International Indian Ocean Expedition

Collected reprints VI

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Preface

The sixth volume of collected reprints of the International Indian Ocean Expedition consists of papers received by Unesco between October 1967 and November 1968.

For convenience of presentation the papers have been grouped, in a very approximate classification, under the following main headings:

I. Marine biology;
II. Physical oceanography and marine meteorology;
III. Marine geology and geophysics;
IV. Marine chemistry;
V. Papers presented by title or abstract only.

Author and subject indexes are now in preparation. Their publication is expected after termination of the series.

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Part I

Marine biology

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ÉPONGES CALCAIRES DE KERGUELEN

Systématique et écologie

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La présente collection a été réunie au cours d'une série de plongées en scaphandre autonome, du 23 décembre 1962 au 5 février 1963, à Kerguelen. Les récoltes ont eu lieu en divers points de la Baie du Morbihan et à l'entrée de la Passe Royale. Les stations ont été choisies en fonction de conditions écologiques variées, et représentatives dans la mesure du possible. Les difficultés de transport n'ont pas permis des prélèvements en d'autres endroits, sur le pourtour extérieur de l'Archipel notamment. L'investigation portait sur la faune d'Invertébrés sédentaires ou sessiles de substrat rocheux, répartis entre la surface et 15 m de profondeur. L'étude systématique a été rédigée par R. BOROJEVIĆ et les données écologiques sont dues à P. GRUA. (Cet article précède une revue systématique et écologique des peuplements d'Invertébrés de Kerguelen.)

1. — CONDITIONS HYDROLOGIQUES LOCALES ET ÉCOLOGIE

Les conditions hydrologiques régnant autour de Kerguelen (48°39′-49°43′ S. et 68°40′-70°34′ E.) restent encore très mal connues. La convergence antarctique pourrait être à quelques degrès seulement au Sud de l'Archipel (DELÉPINE, 1963). Alors que la température des eaux du large oscille annuellement entre 3° et 7° C., celle des eaux intérieures

de la Baie du Morbihan varie entre des limites plus larges. Des enregistrements thermométriques peu précis, entrepris en avril 1962 à Port-aux-Français, indiquent cependant, pour la couche superficielle, des chiffres ayant une valeur encore restreinte, compris entre 2° et 8°5 C. environ (respectivement pour la moyenne mensuelle la plus basse et la plus élevée). Des mesures de température faites en plongée à 15 m de profondeur ont donné 5° C. à l'Ile Buchanan et 5°5 C. à l'Ile du Chat en janvier 1963 (GRUA, 1964 *c*), tandis que la température de surface s'établissait à Port-aux-Français entre 7°5 et 8° C. PAULIAN (1953) rapporte des températures qu'il a prises à 8-10 m sous la surface, au-dessus de fonds à 30-60 m : minimum 2°8 le 27 juillet, maximum 4°8 le 30 décembre 1951.

La Baie du Morbihan est une vaste étendue abritée, de 25 km sur 18 km, semée d'iles et de fjords dans sa moitié Ouest, et communiquant vers l'Est avec le large par la Passe Royale, de 13 km de largeur. Son pourtour terrestre la protège des houles du large et des vents dominants d'Ouest. Les eaux n'y sont jamais profondément remuées par les vents. C'est une méditerranée typique avec un seuil au voisinage de 40 m de profondeur et des fonds dépassant souvent 70 m pour atteindre 131 m au point relevé le plus profond.

La hauteur des pleines mers dans la Baie (Port-aux-Français, Baie de l'Observatoire, Port Jeanne d'Arc) est au maximum de 2 m par vive eau, et de 1,5 m en morte eau.

La transparence des eaux est moindre dans la Baie qu'à l'extérieur. Cette transparence est variable, elle est essentiellement fonction de la mise en suspension, par les vagues, du sédiment qui apparaît le plus souvent à petite distance des rivages ; autour des iles intérieures, l'eau est fréquemment plus claire qu'au long des côtes de la Baie, où se produisent en outre des apports d'eau douce par suintements ou par torrents locaux. Ces arrivées d'eau douce sont plus importantes dans la moitié Ouest où sont drainés des bassins versants de quelque étendue. Les précipitations moyennes sont de 1.116 mm d'eau à Port-aux-Français (DUMAS, 1963).

Dans la Baie, la visibilité sous-marine horizontale, estimée à chaque plongée, a été en moyenne de 4,7 m près des côtes et de 6,1 m près des iles, à l'exclusion des deux station situées à l'entrée de la Passe Royale. Ces valeurs ne sont pas la limite extrême, mais la limite pratique de visibilité. Les mesures relevées au disque de Secchi ont varié, hors des

ressacs côtiers, entre 4 m et 15 m. La seule valeur obtenue à Buchanan était 15 m.

La couleur des eaux était généralement jaune-verte, avec parfois une teinte grise due à la suspension de matières terrigènes inorganiques foncées de nature volcanique. Il est peut-être opportun de garder à l'esprit que les parois verticales faisant face au Sud sont abritées de l'ensoleillement direct dans l'hémisphère austral.

La valeur de la turbulence moyenne des eaux au rivage peut être obtenue à chaque station par l'implantation des *Durvillea antarctica*. Ces algues sont fixées, sur substrat rocheux solide, selon une ceinture de quelques décimètres seulement de hauteur verticale, découvrant aux basses mers de vive eau, lorsque le mode est peu battu ; dans les secteurs battus, cette ceinture s'élève par contre au-dessus de la surface, d'autant plus que l'humectation est plus considérable dans les horizons de l'étage littoral.

Une caractéristique de l'étage infralittoral est la présence de *Macrocystis pyrifera* (GRUA, 1964 *a*), implantées sur substrat rocheux, dont les limites supérieures et inférieures varient selon les lieux avec la transparence des eaux. Dans les stations visitées, ces limites sont respectivement 1 m et 12 m en eaux peu claires, tandis que dans des eaux progressivement plus claires, ces limites sont déplacées vers la profondeur : à l'extérieur de la Passe (I. Buchanan), le peuplement s'établit à 8 m et descend bien au-delà de 15 m. Remarquons qu'à Kerguelen, dans les eaux extérieures, l'implantation de ces algues est mentionnée sur la carte jusqu'à 60 m sous la surfvace. L'indication est-elle rigoureuse ? Il semble bien que les limites inférieures de peuplement de *Macrocystis* ne puissent être précisées depuis la surface qui n'est atteinte que par des individus situés dans des conditions précises d'éclairement. Nous avons pu voir dans les eaux de la Baie, qu'au delà de ces conditions le peuplement se poursuit avec une végétation dont la partie supérieure s'éloigne progressivement de la surface, tandis que les pieds s'espacent peu à peu. Dès qu'il y a du courant, sur l'eau les limites visibles des bancs se rétrécissent. Du côté des forts éclairements, l'herbier au contraire, s'élève subitement du fond jusqu'à la surface en une bordure précise.

Ces algues, souvent réparties sur de larges surfaces entourant les rivages, amortissent les vagues sans arrêter la houle à la côte.

La sous-strate des *Macrocystis* n'est jamais agitée fortement. Des

Desmarestia sp. ténues et fragiles, qui se sont révélées indicatrices d'eaux calmes, y poussent souvent. L'agitation de l'eau peut avoir une influence sur la profondeur d'implantation de *Macrocystis*, du moins pour la limite supérieure (BATHAM, 1956) ; cependant, ce facteur n'a pas paru caractéristique. Les *Desmarestia* fines peuvent, en eau calme, pousser plus près du rivage que les *Macrocystis*.

Dans l'indication des stations mentionnées dans cet article, un ensemble d'éléments complémentaires est rapporté. La valeur de la biomasse est indiquée pour le lieu exact de récolte et n'est pas une moyenne ; elle procure une idée de la richesse du peuplement animal détaché de la surface étudiée. Les *Macrocystis* ne sont jamais incluses dans ces chiffres. Une liste succincte est donnée des animaux prédominants et caractéristiques.

2. — LISTE DES STATIONS

Station 2. — Est de l'Ilôt Channer à 2,4 milles au Sud-Ouest de Port-aux-Français. Ile haute d'une dizaine de mètres, entourée de fonds peu inclinés. Rivages rocheux soumis aux houles venant de la Passe. Récolte à 5 m de profondeur sur une verticale faisant face au Sud, à 0,8 m au-dessus du fond constitué de galets azoïques et de graviers. Biomasse estimée à 1 ou 1,2 kg par dm^2, à peu près exclusivement animale.

— *Leuconia gaussii* Brøndsted.

Station 4 c. — Pointe Sud-Est de l'Ile du Chat, à 8,5 milles au Sud-Ouest de Port-aux-Français. (Voir la station 13). Récolte sur des cailloux remontés par un engin de pêche depuis une profondeur de 25 m environ. Faible couverture biologique.

— *Leucettusa vera* Poléjaeff ; — *Sycon kerguelensis* Urban ; — *Leuconia kerguelensis* Urban.

Station 10. — Nord de l'Ilôt Channer, à 2,4 milles au Sud-Ouest de Port-aux-Français. Eau peu influencée par la houle. Récolte à 7 m de profondeur dans l'herbier de *Macrocystis*, à la face supérieure d'un bloc de roche. Fond rocheux irrégulier. Biomasse environ 1,5 kg par dm^2, à grande majorité animale.

— *Leucetta primigenia* Haeckel.

Station 12. — Sud de la Pointe Suzanne, à l'entrée de la Passe Royale, à 9 milles au Sud-Est de Port-aux-Français. (Voir la station 16). Côte élevée se transformant en un platier horizontal de roche en place, échancré de criques. Rivage exposé au large. Récolte sous 1 à 4 m d'eau sur des faces rocheuses diversement inclinées. Travail difficile et fragmentaire dû à la vive agitation de l'eau. Biomasse estimée à 100 g par dm^2.

— *Clathrina coriacea* Montagu.

Station 13. — Pointe Sud-Est de l'Ile du Chat, à 8,5 miles au Sud-Ouest de Port-aux-Français. Ile élevée aux bords raides, s'enfonçant verticalement sous la surface jusque vers 12 ou 15 m, puis apparition d'une pente de faible inclinaison moyenne. Secteur généralement peu agité. Récolte à 12-15 m sous la surface.

Station 13 a. — Sur la paroi verticale faisant face au Sud-Est. Biolasse de 360 g par dm^2, à minorité végétale.

— *Leucettusa vera* Poléjaeff ; — *Leucetta primigenia* Haeckel ; — *Sycon kerguelensis* Urban ; — *Leuconia anfracta* Urban.

Station 13 b. — Sur le plateau légèrement incliné, sur une face horizontale de roche. Biomasse de 150 g par dm^2, à majorité végétale.

— *Leucetta primigenia* Haeckel.

Station 13 c. — Faune fixée sur les haptères de *Leissonia*.

— *Leucetta primigenia* Haeckel.

Station 16. — Nord de l'Ile Buchanan, à 13,5 milles au Sud-Sud-Est de Port-aux-Français, à l'entrée de la Passe Royale (voir la station 12). Ilôt élevé dont les bords tombent selon une forte inclinaison jusqu'à 15 m sous la surface, puis la pente s'adoucit. Côte battue par les vagues et la houle. Récolte sur des roches à 15 m de profondeur dans la sous-strate de *Macrocystis* établies là en un peuplement peu dense.

Station 16 a. — Face verticale. Biomasse de 130 g par dm^2, à minorité végétale.

— *Clathrina challengeri* Poléjaeff ; — *Leucetta primigenia* Haeckel ; — *Leucettusa vera* Poléjaeff ; — *Leucosolenia discoveryi* Jenkin ; — *Leucosolenia minchini* Jenkin ; — *Sycon kerguelensis* Urban ; — *Leuconia anfracta* Urban ; — *Leuconia minor* Urban.

Station 16 b. — Face horizontale. Biomasse 190 g par dm², à grande majorité végétale.

— *Leucetta primigenia* Haeckel ; — *Leuconia astricta* Tanita.

Station 22. — Cap Kidder, à 6,6 milles à l'Ouest de Port-aux-Français. Côte rocheuse élevée tombant en éboulis dans la mer en cet endroit, puis fonds descendant en faible pente vers le Sud. Eaux généralement peu agitées. Récolte à 7 m de profondeur sur des roches, dans le peuplement de *Macrocystis* très serré. Zone abondamment recouverte de *Desmarestia*. Biomasse à minorité animale variant entre 56 et 177 g par dm² selon l'épaisseur du couvert de *Desmarestia*.

— *Leucetta primigenia* Haeckel.

Station Vb. — A proximité du mouillage de Port-aux-Français. Large étendue de sédiment généralement fin dans une anse soumise aux vagues venant de l'Ouest et du Sud-Ouest. Échantillons rapportés à la drague d'une profondeur de 25 m environ.

— *Leuconia gaussii* Brøndsted.

3. — SYSTÉMATIQUE

La faune des Éponges Calcaires des régions antarctiques et subantarctiques est relativement bien connue, grâce aux travaux des nombreuses expéditions scientifiques qui ont recueilli un vaste matériel faunistique dans ces régions. Les expéditions des navires *Challenger* (Poléjaeff, 1883), *Valdivia* (Urban, 1908) et *Gauss* (Brøndsted, 1928) ont travaillé à Kerguelen, ce qui a permis d'établir une liste de 14 espèces d'Éponges Calcaires de cet Archipel. Notre collection ajoute trois espèces à cette liste : *Clathrina coriacea* Montagu, *Clathrina challengeri* Poléjaeff et *Leuconia astricta* Tanita. Nous donnons à la fin de cet article un inventaire actuel des espèces de Kerguelen, avec les références nécessaires.

Parmi 17 espèces actuellement connues des Kerguelen, 2 sont cosmopolites, 9 ont été décrites seulement à Kerguelen et les autres sont typiques de régions antarctiques et subantarctiques.

Le système des Éponges Calcaires adopté dans ce travail est celui de Bidder, revisé par Hartman (1958).

Clathrina coriacea Montagu (Fig. 1).

Leucosolenia coriacea Topsent, 1936.

L'unique échantillon a la forme d'un petit coussin formé de tubes anastomosés. Les spicules, triactines et tétractines correspondent à ceux de *C. canariensis* Miklucho-Maclay (synonyme de *C. coriacea*, Topsent, 1936). Les triactines (fig. 1 *a*) peu variables ont des actines

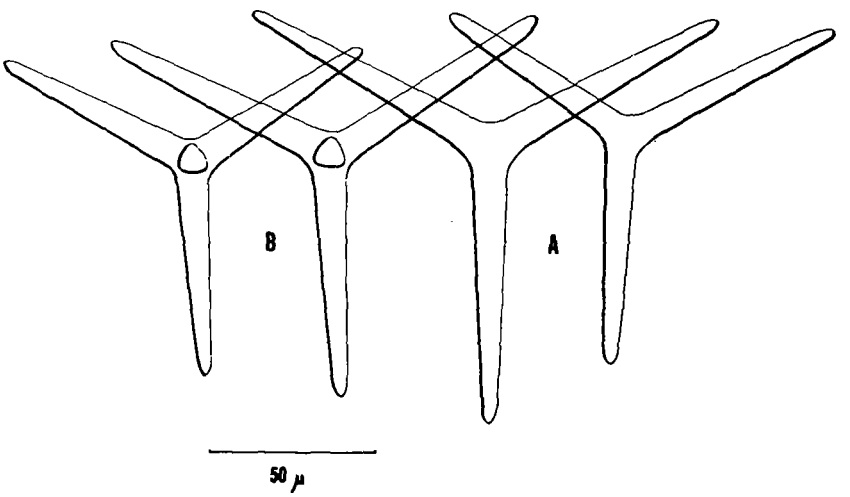

FIG. 1. — *Clathrina coriacea* Montagu.
A. Triactines ; B. Tetractines.

de 60-90 µ de long et 9-10 µ d'épaisseur. Les tétractines (fig. 1 *b*) ont les actines basales semblables aux triactines ; l'actine apicale, 30-50 µ de long est un peu plus mince que les basales.

Distribution géographique : cosmopolite.

Station : 12 ; Kerguelen, Pointe Suzanne (localité nouvelle).

Clathrina challengeri Poléjaeff (Fig. 2.).

Leucosolenia challengeri Poléjaeff, 1883 ; Kirk, 1895 ; Dendy et Row, 1913 ; Tanita, 1942.

Ascetta challengeri von Lendenfeld, 1885.

Leucetta chathrata Carter, 1883.

Clathrina tripodifera var. *gravida* Dendy, 1891.

Leucosolenia intermedia Kirk, 1895 ; Brøndsted, 1926.

Leucosolenia clathrata Dendy et Row, 1913 ; Row et Hozawa, 1931 ; Hozawa, 1940 ; Tanita, 1942.

En 1883 POLÉJAEFF décrit une *Clathrina* provenant de Cape York (Australie) qu'il nomme *Leucosolenia challengeri*. Son squelette consiste

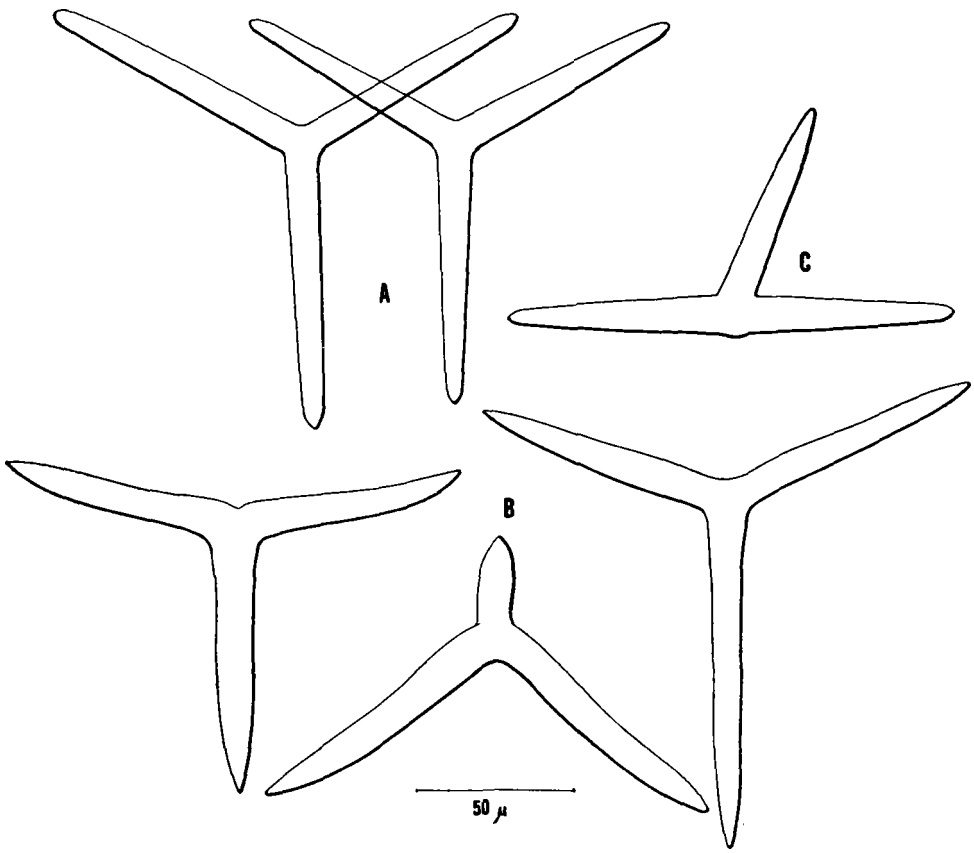

FIG. 2. — *Clathrina challengeri* Poléjaeff.
A. Triactines réguliers ; B. Tripodes ; C. Triactine anormal.

en triactines de deux sortes : les uns réguliers, avec des actines cylindriques, de 180 µ de long, qui rarement, développent une quatrième actine ; les autres, triactines sont sagittaux avec un centre élevé et des actines de forme inconstante ; l'angle compris entre l'actine impaire et chaque actine paire varie de 97° à 120°. Le dessin (Pl. III, n° 4) et la description donnés montrent qu'il s'agit d'un spicule de forme tripode.

La même année, CARTER (1883) décrit *Leucetta clathrata*, provenant des Côtes SW de l'Australie avec exactement les mêmes catégories de spicules. Plus tard (1885-1886) il corrige sa description et nomme cette éponge *Clathrina tripodifera* var. *gravida*. BIDDER (1898) crée le nouveau genre *Dendya* dont *Clathrina tripodifera* Carter devient le type, mais la variété *gravida* reste dans le genre *Clathrina*, gardant le nom *C. clathrata* Carter. ROW et HOZAWA (1931) ont donné une description précise de cette espèce, en considérant *Leucosolenia intermedia* Kirk comme synonyme. D'après leur description les actines des triactines réguliers ont 100-120 μ de long ; elles développent rarement une quatrième actine. Les tripodes ont une forme très variable mais « seen from the facial plane they are markedly sagittal » bien qu'on puisse trouver des tripodes avec des angles à peu près égaux. On remarque que cette description correspond presque exactement à la description de *Clathrina challengeri* Poléjaeff.

TANITA (1942) place *C. challengeri* dans sa section 4 parmi les *Clathrina* à spicules sagittaux et *C. clathrata* dans la section 5 parmi celles à tripodes. Il est évident que cette distinction ne peut pas être maintenue, car les spicules des deux espèces varient du type sagittal au type equiangulaire. Leur forme extérieure (les grands spécimens en forme de coussin, les jeunes avec un court pédoncule) les catégories de spicules et la distribution géographique sont identiques : elles doivent donc être considérées comme synonymes. Comme les deux espèces sont décrites la même année nous retenons le nom spécifique *C. challengeri* Poléjaeff, car la première description de CARTER (1883) est partiellement incorrecté et son espèce *C. clathrata* était placée dans le genre *Leucetta*.

Les deux échantillons de la collection ont la forme typique clathroïde. L'un est fixé sur une algue par un court pédoncule l'autre a la forme de coussin. La couleur est brune (dans l'alcool) ses tubes, très anastomosés, ont 200-350 μ de diamètre. Leurs parois consistent en plusieurs couches de triactines qui sont en forme de tripode sur la surface. Les triactines réguliers (fig. 2 *a*) ont leurs actines cylindriques et obtuses, ayant 80-110 μ de longueur et 8-9 μ d'épaisseur à la base. La forme des tripodes (fig. 2 *b*) est très variable. Parfois leurs actines sont un peu plus robustes que celles des triactines réguliers et leur centre est légèrement élevé ou bien leurs actines sont très courbées, les angles sont inégaux le centre est très élevés et ces spicules ont la forme d'un tripode typique et sagittal.

Station : 16 *a*, Kerguelen. N. Ile Buchanan (localité nouvelle).

Distribution géographique : Côte SW et S de l'Australie (Carter, v. Lendenfeld, Poléjaeff, Dendy, Row et Hozawa) ; New Zealand (Kirk, Brøndsted) Japon (Hozawa).

Leucetta primigenia Haeckel (Fig. 3.).

Leucetta primigenia var. *isoraphis* Haeckel, 1872.
Leuconia fruticosa Poléjaeff, 1883.
Leucetta primigenia Urban, 1908.
Leucetta isoraphis Brøndsted, 1928.

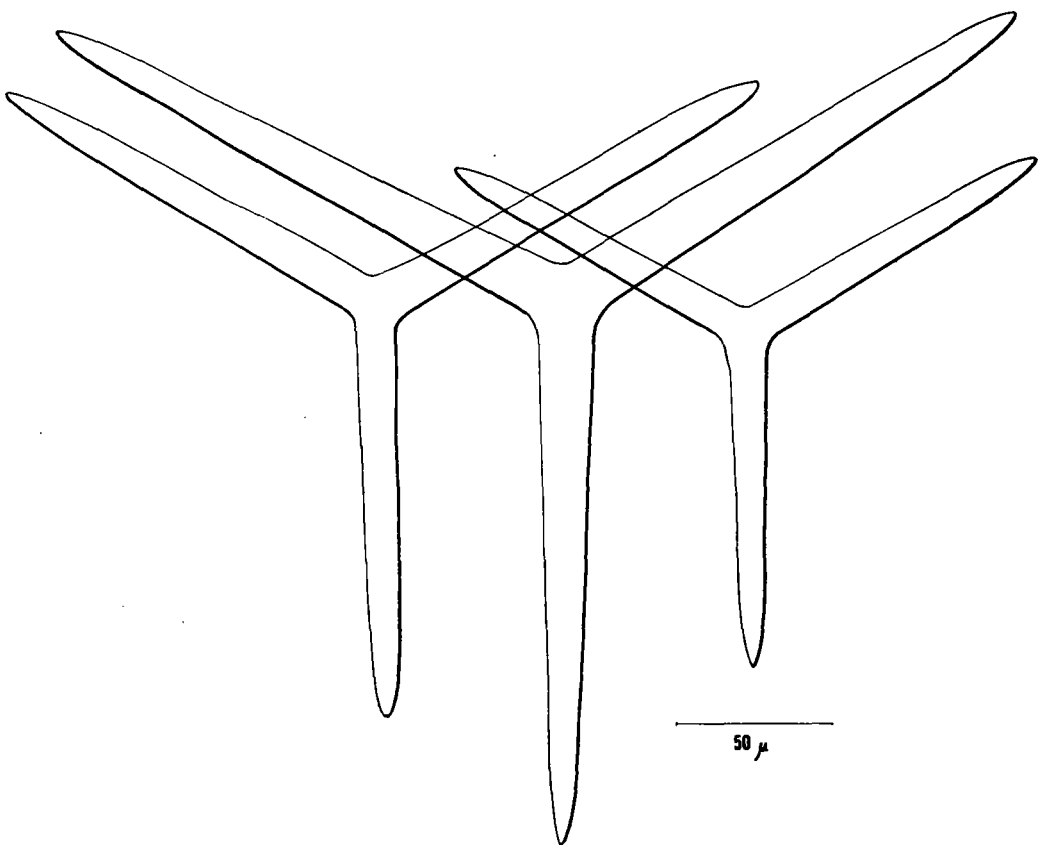

FIG. 3. — *Leucetta primigenia* Haeckel.
Triactines.

La collection renferme 17 échantillons de cette espèce, trouvée plusieurs fois et en abondance dans les eaux Antarctiques (notamment dans la collection de l'expédition « Gauss » et la collection présente)

et qu'on peut ainsi considérer comme l'espèce la plus commune des éponges calcaires de cette région.

Les trois variétés décrites par HAECKEL (1872) : *isoraphis, microraphis* et *megaraphis* ont été séparées déjà par VON LENDENFELD (1895). DENDY (1892) identifie la forme *microraphis* avec *Leuconia dura* Poléjaeff et la nomme *Leucetta microraphis* Haeckel. POLÉJAEFF (1883) cite *Leuconia fruticosa* aux Kerguelen et cette espèce correspond à la forme *isoraphis* ; le nom *fruticosa* (HAECKEL, 1870) qui est antérieur au nom *primigenia* est un « nomen nudum » sans diagnose et doit être abandonné (DENDY et ROW, 1913). BRØNDSTED (1928), en étudiant le vaste matériel de l'expédition « Gauss » élève les formes *isoraphis* et *megaraphis* au rang d'espèces nommées alors *Leucetta isoraphis* avec la variété *apicalis* et *Leucetta megaraphis*. Puisque le nom original d'espèce est ainsi disparu, nous retenons le nom de *L. primigenia* pour la forme *isoraphis* en nous accordant ainsi avec URBAN (1908).

Les spécimens présents sont tous de forme plus ou moins ovoïde, avec une surface lisse et ils ont soit un, soit, rarement, plusieurs oscules. Leur taille varie de 1 à 3 mm de diamètre, sauf les spécimens fixés sur des colonies de Bryozoaires qui sont plus petits. Le choanocoele est réduit à un ou plusieurs canaux très ramifiés, qui s'ouvrent directement à l'oscule.

Tous les spicules sont des triactines réguliers de taille variable. Leurs actines ont environ 120-160 μ de long et 12 μ d'épaisseur à la base. Parmi les autres spicules, certains, de taille nettement inférieure, sont probablement des formes jeunes. Il n'y a aucune différence de taille entre les spicules provenant des différentes parties de l'éponge.

Stations : 10 ; Kerguelen, N. Ilôt Channer ; 13 *a, b, c*, Kerguelen, SE Ile du Chat ; 16 *a, b*. Kerguelen, N Ile Buchanan ; 22, Kerguelen, Cap Kidder.

Distribution géographique : cosmopolite.

Leucettusa vera Poléjaeff. (Fig. 4).

Leucetta vera Poléjaeff (1883).

Les six échantillons étudiés s'accordent bien avec le type de l'espèce, décrit d'après le matériel rapporté de Kerguelen par le *Challenger*. Leur taille varie de 1 à 6 cm de long. Ces éponges sont ovales, souvent

comprimées, avec la surface extérieure lisse, la surface intérieure hispide. Une grande cavité centrale occupe le centre du corps. Tous les spécimens ont un seul oscule et ils sont tous fixés sur le substrat par un pédoncule plus ou moins long.

L'organisation des chambres vibratiles s'accorde bien avec le des-

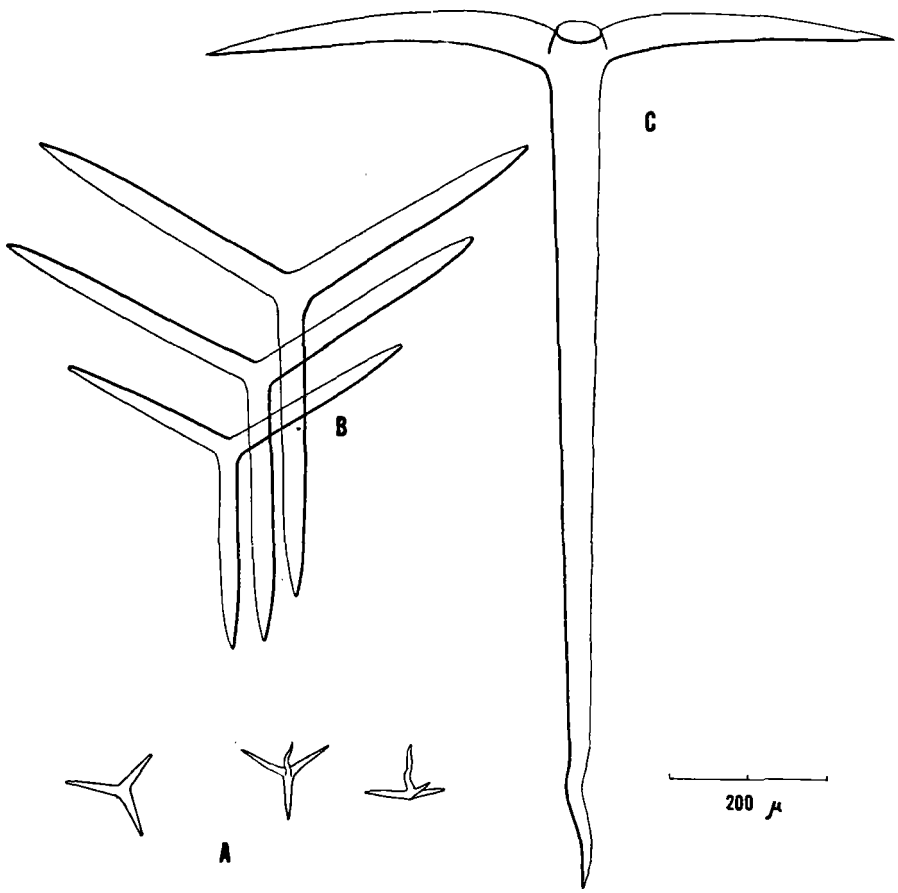

FIG. 4. — *Leucetusa vera* Poléjaeff.
A. Triactine et tetractines gastriques ; B. Triactines dermiques ; C. Tetractine.

sin et la description de POLÉJAEFF (1883), mais la partie comprenant les chambres tubiformes occupe plus de 2/3 de l'épaisseur du corps. Les actines centripetes des tetractines dermiques représentent le seul squelette de cette région. La surface gastrique et celle des grands canaux exhalants sont renforcées d'une couche de triactines et tetractines réguliers (fig. 4 *a*) dont les actines mesurent 55-100 µ de long sur 10 µ d'épaisseur à la base. Souvent plus longue que les actines basales, l'actine

apicale est pointue et présente une ou deux courbures dans la partie intérieure de la paroi comprenant les chambres sphériques. La surface externe est couverte de plusieurs couches de triactines réguliers (fig. 4 *b*) avec des actines coniques et pointues, mesurant de 150 à 350 μ de long sur 10-20 μ d'épaisseur à la base. Ils forment avec les tetractines un cortex robuste de 20 μ d'épaisseur. Les tetractines (fig. 4 *c*) ont les actines basales régulières, mesurant 300-500 μ de long sur 50 μ d'épaisseur à la base. L'actine apicale est rectiligne ou courbée dans sa partie distale et pointue ; elle mesure jusqu'à 2 mm de long et elle traverse souvent toute l'épaisseur de l'éponge.

Stations : 4 *c*, Kerguelen, SE Ile du Chat ; 13 *a*, Kerguelen, SE Ile du Chat ; 16 *a*, Kerguelen, N Ile Buchanan.

Distribution géographique : Kerguelen (Poléjaeff).

Leucosolenia discoveryi Jenkin (Fig. 5).

Leucosolenia discoveryi Jenkin, 1908 ; Burton, 1942.
Leucosolenia botryoides var. *macquariensis* Dendy, 1918.
Leucosolenia australis Brøndsted, 1928, Tanita, 1943.

La seule différence entre ces trois espèces décrites d'après le matériel provenant de l'Antarctique est la différenciation de la partie distale des diactines en fer de lance chez *L. discoveryi* Jenkin et *L. botryoides* var *macquariensis* Dendy, qui n'est pas signalée chez *L. australis* Brøndsted. D'autre part elles montrent toutes la tendance à former sur le substrat un reticulum dense de tubes ramifiés, semblables aux petits coussins. Cette forme, exceptionnelle chez une *Leucosolenia* semble bien caractériser cette espèce australe et la distinguer des autres espèces de *Leucosolenia*.

Les tubes des spécimens de notre collection, très ramifiés et hispides, ont 500-800 μ de large et forment souvent des petits coussins de 3-4 mm de large. Leurs diactines (fig. 5 *a*) varient entre des formes légérement courbées, ayant deux extrémités presque semblables, et des formes à partie distale différenciée en fer de lance. Leur taille varie d'une façon continue de 70-300 μ de long sur 5-12 μ d'épaisseur. La partie proximale est d'habitude plus épaisse que la partie distale. Les triactines (fig. 5 *b*) et les tetractines (fig. 5 *c*) ont l'actine impaire plus longue ou rarement, égale, aux actines paires. Elles est rectiligne et

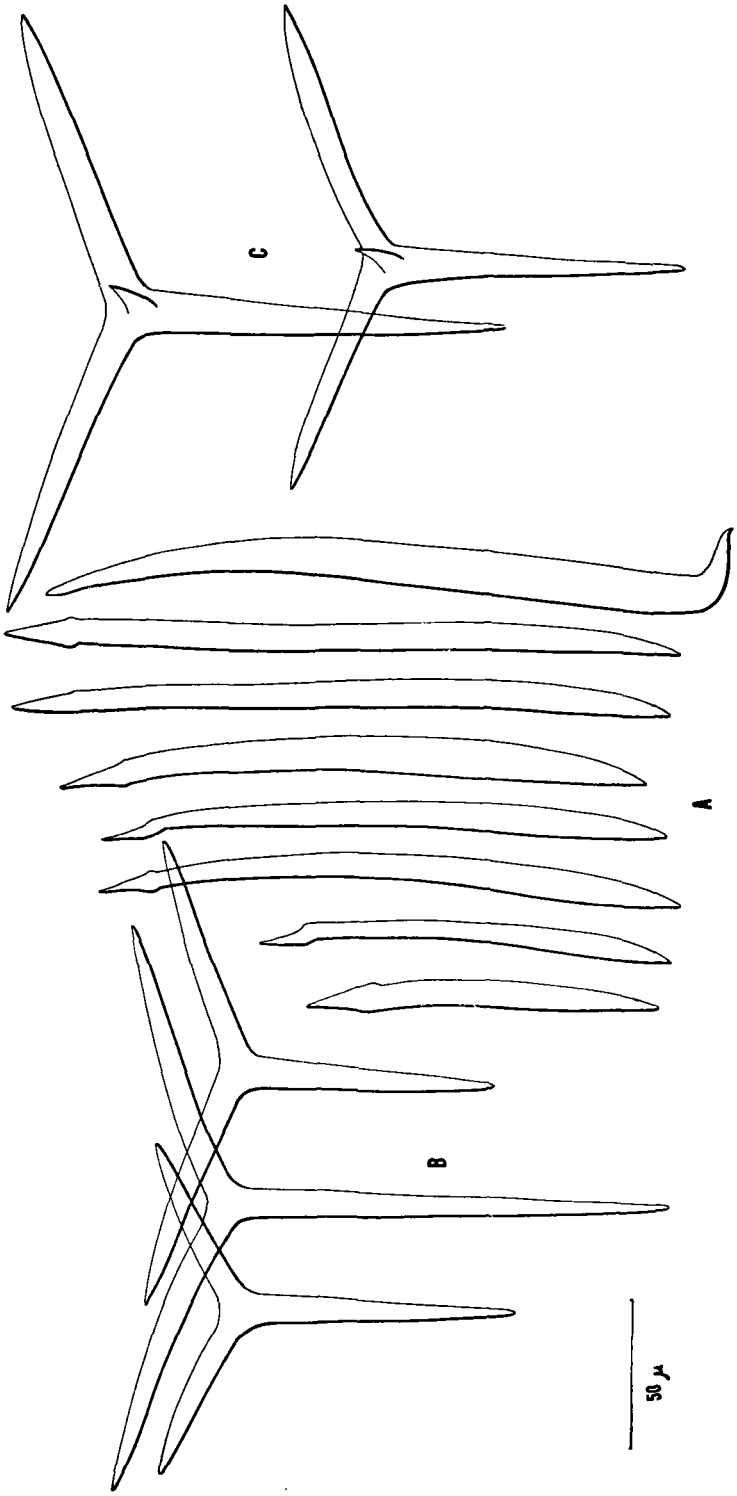

FIG. 5. — *Leucosolenia discoveryi* Jenkin.
A. Diactines ; B. Triactines ; C. Tetractines.

pointue, sa longueur varie entre 80 et 140 μ. Les actines paires sont plus robustes, mesurant 60-120 μ de long sur 8-10 μ d'épaisseur. Les actines basales des tetractines sont semblables aux triactines, mais elles sont plus grandes que la moyenne des tetractines. La longueur de l'actine apicale varie de 30 à 60 μ.

Station : 16 *a*, Kerguelen. N Ile de Buchanan.

Distribution géographique : Victoria Land (Jenkin) ; Kaiser Wilhelm II Land, Kerguelen, Baie d'Observatoire (Brøndsted) ; Iles Falkland (Burton) ; Iles Macquarie (Dendy) ; Detroit de Magellan (Tanita).

Leucosolenia minchini Jenkin (Fig. 6).

Leucosolenia minchini Jenkin, 1908, Brøndsted, 1928.

Le seul échantillon de cette espèce se présente sous forme de tubes ramifiés de 0,5 mm de diamètre, rampant à la surface du substrat.

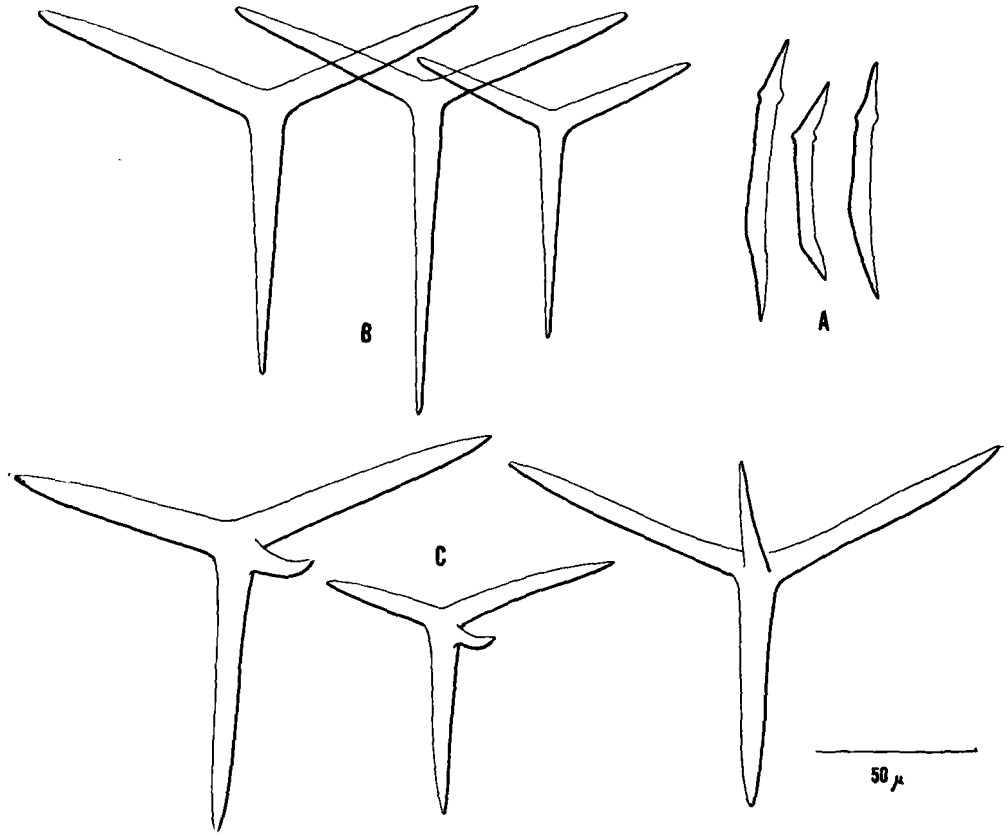

FIG. 6. — *Leucosolenia minchini* Jenkin.
A. Diactines ; B. Triactines ; C. Tetractines.

Les diactines (fig. 6 *a*) sont petits, courbés, mesurant 60-100 μ de long sur 5-8 μ d'épaisseur avec la partie distale marqué par un épaississement en forme d'anneau. Les triactines (fig. 6 *b*) sont sagittaux et leurs actines paires sont plus courtes que l'actine impaire, mesurant 70-90 μ de long en général. Plus rarement, lorsque l'angle oral est voisin de 180° l'actine impaire est de longueur égale ou inférieure aux actines paires. Celles-ci mesurant 50-80 μ de long et sont toujours légérement courbées. Dans les tetractines (fig. 6 *c*) les actines sont semblables aux triactines ou quelquefois plus robustes ; l'actine apicale est très pointue et courbée. L'échantillon correspond bien au type.

Station : 16 *a*, Kerguelen, N Ile Buchanan.

Distribution géographique : Victoria Land (Jenkin) ; Kaiser Wilhelm II Land ; Kerguelen, Baie d'Observatoire, (Brøndsted).

Sycon kerguelensis Urban (Fig. 7).

Sycon kerguelensis Urban, 1908.

URBAN (1908) a donné une excellente description de cette espèce, établie d'après deux spécimens provenant du Bassin de la Gazelle. Les quatres échantillons de la collection diffèrent peu du type. Ceux de l'Ile du Chat ont la forme d'un sac comprimé de 12-15 mm de haut sur 5-9 mm de large, les parois ont 1-1,5 mm d'épaisseur. La surface extérieure est hispide alors que l'intérieure est glabre mais irrégulière. L'oscule est nu, limité par des parois qui s'amincissent et forment un tube de 300-500 μ de haut, renforcé par des triactines sagittaux L'échantillon de l'Ile Buchanan est représenté par deux individus unis à la base chacun en forme de tube de 2 cm de haut sur 0,3 cm de diamètre. Une collerette de 1 mm de haut borde l'oscule. Elle est formée des triactines sagittaux serrés dont les actines impaires sont parallèles et dirigées vers la base, renforcées ici et là par des diactines semblables à ceux des cônes distaux des tubes radiaires.

L'organisation des canaux inhalants des tubes et des pores exhalants correspond exactement aux descriptions d'URBAN (1908).

Les grands diactines (fig. 7 *a*) des parties distales des tubes radiaires ont une taille variable. Ceux des exemplaires de l'Ile Buchanan ont 500-900 μ de long, celles de l'Ile du Chat 200-500 μ or les exemplaires d'URBAN avaient des diactines de 400-600 μ. La présence des trichoxes

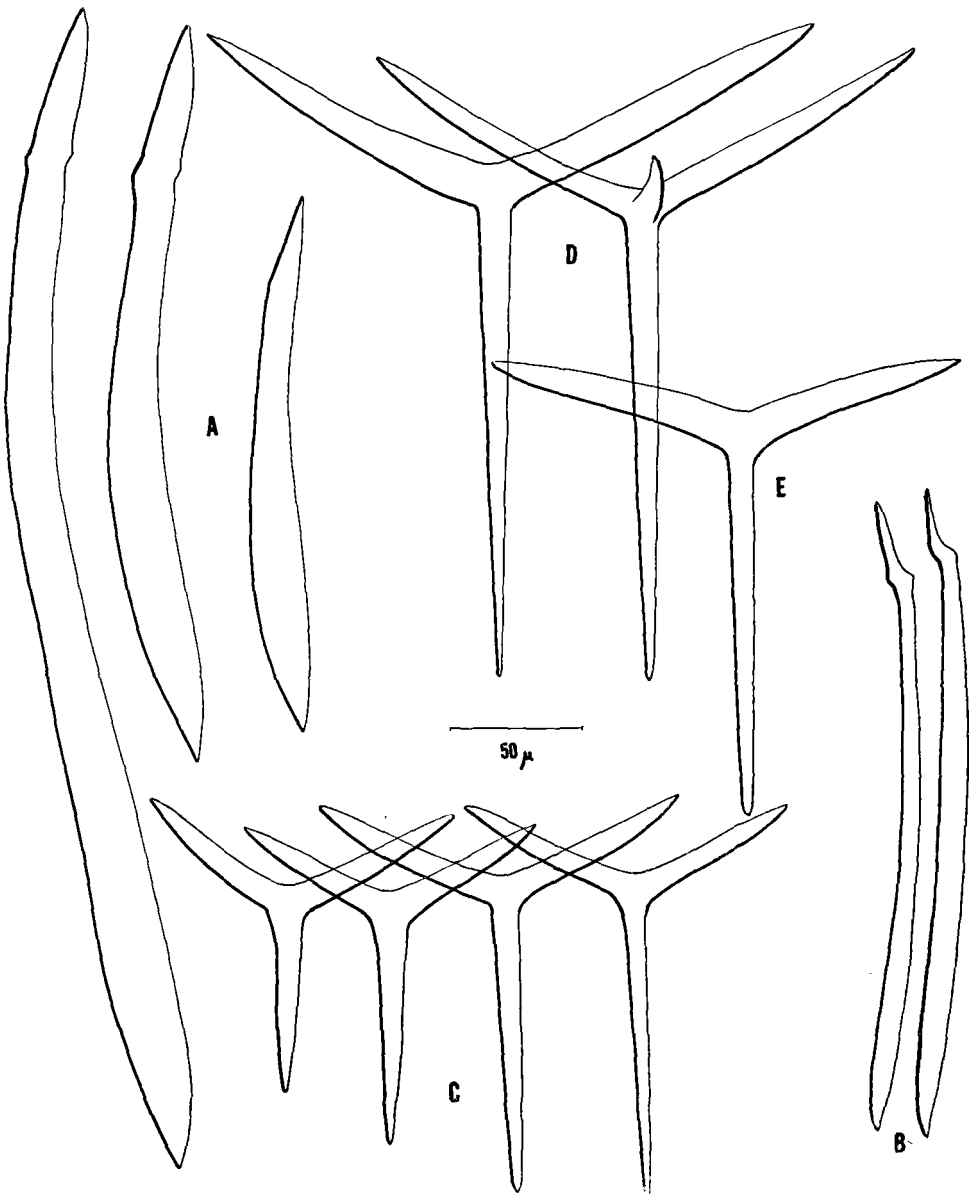

FIG. 7. — *Sycon kerguelensis* Urban.
A. Diactines ; B. Petits diactines ; C. Triactines ;
D. Triactine et tetractine gastriques ; E. Triactine de l'oscule.

est facultative. Le nombre des diactines minces ayant la partie distale différenciée en baionnette (fig. 7 *b*) varie beaucoup, mais elles sont toujours présentes. La taille des triactines (fig. 7 *c*) augmente de façon continue en passant des cônes distaux aux pores exhalants. Les triactines des cônes ont des actines mesurant 60 µ de long tandis que l'actine

impaire des triactines subgastriques atteint 120 μ. Les triactines et les tetractines gastriques (fig. 7 *d*) sont plus grands. Leur actine impaire mesure de 120-200 μ de long, les paires 100-140 μ. L'actine apicale est courbée et pointue, mesurant environ 40 μ. Les triactines de l'oscule (fig. 7 *e*) sont sagittaux, d'angle impair très ouvert, affectant souvent la forme de « T ». L'actine impaire est droite, mince et pointue, mesurant de 120-170 μ de long sur 10 μ d'épaisseur à la base. Les actines paires ont 90-120 μ de long sur 13 μ à la base. Les spicules de l'échantillon de l'Ile Buchanan sont en moyenne de taille supérieure aux spicules de l'échantillon de l'Ile du Chat.

Stations : 4 *c*, Kerguelen, SE Ile du Chat ; 13 *a*, Kerguelen, SE Ile du Chat ; 16 *a*, Kerguelen, Ile Buchanan.

Distribution géographique : Kerguelen, Bassin de la Gazelle (Urban).

Leuconia anfracta Urban (Fig. 8).

Leuconia anfracta Urban, 1908, Brøndsted, 1928.

Les échantillons de cette collection concordent très bien avec la description que donne URBAN (1908) de cette espèce typique des Iles Kerguelen. Ce sont toutes des petites éponges, mesurant de 4 à 12 mm de haut et ayant un seul oscule entouré d'une frange de trichoxes. Les éponges sont souvent fixées sur des colonies de Bryozoaires.

Au-dessous de la couche dermique chargée de triactines tangentiels et des rares microdiactines se trouve une zone de cavités subdermiques très caractéristiques de cette espèce. Cette zone a jusqu'à 400 μ d'épaisseur et elle est traversée par des diactines et des faisceaux des triactines. Les chambres vibratiles ovales, de 100 μ de diamètre environ, se trouvent dans le parenchyme soutenu par des triactines sagittaux disposés sans ordre. La surface gastrique contient des triactines et des tetractines.

Les diactines (fig. 8 *a*) courbées sont très caractéristiques de cette espèces et mesurent jusqu'à 900 μ de long. Les microdiactines (fig. 8 *b*) sont minces avec un épaississement annulaire et mesurent 50-90 μ de long. Les triactines (fig. 8 *c*) et les tetractines (fig. 8 *d*) sont sagittaux, leurs actines sont minces et souvent plus ou moins courbées ; leur taille varie de 80 μ (triactines dermiques) jusqu'à 280 μ (triactines subgastriques. L'actine apicale des tetractines ne dépasse pas 80 μ.

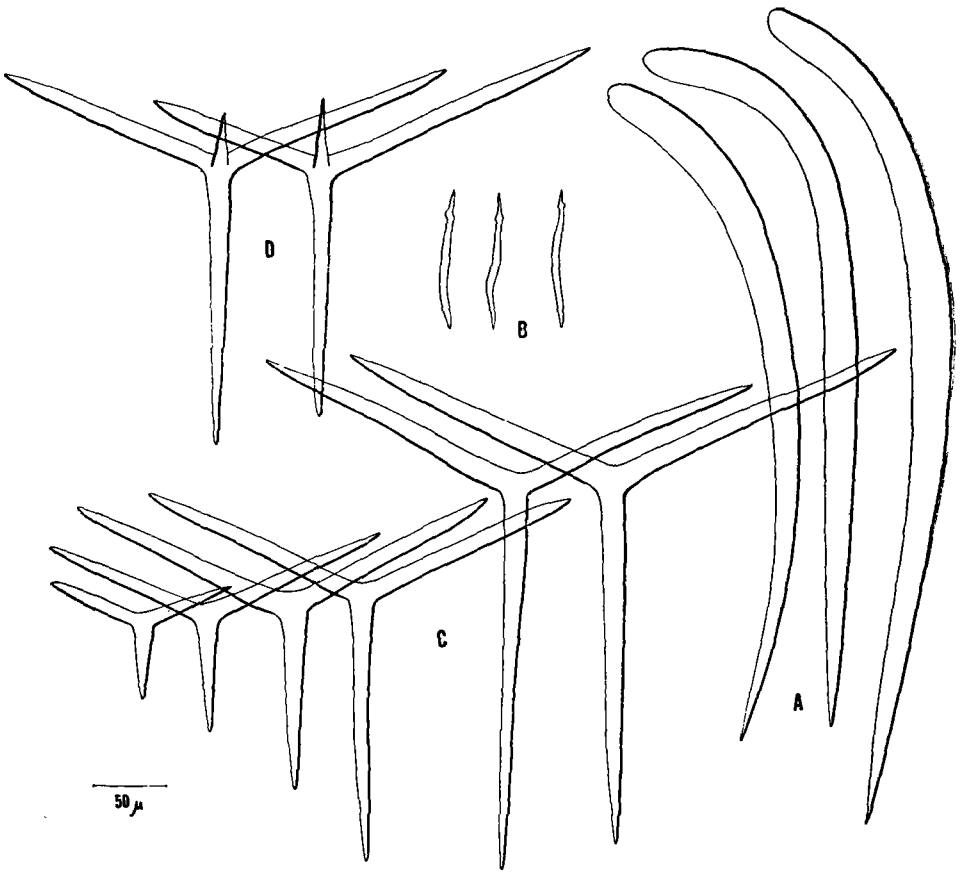

FIG. 8. — *Leuconia antracta* Urban.
A. Diactines ; B. Microdiactines ; C. Triactines ; D. Tetractines.

Stations : 13 *a*, Kerguelen, SE Ile du Chat ; 16 *a*, Kerguelen, N Ile Buchanan.

Distribution géographique : Kerguelen, Bassin de la Gazelle (Urban) Kerguelen, Baie d'Observatoire (Brøndsted).

Leuconia astricta Tanita (Fig. 9).

Leuconia astricta Tanita, 1943.

Nous assimilons les échantillons de l'Ile Buchanan à l'espèce décrite de Georgia du Sud par TANITA (1943), malgré certaines différences, notamment :

— La présence d'une grande quantité de microdiactines dans la couche extérieure de l'éponge, qui n'est pas signalée chez *L. astricta*.

— L'épaisseur des spicules qui est nettement inférieure à celle décrite par TANITA (1943).

— Et la présence de franges osculaires sur nos exemplaires qui semblent manquer aux spécimens de Georgia du Sud.

Par contre l'habitat, la présence de triactines en forme de tripode à la surface de l'éponge et la forme caractéristique des diactines et des spicules gastriques indiquent une proche parenté entre les spécimens de Kerguelen et ceux de Georgia du Sud. Puisque plusieurs auteurs ont déjà montré que la présence des microdiactines, l'épaisseur de l'ensemble des spicules et la présence d'une frange osculaire varient beaucoup à l'intérieur d'une même espèce, les différences mentionnées doivent être considérées comme des variantes individuelles ou locales.

Les trois échantillons sont petits, fixés sur une colonie de Bryozoaires, mesurant 6-10 mm de long sur 3-6 mm de large. La surface extérieure est irrégulière, elle parait glabre car les diactines sont rares et courbés dans la partie distale. L'orifice osculaire est entouré par un tube de triactines et tetractines sagittaux parallèles et de même orientation, soutenant une belle frange de trichoxes. La disposition des chambres vibratiles est typiquement leuconoide, les chambres sont sphériques ou ovales, mesurant 60-80 μ de diamètre. La cavité gastrique est en forme de canal ramifié, dont la surface est rendue hispide par les actines apicales des tetractines gastriques.

Les diactines (fig. 9 *a*) ont une forme très caractéristique. Leur partie proximale est pointue et presque droite, la partie distale présente une courbure brusque : ainsi l'extrémité de spicules d'environ 50 μ de long forme un angle de 120-140° avec la partie proximale. L'extrémité distale est d'habitude arrondie. Leur taille varie peu : de 350 à 450 μ de long sur 20-30 μ d'épaisseur. Les microdiactines (fig. 9 *b*) mesurent 50-60 μ de long. Leur partie distale est différenciée en fer de lance ou en baïonnette. Les triactines de la surface dermique ont la forme de tripode (fig. 9 *c*), leur angle oral est très ouvert mais n'atteint jamais 180°. L'actine impaire est plus ou moins droite, les actines paires sont plus longues et courbées vers l'avant dans leur moitié distale. Elles mesurent 100-130 μ de long sur 15-20 μ d'épaisseur à la base. Les triactines du parenchyme (fig. 9 *d*) sont légèrement sagittaux mesurent 150-170 μ de long. Les triactines (fig. 9 *e*) et tetractines (fig. 9 *f*) gastriques sont très sagittaux avec les actines droites. Leurs actines paires mesurent 150-200 μ, leur actine impaire est beaucoup plus courte :

70-100 μ. Leur épaisseur varie de 8 à 10 μ. L'actine apicale est pointue et droite ou légèrement arquée et, sa longueur ne dépasse pas 80 μ.

Station : 16 *b*, Kerguelen, N Ile Buchanan (localité nouvelle).

Distribution géographique : Georgia du Sud, Tanita (1943).

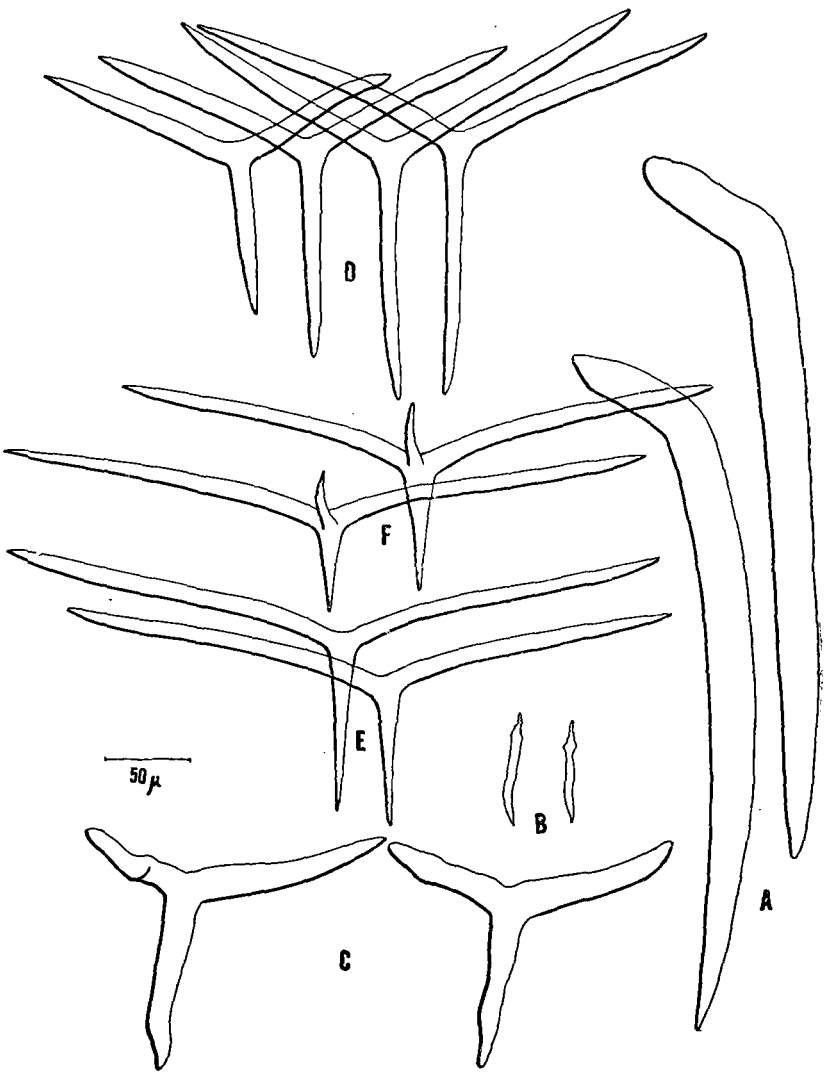

FIG. 9. — *Leuconia astricta* Tanita.
A. Diactines ; B. Microdiactines ; C. Tripodes ;
D. Triactines du parenchyme ; E. Triactines gastriques ; F. Tetractines gastriques.

Leuconia gaussii Brøndsted (Fig. 10).

Leucetta gaussii Brøndsted 1928.

BRØNDSTED (1928) a placé cette éponge dans le genre *Leucetta* à cause de l'absence d'organisation radiaire du choanosquelette et des spicules subgastriques qui caractérisent d'habitude le genre *Leuconia*. Il est vrai qu'à cette éponge manquent toutes traces de cette organisation et que les triactines assez réguliers forment un vague réseau réticuleux avec des mailles hexagonales qui est caractéristique par exemple pour le choanosquelette de *Leucetta primigenia* H. Mais d'autre part les spicules présentent une forme typique pour la sous classe des *Calcaronea* avec les angles pairs nettement plus petits que l'angle impair et ils ne peuvent certainement pas dériver de la forme régulière et equiangulaire des *Calcinea*. Notre matériel est suffisamment bien conservé pour nous permettre aussi d'établir la position du noyau dans les choanocytes : il est toujours apical ce qui montre que l'espèce doit être placée sans doute dans le genre *Leuconia*.

Les échantillons concordent bien avec la description de BRØNDSTED (1928). Ils ont la forme d'un grand sac comprimé ; les deux spécimens récoltés en dragage mesurent 8 × 3 cm et 5 × 4 cm. L'oscule est en forme de large ouverture sur le bout apical. Les parois sont relativement minces et irrégulièrement plissées, ce qui donne à l'éponge un aspect particulier avec la surface irrégulièrement mamelonnée. La surface extérieure est faiblement hispide, la surface de la vaste cavité gastrique est presque glabre.

La couche dermique est mince, contenant des triactines sagitaux percée par des diactines qui sont profondément plantés dans le parenchyme et au maximum 1/4 de leur longueur dépasse de la surface. Le parenchyme est percé par des canaux exhalants. Les chambres vibratiles sont ovales et mesurent jusqu'à 100 μ de diamètre. La surface gastrique est couverte par une mince couche de triactines et d'assez rares tetractines.

Les diactines ont jusqu'à 600 μ de long ; ils sont légèrement courbés et pointus chez les spécimens de Mouillage (fig. 10 *a*) mais le spécimen de l'Ilôt Channer a la partie distale des diactines épaissie, courbée et arrondie (fig. 10 *b*). Les triactines (fig. 10 *c*) sont sagittaux, leurs actines

paires et impaires ont la longueur à peu près égale ; elle varie de 100 à 250 μ sur 10 μ d'épaisseur. L'actine apicale des tetractines (fig. 10 *d*) est courte, courbée et pointue.

Stations : Vb, Kerguelen, SW Mouillage ; 2, Kerguelen, E Ilôt Channer.

Distribution géographique : Kerguelen, Baie du Canard, Baie d'Observatoire (Brøndsted).

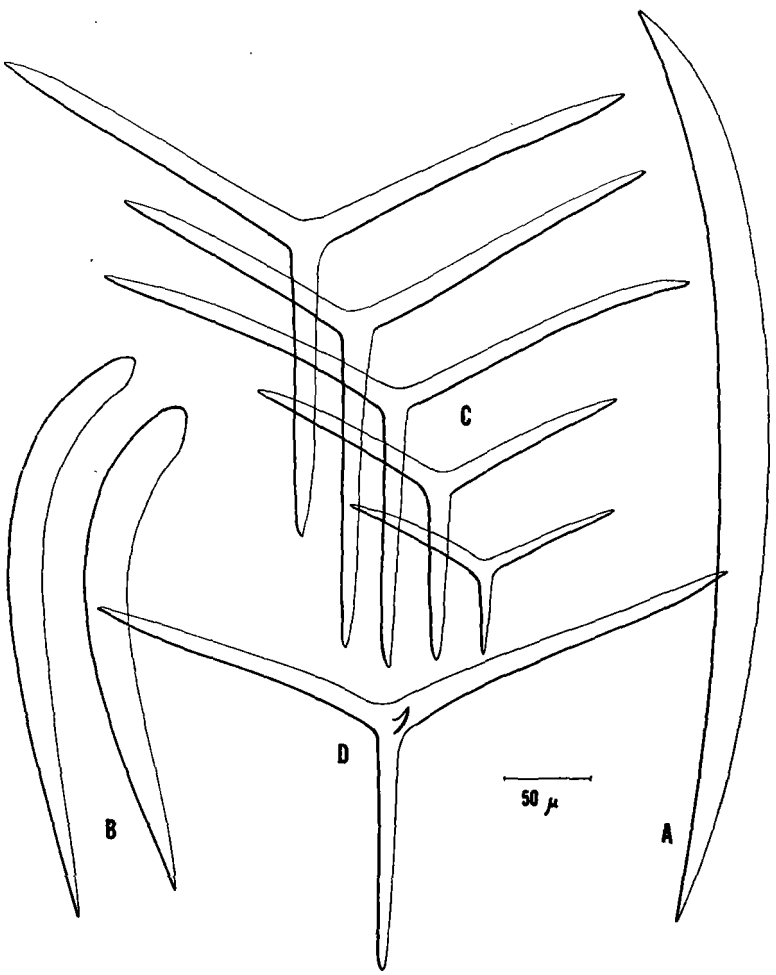

FIG. 10. — *Levconia gaussii* Brøndsted.
A. Diactine du spécimen de Mouillage ; B. Diactine du spécimen de l'Ilot Channer ; C. Triactines ; D. Tetractines.

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Leuconia kerguelensis Urban (Fig. 11).

Leuconia kerguelensis Urban, 1908.

Le spécimen de l'Ile du Chat correspond exactement aux descriptions d'URBAN (1908). Il a la forme d'un tube courbé de 22 mm de haut sur 4 mm de diamètre. Une vaste cavité centrale est entourée de parois de 1 mm d'épaisseur.

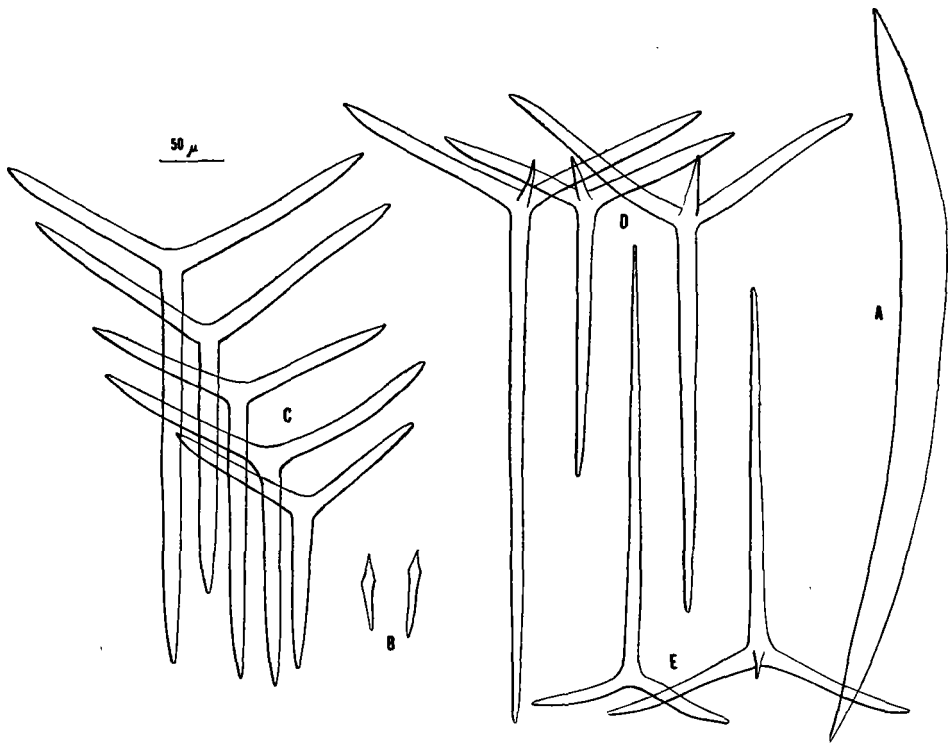

FIG. 11. — *Leuconia kerguelensis* Urban.
A. Diactine ; B. Microdiactines ; C. Triactines ; D. Tetractines ; E. Triactine et tetractines subgastriques.

Les triactines dermiques forment une couche serrée mais mince chargée de nombreux microdiactines et percée par les diactines et trichoxes. L'actine impaire de la plupart des triactines du parenchyme est orienté vers l'extérieur du corps. Le squelette de la partie intérieure du corps est constitué presque exclusivement de triactines et tetractines subgastriques, qui s'appuient sur une couche dense de triactines et tetractines gastriques.

Les diactines (fig. 11 *a*) sont robustes : 400-700 μ de long sur 20-35 μ d'épaisseur, légèrement courbées et pointues. Les microdiactines (fig. 11 *b*) de 40 μ de long sont différenciés en fer de lance ; les triactines (fig. 11 *c*) et les tetractines (fig. 11 *d*) sont sagittaux leur actine impaire est souvent beaucoup plus longue que les actines paires. En passant de la partie dermique à la partie subgastrique l'actine impaire des triactines passe de 150-340 μ tandis que les actines paires passe de 150 à 250 μ. La surface gastrique contient des triactines et tetractines dont l'actine impaire mesure 400 μ et l'actine apicale 20 μ.

Station : 4 *c*, Kerguelen, SE Ile du Chat.

Distribution géographique : Kerguelen, Bassin de la Gazelle (Urban).

Leuconia minor Urban (Fig. 12).

Leuconia minor Urban, 1908.

La collection ne renferme qu'un seul spécimen de 7 mm de haut. Son aspect extérieur est semblable à celui des autres *Leuconia* de cette région, mais cette espèce est caractérisée par la présence des grands tetractines gastriques avec des actines apicales très longues qui rendent la surface gastrique très hispide.

L'oscule est entouré d'une faible frange de trichoxes supportée par un court tube osculaire composé de triactines et tetractines sagittaux.

Une zone de cavités subdermiques est présente, mais elle est moins régulière que celle de *Leuconia anfracta* Urban. Sa largeur maxima est 150 μ. Les chambres vibratiles sont sphériques ou ovales de 60 à 80 μ de diamètre. Les canaux inhalants s'enfoncent souvent très profondément dans le parenchyme. Les canaux exhalants sont renforcés par un squelette semblable à celui de la surface gastrique mais les actines apicales des tetractines sont ici moins longues.

La taille des diactines (fig. 12 *a*) varie de 100 à 600 μ. Les plus petits ont un épaississement en forme d'anneau, aux 2/3 de leur longueur. Ils sont assez nombreux et couvrent la surface d'une hispidation haute et dense. Les trichoxes sont abondants et plantés profondément dans le corps ; leur extrémité distale est toujours brisé. Les triactines (fig. 12 *b*) sont sagittaux. Dans la couche dermique leurs actines sont de longueur à peu près égale, alors que dans ceux du parenchyme l'actine impaire est souvent plus longue. La longueur des actines varie de 60 à 200 μ, elles

développent rarement une quatrième actine rudimentaire. Les tetractines gastriques (fig. 12 *c*) sont très remarquables. L'actine apicale est souvent de même longueur que les basales soit 200 μ environ. Les actines basales sont arquées, l'actine apicale est le plus souvent rectiligne. Les spicules du tube osculaire diffèrent des autres spicules par l'angle oral plus ouvert (fig. 12 *d*).

Station : 16 *a*, Kerguelen, N Ile Buchanan.

Distribution géographique : Kerguelen, Bassin de la Gazelle (Urban).

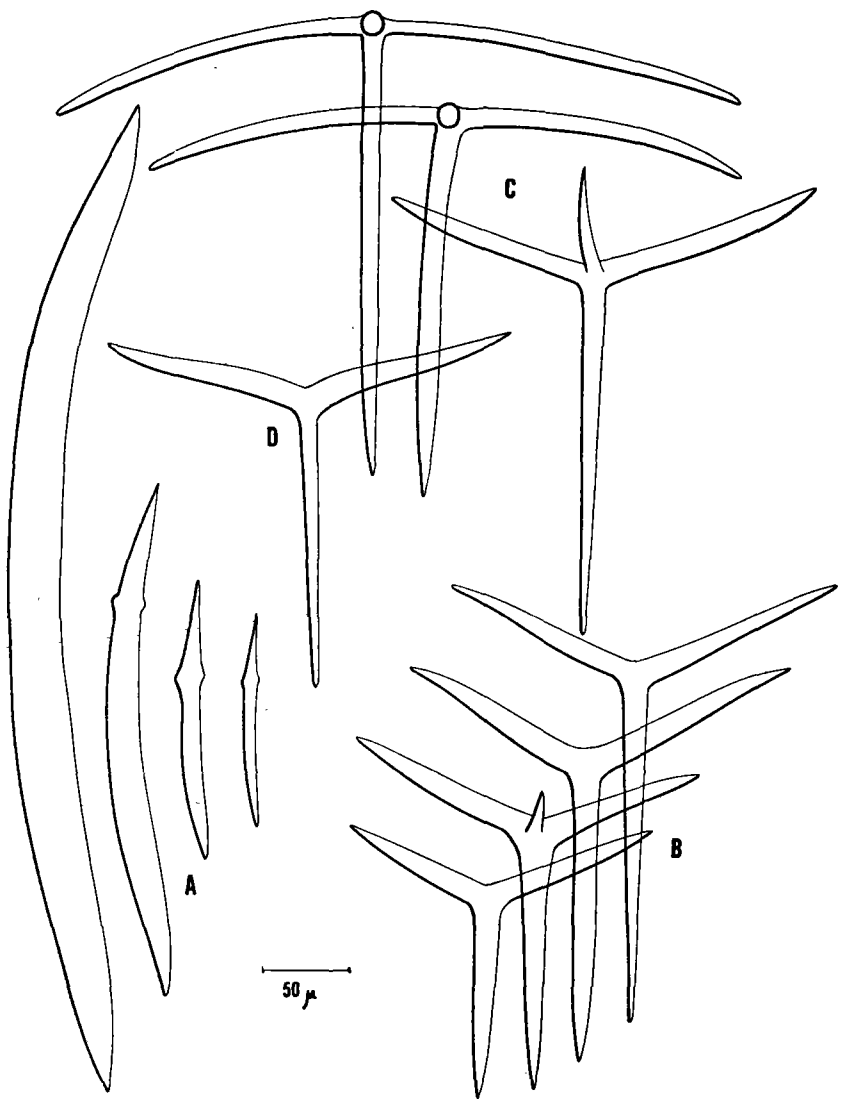

FIG. 12. — *Leuconia minor* Urban.
A. Diactines ; B. Triactines et tetractines du parenchyme ; C. Tetractines gastriques ; D. Triactine du tube oscu'aire.

LISTE DES ÉPONGES CALCAIRES DE KERGUELEN.

Clathrina coriacea Montagu. — Pointe Suzanne, 1-4 m (mission 1962/63).

Clathrina challengeri Poléjaeff. — N Ile Buchanan, 15 m (mission 1962/63).

Leucetta primigenia Haeckel. — Baie Balfour, 20-60 brasses (POLEJAEFF, 1883, p. 64) ; Bassin de la Gazelle, sur un banc à l'Est de Kerguelen, (URBAN, 1908, p. 19) ; Baie d'Observatoire (BRØNDSTED, 1928, p. 18) ; N Ilôt Channer, 7 m, SE Ile du Chat, 15 m, N Ile Buchanan, 15 m, Cap Kidder, 7 m, (mission 1962/63).

Leucettusa vera Poléjaeff. — Kerguelen, 10-100 brasses, (POLÉJAEFF, 1883, p. 68) ; SE Ile du Chat, 15-25 m, N Ile Buchanan, 15 m (mission 1962/63).

Leucosolenia discoveryi Jenkin. — Baie d'Observatoire (BRØNDSTED, 1928, p. 15) ; N Ile Buchanan, 15 m (mission 1962/63).

Leucosolenia minchini Jenkin. — Baie d'Observatoire (BRØNDSTED, 1928, p. 14) ; N Ile Buchanan, 15 m (mission 1962/63).

Leucosolenia incerta Urban. — Sur un banc à l'Est de Kerguelen, 88 m (URBAN, 1908, p. 5).

Sycon kerguelensis Urban. — Bassin de la Gazelle, 9-33 m (URBAN, 1908, p. 5) ; SE Ile du Chat, 15-25 m, N Ile Buchanan, 15 m (mission 1962/63).

Grantia aculeata Urban. — Bassin de la Gazelle, 9-33 m (URBAN, 1908, p. 10).

Grantia tenuis Urban. — Bassin de la Gazelle, 9-33 m (URBAN, 1908, p. 14) ; Baie d'Observatoire (BRØNDSTED, 1928, p. 27).

Leuconia anfracta Urban. — Bassin de la Gazelle, 9-33 m (URBAN, 1908, p. 34) ; Baie d'Observatoire (BRØNDSTED, 1928, p. 38) ; SE Ile du chat, 15 m, N Ile Buchanan, 15 m (mission 1962/63).

Leuconia astricta Tanita. — N Ile Buchanan, 15 m (mission 1962/63).

Leuconia gaussii Brøndsted. — Baie de Canard, Baie d'Observatoire, (BRØNDSTED, 1928, p. 20) ; SW Mouillage, 25 m, E Ilôt Channer, 5 m (mission 1962/63).

Leuconia cirrhosa Urban. — Bassin de la Gazelle, 9-33 m (URBAN, 1908, p. 26).

Leuconia kerguelensis Urban. — Bassin de la Gazelle, 9-33 m (URBAN, 1908, p. 29) ; SE Ile du Chat, 25 m (mission 1962/63).

Leuconia minor Urban. — Bassin de la Gazelle, 9-33 m (URBAN, 1908, p. 32) ; N Ile Buchanan, 15 m (mission 1962-63).

Leuconia ovata Poléjaeff. — Kerguelen 70 brasses (POLÉJAEFF, 1883, p. 61).

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NEW LICHOMOLGID COPEPODS (CYCLOPOIDA) FROM ZOANTHID COELENTERATES IN MADAGASCAR

by ARTHUR G. HUMES* and JU-SHEY HO*

RÉSUMÉ

Les auteurs décrivent deux genres nouveaux (Temnomolgus *et* Indomolgus) *et cinq espèces nouvelles des copépodes cyclopoïdes lichomolgides associés aux zoanthides* (Palythoa tuberculosa *et* Palythoa liscia) *du nord-ouest de Madagascar:* Lichomolgus inaequalis *n. sp.*, Temnomolgus eurynotus *n. gen., n. sp.*, Indomolgus brevisetosus *n. gen., n. sp.*, Indomolgus diversus *n. gen. n. sp. et* Indomolgus mutatus *n. gen., n. sp.*, Indomolgus panikkari *(Gnanamuthu, 1955), une combinaison nouvelle, devient la quatrième espèce du genre* Indomolgus.

* * *

Although lichomolgid copepods are known to be commonly associated with members of the Actiniaria and the Madreporaria, they have not been reported to our knowledge from the Zoanthidea. The five copepods described below were recovered from two species of the zoanthid genus *Palythoa* in the region of Nosy Bé, Madagascar.

The copepods were collected by the first author in 1963-64 as part of the work of the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the material has been aided by a grant from the National Science Foundation of the United States.

We wish to thank Mr. Charles E. Cutress of the United States National Museum, who has identified the zoanthids, and to acknowledge the generous assistance given to the field work by the staff of the Centre d'Océanographie et des Pêches at Nosy Bé (1).

LICHOMOLGIDAE KOSSMANN 1877

LICHOMOLGUS INAEQUALIS n. sp.

Figs. 1-28

Type material. — 17 females from pieces of a colony of the zoanthid *Palythoa tuberculosa* (Esper), in 2 m, at Ambariotelo, a small island between Nosy Bé and Nosy Komba, Madagascar. Collected May 24, 1964. Holotype female and 10 paratypic females deposited in the United States National Museum, Washington.

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(1) Centre O.R.S.T.O.M. de Nosy-Bé (Madagascar).

4 females and 6 males from *Palythoa liscia* Haddon and Duerden, in 2 m, at Pte. Ambarionaomby, Nosy Komba (a locality only 2 kms distant from Ambariotelo). Collected October 1, 1963. Allotype and 6 paratypes (3 females and 3 males) deposited in the United States National Museum. The remaining paratypes in the collection of A. G. Humes.

Other specimens. — 20 females from *Palythoa tuberculosa*, in 2 m, Ambariotelo, May 23, 1964 ; 1 female from *Palythoa liscia*, in 2 m, Ambariotelo, September 10, 1964 ; and 11 females from *Palythoa tuberculosa*, intertidal, Ambariobe, near Ambariotelo, July 6, 1963.

Female. — The body (fig. 1) has a moderately broadened prosome. Its length (not including the setae on the caudal rami) is 0.81 mm (0.72-0.90 mm) and its greatest width (at the level of the posterior part of the head) is 0.43 mm (0.38-0.47 mm), based on 10 specimens. The length of the prosome in relation to its width is about 1.4 : 1. The segment of leg 1 is separated dorsally and laterally from the head by a distinct furrow. The epimeral areas of the segments of legs 2-4 are rounded.

The segment of leg 5 is slightly produced ventrolaterally on each side under the insertion of the free segment of leg 5 (fig. 2) ; dorsally this segment bears a transverse line with its two ends turned forward. The genital segment is a little longer than wide, 114 μ in length, 104 μ in greatest width in the anterior third, and 84 μ in width in the posterior third. The areas of attachment of the egg sacs are situated dorsolaterally in the anterior half of the segment, and each area (fig. 3) bears two small setae 8 μ in length plus a small spiniform process. The three postgenital segments are 40×63, 33×56, and 44×61 μ respectively from anterior to posterior. The anal segment has a row of minute spinules along the outer posteroventral margin on either side.

The caudal ramus (fig. 4), inserted dorsally on the anal segment, is not much elongated, 50×28 μ in greatest dimensions, or 1.8 times longer than wide. The naked outer lateral seta, 68 μ long, is inserted at a slight indentation midway on the outer margin. The naked pedicellate dorsal seta is 40 μ long. Of the four terminal setae, the outermost is naked and 68 μ in length, the innermost is 100 μ long with inner hairs, and the remaining two long setae are 213 μ (outer) and 370 μ (inner) in length, both with the usual basal « peg » and with extremely short lateral spinules on the distal half.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome have very sparse minute refractile points and setules. The ratio of the length of the prosome to that of the urosome is 2 : 1.

The egg sac (fig. 1) is moderately elongated (in one female 360×155 μ, in another 426×179 μ, and contains numerous eggs each about 52 μ in diameter.

The rostral area (fig. 5) is fairly well-defined.

The first antenna (fig. 6) is 7-segmented, with the second segment the longest. The lengths of the segments (measured along their posterior non-setiferous margins) are : 30 (66 μ along the anterior margin), 112, 25, 56, 56, 39, and 30 μ respectively. The formula for the armature is 4, 12 (3+2+7), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All the setae are naked.

The second antenna (fig. 7) is slender and 4-segmented. Each of the first two segments bears a small hyaline naked inner seta, the third segment bears three such setae, and the elongated fourth segment bears two very unequal terminal claws (one 47 μ in length, distinctly unguiform and well-sclerotized, the other less claw-like, slender, somewhat shorter, and weakly sclerotized) plus five small hyaline naked setae near the bases of the claws.

The labrum (fig. 8) has two lobes without ornamentation.

The mandible (fig. 9) bears on its inner basal area a scale-like spinulose sclerotization and a more distal striated flange, and on its outer basal area a row of long, very slender spinules. The greatly attenuated flagellum bears lateral spinules. The paragnath is similar to that of the male (see fig. 23), where it is an elongated lobe bearing a few hairs. The first maxilla (fig. 10) is a single segment bearing four setae, three more or less terminal and one subterminal. The second maxilla

(fig. 11) is 2-segmented, the stout basal segment unarmed, the slender second segment attenuated to form a long flagellum having along one side a row of spines (large proximally but gradually reduced in size distally) and along the opposite side a few small spinules. On the second segment there is a minute hyaline naked basal seta, distally a larger hyaline naked seta, and still more distally a long flagelliform seta ornamented like the terminal flagellum. The maxilliped (fig. 12) is 3-segmented and slender, the first segment being elongated and unarmed, the second of about the same length with two hyaline naked setae, the third short, bearing two small hyaline naked setae and terminating in a pointed process.

The area between the maxillipeds and the first pair of legs (fig. 13) is not produced ventrally, and a line can be seen connecting the bases of the maxillipeds.

The rami of legs 1-4 (figs. 14, 16, 17, and 18) are 3-segmented except for the endopod of leg 4 which is 2-segmented. The spine and setal formula is as follows (the Roman numerals representing the spines, the Arabic numerals the setae) :

P 1	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-1
				end.	0-1 ;	0-1 ;	I-5
P 2	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-II-3
P 3	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-II-2
P 4	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	II-I-5
				end.	0-1 ;	II	

The inner seta on the coxa is feathered in legs 1-3, but smaller and naked on leg 4. On the last segment of the endopod in legs 1-3 there are conspicuous spinules near the insertions of the terminal armature, as shown for leg 1 in fig. 15. In the endopods of leg 4 there is a slight but readily observable asymmetry in the proportions. The first segment appears to have the same size in both legs, about 31×22 μ, though its seta on the right leg is 45 μ and on the left leg 41 μ in length. The second segment on the right side measures 72 μ (the greatest length including the spinous process) $\times$ 18 μ (the greatest width), with its two terminal spines 40 (inner) and 28 μ (outer) ; on the left side this segment is 78×15 μ and the spines 45 and 26 μ. Such asymmetry in proportions was observed in each of the four females dissected.

Leg 5 (fig. 19) has an elongated free segment, 75 μ in greatest length, 31 μ wide at the proximal inner expansion and 19 μ wide in the slender distal portion. The two unequal naked terminal setae are 72 (outer) and 44 μ (inner) in length. The seta on the body near the insertion of the free segment is 39 μ long and feathered.

Leg 6 is represented by the two setae on the area of attachment of the egg sac (see fig. 3).

The color in life in transmitted light is slightly opaque, the eye red, the egg sacs opaque gray.

Male. — The body (fig. 20) is a little less broadened than in the female. The length (excluding the setae on the caudal rami) is 0.69 mm (0.65-0.74 mm) and the greatest width is 0.24 mm (0.22-0.26 mm), based on 6 specimens. The ratio of the length of the prosome to its width is 1.7 : 1.

The genital segment (fig. 21) is about as long as wide, 130×126 μ, with its lateral margins in dorsal view only slightly rounded. The four postgenital segments are 33×51, 23×47, 21×44, and 28×46 μ from anterior to posterior. The minute spinules seen in the female on the posterior ventral margin of the anal segment appear to be absent in this sex.

The caudal ramus resembles that of the female.

There are fewer refractile points and setules on the surfaces of the prosome and urosome than in the female. The ratio of the length of the prosome to that of the urosome is 1.44 : 1.

The rostral area is like that of the female.

The first antenna (fig. 22) resembles that of the female except for the addition of two aesthetes

on segment 2 and one aesthete on segment 4, creating the formula 4, 12 and 2 aesthetes (3+1 aesthete, 2, 7+1 aesthete), 6, 3+1 aesthete, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete.

The second antenna, labrum, mandible, paragnath (fig. 23), first maxilla, and second maxilla are like those in the female.

The maxilliped (fig. 24) is 4-segmented and slender. The basal segment is unarmed, the second segment bears two naked setae and rows of spinules arranged as in the figure, the third segment is very short and unarmed, and the fourth segment, forming part of the claw, bears two setae, one short and naked, the other longer with short hairs along one edge. The gently recurved slender claw is 109 μ in greatest length (measured along its axis and not along its curvature), and shows a suggestion of division midway along its length. On the tip of the claw there is a rather prominent lamella.

The area between the bases of the maxillipeds and the first pair of legs resembles that of the female.

Legs 1-4 resemble those of the female, except that the last segment of the endopod of leg 1 (fig. 25) has the formula I-I-4 instead of I-5 as in the female, the outermost of the setae here being replaced by a spine. The endopods of the fourth legs show asymmetry as in the female, though somewhat less pronounced. In one male the second segment of the endopod (fig. 26) measured on the right side 46×15 μ, with the two spines 39 and 32 μ, on the left side 50×15 μ, with the spines 40 and 29 μ.

Leg 5 (fig. 27) has an elongated free segment, 23×8 μ, without a basal expansion. The two terminal setae, separated by a spinous process, are 39 and 17 μ in length, the longer one naked, the shorter one with a slight lamella.

Leg 6 (fig. 28) consists of a posterolateral flap on the ventral surface of the genital segment. It is armed with two naked setae 33 and 20 μ in length arising near a small spiniform process.

Spermatophores were not observed.

The color in life in transmitted light resembles that of the female.

[The specific name *inaequalis* (Latin = unequally matched, asymmetrical) refers to the unequal size of the terminal claws of the second antenna and to the differences in proportions of the two endopods of the fourth leg.]

Relationship to the host. — *Lichomolgus inaequalis* apparently lives chiefly on the outer surface of the zoanthid colony. This species was recovered in washings of the entire masses of the colony. Later, after the zoanthid had been broken up into small fragments, the washings contained very few of these copepods.

Comparison with other species. — Having the combination of II-I-5 for the third segment of the exopod of leg 4, with the caudal ramus moderately elongated (not subquadrate or very long) and possessing two claws on the second antenna, *Lichomolgus inaequalis* appears to be near *L. furcillatus* Thorell, 1860, and *L. spinulifer* Humes and Frost, 1964. It differs from these two species, however, in readily observable characters. *L. furcillatus* is larger (the female 1.30 mm in length, according to Sars, 1917), one of the three elements on the third segment of the second antenna is a strong spine, and the free segment of leg 5 in the female lacks a basal expansion but instead has a notch in the middle of the outer edge. *L. spinulifer* is also larger, the two terminal claws on the second antenna are subequal, the caudal ramus is 3.3 : 1, and there is a row of spinules instead of hairs along the outer side of the second segment of the endopod of leg 4.

TEMNOMOLGUS n. gen.

Prosome broad and swollen. Segment of leg 1 separated dorsally and laterally from the head by a furrow. Urosome relatively short, 4-segmented in the female and 5-segmented in the male (though in both sexes the last two segments are clearly separated only on the dorsal side). First

antenna 7-segmented. Second antenna 4-segmented with two terminal claws. Mouthparts lichomolgid. Legs 1 and 2 with 3-segmented rami. Leg 3 represented only by two setae. Leg 4 absent. Leg 5 rudimentary, without a free segment and comprising three setae.

Other features as in the species described below.

Living in zoanthids.

Type and only known species : *Temnomolgus eurynotus* n. sp. (The generic name is a combination of τέμνειν = to amputate, referring to the reduced leg 3 and the missing leg 4, and μολγός = a sack made of leather.)

Gender masculine.

TEMNOMOLGUS EURYNOTUS n. sp.

Figs. 29-55

Type material. — 147 females, 143 males, and 15 copepodids from a piece (area about 0.25 square meter and thickness 1 cm) of the colonial zoanthid *Palythoa tuberculosa* (Esper), growing on dead coral in 2 m, at Ambariotelo, a small island between Nosy Bé and Nosy Komba, Madagascar. (This is the same zoanthid colony from which *Lichomolgus inaequalis* was recovered). Collected May 24, 1964. Holotype female, allotype, and 185 paratypes (91 females and 94 males) deposited in the United States National Museum, Washington ; 35 paratypes (20 females and 15 males) in the Zoölogisch Museum, Amsterdam ; and the remaining paratypes in the collection of A. G. Humes.

Other specimens. — 37 females, 40 males, and 39 copepodids from *Palythoa tuberculosa*, in 2 m, Ambariotelo, September 10, 1964.

Female. — The form of the body (figs. 29, 30, and 31) is rather different from that in many lichomolgid genera. The length (excluding the setae on the caudal rami) is 1.18 mm (1.03-1.32 mm) and the greatest width, near the junction of the cephalosome and the first pedigerous segment, is 0.82 mm (0.74-0.90 mm), based on 10 specimens. The prosome is broad and swollen, the proportions of length to width to thickness being about 1.2 : 1.5 : 1.0. The segment of leg 1 is separated dorsally and laterally from the head by a furrow. The epimeral areas of the metasomal segments are more or less rounded. The segment corresponding to leg 4 has a distinct narrow tergal area (390 μ in width) but is not clearly defined ventrally.

The segment of leg 5 (fig. 32) is a little broader (414 μ) than the preceding segment. The setae of the fifth legs arise dorsally. The genital segment is wider than long, being broadest in its anterior half and tapering posteriorly. Its greatest width is 314 μ and its length 185 μ. The areas of attachment of the egg sacs are dorsal and anterior in position, with each area showing two small spines about 7 μ in length (fig. 33). There are three postgenital segments, but the last two are clearly separated only dorsally. In a ventral view these two segments appear as a single segment (compare fig. 30). The first postgenital segment is 101 μ long × 190 μ wide ; the second 50 × 159 μ, and the third 85 × 159 μ, making an overall length of 135 μ. The last segment has an anal operculum and at the insertion of each caudal ramus is slightly truncated.

The caudal ramus (fig. 34), which is inserted a little ventrally on the anal segment, is hyaline, somewhat subelliptical in outline, measuring 55 × 28 μ in greatest dimensions, or two times longer than wide. On the border of the distal half of the ramus there are five hyaline naked setae, the outermost being a little set apart and corresponding to the usual outer lateral seta of lichomolgids. The naked dorsal pedicellate seta is a little more slender than the others. There are refractile areas bearing minute hyaline setules on both dorsal and ventral surfaces of the ramus. There are no spinules on the anal segment near the insertion of the ramus nor are there any on the distal end of the ramus.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear

numerous refractile points with minute setules. The ratio of the length of the prosome to that of the urosome is about 1.8 : 1. In lateral view (fig. 30) the body is arcuate, making it difficult to achieve a complete dorsal view of the animal.

The egg sacs are small and spherical (fig. 35), about 280 μ in diameter, and contain a relatively small number of eggs each with a diameter of about 100 μ.

The rostral region (fig. 36) in ventral view is well-defined, forming a rather narrow linguiform area between the bases of the antennae.

The first antenna (fig. 37) is 7-segmented, the second segment being longer than any of the others. The lengths of the segments (measured along their posterior non-setiferous margins) are : 28 (94 μ along the anterior margin), 93, 44, 40, 39, 22, and 14 μ respectively. The first segment bears 3 setae, the second 13 setae (in groups of 5+2+6), the third 4 setae, the fourth 5 setae, the fifth 3 setae and 1 aesthete, the sixth 2 setae and 1 aesthete, and the seventh 7 setae and 1 aesthete. The formula thus is 3,13 (5+2+6), 4,5,3+1 aesthete, 2+1 aesthete, and 7+1 aesthete. The entire first antenna is hyaline and lightly sclerotized. All the setae are naked and hyaline with delicate annulations.

The second antenna (fig. 38) is 4-segmented, and rather short and robust. Each of the broad first two segments bears a small naked seta. The third segment is less broad and bears three naked setae. The fourth segment is longer than the third and bears four small hyaline setae and two well-sclerotized recurved subequal terminal claws (see fig. 39).

The labrum (fig. 40) has two widely diverging lobes without ornamentation.

The mandible (fig. 41) consists of a basal region (its inner edge with a scale bearing a row of slender setules and its expanded outer edge with a row of hair-like setules and another similar scale) and a distal flagellum basally with an inner striated fringe and distally with bilaterally disposed spinules. The paragnath (fig. 42) is an elongated lobe with groups of hairs ; in ventral view it is seen lying under the lobe of the labrum (see fig. 40). The first maxilla (fig. 43) consists of a single segment with two unequal apical setae, one stout, 21 μ in length, with a well-sclerotized proximal half, the other slender, 10 μ long. The second maxilla (fig. 44) is 2-segmented. The large basal segment is unornamented. The slender arcuate distal segment terminates in a spiniform flagellum provided first with a row of 5-6 sclerotized teeth along its medial margin and then more distally with bilaterally disposed spinules. On this segment there is proximally a small unilaterally barbed seta and distally a large spine bearing two rows of prominent spinules. The maxilliped (fig. 45) is 3-segmented, the first segment the largest and unarmed, the second smaller and bearing two small inner setae, and the third the smallest, bearing two minute hyaline spinules and terminating in two processes, one well-sclerotized and slightly obtuse, the other hyaline and pointed.

The area between the maxillipeds and the first pair of legs (fig. 46) is not produced ventrally. There seems to be no connecting line between the bases of the maxillipeds.

The first two pairs of legs (figs. 47 and 48) have 3-segmented rami. The third leg is rudimentary. The fourth leg is entirely absent. The spine and setal formula is as follows (the Roman numerals indicating the spines, the Arabic numerals the setae) :

P 1	protopod	0-0 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-4
				end.	0-1 ;	0-1 ;	I-I-4
P 2	protopod	0-0 ;	1-0	exp.	I-0 ;	0-1 ;	II-I-4
				end.	0-1 ;	0-1 ;	I-II-2
P 3		—			2		
P 4	absent						

The coxae of legs 1 and 2 are unarmed. The basis of both of these legs has an outer seta but otherwise is unornamented. The spines on the rami are naked and recurved ; the setae are relatively short, naked, and show sclerotized bases, giving the appearance of a « joint ». On the second segment of the exopod of leg 2 the outer spine is absent, an unusual condition in licho-

molgid copepods. Leg 3 (fig. 49) consists only of a small sclerotization bearing two unequal naked setae, the outer one 31 μ, the inner one 21 μ in length. No trace could be found of a fourth leg.

Leg 5 (see fig. 32) is rudimentary and consists only of three naked setae, two closely approximated (28 μ and 12 μ in length) and probably corresponding to the setae found on the free segment in other lichomolgids, and one more distant (28 μ long) corresponding to the seta on the body adjacent to the free segment.

Leg 6 may be represented by the two small spines in the area of attachment of the egg sac (see fig. 33).

The color in life in transmitted light is somewhat opaque, with fine red speckling over the rostral region, the eye dark red, the ovary dark gray, the intestine light brown, the egg sacs dark greenish gray.

Male. — The form of the body (fig. 50) resembles that of the female, but the proportions of the prosome and urosome are somewhat different. The length (not including the setae on the caudal rami) is 1.21 mm (1.07-1.35 mm) and the greatest width near the junction of the cephalosome and the segment of leg 1 is 0.60 mm (0.54-0.66 mm), based on 10 specimens. The prosome is broad and inflated as in the female, the ratio of length to width being about 1.1 : 1. The epimeral areas of the metasomal segments are rounded as in the female. The tergal area of the segment of leg 4 is rather narrow.

The segment of leg 5 (fig. 51) is a little wider than the following segment and bears dorsolaterally the rudimentary fifth legs. The genital segment is much wider than long, 150×328 μ. There are four postgenital segments, but as in the female the last two segments are separated only on the dorsal side. These segments are 135×177, 117×151, 62×124, and 78×121 μ respectively.

The caudal ramus resembles that of the female but is a little larger, measuring about 62×38 μ.

The surfaces of the prosome and urosome bear refractile points as in the female. The ratio of the length of the prosome to that of the urosome is about 1.1 : 1.

The rostral area is like that of the female.

The first antenna resembles that of the female, with the same armature except for the replacement by an aesthete of one seta in the first group on segment 2 and of one seta on segment 4. The formula thus is : 3, 12+1 aesthete (4+1 aesthete, 2, 6), 4, 4+1 aesthete, 3+1 aesthete, 2+1 aesthete, and 7+1 aesthete.

The second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla resemble those of the female.

The maxilliped (fig. 52) is 4-segmented. The first segment is the largest and unarmed ; the second is smaller, with two inner setae and a small patch of spinules on its posterior surface ; the third is very small and unarmed ; and the fourth is elongated, forming part of the claw, and bearing two unequal setae. The claw proper is delimited from the fourth segment by interruptions in the sclerotization. The functional claw (including the fourth segment and the recurved tip) is 66 μ in length (measured along its axis and not along its curvature).

The area between the maxillipeds and the first pair of legs (fig. 53) is not produced ventrally, and shows only indistinct lines between the bases of the maxillipeds.

The first two pairs of legs (figs. 54 and 55) have 3-segmented rami, the third leg is rudimentary, and the fourth leg is absent, all as in the female. The spine and setal formula is the same as in the female. In legs 1 and 2 the spines on the exopods sometimes show minute subterminal flagella ; the setae are longer than in the female, feathered, and do not show the basal « joints ». Leg 3 is like that in the opposite sex. No evidence of leg 4 could be found.

Leg 5 (see fig. 51) resembles that of the female, with the two adjacent setae 42 and 26 μ in length and the more distant seta 39 μ long.

Leg 6 (see fig. 51) consists of a posterolateral flap on the ventral surface of the genital segment, bearing two naked setae 44 and 39 μ in length.

Spermatophores were not observed.

The color in life in transmitted light is somewhat opaque, the eye red.

(The specific name is from εὐρύνωτος = broad-backed, alluding to the form of the prosome.)

Relationship to the host. — *Temnomolgus eurynotus* appears to live in the polyps of the zoanthids. When the pieces of the zoanthid colonies were washed intact in alcoholized sea water, no copepods were recovered. When, however, the zoanthid colonies were broken into small pieces and then washed, large numbers of the copepods were found in the sediment. The living copepods recovered in this way are unable to swim, suggesting that of necessity they inhabit protected places such as the gastrovascular cavities of the polyps.

Systematic position of the new genus. — *Temnomolgus* belongs to the large family Lichomolgidae, in which some 25 apparently valid genera have already been placed. These genera show in varying degrees a reduction of legs 1-4. Several genera have 3-segmented rami on all four legs (for example, *Herrmannella*, *Modiolicola*, and *Paranthessius*). Others have 3-segmented rami except for the endopod of leg 4 which is 2-segmented (for example, *Lichomolgus* and *Stellicola*). Still others have 3-segmented rami but the endopod of leg 4 is reduced to a single segment (for example, *Kelleria*, *Octopicola*, and *Pseudanthessius*). (In *Scambicornus* the reduction occurs only in the male, where the endopods of legs 1 and 2 are 2-segmented). In *Heteranthessius* the reduction is carried further, and, while the other rami are 3-segmented, the endopod of leg 4 is represented only by a small mucronate knob (Bocquet, Stock, and Bénard, 1959). The genus *Meomicola* shows the most extreme reduction known in the family until now. Here the endopod of leg 3 is absent and the ramus of leg 4 is reduced to a single segment (Stock, Humes, and Gooding, 1964). *Temnomolgus* exhibits still more dramatic reduction, having lost leg 4 entirely and leg 3 being reduced to a small sclerotization bearing two setae.

Most of the known lichomolgid genera have a free segment on leg 5. In some, however, the free segment is absent and the leg is represented only by two or three setae (for example, *Heteranthessius*, *Meomicola*, *Pseudanthessius*, and *Urocopia*). *Temnomolgus* shows a similar reduction of leg 5 to a condition of having only three setae.

As pointed out by Stock, Humes, and Gooding (1964, p. 56), the number of body segments in the Lichomolgidae is generally constant, there being five urosomal segments in the female and six in the male. In certain species of *Pseudanthessius*, however, this number is reduced, as in *P. deficiens* Stock, Humes, and Gooding, 1964, and in *P. dubius* Sars, 1918, where there are four segments in the urosome of the female and five in the male. *Temnomolgus* shows a condition intermediate between these, having five urosomal segments in the female and six in the male, but in both sexes the last two segments incompletely separated. In *Meomicola* the urosome has three segments in the female and four in the male.

Sexual dimorphism among the appendages of the Lichomolgidae occurs in several genera. In *Temnomolgus* it is seen not only in the first antennae and maxillipeds, but also in legs 1 and 2, where, although the segmentation and spine and setal formula is similar in both sexes, the nature of the setae is markedly different (short, naked, and « jointed » in the female, but longer, feathered, and entire in the male).

The absence of an outer spine on the second segment of the exopod of leg 2 in both sexes of *Temnomolgus* is unusual among lichomolgid copepods. This spine may be absent, however, in certain other cyclopoids, such as species of *Ergasilus*.

Temnomolgus does not seem to be very close to any other genus in the family, although in the reduction of legs 3 and 4, in the rudimentary condition of leg 5, and in the tendency toward reduction in the number of urosomal segments it approaches *Pseudanthessius*, *Meomicola*, and *Heteranthessius*.

INDOMOLGUS n. gen.

Body elongated, the prosome not much widened. Segment of leg 1 separated partially or completely from the head by a furrow. Urosome 5-segmented in the female, 6-segmented in the

male. Caudal ramus with relatively short setae. First antenna 7-segmented, with short setae. Second antenna 4-segmented with two sometimes unequal terminal claws. Mouthparts lichomolgid. Legs 1-4 with 3-segmented rami except for leg 4 which has a 2-segmented endopod. Armature of the legs somewhat variable. Last segment of the endopod of leg 4 with the formula II-2, I-3, or II-3. Free segment of leg 5 relatively small and provided with two terminal setae.

Living in actiniarians and zoanthids.

Type species : *Indomolgus brevisetosus* n. sp. (The generic name is derived from Ἰνδός = Indian, alluding to the occurrence of this genus in the Indian Ocean, and μολγός = a sac made of leather).

Gender masculine.

INDOMOLGUS PANIKKARI (Gnanamuthu, 1955), new combination

Lichomolgus panikkari Gnanamuthu, 1955, from the brackish water sea anemone *Phytocoeleopsis ramunni* Panikkar in Madras, India, conforms to the generic diagnosis of *Indomolgus* and should be transferred to that genus. Although the original description of *I. panikkari* antedates the descriptions of the three new species from Madagascar, *I. panikkari* has not been selected as the type species (on the basis of Recommendation 69B(6) of the International Code of Zoological Nomenclature). Certain discrepancies seem to exist between the spine and setal formula of legs 1-4 given in th text (p. 152) and the armature shown in text-fig. 1b, c, d, and e. (The legends for text-figs. 1 and 2 are reversed). We have been unable to obtain type or other specimens of *I. panikkari* for study (1).

INDOMOLGUS BREVISETOSUS n. sp.
Figs. 56-85

Type material. — 49 females, 21 males, and 16 copepodids from the colonial zoanthid *Palythoa tuberculosa* (Esper) (the same colony from which *Lichomolgus inaequalis* and *Temnomolgus eurynotus* were taken), in 2 m, at Ambariotelo, a small island between Nosy Bé and Nosy Komba, Madagascar. Collected May 24, 1964. Holotype female, allotype, and 42 paratypes (30 females and 12 males) deposited in the United States National Museum, Washington, and the remaining paratypes in the collection of A. G. Humes.

Other specimens. — 39 females, 31 males, and 11 copepodids from *Palythoa liscia* Haddon and Duerden, in 2 m, Ambariotelo, September 10, 1964 ; 1 female and 1 copepodid from *Palythoa tuberculosa*, in 2 m, Ambariotelo, September 10, 1964 ; 2 females and 1 male from *Palythoa liscia*, in 2 m, Ambato Rano, an islet between Nosy Komba and Ankify, October 20, 1964 ; 7 females, 8 males, and 5 copepodids from *Palythoa liscia*, in 2 m, Pte. Ambarionaomby, Nosy Komba, October 1, 1963 ; and 4 females and 5 males from *Palythoa liscia*, in 2 m, Tany Kely, near Nosy Bé, October 3, 1963.

Female. — The body (figs. 56 and 57) is elongated, with the prosome not unusually expanded. The length (not including the setae on the caudal rami) is 2.02 mm (1.83-2.20 mm) and the greatest width, near the junction of the cephalosome and the first pedigerous segment, is 0.69 mm (0.63-0.75 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.6 : 1. The segment of leg 1 is separated from the head by a furrow which, though readily visible laterally, is indistinct dorsally. The epimeral areas of the metasomal segments are rounded in dorsal view, those of the fourth pedigerous segment being more acutely so.

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(1) The type specimens of L. *panikkari* are not in the collections of the Zoological Survey of India. Personal inquiry indicates that no specimens of this species are now in Dr. Gnanamuthu's collection (letter from Dr. K. Reddiah, April 3, 1965).

The segment of leg 5 (fig. 58) is a little broader (526 μ) than the preceding segment. The fifth legs arise slightly dorsally. The genital segment is only a little longer than wide (336×325 μ), with its lateral margins in dorsal view smooth and only gently expanded. The areas of attachment of the egg sacs lie dorsally and far anteriorly, and each area (fig. 59) bears two small spines, each about 10 μ in length and with an extremely minute lateral tooth. The three postgenital segments are 143×221, 86×180, and 156×188 μ respectively. The anal segment shows an anal operculum and is slightly truncated at the insertion of each caudal ramus.

The caudal ramus (fig. 60), inserted a little dorsally in the anal segment, is elongated, 218× 81 μ in greatest dimensions, or 2.7 times longer than wide. It bears six short naked setae, each about 57 μ in length. One of these is inserted about midway on the outer margin, one is located subterminally on the inner margin, and the remaining four are more or less terminal. One of these setae certainly represents the usual dorsal seta, but since all the setae are inserted marginally this could not be identified with certainty. Both dorsal and ventral surfaces of the ramus bear scattered minute setules. There are no spinules terminally on the ramus nor are there any on the anal segment near its insertion.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear relatively few refractile points with minute hyaline setules. The ratio of the length of the prosome to that of the urosome is about 1.19 : 1.

The egg sacs are moderately elongated (fig. 61), 672×300 μ, and contain numerous eggs, each about 112 μ in diameter.

The rostral area (fig. 62) is poorly defined.

The first antenna (fig. 63) is 7-segmented, with the second segment by far the longest. The lengths of the segments (measured along their posterior non-setiferous margins) are : 25 (62 μ along the anterior margin), 95, 23, 31, 33, 15, and 17 μ respectively. The formula for the armature is : 4, 11 (3 and 1 minute setule+2+6), 6 (+2 minute setules), 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. (One female showed on one first antenna 7 setae instead of 6 in the distal group on segment 2). All the setae are naked and relatively short.

The second antenna (fig. 64) is 4-segmented. Each of the rather large first two segments bears a slender naked inner seta. The small third segment bears three similar inner setae. The fourth segment is elongated and bears seven elements : subterminally three slender naked setae and a larger seta unilaterally with spinules, terminally a small naked setule and two nearly equal claws 39 and 34 μ in length. Both claws are smooth except for a slight knob-like projection at the break in the sclerotization along the convex margin (fig. 65).

The labrum (fig. 66) has two widely diverging lobes devoid of ornamentation.

The mandible (fig. 67) shows on the inner basal region a sclerotization suggesting a scale and a broad hyaline lamella bearing a distal marginal row of minute spinules, and on the outer basal area a row of rather stout spinules. The distal flagellum is short, not finely attenuated, and has serrated margins. The paragnath (fig. 68) is a small lobe bearing two groups of hairs. The first maxilla (fig. 69) is a single segment with three subequal naked terminal setae. The second maxilla (fig. 70) is 2-segmented, the large basal segment bearing a few minute setules, the distal segment terminating in a spiniform flagellum armed on one side with a row of teeth which gradually become more slender distally. On the second segment there is a small outer basal sclerotized knob, a naked seta on the posterior surface, and more distally an inner seta unilaterally with a row of spinules. The maxilliped (fig. 71) is 3-segmented. The first segment is large and unarmed ; the second is smaller and flattened in posterior view (fig. 72), bearing two small hyaline naked setae ; and the third is the smallest, terminating in a pointed, rather weakly sclerotized process, and bearing two unequal hyaline naked setae.

The area between the maxillipeds and the first pair of legs (fig. 62) shows a balloon-like expansion just behind the level of the maxillipeds. This is prominent in lateral view (fig.73).

The rami of legs 1-4 (figs. 74, 76, 77, and 78) are 3-segmented except for the endopod of leg 4

which is 2-segmented. The spine and setal formula is as follows (the Roman numerals indicating the spines and the Arabic numerals the setae) :

P 1	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-4
				end.	0-1 ;	0-1 ;	I-I-4
P 2	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-II-3
P 3	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-II-2
P 4	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	II-3	

The distalmost spine on the third segment of the exopod in all four legs has a subterminal process as shown for leg 1 in fig. 75. The setae on these legs are not as finely attenuated as in many other species of lichomolgids. The first segment of the endopod of leg 4 measures 36×51 μ, the second 95×55 μ. The row of hairs along the outer margin of the second segment is interrupted, perhaps indicating the dual nature of this segment. On this segment the two spines are 30 and 37 μ in length and the setae 51, 63, and 80 μ, from outer to inner.

Leg 5 (fig. 79) has a relatively small free segment, 63×32 μ, two times longer than wide, bearing two naked unequal terminal setae 16 and 36 μ in length and a few small hyaline setules on dorsal and ventral surfaces. The naked seta arising from the body near the free segment is 31 μ in length.

Leg 6 is probably represented by the two minute spines on the area of attachment of the egg sac (see fig. 59).

The color in life in transmitted light is opaque, with the eye red and the egg sacs dark greenish gray. The posterior borders and the epimera of the pedigerous segments, the genital segment, and the caudal rami are tinged with pale amber.

Male. — The form of the body (fig. 80) resembles that of the female. The length (excluding the setae on the caudal rami) is 2.20 mm (2.04-2.36 mm) and the greatest width is 0.68 mm (0.63-0.72 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.57 : 1.

The genital segment (fig. 81) is broad with rounded margins in dorsal view, wider than long, 403×482 μ. The four postgenital segments are 138×195, 122×169, 70×151, and 153×164 μ respectively.

The caudal ramus resembles that of the female, but is a little longer and more slender, 234×64 μ.

The surfaces of the prosome and urosome, as in the female, bear refractile points with minute setules. The ratio of the length of the prosome to that of the urosome is about 1 : 1.

The rostral area is like that of the female.

The first antenna (fig. 82) resembles that of the female but two aesthetes are added on segment 2 and one on segment 4, making the formula as follows : 4, 11+2 aesthetes (3 and 1 minute setule plus 1 aesthete+2+6 and 1 aesthete), 6,3+1 aesthete, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete.

The second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla are like those in the female.

The maxilliped (fig. 83) is 4-segmented. The large first segment bears on its distal inner area a pointed sclerotized knob and a low ridge. The second segment bears two naked inner setae, a postero-inner row of small spines, and two small sclerotized ridges. The small third segment is unarmed. The fourth segment forms part of the claw and bears two basal naked setae. The slightly recurved claw is 318 μ in length (measured along its axis and not along its curvature). It shows a slight indication of division about midway along its length and has a small terminal lamella.

The area between the maxillipeds and the first pair of legs resembles that in the female.

Legs 1-4 are similar to those of the female, except that on legs 1-3 the outer process adjacent to the distalmost spine on the endopods is relatively longer (fig. 84).

Leg 5 (fig. 85) resembles that of the female, but the free segment is relatively much smaller, $31 \times 19\ \mu$, with the two terminal naked setae relatively longer, 33 and 22 μ respectively. The seta arising from the body near the base of the free segment is 31 μ long.

Leg 6 (fig. 81) consists of a posterolateral flap on the ventral surface of the genital segment, bearing an inner rounded protuberance and two outer small naked setae 17 and 13 μ long respectively.

Spermatophores were not observed.

The color in life in transmitted light resembles that of the female, though the pale amber color on the genital segment and the caudal rami appears to be a little more intense.

[The specific name *breviselosus* (Latin, *brevis* = short, and *selosus* = full of setae) alludes to the relatively short setae in this species on the first antennae and on the caudal rami].

Relationship to the host. — Like *Temnomolgus eurynotus*, these copepods apparently inhabit the gastrovascular cavities of the polyps. They were recovered only from washings of zoanthid colonies which had been broken into small pieces, never from washings of intact colonies. When removed from the host, the copepods are unable to swim.

Comparison with related species. — *Indomolgus breviselosus* may be readily distinguished from the following two new species by the armature of the second segment of the endopod of leg 4. It differs in several ways from *I. panikkari* (Gnanamuthu), being smaller [the females of *I. panikkari* have a length of 2.9 mm (2.7-3.1 mm) and the males 2.7 mm (2.4-2.8 mm), the size ranges in both sexes in these two species not overlapping], and having a caudal ramus only a little longer than the anal segment (whereas in *I. panikkari* it is longer than the last two postgenital segments together). The spine and setal formula for legs 1-4 in *I. panikkari* is apparently somewhat different from that in *I. breviselosus*, but the discrepancies between Gnanamuthu's description and figures make a comparison uncertain. The armature of the second segment of the endopod of leg 4 resembles that of *I. breviselosus*.

INDOMOLGUS DIVERSUS n. sp.

Figs. 86-114

Type material. — 165 females, 56 males, and 40 copepodids washed from the colonial zoanthid *Palythoa tuberculosa* (Esper) (the same colony from which *Lichomolgus inaequalis*, *Temnomolgus eurynotus*, and *Indomolgus breviselosus* were recovered), in 2 m, at Ambariotelo, a small island between Nosy Bé and Nosy Komba, Madagascar. Collected May 24, 1964. Holotype female, allotype, and 144 paratypes (110 females and 34 males) deposited in the United States National Museum, Washington ; 30 paratypes (20 females and 10 males) in the Zoölogisch Museum, Amsterdam ; and the remaining paratypes in the collection of A. G. Humes.

Other specimens. — 2 females, 5 males, and 3 copepodids from *Palythoa tuberculosa*, in 2 m, Ambariotelo, May 23, 1964 ; 13 females, 21 males, and 3 copepodids from *Palythoa liscia*, in 1 m, Ambariotrimaramara, off Ampombilava, Nosy Bé, June 12, 1964 ; 58 females, 13 males, and 15 copepodids from *Palythoa liscia*, in 2 m, Ambariotelo, September 10, 1964 ; 35 females, 13 males, and 19 copepodids from *Palythoa tuberculosa*, in 2 m, Ambariotelo, September 10, 1964 ; 44 females 15 males, and 5 copepodids from *Palythoa liscia*, in 2 m, Ambato Rano, an islet between Nosy Komba and Ankify, October 20, 1964 ; 2 females from *Palythoa liscia*, in 2 m, Pte. Ambarionaomby, Nosy Komba, October 1, 1963 ; and 4 females, 2 males, and 3 copepodids from *Palythoa liscia*, in 2 m, Tany Kely, near Nosy Bé, October 3, 1963.

Female. — The body (figs. 86 and 87) is elongated, with the prosome not greatly broadened. The length (not including the setae on the caudal rami) is 1.43 mm (1.36-1.49 mm) and the greatest width, just in front of the junction between the cephalosome and the segment of leg 1, is 0.53 mm (0.50-0.55 mm), based on 10 specimens. The ratio of the length of the prosome to its width is about 1.8 : 1. The segment of leg 1 is separated dorsally and laterally from the head by a distinct furrow. The segments of legs 3 and 4 are often expanded in length (as shown in the figures) but in some specimens they are short. The rounded epimeral areas of the metasomal segments are less prominent than in the preceding species.

The segment of leg 5 (fig. 88) is narrower (240 μ) than either the fourth pedigerous segment or the genital segment. The free segment of leg 5 is inserted slightly ventrally. The genital segment is wider than long (220 × 250 μ), with the areas of attachment of the egg sacs protruding laterally in the anterior half of the segment. Each such area (fig. 89) bears two small spines about 6 μ in length. The three postgenital segments are 91 × 159, 60 × 140, and 96 × 140 μ respectively. The anal segment shows an anal operculum, and bears posteriorly near the insertion of each caudal ramus a dorsolateral row of minute spinules.

The caudal ramus (fig. 90), inserted dorsally on the anal segment, is moderately elongated and held in a widely diverging position. The length along the inner margin is 74 μ, along the outer margin 79 μ, and its greatest width is 41 μ. The ramus is broadest near its base and tapers distally. Taking the greatest dimensions, the ratio of length to width is about 1.9 : 1. The outer lateral seta (33 μ in length) is inserted about midway on the margin. The pedicellate dorsal seta is 27 μ long. Of the four terminal setae, the outermost and innermost are short, 35 and 38 μ respectively ; the remaining two setae are longer but very unequal, the outer 67 μ and indistinctly « pegged », the inner 168 μ and showing the usual sclerotization or « peg ». All the setae are naked. A minute setule is borne on the dorsal surface of the ramus.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome are very sparsely provided with minute hyaline setules. The ratio of the length of the prosome to that of the urosome is about 1.85 : 1.

The egg sacs are moderately elongated (fig. 91), 548 × 235 μ, and each contains a relatively small number of eggs about 78 μ in diameter.

The rostral area (fig. 92) is well-defined, forming a tongue-shaped region between the bases of the first antennae.

The first antenna (fig. 93) is 7-segmented, with the second segment the longest. The lengths of the segments (measured along their posterior non-setiferous margins) are : 15 (40 μ along the anterior margin), 77, 24, 45, 39, 25, and 27 μ respectively. The formula for the armature is 3, 12 (4+2+6), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. On the dorsal surface of segment 1 there is a row of minute spinules. In one female an aesthete was present on segment 4 on both antennae in addition to the three setae. All the setae are naked. The posteriormost distal seta of segment 3 often appears to arise on the extreme basal part of segment 4, but this seta is considered here to belong to segment 3.

The second antenna (fig. 94) is slender and 4-segmented. The armature consists of the same number of elements as in the preceding species. The first and second segments have a single inner seta, the third three inner setae, and the fourth seven elements, — five small setae and two gently recurved claws, 69 and 63 μ in length respectively. All the setae are naked.

The labrum (fig. 95) has two lobes without conspicuous ornamentation.

The mandible (fig. 96) bears on its inner basal region a spinulose scale, a hyaline lamella forming a pointed process and more distally a striated flange, and on its outer basal area three spines (two close together, the other more distant) and an interrupted row of very slender spinules. The distal flagellum is long and attenuated, with spinulose margins. The paragnath (fig. 97) is an elongated smooth lobe. The first maxilla (fig. 98) is a single segment bearing three terminal setae 55, 58, and 15 μ in length. The second maxilla (fig. 99) is 2-segmented, the large basal segment being unarmed, the second segment attenuated to form a distal flagellum armed with 4-5 stout teeth on

its medial margin beyond which its margins are spinulose. The second segment bears a small outer basal hyaline seta (5 μ in length), a larger seta with two lateral spinules, and more distally a still longer seta with four prominent spinules along the medial margin. The maxilliped (fig. 100) is slender and 3-segmented, with the same armature as in the previous species, though the terminal process is recurved and more acutely pointed.

The area between the maxillipeds and the first pair of legs shows only a very slightly raised area just behind the level of the maxillipeds. A line connects the bases of the maxillipeds.

The rami of legs 1-4 (figs. 101, 102, 103, and 104) are segmented as in *I. brevisetosus*. The spine and setal formula is as follows (the Roman numerals indicating the spines, the Arabic numerals the setae) :

P 1	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-4
				end.	0-1 ;	0-1 ;	I-I-4
P 2	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-II-3
P 3	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-I-2
P 4	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-4
				end.	0-1 ;	II-2	

The hairs on the inner margin of the basis of leg 1 appear to be absent, though they are present on legs 2-4. The second segment of the endopod of leg 4 measures 72×37 μ. The outer row of hairs on this segment is interrupted, and at the break there may be in some specimens a minute spinous process. The two spines are 35 and 80 μ and the two setae 90 and 92 μ in length respectively from outer to inner. The setation on this segment seems to be somewhat plastic. One female showed the formula II-3 on both fourth legs (fig. 105). In another the innermost seta on one leg was haired evenly throughout instead of being proximally with long hairs and distally with short spinules as in fig. 104.

Leg 5 (fig. 106) has a slender elongated free segment, 46×12 μ in greatest dimensions, about 4 times longer than wide. It bears two terminal naked setae 57 and 40 μ in length. Along the distal half of its outer margin there are extremely minute spinules. The naked seta arising from the body near the base of the free segment is 36 μ in length. In one female one of the fifth legs showed a short seta (12 μ long) on the ventral surface of the free segment near the insertions of the two terminal setae.

Leg 6 is probably represented by the two small spines on the area of attachment of the egg sac (see fig. 89).

The color in life in transmitted light is opaque to translucid, with the eye red, the egg sacs opaque gray, and with a few minute reddish granules lateral and posterior to the maxillipeds and small reddish areas on the inner sides of the bases of legs 1-4.

Male. — The body (fig. 107) has the same general form as in the female. The length (without the setae on the caudal rami) is 1.21 mm (1.15-1.26 mm) and the greatest width is 0.39 mm (0.37-0.40 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.8 : 1.

The genital segment (fig. 108) is only slightly longer than wide, 246×235 μ, with gently rounded margins in dorsal view. The four postgenital segments are 63×110, 60×107, 44×99, and 63×100 μ respectively. The anal segment bears small spinules on its ventral posterior border.

The caudal ramus is very similar to that of the female, its greatest dimensions being 68×33 μ.

The surfaces of the prosome and urosome are very sparsely provided with minute setules as in the female. The ratio of the length of the prosome to that of the urosome is about 1.35 : 1.

The rostral region resembles that of the female.

The first antenna (fig. 109) resembles that of the female, but, as in *Indomolgus brevisetosus*, two aesthetes are added on segment 2 and one on segment 4, creating the formula 3, 12+2 aesthe-

tes (4 and 1 aesthete+2+6 and 1 aesthete), 6,3+1 aesthete, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. The aesthetes are long and slender, with one edge more sclerotized than the other.

The second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla are like those of the female.

The maxilliped (fig. 110) is 4-segmented. The basal segment is unarmed ; the slender second segment bears the usual two setae, both naked, and a row of short spinules ; the third segment is small and unarmed ; and the fourth segment forms part of the claw and bears two setae, one on the anterior surface minute, the other on the posterior surface large and with spinulose margins. The slightly recurved claw is 121 μ in length (measured along its axis and not along its curvature) and shows a slight indication of division about midway on its length. There is a minute terminal lamella.

The area between the maxillipeds and the first pair of legs (fig. 111) resembles that of the female.

Legs 1-4 are like those of the female.

Leg 5 (fig. 112) has a much shorter free segment than in the female, measuring 25×10 μ, with the two subqual terminal setae relatively longer, 33 and 31 μ in length. The seta on the body near the base of the segment is 35 μ long.

Leg 6 (figs. 108 and 113) consists of a posterolateral flap on the ventral surface of the genital segment. It is armed with two naked setae 29 and 35 μ in length, medial to which there is a small marginal spinous process. The surface of the flap is ornamented with spinules as indicated in the figures.

The spermatophore (fig. 114) attached to the female, is elongated, 255×114 μ, not including the neck of 13 μ.

The color in life resembles that of the female, though the body is perhaps a little more translucid.

[The specific name *diversus* (Latin = turned from one another, diverging) refers to the divergent position of the caudal rami.]

Relationship to the host. — Just as in *Temnomolgus eurynotus* and *Indomolgus brevisetosus*, these copepods were not found in washings of the intact masses of the zoanthid colonies, but only after these masses had been thoroughly broken up. This indicates that *I. diversus* also inhabits the gastrovascular cavities of the polyps. All three species of copepods may occur in the same colony of zoanthid (as in the case of the type material from Ambariotelo in May, 1964, and in a second collection from Ambariotelo in September, 1964).

Comparison with related species. — *I. diversus* differs from both *I. panikkari* and *I. brevisetosus* in being much smaller, the female only 1.43 mm in length instead of 2.9 and 2.02 mm for the other two species respectively. The caudal ramus in *I. diversus* is shorter than the anal segment, whereas in *I. panikkari* and *I. brevisetosus* it is longer. The spine and setal formula for legs 3 and 4 in this species is also somewhat different from that in either *I. panikkari* or *I. brevisetosus*. The armature of the second segment of the endopod of leg 4 is II-2. instead of II-3 as in *I. panikkari* and *I. brevisetosus*, or I-3 as in the following species.

INDOMOLGUS MUTATUS n. sp.

Figs. 115-143

Type material. — 21 females, 19 males, and 11 copepodids from the zoanthid *Palythoa tuberculosa* (Esper), growing on dead coral exposed at low tide at Antafianambitry, Nosy Bé, Madagascar. Collected September 8, 1964. Holotype female, allotype, and 31 paratypes (16 females and 15 males) deposited in the United States National Museum, Washington ; the remaining paratypes in the collection of A. G. Humes.

Female. — The body (figs. 115 and 116) resembles in general form the two species of *Indomolgus* described above. The length (without the setae on the caudal rami) is 2.59 mm (2.24-2.95 mm) and the greatest width in the cephalosome is 0.92 mm (0.77-1.07 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.68 : 1. The segment of leg 1 is separated from the head by a weak suture. The epimera of the metasomal segments are rounded or slightly angular as indicated in the figure.

The segment of leg 5 (fig. 117) is nearly as wide as the genital segment, $168 \times 414\ \mu$, and the fifth legs are borne a little ventrally. The genital segment is expanded in the midregion at the level of the attachment of the egg sacs ; its greatest dimensions are $392 \times 437\ \mu$, being a little wider than long. The area of attachment of each egg sac is situated dorsolaterally and bears two small setae 13 μ in length (fig. 118). The three postgenital segments are 180×336, 135×302, and $247 \times 302\ \mu$ respectively from anterior to posterior. (The boundaries between the genital and the postgenital segments are weak and difficult to distinguish ; hence the measurement of their lengths may be less exact than in other species). The anal segment shows an anal operculum.

The caudal ramus (fig. 119), inserted terminally, is elongated and held in a rather diverging position. The ramus is widest at its base and tapers gradually distally. Its greatest length is 161 μ, and its width at the level of the outer lateral seta is 58 μ. These dimensions give a ratio of length to width of about 2.8 : 1. The outer lateral seta is inserted midway on the margin. The dorsal seta is shorter than the four terminal setae. All the setae are relatively short (the longest only 33 μ in length), hyaline, and naked. The two median terminal setae show a weak « peg » near the base.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome appear to be devoid of refractile points or setules. The ratio of the length of the prosome to that of the urosome is 1.33 : 1.

None of the females found had egg sacs attached, but one detached egg sac (fig. 120) is elongated and arcuate, measuring $1150 \times 730\ \mu$, with each of the numerous eggs about 94 μ in diameter. (It is possible that this egg sac may not be complete).

The rostral area (fig. 121) is well-defined.

The first antenna (fig. 122) is 7-segmented, with the second segment the longest. The lengths of the segments (measured along their posterior non-setiferous margins) are : 51 (105 μ along the anterior edge) 106, 54, 69, 79, 52, and 41 μ. The formula for the armature is 4, 13 (5+8), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All the setae are naked and relatively short. The entire appendage is weakly sclerotized.

The second antenna (fig. 123) is 4-segmented and rather slender. The armature of the first three segments resembles that of the two species of *Indomolgus* described above, though one of the three setae on segment 3 is stouter and more sclerotized than the other two. The two terminal claws are slender and weak, one 39 μ, the other 34 μ in length ; only three small hyaline setae near the bases of the claws could be identified. All the setae are naked.

The labrum (fig. 124) has a ventrally protruding longitudinal ridge in front of the two unornamented rounded lobes.

The mandible (fig. 125) has on its inner basal area a long sclerotization bearing a row of graduated spinules distal to which there is a striated flange, and on its outer basal region a row of hairs. The distal flagellum is rather short, with very small lateral spinules. The paragnath (figs. 126 and 124) is a rather large lobe with hairs. Between the paragnaths there is a ventral protuberance as shown in fig. 124. The first maxilla (fig. 127) is a single segment bearing three long terminal setae and one short subterminal seta. The second maxilla (fig. 128) is 2-segmented, the large basal segment unarmed, the second segment attenuated to form a moderately long distal flagellum provided with seven teeth along one side. This segment bears a hyaline naked seta on its posterior surface and more distally a prominent seta with a row of spinules along its medial margin. The 3-segmented maxilliped (fig. 129) resembles that of *I. diversus*.

The area between the maxillipeds and the first pair of legs (fig. 130) is only slightly protuberant. There is a faint line between the bases of the maxillipeds.

The rami of legs 1-4 (figs. 131, 132, 133, and 135) are segmented as in the above species of *Indomolgus*. The spine and setal formula is as follows (the Roman numerals indicating the spines, the Arabic numerals the setae) :

P 1	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	IV-4
				end.	0-1 ;	0-1 ;	I-5
P 2	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	IV-5
				end.	0-1 ;	0-2 ;	III-3
P 3	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	IV-5
				end.	0-1 ;	0-2 ;	I-3
P 4	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	I-1-I-5
				end.	0-1 ;	I-3	

The outer seta on the basis of all four legs is short and naked. The inner coxal seta on leg 4 is shorter than those on the other legs and is naked. On the exopods of legs 1-3 the proximal outer spines tend to be less ornamented with spinules than the distal ones. In leg 1 the distalmost spine on the last segment of the exopod may have hairs instead of spinules along part or all of its inner margin. The distal outer angle of the second segment of the endopod of leg 1 is distinctly bifurcated, instead of being a single spiniform process as in legs 2 and 3. On the third segment of one endopod of leg 3 in one female the formula I-2 was seen (fig. 134), the other endopod being I-3 which is the usual condition. The armature of the last segment of the exopod of leg 4 is unusual, the middle spine of the outer row of three being here transformed to a short slender naked seta. In one female the second segment of this ramus lacked the outer spine and was only weakly separated from the third segment. The second segment of the endopod measures 88×41 μ in greatest dimensions (including the spiniform process) ; its spine is 45 μ in length and the setae beginning with the outermost 80, 77, and 70 μ. There may be very slight variation in the form and armature of this segment as shown in fig. 136 (the left endopod of the same female from which fig. 135 was drawn).

Leg 5 (figs. 137 and 138) is small, its « free » segment not clearly separated from the body and forming a rounded lobe about 55 μ long. The two distal naked setae are 22 and 37 μ in length. The naked seta arising from the body near the lobe is 35 μ in length.

Leg 6 is represented by the two small setae near the attachment of the egg sac (see fig. 118).

The color in life in transmitted light is opaque, the eye dark red, the egg sacs gray.

Male. — The body (fig. 139) resembles in general form that of the female. The length (excluding the setae on the caudal rami) is 1.35 mm (1.16-1.54 mm) and the greatest width is 0.45 mm (0.40-0.51 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.6 : 1.

The genital segment (fig. 140) is a little wider than long, 246×269 μ, with slightly rounded lateral margins in dorsal view. The four postgenital segments are from anterior to posterior 83×172, 62×161, 44×158, and 112×155 μ (the length of the last segment taken along its margin).

The caudal ramus resembles that of the female, though its distal part may be a little less tapered than in that sex.

The surfaces of the prosome and urosome appear to lack ornamentation, as in the female. The ratio of the length of the prosome to that of the urosome is about 1.34 : 1.

The rostral area, first antenna (with no aesthetes added), second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla resemble those of the female.

The maxilliped (fig. 141) is 4-segmented, slender, and elongated. The first segment is long and unarmed ; the second is not quite as long and bears the usual two setae and a row of spinules ; the third is very short and unarmed ; and the fourth, forming part of the claw, bears two very unequal setae. All the setae are naked. The slender claw, 130 μ in length (measured along its axis and not along its curvature), is rather strongly recurved beyond the proximal indentation and

terminates in a sharp point without a lamella. A distinct line of division may be seen about midway on the claw, presumably indicating the distal limit of the fourth segment.

The area between the maxillipeds and the first pair of legs is like that in the female.

Legs 1-4 are like those in the female. One male had the formula 0-1 ; 0-2 ; I-5 for both endopods of leg 1, an extra seta having been added on the second segment.

Leg 5 (fig. 142) resembles in general form that of the female, but is smaller, the lobe being about 20 μ in length, the two terminal setae 11 and 24 μ, and the seta on the body near the lobe 22 μ in length.

Leg 6 (fig. 143) consists of the usual posterolateral flap on the ventral surface of the genital segment. It bears two hyaline naked setae 28 and 24 μ in length and a minute spiniform process.

Spermatophores were not observed.

The color in life in transmitted light resembles that of the female.

[The specific name *mutatus* (Latin = altered, changed) alludes to the transformation of the usual spine to a seta on the third segment of the exopod of leg 4].

Relationship to the host. — No copepods were recovered in washings until the zoanthid had been thoroughly broken into small fragments. This indicates that *I. mutatus*, like *I. brevisetosus* and *I. diversus*, inhabits the gastrovascular cavity of the polyps. *I. mutatus* was collected only once, and on that occasion it was the only copepod present.

Comparison with related species. — *Indomolgus mutatus* may be distinguished from the other three members of the genus by the spine and setal formula of the last segment of both rami of leg 4, where its exopod is I-1-I-5 and its endopod is I-3. In addition, *I. mutatus* may be readily separated from *I. brevisetosus* by the size and form of leg 5, the shape of the genital segment, and the form and position of the caudal rami. It is unlike *I. diversus* in having a more elongated urosome, in the size and form of leg 5, and in having very short setae on the caudal rami. It has several features which distinguish it from *I. panikkari*, notably, the size of the male (1.35 mm against 2.7 mm for the Indian species), the size and form of leg 5, and the nature of the caudal rami.

REMARKS ON THE GENUS *INDOMOLGUS*

The establishment of a new genus to receive the three new species from Madagascar and *I. panikkari* (Gnanamuthu) from India brings together four species which form a group different from other lichomolgids in several major respects. Among the notable features of this genus are the elongated body form, the two claws on the 4-segmented second antenna, and the armature of the second segment of the endopod of leg 4. This endopod may have the following typical and variant arrangement of spines and setae on the last segment :

	typical	*variant*
I. panikkari	II-3	—
I. brevisetosus	II-3	none observed
I. diversus	II-2	II-3
I. mutatus	I-3	I-2

It has become customary to assign great importance to the segmentation and armature of the endopod of leg 4 in defining lichomolgid genera. In those genera with a 2-segmented endopod the terminal segment may bear only a single element as in *Monomolgus*, two as in *Lichomolgus*, or three as in *Stellicola*. Such armature appears to be fixed throughout the species in those genera, with little or no individual variation. In the four species of *Indomolgus*, however, the armature consists of 4 or 5 elements, of three types : II-3, II-2, or I-3. Considering only this armature, one

might be tempted to recognize the species having the three types as belonging to separate genera. However, a comparison of the other appendages and the body form in the four species demonstrates their close relationship. Furthermore, it would be unwise to make generic distinctions based only on the armature of the endopod of leg 4 when this armature shows a certain amount of variation within a species. Thus it seems best to regard *Indomolgus* as having on the second segment of the endopod of leg 4 a typical armature of II-3, II-2, I-3.

List of zoanthid hosts and their copepods at Nosy Bé

Palythoa tuberculosa:

Lichomolgus inaequalis;
Temnomolgus eurynotus;
Indomolgus brevisetosus;
Indomolgus diversus;
Indomolgus mutatus.

Palythoa liscia:

Lichomolgus inaequalis;
Indomolgus brevisetosus;
Indomolgus diversus.

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Explanation of the figures

All the figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which the figure was drawn.

Fig. 1-12. — *Lichomolgus inaequalis* n. sp., female

1. — Body, dorsal (A)
2. — Urosome, dorsal (B)
3. — Area of attachment of egg sac, dorsal (C)
4. — Caudal ramus, dorsal (D)
5. — Rostral area, ventral (B)
6. — First antenna, dorsal (E)
7. — Second antenna, posterior (E)
8. — Labrum, ventral (D)
9. — Mandible, ventral (D)
10. — First maxilla, ventral (D)
11. — Second maxilla, ventral (D)
12. — Maxilliped, posterior (D).

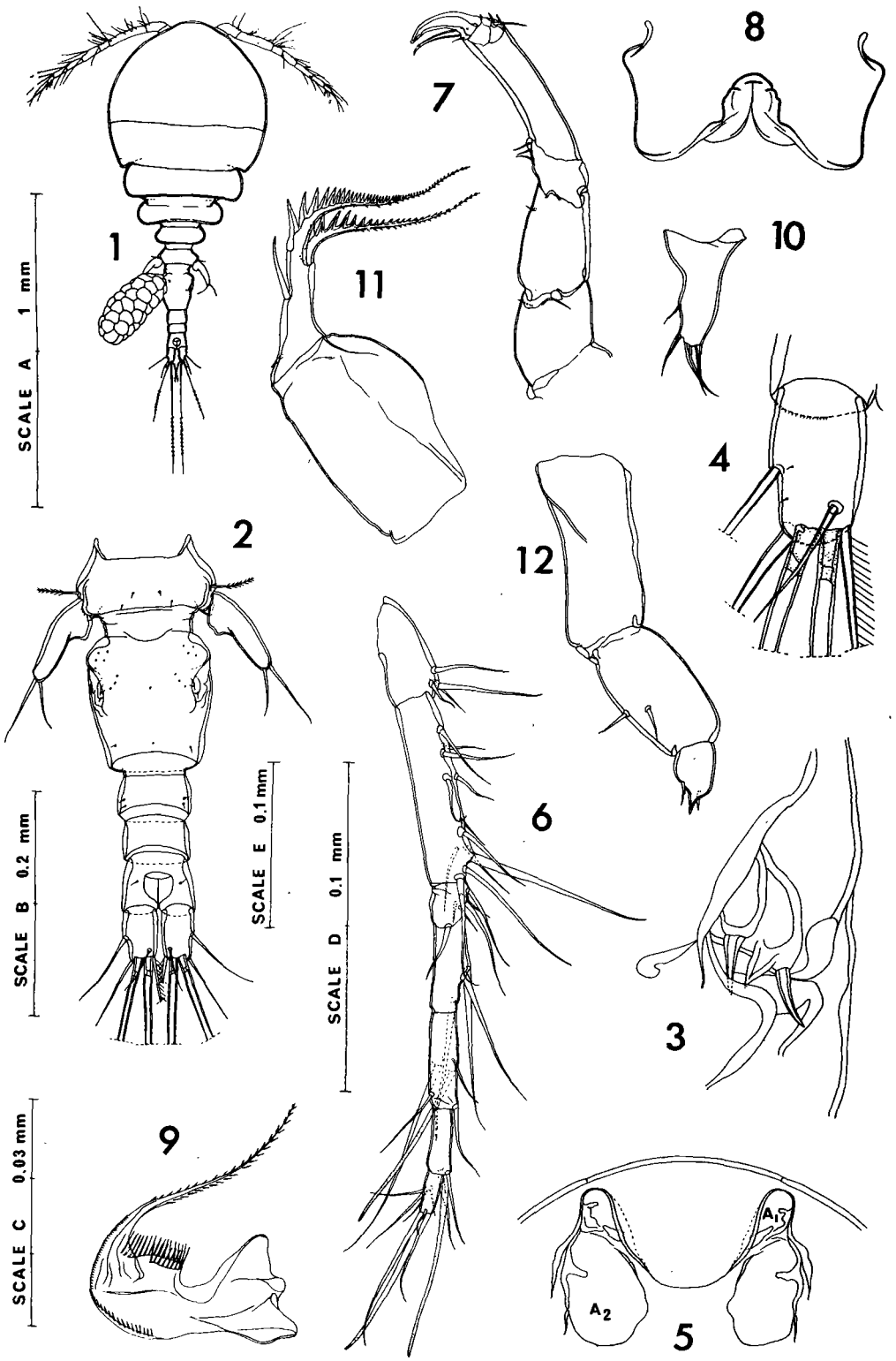

1
SCALE A 1 mm
2
SCALE B 0.2 mm
SCALE E 0.1 mm
SCALE C 0.03 mm
9
SCALE D 0.1 mm
6
7
8
10
11
12
4
3
5
A1?
A2

Fig. 13-19. — *Lichomolgus inaequalis* n. sp., female (continued)

13. — Area between maxillipeds and first pair of legs, ventral (E)
14. — Leg 1, anterior (E)
15. — Tip of endopod of leg 1, anterior (C)
16. — Leg 2, anterior (E)
17. — Leg 3, anterior (E)
18. — Leg 4, anterior E)
19. — Leg 5, dorsal (F).

Fig. 20-21. — *Lichomolgus inaequalis* n. sp., male

20. — Body, dorsal (G)
21. — Urosome, dorsal (B).

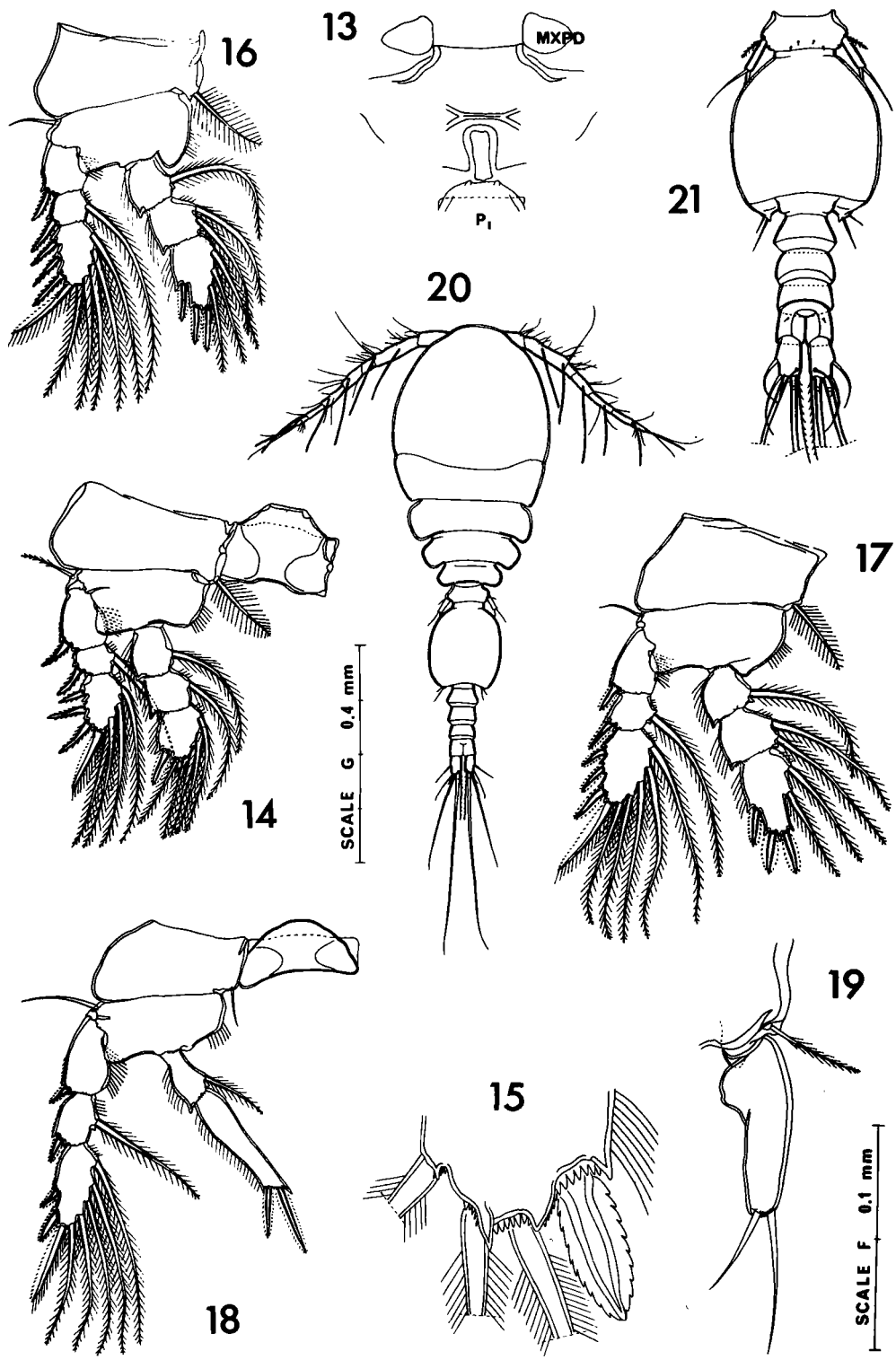

16
13
MXPD
P1
21
20
14
SCALE G 0.4 mm
17
18
15
19
SCALE F 0.1 mm

Fig. 22-28. — *Lichomolgus inaequalis* n. sp., male (continued)

22. — First antenna, dorsal (E)
23. — Paragnath, ventral (C)
24. — Maxilliped, inner (F)
25. — Last segment of endopod of leg 1, anterior (D)
26. — Endopod of leg 4, anterior (F)
27. — Leg 5, ventral (H)
28. — Leg 6, ventral (F) .

Fig. 29-33. — *Temnomolgus eurynotus* n. gen., n. sp., female

29. — Body, dorsal (A)
30. — Body, lateral (A)
31. — Body, ventral (A)
32. — Urosome, dorsal (I)
33. — Area of attachment of egg sac, dorsal (F).

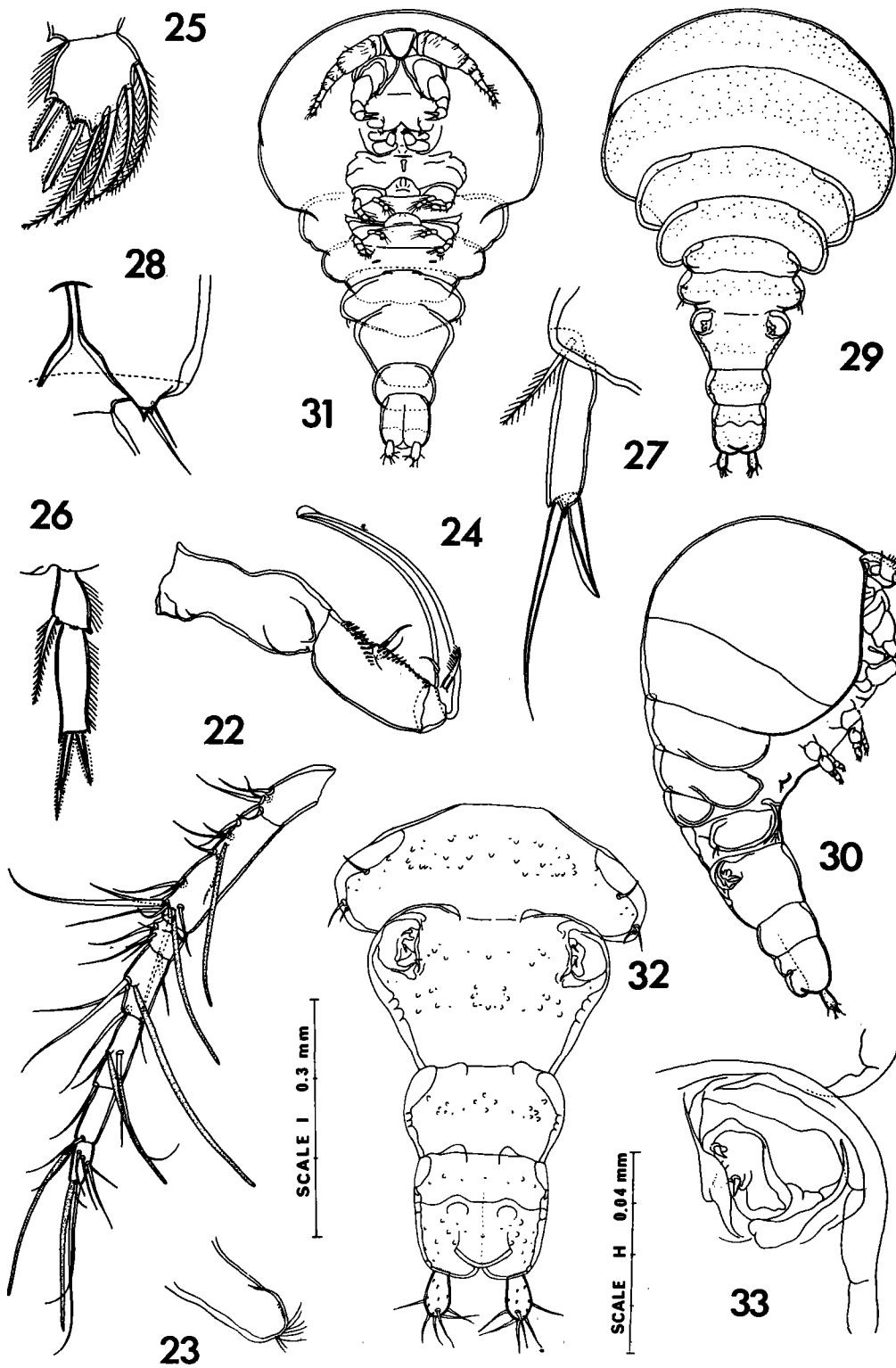
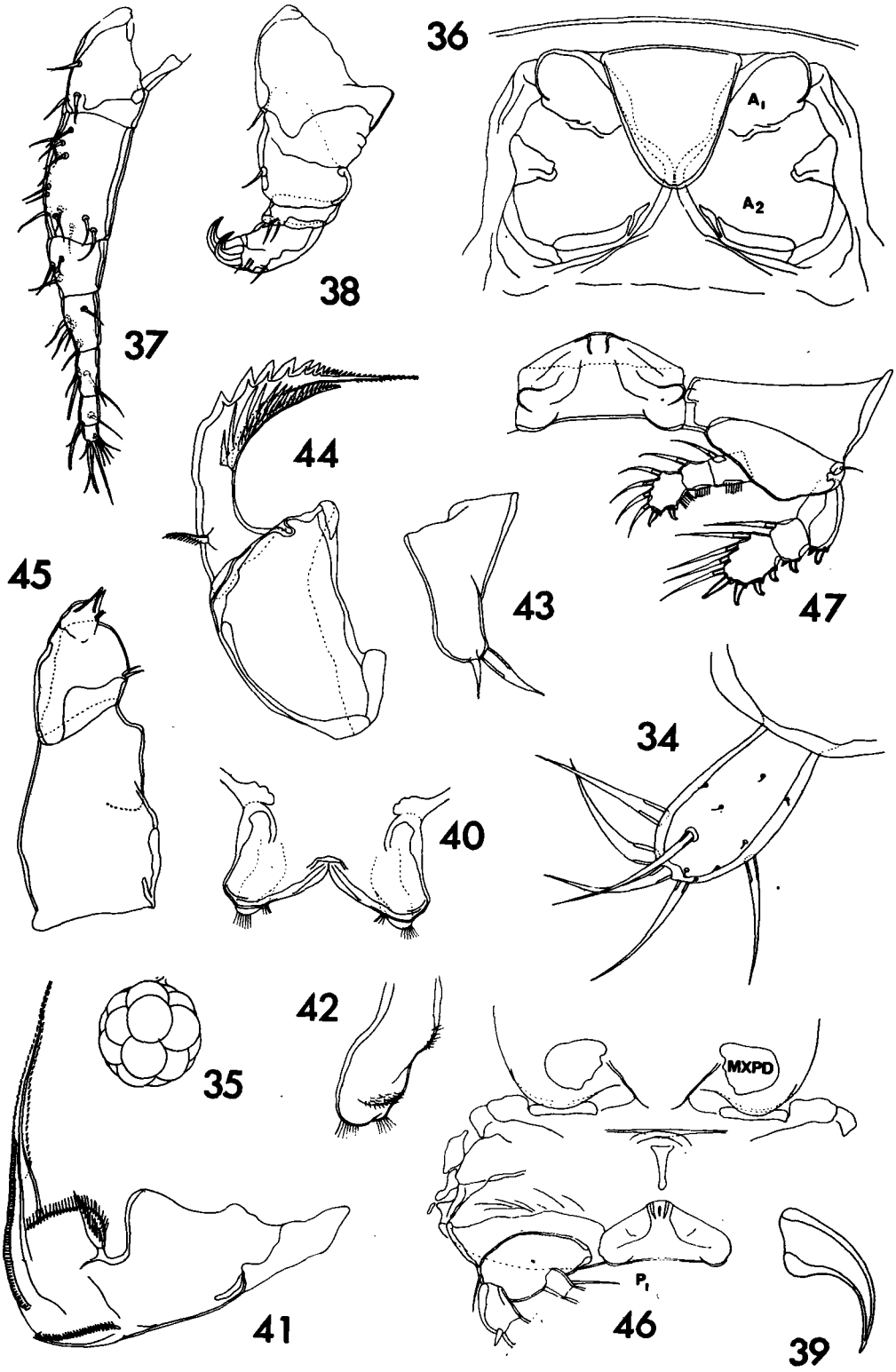

25
28
31
29
27
26
24
22
30
32
SCALE I 0.3 mm
SCALE H 0.04 mm
33
23

Fig. 34-47. — *Temnomolgus eurynotus* n. gen., n. sp., female (continued)

34. — Caudal ramus, dorsal (D)
35. — Egg sac, dorsal (A)
36. — Rostral area, ventral (B)
37. — First antenna, dorsal (B)
38. — Second antenna, anterior and ventral (B)
39. — Claw of second antenna (D)
40. — Labrum with paragnaths, ventral (E)
41. — Mandible, ventral (D)
42. — Paragnath, ventral (D)
43. — First maxilla, ventral (D)
44. — Second maxilla, ventral (D)
45. — Maxilliped, anterior (F)
46. — Area between maxillipeds and first pair of legs, ventral (B)
47. — Leg 1, anterior (E)


36
A1
A2
38
37
44
47
43
45
34
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42
35
MXPD
41
P1
46
39

Fig. 48-49. — *Temnomolgus eurynotus* n. gen., n. sp., female (continued)

48. — Leg 2, anterior (E)
49. — Leg 3, ventral (D).

Fig. 50-55. — *Temnomolgus eurynotus* n. gen., n. sp., male

50. — Body, dorsal (A)
51. — Urosome, ventral (G)
52. — Maxilliped, posterior and ventral (F)
53. — Area between maxillipeds and first pair of legs, ventral (B)
54. — Leg 1, anterior (B)
55. — Leg 2, anterior (B).

Fig. 56-57. — *Indomolgus brevisetosus* n. gen., n. sp., female

56. — Body, dorsal (A)
57. — Body, lateral (A).

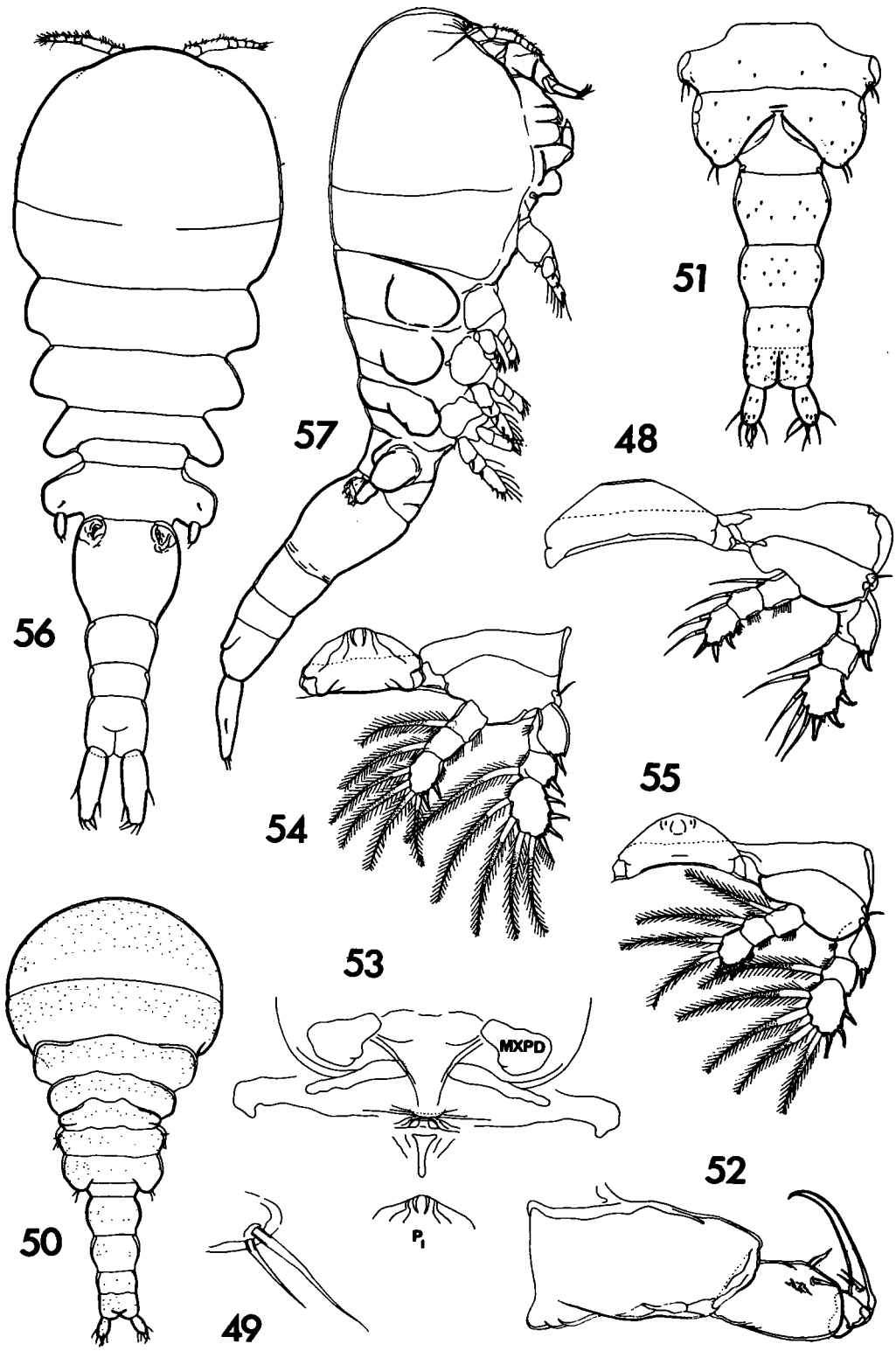
56
57
51
48
54
55
53
MXPD
50
52
49
P1

Fig. 58-70. — *Indomolgus brevisetosus* n. gen., n. sp., female (continued)

58. — Urosome, dorsal (G)
59. — Area of attachment of egg sac, dorsal (F)
60. — Caudal ramus, ventral (E)
61. — Egg sac, lateral (A)
62. — Midregion of cephalosome, ventral (I)
63. — First antenna, ventral (E)
64. — Second antenna, anterior (E)
65. — Claw on second antenna (H)
66. — Labrum, ventral (E)
67. — Mandible, ventral (F)
68. — Paragnath, ventral (D)
69. — First maxilla, ventral (D)
70. — Second maxilla, anterior (F).

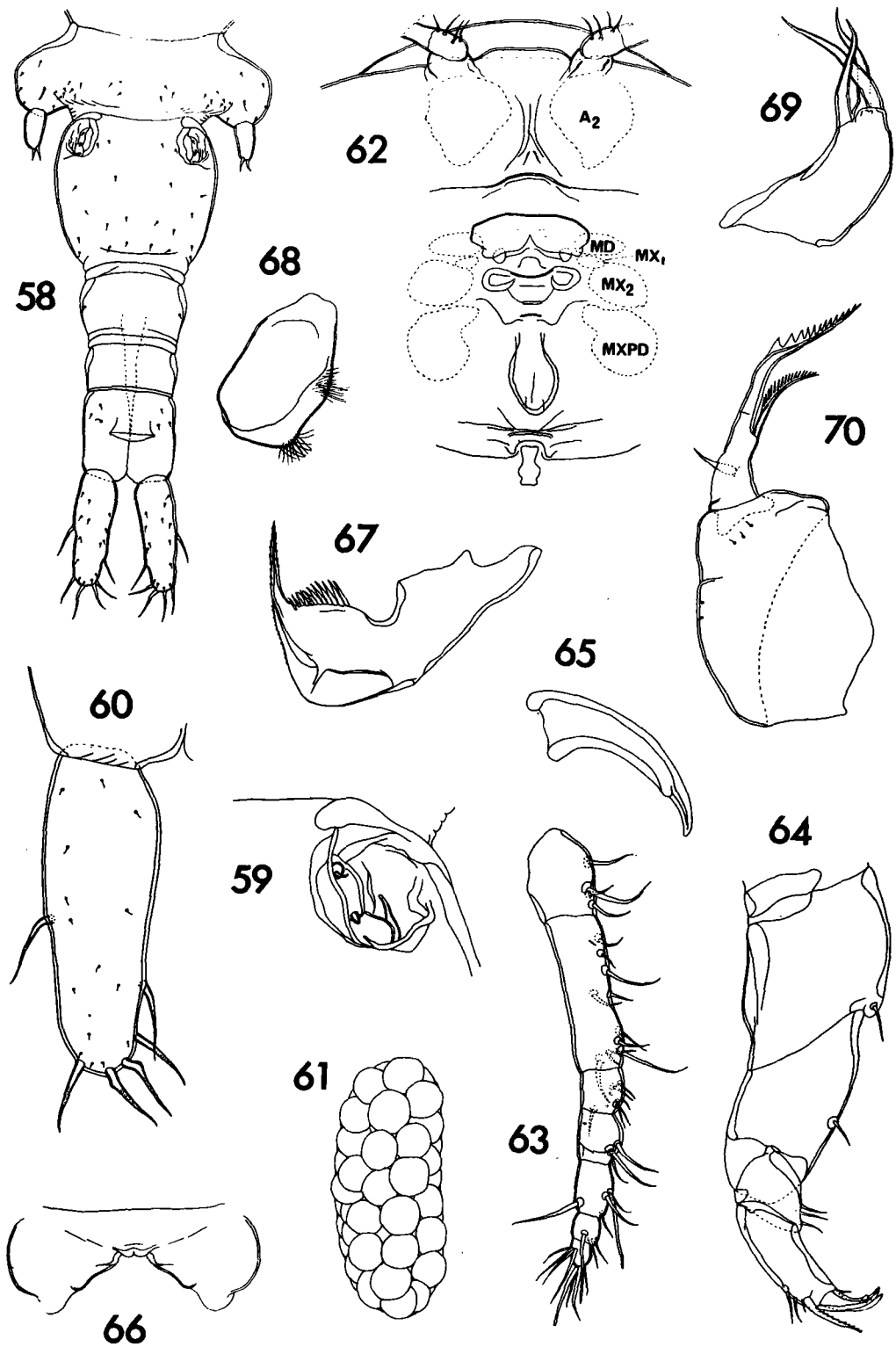
58
62
A2
69
MD
MX1
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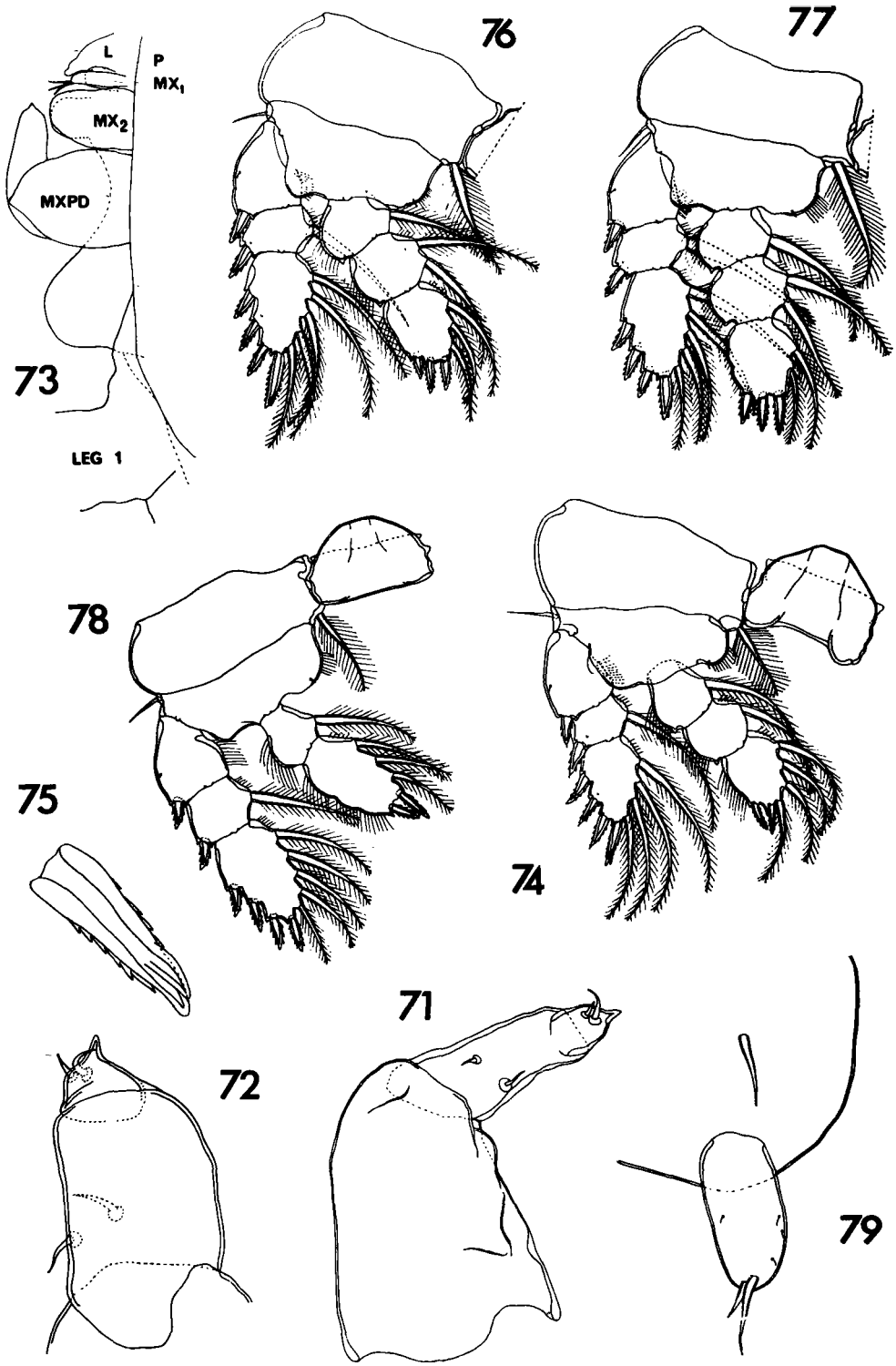
Fig. 71-79. — *Indomolgus brevisetosus* n. gén., n. sp., female (continued)

71. — Maxilliped, anterior and dorsal (F)
72. — Segments 2 and 3 of maxilliped, posterior and ventral (D)
73. — Mouthparts and postoral protuberance, lateral (B)
74. — Leg 1, anterior (B)
75. — Distalmost spine on third segment of exopod of leg 1 (H)
76. — Leg 2, anterior (B)
77. — Leg 3, anterior (B)
78. — Leg 4, anterior (B)
79. — Leg 5, dorsal (F).


L
P
MX1
MX2
MXPD
73
LEG 1
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79

Fig. 80-85. — *Indomolgus brevisetosus* n. gen., n. sp., male

80. — Body, dorsal (A)
81. — Urosome, ventral (G)
82. — First antenna, dorsal (E)
83. — Maxilliped, posterior and inner (B)
84. — Terminal spine and adjacent outer process on last segment of endopod of leg 1, anterior (D)
85. — Leg 5, dorsal (F).

Fig. 86-88. — *Indomolgus diversus* n. gen., n. sp., female

86. — Body, dorsal (A)
87. — Body, lateral (A)
88. — Urosome, dorsal (I).

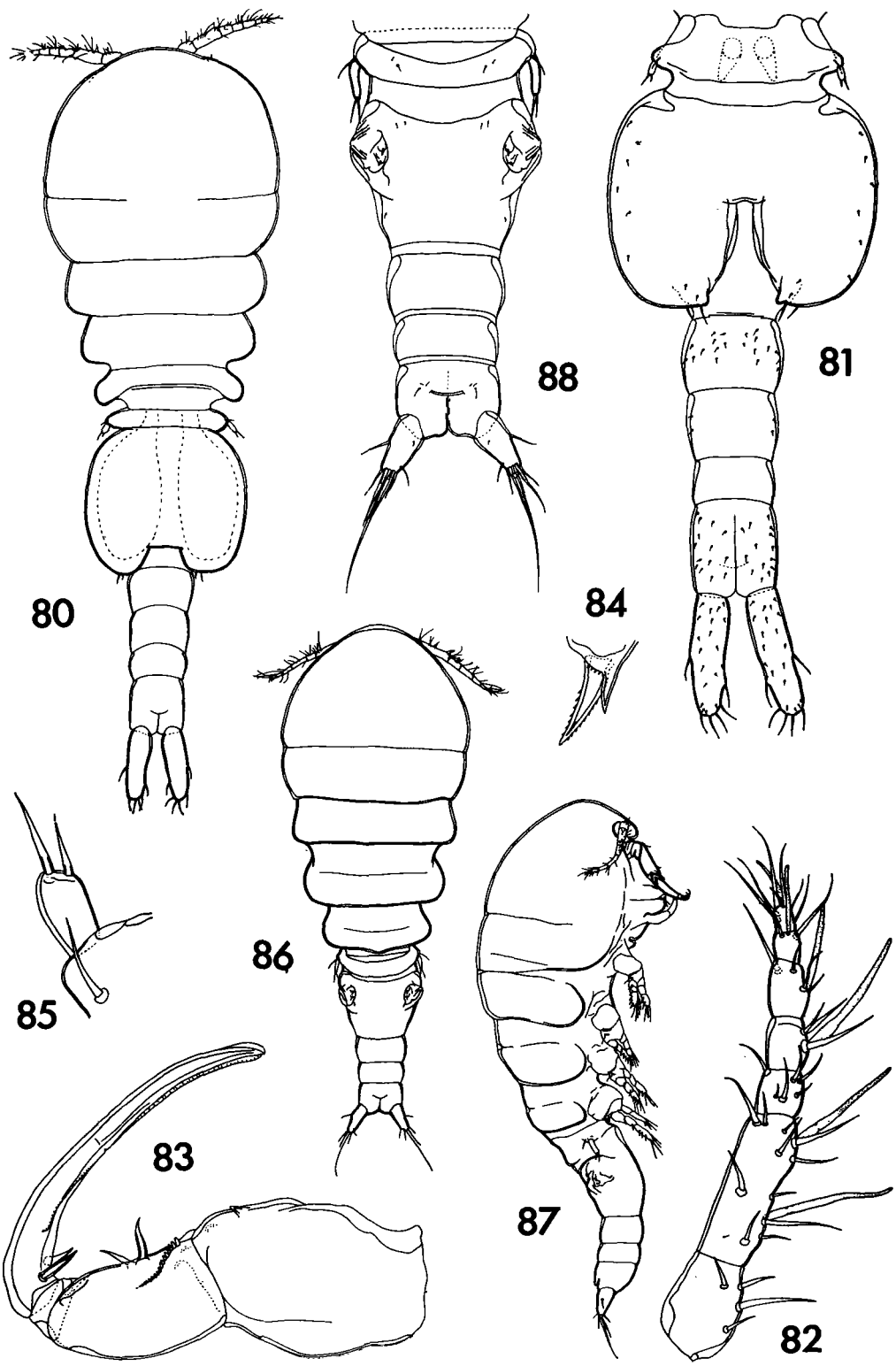
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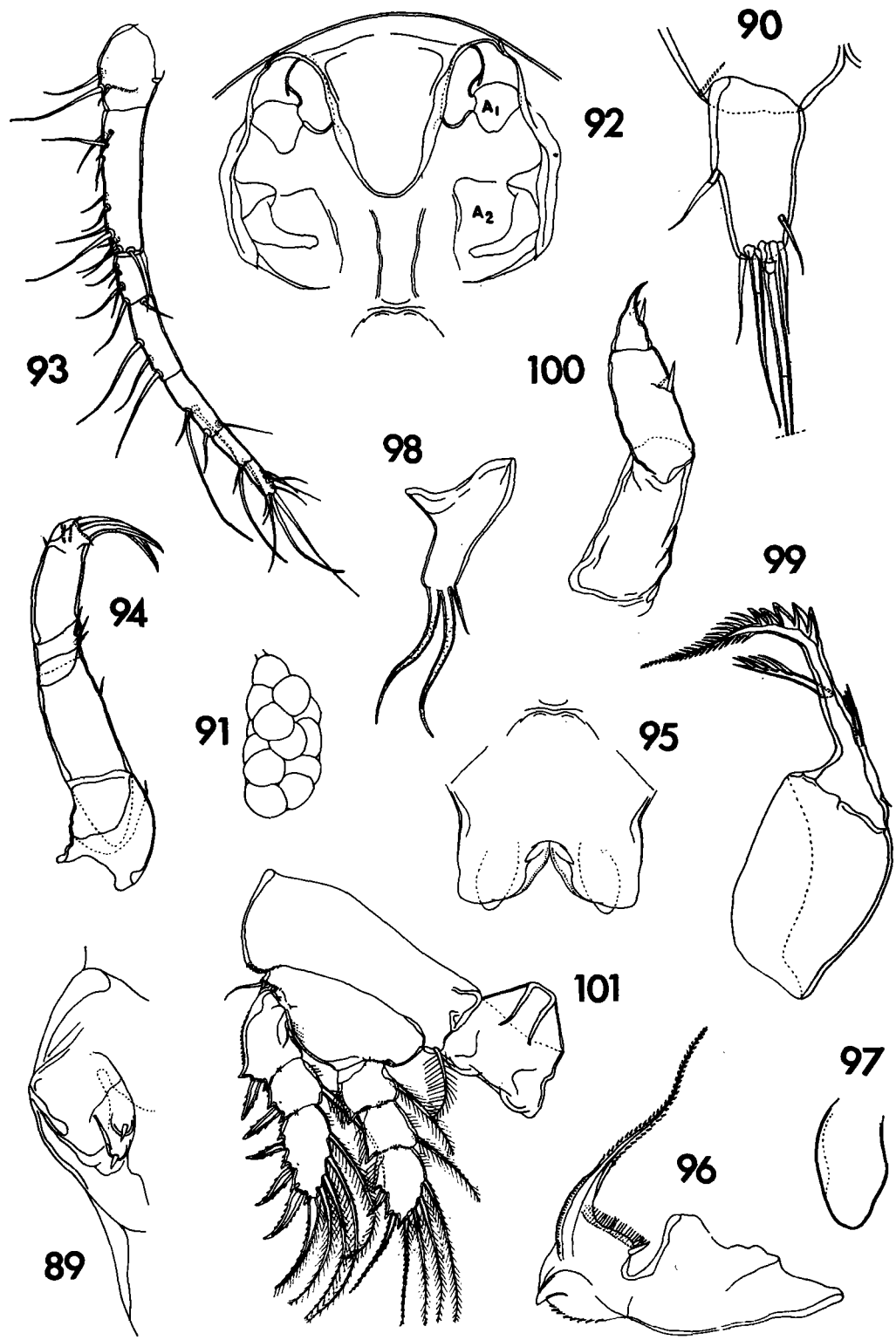
Fig. 89-101. — *Indomolgus diversus* n. gen., n. sp., female (continued)

89. — Area of attachment of egg sac, dorsal (F)
90. — Caudal ramus, dorsal (F)
91. — Egg sac, lateral (A)
92. — Rostral area, ventral (E)
93. — First antenna, dorsal (E)
94. — Second antenna, inner and posterior (E)
95. — Labrum, ventral (E)
96. — Mandible, anterior (D)
97. — Paragnath, ventral (D)
98. — First maxilla, ventral (D)
99. — Second maxilla, anterior (D)
100. — Maxilliped, posterior (F)
101. — Leg 1, anterior (E)


90
92
A1
A2
93
100
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96

Fig. 102-106. — *Indomolgus diversus* n. gen., n. sp., female (continued)

102. — Leg 2. anterior (E).
103. — Leg 3, anterior (E)
104. — Leg 4, anterior (E)
105. — Abnormal endopod of leg 4, anterior (E)
106. — Leg 5, dorsal (D).

Fig. 107-110. — *Indomolgus diversus* n. gen., n. sp., male

107. — Body, dorsal (A)
108. — Urosome, ventral (I)
109. — First antenna, anterior (E)
110. — Maxilliped, posterior (F).

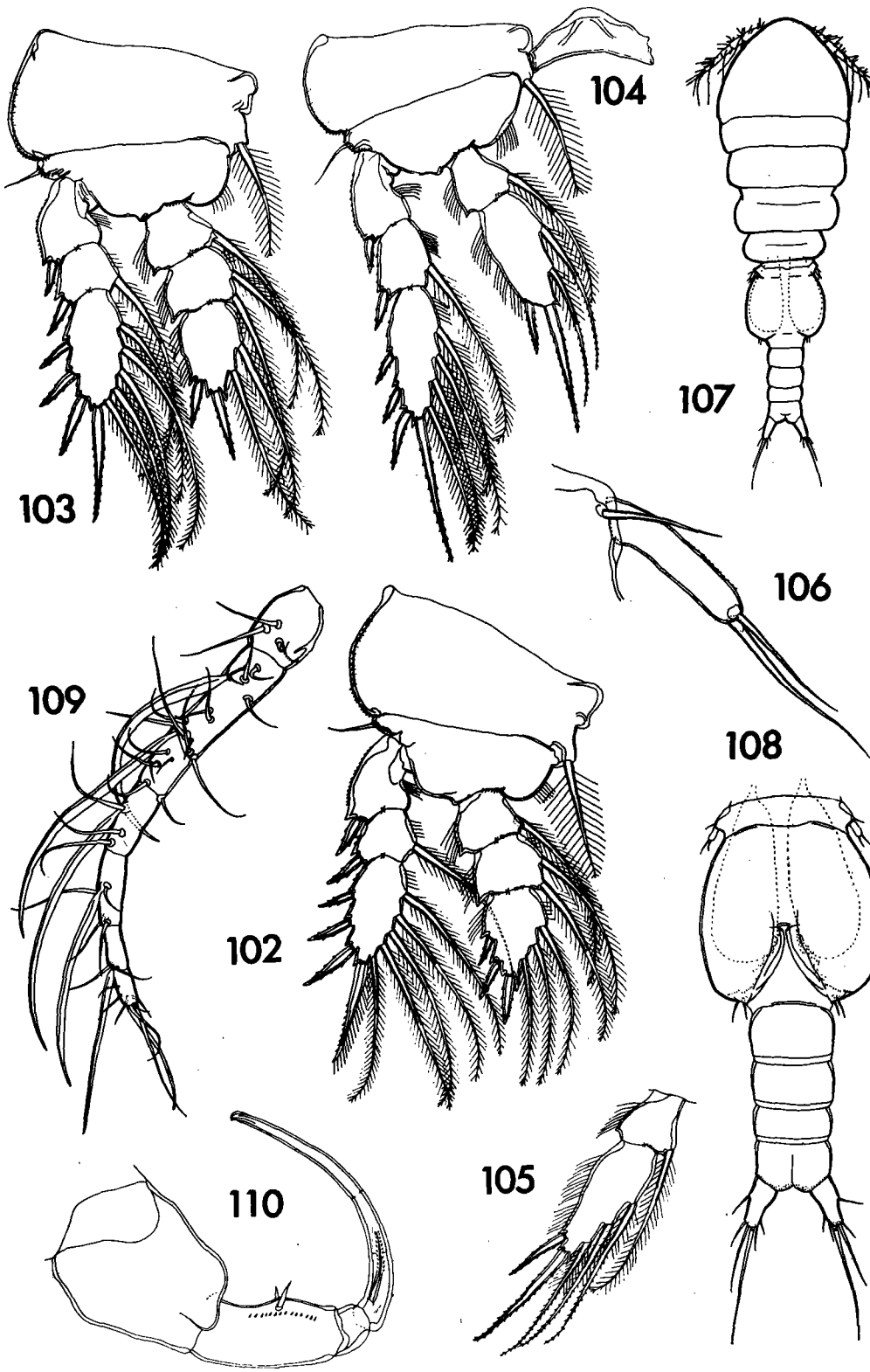
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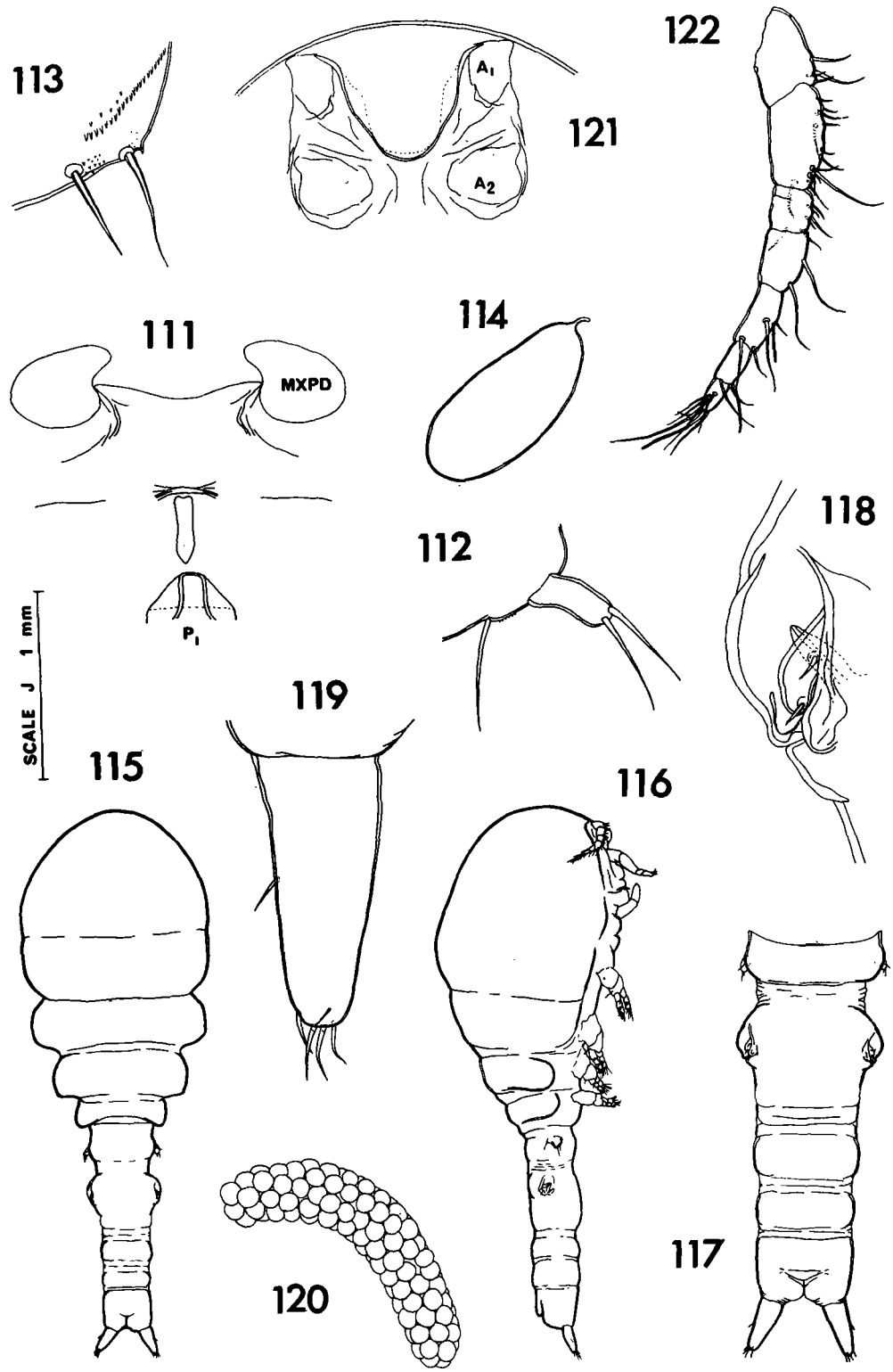
Fig. 111-114. — *Indomolgus diversus* n. gen., n. sp., male (continued)

111. — Area between maxillipeds and first pair of legs, ventral (E)
112. — Leg 5, lateral (D)
113. — Leg 6, ventrolateral (D)
114. — Spermatophore attached to female (I).

Fig. 115-122. — *Indomolgus mutatus* n. gen., n. sp., female

115. — Body, dorsal (J)
116. — Body, lateral (J)
117. — Urosome, dorsal (A)
118. — Area of attachment of egg sac, dorsal (F)
119. — Caudal ramus, dorsal (E)
120. — Egg sac (J)
121. — Rostral area, ventral (I)
122. — First antenna, ventral (I).


113
121
A1
A2
122
111
MXPD
114
P1
112
118
SCALE J 1 mm
119
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117

Fig. 123-132. — *Indomolgus mutatus* n. gen., n. sp., female (continued)

123. — Second antenna, anterior (B)
124. — Labrum, paragnaths, and associated oral area, ventral (E)
125. — Mandible, anterior (F)
126. — Paragnath, ventral (D)
127. — First maxilla, anterior (D)
128. — Second maxilla, posterior (E)
129. — Maxilliped, anterior and dorsal (E)
130. — Area between maxillipeds and first pair of legs, ventral (I)
131. — Leg 1, anterior (B)
132. — Leg 2, anterior (B).

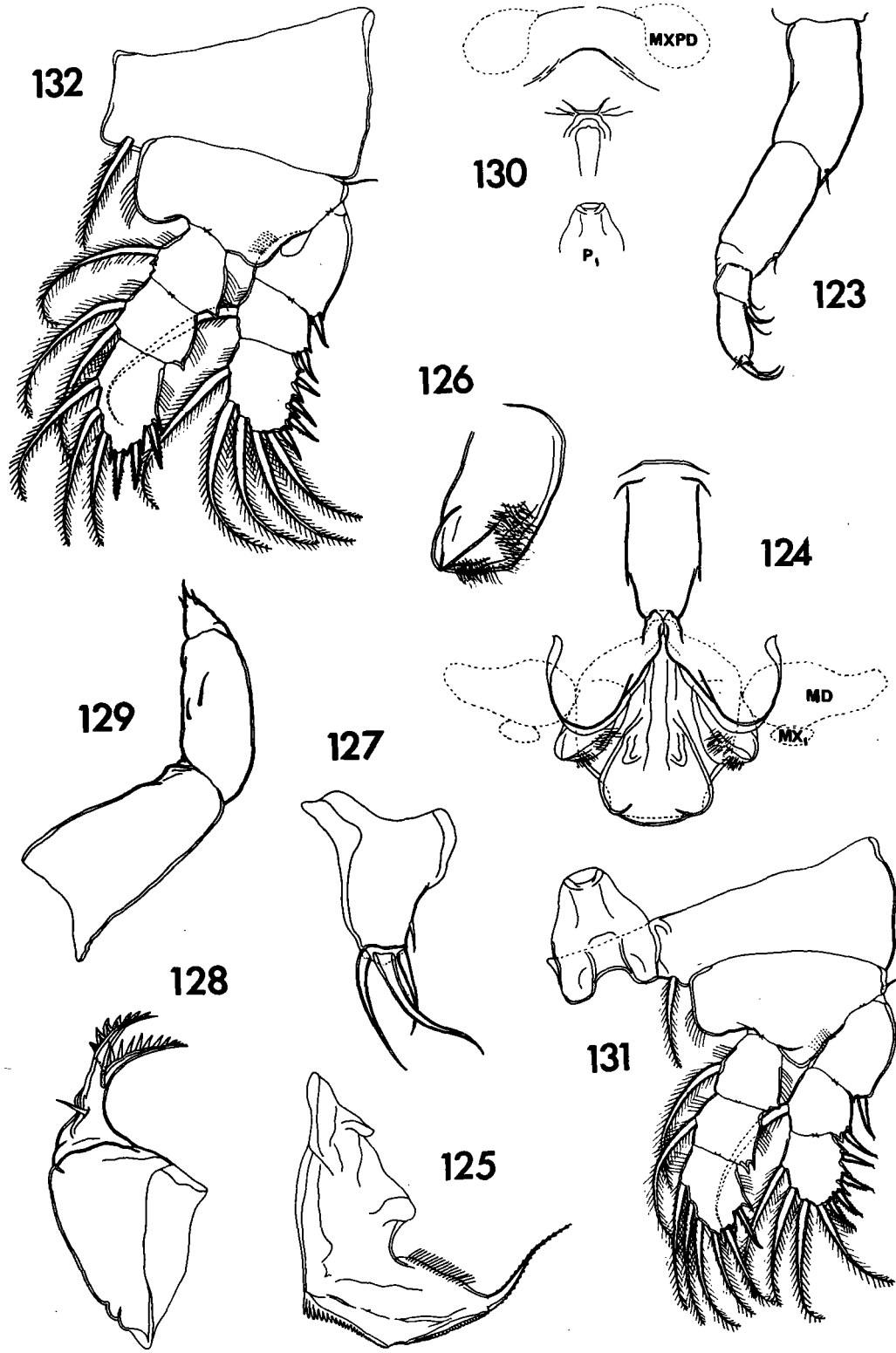
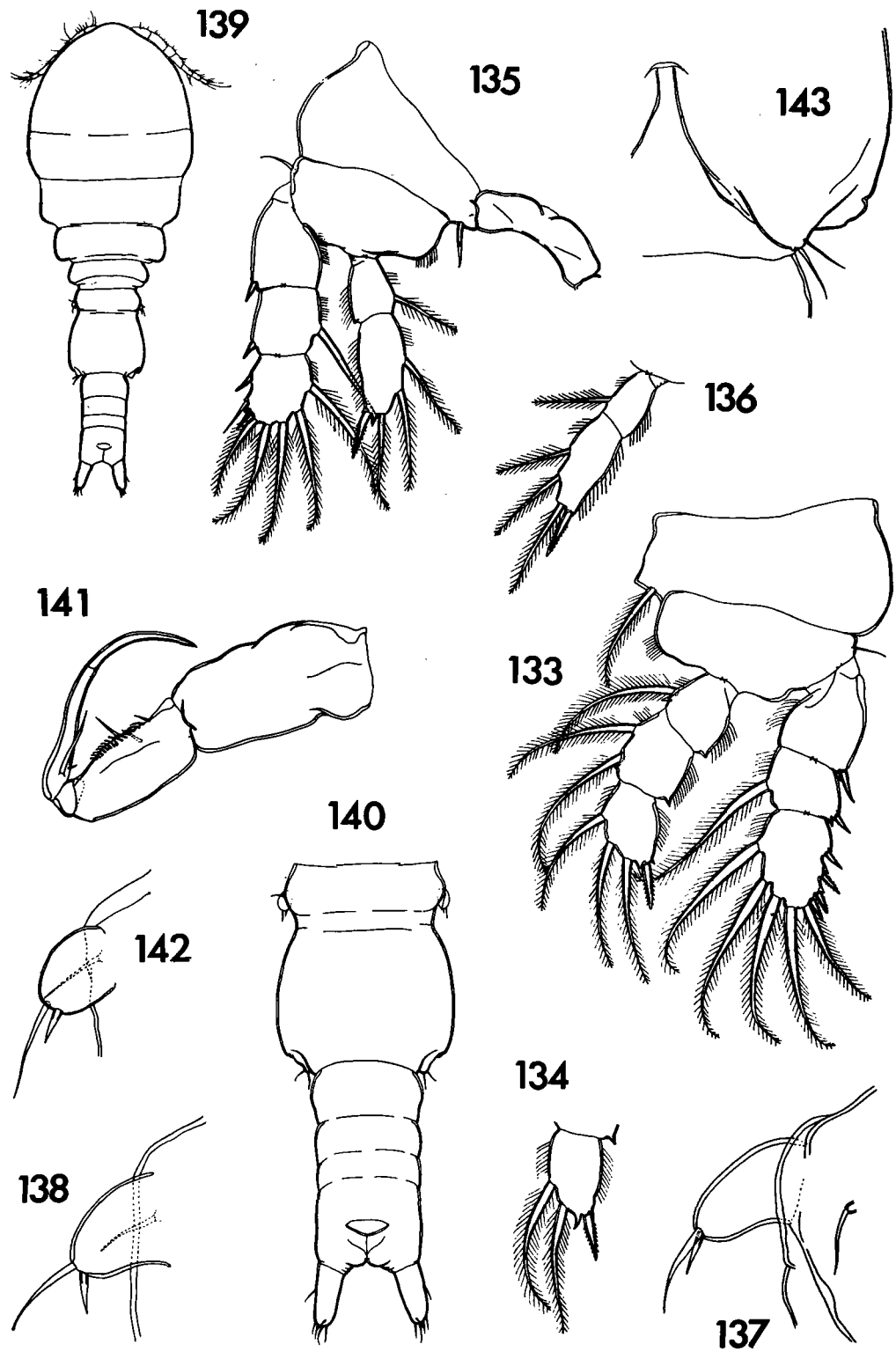

132
MXPD
130
P1
123
126
124
MD
MX1
129
127
128
131
125

Fig. 133-138. — *Indomolgus mutatus* n. gen., n. sp., female (continued)

133. — Leg 3, anterior (B)
134. — Abnormal last segment of endopod of leg 3, anterior (B)
135. — Leg 4, anterior (B)
136. — Endopod of same leg 4, but opposite side of body, anterior (B)
137. — Leg 5, dorsal (F)
138. — Leg 5, ventral (F)

Fig. 139-143. — *Indomolgus mutatus* n. gen., n. sp., male

139. — Body, dorsal (A)
140. — Urosome, dorsal (I)
141. — Maxilliped, posterior (E)
142. — Leg 5, ventral (D)
143. — Leg 6, ventral (F).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CYCLOPOID COPEPODS ASSOCIATED WITH THE STARFISH *CHORIASTER GRANULATUS* (LÜTKEN) IN MADAGASCAR

by Arthur G. HUMES *and* JU-SHEY HO*

RÉSUMÉ

Quatre espèces des copépodes cyclopoïdes s'associent à l'étoile de mer Choriaster granulatus *à Tany Kely (près de Nosy Bé) et à Nosy Ovy (Isles Radama), au nord-ouest de Madagascar :* Asterocomes indica *Padmanabha Rao*, Stellicomes tumidulus *Humes et Cressey*, Stellicola pichoni *n. sp.*, *et* Stellicola oreastriphilus *Humes et Cressey. Certains traits d'*Asterocomes indica *et de* Stellicomes tumidulus *sont décrits, et cette dernière espèce est comparée avec* Stellicomes guineensis *Humes et Cressey (une espèce de l'Afrique Occidentale).*

The region of Nosy Bé, in northwestern Madagascar, has a rich fauna of echinoderms, including numerous species of asteroids. Many of these live intertidally or in shallow water. During several months collecting in these areas *Choriaster granulatus* (Lütken) was never seen. It was only when diving with aqualungs to greater depths (10-40 meters) began that this starfish was found, often in abundance. The 76 *C. granulatus* examined in this study came partly from Tany Kely (collected by Dr. Michel Pichon, to whom we wish to express our thanks) and partly from Nosy Ovy (collected by the first author).

The copepods were collected during 1963-64 as part of the work of the U.S. Program in Biology of the International Indian Ocean Expedition.

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Asterocomes indica Padmanabha Rao, 1962 (1)
Figs. 1-23

This species, known previously only from India, was recovered from washings of *Choriaster granulatus* in two localities as follows :

a) in 10-15 m at Tany Kely, a small island about 8 kms to the south of Nosy Bé, Madagascar : 27 females and 37 males from 5 starfishes, July 11, 1963 ; 10 females and 10 males from 4 hosts,

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(1) For the use of the feminine form of the adjective with *comes*, a Latin noun of either masculine or feminine gender, see the International Code of Zoological Nomenclature 1961, art. 30 (a) (i) (2).

August 1, 1963 ; 11 females and 8 males from 8 hosts, August 28, 1963 ; 5 females and 2 males from 6 hosts, September 10, 1963 ; 53 females, 64 males, and 2 copepodids from 12 hosts, September 17, 1963 ; 9 females and 27 males from 13 hosts, February 19, 1964; 6 females and 14 males from 6 hosts, March 20, 1964 ; and 32 females and 44 males from 13 hosts, April 11, 1964.

b) in 10 m at Nosy Ovy (= Berafia), Isles Radama, 13°59'S, 47°46'30"E, to the southwest of Nosy Bé : 31 females and 28 males from 9 hosts, October 1, 1964.

These collections represent a total number of 184 females, 234 males, and 2 copepodids from the 76 starfishes.

Through the kindness of Dr. S. Jones of the Central Marine Fisheries Research Institute at Mandapam Camp, India, we have been able to examine paratypes (a male and a female) of *A. indica*. The specimens from Madagascar agree in all significant characters with these paratypic specimens from the starfish *Pentaceros hedemanni* (Lütken) (1) from the southeastern coast of India. Based on our study of the abundant material from Madagascar, certain additions and modifications can be made, however, to Padmanabha Rao's original description. (In the following paragraphs those characters not discussed or figured may be considered as like those in the original description.)

Female. — The body (figs. 1 and 2) has a length of 0.76 mm (0.70-0.81 mm) and a greatest width of 0.36 mm (0.32-0.41 mm), based on 10 specimens. The urosome (fig. 3) is broader than long., 140 × 174 μ. The areas of attachment of the egg sacs lie dorsolaterally, overlapped by the posterolateral borders of the prosome; each area is unarmed. The egg sac (fig. 4) is oval, 143 × 120 μ, and contains a single egg. The caudal ramus (fig. 5) is represented by four naked hyaline setae, the longest 36 μ.

The rostrum is undeveloped (see fig. 21 for the male).

The first antenna (fig. 6) is probably composed of fourteen segments, though the segmentation is obscure. The second antenna (fig. 7) has two subequal terminal claws 28 μ in length. Other setae and spinules occur as shown in the figure; apparently there is no seta on the first segment. The mouth cone is shown in anteroventral view in fig. 8 and in ventral view *in situ* in fig. 9; in lateral view the cone projects slightly (fig. 10).

The mandible (fig. 11) consists of a protuberant area lateral to the mouth cone (see fig. 21 for the male) and bears a large spiniform seta and two adjacent slender setae. Paragnaths could not be identified. The first maxilla (fig. 11) is a small lobe bearing four terminal setae and located near the mandible. The second maxilla (fig. 12) has an indistinctly divided claw 110 μ in length (measured along its axis and not along its curvature) with a small subterminal hyaline process on its concave margin. The maxilliped (fig. 13) has a terminal claw 34 μ in length ; there are spinules along the inner margin of the slender fourth segment.

Leg 1 (fig. 14) has a small seta on the proximal anterior surface of the exopod (on the first segment, if the interruption in the inner sclerotization of the ramus indicates a joint). The hyaline endopod is long and slender, about 86 × 16 μ.

Leg 2 (fig. 15) apparently lacks the outer seta on the protopod. The distal part of the exopod is attenuated and hyaline. There are small spinules on the distal inner area of the endopod; this ramus bears two terminal setae.

Leg 3 (fig. 16) also lacks the outer seta on the protopod. The segments and their spines are ornamented as indicated in the figure.

Leg 4 (fig. 17) lacks the outer seta on the protopod. There is a short naked seta on the last segment as in the previous leg. The fourth leg lacks an intercoxal plate.

The spine and setal formula for legs 1-4 is as follows (the Roman numerals indicating the spines, the Arabic numerals the setae) :

(1) This name is a synonym of *Pentaceraster multispinosus* (von Martens).

P 1	protopod	1:0	exp.	1; 3,3
			end.	2
P 2	protopod	0:0	exp.	0:0; 0:1; 3,1
			end.	2
P 3	protopod	0:0	exp.	1:0; 1:0; 1,3
P 4	protopod	0:0	exp.	1:0; 1:0; 1

Leg 5 (fig. 18) is elongated, 25×10 μ, bearing four naked steae, one distinctly larger than the others.

Leg 6 is absent.

The color in life in transmitted light in only slightly opaque, the eye red, the egg sacs dark gray.

Male. — The body (fig. 19) has a length of 0.71 mm (0.67-0.76 mm) and a greatest width of 0.35 mm (0.33-0.38 mm), based on 10 specimens. The urusome (fig. 20) has a somewhat different form than in the female.

The rostral area, first antenna, second antenna, mouth cone, mandible, first maxilla, second maxilla, and maxilliped are like those in the female. Their relationships are shown in fig. 21.

Legs 1-4 resemble those in the female.

Leg 5 (see fig. 20) is similar to that of the female but smaller, the dimensions being 22×7 μ, and the four setae are relatively longer than in the female.

Leg 6 (see fig. 20) is a posterolateral protuberance on the genital area of the urosome bearing a single hyaline seta 7 μ in length

The spermatophore (fig. 22), dissected from the body of a male, is oval, 115×85 μ, not including the neck of 39 μ. *In situ* on the body of the male the spermatophore appears less oval (fig. 23), 100×86 μ, with the neck extending dorsally.

Relationship to the host. — The copepods are closely associated with the starfish and even under abnormal conditions (for example, when several starfishes are kept in a pail of sea water for several hours) do not leave the host. When the starfishes are washed in sea water plus a small amount of ethyl alcohol, very often no copepods will be recovered. If, however, the starfishes are left undisturbed in this weakly alcoholized sea water overnight, and then quickly and vigourously washed, the copepods appear in the sediment. Once the starfishes have been stimulated to the point where their ambulacral grooves close, no more copepods are obtained. It is then necessary to wait for the starfishes to relax the grooves, when the washing may be repeated. In this way specimens of *A. indica* were recovered even after nine successive washings. The copepods evidently cling to the host within the ambulacral grooves and only these successive vigorous washings can dislodge them all.

Behavior. — *A. indica* is unable to swim. When removed from the host to a dish of sea water, the copepods lie on their backs, with their appendages actively moving and clinging to any available debris. Their bodies are slightly contractile, and bend back and forth in very active motions. This contractility may produce slightly different body sizes in specimens treated with alcohol or formalin. In fact, this may be the explanation for the smaller body size of the Indian specimens compared to the specimens from Madagascar, since Padmanabha Rao's specimens were washed from the starfishes in 5 per cent formalin rather than with ethyl alcohol.

Stellicomes tumidulus Humes and Cressey, 1958
Figs. 24-29

This small species was recovered from washings of *Choriaster granulatus* as follows:

1 male from 5 starfishes, in 10 m, Tany Kely, near Nosy Bé, July 11, 1963.

1 female from 8 hosts, from the same locality, August 28, 1963.

1,012 copepods representing both sexes from 9 hosts, in 10 m, Nosy Ovy, Isles Radama, 13°59'S, 47°46'30"E, to the southwest of Nosy Bé, October 1, 1964.

During the study of these specimens from *Choriaster*, certain details of the external anatomy were noticed which at first seemed to be at variance with *Stellicomes tumidulus* as originally described. A comparison of the copepods from *Choriaster* with paratypes of *S. tumidulus* from *Proloreaster* and with other specimens from *Poraster* and *Culcita* shows, however, that all these copepods represent the same species. There are, nevertheless, certain minor modifications necessary in the original description of *S. tumidulus*. These slight inaccuracies have their origin in part on the fact that Humes and Cressey studied unstained dissections in glycerine, which is a rather inferior clearing medium for these very small copepods. We are now using lactic acid (after a light stain with chlorazol black E) with much more satisfactory results. The several features mentioned below are to be regarded as common to all specimens of *S. tumidulus* at Nosy Bé.

a) The body (fig. 24) shows dorsally a rather elaborate sclerotized framework.

b) The second segment of the first antenna (fig. 25) bears only setae, the element originally described as an aesthete being actually a seta.

c) The second antenna (fig. 26) has on the third segment a row of small spinules on the side opposite to the row of large spinules. The armature of the last segment consists of two long spinules on the outer side, two short spinules on the inner side, one seta, a simple subterminal claw, and a terminal claw (or claw-like process, since its articulation is indistinct) with a tripartite tip. (Figure 26 should be compared with Humes and Cressey's Pl. I, fig. 5.)

d) In leg 1 (fig. 27) the exopod has a short naked inner seta at one-third the distance from its base and all three long terminal setae have hairs along one side. (Compare Humes and Cressey's Pl. II, fig. 10).

e) In leg 3 (fig. 28) the exopod has a short naked seta on the terminal segment (in addition to the four long haired setae), and the two terminal setae of the endopod are lightly haired.

f) In the male leg 6 is represented by a single small seta (fig. 29). In connection with the restudy of *S. tumidulus* we have also reexamined paratypes of *S. guineensis* Humes and Cressey, 1958, from *Oreaster clavatus* Müller and Troschel in Sierra Leone, and find that corrections a, c, d, e, and f apply here also. In addition, on the terminal segment of the expod of leg 4 there is only one short naked seta (instead of two as in Humes and Cressey's Pl. V, fig. 28).

The major differences between *S. tumidulus* and *S. guineensis* may be summarized, after reexamination of paratypes of both species, as follows : .

	S. tumidulus	*S. guineensis*
mouth cone	dentition rather weak	dentition coarser
terminal claw on maxilliped	simple, with a feeble subterminal tooth	forked (or with a strong subterminal tooth)
endopod of leg 1	with a single terminal seta	with two terminal setae
protopods of legs 2-4	with a seta	without setae
first segment of endopod of leg 2	with a simple naked seta	with a spiniform process instead of a seta
terminal segment of exopod of leg 3	no spinules	with a row of spinules
exopod of leg 4	1-0; I-1; 0-2	I-0; I-1; 0-1
egg sacs	oval (1.4:1)	more elongated (1.7:1).

A third species of *Stellicomes*, *S. pambanensis*, has recently been described by Padmanabha Rao (1964) from the starfish *Pentaceros hedemanni* (Lütken) in the Gulf of Mannar, southeastern India.

Stellicomes tumidulus is now known to occur on five asteroids in the region of Nosy Bé: *Protoreaster lincki* (Blainville), *Poraster superbus* (Möbius), *Pentaceraster mammillatus* (Audouin), *Culcita schmideliana* (Retzius), and *Choriaster granulatus* (Lütken).

Stellicola pichoni n. sp.
Figs. 30-59

Type material. — 25 females and 23 males washed from 9 *Choriaster granulatus* (Lütken), in 10 m, at Nosy Ovy, Isles Radama, 13°59'S, 47°46'30"E, to the southwest of Nosy Bé, Collected October 1, 1964. Holotype, allotype and 35 paratypes (18 females and 17 males) deposited in the United States National Museum, Washington, and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Choriaster granulatus* in 10 m at Tany Kely, a small island about 8 kms to the south of Nosy Bé). — 5 females and 2 males from 6 hosts, September 10, 1963; 4 females and 4 males from 13 hosts, February 19, 1964; 7 females and 2 males from 6 hosts March 20, 1964; and 12 females and 7 males from 13 hosts, April 11, 1964.

Female. — The body (fig. 30) has a moderately broadened prosome and a relatively slender urosome. The length (not including the setae on the caudal rami) is 0.79 mm (0.70-0.87 mm) and the greatest width, at the junction of the head and the segment of leg 1, is 0.37 mm (0.34-0.40 mm), based on 10 specimens. The ratio of length to width of the prosome is about 1.46:1. The segment of leg 1 is separated from the head dorsally and laterally by a furrow. The epimeral areas of the metasomal segments are rounded.

The segment of leg 5 (figs. 31 and 32) is narrow anteriorly but widened posteriorly where it bears laterally the two legs. The genital segment is elongated, with the posterior fourth (behind the areas of attachment of the egg sacs) constricted. The length is 143 μ, the greatest width 107 μ, and the width in the narrowed posterior fourth is 75 μ. The areas of attachment of the egg sacs are dorsolateral in position and each bears two unusually prominent setae, one 20 μ long and haired, the other 44 μ and annulated but naked; between the two setae there is a small spiniform process (fig. 33). The posteroventral margin of the genital segment bears a row of slender spinules on each side and between them a membrane with a ragged edge simulating small spinules. There are only two postgenital segments, the first 40×64 μ with its posteroventral margin ornamented as on the genital segment, the second (anal segment) 28×53 μ and lacking this posteroventral ornamentation. The posterodorsal margins of the genital and postgenital segments lack any special ornamentation.

The caudal ramus (fig. 34) is inserted ventrally on the anal segment and is only slightly longer than wide, 28×23 μ. On the outer side there is a long hyaline submarginal setule. The pedicellate dorsal seta is 52 μ long and haired. The naked outer lateral seta is 78 μ long and inserted close to the outermost subterminal seta which is 117 μ long and haired. The innermost subterminal seta is 175 μ long and apparently naked. The two long terminal setae, 314 and 470 μ long respectively, bear short lateral spinules, and their basal portions proximal to the « joint » are finely punctate ; these two setae are inserted somewhat ventrally on the ramus between two slight flaps, the ventral one of which bears a marginal row of long slender spinules. There is a small hair on the ventral surface of the ramus.

The dorsal surface of the prosome bears scattered refractile points and hairs. The dorsal and ventral surfaces of the urosome bear hairs and refractile points as shown in the figures. The ratio of the length of the prosome to that of the urosome is 2:1.

The egg sac (fig. 35) is moderately elongated about 325 × 112 μ, and contains numerous small eggs. (In the egg sac drawn, which was the only relatively intact sac found, part of the eggs had already hatched.)

The rostral area (fig. 36) is well-defined.

The seven segments of the first antenna (fig. 37) have the following lengths (measured along their posterior non-setiferous margins): 20 (44 μ along the anterior margin), 65, 26, 36, 25, 13, and 12 μ respectively. The formula for the armature is 4, 13 (5+2+6), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. The setae are naked except for certain ones with short lateral hairs (one in the distal group on segment 2, one on segment 3, one on segments 5 and 6, and five on segment 7). The aesthetes are very slender and often resemble setae; the aesthete on segment 7 arises from a common base with one of the long terminal setae and shows a few annulations in its proximal half. On the proximal ventral region of segment 3 there is a sclerotization suggesting an intercalary segment.

The second antenna (figs. 38 and 39) is slender and 3-segmented, though the last segment is incompletely divided. The first segment bears a smooth annulated seta and more proximally a cluster of short hairs. The second segment has a pilose seta and the third three such setae. The anterior surfaces of segments 2, 3, and 4 bear numerous long hairs as indicated in fig. 38. Terminally there is a single claw 42 μ in greatest length along its axis, near the base of which there are three slender setae and one shorter and rather blunt seta.

The labrum (fig. 40) has two posteroventral lobes without ornamentation.

The mandible (fig. 41) has on its basal region an outer row of spinules and an inner large proximal spine-like process (articulated?) followed by a row of fairly stout spinules; the terminal lash has short lateral spinules. The paragnath (fig. 42) is a short rounded lobe bearing hairs.

The first maxilla (fig. 43) is a single segment bearing four setae, the outermost long and slender with lateral hairs, the next stout with coarser hairs, and the two inner setae short and naked. The second maxilla (fig. 44) is 2-segmented. The basal segment is large and unarmed. The slender distal segment terminates in a spiniform process bearing lateral spinules; on the outer base of this process there is a large sclerotized spine. On the inner side of the second segment there are two setae, one slender and haired, the other large, spiniform, and provided with spinules. The maxilliped (fig. 45) is 3-segmented, the first segment being unarmed, the second with two haired setae and an elliptical row of slender spinules. The short third segment (fig. 46) terminates in a spiniform process with lateral digitiform ornamentations and bears two setae, one slender and naked, the other stout and spiniform with short lateral digitiform processes.

The area between the maxillipeds and the first pair of legs (fig. 47) is only slightly produced, and a weak sclerotization connects the bases of the maxillipeds.

The rami of legs 1-4 (figs. 48, 49, 51, and 52) are 3-segmented, except for the endopod of leg 4 which is weakly 2-segmented. The spine and setal formula is as follows (the Roman numerals representing the spines, the Arabic numerals the setae):

P 1	protopod	0-1;	1-0	exp.	I-0; I-1; III-1-4
				end.	0-1; 0-1; I-5
P 2	protopod	0-1;	1-0	exp.	I-0; I-1; III-1-5
				end.	0-1; 0-2; I-II-3
P 3	protopod	0-1;	1-0	exp.	I-0; I-1; III-1-5
				end.	0-1; 0-2; I-II-2
P 4	protopod	0-1;	1-0	exp.	I-0; I-1; II-1-5
				end.	0-1; II-1

The inner seta on the coxa is long and feathered in legs 1-3, but short (33 μ) and naked in leg 4. A row of hairs is present on the inner margin of the basis in legs 1-3, but these hairs appear to be absent in leg 4. The expansion of the basis lying over the anterior surface of the first segment of the exopod is rather acute, instead of being broadly rounded as is often the case in

other lichomolgids. Between the two terminal spines on the last segment of the endopod of leg 2 there is a bifurcated spinous process (fig. 50). On the second segment of the exopod of leg 4 the inner seta lies (in alcoholic specimens) at an angle across the posterior surface of the ramus and is shorter and less conspicuously haired than in the seta on the last segment. The endopod of leg 4 (fig. 53) is only indistinctly divided into two segments. The overall length of this ramus is 57 μ; the first segment being 19×19 μ, the second 38×16 and 10 μ (the greatest and least widths respectively). The seta on the first segment is 100 μ, the seta on the second segment 45 μ, and the two terminal spines 80 and 51 μ in length. The second segment is ornamented with a row of hairs along the proximal half of its outer margin and with a distal row of minute spinules at the insertions of the two terminal spines.

Leg 5 (fig. 54) has an elongated free segment 65×21 μ. The two terminal setae are very unequal in length, one 120 μ and the other 40 μ, both with short lateral spinules. The seta on the body near the insertion of the free segment is 40 μ long and lightly feathered.

Leg 6 is probably represented by the two setae on the area of attachement of the egg sac (see figs. 31 and 33).

The color in life in transmitted light is pale amber, the eye red.

Male. — The body form (fig. 55) resembles that of the female, though the urosome is relatively more elongated. The length (without the setae on the caudal rami) is 0.64 mm (0.60-0.68 mm and the greatest width is 0.27 mm (0.24-0.27 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.44:1. The segment of leg 1 is separated from the head only by lateral furrows.

The genital segment (fig. 56) is elongated, 107×88 μ, with its lateral margins in dorsal view slightly rounded. There are three postgenital segments, 51×62, 41×56, and 25×47 μ respectively from anterior to posterior, ornamented ventrally as in the female.

The caudal ramus resembles that of the female.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear refractile points and hairs. The ratio of the length of the prosome to that of the urosome is 1.46:1.

The rostral area, first antenna, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla are similar to those in the female.

The maxilliped (fig. 57) is 4-segmented and slender. The basal segment is unarmed. The second segment bears two slender naked setae and two rows of spinules. The third segment is very short and unarmed. The fourth segment forms part of the terminal claw and bears two setae, one very small and hyaline (8 μ long), the other long (47 μ), recurved and bearing a row of spinules along the distal half of its concave edge. The entire claw is 110 μ long (measured along its axis and not along its curvature), is slightly arcuate, and has along its concave edge a striated fringe which is interrupted near the middle of the claw. At the level of this interruption a break in the sclerotization of the claw may be seen, apparently indicating the distal limit of the fourth segment. The tip of the claw lacks a lamella.

The area between the maxillipeds and the first pair of legs is like that of the female.

Legs 1-4 resemble those of the female. The endopod of leg 4, however, seems to be slightly longer and more slender (52×15 μ in greatest overall dimensions) and the outer hairs on the second segment appear to be less prominent.

Leg 5 is similar to that of the female, but smaller, the free segment being 23×6 μ, the two terminal setae 91 and 32 μ, and the seta on the body near the free segment 30 μ.

Leg 6 (fig. 58) consists of a posterolateral flap on the ventral surface of the genital segment. It bears a minute spiniform process (6 μ), a long naked seta (104 μ), and an adjacent feathered seta (40 μ long). In a view of the entire urosome, as in fig. 56, the long setae of this leg are unusually conspicuous.

The spermatophore (fig. 59), attached to a female, is elongated, 85×34 μ, not including the neck.

The color in life in transmitted light resembles that of the female.

(This species is named for Dr. Michel Pichon, of the Centre d'Océanographie et des Pêches at Nosy Bé, who made collections of the host starfishes at Tany Kely while diving with aqualungs.)

Relationship to the host. — *Stellicola pichoni* was mostly recovered after only a single washing of the starfishes, in contrast to the case of *Asterocomes indica*, where several consecutive washings were required. This could indicate that these lichomolgids live more freely on the surface of the host, from which they are easily dislodged by the alcoholized sea water.

Comparison with other species. — Stock (1957) has briefly defined the genus *Stellicola* Kossmann, 1877, as comprising those lichomolgids which have a 3-segmented second antenna armed with a single terminal claw and in which the second segment of the endopod of leg 4 has two terminal and one inner setae. In this sense he included *S. thorelli* Kossmann, 1877, *S. pleurobranchi* Kossmann, 1877, *S. oreastriphilus* Kossmann, 1877, *S. caeruleus* (Stebbing, 1900), *S. curticaudatus* (Thompson and A. Scott, 1903), *S. gracilis* (Thompson and A. Scott, 1903), *S. lankensis* (Thompson and A. Scott, 1903), and *S. asterinae* (Bocquet, 1952). Bocquet and Stock (1962, p. 90) have pointed out that the four West African species of *Lichomolgus* described by Humes and Cressey (1958) belong to *Stellicola*, namely, *S. frequens*, *S. astropectinis*, *S. luidiae*, and *S. lautus*. The genus also includes *S. holothuriae* (Ummerkutty, 1961) and probably *S. longicaudatus* (Thompson and A. Scott, 1903). Adding to these *S. pichoni*, there are fifteen species about which we have sufficient information to place them in the genus *Stellicola* as defined by Stock. The members of this genus, judging from those cases where an association with a host is known, are associated with starfishes, except for *S. pleurobranchi* which lives on a gastropod and *S. holothuriae* which was recovered from washings of holothurians.

Stellicola pichoni is rather unusual in having a reduced number of postgenital segments (two instead of three in the female and three instead of four in the male). Only two other species in the genus show such a reduction, namely, *S. gracilis* and *S. lankensis*. From both of these Ceylonese species *S. pichoni* differs in several important respects. In them the prosome of the female is relatively narrower (a ratio of length to width of about 1.7:1 being obtained by measuring figs. 1 and 25, pl. XV, of Thompson and A. Scott), the caudal ramus is more elongated (about 4 times longer than wide in *S. gracilis* and about 2.2 times, based on measurement of fig. 25, pl. XV, in *S. lankensis*), the free segment of leg 5 is shorter and less slender, and the genital segment has a rather different form.

The number of urosomal segments within the genera of the Lichomolgidae is usually constant, except for sexual differences. A reduction in the number of these segments as seen in the three species of *Stellicola* is not unknown, however, in other lichomolgids. Ummerkutty (1961) described it in his *Lichomolgus indicus*, and Stock, Humes and Gooding (1963, pp. 56-57 and p. 70) have shown it to exist in *Pseudanthessius* and *Meomicola*.

Stellicola oreastriphilus Kossmann, 1877

Three females were recovered from 9 *Choriaster granulatus* in 10 m at Nosy Ovy, Isles Radama October 1, 1964. This species is already known from four starfishes in the region of Nosy Bé: *Protoreaster lincki* (Blainville), *Culcita schmideliana* (Retzius), *Pentaceraster mammillatus* (Audouin) and *Poraster superbus* (Möbius) (see Humes and Cressey, 1961).

The specimens from *Choriaster* agree in all significant details with those from the other starfishes at Nosy Bé.

It is of interest that *S. oreastriphilus* in the Nosy Bé area has been found in relatively large numbers on *Protoreaster*, *Culcita*, and *Pentaceraster*, which were collected intertidally or in very

shallow water (1 m or less), while it is much rarer on *Porastor* and *Choriaster*, both of which were collected in deeper water (4-10 m or more) This copepod thus seems to prefer starfishes in intertidal areas or in very shallow water, and its presence on hosts in deeper water may be more or less accidental.

That *S. oreastriphilus* should occur on *Choriaster* even accidentally is perhaps not surprising. however, since all five genera of hosts belong to the same family, the Oreasteridae.

On the *Choriaster* from Nosy Ovy *S. oreastriphilus* occurred in company with *Asterocomes indica*, *Stellicomes tumidulus*, and *Stellicola pichoni*.

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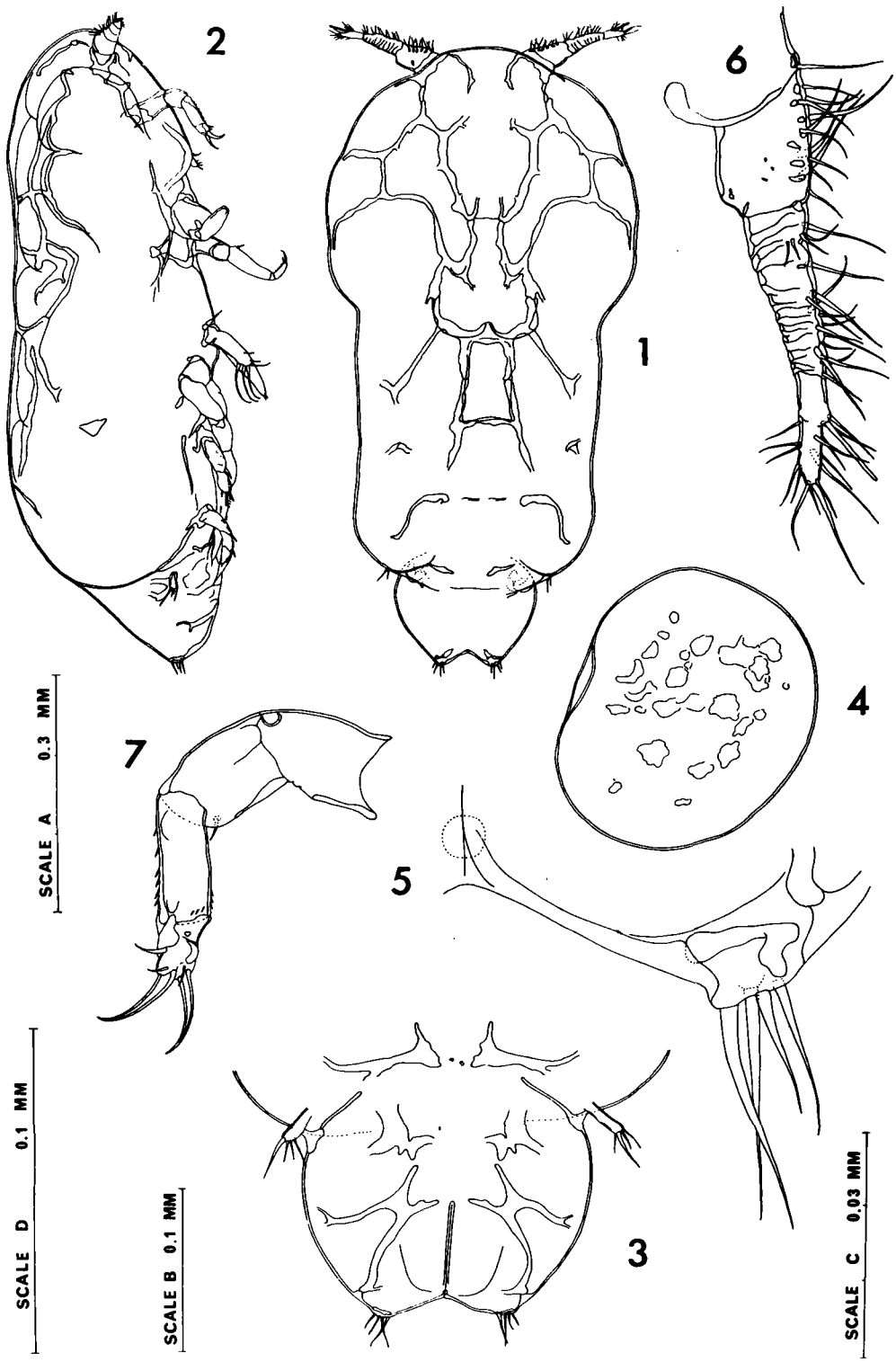
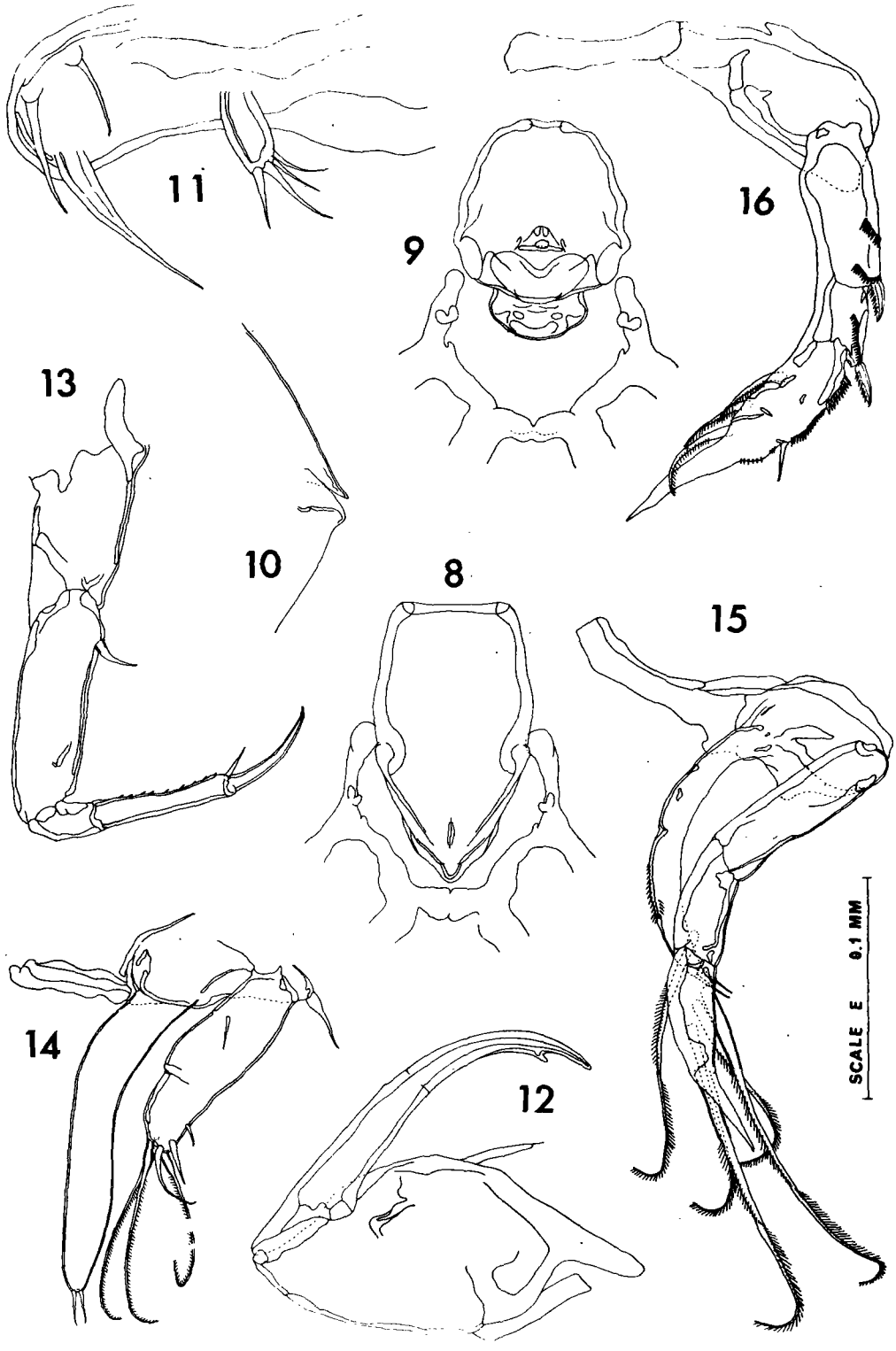
Explanation of the figures

All the figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which the figure was drawn.



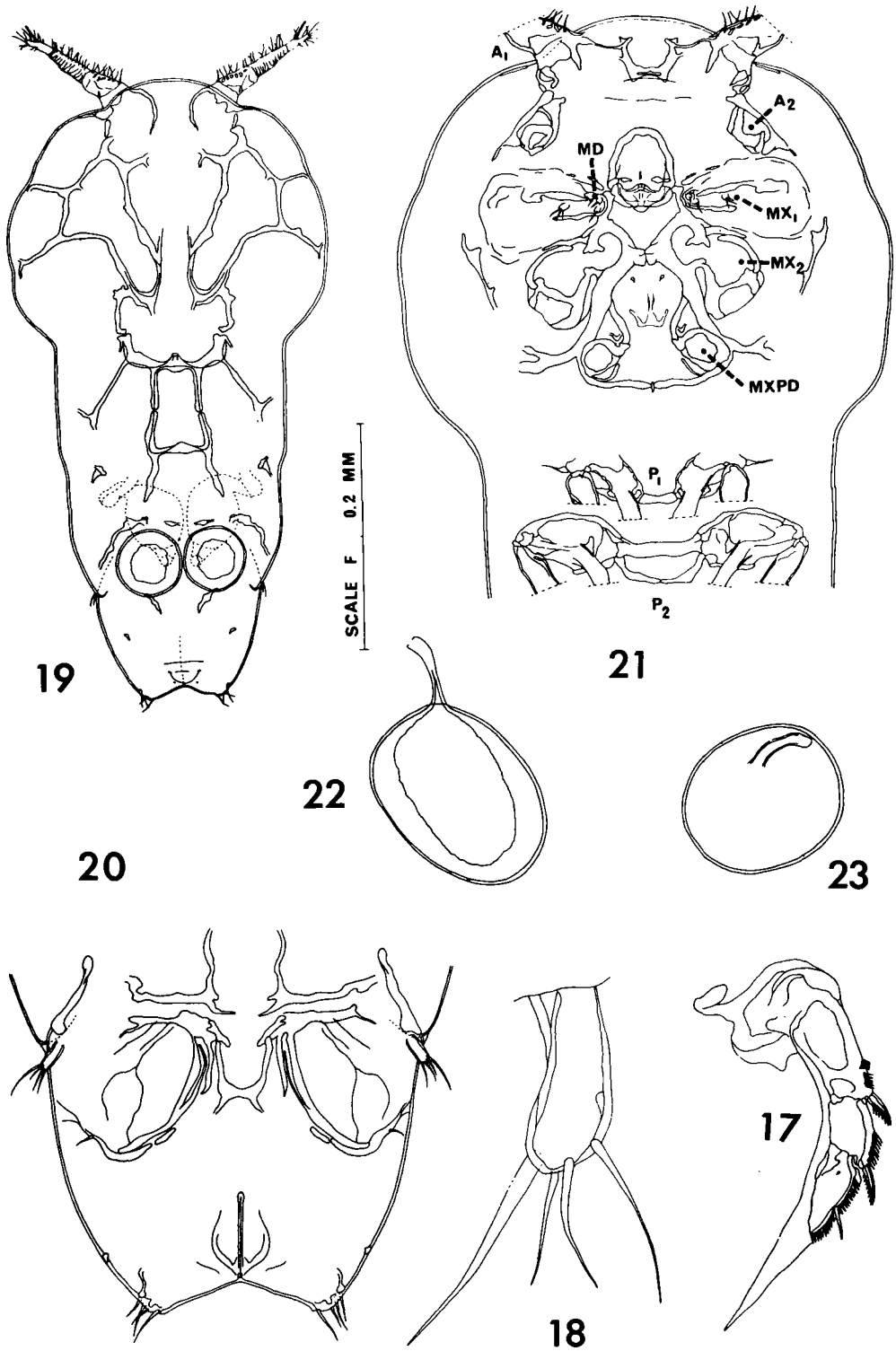
Figs. 1-7. — *Asterocomes indica* Padmanabha Rao, 1962, female

1. Body, dorsal (A) ; 2. Body lateral (A) ; 3. Urosome, ventral (B) ; 4. Egg sac (B) ; 5. Caudal ramus, ventral (C) ; 6. First antenna, dorsal (D) ; 7. Second antenna, anterior and ventral (D).



Figs. 8-16. — *Asterocomes indica* Padmanabha Rao, 1962, female (continued)

8. Labrum, ventral and anterior surface (D) ; 9. Mouth cone and labrum, ventral *in situ* (D) ; 10. Outline of mouth cone, lateral (D) ; 11. Mandible and first maxilla, ventral (C) ; 12. Second maxilla, posterior (D) ; 13. Maxilliped anteromedial (D) ; 14. Leg 1, anterior (D) ; 15. Leg 2, anterior (E) ; 16. Leg 3, anterior (D).

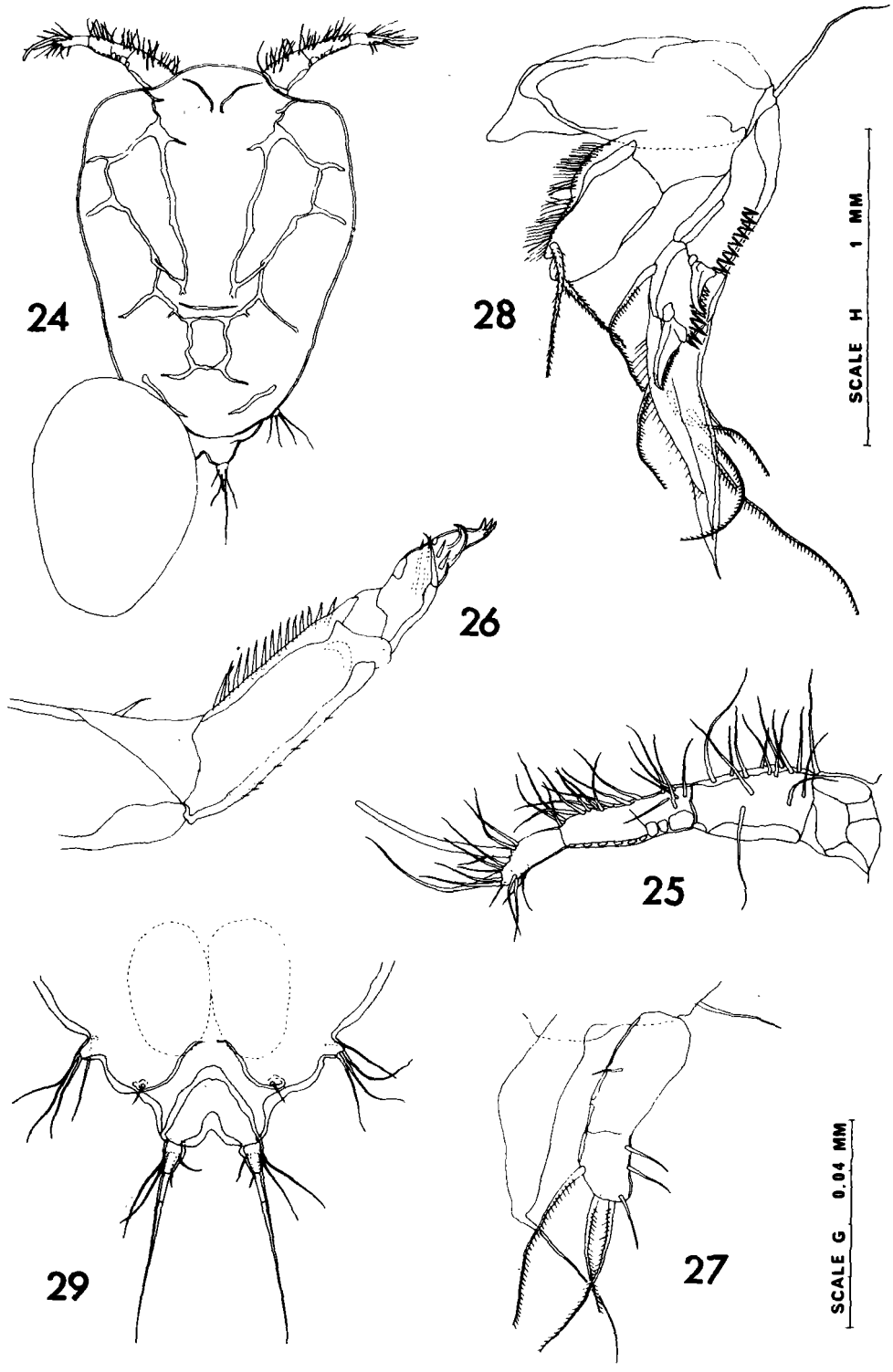


Figs. 17-18. — *Asterocomes indica* Padmanabha Rao, 1962, female (continued)

17. Leg 4, posterior (D) ; 18. Leg 5, ventral (C).

Figs. 19-23. — *Asterocomes indica* Padmanabha Rao, 1962, male

19. Body, dorsal (A) ; 20. Urosome, ventral (B) ; 21. Cephalosome, ventral (F) ; 22. Spermatophore, dissected out of male (B) ; 23. Spermatophore *in situ* in male (B).

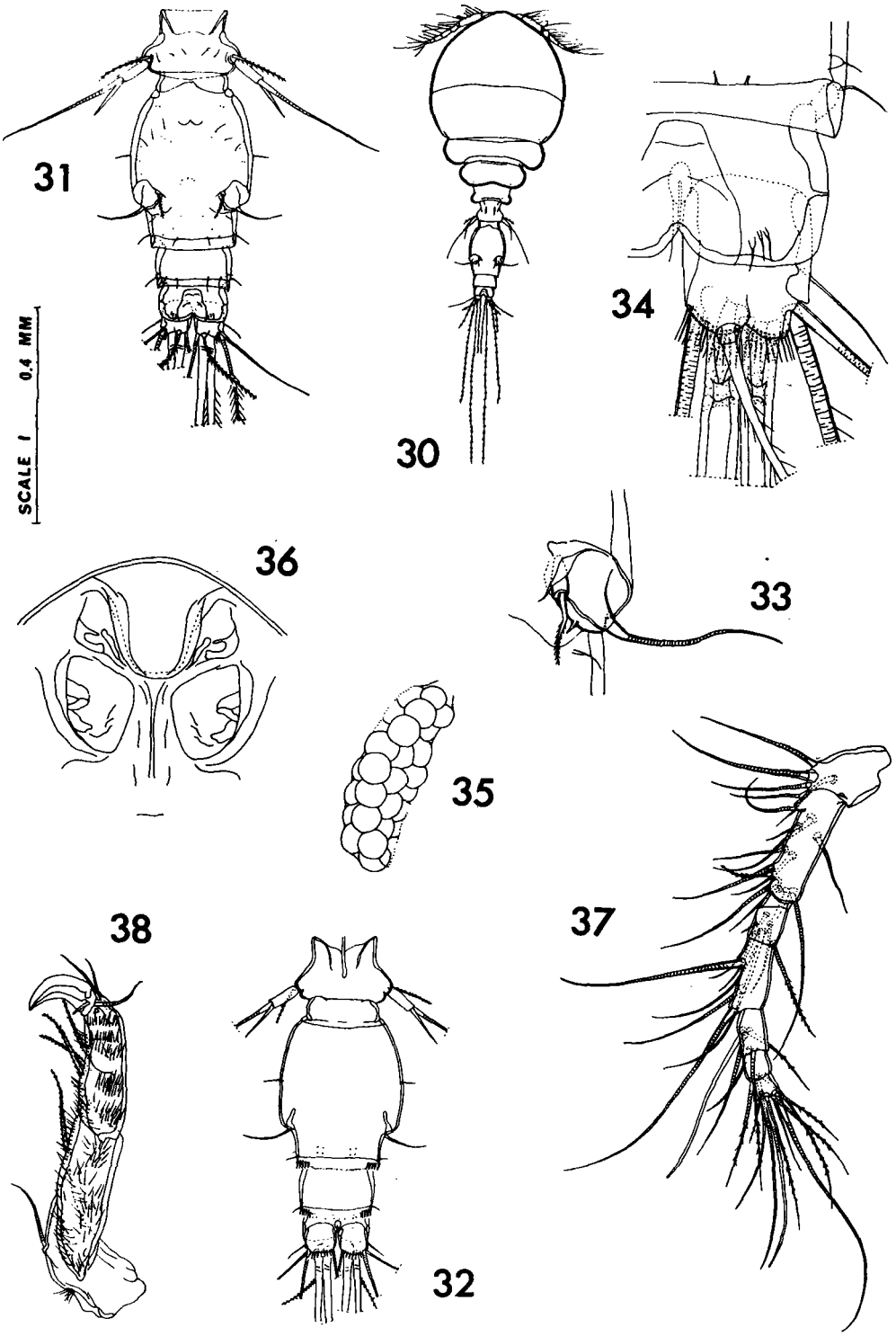


Figs. 24-28. — *Stellicomes tumidulus* Humes and Cressey, 1958, female.

24. Body, dorsal (F) ; 25. First antenna, dorsal (D) ; 26. Distal half of second antenna, inner (C) ; 27. Leg 1, anterior (G) ; 28. Leg 3, anterior (G).

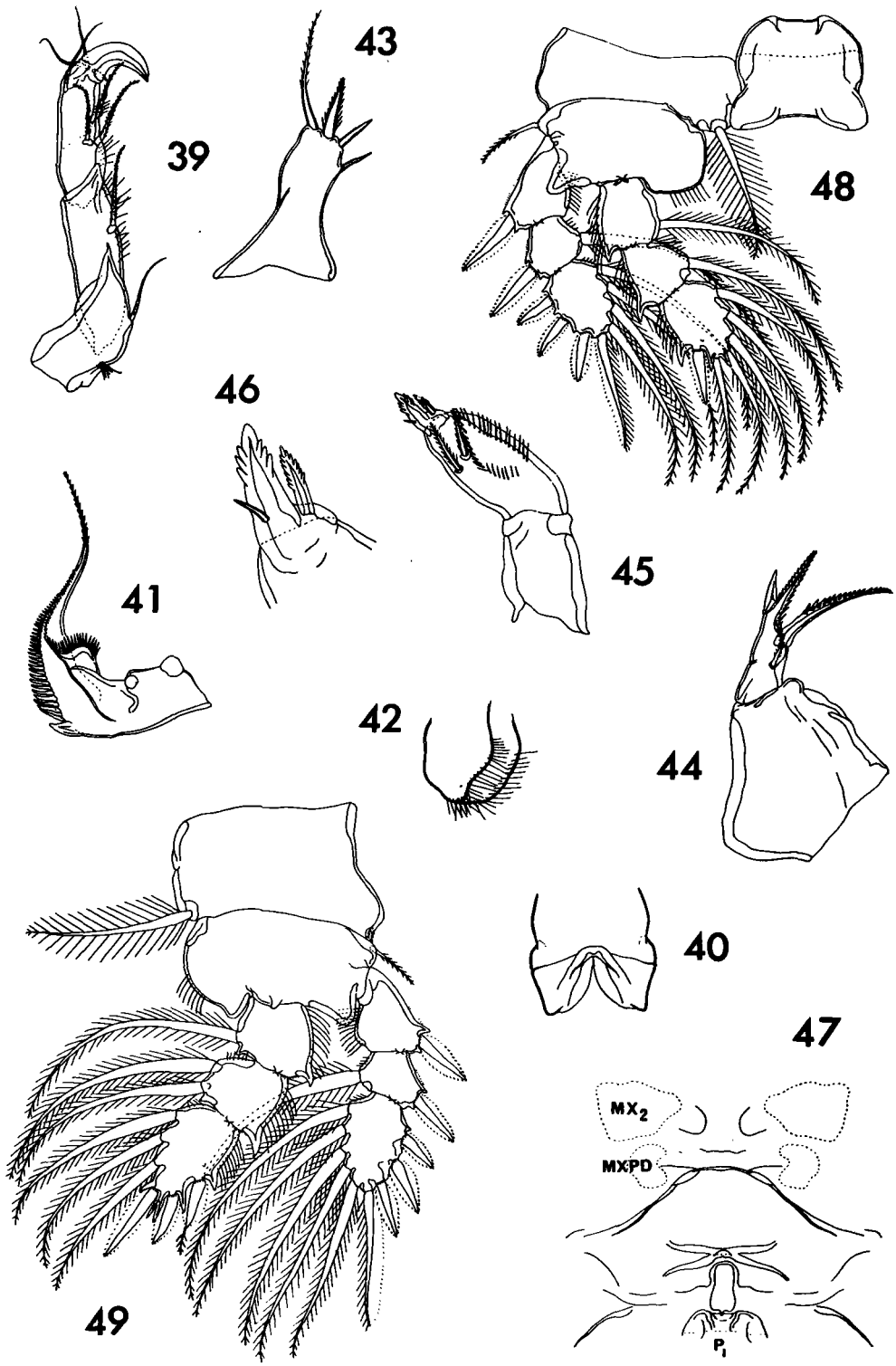
Fig. 29. — *Stellicomes tumidulus* Humes and Cressey, 1958, male.

29. Urosome, ventral (H).



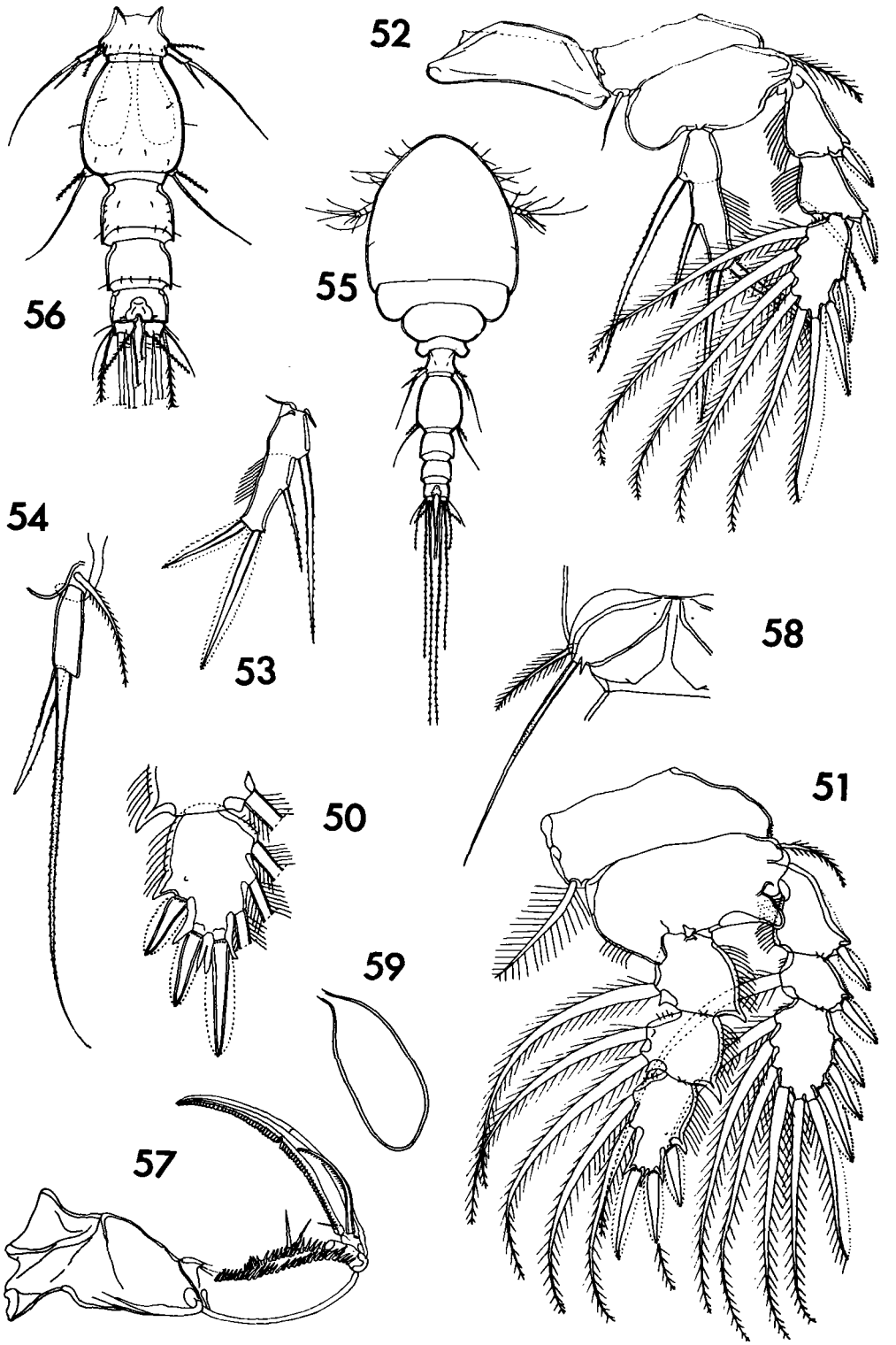
Figs. 30-38. — *Stellicola pichoni* n. sp., female.

30. Body, dorsal (H) ; 31. Urosome, dorsal (F) ; 32. Urosome, ventral (F) ; 33. Area of attachment of egg sac, dorsal (D) ; 34. Caudal ramus, dorsal (G) ; 35. Egg sac, dorsal (I) ; 36. Rostral area, ventral (B) ; 37. First antenna, ventral (B) ; 38. Second antenna, anterior (B).



Figs. 39-49. — *Stellicola pichoni* n. sp., female (Continued)

39. Second antenna, posterior (B) ; 40. Labrum, ventral (B) ; 41. Mandible, posterior (D) ; 42. Paragnath, ventral (G) ; 43. First maxilla, anterior (G) ; 44. Second maxilla, posterior (D) ; 45. Maxilliped, anterior (D) ; 46. Last segment of maxilliped, anterior (C) ; 47. Area between maxillipeds and leg 1, ventral (B) ; 48. Leg 1, anterior (E) ; 49. Leg. 2, anterior (E).



Figs. 50-54. — *Stellicola pichoni* n. sp., female (continued)

50. Third segment of endopod of leg 2, anterior (D) ; 51. Leg 3, anterior (E) ; 52. Leg 4, anterior (E) ; 53. Endopod of leg 4, anterior (E) ; 54. Leg 5, dorsal (D).

Figs. 55-59. — *Stellicola pichoni* n. sp., male.

55. Body, dorsal (I) ; 56. Urosome, dorsal (F) ; 57. Maxilliped, anterior (E) ; 58. Leg 6, ventral (E) ; 59. Spermatophore attached to female (E).

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Е. П. Делало

РАСПРЕДЕЛЕНИЕ БИОМАССЫ ЗООПЛАНКТОНА В КРАСНОМ МОРЕ И АДЕНСКОМ ЗАЛИВЕ ЗИМОЙ 1961/62 г.

Данная статья является результатом первичной обработки части материалов, собранных во время рейса э/с «Академик А. Ковалевский» в восточную часть Средиземного моря, в Красное море и Аденский залив, длившегося с 3 декабря 1961 г. по 3 марта 1962 г. Эти материалы собраны ихтиопланктонной сетью (диаметр входного отверстия 80 *см*, газ № 23) по слоям: 0—10, 10—25, 25—50, 50—100, 100—200, 200—500, 500—1000, 1000—2000 *м*. В Красном море преобладали станции над глубинами в 1000 *м*, а в Аденском заливе и в северо-восточной части Средиземного моря — над глубинами 2000 *м* и более (рис. 1) С помощью волюминометра В. А. Яшнова [1] в пробах определялся объем сестона, который затем перечислялся на вес. Почти полное отсутствие в наших пробах фитопланктона (вследствие применения относительно редкого газа) и минеральных частиц позволяет считать полученный вес сестона близким к величине биомассы зоопланктона.

Для собранных материалов определены массовые формы зоопланктона, главным образом копеподы (см. приложение), гидромедузы, сифонофоры, сальпы.

Красное море является одним из водоемов, чрезвычайно слабо изученных в отношении биологической продуктивности, что проявляется и в малой изученности зоопланктона, количественная характеристика которого совершенно отсутствует. Известная нам литература по зоопланктону Красного моря содержит, в основном, некоторые сведения о его качественном составе, фаунистической общности его с планктоном Аденского залива и Индийского океана. Изучался также обмен фаун Средиземного и Красного морей через Суэцкий канал и фауна канала [2—7].

В настоящей работе мы делаем попытку дать характеристику зоопланктона Красного моря с количественной стороны.

Известно, что фаунистические и продукционные особенности Красного моря определяются в основном водообменом с Аденским заливом [8]. Влияние вод Аденского залива особенно сильно в зимний период в связи с господством северо-восточного муссона, что подтверждается и наибольшим видовым разнообразием планктона в это время в Красном море [7, 9]. Можно предположить поэтому, что наши материалы, собранные в зимний период, когда зимний муссон вполне установился, характеризуют наиболее обильный для планктона Красного моря сезон. Результаты произведенных исследований представлены в таблице и на рисунках 2 и 3.

Как видно из таблицы и рисунков, биомасса зоопланктона Красного моря в зимний период 1961/62 г. возрастала по направлению с севера на юг: от 11,1 *мг/м*^{3} в северной части моря (в слое 0—1000 *м*) до 20,1—28,8 *мг/м*^{3} в средней и южной частях (в слое 0—800 *м*).

В наиболее богатом верхнем 100-метровом слое биомасса зоопланктона составляла в северной части моря 47,7, в средней и южной частях она была в 2—2,5 раза больше.

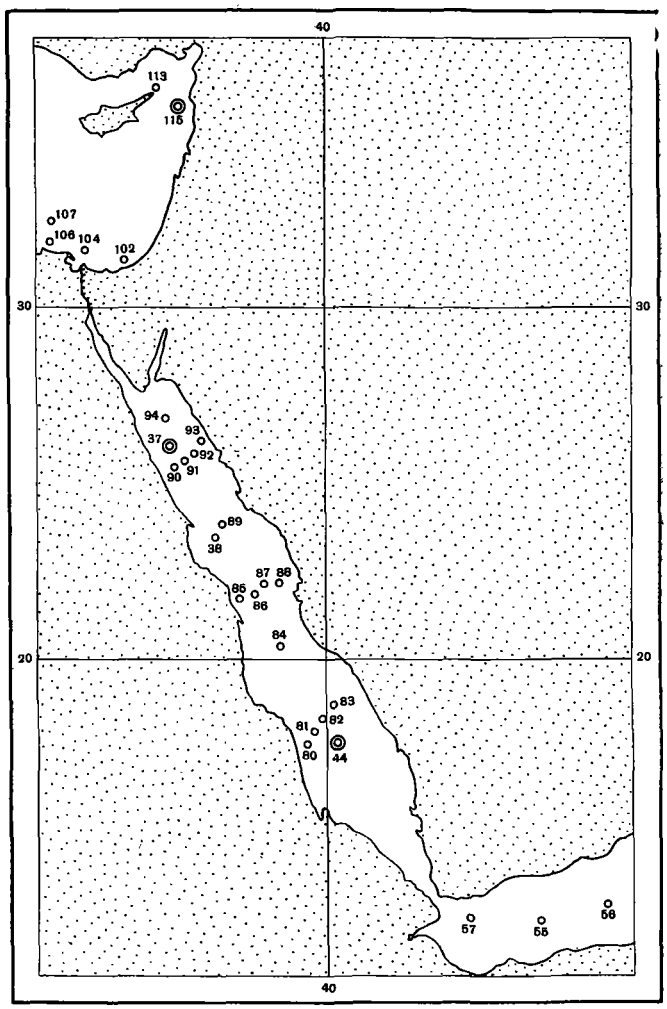

Рис. 1. Схема станций

Наряду с общим количеством зоопланктона несколько менялся по направлению от Суэцкого залива к Баб-эль-Мандебскому проливу и качественный состав зоопланктона. Целый ряд форм копепод, зарегистрированных в планктоне южной части Красного моря, отсутствовали в северной его части (Euchaeta *concinna,* Paracalanus *denudatus,* Paracalanus *nanus*).

В Суэцком канале (пробы из Большого Горького озера и из канала в районе 146 *км*) в массовом количестве обнаружена копепода, ранее для канала не указанная — Oithona *brevicornis* [4, 6]. Трудно предположить,

что эта форма была пропущена в предыдущих исследованиях Гарнея и Макдональда. Очевидно, она проникла в канал позднее и успешно размножилась и расселилась как в самом канале, так и в системе Горьких

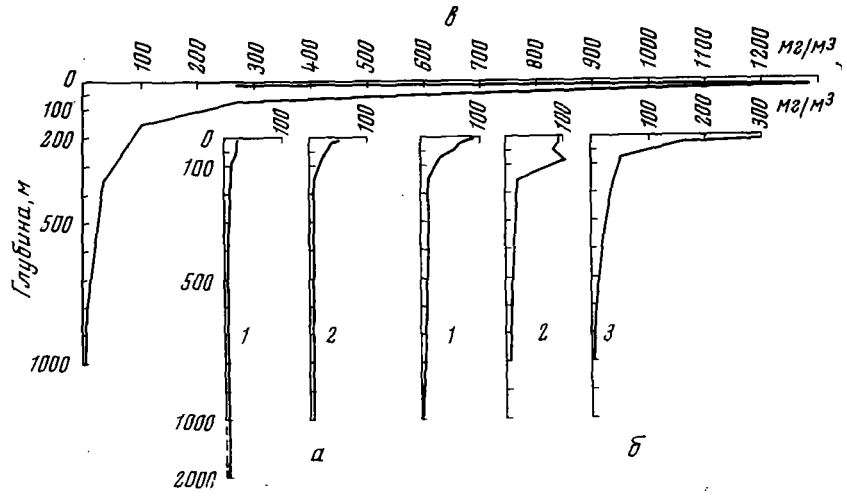

Рис. 2. Вертикальное распределение биомассы зоопланктона

а — Средиземное море: *1* — район о-ва Родос, *2* — Северо-восточный район; *б* — Красное море: *1* — северная часть, *2* — средняя часть, *3* — южная часть; *в* — Аденский залив у Баб-эль-Мандебского пролива

озер. Более систематические исследования, несомненно, помогли бы точнее уловить моменты появления новых элементов в фауне и флоре Суэцкого канала, а также ход миграций элементов фаун Средиземного и

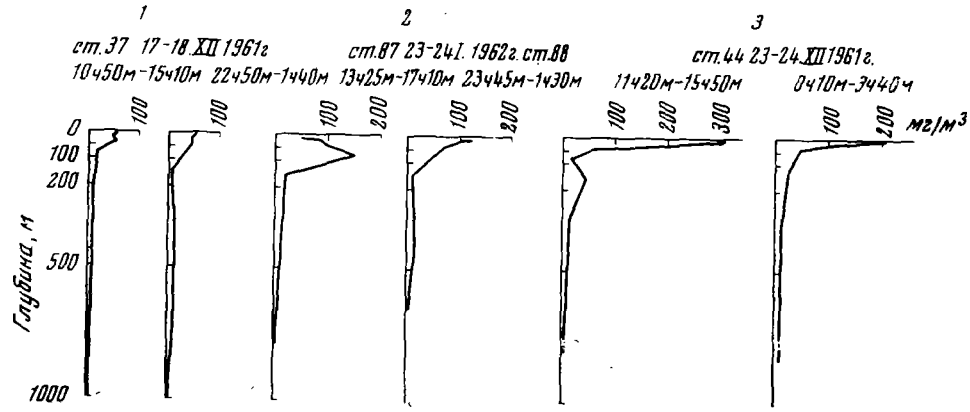

Рис. 3. Суточное вертикальное распределение биомассы зоопланктона в Красном море

1 — северная часть; *2* — средняя часть; *3* — южная часть

Красного морей через канал, так как уже сейчас можно отметить изменение границ распространения вдоль канала многих видов зоопланктона. Эти изменения границ распределения фауны зоопланктона Суэцкого канала, возможно, являются свидетельством интенсивности и направления водообмена через Суэцкий канал.

В южной части Красного моря при большем качественном разнообразии преобладали в планктоне относительно крупные копеподы (2—4 *мм*) из родов Euchaeta, Candacia, Eucalanus, Pleuromamma, Calanus.

Биомасса зоопланктона в зимний период 1961—1962 гг.

Район	Средняя биомасса по слоям, *мг/м³*				Общая биомасса во всей толще, *г/м²*
	0—100	100—200	200—500	500—1000	
I. Средиземное море					
а) р-н северо-восточный (ст. 115,2 серии; 122)	24,0	8,4	2,3	0,2	4,0
б) р-н Присуэцкий (ст. 102, 104) . .	18,4 *				0,9
II. Красное море					
а) Северная часть (ст. 37, 2 серии; 38, 89)	47,7	8,7	10,1	4,9	11,1
б) Средняя часть (ст. 87, 88) . . .	81,1	13,5	17,0	5,0 **	16,1
в) Южная часть (ст. 44, 2 серии; 82, 83)	104,8	38,0	17,8	11,5 **	23,1
III. Аденский залив					
У Баб-эль-Мандебского пролива (ст. 57)	570,7	102,0	34,0	0,7	77,8

* В слое 0—50 *м*. ** В слое 500—800 *м*.

Из некопеподного планктона по направлению с севера на юг относительно возрастало количество аппендикулярий, сальп, сагитт, сифонофор и некоторых других животных.

Такое увеличение количества относительно крупных копепод и других планктонных организмов с севера на юг несомненно, и обусловливает большие богатства южных районов Красного моря по сравнению с северными.

Характер горизонтального распределения биомассы зоопланктона в Красном море подтверждает исключительное влияние вод Аденского залива на продуктивность Красного моря. Район Аденского залива отмечен рядом исследователей как высокопродуктивный. По данным [10], при исследованиях в Аравийском море и Бенгальском заливе в октябре — ноябре 1960 г., наибольшая биомасса зоопланктона (более 2 *г/м³*) наблюдалась в Баб-эль-Мандебском проливе, Аденском заливе и в северной и центральной частях Аравийского моря. Во время наших работ район Аденского залива также был наиболее богатым (таблица, рис. 1, ст. 57). Биомасса зоопланктона здесь в среднем для слоя 0—1000 *м* составляла 78 *мг/м³*, а в слое 0—100 *м* — 571 *мг/м³*. Такая биомасса в 5—12 раз больше наблюдавшейся в Красном море. Наибольшая для Аденского залива биомасса — 1,3 *г/м³* — была отмечена по нашим материалам на ст. 57 в слое 9—20 *м*.

Причиной относительно высокой продуктивности этого района является отмечаемое в литературе поднятие водных масс, наблюдаемое вдоль южной оконечности Аравийского полуострова и у Сомалийского побережья в период летнего муссона [10—12].

Благоприятное влияние вод Аденского залива на красноморский планктон проявляется, по-видимому, как в приносе массы океанического планктона [7, 9], так и в обогащении вод Красного моря биогенными веществами, усиливающими развитие местного планктона. Явление приноса аденского планктона в Красное море с аденским течением подтверждается общностью фаунистического состава планктона обоих водоемов. Как показали исследования качественного состава зоопланктона, преобладающими в планктоне южной части Красного моря формами были те же относительно крупные копеподы (приложение) сальпы, сифонофоры, сагиты, птероподы, остракоды, что и в Аденском заливе.

Обогащающее влияние вод Аденского залива наиболее сильно в южной части Красного моря. По мере удаления от Аденского залива такое влияние все более и более ослабевает, достигая минимума в северной

части Красного моря. Причиной относительной бедности зоопланктоном северной части Красного моря, по сравнению со средней и южной его частями, возможно, является и повышенная соленость этого района (до 42% и выше) [13—15], которая может ограничивать развитие некоторых слабо эвригалинных океанических форм. Кроме того, интенсивное опускание поверхностных вод в северной части моря в зимнее время, вызванное повышенной соленостью и охлаждением, может приводить к тому, что планктон, поступающий с поверхностным аденским течением, попадает в глубинные слои, обедненные кислородом до 0,5 *мг/л* и менее [13, 15], и частично погибает.

На двух суточных и двух близко расположенных на разрезе станциях, взятых в течение одних суток днем и ночью в районе с однородными гидрологическими условиями (рис. 3), заметно вертикальное перераспределение количеств зоопланктона, связанное, по-видимому, с суточными вертикальными миграциями последнего. Наиболее заметно перемещение величин биомассы на станциях 87 и 88. Эти суточные перераспределения величин биомассы по слоям в основном ограничены верхними 200 *м* и выражены относительно слабо, что характерно для тропических морей со значительно более глубинным, чем в морях умеренных широт, распределением фитопланктона (до 200 *м* и глубже [16]), являющегося кормом для зоопланктона.

В связи с малой амплитудой суточных вертикальных миграций, зоопланктон Красного моря в любое время суток находится в наибольшем количестве в верхнем 100—200-метровом слое.

В северо-восточной части Средиземного моря зимой 1961/62 г. зоопланктон количественно был еще беднее, чем в северной части Красного моря (таблица, рис. 2). Здесь в наиболее богатом слое 0—100 *м* биомасса его, равная 24 *мг/м*^{3}, была в 2—4 раза ниже, чем в Красном море. Следовательно, продуктивность этого района, сравнительно с Красным морем, относительно невысока.

Сравнение полученных данных с материалами по сырому весу сестона для других морей Средиземноморского бассейна [17] и Черного моря [18] позволяет сделать вывод, что биомасса зоопланктона северной и средней частей Красного моря приблизительно равна таковой в открытых частях Средиземного моря (моря Ионическое, Тирренское, Сирта и Леванта — 64—80 *мг/м*^{3} в слое 0—200 *м*). По количеству зоопланктона южная часть Красного моря соответствует наиболее богатому району Средиземного моря — Адриатике со среднегодовой биомассой около 110 *мг/м*^{3} в слое 0—200 *м*.

По сравнению с Черным морем, где биомасса зоопланктона зимой составляет 300—400 *мг/м*^{3}, зоопланктон Красного моря в 4—6 раз количественно беднее, а зоопланктон Аденского залива в 1,5—2 раза богаче.

ABSTRACT

The determination of volume and weight of seston was made in 110 samples (from 13 stations). The samples were taken by egg net (D — 80/113 cm, silk gauze N 23) during the cruise of the r/v «Academician A. Kovalevsky» of the Institute of Biology of Southern Seas of the Academy of Sciences of USSR into the Gulf of Aden in December 1961 — March 1962.

Zooplankton in the Red Sea in the period of investigation was distributed unequally: in the Northern part of the Sea in the layer 0—100 m it amounted up to 47,7 mg/m^3, in the middle and in the Southern parts — 81,1—104,8 mg/h^3. The area of the Gulf of Aden appeared to be the richest in zooplankton — 571 mg/m^3 in the layer 0—100 m, the North-Eastern part of the Mediterranean Sea was the most poor — 24 mg/m^3 in the same layer.

At the diurnal stations in the Red Sea diurnal vertical redistribution of zooplankton biomass were observed, mostly in the upper layer 200 m.

In the plankton of the Red Sea 118 species of the copepoda were found; 48 of them were unknown before for this basin. New species was found in the fauna of the Suez Canal.

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ПРИЛОЖЕНИЕ

Копеподы Суэцкого канала, Красного моря и Аденского залива и их встречаемость по районам

Виды	Суэцкий канал	Красное море			Аденский залив
		северная часть	средняя часть	южная часть	
Calanus vulgaris (Dana)		+	+	+	+
* C. tenuicornis Dana		+	+	+	+
C. minor Claus		+	+	+	+
* Eucalanus bungii bungii Giesbr.			+	+	+
* E. attenuatus (Dana)				+	+
E. subcrassus Giesbr.		+	+	+	+
E. crassus Giesbr.				+	+
* E. mucronatus Giesbr.				+	+
Rhincalanus nasutus Giesbr.		+	+	+	+
Mecynocera clausi J.—C. Thompson		+	+	+	+
Paracalanus aculeatus Giesbr.		+	+	+	+
P. parvus Claus	+	+	+	+	
* P. denudatus Sewell				+	+
* P. nanus Sars		+	+		
P. crassirostris Dahl	+	+	+		
Acrocalanus gibber Giesbr.	+	+	+	+	+
A. gracilis Giesbr.		+	+	+	+
A. longicornis Giesbr.		+	+	+	+
Calocalanus pavo Dana		+	+	+	+
C. plumulosus Claus			+	+	+
* C. pavoninus Farran		+	+		
* C. contractus Farran		+	+		
Clausocalanus arcuicornis Dana		+	+	+	+
C. furcatus Brady		+	+	+	+
* C. pergens Farran		+	+	+	+
* C. paululus Farran		+	+		
* Ctenocalanus vanus Giesbr.		+	+	+	
* C. longicornis Mori (?)		+	+		
* Bradyidius armatus (Brady)		+	+	+	
Euchaeta concinna Dana			+	+	+
E. spinosa Giesbr.					+
* E. plana Mori		+	+	+	
* Scaphocalanus? sp.		+			
* Scolecithricella minor (Brady)		+	+	+	+

ПРИЛОЖЕНИЕ (продолжение)

Виды	Суэцкий канал	Красное море			Аденский залив
		северная часть	средняя часть	южная часть	
* S. orientalis Mori		+	+	+	+
* S. tropica Grice		+		+	
* S. spinipedata Mori				+	
Centropages gracilis (Dana)			+	+	+
C. violaceus (Claus)			+	+	
C. furcatus (Dana)	+			+	
C. kroyeri var. ponticus Karawiew	+				
* Phaenna spinifera Claus		+	+		
Temora stylifera (Dana)	+				
T. discaudata Giesbr.				+	+
* Pleuromamma robusta (Dahl)		+	+	+	+
* P. xiphias (Giesbr)					+
Lucicutia flavicornis Claus		+	+	+	+
* L. clausi Giesbr.		+	+	+	+
* L. ovalis Wolfenden		+	+	+	+
* L. gemina Farran		+	+	+	
* Haloptilus longicornis Claus		+	+	+	+
* H. plumosus Claus		+	+	+	+
* H. acutifrons Giesbr.		+	+	+	+
* H. ornatus (?) Giesbr.				+	
* Euaugaptilus hecticus Giesbr.				+	
Candacia truncata (Dana)		+	+	+	+
C. longimana Claus				+	+
C. curta Dana		+	+	+	+
C. bradyi Scott				+	
Calanopia elliptica (Dana)		+	+	+	+
* C. minor A. Scott				+	
Labidocera acuta (Dana)				+	+
Pontellopsis villosa Brady		+	+	+	
Pontellina plumata Dana		+	+	+	
Acartia negligens Dana		+	+	+	+
A. danae Giesbr.		+	+		
A. centrura Giesbr.	+				
A. aerythraea Giesbr.				+	
* Temoropia mayumbaensis T. Scott		+	+	+	
Tortanus gracilis Brady	+				
* Mormonilla minor Giesbr.		+	+	+	
Oithona setigera Dana		+	+	+	+
* O. attenuata Farran		+	+		
O. plumifera Baird.		+	+	+	+
* O. atlantica Farran		+	+		
* O. brevicornis Giesbr.	+			+	
* O. vivida Farran		+	+		
O. robusta Giesbr.		+	+	+	+
* O. decipiens Farran		+	+		
O. simplix Farran	+	+	+		
* O. tenuis Rosendorn		+	+	+	
O. nana Giesbr.	+	+			
* O. minuta (?) Scott	+	+			
* Paroithona pulla Farran		+			
Microsetella rosea Dana		+	+	+	+
M. norvegica Boeck.	+				
Macrosetella gracilis Dana		+	+	+	+

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ПРИЛОЖЕНИЕ (окончание)

Виды	Суэцкий канал	Красное море			Аденский залив
		северная часть	средняя часть	южная часть	
Euterpina acutifrons Dana	+				
Clytemnestra scutellata Dana	+?			+	
Aegistus mucronatus Giesbr.					+
Oncaea media Giesbr.	+	+	+	+	+
* O. similis G. O. Sars		+	+		
O. conifera Giesbr.		+	+	+	+
O. venusta Philippi		+	+	+	+
O. mediterranea Claus				+	
O. minuta (?) Giesbr.	+				
* Conaea rapax Giesbr.				+	
Lubbockia aculeata Giesbr.		+	+	+	
L. squillimana (?) Claus		+			
Sapphirina nigromaculata Claus			+	+	
S. darwini Haeckel			+	+	
S. gemma Dana			+	+	
S. gastrica Giesbr.		+	+	+	
S. scarlata Giesbr.			+	+	
S. metallina Dana.		+	+	+	+
Copilia mirabilis Dana		+	+	+	+
Coricella rostrata Claus		+	+	+	
C. carinata Giesbr.		+	+	+	+
* C. curta Farran		+			
* C. sp.				+	
* Corycaeus limbatus Brady		+	+	+	+
C. latus Dana				+	
C. speciosus Dana		+	+	+	+
C. crassiusculus Dana				+	+
C. agilis Dana		+	+	+	+
* C. japonicus Mori				+	
* C. trukicus Mori				+	
C. erythraeus Farran	+				
C. sp.				+	
* Pontoeciella abyssicola Farran		+		+	

* Виды, ранее для Красного моря не указанные.

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A REVISION OF THE MASCARENE WHITE-EYE, *ZOSTEROPS BORBONICA* (AVES)

BY ROBERT W. STORER AND FRANK B. GILL

IN THE course of field work on the island of Reunion (Fig. 1) (Indian Ocean) in the fall of 1964, we found that the well-known color variation of the "Oiseau-blanc" *(Zosterops borbonica)* on that island follows a geographic pattern, there being no fewer than four well-marked subspecies, two in the highlands and two in the lowlands. One of the former, a gray-backed, gray-flanked form, is found in the highland heaths and savannas, and the other, which has warm brown flanks and breast and a brownish back, is found in the wet upland forests. Of the two lowland forms, one, a bird with gray crown and nape, brownish back, and warm brown flanks, is found on the wet, northern side of the island, and the other, brownish on the flanks and upper parts, is found on the dry lowlands on the southern side of the island. In all forms the males average slightly larger than the females, but there are no sexual differences in color. The upland birds average somewhat larger than the lowland ones (Table 1), and there appear to be other average differences in size between the races. Color, however, is the best means of distinguishing these subspecies.

Elsewhere, the species is known only on Mauritius, where a gray-backed, brown-flanked subspecies occurs.

The names which appear to be available for two of these forms are *Motacilla borbonica* Gmelin (1789, Syst. Nat., vol. i, p. 981) and *Zosterops E. Newtoni* Hartlaub (1877, Vögel Madagascars, pp. 97–98). Gmelin's name is based primarily on Brisson's *Ficedula borbonica* (1760, Orn., vol. iii, p. 510, pl. 28, fig. 3), the description of which reads "Ficedula superne griseo-fuscá, inferne sordide cinereo-albo-flavicans; rectricibus fuscis, oris exterioribus griseo-fuscis." Neither this description nor Brisson's figure is identifiable to species, although the description fits the present species better than any other native bird of Re-

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union. The "griseo-fusca" of the upper parts is translated "gris-brun" in Brisson's description in French, and the rump ("crupion") is said to be this color also. (The white rump characteristic of this species is not mentioned in early accounts, possibly because these feathers were lost either in the catching or skinning process.) Brisson specifically stated that the upper parts of the head, neck, back, and rump are gray-brown, a description which could apply to at least some examples of three of the subspecies, but not the gray-headed, brownish-backed birds of the northern lowlands unless badly soiled or foxed. Gmelin also used Buffon (1786, Hist. Nat. Ois., 5:280) and D'Aubenton's Planches Enluminées (no. 705, fig. 2) as sources of his description. Of these, the plate shows a bird most like the warm brown bird of the upland forests, but not certainly distinguishable from the dry lowland population.

Pollen and van Dam (1868, Faun. Madag., Ois., p. 74) appear to be the first to point out variation within this species, describing birds resembling the two highland forms and the gray-headed, brown-flanked bird of the wet lowlands. They stated that the color of this species is more or less subject to individual variation, but not sexual variation.

Hartlaub (*op. cit.*: 95) restricted the name *borbonica* to the gray-headed, brown-flanked population and described (pp. 97–98) as *Zosterops E. Newtoni* [*sic*] both of the two upland types, the gray one first, as the probable male, and the rich brown one as the probable female.

Brisson's description was based on a bird from the Réaumur Collection. Christian Jouanin, who kindly looked into the matter for us, wrote that this specimen is no longer extant. In the absence of a type specimen, we prefer to follow Hartlaub in assigning the name "*borbonica*" to the form of the lowlands on the north side of the island. We do this because, being common in the capital, St. Denis, it is the form most likely to be encountered by a visitor to the island and because the discrepancy between the birds and the inadequate original description could easily have resulted from soiling of the type.

The cotypes of *E. Newtoni* also appear to be lost. Mrs. Susan Hubbard kindly looked for them in the Cambridge Museum, where she could find no specimens of this form and none listed in the catalogue of the Newton Collection. In order to fix the name, we hereby restrict it to the gray bird, the first described under the name. Hartlaub gave only "Bourbon" (= Réunion) as the type locality. Because gray birds are occasionally found within the range of the warm brown upland form, we restrict the type locality to Nez de Boeuf, 5 kilometers east of le Vingt-Septième, 2100 meters elevation, a locality well within the range of the gray race.

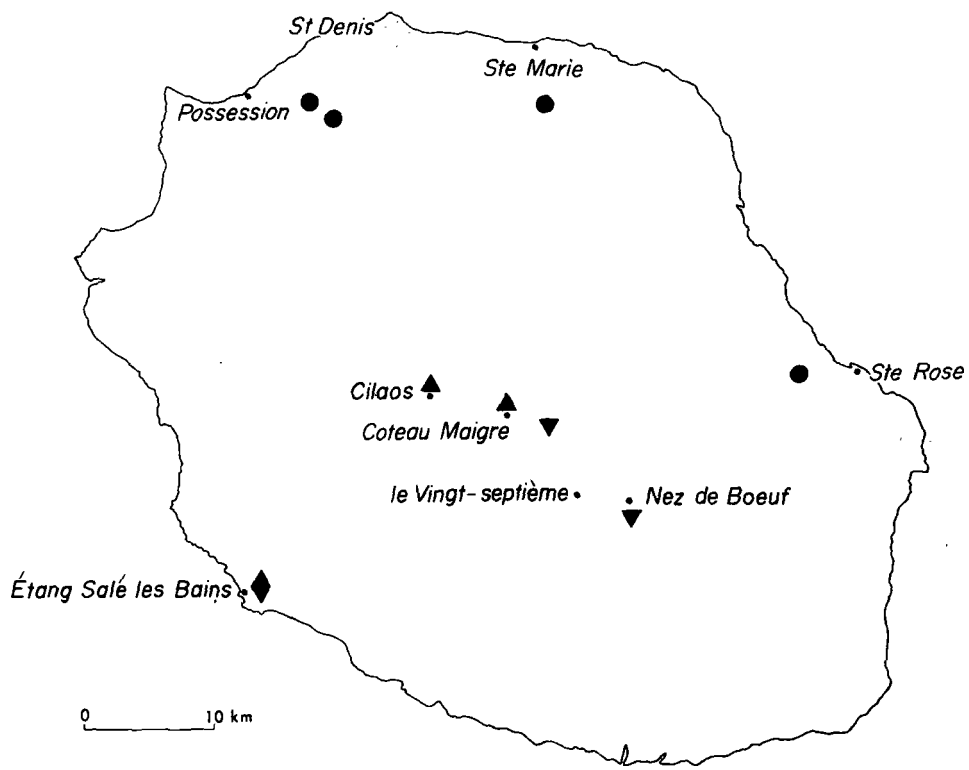

FIG. 1. Map of Reunion Island showing localities from which specimens of *Zosterops borbonica* were examined. Solid circles, *borbonica;* diamonds, *xerophila;* triangles, *alopekion;* and inverted triangles, *edwardnewtoni.*

The orthography of this name as originated by Hartlaub is currently incorrect under the present rules. Dr. Ernst Mayr writes us that as "the letter 'E' in *Zosterops E. Newtoni* is not 'a Latin letter used to denote a character of the taxon' (Article 26c) one is almost forced to assume that it should be spelt out as is demanded for numerals in Article 26b." We therefore emend it to *edwardnewtoni.*

The five forms should therefore stand as follows:

Zosterops borbonica borbonica (Gmelin)

Motacilla borbonica Gmelin, Syst. Nat., vol. 1, p. 981, 1789 ("insulis Bourbon et Madagascar").

CHARACTERS.—Above, the light gray (Neutral Grey[1]) of the head and nape contrasts with the gray-brown (Saccardo's Umber) of the back. The throat and upper breast are grayish white (Light Brownish Olive or

[1] Capitalized colors are those of Ridgway, Color Standards and Color Nomenclature, 1912.

Pale Smoke Grey to Light Gull Grey) without the creamy wash characteristic of the next subspecies. The brownish flanks vary from Tawny Olive to Sayal Brown.

RANGE.—The slopes of the northern side of Réunion from sea level to at least 1100 meters elevation. Specimens examined from 4.6 kilometers S of Ste. Marie, 360 meters (9); 6 km. E of La Possession, 634 meters (6); 4 km. W of Ste. Rose, near sea level (1); and 8 km. SSW of St. Denis, 1100 meters (1).

REMARKS.—The single specimens from 4 km. W of Ste. Rose and from 8 km. SSW of St. Denis approach specimens from the south side of the island in the color of the crown and nape, but they do not have the creamy wash on the under parts characteristic of birds from Étang Salé les Bains.

Zosterops borbonica xerophila new subspecies

CHARACTERS.—Upper parts uniform grayish brown (Light Brownish Olive); under parts grayish white (Pale Olive Grey) with a light creamy wash (near Ivory Yellow), which is strongest on the abdomen; flanks brownish (Tawny Olive). Differs from *borbonica* in its brownish crown and nape, creamy wash on the under parts, and duller brown flanks.

TYPE.—U. S. National Museum No. 486,226, male, from Étang Salé les Bains, sea level, Ile de La Réunion, 18 November 1964, collected by Frank B. Gill, no. GI-926 (skull ossified, testes 6 × 4 mm., weight 6.8 grams). Wing, 55; tail, 39.5; tarsus, 18.5; culmen, 12; bill from nostril, 7.0 mm.

RANGE.—Known from only 7 specimens taken at Étang Salé les Bains, but presumably occurs over much of the lowlands on the dry south side.

REMARKS.—The single specimens from 4 km. W of Ste. Rose and from 8 km. SSW of St. Denis approach examples of this race in the color of the upper parts but do not have the creamy wash on the under parts. The subspecific name alludes to the bird's arid habitat.

Zosterops borbonica edwardnewtoni Hartlaub

Zosterops E. Newtoni Hartlaub, Vögel Madagascars, 1877, pp. 97–98 ("Bourbon"), part ("1").

CHARACTERS.—Crown, nape, and back uniformly gray (Deep Mouse Grey); breast lighter, shading to whitish on the chin and slightly paler gray on the abdomen; flanks gray or tinged with brownish.

TYPE LOCALITY.—Here restricted to Nez de Boeuf, 5 kilometers east of le Vingt-Septième, 2100 meters elevation.

RANGE.—The high heaths and savannas of the interior of the island (above 1500 meters), extending into some of the wet forested slopes of the inland ravines. Specimens examined from Nez de Boeuf (12); Pon de Sable, 6 km. ENE of le Vingt-Septième, 2100 meters elevation (2); and 6 km. NNW of le Vingt-Septième, 1600 meters elevation (6).

REMARKS.—Two specimens from Nez de Boeuf, an adult male and an immature female, are intermediate between this subspecies and the next in both the color of the back and that of the under parts. The intermediacy of these birds and the pale brownish wash on the flanks of several other specimens indicate introgression with the next form.

Zosterops borbonica alopekion new subspecies

Zosterops E. Newtoni Hartlaub, Vögel Madagascars, 1877, pp. 97–98 ("Bourbon"), part ("2").

CHARACTERS.—Uniformly grayish brown above (Saccardo's Umber), averaging somewhat darker and richer brown than *xerophila;* below extensively warm brown (Tawny Olive) on flanks, breast, and lower throat, leaving only the chin and center of the abdomen light gray.

TYPE.—U. S. National Museum No. 486,227, female, from one km. N of Cilaos, 1500 meters elevation, Ile de La Réunion, 20 November 1964, collected by Frank B. Gill, no. GI-978 (skull ossified; ovary 5 mm., 2 collapsed follicles, brood patch; weight, 8.8 grams). Wing, 56; tail, 41; tarsus, 19.3; culmen, 14; bill from nostril, 6.9 mm.

RANGE.—Known only from near Cilaos and from a series purchased from a native bird catcher and said to have come from Coteau Maigre, approximately 5 km. E of Cilaos.

REMARKS.—Of twelve specimens taken near Cilaos, nine are as described above, two answer the description of *edwardnewtoni,* and one is intermediate, having a gray back but nearly as much warm brown on the under parts as typical *alopekion.* Of the ten birds from Coteau Maigre, all are extensively warm brown above and below, but one shows a reduction of brown on the breast. The existence of occasional gray individuals and one intermediate in the Cilaos population suggests that some mixing of the populations occurs in this region.

The name *alopekion* comes from the Greek for little fox and is an allusion to the reddish brown color of the birds.

Zosterops borbonica mauritiana (Gmelin)

Motacilla mauritiana Gmelin, Syst. Nat., vol. 1, p. 981, 1789 ("in insula Franciae").

CHARACTERS.—Upper parts, except rump, light gray (Neutral Grey); flanks pinkish brown (Avellaneous); throat and upper breast white, shading to very pale gray on the lower breast.

TABLE 1

MEASUREMENTS (IN MILLIMETERS) AND WEIGHTS (IN GRAMS) OF THE SUBSPECIES OF *Zosterops borbonica*

	borbonica	*xerophila*	*alopekion*	*edwardnewtoni*	*mauritiana*
			Males		
Number	12	5	12	12	9
Wing (arc)	52.0–57.0 (54.0)	54.5–56.0 (55.2)	53.0–60.0 (57.0)	55.5–60.0– (57.7) [1]	52.0–57.5 (55.7)
Tail	39.0–42.0 (40.5)	39.5–13.0 (40.7)	41.0–45.5 (42.6) [2]	42.0–45.0 (43.1) [1]	37.0–43.0 (40.4)
Tarsus	17.6–19.6 (18.7)	18.4–19.5 (18.7)	18.8–20.1 (19.6)	19.3–21.1 (20.4)	17.0–18.3 (17.6)
Culmen	13.5–15.0 (14.1)	12.0–13.0 (12.8)	13.0–15.0 (14.0) [1]	12.8–14.1 (13.6)	12.0–13.9 (13.0)
Bill from nostril	6.9– 7.4 (7.1)	6.5– 7.0 (6.7)	6.7– 7.5 (7.1) [1]	6.5– 7.1 (6.8)	6.6– 7.8 (7.1)
Weight	7.5– 8.7 (8.2) [1]	6.8– 7.8 (7.4)	7.8– 9.0 (8.5) [3]	7.4–10.0 (8.5)	7.6– 9.2 (8.3)
			Females		
Number	5	2	10	9	4
Wing (arc)	52.0–54.0 (53.6)	53.0–51.5 (53.8)	51.0–58.0 (55.6)	54.0–59.0 (56.1) [6]	53.5–56.0 (51.9)
Tail	39.5–41.0 (40.3) [4]	39.0–39.0 (39.0)	39.0–45.0 (41.6) [5]	39.0–44.0 (41.2) [6]	40.0–41.0 (40.5) [7]
Tarsus	17.1–19.2 (18.2)	17.9–18.1 (18.0)	18.9–20.7 (19.6)	19.2–22.5 (20.2)	17.5–17.9 (17.7)
Culmen	13.0–14.0 (13.8)	13.0–13.0 (13.0)	13.0–14.0 (13.9)	12.8–14.0 (13.5)	13.4–13.6 (13.5)
Bill from nostril	6.9– 7.5 (7.2)	6.5– 6.7 (6.6)	6.5– 7.8 (6.9)	6.6– 7.6 (7.1)	6.8– 7.4 (7.2)
Weight	7.3– 8.5 (7.9)	8.1– 8.3 (8.2)	8.5–10.1 (9.4) [3]	7.6–11.0 (8.8)	7.8– 8.4 (8.0)

[1] 11 specimens
[2] 10 specimens
[3] 6 specimens
[4] 4 specimens
[5] 9 specimens
[6] 8 specimens
[7] 3 specimens

RANGE.—Found nearly throughout the island of Mauritius. Specimens examined from near the Macabe Forest (3), Bel Ombre, Savanne District (3), Plaine Champagne, Savanne District (2), and Rivière de Rempart District (5).

REMARKS.—Our thirteen specimens from various localities on Mauritius show little variation in color, aside from the intensity of the shade on the flanks. Virtually the whole range in intensity is found in the sample from one population (the Rivière de Rempart District).

The presence of four morphologically distinct populations of a species of bird within as small a geographic area as Reunion Island (1000 square miles) is a most unusual occurrence. Similar situations are found more frequently in terrestrial mammals and reptiles, but the only comparable case in birds is that of the Song Sparrows *(Melospiza melodia)* in the San Francisco Bay region of California (Marshall, 1948, Condor, 50:193–215; 233–256). Because of the unusual nature of this case we have in preparation a second paper analyzing the situation in more detail and discussing its implications at greater length.

KEY TO THE SUBSPECIES OF *Zosterops borbonica*

1. Top of head and nape gray, back brown ..... *borbonica*
   Top of head, nape, and back concolor 2
2. Upper parts gray 3
   Upper parts brown 4
3. Throat and upper breast white, flanks pinkish brown ..... *mauritiana*
   Under parts gray (flanks occasionally tinged with brownish) ..... *edwardnewtoni*
4. Breast largely reddish brown ..... *alopekion*
   Breast grayish white with creamy wash ..... *xerophila*

We wish to thank M. Christian Jouanin for his invaluable assistance with the formalities on Réunion, for the loan of material, for his assistance in looking for the type of *borbonica,* and for his help and companionship in the field. We are indebted also to M. Armand Barau, who kindly offered us hospitality and assistance in many other ways, and to John Tottenham, who prepared the map.

This work was supported by the National Science Foundation as part of the U. S. Program in Biology, International Indian Ocean Expedition. The field work was conducted under the auspices of the U. S. National Museum, Smithsonian Institution, Washington, D. C.

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NOTES UPON A COLLECTION OF BIRDS MADE BY FRANK GILL ESQ. OFF THE WEST COAST OF PENINSULAR THAILAND

by

E.C. DICKINSON

SUMMARY

Notes are made upon a collection of 73 specimens of 30 species of birds collected off the West coast of Thailand in November 1963 as part of the International Indian Ocean Expedition. These add to our knowledge of the distribution within Thailand of ten species, none of the extensions in range being unexpected. Five other species seen in areas where they have not previously been recorded are also included.

Introduction: FRANK B. GILL visited 6 Thai localities on or off the West coast of peninsular Thailand during the period November 1st. to 16th. 1963 on board the R/V *Te Vega;* a research vessel from Stanford University, California; which was participating in the United States Programme in Biology as part of the International Indian Ocean Expedition. In the course of this visit he collected with the aid of several colleagues 73 bird specimens; these were preserved either as skins or as skeletons or in alcohol. The specimens have been deposited with the Smithsonian Institution, Washington D.C., which administered the National Science Foundation grant making possible Mr. GILL's fieldwork.

A number of the records which emerge from this collection extend the known range within Thailand of the species concerned. This paper is not intended to resolve subspecific identifications as the material is drawn from the records of the collector and the museum catalogue at the Smithsonian Institution where specimens are entered prior to study. Nonetheless some points are touched upon at sub-specific level. Certain further points may emerge from a serious examination of the material.

Itinerary: To avoid any possible future confusion the names used on U.S. Maps are here shown as well as those used on the labels of the specimens.

Date	Name used on British Admiralty Charts and on specimen labels	Name shown on U.S. Army Map Service Sheets NB 47 and NC 47 if different	Position	Changwad
Nov. 1-2	Phuket Harbour			Phuket
Nov. 3-4	Goh Huyong, Similan Is.	Ko Tai (meaning South Island)	8°29'N:97°37'E	Phang-nga
Nov. 5-7	Goh Sindarar Nua	Ko Chan	9°26'N:97°50'E	Ranong
Nov. 8	Goh Similan, Similan Is.	Ko Nua (meaning North Island)	8°38'N:97°39'E	Phang-nga
	Goh Huyong			
Nov. 9	Phuket Harbour			
	Goh Pipidan	Ko Bida	7°47'N:98°47'E	Krabi
Nov. 11-13	In Malaysian waters			
Nov. 14	Pulau Tenga	Ko Ta Nga, Butang Islands	6°35'N:99°28'E	Satun
Nov. 15	Goh Pipidan			
Nov. 16	Phuket Harbour			

Throughout this paper I use the spelling Ko for Goh meaning island (Pulau in Malay).

Specific List:

The specific names are those used by DEIGNAN (1963).

Egretta sacra (GMELIN)

2 ♂ 2 ♀ as skins. 2 ♀ as skeletons.

Collected from Ko Sindarar Nua and Ko Pipidan. All birds collected and most seen were dark phase. Nests were found on Ko Pipidan.

Egretta alba (LINNÉ)

6 to 8 were seen in Phuket Harbour on November 16th. This appears to be the first record for the West coast of peninsular Thailand.

Goisakius melanolophus (RAFFLES)

1 immature ♂ as skeleton.

Taken in deep forest on Ko Huyong 4.11.63.

Haliastur indus (BODDAERT)

1 in alcohol.

Collected on Ko Pipidan 15.11.63.

Pandion haliaetus (LINNÉ)

Seen on Ko Huyong, Ko Ta Nga and Ko Pipidan. There are no formal records from the West coast of the Peninsula.

Falco peregrinus TUNSTALL

Seen at Phuket 16.11.63. There appears to be no formal record from peninsular Thailand, although there are records from Malaya.

Charadrius alexandrinus LINNÉ

1 ♂ as a skin.

Taken on Ko Huyong 3.11.63. The skin has been entered in the Museum catalogue as *C. a. dealbatus* after comparison with specimens of *C. a. dealbatus* and birds taken in the Gulf of Thailand which have been given the name *C. a. nihonensis* by DEIGNAN (1941). It would thus appear to represent a new subspecies for the Thai list and although the species is known as a visitor to Malaya this extends the known range of the species in Thailand.

Charadrius mongolus PALLAS

2 ♀ as skins, 4 as skeletons and 2 in alcohol.

4 birds were taken in Phuket Harbour and the other 4 on Ko Sindarar Nua. A ♀ from the latter place showed body moult.

Charadrius leschenaultii LESSON

1 ♂ as a skin, 1 ♀ as a skeleton and 2 in alcohol.

Collected from Ko Huyong and Phuket.

Numenius phaeopus (LINNÉ)

Up to 7 seen regularly on Ko Sindarar Nua 5-7.11.63. There are no formal records for the West coast of peninsular Thailand.

Xenus cinereus (GÜLDENSTÄDT)

1 ♀ as a skeleton.

Taken at Phuket 16.11.63. This is the first record from the Changwad though it has been recorded from neighbouring Phang-nga.

Actitis hypoleucos (LINNÉ)

1 ♂ 2 ♀ as skins.

Taken from Ko Sindarar Nua and Ko Ta Nga. The pair from Ko Ta Nga collected on 10.11.63 constitute the first formal records from Changwad Satun and fill a gap in our knowledge of this bird's distribution in Thailand. It occurs widely in Malaya in the winter months.

Arenaria interpres (LINNÉ)

2 seen at Phuket 2.11.63. Previous West coast records come from Satun, further South.

Calidris ruficollis (PALLAS)

1 ♂ as a skin, 2 ♂ as skeletons and 2 birds in alcohol.

All taken in Phuket Harbour on 16.11.63

Calidris ferruginea (PONTOPPIDAN)

1 ♂ as a skeleton, 1 bird in alcohol.

Collected in Phuket Harbour from a large flock 16.11.63. Gill observed "400-500" there on 2.11.63. The species has not been formally recorded from the West coast of peninsular Thailand although it occurs on that coast further South.

Limicola falcinellus (PONTOPPIDAN)

1 ♀ as a skin, 1 ♂ as a skeleton and 1 bird in alcohol.

All collected in Phuket Harbour 16.11.63. The ♀ showed heavy body moult. No formal records exist for peninsular Thailand. The species occurs in winter in Malaya. These specimens were collected from "several dozen" birds.

Esacus magnirostris (VIEILLOT)

1 specimen in alcohol.

Collected on Ko Huyong 3.11.63 from a pair. Also seen on Ko Sindarar Nua. The species has not been formally

recorded from Changwad Pang-nga but is known from Ranong and Satun.

Sterna bergii LICHTENSTEIN

1 ♂ as skeleton.

Taken in Phuket Harbour 2.11.63. The from *S. b. velox* Cretzschmar is reported from Satun, farther South on this coast, but there appears to be no formal record of the species from Changwad Phuket. GILL noted some 25 birds in the harbour on this date.

Ducula aenea (LINNÉ)

1 ♂ as skeleton.

From Ko Sindarar Nua.

Ducula bicolor (SCOPLI)

1 in alcohol.

Collected on Ko Huyong 3.11.63 from a flock of 6-10 birds. GILL also saw this species on Ko Ta Nga on 10.11.63. This bird is listed by DEIGNAN (1963) from islets off the Eastern coast of peninsular Thailand; this appears to be the first formal report from the West coast.

Caloenas nicobarica (LINNÉ)

1 ♂ 1 imm. ♀ as skins.

The male, taken on Ko Huyong on 3.11.63 from a flock of 6 was in mating condition. The immature ♀ was collected on Ko Ta Nga.

Surniculus lugubris (HORSFIELD)

1 ♀ as a skeleton.

From Ko Huyong 4.11.63.

Eudynamys scolopacea (LINNÉ)

1 skin, 1 skeleton and 1 in alcohol–all males.

All from Ko Huyong on 3.11.63.

Alcedo atthis (LINNÉ)

2 skins and 1 in alcohol–all immature females.

Collected on Ko Sindarar Nua and Ko Ta Nga.

Halcyon pileata (BODDAERT)

1 imm. ♀ as a skin, 1 bird in alcohol.

The ♀, from Ko Sindarar Nua, was in moult; the other bird was taken on Ko Similan.

Halcyon chloris (BODDAERT)

4 ♂ 2 ♀ as skins.

From Ko Sindarar Nua and Ko Ta Nga. The birds from Ko Sindarar Nua, a male and a female, showed body moult.

Hirundo tahitica GMELIN

1 ♂ as a skeleton.

From Ko Sindarar Nua.

Dicrurus annectens (HODGSON)

1 imm. ♂ as a skin.

Taken on Ko Huyong 4.11.63.

Monticola solitarius (LINNÉ)

1 ♂ 1 ♀ as skins, 1 in alcohol.

Collected on Ko Pipidan 15.11.63. The bird preserved in alcohol was in male plumage. These birds have been identified by HERBERT G. DEIGNAN as *M. s. affinis* (Blyth).

Phylloscopus borealis (H. BLASIUS)

1 ♂ 1 ? as skins, and 2 as skeletons.

The skins were made of birds collected on Ko Huyong, the skeletons from a bird taken on Ko Similan and a bird found on board at Ko Pipidan.

Acrocephalus arundinaceus (LINNÉ)

1 ♀ as a skin.

This bird was taken in low vegetation at the edge of a swamp on Ko Similan on 8.11.63. This species has been recorded in the province of Ranong to the North and of Phuket to the South; this is the first formal record from Changwad Pang-nga.

Muscicapa latirostris (RAFFLES)

1 ♀ as a skin, 1 bird in alcohol.

The ♀ was collected on Ko Huyong, the other bird on Ko Similan.

Muscicapa tickelliae (BLYTH)

1 ♀ as a skin.

From Ko Ta Nga 10.11.63 in moult.

Anthreptes malacensis (SCOPOLI)

1 imm. ♂ as a skin.

From Ko Sindarar Nua 6.11.63 showing slight moult.

Nectarinia jugularis LINNÉ

1 ♂ 1 ♀ as skins, 1 ♂ in alcohol,

Collected on Ko Sindarar Nua and Ko Similan.

Acknowledgements : My first thanks are due to the collector, FRANK B. GILL, for allowing me to write up this material, to HERBERT G. DEIGNAN who suggested it and to PROF. S. DILLON RIPLEY and Dr. GEORGE WATSON both of the Smithsonian Institution who made it possible.

I should also like to thank GROUP CAPTAIN P. MALLORIE R.A.F. for help with maps. Messrs. GILL, DEIGNAN and WATSON have all been of considerable help in the actual preparation of the text which has been read and criticized by each of them.

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THE GENERAL DISTRIBUTION OF SPECIES OF THE CALANOID COPEPOD FAMILY CANDACIIDAE IN THE INDIAN OCEAN WITH NEW RECORDS

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ABSTRACT

As manifested in the distribution of species of the copepod family Candaciidae, the western Indian Ocean can be divided into three main plankton communities. North of about latitude 20° South, equatorial species predominate. In the extreme western limits, those species are carried southward by the Agulhas Stream.

From latitude 20° South to about 38° South, species characteristic of the southern Central Water are found.

In the Arabian Sea and the Bay of Bengal, neritic or intermediate forms are found. These are apparently associated with the chemical or physical influence of land and the outflow of rivers.

New records include *Candacia samassae* reported for the first time from the Arabian Sea and the Bay of Bengal. This species was originally described from the Red Sea and has not until now been found elsewhere. Another new record is that of *C. guggenheimi* Grice and Jones reported here from the western Indian Ocean and previously known only from the Central Pacific.

THE calanoid copepod family Candaciidae contains 2 genera and 27 described species, according to Grice (1963). With the exception of the extreme polar waters, one or more of the species appear to be endemic to each of the major circulation patterns of the oceans. A few tropical and temperate species usually are found in neritic waters. With such a relatively large number of species so widely distributed, the members of this family appear to have considerable potential value as indicator organisms.

Sewell (1932 and 1947) summarized most of the reports of the occurrences of Candaciidae in the Indian Ocean. Since then Tanaka (1960), Vinogradov and Voronina (1962), Krishnaswamy (1953), and Chiba and Tsuruta (1955) have added to Sewell's records. Vinogradov and Voronina (1962) presented a map of the distribution of *Paracandacia bispinosa* (Claus), and their data were incorporated into the general distribution map of that species in this report.

The purpose of this paper is to present, in a very preliminary manner, the general distribution of several species of the family Candaciidae in the Indian Ocean. The results are based, for the most part, on samples collected during cruises 1 and 2 of the *ANTON BRUUN*.[1] In addition, two new records from the Indian Ocean are presented. In a later publication, more quantitative data will be included. Furthermore, a study also will be made of the changes in the distribution of species with those in the environment. The following are the results of this preliminary study.

Candacia samassae Pesta

New record for the Indian Ocean. The only previous record of this species known to me is he original description (Pesta, 1941) in which the female was found in the Red Sea. In the present

[1] The operation of the *ANTON BRUUN* was supported by the National Science Foundation as a part of the U.S. Program in Biology, International Indian Ocean Expedition.

study, both sexes of *C. samassae* were found in abundance in the zooplankton hauls made in the Bay of Bengal (*ANTON BRUUN* Cruise 1) and the Arabian Sea (*ANTON BRUUN* Cruise 2). The general distribution of this species is given in Fig. 1. In the Arabian Sea, *C. samassae* appeared most frequently in the day hauls made between the depths of 125 and 250 meters, while in the Bay of Bengal this species was collected in the nets towed obliquely from the surface to 100 or 200 meters. None was found in the night surface samples.

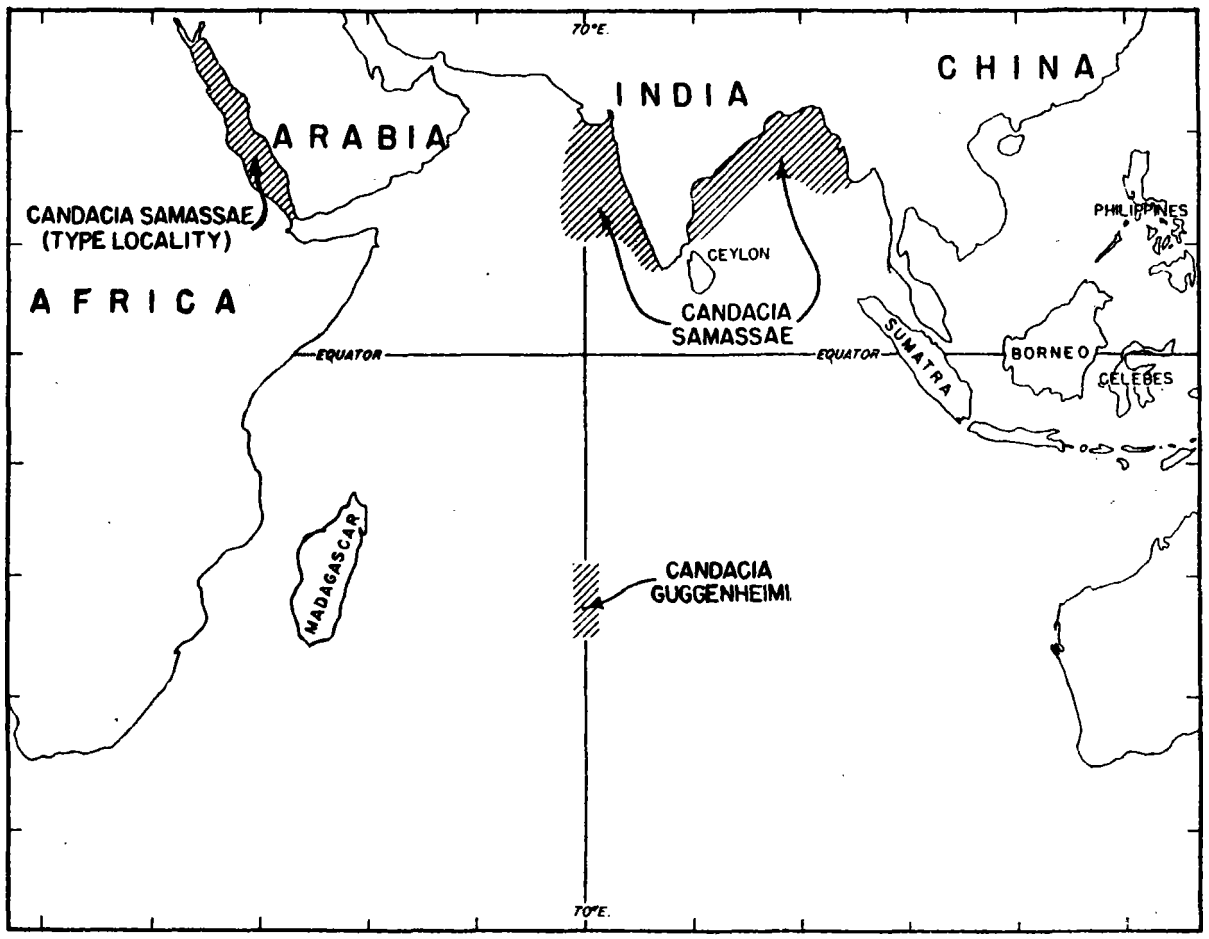

FIG. 1. New records of Candaciidae from the Indian Ocean.

Considering the thorough sampling in those waters as reported by Sewell (1932 and 1947), his failure to find this species presents somewhat of a mystery. The sampling pattern of the two *ANTON BRUUN* cruises did not permit a conclusion regarding the degree of contiguity of the distribution of *C. samassae* from the Red Sea to the Bay of Bengal, but the observed distribution does suggest exchange among those bodies of water.

Candacia guggenheimi Grice and Jones

New record for the Indian Ocean. This species has been reported only from the area of its original discovery in the central North Pacific between the Equator and latitude 35° N. (Grice and

Jones, 1960). In the *ANTON BRUUN* samples, *C. guggenheimi* was collected in small numbers along longitude 70° E., between latitudes 19° and 26° S. (Fig. 1). For the most part, it was found between 125 and 250 metre depths and only in day hauls. It was not found in any of the night surface hauls.

Candacia norvegica (Boeck)

Second record from the Indian Ocean. This species was first described from specimens collected off the Norwegian coast; since then it has been reported as being prevalent in the cold, North

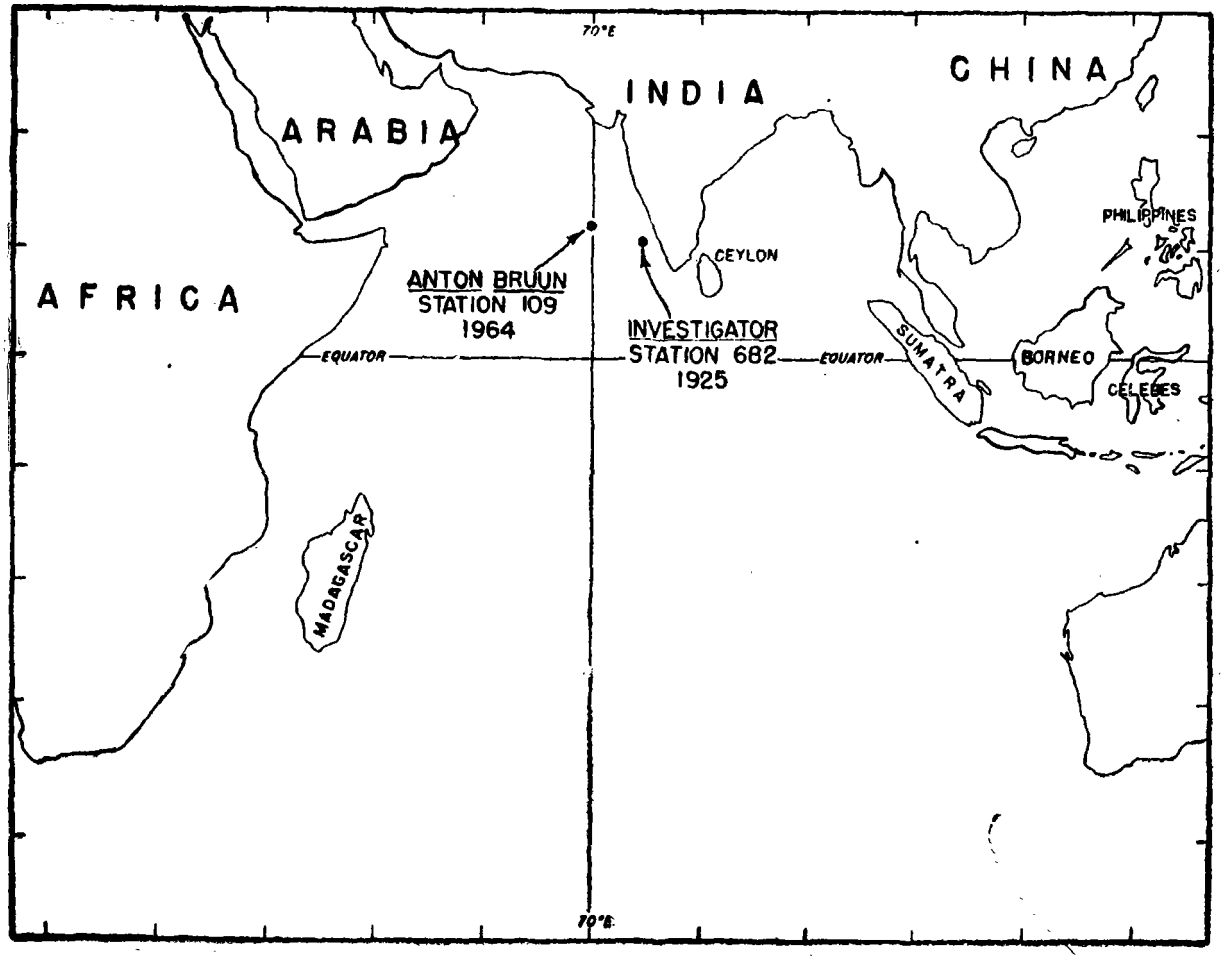

FIG. 2. Records of *Candacia norveica* (Bloeck) from the Indian Ocean

Atlantic. Grice (1963) reported *C. norvegica* as occurring in the area of the Benguela Current off the west coast of southern Africa between latitudes 8° and 15° S. Wilson (1942 and 1950) recorded it from many stations in the tropical and temperate Pacific. Fleminger and Bowman (1956), however, believed that all of Wilson's records of the species were in error. Tanaka (1953) included *C. norvegica* in his list of copepods from the Izu region off Japan and Grice and Jones (1960) reported it as from the central North Pacific. Sewell (1932) described a variety *tropica* from *Investigator* station 682, collected in April 1925 at latitude 10° 26′ N., longitude 74° 32′ E., in the Arabian Sea from a haul made from the surface to 700 fathoms. In this sample he found two females.

Thirty-eight years later, one female was found in a sample collected during cruise 2 of the *ANTON BRUUN* at station 109, latitude 11° 59′ N., longitude 69° 55′ E., less than 300 miles from Sewell's locality (Fig. 2). The terminal spines of the fifth feet of the *ANTON BRUUN* specimen are unequal with the outer spine being longer. In this respect it differs from Sewell's *tropica* and agrees with Pacific and Atlantic specimens as reported by Grice and Jones (1960). This suggests that *tropica* is not a valid variety, but only a manifestation of morphological variation within the species.

Candacia longimana (Claus)

Grice (1963) reported this species as being present in the Indian Ocean only north of latitude 20° S. However, in samples collected along longitude 70° E. during cruise 2 of the *ANTON BRUUN*, *C. longimana* was found, for the most part, south of that position. *C. longimana* was present in one night surface haul and in six night oblique hauls made to the top of the thermocline. This species was absent from all of the day hauls collected on the same dates and at nearby locations (Fig. 3).

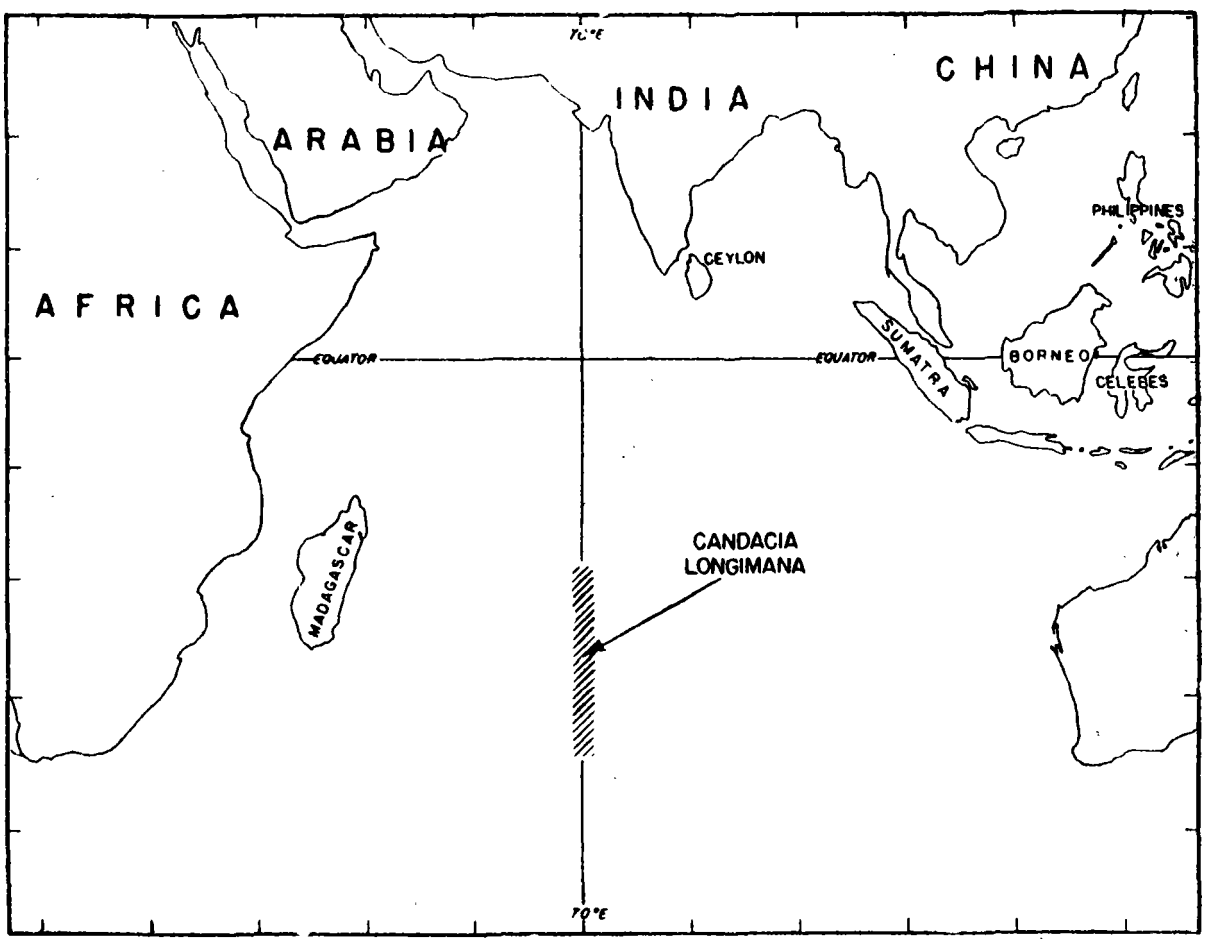

FIG. 3. Location of *Anton Bruun* cruise 2 records of *Candacia longimana* (Claus) in the Indian Ocean.

These day hauls were made with closing nets down to 2,000 meters. It is difficult to explain the circumstances which resulted in such observed distribution. Diel movement does not appear to be as plausible an explanation as does net dodging.

Candacia pachydactyla (Dana), *C. catula* (Giesbrecht) and *Paracandacia truncata* (Dana)

These three species inhabit equatorial waters in the Indian Ocean, for the most part, north of latitude 20° S. (Fig. 4). In *ANTON BRUUN* samples, they usually were found in the upper 250 metres of water and were most abundant in night surface samples. In the extreme western regions of the Indian Ocean, they are carried southward by the Agulhas Stream to the southern extreme of Africa, but apparently do not enter the Atlantic. They were not found in southern central waters of the Indian Ocean nor in the coastal neritic waters of the Arabian Sea and the Bay of Bengal.

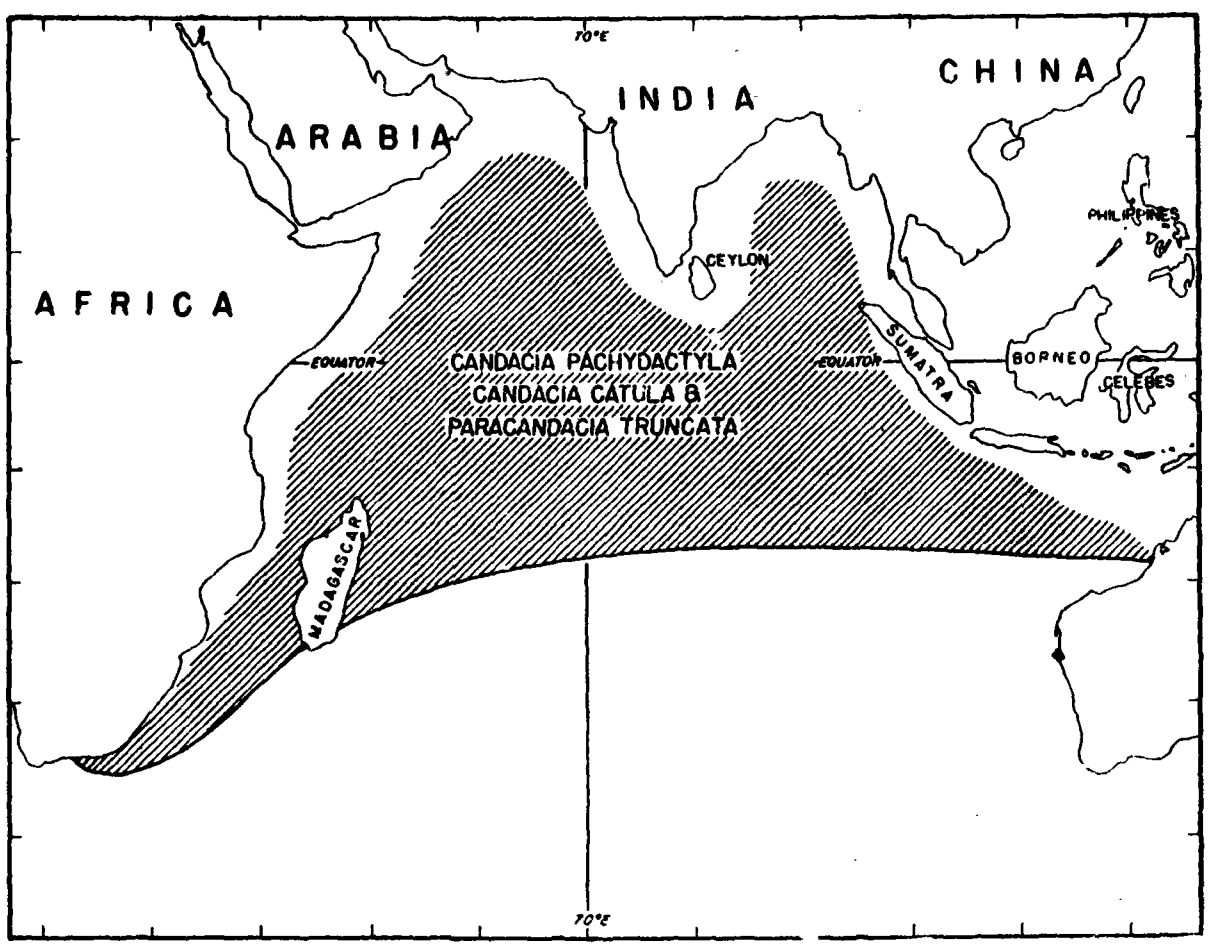

FIG. 4. General distribution of equatorial species of Candaciidae in the Indian Ocean.

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Candacia ethiopica (Dana) and *Paracandacia bispinosa* (Claus)

These two species are most abundant in the southern central waters of the Indian Ocean, but they also occur in smaller numbers in equatorial waters. In samples collected during cruise 2 of the *ANTON BRUUN*, these species were most abundant between latitudes 20° and 30° S. (Fig. 5). *C. ethiopica* appeared in small numbers as far south as lattitude 38° S. where its limits coincided with the surface isotherm of 15° C.

In addition to the species discussed, the following species were collected in such small numbers that their distribution patterns cannot yet be determined: *C. varicans* (Giesbrecht), *C. bipinatta* (Giesbrecht), *C. tenuimana* (Giesbrecht), *C. curta* (Giesbrecht). Two of these, *C. bradyi* and *C. discaudata*, were found most often in neritic waters and may be considered indicators of such waters.

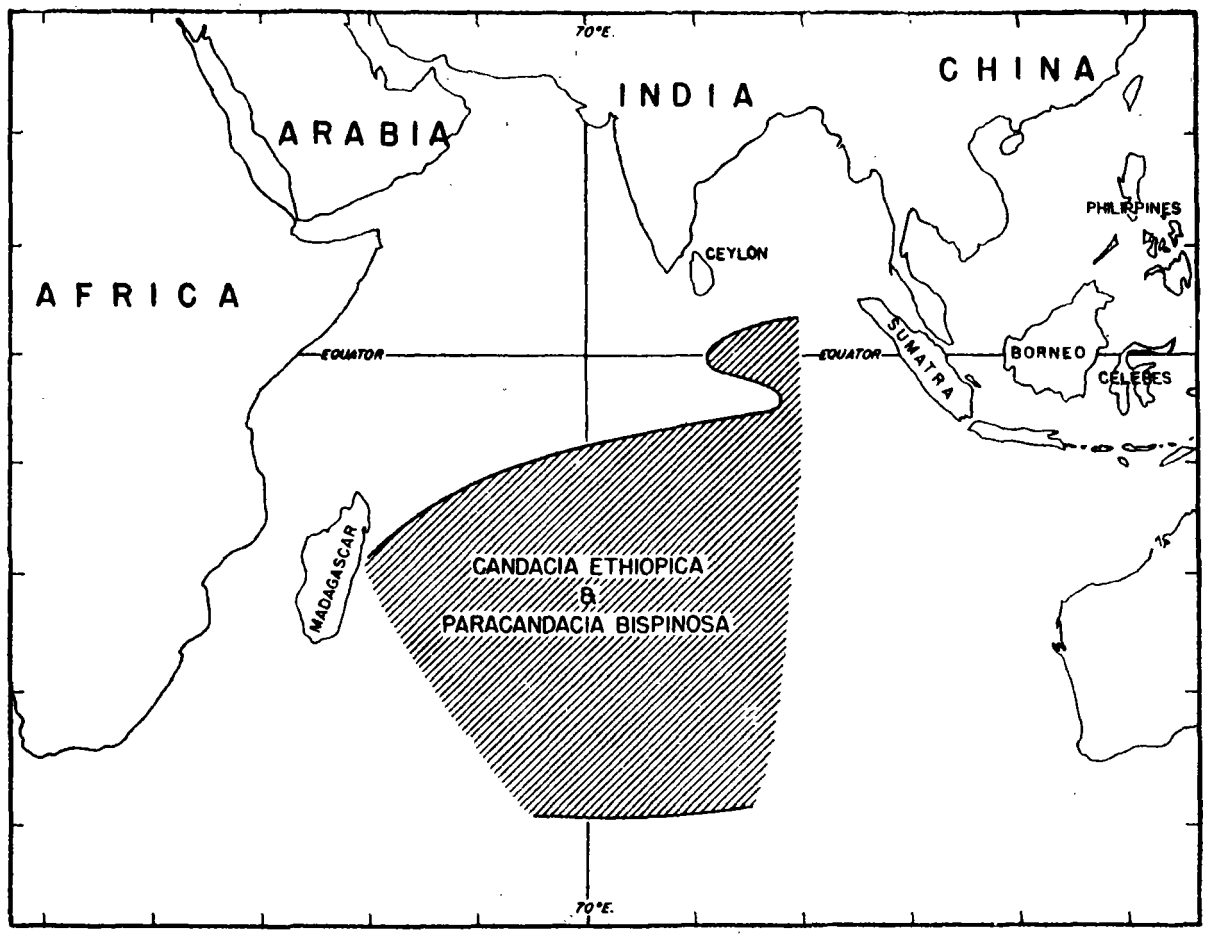

FIG. 5. General distribution of *Candacia] ethiopica* (Dana) and *Paracandaeia bispinosa* (Claus) in the Indian Ocean.

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EVIDENCE OF ISOLATION BETWEEN POPULATIONS OF *CANDACIA PACHYDACTYLA* (DANA) (COPEPODA: CALANOIDA) IN THE ATLANTIC AND THE INDO-PACIFIC OCEANS

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ABSTRACT

Atlantic and Indo-Pacific samples of *Candacia pachydactyla*, a calanoid copepod inhabiting equatorial waters, were examined for differences in morphological characteristics. Such differences were found between samples from the two oceans and are believed to be evidence of genetic isolation of two populations.

Distribution data indicated that the Indo-Pacific population is not carried around the tip of Southern Africa into the Atlantic by the Agulhas Stream. About 2000 miles of water appeared to separate the two populations.

SEWELL (1948) summarized the investigations on the effect of the southern portion of the continent of Africa as a barrier to the mixing of warm water Atlantic and Indo-Pacific pelagic copepods. Two questions seemed to have been considered: (1) Does warm, tropical water from the Agulhas Stream of the south-western Indian Ocean enter the Atlantic after rounding the Cape of Good Hope, and (2) if this takes place, do the tropical copepods from the Indian Ocean survive and enter the gene pool of their Atlantic counterparts? Sewell listed 138 species of warm water copepods he considered to be "Indo-Pacific species", which also are found in the Atlantic: from this he concluded that the African continent does not form an effective barrier to the mixing of populations of the two oceans.

Steuer (1928) concluded it is likely that Africa forms an effective barrier most of the time but occasionally, under certain circumstances, this barrier is broken down. He believed that Indian Ocean populations carried to the Atlantic generally did not survive there. DeDecker (1964) stated that Indo-Pacific copepods carried by the Agulhas Stream disappeared over the Agulhas Bank and were seldom if ever carried further west.

The problem originally was defined because the passage of Agulhas water represents the only possible source of mixing of warm water populations of animals from the two oceans. The probability of such mixing increases with the length of time and the number of species considered. That is, if given sufficient time and if all existing warm water species and fluctuating marginal conditions are considered, mixing between the Atlantic and Indo-Pacific populations is virtually certain to occur at some time at least among some of the species. Because the frequency of such occurrences is not known, it appears to be inappropriate to reach general conclusions which imply that warm water species are never transported around the Cape, or that the Cape does not, in any sense, form a barrier to such transport. Such general conclusions cannot gain merit until the frequency of mixing can be estimated from the analysis of large amounts of data on the distribution of restricted and *well-defined* taxons within the areas under consideration.

This investigation was narrowed to concern a single species inhabiting the equatorial waters of both oceans rather than the broader "warm waters" which include the central water masses of middle latitudes. Because the southern central water masses of the two oceans are separated by less distance than are the equatorial waters, and because the range of environmental conditions of

the former are greater, the frequency of mixing between central water mass populations would appear to be greater than between equatorial populations. The results of a study of the distribution of *Candacia pachydactyla* (Dana) are presented along with evidence of morphological differences between the Atlantic and the Indo-Pacific populations. The presence of such morphological differences suggests a high degree of isolation between those populations.

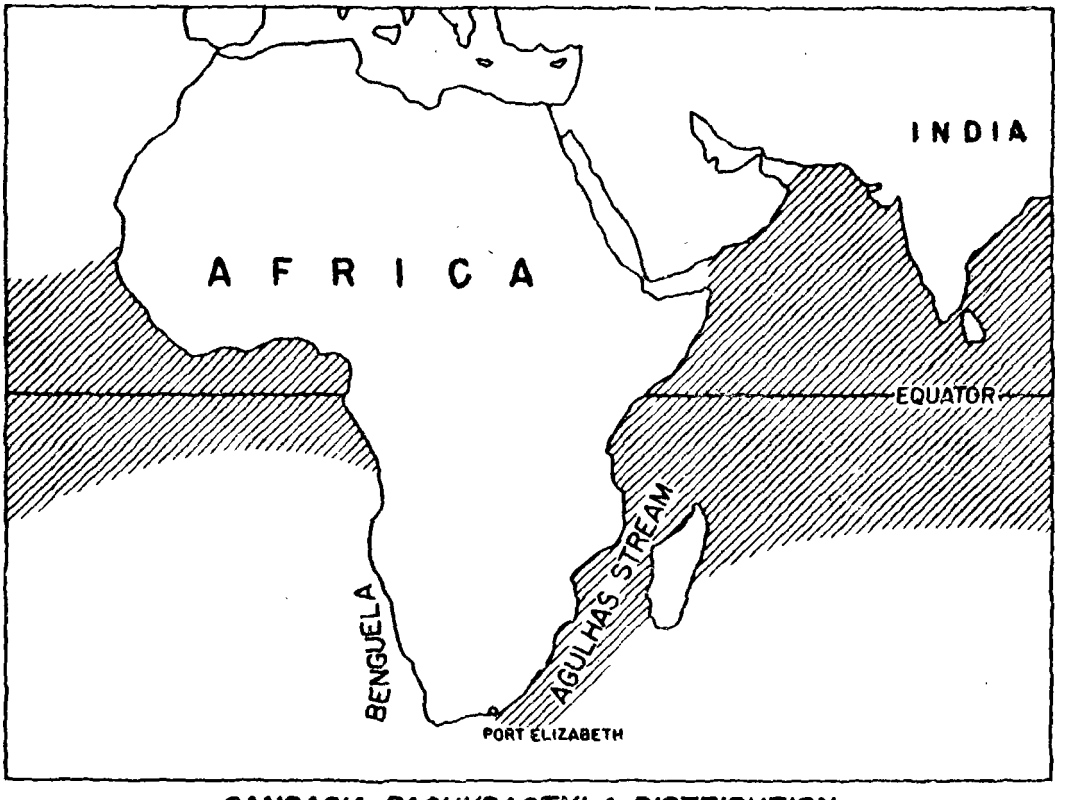

FIG. 1. The general distribution of *Candacia pachydactyla* (hatched area).

A series of plankton samples collected on cruises of the *R. V. Vema* of the Lamont Geological Observatory of Columbia University was examined for the presence of *C. pachydactyla*. This series was collected from stations along the eastern coast of Africa from the Arabian Sea to the Cape of Good Hope, around the Cape, through the area of the Benguela Current and into equatorial waters just south of the Gulf of Guinea. Additional samples from the Gulf of Guinea were made available by the Bureau of Commercial Fisheries Biological Laboratory in Washington, D.C. From this material, it was determined that *C. pachydactyla* was carried by the Agulhas Stream southward and eastward to a point just offshore from Port Elizabeth, South Africa. This species was not encountered in the Atlantic samples south of latitude 8° S. in the vicinity of longitude 10° E. Thus, the Atlantic and Indo-Pacific populations were separed by about 2,000 miles of ocean which included the cold Benguela Current. Unpublished data from the *Vema* cruises indicated that during the period of sampling, this cold, neritic, coastal water extended at least 300 miles off shore from south-west Africa. The Benguela Current therefore appears to constitute an additional barrier to Indo-Pacific individuals mixng with their counterparts in the Atlantic.

Figure 1, based on the samples described and also upon published records, presents the general distribution of *C. pachydactyla* in the areas under consideration.

Samples of *C. pachydactyla*, both males and females, from the central equatorial Pacific Ocean, the Indian Ocean, the Gulf of Guinea in the eastern Atlantic Ocean, and the Straits of Florida in the western Atlantic Ocean were examined in detail for morphological differences among or between populations.

No consistent differences were found between samples from the Indian Ocean and the central Pacific; likewise, none were found between the two Atlantic samples. However, the following differences between Atlantic and Indo-Pacific populations were consistent:

(1) In the females from the Atlantic, a low rounded process is sometimes present between the middle and internal terminal spines of the fifth feet; when present, however, this is never strong or pointed (Fig. 2 *a*). In the Indo-Pacific females, this process is prominent and often pointed (Fig. 2 *b*).

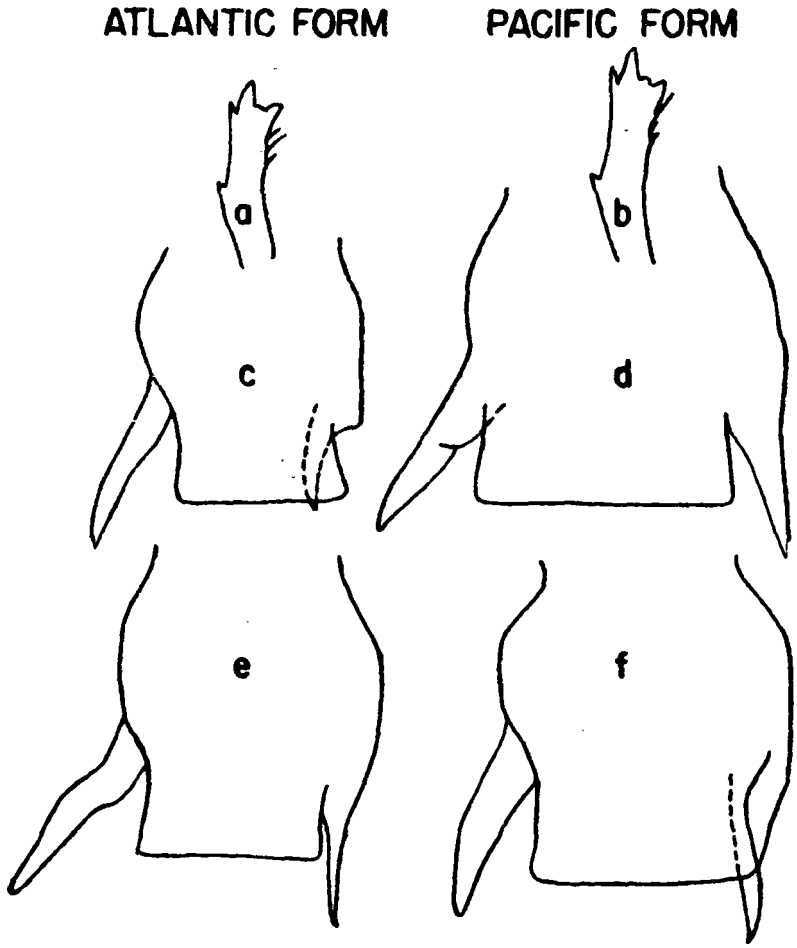

FIG. 2. (*a*) Female fifth foot, Atlantic form; (*b*) female fifth foot, Pacific form; (*c*) female genital segment, Atlantic form; (*d*) female genital segment, Pacific form; (*e* and *f*) female genital segments showing intermediate forms of right spine.

(2) In the Atlantic females, the caudally directed spine on the right margin of the genital segment (in dorsal view) usually points slightly mediad and is usually partially hidden from view (Fig. 2 *c*). The external margin of this spine is usually concave. In most Indo-Pacific females, the right spine points straight caudad or slightly laterad and the tip is not usually hidden in dorsal view (Fig. 2 *d*). Extremes of these two forms appear to be peculiar to the Atlantic or the Indo-Pacific, but intermediacy occurs (Figs. 2 *e,f*) so that this characteristic is not, by itself, enough to distinguish the two populations.

(3) In the males from the Atlantic samples, the posterior margin of the dextral genital process is indented or concave (Fig. 3 *a*). In the Indo-Pacific males, that margin is straight or slightly convex (Fig. 3 *b*).

(4) In all males of this species, the elongated process on the right corner of the fifth thoracic segment has, when viewed laterally, the superficial form of a foot with a pointed "toe" and a smaller "heel". In the Atlantic males, the "heel" is weak or nearly absent and slightly rounded (Fig. 3 *c*). In the Indo-Pacific specimens, the "heel" is stronger, pointed and there is a definite indentation in the "arch" of the "foot" (Fig. 3 *d*).

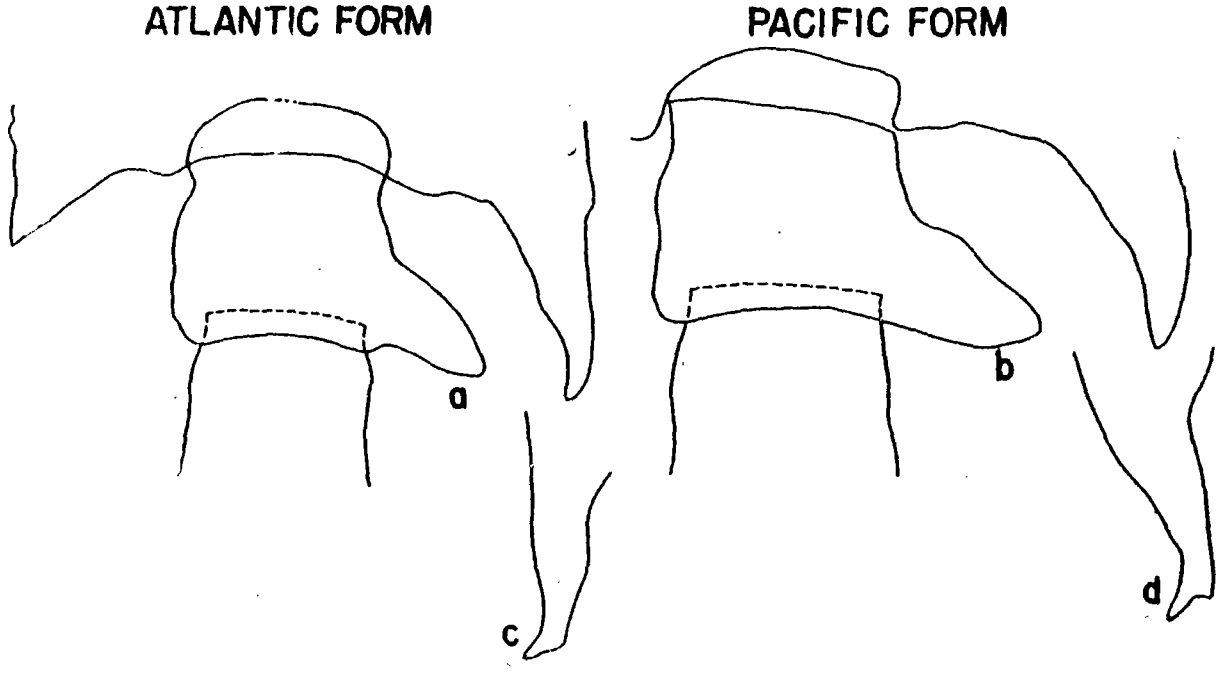

FIG. 3. (*a*) Male genital segment, Atlantic form; (*b*) male genital segment, Pacific form; (*c*) male thoracic process, lateral view, Atlantic form; (*d*) male thoracic process, lateral view, Pacific form.

Other parts of the appendages and body of many individuals from both oceans were examined for differences and while some were found, none appeared to be constant enough to be useful as distinguishing marks.

As a test of the integrity and objectivity of the observed differences, 20 specimens, drawn at random from the two Indo-Pacific and the two Atlantic samples and stained to remove possible color differences, were presented to the author. These were examined and on the basis of the criteria described above, the author was able to correctly relate 19 out of 20 to the proper ocean. He was unable, however, to consistently disinguish beween the two Atlantic samples or the two Indo-

Pacific samples. No elaboration or statistical tests seemed necessary to support this 95 per cent. success in separation.

The conclusion that populations of *C. pachydactyla* in the Atlantic and the Indo-Pacific are separated by the barrier of southern Africa and by associated oceanographic conditions is supported by distribution records of certain other species within the family Candaciidae. Two other Pacific equatorial species, *C. catula* (Giesbrecht) and *Paracandacia truncata* (Dana), are not found in the Atlantic (Grice, 1963). Except for the Atlantic form of *C. pachydactyla*, the Atlantic Ocean appears not to contain any species peculiar to equatorial waters.

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RECHERCHE DU PETREL DE BARAU, *PTERODROMA BARAUI*

par Christian JOUANIN et Frank B. GILL

La découverte en avril 1963 d'un Pétrel nouveau de la Réunion a marqué le début de l'année internationale de l'océan Indien d'un événement surprenant et bien fait pour justifier la reprise de l'exploration ornithologique dans une région du monde que l'on aurait pu croire mieux connue à cet égard. Déjà cependant la mise en évidence, en 1948 seulement, sur un îlot voisin de Maurice, d'une colonie de *Pterodroma arminjoniana* (Giglioli et Salvadori), espèce jusqu'alors insoupçonnée dans l'océan Indien, donnait à penser qu'il pouvait subsister d'importantes lacunes dans notre connaissance de l'avifaune des Mascareignes.

Comment un oiseau de la taille de *Pterodroma baraui* (1) a-t-il

(1) Cet oiseau a été décrit sous le nom de genre *Bulweria*. Rappelons ici que G. M. MATHEWS, en 1948, avait proposé de réunir en un seul les deux genres *Pterodroma* (qui comprend une quarantaine d'espèces) et *Bulweria* (monospécifique à l'époque), qui se trouve avoir la priorité. J'étais parvenu à la même conclusion à la suite de la découverte de *Bulweria fallax* (JOUANIN, 1955), espèce étroitement apparentée à *B. bulweri* (Jardine et Selby) au point que divers auteurs le tiennent pour une forme géographique de celui-ci, et dont cependant plusieurs exemplaires depuis longtemps déposés dans divers musées d'Europe avaient jusqu'alors été confondus avec un *Pterodroma* typique, *Pt. aterrima* Bonaparte. C'est assez dire que la distinction générique ne sautait pas aux yeux. En fait pour l'ornithologiste de musée, examinant des peaux, le seul caractère diagnostique entre les deux genres présumés paraissait être la queue cunéiforme, allongée des *Bulweria* proprement dits, mais ce caractère est partagé par un *Pterodroma* indiscutable, *Pt. hypoleuca* (Salvin).

Des faits nouveaux m'ont amené à réviser ma position. Je ne citerai que pour mémoire l'expérience récemment acquise *in natura* que *Bulweria bulweri* d'une part, *Pterodroma arminjoniana* et *baraui* d'autre part ont une allure de vol et des vocalisations bien différentes, car ces exemples sont peut-être insuffisants pour généraliser. Plus déterminante est l'acquisition par le British Museum d'un spécimen en chair de *B. fallax* dont l'étude anatomique a révélé de sensibles différences de structure avec les *Pterodroma*. C'est pourquoi je me suis associé à la rédaction de l'article publié récemment par ALEXANDER, BOURNE *et al.* en vue de stabiliser la nomenclature des Procellariidés et en particulier de maintenir le genre *Pterodroma*. — Christian JOUANIN.

PLANCHE I.

A gauche : *Pterodroma baraui*, pattern du dessous de l'aile.

A droite : *Pterodroma baraui*, palmures étalées montrant la coloration bicolore des pattes. (*Photos R. W. Storer*).

pu passer inaperçu des hommes de science qui ont travaillé dans une île occupée depuis trois siècles et densément peuplée ? S'agissant d'un représentant du groupe des Pétrels, qui ont pour la plupart des mœurs nocturnes, hypogées, et choisissent souvent pour nicher de hautes altitudes, le fait s'avère plus explicable. Nous sommes convaincus que dans le vaste domaine indopacifique, dont beaucoup d'îles ne sont fréquentées que dans les zones littorales basses, des recherches minutieuses offriraient d'autres exemples comparables, soit découvertes de formes inédites, soit redécouvertes de formes qui passent pour disparues ou qui ne sont connues que par un tout petit nombre de spécimens (cf. BOURNE, 1965). A preuve que dans le monde atlantique pourtant infiniment mieux prospecté, des faits semblables se sont produits : redécouverte aux Bermudes en 1951 de *Pterodroma cahow* (Nichols et Mowbray) (MURPHY et MOWBRAY, 1951) et en 1963 à Haïti de *Pt. hasitata* (Kuhl) (WINGATE, 1964), deux espèces qui, pendant un temps, avaient été considérées comme éteintes. C'est précisément à la découverte d'un Pétrel inédit apparenté aux deux formes que nous venons de citer, qu'aboutissaient les tentatives faites, sur les suggestions de l'un de nous, par Armand BARAU, Conseiller général de la Réunion, Correspondant du Muséum de Paris, pour redécouvrir le Pétrel noir de Bourbon, *Pterodroma aterrima* Bonaparte, dont on est sans nouvelles depuis le siècle dernier.

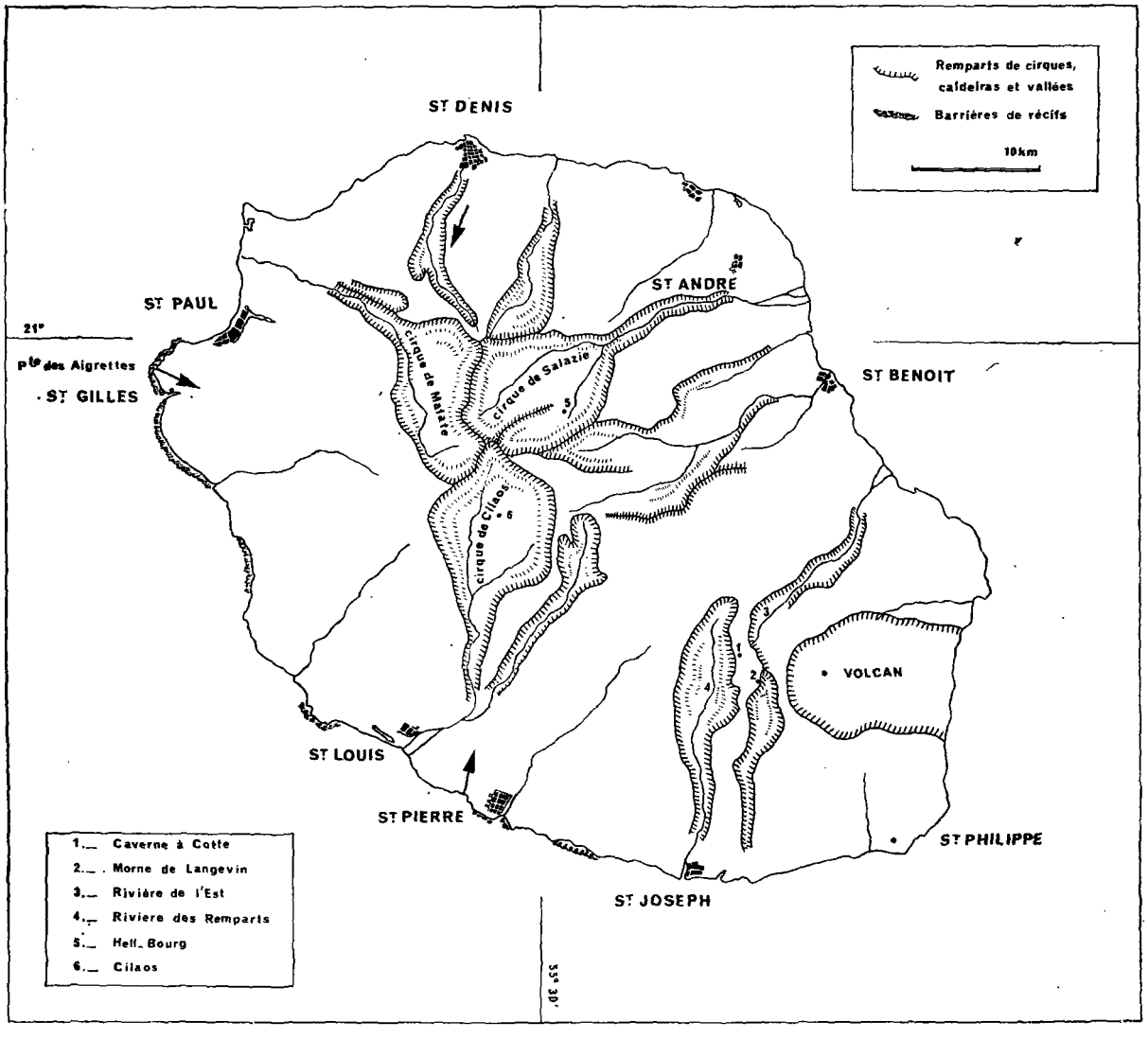
Lorsque JOUANIN (1964) a décrit *Pt. baraui*, il n'en connaissait que deux spécimens : le type, capturé vivant sur une plage de Saint-Denis, en avril 1963, et un vieux spécimen monté, conservé au Muséum d'Histoire Naturelle de Saint-Denis, sous l'appellation trompeuse de *Pt. cooki*, sans référence de date.

Mais à la fin de l'année 1964, nous avons eu l'un et l'autre la possibilité de nous rendre à la Réunion et d'y rechercher le Pétrel de Barau. Nos efforts ont été récompensés par de nombreuses observations et par la capture d'une dizaine d'autres exemplaires. Nous faisons ici le point de nos connaissances sur cette espèce restée ignorée de la science jusqu'en 1963 et pourtant suffisamment commune en certains points de l'île pour y avoir reçu un nom local, celui de Taille-vent.

HISTORIQUE

Le nom local de Taille-vent, que nous venons de citer, a déjà été mentionné dans la littérature. Il apparaît dans l'ouvrage que BORY DE SAINT-VINCENT a consacré à son séjour à la Réunion, au cours du chapitre où il retrace son excursion à la plaine des

Sables par la plaine des Cafres. La nuit du 27/28 brumaire an X (18/19 novembre 1801), il bivouaqua à la caverne à Cotte (cf. carte 1) qu'il décrit en ces termes (2 : 411 *et seq.*) :



Carte 1. — L'île de la Réunion.

N. B. Les flèches indiquent la direction du vol des *Pterodroma baraui* que nous avons observés gagnant l'intérieur de l'île.

« *La caverne où nous nous arrêtâmes, se nomme caverne à* Cotte, *d'un fameux marron* (1) *qui y fut tué. Elle est située dans une cassure, à la cime de ce qu'on nomme le* morne de Langevin, *et dont nous avons déjà parlé quand nous nous arrêtâmes sur le*

(1) Les marrons étaient les esclaves noirs en fuite.

piton de la rivière des Remparts. A quelques pas de la caverne on distingue ce piton ; l'horizon n'a plus de limites ; le quartier sauvage de Saint-Joseph présente à la gauche ses laves et ses forêts ; Saint-Pierre disparaît vers la droite ; deux affreux torrens (1), *dont on ne voit que la cime des parois, fuient vers la mer : ces torrens sont celui de Langevin et la rivière des Remparts, que nous allons abandonner.*

« *Une petite ravine, dans les trous de laquelle on trouve toujours de l'eau, indique le lieu où l'on doit chercher le gîte. Ce gîte est situé sur le côté d'un creux, qui peut avoir vingt-cinq pieds d'évasement, et duquel commence l'escarpement du morne de Langevin. La proximité de l'eau et des* ambavilles (2) *à brûler, en feraient une retraite excellente, si la grotte était moins basse, plus spacieuse, et si dans les longues pluies, les substances poreuses et scorieuses, dans lesquelles elle est creusée, ne laissaient filtrer l'eau de toutes parts.*

« *Tous les environs de la grotte étaient remplis de têtes d'oiseaux de mer, du genre des* pétrels. *Les tas assez considérables de ces débris sans corps, ayant attiré mon attention, j'appris que c'étaient des têtes de* fouquet. *Le* fouquet *me paraît être le même oiseau dont Labat* (3) *a tant parlé, et que de son tems* (1) *on nommait diablotins, dans les Antilles. Ne m'étant pas trouvé dans la saison où l'on prend les* fouquets, *je me bornerai à en rapporter ce qu'on m'en a dit.*

« *Dans le printems* (1), *un oiseau des côtes, brun, fort ressemblant au* goëland, *et qu'on nomme* taille-vent, *abandonne les rivages, et vient faire ses œufs dans ces lieux escarpés, que la nature semble avoir voulu rendre inaccessibles : c'est dans le tems du solstice que les petits* taille-vents *ont acquis une certaine grosseur et cette graisse excessive qui les fait rechercher ; alors*

(1) Nous respectons l'orthographe originale du texte de Bory.

(2) Bory de Saint-Vincent (1804, 1 : 335), bien que parfaitement averti de l'hétérogénéité botanique incluse dans le terme, a adopté dans son ouvrage la dénomination d'ambaville pour désigner collectivement tous les arbustes à port éricoïde qui peuplent les hautes altitudes de la Réunion. *Sensu stricto* le terme d'ambaville ne s'applique qu'aux diverses formes de l'une des plantes caractéristiques de cette zone de végétation, *Senecio Hubertia*. D'après Rivals (1952 : 95) on l'applique encore par extension à d'autres végétaux, en particulier à une Rhamnacée, *Phylica leucocephala*. Mais les Ericacées du genre *Philippia*, qui couvrent de grandes étendues, sont appelées brandes, un nom vernaculaire que Bory ne semble pas avoir connu. Ces *Philippia*, grâce à une huile essentielle de leurs feuilles, sont très faciles à enflammer, malgré la pluie et l'humidité qui règnent si souvent dans les hauts.

(3) Bory fait ici référence au récit publié par le Père Labat (1724, 1 : 209) de la chasse aux jeunes *Pterodroma hasitata* sur les pentes de la Soufrière à la Guadeloupe à la fin du XVII[e] siècle.

les créoles vont à leur recherche, et tout ce qu'ils en trouvent, est préparé dans du sel qu'ils portent avec eux. Ces oiseaux, ainsi salés, se conservent quelque tems, et prennent à-peu-près le goût des vieux harengs-saurs ; *leur graisse est onctueuse ; elle a assez l'odeur d'huile de poisson, ainsi que celle de tous les oiseaux de mer. Le morne de Langevin, le volcan, les hauts de la rivière de l'Est et les Salazes sont les lieux où les* fouquets *se trouvent le plus fréquemment* ».

Le texte de BORY DE ST-VINCENT appelle plusieurs remarques. Tout d'abord le terme de Taille-vent y est mêlé à celui de Fouquet de telle sorte qu'il est difficile à la première lecture de saisir s'ils sont synonymes ou, dans le cas contraire, ce qui se rapporte à l'un ou à l'autre. Fouquet est dans le langage créole actuel une désignation assez vague qui s'applique, indistinctement, nous a-t-il semblé, à tous les Procellariens. Mais BORY assimile le Fouquet dont il fait mention, au Diablotin des Antilles : l'assertion prend toute sa valeur quand on sait quelle étroite parenté existe entre *Pt. baraui* et *Pt. hasitata.* On peut très raisonnablement tenir celui-là pour une sous-espèce de celui-ci (cf. JOUANIN, 1964 b et ci-dessous). La comparaison du Taille-vent au Goéland n'est pas dépourvue non plus de valeur descriptive : avec son manteau gris et ses parties inférieures blanches, *Pt. baraui* présente bien en effet la pattern d'un Goéland. La comparaison s'applique en tous cas indiscutablement mieux à *Pt. baraui* qu'à l'une quelconque des trois autres espèces de Procellariens qui peuplent ou ont peuplé la Réunion.

En revanche, d'autres points du texte de BORY ne conviennent pas au Pétrel de Barau. Quiconque en a vu des exemplaires — mais ce n'était peut-être pas le cas de BORY, malgré son observation de la nuit du 29/30 brumaire an X (20/21 novembre 1801) (cf. ci-dessous) — ne saurait le décrire comme un oiseau « brun ». Autre contradiction : BORY signale qu'il pond au printemps, ce qui est vrai tant du Pétrel de Barau que du Puffin du Pacifique, *Puffinus pacificus* (Gmelin), et du Puffin de Baillon, *Puffinus lherminieri bailloni* (Bonaparte), mais que les jeunes ont atteint leur poids maximum « dans le temps du solstice ». Duquel solstice s'agit-il ? Du solstice d'été, 22 décembre, dont la visite de BORY n'était guère éloignée, ou du solstice d'hiver, 22 juin ? Dans les deux cas, il ne peut s'agir du Pétrel de Barau qui pond certes au printemps (fin novembre-début décembre, cf. ci-dessous), mais dont les jeunes s'envolent à la fin d'avril : c'est donc en fait dans les jours qui suivent l'équinoxe d'automne (21 mars) que les poussins atteignent leur engraissement maximum. Tout porte à croire

que BORY a ici mêlé des informations se rapportant à deux espèces distinctes : l'une appelée Fouquet, dont le plumage est brun (peut-être le mystérieux Pétrel noir de Bourbon, *Pterodroma aterrima,* qui n'a pas été signalé depuis 1890 ; peut-être aussi le Puffin du Pacifique, *Puffinus pacificus,* mais la date indiquée pour la collecte des jeunes ne convient pas plus à ce dernier qu'au Pétrel de Barau), l'autre appelée Taille-vent, dont la pattern est voisine de celle des Goélands.

La confusion n'enlève rien à l'exactitude de la relation de BORY quant aux déchets de cuisine dont il vit encombrés les environs de la caverne à Cotte. Que son texte fasse, à cet égard tout au moins, allusion à *Pt. baraui,* on en trouve une confirmation indiscutable dans la nature des restes osseux qui existent encore de nos jours dans le sol de la caverne.

163 ans après BORY DE SAINT-VINCENT, notre curiosité ayant été éveillée par son récit, nous nous sommes rendus à la caverne à Cotte que nous avons trouvée parfaitement conforme à la description de BORY. Moins basse et moins humide, elle ferait une excellente retraite. Les « ambavilles » du voisinage nous servirent à faire un grand feu au bord de l'escarpement qui domine la rivière des Remparts, mais sans attirer aucun Pétrel bien que le temps fût couvert et qu'il plût, circonstances favorables selon WINGATE (1964 : 154). Mais nous eûmes la satisfaction de trouver dans l'horizon superficiel du sol des deux cavernes à Cotte — car à une dizaine de mètres de la caverne principale, il en existe une seconde beaucoup plus basse encore et plus exiguë que la première — les restes osseux dont parle BORY : débris crâniens, tarses, os longs des ailes.

La composition du lot d'ossements que nous avons recueilli, paraît homogène et ne comprendre qu'une seule espèce. Pour les déterminer, nous avons comparé ces restes osseux au squelette conservé de l'un de nos exemplaires de *Pt. baraui* et aux radiographies des spécimens naturalisés de *Pt. aterrima* du Muséum de Paris. Les épiphyses des os longs sont malheureusement très altérées de sorte qu'on ne saurait en prendre de mesures précises, sauf en ce qui concerne trois tarses, en bon état (36,5 ; 37 ; 37,6 mm) dont la longueur peut convenir tout aussi bien à *Pt. aterrima* (longueur du tarse : 36-39 mm, cf. JOUANIN, 1955 : 160) qu'à *Pt. baraui* (longueur du tarse : 36-41, cf. ci-dessous). Mais les os longs des ailes, même avec leurs épiphyses abîmées, paraissent plus longs que ceux d'*aterrima.* Les crânes présentent les caractères des *Pterodroma* avec l'apophyse antorbitaire des lacrymaux très élargie en aile. L'un d'entre eux, bien conservé, peut être

mesuré : longueur totale du supraoccipital à l'extrémité des prémaxillaires : 81,4. Par ses caractères comme par ses dimensions, il s'accorde parfaitement au crâne de notre squelette de *Pt. baraui* (longueur totale : 79,3) alors qu'il est beaucoup trop grand pour être attribué à *Pt. aterrima* (longueur totale : 71 mm, mesurée à travers la peau du plus grand des deux exemplaires du Muséum de Paris).

Cependant le guide qui nous conduisit à la caverne à Cotte, un homme âgé, nous a affirmé que, de toute sa vie, il n'avait jamais vu ni entendu de « Fouquet », dans toute cette région, morne de Langevin, volcan, hauts de la rivière de l'Est, où selon BORY, les Fouquets se trouveraient le plus fréquemment. L'affirmation de BORY se trouvant étayée par des restes osseux déterminables, il faut conclure que l'espèce, commune autrefois dans cette zone, en a disparu depuis le XVIII[e] siècle.

Notons encore que BORY lui-même eut l'occasion d'apercevoir des Procellariens. 48 heures après son passage à la caverne à Cotte, il décida de passer la nuit « *au pied du mamelon Central, du côté qui regarde le cratère Dolomieu* ». Il écrivit : « *Quand la nuit fut tout à fait close, <...>, le vent portait des fumées du côté opposé où nous étions. J'aperçus des oiseaux de mer que dans le pays on nomme* Fouquets, *et qui se retirent la nuit dans les hautes montagnes, passer sous le vent du cratère sans en paraître incommodés : l'un d'eux traversa par-dessus le cratère même sans se déranger de sa route et sans paraître ébloui* » (3 : 51 *et sq.*).

Il reste étonnant que ces « Taille-vent » soient demeurés ignorés des responsables du Muséum d'Histoire naturelle de Saint-Denis. Le musée de St-Denis a eu son temps de prospérité au XIX[e] siècle, pendant la quarantaine d'années qu'Auguste LANTZ, un alsacien d'origine formé au Muséum de Paris, en fut le conservateur. LANTZ s'était efforcé de réunir une collection complète des productions de l'île. A diverses reprises, notamment à l'occasion de l'exposition de 1889, il adressa à Paris une série représentative de l'avifaune de l'île. Pourquoi le « Taille-vent » des pêcheurs de St-Pierre n'y figurait-il pas ? Nous avons lu attentivement les catalogues où LANTZ notait les spécimens qui entraient dans son musée, ceux qu'il proposait en échange ou qu'il offrait à la métropole. Nous n'avons rien trouvé qui semble s'appliquer au Pétrel de Barau, et nous ignorons à quelle date ont été incorporés dans les collections de St-Denis les trois exemplaires de *Pt. baraui* que MILON (1951 : 154) y a vus en 1948 et dont il ne reste plus de nos jours qu'un seul, faussement étiqueté d'ailleurs jusqu'à notre intervention *Pterodroma cooki*.

AFFINITÉS ET MENSURATIONS

Pterodroma baraui est un Pétrel de taille moyenne, au front et aux parties inférieures blanches, sous-caudales comprises, au dos gris contrastant avec le dessus de la tête brun noirâtre, au-dessous de l'aile blanc, sauf la bordure. Par ces caractères, il appartient, comme nous l'avons déjà indiqué (JOUANIN, 1964 b) au groupe de formes tropicales, récemment rassemblées dans l'espèce polytypique *hasitata* (BOURNE, *in* PALMER, 1962 : 204) qui comprend le « Black-capped Petrel » des auteurs anglais et américains, le Pétrel à capuchon noir, dont le dessus de la tête contraste avec le dos gris. Néanmoins, il est aisément discernable de chacune des sous-espèces d'*hasitata* et représente dans ce groupe un élément original, isolé depuis longtemps. Des trois races atlantiques, *hasitata* (Kuhl), *caribbaea* Carte, *cahow* (Nichols et Mowbray), on le distingue immédiatement par l'absence de croupion blanc, ou blanchâtre ; d'*externa* (Salvin) et de *cervicalis* (Salvin), par l'absence de collier nuchal et par les rémiges plus pigmentées ; de *phaeopygia* (Salvin) et de *sandwichensis* (Ridgway) par la pattern des parties supérieures et des côtés du cou. Dans ses proportions, il possède en outre un caractère original : la relative brièveté de sa queue, plus courte même, en moyenne tout au moins, que celles des plus petites races du groupe (*cahow, caribbaea*), alors que par l'aile, le bec et le tarse, il est équivalent à *sandwichensis*, et se trouve ainsi occuper une situation moyenne dans la progression de taille qui va de *cahow* à *cervicalis*.

Notre lot de spécimens comprend 6 adultes et 7 jeunes de l'année (dont le type de l'espèce). L'un des adultes est le spécimen monté du musée de St-Denis : ses dimensions s'écartent assez sensiblement, pour le bec et les pattes, de celles des autres spécimens ; un cas semblable a déjà été signalé par BOURNE (*in* PALMER, 1962 : 204) pour un exemplaire de *Pt. hasitata hasitata* de la Guadeloupe (au Muséum de Paris). Les cinq autres adultes ont été capturés en novembre et décembre en mer au voisinage immédiat de la côte ou à 5-6 milles de celle-ci. Les douze spécimens en peau se répartissent en 9 ♂♂ et 3 ♀♀. Nous n'avons pas constaté de différences entre les dimensions des unes et des autres, pas plus d'ailleurs qu'entre les jeunes de l'année et les oiseaux nés à une saison de reproduction antérieure (cf. le tableau de mensurations). C'est pourquoi nous ne les avons pas séparés en différents lots pour le synopsis des dimensions que nous donnons sous la forme condensée : (spécimen monté du musée de St-Denis), minimum-maximum, *moyenne*. La moyenne est calculée sur les onze

Mensurations des spécimens de *Pterodroma baraui*

				Aile	Rectrices médianes	Tarse	Doigt médian armé	Culmen exposé	
♂ adulte	St-Pierre	4	décembre 64	288	122	37	49	32,5	conservé en peau
♂ adulte	St-Pierre	4	décembre 64	299	123	38,5	50	32,5	conservé en peau
♂ adulte	St-Pierre	4	décembre 64	295	121	40,5	52	32,5	conservé en peau
♂ jeune	St-Denis	28	avril 63	281	114	36	47	30,5	conservé en peau. Type de l'espèce
♂ jeune	Cilaos	22	avril 65	284	116	37,5	46	30	conservé en peau
♂ jeune	Hell-Bourg	29	avril 65	296	121	41	53	32	conservé en peau
♂ jeune	St-Denis	23	avril 66	(268)	113	36	49	32,5	conservé en peau
♂ jeune	Cilaos	22	avril 65	285	118,5	40,5	54	33	conservé en peau
♂ jeune	Cilaos	22	avril 65	289	120	37,5	50	31	conservé en peau
♀ adulte	au large de St-Paul	15	novembre 64	283	—	39	50,5	32	peau et squelette conservés
♀ adulte	St-Pierre	4	décembre 64	277	116	37	49	31,5	conservé en peau
♀ jeune	Hell-Bourg	29	avril 65	286	108	38	47,5	31,5	conservé en peau
— adulte	—	—		279	116	32	44	28,5	monté. Au Muséum de St-Denis

N. B. : Par jeunes, nous entendons les oiseaux qui viennent de quitter leur terrier natal.

exemplaires en peau capturés en 1963-64-65, sans tenir compte du spécimen monté du Muséum de St-Denis, ni du spécimen de 1966 dont les rémiges présentent encore des traces de calamus à la base. Ailes : (279), 277-299, *287,5* ; queue : (116), 108-123, *118* ; tarse : (32), 36-41, *38,4* ; doigt médian armé : (44), 46-54, *49,8* ; culmen : (28,5), 30-33, *31,7*.

Observations en mer

Le 3 et le 4 mars, l'un de nous, naviguant à bord de l' « Anton Brunn », remarque un Pétrel, qu'à l'époque il ne pouvait identifier, mais dont la description coïncide avec celle de *Pt. baraui*, à plusieurs reprises entre le 20e et le 24e parallèles Sud et 54°34' et 54°58' E. Les lieux d'observation se trouvent situés approximativement à 70, 90, 130 et 300 km de la Réunion, qui, rappelons-le, est située sur le 21e parallèle Sud, par 55°40' de longitude E. D'autres oiseaux, peut-être référables à la même espèce, mais dans ce cas l'identification est beaucoup plus douteuse, sont aperçus les 5 et 12 mars entre le 26e et le 27e parallèles, approximativement le long du 55e méridien. Ces points sont distants de 500 à 600 km de la Réunion.

Gill ne vit aucun autre Pétrel référable à *baraui* pendant sa traversée de l'océan Indien le long du 55e méridien, depuis la mer d'Oman jusqu'au 35e parallèle Sud. Il n'en vit pas non plus dans le voisinage de l'île Maurice, ni d'ailleurs dans les eaux situées à l'est de la Réunion. De même R. Bailey qui, embarqué sur le « Discovery », fit le relevé des oiseaux de mer entre la mer d'Oman et Maurice, en février-mars et juin-juillet 1964, ne rencontra jamais l'espèce (Bailey, *in litt.*). Confronté aux observations positives de Gill, ci-dessus mentionnées, entre le 20e et le 27e parallèle Sud, le manque de record dans les eaux situées au nord des Mascareignes donne à penser que *Pt. baraui* va chercher sa nourriture au sud de celles-ci. Il serait intéressant de connaître avec précision la position dans ce secteur de la convergence tropicale aux différentes époques de l'année et d'étudier ses relations éventuelles avec la saison de nidification et l'aire de dispersion de *Pt. baraui*. Dans l'est de l'océan Indien (le long du méridien 90) la convergence tropicale a été repérée en octobre au voisinage du 20e parallèle (Baker, 1965 : 324). Mais le relief des fonds dont émergent les Mascareignes, peut modifier sensiblement son tracé à leur niveau. Par ailleurs, la convergence tropicale ne présente jamais le caractère de discontinuité brutale de ses homologues subtropicale et antarctique. Néanmoins, Baker (*loc. cit.*) lui recon-

naît une influence sur la distribution des *Euphausia*. En attendant la publication de données océanographiques qui font actuellement défaut, retenons l'hypothèse que *Pt. baraui* soit une espèce liée aux eaux subtropicales plutôt que tropicales.

Tout semble indiquer d'autre part que *Pt. baraui* se nourrit à grande distance en mer et qu'il ne se rapproche des côtes de la Réunion qu'en fin de journée. Il est très rare pendant le jour parmi les vols d'oiseaux qui, à quelques milles de la côte, quêtent des Céphalopodes. Dans la région ouest de la Réunion, la pêche à la traîne avec des canots équipés d'un moteur hors-bord est couramment pratiquée. On attrape dans ces conditions des thons et des bonites. Les bancs de poissons sont repérés grâce aux oiseaux qui les survolent et qui cherchent sans doute la même nourriture qu'eux. Les pêcheurs partent donc vers le large, et à 5-6 milles de la côte se dirigent vers les groupes d'oiseaux. A l'époque de notre passage, ces groupes comprenaient surtout des Puffins de Baillon, *Puffinus lherminieri bailloni* (Bonaparte), et des Noddis niais, *Anoüs stolidus pileatus* (Scopoli), connus localement sous le nom de Macoas. Au cours des deux matinées en mer où l'un de nous eut l'occasion de voir de nombreux oiseaux, un seul exemplaire de *Pt. baraui* a été rencontré. D'après Armand Barau, la composition spécifique de ces groupes d'oiseaux est la même en avril. En revanche à partir de 16-17 heures *Pt. baraui* apparaît en nombre dans les eaux côtières. Le fait est bien connu des pêcheurs de Saint-Pierre.

Observations de la côte

Pt. baraui est communément aperçu le long de la côte, en fin de journée, dans la région ouest - sud-ouest de la Réunion, entre St-Paul et St-Philippe. Nous avons eu l'occasion d'en observer dans ces conditions le 17 novembre de St-Gilles, le 18 novembre à 3 km à l'est de St-Pierre, le 29 novembre de la Pointe des Aigrettes (N de St-Gilles). Les oiseaux volent au ras des flots, parallèlement à la côte, d'un mouvement rapide de battements d'ailes prononcés avec des phases de vol plané. Jusqu'à la nuit des oiseaux sont aperçus, faisant ce manège, allant et venant parallèlement à la côte, à quelques dizaines de mètres seulement parfois de la barrière récifale. D'autres cessent ce manège beaucoup plus tôt (6 à 18 h 45 à St-Pierre le 18 novembre, un à 18 h 10 à la Pointe des Aigrettes le 29 novembre) et soudain se mettent à prendre de l'altitude en décrivant sans discontinuer de larges cercles. La spire hélicoïdale ainsi tracée a son axe incliné vers la terre. Parvenus

à une grande hauteur, ils cessent de tournoyer et d'un vol droit ils mettent le cap sur les massifs montagneux de l'intérieur.

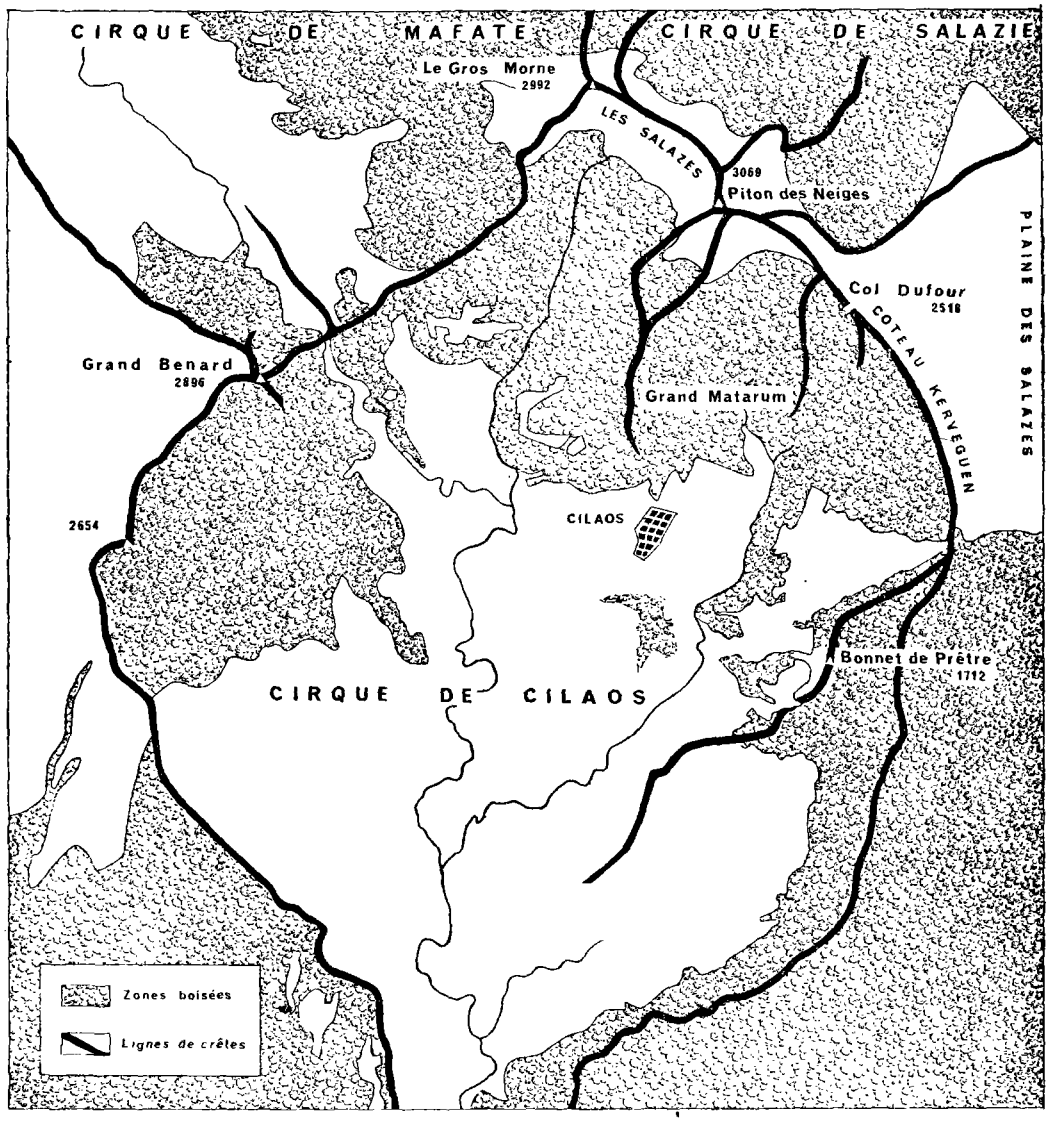
La densité maximum semble être atteinte dans le voisinage de St-Pierre. C'est là en effet que l'on peut observer le plus grand nombre d'individus en se postant sur le rivage à la tombée du jour ; l'espèce est même suffisamment commune dans cette région pour que les pêcheurs locaux lui aient attribué un nom, « Taille-vent », et ses habitudes de retour à la fin de la journée leur sont bien connues. A St-Pierre, le nom de Taille-vent ne prête à aucune confusion spécifique : ayant demandé le 6 décembre à Gilbert de LAVERGNE de nous procurer quelques exemplaires de « Taille-vent », il nous fit parvenir le jour même quatre exemplaires de *Pt. baraui,* tués en mer à 17 heures, à quelques centaines de mètres de la côte.

Inversement l'oiseau semble inhabituel sur le versant est - nord-est de l'île. Les investigations poursuivies depuis près de quatre ans dans la région St-Denis - St-Benoît par Armand BARAU et par Harry GRUCHET ont permis de découvrir de nombreux *Puffinus lh. bailloni,* quelques *Puffinus pacificus,* pour deux *Pt. baraui* seulement, dont le type de l'espèce, l'un et l'autre capturés à la même époque de l'année sur la plage du Barachois à St-Denis (28 avril 1963 et 23 avril 1966). L'observation par nous-mêmes au Brûlé de St-Denis, à 800 mètres d'altitude, d'un autre individu, est sans doute peu banale aussi : le 2 novembre un oiseau isolé passe à 18 h 20 au-dessus de la route, en volant silencieusement avec des battements d'ailes réguliers, prenant de l'altitude et se dirigeant vers le SSW. Nous avons essayé de réitérer l'observation au même endroit ou dans des localités voisines comme la Montagne St-Denis, mais sans aucun succès, alors qu'à St-Gilles ou à St-Pierre, il suffit de se poster sur la plage à partir de 18 heures pour en apercevoir à coup sûr.

OBSERVATIONS A TERRE

Nous avons vu que le Pétrel de Barau commençait à quitter la mer pour rejoindre ses territoires de nidification bien avant la tombée du jour. C'est un point important de son comportement, très différent à cet égard de beaucoup d'autres espèces de Procellariens.

On le retrouve ensuite dans les régions montagneuses de l'île où il a été observé dans le cirque de Cilaos (cf. carte 2), soit de Cilaos même ou du Grand Matarum, soit du col Dufour, les 19, 20, 26 et 30 novembre. Dès 17 h 45, il apparaît en nombre dans le



Carte 2. — Le cirque de Cilaos.

ciel dont un examen minutieux ne laisse alors apercevoir aucune autre espèce de Procellarien. Les individus sont parfois isolés, mais plus souvent réunis en groupes de 4 à 8 qui décrivent des cercles haut dans le ciel. Parfois un oiseau semble poursuivre l'autre et quand plusieurs individus se trouvent ensemble, des vocalisations peuvent en général être perçues. L'évaluation de l'altitude à laquelle se situent ces évolutions, a son importance pour localiser les territoires de nidification éventuels. On doit à WINGATE (1964 : 156) une estimation de la distance à laquelle les cris de *Pt. hasitata* (espèce ou sous-espèce voisine de *baraui*) peu-

vent être entendus latéralement (1000 m) et verticalement (500 m), Mais elle dépend évidemment de nombreux facteurs, acoustique des lieux, force et direction du vent, etc. Les individus entendus le 20 novembre du Grand Matarum (alt. : 1500 m), criant dans le ciel, pouvaient se trouver à une altitude voisine de 2000 m environ. Ceux qui furent observés du col Dufour le 26 novembre volaient à des altitudes comprises, au jugé, entre 2000 et 2800 mètres. C'est entre ces deux limites approximatives qu'il faut chercher, croyons-nous, les terriers de *Pt. baraui*.

Ces évolutions aériennes semblent se poursuivre jusqu'à la tombée de la nuit. Il faut certes tenir compte des arrivées successives d'individus dont les rythmes nycthéméraux respectifs ne sont pas nécessairement synchronisés, comme le prouve d'ailleurs l'observation d'exemplaires quittant le rivage de la mer à 18 h 45, alors que d'autres survolent Cilaos dès 17 h 45. Cependant on retire l'impression que ces oiseaux, certains d'entre eux tout au moins, se livrent dans l'intérieur de l'île, avant de gagner les approches immédiates de leurs lieux de nidification, à des parades prolongées. Il est possible à ce propos que leur comportement varie selon qu'ils sont plus ou moins engagés dans le processus de la reproduction, les parades bruyantes et prolongées étant le fait d'individus « inemployés ».

Où se trouvent exactement les points de ponte ? Nous ne sommes malheureusement pas en mesure d'apporter une réponse certaine à cette question. Le versant occidental du Piton des Neiges semble un site probable. Le 26 novembre, GILL, en observation de 17 h 30 à 19 h 30 au col Dufour, c'est-à-dire au bord du rempart, à l'issue du sentier qui monte de Cilaos, en vit de nombreux volant devant les pentes qui descendent du Piton des Neiges. Les oiseaux étaient très bruyants et leurs cris, malgré un fort vent d'est, pouvaient être entendus en prêtant une oreille attentive ; même le bruissement de leurs ailes était audible et parfaitement distinct. Une activité considérable régnait ; les oiseaux, se suivant de très près, se poursuivaient en planant les uns autour des autres, par deux ou par trois, bien visibles quand ils se silhouettaient sur le ciel au-dessus de l'arête qui descend du Piton des Neiges. Quand l'observateur quitta l'endroit (19 h 30), l'activité vocale donnait son plein et il est possible qu'elle ait encore augmenté ensuite. Les conclusions que l'on serait tenté de tirer de cette observation fort précise sont malheureusement infirmées par JOUANIN qui, le 30 novembre, en poste au même endroit de 17 h 45 à 20 h, ne vit aucun Pétrel devant les pentes du Piton des Neiges. A grande distance dans la direction du Grand Bénard, des oiseaux tournoyaient

à une altitude un peu inférieure à celle du col Dufour (2500 m) mais aucun n'a traversé le cirque pour se diriger vers le Piton des Neiges. Cependant à deux reprises, après la disparition du soleil derrière les remparts occidentaux du cirque, des cris de *Pterodroma* ont été entendus. Il fallait prêter l'oreille attentivement pour les percevoir. Ils ne provenaient cependant évidemment pas du Grand Bénard (distant de plus de 7 km) mais d'un point situé à quelques centaines de mètres à l'ouest du col Dufour sur les pentes du Piton des Neiges.

Il serait donc prématuré de parler déjà d'une colonie à cet endroit, mais il doit y avoir quelques nids dans le voisinage, sans quoi les cris entendus par JOUANIN vers 19 h 30, alors qu'il faisait déjà sombre, seraient autrement difficiles à expliquer.

Une autre « colonie » est probable sur les pentes orientales du Grand Bénard où des rassemblements d'oiseaux tournoyant dans le ciel ont été aperçus régulièrement les 19, 20, 26 et 30 novembre. Mais il doit encore exister des points de nidification ailleurs : le 20 novembre un individu est noté à 18 h 50 volant vers les falaises du Bonnet de Prêtre en perdant rapidement de l'altitude (les nuages n'ont pas permis malheureusement de le suivre jusqu'au bout de sa route). Le 26 novembre, à 18 h 15, trois individus quittent le cirque de Cilaos et, passant au-dessus du coteau Kerveguen, continuent leur vol vers la plaine des Salazes.

Il est peu douteux que les lieux de nidification, qui subsistent encore de nos jours, se trouvent dans des endroits particulièrement inaccessibles. Cela seul peut expliquer l'ignorance où se trouvent tous les habitants des « îlets » (1) que nous avons interrogés au sujet de cette espèce. Alors que les habitants de la côte voisine de St-Pierre connaissent bien l'oiseau, comme nous l'avons rapporté ci-dessus, ceux des montagnes l'ignorent. Ils en ont vu des exemplaires de temps à autre, quand, par temps couvert, des oiseaux désorientés se font prendre au sol dans les rues de Cilaos ou de Hell-Bourg, mais ils n'en connaissent pas les lieux de nidification, en dépit de leur aptitude à gravir les pentes les plus difficiles, aptitude qui vaut aux plus habiles le pittoresque sobriquet local de « chats de rempart ».

Les parois du Piton des Neiges, des Salazes et du Grand Bénard, du coteau Kerveguen, qui dominent de plusieurs centaines de mètres (2) le cirque de Cilaos sont particulièrement abruptes. Seuls

(1) Dans le langage créole de la Réunion, îlet désigne non pas de petites îles en mer (le littoral de la Réunion en est d'ailleurs dépourvu), mais des villages isolés dans les montagnes.

(2) Altitude des sommets : Piton des Neiges 3069 m ; Grand Bénard 2896 m.

des alpinistes éprouvés descendant en varappe depuis les crêtes pourraient en tenter l'exploration. Les falaises du Piton des Neiges et des Salazes sont en outre dépourvues de couvert végétal et la présence éventuelle de Procellariens nicheurs dans un tel biotope pose un problème jusqu'ici sans réponse. A l'altitude en cause, le refroidissement nocturne est important. Des abris profonds sont nécessaires pour protéger les poussins de variations de température qui leur seraient fatales. Les terriers où nichent, à 1500 m d'altitude, en Nouvelle-Zélande, les *Puffinus huttoni,* ont environ 2 mètres de longueur (HARROW, 1965). Il en est de même pour les terriers creusés par *Pterodroma mollis feae* dans la terre de remblai qui meuble les interstices entre les blocs des éboulis, au volcan de Fogo, dans l'archipel du Cap Vert, pourtant situé à une latitude tropicale (R. DE NAUROIS *in litt.*). A Haïti, WINGATE a trouvé *Pterodroma hasitata* nichant entre 1500 et 2000 m d'altitude sur des pentes très escarpées, mais abondamment garnies de végétation : la présence d'un sol meuble où il est possible de creuser un terrier y est donc probable. Mais dans l'abrupt désert rupestre qui descend, quasi verticalement, du Piton des Neiges ou du Grand Morne vers Cilaos, où le Pétrel de Barau trouve-t-il la possibilité d'aménager de profonds terriers ?

VOCALISATIONS

C'est de Cilaos et du col Dufour uniquement qu'ont été entendus des cris de *Pt. baraui.* Le cri le plus fréquent comprend une sourde et rauque aspiration « oaoou » suivie d'un rapide « kekekeke ». La phrase est souvent répétée deux fois, parfois trois. Il ne semble pas que les deux termes de la séquence soit obligatoirement liés, car l'un et l'autre ont été entendus séparément. or, si l'éloignement devait avoir masqué l'un des termes, c'eût été, nous semble-t-il, plutôt exclusivement au détriment de la première note, sourde et gutturale. GILL a pu distinguer deux variantes de la seconde partie, l'une plus basse, l'autre plus haute, qui correspondent peut-être à un aspect de dimorphisme sexuel. Un autre cri, entendu de temps à autre, est un « Pic-teck » qui ressemble à celui des Phaétons. GILL a également noté un rauque « Kre-Kre » qui peut être une altération de l'appel tétrasyllabique « Kekekeke ».

EPOQUE DE LA NIDIFICATION

Rappelons ici que la Réunion ne connaît que deux saisons, en général bien délimitées. La saison chaude et pluvieuse, également

appelée hivernage, qui correspond à l'été austral, dure cinq mois, de décembre à avril. C'est durant cette période que soufflent les cyclones et que se reproduisent *Puffinus pacificus, Puffinus bailloni* comme *Pt. baraui*. La saison fraîche et sèche, qui correspond à l'hiver, est nettement établie de juin à septembre. Le passage d'une saison à l'autre dure environ un mois et demi. Avril et mai, octobre et novembre sont les mois de transition.

A la fin de novembre, la saison de nidification de *Pt. baraui* semble en être juste à son début. Sur les cinq spécimens collectés au printemps austral 1964, trois (4 décembre) ont encore la plaque incubatrice complètement recouverte de duvet, un (17 novembre) montre un début de dénudation, un autre (4 décembre) a la plaque incubatrice presque entièrement dénudée. Les trois mâles collectés ont des testicules petits (7×4 ; $7 \times 4.4 \times 5$; $7 \times 4.8{,}5 \times 3$; 5×3 mm) avec le pôle antérieur gris.

Des renseignements concordants sont fournis par les captures de plusieurs jeunes à l'envol en avril. Durant les derniers jours d'avril 1965, cinq spécimens ont été attrapés à la main dans les rues de Cilaos et d'Hell-bourg. D'après la fraîcheur homogène de leur plumage, nous pensons que ces cinq spécimens sont des jeunes, ce qui est confirmé par la présence chez deux d'entre eux, qui nous ont été adressés en chair, d'une bourse de Fabricius non résorbée. Pour une raison ou pour une autre, ces oiseaux avaient manqué leur premier envol vers la mer. Les mêmes incidents doivent se reproduire chaque année (nous avons cité ci-dessus cette cause de mortalité) : en 1965, ils sont parvenus à notre connaissance grâce aux nombreuses tournées d'information que nous avions effectuées quelques mois auparavant dans les villages de l'intérieur.

Ces jeunes oiseaux ont été capturés entre le 22 avril et le 29 avril. En assimilant ces dates à celle de leur premier envol et en supposant que les durées d'incubation et d'élevage sont identiques à celles de *Pt. cahow* (en tout état de cause, elles sont sans doute peu différentes), il est possible de calculer les dates de ponte et d'éclosion correspondantes. WINGATE (*in* PALMER, 1962 : 207) indique pour *Pt. cahow* une durée d'incubation variant de 51 à 54 jours, une durée de croissance au nid variant de 90 à 100 jours. Des jeunes à l'envol le 22 et le 29 avril correspondraient donc à des œufs pondus entre le 19 novembre et le 9 décembre et éclos entre le 12 et le 29 janvier. En termes moins rigoureux et par conséquent mieux conformes à l'imprécision des hypothèses de notre calcul, retenons que *Pt. baraui* pond vraisemblablement à la fin de novembre, que les éclosions se placent à la fin de janvier et que les jeunes s'envolent à la fin d'avril.

Pterodroma baraui est donc un nicheur d'été comme *Pt. externa, cervicalis* et *sandwichensis,* alors que *hasitata, cahow* et *phaeopygia* sont des nicheurs d'hiver. Mais par suite du changement d'hémisphère, il se trouve que *baraui, externa, cervicalis, hasitata* et *cahow* se reproduisent sensiblement à la même époque de l'année. Dans l'ensemble des formes incluses dans la super-espèce *hasitata, sandwichensis* et *phaeopygia* font exception avec une ponte en mai, juin ou juillet.

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Nous ne saurions le terminer sans exprimer notre profonde gratitude à l'égard de toutes les personnalités qui nous ont accordé leur appui ou leur concours dans l'accomplissement de notre mission et sans rendre hommage à l'accueil chaleureux que nous avons trouvé sur cette lointaine terre de France. Il nous est impossible de citer ici tous ceux envers lesquels nous avons contracté une dette de reconnaissance, mais qu'ils soient assurés que nous ne l'oublions pas. Nous mentionnerons seulement ceux qui ont partagé sur le terrain les observations qui sont la substance de cet article : MM. Armand BARAU, Ingénieur agronome, Conseiller général de la Réunion, son frère Georges BARAU, Harry GRUCHET, Conservateur du Muséum d'Histoire Naturelle de Saint-Denis, Gilbert de LAVERGNE, et R. W. STORER, Professeur à l'Université de Michigan. Ce dernier, qui nous avait rejoints à la Réunion, nous a laissé le soin d'assurer seuls cette publication : nous l'en remercions ainsi que des commentaires avisés qu'il fit à la lecture de notre manuscrit. Nous remercions aussi les Drs W. R. P. BOURNE et G. E. WATSON qui se sont intéressés à notre travail et nous ont fait part de leurs réflexions judicieuses.

SUMMARY

Pterodroma baraui belongs to the group of tropical petrels currently included in the polytypic species *Pterodroma hasitata.* Nevertheless it is easily distinguished from the other forms of this group by means of both plumage and mensural characters. It has apparently been isolated from the other members of this complex for some time.

Although it was described only recently, *Pt. baraui* is not uncommon on Reunion Island in the Indian Ocean. It is encountered only infrequently on the northern side of the island, whereas on the southern side in the vicinity of Saint-Pierre it is well known under the local name « Taille-vent ».

The « Taille-vent » was mentioned in 1804 by Bory de Saint-Vincent, who spoke of bones of seabirds, which were captured for food by maroons, in a remote cave in the eastern highlands of Reunion. Bones which are referable to *Pterodroma baraui* can still be found there but the species no longer inhabits the cliffs in that region.

Pt. baraui does not feed in the coastal waters where it appears only in the late afternoon, approximately one hour before going inland to its breeding grounds. We suggest that its distribution is determined by the tropical

convergence, which lies close to the Mascarene islands, and that it feeds in subtropical rather than tropical waters.

In late November *Pt. barau*i can be seen circling above the mountainous cirque of Cilaos and gathering about some of the inland cliffs. Intense vocal activity and chasing, presumably indicative of prebeeding behaviour, characterize these congregations. Nests were not located but presumably are to be found on the inaccessible cliffs of the interior, particularly those of Piton des Neiges, les Salazes and Grand Benard.

*Pt. barau*i breeds in the summer, laying at the end of November. The young probably hatch by the end of January and fledge at the end of April or beginning of May when some of them, grounded by bad weather, are caught annually in the streets of the mountain villages.

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Observations On the Pelagic Distribution of Seabirds In the Western Indian Ocean

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In 1952, regarding our knowledge of seabirds, the Indian Ocean was considered to be the least-explored part of the world ocean (Murphy, 1952). The validity of this statement was dramatized soon thereafter by the discovery of two new petrels, *Bulweria fallax* (Jouanin, 1955) and *Pterodroma baraui* (Jouanin, 1963), and an Indian Ocean breeding colony of a third petrel, *Pterodroma arminjoniana* (Murphy and Pennoyer, 1952). Still, the need for information on the pelagic distribution and behavior of seabirds in the Indian Ocean remains (Bourne, 1963), for, although summaries of the scattered accounts are available (Bourne, 1960, 1963; Jouanin, 1957; Watson, Zusi, and Storer, 1963), the information on which they are based comes primarily from well-travelled commercial routes. By contrast, the rest of that ocean has received scant attention.

The International Indian Ocean Expedition (IIOE), a multination endeavor coordinated and sponsored by UNESCO, has been

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making possible the accumulation of seabird observations by scientific personnel aboard oceanographic research vessels that are systematically transecting the entire Indian Ocean. Some of the resulting information has already been published (Bailey, 1964, 1965, 1966; Pocklington, 1965; Pocklington and Risebrough, 1964; Rand, 1962, 1963). The present report is based on observations and collections made by the author during IIOE cruise 5 of the R/V *Anton Bruun* from January through April 1964 and also during a voyage of the commercial vessel S.S. *Kampala* in May 1964.

The cruise tracks of these two voyages are outlined in figure 1 and the details of the itineraries are included in table 1. Cruise 5 of the *Anton Bruun* originated and terminated in Bombay, India, on Jan. 26 and May 4, 1964, respectively and consisted of a direct transit across the Arabian Sea from Bombay to the Gulf of Aden followed by a north-south transect of the western Indian Ocean on longitude 55° E and a south-north transect on longitude 75° E. A direct run from Mauritius to 40° S, 75° E, connected the two transects. The passage from Bombay to the Seychelles from May 17 to June 2, 1964, was a scheduled run of the *Kampala* (British-India Lines) and included stops at Karachi, Mombasa, and Zanzibar.

At each station on the *Anton Bruun*'s itinerary, I maintained a 2–3-hour standardized watch for seabirds from the bridge of the ship. During this period the ship was essentially stationary. In the evening, while in transit to the next day's station at an average speed of 10–12 knots, I counted seabirds again for an hour before dusk. Records also were kept of all birds sighted between watch periods; when I was not on deck, I was alerted to the presence of seabirds by the officers on watch.

The main difference influencing the observations made from the *Kampala* was the continuous movement of the ship (15 knots) and the fact that I could only watch from one side of the ship at a time, narrowing the radius of observation from 360° to slightly less than 180°.

Some seabirds were collected from a small rubber "Zodiac" boat in subantarctic waters and during our brief visits to the Seychelles, Mauritius, Amsterdam, and St. Paul Islands. Although the latter two islands will be included in this report, only those birds seen at sea in the vicinity of the Seychelles and Mascarene Islands are discussed here, as studies on these islands were continued from June to November 1964 and will be published elsewhere.

In the course of this work I have kept detailed notes and descriptions of all unfamiliar seabirds and have found the following references especially useful for identification: "Birds of the Ocean" (Alexander, 1954), "The Petrels of the Indian Ocean" (Bourne, 1960), "A Preliminary Field Guide to Birds of the Indian Ocean" (Watson, Zusi, and

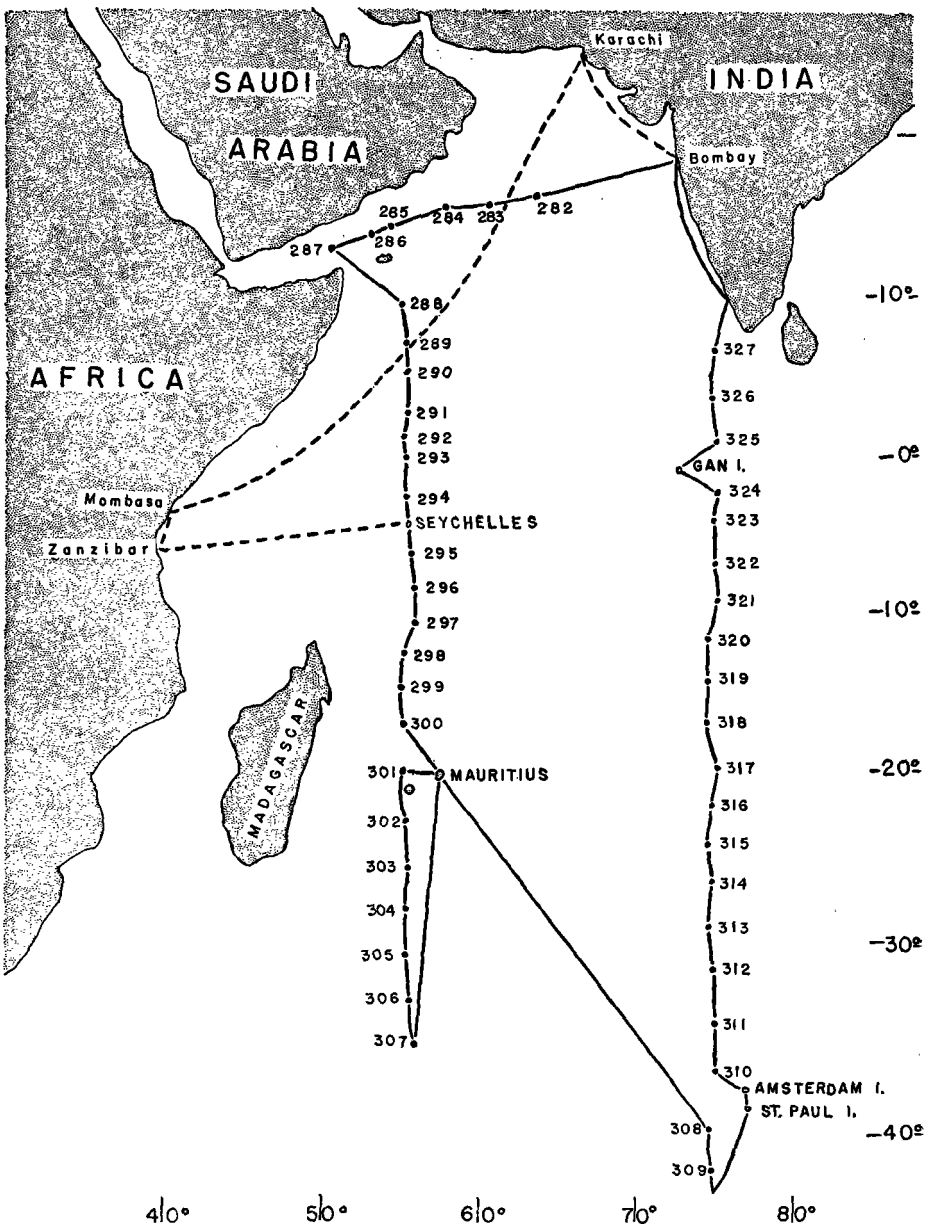

FIGURE 1.—Cruise tracks and station positions.
——— R/V *Anton Bruun:* Jan. 26 to May 4, 1964
------ T.S.S. *Kampala:* May 17 to June 2, 1964

Storer, 1963). The nomenclature used follows that of Peters (1931, 1934) except in a few cases wherein recent revisions or descriptions were applicable. All specimens have been cataloged in the collections of the U.S. National Museum in Washington, D.C.

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SEABIRD ABUNDANCE.—Included in table 1 are the numbers of seabirds (grouped by order) observed during the standardized watch periods and a calculated figure for the number of birds seen per hour during each watch. The relationship of the latter figure to the actual density of seabirds in a given area is biased by many variables including the movement of the ship, movement of the birds, conditions for observation, and perhaps time of day. The first of these may be particularly important (compare Bailey, 1966, p. 261) since seabirds rarely are distributed uniformly at sea but instead congregate at and move with localized sources of food. Hence, any substantial movement of the ship should increase the likelihood of encountering nonrandomly distributed seabirds. If this is true, the counts I made during the morning watches on station are not directly comparable to evening watches or others made when the ship was cruising at normal speeds. An additional complication is the possibility that the greater duration of the morning watches increased the chances of seeing small groups of moving birds and partially compensated for the lack of movement of the ship. Despite these and other problems inherent in the quantification of at-sea observations, at least five regions were found where seabirds were more common than in the intervening areas. These were: (1) the western Arabian Sea and south along the coast of Somalia; (2) the Seychelles Islands and surrounding seas; (3) the waters near the Mascarene Islands; (4) subantarctic waters below 33° S; (5) the seas east of the Maldive Islands and north to the Indian coast. A sixth region near the equator also might be distinguished though the increase there was less pronounced than in the other areas. In these regions the number of seabirds seen per hour was definitely greater than 2–3, usually 10–30, and on some occa-

sions reached 100–200.[2] In the intervening seas an average of one bird or less was seen per hour.

REGIONAL SUMMARIES.—In the Arabian Sea, Jouanin's petrel (*Bulweria fallax*) and the red-billed tropicbird (*Phaëthon aethereus*) were the two species most commonly encountered in January although, close to the Gulf of Aden and Socotra, Audubon's shearwaters (*Puffinus lherminieri*) were quite common and the lesser black-backed gull (*Larus fuscus*), Aden gull (*Larus hemprichii*), masked booby (*Sula dactylatra*) and brown booby (*Sula leucogaster*) also were found. The primary difference within this general region in the following May was the appearance of several storm petrels, i.e., Wilson's petrel (*Oceanites oceanicus*), frigate petrel (*Pelagodroma marina*), and either the white-bellied storm petrel (*Fregetta grallaria*) or the black-bellied storm petrel (*Fregetta tropica*). Storm petrels also were seen at this time south along the African coast to Mombasa and east to the Seychelles Islands (see table 4).

Most of the breeding seabirds of the Seychelles Islands forage in large mixed flocks in the relatively shallow waters around these islands. Few species, however, except the sooty tern (*Sterna fuscata*) and the wedge-tailed shearwater (*Puffinus pacificus*), stray into the surrounding open seas with any regularity. Although flocks of up to several hundred sooty terns were seen near the Seychelles and east to the African coast in May and June, no sooty terns were seen in this region in January and February.

In the equatorial regions two all-dark storm petrels of uncertain identification (possibly *Oceanodroma monorhis* and *O. matsudairae;* see "Species Accounts") were encountered, as well as a tern, apparently the fairy tern (*Gygis alba*).

The numbers of seabirds found in the waters near the Mascarene Islands seemed impressive to me after having passed through the relatively barren region south of the Seychelles Islands. Flocks of sooty terns and wedge-tailed shearwaters, as well as scattered white-tailed tropicbirds (*Phaëthon lepturus*), appeared within 50 miles of Mauritius. A few common noddies (*Anous stolidus*) also were seen. Further to the southwest, Barau's petrel (*Pterodroma baraui*) from Reunion was a common pelagic species, occurring with tropicbirds (*P. lepturus*) and Audubon's shearwaters (*Puffinus lherminieri*).

Below 34° S we encountered the albatrosses and petrels, characteristic of the cool water oceans of the southern hemisphere. The wandering albatross (*Diomedea exulans*), white-chinned petrel (*Procellaria aequinoctialis*), soft-plumaged petrel (*Pterodroma mollis*), and

[2] The increase near the Maldives was only subjectively apparent, as standardized watches permitting computations of birds seen per hour were not made in this region.

prions (*Pachyptila*) were the most abundant and conspicuous species while others such as the sooty albatross (*Phoebetria fusca*), shy albatross (*Diomedea cauta*), black-browed albatross (*Diomedea melanophris*), yellow-nosed albatross (*Diomedea chlororhynchos*), and great-winged petrel (*Pterodroma macroptera*) were seen regularly but in smaller numbers. Scattered individuals of only six other species were seen at sea in this region: Schlegel's petrel (*Pterodroma incerta*), giant petrel (*Macronectes giganteus*), pediunker (*Adamastor cinereus*), sooty shearwater (*Puffinus griseus*), Wilson's petrel (*Oceanites oceanicus*), and white-bellied storm petrel (*Fregetta grallaria*).

St. Paul and Amsterdam Islands were once very important seabird breeding stations (Jouanin, 1953; Murphy and Irving, 1951). During cruise 5 of the *Anton Bruun*, we visited each of these islands briefly, St. Paul for a few hours in the late afternoon of Apr. 7 and Amsterdam Island the following day. Seabirds were numerous in the waters around both of these islands and included most of the common petrel and albatross species seen elsewhere at sea in this region; however, sooty albatrosses and white-chinned petrels were especially numerous near Amsterdam Island. Flocks of Antarctic terns (*Sterna vittata*) were feeding near both islands and, within one mile of St. Paul, we also found feeding flocks of the little shearwater (*Puffinus assimilis*). Aside from Rockhopper penguins (*Eudyptes crestatus*), we could find no seabirds on St. Paul Island itself, though a number of "petrel nests" were located in small crevices and under rocky overhangs. Although the island was infested with both rats and hares, the absence of seabirds may be attributed to the fact that most species would have finished breeding and left the island by this date. We therefore spent little time on Amsterdam Island but instead confined our collecting efforts to the waters just offshore.

On the 75° E transect few seabirds were seen north of 31° S until we reached the latitudes of the Chagos and Maldive Islands. Here we found dark shearwaters, apparently the pale-footed shearwater (*Puffinus carneipes*), and scattered flocks of sooty terns. Occasional tropicbirds (*P. lepturus*) also were seen.

Several species of seabirds known to breed on the Seychelles or Mascarene Islands were not observed in the course of the two voyages. These include the Trinidad petrel (*Pterodroma arminjoniana*), red-tailed tropicbird (*Phaëthon rubricauda*), greater frigate-bird (*Fregata minor*), red-footed booby (*Sula sula*), lesser noddy (*Anous tenuirostris*), and roseate tern (*Sterna dougallii*). All of these species were encountered during subsequent field work on these islands and will be included in other reports.

OCEANOGRAPHIC DATA.—Concurrent with my seabird observations, standard oceanographic measurements (temperature profiles, nutri-

ents, plankton abundance, and primary productivity) were being taken by other members of the *Anton Bruun*'s scientific party. These data and the methods used in their determination are presented in detail in the "Final cruise report, *Anton Bruun* cruise #5" (Woods Hole Oceanographic Institution, March 1965), and will be summarized only briefly here. The values obtained for surface salinity (36.0–36.35°/$_{oo}$), nutrient concentrations (PO_4, .46–.49μg A/l.; NO^2–N, .35–.60μg A/l.), and primary productivity (18–44μg C/1./d)[3] in the western Arabian Sea near the Gulf of Aden and Socotra (sta. 282–287) were consistently higher than most other locations visited. Although nutrient concentrations at a few of our southernmost stations (308–310) were comparable to or higher than Arabian Sea values, primary productivity levels were much lower (6–7μg C/1./d.). Unfortunately, the results of analyses of plankton samples are not yet available. Surface water temperatures in the western Arabian Sea were several degrees lower than in the seas immediately to the south. This decrease in temperature and concomitant increase in the nutrient concentrations and productivity are indicative of strong local upwelling which is known to occur in that region and which is believed to be the major determinant of the composition and density of the seabird community there (Bourne, 1963; Bailey, 1966). Between the Arabian Sea and the Mascarene Islands on the 55° E transect, surface temperatures ranged from 26° to 29.2° C. At comparable latitudes on the 75° E transect they ranged from 27° to 30.1° C. A progressive decrease in temperature was noted south of the Mascarenes, but the drop (from 19° to 15° C) was especially pronounced from 35° to 40° S, the region of the subtropical convergence. It was also in this region that the numbers of seabirds increased markedly.

Species Accounts

Eudyptes crestatus **Rockhopper Penguin**

Common at St. Paul Island on Apr. 7, where they were breeding in colonies on the steep grassy slopes though they were not nearly as abundant as Jeannel found them on these same slopes in February 1939 (Jeannel, 1941, pl. x). Many full-size young, which had lost most of the down tips on their juvenal feathers, were present, but no small young or eggs were found. The soft part colors recorded from five specimens were as follows: irides orange; bill dull orange; feet dark grey below, white above. Weights ranged from 1915 to 2475 grams (mean 2205 grams). The measurements (in mm)[4] of

[3] Average of combined values to depths of 25 percent incident light.

[4] Made by George E. Watson, Division of Birds, U.S. National Museum, Washington, D.C.

two female specimens are as follows: wing 158,162; tail molting; crest 70, 72; culmen 46.5; bill from gape 56, 57; width of bill 13.5, 14; depth of maxilla 11; foot from heel 105, 110; middle toe and claw 70, 75.

Diomedea exulans **Wandering Albatross**

One of the most common and conspicuous species in subantarctic waters below 33°52′ S on Mar. 8–9 and Apr. 3–10, 1964, its numbers reaching a maximum (25) at our southernmost station (see table 2).

Six specimens were taken, two at sea at 40°04′ S on Apr. 4 and four just off the coast of Amsterdam Island three days later. The weights of these specimens ranged from 14 to over 20 pounds. The soft part colors, including those of a brown-bodied immature were as follows: feet bluish grey to bluish white; irides brown; orbital ring light blue; bill flesh color. The gonads of these specimens were not enlarged.

On several occasions I observed a pair of birds that were sitting on the water engage in a ceremony in which one bird with its wings raised slightly over its back was fed regurgitated morsels by the other. The ceremony terminated when the receiving partner spread its wings fully, stretched its neck, pointing its bill upward, and uttered a high-pitched squealing note. It then relaxed its position. On several other occasions two birds nibbled simultaneously at the end of each other's bill without the exchange of any food or use of vocalizations. Murphy (1936, p. 558) describes similar courtship-like activities being engaged in at sea often by large groups of albatrosses.

Diomedea melanophris **Black-browed Albatross**

We observed this small mollymauk only occasionally in subantarctic waters, primarily below 40° S on Apr. 4–6 (see table 2). A single individual was present at 36°58′ S on Apr. 9.

Diomedea cauta **Shy or White-capped Albatross**

Only occasional individuals were noted in subantarctic waters south of 36°58′ S on Apr. 3–9 (see table 2).

Diomedea chlororhynchos **Yellow-nosed Albatross**

We observed this mollymauk only occasionally between latitudes 34° S and 40° S on Apr. 3–10 (see table 2).

Two specimens collected off the coast of Amsterdam Island on Apr. 8 had the following soft part colors: bill black with yellow culminocorn becoming reddish toward the tip; irides brown; feet pink. They weighed 2370 grams (male) and 2395 grams (female) and both had small gonads. The female specimen, prepared as a study skin,

measured (in mm): wing 436; tail 191; culmen 114; tarsus 75; middle toe 109. The stomach of this specimen contained the remains of a fish and a sponge.

Phoebetria fusca **Sooty Albatross**

Common in subantarctic waters below 34°32′ S on Apr. 3–10, being most abundant near Amsterdam and St. Paul Islands on Apr. 7–8 (see table 2). Many buff-headed immatures were seen.

Twelve specimens were obtained, five at sea at 40°04′ S, 75°00′ E, on Apr. 4 and seven off the coast of Amsterdam Island on Apr. 8. The soft part colors of these specimens were recorded as follows: irides brown; feet flesh-color; bill black with yellowish stripe (dull white in immatures) on lower mandible. The weights (in grams) of seven specimens were as follows: 3 males 2600, 2650, 2545; 3 females 2930, 2390, 2370; immature (sex unknown) 2440. The gonads of adults were slightly enlarged, ovaries averaging 19 x 9 mm, testes 11 x 6 mm. Three skinned specimens, two adult males and an immature, measured (in mm): wing 496, 496, 483; tail 243, 266, 245; culmen 116, 113, 106; tarsus 87, 84, 82. Of seven stomachs examined, three contained fish remains, two contained large cephalopod beaks, one contained 13 cephalopod beaks, several large shrimp, and the remains of a fish, and one stomach was empty.

Phoebetria palpebrata **Light-mantled Sooty Albatross**

One dark albatross with a light back seen at 43°31′ S, 75°27′ E, on Apr. 6 may have been this species.

Macronectes giganteus **Giant Petrel**

Only two individuals, both dark phase, were seen, one at 42°23′ S, 74°56′ E, on Apr. 5 and the other just off the coast of Amsterdam Island on Apr. 8.

Daption capense **Cape Pigeon**

I saw only one Cape pigeon briefly at 34°53′ S, 69°37′ E, on Apr. 2.

***Pachyptila* species** **Prion**

Prions, of undetermined species, were fairly common in the waters near St. Paul Island on Apr. 7 and south to 43°31′ S on Apr. 4 to 7 (see table 3).

A single *Pachyptila desolata* came aboard the *Anton Bruun* on Apr. 8 when we were about 20 miles west of Amsterdam Island. It was a female with a small ovary and weighed 121.6 grams. The bill and feet were light blue, the irides brown. It measured as follows (in mm): wing 187; tail 96; culmen 26; width bill at base 13; tarsus 34; middle toe 34. The stomach contained several small white pebbles, very likely floating pumice.

Adamastor cinereus **Pediunker**

We saw only two, possibly three, individuals in subantarctic waters (see table 3).

Procellaria aequinoctialis **White-chinned Petrel**

White-chinned petrels were common south of the subtropical convergence where they frequently followed our ship. Our northernmost record was of a single individual at 30°50′ S, 55°09′ E, on Mar. 7. Maximum numbers were encountered at 40°04′ S, 75°00′ E, on Apr. 4 and off the coast of Amsterdam Island on Apr. 8 (see table 3).

Twelve specimens were obtained, primarily off the coast of Amsterdam Island. The soft part colors noted were: feet black; irides brown; bill light grey green with black markings. The ovaries of ten females varied in size from 7 x 4 to 15 x 8 mm; testes of two males measured 7 x 5 and 8 x 5 mm. Of nine stomachs examined, three contained cephalopods; two contained fish; two contained both fish and cephalopods; one contained pieces of fish and bologna, the latter presumably from discarded galley refuse; and one was empty.

Although I never saw this species hover like a kestrel (Watson, Zusi, and Storer, 1963), it often stops short in midair and flutters to the surface of the water. Then, preceding diving, the petrel submerges its head as if looking about under water. When it finally dives, the wings are held partially outstretched and may, therefore, be used for underwater propulsion.

Puffinus carneipes **Pale-footed Shearwater**

This dark shearwater can usually be distinguished by its large size, pale bill, and, from *P. pacificus*, by its short rounded tail. At a distance its large size and heavy flight are diagnostic. Many of the shearwaters seen near the Maldive Islands and west coast of India in late April (see table 4) were identified as this species as were four shearwaters seen on May 21 in the Arabian Sea. At least one of the birds seen near the Maldive Islands was molting its remiges.

Puffinus pacificus **Wedge-tailed Shearwater**

Only one wedge-tailed shearwater was identified positively in the Arabian Sea, on May 17 at 17°29′ N (see table 5). Some of the other dark petrels also may have been this species, but I was unable to separate them from *Bulweria fallax*, which is very similar in appearance. Several wedge-tailed shearwaters were seen as we approached the Seychelles in February, and they were numerous in this region in early June. It was common near Mauritius in February and March, and a few were seen near Reunion. Large dark shearwaters were encountered in the vicinity of the Maldive Islands in April,

but most of these seemed to be *P. carneipes;* however, 40 shearwaters seen resting on the water on Apr. 20 were identified as this species.

Puffinus griseus **Sooty Shearwater**

In early April south of the subtropical convergence we encountered several dark brown shearwaters with whitish underwings, short rounded tails, and flutter-and-glide flight. They were most common near Amsterdam Island (5–6 total) but single birds also were seen at 38°01′ S, 79°19′ E, at 40°04′ S, 75°00′ E, and near St. Paul Island. I have identified tentatively these shearwaters as *P. griseus* rather than *P. tenuirostris* on the basis of the whitish as opposed to grayish underwing coloration. Neither of these species occurs regularly in the Indian Ocean though it seems likely that *P. griseus* could stray northward from the Antarctic regions, where it is abundant during migration (Oordt and Kruijt, 1953).

Puffinus assimilis **Little Shearwater**

A single small, black and white shearwater with flutter-and-glide flight was seen at 33°52′ S, 55°05′ E, on Mar. 8. Large numbers (250+) of *P. assimilis* were found in the waters close to St. Paul Island.

Three specimens with slightly enlarged gonads were taken from the flocks feeding just off the coast of St. Paul Island on Apr. 7, 1964. The soft part colors were as follows: bill light greyish blue; feet bright blue with pink webs and some blackish on the underside; irides brown with bluish outer ring. The weights (in grams) and measurements (in mm) are included in the table below:

specimen	*sex*	*weight*	*culmen*	*wing (chord)*	*tail*	*tarsus*
GI-279	M	289	25	184	68	38
GI-280	?	263.5	25	184	68	38
GI-281	M	250.5	24.6	183	67.5	40.3

The two stomachs examined both contained the remains of many tiny cephalopods.

Conspicuous white edgings were present on the terminal portions of the dark grey feathers of the upperparts and in this respect, as well as mensural characters, the specimens resemble *P.a. munda* as described by Murphy (1927). George E. Watson, who kindly compared the one skinned specimen[5] with available material, writes that it "agrees exactly with two *'munda'* collected February 16, 1926 at 49° S, 179′ W by Beck and Correia (AMNH 211648, 211652).

[5] Careful comparison of the three specimens before preservation revealed no differences in plumage pattern or coloration.

Very similar but lacking the white tipping are a *kempi* from Chatham Island, May 1892 (USNM 208603), and an *elegans* from Nightingale Island, November 1950 (AMNH 648710)." A new subspecies, *P.a. myrtae*, with distinct white feather edgings, however, has been described recently (Bourne, 1959) and it appears that immatures and fresh-plumaged adults frequently possess white feather edgings that soon wear off (Bourne, 1959; Palmer, 1962). The specimens from St. Paul fit into the complex of southern *P. assimilis* populations, but, in view of the uncertain taxonomic relationships of these shearwaters, it seems inadvisable to assign them to subspecies on the basis of the specimen material presently available.

A breeding population of *P. assimilis* has not yet been described from St. Paul Island. Jouanin and Paulian (1960) reported the species from a single subfossil tarsus and there is a recently fledged young specimen, which was collected near St. Paul Island on Jan. 26, 1956, by P. Paulian, in the collections of the Museum National D'Histoire Naturelle in Paris (Jouanin, in litt.).

Puffinus lherminieri **Audubon's Shearwater**

This small shearwater was common in the vicinity of Socotra, the Seychelles, Mauritius, and Reunion Islands, but not in the intervening seas (see table 5). A flock of 15 small black and white shearwaters (*P.l. persicus?*) was also seen near the Pakistani coast between Bombay and Karachi on May 18, 1964.

Four *P. lherminieri* came aboard the *Anton Bruun* just north of the Seychelles during the evening of Feb. 11, and were collected. These specimens, however, will be included in a more comprehensive discussion of the seabirds of the Seychelles (Gill, in prep.).

Pterodroma baraui **Barau's Petrel**

A *Pterodroma* petrel, which I was unable to identify at the time, was fairly common in the vicinity of Reunion Island on Mar. 3 and 4, 1964. Scattered individuals, apparently of the same species were seen as far south as 27°02′ S (see table 6). Subsequent observations and study of Barau's petrel on Reunion (Jouanin and Gill, MS) convinced me that I had been seeing this recently described species.

Description (from at-sea observations): upperparts light brown, primaries darker; underparts white including the undersurface of the wing, except for a narrow black band on the fore-edge of the wing becoming widest in the primaries; face white; whitish collar; tail rounded; flight with pronounced soaring and swooping, rising high on the upswing, no flapping. Especially confusing was the fact that the back appeared brown, not the characteristic grey of *P. baraui* in the hand, but this undoubtedly resulted from the phenomenon whereby

grey or blackish birds at sea often appear brown against the blue of the ocean.

Pterodroma macroptera **Great-winged Petrel**

Occasional individuals were seen in subantarctic waters, primarily south of Amsterdam Island (see table 3). Two dark, fast-flying petrels seen at 27°02′ S, 55°49′ E, on Mar. 12 may have been this species though the proximity of the location to Reunion Island also suggests the possibility of *P. aterrima*.

Pterodroma incerta **Schlegel's Petrel**

Three individuals seen at 34°34′ S, 69°03′ E, on Apr. 2 constitute my only records of this species. Their flight consisted primarily of low gliding over the water with only occasional flapping or swooping.

Pterodroma m. mollis **Soft-plumaged Petrel**

We saw this petrel commonly in subantarctic waters south of 31°31′ S and recorded the highest numbers (30) at our southernmost station (see table 3). A petrel seen at 28°58′ S, 55°08′ E, on Mar. 6 was probably this species.

A single specimen was obtained at 40°04′ S, 75°00′ E, on Apr. 4. It was a male with small gonads and weighed 277.4 grams. The bill was black, the irides brown, and the feet were flesh colored, except for the outer toe and distal two-thirds of the web, which were black. The stomach contained cephalopod beaks. The measurements (in mm) were: wing 256.5; tail 115; culmen 28; tarsus 36; middle toe 45.

Pterodroma mollis is recognized easily by its small size, greyish-brown upperparts, and dark chest band against the white underparts. Its flight is fast and erratic with rapid swooping and swift, deep wing strokes, reminding one of a small jaeger (*Stercorarius*). Frequently it flies very high and then dives to the surface of the ocean, appearing to make "passes" at other birds. After dark (2100 hours) on Apr. 5, I saw a soft-plumaged petrel (made visible by the deck lights) feeding; it landed briefly on the water several times, picked up something from the surface, and then flew a short distance before repeating this procedure.

Pterodroma (leucoptera)

I saw a single, small, grey, black and white petrel on Mar. 13 at 24°10′ S, 56°24′ E. Apparently it was a member of the South Pacific *Cookilaria* complex though the possibility of *P. hypoleuca* could not be eliminated with certainty. Patrick J. Gould, who is familiar

with the Pacific gadfly petrels at sea, concurs in this identification after examining my field notes and sketches.

***Pterodroma* species**

An unidentified large, greyish-brown (=grey?) petrel with a darker head and tail and white underparts was observed west of the Seychelles Islands at 05°23′ S, 48°08′ E, on June 1. There was a pronounced dark stripe on the upper wing surface and the underwings were white with broad black margins. The flight consisted entirely of pendulum-like swooping motions with no flapping.

Bulweria fallax **Jouanin's Petrel**

In January and February medium-sized, all-dark petrels were seen regularly over most of the Arabian Sea between Bombay and Socotra. The majority of these could not be identified positively because of the difficulties involved in the separation of this species from *Puffinus pacificus* and perhaps some *Pterodroma* petrels; however, a few positive identifications of *B. fallax* were obtained and all individuals seen at close range proved to be this species; consequently, I have included here all unidentified dark brown petrels seen in the Arabian Sea from the *Anton Bruun*. Positive identifications are indicated in table 7 by an asterisk.

Using these criteria, 104 "*Bulweria fallax*" were seen during 64 hours of intensive surveillance between Jan. 27 and Feb. 10. Several small flocks (up to 50 birds) were encountered near Socotra, where the species was most common. My southernmost record was of four individuals at 00°31′ S, 54°56′ E, on Feb. 10.

In late May, Jouanin's petrel was the most commonly observed pelagic species on a course paralleling the Arabian coast. At least 53 *B. fallax* plus an additional 16 petrels that were either this species or *Puffinus pacificus* were seen between 22°59′ N, 65°42′ E, and 02°02′ N, 51°11′ E, in 17 hours of observation.

The flight of *B. fallax* consists of five or six quick flaps followed by a glide low over the water or a swoop down to the water from the extra height it has gained. Only occasionally does the petrel swoop in the pendulum fashion of some *Pterodroma* and, when it does, its flight hardly seems fast or erratic. The shearwater-like flight pattern seems to be used when the bird is foraging and the pendulum motion when it is travelling, though the force of the wind is also an important factor (see Bailey, 1966, p. 240). Although I saw groups of this petrel near Socotra, single individuals usually were encountered. On occasion they were seen to land on the water for extended periods of time and appeared to be feeding on squid.

Oceanites oceanicus **Wilson's Petrel**

Five scattered individuals were seen south of the subtropical convergence in early April (see table 8). None were seen in the Arabian Sea in January and February, but in May a flock of more than 50 Wilson's petrels was passed between Bombay and Karachi and still others were found near the African coast during the last week of May.

Pelagodroma marina **Frigate Petrel**

Nine frigate petrels were seen in late May between Karachi and the Seychelles Islands (see table 8). Instead of the characteristic grey, they appeared "light brown" to my eye.

Fregetta grallaria **White-bellied Storm Petrel**

Several dark storm petrels with white rumps and bellies were seen near Amsterdam and St. Paul Islands and in the waters to the south (see table 8). Although I had excellent looks at some of these, I was unable to discern any black in the middle of the white underparts. An additional 10 *Fregetta* species (probably *F. tropica:* see Bailey, 1966, p. 243) were seen in the Arabian Sea (and vicinity) between May 22 and June 2.

Oceanodroma monorhis **Swinhoe's Storm Petrel**

On two occasions (00°58′ N, 55°00′ E, on Feb. 9; 10°46′ S, 55°00′ E, on Feb. 18), I saw an all-dark storm petrel with a forked tail and very fast, erratic flight. Bailey (1965) found two species of all-dark storm petrels, the smaller of which was *O. monorhis*, verified by the capture of specimens. It seems reasonable, therefore, to assign my two observations to this species.

Oceanodroma matsudairae **Matsudaira's Storm Petrel**

Scattered individuals (12 total) of an unidentified storm petrel were seen between latitudes 07°17′ N and 21°00′ S; over one-half of these observations were made near the equator (see table 9). This petrel was the size of a large *Oceanodroma* (or *Bulweria bulweria*) but was not nearly as large as *B. fallax*. It was entirely dark brown in color though some individuals had conspicuously paler upper wing coverts. The flight was deliberate, almost sluggish, consisting of four or five deep wing strokes followed by a short glide with the wings bowed downward. The tail appeared either square or slightly forked.

Bailey (1964, 1965) observed a large *Oceanodroma* commonly in the vicinity of the equator from March to May 1964 and suggested that it was *O. matsudairae* from the Pacific. Since then, two specimens confirming this tentative identification have been collected in the

Indian Ocean off Western Australia by Pocklington, Willis, and Palmieri (unpubl.).

Phaëthon aethereus **Red-billed Tropicbird**

In late January and early February this tropicbird was fairly common in the western Arabian Sea east to 69°11′ E and south to 11°01′ N, often very far from land (see table 10). In late May, five were seen only 17°29′ N, 62°31′ E, and three at 02°02′ N, 51°11′ E. No other species of tropicbirds were identified in this region.

Phaëthon lepturus **White-tailed Tropicbird**

White-tailed tropicbirds were first encountered at 08°42′ S, 55°07′ E, on Feb. 17 and were not seen south of 24° S on this transect of the cruise (see table 11). On the 75° E transect the first one was seen at 16°42′ S; we noted the species at only two of the remaining stations to the north. Many white-tailed tropicbirds were present near the the Seychelles Islands on June 2.

Sula dactylatra **Masked Booby**

Scattered individuals were seen in the southwestern Arabian Sea and near the Seychelles Islands in January–February and again in late May (see table 10).

Sula leucogaster **Brown Booby**

Four adults were seen near Socotra, one at 14°40′ N, 55°25′ E, on Feb. 1 and three at 11°30′ N, 52°53′ E, on Feb. 4.

Fregata ariel **Lesser Frigatebird**

I saw this species only twice; three at 07°02′ S, 55°11′ E, on Feb. 16, and two near the Seychelles Islands on June 2.

Lobipes lobatus **Northern Phalarope**

Ten northern phalaropes were seen near the Indian coast (17°44′ N, 69°11′ E) on Jan. 27.

Catharacta skua **Skua**

A single individual was seen five miles west of Mauritius on Mar. 2. Three skuas were observed at St. Paul Island on Apr. 7.

Larus fuscus **Lesser Black-backed Gull**

Several were seen near the Gulf of Aden, one on Feb. 2 and five on Feb. 3.

Larus hemprichii **Aden Gull**

Two, possibly three, individuals were seen in the Gulf of Aden on Feb. 1–2.

Larus brunneicephalus **Indian Black-headed Gull**

A flock of 12 was passed about 75 miles east southeast of Bombay on Jan. 27.

Sterna vittata tristanensis **Murphy** **Antarctic Tern**

This tern was common near both St. Paul and Amsterdam Islands, where flocks of up to 100 individuals were seen just offshore.

Thirteen specimens in molt and nonbreeding condition were collected, one at St. Paul Island on Apr. 7 and the rest at Amsterdam Island on Apr. 8. In addition to winter-plumaged adults, they include several heavily barred immatures. Measurements of the skins from Amsterdam Island are included in table 12. Although the wings of this series are small (cf. Murphy, 1938), the culmen and tarsus lengths seem sufficient to separate this race from the smaller *S. v. vittata*, which breeds on Kerguelen. Of 10 stomachs examined, four contained tiny cephalopods, four contained fish, one had both fish and cephalopods, and one contained the remains of small crustacea.

Sterna repressa **White-cheeked Tern**

Common at sea between Bombay and Karachi on May 18.

Sterna anaethetus **Bridled Tern**

Seen at sea only in the vicinity of the Seychelles Islands on June 2.

Sterna fuscata **Sooty Tern**

Although sooty terns were absent from the Arabian Sea south to the Seychelles in January and February, large flocks were seen 200–300 miles east of the Somalian coast of East Africa (between 06°46′ N, 55°00′ E, and 06°05′ S, 42°11′ E) and east to the Seychelles Islands in late May (see table 11). Sooty terns were common near Mauritius in February and March, and scattered individuals and flocks were seen near the Chagos and Maldive Islands in late April.

Thalasseus bergii **Crested Tern**

Five *Thalasseus* terns were seen at 06°05′ S, 42°11′ E, on May 31 and a single *T. bergii* was observed near the Seychelles on June 2.

Anous stolidus **Common Noddy**

Common noddies were numerous near both the Seychelles Islands and Mauritius, but only two individuals were seen at sea, one at 00°27′ S, 54°57′ E, on Feb. 10 and the other at 22°51′ S, 54°58′ E (southwest of Reunion), on Mar. 4.

Gygis alba **Fairy Tern**

Fairy terns were seen close to the Seychelles Islands in both February and June.

In early February between 08°00′ N and 00°49′ S on the 55° E transect, a species of tern was noted flying around the *Anton Bruun* at night (see table 13). Using spot lights, we obtained good observations, discerning an *all*-white tern with a slightly forked tail that left, in my opinion, little doubt as to the identity. The birds were quite vocal, emitting short, low notes, especially when two were together. The presence of fairy terns so far out to sea and only at night (none were seen during the daytime watches) is surprising, for the nearest possible source of these birds, the Seychelles Islands, was well over 600 miles to the south and *Gygis* is usually known as a coastal or inshore species, not a pelagic one (Murphy, 1936). One wonders, however, whether scattered individuals were drawn to and concentrated around the ship at night, thereby becoming conspicuous, and also whether the species might not be as highly nocturnal as the huge eyes and pure white plumage suggest. These observations should remain hypothetical pending future confirmation.

Discussion

The distribution of seabird species and numbers is related to oceanographic factors that produce a suitable variety and abundance of food items (Jespersen, 1929; Hutchinson, 1950; Murphy, 1936). Although the data presented in this paper are insufficient in themselves, it is hoped that the total information gathered during the International Indian Ocean Expedition eventually will provide the basis for a detailed analysis of the factors underlying seabird distributional patterns in the Indian Ocean. A noteworthy step in this direction has been made recently by Bailey (1966) for the important region of upwelling off the southern Arabian coast. The rest of the Indian Ocean, however, awaits comparable attention.

One of the conclusions that is readily apparent from the data presented in this paper is the paucity of seabirds in the major part of the western Indian Ocean. In this respect, the Indian Ocean is similar to other tropical oceans, which are characterized by the relative infertility of their waters and a consequent scarcity of seabirds, except in the vicinity of land, either islands or continental coasts, and regions of local enrichment. It was only in the western Arabian Sea and below the subtropical convergence, regions where upwelling, cooler surface temperatures or other factors permit nutrient replenishment and continued productivity, and near the Seychelles and Mascarene Islands, which provide land necessary for breeding and roosting, that seabirds were at all numerous. But even the maximum numbers (200+/hour) I recorded in these regions were certainly small compared to what is possible in other parts of the world ocean (see Murphy, 1914; Oordt and Kruijt, 1955), especially

at higher latitudes. The numbers of seabirds recorded by Bailey (1966) off Arabia were also considerably greater than my counts and serve to emphasize the highly localized nature of seabird distribution in the Indian Ocean.

The composition of seabird communities often changes markedly during a year because of movements of seabirds that correspond to changes in the availability of food items and/or that are a part of extensive postbreeding migrations. In the Indian Ocean the most striking seasonal differences are those found in the western Arabian Sea (see Bailey, 1966; Bourne, 1960, 1963; Jouanin, 1957). In this area there is, first of all, a resident seabird community, which includes no less than eight endemic forms (four species and four subspecies). The majority of its species occur primarily in the inshore waters close to breeding and/or roosting stations (Bailey, 1966) with the result that only a few, e.g., *Bulweria fallax* and *Phaëthon aethereus*, are encountered regularly as far out to sea as were the stations included in this report. The presence of dark petrels, all apparently *B. fallax*, at our stations in the Arabian Sea in January and February east as far as 69°11′ E suggests that Jouanin's petrel disperses widely at sea from its yet undiscovered breeding stations near the Arabian coast, at least during the nonbreeding season. Unfortunately, the southern limits of these movements remain uncertain because of the difficulty of separating it from other dark petrels. All my records were made north of the equator (actually 00°31′ S), but there is a specimen from Kenya (Jouanin, 1957), and Bailey (in prep.) saw dark petrels "inseparable from *B. fallax* south to 15° S."

In May, coinciding with the onset of the monsoon winds, with the consequent offshore upwelling, and with increased productivity, the resident species of the western Arabian Sea are subjected to an influx of large numbers of several migrant species from the subantarctic Indian Ocean. Included in this arriving assemblage are three species of storm petrels: *Oceanites oceanicus* and *Fregetta tropica* from Kerguelen and the Crozet Islands (Bourne, 1960), and *Pelagodroma marina* from breeding stations off southwest Australia (Mörzer Bruyns and Voous, 1964). All of my observations are in accord with the known arrival times and distribution of these species in the northern Indian Ocean, though actual records of Wilson's petrels near the African coast may be noteworthy.

Arriving from the same area as *Pelagodroma* is the large pale-footed shearwater, *Puffinus carneipes*. Unfortunately, the majority of shearwaters I saw near the Maldive Islands in April did not come close enough to permit positive identification; however, most appeared too large, with too heavy a flight to be *P. pacificus* and consequently were considered to be *P. carneipes*. A light bill could be discerned on a

few individuals. Although large numbers do not appear until late May, pale-footed shearwaters are known to arrive in the Arabian Sea as early as mid-April (see Bailey, 1966) and, hence, records near the Maldives would not be unexpected at this time.

The status of the other dark shearwater in the Arabian Sea, the wedge-tailed shearwater, is particularly hazy because of the ease of confusion with *Bulweria fallax*. For years it was considered to be the common dark petrel in the western Arabian Sea (Alexander, 1931; Phillips, 1954) until these records were reexamined (Jouanin, 1957) in light of the discovery of *B. fallax*, which is very similar in appearance. Although a few specimens have been taken in the Arabian Sea, wedge-tailed shearwaters certainly appear to be rare there, for Bailey (1966) recorded none positively north of 10° N and I saw but one. It seems necessary, therefore, to establish just how common this species actually is in order to determine whether only occasional stragglers are involved or whether there are enough to justify postulations of either a local population or a migratory movement from another part of the Indian Ocean. The latter possibilities have been suggested (Bourne, 1960), and the idea of a local undiscovered breeding population seems especially attractive in view of several recent discoveries of small breeding populations of this species on tiny rock offshore islets, for example near Madagascar (Appert, 1965), Reunion (Jouanin, pers. comm.) and Roderigues (Vinson, 1965). In this connection also, the Maldive Islands may harbor a population of wedge-tailed shearwaters, thereby accounting for some of the shearwaters seen at sea in that area.

Just now being established is the regular occurrence in the equatorial regions of the Indian Ocean of two storm petrels from the Pacific, *Oceanodroma monorhis* and *O. matsudairae*. Although their numbers seem to be greatest during the northern summer (Bailey, in prep.), my observations indicate that at least small numbers are present throughout the year. One cannot help but wonder if there are also undiscovered breeding populations of storm petrels in the Indian Ocean, and again the Maldive or perhaps the Chagos Islands seem likely locations. In addition to *Oceanodroma* species, *Bulweria bulweria*, which has been recorded in the Indian Ocean (Phillips, 1959; Bourne, 1960; Jouanin, 1957), might also be sought.

Perhaps the least understood seasonal change in the western Indian Ocean are the movements of the sooty terns that breed in the Seychelles and Amirante Islands in huge numbers from May to October and that then disappear for the remainder of the year. Whether they move to other island groups, such as the Aldabras, Chagos, or perhaps Cargados Carajos Shoals, or spend these six months at sea is unknown. In February I saw no sooty terns north

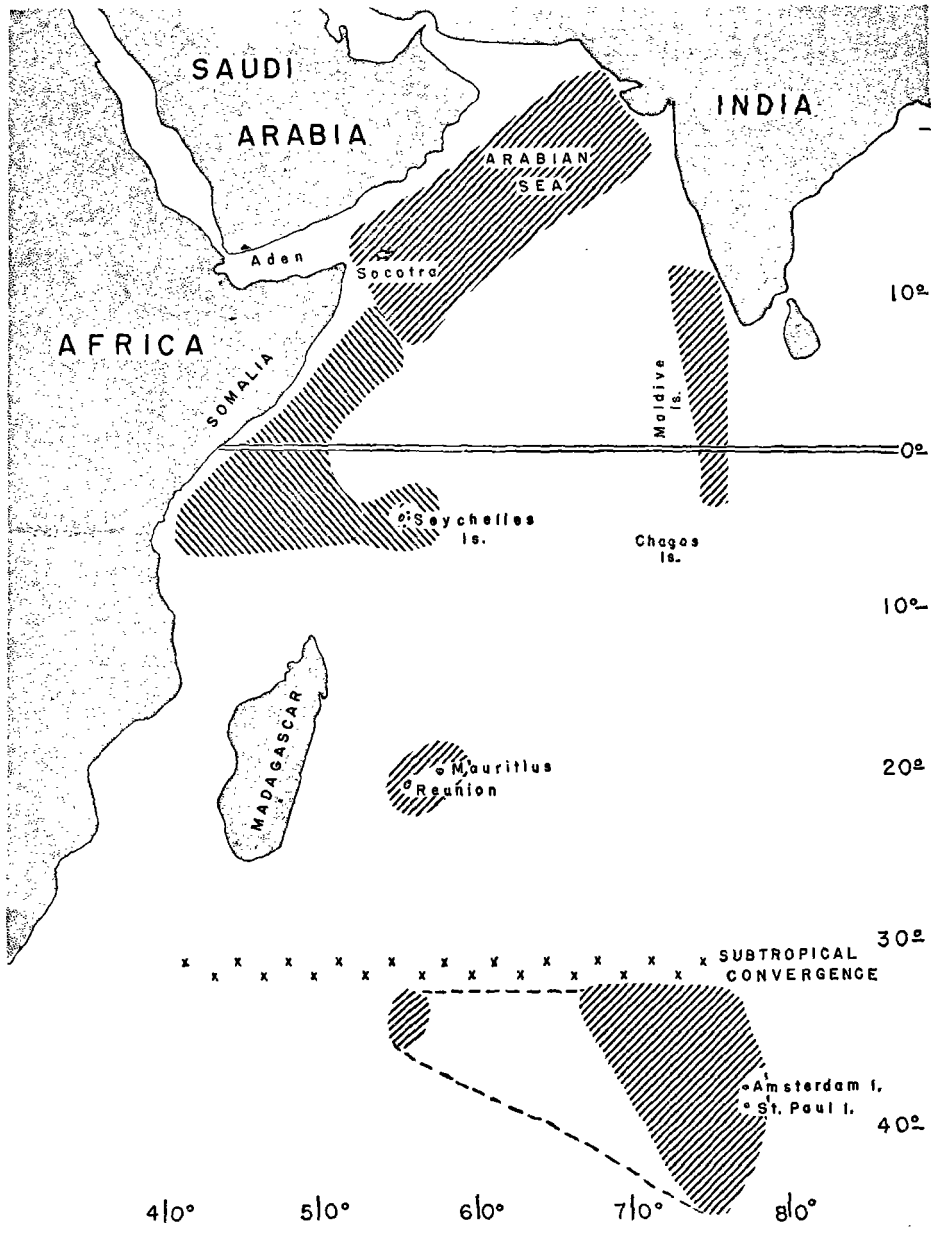

FIGURE 2.—Regions of observed seabird abundance in the western Indian Ocean.

of the Mascarene Islands on our 55° E transect, whereas in May large flocks were present at 06°46′ N on this same longitude, as well as the seas south to the Seychelles and southwest to the African coast. Other observers (e.g., Bailey, in prep.) report a similar seasonality in their observations of sooty terns in this region.

The Mascarene region is of particular interest because it is the only place in the tropical or subtropical Indian Ocean where breeding

petrels of the genus *Pterodroma* are found. No less than three species of *Pterodroma* breed (or did) in the Mascarenes: the Trinidad petrel (*P. arminjoniana*) on Round Island off the north coast of Mauritius; Barau's petrel (*P. barau*i) and the little known Mascarene petrel (*P. aterrima*), presumably on Reunion. This latter species is apparently extinct as it has not been seen alive in this century (Bourne, 1965) and was not found during an intensive search for petrels on Reunion in 1964 (Jouanin and Gill, MS). Barau's petrel is the most recently described species of petrel (1964), despite its being a fairly common species on Reunion; however, it is not known whether this petrel remains near Reunion throughout the year or disperses to sea in some direction during the nonbreeding season (austral winter). It does appear to confine its pelagic activities during the breeding season to the south and west of Reunion Island, as none were seen to the north or immediately to the east by either Roger Bailey or myself. Since the tropical convergence in the western Indian Ocean is located at approximately the same latitude as the Mascarene Islands (Baker, 1965), these observations suggest that Barau's petrel feeds primarily in subtropical waters. Similarly, the location of the only other breeding population of *Pterodroma a. arminjoniana* (on Trinidad Island in the South Atlantic) at almost precisely the same latitude as the Mascarene population might imply a dependence on the proximity of subtropical waters, but unfortunately this species rarely has been noted at sea.

Oceanographically, the position of the subtropical convergence, where cooler subantarctic waters sink below the warm water mass of the central (tropical) ocean, delimits the southern boundary of the Indian Ocean (Sverdrup, Johnson and Fleming, 1942). This is a *region* rather than a well-marked line and generally is considered to lie at about 40° S. Ornithologically it is of interest because it seems to coincide with the northern limits of the distributions of a variety of procellariiform species. Our northernmost records of certain southern petrels, such as the white-chinned petrel and soft-plumaged petrel, were at 31° S; nevertheless, these species were found primarily south of 34° S as were the majority of others including the albatrosses. On a transect in early July, comparable to our 55° E transect, Rand (1962) also encountered the first southern petrels at about 30° S and noted a marked increase just below 35° S; however, the numbers of individuals and the variety of species he recorded were slightly greater than ours and, in addition, he found them as far north as 26° S at stations closer to the African coast. The surface water temperatures recorded by Rand averaged several degrees lower than our measurements.

Although many of the species encountered by Rand below 30° S were the same as we found, there were several important differences. Conspicuous by their absence on our March–April cruise were Cape pigeons (*Daption capense*) which were the "most abundant of small petrels" on his cruise in June–July. Also, on a previous cruise of the *Anton Bruun* through these latitudes in September (1963) Cape pigeons were common (P. Willis, pers. comm.). On the other hand, Rand saw few white-chinned petrels (*Procellaria aequinoctialis*) except near the African coast, whereas in March and April this was a predominant species at our southern stations. Similarly, the soft-plumaged petrel (*Pterodroma mollis*), which was a common species at our stations, was not even recorded by Rand. It is unfortunate that so few detailed reports of seabird species and numbers are available for this region as there seem to be marked seasonal fluctuations in the composition, distribution, and perhaps size of its seabird community. Some of these may be related only to reduced pelagic activity during the breeding season but others may be correlated with seasonal changes in productivity. Also interesting would be an elucidation of the subtropical convergence's role in limiting seabird distribution.

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TABLE 1.—*Seabird numbers recorded during standardized watch periods* (station = IIOE Oceanographic Station, *Anton Bruun;* A = Procellariiformes; B = Pelecaniformes; C = Charadriiformes)

Date	Locality	Sta. No.	Water temp. (° C)	Time	A	B	C	Birds/ Hr.
Jan. 27	17°44′ N, 69°11′ E	-	-	0900-1100	6	4	22	16
" 28	17 12 N, 67 00 E	-	-	0755-1045	6	2	0	2.5
" 29	16 13 N, 63 29 E	282	25.2	0830-1130	2	1	0	1
" 30	15 42 N, 60 52 E	283	25.1	0830-1100	2	2	0	1.6
" 31	15 22 N, 58 12 E	284	23.9	0830-1130	3	1	0	1.3
" 31	15 18 N, 57 59 E	-	-	1530-1630	12	1	0	13
Feb. 1	14 22 N, 55 18 E	285	24.0	0800-1100	4	0	0	1.3
" 2	13 50 N, 52 59 E	286	24.9	0815-1115	4	3	1	2.6
" 3	13 11 N, 50 22 E	287	24.8	0805-1105	0	0	6	2
" 3	13 08 N, 50 36 E	-	-	1600-1700	9	0	0	9
" 4	11 30 N, 52 53 E	-	-	0835-1135	80+	3	0	27
" 4	11 01 N, 53 30 E	-	-	1345-1645	7	0	16	7.6
" 5	09 28 N, 54 52 E	288	26.0	0820-1120	3	0	0	1
" 6	07 10 N, 55 05 E	289	26.5	0815-1045	4	0	0	1.3
" 6	06 52 N, 55 06 E	-	-	1730-1830	2	0	0	2
" 7	05 02 N, 55 01 E	290	26.5	0800-1100	0	0	0	0
" 8	02 31 N, 55 04 E	291	27.6	0810-1110	0	0	0	0
" 8	02 15 N, 54 57 E	-	-	1720-1820	1	0	0	1
" 9	01 03 N, 54 56 E	292	28.0	0820-1120	1	0	0	0.3
" 9	00 58 N, 54 53 E	-	-	1720-1820	2	0	0	2
" 10	00 31 S, 54 56 E	293	28.2	0820-1120	6	0	1	2.3
" 10	00 49 S, 54 49 E	-	-	1720-1820	2	0	0	2
" 11	02 51 S, 54 58 E	294	28.3	0830-1130	5	0	0	1.6
" 11	03 20 S, 55 13 E	-	-	1725-1825	6	0	6	12
" 15	Seychelles, east coast of Mahe	-	-	1730-1830	11	0	2	13
" 16	06 28 S, 55 12 E	295	29.2	0810-1110	1	0	0	0.3
" 17	08 42 S, 55 07 E	296	28.4	0800-1120	2	2	0	1.3
" 17	09 02 S, 55 13 E	-	-	1720-1820	0	0	0	0
" 18	10 47 S, 55 15 E	297	28.9	0800-1100	3	0	0	1
" 19	12 33 S, 54 33 E	298	28.4	0840-1140	1	1	0	0.6
" 19	13 04 S, 54 37 E	-	-	1720-1820	0	0	0	0
" 20	14 57 S, 54 43 E	299	27.6	0810-1050	0	1	0	0.3
" 20	15 34 S, 54 50 E	-	-	1720-1820	0	0	0	0
" 21	17 14 S, 54 38 E	300	28.0	0815-1115	-	1	0	0.3
" 22	Mauritius (50 to 20 miles west)	-	-	0900-1130	40	5	170	86
Mar. 2	Mauritius (0 to 30 miles west)	-	-	1430-1630	12	2	15	14.5
" 3	19 57 S, 54 58 E	301	26.8	0810-1110	4	5	4	4.3
" 3	20 34 S, 54 58 E	-	-	1745-1830	6	2	0	10.6
" 4	23 07 S, 54 50 E	302	25.8	0805-1105	9	0	1	3.3
" 4	24 07 S, 54 55 E	-	-	1730-1830	2	0	0	2
" 5	26 00 S, 54 52 E	303	25.4	0830-1130	1	0	0	0.3
" 5	26 25 S, 55 01 E	-	-	1730-1830	1	0	0	1
" 6	28 22 S, 55 02 E	304	24.8	0815-1115	0	0	0	0
" 6	28 58 S, 55 08 E	-	-	1720-1820	0	0	0	0
" 7	30 50 S, 55 09 E	305	22.4	0820-1120	1	0	0	0.3
" 7	31 25 S, 54 59 E	-	-	1720-1820	0	0	0	0
" 8	33 13 S, 55 10 E	306	21.0	0805-1125	6?	0	0	2
" 8	33 52 S, 55 05 E	-	-	1730-1845	4	0	0	3.2
" 9	35 42 S, 55 15 E	307	19.7	0800-1100	11	0	0	3.6
" 9	35 00 S, 55 16 E	-	-	1725-1825	5	0	0	5
" 12	27 02 S, 55 49 E	-	-	1730-1830	1	0	0	1
" 13	24 10 S, 56 24 E	-	-	0825-1025	1	0	0	0.5

TABLE 1.—Continued

Date	Locality	Sta. No.	Water temp. (° C)	Time	A	B	C	Birds/ Hr.
Mar. 14	21°00′ S, 57°00′ E	-	-	0830-1130	4	1	145	50
" 14	20 40 S, 57 07 E	-	-	1220-1420	300	1	100	200
" 29	21 43 S, 57 43 E	-	-	0825-0925	0	0	1	1
" 29	22 33 S, 58 22 E	-	-	1420-1620	3	0	5	4
" 30	24 57 S, 60 09 E	-	-	0835-1035	0	0	0	0
" 31	28 44 S, 63 36 E	-	-	1415-1615	0	0	0	0
Apr. 1	31 29 S, 65 58 E	-	-	0815-1115	0	0	0	0
" 1	32 20 S, 66 47 E	-	-	1545-1645	0	0	0	0
" 2	34 24 S, 69 03 E	-	20-19.2	0830-1130	5	0	0	1.6
" 2	34 53 S, 69 37 E	-	-	1345-1445	1	0	0	1
" 3	37 55 S, 72 23 E	-	-	0800-1100	29+	0	0	10
" 3	38 01 S, 73 19 E	-	-	1400-1700	25	0	0	8.3
" 4	40 04 S, 75 00 E	308	15.0	0600-0930	92	0	0	23.4
" 5	42 23 S, 74 54 E	309	12.1	0830-1430	37	0	0	6
" 6	43 31 S, 75 27 E	-	-	0700-1600	126	0	0	14
" 7	39 48 S, 77 20 E	-	-	0845-1100	32	0	0	14
" 7	St. Paul Island (within 30 miles)	309C	-	1200-1500	300+	0	53+	120
" 8	Amsterdam Island (offshore)	309E	-	all day	120	0	150	-
" 9	37 01 S, 75 19 E	310	17.0	0630-0930	21	0	0	7
" 10	34 31 S, 74 47 E	311	19.3	0630-0930	15	0	0	5
" 11	31 26 S, 74 57 E	312	22.6	0800-1000	2	0	0	1
" 12	29 00 S, 74 51 E	313	22.5	0630-0930	1	0	0	0.3
" 13	26 27 S, 75 02 E	314	24.5	0630-0730	0	0	0	0
" 14	24 20 S, 74 52 E	315	24.7	0800-1000	0	0	0	0
" 15	21 58 S, 74 55 E	316	26.0	0830-1030	0	0	1	0.5
" 16	19 44 S, 75 20 E	317	27.0	0800-1000	0	0	0	0
" 17	16 43 S, 74 53 E	318	28.1	0825-1025	0	1	0	0.5
" 18	14 10 S, 74 55 E	319	28.3	0830-1030	1?	0	0	0.5
" 19	11 47 S, 74 42 E	320	28.8	0820-1020	0	0	0	0
" 20	09 21 S, 75 08 E	321	29.3	0810-1010	0	0	0	0
" 21	06 50 S, 75 02 E	322	29.2	0820-1020	0	0	0	0
" 22	04 11 S, 75 00 E	323	29.1	0820-1020	1	0	0	0.5
" 24-27	Maldive Islands (Addu Atoll)	-	-	no standardized watch	-	-	-	-
" 28-30	Maldives to Cochin, India	325-327	-	no standardized watches	-	-	-	-
May 18	Bombay to Karachi	-	-	0900-1300	65	0	200+	66
" 20	22 59 N, 65 42 E	-	-	0905-1105	2	0	0	1
" 21	17 29 N, 62 31 E	-	-	0915-1245	28	4	0	91
				1400-1545	11	1	0	6.8
" 22	12 05 N, 58 58 E	-	-	0910-1130	26	0	0	11.3
				1410-1530	5	0	0	3.8
" 23	06 46 N, 55 00 E	-	-	0845-0945	1	0	0	1
				1400-1600	6+	0	8+	7
" 24	02 02 N, 51 11 E	-	-	0925-1225	9	3	275	96
" 25	01 42 S, 45 46 E	-	-	0910-1110	10	0	500	255
" 26	Mombasa—32 miles northeast	-	-	0910-1010	1	0	0	1
" 31	06 05 S, 42 11 E	-	-	0915-1215	2	0	76	26
June 1	05 23 S, 48 08 E	-	-	0915-1215	2	1	360+	120
" 2	04 33 S, 54 17 E (Seychelles Is.)	-	-	0910-1210	11	2	226	80

TABLE 2.—*Observations of albatrosses (Diomedeidae)*

Date	Location	Time	*Diomedea exulans*	*Diomedea melanophris*	*Diomedea chlororhynchos*	*Diomedea cauta*	*Phoebetria fusca*
Mar. 8	33°52′ S, 55°05′ E	1730–1845	1	0	0	0	0
" 9	35 42 S, 55 15 E	0800–1100	1	0	0	0	0
Apr. 3	37 55 S, 72 23 E	0800–1100	12	0	2	1	0
" 3	38 01 S, 73 19 E	1400–1700	6	0	2	0	0
" 4	40 04 S, 75 00 E	all day	20	4–5	0	2–3	10
" 5	42 23 S, 74 54 E	all day	6	1	0	0	2–3
" 6	43 31 S, 75 27 E	all day	25	2–3	0	2–3	4–5
" 7	38 48 S, 77 20 E	0845–1100	17	0	1	2	3
" 7	St. Paul Island (within 30 miles)	1200–1500	12	0	0	0	10
" 8	Amsterdam Island (off-shore)	all day	15	0	4–5	0	25–30
" 9	37 01 S, 75 19 E	all day	6	1	0	1	1
" 10	34 31 S, 74 47 E	0630–0930	1	0	4 (repeats)	0	1

TABLE 3.—*Observations of subantarctic petrels (Procellaridae)*

Date	Location	Time	*Procellaria aequinoctialis*	*Adamastor cinereus*	*Pterodroma macroptera*	*Pterodroma mollis*	*Pachyptila* species
Mar. 7	30°50′ S, 55°09′ E	0820–1120	1	0	0	0	0
" 8	33 13 S, 55 05 E	0805–1125	8	0	0	0	0
	33 52 S, 55 05 E	1730–1845	2	0	0	0	0
" 9	35 42 S, 55 15 E	0800–1100	11	0	0	8	0
" 12	27 02 S, 55 49 E	0930	0	0	2?	0	0
Apr. 2	34 24 S, 69 03 E	0830–1130	1?	0	0	0	0
" 3	37 55 S, 72 23 E	0800–1100	10	0	0	5	0
	38 01 S, 73 19 E	1400–1700	8	0	0	4	0
" 4	40 04 S, 75 00 E	all day	30	0	1	15	5–6
" 5	42 23 S, 74 54 E	all day	10	0	1–2	3–4	20
" 6	43 31 S, 75 27 E	all day	20	1–2	6	30	30
" 7	38 48 S, 77 20 E	0845–1100	5	1	3	2	7
" 7	St. Paul Island (0–30 miles)	1200–1500	10	0	0	0	10
" 8	Amsterdam Island (offshore)	all day	40	0	4–5	4	1
" 9	37 01 S, 75 19 E	all day	7	0	0	3–4	0
" 10	34 31 S, 74 47 E	0630–0930	5	0	2?	1	0
" 11	31 26 S, 74 57 E	0800–1000	0	0	0	2	0
" 12	29 00 S, 74 51 E	0630–0930	0	0	0	1?	0

TABLE 4.—*Observations of* Puffinus carneipes

Date	Location	Time	Number
		1415	
Apr. 19	11°47′ S, 74°42′ E	0820–1020	1
" 22	04 11 S, 75 00 E	1200, 1800	1?
" 23	02 14 S, 75 14 E	0630–0730	1, 1
" 24	Maldive Islands (Addu Atoll, Gan Is.)		2
" 28	02 01 N, 75 13 E	1600	1 (reported)
" 29	04 49 N, 74 55 E	1400	2
" 30	06 51 N, 75 02 E	1030	4
May 3	14 48 N, 73 41 E	1200	8 (reported)
" 21	17 29 N, 62 31 E	0915–1245	3
		1400–1545	1

TABLE 5.—*Observations of tropical shearwaters* (Puffinus)

Date	Location	Time	*pacificus*	*lherminieri*
Jan. 29	16°13′ N, 63°29′ E	0830–1130	2?	0
Feb. 1	14 22 N, 55 18 E	0800–1100	0	4
	14 09 N, 54 38 E	1830	0	1
" 2	13 50 N, 52 59 E	0815–1115	0	3
	13 51 N, 52 45 E	1600–1700	0	7
" 3	12 55 N, 50 54 E	1830	0	1
" 4	11 30 N, 52 53 E	0835–1135	0	3
	11 01 N, 53 30 E	1345–1645	0	1
" 11	02 51 S, 54 58 E	0830–1130	0	1
	03 22 S, 55 13 E	1725–1825	5	0
	03 30 S, 55 19 E	2000	0	12
" 15	Seychelles Islands (east coast of Mahe)	1700–1800	0	11
" 16	06 28 S, 55 12 E	0810–1110	1	0
" 18	10 47 S, 55 15 E	0800–1100	2	0
" 22	Mauritius—50 to 20 miles west	0900–1130	38	1
Mar. 2	Mauritius—0 to 30 miles west	1430–1630	21	1
" 3	19 57 S, 54 58 E	0810–1110	0	1
	20 34 S, 54 58 E	1745–1830	1	3
" 14	20 40 S, 57 07 E	0830	0	2
	Mauritius—20 miles south southeast	1220–1420	300	0
Apr. 20	09 00 S, 75 00 E	1500	40?	0
May 18	Bombay to Karachi	1130	0	15
" 21	17 29 N, 62 31 E	0915–1245	1	0
" 22	12 05 N, 58 58 E	1410–1530	0	1
" 24	02 02 N, 51 11 E	0925–1225	8?	0
June 2	04 33 S, 54 17 E	0910–1210	2	8

TABLE 6.—*Observations of* Pterodroma baraui

Date	Location	Time	Number
Mar. 3	19°57′ S, 54°58′ E	0810–111	1
	20 35 S, 54 58 E	1745–1830	4
" 4	23 07 S, 54 50 E	0805–1105	9
	24 07 S, 54 55 E	1650, 1730–1830	1, 2
" 5	26 00 S, 54 52 E	0830–1130	1?
	26 25 S, 55 01 E	1730–1830	1?
" 12	27 02 S, 55 49 E	1730–1830	1?
" 13	23 41 S, 56 23 E	1230–1400	1?

TABLE 7.—*Observations of* Bulweria fallax

Date	Location	Time	Number
Jan. 27	17°44′ N, 69°11′ E	0900–1100	6
" 28	17 12 N, 67 00 E	0755–1045	*6
" 30	15 42 N, 60 52 E	0830–1130	2
" 31	15 22 N, 58 12 E	0830–1130	3
	15 18 N, 57 59 E	1530–1630	*12
Feb. 1	14 08 N, 54 34 E	1830	1
" 2	13 50 N, 52 59 E	0815–1115	1
	13 51 N, 52 45 E	1600–1700	2
" 4	11 30 N, 52 53 E	0835–1135	*53+
	11 01 N, 53 30 E	1345–1645	*7
" 5	09 28 N, 54 52 E	0820–1120	2
" 6	07 10 N, 55 05 E	0815–0145	4
	06 52 N, 55 06 E	1730–1830	*2
" 8	02 15 N, 54 57 E	1720–1820	1
" 9	00 58 N, 54 53 E	1720–1820	1
" 10	00 31 S, 54 56 E	0820–1120	4
May 20	22 59 N, 65 42 E	0905–1105	2
" 21	17 29 N, 62 31 E	0915–1245	*15
		1400–1545	*10
" 22	12 05 N, 58 58 E	0810–1130	*22
		1430–1530	2
" 23	06 56 N, 55 90 E	0845–0945	1
" 24	02 02 N, 51 11 E	0925–1225	1
" 25	01 42 S, 45 46 E	0910–1110	1?

*Positive identification.

TABLE 8.—*Observations of storm petrels (Hydrobatidae)*

Date	Location	Time	*Oceanites oceanicus*	*Pelagodroma marina*	*Fregetta* sp.
Apr. 2	34°24′ S, 69°03′ E	0830–1130	1	0	0
" 3	37 55 S, 72 23 E	0800–1100	1	0	0
	38 01 S, 73 19 E	1400–1600	1	0	1
" 5	42 23 S, 74 54 E	all day	1	0	0
" 6	43 31 S, 75 27 E	all day	1	0	1
" 7	39 48 S, 77 20 E	0845–1100	0	0	1
	St. Paul Island—within 30 miles	1200–1500	0	0	6
" 8	Amsterdam Island (offshore)	all day	0	0	3–4
May 18	Bombay, Karachi	1220	50+	0	0
" 21	17 29 N, 62 31 E	0910–1245	0	1	0
" 22	12 05 N, 58 58 E	0910–1130	0	4	0
		1410–1530	0	0	2
" 23	06 46 N, 55 00 E	1400–1600	0	0	5
" 25	01 42 S, 45 46 E	0910–1110	6	1	2
" 26	32 miles northeast of Mombasa	0910–1010	1	0	0
" 31	06 05 S, 42 11 E	0915–1215	0	2	0
June 1	05 23 S, 48 08 E	0915–0215	0	0	1?
" 2	04 33 S, 54 17 E	0910–1210	0	0	1

TABLE 9.—*Observations of* "Oceanodroma matsudairae"

Date	Location	Time	Number
Feb. 6	07°10′ N, 55°05′ E	0815–1945	1
" 10	00 49 S, 54 59 E	1720–1820	2
" 11	02 51 S, 54 58 E	0830–1030	4
	03 20 S, 55 13 E	1725–1825	1
" 18	10 47 S, 55 15 E	0800–1100	1
Mar. 14	21 00 S, 57 00 E	0830–1130	2
Apr. 19	11 47 S, 74 43 E	1415	1

TABLE 10.—*Observations of* Phaëthon aethereus *and* Sula dactylatra

Date	Location	Time	*Phaëthon aethereus*	*Sula dactylatra*
Jan. 27	17°44′ N, 69°11′ E	0900–1100	4	0
		1600	2	0
" 28	17 12 N, 67 00 E	0755–1045	2	0
" 29	16 14 N, 63 27 E	0800–1130	1	1
		1500–1715	2	0
" 30	15 52 N, 60 52 E	0830–1100	4	1
	15 42 N, 60 38 E	1730	2	0
" 31	15 22 N, 58 12 E	0830–1130	1	0
	15 18 N, 57 59 E	1530–1630	0	1
Feb. 2	13 50 N, 52 59 E	0815–1115	1?	1
" 4	11 01 N, 53 30 E	1725	1	0
" 17	08 42 S, 55 07 E	0800–1120	0	1
May 20	22 59 N, 65 42 E	1400	0	1
" 21	17 29 N, 62 31 E	0915–1245	4	0
		1400–1545	1	0
" 24	02 02 N, 51 11 E	0925–1225	3	0
June 1	05 23 S, 48 08 E	0925–1225	0	1

TABLE 11.—*Observations of* Phaëthon lepturus *and* Sterna fuscata

Date	Location	Time	*Phaëthon lepturus*	*Sterna fuscata*
Feb. 17	08°42′ S, 55°07′ E	0800–1120	1	0
" 21	17 14 S, 54 38 E	0815–1115	1	0
" 22	Mauritius—50 to 20 miles west	0900–1130	5	170+
Mar. 2	Mauritius—zero to 30 miles west	1430–1630	3	13
" 3	19 57 S, 54 58 E	0810–1110	5	4
	20 34 S, 54 58 E	1745–1830	2	0
" 4	23 07 S, 54 50 E	0700–1600	1, 1 (reported)	0
" 13	24 10 S, 56 24 E	1030	1 (reported)	0
" 14	21 00 S, 57 00 E	0830–1130	1	145
	20 40 S, 57 07 E	1220–1420	1	100
" 29	21 43 S, 57 43 E	0825–0925	0	1
Apr. 17	16 43 S, 74 53 E	0825–1025	1	0
" 20	09 21 S, 75 08 E	1500	0	flock on horizon
" 28	01 34 N, 75 13 E	1400	1	0
" 29	03 54 N, 74 56 E	1100	0	2
" 30	06 51 N, 75 02 E	1030	1	100+
May 23	06 46 N, 55 00 E	1400–1600	0	8+
" 24	02 02 N, 51 11 E	0925–1125	0	275+
" 25	01 42 S, 45 46 E	0910–1110	0	500
" 31	06 05 S, 42 11 E	0915–1215	0	70
June 1	05 23 S, 48 08 E	0915–1215	0	360+
" 2	04 33 S, 54 17 E	0910–1210	0	180

TABLE 12.—*Weights (in grams) and measurements (in mm) of* Sterna vittata

Specimen	Age/Sex	Wing (arc)	Tail	Culmen	Tarsus	Weight
GI-315	ad. M	250	131	38	19	158.7
GI-316	imm. F	243	125	35	20.5	135.7
GI-317	ad. F	242	154	35	20	128.0
GI-318	ad. F	236	153	35	19	124.5
GI-319	ad. M	249	132	37.5	19.5	152.5
GI-320	imm. M	245	120	39.5	20.5	152.6
GI-321	ad F.	252	172	37	20	136.5
GI-322	ad. M	246	160	39	20	146.7
GI-323	imm. F	240	122	35	20	152.8
S. v. tristanensis [1]		258	172	36.5	19.5	
S. v. vittata [1]		267	139.5	33	18	

[1] Taken from Murphy, 1938, p. 16.

TABLE 13.—*Observations of* Gygis alba

Date	Location	Time	Number	Remarks
Feb. 5–6	08°00′ N, 54°58′ E	2200–0500	1?	reported
" 6	06 28 N, 55 04 E	2100	1+	heard several, saw one
" 7	03 54 N, 55 01 E	2100–2400	15+	heard and seen
" 8	01 59 N, 54 57 E	2100	1–2	
" 10	01 47 S, 54 56 E	2300	1	reported
" 11	03 20 S, 55 13 E	1745	6	
June 2	04 33 S, 54 17 E	0910–1210	24	

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BIRDS OF RODRIGUEZ ISLAND (INDIAN OCEAN)

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INTRODUCTION

The island of Rodriguez is the smallest and most remote of the three Mascarene islands. It is located at latitude 19° 41′ S. and longitude 63° 23′ E. in the Indian Ocean, over 800 miles east of Madagascar and 365 miles from the island of Mauritius upon which it is economically and politically dependent. Its oblong shape, 10·5 miles long by 4·75 miles wide, contains a land area of only 42 square miles (Mauritius includes 720 square miles). Like both Mauritius and Réunion, Rodriguez is primarily of volcanic origin but its topographic features are gentle by comparison and reach a maximum elevation of only 1300 feet. When the island was settled the natural vegetation was quickly cleared and replaced by exotic or cultivated species and today remnants of the indigenous vegetation are left only at the tops of some of the hills and in a few of the ravines (see Wiehe 1949 for details). An extensive coral reef studded with small islets surrounds the main island. Some of these islets are composed of volcanic rock whereas others are simply accumulations of coral and sand.

Twelve unique species of birds were once found on Rodriguez. Nine of these, however, were exterminated soon after the island was settled in the 18th century and are known only from descriptions contained in the journals of early visitors and from partially fossilized bones found in the caverns in the southwestern portion of the island. Included in this assemblage were two owls (*Bubo leguati* and *Athene murivora*), a flightless heron (*Megaphoyx megacephala*), a flightless egg-eating rail (*Erythromachus leguati*), the Solitaire (*Pezophaps solitarius*) usually considered closely related to the Dodo of Mauritius, a pigeon (*Alectroenas rodericana*), a ground parrot (*Necropsittacus rodericanus*), a starling (*Necropsar rodericanus*) and perhaps a chough (*Testudophaga bicolor*) though the evidence for this latter species is not convincing (see Hachisuka 1953). The parrot *Psittacula exsul* survived into the 19th century but has not been reported since. Today only two endemic land-birds are left on Rodriguez, a weaver (*Foudia flavicans*) and a brush warbler (*Bebrornis rodericana*). There are also a number of birds which have been widely introduced in the Mascarene region and small sea-bird colonies occupying some of the offshore islets.

The only available information on the surviving species is in the notes made by Newton during a brief visit in 1864 (Newton 1865) and by the scientific party of the Transit of Venus Expedition in 1874 (Sharpe 1879). Watson, Zusi & Storer (1963) summarized the species known from the island and their present status but emphasized the lack of current information. Hence, the observations and collections I made during a week's stay on Rodriguez in September-October 1964 may be of interest.

I arrived at Rodriguez on 26 September 1964 after a two-day voyage from Mauritius aboard *La Perle*, a commercial fishing vessel bound for the shoals of Cargados Carajos to the north. The following day, after making necessary arrangements in Port Mathurin, the island's capital, I moved to Solitude, a location which provided access to the forests in Cascade Pigeon. The majority of my field work was conducted in this area which includes Mt. Limon, La Source and Cascade Pigeon. On 29 September, however, I visited the two offshore islets known to have sea-birds, Sandy and Cocoa Islands. The morning of 1 October was spent in the hills of the interior near La Ferme. I left Rodriguez on 3 October, returning to Mauritius aboard the S.S. 'Mauritius', whose

monthly calls constitute the only regular contact Rodriguez's population of 20,000 has with the outside world.

In the course of this week of field work I obtained 74 bird specimens, which have since been deposited in the collections of the Smithsonian Institution in Washington, D.C. In addition, I recorded on magnetic tape the vocalizations of many of the species encountered and attempted to learn as much as possible about the status and behaviour of the endemic fody. Below I have summarized the results of this work in species accounts followed by a more comprehensive discussion of the islands avifauna as a whole.

1. SEA-BIRDS

ANOUS STOLIDUS PILEATUS (Scopoli) Brown Noddy

Brown Noddies were found on both Cocoa Island (200) and Sandy Island (100), but no nests, eggs or young were found and the two specimens collected both had small gonads. A few Brown Noddies were seen at sea west of Rodriguez.

ANOUS TENUIROSTRIS TENUIROSTRIS (Temminck) Black Noddy.

The Black Noddy was a common breeding species on both Cocoa Island (200) and Sandy Island (400). Although there were many nests of this species in the *Casuarina* trees on these islands, there was no evidence that they were being used at the time of my visit. On Sandy Island, however, there were many full-grown immatures. The gonads of ten adult specimens were not enlarged. Six of these specimens were moulting.

GYGIS ALBA MONTE Mathews Fairy Tern

Breeding Fairy Terns with both eggs and unfledged young were found on Cocoa Island (400) and Sandy Island (100). The gonads of six adult specimens exhibited various degrees of enlargement. One specimen was moulting.

2. SHORE-BIRDS

BUTORIDES STRIATUS RUTENBERGI (Hartlaub) Little Green Heron

This small heron was common along the coast of Rodriguez especially on the exposed mud flats at low tide. It was also seen inland near Solitude and Cascade Pigeon. I collected an adult female (ovary enlarged) near a nest by the reservoir at Cascade Pigeon.

EROLIA TESTACEA Curlew Sandpiper

I saw approximately 30 Curlew Sandpipers in winter plumage on the mud flats and beaches at Sandy and Cocoa Islands.

ARENARIA INTERPRES Ruddy Turnstone

About 12 turnstones were feeding on the shores of Sandy and Cocoa Islands.

SQUATAROLA SQUATAROLA Grey Plover

Six Grey Plovers were seen at Sandy and Cocoa Islands.

CROCETHIA ALBA Sanderling

A single Sanderling in winter plumage was collected at Cocoa Island.

3. LAND-BIRDS

FRANCOLINUS PONDICERANUS Grey Francolin (Perdrix)

This introduced partridge was fairly common on the higher parts of the island. I heard it several times near Solitude and flushed many pairs in the hills near La Ferme. The partridges are found primarily in the open grass fields near cultivated maize and are considered a pest because of the considerable damage they do to these (young) plants. The Perdrix is frequently hunted for both food and sport.

GEOPELIA STRIATA STRIATA (Linnaeus) Barred Ground Dove (Tourterelle)

This small introduced dove was very common at all localities visited including the offshore islets. The gonads of four specimens were enlarged.

ACRIDOTHERES TRISTIS TRISTIS (Linnaeus) Indian Mynah (Martin)

This starling has been widely introduced in the Indo-Pacific region and was abundant on Rodriguez. Several specimens with enlarged gonads and brood patches were taken.

BEBRORNIS RODERICANA Newton Rodriguez Brush Warbler

At Dr. Jean Vinson's suggestion I made a thorough but unsuccessful search for this endemic species at La Source, the locality of its last known occurrence. On 1 October 1964 I observed a lone singing male feeding about 15 feet above the ground in the forest in Cascade Pigeon. Its song consisted of an introductory " *sueeee* " followed by several sweet warbled trills at a lower frequency. (Newton described the song of this species as a " melodius single-noted whistle followed by a Nightingale-like *tchou-ti- tchou*".) On 3 October I heard a similar song emanating from the vegetation along a stream at Solitude but I was unable to locate the bird. It was, however, almost certainly this species as the song of *Bebrornis* is quite distinct from the vocalizations of both *Foudia flavicans* and *Serinus mozambicus*, the only other " singers " on the island.

SERINUS MOZAMBICUS MOZAMBICUS (Muller) Yellow-fronted Canary (Serin)

I saw this small introduced finch only occasionally in the forests at Solitude and Cascade Pigeon. The two specimens taken both had small gonads and were moulting.

ESTRILDA ASTRILD sub spp. Red-eared Waxbill (Bengali)

The wax-bill was common over most of the island, particularly in the gardens and in the lush vegetation along streams. Several birds carrying nesting material were seen and four of the seven specimens taken had enlarged gonads. These specimens are slightly darker than a series of *E. a. astrild* used for comparison, but are greyer than *E. a. cavendishi*. Consequently subspecific identification will be deferred until a more complete analysis of the Mascarene island populations can be made.

PASSER DOMESTICUS INDICUS Jardine & Selby House Sparrow (Moineau)

The House Sparrow was common on Rodriguez as well as one of the offshore islets (Cocoa).

FOUDIA MADAGASCARIENSIS Madagascar Fody (Cardinal)

The Cardinal was abundant over most of Rodriguez, occurring even in the forests of Cascade Pigeon. Males moulting into the red breeding plumage were ever present and conspicuous, whereas females (and immatures?) were usually found in the dense vegetation along streams and in the undergrowth in the forest. The specimens taken possessed large gonads and were moulting.

FOUDIA FLAVICANS Newton Rodriguez Fody (Zo Zo du Pays)

The yellow-headed fody of Rodriguez can still be found with ease in the forests and wooded areas near La Source, Solitude and Cascade Pigeon, where its loud distinctive warbling is one of the dominant bird sounds. In this region, however, it is restricted to relatively dense vegetation, particularly near streambeds and/or stands of *Araucaria*. Of the eight pairs I had a chance to observe, three were in *Araucaria* stands near streams, three near streams only, one in *Araucaria* a short distance from a stream, and one in the scrub vegetation at the edge of a maize field. Many others were heard but time did not permit an evaluation of their habitats.

In 1864 *Foudia flavicans* was apparently very common on Rodriguez, occurring not only in the forests but on relatively barren hillsides as well (Newton 1865). By 1958 *Foudia madagascariensis*, which was introduced sometime after 1874 (Moreau 1960), outnumbered *F. flavicans* 3 : 1, the latter species being restricted at this time to the evergreen thickets in the interior of the island (Moreau 1960). During my visit, however, I estimated the ratio to be closer to 10 : 1 in favour of *madagascariensis* in the region near Solitude where *flavicans* is most common. Elsewhere, of course, the ratio was much higher. This does not necessarily mean that *flavicans* has decreased in abundance

since 1958 as *madagascariensis* may be increasing its numbers while *flavicans* is simply maintaining a given population level.

Foudia flavicans appears to be entirely insectivorous. It forages from ground level to heights of over 30 feet and extracts small insects from crevices or the undersides of leaves and branches. On one occasion I watched a female capture a 1·5 in. stick insect (Phasmidae) which it found on the underside of a *Pandanus* leaf. The six stomachs of this fody that I examined contained the remains of insects and spiders. The Rodriguez Fody frequently hangs upside down like some parids as it extracts or captures food.

The feeding behaviour of *Foudia flavicans* is of interest in view of the possibility of competition with its congener, *Foudia madagascariensis*. Moreau (1960) has attributed the decline of the Rodriguez Fody to the presence of this introduced species, which he considers competitively superior at least in the open areas. The Rodriguez Fody is now restricted to the forests of the interior where it is presumably no longer at such a disadvantage. The possibility of *flavicans* having had a more plastic ecology before the arrival of *madagascariensis* is an interesting one. Today, however, it is a question of defining the relationship of an insectivorous species to a graminivorous one. Elsewhere the introduced Madagascar Fody does not seem to compete with endemic insectivorous fodies, i.e. on Mauritius with *Foudia rubra* (Newton 1959) and on the Seychelles with *Foudia seychellarum* (Crook 1961). Rather the decline of the endemic species can be attributed to the destruction of indigenous vegetation or other factors (Moreau 1960). Such an interpretation may also be valid for the situation on Rodriguez. It is surprising, however, that on Rodriguez the two fodies are found side by side throughout the Solitude-Cascade Pigeon region, including the relatively dense forest, a habitat rarely occupied by *madagascariensis* on Mauritius. In this connection I made several relevant observations of male *madagascariensis* feeding in the tall trees in this area, probing into the conspicuous red flowers of the flame tree (*Poinsiana*) and foraging among the leaves and buds of other species. The crop of one of my specimens of *madagascariensis* was full of small caterpillars. *F. madagascariensis* is known to feed small insects to its young (Delacour 1933, Crook 1961) but there was no evidence that breeding had progressed this far at the time of my visit to Rodriguez. Whether such departures from the usual seed-eating habits of this species are frequent and in the direction of a competitive relationship with *flavicans* remains to be demonstrated. The possibility is also to be considered that the feeding behaviour of *madagascariensis* on Rodriguez has been influenced by the absence of a small insectivorous bird, such as the white-eye *Malacirops borbonica*, which is abundant on the other two Mascarene islands.

Foudia flavicans was always found in pairs, quite unlike *Foudia madagascariensis* which often occurs singly or in flocks. The six specimens taken of *flavicans* were in breeding condition and one nearly completed nest was found. This nest was located ten feet above the ground at the end of a branch of an *Araucaria cunninghami*. It was a globose, domed structure composed of fine grasses and palm fibres with scattered pieces of cotton and occasional feathers. Only the female of this pair was observed carrying nesting material to the nest, presumably for the lining of the interior.

The Rodriguez Fody is very vocal and hence easily located by means of either its emphatic "*chip*" notes or its characteristic song, which consists of a variable assortment of repeated clear whistles, trills and notes of scolding quality. Both males and females sing, the song of the female being indistinguishable from that of the male. The two sexes even duet on occasion, i.e. sing identical songs simultaneously when they are near one another. In the presence of the female the male frequently displays actively, flapping its wings slowly or letting them hang forward as if they were broken. Other displays of the male included a slow deliberate flapping of the wings while singing and an exaggerated moth-like flight. The female frequently flicked and quivered her wings when she was foraging and when near the male begged or solicited with rapid wing

quivering while uttering short squeaking notes. No copulations or courtship feedings were observed however.

DISCUSSION

The birds found on the main island of Rodriguez are now primarily introduced species, only three of the twelve species (Rodriguez Brush Warbler, Rodriguez Fody and Little Green Heron) being undoubtedly indigenous. Seven of the introduced species, the Grey Francolin, Indian Mynah, Ground Dove, House Sparrow, Madagascar Fody, Red-eared Waxbill and to a lesser degree the Yellow-fronted Canary are now highly successful, maintaining flourishing populations that are the dominant elements of the islands' avifauna. Newton (1865) apparently saw none of these species during his visit in 1864 although he was told that a Serin (=*Serinus mozambicus*?), Bengali (=*Estrilda astrild*?) and a Tourterelle (=*Geopelia striata*) could be found on the island. Ten years later Sclater obtained specimens of the mynah and francolin (Sharpe 1879) but no mention is made of the remaining five species. If they were present therefore, they could not have been numerous, having eluded two zealous collectors; they must have greatly increased in numbers in the last hundred years.

Three species have declined in abundance in the past century and are now either extinct or very nearly so. The guinea-fowl (*Numidia meleagris*) was numerous in 1864 (Newton 1865) and maintained its population up to only a few years ago. I saw none during my visit and was told by several persons that the species had disappeared from the island within the past two or three years. My informants believed that the cyclones were responsible. Similarly the Madagascar Lovebird *Agapornis cana* was common in the 19th century. Whether its numbers declined gradually or suddenly is uncertain, but it is now very rare and localized. I saw none, but was informed that it could still be seen occasionally in the vicinity of Grande Montagne. This species has been unable to maintain a population on the other two Mascarene islands as well, for it was eliminated from Mauritius by the cyclone of 1892 and only a few individuals still exist on Réunion. The endemic brush warbler *Bebrornis rodericana* has certainly decreased since Newton's time and may be on the verge of extinction. Unlike the previous two species, however, its decline has probably been due to the destruction of natural vegetation rather than to the effects of cyclones.

The Rodriguez Parrot *Psittacula exsul* might also be considered with those species which have decreased in abundance or recently become extinct. It has, however, not been reported since 1874 (Newton 1875) at which time it was exceedingly scarce. This parrot is almost certainly extinct and presumably has been for most of this century. The possibility of a few individuals still existing on one of the offshore islets (Watson, Zusi & Storer 1963) seems very remote.

Rodriguez's importance as an Indian Ocean sea-bird breeding locale has been the subject of considerable speculation and uncertainty (Bourne 1965, Watson, Zusi & Storer 1963). In 1864 Newton found many Wedge-tailed Shearwaters *Puffinus pacificus* on one islet and on another, a colony of Red-footed Boobies *Sula sula*. He also reported four species of terns: *Gygis alba, Anous stolidus, Sterna fuscata* and *Sterna velox* (= *Thalasseus bergii*). The Transit of Venus Expedition collections contained specimens of all these species as well as the tropic-bird *Phaëthon lepturus* and two additional terns, *Sterna dougallii* and *Anous tenuirostris*. During my visit I found only three species of terns, *Gygis alba*, *Anous tenuirostris* and *Anous stolidus*, all of which were present in numbers on the two offshore islets, Sandy and Cocoa islands. These were, I was informed, the only two islets with sea-birds. No other species of sea-birds were seen at Rodriguez or in the seas surrounding the island, but I was told that tropic-birds could be seen in some of the ravines on the island. Wedge tailed Shearwaters may also still be present since Vinson has recently taken specimens of this species. These are in the collections

of the Mauritius Institute Museum in Port Louis. I was particularly surprised at the absence of Sooty Terns *Sterna fuscata* since Vinson has also obtained specimens, but several persons who were familiar with the species (Ye Ye) assured me that they had never seen it at Rodriguez. It is possible that more complete coverage of the many offshore islets would have revealed other sea-birds, but it seems unlikely that significant numbers of breeding sea-birds would have escaped the notice of the residents of Rodriguez. Apparently therefore, a loss of breeding sea-birds has accompanied the increase in the island's human population and the inevitable concommitant disturbance of the offshore islets.

Bourne (1965) and others have suggested that Rodriguez may have an undiscovered population of an unknown petrel, apparently feeling that if both Mauritius and Réunion have unique petrel populations, so also should Rodriguez. In my opinion, however, Rodriguez lacks cliffs or isolated islands suitable for breeding petrels, or at least a population of any size that could have escaped detection. I would not, however, discount the possibility of a more widespread species of petrel or shearwater (*Puffinus lherminieri*, for example) occurring in small numbers on some of the more remote islets.

A final category of birds found on Rodriguez is that of non-breeding migrants or vagrants. The ancient record of "*Leguatia gigantea*" belongs here (Hachisuka 1953) if such a species ever existed and was capable of a 300 mile flight from Mauritius! The frigate-bird (*Fregata* sp.) observed by Newton (1865) was probably attracted by the booby (*Sula*) colony as there is no evidence that frigate-birds ever bred on Rodriguez. All the remaining species in this category are migrant or non-breeding waders. Newton recorded only the turnstone *Arenaria interpres* and an unidentified curlew (*Numenius*). Sclater obtained specimens of the turnstone, a whimbrel *Numenius phaeopus* and the Greater Sand Plover *Charadrius leschenaultii*. During my visit I saw numbers of both the whimbrels and turnstones and also found three species which have not been recorded previously from Rodriguez, i.e. *Squatarola squatarola*, *Erolia testacea* and *Crocethia alba*.

Thus in summary (see below), a total of 38 species of birds has been recorded from Rodriguez. Nine of these became extinct soon after the island was settled and an additional four species have become extinct or extremely rare within the last 100 years. Seven species of introduced land-birds and two endemic species exist on the island today. The Little Green Heron is also presumed to be indigenous. The endemic fody still maintains a substantial population in the vicinity of Cascade Pigeon but the endemic brush warbler is now extremely rare. Sea-birds inhabiting the outer islets have decreased in abundance and variety (from nine to five species) in the past century. Finally six species of non-breeding waders and one vagrant frigate-bird have been recorded on Rodriguez.

Rodriguez has always had a much less varied avifauna than either Mauritius or Réunion. Mauritius, for example, whose avifauna both past and present is much better known than Réunion's, claims a total of 69 established species plus an additional 33 accidentals or vagrants (Rountree, Guérin, Pelte & Vinson 1952). The determinants of insular faunas have been analysed in considerably more detail than is possible here (see MacArthur & Wilson 1965, Watson 1965) though an analysis of the Mascarene region from this standpoint is in preparation (Gill, in prep.). Suffice it to say here that the size of an island and the associated ecological diversity are among the primary factors and on this basis alone Rodriguez could not be expected to support as large a fauna as Mauritius or Réunion. In addition Rodriguez's remote location dictates in effect, that only a fraction of the species colonizing Mauritius and Réunion will reach it. (In this connection it seems surprising that Rodriguez does not have a white-eye (Zosteropidae) in view of this group's extraordinary ability to colonize remote oceanic islands and the fact that Mauritius and Réunion have had several successful invasions by these birds.)

BIRD SPECIES KNOWN FROM RODRIGUEZ ISLAND (INDIAN OCEAN

ENDEMIC LAND-BIRDS

**Megaphoyx megacephala*
**Erythromachus leguati*
**Athene* (Carine) *murivora*
**Bubo leguati*
**Necropsittacus rodericanus*
**Psittacula exsul*
**Pezophaps solitarius*
**Alectroenas rodericana*
**(Testudophaga bicolor)*
**Necropsar rodericanus*
†*Bebrornis rodericana*
Foudia flavicans

INTRODUCED LAND-BIRDS

**Numidia meleagris mitrata*
Francolinus pondiceranus
**Agapornis cana*
Geopelia striata striata
Acridotheres tristis tristis
Passer domesticus indicus
Foudia madagascariensis
Estrilda astrild sub spp.
Serinus mozambicus mozambicus

SEA-BIRDS

Puffinus pacificus chlororhynchos
Phaethon lepturus lepturus
‡*Sula sula*
‡*Sterna dougallii*
Gygis alba monte
‡*Sterna fuscata nubilosa*
‡*Thalasseus bergii*
Anous stolidus pileatus
Anous tenuirostris tenuirostris
§(*Fregata* sp.)

SHORE-BIRDS

§*Numenius phaeopus*
§*Charadrius leschenaultii*
§*Arenaria interpres*
§*Crocethia alba*
§*Squatarola squatarola*
§*Erolia testacea*
Butorides striatus rutenbergi

Note.—* Extinct.
† Extant but rare.
§ Vagrant or migrant only.
‡ Doubtfully still present as a breeding species.
( ) Hypothetical—occurrence not substantiated.

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SUMMARY

A description is given of Rodriguez, the most remote of the Mascarene Islands, and of its avifauna, with special reference to the two surviving endemic land-birds.

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TWO NEW SPECIES OF *LICHOMOLGUS* (COPEPODA, CYCLOPOIDA) FROM AN ACTINIARIAN IN MADAGASCAR

by ARTHUR G. HUMES* and JU-SHEY HO*

RÉSUMÉ

Les auteurs décrivent deux espèces nouvelles des copépodes cyclopoïdes, Lichomolgus politus *n. sp. et* Lichomolgus simulans *n. sp., associées à une petite actinie* Rhodactis rhodostoma *à Nosy Komba (près de Nosy Bé), au nord-ouest de Madagascar.*

* * *

Three species of *Lichomolgus* have already been recorded from actiniarians in Madagascar. They are *L. cuspis*, *L. gemmatus*, and *L. magnificus*, all described by Humes (1964). These copepods live in association with two members of the family Stoichactinidae, *Stoichactis giganteum* (Forskål) and *Radianthus ritteri* (Kwietniewski). The two new lichomolgids described below came from the small sea anemone *Rhodactis rhodostoma* (Ehrenberg), family Actinodiscidae.

The collection of the copepods (by the first author) occurred partly in 1960 during an expedition to Nosy Bé by the Academy of Natural Sciences of Philadelphia and partly in 1963-64 during the work of the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the material has been aided by a grant from the National Science Foundation of the United States.

We wish to thank Mr. Charles E. Cutress of the United States National Museum for the identification of the actiniarian and the staff of the Centre d'Océanographie et des Pêches at Nosy Bé for assistance with the field work.

LICHOMOLGUS POLITUS n. sp.

Figs. 1-28

Type material. — 47 females and 13 males from 60 *Rhodactis rhodostoma* (Ehrenberg), attached to dead *Acropora* in 1 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar. Collected May 29, 1964. Holotype female, allotype, and 48 paratypes (39 females and 9 males) deposited in the United States National Museum, Washington, and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Rhodactis rhodostoma* at Pte. Ambarionaomby). — 11 females, 17 males, and 1 copepodid from 50 hosts in 2 m, August 18, 1960 ; 12 females and 19 males from 30 hosts in 0,5 m, June 24, 1963 ; and 9 females and 4 males from 40 hosts in 1 m, July 3, 1963.

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Female. — The body (fig. 1) has a moderately broadened prosome and slender urosome. The length (not including the setae on the caudal rami) is 1.78 mm (1.61-1.94 mm) and the greatest width, at the junction of the head and the segment of leg 1, is 0.74 mm (0.70-0.78 mm), based on 10 specimens. The ratio of length to width of the prosome is 1.43 : 1. The segment of leg 1 is separated dorsally and laterally from the head by a distinct furrow. The epimeral areas of the metasomal segments are rounded.

The segment of leg 5 (fig. 2) is narrowed anteriorly and broadened posteriorly where its greatest width is 224 μ. The free segment of leg 5 is attached somewhat ventrally on the posterolateral edge. The genital segment is longer than wide, 275×224 μ ; it is moderately swollen in its midregion where the egg sacs are attached dorsolaterally. Each area of attachment of the egg sacs (fig. 3) bears two small blunt spines 8 μ in length, with their tips very finely punctate. The three postgenital segments measure 96×122, 68×155, and 115×130 μ respectively from anterior to posterior. The posteroventral margin of the anal segment along the insertions of each caudal ramus bears a row of minute spinules.

The caudal ramus (fig. 4) is elongated, 3.8 times longer than wide, 190×52 μ in greatest dimensions, and inserted a little dorsally on the anal segment. The outer lateral seta and the outer terminal seta are both 91 μ in length and naked. The inner terminal seta is 143 μ in length and has a few proximal inner hairs. The two long terminal setae, inserted between a slight dorsal flap and a larger ventral flap (with a row of minute spinules along its edge), are 360 μ (outer) and 505 μ (inner) in length and naked. The small pedicellate dorsal seta is 38 μ long. The dorsal and ventral surfaces of the ramus have minute scattered spinules.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear scattered refractile points and hairs. The ratio of the length of the prosome to that of the urosome is 1.55 : 1.

The egg sac (fig. 5) is moderately elongated, 784×358 μ, with each of the many eggs about 83 μ in diameter.

The rostral area (fig. 6) is well-defined.

The seven segments of the first antenna (fig. 7) have the following lengths (measured along their posterior non-setiferous margins) : 50 (99 μ along the anterior margin), 211, 34, 92, 72, 55, and 32 μ respectively. The formula for the armature is 4, 13 (3+2+8), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All the setae are naked. On the proximal ventral region of segment 3 there is a sclerotization suggesting an intercalary segment.

The second antenna (fig. 8) is slender and 4-segmented. The elongated first and second segments bear a small inner seta. The short third segment bears three inner setae, one much smaller than the other two. The elongated fourth segment measures about 100×21 μ and bears terminally seven elements (one large setule and six smaller setules) and a single claw 55 μ long (measured along its axis). All the setae and setules are naked.

The labrum (fig. 9) has two broad lobes, each with a minute medial marginal spiniform hyaline process.

The mandible (fig. 10) has a basal region separated into two parts by a waist-like constriction. The distal of these two areas has on its outer margin a sclerotization bearing a row of prominent spinules followed by a hyaline striated fringe, and on its inner margin a row of slender spinules ; the terminal lash has lateral spinules. The paragnath (fig. 11) has its hairy distal region bilobed, with the posterior lobe bearing a small knob-like excrescence. The first maxilla (fig. 12) is a single segment bearing four setae, one subterminal small and naked, and three terminal of which one is armed bilaterally with minute spinules and the two others are naked. The second maxilla (fig. 13) is 2-segmented. The basal segment is large and unarmed. The distal segment is gradually attenuated into a spiniform process with its outer edge bearing teeth along its first three-fourths and slender spinules on its distal fourth ; the segment bears two inner setae (one with prominent bilateral spinules, the other with a row of minute spinules along one side) and a small hyaline

proximal outer setule. The 3-segmented maxilliped (fig. 14) has the first segment elongated and unarmed, the second segment somewhat stouter with two very unequal setae (one of them long and scythe-shaped), and the third segment small with a terminal spiniform barbed process, a spine with minute spinules along one side, and a slender hyaline seta.

The area between the maxillipeds and the first pair of legs (fig. 15) is not produced ventrally and a lightly sclerotized line connects the bases of the maxillipeds.

The rami of legs 1-4 (figs. 16, 17, 18, and 19) are 3-segmented, except for the endopod of leg 4 which is 2-segmented. The spine and setal formula is as follows (the Roman numerals representing the spines, the Arabic numerals the setae) :

P 1	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-4
				end.	0-1 ;	0-1 ;	I-5
P 2	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-II-3
P 3	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	III-I-5
				end.	0-1 ;	0-2 ;	I-II-2
P 4	protopod	0-1 ;	1-0	exp.	I-0 ;	I-1 ;	II-I-5
				end.	0-1 ;	II	

The inner seta on the coxa is long and feathered in legs 1-3, but short (9 μ) and naked in leg 4. A row of hairs is present on the inner margin of the basis in legs 1-3, but these hairs are absent in leg 4. The endopod of leg 4 is distinctly 2-segmented, the first segment 46 × 51 μ, with its inner seta 80 μ long. The second segment is 88 μ long (95 μ including the spinous processes) × 40 μ in greatest width, ornamented with an outer interrupted row of hairs and a terminal row of spinules, and armed with two terminal spines 64 μ (inner) and 42 μ (outer) in length.

Leg 5 (fig. 20) has a moderately elongated free segment of somewhat irregular outline, measuring 94 μ along the outer edge, 77 μ along the inner edge, and 41 μ in greatest width, or about 2.1 times longer than wide. It bears small dorsolateral spinules along the outer margin and is armed with two terminal naked setae 63 μ (inner) and 53 μ (outer) in length. The seta arising from the body near the base of the free segment is about 30 μ long and unornamented.

Leg 6 is doubtless represented by the two spines on the area of attachment of the egg sac (see fig. 3).

The color in life in transmitted light is very slightly amber, the eye red, the egg sacs grayish green.

Male. — The body form (fig. 21) resembles that of the female. The length (excluding the setae on the caudal rami) is 1.33 mm (1.26-1.40 mm) and the greatest width is 0.44 mm (0.42-0.46 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.7 : 1.

The genital segment (fig. 22) is subquadrated, 285 × 280 μ. There are four postgenital segments, 50 × 86, 50 × 82, 41 × 78, and 77 × 85 μ respectively from anterior to posterior.

The caudal ramus, measuring 138 × 36 μ, is similar to that of the female.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear refractile points and hairs. The ratio of the length of the prosome to that of the urosome is 1.16 : 1.

The rostral area is like that of the female.

The first antenna (fig. 23) resembles that of the female, but there are three long aesthetes added (two on segment 2 and one on segment 4), making the formula 4, 13+2 aesthetes (3+1 aesthete, 2, 8+1 aesthete), 6, 3+1 aesthete, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete.

The second antenna is like that of the female, but there are many small refractile knobs on the inner surface of the first two segments (fig. 24).

The labrum, mandible, paragnath, and first maxilla resemble those of the female. The second maxilla is also like that in the opposite sex but the first segment is a little more swollen.

The maxilliped (fig. 25) is 4-segmented and slender. The first segment is unarmed, the second bears two inner setae and two rows of spinules, the third is very short and unarmed, and the fourth forms the proximal part of the claw and bears two setae, one hyaline and naked, 15 μ long, the other minutely barbed and 46 μ long. The entire claw is 211 μ long (measured along its axis and not along its curvature). The narrow hyaline membrane along the concave edge of the claw is indented at about midway, at which point there is a break in the sclerotization. There is a prominent terminal lamella.

The area between the maxillipeds and the first pair of legs is like that of the female.

Legs 1-4 resemble those of the female and have the same spine and setal formula except for the last segment of the endopod of leg 1 (fig. 26) where the formula is I-I-4, the outermost seta here being transformed to a spine.

Leg 5 (fig. 27) is much more slender than in the female, the free segment measuring 59 × 17 μ, or 3 times longer than wide. The two terminal naked setae are 47 and 45 μ in length and the seta arising from the body near the insertion of the free segment is 44 μ long.

Leg 6 (fig. 28) consists of a ventrolateral flap on the ventral surface of the genital segment. It bears two slender naked setae 44 and 35 μ in length.

Spermatophores were not observed.

The color in life in transmitted light resembles that of the female, but often there is a greenish area in the middle of the cephalosome.

(The specific name *politus* is a Latin adjective meaning polished, elegant.)

Relationship to the host. — It is apparent that *Lichomolgus politus* lives within the coelenterates, since the copepods were recovered only after the hosts had been thoroughly torn apart, never in washings of the intact anemones.

Comparison with other species. — *Lichomolgus politus* may be compared with those species ascribed to *Lichomolgus* which have the armature of II-I-5 on the last segment of the endopod of leg 4, the caudal ramus more than 3 times but less than 4 times longer than wide, and only a single terminal claw on the second antenna. It thus resembles *L. simplex* and *L. gigas*, both described by Thompson and A. Scott in 1903 from Ceylon. *L. simplex*, based on a few specimens found in sponge washings in the Gulf of Manaar, is much smaller (female 0.88 mm, male 0.8 mm), the first antenna is described as 6-segmented (the second segment shown in Thompson and Scott's fig. 28, Pl. XV, being of about the same length as the fourth), the maxilliped of the female apparently lacks the large conspicuous seta on the second segment, and the general aspect of the female is different.

L. gigas, based on one male and one female, from general washings of dredged invertebrates, is a little larger (female 2 mm, male 1.4 mm), the ratio of the length of the prosome of the female to that of the urosome (measured from Thompson and Scott's fig. 21, Pl. XVI) is 1.25 : 1, the form of the free segment of leg 5 in the female appears to be somewhat different, and the outline of the genital segment in the male is not as subquadrate as in *L. politus*. The proportional lengths of the segments of the first antenna, however, closely resemble those of *L. politus*. (One male of *L. gigas* was listed by A. Scott, 1909, p. 264, in washings from dredged invertebrates, in 1595 m, Siboga Station 226, 5° 26'.7S, 127° 36'.5E, midway between the Lucipara and Schildpad Islands, but no description or figures were given.)

LICHOMOLGUS SIMULANS n. sp.

Figs. 29-53

Type material. — 11 females and 12 males from 30 *Rhodactis rhodostoma* (Ehrenberg), attached to dead *Acropora* in 0.5 m, at Pte. Ambarionaomby, Nosy Komba, near Nosy Bé,

Madagascar. Collected June 24, 1963. Holotype female, allotype, and 17 paratypes (8 females and 9 males) deposited in the United States National Museum, Washington, and the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens (all from *Rhodactis rhodostoma* at Pte. Ambarionaomby). — 3 females and 1 male from 50 hosts, in 2 m, August 18, 1960 ; 3 females and 1 male from 60 hosts, in 1 m, May 29, 1964 ; and 3 females from 40 hosts, in 1 m, July 3, 1963.

Female. — The body form (fig. 29) resembles that of *L. politus*. The length (without the setae on the caudal rami) is 1.40 mm (1.30-1.51 mm) and the greatest width is 0.61 mm (0.56-0.66 mm), based on 10 specimens. The ratio of length to width of the prosome is 1.4 : 1.

The segment of leg 5 (fig. 30) is 211 μ wide. The genital segment is longer than wide, 221 ×174 μ, its sides not as swollen as in the previous species and with small indentations just posterior to the attachment areas of the egg sacs. Each area of attachment of the egg sacs (fig. 31) is dorsolateral in position and bears two blunt naked spines 12 μ in length. The dorsolateral surface of the genital segment in the vicinity of the attachment areas is very delicately pilose. The three postgenital segments are 55×107, 44×100, and 70×104 μ respectively from anterior to posterior.

The caudal ramus (fig. 32) measures 68×45 μ in greatest dimensions, or 1.5 times longer than wide. The outer lateral seta is 146 μ in length and naked. The outer terminal seta is 150 μ and haired along its proximal half. The inner lateral seta is 295 μ and bears fine spinules along its proximal half. The two long terminal setae are 448 μ (outer) and 571 μ (inner) and naked. The pedicellate dorsal seta is 42 μ in length and feathered. The surface of the ramus lacks fine ornamentation.

The ratio of the length of the prosome to that of the urosome is 1.8 : 1.

The egg sac resembles that of *L. politus*, 661×224 μ, with each egg about 60 μ in diameter.

The rostral area (fig. 33) is well-defined.

The first antenna (fig. 34) has seven segments of somewhat different relative lengths than in the preceding species. The lengths of the segments (measured along their posterior non-setiferous margins) are 39 (83 μ along the anterior edge), 160, 29, 91, 74, 55, and 34 μ. The armature is like that of *L. politus*, but one seta on segment 1 and another on the distal end of segment 2 are much longer.

The 4-segmented second antenna (fig. 35) is similar to that of *L. politus*, but there are a few spinules on the postero-inner surface of the second segment, and the last segment is more elongated and slender, 133×18 μ, bearing only six terminal elements and a claw 60 μ long.

The lobes of the labrum (fig. 36) lack the small medial spiniform processes seen in *L. politus*.

The mandible (fig. 37) closely resembles that of the previous species, but the spinules on the sclerotization on the outer margin of the basal region are smaller. The paragnath (fig. 38) has an undivided hairy tip bearing a small knob-like process. The first maxilla (fig. 39) is a single segment, with the subterminal element not articulated with the segment and the three terminal setae minutely barbed. The second maxilla (fig. 40) resembles very closely that of *L. politus*. The maxilliped (fig. 41) is also much like that of the preceding species except for minor differences in the ornamentation of the elements.

The area between the maxillipeds and the first pair of legs (fig. 42) resembles that of *L. politus*.

Legs 1-4 (figs. 43, 44, 45, and 46) resemble in major respects those of the previous species, and have the same spine and setal formula. In leg 4 (fig. 46) the inner seta on the coxa is short (25 μ) and naked, and there are hairs on the inner margin of the basis as in the other legs. The first segment of the endopod is 43×49 μ, with its inner seta 94 μ long. The second segment is 104 μ long (109 μ including the spinous processes)×49 μ at its widest part (or 32 μ at the narrowest part), with its two terminal spines 69 μ (inner) and 40 μ (outer) in length.

Leg 5 (fig. 47) has a moderately elongated free segment, 143 μ in greatest length along the

spinulose outer margin and 65 μ in greatest width at the level of the inner basal expansion. The inner margin distal to the expansion is slightly irregular with a slight notch about midway to the extremity. The two naked terminal setae are 130 μ (inner) and 78 μ (outer) in length. The seta on the body near the insertion of the free segment is 45 μ in length and feathered.

Leg 6 is represented by the two spines located on the area of attachment of the egg sacs (see fig. 31).

The color in life in transmitted light is translucent, the eye red, the ovary dark gray.

Male. — The body form (fig. 48) resembles that of *L. politus*. The length (not including the setae on the caudal rami) is 0.96 mm (0.85-1.08 mm) and the greatest width is 0.38 mm (0.36-0.40 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 1.56 : 1

The genital segment (fig. 49) is a little longer than wide, 265×224 μ, with nearly parallel sides. The four postgenital segments measure 38×73, 38×73, 23×69, and 53×76 μ respectively from anterior to posterior.

The caudal ramus is like that of the female, though smaller (52×34 μ).

The ratio of the length of the prosome to that of the urosome is 1.35 : 1.

The rostral area is like that of the female.

The first antenna resembles that of the female, but has three added aesthetes as in the male of *L. politus*.

The second antenna is similar to that of the female, but both first and second segments have numerous conspicuous spinules on their postero-inner surfaces (fig. 50).

The labrum, mandible, paragnath, and first maxilla resemble those of the female. As in *L. politus*, the basal segment of the second maxilla is slightly more swollen than in the female.

The maxilliped (fig. 51) resembles that of *L. politus*, but the claw (213μ in length) is more evenly arcuate and the terminal lamella is less conspicuous.

The area between the maxillipeds and the first pair of legs is like that in the female.

Legs 1-4 resemble those of the female, with the same spine and setal formula except for the last segment of the endopod of leg 1 (fig. 52) where the formula is I-I-4, the outermost seta here transformed to a spine as in *L. politus*.

Leg 5 (fig. 53) has a free segment measuring 62×18 μ, without a basal expansion. The surficial spinules are more numerous than in the female. The two terminal naked setae are 28 μ (inner) and 70 μ (outer) in length. The seta arising on the body near the insertion of the free segment is 35 μ long and feathered.

Leg 6 is like that of *L. politus*, but the two setae are longer, 52 and 44 μ.

Spermatophores were not observed.

(Features not mentioned in the description of *L. simulans* but described in *L. politus* may be assumed to be similar to the latter species.)

The color in life in transmitted light is similar to that of the female.

(The specific name *simulans*, Latin = imitating, refers to the many similarities of this species with *L. politus*.)

Relationship to the host. — As in the case of *L. politus*, this species was recovered only from washings of well-dissected *Rhodactis* and may be assumed to inhabit the gastrovascular cavity of these coelenterates rather than the outer surface.

Comparison with other species. — *Lichomolgus simulans* may be compared with those species of the genus *Lichomolgus* which have the formula II-I-5 for the last segment of the exopod of leg 4, the caudal ramus 1.5 times or less longer than wide, and a single claw on the second antenna. *L. anomalus* A. Scott, 1909, p. 264 (collected from washings of dredged invertebrates, in 1595 m, Siboga Station 226, between the Lucipara and Schildpad Islands), though possessing these features,

is much smaller (both male and female 0.67 mm), the prosome in the female is fully 3 times longer than the urosome, the fifth leg in the female is attenuated distally and is armed with a single seta, and the endopod of leg 1 in the male is curiously modified.

L. elegans Thompson and A. Scott, 1903, originally described from a single female found in washings of dredged invertebrates in Ceylon, has a notched genital segment, and leg 5 (in Thompson and Scott's fig. 8, Pl. XVI) does not show the prominent basal expansion seen in *L. simulans*. The relative lengths of the segments of the first antenna are, however, rather similar to those of *L. simulans*. (A. Scott, 1909, p. 264, lists one specimen of *L. elegans* in washings of dredged invertebrates, in 1595 m, Siboga Station 226, but gives no further description.)

L. simulans may be readily distinguished from *L. politus* by its smaller size, the shorter caudal rami, and the basal expansion on leg 5 in the female. These two species from *Rhodactis* in Madagascar have many features in common, however, such as the proportional lengths of the segments of the first antenna, the general structure and armature of the second antenna, the form of the mouthparts, and the spine and setal formula of legs 1-4. Thus, in spite of the obvious differences between them, they appear to be rather closely related.

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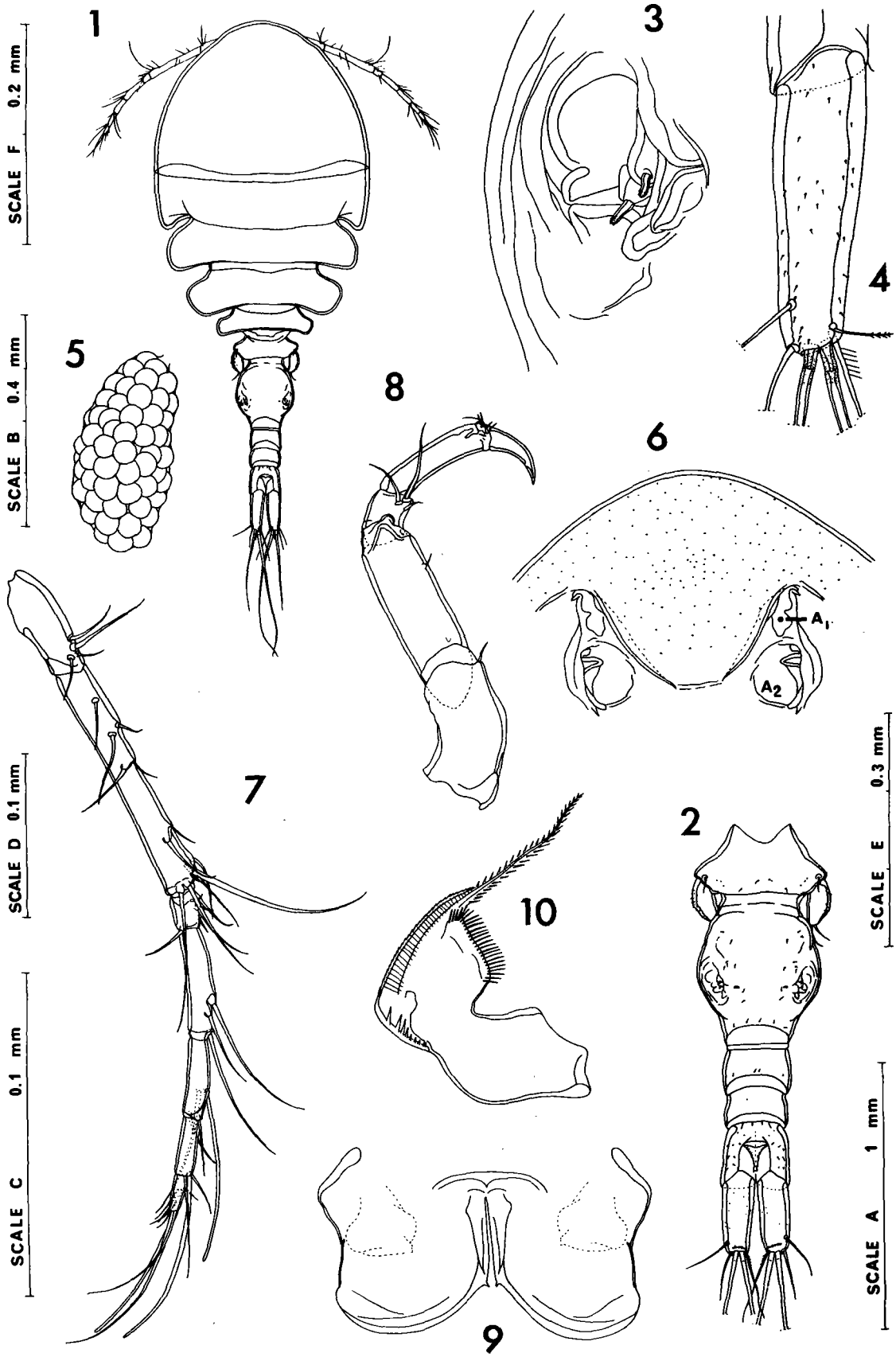
Explanation of the figures

All the figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which the figure was drawn.

Fig. 1-10. — *Lichomolgus politus* n. sp., female

1. — Body, dorsal (A)
2. — Urosome, dorsal (B)
3. — Area of attachment of egg sac, dorsal (C)
4. — Caudal ramus, dorsal (D)
5. — Egg sac, dorsal (A)
6. — Rostral area, ventral (E)
7. — First antenna, dorsal (F)
8. — Second antenna, slightly inner (F)
9. — Labrum, with paragnaths indicated by dashed lines, ventral (D)
10. — Mandible, posterior (D)


1
3
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5
8
6
7
10
2
9
A1
A2
SCALE F 0.2 mm
SCALE B 0.4 mm
SCALE D 0.1 mm
SCALE C 0.1 mm
SCALE E 0.3 mm
SCALE A 1 mm

Fig. 11-19. — *Lichomolgus politus* n. sp., female (continued)

11. — Paragnath, ventral (G)
12. — First maxilla, posterior (D)
13. — Second maxilla, posterior (D)
14. — Maxilliped, postero-inner (D)
15. — Area between maxillipeds and first pair of legs, ventral (E)
16. — Leg 1, anterior (F)
17. — Leg 2, anterior (F)
18. — Leg 3, anterior (F)
19. — Leg 4, anterior (F)

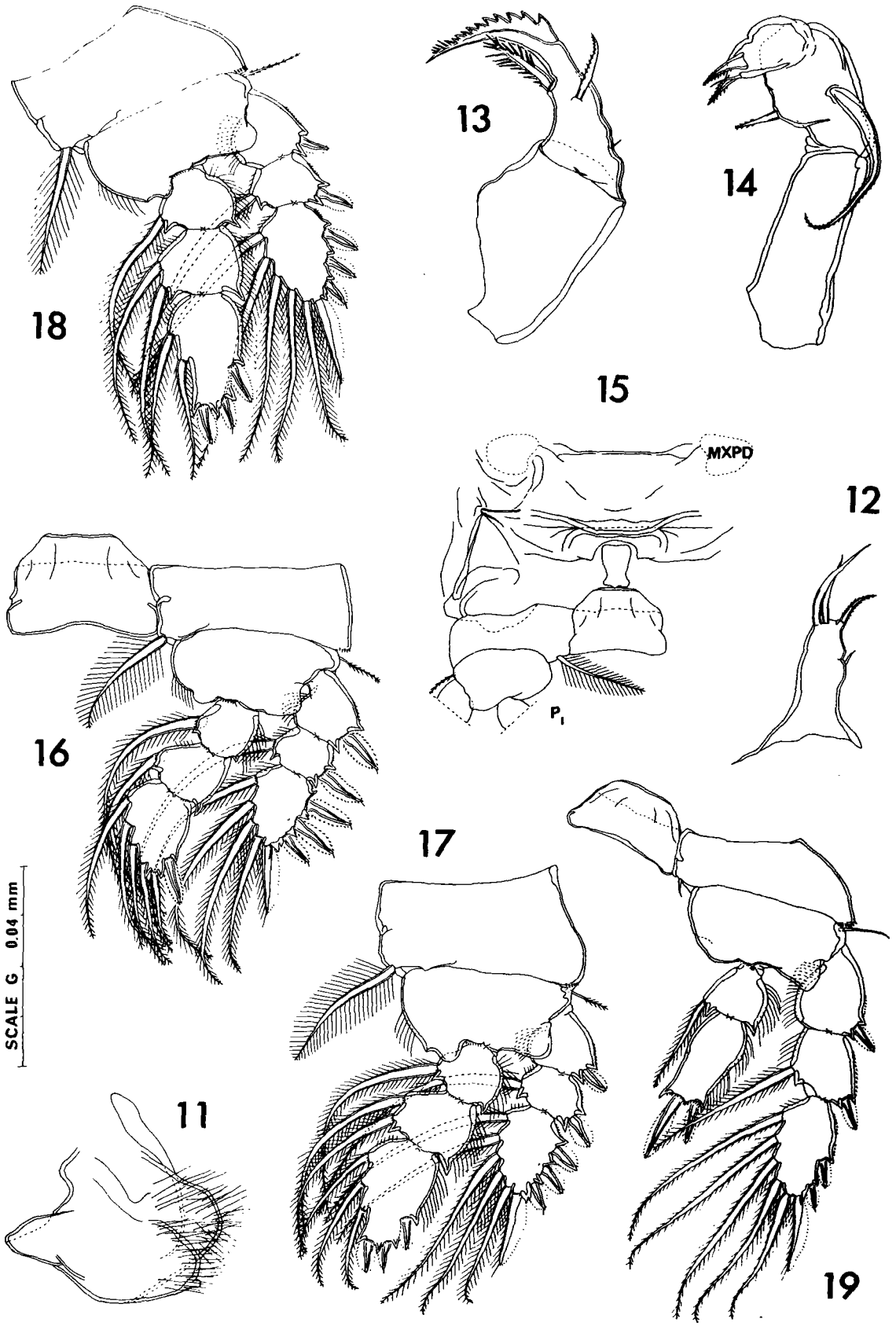

18
13
14
15
MXPD
12
P1
16
17
SCALE G 0.04 mm
11
19

Fig. 20. — *Lichomolgus politus* n. sp., female (continued)
20. — Leg 5, dorsal (H)

Fig. 21-28. — *Lichomolgus politus* n. sp., male

21. — Body, dorsal (I)
22. — Urosome, dorsal (E)
23. — First antenna, ventral (F)
24. — First two segments of second antenna, inner (H)
25. — Maxilliped, inner (F)
26. — Last segment of endopod of leg 1, anterior (H)
27. — Leg 5, dorsal (C)
28. — Leg 6, ventral (F)

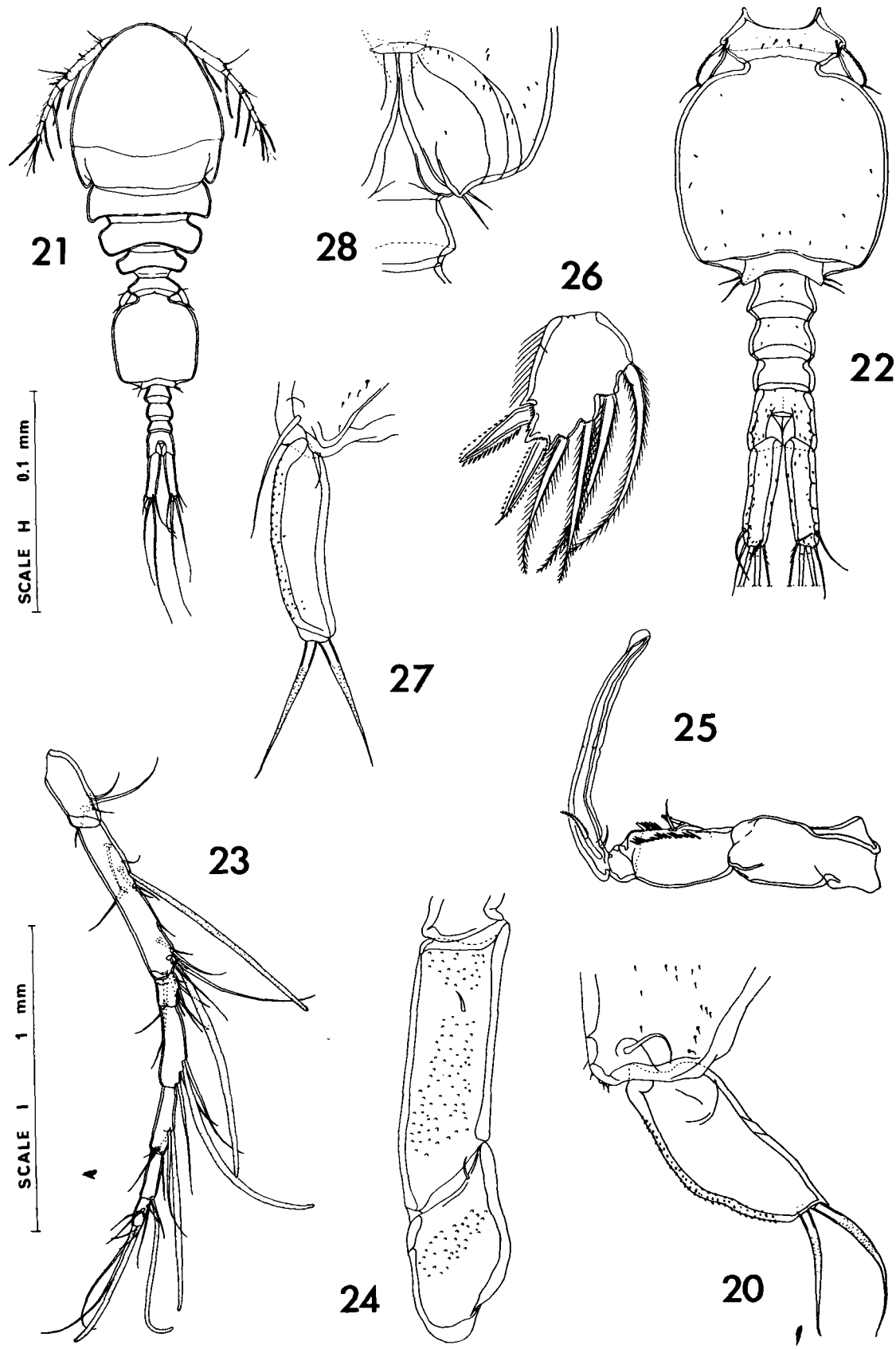
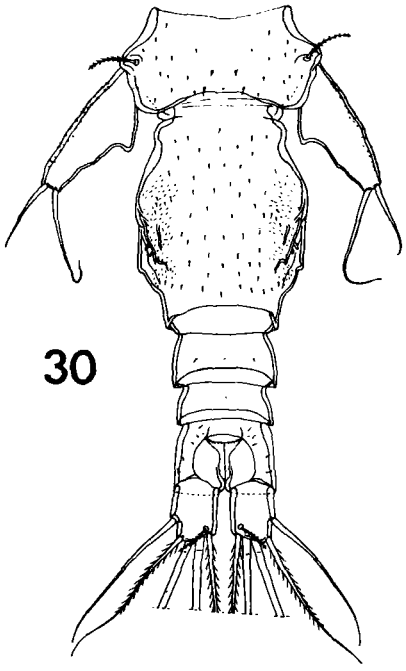

21
28
26
22
SCALE H 0.1 mm
27
25
23
SCALE I 1 mm
24
20

Fig. 29-37. — *Lichomolgus simulans* n. sp., female

29. — Body, dorsal (A)
30. — Urosome, dorsal (E)
31. — Area of attachment of egg sac, dorsal (C)
32. — Caudal ramus, dorsal (H)
33. — Rostral area, ventral (E)
34. — First antenna, ventral (F)
35. — Second antenna, posterior (F)
36. — Labrum, with paragnaths indicated by dashed lines, ventral (D)
37. — Mandible, posterior (D)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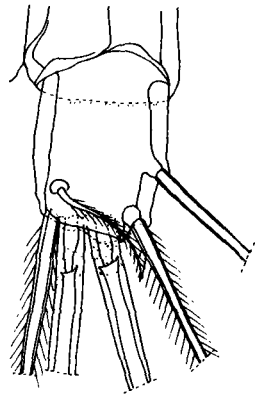
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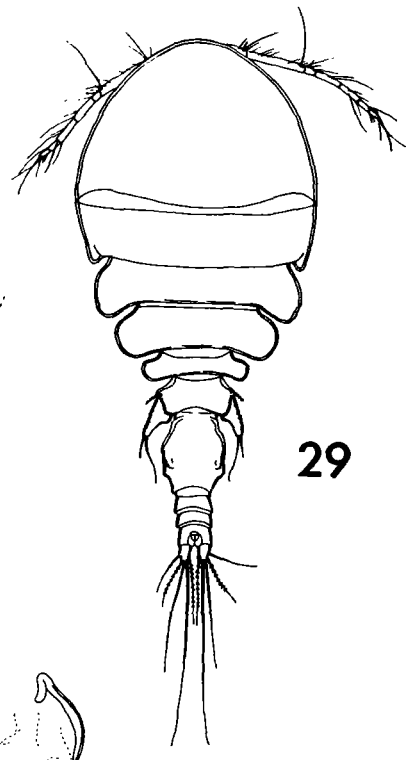
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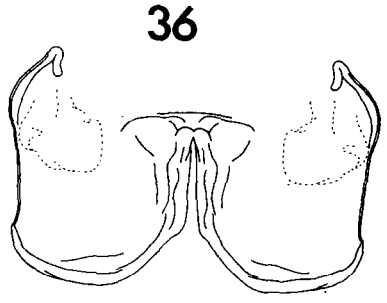
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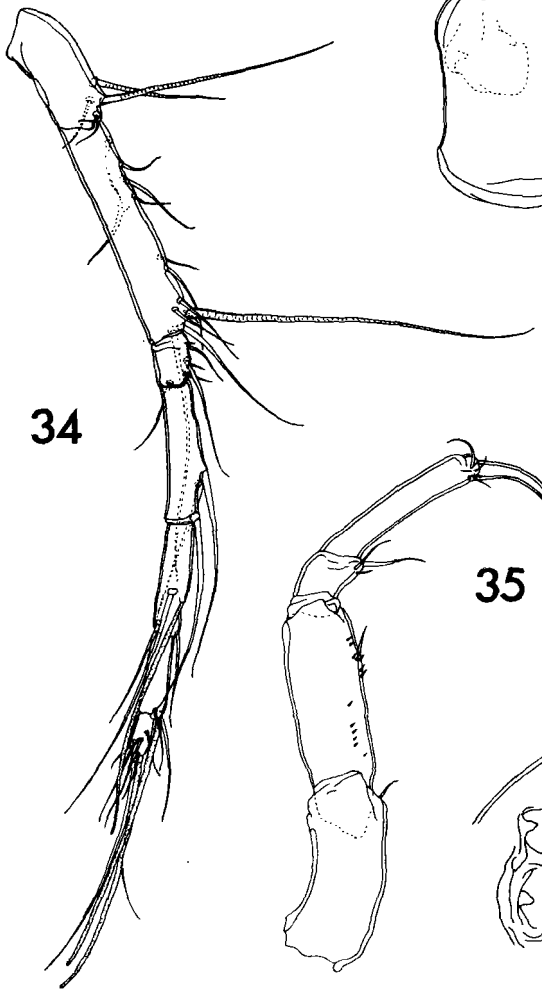
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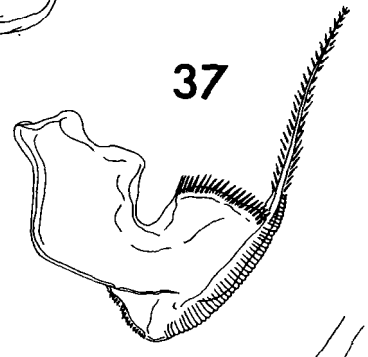
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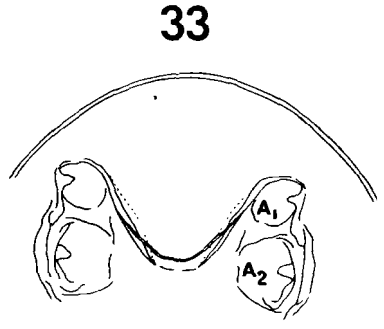
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A1
A2

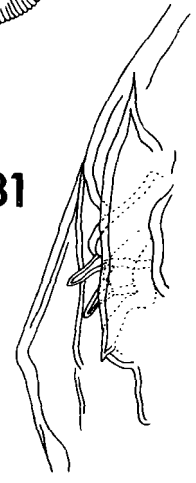
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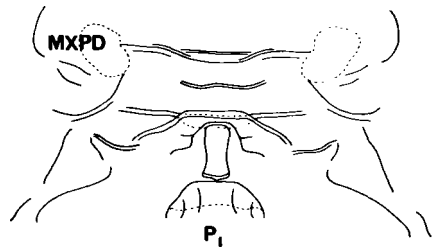
Fig. 38-45. — *Lichomolgus simulans* n. sp., female (continued)

38. — Paragnath, ventral (G)
39. — First maxilla, anterior (D)
40. — Second maxilla, posterior (D)
41. — Maxilliped, posterior (D)
42. — Area between maxillipeds and first pair of legs, ventral (E)
43. — Leg 1, anterior (F)
44. — Leg 2, anterior (F)
45. — Leg 3, anterior (F)



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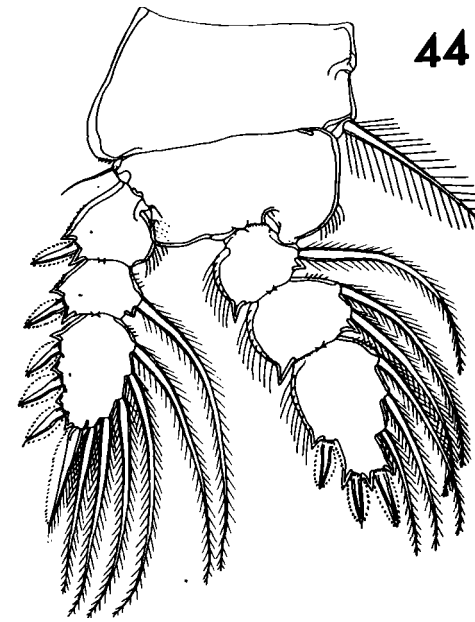

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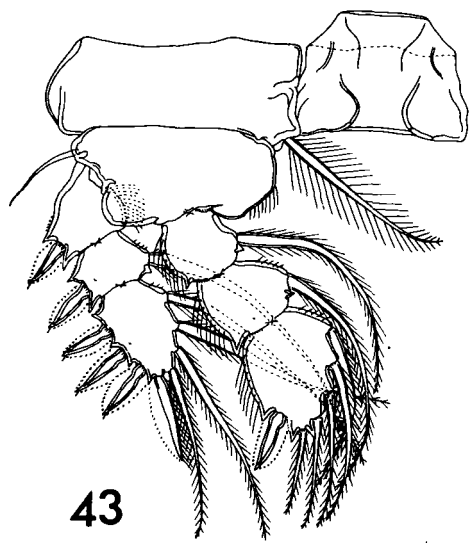

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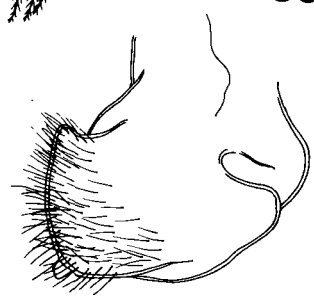

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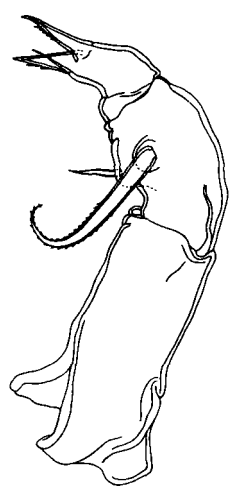

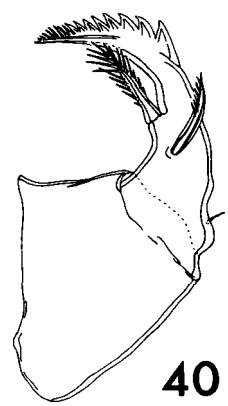

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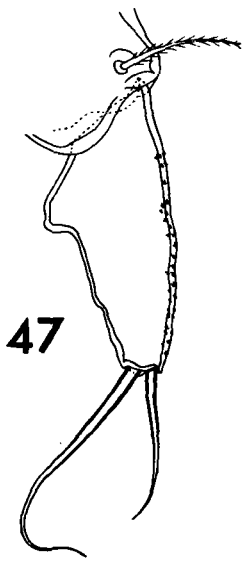
Fig. 46-47. — *Lichomolgus simulans* n. sp., female (continued)

46. — Leg 4, anterior (F)
47. — Leg 5, dorsal (D)

Fig. 48-53. — *Lichomolgus simulans* n. sp., male

48. — Body, dorsal (I)
49. — Urosome, dorsal (E)
50. — First two segments of second antenna, posterior (D)
51. — Maxilliped, inner (F)
52. — Last segment of endopod of leg 1, anterior (H)
53. — Leg 5, dorsal (C)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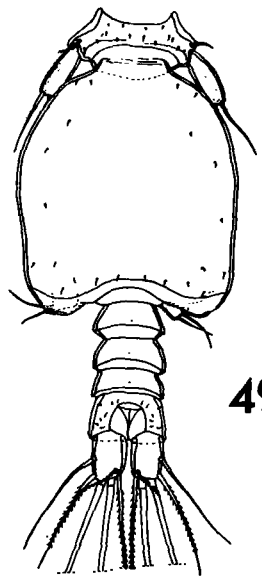
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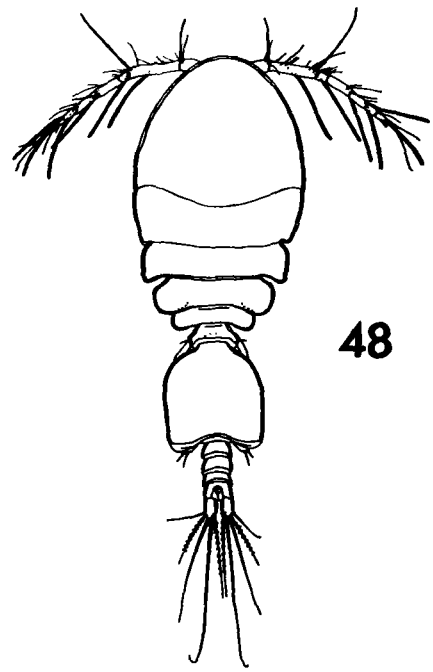
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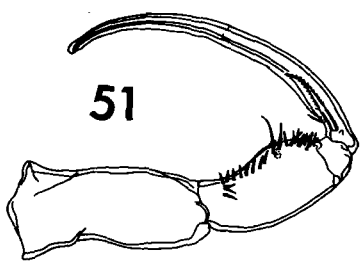
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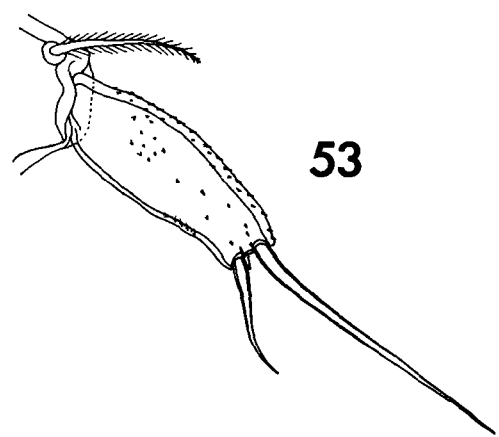
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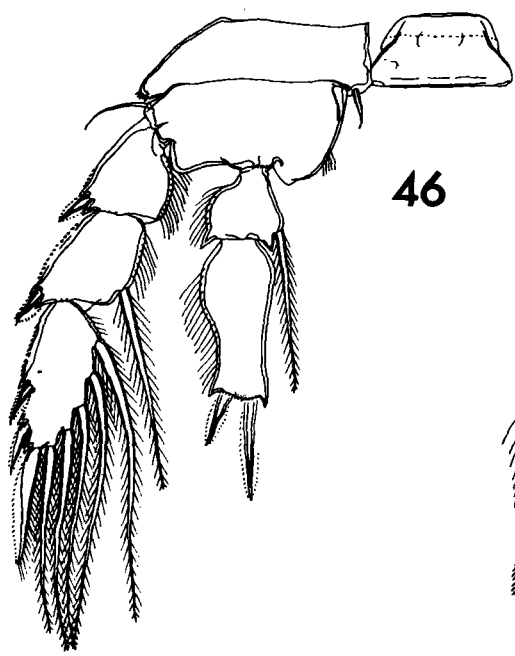
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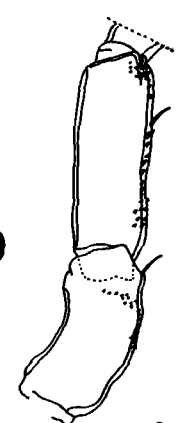
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NEW SPECIES OF *STELLICOLA* (COPEPODA, CYCLOPOIDA) ASSOCIATED WITH STARFISHES IN MADAGASCAR, WITH A REDESCRIPTION OF *S. CAERULEUS* (STEBBING, 1900)

By ARTHUR G. HUMES & JU-SHEY HO

INTRODUCTION

Two species of the lichomolgid genus *Stellicola* (a genus usually living in association with asteroid echinoderms) are known from starfishes in the region of Nosy Bé, in northwestern Madagascar. *S. oreastriphilus* Kossmann, 1877, occurs commonly on *Protoreaster lincki* (Blainville), *Culcita schmideliana* (Retzius), *Pentaceraster mammillatus* (Audouin), and *Poraster superbus* (Möbius) (Humes & Cressey, 1961), and more rarely on *Choriaster granulatus* (Lütken) (Humes & Ho, in press). A second species of *Stellicola*, whose description by Humes and Ho is in press, also occurs on *Choriaster granulatus*. Five new species from the region of Nosy Bé are now to be added, bringing the total number of species in that area to seven.

The field work was done by the first author, in 1960 while a member of an expedition sent to Madagascar by the Academy of Natural Sciences of Philadelphia, and in 1963–64 while participating in the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the material has been aided by a grant (GB-1809) from the National Science Foundation of the U.S.

We wish to thank Dr. H. Barraclough Fell and Mr. James F. Clark of the Museum of Comparative Zoology, Harvard University, for the identifications of the starfishes collected in 1963–64 (with the exception of the *Retaster cribrosus* from Ankify which was determined by Dr. G. Cherbonnier of the Muséum National d'Histoire Naturelle in Paris) and Dr. Elisabeth Deichmann, also of the Museum of Comparative Zoology, for determining the starfishes collected in 1960. It is a pleasure also to acknowledge the assistance given to the field work by the staff at the Centre d'Océanographie et des Pêches et Nosy Bé during the eighteen months while the first author was resident there.

We are also indebted to Dr. J. P. Harding of the British Museum (Natural History) for information on the whereabouts of Thompson and A. Scott's Ceylonese copepods and to Miss Patricia D. Lofthouse of the same museum for arranging the loan of syntypes of *S. caeruleus* with permission to dissect a male and a female.

The material covered in this paper comprises :

Stellicola kossmanni, new species
Stellicola affinis, new species
Stellicola longiseta, new species
Stellicola femineus, new species
Stellicola pollex, new species
Stellicola oreastriphilus Kossmann, redescription in part
Stellicola caeruleus (Stebbing), redescription of syntypes

STELLICOLA Kossmann, 1877

Stellicola kossmanni n. sp.

Pl. 1, figs. 1–6; Pl. 2, figs. 7–15; Pl. 3, figs. 16–21; Pl. 4, figs. 22–24.

TYPE MATERIAL. 4 ♀ and 14 ♂ from washings of 83 starfishes, *Protoreaster lincki* (Blainville), in a depth of 0·5 m. at Pte. Antsamantsara, west of Madirokely, Nosy Bé, Madagascar. Collected 7th July, 1963. Holotype female, allotype, and 13 paratypes (2 ♀, 11 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.1–3; the remaining 3 paratypes (dissected) in the collection of A. G. Humes.

Other specimens (all from *Protoreaster lincki* in 0·5 m.): 6 ♀, 6 ♂ from 7 hosts, Pte. Mahatsinjo, Nosy Bé, 4th July, 1963; 1 ♀, 6 ♂ from 60 hosts at Pte. Lokobe, Nosy Bé, 11th July, 1963.

FEMALE. Body (Pl. 1, fig. 1) with moderately broadened prosome. Length (not including setae on caudal rami) 1·0 mm. (0·95–1·03 mm.) and greatest width 0·46 mm. (0·44–0·47 mm.), based on 10 specimens (holotype, 3 paratypes, and 6 specimens from Pte. Mahatsinjo, 4th July, 1963). Ratio of length to width of prosome 1·45 : 1. Segment of leg 1 separated dorsally and laterally from head by a furrow. Epimeral areas of segments of legs 1–4 rounded; lateral margins of segments of legs 1–3 with membrane (Pl. 1, fig. 2).

Segment of leg 5 (Pl. 1, fig. 3) 83 μ long and 105 μ in greatest width; fifth legs borne slightly dorsally. Between this segment and genital segment a short intersegmental sclerite ventrally. Genital segment longer than wide, 146 μ in length, 127 μ in width in its anterior three-fourths where its lateral margins are somewhat irregular, and 85 μ in width in its constricted posterior fourth. Areas of attachment of egg sacs situated dorsolaterally just in front of posteriormost fourth; each area (Pl. 1, fig. 4) with 2 long setae (outer 82 μ long and bearing minute unilateral spinules, inner 36 μ and feathered) and between them a small spinous process 6 μ long. Posterior margin of segment with a membrane having a ragged edge simulating small spinules especially laterally. Three postgenital segments, first 44 × 75 μ with a similar posterior membrane, second 18 × 68 μ, and third 28 × 65 μ.

Caudal ramus (Pl. 1, fig. 5), inserted ventrally on anal segment, quadrate, 31 × 29 μ. Long naked setule (34 μ) midway on outer margin. Pedicellate dorsal seta 65 μ and haired. Outer lateral seta 109 μ and naked, inserted close to outermost terminal seta (156 μ, with a few spinules on each side in its proximal third). Innermost terminal seta 216 μ and naked. Two long terminal setae, inserted between dorsal (smooth) and ventral (with a row of prominent setules) flaps, 429 μ (outer) and 600 μ (inner) and both with lateral spinules; " pegged " region of these two setae finely punctate. A small hair on ventral surface of ramus.

Dorsal surface of prosome with scattered hairs (sensilla). Dorsal surface of urosome with hairs as shown in Pl. 1, fig. 3; ventral surface less ornamented with hairs. Ratio of length of prosome to that of urosome 1·87 : 1.

Egg sac (Pl. 1, fig. 1) elongated, 520 × 275 μ, extending far beyond caudal rami, and containing many eggs about 50 μ in diameter.

Rostral area (Pl. 1, fig. 6) rounded, not strongly sclerotized.

First antenna (Pl. 2, fig. 7) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 39 (50 μ along anterior margin), 74, 31, 41, 34, 18, and 16 μ respectively. Formula for armature: 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All setae naked except 1 on second segment and 4 on last 3 segments which are delicately haired. Terminal seta on segment 7 very long (260 μ), equal to length of entire first antenna. Aesthete on segment 7 arising from common base with adjacent long naked seta. Ventral surface of segment 3 with sclerotization suggesting an intercalary segment.

Second antenna (Pl. 2, fig. 8) relatively slender and 3-segmented, third segment showing a partial division on anterior surface but entire posteriorly. First segment with a smooth seta, second with a haired seta, and third with 3 haired setae near the incomplete division and terminally with 6 elements: a stout claw 42 μ along its axis, 4 long naked setae, and a short blunt naked seta. Anterior surface of second antenna pilose, with 4 slender setules subterminally on last segment. Long setae annulated.

Labrum (Pl. 2, fig. 9) with its two posteroventral lobes somewhat angular and unornamented.

Mandible (Pl. 2, fig. 10) with an outer row of slender spinules and an inner row of rather stout blunt teeth preceded proximally by a prominent dentiform process; both rows diminishing to minute spinules along the slender terminal lash. Paragnath a small lobe hidden under lobe of labrum in ventral view. First maxilla (Pl. 2, fig. 11) an elongated lobe with 3 naked setae and 1 stout spiniform element strongly spinose on its posterolateral surface. Second maxilla (Pl. 2, fig. 12) 2-segmented; first segment unarmed, its proximal ventral margin projecting strongly; second segment with 2 postero-inner elements (a slender seta with short lateral spinules and a spine with rows of spinules) and terminating in a spiniform process bearing rows of teeth as in the figure (proximal tooth larger than others, producing a bifurcated appearance). Maxilliped (Pl. 2, fig. 13) 3-segmented; first segment unarmed, second with 2 setae and anterior surficial spinules, and third with 2 setae (1 with lateral spinules, other naked) and terminating in a spiniform process bearing lateral spinules.

Area between maxillipeds and first pair of legs (Pl. 2, fig. 14) not protuberant, with a distinct sclerotized line between bases of maxillipeds.

Rami of legs 1–4 (Pl. 2, fig. 15, Pl. 3, figs. 16, 17, and 18) 3-segmented, except endopod of leg 4 which is weakly 2-segmented. Spine and setal formula as follows (Roman numerals indicating spines, Arabic numerals setae):

P_1	protopod	0–1;	1–0	exp	I–0;	I–1;	III, I, 4
				end	0–1;	0–1;	I, 5
P_2	protopod	0–1;	1–0	exp	I–0;	I–1;	III, I, 5
				end	0–1;	0–2;	I, II, 3
P_3	protopod	0–1;	1–0	exp	I–0;	I–1;	III, I, 5
				end	0–1;	0–2;	I, II, 2
P_4	protopod	0–1;	1–0	exp	I–0;	I–1;	II, I, 5
				end	0–1;	II, 1	

Inner seta on coxa feathered in legs 1–3 but naked (42 μ long) in leg 4. Hairs on inner margin of basis in legs 1–3 absent in leg 4. Expansion of basis over anterior surface of first segment of exopod rather acute. Between 2 terminal spines on last segment of endopod of leg 2 a bifurcated spinous process. On second segment of exopod of leg 4 relatively short inner seta lying (in alcoholized specimens) nearly parallel to ramus and having short lateral spinules instead of the usual long hairs. Endopod of leg 4 two-segmented, with a line of separation visible on both anterior and posterior surfaces, but with the lateral sclerotization continuous between the two segments. First segment 26 × 24 μ (greatest dimensions) with inner distal seta 84 μ long, spiniform, with short lateral spinules. Second segment 46 × 21 μ (greatest dimensions), the feathered inner seta 67 μ, the 2 terminal spines 105 μ (inner) and 58 μ (outer) both with delicately serrate lamellae; a row of minute spinules anteriorly across end of segment near insertions of 2 spines, and a row of hairs on proximal half of outer margin of segment.

Leg 5 (Pl. 3, fig. 19) with free segment elongated, 32 × 14 μ. Two very unequal terminal setae, outer 102 μ long, with minute lateral spinules, inner 55 μ, with delicately serrate lamellae. Seta on body near insertion of free segment 40 μ and feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 1, figs. 3 and 4).

Colour in life in transmitted light faintly reddish, eye red, intestine dark brown, ovary reddish brown.

MALE. Body form (Pl. 3, fig. 20) resembling that of female, though prosome somewhat narrower. Length (excluding setae on caudal rami) 0·71 mm. (0·69–0·74 mm.) and greatest width 0·27 mm. (0·26–0·28 mm.), based on 10 specimens. Ratio of length to width of prosome 1·72 : 1.

Segment of leg 5 (Pl. 3, fig. 21) 33 × 70 μ. Ventral intersegmental sclerite absent. Genital segment about as long as wide, 99 × 94 μ, with slightly rounded lateral margins in dorsal view. Four postgenital segments 42 × 66, 34 × 58, 11 × 50, and 21 × 52 μ from anterior to posterior.

Caudal ramus like that of female but smaller, 23 × 23 μ.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 1·85 : 1.

Rostral area, first antenna, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla like those of female. Maxilliped (Pl. 4, fig. 22) slender and 4-segmented. First segment unarmed, second with 2 naked setae and 2 rows of spinules, and third small and unarmed. Proximal part of terminal claw probably representing fourth segment. Claw 101 μ in length (measured along its axis), recurved, showing a slight evidence of division about midway and having a fringe of delicate hyaline spinules along its concave edge; bearing 2 setae proximally, one small naked and hyaline 12 μ long, other long (50 μ) with a few distal spinules.

Area between maxillipeds and first pair of legs like that in female.

Legs 1–4 resembling those of female, with same spine and setal formula. Endopod of leg 4 with 2 terminal spines differing in their proportional lengths. Measurements

for this ramus : first segment 19 × 18 μ with seta 66 μ, second segment 33 × 17 μ with seta 45 μ and 2 terminal spines 80 μ and 47 μ (ratio of these 2 spines 1·7 : 1, instead of 1·8 : 1 in female).

Leg 5 resembling that of female, with free segment 21 × 8 μ and 2 terminal elements 70 μ and 34 μ respectively.

Leg 6 (Pl. 4, fig. 23) consisting of posterolateral flap on ventral surface of genital segment and bearing a minute spiniform process and 2 unequal setae, one naked (69 μ), other feathered (33 μ). In view of entire urosome these setae conspicuous (see Pl. 3, fig. 21).

Spermatophore (Pl. 4, fig. 24), inside body of male, elongated, 86 × 31 μ without neck.

Colour in life in transmitted light resembling that of female.

(This species is named for Dr. Robby Kossmann, who originally described the genus *Stellicola*).

COMPARISON WITH RELATED SPECIES. There are at present fifteen species known with some certainty to belong to the genus *Stellicola* (14 with published descriptions and 1 whose description by Humes and Ho is in press). Stock (1957) included *S. thorelli* Kossmann, 1877, *S. pleurobranchi* Kossmann, 1877, *S. oreastriphilus* Kossmann, 1877, *S. caeruleus* (Stebbing, 1900), *S. curticaudatus* (Thompson & A. Scott, 1903), *S. gracilis* (Thompson & A. Scott, 1903), *S. lankensis* (Thompson & A. Scott, 1903), and *S. asterinae* (Bocquet, 1952), a species later synonymized with *S. clausi* (Rosoll, 1889) by Bocquet and Stock (1962). The four West African species (*S. frequens, S. astropectinis, S. luidiae,* and *S. lautus*) originally described by Humes & Cressey (1958) in the genus *Lichomolgus* also belong to *Stellicola,* as pointed out by Bocquet and Stock (1962). In *Stellicola* there should also be included *S. holothuriae* (Ummerkutty, 1961) and probably *S. longicaudatus* (Thompson & A. Scott, 1903).

S. kossmanni may be separated from these fifteen species as follows : in *gracilis, lankensis,* and the new species of Humes & Ho (in press) there are two postgenital segments in the female and three in the male ; in *frequens, astropectinis, luidiae,* and *lautus* there are three claws on the second antenna ; in *clausi* there are two claws on the second antenna ; and in *oreastriphilus, holothuriae, thorelli, pleurobranchi, curticaudatus, longicaudatus,* and *caeruleus,* although the second antenna has only a single claw, the length ratio of prosome to urosome in the female (ranging from 2·3–3·3 : 1) is distinctly more than 2 : 1.

S. kossmanni shows several features which may be used as identifying characters : the very long terminal seta on the first antenna (as long as the antenna itself), the four slender subterminal setules on the second antenna (these in addition to the six terminal elements), the strongly spinose element on the first maxilla, and in leg 4 the detailed ornamentation of the four elements on the endopod and the nature of the inner seta on the second segment of the exopod.

Stellicola affinis n. sp.

Pl. 4, figs. 25–31; Pl. 5, figs. 32–41; Pl. 6, figs, 42–48.

TYPE MATERIAL. 84 ♀ and 26 ♂ washed from 2 starfishes, *Maculaster maculata maculata* (Müller & Troschel), exposed on sand bar at low tide on the eastern side of Ankify, on the mainland of Madagascar, opposite Nosy Komba, and about 15 kilometers south of Nosy Bé. Collected 8th August, 1964. Holotype female, allotype, and 51 paratypes (40 ♀, 11 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.4–6 ; 27 paratypes (20 ♀, 7 ♂) in the United States National Museum, Washington ; and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all in the vicinity of Nosy Bé). From *Maculaster maculata maculata :* 16 ♀, 8 ♂ from 1 host, exposed on sand bar at Ankify (the type locality), 9th September, 1964. From *Maculaster savignyi* (Audouin) : 38 ♀, 6 ♂ from 9 hosts, exposed on sand bar at Ankify, 8th August, 1964 ; 60 ♀, 27 ♂ from 1 host, in 2 m., eastern shore of Ambariobe, a small island between Nosy Komba and Nosy Bé, 4th October, 1964 ; 12 ♀, 3 ♂ from 1 host, on sand exposed at low tide, Ambariobe, 21st July, 1963. From *Retaster cribrosus* von Martens : 11 ♀, 5 ♂ from 1 host, exposed on sand bar, Ankify, 2nd November, 1963. From *Luidia maculata* Müller & Troschel : 35 ♀, 16 ♂ from 2 hosts, dredged in 17 m., 13° 16′ S, 48° 31′ 30″ E, northeast of Nosy Faly, 14th September, 1960.

FEMALE. Body (Pl. 4, figs. 25 and 26) relatively slender. Length (not including setae on caudal rami) 1·01 mm. (0·98–1·04 mm.) and greatest width 0·35 mm. (0·32–0·37 mm.), based on 10 specimens. Ratio of length to width of prosome 1·56 : 1. Epimeral areas of segment of leg 4 pointed.

Segment of leg 5 (Pl. 4, fig. 27) 61 × 97 μ. Between this segment and genital segment a short intersegmental sclerite ventrally. Genital segment elongated, 156 μ in length, being somewhat wider in its anterior two-thirds (109 μ) than in its posterior third (80 μ). Areas of attachment of egg sacs located dorsolaterally on anterior part of middle third ; each area (Pl. 4, fig. 28) bearing 2 short naked setae (outer 13 μ long, inner 17 μ), with a small spinous process about 5 μ long between them. Two postgenital segments, first 56 × 63 μ, second (anal) 43 μ long and 72 μ in greatest width (this segment deeply incised).

Caudal ramus (Pl. 4, fig. 29) divergent, inserted a little ventrally on anal segment, elongated and somewhat narrowed distally, in one female 106 μ (greatest length) × 15 μ (width taken at level of outer seta) making a ratio of 7 : 1, in another female 108 × 17 μ, ratio of 6·3 : 1. Minute setule (4 μ long) on outer proximal margin. Another small setule (8 μ) on outer margin just beyond midpoint of ramus (perhaps corresponding to long marginal setule in *S. kossmanni*). Pedicellate dorsal seta 25 μ. Outer lateral seta 74 μ, inserted near end of ramus. Innermost terminal seta 130 μ, outermost terminal seta 88 μ, and 2 long median terminal setae, inserted between dorsal (smooth) and ventral (with a row of minute spinules) flaps, 242 μ (outer) and 363 μ (inner). All setae naked. Both outer and inner walls of ramus with an interruption in sclerotization as shown in figure. Two minute hairs on ventral surface of ramus.

Dorsal surface of prosome with scattered hairs. Dorsal surface of urosome with hairs as shown in Pl. 4, fig. 27; ventral surface much less ornamented with hairs. Ratio of length of prosome to that of urosome 1·30 : 1.

Egg sac (Pl. 4, fig. 25) fairly elongated, 374 × 143 μ, extending not quite to the ends of caudal rami, and containing a moderate number of eggs about 50 μ in diameter.

Rostral area (Pl. 4, fig. 30) rounded.

First antenna (Pl. 4, fig. 31) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 30 (47 μ along anterior margin), 67, 23, 25, 31, 19, and 14 μ respectively. Formula for armature as in *S. kossmanni*. Setae naked except for 1 on antepenultimate segment, 1 on penultimate segment, and 2 on last segment which are delicately haired. Long terminal seta 213 μ in length, nearly as long as entire first antenna. Aesthete on last segment having a common base with adjacent seta. Sclerotization on ventral surface of segment 3 suggesting an intercalary segment.

Second antenna (Pl. 5, fig. 32) 3-segmented, with no evidence of division of third segment. Armature 1; 1; 3 + 5 + 1 claw, as in *S. kossmanni*, though relative lengths and fine ornamentation of setae different (compare Pl. 2, fig. 8 and Pl. 5, fig. 32). Claw 41 μ along its axis. Anterior surface of second antenna not pilose as in *S. kossmanni*; posterior surface with very fine punctations.

Labrum (Pl. 5, fig. 33) with subtriangular unornamented lobes.

Mandible (Pl. 5, fig. 34) in general resembling that of *S. kossmanni*, but first element in inner row of teeth less prominent and terminal lash relatively shorter. Paragnath a small indistinct lobe medial to insertions of mandible and first maxilla (Pl. 5, fig. 38). Four elements on first maxilla (Pl. 5, fig. 35), including spine with lateral rows of spinules. Second maxilla (Pl. 5, fig. 36) 2-segmented, with proximal ventral margin of unarmed first segment rather angularly produced; second segment with long inner spine having serrated flanges (with serrations especially prominent along distal flange) and with terminal process bifurcated as shown in figure. Maxilliped (Pl. 5, fig. 37) 3-segmented, with armature resembling that of *S. kossmanni*; second segment lacking rows of small spinules seen in that species.

Area between maxillipeds and first pair of legs only slightly protuberant (Pl. 4, fig. 26); a sclerotized line connecting bases of maxillipeds (Pl. 5, fig. 38).

Rami of legs 1–4 (Pl. 5, figs. 39, 40, 41, and Pl. 6, fig. 42) with same segmentation and spine and setal formula as in *S. kossmanni*. Inner seta on coxa relatively long and feathered in legs 1–3 but short (19 μ) and naked in leg 4. Hairs on inner margin of basis absent in leg 4 and apparently also in leg 1. In legs 1–3 expansion of basis over anterior surface of first segment of exopod with membranous tip; this expansion absent in leg 4. Second segment of exopod of leg 4 with inner seta like that in *S. kossmanni*. Endopod of leg 4 two-segmented, with distinct articulation between these segments. First segment 31 × 25 μ (greatest dimensions) with finely barbed inner seta 91 μ long. Second segment 50 × 24 μ (greatest dimensions), the inner seta finely barbed and 48 μ, the 2 terminal spines 62 μ (inner) and 51 μ (outer), both with delicately serrate lamellae. Rows of long hairs along outer margins of both segments, with row on second segment interrupted. Row of minute spinules

on anterior surface across end of segment near insertions of 2 spines.

Leg 5 (Pl. 6, fig. 43) with elongated free segment, 28 × 13 μ. Two unequal terminal setae, outer 61 μ long with a few minute barbs distally, inner 39 μ with outer serrated fringe. Seta on body near insertion of free segment 25 μ long and delicately feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 4, fig. 28).

Colour in life in transmitted light slightly opaque, ovary dark gray, eye dark blackish red, egg sacs dark gray.

MALE. Body form (Pl. 6, fig. 44) resembling that of female but more slender. Length (without ramal setae) 0·78 mm. (0·75–0·82 mm.) and greatest width 0·22 mm. (0·21–0·23 mm.), based on 10 specimens. Ratio of length to width of prosome 1·84 : 1.

Segment of leg 5 (Pl. 6, fig. 45) 31 × 65 μ. Ventral intersegmental sclerite absent. Genital segment subquadrate, 133 × 117 μ, a little longer than wide, with lateral borders nearly parallel in dorsal view. Three postgenital segments 47 × 59, 43 × 46, and 26 × 46 μ from anterior to posterior.

Caudal ramus (see Pl. 6, fig. 45) resembling that of female, but proportionately more slender, 90 × 12 μ, with ratio of 7·5 : 1, and a little more narrowed in its distal half.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 1·16 : 1.

Rostral area, first antenna, second antenna, labrum, mandible, paragnath, and first maxilla like those of female. Second maxilla also resembling that of female but proximal ventral margin of first segment less produced and more rounded. Maxilliped (Pl. 6, fig. 46) slender and 4-segmented. First segment unarmed. Second segment with 2 slender naked setae and 2 rows of spinules (1 row short, consisting of only about 5 spinules.) Third segment short and unarmed. Proximal part of claw probably representing fourth segment. Slender gently recurved claw 111 μ along its axis, with evidence of division about midway and having a fringe of delicate hyaline spinules along its concave margin ; bearing proximally 2 setae, one 11 μ and naked, other 29 μ long with a few minute barbs near its tip.

Area between maxillipeds and first pair of legs like that in female.

Legs 1–4 resembling those of female, with same spine and setal formula. Endopod of leg 4 much like that in female, with 4 elements from inner to outer 72, 35, 43, and 34 μ long.

Leg 5 (Pl. 6, fig. 47) with free segment 21 × 8 μ, more slender than in female, and 2 terminal setae more unequal, 53 μ and 22 μ (ratio of 2·4 : 1, instead of 1·56 : 1 in female).

Leg 6 (Pl. 6, fig. 48) consisting of posterolateral flap on ventral surface of genital segment and bearing 2 slender naked setae 25 and 38 μ long.

Spermatophores not observed.

Colour in life in transmitted light resembling that of female.

[The specific name *affinis*, Latin = adjoining or related, refers to the close similarity of this species with *Stellicola gracilis* (Thompson & A. Scott) as discussed below].

COMPARISON WITH OTHER SPECIES. At present there are three species known in the genus *Stellicola* which, like *S. affinis*, have two postgenital segments in the female and three in the male. These are *S. gracilis* (Thompson & A. Scott, 1903), *S. lankensis* (Thompson & A. Scott, 1903), and the species whose description by Humes and Ho is in press. *S. lankensis* (of which only the female is known), from washings of dredged invertebrates in Ceylon, has a much shorter caudal ramus (proportions of about 2·37 : 1 in T. & S.'s pl. XV, fig. 25). The new species of Humes and Ho differs in having a quadrate caudal ramus, in its smaller size (female 0·79 mm., male 0·64 mm.), and in many other features.

S. gracilis, from washings of dredged invertebrates in Ceylon, is known only from the original description and figures by Thompson & A. Scott. The existence of type material (the " several males and females " of Thompson & A. Scott) is extremely doubtful. The type specimens of *S. gracilis* were apparently deposited in the University of Liverpool, where Dr. W. A. Herdman, the author of the Report on Pearl Oyster Fisheries, was professor of natural history. An inquiry recently made by Dr. J. P. Harding of the British Museum to the Department of Oceanography of Liverpool University drew the reply that the Andrew Scott collection had been discarded. Our only available information on *S. gracilis* is, then, to be found in the brief original description.

When *S. affinis* is compared with *S. gracilis* certain similarities are obvious. The two species are of about the same length and have the same number of postgenital segments. In the female of both the anal segment is cleft deeply, the caudal rami are divergent, the genital segment has a similar shape, the second antenna appears to have the same general form, the base of the mandible is somewhat angular. and the first segment of the second maxilla seems to project. In the male of both the maxilliped is rather similar.

There exist, however, differences between the two species which in our opinion make it impossible to regard them as one and the same species. In the female of *S. gracilis* the proportions of the caudal ramus are about 4 : 1 (instead of 6·3 : 1 or 7 : 1 as in *S. affinis*), the two inner setae on the endopod of leg 4 are distinctly feathered (while in *S. affinis* these setae have very minute barbs), and (based on measurements of T. & S.'s pl. XV, fig. 1) the ratio of the length of prosome to urosome is 1 : 1 (1·30 : 1 in *S. affinis*) and the ratio of length to width of the prosome is 1·75 : 1 (1·56 : 1 in *S. affinis*). T. & S.'s pl. XV, fig. 4, shows only three elements on the first maxilla, but a fourth minute seta may have escaped their notice. They describe the tip of the second maxilla as " triangular, sharp and wedge-shaped ", illustrated on pl. XV, fig. 5, but their description is wanting in detail.

We conclude that *S. affinis*, while related to *S. gracilis*, is a separate species.

Stellicola longiseta n. sp.

Pl. 6, figs. 49–50; Pl. 7, figs. 51–60; Pl. 8, figs. 61–66.

TYPE MATERIAL. 2 ♀ and 3 ♂ from washings of 1 starfish, *Mithrodia clavigera* (Lamarck), under dead coral (*Acropora*) in a depth of 1 m., Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar. Collected 3rd September, 1963. Holo-

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type female, allotype, and 2 paratypes (1 ♀, 1 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.7–9; the remaining paratypic male (dissected) in the collection of A. G. Humes.

Other specimens (from *Mithrodia clavigera* in the same locality). 2 ♀ from 1 host in 1 m., 14th December, 1963.

FEMALE. Body (Pl. 6, fig. 49) with prosome relatively thickened as in *S. affinis*, but broader than in that species. Length (excluding setae on caudal rami) 1·18 mm. (1·14–1·22 mm.) and greatest width 0·60 mm. (0·58–0·62 mm.), based on 4 specimens (holotype, 1 paratype, and 2 specimens collected on 14th December, 1963). Ratio of length to width of prosome 1·36 : 1. Segment of leg 1 separated from head by a dorsal and lateral furrow. Epimeral areas of segment of leg 2 rather pointed posteriorly; those of segments of legs 1, 3, and 4 rounded.

Segment of leg 5 (Pl. 6, fig. 50) 88 × 146 μ. Between this segment and genital segment a short intersegmental sclerite ventrally. Genital segment a little longer than wide, 177 μ in length, 159 μ in width in its anterior two-thirds, and 114 μ in width in its constricted posterior third, and showing a slight middorsal hump anteriorly. Areas of attachment of egg sacs situated dorsolaterally on anterior part of posterior third; each area (Pl. 6, fig. 50) with 2 setae (outer 77 μ long and naked, inner 23 μ and feathered) and between them a small spinous process 6 μ long. Posterior margin of genital segment with a membrane which simulates spinules laterally. Two postgenital segments 52 × 95 and 34 × 88 μ respectively.

Caudal ramus (Pl. 7, fig. 51), inserted ventrally on anal segment, a little wider than long, 28 × 35 μ, taking average length as 28 μ, the ramus being longer ventrally (31 μ) than dorsally (25 μ). Long naked setule on outer margin 31 μ long. Outer lateral seta 120 μ and naked. Outermost terminal seta 180 μ with lateral spinules. Innermost terminal seta long, 451 μ, and naked. Two long median terminal setae 460 μ (outer) and 660 μ (inner), both with lateral spinules and their "pegged" regions punctate. These 2 setae inserted between ventral flap (with rows of spinules) and dorsal flap of form shown in figure and bearing very small spinules near pedicellate dorsal seta (33 μ long and naked). Group of 2–3 minute hairs on dorsal surface of ramus.

Dorsal surface of prosome with only a few hairs. Dorsal surface of urosome with more abundant hairs as in Pl. 6, fig. 50; ventral surface with very few hairs. Ratio of length of prosome to that of urosome 2·45 : 1.

Egg sac (Pl. 6, fig. 49) elongated and rather stout, about 810 × 300 μ, more than twice as long as the urosome, and containing many eggs about 52 μ in diameter.

Rostral area (Pl. 7, fig. 52) rather pointed.

First antenna with armature as in *S. kossmanni* and *S. affinis*. All setae apparently naked. Lengths of segments (measured as before) 30 (67 μ along anterior edge), 107, 29, 53, 46, 23, and 15 μ respectively. Terminal aesthete and adjacent seta with common base. Sclerite on ventral surface of third segment. Long terminal seta 234 μ in length, distinctly less than length of antenna (340 μ).

Second antenna (Pl. 7, fig. 53) 3-segmented, third segment showing no evidence of division. Armature 1; 1; 3 + 5 + 1 claw, as in 2 previous species. Seta on

segment 1 unusually long (165 μ) and setose. Seta on segment 2 relatively short (44 μ) and naked. Claw 68 μ along its axis. On anterior surface near base of claw a short vermiform protrusion (aesthete ?). Anterior surface of second antenna pilose as in figure.

Labrum (Pl. 7, fig. 54) with attenuated unornamented lobes.

Mandible (Pl. 7, fig. 55) with elements of outer row beginning as stout spines and diminishing to slender spinules ; first element in inner row not much larger than rest ; a patch of spinules on posterior proximal surface of mandible. Paragnath a small lobe as in *S. affinis*. First maxilla with 4 elements as in 2 previous species, but ornamented spiniform element only very finely spinulose. Second maxilla (Pl. 7, fig. 56) with first segment ornamented with a few spinules on both anterior and posterior surfaces and with its proximal ventral margin angularly produced. Second segment with postero-inner finely barbed seta, long inner spiniform seta with its posterior surface spinulose but anterior surface smooth, and with terminal spiniform process spinulose and showing 2 prominent spines near base. Maxilliped (Pl. 7, fig. 57) with first segment unarmed, second with usual 2 setae and with spinules as in figure, and third with 2 setae (one spinulose, other naked) and terminal spiniform process.

Area between maxillipeds and first pair of legs not protuberant and resembling that in *S. kossmanni*.

Rami of legs 1–4 like those in 2 previous species, with same spine and setal formula. Fine ornamentation much like that in *S. kossmanni*. Last segment of endopod of leg 2 without a bifurcated spinous process (Pl. 7, fig. 58), and having a form somewhat different from that in *S. kossmanni*. Last segment of endopod of leg 3 (Pl. 7, fig. 59) of a form slightly different from *S. kossmanni*. Leg 4 (Pl. 7, fig. 60) with inner seta on coxa relatively short (26 μ) and, naked. Slightly barbed inner seta on second segment of exopod shorter than setae on third segment, recurved, and lying (in alcoholized specimens) over the posterior surface of ramus. Endopod (Pl. 8, fig. 61) with 2 segments clearly separated. First segment 31 $\times$ 28 μ, with inner seta 58 μ long and feathered. Second segment 69 μ long, 28 μ in greatest width, and 18 μ wide at narrowest point, its feathered inner seta 74 μ, inner terminal spine 76 μ with a very narrow lamella along one edge, and outer terminal spine 55 μ with finely serrated lamellae and with a delicately trifurcate tip. Row of hairs on outer margin of this segment interrupted at slight indentation.

Leg 5 (Pl. 8, fig. 62) with free segment swollen on inner margin, its greatest dimensions 39 $\times$ 19 μ. Two terminal naked setae extremely unequal, inner 34 μ, outer 170 μ. Seta on body near insertion of free segment about 35 μ and feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 6, fig. 50).

Colour in life in transmitted light translucent to grayish, eye red, egg sacs gray.

MALE. Body (Pl. 8, fig. 63) with prosome more slender than in female. Length (without ramal setae) 0·73 mm. (0·72–0·73 mm.) and greatest width 0·29 mm. (0·28–0·29 mm.), based on 3 specimens (allotype, 1 paratype, and 1 specimen collected 14th December, 1963). Ratio of length to width of prosome 1·62 : 1.

Segment of leg 5 (Pl. 8, fig. 64) 46 × 79 μ. Ventral intersegmental sclerite absent. Genital segment a little longer than wide, 125 × 104 μ, with sides in dorsal view nearly parallel. Three postgenital segments 42 × 69, 33 × 55, and 20 × 53 μ from anterior to posterior.

Caudal ramus like that of female. Surfaces of prosome and urosome, as in female, sparsely ornamented with hairs. Ratio of length of prosome to that of urosome 1·70 : 1.

Rostral area, first antenna, second antenna, labrum, mandible, paragnath, and first maxilla resembling those in female. Second maxilla much like that of female, with same process on first segment, but with long inner seta less strongly developed and with terminal spiniform process weaker and showing near base only 1 prominent spine, the second being greatly reduced in size. Maxilliped (Pl. 8, fig. 65) slender. Spinules on second segment arranged differently than in 2 previous species. Claw 117 μ long (measured along its axis) and showing 2 slight flexures, with only indication of division being an interruption in fringe of delicate hyaline spinules along concave margin. Two setae near base of claw 67 μ (with a few barbs near tip) and 8 μ (naked).

Area between maxillipeds and first pair of legs resembling that of female.

Legs 1–4 resembling those of female, with same spine and setal formula.

Leg 5 (Pl. 8, fig. 66) with free segment lacking inner swelling, 18 × 9 μ. Two terminal setae 20 μ (inner) and 58 μ (outer), ratio between them being 2·9 : 1, instead of 7 : 1 as in female. Seta on body near insertion of free segment about 20 μ long and slightly feathered.

Leg 6 (see Pl. 8, fig. 64) resembling that of *S. kossmanni*, with a minute spinous process and 2 unequal setae, one naked (64 μ), other feathered (20 μ).

Spermatophores not observed.

Colour in life in transmitted light as in female.

(The specific name *longiseta*, Latin = long seta, alludes to the unusually long terminal seta on the fifth leg in the female).

Comparison with related species. From the four species of *Stellicola* known to have two postgenital segments in the female, *S. longiseta* may readily be separated by its very long seta on leg 5. In addition, this species from *Mithrodia* has a caudal ramus which is a little wider than long, instead of 4 : 1 as in *S. gracilis* (Thompson & A. Scott, 1903), about 2 : 1 as in *S. lankensis* (Thompson & A. Scott, 1903), and 6·3 : 1 or 7 : 1 as in *S. affinis*. The female of the species from Madagascar whose description by Humes and Ho is in press, although having a nearly quadrate caudal ramus, differs from *S. longiseta* in having a rounded rostrum, in the seta on the first segment of the second antenna being not unusually long, in the two setae on the endopod of leg 4 being finely barbed instead of feathered, in the two terminal setae on leg 5 having a ratio of 3 : 1 instead of 7 : 1, and in the ratio of the length of the prosome to that of the urosome being 2·0 : 1 instead of 2·45 : 1. In the male, the species of Humes and Ho differs from *S. longiseta* in having the genital segment somewhat tapered anteriorly instead of having nearly parallel sides, and in the claw of the maxilliped being evenly recurved instead of showing two flexures.

From all four of these species *S. longiseta* may be further distinguished by details in ornamentation of the appendages.

S. longiseta appears to be closest to the species to be described by Humes and Ho, both having a very short caudal ramus and a somewhat similar genital segment in the female.

Stellicola femineus n. sp.

Pl. 8, fig. 67 ; Pl. 9, figs. 68–75 ; Pl. 10, figs. 76–84 ; Pl. 11, figs. 85–92

TYPE MATERIAL. 8 ♀, 9 ♂, and 1 copepodid from 1 starfish, *Leiaster leachi* Gray, in a depth of 0·5 m., Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected 8th August, 1960. Holotype female, allotype, and 11 paratypes (5 ♀, 6 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.10–12, and the remaining paratypes in the collection of A. G. Humes.

Other specimens. 4 ♀, 9 ♂ from 1 starfish, *Leiaster speciosus* von Martens, in 0·5 m., Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar, 2nd October, 1960.

FEMALE. Body (Pl. 8, fig. 67) with broad flattened prosome. Length (not including setae on caudal rami) 1·41 mm. (1·32–1·49 mm.) and greatest width 0·94 mm. (0·88–0·99 mm.), based on 10 specimens (holotype, 7 paratypes, and 2 specimens from *Leiaster speciosus*). Ratio of length to width of prosome 1·06 : 1. Segment of leg 1 completely fused with head. Epimeral areas of segments of legs 1 and 2 pointed posteriorly ; those of segment of leg 3 also pointed but indented as in figure. Segment of leg 4 small, with its tergum and rounded epimeral areas partly overlapped by preceding segment.

Segment of leg 5 (Pl. 9, fig. 68) 164 × 257 μ. Intersegmental sclerite not evident. Genital segment broad and flattened, 135 × 239 μ, wider than long, with expanded rounded lateral margins. Areas of attachment of egg sacs located posteriorly and slightly dorsally ; each area (Pl. 9, fig. 69) with 2 unequal feathered setae 34 and 17 μ in length, each arising from a pedicel. Three postgenital segments 44 × 99, 39 × 89, and 59 × 77 μ from anterior to posterior.

Caudal ramus (Pl. 9, fig. 70), inserted slightly ventrally, subquadrate, 30 × 33 μ, a little wider than long. Long naked setule (55 μ) midway on outer margin. Pedicellate dorsal seta 60 μ and feathered. Outer lateral seta 101 μ and naked, inserted close to outermost terminal seta (208 μ with straight lateral spinules). Innermost terminal seta 234 μ with straight lateral spinules. Two long terminal setae, inserted between dorsal (smooth) and ventral (with row of minute spinules) flaps, 396 μ (outer) and 540 μ (inner) and both with unusually long hairlike recurved lateral spinules.

Dorsal surface of prosome with short hairs. Dorsal and ventral surfaces of urosome with many hairs as shown in Pl. 9, fig. 68. Ratio of length of prosome to that of urosome 2·32 : 1.

Egg sac (see Pl. 8, fig. 67) moderately elongated and stout, 682 × 341 μ, extending far beyond ends of caudal rami, and containing many eggs about 70 μ in diameter.

Rostral area (Pl. 9, fig. 71) prominent, its posterior margin a little truncated.

First antenna (Pl. 9, fig. 72) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 46 (35 μ along anterior margin), 107, 34, 36, 25, 13, and 12 μ respectively. Formula for armature as in 3 previous species. Certain setae with short hairs as in figure. Ventral sclerite on third segment. Long terminal seta 203 μ in length, distinctly less than length of antenna (270 μ).

Second antenna (Pl. 9, fig. 73) 3-segmented, 495 μ in length, with no evidence of division in segment 3. Armature 1 ; 1 ; 3 + 5 + 1 claw as in 3 previous species. Third segment elongated, 300 μ along outer edge, 187 μ along inner edge, with a sclerotized strongly bent pointed process near base of claw (Pl. 9, fig. 74). Claw 96 μ along its axis. All setae naked.

Labrum (Pl. 9, fig. 75) with moderately rounded unornamented lobes.

Mandible (Pl. 10, fig. 76) in general resembling that of *S. longiseta* but without proximal patch of spinules. Paragnath (see Pl. 9, fig. 71) a small lobe. First maxilla (Pl. 10, fig. 77) with 4 elements. Second maxilla (Pl. 10, fig. 78) showing second segment with long inner spiniform seta bearing a row of spinules, those in middle of row much longer and stronger ; terminal spiniform process with a single large tooth-like proximal spine (2 such spines seen on left second maxilla in 1 female). Maxilliped (Pl. 10, fig. 79) with first segment having a distal patch of spinules, second with 1 naked and 1 feathered seta and rows of spinules as in figure, and third with 2 small unequal setae and terminal spiniform process.

Area between maxillipeds and first pair of legs not protuberant and formed as in Pl. 9, fig. 71.

Rami of legs 1–4 (Pl. 10, figs. 80, 81, 82, and 83) like those in 3 previous species with same spine and setal formula. Endopods of legs 1–3 rather elongated ; last segment of endopod of leg 2 without a bifurcated spinous process. In leg 4 coxa with inner seta apparently reduced to a mere vestige. Feathered inner seta on second segment of exopod short and lying free of ramus. Endopod (Pl. 10, fig. 84) slender, 2 segments clearly separated. First segment 38 × 15·5 μ with its inner seta short, 30 μ, and finely barbed distally. Second segment 50 × 12 μ (greatest dimensions), its feathered inner seta 52 μ, inner terminal spine 76 μ, and outer terminal spine 31 μ, both spines finely barbed. (In another female first segment 33 × 20 μ, and second segment 58 × 14·5 μ). Marginal hairs on segments as in figure.

Leg 5 (Pl. 11, fig. 85) with elongated slightly recurved slender free segment, 71 × 22 μ (greatest dimensions), tapering slightly distally. Two terminal setae naked and very unequal, inner 22 μ, outer 113 μ. Seta on body near insertion of free segment about 48 μ and feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 9, fig. 69).

Colour in life in transmitted light orange-red to deep red, eye red, egg sacs red.

MALE. Body (Pl. 11, fig. 86) with broad flattened prosome as in female. Length (excluding setae on caudal rami) 0·85 mm. (0·82–0·88 mm.) and greatest width 0·48 mm. (0·46–0·49 mm.), based on 10 specimens (allotype, 8 paratypes, and 1

specimen from *Leiaster speciosus*). Ratio of length to width of prosome 1·11 : 1.

Segment of leg 5 completely fused dorsally with genital segment (Pl. 11, fig. 87), and only a faint indication of separation between these 2 segments ventrally; segment of leg 5 and genital segment combined a little longer than wide, 221 × 195 μ. No intersegmental sclerite. Four postgenital segments 28 × 68, 27 × 62, 24 × 57, and 29 × 52 μ, from anterior to posterior.

Caudal ramus similar to that of female but smaller, 18 × 21 μ.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 1·73 : 1.

Rostral area, first antenna, and second antenna as in female. Labrum (Pl. 11, fig. 88) with 2 lobes apparently somewhat more pointed than in female. Mandible, paragnath, first maxilla, and second maxilla like those of female. Maxilliped (Pl. 11, fig. 89) without long terminal claw, but instead having a form rather like that of female. First segment without ornamentation, second with 2 small naked setae (one hyaline and with a blunt tip) and bearing a patch of spinules, and third with one of 2 setae at base of naked terminal spiniform process greatly elongated.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 resembling in major features those of female, having same spine and setal formula. In legs 2 and 3 apparently a slight sexual dimorphism in lengths of 3 spines on last segment of endopod (from proximal to distal in leg 2 of male 12, 13, and 24 μ, but in female 22, 21, and 34 μ; in leg 3 of male 12, 13, and 25 μ, but in female 23, 24, and 40 μ). Dimensions of endopod of leg 4 : first segment 22 × 13 μ, with its seta 21 μ; second segment 31 × 11 μ, with its seta 34 μ and spines 50 μ (inner) and 24 μ (outer).

Leg 5 (Pl. 11, fig. 90) with rectangular free segment relatively shorter than in female, 19 × 9 μ, with 2 terminal setae 16 μ (inner) and 56 μ (outer), with ratio of 3·5 : 1, instead of 5 : 1 as in female. Seta on body near insertion of free segment about 22 μ long and feathered.

Leg 6 (Pl. 11, fig. 91) consisting of a posterolateral flap on ventral surface of genital segment and bearing at either side of a small spinous process 2 slender naked setae 46 and 29 μ long.

Spermatophore, observed only inside body of male, of elongated form (Pl. 11, fig. 92).

Colour in life in transmitted light paler orange-red than in female, eye red.

(The specific name *femineus*, Latin = womanly or feminine, alludes to the weakly prehensile, female-like maxilliped in the male of this species).

COMPARISON WITH RELATED SPECIES. The female of *S. femineus* differs from almost all other known species in the genus in having the free segment of leg 5 at least three times longer than wide. The only species which has similar proportions in leg 5 is the species of Humes and Ho (in press) where the free segment is 65 × 21 μ. In this species, however, there are only two postgenital segments in the female.

The male of *S. femineus* is unique in the genus in having a female-like maxilliped, without a well-formed prehensile claw.

Stellicola pollex n. sp.

Pl. 11, fig. 93 ; Pl. 12, figs. 94–101 ; Pl. 13, figs. 102–109 ; Pl. 14, figs. 110–114.

TYPE MATERIAL. 5 ♀ and 4 ♂ from 2 starfishes, *Linckia laevigata* (L.), in a depth of 10 m., at Nosy Ovy (=Berafia), 13° 59′ S, 47° 46′ 30″ E, to the southwest of Nosy Bé, Madagascar. Collected 1st October, 1964. Holotype, allotype, and 5 paratypes (3 ♀, 2 ♂) deposited in the British Mus. (Nat. Hist.) Reg. No. 1966.12.7.13–15, and the remaining 2 paratypes (dissected) in the collection of A. G. Humes.

FEMALE. Body (Pl. 11, fig. 93) with broad flat prosome. Length (without setae on caudal rami) 0·99 mm. (0·94–1·03 mm.) and greatest width 0·78 mm. (0·68–0·88 mm.), based on 5 specimens. Ratio of length to width of prosome 0·95 : 1, prosome being slightly wider than long. Segment of leg 1 separated dorsally and laterally from head by a distinct furrow. Epimera of metasomal segments as in *S. femineus*.

Segment of leg 5 (Pl. 12, fig. 94) 91 × 180 μ. Ventrally between this segment and genital segment a very short intersegmental sclerite. Genital segment broad and flattened, 161 × 198 μ, wider than long, with expanded rounded lateral margins lobed posteriorly. Areas of attachment of egg sacs located ventrally and hidden in dorsal view by the lobes ; each area (Pl. 12, fig. 95) with 2 naked setae, 39 and 35 μ in length, borne on pedicels. Three postgenital segments 35 × 64, 36 × 62, and 34 × 57 μ from anterior to posterior.

Caudal ramus (Pl. 12, fig. 96), inserted ventrally, quadrate, 20 × 20 μ, with naked setule on outer margin 19 μ long. Pedicellate dorsal seta 36 μ and feathered. Outer lateral seta 60 μ and naked. Outermost terminal seta 127 μ and innermost 96 μ, both with lateral spinules. Two long terminal setae, inserted between flaps as in *S. femineus*, 320 μ (outer) and 495 μ (inner), both with short spinules.

Dorsal surface of prosome with scattered hairs (not shown in Pl. 11, fig. 93, because of the reduced scale). Dorsal surface of urosome with hairs and refractile points as in Pl. 12, fig. 94 ; ventral surface with very little ornamentation. Ratio of length of prosome to that of urosome 2·5 : 1.

Egg sacs not present on any of females collected.

Rostral area as in *S. femineus*, though posterior margin less truncated.

First antenna (Pl. 12, fig. 97) more slender than in *S. femineus*, but with same segmentation and armature. Lengths of segments (measured as before) 44 (35 μ along anterior margin), 116, 45, 50, 33, 20, and 16 μ respectively. One seta on segment 6 and 4 setae on segment 7 with lateral hairs ; rest of setae naked. Terminal seta 117 μ, about one-third length of antenna (330 μ).

Second antenna (Pl. 12, fig. 98) slender as in *S. femineus*, with third segment showing no indication of division. Armature 1 ; 1 ; 3 + 5 + 1 claw as in 4 previous species. Near base of claw a small spinous process. Claw 61 μ along its axis. All setae naked.

Labrum as in *S. femineus*, though lobes a little more rounded.

Mandible (Pl. 12, fig. 99) with slender spinules along outer margin and row of dentiform spinules along inner margin (proximal spinule enlarged and preceded by

a slight flange). Paragnath (Pl. 12, fig. 100) a small lobe with very slender spinules. First maxilla in general like that of *S. femineus*. Second maxilla (Pl. 12, fig. 101) with first segment unarmed, second with 2 postero-inner elements (a slender barbed seta and a long spiniform seta ornamented with a row of spinules along its distal edge and showing a very weak line of division proximally) and terminating in a spiniform process bearing rows of teeth as in figure. Maxilliped (Pl. 13, fig. 102) resembling in major features that of *S. femineus*, though details of ornamentation somewhat different.

Area between maxillipeds and first pair of legs as in *S. femineus*.

Rami of legs 1–4 (Pl. 13, figs. 103, 104, 105, and 106) segmented as in previous 4 species, with similar spine and setal formula, except for endopod of leg 4 which is 0–0 ; II. Endopods of legs 1–3 rather elongated as in *S. femineus ;* last segment of endopod of leg 2 without a bifurcated spinous process. Leg 4 with only a vestige of inner coxal seta. Inner seta on second segment of exopod short (22 μ) and apparently naked. Endopod (Pl. 13, fig. 107) 41 $\times$ 10 μ, only incompletely divided into 2 segments, its inner margin entire. Two inner setae usually seen in *Stellicola* here absent, and only armature of endopod consisting of 2 terminal smooth spines 60 μ (inner) and 31 μ (outer) in length. Rows of hairs along outer and inner margins of endopod, outer row interrupted at incomplete division of ramus.

Leg 5 (Pl. 13, fig. 108) with free segment 55 $\times$ 27 μ (greatest dimensions, its inner proximal margin somewhat irregular and produced). Two terminal setae naked and unequal, inner 43 μ, outer 56 μ. Seta on body near insertion of free segment about 37 μ and slightly feathered.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 12, fig. 95).

Colour in life in transmitted light slightly opaque, eye red, egg sacs gray.

MALE. Body (Pl. 13, fig. 109) resembling that of female. Length (excluding setae on caudal ramus) 0·55 mm. (0·53–0·56 mm.) and greatest width 0·36 mm. (0·35–0·37 mm.), based on 4 specimens. Ratio of length to width of prosome 1·07 : 1.

Segment of leg 5 and genital segment fused (Pl. 14, fig. 110) as in *S. femineus ;* these fused segments 127 μ long, 115 μ wide just in front of leg 5, and 105 μ wide behind leg 5. No intersegmental sclerite. Four postgenital segments 28 $\times$ 46, 23 $\times$ 43, 22 $\times$ 40, and 18 $\times$ 36 μ from anterior to posterior.

Caudal ramus similar to that of female but smaller, 12·5 $\times$ 13 μ.

Surfaces of prosome and urosome, as in female, ornamented with hairs. Ratio of length of prosome to that of urosome 2·07 : 1.

Rostral area and first antenna as in female. Second antenna also resembling that of female, but having a conspicuous thumb-like process on inner margin of third segment (Pl. 14, fig. 111). Labrum, mandible, paragnath, first maxilla, and second maxilla like those in female. Maxilliped (Pl. 14, fig. 112) slender, with long terminal claw. First segment unarmed, second with 2 naked setae and 2 patches of spinules, third short and unarmed. Proximal half of claw probably representing fourth segment. Claw only slightly recurved, 130 μ in length along its axis, showing

faint indication of division about midway, with a fringe of small spinules along its concave margin and 2 unequal setae 8 μ (naked) and 26 μ (slightly barbed) near its base.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 resembling those of female, with same spine and setal formula. As in *S. femineus* a slight sexual dimorphism in lengths of 3 spines on last segment of endopod of legs 2 and 3 (from proximal to distal in leg 2 of male 9, 10, and 22 μ, but in female 16·5, 17·5, and 35 μ; in leg 3 of male 8, 10, and 20 μ, but in female 16·5, 18·5, and 35 μ). Dimensions of endopod of fourth leg 22 × 8 μ, with inner spine 31 μ and outer spine 17 μ.

Leg 5 (Pl. 14, fig. 113) with free segment smaller and having nearly parallel sides, 20 × 8 μ, the terminal setae 18 μ (inner) and 52 μ (outer), with ratio of 2·9 : 1, instead of 1·3 : 1 as in female.

Leg 6 (Pl. 14, fig. 114) consisting of a posterolateral flap on ventral surface of genital segment and bearing 2 slender naked setae 21 and 36 μ.

Spermatophores not observed.

Colour in life in transmitted light as in female.

(The specific name *pollex*, Latin = a thumb, refers to the thumb-like process on the third segment of the second antenna of the male).

COMPARISON WITH OTHER SPECIES. *S. pollex* has two readily observable characters by which it may be distinguished from all other species in the genus, namely, the thumb-like process on the third segment of the second antenna in the male and the armature of the endopod of leg 4 (0–0; II) in both sexes.

In the fifteen previously known species and in the four species described above the formula for the endopod of leg 4 is 0–1; II, 1. Such an armature seems to be a stable and constant feature in the genus. The unusual armature in *S. pollex* might suggest at first glance that this species should be removed to a separate genus. However, other features of *S. pollex* (first antenna, second antenna, mouthparts, legs 1–5, and body form) conform very closely to the pattern of *Stellicola*. The structure of the mandible (which is an important generic character in the Lichomolgidae) is very much like that in other species of the genus. Therefore, in spite of the rather remarkable difference in the armature of this endopod, we are considering the species to belong to *Stellicola*.

Stellicola oreastriphilus Kossmann, 1877

Pl. 14, figs. 115–120

Two females and one male were recovered from washings of a single starfish, *Protoreaster nodosus* (L.), in a depth of 2 m., on *Cymodocea*, at Ambatoloaka, Nosy Bé, 15th October, 1960. This represents a new host record, the species having been previously found on six other starfishes—*Asterope carinifera* (Lamarck) in the Red Sea by Kossmann (1877), on *Protoreaster lincki* (Blainville), *Culcita schmideliana* (Retzius), *Pentaceraster mammillatus* (Audouin), and *Poraster superbus* (Möbius) in Madagascar by Humes & Cressey (1961), and on *Choriaster granulatus* (Lütken) in Madagascar by Humes & Ho (in press).

In connection with the description of the five new species above, specimens of *S. oreastriphilus* (from a lot of approximately 1,000 individuals washed from 200 *Protoreaster lincki*, in a depth of 10 cm., at Pte. Mahatsinjo, Nosy Bé, 6th September, 1964) were restudied. The dissections were done in lactic acid (see Humes & Gooding, 1964), enabling us to see certain details not easily observed in the original dissections in glycerine. Notes on these features are offered here as a supplement to the work of Humes & Cressey (1961).

FEMALE. The flattened genital segment (Pl. 14, fig. 115) expanded laterally, with subparallel lateral margins. A pair of ventral refractile sclerotizations present on sides of segment. Tip of second antenna (Pl. 14, fig. 116) bearing 5 setae and 1 claw. Paragnath (Pl. 14, fig. 117) a hairy lobe bearing a sclerotized process. Maxilliped (Pl. 14, fig. 118) with second segment having 2 setae (one surficial, other on a hyaline base at inner marginal angle) and a crescentic row of spinules; third segment with 2 very unequal small setae at base of terminal spiniform process. Endopod of leg 4 (Pl. 14, fig. 119) with marginal hairs as in figure.

MALE. Segment of leg 5 and genital segment (Pl. 14, fig. 120) fused completely dorsally and their ventral separation suggested by a very indistinct line. Fused segments 120 μ long, 109 μ wide just in front of leg 5, and 101 μ wide posterior to leg 5. (The rather distinct separation of the two segments shown by Humes & Cressey, 1961, fig. 25, is not present in the material which we have re-examined).

Stellicola caeruleus (Stebbing, 1900)

Pl. 15, figs. 121–128; Pl. 16, figs. 129–134; Pl. 17, figs. 135–141

This species was placed by Stebbing (1900, pp. 664–666, plate LXXIVB) in a new genus *Linckiomolgus*, but, as Stock (1957) has pointed out, and as will be seen from the redescription below, it belongs more properly to *Stellicola*.

Through the kindness of Miss Patricia D. Lofthouse we have been able to study syntypes (1 female and 1 male) of *S. caeruleus* [Brit. Mus. (Nat. Hist.) reg. no. 1928.12.1.3020]. These are labelled "China Sea on blue *Linckia*", though the type locality given by Stebbing was Feather Island, China Straits, New Guinea. The dissections of these specimens, mounted on two slides, have been returned to the British Museum (Nat. Hist.). Although the condition of the specimens (which were in amplexus) was less than perfect, with certain setae broken or missing, the major features could be observed in the dissections. Stebbing's original description being inadequate in many respects, especially regarding the mouthparts, a redescription of the species based on syntypic material is desirable.

FEMALE. Body (Pl. 15, fig. 121) with greatly expanded prosome. Length (without setae on caudal rami) 1·23 mm. and greatest width 0·88 mm. Ratio of length to width of prosome 0·97 : 1, being a little wider than long. Segment of leg 1 completely fused with head. Epimeral areas of metasomal segments resembling those of *S. femineus*.

Genital segment (Pl. 15, fig. 122) wider than long, 156 × 208 μ, broadly rounded laterally in its anterior half and tapering in its posterior half where the areas of

attachment of the egg sacs are located laterally. Dorsally with two longitudinal posterior elevations with sclerotization as in figure. Each egg sac attachment area with 2 unequal setae, one arising from a prominent slender pedicel 31 × 8 μ. Three postgenital segments 60 × 86, 42 × 78, and 52 × 72 μ from anterior to posterior.

Caudal ramus (Pl. 15, fig. 123) only a little longer than wide, 32 × 28 μ.

Ratio of length of prosome to that of urosome 2·32 : 1.

Egg sac broken on female examined; an isolated egg about 74 μ in diameter.

Rostral area (Pl. 15, fig. 124) incomplete posteriorly.

First antenna (Pl. 15, fig. 125) 7-segmented, lengths of segments (measured along their posterior non-setiferous margins) being 55 (44 μ along anterior margin), 113, 39, 43, 33, 15, and 14 μ respectively. Formula for armature 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in all 5 new species described above and as in *S. oreastriphilus*. Ventral sclerite present on third segment.

Second antenna (Pl. 15, fig. 126) with a single claw 79 μ along its axis and with armature as in *S. femineus*. Third segment 166 μ along outer side, 91 μ along inner side, with no evidence of division.

Labrum as in Pl. 15, fig. 124.

Mandible (Pl. 15, fig. 127) with first 2 elements of inner row only slightly larger than succeeding ones. Paragnath a small lobe with coarse hairs. First maxilla with 4 elements. Second maxilla (Pl. 15, fig. 128) with second segment with long inner spiniform seta bearing a row of spinules, those in middle of row somewhat longer; terminal spiniform process with strong graduated teeth. Maxilliped (Pl. 16, fig. 129) 3-segmented, with second segment apparently having only 1 seta, and with 2 very unequal spinules near base of short terminal claw-like process.

Area between maxillipeds and first pair of legs resembling that of *S. femineus*.

Rami of legs 1–4 (Pl. 16, figs. 130, 131, 132, and 133) segmented and armed as in *S. kossmanni*, *S. affinis*, *S. longiseta*, and *S. femineus*, except for last segment of exopod of leg 3 which has formula of II, I, 5. In leg 4 coxa with only a minute knob probably representing a vestige of inner coxal seta seen in other species. Inner seta on second segment of exopod 25 μ long and naked. Endopod 2-segmented, 2 segments distinctly separated. First segment 27 × 15 μ, with its inner seta 36 μ and finely barbed. Second segment 31 × 12 μ, its inner seta 42 μ and feathered, inner terminal spine 66 μ and barbed, outer spine 29 μ with only a few minute barbs. (Marginal hairs on endopod segments not discernible).

Leg 5 (Pl. 16, fig. 134) with free segment about 44 × 17 μ, bearing 2 very unequal terminal setae.

Leg 6 probably represented by the 2 setae on area of attachment of egg sac (see Pl. 15, fig. 122).

MALE. Body (Pl. 17, fig. 135) with prosome somewhat less expanded than in female. Length (excluding ramal setae) 0·52 mm. and greatest width 0·32 mm. Ratio of length to width of prosome 1·09 : 1, being a little longer than wide.

Segment of leg 5 fused with genital segment (Pl. 17, fig. 136), as in *S. femineus*, *S. pollex*, and *S. oreastriphilus*. These 2 segments combined longer than wide: 110 μ in length, 83 μ wide at level of fifth legs, and 75 μ wide posterior to these

legs, where lateral margins are subparallel. Four postgenital segments 30 × 47, 30 × 44, 20 × 40, and 22 × 37 μ from anterior to posterior.

Caudal ramus similar to that of female but smaller, 19 × 15 μ.

Ratio of length of prosome to that of urosome 2·05 : 1.

Rostral area (Pl. 17, fig. 137) well-defined posteriorly, with its border there slightly indented.

First antenna, second antenna, labrum, mandible, paragnath, and first maxilla like those of female. Second maxilla (Pl. 17, fig. 138) with second segment much like that of female, but with first segment showing 3 peculiar sclerotized processes arising ventrally. (Possibly these are adhesive pads). Maxilliped (Pl. 17, fig. 139) small, 2-segmented, with terminal claw 22 μ along its axis. Both segments without ornamentation or armature ; a small knob on basal area of claw.

Legs 1–4 like those in female, with same spine and seta formula.

Leg 5 (Pl. 17, fig. 140) with a small free segment, 12 × 7 μ, bearing 2 terminal setae 18 μ (inner) and 55 μ (outer).

Leg 6 (Pl. 17, fig. 141) consisting of the usual posterolateral flap on ventral surface of genital segment and bearing 2 unequal setae.

Spermatophores not observed.

COMPARISON WITH OTHER SPECIES. Based on our study of syntypes, *S. caeruleus* shows three features not found in the other nineteen species of the genus, as far as known : the two posterior sclerotized elevations on the dorsal surface of the genital segment of the female, the three peculiar sclerotized processes on the first segment of the second maxilla in the male, and the formula of II, I, 5 on the last segment of the exopod of leg 3 in both sexes. A small 2-segmented maxilliped with a short claw is also found in the male of *S. holothuriae* (Ummerkutty), but this Indian species differs from *S. caeruleus* in having the formula III, I, 5 on the last segment of the exopod in leg 3 and in the shape of the caudal ramus (much wider than long). *S. caeruleus* may thus readily be distinguished from other members of the genus.

NOTES ON THE VARIABILITY OF CERTAIN FEATURES IN THE GENUS *STELLICOLA*

The twenty species here recognized in the genus *Stellicola* exhibit certain variations in external structure worthy of note. The second antenna may bear terminally a single claw, two claws, or three claws. Those with three claws are the four West African species : *S. frequens*, *S. astropectinis*, *S. luidiae*, and *S. lautus*. (In all of these the middle spine on the last segment of the endopod of leg 2 is unusually short, whereas in other species, as far as known, this spine is not thus shortened ; the second segment of the endopod of leg 4 has a sharp spinous process midway on its outer margin opposite the inner seta). The only species with two claws is *S. clausi*. The remaining fifteen species have a single claw. The third segment of the second antenna in some species may show an incomplete division (as in the species to be described by Humes and Ho, in press, and in *S. kossmanni*).

The armature of legs 1–4 is similar in all species (where it has been described) except for *S. caeruleus*, where the formula for the last segment of the exopod of leg 3 is II, I, 5, and *S. pollex*, where the endopod of leg 4 has a formula of 0–0 ; II.

In a few species the basis of leg 4 is greatly elongated and the inner coxal seta is absent, this seta being perhaps represented by a small knob, as in *S. femineus*, *S. pollex*, and *S. caeruleus*. *S. thorelli*, *S. pleurobranchi*, *S. curticaudatus*, *S. longicaudatus*, and *S. holothuriae* appear to be similarly constructed, but the exact nature of the protopodal segments of leg 4 is impossible to determine from the descriptions and figures of these species. *S. oreastriphilus* represents an intermediate form between those species with an elongated basis and those with a short basis (as in *S. kossmanni*, for example).

The maxilliped of the male in most species is elongated and bears a long prehensile claw, but in *S. femineus* it is female-like and only weakly prehensile, and in *S. caeruleus* it is small, 2-segmented, with a short claw.

The second maxilla of the male of *S. caeruleus* is remarkable in the development of three peculiar sclerotized processes on the first segment. In most other species, as far as known, there is no sexual dimorphism in this appendage, but in *S. longiseta* and *S. affinis* the second maxilla of the male shows slight differences from that of the female.

In the males of certain species the segment of leg 5 and the genital segment are almost completely fused, as in *S. oreastriphilus*, *S. femineus*, *S. pollex*, and *S. caeruleus*. It may be noted that the tendency in leg 4 toward elongation of the basis and loss of the inner coxal seta occurs in the same four species.

The males of five species (*S. thorelli*, *S. pleurobranchi*, *S. lankensis*, *S. curticaudatus*, and *S. longicaudatus*) are unknown, and the available descriptions of the females are lacking in detail. Hence, it is impossible at present to determine whether or not these variations exist in them.

The significance of such variations as mentioned above is not clear. The four West African species seem to be closely related and set apart from the rest, perhaps constituting an evolutionary line within the genus. It will be necessary, however, to have much more information on the species within the genus before well-founded conclusions regarding evolutionary relationships can be made. Undoubtedly many more species of *Stellicola* remain to be discovered, since relatively few species of potential asteroid hosts have been examined.

KEYS TO THE SPECIES OF *STELLICOLA*

The preparation of keys for the identification of the species of *Stellicola* presents certain difficulties, since detailed information regarding various structures in several species is not available in the existing descriptions or figures. Furthermore, the males of five species (*thorelli*, *pleurobranchi*, *lankensis*, *curticaudatus*, and *longicaudatus*) are unknown and consequently cannot be included in the key. The keys given here are entirely artificial and are presented only as aids in identification. Final determination of a species should be made by reference to the original descriptions and figures, or to actual specimens, if available.

FEMALES

1	Two postgenital segments	2
	Three postgenital segments	6
2	Caudal ramus 2× or more than 2× longer than wide	3
	Caudal ramus short, nearly quadrate	5

3 Caudal ramus at least 4× longer than wide 4
Caudal ramus about 2× longer than wide . . . . . ***lankensis***
4 Caudal ramus 6·3–7× longer than wide . . . . . ***affinis***
Caudal ramus 4× longer than wide . . . . . ***gracilis***
5 Seta on first segment of second antenna unusually long, reaching nearly to end of appendage ; free segment of leg 5 swollen on inner margin ; caudal ramus slightly wider than long, 28 × 35 μ . . . . . ***longiseta***
Seta on first segment of second antenna not unusually long ; free segment of leg 5 with sides nearly parallel ; caudal ramus slightly longer than wide, 28 × 23 μ
species of Humes and Ho, in press
6 With more than 1 claw on last segment of second antenna 7
With only 1 claw on last segment of second antenna 11
7 With 3 claws on last segment of second antenna 8
With 2 claws on last segment of second antenna . . . . . ***clausi***
8 Length about 1·0 mm. ; genital segment a little longer than wide . . . 9
Length 1·3–1·6 mm. ; genital segment about as long as wide 10
9 Caudal ramus 48 × 36 μ, ratio of 1·33 : 1 . . . . . ***frequens***
Caudal ramus 60 × 28 μ, ratio of 2·14 : 1 . . . . . ***astropectinis***
10 Caudal ramus 61 × 38 μ, ratio of 1·61 : 1 . . . . . ***luidiae***
Caudal ramus 96 × 43 μ, ratio of 2·23 : 1 . . . . . ***lautus***
11 Formula of endopod of fourth leg 0–0 ; II . . . . . ***pollex***
Formula of endopod of fourth leg 0–1 ; II, 1 12
12 With 2 posterior dorsal sclerotized elevations on genital segment . ***caeruleus***
Without such elevations 13
13 Free segment of leg 5 a little more than 3× longer than wide and slightly recurved ; length 1·41 mm. . . . . ***femineus***
Free segment of leg 5 less than 3× longer than wide and not recurved ; length 1·2 mm. or less 14
14 Ratio of length of prosome to urosome 1·87 : 1, ratio of length to width of prosome 1·45 : 1 . . . . . ***kossmanni***
Ratio of length of prosome to urosome 2·4–3·3 : 1 ; ratio of length to width of prosome 0·94–1·22 : 1 15
15 Ratio of body length to width about 1·28 : 1 . . . . . ***longicaudatus***
Ratio of body length to width about 1·5 : 1 16
16 Two setae on free segment of leg 5 about equal in length 17
Two setae on free segment of leg 5 distinctly unequal in length 18
17 Basis of leg 4 greatly elongated, ratio of its length to length of exopod about 13·5 : 5 ***pleurobranchi***
Basis of leg 4 not as elongated, ratio of its length to length of exopod about 9 : 5 ***oreastriphilus***
18 Postgenital segments and caudal rami together more than 4× as long as genital segment . . . . . ***thorelli***
Postgenital segments and caudal rami together only a little longer than genital segment or shorter than that segment 19
19 Postgenital segments and caudal rami together a little longer than genital segment ***curticaudatus***
Postgenital segments and caudal rami together a little shorter than genital segment ***holothuriae***

MALES

1 Three postgenital segments 2
Four postgenital segments 5
2 Caudal ramus distinctly elongated 3
Caudal ramus nearly quadrate 4

3 Caudal ramus 7·5 × longer than wide . . . . . ***affinis***
Caudal ramus about 4 × longer than wide . . . . . ***gracilis***
4 Caudal ramus slightly longer than wide ; claw of maxilliped evenly recurved ; free segment of leg 5 nearly 4 × longer than wide . species of Humes and Ho, in press
Caudal ramus a little wider than long ; claw of maxilliped with 2 slight flexures ; free segment of leg 5 about 2 × longer than wide . . . . . ***longiseta***
5 With more than 1 claw on last segment of second antenna 6
With only 1 claw on last segment of second antenna 10
6 With 3 claws on last segment of second antenna 7
With 2 claws on last segment of second antenna . . . . . ***clausi***
7 Length less than 1 mm. ; free segment of leg 5 about 24–25 × 12 μ . . . 8
Length somewhat more than 1 mm. ; free segment of leg 5 about 36–38 × 17 μ . 9
8 Caudal ramus a little longer than wide, ratio about 1·3 : 1 . . ***frequens***
Caudal ramus more elongated, ratio about 2·1 : 1 . . . . ***astropectinis***
9 Caudal ramus somewhat elongated, ratio about 1·6 : 1 . . . . ***luidiae***
Caudal ramus more elongated, ratio about 2·2 : 1 . . . . . ***lautus***
10 With thumb-like process on third segment of second antenna ; formula of endopod of fourth leg 0–0 ; II . . . . . ***pollex***
Without thumb-like process on third segment of second antenna ; formula of endopod of fourth leg 0–1 ; II, 1 11
11 Maxilliped not elongated, 2- or 3-segmented, with relatively short claw . . 12
Maxilliped elongated, 4-segmented, with long prehensile claw 14
12 Maxilliped small, 2-segmented, with relatively small but distinctly prehensile claw 13
Maxilliped female-like, 3-segmented, with terminal spiniform process instead of a claw ***femineus***
13 First segment of second maxilla with 3 peculiar sclerotized processes . ***caeruleus***
First segment of second maxilla without such processes . . . ***holothuriae***
14 Segment of leg 5 and genital segment separated . . . . . ***kossmanni***
Segment of leg 5 and genital segment almost completely fused . ***oreastriphilus***

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EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

Abbreviations used : A_1 = first antenna, A_2 = second antenna, MD = mandible, P = paragnath, MX_1 = first maxilla, MX_2 = second maxilla, MXPD = maxilliped, P_1 = leg 1.

PLATE 1

Stellicola kossmanni n. sp., female

FIG. 1. Dorsal (A).
FIG. 2. Marginal membrane on prosomal segments, dorsal (B).
FIG. 3. Urosome, dorsal (C).
FIG. 4. Area of attachment of egg sac, dorsal (D).
FIG. 5. Caudal ramus and part of anal segment, dorsal (E).
FIG. 6. Rostral area, ventral (C).

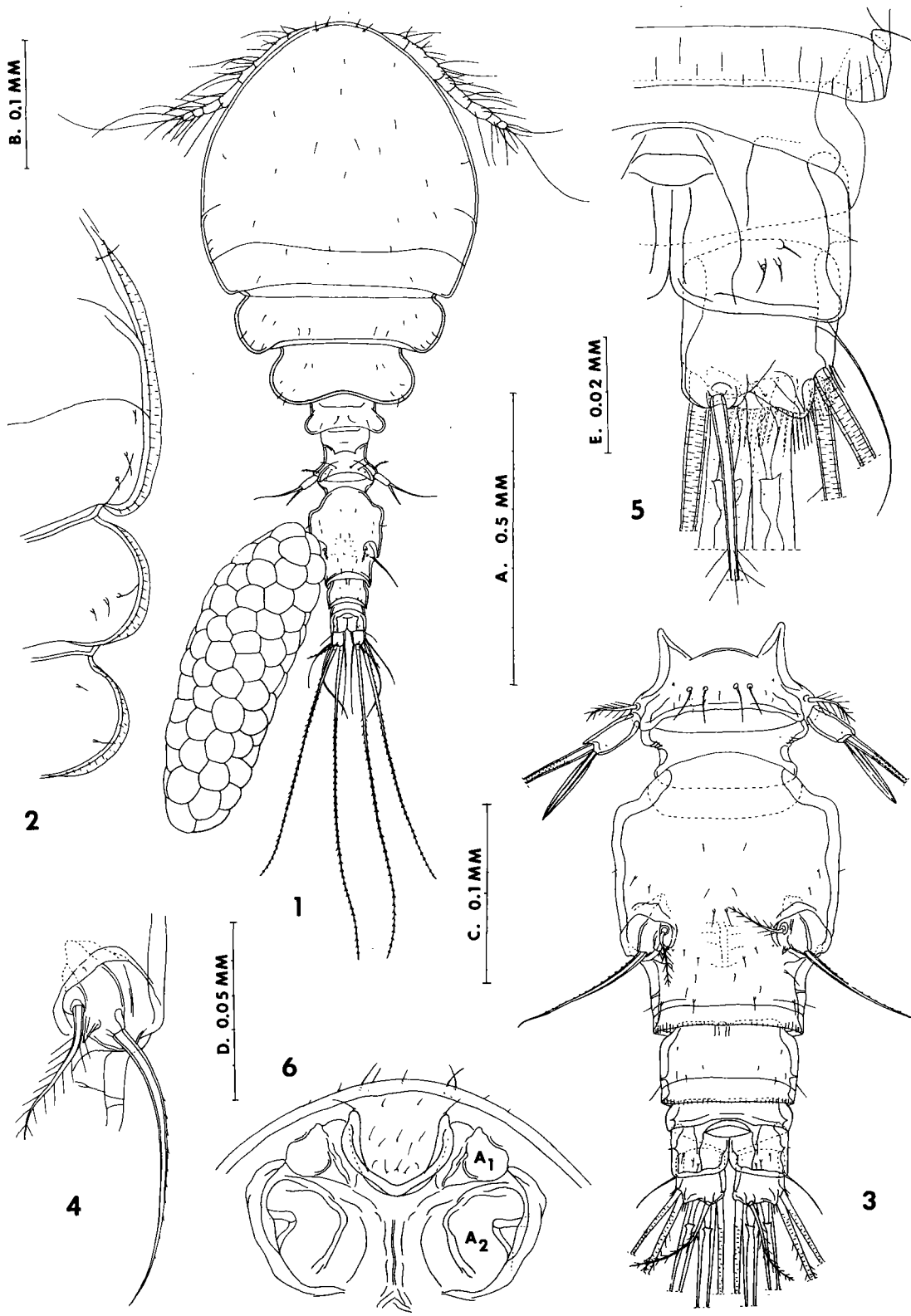

B. 0.1 MM
A. 0.5 MM
E. 0.02 MM
C. 0.1 MM
D. 0.05 MM
1
2
3
4
5
6
A1
A2

PLATE 2

Stellicola kossmanni n. sp., female (continued)

FIG. 7. First antenna, anterodorsal (C).
FIG. 8. Second antenna, anterior (F).
FIG. 9. Labrum, ventral (D).
FIG. 10. Mandible, posterior (D).
FIG. 11. First maxilla, posterolateral (G).
FIG. 12. Second maxilla, posterior (D).
FIG. 13. Maxilliped, anterior (D).
FIG. 14. Area between maxillipeds and first pair of legs, ventral (C).
FIG. 15. Leg 1 and intercoxal plate, anterior (C).

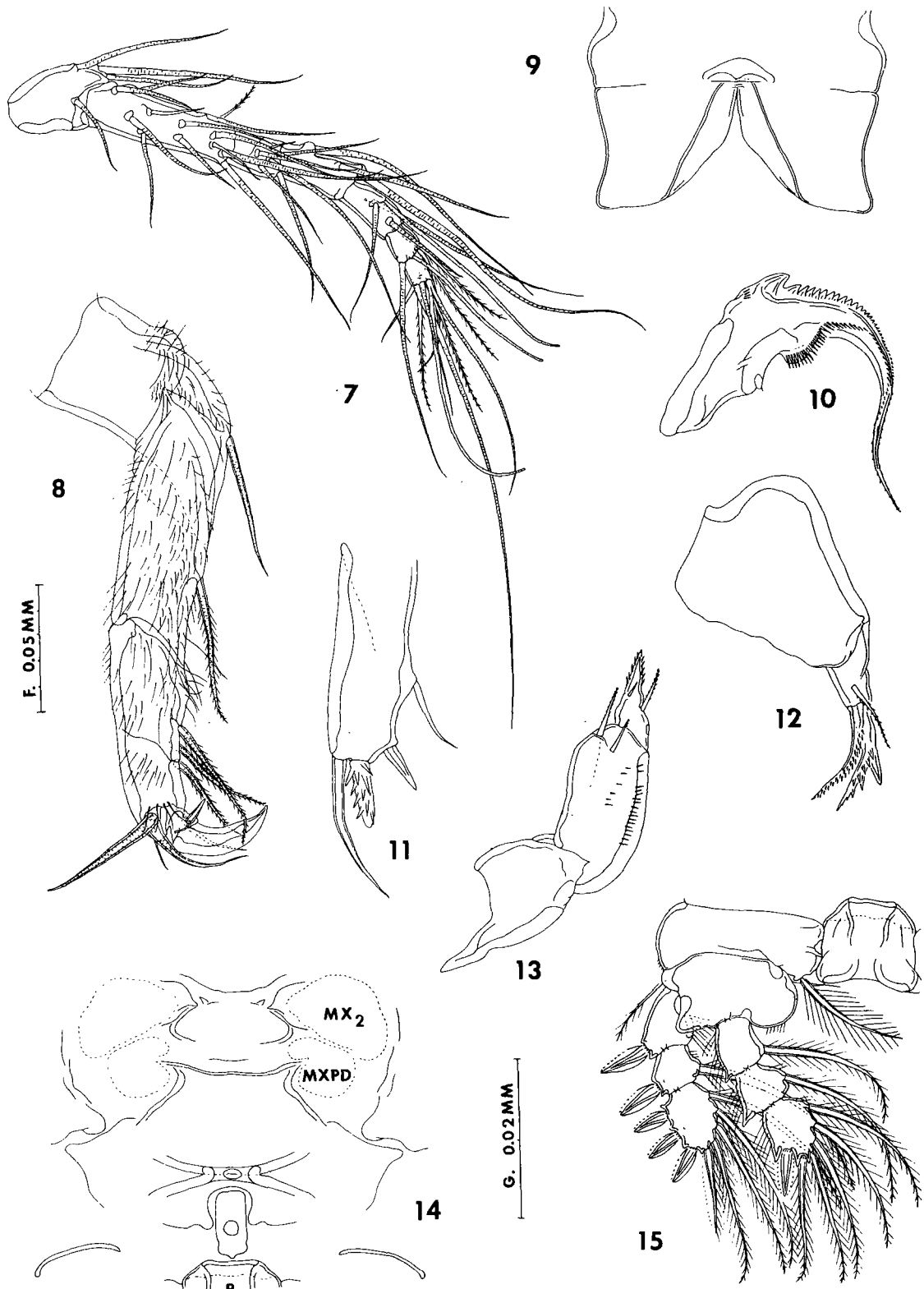

9
7
10
8
F. 0.05MM
11
12
13
MX2
MXPD
G. 0.02MM
14
15
P1

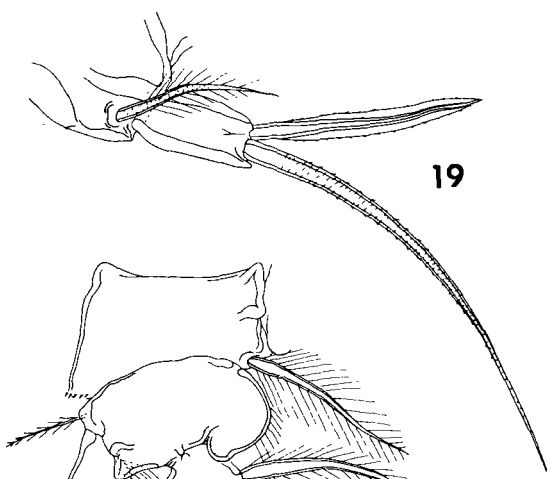
PLATE 3

Stellicola kossmanni n. sp., female (continued)

FIG. 16. Leg 2, anterior (C).
FIG. 17. Leg 3, anterior (C).
FIG. 18. Leg 4 and intercoxal plate, anterior (C).
FIG. 19. Leg 5, dorsal (D).

Stellicola kossmanni n. sp., male

FIG. 20. Dorsal (A).
FIG. 21. Urosome, dorsal (C).



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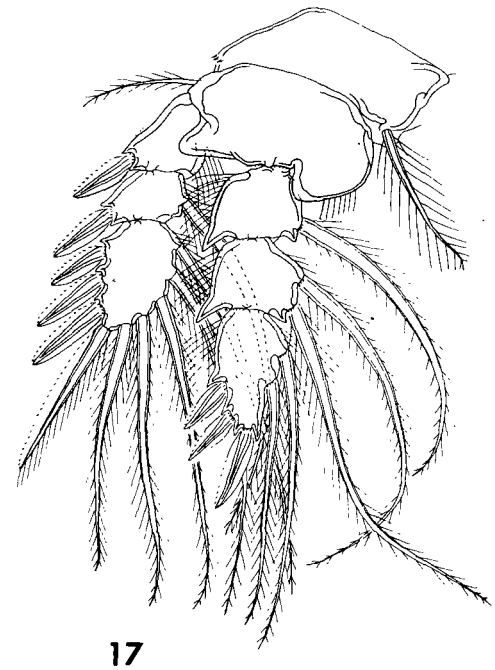

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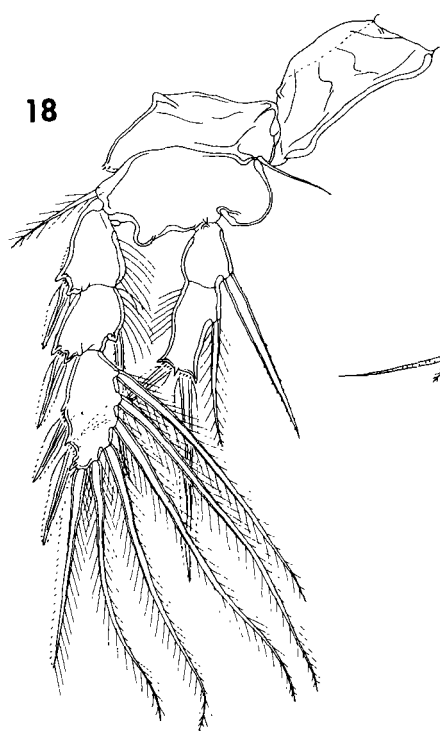

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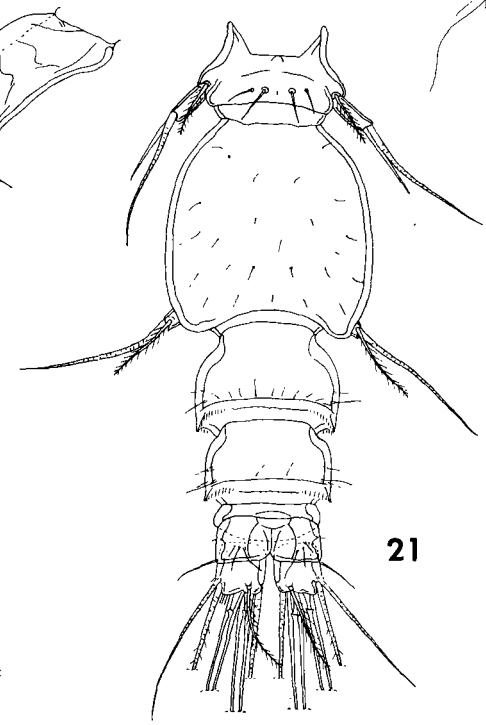

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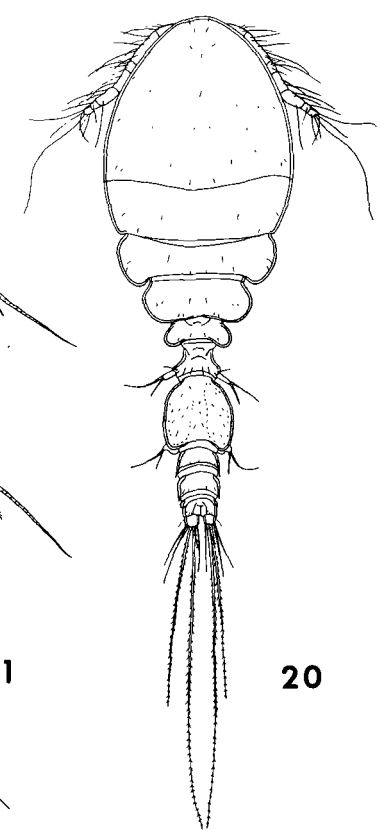


20

PLATE 4

Stellicola kossmanni n. sp., male (continued)

FIG. 22. Maxilliped, anterior (F).
FIG. 23. Leg 6, ventral (F).
FIG. 24. Spermatophore, in body of male, dorsal (C).

Stellicola affinis n. sp., female

FIG. 25. Dorsal (A).
FIG. 26. Lateral (A).
FIG. 27. Urosome, dorsal (B).
FIG. 28. Area of attachment of egg sac, dorsal (D).
FIG. 29. Caudal ramus, dorsal (F).
FIG. 30. Rostrum, ventral (C).
FIG. 31. First antenna, anterodorsal (C).

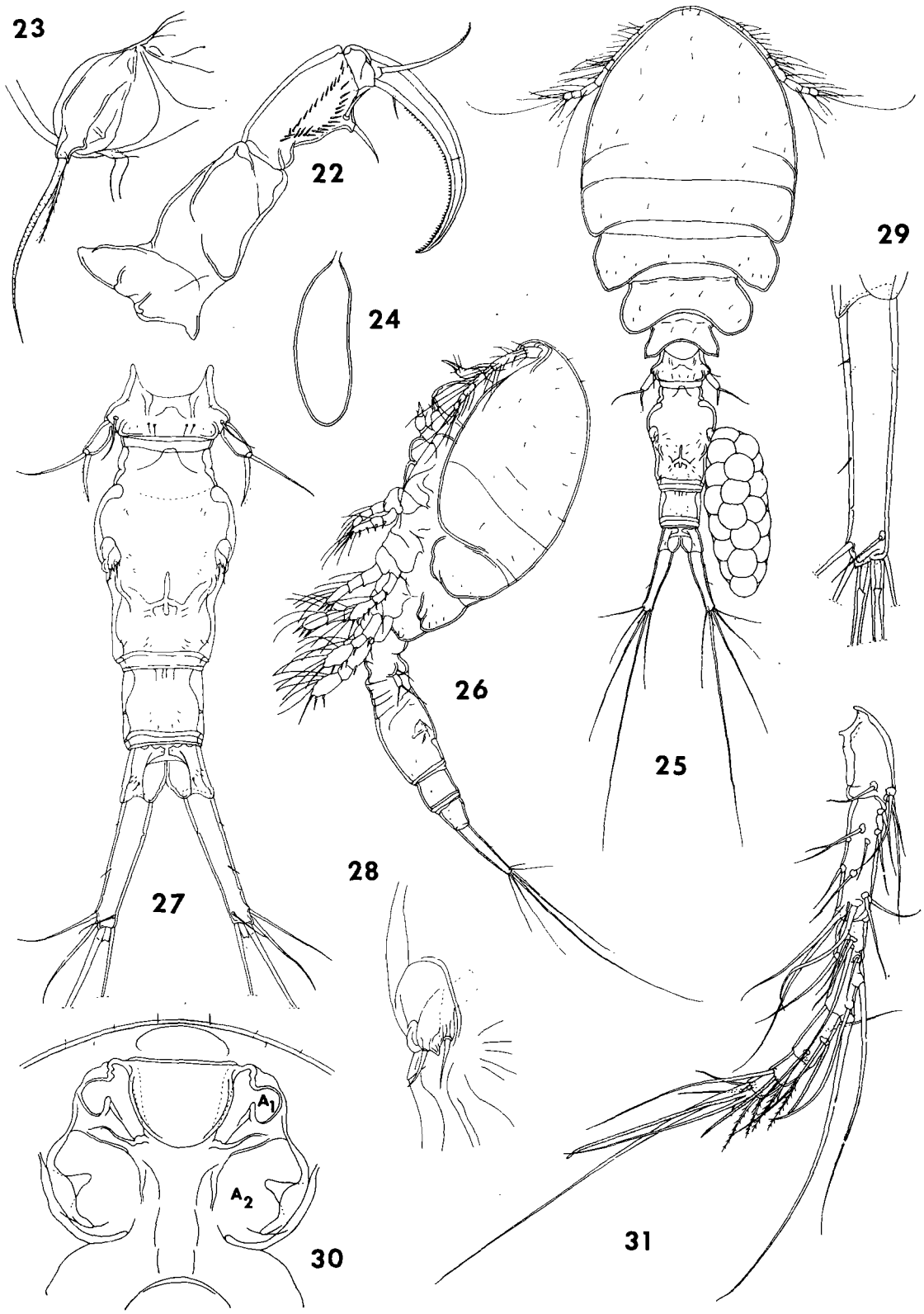
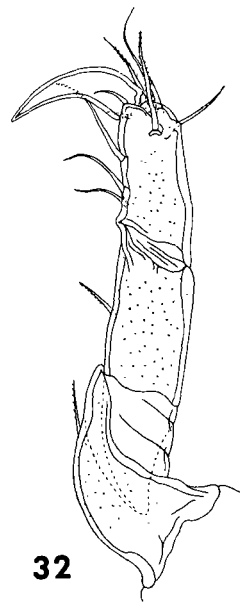

23
22
24
29
26
25
27
28
A1
A2
30
31

PLATE 5

Stellicola affinis n. sp., female (continued)

FIG. 32. Second antenna, posterior (F).
FIG. 33. Labrum, ventral (D).
FIG. 34. Mandible, posterior (D).
FIG. 35. First maxilla, posterior (E).
FIG. 36. Second maxilla, posterior (D).
FIG. 37. Maxilliped, posterior (D).
FIG. 38. Oral and postoral areas, ventral (C).
FIG. 39. Leg 1 and intercoxal plate, anterior (C).
FIG. 40. Leg 2, anterior (C).
FIG. 41. Leg 3, anterior (C).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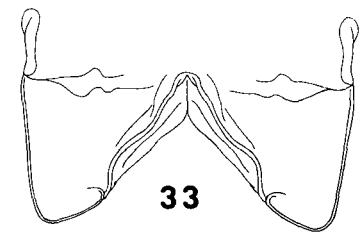
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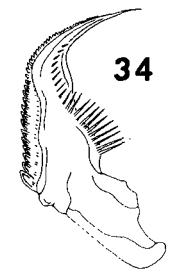
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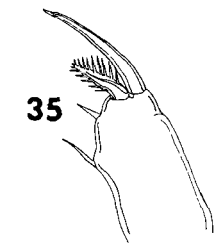
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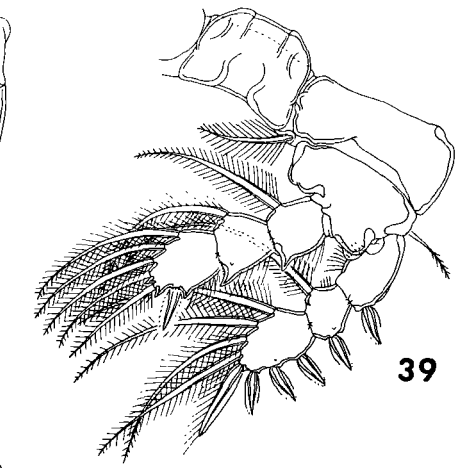
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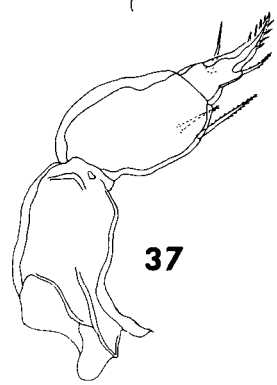
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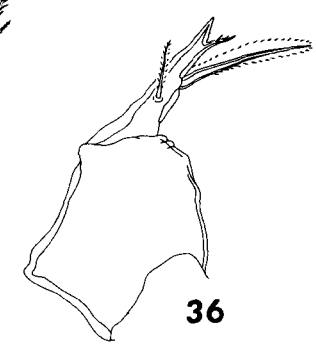
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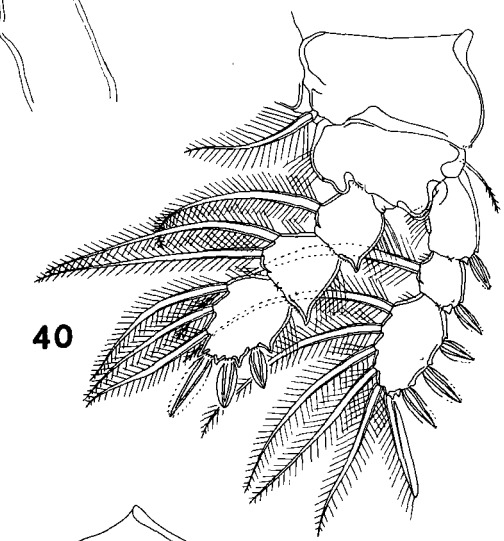
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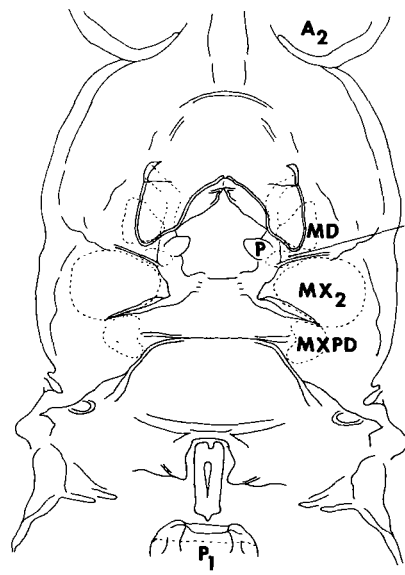

A2
38
MD
MX1
P
MX2
MXPD
P1

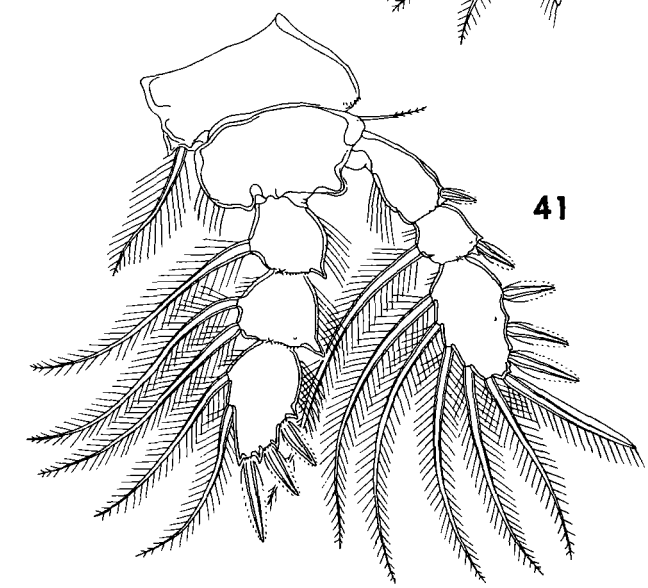

41

PLATE 6

Stellicola affinis n. sp., female (continued)

FIG. 42. Leg 4 and intercoxal plate, anterior (C).
FIG. 43. Leg 5, dorsal (D).

Stellicola affinis n. sp., male

FIG. 44. Dorsal (A).
FIG. 45. Urosome, dorsal (B).
FIG. 46. Maxilliped, anterior (F).
FIG. 47. Leg 5, ventral (D).
FIG. 48. Leg 6, ventral (F).

Stellicola longiseta n. sp., female

FIG. 49. Dorsal (H).
FIG. 50. Urosome, dorsal (B).

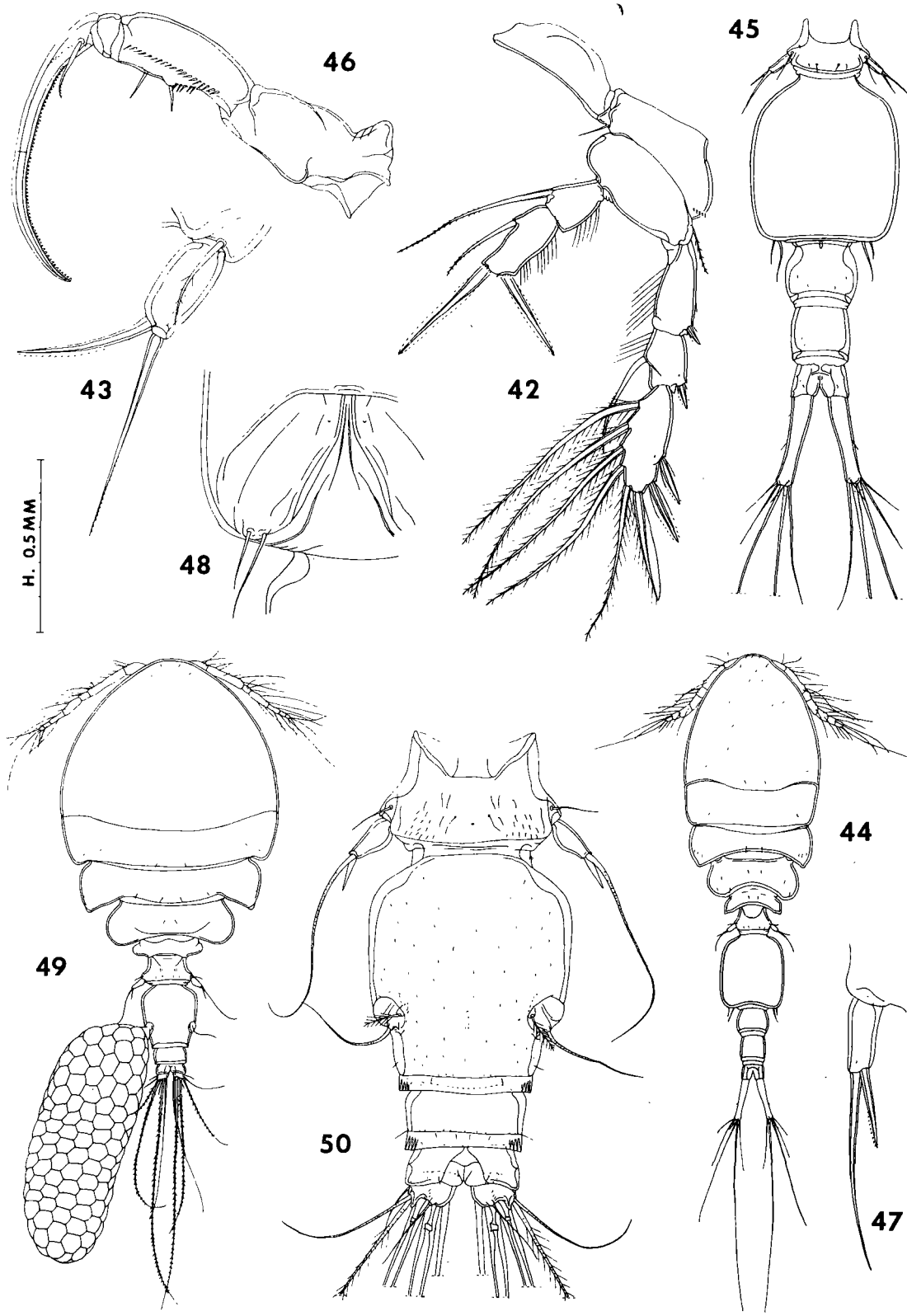

46
45
43
42
48
H. 0.5MM
49
50
44
47

PLATE 7

Stellicola longiseta n. sp., female (continued)

FIG. 51. Caudal ramus, dorsal (E).
FIG. 52. Rostrum, ventral (C).
FIG. 53. Second antenna, anterior (F).
FIG. 54. Labrum, ventral (F).
FIG. 55. Mandible, posterior (D).
FIG. 56. Second maxilla, posterior (D).
FIG. 57. Maxilliped, anterior (D).
FIG. 58. Last segment of endopod of leg 2, anterior (F).
FIG. 59. Last segment of endopod of leg 3, anterior (F).
FIG. 60. Leg 4 and intercoxal plate, anterior (C).

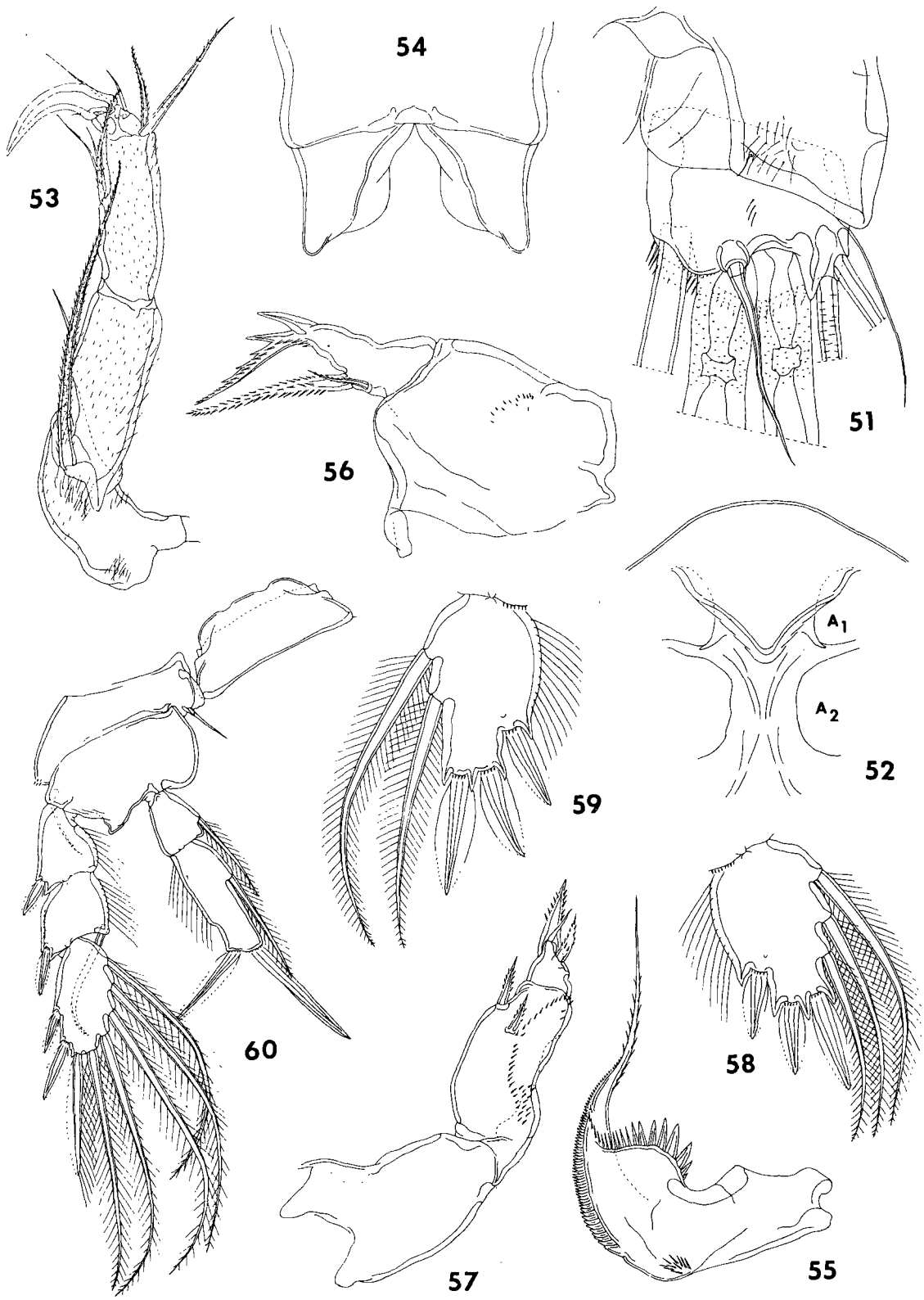

53
54
51
56
A1
A2
52
59
60
58
57
55

PLATE 8

Stellicola longiseta n. sp., female (continued)

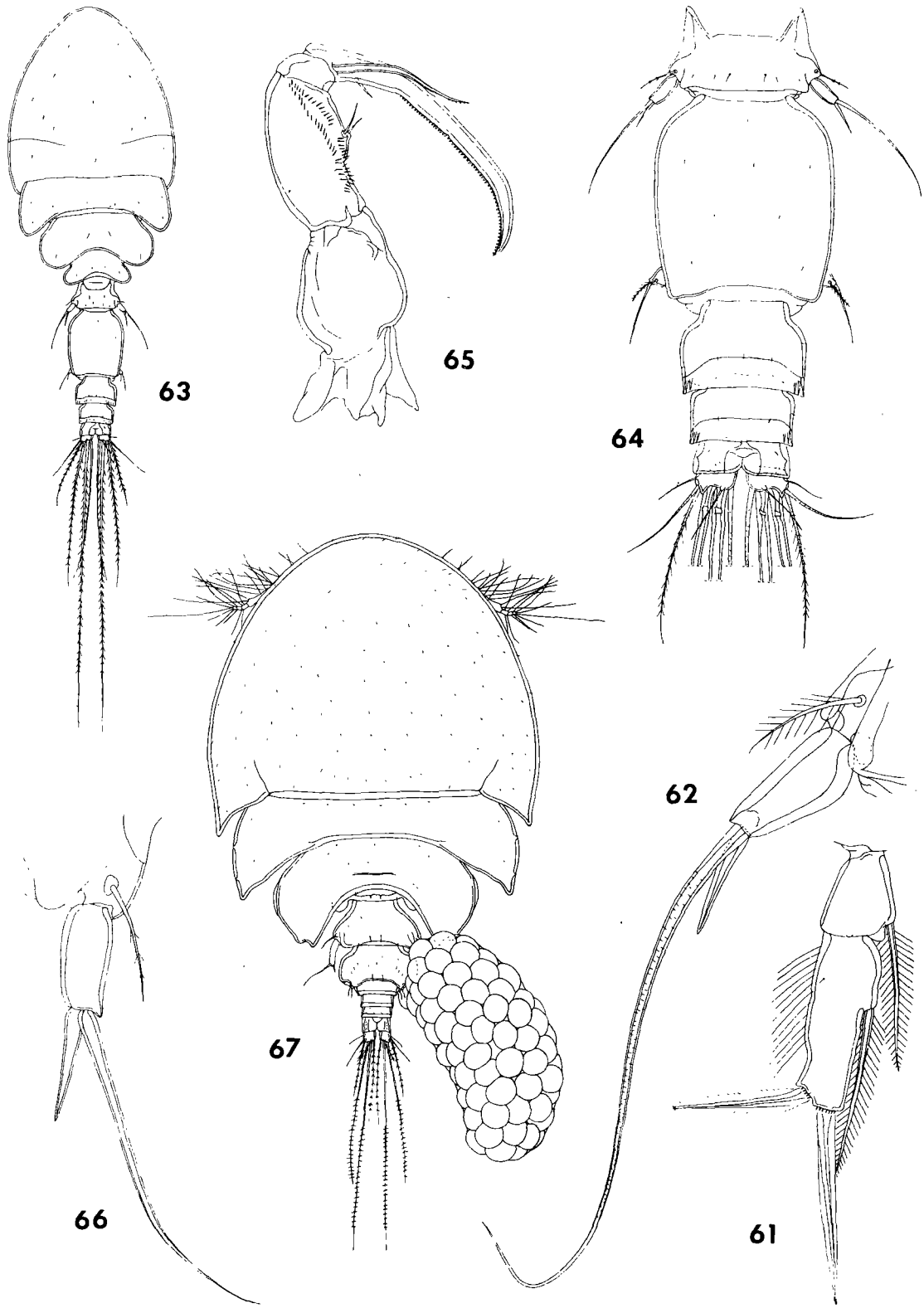
FIG. 61. Endopod of leg 4, anterior (F).
FIG. 62. Leg 5, dorsal (D).

Stellicola longiseta n. sp., male

FIG. 63. Dorsal (A).
FIG. 64. Urosome, dorsal (C).
FIG. 65. Maxilliped, anterior (F).
FIG. 66. Leg 5, dorsal (E).

Stellicola femineus n. sp., female

FIG. 67. Dorsal (H).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61

PLATE 9

Stellicola femineus n. sp., female (continued)

FIG. 68. Urosome, dorsal (I).
FIG. 69. Area of attachment of egg sac, dorsal (F).
FIG. 70. Caudal ramus, dorsal (E).
FIG. 71. Rostrum, oral and postoral areas, mouthparts not labelled but in same relative positions as in Plate 5, fig. 38, ventral (A).
FIG. 72. First antenna, dorsal (C).
FIG. 73. Second antenna, posterior (B).
FIG. 74. Tip of second antenna, anterior (F).
FIG. 75. Labrum, ventral (C).

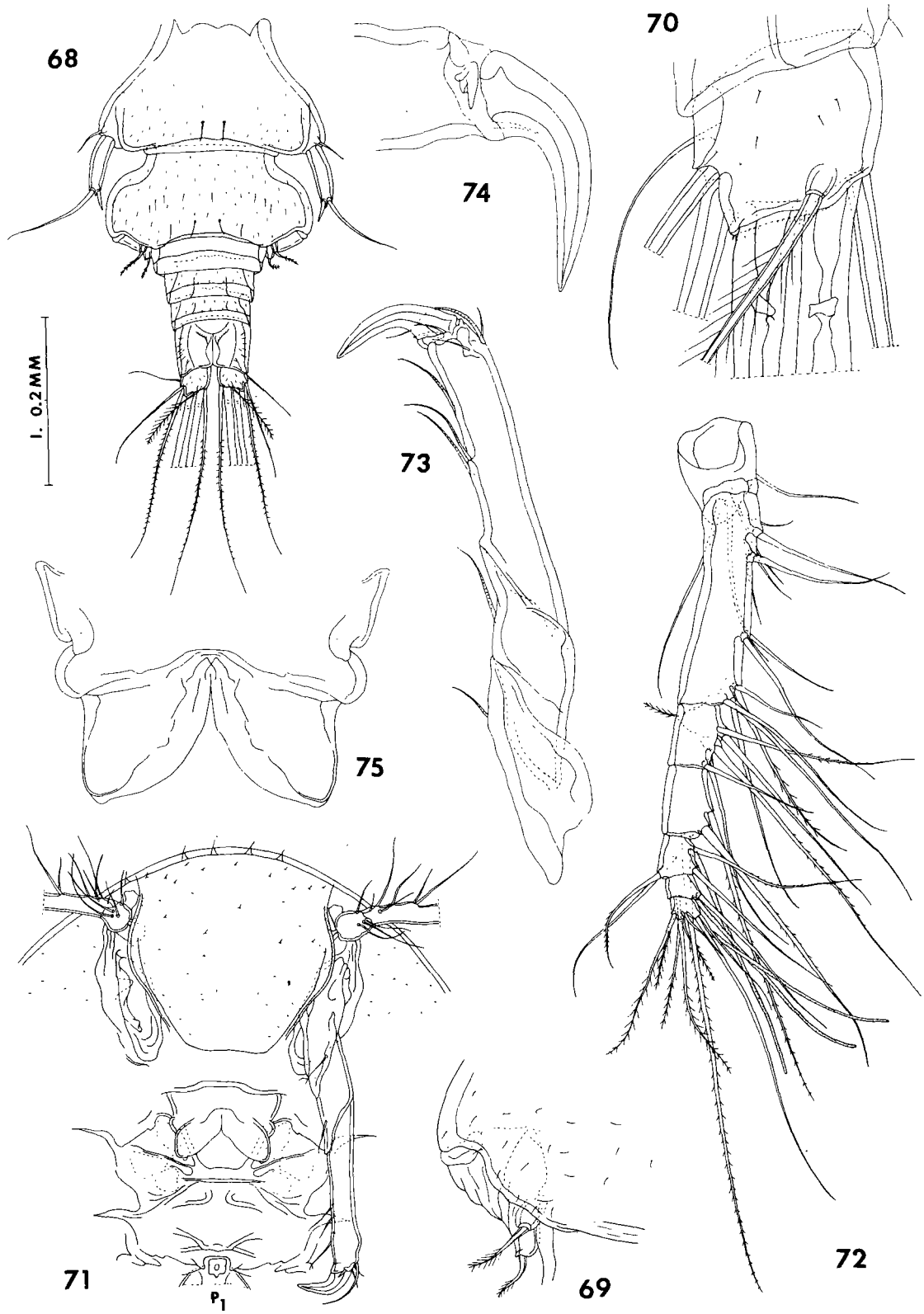
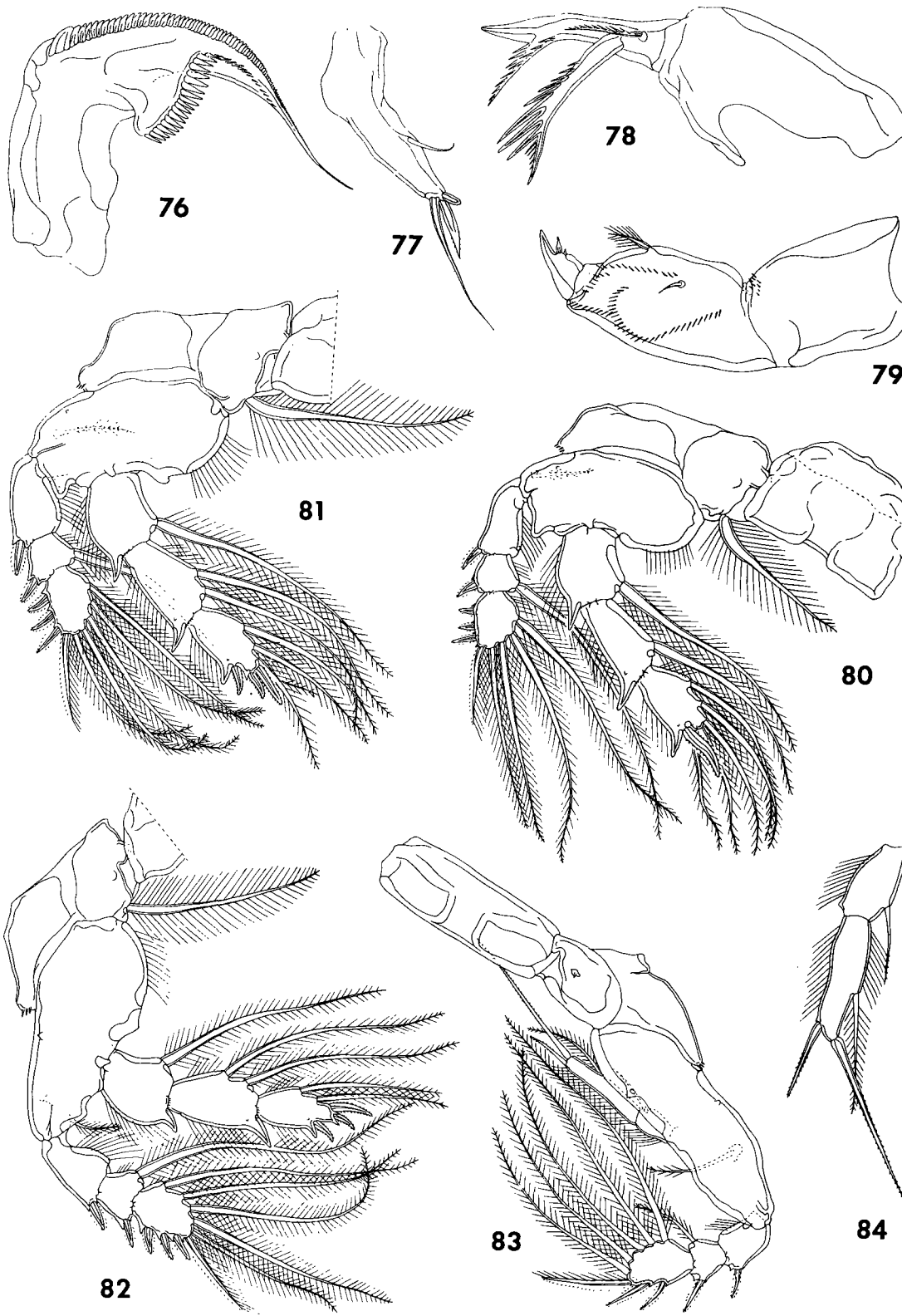

68
I. 0.2 MM
74
70
73
75
72
71
P1
69

PLATE 10

Stellicola femineus n. sp., female (continued)

FIG. 76. Mandible, posterior (F).
FIG. 77. First maxilla, anterolateral (F).
FIG. 78. Second maxilla, posterior (F).
FIG. 79. Maxilliped, posterior (F).
FIG. 80. Leg 1 and intercoxal plate, anterior (B).
FIG. 81. Leg 2, anterior (B).
FIG. 82. Leg 3, anterior (B).
FIG. 83. Leg 4 and intercoxal plate, anterior (B).
FIG. 84. Endopod of leg 4, anterior (F).


76
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80
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83
84

PLATE 11

Stellicola femineus n. sp., female (continued)

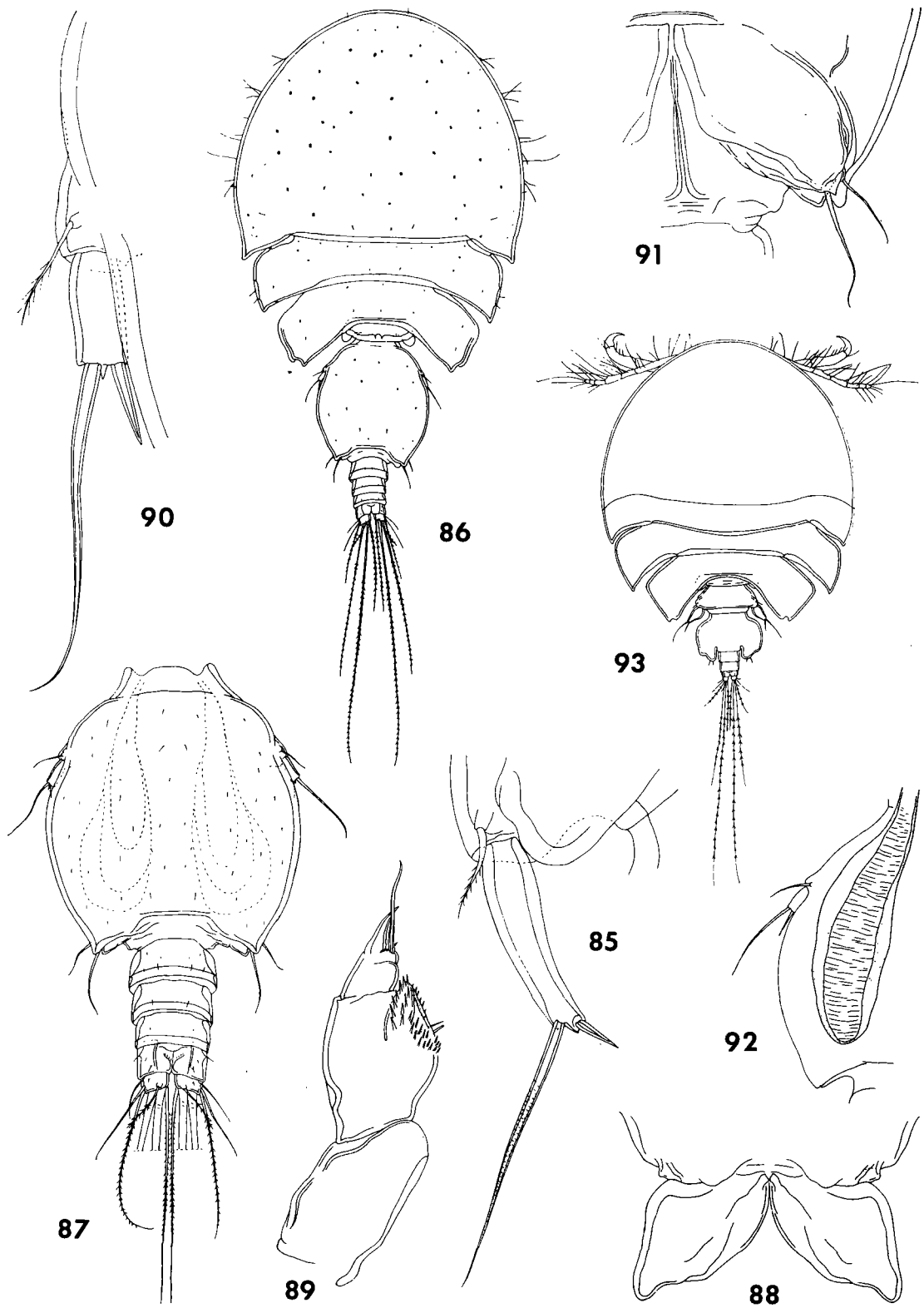
FIG. 85. Leg 5, dorsal (F).

Stellicola femineus n. sp., male

FIG. 86. Dorsal (A).
FIG. 87. Urosome, dorsal (B).
FIG. 88. Labrum, ventral (F).
FIG. 89. Maxilliped, postero-inner (D).
FIG. 90. Leg 5, dorsal (E).
FIG. 91. Leg 6, ventral (F).
FIG. 92. Spermatophore, inside male, dorsal (B).

Stellicola pollex n. sp., female

FIG. 93. Dorsal (H).


90
86
91
93
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92
88

PLATE 12

Stellicola pollex n. sp., female (continued)

FIG. 94. Urosome, dorsal (C).
FIG. 95. Area of attachment of egg sac, ventral (D).
FIG. 96. Caudal ramus, dorsal (E).
FIG. 97. First antenna, ventral (C).
FIG. 98. Second antenna, posterior (C).
FIG. 99. Mandible, posterior (F).
FIG. 100. Paragnath; ventral (G).
FIG. 101. Second maxilla, posterior (D).

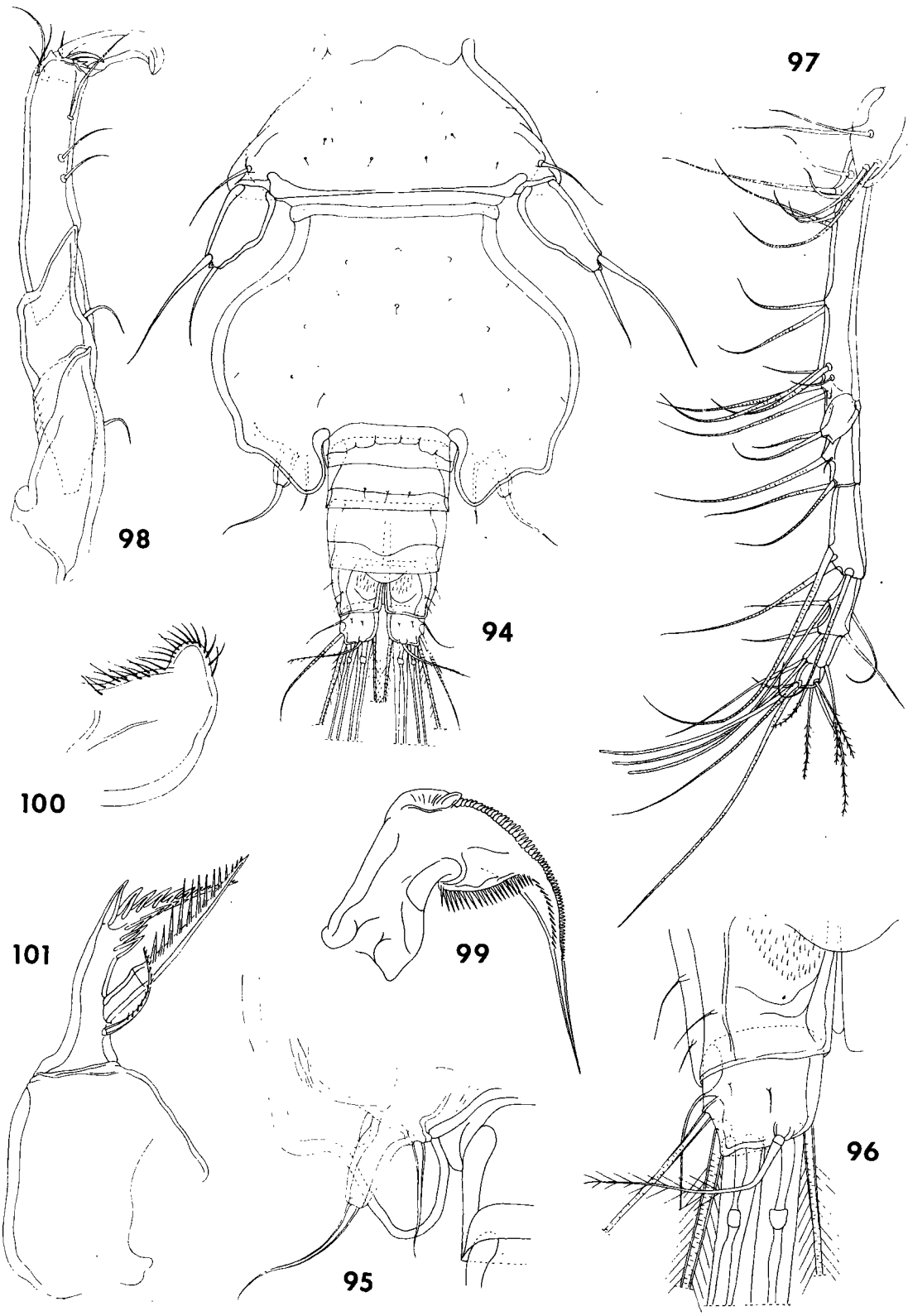

97
98
94
100
99
101
96
95

PLATE 13

Stellicola pollex n. sp., female (continued)

FIG. 102. Maxilliped, posterior (D).
FIG. 103. Leg 1 and intercoxal plate, anterior (C).
FIG. 104. Leg 2, anterior (C).
FIG. 105. Leg 3, anterior (C).
FIG. 106. Leg 4 and intercoxal plate, anterior (C).
FIG. 107. Endopod of leg 4, anterior (E).
FIG. 108. Leg 5, dorsal (D).

Stellicola pollex n. sp., male

FIG. 109. Dorsal (I).

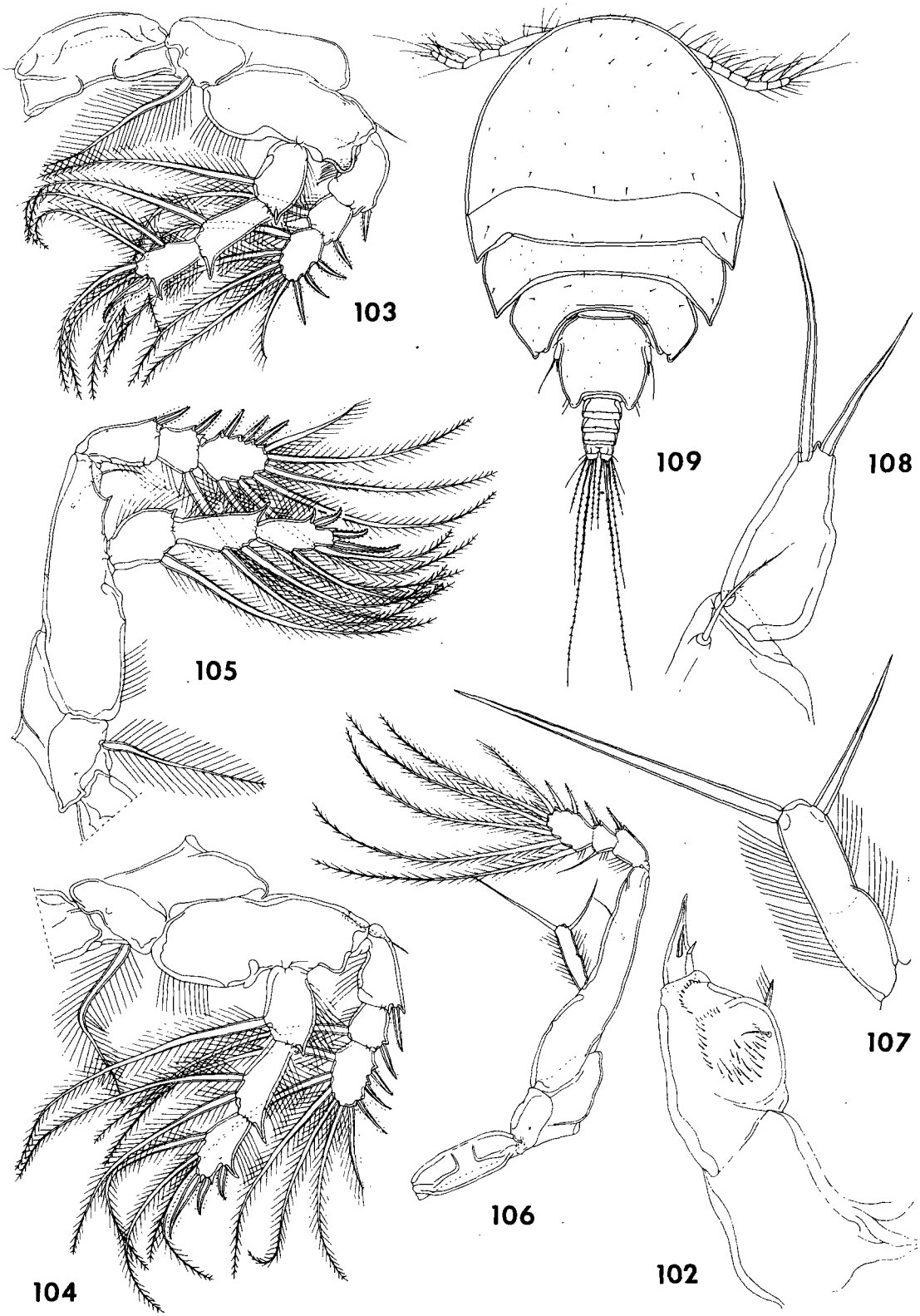

103
109
108
105
107
106
104
102

PLATE 14

Stellicola pollex n. sp., male (continued)

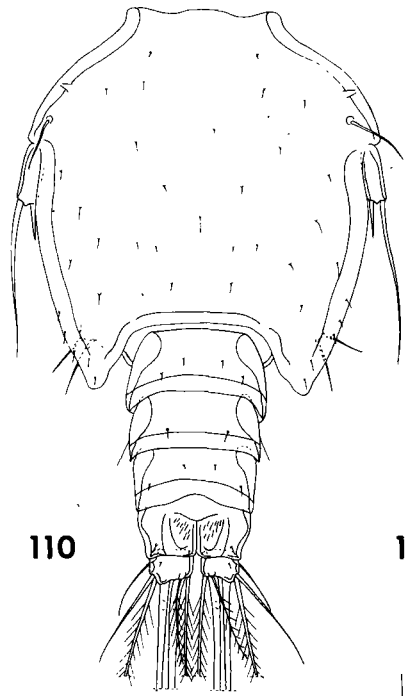
FIG. 110. Urosome, dorsal (F).
FIG. 111. Third segment of second antenna, anterior (E).
FIG. 112. Maxilliped, postero-inner (D).
FIG. 113. Leg 5, dorsal (G).
FIG. 114. Leg 6, ventral (D).

Stellicola oreastriphilus Kossmann, 1877, female

FIG. 115. Genital segment, dorsal (C).
FIG. 116. Tip of second antenna, posterior (F).
FIG. 117. Paragnath, ventral (E).
FIG. 118. Maxilliped, anterior (D).
FIG. 119. Endopod of leg 4, anterior (F).

Stellicola oreastriphilus Kossmann, 1877, male

FIG. 120. Segment of leg 5 and genital segment, dorsal (C).



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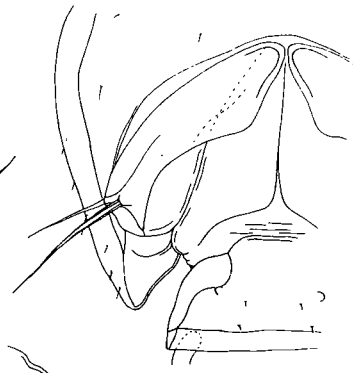

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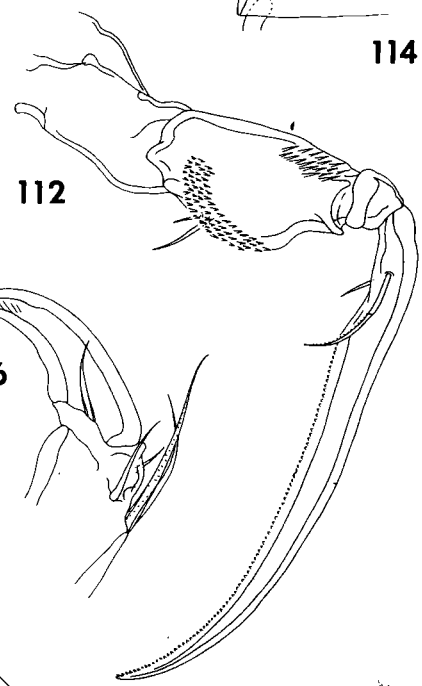

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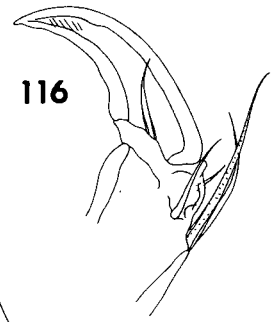

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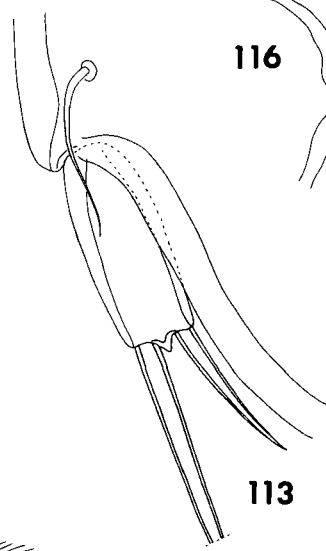

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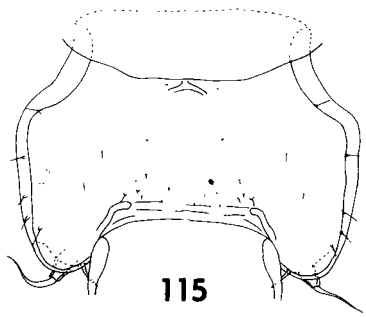

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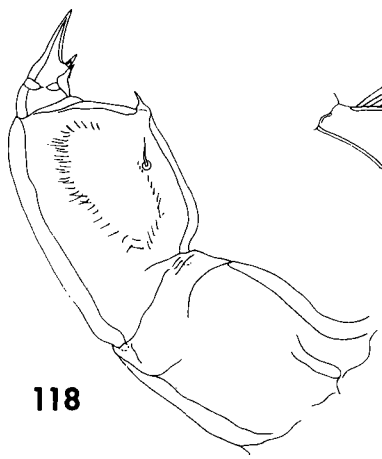

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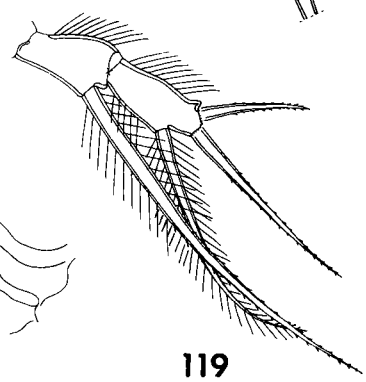

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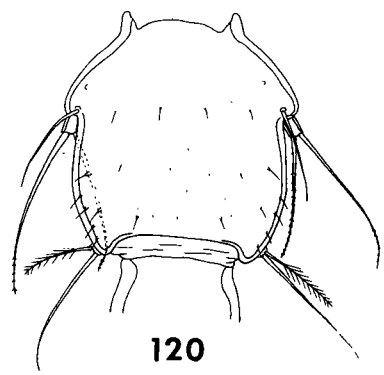

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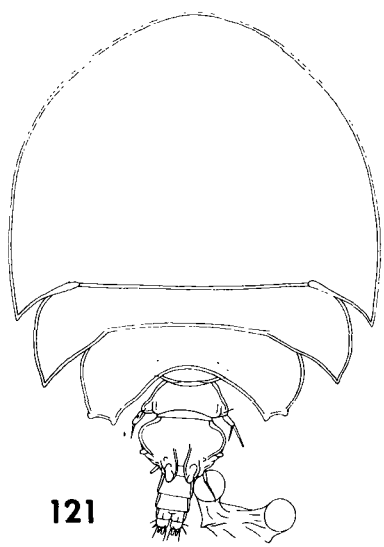
PLATE 15

Stellicola caeruleus (Stebbing, 1900), syntypic female

FIG. 121. Dorsal (H).
FIG. 122. Urosome, dorsal (B).
FIG. 123. Caudal ramus, dorsal (E).
FIG. 124. Rostrum and labrum, ventral (I).
FIG. 125. First antenna, ventral (C).
FIG. 126. Second antenna, anterior (B).
FIG. 127. Mandible, posterior (F).
FIG. 128. Second maxilla, posterior (F).



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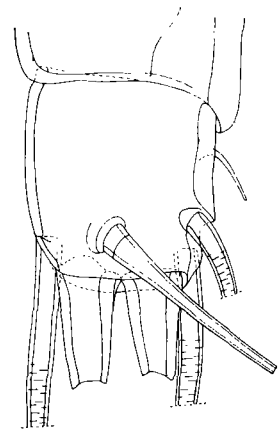

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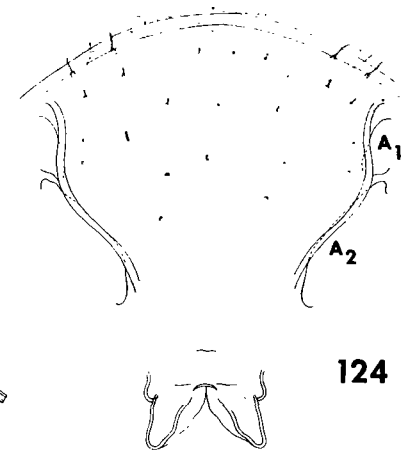

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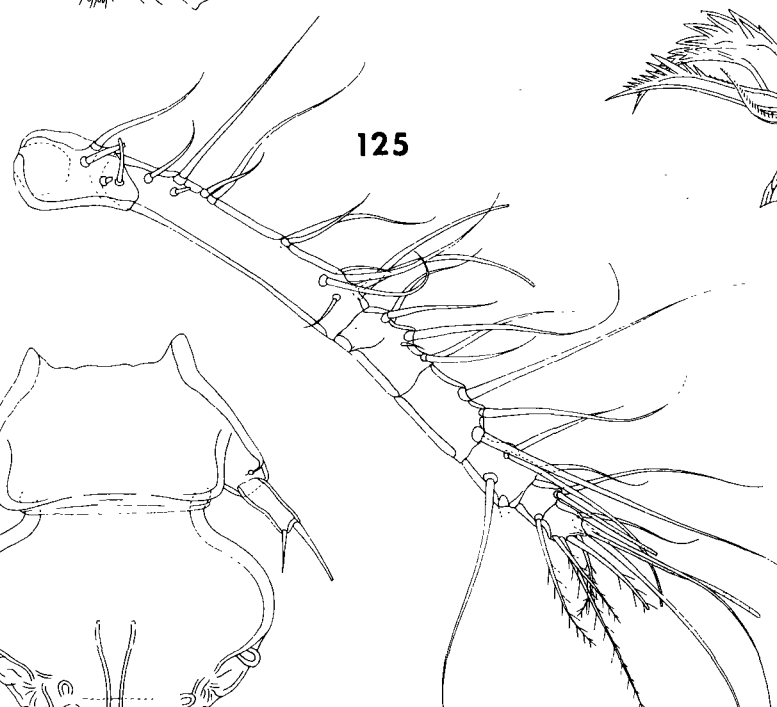

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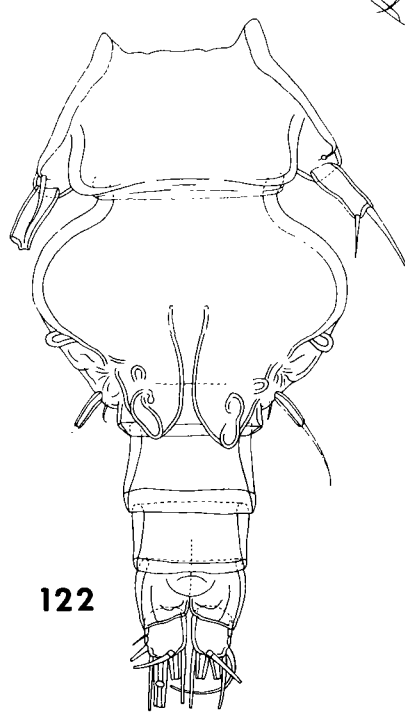

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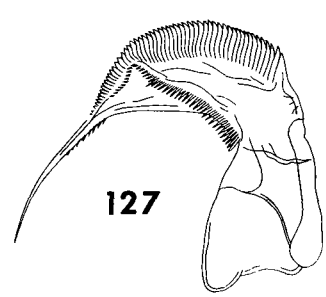

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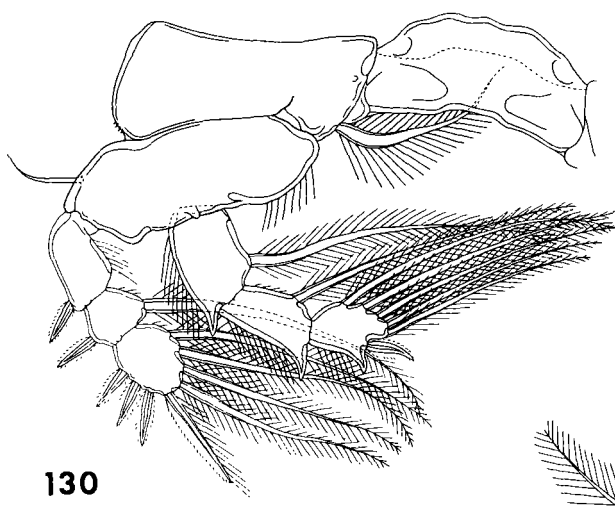
PLATE 16

Stellicola caeruleus (Stebbing, 1900), syntypic female (continued)

FIG. 129. Maxilliped, posterior (F).
FIG. 130. Leg 1 and intercoxal plate, anterior (C).
FIG. 131. Leg 2, anterior (C).
FIG. 132. Leg 3, anterior (C).
FIG. 133. Leg 4, anterior (F).
FIG. 134. Leg 5, dorsal (D).



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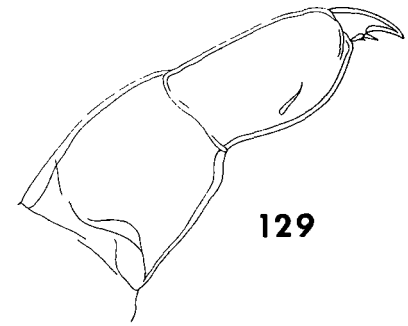

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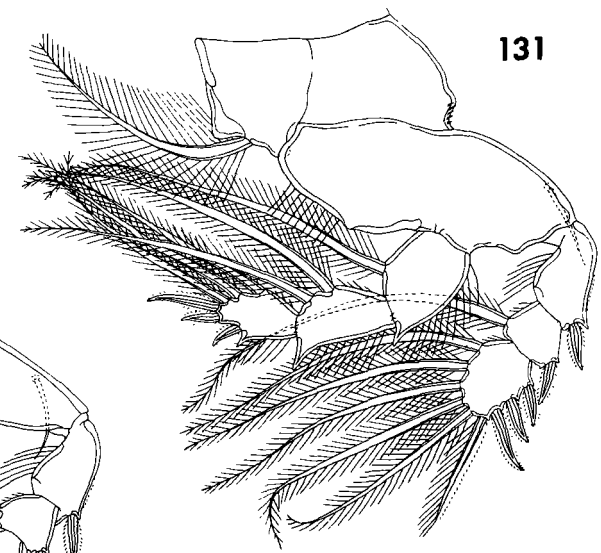

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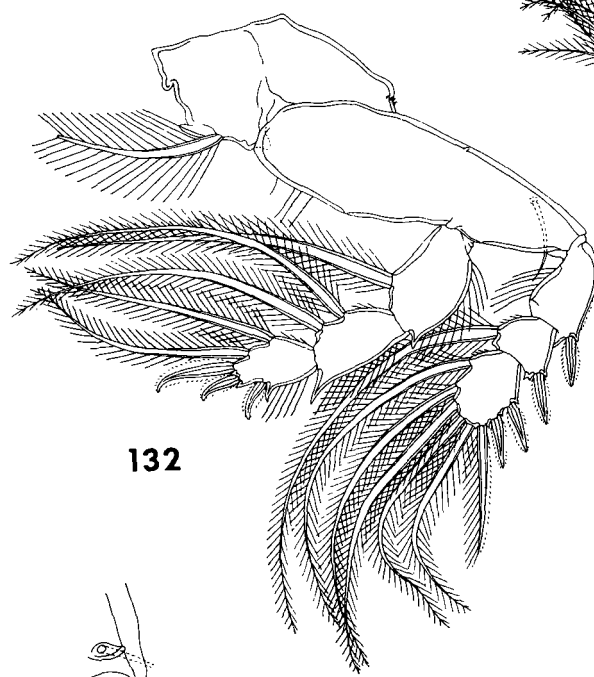

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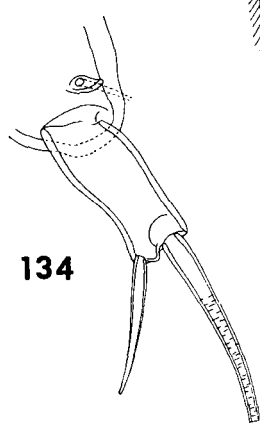

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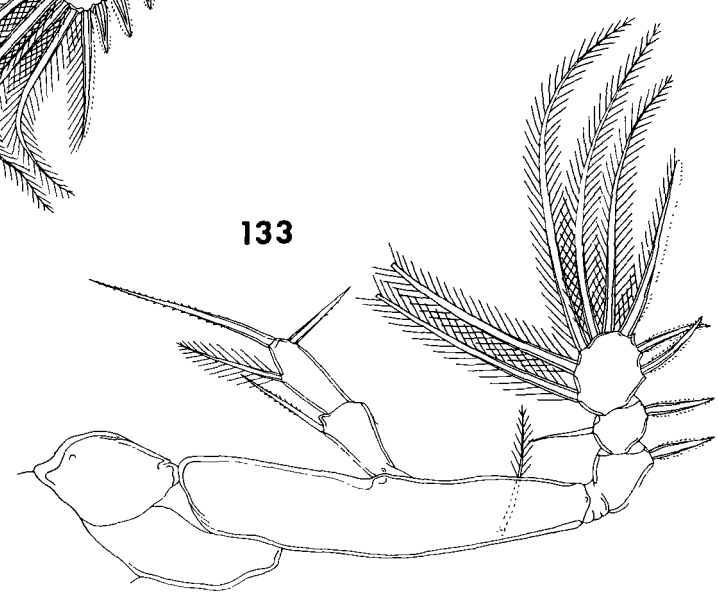

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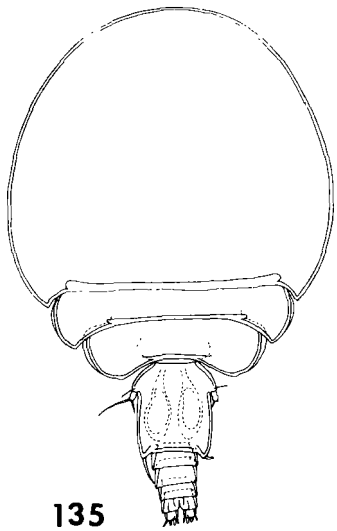
PLATE 17

Stellicola caeruleus (Stebbing, 1900) syntypic male

FIG. 135. Dorsal (I).
FIG. 136. Urosome, dorsal (F).
FIG. 137. Rostrum, ventral (C).
FIG. 138. Second maxilla, dorsal (E).
FIG. 139. Maxilliped, dorsal (G).
FIG. 140. Leg 5, dorsal (G).
FIG. 141. Leg 6, ventral (E).



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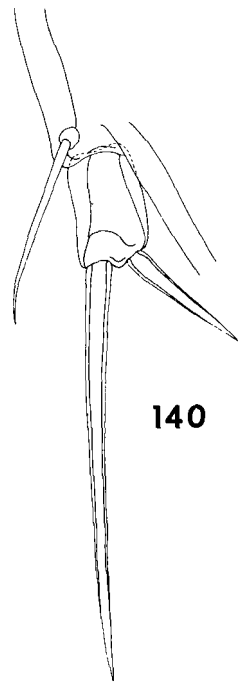

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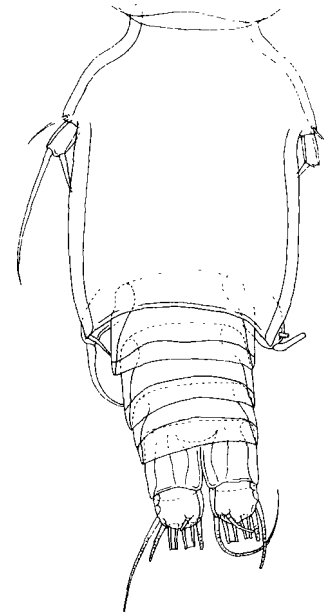

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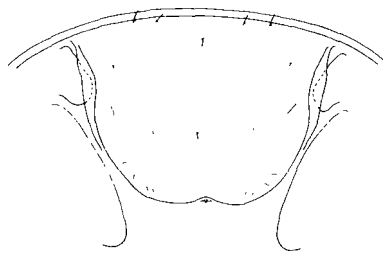

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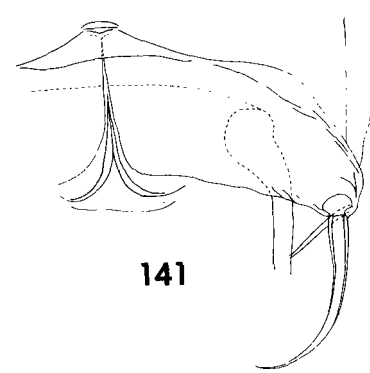

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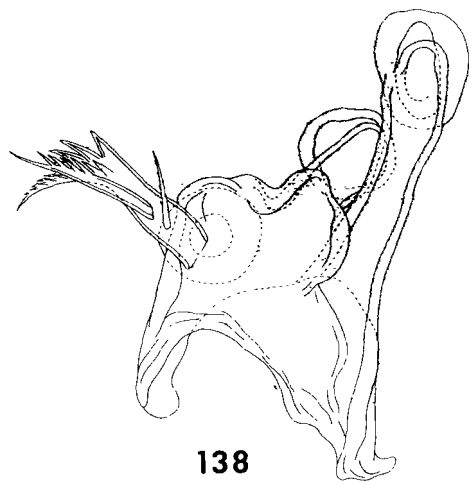

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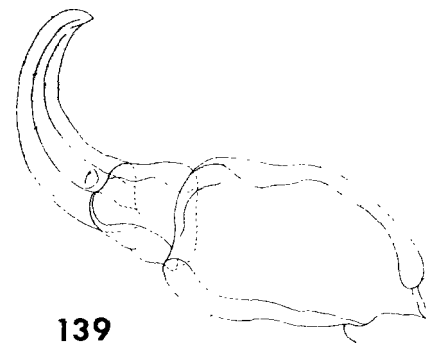

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Reprinted from *Boll. Mus. Ist. Biol. Univ. Genova*, vol. XXXV, no. 226, 1967, p. 55-73

R.W. INGLE - N. DELLA CROCE

Natural History Museum, London

Istituto di Zoologia della Università di Genova

Stomatopod larvae from the Mozambique Channel

The present collection of stomatopod larvae was made on cruise no. 8 of the U.S. National Science Foundation research vessel « Anton Bruun », during the International Indian Ocean Expedition (WHOI, 1965; Della Croce, 1964-65).

Most of the tows were carried out at night, in surface waters, at depths where heavy traces of scattering were recorded by the PGR; or at day-time at different depths. Details on the sampling net and on sampling stations have been reported elsewhere (Della Croce & Frontier, 1966).

Many stomatopod larvae from the Indian Ocean have been described and figured (Claus, 1871; Lanchester, 1903; Tattersall, 1906; Borradaile, 1907; Foxon, 1939), but very few have been satisfactorily assigned to known adult species of the order. Alikunhi (1944; 1952) has succeeded in rearing later larval forms (particularly of *Alima* larvae) into post-larval stages, and in many instances to attribute them to known species of adult stomatopods.

A small proportion of the collection has been definitely identified as late larval stages of the following four species: *Odontodactylus brevirostris* (Miers), *Pseudosquilla ciliata* (Fabricius), *Lysiosquilla maculata* (Fabricius), *Acanthosquilla multifasciata* (Wood-Mason).

The remaining specimens, mostly *Alima* larvae, have not provided such a satisfactory study, presumably because too immature. For the

The Authors are grateful to Dr. A.L. Rice for his constructive suggestions.

most part these have been identified as far as practicable to the *Alima* stages of *Squilla*, according to the key by Alikunhi (1952). Unfortunately it has not been possible to assign any specimen to the last couplet of that key denoting a particular species of *Squilla*. Each specimen therefore has been placed into one of five « species-groups » according to the characters of the same key. An example from each group has been figured and variations of the material noted in the text. The figures have been drawn with the aid of a camera lucida and all measurements, unless otherwise stated, are from the apex of the rostrum to the median posterior margin of the telson, or larval carapace.

Sampling stations and Identifications

A. Bruun Station 398 D: 25° 46' S - 34° 29' E; 30-9-1964; surface tow at 0415; sonic depth 400 m.

Lysierichthus stages of *Acanthosquilla multifasciata* (Wood-Mason);
Alima stages of *Squilla hieroglyphica-gonypetes-woodmasoni* group.

A. Bruun Station 398A: 22° 46' S - 35° 50' E; 1-10-1964; surface tow at 0415.

Lysierichthus stages of *Lysiosquilla* sp.

A. Bruun Station 400B: 21° 41' S - 35° 39' E; 3-10-1964; surface tow at 0415.

Pseudorichthus stages of *Pseudosquilla ciliata* (Fabricius);
Coroniderichthus bituberculatus Hansen (larv. st. of *Coronida* sp.);
Alima stages of *Squilla holochista-nepa-oratoria* group.

A. Bruun Station 406C: 18° 27' S - 41° 20' E; 12-10-1964; tows at 1455; sonic depth 2150 m.

Odonterichthus stages of *Odontodactylus brevirostris* (Miers);
Pseuderichthus stages of *Pseudosquilla* sp.;
Coroniderichthus bituberculatus Hansen (larv. st. of *Coronida* sp.);
Alima stages of *Squilla holochista-nepa-oratoria* group.

A. Bruun Station 407B: 17° 34' S - 42° 43' E; 13-10-1964; tow at 1530; sonic depth 1950 m.

Odonterichthus stages of *Odontodactylus brevirostris* (Miers);
Pseuderichthus stages of *Pseudosquilla* sp.

A. Bruun Station 407H: 17° 22' S - 43° 10' E; 14-10-1964; tow at 1330; sonic depth 710 m.

Lysierichthus stages of *Lysiosquilla maculata* (Fabricius);
Alima stages of *Squilla hieroglyphica-gonypetes-woodmasoni* group;
Squilla interrupta-boops-quinquedentata group;
Squilla latreillei-lata-fasciata group;
Squilla holochista-nepa-oratoria group;
Harpiosquilla raphidea-harpax group.

A. Bruun Station 408E: 16° 11' S - 43° 29' E; 16-10-1964; surface tow at 0415; sonic depth 1600 m.

Odonterichthus stages of *Odontodactylus brevirostris* (Miers);
Odonterichthus tenuicornis Jurich (larv. st. of *Odontodactylus* sp.);
Pseuderichthus stages of *Pseudosquilla ciliata* (Fabricius);
Lysierichthus stages of *Lysiosquilla* sp.;
Alima stages of *Squilla latreillei-lata-fasciata* group;
Squilla holochista-nepa-oratoria group;
Harpiosquilla raphidea-harpax group.

A. Bruun Station 409D: 16° 12' S - 43° 41' E; 18-10-1964; surface tow at 0415; sonic depth 600 m.

Odonterichthus stages of *Odontodactylus brevirostris* (Miers);
Alima stages of *Squilla hieroglyphica-gonypetes-woodmasoni* group;
Squilla interrupta-boops-quinquedentata group;
Squilla latreillei-lata-fasciata group;
Squilla holochista-nepa-oratoria group;
Harpiosquilla raphidea-harpax group:
Alima gracillima.

A. Bruun Station 409N: 15° 29' S - 44° 42' E; 20-10-1964; surface tow at 0415; sonic depth 1600 m.

Coronideríchthus bituberculatus Hansen (larv. st. of *Coronida* sp.);
Alima stages of *Squilla latreillei-lata-fasciata* group;
Harpiosquilla raphidea-harpax group.

A. Bruun Station 410B: 14° 33' S - 45° 47' E; 21-10-1964; surface tow at 0410; sonic depth 2000 m.

Alima stages of *Harpiosquilla raphidea-harpax* group.

Systematic account

Genus *Odontodactylus* Bigelow 1894

Specimens of larvae have been ascribed to the genus *Odontadactylus* by various authors under different names:

Gonodactylus form, Claus, 1871, p. 139, pl. 5, figs., 21 & 21c;

Odonterichthus larvae, Bigelow, 1894, pp. 554-6, figs., 25 & 26;

Odonterichthus tenuicornis Jurich, 1904, p. 396, pl. 28, fig. 4 (doubtful according to Hansen, 1926, p. 43);

Odonterichthus rostratus Borradaile, 1907, p. 214 (somewhat doubtful, see below);

Pseuderichthus distinguendus Borradaile, 1907, p. 215 (at least one specimen, see below);

Odontodactylus sp. (= *Odonterichthus* sp.) Calman, 1917, p. 145; Verrill, 1923, p. 201, pl. 49, fig. 6 (« Odontosyllis » in legend to fig.);

Odontodactylus (?) *scyllaris*, larval stages, Hansen, 1926, pp. 43-4, figs., 6-9.

There would appear to be few reliable characters on which to distinguish between the larval forms of *Odonterichthus* (= *Odontodactylus*), *Pseuderichthus* (= *Pseudosquilla*) and *Gonerichthus* (= *Gonodactylus*), although Bigelow (1894, p. 543) suggested that the more mature stages of *Odonterichthus* differed from *Gonerichthus* in having traces of lateral teeth on the raptorial dactylus, which were absent in *Gonerichthus* larvae. Bigelow substantiated his remarks by describing two advanced forms of *Odontodactylus* in which the dactylus of each had five and eight incipient teeth respectively on the inner margin. Hansen (1926, p. 43) suggested that the late larvae of *Pseuderichthus* (*Pseudosquilla*) could be distinguished from *Odonterichthus* (*Odontodactylus*) and *Gonerichthus* (*Gonodactylus*) by the slender proximal merus of the raptorial claw articulating terminally with the ischium. In *Odonterichthus* and *Gonerichthus* this corresponding portion of the merus is considerably thickened and its articulation with the ischium is situated at a point on the inner side and at a short distance from the posterior meral edge. Thus the merus has a posterior prolongation. Hansen also suggested that mature larvae of *Odonterichthus* have exceptionally long marginal submedian spines on the telson, a long rostrum and long postero-lateral processes

on the larval carapace (see his pl. 2, figs. 6b, cf. 10b & figs. 7a cf. 11a).

Of the twenty-four described larvae attributed to *Odonterichthus*, only four figured examples appear to show the posterior prolongation of the raptorial merus (viz. Bigelow 1894, fig. 26; Hansen 1926, pl. 2, figs. 6a, 7c, 9b). The examples figured by Claus (1871, pl. 5, figs. 21 & 21'), Bigelow (1894, fig. 25), Jurich (1904, pl. 28, fig. 4) and Verrill (1923, pl. 49, fig. 6) do not show the raptorial merus as being prolonged. The specimens in the B.M. (N.H.) Collection identified as *Odonterichthus tenuicornis and O. rostratus* by Borradaile (1907, p. 214) and those identified as *Odontodactylus* (*Odonterichthus*) sp. by Calman (1907, p. 145) also lack the posterior prolongation of the raptorial merus. In addition, the telsons of all the specimens attributed to *O. rostratus* have short submedian spines. This feature, combined with the terminal articulation of the raptorial merus, would seem to indicate that they are *Pseuderichthus* rather than *Odonterichthus* larvae. In contrast the telsons of the specimens of *O. tenuicornis* and of *Odontodactylus* (*Odonterichthus*) sp. are furnished with long submedian spines and it seems that these larvae are true *Odonterichthus* type but not sufficiently mature to show the posterior prolongation of the raptorial merus, a condition which also obtains in the specimens described below as the late larval stages of *Odontodactylus brevirostris* (Miers).

Late *Odonterichthus* stages of *Odontodactylus brevirostris* (Miers) (Figs. 1-9)

Gonodactylus brevirostris Miers, 1884, p. 567, pl. 52, fig. c;

Odontodactylus brevirostris Bigelow, 1894, p. 496; Tattersall, 1906, p. 172, pl. ii, figs. 16-18; Borradaile, 1907, p. 212; Kemp, 1913, p. 143-4;

Pseuderichthus distinguendus Borradaile, 1907, p. 215 (part).

Material examined: 5 specimens. Station 406C: 1 specimen (length 12 mm); Station 407B: 1 specimen (length 12,5 mm); Station 408E: 2 specimens (length 9-18 mm); Station 409 D: 1 specimen (length 10 mm).

Descriptive notes. - The following description is of the 18 mm specimen from Station 408E. The larval rostrum has five spines on the lower margin. The carapace (fig. 1), beneath the larval skin, is without a cervical groove; the gastric carinae are well developed and the rostrum is ovate. The thoracic and abdominal somites (figs. 1, 2) are without carinae. The telson (figs. 1, 8) has a dorsal median carina and distally

a small spinule. There is a faint intermediate carina on either side of the mid-line. The median edge of the telson bears fifteen sub-median denticles on either side of the mid-line and two intermediate and one lateral denticle. All these are visible beneath the larval skin. The sub-median and intermediate spines are long and movable. The outer endite of the antennular flagellum has eight groups of setae (fig. 3). The antenna (fig. 4) has an incipient papilla on the protopodite (fig. 4,y) and a broad distal endite (s). The merus (m) of the raptorial claw (fig. 6) is without a pronounced proximal expansion and articulates terminally with the ischium (i); the lower margin of the merus is grooved throughout its length. The propodus has a number of fine, well spaced setules on its outer edge and the dactylus has at least six rudimentary teeth on its inner edge (right inset to fig. 6). Each of the third to fifth thoracic appendages (the fifth is depicted in fig. 5) has the propodus longer than broad and the inner edge of this segment beset with spines and setules. The sixth thoracic appendage is shaped as in fig. 7. The proximal segment of the uropod exopodite (fig. 9) has ten graded spines; the distal segment is broader than long. The outer prolongation of the protopodite is longer than the inner one; the length of the endopod (fig. 9, en) is approximately 2½ times its width.

The remaining specimens, measuring 9-12,5 mm, differ from the largest example described above in the following features: 1. There are, on average, three spinules on the lower rostral margin. 2. The intermediate denticles of the telson are only just discernible. 3. There are no teeth visible on the inner raptorial dactylus.

Remarks. — The following reasons would seem adequate for assigning these specimens to the genus *Odontodactylus*:

1. The propodi of the third and fourth thoracic appendages are longer than broad and not much longer than the fifth pair. It is thus excluded from the genus *Lysiosquilla* (*Lysierichthus* larvae).

2. The telson has sub-median denticles and the dactylus has at least six teeth. This excludes it from *Pseudosquilla* (dactylus with 3 teeth), *Pseudosquillopsis* (dactylus with 3 teeth), *Manningia* (dactylus with 4 teeth), *Coronidopsis* (dactylus with 4 teeth) as all the species attributed to these genera are without sub-median denticles. (see Manning, 1963, pp. 311-14).

3. It is likewise excluded from *Parasquilla* in not having a bilobed eye cornea and from *Eurysquilloides* because the antennular somite is not elongated.

4. It has long sub-median, intermediate and lateral spines on the telson, a character regarded by Hansen (1926, p. 43) as being typical of *Odontodactylus* larvae. Finally there is no indication of a cervical groove on the carapace beneath the larval skin and this groove is absent in species of *Odontodactylus* according to Kemp (1913, p. 133).

Of the described species of *Odontodactylus* only five (*) are known from Indo-Pacific waters, all with at least six teeth on the raptorial dactylus. Only one of these species, *O. brevirostris*, is without lateral carinae on the telson (Kemp, 1913, pp. 135 & 143). This species is known to occur in Seychelle waters (Miers, 1884, p. 567; Borradaile, 1907, p. 212) and in the Gulf of Manaar (Tattersall, 1906, p. 172).

An examination of a female specimen of *O. brevirostris* (14 mm) from Oyster Banks, Manaar, Ceylon (det. W.M. Tattersall) has shown that the larvae described above have the following features in common with this specimen:

1. The shape of the antennal endite and the position of the protopodite papilla (fig. 4, cf. 10).

2. The shape and spinulation of the uropods (fig. 7, cf. 13).

3. The shape and proportions of the sixth thoracic appendage (fig. 7 cf. 11).

4. The telson of both examples figured are without lateral carinae.

Borradaile (1907, p. 215) attributed several specimens from the Western Indian Ocean to the larval *Pseuderichthus distinguendus* Hansen. He mentions a number of « smaller individuals in which the zoaea spine... is wanting ». One of these specimens, in the B.M. (N.H.) Collections, is identical with the larva attributed to *O. brevirostris*. It is therefore now assigned to this species.

(*) Manning (in press) is of the opinion that *Odontodactylus* is a monotypic genus and that many of the characters used by Kemp to separate the several species are juvenile ones (personal communication from R.B. Manning, March 1967).

Odonterichthus tenuicornis Jurich

Odonterichthus tenuicornis Jurich, 1904, p. 396, pl. 28, fig. 4; Borradaile, 1907, p. 214.

Material examined: 4 specimens. Station 406C: 1 specimen (length 16 mm); Station 408E: 3 specimens (length 11-17 mm).

Remarks. - These specimens agree in every detail with Borradaile's material from Stn. 66, W. Indian Ocean, « Sea-lark » Exped. and also with Jurich's (1904, pl. 28, fig. 4).

Genus *Pseudosquilla* Dana 1852
Pseuderichthus stages of
Pseudosquilla ciliata (Fabricius)
(Figs. 14 & 15)

?*Almerichthus cylindricus* Guerin-Meneville, 1857, pl. 3, Figs. 12, 12a;

Squilloid-*Pseudosquilla* Claus, 1871, p. 32, Fig. 26;

Pseuderichthus communis Hansen, 1895, p. 86, pl. 8, figs. 5, 5a, and 5b; Jurich, 1904, p. 395, pl. 29, fig. 1; Borradaile, 1907, p. 214;

Pseudosquilla ciliata (*Pseuderichthus communis*) Calman, 1917, p. 142; Foxon, 1939, p. 260.

Material examined: 3 specimens. Station 400B: 2 specimens (length 21-24 mm); Station 408E: 1 specimen (length 24 mm).

Descriptive notes. - The specimen of 24 mm from Station 408E shows, beneath the larval skin, a telson approaching in shape the « monodactyla » or early post-larval stage of *Pseudosquilla ciliata* as figured by Bigelow (1931, fig. 5). The telson and left uropod of this specimen are depicted in figs. 14 and 15 respectively to show the change of shape attained at the next moult. The raptorial dactylus has two faint indentations indicating the origin of the dactylar teeth.

Pseuderichthus stages of unidentified
Pseudosquilla sp.

Material examined: 2 specimens. Station 406C: 1 specimen (length 17 mm); Station 407B: 1 specimen (length 22,5 mm).

Descriptive notes. - These two specimens agree in many features with the *Pseuderichthus* stages of *Pseudosquilla ciliata*, but the rostrum of each is more strongly concave in the anterior part than is shown in

the figure by Claus (1871, fig. 26) of the « Squilloid-larva » which, according to Hansen (1926, p. 84) is the larva of *Pseudosquilla ciliata*. In the two specimens collected by the « Anton Bruun » a prominent zoeal spine is present, a feature not apparent in *P. ciliata* larvae.

Genus *Lysiosquilla* Dana 1852
Lysierichthus stage of
Lysiosquilla maculata (Fabricius)

Lysiosquilla maculata (final pelagic stage), Alikunhi, 1951, p. 285, fig. 17.

Material examined: 1 specimen (length 24 mm), Station 407H.

Remarks. - This specimen agrees with the description and figures by Alikunhi (1951, fig. 17), who remarked that the larva reared by him into *L. maculata* was distinctly different from the larval form originally described as *Erichthus* (= *Lysierichthus*) *duvaucelli* Guerin-Meneville 1857, which has generally been supposed to be the pelagic larva of *Lysiosquilla maculata* by subsequent authors.

Lysierichthus stages of unidentified
Lysiosquilla sp.

Material examined: 4 specimens. Station 398A: 1 specimen (length 8,5 mm); Station 408E: 2 specimens (length 11,5-12 mm); Station 410B: 1 incomplete specimen.

Descriptive notes. - The following description is of the 12 mm specimen from Station 408E. Carapace without a zoeal spine, postero-lateral spines present. Rostrum with eight spinules on lower margin. Abdominal somites with postero-lateral angles acutely pointed; the last somite with a pair of median dorsal spinules. Telson with thirty two sub-median denticles; sub-median, intermediate, lateral and pre-lateral spines all well developed. Raptorial dactylus with ten vestigial teeth. Uropods with distal and proximal exopodite segments not yet articulate, the latter has the outer edge beset with two well developed and one rudimentary spine, bifurcate protopodite process with outer spine longer than inner one.

The smallest specimen (8,5 mm) from Station 398A is very juvenile. The carapace has a zoeal spine and the lower rostral edge is beset with four spinules. There are no vestigial teeth on the raptorial dactylus.

Genus *Acanthosquilla* Manning 1963
Lysierichthus stages of
Acanthosquilla multifasciata (Wood-Mason)

?Erichthoidina brevispinosa Claus, 1871, pl. 1, fig. 4, pl. 2, fig. 5; Gurney, 1946, p. 149, figs. 9, A-C;

Lysierichthus sp. Komai & Tung, 1929, pl. 7, figs. 13-19, pl. 8, figs. 1-9;

Lysiosquilla multifasciata (final pelagic stage), Alikunhi, 1952, p. 289, fig. 19, a-c.

Material examined: 2 specimens. Station 398D: 1 specimen (length 16 mm); Station 409D: 1 specimen (length 15 mm).

Descriptive notes. - The specimens collected by the « Anton Bruun » agree with other descriptions (Komai & Tung, 1929; Alikunhi, 1952) except that the three spines on the rostral ventral edge are much smaller than depicted by these authors. According to Alikunhi, the *Erichthoidina brevispinosa* figured by Claus (1871) and by Gurney (1946) are probably stages of *A. multifasciata.* However, the figures of these two authors show respectively six and eight prominent spinules on the rostral ventral edge, and the sub-median denticles on the telson are arranged somewhat differently to those depicted by Alikunhi's fig. 19 b-c.

Genus *Coronida* Brooks 1886
Coronide richthus bituberculatus Hansen
larval stages of *Coronida* sp.

Erichthus armatus Claus, 1871, p. 25, pl. 4, figs. 15 & 15';

Coronide richthus bituberculatus Hansen, 1895, p. 83; Jurich, 1904, p. 394, pl. 28;

Coronida sp. (*?trachurus*) Foxon, 1939, p. 264, fig. 4.

Material examined: 4 specimens. Station 400B: 2 specimens (length 8-11 mm); Station 406C: 1 specimen (length 15 mm); Station 409N: 1 specimen with atrophied telson (length 14 mm).

Descriptive remarks. - The specimens from « John Murray » Stn. 172, (Foxon, 1939) have undeveloped uropods in contrast to those

collected by « Anton Bruun » all of which have these appendages well developed. The smaller specimens of 11 & 14 mm respectively have the outer prolongation of the uropod protopodite longer than the inner, whilst in the 15 mm example the outer prolongation is shorter than the inner.

Genus *Squilla* Fabricius 1787

The *Alima* larvae are arranged here in five « species-groups » using the characters given in Alikunhi's (1952) key for the indentification of larvae, except for *Alima gracillima* Borradaile which does not fit his key satisfactorily.

Alima stages of *Squilla hieroglyphica-gonypetes-woodmasoni* group (Figs. 16, 21 & 26)

Material examined: 2 specimens. Station 398D: 1 specimen (length 11,5 mm); Station 407H: 1 specimen (length 19 mm).

Descriptive remarks. - The 11,5 mm specimen from Station 398D is depicted in figs. 16, 21 & 26. The spinules on the lateral left margin of the carapace are labelled 1-4 respectively. No. 4 is visible from lateral and dorsal aspects. The raptorial dactylus and propodus is shown in fig. 26. The lateral margins of the carapace of the 19 mm specimen from Station 407H is beset with three spinules corresponding to nos. 1, 3 & 4 in fig. 16. The carapace of this specimen is narrower than the one shown in fig. 21.

Alima stages of *Squilla interrupta-boops-quinquedentata* group (Figs. 17, 22 & 27)

Material examined: 3 specimens. Station 407H: 1 specimen (length 12 mm); Station 409D: 2 specimens (length 12-13 mm).

Descriptive remarks. - The 12 mm specimen from Station 407H is depicted in figs. 17 & 22. The lateral margin of the carapace has four

spinules; the first (no. 1) is visible in lateral and dorsal aspects. The raptorial appendage however is very similar in shape and proportions to the one shown in fig. 26. The examples measuring 12 & 13 mm from Station 409D each have a carapace corresponding in shape with figs. 17 e 22, but the raptorial claw shown in fig. 27 has only two spines on the upper part of the propodus which is narrow and elongate.

Alima stages of *Squilla latreillei-lata-fasciata* group (Figs. 18 & 23)

Material examined: 8 specimens. Station 407H: 4 specimens (length 9-13 mm); Station 408E: 2 specimens (length 9-10 mm); Station 409D: 1 specimen (length 14 mm); Station 409N: 1 specimen (length 8,5 mm).

Descriptive notes. - Figs. 18 & 23 are of the 14 mm specimen from Station 409D and the following remarks apply to this and to the examples of 9-10 mm from Station 408E. The carapace lateral margin has six spinules and no. 2 is visible in both lateral and dorsal aspects. The raptorial dactylus has two teeth on its inner margin and three proximal propodal spines similar to those shown in fig. 26. These specimens appear to correspond with the form described by Borradaile (1907, p. 215) as *Alima spinigera* which, according to Alikunhi (1951, p. 278), is the larva of *Squilla fasciata* de Haan. The four specimens, 9-13 mm, from Station 407H have a broader carapace than shown in fig. 23 and there are only five spines on the lateral margins; the one corresponding to no. 15 (shown in fig. 18) is absent in these specimens. The raptorial dactylus has one tooth.

Alima stages of *Harpiosquilla raphidea-harpax* group (Figs. 19 & 24)

Material examined: 7 specimens. Station 407H: 1 specimen (length 9,5 mm); Station 408E: 1 specimen (length 11 mm); Station 409D: 2 specimens (length 10 mm); Station 409N: 2 specimens (length 6,5-10 mm); Station 410B: 1 specimen (length 6 mm).

Descriptive remarks. - The specimen measuring 9,5 mm from Station 407H is depicted in figs. 19 & 24. It has 8 spinules on the ca-

rapace lateral margin; nos. 3 & 4 are sible in dorsal view as shown in fig. 24. There is considerable variation among the remaining specimens of spinule investiture as follows. The 11 mm specimen, Station 408E, and the 6,5 mm specimen, Station 409N, have the complement and arrangement of spinules as depicted in the figures 19 & 24. The 10 mm specimen from Station 409N has spinule 3 deflected ventrally and not visible from dorsal aspect; the 6 mm example from Station 410B has spinules nos. 2 & 7 missing but otherwise agrees with the figured specimen; one 10 mm specimen from Station 409D has spinules 1, 2 & 3 missing and in the other example from this station spinule no. 2 is absent. The raptorial claw of every specimen is similar in shape to the fig. 26.

Alikunhi (1952, p. 265) attributes Foxon's (1932, p. 381) material of *Alima pyramidalis* (Lanchester) to the adult species *Squilla raphidea* Fabricius. These particular specimens in the B.M. (N.H.) Collections do not quite correspond to Alikunhi's description and figures as most of them have spinule no. 5 (as shown in fig. 19) poorly developed and one or more teeth on the inner margin of the raptorial dactylus.

The specimens identified by Foxon (1939, p. 258) as atypical forms of *Alima multispinosa* (Claus) agree with Alikunhi's figures and description of late *S. raphidea* larvae.

Alima stages of *Squilla holochista-nepa-oratoria* group (Figs. 20, 20a & 25)

Material examined: 31 specimens. Station 400B: 2 specimens (length 32-34,5 mm); Station 406C: 2 specimens (length 14-23 mm); Station 407H: 3 specimens (length 11,5-20 mm); Station 408E: 12 specimens (length 14-30 mm); Station 409D: 12 specimens (length 14-29 mm).

Descriptive remarks. - The figured specimen, from Station 408E, measures 26,5 mm. It has 17 small spinules on the carapace lateral edge; the posterior ones are visible in lateral aspect as shown in fig. 20, but those situated anteriorly are directed inwardly and are therefore visible only in ventral view (fig. 20a). The raptorial propodus has 3

spines as depicted in fig. 26. The remaining specimens agree with the on figured except for an example of 14 mm from Station 409D. This has 12 spinules on the carapace edge, no. 9 being visible from dorsal aspect. The carapace is also slightly deeper and somewhat broader than as shown in the figured specimen. The raptorial propodus has only two well spaced spines on the inner proximal edge.

Alima gracillima Borradaile

Alima gracillima Borradaile, 1907, p. 22, figs. 5a-b; Gurney, 1946, p. 158.

Material examined: 1 specimen (length 17 mm), Station 409D.

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RIASSUNTO

Larve di Stomatopodi vennero raccolte nel Canale di Mozambico nel corso della crociera no. 8 del R./V. « A. Bruun » in occasione della Spedizione Internazionale nell'Oceano Indiano. Tale raccolta, che avvenne prevalentemente di notte ed in acque superficiali caratterizzate da « scattering » registrato al PGR, comprendeva settantasette esemplari. Sono stati identificati gli ultimi stadi larvali di *Odontodactylus brevirostris*, *Pseudosquilla ciliata*, *Lysiosquilla maculata* e *Acanthosquilla multifasciata*. Le rimanenti forme, riconosciute in prevalenza come stadio *Alima* di *Squilla*, vennero incluse nei cinque gruppi di specie descritti nella sistematica usata per la loro classificazione.

SUMMARY

Stomatopod larvae have been collected in the Mozambique Channel on cruise no. 8 of the R./V. « A. Bruun », during the International Indian Ocean Expedition. The collection, which took place mainly at night in surface waters where scattering was recorded by the PGR, included seventy-seven larvae. The late larval stages of *Odontodactylus brevirostris*, *Pseudosquilla ciliata*, *Lysiosquilla maculata* and *Acanthosquilla multifasciata* have been definitely identified. The remaining larvae have been referred mostly to *Alima* stages of *Squilla* and included into five species-groups, according to the systematic used for their classification.

Figs. 1-9: Late *Odonterichthus* stage of *Odontodactylus brevirostris* (Miers), 18 mm. *A. Bruun* Station 408E.

Fig. 1. Dorsal aspect of whole specimen excluding appendages - Fig. 2. Left lateral aspect of same - Fig. 3. Left antennule, dorsal aspect - Fig. 4. Right antenna, ventral aspect - Fig. 5. Fifth thoracic appendage from left side of body, ventral aspect. - Fig. 6. Left raptorial appendage, inner aspect. Lower inset shows merus and carpus from outer view; right inset shows terminal part of dactylus at higher magnification - Fig. 7. Sixth thoracic appendage from left side of body, ventral aspect. The right inset shows penultimate segment from dorsal aspect - Fig. 8. Right half of telson, dorsal aspect - Fig. 9. Left uropod, ventral aspect.

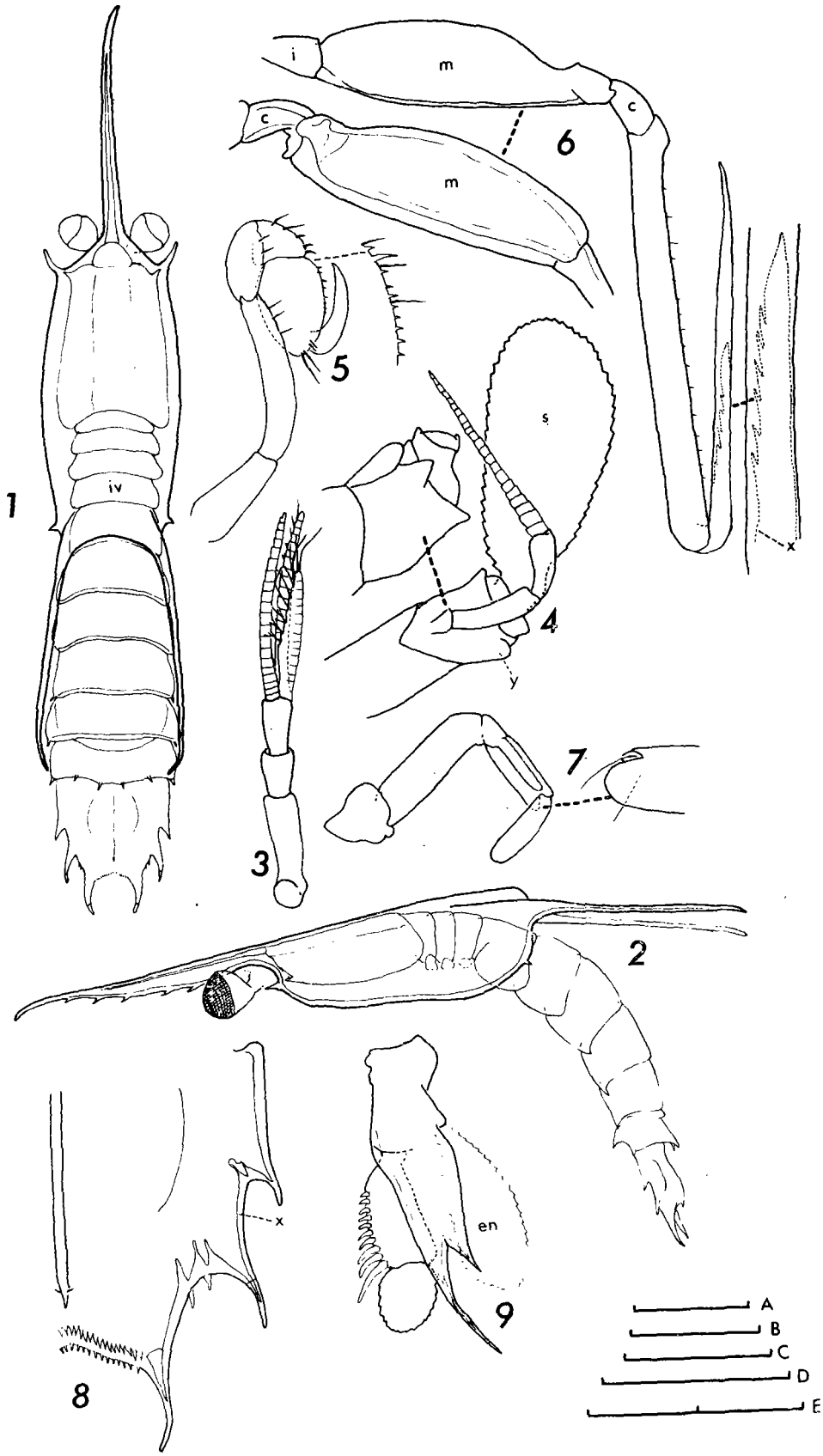
x = outline of telson and dactylus beneath larval skin; c = carpus; m = merus; y = incipient papilla.
Figs. 1, 2 & 6 to scale A = 4 mm; Fig. 5 to scale B = 0,5 mm; Figs. 4 & 9 to scale C = 2 mm; Fig. 3 to scale D = 2,5 mm; Figs. 7 & 8 to scale E = 2 mm.

Figs. 10-13: *Odontodactylus brevirostris* (Miers), ♀, 14 mm.
Oyster Banks, Manaar, Ceylon. B.M. (N.H.) Reg.no. 1906.10.27.5.
Fig. 10. Antenna from right side of body, ventral aspect (lower fig.); dorsal aspect (upper fig.) of protopodite. Fig. 11. Sixth thoracic appendage from left side of body, ventral aspect (lower inset shows dorsal aspect of propodus-dactylus articulation). Fig. 12. Left uropod, ventral aspect - Fig. 13. Right half of telson, dorsal aspect.
y = papilla

Figs. 14-15: Telson and left uropod of *Pseuderichthus* stage of *Pseudosquilla ciliata* (Fabricius).
Figs. 10 & 11 to scale 0,5 mm; Figs. 12-15 to scale 1 mm.

Figs. 16-27: Left lateral (16-20), ventral aspect (20a), dorsal aspects (21-25) and left raptorial appendages (26-27), respectively of the *Alima* stages assigned to the following « species-groups » of *Squilla*.

Figs. 16, 21 & 26. *Squilla hieroglyphica-gonypetes-woodmasoni*, 11,5 mm, *A. Bruun* Station 398D.
Figs. 17 & 22. *Squilla interrupta-boops-quinquedentata*, 12 mm, *A. Bruun* Station 407H.
Fig. 27. Same, 12 mm, *A. Bruun* Station 409D.
Figs. 18 & 23. *Squilla latreillei-lata-fasciata*, 14 mm, *A. Bruun* Station 409D.
Figs. 19 & 24. *Harpiosquilla raphidea-harpax*, 9,5 mm, *A. Bruun* Station 407H.
Figs. 20, 20a & 25. *Squilla holochista-nepa-oratoria*, 26,5 mm, *A. Bruun* Station 408E.
Scales. Total lengths of figured specimens are quoted above. Figs. 26 to scale A and 27 to scale E respectively. Each division = 1,0 mm.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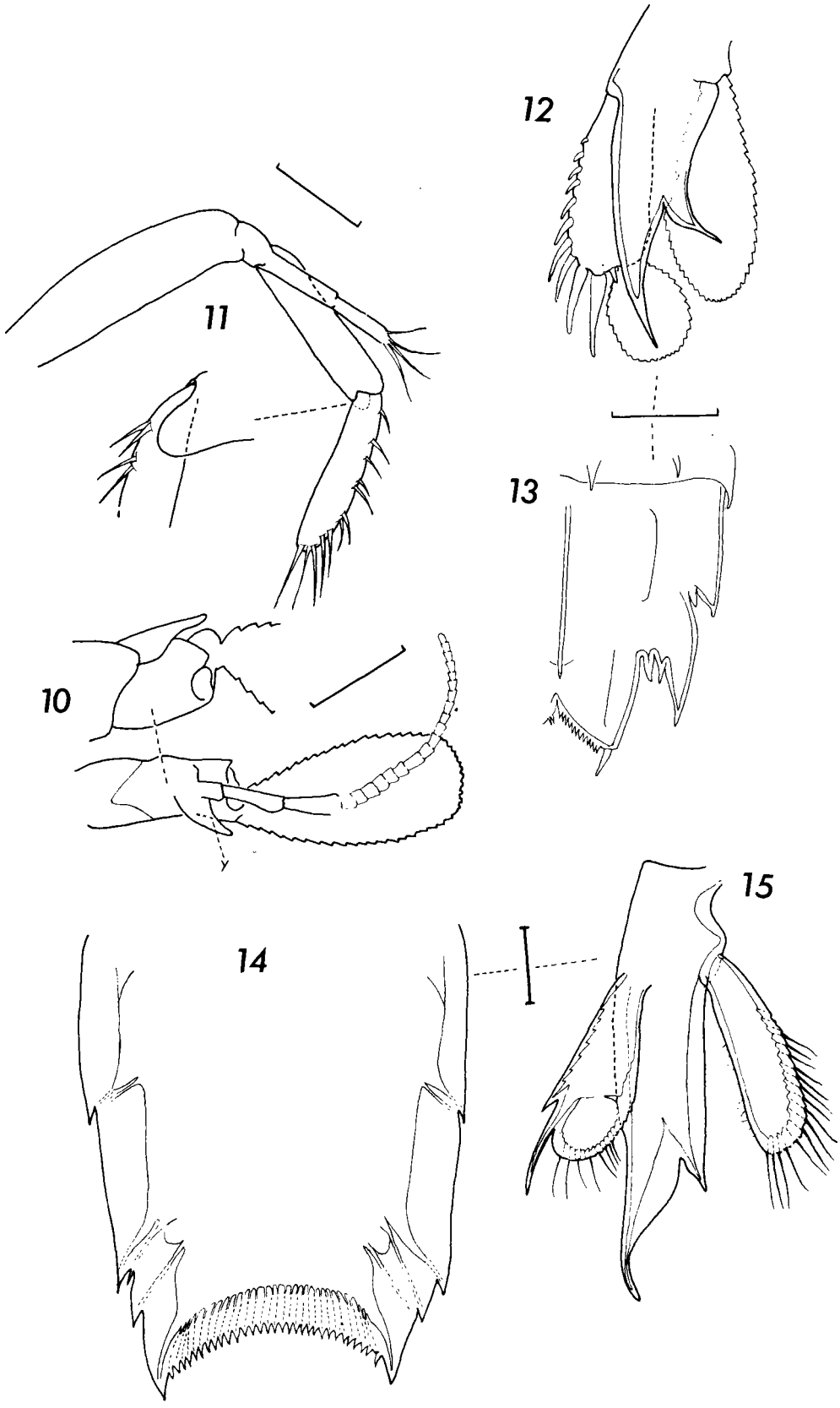
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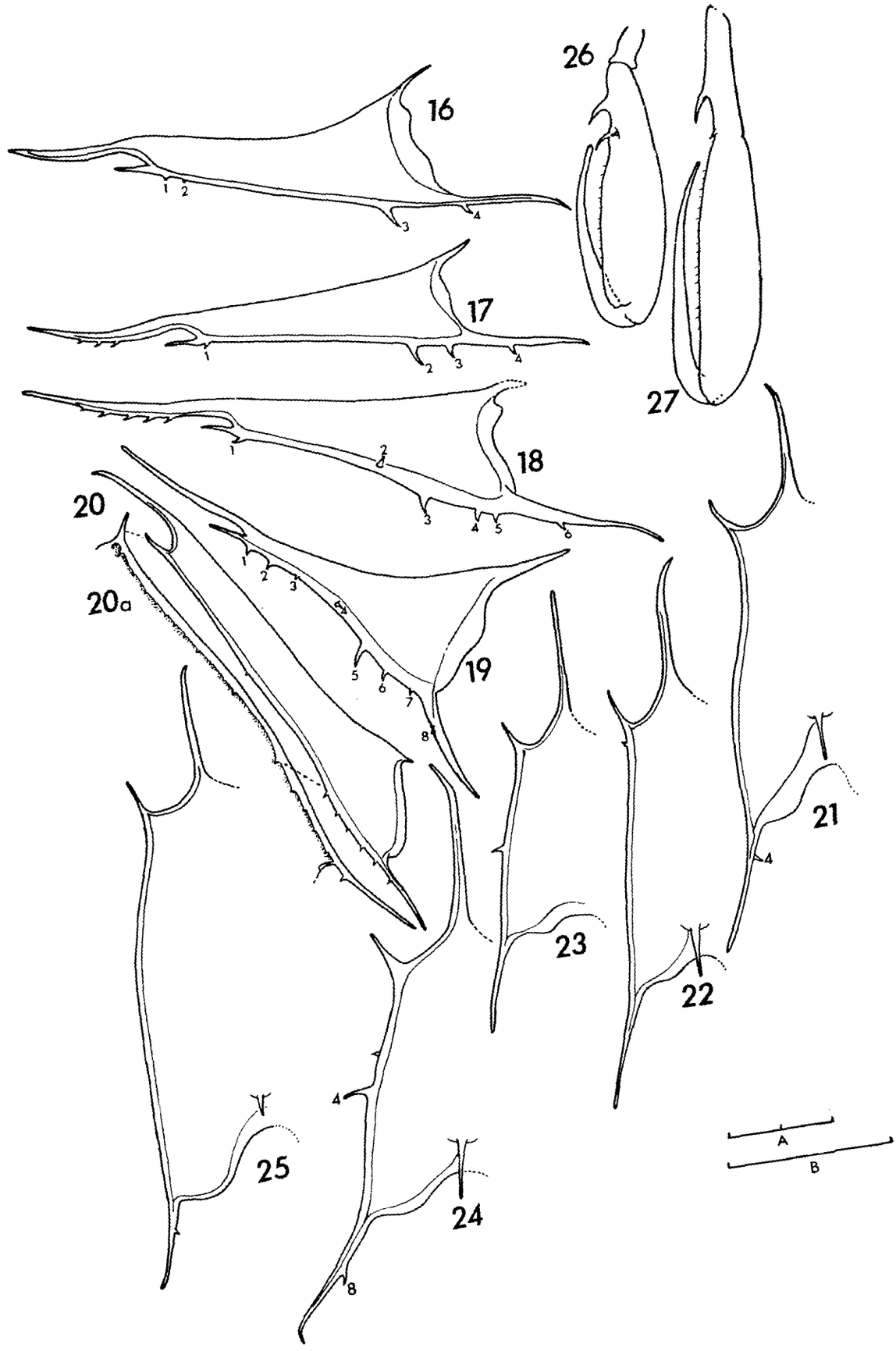
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The American Museum of Natural History, New York (USA)
Department of Living Invertebrates

New Marine Nemerteans from Nossi Be, Madagascar

Results of the Austrian Indo-Westpacific Expedition 1959/60

Part VIII

By

Ernst Kirsteuer[1]

With 4 figures

(Eingegangen am 6. April 1966)

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Introduction

The present paper continues the study of marine nemerteans from the Indian Ocean, which were collected during the Austrian Indo-Westpacific Expedition 1959/60. Although the primary objective of the expedition was the study of metazoan invertebrates and their distribution in the fringing coral reef of the Island of Tanikely (KIRSTEUER 1965), a few mud samples were taken by the author while at the Institut Recherche Scientifique a Madagascar, Station Oceanographique Nossi Be, in December 1959. Two dredge hauls were

made with an 18 × 40 cm steel frame dredge in the Bay of Ambanoro near the Oceanographic Station. The collecting station data are as follows: Nossi Be — South Coast, Bay of Ambanoro, 13° 24,4′ S, 48° 17,3′ E; mud mixed with sand in 20 m depth; December 29, 1959.

To obtain the nemerteans, the substrate was placed in glass jars with sea water and gently stirred. After the sediment had settled, the mud surface was examined and the worms removed. Of the nemerteans here recorded two species belong to the Palaeonemertini and one to the Hoplonemertini Monostilifera. The types are deposited in the private collection of the author.

Description

Hubrechtella sarodravayensis n. sp.

External Characters: The animal was found in a mucous tube covered with mud particles, which was about twice as long as the 30 mm long worm. The body is slender and the head is slightly constricted at the beginning of the mouth slit. The maximum body width, 1.2 mm, occurs in the middle of the gonad region. The color of the anterior one-third of the animal is a milky white, and posteriorly it gradually changes into a light orange with the white ovaries shining through. Coiling of the caudal portion of the body into a spiral as is typical for *Hubrechtella dubia* was not observed. After it was removed from its tube, the animal coiled like a cork screw, and constrictions were noted at short intervals throughout the gonad region (Fig. 1, A). Eyes could not be found either in the living animal or in crossections.

Anatomy: As in *Hubrechtella dubia*, the epidermis is high in the anterior part of the body where it is also rich in gland cells, but it decreases in height caudad to the foregut. Large elliptic, acidophile gland cells frequently attain the height of the epidermis, as in *H. dubia* (Hylbom 1957, p. 558). However, in the present species these gland cells are restricted to the anterior region of the animal. The homogenous-looking secretion from these cells sometimes penetrates the epidermis and extends over the surface of the body. Beneath the thin but distinct basement membrane there is a nervous layer in which, anterior to the brain, subepidermal gland cells are imbedded. The musculature of the body wall is composed of an outer circular and an inner longitudinal muscle layer, the circular layer always being much thinner than the longitudinal one. There is no differentiation in the longitudinal layer as found in *Hubrechtella dubia* (Hylbom 1957, p. 559). In the posterior foregut region a radial musculature occurs, which consists of fibers derived from the longitudinal fiber stratum.

The ganglia of the cerebral complex are of almost the same size. Inasmuch as the ganglia have a lateral position in the head, the cerebral commissures are of an equal length, but the ventral commissure is more than twice as thick as the dorsal commissure (Fig. 2, *dc, vc*). The lateral nerve cords originate from the caudal ends of the ventral ganglia, and a giant nerve fiber can be seen throughout their whole length. An upper dorsal nerve arises from the dorsal brain commissure and continues caudad to the beginning of the midgut. The

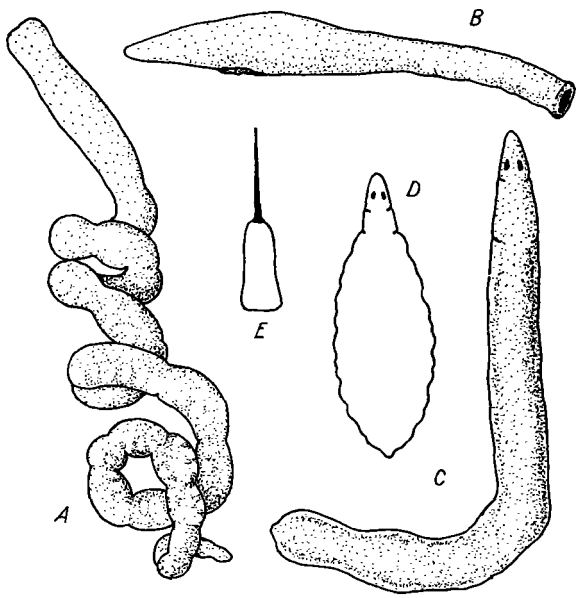

Fig. 1. A) *Hubrechtella sarodravayensis*, removed from its mucous tube. B) *Hubrechtella indica*, anterior part of the animal in lateral view. C) *Poseidonemertes gondwanae* in dorsal view. D) *Poseidonemertes gondwanae*, strongly contracted. E) *Poseidonemertes gondwanae*, proboscis stilet on its basis

posterior ends of the dorsal ganglia point dorsad, and from their caudo-ventral side, a rather strong nerve arises, which, shortly afterward, enters the cerebral sense organs (Fig. 2, *nco*). The latter are situated inside the lateral blood vessels, as is also the case in *Hubrechtella dubia.* The cerebral sense organs extend from the posterior end of the brain region to the beginning of the mouth, and they open over a short canal on the latero-dorsal body surface (Fig. 2, *co*).

The rhynchodaeum is short, but different from that in *Hubrechtella dubia,* because its lining epithelium is thin and contains only a few gland cells. The proboscis is inserted anterior to the brain by muscles coming from the dorsal and ventral side of the body wall. As in the other two species of the genus, there are no musclus turning inward on the lateral sides due to the presence of the large blood vessels. The musculature of the proboscis consists of an outer longitudinal and an inner circular fiber layer. The epithelium of the proboscis is high and rich in glands, but it does not contain the peculiar gland cells with a thread-like secretion which were observed in *Hubrechtella dubia.* The proboscis sheath extends approximately through 4/5 of the length of the body, and is therefore much longer than in *H. dubia.* Its wall is weakly developed and in the caudal half, it has irregularly scattered areas where the outer circular and inner longitudinal muscle layers are only one fiber thick.

The simple digestive system begins with the mouth slit immediately behind the brain. It is a uniform tube. The only difference between the foregut

and the midgut is the structure of the epithelium, which is high and folded in the foregut, becoming thinner and also much poorer in gland cells in the midgut. Midgut pouches occur in the gonad region. These pouches are caused by the ovaries, which are arranged in a lateral row on each side of the body.

The lateral blood vessels are extremely wide in the precerebral region (Fig. 2, *lv*). They unite in the tip of the head and anastomose ventrally behind the ventral brain commissure. Although they are still wide in the foregut area, they do not spread into a lacunar system as is the case in *H. dubia*. At the end

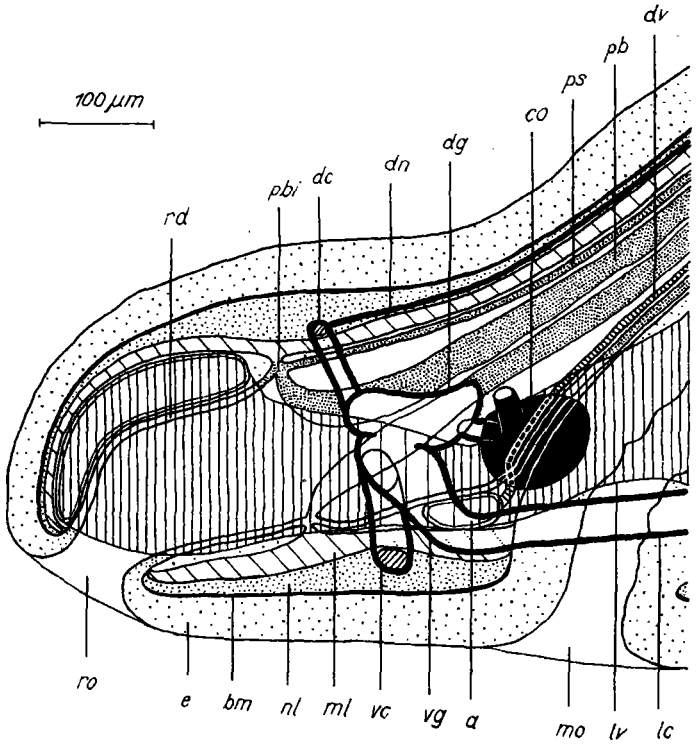

Fig. 2. *Hubrechtella sarodravayensis*. Reconstruction of the head region. (The organs of the left side of the animal are projected into the median-sagittal screen. For explanation of the abbreviations, see p. 122)

of the foregut, the vessels become narrow and continue in a latero-dorsal position. The dorsal blood vessel, which arises from the ventral anastomosis, penetrates the proboscis sheath and extends along the ventral inner side of it throughout the foregut and the most anterior part of the midgut region (Fig. 2, *dv*). No excretory organs could be found in the present species.

Discussion: *Hubrechtella sarodravayensis* n. sp. differs from *H. dubia* Bergendal (1902), the hitherto only recorded species of the genus, by the following characters: In the longitudinal muscle layer of the body wall, no central zigzag fiber layer occurs; the proboscis sheath extends over 4/5 of the body length; the dorsal nerve reaches caudad only to the end of the foregut (while in *H. dubia* it is as long as the proboscis sheath); the epithelium of the rhynchodaeum is thin and contains almost no gland cells; the peculiar gland cells

with a thread-like secretion are not be be found in the epithelium of the proboscis. Furthermore, there are differences in the body coloration, and in the behavior of the living animal.

Hubrechtella indica n. sp.

External characters: The body is slender and the present specimen, which lacks the caudal part of the body owing to autotomisation, measures 10 mm in length and 0.7 mm in maximum width. The maximum width occurs a short distance behind the mouth. The remainder of the body, posterior to the oral expansion, is 0.5 mm in width. Terminally, the head is rounded and dorso-ventrally flattened. The specimen is white, as is *Hubrechtella dubia.* However, the head region of this new species is not translucent as was observed by Hylbom (1957) and Brunberg (1964). In the present animal, the body is semitransparent caudal to the head, and in this area, the gray intestine shows through (Fig. 1, B). No eyes were found in the new species.

Anatomy: The internal organization is very similar to that in *Hubrechtella dubia* and *H. sarodravayensis.* The epidermis reaches its greatest height in the head and foregut regions, and in cross sections posterior to the brain, the epidermis is always thinner peripheral to the lateral nerve cords. The large acidophile gland cells which were observed in *H. dubia* and *H. sarodravayensis* do not occur in the epidermis of the present species. The basement membrane is thin, but can be easily observed throughout the body. A cutis-like stratum between the basement membrane and the circular muscle layer is present in front of the brain. This structure was first described in *H. dubia* by Hylbom (1957, p. 559), who also mentioned that no ducts lead away from the gland cells in this particular layer. In the present species, however, ducts coming from the gland cells can be seen penetrating the basement membrane.

The musculature of the body wall consists of an outer circular and an inner longitudinal layer. Both continue towards the anterior end of the body, but are very weak in this region. Posterior to the brain, the circular muscle layer remains thin, and only the longitudinal layer is well developed. The longitudinal fiber stratum does not have fibers running in a zigzag manner, as is the case in *Hubrechtella dubia* (Hylbom 1957, p. 559).

The dorsal ganglia of the cerebral complex are much larger than the ventral ganglia, but the diameters of the dorsal and ventral cerebral commissure are equal (Fig. 3). Both commissures are rather thick and situated at the anterior ends of the ganglia. The upper, single dorsal nerve arises from the dorsal commissure. A giant nerve fiber runs through the dorsal and ventral ganglia of each side, and it can be traced throughout the lateral nerve cords. The latter originate from the caudal ends of the ventral ganglia. The cerebral sense organs follow immediately behind the brain. They are innervated by a comparatively thick nerve coming from the dorso-median side of the dorsal ganglia and entering the organs dorsally (Fig. 3, *co, nco*). The cerebral organs are situated inside the lateral blood vessels and open latero-dorsally over a very short canal on

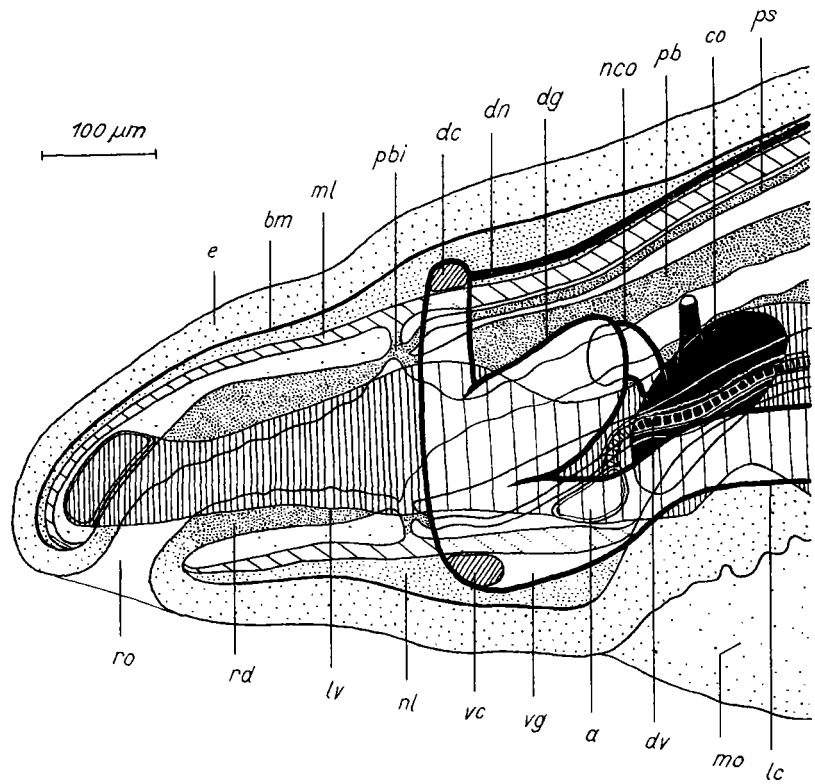

Fig. 3. *Hubrechtella indica*. Reconstruction of the head region. (The organs of the left side of the animal are projected into the median-sagittal screen. For explanation of the abbreviations, see p. 122.

the body surface. Both brain and cerebral sense organs are considerably larger in the present species than in *H. sarodravayensis* (Fig. 2. Fig. 3).

The epithelium of the rhynchodaeum is the same as in *H. dubia* (Hylbom 1957, Pl. 4, Fig. 25). It is high and provided with a large number of gland cells. The rhynchodaeum opens ventro-terminally near the tip of the head, and ends caudally with the insertion of the proboscis close to the anterior border of the brain. In this region, muscle fibers from the longitudinal muscle layer bend inward to form the attachment of the proboscis. Inasmuch as the lateral blood vessels are very voluminous, only fibers from the dorsal and ventral side extend to the proboscis. The musculature of the proboscis sheath is composed of an outer circular and an inner longitudinal layer, both of equal thickness. In the proboscis wall, there is an outer longitudinal and an inner circular muscle layer, a condition which agrees with that found in *H. dubia* and *H. sarodravayensis*. Gland cells of the type with a thread-like secretion, which were observed in the proboscis epithelium of *H. dubia* (Bergendal 1902, p. 10; Hylbom 1957, p. 559), are also present in the species described here.

The alimentary tract is simple. The mouth is situated behind the brain and begins a short distance anterior to the caudal ends of the cerebral sense organs. The foregut is short, and continues into the midgut without significant morphological change. Aside from the different histological nature of the epithelium in

these two portions of the gut (which is the same as in *H. dubia*), the only difference is that the epithelium of the foregut is much more folded than that of the midgut.

Beginning with a blood lacuna in the terminal part of the head, the circulatory system shows two lateral vessels, which have an anastomosis in the ventral brain region (Fig. 3, *lv, a*). Farther back, they widen greatly and surround the foregut from the lateral sides, but do not split up into a lacunar system as in *H. dubia*. Caudal from the foregut, the lateral vessels become narrow and continue in a lateral position. The dorsal vessel originates from the broad anastomosis of the lateral vessels. It enters the wall of the proboscis sheath where it is found between the muscle layers over the whole foregut region. After leaving the proboscis sheath wall, the dorsal vessel runs along the dorsal side of the intestine. It was not possible to locate the excretory organs, and since the caudal part of the animal is missing, no gonads were observed.

Discussion: As mentioned above, *Hubrechtella indica* n. sp. has many characters in common with *Hubrechtella dubia* and *H. sarodravayensis*, but it can be distinguished from both of these species by the following characters: the dorsal blood vessel in the foregut region which does not enter the rhynchocoelom, but which is situated instead in the wall of the proboscis sheath; no radial muscle fibers occur in *H. indica*; and no large, elliptic acidophile gland cells are found in the epidermis. Further differences between this new species and *Hubrechtella dubia* are: the absence of zigzag running fibers in the longitudinal muscle layer of the body wall, and the lack of a lacunar system around the foregut. Additional characteristics that serve to distinguish *H. indica* from *H. sarodravayensis* are as follows: the possession of high epithelium with many gland cells in the rynchodaeum, and gland cells with a thread-like secretion in the proboscis epithelium.

Poseidonemertes gondwanae n. g., n. sp.

External characters: The body is rather stout as shown in Fig. 1, C, and during normal gliding, the head is pointed whereas the posterior end is rounded. Situated near the front margin of the head are two comparatively large ocelli which can be seen easily in life. The mature worm measured 12 mm in length and 1.3 mm in maximum width. When disturbed, the animal showed a high contractability, and then only the head region retained its normal shape (Fig. 1, D). The body color is a whitish yellow, but the orange intestine, which can be seen throughout its whole length, influences the appearance very much, and gives the impression of an orange body-coloration. There are two pairs of inconspicuous, transverse cephalic furrows which do not meet dorsally. The first pair, into which the canals of the cerebral sense organs open, passes upward on the sides of the head at the level of the eyes, and the second pair of furrows is found near the posterior end of the brain (Fig. 1, C). Due to the coloration and the possession of only two eyes, this species shows a certain similarity to *Amphiporus bioculatus* as described initially by McIntosh (1873, p. 162, Pl. 8, Fig. 3), and later by Verrill (1892, p. 21, Pl. 34, Fig. 4), Bergendal (1903,

p. 107), Southern (1913, p. 15), Correa (1958, p. 450) and Brunberg (1964, p. 96, Pl. 3, Fig. 2). It can be distinguished, however, from the latter by means of the number and arrangement of the cephalic furrows. It is important to note that the existing data on the cephalic furrows in *Amphiporus bioculatus* do not agree, and considering also the differences in the internal organization as will be shown below, it seems that there is more than one species described under the name of *A. bioculatus*. Nevertheless, the cephalic furrows have not been described as they appear in the species under consideration here. McIntosh (1873) mentions one pair of furrows, but illustrates two pairs in text-fig. 10 and /Plate 8, Fig. 3; one time pointing with their dorsal angles together (><), the other time running in the opposite direction (<>). Verrill (1892) found only one pair running backward on the dorsal side of the head (V), and the same was reported by Correa (1958, Pl. 3, Fig. 19). Brunberg (1964) does not refer to the furrows in the text, but outlines a $\wedge$-shaped figure in Fig. 12, which seemingly is identical with the cephalic furrows. Joubin (1890) described a green variety of *Amphiporus bioculatus* with furrows arranged in the same way as in Brunberg's specimen.

Anatomy: The epidermis is moderately high and richly provided with glandular cells, particularly mucous glands which are more numerous in the postcerebral part of the animal than in the head region. The basement membrane is well developed throughout the body and reaches an average thickness of 5 μm, which is about one-third of the thickness of the circular muscle layer beneath it. The longitudinal muscle layer is massive and in the area of the brain it is divided into an outer and inner portion, separated by a distinct stratum of connective tissue. The circular and the outer component of the longitudinal muscle layer continue into the tip of the head. Only a few bundles of the outer longitudinal muscles bend inward and pass through the connective tissue to take part in composing the precerebral septum, which is split up into bundles of muscles, and consists mainly of fibers originating from the inner longitudinal muscle layer. The remaining fibers of the inner layer, which extend terminad over the septum, lie between the clusters of the rather large cephalic gland. The cephalic gland occupies nearly all of the space anterior to the brain, and it reaches backward to the level of the dorsal cerebral commissure (Fig. 4, *cg*). There are a few, but conspicuous, submuscular glands (which stain intensive red with acid fuchsin) imbedded in the scanty mesenchyme of the head.

The cerebral complex is situated immediately behind the septum. Dorsal and ventral ganglia are superficially marked in the posterior half of the brain, and they are connected by a thinner, dorsal, and a thicker, ventral, commissure (Fig. 4). The lateral nerve cords arise from the lateral sides of the ventral ganglia and show only one fibrous core in cross sections. The cerebral sense organs, which open over a rather long canal into the first cephalic furrows, are relatively small and simple, dorso-ventrally flattened, and their caudal ends lie near the anterior border of the ventral ganglia (Fig. 4, *co*).

The rhynchocoel extends to the extreme posterior end of the body. In the

wall of the proboscis sheath, the two muscle layers are clearly separated. The proboscis was everted before the animal was fixed even though it was narcotized by Urethanum. Unfortunately, the proboscis was lost, and the only morphological data was obtained from a squeeze preparation, that showed the amature, which consists of a slender central stilet resting on a pear-shaped basis (Fig. 1. E). The stilet is almost as long as the basis. Two pouches were observed containing one and three accessory stilets, respectively.

The rhynchodaeum, whose sphincter near the proboscis insertion is well developed, widens before it communicates with the exterior. The enlarged portion of the rhynchodaeum is lined with a thicker epithelium than the rest of the rhynchodaeum.

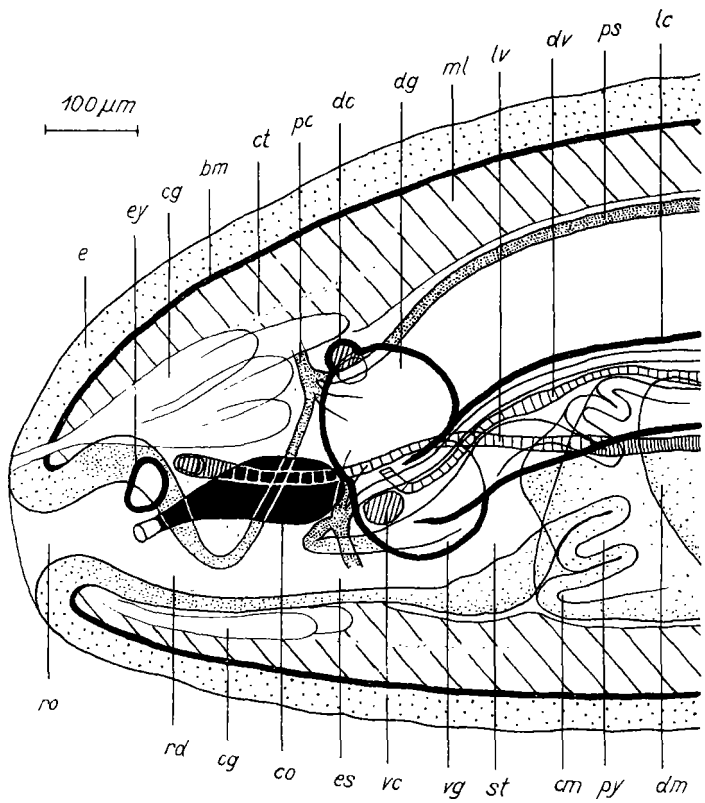

Fig. 4. *Poseidonemertes gondwanae*. Reconstruction of the anterior body region. (The organs of the left side of the animal are projected into the median-sagittal screen. For explanation of the abbreviations, see p. 122)

The foregut is differentiated into three regions. The esophagus, a short and narrow tube, opens into the rhynchodaeum a small distance in front of the brain and is followed caudad by a barrel-shaped and simple stomach. The pylorus overlaps the posterior end of the stomach as a collar, and it has two short lateral pouches (Fig. 4, *py*). This part of the foregut does not qualify as a pylorus in the morphological sense, and it obviously has also lost its original function since it opens widely into the intestine at almost the same level as the

stomach communicates with the midgut (Fig. 4, *st*), but on the basis of the histological structure of the wall, this portion of the foregut has to be considered a pylorus. From the midgut a short caecum projects forward under the stomach. It does not possess lateral diverticula or terminal pouches. The lateral diverticula of the midgut are wide (Fig. 4, *dm*), unbranched, and in the middle part of the body, they ascend laterally as high as the dorsal level of the proboscis sheath. A very weak, dorso-ventral musculature appears on both sides of the stomach and the midgut between the brain and the beginning of the gonads.

The two cephalic blood vessels unite terminally near the eyes, pass through the brain ring, and as there is no postcerebral anastomosis, they continue as lateral vessels. At the end of the gastric region, the lateral vessels reach their position ventral to the nerve cords. The dorsal vessel originates from the right lateral vessel, and does not enter the wall of the rhynchocoel (Fig. 4, *dv*).

The excretory apparatus is limited to a comparatively short region behind the cerebral ganglia and it does not extend farther back than the stomach. Nephridiopores were not discernible in the sections. The mature male specimen was collected in November. The testes are arranged on the lateral sides of the body and they alternate with the diverticula of the intestine. The gonad region occurs in the posterior two-thirds of the body.

Discussion: By the separation of the longitudinal muscle layer in the body wall, the present species shows similarity to *Nemertes* Johnston (1837), *Paranemertes* Coe (1901), *Paramphiporus* Kirsteuer (1965)[2] and the *Hastatus*-Group, which was isolated from *Amphiporus* by Friedrich (1955). However, a comparison of several anatomical features indicated that it is not congeneric, and therefore, it cannot be included in one of these genera. A distinct difference between the present species and *Nemertes,* as well as most species of *Paranemertes,* exists in the length of the proboscis sheath, which normally does not reach into the posterior half of the body. Only *Paranemertes biocellatus* Coe (1944) has a rhynchocoelom almost as long as its body. Inasmuch as the cerebral sense organs are situated far anterior to the brain, the intestinal caecum is provided with diverticula, and the proboscis has four or eight pouches of accessory stilets, one can easily distinguish *P. biocellatus* from the species described as new herein. On the other hand, the *Hastatus*-Group, which comprises *Amphiporus hastatus,* McIntosh (1873), *A. nebulosus* Coe (1901), *A. korschelti* Friedrich (1940) and *A. bioculatus* McIntosh (1873) is heterogenic due to the fact that the first three species have extracerebral blood vessels, and furthermore, in *A. korschelti* a precerebral septum is lacking. Therefore, only *Amphiporus bioculatus* can be compared with this new form, but, as already mentioned, *A. bioculatus* is not clearly defined. In the few papers dealing with the anatomy of *Amphiporus bioculatus,* different information is given concerning the configuration of the foregut and the intestine. Joubin (1890, p. 568) does

[2] *Paramphiporus albimarginatus* n. g., n. sp. Kirsteuer (1965): type species of *Paramphiporus* here designated: *P. albimarginatus* Kirsteuer (1965).

not describe a gastric caecum or pouches on the intestinal caecum. BERGENDAL (1903, p. 112) found pouches on the intestinal caecum but no caecum on the stomach. CORREA (1958, p. 451) reports both pouches on the caecum of the midgut, and a ventral caecum of the stomach.

The blood vessel system, especially the dorsal vessel in its relation to the rhynchocoel, also indicates that we have undoubtedly at least two different species under the name *Amphiporus bioculatus*. JOUBIN (1890) did not give any account of the circulatory system in his description (and in the cross section in Pl. 31, Fig. 5, only the position of the lateral vessels ventral to the nerve cords is shown; the absence of a dorsal vessel in this drawing might be a mistake), but BERGENDAL (1903, p. 113) points out that in his Scandinavian specimens, the dorsal vessel enters the muscle wall of the rhynchocoel in the caudal brain region, thus creating a situation contrary to the observations made by CORREA (1958, p. 451) on Brazilian specimens, where the dorsal vessel does not pass into the proboscis sheath.

As CORREA's species is not considered to be identical with *Amphiporus bioculatus* MCINTOSH sensu BERGENDAL and also is not referable to any of the existing genera of the Monostilifera with a divided longitudinal muscle layer of the body wall, it is here proposed to place it in a new genus, *Correanemertes* n. g., with *Correanemertes* (*Amphiporus*) *bioculatus* (CORREA 1958) as the type species. The diagnosis for *Correanemertes* is as follows: Body shape resembling that of smaller *Amphiporus* species; cerebral sense organs small, simple and far anterior to the brain. In the brain region the longitudinal muscle layer of the body wall is divided into two portions. The precerebral septum is closed dorsally, ventrally split up, and its muscles originate from the inner longitudinal muscle layer only. The proboscis sheath is as long as the body, and it does not possess appendages. The foregut has differentiations, and the intestinal caecum possesses pouches. Dorso-ventral muscles are present. The lateral nerve cords have one fibrous core. The circulatory system is simple, lacking extracerebral vessels.

More information on the anatomy of the European and North American representatives of *Amphiporus bioculatus* is necessary to decide whether or not they should be included in the genus *Paramphiporus*.

The species here described differs from *Amphiporus bioculatus* MCINTOSH sensu BERGENDAL in that the dorsal blood vessel does not enter the proboscis sheath, and the caecum of the intestine is not provided with pouches. The latter feature also distinguishes it from *Correanemertes bioculatus*, and further differences between these two species are given in the configuration of the foregut and the position of the cerebral sense organs. The split precerebral septum, which is composed of fibers from both longitudinal muscle layers is an important separating characteristic not only for *Amphiporus bioculatus* and *Correanemertes bioculatus* but also for *Paramphiporus*, which, furthermore, has a normal and simple foregut, and pouches on the caecum of the intestine.

The preceding discussion shows that it was necessary to constitute a new genus for the present species. The diagnosis for *Poseidonemertes* n. g. is as fol-

lows: Body rather stout and capable of great contraction, head not demarcated from the body. Cerebral sense organs small, simple, and in front of the brain. Longitudinal muscle layer of the body wall divided into two portions in the area of the brain. Precerebral septum split and composed of muscles from the outer and inner longitudinal muscle layer. Proboscis sheath as long as the body and without appendages. Dorso-ventral muscles present. Lateral nerve cords with one fibrous core. Circulatory system simple (without extracerebral vessels).

The type species of this genus is *Poseidonemertes gondwanae* n. sp.

Zusammenfassung

Die vorliegende Schrift behandelt drei neue Nemertinen-Arten, welche vom Verfasser im Verlaufe der Österreichischen Indo-Westpazifik Expedition 1959/60 auf Nossi Be, Madagaskar, im Dezember 1959 aufgesammelt wurden. Der Fundort lag an der Südküste von Nossi Be in der Bucht von Ambanoro in der Nähe des Ozeanographischen Instituts. Das behandelte Tiermaterial entstammt Sedimentproben aus 20 m Tiefe. Das Substrat, sandvermischter Schlamm, wurde mit Seewasser aufgerührt und in Glaswannen abgestellt. Nach einigen Stunden wurde die Schlammoberfläche auf Nemertinen abgesucht. Von den gefundenen Arten erwiesen sich zwei als Vertreter der Palaeonemertini, es sind dies *Hubrechtella sarodravayensis* n. sp. und *Hubrechtella indica* n. sp. Die dritte Art, *Poseidonemertes gondwanae* n. g., n. sp. gehört zu den Hoplonemertini Monostilifera.

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Abbreviations

a	anastomosis of lateral blood vessels	*lv*	lateral blood vessel
bm	basement membrane	*ml*	muscle layers
cg	cephalic gland	*mo*	mouth opening
cm	caecum of midgut	*nco*	nerve to cerebral sense organ
co	cerebral sense organ	*nl*	nervous layer
ct	connective tissue	*pb*	proboscis
dc	dorsal cerebral commissure	*pbi*	proboscis insertion
dg	dorsal ganglion	*pc*	precerebral septum
dm	diverticulum of midgut	*ps*	proboscis sheath
dn	dorsal nerve	*py*	pylorus
dv	dorsal blood vessel	*rd*	rhynchodaeum
e	epidermis	*ro*	rhynchodaeum opening
es	esophagus	*st*	stomach
ey	eye	*vc*	ventral cerebral commissure
lc	lateral nerve cord	*vg*	ventral ganglion

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DISTRIBUTION OF YEASTS IN THE INDIAN OCEAN[1]

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ABSTRACT

Yeasts and molds were collected from 16 stations during Cruise 3 of the R/V ANTON BRUUN for the U. S. Program in Biology, International Indian Ocean Expedition. The transect investigated extended along the 60°E meridian from 11°56'N to 40°54'S at depths of 0-2,000 meters. Population densities of yeasts ranged from 0-513 cells/liter, with greatest concentrations in the Somali Current and Antarctic Intermediate waters. A total of 25 species of yeasts were isolated, 19 of which occurred infrequently, *i.e.*, in less than 6 per cent of the positive samples. The commonly isolated species were classified ecologically into three arbitrary groups: (1) cosmopolitan species (*Rhodotorula rubra* and *Candida atmosphaerica*) present in all water masses studied; (2) widely distributed species (*C. polymorpha* and *Rh. glutinis*) absent from Red Sea water; (3) regionally distributed organisms obtained either from waters north of 22°S (*Sporobolomyces hispanicus* and *Sp. odorus*) or from southern waters (*Candida* sp. I and *Rh. crocea*). The relationship of yeast distribution to hydrographic and biological conditions is discussed. The incidence of molds appeared to be partially dependent on the proximity of terrigenous materials.

INTRODUCTION

Yeast species of the genera *Candida*, *Cryptococcus*, *Rhodotorula*, and *Debaryomyces* have been reported (Bhat & Kachwalla, 1955; Kriss, 1963; Fell & van Uden, 1963) in the sea from surface waters to the bottom from tens to thousands of cells per liter. The present study examines some of the environmental conditions in the Indian Ocean associated with the distributions of these species and their fluctuations in population densities.

METHODS AND MATERIALS

Samples were collected at 16 stations (Fig. 1) in the Indian Ocean during Cruise 3 of the R/V ANTON BRUUN for the U. S. Program in Biology of the International Indian Ocean Expedition. Two-liter quantities of water were collected aseptically (at selected depths from the surface to 2,000 meters) with Niskin Bio-samplers (Niskin, 1962). The latter were placed on the hydrographic cast in tandem with Nansen bottles used for obtaining hydrographic data. Oxygen, temperature, and salinity were determined by the shipboard scientific staff. The physical data were compiled and the location of water masses estimated by the definitions of Sverdrup *et al.* (1942).

Yeasts also were obtained from fish caught in surface and mid-water

[1] Contribution No. 783 from the Institute of Marine Science, University of Miami.

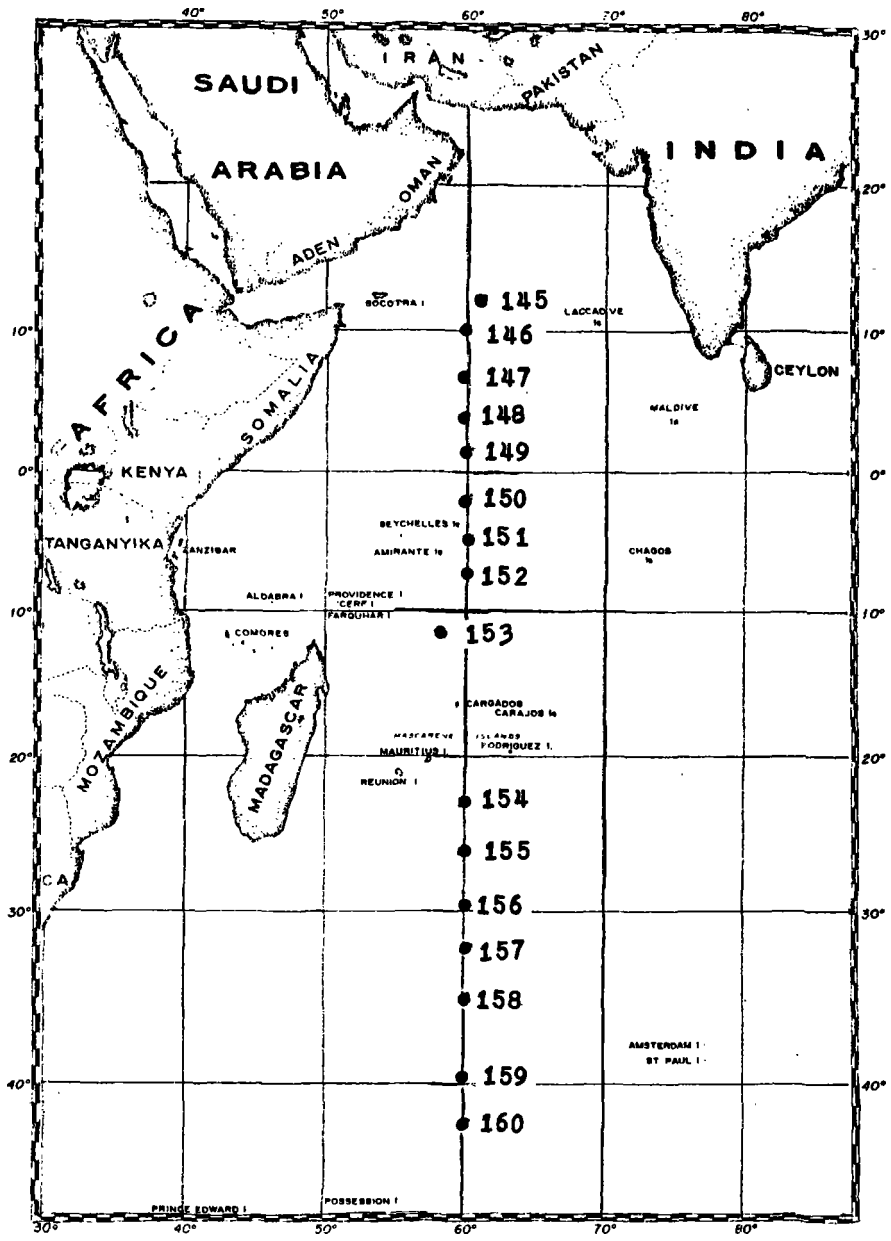


FIGURE 1. Station locations of Cruise 3, R/V ANTON BRUUN, Aug. 5-Sept. 20, 1963.

collections (Table 2) and from fresh and inshore marine waters at the island of Mauritius, U. K.

Methods of yeast isolation and enumeration followed those described by Fell & van Uden (1963). Yeast systematics employed recommendations of Lodder & Kreger-van Rij (1952) and Wickerham (1951). The molds (Deuteromycetes) present were collected and counted by these methods.

TABLE 1
SPECIES OF YEASTS ISOLATED FROM THE INDIAN OCEAN

Species	Number of Samples in Which Species Occurred	Frequency of Occurrence*
Candida Berkhout		
C. atmosphaerica Santa Maria 1959**	55	47%
Candida sp. I (nov. sp.)	33	28
C. polymorpha Ohara et Nonomura 1954	27	23
C. tenuis Diddens et Lodder 1942	7	6
C. parapsilosis (Ashf.) Langeron et Talice 1928	4	3
C. guilliermondii (Cast.) Langeron et Guerra 1912	2	2
C. mycoderma (Reess) Lodder et Kreger-van Rij 1870	2	2
C. tropicalis (Cast.) Berkhout 1910	2	2
C. albicans (Robin) Berkhout 1853	1	1
C. rugosa (Anderson) Diddens et Lodder 1917	1	1
Candida sp.	1	1
Cryptococcus Kutzing *emend.* Vuillemin		
Cr. albidus (Saito) Skinner 1922	1	1
Rhodotorula Harrison		
Rh. rubra (Demme) Lodder 1889	54	46
Rh. glutinis (Fres.) Harrison 1852	16	14
Rh. crocea Shifrine et Phaff 1956	5	4
Rh. graminis di Menna 1958	2	2
Rh. pallida Lodder 1934	1	1
Sporobolomyces Kluyver et van Niel		
Sp. odorus Derx 1930	33	28
Sp. hispanicus Palaez et Ramirez 1956	2	2
Sterigmatomyces Fell		
St. halophilus Fell 1966	1	1
St. halophilus var. *indicus* Fell 1966	2	2
Debaryomyces Lodder et Kreger-van Rij		
D. hansenii (Zopf) Lodder et Kreger-van Rij 1889	8	7
Hanseniaspora Zikes		
H. uvarum (Niehaus) Chehata, Mrak et Phaff 1932	1	1
Pichia Hansen		
P. fermentans Lodder 1932	1	1
Saccharomyces (Meyer) Reess		
S. cerevisiae Hansen 1883	5	4

* Frequency (%) in water samples with yeasts present.
** *C. atmosphaerica* is identical to *Trichosporon diddensii* Mrak, Phaff, et Williams, 1952. As Arthrospores have not been found, the species will be transferred to the genus *Candida* (Fell & Meyers, Mycopath. et Mycol. Apply, in press).

RESULTS

Hydrographic Conditions.—The southwest monsoon, which influenced the sampled region during the study period, caused upwelling along the Somali

TABLE 2
YEASTS ISOLATED FROM FISH

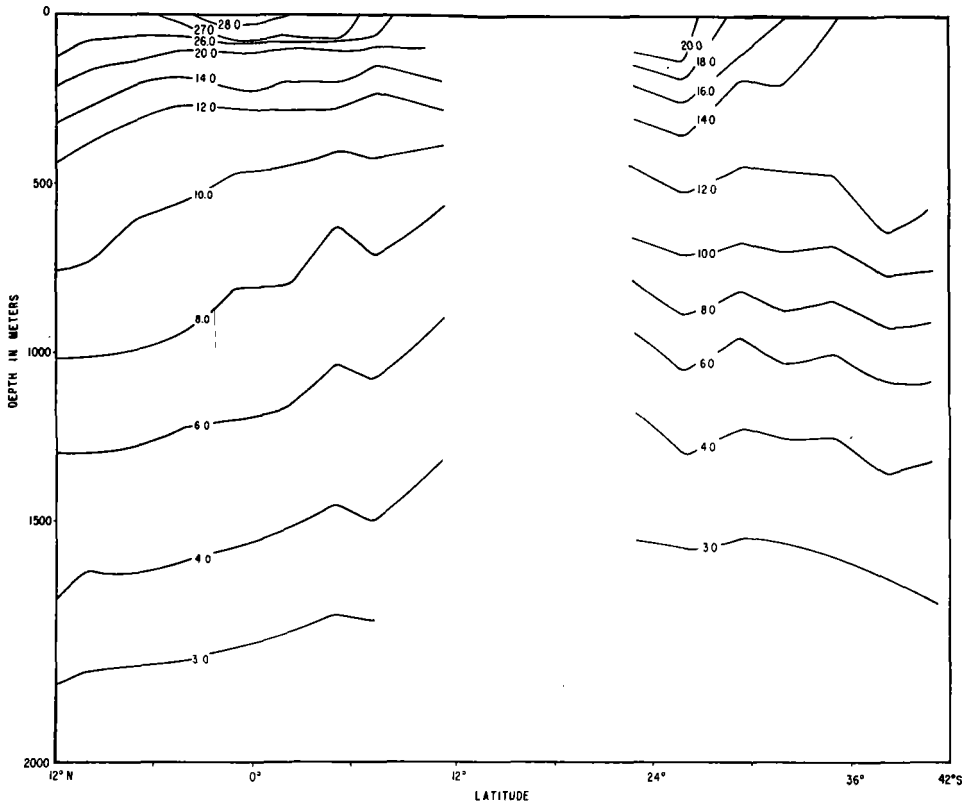
Species of Fish	Sample Examined	Collection Location	Yeasts Present
Pterolamiops longimanus	Intestine	Sta. 147-surface	*C. atmosphaerica*
Coryphaena hippuris (3 specimens)	Intestine	Sta. 148-surface	none
Cypseluras sp.	Intestine	Sta. 151-surface	none
Scopelenges alcocki	Intestine	Sta. 151-150-685 m	*C. guilliermondii*, *C. tenuis*
S. alcocki		Sta. 151-150-685 m	none
C. hippuris	Intestine	Sta. 151-surface	*C. tenuis*
	Nasal cavity		*C. viswanathii*
	Gill		*C. viswanathii*
Lampanyctus sp.	Intestine	Sta. 158-150-680 m	*C. guilliermondii*

coast and consequently an increase in productivity. The surface currents along this coast flow northward and veer east at Socotra to the Indian coast (U. S. Hydrographic Office, 1960), also influencing offshore productivity.

The waters in the northern stations (11°56′N-11°39′S) consist of three water masses (Fig. 2): the high-salinity Arabian Sea Water in the upper layers; the high salinity, low oxygen, Red Sea Water in the limits defined by temperature T = 5-12°C, salinity S = 35.0-35.4‰; and the Indian Ocean Equatorial Water below and south of the Red Sea Water. The equatorial water is formed *in situ* from mixing of adjacent water masses. The southern stations (22°58′S-40°54′S) consist of three distinguishable water masses (Fig. 2); the Indian Central Water, T = 7-16°C, S = 35.5-34.6‰; the Antarctic Intermediate Water T = 3-7°C, S = 34.46-34.6‰; and the Upper Deep Water below the Antarctic Intermediate Water.

Yeast Distributions.—A total of 179 water samples were taken, of which 117 or 65 per cent were positive for yeasts. Concentrations (Fig. 3) ranged from 1-513 cells/liter. Dense populations were found at Sta. 145 in the Somali Current, surface waters of Sta. 152, 153, 156, and 157, and in Antarctic Intermediate waters. Red Sea, Arabian Sea, Equatorial and Central waters were noticeably low in yeasts.

Of the twenty-five species isolated (Table 1), 19 occurred infrequently, *i.e.*, in less than 6 per cent of the positive samples. The most commonly isolated species can be classified ecologically into three groups: (1) Present in all the water masses studied: *Rh. rubra* (Fig. 5) and *C. atmosphaerica* (Fig. 6); (2) Widely distributed but apparently absent from Red Sea water: *C. polymorpha* (Fig. 7) and *Rh. glutinis* (Fig. 9); and (3) Regionally


0
500
1000
1500
2000
DEPTH IN METERS
28.0
27.0
26.0
20.0
14.0
12.0
10.0
8.0
6.0
4.0
3.0
20.0
18.0
16.0
14.0
12.0
10.0
8.0
6.0
4.0
3.0
12° N
0°
12°
24°
36°
42°S
LATITUDE

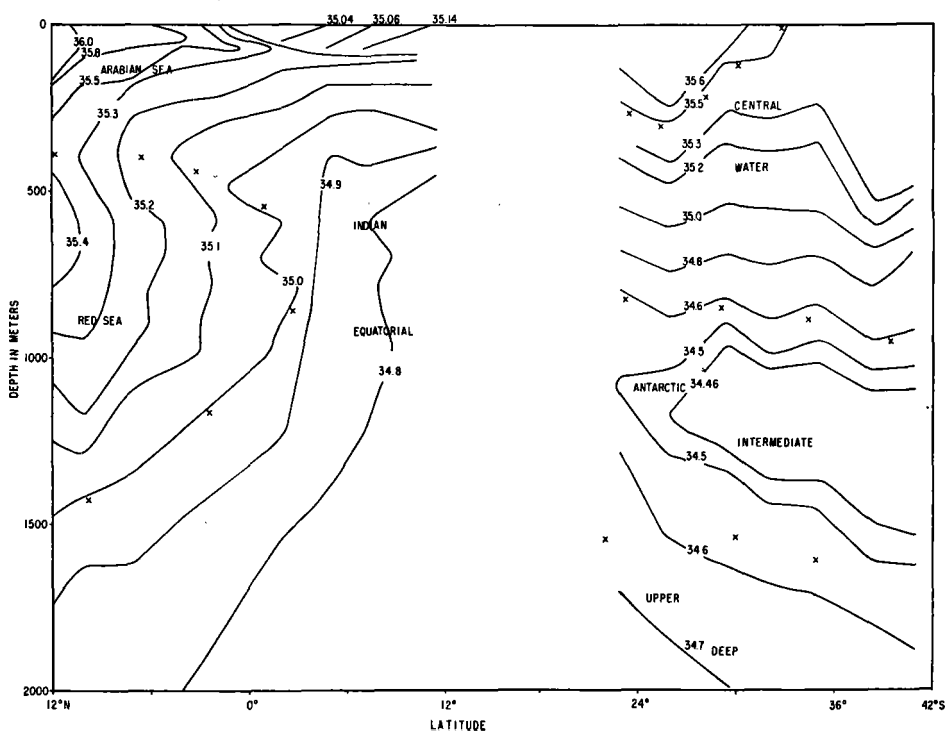

0
500
1000
1500
2000
DEPTH IN METERS
35.04
35.06
35.14
36.0
35.8
ARABIAN SEA
35.5
35.3
35.2
35.4
35.1
35.0
34.9
INDIAN
RED SEA
EQUATORIAL
34.8
35.6
35.5
CENTRAL
35.3
35.2
WATER
35.0
34.8
34.6
34.5
ANTARCTIC 34.46
INTERMEDIATE
34.5
34.6
UPPER
34.7 DEEP
12°N
0°
12°
24°
36°
42°S
LATITUDE

TABLE 3

YEASTS ISOLATED AT THE ISLAND OF MAURITIUS, U. K.

Fresh Water (2)*	Estuarian (3)	Marine (4)
H. uvarum (1)†	*C. rhagii* (2)	*Cr. laurentii* (1)
C. rhagii (1)	*H. uvarum* (2)	*C. guilliermondii* (1)
Rh. sp. (1)	*Rh. glutinis* (1)	*C. polymorpha* (1)
	Cr. albidus (1)	*Hansenula anomala* (1)
	Cr. laurentii (1)	*C. atmosphaerica* (1)
	Rh. rubra (1)	*D. hansenii* (1)
	Rh. glutinis var. *infirmo-minuta* (1)	
	Rh. graminis (1)	

* Number of stations examined.
† Number of stations with the particular species present.

distributed in northern waters, *Sp. hispanicus*, *Sp. odorus* (Fig. 4), and *C. tenuis* (Fig. 8) or in southern waters, *Candida* sp. I (Fig. 4) and *Rh. crocea* (Fig. 9).

Four species of yeasts, *C. atmosphaerica*, *C. guilliermondii*, *C. tenuis*, and *C. viswanathii*, were isolated from four of the nine fish examined from surface and mid-water catches (Table 2).

Twelve species (Table 3) were isolated in inshore and fresh waters of Mauritius. Four of these, *C. rhagii*, *Cr. albidus*, *Cr. laurentii*, and *H. anomala*, were not found offshore, while two abundant offshore organisms, *C. polymorpha* and *C. atmosphaerica*, were found at Mauritius marine stations but not in estuarine or fresh waters.

Molds were isolated in 30 per cent of the samples in concentrations of from 1-26 cells/liter (Fig. 11). Highest numbers occurred at Sta. 145, upper waters of Sta. 151, 152, 153, 155, and at other scattered locations.

Yeast Identifications.—The characteristics of the species from the Indian Ocean were generally the same as presented by Lodder & Kreger-van Rij (1952) and/or the original descriptions, with the exception of two unidentified species of *Candida*, designated "*Candida* sp. I" and "*Candida* sp. II."

Candida sp. I ferments dextrose and assimilates galactose, cellobiose, salicin, D-xylose, L- and D-arabinose, D-ribose, i-erythritol, adonitol, D-mannitol, D-sorbitol and ethanol, with negative to latent reactions on

←

FIGURE 2. Distribution of temperature °C, salinity ‰, and estimated location of water masses (x x x) in the Indian Ocean as observed on Cruise 3, R/V ANTON BRUUN (60°E Lon.).

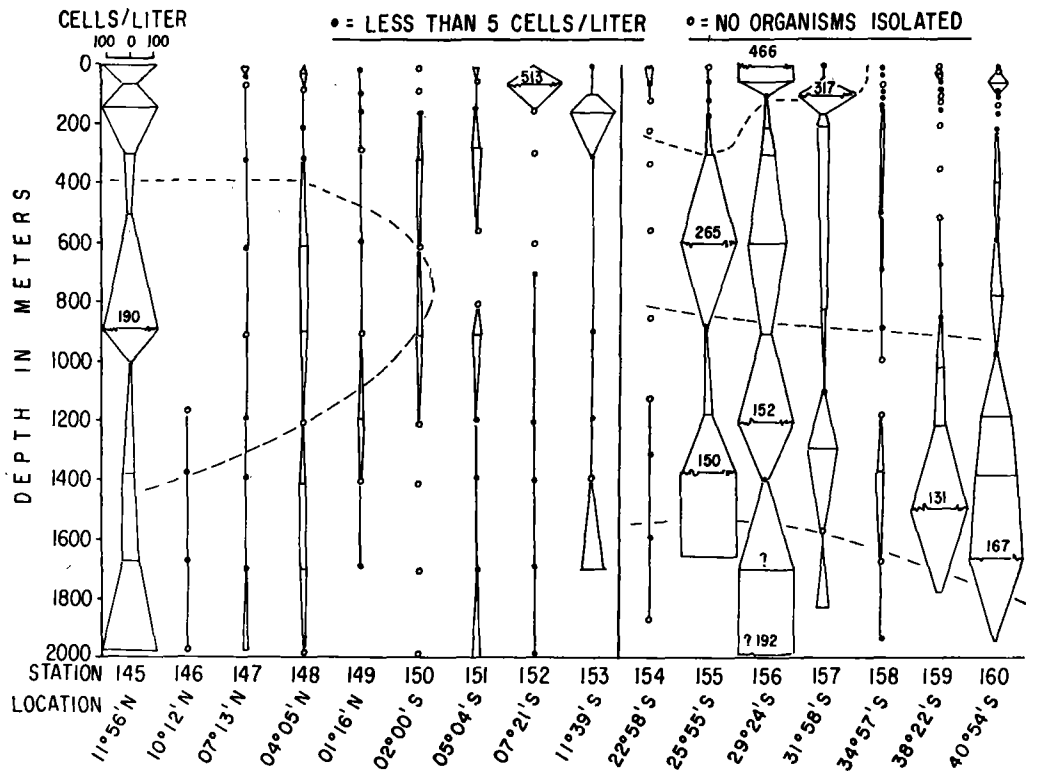


FIGURE 3. Quantitative distribution of yeasts in the Indian Ocean (60°E) Aug. 5-Sept. 20, 1963. ? = exact sampling depth unknown due to faulty samplers. ——— water mass distribution (see Figure 2).

maltose and sucrose. Carbon compounds not assimilated were lactose, melibiose, raffinose, melezitose, trehalose, and inositol. KNO_3 was not assimilated. Urea is hydrolyzed. *Candida* sp. I is similar to a group of candidas, *i.e.*, *C. rugosa*, *C. ingens*, *C. krusei*, *C. lipolytica*, *C. mesenterica*, *C. norvegensis*, *C. mycoderma*, and *C. rugosa*, that do not assimilate lactose, trehalose, or KNO_3. *Candida* sp. I also is similar to *C. atmosphaerica* with the exception that the latter assimilates trehalose and does not hydrolyze urea. A complete description of *Candida* sp. I is being prepared for publication (Fell & Meyer, Mss.).

Candida sp. II ferments dextrose and assimilates maltose, sucrose, cellobiose, trehalose, melezitose, mannitol, sorbitol, and salicin, but not galactose, D-xylose, lactose, melebiose, raffinose, L- or D-arabinose, D-ribose, L-rhamnose, dulcitol, inositol, or KNO_3. This species is similar to *C. solani* Lodder & Kreger-van Rij 1952 except for the abilities to assimilate xylose and sorbitol.

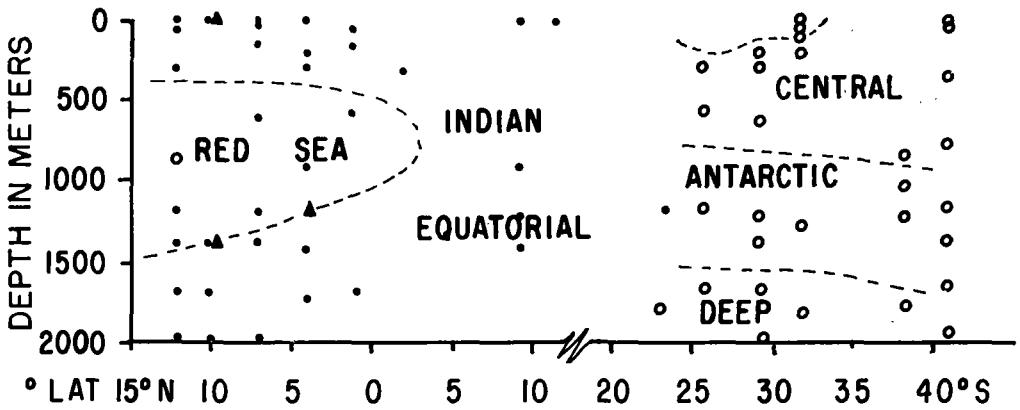


FIGURE 4. Distribution of *Sporobolomyces hispanicus* (▲), *Sp. odorus* (●), and *Candida* sp. I (○) in the Indian Ocean.

DISCUSSION

Distribution of Yeasts.—Kriss (1960, 1963) found heterotrophic bacteria in surface and deep waters of the Indian Ocean in quantities of hundreds and thousands of cells/50 ml and characterized water masses and their circulation on these data. He stated: "Antarctic waters are characterized by low concentrations of heterotrophs, whereas the equatorial-tropical waters are characterized by high concentrations of these organisms." However, Kriss collected his samples with non-sterile containers, *viz.* Nansen bottles, a technique severely questioned by Sorokin (1964). The latter worker, using aseptic samplers, demonstrated that Nansen bottles were heavily contaminated, and data thus obtained could lead to erroneous conclusions. Separate tests in our laboratory (Fell, unpublished) and by Willingham & Buck (1965) have shown that van Dorn samplers also may be contaminated by filamentous fungi and yeasts. Sorokin concluded that heterotrophic bacteria in the central Pacific were most abundant in the

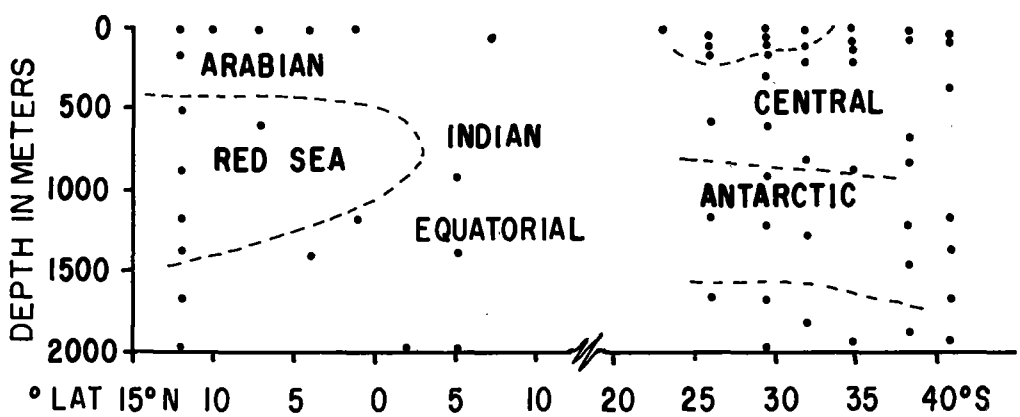


FIGURE 5. Distribution of *Rhodotorula rubra* in the Indian Ocean.

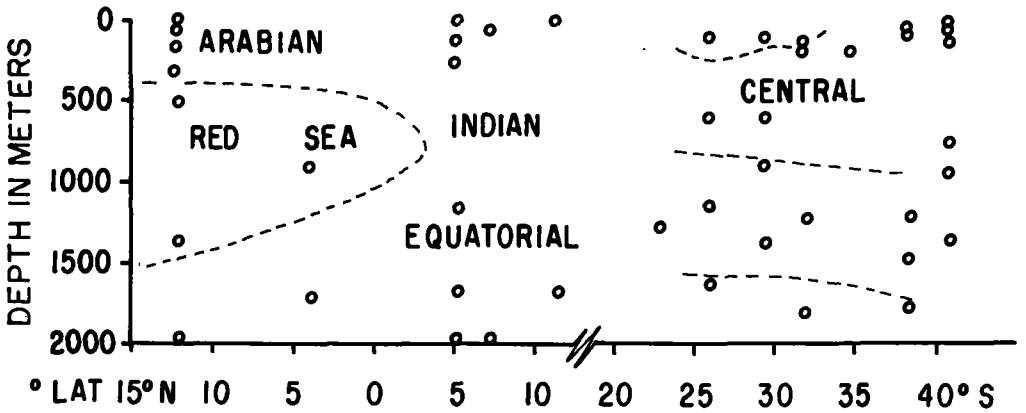


FIGURE 6. Distribution of *Candida atmosphaerica* in the Indian Ocean.

photosynthetic zone where assimilable organics were concentrated and were relatively sparse in deep-sea waters due to a lack of available organics. In contrast, the distribution of yeasts in the Indian Ocean was somewhat different from that found by Kriss or Sorokin for bacterial populations.

Yeasts were abundant at the northernmost station, Sta. 145, but decreased at Sta. 146 and 147 (Fig. 3). The former dense populations possibly arise in the rich Somali Current that carries yeasts and/or nutrients offshore, while the reduction in numbers of yeast suggests a southern boundary of the Somali influence near 12°N. Difficulties prevented our obtaining data in the upper waters at Sta. 146; thus, an extension of the Somali Current populations into those waters was not established.

Yeasts were few in number in the Red Sea, Arabian Sea, and in Equatorial waters, but were concentrated in Antarctic Intermediate waters. The latter intrusion arises from the highly productive Antarctic surface waters that presumably carry yeasts and assimilable nutrients into deeper waters. This suggests that Antarctic waters may contain dense concentrations of

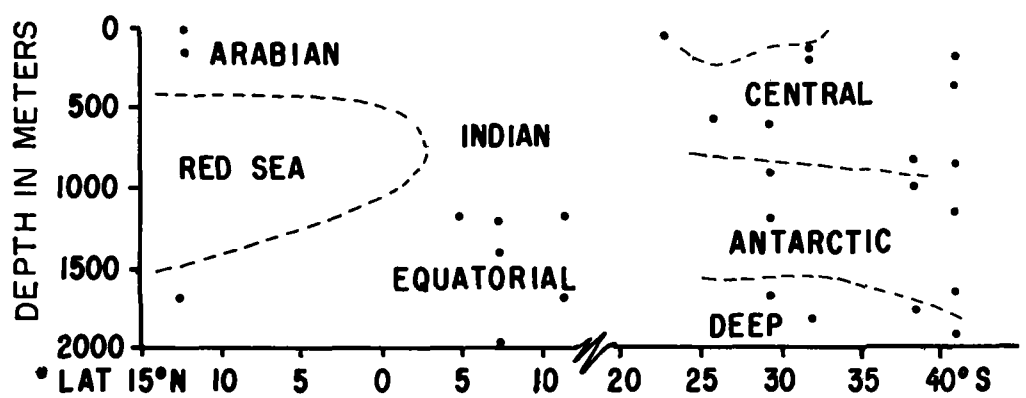


FIGURE 7. Distribution of *Candida polymorpha* in the Indian Ocean.

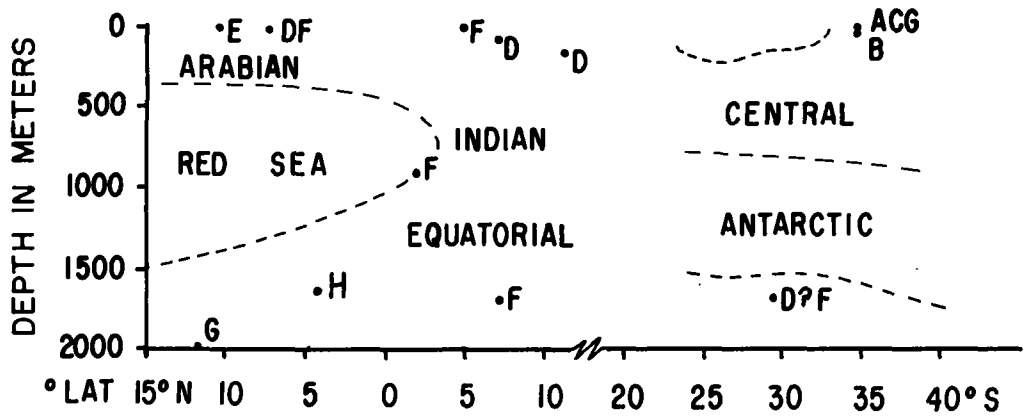


FIGURE 8. Distribution of: A, *Candida albicans*; B, *C. guilliermondii*; C, *C. mycoderma*; D, *C. parapsilosis*; E, *Candida* sp. II; F, *C. tenuis*; G, *C. tropicalis*; H, *C. rugosa*.

micro-organisms in contradiction to Kriss's observations of low numbers of heterotrophs. An abundance of Antarctic micro-organisms would agree with Sorokin's findings of high bacterial concentrations in surface waters. Significant quantities of micro-organisms, however, are found in deep waters, but their origin and sustained reproduction in certain locales may be directly dependent on the productivity of the photosynthetic zone.

Kriss (1963) suggested that an interface is formed at convergences of water of different densities; organic substances might accumulate, thus producing a potential area for bacterial development. Increases in bacterial biomass were observed at the thermocline layer at all stations examined by Kriss in the Caspian Sea. Kriss also reported dense bacterial populations in the Arctic at boundaries of water masses with different temperatures. Similar numerical increases in yeasts were observed in the Florida

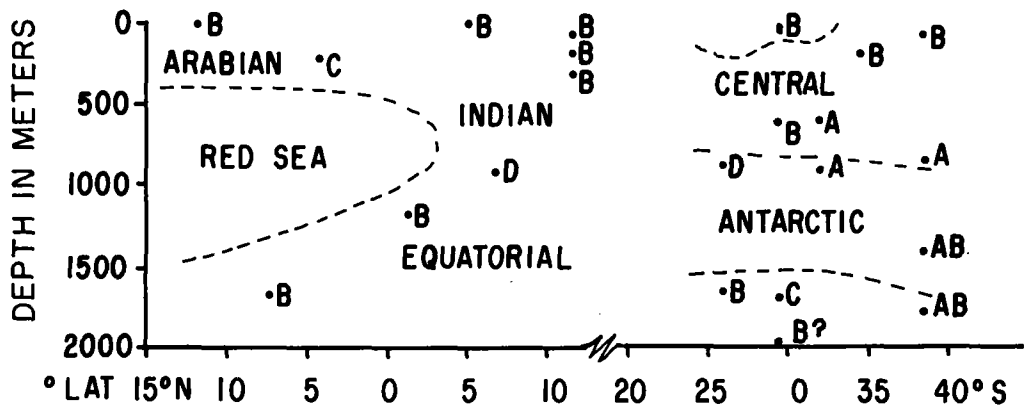


FIGURE 9. Distribution of: A, *Rhodotorula crocea*; B, *Rh. glutinis*; C, *Rh. graminis*; D, *Rh. pallida*.

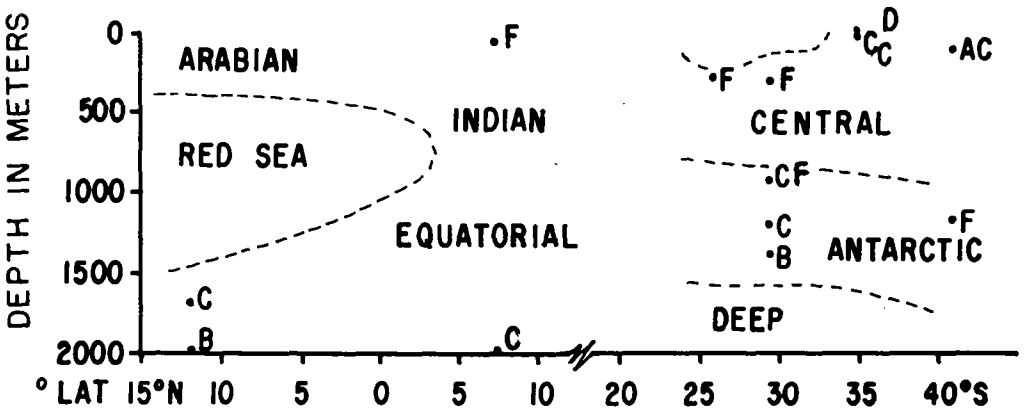


FIGURE 10. Distribution of: A, *Sterigmatomyces halophilus*; B, *St. halophilus* var.; C, *Debaryomyces hansenii*; D, *Hanseniaspora uvarum*; E, *Pichia fermentans*; F, *Saccharomyces cerevisiae*.

Straits (Fell & van Uden, 1963), and in the Indian Ocean in the thermocline at Sta. 152 (Fig. 11); however, evidence to suggest a causal relationship is insufficient.

Biological Conditions.—A preliminary study of values of phytoplankton productivity and volumes of standing crops from ANTON BRUUN Cruise 3 (Woods Hole Oceanographic Institution, 1965) indicates that the Indian Ocean comprises three biologically distinct regions. First, a region north of the Equator associated with the Gulf of Arabia and Monsoon Current is characterized by a high standing crop of phytoplankton as measured by the concentration of chlorophyll *a*, unusually high carbon-14 productivity, and associated physical features such as shallow thermocline depths and current divergences, which usually denote vertical mixing of nutrient-rich deeper waters with the surface layers. Maximum biomass and productivity values were obtained at 7°N. South of 11°S, values decreased to a minimum at 23°S in the midst of the relatively sterile Indian Central Water Mass. Productivity and biomass values tended to increase near the Subtropical Convergence, so that the Indian Central Water Mass appeared to be bordered by two fertile regions, the Indian Equatorial Water to the north and the Subantarctic Water to the south. In the latter area, volumes of shallow invertebrates abruptly increased at 26-32°S then decreased to the south; those of deep invertebrates increased at 32-41°S (W.H.O.I., 1965; Ebeling, in press).

Yeast productivity, as indicated by total numbers, was high near 12°N. In contrast to other biological activity, dense concentrations of yeast populations were not found to 7°N. Presumably the Somali Current had a greater effect on yeast abundance than the values of productivity would indicate. The abundance of shallow-water invertebrates at 26-32°S and

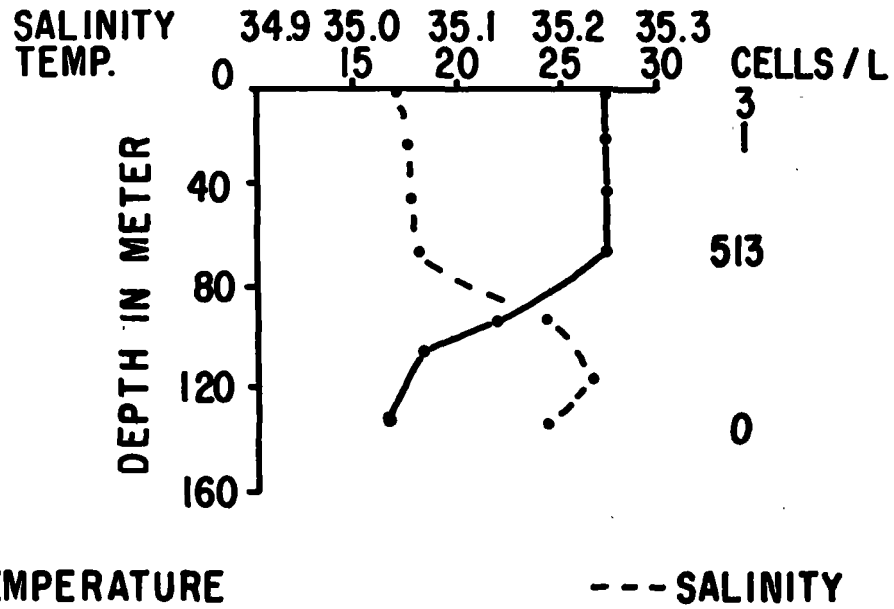


FIGURE 11. Distribution of yeasts (cells/liter) near the thermocline at Sta. 152.

the deep-water concentration at 32-41° was mirrored by an increase in yeasts. Yeasts are dependent, for growth, on available organics so that biological activity and subsequent decay of materials make food available. Conversely, yeasts may be included in the diet of invertebrates as ancillary source of protein and vitamins, particularly in deep waters where the quantity of phytoplankton is appreciably reduced.

No strong evidence has been presented to indicate that marine yeasts are symbiotic with living plants or animals (Fell & van Uden, 1963). The yeasts probably utilize organic material that becomes available after death and dissolution of various marine organisms. Other than by the examination of several fish from the Indian Ocean, the presence of yeasts in marine organisms was not established. With the exception of *C. atmosphaerica*, the yeast species isolated (Table 2) were not common pelagic forms. *C. viswanathii* was recorded for the first time outside human sources. Sandhu *et al.* (1965) suggested that *C. viswanathii* may be pathogenic to humans and laboratory animals.

General Considerations.—In view of our earlier extensive collections of yeasts in the subtropical Atlantic (Fell *et al.*, 1960; Fell & van Uden, 1963; van Uden & Fell, unpublished data), a comparison of yeasts from that region with those found in the Indian Ocean is worthwhile. The subtropical Atlantic studies, which included Florida and the Bahamas, indicated diverse yeast populations both in inshore and offshore environments. Estuarine

areas, affected by terrestrial runoff, contained a diversity of terrestrial species, *e.g.*, *C. tropicalis*, *C. parapsilosis*, *T. glabrata*, *Tr. cutaneum*, usually associated with animals. Apparently, not all of these terrestrially-introduced species can survive in sea water. The human pathogen, *C. albicans*, was routinely isolated in a bathing lagoon in Biscayne Bay, Florida, but rarely found in regions within a mile or so from the source of introduction. Kawakita & van Uden (1965) have suggested that optimal temperatures for growth may be a limiting factor in the survival of animal-associated yeasts in temperate regions. Other factors also may exist. Summer water temperatures (June-Sept.) of Biscayne Bay (27-34.5°C; McNulty, unpublished data) are well within the temperature range for optimal growth of *C. albicans*; furthermore, *in vitro* studies indicate that *C. albicans* can survive and proliferate in sea water for three-week periods at 22°C.

Concentrations of yeasts in these inshore areas ranged from 0-5,000 cells/liter with highest counts obtained around terrestrial outflows and in highly productive regions as algal beds and coral reefs. The animal-associated species diminished in numbers offshore and in estuarine regions free from terrestrial outflow. Instead, the predominant organisms were species of *Cryptococcus*, *Rhodotorula*, *Debaryomyces*, and less fermentative *Candida* spp., *e.g.*, *C. atmosphaerica*, *C. polymorpha*, and *C. natalensis*. While these species were also found in estuaries, the distributional limitation of the estuarine species was probably due to differences in ambient temperatures and in organic content of the two regions. Occasionally, the offshore yeast populations of Florida and Bahamian waters were as great as those found inshore. This may be attributed in part to the inter-island effect (Doty & Oguri, 1956).

The distribution of many yeasts in Florida and Bahamian waters was influenced by the proximity to land and by the ability of terrestrial organisms to survive offshore; however, generally the occurrence of species in the offshore Indian Ocean was not affected by these factors. Two species, *C. atmosphaerica* and *Rh. rubra* were cosmopolitan, inhabiting all water masses studied. The Red Sea water appeared limiting to certain ubiquitous forms such as *C. polymorpha*, *Rh. glutinis*, and the sporogenous yeasts. This limitation may be a function of the source and/or physical properties (*e.g.*, low salinity, oxygen, and nutrients) of the water mass. *Sp. odorus* was abundant in Red Sea water and other water masses of the northern stations, but was not isolated south of 22°S, while *Candida* sp. I was abundant in the latter region. The separation of two apparent floral zones by distribution of *Sp. odorus* and *Candida* sp. I corresponds to the faunal discontinuity between the distributions of species of equatorial and subtropical-subantarctic fishes in the deep-sea family Melamphaidae (Ebeling, in press).

The subtropical Atlantic and the Indian Ocean have similar species (*C. atmosphaerica*, *C. polymorpha*, *Rh. glutinis*, and *Rh. rubra*) that apparently are ubiquitous oceanic forms. Other abundant Atlantic forms (*C. guilliermondii*, *C. parapsilosis*, *Cr. albidus*, and *Cr. laurentii*) were not prevalent in the Indian Ocean, but were isolated at Mauritius, suggesting their offshore occurrence possibly may be dependent on terrigenous sources. Several land-animal associated yeasts (*C. albicans*, *C. mycoderma*, *C. tropicalis*, and *C. parapsilosis*) were isolated in the Indian Ocean (Fig. 8). In most cases, these occurrences can be attributed to the proximity to land or to contamination. *C. albicans*, *C. tropicalis*, and *C. mycoderma* were isolated from surface waters at Sta. 158. However, to avoid ship or bird contamination, surface waters generally were not sampled. At Sta. 158 numerous species of petrels and albatrosses were present. Kawakita & van Uden (1965) have shown that the intestinal tract of sea birds (gulls and terns) contain *C. albicans*, *C. tropicalis*, and *T. glabrata*.

C. parapsilosis was isolated in four locations, three of which were in upper 160 meters (above 16°C). Laboratory tests indicated that this species does not grow below 7°C (at atmospheric pressure) suggesting that *C. parapsilosis* does not inhabit deep waters. The only deep isolation of *C. parapsilosis* was at 1,696 meters, Sta. 156 (2.7°C). However, due to a leak in the sampler, there is some question as to the validity of this particular sample.

Collections by Bhat & Kachwalla (1955) in the Indian Ocean also indicated the presence of terrestrial yeasts. Their samples, taken two miles off the coast of India, contained *S. steineri*, *S. fructuum*, *S. rosei*, *D. hansenii*, *D. nicotinae*, *D. subglobosus*, *D. kloeckeri*, *C. tropicalis*, *C. guilliermondii*, *C. melibiosi*, *T. glabrata*, *T. candida*, and *T. famata*. The presence of the animal pathogens *T. glabrata* and *C. tropicalis* suggests a terrestrial origin of these yeasts. In Florida and Bahamian waters, both of the latter animal-associated species were found only in inshore regions with terrestrial outflow. *C. tropicalis* was the most abundant species in Bhat & Kachwalla's samples as it was in those of Fell *et al.* (1960) from Biscayne Bay, Florida.

Filamentous Fungi.—Few studies have been made of filamentous fungi (molds) in the open oceans (Johnson & Sparrow, 1961). Roth *et al.* (1964) reported an abundance of molds in the inter-island offshore regions of the Bahamas. Eighty per cent of their samples contained fungi at an average concentration of 10 cells/liter. The methods of Roth *et al.* included both non-sterile and sterile collecting techniques, but their results did not distinguish between the two methods. Thus, it is not possible to evaluate the presence and significance of these filamentous fungi in offshore regions.

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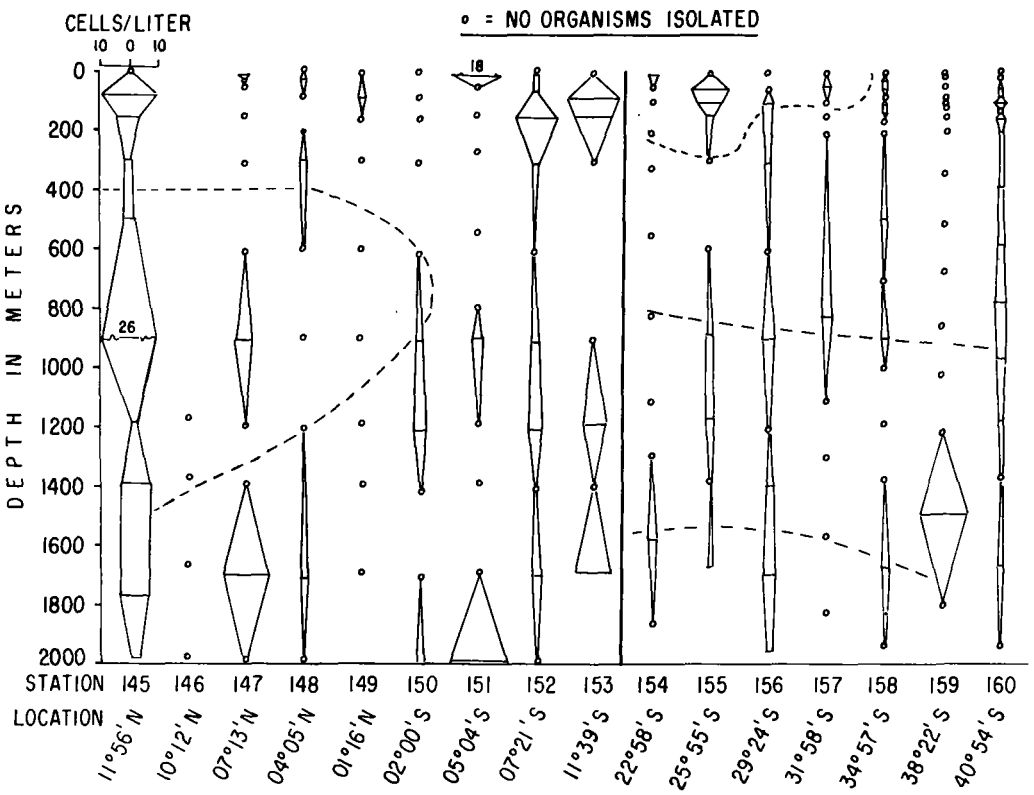

FIGURE 12. Distribution of filamentous fungi in the Indian Ocean (60°E Lon.) Aug. 5-Sept. 20, 1963.

In the Indian Ocean, 30 per cent of the samples (Fig. 12) contained molds at an average of 3 cells/liter. Highest concentrations were at Sta. 145 in the Somali Current and in the upper waters of Sta. 151-153. The latter region, which showed a similar increase in yeast numbers, is near the Seychelles Islands. The collection of molds relatively near land and the observation of large numbers of these organisms in the Somali Current suggests that the presence of molds in the ocean may be strongly influenced by terrigenous sources.

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The author wishes to express his appreciation to Dr. D. G. Ahearn, Department of Microbiology, University of Miami, Florida, for identifying the species of *Rhodotorula* and *Sporobolomyces*; to Dr. Alfred Ebeling, University of California at Santa Barbara, California, for his discussions and pre-publication information on productivity and animal populations in the Indian Ocean; to Drs. Ebeling and S. P. Meyers, Institute of Marine Science, University of Miami, for reviewing the manuscript; to Miss Ingrid

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SUMARIO

DISTRIBUCIÓN DE LEVADURAS EN EL OCÉANO ÍNDICO

Se colectaron levaduras y mohos en 16 estaciones durante el crucero 3 del barco de investigaciones ANTON BRUUN para el Programa de los Estados Unidos en Biología, Expedición Internacional del Océano Índico. El crucero investigado se extendió a lo largo del meridiano 60°E desde la latitud 11°56'N a la 40°54'S, a profundidades de 0-2,000 m. Las densidades de poblaciones de levaduras fueron de 0-513 cel/lit, con las mayores concentraciones en las aguas de la Corriente de Somali y el Antártico Intermedio. Se aislaron un total de 25 especies de levaduras, 19 de las cuales se presentaron con poca frecuencia, *i.e.*, en menos del 6 por ciento de las muestras positivas. Las especies más comúnmente aisladas fueron clasificadas ecológicamente en tres grupos arbitrarios: (1) especies cosmopolitas (*Rhodotorula rubra* y *Candida atmosphaerica*) presentes en todas las masas de agua estudiadas; (2) especies ampliamente distribuídas (*C. polymorpha* y *Rh. glutinis*) ausentes en las aguas del Mar Rojo; (3) organismos regionalmente distribuídos, obtenidos bien de aguas al norte de los 22°S (*Sporobolomyces hispanicus* y *Sp. odorus*) o de aguas más al sur (*Candida* sp. I y *Rh. crocea*). Se discute la relación de la distribución de levaduras con las condiciones hidrográficas y biológicas. La incidencia de mohos parecieron ser parcialmente dependientes de la proximidad de material terrígeno.

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No. 173 Volume 14 September 1, 1967

A new species of *Scambicornus* (Copepoda, Cyclopoida, Lichomolgidae) associated with a holothurian in Madagascar, with notes on several previously described species

ARTHUR G. HUMES

ABSTRACT

A new lichomolgid copepod, *Scambicornus lobulatus*, associated with a holothurian, *Bohadschia graeffei*, is described from the region of Nosy Bé, Madagascar. Certain previously described species of *Scambicornus* in that area are redescribed in part. New host records are: *S. campanulipes* from *Actinopyga lecanora* and *A. miliaris*, *S. idoneus* from *Argiodia nobilis* and *Holothuria scabra*, *S. modestus* from *Brandtothuria impatiens* and either *Microthele difficilis* or *Urodemas ehrenbergi*, and *S. tuberatus* from *Bohadschia marmorata*.

INTRODUCTION

Field investigations in 1955 resulted in the description of seven species of *Scambicornus* (= *Preherrmannella*) associated with nineteen holothurians (distributed in eight genera) and one echinoid at Nosy Bé, in northwestern Madagascar (Humes & Cressey, 1961). Later collections in 1960 and 1963-64 at Nosy Bé have produced the new species described below.

The copepods formerly placed in the genus *Preherrmannella* Sewell, 1949, must now be removed to *Scambicornus* Heegaard, 1944, since Stock (1964) has shown, after an examination of type specimens of *Scambicornus hamatus* Heegaard, 1944, that *Scambicornus* and *Preherrmannella* represent the same genus, with Heegaard's name having clear priority.

The holothurians examined in this study were isolated in sea water in plastic bags immediately after collection. Later a small amount of ethyl alcohol (about five per cent) was added, the holothurians thoroughly rinsed for several minutes, and the copepods then recovered by pouring the water through a fine net. With this technique there was little possibility of accidental contamination of the samples.

Received: May 15, 1967

All figures were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The abbreviations used are: A_1 = first antenna, A_2 = second antenna, MX_2 = second maxilla, MXPD = maxilliped, and P_1 = leg 1.

ACKNOWLEDGEMENTS

The collections were made by the author, during four months in 1960 while a member of an expedition sent to Madagascar by the Academy of Natural Sciences of Philadelphia, and during eighteen months in 1963-64 while participating in the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the material has been aided by grants (GB-1809 and GB-5838) from the National Science Foundation of the U.S.

I thank Dr. H. Barraclough Fell and Mr. James F. Clark, of the Museum of Comparative Zoology, Harvard University, for the identifications of the holothurians collected in 1963-64 and Dr. Elisabeth Deichmann, also of the Museum of Comparative Zoology, for the determination of those collected in 1960. The field work was aided in many ways by the staff of the Centre d'Océanographie et des Pêches at Nosy Bé.

Scambicornus lobulatus n. sp. Figs. 1—35.

Type material. — 29 ♀♀, 49 ♂♂, and 27 copepodids washed from the body surface of 10 holothurians, *Bohadschia graeffei* (Semper), in a depth of 2 m, Antsiabe, on the southern end of Nosy Komba, near Nosy Bé, Madagascar. (Seventeen of these males were in amplexus with adult females and five were in amplexus with apparently last copepodids.) Collected November 30, 1963. Holotype female, allotype, and 45 paratypes (18 ♀♀, 27 ♂♂) deposited in the Zoölogisch Museum, Amsterdam; 15 paratypes (6 ♀♀, 9 ♂♂) in the United States National Museum, Washington; and the remaining paratypes in the collection of the author.

Other specimens (all from *Bohadschia graeffei*). — 7 ♀♀, 13 ♂♂, and 1 copepodid from 1 host in 12 m, Ambatoloaka, Nosy Bé, August 17, 1960; 1 ♀ from 1 host in 1 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, August 18, 1960; 6 ♀♀ and 1 copepodid from 1 host in 2 m, Tany Kely, a small island to the south of Nosy Bé, August 26, 1960; 37 ♀♀, 25 ♂♂, and 6 copepodids from 4 hosts in 2 m, Pte. Ambarionaomby, October 2, 1960; 40 ♀♀, 20 ♂♂, and 2 copepodids from 21 hosts in 3 m, northern end of Nosy Sakatia, near Nosy Bé, October 8, 1960; 11 ♀♀ and 4 ♂♂ from 6 hosts in 2 m, southern end of Nosy Sakatia, October 23, 1960; 24 ♀♀, 11 ♂♂, and 1 copepodid from 2 hosts in 1 m, Tany Kely, July 9, 1963; and 12 ♀♀, 3 ♂♂, and 1 copepodid from 5 hosts in 2 m, Nosy N'Tangam, near Nosy Bé, August 8, 1963. (These collections include 60 pairs in amplexus.)

Female. — Body (fig. 1) with a moderately broadened prosome. Length (not including the setae on the caudal rami) 1.39 mm (1.34—1.44 mm) and greatest width 0.73 mm (0.68—0.79 mm), based on 10 specimens. Ratio of length to width of the prosome 1.27 : 1. Segment of leg 1 separated from the head by a dorsal furrow. Epimeral areas of the segments of legs 1 and 2 pointed posteriorly, those of the segment of leg 3 rounded, and those of the segment of leg 4 small and outlined as shown in the figure.

Segment of leg 5 (fig. 2) 117 × 203 μ. Between this segment and the genital segment a weakly developed ventral intersegmental sclerite. Genital segment wider than long, 161 × 237 μ, with posteriorly directed lateral wings. Areas of attachment of the egg sacs situated laterally at the tips of the wings, each area (fig. 3) bearing two naked setae 47 and 80 μ in length and a ventral row of

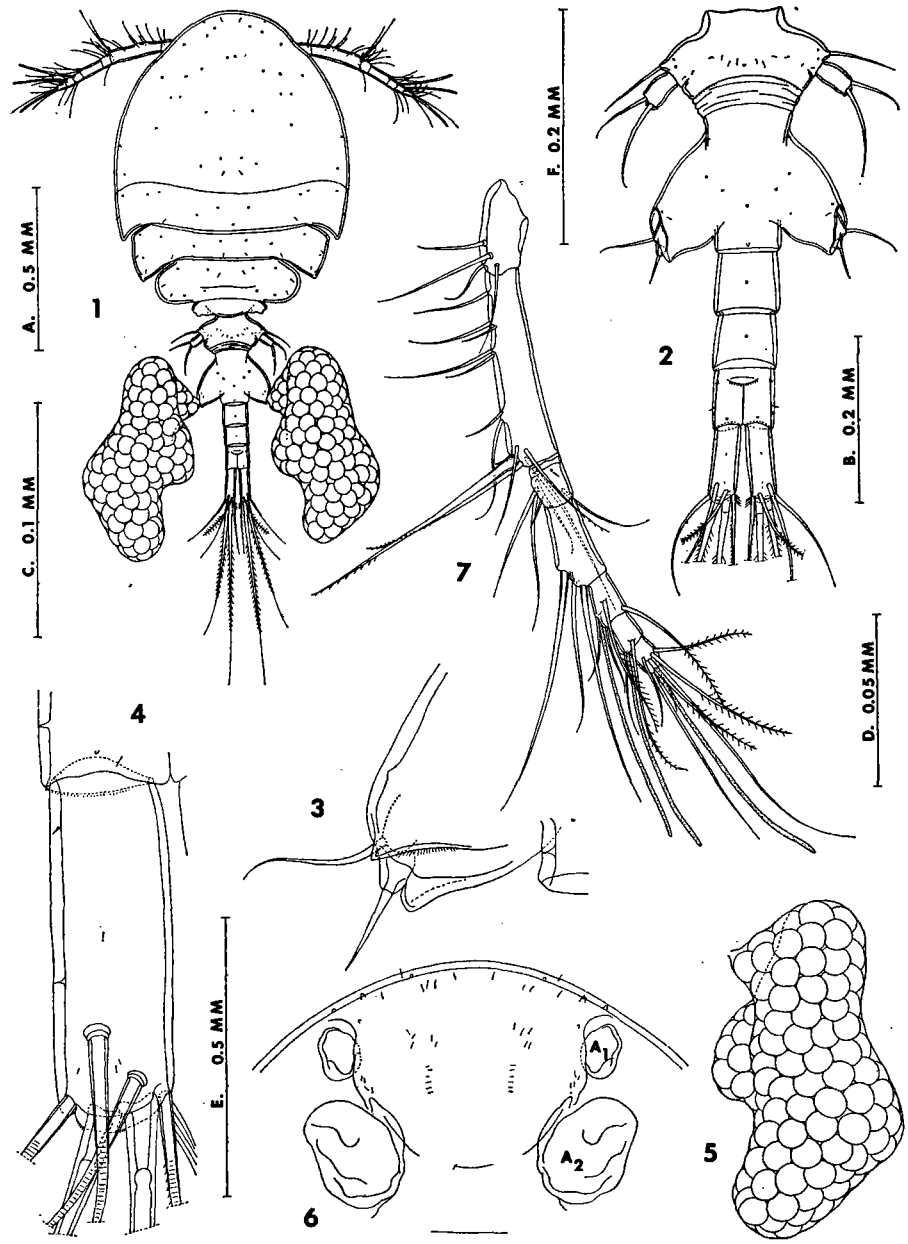

FIG. 1—7. *Scambicornus lobulatus* n. sp., female: 1, body, dorsal (A); 2, urosome, dorsal (B); 3, area of attachment of egg sac and leg 6, ventral (C); 4, caudal ramus, dorsal (D); 5, egg sac, ventral (E); 6, rostral area, ventral (B); 7, first antenna, ventral (F).

minute spinules. Three postgenital segments 70 × 81, 68 × 78, and 76 × 73 μ from anterior to posterior. Anal segment with a row of minute spinules along its posteroventral margin on each side.

Caudal ramus (fig. 4) moderately elongated, 99 × 34 μ in greatest dimensions, about 2.9 times longer than wide. Outer lateral seta (placed dorsally on the ramus) 185 μ and naked; outermost terminal seta 174 μ and naked; innermost terminal seta 156 μ with a short row of hairs proximally on the inner side and barbed along the outer side. Two long median terminal setae 715 μ (inner) and 451 μ (outer), both with lateral spinules in their midregions; these two setae inserted between dorsal (smooth) and ventral (with a row of minute spinules) flaps. Dorsal seta 143 μ with lateral hairs distally. A minute spinule basally near the outer margin of the ramus. A few hairs on the dorsal surface of the ramus.

Dorsal surface of the prosome and urosome with hairs and refractile points as in figs. 1 and 2; ventral surface of the urosome with a few hairs and refractile points. Ratio of the length of the prosome to that of the urosome 1.59 : 1.

Egg sac (figs. 1 and 5) of a peculiar lobulate form and rather flattened dorsoventrally, its greatest dimensions in dorsal aspect 605 × 352 μ. Large number of relatively small eggs (about 100), each about 55 μ in diameter. Actual attachment of the egg sac dorsal to the two setae.

Rostral area (fig. 6) not well defined posteroventrally.

First antenna (fig. 7) 7-segmented, 418 μ in length, with a sclerite on the ventral side of the third segment suggesting an intercalary segment. Lengths of the segments (measured along their posterior non-setiferous margins) 42 (70 μ along the anterior edge), 153, 34, 69, 36, 27, and 29 μ respectively. Formula for the armature: 4, 13 (5 + 8), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Several setae with lateral hairs as indicated in the figure.

Second antenna (fig. 8) 4-segmented, 290 μ long, including the claw. Armature: 1, 1, 3 + claw, and 7. All setae naked. Second segment 200 μ along its outer margin and 109 μ along its inner margin. Claw 90 μ along its axis. Last segment with five of the seven setae arising from a lobe which appears to be somewhat separated from the proximal part of the segment (fig. 9).

Labrum (fig. 10) with two posteroventral lobes, their distal margins hyaline.

Mandible (fig. 11) with the convex margin of the blade serrated, the concave margin with a proximal spiniform recurved process followed by a row of hairs. Paragnath (fig. 12) a small lobe with hairs distally. First maxilla (fig. 13) with three terminal setae and a prominent subterminal digitiform process hyaline in its distal two-thirds. Second maxilla (fig. 14) 2-segmented. First segment unarmed. Second segment having on its outer (ventral) margin a proximal setule, on its posterior surface a naked seta and a spinulose spine, and terminating in a lash with a few small spines on its posterior proximal area, a row of teeth along one edge, and a few short spinules on the opposite edge. Maxilliped (fig. 15) 3-segmented. First segment unarmed. Second segment with two naked setae, an inner oblique row of spinules, and two patches

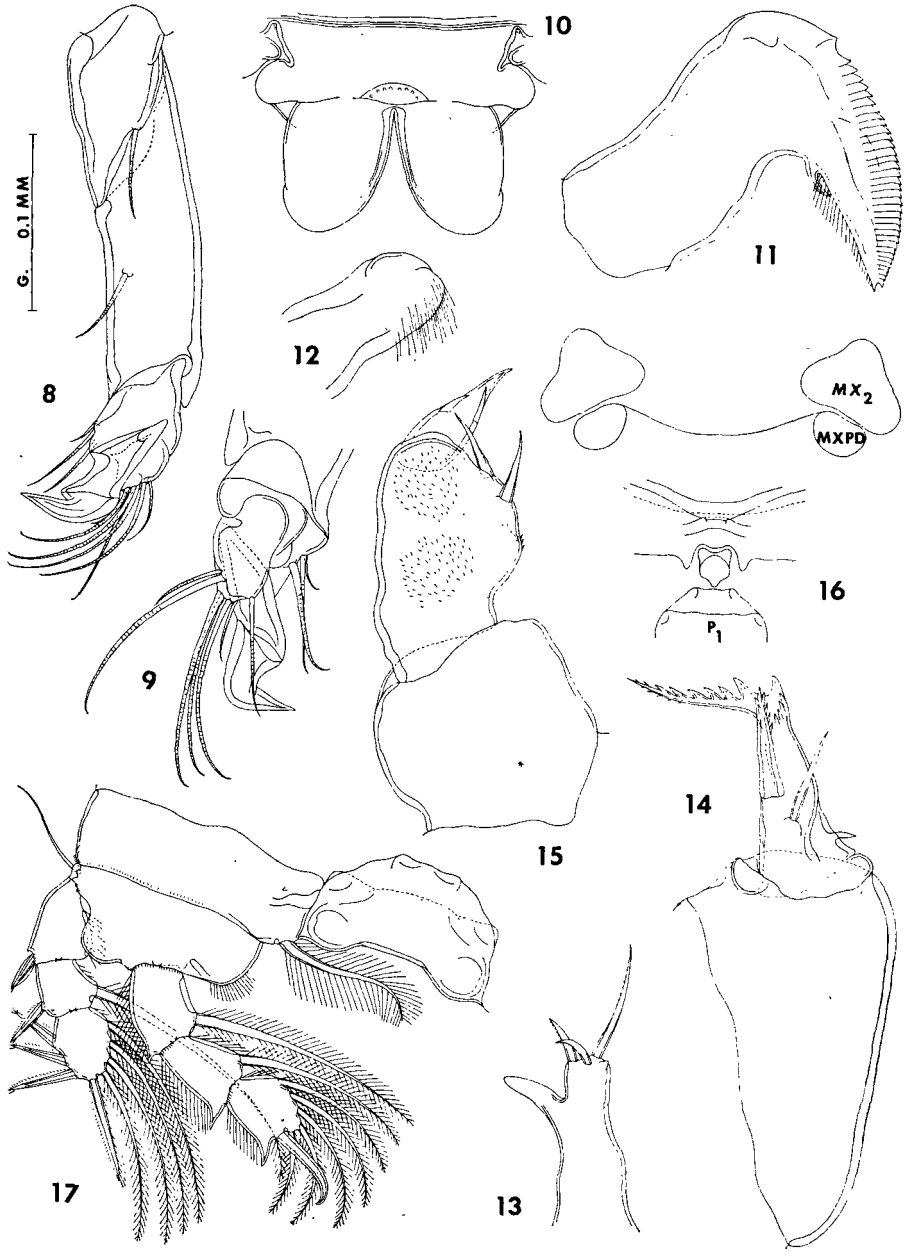

FIG. 8—17. *Scambicornus lobulatus* n. sp., female (continued): 8, second antenna, anterior (G); 9, segments 3 and 4 of second antenna, posterior (C); 10, labrum, ventral (C); 11, mandible, posterior (D); 12, paragnath, ventral (D); 13, first maxilla, posterior (D); 14, second maxilla, posterior (D); 15, maxilliped, antero-inner (D); 16, area between maxillipeds and first pair of legs, ventral (F); 17, leg 1, anterior (G).

of minute spinulus on its antero-inner surface. Third segment with two hyaline spinules and terminating in a spiniform process.

Area between the maxillipeds and the first pair of legs (fig. 16) not protuberant; a sclerotized line between the bases of the maxillipeds.

Legs 1—4 (figs. 17, 18, 19, and 20) with 3-segmented rami. Armature as follows (Roman numerals indicating spines, Arabic numerals setae):

P_1	protopod	0—1	1—0	exp	I—0	I—1	III, I, 4
				end	0—1	0—1	I, 5
P_2	protopod	0—1	1—0	exp	I—0	I—1	III, I, 5
				end	0—1	0—2	I, II, 3
P_3	protopod	0—1	1—0	exp	I—0	I—1	III, I, 5
				end	0—1	0—2	I, III, 2
P_4	protopod	0—1	1—0	exp	I—0	I—1	II, I, 5
				end	0—1	0—1	I, II, II

Inner seta on the coxa of legs 1—3 long and plumose, but in leg 4 short (15 μ) and naked. Outer seta on the basis moderately long in legs 1 and 2, but much longer (about 150 μ, or a little longer than the entire exopod) in legs 3 and 4. Outer spines on the exopod of leg 1 flagellated. Five spines on the last segment of the endopod of leg 4 measuring in length from outer to inner 27.5, 43, 70, 62, and 42 μ.

Leg 5 (fig. 21) with a relatively short free segment, 43 $\times$ 23 μ in greatest dimensions (in leg shown in figure) including the distal fringe, or 1.9 : 1. (Opposite leg in this individual 46 $\times$ 23 μ or 2 : 1, and both legs in another female 41 $\times$ 26 μ or 1.58 : 1). Outer terminal seta 75 μ long and naked; inner terminal seta, inserted dorsally to the serrated fringe, 104 μ with a few inner barbules. Seta on the body near the insertion of the free segment 78 μ and haired distally.

Leg 6 probably represented by the two setae near the attachment of each egg sac (see fig. 3).

Color in life in transmitted light translucent, eye red, egg sac grayish.

Male. — Body (fig. 22) resembling that of the female but the cephalosome a little more rounded anteriorly. Length (without the setae on the caudal rami) 0.71 mm (0.66—0.75 mm) and greatest width 0.33 mm (0.31—0.34 mm), based on 10 specimens. Ratio of length to width of the prosome 1.36 : 1.

Segment of leg 5 (fig. 23) 36 $\times$ 73 μ. Between this segment and the genital segment no ventral intersegmental sclerite. Genital segment 99 $\times$ 109 μ, slightly wider than long. Four postgenital segments 22 $\times$ 46, 23 $\times$ 45, 21 $\times$ 44, and 24 $\times$ 46 μ from anterior to posterior.

Caudal ramus (fig. 24) much shorter than in the female, 29 $\times$ 19 μ in greatest dimensions or 1.47 times longer than wide.

Dorsal surface of the body ornamented with hairs and refractile points as in figs. 22 and 23; ventral surface of the urosome with almost no ornamentation. Ratio of the length of the prosome to that of the urosome 1.83 : 1.

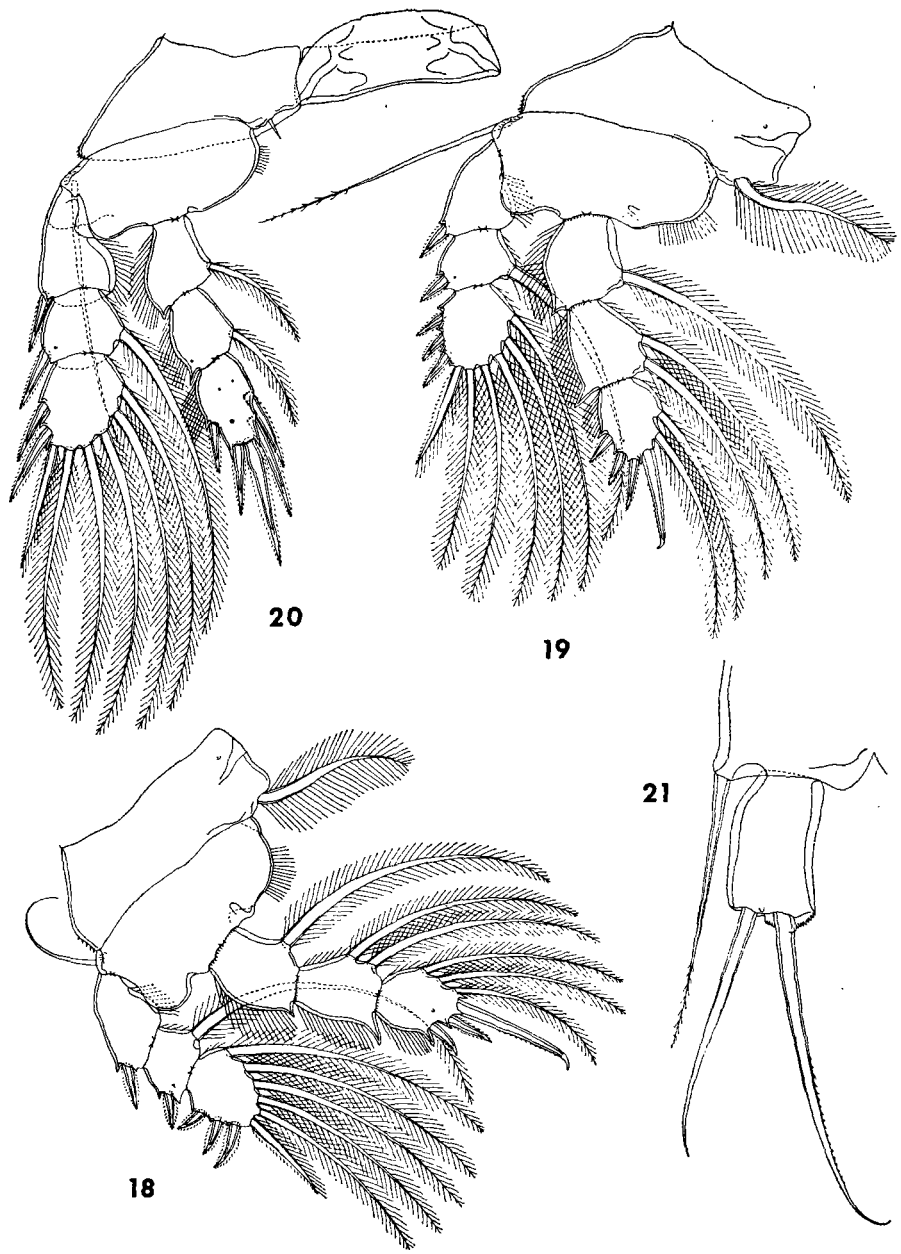

FIG. 18—21. *Scambicornus lobulatus* n. sp., female (continued): 18, leg 2, anterior (G); 19, leg 3, anterior (G); 20, leg 4, anterior (G); 21, leg 5, dorsal (D).

Rostral area as in the female.

First antenna resembling that of the female, but with a short aesthete added on segment 3 (fig. 25) and with lateral hairs on certain of the setae much less prominent. Second antenna (fig. 26) similar to that of the female, but with a patch of spinules on the inner surface of the second segment proximal to the seta and with all setae less obviously annulated.

Labrum resembling that of the female but the distal edges of the two lobes a little less hyaline.

Mandible, paragnath, and first maxilla like those in the female. Second maxilla (fig. 27) resembling that of the female but the lash has two large teeth followed by 5—6 slender teeth, and spinules are absent on the opposite side. Maxilliped (figs. 28 and 29) 4-segmented, assuming that the proximal part of the claw represents a fourth segment. First segment short and unarmed. Second segment elongated, its inner surface with two naked setae and an elongated patch of small spines, its posterior surface covered with minute spinules. Third segment short and unarmed. Claw 135 μ along its axis, recurved, bearing two unequal setae proximally, showing a slight indication of division about midway, and having terminally a few denticles and a conspicuous lamella (fig. 30) which fits like a hood over the end of the claw. (In amplexus the claws of the maxillipeds are held around the anterior part of the genital segment of the female, with their tips crossed below that segment.)

Exopods of legs 1—3 and both rami of leg 4 segmented and armed as in the female (except that the outer seta on the basis of legs 3 and 4 is shorter than in the female, being not much longer than on legs 1 and 2). Endopods of legs 1—3 with the same arrangement of spines and setae as in the female, but showing sexual dimorphism. (Spine and setal formula of the male is thus similar to that of the female, allowing for the fusion of the second and third segments of the endopods in legs 1 and 2.) Endopod of leg 1 (fig. 31) 2-segmented, with the last two segments completely fused. Outer spine 17 μ long and rather hyaline in its distal three-fourths. Outermost seta 39 μ, with hairs proximally but with barbules distally. Endopod of leg 2 (fig. 32) 2-segmented, with the last two segments fused, there being only an extremely indistinct suggestion of division, without a definite line. Outer spine 22 μ, two terminal spines 31 μ (outer) and 55 μ (inner), all three spines hyaline distally. Endopod of leg 3 (fig. 33) 3-segmented. Four spines, all hyaline distally with obtuse tips, from outer to inner 44, 20, 37, and 65 μ long. Outer spine and outermost of the three terminal spines recurved so that they oppose each other. Five spines on the last segment of the endopod of leg 4, from outer to inner, 18, 32, 52, 30, and 24 μ long, similar to those in the female.

Leg 5 (fig. 34) small, the free segment being only 16 $\times$ 10 μ and slightly tapered distally, with only a trace of a distal fringe. Outer terminal seta 44 μ and naked, inner terminal seta 55 μ with lateral barbules. Seta on the body near the insertion of the free segment 30 μ and haired.

Leg 6 (fig. 35) a posteroventral flap on the genital segment bearing two setae (both 33 μ long), one naked, the other with lateral hairs; ventrad to the

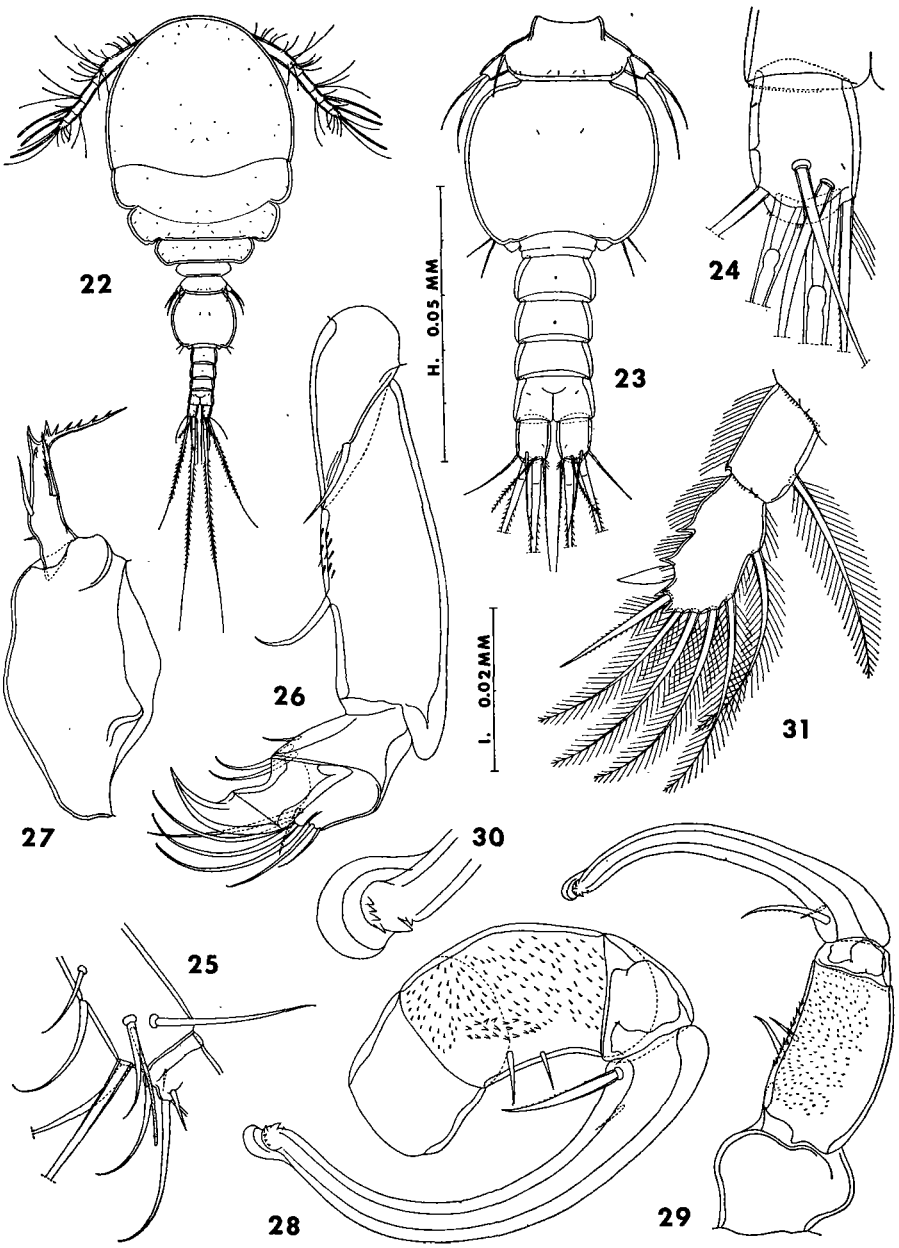

FIG. 22—31. *Scambicornus lobulatus* n. sp., male: 22, body, dorsal (E); 23, urosome, dorsal (G); 24, caudal ramus, dorsal (H); 25, distal part of segment 2 of first antenna, ventral (D); 26, second antenna, anterior (D); 27, second maxilla, posterior (D); 28, maxilliped, posteroventral (D); 29, maxilliped, posterior (C); 30, tip of claw of maxilliped, posterior (I); 31, endopod of leg 1, anterior (D).

insertions of these setae a pointed projection with an outer row of spinules.

Spermatophore not observed.

Color in life in transmitted light similar to that of the female.

(The specific name *lobulatus*, derived from Neo-Latin *lobulus* = provided with lobes, refers to the unusual form of the egg sacs.)

Comparison with related species. — Stock (1964) recognized twenty species in the genus *Scambicornus* which he devided into three groups according to the armature of segments 3 and 4 of the second antenna. (A similar division had been previously suggested by Bocquet, Stock & Kleeton, 1963). *Scambicornus lobulatus* differs from *S. propinquus* (Nicholls, 1944) and *S. armoricanus* (Bocquet, Stock & Kleeton, 1963), both members of Stock's group b, where there is a moderately prehensile element on segment 3 and where segment 4 is normally developed (i.e., elongated). The new species differs also from *S. finmarchicus* (T. Scott, 1903), *S. tenuicaudis* (Sars, 1918), and *S. brevicauda* (Sewell, 1949), all belonging to Stock's group c, where prehensile elements on segment 3 are absent or setiform and where segment 4 is normally developed.

The remaining fifteen species, representing Stock's group a, have a strongly prehensile and usually 2-segmented claw on segment 3 of the second antenna. Three of these, *S. poculiferus* (Humes & Cressey, 1961), *S. nicobaricus* (Sewell, 1949), and *S. changeuxi* (Stock & Kleeton, 1963) have the last segment of the second antenna elongated (longer than the third segment) and thus may be separated from *S. lobulatus*. Four of the remaining twelve species, *S. idoneus* (Humes & Cressey, 1961), *S. petiti* (Stock & Kleeton, 1963), *S. prehensilis* (Sars, 1918), and *S. serendibicus* (Thompson & A. Scott, 1903), have a ratio of length to width of the caudal ramus in the female of more than 4 : 1; and three species, *S. campanulipes* (Humes & Cressey, 1961), *S. subtilis* (Humes & Cressey, 1961), and *S. robustus* (Thompson & A. Scott, 1903), have this ratio only 2 : 1 or less, thus distinguishing them all from *S. lobulatus*.

The five remaining species show certain features by which each may be separated from *S. lobulatus*. In *S. tuberatus* (Humes & Cressey, 1961) the genital segment in the female has rounded lateral borders, lacking wings entirely, and the inner surface of the claw in the maxilliped of the male has a digitiform protuberance. In *S. hamatus* Heegaard, 1944, the genital segment of the female has the central part enlarged to form lateral lobes, the rostrum has a clearly defined point, and the second antenna is rather short and robust. In *S. modestus* (Humes & Cressey, 1961) the body is shorter, the female 1.18 mm (1.06—1.25 mm), the male 0.58 mm (0.54—0.61 mm), not overlapping the size range of *S. lobulatus*, and the inner surface of the second segment of the maxilliped of the male has rows of slender spines. In *S. subgrandis* (Humes & Cressey, 1961) the ratio of the length to width of the caudal ramus of the female is 2.5 : 1, and the spines on the second segment of the endopod of leg 2 in the male are acute and have proportional lengths (26, 46, and 28 μ) different from those in *S. lobulatus*.

The last of the twenty species, *S. adduensis* (Sewell, 1949), seems to be closest to *S. lobulatus*, resembling it in having a comparable size in both sexes,

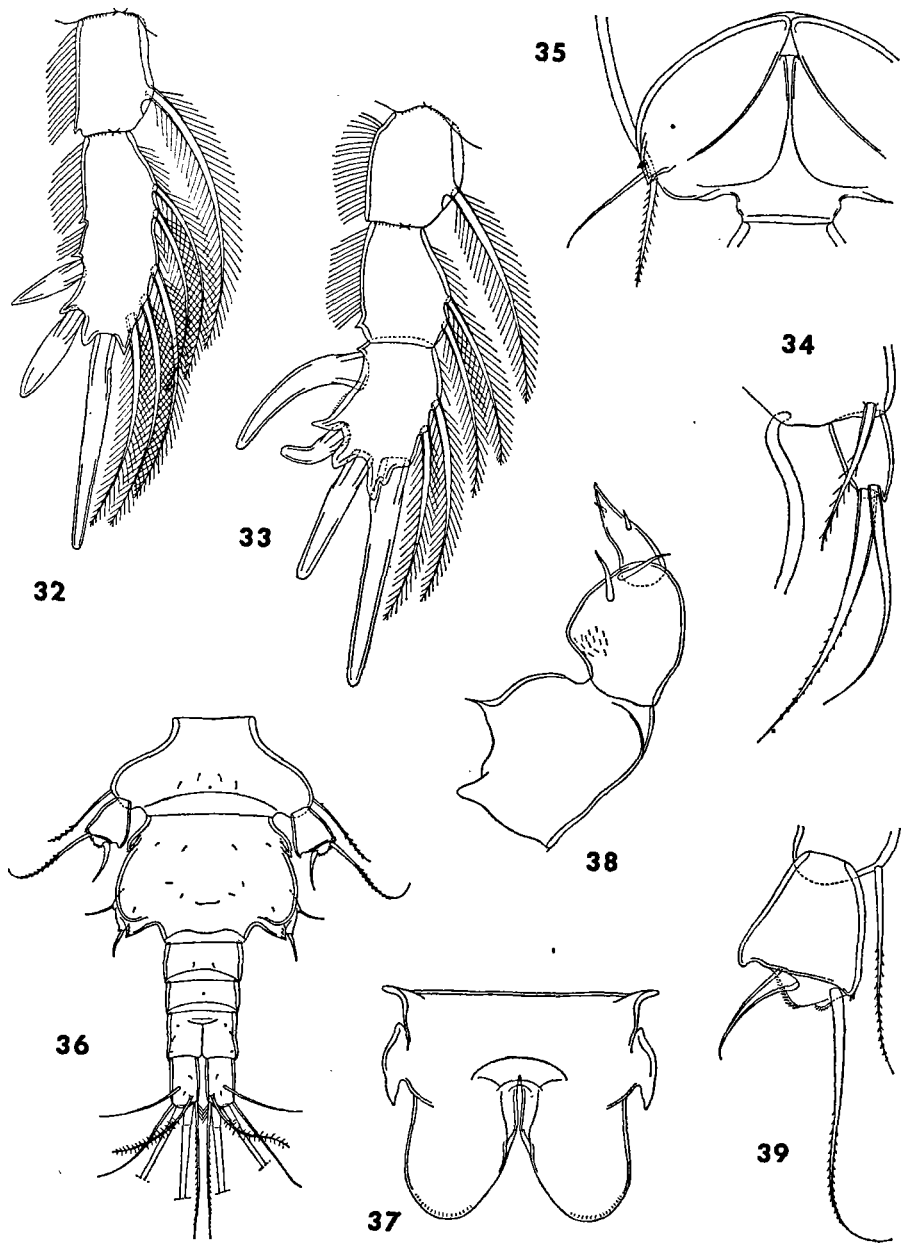

FIG. 32—35. *Scambicornus lobulatus* n. sp., male (continued): 32, endopod of leg 2, anterior (D); 33, endopod of leg 3, anterior (D); 34, leg 5, dorsal (H); 35, leg 6, ventral (D).

FIG. 36—39. *Scambicornus campanulipes* (Humes & Cressey, 1961), female: 36, urosome, dorsal (B); 37, labrum, ventral (C); 38, maxilliped, anterior (C); 39, leg 5, dorsal (C).

in the similar body proportions, and in the pronounced lateral wings on the genital segment in the female. In *S. adduensis*, however, the egg sac (not figured by Sewell) contains only about twelve eggs. (Sewell did not describe its shape, but presumably it is not strongly lobulated as in the new species; otherwise Sewell would surely have made mention of such an unusual form.) The shape of the genital segment of the female is somewhat different (compare fig. 2 with Sewell's text-fig. 20A). The mandible, as shown by Sewell in text fig. 20E, has a short terminal lash, quite unlike the new species.

In the male of *S. adduensis* the cephalosome is more pointed anteriorly than in *S. lobulatus*, the caudal ramus is about as long as broad (instead of 1.47 : 1 as in the new species), the terminal spine on the endopod of leg 2 is relatively shorter, and the outer spine on the last segment of the endopod of leg 3 is straight rather than recurved in opposition to the outermost terminal spine as in *S. lobulatus*.

Remarks on the nature of the egg sacs. — Most cyclopoid copepods have symmetrical egg sacs. In the eleven species of *Scambicornus* whose egg sacs are known, the sacs are elongated, have a regular form without lobes, and usually contain numerous eggs (in several species 75—100, but in *S. adduensis* only about 12). The lobulate form of the egg sacs in *S. lobulatus* is unusual, if not unique, in the suborder Poecilostoma.

The mechanism of the formation of such a lobulate egg sac is difficult to explain. Perhaps the eggs are extruded in spurts so that the cement substance, when hardening, fixes the eggs in lobes. In any case, the mechnism must be inherent and similar in all females of *S. lobulatus*, since all egg sacs produced have the same lobulate form.

Heegaard (1959) suggested that in *Caligus*, parasitic on fishes, the shape of the egg strings may be determined by the movements of the female and by the pressure (currents) of the water related to the movements of the fish host. In the case of *S. lobulatus*, however, the holothurian host is so sluggish that it does not seem possible that its body movements could create water currents rapid enough to influence the form of the egg sacs. Furthermore, other species of *Scambicornus* living on holothurians have regular egg sacs.

Gotto (1962), in an interesting discussion of egg number and ecology in parasitic copepods, made certain assumptions by way of explanation of large numbers of eggs in the egg sacs. He suggested that a high egg number might be related to: the host being sparsely distributed, somewhat inaccessible, or not obviously attractive from a distance; the host being highly mobile; or the environment of the host being inimical to successful infestation (e.g., swift currents, wavebeaten shores, or exposure during low tides). Little correlation has been observed at present, however, between the ecology of the holothurian host and the relatively large numbers of eggs in *S. lobulatus*. The holothurians collected, conspicuous by their size (30 cm or more in length), were found in depths of 1—12 meters, exposed on the surfaces of masses of coral. Sometimes several holothurians occurred within an area of 2 to 3 square meters. They lived in situations where there was considerable water current resulting

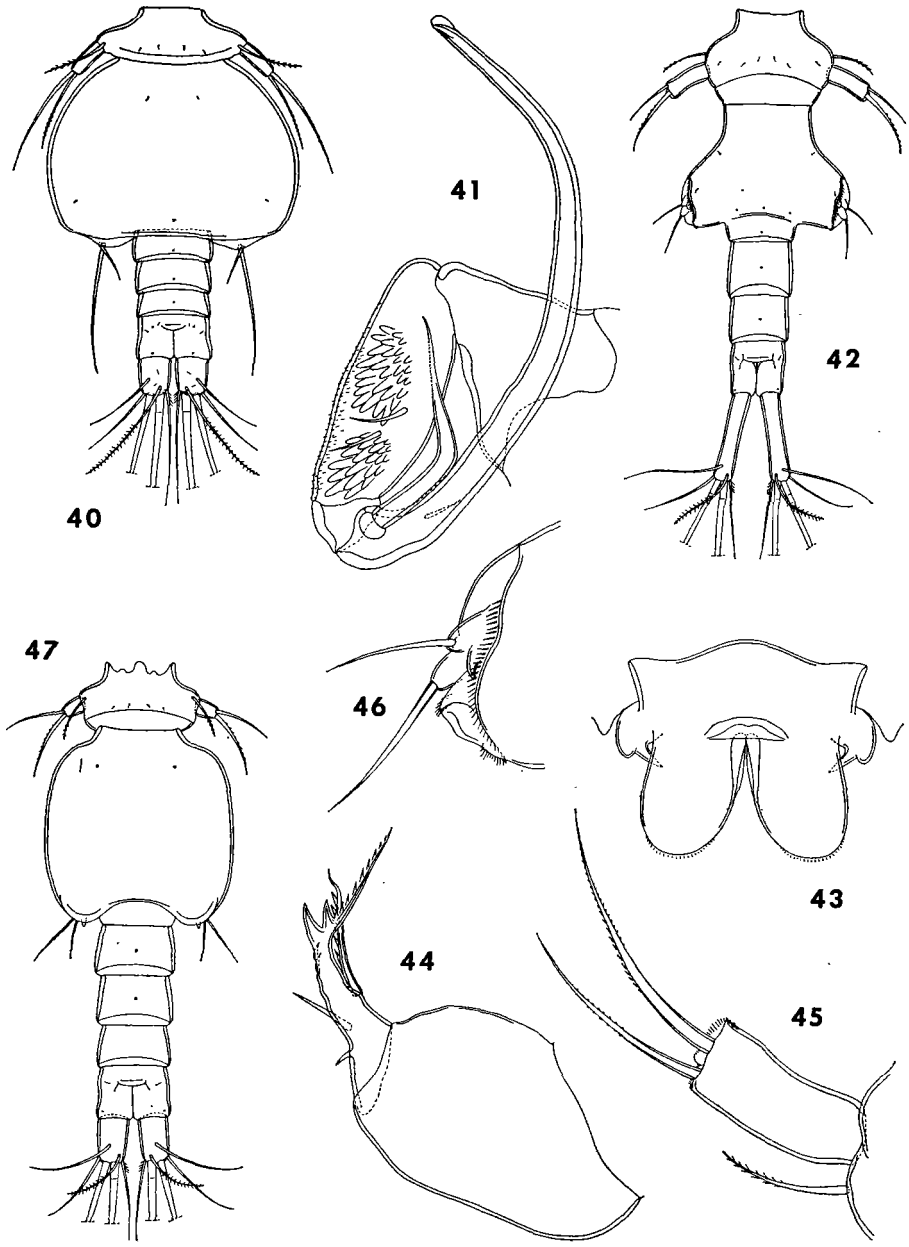

FIG. 40—41. *Scambicornus campanulipes* (Humes & Cressey, 1961), male: 40, urosome, dorsal (C); 41, maxilliped, postero-inner (C).

FIG. 42—46. *Scambicornus idoneus* (Humes & Cressey, 1961), female: 42, urosome, dorsal (B); 43, labrum, ventral (C); 44, second maxilla, anterior (D); 45, leg 5, dorsal (D); 46, area of attachment of egg sac and leg 6, dorsal (D).

FIG. 47. *Scambicornus idoneus* (Humes & Cressey, 1961), male: 47, urosome, dorsal (G).

from tidal change. Possibly this water movement may be related to the large numbers of eggs produced.

Redescription of certain *Scambicornus* species

The following five species are redescribed in part. The dissections upon which the original descriptions by Humes & Cressey (1961) were based were done in glycerine and studied in glycerine jelly mounts. I have restudied specimens of each of these species in lactic acid, using the method described by Humes & Gooding (1964). This technique better retains the original shape of the parts and allows greater visual discrimination of details. I find that certain features in the original descriptions need additions or corrections.

Scambicornus campanulipes (Humes & Cressey, 1961). Figs. 36—41.

Material examined. — From *Actinopyga lecanora* (Jaeger): 60 ♀♀, 84 ♂♂, and 38 copepodids from 5 hosts, intertidal, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, October 6, 1963; 21 ♀♀, 27 ♂♂, and 4 copepodids from 3 hosts, intertidal, Ambariobe, August 7, 1963; 14 ♀♀, 13 ♂♂, and 4 copepodids from 5 hosts in 1 m, Pte. Ambarionaomby, Nosy Komba, June 8, 1964; and 48 ♀♀, 61 ♂♂, and 57 copepodids from 5 hosts, intertidal, Ambariotelo, near Ambariobe, September 9, 1960. From *Actinopyga mauritiana* (Quoy & Gaimard): 17 ♀♀, 14 ♂♂, and 2 copepodids from 1 host in 0.5 m, Nosy Sakatia, near Nosy Bé, October 8, 1960; 62 ♀♀, 44 ♂♂, and 19 copepodids from 7 hosts in 2 m, Nosy Taolankena, near Nosy Bé, November 15, 1963; 2 ♀♀, 3 ♂♂, and 6 copepodids from 1 host in 2 m, Antsamantsara, north of Madirokely, Nosy Bé, December 15, 1963; 92 ♀♀, 29 ♂♂, and 7 copepodids from 10 hosts in 10 cm, Tany Kely, a small island to the south of Nosy Bé, May 27, 1964; and 84 ♀♀, 61 ♂♂, and 9 copepodids from 10 hosts, intertidal, Antsakoabe, Nosy Bé, September 7, 1964. From *Actinopyga miliaris* (Quoy & Gaimard): 20 ♀♀, 10 ♂♂, and 1 copepodid from 1 host in 20 cm, Ambariobe, August 6, 1960; 52 ♀♀, 151 ♂♂, and 114 copepodids from 16 hosts in 2 m, Pte. Lokobe, Nosy Bé, August 16, 1960; 93 ♀♀, 30 ♂♂, and 16 copepodids from 21 hosts in 0.5 m, Ambatoloaka, Nosy Bé, September 25, 1960; 5 ♀♀ from 60 hosts in 10 cm, Pte. Mahatsinjo, Nosy Bé, September 29, 1960; 19 ♀♀, 2 ♂♂, and 1 copepodid from 35 hosts in 1 m, Ambatoloaka, October 15, 1960; 11 ♀♀, 6 ♂♂ from 50 hosts in 1 m, Antsamantsara, October 31, 1960; and 13 ♀♀, 2 ♂♂ from 200 hosts in 10 cm, Ambatoloaka, May 26, 1964. From *Actinopyga echinites* (Jaeger): 3 ♀♀ from 10 hosts in 1 m, Tany Kely, May 27, 1964; and 65 ♀♀, 28 ♂♂, and 1 copepodid from 100 hosts in 1 m, Tany Kely, May 28, 1964.

New host records for this species are *Actinopyga lecanora* and *A. miliaris*.

Female. — Genital segment (fig. 36) with rounded lateral edges in dorsal view and with the two toothlike protuberances dorsolateral in position. Caudal ramus 60 × 35 μ. Rostral area lacking a well defined posteroventral border. Formula for the armature of the first antenna the same as in *S. lobulatus*. Labrum (fig. 37) with an auricular sclerotization at the outer base of each lobe. Maxilliped ornamented as in fig. 38. Formula for the armature of legs 1—4 the same as in *S. lobulatus*. Free segment of leg 5 (fig. 39) 62 × 49 μ, form than the longer barbed element (130 μ).

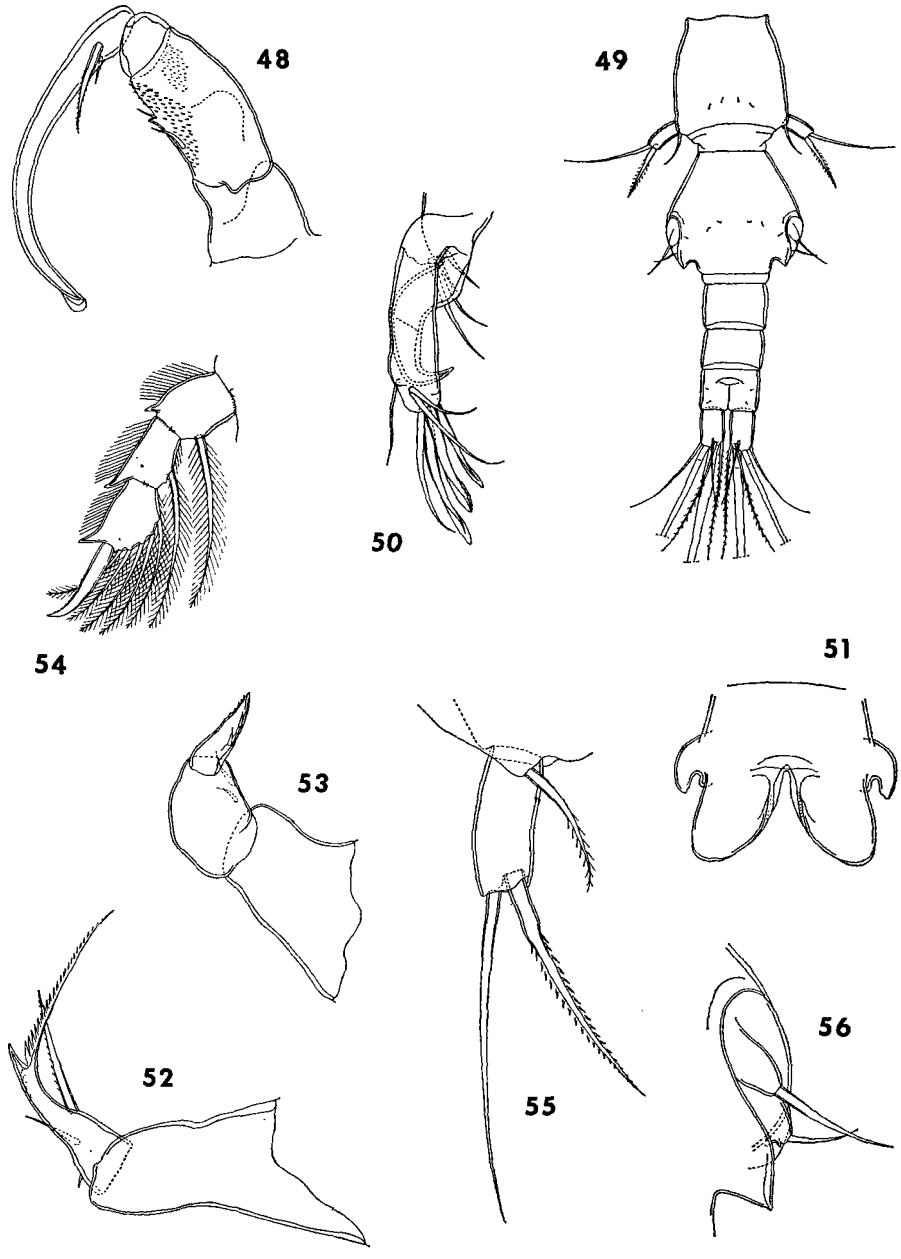

FIG. 48. *Scambicornus idoneus* (Humes & Cressey, 1961), male (continued): 48, maxilliped, posterior (C).

FIG. 49—56. *Scambicornus poculiferus* (Humes & Cressey, 1961), female: 49, urosome, dorsal (B); 50, distal part of second antenna, outer (C); 51, labrum, ventral (C); 52, second maxilla, anterior (D); 53, maxilliped, antero-outer (C); 54, endopod of leg 1, anterior (G); 55, leg 5, dorsal (D); 56, area of attachment of egg sac and leg 6, dorsal (D).

Male. — Genital segment (fig. 40) 156 × 203 μ, rounded laterally in dorsal view. Rostral area as in the female. First antenna with the formula for the armature as in *S. lobulatus*. Maxilliped as in fig. 41, with the two elements on the proximal region of the claw very unequal, the larger one strongly geniculate and delicately serrate distally.

Scambicornus idoneus (Humes & Cressey, 1961). Figs. 42—48.

Material examined. — From *Ludwigothuria atra* (Jaeger): 38 ♀♀ from 30 hosts in 10 cm, Nosy Faly, near Nosy Bé, October 21, 1960; and 22 ♀♀, 11 ♂♂, and 5 copepodids from 110 hosts in 1 m, Pte. Lokobe, Nosy Bé, October 27, 1960. From *Argiodia nobilis* (Selenka): 15 ♀♀, 25 ♂♂, and 2 copepodids from 2 hosts in 2 m, Nosy N'Tangam, near Nosy Bé, August 25, 1960; 3 ♀♀, 1 ♂ from 1 host in 2 m, Nosy N'Tangam, October 5, 1960; 1 ♀ from 1 host in 3 m, northern end of Nosy Sakatia, near Nosy Bé, October 8, 1960; 2 ♀♀ from 1 host in 2 m, Tany Kely, near Nosy Bé, October 9, 1960; 2 ♀♀, 7 ♂♂, and 1 copepodid from 4 hosts in 3 m, Nosy N'Tangam, August 8, 1963; 2 ♀♀ from 2 hosts in 2 m, Nosy Taolankena, near Nosy Bé, November 15, 1963; 2 ♂♂ from 3 hosts in 15 cm, Tany Kely, May 27, 1964; and 12 ♀♀, 14 ♂♂, and 7 copepodids from 10 hosts in 3 m, Sanitry, Nosy Bé, October 6, 1964. From *Holothuria scabra* Jaeger: 5 ♀♀, 3 ♂♂, and 1 copepodid from 8 hosts, intertidal, Antafianambitry, Nosy Bé, November 5, 1963; and 1 ♀ from 79 hosts, intertidal, Antafianambitry, December 4, 1963.

New host records for this species are *Argiodia nobilis* and *Holothuria scabra*.

Female. — Genital segment with lateral wings as in fig. 42. Rostral area without a well developed posteroventral border. First antenna segmented and armed as in *S. lobulatus*. Labrum (fig. 43) with a sclerotized expansion bearing a spiniform process at the outer base of each lobe. Second maxilla as in fig. 44. Formula for the armature of legs 1—4 as in *S. lobulatus*. Leg 5 as in fig. 45. Leg 6 as in fig. 46.

Male. — Genital segment (fig. 47) 110 × 105 μ, with subparallel lateral margins in dorsal view. Caudal ramus 28 × 17 μ, a little longer than wide. Rostral area as in the female. First antenna with the same formula for the armature as in *S. lobulatus*. Maxilliped (fig. 48) with an inner prominence near the base of the distal seta on the second segment.

Scambicornus poculiferus (Humes & Cressey, 1961). Figs. 49—60.

Material examined. — From *Synapta maculata* (Chamisso & Eysenhardt): 134 ♀♀, 117 ♂♂, and 22 copepodids from 1 host in 10 cm, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, October 6, 1963; 157 ♀♀, 310 ♂♂, and 122 copepodids from 1 host in 0.5 m, Ampombilava, Nosy Bé, October 31, 1963; 17 ♀♀, 15 ♂♂, and 4 copepodids from 1 host, intertidal, Antsakoabe, Nosy Bé, December 1, 1963; 14 ♀♀, 8 ♂♂ from 1 host in 1 m, crater at Ambatoloaka, Nosy Bé, January 7, 1964; and 36 ♀♀, 37 ♂♂, and 35 copepodids from 1 host in 1.5 m, Ambatoloaka, January 11, 1964.

Female. — Genital segment (fig. 49) with moderately developed wings. Caudal ramus 44 × 28 μ. Rostral area without a defined posteroventral

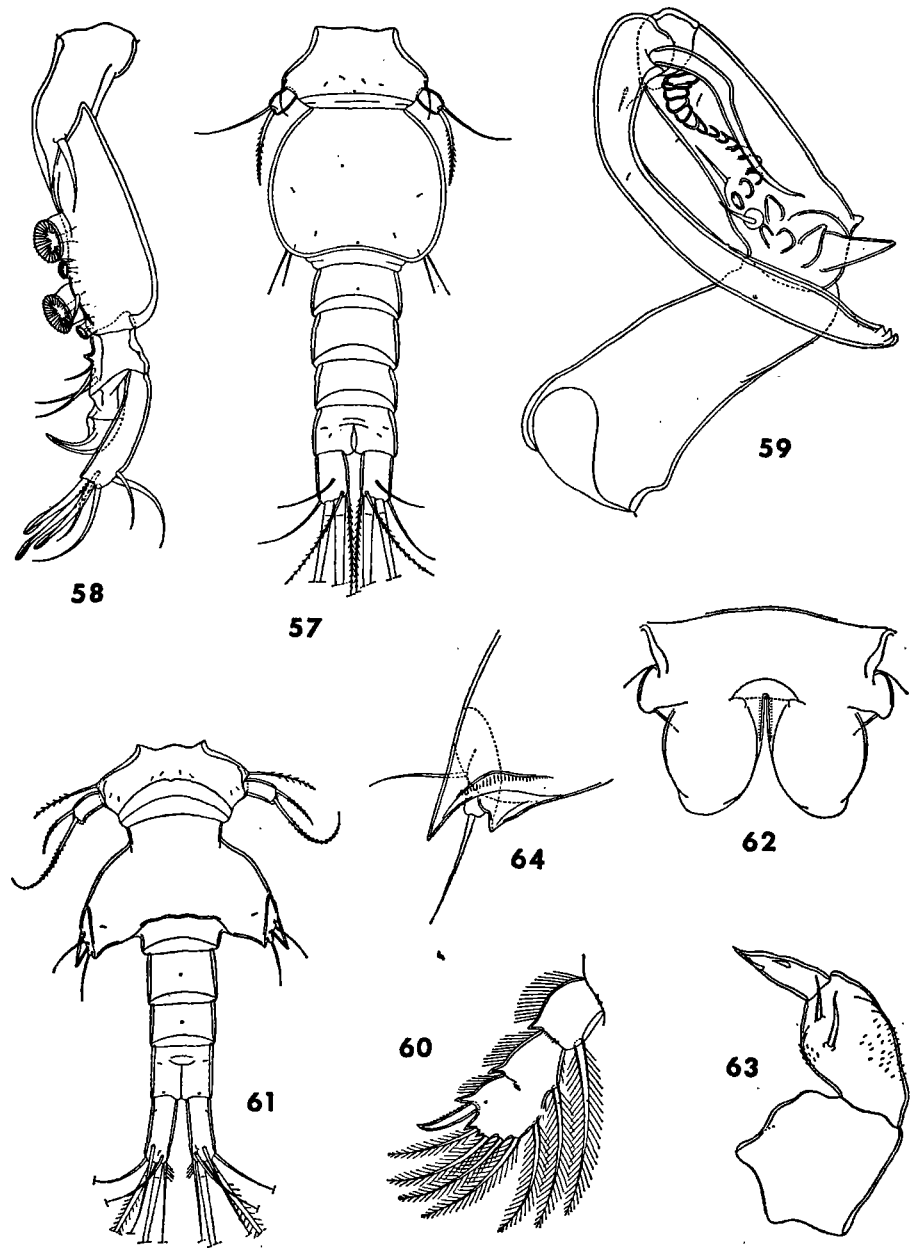

FIG. 57—60. *Scambicornus poculiferus* (Humes & Cressey, 1961), male: 57, urosome, dorsal (G); 58, second antenna, anterior (C); 59, maxilliped, postero-inner (C); 60, endopod of leg 1, anterior (C).

FIG. 61—64. *Scambicornus modestus* (Humes & Cressey, 1961), female: 61, urosome, dorsal (B); 62, labrum, ventral (C); 63, maxilliped, anterior (C); 64, area of attachment of egg sac and leg 6, ventral (C).

margin. First antenna segmented and armed as in *S. lobulatus*. Second antenna with the elongated last segment 64 × 18 μ (fig. 50). Labrum (fig. 51) with a recurved sclerotized expansion at the outer base of each lobe. Second maxilla as in fig. 52. Maxilliped as in fig. 53. Formula for the armature of legs 1—4 as in *S. lobulatus*. Endopod of leg 1 (fig. 54) with the formula for the last segment I, 5, not I, 4 as shown in fig. 136 of Humes & Cressey (1961). Free segment of leg 5 (fig. 55) 40 × 18 μ. Leg 6 as in fig. 56.

Male. — Genital segment (fig. 57) with rounded lateral margins in dorsal view. Caudal ramus 31 × 18 μ, longer than wide. Rostral area as in the female. First antenna apparently lacking an aesthete on the second segment, so that the formula is the same as for the female. Second antenna as in fig. 58. Maxilliped as in fig. 59, with two proximal elements on the claw. Endopod of leg 1 as in fig. 60.

Scambicornus modestus (Humes & Cressey, 1961). Figs. 61—66.

Material examined. — From *Stichopus chloronotus* (Brandt): 16 ♀♀, 18 ♂♂, and 2 copepodids from 2 hosts in 2 m, Pte. Lokobe, Nosy Bé, August 16, 1960; 28 ♀♀, 21 ♂♂, and 5 copepodids from 8 hosts in 15 cm, Tany Kely, near Nosy Bé, July 9, 1963; 3 ♀♀, 5 ♂♂, and 8 copepodids from 1 host in 1 m, Pte. Ambarionaomby, Nosy Komba, July 18, 1963; 3 ♀♀, 3 ♂♂ from 1 host in 10 cm, Ankify, on the mainland of Madagascar opposite Nosy Komba, July 22, 1963; 8 ♀♀, 6 ♂♂ from 4 hosts in 0.5 m, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, August 7, 1963; 5 ♀♀, 5 ♂♂ from 1 host in 1 m, Nosy N'Tangam, Nosy Bé, August 8, 1963; 9 ♀♀, 14 ♂♂, and 9 copepodids from 1 host in 10 cm, Nosy N'Tangam, September 5, 1963; 8 ♀♀, 7 ♂♂, and 2 copepodids from 1 host in 1 m, Pte. de Tafondro, Nosy Bé, October 2, 1963; 17 ♀♀, 24 ♂♂ from 8 hosts in 1 m, Nosy Mamoko, south of Nosy Bé in the Bay of Ampasindava, November 16, 1963; 29 ♀♀, 49 ♂♂, and 14 copepodids from 4 hosts in 1 m, Pte. Ambarionaomby, December 14, 1963; and 31 ♀♀, 29 ♂♂, and 4 copepodids from 2 hosts in 1 m, Pte. Ambarionaomby, June 8, 1964. From *Stichopus variegatus* Semper: 1 ♀, 1 ♂, and 2 copepodids from 1 host in 1 m, west of Pte. de Tafondro, October 19, 1960; and 48 ♀♀, 22 ♂♂, and 1 copepodid from 9 hosts in 10 cm, Ankify, June 11, 1964. From either *Microthele difficilis* (Semper) or *Urodemas ehrenbergi* Selenka (hosts mixed at time of collection): 1 ♀ from 5 hosts in 2 m, Pte. Ambarionaomby, August 18, 1960. From *Brandtothuria impatiens* (Forskål): 1 ♀ from 1 host in 2 m, Pte. Ambarionaomby, August 19, 1960.

New host records for this species are *Brandtothuria impatiens* and either *Microthele difficilis* or *Urodemas ehrenbergi*.

Female. — Genital segment (fig. 61) with expanded wings. Caudal ramus 72 × 33 μ. Rostral area lacking a definite posteroventral border. Segmentation and formula for the armature of the first antenna as in *S. lobulatus*. Labrum (fig. 62) with an expanded sclerotized expansion at the outer base of each lobe. Maxilliped as in fig. 63. Formula for the armature of legs 1—4 as in *S. lobulatus*, with the outer seta on the basis of legs 3 and 4 very long as in that species. Leg 6 as in fig. 64.

Male. — Genital segment (fig. 65) with rounded lateral margins in dorsal view. Caudal ramus 28 × 18 μ. Rostral area as in the female. First antenna

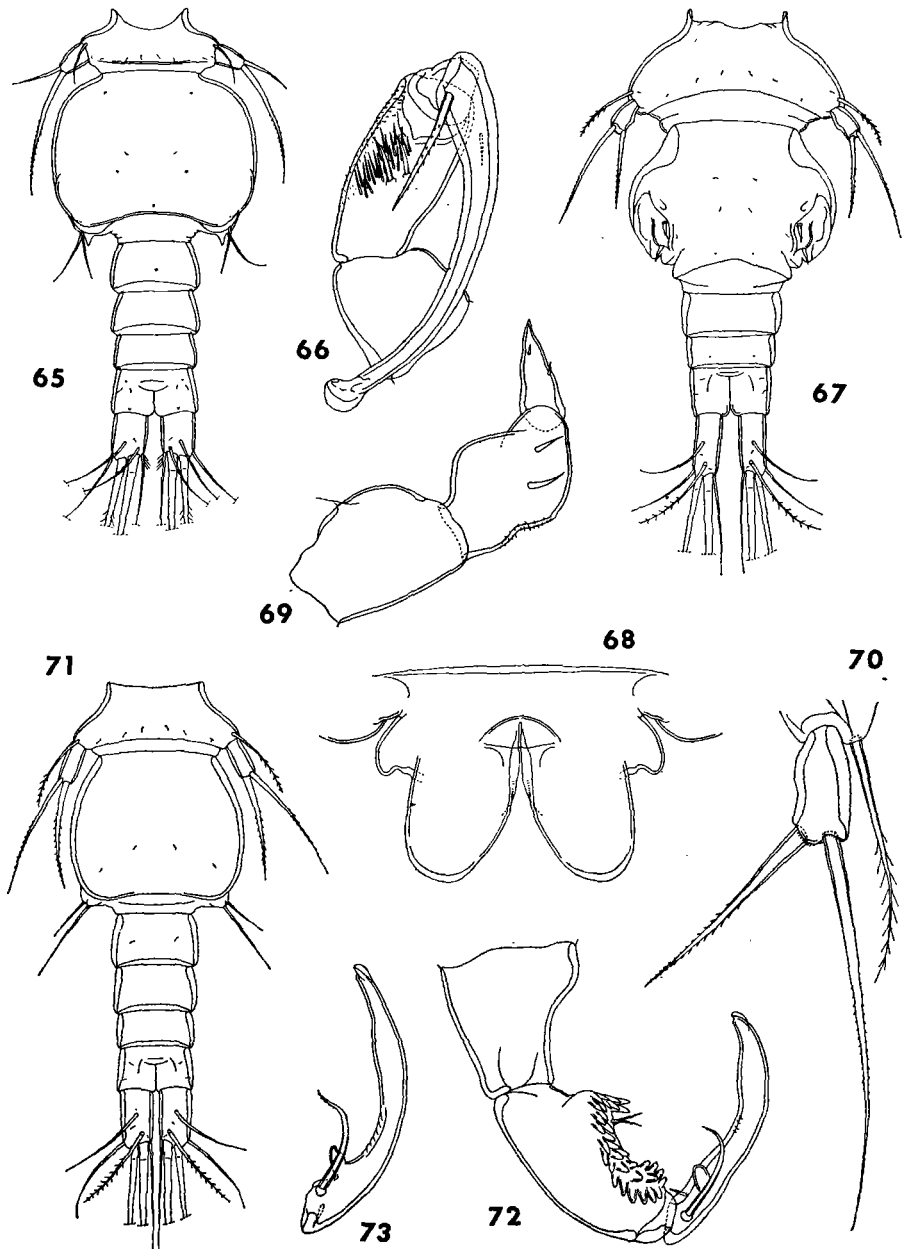

FIG. 65—66. *Scambicornus modestus* (Humes & Cressey, 1961), male: 65, urosome, dorsal (G); 66, maxilliped, postero-inner (C).

FIG. 67—70. *Scambicornus tuberatus* (Humes & Cressey, 1961), female: 67, urosome, dorsal (F); 68, labrum, ventral (C); 69, maxilliped, antero-inner (C); 70, leg 5, ventral (D).

FIG. 71—73. *Scambicornus tuberatus* (Humes & Cressey, 1961), male: 71, urosome, dorsal (G); 72, maxilliped, posterior (C); 73, claw of maxilliped, posterior (C).

with the formula for the armature as in *S. lobulatus*. Maxilliped as in fig. 66, the claw 153 μ in length, with two unequal proximal elements.

Scambicornus tuberatus (Humes & Cressey, 1961). Figs. 67—73.

Material examined. — From *Bohadschia marmorata* Jaeger: 8 ♀♀, 8 ♂♂, and 1 copepodid from 1 host in 2 m, Pte. Mahatsinjo, Nosy Bé, November 2, 1960; 53 ♀♀, 45 ♂♂, and 22 copepodids from 2 hosts in 1 m, Pte. Lokobe, Nosy Bé, November 5, 1960; 4 ♀♀, 1 ♂ from 4 hosts in 1 m, Antsamantsara, north of Madirokely, Nosy Bé, November 6, 1960; and 12 ♀♀, 5 ♂♂ from 5 hosts in 2 m, Nosy N'Tangam, near Nosy Bé, August 8, 1963.

Bohadschia marmorata is a new host record for this species.

Female. — Genital segment (fig. 67) in dorsal view with somewhat expanded and rounded lateral margins. Caudal ramus 50 × 21 μ. Rostral area lacking a definite posteroventral border. First antenna segmented and armed as in *S. lobulatus*. Labrum (fig. 68) with a sclerotized expansion at the outer base of each lobe. Maxilliped as in fig. 69. Formula for the armature of the legs as in *S. lobulatus*. Leg 5 (fig. 70) with the free segment 32 × 15 μ in greatest dimensions and with a sinuous inner margin; the two terminal elements 66 μ (inner) and 100 μ (outer) in length.

Male. — Genital segment (fig. 71) 88 × 97 μ, with rounded margins in dorsal view. Caudal ramus 39 × 18 μ. Rostral area as in the famele. First antenna with the same formula for the armature as in *S. lobulatus*, the aesthete on the second segment being very short. Maxilliped as in fig. 72, with two unequal proximal elements on the claw (fig. 73).

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VAHINIUS PETAX N. GEN., N. SP., A CYCLOPOID COPEPOD PARASITIC IN AN ANTIPATHARIAN COELENTERATE IN MADAGASCAR

BY

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During an expedition of the Academy of Natural Sciences of Philadelphia in 1960 several specimens of an antipatharian were dredged near Nosy Bé, in the northwestern part of Madagascar. From these coelenterates I recovered 42 individuals of the much modified cyclopoid copepod described below.

All figures in this paper were drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which the figure was drawn.

The study of the specimens has been aided by a grant from the National Science Foundation of the United States.

I wish to thank Dr. Elisabeth Deichmann of the Museum of Comparative Zoology, Harvard University, for the identification of the antipatharian.

VAHINIIDAE N. FAM.

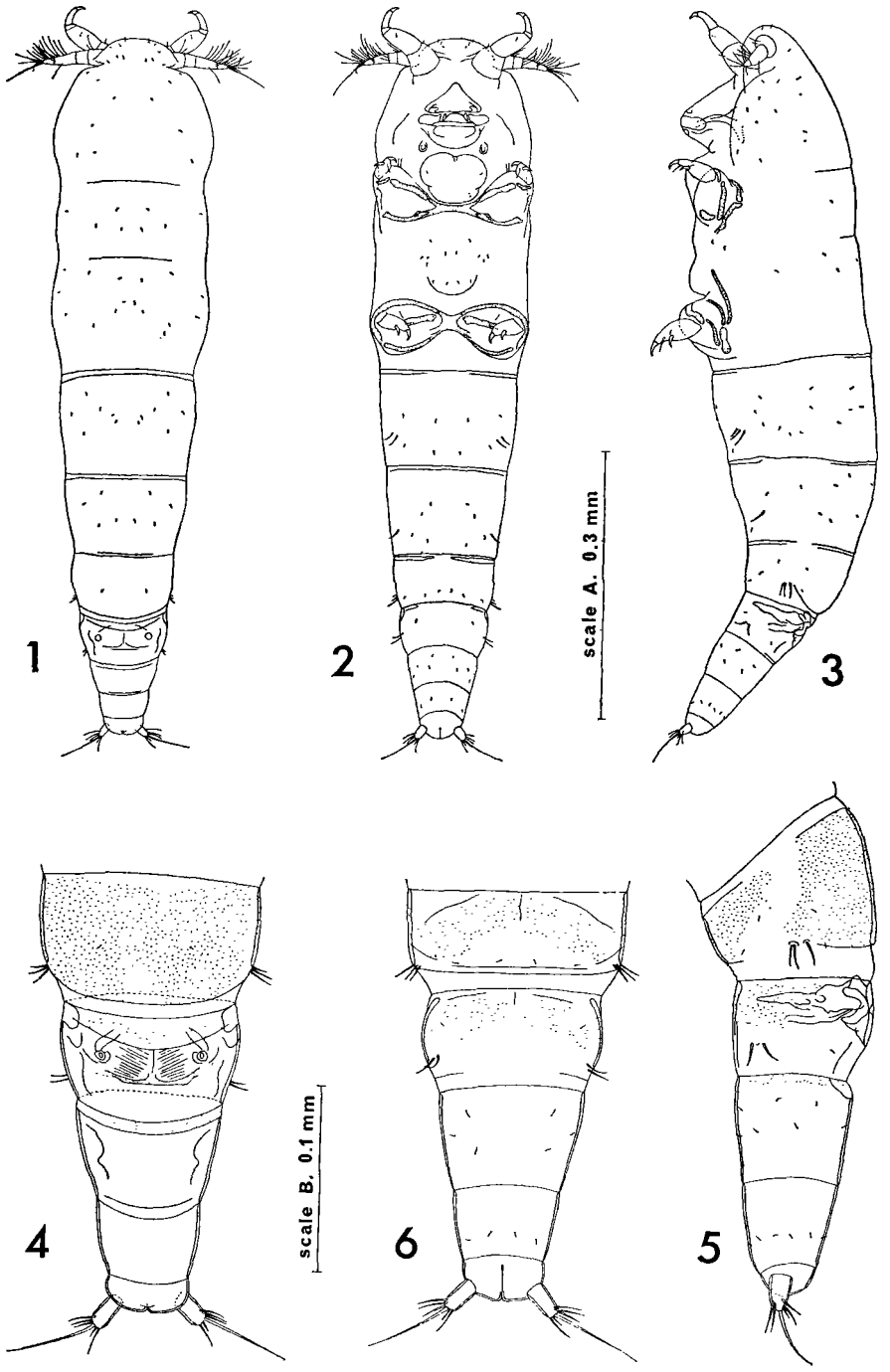
Vahinius n. gen.

Body elongated and slender. Metasomal segments without projecting lateral areas. Segment of leg 1 weakly delimited from the cephalosome. Urosome 5-segmented in both sexes. Caudal ramus with six setae. First antenna 3-segmented, with the middle segment incompletely divided. Second antenna 4-segmented with a terminal claw. Labrum and "labium" raised, embracing the mandibles and the two pairs of maxillae, forming thus a low cone. Both mandible and first maxilla minute, slender, styliform. Second maxilla much larger, unsegmented, with obtuse oblique tip and a subterminal setule. Maxilliped in the female reduced to a small rounded sclerotized process, but well-formed in the male, where it is 4-segmented (the fourth segment being interpreted as part of the claw).

Leg 1 with a 2-segmented exopod, the endopod consisting of two setae. Leg 2 with a similar 2-segmented exopod, the endopod represented by a single seta. Leg 3 indicated by three setae and leg 4 by a single seta. Leg 5 consisting of three setae and leg 6 of two setae in both sexes.

Other features as in the species described below.

Living in Antipatharia.



Figs. 1-6. *Vahinius petax* n. gen., n. sp., female. 1, dorsal (A); 2, ventral (A); 3, lateral (A); 4, urosome, dorsal (B); 5, urosome, lateral (B); 6, urosome, ventral (B).

Type and only known species: *Vahinius petax* n. sp.

The generic name is a Latinized form of *vahiny*, a Madagascan word meaning a guest or visitor, and thus alluding to the association with the antipatharian.

Gender masculine.

Vahinius petax n. sp.

(figs. 1-25)

Type material. — 24 females and 18 males from washings of several incomplete specimens of the antipatharian *Stichopathes echinulata* Brook, dredged in 30 m, 13° 32′ 18″ S, 48° 12′ 30″ E, south of Tany Kely, near Nosy Bé, Madagascar. Collected September 17, 1960. Holotype female, allotype, and 31 paratypes (17 females and 14 males) deposited in the United States National Museum, Washington; the remaining paratypes in the author's collection.

Female. — The body (figs. 1, 2, 3) is elongated, the prosome being somewhat cylindrical with the metasomal segments not produced laterally. The length (without the caudal setae) is 0.78 mm (0.74-0.81 mm) and the greatest width (at the level of the segment of leg 2) is 0.19 mm (0.17-0.20 mm), based on 10 specimens. The segment of leg 1 is separated from the cephalosome only by a weak transverse dorsal furrow, and from the segment of leg 2 by a similar furrow. The segments of legs 3, 4, and 5 are more distinctly separated from each other and from the genital segment. The cephalosome is nearly as wide as the segment of leg 2. In front of the second pair of legs there is a midventral protrusion (figs. 2, 3); at this point the thickness of the body is about 175 μ. The ratio of the length to the width of the prosome is about 3.22 : 1.

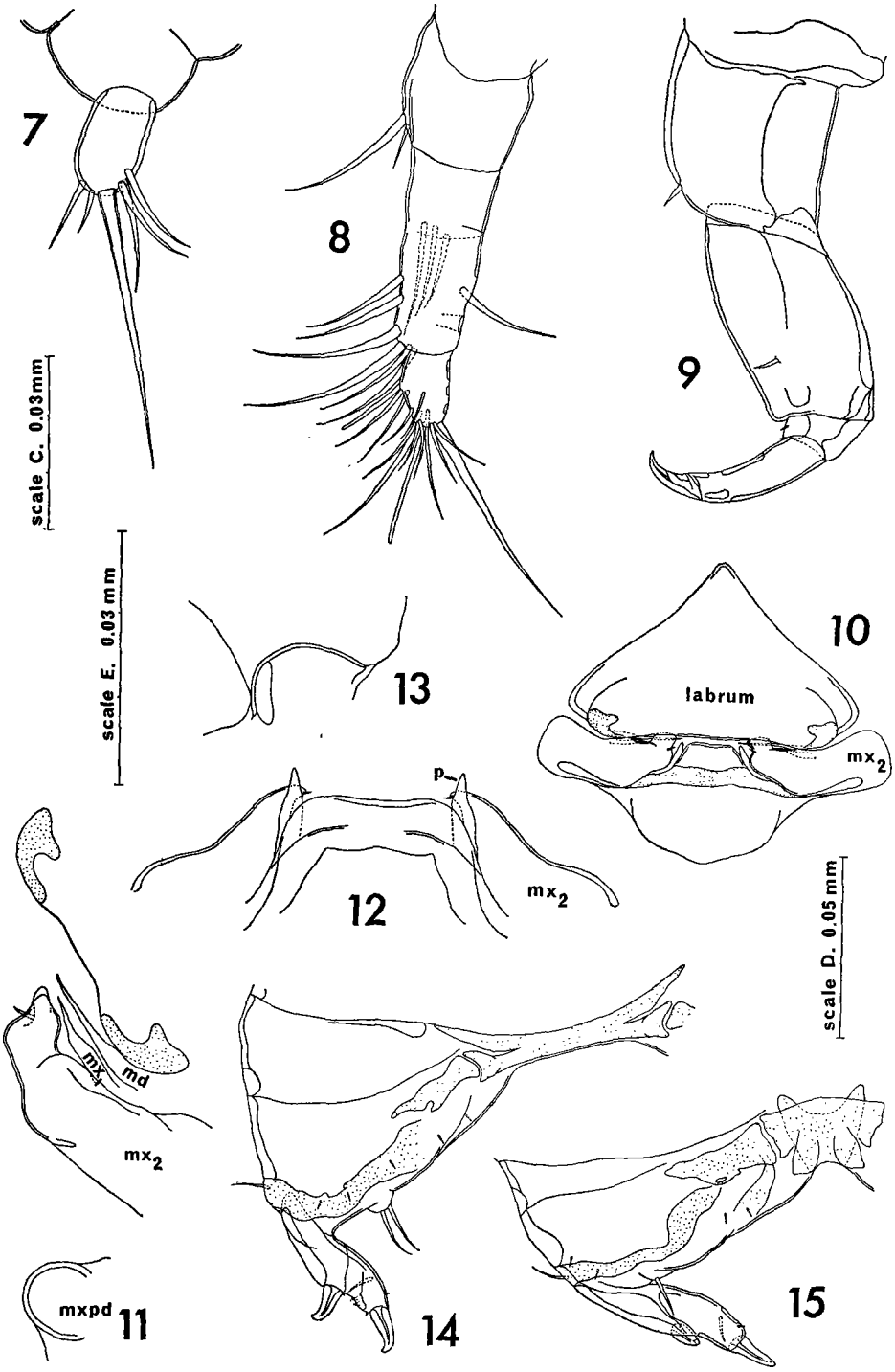
The 5-segmented urosome (figs. 4, 5, 6) is bent slightly ventrally in specimens preserved in alcohol, the segment of leg 5 being longer dorsally than ventrally, and measuring in dorsal view 65 × 118 μ. The genital segment, 55 × 100 μ, bears the oviducal openings dorsally in its anterior half (fig. 4). There are no setae close to these openings (as there are in many other cyclopoids), but instead there are two setae rather far removed, located ventrolaterally on the segment (figs. 5, 6) and probably representing leg 6. No egg sacs were present on the females examined. The three postgenital segments diminish in width posteriorly, and measure 57 × 70, 44 × 52, and 20 × 44 μ respectively.

The minute caudal rami are held in a diverging position. Each unornamented ramus (fig. 7) is 21 × 12 μ, and bears six naked setae, one of them much longer (53 μ) and stouter than the others.

The surfaces of the prosome and urosome bear minute setules as indicated in the figures. In addition, there are regions of very minute surficial punctations (shown in figs. 4, 5, and 6, but omitted from figs. 1, 2, and 3). The ratio of the length of the prosome to that of the urosome is about 2.8 : 1.

The rostral area is not developed.

The first antenna (fig. 8) has three distinct segments, with the middle one showing an indistinct division on its anteroventral surface. The lengths of the segments are 23, 35, and 12 μ respectively (measured along their anterior margins),



Figs. 7-15. *Vahinius petax* n. gen., n. sp., female. 7, caudal ramus, ventral (C); 8, first antenna, posterodorsal (C); 9, second antenna, postero-inner (C); 10, labrum, "labium", and associated mouthparts, forming oral cone, ventral (D); 11, edge of labrum, mandible, first maxilla, second maxilla, and maxilliped, the parts slightly separated, ventral (C); 12, edge of "labium" showing paragnaths (?), posterior (C); 13, maxilliped, lateral (E); 14, leg 1, anterior (D); 15, leg 2, anterior (D).

the entire appendage being only 70 μ long. The first segment bears two unequal setae. The second segment has ten setae, three of them on the anteroventral surface proximal to the incomplete division. The third segment bears twelve setae and two short aesthetes, the proximal aesthete being very slender and setiform. The longest terminal seta is 39 μ in length. All the setae are naked.

The second antenna (fig. 9) is 4-segmented, the segments measuring 30, 34, 9, and 20 μ respectively along their outer margins. Including the claw, this appendage is distinctly longer (about 105 μ) than the first antenna. Each of the first two segments bears a small inner seta. The short third segment has two minute inner setules. The slender fourth segment is unarmed. The terminal claw is 13 μ long (measured along its greatest axis).

The labrum and "labium" (fig. 10) consist of broad flaps raised ventrally from the surface of the cephalosome to form a low cone (see fig. 3). Between these two structures lie the mouthparts, with the exception of the maxillipeds. Just posterior to the labrum and largely obscured by it in ventral view there are on either side two elongated styliform elements (fig. 11), the anterior one being interpreted as the mandible and the other as the first maxilla. The unsegmented second maxilla (fig. 11) largely fills the space between the labrum and "labium". Its distal part is somewhat irregular in shape, with an oblique obtuse tip and a subterminal setule. Just anterior to the "labium" there are two pointed hyaline processes (fig. 12) which may be paragnaths. They appear to be rather distant from the region of the mandibles and first maxillae where one would expect to find them. On the other hand, it is virtually impossible to distinguish these minute mouthparts without dissection, and once a dissection has been made the true spatial relationships of the appendages are usually distorted.

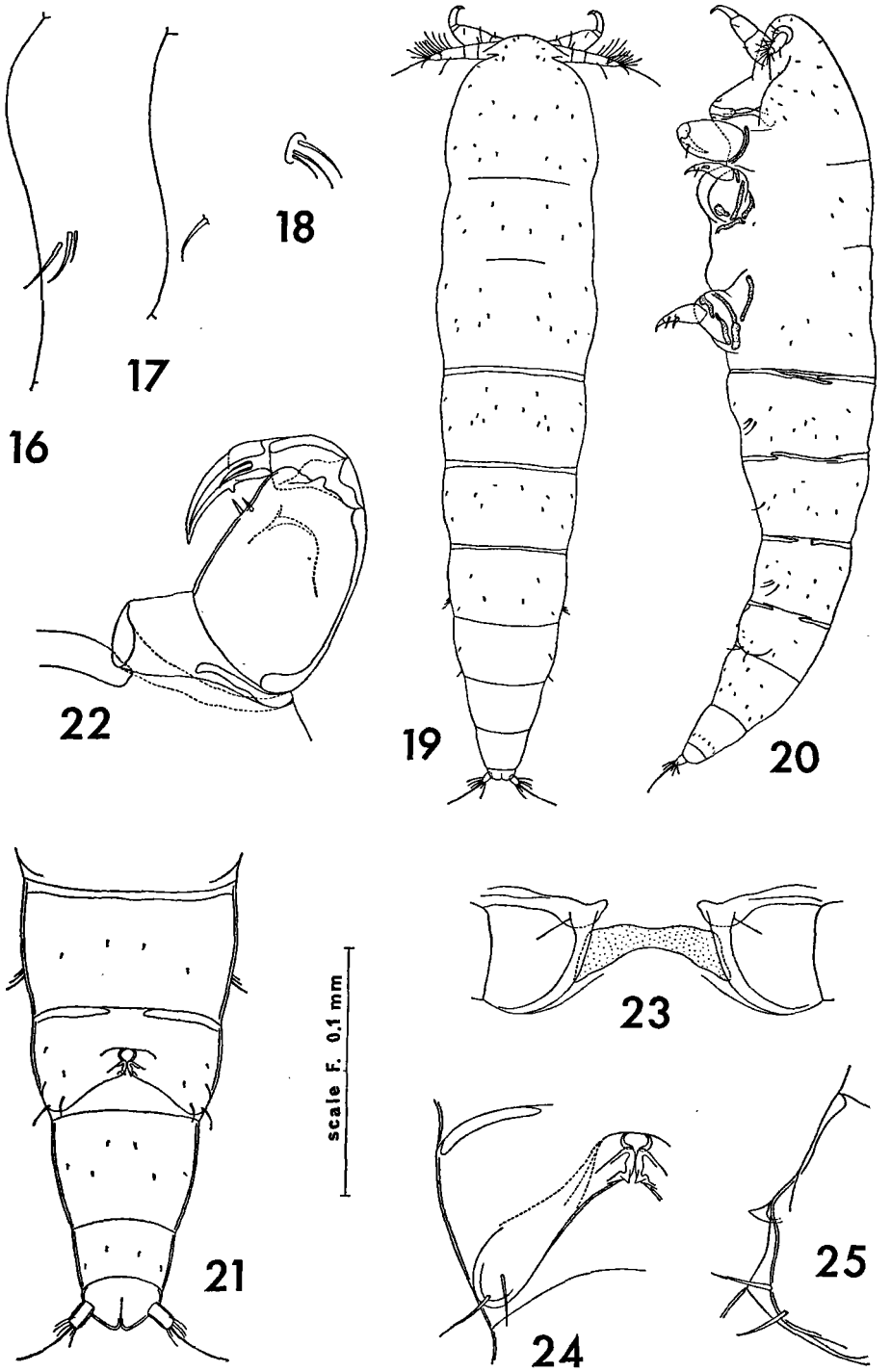
The maxilliped (figs. 2, 11, 13) consists of a small sclerotized rounded knob located posteriorly and somewhat laterally to the oral cone.

Between the maxillipeds and the first pair of legs the ventral surface of the cephalosome is expanded into a tripartite balloonlike swelling (see figs. 2 and 3).

The first two pairs of legs are prominent, both with sclerites in the protopodal area (figs. 2, 3). The third and fourth legs are vestigial, represented only by a few setae and lacking a protopod and sclerites. The spine and setal formula for legs 1-4 (figs. 14, 15, 16, 17) may be shown as follows (the Roman numerals indicating spines, the Arabic numerals setae):

P 1	protopod	1-0	exp	I-0; I-1
			end	2
P 2	protopod	1-0	exp	I-0; I-1
			end	1
P 3			3	
P 4			1	

The two legs of the first pair (fig. 14) are set rather far apart (fig. 2) with a long intercoxal sclerite between them. No evidence of a distinction between



Figs. 16-18. *Vahinius petax* n. gen., n. sp., female. 16, leg 3, lateral (D); 17, leg 4, lateral (D); 18, leg 5, lateral (D).

Figs. 19-25. *Vahinius petax* n. gen., n. sp., male. 19, dorsal (A); 20, lateral (A); 21, urosome, ventral (B); 22, maxilliped, posterior (D); 23, bases of maxillipeds and intermaxillipedal sclerite, ventral (F); 24, leg 6, ventral (D); 25, leg 6, lateral (D).

coxa and basis was seen, the basal area of the leg consisting of an undivided protopod. On the posterior distal surface of the protopod there is a row of five widely spaced small hyaline setules. The outer protopodal seta is small and naked. The exopod is 2-segmented, each of the segments bearing a clawlike naked outer spine directed posteriorly. In addition, the second segment has a small naked seta on its posterior surface and is ornamented on its outer edge with two small spine-like processes and a minute setule and on its inner edge with a minute hyaline setule. The endopod is represented only by two slender naked setae about 15 μ in length.

The two legs of the second pair (fig. 15) are set rather close together (fig. 2) with a short intercoxal sclerite between them. In general, the second leg is similar to the first, except that there are four setules on the posterior distal surface of the protopod, the second segment of the exopod has a fine ornamentation of only an inner setule, and the endopod consists of a single seta.

Leg 3 (fig. 16) is ventrolateral in position and is represented by three naked setae, one 17 μ long and slightly set apart from the other two which are 17 and 8 μ in length.

Leg 4 (fig. 17) is reduced to a single naked seta 16 μ long and ventrolateral in position.

Leg 5 (fig. 18) is lateral in position (figs. 3, 5) and consists of three naked setae, the dorsal one 17 μ long and set apart from the other two which are 17 and 10 μ long.

Leg 6 (fig. 5) is represented by the two setae already mentioned on the ventrolateral areas of the genital segment. Between these two setae there is a minute sclerotization.

The color in life in transmitted light is slightly amber, the eye red.

Male. — The form of the body (figs. 19, 20) resembles that of the female. The length (not including the setae on the caudal rami) is 0.80 mm (0.74-0.85 mm) and the greatest width (at the level of the segment of the second pair of legs) is 0.19 mm (0.17-0.20 mm), based on 10 specimens. The ratio of the length of the prosome to its width is 3.17 : 1.

The urosome (fig. 21) is 5-segmented as in the female. The segment of leg 5 is 72 $\times$ 117 μ in ventral view. The genital segment is 57 $\times$ 104 μ. The three postgenital segments are 60 $\times$ 78, 34 $\times$ 52, and 24 $\times$ 43 μ respectively.

The caudal ramus is like that of the female.

The ratio of the length of the prosome to that of the urosome is about 2.2 : 1.

The rostral area, first antenna, second antenna, labrum, mandible, paragnath (?), first maxilla, second maxilla, and "labium" resemble those of the female.

The maxilliped (fig. 22), in contrast to the condition in the female, is well-developed. It consists of four segments (assuming that the basal part of the claw represents the fourth segment). The first segment is short and poorly delimited from the body, being expanded on the inner side. The second segment

is large and bears two small naked hyaline inner setae 4.5 μ in length, but has no fine ornamentation. The third segment is short and turned inwardly. The claw, 33 μ in length (measured along its greatest axis), is directed back along the second segment, and bears a small knob (2.2 μ long) on its concave edge and a naked seta (15 μ long) on the basal area of its posterior surface. Just distal to the insertion of this seta there may be seen a slight indication of division in the claw, perhaps marking the distal boundary of the fourth segment. Between the bases of the maxillipeds there is a well-formed intermaxillipedal sclerite (fig. 23).

There is a balloonlike swelling between the maxillipeds and the first pair of legs as in the female.

Legs 1, 2, 3, 4, and 5 resemble those of the female.

Leg 6 (fig. 24) consists of a posteroventral flap on the genital segment bearing two slender naked setae. Medially at the junction of the two flaps of leg 6 there are two small erect spinelike sclerotizations, best seen in lateral view (fig. 25).

Spermatophores were not observed.

The color in life in transmitted light resembles that of the female.

The specific name *petax* (Latin, = striving or seeking after) refers to the grasping nature of the second antenna and the first two pairs of legs.

Relationship to the host. — The 42 specimens of *V. petax* were recovered from the sediment obtained after washing the antipatharian twice in sea water with about 2 per cent ethyl alcohol. The second such washing produced 10 copepods, suggesting that the copepods live in the polyps. (In the case of loosely associated external copepods all would probably be dislodged from the host during the first washing.) The recovery of relatively large numbers of copepods from the first washing may be accounted for by the fact that a lapse of about 10 hours occurred between the placing of the live antipatharian in a pail of sea water and the first washing in the same sea water plus alcohol. Presumably these copepods, subjected in the laboratory to increased temperatures and to the accumulation of products of decay after the death of the antipatharian, gradually leave the polyps. Furthermore, the weak alcohol may stimulate the copepods to emerge from the polyps. Similar recovery of large numbers of copepods after the hosts had remained in the laboratory for several hours was observed in the case of *Xarifia* by Humes (1962a) and *Kombia* by Humes (1962b).

Systematic relationships. — The general aspect of *Vahinius* suggests possible affinity with the family Lamippidae De Zulueta, 1908, the genera of which are parasitic in octocorals. There are, however, rather fundamental differences in the detailed external structure. Bouligand (1960a) included six genera in the Lamippidae (*Lamippe* Bruzelius, 1858, *Lamippina* Bouligand, 1960, *Enalcyonium* Olsson, 1869, *Lamippella* Bouligand & Delamare Deboutteville, 1959, *Linaresia* De Zulueta, 1908, and *Isidicola* Gravier, 1914). In this family the thin integument

lacks evident segmentation; there is usually a characteristic triangular sclerotized buccal complex and the mouthparts are extremely reduced or absent though Bouligand (1960b, fig. 6, b''_1) shows what is presumed to be a mandible in *Enalcyonium rubicundum* (Olsson, 1869) and Heegaard (1949) describes a small 2-segmented mandible and a rudimentary maxilliped in *Lamippe rubra* Bruzelius, 1858 (which Bouligand, 1960, holds to be a new species, *Enalcyonium heegaardi*); the maxillipeds may be 3-segmented or absent; there are only two pairs of legs; and the reduced caudal ramus is variable in form. These features indicate a natural assemblage of genera forming the Lamippidae. *Vahinius,* on the other hand, has rather distinct segmentation, well-developed caudal rami, better developed mouthparts, strongly sexually dimorphic maxillipeds, and legs 1-4 (though legs 3 and 4 are reduced), leg 5, and leg 6. These features exclude the new genus from the Lamippidae.

A second family of copepods living in anthozoans, the Xarifiidae Humes, 1960, has a general aspect quite different from *Vahinius.* This family includes two genera, *Xarifia* Humes, 1960, and probably also *Kombia* Humes, 1962, both of which live in madreporarian corals. In the ten species of *Xarifia* the segmentation is weakly defined, the region dorsal to the fifth legs in the female usually bears posteriorly directed processes, the maxilliped in the female is 2-segmented, and legs 1-4 are biramous and nearly equally developed (Humes, 1960, 1962a). In the single known species of *Kombia* the prosome is distinctly stouter than the urosome; the mouthparts are lichomolgic with a relatively well-developed mandible, first maxilla, and second maxilla; the maxilliped in both sexes is apparently 3-segmented though larger in the male; and legs 1 and 2 are biramous, leg 3 uniramous, and leg 4 absent (Humes, 1962b). On the basis of these differences it does not seem possible to include *Vahinius* in the Xarifiidae.

The structure of the mouthparts would seem to offer the soundest basis for determining the systematic position of *Vahinius.* Previous workers have emphasized the great significance of the structure and general arrangement of the buccal appendages in the Copepoda (for example, Bocquet & Stock, 1957). The mouthparts of *Vahinius* appear to be fundamentally different from those of either the Lamippidae or the Xarifiidae, and indeed from those of any poecilostome known to me. It is primarily for this reason that *Vahinius* is regarded as sufficiently distinct from other poecilostomes to warrant the establishment for it of a new family, the Vahiniidae.

The conclusions reached here regarding the systematic position of *Vahinius* are based upon the external morphology of what are presumed to be adult animals. Since none of the females carried egg sacs, it was impossible to attempt to learn anything of the developmental stages. Perhaps, as Bouligand (1960b) has reported for the Lamippidae, *Vahinius* does not form egg sacs.

The morphological aberrations of the adults in many parasitic genera of poecilostomes make it extremely difficult to determine their systematic relationships. In spite of the great technical difficulties in obtaining information on the develop-

mental stages of parasitic groups such as *Vahinius,* it is hoped that future investigations will elucidate their ontogeny and thus clarify their systematic relationships.

For the present, the poecilostomatous family Vahiniidae may be placed near the Lamippidae and the Xarifiidae.

RÉSUMÉ

Description de *Vahinius petax,* nouveau genre et nouvelle espèce de copépode cyclopoïde parasite d'un antipathaire, *Stichopathes echinulata* Brook, à Madagascar. Ce copépode se place dans une famille nouvelle, les Vahiniidae, près des Lamippidae et des Xarifiidae.

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Die physiographische Zonierung der Saumriffe von Sarso

4. Beitrag der Arbeitsgruppe Litoralforschung

von

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The physiographic zonation of the margin reefs of Sarso

Summary

1. The physiographical zones of the coast of the islands Sarso and Sindi Sarso (Farsan Archipelago, Red Sea) were analyzed by 3 profiles. As shore types a steep coast with an eroded eulitoral platform, a steep coast without such a platform and a sandbeach were selected.

2. The most conspicuous and characteristic fishes, invertebrates and algae were identified, their distribution and zonational limit were studied.

3. In contrast to a normal fringing reef the whole litoral area of these islands is of coral origin. The islands themselves are raised subfossil reefs from the early pleistocene or late tertiary. The recent reefs are based on eroded platforms of these subfossil reefs.

4. Terrestially and subaquatically there are distinguishable different water level marks. They may be the result not only of tectonic occurrences, but also of eustatic changes of the sea-level by glacial origin.

5. The litoral area along the NE coast of the island Sarso was mapped. The 3 zones were studied and described as cross-sections.

6. Samples of the characteristic lime stone of different zones were studied and identified as of only corallogene.

7. As profile II is distinguished from profile I only by the sedimentation of sand upon the eroded platform along the beach there are great morphological and ecological differences between profile I and III.

8. A reconstruction of the reef development of profiles I and III by raising sea-level was tried. Despite the morphological differences there are many important geological coincidences.

Zusammenfassung

1. An den Küsten der Inseln Sarso und Sindi Sarso der Farasan-Gruppe (Rotes Meer) wurden zur Feststellung der physiographischen Zonierung drei Profile gelegt. Als Küstentypen wurden eine Steilküste mit Abrasionsterrasse, eine Steilküste ohne Abrasionsterrasse und eine Sandküste gewählt.

2. Die auffälligsten Bewohner unter den Fischen, Evertebraten und Algen sowie deren Verbreitung bzw. zonale Bindung wurden festgestellt.

3. Im Gegensatz zu einem Saumriff normalen Typs ist bei diesen Inseln das gesamte Litoral corallogenen Ursprungs. Die Inseln sind gehobene subfossile Riffe, die wahrscheinlich im frühen Pleistozän oder späten Tertiär entstanden sind. Die rezenten Riffe ruhen auf erodierten Plattformen, die die Abrasionsterrassen jener subfossilen Riffe sind.

4. Emers und submers sind ± deutliche Wasserstandsmarken festzustellen. Sie dürften nicht nur auf tektonische Vorgänge, sondern auch auf glaziale eustatische Schwankungen des Wasserspiegels zurückzuführen sein.

5. Vor der Nordost-Küste von Sarso wurde das Litoral mit den Zonen kartiert. Die drei Profile wurden im Schnitt dargestellt und beschrieben.

6. Gesteinsproben der durch Kalkstein geprägten Zonen wurden durch Schnitte analysiert und bewiesen deren rein corallogenen Charakter.

7. Während sich Profil II von Profil I nur durch die Überlagerung von Sand auf der Abrasionsplatte im Küstenbereich unterscheiden, bestehen zwischen Profil I und III zahlreiche wesentliche morphologische und ökologische Unterschiede.

8. Es wurde eine Rekonstruktion der Riffbildung beider Inseln im Bereich der Profile I und III bei ansteigendem Wasserstand versucht. Trotz der morphologischen Unterschiede lassen sich an beiden Riffen zahlreiche historische Koinzidenzen erkennen.

I. Einleitung

Während des zweiwöchigen Aufenthaltes auf der Insel Sarso (arab. Sarso kebir) des Farasan-Archipels im südlichen Roten Meer (vgl. GERLACH, 1967a) untersuchte der Verfasser nicht nur die Fischwelt der küstennahen Gewässer, sondern auch deren Lebensraum von der Strandzone bis zum Außenriff. Wie zu erwarten, erwies sich dieser Abschnitt nicht als einheitlich, sondern ließ verschiedene physiographische Zonen erkennen. Durch drei Profile (Abb. 1) konnte die Zonierung drei verschiedener Küstentypen, nämlich einer Steilküste mit Abrasionsplatte, einer Sandküste und einer Steilküste ohne Abrasionsplatte miteinander verglichen werden.

Abb. 1. Die beiden Inseln Sarso (arab. Sarso kebir) und Sindi-Sarso (arab. Sarso seghir) mit den drei von uns gelegten Profilen. Sämtliche Originalzeichnungen: R. KLEIN-RÖDDER, Senckenberg-Museum.

Fig. 1. The two islands Sarso and Sindi-Sarso (arab. Sarso kebir and seghir) with the location of the three described profiles. All original drawings by R. KLEIN-RÖDDER, Senkenberg-Museum, Frankfurt a. M.

Die auffälligsten Bewohner unter den Fischen, Evertebraten und Algen wurden festgestellt (eine genaue botanische Analyse der physiographischen Zonen folgt von SIMONSEN). Die in diesem Bericht angeführten Pflanzen wurden in dankenswerter Weise von Dr. Y. LIPKIN, Tel-Aviv, und Dr. H. LANGE, Frankfurt a. M., determiniert. Ebenso danke ich den Herren Dr. G. SCHEER und Dr. A. ZILCH für die Bestimmung von Korallen bzw. Mollusken, Herrn Dr. S. RIETSCHEL für die Schnitte und Aufnahmen der Gesteinsproben. Für die finanzielle Unterstützung zur Teilnahme an der „Meteor"-Expedition möchte ich auch an dieser Stelle der Deutschen Forschungsgemeinschaft meinen Dank aussprechen.

Aus Mangel an Zeit, Personal und technischem Gerät war es uns allerdings nur möglich, örtliche Profile anzulegen und weder die Inseln in ihrer vollen Größe kartographisch aufzunehmen, noch die weiteren Verhältnisse unter Wasser zu untersuchen. So wäre besonders eine Vermessung durch Echolot westlich von Sarso und östlich von Sindi Sarso* (arab. Sarso seghir) nötig. Im erstgenannten Fall scheint ein breites submerses, aber sehr flaches Plateau vorzuliegen, während im zweiten Fall abrupt ein tiefer Abschnitt anschließt. Hierzu wäre ein geeignetes Litoralschiff oder zumindest ein entsprechend ausgestattetes Verkehrsboot notwendig.

II. Historischer Überblick

Schon recht frühzeitig haben topographische Untersuchungen verschiedener Autoren ergeben, daß Korallenriffe keine einheitlich gestalteten Komplexe sind, sondern aus einer Reihe ± deutlich abgrenzbarer Abschnitte bestehen. Bedingt ist solche morphologische und ökologische Aufgliederung vorzugsweise durch verschiedene abiotische Faktoren, wie Wellenbildung, Brandung, dominierende Wellen- und Strömungsrichtung, Gestaltung des Untergrundes, mögliche Küstennähe, Inselbildung innerhalb eines Riffes usw. Als erster hat DARWIN (1842) die Strukturierung von Riffen erkannt und geschildert. In der Folgezeit haben GARDINER (1902, 1903a, b, 1905/6) und AGASSIZ (1903) verschiedene Riffabschnitte unterschieden. Während diese Autoren aber ausschließlich Atollriffe untersuchten und beschrieben, hatte KLUNZINGER (1870) als erster ein Saumriff, und zwar bei Qoseir (= Kosseir) an der Westküste des Roten Meeres, mit dessen Zonierung und Tierwelt sehr genau dargestellt.

Da diese Arbeit nicht nur auf einer achtjährigen Untersuchungszeit am Ort beruhte, sondern trotz der beschränkten Beobachtungsmöglichkeiten (Schwimmtauchen kannte der Zoologe jener Zeit noch nicht) die einzelnen Abschnitte sehr genau beschrieben und zahlreiche Tiere der verschiedensten systematischen Einheiten als Charakterarten genannt wurden, stellt dieser Bericht KLUNZINGERS eine Pionierleistung in der Riff-Forschung dar, die bisher keine genügende Würdigung fand. Aus diesem Grunde wollen wir auf diese Beschreibung näher eingehen.

Über die Gliederung des Küstenabschnitts schreibt KLUNZINGER wörtlich: „Es ist nicht willkürlich,

* Auf manchen deutschen Karten und in der wissenschaftlichen Literatur auch als Sarad Sarso bezeichnet.

wenn man die Klippe in Zonen von außen nach innen eintheilt; jede Zone hat ihren bestimmten äußeren Charakter und ihre eigenen Thier- und Pflanzenformen". Insgesamt handele es sich um ein Küstenriff. Vom Ufer bis zur Basis des lebenden Außenriffs sei diese Klippe eine horizontale Fläche mit allmählichem Niveauabfall und zahlreichen brunnenartigen Vertiefungen. Dieser Niveauabfall betrage mehr als 2 m. Das Riffgestein stelle im wesentlichen ein „Backwerk von abgestorbenen Korallblöcken, Kalk, Muschelschalen und Wurmröhren" dar. Vier Hauptzonen mit einigen Unterzonen, zwischen der obersten Wasserlinie und dem äußeren Riffhang gelegen, wurden von diesem Autor beschrieben (die folgende Gliederung wurde allerdings als Verarbeitung des beschreibenden Textes von uns aufgestellt).

1. Uferzone

a) Äußere Uferzone: Bei Flut liegt sie nur kurz unter Wasser, ist also meist trockenliegend. Charakterarten sind *Nerita*, *Patella*, *Chiton* auf dem Gestein, somit trockenfallend; in Löchern und Rinnen, also stets weitgehend submers bleibend, *Gelasimus*, *Macrophthalmus*, *Chlorodius*; an den Rändern der Löcher sind *Mytilus* in Menge; in Pfützen und an Steinen *Cerithium*, *Littorina*, *Planaxis* und *Purpurea* sowie *Pagurus*. An Fischen gäbe es dort junge *Gobius*- und *Salarias*-Arten.

b) Innere Uferzone oder Seegraszone: Auf der Klippe die vorgenannten Uferschnecken, ferner *Pirula*, *Natica*, *Terebra* und *Nassa*; in Spalten und Ritzen *Ophiocoma*, in Löchern *Echinometra*. In die Felsplatte eingelagert sind Tümpel, mit Sand gefüllt, in denen phanerogame Seegräser wachsen; daran *Aplysia*, *Pleurobranchus*, *Bulla*, *Dolabella*, *Doris*; im Wasser dieser Vertiefungen schwimmend *Palemon*, *Hippolyte* und *Mysis*; am Boden *Conus*, *Strombus*, *Calappa*, *Lupea*, *Portunus*, *Thalamita*; im Sande *Pinna* und gelegentlich *Pinnotheres*, ferner *Tellina* und *Lucina*.

2. Stilophoren-Zone

Die Klippe bleibt weiterhin bestehen, jedoch ist sie durch die Form, Größe und Tiefe der Tümpel, die auch als Klippenbrunnen bezeichnet werden, stärker charakterisiert. Auf dem Fels wächst eine moosartige Alge. An den Riffkanten sind allenthalben *Chama* angemauert. *Ophiocoma* ist noch häufiger. An Stelle einer schwarz-gelben *Pagurus*-Art der I. Zone ist hier eine graugescheckte Spezies der Leitkrebs. Die Neriten sind ersetzt durch *Columbella* und *Monodonta pharaonis*.

Die Klippenbrunnen sind 2 bis 4 Fuß (= 60 bis 120 cm) tief. Dementsprechend ist das Wasser relativ ruhig und klar. Hier wachsen bereits die ersten Korallinen (worunter offensichtlich Kalkalgen der Familie Corallinaceae der Rhodophyceen verstanden wurden) sowie Steinkorallen der Gattung *Stilophora* (= *Stylophora*). Der Boden ist mit Sand und groben Steinen bedeckt, auf denen struppige Algen wachsen. An den Brunnenwänden befinden sich die ersten Exemplare der Gattungen *Tridacna* sowie *Diadema*, auf dem Sand Holothurien und Synapten.

Während auf der Klippenoberfläche noch *Gobius* und *Salarias* vorherrschen, findet man in diesen Klippenbrunnen die ersten, wohl meist jungen Korallenfischchen, besonders Pomacentriden.

3. Vorkorallzone

Die Klippe bleibt weiterhin als einheitliche Platte bestehen, jedoch ist dieser Abschnitt stets vom Wasser bedeckt und fällt nur ausnahmsweise bei extremem Niedrigwasser zum Teil trocken. Auch hier sind die Klippenbrunnen vorhanden. An deren Rändern und Böden wachsen außer der nun dominierenden *Stylophora* „Frühkorallen" (offensichtlich jüngere Stadien) der Korallengattungen *Heliastraea*, *Solonastraea*, *Leptastraea*, *Lophoseris*, ferner knollige *Millepora* und *Porites* sowie *Favia* und *Coeloria*. Diese Korallen bilden meist Überzüge, Kugeln und Knollen auf dem Boden sowie friesartige Abgrenzungen an den Rändern der Tümpel und Brunnen. Auf der Klippe selbst findet man nur gelegentlich *Stylophora*. Die übrige Tierwelt der Brunnen sowie der Klippe stellt eine Mischfauna der beiden benachbarten Zonen dar.

4. Korall-, Abhangs- oder Brandungszone

Sie bildet den äußeren Abschluß der Klippe. Das Wasser weist starke Strömung und erhebliche Wellenbewegung auf.

a) Die Klippe: Der Fels ist mit einer „schlüpfrigen Algensteppe" bedeckt. Die Brunnen sind tiefer, haben teilweise überhängende Ränder und stehen vielfach mit dem angrenzenden Meer in Verbindung. Die Klippe ist zum Rand hin zerklüftet und schluchtartig zergliedert. Zahlreiche Spalten, Löcher und kraterartige Vertiefungen lassen ein großartiges Höhlensystem vermuten.

Das Korallenleben ist noch reicher. An den Brunnen- und Schluchtenrändern treten große Anemonen der Gattungen *Discosoma* und *Thalassianthus* sowie *Eunice gigantea* auf. In Vertiefungen findet man *Conus*, *Ricinula*, *Turbellina*, *Fasciolaria*, *Trochus* und *Turbo*. Unter den Algen leben zahlreiche Spitzkrabben. In tieferen Abschnitten sowie Spalten kommen verschiedene Rundkrabben-Arten vor, eine neue *Pagurus*-Art sowie als neue Echinodermen Vertreter der Gattungen *Ophiothrix* und *Ophionyx*.

b) Der Klippenabhang: Er ist teilweise jäh abfallend, oft mit überhängendem Oberrand, oder

allmählich sich senkend oder terrassenartig nach außen abgesetzt. An diesen Abhang schließt ein „5—8 Mannshöhen" (also etwa 8—13 m) tiefer Sandgrund an, der aber rasch abfällt, so daß die tiefe Freiwasserzone bereits nach wenigen Metern beginnt.

Am Klippenabhang dominiert bei weitem die Korallengattung *Madrepora* (= *Acropora*), und zwar in drei Grundformen, von denen jede einen bestimmten Abschnitt bewohnt. Auf der Höhe des Riffs befindet sich vorzugsweise eine rasige Form, auf dem Abfall selbst wachsen hauptsächlich Arten mit Blattnetz- und Vasenform, während höhere Busch- und Baumformen fast ausschließlich den tiefsten Abschnitt dieses Hangs bewohnen. Der äußere Klippfels wird hier von großen Blöcken der Gattungen *Porites* sowie von Mäandrinen und Asträen gebildet; charakteristisch sind ferner die Krusten von *Montipora* und Tafeln von *Echinopora*. Zum Teil bankweise tritt hier auch die solide *Hydrophora* auf. *Coenopsammia*, *Fungia*, *Seriatopora*, *Poecilopora* und *Galaxea* sind zwar auch häufig, spielen bei der Klippenbildung aber keine entscheidende Rolle. In der Tiefe kommt die schwarze Koralle *Antipathes glaberrima* vor. Während am Abhang Algen fehlen, treten kolonienweise Alcyonien auf.

Anschließend folgt das tiefe Meer, von dem aus Scomberoiden, Clupeoiden, Scomberesoces sowie Haie, Säge- und Hammerhaie, ferner Delphine, Sirenen, Seeschildkröten usw. bis zum Riff vorstoßen können.

D. B. E. MAGNUS, der durch seine zahlreichen Forschungsreisen (vgl. MAGNUS 1961, 1963a, b und KLAUSEWITZ 1964a) weite Teile des Roten Meeres kennt und auch die Riffe bei Kosseir untersucht hat, teilte uns in dankenswerter Weise mündlich mit, daß dieser Rifftyp direkt südl. des Hafens dieser Stadt zu finden ist. Er bestätigte, daß die Brunnen bereits in der Gezeitenzone vorkämen, die umliegende Abrasionsterrasse also trockenfalle. Zur See hin würden diese Brunnen allmählich tiefer werden und eine maximale Tiefe bis zu 4 m erreichen. Es sei ohne weiteres möglich, in diesen Brunnen zu tauchen. Nahe des äußeren Kliffendes sei die Felsterrasse cañonartig zerklüftet, die Brunnen in der Tiefe miteinander und mit dem Meer durch ein Höhlensystem und Kanäle verbunden (was auch KLUNZINGER bereits erkannt hatte). Allgemein herrschten an diesem Riff sowie in den Cañons und auch den Brunnen gefährliche Strömungen. MAGNUS betont, daß nach seinen Erfahrungen dieser Klifftyp mit den beschriebenen Brunnen eine einmalige Erscheinung sei, die er an keiner anderen Stelle der Rotmeer-Küste gefunden hätte. KLUNZINGER hat also kein normales Saumriff dargestellt, vielmehr eine Sonderbildung, die zum einen durch den corallogenen Ursprung des gesamten Litorals bedingt ist (eine für das Rote Meer charakteristische Erscheinung), zum anderen aber durch die beschriebene Brunnenbildung eine sehr starke Differenzierung aufweise. Demgegenüber haben die späteren Autoren zur Beschreibung physiographischer Zonierungen vorwiegend normal gestaltete Rifftypen untersucht.

PLATE hat das Saumriff von der Sinai-Küste bei Thor näher untersucht und festgestellt, daß sich zwischen der Küste und dem Riff ein 1—2 km breiter Abschnitt befindet, den er als „Strandkanal" bezeichnet hat. Am oberen Abschnitt des ziemlich steil abfallenden seeseitigen Hanges, den er „Riffkante" genannt hat, würden die Korallen wegen des stark bewegten Wassers, des Nahrungsreichtums und der hohen Sauerstoffzufuhr besonders gut entwickelt sein. Der küstenseitige Hang, der nur allmählich zum Strandkanal hin abfällt und als „flache Innenzone" bezeichnet wird, wiese ein erheblich schwächeres Korallenwachstum auf.

Eine erste systematische und vergleichende Gliederung von Korallenriffen erarbeitete DAVIS (1928). Seit diesem Autor ist man nicht nur bemüht, die einzelnen Riffzonen zu definieren, sondern auch die Terminologie zu vereinheitlichen. Für ein Saumriff (fringing reef) unterschied DAVIS folgende drei Abschnitte: reef flat, coastal slope, spur slope. Dieser Autor beschränkte sich also auf das eigentliche Riff, ohne auf die benachbarten, insbesondere die zur Küste hin gelegenen Abschnitte einzugehen. Wesentliche neuere Arbeiten, verbunden mit einer anerkannten englischen Terminologie der Zonen, stammen einerseits von CLOUD (1952) sowie TRACY, CLOUD & EMERY (1955) nach rein topographischen Prinzipien und andererseits von ODUM & ODUM (1957) sowie WELLS (1957) vorwiegend nach Korallenformationen. Allerdings beruhen die Arbeiten dieser Autoren hauptsächlich auf Untersuchungen an Atollriffen, die bekanntlich eine andersartige Struktur aufweisen als küstennahe Saumriffe.

In jüngerer Zeit beschrieben die spezifischen Küstenverhältnisse des Roten Meeres CROSSLAND (1938), MAGNUS (1961, 1963a, b, 1964) sowie SAFRIEL & LIPKIN (1964). MAGNUS unterscheidet an der Supralitoralzone eine Abbruchkante des alten, stets trockenliegenden pleistozänen Riffs (an anderer Stelle als Kliff bezeichnet), sowie, falls vorhanden, einen flachgründigen Sandstreifen. Ferner nennt dieser Autor die Gezeitenstufe mit einer 200—300 m breiten Abrasionsterrasse, die einzelne, freistehende Klippen enthalten kann, sowie eine Gezeitentümpelzone, an die sich eine flache Schlickschicht oder direkt ein rezentes Saumriff anschließen. Nach Angaben von MAGNUS unterschied KLAUSEWITZ (1964b) das kliffartige Ufer, Tidenrinne mit Gezeitentümpeln, eine meist breite Abrasionsterrasse, eine anschließende Sand-Schlick-Zone, die

stellenweise wiesenartigen Seegrasbewuchs aufweist und das erste lebende Saumriff; den seeseitigen Abschluß der Küstenzone bildet ein Außenriffriegel.

SAFRIEL & LIPKIN (1964) haben vorwiegend auf Grund des Algenbewuchses und bestimmter Evertebraten eine genaue Zonierung der „intertidal zone" (Gezeitenzone) der Küste von Eilat vorgenommen. Es handele sich hierbei ausschließlich um „beach rock" als eine rein felsige Abrasionsterrasse. Diese Autoren unterteilen den Gezeitenabschnitt in 7 verschiedene Zonen:

1. „Terrestrial zone", die nahezu stets trocken liegt.
2. „Littorinid zone" mit *Tectarius* und *Littorina*.
3. „*Chthamalid* zone", vorwiegend mit kleinen Chthamaliden (Seepocken).
4. „*Tetraclita* zone", charakterisiert durch große Seepocken der Gattung *Tetraclita*, zahlreiche Schnecken, ferner *Chiton*, *Acanthopleura*, Krabben, Blaualgen usw.
5. „*Sphacelaria* zone", charakterisiert durch eine filamentöse Braunalge der Gattung *Sphacelaria*, in Gemeinschaft mit einer Reihe weiterer Algenarten. Mit diesem Abschnitt endet die eigentliche Gezeitenzone. Denn während die Zonen 2—5 täglich mindestens einmal trocken fallen, sind die folgenden Zonen normalerweise ständig von Wasser bedeckt.
6. „Rhodophyta-*Serpulorbis*-zone"; sie enthält vorzugsweise Rotalgen und Grünalgen. Ferner ist sie charakterisiert durch einen Gastropoden der Gattung *Serpulorbis*.
7. „Reef-forms zone"; bei ihr beginnt das Korallenwachstum; sie fällt nur ausnahmsweise trocken.

III. Topographische Übersicht

Ein normales tropisches Küstenriff ist saumartig der Strandlinie vorgelagert (Abb. 2) und unterscheidet sich sehr deutlich von den übrigen Litoralbildungen. Normalerweise weist es in der Genese keine direkte Beziehung zur Küste auf, was besagen soll, daß die Küstenzone und die Basis des Riffs verschiedenen geologischen Ursprungs sind und aus unterschiedlichem Material bestehen. Hingegen sind die meisten Küstenriffe des Roten Meeres dadurch charakterisiert, daß die Küste und die vorgelagerten Riffe aus demselben Material bestehen und gleichen geologischen, nämlich corallogenen Ursprungs sind. Die Küstenzone ist nämlich fast am ganzen Roten Meer dadurch gekennzeichnet, daß sich oberhalb der Wasserlinie trockenliegende Riffe befinden. KLUNZINGER (1870) stellt diese Tatsache in folgender Weise dar: „Das rothe Meer nimmt ab, sein Ufer wächst, und zwar sehr rasch ... Das, was jetzt Ufer ist, war noch zum Theil zu Menschengedenken Meeresboden." WALTHER (1888) spricht von einer „negativen Strandverschiebung, die durch eine regredierende Bewegung des Meeres bedingt sei". Nach CROSSLAND (1939) seien die Saumriffe des Roten Meeres "mainly erosion platforms cut into the 'raised' reef", d. h. das gehobene pleistozäne Riff.

Nicht nur an den Sarso-Inseln bildet das Ufer vielfach bis 30 m hohe Steilküsten, deren Felsen rein corallogenen Ursprungs sind (vgl. KLAUSEWITZ & SCHÄFER, 1965, SCHÄFER, 1965), das gleiche Bild zeigen alle anderen Farasan-Inseln (vgl. hierzu MACFADYEN, 1930, GUILCHER, 1952, 1955, TAZIEFF, 1952, und NESTEROFF, 1955, 1959), und man findet es auch an vielen anderen Stellen im nördlichen, mittleren und südlichen Bereich des Roten Meeres (vgl. CROSSLAND, 1907, 1938, 1939). Diese Tatsache deutet darauf hin, daß es sich hierbei nicht um lokale tektonische Hebungen bestimmter Küstenabschnitte handeln kann, sondern um Abläufe, die das gesamte Rotmeer-Becken betrafen. Ob eine als Kompensation zur Absenkung der Grabensohle verstandene Hebung des gesamten Schelfgebietes während der Würmeiszeit, also vor etwa 35 000 Jahren, die Ursache für das Trockenfallen dieser alten Riffe war, wie es NESTEROFF (1959) annimmt, oder ob allein eustatische Schwankungen des Meeresspiegels, besonders der 30 m betragende Niveauanstieg während des Riß-Würm-Interglazials (vor etwa 100 000 Jahren), der mit der Maximalhöhe der fossilen, trockenliegenden Riffe übereinstimmt, als Grund für deren Entstehung angesehen werden können (vgl. KLAUSEWITZ, 1960), sei dahingestellt; auf jeden Fall dürfte kaum daran gezweifelt werden, daß diese corallogenen Inseln pleistozänen Ursprungs sind (GUILCHER, 1952, meint, daß sie auch aus dem Pliozän stammen könnten). Nach SCHÄFER (1966) handelt es sich bei diesen rezenten Riffen um Teile eines Wallriffs (Barriereriffs), das pleistozänen Ur-

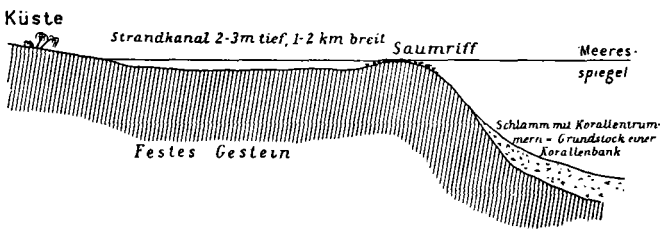

Abb. 2. Schnitt durch ein Saumriff normalen Typs. Nach PLATE, aus dem „Führer durch das Museum für Meereskunde in Berlin", 1907.

Fig. 2. Zonation of a normal margin reef. After PLATE.

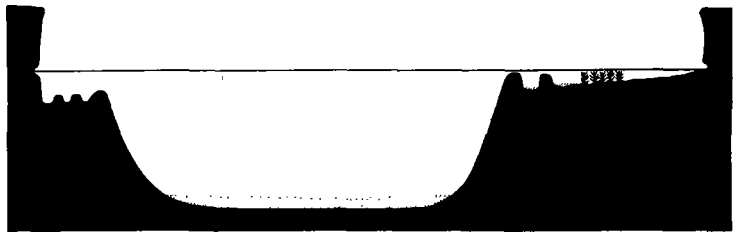

Fig. 3. Diagrammatic cross-section of the two Sarso-Islands with their litoral zones, opposite to each other, morphological very different and separated by a deep channel.

Abb. 3. Stark schematisierter Schnitt durch die einander gegenüberliegenden, morphologisch deutlich voneinander unterschiedenen Litoralzonen der beiden Sarso-Inseln, die durch einen tiefen und breiten, in der Abb. stark verkürzt dargestellten Kanal getrennt sind. Links Sindi-Sarso, rechts Sarso.

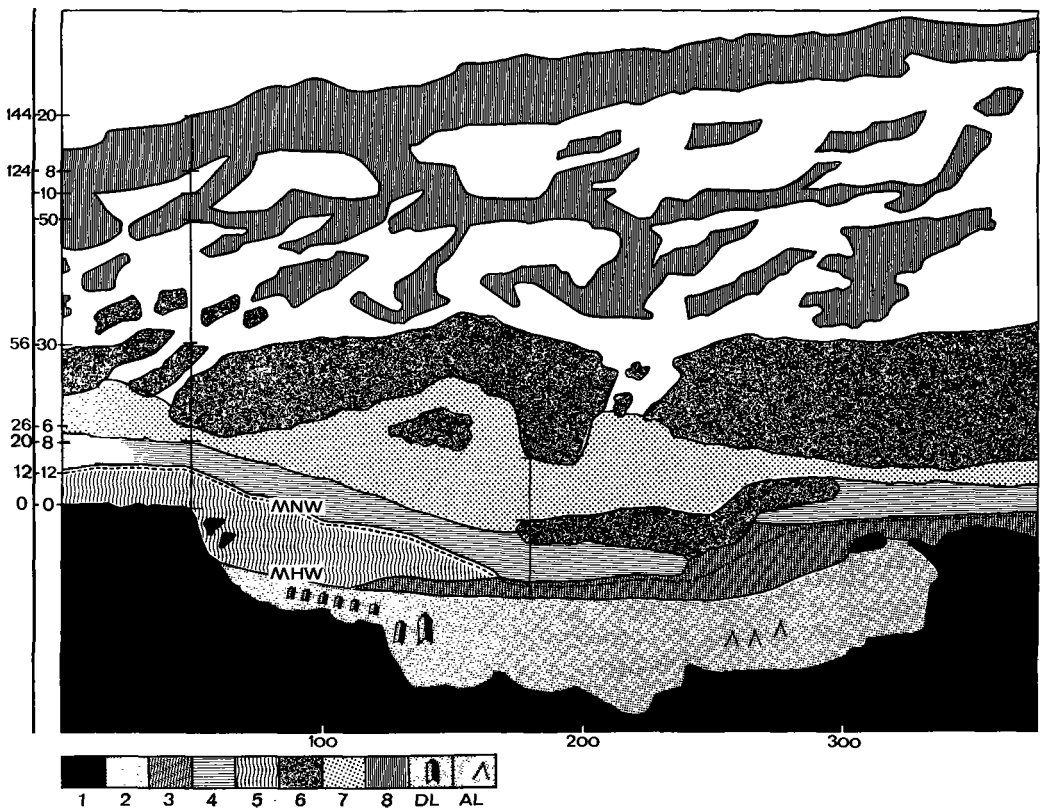

Abb. 4. Schematische Kartierung des Küstenabschnitts vor dem Lagerstrand (Araberbucht). 1 = Gehobenes Kliff mit seeseitiger Steilkante; 2 = Sandbucht; 3 = Eulitorale Sandablagerung; 4 = Sublitorale knubbelige Abrasionsterrasse; 5 = Eulitorale glatte Abrasionsplatte; 6 = Tangwälder; 7 = Sand-Schlick-Zone; 8 = Vorriffe und seeseitiges Hauptriff; DL = Deutsches Expeditionslager; AL = Lager der arabischen Fischer. MNW = Mittlere Niedrigwasser-Linie; MHW = Mittlere Hochwasser-Linie. Die linke Zahlenreihe bedeutet den jeweils absoluten Abstand der Zonengrenzen von der Küstenlinie, die rechte die relative Breite der einzelnen physiographischen Zonen, beides bezogen auf das Profil I (links). Zahlenreihe am unteren Rand: Abstände in Meter.

Fig. 4. Map of the coastal area with the physiographical zonation of the sandbay of Sarso Island. 1 = Raised cliff with steep edge; 2 = Sand bay; 3 = Eulitoral sand sediments; 4 = Sublitoral tuberoused terrace; 5 = Eulitoral abraded terrace; 6 = Areas of seaweed; 7 = Sand-mud zone; 8 = Inner reefs and main reef; DL = Camp of the German group; AL = Camp of the Arabian fishermen. MNW = Average level of the low tide, MHW = High tide. The left series of figures indicates the absolute distances of the zone borders from the coastal line, the right series the width of the different physiographical zones, both related to the profile no. I. The series of figures on the lower margin indicates distances in meter.

sprungs ist. Nach CROSSLAND (1939) seien diese breiten Barriereriffe des Roten Meeres "shallow caps of coral covering eroded ridges which are tectonic in origin".

Daß außer den eustatischen Schwankungen, welche dem Roten Meer auch in biologischer Hinsicht ein eigenes Gepräge geben (vgl. KLAUSEWITZ, 1960, 1964a) und welche die rings um das Rote Meer heute weit im Küstenhinterland liegenden Korallenriffe bedingt haben, höchstwahrscheinlich auch tektonische Abläufe eine Rolle spielten und möglicherweise auch heute noch spielen, lassen die beiden Sarso-Inseln (Abb. 3) vermuten. Oberflächlich sind sie durch einen $^1/_2$ Seemeile breiten und nahezu 100 m tiefen Kanal voneinander getrennt, submers liegen sie durch die Riffe jedoch bedeutend dichter nebeneinander, was eine einstige Verbindung beider Inseln vermuten läßt. Darüber hinaus fanden wir auf Sindi Sarso eine Reihe von in Längsrichtung verlaufenden Rissen, kleineren Verwerfungen und partiellen Absenkungen, die vielleicht auf heute noch aktive tektonische Kräfte zurückzuführen sind.

Durch die historisch bedingte, erheblich breitere Ausbildung der Riffe und das Vorhandensein jener subfossilen Komplexe, entweder unter Wasser als ausgedehnte Flachzonen oder über Wasser als steile Kliffe, sind die Saumriffe allgemein am Roten Meer und speziell bei den Sarso-Inseln im Vergleich zu einem Saumriff normalen Typs stark differenziert. Aus diesem Grunde wurde jener Teil, in den die Profile I und II gelegt wurden, zuvor schematisch kartiert (Abb. 4).

Die submerse Terrasse, die sich von dem gehobenen Kliff bzw. von dessen Steilküste bis zum 150—200 m entfernten Außenriff hinzieht, gibt dem litoralen Bereich in seiner vollen Breite einen spezifischen Charakter. Angefangen von der Steilküste, ihrer Hohlkehle und den teilweise abgebrochenen Überhängen über die kahle Abrasionsterrasse, die die Gezeitenzone bildet, gefolgt von den Tangwäldern, die auf toten, aber noch nicht abradierten Riffen stehen und den ungewöhnlich breiten Vorriffen bis zum seeseitigen Hauptriff, bildet das Fundament eine nach außen hin leicht geneigte Plattform aus organogenem Kalk. Sie scheint die Abrasionsterrasse eines pleistozänen erodierten Riffs zu sein.

Bei einem typischen Saumriff (Abb. 2), das aus der Küste, einem lagunenartigen Strandkanal und dem ± einheitlichen Hauptriff mit küsten- und seeseitigem Abhang zu bestehen pflegt, wäre die Ausbildung derartig breiter Vorriffe und breiter Tangwälder nicht möglich, da die zwischen Riff und Küste liegende Sandzone normalerweise keinerlei Fundamente für solche Ausbildungen zu bieten pflegt. Dasselbe gilt für die der Wasserlinie vorgelagerte kahlfelsige oder nur schwach sedimentierte Abrasionsterrasse, durch die Zonen entstanden sind, die bei einem typischen Saumriff nicht vorkommen (jedoch bei corallogenen Inseln auf breiten Riffplatten von Atollriffen).

Beim Saumriff von Sarso ist auch an jenen Stellen des Litorals, an denen Sand liegt, submers diese Sedimentschicht nur relativ dünn und befindet sich auf der litoralen Plattform. Auf dem Trockenen ist auf dieser Felsschicht der Sand durch die Windwirkung recht hoch angehäuft. Eine solche Situation fanden wir in einer Bucht nahe der Nordostecke der Insel Sarso (in dieser Bucht kampieren die arabischen Fischer, dort hatten auch wir unser Lager aufgeschlagen, vgl. GERLACH, 1967a).

Eine gänzlich andere Riffbildung haben wir allerdings nahe der Nordwestecke von Sindi Sarso. Dort fehlt eine flache Abrasionsplatte, die Steilküste reicht unter die Wasserlinie, das Riff beginnt sofort an der Küstenlinie, ist relativ schmal und zeigt eine ganz andere Zonierung als das Litoral der gegenüberliegenden Insel. Allerdings ist die Riffausbildung in dieser typischen Form nur nahe der Nordwestecke dieser Insel zu finden. Während der anschließende Nordabschnitt von Sindi Sarso ohne jegliche Riffbildung von der Steilküste sofort ins Tiefe geht, haben wir weiter südlich im eigentlichen Kanal ähnliche Verhältnisse, wie wir sie vom Profil der gegenüberliegenden Insel beschreiben.

IV. Beschreibung der Profile

Insgesamt wurden drei Profile durch die Küstenzone von der Wasserlinie bis zum seeseitigen Hang des Außenriffs an drei deutlich voneinander abweichenden Stellen gelegt (Abb. 1). Profil I und II wurden senkrecht zur Küstenlinie und parallel zueinander nahe der Nordostecke der Insel Sarso, Profil III nahe der Nordwestecke von Sindi Sarso vermessen. Alle drei sind zur Kanalmitte hin gerichtet, III liegt ungefähr gegenüber von I.

Die dabei festgestellten physiographischen Zonen stellen klar abgrenzbare größere Abschnitte dar, die sich sowohl im Untergrund als auch im Bewuchs durch Algen und Korallen sowie durch die tierischen Bewohner voneinander deutlich unterscheiden. Wir haben nicht jene Subzonen berücksichtigt, wie sie von SAFRIEL & LIPKIN (1964) bearbeitet wurden.

Profil Nr. I (Abb. 5)

Dieses Profil, das unterhalb einer etwa 10 m hohen Steilküste lag, wies folgende 6 Zonen auf:

1. Zone: Hohlkehle

Der untere, an der Wasserlinie liegende Abschnitt des Steilhangs ist charakterisiert durch eine ± deutlich ausgebildete Hohlkehle. In dem hier vor-

liegenden Fall hat diese Vertiefung eine Höhe von nur 50 cm (an anderen Stellen war diese Hohlkehle erheblich höher, bis etwa 4 m).

Bei mittlerem Hochwasser sind die unteren 15 cm dieser vertikal-konkaven Fläche mit Wasser bedeckt. Bei mittlerem Niedrigwasser fällt die Wand trocken. In ihrer vollen Höhe liegt die Hohlkehle nur bei Springflut unter Wasser.

Diese Maße besagen, daß während des größten Teils des Tidenablaufs diese Zone trockenliegt und daß bei geringem Tidenhub dieser Abschnitt über mehrere Gezeiten trocken bleibt. Da der Wellengang normalerweise an dieser Stelle schwach ist und keine eigentliche Brandung vorliegt, kann man kaum von einer Spritzwasserzone sprechen. Trotzdem dringt kapillar durch das poröse Gestein das Seewasser auch in die höheren Bereiche der Hohlkehle vor. Dieser obere Abschnitt gehört somit zum Supralitoral, während die unteren 15 cm zum Eulitoral gerechnet werden müssen (vgl. GERLACH, 1963).

Wohl bedingt durch diese geringen Befeuchtungsperioden ist diese Zone nur von einer Schicht mit Cyanophyceen bedeckt, die relativ trockenresistent sind. Charakteristische Evertebraten sind *Nerita* und *Patella*. Fische fehlen völlig.

2. Zone: Nackte Abrasionsterrasse

Während die 1. Zone ± vertikal orientiert ist, liegen von der 2. an alle Zonen mit leichter Schrägneigung horizontal.

Die nackte Abrasionsterrasse beginnt am Fuß der Hohlkehle, ist etwa 12—14 m breit und endet recht abrupt an der Grenze zur folgenden Zone.

Diese Abrasionsterrasse besteht aus einer ziemlich glatten Felsplatte, deren Oberfläche eine nur geringe Strukturierung aufweist. Allerdings ist sie durch einige Rinnen durchschnitten, die offensichtlich ausgewaschene Spalten sind. Sie wurden durch das Zerbrechen dieser Terrasse bedingt und stellen heute Flutrinnen dar. Durch sie kann man diese Zone in folgende drei Subzonen unterteilen: Anschließend an den unteren Rand der Hohlkehle (1. Zone) bildet den äußersten Abschnitt ein 1 m breites Band (Subzone a), dessen Oberfläche glatt und kompakt ist. Es folgt eine parallel zur Küstenlinie verlaufende, etwa 15 cm tiefe und 25 cm breite Flutrinne. Daran schließt die eigentliche Abrasionsterrasse an (Subzone b), die leicht gewölbt ist und etwa zwei Drittel der Fläche ausmacht. Das letzte Drittel (Subzone c) ist eine Terrasse, die durch enge Längs- und Querrinnen zerfurcht ist. Den seeseitigen Abschluß stellt ein recht abrupter Abfall dar, der den Rand einer weiteren, größeren, parallel zur Küste verlaufenden Querrinne bildet.

Bei mittlerem Hochwasser ist die ganze Zone bedeckt, bei mittlerem Niedrigwasser fällt sie völlig trocken. Diese Abrasionsterrasse bildet sozusagen ein Felswatt, dessen Flutrinnen die Bedeutung von Prielen haben.

An den Rändern dieser Rinnen ist das Gestein (Abb. 6a) stärker strukturiert; es ist besonders durch bohrende Organismen ziemlich porös; ferner bilden Bohrmuscheln größere Gänge. An diesen Rändern des Rinnenbodens haben sich auch kleine Überhänge

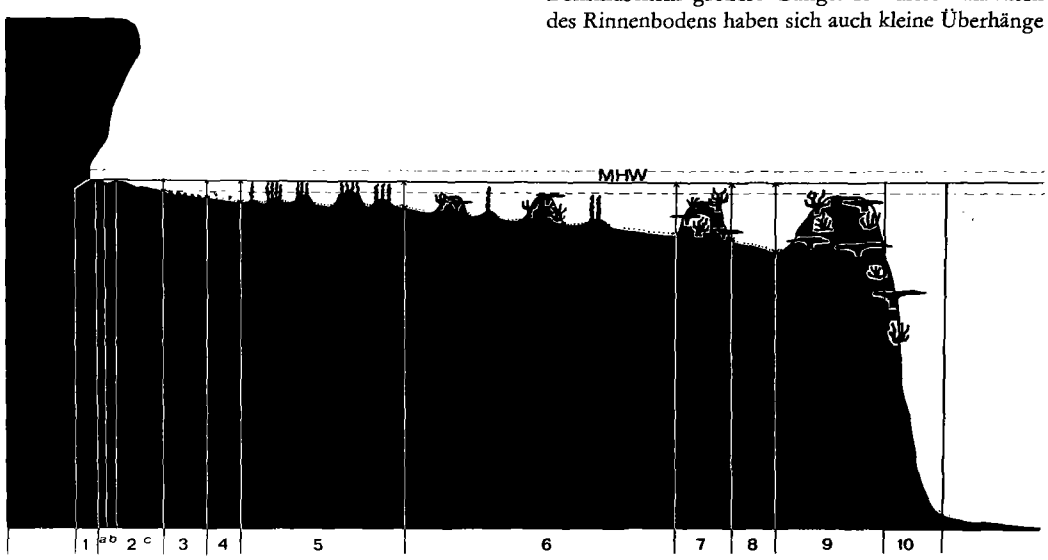

Abb. 5. Schematische Darstellung durch das Profil I von der Küstenlinie des gehobenen Kliffs zu dem seeseitig an das Hauptriff anschließenden tiefen Kanal. 1—10 sind die durch die Profillegung ermittelten physiographischen Zonen.
Fig. 5. Profile I with the 10 physiographic zones.

gebildet (Verstecke für Fische, Schlangensterne usw.).

Im Gegensatz zu diesen Randpartien weist das Gestein der Abrasionsflächen eine verminderte Porierung auf und ist verhältnismäßig glatt. Bohrmuscheln sind nicht vorhanden, die Zahl der Poren der Bohrschwämme ist ziemlich gering. Eine recht dichte und manchmal etwas glitschige Kalkschicht, die offenbar von Kalkalgen stammt, bildet hier die Oberfläche. Nur an wenigen Stellen sind eingebaute tote Korallenskelette zu erkennen. Entsprechend diesem äußeren Eindruck weist das Gestein selbst einen für Kalk recht ungewöhnlichen Härtegrad auf.

Der angeschliffene und durch Azetatfolienabzug dargestellte Querschnitt (Abb. 6b) einer solchen Probe (9 cm lang, 8 cm breit, 6 cm hoch) läßt folgende Merkmale erkennen: Den größten Teil nimmt das Skelett eines *Porites*-Stockes ein. Wenngleich auch das Skelett einer lebenden *Porites* stets relativ dicht ist, erweist sich dieses subfossile Stück in seinem inneren Aufbau als noch erheblich dichter. Zwar sind die einstigen Polypenkelche noch erkennbar, aber die einzelnen Querlamellen sind vielfach verbacken und die Gänge sind angefüllt. Ob es sich hierbei um den Beginn des Umzementierungsprozesses handelt, wie er für Korallenstöcke im Basalbereich üblich ist, oder um Anfüllung mit feinsten, inzwischen verhärteten Schlammpartikeln, ist ungeklärt. Die Färbung des Skeletts ist nicht rein weiß, wie bei der Basis einer lebenden *Porites*, sondern hell sandfarben. Zwei Bohrmuschelgänge sind nahe der Oberfläche zu erkennen, sie sind aber angefüllt mit feinstem, verfestigtem Sediment zu Gesteinskernen.

Die Oberfläche ist nicht relativ gerade bzw. leicht gewölbt, wie bei einer lebenden oder frischtoten *Porites*, sondern unregelmäßig ausgebildet. Sie entspricht also nicht mehr der einstigen oberen Begrenzung; nach dem Absterben muß ein unbekannter Teil des peripheren Bereichs dieser Koralle abgebaut worden sein. Die heutige Oberfläche bildet eine dünne Kalkschicht, die von Kalkalgen stammt. Auch am äußeren Rand (der die Kante einer Flutrinne bildet) ist der *Porites*-Stock unnatürlich abgeschnitten, worauf der unterbrochene Verlauf der Polypengänge eindeutig hinweist.

Während das *Porites*-Skelett die volle Breite der Gesteinsprobe einnimmt, reicht es nicht in die Tiefe. Denn die untere 5—15 mm starke Schicht ist verfestigtes Sediment, aus einer Mischung von feinstem Kalkschlamm und Grobteilen, wie Schalenstückchen von Muscheln usw., bestehend. Wegen des relativ glatten Verlaufs der Begrenzung des Korallenstocks zur Sedimentschicht hin könnte es möglich sein, daß die *Porites* auf diesem Untergrund gewachsen ist und somit in ihrer ursprünglichen Lage erhalten ist. Allerdings verlaufen die Polypengänge nicht radiär, wie normalerweise bei einer *Porites*, sondern ± parallel, was man aber auch bei einem geschnittenen rezenten *Porites*-Skelett im Bereich der Randzone gelegentlich feststellen kann. Dies bedeutet ein seitliches Anwachsen und Überwachsen einer Sedimentschicht, wodurch die parallel verlaufenden Wachstumsgänge entstanden sind.

Mit Sicherheit hat diese Untersuchung der Gesteinsprobe ergeben, daß die Abrasionsterrasse Korallenskelette enthält (vgl. hierzu auch SCHÄFER, 1966). Wahrscheinlich ist, daß sie weitgehend von Korallenstöcken aufgebaut wurde. Es muß angenommen werden, daß an dieser Stelle sich einst größere Blöcke befanden (vgl. hierzu Profil Nr. III, 3. Zone), die durch die gemeinsame Einwirkung von Wasser und Luft so weit erodierten, bis im Gezeitenbereich eine relativ ebene Platte übrig blieb. Nach GUILCHER (1952) handelt es sich weniger um eine mechanische, als vielmehr um eine chemische Erosion.

Der dominierende Pflanzenbewuchs wird auf der Subzone b) von fädigen Grünalgen (Cyanophyceen: Oscillatoriaceae, wahrscheinlich *Phormidium*) als feiner Rasenüberzug gebildet; auf der Subzone c) von der bartförmigen Cyanophycee *Lyngbia* spec. (Nostocaceae).

Die häufigsten Evertebraten der nackten Abrasionsterrasse sind: Einsiedlerkrebse der Gattung *Clibanarius*, die in großer Zahl vorkommen. Ferner die Schnecken *Canarium fasciatum* BORN, *Cerithium erythaeonense* LAM., *Conus* (*Cylinder*) *textile vicarius* LAM., *Erosaria turdus* LAM., *Galeodes* (*Volema*) *paradisiaca* (ROEDING), *Latirus polygonus* LAM., *Tectus noduliferus* LAM. Außerdem befand sich dort die solitär festgewachsene Muschel *Chama rüppellii* REEVE sowie festsitzende Arten der Gattungen *Nerita*, *Patella* und *Chiton*.

Charakteristische Fische (nur Namensangabe, auf das gesammelte Material wird in einer gesonderten Arbeit näher eingegangen; außerdem hat D. ZANDER die Ichthyofauna der Gezeitenzone näher untersucht, vgl. ZANDER 1967):

a) Auf der Abrasionsplatte und in deren Rinnen leben:

Blenniidae
Antennablennius hypenetes (KLZGR.)
Istiblennius edentulus (BL., SCHN.)
Istiblennius flavoumbrinus (RÜPP.)
Gobiidae
Acentrogobius ornatus (RÜPP.)
Acentrogobius meteori KLAUSEW. & ZAND. (im Druck)

b) In den Rinnen schwimmen:

Cyprinodontidae
Aphanius dispar (RÜPP.)
Teraponidae
Terapon jarbua (FORSK.), Jungtiere

Abb. 6 a

Abb. 6 b

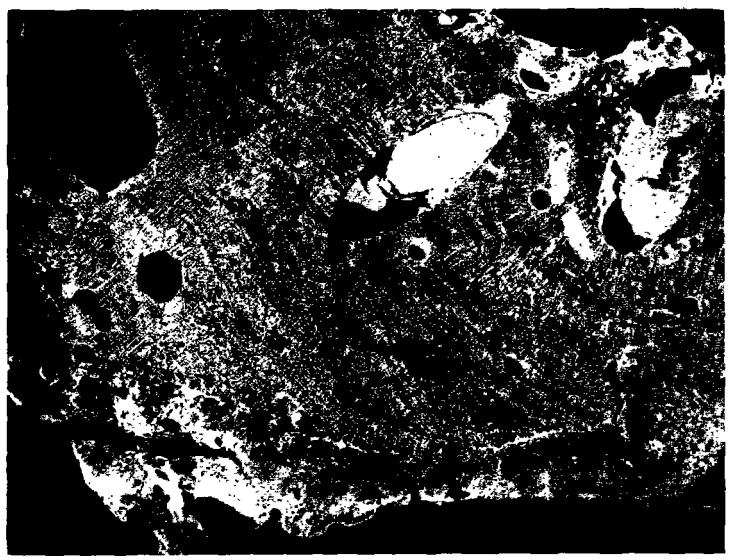

Abb. 6. Querschnitt durch eine Gesteinsprobe der 2. Zone (nackte Abrasionsterrasse). Die linke Begrenzung bildet den überhängenden Rand einer Rinne. Nur die rechte Hälfte des Unterrandes sowie die rechte Seite waren fest mit dem Untergrund verbunden. a) Gesteinsprobe angeschliffen. b) Darstellung der rein corallogenen Struktur durch Azetatfolienabzug (Ausschnitt). — Sämtliche Photos: ERWIN HAUPT, Senckenberg-Museum.

Fig. 6. Section of a sample of the second zone. a) Polished. b) Proof of the corallogene structure by the print of an acetate film. — All photos by ERWIN HAUPT, Senckenberg-Museum.

Abb. 7a

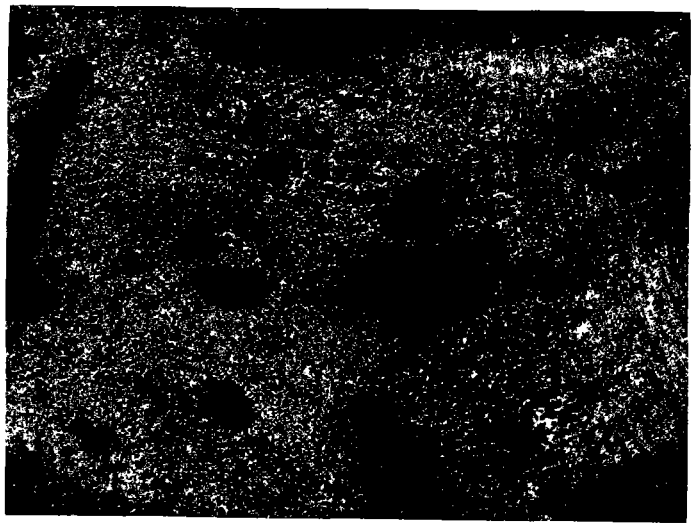

Abb. 7b

Abb. 8

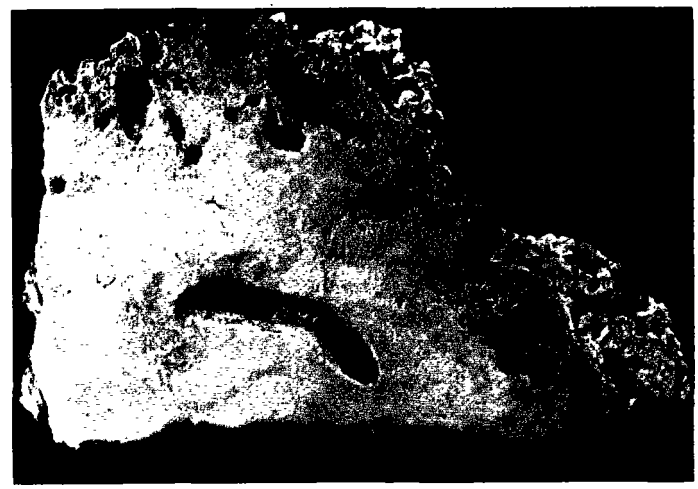

Abb. 9

Abb. 11

Abb. 7a. Angeschliffener Schnitt durch eine Gesteinsprobe der 3. Zone (knubbelige Abrasionsterrasse). Der vorliegende Stein wurde ausschließlich von *Porites solida* (FORSK.) aufgebaut.

Fig. 7a. Polished section of a sample of the third zone. The stone was exclusively built up by the coral species *Porites solida*.

Abb. 7b. Der rein corallogene Aufbau ist durch diesen Azetatfolienabzug erkennbar. Die dunklen Zwischenräume sind Gänge bohrender Organismen.

Fig. 7b. The corallogene structure of the sample demonstrated by the print of an acetate film. The dark spaces are ducts of boring organisms.

Abb. 8. Struktur der großlumigen *Favites complanata* (EHR.), die ebenfalls häufig in den Gesteinsproben der 3. Zone zu finden ist.

Fig. 8. Structure of the coral *Favites complanata*, which frequently is embedded in the limestone of the third zone.

Abb. 9. Schnitt durch eine kleine Erhebung der 3. Zone. Die Oberfläche ist vielfach mit *Lithothamnion*- und *Lithophyllum*-Kalkalgen besetzt. Das Gestein ist auch in der Tiefe durch Röhren durchlöchert.

Fig. 9. Section through a tuber of the third zone. The surface layer is built by living chalk algae *Lithothamnion* and *Lithophyllum*.

Abb. 11. Ausschnitt aus der Oberfläche eines Hügels der 5. Zone (Tangwald-Streifen) mit Kalkalgen und je einer jungen *Stylophora pistillata* (ESP.) (links) und *Montipora tuberosa* KLZGR. (rechts).

Fig. 11. Part of the surface of a small knoll of the fifth zone with chalky algae and young specimens of the corals *Stylophora pistillata* (left) and *Montipora tuberosa* (right).

Abb. 12

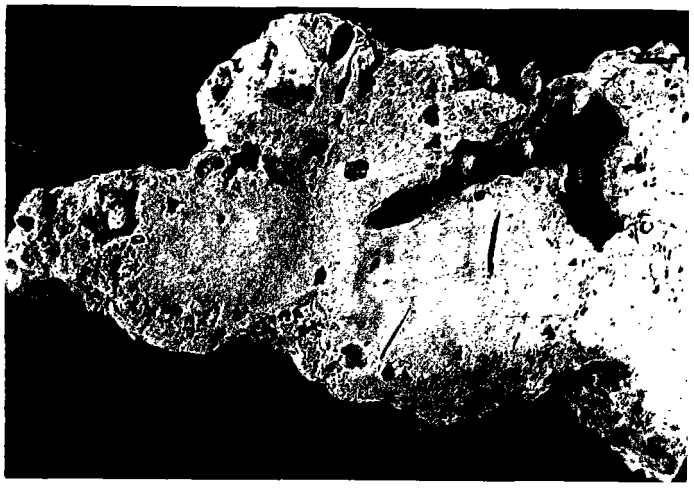

Abb. 13a

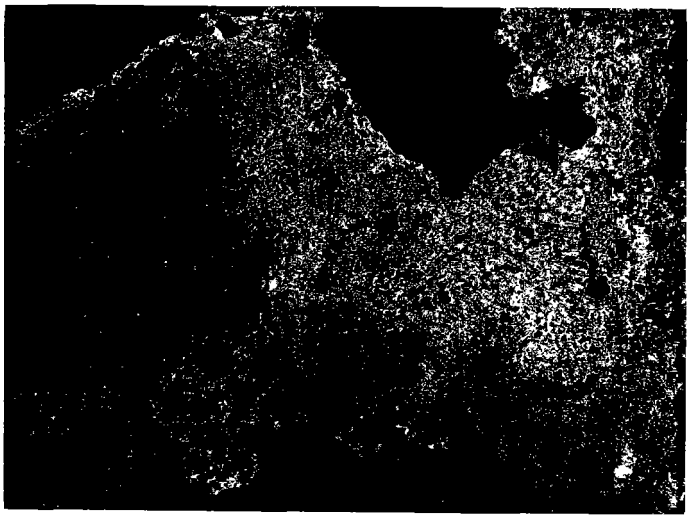

Abb. 13b

c) Bei Flut schwimmen am Tage über der Abrasionsterrasse:

Cyprinodontidae
Aphanius dispar (RÜPP.)
Teraponidae
Terapon jarbua (FORSK.), Jungtiere
Lutianidae
Lutianus ehrenbergi (PETERS), Jungtiere
Labridae
Cheilinus fasciatus quinquecinctus (RÜPP.), Jungtiere
Acanthuridae
Acanthurus gahhm (FORSK.), Jungtiere

d) Bei Nacht freischwimmend über der Abrasionsterrasse:

Mugilidae
Crenimugil crenilabis (FORSK.), Jungtiere
Atherinidae
Allanetta forskali (RÜPP.), subad. Exemplare
Lutianidae
Lutianus ehrenbergi (PETERS), juv.

3. Zone: Knubbelige Abrasionsterrasse

Zone 2 und 3 sind deutlich voneinander getrennt durch eine etwa 30 cm breite, verschlickte, parallel zur Küste verlaufende Flutrinne.

Bei mittlerem Niedrigwasser verläuft die Wasserlinie entlang dieser Rinne. Nur bei Springtide fällt die 3. Zone kurzzeitig trocken. Mit dieser Zone beginnt somit das Sublitoral.

Diese Zone ist etwa 10 m breit und weist bei mittlerem Hochwasser am seeseitigen Außenrand eine maximale Tiefe von 70—80 cm auf.

Auch diese Zone besteht aus einer Felsplatte, ihre Oberfläche ist aber nicht ± glatt wie bei Zone 2, sondern mit zahlreichen knubbelartigen, bis 10 cm hohen, sehr unregelmäßig gestalteten Erhebungen überzogen. Nur zwischen diesen befindet sich ± glatter Fels.

Die Oberfläche dieser Knubbel ist überzogen von blasenförmigen, rotweinfarbenen Kalkalgen der Gattung *Lithothamnion* (zwei Arten), die diesen Erhebungen zusätzlich ein unebenes, fast schaumiges Gepräge geben.

Während die tiefer liegenden Zwischenräume zwischen diesen Knubbeln mit einem wenige Millimeter hohen Schlicksand-Sediment bedeckt sind, wachsen auf den Erhebungen büschelförmige, etwa 20 cm hohe Braunalgen der Gattung *Cystoseira* (auch auf diesen Algen findet man einen feinen Überzug mit Schlamm- und Mulmpartikelchen).

Durch die *Lithothamnion*-Knubbel, die *Cystoseira*-Büsche und den Sedimentbelag der Zwischenräume ist diese Zone charakterisiert.

Da die Oberfläche nur gelegentlich trockenfällt und normalerweise zumindest mit einem geringen Wasserstand bedeckt bleibt, ist offensichtlich die kombinierte Erosionswirkung von Wasser und Luft bedeutend weniger wirksam. Dadurch ist die viel stärkere Strukturierung des Gesteins und die erheblich größere Oberfläche gegeben. Denn trotz der hier ebenso großen oder schwachen Wellenwirkung wie bei Zone 2 sind in Zone 3 die subfossilen Korallenblöcke und -Stöcke erheblich besser erhalten als auf der nackten Abrasionsterrasse.

Die innere Struktur von Gesteinsproben (Abb. 7a u. b) und gelegentlich erkennbare Merkmale an der Gesteinsoberfläche lassen mit Sicherheit feststellen, daß der Kalkfels dieser Zone ebenfalls vorwiegend von Blöcken der Gattung *Porites*, und zwar besonders von *P. solida* (FORSK.) aufgebaut worden ist. Auch die kleinen Erhebungen lassen das Innenskelett dieser Korallenart deutlich erkennen. Daneben findet man oft die Struktur der relativ großlumigeren *Favites complanata* (EHRENBERG, Abb. 8). Querschnitte der etwa zentimetergroßen Poren sind oft auch an der Oberfläche festzustellen. Es versteht sich von selbst, daß auch diese Korallen abgestorben und sozusagen subfossil sind und daß deren Skelette an der Oberfläche schon mancherlei Veränderung erfahren haben. Sehr reich ist bei den Knubbeln, weniger häufig beim Basalgestein, die bohrende Fauna, bzw. deren Gänge zu finden. Auch scheinen diese kavernikolen Formen erheblich tiefer in das Gestein vorzudringen, als dies bei Zone 2, also der nackten Abrasionsplatte, der Fall ist. Die äußerste Oberfläche bildet auch hier einen Kalkalgen-Überzug (Abb. 9).

Die dominierenden Pflanzen sind *Melobesia*, ferner die buschförmige *Cystoseira* spec., außerdem in geringer Menge als Aufwuchs grüne Fadenalgen und die Kalkalge *Halimeda opuntia* in niedrigen Büschen.

Die Tierwelt ist oberflächlich recht schwach vertreten. An den Knubbeln und den dadurch gegebenen Spalten und Höhlungen sind die Miesmuscheln *Modiola auriculata* KRAUSS, *Erosaria turdus* LAM., *Cypraea vinosa* GMELIN und *Lyncina camelopardalis* LINN. sowie Einsiedlerkrebse der Gattung

Abb. 12. Angeschnittene Gesteinsprobe eines lebenden *Porites*-Stockes mit kompakter innerer Struktur. 5. Zone.

Fig. 12. Section of a sample of a living *Porites* with a very compact internal structure 5. Zone.

Abb. 13a. Stark durchlöcherter Teil eines abgestorbenen *Porites*-Stockes derselben Gesteinsprobe wie Abb. 11.

Fig. 13a. A poroused part of a dead *Porites* specimen of the same sample as in fig. 11.

Abb. 13b. Azetatfolienabzug (Ausschnitt) der Gesteinsprobe von Abb. 13a zum Nachweis der corallogenen Struktur.

Fig. 13b. Print of an acetate film of the same sample as in fig. 13a, demonstrating the corallogene structure.

Clibanarius zu finden. Letztgenannte Form ist hier aber bedeutend weniger häufig als im Bereich der nackten Abrasionsterrasse (2. Zone). Das gleiche gilt für die festgewachsene solitäre Muschel *Chama rüppellii* REEVE, die hier am unteren Rand der kleinen Erhebungen und auch auf dem Gestein der tiefer gelegenen Zwischenräume zu finden ist.

Unter den Fischen ist die häufigste Form und schlechthin die Charakterart dieser Zone das adulte Stadium von *Acentrogobius ornatus* (RÜPP.). Während die Jugendform vorwiegend Zone 2 besiedelt, sind die erwachsenen Tiere fast ausschließlich auf Zone 3 zu finden. Daneben kommt von den Salariidae gelegentlich *Salarias fasciatus* (BLOCH) vor. Außerdem haben wir von derselben Familie *Cirripectus variolosus* (VAL.) beobachtet.

Bei Flut schwimmen zwischen den Knubbeln jeweils junge Exemplare von *Parupeneus auriflamma* (FORSK.) (Fam. Mullidae) sowie die bereits erwähnten *Lutianus ehrenbergi* und *Cheilinus fasciatus quinquecinctus)*.

4. Zone: Sand-Schlick-Feld

Der Übergang von der 3. Zone zu der nun folgenden ist ziemlich abrupt: Die kleinen Erhebungen hören in einer geraden, parallel zur Küste verlaufenden Linie auf. Was sich hingegen fortsetzt, ist das Sand-Schlick-Sediment, das nun aber durchgehend den Boden bedeckt.

Die Sand-Schlick-Zone ist etwa 6 m breit. Ihre maximale Tiefe beträgt 85—100 cm.

Die in der 3. Zone häufigen und kennzeichnenden büschelförmigen Braunalgen *Cystoseira* spec. sind hier nur noch spärlich vertreten. In der seeseitigen Hälfte der 4. Zone werden diese Braunalgen gelegentlich ersetzt durch ebenfalls solitär stehende „Kandelaber-Algen" der Gattung *Turbinaria* (an anderer Stelle, aber nicht im Bereich dieses Profils, fanden wir in dieser Zone an Stelle der beiden vorgenannten Algen vorwiegend Seegras der Gattung *Cymodocea)*.

Läuft man von Zone 3 in Zone 4, so verspürt man unter den Füßen einen deutlichen Wechsel in der Konsistenz des Bodens. Denn während der Untergrund der knubbeligen Abrasionsterrasse sehr fest ist und sich auf dem Fels nur wenig Sediment befindet, gibt hier der Boden durch eine dicke Sandschicht deutlich nach.

Eine Überprüfung des Sediments ergibt, daß hier oberflächlich keine Felsplatte mehr vorhanden ist, sondern eine tiefe Sedimentablagerung vorliegt. Sie wies folgende konstante Schichtung auf:

An oberster Stelle liegt eine dünne Schicht mit feinstem Schlick,

gefolgt von einer dicken Lage mit feinem Sand, darunter befindet sich eine etwas weniger dicke Schicht mit grobkörnigem Sand

(insgesamt haben diese drei Sedimentschichten eine Dicke von etwa 15 cm).

Darunter befindet sich eine mindestens ebenso dicke Schicht von ± fest aneinandergelagertem, aber nicht verbackenem Korallengeröll. Dieses Geröll besteht aus zentimetergroßen Bruchstücken bis zu ganzen *Acropora*-Ästen. Durchmischt ist es mit verschiedenkörnigem Sand.

Diese völlig andersartige Zusammensetzung des Untergrundes gegenüber der 3. Zone ist darauf zurückzuführen, daß die Abrasionsterrasse an der Grenze zwischen der 3. und 4. Zone abrupt endet und mit einer Stufe abschließt. Erst in etwa 30 cm Tiefe unterhalb der Sedimentschicht beginnt eine neue ± horizontal verlaufende Abrasionsterrasse, auf der die oben beschriebenen Sand- und Geröllschichten abgelagert sind (Abb. 10).

Abb. 10. Schematische Darstellung der Grenze zwischen 3. und 4. Zone, die durch eine Stufe des basalen Felsbodens ausgezeichnet ist. Die tiefer gelegene Sohle der 4. Zone ist durch verschiedenartige Sedimentablagerungen gekennzeichnet.

Fig. 10. Diagrammatic section of the border area between the third and fourth zone. The deeper floor of the fourth zone is filled up by different sediments.

Oberflächlich gekennzeichnet ist der Boden durch eine recht dichte Verteilung von größeren oder kleineren, meist senkrechten Löchern. Sie stammen teilweise von Fischen der Gattung *Cryptocentrus* bzw. den mit ihnen in Gemeinschaft lebenden Knallgarnelen der Gattung *Alpheus*. In anderen Röhren mit großen runden Öffnungen leben nachtaktive Anemonen der Gattung *Cerianthus*. Hinzu kommen zahlreiche kleinere Löcher im Boden, die einen Abstand von etwa 10 cm haben. Sie scheinen vorzugsweise von Polychaeten und Muscheln zu stammen. Die großen Röhren reichen in der Tiefe bis in den Bereich des Korallenschutts.

Auf dem schlickigen Boden trifft man gelegentlich große Exemplare der Schnecke *Strombus tricornis* LAM. sowie häufig die kleine Schnecke *Canarium fasciatum* BORN. an.

An Fischen sind häufig zu beobachten:

a) Obligatorisch vor Höhlen am Boden sitzend:

Gobiidae
Amblygobius albimaculatus (RÜPP.)
Cryptocentrus caeruleopunctatus (RÜPP.)
Cryptocentrus lutheri KLAUSEW.
Ctenogobiops maculosus (FOURMANOIR)

b) Am Boden ruhend ohne Höhle:

Eleotridae
Eleotriodes sexguttatus (VAL.)

c) Fakultativ am Boden ruhend:

Serranidae
Epinephelus areolatus (FORSK.), juv.-s. ad.
Bothidae
Bothus pantherinus (RÜPP.), juv.

d) Im Freiwasser, das bei Flut bis 100 cm hoch stehen kann, schwimmen:

Atherinidae
Allanetta forskali (RÜPP.), (juv.-ad. Exemplare)
Lutianidae
Lutianus ehrenbergi (PETERS), (jüngere Tiere)
Gerreidae
Gerres oeyena FORSK., (ad. Exemplare)
Mullidae
Parupeneus auriflamma (FORSK.), (Jungtiere)
Acanthuridae
Acanthurus xanthopterus CUV., (Jungtiere)
Labridae
Cheilinus fasciatus quinquecinctus RÜPP., (meist jüngere Tiere)

(Alle vorgenannten leben gesellig, teilweise im Schwarm beisammen.)

Platacidae
Platax orbicularis (FORSK.), (ad. Einzeltier)
Tetraodontidae
Arothron diadematus (RÜPP.), (ad. Einzeltier).

An einer abseits liegenden Stelle fehlte diese Sand-Schlick-Zone völlig, so daß Zone 3 direkt in die folgende Zone 5 überging.

5. Zone: Tangwald-Streifen

Diese Zone ist etwa 30 m breit und hat eine Wassertiefe von 130—180 cm.

Der Boden der Tangwald-Zone besteht aus einer ± ebenen Abrasionsterrasse, die hier also wieder zutage tritt, während in Zone 4 dieselbe Terrasse hoch mit Sediment bedeckt ist. Das Gestein dieser Basalplatte ist relativ fest und scheint nur wenig strukturiert zu sein.

Auf dieser planen, leicht geneigten Abrasionsterrasse befinden sich als Sekundärstruktur hügelartige Erhebungen (bolders) von 50—100 cm Höhe und 200—300 cm Durchmesser. Während die Oberfläche vorwiegend mit knubbeligen *Lithothamnion-* und *Lithophyllum*-Kalkalgen besetzt ist, findet man an den Außenrändern einige solide Korallenstöcke, besonders von *Porites solida* (FORSK.), *Gonastraea cutiformis* (LAM.) sowie *Stylophora pistillata* (ESPER). Meist bilden diese Stöcke nur Zwergformen im Vergleich zur üblichen Wuchsgröße. Oft stehen diese Hügel dicht nebeneinander, an anderer Stelle haben sie mehrere Meter Abstand voneinander. Die Oberfläche dieser Erhebungen ist sehr unregelmäßig. Das Gestein macht einen porösen und lockeren Eindruck. Auf der ebenen Basalplatte zwischen den Hügeln befindet sich eine nur dünne Schicht von Sand und Schlick. Auf den hügelartigen Erhebungen sind zahlreiche Großalgen verankert. Es handelt sich um zwei Arten, nämlich *Sargassum* spec. und die „Kandelaber-Alge", *Turbinaria* spec. (? *decurrens*). Beide Tange werden etwa 1,50 m hoch und reichen somit auch bei Flut bis an die Wasseroberfläche. Sie sitzen dicht beieinander auf den Hügeln und bilden ganze „Wälder". Diese Tange sind das Charakteristikum dieser Zone.

Unterbrochen werden diese Tangwälder durch unbewachsene, schmale und oft kanalartige Einschnitte. Diese freien Abschnitte sind dadurch bedingt, daß beide Tangarten ausschließlich auf den toten Korallenhügeln wachsen und niemals auf der dazwischenliegenden basalen Terrasse und somit auch nicht auf dem sandigen Boden.

An den Rändern mancher Hügel wachsen gelegentlich kleinere solitäre Kolonien von Octocorallia (Alcyonarien).

An der Basis der hohen Tange findet man auf dem Gestein Cyanophyceen als Algenrasen, u. a. *Lyngbia* spec.

Gesteinsanalysen des Untergrundes der Tangwald-Zone (Abb. 11) lassen folgende Einzelheiten erkennen. Bei den großen Hügeln weist die Oberfläche zahlreiche kleinere Erhebungen, Vertiefungen, Spalten und Löcher auf. Der größte Teil des Gesteins ist vorwiegend mit Kalkalgen der Gattungen *Lithothamnion* und *Lithophyllum* überzogen. Dazwischen befinden sich kleine, eventuell junge Stöcke und Stockansätze folgender Korallen: *Platygyra lamellina* (EHRENB.), *Galaxea fascicularis* (L.), *Porites solida* (FORSK.), *Stylophora pistillata* (ESPER), *Montipora tuberosa* KLZGR. und *Echinopora* spec. An anderen Stellen, die stärker exponiert und nicht Ansatzgebiet der Großalgen (*Sargassum*) sind, haben sich größere Stöcke von *Porites solida* (FORSK.) entwickelt.

Die innere Struktur der Hügel läßt in Anschnitten nur einen Korallenvertreter erkennen, nämlich das sehr kompakte Skelett von *Porites solida* (FORSK.). Alle hügelartigen Erhebungen sind also von dieser einen Art aufgebaut worden. Sofern Teile dieser Koralle noch leben, ist das Skelett völlig unverändert (Abb. 12). Da der größte Teil aber abgestorben ist, sind die oberflächennahen Bereiche, gelegentlich aber auch tiefere Bezirke eines einstigen Stockes mit zahlreichen Löchern und Gängen von Bohrschwämmen und Bohrmuscheln durchzogen (Abb. 13a). Die Gesteinsanalyse der hügeligen Sekundärstruktur läßt also mit Sicherheit erkennen, daß hier einst ein lebendes Riff stand, das vorwiegend von *Porites* aufgebaut worden war (Abb. 13b).

Eine Gesteinsprobe des Bodens zwischen den Hügeln, also der eigentlichen Basalplatte, zeigt

hingegen eine ganz andere Zusammensetzung. Hier ist kein Korallenskelett erkennbar. Vielmehr scheint dieser Boden ausschließlich aus verbackenem grobkörnigem Kalksand zu bestehen. Zwar ist auch diese Basalplatte corallogen, aber nicht aus primärer Skelettstruktur, sondern aus deren, zu Sand abgebauten und schichtweise verbackenen Resten. Sicher finden sich auch hier erhaltene Skelette, ebenso wie Teile anderer hartschaliger Tiere, doch ist unsere Probe zu klein für einen solchen Nachweis gewesen.

Man hat den Eindruck, daß sich am Fuße der einstigen *Porites*-Blöcke Sand abgelagert hat, der zu Kalkgestein verbacken wurde. Darüber liegt eine Sedimentschicht noch lockeren Sandes.

An Oberflächenbewohnern der Tangwald-Zone konnten wir unter den Evertebraten außer den genannten Korallen keine Leitarten feststellen. Gelegentlich kommt die große Schnecke *Strombus tricornis* LAM. vor, die wir bereits in der 4. Zone fanden.

An Fischen sind häufig zu beobachten:

a) Bodenbewohnende Arten:

Gobiidae
Amblygobius albimaculatus (RÜPP.)
Cryptocentrus caeruleopunctatus (RÜPP.)
Cryptocentrus lutheri (KLAUSEW.)
Eleotriodes sexguttatus (VAL.)

b) Freischwimmende und am Boden fressende Arten:

Apogonidae
Cheilodipterus lineatus (L.)
Gerreidae
Gerres oyena (FORSK.)
Scolopsidae
Scolopsis ghanam (FORSK.)
Mullidae
Parupeneus auriflamma (FORSK.)
Acanthuridae
Acanthurus xanthopterus CUV.
Labridae
Halichoeres centriquadrus (LAC.)
Halichoeres scapularis (BENN.)
Thalassoma lunare (L.)
Callyodontidae
Zahlreiche kleine Exemplare verschiedener *Callyodon*-Arten

c) Zwischen dem Tang lebende Arten:

Pomacentridae
Abudefduf sexfasciatus (LAC.), (nur im tieferen Bereich dieser Zone)
Labridae
Cheilinus fasciatus quinquecinctus RÜPP. (juvenile u. subadulte Exemplare)
Cheilio inermis (FORSK.)

d) An den toten Blöcken lebende Arten:

Lutianidae
Lutianus fulviflamma (FORSK.), (jüngere Einzeltiere)
Siganidae
Siganus stellatus (FORSK.)
Pomacentridae
Abudefduf sexfasciatus (LAC.)
verschiedene *Pomacentrus*-Arten
Salariidae
Salarias fasciatus (BLOCH)

e) In den wenigen lebenden Korallenstöcken der Gattung *Stylophora:*

Pomacentridae
Einige *Pomacentrus*-Arten in geringer Individuendichte

f) In den Kanälen zwischen den Tangwäldern:

Clupeidae
Harengula punctata RÜPP. (schwarmweise in sehr großer Zahl).

6. Zone: Vorriff mit Sandfeld

Diese Zone ist gekennzeichnet durch die Kombination von Korallenhügeln auf sandigem Untergrund. Sie reicht von der Außengrenze der Tangwaldzone bis zur Innenwand des Hauptriffs. Im Bereich unseres Profils ist die 6. Zone etwa 70 m breit, in unserem Abschnitt variierte ihre Breite zwischen 50 und 100 m. Der Wasserstand (MHW) liegt zwischen 1,50 und 3 m.

Der Boden besteht aus feinem Sand. An der Grenze zur Tangwald-Zone ist die Sandschicht noch sehr dünn; darunter befindet sich glatter Fels. Aber bereits 10 m weiter seewärts ist die Sedimentschicht mindestens 15 cm dick.

Durchzogen ist diese Zone von zahlreichen Korallenhügeln. Zur Tangwald-Zone hin sind sie teilweise solitär, im übrigen sind sie mäanderförmig miteinander verbunden. Sie dürften teilweise abgestorbene Riffe sein, auf denen aber weitere Korallen wachsen. Im flachen Bereich haben diese Riffe eine Höhe von etwa 1,50 m, im tieferen bis etwa 2,50 m.

In der Nähe der Tangwald-Zone kommen noch kleinere isolierte Tangkomplexe (*Sargassum* spec. und *Turbinaria* spec.) vor, die aber keinen durchgehenden Tangwald bilden. Nach außen, also zum tieferen Bereich hin wird dieser Großtang immer seltener. Im Gegensatz zur Tangwald-Zone wächst auf den Riffhügeln kein Tang. Auf abgestorbenen Randpartien dieser Hügel finden sich flächige Krusten der Kalkalgen-Gattung *Lithophyllum*, ferner Algenrasen mit *Amphiroa* spec. und *Laurencia* spec. (Rhodophyta).

Auf den Riffhügeln dominiert bei weitem das tierische Leben. Im flacheren Bereich, also nahe der Tangwald-Zone, überwiegen auf den Korallenhügeln die Octocorallia (Alcyonaria) der Gattungen *Xenia*, *Lobophyton* und *Sarcophyton*, die ganze wogende Flächen bilden. Ferner kommen hier häufig klobig gebaute Madreporaria vor, wie *Porites solida* FORSK.,

Favites complanata (EHRENB.), *Goniastrea retiformis* (LAM.), *Favia stelligera* (DANA), *Galaxea fascicularis* (L.), *Echinopora gemmacea* (LAM.) und *Platygyra lamellina* (EHRENB.); ferner Stöcke kolbig-zweigiger *Stylophora pistillata* (ESPER.). In die großen Blöcke eingebettet und von den gröber gebauten Korallen bis zu einem gewissen Grade gegen mechanische Einwirkung der Wellen geschützt sind einzelne Stöcke der grazil gebauten *Seriatopora angulata* KLZGR. Von der Gattung *Acropora* kommt hier nur vereinzelt die durch kräftige Stangen charakterisierte Spezies *A. humilis* (DANA) vor. Nach außen hin wird das Wachstum an Steinkorallen immer üppiger, die Arten werden immer zahlreicher. Auch wird das Vorkommen von *Acropora* allmählich häufiger.

Auf den nicht mit lebenden Korallen besetzten Zwischenbereichen des Vorriffs wächst vorzugsweise ein dichter, aber niedriger Algenrasen.

Auf der Oberfläche der Vorriffe ist außer den Leder- und Kalkkorallen nur der langstachelige Seeigel *Diadema setosa* LESC. dominierend (daß die zahlreichen Löcher, Höhlen, Spalten und die Korallenstöcke vielfach von Evertebraten, besonders Krebsen und Stachelhäutern, besiedelt sind, versteht sich von selbst).

Der Sandboden ist sehr stark porig durchlöchert, vorwiegend durch den Sipho von Muscheln. Oberflächlich fanden wir aber auch hier keine dominierenden Evertebraten.

Folgende Fischarten haben wir häufig beobachtet:

a) Auf dem Boden lebend:

Synodidae
Saurida tumbil (BL.)
und verwandte Arten (lauernd auf dem Sande ruhend, nicht eingegraben)

Mullidae
Parupeneus auriflamma (FORSK.)
und einige verwandte Arten (mit der Schnauze im Sande wühlend)

Labridae
Halichoeres scapularis (BENN.), (in Gemeinschaft mit *Parupeneus auriflamma*)

Parapercidae
Parapercis polyophthalma (C. & V.), (lauernd auf dem Boden ruhend)

Eleotridae
Eleotriodes sexguttatus (VAL.)

Bothidae
Bothus pantherinus (RÜPP.), (leicht in das Sediment eingewühlt)

b) Im Boden Höhlen bauend:

Gobiidae
Acentrogobius ornatus (RÜPP.)
Amblygobius albimaculatus (RÜPP.)
Cryptocentrus lutheri KLAUSEW.
und einige verwandte Arten
(alle mit kaminartigen Röhren im Sandboden, meist in Wohngemeinschaft mit Knallgarnelen der Gattung *Alpheus*)

c) Bewohner der Vorriffe:

Apogonidae
Apogon aureus annularis RÜPP.
Apogon chrysotaenia BLKR.
Apogon taeniatus C. & V.
Cheilodipterus lineatus (L.)
Cheilodipterus lachneri KLAUSEW.

Serranidae
Epinephelus hemistictos (RÜPP.)
und einige verwandte Arten

Chaetodontidae
Chaetodon fasciatus FORSK.
Chaetodon larvatus CUV.
Chaetodon mesoleucos FORSK.
Chaetodon semilarvatus CUV.

Pomacanthidae
Pomacanthodes maculosus (FORSK.)

Acanthuridae
Acanthurus gahhm (FORSK.)
Acanthurus sohal (FORSK.)
Ctenochaetus striatus (C. & V.)
Zebrasoma veliferum (BL.)

Pomacentridae
Abudefduf saxitilis (L.)
Amphiprion bicinctus (RÜPP.)
Chromis caeruleus (C. & V.)
Chromis dimidiatus (KLZGR.)
Dascyllus aruanus (L.)
Dascyllus marginatus (RÜPP.)
Pomacentrus sulfureus (KLZGR.)

Labridae
Halichoeres centriquadrus (LAC.)
Hemigymnus melapterus BL.
Labroides dimidiatus C. & V.
Stethojulis axillaris (Q. & G.)
Thalassoma purpurea (FORSK.)

Callyodontidae
Callyodon harid (RÜPP.)
und zahlreiche weitere Arten

Scorpaenidae
Pterois radiata (C. & V.)

Balistidae
Rhinecanthus assasi (FORSK.)

d) Auf abgestorbenen Riffabschnitten:

Salariidae
Salarias fasciatus (BL.)

Hinsichtlich der Ichthyofauna ist diese Zone durch die Heterogenität des Biotops, also einerseits durch typische Sandbewohner, andererseits durch charakteristische „Korallenfische" gekennzeichnet.

7. Zone: Hauptriff

Etwa parallel zur Küstenlinie und in 150 bis 200 m von dieser entfernt verläuft als Abschluß des oberen Küstenabschnitts zum tieferen Wasser hin das Hauptriff. Es ist etwa 20 m breit und 3—4 m hoch. An seiner inneren Basis beträgt der Wasserstand (MHW) etwa 3,50—4,50 m. Nach außen hin reicht ein Steilhang mit einer Neigung von etwa 70° bis in 15—20 m Tiefe. Dort beginnt der Kanalboden, der am Fuße des Außenhangs vorzugsweise mit Korallenschutt und grobem Sand bedeckt ist.

Das Hauptriff ist vollständig mit lebenden Steinkorallen besetzt. Hier dominiert bei weitem die Gattung *Acropora: A. hemprichi* EHRENB., *A. erythraea* (KLZGR.). Am Außenhang befinden sich bis in etwa 6 m Tiefe große „Tischkorallen", *A. corymbosa* (LAM.), buschförmige *Acropora* fehlen hier fast gänzlich.

Die häufigsten Fische:

a) An dominierenden Arten kommen alle jene vor, die bereits beim Vorriff aufgezählt wurden. Hinzu kommen:

Serranidae
Cephalopholis miniatus (FORSK.)
Epinephelus summana (FORSK.)
Lutianidae
Lutianus fulviflamma (FORSK.)
Chaetodontidae
Chaetodon auriga FORSK.
Chaetodon lineolatus CUV.
Pomacanthidae
Arusetta asfur (FORSK.)
Pomacanthodes imperator (BL.), (selten)
Pygoplites diacanthus (BODD.), (selten)
Labridae
Gomphosus caeruleus LAC.

b) Im Freiwasser über dem Riff:

Caesiodidae
Caesio caerulaureus LAC.
Caesio lunaris C. & V.
Mugilidae
Crenimugil crenilabis (FORSK.)
und einige weitere Arten

c) An den Korallen des Außenhangs:

Holocentridae
Holocentrus caudimaculatus (RÜPP.)
Holocentrus sammara (FORSK.)
Myripristis murdjan (FORSK.)
Serranidae
Aethaloperca rogaa (FORSK.)
Cephalopholis miniatus (FORSK.)
Epinephelus tauvina (FORSK.)
Anthiidae
Anthias squamipinnis (PETERS)
Chaetodontidae
Chaetodon austriacus RÜPP.
Gaterinidae
Gaterin gaterinus (FORSK.)
Labridae
Cheilinus undulatus RÜPP.
Muraenidae
Gymnothorax flavimarginatus (RÜPP.)
Balistidae
Rhinecanthus assasi (FORSK.)
Ostraciidae
Ostracion cyanurus RÜPP.
Ostracion tuberculatus L.
Tetraodontidae
Arothron hispidus perspicillaris (RÜPP.)

d) Im Tiefenwasser entlang des Riffs:

Carcharhinidae
Carcharhinus melanopterus (Q. & G.)
Triakidae
Triaenodon obesus (RÜPP.)
Mobulidae
Manta birostris (WALB.)
Hemirhamphidae
Hemirhamphus far (FORSK.)
Hemirhamphus marginatus (FORSK.)
Tylosuridae
Tylosurus crocodilus (LES.)
Sphyraenidae
Sphyraena jello C. & V.
Carangidae
Caranx fulvoguttatus (FORSK.)
Caranx speciosus (FORSK.)

Profil Nr. II (Abb. 14)

Dieses Profil, das in der Fischerbucht (Lagerstrand) gelegt wurde, ist durch den Sandstrand charakterisiert. Die felsige Steilküste, die weiter nördlich (siehe Profil Nr. I) bis an die Wasserlinie reicht, ist hier buchtartig zurückgeschwenkt. Diese Bucht ist mit Sand angefüllt, der bereits an der Küste bei mittlerem Wasserstand etwa um 1 m Höhe die Wasserlinie überragt. Landseitig bis zur Felswand hin steigt die Sandschicht noch um etwa einen weiteren Meter an. Trotz dieser Ablagerung ist an der völlig trockenliegenden Felswand eine tiefe Hohlkehle zu erkennen (die von den arabischen Fischern als höhlenartige Überdachung zum Schlafen

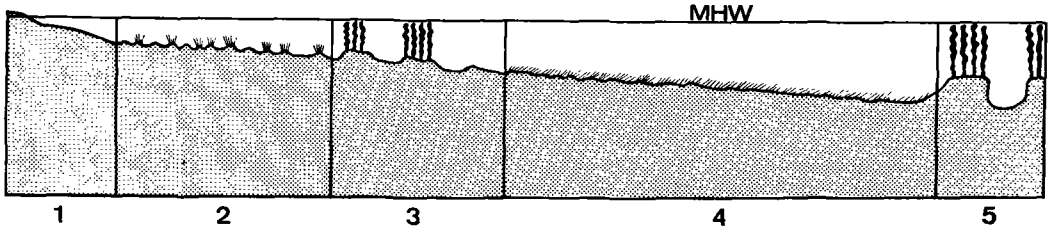

Abb. 14. Schematisiertes Schnitt von Profil II vom Sandufer bis zur Tangwald-Zone. 1—5 sind die physiographischen Zonen.

Fig. 14. Section of profile no. II with the five (1—5) physiographic zones from the sand beach until the seaweed area.

verwendet wird); doch bildet sie zweifelsohne nur den obersten Abschnitt einer viel größeren und tieferen Hohlkehle, die in der Größe und Überdachung jenen tiefen Brandungskehlen entsprechen dürfte, wie wir sie vorzugsweise auf der Westseite von Sarso und Sindi Sarso gefunden haben.

Bei der Profilnahme habe ich mich auf den küstennahen Teil beschränkt, der direkt oder indirekt von dieser Sandablagerung her beeinflußt wurde und sich somit von der Zonierung des Profils I unterscheidet. Demgegenüber erwies sich der küstenferne, riffnahe Abschnitt als identisch mit den entsprechenden Zonen von Profil I, was eine nähere Untersuchung erübrigte.

Im einzelnen wurden bei Profil II folgende Zonen festgestellt:

1. Zone: Küstensand

Diese Zone ist vollständig geprägt von dem durch die Wellen abgelagerten Sand. Die Wasserlinie liegt an einem rein sandigen Schräghang, der bis zu 1 m hoch sein kann. Die Sandzone selbst ist bei mittlerem Wasserstand etwa 2 m breit und fällt rasch ab. Entsprechend dieser Neigung fällt sie normalerweise bei Ebbe nie völlig trocken: Bei mittlerem Niedrigwasser bleiben die unteren 1,2—1,5 m dieser Zone bedeckt.

Den Untergrund dieser Sandzone bildet eine Abrasionsterrasse, wie wir sie bei Zone 2 des Profils I kennengelernt haben. Hier ist diese Terrasse völlig mit Sand zugedeckt und wird erst durch Freischaufeln sichtbar, während sie einige Meter weiter nördlich, also zwischen Profil I und II, noch offenliegt; denn dort beginnt die Sandablagerung erst direkt an der Strandlinie. Im Bereich des II. Profils ist die Abrasionsterrasse aber bis zur Grenze der anschließenden Zone völlig mit sandigem Sediment bedeckt. Ökologisch dürfte sie in keiner Weise mehr wirksam sein.

Während im trockenen Strand oberhalb der Wasserlinie und des Spülsaumes der Einsiedlerkrebs *Coenobita staevola* FORSK. und die Gespenstkrabbe *Ocypode saratan* FORSK. charakteristisch sind, scheint nach den Beobachtungen von ZANDER für die weitgehend submers liegende Sandzone die Muschel *Mesodesma* eine Charakterform zu sein. Oberflächlich, also ständig auf dem Sediment, konnten wir hingegen weder unter den Evertebraten noch unter den Fischen kennzeichnende Arten finden. Diese Zone dürfte einerseits zu schmal und klein sein und ihr Sediment dürfte andererseits durch die dauernde, wenn auch meist schwache Brandung zu unruhig sein, um einer eigenen Population genügend Lebensraum und Existenzmöglichkeiten zu geben. Über die Mikrofauna des Küstensandes berichtet GERLACH (1967b).

2. Zone: Knubbelige Abrasionsterrasse

Am Ende der recht stark geneigten Sandzone tritt wieder die Abrasionsterrasse heraus. Hier aber nicht die glatte und nackte Platte (die der 2. Zone des I. Profils entspricht), sondern jene Terrasse, die durch zahlreiche knubbelartige, bis zu 10 cm hohe und sehr unregelmäßige Erhebungen charakterisiert ist. Sie entspricht vollkommen der 3. Zone des I. Profils.

Wie dort, werden diese Knubbel vorwiegend von Kalkalgen der Gattungen *Melobesia* und *Lithothamnion* gebildet, sind die vertieften Zwischenräume mit einer dünnen Schlicksand-Schicht bedeckt und wachsen auf den Erhebungen niedrige büschelförmige Braunalgen der Gattung *Cystoseira*.

Im Bereich des II. Profils ist diese knubbelige Abrasionsterrasse etwa 7 m breit und stets mit Wasser bedeckt.

Die tierischen Bewohner sind die gleichen wie bei der 3. Zone des I. Profils.

3. Zone: Tangwald-Zwischenfeld

Auf einem relativ schmalen Abschnitt von etwa 8 m Breite tritt nun eine Zone mit niedrigen abgestorbenen Korallenhügeln auf. Sie sind nicht mit lebenden Korallen, sondern nur noch mit Kalkalgen besetzt. Außerdem wachsen auf der Oberseite dieser Hügel höhere Braunalgen, allerdings nicht mehr die kleine buschförmige *Cystoseira* spec. der 2. Zone, sondern dieselben Arten von *Sargassum* und *Turbinaria* der Tangwald-Zone (5. Zone) des I. Profils. Die Zwischenräume sind mit einer dünnen Sandschlick-Schicht bedeckt.

Da diese Tangwald-Zwischenzone zu schmal ist, weist sie keine eigene ökologische Population auf. Man findet unter den Evertebraten wie den Fischen eine Mischfauna, wie sie sowohl in der umgebenden Sandzone wie auch in der eigentlichen Tangwald-Zone vorkommt.

4. Zone: Sandschlick-Feld mit Seegras

Dieser Abschnitt, der etwa 20 m breit ist, entspricht hinsichtlich der Bodenverhältnisse völlig der Sandschlick-Zone (Zone 4) des I. Profils. Das Sediment besteht vorwiegend aus einer hohen Lage Sandschlick; darunter befindet sich Korallenschutt. Die Abrasionsplatte liegt auch hier erheblich tiefer als bei den benachbarten Zonen.

Der wesentlichste Unterschied, der zugleich diese Zone charakterisiert, besteht im Bewuchs durch eine „Seegras"-Art der Gattung *Cymodocea*. Die einzelnen grasbüschelähnlichen Pflanzen stehen ± solitär, d. h. sie bilden keinen dichten Rasen, sondern zwischen den einzelnen Stücken befindet sich ein kleiner Abstand.

Der Boden zwischen den *Cymodocea*-Büscheln ist mit zahlreichen Löchern durchsetzt. Auch hier sind die Verhältnisse die gleichen wie bei Zone 4 des I. Profils; dasselbe gilt für die Fischwelt.

5. Zone: Tangwald-Streifen

Diese sowie die weiteren Zonen bis zum Hauptriff und dem Außenhang entsprechen vollauf den Verhältnissen von Profil I. Daher verzichten wir auf eine Beschreibung, die nur eine Wiederholung des bereits Gesagten sein würde.

Profil Nr. III (Abb. 15)

Dieses Profil wurde nahe der Nordwestecke der Insel Sindi Sarso (Sarso seghir), und zwar ungefähr gegenüber dem Profil I gelegt. Auch hier verlief die Profillinie senkrecht zur Küstenlinie in Richtung zur Kanalmitte. Das Profil verlief von der Küste bis zum äußeren Riffhang (vgl. auch ZANDER 1967).

Gegenüber der bisher beschriebenen Küste von Sarso (Profil I und II) weist die Küstenzone einen erheblichen Unterschied auf. Wie bei Profil I liegt auch hier eine Steilküste vor. Es fehlt aber eine Abrasionsterrasse in Höhe der heutigen Wasserlinie. Zwar findet man an dieser Stelle auch eine Hohlkehle, von deren Basis fällt aber die Küste weiter senkrecht ab bis in etwa 2,50 m Tiefe. Erst dort setzt eine ± waagerechte Platte an, die bis zum Außenriff verläuft. Diese Platte hat von der Küste bis zum Außenhang eine Breite von etwa 20 m. Trotz dieser relativ kurzen Strecke glaube ich, vier verschiedene physiographische Zonen unterscheiden zu können.

Die Wasserbewegung ist hier relativ stark. Der Kanal zwischen den beiden Inseln ist schon so breit und dieser Punkt liegt so weit nach Norden, daß dieser Küstenabschnitt ziemlich exponiert und dem Wellengang der vorherrschenden Nordwinde ausgesetzt ist. Auf jeden Fall haben wir hier eine deutliche Brandung festgestellt. Für stärkere Wasserbewegungen sprechen auch die Ausbildung des Terrassenbodens sowie die Wuchsformen der Korallen, worauf bei der Beschreibung der Zonen näher eingegangen wird.

1. Zone: Hohlkehle

Dicht oberhalb der mittleren Niedrigwasserlinie verläuft in den Fels hinein eine etwa 1 m breite waagerechte Terrasse, die am inneren Ende abgerundet ist und von dort schräg nach oben führt. Überdacht ist sie von einem weit ausladenden Felsvorsprung, der darauf hindeutet, daß auch hier die Insel weiter in das Wasser hineinragte als es heute der Fall ist.

Der Fels der Hohlkehle besteht, wie bei der Insel selbst, aus subfossilem Korallengestein, teils aus kalkigem Sandschlickstein, teils aus Korallenskelet-

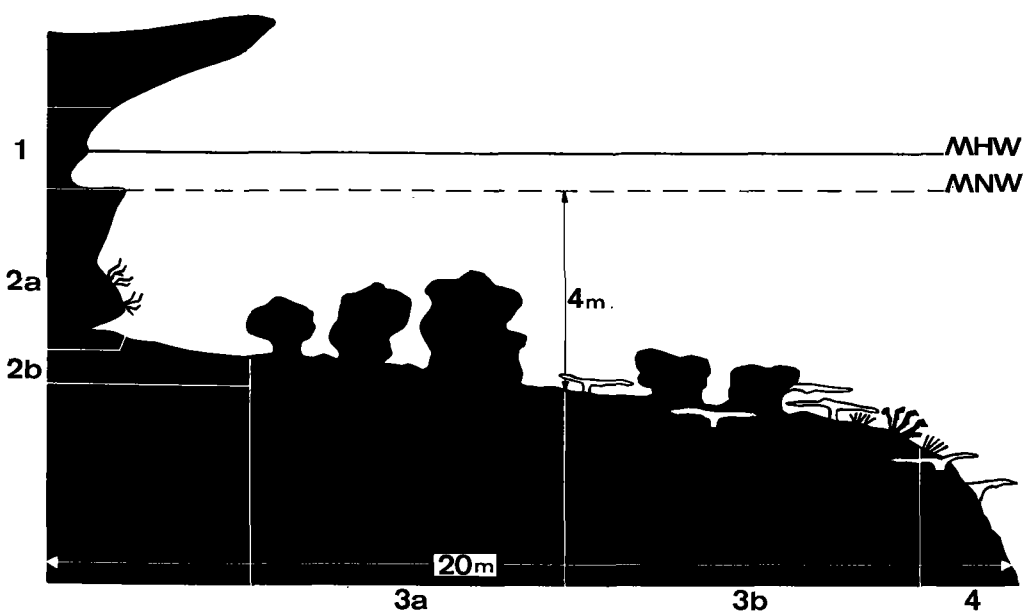

Abb. 15. Schematisierter Schnitt durch den Küstenabschnitt der Insel Sindi-Sarso (Sarso seghir). 1—4 = Physiographische Zonen. MHW = Mittlere Hochwasser-Linie, MNW = Mittlere Niedrigwasser-Linie.

Fig. 15. Section of the four (1—4) coastal zones of the island Sindi-Sarso. MHW = HT, MNW = LT.

ten, und überall mit eingelagerten anderen tierischen Resten, wie Muschelschalen, Seeigelstacheln usw. Durch die erodierende Wirkung des Wassers ist der Fels an jenen Teilen, die im Bereich der 1. Zone im Verlauf einer Flut mit Wasser bedeckt oder benetzt werden, ziemlich glatt; an der rückwärtigen steilen Fläche findet man allerdings auch zahlreiche Spalten und andere Vertiefungen.

Überwachsen ist der Fels der Hohlkehle mit einem Rasen feinfädiger Cyanophyceen, besonders auf der waagerechten Sohle dieser Vertiefung. Außerdem findet man dort niedrige, mehr schichtenförmig gebaute Kalkalgen.

Zwei Charaktertiere findet man in dieser 1. Zone: die Krabbe *Grapsus* spec. und den Fisch *Lophalticus kirkii magnusi*. Beide leben amphibisch und bewegen sich vorzugsweise im Bereich der Spritzzone oberhalb der eigentlichen Wasserlinie.

2. Zone: Submerse Steilwand

Diese Zone besteht aus zwei Abschnitten:

a) Der Steilwand von der Wasserlinie bis in 2—2,5 m Tiefe mit einer abschließenden kleinen Hohlkehle;

b) dem ersten, noch recht schräg, hangartig verlaufenden Teil der Basalterrasse.

Nach dem Korallenwachstum bilden beide noch eine Einheit.

Die eigentliche, stets submerse Steilwand verläuft nicht völlig senkrecht und auch nicht in gerader Linie, sondern weist in etwa 1 m Tiefe eine deutliche Einbuchtung nach innen auf, eine nicht völlig ausgeprägte offene Höhlung. An der Basis dieser Steilküste befindet sich eine weitere deutliche Eintiefung, die zudem noch eine echte Überdachung aufweist. Beide machen den Eindruck einstiger Hohlkehlen.

Auch der Steilhang mit den beiden genannten Aushöhlungen sowie der seeseitig anschließende weniger stark geneigte Abschnitt, der zugleich den Beginn der großen Basalterrasse bildet, bestehen ausschließlich aus ziemlich kompakt gebautem Kalkgestein, das corallogenen Ursprungs ist.

An lebenden Korallen finden sich sowohl am Steilhang als auch am Basalabschnitt dieser Zone stabil und recht niedrig gebaute, buschförmige Stöcke der Gattungen *Acropora, Pocillopora* usw.

An Fischen bilden drei Arten der Familie Salariidae Leitformen für drei verschiedene Höhenstufen dieser Zone.

Istiblennius edentulus (Bl., Schn.) bewohnt den Bereich direkt unter der Wasserlinie und findet sich am oben leicht überhängenden Abschnitt dicht unterhalb der obersten Hohlkehle; bei Hochwasser wandert dieser Fisch auch auf die dann submers liegende Basalplatte dieser Hohlkehle.

Ecsenius frontalis (Val.) bewohnt die Korallenstöcke des eigentlichen submersen Steilhanges (außerdem findet man hier kleinere Exemplare der Gattung *Cheilinus*).

Salarias fasciatus (Bl.) lebt an den Korallenstöcken, die auf dem schwächer geneigten basalen Abschnitt wachsen.

3. Zone: Große Basalterrasse

Diese Terrasse bildet den größten Teil des Bereiches zwischen der Steilküste und dem seeseitigen Steilhang. An ihrer landseitigen Grenze ist diese Zone etwa 2,5 m, im mittleren Bereich 4 m, an der äußeren Grenze etwa 5 m tief.

Der Boden dieser Basalterrasse ist glatter Kalkfels. Er weist nur wenig Sand und keinerlei Schlick auf.

Nach dem Korallenwachstum lassen sich zwei Unterzonen unterscheiden:

a) Der innere Abschnitt lebender *Porites*-Blöcke, und
b) der äußere Abschnitt toter *Porites*-Blöcke und lebender Korallen des „Kriechweiden-Typs".

Der innere Abschnitt, der in der Breite ein Drittel bis die Hälfte der Zone einnimmt, besteht vorwiegend aus normal gewachsenen, etwa 1—1,50 m hohen Blöcken der Gattung *Porites*. Normalerweise ist die ganze Oberfläche lebend.

Auch der äußere Abschnitt wurde charakterisiert durch *Porites*-Blöcke, die aber höchstens die halbe Höhe aufwiesen und durchweg abgestorben sind. Nur an wenigen Stellen konnten lebende Polypenkomplexe festgestellt werden. Zwischen diesen toten *Porites*-Blöcken und noch niedriger als diese stehen ± als Kriechformen ausgebildete lebende Korallen der Gattung *Acropora, Pocillopora* usw. Besonders häufig sind hier sehr niedrig gebaute Schirmkorallen. Gelegentlich kommen „Feuerkorallen" (Milleporidae) vor. Auf den toten Blöcken finden sich oft Felder im Wasserstrom wogender Alcyonaria. Diese Lederkorallen nehmen nach außen zum Riffhang hin stark zu und bedecken wesentliche Teile der obersten Abschrägung zum eigentlichen Außenhang.

Die häufigsten Fische dieser Zone sind:

a) An den Korallen:

Serranidae
Cephalopholis miniatus (Forsk.)
Epinephelus areolatus (Forsk.)
Epinephelus hemistictos (Rüpp.)
Epinephelus summana (Forsk.)
Lutianidae
Lutianus ehrenbergi (Pet.)
und einige weitere Arten
Pomacanthidae
Arusetta asfur (Forsk.), (selten, meist paarweise)
Pomacanthodes maculosus (Forsk.)

Chaetodontidae
Chaetodon fasciatus FORSK. (paarweise)
Chaetodon larvatus CUV. & VAL. (solitär)
Chaetodon mesoleucos FORSK. (paarweise)
Chaetodon semilarvatus CUV. (paarweise)
Heniochus intermedius STEIND.
Acanthuridae
Acanthurus xanthopterus CUV. & VAL.
Acanthurus sohal (FORSK.)
Zebrasoma veliferum (BL.)
Pomacentridae
Pomacentrus sulfureus KLZGR.
Callyodontidae
Zahlreiche *Callyodon*-Arten

b) Im freien Wasser oberhalb der Korallen:

Clupeidae
Harengula punctata RÜPP. (in riesigen Schwärmen)
Mugilidae
Crenimugil crenilabis (FORSK.), (schwarmweise)
Hemirhamphidae
Hemirhamphus marginatus (FORSK.), (schwarmweise)
Caesiodidae
Caesio caerulaureus LAC.
Caesio lunaris CUV. & VAL. (beide schwarmweise)
Carangidae
Trachinotus bailloni (LAC.)

4. Zone: Außenhang

Im Prinzip ähnelt der Außenhang der entsprechenden Zone bei Profil I. Allerdings bestehen zwei wesentliche Unterschiede: Während bei Profil I den äußeren Abschluß der Küstenzone ein Hauptriff bildet, das dammartig bis dicht unter die Wasseroberfläche reicht, fehlt bei Profil III ein solches Hauptriff völlig. Dementsprechend liegt die obere Kante des Außenhangs nicht in 100 cm oder weniger Tiefe, sondern mindestens 5 m tief. Dementsprechend ist die Lichtmenge geringer und das Korallenwachstum weniger üppig. Im oberen Bereich des Hanges wachsen besonders kleinere *Porites* und tischförmige *Acropora*, die aber bald zur Tiefe hin verschwinden.

Die Fischwelt entspricht der der genannten Ichthyofauna des Außenhangs von Profil I.

V. Vergleichend-topographische Untersuchungen

Vergleicht man den Aufbau von Profil I und Profil III (Abb. 16), so finden sich einige grundlegende Unterschiede, wie aus der folgenden Gegenüberstellung ersichtlich ist:

	Profil I	Profil III
Breite	200 m	20 m
Submerse Küstenlinie	flach	steil
Flache Abrasionsterrasse	vorhanden	fehlt
Größere Sandschlick-Sedimente	vorhanden	fehlen
Großalgenzone	vorhanden	fehlt
Äußeres Hauptriff	vorhanden	fehlt
Dominierende Korallen-Gattung	*Acropora*	*Porites*

Trotz dieser grundlegend erscheinenden Unterschiede in der Morphologie dieser beiden Riffe lassen sich doch bestimmte Gemeinsamkeiten feststellen, bzw. Kriterien, die auf eine gemeinsame Geschichte hindeuten.

An Profil III sind deutlich drei Wasserstandsmarken erkennbar: Die Hohlkehle in der heutigen MW-Linie, eine weitere, etwas weniger ausgeprägte in — 1 m MW und eine dritte, deutlichere in 2 m Tiefe. Diese Markierungen deuten auf Schwankungen des Wasserstandes hin, in dem Sinne, daß die MW-Linie stufenweise tiefer gelegen haben muß als heute.

Wie bereits erwähnt, gab KLUNZINGER (1870) an, daß der Wasserstand des Roten Meeres zur Zeit deutlich absinke, was allerdings unseren Beobachtungen zu widersprechen scheint. Das gleiche gilt für die Beobachtung von NESTEROFF (1955), der von der Insel Abulat im nördlichen Bereich der Farasan-

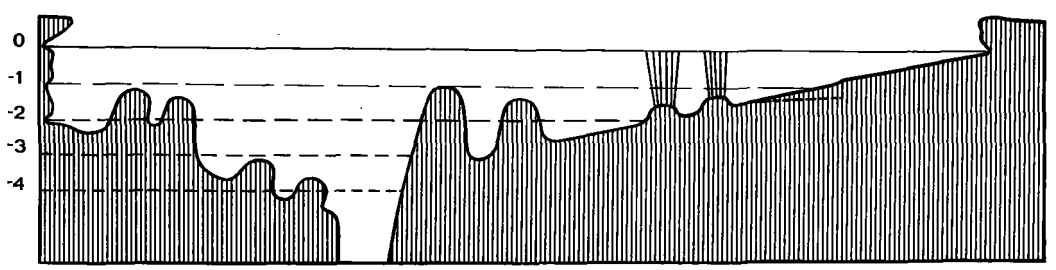

Abb. 16. Stark schematisierte vergleichende Gegenüberstellung der beiden Küstenriffe von Sarso und Sindi-Sarso mit Wasserstandsmarken bei entsprechend abgesenktem Niveau. Durch diese Gegenüberstellung läßt sich die Entwicklung der Riffe konstruieren.

Abb. 16. Diagrammatic cross-section of the both opposite coastal and reef areas of Sarso and Sindi-Sarso, with the marks of different depressed water- levels. This confrontation of both areas allows a reconstruction of the development of the reefs.

Bank drei deutliche Hohlkehl-Linien oberhalb des heutigen Wasserstandes feststellte. Wenn man auch einen Teil dieser Zeitmarken und insbesondere die Entstehung der rein corallogenen Inseln selber möglicherweise auf einen Hebungsvorgang des ganzen Gebietes zurückführen kann (wogegen allerdings erhebliche Einwände bestehen), so sind zumindest jene heute submers liegenden Hohlkehl-Linien sicher nur auf eustatische Schwankungen zurückzuführen.

Versuchen wir nun, die Zeitmarken des Profils III auf das I. Profil zu übertragen, so finden wir einigen Aufschluß hinsichtlich der historischen Abläufe der beiden Riffe. Die — 2 m-Linie verläuft im Profil III durch die lebenden *Porites*-Blöcke, liegt aber über den seeseitig befindlichen toten *Porites*-Blöcken. Bei Profil I läuft sie durch das Hauptriff und die Vorriffe und endet vor den Hügeln der Tangwaldzone.

Die — 1 m-Linie liegt im Profil III oberhalb aller heutigen Korallen, beim I. Profil berührt sie den Rücken des Hauptriffs und läuft dicht über die Oberseite der Vorriffe; sie liegt auch normalerweise dicht über dem Kamm der Hügel, die die Algen der Tangwaldzone tragen, und sie endet in der Sandschlick-Zone vor dem oberflächlich kleinen, aber tiefer reichenden Absatz der heutigen Abrasionsterrasse. Die — 4 m-Linie berührte die Basis der heutigen Außenriffe. Welche historischen Rückschlüsse lassen sich nun aus den verschiedenen Marken ziehen?

Man könnte sich folgenden zeitlichen Ablauf bei steigendem Wasserstand vorstellen.

Die Steilwände des gehobenen Kliffs reichten bis zum Außenhang der heute lebenden Korallenriffe.

Bei der heutigen — 4 m-Linie, also einem Wasserstand, der 4 m tiefer lag als die jetzige Oberfläche, entstanden durch Bildung von Hohlkehlen und folgendem Abbruch des überhängenden Gesteins sowie durch dessen Abbau die Anfänge einer Abrasionsterrasse. Bei — 3 m, also 1 m Wasserstand für die jeweilige Außenkante, entstand an dieser Kante das Riff, wahrscheinlich mit *Porites*-Blöcken. Gleichzeitig vergrößerte sich bei allmählichem Wasseranstieg die Abrasionsterrasse, allerdings der Insel Sarso stärker als bei Sindi Sarso. Dieser Prozeß hielt bei der heutigen — 2 m-Marke an. Damit hatte bei Sindi Sarso das Wasser die heutige Steilwand erreicht, bei Sarso war die Abrasionsterrasse bis zur seeseitigen Grenze der heutigen Tangwaldzone vorgedrungen. Deren *Porites*-Blöcke, die jetzt die Basis für die Tange bilden, existierten zu jener Zeit noch nicht, da dort die Steilwand der gehobenen Insel gestanden haben muß. Hingegen vergrößerte sich das Außenriff (= Hauptriff) und entstanden auch die (heute mit anderen Korallen überwachsenen) *Porites*-Blöcke des Vorriffs. Vor der Insel Sindi Sarso entwickelten sich die äußeren *Porites*-Blöcke weiter, die heute lebenden dürften in den ersten Anfängen entstanden sein.

Das Wasser stieg weiter auf die heutige — 1 m-Marke und verblieb wiederum eine Weile auf dieser Höhe. Vor Sarso wuchsen Hauptriff und Vorriffe weiter, wobei die *Porites* sicher schon größtenteils von anderen Korallen, die ein schnelleres Höhenwachstum haben, überlagert wurden. Es entstanden dafür die *Porites*-Blöcke, die heute den Tangwald tragen. Das Wasser reichte bis zur heutigen Grenze zwischen der Sandschlick-Zone und der folgenden heutigen Abrasionsterrasse. Diese Terrasse war noch eingebaut in das steile Kliff der Insel, während die heutige Sandschlick-Zone die eulitorale und nackte Abrasionsterrasse war.

Vor Sindi Sarso starben die äußeren *Porites*-Blöcke, die den äußeren Riegel bildeten, ab, da nun der Wasserstand für diese Korallen zu hoch war (*Porites* ist eine reine Seichtwasserform). Zu starke Brandung mag die Entwicklung anderer Kalkkorallen, wie sie als dichtes Riff vor Sarso stehen, verhindert haben. Dafür aber hat sich jetzt auf der kurzen Basalplatte vor Sindi Sarso die heute noch lebende zweite Garnitur von *Porites*-Blöcken entwickelt.

Der folgende Wasseranstieg dürfte sprunghaft auf etwa — 50 cm erfolgt sein. Darauf deutet vor Sarso der scharfe Absatz (Abb. 10) an der Grenze zwischen der Sandschlick-Zone und der knubbeligen Abrasionsterrasse (I. Profil, 3. und 4. Zone) und an der submersen Steilwand eine weitere kleine Vertiefung (es ist keine echte Hohlkehle) dicht unter dem heutigen Wasserstand hin. Dann erst stieg das Wasser bis zum jetzigen MW-Stand, wobei sich vor Sarso die heute schwach bewachsene und die nackte Abrasionsterrasse bildeten. Da das Hauptriff und die Vorriffe zu hoch wurden und wesentliche Nahrungskonkurrenten darstellten, da ferner wahrscheinlich durch die Abrasion des gehobenen Felsens erhebliche Sedimentmengen anfielen und da außerdem der Wasserstand zu hoch wurde, starben die inneren *Porites*-Blöcke ab und wurden zur Basis großwüchsiger Algen, dem heutigen Tangwald. An der Insel Sindi Sarso hat sich nur eine neue Hohlkehle gebildet, sonst sind keine weiteren größeren Veränderungen eingetreten.

Die einzige, wenn auch nicht unerhebliche Unklarheit bleibt sowohl bei diesem hypothetischen Ablauf der Riffentwicklung als auch bei dem äußeren Vergleich der Profile beider Inseln bestehen, nämlich die Frage nach der Ursache für die beträchtlichen Unterschiede in der heutigen Riffbreite. Dies aber ist eine Frage der erodierenden Kräfte, die allgemein noch einer Analyse bedürfen. Sicher sind sie auf Wellenbildung allein nicht zurückzuführen, die chemische Erosion ist wahrscheinlich viel bedeutsamer, und mit ihr zusammen sind es die bohrenden

Lebewesen, die ein Gestein zermürben. Weshalb diese Kräfte aber an der einen Insel erheblich stärker wirksam werden konnten als an der anderen, bleibt bisher ungeklärt.

Wenn wir den Vermerk gemacht haben, die Entstehung der Riffe und physiographischen Zonen und die heutigen topographisch-morphologischen Gegebenheiten von der historischen Seite her zu beleuchten, so betrifft dies jedoch nur die relativ jüngste Zeit der Riffbildung. Die Abläufe während der Entstehung der eigentlichen Inseln bzw. des ganzen Komplexes der Farasan-Bank sowie die zweifelsohne vorhandenen tektonischen Vorgänge, wie sie in unserem Falle durch die Grabenbildung zwischen den beiden Sarso-Inseln gegeben ist, sind damit nicht betroffen und sind sicher erheblich älteren Datums als die Entstehung der beschriebenen Riffe und ihrer physiographischen Zonen.

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Beiträge zur Ökologie und Biologie litoralbewohnender Salariidae und Gobiidae (Pisces) aus dem Roten Meer

5. Beitrag der Arbeitsgruppe Litoralforschung

von

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Contribution to the ecology and biology of littoral inhabiting Salariidae and Gobiidae (Pisces) of the Red Sea

Summary

At the shores of the islands of Sarso and Sindi Sarso (Farasan Archipelago, Red Sea) the supra-, mid- and sublittoral zones of four different localities were investigated. Cross sections of a sand-rock beach, a rock beach, a rocky cliff and a mangrove beach have been drawn to find out different habitats. The largest part of the bottom is formed by creviced coral rocks.

Fishes of the families Salariidae and Gobiidae were examined in detail and referred to distinct habitats. The habits and ecological demands of the species mentioned are discussed:

Salariidae: *Lophalticus kirkii* prefers the supralittoral region of the steep cliffs, from which it can easily reach the water level. Feeds on algae. — *Istiblennius edentulus* inhabits the horizontal as well as the vertical rock walls of the midlittoral region. Periods of low tide are passed in tide pools. Goes ashore only at night and feeds on algae. — *Halmablennius flaviumbrinus* occurs on the horizontal rock walls of the midlittoral region only. Periods of low tide are passed in tide pools, too. Feeds on algae. — *Antennablennius hypenetes* exists on plain and steep rocks of the midlittoral region and prefers holes of adequate diameter to hide in. Periods of low tide are spent in little tide pools. Feeds on algae. — *Salarias fasciatus* is very common in those parts of the sublittoral region where sufficient hiding-places are present. It seems to avoid turbulent water. Feeds on algae, eventually Bryozoa, too. —

Gobiidae: *Acentrogobius ornatus* and *A. meteori* live in the midlittoral and upper sublittoral regions on sand or in sand-filled trenches of horizontal rock walls. — *Cryptocentrus:* species of this genus are very common below the midlittoral region. Since they are living in sand burrows, they are dependent on sandy areas.

It is discussed, why Salariidae and Gobiidae prefer different environments in their trend towards an amphibian habit. On the rocky shores there seems to be a more favorable food supply for the algae-feeding Salariidae than for the predatory Gobiidae; the representatives of Gobiidae have turned to terrestrial habits in the mangrove region, less at rocky shores.

Zusammenfassung

An den Inseln Sarso und Sindi Sarso (Farasan-Inselgruppe — Rotes Meer) wurden das Supra-, Eu- und das unmittelbar angrenzende Sublitoral von vier verschiedenen Stellen untersucht. Es wurden Profile eines Sand-Fels-Strandes, eines Felsstrandes, eines Felskliffs und eines Mangrovestrandes gezeichnet und eine Zonierung vorgenommen. Der weitaus größte Teil des Untergrundes wird aus Korallenfelsen gebildet.

Von der Fauna konnten Fische der Familien Salariidae und Gobiidae genauer beobachtet und einzelnen Zonen zugeordnet werden. Die Besonderheiten in der Lebensweise und die ökologischen Ansprüche der einzelnen Arten seien kurz aufgezählt.

Salariidae: *Lophalticus kirkii:* Lebt im Supralitoral an steilen Felsklippen, von denen er leicht das

Wasser erreichen kann. Algenfresser. — *Istiblennius edentulus:* Bewohnt sowohl horizontale als auch vertikale Stellen des Eulitorals. Die Ebbezeit wird in Resttümpeln überdauert. Geht nur nachts aktiv an Land. Algenfresser. — *Halmablennius flaviumbrinus:* Nur am horizontalen Felsen des Eulitorals vorkommend. Die Ebbezeit wird ebenfalls in Resttümpeln überdauert. Algenfresser. — *Antennablennius hypenetes:* Lebt an flachen und steilen Felsen des Eulitorals. Bevorzugt dem Körperdurchmesser entsprechende Löcher als Wohnröhren. Die Ebbezeit verbringt er in kleinen Wasseransammlungen. Algenfresser. — *Salarias fasciatus:* Im Sublitoral dort sehr weit verbreitet, wo genügend Versteckmöglichkeiten vorhanden sind. Weicht anscheinend sehr bewegtem Wasser aus. Algen-, evtl. auch Bryozoenfresser.

Gobiidae: *Acentrogobius ornatus* und *A. meteori:* Leben im Eu- und oberen Sublitoral auf Sand oder in sandgefüllten Rinnen des zerklüfteten horizontalen Felsens. *Cryptocentrus:* Arten dieser Gattung sind vom oberen Sublitoral an weit verbreitet. Sind von Sandzonen abhängig, da sie dort ihre Höhlen anlegen.

Es wird die Frage diskutiert, ob die Salariidae und Gobiidae beim Übergang zu einer amphibischen Lebensweise verschiedene Lebensräume bevorzugen. Es hat den Anschein, daß im Felslitoral für die algenfressenden Salariidae ein günstigeres Nahrungsangebot besteht als für die räuberischen Gobiidae, deren Vertreter besonders in der Mangrove zur Landlebensweise übergegangen sind.

I. Einleitung

Im Eulitoral und Supralitoral der Meeresküste kann nur eine Fauna existieren, die sich durch Spezialisierung an die Besonderheiten des Lebensraumes angepaßt hat. Diese Zonen sind nämlich dadurch gekennzeichnet, daß durch die Gezeiten (Eulitoral) oder auch nur durch Brandung, Sturmflut und Springflut (Supralitoral) abwechselnd marine und terrestrische Bedingungen geschaffen werden, die weder echten Meerestieren noch echten Landtieren Lebensmöglichkeiten bieten (GERLACH 1963). In verschiedenen Tiergruppen sind aber bei einigen Arten bestimmte Organe und Organsysteme so verändert, daß diese Formen in solche ökologische Nischen eindringen konnten. Es hat sich erwiesen, daß die Besiedlung des Eulitorals und Supralitorals vornehmlich von Tieren erfolgte, die sich von Meeresbewohnern ableiten lassen; der nächste phylogenetische Sprung solcher Formen könnte die Eroberung des Landes bedeuten. Es ist möglich, diese progressive Evolution an Hand von Zwischenformen in ihren Einzelschritten annähernd zu verfolgen.

Als solche Zwischenformen können amphibisch lebende Fische angesehen werden, die bevorzugt an tropischen Meeresküsten, ausnahmsweise (*Blennius galerita*) am Mittelmeer vorkommen. Unter den Gobiiden konnte nach den Untersuchungen von HARMS (1928), EGGERT (1929, 1931, 1935) und SCHÖTTLE (1931) mehrmalige parallele Evolution zum Landleben festgestellt werden; sogar innerhalb der Gattung *Periophthalmus* lassen sich zwei phylogenetische Reihen aufstellen. Die Blennioidea mit ihren Familien Blenniidae und Salariidae haben ebenfalls amphibisch lebende Vertreter hervorgebracht. Es gibt über diese Familien zwar einige morphologische und ökologische Untersuchungen von HARMS (1928), EGGERT (1931), SOLJAN (1932), RAO & HORA (1938), ABEL (1960, 1962), MAGNUS (1963, 1966) und KLAUSEWITZ (1964), doch sind die Zusammenhänge zwischen Lebensweise und Körperbau sowie der phylogenetische Wert der Anpassungen bisher nicht geklärt worden.

Im Herbst 1964 hatte ich Gelegenheit, für eine kurze Zeit im südlichen Roten Meer auf den Inseln Sarso und Sindi Sarso, die zur Farasan-Inselgruppe gehören, den Lebensraum und die Lebensweise küstenbewohnender Salariiden und Gobiiden zu untersuchen, sowie auch einige Exemplare zu sammeln und für morphologische Untersuchungen zu fixieren. Diese Reise fand im Rahmen der Expedition des Forschungsschiffes „Meteor" statt und wurde finanziert von der Deutschen Forschungsgemeinschaft, der ich zu Dank verpflichtet bin. Ebenfalls danken möchte ich Herrn Prof. Dr. C. KOSSWIG, der diese Expedition förderte, sowie den Herren W. FISCHER, Prof. Dr. S. GERLACH, Dr. W. KLAUSEWITZ, Dr. W. KOST, Prof. Dr. W. SCHÄFER, L. SILLNER und Dr. R. SIMONSEN, die mit mir zusammen die 14 Tage auf der Insel verbrachten und mir in jeder Weise behilflich waren. Herrn Prof. Dr. G. DIETRICH, Herrn Kapitän LEMKE und der Besatzung von der „Meteor" gebührt großer Dank für ihr Verständnis und Entgegenkommen bei den Schwierigkeiten, die das Inselunternehmen forderte.

Die vorliegende Schrift soll ein Beitrag zur Ökologie und Lebensweise litoralbewohnender Salariiden und Gobiiden der beiden Inseln sein. Die morphologischen und anatomischen Untersuchungen werden einer weiteren Veröffentlichung vorbehalten sein.

II. Ökologische und biologische Untersuchungen

a) Untersuchungsgebiet und Methode

Die Inseln Sarso und Sindi Sarso liegen im Nordwesten der Farasan-Inselgruppe, die als der arabischen Küste zugehörige Landteile zu betrachten sind (Abb. 1). Bei den genannten Inseln handelt es sich um kleine langgestreckte Erhebungen eines pleistozänen Korallenriffes (KLAUSEWITZ & SCHÄFER 1965) von 12 bzw. 6 km Länge und 1,3 bzw. 0,5 km Breite. Das aride Klima und der Mangel an süßem Grundwasser haben nur stellenweise eine kärgliche Landvegetation aufkommen lassen. Die Inseln erheben sich bis zu 40 m über den Meeresspiegel; an der Westküste sind sie, da der Wind hauptsächlich aus dem Westen oder Nordwesten kommt, stark zerklüftet und unterhöhlt; an der Ostküste dagegen sind größere Buchten mit angespültem Korallensand zu finden. Während des Aufenthaltes vom 24. November bis zum 8. Dezember 1964 waren maximale Temperaturen von 38 °C zu verzeichnen; in den Dezembertagen kam ein leichter Sturm mit Windstärke 6 auf, der die Höchstwerte auf 32 °C senkte, in dieser Zeit gab es auch einige kurze Regenschauer. Die Werte lagen nachts um 10—15° niedriger als die Maximaltemperaturen. Das Wasser war anfangs mit etwa 27° sehr warm, kühlte aber nach dem Sturm etwas ab, der außerdem eine leichte Trübung des sonst sehr klaren Wassers verursachte. Die Gezeiten wechselten zweimal täglich, der Tidenhub betrug 60—70 cm.

Für die Beobachtungen wurden an der Ostküste von Sarso und an der Westküste von Sindi Sarso je zwei Stellen ausgesucht: es wurden ihre Strukturierungen in Form von Profilen aufgezeichnet und die dort lebenden Salariiden und Gobiiden vom oberen Litoral manchmal bis zu einer Wassertiefe von 1,5 m unter der Hochwasserlinie registriert. Diese Untersuchungen erfolgten zum größten Teil durch Schwimmtauchen mit einer Beobachtungsmaske. Für eingehendere Beobachtungen stand ein 30 l fassendes Plastikaquarium zur Verfügung, in dem einige Fische eine kurze Zeit gehältert werden konnten.

Es ist offensichtlich, daß wegen der kurzen Untersuchungszeit noch viele Fragen ungeklärt bleiben mußten: so können z. B. keine Angaben über die Fortpflanzungsbiologie gemacht werden. Außerdem muß bei der Beurteilung der unten beschriebenen Ergebnisse berücksichtigt werden, daß Klimaunterschiede evtl. jahreszeitliche Veränderungen der Lebensweise der Tiere bedingen, die nicht erfaßt werden konnten.

Für die Nomenklatur der Fische wurde das System von SMITH (1959a, b) berücksichtigt, obwohl es Auffassungssache zu sein scheint, ob z. B. die alte Gattung *Salarias* in viele neue Gattungen aufgespalten werden mußte. Einer der gesammelten Gobiiden stellte sich als neue Art heraus (KLAUSEWITZ & ZANDER 1967). Für die Bestimmung einiger Mollusken danke ich Herrn Dr. P. KAISER, Hamburg.

b) Die untersuchten Profile und ihre Fischfauna

Profil I: Sand-Fels-Strand der Lagerbucht

Im Norden der Insel Sarso befindet sich eine größere Bucht, in der das steil abfallende Felskliff zurückweicht und einen breiten Strand aus Korallensand

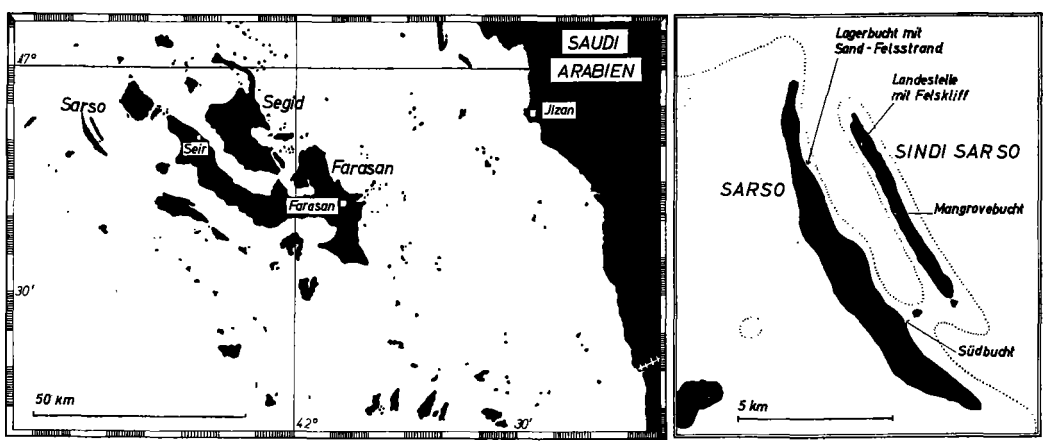

Abb. 1. Übersichtskarte der Farasan-Inseln, rechts im Detail die Inseln Sarso (Sarad Sarso) und Sindi Sarso mit der Angabe der Küstenstellen, an denen von der Litoralgruppe vorwiegend gearbeitet worden ist.

Fig. 1. Plan of Farasan Archipelago; right: detailed plan of Sarso Island (Sarad Sarso) and Sindi Sarso. Indicated are the localities where the litoral group worked.

freigibt, welcher bis über die Hochwasserlinie reicht. Der Sand ist jedoch kaum mächtiger als 1 m auf eine langsam zum Meer hin abfallende Abrasionsterrasse aus massivem Korallenkalk aufgelagert. An den sandigen Prallhang des Strandes schließt sich in der mittleren eulitoralen Region diese sandfreie Abrasionsterrasse an, welche etwa 5 m breit ist. Ein etwa 30 cm hoher Absatz trennt die eulitorale Abrasionsterrassse von dem sublitoralen, ständig wasserbedeckten Flachwassergebiet. Die sublitorale Zone gliedert sich in eine strandnahe Sand- und Geröllzone, eine schmale sublitorale Abrasionsterrasse und die Zone der Kleinriffe mit *Sargassum*-Tangen, welche in einer Wassertiefe von mehr als 60 cm ausgedehnte Bestände bilden. Seewärts der Zone der Kleinriffe mit *Sargassum* beginnt die eigentliche Riffzone mit abwechselnd Riffen und Sandflächen in 2—5 m Wassertiefe. Etwa 150 m vom Ufer entfernt liegt der Riffabfall zu dem bis 80 m tiefen Meeresarm zwischen den Inseln Sarso und Sindi Sarso. Die ufernahen Zonen des Profils bis etwa 1,5 m Wassertiefe sind in der Abb. 2 eingetragen, zusammen mit dem Vorkommen der Salariidae und Gobiidae, denen diese Studie in erster Linie gewidmet ist.

In der supralitoralen Zone liegt der obere Bezirk des Sandstrandes (Abb. 3). Ein Anwurfstreifen von losgerissenen *Sargassum*-Thalli ist vorhanden, die bei Sturm frisch an den Strand angeschwemmt werden und dann auch kleinere Fische enthalten, die schnell absterben. In den sich zersetzenden Tangen siedelt sich eine individuenreiche Kleinlebewelt an, insbesondere Collembolen.

Die eulitorale Zone wird im oberen Teil vom Prallhang des Sandstrandes gebildet. Die gröbsten Körner sammeln sich im unteren Prallhanggebiet an. Im Sand findet man lebende Muscheln der Gattung *Mesodesma* und sehr zahlreich leere Schalen dieser Tiere.

Der untere Teil des Eulitorals wird von der Abrasionsterrasse gebildet. Sie weist trotz der abschleifend wirkenden Wellenbewegung sehr viele Vertiefungen in Form von Löchern und Rinnen auf; die größeren Vertiefungen sind oft mit Sand und kleinem Geröll ausgefüllt. Zur Niedrigwasserzeit liegt die Abrasionsterrasse gewöhnlich trocken (Abb. 4). In den Löchern und Rinnen bleibt jedoch eine geringe Restwassermenge zurück, welche sich unter der starken Sonneneinstrahlung beträchtlich erwärmt. Die vielen Unebenheiten und Spalten bieten Tieren ebenso wie das vereinzelt vorkommende Geröll Versteckmöglichkeiten. Die Felsoberfläche ist mit einem feinen Rasen grüner Algen bewachsen. An Wirbellosen sind in dieser Zone besonders Paguriden vertreten, welche ihr Abdomen in den Schalen von *Conus*-Schnecken bergen. Die versteckt lebenden Krebse der Gattung *Alpheus* sind durch das knackende Geräusch ihrer Scheren zu bemerken. Nachts dringen Exemplare von *Octopus* bis in diese Zone vor.

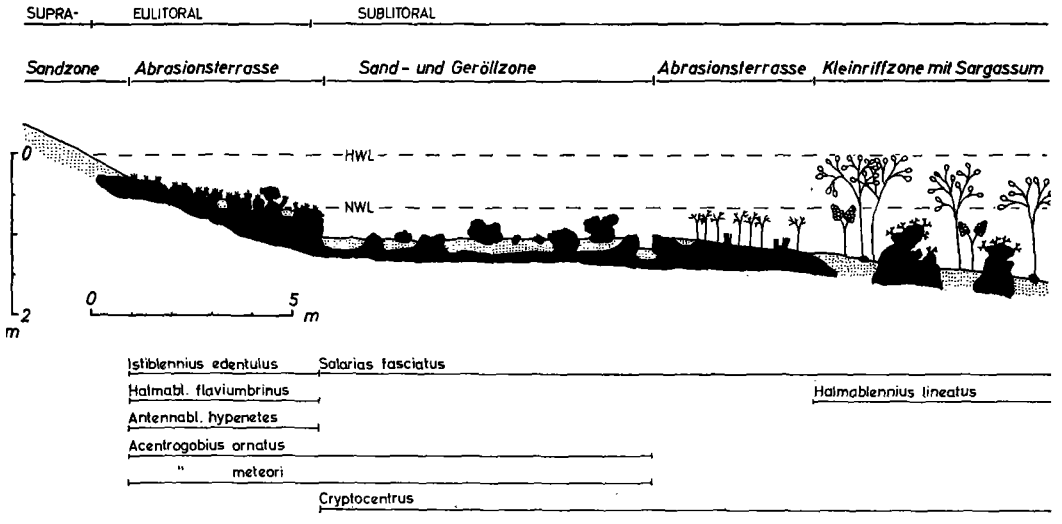

Abb. 2. Schematisches Profil des Sand-Fels-Strandes. Die einzelnen Zonen sind im Text genauer beschrieben, nur Fische aus den Familien Salariidae und Gobiidae sind jeweils angeführt. Die Hochwasser- und Niedrigwasser-Linie sind mit HWL bzw. NWL gekennzeichnet. Das Profil ist doppelt überhöht dargestellt. Diese Erklärungen gelten auch für die Abbildungen 5, 9, 10 und 12.

A diagram showing the cross-section of the sand-rock-beach. The different regions are described more precisely in the text, only fishes of the families Salariidae and Gobiidae are considered. HWL and NWL mark the high water level resp. the low water level. The drawing of the cross-section is twice increased. These explanations are also valid to figures 5, 9, 10 and 12.

Abb. 3. Der Sand-Fels-Strand bei Flut.
The sand-rock-beach at high tide.

Abb. 4. Der Sand-Fels-Strand bei Ebbe. Auf die Sandzone folgt eine eulitorale Abrasionsterrasse mit Restwassertümpeln und Spalten, in denen *Istiblennius edentulus*, *Halmablennius flaviumbrinus*, *Antennablennius hypenetes*, *Acentrogobius ornatus* und *A. meteori* die Trockenzeit überdauern können.

The sand-rock-beach at low tide. The sand-region is followed by a well cleavaged midlittoral rock-terrace with tide-pools and fissures, in which *Istiblennius edentulus*, *Halmablennius flaviumbrinus*, *Antennablennius hypenetes* as well as *Acentrogobius ornatus* and *A. meteori* may survive periods of desiccation.

Abb. 6. Der Felsstrand bei Ebbe. Links ein Graben, der auch bei Ebbe Wasser führt, daran schließt sich eine trocken gefallene Abrasionsterrasse an.

The rock-beach at low tide. On the left you see a flat pit filled with water, followed by a rock-terrace which had turned dry.

Abb. 7. Felskliff. Links ein Teil des Pilzfelsens, rechts die Küste von Sindi-Sarso.

Rocky cliff. On the left you see a part of the fungoid rock, on the right the coast of Sindi-Sarso.

Abb. 8. Felskliff. In der Mitte befindet sich ein Felsblock, an dem über der Wasserlinie *Lophalticus kirkii*, unter der Wasserlinie *Istiblennius edentulus* und *Antennablennius hypenetes* gefunden wird.

Rocky cliff. In the center there lies a boulder on which above water level *Lophalticus kirkii* may be found, below it *Istiblennius edentulus* and *Antennablennius hypenetes.*

Abb. 11. Mangrovestrand. Am sandigen Ufer befindet sich ein Gebüsch der Mangrovepflanze *Avicennia*, davor sind ihre Luftwurzeln zu sehen.

Mangrove-beach. On the sandy beach bushes of the mangrove plant *Avicennia* and its pneumatophores are to be seen.

Abb. 14. *Lophalticus kirkii* auf dem trocken gefallenen Felsen beim Abweiden von Algen. Sehr typisch ist die Drehung des Schwanzes um 90°.

Lophalticus kirkii feeding off algae from the rock which had turned dry. The 90° torsion of the tail is a very typical position.
Photo: D. E. B. MAGNUS.

Von Fischen wurden *Istiblennius edentulus* (SCHNEIDER 1801), *Halmablennius flaviumbrinus* (RÜPPEL 1828) und *Antennablennius hypenetes* (KLUNZINGER 1871)[1] ausschließlich in dieser Zone gefunden. Sie halten sich vorwiegend in kleinen Löchern oder unter Steinen auf und überdauern auch dort die Niedrigwasserzeit, obwohl sie dann unter Umständen nur sehr knapp mit Restwasser bedeckt sein können. Jungtiere dieser Arten leben zusammen mit den Gobiiden *Acentrogobius ornatus* (RÜPPELL 1828) und *A. meteori* KLAUSEWITZ & ZANDER 1967 in den Felsspalten, welche bei Ebbe als wasserführende Rinnen erhalten bleiben. Die beiden Gobiiden kommen jedoch nicht nur hier vor, sondern auch in der seewärts anschließenden sublitoralen, dauernd von Wasser bedeckten Sand- und Geröllzone.

Hier bilden Sand, Geröll und vorspringende Felsen die Hauptelemente des Bodengrundes; das Gestein ist mit einem schmutzigen Diatomeenüberzug oder mit Kalkalgen bewachsen. Die Schnecke *Conus textile* L. ist häufig. Neben anderen Fischen, die durch ihre Färbung dem Sand angepaßt sind, kommen hier Jungtiere verschiedener *Cryptocentrus*-Arten vor. In dieser Zone beginnt auch der Lebensraum von *Salarias fasciatus* (BLOCH 1786), welcher bis ins Korallenriff herunterreicht. Obwohl diese Art meistens wenige Zentimeter über dem Bodengrund schwimmt, dient ihr das zerklüftete Geröll bei Gefahr als Versteck. In tieferen Gebieten haben diese Funktion die dichten *Sargassum*-Bestände oder Korallenblöcke übernommen.

Die schmale sublitorale Abrasionsterrasse zeichnet sich durch das Fehlen von Sand aus; darum kommen hier viele Fische der Sand- und Geröllzone nicht vor, und auch *Salarias fasciatus* ist seltener. Der Felsen ist glatter, nicht so zerklüftet wie in der eulitoralen Abrasionsterrasse. Braunalgen (eine fadenförmige und eine verzweigte Form) sind häufig, seltener *Sargassum* und eine Art der Gattung *Turbinaria*.

Bei etwa 60 cm unter der Niedrigwasserlinie beginnen die Kleinriffe und der dichte Bestand von *Sargassum*. Der Bodengrund besteht aus Sand und etwas Geröll, zwischen dem dichten *Sargassum*-Wald befinden sich auch Thalli von *Turbinaria*. Die kleinen Riffe werden von Korallen der Gattungen *Porites* und *Stylophora* aufgebaut. An Blöcken der letzten Gattung lebt *Salarias fasciatus* und einmal wurde dort auch *Halmablennius lineatus* (VALENCIENNES 1836) beobachtet. Adulte Tiere von *Cryptocentrus sp.* sind sehr zahlreich vertreten. Es konnten aber keine Exemplare gefangen werden, weshalb eine Artbestimmung nicht möglich ist. Diese Fische haben Höhlen im Sand und leben in Symbiose mit dem Krebs *Alpheus* (LUTHER 1958). In den seewärts anschließenden Riffzonen lebt *Salarias fasciatus* zusammen mit *Escenius* (*Salarias*) *frontalis* (VALENCIENNES 1836) an Korallenstöcken.

[1] KLAUSEWITZ (in MERTENS 1965) schreibt, daß das Eulitoral dieser Zone auch Vertreter der Blenniidae und von den Salariidae besonders *Istiblennius rivulatus* bewohnen. Jedoch gerade diese Art konnte trotz genauer Beobachtungen bei den Sarso-Inseln nicht gefunden werden und Vertreter der Blenniidae fehlen im Supra- und Eulitoral vollkommen.

Profil II: Felsstrand

Am nördlichen Ende der Lagerbucht tritt das Felskliff wieder fast bis an die Wasserlinie heran. Das bedeutet, daß die ufernahen Zonen dieser im folgenden beschriebenen Untersuchungsstelle nachmittags im Schatten liegen. An die unterhöhlten Steilfelsen schließt sich seeseitig eine schmale horizontale Felsplatte an, die sich mit geringer Neigung im Eulitoral in eine Abrasionsterrasse fortsetzt. Noch innerhalb des Gezeitenbereiches wird diese durch eine schmale grabenartige Vertiefung unterbrochen, die auch bei Ebbe mit Wasser gefüllt bleibt. Die eben erwähnte Abrasionsterrasse reicht bis in das Sublitoral, wird aber schon im oberen Bereich von einer Sand- und Geröllzone überlagert, der die Zone der Kleinriffe mit *Sargassum* folgt. Im Flachwassergebiet liegen größere Felsblöcke verstreut, die für die Fauna eine Bereicherung an Lebensraummöglichkeiten bedeuten.

In Abb. 5 wird ein Profil von dieser Stelle mit den in den einzelnen Zonen vorkommenden Salariidae und Gobiidae dargestellt. Die dem Steilfelsen vorgelagerte horizontale Felsplatte liegt noch im supralitoralen Bereich. Bei Hochwasser ist sie infolge kleiner Brandungswellen Spritzwasser ausgesetzt, das eine Besiedlung mit *Acanthopleura spiniger* SOWERBY und *Nerita stella* CHEMNITZ ermöglicht. An der Grenze zur Hochwasserlinie liegen angeschwemmte Tange, die verfaulen und eine große Anzahl von Collembolen enthalten; sie bieten zahlreichen Einsiedlerkrebsen der Gattung *Coenobita* Nahrung. An dieser Stelle konnte nachts die Natter *Coluber insulanus* MERTENS 1965, die auch auf dem flachen Wasser der nächsten Zone angetroffen wurde, beobachtet werden. Es hatte den Anschein, als ob sie dem Salariiden *Istiblennius edentulus* nachstellte, der zu dieser Zeit ebenfalls aktiv an Land geht und im Schein der Taschenlampe gesehen wurde. Am Tage wurde diese Art niemals im supralitoralen Bereich gefunden, um so häufiger aber in der seewärts sich anschließenden, eulitoralen Abrasionsterrasse.

Diese Zone gleicht weitgehend der entsprechenden Abrasionsterrasse des Sand-Fels-Strandes (Abb. 2), unterscheidet sich aber von ihr durch eine stärkere Besiedlung von Schnecken, die wohl auf die schattige Lage zurückzuführen ist. Es handelt sich um *Nerita stella* CHEMNITZ, *Cerithium adustum* KIENER und *Littorina sp.* Der mit feinen Grünalgen bewachsene Felsen fällt bei Niedrigwasser bis auf einige kleine Resttümpel und tiefe Spalten vollkommen trocken.

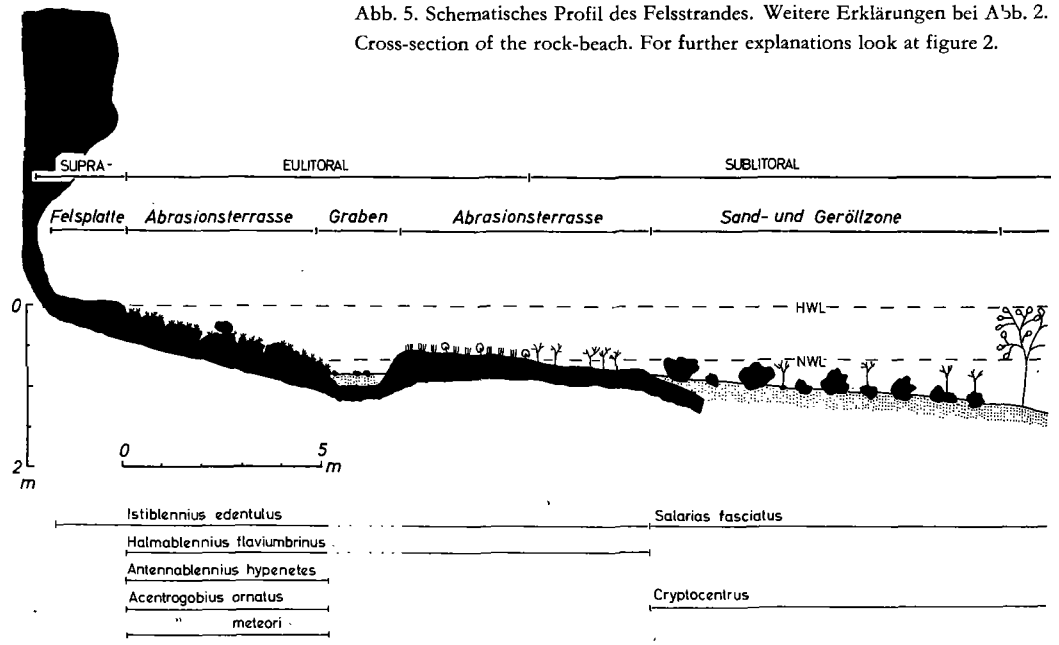

Abb. 5. Schematisches Profil des Felsstrandes. Weitere Erklärungen bei Abb. 2.
Cross-section of the rock-beach. For further explanations look at figure 2.

Neben *Istiblennius edentulus* (SCHNEIDER 1801) leben hier *Halmablennius flaviumbrinus* (RÜPPELL 1828) und *Antennablennius hypenetes* (KLUNZINGER 1871), sowie die Gobiiden *Acentrogobius ornatus* (RÜPPELL 1828) und *A. meteori* KLAUSEWITZ & ZANDER 1967 in größerer Anzahl.

Die eulitorale Abrasionsterrasse wird nach etwa 5 m durch den oben erwähnten Graben unterbrochen, der auch bei Ebbe einen Wasserstand von 20 cm aufweist. Er ist etwa 2 m breit und verläuft diagonal zur Küste, allmählich aber in der landwärts gelegenen Abrasionsterrasse verflachend. Der Bodengrund besteht aus Sand und kleinem Geröll, das mit Fadenalgen bewachsen sein kann. Hier lebt u. a. der Zahnkarpfen *Aphanius dispar* (RÜPPELL 1826), aber kein Vertreter der Salariiden oder Gobiiden.

Seewärts folgt darauf der untere Teil der Abrasionsterrasse (Abb. 6), die allerdings hier stärker abgeschliffen zu sein scheint als in der strandnahen Zone. Ihr oberer Teil, der noch zum Eulitoral gehört, ist mit Fadenalgen und *Padina* bewachsen. Das Fehlen von geeigneten Versteckmöglichkeiten ist offenbar verantwortlich für das seltene Vorkommen von *Istiblennius edentulus* und *Halmablennius flaviumbrinus*. *Antennablennius hypenetes* und Gobiiden sind nicht vertreten. Der untere, sublitorale Abschnitt der 7 m breiten Abrasionsterrasse ist mit einer verzweigten Braunalge bewachsen. Nur gelegentlich schwimmen *Istiblennius edentulus* und *Halmablennius flaviumbrinus* bis in diese Region.

Mit sanftem Gefälle geht diese Zone in die sublitorale Sand- und Geröllzone über, die der entsprechenden Zone des Sand-Stein-Strandes gleicht (Abb. 2). Von hier an ist wieder *Salarias fasciatus* (BLOCH 1786) vertreten, ebenfalls die Gobiidengattung *Cryptocentrus*, von der wenigstens zwei verschiedene Arten (*cryptocentrus* VALENCIENNES 1837 und *caeruleopunctatus* RÜPPELL 1828) bestimmt werden konnten. Bei Niedrigwasser ist diese Zone mit 20 bzw. 50 cm Wasser bedeckt.

Profile III und IV: Felskliff

Im Norden der Insel Sindi Sarso liegt etwa gegenüber vom Lagerstrand eine Bucht, die als Landeplatz geeignet war. Sie ist von senkrechten, an der Unterkante durch Brandungswellen ausgehöhlten Korallenfelswänden umgeben (Abb. 7); nur im inneren Teil der Bucht ist ein schmaler, steil ansteigender Sandstrand vorhanden. Im ufernahen Flachwasserbereich liegen einzelne große Geröllblöcke, die sich als besonders interessant hinsichtlich der Fischfauna erwiesen (Abb. 8). In einer Entfernung von 10 m vom Inselkliff erhebt sich aus dem 80 cm tiefen Wasser ein großer Pilzfelsen, dessen Längsachse in Nordwest-Südost-Richtung verläuft. Unter normalen Bedingungen schon herrscht eine Brandung mit Wellen von 80 cm Höhe, die gegen die Felsen schlagen und eine ausgedehnte Spritzwasserzone schaffen. Die senkrechten Felswände enden unter der Hochwasserlinie in einer horizontalen Platte („Felsplatte") von 1–2 m Breite; ins Sublitoral fällt sie etwa 90 cm steil ab. Dort können eine Sandzone, eine Sand- und Geröllzone oder eine Abrasionsterrasse folgen. Von der seeseitigen Wand des Pilz-

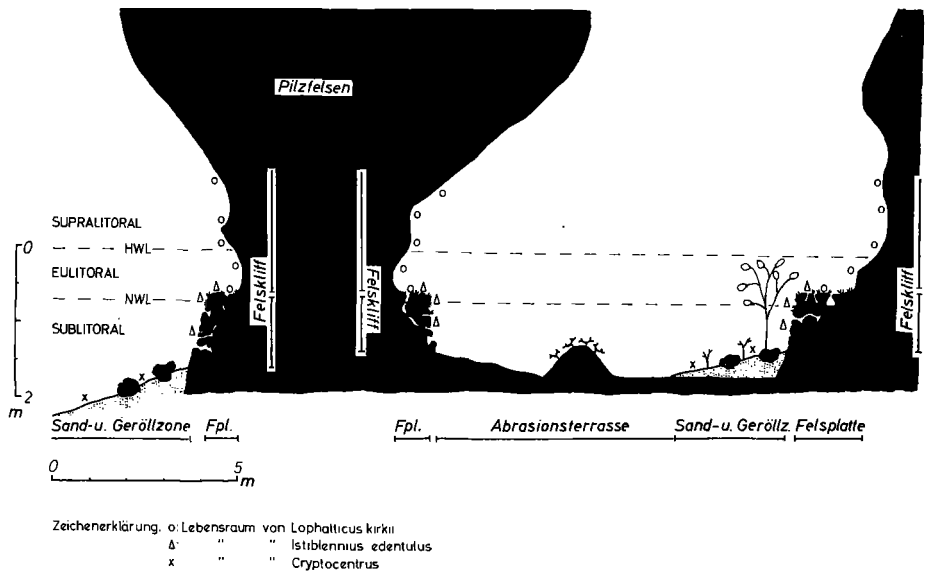

Abb. 9. Schematisches Profil des Felskliffs, senkrecht auf die Längsachse des Pilzfelsens geführt. Weitere Erklärungen bei Abb. 2.

Cross-section of the rocky cliff, vertically cut to the longitudinal axis of the fungoid rock. For further explanations look at figure 2.

felsens geht eine Sand- und Geröllzone in sehr steilem Abfall in die 4 m tief gelegene Riffzone über.

Um alle genannten Zonen erfassen zu können, mußten von dieser Bucht zwei Profile gezeichnet werden. Das eine verläuft in West-Ost-Richtung und schneidet den Pilzfelsen (Profil III, Abb. 9); das andere ist in der Fortsetzung seiner Längsachse über das Flachwassergebiet zum Inselufer gelegt worden (Profil IV, Abb. 10). Die in den einzelnen Zonen vertretenen Salariiden und Gobiiden werden mit Symbolen gekennzeichnet.

Das supralitorale Felskliff des Inselufers besteht aus senkrechten oder ausgehöhlten Korallenkalkwänden, die durch kleine Löcher, Mulden oder Spalten reich strukturiert sind. In der Spritzwasserzone leben *Acanthopleura spiniger* SOWERBY, *Nerita stella* CHEMNITZ und *Patella sp.* Während des Hochwassers befindet sich hier auch der Lebensraum von *Lophalticus kirkii* (GUENTHER 1868)[2], der tagsüber aktiv aus dem Wasser an die Felsen springt. Er sitzt meistens so weit von der Wasseroberfläche entfernt, daß ihn die Brandungswellen nicht mehr erreichen können. Die Tiere können an sonnigen und schattigen Stellen gefunden werden; einige verstecken sich in Löchern oder pressen sich in Mulden. Bei Niedrigwasser werden sie in den folgenden Zonen des eulitoralen Felskliffs und, allerdings nicht so häufig, der eulitoralen Felsplatte angetroffen.

Das Eulitoral besteht also aus der unteren Fortsetzung der senkrechten oder ausgehöhlten Felswand und einer sich daran anschließenden 1—2 m breiten horizontalen Felsplatte, die mit kleinen Grün-, Braun- und Rotalgen bewachsen ist; an einigen Stellen befindet sich auch ein Überzug von Cyanophyceen und Diatomeen. Die Felsplatte ist mit vielen Löchern aller Größen versehen, die sich als Höhlen in das Innere des Gesteins fortsetzen können und teilweise Verbindung mit Hohlräumen des sublitoralen Felskliffs haben. Die Grenze zwischen Eu- und Sublitoral liegt an einem weiteren steil abfallenden Felskliff. An diesen Stellen konnte oft *Istiblennius edentulus* (SCHNEIDER 1801) beobachtet werden, wo er zwischen zwei Brandungswellen auf dem Trockenen sitzt, wenn Ebbe herrscht. Als Versteck genügt ihm eine Mulde, in die er sich schmiegt, und in der er sich beim Trockenfallen festhaftet.

Von der eulitoralen Felsplatte fällt das Felskliff, von dem der größte Teil im sublitoralen Bereich liegt, insgesamt 90 cm tief ab. *Istiblennius edentulus* wird dort seltener angetroffen.

Es folgt, zum Pilzfelsen sich erstreckend, eine drei Meter breite, fast horizontal liegende Sand- und Geröllzone. Am Rand zum sublitoralen Felskliff stehen meist in einem schmalen Streifen angeordnet *Sargassum*-Tange (Abb. 9). Hier wurden von Salariiden oder Gobiiden nur Arten der Gattung *Crypto-*

[2] Nach KLAUSEWITZ (1964) gehört diese Population der Unterart *magnusi* an, die sich von der Nominatform durch die Gestalt des Kopflappens unterscheidet.

centrus angetroffen. Das Fehlen von *Salarias fasciatus* mag seinen Grund in der durch die Brandung hervorgerufenen starken Wasserbewegung haben.

Die sich anschließende sublitorale Abrasionsterrasse besitzt eine sehr glatt abgeschliffene Oberfläche. Die Kraft der Strömung läßt keinen Bewuchs mit größeren Algen außer wenigen *Sargassum*-Büschen zu. Dagegen kommen hier kleine Korallenstöcke vereinzelt vor. Diese Zone scheint als Lebensraum von Bodenfischen sehr ungünstig zu sein, denn Vertreter von Salariiden und Gobiiden fehlen vollkommen.

Die Abrasionsterrasse reicht bis an den Fuß des Pilzfelsens heran. Dieser weist sowohl an seiner land- als auch an seiner seeseitigen Wand die gleiche vertikale Zonierung auf wie am Inselufer. Anschließend an sein sublitorales Felskliff fällt seewärts eine Sand- und Geröllzone sehr schnell zur Riffzone ab. Auf dem Sand leben *Cryptocentrus*-Arten. Erst an den Korallenstöcken der tiefgelegenen Riffe wird *Salarias fasciatus* (BLOCH 1786) zusammen mit *Escenius frontalis* (VALENCIENNES 1836) gefunden.

Das Profil IV (Abb. 10) verläuft, wie schon erwähnt, in der Längsachse des Pilzfelsens. Den supralitoralen Teil des Inselfelsens bildet eine ausgehöhlte Felswand, auf der bei Flut *Lophalticus kirkii* herumspringt. An den eulitoralen Teil des Felskliffs schließt sich eine breite Sandzone an, die durch ein starkes Gefälle bis in das Sublitoral herunterreicht. Sie wird von Salariiden oder Gobiiden nicht bewohnt.

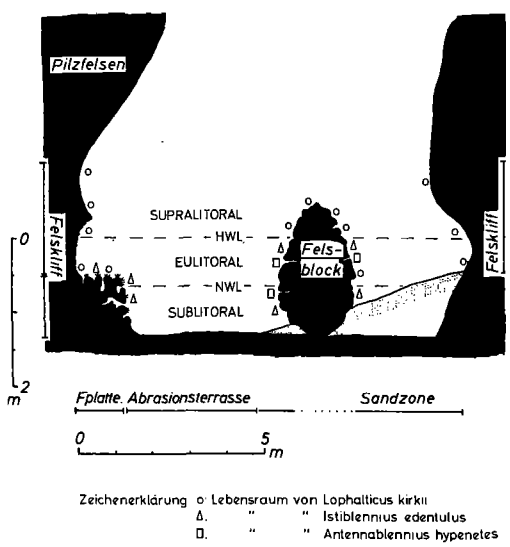

Abb. 10. Schematisches Profil des Felskliffs, in der Längsachse des Pilzfelsens geführt. Weitere Erklärungen bei Abb. 2.

Cross-section of the rocky cliff in the longitudinal axis of the fungoid rock. For further explanations look at figure 2.

Von der sublitoralen Sandzone erhebt sich bis 40 cm über die Hochwasserlinie ein großer Felsblock, der sich als günstiger Lebensraum für verschiedene Salariiden erweist (Abb. 8). Das Gestein ist nur wenig zerklüftet, doch sind neben Mulden und Spalten kleine Löcher zu finden, die offenbar von Bohrmuscheln herrühren. Der Felsblock ist mit feinen Grünalgen bewachsen. Der supralitorale Teil wird häufig von *Lophalticus kirkii* aufgesucht, der bei Niedrigwasser auch den trockenfallenden Abschnitt des Eulitorals aufsucht. Diesen bewohnen jedoch hauptsächlich *Istiblennius edentulus* und *Antennablennius hypenetes* (KLUNZINGER 1871), die teilweise infoge der Brandungswellen abwechselnd unter Wasser und auf dem Trockenen sitzen können. Während *Istiblennius* sich bei Gefahr auch hier in eine Mulde preßt, sucht *Antennablennius hypenetes* die Bohrmuschel-Löcher auf, die dem Körperdurchmesser des Fisches entsprechen.

Zwischen der Sandzone und dem Pilzfelsen liegt eine sublitorale Abrasionsterrasse, die sehr glatt abgeschliffen ist und ungefähr 3 m mißt. Am Pilzfelsen findet man die gleiche Zonierung wieder, wie sie beim Profil III schon besprochen wurde.

Profile V und VI: Mangrovestrand

Wenige Kilometer südlich des Felskliffs liegt auf der Insel Sindi Sarso eine geschützte Sandbucht, die als Besonderheit einen Bestand an *Avicennia* aufzuweisen hat. Diese baumartigen Pflanzen besitzen Luftwurzeln und besiedeln gewöhnlich den Lebensraum der Mangrove. An der genannten Bucht ziehen sie sich in einem 5 m breiten Gürtel etwa 200 m der Küste entlang (Abb. 11). Da aber eine ständige Zufuhr von Süßwasser fehlt, kann dort nicht der Lebensraum gebildet werden, der für eine echte Mangrove typisch ist. Unter Wasser findet man daher ganz ähnliche Verhältnisse wie bei den bisher beschriebenen Lebensräumen. Weil es aber geringe Unterschiede gibt, sollen sie hier geschildert werden, da sie helfen, das Bild von den ökologischen Ansprüchen der bereits erwähnten Salariiden und Gobiiden zu vervollständigen (Abb. 12).

Das Supralitoral ist ein Sandstrand, der mit der oben erwähnten *Avicennia* bestanden ist. Die Pflanzen und ihre Luftwurzeln stehen teilweise noch im oberen eulitoralen Bereich, der von dem Prallhang der Sandzone gebildet wird. Ihr folgt, bei einem Profil, das in der Mitte der Bucht gelegt wurde (Abb. 12a), eine eulitorale Abrasionsterrasse, die sich langsam abfallend in eine sublitorale Abrasionsterrasse fortsetzt. Sie erscheint glatter abgeschliffen zu sein als die entsprechenden Zonen des Sand-Fels-Strandes oder des Felsstrandes (Abb. 2 und 5).

Im Eulitoral lebt an dem mit feinen Grünalgen bewachsenen Felsen *Istiblennius edentulus* (SCHNEIDER 1801), allerdings nicht häufig. Für eine dichtere

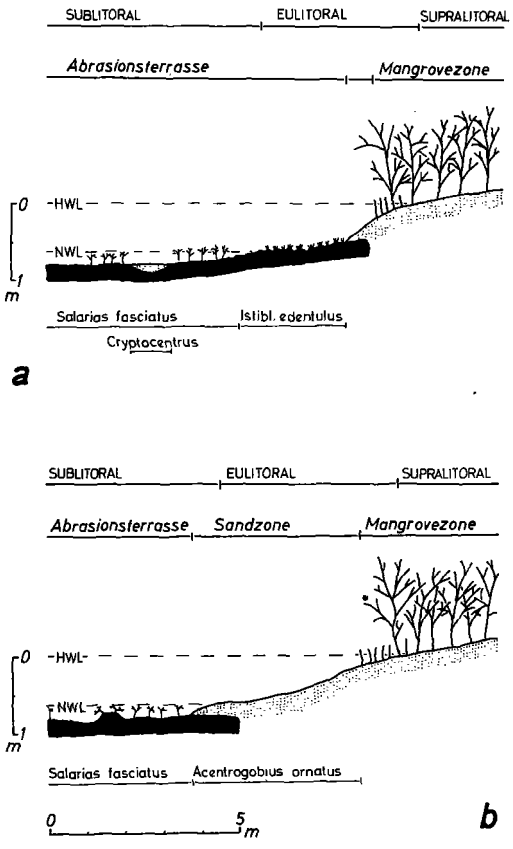

Abb. 12. Schematische Profile des Mangrovestrandes. Weitere Erklärungen bei Abb. 2.

Cross-sections of the mangrove-beach. For further explanations look at figure 2.

Besiedlung ist der Felsen anscheinend zu wenig strukturiert.

Die sublitorale Abrasionsterrasse, die fast horizontal liegt, ist mit einer verzweigten Braunalge bewachsen und weist an ihren Vertiefungen Sandablagerungen auf. An den größeren solcher Sandinseln legen *Cryptocentrus*-Arten ihre Löcher an, während *Salarias fasciatus* (BLOCH 1786) zwischen den Braunalgen reichlich Versteckmöglichkeiten findet.

Am südlichen Ende der Mangrovebucht wird der gesamte eulitorale Bereich von dem Prallhang der Sandzone eingenommen, der sogar bis ins obere Sublitoral herabreicht (Abb. 12b). In der ganzen Sandzone wird *Acentrogobius ornatus* (RÜPPELL 1828) angetroffen. Seewärts schließt sich eine wenig strukturierte sublitorale Abrasionsterrasse an, die mit Braunalgen bewachsen ist. Vereinzelt befinden sich dort kleine Korallenstöcke. Diese Zone stellt den Anfang des ausgedehnten Lebensraumes von *Salarias fasciatus* dar.

c) Einige Beobachtungen über die Lebensweise von Vertretern der Salariidae

Lophalticus kirkii (GUENTHER 1868)[3] (Abb. 16a). Diese Art, die von den beschriebenen Formen am besten dem Landleben angepaßt erscheint, wurde bereits von MAGNUS (1963, 1966) eingehender untersucht. Es seien an dieser Stelle noch einige Ergänzungen gebracht. Es handelt sich um sehr aktive Tiere, die viel auf dem trockenen Felsen herumspringen und in den Bewegungspausen von dem Gestein kleine Algen abweiden. Die Anpassung an das Landleben geht sogar soweit, daß die Tiere bei Gefahr aus dem Wasser an das Land springen (MAGNUS, 1966). Beim Transport in einem Plastikkanister versuchen sie sofort aus dem Wasser zu gelangen und sich an der rauhen Wand des Behälters festzuhalten.

Unter Wasser ist die Bewegung wie bei anderen Blenniiden und Salariiden ein Schlängelschwimmen. Aus der Ruhelage wird mit einem kräftigen Schlag der Pektoralen gestartet. In der Bewegungspause dienen die Ventralen zum Abstützen, die unpaaren Flossen sind während dieser Zeit auseinandergespreizt. Die Tiere versuchen, sich eng an den Felsen anzuschmiegen.

Beim Wechsel vom Wasser an das Land heben sie sich mit schnellen Schwanzschlägen von der Wasseroberfläche empor und springen auf die nächste Felskante. Für die Weiterbewegung auf dem Gestein wird der ganze Schwanz meistens um 90° gedreht (Abb. 14); er dient beim Emporschnellen als Sprungbasis, beim Klettern an einer senkrechten Wand mit dem „Stemmschritt" als Stütze oder beim Abwärtsklettern als Greiforgan. Bei letzterer Bewegung kann beobachtet werden, wie sich die Anale Strahl für Strahl langsam nach vorne schiebt. Beim Stemmschritt wird der Schwanz nach der Drehung zur Seite gekrümmt und darauf der übrige Körper hochgeschoben, bis er wieder senkrecht steht (Abb. 13). Die Pectoralen sind beim Hochstemmen zusammengefaltet, während sie in der Ruhephase ausgebreitet werden. Meist wird der Schwanz in

[3] Vergl. Fußnote Seite 77.

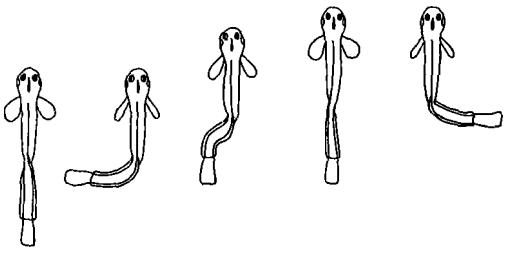

Abb. 13. Schema der Fortbewegung von *Lophalticus kirkii* an einer senkrechten Fläche mit Hilfe des „Stemmschrittes".

A model of movement of *Lophalticus kirkii* by the "stemming step" on a vertical surface.

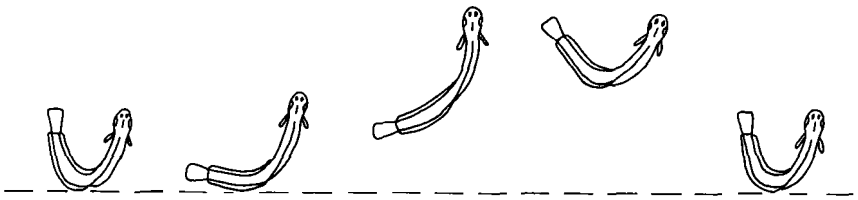

Abb. 15. Schema der Fortbewegung von *Lophalticus kirkii* durch Springen auf der Wasseroberfläche.

A model of movement of *Lophalticus kirkii* by jumping on the water surface.

schneller Folge nach rechts und links gekrümmt, es kommt aber auch vor, daß er mehrere Male nur nach einer Seite gebogen wird. RAO & HORA beobachteten 1938 die gleiche Bewegungsweise bei *Andamia*. Die in der Ruhephase ausgebreiteten Pectoralen sind löffelförmig an die senkrechte Wand angepreßt, so daß sich innen ein Hohlraum bildet, in dem oft eine von wenig Wasser umgebene Luftblase zu erkennen ist. In ähnlicher Weise werden die Dorsale, Anale und Caudale als Haftorgane benutzt, indem die Flossen nur mit ihrem äußeren Rand fest an den Untergrund gepreßt werden. Und schließlich liegen Kehle, Brust und das gedrehte Schwanzende sehr dicht dem Substrat angeschmiegt, wobei sich unter der Kehle ebenfalls ein Hohlraum ausbilden kann. Das Auseinanderspreizen der zwei längeren Strahlen der Ventralen mag auch dabei helfen, ein Zurückgleiten zu verhindern. Von den Tieren werden damit während ihres Aufenthaltes am steilen oder senkrechten Felsen sowohl mechanische als auch Adhäsions- und Kapillarkräfte ausgenutzt. — Beim Klettern am weniger steilen Felsen wird nicht immer der Schwanz gedreht, in diesem Fall wird aber die Anale zum Substrat hin gekrümmt.

Zu einer anderen sehr merkwürdigen Bewegung ist *Lophalticus* auf der Wasseroberfläche fähig. Bei Störung läßt er sich oft vom Felsen auf das Wasser fallen, krümmt sich U-förmig und schnellt sich seitlich liegend mit seinem Schwanz vom Wasser ab (Abb. 15). Dieses Springen kann mehrere Male hintereinander erfolgen, ehe sich das Tier wieder an Land begibt.

Im Beobachtungsaquarium sucht sich jedes Tier sowohl unter als auch über Wasser einen festen Platz, der gegenüber Artgenossen verteidigt wird. Die beiden Gegner spreizen dann ihre Dorsalen und springen im nächsten Moment aufeinander zu. Der darauffolgende kurze Kampf endet mit einer schnellen Bewegung des Kopfes, die von oben nach unten erfolgt; danach räumt einer der Gegner den Platz. Im natürlichen Lebensraum wurden dagegen auch mehrere Tiere in einer Mulde zusammenliegend beobachtet, ohne daß es zu einem Kampf kam.

Die Hauptnahrung besteht aus dem feinen Algenbewuchs der Felsen, der abgeweidet wird. Dabei wird der Kopf des Tieres von vorne und von oben nach hinten auf das Substrat bewegt. Von Urinsekten, die im Beobachtungsaquarium auf den Felsen herumliefen, wurde keine Notiz genommen. Die Nahrungsaufnahme erfolgt anscheinend ausschließlich an Land.

Die Kiemenbewegung unter Wasser erfolgt sehr viel schneller als an Land: im ersten Fall wurden bis 130, im letzten Fall höchstens 25 Bewegungen in der Minute festgestellt. Im Aquarium konnten die Tiere mehrere Minuten an Land bleiben, ehe sie nur kurz den Kopf in das Wasser steckten oder seltener ganz ins Wasser sprangen. Damit soll anscheinend erreicht werden, daß die Kiemen (oder zusätzliche Atmungsorgane der Mundhöhle?) feucht gehalten werden. Im natürlichen Lebensraum ist eine häufigere Wasserbenetzung durch die Brandungswellen gegeben, vor denen die Tiere allerdings durch Aufwärtsklettern zu entkommen versuchen.

Es hat den Anschein, daß die Augen die Hauptsinnesleistungen übernehmen. Sie stehen weit oben, etwas hervorragend am Kopf (Abb. 14) und können nach allen Richtungen bewegt werden. Die Pupille ist elliptisch gestaltet. Erschütterungen führen zu keiner Reaktion: entweder werden sie nicht wahrgenommen, oder die Reaktionen sind durch das Leben in der Brandungszone abgestumpft.

Die Tiere sind zu einem schnellen Farbwechsel befähigt; während die Zeichnung unter Wasser sehr aufgehellt erscheint, kann sie an Land einem dunklen Felsen durch Ausbreitung von Melanophoren angepaßt werden. Dieser Umschwung erfolgt innerhalb weniger Sekunden.

Istiblennius edentulus (SCHNEIDER 1801) (Abb. 16b)

Tiere dieser Art werden tagsüber auf dem Felsen des Eulitorals gefunden, den sie auch nicht bei Niedrigwasser verlassen. Zu dieser Zeit liegen sie vor der Sonne geschützt unter Steinen oder in Ritzen und springen nur ab und zu über die trockengefallene Felsterrasse. Am Ruheplatz sind sie dann nur teilweise oder auch gar nicht von Wasser bedeckt. An anderen Stellen haben sie an senkrechten Felswänden ihren Lebensraum gefunden (Felskliff), dort halten sie sich gerne an solchen Plätzen auf, die zwischen

zwei Brandungswellen trocken fallen können. Dagegen verlassen die Tiere nachts ihre spezielle Lebenszone und suchen aktiv das Land auf, auf dem sie herumspringen und nach Nahrung suchen.

Das Schwimmen unter Wasser erfolgt auf die gleiche Weise wie bei *L. kirkii*. Während des Aufenthaltes an Land wird ebenfalls das ganze Schwanzende um 90° gedreht; der Schwanz dient beim Sprung als Basis zum Abschnellen. Sehr auffällig ist, daß die Tiere mit sehr flachen und schnell aufeinanderfolgenden Sätzen über die Felsterrasse springen. Wenn sie sich in ihren Verstecken aufhalten, schauen sie normalerweise mit dem Vorderende bis zum Ansatz der Pectoralen hervor. Am senkrechten Felsen suchen sie keine Löcher oder dergl. auf, sondern pressen sich bei Störung in eine Mulde; sonst sind sie überall auf dem Gestein zu finden. Dort widerstehen sie auch der Kraft der Brandungswellen, indem sie sich mit Hilfe der Flossen fest an der rauhen Unterlage verankern. Wenn der Wasserspiegel plötzlich unter ihren Aufenthaltsort sinkt, vermögen sie sich in der gleichen Weise vor dem Abrutschen zu bewahren.

Als Nahrung dienen auch dieser Art feine Grünalgen, die als Bewuchs überall auf den Felsen des Eulitorals zu finden sind. Das Abweiden geschieht mit der gleichen eigentümlichen Kopfbewegung, wie sie bei *L. kirkii* bereits beschrieben wurde.

Eine Revierbildung oder eine Rangordnung gibt es anscheinend innerhalb dieser Art nicht. Oft wurde beobachtet, daß die Tiere gesellig zusammenleben.

Auch *I. edentulus* kann sich in seiner Färbung dem Untergrund anpassen.

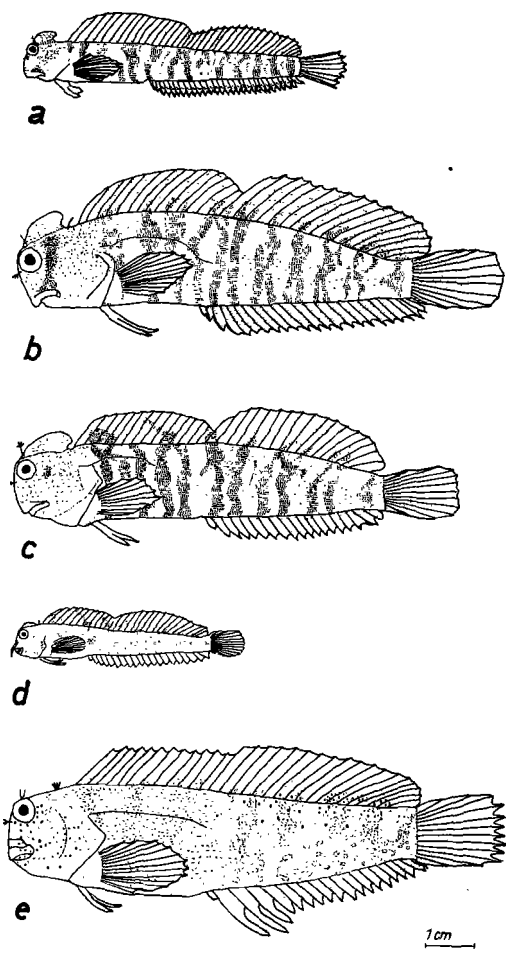

Abb. 16. Zeichnungen der untersuchten Salariidae.
a: *Lophalticus kirkii*. b: *Istiblennius edentulus*. c: *Halmablennius flaviumbrinus*. d: *Antennablennius hypenetes*. e: *Salarias fasciatus*.

Drawings of the Salariidae examined.

Halmablennius flaviumbrinus (Rüppell 1828) (Abb. 16c)

Bei dieser, mit *I. edentulus* sympatrisch lebenden Art, können keine Angaben über die Lebensweise gemacht werden.

Antennablennius hypenetes (Klunzinger 1871) (Abb. 16d)

Auch diese Form lebt sowohl am horizontalen als auch am senkrechten Felsen des Eulitorals, wurde aber niemals außerhalb des Wassers gefunden. Bedingt durch die geringe Größe gelingt es *A. hypenetes*, sich auch bei Niedrigwasser in Restwassertümpeln aufzuhalten, ohne in das Sublitoral hinabschwimmen zu müssen. Es handelt sich um sehr lebhafte Tiere, die sich bei Gefahr blitzschnell in einem Loch verstecken; nach kurzer Zeit aber schieben sie ihren Vorderkörper bis zum Ansatz der Pectoralen hervor, um die Umgebung beobachten zu können. Am senkrechten Felsen wurden sie meist in Bohrmuschellöchern gesehen, aus denen sie in allen Lagen, sogar mit dem Bauch nach oben, herausschauen. Offenbar besteht bei ihnen ein Bedürfnis nach einem thigmotaktischen Berührungsreiz.

Die Nahrung und die Nahrungsaufnahme ist die gleiche wie sie schon bei *L. kirkii* beschrieben wurde.

Salarias fasciatus (Bloch 1786) (Abb. 16e)

Es handelt sich um einen sehr aktiven Fisch, der ausschließlich im Sublitoral seinen Lebensraum findet. Sein Schwimmen ist eine Art Hüpfen unter Wasser: er schwimmt blitzschnell etwa $^1/_2$ m, ruht einen Moment aus, um danach wieder die gleiche Strecke zurückzulegen. Längere Ruhepausen werden beim Fressen oder nach Störung im Versteck gemacht, es kommt aber auch vor, daß die Fische einfach nur auf dem Untergrund stehen und beobachten. Dabei wird der Kopf durch Aufrichten der

Ventralen hochgestützt, oft wird dabei auch eine schräge Körperlage eingenommen, indem die Ventralen an einer Seite mehr abgespreizt werden als an der anderen. Als Verstecke benutzen die Tiere nicht nur Höhlungen im Gestein oder im Korallenriff, sondern auch dichte Algenbüschel. Dem Felsen vermögen sie sich ganz eng anzupressen. Die Tiere scheinen nicht scheu zu sein, denn kurze Zeit nach einer Störung verlassen sie bereits ihr Versteck vollkommen, um ihr normales Treiben im freien Wasser wieder aufzunehmen.

Anscheinend bilden die Tiere Reviere, da Artgenossen immer aus der Nähe vertrieben werden. Einmal wurde sogar beobachtet, wie am Sand-Fels-Strand ein *Istiblennius edentulus*, der sich an der Grenze von Eu- und Sublitoral befand, von einem *S. fasciatus* verjagt wurde.

Als Nahrung dienen nicht nur feine Grünalgen und evtl. Diatomeen, sondern anscheinend auch Bryozoen, die auf den Riffblöcken festsitzen und dort abgeweidet werden.

S. fasciatus ist zu einem sehr intensiven Farbwechsel befähigt. Wenn die Tiere aus einem Versteck herauskommen, ist die Grundfärbung blaß graubraun, nur in der Körperlängsachse sind sie etwas intensiver gemustert. Kurz darauf ist aber ein Umschlagen ins Olivbraune festzustellen, wobei dann auch die Zeichnung deutlicher hervortritt. Die Zeichnung bewirkt, daß die Tiere trotz der auffälligen Färbung in ihrem natürlichen Lebensraum durch Somatolyse gut getarnt erscheinen.

III. Die ökologischen Ansprüche der untersuchten Salariiden und Gobiiden

Alle oben beschriebenen Salariiden erweisen sich als Bewohner der verschiedenen Felszonen des Litorals. Die Ursache für diese besondere Substratverbundenheit mag einmal in der Art der Nahrung liegen, die zum größten Teil aus kleinsten fadenförmigen Grünalgen besteht, welche nur auf Gestein wachsen können; *Salarias fasciatus* frißt möglicherweise auch Diatomeen und Bryozoen, die an Hartbodenstrukturen gedeihen. Ein zweiter Grund ist, daß die Tiere das Bedürfnis haben, Hohlräume des Gesteins aufzusuchen, die z. T. nur als Versteck bei Gefahr, z. T. auch als Wohnröhren dienen. Auch bei diesem zweiten Faktor erweist sich *Salarias fasciatus* als weiter anpassungsfähig, da die Art beim Verbergen auch auf dichte Algenbüsche ausweichen kann.

Die Verteilung der genannten Arten auf Sublitoral, Eulitoral und Supralitoral ist nun durch eine verschiedene Lebensweise bedingt, welcher spezielle Anpassungen des Körperbaues zugrunde liegen müssen. Am wenigsten sind sie bei *Salarias fasciatus* zu erwarten, der ausschließlich das Sublitoral bewohnt. In diesem Bereich erweist er sich aber als sehr euryök, da er von den oberen Zonen des Sublitorals bis zum Korallenriff in einer Wassertiefe bis zu 4 m gefunden wird. Dennoch muß diese Form als sehr standortstreu angesehen werden, da sie auch während der Hochwasserzeit nicht vom angrenzenden Sublitoral in den strukturierten Felsbiotop des Eulitorals schwimmt. Ihr Fehlen im flachen Sublitoral des Felskliffs ist anscheinend durch den Mangel an Versteckmöglichkeiten in der sublitoralen Abrasionsterrasse, sowie durch die starke Wasserbewegung bedingt: die Tiere schwimmen viel umher und sind anscheinend nicht fähig, sich in der gleichen Weise am Substrat festzuhalten wie *Istiblennius edentulus* oder *Lophalticus kirkii*.

Das andere Extrem unter den untersuchten Arten ist ohne Zweifel *Lophalticus kirkii*, der als hoch spezialisiert angesehen werden muß. Sein Lebensraum befindet sich vor allen Dingen an senkrechten Felswänden des Supralitorals, die auch bei Ebbe vom Wasser her direkt zu erreichen sind (vergl. MAGNUS 1963, 1966). Es darf vermutet werden, daß besondere Organe für die Veratmung atmosphärischer Luft vorhanden sind, die ihre Funktion besser erfüllen können als die Kiemen unter Wasser. Obwohl die Tiere sogar Brandungswellen ausweichen, sind sie vom Wasser nicht unabhängig, da Mundhöhle, Kiemen und Haut regelmäßig befeuchtet werden müssen, um eine Austrocknung zu vermeiden. Es ist daher einfacher für die Tiere, ein Stück am senkrechten Felsen herabzuklettern oder direkt auf das Wasser zu springen, als — besonders bei Ebbe — längere Strecken am schwach geneigten Ufer zurückzulegen. Beim Fluchtweg, der oft über das Wasser führt, brauchen sich die Fische ebenfalls nur auf die Wasseroberfläche herabfallen zu lassen. Vielleicht ist für die Tiere auch das Klettern an steilen oder senkrechten Flächen leichter als an horizontalen, an denen sie ihren typischen Stemmschritt nicht ausnutzen können, sondern sich durch Springen fortbewegen. Von den beschriebenen Lebensräumen wird daher nur das Felskliff den Anforderungen von *Lophalticus kirkii* gerecht; der Felsstrand, der auch von steilen Felsen begrenzt wird, erweist sich deshalb als ungeeignet, weil die davorliegende Zone des Supra- und Eulitorals sehr ausgedehnt ist.

An dieser Stelle sei noch eine Art Mimikry erwähnt: Wenn *Lophalticus kirkii* mit Kopf-Schwanzberührung fast kreisförmig auf dem Felsen liegt, ähnelt er weitgehend der Schnecke *Patella*, die an ihrem Schalenrand eine ähnliche Zeichnung aufweist wie der Körper der Fische; die Schnecke wurde ebenfalls nur am Felskliff gefunden.

Als Formen, die einen Kontakt zu der Atmosphäre suchen, die aber an das Landleben nicht so gut angepaßt sind wie *Lophalticus kirkii*, müssen *Istiblennius edentulus*, *Halmablennius flaviumbrinus* und *Antennablennius hypenetes* angesehen werden. Ihr Lebensraum

wird von den Felsen des Eulitorals gebildet, die bis auf Resttümpel und tiefere Spalten bei Ebbe trocken fallen. Während der Niedrigwasserzeit halten sich die Tiere in diesen Resttümpeln auf, wobei sie nur teilweise mit Wasser bedeckt zu sein brauchen. Der durch die Sonneneinstrahlung verursachten starken Erwärmung des Wassers und dem damit verbundenen Sauerstoffmangel können sie dadurch entgehen, daß ihre Atmungsorgane auch an Land funktionsfähig sind; das Aufsuchen schattiger Stellen schützt sie außerdem vor einer allgemeinen Austrocknung. Der Lebensraum wird auch bei Flut, wenn der Wasserstand mindestens 40 cm beträgt, am Tage beibehalten; bei den kühleren Temperaturen der Nacht geht *Istiblennius edentulus* dagegen aktiv an Land. Diese Art kommt an allen vier untersuchten Stellen vor, ihre Frequenz läßt jedoch stark nach, wenn der Felsen zu wenig strukturiert ist (Mangrovestrand). An den senkrechten Wänden des Felskliffs befindet sie sich häufig an den Stellen, die zwischen den Brandungswellen kurz trocken fallen. *Halmablennius flaviumbrinus* ist dort nicht vertreten, evtl. fehlen dieser Art die besonderen Anpassungen, um sich wie *Istiblennius edentulus* am Substrat festhalten zu können und damit der Brandung zu widerstehen. Für *Antennablennius hypenetes* kommt zu den anderen Ansprüchen eine Bevorzugung enger, seinem Körperdurchmesser angepaßter Löcher, in denen er am Sand-Fels-Strand und Felsstrand die Ebbezeit überdauert, am Felskliff vor der Brandung ausweichen kann. Nach KLUNZINGER (1871) geht die Art sogar auf den trockenen Felsen; an den Sarso-Inseln wurden sie aber höchstens dabei beobachtet, wie sie in den Resttümpeln beim Überqueren sehr flacher Stellen teilweise mit dem Körper herausragen. Im Profil IV sind durch das Fehlen von geeigneten Löchern für diese Art offenbar keine günstigen Lebensbedingungen vorhanden.

Die Gobiiden *Acentrogobius ornatus* und *A. meteori* erweisen sich nur als fakultative Bewohner des Eulitorals. Dort leben sie zur Ebbezeit in tiefen Felsrinnen, in denen genügend Restwasser stehenbleibt. Da sie aber auch in der sublitoralen Sand- und Geröllzone des Sand-Fels-Strandes und *A. ornatus* auch in der Sandzone des Mangrovestrandes vorkommen, scheinen sie Sanduntergrund in flacheren Wasserbereichen zu bevorzugen; auch in den Felsspalten der eulitoralen Abrasionsterrasse befinden sich eingeschwemmte Sandablagerungen. Das Fehlen der beiden Arten an dem Felskliff mag darauf zurückzuführen sein, daß die Sandflächen relativ tief unter dem Wasserspiegel liegen; möglicherweise ist die dort herrschende starke Wasserbewegung ein weiterer ungünstiger Umweltfaktor für diese Fische. Die Arten der Gattung *Cryptocentrus* halten sich dagegen auf den Sandflächen des Sublitorals auf. Sie sind in der Riffzone häufiger vertreten als in den flacheren Gebieten. Nur Jungfische leben bereits in der sublitoralen Sand- und Geröllzone des Sand-Fels-Strandes, adulte Tiere treten erst in der Zone der Kleinriffe mit *Sargassum* auf.

IV. Die Lebensräume amphibisch lebender Blennioidea und Gobioidea

Es erscheint auffällig, daß unter den untersuchten Fischen vier Arten der Salariidae eine amphibische Lebensweise führen können, während die Gobiidae durch keine in der Weise spezialisierte Form an den Sarso-Inseln vertreten sind. Diese Tatsache wirft die Frage auf, ob das dort vorherrschende Felslitoral für die erste Gruppe günstig, für letztere ungünstig beim Übergang vom Wasser zum Landleben ist. Die Gobiiden-Gattungen *Periophthalmus* und *Boleophthalmus* „sind die charakteristischen Bewohner der Riff- und besonders der Schwemmlandmangrove" (EGGERT 1935), doch haben sich *Periophthalmus koelreuteri* und *P. harmsi* an das Leben am Felsufer anpassen können (HARMS 1928, EGGERT 1935). Andererseits berichtet GERLACH (1958) über das Vorkommen des Salariiden *Scartichthys* in der brasilianischen Mangrove, wo sich das Tier an einem Baumstamm aufhielt. Diese Beispiele sind jedoch als sekundäre Spezialisierungen aufzufassen. Anscheinend sind die Unterschiede bei der Bevorzugung bestimmter Lebensräume in den Nahrungsansprüchen begründet. Die Gobiidae als Raubfische finden dort ihr Existenzoptimum, wo eine Vielzahl anderer Tiere, die ihnen als Nahrung dienen, leben können. Nach den Schilderungen von HARMS (1928) und GERLACH (1958) ist der eulitorale Bereich der Mangrove sehr reich an kleinen Krebstieren und Insekten, die infolge der hohen Luftfeuchtigkeit gute Lebensbedingungen finden; diese Tiere bilden die Hauptnahrung der *Boleophthalmus*- und *Periophthalmus*-Arten. Die Salariidae sind dagegen auf Pflanzennahrung angewiesen, die sie als feinen Algenbewuchs von dem Gestein abweiden. Wie von RAO & HORA (1938), MAGNUS (1963, 1966) und in der vorliegenden Arbeit beschrieben wurde, behalten auch amphibisch lebende Vertreter der Familie diese Lebensweise bei. Sie nehmen daher im felsigen Eu- oder Supralitoral den Platz der Periophthalmen ein, die dort bis auf die genannten Ausnahmen keine günstigen Bedingungen finden würden, weil ihre Nahrungstiere nicht in der Häufigkeit auftreten wie in der Mangrove. Die eng mit den Salariidae verwandten Blenniidae sind meist ebenfalls Räuber, bevorzugen aber im allgemeinen Felsbiotope; es ist wenig darüber bekannt, ob Vertreter dieser Familie zu einer amphibischen oder Landlebensweise übergegangen sind. Nur über *Blennius galerita* liegen sehr genaue Untersuchungen von SOLJAN (1932) vor: es handelt sich um einen hoch-

angepaßten Nahrungsspezialisten, der sich von dem Cirripedier *Chthamalus stellatus* ernährt. Dieser lebt in der Brandungszone an Felsen und öffnet nur, während er von Wellen überspült wird, den Deckel und streckt seine Extremitäten heraus; dieses ist der Moment, in dem *Blennius galerita* seine Beute fassen kann.

Etwas mehr überschneiden sich die Ansprüche bei dem Faktor Wasserbewegung, wenn verallgemeinert wird, daß die Gobiidae ruhiges Wasser bevorzugen, die Salariidae (und Blenniidae) aber durchaus in der Brandung zu leben vermögen. *Periophthalmus harmsi* lebt aber in Felsbuchten der Nordwestküste Javas, an der bei Flut eine starke Brandung herrscht (HARMS 1928). Wie in der vorliegenden Arbeit gezeigt werden konnte, kommen *Istiblennius edentulus*, *Halmablennius flaviumbrinus* und *Antennablennius hypenetes* durchaus im Felswatt vor, in dem das Wasser ziemlich ruhig aufläuft. Auf S. 82 wurde bereits angenommen, daß das Fehlen von *Salarias fasciatus* im flacheren Bereich von Profil III evtl. auf die dort herrschende starke Wasserbewegung zurückgeführt werden kann. Daher wäre es möglich, daß bei *Lophalticus kirkii* der Aufenthalt in der Brandungszone eine sekundäre Folge der amphibischen Lebensweise ist, der erst durch die Ausbildung bestimmter Festhalteorgane ermöglicht wurde. Da *Istiblennius edentulus* und *Antennablennius hypenetes* sowohl in ruhigem als auch in stark bewegtem Wasser (Sand-Fels-Strand, Felskliff) leben können, erweisen sie sich auch in dieser Hinsicht als Übergangsformen.

Es wird daher vermutet, daß die Nahrung, die in einer konkurrenzärmeren Umgebung geboten werden kann, der Hauptfaktor für das Aufsuchen des neuen Lebensraumes über der Wasserlinie ist. Nach GERLACH (1963) sind die Mangroveregion und die tropische Felsküste besonders reich an Beispielen für den Übergang zum Landleben. Es kann noch nicht beurteilt werden, welcher der beiden Lebensräume günstiger für die Eroberung dieser ökologischen Nische ist. Nachdem aber aus der besser untersuchten Mangrove eine Menge an Arten bekannt geworden ist, die eine amphibische Lebensweise führen, sollen die oben beschriebenen Untersuchungen dazu beitragen, den Prozeß der Landtierwerdung am Felslitoral näher kennenzulernen.

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Acentrogobius meteori n. sp. (Pisces, Gobiidae)

6. Beitrag der Arbeitsgruppe Litoralforschung

von

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Summary

Acentrogobius meteori is a new species of the family Gobiidae. It was found on the coast of the island Sarso of the Farsan Archipelago (Red Sea). It seems to be related to the species *A. baltea*, *decoratus*, *leptochilus*, and *reichei*. The new gobiid fish lives within the eulitoral and upper sublitoral.

Während des zweiwöchigen Aufenthaltes auf den Sarso-Inseln (Farasan Archipel, südliches Rotes Meer) wurden in den Flutrinnen der Abrasionsplatte der Gezeitenzone mehrere kleine Gobiiden gesammelt, die sich bei der Untersuchung durch den erstgenannten Autor als Angehörige einer bisher unbekannten Art erwiesen. Zur Bestimmung wurden KLUNZINGER (1871), KOUMANS (1953) sowie J. L. B. SMITH (1959, 1960) verwendet. Während die folgende systematische Beschreibung der neuen Art von KLAUSEWITZ stammt, hat ZANDER die Darstellung des Lebensraumes und der Lebensweise übernommen. Wir benennen den Fisch nach dem deutschen Forschungsschiff „Meteor", da wir die Entdeckung dieser neuen Art letzten Endes diesem Forschungsschiff verdanken.

Die Abkürzungen SMF und ZMH bedeuten: Senckenberg-Museum Frankfurt bzw. Zoologisches Museum Hamburg. Ttl = Gesamtlänge, Stdl = Standardlänge.

Acentrogobius meteori n. sp.

MATERIAL: 6 Expl., wahrscheinlich adult bis subadult; Holotypus, SMF 8188, und 1 Paratypus, SMF 8527 (Senckenberg-Museum, Frankfurt), 4 Paratypen, Nr. ZMH 2902—2905 (Zoologisches Museum, Hamburg); Rotes Meer, Farasan-Archipel, Insel Sarso khebir, Tidenrinnen auf der Abrasionsplatte der eulitoralen Küstenzone.

MASSE (in mm):

	Ttl	Stdl	Kopf	Körperhöhe
SMF 8188	21,0	17,0	5,25	3,35
SMF 8527	24,9	20,8	5,7	4,0
ZMH 2902	25,4	20,2	5,7	3,8
ZMH 2903	20,5	17,15	4,8	3,25
ZMH 2904	16,1	13,4	4,0	2,45
ZMH 2905	16,1	13,2	3,9	2,55

DIAGNOSE: Eine kleine Art der Gattung *Acentrogobius* mit weniger als 30 Schuppen auf der Seitenlinie, D_2 1.8, A 1.7 und 8 Praedorsal-Schuppen, mit je einem schwarzbraunen Postorbitalfleck, Schachbrettzeichnung auf den Flanken und schwärzlichem Transversalfleck auf der C-Basis.

BESCHREIBUNG: D VI + 1.8, A 1.7, P 1.14. Ll 26, Sq tr 9, praedorsal 8. Körper langgestreckt, von den Brustflossen an nach rückwärts lateral kompreß. Kopf vorn deutlich konisch zulaufend, länger als breit, breiter als hoch. Schnauze ebenso lang wie Augendurchmesser. Mundspalte schräg abwärts geneigt. Schnauzenspitze liegt in Höhe des unteren Augenrandes. Unterkiefer vorragend. Oberkiefer

breit, reicht bis in Höhe des Pupillenvorderrandes. Kopf ohne Barteln. Jedoch befindet sich an der Symphyse ein kleiner lappenartiger Hautfortsatz; ferner sind die Hautfalten der Kopfunterseite mit Papillen besetzt. Kopfoberseite und Wangenregion nackt. Auf der Nackenregion etwa eine Schnauzenlänge hinter den Augen die ersten Schuppen, cycloid, unter der Haut befindlich. Hinterer Praeopercular-

FÄRBUNG: Im Alkoholpräparat Kopf dunkelolivbraun, Grundfarbe des Rückens mittel- bis hellbraun, der Bauchseite schmutzig weiß bis hell sandfarben. Hinter dem Auge ein schwarzer Fleck, der mindestens zwei Drittel des Augendurchmessers entspricht. Praedorsal eine helle Transversalbinde; unter der 1. D eine breite mittel- bis dunkelbraune Zone, die sich auf der Unterseite der Flanken in zwei etwas

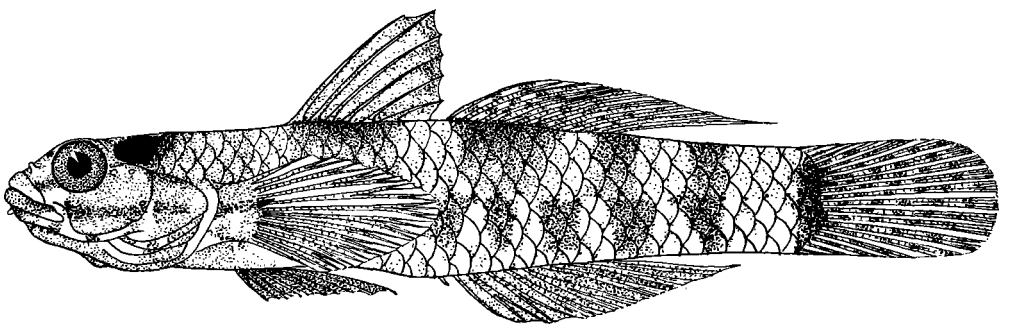

Abb. 1. *Acentrogobius meteori* n. sp. Holotypus, SMF 8188. Ttl. 21 mm. Zeichnung: INGEBORG SCHRÖDER.

Acentrogobius meteori n. sp., holotype, SMF 8188. Total length 21 mm. Drawing by INGEBORG SCHRÖDER.

rand glatt, ohne Stachel; der Hautteil des unteren Randes ist mit Papillen besetzt. Vordere Nasenöffnung röhrenförmig, hintere eine große Pore mit leicht angehobenem Hautrand. Auf der Kopfoberseite und der Wangenregion Reihen von Poren und Röhren des Seitenliniensystems, jedoch keine dichten Papillarreihen. Kiemenspalten verkürzt, enden dicht unter der P-Basis.

Körper völlig mit relativ großen Schuppen bedeckt. Nur die Brust und die P-Basis nackt. Mit Ausnahme derjenigen des Nackens sämtliche Schuppen deutlich ctenoid, zum Bauch hin werden die Kammränder allerdings erheblich schmaler.

1. und 2. D durch einen Abstand von etwa einer Schuppenbreite voneinander getrennt. Der jeweils erste Strahl beider Flossen ist normal entwickelt. Der II. D-Strahl ist am längsten. Beide Flossen sind etwas höher als die größte Körperhöhe. 2. D spitzig auslaufend. A der weichen D sehr ähnlich. P breit, gerundet; ohne Basis etwas kürzer als der Kopf, mit Basis deutlich länger; ohne fadenförmige Solitärstrahlen und ohne fleischigen Fortsatz im Schulterbereich. Beide V in ganzer Länge miteinander verschmolzen. Basalmembran (Fraenum) deutlich entwickelt, wenn auch nicht sehr stark. C gerundet, etwas kürzer als der Kopf.

Ober- und Unterkiefer jeweils mit mehreren Reihen kleiner spitziger Zähne besetzt, Vomer und Palatina unbezahnt. Zunge leicht zweilappig.

dunklere Flecken aufspaltet. Von der 2. D bis zum Schwanzstiel drei verwaschene dunkelbraune Sattelflecken, die auf der Körperunterseite durch 4—5 etwas dunklere und schärfer abgesetzte Flecken abgelöst werden. Auf der C-Basis eine schmale schwärzliche Querbinde. 1. D schwach gebändert, 2. D und C durch transversale Reihen schwarzer Punkte deutlich gebändert; A und P wiederum nur schwach gebändert. A kann auch einheitlich mittel- bis dunkelgrau sein; V einheitlich mittel- bis schwarzgrau.

LEBENDFÄRBUNG: Im Leben ist die Grundtönung braunoliv, die Zeichnung dunkelbraun, postorbitaler Fleck und Schwanzwurzel sind schwarz. Am Rande des Praeoperculum einige orangefarbene Punkte. D, A und C hell bräunlich mit dunkelbrauner Zeichnung.

BEZIEHUNGEN: *A. meteori* n. sp. scheint nach den Flossenformeln recht nahe verwandt zu sein mit *A. baltea, decoratus, leptochilus* und *reichei*, von denen sich die neue Art aber durchweg durch ihre Zeichnung unterscheidet. Nach dem Bestimmungsschlüssel von KOUMANS (1953) müßte *meteori* zur Gattung *Quisquilius* gehören, wovon sie sich aber durch die Restriktion der Kiemenspalten deutlich unterscheidet. Eine gewisse Ähnlichkeit hat *A. meteori* mit *Palutrus reticularis* J. L. B. SMITH, wovon sich unsere neue Art aber allein schon durch die Gattungsmerkmale sowie durch die Ausbildung der V und durch die

postorbitale Fleckung unterscheidet. *A. meteori* gehört in den Grenzbereich dieser Gattung, da das Fraenum der Ventralflossen nur schwach ausgebildet ist. Es gibt aber keine andere Gattung, in die unsere neue Art mit Sicherheit eingegliedert werden kann.

ÖKOLOGIE: *Acentrogobius meteori* wurde an der Ostküste von Sarso (Sarso kebir) im Eulitoral und oberen Sublitoral entdeckt. Der Untergrund des Eulitorals besteht an der Fundstelle aus einem reich gegliederten, schwach geneigten Abrasionsfelsen eines möglicherweise gehobenen Korallenriffes. Seine Oberfläche ist mit vielen Spalten, Rissen und Löchern versehen (Abb. 2), von denen einige größere Rinnen am Grunde mit Sand oder kleinem Geröll angefüllt sein können. Das Gestein ist mit einem Überzug von feinen, fadenförmigen Grünalgen bewachsen. Diese Region wird während einer normalen Flut von 30—60 cm Wasser bedeckt, fällt aber zweimal täglich bei Ebbe zum größten Teil trocken. Nur in einigen Vertiefungen der Felsplatte bleiben dann Restwasseransammlungen bestehen, die *A. meteori* auch bei Ebbe die Existenz in dieser Region ermöglichen. Bevorzugt werden Gezeitenrinnen, die am Grunde Sandablagerungen enthalten; dort liegen die Fische meist ruhig auf dem Grunde, nur bei Gefahr schwimmen sie blitzschnell davon, um sich in einem Versteck am Rande der Vertiefung zu verbergen. Die starke Erwärmung der Gezeitentümpel, die durch die direkte Sonneneinstrahlung verursacht wird, wird von *A. meteori* vertragen. Die Art ist vergesellschaftet mit dem viel häufiger vertretenen *Acentrogobius ornatus* und dem Salariiden *Antennablennius hypenetes* sowie Jungfischen von *Istiblennius edentulus* und *Halmablennius flaviumbrinus*.

Außer im Eulitoral wurde die neue Art auch im unmittelbar angrenzenden Sublitoral gefunden, dessen Bodengrund aus Sand und herausragendem Gestein mit aufgelagertem Geröll jeder Größe besteht. Der Wasserstand beträgt in dieser fast waagerechten Region bei Ebbe etwa 30 cm. Die Tiere halten sich dort bevorzugt unter dem Geröll auf dem Sand auf.

Nicht gefunden wurde die neue Art an solchen Stellen, an denen die Abrasionsterrasse zu sehr abgeschliffen ist und daher kaum eine Strukturierung aufweist. *A. meteori* fehlt außerdem in der reinen Sandregion (Gegensatz *A. ornatus*) und an Plätzen mit starker Brandung, da die schwach entwickelte Membran an den Ventralflossen anscheinend die Leistungsfähigkeit des Saugorgans beeinträchtigt und die Tiere sich der Turbulenz nicht widersetzen können.

Abb. 2. Lebensraum von *Acentrogobius meteori* n. sp. bei Ebbe. Die Tiere halten sich vorwiegend in den wasserführenden Spalten des Abrasionsfelsens auf. Photo: C. D. ZANDER.

Da *A. meteori* auch im oberen Sublitoral vorkommt, kann er nur bedingt als eine Form angesehen werden, die einer Lebensweise in der Gezeitenzone angepaßt ist. Eventuell steht diese Art am Anfang einer Entwicklungsreihe, die zu einer amphibischen Lebensweise hinführt; diese Tatsache wäre am Felslitoral für einen Vertreter der Gobiidae bemerkenswert.

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OSTRACODES PÉLAGIQUES DU SUD-OUEST DE L'OCÉAN INDIEN (RÉGION DE TULÉAR)

par Michel LEVEAU

INTRODUCTION.

A la fin du siècle dernier les expéditions de la "Valdivia" et de la "Siboga", qui eurent lieu en partie dans l'Océan Indien nous permirent d'avoir un relevé assez complet de la faune pélagique de cet Océan. De ce fait, les Ostracodes pélagiques, qui offrent une très vaste répartition géographique, furent pour la plupart décrits par MULLER (1906 a, 1906 b).

Si la systématique des Ostracodes de l'Océan Indien est assez bien connue, par contre la distribution verticale et l'abondance des différentes espèces l'est beaucoup moins. Je me suis donc tout particulièrement attaché à l'étude de ces deux facteurs au cours d'une mission à Madagascar, pendant les mois d'avril et mai 1963, dans une zone proche de Tuléar (Sud-Ouest de l'Océan Indien).

En effet, le secteur de Tuléar offre un intérêt tout particulier, de par sa situation géographique (il est situé sous le tropique) et de par sa morphologie sous marine si variée, dûe à la présence d'un récif barrière limité au Nord et au Sud par l'embouchure de deux fleuves : l'Onilahy et le Fiherenana.

La prospection de biotopes interessants et variés, tels le chenal d'arrière-récif dont les fonds ne dépassent guère 20 m, la grande vasque récifale presque entièrement isolée à marée basse, le canyon très abrupt au niveau de l'embouchure de l'Onilahy, et les eaux situées plus au large du récif, me permit d'avoir une idée assez bonne de la distribution horizontale et verticale des ostracodes pélagiques.

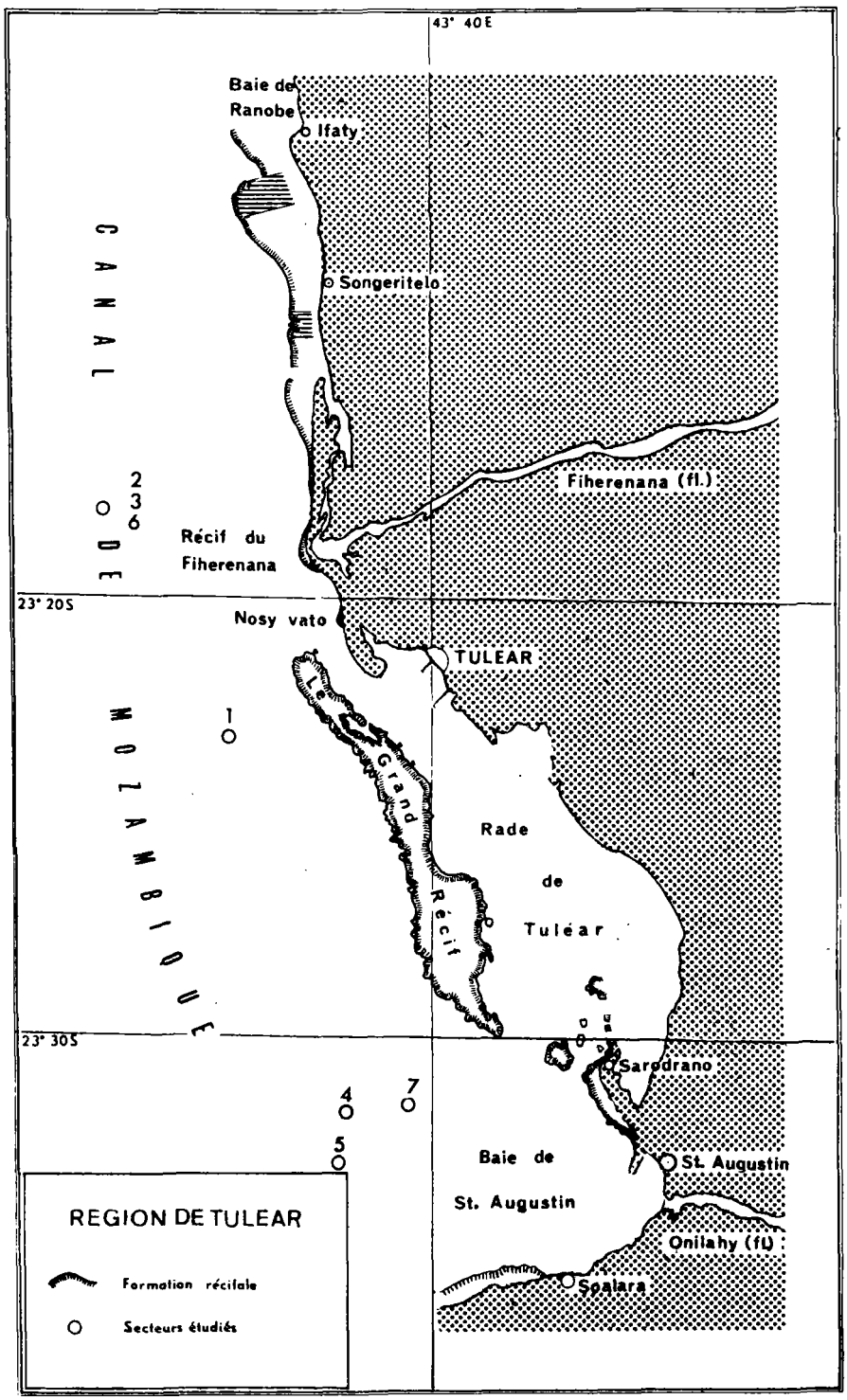
METHODES

J'ai utilisé pour l'ensemble de ces prélèvements deux types de filets fermants : le filet JUDAY - BOGOROV, fréquemment employé en Méditerranée, et le grand filet "Indian Ocean Standard Net" (Ronald I. Currie. N.I.O. Internal report n° B1) que j'appelerai I.O.S.N. par la suite. Ce dernier filet fut adopté pour l'étude du zooplancton par l'Expedition Internationale de l'Océan Indien. J'ai effectué à chaque station avec le filet I.O.S.N. deux traits verticaux, l'un entre 200 m et la surface, donc exactement comme il avait été préconisé d'employer ce filet pour l'étude de la biomasse planctonique, et l'autre entre 400 m et 200 m. En outre, j'ai réalisé un certain nombre de traits horizontaux et verticaux à l'aide du filet JUDAY BOGOROV dans le chenal d'arrière récif, dans une des grandes vasques récifales et enfin au large du récif.

A chacun de ces filets utilisés en vertical, je fixais une gueuse en plomb de 25 kg nécessaire à leur enfoncement, ainsi qu'un enregistreur de profondeur du même type que celui décrit par MILLER S.M, MOORE H.B et KVAMMEN (1958). La vitesse de remontée du filet variait entre 0,33 m/s et 0,5 m/s suivant le type de filet utilisé.

Les facteurs physico-chimiques du milieu furent étudiés à l'aide de moyens classiques : thermomètres fixés sur des bouteilles d'hydrologie à renversement, et disque de Secchi pour évaluer la transparence de l'eau.

Au laboratoire je n'ai pas eu à utiliser une méthode de sous échantillonnage du fait de la pauvreté numérique de certaines espèces telles *Conchoecia ametra* et *C. daphnoides*. J'ai donc trié en totalité chaque prélèvement.


43° 40E
Baie de Ranobe
Ifaty
Songeritelo
CANAL DE MOZAMBIQUE
2
3
6
Récif du Fiherenana
Fiherenana (fl.)
23° 20S
Nosy vato
TULEAR
1
Grand Récif
Rade de Tuléar
23° 30S
Sarodrano
4
7
5
Baie de St. Augustin
St. Augustin
Onilahy (fl)
Soalara
REGION DE TULEAR
Formation récifale
Secteurs étudiés

RESULTATS : -

Je dois tout d'abord signaler que dans tous les prélèvements effectués en eau peu profonde (vasque récifale et chenal d'arrière récif) je n'ai pas recueilli un seul ostracode pélagique. Ceci vient donc dans une certaine mesure corroborer les observations que j'avais pu faire dans le golfe de Marseille, ou le nombre d'individus et d'espèces d'ostracodes pélagiques diminuait au fur et à mesure que les fonds remontaient, pour devenir totalement nul près des côtes. ILES (1954), sur la côte Ouest Atlantique avait pu constater le même phénomène.

Ce n'est donc que dans les prélèvements verticaux réalisés au large du récif et dans le canyon de St Augustin que les ostracodes pélagiques se sont révélés être abondants. Je me bornerai donc ici à donner les résultats des douze prélèvements effectués avec le filet I.O.S.N. et à discuter ces résultats en tenant compte des traits réalisés avec le filet JUDAY BOGEROV.

J'ai trié et déterminé une trentaine d'espèces appartenant pour la plupart au genre *Conchoecia*, et décrit une nouvelle espèce *Conchoecia pectinata* (sous presse), ce qui prouve la richesse qualitative en ostracodes pélagiques des eaux de cette partie de l'Océan Indien.

Je donne ci-dessous un tableau récapitulatif de l'ensemble des espèces avec leur fréquence. Il ressort de ce tableau plusieurs points intéressants :

- Tout d'abord la fréquence très élevée de quelques espèces telles *Conchoecia procera*, *C. tetivalvata*, *C. spinirostris* *C. magna*, *Euconchoecia chierchiae* et *Halocypris inflata*, alors que d'autres espèces ne sont représentées que par quelques individus isolés telles *C. loricata* et *C. daphnoides*.

- Il faut noter également, que sur 4 058 individus capturés dans 10 traits verticaux, dont cinq entre 400 et 200 m et cinq entre 200 m et la surface, il n'y avait que 1174 individus entre 400 et 200 m, soit 28 % seulement du nombre total d'individus.

- En outre, on constate une répartition verticale variable selon les espèces que l'on pourra classer en :

  - espèces fréquentes entre 200 m et la surface
  - espèces fréquentes entre 400 m et 200 m.
  - espèces sans niveau préférentiel apparent.

ESPECES FREQUENTES ENTRE 200 m ET LA SURFACE.

Ce sont toutes les espèces récoltées en très grand nombre citées ci-dessus, auxquelles viennent s'ajouter *C. acuminata* et *C. decipiens*.

Euconchoecia chierchiae Muller

E. chierchiae est l'espèce épiplanctonique la plus fréquente. J'avais pu m'en rendre compte en étudiant le plancton dé quelques pêches verticales réalisées entre 100 m et la surface avec le filet JUDAY BOGOROV, où elle s'était montrée particulièrement abondante, associée à d'autres espèces telles *C. spinirostris* et *Halocypris inflata*. J'ai remarqué un phénomène analogue en observant les prélèvements effectués par SEGUIN en Atlantique, près de Dakar, uniquement en surface, où les *E. chierchiae* étaient les seuls ostracodes recueillis en grandes quantité. Cette espèce comme le pense MULLER (1906 a) semble liée aux eaux superficielles où la température et la luminosité sont élevées. En effet à Tuléar lorsque la température de surface est descendue de 25, 6° C à 22, 9° C, le nombre d'*E. chierchia* a fortement diminué puisque je n'ai recueilli que deux individus (trait n° 7) contre 335 (trait n° 2) lorsque la température était de 25, 6° C.

Conchoecia spinirostris Claus

Ils sont également très abondants dans la couche d'eau des 200 premiers mètres. FOWLER (1909) dans le golfe de Gascogne leur assigne comme niveau moyen probable 180 m. Il pense que cette espèce est localisée dans la couche des 180 m puisqu'il l'a recueillie depuis cette profondeur jusqu'à la surface. Il lui fixe comme limite de température inférieure et supérieure 11° 5 C et 17°2 C. HURE (1955) fixe pour cette même espèce comme niveau moyen journalier la profondeur de 85 m, et l'a rencontrée toute l'année entre 50 m et 150 m dans des eaux dont la température varie entre 13° C et 25° 6 C.

Dans l'Océan Indien, *C. spinirostris* présente un maximum d'abondance entre 200 m et 0 m, mais on la rencontre encore entre 400 m et 200 m, dans des eaux dont la température varie entre 11°9 C et 25°6 C. Je pense que, pour cette région de l'Océan Indien, le maximum d'abondance se situe entre 160 m et 50 m. En effet, dans les prélèvements que j'ai réalisé avec le filet standard entre ces deux profondeurs, elle était fréquemment capturée alors que de 50 m à la surface elle était totalement absente.

Il me semble bon de signaler que j'ai recueilli *C. spinirostris* sous ses deux formes sexuées. Au stade le plus âgé la longueur des femelles oscillait autour de 1,80 mm, celle des mâles était peu différente de 1,40 mm (forme *C. porrecta* de CLAUS 1891). Je pense comme MULLER et FOWLER (1909) qu'il s'agit en fait du stade le plus âgé de *C. spinirostris*. Les mâles ne présentent que quelques différences morphologiques minimes avec les *C. spinirostris* typiques ; ils possèdent, par exemple, un plus grand nombre d'épines sur la soie (e) de la première antenne, mais ces épines ont une forme tout à fait identique à celles rencontrées chez les mâles qui ne mesurent que 1,10 mm. Les femelles ne présentent pas de différences fondamentales si ce n'est la taille qui est de 1,20 mm chez les plus petites formes.

Conchoecia magna - Claus

Cette espèce, fréquemment recueillie dans les traits 200 m - 0 m, ne doit pourtant pas être superficielle, car elle est totalement absente des pêches verticales que j'ai effectuées avec le filet JUDAY BOGOROV entre 50 m et la surface. HURE en Adriatique la trouve toute l'année entre 100 m et 150 m et entre 50 m et 100 m en hiver. MULLER (1894) et LO BIANCO en Méditerranée s'accordent pour penser qu'il s'agit d'une espèce d'eau profonde. Pour la région que j'ai prospectée son maximum de fréquence doit se trouver entre 50 m et 200 m car dans les prélèvements 400 - 200 m elle est peu abondante.

Conchoecia procera - Müller

C'est une espèce très répandue dans les eaux de l'Océan Indien et de la région de Tuléar. Elle est surtout fréquente entre 200 m et la surface bien qu'encore présente entre 400 et 200 m. FOWLER dans le golfe de Gascogne lui donne comme niveau probable le plus bas 450 m et comme niveau supérieur possible 0 m, avec un maximum d'abondance vers 180 m. Les températures extrêmes entre lesquelles il a pu recueillir cette espèce sont 8° C et 17°2 C. En Adriatique HURE la trouve d'octobre à mars entre 50 m et 150 m. Cette espèce, en Adriatique, semble localisée dans les eaux dont la température est proche de 13° C.

MULLER, LO BIANCO en Méditerranée, et FOWLER pour le golfe Gascogne, signalent que cette espèce est assez rare alors qu'elle est très fréquente dans les eaux proches de Tuléar.

Conchoecia decipiens - Muller

Cette espèce était présente à toutes les stations en assez grande quantité, tout particulièrement entre 200 m et la surface. C'est d'après MULLER (1906) une forme superficielle, ce que semble confirmer sa répartition verticale dans les eaux que j'ai prospectées.

Conchoecia pectinata Leveau et *C. atlantica Lubbock*

Bien que peu abondantes ce sont toutefois des espèces typiquement épiplanctoniques.

Halocypris inflata Dana

Dans les pêches que j'ai effectuées, elles sont très nombreuses, tout particulièrement dans les 200 premiers mètres. MULLER pense pourtant que cette espèce a une large distribution verticale puisqu'il a trouvé un jeune exemplaire entre 2 700 m et 2 400 m et un autre entre 3 300 m et 2 700 m. A Tuléar (cf tableau) leur maximum d'abondance est localisé à un niveau beaucoup plus superficiel.

ESPECES FREQUENTES ENTRE 400 m ET 200 m

Conchoecia imbricata - Brady

C'est une espèce peu abondante. Si elle est surtout récoltée entre 400 m et 200 m, elle est encore présente entre 200 m et la surface. FOWLER avait également signalé son absence totale dans l'épiplancton du golfe de Gascogne, alors qu'il l'a capturée encore vers 900 m.

Températures observées aux différentes stations et profondeurs

Profondeurs	0 m	100 m	200 m	300 m	400 m
Stations					
II	25°6 C	21°8 C	18°10 C	14°8 C	13°4 C
III	25°8	21°95	18°8	14°9	13°25
IV	24°8	23°2	18°7	15°2	12°95
V		Pas de relevé de température			
VI	24°2	19°4	15°95	13°4	11°95
VII	22°9	21°25	15°85	13°45	11°62

Tableau récapitulatif des différents genres et espèces d'ostracodes pélagiques recueillis dans le sud ouest de l'Océan Indien.

Station	I	II	III		IV		V		VI		VII	
	200-0	200-0	200-0	400-200	200-0	400-200	200-0	400-200	200-0	400-200	200-0	400-200
Conchoecia												
C. acuminata	84	30	12	0	15	1	25	1	12	0	8	0
C. atlantica	6	7	2	0	0	0	3	0	1	0	0	1
C. bispinosa	1	0	3	14	0	18	4	5	3	7	0	2
C. concentrica	0	1	0	0	0	0	1	0	0	0	0	0
C. curta	11	79	111	196	48	83	36	8	73	29	5	3
C. daphnoides	2	3	6	1	1	1	2	1	2	2	1	0
C. decipiens	55	72	22	2	23	8	15	0	30	0	1	1
C. echinata	1	1	1	1	3	12	1	5	6	0	0	2
C. elegans	1	14	36	74	5	72	5	77	42	14	3	8
C. glandulosa	-	-	-	-	-	2	-	-	-	-	-	-
C. imbricata	0	1	0	3	0	7	0	9	2	13	1	4
C. kyrtophora	0	0	0	10	0	15	0	0	0	0	2	1
C. loricata	0	0	0	0	0	0	0	0	0	1	1	7
C. magna	80	16	18	2	22	9	24	1	40	0	54	1
C. oblonga	9	35	30	22	23	47	10	24	37	7	13	4
C. parthenoda	14	8	15	4	3	3	3	0	10	2	2	0
C. pectinata	16	4	3	0	2	0	3	0	3	0	0	0
C. procera	273	155	144	22	83	35	44	6	147	12	85	4
C. pusilla	1	0	0	0	0	0	0	2	1	0	3	1
C. sibogae	0	0	0	0	0	0	0	0	0	0	0	2
C. spinifera	0	0	0	0	0	4	0	0	0	3	0	0
C. spinirostris	203	90	123	24	174	17	188	10	108	11	75	11
C. teretivalvata	66	58	51	20	15	27	1	16	30	7	24	10
Archiconchoecia												
A. cucullata	0	0	0	0	0	1	0	0	1	0	0	0
A. striata	1	2	0	0	0	0	0	0	1	1	1	0
Euconchoecia												
E. chierchiae	335	280	95	2	84	1	90	0	204	0	2	1
Cypridina												
C. serrata	0	0	0	0	0	0	3	0	0	0	0	0
C. sp.	0	0	0	0	0	0	2	0	0	0	0	0
Conodocera												
C. pusilla	0	0	0	0	0	0	1	0	0	0	0	0
Halocypris												
H. inflata	97	100	50	10	44	8	90	4	24	3	7	0

Traits IOSN	Dates	heures des pêches	Stations	Profondeur où fut effectué le trait.	Etat de la mer	vitesse de remontée du filet.	transparence disque de Secchi.
I	9/5/63	10 h	1 Large passe nord du chenal	# 300 m	légère houle de S. W.	0, 5 m/s	
II	11/5/63	11 h 23 12 h 15	1	# 500 m	mer calme temps superbe	0, 5 m/s	eau transparente 30 m.
III	13/5/63	10 h 30 11 h 20	3	# 500 m	Beau temps très faible houle.	0, 33 m/s	eau transparente.
IV	15/5/63	8 h 45 9 h 40	4 Flanc nord canyon St Augustin Long. 43°38'1/10 W Lat. 23°31'3/10 S	# 900 m	calme plat	0, 33 m/s	eau bleue 20 m.
V	15/5/63	12 h 55 13 h 54	5 Long. 43°38'6/10 W Lat. 23°33'4/10 S	# 650 m	calme plat légère brise	0, 33 m/s	21 m.
VI	27/5/63	9 h 20 10 h 15	6 large passe nord	# 500 m	mer 2 temps clair	0, 33 m/s	28 m.
VII	29/5/63	8 h 32	7 Long. 43°40'3/10 W Lat. 23°31'8/10 S	# 1 200 m	mer belle	0, 33 m/s	eau sale 8 m.

Conchoecia bispinosa Claus

C'est une espèce également peu abondante, en particulier entre 200 m et la surface, mais elle est déjà plus fréquente entre 400 m et 200 m. FOWLER en fait une espèce mésoplanctonique, ce que confirme la répartition verticale observée dans l'Océan Indien.

Conchoecia elegans - Sars.

C. elegans peut également être considérée comme une espèce de profondeur. Elle est en effet toujours plus abondante entre 400 m et 200 m, sauf pour la sixième station où j'ai recueilli 42 individus entre 200 m et 0 m et seulement 14 entre 400 m et 200 m. Ceci peut s'expliquer si l'on constate que la température à 200 m n'est que de 15, 95° C soit inférieure de près de 3° C à celle des autres stations pour la même profondeur.

ESPECES SANS NIVEAU PREFERENTIEL APPARENT

Conchoecia teretivalvata Iles = *C. rotundata* MULLER 1894-1906 - 1962.

FOWLER 1909 "short forms" et *C. curta* Lubbock ces deux espèces sont si fréquentes entre 400 m et 200 m puis entre 200 et 0 m qu'il m'est impossible de leur attribuer un niveau préférentiel. Pourtant on ne peut assurer qu'elles soient réparties dans toute la tranche d'eau plutôt qu'à 200 m qui serait alors leur niveau moyen de distribution verticale et qui, de ce fait expliquerait leur présence dans les deux séries de prélèvements.

ILES (1953) sur la côte ouest africaine, dans le courant de Benguela, note que le maximum de fréquence pour *C. teretivalvata* se situe entre 250 m et 100 m, mais il a encore capturé quelques individus entre 750 m et 500 m.

FOWLER (1909) pense que ces deux espèces sont épiplanctoniques mais que les plus vieux stades de développement seraient uniquement mésoplanctoniques. N'ayant pas fait de discrimination entre les différents stades de développement, je ne puis confirmer ou infirmer ceci, pourtant je puis dire que les *C. teretivalvata* arrivée à maturité sexuelle, n'étaient pas absents de la couche d'eau des 200 premiers mètres.

SOMMAIRE :

J'ai pu examiner les ostracodes pélagiques recueillis lors d'une mission dans le sud ouest de l'Océan Indien, en avril - mai donc pendant la période du refroidissement des eaux dans l'hémisphère austral.

Vingt quatre espèces du genre *Conchoecia* ont été déterminées ainsi qu'une espèce des genres *Cypridina* et *Conodocera*. Deux autres espèces de *Cypridina* dont je n'avais que de jeunes exemplaires ont été récoltées. J'ai également récolté une espèce nouvelle épiplanctonique : *C. pectinata* décrite précédemment (sous presse). En outre je me suis rendu compte de l'absence totale des *Conchoecia* sur les fonds peu importants, alors qu'au niveau du canyon de St Augustin et des grands fonds situés plus au large du récif les eaux étaient riches en ostracodes pélagiques tant du point de vue qualitatif que quantitatif.

La couche d'eau des 200 premiers mètres est la plus riche en espèces mais aussi en individus : 72 % des individus entre 200 et 0 m contre 28 % entre 400 m et 200 m.

Enfin les différentes espèces ont pu être réparties en trois groupes en fonction de leur répartition bathymètrique.

SUMMARY :

The présent report is based on the material collected during a survey in the south-west Indian Ocean (Madagascar), during the cooling periode of waters in the Southern hemisphere (april - may).

Twenty four species of Conchoecia were identified as well as one genus each of *Cypridina* and *Conodocera*. Two other species of *Cypridina* of which I have only a few young specimens were listed as "unidentified juveniles". I have also collected a new epiplanctonic species : *C. pectinata* which previously I have described (under press).

In addition, I have noticed an almost complete absence of the genus *Conchoecia* in shallow areas which is in contrast to deeper water stations (St Augustin's canyon, and off barrier reefs) where planktonic ostracods were very abundant quantitatively and qualitatively.

The superficial layer from zero to two hundred meters is the richest both in the number of individuals and species : 72 % of specimens between 200 m and 0 m and only 28 % between 400 m and 200 m.

Lastly, the different species were divided into three groups according to their bathymetric distribution.

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NOTE PRÉLIMINAIRE SUR LA SYSTÉMATIQUE ET LA RÉPARTITION ANNUELLE DES COPEPODES DES EAUX SUPERFICIELLES DE TULEAR (MADAGASCAR)

par Raymond GAUDY

La systématique des Copépodes pélagiques des mers tropicales est connue surtout d'après le matériel recueilli par les grandes expéditions océanographiques (Challenger, Valdivia, Siboga, Albatross, Terra-nova, Carnegie, Dana, Snellius, Galathea, etc...). La faune de l'Océan Indien fait ainsi l'objet d'importants travaux de A. SCOTT (1909) basés sur les prélèvements de plancton du "Siboga" dans les parages de l'archipel malais. Les différentes études de SEWELL (1929, 1932, 1940, 1947, 1948) concernent plus spécialement les mers avoisinant la péninsule Indienne. WOLFENDEN (1906) est l'auteur d'une interessante note systématique sur les copépodes des Maldives et des Laquedives. Enfin divers travaux d'auteurs indiens sont relatifs à des zones côtières. KRISHNAWAMY (1953 a, b, c, 1956) s'est ainsi intéressé à la systématique des copépodes des côtes occidentales de l'Inde.

Les Copépodes du plancton méridional et occidental d'Afrique du Sud ont été initialement étudiés par CLEVE (1904) entre Durban et Le Cap, puis par BRADY (1914 a, b, 1915), au voisinage de Durban. Les récents travaux systématiques et écologiques de DE DECKER (1963) viennent compléter dans une large mesure la connaissance de la systématique des copépodes de surface de la même zone sud-africaine Durban - Le Cap. Plusieurs stations de WOLFENDEN (1811) et de TANAKA (1960) intéressent également le sud de la Province du Cap. En dehors de ces travaux consacrés surtout aux Copépodes, quelques études d'ordre plus général peuvent apporter néanmoins des précisions pour certaines espèces de Copépodes (CLEVE 1901). D'autres travaux, plus spécialisés, constituent en quelque sorte des monographies de genres dans l'Océan Indien. (GIANFERRARI 1921 et STEUER 1923 pour le genre *Acartia*, FARRAN 1911, 1913 pour les genres *Corycaeus*, *Corycella*, *Oithona*, *Paroithona* de l'Ile Christmas, au sud de Java).

Ces divers travaux systématiques sont le plus souvent basés sur des prélèvements faits dans un temps limité, à l'occasion d'un voyage ou d'une brève mission. On sait en fait peu de choses sur l'évolution annuelle des communautés planctoniques tropicales, et, contrairement à ce qu'il en est pour les mers tempérées de l'hémisphère nord, les mers chaudes ont un cycle biologique encore mal élucidé, particulièrement en ce qui concerne les copépodes pélagiques, dont l'importance au sein de la productivité secondaire n'est plus à démontrer. C'est ainsi que dans l'Océan Indien, seules certaines zones des côtes de l'Inde font l'objet de travaux basés sur des prélèvements réguliers (GANAPATI et RAO 1954, GANAPATI et SHANTHAKUMARI 1961).

Nous aurons souvent recours, pour établir des comparaisons au travail de FARRAN 1949 sur la distribution saisonnière et verticale des copépodes de la Grande Barrière, qui présente des conditions écologiques assez voisines de celles du Grand Récif de Tuléar.

Pour la région malgache, n'existait en particulier aucun travail d'ordre systématique ou biologique sur les Copépodes pélagiques marins. Il y avait donc là une certaine lacune, d'autant plus que la situation de la Grande Ile au cœur d'une zone peu étudiée, son environnement courantologique, l'endémisme de sa faune intérieure, sont autant de facteurs qui permettent de supposer des problèmes biogéographiques intéressants. L'objet du présent travail, conduit dans le cadre de l'Année Internationale d'Etude de l'Océan Indien, est de dresser une première liste des Copépodes de surface des eaux de Tuléar, et de faire quelques remarques sur leur distribution et leur signification écologique.

Dans un travail ultérieur, nous examinerons également la faune méso et bathypélagique de la même région.

LES CONDITIONS DU MILIEU

Zone d'étude :

Le matériel dont l'étude fait l'objet du présent travail provient d'une station côtière comprise entre les deux bouées balisant la passe nord du Grand Récif de Tuléar, et dont la position moyenne est : latitude 23° 21' S ; longitude 43° 37' 30" E.

Cette zone présente un caractère néritique accentué, de par la proximité de la côte, la faible profondeur (12 à 18 m), la présence à quelques miles au nord du débouché d'un fleuve à régime très irrégulier, le Fiherena. L'arrivée d'espèces océaniques n'est cependant pas exclue sous certains régimes de vent. En effet, la passe est largement ouverte vers le large, et le plateau continental peu étendu : à cinq miles au large, on trouve des fonds supérieurs à 400 m.

Méthodes de prélèvements :

Les prélèvements ont été faits le plus régulièrement possible (trois à quatre fois par mois). Le filet, de 50 cm de diamètre d'ouverture et à mailles de 250 microns, était trainé horizontalement entre les deux bouées, ce qui représente une distance de 600 m, aux niveaux de 0 et 8 mètres, afin de réduire dans une certaine mesure les irrégularités de distribution. Un petit filet à mailles de 60 microns, accouplé au grand filet, était plus spécialement déstiné à la capture du phytoplancton ou des très petites formes (nauplii de copépodes en particulier).

La période d'étude est comprise entre le 3 octobre 1963 et le 8 octobre 1964.

Température :

Le tableau I indique un intervalle de températures compris entre 22° (18 août) et 30°02 (20 février). La température moyenne est proche de 25°.

Salinité :

Les dosages de salinités concernant la station d'étude n'ont pas encore été effectués. A titre indicatif, les eaux du large ont en surface une salinité égale ou légèrement supérieure à 35°/$_{oo}$ presque toute l'année. En janvier et février, ces valeurs peuvent s'abaisser jusqu'à 34°/$_{oo}$. Il est probable que les eaux côtières présentent à ce moment là des valeurs encore inférieures, de l'ordre de 33 à 33,5°/$_{oo}$. Cet abaissement saisonnier de salinité résulte évidemment de la fréquence des pluies en saison chaude, qui provoquent des crues brutales du Fiherena. Pour la période considérée, le Service Météologique de Tuléar cite les chiffres de précipitations suivants :

Pluies ; Hauteur totale du mois en mm et dixièmes

Septembre 1963	0,0	Avril	0,0
Octobre	0,5	Mai	0,0
Novembre	60,1	Juin	9,4
Décembre	29,9	Juillet	12,8
Janvier	53,7	Août	30,0
Février	15,9	Septembre	0,0
Mars	62,5	Octobre	9,5

Turbidité :

Les mesures de turbidité par immersion d'un disque de Secchi (Tableau I) traduisent également les inégalités du régime pluvial. En période de crue, le Fiherena déverse des eaux très turbides, réduisant parfois la visibilité du disque à des valeurs inférieures à 2 mètres. Par suite de la proximité de la côte, il est rare que cette visibilité soit supérieure à 15 mètres. A titre indicatif, les eaux du large offrent couramment une clarté permettant l'observation du disque jusqu'à 25 ou même 30 mètres.

P.h. ; Oxygène dissous :

A partir de juillet 1964, des mesures de Ph de l'eau de mer ont été faites à chaque sortie. Les valeurs relevées varient très peu autour de 8,1 à 8,25. Les eaux sont largement oxygénées (plus de 8,20 ml/L).

Courants :

A côté des courants de marée portant alternativement nord-sud ou sud-nord, de peu d'importance biologique, il existe à l'extérieur du récif un courant de direction générale sud-nord, dont les caractéristiques mériteraient d'être précisées ultérieurement. Ce courant, favorisé par l'action des vents dominants de secteur sud à sud-ouest, paraît correspondre à la branche infléchie du courant du Mozambique : MENACHE (1961), à la suite de la Campagne du Robert-Giraud dans le Mozambique, signale en effet que : "Le courant du Mozambique descend vers le sud le long des côtes d'Afrique. Contrairement aux schémas classiques, ce courant ne rejoint pas celui des Aiguilles, mais s'infléchit vers l'Est vers 24° S, puis remonte au nord, le long de la côte de Madagascar".

Phytoplancton :

Nous n'avons pas encore examiné de manière systématique les prélèvements de Phytoplancton. Lors des périodes de développement ; l'élément prédominant est le genre *Chaetoceros*.

Plusieurs maxima ont été notés, peu après d'importantes précipitations (novembre, janvier, février, juillet).

SYSTEMATIQUE ET REPARTITION ANNUELLE

Les tableaux de distribution placés à la fin de ce travail résument pour chaque prélèvement effectué la présence et l'abondance des espèces récoltées. Pour donner un premier aperçu de l'abondance relative des espèces, l'échelle suivante a été adoptée :

\+ individus isolés ou rares

1 abondance faible

2 commun

3 très abondant

CALANIDAE

Undinula vulgaris (Dana)

Cette espèce, de taille relativement importante, est fréquente dans les mers tropicales, ce qui lui a valu d'être comparée au *Calanus finmarchicus* des mers boréales dont on sait le rôle économique de premier plan pour l'alimentation des poissons (DELSMAN 1939).

Du point de vue écologique, il s'agit d'une forme néritique tropicale, distribuée dans les trois océans. TSURUTA (1962) lui accorde une tolérance aux salinités variant de 33,5 à près de 36°/$_{oo}$ et aux températures comprises entre 18 et 28° C. BJORNBERG (1963) constate également la prédominance de ce Copépode dans les eaux chaudes (plus de 25°) et salées (plus de 36°/$_{oo}$) des côtes du Brésil. A Dakar (GAUDY et SEGUIN 1964), la répartition de *U. vulgaris* dépend surtout de la température (qui doit être supérieure à 23°).

La plupart des auteurs attribuent à cette espèce une répartition surtout néritique (FARRAN 1947 ; BJORNBERG 1963).

D'après FARRAN (1947), *U. vulgaris* présente à la Grande Barrière des fluctuations saisonnières, avec des maxima en octobre, novembre, décembre et avril. Il est probable que ces irrégularités d'abondance sont dûes aux développements successifs de plusieurs générations.

Dans l'Océan Indien, *U. vulgaris* a été souvent signalé. Il est connu en particulier sur les côtes occidentales de l'Inde (GANAPATI et SHANTHAKUMARI 1961), et en Afrique du sud (CLEVE 1904 BRADY 1914. DE DECKER (1963) le considère comme caractéristique des eaux du Courant des Aiguilles.

A Tuléar, l'espèce est présente dans presque tous les prélèvements, sauf en janvier (influence probable de la dessalure). Elle est particulièrement abondante en novembre et en avril. Le 11 juillet, j'ai récolté une forme particulière de cette espèce, caractérisée par l'existence à la partie postérieure du dernier segment thoracique de deux crochets superposés, correspondant à la description d'une variété analogue des mers de l'Inde (SEWELL-1929).

Undinula darwini (Lubbock)

Circumtropicale, et présentant sensiblement les mêmes tolérances aux températures et aux salinités que *U. vulgaris*, cette espèce est généralement considérée comme une forme océanique (FARRAN 1947).

U. darwini est citée sur les côtes orientales d'Afrique du Sud (CLEVE 1904, BRADY 1914) DE DECKER (1963) montre que sa distribution reste localisée au voisinage de Durban, dans les eaux influencées par le courant des aiguilles.

Dans nos prélèvements, l'espèce apparaît sporadiquement en saison chaude. En saison fraîche, elle est plus fréquente, mais demeure peu abondante.

Undinula caroli (Giesbrecht)

Cette espèce océanique, très voisine de la précédente, n'est généralement récoltée qu'en très faible abondance. Elle est typiquement Indo-Pacifique, mais n'est pas citée en Afrique du sud.

A Tuléar, quelques individus ont été capturés, le 6 juillet et le 6 août.

Calanus tenuicornis Dana

Forme cosmopolite, ce copépode se rencontre dans les eaux tropicales, mais BJORNBERG (1963) la classe comme eurythermique préférentielle de la limite inférieure de l'intervalle de température des eaux chaudes. De ce fait, l'espèce est souvent rencontrée dans les couches sub-superficielles (100-200 m) des mers chaudes (FARRAN 1926, VERVOORT 1946).

C. tenuicornis est cité en Afrique du Sud par CLEVE (1904) et DE DECKER (1963). Ce dernier auteur note sa rareté en surface et signale qu'il a pu retrouver l'espèce en profondeur (3000 m) au sud de Madagascar, en compagnie de *Calanoïdes carinatus* Kroyer et *Calanus tonsus* Brady, qui sont connues comme préférentielles d'eaux tempérées froides.

Dans les eaux de surface de la région de Tuléar, *Calanus tenuicornis* se montre rare en octobre, février, juillet.

Calanus minor (Claus)

Forme cosmopolite de par son euryhalinité et son eurythermie, *C. minor* semble cependant plus abondamment et régulièrement distribué dans les eaux chaudes. Les auteurs s'accordent pour en faire une espèce océanique (FARRAN 1949 pour la région de la Grande barrière, DEEVEY (1952), pour la côte atlantique nord-américaine). A Dakar, également, elle n'est régulièrement et abondamment distribuée que de juin à novembre, en compagnie de *Undinula vulgaris* (GAUDY et SEGUIN 1964), à des températures supérieures à 23°.

C. minor est épipélagique, mais peut se rencontrer en profondeur en faible abondance (BJORNBERG 1963).

Dans l'Océan Indien, cette forme, rare sur les côtes occidentales de l'Inde, d'après GANAPATI et SHANTHAKUMARI (1961) est citée au voisinage de l'Afrique du sud par CLEVE (1904), TANAKA (1960), DE DECKER (1963). Ce dernier en fait une des espèces les plus abondantes de la faune épipélagique qu'il examine.

A Tuléar, *Calanus minor* se rencontre surtout en saison froide, en compagnie d'autres espèces océaniques, telles *Undinula darwini*.

Calanus gracilis Dana

Cosmopolite de mers tempérées-chaudes et tropicales, cette espèce océanique est affectée de migrations verticales nycthémérales importantes, mais reste en général mieux distribuée dans les eaux sub-superficielles de 100 à 200 m (BJORNBERG 1963).

Calanus gracilis ne semble pas avoir atteint les rivages d'Afrique du sud. A Tuléar, elle demeure exceptionnelle dans les eaux superficielles.

Canthocalanus pauper (Giesbrecht)

Cette forme, dont la distribution est limitée à l'Indo-Pacifique est un des composants habituels des communautés néritiques tropicales du Pacifique (FARRAN 1929) ou de l'Océan Indien (SEWELL 1948, GANAPATI et SHANTHAKUMARI 1961).

DE DECKER (1963) en fait mention sur les côtes orientales d'Afrique du sud, où l'espèce atteint sa limite extrême de répartition, à la longitude du Cap Agulhas (TANAKA 1960).

Dans les eaux de surface de Tuléar, *C. pauper* est une espèce fréquente et souvent abondante. Elle disparaît pratiquement en août et septembre, époque du minimum thermique.

EUCALANIDAE

Eucalanus subcrassus Giesbrecht

Cette forme circum-tropicale d'eaux néritiques et côtières évite les hautes salinités et peut atteindre des valeurs numériques élevées dans les zones soumises à l'influence côtière. Devant les côtes du Brésil en particulier, l'espèce est souvent récoltée en abondance (FARRAN 1929, BJORNBERG 1963, GAUDY 1963). Dans les eaux de la Grande Barrière, FARRAN (1946) considère que cette espèce constitue, en compagnie de *Undinula vulgaris* et de *Euchaeta concinna* une des formes économiquement les plus intéressantes dans le zooplancton de ce secteur. Là aussi, les hautes salinités rencontrées pendant les mois froids semblent gêner le développement de l'espèce.

Dans l'Océan Indien, *E. subcrassus* est un des éléments les plus constants du plancton de Lawson's bay où les salinités varient entre 21 et 31°/$_{oo}$ (GANAPATI et SHANTHAKUMARI 1961).

Elle est présente également à l'Ouest de la colonie du Cap (CLEVE 1904). DE DECKER (1963) la cite en compagnie d'autres *Eucalanus*, en une seule station.

A Tuléar, *E. subcrassus* apparaît à la mi-décembre, prend une grande importance de février à la mi-mai, puis en juillet et août, époques de nouvelles précipitations pluviométriques. Il semble que là aussi sa répartition dépende essentiellement de la salinité, défavorable quand elle est trop forte.

Eucalanus mucronatus Giesbrecht

De large distribution, ce copépode semble habituellement distribué dans les eaux profondes (SEWELL 1947). Il est cité en divers points de l'Océan Indien, notamment en Afrique du sud (CLEVE 1904, TANAKA 1960, DE DECKER 1963), où il demeure peu abondant.

A Tuléar, l'espèce se rencontre quelque fois en surface surtout pendant la saison froide. En profondeur, elle est souvent abondante (observations personnelles).

Eucalanus subtenuis Giesbrecht

Il s'agit là encore d'une forme largement distribuée, mais présentant un caractère sténotherme chaud. Elle accompagne souvent dans les communautés néritiques tropicales *E. subcrassus*.

Citée par CLEVE (1904) à l'est de l'Afrique du Sud, cette forme est présente à Tuléar, mais n'atteint pas l'abondance de *Eucalanus subcrassus*.

Eucalanus crassus Giesbrecht

Forme à large répartition, ce copépode est à caractère sténotherme chaud, selon TSURUTA (1963). En fait, il semblerait que cette espèce, comme *Calanus tenuicornis*, soit une forme de mers chaudes se cantonnant dans des eaux dont la température est de l'ordre de 22°C. *E. crassus* est en effet souvent rencontrée en profondeur, vers 200 m ou plus. (SEWELL 1947). A la latitude de Dakar, on peut la considérer comme un indicateur d'eaux froides et salées (BAINBRIDGE 1960, GAUDY et SEGUIN 1964).

Bien connue dans l'Océan Indien, cette forme est citée par CLEVE à l'est de l'Afrique du Sud. (1904).

A Tuléar, elle est peu abondante. En période froide, elle semble se maintenir quelque temps dans les eaux superficielles refroidies (températures voisines de 22°).

Eucalanus attenuatus Dana

Cette grande forme océanique est rencontrée souvent en profondeur, comme la précédente (SEWELL 1947) DEEVEY (1952) la considère comme un indicateur des eaux salées du Gulf-Stream BJORNBERG, devant les côtes du Brésil, pense au contraire qu'il s'agit d'une espèce océanique préférentielle des salinités moyennes ou basses, en mers tropicales. Dans les eaux de surface de Dakar, j'ai constaté au contraire que cette forme accompagnait *E. crassus* et *Calanoides carinatus* pendant la période des eaux froides et salées.

Citée sur les côtes orientales ou méridionales d'Afrique du Sud (CLEVE 1904, WOLFENDEN 1911, BRADY 1914, DE DECKER 1963) *E. attenuatus* ne semble pas montrer à Tuléar de préférence saisonnière stricte.

Une forme particulière de cette espèce est apparue le 9 juin. Elle se signale par sa taille plus grande (5,80 mm), la présence de soies antennaires et caudales plumeuses, la pilosité du segment génital.

Eucalanus elongatus (Dana)

Il s'agit là encore d'une espèce océanique tropicale à tendance tempérée chaude, largement distribuée. Elle est rare dans les eaux de surface, mais recherche les couches sub-superficielles dont la température varie entre 20 et 25° (VERVOORT 1946, BJORNBERG 1963). A Dakar, ce Copépode n'apparaît effectivement que sporadiquement, en février, mars, avril, à des températures inférieures à 20°. (GAUDY et SEGUIN 1964).

L'espèce est citée comme rare sur les rivages orientaux d'Afrique du Sud (CLEVE 1904, DE DECKER 1963).

Dans les eaux de Tuléar, quelques individus sont apparus épisodiquement en saison froide (juin, juillet, 27 août).

Rhincalanus cornutus (Dana)

Cette espèce océanique, mondialement distribuée, est particulièrement bien représentée dans les eaux chaudes de surface ou de sub-surface (VERVOORT 1946). Bien connue en Océan Indien, elle est notamment citée au large des côtes d'Afrique du sud (CLEVE, BRADY, DE DECKER). Selon ce dernier auteur, elle caractériserait le courant des Aiguilles.

Son arrivée dans les eaux néritiques de Tuléar n'est pas exceptionnelle, surtout à l'époque du minimum thermique. D'après des examens préliminaires du plancton de profondeur de St Augustin, ce Copépode constitue bien souvent aux niveaux de 100 et 200 m, l'élément le mieux représenté parmi les Copépodes.

Rhincalanus nasutus Giesbrecht.

On sait, à la suite des travaux de SCHMAUS et LEHNHOFFER (1927) et de STEUER (1931) que cette forme est bathypélagique sous les basses latitudes, alors qu'elle devient superficielle au voisinage des pôles. SEWELL (1948) remarque à son tour les mêmes faits dans l'Océan Indien. D'après sa carte de distribution, on devrait rencontrer l'espèce à près de 800 m à la latitude de Tuléar, les couches supérieures abritant l'autre espèce, *R. cornutus*.

En fait, *R. nasutus* à été noté plusieurs fois en surface mais toujours en saison froide, et en nombre très restreint.

Des faits analogues sont relevés en Afrique du Sud, où l'espèce, signalée par CLEVE (1904) et DE DECKER (1963), n'est jamais abondante dans les eaux de l'Océan Indien. DE DECKER fait à ce propos remarquer que *R. nasutus* n'est pas rare dans le courant froid du Benguela, et, dans le SW de l'Océan Indien, vers 500 m de profondeur. L'espèce apparaît donc avant-tout comme une forme océanique, préférentielle d'eaux fraîches.

Mecynocera clausi J.C. Thompson.

Ce petit eucalanide cosmopolite est une forme océanique de surface et de sub-surface, dans les eaux tropicales ou tempérées chaudes. D'après BJORNBERG (1963), son environnement optimum correspond à des températures inférieures à 18°.

DE DECKER le cite en deux stations sud-africaines.

A Tuléar, il est présent parfois dans les eaux de surface, mais ne semble pas s'y maintenir. Par contre, dans les couches de 100-200 m, il montre une certaine abondance. (Données de St. Augustin).

PARACALANIDAE

Paracalanus parvus (Claus)

Cette forme néritique est mondialement distribuée. Très eurytherme et euryhaline, elle constitue un des éléments caractéristiques des communautés néritiques. C'est le cas à Tuléar, où ce

petit calanide est rencontré pratiquement toute l'année, en compagnie de l'espèce voisine, *P. aculeatus*.

Paracalanus aculeatus Giesbrecht

Ce *paracalanus* est reconnu comme une forme néritique d'eaux tropicales et tempérées chaudes. C'est le mieux représenté des Copépodes dans la plupart des communautés néritiques tropicales (BJORNBERG 1963, FARRAN 1947).

Dans l'Océan Indien, il est cité en particulier sur les côtes orientales de l'Inde (GANAPATI et SHANTHAKUMARI 1961) où il est abondant toute l'année. Sur les côtes d'Afrique du sud, il se révèle également très abondant (DE DECKER 1963).

Dans les eaux de surface de Tuléar, c'est avec *Clausocalanus furcatus* le plus abondamment et régulièrement représenté des Copépodes.

Paracalanus crassirostris F. Dahl

Cette très petite espèce est, d'après BJORNBERG (1963) un excellent indicateur des eaux côtières, soumises à de grandes variations de salinité et de température.

De même qu'en Afrique du sud (DE DECKER 1963), la forme rencontrée à Tuléar est la *typica* (Früchtl). Elle est peu abondante, et n'apparaît qu'en octobre et en fin décembre dans les prélèvements étudiés ici, présentant, il est vrai, un caractère plus néritique que côtier, au sens où l'entend BJORNBERG.

Acrocalanus gracilis Giesbrecht.

Cette espèce représente un élément caractéristique des communautés néritiques de l'Indo-Pacifique. C'est le cas en particulier pour la Grande Barrière (FARRAN 1947). En Océan Indien, *A. gracilis* est présent toute l'année à Lawson's bay (GANAPATI et SHANTHAKUMARI 1961). Il est noté en de nombreux points du South Burma, des îles Nicobar (SEWELL 1947), de la côte du Madras, des Maldives (WOLFENDEN 1906) etc... .

Citée également en Afrique du Sud (CLEVE 1904, WOLFENDEN 1911), cette forme semble particulièrement abondante dans les eaux chaudes influencées par le courant des Aiguilles (DE DECKER 1963). Ce dernier auteur signale également qu'il a rencontré l'espèce à 100 miles à l'Ouest du Cap de Bonne Espérance, ce qui semble représenter sa localisation occidentale le plus extrême.

Dans les eaux superficielles de Tuléar, cette espèce est le représentant le plus abondant de son genre. Elle disparait en période froide, d'août à octobre.

Acrocalanus monachus Giesbrecht

Cette petite forme est également strictement Indo-Pacifique. Rare dans les eaux côtières, orientales de l'Inde (Lawson's bay), elle est citée pour la première fois en Afrique du sud par DE DECKER (1963). Elle est également très rare à Tuléar, où on la rencontre surtout pendant la période froide.

Acrocalanus gibber Giesbrecht

Comme les précédentes, il s'agit d'une forme néritique Indo-Pacifique (FARRAN 1949, WICKSTEAD 1961, GANAPATI et SHANTHAKUMARI 1961).

Sa répartition à Tuléar semble se limiter surtout aux périodes froides. Son abondance reste toujours très faible.

Acrocalanus andersoni Bowman ?

Cette espèce, recemment décrite sur la côte atlantique des Etats Unis ; a été depuis retrouvée dans le Pacifique équatorial par GRICE (1961).

Une forme qui semble devoir se rattacher à cette espèce a été souvent rencontrée dans le plancton de Tuléar.

Acrocalanus longicornis Giesbrecht

En Atlantique, cette espèce paraît bien représentée dans les eaux tropicales proches des côtes américaines (T. SCOTT 1912, FARRAN 1929). Ce dernier la trouve souvent en compagnie de *P.*

aculeatus, au voisinage de Rio de Janeiro. BJORNBERG (1963) estime que sa fréquence est la plus grande dans les eaux chaudes et salées, opinion que j'ai partagé (GAUDY 1963) en faisant de cette espèce une forme caractérisant dans le secteur envisagé, les eaux chaudes du courant du Brésil.

A. longicornis est cité en divers points de l'Océan Indien, mais pas encore, à ma connaissance, sur les rivages d'Afrique du Sud.

A Tuléar, c'est une forme rare, rencontrée surtout pendant la saison froide.

Calocalanus pavo (Dana)

Forme océanique de mers chaudes, mondialement distribuée, cette espèce est citée notamment en Afrique du Sud (CLEVE 1904, DE DECKER 1963).

Sa présence dans les eaux de Tuléar est rare et transitoire.

Calocalanus plumulosus (Claus)

Cette espèce océanique cosmopolite, mais en général plus rare que la précédente, n'a été capturée qu'une seule fois dans la station étudiée.

Calocalanus stylremis Giesbrecht

Océanique également, cette petite forme est citée, comme la précédente, près des côtes d'Afrique du Sud (DE DECKER 1963).

Elle est exceptionnelle dans les eaux côtières de Tuléar.

PSEUDOCALANIDAE

Clausocalanus arcuicornis (Dana)

Constituant habituel des communautés néritiques, de distribution mondiale, ce Copépode est, par rapport à l'espèce suivante, mieux représenté dans les eaux fraîches, de salinité moyenne. C'est ce que démontrent BJORNBERG (1963) pour les eaux brésiliennes, et les observations de nombreux auteurs qui remarquent sa prépondérance dans les eaux tempérées ou tempérées chaudes.

En Océan Indien, l'espèce est signalée en particulier dans les eaux de faible salinité de Lawson's bay, surtout en hiver (GANAPATI et SHANTHAKUMARI 1961), et dans les eaux côtières d'Afrique du sud (CLEVE, 1904, TANAKA 1960, DE DECKER 1963).

A Tuléar, *C. arcuicornis* est moins abondant et régulièrement distribué que *C. furcatus*. Les individus recueillis appartiennent pour la presque totalité à la forme *minor*.

Clausocalanus furcatus (Brady)

Très fréquente, cette espèce se rencontre aussi bien dans les eaux néritiques qu'océaniques, mais elle n'est dominante que dans des eaux de forte salinité (plus de 35°/$_{oo}$) et à température élevée. (BJORNBERG 1963). Dans les eaux tropicales salées, cette forme prédomine en général l'espèce *arcuicornis*.

Dans l'Océan Indien, elle est absente des zones soumises à des salinités trop faibles, comme Lawson's bay. Par contre, elle est abondante en Afrique du Sud (CLEVE 1904 DE DECKER 1963).

C. furcatus est à Tuléar l'élément le plus abondant et régulièrement présent du plancton.

Clausocalanus paululus Farran.

Cette petite forme, connue du golfe de Biscaye et du SW Pacifique (FARRAN 1926, 1949), est citée également par TANAKA 1960 près de Maurice. DE DECKER (1963) la signale dans les eaux sud-africaines en une seule station.

A Tuléar, l'espèce, rare, apparaît surtout en juin et en septembre.

AETIDEIDAE

Aetideus bradyi A. Scott.

Cette espèce psichrophile présente en général une répartition meso-pélagique. Elle a été retrouvée en surface à Tuléar le 27 août, ce qui correspond à l'époque du minimum thermique annuel.

EUCHAETIDAE

Euchaeta marina (Prestandrea)

Espèce cosmopolite de mers tempérées et chaudes, cette forme est, d'après les notes écologiques de BJORNBERG (1963), caractéristique des eaux superficielles chaudes et salées de la Province Océanique ou néritique, mais évitant les eaux côtières. La tolérance thermique de l'espèce est cependant assez large, puisque, d'après WILSON 1950, l'espèce n'est pas rare devant les côtes d'Alaska.

En Océan Indien, elle est citée notamment à Lawson's bay (GANAPATI et SHANTHAKUMARI 1961), aux Ceylon Pearl banks (SEWELL, A. SCOTT), aux Maldives et Laquedives (WOLFENDEN 1906), près de Durban (BRADY 1913), dans le courant des Aiguilles (CLEVE 1904).

A Tuléar, l'espèce est représentée en surface toute l'année, mais surtout à l'état de copépodites 4 ou 5. Les adultes semblent en effet se cantonner dans des eaux plus profondes : c'est ainsi qu'à St. Augustin, au sud de Tuléar, on les retrouve avec une certaine abondance entre 100 et 300 mètres (observations personnelles).

Euchaeta longicornis Giesbrecht

Forme tropicale de caractère strictement Indo-Pacifique, cette espèce est citée en particulier au cœur du Pacifique (GRICE 1961), à la Grande Barrière (FARRAN 1929) dans l'Archipel Malais (CLEVE 1901, A. SCOTT 1909).

En Océan Indien, CLEVE 1904 la signale à l'est de l'Afrique du sud, localisation qui n'a pas été reconfirmée par les auteurs ayant étudié le même secteur : l'espèce semble en effet assez rare, dans la zone occidentale de l'Océan Indien.

Dans les eaux de surface de la région de Tuléar, *E. longicornis* n'apparaît que rarement et de façon transitoire, ce qui semble dû au caractère océanique de l'espèce.

Euchaeta wolfendeni A. Scott.

Il s'agit comme la précédente d'une forme Indo-Pacifique, décrite sur du matériel de l'Archipel malais. De caractère océanique, elle est présente en Afrique du sud orientale, probablement apportée par le courant des Aiguilles (DE DECKER 1963).

Rare dans les eaux de surface de Tuléar, sauf pendant la saison froide, elle semble, en compagnie de l'espèce précédente, mieux distribuée dans les eaux sub-superficielles, vers 200 mètres (Stations de St. Augustin et du large de Tuléar ; observations personnelles).

SCOLECITHRIDAE

Scolecithrix danae (Lubbock)

Espèce cosmopolite, habituellement rencontrée dans les eaux superficielles de la Province Océanique, ce copépode acquiert son maximum d'importance dans les eaux chaudes et salées. Il est à ce titre indicateur du courant du Brésil (BJORNBERG 1963 ; GAUDY 1963). On le rencontre également dans la plupart des grands courants chauds océaniques (SEWELL 1948). Cité en de nombreux points du Pacifique, il est en particulier noté par GRICE (1961) comme un des éléments les plus fréquents du plancton de la zone pacifique intéressée par le courant équatorial.

Dans l'Océan Indien, il est rare dans les zones côtières ou trop dessalées, comme Lawson's bay (GANAPATI et SHANTHAKUMARI 1961), mais présent en Afrique du sud (CLEVE 1904, WOLFENDEN 1911, BRADY 1913, DE DECKER 1963), où il semble apporté par le courant des Aiguilles.

S. danae est bien représenté à Tuléar pendant la saison froide, époque à laquelle beaucoup d'espèces océaniques atteignent les eaux de la Province néritique.

Scolecithrix bradyi Giesbrecht

Océanique également, mais rencontrée le plus souvent dans des récoltes sub-superficielles, contrairement à la précédente, cette espèce est en général beaucoup plus rare (A. SCOTT 1909).

Elle n'est présente à Tuléar que pendant la saison fraîche, et toujours avec une abondance très réduite.

Scolecithricella ovata Farran.

Comme la plupart des représentants de son genre, ce Copépode est habituellement récolté en profondeur, ce qui laisse supposer une certaine psichrophilie. On ne le trouve dans les eaux de surface de Tuléar que dans un prélèvement de juillet, époque du minimum thermique.

Scolecithricella minor (Brady)

Comme la précédente, cette espèce cosmopolite de répartition mésopélagique a été recueillie en surface en période froide, le 27 août.

TEMORIDAE

Temora discaudata Giesbrecht

Bien que très voisine de *T. stylifera*, à distribution très large, cette espèce est localisée essentiellement dans le Pacifique et l'Océan Indien. WILSON (1950) la cite cependant devant les côtes d'Argentine. Si aucune confusion n'a été faite il s'agirait là de son unique signalisation dans l'Océan Atlantique.

FARRAN (1949) la considère, à la Grande Barrière, comme une espèce indicatrice d'eaux à basse salinité.

T. discaudata est cité dans de nombreuses communautés néritiques tropicales de l'Océan Indien (Iles Nicobar, Ceylon Pearl bank : SEWELL 1947, Maldives et Laquedives : WOLFENDEN 1906 ; Lawson's bay : GANAPATI et SHANTHAKUMARI 1961). CLEVE (1904) et DE DECKER (1963) capturent l'espèce assez communément dans les eaux chaudes du courant des Aiguilles.

A Tuléar, l'espèce est assez fréquente, mais peu abondante. Elle semble absente ou rare de septembre à novembre.

Temora turbinata (Dana)

Il s'agit d'une forme côtière répandue dans les eaux tropicales des trois grands océans. En Océan Indien, elle est notamment citée sur les côtes de l'Inde (SEWELL (1947), MENON (1931), GANAPATI et SHANTHAKUMARI (1961), près de Durban, sous le nom de *T. africana* (BRADY 1914), entre Durban et Le Cap (DE DECKER 1963), où elle est assez commune.

Au contraire, l'espèce est rare à Tuléar, où elle n'est guère représentée que par des individus isolés, au mois de décembre.

METRIDIIDAE

Pleuromamma abdominalis (Lubbock)

Forme méso-pélagique affectée de puissantes migrations verticales, ce gros Calanide est habituellement trouvé dans les eaux océaniques tropicales et les eaux néritiques influencées par l'arrivée d'eaux du large (BJORNBERG 1963).

DE DECKER (1963) le signale en Afrique du Sud, à l'occasion de pêches nocturnes.

Il est présent à Tuléar en de rares occasions (4 avril 6 août). Sa localisation en profondeur est par contre beaucoup plus habituelle. (Prélèvements de St. Augustin ; observations personnelles).

Pleuromamma gracilis (Claus)

Comme la précédente, cette espèce se situe généralement en profondeur, mais atteint la surface la nuit. Les auteurs s'accordent à en faire une forme relativement Psichrophile (BJORNBERG 1963).

Citée en Afrique du sud par CLEVE et DE DECKER, l'espèce, fréquente à Tuléar en profondeur, n'apparaît en surface de jour que dans un prélèvement de la période froide.

Pleuromamma robusta (F. Dahl)

Capturée généralement à des profondeurs relativement importantes (plus de 400 m), cette espèce n'en est pas moins sujette à des migrations nycthémérales pouvant l'amener en certains cas en surface. CLEVE et DE DECKER en font mention à l'est de l'Afrique du sud. Le premier la capture au niveau de 900 m. Le second, en surface, lors d'un prélèvement nocturne.

A Tuléar, quelques individus appartenant à cette espèce sont apparus en surface le 5 juillet, en période froide.

CENTROPAGIDAE

Centropages furcatus (Dana)

Ce Copépode est un des éléments caractéristique des communautés néritiques des mers chaudes (BJORNBERG 1963 pour les côtes du Brésil ; FLEMINGER 1959 pour le Golfe du Mexique ; BAINBRIDGE 1960, pour le Golfe de Guinée). Dans les eaux de Dakar (GAUDY et SEGUIN 1964), l'espèce est caractéristique des eaux de surface, pendant la période juillet-mi-décembre, à des températures supérieures à 24° et des salinités fluctuant entre 33,5 et 36°/$_{oo}$. Ce caractère d'euryhalinité avait déjà été noté par BJORNBERG devant les côtes brésiliennes.

L'espèce est fréquente également dans le Pacifique, au voisinage des côtes. FARRAN (1949) lui assigne à la Grande Barrière un maximum d'abondance net en avril mai, le minimum se situant en octobre-novembre. GRICE (1961) ne cite pas cette forme dans les eaux océaniques du Pacifique équatorial, alors que les espèces du large *Centropages gracilis, elongatus* et *calaninus* n'y sont pas rares.

Dans l'Océan Indien, *C. furcatus* est présente toute l'année dans les eaux peu salées de Lawson's bay (GANAPATI et SHANTHAKUMARI 1961). WOLFENDEN (1906) note sa fréquence dans le matériel des Maldives et Laquedives. CLEVE (1904), BRADY (1913) et DE DECKER la signalent dans le plancton côtier d'Afrique du Sud. Ce dernier auteur indique que la forme se trouve dans les eaux influencées par le courant des Aiguilles.

A Tuléar, *C. furcatus* est présent une grande partie de l'année. Il n'atteint jamais une grande abondance. Il est rare ou absent de fin août à novembre.

Centropages violaceus (Claus)

Centropages gracilis (Dana)

Centropages calaninus (Dana)

Centropages elongatus Giesbrecht

Ces espèces sont des formes océaniques de mers chaudes.

La première de ces espèces est assez fréquente en Atlantique. BJORNBERG (1963) la trouve fréquemment dans les eaux chaudes et salées du courant du Brésil. Elle peut être considérée à Marseille comme une espèce caractérisant l'intrusion d'eaux atlantiques en Méditerranée (GAUDY 1963).

Les autres espèces citées sont signalées dans les eaux équatoriales du Pacifique (GRICE 1962) et dans les eaux océaniques des mers tropicales atlantiques ou indiennes. DE DECKER les cite dans les eaux sud-africaines influencées par le courant des Aiguilles.

Leur présence dans les eaux côtières de Tuléar est exceptionnelle et dénote probablement l'arrivée d'eaux du large.

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DIAPTOMIDAE

Pseudodiaptomus sp.

Un *pseudodiaptomus* non encore identifié à été remarqué dans plusieurs prélèvements (décembre, janvier), à une époque où les eaux présentaient une salinité diminuée, à la suite de grandes pluies. D'après les données de BJORNBERG (1963), ce genre est strictement côtier, et par celà, très eurytherme et euryhalin. Cette stenoecie se retrouve effectivement quand on examine la signalisation du genre dans des aires côtières sujettes à fortes variations écologiques, telles l'embouchure du Tocantin (F. DAHL) 1894, le Brésil dans les baies ou les lagunes (BJORNBERG 1963, carte 1) les zones côtières de l'Inde (SEWELL 1949), la région du banc des Aiguilles (CLEVE 1904, DE DECKER 1963).

Il est probable que ce genre est habituellement présent à Tuléar, dans les zones les plus éloignées de l'influence du large, et qu'il peut s'étendre lorsque la dessalure est suffisante. L'examen ultérieur du matériel des autres stations permettra peut-être de confirmer cette idée.

LUCICUTIIDAE

Lucicutia flavicornis (Claus)

Cette forme océanique cosmopolite présente le plus souvent un caractère *mésopélagique*. On la rencontre donc surtout dans les eaux sub-superficielles pendant la journée. Elle atteint la surface la nuit. D'après BJORNBERG, elle semble éviter les eaux de température supérieure à 24°, devant les côtes du Brésil, et serait une caractéristique des eaux de transition sub-tropicales. En fait, sa présence dans la zone néritique indique souvent un renouvellement de la faune par arrivée d'eaux sub-superficielles, plus froides. C'est en particulier le cas dans le Golfe de Marseille (GAUDY 1962).

Lucicutia flavicornis, qui est absente du matériel de surface récolté par DE DECKER en Afrique du Sud, est par contre citée dans le même secteur par CLEVE (1904), dans des pêches profondes.

A Tuléar, l'espèce est présente sporadiquement en surface, particulièrement au cours de la période froide.

Lucicutia ovalis (Giesbrecht)

Plus rare que la précédente, cette forme paraît, d'après les données de divers auteurs, avoir une distribution plus profonde (SEWELL 1948).

Elle n'apparaît qu'une seule fois, en période froide, dans les eaux de Tuléar.

HETERORHABDIDAE

Heterorhabdus papilliger (Claus)

Comme les précédentes, cette forme évite en général les eaux de surface, mais présente des migrations nycthémérales importantes.

Elle n'a été capturée en surface à Tuléar qu'une seule fois, le 27 août, à l'époque du minimum thermique.

AUGAPTILIDAE

Haloptilus longicornis (Claus)

Il s'agit également d'une espèce cosmopolite vivant ordinairement vers 200 mètres de profondeur et présentant des migrations verticales importantes. Elle serait selon BJORNBERG (1963) un indicateur d'eaux salées et chaudes de la Province Océanique, mais elle reste fréquente dans les eaux sub-tropicales.

Presque constante à Tuléar en profondeur, elle n'est que rarement récoltée dans les eaux néritiques superficielles.

Haloptilus mucronatus (Claus)

Haloptilus oxycephalus (Giesbrecht)

Haloptilus spiniceps (Giesbrecht)

Enaugaptilus hecticus (Giesbrecht)

Toutes ces espèces bathypélagiques n'ont été capturées qu'exceptionnellement dans les eaux de surface de Tuléar.

ARIETELLIDAE

Metacalanus aurivilli Cleve

Cette espèce n'était jusque là connue que dans les mers de l'Archipel malais (CLEVE 1901) et sur les côtes de l'Inde (GANAPATI et SHANTHAKUMARI 1961).

Quelques individus sont présents à Tuléar, le 17 septembre.

Paraugaptilus mozambicus Gaudy

Récemment décrite sur du matériel de profondeur de St. Augustin (GAUDY 1965), cette forme rare apparaît quelque fois en surface (19 juin, 5 mars). Tous les individus capturés sont des copépodites des stades 4 ou 5.

CANDACIIDAE

Candacia pachydactyla (Dana)

Candacia aethiopica (Dana)

Candacia bispinosa (Claus)

Candacia truncata (Dana)

Candacia catula (Giesbrecht)

Candacia curta (Dana)

Candacia simplex (Giesbrecht)

Toutes ces espèces sont des formes du large. *C. catula* est strictement Indo-Pacifique. *C. curta* et *truncata* sont limitées aux régions chaudes des trois océans. *C. simplex, pachydactyla, aethiopica, bispinosa* sont cosmopolites et de tendance plus eurytherme. (BJORNBERG 1963). On constate dans le genre *Candacia* une tendance marquée à "préférer" les hautes salinités.

Ces diverses espèces apparaissent temporairement dans le plancton de Tuléar, mais semblent se maintenir difficilement dans des eaux néritiques de caractère trop fluctuant. Il nous faut signaler l'absence de deux formes représentées en Afrique du Sud, qui sont de tendance cryophile (*C. armata* (Boeck) et *C. bipinnata* (Giesbrecht)).

PONTELLIDAE

Calanopia thompsoni A. Scott.

Le genre *Calanopia* caractérise de nombreuses communautés néritiques de mers chaudes (BJORNBERG 1963 Table IV). *C. Thompsoni* est limité à la région Indo-Pacifique. C'est un élément fréquent dans les communautés néritiques japonaises (YAMAZI 1958), malaises (A. SCOTT 1909) ou indiennes (SEWELL 1948 GANAPATI et SHANTHAKUMARI 1961).

Cette espèce n'est pas signalée sur les côtes d'Afrique du sud. C'est par contre une des formes les mieux représentées du plancton de surface de Tuléar.

Calanopia elliptica (Dana)

Il s'agit aussi d'une espèce Indo-Pacifique, connue en particulier de la Grande Barrière (FARRAN 1936), des mers indiennes (SEWELL 1948, GANAPATI et SHANTHAKUMARI 1961), du canal de Suez (GURNEY 1927).

Moins abondante que la précédente, l'espèce apparaît à Tuléar, présentant un léger maximum d'abondance en avril. Il est à noter que FARRAN (1949) signale dans les eaux de la Grande Barrière, un maximum analogue, à la même époque.

Calanopia minor A. Scott

Ce petit Calanide, signalé à Lawson's bay, et en Afrique du sud, demeure exceptionnel à Tuléar.

Labidocera acuta (Dana)

Cette espèce tropicale est une caractéristique de communautés néritiques. FARRAN la cite dans les eaux de la Grande Barrière (1949) où son maximum d'abondance se situe en janvier. Elle est fréquente dans l'archipel malais (CLEVE 1901 ; A. SCOTT 1909, VORONINA 1962) dans les mers de l'Inde (SEWELL 1948), GAN APATI 1961), les Maldives et Laquedives (WOLFENDEN 1906). CLEVE, WOLFENDEN, BRADY, DE DECKER la citent à l'est de l'Afrique du sud.

A Tuléar, elle acquiert son maximum d'importance en janvier-février, époque du maximum thermique.

Labidocera minuta Giesbrecht

Autre forme néritique tropicale, mais limitée à l'Indo-Pacifique, cette petite espèce accompagne souvent la précédente. FARRAN (1949) lui assigne dans les eaux de la Grande Barrière un maximum en décembre, avec des pointes d'abondance en février et avril. Elle est connue dans diverses régions septentrionales de l'Océan Indien (SEWELL 1949, WOLFENDEN 1906) DE DECKER (1963) la cite à l'est de l'Afrique du Sud.

A Tuléar, elle est plus abondante pendant l'été austral.

Labidocera acutifrons (Dana)

Cette forme cosmopolite de mers chaudes paraît être, contrairement à la plupart des représentants de son genre, une espèce océanique (YAMAZI 1958). Dans le Pacifique, SHERMAN KENNETH (1963) l'associe avec les N. P. C. (north Pacific central waters). Dans l'Océan Indien, on la rencontre parfois transitoirement dans les eaux néritiques, comme à Lawson's bay (GANAPATI et SHANTHAKUMARI 1961). BJORNBERG (1963) qui cite l'espèce au large des côtes du Brésil, fait remarquer que son environnement optimum est celui de la mer-ouverte, sans aucune influence limimitante de salinité.

A Tuléar, l'espèce est rare et n'apparaît que dans des prélèvements de juin-juillet, en compagnie d'autres espèces océaniques.

Labidocera laevidentata (Brady)

Cette forme Indo-Pacifique semble être d'après les données connues une espèce néritique. (FARRAN 1949 ; SEWELL 1948). Elle est cependant très rare à Tuléar.

Labidocera kroyeri (Brady)

Il s'agit d'une espèce cosmopolite de mers chaudes. Quelques individus, très rares, semblent former à Tuléar une variété nouvelle qui sera précisée ultérieurement.

Labidocera madurae A. Scott.

Ce copépode, décrit sur du matériel de l'Archipel Malais doit être considéré comme une forme côtière. SHERMAN (1963), en effet, la signale en abondance près des Iles Necker, dans la région des Hawaï et remarque que l'espèce n'a cependant été récoltée que dans deux stations. L'auteur note qu'elle avait été déjà trouvée en abondance dans des zones proches d'îles (SCOTT 1909, SEWELL 1929, E. C. JONES personnal communication), et pense que cette aggrégation dépend plus étroitement de l'influence insulaire que de la "North pacific central water" dans laquelle elle a été récoltée.

A Tuléar, la forme semble se maintenir et se reproduire dans les eaux côtières, particulièrement en saison chaude. Les femelles présentent certaines différences avec la forme type (légère asymétrie de la cinquième paire de pattes, protubérances du segment génital plus anguleuses).

Pontellina plumata (Dana)

Cette espèce océanique cosmopolite est largement répandue dans les eaux chaudes. BJORNBERG (1963) remarque devant les côtes brésiliennes sa préférence pour les eaux très salées (plus de 36°/$_{oo}$) et de température supérieure à 22° C. TSURUTA (1962) la classe parmi les espèces indicatrices d'eaux chaudes dans l'Indo-Pacifique. *Pontellina plumata* est fréquente dans les eaux océaniques du Pacifique, dans la N. P. C. Water (SHERMAN 1963). Elle peut cependant tolérer des salinité plus basses que *Labidocera acutifrons*, qui caractérise cette même eau.

CLEVE (1904), BRADY (1913), DE DECKER (1963) la signalent à l'est de l'Afrique du Sud, dans les régions intéressées par le courant des Aiguilles.

A Tuléar, *P. plumata* n'est pas rare dans les eaux de surface, à diverses époques de l'année. Son abondance reste toujours faible.

ACARTIIDAE

Acartia (odontacartia) amboinensis Carl

Cette forme Indo-Pacifique a été retrouvée par STEUER (1923) en deux stations (Archipel malais, Aden) SEWELL la signale pour sa part en Océan Pacifique, et en divers points du nord de l'Océan Indien. L'espèce est également présente sur les côtes orientales d'Afrique du Sud (DE DECKER 1963). Cet auteur fait remarquer en outre que BRADY avait cité à Durban une forme très voisine, *Acartia erythrea* Giesbrecht, forme répandue dans l'Indo-Pacifique, mais qui n'a jamais été retrouvée depuis dans le sud-ouest de l'Océan Indien, ce qui laisse supposer une confusion possible entre les deux espèces, que seul un examen attentif permet de différencier.

A Tuléar, *A. amboinensis* est une forme des plus communes, particulièrement pendant l'été austral.

Acartia (acanthacartia) fossae Gurney

Cette forme, très proche de *Acartia bifilosa* avait été considérée par GURNEY (1927) comme une originaire du sud du Canal de Suez. Des recherches ultérieures ont permis d'élargir sa distribution. VAISSIERE 1954 cite l'espèce dans les Tuamotu, sous le nom de *A. ransoni*. GRICE (1964) la retrouve dans du matériel des Iles de la Société et Tuamotu, et estime que *A. hamata* Mori décit en mer de Chine doit entrer en synonymie avec *A. fossae*.

A Tuléar, cette forme est surtout abondante d'octobre à décembre, mais se retrouve pratiquement à toutes les saisons.

Acartia (planktacartia) negligens Dana

Espèce océanique mondialement distribuée, elle apparaît d'après les données de BJORNBERG (1963) comme fréquente dans les eaux à plus de 35°/$_{oo}$ de salinité, et de température assez basse. De ce fait, l'espèce caractérise surtout les eaux sub-tropicales.

WOLFENDEN (1911), TANAKA (1960), DE DECKER (1963) la citent dans le sud-ouest de l'Océan Indien.

A Tuléar, cette forme est souvent présente dans les eaux de surface. Elle est assez abondante de septembre à décembre.

Acartia (planktacartia) danae Giesbrecht

Il s'agit aussi d'une espèce océanique cosmopolite, mais rencontrée plus souvent dans des eaux tempérées. Elle est habituellement plus fréquente dans les couches superficielles.

Citée par CLEVE (1904) en Afrique du sud, on la trouve souvent à Tuléar en compagnie de l'espèce précédente.

Tortanus barbatus (Brady)

Comme les autres représentants du genre, il s'agit d'une forme néritique rencontrée dans de nombreuses communautés côtières tropicales (archipel malais, mer rouge, etc).

A Tuléar, elle est rare, et de distribution éparse (avril-mai, août-septembre).

Tortanus gracilis (Brady)

C'est la plus répandue des espèces du genre. Dans le plancton de la Grande Barrière, FARRAN (1948) observe des maxima d'abondance de mars à juin, le minimum se situant de septembre à novembre. A Lawson's bay, elle apparaît en mars, et de mai à juillet, aux époques du maximum de salinité (plus de 30°/$_{oo}$).

A Tuléar, par contre, la plus grande fréquence de l'espèce se note de janvier à mars, saison où la salinité en surface est très fluctuante, bien que supérieure à 32°/$_{oo}$).

Tortanus forcipatus (Giesbrecht)

Voisine de la précédente, cette espèce est à Tuléar beaucoup plus rare, n'ayant été capturée que dans trois prélèvements.

Tortanus A

Tortanus B

Tortanus C

Ces trois formes n'ont pu encore être déterminées avec certitude.

OITHONIDAE

Oithona helgolandica Claus

Il s'agit d'une forme néritique mondialement distribuée et de caractère particulièrement eurytherme. Elle est très fréquente dans les eaux tempérées, en particulier.

Présente toute l'année à Tuléar, elle s'y montre peu abondante.

Oithona plumifera Baird

Cette espèce cosmopolite est au contraire une forme océanique de mers chaudes, préférentielle des hautes salinités (BJORNBERG 1963). Elle n'est pas rare dans les eaux de Tuléar.

Oithona linearis Giesbrecht

Forme peu abondante, mais assez souvent présente dans nos prélèvements.

Oithona robusta Giesbrecht

Relevée par BJORNBERG dans les eaux chaudes et très salées du Brésil, cette espèce semble être un indicateur d'eaux du large. On ne la trouve à Tuléar que rarement.

Oithona brevicornis Giesbrecht

Il s'agit, d'après BJORNBERG d'une forme d'eaux côtières ou même saumâtres, d'abondance très irrégulière. Elle semble très rare dans la station étudiée.

Oithona oculata Clève

Espèce d'eaux chaudes et salines, d'après BJORNBERG, cette forme paraît avoir souvent une distribution sub-superficielle, dans la région de Tuléar (observations personnelles). Elle est peu abondante dans les stations de surface.

Oithona rigida Giesbrecht

Rencontrée par DE DECKER (1963) dans les eaux influencées par le courant des Aiguilles, cette espèce n'apparaît dans le biotope étudié qu'en fin de saison fraîche, en compagnie d'autres formes océaniques.

ONCAEIDAE

Oncaea venusta Philippi

Cette espèce cosmopolite est, selon BJORNBERG (1963) un bon indicateur des eaux tropicales et subtropicales devant les côtes du Brésil.

A Tuléar, cette forme est très fréquemment rencontrée dans les eaux côtières.

Oncaea media Giesbrecht

Plus strictement localisé aux eaux côtières, ce copépode est à Tuléar le représentant le plus abondant de son genre, et souvent de l'ensemble de la communauté.

Oncaea conifera Giesbrecht

De caractère plus cryophile que les espèces précédentes ce cyclopoïde est souvent rencontré dans les eaux sub-superficielles. Son abondance, en surface, à Tuléar, reste toujours limitée.

SAPPHIRINIDAE

Sapphirina opalina Dana - *darwini* Haeckel

Sapphirina scarlata Giesbrecht - *nigromaculata* Claus

Sapphirina metallina Dana

Copilia mirabilis Dana

Copilia vitraea Haeckel

Copilia quadrata Dana

Sapphirines et copilies sont des formes océaniques de mer chaude. Leur présence dans les eaux côtières de Tuléar est toujours éphémère. Très souvent accompagnée de salpes ou de méduses, elle indique une arrivée temporaire d'eaux du large.

CORYCAEIDAE

Corycaeus speciosus Dana

Cette forme d'eaux chaudes et salées est considérée par BJORNBERG (1963) comme un indicateur typique des eaux océaniques chaudes tropicales, quand on la rencontre en grand nombre.

Elle est assez fréquente à Tuléar, mais toujours en abondance réduite.

Corycaeus crassiusculus Dana

Forme circum-tropicale à caractère océanique, cette espèce accompagne souvent la précédente dans les eaux de Tuléar.

Corycaeus (agetus) flaccus Giesbrecht

Il s'agit d'une forme cosmopolite, classée par BJORNBERG parmi les subtropicales.

Elle est très rare dans nos prélèvements.

Corycaeus (agetus) limbatus

Corycaeus (agetus) typicus

Appartenant au même environnement que *C. flaccus*, elles sont considérées par BJORNBERG comme un index d'arrivée d'eau du large devant les côtes du Brésil.

Elles ne sont jamais abondantes dans les eaux néritiques de Tuléar.

Corycaeus (onychocorycaeus) giesbrechti F. Dahl

Corycaeus (onychocorycaeus) latus Dana

Corycaeus (onychocorycaeus) ovalis Claus

Corycaeus (onychocorycaeus) gracilicaudatus Giesbrecht

Le genre *onychocorycaeus* est étroitement localisé aux eaux côtières. Toutes ces espèces sont bien représentées dans les eaux de Tuléar, particulièrement la première citée.

Corycaeus (dithrichocorycaeus) africanus F. Dahl

Ce sous genre est également à répartition côtière, particulièrement dans les aires à faible salinité. Il est rare à Tuléar.

Corycaeus (urocorycaeus) longistylis Dana

Espèce à tendance océanique, elle disparaît du milieu néritique lorsque la salinité est amoindrie.

Corycella gracilis Dana

Corycella gibbula Giesbrecht

Corycella carinata Giesbrecht

Les représentants de ce genre d'eaux oligothrophiques se rencontrent sporadiquement dans les eaux de Tuléar. Le premier est le plus abondant et régulièrement distribué.

ECTINOSOMIDAE

Microsetella rosaea (Dana)

Microsetella norvegica (Boeck)

Ces petites formes côtières (YAMAZI 1956) présentent en général une répartition différente. L'espèce *rosaea* est en effet une forme de surface, tandis que *norvegica*, souvent récoltée en profondeur, semble adaptée à des plus basses températures ;

Elles n'apparaissent à Tuléar que dans un seul prélèvement, pour la station étudiée.

MACROSETELLIDAE

Macrosetella gracilis (Dana)

Forme cosmopolite d'eaux chaudes et salées, elle est citée en Afrique du Sud comme particulièrement abondante dans le courant des Aiguilles (DE DECKER 1963). BJORNBERG (1963) en fait également un indicateur du courant du Brésil.

Macrosetella est assez fréquent en surface à Tuléar.

Miracia efferata Dana

Il s'agit également d'une espèce océanique tropicale. Elle n'a été retrouvée à Tuléar que dans un prélèvement, le 28 novembre.

TACHYDIIDAE

Euterpina acutifrons (Dana)

Ce petit harpacticoïde est mondialement distribué dans les eaux côtières. Il est très euryhalin et eurytherme (YAMAZI 1956).

Dans la station qui fait l'objet de cette étude, cette forme reste cependant assez rare. Elle est beaucoup plus commune dans les zones proches de l'embouchure de l'Onilahi, au sud. (observations personnelles), où la salinité est réduite.

DISCUSSION

1) COMPOSITION DE LA COMMUNAUTE NERITIQUE

Si l'on se réfère au tableau de présence-abondance placé en appendice, on remarque que la population de copépodes peut se répartir en plusieurs groupes :

espèces très fréquentes et abondantes :

Clausocalanus furcatus
Paracalanus aculeatus
Oncaea media
Oncaea venusta
Undinula vulgaris
Paracalanus aculeatus
Clausocalanus furcatus
Calanopia thompsoni
Acartia amboinensis
Acartia fossae
Oncaea media
Oncaea venusta

espèces fréquentes et moins abondantes

Calanus minor
Canthocalanus pauper
Eucalanus subcrassus
Paracalanus parvus
Acrocalanus gracilis
Clausocalanus arcuicornis

espèces moins fréquentes

Eucalanus mucronatus
Eucalanus subtenuis
Euchaeta marina
Temora discaudata
Centropages furcatus
Labidocera acuta
Labidocera minuta
Onychocorycaeus sp.

Il n'a pas été observé chez les espèces du premier groupe, de répartition saisonnière bien nette ; tout-au-plus, peut-on remarquer une absence ou une rareté plus grande de certaines formes relativement sténohalines, pendant l'été austral, caractérisé par une certaine pluviosité.

Acartia amboinensis et *Acartia fossae* montrent par contre des préférences écologiques distinctes, la première forme étant plus abondante de janvier à septembre, la seconde, d'octobre à décembre.

Certaines espèces du second groupe présentent des irrégularités de distribution plus évidentes. (maximum de *Calanus minor* en mai-juin, minimum en hiver austral de *Canthocalanus* et *Acrocalanus*).

Enfin, il faut noter la répartition de *Labidocera acuta* et *L. minuta*, limitée à la période décembre-mars.

La plupart de ces espèces ou de ces genres sont, nous l'avons vu, communs dans les zones côtières des mers chaudes.

C'est ainsi que FARRAN (1949) cite dans les eaux côtières de la Grande Barrière *Paracalanus aculeatus, Oncaea, Oithona, Canthocalanus pauper, Acrocalanus, Eucalanus subcrassus, Undinula vulgaris, Centropages furcatus, Temora discaudata, Clausocalanus furcatus, Tortanus gracilis, Labidocera acuta* et *minuta*, soit sensiblement les mêmes espèces que celles rencontrées à Tuléar.

Cette analogie de la composition spécifique des formes néritiques tropicales a été mise en évidence par BJORNBERG (1963) qui fait remarquer la fréquence des genres *Centropages, Temora, Acartia, Labidocera, Paracalanus, Oithona, Oncaea, Corycaeus, Pseudodiaptomus, Euterpina* et *Microsetella*. Il faut ajouter à cette liste certaines formes propres aux aires tropicales : *Tortanus, Calanopia, Eucalanus*.

Dans la partie nord de l'Océan Indien, l'existence d'eaux côtières de basse salinité peut être néfaste à la présence de certaines formes peu euryhalines, telles *Calanopia thompsoni* et *Undinula vulgaris*. C'est en particulier le cas à Lawson's bay où la salinité peut descendre jusqu'à 28°/$_{oo}$ (GANAPATI et SHANTHAKUMARI 1961). Il est fréquent par contre de voir dans ces eaux des genres très euryhalins tels les *Pseudodiaptomus*. *Schmackeria* et *Euterpina* dont la présence dans les eaux salées de Tuléar demeure exceptionnelle.

La station côtière qui fait l'objet de cette étude possède donc une population néritique typique. Mais, la proximité relative des fonds moyens, par suite de l'étroitesse du plateau continental, et l'existence d'un courant océanique d'origine sud-équatoriale, sont la cause d'arrivées périodiques de faune océanique. Les eaux du large vectrices de cette faune peuvent être mises en évidence par leur transparence plus grande, leur couleur bleue s'opposant au vert-jaunâtre des eaux côtières, leur température souvent plus basse, leur salinité plus forte, ainsi qu'il apparaît dans les premiers dosages effectués à ce jour.

Ainsi, le 27 décembre, on relève, corrélativement à un abaissement de température de plus d'un degré centigrade en surface, et de près de 2°,5 C à 8 mètres, et à une légère augmentation de la transparence, l'arrivée des espèces suivantes :

Undinula darwini
Rhincalanus cornutus
Mecynocera clausi
Aetideus bradyi
Euchaeta marina
Euchaeta longicornis
Haloptilus longicornis
Haloptilus mucronatus
Candacia aethipica
Candacia catula
Candacia simplex
Acartia negligens
Acartia danae
Oithona plumifera
Oithona linearis
Macrosetella gracilis
Sapphirina scarlata
Copilia mirabilis

Le mois d'avril a été marqué par une chûte très rapide de la température. Le 4 et le 27, les valeurs relevées au disque de Secchi sont respectivement de 8,5 m et 13 m. On constate à ce moment là la présence des espèces océaniques suivantes :

Undinula darwini
Calanus gracilis
Rhincalanus cornutus
Mecynocera clausi
Eucalanus mucronatus
Euchaeta wolfendeni
Scolecithrix danae
Pleuromamma abdominalis
Centropages violaceus
Centropages gracilis
Centropages elongatus
Haloptilus longicornis
Haloptilus oxycephalus
Acartia danae
Acartia negligens
Macrosetella gracilis
Corycella gracilis

La période du 19 juin au 6 août (hiver austral) est remarquable par la fréquence d'espèces du large. Les eaux sont claires (20 mètres le 19 juin) et fraîches (22 à 23.40° C).

On rencontre à cette époque les espèces suivantes :

Undinula darwini	*Scolecithricella ovata*
Undinula caroli	*Lucicutia flavicornis*
Calanus tenuicornis	*Paraugaptilus mozambicus*
Eucalanus mucronatus	*Candacia* 5 espèces
Eucalanus crassus	*Labidocera acutifrons*
Eucalanus elongatus	*Pontellina plumata*
Rhincalanus cornutus	*Oncaea conifera*
Rhincalanus nasutus	*Sapphirina* 3 espèces
Euchaeta longicornis	*Copilia* 3 espèces
Euchaeta wolfendeni	*Corycaeus speciosus*
Scolecithrix danae	*Corycaeus crassiusculus*
Scolecithrix bradyi	

Enfin, à la date du 27 août, on peut noter un afflux d'espèces inhabituelles aux eaux néritiques :

o *Calanus gracilis*	o *Enaugaptilus hecticus*
o *Eucalanus attenuatus*	o *Heterorhabdus papilliger*
Rhincalanus cornutus	*Candacia* 4 espèces
Mecynocera clausi	*Labidocera acutifrons*
o *Euaetideus bradyi*	*Acartia danae*
Euchaeta longicornis	*Oithona linearis*
Scolecithrix danae	*Oithona rigida*
o *Pleuromamma gracilis*	*Corycaeus speciosus*
o *Lucicutia ovalis*	*Corycaeus crassiusculus*
o *Haloptilus longicornis*	*Corycaeus limbatus*
o *Haloptilus spiniceps*	*Corycella gracilis*

Il est à signaler que beaucoup d'espèces citées ci-dessus sont des formes mésopélagiques à tendance froide, présentant habituellement une abondance maximum entre 200 et 400 mètres. Ces espèces (marquées d'un cercle sur la liste qui précède) sont surtout abondantes à l'époque du minimum thermique.

Il semble en fait que les eaux vectrices de cette faune soient constituées d'un mélange d'eaux superficielles du large et d'eaux plus profondes, ce qui expliquerait la chûte de température observée à l'occasion de leur arrivée. Une étude ultérieure des prélèvements faits au filet vertical fermant jusqu'à 400 mètres de profondeur, au voisinage de Tuléar, permettra peut-être d'élucider cette question.

2) ASPECT BIOGEOGRAPHIQUE :

Le nombre d'espèces déterminées dans les eaux de surface de Tuléar est important : 121 espèces sont présentes en une seule station. Ce chiffre est à rapprocher des nombres que cite WOLFENDEN (1904) pour la faune des Maldives et des Laquedives (120 espèces) WICKSTEAD (1961) dénombre en diverses stations de l'Archipel malais (Malacca) 82 espèces. GANAPATI (1961) recense 109 espèces dans les eaux de Lawson's bay, sur la côte occidentale de l'Inde.

Les chiffres relevés dans le sud-ouest de l'Océan Indien au voisinage des côtes d'Afrique semble marquer par contre un certain appauvrissement, dû certainement à la présence d'eaux plus froides, moins propices en général au développement du nombre d'espèce, mais aussi à l'éloignement des zones malaises et ouest-pacifiques, qui sont du points de vue biogéographique des "réservoirs de faune", comme l'a montré SEWELL (1948) pour le groupe des Copépodes pélagiques.

CLEVE (1904) cite ainsi 110 espèces dans les mers de la Province du Cap, mais ce nombre relativement élevé est dû au fait qu'il inclut dans ce chiffre des espèces capturées au cours de pêches en profondeur. BRADY (1914-1915), décrivant la faune de surface de Durban, y rapporte un nombre réduit de formes, dont plusieurs n'on jamais été retrouvées par la suite, et par celà, apparaissent comme suspectes. (*Acartia longisetosa, A. nana, Aphelura typica, Oithonopsis farrani, Calanoides natalis,* etc...).

DE DECKER (1963), dans son interessant travail basé sur des prélèvements entre Durban et le Cap (1963) ne cite que 93 espèces.

La richesse en espèces de la faune de Tuléar doit s'expliquer en partie par la proximité du courant du Mozambique, issu du courant sud-équatorial. MENACHE (1961) et Mac NAE (1961) ont en effet montré que ce courant, après avoir longé la côte d'Afrique en direction nord-sud, changeait de direction à la latitude du sud de Madagascar, remontant vers le nord le long de la côte occidentale de l'île. Ainsi, des formes particulièrement thermophiles sont présentes à Tuléar, mais n'atteignent pas la latitude de Durban, d'après les données actuelles : *Undinula caroli, Acrocalanus gibber, A. longicornis, A. andersoni, Euchaeta longicornis, Metacalanus aurivilli, Paraugaptilus mozambicus, Calanopia thompsoni, C. elliptica, Labidocera acutifrons, laevidentata, Kroyeri, madurae, Acartia fossae, Tortanus sp., Miracia efferata, Onychocorycaeus gracillicaudatus.*

Certaines de ces formes sont originaires de l'est-pacifique (*Acartia fossae, labidocera acutifrons, Tortanus forcipatus, Onychocorycaeus gracillicaudatus, Miracia efferata, Undinula caroli, Euchaeta longicornis.* D'autres proviennent de la région ouest-pacifique - archipel malais : *Metacalanus aurivilli, Tortanus barbatus, Labidocera laevidentata, L. madurae, L. kroeri, Calanopia thompsoni C. elliptica.* Le cas de *Paraugaptilus mozambicus,* espèce de profondeur, est particulier : on peut la considérer comme une endémique méso-pélagique de cette partie de l'Océan Indien. Mais les informations d'ordre systématique sur le plancton de profondeur sont encore trop fragmentaires pour confirmer cet endémisme.

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ABSTRACT

An account is given of the systematic and annual repartition of pelagic copepods from the superficial waters of the région of Tuléar (Madagascar). One hundred and twenty-one species were recorded. Among neritic species, the more frequent throughout the year were *clausocalanus furcatus, Paracalanus aculeatus, Oncaea* sp., *undinula vulgaris, calanopia thompsoni, Acartia ambainensis, Acartia fossae. Labidocera acuta* and *Labidocera minuta* were noted particularly during the warm season (december to march). The occurrence of oceanic and mesopelagic species was observed during the cold months (july - august) which corresponds to the arrival of clear, cold oceanic waters.

Tableau I

Température et turbité des eaux de surface

Date	Température	Turbidité	Date	Température	Turbidité
3 X 63	24°30	12 m	26 III	26°90	13 m
10 X	24°85	6	4 IV	25°20	8,5
21 X	24°95	15	27 IV	23°25	13
29 X	24°05	8	4 V	22°80	4
11 XI	25°80	6	11 V	22°90	6,5
20 XI	26°30	6	21 V	24°40	12
28 XI	27°00		29 V	22°60	4
5 XII	25°00	8	9 VI	24°10	6
14 XII	27°50	2	19 VI	23°40	20
19 XII	27°85	1,5	6 VII	22°20	8
27 XII	26°70	3	15 VII	22°05	14,5
6 II 64	28°10	4,5	27 VII	22°30	10
15 I	28°10	4,5	6 VIII	22°65	7,5
25 I	27°45	14,5	18 VIII	22°00	5
4 II	29°05	2,5	27 VIII	22°12	10
10 II	28°65		9 IX	22°40	5,5
20 II	30°02	4	17 IX	23°55	23
5 III	27°30	1,5	27 IX	23°02	5
16 III	27°55	3,5	8 X	24°60	8

Tableau II

Répartition saisonnière des copépodes

	oct. 3,10,21,29	nov. 11,18,28	dec. 5,14,19,27	janv. 6,15,25	fevr. 4,10,20	mars 5,16,26	avr. 4,27	mai 4,11,21,29	juin 9,19	juil. 6,15,27	août 6,18,27	sept. 9,17,27	oct. 8
Undinula													
vulgaris	2 2 2 2	3 3 3	3 2 2 1	.....	2 2 2	2 2 2	3 3	2 2 2 2	3 2	2 1 1	1 1 1	1 2 2	2
darwini	+	... + ..	..... +	.....	.....	.....	+ ..	.... + +	.. +	+ + +	+	+ + +	+
caroli	.....	.....	.....	.....	.....	.....	....	.....	....	+	+	.....	..
Calanus													
tenuicornis	.... + +	.....	.....	.....	.... +	.....	....	.....	....	+	.....	.....	..
minor	 1	1 1 ..	1 1 1 1	.....	1 .. 1	1 1	1	1 2 2	2 2	1 1 1	1 1 1	1	..
gracilis	.... + +	.....	.....	.....	.....	.....	+ ..	.....	....	.....	.... +	+	..
Canthocalanus	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
pauper	.. 2 2 2	2 2 ..	 2	2 2 2	2 2 2	2 1	.. 1	1 2 2 2	2 2	2 2 2	.....	1	..
Eucalanus													
subcrassus	.....	.....	..... 1 1	1 1	2 2 2	2 2 2	2 2	2 2	1 1	2 2 2	2 2 2	2 2	1
mucronatus	.....	.....	.....	1	.....	 1	2	2	1	1 1 1	1 1 1	.....	..
subtenuis	..... 1 ...	.....	..... 1 1	1	1	1	1 ...	.... 1 1	....	.. 1 1	1	.....	..
crassus	.....	.....	.....	1	1	1	....	.....	+	+ + +	.... +	.....	..
attenuatus	..... 1 ...	 1	..... 1 ...	1	1 1	1 1	....	. + + +	+ +	+	.....	.....	..
elongatus	.....	.....	.....	.....	.....	.....	....	.....	+	+ +	.... +	.....	..
Rhincalanus													
cornutus	.....	.....	+ ..... +	.....	..... +	.....	+ ..	.....	1	1 1 1	.... +	.....	..
nasutus	.....	.....	.....	.....	.....	.....	....	.....	+	+ +	.....	.....	..
Mecynocera													
clausi	+ + ...	... + ..	..... +	.....	.....	.....	+ +	.....	....	.....	.... +	+	+
Paracalanus													
parvus	1 1 1	1 1	1 2 2 1	1 1 1	1 1 1	1 1 1	1 1	1 1 1 1	1	1 1 1	1 1 1	1 1 1	1
aculeatus	2 2 2 2	2 2	2 2 1	1 1	2 2 2	2 2 2	2 2	2 2 2 2	2 2	2 2 2	2 2 2	2 2 2	2
crassirostris	+ +	.....	..... +	.....	.....	.....	....	.....	....	.....	.....	.....	..
Acrocalanus													
gracilis	.. 1 1 ...	... 1 ..	.. 2 1 1	1 1 1	1 1 1	1 1	1 1	1 1 1 1	1 1	1 1 1	.....	.....	..
monachus	.....	... + ..	.....	.....	.....	.....	....	.....	.. +	+ + ..	.. + ..	.....	..
gibber	.....	.....	..... +	.....	.....	.... +	....	.....	....	+ + +	+ + ..	.....	..
longicornis	.....	.....	+ ... + ...	.....	+ ... +	.....	....	. + + ..	.. +	+ + +	+ + +	.....	..
andersoni	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
Calocalanus													
pavo	1	.....	.. 1 1 ...	.....	1 1 ...	.....	....	.....	....	.....	.. + ..	.....	+
plumulosus	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.....	.....	+
styliremis	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..

	oct. 3,10,21,29	nov. 11,18,28	dec. 5,14,19,27	janv. 6,15,25	fevr. 4,10,20	mars 5,16,26	avr. 4,27	mai 4,11,21,29	juin 9,19	juil. 6,15,27	aôut 6,18,27	sept. 9,17,27	oct. 8
Clausocalanus													
arcuicornis	1 1 1	1 1 1	1 1	.....	.. 1 1	1	1 ...	.... 1 1	1 1	1	.....	.....	+
furcatus	1 3 3 3	3 3 3	3 3 3 3	 2	2 2 ...	2 2 2	2 2	3 ... 3	3 3	3 3 3	3 3 2	3 3 3	3
paululus	.....	.....	..... +	.....	.....	.... +	....	.....	+ ..	+ + ...	.... +	+ + +	+
Euaetideus													
bradyi	.....	.....	..... +	.....	.....	.....	....	.....	....	.... +	.....	.....	..
Euchaeta													
marina	+ ... 1 1	1 1 1	..... +	.....	+ +	+ + +	....	.... 1 1	1 ..	1 1 1	1 1 1	1 1 1	1
longicornis	..... +	.....	..... +	.....	.....	.....	....	.... + ..	....	. +	.... +	.. +...	..
wolfendeni	+..... +	.....	.....	+	.....	.....+	+ ..	.....	1 1	1 1 1	.....	.....	..
Scolecithrix													
danae	.....	.....	..... +	.....	.....	.....	+ ..	.....	1 1	1 1	1 1 1	.....	..
bradyi	.....	.....	.....	.....	.....	.....	....	..... + +	+	+	.....	.....	..
Scolecithricella													
ovata	.....	.....	.....	.....	.....	.....	....	.....	+	.....	.....	.....	..
minor	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
Temora													
discaudata	.....	.....	.. + 1 1	1 1 1	1 1 1	1	....	.... 1 1	1 1	1 1 1	1 1 1	1	1
turbinata	.....	.....	.. + ...	.....	.....	.....	....	.....	....	.....	.....	.....	..
Pleuromamma													
abdominalis	.....	.....	.....	.....	.....	.....	+ ..	.....	....	.....	+	.....	..
gracilis	.....	.....	.....	.....	.....	.....	....	.....	....	.....	..... +	.....	..
robusta	.....	.....	.....	.....	.....	.....	....	.....	....	+	.....	.....	..
Centropages													
furcatus	.....	.....	1 1 1 1	1 1 ...	.....	1 1 1	....	.. 1 1 1	1 1	1 1	1 1 ...	 1	1
violaceus	.....	... +...	.. + ...	.... +.	.....	.....	+ ..	.....	+...	.....	.....	.....	..
elongatus	..... + ..	.....	.....	.....	.....	.....	+ ..	.....	....	.....	.....	.....	..
gracilis	.....	.....	.....	.....+	+ + ..	+	.. +	.....	....	.....	+	.....	..
calaninus	.....	.....	.....	.....	+ + ..	.....	....	.....	....	.....	.....	.....	..
Pseudodiaptomus													
sp.	.....	.....	..... +	.... +	.....	.....	....	.....	....	.....	.....	.....	..
Lucicutia													
flavicornis	.....	... + ..	.....	.....	.....	+.. +	....	.....	....	+ + +	.....	.....	..
ovalis	.....	.....	.....	.....	.....	.....	....	.....	....	.....	..... +	.....	..
Heterorhabdus													
papilliger	.....	.....	.....	.....	.....	.....	....	.....	....	.....	..... +	.....	..

	oct. 3,10,21,29	nov. 11,18,28	dec. 5,14,19,27	janv. 6,15,25	févr. 4,10,20	mars 5,16,26	avr. 4,27	mai 4,11,21,29	juin 9,19	juil. 6,15,27	août 6,18,27	sept. 9,17,27	oct. 8
Haloptilus													
longicornis	.....	.....	..... +	.....	.....	.....	.. +	.....	....	.....	..... +	.....	..
mucronatus	.....	.....	..... +	.....	.....	.....	....	.....	....	.....	.....	.....	..
oxycephalus	.....	.....	.....	.....	.....	.....	.. +	.....	....	.....	.....	.....	..
spiniceps	.....	.....	.....	.....	.....	.....	....	.....	....	.....	..... +	.....	..
Enaugaptilus													
hecticus	.....	.....	.....	.....	.....	.....	....	.....	....	.....	..... +	.....	..
Metacalanus													
aurivilli	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.....	.... +	..
Paraugaptilus													
mozambicus	.....	.....	.....	.....	.....	+	....	.....	.. +	.....	.....	.....	..
Candacia													
pachydactyla	.....	.....	.....	.....	.....	+	....	.....	.. +	.. + ..	+ + ...	..... +	..
aethiopica	.....	.....	..... +	.....	.....	.....	....	.....	....	.....	.....	.....	..
bispinosa	..... +	.....	.....	.....	.....	+	....	.....	....	.....	..... +	.....	..
truncata	.....	.....	.....	.....	.....	..... +	....	.....	....	+ + ..	..... +	.....	..
catula	.....	.....	..... + +	.. + ..	.....	+	....	.....	+ +	+	.....	.....	..
curta	.....	.....	..... + ..	.....	.....	.....	....	.....	....	+	..... +	.....	..
simplex	+	.....	..... + +	.....	+ + ...	.. + +	....	.....	....	+	..... +	.....	..
Calanopia													
thompsoni	2 3 3 2	2 2 ..	..... 1 1	 1	 2	3 3 3	3 2	.....	2 2	2 2 ..	.. + +	..... +	..
elliptica	.....	.....	..... +	.....	..... +	+ ... +	+ +	..... +	.. +	+ + ..	+ ... +	.....	..
minor	.....	.....	.....	.....	.....	+	....	.....	.. +	+ ..	.....	.....	..
Labidocera													
acuta	.....	.....	.. 1 1 ..	1 1 1	1 1 1	.....	.. +	.....	.. +	.....	..... +	.....	..
minuta	.....	.....	.. 1	1 1 1	1 1 1	1 1 1	....	.... + ..	+ ..	.....	+ ... +	.....	..
acutifrons	.....	.....	.....	.....	.....	.....	....	.....	.. +	+ + ..	.....	.....	..
laevidentata	.....	.....	.....	.. + ..	.....	..... +	....	.....	....	.....	.....	..... +	..
kroyeri	.....	.....	.....	.....	..... +	.....	....	.....	....	.....	.....	..... +	..
madurae	.. + ...	+ + +	+ + + ..	.....	.....	.....	....	.. + + ..	....	.....	.....	..... +	..
Pontellina													
plumata	..... +	.....	.....	+ + +	+	+	....	.. + ...	+ +	+ + ..	.. + +	.....	+
Acartia													
amboinensis	+ + +	....1 2	2 2 3 ..	3 3 2	3 3 2	3 3 3	3 3	3 3 3 3	3 2	2 2 2	2 2 2	2	..
fossae	3 3 3	+ 3 3	3 3 2 ..	.. 1 3	1 1 1	1 1 3	1 2	1 1 1 1	1 1	1 2 1	1 1 1	1 ... +	+
negligens	+ +	+ + +	+ + ..	.... +	.. + ..	..... +	....	.....	.....	.....	.....	.....	..
danae	+ + +	+ + +	+ + + ..	.....	.. + ..	+	+ ..	.....	.....	.....	.....	.....	..

	oct. 3,10,21,29	nov. 11,18,28	dec. 5,14,19,27	janv. 6,15,25	févr. 4,10,20	mars 5,16,26	avr. 4,27	mai 4,11,21,29	juin 9,19	juil. 6,15,27	août 6,18,27	sept. 9,17,27	oct. 8
Tortanus													
barbatus	.....	.....	..... +	.....	.....	.....	+ ..	.....	....	.....	.....	.....	..
gracilis	.....	.....	.....	.. + +	..... +	..... +	....	.....	....	.....	.. + +	.....	..
forcipatus	.....	.....	..... +	.....	.. +...	.....	....	.....	....	.....	.. + +	..... +	..
A	..... + ..	.....	+ + ...	.....	.....	.....	....	.....	....	.....	.....	.....	..
B	.....	+.....	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
C	.....	.....	.....	.....	.....	.....	....	..... +	....	..... +	.....	.....	..
Oithona													
helgolandica	..... +	..... +	.. + ... +	.....	.. + ..	.. + ..	+ ..	.. + .. +	.. +	.....	.....	+	..
plumifera	..... + ..	+ .. +	+ ..... +	.....	..... +	+ ... +	....	.. + .. +	.. +	.....	.. + ..	.....	..
linearis	+ .. + ..	+	+ ..... +	.....	.....	..... +	....	.. + ...	....	.....	.... +	.....	..
robusta	.... + ..	.....	..... +	.....	.....	.....	....	..... +	....	.....	.....	.....	..
brevicornis	.....	.....	.....	.....	.....	.....	.. +	.....	....	.....	.....	.....	..
oculata	.. + + ..	.+	.. + ...	.....	.....	..... +	....	.....	....	.....	.....	.....	..
rigida	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.. + +	.....	..
Microsetella													
rosaea	.....	..... +	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
norvegica	.....	..... +	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
Macrosetella	.....	.....	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
gracilis	+	..... +	..... + +	+	.. +..	+ + +	+ +	.. +... +	.....	+	+ + ..	+ +..	..
Miracia													
efferata	.....	..... +	.....	.....	.....	.....	....	.....	....	.....	.....	.....	..
Euterpina													
acutifrons	.....	..... +	.....	+ +...	.....	.. + ..	....	.. + ...	.....	.....	.....	.....	..
Oncaea													
venusta	.. + + +	 2	2 2 2...	1 1 1	.. 1 1	2 2 2	+ +	+ + 1 1	1 +	1 1 1	1 1 1	1	..
media	1 2 2 2	2 2 2	3 3 3 2	2 2	2 3 3	2 1 2	2 2	2 2 2 2	2 2	2 2 2	2 2 2	2	..
conifera	.. + ... +	... + ..	.....	.....	.....	..... +	+ ..	.....	....	+	.....	.....	..
Sapphirina													
opalina-darw.	.....	.....	.....	.....	.....	.....	....	.....	....	.. + +	.....	.....	..
scarlata	.....	.....	.. ..	.....	.....	.....	....	.....	....	.. +...	.....	.....	..
metallina	..... +	.....	..... +	.....	.....	.....	....	.....	....	+.....	.....	.....	..
Copilia													
mirabilis	+	.....	..... +	+ + ..	.. +..	+ +...	....	.....	....	+.....	.... +	.....	..
vitraea	.....	.....	.....	.....	.....	.....	....	.....	....	.. + ..	..+ +	.....	..
quadrata	.....	.....	.....	.. + ..	.....	.....	....	.....	....	.. + ..	.....	.....	..

	oct. 3,10,21,29	nov. 11,18,28	dec. 5,14,19,27	janv. 6,15,25	févr. 4,10,20	mars 5,16,26	avr. 4,27	mai 4,11,21,29	juin 9,19	juil. 6,15,27	août 6,18,27	sept. 9,17,27	oct. 8
Corycaeus													
speciosus	.. + + ..	... + ..	..... +...	.. + ..	.. + +	+.... +	....	+.....	...+	+ + +	+ .. +	+....	..
crassiusculus	.....	... + ..	..... + ..	+	..... +	+ ... +	....	+ + + +	+ +	+	+ + +	+ +..	..
flaccus	..... +	.....	+.....	.....	.....	.....	....	.....	....	.....	.... +	.....	..
limbatus	.....	.....	..... +...	.....	.....	.....	....	.....	....	.....	.....	.....	..
typicus	.... + +	... +...	+.....	.....	.....	.. + ..	+ ..	.....	....	.....	.....	.....	..
giesbrechti	+.....	+ + +	...+ +...	+ + +	...+ +	+ +...	....	.. + ...	....	...+ ..	.. +..	+ +..	..
latus	.....	... +...	..... + +	+	.....	.....	.. +	+... +..	...+	.....	.....	.....	..
ovalis	.. +.....	... +...	...+.....	+	.....	..... +	.. +	+... +.	...+	..... +	.....	.....	..
gracilicaudatus	.....+ ..	... + ...	...+.....	.....	...+...	+ + +	....	.....	+..	.....	.. + +	.....	..
africanus	.....	.....	+	+.....	.....	.....	....	.....	....	.....	.....	+	..
longistylis	.. + ...	... + +	+... + ..	.....	.. + +	.....	....	+ +.....	.. +	.....	.....	.....	..
Corycella													
gracilis	+ + + ..	+ + +	+ + ...	.. + ..	..... +	.....	+ +	+.....	....	+.....	+ .. +	.....	..
gibbula	+	.....	..... + ..	..... +	.. +...	+.....	....	.....	+..	.....	.. +..	+....	..
carinata	.....	... +...	.....	.....	.....	.....	....	.. +.....	....	.....	.....	+....	..

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CONTRIBUTION A L'ÉTUDE DES ASCIDIES DE L'ILE MAURICE (ARCHIPEL DES MASCAREIGNES, OCÉAN INDIEN)

par P. VASSEUR

INTRODUCTION.

La collection d'Ascidies des eaux côtières de l'Ile Maurice, qui fait l'objet du présent travail, a été réalisée par Mr. C.M. MICHEL du Mauritius Institute à Port-Louis, qui a bien voulu me confier l'étude de ce matériel. Il m'est agréable de lui exprimer ici ma plus vive et ma plus sincère reconnaissance.

En effet, ce travail apporte une contribution indéniable à la connaissance de la faune ascidiologique de cette intéressante aire maritime qui n'était connue, jusqu'à présent, que par deux publications anciennes, celle de DRASCHE (1883) qui porte sur une seule espèce nouvelle et celle de HARTMEYER (1905) qui renferme 8 espèces dont 4 sont nouvelles.

La collection décrite dans ce travail contient 21 espèces d'Ascidies, dont une est nouvelle. Des 9 espèces, au total, figurées dans les publications de DRASCHE et de HARTMEYER, 3 espèces seulement figurent dans les récoltes de Mr MICHEL, à savoir : *Halocynthia pallida* (Heller) = *Pyura momus* (Savigny), *Polycarpa nigricans* Heller et *Colella möbiusi* Hartmeyer [= *Eudistoma möbiusi* (Hartmeyer)]. Les autres espèces, figurant dans ma liste systématique, constituent donc de nouvelles localisations pour la faune de l'Ile Maurice, dont une, l'espèce nouvelle, est momentanément caractéristique de cette zone de l'Océan Indien.

La collection a été faite dans les localités suivantes : Rade de Port-Louis, Ilot Barkly, Cassis, Flic en Flac, Pointe d'Esny, Trou d'eau douce et Trou aux Biches. Ces localités, toutes littorales, s'étendent largement autour des côtes de l'Ile Maurice (voir la carte) et suggèrent, par conséquent, des conditions hydrodynamiques et de milieu très différentes.

LISTE SYSTEMATIQUE.

APLOUSOBRANCHES

SYNOICIDAE

Pseudodistoma mauritiana n. sp.

DIDEMNIDAE

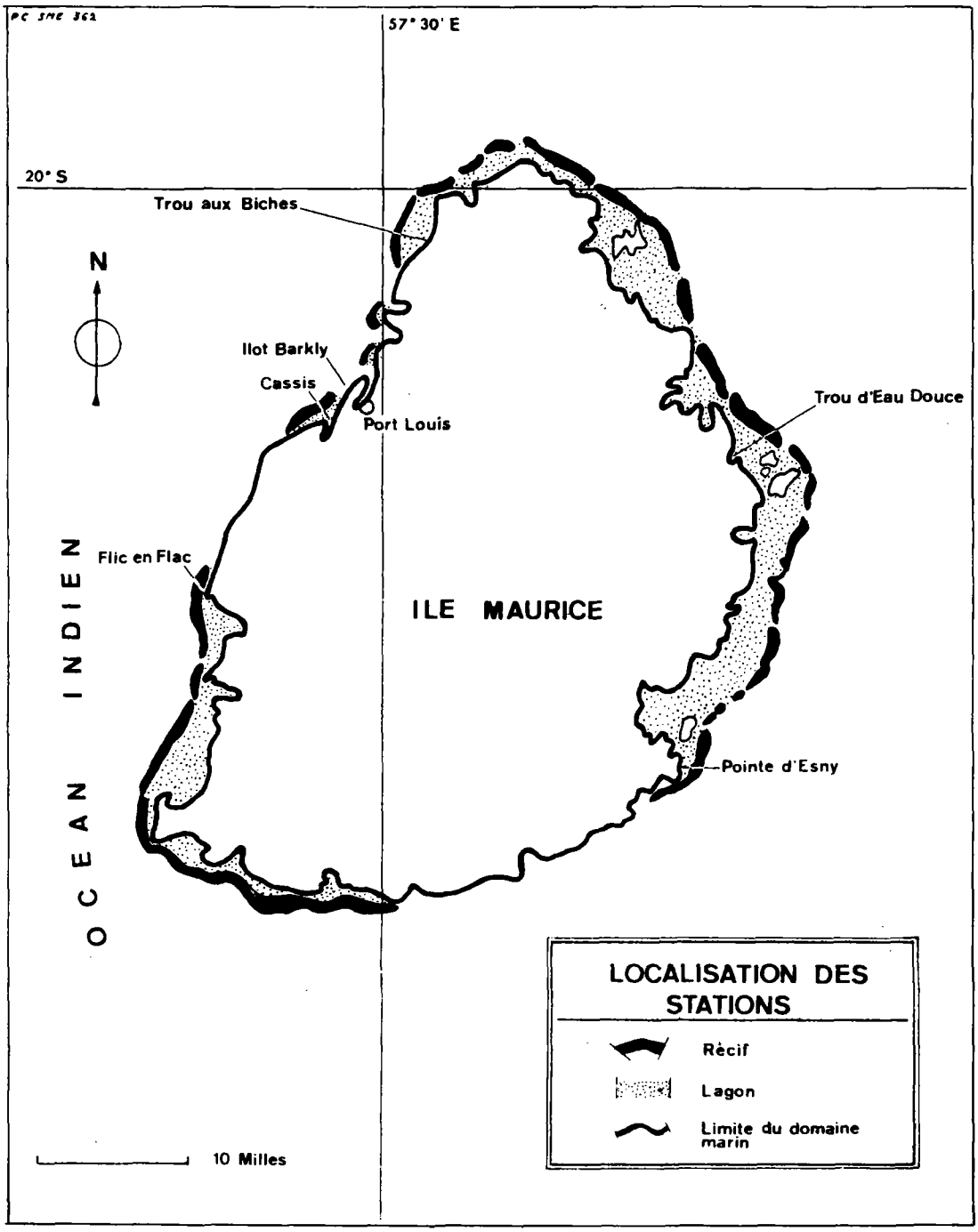
Didemnum candidum Savigny.
Tridemnum sansibaricum (Michaelsen).
Tridemnum natalense Michaelsen.
Tridemnum meridionale Millar.

POLYCITORIDAE

Eudistoma rhodopyge (Sluiter).
Eudistoma möbiusi (Hartmeyer).

PHLEBOBRANCHES

ASCIDIIDAE


57° 30' E
20° S
Trou aux Biches
N
Ilot Barkly
Cassis
Port Louis
Trou d'Eau Douce
Flic en Flac
ILE MAURICE
OCEAN INDIEN
Pointe d'Esny
LOCALISATION DES STATIONS
Récif
Lagon
Limite du domaine marin
10 Milles

Ascidia sydneiensis Stimpson.
Ascidia munda Sluiter.

STOLIDOBRANCHES

STYELIDAE

Symplegma viride Herdman.
Amphicarpa inhacae (Millar).
Polyandrocarpa anguinea (Sluiter).
Polyandrocarpa (Eusynstyela) tincta (Van Name).
Polycarpa nigricans Heller.
Cnemidocarpa madagascariensis Hartmeyer.
Styela partita (Stimpson).
Styela pupa Heller.

PYURIDAE

Pyura pulla (Sluiter).
Pyura momus (Savigny).
Microcosmus exasperatus Heller.

MOLGULIDAE

Molgula natalensis (Michaelsen).

DESCRIPTION DES ESPECES.

SYNOICIDAE

Pseudodistoma mauritiana n. sp.
(Pl. I : figure 1).

Localité.

62/64, Flic en Flac, 6/2/62.

Diagnose.

Petites colonies encroûtantes, irrégulières, molles ou semi-cartilagineuses, translucides. Zoïdes divisés en 3 parties distinctes : thorax, abdomen, postabdomen. Manteau sans musculature apparente. Environ 20 filets tentaculaires en deux cercles. Trois rangs de trémas avec 12 à 15 trémas par demi-rangée. Estomac à 4 plis longitudinaux très nets. Une dizaine de follicules testiculaires dans la région distale du post-abdomen. Extrémité distale du pos-abdomen avec cardio-péricarde.

Description.

Trois petites colonies encroûtantes, irrégulières, de coloration bistre très pâle dans le formol. Tunique molle ou semi-cartilagineuse, d'aspect translucide. La surface du cormus est lisse mais renferme quelques incrustations de grains de sable, de tests de Foraminifères et de débris coquilliers. Dimensions des colonies : Longueur : 8 à 15 mm ; Largeur : 4 à 5 mm ; Epaisseur : 1,3 à 3 mm.

Les zoïdes, peu nombreux, apparaissent en brun clair à travers la tunique commune ; ils ne sont pas disposés en systèmes. La longueur des zoïdes varie de 4 à 11 mm suivant le degré de contraction du post-abdomen : thorax : 1 mm, abdomen : 2 mm, post-abdomen : 8 mm.

Le thorax est presque aussi large que long. Les deux siphons sont antérieurs et 6-lobés ; les lobes sont courts, à extrémités arrondies. L'axe du siphon cloacal qui s'ouvre en face du premier rang de trémas, est nettement oblique par rapport à l'axe du siphon buccal. Environ 20 filets tentaculaires disposés en deux cercles. Le sac branchial, à 3 rangs de trémas, compte 12 à 15 trémas par demi-rangée.

Aucun faisceau musculaire apparent sur le thorax et l'abdomen.

L'abdomen est deux fois plus long que le thorax. Le tube digestif, non tordu, a un oesophage très long et assez étroit ; l'estomac, situé dans le dernier tiers abdominal, possède 4 plis longitudinaux bien marqués ; l'intestin est divisé nettement en trois chambres. L'extrémité proximale de la branche intestinale ascendante présente deux éperons dorsaux, comme des coecums. L'extrémité rectale, qui atteint le deuxième rang de trémas, est légèrement bifide.

Les post-abdomens semblent pour la plupart immatures, sauf un qui présentait une dizaine de petits follicules testiculaires irrégulièrement répartis au niveau du dernier quart post-abdominal. Ovaire non apparent.

L'extrémité du post-abdomen contient le cœur.

Discussion.

Depuis l'espèce type *Pseudodistoma cereum* Michaelsen, 1924, de l'Ile Stewart, Nouvelle-Zélande, seulement 9 espèces du genre *Pseudodistoma* ont été décrites. Pour l'ensemble de ces espèces, 6 ont l'estomac lisse et 3 ont l'estomac avec quatre plis.

Pour les espèces à estomac lisse qui, de ce fait, diffèrent de l'espèce de l'Ile Maurice, il faut citer : *P. cereum* Michaelsen que KOTT P. (1963) place dans la catégorie des espèces à "estomac sans plis" et met en synonymie l'espèce *P. novae-zealandiae* (Brewin), 1950, Ile de la Grande Barrière, Nouvelle-Zélande ; *P. antinboja* Tokioka, 1949, de Seto, Japon ; *P. brieni* Pérès, 1949, du Sénégal, Afrique de l'Ouest ; *P. cyrnusense* Pérès, 1952, de la Méditerranée ; *P. australis* Kott, 1957, de la Côte Ouest de l'Australie ; *P. fragilis* Tokioka, 1958, du Japon.

En ce qui concerne les 3 espèces décrites avec un estomac à quatre plis : *P. opaca* (Brewin), 1957, de l'Ile de la Grande Barrière, Nouvelle-Zélande ; *P. aurea* (Brewin), 1957, de Nouvelle-Zélande et *P. africanum* Millar, 1954, de l'Afrique du Sud, seules les espèces *P. opaca* et *P. africanum* diffèrent essentiellement de *P. mauritiana* n. sp. par la forme des colonies, en massues pour la première espèce et en petits lobes capités pour la seconde ; d'autre part, à la différence de *P. mauritiana*, *P. opaca* ne présente aucune constriction intestinale et *P. africanum* montre des acinis testiculaires régulièrement répartis en séries longitudinales. Bien que l'état de maturité des cormus de l'Ile Maurice ne permette pas de préciser le nombre exact d'acini testiculaires et la position de l'ovaire, *P. mauritiana* ne paraît pouvoir être assimilé également à *P. aurea* bien qu'il présente par certains caractères de l'anatomie des zoïdes quelques ressemblances surtout en ce qui concerne le cormus, la longueur des zoïdes, le nombre approximatif des filets tentaculaires et le sac branchial ; les différences dans la morphologie du tube digestif (intestin étroit immédiatement après l'estomac, puis très large jusqu'au siphon atrial, ouverture anale lisse chez *P. aurea* ; intestin en trois chambres assez larges avec deux éperons nets au début de la chambre intestinale ascendante, ouverture anale bifide chez *P. mauritiana*) et l'éloignement géographique les séparent.

Seule la récolte d'autres cormus présentant des zoïdes à gonades développées, permettra de préciser les caractères de cette espèce qui, je pense, est bien nouvelle et d'apprécier ses affinités avec les espèces connues.

DIDEMNIDAE

Didemnum candidum Savigny, 1816
(Pl. I : figs. 2-4).

Pour la synonymie, voir VAN NAME, 1945, p. 83.

Distribution.

Méditerranée ; Mer Rouge ; Océan Indien ; Malaisie ; Australie ; "Indes Occidentales" ; Bermudes ; Brésil.

Localité.

61/202, Trou aux Biches, 7/12/61.

Description.

Quelques cormus, blanchâtres à l'état fixé, encroûtants sur le substrat, aux contours légèrement sinueux, d'aspect opaque et de consistance friable. Dimensions d'un cormus : Longueur : 40 mm ; Largeur : 25 mm ; Epaisseur : 1 à 2 mm.

La spiculation de la tunique commune est très dense à la surface et dans la couche basale. Entre ces deux couches, une gaine de la tunique enveloppe les abdomens de chaque zoïde. Les spicules sont un peu moins denses au niveau des ouvertures buccales. Ils sont d'une seule catégorie, de taille variable (12 à 27 µ), étoilés à nombreux rayons. Les rayons sont courts à sommets coniques ou légèrement arrondis.

Les zoïdes, très petits, ne dépassent pas 0,9 mm. Le thorax mesure 0,35 mm. L'abdomen est presque deux fois plus long avec 0,7 mm. L'appendice musculaire, situé à la base du thorax et présent à chaque zoïde, reste assez court.

Le siphon buccal, tubulaire avec 6 lobes triangulaires, a des fibres musculaires circulaires et longitudinales. L'orifice du siphon cloacal s'ouvre au milieu du thorax. Environ 12 filets tentaculaires.

Le sac branchial a 4 rangs de trémas avec 6 à 7 trémas, assez courts, par demi-rangée.

Le tube digestif montre un oesophage étroit ; l'estomac, assez large, est de forme ovoïde ou rectangulaire ; l'intestin dessine une large boucle et se divise en trois chambres bien nettes avant la branche intestinale ascendante.

L'appareil sexuel est constitué d'un seul follicule testiculaire situé dans la boucle intestinale et chez certains zoïdes, d'un ovaire accolé contre le follicule. L'ovaire est constitué par un œuf atteignant jusqu'à 0,2 mm. Le spermiducte dessine 4 à 5 tours de spire.

Larve petite de 0,4 mm, des papilles à la base de la queue, avec 4 paires d'ampoules antérieures et 3 papilles adhésives médianes. Vésicule sensorielle avec un ocelle et un otolithe.

Discussion.

Je pense que l'on peut attribuer à *Didemnum candidum* Savigny, espèce très polymorphe et à distribution circumtropicale, les cormus blanchâtres, d'aspect homogène, aplatis et très minces, de l'Ile Maurice. Aucune différence essentielle ne peut être recherchée dans les zoïdes de ces colonies, à part le faible diamètre des spicules dont les figures correspondent parfaitement à certaines de celles figurées par VAN NAME (1945), et le nombre restreint de tours de spire du spermiducte ; mais ces deux caractères varient chez les *Didemnum* et ne peuvent, par conséquent, être retenus comme critères de discrimination spécifique. Les zoïdes restent assez typiques en ce qui concerne les siphons, le sac branchial et le tube digestif.

Trididemnum sansibaricum (Michaelsen), 1920
(Pl. I : fig. 5).

Didemnopsis sansibaricum Michaelsen, 1920, p. 6.
MILLAR, 1956, p. 922.

Distribution.

Zanzibar ; Ile du Moçambique.

Localités.

62/1/7. Flic en Flac, 24/4/62 ; 62/Ib, Trou d'eau douce, 5/1/62.

Description.

Trois petites colonies de forme oblongue ou presque globuleuse. Dimensions : Longueur : 5 à 15 mm ; Largeur ; 5 à 8 mm ; Epaisseur : 4 mm. Les cormus ont une consistance assez ferme, semi-cartilagineuse, de coloration vert-brunâtre vers la périphérie à pourpre noirâtre au centre, à l'état fixé.

La tunique est lisse au toucher, d'aspect translucide, les zoïdes apparaissant en plus sombres car plus fortement pigmentés. Présence de nombreuses cellules pigmentaires, de façon dense, à la surface de la tunique commune, la substance fondamentale étant jaunâtre. Il y a deux types de cellules pigmentaires, soit des cellules très allongées ou étoilées, soit des cellules ellipsoïdales renfermant des grains arrondis de pigments bruns-verdâtres.

Absence totale de spicules.

Les zoïdes sont jaunes-verdâtres et leur taille varie de 1,5 à 2 mm, l'abdomen étant généralement une fois et demi plus long que le thorax. L'appendice musculaire, situé à la base du

thorax, dépasse largement l'extrémité abdominale, ayant deux à trois fois la longueur du thorax. Le thorax est plus large que long. Le siphon buccal et le manteau, au niveau de la partie antérieure du thorax et de l'endostyle, sont fortement pigmentés en brun verdâtre. La pigmentation du manteau abdominal est plus faible mais uniforme.

Le siphon buccal, en forme de tube, est 6-lobé avec des lobes courts et aigus. Le siphon cloacal, à orifice circulaire, s'ouvre latéralement en face du 3e rang de trémas. On compte 10 filets tentaculaires de même taille.

Généralement, les thorax sont plus ou moins contractés et opaques. Dans les thorax dilatés et transparents, le sac branchial montre 3 rangs de trémas avec 15 à 13 trémas par demi-rangée du 1er au 3e rang. La première rangée de trémas est situé à une distance de la couronne tentaculaire au moins égale à la hauteur d'un tréma. Les 2 languettes dorsales sont aussi longues que les trémas. Sur toute la longueur du thorax, de très fins filets musculaires longitudinaux (une quinzaine de chaque côté du corps) parcourent les espaces intertrématiques.

Dans la partie abdominale, le tube digestif ne présente aucun caractère particulier ; oesophage court ; estomac assez gros, ovoïde ou globuleux ; intestin large en trois chambres bien nettes séparées par deux profondes constrictions.

Le testicule est formé d'un seul follicule de taille variable (de 0,2 à 0,5 mm), subsphérique ou en forme de lentille, situé au milieu de l'anse intestinale. Le spermiducte décrit 7 à 8 tours de spire avant de remonter le long du rectum. Ovaire non apparent. Pas de larves.

Discussion.

Ces spécimens de l'Ile Maurice sont parfaitement identifiables à *D. sansibaricum* (Michaelsen) aussi bien par les caractères du cormus que par l'anatomie des zoïdes. La consistance de la tunique commune, la coloration, la pigmentation et l'absence de spicules sont tout à fait comparables à la description de MICHAELSEN. De même, le nombre de filets tentaculaires, le nombre de trémas dans les 3 rangs du sac branchial, la forme lenticulaire du testicule, plus grand que l'estomac, recouvrant entièrement l'anse intestinale et débordant sur l'intestin, le nombre de tours de spire du spermiducte sont suffisamment proches de l'espèce type pour qu'aucune séparation soit possible.

Trididemnum natalense Michaelsen, 1920
(Pl. I : figs. 6-8).

Trididemnum natalense Michaelsen, 1920, p. 3. HASTINGS, 1931, p. 92. KOTT, 1962, p. 278.

Distribution.

Afrique du Sud : Natali Australie.

Localité.

62/1b, Trou d'eau douce, 5/1/62.

Description.

Une petite colonie irrégulière, encroûtante, molle, d'aspect translucide, de coloration bistre dans le formol. Les ascidiozoïdes apparaissent comme des points brunâtres à travers la tunique commune. La tunique est lisse, assez facile à déchirer. Dimensions du cormus : Longueur : 15 mm ; Largeur : 7 mm ; Epaisseur : 1 mm.

Les spicules, étoilés, blanchâtres et peu nombreux, sont disposés en une mince couche uniquement au centre du cormus, entre le thorax et l'abdomen des zoïdes. Ces spicules, sans caractères spécifiques, à rayons assez nombreux de forme conique, ont un diamètre qui varie de 35 à 60 µ. Le reste de la tunique est envahie par les lacunes tunicales et entre les lacunes se trouvent disséminés de petites cellules pigmentaires plus ou moins rondes renfermant des grains de pigments bruns.

Les zoïdes sont de très petite taille, de 0,7 à 0,9 mm. Le pédicule oesophagien peut être très étroit. Absence ou présence d'un court appendice musculaire à la base du thorax. Le thorax est opaque, pigmenté en brun. Siphon buccal court, mais assez large, avec 6 lobes aigus triangulaires. Siphon cloacal un peu plus étroit, situé en face du dernier rang branchial, allongé soit latéralement ou obliquement vers le bas. Le sac branchial, à 3 rangs, compte 10 à 7 trémas par demi-rangée, du 1er au 3e rang. Les deux languettes dorsales atteignent le tiers de la largeur du sac branchial. L'endostyle est large, épais, très foncé. Le tube digestif est sans caractères spécifiques. L'intestin peut être tordu.

Le testicule est constitué d'un seul follicule subsphérique ou en forme de lentille, situé dans l'anse intestinale. Le spermiducte décrit 5 à 6 tours de spire sur le follicule puis, court droit le long du rectum. L'ovaire se compose soit d'un ou deux petits œufs situés entre le testicule et l'estomac soit, chez certains zoïdes, d'un seul œuf volumineux (jusqu'à 0,4 mm de diamètre) situé à la partie postérieure de l'abdomen.

Dans la colonie, présence de larves mesurant 0,7 mm avec 3 paires d'ampoules antérieures et 3 papilles adhésives.

Discussion.

Après avoir longuement hésité, je me suis cependant résolu à attribuer à ce petit cormus, l'espèce *Trididemnum natalense* Michaelsen. En effet, sur l'ensemble des espèces indo-pacifiques du genre *Trididemnum*, l'espèce de l'Ile Maurice, par la distribution des spicules et les caractères de la tunique, ainsi que par les points communs dans l'anatomie des zoïdes et dans la ressemblance des larves, paraît davantage se rapporter à *T. natalense*, bien que cette espèce soit assez polymorphe.

Trididemnum meridionale Millar, 1953.
(Pl. II : figs. 9-10)

Trididemnum meridionale Millar, 1953, p. 205.

Distribution.

Afrique de l'Ouest : Côte de l'Or.

Localité.

61/203, Trou aux Biches, 20/3/61.

Description.

Une seule colonie encroûtante à contours irréguliers, de coloration grisâtre à l'état fixé. Dimensions du cormus : Longueur : 35 mm ; Largeur : 20 mm ; Epaisseur : 2 mm. La surface du cormus montre de très nombreuses petites surélévations, comme des papilles, qui correspondent à l'emplacement des orifices buccaux. La tunique commune est spongieuse, molle au toucher, d'aspect translucide, exceptée la présence de spicules.

Les spicules sont presque uniquement répartis dans les couches supérieure et basale de la tunique, le centre étant occupé par les ascidiozoïdes avec les spicules très rares ou absents. Pour la couche supérieure, les spicules blanchâtres sont très denses dans les dépressions entre les papilles et moins denses sur les papilles. Dans la couche basale, les spicules sont plutôt disséminés. Ces spicules sont étoilés et le nombre de rayons est variable suivant leur diamètre ; ils mesurent de 25 à 70 µ de diamètre. Les rayons sont coniques, courts, avec un sommet étroit et une base large. Certains spicules ont des rayons dont les côtés sont légèrement concaves.

Les zoïdes très serrés, assez difficiles à extraire de la tunique, mesurent de 0,9 à 1,2 mm. Le thorax et l'abdomen sont d'égale longueur. L'appendice musculaire, à la base du thorax, reste court. Il y a une constriction étroite entre le thorax et l'abdomen. Le siphon buccal et la partie antérieure du thorax sont pigmentés en brun, les grains pigmentaires étant régulièrement répartis.

Le siphon buccal est tubulaire avec 6 lobes triangulaires très nets à extrémités aiguës. Le siphon atrial également tubulaire mais plus petit, se trouve situé à la partie postérieure du thorax et dirigé obliquement vers le bas. La marge de l'orifice atrial est apparemment lobée.

On compte 8 tentacules simples, 2 grands et 6 petits, les deux plus grands étant placés aux deux extrémités du diamètre dorso-ventral.

Le sac branchial a 3 rangs de trémas, avec 8 trémas au 1er rang, 7 trémas au 2e rang et 6 trémas au 3e rang. La première rangée de trémas, la plus large, est située à une distance de la couronne tentaculaire au moins supérieure à la hauteur d'un tréma. Les trémas sont elliptiques ou ovales, ceux des extrémités de chaque rang étant plus courts que ceux du centre. Les languettes dorsales, étroites et pointues, sont égales à la hauteur d'un tréma et nettement incurvées vers le bas.

Le tube digestif est sans caractères spécifiques : l'oesophage reste étroit ; l'estomac est globuleux ; l'intestin montre les trois chambres bien visibles. Le rectum présente un léger renflement avec semble-t-il à l'extrémité, deux oreillettes anales très courtes, peu distinctes.

Les zoïdes sont à maturité. Le testicule est constitué d'un seul follicule, sphérique ou subsphérique, qui est situé dans la boucle intestinale et d'où s'échappe un spermiducte décrivant 5 tours de spire avant de remonter le long du rectum. Ovaire peu développé, sans caractères spécifiques, constitué de un ou deux petits œufs entre le testicule et l'estomac.

Discussion.

A part le diamètre légèrement plus grand des spicules et le nombre un peu plus faible de tours de spire du spermiducte, les affinités de ce cormus concordent parfaitement avec l'espèce *Tridemnum meridionale* Millar. Néanmoins, cette espèce fait vraisemblablement partie d'un lot de formes très proches les unes des autres. En effet, d'après MILLAR (1953), *T. meridionale* ressemble essentiellement à *T. savignii* (Herdman), "Indes occidentales" et Sénégal que VAN NAME (1945) apparente à *T. natalense* Michaelsen, Natal, et à *T. cyclops* Michaelsen, Madagascar, ainsi qu'à *T. solidum* (Van Name), Bermudes, mais en diffère par les spicules plus petits, par le nombre plus faible de trémas dans chaque rang, par le nombre moins important de tours de spire du spermiducte et enfin par l'appendice thoracique nettement plus court. *T. meridionale* est également très semblable à *T. lüderitzi* Michaelsen, Afrique du Sud-Ouest - que KOTT (1962) rapproche de *T. cerebriforme* Hartmeyer, Sud et Ouest de l'Afrique, Australie -, mais qui a cependant un siphon atrial plus court et un plus grand nombre de trémas dans chaque rang.

POLYCITORIDAE

Fudistoma rhodopyge (Sluiter), 1898.
(Pl. II : fig. 11).

Distoma rhodopyge Sluiter, 1898, p. 12.

Polycitor (Eudistoma) rhodopyge Hartmeyer, 1909, p. 1432.

MICHAELSEN, 1919, p. 72. MILLAR, 1956, p. 917.

Pour la synonymie, voir MICHAELSEN, 1934, p. 141.

Distribution.

Afrique du Sud ; Côte Sud-Ouest de Madagascar.

Localité.

473, Ilot Barkly.

Description.

Cinq colonies massives, compactes, en forme de coussin ou constituées de plusieurs lobes peu élevés, d'aspect vitreux et de coloration bistre à brun sombre dans le formol. Pour les colonies en coussins, l'aire de fixation des cormus est très plane, tandis que la surface est bombée avec les contours arrondis. La tunique, assez ferme, difficile à déchirer et lisse au toucher, n'agglutine pas le sable et les débris coquillers, sauf à la base. Dimensions des colonies : Longueur : 30 à 50 mm ; Largeur : 20 à 30 mm ; Epaisseur : 5 à 10 mm.

Les zoïdes sont nombreux et bien visibles. Il n'y a pas de systèmes apparents. La longueur des zoïdes varie de 2,5 à 4,5 mm suivant l'état de développement de l'abdomen. Le thorax mesure entre 0, 7 et 1 mm.

Les siphons sont tous les deux 6-lobés et dirigés vers l'avant. Les lobes sont courts, triangulaires, avec les extrémités aiguës ou un peu arrondies. Le siphon cloacal forme un tube un peu plus long que le siphon buccal.

Environ 10 filets tentaculaires, tous de même taille.

La branchie a 3 rangs de trémas bien visibles, malgré la légère opacité du thorax. Les trémas paraissent peu nombreux mais serrés : une dizaine par demi-rangée.

L'abdomen est long. Le tube digestif présente la torsion habituelle : l'oesophage reste étroit ; l'estomac à paroi lisse, situé dans le quart postérieur de l'abdomen, est peu volumineux, plus haut que large, de forme ovale (dans les zoïdes contractés, l'estomac est plutôt globuleux) ; l'intestin, large, est droit dans les abdomens en extension, ou circonvolutionné dans les abdomens contractés ; le rectum atteint le 2e rang de trémas.

On compte jusqu'à 15 follicules testiculaires sous la forme d'une grappe massive, disposée dans la boucle intestinale, en arrière de l'estomac. L'ovaire à 1, 2 ou 3 œufs, est au centre de l'amas folliculaire. Le spermiducte, nettement blanchâtre, assez large, accompagne l'intestin sur toute sa longueur.

Discussion.

Je rattache ces cormus à *Eudistoma rhodopygæ* (Sluiter) bien que leur forme soit différente de l'espèce-type qui montre soit de courtes masses coniques très serrées ou de grandes élévations en doigts de gant largement séparées. Or, MICHAELSEN (1934) et MILLAR (1956) considèrent cette espèce comme très polymorphe et n'accordent, par conséquent, qu'une faible valeur systématique aux différences de forme des colonies. Les caractères tirés des zoïdes paraissent plus conformes pour justifier ma détermination.

Eudistoma möbiusi (Hartmeyer), 1905.

(Pl. II : figure 12)

Colella möbiusi Hartmeyer, 1905, p. 396.
Polycitor möbiusi Hartmeyer, 1912, p. 305.
Polycitor (Eudistoma) möbiusi Michaelsen, 1919, p. 73.

Distribution.

Ile Maurice ; Province du Cap ; Moçambique ; Tanganyika ; Zanzibar ; Sud de Madagascar : Baie de Tuléar (collection VOELTZKOW, 1898), Grand Récif de Tuléar (R. PLANTE et P. VASSEUR, 1966).

Localités.

61/184, Pointe d'Esny, 28/12/61 ; 62/1a, Trou d'eau douce, 5/1/62.

Description.

Plusieurs petites colonies molles ou semi-cartilagineuses dont les dimensions varient de 6,5 à 13 mm pour la longueur, de 2,5 à 5 mm pour la largeur et de 2,5 à 7 mm pour l'épaisseur. La tunique est incolore ou blanchâtre dans le formol, l'aspect étant vitreux ; sa surface est, pour certains cormus, légèrement incrustée de débris, soit des grains de sable ou des tests brisés de Foraminifères et de Mollusques.

Les zoïdes, très fortement pigmentés et opaques, apparaissent en bleu très sombre à travers la tunique commune où ils sont disposés soit verticalement, soit plus ou moins horizontalement.

Les caractères anatomiques des zoïdes, mesurant entre 2 et 3 mm, correspondent parfaitement à l'espèce type ainsi qu'aux spécimens récoltés à Tuléar, qui, cependant, étaient tous immatures et avaient un abdomen moins opaque, donc moins pigmenté, et une tunique nettement colorée en bleu sombre qui est la couleur caractéristique de l'espèce.

En ce qui concerne les échantillons de l'Ile Maurice, on peut ajouter les remarques suivantes. Un certain nombre de zoïdes présentent des stolons vasculaires post-abdominaux. Les siphons buccal et cloacal sont 6-lobés. Il y a 12 filets tentaculaires, toujours 8 grands et 4 petits. La branchie à 3 rangs, présente environ 20 trémas par demi-rangée ; les sillons transverses sont pigmentés en bleu sombre ; les languettes dorsales sont très longues, effilées, atteignant la moitié de la largeur du sac branchial. L'extrémité rectale est bifide. On compte environ 20 follicules testiculaires, groupés sous la forme d'une "grappe de raisin" dans l'anse intestinale (diamètre des follicules : de 105 à 140 µ).

ASCIDIIDAE

Ascidia sydneiensis Stimpson, 1855
(Pl. II : figs. 13-20)

Ascidia sydneiensis Stimpson, 1855, p. 387. HARTMEYER, 1919, p. 98-99. VAN NAME, 1945, p. 189-190. TOKIOKA, 1950, p. 133 ; 1952, p. 105-106 ; 1953, p. 223-227. MILLAR, 1955, p. 190-191 ; 1956, p. 411-413 ; 1962, p. 173-174. Pour la synonymie voir KOTT, 1952, p. 310-311.

Distribution

Espèce largement distribuée dans les mers chaudes du globe : "Indes occidentales" ; Hawaï ; Archipel malais ; Amboine ; Japon ; Afrique du Sud ; Australie ; Nouvelle-Calédonie ; Afrique de l'Ouest : Sierra Leone et Gambie.

Localités.

61/199, Flic en Flac, 23/10/61 : 2 spécimens. 62/128, Bouée Rade de Port-Louis, 11/5/62 : 2 spécimens, 62/59 : 4 spécimens, 62/60 : 1 spécimen, 62/62 : 1 spécimen fixé sur *Polyandrocarpa anguinea* (Sluiter), 62/63 : 3 spécimens, sur une bouée Rade de Port-Louis, 5/4/62.

Description.

Je ne décrirai que les deux spécimens les plus typiques numérotés 61/199. Leur longueur ne dépasse pas 25 mm. Leur forme est allongée et modérément comprimée latéralement. La tunique est mince, transparente, hyaline, de consistance semi-cartilagineuse, sans aucune incrustation de débris.

Le siphon branchial, assez long, se termine par 8 lobes bien marqués. Le siphon atrial, plus court et plus étroit, n'a que 6 lobes ; il se trouve situé vers le milieu de la ligne dorsale, et a une direction oblique légèrement dirigée vers le bas.

La musculature du manteau est très bien marquée au niveau des siphons et à la périphérie des marges dorsale et ventrale du corps. Les siphons ont une couronne de nombreuses fibres musculaires très fines et quelques fibres musculaires longitudinales plus épaisses. Tout le manteau du côté gauche, mince et transparent, ne possède aucune musculature, mais du côté droit, par contre, les marges dorsale, ventrale et postérieure sont largement bordées de bandes musculaires courtes et épaisses qui s'entrecroisent.

Un seul cercle de tentacules oraux, longs, filiformes, nombreux (60 environ), de tailles différentes.

Le tubercule dorsal, situé derrière la couronne tentaculaire, a la forme d'un cercle ouvert vers l'avant. La lame dorsale, à bord denticulé et présentant des côtes, s'étend au-delà de la région oesophagienne.

Le sac branchial atteint la partie postérieure du corps. La branchie est finement plissée avec 4 à 5 stigmas pour chaque champ branchial. De larges papilles se trouvent à l'intersection des vaisseaux longitudinaux très minces et des vaisseaux transverses. Il n'y a pas de papilles intermédiaires.

Le tube digestif s'étend sur tout le côté gauche et atteint la base du siphon buccal. L'estomac et l'intestin sont remplis de fèces. L'estomac, assez gros, est plissé longitudinalement. L'intestin, de même diamètre sur toute sa longueur, dessine deux boucles, la première boucle dépassant largement le niveau de l'ouverture anale.

Les follicules testiculaires sont très petits et apparaissent en surface sur les parois de l'intestin et au niveau des deux anses intestinales. L'ovaire est situé dans les deux anses intestinales ; l'oviducte, rempli d'œufs, accompagne le rectum jusqu'au siphon cloacal.

Discussion.

Tous les spécimens de ces différentes localités sont incontestablement référables à *A. sydneiensis*, espèce largement distribuée dans les eaux tropicales ou subtropicales mais qui présente des variations dans l'apparence externe et dans les caractères anatomiques. Parmi tous les individus de cette collection, provenant soit d'une même station ou de différentes localités, j'ai pu observer différentes morphoses : tout d'abord la taille des spécimens varie considérablement, de 10 à 50 mm pour la longueur et de 5 à 20 mm pour la largeur ; ensuite la tunique chez les individus de grande taille, est généralement sale, d'aspect grisâtre, agglutinant de la boue, des débris coquilliers et du sable ; enfin, certains points de l'anatomie comme la forme du tubercule vibratile ou la position de l'anse intestinale la plus antérieure par rapport au siphon atrial changent d'un individu à l'autre. Le tubercule vibratide, simple en demi-cercle, peut devenir complexe, soit en forme de fer à cheval avec les extrémités enroulées, soit divisé en plusieurs parties. En ce qui concerne le tube digestif, souvent distendu par les fèces, la partie antérieure de l'anse intestinale dépasse largement la base du siphon atrial ou ne s'étend pas au-delà.

A partir de ces différentes variations morphologiques, j'ai pu reconnaître parmi les 13 spécimens de l'Ile Maurice les trois sous-espèces redécrites par TOKIOKA (1953) : *A. s. sydneiensis*

(Stimpson, 1855), *A. s. divisa* (Sluiter, 1898) et *A. s. samea* (Oka, 1935), mais momentanément, je préfère retenir plus simplement la détermination spécifique.

Ascidia munda Sluiter, 1890
(Pl. III : figs. 21-23)

Ascidia translucida, Sluiter, 1890, p. 344.
Phallusia munda, Hartmeyer, 1909, p. 1403.
Ascidia munda, Hartmeyer, 1919, p. 97. Hartmeyer et Michaelsen, 1928, p. 295.

Distribution.

Australie du Nord ; Archipel malais.

Localité.

61/199, Flic en Flac, 23/10/61.

Description.

Deux spécimens à corps irrégulièrement ovale, de 30 mm de long sur 10 mm de large, aplati latéralement. La tunique est lisse, de 1 à 3 mm d'épaisseur, de consistance semi-cartilagineuse, d'aspect transparent et hyalin.

Le siphon buccal est tubulaire, de faible longueur, à 8 lobes. Le siphon atrial, situé au niveau du tiers postérieur, se réduit à un simple orifice dont la marge est 6-lobée.

Le manteau, mince et transparent, ne possède aucune musculature sauf au niveau des siphons. Le siphon buccal a de très nombreux muscles circulaires très fins et plusieurs faisceaux de muscles longitudinaux plus épais. Le siphon atrial possède un anneau de muscles circulaires très minces et toute la marge dorsale, entourant l'aire siphonale, présente des bandes musculaires longitudinales, très larges et épaisses, qui s'entrecroisent plus ou moins.

On compte jusqu'à 160 tentacules filiformes, de différentes tailles, disposés en un seul cercle.

Le tubercule dorsal est petit, en fer à cheval, ouvert vers l'avant et dont les extrémités sont légèrement recourbées. Le raphé dorsal, relativement étroit dans la région antérieure, devient plus large postérieurement ; il porte, sur toute sa longueur, des côtes et des dents.

Le sac branchial est entièrement rempli de sable. La branchie, non plissée, possède 30 sinus longitudinaux de chaque côté. Les papilles principales sont simples. Absence de papilles intermédiaires. Il y a 4 à 5 trémas par champ branchial. Les sinus tranverses sont de 4 ordres : 1, 4, 3, 4, 2, 4, 3, 4, 1.

L'oesophage est court et s'incurve vers l'estomac plissé longitudinalement. L'intestin dessine une première boucle puis se dilate en ampoule remplie de fèces et de sable. Le rectum, en partie caché, court droit en direction de l'orifice cloacal.

Les gonades sont en partie dissimulées par le tube digestif. Les follicules testiculaires sont visibles sur la paroi de l'intestin. L'ovaire est présent dans la première anse intestinale. Le spermiducte blanchâtre et l'oviducte très large, rempli d'oeufs, accompagnent côte à côte le rectum jusqu'à l'orifice cloacal.

Discussion.

Il semble qu'un certain nombre de caractères des deux exemplaires de l'Ile Maurice cadrent bien avec l'étude détaillée de HARTMEYER et MICHAELSEN (1928) sur *Ascidia munda*. En effet, l'aspect de la tunique, la position des siphons et leur musculature développée, la transparence du manteau, la forme du tubercule vibratile et l'aspect du raphé dorsal, la branchie et ses papilles simples sont tout à fait comparables à *Ascidia munda* , mais surtout cette espèce présente un intestin dilaté en "ampoule" et c'est sur ce dernier caractère, absent des autres espèces du genre Ascidia de l'Océan Indien sauf chez *A. sydneiensis* Stimpson, *A. obesa* (Herdman) et *A. julinea* Sluiter, que j'ai fondé ma détermination.

STYELIDAE

Symplegma viride Herdman, 1886
(Pl. III : figs. 24-25).

Symplegma viride Herdman, 1866, p. 144. VAN NAME, 1945, p. 232. PERES, 1948, p. 94 ; 1949, p. 198. MILLAR, 1953, p. 315 ; 1955, p. 196.
Diandrocarpa botryllopsis Van Name, 1902, p. 384.
Diandrocarpa brakenhielmi Michaelsen, 1904, p. 50.
Symplegma elegans Michaelsen, 1934, p. 154.

Distribution.

Espèce très largement répandue dans les mers chaudes du globe : Bermudes ; "Indes occidentales" ; région de Dakar ; Côte de l'Or, Afrique de l'Ouest ; Côtes Est et Sud de l'Afrique ; Madagascar : région de Tuléar ; Mer Rouge ; Australie ; Phillipines.

Localités.

62/124 (colonies de teinte jaune), 62/125 (colonies de teinte rouge), 62/126 (colonies de teinte grise), 62/127 (colonies de teinte orangée), Bouée Rade de Port-Louis, 11/5/62.

Description.

Très nombreuses colonies minces et encroûtantes, d'épaisseur variable, molles, gélatineuses, transparentes de tunique. Les zoïdes, non disposés en systèmes, sont nombreux et très serrés. A l'état vivant et suivant les colonies, la coloration des zoïdes était vive et variée : jaune, orange, rouge ou grise ; dans le formol, les colorations sont uniformément grisâtres.

Œufs en division (stades blastula et grastrula) et larves développées dans la cavité atriale. Longueur totale des larves : 1,5 mm ; longueur depuis le sommet des papilles jusqu'à la base de la queue : 0,4 mm. Les larves possèdent trois papilles frontales adhésives et une couronne de huit renflements ectodermiques.

Il y a 24 filets tentaculaires : 6 de grande taille, 6 de taille moyenne et 12 de petite taille.

Le sac branchial, le système digestif et les gonades sont parfaitement conformes à la diagnose de VAN NAME (1945).

Amphicarpa inhacae (Millar), 1956
(Pl. IV : figs. 26 - 29).

Polyandrocarpa inhacae Millar, 1956, p. 927-929.

Distribution.

Moçambique : Ile d'Inhaca.

Localité.

51/41, Ilot Barkly, 2/11/51.

Description.

Colonie assez compacte, ayant 70 × 20 mm de surface et 15 mm d'épaisseur, formé de nombreux individus serrés, réunis à la base par des stolons. L'aspect est celui d'une grappe de "raisins" et la coloration est grisâtre dans le formol.

Les zoïdes mesurent entre 4 et 8 mm en hauteur, en moyenne 6 mm. Ils sont dressés, de forme ovoïde ou en massue. Toute la tunique ainsi que les prolongements des zoïdes et les stolons sont incrustés de sable et de fins débris coquilliers sauf au niveau des deux siphons très petits, 4-lobés, situés au sommet du corps.

Le manteau, brunâtre, mince, un peu translucide, possède de nombreuses fibres musculaires, longitudinales et circulaires, fines. Il renferme, ainsi que les organes internes, de nombreuses cellules pigmentaires colorées en brun foncé.

Le siphon buccal, terminal, est un peu plus long et plus large que le siphon atrial, subterminal.

Le nombre de tentacules est supérieur à 20.

Le tubercule vibratile est une simple fente longitudinale. Sous le tubercule vibratile se trouve situé le ganglion dorsal, globuleux, et de part et d'autre du ganglion, on observe deux masses du tissu neural.

Le sac branchial présente 2 à 3 plis, très peu élevés, suivant la taille des zoïdes. Pour un individu de 6 mm, l'arrangement des sinus longitudinaux est le suivant :

GAUCHE R.D. 3 (6) 5 (4) 5 (2) 0 E.

DROITE R.D. 0 (8) 5 (5) 5 (5) 5 E.

Nombre de trémas entre deux sinus longitudinaux dans l'intervalle des plis : 2 à 4 trémas. Pour un individu de 4,5 mm avec seulement 2 plis de chaque côté, la formule branchiale est :

R.D. 0 (6) 5 (5) 5 E.

La lame dorsale est lisse, un peu épaisse, assez étroite. L'endostyle est assez haut.

L'oesophage est court, étroit, faiblement tordu. L'estomac est globuleux avec 12 plis longitudinaux et un coecum pylorique assez large, très courbé. L'intestin, large, dessine une boucle simple. L'anus a la bordure faiblement lobée.

Les gonades sont unisexuées. Les testicules piriformes sont disposés en lignes irrégulières de chaque côté du corps le long de l'endostyle, ainsi qu'en plusieurs amas dans la région médiane transversalement. J'ai compté pour un individu 24 follicules à gauche et 22 à droite. Les ovaires sont disposés en avant des testicules, grossièrement alignés le long de l'endostyle ; ils sont très larges et de forme globuleuse par rapport aux follicules. On compte 3 ovaires à gauche et 4 à droite.

Présence d'endocarpes sur le manteau de chaque côté, dont un très gros dans l'anse intestinale.

Les larves sont de grande taille, entre 1,06 et 1,2 mm depuis l'extrémité des papilles jusqu'à la base de la queue, avec trois courtes papilles et un double rang d'ampoules nombreuses.

Discussion.

L'appartenance de cette espèce au genre *Amphicarpa*, caractérisé par 2 ou 3 plis branchiaux et par de nombreuses gonades mâles et femelles irrégulièrement disposées de chaque côté du corps, ne fait aucun doute. Mais cette colonie montre aussi bien par son apparence externe que par de nombreux points de son anatomie des affinités tout à fait comparables à l'espèce *Polyandrocarpa inhacae* Millar, 1956. Or, MILLAR, par suite de l'état de maturité de sa colonie de l'Ile d'Inhaca, n'a justement pu préciser la structure exacte, ainsi que le nombre, des follicules et des ovaires et lui a donné, par conséquent, une détermination générique sous toute réserve.

Je n'ai point voulu faire du cormus de l'Ile Maurice une espèce nouvelle mais je pense qu'il doit être placé dans le genre *Amphicarpa* tout en conservant l'espèce de MILLAR. Cette décision est justifiée par le fait de la très grande similitude des deux cormus, celui de l'Ile d'Inhaca et celui de l'Ile Maurice.

Polyandrocarpa anguinea (Sluiter), 1898
(Pl. IV : figs. 30-32).

Pandocia anguinea Hartmeyer, 1913, p. 128.
Polycarpa anguinea Michaelsen, 1934, p. 132.
Styela (Polycarpa) anguinea Sluiter, 1898, p. 52.
Polycarpa anguinea Millar, 1955, p. 203-204 : 1958, p. 507-509.
Polyandrocarpa anguinea Millar, 1962, p. 186.

Distribution.

Afrique du Sud ; Brésil.

Localité.

62/62, Rade de Port-Louis, sur une bouée, 5/4/62.

Description.

Large colonie massive, encroûtante, épaisse, formée de nombreux individus très serrés, fusionnés par coalescence des cormus postérieurs de chaque zoïde, la partie antérieure libre avec les siphons se projetant un peu au-dessus de la masse commune.

Le test, surtout épais à la base, est de consistance cartilagineuse, résistant à la déchirure. La coloration dans le formol est gris foncé. L'aire de fixation des cormus est incrustée de débris coquilliers. La colonie est associée à d'autres organismes surtout des Ascidies comme *Ascidia sydneiensis* Stimpson, *Microcosmus exasperatus* Heller, *Styela pupa* Heller.

Les deux siphons, tubulaires, sont très longs avec des fibres musculaires circulaires nombreuses et des fibres longitudinales. Le siphon buccal est terminal tandis que le siphon cloacal, situé vers le milieu de la ligne dorsale, est perpendiculaire.

Le manteau est mince, sa musculature restant très faible.

Il y a environ 35 tentacules simples en trois tailles dont 12 grands, épais.

Le sac branchial présente 4 plis méridiens de chaque côté avec généralement 6 à 8 sinus longitudinaux entre les plis et 2 à 4 trémas par champ branchial. Présence de vaisseaux parastigmatiques. Formule branchiale d'un individu :

GAUCHE R.D. 4 (11) 8 (16) 6 (15) 7 (12) 6 E.

DROITE R.D. 7 (12) 6 (15) 7 (15) 8 (11) 6 E.

Le tubercule dorsal a la forme d'un S, à direction oblique vers la gauche. La lame dorsale est large et présente régulièrement des côtes sur la face interne.

L'oesophage est court. L'estomac, assez large, ovoïde, sans coecum pylorique, à surface lisse, montre l'indication d'un plissement interne : il y a 12 plis bien marqués. L'intestin remonte droit vers le siphon atrial ou dessine la forme d'un S. L'anus est à bordure simple.

Nombreux polycarpes (20 à 25 au total), de forme allongée, disposés transversalement par rapport à l'axe du corps. Chaque gonade est constituée d'un double rang de testicules coiffant l'ovaire.

Absence d'endocarpe dans l'anse intertinale.

Remarque.

La station de l'Ile Maurice accroît notablement l'aire de dispersion de cette espèce qui semblerait être circumtropicale.

Polyandrocarpa (Eusynstyela) tincta (Van Name), 1902.
(Pl. IV : figs. 33 - 36).

Eusynstyela tincta Michaelsen, 1904, p. 37.
Michaelsenia tincta Van Name, 1902, p. 381.
Polyandrocarpa tincta Van Name, 1921, p. 414 : 1945, p. 250. PERES, 1949, p. 200 ; 1951, p. 1065. MILLAR, 1956, p. 926.

Distribution.

Bermudes et Floride ; Sénégal : Moçambique : Ile d'Inhaca.

Localité.

62/123, Bouée Rade de Port-Louis, 11/5/62.

Description.

Une grande colonie encroûtante avec de larges surélévations épaisses de forme ovale. Dimensions du cormus encroûtant : 70 × 50 × 2-3 mm. Dimensions des lobes : 25 × 10 × 5 mm. La coloration est rose-violacée-pourpre à l'état vivant et dans le formol.

Les zoïdes, très serrés, sont enveloppés dans une tunique commune fortement cartilagineuse, coriace, difficile à déchirer. Des zoïdes nombreux, à contours ovales ou elliptiques, s'élèvent deux siphons proéminents de 1 à 2 mm de long. La base du cormus contient des agglomérations de petites coquilles.

Les zoïdes, colorés en jaune, mesurent 3,5 à 6 mm de long, 2 à 3,5 mm de large et 1 mm d'épaisseur. Ils sont comprimés dorso-ventralement.

Le manteau est mince, plus ou moins transparent ; sa musculature est très fine. Les siphons, largement séparés sur la face dorsale, sont colorés en rose-pourpre.

Les tentacules sont simples et filiformes : environ 25 filets tentaculaires en trois tailles (3 grands, 7 de taille moyenne et 15 de petite taille). Le tubercule dorsal est ovale, allongé dans le sens antéro-postérieur.

Le sac branchial présente 4 plis méridiens de chaque côté, le 1er et le 3e pli étant généralement les plus élevés. Formule branchiale :

GAUCHE R.D. 0 (7) 2 (8) 2 (4) 0 (1) 0 E.
ou R.D. 1 (10) 1 (4) 1 (6) 2 (4) 1 E.
DROITE R.D. 0 (6) 0 (4) 2 (10) 2 (6) 1 E.
ou R.D. 0 (10) 0 (4) 2 (8) 0 (4) 0 E.

Environ 6 trémas dans chaque champ branchial pour la plus grande partie du sac branchial ; 7 à 8 trémas dans les champs branchiaux au niveau de l'endostyle et 12 trémas au niveau de la ligne dorsale. Vaisseaux parastigmatiques présents.

L'oesophage est court, bien courbé. L'estomac est allongé, de teinte jaune-orangée avec 13 à 14 plis longitudinaux et un coecum pylorique bien net. L'intestin dessine un S. Le rectum croise l'oesophage. L'anus, avec deux lèvres bien marquées, est situé à peu près à la même hauteur que l'entrée de l'oesophage.

Les gonades, attachées à la paroi interne du manteau dans la région ventrale, sont présentes des deux côtés du corps et forment deux rangs parallèles à l'endostyle, de 4 à 6 gonades dans chaque rang. Chaque gonade est une sphérule contenant 2 testicules en forme "d'haricot", faisant face à la paroi interne du manteau, et un nombre variable d'œufs.

Endocarpes piriformes s'élevant de la paroi interne du manteau.

Polycarpa nigricans Heller, 1877.
(Pl. V : figs. 37 - 40)

Polycarpa nigricans Heller, 1877, p. 102. HERDMAN, 1891, p. 583. HARTMEYER, 1905, p. 390. KOTT, 1952, p. 229.

Distribution.

Ile Maurice.

Localité.

703, Cassis, 6/11/41.

Description.

Cinq spécimens de 25 à 30 mm de long. La forme du corps est allongée, oblongue, avec les deux ouvertures des siphons situées dans la région antérieure. L'aire de fixation des individus est postérieure et présente des expansions de la tunique.

La tunique est peu épaisse de 0,5 à 2 mm mais très coriace. Sa surface est ridée mais sans incrustation de débris. La coloration est brunâtre.

Les deux siphons tubulaires sont assez courts, 4 mm environ. Le siphon buccal, plus large, est antérieur. Le siphon cloacal est situé au tiers antérieur de la ligne dorsale.

Le manteau, brun très foncé, est fortement musclé avec surtout des faisceaux très serrés de fibres circulaires qui s'entrecroisent formant une couverture continue, rendant le manteau entièrement opaque.

Environ 40 tentacules simples en trois tailles, les plus grands fins et assez longs.

Le tubercule dorsal en forme d'S a une disposition dorso-ventrale. L'aire péri-tuberculaire semble mamelonnée.

Le sac branchial a 4 plis méridiens bien marqués de chaque côté du corps. Formule branchiale pour un individu détuniqué de 18 mm de long :

GAUCHE R.D. 1 (6) 3 (10) 3 (11) 3 (9) 3 E.
DROITE R.D. 0 (11) 2 (10) 2 (10) 3 (8) 1 E.

On compte 10 trémas entre deux sinus longitudinaux dans l'intervalle des plis et 4 trémas entre deux sinus longitudinaux sur les plis. Le raphé dorsal est lisse.

L'oesophage est court, étroit. L'estomac, ovoïde, peu volumineux, ne présente pas de plis externes longitudinaux. L'intestin, large, dessine une simple boucle dans la partie postérieure du corps. Le rectum, un peu plus étroit que l'intestin, remonte droit le long de la ligne dorsale du sac branchial. L'anus, avec deux lèvres assez larges, a sa bordure finement crenelée. Pas de coecum pylorique.

Il y a 22 polycarpes sous formes de petits sacs du côté droit du corps et 13 du côté gauche. Les polycarpes sont arrangés plus ou moins en rangs parallèles de chaque côté de l'endostyle : il y a 3 à 4 rangs. Chaque polycarpe est constitué, côté manteau, d'un amas de testicules réunis à un spermiducte commun ; l'ovaire, du côté du sac branchial, se prolonge par un oviducte s'ouvrant en avant du spermiducte.

Un seul endocarpe, large, en forme de feuille, dans la boucle intestinale.

Présence de nombreuses poches d'air enveloppées dans le manteau.

Discussion.

Ces nouveaux spécimens récoltés à l'Ile Maurice, ne diffèrent pas de façon appréciable de la description de HARTMEYER (1905) ; néanmoins, je n'ai pas pu préciser comme dans cette description, si les individus, très nombreux, croissaient ensemble.

Mais le très large endocarpe enveloppé par l'anse intestinale, la simplicité du tubercule vibratile, la présence de glandes hermaphrodites disposés sur plusieurs rangs vers le milieu du corps, la teinte brune des individus, sont des caractères tout à fait comparables à la diagnose de *Polycarpa nigricans* Heller, espèce qui par ses affinités anatomiques, se rapproche également de *P. obtecta* Traustedt (1883), de *P. obscura* Heller (1878) et de *P. moebi* Michaelsen (1905).

Cnemidocarpa madagascariensis Hartmeyer, 1916.
(Pl. V : figs. 41 - 43)

Cnemidocarpa madagascariensis Hartmeyer, 1916, p. 222-224.

Distribution.

Sud-Ouest de Madagascar : Baie de Tuléar (collection VOELTZKOW, 1898).

Localité.

62/118, Flic en Flac, 24/4/62.

Description.

Unique spécimen, en assez mauvais état, mesurant au total 25 mm de long et 10 mm de large, pour une distance intersiphonale de 10 mm environ.

La tunique, opaque, brunâtre, mince mais coriace, était fixée au substrat par un prolongement postérieur plus épais. La surface de cette tunique apparait fortement ridée.

Les siphons sont nets, fortement musclés. Le siphon cloacal se situe au milieu de la ligne dorsale du corps. Le manteau, également coloré en brun, est rendu opaque par une couverture continue de fibres musculaires circulaires fines ; les fibres musculaires longitudinales sont nettement moins nombreuses mais plus épaisses.

Il y a environ une quinzaine de grands tentacules simples et un à deux petits tentacules entre chaque intervalle laissé par les plus grands. A la base du siphon cloacal, il y a de nombreux tentacules très petits et fins.

Le tubercule vibratile a la forme d'un C ouvert vers l'avant avec les extrémités enroulées.

La branchie, contractée et déchirée, est d'observation difficile. Les plis méridiens ont 12 à 14 sinus longitudinaux. Dans l'intervalle des plis, on compte 3 à 4 sinus longitudinaux et 5 trémas entre deux sinus. Le raphé dorsal est une membrane lisse et élevée.

Le tube digestif, également en mauvais état, présente un estomac avec des cannelures internes marquées et un rebord anal découpé en 11 languettes arrondies.

Les gonades, toutes hermaphrodites, sont plus ou moins allongées, avec l'ovaire du côté de la branchie et les testicules du côté de la paroi du corps. Elles sont au nombre de 5 du côté droit du corps et sont localisées dans la zone médiane de la masse viscérale. La partie gauche du corps, en partie manquante, ne présentait qu'une gonade.

De gros endocarpes entourent les gonades.

Discussion.

Malgré son mauvais état, je pense que l'on peut attribuer ce *Cnemidocarpa* de l'Ile Maurice à l'espèce de HARTMEYER, *C. madagascariensis*. En effet, la taille et la consistance de la tunique, l'écartement des siphons, la musculature du manteau sont peu différents de l'espèce type ; d'autre part, le nombre de tentacules du siphon buccal, la forme du tubercule vibratile, l'aspect et la disposition des gonades, la présence de gros endocarpes entre les gonades sont des caractères anatomiques suffisamment proches de la description de HARTMEYER (1816) ; enfin, le faible éloignement géographique est en faveur de l'appartenance de ce *Cnemidocarpa* à l'espèce connue des eaux malgaches.

Styela partita (Stimpson), 1852
(Pl. V : figs. 44-47).

Cynthia partita Stimpson, 1852, p. 231.

Pour la synonymie voir VAN NAME, 1945, p. 290 ; TOKIOKA, 1954, p. 88.

Distribution.

Côte Est de l'Amérique du Nord ; Côte Sud-Ouest de l'Europe ; Méditerranée ; Adriatique ; Afrique de l'Ouest ; Japon ; Nouvelle-Calédonie.

Localités.

62/60, Rade de Port-Louis sur une bouée, 5/4/62 : 10 spécimens ; 62/129, Bouée Rade de Port-Louis, 11/5/62 : 1 spécimen.

Description.

Les spécimens mesurent de 13 mm à 25 mm de long. Le corps est ovale, attaché soit par le côté gauche ou par les parties postérieures droite ou gauche. L'ouverture branchiale est terminale ; l'ouverture atriale est subterminale ou située près du milieu du corps. Les deux ouvertures, proéminentes, de teinte orangée, sont 4-lobées. La tunique est peu épaisse mais résistante, de coloration jaune-grisâtre à brun, à surface plus ou moins ridée. La surface intérieure de la tunique est gris perle.

Le manteau est mince, translucide, jaunâtre ; sa musculature est faible.

Il y a plus de 30 tentacules en deux tailles alternées.

Le tubercule dorsal a la forme d'un C.

Les sinus longitudinaux du sac branchial qui compte 4 plis méridiens de chaque côté, sont arrangés de la façon suivante pour un individu de 20 mm de long :

GAUCHE R.D. 4 (9) 4 (8) 6 (10) 4 (6) 3 E.

DROITE R.D. 4 (9) 6 (9) 6 (8) 6 (6) 3 E.

Vaisseaux parastigmatiques présents. Il y a 5 à 6 trémas entre deux sinus longitudinaux dans l'intervalle des plis et 3 trémas entre deux sinus longitudinaux sur les plis.

Oesophage court, estomac allongé avec 22 plis longitudinaux. Pas de coecum pylorique. Intestin en forme d'S. Anus lobé. Présence de très petits tentacules atriaux.

Deux longues gonades de chaque côté du corps ; la gonade postérieure du côté gauche est située dans la 2e boucle intestinale.

Nombreux endocarpes sur les faces internes gauche et droite du manteau.

Styela pupa Heller, 1878.
(Pl. VI : figs. 48-50)

Styela pupa Heller, 1878, p. 107. HERDMAN, 1891, p. 586. MICHAELSEN, 1934, p. 132. MILLAR, 1955, p. 204.
Tethyum pupa Hartmeyer, 1911, p. 569.

Distribution.

Afrique du Sud.

Localité.

62/62, Rade de Port-Louis sur une bouée, 5/4/62 : 1 spécimen fixé sur *Polyandrocarpa anguinea* (Sluiter).

Description.

Un seul spécimen dont les dimensions sont : Longueur : 12 mm ; Distance dorsoventrale : 8 mm ; Epaisseur : 5 mm. Aire de fixation par l'extrémité postérieure. Les ouvertures des siphons, antérieures et 4-lobées, sont médiocrement écartées et non proéminentes. La tunique est mince mais résistante, opaque, de coloration beige à la base mais devenant brunâtre vers le sommet. La forme est ovale, presque quadrangulaire. La surface est ridée.

Le manteau est assez musclé avec des fibres musculaires circulaires et longitudinales. Le manteau a une teinte brune par suite de la présence de cellules pigmentaires dans son épaisseur.

Les siphons sont courts. Le siphon atrial est peu décalé sur la ligne dorsale par rapport au siphon buccal.

Les tentacules sont simples de trois ordres dont 20 grands.

Le tubercule dorsal, en fer à cheval, est ouvert vers la gauche. Le raphé dorsal est lisse, assez large postérieurement.

Le sac branchial présente 4 plis méridiens de chaque côté. Formule branchiale :

GAUCHE R. D. 4 (14) 5 (11) 6 (14) 6 (8) 3 E.

DROITE R. D. 4 (13) 6 (12) 6 (16) 5 (10) 2 E.

Les 1er et 3e plis sont plus élevés que les 2e et 4e. On compte 8 trémas entre deux sinus longitudinaux dans l'intervalle des plis et 5 trémas sur les plis. Vaisseaux parastigmatiques présents.

Estomac avec 20 plis longitudinaux. Rectum évasé en forme de "trompette". Bordure anale lobée.

Une paire de gonades de chaque côté du corps.

Nombreux endocarpes sur toute la face interne du manteau.

PYURIDAE

Pyura pulla (Sluiter), 1900
(Pl. VI : figs. 51-55).

Cynthia pulla Sluiter, 1900, p. 28.
Pyura pulla Hartmeyer, 1909, p. 1341. MICHAELSEN, 1922, p. 385. BREWIN, 1946, p. 124.

Distribution.

Nouvelle-Zélande.

Localité.

57/64, Trou d'eau douce, 3/12/57.

Description.

Un seul spécimen de 70 mm de long, fixé par la partie postérieure et ventrale de la tunique. La tunique, opaque, cartilagineuse, est très épaisse (environ 5 mm), dure surtout au niveau de l'aire de fixation, à la partie droite du corps ainsi qu'autour des ouvertures siphonales et plus mince (environ 1 mm) à la partie gauche du corps. La surface de la tunique est parcourue par des rides bien marquées ; sa coloration est blanchâtre sauf l'aire des ouvertures siphonales qui est rose.

L'ouverture buccale est terminale et l'ouverture atriale subterminale. Les spinules sont fines, grandes et serrées, mesurant de 0,05 à 0,07 mm en longueur. Les siphons sont tubulaires, d'égale longueur, mais le siphon atrial est plus étroit que le siphon buccal. La tunique interne des siphons est colorée en rouge vif. Les siphons ont de très fins et nombreux muscles circulaires et longitudinaux tandis que les aires siphonales possèdent de très fortes bandes musculaires épaisses, longitudinales et circulaires. Le manteau, de teinte jaune-orangée, a des bandes musculaires larges et épaisses du côté dorsal devenant plus fines et nombreuses du côté ventral ; ces bandes musculaires s'entrecroisent plus ou moins.

On observe environ 12 tentacules coronaux, falciformes, grands ou moyens, disposés sans ordre. Chaque tentacule porte deux séries de ramifications dont la longueur peut atteindre le tiers de la taille du tentacule. Ces ramifications portent elles-mêmes de très petites digitations plus ou moins divisées.

Le tubercule vibratile, assez élevé, a la forme d'un S dont la corne droite s'enroule nettement en colimaçon. La lame dorsale est divisée en une série de languettes très serrées, longues et effilées. L'endostyle forme un sillon net.

La branchie compte 6 plis méridiens de chaque côté. L'arrangement des vaisseaux longitudinaux est le suivant :

GAUCHE R.D. 2 (20) 5 (24) 6 (23) 6 (21) 5 (20) 5 (18) 4 E.

DROITE R.D. 2 (18) 4 (22) 5 (26) 6 (23) 5 (20) 4 (20) 4 E.

Nombre de trémas dans l'intervalle des plis entre deux sinus longitudinaux : 8 trémas. Nombre de trémas sur les plis entre deux sinus longitudinaux : 5 à 6 trémas. Des vaisseaux parastigmatiques recoupent les trémas sur les plis et entre les plis.

Le tube digestif forme une simple boucle fermée et le sommet de l'anse intestinale visible au-dessus de la gonade, remonte très haut sur la face gauche du manteau. La glande hépatique semble d'une seule masse.

Les gonades, une de chaque côté, sont formées de plusieurs lobes massifs plus ou moins sphériques, en deux rangs du côté droit. La gonade gauche est située dans la boucle intestinale.

Discussion.

A part le nombre plus faible de filets tentaculaires, cette *Pyura* se rapproche de *P. pulla* (Sluiter) par des caractères très voisins de ceux indiqués par SLUITER (1900), par MICHAELSEN (1922) et par BREWIN (1946). Ces caractères concernent principalement la forme générale du corps, la musculature très puissante du manteau, la présence des épines tunicales, longues et effilées des siphons, la structure de la branchie et enfin, la disposition et la forme des gonades.

Pyura momus (Savigny), 1816.
(Pl. IV : figs. 56-58 ; Pl. VII : figs. 59-60).

Cynthia momus Savigny, 1816, p. 143.
Cynthia pallida Heller, 1878, p. 96.
Halocynthia pallida Michaelsen, 1905, p. 83.
Pyura momus f. *pallida* Michaelsen, 1918, p. 10.
Pyura pallida Michaelsen, 1908, p. 269.
Rhabdocynthia pallida Herdman, 1891, p. 575.
Herdmania momus Van Name, 1945, p. 341.
Pyura momus Monniot, 1965, p. 102.

Distribution.

Espèce très largement distribuée dans toutes les mers chaudes du globe : Côtes américaines de l'Atlantique entre Cuba et Rio de Janeiro ; Mer Rouge : Golfe de Suez, Golfe d'Akaba ; Océan Indien : Golfe de Tadjourah, Ile du Moçambique, Ile Maurice, Ceylan, Archipel malais ; Océan Pacifique : Japon, Philippines, Nouvelle-Calédonie.

Localités.

62/128, Bouée Rade de Port-Louis, 11/5/62 : 1 spécimen ; 62/60, Rade de Port-Louis sur une bouée, 5/4/62 : 3 spécimens.

Description.

Le plus grand de ces 4 spécimens mesure 50 mm de long sur 40 mm de distance dorso-ventrale. La forme du corps est ovale. La tunique est cartilagineuse, molle, opaque, incolore, de 1 à 4 mm d'épaisseur ; sa surface est irrégulière, ridée, recouverte de vase et d'organismes et incrustée de débris coquilliers.

Les ouvertures siphonales sont subterminales.

Le manteau présente les spicules calcaires caractéristiques en forme d'oxes ou de styles de Spongiaires. Il est modérément épais dorsalement, où la musculature longitudinale forme des bandes épaisses, plus mince et transparent ventralement.

Les spicules sont également présents dans les organes internes divers comme les tentacules, le tubercule dorsal, la sac branchial.

Les tentacules coronaux, falciformes, de taille inégale, sont disposés irrégulièrement : le nombre varie de 13 à 15 suivant les individus.

Le tubercule vibratile est en forme de fer à cheval avec les cornes enroulées. La lame dorsale est divisée en une série de languettes.

Le sac branchial compte 7 à 8 plis de chaque côté. L'arrangement des vaisseaux longitudinaux est le suivant chez l'individu de 50 mm :

GAUCHE R.D. 2 (12) 2 (16) 2 (18) 2 (20) 3 (16) 3 (12) 2 (10) 2 (8) 1 (2) 0 E.

DROITE R.D. 1 (12) 2 (16) 2 (20) 2 (18) 2 (16) 2 (16) 2 (12) 1 (10) 0 E.

Nombre de trémas dans l'intervalle des plis et sur les plis entre deux sinus longitudinaux : 10 trémas.

Le système digestif est simple. La boucle intestinale est fermée. L'oesophage est court, légèrement courbé. L'estomac est allongé et contre sa paroi dorsale se trouve accolé le foie. Le rectum est court.

Il y a une gonade de chaque côté, de forme massive et allongée. L'ovaire, aux contours irréguliers et sinueux, est entouré par les follicules testiculaires. La gonade gauche est située dans l'anse intestinale.

Microcosmus exasperatus Heller, 1878.
(Pl. VII : figs. 61-62).

Microcosmus exasperatus Heller, 1878, p. 99.

Pour la synonymie voir VAN NAME, 1945, p. 346. TOKIOKA, 1952, p. 130.

Distribution.

Espèce à très large répartition dans les eaux tropicales du globe : Bermudes ; "Indes occidentales" ; Mer Rouge ; Côtes Est et Sud de l'Afrique ; Archipel malais ; Côte Est de l'Australie ; Japon ; Nouvelle-Calédonie ; Hawaï.

Localités.

62/129, Bouée Rade de Port-Louis, 11/5/62 : 2 spécimens ; 62/60, Rade de Port-Louis sur une bouée, 5/4/62 : 6 spécimens ; 62/62, Rade de Port-Louis sur une bouée, 5/4/62 : 1 spécimen fixé sur *Polyandrocarpa anguinea* (Sluiter).

Description.

Neuf spécimens dont le plus grand mesure 50 mm de long et le plus petit 15 mm. Le corps est irrégulièrement allongé ou ovale, de couleur orangée à rouge sombre, attaché ventralement. Les ouvertures sont largement séparées sur le côté dorsal.

La tunique est peu épaisse mais coriace, ridée, plus ou moins recouverte de débris coquilliers et d'organismes tel que l'Ascidie composée *Symplegma viride* Herdman. Intérieurement, la tunique est rose-blanc nacré.

Les siphons subterminaux, mesurent 6 mm pour les plus grands individus.

Le manteau possède de très nombreuses bandes musculaires circulaires sur les siphons et à la base des siphons ainsi que des fibres radiaires sur les siphons et sur les aires siphonales gauche et droite du corps où elles s'entrecroisent.

Les tentacules sont au nombre de 20 dont 10 très grands.

Le tubercule dorsal, en forme de C avec les branches enroulées, s'ouvre en avant et obliquement vers la gauche. La lame dorsale est large et lisse. L'endostyle forme un sillon net.

Le sac branchial compte 9 plis méridiens à droite et 8 plis méridiens à gauche. La formule branchiale s'établit ainsi pour un individu de 30 mm de long :

GAUCHE R.D. 4 (16) 4 (8) 4 (20) 5 (20) 5 (20) 5 (18) 4 (12) 2 (3) 0 E.

DROITE R.D. 4 (14) 4 (16) 4 (21) 5 (20) 5 (18) 5 (16) 4 (14) 4 (10) 3 (3) 0 E.

On observe 8 stigmas entre deux sinus dans l'intervalle des plis branchiaux.

Le tube digestif forme une boucle fermée ; l'anse intestinale renferme le lobe antérieur de la gonade gauche. La glande hépatique, large, est constituée de ponctuations verdâtres.

Les gonades, une de chaque côté du corps, sont formées de plusieurs lobes massifs : 4 lobes à droite et 3 lobes à gauche.

MOLGULIDAE

Molgula natalensis (Michaelsen), 1918.
(Pl. VII : figs. 63-68).

Ctenicella natalensis Michaelsen, 1918, p. 2.

Distribution.

Afrique du Sud : Natal (Durban).

Localité.

52/79, Ilot Barkly, 24/4/52.

Description.

Nombreux individus au corps ovoïde, globuleux ou comprimé latéralement. La tunique est translucide, incolore mais très généralement recouverte d'une couche de vase, de menus débris et d'Algues filamenteuses qui adhèrent fortement à la paroi de la tunique. Cette adhérence est favorisée par la présence d'un chevelu de poils sur toute la surface de la tunique.

Les ouvertures des siphons sont très rapprochées sur la ligne dorsale et apparaissent au sommet de boursoufflures de la tunique. La tunique est mince mais résistante à la déchirure. Intérieurement, la tunique est lisse, brillante et d'aspect nacré.

Dimensions des spécimens : Longueur : 10 à 16 mm.
Distance dorso-ventrale maxima : 6 à 10 mm.
Epaisseur : 5 à 9 mm.
Distance intersiphonale : 2 à 3 mm.

Les siphons sont d'égale longueur, orangés, tubulaires et coniques.

Le manteau est une très fine membrane incolore, transparente qui se déchire très facilement. Autour des siphons, le manteau est fortement musclé : présence de larges bandes, très épaisses, circulaires et longitudinales. Dans la région ventrale, le manteau présente quelques fibres musculaires qui s'entrecroisent.

La couronne tentaculaire ferme complètement le siphon buccal : il y a 16 tentacules de deux ordres, les plus grands étant doublement pennés.

Le tubercule vibratile est simple en forme d'S. Le raphé dorsal, lisse, forme une membrane continue plus ou moins plissée, devenant assez large au niveau de l'oesophage.

La branchie montre 7 plis méridiens de chaque côté. Les plis, longs et aplatis ventralement, deviennent courts, épais et plus développés dorsalement. Les trémas longitudinaux, droits et arrangés régulièrement en rangs transverses, sont parallèles aux plis sauf dans les régions du raphé dorsal et de l'endostyle où ils deviennent plus ou moins courbés, en forme de petites spirales disposées irrégulièrement. Formule branchiale d'un individu de 13 mm de long :

GAUCHE R. D. 0 (7) 0 (7) 0 (7) 0 (7) 0 (5) 0 (5) 0 (3) 0 E.

DROITE R. D. 0 (7) 0 (7) 0 (7) 1 (7) 0 (5) 0 (5) 0 (3) 0 E.

Nombre de trémas dans l'intervalle des plis entre deux sinus longitudinaux : 15 trémas. Nombre de trémas sur les plis entre deux sinus longitudinaux : 6 à 7 trémas. Les trémas sur les plis sont fins, allongés, régulièrement recoupés par un sinus parastigmatique ; dans l'intervalle des plis, ils sont plus larges, ovales ou elliptiques.

Le tube digestif de diamètre presque uniforme, présente une boucle primaire très serrée et une boucle secondaire qui dessine un C remontant très haut sur la face gauche du manteau. La glande hépatique est constituée d'une seule masse.

Les gonades, une de chaque côté, constituent deux masses compactes, rondes ou oblongues. Chaque masse comprend un ovaire central entouré par les follicules testiculaires plus ou moins piriformes ou lobés. L'ovaire est orangé ; les glandes mâles sont jaunes. La gonade de gauche se trouve en partie à l'intérieur de l'anse intestinale secondaire.

Le rein, en forme d'haricot, est situé à droite de la branchie.

Discussion.

Cette espèce a été, à l'origine, décrite par MICHAELSEN pour un spécimen récolté au Sud de l'entrée du Port de Durban, sur un fond de sable au niveau de la zone rocheuse à basse-mer. En ce qui concerne les spécimens récoltés à l'Ile Maurice, c'est une nouvelle localisation de cette espèce dont la diagnose est tout à fait conforme à la description de MICHAELSEN, à part la présence sur la tunique de poils, qui peuvent être confondus avec le revêtement végétal, et le nombre légèrement plus élevé de filets tentaculaires.

CONCLUSION.

La liste des Ascidiès, décrites dans ce présent travail, permet d'établir quelques considérations générales sur leur répartition dans le reste du monde.

1° On peut constater, tout d'abord, un fort pourcentage (30 %) d'espèces propres à la faune de l'Afrique du Sud et de Madagascar : *Tridemnum sansibaricum*, *Eudistoma rhodopyge*, *Eudistoma möbiusi*, *Amphicarpa inhacae*, *Styela pupa*, *Cnemidocarpa madagascariensis*, *Molgula natalensis*.

2° La collection de l'Ile Maurice montre également un pourcentage aussi élevé d'espèces largement distribuées dans toutes les mers chaudes du globe : *Didemnum candidum*, *Ascidia sydneiensis*, *Symplegma viride*, *Styela partita*, *Pyura momus*, *Microcosmus exasperatus*.

3° La station de l'Ile Maurice étend considérablement l'aire de répartition circumtropicale de trois espèces : *Tridemnum meridionale*, *Polyandrocarpa anguinea*, *Polyandrocarpa (Eusynstyela) tincta*.

4° Deux espèces sont communes à l'Océan Indien et au Pacifique : *Tridemnum natalense* et *Pyura pulla*.

5° Une seule espèce semble provisoirement propre à l'Océan Indien : *Ascidia munda*.

6° Enfin, deux espèces sont momentanément endémiques des eaux de l'Ile Maurice : *Pseudodistoma mauritiana* et *Polycarpa nigricans*.

En conclusion, la faune ascidiologique de l'Ile Maurice présente avec les régions voisines de l'Afrique du Sud et de Madagascar de larges affinités ; d'autre part, elle renferme également un nombre assez élevé d'espèces cosmopolites ou à peu près cosmopolites de toutes les mers chaudes du globe, les localisations des récoltes étant très littorales.

ABSTRACT.

A systematic account is given of the ascidians from Maurice Island, Indian Ocean. Twenty-one species are identified. Of the total, one is described as new species. The distribution of the species is briefly discussed.

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PLANCHES

PLANCHE I

Pseudodistoma mauritiana sp. n.

Figure 1 : Zoïde isolé, 10 × 4.

Didemnum candidum Savigny.

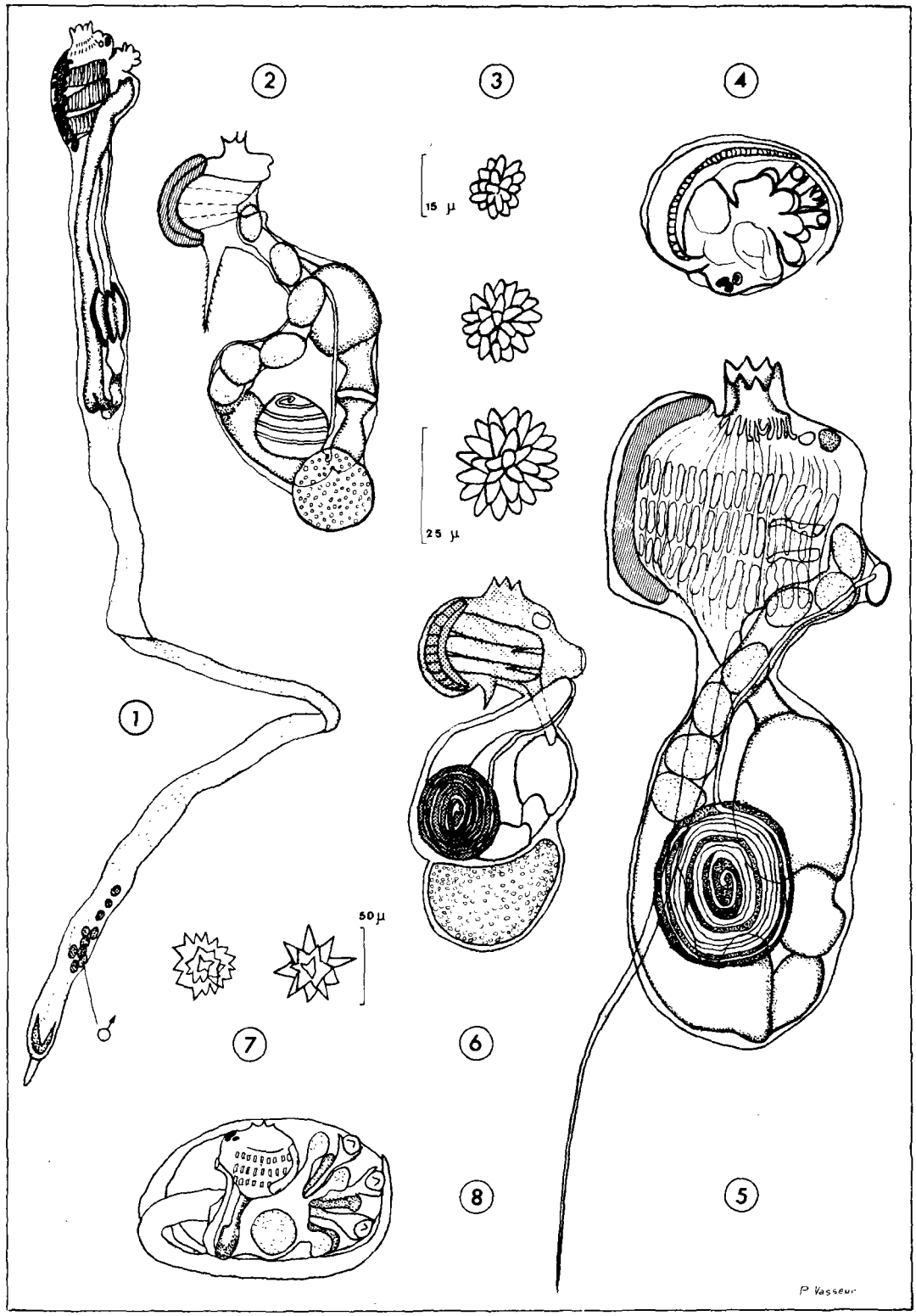
Figure 2 : Zoïde isolé, 10 × 10.
Figure 3 : Spicules.
Figure 4 : Larve, 15 × 10.

Tridemnum sansibaricum (Michaelsen)

Figure 5 : Zoïde isolé, 10 × 10.

Tridemnum natalense Michaelsen.

Figure 6 : Zoïde isolé, 10 × 10.
Figure 7 : Spicules.
Figure 8 : Larve, 10 × 10.



PL. I

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PLANCHE II

Tridemnum meridionale Millar.

Figure 9 : Zoïde isolé, 10 × 10.
Figure 10 : Spicules.

Eudistoma rhodopyge (Sluiter).

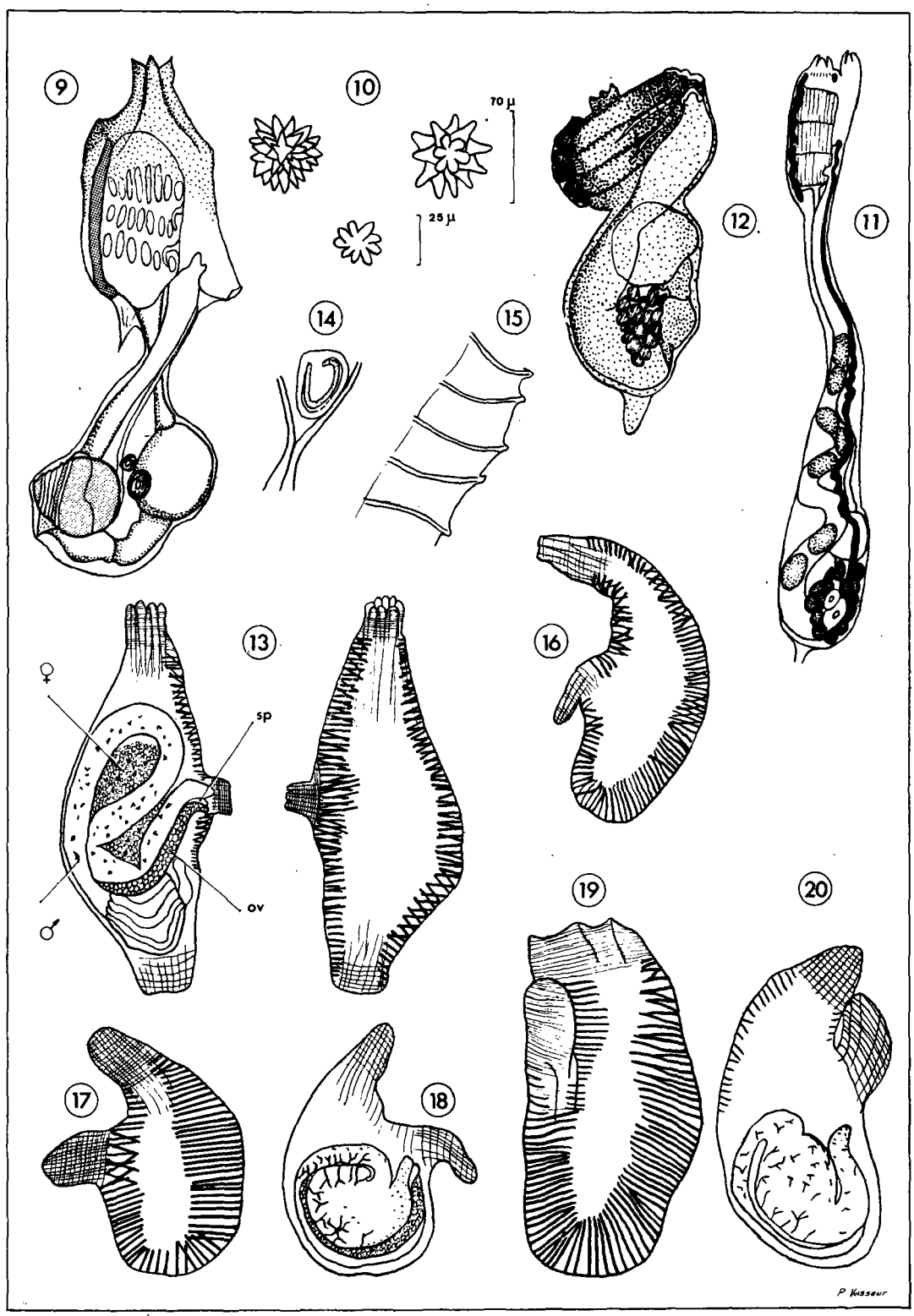
Figure 11 : Zoïde isolé, 10 × 4.

Eudistoma mobiusi (Hartmeyer).

Figure 12 : Zoïde du côté gauche, 10 × 4.

Ascidia sydneiensis Stimpson.

Figure 13 : Individu type, côtés gauche et droit du corps, × 5.
Figure 15 : Lame dorsale, 15 × 4.
Figures 16-20 : Un groupe de trois individus morphologiquement différents :
Figure 16 : Animal détuniqué vu du côté droit.
Figure 17-18 : Animal détuniqué vu du côté droit et du côté gauche.
Figure 19-20 : Animal détuniqué vu du côté droit et du côté gauche.



PL.II

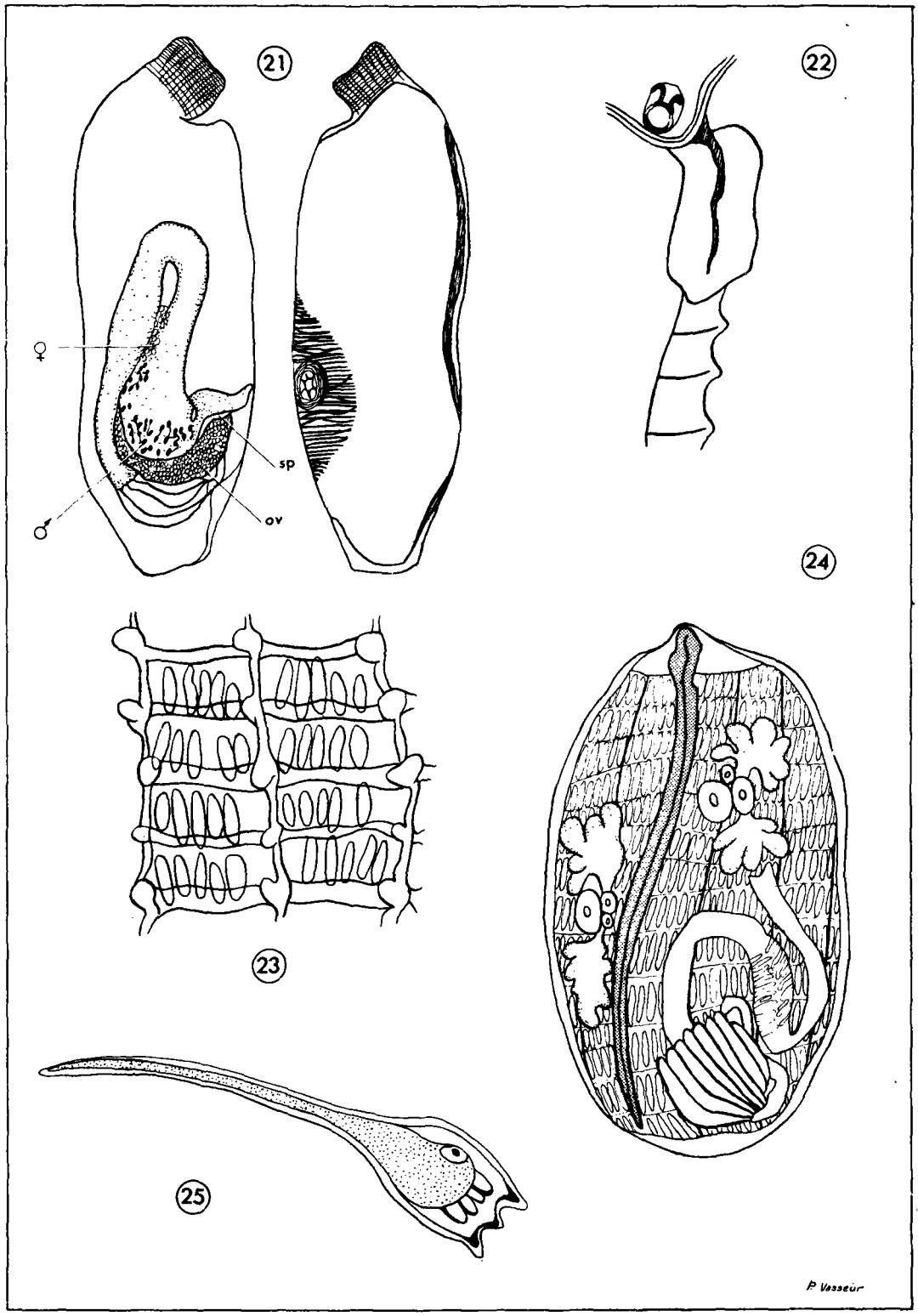
PLANCHE III

Ascidia munda Sluiter.

Figure 21 : Animal détuniqué, côtés gauche et droit du corps, × 5.
Figure 22 : Tubercule vibratile et raphé dorsal, 10 × 10.
Figure 23 : Détail du sac branchial, 10 × 15.

Symplegma viride Herdman.

Figure 24 : Zoïde isolé en vue ventrale, 4 × 10.
Figure 25 : Larve, 10 × 10.



PL. III

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PLANCHE IV

Amphicarpa inhacae (Millar).

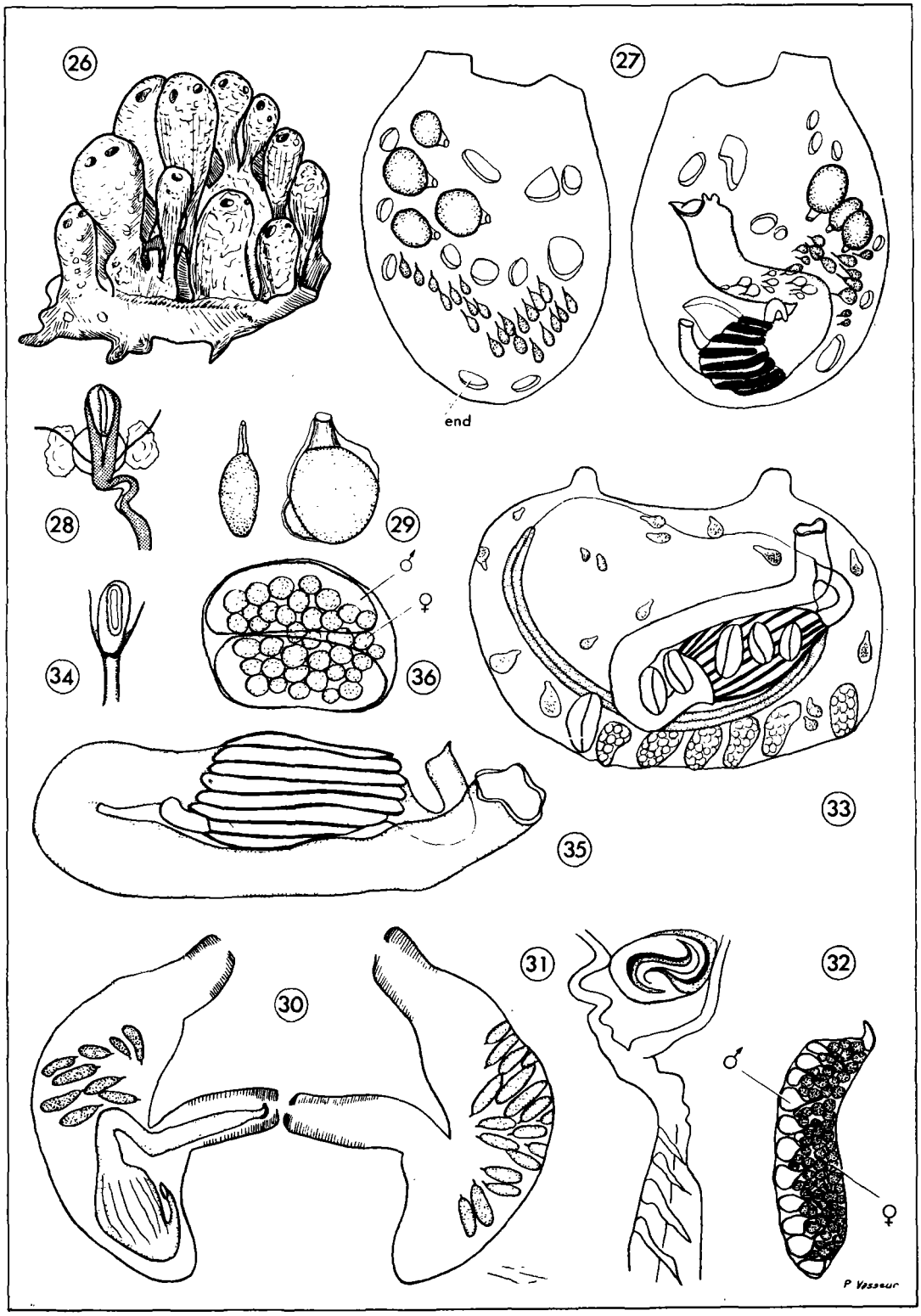
Figure 26 : Une partie de la colonie, × 5.
Figure 27 : Individu ouvert pour montrer la disposition du tube digestif, des gonades et des endocarpes, 5 × 4.
Figure 28 : Tubercule vibratile, raphé dorsal, ganglion et glande neurale divisée, 5 × 10.
Figure 29 : Un testicule et un ovaire, 5 × 10.

Polyandrocarpa anguinea (Sluiter).

Figure 30 : Côtés gauche et droit du corps de l'animal vu de l'intérieur pour montrer la disposition des gonades et du tube digestif, × 5.
Figure 31 : Tubercule vibratile et début du raphé dorsal, 5×10.
Figure 32 : Détail d'une gonade, 5 × 4.

Polyandrocarpa (Eusynstyela) tincta (Van Name).

Figure 33 : Zoïde isolé, vu ventralement et du côté gauche, 5 × 4.
Figure 34 : Tubercule vibratile, 10 × 10.
Figure 35 : Détail du tube digestif, 10 × 4.
Figure 36 : Gonade, 10 × 10.



PL. IV

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PLANCHE V

Polycarpa nigricans Heller

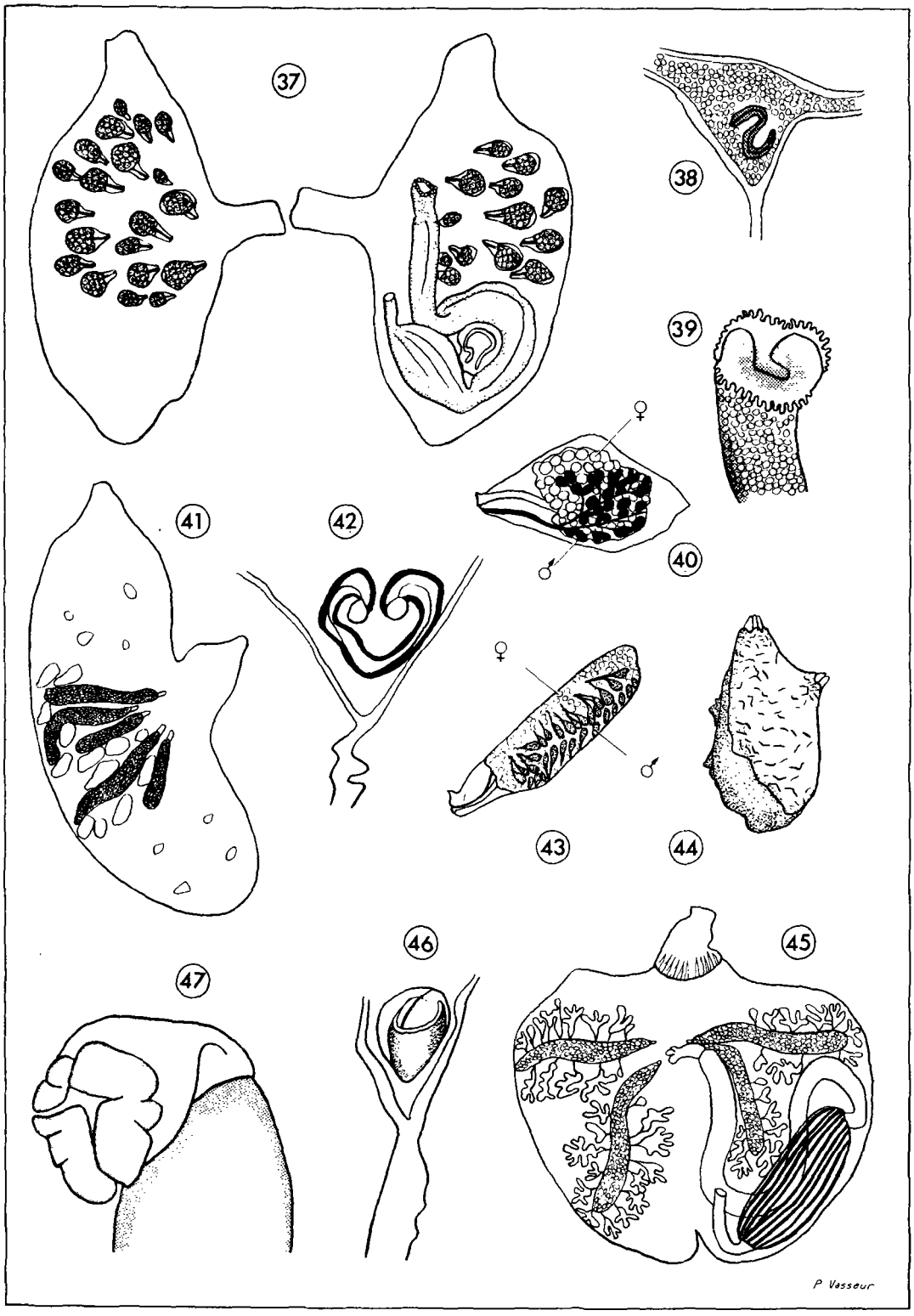
Figure 37 : Côtés droit et gauche du corps de l'animal vu de l'intérieur montrant la disposition du tube digestif et des gonades, × 5.
Figure 38 : Tubercule vibratile, 5 × 4.
Figure 39 : Détail de la bordure anale, 5 × 4.
Figure 40 : Une gonade vue de profil, 5 × 4.

Cnemidocarpa madagascariensis Hartmeyer.

Figure 41 : Côté droit du corps en vue intérieure, × 10.
Figure 42 : Tubercule vibratile, 10 × 6.
Figure 43 : Une gonade, 10 × 3.

Styela partita (Stimpson).

Figure 44 : Animal entier, × 5 la grandeur naturelle.
Figure 45 : Animal ouvert pour montrer la disposition du tube digestif et des gonades, × 5.
Figure 46 : Tubercule vibratile, 10 × 5.
Figure 47 : Détail des lobes de l'anus, 10 × 5.



PL. V

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PLANCHE VI

Styela pupa Heller.

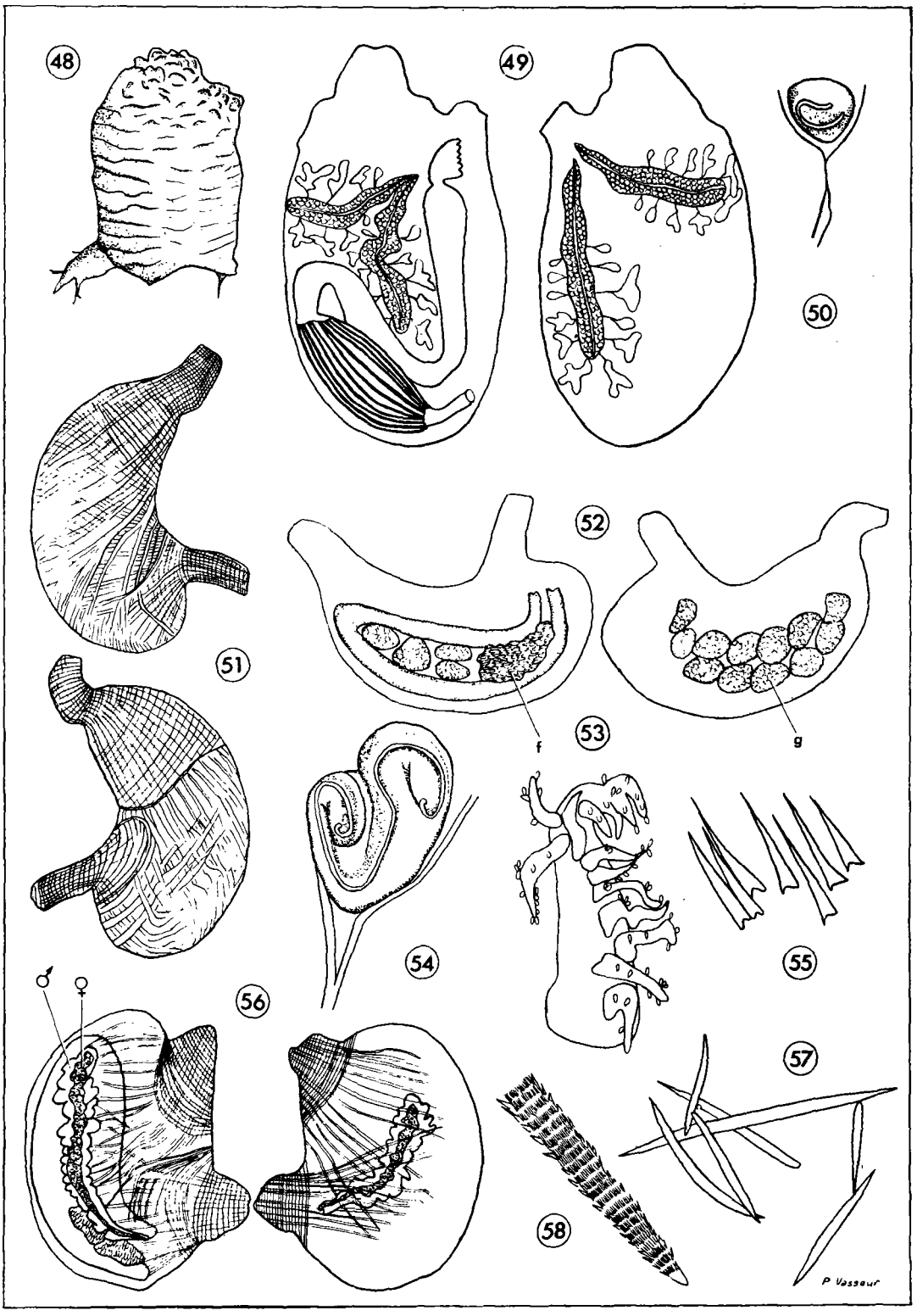
Figure 48 : Animal entier, × 5 la grandeur naturelle.
Figure 49 : Animal vu du côté droit et du côté gauche, × 10.
Figure 50 : Tubercule vibratile, 5 × 4.

Pyura pulla (Sluiter).

Figure 51 : Animal dépouillé de sa tunique en vues gauche et droite m rant le détail de la musculature du manteau.
Figure 52 : Animal ouvert, côtés gauche et droit du corps.
Figure 53 : Un tentacule buccal, 5 ×4.
Figure 54 : Tubercule vibratile, 5 × 4.
Figure 55 : Spinules, 40 × 6.

Pyura momus (Savigny).

Figure 56 : Individu détuniqué vu du côté gauche et du côté droit.
Figure 57 : Un groupe de spicules calcaires, 15 × 10.
Figure 58 : Détail d'un spicule montrant les rangs d'aiguilles dirigées postérieurement, 40 × 15.



PL. VI

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PLANCHE VII

Pyura momus (Savigny).

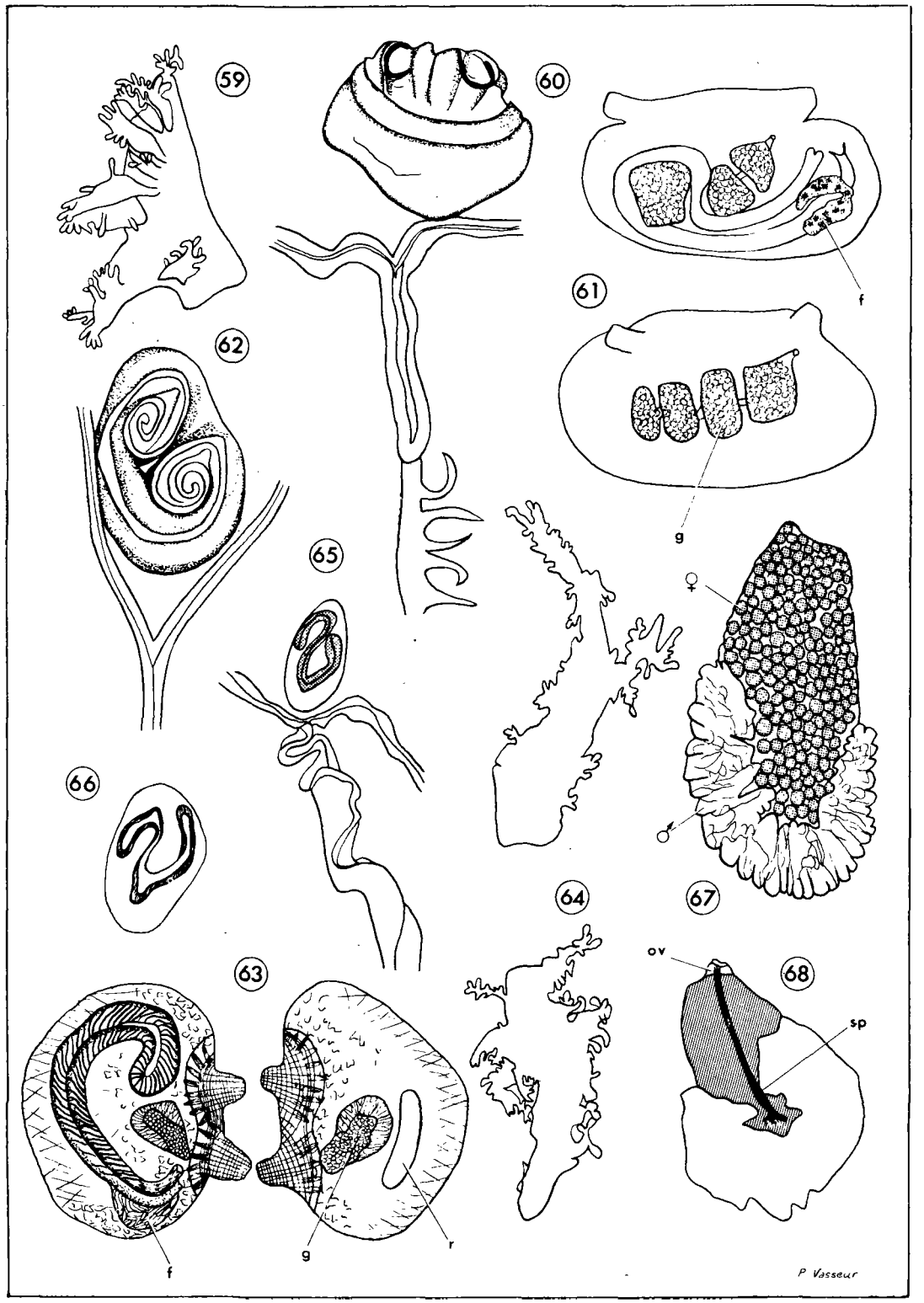
Figure 59 : Tentacule de petite taille, 15 × 4.
Figure 60 : Détail du tubercule vibratile et de la lame dorsale découpée en languettes, 10 × 4.

Microcosmus exasperatus Heller.

Figure 61 : Animal ouvert, côtés gauche et droit du corps.
Figure 62 : Tubercule vibratile, 5 × 4.

Molgula natalensis (Michaelsen).

Figure 63 : Animal ouvert, côtés gauche et droit du corps, × 5.
Figure 64 : Tentacules du siphon buccal, 15 × 4.
Figure 65 : Tubercule vibratile et raphé dorsal, 15 × 4.
Figure 66 : Tubercule vibratile d'un second spécimen, 10 × 5.
Figure 67 : Gonade, côté du manteau, 5 × 4.
Figure 68 : Gonade, côté du sac branchial, 5 × 4.



PL. VII

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CONTRIBUTION A LA CONNAISSANCE DES PÉRIDINIENS MICROPLANCTONIQUES DU CANAL DE MOZAMBIQUE

Par A. SOURNIA

L'épithète « microplanctoniques », opposée ici à « nannoplanctoniques », désigne les Péridiniens de grande taille, susceptibles d'être récoltés au filet fin. Rappelons que les Flagellés nannoplanctoniques relèvent de techniques différentes (centrifugation, ultrafiltration), ont un rôle océanographique distinct (leur productivité est sans doute beaucoup plus élevée), et sont d'ailleurs considérablement plus mal connus.

Cette seconde catégorie d'organismes étant mise à part, il convient encore d'exclure ici le genre *Ceratium*, le plus notoire parmi les Péridiniens microplanctoniques, et dont une étude est en cours de publication (Sournia, sous presse).

Ces deux réserves étant faites, une vue d'ensemble sur la bibliographie mondiale conduit aux trois remarques suivantes :

1) Canal de Mozambique :

Comparativement au reste de l'océan indien, les Péridiniens n'apparaissent ni mieux, ni plus mal connus, dans le canal de Mozambique. Cette région a en effet prêté à deux travaux de Silva (1956, 1960) relatifs à la côte du Mozambique, d'Inhaca au cap Delgado, ainsi qu'à l'inventaire de Travers (1965) pour la région de Tuléar ; de plus, aux confins du canal, le plancton de Zanzibar a été étudié par Ballantine (1961). Quant aux « grandes expéditions », on peut citer, ou omettre, celle de la « Valdivia », qui a longé l'extrême nord du canal. (Rappelons au sujet du « Dana », qui a parcouru toute la région concernée, que seul les *Ceratium* ont donné lieu à publication).

2) Océan indien :

Par rapport au reste du globe, les Péridiniens de l'océan indien ont été relativement peu étudiés. On ne compte qu'une seule « grande expédition », celle de la « Valdivia » ; encore le mémoire qui en a résulté (Karsten, 1907) a-t-il notablement vieilli du point de vue de la nomenclature, c'est-à-dire que de nombreux noms sont tombés depuis en synonymie. Par ailleurs, divers voyages ou croisières de moindre importance ont donné lieu aux travaux suivants, qui datent eux aussi, pour la plupart, du début du siècle : Cleve (1900 a, 1901, 1903), Ostenfeld & Schmidt (1901),

Schröder (1906), Czapek (1909), Ostenfeld (1915), Böhm (1931), et Matzenauer (1933). Les principales recherches récentes sont celles de Wood (1954, 1963 b et c) dans les parages de l'Australie.

Il est donc à souhaiter que le matériel récolté par les nombreux participants de l'Expédition internationale dans l'océan indien soit exploité au mieux de façon à combler cette lacune.

Notons cependant que cet océan possède sur les autres l'avantage de disposer d'un index bibliographique des espèces : la « check-list » de Wood (1963 a).

3) Connaissances mondiales :

Passant, dans cette vue d'ensemble, du canal de Mozambique à l'océan indien, puis de ce dernier à l'océan mondial, on serait amené, dans ce troisième paragraphe, à une synthèse des connaissances modernes... Sujet qui dépasse la portée de la présente note. Une remarque cependant s'impose, concernant l'état actuel de la bibliographie :

La révision mondiale de Schiller (1933-1937) doit son autorité au simple fait qu'elle est la seule de son espèce. Elle constitue certes une base bibliographique indispensable, mais nullement un manuel infaillible pour la détermination des espèces : il s'agit en effet d'une compilation souvent rapide, et qui pêche par de fréquentes erreurs ou omissions « de détail ». De trop nombreux planctologistes ont suivi cet ouvrage en toute confiance, et, de fait, les travaux postérieurs « d'inspiration originale » sont relativement peu nombreux (Cf. Balech, Chatton, Graham, et quelques autres). Par ailleurs, la notion d'espèce (et de taxons infraspécifiques), telle qu'utilisée dans l'œuvre de Schiller, s'oppose souvent aux données actuelles sur la variabilité morphologique chez les Péridiniens.

Matériel étudié, et objet de la présente note.

Le matériel ici étudié, et dont j'ai antérieurement examiné les *Ceratium* ainsi que les Diatomées (également sous presse), provient de trois séries de récoltes au filet :

— Nossi-Bé (Madagascar) : prélèvements hebdomadaires, en surface, dans la baie du Centre océanographique de l'O.R.S.T.O.M. (Février 1963 à juillet 1964).

— Tuléar (Madagascar) : divers prélèvements en surface, de part et d'autre du grand récif et dans le canyon de St. Augustin (Août-septembre 1964).

— Croisière nº 8 de l' « Anton Bruun » (Woods Hole oceanogr. Inst.) dans le canal de Mozambique, de Durban à Mombasa (Septembre-novembre 1964). Récoltes horizontales et verticales.

Dans la présente note seront étudiés neuf genres essentiellement tropicaux (sauf peut-être *Pyrophacus*), et, pour la plupart, préférentiellement

océaniques (donc provenant principalement des récoltes de l' « Anton Bruun »).

Ces neuf genres peuvent être appelés « mineurs », en ce sens qu'ils jouent dans l'économie des mers un rôle plus « décoratif » que productif ; toutefois, en raison de leur rareté, ils demeurent mal connus, et justifiaient à ce titre une brève mise à jour.

A PROPOS DES RÉFÉRENCES GÉNÉRIQUES ET SPÉCIFIQUES :

— La pagination et l'iconographie ne sont précisées que dans le cas des descriptions *princeps*.

— Les références antérieures à la monographie de SCHILLER ne sont ici reportées que si elles sont erronées, ou absentes, *in* SCHILLER, ou si elles offrent un intérêt essentiel.

— Pour éviter les répétitions, j'omets de reproduire à propos des espèces les références déjà citées à propos des genres, sauf intérêt particulier.

NOMENCLATURE :

Les règles suivies dans cette note sont celles du Code international de la nomenclature botanique (LANJOUW *et al.*, 1961).

Genre *Amphisolenia* Stein, 1883.

STEIN, 1883, p. 24.
KOFOID, 1907. PAULSEN, 1908. KOFOID & MICHENER, 1911. JÖRGENSEN, 1923. KOFOID & SKOGSBERG, 1928. LINDEMANN, 1928. SCHILLER, 1933. BALECH, 1962.

Comme le note BALECH (1962), l'essentiel des connaissances relatives à ce genre réside dans la remarquable monographie de KOFOID & SKOGSBERG, dont SCHILLER ne donne qu'une reproduction sommaire. Quelques nouvelles espèces ont été décrites par la suite (BÖHM, 1933 ; BALECH, 1962 ; WOOD, 1963 c ; HALIM, 1965 ; voir aussi deux espèces indéterminées, *in* Silva, 1955, 1958) ; d'autre part, au vu des divers travaux phytoplanctologiques postérieurs, il apparaît de plus en plus probable que toutes les espèces sont, quoique rares, distribuées dans toutes les mers chaudes et, occasionnellement, tempérées. Ces deux points mis à part, le genre demeure mal connu.

KOFOID & SKOGSBERG ont insisté sur les difficultés de détermination et les incertitudes qui subsistent quant à la position et la délimitation de certaines espèces : ceci tient à une connaissance insuffisante de la variabilité spécifique, ainsi que du mode de croissance (la vitesse de régénération des cellules après la division reste inconnue).

Mes récoltes dans le canal de Mozambique confirment, outre la thermophilie du genre, les trois données actuelles de l'écologie des *Amphisolenia* : rareté numérique des individus ; oligophotisme (ces organismes sont nettement plus nombreux dans les prélèvements verticaux) ; enfin, répartition préférentiellement eupélagique.

Amphisolenia bidentata Schröder, 1900.

Schröder, 1900, p. 20, pl. 1, fig. 16.
Böhm, 1936. Rampi, 1940. Gaarder, 1954. Wood, 1954, 1963 *a*. Silva, 1955, 1956. Balech, 1962.

La plus commune du genre, cette espèce est effectivement la plus abondante dans mes récoltes. Sa répartition verticale fait exception : l'oligophotisme n'est ici nullement évident.

Amphisolenia extensa Kofoid, 1907.

Kofoid, 1907, p. 198, pl. 13, fig. 78.
Böhm, 1933. Pavillard, 1937. Silva, 1958.

Cette espèce semble nouvelle pour l'océan indien. Bien que plus courante dans le Pacifique, elle est donc maintenant connue, quoique sporadiquement, dans toutes les mers : Atlantique (Böhm, Silva), Méditerranée (Jörgensen, Pavillard, Tregouboff & Rose).

Amphisolenia globifera Stein, 1883.

Stein, 1883, p. 24, pl. 21, fig. 9-10.
Gaarder, 1954. Silva, 1958. Halim, 1960. Wood, 1963 a et b.

Espèce nouvelle pour le canal de Mozambique.

Amphisolenia Lemmermannii Kofoid, 1907.

Kofoid, 1907, p. 199, pl. 14, fig. 88-89.
Böhm, 1933, 1936. Gaarder, 1954. Balech, 1962. Wood, 1963 a et b (*vix* fig. 25).

Espèce nouvelle pour la région étudiée, mais particulièrement mal connue et, semble-t-il, très rare en dehors de l'Indopacifique : Atlantique sud ? (Böhm, 1933), Gibraltar (Gaarder). Son autonomie par rapport à *A. bidentata* est en effet discutable (Cf. Kofoid & Skogsberg, Böhm 1936, et Balech). Je maintiens cependant la distinction, sur la base des caractères suivants :

Longueur totale 500-700 μ (chez *A. bidentata* : 700-1000). Extrémité antapicale courbée vers la gauche, mais non tordue ventralement (à la différence de l'espèce voisine). La largeur du corps central, très variable, ne constitue pas un critère certain : 20-53 μ, au lieu de 14-30 μ chez *A. bidentata*. Le quatrième caractère distinctif est d'ordre écologique : répartition nettement oligophotique chez *A. Lemmermannii*.

Amphisolenia mozambica nov. sp. (Fig. 1-3).

Epitheca convexa ; tenue caput, bis aut ter latior quam longior. Corpus centrale fusiforme, angustum, paulatim utrimque decrescens. Pars antapicalis bis aut ter quam pars reliqua longior, ad extremitatem in dexteram incurvata, sed non ad ventrem detorta. Extremitas leviter inflata, tenuissime denticulata ; spinae nullae.

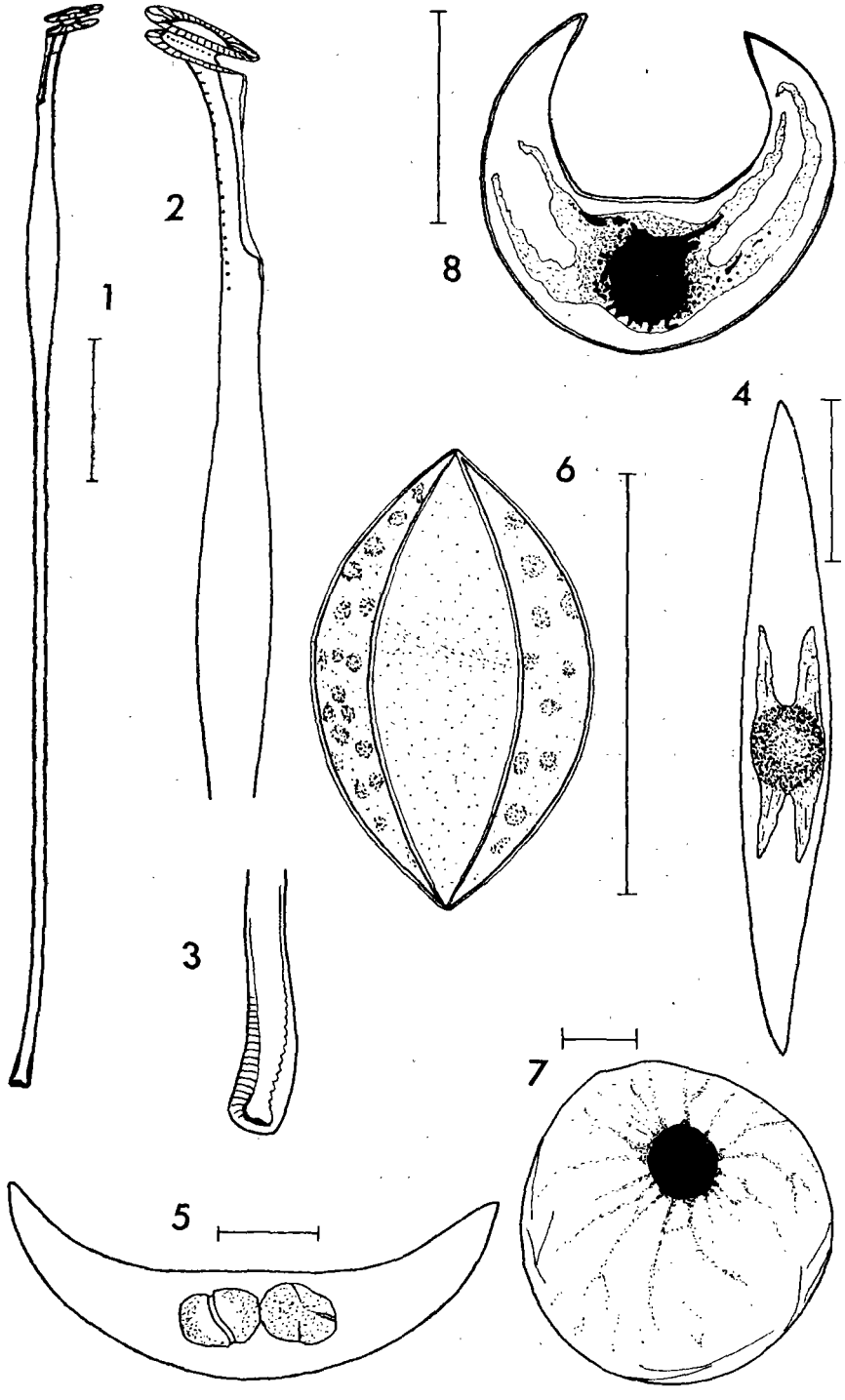


FIG. 1. — *Amphisolenia mozambica n. sp.*, vue latérale gauche. — 2 : *Id.*, détail de la partie antérieure, vue latérale droite. — 3. *Id.*, détail de la partie postérieure, vue latéro-ventrale. — 4 : *Pyrocystis fusiformis* Wyv. Thomson *ex* Murray. — 5 : *P. Gerbaultii* Pavillard. — 6 : *P. lunula* (Schütt) Schütt. — 7 : *P. pseudonoctiluca* Wyv. Thomson *ex* Murray. — 8 : *P. robusta* Kofoid.

L'échelle indique, dans tous les cas, une longueur de 100 μ.

Description (Selon la terminologie de Kofoid & Skogsberg). — Epithèque convexe ; tête fine, environ 2-3 fois plus large que longue. Cou deux fois moins large que le processus antérieur. Corps central fusiforme, relativement étroit, se rétrécissant de façon identique à ses deux extrémités, et de convexité identique sur ses faces ventrale et dorsale ; largeur du corps central légèrement inférieure au double de celle du processus antérieur, et légèrement supérieure au double de celle de la partie antapicale. Cette dernière, 2-3 fois plus longue que le reste de la cellule. Région terminale régulièrement recourbée vers la droite, mais non tordue ventralement (sur ce dernier point, la pression exercée par la lamelle couvre-objet peut faire illusion). Extrémité antapicale légèrement renflée, et bordée d'une très fine denticulation marquant la suture sagittale. Épines terminales et épine subterminale absentes.

Longueur totale : 740-800 µ.

Récoltes. — Centre du canal de Mozambique (« Anton Bruun », station 404, filet vertical), et au large de Mombasa (station 419, filet horizontal). Les conditions hydrologiques, peu différentes dans les deux cas, étaient respectivement (eaux de surface) :

Température : 24,69 et 25,58° C. Salinité : 35,22 et 35,37 ‰.

Affinités. — *A. elongata* Kof. & Skogsb., voisine de la présente espèce, s'en distingue comme suit : chez *A. mozambica*, la tête est relativement plus large ; la partie antapicale est proportionnellement plus longue (par rapport au reste du corps), et son extrémité n'est pas tordue ventralement ; la denticulation terminale de la suture sagittale semble en outre caractéristique, mais une telle observation est nouvelle pour le genre : ce caractère, peut-être « accessoire », mérite d'être recherché chez d'autres espèces.

Amphisolenia palmata Stein, 1883.

Stein, 1883, p. 24, pl. 21, fig. 11-15.
Wood, 1954 (*vix* fig. 56) et 1963 a. Silva, 1956.

Amphisolenia Schauinslandii Lemmermann, 1899.

Lemmermann, 1899, p. 350, pl. 1, fig. 18-19.
Böhm, 1933, 1936. Ballantine, 1961. Wood, 1963 a et b.

Très peu signalée en dehors de l'Indo-pacifique (Böhm, 1933 : Atlantique sud).

Amphisolenia thrinax Schütt, 1893.

Schütt, 1893, fig. 25.
Wood, 1954 et 1963 a. Balech, 1962.

Genre *Triposolenia* Kofoid, 1906.

Kofoid, 1906 a, p. 102 et suiv.
Kofoid, 1906 b et c, 1907. Jörgensen, 1923. Kofoid & Skogsberg, 1928. Schiller, 1933. Pavillard, 1937. Gaarder, 1954. Silva, 1958. Halim, 1960.

Plus encore que le genre précédent, celui-ci est principalement connu par la monographie de Kofoid & Skogsberg, résumée par Schiller. Les références postérieures à ces deux travaux sont très rares : aucune innovation ne s'est depuis ajoutée aux neuf espèces connues en 1928 ; la distribution géographique du genre a seulement acquis quelques points nouveaux en Méditerranée et dans l'Atlantique. Les *Triposolenia* sont en effet plus rares encore que les *Amphisolenia*, parce que sans doute plus nettement encore eupélagiques et oligophotiques.

Nouveau pour le canal de Mozambique, ce genre n'était précédemment connu dans l'océan indien que par Wood (1963 c), qui signale *T. bicornis* dans la mer de Timor. J'ai récolté à Tuléar (eaux du large) et dans le centre du canal (prélèvements verticaux) quelques spécimens des trois espèces suivantes :

Triposolenia bicornis Kofoid, 1906.

Kofoid, 1906 a, p. 105, pl. 15, fig. 1-2, et pl. 16, fig. 6.

Triposolenia depressa Kofoid, 1906.

Ibid., p. 104, pl. 16, fig. 3-4.

Triposolenia truncata Kofoid, 1906.

Ibid., p. 102, pl. 16, fig. 5.

Genre *Ornithocercus* Stein, 1883.

Stein, 1883, p. 25 et suiv.
Schütt, 1893, 1895, 1896, 1900. Jörgensen, 1923. Kofoid & Skogsberg, 1928. Schiller, 1933. Chatton, 1952.

Ici encore, la monographie de Kofoid & Skogsberg fait autorité. Neuf espèces y sont décrites, avec les réserves suivantes : le cas d'*O. orbiculatus* est douteux (cette espèce semble en effet n'avoir été signalée ultérieurement que par Matzenauer, 1933), et, d'autre part, les cinq formes d'*O. quadratus* représentent peut-être plusieurs espèces. Ces neuf unités sont reportées par Schiller, qui en ajoute une dixième (*O. geniculatus* Dang.). Postérieurement à ces deux travaux, le nombre des espèces a été porté au double, du fait des contributions de Matzenauer (1933), Rampi (1950), Wood (1954, 1963 b et c) et Balech (1962). Cependant, toutes les espèces actuellement connues ne peuvent être données comme « sûres », car la variabilité morphologique et les modalités de la croissance restent à préciser.

Dans mes récoltes, le genre était représenté à la presque totalité des stations au nord de la latitude 25° sud ; les exigences écologiques étaient peu marquées : seule une variation d'abondance en fonction de la profondeur a pu être observée dans certains cas.

Ornithocercus magnificus Stein, *emend.* Schütt, 1895.

Stein, 1883, *pro parte* : p. 26, pl. 23, fig. 1-2, *non al.* (A propos d'*O. magnificus* Stein, voir autres références et restrictions, *in* Kofoid & Skogsberg). Schütt, 1895, p. 16 et suiv., pl. 4, fig. $21/_{9}$, et pl. 5, fig. $21/_{1\text{-}8}$ (*vix* $21/_{2}$).

Schütt, 1896, 1900. Rampi, 1940. Gaarder, 1954. Wood, 1954, 1963 a. Silva, 1955. Ballantine, 1961.

Ornithocercus quadratus Schütt, 1900 (Pl. I, fig. 1).

Schütt, 1900, p. 254, fig. 1-4, 12-13.

Rampi, 1939. Silva, 1956. Gaarder, 1954. Wood, 1954, 1963 a.

Cette espèce, la plus complexe du genre, pose au systématicien un problème qui rappelle, chez un autre genre de Péridinien, le cas du *Ceratium tripos* : on serait tenté de distinguer autant de taxons que d'individus. L'analogie entre ces deux cas peut-elle être poussée plus loin ?

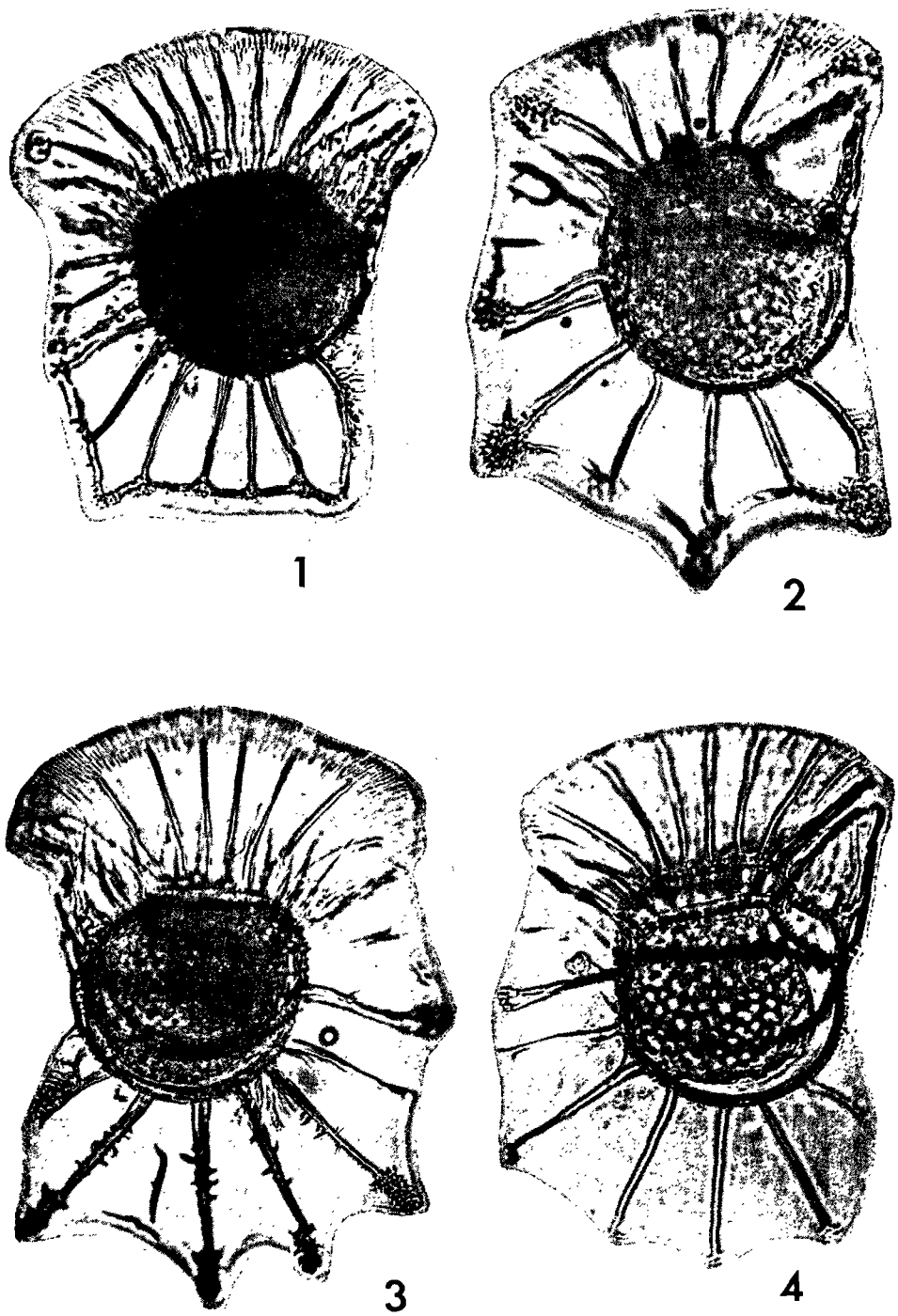
Dans l'état actuel des connaissances, c'est-à-dire, à défaut de données biométriques et statistiques, les diverses formes connues d'*O. quadratus* (ou du moins une partie d'entre elles) pourraient être considérées comme une série de variations comprise entre deux stades extrêmes : l'un (f. *quadratus*) de grande taille, à aileron sulcal gauche abondamment réticulé (principalement dans sa partie marginale) ; l'autre (f. *simplex*) de petite taille, à aileron gauche relativement moins développé et dépourvu de réticulation ainsi que, souvent, de zone marginale. Seraient considérées comme intermédiaires les formes *Schuettii* et *assimilis* (cette dernière, traitée comme espèce distincte par Jörgensen, 1923 et Böhm, 1936). La cinquième et dernière forme, f. *intermedius*, devrait être tenue à l'écart de cette série.

Cette conception est toute personnelle et purement intuitive : seule une étude statistique des différents caractères morphologiques pourra, à l'avenir, la confirmer ou lui substituer une meilleure interprétation. Dans le premier cas, c'est-à-dire, si l'existence d'une suite continue de variations apparaît évidente, on pourra employer le mode de désignation infraspécifique que j'ai précédemment proposé (1966) pour le genre *Ceratium*.

J'ai récolté assez fréquemment les formes *intermedius*, *quadratus* et *Schuettii*, sans pouvoir établir entre elles une discrimination écologique. L'espèce est, dans son ensemble, préférentiellement oligophotique.

LÉGENDE DE LA PLANCHE I

Fig. 1 : *Ornithocercus quadratus* Schütt f. *quadratus* ; hauteur du corps central : 65 µ. 2 : *O. Thumii* (Schmidt) Kof. & Skogsb. ; hauteur : 50 µ. 3 : *O. Steinii* Schutt *emend.* Kof. & Skogsb. ; individu probablement âgé ; hauteur 65 µ (aileron sulcal gauche accidentellement interrompu dans sa partie ventrale). 4 : *Id.*, individu probablement jeune ; hauteur 55 µ. Fig. 1, 2, 4 : vue latérale gauche. Fig. 3 : Vue latérale droite.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Ornithocercus splendidus Schütt, 1893.

Schütt, 1893, p. 272, fig. 82-83.
Schütt, 1895, 1896 (« *O. splendens* »), 1900. Gaarder, 1954. Wood, 1954, 1963 a. Silva, 1955.

Dans mes prélèvements, toujours en très faibles quentités numériques, et résolument oligophotique.

Ornithocercus Steinii Schütt, *emend.* Kof. & Skogsb., 1928 (Pl. I, fig. 3-4).

Schütt, 1900, *pro parte* : p. 260, fig. 5-6, *non* 7. Kofoid & Skogsberg, 1928, p. 551, fig. 83-84, et pl. 16, fig. 1 : « *O. Steinii* Schütt, *s. str.* ». « *O. Steinii* Schütt » *in plur. auct.* : Böhm, 1936. Gaarder, 1954. Wood, 1954, 1963 a. *Vix* Silva, 1955 (*non* pl. 3, fig. 6 ?).

La présente désignation est imposée par le fait que Kofoid & Skogsberg ont modifié l'acception originelle de Schütt (la figure 7 de cet auteur se rapporte en effet à l'espèce suivante).

Ornithocercus Thumii (Schmidt) Kof. & Skogsb., 1928 (Pl. I, fig. 2).

Schmidt, 1888 (Atlas Diatomeenk.), pl. 144, fig. 59-61 : « *Parelion Thumii* ». Kofoid & Skogsberg, 1928, p. 540, fig. 81-82, et pl. 18, fig. 4-6.
Böhm, 1936. Gaarder, 1954. Wood, 1954, 1963 a. Ballantine, 1961.

(La graphie courante « *Thurnii* » est erronée).

Rencontrée plusieurs fois en quantités relativement importantes, et, à la différence également des espèces précédentes, plus abondante en surface.

Genre *Pyrophacus* Stein, 1883.

Unique espèce :

Pyrophacus horlogium Stein, 1883.

Stein, 1883, p. 28, pl. 24, fig. 1-13.
Wang, 1936. Schiller, 1937. Gaarder, 1954. Wood, 1954, 1963 a. Silva, 1956.
? Incl. : var. *Steinii* Schiller, 1937.
Schiller, 1937, p. 87, fig. 74.
Wood, 1954 (fig. 84 b-c douteuses). Silva, 1956. Ballantine, 1961.

(Les graphies : « *horologium* », « *horologicum* » et « *horlogicum* » sont erronées).

La distinction proposée par Schiller d'une variété *Steinii* reste à justifier : il est seulement probable que cette dernière soit préférentiellement thermophile, et la discrimination morphologique, basée sur le nombre des plaques et les dimensions générales, me semble arbitraire ; il reste de plus à prouver que ces deux caractères sont effectivement liés : mes

observations ne le laissent pas penser, et les données numériques de Silva contredisent sur ce point celles de Schiller.

Genre *Acanthogonyaulax* (Kofoid) Graham, 1942.

Kofoid, 1911 a, p. 202 : « *Gonyaulax* subg. *Acanthogonyaulax* ».
Graham, 1942, p. 52.

Unique espèce :

Acanthogonyaulax spinifera (Murray & Whitt.) Graham, 1942.

Murray & Whitting, 1899, *pro parte* : p. 329, pl. 30, fig. 6 a-b, e, *non* c-d : « *Ceratocorys spinifera* ». Graham, 1942, p. 53, fig. 64-65. Balech, 1962.
= *Gonyaulax ceratocoroides* Kofoid, 1910.
Kofoid, 1910, p. 182.
Kofoid, 1911 a. Pavillard, 1931. Schiller, 1937.
Non : Gonyaulax spinifera (Clap. & Lachm). Diesnig, 1866.

Cette espèce, dont je n'ai récolté que deux spécimens (centre du canal de Mozambique, et au large des Comores), se trouve nouvelle pour l'océan indien. Elle est par ailleurs connue, très sporadiquement, dans l'Atlantique tropical et tempéré ainsi que dans le Pacifique tropical ; c'est par erreur semble-t-il que Schiller la signale en Méditerranée.

Genre *Spiraulax* Kofoid, 1911.

Kofoid, 1911 b, p. 295 et suiv.

Spiraulax Kofoidii Graham, 1942.

Graham, 1942, p. 55, fig. 66.
= *Spiraulax Jollifei* (Murray & Whitt.) Kofoid, 1911, *pro parte*.
Kofoid, 1911 b, p. 296, pl. 19, fig. 1-5.
Forti, 1922. Schiller, 1937. Silva, 1956 (*vix* pl. 11, fig. 11). ? Pavillard, 1931, 1937. ? Matzenauer, 1933. ? Wood, 1954, 1963 a.
Non : Gonyaulax Jollifei Murray & Whitting, 1899.
Murray & Whitting, 1899, p. 324, pl. 28, fig. 1. Autres références : incertaines : Cleve, 1903. Schröder, 1906. Karsten, 1907. Pavillard, 1909.

Graham a montré que le *Spiraulax Jollifei* de Kofoid ne peut être assimilé au *Gonyaulax Jollifei* de Murray & Whitting. De plus, la diagnose de cette dernière espèce étant insuffisante, Graham lui substitue un nouveau taxon, *Gonyaulax fusiformis* (celui-ci absent de mes récoltes). Il importe donc que les noms de *Spiraulax Jollifei* et de *Gonyaulax Jollifei*, prêtant à confusion, soient à l'avenir abandonnés.

Genre *Ceratocorys* Stein, 1883.

Stein, 1883, p. 20.
Kofoid, 1910. Pavillard, 1931, 1937. Schiller, 1937, Graham, 1942. Wood, 1954, 1963 a, b et c. Balech, 1962.

Ce genre compte aujourd'hui, outre les six espèces reportées par Schiller, six autres décrites depuis par divers auteurs (Matzenauer, 1933 ; Graham, 1942 ; Osorio Tafall, 1942 ; Wood, 1963 c. Voir aussi *Ceratocorys sp., in* Wood, 1963 b).

Les trois espèces suivantes ont été récoltées (les deux premières très rarement) dans les zones littorales :

Ceratocorys armata (Schütt) Kofoid, 1910.

Schütt, 1895, p. 153, pl. 9, fig. 32 : « *Goniodoma acuminatum* Stein var. ***armatum*** ».
Kofoid, 1910, p. 181.
Paulsen, 1931.

Ceratocorys Gourretii Paulsen, 1931.

Paulsen, 1931, p. 36.
Silva, 1956.

Ceratocorys horrida Stein, 1883.

Stein, 1883, p. 20, pl. 6, fig. 4-11.
Dangeard, 1927. Gaarder, 1954. Silva, 1955. Ballantine, 1961.
Incl. *C. horrida* var. *africana* Karsten, 1907.
Karsten, 1907, p. 419, pl. 52, fig. 1-3.

— var. *extensa* Pavillard, 1931.

Pavillard, 1931, p. 101, pl. 3, fig. 17 b.
Böhm, 1936. Balech, 1949.
? = *C. horrida* var. *longicornis* Lemm., 1899.
Lemmermann, 1899, p. 350.

L'autonomie de cette variété reste à confirmer : la longueur des cornes varie en effet considérablement selon l'intervalle de temps qui sépare l'individu de sa dernière division cellulaire. Cette longueur est également supposée varier avec la température (Kofoid), mais le rôle de ce facteur n'a pas été prouvé, pas plus que l'existence de transitions morphologiques continues entre les cas extrêmes.

Genre *Podolampas* Stein, 1883.

Stein, 1883, p. 22.
Kofoid, 1907, 1909. Lindemann, 1928. Pavillard, 1931, 1937. Schiller, 1937. Rampi, 1943. Gaarder, 1954. Wood, 1963 a. Balech, 1963. Balech & el Sayed, 1965.

J'ai récolté dans le canal de Mozambique les quatre espèces principales du genre, nettement confinées aux stations néritiques, et qui toutes, à l'exception de *P. palmipes*, étaient déjà connues dans cette région.

A propos des trois autres espèces actuellement décrites, rappelons

que l'une (*P. curvata* Schiller, 1937) est douteuse, que la seconde (*P. reticulata* Kofoid, 1907) peut-être considérée comme une variété de *P. bipes*, et que la troisième, tout dernièrement décrite (*P. antarctica* Balech, 1965), est antarctique.

Les *Podolampaceae* ayant fait l'objet d'observations plus ou moins récentes, reportées ci-dessus, ainsi que d'une révision détaillée, celle-ci toute récente, de Balech (1963), je ne ferai que préciser ou ajouter quelques références relatives aux quatre espèces annoncées plus haut :

Podolampas bipes Stein, 1883.

Stein, 1883, p. 22, pl. 8, fig. 6-8.
Wood, 1954. Halim, 1960. Ballantine, 1961.

Podolampas elegans Schütt, 1895.

Schütt, 1895, p. 161, pl. 18, fig. 57.

Podolampas palmipes Stein, 1883.

Stein, 1883, p. 22, pl. 8, fig. 9-11. Wood, 1954.

Cette espèce semble la plus eurytherme des quatre.

Podolampas spinifera Okamura, 1912.

Okamura, 1912, p. 20, pl. 2, fig. 35.
Rampi, 1939. Halim, 1960. Wood, 1963 b (fig. 187 douteuse).

Genre *Pyrocystis* Murray, 1876.

Murray, 1876, p. 533, pl. 21.
Murray, *in* Tizard *et al.*, 1885. Schütt, 1895, 1896. Blackmann, 1902. Dogiel, 1906. Apstein, 1906, 1909. Karsten, 1907. Kofoid & Swezy, 1921. Pascher, 1927. Peters, 1930. Pavillard, 1931. Schiller, 1937. Chatton, 1952. Wood, 1954, 1963 a.

Le problème des *Pyrocystis* demeure un nœud gordien dans l'étude des Dinoflagellés. L'existence d'un cycle évolutif complexe (stades globulaires, stades en croissant et stades *Gymnodinium*), pressentie par Schütt, a été prouvée au début du siècle (1906), simultanément par Dogiel et par Apstein. Mais les connaissances ont très peu progressé depuis cette date, et peuvent être inventoriées comme suit : d'une part, un cycle incomplet, relatif à *Pyrocystis* (*Gymnodinium*) *lunula* ; d'autre part, divers stades isolés, décrits sous des noms spécifiques, mais ne justifiant probablement pas tous ce rang. Au total, le nombre de cycles (ou d'espèces) distincts est inconnu.

Devant ces incertitudes, « le maintien du genre *Pyrocystis* s'impose comme une nécessité » (Pavillard, 1931, p. 35). Rappelons d'ailleurs que la priorité de ce nom sur celui de *Gymnodinium* posera, le moment venu, une délicate question de nomenclature.

Le cycle classique de Dogiel, reproduit ou légèrement modifié par divers auteurs (Kofoid & Swezy, Peters, Schiller, Chatton) pose actuellement quatre problèmes :

1) Passage des stades gymnodiniens aux stades sphériques de grande taille. (*In* Schiller, 1937, fig. 559 : passage de (11) à (1)).

2) Emplacement (probable ?) d'une phase sexuée.

3) Position systématique, et affinités avec *P. lunula*, des diverses autres « espèces » du genre : type globulaire (*P. pseudonoctiluca*) ; type fusiforme (*P. lanceolata*, *P. fusiformis*) ; type lunulaire (*P. elegans*, *P. ellipsoides*, *P. Gerbaultii*, *P. minima*, *P. obtusa*, *P. robusta*, et *Gymnodinium bicorne*).

4) Généralisation et extension d'un tel cycle à divers genres et espèces de Péridiniens, *Gonyaulax* par exemple (Cf. Kofoid & Swezy, p. 62).

Je ne puis apporter ici qu'une maigre contribution au troisième problème, sous la forme de quelques données complémentaires relatives aux diverses « espèces » observées dans mes récoltes.

Pyrocystis fusiformis Wyv. Thomson *ex* Murray, 1876 (Fig. 4).

Murray, 1876, (p. 553), pl. 21 : « *P. fusiformis* (Wy. T.) ».
Murray, *in* Tizard *et al.*, 1885 : « *P. fusiformis* Murray ».
Lemmermann, 1899. Okamura, 1907. Gaarder, 1954. Silva, 1956, 1958.

Ma figure 4 en représente un cas quelque peu particulier : contour très légèrement sigmoïde, et taille relativement réduite (longueur : 420 µ).

Pyrocystis Gerbaultii Pavillard, 1935 (Fig. 5).

Pavillard, 1935, p. 4, fig. 2.

Cette espèce n'a été que récemment signalée dans l'océan indien (Travers, 1965). J'en reporte ici un stade inédit, renfermant deux spores gymnodiniennes (Fig. 5).

Pyrocystis lunula (Schütt) Schütt, 1896 (Fig. 6).

Schütt, 1895, p. 4 et suiv., fig. 80 (*pro parte* ?) : « *Gymnodinium lunula* ». Schütt, 1896, p. 4, fig. 2 b-f.
Apstein, 1906, 1909. Okamura, 1907. Paulsen, 1908. Forti, 1922. Gaarder, 1954.
= *Gymnodinium lunula* Schütt, 1895.
Schütt, 1895, *loc. cit.* Dogiel, 1906. Kofoid & Swezy, 1921. Lindemann, 1928.

Deux stades remarquables du cycle évolutif de cette espèce ont été dénommés par Apstein (1906) : f. *lunula* (en croissant) et f. *globosa* (sphérique). Mais le rang de forme, dans l'esprit de la nomenclature classique, ne peut être utilisé ici. Apstein lui-même lui substitue postérieurement (1909) l'expression « *generatio* » mieux justifiée, mais parataxinomique.

Outre les stades solitaires en croissant, assez communs dans divers prélèvements néritiques (*in* Schiller, fig. $559/_{5\text{-}6}$), j'ai récolté une forme inédite, constituée par une paire de spores, dont je ne puis malheureusement préciser le contenu (Fig. 6).

Par suite des incertitudes concernant les limites de l'espèce (voir plus haut), la répartition mondiale est ici particulièrement incertaine. Signalé par plusieurs auteurs dans l'océan indien (Cf. Wood, 1963 a), *P. lunula* semble nouveau pour le canal de Mozambique.

Pyrocystis pseudonoctiluca Wyv. Thomson *ex* Murray, 1876 (Fig. 7).

Murray, 1876, (p. 533), pl. 21 : « *P. pseudonoctiluca* (Wy. T.) ». Schütt, 1893. Lemmermann, 1901, 1906. Okamura, 1907. Karsten, 1907. Forti, 1922. Pavillard, 1931, 1937. Gaarder, 1954. Wood, 1954 (fig. 255 douteuse) et 1963 a.

= *Pyrocystis noctiluca* Murray, *in* Tizard *et al.*, 1885.

Murray, *in* Tizard *et al.*, 1885, p. 935, fig. 335-337 : « *Pyrocystis noctiluca* Murray ».

Lemmermann, 1899. Schütt, 1896. Schröder, 1900.

Non : Gymnodinium pseudonoctiluca Pouchet, 1885.

Pouchet, 1885, p. 71, pl. 4, fig. 34-37.

Kofoid & Swezy, 1921. Schiller, 1937.

Point n'est besoin d'être un « Œdipe de la Systématique », comme le postulait Pavillard (1931, p. 36) pour découvrir l'origine bibliographique légale de ce taxon : la première publication en remonte à Murray (1876), qui attribue toutefois le nom à Wyville Thomson. L'auteur de l'espèce doit donc être désigné comme ci-dessus, ou abrégé ainsi : *P. pseudonoctiluca* Murray.

Cette espèce se distinguerait de toutes les autres par sa distribution exclusivement océanique : ce caractère est manifeste dans le nord et l'est de l'océan indien (Sukhanova, 1962, Desrosières, 1965) et plus encore dans le canal de Mozambique, où *P. pseudonoctiluca* semble exclue des eaux néritiques (Cf. Silva, 1956, 1960. Ballantine, 1961, Travers, 1965) ; mes récoltes personnelles confirment ce point : l'espèce, absente à Nossi-Bé et Tuléar, a été rencontrée en abondance dans le domaine océanique, au cours de la croisière de l' « Anton Bruun ».

Du point de vue de ses affinités morphologiques avec la forme sphérique du *P. lunula*, seules les dimensions constituent un critère distinctif : le diamètre est de 350-800 µ chez *P. pseudonoctiluca*, et de 62-172 µ chez *P. lunula* « f. *globosa* ».

Pyrocystis robusta Kofoid, 1907, (Fig. 8).

Kofoid, 1907, p. 167, pl. 1, fig. 5.

Pavillard, 1931. Silva, 1956. Ballantine, 1961 (fig. 65, *non* ? 64).

= *P. lunula* var. *robusta* (Kofoid) Apstein, 1909.

Apstein, 1909, p. 9.

Notons que, si cette « espèce » appartient effectivement au cycle de *P. lunula*, le terme de variété proposé par Apstein est impropre.

Un stade globulaire de *P. robusta* a été récemment décrit par Ballantine (*loc. cit.*, fig. 64).

Résumé

Observations, et brève mise à jour de la bibliographie mondiale, concernant neuf genres tropicaux, pour la plupart océaniques : *Amphisolenia* (dont *A. mozambica, nov. sp.*), *Triposolenia*, *Ornithocercus*, *Pyrophacus*, *Acanthogonyaulax*, *Spiraulax*, *Ceratocorys*, *Podolampas*, *Pyrocystis*. La bibliographie contient 111 titres, dont 25 relatifs à l'océan indien.

Abstract

A short review and some observations concerning nine tropical and mostly océanic genera : *Amphisolenia* (among which *A. mozambica, nov. sp.*) *Triposolenia*, *Ornithocercus*, *Pyrophacus*, *Acanthogonyaulax*, *Spiraulax*, *Ceratocorys*, *Podolampas*, *Pyrocystis*. Bibliography contains 111 titles, 25 of them relevant to the indian ocean.

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Les travaux concernant, exclusivement ou non, l'océan indien sont précédés d'un astérisque. Le point d'interrogation désigne un ouvrage que je n'ai pu personnellement consulter.
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Reprinted from *C.R. Acad. Sc. Paris*, series D, vol. 265, 1967, p. 1000-1003

OCÉANOGRAPHIE BIOLOGIQUE. — *Rythme nycthéméral du rapport « intensité photosynthétique/chlorophylle » dans le plancton marin.* Note (*) de M. Alain Sournia, présentée par M. Théodore Monod.

Dans le Canal de Mozambique, l'activité photosynthétique du phytoplancton, mesurée en éclairage artificiel constant et rapportée à l'unité de pigment, présente un rythme nycthéméral : maximum le matin ou vers midi, minimum au début de la nuit. Les modalités de ce phénomène diffèrent selon la profondeur.

L'incubation en éclairage artificiel constant de populations naturelles du phytoplancton marin prélevées à diverses heures révèle un cycle nycthéméral de l'intensité photosynthétique (celle-ci exprimée en milligrammes de carbone ou d'oxygène par heure et par mètre cube d'eau de mer) : ce phénomène, mis en évidence par Doty et Oguri [1] et confirmé par plusieurs auteurs [[2] à [7]], se traduit en général par un maximum à l'aube ou dans le cours de la matinée et un minimum en fin d'après-midi ou au début de la nuit.

Dans quelques cas [[2], [3], [5]], les variations *in situ* des teneurs en chlorophylle semblent suivre un rythme synchrone ou voisin, ce qui justifierait l'hypothèse hâtive, mais très répandue, selon laquelle les variations nycthémérales de l'activité photosynthétique sont directement liées à celles de la concentration en pigment — ces dernières étant elles-mêmes soumises au cycle de l'éclairement solaire [8]. Cependant, on observe plus souvent que photosynthèse et chlorophylle évoluent indépendamment, ou de façons opposées, dans le cours de 24 h [[4], [6], [9], [10], [11]] et que, des deux séries de variations considérées, la première possède une amplitude bien supérieure.

L'intérêt se reporte alors sur le quotient *photosynthèse/pigment* (le « $Q O_2$ chl. » des physiologistes), expression fondamentale du rapport *production/biomasse* et qui revêt à ce titre une importance capitale dans les recherches sur la productivité primaire. Deux auteurs [[5], [6]] ont brièvement signalé que ce rapport subit lui-même des fluctuations nycthémérales, mais semblent tenir ce fait pour accessoire : à mon avis, ces variations sont d'un intérêt primordial, et leur existence même justifie une preuve substantielle.

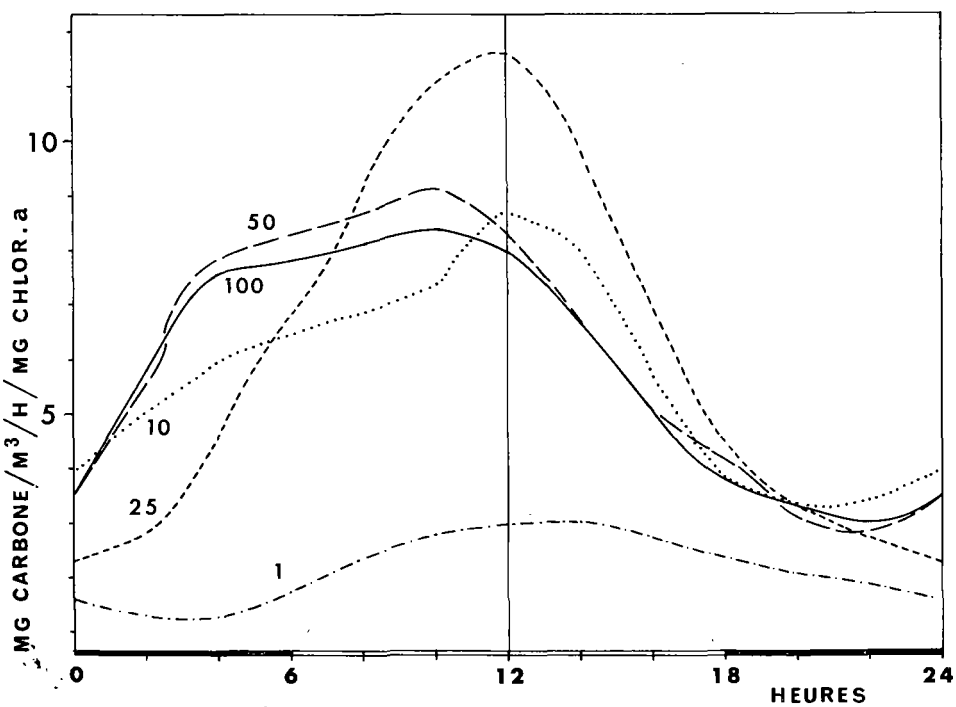
Prélèvements. — Les présentes observations ont été recueillies dans le cadre de l'Expédition internationale dans l'océan indien, au cours de la croisière n° 8 du *R/V Anton Bruun* dans le Canal de Mozambique [12] : 29 stations ont été occupées dans cette région, entre les latitudes 30° et 3° Sud, à diverses heures du jour ou de la nuit. A chaque station, des échantillons d'eau de mer étaient prélevés à cinq profondeurs déterminées par photométrie : 100, 50, 25, 10 et 1 % de l'énergie lumineuse en surface.

Expérimentation. — L'activité photosynthétique a été mesurée par la méthode du ^{14}C de Steemann-Nielsen; les flacons étaient exposés pendant 4 h à un éclairement infra-optimal constant d'environ 10 000 lx (soit une énergie approximative de

40 000 ergs.cm^{-2}.s^{-1}). Les teneurs initiales en chlorophylle *a* ont été mesurées sur une partie aliquote des échantillons par la méthode spectrophotométrique de Richards et Thompson, les concentrations étant calculées selon les équations de Parsons et Strickland.

UNITÉS. — Les résultats sont exprimés en milligrammes de carbone (flacon clair — flacon noir, sans autre correction) assimilé par heure et par milligramme de chlorophylle *a*.

Les résultats reportés sur la figure montrent que, aux cinq niveaux étudiés, c'est-à-dire dans l'ensemble de la couche euphotique, la capacité photosynthétique de la chlorophylle *a* décrit un cycle nycthéméral : le maximum survient au milieu de la matinée ou vers midi, le minimum



Cycle nycthéméral de la capacité photosynthétique de la chlorophylle *a*. Chaque courbe joint les moyennes pondérées de 12 classes chevauchantes de 4 h chacune. Les nombres 100, 50, 25, 10 et 1 indiquent les pourcentages de lumière pénétrant aux cinq profondeurs.

au début de la nuit. Ce schéma est très voisin du rythme défini au début de cette Note, d'autant plus que les travaux mentionnés ci-dessus se rapportent en majorité aux eaux superficielles (niveaux 100 et 50 % sur la figure). Le rapprochement conduit à attribuer en grande partie les variations antérieurement décrites à des variations de l'activité propre de l'appareil chlorophyllien. En d'autres termes aussi : dans le cours de 24 h, la production primaire peut, dans une large mesure, varier indépendamment des concentrations en pigment.

Reporté dans le cadre général des connaissances sur la photosynthèse, ce phénomène peut s'expliquer par l'accumulation dans les cellules des substances synthétisées, entraînant une chute de la production *in situ* vers le milieu du jour, selon un mécanisme clairement démontré par la méthode des cultures synchrones ([13]) et connu plus généralement sous le nom de « dépression de midi ». Quoi qu'il en soit, on peut parler ici de rythme endogène, et exclure plusieurs hypothèses répandues dans la littérature océanographique : variations nycthémérales du nombre d'organismes phytoplanctoniques, ou de la concentration en chlorophylle par cellule, ou encore du taux de « broutage » par le zooplancton; il est par ailleurs peu probable que les variations nycthémérales de l'intensité respiratoire puissent à elles seules rendre compte de l'amplitude ici observée.

Soulignons que les présents résultats traduisent le comportement global de diverses populations phytoplanctoniques, quantitativement et qualitativement très dissemblables.

Fait non moins remarquable que ce rythme lui-même, il apparaît ici que le phénomène varie suivant la profondeur :

— Aux niveaux supérieurs (100 et 50 % de lumière), les valeurs les plus élevées surviennent entre 4 et 12 h avec un maximum vers 10 h; la courbe « 25 % » est presque symétrique et axée sur le milieu du jour ou peu avant; enfin, aux niveaux les plus profonds (10 et 1 %), le maximum s'observe vers midi ou peu après. On note donc dans l'ensemble un décalage dans le temps en fonction de la profondeur.

— Les amplitudes des variations, rapportées à l'unité, sont respectivement, dans l'ordre des profondeurs croissantes : 2,8, 3,2, 5,1, 2,6 et 2,3. C'est donc vers le milieu de la couche euphotique que l'écart nycthéméral est le plus considérable.

Sous ces deux aspects, les faits demandent à être précisés sur la base de mesures systématiques plus nombreuses et appuyées de données photométriques rigoureuses (à bord de l'*Anton Bruun*, plusieurs déterminations de la pénétration de la lumière ont dû être « extrapolées »). Toutefois, les présentes mesures (obtenues, rappelons-le, en éclairage artificiel constant) mettent en évidence les différences entre les potentialités photosynthétiques des échantillons récoltés aux diverses profondeurs; quelques remarques à ce sujet :

On sait que l'intensité photosynthétique est d'ordinaire maximale à une certaine profondeur, l'énergie lumineuse étant supposée optimale à ce niveau, excessive au-dessus et insuffisante au-dessous : ceci fournit, sinon une explication, du moins une analogie immédiate avec les différences d'amplitude relevées sur la figure ; notons aussi que les valeurs relativement très faibles mesurées au fond de la couche euphotique (niveau 1 %) peuvent être partiellement attribuées à une accumulation de chlorophylle détritique ([14]).

Deux hypothèses relient l'amplitude des variations nycthémérales de l'intensité photosynthétique, l'une à la latitude du lieu ([15]), l'autre, plus précisément, à la longueur du jour ([5]); or la durée du jour solaire varie en un même lieu en raison inverse de la profondeur. Ce facteur détermine peut-être en partie les différences d'amplitude ici observées, et peut d'autre part aisément expliquer le décalage horaire des maximums et des minimums aux cinq niveaux.

(*) Séance du 25 septembre 1967.

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([10]) J. H. Ryther et D. W. Menzel, *Bull. mar. Sci. Gulf Caribb.*, 11, n° 3, 1961, p. 381-388.
([11]) Diverses observations personnelles, inédites ou sous-presse.
([12]) *Cf.* U. S. Program in biology, Int. indian ocean exped., Cruises Rep., *Woods Hole oceanogr. Instn.*
([13]) Par exemple : A. Pirson et H. Lorenzen, *Naturwiss.*, 45, n° 20, 1958, p. 497.
([14]) *Cf.* C. S. Yentsch, *Mem. Ist. ital. Idrobiol.*, 18 (Suppl.), 1965, p. 323-346.
([15]) M. S. Doty, *J. mar. biol. Ass. India*, 1, n° 1, 1959, p. 66-68.

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LE GENRE *CERATIUM* (PÉRIDINIEN PLANCTONIQUE) DANS LE CANAL DE MOZAMBIQUE. CONTRIBUTION A UNE RÉVISION MONDIALE

PREMIÈRE PARTIE

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— SYSTÉMATIQUE.

Subg. *Archaeceratium*.
Sect. *Poroceratium : C. praelongum* (386). *C. cephalotum* (388). *C. gravidum* (388).

Subg. *Ceratium* (1).
Sect. *Candelabra : C. candelabrum* (390).
Sect. *Furciformia : C. furca* (395). *C. belone* (399). *C. incisum* (400).
Sect. *Pentagona : C. pentagonum* (400). *C. lineatum* (404). *C. teres* (405). *C. Kofoidii* (406). *C. minutum* (406). *C. setaceum* (407).

Subg. *Amphiceratium*.
Sect. *Inflata : C. geniculatum* (407).
Sect. *Fusiformia : C. fusus* (408). *C. extensum* (412). *C. inflatum* (412). *C. longirostrum* (413). *C. falcatum* (414). *C. falcatiforme* (414).

(1) En remplacement du nom illégal de « Subg. *Biceratium* (Vanh.) Gran » (cf. LANJOUW *et al.*, 1966, article 22), puisque ce sous-genre inclut très probablement l'espèce-type du genre *Ceratium : C. pleuroceras* Schrank, 1793, p. 34, pl. 3, fig. 23; quoiqu'imprécise, la description de SCHRANK semble en effet désigner une espère d'eau douce très voisine du *C. cornutum*.

Subg. *Orthoceratium* (1).
Sect. Tripos : *C. tripos* (416). *C. porrectum* (425). *C. breve* (425). *C. arietinum* (429). *C. symetricum* (432). *C. azoricum* (435). *C. Petersii* (436). *C. euarcuatum* (436). *C. declinatum* (438). *C. contortum* (441). *C. giberrum* (446). *C. concilians* (449). *C. lunula* (450), *C. Carnegiei* (452). *C. platycorne* (453).
Sect. *Densa : C. dens* (457).
Sect. *Limulus : C. limulus* (458). *C. paradoxides* (458).
Sect. *Palmata : C. ranipes* (459).
Sect. *Macroceros : C. macroceros* (460). *C. deflexum* (464). *C. massiliense* (466). *C. carriense* (469). *C. trichoceros* (472). *C. contrarium* (473). *C. horridum* (474). *C. vultur* (481). *C. Pavillardii* (483). *C. hexacanthum* (484).
Sect. *Reflexa : C. reflexum* (487).

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APERÇU SUR LA BIBLIOGRAPHIE MONDIALE

Une œuvre capitale domine la bibliographie du genre *Ceratium :* celle de JÖRGENSEN; la monographie mondiale de cet auteur (1911) est en effet la première en date (ainsi d'ailleurs que la dernière, si l'on met de côté, comme on le verra plus loin, le travail de SCHILLER). Cette révision contient la description et l'illustration détaillées de la presque totalité des espèces aujourd'hui connues; elle a cependant vieilli, comme il est naturel en un demi-siècle, d'une part du point de vue nomenclatural (synonymies, priorités, etc.), d'autre part au niveau infraspécifique (variabilité). Enfin, au sujet de cette monographie, signalons qu'elle est malheureusement devenue très rare dans les bibliothèques, et que sa réédition sera très profitable (2).

JÖRGENSEN a publié postérieurement (1920) une seconde étude capitale sur le genre *Ceratium,* mais cette fois limitée à la Méditerranée, et présentée différemment : l'auteur décrit les variations saisonnières et géographiques, et s'attache particulièrement au problème de la variabilité, ce qui le conduit à modifier sur plusieurs points de taxinomie son travail précédent, ainsi qu'à créer de nombreux taxons infraspécifiques.

Les *Ceratium* avaient antérieurement été étudiés dans l'optique océanographique, mais sur des bases systématiques insuffisantes,

(1) En remplacement du non illégal de « Subg. *Euceratium* (Vanh.) Ostf. » (cf. LANJOUW, *ibid.*, article 21).
(2) projetée par les Editions Zentralantiquariat (Leipzig).

par KARSTEN (1905, 1907) au cours des croisières de la *Valdivia*. Ils le sont de nouveau après JÖRGENSEN, par PETERS (1934) et SCHUBERT (1937) dans l'Atlantique (*Meteor, Plankton Exped.*, et *dtsch. antarkt. Exped.*), puis par STEEMANN NIELSEN (1934, 1939) dans l'Indo-pacifique (*Dana*) : PETERS développe la notion de sous-espèce géographique, qu'il appuie toutefois trop souvent sur une discrimination morphologique incertaine. STEEMANN NIELSEN, par contre, traite avec une égale précision les aspects écologique et morphologique et donne la première approche biométrique du problème de la variabilité.

L'histoire, ou plus simplement, les conditions de publication, ont voulu que le travail qui fait actuellement autorité dans le genre *Ceratium* soit celui de SCHILLER (1937) : publiée dans la *Rabenhorsts Kryptogamen-Flora*, la monographie de SCHILLER a probablement bénéficié du renom des Diatomées présentées peu avant par HUSTEDT dans la même Flore, car, de l'avis des Phytoplanctologistes avertis, la comparaison des deux ouvrages n'est guère soutenable. Les *Ceratium* de SCHILLER peuvent être considérés comme une mauvaise copie de ceux de JÖRGENSEN, copie cependant indispensable, car renfermant diverses innovations, et constituant malgré tout la mise à jour taxinomique la plus récente. Ce travail doit être consulté avec précautions, car les « distractions » et les erreurs « de détail » y sont abondantes : erreurs typographiques (?), omissions, références erronées, désignations infraspécifiques (*var.*, *f.*, *subsp.*) employées l'une pour l'autre, enfin figures empruntées à JÖRGENSEN ou à BÖHM et reproduites sous un nom infraspécifique différent...

Quoi qu'il en soit, la monographie de SCHILLER a fait date, et la grande majorité des travaux postérieurs en porte l'empreinte fidèle. Deux exceptions importantes cependant :

GRAHAM & BRONIKOVSKY (1944) ont donné une remarquable étude des *Ceratium* récoltés par le *Carnegie* dans l'Atlantique nord et dans le Pacifique; ce travail, d'importance « semi-mondiale », apporte de nombreuses contributions à la connaissance de l'écologie et de la variabilité chez ces Péridiniens. D'autre part, LOPEZ (1955 et 1966) a appliqué à plusieurs espèces les méthodes biométriques : nous y reviendrons plus loin.

Enfin, remarquons que les méthodes expérimentales ne sont pas encore entrées dans la pratique courante, si bien que les questions de physiologie, et particulièrement celles du métabolisme et de la sexualité, sont encore très mal connues (cf. HASLE & NORDLI, 1951; NIELSEN, 1956; NORDLI, 1953, 1957; STOSCH, 1964).

RÉPARTITION GÉOGRAPHIQUE DANS L'OCÉAN MONDIAL

Les *Ceratium* sont essentiellement thermophiles, mais de tolérance très variable vis-à-vis de la température. Les espèces d'eaux froides (soit sténothermes froides, soit cosmopolites) sont très peu nombreuses. On peut penser, à la suite de GRAHAM (1941) et GRAHAM & BRONIKOVSKY (1944), qu'il n'existe pas d'espèces tempérées proprement dites, mais seulement des espèces tropicales plus ou moins tolérantes, l'eurythermie pouvant conduire au cosmopolitisme.

La répartition géographique mondiale pose ici, comme pour tout être vivant, deux sortes de problèmes : 1) un problème de latitude, qui est celui de la bipolarité : les espèces d'eaux froides sont-elles les mêmes dans les deux hémisphères ? 2) un problème de longitude : à une latitude donnée, les espèces sont-elles réparties tout autour du globe ? Quelques mots sur ces deux questions :

1. BIPOLARITÉ

Ce problème ne peut qu'être évoqué ici pour mémoire, car mes récoltes dans le canal de Mozambique ne l'ont pas mis en jeu.

S'il est universellement admis que les espèces polaires sont différentes dans les deux hémisphères (JÖRGENSEN, 1911, STEEMANN NIELSEN, 1939), cette notion est toutefois plutôt suggérée par la théorie que prouvée par l'observation; celle-ci n'est en effet qu'à demi-probante, et l'on peut résumer comme suit l'état des connaissances : deux espèces arctiques bien connues, *C. arcticum* et *C. longipes*, n'ont pas encore été signalées dans l'Antarctique. (Mais rappelons ici la disproportion de nos connaissances phytoplanctoniques des deux régions... D'autre part, plusieurs taxons sont réputés propres à l'un ou à l'autre hémisphère, mais sont en fait mal définis ou mal connus : *C. lineatum*, *C. pentagonum* var. *robustum*, *C. pentagonum* subsp. *pacificum*, et *C. Petersii*.

Le problème est délicat, car il suppose de décider si deux formes morphologiquement voisines sont ou non distinctes. Une telle question, dans l'état actuel des connaissances et des méthodes de culture, demeure pratiquement insoluble.

2. INDO-PACIFIQUE ET ATLANTIQUE

Le problème de la distribution longitudinale des espèces d'eaux froides ne peut être abordé ici (cf. STEEMANN NIELSEN, 1939, GRAHAM

& BRONIKOVSKY, 1944). Par contre il me semble utile de résumer le cas des espèces tropicales, sous l'aspect de la distinction entre Atlantique et Indo-Pacifique.

La dernière mise à jour de cette question est celle de GRAHAM (1941) et GRAHAM & BRONIKOVSKY (1944) : ces deux auteurs concluent que, par suite des conditions hydrologiques, les communications entre les deux régions s'effectuent « à sens unique », 8 espèces, sténothermes chaudes, étant propres au Pacifique, et aucune n'étant endémique dans l'Atlantique.

Cette thèse doit être modifiée, dans son détail du moins, à la suite des quelques modifications taxinomiques et de la mise à jour que j'expose dans le présent travail :

— une espèce seulement demeure provisoirement « atlantique » : *C. minutum*; encore est-elle très mal connue, du fait de sa petite taille;

— par contre, sept espèces (dont la liste diffère de celle de GRAHAM & BRONIKOVSKY), paraissent « indo-pacifiques » ; quatre d'entre elles sont cependant mal connues (je les indique par un point d'interrogation) :

C. dens	? *C. Aultii*
C. filicorne	? *C. deflexum*
C. humile	? *C. lanceolatum*
	? *C. Petersii*

Précisons que sept espèces données par STEEMANN NIELSEN ou GRAHAM & BRONIKOVSKY comme endémiques de l'une ou de l'autre région sont maintenant connues dans les trois océans, ou sont tombées en synonymie : *C. Boehmii, C. Carnegiei, C. geniculatum, C. longinum, C. scapiforme, C. Schmidtii* et *C. Bigelowii*.

FACTEURS ÉCOLOGIQUES

Il est prouvé que le plus important est la température, dont l'effet se manifeste dans l'espace (variations géographiques) comme dans le temps (variations saisonnières). Ce facteur influe non seulement sur la répartition géographique des espèces, comme on vient de le voir plus haut, mais aussi sur les caractères morphologiques, selon un processus toutefois incertain : deux hypothèses principales tentent d'expliquer la relation entre température et variation morphologique. La première, la plus ancienne, est celle de la flottabilité : les cellules s'adapteraient à une élévation de la température par une diminution de leur masse et une augmentation de leur

surface portante. Selon la seconde hypothèse, la croissance, plus rapide dans les mers chaudes, rendrait compte de ces différences de taille. Quel que soit le mécanisme de ce phénomène (cf. NIELSEN, 1957), il est de règle que les *Ceratium* psychrophiles sont des organismes robustes, souvent pourvus de crêtes lamellaires, tandis que les formes d'eaux chaudes sont plus petites, plus délicates, et possèdent souvent des cornes longues et fines.

Au sujet des autres facteurs écologiques, les données sont contradictoires. Il est du moins assuré que la salinité est de peu d'importance, les *Ceratium* jouissant d'une remarquable euryhalinité. Par contre, l'action des sels nutritifs, des substances organiques, de la richesse planctonique, de la nature du milieu (« océanique » ou « néritique »), etc., demeure confuse (cf. PETERS, STEEMANN NIELSEN, GRAHAM & BRONIKOVSKY, NORDLI) : ceci tient en partie au fait que ces facteurs sont souvent interdépendants, et que seule une étude statistique peut permettre de définir leurs rôles respectifs.

La lumière enfin détermine dans une certaine mesure la distribution verticale des espèces : la notion de « plancton d'ombre » date de KARSTEN (1907), et a été développée par JÖRGENSEN (1920), STEEMANN NIELSEN, SCHUBERT (dont les données contredisent en grande partie celles de l'auteur précédent), PAVILLARD (1937), GRAHAM & BRONIKOVSKY, et HASLE. Cependant, la discrimination est incertaine dans plusieurs cas, ainsi que son mécanisme physiologique.

PROBLÈME DE LA VARIABILITÉ

La variabilité morphologique dans le genre *Ceratium* peut être qualifiée de diabolique. Elle n'a cependant pas lieu d'être supposée infinie, et c'est cet espoir qui doit soutenir dans leurs recherches les Océanographes et les Systématiciens...

Dans l'état actuel des connaissances, la notion d'espèce chez ces Péridiniens ne repose que sur le critère morphologique (que sa variabilité même rend souvent aléatoire), et sur un ensemble d'incertitudes relatives aux mécanismes génétiques (sexualité, hérédité, mutations) et physiologiques (autotomie, régénération, adaptation, hétéromorphisme). Le problème se trouve de plus compliqué par le fait que, dans le domaine de l'Océanographie, le milieu est mobile et constitue, par rapport à la Botanique terrestre, une référence beaucoup moins sûre. Aussi, l'extension de cette notion d'espèce varie-t-elle considérablement selon les auteurs, et s'est-elle trouvée parfois excessivement élargie (ENTZ, ZACHARIAS). Certains ont mul-

tiplié le nombre des formes, des variétés et des sous-espèces (JÖRGENSEN, 1920; PETERS, 1934); d'autres ont renoncé aux désignations infra-spécifiques, comme il apparaît souvent chez GRAHAM & BRONIKOVSKY.

Ce que PAVILLARD disait du *C. furca* (1931, p. 70) est applicable à de nombreuses autres espèces : « Son extension cosmopolite, son irrégularité quantitative, sa variabilité morphologique sont autant d'obstacles à une discrimination systématique et à une délimitation géographique rigoureuses ». La question change d'aspect cependant, dès lors que l'on admet qu'*il n'existe effectivement ni discrimination systématique, ni délimitation géographique rigoureuses,* chez certaines espèces du moins, telles que le *C. furca.* L'écueil principal ne réside plus alors que dans la nomenclature.

Les recherches les plus précises dans le domaine de la variabilité sont représentées, après les premières données numériques de STEEMANN NIELSEN (1934), par les deux travaux de LOPEZ sur *C. tripos* (1955) et le sous-genre *Ceratium* (1966). Les deux contributions que cet auteur a apportées à la connaissance du genre *Ceratium* sont considérables; toutefois c'est là davantage l'œuvre d'un Mathématicien que celle d'un Botaniste ou d'un Océanographe.

Remarquons tout d'abord que les méthodes employées par LOPEZ limitent la portée de ses recherches : 1) le matériel examiné provient exclusivement des côtes espagnoles de la Méditerranée (mais présente l'avantage de couvrir un cycle annuel). Les formes psychrophiles des espèces étudiées sont donc *a priori* écartées, et l'auteur n'a pas cru devoir les traiter « pour mémoire », comme je tente de le faire dans le présent travail, 2) les critères dimensionnels utilisés par LOPEZ (diamètre cingulaire et longueurs des cornes antapicales) représentent également une « option ». Il était certes impossible de « tout » mesurer; cependant, certaines autres dimensions ne sont pas moins intéressantes : longueur totale, longueur de la corne apicale, divergence des cornes postérieures (cf. JÖRGENSEN, 1911; NIELSEN, 1956 et, tout récemment, YARRANTON, 1967).

D'autre part, les conclusions de LOPEZ (génotypes et phénotypes thermiques) sont basées sur l'examen de populations (lots de 1 000 spécimens ou davantage); il en résulte que, au niveau des individus, la détermination reste souvent impossible. Ainsi plusieurs figures données par l'auteur (1955, fig. 13, et 1966, fig. 88, 90, 93) sont-elles dotées chacune de deux noms infra-spécifiques différents... Si les innovations proposées par LOPEZ sont donc pour la plupart inacceptables du point de vue taxinomique, du moins un fait biométrique essentiel (croissance allométrique) est désormais acquis.

PROPOSITIONS DE NOMENCLATURE

Il reste donc, dans le cas des espèces présentant une suite continue de variations morphologiques apparemment liées à la température, à convenir d'un mode de désignation infra-spécifique. On ne peut en effet s'en tenir au seul nom d'espèce : ce serait là refuser la difficulté et enterrer le problème. D'autre part, l'emploi de taxons infra-spécifiques devrait, pour rendre compte de tous les termes d'une série, être multiplié à l'infini...

Dans l'ignorance du fondement génétique des variations (génotypes ou phénotypes ?, mutants ?, clones ?, taxons distincts ou simples morphoses écologiques ?), on ne peut que tenter d'indiquer si le spécimen examiné représente le type thermophile, le type psychrophile, ou un stade intermédiaire :

— dans les deux premiers cas, l'emploi d'un nom de variété se révèle pratique, car les taxons de ce rang abondent dans la bibliographie, et évitent la création de nouvelles combinaisons. L'avenir dira si ce terme est physiologiquement et génétiquement justifié.

— pour ce qui est des stades intermédiaires, je propose une désignation para-systématique composée des épithètes des deux variétés, réunies par un tiret (1), ou par le signe > lorsque le spécimen en question est nettement plus proche de l'une des variétés.

Ainsi, le *Ceratium furca*, nommé plus haut, peut être subdivisé comme suit :

1. variété thermophile : *C. furca* var. *eugrammum* (Ehr.) Schiller.
2. variété psychrophile : *C. furca* (Ehr.) Clap. & Lachm. var. *furca*.
3. stades apparemment transitoires entre les deux variétés : *C. furca* (Ehr.) Clap. & Lachm., « *furca-eugrammum* », ou « *furca* > *eugrammum* », ou « *eugrammum* > *furca* » (voir détail p. 395).

Les guillemets précisent que ce mode de désignation se situe en marge de la Taxinomie classique. Cette innovation ne sera peut-être pas appréciée des Systématiciens, mais n'aura pas été inutile si elle suggère à l'un d'eux le désir de mieux faire dans cette voie. Du moins l'Océanographe peut-il par ce moyen apporter une précision écologique à la détermination spécifique.

L'on peut réserver l'emploi des noms de formes à des cas morphologiques particuliers qui ne peuvent être intégrés à une série de

(1) Chez de tels binômes, le choix du premier des deux noms à écrire sera fixé par les règles de priorité : ainsi, « *furca-eugrammum* », « *atlanticum-pulchellum* », etc., et non l'inverse.

variations thermiques : ainsi le *C. furca* f. *corpulentum* Jörg. (voir p. 399) à thèque épaisse et anguleuse, et pourvue d'une ornementation particulière; ou encore, le *C. horridum* f. *claviger* (Kof.) nov. comb., dont les extrémités des cornes postérieures sont claviformes.

A PROPOS DES TYPES SPÉCIFIQUES

J'ai dû à plusieurs reprises dans le cours de ce travail remplacer une épithète infra-spécifique superflue par le nom de l'espèce, selon les prescriptions du Code international de la nomenclature botanique (LANJOUW *et al.*, 1961). Ces innovations ne constituent nullement des combinaisons nouvelles (*ibid.*, art. 26). C'est ainsi que le nom de *C. furca* var. *Berghii* Lemm., qui représente le type de l'espèce, doit être remplacé par celui de *C. furca* (Ehr.) Clap. & Lachm. var. *furca*, et pareillement :

C. candelabrum var. *curvatulum* Jörg., par : var. *candelabrum*.

C. tripos var. *genuinum* Pav., par : var. *tripos*., etc.

Inversement, le type de l'espèce peut souvent désigner une des variétés de celle-ci; quelquefois aussi une forme particulière, comme c'est le cas pour *C. pentagonum*, dont la diagnose originelle de GOURRET décrit un cas physiologique « anormal » (corne antérieure vestigiale), pour lequel le nom légal est *C. pentagonum* Gourr. f. *pentagonum*.

Il se peut enfin que le type originel, dans le cas d'une forte variabilité, corresponde non pas à une subdivision de l'espèce, mais à un stade de transition entre deux variétés : c'est le cas de *C. breve* dont le type représente un intermédiaire entre les var. *parallelum* et *Schmidtii*. De telles situations, embarrassantes du point de vue de la nomenclature, ne peuvent être actuellement démêlées, devant l'ignorance de la nature génétique de ces « transitions ».

Notons que LOPEZ (1966) considère arbitrairement les variétés psychrophiles comme types spécifiques : cette position, anti-systématique, ne peut être retenue.

RECHERCHES ANTÉRIEURES DANS LA RÉGION ÉTUDIÉE

De même que les Diatomées planctoniques (cf. SOURNIA, s. presse), les *Ceratium* ne sont, dans l'océan Indien et dans la région du canal de Mozambique, ni mieux ni plus mal connus qu'ailleurs dans le monde, exception faite de l'Atlantique Nord, région océanographique privilégiée entre toutes. On peut d'autre part espérer

d'intéressantes contributions du dépouillement final de l'Expédition internationale dans l'océan Indien.

Les deux grandes expéditions océanographiques de la *Valdivia* et du *Dana* ont donné lieu aux importants mémoires de KARSTEN (1907) et de STEEMANN NIELSEN (1939). De plus, diverses croisières ou voyages non océanographiques ont fourni matière aux travaux de CLEVE, 1900b (sud de l'océan), 1900c (mer Rouge), 1901 (océan Indien et régions indonésiennes), 1903 (mer Rouge et mer d'Arabie), d'OSTENFELD & SCHMIDT, 1901 (mer Rouge et golfe d'Aden) et de SCHRÖDER, 1906 (*id.*, Ceylan, Indonésie, côte d'Australie). La région australienne a été abondamment étudiée par WOOD (1954, 1963b et c). On compte enfin quelques inventaires localisés, tels celui d'OSTENFELD, 1915 (Célèbes), de SUBRAHMANYAN, 1958 (côte occidentale des Indes) ainsi que plusieurs travaux propres au canal de Mozambique :

Cette dernière région (voir carte 1) a été relativement bien explorée. Le *Dana* l'a traversée du Nord au Sud, et la *Valdivia* l'a longée au Nord. Les inventaires locaux annoncés ci-dessus concernent la côte du Mozambique (SILVA, 1956a et 1960), les parages de Zanzibar (BALLANTINE, 1961) et de Tuléar (TRAVERS, 1965).

Enfin, au sujet du genre *Ceratium* dans l'océan Indien, WOOD (1963a) a donné, sous forme d'une « check-list », une base bibliographique indispensable.

MÉTHODES, BUTS ET LIMITES DU PRÉSENT TRAVAIL

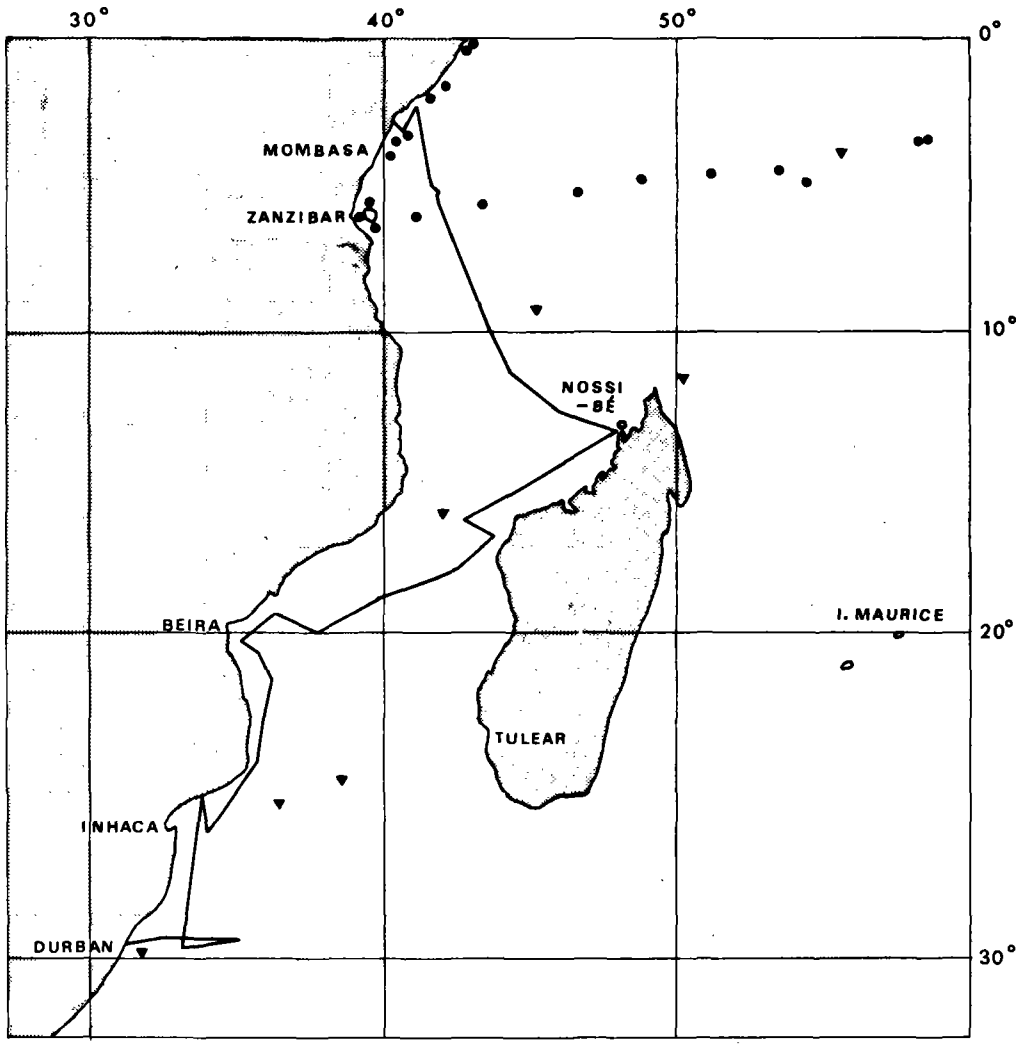
1. RÉCOLTES

Le matériel ici étudié provient de trois groupes de récoltes (voir carte 1).

— A Nossi-Bé : pêches au filet de surface, hebdomadaires, de février 1963 à juillet 1964, dans la baie de la Station océanographique de l'ORSTOM (baie d'Ambanoro). Il s'agit donc là de récoltes purement littorales, mais échelonnées sur un cycle annuel.

— A Tuléar : pêches au filet de surface, en août et septembre 1964, en diverses stations plus ou moins littorales (de part et d'autre du grand récif, et dans le canyon de St. Augustin).

— A bord du R/V *Anton Bruun* (Woods Hole), croisière océanographique du sud au nord du canal de Mozambique, de septembre à novembre 1964 (le parcours en est reporté sur la carte 1 par une ligne brisée. Voir aussi Anonyme, 1965). Pêches horizontales et verticales.



CARTE 1 : Etat actuel des recherches sur le genre *Ceratium* dans le canal de Mozambique. Voir page précédente.
— triangles : stations du *Dana*;
— cercles : stations de la *Valdivia*;
— ligne brisée: croisière n° 8 de l'*Anton Bruun*.

Dans les trois cas, des échantillons d'eau de mer étaient prélevés aux fins d'études quantitatives (méthode d'UTERMÖHL), mais se sont révélés de peu d'intérêt pour l'observation des *Ceratium*, étant donné la rareté numérique de ces Péridiniens. Ce moyen a cependant permis d'examiner les quelques petites espèces qui échappent ordinairement au filet.

Enfin, pour des raisons de commodité, j'intègre au présent travail quelques prélèvements effectués à l'Ile Maurice, et dont un inventaire préliminaire a déjà été publié (SOURNIA, 1965).

2. RÉSULTATS

L'objet de la présente étude est essentiellement taxinomique. Les données quantitatives et écologiques, ainsi que les mesures de productivité que j'ai pu effectuer dans la même région, seront exposées ultérieurement.

Par suite de la thermophilie générale du genre, j'ai pu récolter dans le canal de Mozambique la majorité des espèces, et du moins les plus embarrassantes du point de vue systématique. Ayant de plus disposé des possibilités bibliographiques considérables du Muséum d'Histoire naturelle de Paris, j'ai été amené à un compromis entre l'inventaire régional et la révision mondiale. C'est ainsi que, conjointement aux *Ceratium* que j'ai observés, je traite « pour mémoire » plusieurs taxons que je ne connais que par la bibliographie, mais dont la position taxinomique était directement mise en cause par les premiers. Dans une note préliminaire (SOURNIA, 1966) ont été exposées les conclusions essentielles de cette étude, ainsi que les principales nouvelles combinaisons taxinomiques que celle-ci m'a conduit à proposer.

Toutes les illustrations sont accompagnées d'une échelle de 50 µ. Dans le cas des figures non originales, l'échelle a été calculée d'après les dimensions indiquées par l'auteur cité.

Mes remerciements vont à l'Office de la recherche scientifique et technique outre-mer, qui m'a accueilli pendant dix-huit mois dans son centre de Nossi-Bé; à la Faculté des sciences de Tananarive et à la Station marine d'Endoume-Marseille, pour les possibilités de travail dont j'ai bénéficié à Tuléar; enfin à la Woods Hole oceanographic Institution et la National Science Foundation, qui m'ont permis de participer à la croisière de l'*Anton Bruun* dans le canal de Mozambique.

SUBG. ***ARCHAECERATIUM*** JÖRGENSEN
SECT. *POROCERATIUM* VANHÖFFEN) JÖRGENSEN

Ceratium praelongum (Lemmermann) Kofoid *ex* Jörgensen, 1911
(Pl. I, fig. 1)

LEMMERMANN, 1899, p. 349, pl. 1, fig. 15 : *C. gravidum* var. *praelongum* ; KOFOID, 1907*b*, p. 182 ; JÖRGENSEN, 1911, p. 9, pl. 1, fig. 9 ; OKAMURA, 1912, p. 6, pl. 3, fig. 48 ; PETERS, 1934, p. 28, pl. 2, fig. 12*f* ; STEEMANN NIELSEN, 1934, p. 7, fig. 1, et 1939, p. 6 ; SCHILLER, 1937, p. 356, fig. 387 ; GRAHAM & BRONIKOVSKY, 1944, p. 14, fig. 1*a-d* ; SILVA, 1958, p. 32, pl. 3, fig. 4 ; WOOD, 1963*b*, p. 40, fig. 148.

= *Ceratium gravidum* var. *praelongum* Lemmermann.
LEMMERMANN, 1899; OSTENFELD & SCHMIDT, 1901; KARSTEN, 1907.

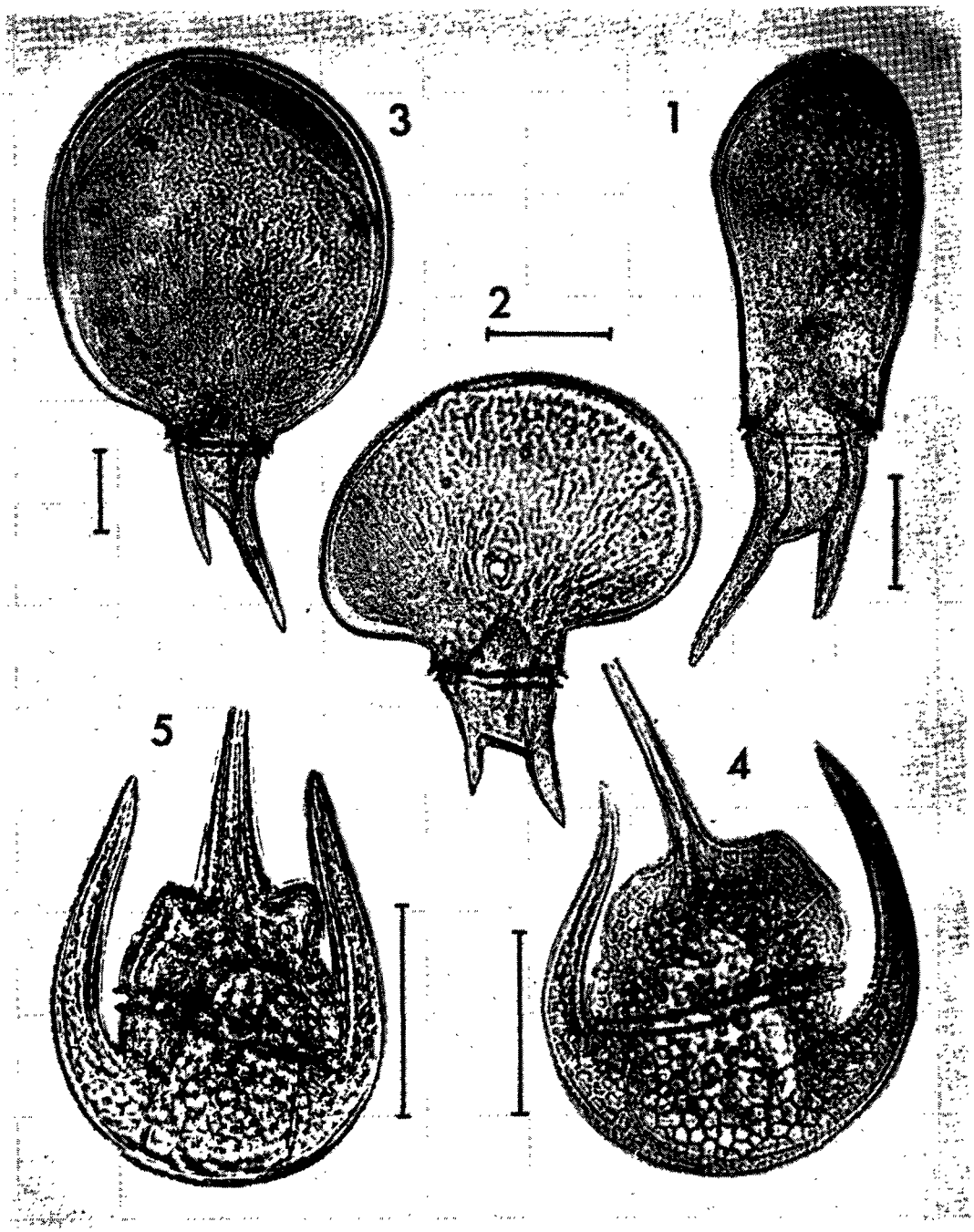


PLANCHE I

FIG. 1 : *Ceratium praelongum* (Lemm.) Jörg. — 2 : *C. cephalotum* (Lemm.) Jörg. — 3 : *C. gravidum* Gourret. — 4 : *C. paradoxides* Cleve. — 5 : *C. limulus* (Pouchet) Gourret.

Le nom de *C. praelongum* se trouve seulement « mentionné incidemment » par KOFOID (*loc. cit.*), sans nom d'auteur, et sans que rien n'indique que l'auteur eût voulu créer là une espèce nouvelle. La publication valide de ce taxon doit donc être attribuée à JÖRGENSEN.

RÉCOLTES PERSONNELLES : Au large de Durban. Centre du canal de Mozambique. Au large de Nossi-Bé et des Comores. Espèce rare, et seulement récoltée dans les prélèvements verticaux.

OCÉAN INDIEN : Distribution très sporadique : mer Rouge. Ceylan. Diverses stations pélagiques de la zone tropicale. Dans le canal de Mozambique, ce *Ceratium* n'était connu jusqu'ici qu'à Tuléar (TRAVERS, 1965).

DISTRIBUTION MONDIALE : Espèce oligophotique, océanique, intertropicale, de distribution sporadique. En Méditerranée, seulement signalée par PAULSEN (1930) en mer d'Alboran.

Ceratium cephalotum (Lemmermann) Jörgensen, 1911
(Pl. I, fig. 2)

LEMMERMANN, 1899, p. 349, pl. 1, fig. 16 : *C. gravidum* var. *cephalotum* ; JÖRGENSEN, 1911, p. 10, pl. 1, fig. 10 ; OKAMURA, 1912, p. 6, pl. 3, fig. 49 ; PETERS, 1934, p. 28 ; STEEMANN NIELSEN, 1934, p. 7, fig. 2, et 1939, p. 6 ; SCHILLER, p. 356, fig. 388 ; GRAHAM & BRONIKOVSKY, 1944, p. 15, fig. 2*a-c* ; WOOD, 1954, p. 271, fig. 185.

= *C. gravidum* var. *cephalotum* Lemmermann.
LEMMERMANN, 1899; KARSTEN, 1907.

= *C. gravidum* var. *hydrocephalum* Schröder.
SCHRÖDER, 1906

RÉCOLTES PERSONNELLES : Tuléar. Centre du canal de Mozambique. Très rare.

OCÉAN INDIEN : Comme *C. praelongum*.

DISTRIBUTION MONDIALE : Semblable à celle de l'espèce précédente; toutefois *C. cephalotum* est notablement plus rare, et demeure inconnu en Méditerranée.

Ceratium gravidum Gourret, 1883
(Pl. I, fig. 3)

GOURRET, 1883, p. 58, pl. 1, fig. 15 ; KOFOID, 1907*b*, p. 182, fig. 7-8 ; JÖRGENSEN, 1911, p. 10, pl. 1, fig. 8, et 1920, p. 8, fig. 4 ; PETERS, 1934, p. 28, pl. 2, fig. 12*g* ; STEEMANN NIELSEN, 1934, p. 8, fig. 3-4, et 1939, p. 6 ; SCHILLER, 1937, p. 357, fig. 389 ; GRAHAM & BRONIKOVSKY, 1944, p. 15, fig. 3*a-c*, 4*p-u* ; WOOD, 1954, p. 272, fig. 186 ; SILVA, 1955, p. 49, pl. 7, fig. 1 ; HALIM, 1960, pl. 4, fig. 21.

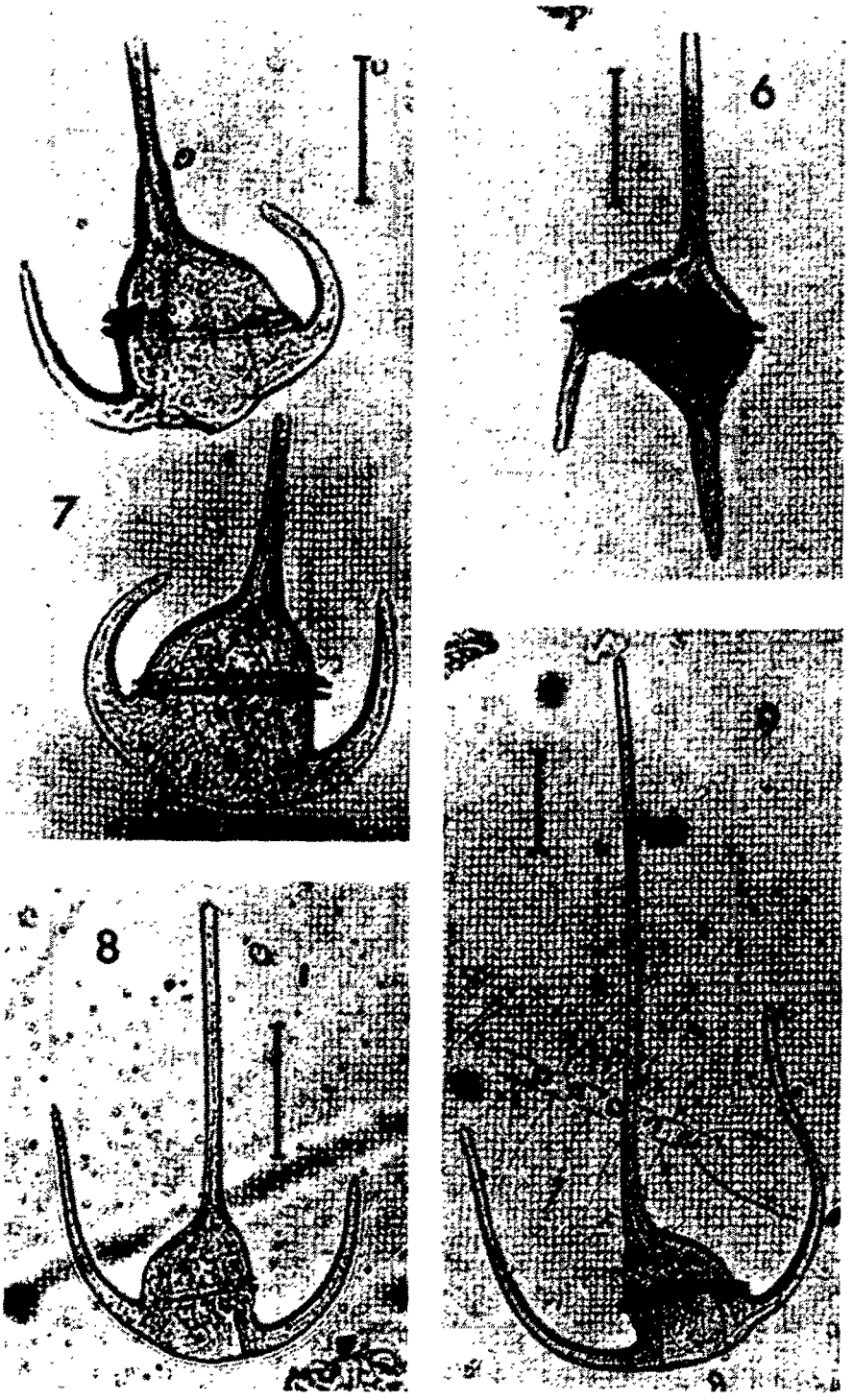


PLANCHE II

FIG. 6 : *Ceratium candelabrum* (Ehr.) Stein, « *candelabrum-depressum* ». — 7 : *C. breve* (Ostf. & Schm.) Schröder, « *Schmidtii* > *parallelum* ». — 8 : *C. declinatum* f. *normale* Jörg. — 9 : *C. contortum* (Gourret) Cleve, « *Karstenii* > *contortum* ».

ARCHIVES

= *C. gravidum* var. *latum*, var. *angustum*, var. *elegans*, et f. *obovatum* Jörgensen.

JÖRGENSEN, 1911, 1920; PAVILLARD, 1935.

= *C. gravidum* var. *elongatum* Wood.

WOOD, 1963b.

RÉCOLTES PERSONNELLES : Tuléar (rare).

OCÉAN INDIEN : Mer Rouge, golfe d'Aden, mer d'Arabie, parages de l'Australie, Tuléar, et diverses stations océaniques.

DISTRIBUTION MONDIALE : Espèce océanique, tropicale et subtropicale, occasionnellement tempérée. Notablement plus fréquente que les deux précédentes et, notamment, bien connue en Méditerranée.

GRAHAM & BRONIKOVSKY ont montré qu'il est inutile de retenir les désignations infra-spécifiques introduites par JÖRGENSEN : D'après ces auteurs, la variabilité du *C. gravidum* serait indépendante des conditions géographiques, mais ceci reste à confirmer par une méthode statistique appropriée.

SUBG. *CERATIUM*

SECT. *CANDELABRA* JÖRGENSEN

Ceratium candelabrum (Ehrenberg) Stein, 1883

EHRENBERG, 1860, p. 792, et 1873, p. 3, pl. 1, fig. 2-3 : *Peridinium candelabrum* ; STEIN, 1883, pl. 15, fig. 15-16.

Une lourde méprise entache et complique la bibliographie de cette espèce, et justifie ici un bref historique :

JÖRGENSEN (1920) a apporté deux modifications majeures à l'exposé qu'il avait précédemment donné dans sa monographie (1911). En premier lieu, il substitue au terme « var. *dilatatum* (Gourret) Jörgensen, 1911 » celui de « var. *depressum* (Pouchet) Jörgensen, 1920 ». Les deux figures données à l'appui (1920, fig. 5-6) correspondent en effet fidèlement à l'iconographie de la variété *dilatatum* (respectivement : 1911, pl. 1, fig. 5, et pl. 2, fig. 22). Rappelons que PAVILLARD (1931) conteste l'identité des deux taxons, mais admettons pour définitive l'interprétation que donne JÖRGENSEN des diverses figures très douteuses de GOURRET, et passons outre. En second lieu, JÖRGENSEN désigne (illégalement) le type de l'espèce sous le nom de « var. *α-curvatulum* », cette épithète évoquant l'inflexion de la corne apicale, inflexion donnée par l'auteur comme caractéristique du type (ce caractère est en fait tout à fait accessoire, mais passons encore). STEEMANN NIELSEN (1934) doute de la signification de cette innovation ; il est vrai que la variété *curvatulum* n'est pas illustrée par JÖRGENSEN dans son travail de 1920, mais tout porte à croire que l'auteur

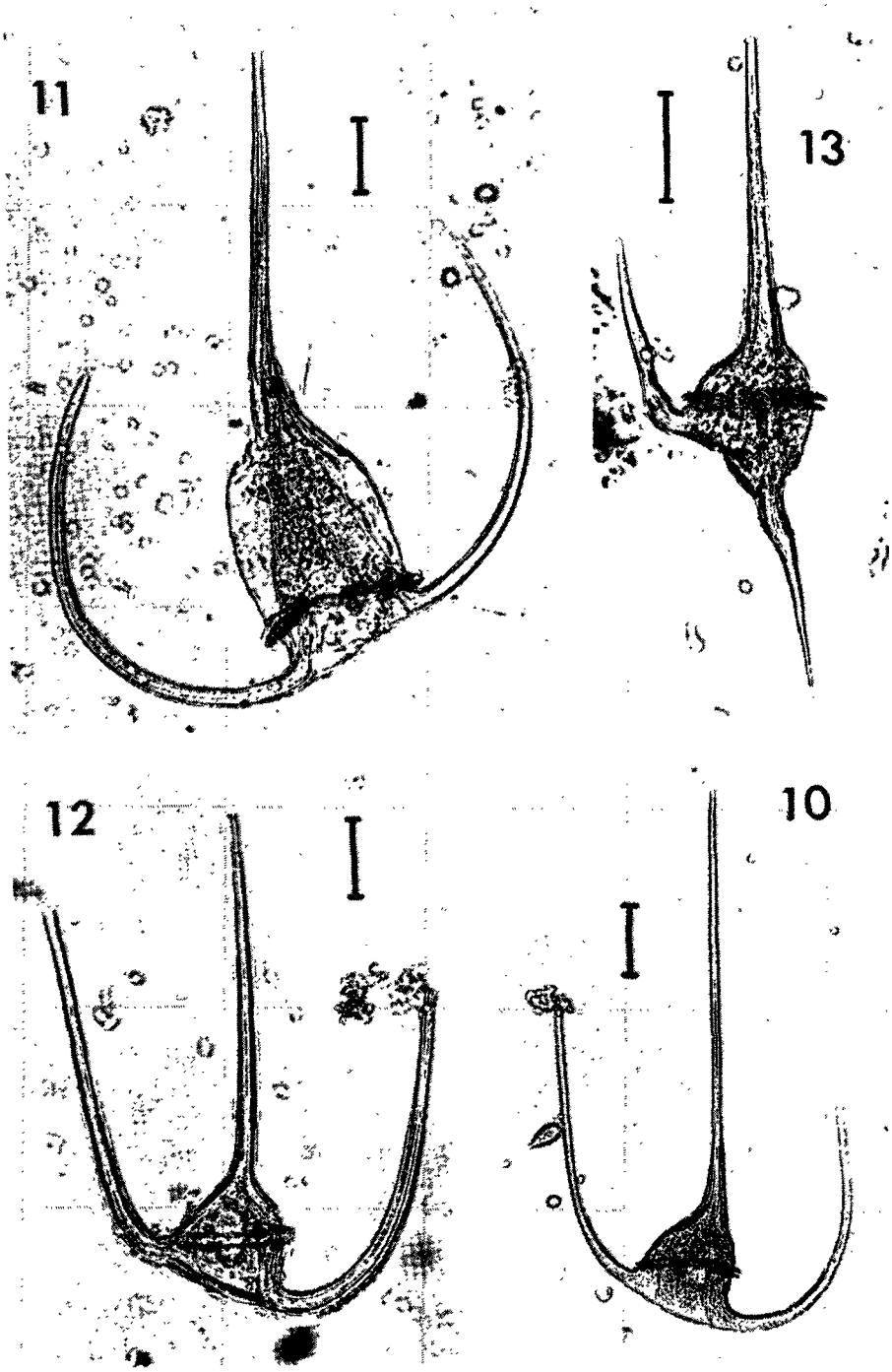


PLANCHE III

FIG. 10 : *Ceratium contortum* var. *Karstenii* (Pav.) Sournia. — 11 : *C. Carnegiei* Graham & Bron. — 12 : *C. horridum* (Cleve) Gran, « *horridum* > *buceros* ». — 13 : *C. reflexum* Cleve.

renvoie implicitement à la figure donnée précédemment pour le type de l'espèce : 1911, pl. 2, fig. 21. L'erreur annoncée plus haut est le fait de Böhm (1931*a*) qui attribue la figure 6 de Jörgensen, 1920, à la variété *curvatulum*. Böhm crée de plus illégalement la forme « f. *commune* (*nov. nom.*) = Jörgensen, 1911, fig. 21 ». Enfin, dans le même travail, Böhm ajoute à l'espèce deux formes nouvelles : f. *eucandelabrum* et f. *hiemale*, qui toutes deux, à mon avis, sont assimilables au type. La conception erronée et illégale de Böhm est intégralement reprise par Schiller (1937); ce dernier figure donc sous le nom impropre de « f. *curvulatum* » (fig. 402*a-c*) deux spécimens appartenant en fait à la variété *depressum*.

Il résulte de cet historique que :

— le terme « var. *curvatulum* » est, postérieurement à Jörgensen, employé à tort, puisqu'à l'opposé du sens primitif. Ce terme est de plus illégal, puisqu'il désigne le type de l'espèce, et doit être remplacé par celui de « var. *candelabrum* ».

— le terme « f. *commune* », semblablement illégal, doit lui aussi être rejeté.

Quant à la variabilité de l'espèce, elle se manifeste sous la forme de deux types extrêmes reliés par une série continue de transitions. Parmi les divers taxons subspécifiques décrits jusqu'ici, un seul doit être maintenu à l'écart de ce « spectre » de variations : il s'agit de la variété *subrotundum* Pav. qui représente vraisemblablement un cas physiologique particulier, et que je préfère considérer comme une forme (voir références ci-dessous).

Cependant *C. candelabrum* présente un cas quelque peu particulier : sa distribution géographique est, autant qu'on en puisse juger actuellement, remarquablement homogène, toutes les variations morphologiques se rencontrant à peu près uniformément dans l'aire de répartition de l'espèce. Seul Steemann Nielsen (1934) remarque, dans le Pacifique tropical, une certaine discrimination latitudinale. Cette homogénéité géographique, jointe à la continuité des variations morphologiques, a conduit Peters (1934) et Graham & Bronikovsky (1944), à considérer l'espèce comme indivisible. En fait, la variabilité du *C. candelabrum* est bien liée aux facteurs écologiques, mais se manifeste plus nettement « dans le temps » que « dans l'espace » : Pavillard (1916) note que la « forme *dilatatum* » remplace le type en été dans le golfe du Lion; Jörgensen (1920) a montré le rôle de l'alternance saisonnière dans la répartition des variétés « *depressum* » et « *curvatulum* » en Méditerranée; et, plus récemment, la remarquable étude de Lopez (1966) expose clairement le cycle annuel de l'espèce sur les côtes de Castellon.

La nature même des variations porte essentiellement sur la longueur des cornes antapicales, et le rapport de cette longueur au diamètre cingulaire; tel est du moins le système adopté par Lopez. La divergence des cornes antapicales, ainsi que la hauteur de l'épi-

thèque et de l'hypothèque, semblent être des caractères concomitants, quelque peu plus instables, et aussi d'emploi moins aisé.

Quelle nomenclature adopter ? Lopez distingue deux variétés, *candelabrum* et *dilatatum*, la première composée de deux formes dont l'une est en quelque sorte transitionnelle. Je préfère adopter le système proposé p. 382 et qui trouve ici sa première application :

var. ***candelabrum***
Fig. 14

= *Ceratium candelabrum* (Ehrenberg) Stein, *pro parte.*

Stein, 1883; *Vix* Ehrenberg, 1873; Jörgensen, 1911 (fig. 21, *non al.*); Forti, 1924; Lebour, 1925; Steemann Nielsen, 1934; Nie, 1936; Graham & Bronikovsky, 1944 (fig. 6e, f, h, *non al.*).

= *C. candelabrum* f. *commune* Böhm.

Böhm, 1931a; Schiller, 1937; Rampi, 1939; Wood, 1954; Klement, 1964.

= *C. candelabrum* f. *hiemale* Böhm, et f. *eucandelabrum* Böhm.
Böhm, 1931a et b.

= *C. candelabrum* var. *genuinum* Pavillard.
Pavillard, 1931.

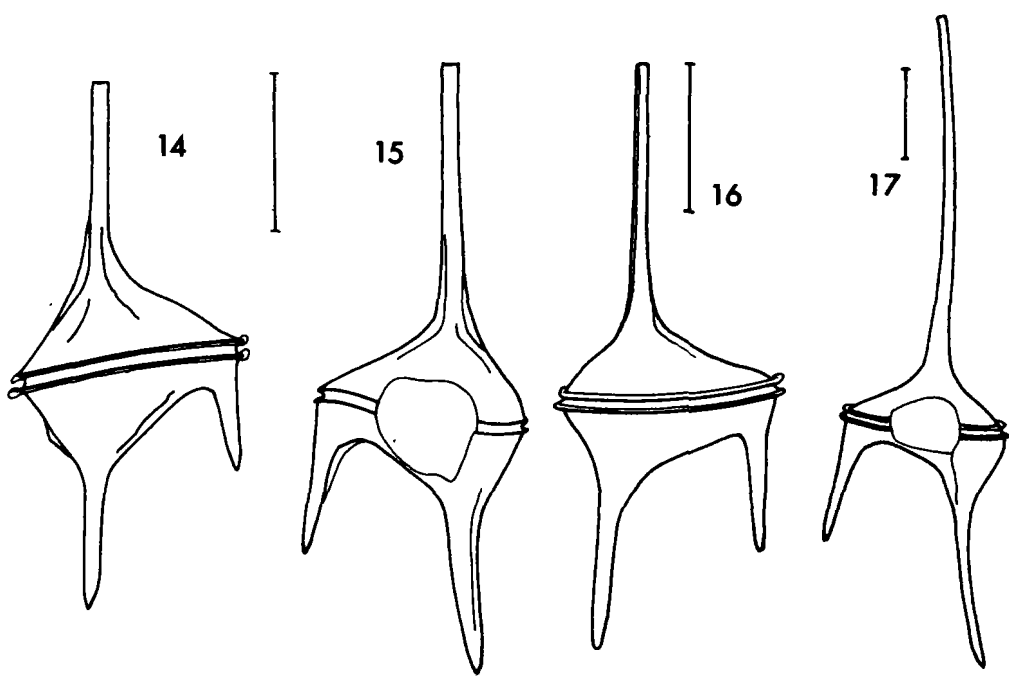


Fig. 14 : *Ceratium candelabrum* (Ehr.) Stein var. *candelabrum*. — 15 : *C. candelabrum* (Ehr.) Stein, « *candelabrum* > *depressum* ». — 16 : *C. candelabrum* (Ehr.) Stein, « *candelabrum-depressum* ». — 17 : *C. candelabrum* var. *depressum* (Pouchet) Jörg.

= *C. candelabrum* var. α *curvatulum* Jörgensen, *pro parte.*
Jörgensen, 1920; Wood, 1954; Klement, 1964. *Non al.*

= *C. candelabrum* var. *candelabrum* f. *subcandelabrum* Lopez.
Lopez, 1966.

Cornes antapicales peu développées : longueur de la corne gauche (la plus longue des deux) inférieure au diamètre cingulaire. Corps central non comprimé (Diam. cing. : 55-75 μ).

Variété psychrophile, ou du moins hivernale.

var. ***depressum*** (Pouchet) Jörgensen, 1920
Fig. 17

Pouchet, 1883, p. 417, *vix* pl. 18, fig. 1*a-b* : *Ceratium furca* var. *depressum* ; Jörgensen, 1920, p. 12, fig. 5-6 ; Forti, 1924, p. 34, pl. 1, fig. 16 ; Böhm, 1931*a*, p. 351, et 1931*b*, p. 8, fig. 8*a, c, d, non b* ; Steemann Nielsen, 1934, p. 8, fig. 7 ; Schiller, 1937, p. 366, fig. 403 : « f. *depressum* Pouchet » ; Rampi, 1939, p. 302, fig. 7 ; Wood, 1954, p. 273, fig. 187*b* ; Klement, 1964, p. 354.

= *C. candelabrum* var. *dilatatum* (Gourret) Jörgensen.
Gourret, 1883 : *Ceratium dilatatum;* Jörgensen, 1911, (1920); Lebour, 1925; Pavillard, 1931; Lopez, 1966 (fig. 89 droite, *non* gauche).

= *C. candelabrum* var. α *curvatulum* Jörgensen, *pro parte.*
Böhm, 1931a ; Schiller, 1937; Halim, 1963 et *plur. auct. Non* Jörgensen, 1920.

= *C. candelabrum* var. *algerense* Schiller.
Schiller, 1929, (1937). *Vix* Pavillard, 1931.

= *Ceratium candelabrum* (Ehrenberg) Stein, *pro parte.*
Graham & Bronikovsky, 1944 (fig. 6 b-d, g, *non al.*).

Cornes antapicales très développées, souvent divergentes; longueur de la corne gauche (la plus longue des deux) égale ou supérieure au diamètre cingulaire. Corps central généralement comprimé : épithèque et hypothèque beaucoup plus « larges » que « hautes » (Diam. cing. : 80-105 μ).

Variété thermophile, ou du moins estivale.

Transitions entre les deux variétés précédentes :
Fig. 15-16 et pl. II, fig. 6

= *Ceratium candelabrum* (Ehrenberg) Stein, *pro parte.*
Graham & Bronikovsky, 1944, fig. 6a, i-k, *non al.*
= *C. candelabrum* var. *candelabrum* f. *candelabrum, in* Lopez, 1966.
Lopez, 1966, fig. 56-58, et 88 II et III.

POUR LES DEUX VARIÉTÉS ET LEURS TRANSITIONS :

RÉCOLTES PERSONNELLES : *C. candelabrum* est assez rare en domaine néritique (Nossi-Bé, Tuléar, Ile Maurice), mais plus fréquent, encore que sporadique, en domaine océanique (croisière de l'*Anton Bruun*), et là, également présent dans les prélèvements horizontaux et verticaux. Dans l'ensemble, aucune discrimination écologique entre les deux variétés n'est évidente.

OCÉAN INDIEN : Espèce largement répandue dans toutes les régions de l'océan.

DISTRIBUTION MONDIALE : Espèce commune dans toute la zone tempérée-tropicale. Euphotique. Peut-être, mais non exclusivement océanique. Au sujet des exigences écologiques des deux variétés, voir plus haut.

Pour mémoire :

C. candelabrum f. ***subrotundum*** (Pavillard) nov. comb.

= *C. candelabrum* var. *subrotundum* Pavillard.
PAVILLARD, 1930 et 1931.

Il semble s'agir ici d'un cas physiologique particulier (réduction des trois cornes) qui dériverait de la variété *candelabrum*.

SECT. *FURCIFORMA* JÖRGENSEN

Ceratium furca (Ehrenberg) Claparède & Lachmann, 1859

EHRENBERG, 1836, p. 574, pl. 2, fig. 2, et 1838, p. 256, pl. 22, fig. 21 : *Peridinium furca* ; CLAPARÈDE & LACHMANN, 1859, p. 399, pl. 19, fig. 5.

Cette espèce est souvent attribuée à tort à DUJARDIN : cet auteur ne fait cependant que mentionner (1841, p. 379) le *Peridinium furca* Ehr. comme espèce voisine du *Ceratium fusus*, ce qui ne saurait constituer une publication valide.

JÖRGENSEN (1911) distinguait chez *C. furca* deux sous-espèces, *Berghii* et *eugrammum*, l'une relativement grande et psychrophile, l'autre plus petite et thermophile. Cette dualité n'a été que renforcée par les observations ultérieures, en même temps que s'est confirmée la présence d'une suite ininterrompue de transitions entre les deux extrêmes ; ce dernier point a découragé certains auteurs tels que GRAHAM & BRONIKOVSKY

(1944), qui traitent l'espèce comme un complexe indivisible. Notons encore, dans l'historique du *C. furca*, quelques divergences d'opinion :

JÖRGENSEN (1920) adjoint à la sous-espèce *eugrammum* diverses formes qui, à l'exception d'une f. *corpulentum*, peuvent être sans difficulté intégrées au spectre de variations spécifiques, et ne seront donc pas conservées ici. Les références de la forme *corpulentum* (non rencontrée dans mes récoltes), sont données plus bas pour mémoire. BÖHM (1931*b*) voit ensuite en *C. furca* deux génotypes différant l'un de l'autre par leur longueur totale, mais appartenant tous deux « de toute évidence » (?) à la variété *eugrammum* ; les deux groupes sont eux-mêmes, selon BÖHM, soumis à des variations écologiques et, dans la marge de variations qui leur est commune, sont indiscernables l'un de l'autre. Dans son détail cependant, cette conception très souple n'est pas défendable, car elle repose sur une étude statistique trop sommaire et sur des chiffres tout à fait contradictoires, dont STEEMANN NIELSEN (1934) a fait avant moi la critique. Ce dernier auteur reconnaît les deux sous-espèces initiales de JÖRGENSEN, mais ses données montrent que la distinction est rarement évidente. Pour GRAHAM & BRONIKOVSKY (1944), comme on l'a vu, *C. furca* représente la juxtaposition de plusieurs (et non pas deux) « races » et variétés impossibles à définir.

Le problème de la variabilité chez *C. furca* n'a été abordé de façon réellement statistique que tout récemment, par LOPEZ (1966). Cet auteur, ayant mesuré la longueur des cornes antapicales et du diamètre cingulaire chez 1841 individus méditerranéens, confirme l'existence de deux variétés distinctes, et divise la seconde (var. *Berghii*) en deux formes. La critique générale du travail de LOPEZ a été faite au début de ce travail (p. 381) ; pour les raisons que j'y expose, je préfère voir en la présente espèce deux variétés, réunies par des stades de transition.

Rappelons en outre que la var. *Berghii* Lemm. n'a pas été décrite par LEMMERMANN (1899), qui renvoie simplement à la figure 20 de BERGH (1882). La description de cette variété est due à JÖRGENSEN (1911, et de façon allusive *in* 1920) qui la considère à la fois comme le type de l'espèce et comme une sous-espèce nordique. Il est en effet indiscutable que la var. *Berghii* correspond au type d'EHRENBERG et de CLAPARÈDE & LACHMANN. Aussi le nom de ce taxon est-il illégal, et doit être remplacé par celui de var. *furca*.

var. ***furca***
Fig. 20

= *C. furca* var. *Berghii* Lemmermann = subsp. *Berghii* (Lemmermann) Jörgensen.

BERGH, 1882 (fig. 20, *non al.*, « Varietät von *C. furca* » ; LEMMERMANN, 1899; JÖRGENSEN, 1911, (1920); STEEMANN NIELSEN, 1934, 1939; SCHILLER, 1937 (fig. 404a, *vix* b, *non* c); ? WOOD, 1954 (*non* fig. 189a).

= *Ceratium furca* (Ehrenberg) Claparède & Lachmann, *pro parte.*
EHRENBERG, 1836, 1838 (*Peridinium furca*); CLAPARÈDE & LACHMANN, 1859. *Non* BERGH, 1882; WAILES, 1928; SOUZA, 1950. *Vix* HALIM, 1960.

= *Ceratium furca* var. *singulare* Gourret.
GOURRET, 1883.

= *Ceratium furca* f. *magnipes* Jörgensen.
JÖRGENSEN, 1920.

= *C. furca* var. *Berghii* f. *Berghii, in* LOPEZ, 1966.

Epithèque sub-conique, se rétrécissant rapidement et, de ce fait, distincte de la corne apicale proprement dite. Celle-ci longue, souvent légèrement recourbée. Hauteur de l'épithèque inférieure ou quelquefois égale à la longueur de la corne apicale. Cornes antapicales bien développées par rapport au diamètre cingulaire; longueur de la corne antapicale droite (la plus courte des deux) égale ou supérieure à ce diamètre. Cornes antapicales parallèles entre elles, ou divergentes, et généralement denticulées à leur extrémité.

Variété psychrophile, quoique probablement cosmopolite.

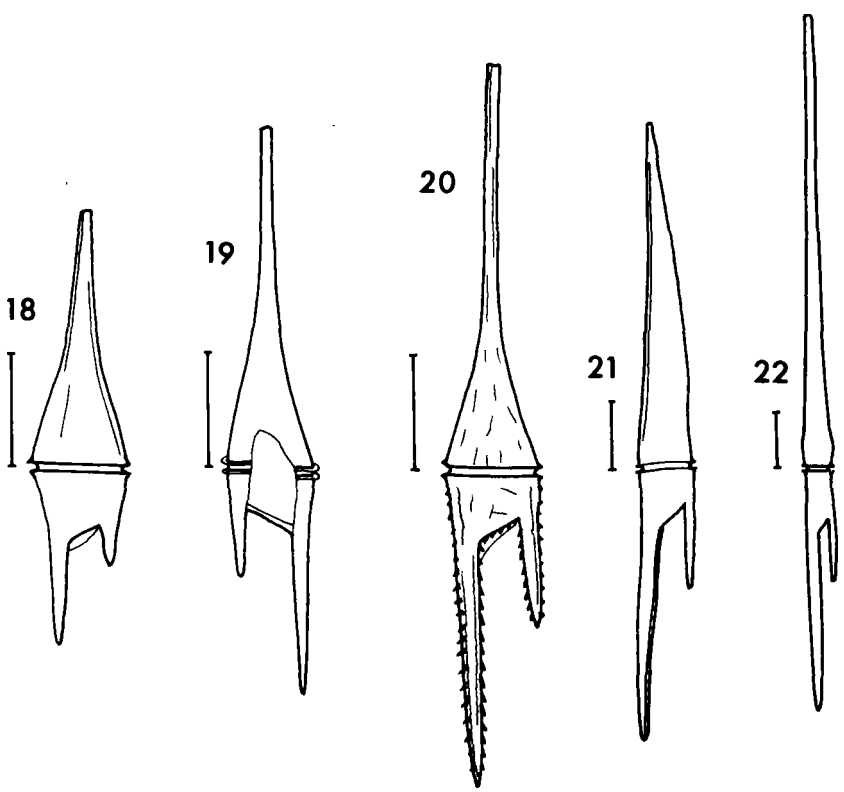


FIG. 18 : *Ceratium furca* var. *eugrammum* (Ehr.) Schiller. — 19 : *C. furca* (Ehr.) Clap. & Lachm., « *furca-eugrammum* ». — 20 : *C. furca* (Ehr.) Clap. & Lachm. var. *furca.* — 21 : *C. incisum* (Karsten) Jörg. — 22 : *C. belone* Cleve.

var. **eugrammum** (Ehrenberg) Schiller, 1937
Fig. 18

Ehrenberg, 1860, p. 792 et 1873, p. 3, pl. 1, fig. 4 : *Peridinium eugrammum*; Schiller, 1937, p. 368, fig. 405a; Rampi, 1939, p. 302, fig. 8; Wood, 1954, p. 275, *vix* fig. 189b-c; Klement, 1964, p. 364; Lopez, 1966, p. 417, fig. 92.

= *C. furca* subsp. *eugrammum* (Ehrenberg) Jörgensen.

Jörgensen, 1911 (fig. 24, 25, *non* 26), 1920; Pavillard, 1916; Forti, 1924; Abé, 1927; Steemann Nielsen, 1934, 1939.

= *C. furca* (Ehrenberg) Clap. & Lachmann *pro parte*.

Wailes, 1928 (pl. 1, fig. 8, *non al.*); Wang & Nie, 1932; Halim, 1963. *Non* Souza, 1950.

= *C. furca* var. *medium* Gourret.

Gourret, 1883.

Il faut attribuer cette variété à Schiller qui, dans le cas présent, a nettement indiqué qu'il considérait comme une variété la sous-espèce de Jörgensen.

Cellule plus petite. Epithèque se rétrécissant lentement et, de ce fait, peu distincte de la corne apicale proprement dite. Longueur de la corne apicale nettement inférieure à la hauteur de l'épithèque. Cornes antapicales parallèles, peu développées par rapport au diamètre cingulaire; longueur de la corne antapicale droite nettement inférieure à ce diamètre. Cornes antapicales rarement denticulées à leur extrémité.

Variété thermophile.

Transitions entre les deux variétés précédentes :
Fig. 19

= *C. furca* var. *Berghii* f. *sub-Berghii* Lopez.

Lopez, 1966.

= *C. furca* var. *tertium* Gourret.

Gourret, 1883.

= *C. furca* f. *nannofurca* et f. *belonoides* Jörgensen.

Jörgensen, 1920; Schiller, 1937.

POUR LES DEUX VARIÉTÉS ET LEURS TRANSITIONS :

Récoltes personnelles : A Nossi-Bé, cette espèce est quasi pérennante, mais toujours rare, si bien qu'une alternance saisonnière des deux variétés n'a pu être décelée avec certitude. *Ceratium*

furca était également présent à Tuléar, et, de façon très sporadique, dans tout le canal de Mozambique, où la variété *eugrammum* dominait nettement.

Océan Indien : Espèce assez courante.

Distribution mondiale : L'espèce est probablement cosmopolite, mais sa variété *furca* est préférentiellement psychrophile, tandis que sa variété *eugrammum* est plus strictement tropicale et subtropicale. Enfin l'espèce semble préférentiellement néritique. Répartition verticale incertaine.

Signalons pour mémoire la très courte note de Minkiewicz (1900) sur le dimorphisme saisonnier du *C. furca* dans la mer Noire : selon cet auteur, les formes estivales ont une longueur double de celle des formes hivernales. Cette observation hâtive est manifestement due au fait que les deux variétés *furca* et *eugrammum* n'ont pu être distinguées par l'auteur.

Pour mémoire :

C. furca* f. *corpulentum Jörgensen

Jörgensen, 1920, p. 19, fig. 8.

? = *Ceratium hircus* Schröder = *C. furca* var. *hircus* (Schröder) Margalef. Schröder, 1909; Jörgensen, 1911; Nie, 1936 (et cf. *C. hircus* var. *sinicum* Nie, *ibid.*); Schiller, 1937; Margalef, 1961.

Ceratium belone Cleve, 1900

Fig. 22

Cleve, 1900a, p. 13, pl. 7, fig. 13 : *C. (furca var. ?) belone*; Jörgensen, 1911, p. 19, pl. 2, fig. 28, et 1920, p. 22, fig. 14; Peters, 1934, p. 29, pl. 3, fig. 14d; Steemann Nielsen, 1934, p. 10, fig. 10, et 1939, p. 7; Schiller, 1937, p. 369, fig. 407a; Rampi, 1942, p. 222, fig. 2; Graham & Bronikovsky, 1944, p. 18, fig. 8; Silva, 1949, p. 354, pl. 6, fig. 20; Wood, 1954, p. 275; Halim, 1960, p. 191, pl. 4, fig. 6; *Non* Schröder, 1906, *nec* Okamura & Nishikawa, 1904.

= *Ceratium pacificum* Schröder. *Non C. pacificum* Wood.
Schröder, 1906; Stüwe, 1909; Kofoid, 1907d; Pavillard, 1931.

Récoltes personnelles : Ile Maurice, Tuléar (très rare).

Océan Indien : Mer Rouge, mer d'Arabie, canal de Mozambique, et diverses stations océaniques très clairsemées.

Distribution mondiale : Espèce tropicale peu courante, rencontrée sporadiquement dans les trois grands océans et en Méditerranée. Océanique et euphotique.

Ceratium incisum (Karsten) Jörgensen, 1911
Fig. 21

KARSTEN, 1905b, p. 149, pl. 23, fig. 6a-b : *C. furca* var. *incisum*; JÖRGENSEN, 1911, p. 19, pl. 2, fig. 29-30, et 1920, p. 22, fig. 13; PETERS, 1934, p. 29; STEEMANN NIELSEN, 1934, p. 10, fig. 11, et 1939, p. 8; SCHILLER, 1937, p. 370, fig. 407b; GRAHAM & BRONIKOVSKY, 1944, p. 19; fig. 9a-e; WOOD, 1954, p. 275, fig. 190; SILVA, 1955, p. 50, pl. 7, fig. 2.

= *Ceratium belone* Cleve, *pro parte.*

SCHRÖDER, 1906; OKAMURA & NISHIKAWA, 1904. *Non al.*

? = *Ceratium Brunellii* Rampi.

RAMPI, 1942.

RÉCOLTES PERSONNELLES : Au large de Nossi-Bé (très rare).

OCÉAN INDIEN : Mer Rouge, Ceylan, Tuléar, et quelques rares stations océaniques.

DISTRIBUTION MONDIALE : Comme *C. belone,* mais probablement plus rare encore. Répartition verticale incertaine.

Il faut probablement rattacher à cette espèce le *Ceratium Brunellii* de RAMPI, connu par l'unique spécimen récolté par cet auteur (1942, p. 222, fig. 1).

SECT. *PENTAGONA* JÖRGENSEN

Ceratium pentagonum Gourret, 1883

GOURRET, 1883, p. 45, pl. 4, fig. 58.

Cette espèce a été subdivisée en divers taxons infra-spécifiques, dont certains sont mal définis, et qui tous peuvent être intégrés à une suite continue de variations limitée par deux types extrêmes : une variété *robustum* psychrophile, et une variété *tenerum* thermophile. Deux formes cependant, selon le sens donné à ce mot p. 382, doivent être tenues à l'écart de cette série : l'une correspond au type originel de l'espèce; l'autre est la f. *turgidum* de Jörgensen. Toutes deux, absentes de mes récoltes, seront ici traitées « pour mémoire », ainsi d'ailleurs que la variété *robustum.*

Avant de passer au détail, un mot du travail de LOPEZ (1966) : l'étude biométrique menée par cet auteur le conduit à diviser l'espèce en deux formes estivale et hivernale, la seconde étant la plus abondante et possédant des cornes antapicales plus développées. LOPEZ déclare n'avoir pu distinguer de variétés chez *C. pentagonum*; ceci tient apparemment au fait que, comme l'on peut en juger d'après l'illustration fournie par cet auteur, le matériel examiné

ne renfermait que la variété *tenerum*, ainsi que les stades intermédiaires. La variété *robustum* est en effet inconnue en Méditerranée.

Pour mémoire :

var. ***robustum*** (Cleve) Jörgensen, 1920, *non* 1911

Cleve, 1900b, p. 925, fig. 6 : *C. lineatum* var. *robustum;* Jörgensen, 1920, p. 26, fig. 17a-b, *non* 1911, p. 20, pl. 2, fig. 32; Peters, 1934, p. 32, pl. 4, fig. 18 (« subsp. »); Wood, 1954, p. 276, fig. 191b, f, *vix* a; Balech, 1962, p. 179, fig. 379, *vix* fig. 380, 383, *non* fig. 381-382. *Vix* Silva, 1955, p. 51, pl. 7, fig. 3 (« subsp. »). *Non* Schiller, 1937, p. 371, fig. 408a. *Nec* Halim, 1963.

= *C. furca* var. *balticum* Moebius = *Ceratium balticum* (Moebius) Balech; Schütt, 1895; Balech, 1944. *Non* Souza, 1950 (hétéromorphisme).

? = *C. pentagonum* subsp. *pacificum* Graham & Bronikovsky. Graham & Bronikovsky, 1944 (fig. 10i, *non al.*).

Cellules d'apparence robuste, à thèque épaisse, ornée de sillons et de crêtes. Crête postérieure (entre les deux cornes antapicales) bien développée. Cornes antapicales longues et divergentes, la droite (la plus courte) étant de longueur égale à l'espace compris entre les bases des deux cornes.

Rappelons que Jörgensen a modifié en 1920 la diagnose de ce taxon, et précisé que la f. *robustum* décrite par lui en 1911 appartient en fait à la variété *subrobustum*. Schiller (1937) a malheureusement commis la confusion (*loc. cit.*, fig. 408a).

Océan Indien : Cette variété n'y est connue avec certitude que dans les régions subantarctiques (Cleve, Jörgensen). La référence d'Ostenfeld & Schmidt, 1901 (mer Rouge) est douteuse .

Distribution mondiale : Variété psychrophile, peu connue. Seulement signalée sous ce nom dans les régions subantarctiques de l'Atlantique et de l'océan Indien. La référence de Silva, 1955 (Angola) est douteuse. Mais cette variété a vraisemblablement été confondue dans l'Atlantique Nord avec l'énigmatique *Ceratium lineatum*, et rapportée sous ce nom. Enfin, sa présence dans le Pacifique Nord est très probable : Graham & Bronikovsky ont créé sous le nom de subsp. *pacificum* une sous-espèce « endémique » de cette région, mais de caractères morphologiques très imprécis : les quatre figures données par ces auteurs sont pour le moins hétérogènes, mais l'une d'elles ressemble de très près à la variété *robustum*. Il semble que Graham & Bronikovsky, voulant prouver l'isolement hydrologique du Pacifique Nord et la bipolarité du *C. pentagonum*, aient fait preuve de parti pris, ayant en quelque sorte choisi

l'aire de répartition avant de définir la sous-espèce. Ces deux auteurs reconnaissent d'ailleurs n'avoir pas observé la var. *robustum*, et n'ont donc pu établir de comparaison.

(Le problème de la bipolarité chez *Ceratium* a été évoqué p. 378).

var. ***tenerum*** Jörgensen, 1920
Fig. 24

JÖRGENSEN, 1920, p. 26, fig. 16a-b; PETERS, 1934, p. 32, pl. 1, fig. 1b (subsp.); SCHILLER, 1937, p. 371, fig. 408c (forma); RAMPI, 1939, p. 303, fig. 17; GRAHAM & BRONIKOVSKY, 1944, p. 20, fig. 10h, k-n (subsp.); WOOD, 1954, p. 276, fig. 191c (forma); SILVA, 1955, p. 51, pl. 7, fig. 4 (subsp.); HALIM, 1960, pl. 4, fig. 8; BALLANTINE, 1961, p. 224, fig. 48 (forma); BALECH, 1962, p. 180, pl. 25, fig. 384.

= *C. lineatum* var. *longisetum* Ostenfeld & Schmidt = *C. pentagonum* f. *longisetum* (Ostenfeld & Schmidt) Jörgensen.
OSTENFELD & SCHMIDT, 1901; OKAMURA, 1907; JÖRGENSEN, 1911, 1920.

= *C. pentagonum* subsp. *pentagonum*.
PETERS, 1934.

= *C. pentagonum* f. *subpentagonum* Lopez.
LOPEZ, 1966.

Cellules plus petites. Thèque mince, cornes délicates. Crête postérieure de l'hypothèque absente ou réduite. Cornes antapicales courtes, la gauche (la plus longue) nettement plus courte que l'espace compris entre les bases de ces cornes.

RÉCOLTES PERSONNELLES : Nossi-Bé (plutôt « hivernale »). Tuléar. Ile Maurice. Sporadique dans le canal de Mozambique, dans les prélèvements horizontaux et verticaux.

OCÉAN INDIEN : Cette variété y est courante, mais de répartition difficile à distinguer de celle des formes transitionnelles.

DISTRIBUTION MONDIALE : Variété thermophile, tropicale et subtropicale (Méditerranée incluse). Répartition verticale incertaine, peut-être euphotique.

Transitions entre les deux variétés précédentes
Fig. 23

1. « *C. pentagonum* var. *subrobustum* Jörgensen »

Considérée par PETERS comme une sous-espèce, puis par STEEMANN NIELSEN et, à la suite de ce dernier, par GRAHAM & BRONIKOVSKY et SILVA, comme une espèce distincte. Ses caractères morphologiques sont cependant très vagues, et son aire géographique, de même que sa distribution verticale, sont controversées.

On ne peut nullement assurer, comme le veut BALECH (1962) que la thèque soit ici plus « robuste » que celle de la variété *robus-*

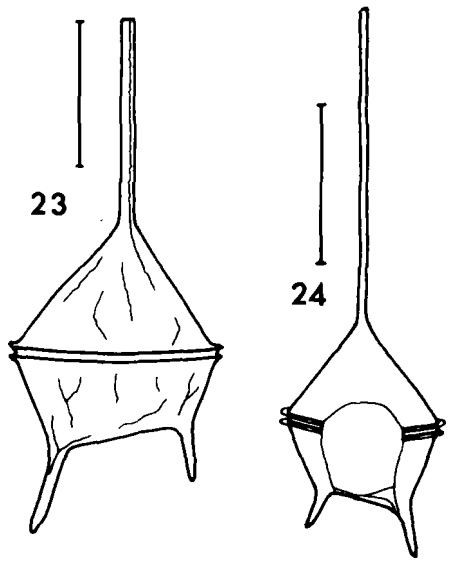


FIG. 23 : *Ceratium pentagonum* Gourret « *robustum-tenerum* ». — 24 : *C. pentagonum* var. *tenerum* Jörg.

tum. Il s'agit, dans l'ensemble, d'une transition entre les deux variétés, plus proche cependant du terme psychrophile, et que l'on peut désigner sous l'expression : *C. pentagonum* Gourret, « *robustum* > *tenerum* ».

2. « *C. pentagonum* f. *pentagonum* », *in* LOPEZ, 1966

L'iconographie de cet auteur (fig. 63, moitié droite de la planche, et fig. 90 II-III) donne divers exemples de transitions : « *robustum-tenerum* » et « *tenerum* > *robustum* ».

Pour mémoire :

f. ***pentagonum***

= *Ceratium pentagonum*, et var. *rectum* Gourret.
GOURRET, 1883, p. 45, pl. 4, fig. 58-59.

? = *Ceratium Ehrenbergii* Kofoid.
KOFOID, 1907d, p. 171, pl. 2, fig. 16; NIE, 1936, p. 38, fig. 9.

= *Ceratium furca* var. *pentagonum* (Gourret) Lemmermann.
LEMMERMANN, 1899, p. 368; KARSTEN, 1905b, pl. 23, fig. 8.

= *C. pentagonum* f. *tenerum* Jörgensen, *pro parte*.
GAARDER, 1954, p. 15, fig. 14, *Non al.*

= *C. pentagonum* Gourret, *pro parte*.
KLEMENT, 1964, p. 354, pl. 2, fig. 6. *Non al.*

Le type originel de GOURRET représente en effet une forme « anormale », ou du moins particulière, de l'espèce : corne apicale vestigiale.

Pour mémoire :

f. ***turgidum*** (Jörgensen) Jörgensen, 1920.

JÖRGENSEN, 1920, p. 26; RAMPI, 1939, p. 303, fig. 20, et 1951, p. 9.

= *C. pentagonum* var. *turgidum* Jörgensen.

JÖRGENSEN, 1911; PAVILLARD, 1916; SILVA, 1955.

Epithèque « anormalement » renflée.

Pour mémoire :

Ceratium lineatum (Ehrenberg) Cleve, 1899
Fig. 25-26

EHRENBERG, 1854, pl. 35a, fig. 24c : *Peridinium lineatum;* CLEVE, 1899, p. 36, 1900b, p. 925, 1900c, p. 1030 et 1900d, p. 224; GRAN, 1902, p. 197; OSTENFELD, 1903, p. 587, fig. 144; PAVILLARD, 1905, p. 55, et 1907, p. 230; KOFOID, 1907a, fig. 2; PAULSEN, 1909, p. 16, fig. 3 (?); JÖRGENSEN, 1911, p. 22, pl. 2, fig. 36-37, 1911b, p. 207, et 1920, p. 34; MEUNIER, 1919, p. 86,

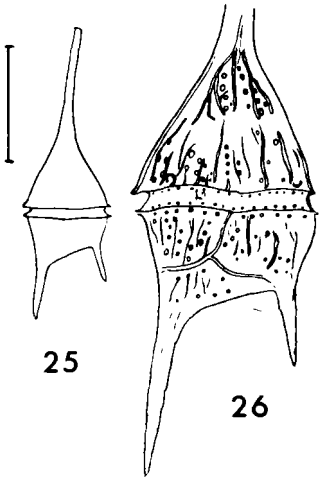


FIG. 25-26 : *Ceratium lineatum* (Ehr.) Cleve. *In* BALECH, 1944, fig. 2-3.

pl. 20, fig. 33-34; LEBOUR, 1925, p. 145, fig. 45d-e; DANGEARD, 1926, p. 313, fig. 2c; WAILES, 1928, pl. 2, fig. 9; OSTENFELD, 1931, p. 616; WANG, 1936, p. 152, fig. 24; SCHILLER, 1937, p. 372, fig. 410; SCHUBERT, 1937, p. 388; BALECH, 1944, p. 424, pl. 1, fig. 2-3; SILVA & PINTO, 1948, p. 171, pl. 2, fig. 12; WOOD, 1954, p. 277, fig. 192; ?GRAHAM & BRONIKOVSKY, 1944, p. 22, fig. 11e-g (incl. *C. minutum*); TRAVERS, 1962, p. 58.

= *fide* CLEVE : *C. furca* var. *balticum* Moebius.

SCHÜTT, 1895; ZACHARIAS, 1906. (Mais ce taxon désigne en fait *C. pentagonum*).

= *C. tripos* var. *subsalsum* f. *lineatum* (Ehr.) Lohmann.
LOHMANN, 1908; PAULSEN, 1908.

Espèce énigmatique, certainement hétérogène, confondue en grande partie (du moins à l'origine) avec *C. pentagonum*. Ses caractères morphologiques sont mal définis et sa distribution, en conséquence, oppose diverses contradictions : CLEVE la donne comme espèce d'eaux chaudes (océan Indien et Atlantique tropicaux) quoique rencontrée dans l'Atlantique Nord jusqu'au Groenland. Mais, depuis JÖRGENSEN, *C. lineatum* est généralement considérée comme une espèce boréale et australe.

La dernière description détaillée du *C. lineatum* est celle de BALECH (1944), qui passe malheureusement sous silence les affinités avec *C. pentagonum*.

Ceratium teres Kofoid, 1907
Fig. 28

KOFOID, 1907c, p. 308, pl. 29, fig. 34-36, et 1907a, fig. 4; JÖRGENSEN, 1911, p. 21, pl. 2, fig. 34-35, et 1920, p. 28, fig. 18 (incl. *C. teres* f. *subturgidum*); PETERS, 1934, p. 32, pl. 3, fig. 14e (?); STEEMANN NIELSEN, 1934, p. 11, fig. 14 (?), et 1939, p. 8; SCHILLER, p. 372, fig. 409; GRAHAM & BRONIKOVSKY, 1944, p. 21, fig. 11b-d; SILVA, 1949, p. 355, pl. 6, *vix* fig. 21; WOOD, 1954, p. 277, fig. 193 (?); HALIM, 1960, pl. 4, fig. 10, et 1963, p. 493, *vix* fig. 5; LOPEZ, 1966, p. 415, fig. 91.

RÉCOLTES PERSONNELLES : Nossi-Bé, Tuléar, Ile Maurice. Rare et toujours en petit nombre.

OCÉAN INDIEN : Mer d'Arabie, Indonésie, Canal de Mozambique, région du Cap, Ceylan, et quelques stations océaniques.

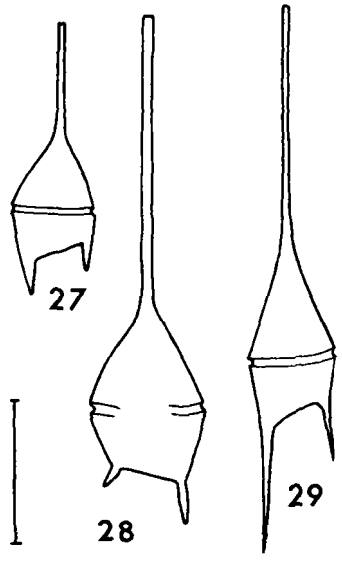


FIG. 27 : *Ceratium minutum* Jörg. — 28 : *C. teres* Kofoid. — 29 : *C. Kofoidii* Jörg.

DISTRIBUTION MONDIALE : Espèce tropicale et sub-tropicale, rencontrée occasionnellement sous les latitudes tempérées. Selon STEEMANN NIELSEN, SCHUBERT et PAVILLARD (1937), espèce de « surface », et, selon WOOD, océanique, mais ces deux points restent l'un et l'autre à vérifier.

Ceratium Kofoidii Jörgensen, 1911
Fig. 29

JÖRGENSEN, 1911, p. 23, pl. 2, fig. 38-39, et 1920, p. 33, fig. 20; BÖHM, 1931b, p. 12, fig. 9c, e-g; PETERS, 1934, p. 33; STEEMANN NIELSEN, 1934, p. 11, fig. 15; SCHILLER, 1937, p. 373, fig. 412; *vix* RAMPI, 1942, p. 223, fig. 5; GRAHAM & BRONIKOVSKY, 1944, p. 21, *vix*, 11h; WOOD, 1954, p. 278, fig. 195; SILVA, 1955, p. 55, pl. 7, fig. 7 (?).

= *Ceratium Boehmii* Graham & Bronikovsky.
GRAHAM & BRONIKOVSKY, 1944.

RÉCOLTES PERSONNELLES : Nossi-Bé (rare, et seulement hivernal). Tuléar. Au large de Lourenço Marques.

OCÉAN INDIEN : Espèce surtout répandue dans la région indonésienne, connue également en mer d'Arabie, dans le canal de Mozambique, et en diverses stations tropicales.

DISTRIBUTION MONDIALE : Zone intertropicale (Méditerranée incluse); la rareté apparente de cette espèce est peut-être seulement due à sa petite taille.

Ceratium minutum Jörgensen, 1920
Fig. 27

JÖRGENSEN, 1920, p. 34, fig. 21-23; LEBOUR, 1925, p. 145, pl. 30, fig. 4; DANGEARD, 1926, p. 313, fig. 2 d; MARTIN, 1929, p. 30, pl. 2, fig. 17-19, et pl. 5, fig. 13-14; PETERS, 1934, p. 33; SCHILLER, 1937, p. 374, fig. 413; RAMPI, 1942, p. 223, fig. 6, et 1951, p. 8; *vix* WOOD, 1954, p. 279, *non* fig. 196; HALIM, 1960, pl. 4, fig. 9.
? GRAHAM & BRONIKOVSKY, 1944 (incl. *C. lineatum*), p. 22, fig. 11e-g.

Cellules délicates et de petite taille (diamètre cingulaire : 25-35 µ). Epithèque sub-triangulaire, de contour rectiligne ou légèrement convexe. Longueur de la corne apicale généralement inférieure ou égale à la hauteur totale du corps central. Cornes antapicales peu développées, sub-parallèles, effilées à leur extrémité. Longueur de la corne antapicale gauche (la plus longue) inférieure au diamètre cingulaire.

RÉCOLTES PERSONNELLES : Nossi-Bé. Très rare, observé seulement par sédimentation (absent des prises au filet).

OCÉAN INDIEN : Cette espèce aurait seulement été rencontrée par

Wood dans les parages de l'Australie et dans le centre de l'océan. Mais la description donnée par cet auteur diffère quelque peu de celle de Jörgensen.

Distribution mondiale : Sauf confusion avec les espèces voisines (*C. Kofoidii, C. lineatum* et peut-être même *C. pentagonum*), espèce rare, de distribution incertaine : connue principalement dans l'Atlantique tempéré, et sur les côtes d'Australie : en Méditerranée, seulement récoltée à Gibraltar (Jörgensen) et en mer Ligure (Rampi, Halim). Semble néritique. Comme pour *C. Kofoidii*, la petite taille de cette espèce expliquerait en partie sa rareté.

Pour mémoire :

Ceratium setaceum Jörgensen, 1911

Jörgensen, 1911, p. 23, pl. 2, fig. 40, 41, et 1920, p. 31, fig. 49; Mangin, 1912, p. 26, fig. 12; Forti, 1922, p. 39, pl. 1, fig. 23; Pavillard, 1931, p. 72, et 1937, p. 13; Peters, 1934, p. 33, pl. 3, fig. 15b-c; Steemann Nielsen, 1934, p. 12, fig. 16 (?), et 1939, p. 8; Schiller, 1937, p. 373, fig. 411; Schubert, 1937, p. 388; ? Rampi, 1942, p. 223, fig. 8; Graham & Bronikovsky, 1944, p. 22, fig. 11a; Wood, 1954, p. 278, fig. 194a, *non* b.

Cette espèce, voisine de *C. pentagonum* et de *C. Kofoidii*, me paraît, d'après la bibliographie et l'iconographie consultées, bien distinctes de l'une et de l'autre.

Espèce tropicale et subtropicale, rare (petite taille).

SUBG. *AMPHICERATIUM* (VANHÖFFEN) OSTENFELD

SECT. *INFLATA* JÖRGENSEN

Ceratium geniculatum (Lemmermann) Cleve, 1900
Fig 30-31

Lemmermann, 1899, p. 349, pl. 1, fig. 17 : *C. fusus* var. *geniculatum* Cleve, 1900d, p. 221; Jörgensen, 1911, p. 24, pl. 2, fig. 42-43, et 1920, p. 34, fig. 24; Böhm, 1931b, p. 43, fig. 37c-d; Peters, 1934, p. 36; Steemann Nielsen, 1934, p. 13, fig. 17, et 1939, p. 8; Schiller, 1937, p. 375, fig. 414; Graham & Bronikovsky, 1944, p. 22, fig. 11j; Silva, 1949, p. 355, pl. 9, fig. 2; Wood, 1954, p. 279, fig. 197, et 1963b, p. 40, fig. 45 (« var. »).

= *Ceratium tricarinatum* Kofoid.
Kofoid, 1907d.

Récoltes personnelles : Tuléar (rare).

Océan Indien : Ceylan, Indonésie, Tuléar, et diverses stations océaniques.

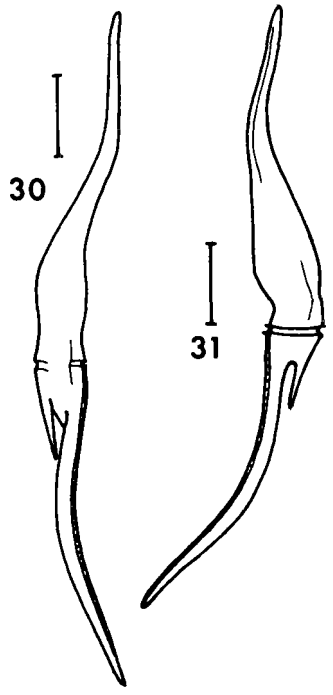


FIG. 30 : *Ceratium geniculatum* (Lemm.) Cleve; vue ventrale. — 31 : *Id.*, autre spécimen, vue dorsale.

DISTRIBUTION MONDIALE : Espèce sporadique dans les zones intertropicales des trois grands océans, ainsi qu'en Méditerranée occidentale. Selon STEEMANN NIELSEN : espèce océanique, de surface.

SECT. *FUSIFORMIA* JÖRGENSEN

Ceratium fusus (Ehrenberg) Dujardin, 1841

EHRENBERG, 1834, p. 271, 1836, p. 574, pl. 2, fig. 3, et 1838, p. 256, pl. 22, fig. 20; DUJARDIN, 1841, p. 378.

Pour JÖRGENSEN (1911, 1920), PAVILLARD (1931), et divers auteurs, la distinction d'une sous-espèce *seta* thermophile, plus fine et plus petite que le type, est évidente. PETERS (1934) a rencontré en abondance des cellules de toutes tailles dans toutes les régions de l'Atlantique explorées par le « METEOR », mais n'a pu établir de discrimination morphologique ni géographique. La position de STEEMANN NIELSEN (1934) n'est pas claire : cet auteur voit en *C. fusus* un génotype unique étroitement soumis aux conditions écologiques, mais par ailleurs doute si le matériel par lui examiné correspond au type nordique de l'espèce, et de plus maintient à l'écart la sous-espèce *seta*... Toutefois, d'après les dimensions qu'il donne (226-550 µ), STEEMANN NIELSEN semble avoir bien récolté et le type et la sous-espèce. Le même auteur soutient encore (1939) l'indivisibilité de *C. fusus*, sans désigner cependant nommément la subsp. *seta* : « Es gibt nicht eine kleine Warmwasserform und eine grosse Kaltwasserform. Wenn die Individuen der kühleren Gebiete am grössten sind, ist dies eine

Folge der allgemeinen Variationstendenz bei den Ceratien. Ein neritischer Einfluss bewirkt eine ganz ähnliche Vergrosserung der Zellen ». Enfin, GRAHAM & BRONIKOVSKY (1944) ne divisent pas l'espèce, mais notent que le diamètre cingulaire est inversement fonction de la température, les variations de la longueur totale restant à élucider.

On ne sait donc si la variabilité de *C. fusus* est le fait d'un seul, de deux ou de plusieurs génotypes, et si elle résulte de l'action de la température, ou de celle des facteurs trophiques (cf. « neritischer Einfluss »...). Une fois de plus, la suite des variations morphologiques est continue, mais, dans le cas présent, l'espèce est, sous ses diverses formes, particulièrement tolérante, si bien que la discrimination géographique n'est qu'approximative.

Pour éclaircir ces divers points, il semble utile de distinguer à l'avenir : 1) le type de l'espèce, sous le nom de var. *fusus*, 2) la variété thermophile *seta*, 3) les transitions.

Je donnerai pour mémoire les références de la « variété *Schuettii* », qui se distingue nettement des deux précédentes par le renflement de l'épithèque, et dont il reste à dire si elle représente une forme ou une espèce distincte.

var. ***fusus***
Fig. 32

= *Ceratium fusus* (Ehr.) Dujardin, *stricto sensu.*
JÖRGENSEN, 1911, 1920; SCHILLER, 1937, *et plur. auct.*

= *C. fusus* subsp. *boreale* Pavillard.
PAVILLARD, 1931.

var. ***seta*** (Ehrenberg) Sournia, 1966
Fig. 33

= *Ceratium fusus* subsp. *seta* (Ehrenberg) Jörgensen = « *C. fusus* var. *seta* (Ehrenberg) Jörgensen » *in plur. auct.* = *Ceratium seta* (Ehr.) Kofoid = *Peridinium seta* Ehrenberg.

EHRENBERG, 1860, p. 792 et 1873, p. 3, fig. 5-6; KOFOID, 1908b; JÖRGENSEN, 1911, 1920; PAVILLARD, 1931; WANG & NIE, 1932; NIE, 1936; SCHILLER, 1937; RAMPI, 1939; WOOD, 1954; BALLANTINE, 1961.

Caractères distinctifs de la variété précédente : Cellules plus petites : longueur totale 280-400 µ (chez le type : 450-650 µ). Cornes plus fines, seulement légèrement recourbées, ou rectilignes. Corne antapicale droite souvent complètement absente.

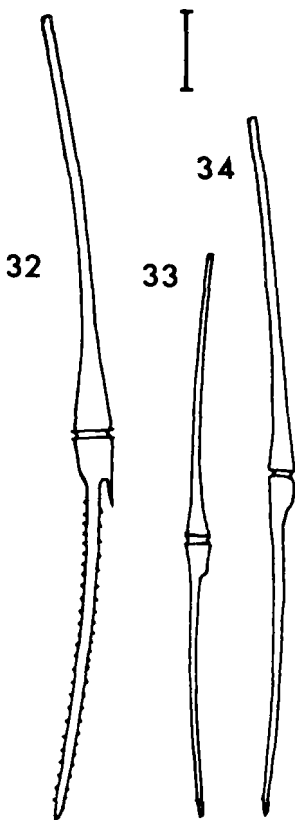


FIG. 32 : *Ceratium fusus* (Ehr.) Duj. var. *fusus*. — 33 : *C. fusus* var. *seta* (Ehr.) Sournia. — 34 : *C. fusus* (Ehr.) Duj. « *fusus-seta* ».

Transitions entre les deux variétés précédentes :
Fig. 34

Cf. STEEMANN NIELSEN, 1934, p. 48, tableau 12; GRAHAM & BRONIKOVSKY, 1944, fig. 13b-d.

POUR LES DEUX VARIÉTÉS ET LEURS TRANSITIONS

RÉCOLTES PERSONNELLES : A Nossi-Bé, espèce pérennante, représentée indifféremment semble-t-il, par les deux variétés et leurs transitions. Tuléar. Ile Maurice. Au cours de la croisière de l'*Anton Bruun*, *C. fusus* a été rencontré dans toute l'étendue du Canal de Mozambique, où la variété *seta* semblait préférentiellement océanique.

OCÉAN INDIEN : Espèce très courante dans les régions tropicales et tempérées.

DISTRIBUTION MONDIALE : Cosmopolite. La variété *fusus* est elle-même quasi cosmopolite, tandis que la variété *seta* est nettement thermophile. Probablement euphotique.

Pour mémoire :

var. (?) ***Schuettii*** Lemmermann
Fig. 35

LEMMERMANN, 1899, p. 367; JÖRGENSEN, 1911, p. 29, pl. 3, fig. 54, et 1920, p. 43; WANG, 1932, p. 154, fig. 25; SCHILLER, 1937, p. 379, fig. 418c; WOOD, 1954, p. 282.

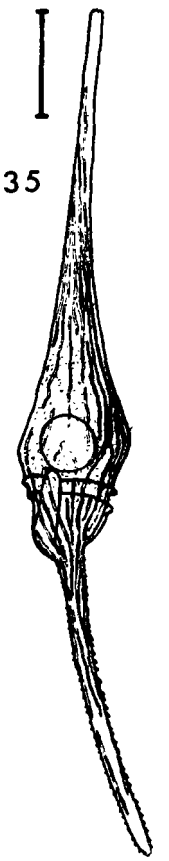


FIG. 35 : *C. fusus* var. *Schuettii* Lemm. D'après SCHÜTT, 1895, fig. 35/4.

Non RAMPI, 1939, p. 303, fig. 13; *Nec* MARGALEF, 1957, p. 47, fig. 1j, *nec* 1961, p. 81, fig. 26e-g. *Nec* HALIM, 1963, p. 497, fig. 8.

= « *Ceratium fusus* Dujardin » *in* SCHÜTT.

SCHÜTT, 1895, p. 154, pl. 9, fig. 35 (4). *Non al.*

Ceratium extensum (Gourret) Cleve, 1900

GOURRET, 1883, p. 52, pl. 4, fig. 56 : *Ceratium fusus* var. *extensum*; CLEVE, 1900d, p. 215 : *Ceratium* (*fusus* var.) *extensum* Gourret; SCHRÖDER, 1906, p. 321 : « *Ceratium extensum* (Gourret) *nob.* »; JÖRGENSEN, 1911, p. 28, pl. 3, fig. 50, et 1920, p. 43, fig. 31; PETERS, 1934, p. 36, pl. 2-3, fig. 10d, 14f; STEEMANN NIELSEN, 1934, p. 14, fig. 24, et 1939, p. 8; SCHILLER, 1937, p. 380, fig. 419; RAMPI, 1939, p. 304, fig. 11; GRAHAM & BRONIKOVSKY, 1944, p. 24, fig. 11bb-dd; SILVA, 1949, p. 356, pl. 6, fig. 22; WOOD, 1954, p. 283, fig. 203; HALIM, 1960, p. 230, pl. 4, fig. 3, et 1963, p. 497, fig. 9.

= *Ceratium strictum* (Okamura & Nishikawa) Kofoid.

OKAMURA & NISHIKAWA, 1904; KOFOID, 1907d; FORTI, 1922; JÖRGENSEN, 1911, 1920; RAMPI, 1939; BALECH, 1962.

= *C. extensum* f. *strictum* (Okamura & Nishikawa) Steemann Nielsen.

STEEMANN NIELSEN, 1934; SCHILLER, 1937; WOOD, 1954; SILVA, 1955; HALIM, 1963.

RÉCOLTES PERSONNELLES : Nossi-Bé (très rare). Tuléar. Ile Maurice. Sporadique dans le canal de Mozambique, et là, plutôt océanique, et euphotique.

OCÉAN INDIEN : Espèce assez courante dans les régions tropicales et subtropicales.

DISTRIBUTION MONDIALE : Espèce tropicale ou sub-tropicale, commune dans les trois océans et en Méditerranée. Euphotique.

La présence de la corne antapicale droite (« *C. strictum* ») ne semble pas justifier de désignation particulière. Ce caractère est en effet très variable et, apparemment, sans signification écologique.

Ceratium inflatum (Kofoid) Jörgensen, 1911
Fig. 36

KOFOID, 1907d, p. 172, pl. 2, fig. 13 : *C. pennatum* f. *inflatum*; JÖRGENSEN, 1911, p. 25, pl. 3, fig. 45, 46, 48a (incl. *C. pennatum*), et 1920, p. 35, fig. 25; FORTI, 1922, p. 39, pl. 1, fig. 24; BÖHM, 1931b, p. 14, fig. 10a-b; PETERS, 1934, p. 33 (*C. inflatum* subsp. *inflatum*); STEEMANN NIELSEN, 1934, p. 13, fig. 20, et 1939, p. 8; SCHILLER, 1937, p. 376, fig. 415; RAMPI, 1939, p. 303, fig. 15; GRAHAM & BRONIKOVSKY, 1944, p. 23, fig. 11o-s; WOOD, 1954, p. 281, fig. 198; SILVA, 1955, p. 56, pl. 7, fig. 9.

= *C. furca* f. *recurvatum* Stüwe.

STÜWE, 1909.

RÉCOLTES PERSONNELLES : Centre du canal de Mozambique (très rare).

OCÉAN INDIEN : Diverses stations tropicales, principalement océaniques.

DISTRIBUTION MONDIALE : Espèce inter-tropicale (Méditerranée incluse), océanique. Répartition verticale incertaine.

Voir aussi remarque, page suivante.

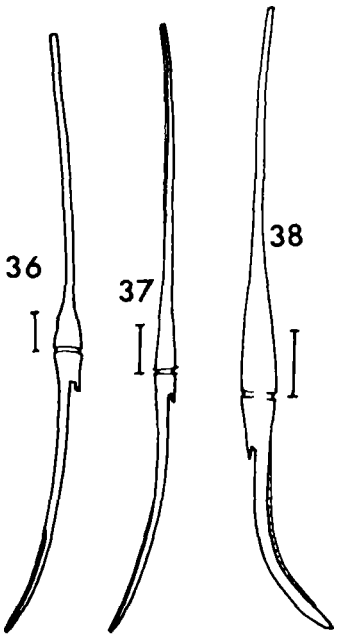


FIG. 36 : *Ceratium inflatum* (Kofoid) Jörg. — 37 : *C. longirostrum* Gourret. — 38 : *C. falcatum* (Kofoid) Jörg.

Ceratium longirostrum Gourret, 1883
Fig. 37

GOURRET, 1883, p. 55, pl. 4, fig. 65; JÖRGENSEN, 1920, p. 37, fig. 26-27; FORTI, 1922, p. 40, pl. 2, fig. 25; PETERS, 1934, p. 33 (*C. falcatum* subsp. *longirostrum*); STEEMANN NIELSEN, 1934, p. 13, fig. 21, et 1939, p. 8; SCHILLER, 1937, p. 376, fig. 416; RAMPI, 1939, p. 303, fig. 9; GRAHAM & BRONIKOVSKY, 1944, p. 24, fig. 11t-v; WOOD, 1954, p. 281, fig. 199; SILVA, 1955, p. 57, pl. 7, fig. 10; HALIM, 1960, pl. 4, fig. 4, et 1963, p. 496, fig. 6.

= *C. pennatum* var. *scapiforme* (Kofoid) Jörgensen.
JÖRGENSEN, 1911. *Vix* KOFOID, 1907d (*Ceratium scapiforme*).

RÉCOLTES PERSONNELLES : Nossi-Bé (très rare). Tuléar. Ile Maurice.

OCÉAN INDIEN ET DISTRIBUTION MONDIALE : Répartition et biologie non distinguables de celles de *C. inflatum*.

Voir aussi remarque, page suivante.

Ceratium falcatum (Kofoid) Jörgensen, 1920
Fig. 38

KOFOID, 1907d, p. 172, pl. 2, fig. 14 : *C. pennatum* f. *falcatum*; JÖRGENSEN, 1920, p. 39, fig. 28; FORTI, 1922, p. 41, pl. 2, fig. 26; PETERS, 1934, p. 33 (*C. inflatum* subsp. *falcatum*); STEEMANN NIELSEN, 1934, p. 14, fig. 22, et 1939, p. 8; SCHILLER, 1937, p. 377, fig. 417a; RAMPI, 1939, p. 303, fig. 14; GRAHAM & BRONIKOVSKY, 1944, p. 24, fig. 11w-aa; WOOD, 1954, p. 281, fig. 400; SILVA, 1955, p. 57, pl. 7, fig. 11; HALIM, 1963, p. 496, fig. 7.

= *C. pennatum* var. *falcatum* (Kofoid) Jörgensen.
KOFOID, 1907d; JÖRGENSEN, 1911.

RÉCOLTES PERSONNELLES : Nossi-Bé (rare). Au large du cap St André.

OCÉAN INDIEN ET DISTRIBUTION MONDIALE : Cf. *C. inflatum*, avec cette différence que *C. falcatum* serait une espèce de surface, et qu'elle paraît plus fréquente que les deux précédentes.

Voir aussi remarque, ci-dessous.

Pour mémoire :

Ceratium falcatiforme Jörgensen, 1920
Fig. 39

JÖRGENSEN, 1920, p. 40, fig. 29; PETERS, 1934, p. 33 (*C. inflatum* subsp. *falcatiforme*); STEEMANN NIELSEN, 1934, p. 14, fig. 23, et 1939, p. 8; SCHILLER, 1937, p. 378, fig. 417b; PAVILLARD, 1937, p. 10; WOOD, 1954, p. 282, fig. 201; HALIM, 1960, p. 191, pl. 4, fig. 5; BALECH, 1962, p. 181, pl. 25, fig. 387.

= syn. de *C. falcatum*, *in* GRAHAM & BRONIKOVSKY, 1944.

Remarques sur les quatres espèces précédentes :

C. inflatum, *C. longirostrum* et *C. falcatum* sont considérées par KOFOID (1907d) comme les formes d'une espèce unique, sous les noms respectifs de *C. pennatum* f. *inflatum*, f. *proprium* et f. *falcatum*; par PETERS (1934) comme des sous-espèces, ainsi que le *C. falcatiforme* créé entre temps par JÖRGENSEN. STEEMANN NIELSEN maintient séparées les quatre espèces, toutefois sans conviction, et insiste sur le fait que, dans le cas de la fusion en une espèce unique, le nom de *C. pennatum* de KOFOID doit prévaloir sur celui de *C. inflatum* utilisé par PETERS. Enfin, GRAHAM & BRONIKOVSKY conservent provisoirement les trois premières espèces et, pour ce qui est du *C. falcatiforme*, le rattachent à *C. falcatum*.

Ces quatre *Ceratium* sont effectivement très proches les uns des autres (PETERS et STEEMANN NIELSEN emploient l'expression

TABLEAU 1

Caractères morphologiques comparés de *Ceratium inflatum*, *C. longirostrum*, *C. falcatum* et *C. falcatiforme*

	C. inflatum	*C. longirostrum*	*C. falcatum*	*C. falcatiforme*
Longueurs épithèque/ hypothèque (**)	peu différentes	épithèque plus longue	épithèque plus longue	peu différentes
Leur rapport, selon JÖRGENSEN	1,06-1,26 1,26-1,23 (*)	1,26-1,45	1,38-1,70	1,13-1,20
selon GRAHAM & BRONIKOVSKY	0,86-1,25	1,19-1,50	1,00-1,72	
Limite entre épithèque et corne apicale	visible	indistincte (progressive)	visible	presque indistincte
Forme des deux grandes cornes	- corne apicale seulement légèrement infléchie - antapicale nettement infléchie à son extrémité	les deux cornes sont courbées assez régulièrement et de façon analogue	- corne apicale seulement infléchie - antapicale plus forte et nettement infléchie	- corne apicale comme chez *C. longirostrum* - antapicale comme chez *C. falcatum*
Longueur totale selon JÖRGENSEN	570-1024 µ 879-947 µ (*)	548-718 µ	413-480 µ	272-291 µ
selon GRAHAM & BRONIKOVSKY	640-1460 µ	570-730 µ	350-750 µ	

(*) « Autre forme », non nommée par JÖRGENSEN.
(**) Cornes correspondantes incluses.

« Formenkreiss »), et il est probable que les confusions sont fréquentes. Le trop petit nombre de spécimens observés dans mes récoltes m'empêche de former une opinion personnelle sur ce sujet.

Les quatre « espèces » sont tropicales, et réparties toutes quatre de façon très sporadique, si bien que les détails de leurs distributions géographiques respectives demeurent indiscernables.

FIG. 39 : *Ceratium falcatiforme* Jörg. *In* BALECH, 1962, fig. 387.

Dans le tableau 1 sont reportés les caractères morphologiques des quatre espèces, d'après les données de JÖRGENSEN et celles de GRAHAM & BRONIKOVSKY. Remarquons que le critère « longueur totale » doit, comme il convient, être utilisé avec précaution, et que par ailleurs le rapport des longueurs « épithèque/hypothèque » (cornes correspondantes incluses) n'est guère plus sûr : comme le fait remarquer JÖRGENSEN lui-même, ce rapport se trouve détruit à l'occasion de la division cellulaire.

SUBG. ***ORTHOCERATIUM*** nom. nov.

= Subg. *Euceratium* (Vanhöffen) Ostenfeld

SECT. *TRIPOS* OSTENFELD

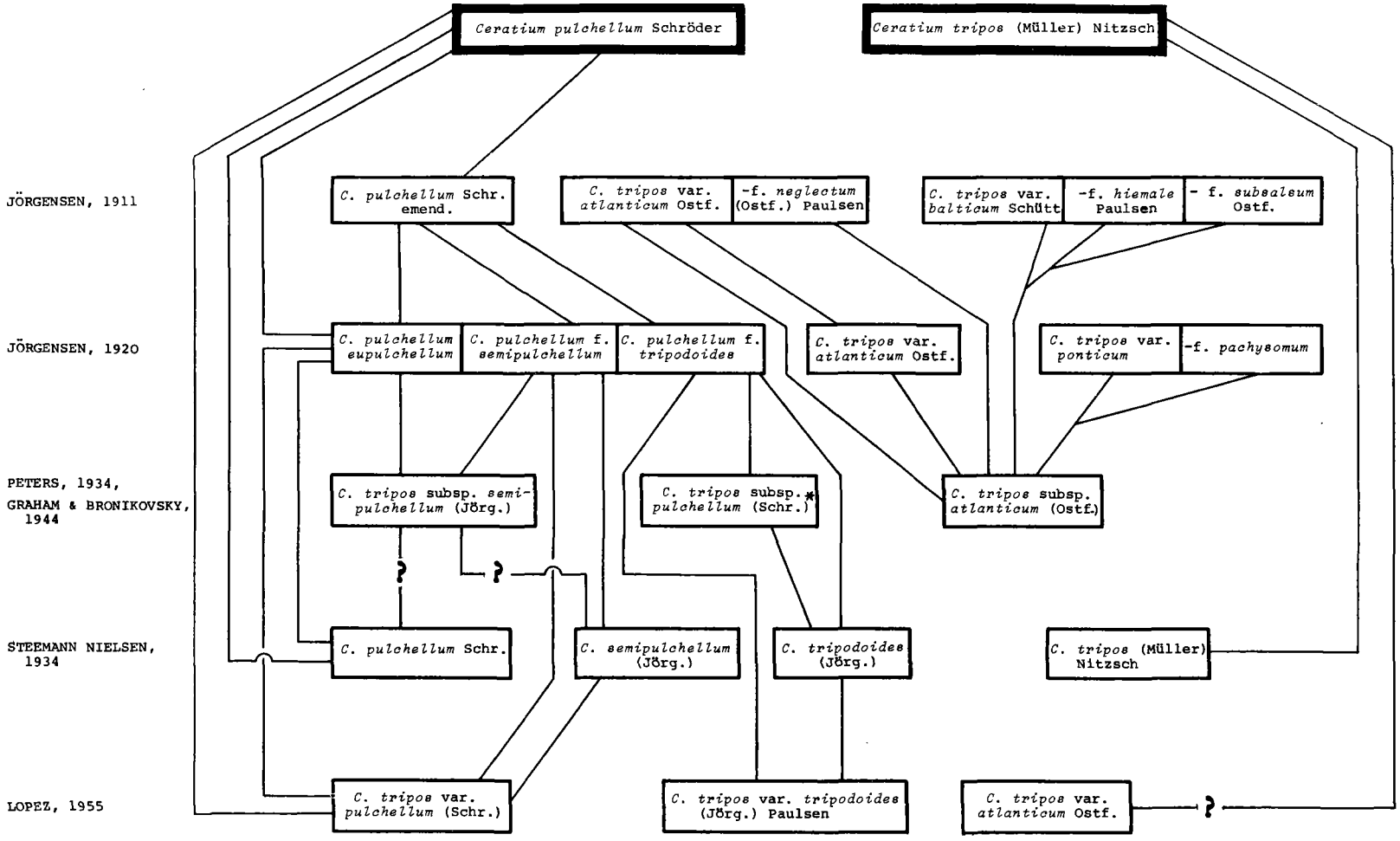
Ceratium tripos (Müller) Nitzsch, 1817

MÜLLER, 1786, p. 136, pl. 19, fig. 22 : *Cercaria tripos*; NITZSCH, 1817, p. 4; EHRENBERG, 1836, p. 573, pl. 2, fig. 1a-e, g, h, *non* f : *Peridinium tripos.*
Incl. *Ceratium pulchellum* Schröder.

TABLEAU 2

« Généalogie bibliographique » du *Ceratium tripos*.

Dans les cas d'innovations nomenclaturales, le nom de l'auteur du taxon est celui qui figure dans la colonne gauche.



(*) Pour GRAHAM et BRONIKOVSKY : *C. pulchellum* Schr., espèce distincte.

« La question de la définition et de la délimitation du *C. tripos* est un des problèmes les plus complexes de la systématique des Péridiniens », écrivait PAVILLARD en 1931. Or cette question a très peu progressé depuis cette date, si ce n'est que les affinités entre *C. tripos* et *C. pulchellum* ont été définitivement établies par divers auteurs et, notamment, par LOPEZ (1955) qui en a donné la démonstration biométrique; toutefois la parenté étroite entre les deux « espèces » était connue depuis JÖRGENSEN (1920).

C. tripos mériterait à lui seul une longue monographie et un historique détaillé. Mon intention ici se limite à une brève mise à jour de la question. Il m'a semblé utile de reporter dans le tableau 2 la « généalogie bibliographique » de cette espèce (*C. pulchellum* inclus), c'est-à-dire l'enchaînement des principales conceptions qui ont été proposées depuis JÖRGENSEN. Il était sans grand intérêt de remonter plus loin dans le temps; signalons pour mémoire seulement la conception *sensu* « *latissimo* » des auteurs anciens (BERGH, STEIN, LEMMERMANN, KARSTEN, ENTZ), qui englobait sous le nom de *C. tripos* presque toutes les espèces du sous-genre *Ceratium* et conduisait à une désignation tri- et quadrinominale qui n'a fait que compliquer la taxinomie.

Ce tableau reproduit les synonymies et les analogies telles que données par les auteurs mentionnés; les points d'interrogation eux-mêmes sont « d'origine ». Si cet « arbre généalogique » manque parfois de clarté et trahit certaines incohérences, il aura atteint son but : montrer les incertitudes qui subsistent actuellement sur les points suivants :

1. — comment désigner les termes de la « série *atlanticum-pulchellum* » ?

2. — où placer certains taxons quelque peu tombés dans l'oubli depuis JÖRGENSEN, et dont la synonymie n'est pas évidente, tels que : *neglectum, balticum, hiemale, subsalsum*, etc.

3. — qu'est-ce que le type du *Ceratium tripos* ?

Examinons successivement ces trois points :

I. — LA « SÉRIE *ATLANTICUM-PULCHELLUM* »

Cette question ne pose plus que des problèmes de nomenclature, car la présence d'une suite continue de variations entre *C. pulchellum* Schröder et *C. tripos* var. *atlanticum* (Ostf.) Paulsen n'est plus à démontrer (PAVILARD, 1931, s'y oppose encore cependant, n'ayant pas observé toutes les transitions). J'ai pu moi-même observer tous les termes de cette série dans mes échantillons.

Je crois devoir modifier comme suit le système de LOPEZ (1955) :

— A propos de la variété *atlanticum :* LOPEZ la traite pour mémoire, disant ne l'avoir pas récoltée dans le secteur méditerranéen étudié (Castellon), et maintient provisoirement le type atlantique comme étranger à la Méditerranée. Toutefois, un rapprochement sommaire entre les figures 6 et 13 c de cet auteur montrerait que cette variété était effectivement présente dans le matériel étudié. D'ailleurs, le même auteur a noté récemment (1966) sa présence dans la même région. De plus TRAVERS (1962) l'a récoltée en abondance, ainsi que les deux autres variétés définies par LOPEZ, au cours d'un cycle annuel dans le golfe de Marseille. Au reste, autant que l'on connaisse le type d'OSTENFELD, aucun caractère morphologique sûr ne permet d'en distinguer les représentants méditerranéens (voir aussi JÖRGENSEN, 1920, p. 47 et suiv., PAULSEN, 1930, p. 79 et PAVILLARD, 1931, p. 77).

— A propos de la var. *pulchellum* (Schr.) Lopez : Parmi les divers synonymes donnés par LOPEZ, certains doivent à mon avis être rejetés, car ils représentent en fait des stades de transition déjà plus ou moins « avancés » : *C. tripos* var. *gracile* Schr., *C. pulchellum* f. *semipulchellum* Jörg., et *C. semipulchellum* (Jörg.) St. Nielsen.

Je propose donc de modifier la diagnose de LOPEZ, et de ne plus voir en cette variété que le type même du *C. pulchellum* de SCHRÖDER.

— A propos de la var. *tripodoides* (Jörg.) Paulsen : Rappelons qu'elle est beaucoup plus proche de la var. *atlanticum* que de la var. *pulchellum* : elle n'a en fait été créée que pour désigner les représentants méditerranéens de la première. Il semble donc, d'après ce qui précède, qu'elle ne soit plus justifiée. Il est en tous les cas illogique et sans doute erroné de grouper sous son nom les stades de transition entre les deux variétés. Je propose plutôt, pour désigner ces derniers, le système exposé p. 382.

var. ***atlanticum*** (Ostenfeld) Paulsen, 1907
Fig. 43

OSTENFELD, 1903, p. 584, fig. 132-133 (« f. *atlantica* »); PAULSEN, 1907, p. 21, fig. 30, et 1908, p. 78, fig. 102; JÖRGENSEN, 1911, p. 36, pl. 4, fig. 69-73, et 1920, p. 47, fig. 33, 34, 36, *vix* 35; ABÉ, 1927, p. 424, fig. 41; *Non* WAILES, 1928, pl. 1, fig. 4, *vix* pl. 3, fig. 1; SCHILLER, 1937, p. 384, fig. 321a; WOOD, 1954, p. 285, fig. 205a; LOPEZ, 1955, p. 156, fig. 13c, et fig. 6 *pro parte* (colonne verticale 4 à partir de la gauche, *non al.*), et 1966, p. 330, fig. 33, et photogr. 2 (3). Ce taxon était jusqu'ici attribué à tort à OSTENFELD.

Non C. tripos (Müller) Nitzsch, *typ.*

Vix C. tripos, in WANG & NIE, 1932.

= *C. tripos* subsp. *atlanticum* (Ostenfeld) Peters.

PETERS, 1934; GRAHAM & BRONIKOVSKY, 1944 (fig. e-f et i-k, *non* g-h).

= *C. pulchellum* f. *tripodoides* Jörgensen = *C. tripos* var. *tripodoides* (Jörgensen) Paulsen = *Ceratium tripodoides* (Jörgensen) Steemann Nielsen = *C. tripos* subsp. *tripodoides* (Jörgensen) Steemann Nielsen.

JÖRGENSEN, 1920; PAULSEN, 1930 (fig. 47a-b, *vix* c-f); STEEMANN NIELSEN, 1934, 1939; LOPEZ, 1955 (fig. 6 *pro parte*, comme ci-dessus, et fig. 13c, *non* b), et 1966 *pro parte* (*vix* fig. 34, *non* photogr. 2 (2); HALIM, 1963.

= *C. tripos* var. *atlanticum* f. *Novae-Scotiae* Pavillard.

PAVILLARD, 1930, 1931.

Diamètre cingulaire : 70-90 µ. Cornes antapicales bien développées, de longueurs peu différentes l'une de l'autre; la droite (la plus courte des deux) de longueur supérieure au diamètre cingulaire. Corps central sensiblement aussi « large » que « haut ».

var. ***pulchellum*** (Schröder) Lopez, 1955
Fig. 40

LOPEZ, 1955, *pro parte* (restrictions formulées plus haut) : fig. 6 (colonne verticale 1 à partir de la gauche, *non al.*), et fig. 13a, *non* b.

= *Ceratium pulchellum* Schröder, *pro parte.*

SCHRÖDER, 1906; JÖRGENSEN, 1911 (fig. 62, *non al.*); *Non* ABÉ, 1927; *Nec* BÖHM, 1931b; PAVILLARD, 1931 (pl. 2, fig. 20a, *non* b-c); STEEMANN

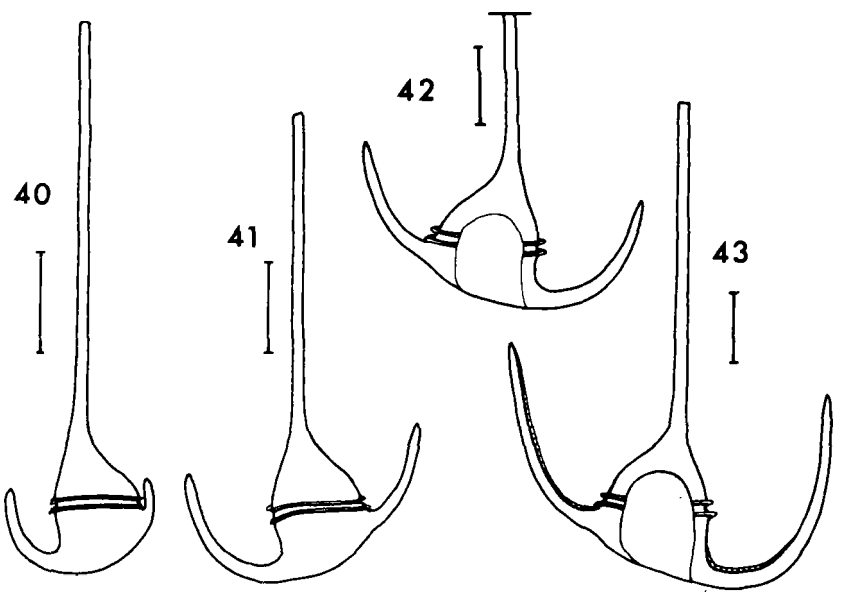


FIG. 40 : *Ceratium tripos* var. *pulchellum* (Schr.) Lopez. — 41 : *C. tripos* (Müller) Nitzsch, « *atlanticum-pulchellum.* — 42 : *C. tripos* (Müller) Nitzsch, « *atlanticum* > *pulchellum* ». — 43 : *C. tripos* var. *atlanticum* (Ostf.) Paulsen.

NIELSEN, 1934; *non* NIE, 1936; SCHILLER, 1937 (fig. 422a, *non* b); RAMPI, 1939 (fig. 2, *non* 21); GRAHAM & BRONIKOVSKY, 1944 (fig. 14c-f, *non* b); WOOD, 1954; HALIM, 1963; LOPEZ, 1966.

= *C. pulchellum* α *eupulchellum* Jörgensen.
JÖRGENSEN, 1920; BÖHM, 1931b; HALIM, 1960.

= *C. tripos* subsp. *semipulchellum* (Jörgensen) Peters, *pro parte.*
PETERS, 1934 (pl. 1, fig. 5a, *non* b). *Non* GRAHAM & BRONIKOVSKY, 1944.
= *Ceratium Schroederi* Nie.
NIE, 1936.

Non C. tripos subsp. *pulchellum* (Jörgensen) Peters, *in* PETERS, 1934.

Nec C. tripos var. *gracile* (Gourret) Schröder, *in* SCHRÖDER, 1901.

Nec C. pulchellum f. *semipulchellum* Jörgensen, *nec Ceratium semipulchellum* (Jörgensen) Steemann Nielsen.

Diamètre cingulaire : 40-60 µ. Cornes antapicales très réduites : la gauche, de longueur peu différente du diamètre cingulaire; la droite, rudimentaire, à peine plus longue que large. Corps central plus « haut » que « large ».

Transitions entre les deux variétés précédentes :
Fig. 41-42

= *Ceratium pulchellum* Schröder, *pro parte.*
JÖRGENSEN, 1911 (fig. 60, 61, *non al.*); PAVILLARD, 1931 (pl. 2, fig. 20b-c, *non* a); GRAHAM & BRONIKOVSKY, 1944 (fig. 14b, *non* c-f); LOPEZ, 1955 (fig. 6, colonnes verticales 2 et 3, et fig. 13b, *non al.*).

= *C. pulchellum* f. *semipulchellum* Jörgensen = *Ceratium semipulchellum* (Jörgensen) Steemann Nielsen, *pro parte.*
JÖRGENSEN, 1920; PAULSEN, 1930; PETERS, 1934 (pl. 1, fig. 5b, *non* a); STEEMANN NIELSEN, 1934; WOOD, 1954.
Non SCHILLER, 1937, *nec* GRAHAM & BRONIKOVSKY, 1944.

= *C. pulchellum* f. *tripodoides* Jörgensen, *pro parte.*
SCHILLER, 1937; WOOD, 1954; LOPEZ, 1955, *pro parte* (comme ci-dessus), et 1966.

= *C. tripos* subsp. *mediterraneum* Pavillard.
PAVILLARD, 1931.

= *C. pulchellum* var. *Joergensenii* Wang.
WANG, 1932.

POUR LES DEUX VARIÉTÉS ET LEURS TRANSITIONS

RÉCOLTES PERSONNELLES : A Nossi-Bé, l'espèce est, dans son ensemble, pérennante, mais la variété *pulchellum* et les formes de transition sont préférentiellement « hivernales ». Tous les stades

ont été observés à Tuléar et à l'île Maurice. Au cours de la croisière de l'*Anton Bruun*, la variété *atlanticum* et les stades voisins étaient représentés en plus ou moins grande abondance dans la presque totalité des prélèvements; par contre, la variété *pulchellum* et les stades intermédiaires n'ont été récoltés que dans le centre du canal, et seulement dans les prélèvements verticaux.

Océan indien : L'espèce y est courante, mais la répartition et l'abondance relative des diverses unités est difficile à préciser. Il apparaît cependant que la var. *pulchellum* est la plus rare.

Distribution mondiale : La « série *atlanticum-pulchellum* » est largement répandue dans toutes les mers tempérées et tropicales; la variété *pulchellum* est plus rare et nettement thermophile (sténothermie, ou sténohalinité ? Ceci reste à définir). Au sujet de la répartition verticale, il n'existe pas de discrimination affirmée.

II. — AUTRES UNITÉS INFRA-SPÉCIFIQUES

La variabilité du *Ceratium tripos* ne se limite manifestement pas à la « série *atlanticum-pulchellum* ». Si le type thermophile, *pulchellum*, semble stable et uniforme (mise à part la forme *dalmaticum* des côtes adriatiques), il n'en va pas de même des formes tempérées et froides. Le matériel qui fait l'objet du présent travail n'était assurément pas propice à l'étude de cette question. J'ai cependant récolté à Tuléar plusieurs spécimens se rapportant au *C. tripos* var. *atlanticum* f. *neglectum*. Par ailleurs, le cas de diverses formes et variétés nordiques, et celui du *Ceratium porrectum*, attendent d'être reconsidérés. Les références de ces divers taxons seront donnés ici pour mémoire (au sujet de *C. porrectum*, voir p. 425).

var. ***atlanticum*** f. ***neglectum*** (Ostenfeld) Paulsen, 1908
Fig. 44

Ostenfeld, 1903, p. 584, fig. 135 : *Ceratium neglectum;* Paulsen, 1908, p. 78, fig. 103; Jörgensen, 1911, p. 37, pl. 4, fig. 74; Dangeard, 1926, p. 314, fig. 3b; Lebour, 1925, p. 150, pl. 30.

Epithèque très élargie, couverte de crêtes lamellaires unissant la corne apicale au corps central. Il semble bien s'agir ici d'un cas de développement particulier de la variété *atlanticum*.

Cette forme paraît nouvelle pour l'océan indien, et demeure peu connue dans le reste du globe.

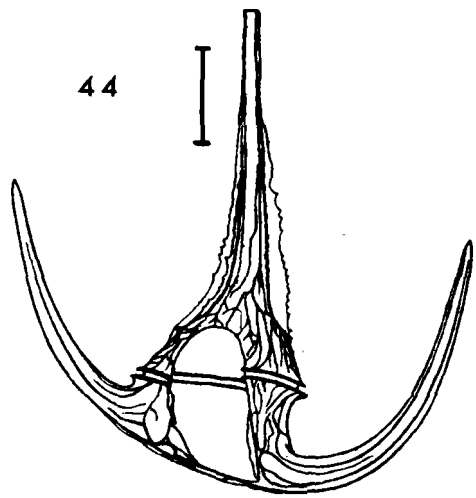


FIG. 44 : *Ceratium tripos* var. *atlanticum* f. *neglectum* (Ostf.) Paulsen. *In* JÖRGENSEN, 1911, fig. 68.

Pour mémoire :

var. ***atlanticum*** f. ***reticulatum*** Dangeard, 1926

DANGEARD, 1926, p. 314, fig. 4a.

var. ***balticum*** « Schütt » (?)

?SCHÜTT, 893, fig. 20 IVa, « *C. tripos* » ; (PAULSEN, 1908) ; JÖRGENSEN, 1911, p. 35, pl. 4, fig. 65 ; LOHMANN, 1908, p. 267, fig. 21 ; SCHILLER, 1937, p. 384, fig. 421d : « f. *balticum* Schütt » ; ? WOOD, 1954, p. 286, fig. 205b ; NIELSEN, 1956.

C. tripos f. ***subsalsum*** Ostenfeld, 1903

OSTENFELD, 1903, p. 584, fig. 134 ; JÖRGENSEN, 1911, p. 36, pl. 4, fig. 66-67 ; LEBOUR, 1925, p. 149, fig. 46d ; ABÉ, 1927, p. 425, fig. 42 : « var. *subsalsum* Ostf. » ; WANG, 1936, p. 157, fig. 27 ; SCHILLER, 1937.

= *C. tripos* var. *subsalsum* (Ostenfeld) Paulsen.

PAULSEN, 1907, 1908 ; APSTEIN, 1910, 1911.

C. tripos f. ***hiemale*** Paulsen, 1907
Fig. 45

PAULSEN, 1907, p. 21, fig. 31, et 1908, p. 80, fig. 107 ; JÖRGENSEN, 1911, p. 36, pl. 4, fig. 68 (« *C. tripos* var. *balticum* f. *hiemale* Paulsen ») ; LEBOUR, 1925, p. 149, fig. 46c.

C. tripos var. ***ponticum*** Jörgensen, 1920

JÖRGENSEN, 1920, p. 47, fig. 37, 38, et f. *pachysomum* Jörgensen, *ibid.*, fig. 39.

A rattacher probablement à la variété *atlanticum*. LOPEZ en a décrit récemment un cas d'hétéromorphie (1966, p. 420, fig. 36).

Hétéromorphisme chez *C. tripos*

LOHMANN, 1908; APSTEIN, 1909, 1910, 1911; JÖRGENSEN, 1911, 1920 (à propos de la variété *ponticum*); LEBOUR, 1925; HASLE & NORDLI, 1951; NORDLI, 1957; STOSCH, 1964.

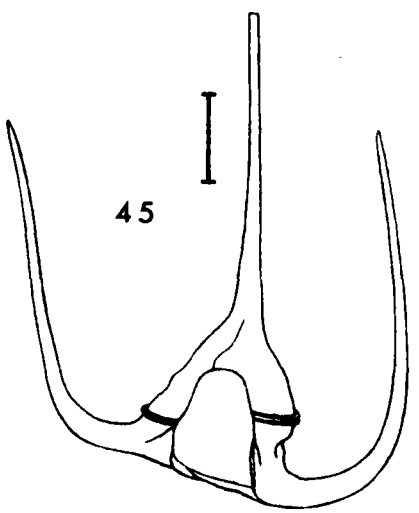


FIG. 45 : *Ceratium tripos* f. *hiemale* Paulsen. *In* JÖRGENSEN, 1911, fig. 68.

III. — QU'EST-CE QUE LE TYPE DU *C. TRIPOS* ?

Cf. MÜLLER et NITZSCH (loc. cit.), et : EHRENBERG, 1836; DUJARDIN, 1841; BERGH, 1882; SCHÜTT, 1892, 1895; LEMMERMANN, 1899; KARSTEN, 1907; JÖRGENSEN, 1911, 1920; PAVILLARD, 1931; STEEMANN NIELSEN, 1934.

La description originelle de MÜLLER ne permet pas de répondre avec certitude à cette question; du moins la figure donnée par cet auteur semble-t-elle à l'écart de la série *atlanticum-pulchellum*. Par la suite, les interprétations les plus diverses ont été données (voir auteurs cités ci-dessus).

Il est finalement très probable que, comme le veut JÖRGENSEN, le type du *C. tripos* se situe au voisinage de la « variété *balticum* » dont le nom serait alors illégal. Rappelons que le terme « var. *genuinum* » de PAVILLARD (1931) doit également être rejeté (cf. p. 383).

IV. — CONCLUSION

Pour conclure cette mise à jour de la question du *C. tripos*, rappelons à nouveau que la série des variations unissant les variétés *atlanticum* et *pulchellum* ne représente nullement la totalité des variations de l'espèce : le cas des formes tempérées et froides reste à étudier, particulièrement celui de la var. *balticum*. A propos de cette dernière, on peut également se demander si elle représente ou non le prolongement et le terme extrême de la série *atlanticum-pulchellum :* la variabilité du *Ceratium tripos* se déroule-t-elle selon deux, ou plusieurs directions ?

Ceratium porrectum (Karsten) Jörgensen, 1911
Fig. 46

Karsten, 1907, pl. 51, fig. 6 : *C. tripos porrectum.*

Sous le nom erroné de « *C. porrectum* Karsten » :

Jörgensen, 1911, p. 34, pl. 3, fig. 63-64 (incl. *f. megasomum*); Dangeard, 1927, p. 376, fig. 41a, *vix* c, *non* ? b; Schiller, 1937, p. 389, fig. 427a; Silva, 1949, p. 357, pl. 7, fig. 1; Wood, 1954, p. 287, fig. 207.

Récoltes personnelles : Deux spécimens seulement, provenant de Tuléar.

Océan indien : Seychelles (Karsten), Sud de l'Australie (Wood) et « océan indien » (Wood, 1963).

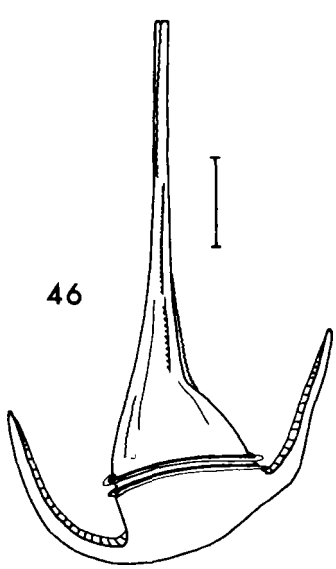


Fig. 46 : *Ceratium porrectum* (Karsten) Jörg.

DISTRIBUTION MONDIALE : Quelques stations seulement à ajouter aux précédentes : Atlantique tropical (DANGEARD) et côte du Portugal (SILVA).

Cette espèce, voisine de *C. tripos*, demeure donc très mal connue. Le spécimen décrit par JÖRGENSEN sous le nom de *f. megasomum* est seulement plus robuste (plus âgé ?) que le type; cette distinction est peut-être superflue.

Ceratium breve (Ostenfeld & Schmidt) Schröder, 1906

OSTENFELD & SCHMIDT, 1901, p. 164, fig. 13 : *C. tripos* var. *breve;* SCHRÖDER, 1906, p. 358.

Incl. : *Ceratium Schmidtii* Jörgensen.

Voici encore une espèce très variable, comme l'ont montré principalement JÖRGENSEN (1911), BÖHM (1931b), STEEMANN NIELSEN (1934) et GRAHAM & BRONIKOVSKY (1944). Elle a été quelquefois rapprochée de *C. tripos* et de *C. arcuatum,* mais ces affinités paraissent superficielles (« convergence » plutôt que « filiation »). Par contre, sa parenté avec *C. Schmidtii* n'a été évoquée que très discrètement par JÖRGENSEN ainsi que par BÖHM (1931a), et n'est devenue évidente qu'assez récemment, à la suite du travail de GRAHAM & BRONIKOVSKY. Ces deux auteurs n'ont cependant pas osé réunir les deux espèces, ce que je ferai aujourd'hui. Une suite homogène de variations unit en effet les deux extrêmes, et la courbure ventrale des cornes antapicales, donnée par JÖRGENSEN comme caractéristique de son *C. Schmidtii,* a été observée chez *C. breve* par GRAHAM & BRONIKOVSKY, ainsi que par moi-même. Aussi n'est-il plus possible de traiter distinctement les deux espèces.

La variabilité du *C. breve* (*sensu lato*) se traduit essentiellement par deux caractères morphologiques : 1) « ouverture » des cornes antapicales, qui sont dans les deux cas extrêmes, soit parallèles (« *C. breve* var. *parallelum* »), soit fortement recourbées l'une vers l'autre (« *C. Schmidtii* »), 2) longueur de la corne apicale. Ces deux variables semblent liées mutuellement : dans la plupart des cas, la corne apicale est d'autant plus courte que les antapicales sont plus « ouvertes ».

Le type de l'espèce lui-même représente une transition : antapicales légèrement convergentes, et apicale très réduite (OSTENFELD & SCHMIDT) ou longue et fine (SCHRÖDER). Aussi, dans l'impossibilité de donner l'épithète spécifique à l'une ou l'autre des deux variétés extrêmes, je désignerai celles-ci sous les noms de var. *parallelum* (Schm.) Jörg., et var. *Schmidtii* (Jörg.) Sournia.

var. *parallelum* (Schmidt) Jörgensen, 1911
Fig. 47-48

SCHMIDT, 1901, p. 213, fig. 1 : *C. tripos balticum* Schütt *f. parallelum*; JÖRGENSEN, 1911, p. 41, pl. 4, fig. 86; BÖHM, 1931b, p. 18, fig. 17, 18a; NIE, 1936, p. 51, fig. 19.

= *Ceratium breve* (Ostenfeld & Schmidt) Schröder, *pro parte*.

WANG & NIE, 1932; STEEMANN NIELSEN, 1934 (fig. 35, *non* 36); SCHILLER, 1937 (fig. 429a, *non* b); GRAHAM & BRONIKOVSKY, 1944 (fig. 14h, k, m, *non al.*); BALLANTINE, 1961.

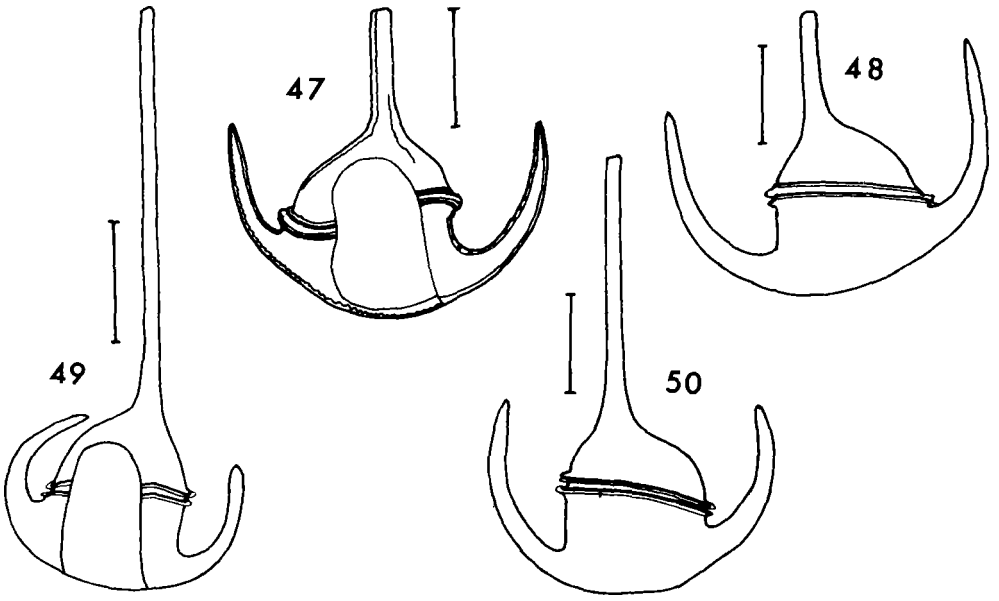


FIG. 47-48 : *Ceratium breve* var. *parallelum* (Schm.) Jörg. — 49 : *C. breve* var. *Schmidtii* (Jörg.) Sournia. — 50 : *C. breve* (Ostf. & Schm.) Schröder, « *parallelum* > *Schmidtii* ».

Parties distales des cornes antapicales parallèles ou légèrement divergentes. Longueur de la corne apicale rarement supérieure à la hauteur du corps central.

var. *Schmidtii* (Jörgensen) Sournia, 1966
Fig. 49

= *Ceratium Schmidtii* Jörgensen.

JÖRGENSEN, 1911, p. 50, pl. 5, fig. 110-111; BÖHM, 1931b (fig. 22c-d, *vix* b, *non* a); STEEMANN NIELSEN, 1943, 1939; NIE, 1936; SCHILLER, 1937; WOOD, 1954 (fig. 216a, *non* b); LOPEZ, 1966.

= *Ceratium curvicorne* (Daday) Cleve, *pro parte*.

SCHMIDT, 1901; *Non* DADAY, 1888 (*vix* fig. 17, *non al.*); *Nec* CLEVE, 1900a

Cornes antapicales très peu écartées du corps central; la gauche grossièrement parallèle à la corne apicale, la droite fortement recourbée et devenant dans sa partie distale perpendiculaire à la corne apicale. Longueur de la corne apicale le plus souvent très supérieure à la hauteur du corps central.

Transitions entre les deux variétés précédentes :
Fig. 50, et pl. II, fig. 7

= *Ceratium breve* (Ostf. & Schmidt) Schröder, *pro parte.*

JORGENSEN, 1911, p. 40, pl. 4, fig. 84; STEEMANN NIELSEN, 1934, p. 18, fig. 36, *non* 35; NIE, 1936, p. 50, fig. 18; GRAHAM & BRONIKOVSKY, 1944, p. 27, fig. 14g, j, l, n-o, *non al.*; SILVA, 1949, p. 357, pl. 9, fig. 4; KLEMENT, 1964, p. 355, pl. 3, fig. 4.

= *Ceratium Schmidtii* Jörgensen, *pro parte.*

WANG & NIE, 1932, p. 308, fig. 20; HALIM, 1963, p. 498, fig. 20-21.

= *C. breve* var. *curvulum* Jörgensen.

JÖRGENSEN, 1911, p. 41, pl. 4, fig. 85; PETERS, 1934, p. 39, pl. 3, fig. 13d; ? SCHUBERT, 1937, p. 393.

= *C. tripos* (Müller) Nitzsch : *in* MARGALEF, 1961, fig. 26j. *Non al.*

POUR LES DEUX VARIÉTÉS ET LEURS TRANSITIONS

RÉCOLTES PERSONNELLES : A Nossi-Bé, cette espèce est assez peu courante. Il n'a pas été possible de déceler d'alternance saisonnière, mais la var. *Schmidtii* domine au sein de l'espèce, en fréquence et en abondance. Par contre, à Tuléar et à l'île Maurice, la var. *parallelum* et les stades voisins ont seuls été observés. Le matériel de l'*Anton Bruun* a montré tous les stades de la série en assez grande abondance, sans qu'il soit possible d'établir une distinction latitudinale ou écologique entre les deux variétés; toutefois la *var. Schmidtii* était la plus rare.

OCÉAN INDIEN : Espèce courante, mais var. *Schmidtii* sensiblement plus rare.

DISTRIBUTION MONDIALE : Espèce tropicale assez sporadique. Presque inconnue en Méditerranée : la variété *Schmidtii* n'y a été que récemment signalée, par HALIM (1963) en mer d'Alexandrie, et par LOPEZ (1966) sur les côtes espagnoles. Il est difficile de distinguer écologiquement les deux types extrêmes; STEEMANN NIELSEN a montré que chez « *C. breve* » (au sens de JÖRGENSEN), le diamètre cingulaire variait en fonction inverse de la température, et que la

proximité des côtes se traduisait par un accroissement de ce diamètre ainsi que de la longueur des cornes postérieures. D'après le même auteur, la variété « *curvulum* » (dont je fais une forme intermédiaire) est seule présente en domaine océanique, alors qu'on la rencontre en même temps que la var. *parallelum* en domaine néritique. D'autre part, pour STEEMANN NIELSEN, « *C. Schmidtii* » est nettement néritique. C'est ce que mes propres observations dans le canal de Mozambique tendent à confirmer. Mais la rareté relative de cette variété peut fausser les observations.

L'espèce serait euphotique.

Ceratium arietinum Cleve, 1900

CLEVE, 1900a, p. 13, pl. 7, fig. 3 : *C.* (*tripos* var. *arietinum.*
Incl. *C. bucephalum* (Cleve) Cleve.

On s'étonne que les deux espèces aient été réunies si tardivement (GRAHAM & BRONIKOVSKY, 1944). En effet, le cas du « *C. heterocamptum* », sous ses divers synonymes, pouvait déjà paraître étrange bien avant cette date et suggérer un rapprochement. Mais l'on peut penser que le *C. bucephalum* a été tenu à l'écart du fait de sa rareté : entre CLEVE et GRAHAM & BRONIKOVSKY, cette espèce ne figure que dans quelques rares travaux; notons que la figure de SCHILLER (1937), « nach PETERS » diffère notablement de celle de ce dernier, et plus encore du type originel de CLEVE. Remarquons aussi que l'iconographie de WOOD (1954) relative à cette espèce est très douteuse.

GRAHAM & BRONIKOVSKY distinguent en *Ceratium arietinum, sensu lato,* deux sous-espèces, *bucephalum* et *gracilentum.* Je crois devoir intercaler entre ces deux extrêmes le terme *arietinum,* et considérer les trois comme des variétés (la première, absente de mes récoltes, sera traitée ici pour mémoire).

Le nom de l'espèce est bien *arietinum,* puisque la publication de ce nom (CLEVE, 1900a) est légèrement antérieure à celle du *C. bucephalum* (CLEVE, 1900d), ainsi qu'à celle du *C. heterocamptum* (OSTENFELD & SCHMIDT, 1901).

Pour mémoire :

var. ***bucephalum*** (Cleve) Sournia, 1966

Fig. 51

= *C. bucephalum* (Cleve) Cleve.

CLEVE, 1897, p. 302, fig. 5 (*C. tripos* var. *bucephalum*); CLEVE, 1900d; PAULSEN, 1908; JÖRGENSEN, 1911, 1920; OKAMURA, 1912; LEBOUR, 1925; *Non ?* DANGEARD, 1926; MARTIN, 1929; PETERS, 1934; SCHILLER, 1937 (? fig. 430); SILVA, 1949; WOOD, 1954 (? fig. 210).

= *C. arietinum* subsp. *bucephalum* (Cleve) Graham & Bronikovsky.

GRAHAM & BRONIKOVSKY, 1944 (fig. 16a-d, h, *non al.*).

= *C. arietinum* f. *regulare* Jörgensen.

JÖRGENSEN, 1920; PAVILLARD, 1931, p. 81; SCHILLER, 1937; WOOD, 1954.

Non Ceratium Petersii Steemann Nielsen (à ce sujet, voir plus loin, p. 435 à propos de *C. azoricum*, et voir aussi GRAHAM & BRONIKOVSKY, 1944, p. 31).

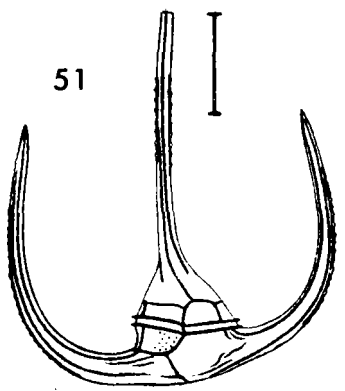


FIG. 51 : *Ceratium arietinum* var. *bucephalum* (Cleve) Sournia. *In* JÖRGENSEN, 1911, fig. 99.

C'est la variété psychrophile de l'espèce (PAULSEN, 1908, la donne pour sub-tropicale, mais ce point a été infirmé par la suite). Répartition bipolaire : zones froides et tempérées des deux hémisphères. Inconnue en Méditerranée.

var. ***arietinum***
Fig. 52

= *C. arietinum* Cleve, *stricto sensu.*

CLEVE, 1900a; JÖRGENSEN, 1911 (fig. 102, 103, *vix* 104, *non* 105); OKAMURA, 1912; FORTI, 1924; BÖHM, 1931a; PETERS, 1934 (« *C. arietinum arietinum* »); SILVA, 1949, GAARDER, 1954.

= *C. heterocamptum* (Jörgensen) Ostenfeld & Schmidt = *C. bucephalum* var. *heterocamptum* (Jörgensen) Jörgensen.

OSTENFELD & SCHMIDT, 1901; PAVILLARD, 1907; PAULSEN, 1908; JÖRGENSEN, 1911; LEBOUR, 1925; ABÉ, 1927.

= *C. arietinum* f. *detortum* (Stüwe) Jörgensen.

JÖRGENSEN, 1920; SCHILLER, 1937; WOOD, 1954 (fig. 221c, *non* b).

= *C. arietinium* f. *valens* Jörgensen.

JÖRGENSEN, 1920; WOOD, 1954 (*non* fig. 221d).

C'est le type originel de l'espèce, et qui se trouve être son type « moyen ». Caractères assez variables, mais cellules toujours relativement robustes, et corne apicale courte; corne postérieure droite fortement recourbée vers l'intérieur, et souvent tordue en sens inverse à son extrémité.

RÉCOLTES PERSONNELLES : Très rare à Nossi-Bé (quelques stations dans le cours du cycle annuel). Tuléar. Ile Maurice. Centre du canal de Mozambique.

OCÉAN INDIEN : Variété assez courante, mais de répartition difficile à distinguer de celle de la suivante.

DISTRIBUTION MONDIALE : Cette variété possède une répartition latitudinale très vaste, presque cosmopolite, mais préférentiellement thermophile.

var. ***gracilentum*** (Jörgensen) Sournia, 1966
Fig. 54

= *C. arietinum* f. *gracilentum* Jörgensen.
JÖRGENSEN, 1920, p. 64, fig. 62; SCHILLER, 1937; RAMPI, 1939; WOOD, 1954 (*non* fig. 221d); HALIM, 1960, 1963.

= *C. arietinum* subsp. *gracilentum* (Jörgensen) Peters.
PETERS, 1934; GRAHAM & BRONIKOVSKY, 1944.

C'est la variété thermophile et la plus « délicate » :

Corne apicale toujours longue, et sub-rectiligne. Corne postérieure droite mince, non tordue à son extrémité. Contour postérieur de l'hypothèque régulièrement convexe, sans gibbosité.

Cette variété est morphologiquement beaucoup plus proche de la précédente que de la var. *bucephalum*. STEEMANN NIELSEN la réunit même à la « forme » *detortum* de JÖRGENSEN, c'est-à-dire à la variété *arietinum*, mais PETERS l'isole de toutes les formes décrites par JÖRGENSEN.

RÉCOLTES PERSONNELLES : Quelques spécimens seulement, à Tuléar et au large de Monbasa.

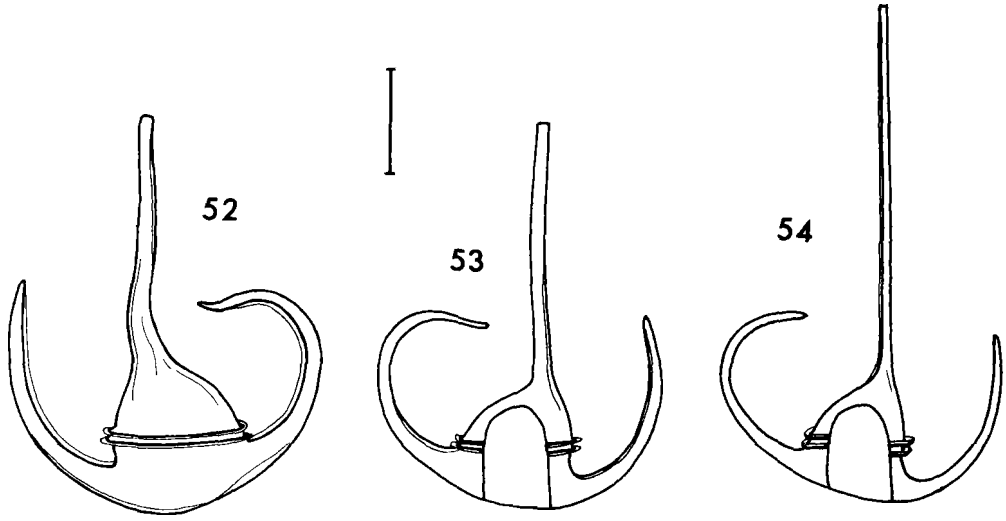


FIG. 52 : *Ceratium arietinum* Cleve var. *arietinum*. 53 : *C. arietinum* Cleve, « *arietinum-gracilentum* ». 54 : *C. arietinum* var. *gracilentum* (Jörg.) Sournia. L'échelle est commune aux trois figures.

OCÉAN INDIEN : Voir variété précédente.

DISTRIBUTION MONDIALE : A la différence de la variété *arietinum*, semble nettement tropicale, comme le montrent PETERS et GRAHAM & BRONIKOVSKY.

Transitions entre les trois variétés précédentes :
Fig. 53

Cf. GRAHAM & BRONIKOVSKY, 1944, fig. 16.

La distinction des deux variétés *arietinum* et *gracilentum* n'est donnée ici qu'à titre d'hypothèse, et dans le but de préciser à l'avenir si les deux distributions géographiques sont effectivement distinctes. On peut également considérer la variété *arietinum* comme un ensemble de termes de passage entre les deux extrêmes psychrophile et thermophile.

Ceratium symetricum Pavillard, 1905

PAVILLARD, 1905, p. 52, pl. 1, fig. 4.
Incl. *C. coarctatum* Pav. et *C. gracile* (Gourret) Jörgensen.

Etant donné les affinités entre ces trois espèces, il est nécessaire de réunir celles-ci en une seule, selon l'opinion de STEEMANN NIELSEN, SCHILLER et GRAHAM & BRONIKOVSKY, et malgré PAULSEN, PAVILLARD et divers auteurs qui maintiennent certaines séparations.

L'historique du *Ceratium gracile* est inextricable, car cette dernière épithète a été employée par divers auteurs, sous divers rangs taxinomiques, et sous diverses acceptions. Aussi l'usage de ce nom prête-t-il à confusion. Il faut de plus admettre que la description et la figure originelles de GOURRET (1883, p. 24, pl. 1, fig. 1 : « *C. tripos* var. *gracile* »), ainsi que la diagnose non illustrée de POUCHET (1883, p. 422, sous le même nom) sont à vrai dire non identifiables spécifiquement. Dans ces conditions, le nom de l'espèce revient bien à *C. symetricum*.

Enfin, l'emploi de désignations infra-spécifiques s'impose (*contra* STEEMANN NIELSEN, SCHILLER, WOOD) car les trois « espèces » originelles sont aisément reconnaissables, et peuvent être considérées comme autant de variétés (GRAHAM & BRONIKOVSKY).

var. ***symetricum***
Fig. 57

GRAHAM & BRONIKOVSKY, 1944, p. 29, fig. 15i.

= *C. symetricum* Pavillard, *stricto sensu*.
PAVILLARD, 1905, 1907, 1923, 1931, 1937; FORTI, 1924; PAULSEN, 1930; STEEMANN NIELSEN, 1934 (fig. 41, *non* 40); SCHILLER, 1937 (fig. 441d, *non* a-c); WOOD, 1954 (fig. 217a, c, *non* b); HALIM, 1960, 1963.

= *C. gracile* var. *symetricum* (Pavillard) Jörgensen.
JÖRGENSEN, 1911, 1920; BÖHM, 1931a; RAMPI, 1939.

Caractères distinctifs des deux autres variétés : cornes fines, subparallèles dans leurs parties distales. Cornes antapicales largement déployées de part et d'autre de la corne apicale.

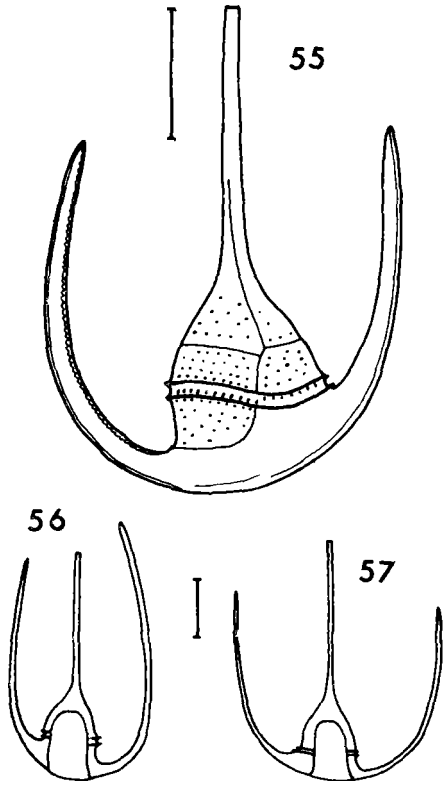


FIG. 55 : *Ceratium symetricum* var. *orthoceras* (Jörg.) Graham & Bron. — 56 : *C. symetricum* var. *coarctatum* (Pav.) Graham & Bron. — 57 : *C. symetricum* Pav. var. *symetricum*.

var. ***coarctatum*** (Pavillard) Graham & Bronikovsky, 1944
Fig. 56

GRAHAM & BRONIKOVSKY, 1944, p. 29, fig. 15 j-l.

= *C. coarctatum* Pavillard.

PAVILLARD, 1905, 1907, 1923, 1931, 1937; PAULSEN, 1930; RAMPI, 1939; HALIM, 1960.

= *C. gracile* (Gourret) Jörgensen, *stricto sensu.*

JÖRGENSEN, 1911; FORTI, 1924.

= *C. gracile* α *coarctatum* (Pavillard) Jörgensen.

JÖRGENSEN, 1920.

= *C. symetricum* Pavillard, *pro parte.*

SCHILLER, 1937 (fig. 441a-b, *non* c-d). *Non al.*

Caractères distinctifs des deux autres variétés : cornes longues; antapicales légèrement convergentes dans leurs parties distales, et

peu éloignées de la corne apicale (la distance de cette dernière à l'une ou l'autre des cornes antapicales est égale ou inférieure au diamètre cingulaire).

var. ***orthoceras*** (Jörgensen) Graham & Bronikovsky, 1944
Fig. 55

Graham & Bronikovsky, 1944, p. 29, fig. 15h; Halim, 1963, p. 498, fig. 25 (« *C. symetricum* var. *orthoceras* Jörgensen ».

= *C. gracile* f. *orthoceras* Jörgensen.
Jörgensen, 1911, 1920; Forti, 1924.

= *C. orthoceras* (Jörgensen) Pavillard.
Pavillard, 1931.

= *C. symetricum* Pavillard, *pro parte.*
Schiller, 1937, fig. 441c, *non* a-b, d. *Non al.*

Caractères distinctifs des deux autres variétés : cornes relativement plus robustes, sub-parallèles dans leurs parties distales; antapicales assez rapprochées de la corne apicale; corne antapicale droite seulement légèrement incurvée à son origine, puis rectiligne.

Cette variété est en quelque sorte intermédiaire entre les deux précédentes. Elle rappelle par ailleurs *C. euarcuatum* (disposition de la corne postérieure droite).

Transitions entre les trois variétés précédentes :

Les trois variétés sont assez stables, et les formes transitionnelles sont rarement observées. La var. *orthoceras,* quelque peu plus fluctuante que les deux autres, ne représente peut-être qu'une transition entre celles-ci.

POUR LES TROIS VARIÉTÉS

Récoltes personnelles : *C. symetricum* est dans l'ensemble assez rare, et aucune différenciation écologique n'est apparue entre les trois variétés. L'espèce semble plutôt océanique : Nossi-Bé (très rare), Tuléar, et diverses stations du canal de Mozambique.

Océan indien : Cette espèce y est principalement connue par la croisière du « *Dana* » (Steemann Nielsen, 1939) et par les travaux récents de Wood (1954), Silva (1956) et Travers (1965). Jörgensen, en 1911, la donnait comme courante, sans préciser de références (probablement Karsten, sous divers synonymes). Elle serait finale-

ment assez commune, compte tenu de confusions possibles sous le nom incertain de « *Ceratium gracile* ».

DISTRIBUTION MONDIALE : Espèce tropicale et sub-tropicale, plutôt océanique. Oligophotique (je n'ai pu vérifier personnellement ce point).

Ceratium azoricum Cleve, 1900
Fig. 58

CLEVE, 1900a, p. 13, pl. 7, fig. 6-7 : *C.* (*tripos* var.) *azoricum;* JÖRGENSEN, 1911, p. 47, pl. 5, fig. 97-98 et 1920, p. 69, fig. 66; LEBOUR, 1925, p. 151, fig. 48; WAILES, 1928, pl. 1, fig. 3; PETERS, 1934, p. 43, pl. 3, fig. 14h; STEEMANN NIELSEN, 1934, p. 20, fig. 43, et 1939, p. 12; SCHILLER, 1937, p. 406, fig. 447; SCHUBERT, 1937, p. 395; RAMPI, 1939, p. 307, fig. 25; GRAHAM & BRONIKOVSKY, 1944, p. 30, fig. 16m-p; *Vix* SILVA, 1949, p. 358, pl. 6, fig. 24; WOOD, 1954, p. 295, fig. 222; HALIM, 1960, pl. 4, fig. 13.

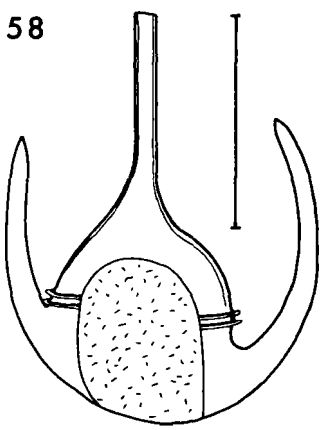


FIG. 58 : *Ceratium azoricum* Cleve.

RÉCOLTES PERSONNELLES : Nossi-Bé (rare). Tuléar. Sud et centre du canal de Mozambique.

OCÉAN INDIEN : Espèce assez rare, distribuée très sporadiquement. Dans la région du canal de Mozambique, *C. azoricum* n'avait jusqu'ici été signalé que sur les côtes du Natal (très rare) par STEEMANN NIELSEN (1939).

DISTRIBUTION MONDIALE : Réputée tropicale ou sub-tropicale, cette espèce est en fait également répandue, quoique sporadiquement, sous toutes les latitudes tempérées ainsi que, plus rarement, sous les basses latitudes. Sa distribution verticale est incertaine.

Selon GRAHAM & BRONIKOVSKY cette espèce est douée d'une large variabilité et évolue entre deux extrêmes, l'un représenté par de petites cellules à cornes rapprochées, l'autre par de grandes cellules à cornes déployées, et il se pourrait que *C. Petersii* St.

Nielsen (absent de mes prélèvements) dût être rattaché à ce dernier type. (Voir aussi BALECH, 1962, p. 183, pl. 26). Cependant, *C. azoricum*, assez rare il est vrai dans mes récoltes, s'y présente sous une forme relativement constante (fig. 58), et dépourvue de crêtes lamellaires.

Finalement cette espèce, du fait sans doute de sa petite taille, demeure imparfaitement connue.

Pour mémoire :

Ceratium Petersii Steemann Nielsen, 1934
Fig. 59-63

STEEMANN NIELSEN, 1934, p. 20, fig. 44; SCHILLER, 1937, p. 406, fig. 446; GRAHAM & BRONIKOVSKY, 1944, p. 31, fig. 16 l; WOOD, 1954, p. 296, fig. 224a-b; BALECH, 1962, p. 183, pl. 26, fig. 395-397.

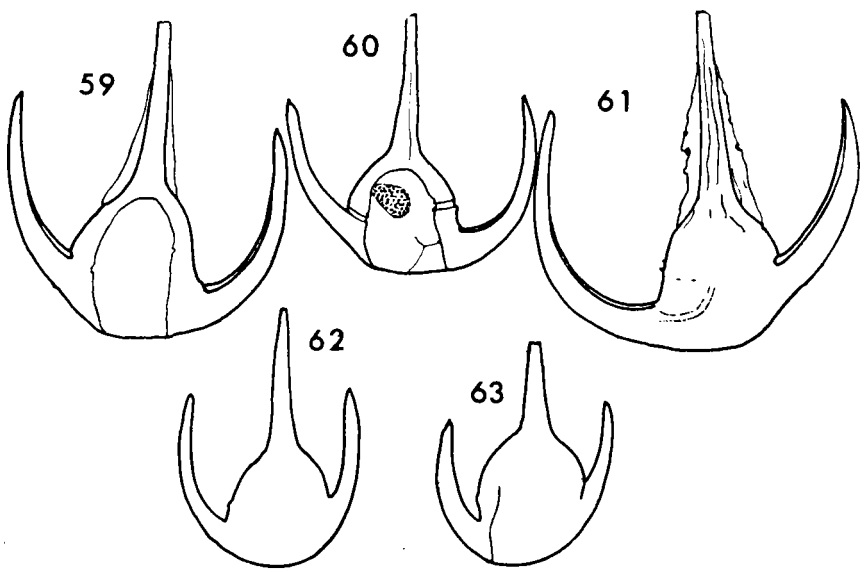


FIG. 59-61 : *Ceratium Petersii* St. Nielsen, « typique ». — 62-63 : « transitions vers *C. azoricum* ». *In* BALECH, 1962, fig. 395-399; échelles non indiquées par l'auteur.

Ceratium euarcuatum Jörgensen, 1920
Fig. 64-65

JÖRGENSEN, 1920, p. 56, fig. 54; PETERS, 1934, p. 40, pl. 1, fig. 4a-c; STEEMANN NIELSEN, 1934, p. 18, fig. 38, et 1939, p. 11; SCHILLER, 1937, p. 402, fig. 443; RAMPI, 1939, p. 306, fig. 30; GRAHAM & BRONIKOVSKY, 1944, p. 28, fig. 15n-m; WOOD, 1954, p. 294, fig. 220; HALIM, 1960, p. 185, pl. 5, fig. 3, et 1963, p. 497, fig. 13.

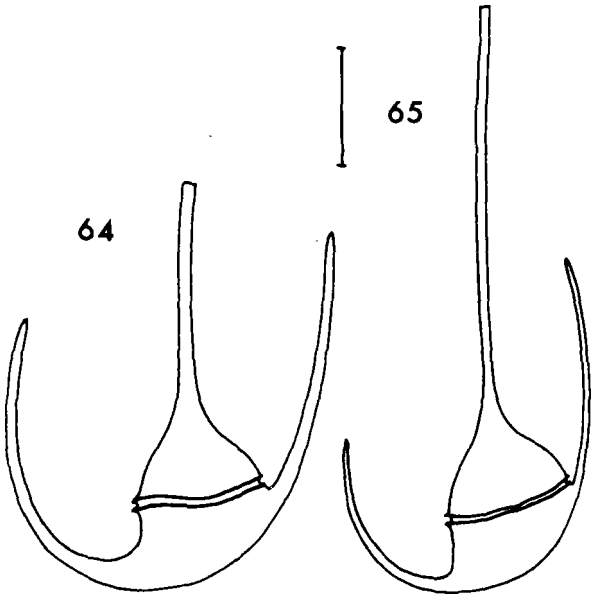


FIG. 64-65 : *Ceratium euarcuatum* Jörg.

Au sujet de la légalité de ce taxon, voir plus loin (deuxième partie), à propos de *C. contortum*.

RÉCOLTES PERSONNELLES : Nossi-Bé (très rare), Tuléar, île Maurice. Au cours de la croisière de l'« *Anton Bruun* », présent dans tous les prélèvements verticaux des eaux du large, mais très rare dans le domaine néritique, ainsi que dans les prélèvements de surface.

OCÉAN INDIEN : De découverte relativement récente, l'espèce n'a été signalée dans cet océan que par JÖRGENSEN (1920), par STEEMANN NIELSEN (1939) qui la donne comme très courante dans la zone tropicale océanique, enfin, plus récemment, par WOOD (1954, 1962) et TRAVERS (1965). Les références de SCHRÖDER et de KARSTEN données par WOOD dans son index (1963a) sont très douteuses.

DISTRIBUTION MONDIALE : Espèce tropicale, vraisemblablement oligophotique (PAVILLARD, 1937, et SCHUBERT contestent ce point), connue dans les trois océans et en Méditerranée. Principalement océanique et oligotrophique, elle n'est pas pour autant exclue des eaux néritiques ou eutrophiques.

Quoique proche de *C. symetricum*, cette espèce en est toujours aisément distinguable, et d'ailleurs peu variable. JÖRGENSEN (1920) en a décrit, sans les nommer, deux « formes » qui ne diffèrent entre elles que par la longueur et l'épaisseur des cornes. Toutes deux étaient présentes dans mon matériel, mais ne semblent pas justifier de désignations infra-spécifiques distinctes. A toutes fins utiles, je les représente l'une et l'autre par les figures 64 et 65 :

— Fig. 64 : corne apicale seulement un peu plus longue que

les cornes postérieures; celles-ci assez robustes; corne gauche plus rapprochée du corps central que dans le cas suivant.

— Fig. 65 : corne apicale nettement plus longue que les postérieures; celles-ci délicates; corne droite s'effilant vers son extrémité.

Ceratium declinatum (Karsten) Jörgensen, 1911 *sensu lato*

Karsten, 1907, p. 406, pl. 48, fig. 2 : *C. tripos declinatum*; Jörgensen, 1911, p. 42, pl. 4, fig. 87-89, et 1920, p. 66, fig. 63-65; Mangin, 1912, p. 24, fig. 8; Peters, 1934, p. 43, pl. 4, fig. 23; Steemann Nielsen, 1934, p. 22, fig. 46-47, et 1939, p. 13; Schiller, 1937, p. 404, fig. 445; Graham & Bronikovsky, 1944, p. 32, fig. 16q-t et 17a-c; Wood, 1954, p. 293, fig. 218; Halim, 1960, p. 185, pl. 4, fig. 22-26.

Récoltes personnelles : Nossi-Bé (espèce rare, mais presque pérennante). Tuléar. Ile Maurice. Rencontrée fréquemment tout au long de la croisière de l'« *Anton Bruun* », dans les prélèvements horizontaux et verticaux, tant océaniques que néritiques.

Océan indien : Espèce courante.

Distribution mondiale : Espèce tropicale et sub-tropicale, occasionnellement tempérée, largement répandue dans les trois océans et en Méditerranée. Répartition verticale douteuse.

Quelle valeur attribuer aux dievrs taxons infra-spécifiques proposés par Jörgensen (1920), Böhm (1931a et b), et Peters (1934) ? Certains sont manifestement à rejeter pour raison de synonymie, ou parce qu'ils sont superflus; mais les autres demeurent assez embarrassants. S'agit-il de formes, de variétés, ou des deux ? Et quels sont leurs rapports mutuels ?

La variabilité du *C. declinatum* paraît en effet, dans son ensemble, plutôt désordonnée. La fragilité particulière de cette petite espèce serait, plus que l'influence des facteurs écologiques, la cause de cette plasticité. Il apparaît du moins qu'aucun des taxons infra-spécifiques ne dispose d'une distribution géographique propre; seule une différenciation saisonnière se manifeste, comme l'a montré Halim (1960) en Méditerranée (baie de Villefranche).

Tous les spécimens que j'ai récoltés dans le canal de Mozambique sont identifiables à la « f. *normale* Jörg. », ou très voisins de celle-ci. Les références bibliographiques de cette forme sont données ci-dessous, ainsi que, pour mémoire, celle des autres subdivisions de l'espèce. La synthèse reste à faire.

f. ***normale*** Jörgensen, 1911
Fig. 66, et pl. II, fig. 8

JÖRGENSEN, 1920; SCHILLER, 1937; RAMPI, 1939; WOOD, 1954 ?; HALIM, 1960, 1963.

= *C. declinatum* f. *orthoceras* Böhm.

BÖHM, 1931a, 1931b.

= *C. declinatum* subsp. *declinatum, sec.* Peters.

PETERS, 1934; STEEMANN NIELSEN, 1934; HALIM, 1960 (« var. *declinatum* Peters »).

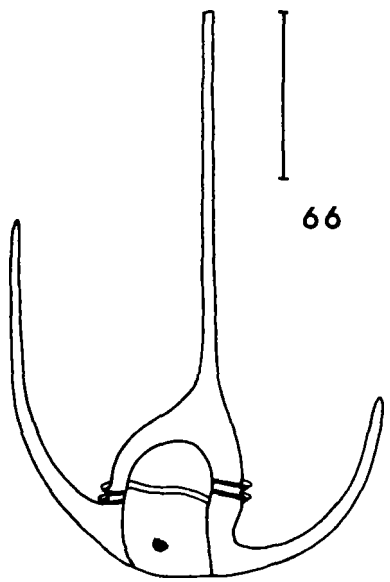


FIG. 66 : *Ceratium declinatum* f. ***normale*** Jörg.

Pour mémoire :

f. ***declinatum***

Il faut ainsi désigner le type de l'espèce, pour lequel JÖRGENSEN a créé illégalement le nom de « f. *debile* Jörgensen » :

JÖRGENSEN, 1920; SCHILLER, 1937; WOOD, 1954 (?).

f. ***brachiatum*** Jörgensen, 1920

JÖRGENSEN, 1920; BÖHM, 1931b; SCHILLER, 1937; RAMPI, 1939; WOOD, 1954; HALIM, 1960.

subsp. ***angusticornum*** Peters, et
subsp. ***laticornum*** Peters, 1934

PETERS, 1934; STEEMANN NIELSEN, 1934.

PETERS donne pour toutes diagnoses deux figures très schématiques et étonnamment ressemblantes, et de plus, pour ces deux sous-espèces, des répartitions géographiques très voisines. STEEMANN NIELSEN (1934) ne retient que la première, dont il semble ultérieurement (1939) vouloir faire une espèce distincte, tout en admettant que sa biologie est en tout point semblable à celle du « type » (f. *normale*).

Ces deux « sous-espèces » sont assez proches de la forme *brachiatum*.

var. ***majus*** Jörgensen, 1920

JÖRGENSEN, 1920; FORTI, 1924; PAULSEN, 1930; SCHILLER, 1937; HALIM, 1960.

(Fin de la première partie).

LE GENRE *CERATIUM* (PÉRIDINIEN PLANCTONIQUE) DANS LE CANAL DE MOZAMBIQUE CONTRIBUTION A UNE RÉVISION MONDIALE (FIN)

par A. SOURNIA

Ceratium contortum (Gourret) Cleve, 1900

GOURRET, 1883, p. 35, pl. 2, fig. 33 (?) : *C. gibberum* var. *contortum;* CLEVE, 1900a, p. 14, pl. 7, fig. 10 : « *C. contortum* Gourret ».

Incl. *C. longinum* Karsten, et *C. Karstenii* Pavillard.

On doit à GRAHAM et BRONIKOVSKY (1944) la réunion des trois espèces; toutefois une fusion partielle avait été proposée par PETERS (1934) qui rapprochait *C. longinum* et *C. Karstenii* sous le nom erroné de *C. arcuatum*. Au sujet de ce dernier nom, admettons comme définitif, à la suite des démonstrations de PAVILLARD (1907, 1923) et de PAULSEN (1930) que :

— *C. tripos* var. *arcuatum* Gourret est « l'ancêtre » du *C. euarcuatum* Jörg.

— *C. arcuatum* (Gourret) Cleve représente une autre espèce : c'est l'ancêtre du *C. Karstenii* Pav.

— Le nom de « *C. arcuatum* » (Gourret) Pav. » est à rejeter, car postérieur à *C. arcuatum* (Gourret) Vanhöffen.

— Le nom de « *C. arcuatum* Cleve » utilisé par PETERS (1934) et JÖRGENSEN (1920) est erroné, et doit être rejeté pour la même raison.

— En conclusion : le nom de *C. arcuatum*, sous toutes ses acceptions, doit être abandonné.

Revenons à notre espèce : j'ai pu, comme GRAHAM et BRONIKOVSKY, observer toutes les transitions entre les *Ceratium contortum, longinum, Karstenii* et leurs variétés, tels que définis par JÖRGENSEN (1911); aussi la réunion des trois « espèces » sous le nom le plus ancien me semble-t-elle inévitable.

Cependant, il est indispensable de distinguer et de pouvoir désigner les stades principaux de l'espèce, ce dont GRAHAM et BRONIKOVSKY ne nous ont pas laissé le moyen. Les types extrêmes sont en effet très dissemblables morphologiquement, et il n'est pas assuré que leur écologie soit uniforme.

Dans le présent cas, le choix et la délimitation des formes principales de l'espèce sont délicats, car la variabilité repose sur un ensemble de caractères morphologiques relativement autonomes : dimensions générales; diamètre et longueur des trois cornes; flexion de la corne apicale; direction des cornes antapicales (de la corne droite principalement). Un caractère général se dégage de cet ensemble, mais il est assez intuitif : *C. contortum* est plus ou moins « robuste ». Sous cet aspect, la variabilité de l'espèce évolue simplement entre deux types extrêmes. Mais des divergences se manifestent dans le détail. Aussi je propose de distinguer quatre variétés principales, et de désigner leurs transitions suivant le système exposé p. 382).

var. ***robustum*** (Karsten) Sournia, 1966
Fig. 72

KARSTEN, 1907, pl. 48, fig. 6 : *C. tripos arcuatum* Gourret var. *robustum*, et 1905 b, pl. 20, fig. 9, 13-15 : sous divers noms infraspécifiques de *C. tripos*.

= *C. Karstenii* var. *robustum* (Karsten) Jörgensen

JÖRGENSEN, 1911 (dont la fig. 118 représente, de l'aveu même de l'auteur (1920), un cas très particulier); *non* BALLANTINE, 1961.

= *Ceratium contortum* (Gourret) Cleve, *pro parte*

GRAHAM & BRONIKOVSKY, 1944 (fig. 18 e, *non al.*); *nec al.*

C'est le stade le plus « robuste » de l'espèce :

Cornes recouvertes de crêtes, du moins sur leurs parties basales. Cornes antapicales largement ouvertes, sub-parallèles (ou légèrement convergentes) dans leurs parties distales; recourbées toutes deux régulièrement, de façon analogue, et chacune selon un sens constant.

var. ***Karstenii*** (Pavillard) Sournia, 1966
Fig. 71 et Pl. III, fig. 10

= *Ceratium Karstenii* Pavillard, *pro parte*

PAVILLARD, 1907, p. 152, et 1923, p. 514; JÖRGENSEN, 1911 (fig. 116, *non*

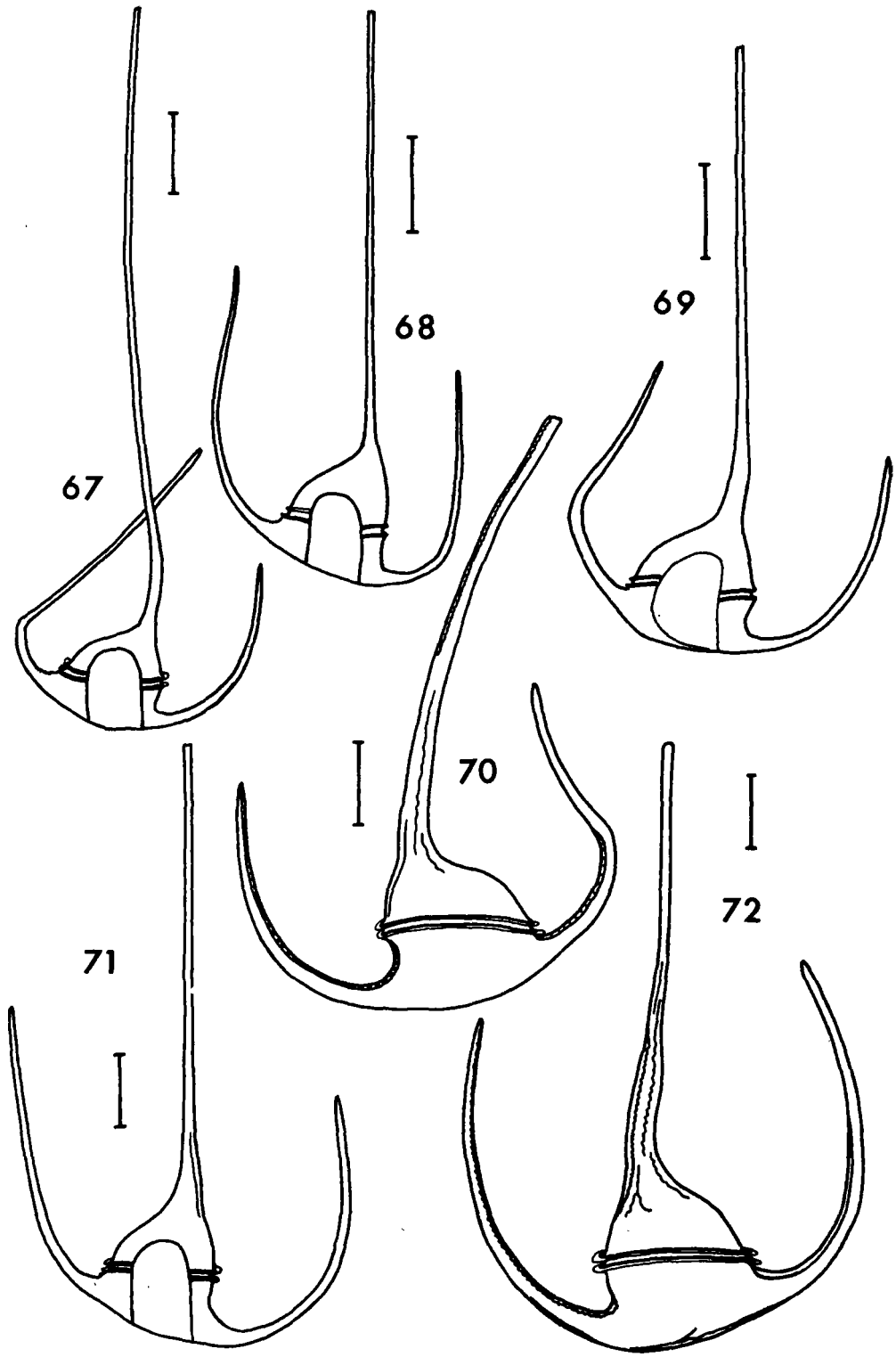


FIG. 67 : *Ceratium contortum* (Gourret) Cleve var. *contortum*. — 68 : *C. contortum* var. *longinum* (Karsten) Sournia. — 69 : *C. contortum* (Gourret) Cleve, « *contortum - Karstenii* ». — 70 : *C. contortum* (Gourret) Cleve, « *contortum - robustum* ». — 71 : *C. contortum* var. *Karstenii* (Pav.) Sournia. — 72 : *C. contortum* var. *robustum* (Karsten) Sournia.

117); PAULSEN, 1930 (fig. 52b, *vix* c, *non* a); ? STEEMANN NIELSEN, 1934 (*non* fig. 51); SCHILLER, 1937 (fig. 431a, *non* b, et 432a, *non* b); RAMPI, 1939; WOOD, 1954 (fig. 211a, *non* b); ? SILVA, 1955 (*non* pl. 8, fig. 1); HALIM, 1960.

= *Ceratium contortum* (Gourret) Cleve, *pro parte*

STEEMANN NIELSEN, 1934; GRAHAM & BRONIKOVSKY, 1944 (fig. 18*l*, *vix* g, *non al.*); SILVA, 1955. *non al.*

= *C. arcuatum* Cleve α *Karstenii* (Pavillard) Jörgensen

JÖRGENSEN, 1920; PETERS, 1934 (« f. *Karstenii* Pavillard »).

C'est le type « moyen » de l'espèce.

Cornes longues et fines, sub-parallèles dans leurs parties distales. Cornes antapicales régulièrement recourbées (la droite beaucoup moins que la gauche), chacune selon un sens constant.

var. ***longinum*** (Karsten) Sournia, 1966
Fig. 68

KARSTEN, 1905b, p. 143, pl. 21, fig. 18 : *C. tripos longinum.*

= *C. longinum* (Karsten) Jörgensen

JÖRGENSEN, 1911; OMAKURA, 1912; PAVILLARD, 1931; NIE, 1936; SCHILLER, 1937; WOOD, 1954.

= *C. contortum* (Gourret) Cleve, *pro parte*

GRAHAM & BRONIKOVSKY, 1944 (fig. 18i ?, *non al.*). *Nec al.*

= *C. Karstenii* Pavillard, *pro parte*

WOOD, 1954 (fig. 211b, *non* a). *Nec al.*

= *C. arcuatum* f. *longinum* (Karsten) Peters

PETERS, 1934.

Cellules plus délicates que chez la variété précédente. Corne apicale souvent beaucoup plus longue que les deux autres. Cornes généralement parallèles dans leurs parties distales. Corne antapicale gauche plus rapprochée que la droite de la corne apicale. Antapicales souvent flexueuses.

var. ***contortum***
Fig. 67

Cf. GOURRET, 1883; CLEVE, 1900a (références données plus haut).

= *C. contortum* (Gourret) Cleve, *pro parte*

OKAMURA, 1907; *vix* JÖRGENSEN, 1911; PETERS, 1934; STEEMANN NIELSEN, 1934, 1939; SCHILLER, 1937; GRAHAM & BRONIKOVSKY, 1944 (fig. 18f, h, j, n, *non al.*); WOOD, 1954 (*vix* fig. 212b-c, *non* a); SILVA, 1955.

= *C. saltans* Schröder = *C. contortum* var. *saltans* (Schr.) Jörgensen

SCHRÖDER, 1906; JÖRGENSEN, 1911; OKAMURA, 1912; BÖHM, 1931b; PAVILLARD, 1931; NIE, 1936.

C'est la forme la plus « délicate » de l'espèce, et aussi son type originel. Il est pratiquement impossible d'en distinguer la « var. *saltans* ». Notons que la description de JÖRGENSEN (1911) concerne un stade relativement robuste de cette variété et représente plutôt une transition entre celle-ci et la var. *Karstenii*.

Transitions entre les quatre variétés précédentes :
Fig. 69-70 et Pl. II, fig. 9

Les transitions les plus fréquemment rencontrées dans la bibliographie ainsi que dans mes récoltes se situent entre les variétés *Karstenii* et *contortum*. Quelques autres cas sont également observables.

1 — *C. contortum* (Gourret) Cl., « *contortum-Karstenii* »
Fig. 69

= *Ceratium subcontortum* Schröder, in SCHRÖDER, 1906, fig. 28 a-b.
= *Ceratium Karstenii* Pavillard, *in* : STEEMANN NIELSEN, 1934, fig. 51; JÖRGENSEN, 1911, fig. 117; PAULSEN, 1930, fig. 52a.

2 — *C. contortum* (Gourret) Cl., « *contortum-robustum* »
Fig. 70

= *C. contortum, in* WOOD, 1954, fig. 212 a.
= « *C. Karstenii* var. *robustum* (Pavillard) Jörgensen », *in* BALLANTINE, 1961, p. 225, *vix* fig. 54.

3 — *C. contortum* (Gourret) Cl., « *contortum-longinum* »

= « *C. contortum* Cleve » *in* GRAHAM & BRONIKOVSKY, 1944, fig. 18m.

4 — *C. contortum* (Gourret) Cl., « *longinum-Karstenii* »

= « *C. contortum* Cleve », *in* GRAHAM & BRONIKOVSKY, 1944, fig. 18k.

POUR LES QUATRE VARIÉTÉS ET LEURS TRANSITIONS

RÉCOLTES PERSONNELLES : Espèce très rare à Nossi-Bé, où quelques spécimens de la var. *Karstenii* seulement ont été récoltés. A Tuléar et à l'île Maurice, presque toutes les formes étaient représentées, à l'exception de la var. *robustum*, mais en nombre très réduit. Au cours de la croisière de l' « *Anton Bruun* » : var. *robus-*

tum très rare (parages de Durban); var. *Karstenii* présente à presque toutes les stations; var. *longinum, contortum,* et formes voisines, nettement océaniques, et seulement récoltées dans les prélèvements de surface.

OCÉAN INDIEN : Espèce très courante sous ses diversees formes.

DISTRIBUTION MONDIALE : *C. contortum, sensu lato,* est une espèce tropicale, assez rare en Méditerranée (où les variétés *Karstenii et robustum* prédominent). La répartition latitudinale semble homogène ,sauf dans le cas de la var. *robustum* qui, selon STEEMANN NIELSEN, serait plus tempérée — ce que mes observations confirmeraient. L'espèce est, dans l'ensemble, préférentiellement océanique et euphotique, mais, dans le détail, les diverses variétés présenteraient des adaptations particulières, difficiles actuellement à préciser du fait de confusions fréquentes. Ainsi STEEMANN NIELSEN attribue-t-il à la « f. *subcontortum* » une distribution géographique et verticale particulière, malheureusement la diagnose de cette forme est obscure.

Ceratium gibberum Gourret, 1883

GOURRET, 1883, p. 34, pl. 2, fig. 33-35.

La taxinomie de cette espèce est complexe; en effet, les caractères morphologiques sont très variables, et la conception originelle de GOURRET (une espèce type et deux variétés), ne pouvant rendre compte de cette variabilité, doit être abandonnée.

Très variables sont en effet : 1) la longueur et la direction des cornes antapicales, particulièrement chez la corne droite qui se trouve, dans les deux cas extrêmes, parallèle à la corne gauche, ou reployée perpendiculairement à celle-ci, 2) la longueur et l'inflexion basilaire de la corne apicale, 3) la convexité du contour postérieur de l'hypothèque, 4) l'ornementation lamellaire superficielle.

Le critère le plus apparent réside dans la direction de la corne antapicale droite, et c'est sur celui-ci que JÖRGENSEN (1920) fonde sa distinction entre les deux formes *dispar* et *subaequale.* Il est de fait probable que ces deux formes représentent les deux extrêmes d'une série de variations; dans cette hypothèse, je crois devoir élever au rang de variété la forme *dispar,* et, concernant la seconde, à laquelle JÖRGENSEN attribue indifféremment les deux rangs, la traiter également comme variété (et pour mémoire ici, puisque absente de mes récoltes). Les relations entre ces deux extrêmes restent à définir, car les stades de transition sont très peu connus. Enfin, sous son aspect écologique, la question reste entièrement à étudier.

Comme il est dit plus haut, la position de GOURRET ne peut être conservée : cet auteur représente en effet sous le nom de *C. gibberum* (*loc. cit.*, fig. 35 et 35a) deux cas morphologiques différents, l'un (35) s'apparentant, sans pouvoir lui être assimilé, à la variété *dispar*, l'autre (35a) correspondant à un stade de transition assez proche de la f. *subaequale*. En outre, le nom de var. *sinistrum* Gourret doit céder la place à celui de var. *dispar*, pour raison de priorité (JÖRGENSEN, 1920). Enfin, la var. *contortum* Gourret doit être rapportée soit au *C. contortum*, soit, comme le veut JÖRGENSEN, au *C. concilians*.

var. ***dispar*** (Pouchet) Sournia, 1966
Fig. 73

= *C. tripos* var. *dispar* Pouchet
POUCHET, 1883, p. 423, *vix* fig. D, et 1893, fig. 13b.

= *C. gibberum* f. *dispar* (Pouchet) Jörgensen
JÖRGENSEN, 1920; PETERS, 1934; STEEMANN NIELSEN, 1934; SCHILLER, 1937; RAMPI, 1939; GRAHAM & BRONIKOVSKY, 1944; KLEMENT, 1964.

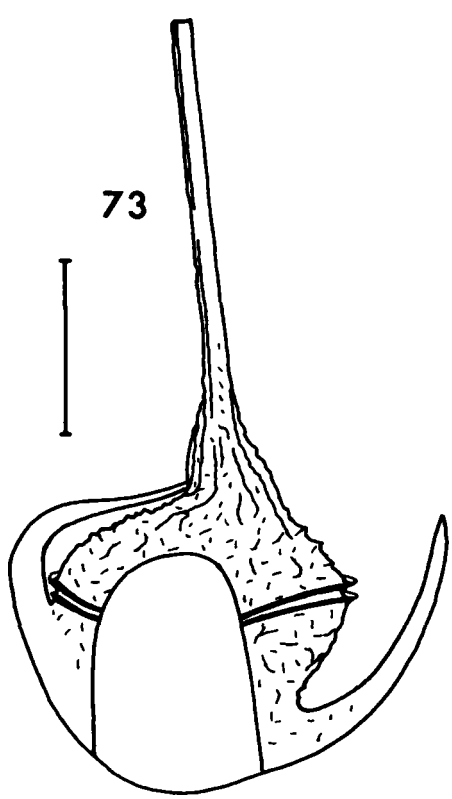


FIG. 73 : *Ceratium gibberum* var. *dispar* (Pouchet) Sournia.

= *C. gibberum* var. *sinistrum* Gourret = « *C. gibberum* f. *sinistrum* Gourret » *in plur. auct.*

GOURRET, 1883; JÖRGENSEN, 1911; OKAMURA, 1912; LEBOUR, 1925; NIE, 1936.

= *C. concilians* f. *dispar* (Pouchet) Böhm

BÖHM, 1931a et b.

= *C. gibberum* Gourret, *pro parte*

OKAMURA, 1907 (fig. 3d-e, *non al.*); WOOD, 1954; HALIM, 1960, *non* ? 1963. *Non* MANGIN, 1912, *nec* BÖHM, 1931a.

RÉCOLTES PERSONNELLES : Variété très rare dans les stations littorales (Tuléar, île Maurice; absente à Nossi-Bé), mais assez courante dans les stations océaniques du Nord du canal de Mozambique, à partir de la latitude de Nossi-Bé.

OCÉAN INDIEN : Assez courante.

DISTRIBUTION MONDIALE : Tropicale (Méditerranée incluse), océanique. Répartition verticale incertaine (euphotique ?).

Cette variété a pu cependant être largement confondue avec *C. concilians* (au sujet de cette espèce, voir plus loin).

Pour mémoire :

var. ***subaequale*** Jörgensen, 1920
Fig. 74

JÖRGENSEN, 1920, p. 70, fig. 68 (« *var.* » et « *f* »); PETERS, 1934, p. 44; SCHILLER, 1937, p. 398, fig. 437; GRAHAM & BRONIKOVSKY, 1944, p. 33, fig. 17f; WOOD, 1954, p. 290, fig. 214c.

= *C. gibberum* Gourret, *pro parte*

GOURRET, 1883 (*vix* fig. 35a, *non al.*); OKAMURA, 1907 (fig. 3a-c, *non al.*); PAULSEN, 1908 (fig. 98, droite, *non* fig. gauche); JÖRGENSEN, 1911; MANGIN, 1912 (formes α et β, *vix* forme γ); LEBOUR, 1925; BÖHM, 1931a.

Il est actuellement impossible de distinguer les répartitions respectives des deux variétés, du fait des trop nombreuses références incertaines sous le nom de « *C. gibberum* ».

Transitions entre les deux variétés précédentes :

Cette question reste à étudier. On ne peut en effet actuellement assurer l'existence d'une suite continue de transitions entre les deux variétés. Quelques stades seulement ont été décrits par :

— DADAY, 1888, pl. 1, fig. 12, 14(?), sous le nom de *C. tripos* var. *curvicorne*.

— MANGIN, 1912, p. 23, fig. 6 (*Ceratium gibberum* Gourret).

— GRAHAM et BRONIKOVSKY, 1944, fig. 17i (*C. concilians* Jörgensen).

— SILVA, 1949, p. 359, pl. 9, fig. 9 (*C. gibberum* Gourret).

Ces transitions, dont je n'ai pu personnellement observer d'exemples, sont à désigner, conformément au système proposé p. 382 sous l'expression : *C. gibberum* Gourret, « *dispar-subaequale* ».

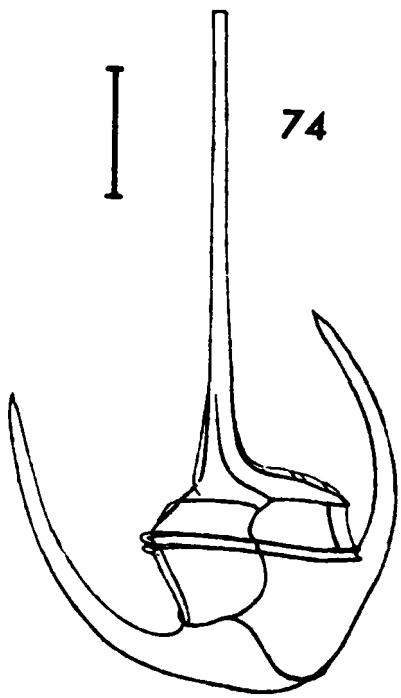


FIG. 74 : *Ceratium gibberum* var. *subaequale* Jörg.
In JÖRGENSEN, 1911, fig. 106.

Pour mémoire :

Ceratium concilians Jörgensen, 1920

JÖRGENSEN, 1920, p. 72, fig. 69; ? BÖHM, 1931b, p. 24, fig. 21; PETERS, 1934, p. 44, pl. 2, fig. 8; STEEMANN NIELSEN, 1934, p. 22, fig. 49, et 1939, p. 13; SCHILLER, 1937, p. 396, fig. 435; RAMPI, 1939, p. 306, fig. 36; GRAHAM & BRONIKOVSKY, 1944, p. 33, ? fig. 17h-i; WOOD, 1954, p. 290, ? fig. 213; HALIM, 1960, pl. 4, ? fig. 20, et 1963, p. 497, fig. 11.

= *C. concilians* f. *contortum* (Gourret) Böhm

BÖHM, 1931a.

Je ne suis pas certain d'avoir observé cette espèce dans mes récoltes, et doute de sa valeur spécifique. En effet, les critères donnés

par JÖRGENSEN comme distinctifs du *C. gibberum* me semblent peu sûrs :

Corne apicale incurvée à sa base. Contour antapical régulièrement convexe, peu saillant. Corne antapicale gauche plus éloignée du corps central que chez *C. gibberum*. Absence d'ornementation lamellaire superficielle.

J'ai pu effectivement observer dans mes récoltes quelques spécimens du *C. gibberum* qui se rapprochaient de cette description. Il est vraisemblable que tous les intermédiaires existent entre les deux « espèces » : WOOD (1954) l'admet (« transitions to *C. gibberum* occur »), ainsi que BÖHM (cet auteur considère les deux espèces comme deux formes du *C. concilians*).

Les distributions mondiales sont semblables dans les deux cas, quoique celle du *C. concilians* soit plus clairsemée. Les répartitions verticales, incertaines, ne s'opposent pas davantage.

L'autonomie de ces deux espèces reste donc à confirmer.

Ceratium lunula (Schimper *ex* Karsten) Jörgensen, 1911
Fig. 75-76

KARSTEN, 1905b, p. 142, pl. 20, fig. 12, *non al.* : *C. tripos lunula* Schimper; JÖRGENSEN, 1911, p. 51, pl. 5, fig. 112-115 : *Ceratium lunula* Schimper *in* Chun.

Sous divers noms d'auteur erronés : OKAMURA, 1912, p. 10, pl. 2, fig. 25-26; JÖRGENSEN, 1920, p. 74, fig. 70; BÖHM, 1931b, p. 30, fig. 26; WANG & NIE, 1932, p. 305, fig. 18; PETERS, 1934, p. 44, pl. 2, fig. 12c; STEEMANN NIELSEN, 1934, p. 23, fig. 50, et 1939, p. 15; NIE, 1936, p. 56, fig. 23; SCHILLER, 1937, p. 399, fig. 439; GRAHAM & BRONIKOVSKY, 1944, p. 33, fig. 17j-n; WOOD, 1954, p. 291, fig. 215; SILVA, 1955, p. 61, pl. 8, fig. 3-5. *Non* CHUN, 1900, p. 73, fig. a-b. *Nec* ZACHARIAS, 1906, p. 523, fig. 10.

L'origine de ce taxon est ténébreuse, et remonte vraisemblablement à un journal de bord manuscrit tenu par SCHIMPER au cours de la croisière de la « *Valvidia* », journal dont fait état KARSTEN (1905a, p. 136, et 1905b, p. 142). Le nom de « *Ceratium lunula* » a été employé sans nom d'auteur par CHUN, sur la foi de ce manuscrit. Des deux figures données par cet auteur (et reprises par ZACHARIAS, 1906), l'une (a) est très douteuse (*C. tripos* ?), l'autre (b) se rapporte au *C. gibberum*. La publication valide et effective revient donc à KARSTEN, qui attribue (quoique sans certitude) à SCHIMPER le nom de « *C. tripos lunula* ». Postérieurement enfin, JÖRGENSEN (1911) a élevé ce taxon au rang d'espèce.

RÉCOLTES PERSONNELLES : Centre du canal de Mozambique (rare).

OCÉAN INDIEN : Espèce répartie sporadiquement dans la zone tropicale et sub-tropicale, moins courante dans l'océan même que

dans les régions indonésiennes; bien connue cependant dans le canal de Mozambique (SILVA, 1956, 1960; TRAVERS, 1965). Les références de KARSTEN et de CZAPEK, citées par WOOD dans son index (1963a) sont douteuses.

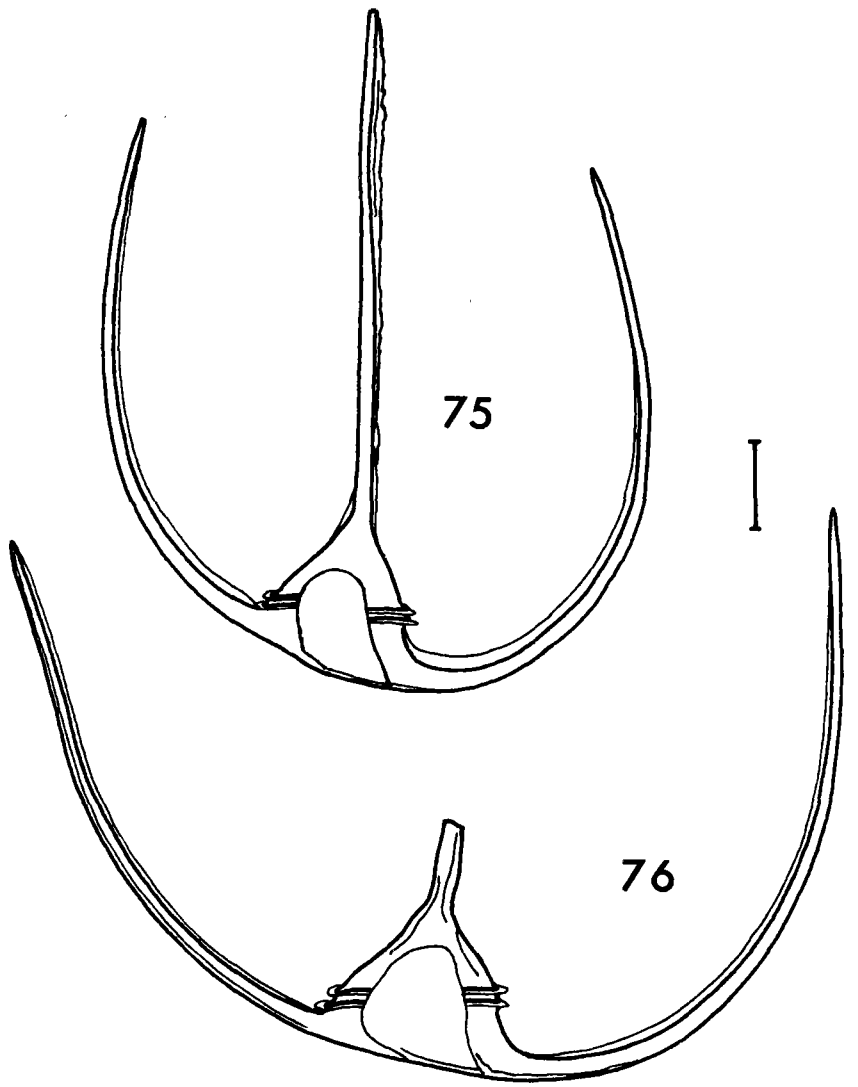


FIG. 75-76 : *Ceratium lunula* (Karsten) Jörg.

DISTRIBUTION MONDIALE : Espèce tropicale, assez rare en Méditerranée. Oligophotique. Réputée océanique, quoique sa distribution dans l'Océan indien soit plutôt du type néritique.

Les deux formes *brachyceros* et *megaceros* de JÖRGENSEN, basées sur les longueurs relatives des cornes antérieure et posté-

rieures, ne font que traduire la situation des cellules dans une même chaîne; aussi n'ont-elles pas lieu d'être conservées.

Ceratium Carnegiei Graham et Bronikovsky, 1944
Fig. 77 et Pl. III, fig. 11

GRAHAM & BRONIKOVSKY, 1944, p. 34, fig. 18a-c; GAARDER, 1954, p. 10, fig. 11.

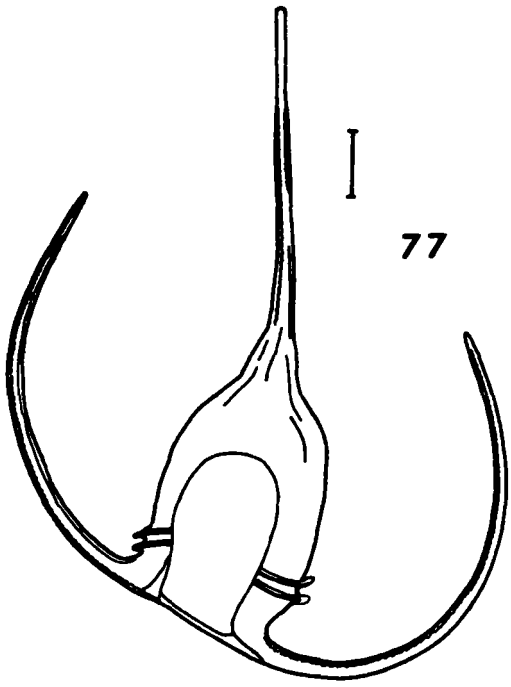


FIG. 77 : *Ceratium Carnegiei* Graham & Bron.

RÉCOLTES PERSONNELLES : Un seul spécimen, au Nord des Comores (filet vertical).

OCÉAN INDIEN : Espèce nouvelle pour cet océan.

DISTRIBUTION MONDIALE : Cette espèce n'est connue que par les deux auteurs cités ci-dessus : quatre stations dans le Pacifique tropical (GRAHAM et BRONIKOVSKY), et une station dans l'Atlantique tempéré, au Sud des Açores (GAARDER).

Au total, compte tenu de l'observation personnelle rapportée ci-dessus, *Ceratium Carnegiei* est connu, quoique très rare, dans les trois grands océans.

GRAHAM et BRONIKOVSKY donnent trois figures de cette espèce; l'une d'elles (18a) rappelle quelque peu le *C. longipes* var. *ventri-*

cosum Ostf. (cf. OSTENFELD, 1903; PAULSEN, 1908; JÖRGENSEN, 1911). Le spécimen que j'ai observé est identique à celui de la figure 18 c de GRAHAM et BRONIKOVSKY, mais, par son aire ventrale plus développée, s'accorde davantage encore à la description de GAARDER.

Ceratium platycorne Daday, 1888

DADAY, 1888, p. 101, pl. 3, fig. 1-2.
Incl. *C. compressum* Gran.

Les deux espèces ont été réunies dès 1912 par GRAN (voir aussi HJORT, 1911) qui a montré, au terme de l'expédition du « *Michael Sars* » dans l'Atlantique nord, que *C. platycorne* et *C. compressum* traduisent l'adaptabilité à la flottaison d'une espèce unique.

Ce rapprochement est d'autant plus digne de foi qu'il est proposé par l'auteur même du *C. compressum*. Cependant, la plupart des Systématiciens, sans s'opposer expressément à cette conception, affectent de l'ignorer (s'ils ne l'ignorent pas effectivement), ou la traitent de façon allusive.

Nommons pour mémoire le *C. lamellicorne*, dont les caractères sont intermédiaires, et qui de ce fait a été rapproché tantôt du *C. compressum*, tantôt du *C. platycorne*.

JÖRGENSEN (1911) mentionne seulement une ressemblance entre les deux espèces, puis (1911b) une parenté étroite, enfin (1920) crée un « *C. platycorne* var. *compressum* (Gran) » sans justifier malheureusement d'un seul mot cette innovation, peut-être parce qu'il n'a pas récolté cette variété en Méditerranée. OSTENFELD (1931) désigne en toutes lettres le *C. compressum* comme une race nordique du *C. lamellicorne*. Le seul argument que puisse opposer PAVILLARD (1931, 1936, 1937) est que *C. compressum* se présente sous un type morphologique constant, et à la même époque de l'année, dans la mer de Monaco. Enfin, GRAHAM & BRONIKOVSKY (1944), qui n'ont récolté qu'un seul spécimen de cette dernière espèce, considèrent celle-ci comme distincte et ne mentionnent aucune affinité avec *C. platycorne*.

La position de SCHILLER (1937) n'est pas claire : cet auteur inclut *C. compressum* dans la liste des synonymes de *C. platycorne* (p. 409), mais par ailleurs (p. 390) traite distinctement la première espèce, tout en se référant dans les deux cas à l'iconographie de JÖRGENSEN (1911). Il faut donc penser à une méprise de SCHILLER et, compte tenu de plus d'une omission, lire p. 409, ligne 8 : « *non C. compressum* Gran : JÖRGENSEN, 1911, T. 3... » au lieu de : « *C. compressum* Gran, 1911, T. 3... ».

La variabilité du *C. platycorne, sensu lato,* semble essentiellement porter sur la largeur des cornes antapicales. Il est en effet délicat de prendre en considération la forme de la partie terminale de celles-ci, qui

a pu être lésée en cours de prélèvement — comme c'est probablement le cas pour le type de DADAY, ainsi que pour le « *Ceratium* sp. » de SILVA (1949) — ou se trouver autotomisée, ou en voie de régénération. Par ailleurs, la forme de l'épithèque, et la longueur de la corne apicale, semblent sujettes à des variations « désordonnées ». Aussi faut-il abandonner les noms de f. α *incisum* et var. *cuneatum* de JÖRGENSEN.

Je propose finalement de distinguer en la présente espèce deux variétés : l'une thermophile, à cornes postérieures larges et aplaties, correspondant au type originel de l'espèce. L'autre psychrophile, à cornes postérieures tubuliformes, déjà nommée var. *compressum* par JÖRGENSEN, et qui sera traitée ici pour mémoire. Les nombreuses transitions, qui correspondent pour la plupart aux « *C. dilatatum* » et « *C. lamellicorne* », seront désignées conformément au système proposé p. 382.

Enfin, d'après ce qui précède, la section *Platycornia* Jörg. n'a plus de raison d'être : *C. platycorne, sensu lato,* peut être intégré sans difficulté à la sect. *Tripos.*

var. ***platycorne***
Fig. 78

= *Ceratium platycorne* Daday, *sensu stricto*

DADAY, 1888; PAULSEN, 1908; JÖRGENSEN, 1911, 1920; SCHRÖDER, 1911; LEBOUR, 1925; STEEMANN NIELSEN, 1934; GRAHAM & BRONIKOVSKY, 1944 (fig. 19d-f, *non al.*); SILVA & PINTO, 1948; WOOD, 1954.

= *C. platycorne* f. *normale* Gran, *pro parte*

HJORT, 1911 (fig. 13/3, *non* 2); GRAN, 1912 (fig. 228/3, *non* 2).

= *C. platycorne* f. α *incisum* Jörgensen

JÖRGENSEN, 1920; BÖHM, 1931a. *Non* RAMPI, 1942.

= *C. platycorne* var. *cuneatum* Jörgensen = f. *cuneatum* (Jörgensen) Jörgensen

JÖRGENSEN, 1911, 1920; SCHILLER, 1937; RAMPI, 1942 et 1951b.

RÉCOLTES PERSONNELLES : Rare : Tuléar, et au large de Beira.

OCÉAN INDIEN : Cette variété y est très sporadiquement répandue. Dans le canal de Mozambique, seulement connue antérieurement par TRAVERS (1965).

DISTRIBUTION MONDIALE : Tropicale ou sub-tropicale, peu courante, oligophotique (?), et préférentiellement océanique.

Pour mémoire :

var. ***compressum*** (Gran) Jörgensen, 1920

Jörgensen, 1920, p. 79 et 81.

= *Ceratium compressum* Gran

Gran, 1902; Paulsen, 1908; Jörgensen, 1911, 1911b; Lebour, 1925; Pavillard, 1931; Schiller, 1937; Graham & Bronikovsky, 1944; Wood, 1954.

Variété psychrophile : mers froides des deux hémisphères. Plus rare dans les mers tempérées et en Méditerranée.

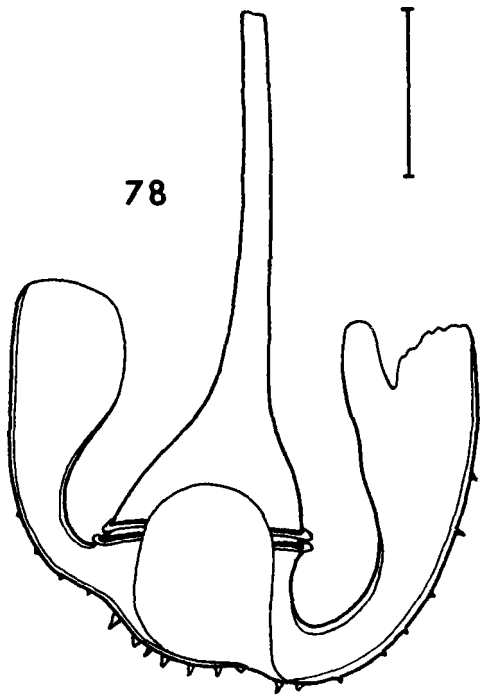


Fig. 78 : *Ceratium platycorne* Daday var. *platycorne*.

Transitions entre les deux variétés précédentes
Fig. 79

Je n'ai personnellement pas observé de formes de transition dans le canal de Mozambique. La bibliographie en montre cependant de nombreux exemples, que je désignerai sous l'expression : *C. platycorne* Daday, « *platycorne-compressum* » :

= *C. tripos* f. *dilatatum* Karsten = *C. dilatatum* (Karsten) Kofoid = *C. platycorne* var. (f.) *dilatatum* (Karsten) Jörgensen = *C. platycorne* subsp. *dilatatum* (Karsten) St. Nielsen.

KARSTEN, 1905a; KOFOID, 1907d; JÖRGENSEN, 1920; STEEMANN NIELSEN, 1934, 1939; SCHILLER, 1937.

= *Ceratium lamellicorne* Kofoid

KOFOID, 1908a et b; JÖRGENSEN, 1911 et 1911b; LEBOUR, 1925.

= *C. platycorne* f. *normale* Gran : *in* GRAN, 1912 (fig. 228/2, *non* 3).

= *C. platycorne* Daday : *in* GRAHAM & BRONIKOVSKY, 1944, fig. 19c, g. *non al.*

= *C. platycorne* f. *incisum* Jörg. : *in* RAMPI, 1942, p. 223, fig. 3.

= *Ceratium sp.* : *in* SILVA, 1949, p. 357, pl. 6, fig. 23, et pl. 9, fig. 3.

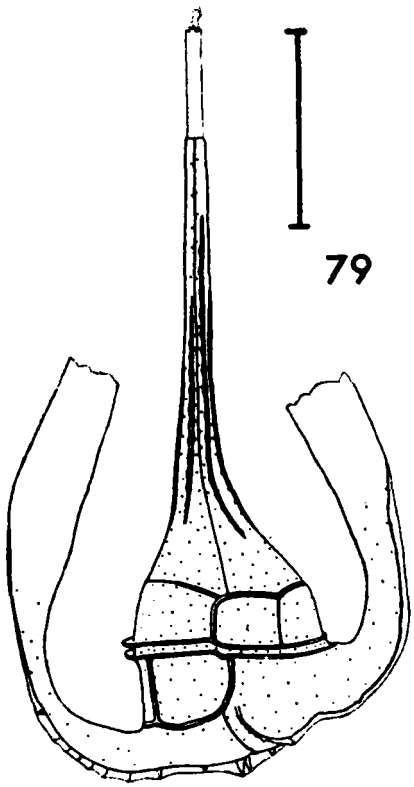


FIG. 79 : *Ceratium platycorne* Daday, « *platycorne - compressum* ». *In* KOFOID, 1908*a*, fig. 28.

Voici de plus, pris également dans la bibliographie, deux exemples de : *C. platycorne* Daday, « *compressum* > *platycorne* » :

— STEEMANN NIELSEN, 1934, fig. 57, sous le nom de *C. platycorne* var. *dilatatum* (Karsten) Jörgensen.

— GRAHAM & BRONIKOVSKY, 1944, fig. 19c (*C. platycorne* Daday).

SECT. *DENSA* JÖRGENSEN

Ceratium dens Ostenfeld & Schmidt, 1901
Fig. 80

OSTENFELD & SCHMIDT, 1901, p. 165, fig. 16; KARSTEN, 1907, p. 414, pl. 48, fig. 8a-b; JÖRGENSEN, 1911, p. 31, pl. 3, fig. 58; SCHILLER, 1937, p. 381, fig. 420; STEEMANN NIELSEN, 1934, p. 15, fig. 27, et 1939, p. 9; NIE, 1936, p. 44, fig. 14; WOOD, 1954, p. 284, fig. 204.

RÉCOLTES PERSONNELLES : Nossi-Bé, très rare (observée une seule fois, sous la forme d'une chaîne d'une quinzaine d'individus).

OCÉAN INDIEN : Mer Rouge, golfe d'Aden, mer d'Arabie, Seychelles, canal de Mozambique, Indonésie.

DISTRIBUTION MONDIALE : Espèce donnée par STEEMANN NIELSEN comme typiquement tropicale et néritique. Elle est très peu connue en dehors de l'Océan indien et du Sud-Ouest asiatique; rencontrée

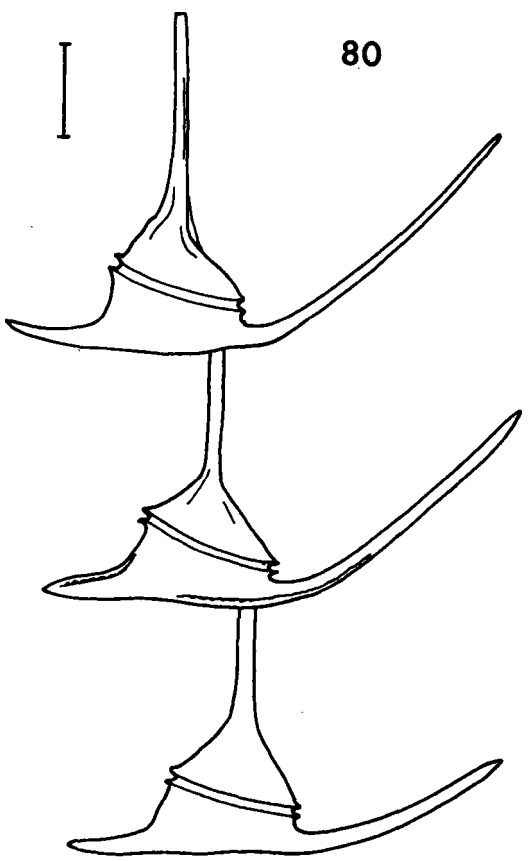


FIG. 80 : *Ceratium dens* Ostf. & Schm.

dans les parages de la côte orientale de l'Australie, elle y jouerait le rôle d'espèce indicatrice des courants (WOOD); plus à l'Est dans le Pacifique, elle n'est reportée que par PAVILLARD (1935) à proximité des îles Marquises. *C. dens* demeure inconnu dans l'Atlantique et en Méditerranée.

SECT. *LIMULUS* JÖRGENSEN

Ceratium limulus (Gourret *ex* Pouchet) Gourret, 1883
Pl. I, fig. 5

POUCHET, 1883, p. 424, pl. 18-19, fig. 4 : *C. tripos* var. *limulus;* GOURRET, 1883, p. 33, pl. 1, fig. 7; PAVILLARD, 1907, p. 149; OKAMURA, 1907, p. 127, pl. 3, fig. 8, et 1912, p. 11; JÖRGENSEN, 1911, p. 57, pl. 6, fig. 122, et 1920, p. 77, fig. 72; BÖHM, 1931a, p. 361, fig. 13-14, et 1931b, p. 31, fig. 27b; PETERS, 1934, p. 46, pl. 1, fig. 6; STEEMANN NIELSEN, 1934, p. 24, fig. 54, et 1939, p. 13; SCHILLER, 1937, p. 407, fig. 448; RAMPI, 1939, p. 307, fig. 19; GRAHAM & BRONIKOVSKY, 1944, p. 35, fig. 19a; SILVA, 1949, p. 360, pl. 9, fig. 10; WOOD, 1954, p. 296, fig. 223; HALIM, 1960, pl. 4, fig. 14.

RÉCOLTES PERSONNELLES : Tuléar. Centre du canal de Mozambique (rare).

OCÉAN INDIEN : Espèce sporadique mais assez courante.

DISTRIBUTION MONDIALE : Espèce tropicale ou sub-tropicale, plutôt océanique. Répartition verticale incertaine, peut-être euphotique.

Au sujet de la nomenclature de cette espèce, une précision : les conditions de publication des deux mémoires de GOURRET et de POUCHET ont été telles que chacun des deux auteurs a pu citer le travail de l'autre : POUCHET, dont le mémoire a paru le premier, a publié le nom de « *C. tripos* var. *limulus* » qui figurait dans le manuscrit que GOURRET lui avait communiqué. Ce dernier, se corrigeant lui-même, a publié peu après le nom de « *C. limulus* ». En application du Code de nomenclature (LANJOUW *et al.*, 1961, recom. 46c), le nom de l'espèce doit donc s'écrire comme ci-dessus, ou abrégé comme suit : *C. limulus* (Pouchet) Gourret.

Ceratium paradoxides Cleve, 1900
Pl. I, fig. 4

CLEVE, 1900a, p. 15, pl. 7, fig. 14; JÖRGENSEN, 1911, p. 57, pl. 6, fig. 123, et 1920, p. 79, fig. 73; PETERS, 1934, p. 47; STEEMANN NIELSEN, 1934, p. 24, fig. 55, et 1939, p. 13; SCHILLER, 1937, p. 408, fig. 449; GRAHAM & BRONIKOVSKY, 1944, p. 36, fig. 19b; WOOD, 1954, p. 296, et 1963b, p. 40, fig. 147; SILVA, 1955, p. 62, pl. 8, fig. 6.

RÉCOLTES PERSONNELLES : Au Nord des îles Comores. Au large du Kénya. Rare, et seulement dans les récoltes verticales.

OCÉAN INDIEN : Espèce rare. Dans la région du canal de Mozambique, seulement signalée jusqu'ici par STEEMANN NIELSEN (1939) dans le secteur même où je l'ai récoltée.

DISTRIBUTION MONDIALE : Espèce tropicale ou sub-tropicale, très clairsemée. Rare en Méditerranée. A la différence de *C. limulus*, c'est très nettement une espèce d'ombre. (STEEMANN NIELSEN, 1934, p. 45, mentionne par erreur sans doute le *C. paradoxides* parmi les espèces de suface, car il développe ailleurs l'opinion contraire : *ibid.*, p. 24, et 1939, p. 13).

SECT. *PALMATA* (PAVILLARD) JÖRGENSEN

Ceratium ranipes Cleve, 1900
Fig. 81-82

CLEVE, 1900a, p. 15, pl. 7, fig. 1; JÖRGENSEN, 1920, p. 82, fig. 76; BÖHM, 1931a, p. 361, et 1931b, p. 31, fig. 28-31; PETERS, 1934, p. 47, pl. 2,

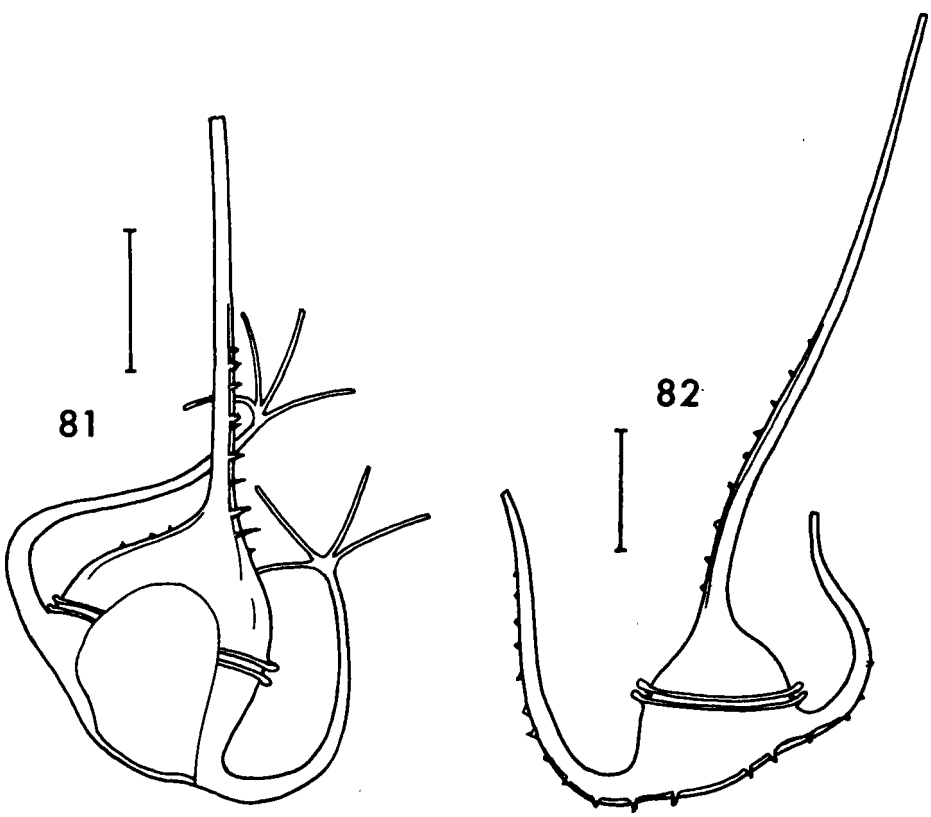


FIG. 81-82 : *Ceratium ranipes* Cleve

fig. 12d-e; STEEMANN NIELSEN, 1934, p. 24, fig. 58, et 1939, p. 13; SCHILLER, 1937, p. 409, fig. 451; GRAHAM & BRONIKOVSKY, 1944, p. 37, fig. 19i-k, 20, 21a; WOOD, 1954, p. 299, fig. 227; SILVA, 1955, p. 62, pl. 9, fig. 1; HALIM, 1960, pl. 4, fig. 16, et 1963, p. 498, fig. 26.

= *Ceratium palmatum* (Schröder) Schröder = *C. tripos* f. *palmatum* Schröder. = *C. ranipes* var. *palmatum* (Schröder) Jörgensen

SCHRÖDER, 1901, 1906; KARSTEN, 1907; JÖRGENSEN, 1911, 1920; OKAMURA, 1912; BÖHM, 1931a et b; SCHILLER, 1937; RAMPI, 1939; KLEMENT, 1964.

= *C. palmatum* var. *furcellatum* (Lemmermann) Jörgensen = *C. tripos* var. *furcellatum* Lemmermann

LEMMERMANN, 1899; JÖRGENSEN, 1911; BÖHM, 1931b.

RÉCOLTES PERSONNELLES : Tuléar. Centre du canal de Mozambique.

OCÉAN INDIEN : Espèce assez courante.

DISTRIBUTION MONDIALE : Espèce tropicale et sub-tropicale, préférentiellement océanique, et largement répandue dans les trois océans et en Méditerranée. Oligophotique.

La variabilité de cette espèce est considérable (voir entre autres les iconographies de BÖHM (1931b) et de GRAHAM & BRONIKOVSKY; elle porte non seulement sur la forme, la direction et le nombre des « doigts », mais aussi sur la longueur, le diamètre et la direction des « bras ». Cette variabilité doit jusqu'à nouvel ordre être considérée comme « désordonnée », ou du moins sans fondement écologique évident. Les formes « sans doigts », quoi qu'en dise PAULSEN (1930), ne sont d'ailleurs pas exceptionnelles : cf JÖRGENSEN, PAVILLARD (1916) et ma figure 82.

SECT. *MACROCEROS* OSTENFELD

Ceratium macroceros (Ehrenberg) Vanhöffen, 1897

EHRENBERG, 1840, p. 201 (?) : *Peridinium macroceros;* VANHÖFFEN, 1897, p. 310, 382, pl. 5, fig. 10 : *Ceratium macroceros* Clap. & Lachmann; CLARAPÈDE & LACHMANN, 1859, p. 397, 481, pl. 19, fig. 1 : « *C. tripos* var. α *Per. macroceros* Ehr. » et « *Ceratium tripos* var. *macroceros* »; CLEVE, 1900d, p. 227 : *Ceratium macroceros* Ehrenberg.

La priorité du nom spécifique revient bien à VANHÖFFEN, comme il apparaît *in* BÖHM, STEEMANN NIELSEN, etc., et non à CLEVE comme l'écrivent certains auteurs.

Il est bien établi aujourd'hui que le type de cette espèce est psychrophile, mais qu'une forme voisine le remplace dans les mers chaudes. La distinction, tant morphologique que géographique, est si nette que JÖRGENSEN a fait du substitut thermophile une sous-

espèce et non une variété; il me semble cependant que le second terme convient mieux, et qu'il s'agit ici d'un cas typique de « variabilité thermique » dont nous avons déjà vu maints exemples (voir aussi p. 382). SCHILLER (1937) et HALIM (1960) ont d'ailleurs avant moi effectué cette modification, toutefois sans la justifier, ce qui peut laisser croire à une méprise (chez SCHILLER en effet les désignations infra-spécifiques se trouvent fréquemment interverties).

La variété psychrophile — puisque variété il y a — correspond au type de l'espèce, et doit de ce fait être appelée var. *macroceros* (traitée ici pour mémoire, puisqu'absente de mes récoltes); rappelons que GRAHAM & BRONIKOVSKY (1944) ont créé, sous la même acception, le terme « subsp. *macroceros* n. subsp. », en partie illégal (cf. p. 383).

Pour la variété thermophile, j'ai proposé (1966) le nom de var. *gallicum* (Kofoid) Sournia.

Quant aux stades de transition, bien qu'ils soient assez rares dans le cas présent, il importe cependant de pouvoir les nommer, ce pour quoi je propose l'expression : *C. macroceros* (Ehr.) Vanh., « *macroceros-gallicum* ».

Pour mémoire :

var. ***macroceros***

Fig. 83

= *Ceratium macroceros* (Ehr.) Vanhöffen, *stricto sensu*

OSTENFELD & SCHMIDT, 1901; OKAMURA, 1907, PAULSEN, 1908; JÖRGENSEN, 1911; LEBOUR, 1925 (*vix* pl. 35); OSTENFELD, 1931; SCHILLER, 1937; GRAHAM & BRONIKOVSKY, 1944, WOOD, 1954; KLEMENT, 1964.

= *C. macroceros* var. *hainanense* Nie : NIE, 1936.

Absente de mes récoltes, cette variété l'est peut-être également de l'océan indien : si divers auteurs cependant la signalent (cf. index de WOOD, 1963a, et SILVA, 1956, 1960, TRAVERS, 1965), peu d'entre eux la décrivent ou la figurent, et dans ce dernier cas l'identification est douteuse : BALLANTINE (1961, p. 225, fig. 56) semble avoir vu sous le nom de « *C. macroceros* » la variété *gallicum*. KARSTEN d'autre part (1907, pl. 49, fig. 26, et pl. 51, fig. 11) mentionne « *C. tripos* var. *macroceros* » mais il s'agit du *C. deflexum*. Il est finalement probable que la plupart des références se rapportent à la variété *gallicum* (1); rappelons en ce sens que STEEMANN NIELSEN (1939) signale, pour l'océan indien et le sud-ouest asiatique, cette variété seulement et non le type.

Au reste, la var. *macroceros* est nettement tempérée et subboréale (très rare en Méditerranée : PAULSEN, 1930 ?, et FORTI, 1922). GRAHAM

(1) J'ai moi-même fait figurer par erreur cette variété dans un inventaire préliminaire du plancton de l'île Maurice (SOURNIA, 1965) : il s'agissait là d'une transition entre les deux variétés.

& BRONIKOVSKY ont posé le problème de sa bipolarité : la forme que ces auteurs ont rencontrée dans le Pacifique sud, et celle que PETERS signale dans l'Atlantique sud, sont-elles semblables au type de l'Atlantique nord ?

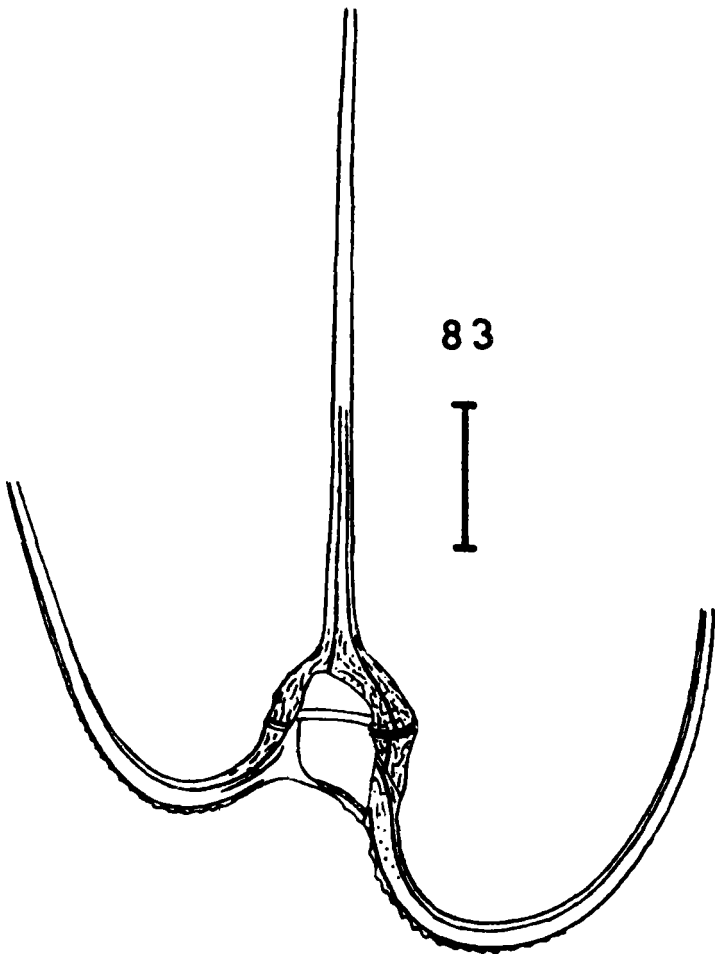


FIG. 83 : *Ceratium macroceros* (Ehr.) Vanh. var. *macroceros*. *In* JÖRGENSEN, 1911, fig. 133.

var. ***gallicum*** (Kofoid) Sournia, 1966
Fig. 84

SCHILLER, 1937, p. 430, fig. 469. *Vix* RAMPI, 1939, p. 310, fig. 42 : chez ces deux auteurs, sous le nom erroné de « var. *gallicum* (Kofoid) Jörgensen ».

= *C. macroceros* subsp. *gallicum* (Kofoid) Jörgensen

JÖRGENSEN, 1911, 1920; FORTI, 1924; ABÉ, 1927; PAULSEN, 1930; BÖHM, 1931b; STEEMANN NIELSEN, 1934, 1939; GRAHAM & BRONIKOVSKY, 1944;

WOOD, 1954; HALIM, 1963 (« f. *gallicum* (Kof.) Jörg. »).

= *Ceratium gallicum* Kofoid

KOFOID, 1907c, 1908a.

? = *C. macroceros* var. *Karstenii* Abé : ABÉ, 1927.

Diffère du type par les caractères suivants :

Cellule plus petite et plus délicate. Cingulum souvent peu apparent ou imparfaitement développé. Cornes antapicales, à leur origine, très peu divergentes entre elles, la base de la corne gauche étant presque parallèle à l'axe apical. Partie basale de ces deux cornes faisant, avec la partie médiane, un angle très brusque, ce caractère étant plus accentué chez la corne droite pour laquelle cet angle est égal ou inférieur à 90° (chez var. *macroceros :* angle supérieur à 90°). Epines et crêtes très réduites ou absentes.

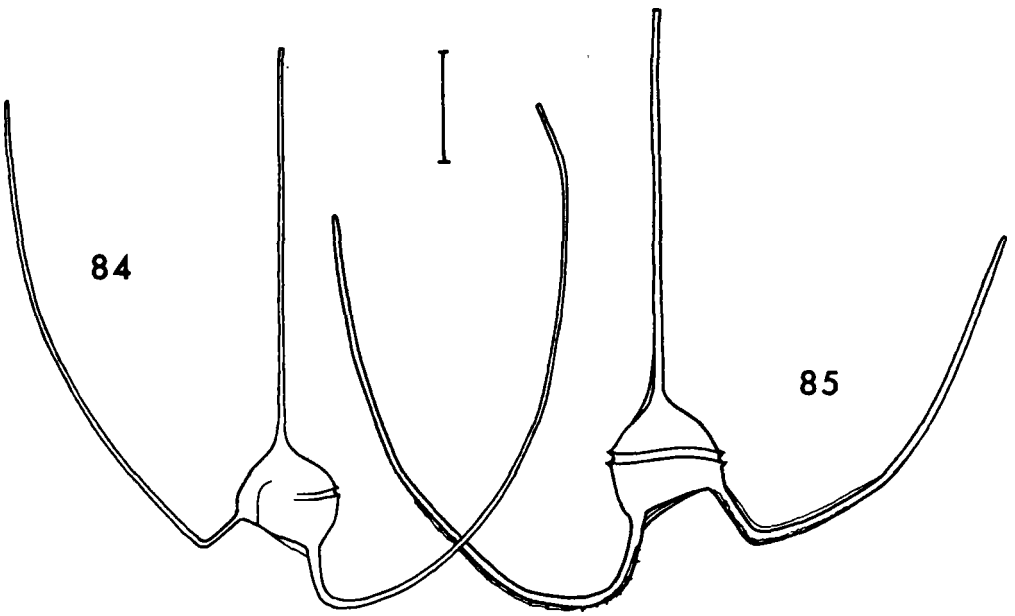


FIG. 84 : *Ceratium macroceros* var. *gallicum* (Kofoid) Sournia. — 85 : *C. macroceros* (Ehr.) Vanh., « *gallicum* > *macroceros* ».

RÉCOLTES PERSONNELLES : Variété rare à Nossi-Bé, où elle est plutôt estivale. Tuléar. Ile Maurice. Au cours de la croisière de l' « *Anton Bruun* », cette variété était largement représentée du Nord au Sud du canal de Mozambique, tant dans les prélèvements horizontaux que verticaux.

OCÉAN INDIEN : Variété courante, quoique le plus souvent désignée sous le nom spécifique, et sous réserve de quelques confusions possibles (voir var. *macroceros*).

DISTRIBUTION MONDIALE : Tropicale et sub-tropicale (Méditerranée incluse). Océanique. Répartition verticale uniforme.

Transitions entre les deux variétés précédentes : Fig. 85

En voici quelques exemples, pour lesquels j'ai proposé plus haut l'expression : *C. macroceros* (Ehr.) Vanh., « *macroceros-gallicum* » :

ABÉ, 1927, fig. 44a-d (*C. macroceros*).
PAULSEN, 1930, fig. 54a-b, *vix* c (*C. macroceros* subsp. *gallicum*).
WANG, 1932, fig. 29 (*C. macroceros*).
GRAHAM & BRONIKOVSKY, 1944, fig. 21f (*C. macroceros*).

Ceratium deflexum (Kofoid) Jörgensen, 1911
Fig. 86

KOFOID, 1907c, p. 304, pl. 24, fig. 13-15 : *C. macroceros* subsp. *deflexum;* JÖRGENSEN, 1911, p. 64, pl. 7, fig. 138; OKAMURA, 1912, p. 12, pl. 2, fig. 20; BÖHM, 1931b, p. 37, fig. 33-34; STEEMANN NIELSEN, 1934, p. 25, fig. 63, et 1939, p. 14; NIE, 1936, p. 63, fig. 29; SCHILLER, 1937, p. 428, fig. 467a, *non* b; GRAHAM & BRONIKOVSKY, 1944, p. 39, fig. 22c-d; WOOD, 1954, p. 310, fig. 237.

RÉCOLTES PERSONNELLES : Nossi-Bé (rare). Tuléar. Diverses stations océaniques et néritiques dans le canal de Mozambique.

OCÉAN INDIEN : Espèce assez peu signalée, car probablement confondue par certains auteurs avec *C. macroceros*. Très abondante cependant, selon STEEMANN NIELSEN (1934).

RÉPARTITION MONDIALE : Espèce tropicale, de surface; indifféremment océanique et néritique : sur ce point, STEEMANN NIELSEN (1939) est revenu sur sa première opinion (1934).

C. deflexum est-il confiné à l'Indo-Pacifique ? PETERS (1934), qui fait de cette espèce une forme de *C. massiliense,* l'aurait récoltée dans l'Atlantique. Toutefois, cet auteur ne donnant ni description ni figure, GRAHAM & BRONIKOVSKY pensent qu'il s'agit effectivement de la forme de cette dernière espèce qu'ils décrivent dans leur travail (p. 38, fig. 22 h), mais non du *C. deflexum* lui-même. D'autre part, PAVILLARD (1931, p. 92) aurait observé *C. deflexum* en diverses stations de l'Atlantique tempéré et tropical, mais précise « Détermination un peu douteuse en raison des ressemblances avec *C. macroceros* ou avec *C. carriense* ». Le même auteur (1937) doute pareillement de ses récoltes dans la mer de Monaco. Plus récemment enfin,

TRAVERS (1962) signale cette espèce dans le golfe de Marseille, sans insister sur l'intérêt de cette découverte, et précisant qu'un seul spécimen a été observé.

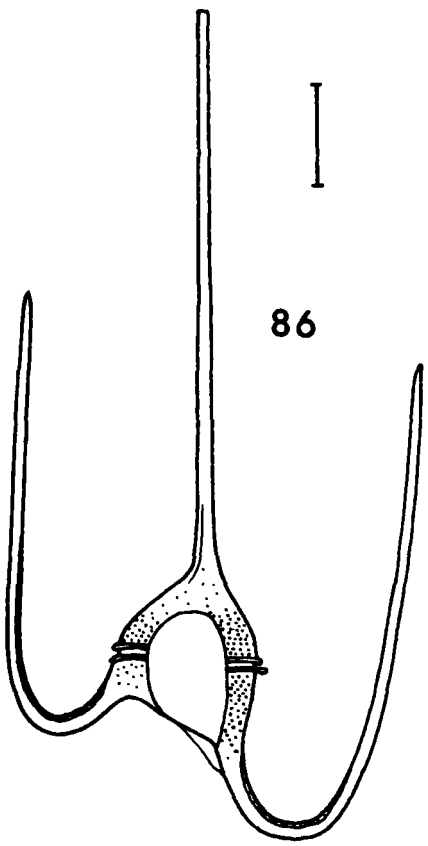


FIG. 86 : *Ceratium deflexum* (Kofoid) Jörg.

A propos de la forme *recurvatum* (Schröder) Jörgensen (= *C. recurvatum* Schröder) que je n'ai pu examiner, il semble préférable de la maintenir au rang de forme plutôt que d'en faire un synonyme de l'espèce comme le voudrait SCHILLER (1937, p. 428, fig. 467 b).

Ceratium massiliense (Gourret) Jörgensen, 1911

GOURRET, 1883, p. 27, pl. 1, fig. 2, *vix* 2a : *C. tripos* var. *massiliense;* KARSTEN, 1905b, p. 145 : *Ceratium massiliense* Gourret; JÖRGENSEN, 1911, p. 66, pl. 7, fig. 140-143, et pl. 8, fig. 144-146 : *Ceratium massiliense* (Gourret).

Le nom de cette espèce pourrait peut-être revenir par priorité au *Ceratium aequatoriale* ou au *C. undulatum* de SCHRÖDER (1906). Cependant, l'épithète *massiliense* ayant été universellement consacrée par

l'usage, il est instamment préférable de la conserver. JÖRGENSEN (1920), qui donne une historique détaillé de ce problème, propose l'expression « *C. massiliense* (Gourret, Karsten) Jörgensen », laquelle est illégale pour la raison principale suivante : aux termes du Code de nomenclature (LANJOUW *et al.*, art. 33-34), la publication par KARSTEN (*loc. cit.*) du nom de « *C. massiliense* Gourret » n'est pas valide.

Cette espèce est généralement considérée comme l'une des plus variables et des plus complexes du genre, mais ce jugement est peut-être excessif. A la suite de JÖRGENSEN, on y reconnaît le plus souvent trois formes ou variétés : *macroceroides, armatum* et *protuberans* (cette dernière étant tenue pour espèce distincte par PAULSEN, 1930). BÖHM (1931a) y ajoute une forme *ellipticum* qui est, du moins partiellement, à rattacher au type. PETERS (1934), qui réunit *C. deflexum* à la présente espèce, voit en celle-ci 5 formes qu'il ne décrit pas, dont une seule, la var. *armatum*, se distingue de l'ensemble par sa répartition géographique. STEEMANN NIELSEN (1939) considère *C. massiliense* comme une espèce collective dont il est impossible d'isoler les parties constituantes; toutefois, il élargit excessivement à mon avis le sens de ce taxon, puisqu'il semble y rattacher *C. deflexum* et *C. carriense* f. *carriense*. Enfin, GRAHAM & BRONIKOVSKY (1944) décrivent 7 (ou 8) formes — tout en en dénombrant 9 au total — sans pouvoir reconnaître de critères biogéographiques ou écologiques distinctifs.

C. massiliense est en effet très polymorphe, la variabilité portant ici sur divers caractères : direction, longueur et diamètre des cornes, forme du corps central, mode d'insertion et divergence des cornes antapicales, présence ou absence de crêtes et d'épines. A titre d'hypothèse, je considère dans leur ensemble ces variations comme réparties entre deux cas extrêmes (voir p. 382) : la variété thermophile est ici représentée par la var. *macroceroides*, c'est-à-dire le type de l'espèce; ce nom illégal doit être remplacé par celui de var. *massiliense*. La variété psychrophile correspond à la var. *protuberans*, ou peut-être à la var. *armatum*, ramenée au rang de forme par JÖRGENSEN (1920), et qui demeure mal connue. (N'ayant pas observé personnellement cette dernière forme, je la traite ici pour mémoire).

var. **massiliense**

= *C. massiliense* var. *α macroceroides* (Karsten) Jörgensen = « f. *macroceroides* » *in plur. auct.*

KARSTEN, 1905b (*C. tripos macroceroides*); JÖRGENSEN, 1920; BÖHM, 1931a et b; SCHILLER, 1937; RAMPI, 1939; WOOD, 1954; HALIM, 1963.

= *Ceratium massiliense* (Gourret) Jörgensen, *stricto sensu*

JÖRGENSEN, 1911; MANGIN, 1912; FORTI, 1924; ABÉ, 1927, PAULSEN, 1930; GRAHAM & BRONIKOVSKY, 1944; HALIM, 1960; MARGALEF, 1961a; KLEMENT, 1964.

= *C. massiliense* f. *ellipticum* Böhm, *pro parte*
Böhm, 1931a (fig. 17a-b, *vix* 18a, *non* 18b).

Récoltes personnelles : L'une des formes les plus courantes du genre. A Nossi-Bé, très fréquente, et quasi pérennante. Tuléar. Ile Maurice. Au cours de la croisière de l' « *Anton Bruun* », rencontrée dans tout le canal de Mozambique, quoique plus rarement dans le Sud, en milieu océanique et néritique, et tant dans les prélèvements horizontaux que verticaux.

Océan indien : Cette variété y est très courante, sous réserve de confusions possibles avec la suivante.

Distribution mondiale : Largement répandue dans les mers tempérées et tropicales; toutefois le maximum d'abondance se situe. selon Jörgensen (1911) et Steemann Nielsen (1934) sous les latitudes purement tropicales. Indifféremment océanique et néritique. Répartition verticale : selon Steemann Nielsen, « résolument » oligophotique; selon Graham & Bronikovsky, moins nettement; enfin. d'après mes propres observations, eurybathe.

var. ***protuberans*** (Karsten) Jörgensen, 1911

Karsten, 1905b, p. 145, pl. 22, fig. 27 : *C. tripos protuberans;* Jörgensen, 1911, p. 67, pl. 7, fig. 143, et pl. 8, fig. 144-145, et 1920, p. 86, fig. 79; Forti, 1922, p. 66, pl. 4, fig. 53; *vix* Dangeard, 1927, p. 379, fig. 43b; Böhm, 1931a, p. 362; *non* Graham & Bronikovsky, 1944, p. 38, fig. 22i.
Sous le nom erroné de « f. *protuberans* (Karsten) Jörgensen » : Schiller, 1937, p. 424, fig. 463c-d; Rampi, 1939, p. 310, fig. 40; Wood, 1954, p. 308, fig. 235c; Halim, 1963, p. 499, fig. 29.

= *Ceratium protuberans* (Karsten) Paulsen
Paulsen, 1930; Pavillard, 1937.

Caractères distinctifs de la variété précédente (d'après Jörgensen, 1911) :

Cellules plus petites et plus robustes; corne antapicale gauche ne dépassant pas, ou dépassant à peine, à son origine, le prolongement du contour postérieur du corps; ce dernier, légèrement concave, surtout en vue ventrale; corne apicale souvent légèrement fléchie, et pourvue de crêtes longitudinales; cornes robustes à leur origine et s'effilant vers leur extrémité; dents plus ou moins développées sur la courbure postérieure des cornes antapicales.

Paulsen donne comme caractère distinctif essentiel : contour général du corps central plus arrondi que chez le type; mais ce critère n'est pas toujours décisif.

La présente diagnose exclut celle de Graham & Bronikovsky (*loc. cit.*).

RÉCOLTES PERSONNELLES : Nossi-Bé (très rare). Tuléar. Sud du canal de Mozambique.

OCÉAN INDIEN : Cette variété semble n'y avoir été signalée que par JÖRGENSEN (1911), du moins comme telle : elle a pu être par ailleurs reportée sous le nom de spécifique.

DISTRIBUTION MONDIALE : Selon JÖRGENSEN (1911) : même distribution que le type, mais plus sporadique. Postérieurement, selon le même auteur (1920) : moins tropicale que le type. Selon STEEMANN NIELSEN (1934) : distribution plutôt tempérée, qui représenterait l'évolution du *C. massiliense* sous les latitudes moyennes.

Transitions entre les deux variétés précédentes ?

Il n'apparaît pas évident que les deux variétés *massiliense* et *protuberans* soient réunies par une suite continue de transitions. Dans mes récoltes, la distinction entre les deux types était toujours aisée.

Il serait hasardeux de nommer stades de transition les quelques cas difficilement identifiables rencontrés dans la bibliographie (cf. GRAHAM & BRONIKOVSKY). La question reste donc posée.

Pour mémoire :

f. ***armatum*** (Karsten) Jörgensen, 1920
Fig. 87-88

KARSTEN, 1905a, p. 132, pl. 19, fig. 8 : *C. tripos macroceros* f. *armatum;* JÖRGENSEN, 1911, p. 67, pl. 8, fig. 146 ; « var. *armatum* (Karsten) », et 1920, p. 86; FORTI, 1924, p. 66, pl. 4, fig. 52; SCHILLER, 1937, p. 424, fig. 463b.
? PETERS, 1934, p. 50, pl. 3, fig. 16a; ? RAMPI, 1939, p. 310, fig. 32; ? GRAHAM & BRONIKOVSKY, 1944, p. 38, fig. 22*l*; ? WOOD, 1954, p. 308, fig. 235b.

Diffère de la var. *protuberans*, selon JÖRGENSEN (1911) par les caractères suivants : cellule plus robuste; cornes plus courtes; crêtes épineuses très développées.

Cette forme, que je n'ai pas récoltée, ne paraît avoir été signalée dans l'Océan indien que par KARSTEN (1907), sous le nom de *C. tripos* var. *cristatum* Karsten, au Sud des îles St Paul et Amsterdam, et tout récemment par TRAVERS (1965) à Tuléar. Sa distribution géographique, pour le reste du globe, serait nettement psychrophile selon les auteurs cités ci-dessus, sauf pour GRAHAM & BRONIKOVSKY

qui réservent leur opinion à ce sujet. Toutefois la diagnose de cette forme est incertaine : telle que représentée par JÖRGENSEN (dont la figure est reproduite *in* SCHILLER) et par FORTI, elle semble bien distincte des deux variétés précédentes, et peu éloignée de *C. horridum* var. *horridum*. Les autres auteurs mentionnés la voient diffé-

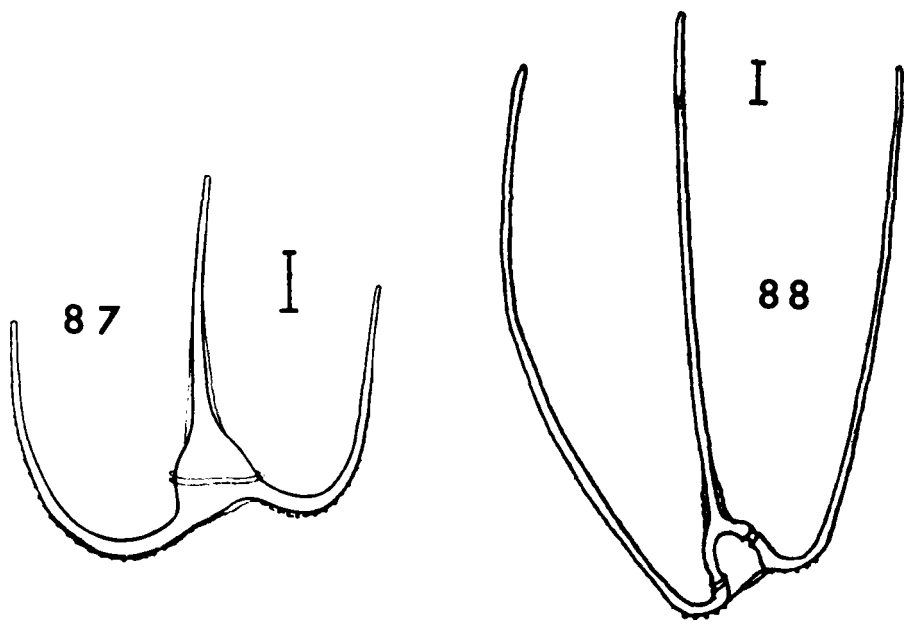


FIG. 87-88 : *Ceratium massiliense* f. *armatum* (Karsten) Jörg. ? — 87 : *in* PETERS, 1934, pl. 3, fig. 16a. — 88 : *in* RAMPI, 1939, fig. 32.

remment (cf. fig. 87-88). Cette divergence mise à part, il reste à décider s'il s'agit là d'une forme secondaire de la var. *protuberans*, ou bien d'une variété propre de l'espèce, dont elle serait le terme psychrophile extrême.

Ceratium carriense Gourret, 1883

GOURRET, 1883, p. 38, pl. 4, fig. 57.

Je maintiens cette espèce distincte de *C. massiliense*. En effet, bien que les deux espèces soient étroitement affines, elles diffèrent cependant assez clairement l'une de l'autre par les caractères définis par JÖRGENSEN (voir ci-dessous). Cependant, cette distinction paraît douteuse à de nombreux auteurs, bien qu'aucun n'eût procédé effectivement au rapprochement; le plus avancé dans cette voie est STEEMANN NIELSEN (1934), qui a observé que *C. massiliense* se développe, en milieu néritique, sous une forme très proche du type de *C. carriense*. Le même auteur semble postérieurement (1939) inclure ce type à « *C. massiliense* (Gourret) Jörg., *sensu lato* ».

D'autre part, la variabilité de cette espèce semble tenir à la présence de deux variétés, que je distingue comme suit :

var. ***carriense***

= *Ceratium carriense* Gourret, *stricto sensu*

Jörgensen, 1911, 1920; Forti, 1924; Schiller, 1937 (fig. 464a, *non* b); Rampi, 1939; *non* Graham & Bronikovsky, 1944; Wood, 1954.

= *C. carriense* f. *eucarriense* Böhm

Böhm, 1931a.

C'est sous cette variété-type que *C. carriense* présente des affinités certaines avec *C. massiliense*. Aussi est-il utile de rappeler les caractères distinctifs donnés par Jörgensen (1911) :

Contour postérieur du corps situé plus profondément entre les deux cornes antapicales; base de la corne gauche nettement détachée du corps et faisant un angle brusque avec le prolongement du contour postérieur; la base de cette corne est tout d'abord dirigée presque parallèlement à la corne apicale, puis rapidement infléchie latéralement; base de la corne droite faisant avec la partie suivante de cette corne un angle nettement obtus, de 135° env. (90° chez *C. massiliense*); le contour postérieur gauche du corps central est rectiligne ou convexe (plutôt concave chez *C. massiliense*).

Comme le montre Jörgensen (1920), le caractère distinctif donné initialement par Gourret (« sillon transversal concave en bas ») ne peut être conservé, car il provient vraisemblablement de la confusion, fréquente chez Gourret, des faces ventrale et dorsale.

A cette variété doit être rattaché en partie (Jörgensen, 1911; Schiller, 1937; *non al.*) le *Ceratium leptosomum* Jörg. voir p. 479).

var. ***volans*** (Cleve) Jörgensen, 1911

Cleve, 1900a, p. 15, *vix* pl. 7, fig. 4 : *C.* (*tripos* var. ?) *volans*; Jörgensen, 1911, p. 70, pl. 8, fig. 148-149, et 1920, p. 90, fig. 82; Pavillard, 1916, p. 17, pl. 1, fig. 4, 1923, p. 918, fig. C (f. *parallelum*) et 1931, p. 89; Forti, 1922, p. 69, pl. 4, fig. 55; Paulsen, 1930, p. 90, fig. 57; Steemann Nielsen, 1934, p. 26, *non* fig. 64; *non* Silva, 1955, p. 66, pl. 9, fig. 5-8.
Sous le nom erroné de « f. *volans* (Cleve) Jörgensen » :
Schiller, 1937, p. 426, fig. 465; Rampi, 1939, p. 310, fig. 37; *non* Wood, 1954, p. 309, fig. 236a.

= *Ceratium volans* Cleve, *pro parte*

Cleve, 1900a; *non* Ostenfeld & Schmidt, 1901; *nec* Pavillard, 1905; *nec* Okamura, 1907.

Diffère du type par les caractères suivants : aspect général plus ténu. Cornes très longues et très fines. Antapicales infléchies perpendiculairement vers l'avant.

Transitions entre les deux variétés précédentes :

La bibliographie présente divers cas de transitions que je propose de désigner ainsi : *C. carriense* Gourret, « *carriense-volans* » :

= *Ceratium carriense* Gourret, *pro parte*
SCHILLER, 1937, fig. 466b.
GRAHAM & BRONIKOVSKY, 1944, fig. 22a.

= *C. carriense* var. *volans* (Cleve) Jörgensen, *pro parte*
STEEMANN NIELSEN, 1934, fig. 64.
SILVA, 1955, pl. 9,fig. 8.
HALIM, 1960, pl. 5, fig. 11.

= *C. massiliense* f. *ellipticum* Böhm, *pro parte*
BÖHM, 1931a, fig. 18a.

= « *C. volans* Cleve *forma* » *in* SCHRÖDER, 1906, fig. 34.

= *Ceratium elegans* Schröder, *in* SCHRÖDER, 1906, fig. 36.

= *Ceratium ceylanicum* Schröder = *C. carriense* var. *volans* f. *ceylanicum* (Schröder) Jörgensen
SCHRÖDER, 1906; JÖRGENSEN, 1911; OKAMURA, 1912; PAVILLARD, 1931; ? SCHILLER, 1937; WOOD, 1954 (? fig. 236b).

= ? *Ceratium Hundhausenii* Schröder = *C. carriense* f. *Hundhausenii* (Schröder) Wood
SCHRÖDER, 1906; OKAMURA, 1912; *non* PAVILLARD, 1931; WOOD, 1954.

POUR LES DEUX VARIÉTÉS ET LEURS TRANSITIONS :

RÉCOLTES PERSONNELLES : Cette espèce est étonnamment rare dans mes prélèvements : exceptionnelle à Nossi-Bé; très rare à Tuléar et à l'île Maurice; sporadique dans le centre et le Nord du canal de Mozambique. Aucune discrimination écologique n'a pu être établie entre les deux variétés; on a seulement noté que la var. *volans* dominait.

OCÉAN INDIEN : Espèce courante.

DISTRIBUTION MONDIALE : Espèce tropicale et sub-tropicale, océanique, largement répandue dans les trois océans et en Méditerranée. Répartition verticale incertaine : hypothétiquement oligophotique pour STEEMANN NIELSEN, plutôt euphotique pour GRAHAM & BRONIKOVSKY.

Il est possible que la var. *volans* possède une distribution plus nettement tropicale que la variété-type : c'est du moins ce qui ressort clairement des observations de PETERS (1934).

Ceratium trichoceros (Ehrenberg) Kofoid, 1908
Fig. 89

EHRENBERG, 1873, p. 3, pl. 1, fig. 1 : *Peridinium trichoceros;* KOFOID, 1908a, p. 361, fig. 16-19 : « *Ceratium trichoceros* », et 1908b, p. 388 : « *Ceratium trichoceros* (Ehrenberg) » ; JÖRGENSEN, 1911, p. 75, pl. 9, fig. 159, et 1920, p. 95, fig. 85; ABÉ, 1927, p. 441, fig. 49; WANG & NIE, 1932, p. 303, fig. 15; PETERS, 1934, p. 51, pl. 1, 4, fig. 3a-c, 17a; STEEMANN NIELSEN, 1934, p. 27, fig. 68, et 1939, p. 15; SCHILLER, 1937, p. 430, *non* fig. 470, *nec* var. *contrarium;* GRAHAM & BRONIKOVSKY, 1944, p. 40, fig. 22b; SILVA, 1949, p. 361, pl. 7, fig. 4; WOOD, 1954, p. 311, fig. 239a, b (b : sous le nom erroné de *C. macroceros* var. *contrarium*); HALIM, 1960, pl. 5, fig. 18, et 1963, p. 499, fig. 31; DAVIS & STEIDINGER, 1966.

A propos de la variété *contrarium*, voir ci-dessous : *Ceratium contrarium*.

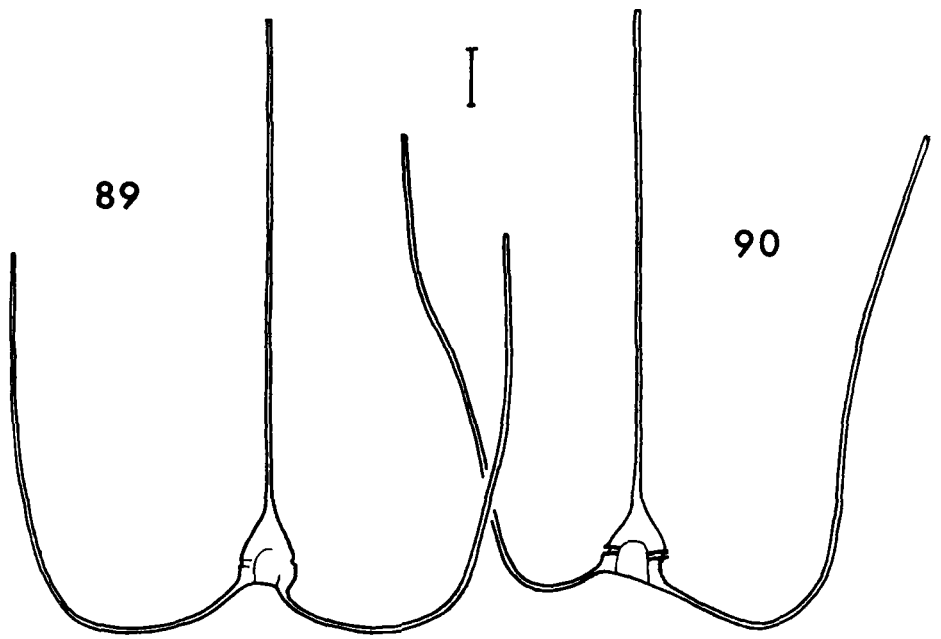


FIG. 89 : *Ceratium trichoceros* (Ehr.) Kofoid. — 90 : *C. contrarium* (Gourret) Pav.

RÉCOLTES PERSONNELLES : L'une des espèces les plus courantes du genre : Nossi-Bé (espèce pérennante, souvent abondante). Tuléar. Ile Maurice. Présente à toutes ou presque toutes les stations de l' « *Anton Bruun* » dans le canal de Mozambique, en quantités plus importantes dans les prélèvements superficiels.

Océan indien : Espèce courante, ou très courante (Steemann Nielsen, 1939).

Répartition mondiale : Espèce tropicale sténotherme, commune dans les trois océans. Jörgensen (1920) la donnait comme assez rare en Méditerranée, mais ceci semble inexact : *C. trichoceros* est pérennant et abondant dans le golfe de Marseille (Travers, 1962). Ce *Ceratium* est indifféremment océanique et néritique; sa distribution verticale est controversée.

La longueur des cornes est particulièrement variable (cf. Kofoid, 1908a et Peters, 1934).

Ceratium contrarium (Gourret) Pavillard, 1905
Fig. 90

Pavillard, 1905, p. 53, pl. 2, fig. 1, 1907, p. 229, 1931, p. 89, pl. 3, fig. 3, et 1937, p. 9; Jörgensen, 1920, p. 93, fig. 84; Paulsen, 1930, p. 90, fig. 58; Peters, 1934, p. 50, pl. 2, fig. 10c; Steemann Nielsen, 1934, p. 77, fig. 67, et 1939, p. 15; Graham & Bronikovsky, 1944, p. 40, fig. 22e, 24a, b; Silva, 1949, p. 361, pl. 9, fig. 12; Margalef, 1957, p. 47, fig. 3f; Halim, 1963, p. 499, fig. 30.

= *Ceratium inflexum* (Gourret) Kofoid.
Jörgensen, 1911; Schröder, 1911; Okamura, 1912; Pavillard, 1916; Abé, 1927 (fig. douteuses).

= *Ceratium trichoceros* var. *contrarium* (Gourret) Schiller.
Schiller, 1937; Wood, 1954 (fig. 239c, *non* b).

Schiller (1937) suivi par Wood (1954, non 1963a) fait de cette espèce une variété de *C. trichoceros*. Les caractères distinctifs du *C. contrarium* sont assez manifestes pour s'opposer à ce rapprochement :

Corps central plus volumineux. Contour gauche de l'hypothèque plus oblique, légèrement concave. Epithèque plus large que haute (chez *C. trichoceros :* plus haute que large). Cingulum normalement développé. Base de la corne antapicale gauche presque en continuité avec le contour postérieur de l'hypothèque. Corne gauche, à son origine, non infléchie, mais régulièrement courbée. Corne droite courbée à peu de distance de son insertion : cette distance est inférieuree ou égale au diamètre cingulaire (chez *C. trichoceros :* distance environ égale au double du diamètre). Courbures majeures des cornes antapicales non symétriques : celle de la corne droite légèrement plus rapide, et nettement plus antérieure.

RÉCOLTES PERSONNELLES : Nossi-Bé (beaucoup plus rare que *C. trichoceros*). Tuléar. Ile Maurice. Diverses stations océaniques de la croisière de l' « *Anton Bruun* ».

OCÉAN INDIEN : Espèce très courante.

RÉPARTITION MONDIALE : Espèce tropicale ou sub-tropicale, très commune dans les trois océans et en Méditerranée. Nettement océanique, selon STEEMANN NIELSEN du moins et mes observations personnelles; euphotique. *C. contrarium* diffère donc de l'espèce précédente non seulement par sa morphologie, mais aussi, comme l'a montré STEEMANN NIELSEN (1939), par sa distribution et sa biologie.

Pour mémoire :

F. ***claviceps*** (Schröder) Jörgensen

Absente de mes prélèvements. Cf. JÖRGENSEN, 1920; GRAHAM & BRONIKOVSKY, 1944; WOOD, 1954 (fig. 239d, *non* c); HALIM, 1960.

Ceratium horridum (Cleve) Gran, 1902

CLEVE, 1897, p. 302, fig. 4 : *C. tripos* var. *horridum;* GRAN, 1902, p. 54, 193 : « *C.* (*macroceros* subsp.) *horridum* Cl. » et « *C. horridum* Cl., *s. dilat.* »; JÖRGENSEN, 1920, p. 96, fig. 86-92.

Incl. *Ceratium tenue* Ostenfeld & Schmidt.

C. intermedium (Jörgensen) Jörgensen.

C. tenuissimum, C. inclinatum, C. claviger, et *C. molle* Kofoid.

C. batavum Paulsen.

C. denticulatum (Jörgensen) Paulsen.

C. buceros Zacharias, *emend.* Böhm *in* Schiller.

Non C. leptosomum Jörgensen, et syn.

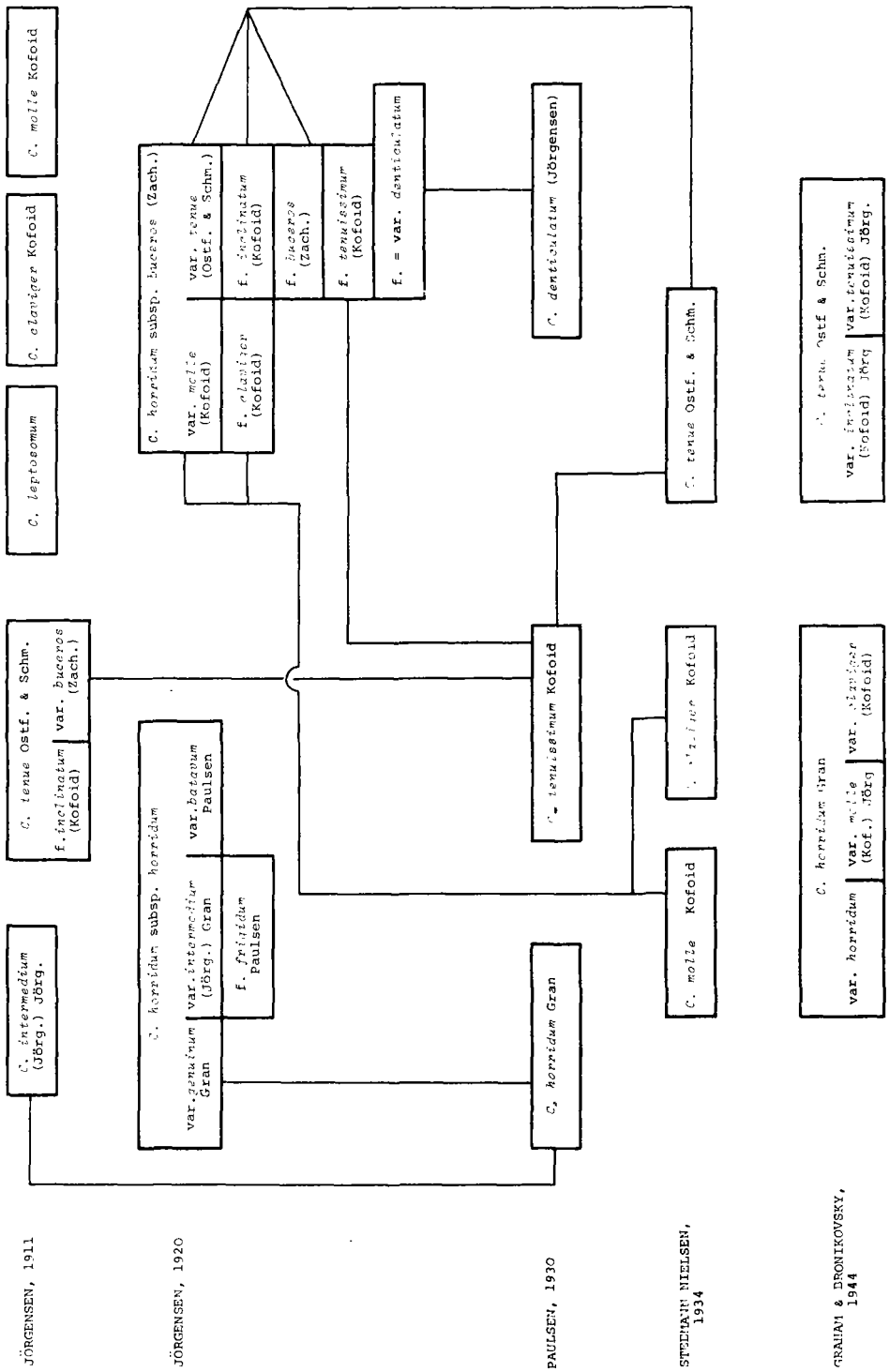
Une des innovations majeures du travail de JÖRGENSEN (1920) réside en la fusion, sous le nom spécifique commun « *C. horridum* Gran *s. dilat.* » de tout un groupe d'espèces considérées jusqu'alors comme distinctes, et qui pour la plupart avaient été précédemment traitées comme telles par JÖRGENSEN lui-même (1911). Notons qu'un tel esprit de synthèse est peu courant dans l'œuvre de cet éminent auteur, plutôt porté à multiplier les formes et les variétés qu'à réunir les espèces voisines. Cette initiative n'a pas été suivie par la suite, mais je pense devoir la reprendre aujourd'hui.

Le tableau 3 reproduit la « généalogie bibliographique » de *C. horridum* et des espèces affines, de JÖRGENSEN « à nos jours », et peut-être résumé comme suit :

En 1920, JÖRGENSEN considère une espèce unique, mais divise celle-ci en deux sous-espèces : l'une, septentrionale, comprenant principalement des formes « robustes » : subsp. α *horridum* (Gran)

TABLEAU III

« Généalogie bibliographique » du *Ceratium horridum* (voir p. 476)
Dans les cas d'innovations nomenclaturales, le nom de l'auteur du taxon est celui qui figure dans la colonne gauche.



Jörg.; l'autre, méridionale comprenant principalement des formes « délicates » : subsp. *buceros* (Zach.) Jörg., *s. dilat.* Chaque sous-espèce est divisée en variétés et en formes. Cependant, JÖRGENSEN n'est pas loin de considérer ses deux sous-espèces comme espèces distinctes (*loc. cit.*, p. 97). C'est ce point de vue qui a été repris par BÖHM, divulgué par SCHILLER (1937) — qui cite le précédent « *in litt.* » —, et généralement admis par la suite (WOOD, 1954, *et plur. auct.*). Par ailleurs, diverses autres scissions ont été proposées par PAVILLARD (1923, 1931), PAULSEN (1930), STEEMANN NIELSEN (1934), GRAHAM & BRONIKOVSKY (1944).

Comme le montre JÖRGENSEN, toutes les transitions sont observables entre les prétendues espèces; l'on rencontre également des cellules atypiques dont les cornes antapicales sont mi-robustes (partie basale), mi-délicates (partie distale) : cf. JÖRGENSEN (1911, pl. 10, fig. 171; 1920, p. 96), GRAHAM & BRONIKOVSKY (1944, fig. 25*d*). De plus, l'exposé des diverses tentatives de scissions spécifiques et infra-spécifiques (voir tableau 3), dont aucune n'est conservable, ne peut que renforcer l'idée de l'unité spécifique du groupe.

La conception de JÖRGENSEN elle-même, dans son détail, ne peut être maintenue : la séparation des deux sous-espèces isole arbitrairement d'un côté ou de l'autre les formes intermédiaires, et, d'autre part, nombre de variétés et de formes sont superflues.

Je propose donc (voir aussi SOURNIA, 1966) la création de trois variétés, au sens défini au début de cette étude. Le nom de l'espèce sera, comme JÖRGENSEN l'a montré, *C. horridum*, selon un sens doublement élargi (par GRAN, 1902, puis par JÖRGENSEN, 1920). Le nom de la variété « robuste » sera celui du type de l'espèce : var. *horridum*. Celui de la variété « délicate » : var. *buceros* (Zach.) Sournia, en remplacement de : subsp. *buceros* (Zach.) Jörg. Les stades de transition seront désignés conformément au système proposé p. 382. Enfin, le *Ceratium claviger* Kofoid sera traité ici (pour mémoire) au rang de forme.

var. ***horridum***
Fig. 91

GRAHAM & BRONIKOVSKY, 1944, p. 42, fig. 24d, *vix* g.

= *Ceratium horridum* (Cleve) Gran, *sensu stricto.*

CLEVE, 1897; LEBOUR, 1925; PAULSEN, 1930; SCHILLER, 1937 (fig. 455b-c, *non* a); GRAHAM & BRONIKOVSKY, 1944 (fig. 24d, 25e-f, *non al.*); WOOD, 1954 (fig. 230a, *non* b).

Non WAILES, 1928;*vix* WANG & NIE, 1932; *vix* HALIM, 1960, 1963.

= *Ceratium intermedium* (Jörgensen) Jörgensen, *pro parte.*

PAULSEN, 1908 : f. *spiniferum* et f. *typicum* Paulsen, *non* f. *frigidum* Paulsen); JÖRGENSEN, 1911 (fig. 175-176, *vix* 174); *vix* DANGEARD, 1926; WANG, 1936.

= *C. horridum* var. *genuinum* Gran.

Gran, 1902; Jörgensen, 1920.

= *C. buceros* f. *tenue* (Ostf. & Schmidt) Schiller, *pro parte.*

Schiller, 1937 (fig. 456a, *non al.*); Böhm, 1931a; *non al.*

Cellules robustes. Cornes relativement épaisses par rapport à leur longueur. Diamètre cingulaire : 40-70 µ. Corne apicale rectiligne; cornes antapicales parallèles ou légèrement divergentes, jamais flexueuses. Crêtes et épines fréquentes.

Récoltes personnelles : Tuléar (très rare).

Océan indien : Très rare ou inconnue (références incertaines).

Distribution mondiale : cette variété psychrophile est en fait, sauf confusions, très tolérante à l'égard de la température, et peut être rencontrée sous les latitudes tempérées et sub-tropicales. Signalons pour mémoire la parenté de cette variété avec *C. arcticum* et *C. longipes* (espèces toutes deux absentes de mes récoltes).

var. ***buceros*** (Zacharias) Sournia, 1966
Fig. 95

= *C. horridum* subsp. *buceros* (Zacharias) Jörgensen, *pro parte.*

Jörgensen, 1920, fig. 87-91, *non al. :* à l'exclusion de *var. molle.*

= *Ceratium buceros* Zacharias, *in* Zacharias, 1906, p. 551, *vix* fig. 15.

= *Ceratium inclinatum* Kofoid = *C. tenue* f. *inclinatum* (Kofoid) Jörgensen = *C. horridum* subsp. *buceros* var. *tenue* f. *inclinatum* (Kofoid) Jörgensen = *C. buceros* f. *inclinatum* (Kofoid) Schiller = *C. tenue* var. *inclinatum* (Kofoid) Graham & Bronikovsky.

Kofoid, 1907c; Jörgensen, 1911, 1920; Schiller, 1937; Graham & Bronikovsky, 1944; Wood, 1954; Halim, 1960.

= *Ceratium tenuissimum* Kofoid = *C. horridum* subsp. *buceros* var. *tenue* f. *tenuissimum* (Kofoid) Jörgensen = *C. buceros* f. *tenuissimum* (Kofoid) Schiller = *C. tenue* var. *tenuissimum* (Kofoid) Graham & Bronikovsky.

Kofoid, 1907c; Jörgensen, 1920; Paulsen, 1930; Schiller, 1937; Graham & Bronikovsky, 1944; Wood, 1954; Halim, 1963.

= *pro parte : Ceratium tenue* Ostenfeld & Schmidt = *C. horidum* subsp. *buceros* var. *tenue* (Ostf. & Schmidt) Jörgensen = *C. buceros* f. *tenue* (Ostf. & Schmidt) Schiller = *C. horridum* subsp. *tenue* (Ostf. & Schmidt) Dangeard.

Non Ostenfeld & Schmidt, 1901; *nec* Jörgensen, 1911; *vix* Okamura, 1912; Mangin, 1912 (fig. 11, *pro parte*); *vix* Pavillard, 1916; *non* Dangeard, 1927; Steemann Nielsen, 1934; *non* Schiller, 1937; Graham & Bronikovsky, 1944; Halim, 1960, 1963.

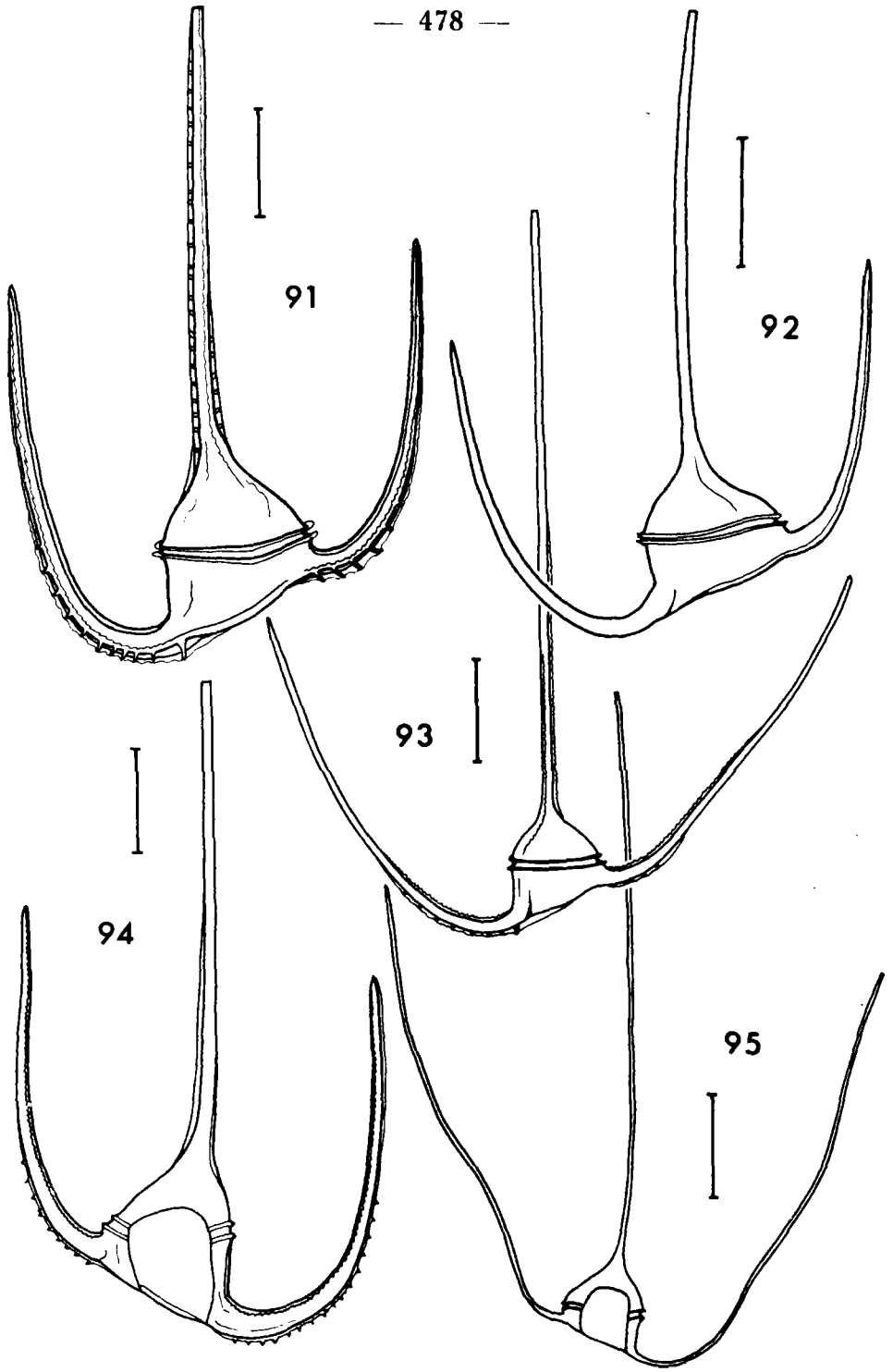


FIG. 91 : *Ceratium horridum* (Cl.) Gran var. *horridum*. — 92 : *C. horridum* (Cl.) Gran, « *horridum - buceros* ». — 93 : *C. horridum* (Cl.) Gran, « *buceros* > *horridum* ». — 94 : *C. horridum* (Cl.) Gran, « *horridum* > *buceros* ». — 95 : *C. horridum* var. *buceros* (Zach.) Sournia.

= *pro parte : Ceratium leptosomum* Jörgensen = *C. buceros* f. *leptosomum* (Jörgensen) Schiller.

DANGEARD, 1927; RAMPI, 1942; WOOD, 1954. *Non* JÖRGENSEN, 1911, *nec* SCHILLER, 1937 : voir à ce sujet *C. carriense,* p. 470.

= *Ceratium horridum* Gran, *pro parte.*

GRAHAM & BRONIKOVSKY, 1944 (fig. 25g, *non al.*). *Nec al.*

Non Ceratium molle Kofoid. (Voir : transitions).

Nec Ceratium denticulatum (Jörgensen) Paulsen. (Voir : transitions).

Cellules délicates. Corne apicale plus ou moins infléchie. Cornes antapicales fines, largement ouvertes, de direction variable, souvent plus ou moins flexueuses. Diamètre cingulaire : 30 - 50 µ. Pas de crêtes lamellaires. Epines présentes ou non sur le bord postérieur des cornes antapicales.

RÉCOLTES PERSONNELLES : Nossi-Bé et île Maurice (très rare). Cette variété était par contre très abondante en domaine océanique, dans le centre et le Nord du canal de Mozambique, et là, seulement dans les prélèvements verticaux.

OCÉAN INDIEN : Cette variété y est assez courante, mais sa répartition est difficile à distinguer de celle des stades de transition.

DISTRIBUTION MONDIALE : Tropicale et sub-tropicale (Méditerranée incluse). Oligophotique.

Transitions entre les deux variétés précédentes :
Fig. 92-94, et Pl. III, fig. 12

Elles sont très fréquentes, tant dans mes récoltes (en milieu océanique principalement) que dans la bibliographie. Elles représentent dans leur ensemble un groupe cosmopolite, et dont la répartition verticale est plutôt oligophotique. Ce sont, *pro parte,* les taxons suivants :

— *Ceratium horridum* Gran.

— *C. tenue* Ostf. & Schmidt, et ses synonymes (ceux-ci énumérés plus haut).

— *C. molle* Kofoid = *C. horridum* subsp. *buceros* var. *molle* (Kofoid) Jörgensen = *C. buceros f. molle* (Kofoid) Schiller.

— *C. denticulatum* (Jörgensen) Paulsen = *C. horridum* subsp. *buceros* var. (f.) *denticulatum* Jörgensen = *C. buceros* f. *denticulatum* (Jörgensen) Schiller.

— *C. intermedium* (Jörgensen) Jörgensen = *C. horridum* subsp. *horridum* var. *intermedium* (Jörgensen) Gran.

— *C. batavum* Paulsen = *C. intermedium* f. *batavum* (Paulsen) Jörgensen = *C. horridum* subsp. *horridum* var. *batavum* (Paulsen) Jörgensen.

En voici quelques exemples, empruntés à l'iconographie mondiale, ainsi qu'à mes propres observations :

C. horridum (Cl.) Gran, « *horridum — buceros* »

JÖRGENSEN, 1911, pl. 10, fig. 171, 172, 174, 177, et 1920, fig. 91.
PAULSEN, 1908, fig. 113, 114, et 1930, fig. 61.
SCHILLER, 1937, fig. 456b.
GRAHAM & BRONIKOVSKY, 1944, fig. 24 g-i, 25 a, c-d.
Et dans le présent travail : fig. 92.

C. horridum (Cl.) Gran, « *horridum* > *buceros* »

JÖRGENSEN, 1911, pl. 9, fig. 169, 170, et 1920, fig. 87.
GRAHAM & BRONIKOVSKY, 1944, fig. 25 b.
Et dans le présent travail : fig. 94, et pl. III, fig. 12.

C. horridum (Cl.) Gran, « *buceros* > *horridum* »

JÖRGENSEN, 1911, pl. 9, fig. 163, 165.
GRAHAM & BRONIKOVSKY, 1944, fig. 24 c, e, f.
Et dans le présent travail : fig. 93.

Pour mémoire :

C. horridum f. ***claviger*** (Kofoid) nov. comb.

= *Ceratium claviger* Kofoid.
KOFOID, 1907 d, p. 170, pl. 4, fig. 27; JÖRGENSEN, 1911 (fig. 168, *non* 169).
non PAVILLARD, 1916; STEEMANN NIELSEN, 1934.

= *C. horridum* subsp. *buceros* var. *molle* f. *claviger* (Kofoid) Jörgensen.
JÖRGENSEN, 1920.

= *C. buceros* f. *claviger* (Kofoid) Schiller.
SCHILLER, 1937; RAMPI, 1942; SILVA, 1955; *non* HALIM, 1960.

= *C. horridum* var. *claviger* (Kofoid) Graham & Bronikovsky.
GRAHAM & BRONIKOVSKY, 1944.

Cornes antapicales claviformes à leurs extrémités.

Cette forme affecte principalement les stades de transition entre les deux variétés.

Ceratium vultur Cleve, 1900

CLEVE, 1900a, p. 15, pl. 7, fig. 5 : *Ceratium* (*tripos* var. ?) *vultur*.
Incl. *C. sumatranum* (Karsten) Jörgensen.
Non C. Pavillardii Jörgensen.

J'inclus sous ce nom *Ceratium sumatranum*, suivant sur ce point l'opinion générale, mais allant à l'encontre de celle de STEEMANN NIELSEN (1939, *non* 1934). Au sujet de *C. Pavillardii*, voir plus loin p. 483.

C. vultur est une espèce assez variable, en laquelle on peut reconnaître quatre formes, plutôt que variétés :

— f. *sumatranum :* cornes antapicales largement déployées, plus ou moins « convexes » vers l'intérieur.

— f. *japonicum :* antapicales complètement reployées vers l'avant, et parallèles à la corne apicale.

— f. *vultur :* antapicales en position intermédiaire entre les deux cas précédents.

— f. *recurvum :* antapicales (surtout la gauche) brutalement infléchies vers l'arrière, à mi-distance de leur longueur.

La répartition géographique et la biologie de ces diverses formes semblent jusqu'à présent uniformes.

La présence ou l'absence de crêtes lamellaires (plus fréquentes chez les formes *japonicum* et *vultur*) ne paraît pas devoir justifier de désignation infra-spécifique particulière (cf. *C. robustum* Ostf. & Schmidt, *in* Ostenfeld & Schmidt, 1901 et Schröder, 1906).

Enfin, il faut exclure de cette espèce les var. *reversum* et *regulare* Graham & Bron, voir à ce sujet *C. Pavillardii*, p. 483) ainsi que la variété *productum* de Wood (1963c), laquelle semble représenter une espèce distincte.

f. *vultur*

= *Ceratium vultur* Cleve, *pro parte.*

Cleve, 1900a; Okamura, 1907, 1912; Jörgensen, 1911 (incl. f. *angulatum*); Pavillard, 1931, *non* 1905; Steemann Nielsen, 1934, 1939; Schiller, 1937 (fig. 459a, *non* b); Wood, 1954; Klement, 1964.

= *C. vultur* var. *tenue,* et var. *divergens* Okamura.

Okamura, 1912.

= *C. vultur* Cleve var. *vultur.*

Graham & Bronikovsky, 1944.

f. *japonicum* (Schröder) Wood, 1954
Fig. 96

Wood, 1954, p. 305, fig. 233b-c.

= *C. vultur* var. *japonicum* (Schröder) Jörgensen.

Jörgensen, 1911; Okamura, 1912; Graham & Bronikovsky, 1944 (fig. 23e, *non* f).

= *Ceratium japonicum* Schröder.

Schröder, 1906; Pavillard, 1931.

= *Ceratium vultur* Cleve, *pro parte.*

Peters, 1934 (fig. 7a, *non* b); Schiller, 1937 (fig. 459b, *non* a).

f. ***sumatranum*** (Karsten) nov. comb.

= *C. tripos vultur* var. *sumatranum* Karsten.

KARSTEN, 1907, p. 530, pl. 48, fig. 15, pl. 51, fig. 14.

= *C. vultur* var. *sumatranum* (Karsten) « Steeman Nielsen ».

? STEEMANN NIELSEN, 1934 (*non* fig. 65-66); SCHILLER, 1937 (fig. 460 b, *non* a-c); GRAHAM & BRONIKOVSKY, 1944; WOOD, 1954; BALLANTINE, 1961.

= *Ceratium sumatranum* (Karsten) Jörgensen.

JÖRGENSEN, 1911 (incl. f. *angulatum* Jörgensen), fig. 154-155, *non* 153; NIE, 1936.

= *Ceratium vultur* Cleve, *pro parte*.

PETERS, 1934 (pl. 1, fig. 7 b, *non* a).

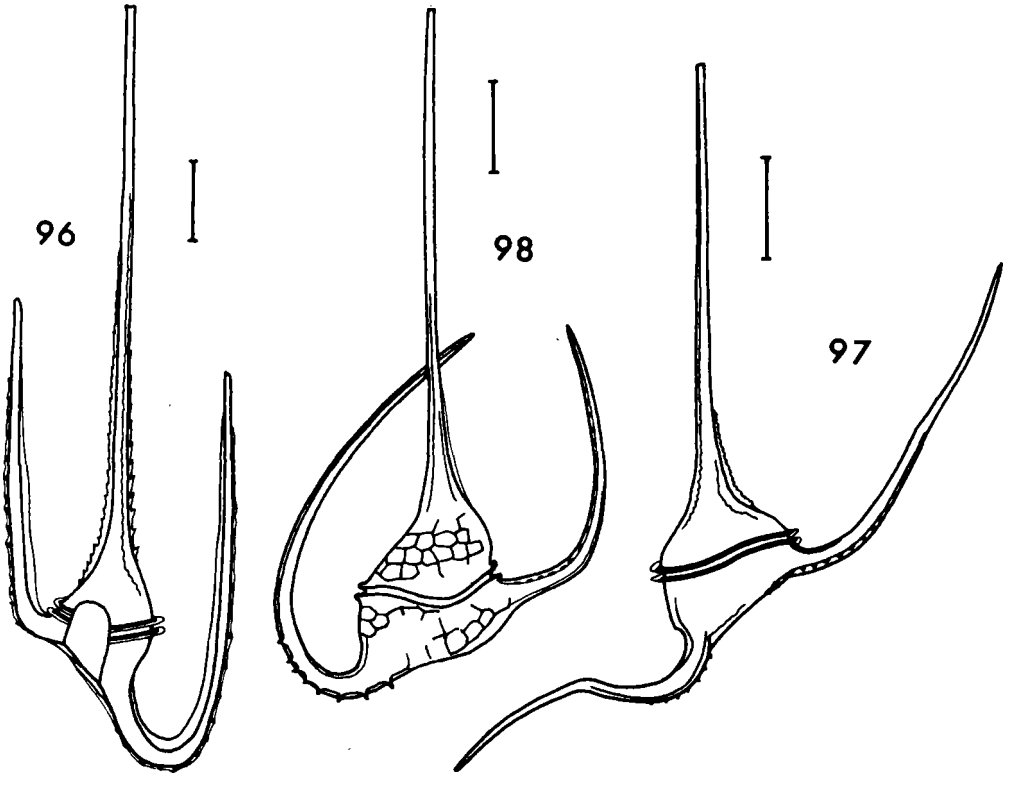


FIG. 96 : *Ceratium vultur* f. *japonicum* (Schr.) Wood. — 97 : *C. vultur* f. *recurvum* (Jörg.) Schiller. — 98 : *C. hexacanthum* Gourret.

f. ***recurvum*** (Jörgensen) Schiller, 1937
Fig. 97

SCHILLER, 1937, p. 419, fig. 460 c.

= *C. sumatranum* var. *recurvum* Jörgensen.

JÖRGENSEN, 1911.

= *C. vultur* var. *recurvum* « Jörgensen ».

STEEMANN NIELSEN, 1934; GRAHAM & BRONIKOVSKY, 1944.

POUR LES QUATRE FORMES :

RÉCOLTES PERSONNELLES : Tuléar. Ile Maurice (rare). Dans le canal de Mozambique, espèce courante dans le domaine océanique, principalement dans les prélèvements verticaux.

La forme *recurvum* n'a été rencontrée qu'une seule fois (au large de Durban).

OCÉAN INDEN : Espèce courante.

DISTRIBUTION MONDIALE : Tropicale, océanique, oligophotique. Jusqu'ici inconnue en Méditerranée.

Pour mémoire :

Ceratium Pavillardii Jörgensen, 1911

JÖRGENSEN, 1911, p. 74, pl. 9, fig. 157-158, et 1920, p. 92, fig. 83; OKAMURA, 1912, ? p. 14, pl. 1, fig. 12, 15; *non* DANGEARD, 1927, p. 378, fig. 42 a; PAVILLARD, 1931, p. 93; SCHILLER, 1937, p. 418, fig. 458; RAMPI, 1939, p. 307, fig. 41; STEEMANN NIELSEN, 1939, p. 15; GRAHAM, 1942, p. 56, fig. 67; WOOD, 1954, ? p. 304, *non* fig. 232; HALIM, 1960, pl. 5, fig. 8.

= *C. vultur* var. *Pavillardii* (Jörgensen) Graham & Bronikovsky.

GRAHAM & BRONIKOVSKY, 1944.

Ce *Ceratium*, que je n'ai pas rencontré dans mes récoltes, me semble distinct du *C. vultur*, avec lequel il a pu cependant être souvent confondu : du moins à l'origine, par PAVILLARD (1905), et plus récemment par WOOD (1954), si l'on en juge par l'iconographie donnée par ce dernier.

GRAHAM & BRONIKOVSKY (1944) font de cette espèce une variété de *C. vultur*, mais ce rapprochement semble encore excessif. Ces deux auteurs décrivent également sous le même nom spécifique deux variétés intéressantes : l'une, var. *reversum*, serait en quelque sorte une inversion du *C. Pavillardii*, l'autre, plus énigmatique encore, rapprocherait *C. massiliense* de *C. vultur*.

La présence de *C. Pavillardii* dans l'Océan indien n'est pas assurée (cf. WOOD, 1963a). Cette espèce n'est en fait guère connue en dehors de la Méditerranée.

Ceratium hexacanthum Gourret, 1883
Fig. 98

Gourret, 1883, p. 36, pl. 3, fig. 49; Jörgensen, 1920, p. 101, fig. 94; Peters, 1934, p. 54, pl. 2, fig. 10a, 11b; Steemann Nielsen, 1934, p. 29, fig. 73, et 1939, p. 15; Schiller, 1937, p. 421, fig. 462; Graham & Bronikovsky, 1944, p. 44, fig. 27f-g; Wood, 1954, p. 306, fig. 234; Halim, 1960, pl. 4, fig. 17, et 1963, p. 499, fig. 35; Davis, 1965.

= *Ceratium reticulatum* (Pouchet) Cleve.

Pouchet, 1883; Cleve, 1903; Jörgensen, 1911; Okamura, 1912; Mangin, 1912; Pavillard, 1905, 1916; Forti, 1922; Lebour, 1925.

Récoltes personnelles : Très rare : Tuléar, île Maurice. Au cours de la croisière de l' « *Anton Bruun* » : au large de Beira, et au large de Mombasa.

Dans l'ensemble, les quelques spécimens récoltés possèdent des cornes antapicales relativement robustes et peu incurvées (fig. 98).

Océan indien : Espèce assez courante.

Distribution mondiale : Tropicale et sub-tropicale, occasionnellement (mais rarement) tempérée. Répartition verticale incertaine.

Plusieurs variétés et formes ont été décrites, sur la considération de la longueur, du diamètre et de la direction des cornes postérieures. Ces caractères sont malheureusement très fluctuants, et difficiles à évaluer; de plus, comme le remarque Jörgensen (1920), l'extrémité des cornes peut se trouver lésée : dans ce cas, la distinction d'une forme *spirale* (extrémités spiralées) devient plus qu'aléatoire.

Selon Pavillard (1916), « *C. reticulatum* », c'est-à-dire *C. hexacanthum*, offre « un des meilleurs exemples de plasticité morphologique en rapport avec l'adaptation saisonnière. Les formes estivales ont une enveloppe moins épaisse et des cornes beaucoup plus longues que les formes hivernales ».

Cette variabilité reste cependant à préciser et à nomenclaturer. Ayant réuni trop peu d'observations personnelles sur cette espèce, je ne puis que donner pour mémoire les références des divers taxons infraspécifiques rencontrés dans la bibliographie :

C. hexacanthum var. *aestuarium* (Schröder) Jörgensen
= *Ceratium aestuarium* Schröder

Schröder, 1911; Jörgensen, 1920; Böhm, 1931a; Pavillard, 1937; Schiller, 1937; Rampi, 1937.

Non C. aestuarium var. *Pavillardii* Rampi : voir plus bas.

Cette variété sera probablement à conserver, car elle représente un cas extrême : cornes antapicales sub-parallèles; crêtes lamellaires absentes; réticulation incomplète.

C. hexacanthum var. ***contortum*** Lemmermann
= *C. reticulatum* f. *contortum* (Lemmermann) Jörgensen

LEMMERMANN, 1899; KARSTEN, ? 1905b, 1907; OKAMURA, 1907, 1912; JÖRGENSEN, 1911, 1920; PAVILLARD, 1916; SCHILLER, 1937; RAMPI, 1939, 1942; HALIM, 1963.

C. hexacanthum f. ***spirale*** (Kofoid) Schiller
= *C. reticulatum* subsp. *spirale* Kofoid
= *C. reticulatum* f. *spirale* (Kofoid) Jörgensen

KOFOID, 1907c; KARSTEN, 1907; STÜWE, 1909; JÖRGENSEN, 1911, 1920; PAVILLARD, 1916, 1937; SCHILLER, 1937; *vix* HALIM, 1963.

Sous la réserve formulée plus haut.

C. hexacanthum f. ***hiemale*** Pavillard = *C. hexacanthum* var. *hiemale* (Pav.) Pav.

PAVILLARD, 1916, 1931, 1937; JÖRGENSEN, 1920; RAMPI, 1942; SILVA, 1949.

C. hexacanthum var. ***Karstenii*** Pavillard

PAVILLARD, 1930, 1931.

C. hexacanthum f. ***Pavillardii*** (Rampi) nov. comb.

= *C. aestuarium* var. *Pavillardii* Rampi.
RAMPI, 1939, p. 308, fig. 34.
= « *C. aestuarium var.* ? » *in* PAVILLARD, 1937, p. 8, fig. 2.

Il s'agit ici d'un cas d'hétéromorphisme (cornes antapicales dirigées postérieurement), que je propose de ramener au rang de forme.

Il convient enfin d'ajouter à cette liste le ***Ceratium obesum*** de PAVILLARD (1930, p. 11, fig. 11, et 1931) : forme robuste, corps central arrondi, cornes courtes et lamellaires, réticulation « très peu apparente ».

SECT. *REFLEXA* JÖRGENSEN

Ceratium reflexum Cleve, 1900
Fig. 99 et pl. III, fig. 13

CLEVE, 1900a, p. 15, pl. 7, fig. 8-9; KARSTEN, 1907, p. 414, pl. 48, fig. 9; JÖRGENSEN, 1911, p. 87, pl. 10, fig. 184; PAVILLARD, 1931, p. 94; STEEMANN NIELSEN, 1934, p. 29, fig. 74, et 1939, p. 15 (?); SCHILLER, 1937, p. 420, fig. ? 461; GRAHAM & BRONIKOVSKY, 1944, p. 45, fig. 27h; WOOD, 1954, p. 305, et 1963b, p. 40, fig. ? 149; *non* SILVA, 1955, p. 66, pl. 9, fig. 9.
= *C. reflexum* Cleve « *forma* » *in* SCHRÖDER, 1906.

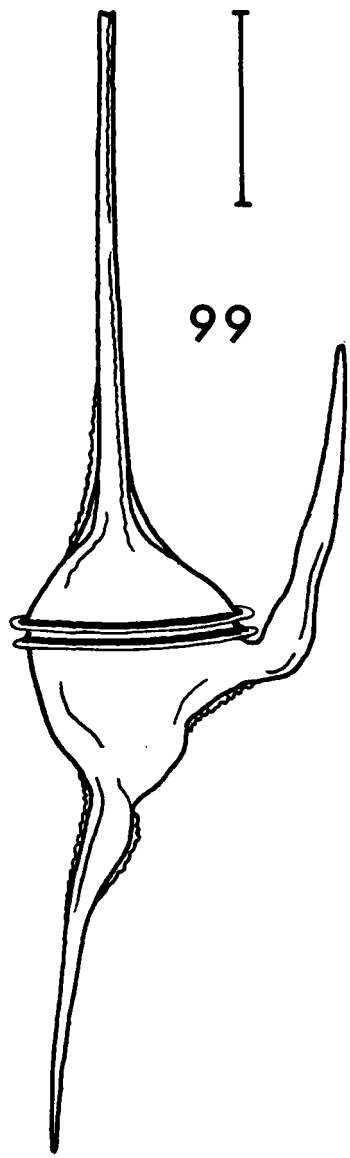


FIG. 99 : *Ceratium reflexum* Cleve.

RÉCOLTES PERSONNELLES : Ile Maurice (très rare). Centre du canal de Mozambique (rare), dans les prélèvements verticaux seulement.

OCÉAN INDIEN : Mer Rouge, golfe d'Aden, Indonésie, et quelques stations océaniques. Espèce nouvelle pour le canal de Mozambique.

DISTRIBUTION MONDIALE : Espèce tropicale de distribution très clairsemée, plus rare peut-être dans l'Atlantique que dans l'Indo-Pacifique et inconnue en Méditerranée. Oligophotique, océanique.

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RÉSUMÉ

Cette étude, essentiellement taxinomique, représente un compromis entre un inventaire régional et une révision mondiale. Plusieurs nouvelles combinaisons sont introduites. Un intérêt particulier est accordé au cas des variations morphologiques continues, de nature apparemment thermique, et pour lesquelles un nouveau mode de désignation infraspécifique est proposé.

SUMMARY

This is a chiefly taxonomic study, at half-way between a regional list and a world revision. Several new combinations are introduced. Special interest is given to continuous morphological variations of apparently thermic origin, for which a new type of infraspecific nomenclature is proposed.

ZUSAMMENFASSUNG

Diese Studie, vornehmlich taxonomischer Art, ist ein Kompromiss zwischen einem Regionalverzeichnis und einer Weltrevision. Mehrere neue Kombinationen werden eingeführt. Den kontinuirlich-morphologischen Variationen, offensichtlich thermischer Art, gilt besonderes Interesse, für die eine neue, infraspezifische Bezeichnung vorgeschlagen wurde.

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LESTIDIUM BIGELOWI, A NEW SPECIES OF PARALEPIDID FISH WITH PHOTOPHORES

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ABSTRACT

Two specimens of a new luminous paralepidid fish were taken in the Indian Ocean during Cruise VI of the R/V *Anton Bruun*. Their main distinguishing feature is the presence of three separate and distinct, circular photophores along the ventral midline that are unlike the light organs found in other paralepidids. The two specimens are described here as a new species, and the structure of one photophore is examined in detail.

INTRODUCTION

Two evolutionary lineages, the myctophoids and the alepisauroids, are generally recognized within the pelagic members of the Myctophiformes (Iniomi). The myctophoid families Myctophidae and Neoscopelidae have discrete photophores lying in rows on each side of the ventral midline, and it has been shown recently (Haneda, 1958; Rofen, 1965) that a few members of the alepisauroid family Paralepididae have elongated luminous glands immediately on, or adjacent to, the ventral midline. One genus also has a small finger-like projection, before the eye, that may be luminous, but this organ does not appear to have the structure found in the myctophoids. This paper is concerned with a unique new species of paralepidid which, though quite similar to other paralepidids in most characters, is distinguished from them by the discrete photophores on the ventral midline.

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LESTIDIUM BIGELOWI, new species

Holotype: MCZ 44881, 37.2 mm in standard length; collected during the International Indian Ocean Expedition, R/V *Anton Bruun,* Cruise VI, trawl 339A; APB label 7227; hydrographic station 339; collected in 10′ Isaacs-Kidd Midwater Trawl, depth 0-615m; 30-V-64. 0140-0645 hrs; 4°01′-4°14′S, 65°00′-65°02′E.

Paratype: MCZ 44880, 28.4mm in standard length; R/V *Anton Bruun,* Cruise VI; trawl 340B; APB label 7241; hydrographic station 340; 10′ IKMT, 0-746m; 31-V-64, 1945-0155 hrs; 5°55′-6°08′S, 64°48′-64°58′E.

Diagnosis: This species is the only paralepidid known to have light organs that are small and discrete, as opposed to long and tubular. There are three of these; all are directed ventrally. One is at the isthmus, one is between the bases of the pectoral fins, and one is just posterior to the bases of the ventral fins. In most characters, *Lestidium bigelowi* is almost intermediate between the genera *Lestidium* and *Lestidiops* (see Table 1).

Description: The following description is based on both types. Body long and slender, very compressed. Keel present for short distance ventrally between anus and anal fin. Anus between tips of appressed ventral fins. Skin smooth; scales absent, with lateral line ossicles insufficiently ossified to be observed. Lateral line extending along side of body from edge of operculum to a vertical with first of procurrent caudal rays, and slightly above middle of body.

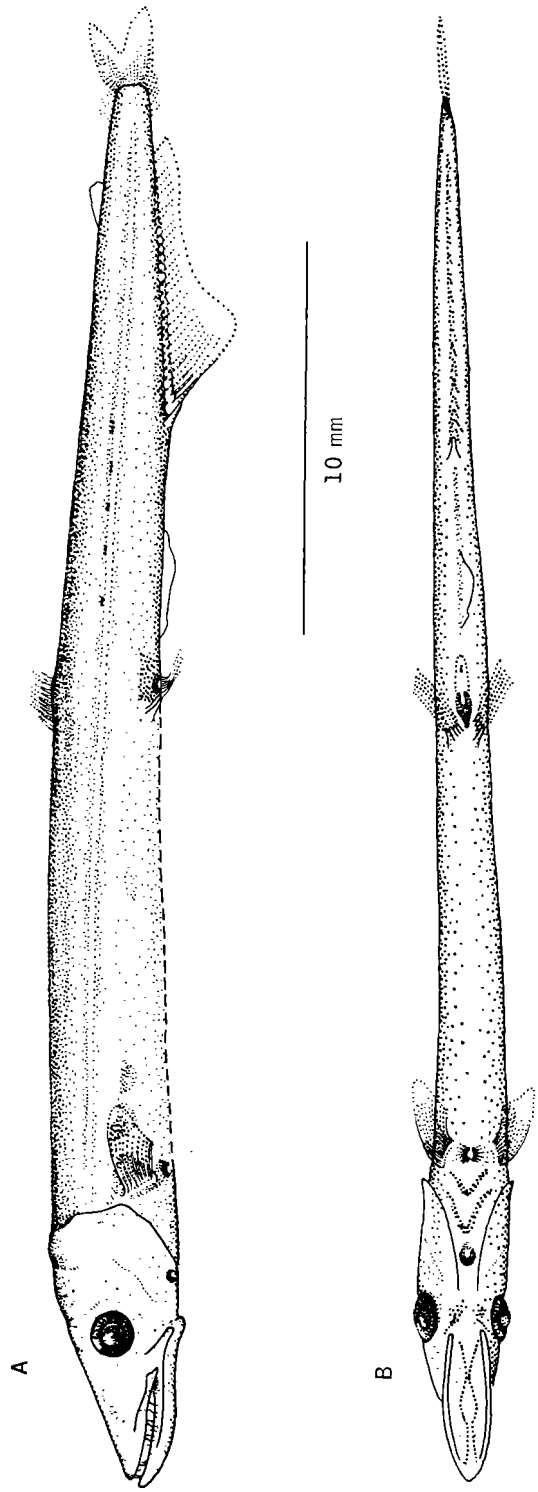

Figure 1. Side and ventral views of *Lestidium bigelowi*, new species, drawn from the holotype — 37.2 mm in standard length (MCZ 44881).

Three luminous organs on the midventral line — one at isthmus, another between bases of the pectoral fins, and the third between bases of ventral fins and anus. Isthmal and pectoral organs imbedded in flesh; anal organ close to skin, possibly open to surface or connected to rectum. In alcohol, these organs are black with a translucent, white layer at center (see discussion of luminous organs, below).

Head pointed and moderately long, widest just posterior to eyes. Snout length slightly more than two in head, about three-quarters as wide as head. Eye and pupil large, about five in head length; eye and pupil round; adipose eyelid present. Interorbital slightly concave, with two lateral, compressed, longitudinal ridges on each side. Occiput rounded, convex. Nasal apertures approximately halfway between tip of snout and eye. Opercle with posterior edge moderately pointed and notched about pectoral fin base. Mouth large, lower jaw with a slight non-ossified projection. Premaxillary extending to a point beneath anterior edge of orbit. Premaxillary with two or three depressible canines, posteriorly followed by fixed teeth. Palatine with a few depressible teeth. Gill rakers present but poorly developed on first two arches.

Dorsal fin origin slightly anterior to origins of ventral fins, a little more than halfway back on body. Posterior edge of adipose fin anterior to caudal peduncle, slightly before last anal fin ray. Inner rays of ventral fins distinctly longer than the outer. Ossification is too incomplete to permit radiographic study of vertebral column or study of lateral line ossicles through staining.

In ethyl alcohol the body is largely colorless. Melanophores, most of them stellate, cover many parts of the fish: the occiput, the edges, ridges and sutures of the jaws, the angular bone, the dorsum, the posterior part of the caudal peduncle, the ventral midline between the anus and the anal fin, the first pectoral and anal fin rays, and the anal and caudal fin ray bases. The angular bone is also covered by heavy black pigment, and the dorsum is covered by light brown pigment in a band becoming denser and darker posteriorly. Three anterior and one posterior peritoneal sections are relatively clearly outlined; the others are indistinct.

All measurements and counts are given in Table 1, and reconstructed lateral and ventral views of the holotype are shown in Figure 1.

This new species is named in honor of Dr. Henry Bryant Bigelow, to whom I wish to express my sincere thanks for his kindness and generosity.

Distribution: Taken only in the Indian Ocean, approximately 650 miles northeast of Madagascar at a depth above 750m.

TABLE 1

Proportional Measurements in Percent of Standard Length

	Lestidium bigelowi	*Lestidium atlanticum*	*Lestidiops jayakari*	*Lestidiops indopacificum*
Head length	20.8-21.8	22.4-22.9	18.5-22.0	20.3
Snout length	8.9-9.2	10.1-12.4	7.6-10.2	7.1
Snout to anus	59.9-60.0	59.8-64.1	55.7-64.6	58.4
Snout to dorsal fin	54.3-54.9	56.3-60.0	56.5-61.0	53.9
Snout to anal fin	75.0-77.4	75.4-79.2	76.7-79.4	76.8
Snout to ventral fin	56.0-56.2	56.8-59.6	48.4-58.0	54.8
Dorsal fin to ventral fin	1.4-1.6	0.0-0.5	2.3-6.5	0.9*-1.2*
Dorsal fin to anal fin	15.5-18.8	19.8-20.0	19.6-22.1	22.0*-22.9*
Dorsal fin rays	9-10	9-10	10	10
Anal fin rays	28-29	29-30	28-30	29-32
Body depth	8.5-8.9	8.0	6.7-9.1	10.0
Caudal peduncle depth	3.2-3.5	2.4-2.7	2.3-3.2	—
Eye diameter	4.0-4.6	3.9-4.4	3.4-4.9	4.5
Upper jaw length	9.7-10.9	10.3-10.5	8.2-10.0	—
Premaxillary to eyes	0.7-0.8	1.4-2.2	0.5-1.4	—
Dorsal fin to caudal fin	41.7-45.1	35.9-36.7	35.2-40.0	41.9[x]
Anal fin to caudal fin	5.9-6.0	5.2-5.9	5.3-6.5	1.9
Adipose fin to caudal fin	6.3-8.3	5.5-5.8	5.1-7.0	2.6
Dorsal fin base length	4.8-5.3	3.6-4.4	3.6-5.0	4.2
Anal fin base length	18.8-19.4	15.2-17.5	15.7-18.5	19.0

* Taken from Ege's illustration.

[x] Computed from: total length — (predorsal + dorsal base length).

Relationships: In relative proportions and numbers of fin rays, *Lestidium bigelowi* closely resembles *Lestidium atlanticum* Borodin, *Lestidiops jayakari* (Boulenger), and *Lestidiops indopacificum* (Ege). The ranges of meristic characters shown by the species in these two genera provide no grounds for separation. Analysis is further impaired by discrepancies evident in the monograph recently published by Rofen (1965), for the proportionality data provided in certain of his tables (e.g., table XXIV, pp. 302-303) are at variance with those reported in his description (e.g. that of *Lestidium atlanticum* on pp. 308-309). The single valid and conservative character which does separate *Lestidium* from *Lestidiops* is the presence or absence of an internal light organ; hence the species described here is relegated to *Lestidium.* The meristic data taken from this species are compared in Table 1 with those for *Lestidium atlanticum* and *Lestidiops jayakari* taken from Rofen's description (1965: 308, 348), and for *Lestidiops indopacificum* taken from Ege (1953).

Anatomy of the luminous organs: The three organs differ somewhat from one another in gross morphology. The anterior one (the isthmal) is buried in the muscle of the isthmus (Fig. 1A, B). It has a black cup-shaped structure with the opening directed

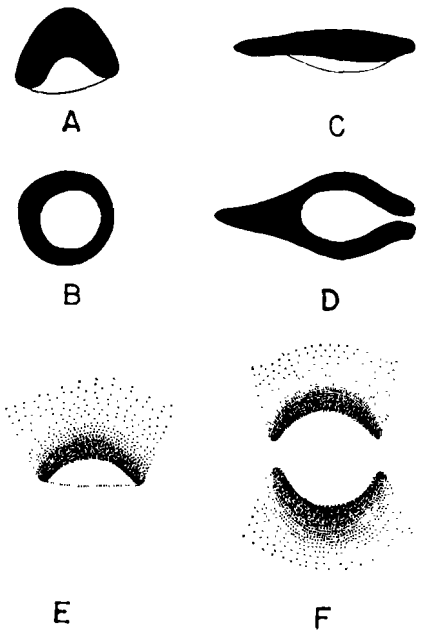

Figure 2. Photophores of holotype: A and B, lateral and ventral views of isthmal photophore; C and D, lateral and ventral views of anal photophore; E and F, lateral and ventral views of pectoral photophore.

posteroventrally and is covered by a mass of translucent tissue (Fig. 2A, B). The middle one (the pectoral) is nearer the surface than the isthmal (Fig. 1A). It too has a black, ventrally directed cup, covered with a translucent cap; its black pigment seems to be associated with the peritoneal lining (Figs. 1A, B; 2E, F). The posterior one (the anal) is close to, or partially embedded in, the skin (Fig. 1A, B). As seen from the ventral side, it has an arrowhead-shaped mass of black tissue surrounding a central translucent cap (Figs. 1B; 2C, D). There may be an opening directed posteriorly toward the anus or the surface from the central part of this photophore (Fig. 2D).

The isthmal photophore of the paratype was removed, and sectioned by William O'Day, using the following procedure: the fish was fixed whole in formalin aboard ship, and then transferred to 72% ethanol for preservation. The photophore was excised and dehydrated for twenty-four hour periods in 100% ethanol, 100% n-propanol, and 100% n-butanol. It was then infiltrated in one cc of pure glycol methacrylate with a polymerization catalyst, and transferred to fresh monomer and polymerized in a gelatin capsule at 60°C. After polymerization, the sections were cut vertically through the photophore at one micron thickness by a Porter-Blum microtome. The sections were stained first with 4% acid fuchsin in water for four minutes, and then with a concentrated solution of toluidine blue in water for five minutes. The sections were mounted on a slide and covered with a Permount cover slip (see Ashley and Feder, 1966).

The isthmal light organ (Fig. 3) is a classical example of a photophore (e.g. see Brauer, 1908, fig. XXX). It consists of a cup of heavy black pigment surrounding an internal body of granular tissue. On examination under high magnification the latter material does not seem to be associated with bacteria, implying that the luminescence of at least this organ is glandular in nature. The cup is closed ventrally by a lens-like layer of cells which separates the luminous tissue from a gelatinous cap. This cap completely covers the ventral aspect of the photophore and may serve to filter, focus, or disperse the light emitted.

The structures of the light organ resemble those found in other fishes, especially the myctophoid inioms. They do not appear to be similar to those described by Haneda (1958) for *Lestidium prolixum* Harry or *Lestrolepis japonicum* (Tanaka). They do, however, look like those found in the family Myctophidae except for the presence of an internal lens. However, since the Paralepididae are so dissimilar to the Myctophidae in other respects, the similarity of the photophore of *L. bigelowi* to those of

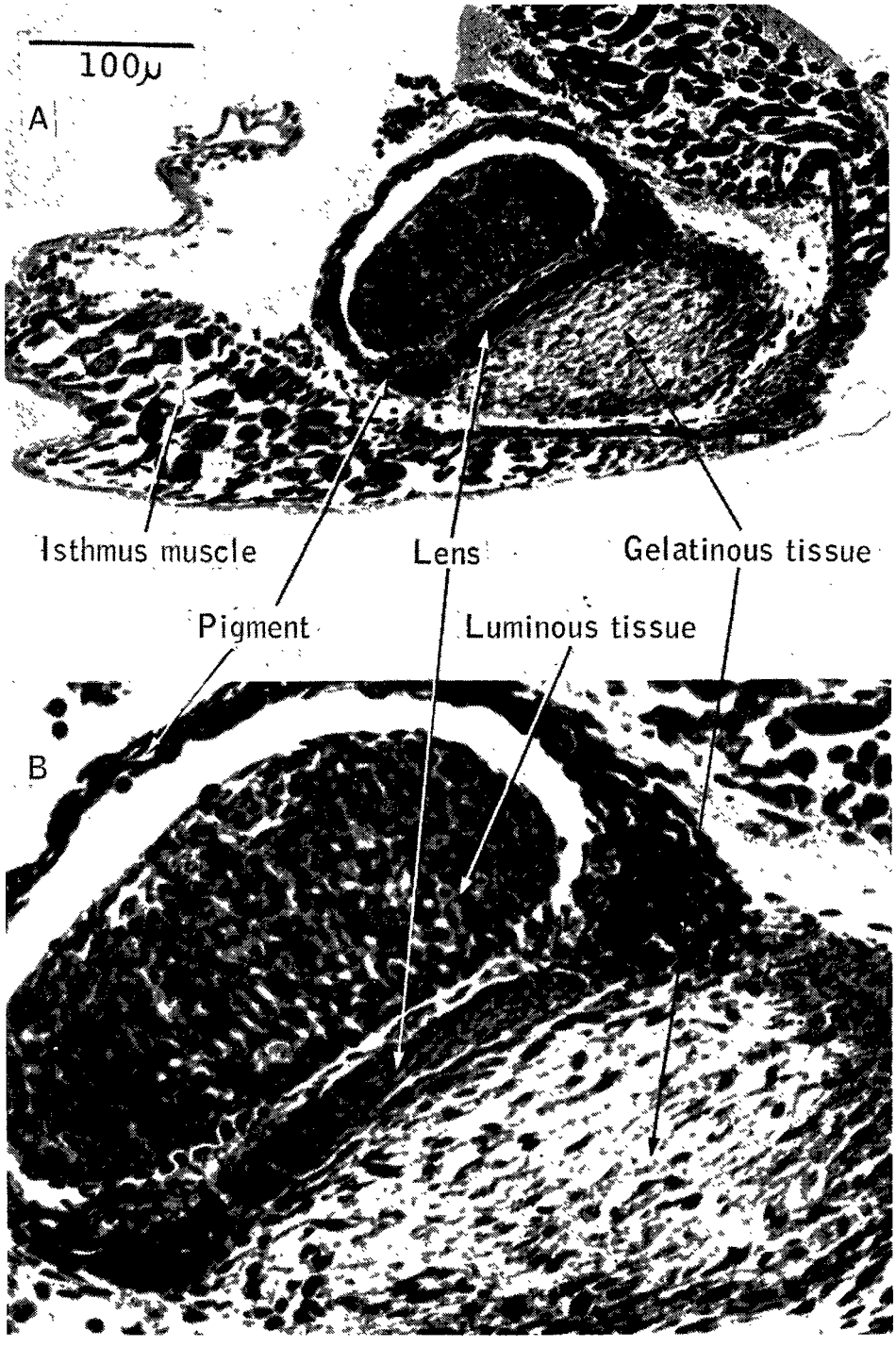

Figure 3. A, a vertical section through isthmal photophore. B, the photophore above, enlarged.

the myctophids is assumed to be due to convergence rather than to close relationship.

The anal photophore of *Lestidium bigelowi* is similar in shape to that discussed by Bertelsen, Theisen, and Munk (1965) for the argentinoid fish, *Rhynchohyalus natalensis* (Gilchrist and von Bonde). Like that of *R. natalensis,* the anal photophore of *L. bigelowi* may be connected to the anus (though posteriorly instead of anteriorly), and its luminescence may thereby also be bacterial in nature. As the anal photophore on the holotype was the only one found, the paratype being mutilated in that region, no sections were made of it; thus the question of whether this luminescence is bacterial or glandular can not now be answered.

SUMMARY

A new species of *Lestidium* was collected in the Indian Ocean in 1964. It most nearly resembles *Lestidium atlanticum* Borodin in proportions and counts, and in some other respects is similar to *Lestidiops jayakari* (Boulenger) and *L. indopacificum* (Ege). It differs from all other paralepidids in possessing discrete photophores. These photophores have a darkly pigmented cap, with opening directed ventrally, and are covered by a gelatinous, translucent mass of tissue. Photomicrographs of the isthmal photophore of the paratype show that it is very similar to those of the Myctophidae, differing significantly only in the possession of an internal lens. This similarity is attributed to convergence rather than to close relationship.

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Systematics and Zoogeography of the Stomiatoid Fishes, *Chauliodus pammelas* and *C. sloani*, of the Indian Ocean

ROBERT H. GIBBS, JR. AND BARBARA A. HURWITZ

Midwater-trawl collections made on two north–south transects in the western Indian Ocean show *Chauliodus pammelas* north of 5° N and *Chauliodus sloani* from 10° N to the Subtropical Convergence. Compared to *C. sloani*, *C. pammelas* has fewer VAV and IC photophores, fewer vertebrae, and greater gill development, with little or no overlap in any of these characters. *C. pammelas* is restricted to the Arabian Sea, the Bay of Bengal, and south of India and Ceylon to 5° N; smaller specimens occur in the upper 300 m, but adults seem most abundant between 500–750 m. The geographic and vertical ranges of *C. pammelas* are correlated with (1) an oxygen-poor layer, where the 1.0 ml/l isopleth occurs at shallow depths, (2) high concentration of nutrients at shallow depths and resultant high productivity, and (3) the distribution of the Red Sea and Persian Gulf water masses. *C. sloani* has wider geographic and vertical ranges than *C. pammelas*, but apparently does not occur at very low oxygen concentrations. There appear to be at least two populations of *C. sloani*: a denser one north of the Frontal Zone (about 10° S) and a less-dense one, with higher photophore and vertebral counts, south of about 23° S, the two separated by a relatively sterile region.

INTRODUCTION

MIDWATER-TRAWL collections from two north–south transects in the western Indian Ocean, from 18° N to 44° S, along latitudes 60° and 65° E, have provided an abundance of specimens of two species of *Chauliodus*, *C. sloani* Bloch and Schneider and *C. pammelas* Alcock, enabling for the first time, a reasonable assessment of their relationship and zoogeography. These collections were made during cruises 3 and 6 of the R/V ANTON BRUUN as part of the American Program in Biology of the International Indian Ocean Expedition and are a portion of the material being used in a cooperative study of the zoogeography of the midwater fishes of the western Indian Ocean.

Recognition of species in the genus *Chauliodus*, in spite of extensive revisionary studies by Ege (1948) and Morrow (1961, 1964) continues to be a perplexing problem. Ege, placing much emphasis on the smaller body photophores, recognized three species in the genus: *C. barbatus* Garman, *C. danae* Regan and Trewavas, and *C. sloani* Bloch and Schneider, the latter with six subspecies. Morrow recognized three of Ege's subspecies of *C. sloani* as species: *C. macouni* Bean, *C. pammelas* Alcock, and *C. schmidti* Ege, but regarded the other two subspecies as invalid. At the same time, he noted geographic variation in *C. sloani*. *C. sloani* has a worldwide distribution, but the other five species are limited to smaller areas, entirely within a single ocean basin. The recent report of the north Atlantic *C. danae* in the Humboldt Current of the southeastern Pacific (Bussing, 1965) provides the only exception, and this needs further study. Crane (1966) discussed the fossil species *C. eximius* (Jordan and Gilbert) relative to the possible evolutionary history of the genus.

Chauliodus sloani and *C. pammelas* are the only species of the genus known from the Indian Ocean. *C. sloani* apparently occurs abundantly throughout most of the Indian Ocean north to about 10° N. In contrast, only about 20 specimens of *C. pammelas* have been reported previously (Alcock, 1890, 1892; Brauer, 1906; Norman, 1939; Ege, 1948; Morrow, 1961), all from north of 5° N, in or adjacent to the Gulf of Aden, Gulf of Oman, Arabian Sea, and Bay of Bengal. Thus, there is little overlap in the geographic ranges of the two species. A record from 7°19′ S, 116°50′ W in the Flores Sea (Weber, 1913) is surely a misidentification.

The two species differ primarily in meristic characters, with *C. pammelas* having fewer photophores and vertebrae than *C. sloani*. With collections available for the first time covering the entire north–south

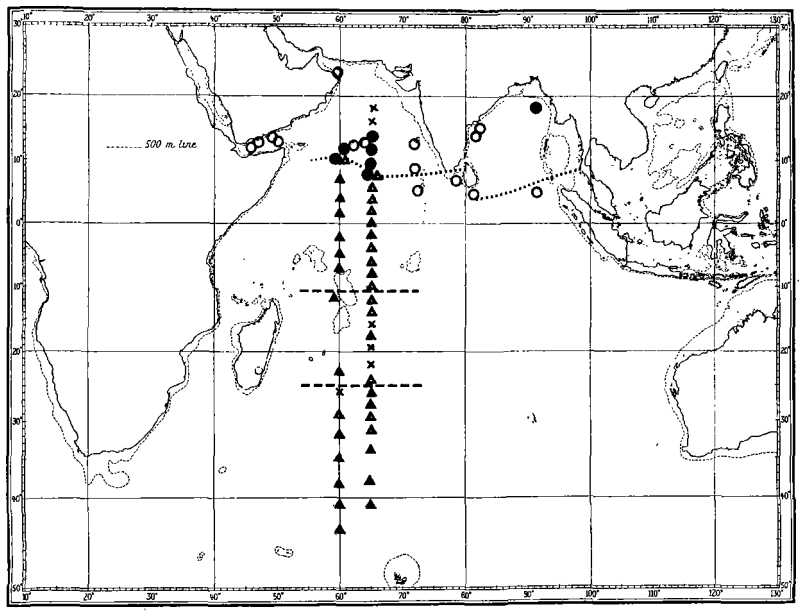

Fig. 1. Midwater-trawl stations of R/V ANTON BRUUN cruises 3 and 6. Unsuccessful trawls indicated by X; captures of *Chauliodus sloani* by triangles, *C. pammelas* by dots; literature records of *C. pammelas* indicated by open circles; dashed lines represent boundaries of three zones of *C. sloani* distribution discussed in text; dotted line is northern limit of *C. sloani* as far as known.

dimension of the ocean as far as the Subtropical Convergence, the possibility that the variability of the meristic characters might be clinal could be examined. Characters other than meristic were scrutinized, but all except one were essentially similar in both species; the structure of the gill rakers proved species-specific. We confirm here that *C. pammelas* is a valid species, on the basis of meristic characters, gill-filament structure, and zoogeography.

MATERIALS

Using a 10-foot Isaacs-Kidd midwater trawl equipped with a cod-end catch-divider (Foxton, 1963), 28 trawls were made on cruise 3, between 13 August and 13 September 1963, and 58 trawls on cruise 6, between 7 May and 4 July 1964. Station positions are shown in Fig. 1, and details of these, as well as of the Foxton device, may be found in the final cruise reports (Anonymous, 1965a, b). During cruise 3, 26 of 28 trawls and 39 of 52 component samples contained *Chauliodus*. For cruise 6, the figures are 20 of 58 trawls and 54 of 103 component samples. The total number of specimens of *Chauliodus* was 52 *C. pammelas* (27 from cruise 3, 25 from cruise 6) and 204 *C. sloani* (74 from cruise 3, 130 from cruise 6). An IIOE collection (USNM 201220, R/V ANTON BRUUN, cruise 1, 18°55′ N, 91°59′ E) of *C. pammelas* confirms the presence of this species in the Bay of Bengal.

The Foxton closing device is designed to collect one sample from the surface to a determined depth and another sample from that depth to the deepest trawling depth. In tests aboard the ANTON BRUUN, the depth of closing for the shallow sample as the trawl descended did not correspond to the depth of opening on the way up. Most of the shallow fraction, however, probably came from the upper 300 m.

The collections are deposited in the U. S. National Museum (USNM) and the Museum of Comparative Zoology, Harvard University.

SYSTEMATICS

Identifications were based initially on the photophore counts given by Morrow (1961). The ranges of these counts, though mutually exclusive, were contiguous, and, with more specimens at hand, we expected overlap. Specimens with atypical photophore counts

TABLE 1. FREQUENCY DISTRIBUTIONS OF THREE MERISTIC CHARACTERS OF INDIAN OCEAN *Chauliodus pammelas* AND *C. sloani*. Northern (N), central (C), and southern (S) populations of *C. sloani* are those shown in Fig. 1 and discussed in the text. Data from specimens collected on R/V ANTON BRUUN cruises 3 and 6 only.

	IC photophores												
	58	59	60	61	62	63	64	65	66	67	68	*N*	$\bar{x}$
pammelas	1	4	12	4								21	59.9
sloani (N)					3	2	24	25	18	11	2	85	65.1
sloani (C)								3	4	3	1	11	66.2
sloani (S)								3	3	8	1	15	66.5
	VAV photophores												
	21	22	23	24	25	26	27	28				*N*	$\bar{x}$
pammelas	11	21	10									42	22.0
sloani (N)			3	22	62	39	16	1				143	25.3
sloani (C)			1	—	9	5	3	1				19	25.6
sloani (S)				2	3	8	9	3				25	26.3
	Total vertebrae												
	50	51	52	53	54	55	56	57	58	59	60	*N*	$\bar{x}$
pammelas	4	10	14	5								33	51.6
sloani (N)				2	7	16	17	31	19	5	2	99	56.6
sloani (C)						2	3	1	1			7	56.1
sloani (S)						3	1	–	6	4		14	57.5

were, indeed, found within the almost allopatric ranges of each species, and there were a number on which photophore counts could not be made.

Vertebral counts, too, were supposedly non-overlapping (Morrow, 1961). The anteriormost several vertebral centra are unossified, only neural and haemal arch elements being present (Crane, 1966; Tchernavin, 1953). When our counts were being made no previous worker on *Chauliodus* had described his method of counting vertebrae, but it seemed logical to us to count only the ossified centra. This method showed a clear modal separation, but did not solve our identification problems. Small specimens have more unossified anterior centra than do larger ones (Crane, 1966). Furthermore, these counts were not comparable with those in the literature. Counts were then made to include the anterior neural arches (omitting the very large, anteriormost element), and this not only conformed to published data, but provided excellent species differentiation. This is the method used by Crane (1966), whose work was published after our study was completed.

Table 1 summarizes the three meristic characters that are considered useful: VAV photophores (in the ventral row between pelvic insertion and anal origin), IC photophores (the total row, from anterior isthmus to end of row on caudal peduncle), and vertebral counts. Frequency distributions of IC counts show no overlap, and those of VAV and vertebral counts barely overlap.

Using a combination of these three counts, we could identify all but two specimens with confidence. One doubtful specimen (USNM 201191, 45.1 mm standard length) was taken during cruise 3 at 6°54′ N, 59°55′ E in a deep Foxton fraction together, with a single specimen that is clearly *C. sloani*. The shallow fraction of the same trawl contained one specimen of *C. sloani*, and the immediately preceding trawl contained four specimens of *C. sloani*. The other doubtful specimen (USNM 201194, 100.2 mm) was taken during cruise 3 at 01°48′ S, 59°50′ E in a fraction that accumulated ahead of the twisted cod-end of the net; if this were *C. pammelas*, the occurrence would be considerably farther south than any other. In the two Foxton fractions of the same trawl were seven specimens of *C. sloani*, and the immediately preceding tow took ten *C. sloani*.

Morrow (1961) and Ege (1948) suggested other possible differentiating characters. Comparison of published morphometric data indicated considerable overlap in every char-

acter, so we made no attempt to check these. The number of lower jaw teeth were recorded as five in *C. pammelas*, usually more than five in *C. sloani*; we found the range of variation similar in both. There are small denticles on the upper posterior edge of the lower jaw, their number varying directly with size. Published data suggested that large *C. pammelas* have more denticles than large *C. sloani*, but in our material both species had a similar high number. The small photophores (SM), in the area between the lateral and ventral rows of serial photophores, have been reported as different in the two species (*C. pammelas* $0+3+1$ or $0+4+0$; *C. sloani* $1+3+1$ or $1+4+0$ in the Indo-Pacific). We found all such variants in both species, and the most common variants were the reverse of those previously used to distinguish the species.

The structure of the gills, not previously used as a taxonomic character in *Chauliodus*, enabled us to identify our two doubtful specimens as *C. sloani*. The gill filaments of *C. pammelas* are longer and have longer, thinner, and more-numerous lamellae than those of *C. sloani* (Fig. 2). Two methods of expressing this relationship are useful. The length of the shortest individual filament at the angle of the first gill arch (from origin at posterior surface of arch to tip) is as long as or longer than the diameter of the lens of the eye in *C. pammelas*; in *C. sloani* it is, at most, about two-thirds of the lens diameter. The length of the filament at the junction of hypobranchial and ceratobranchial of the first arch is equal to or greater than the fleshy orbit diameter in *C. pammelas*, but not more than about three-fourths of the fleshy orbit diameter in *C. sloani*. This relationship holds in both species at least for specimens larger than about 40 mm SL. The number of lamellae on a side of a filament was counted in a single specimen each of *C. pammelas* (USNM 201193, 169.9 mm) and *C. sloani* (USNM 201198, 171.6 mm). The range of number of lamellae per side on a filament was 13–52 for *C. sloani*, 60–117 for *C. pammelas*. The longest filament (at the hypobranchial–ceratobranchial junction) in *C. sloani* was 3.47 mm long and had 52 lamellae—an average of about 15 lamellae per mm. The corresponding filament of *C. pammelas* was 5.87 mm long and had 117 lamellae—averaging about 20 lamellae per mm. The greater gill development of *C. pammelas* must be an adaptation enabling it to inhabit waters of low oxygen content. This type of adaptation has been noted previously, *viz.* Ebeling and Weed (1963) and Parin (1961), for midwater fishes.

Fig. 2. Excised first gill arches: (left) *Chauliodus sloani*, 171.6 mm; (right) *C. pammelas*, 169.9 mm. Greater development of filaments of *C. pammelas* is correlated with its occurrence in the oxygen-poor layer.

ZOOGEOGRAPHY

Geographic distribution.—The almost complete separation of the geographic ranges of *C. pammelas* and *C. sloani* warrants speculation regarding the factors responsible for maintenance of the separation. Probably the integrity of the species results from their adaptation and restriction to different sets of hydrological features (see Haffner, 1952).

The range of *C. pammelas* is indicated in Fig. 1, where, in addition to records from the two north–south transects, all reasonably verifiable literature records are plotted. These include Alcock (1890, 1892), Brauer (1906), Norman (1939), and Ege (1948). Alcock's (1890) records of *C. sloani* from the Bay of Bengal are regarded, on the basis of his photophore counts, as *C. pammelas*. His original description (Alcock, 1892) of *C. pammelas* separates his new species from what he called *C. sloani* by characters that are now considered worthless, but he was comparing his single specimen with others of the same species. Weber (1913) tentatively identified a single specimen from the Flores Sea as *C. pammelas*, but this was certainly a misidentification. The total range appears to include all, or a considerable part, of the Arabian Sea, including the Gulf of

Aden and Gulf of Oman, and the Bay of Bengal south to about 5° N, the two regions narrowly continuous just south of the tip of India and Ceylon.

The northern boundary of the range of *C. sloani* overlaps the southern boundary of *C. pammelas* between 5°–10° N, and, judging mainly from the two transects reported here, *C. sloani* probably occurs throughout the rest of the Indian Ocean, at least into the Subtropical Convergence. The genus *Chauliodus* apparently occurs rarely in true Subantarctic water.

Vertical distribution.—Depths of capture cannot be stated confidently. For this discussion, we use 0–300 m as an approximation for all shallow Foxton fractions. Trawls made without a Foxton device are not considered.

C. pammelas was captured in ten trawl hauls, of which five had both shallow and deep fractions. Two shallow fractions contained *C. pammelas*; the largest of the seven specimens was 140 mm. Four deep fractions were successful: two, towed at depths of 500 to 750 m, caught 14 specimens up to 205 mm; two, towed at depths greater than 750 m, caught only four specimens, none more than 50 mm. This suggests that, while smaller *C. pammelas* may occur in the upper 300 m, the adults occur mostly between 500–750 m, and probably in the upper part of this stratum.

C. sloani was captured in 56 trawl hauls, of which 48 had both shallow and deep fractions. Thirty-four shallow fractions contained *C. sloani*. Five of the 17 shallow fractions representing night collections took specimens longer than 150 mm; of the other 17 shallow fractions (four day only, 13 night and day), only one took a large specimen, the next largest being 108 mm. Although the possibility of net avoidance by larger fish during daylight hours cannot be eliminated, these data suggest that *C. sloani* over 150 mm migrate with darkness to levels above 300 m. This is somewhat at variance with the conclusions of Haffner (1952), who indicated that very few large specimens migrated above 400 m.

Forty deep fractions were successful. The catch of specimens longer than 150 mm could not be associated confidently either with time of day or with depth strata (500–750 m, 750–1000 m, or more than 1000 m). However, the presence of large *C. sloani* in 17 of the 40 deep fractions (compared to six of 34 shallow fractions) indicates that larger specimens probably live predominantly at depths greater than 500 m, and the lack of stratification suggests that they inhabit a wider range of depths than *C. pammelas*.

Oceanographic correlations.—The distribution of *C. pammelas* can be associated with three oceanographic features: (1) well-defined oxygen-poor areas, (2) the relatively shallow occurrence of high nutrient levels, and (3) the Red Sea and Persian Gulf water masses and their movements.

The presence of an oxygen-poor layer throughout the Arabian Sea is fairly well documented (Rochford, 1966; Ryther and Menzel, 1965; Ivanenkov, *et al.*, 1964; Vinogradov and Voronina, 1961; data in Anonymous, 1965a, b). In the upper 200 m to as far south as 5° N, dissolved oxygen decreases rapidly with depth to less than 1.0 ml/l. South of 5° N the 1.0 ml/l isopleth descends to about 800–1000 m, below which depth it recurves northward and descends. The 1.0 ml/l isopleth encloses a core of water in which the oxygen concentration becomes less than 0.1 ml/l or may be undetectable by routine methods; the 0.1 ml/l isopleth appears to reach southward to 10° N. A similar situation apparently exists in the Bay of Bengal (Ivanenkov, *et al.*, 1964; data in Anonymous, 1964), but is not so thoroughly documented. Here, the lowest levels of oxygen, less than 0.1 ml/l, are not as extreme as in the Arabian Sea, but the pattern is otherwise comparable.

The southern limit of the range of *C. pammelas* at about 5° N in the Arabian Sea corresponds closely to the southern extension of the 1.0 ml/l oxygen isopleth in the upper 200 m. The northern limit of *C. sloani* is at about the same latitude; only a few larvae and juveniles were taken at the same stations as *C. pammelas*.

The basic cause of an oxygen minimum layer is probably biological, although its position and extent may depend upon circulation (Wyrtki, 1962). The oxygen minimum of the Arabian Sea is associated with a rapid increase in nutrients with depth (Ryther and Menzel, 1965). For example, phosphate levels at 200 m in the Arabian Sea are about 2.0 mg A/l, a concentration that is not usually reached until 600–1000 m south of 5° S (data in Anonymous, 1965a, b). With such supplies of nutrients in the upper waters.

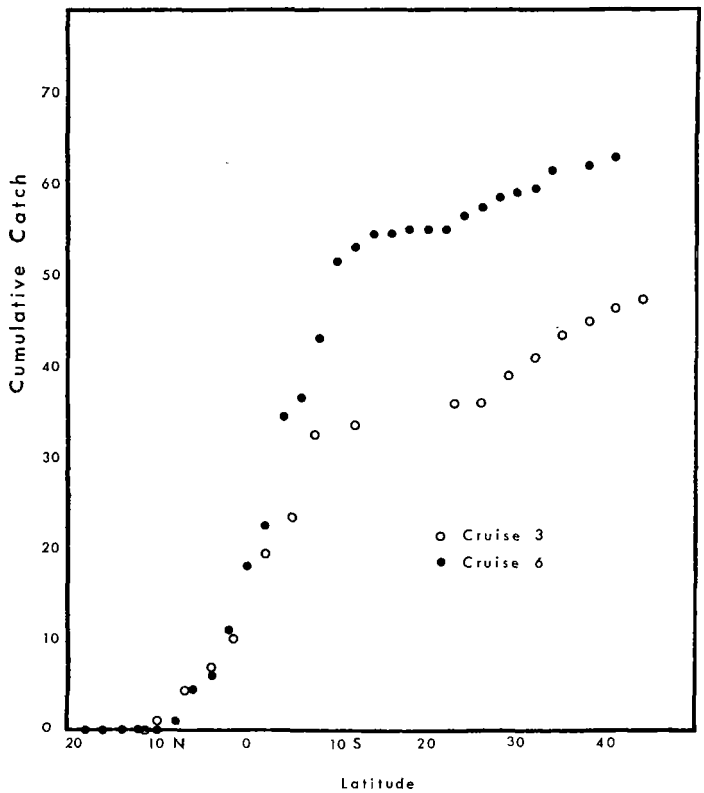

Fig. 3. Cumulative catch of *Chauliodus sloani* taken during R/V ANTON BRUUN cruises 3 (open circles) and 6 (dots). All Foxton fractions of a single trawl counted together. Where two trawls were made at one station, the mean number is used.

oxygen consumption by living organisms and oxidation of dead organic matter doubtlessly rapidly deplete the oxygen supply at relatively shallow depths, and the oxygen is not replenished until the influence of northward-flowing water masses is felt at considerable depths.

Rochford (1964, 1966) has traced paths of flow of two high-salinity water masses from the Arabian Sea region to the Bay of Bengal. One of these, the Red Sea water mass, enters the Arabian Sea with its core at about 700–800 m, becomes slightly shallower as it spreads out to the east at about 500–600 m and deeper as it extends southward at depths up to 1000 m. The eastern portion of the Red Sea water passes south of India mainly in channels between the Maldive and Chagos island- groups, and reaches the Bay of Bengal. The second pertinent water mass has been called Persian Gulf water (Rochford, 1964). At a core depth of 200–300 m, this water occupies all or most of the Arabian Sea, spreads southward and eastward, passes mainly between the Maldive and Chagos islands, and enters the Bay of Bengal. Either of these two water masses could transport, or at least provide a pathway for, *C. pammelas* between the Arabian Sea and the Bay of Bengal. The Red Sea water occurs at the depths which we believe to be the center of abundance of *C. pammelas* adults; Persian Gulf water occupies depths that are probably inhabited by the larvae and juveniles. Although *C. pammelas* has been reported south of the southern tip of India to about 5° N (Norman, 1939; Ege, 1948), we believe that these specimens were transients, and that breeding populations are limited to the Arabian Sea and Bay of Bengal.

In contrast, *C. sloani* appears to inhabit a wide range of water types in the Indian Ocean and around the world, but is not adapted for the kind of environment typified by an oxygen-poor layer. Besides not occurring in such areas in the Arabian Sea and

Bay of Bengal, *C. sloani* apparently also does not inhabit the eastern tropical Pacific, where an oxygen-poor layer and high productivity also prevail (Bennett, 1963; Wooster and Cromwell, 1958); the latter region is occupied by *C. barbatus*.

The close association of the distribution of *C. pammelas* and *C. sloani* with oxygen concentration is confirmed by the relatively greater development of gill filaments and their lamellae in *C. pammelas* than in *C. sloani* (*cf.* Ebeling and Weed, 1963, for melamphaids; Parin, 1961, for myctophids and gonostomatids).

The cumulative catch curve for *C. sloani* (Fig. 3) suggests that this species has at least two distinct populations. Population density is high north of about 10° S. Between 10° and about 25° S, the catch was extremely small, and south of this it was again higher, but not nearly as high as in the north. These zones are correlated with hydrological conditions. Waters to a depth of at least 1000 m from both north and south have a general movement toward 10° S, at which their meeting causes a surface divergence, called the Frontal Zone (Ovchinnikov, 1961; Rochford, 1966). Here, isopleths of salinity and oxygen concentration are essentially vertical to a considerable depth. The Frontal Zone is at the north side of the South Equatorial current and is at the boundary between the Indian Ocean Equatorial and Central water masses as delimited by Sverdrup, Johnson, and Fleming (1942). The movement of the upper waters from the Frontal Zone carries northward at least to 5° N, but southward only to about 20° S. The combined effects of northward transport of nutrient-rich surface waters from the Frontal Zone and southward movement of highly productive Arabian Sea waters maintains a productive situation north of 10° S, but to the southward surface waters rapidly become relatively sterile.

We believe there is a population of *C. sloani* north of the Frontal Zone that has little interchange of adults with a second population that is centered south of 23° S and is perhaps directly associated with the highly productive waters of the Subtropical Convergence. The sterile region that extends to about 23° S is probably an effective, but not an absolute, barrier. Any member of either population that might reach the Frontal Zone would be more likely to be carried northward than southward, so that gene exchange is probably largely from south to north. Meristic data for the southern population are too few to allow confirmation of their distinctness, but counts definitely tend to be relatively high (Table 1).

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RADIOLARIA IN PELAGIC SEDIMENTS FROM THE INDIAN AND ATLANTIC OCEANS

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ABSTRACT

The distribution of Radiolaria in pelagic Indian Ocean sediments from middle (30°–45° S.) and low (10° N.–30° S.) latitudes has been determined and described. Radiolaria have been found to be abundant in two areas: (1) a low (10° N. to approximately 20° S.) latitude belt; and (2) a middle (35° S. to 45° S.) latitude belt. Forty-five species of Radiolaria (Spumellaria and Nassellaria) have been described, including one new species and two new subspecies. Of these twenty-two contribute to a recognizable low latitude assemblage, and seven form a distinctive middle latitude assemblage. The recognition of these assemblages now provides a potentially useful tool in the interpretation of Quaternary stratigraphy.

As an appendix, a preliminary survey of radiolarian distribution in pelagic sediments from the Atlantic Ocean, from between 60° N. and 40° S., was made. In general, Radiolaria are neither as abundant nor as well preserved as in the Indian Ocean where assemblages are comparable in richness to those of the Pacific. However, Radiolaria do occur in some abundance equatorially (10° N.–10° S.), in middle northern (35°–45° N.), and in middle southern (25°–40° S.) latitudes. An examination of nine samples from these areas has shown that, in general, species confined to low or middle latitudes in the Indian Ocean are similarly restricted in the Atlantic.

INTRODUCTION

DURING RECENT YEARS, oceanographic attention has been concentrated to a large degree on the Indian Ocean (Knauss, 1961; Snider, 1961). The primary object of this paper is to describe the distribution of Radiolaria in Recent[1] pelagic Indian Ocean sediments from middle (30°–45° S.) and low (10° N.–30° S.) latitudes. The areas in which Radiolaria occur had first to be determined. Preliminary investigation by Riedel (1951*a*, *b*) had shown that Radiolaria are abundant in tropical areas of the Indian Ocean, but no overall survey had ever been made. Second, it had been suggested by Riedel (1958) that radiolarian assemblages from various latitudes might be distinguished one from another and, therefore, be as useful as foraminifera (see, for example, Phleger, Parker, and Peirson, 1953) for palaeoceanographic interpretation of pelagic sediments. Tropical and Antarctic faunas had been observed to differ markedly, but no previous investigation had been made of transitional stages between the two.

The area treated in this study extends from 20° E. to 120° E., though the limits of the Indian Ocean are usually (International Hydrographic Bureau, 1950; Fairbridge, 1954) taken as 20° E. and about 147° E. A southern limit of 45° S. has

[1] The term Quaternary has been avoided so as not to imply that a stratigraphic study has been made. Since near-surface samples were used, it is probable that all the sediments examined are, in fact, Recent rather than Pleistocene. It is, nevertheless, possible that a few *in situ* or reworked Pleistocene assemblages are included in the material studied. If some older or mixed samples are included, it is unlikely (because of what is known of the rates of evolution of radiolarian species and the "dilution" of older forms during reworking) that they would appreciably affect the taxonomic aspects of this paper. The species–distributional aspects would be affected only to the extent that the geographic ranges indicated herein may be a little wider (or, under certain circumstances, narrower) than those of living organisms.

been imposed so as not to repeat work done in the Antarctic by J. D. Hays. Hays (1965) observed and described a striking change in fossil radiolarian assemblages across the Polar Front.

As an appendix to this study, a preliminary survey of radiolarian distribution in Recent pelagic sediments from the Atlantic Ocean, between 60° N. and 40° S., was made. The object of this part of the paper is to determine whether or not particular species of Radiolaria, characteristic of low or middle latitudes in the Indian Ocean, are similarly distributed in the Atlantic.

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This paper represents a major portion of the author's doctoral dissertation for the University of Cambridge (Clark, 1965). Research was carried out partly in the Department of Geology of the University of Cambridge, where facilities were made available through the kindness of Professor O. M. B. Bulman, and partly at the Scripps Institution of Oceanography, La Jolla, California. I wish to thank my supervisor in Cambridge, Dr. B. M. Funnell, for his guidance and advice throughout the early stages of my work.

In La Jolla, research was under the supervision of W. R. Riedel, to whom I am most grateful, not only for his help and encouragement during the final year of study, but also for instilling in me the initial interest in Radiolaria and for ensuring that that interest never waned. My work in the United States was sponsored by the National Science Foundation (grants G-22255 and GP-3354). Shiptime, during which S.I.O. samples were collected, was financed by the Office of Naval Research, Contract No. 2216(23).

PREVIOUS INVESTIGATIONS IN THE INDIAN AND ATLANTIC OCEANS

Radiolarian literature is divided into two periods by Ernst Haeckel's monumental "Report on the Radiolaria collected by H.M.S. *Challenger* during the years 1873–1876." The most important and most prolific pre-Haeckelian author was C. G. Ehrenberg. Between 1838 and 1876 he published a large number of papers on Quaternary and Tertiary Radiolaria in the Monatsberichte and Abhandlungen of the Könglichen Akademie der Wissenschaften, Berlin. His material included one sample from the Indian Ocean (Ehrenberg, 1872*b*) and several from the Atlantic (Ehrenberg, 1854*a*).

Haeckel (1887), in his report on the Radiolaria collected by the "Challenger" Expedition, monographed his own preliminary work and the work of previous researchers (Ehrenberg and less prolific authors such as Stöhr, 1880). Using, for the most part, skeletal remains collected by H.M.S. *Challenger,* he formulated the almost purely artificial radiolarian classification now used. He was concerned mainly with the description of species, and few distributional data are given. Previously published, quantitative reports of radiolarian occurrences in Indian and Atlantic Ocean sediments are incorporated in the preface to the report.

Even after Haeckel's report, the number of descriptive references to Recent Radiolaria is limited, and there is a particular lack of descriptions of skeletal remains in sediments (i.e., Spumellaria and Nassellaria). Some important contribu-

tions concerning Indian and Atlantic Ocean Spumellaria and Nassellaria are by Cleve (1900, 1902, 1904), Haecker (1908), and Dreyer (1913).

The most extensive post-Haeckelian work on planktonic Spumellaria and Nassellaria is that of Popofsky (1912, 1913) in the reports of the Deutsche Südpolar-Expedition. In 1917 he published "Die Collosphaeriden der Deutschen Südpolar-Expedition 1901–1903. Mit Nachtrag zu den Spumellarien und Nassellarien." This paper, containing 27 species descriptions, has previously been omitted from most bibliographies and synonymies, and was recently brought to the author's attention by Helen P. Foreman. It should be noted that many of Popofsky's 208 species descriptions were based on single specimens. Most of the efforts of early researchers were concentrated on defining a large number of species, rather than on investigating variations within a particular species.

During the last decade, an attempt has been made to relate Recent species distribution to ecology, to carry out population studies, and to seek a more natural classification for the Radiolaria (Riedel, 1957, 1958). Preliminary work by Riedel on these problems in the Pacific and Antarctic has demonstrated the usefulness of Radiolaria, both as indicators of ecological conditions, and as Cenozoic stratigraphic markers.

Quantitative reports of radiolarian distribution in Recent Indian Ocean sediment have been published by Murray (1910), Schott (1939), Keunen (1939), Riedel (1951*a*, *b*), and Olausson (1960). All these papers have now been eclipsed by the work of Bezrukov (1964) (cf. p. 9, below).

A few workers have published quantitative information about the distribution of Radiolaria in Recent Atlantic sediments. The most important of these are by Murray and Chumley (1924), Correns (1939), Prajte (1951), and Olausson (1960). The information contained in these papers has been used in conjunction with data presented below (p. 94) to compile a map of radiolarian distribution in Recent Atlantic Ocean sediments (p. 97).

METHODS OF STUDY

All samples were treated in the following way: The sediment (10–20 gm) was first disaggregated by heating gently in 30 cc of a solution of tetrasodium pyrophosphate (approximately 1.5 gm) and 35 percent hydrogen peroxide until effervescence ceased. The sample was decalcified by adding hydrochloric acid and then sieved wet through a 64μ mesh. The coarse fraction was washed thoroughly, transferred to a beaker, and allowed to settle. Using a wide-mouthed eyedropper, a small amount of residue was then placed on a 3″ × 1″ glass slide, spread evenly, and allowed to dry. A drop of Xylol and of Canada balsam were added, the preparation was covered with a cover glass (1½″ × ⅞″, no. 1 thickness), and was dried in an oven at 65°C for two weeks. The remaining siliceous residue was dried and preserved. Strewn slides prepared in this manner and used in conjunction with an England Finder (Riedel and Foreman, 1961) were found to be most satisfactory for routine examination. A balsam-mounted smear slide of untreated material was also made for each sample.

It is frequently necessary to view radiolarian skeletons from a number of different angles. This is done by preparing a slide as described above, but examining

it while the Canada balsam is still fluid. The skeletons can be made to rotate by pushing gently on the cover glass with a needle or pencil. In some cases, an outer shell must be broken so as to examine the inner structure more closely; this can be done by tapping gently on the cover glass.

Rarely, it is necessary to make a thin section of a radiolarian skeleton in order to see clearly the inner structure. First, the Radiolaria in question must be picked. This is most easily accomplished by using the follicle end of an eyebrow or eyelash rather than a brush. The specimen is then mounted in gum tragacanth in the desired orientation, covered with a thin layer of Canada balsam, and dried on a hot plate. Using the very finest carborundum, the Canada balsam is ground down to the desired plane in the radiolarian skeleton. It is necessary to examine the slide frequently during grinding, and each time it must be cleared and imbedded grains of carborundum washed away with a few drops of Xylol and rehardened on the hot plate.

Both Polaroid and 35 mm photographs were used extensively and were found to be an invaluable aid in routine study. A Zeiss 35 mm attachment camera and Agfa IFF (ASA 25) film were used to take photographs for publication. Prints were made on Kodak Polycontrast paper using a number 5 filter.

Drawings were based on examination of numerous specimens in "wet" preparations and have been reduced to half their original size during reproduction.

INDIAN OCEAN SAMPLE DESCRIPTIONS

Explanation

A number of different sampling methods were used to collect the material on which this study is based. British Museum (Natural History) samples (B.M.) were, in all cases except two, dried sediments which had originally been taken as grab samples by several expeditions during this century and the last. Two samples (Mabahiss 135 and Discovery 2899) were from the tops of dried cores. Samples obtained from the Department of Geodesy and Geophysics, Cambridge (D.G.G.) and from the Scripps Institution of Oceanography (S.I.O.) were from the tops or within 7 cm of the top of deep-sea, open-barrel, gravity cores. These were all received in a wet condition. Samples from the Lamont Geological Observatory (L.G.O.) were from the tops of dried cores.

In the following descriptions (of both Indian Ocean and Atlantic Ocean samples) latitude and longitude are given to the nearest minute; 0.5 of a minute or over has been rounded to the next highest minute. Depths of samples obtained from the Scripps Institution of Oceanography, the Lamont Geological Observatory, and the Department of Geodesy and Geophysics, Cambridge, are considered to be accurate and have been corrected by Matthews' tables (1939) for variations in the velocity of sound in sea water. Depths for British Museum samples have been accepted as originally given and are probably of varying accuracy. Those depths originally recorded in fathoms have been converted to meters (1 fm = 1.83 m).

In most cases the name of the collecting ship is given with the original sample number. Samples obtained from the Scripps Institution of Oceanography are designated according to the code letters of particular expeditions (LSDA,

"Lusiad-Argo"; LSDH, "Lusiad-Horizon"; MSN, "Monsoon"). The letter G indicates a core collected by a simple, open-barrel, gravity corer.

The character of each sample was determined by examining smear slides of untreated material. Sediment descriptions are purely qualitative; for example, a relative decrease in the amount of silica present is indicated by the terms siliceous ooze, siliceous-calcareous ooze, calcareous-siliceous ooze, and calcareous ooze with few siliceous microfossils. Radiolarian abundances are given relative to the non-calcareous fraction larger than 64 microns, and were determined by examining strewn slides.

Samples used for counts of species are marked with an asterisk, and are plotted in figure 1 (p. 9).

Descriptions

Marsden Square

28 5°48′ N., 81°58′ E., 4,532 m; Sealark 191, Oct. 1907; B.M. (M7527); calcareous-silty clay with few siliceous microfossils; few, well-preserved Radiolaria.

*29 2°37′ N., 80°00′ E., 4,033 m; Serpent (?) 96, 16 Mar. 1869; B.M. (M7866); highly calcareous clay with few siliceous microfossils; abundant, quite well-preserved Radiolaria.

29 4°34′ N., 72°30′ E., 2,727 m, top of core; Mabahiss 135, 18 Feb. 1934; B.M. (96626 [A50]); calcareous ooze with few siliceous microfossils, except for many sponge spicules; moderately abundant, well-preserved Radiolaria.

30 2°45′ N., 60°15′ E., 4,810 m, top of core; Discovery 5125, 4 Sept. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; moderately abundant, well-preserved Radiolaria.

30 2°55′ N., 59°53′ E., 4,700 m, top of core; Discovery 5135, 6 Sept. 1963; D.G.G.; calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

*30 5°34′ N., 61°57′ E., 3,566 m, top of core; Discovery 5112, 31 Aug. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; abundant, slightly corroded Radiolaria.

30 5°35′ N., 61°56′ E., 3,557 m, top of core; Discovery 5122, 3 Sept. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; abundant, slightly corroded Radiolaria.

30 5°35′ N., 61°57′ E., 3,566 m, top of core; Discovery 5116, 1 Sept. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; abundant, slightly corroded Radiolaria.

30 5°48′ N., 61°47′ E., 4,042 m, top of core; Discovery 5110, 31 Aug. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; abundant, slightly corroded Radiolaria.

30 6°55′ N., 66°56′ E., 4,111 m, top of core; Discovery 2899, 4 Nov. 1951; B.M. (1954, 35); calcareous ooze with few siliceous microfossils; few, corroded Radiolaria.

31 1°54′ N., 56°11′ E., 4,810 m, top of core; Discovery 5139, 8 Sept. 1963; D.G.G.; calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

*31 2°55′ N., 56°35′ E., approximately 4,796 m, top of core; Owen CB, 19 Apr. 1962; D.G.G.; clayey calcareous-siliceous ooze with many discoasters; abundant, well-preserved Radiolaria.

67 11°07′ N., 54°03′ E., 4,033 m, top of core; Discovery 5226, 11 Nov. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria.

327 5°32′ S., 80°30′ E., 5,167 m, top of core; Vema 19-172, 1 Aug. 1963; L.G.O.; silt, mostly quartz fragments; Radiolaria rare.

*328 5°33′ S., 72°27′ E., 2,551 m; Sealark 17, 20 July 1905; B.M. (M7461); clayey, calcareous ooze with few discoasters and few siliceous microfossils, except for many sponge spicules; abundant, well-preserved Radiolaria.

*329 2°27′ S., 66°59′ E., 3,713 m, 0–2 cm; Vema 14–97, 21 May 1958; L.G.O.; clayey, calcareous ooze with few discoasters and few siliceous microfossils; abundant well-preserved Radiolaria.

Marsden Square

*329 7°33′ S., 61°06′ E., 3,691 m; SEALARK 180, 8 Nov. 1905; B.M. (M7468); clayey, calcareous-siliceous ooze; abundant, well-preserved Radiolaria.

*329 8°25′ S., 65°38′ E., 4,082 m; SEALARK 52, 29 July 1905; B.M. (M7469); clayey, calcareous-siliceous ooze; abundant, well-preserved Radiolaria.

330 2°10′ S., 57°25′ E., 4,389 m, top of core; DISCOVERY 5171, 28 Sept. 1963; D.G.G.; calcareous ooze with many discoasters and few siliceous microfossils; abundant, well-preserved Radiolaria (few admixed Tertiary forms, probably Eocene).

330 2°12′ S., 57°20′ E., 4,407 m, top of core; DISCOVERY 5177, 30 Sept. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; moderately abundant, well-preserved Radiolaria (few admixed Tertiary forms, probably Eocene).

*330 3°33′ S., 51°29′ E., 5,102 m, top of core; DISCOVERY 5165, 25 Sept. 1963; D.G.G.; calcareous-siliceous ooze; abundant, well-preserved Radiolaria.

330 3°34′ S., 50°29′ E., 5,084 m, top of core; DISCOVERY 5207, 30 Oct. 1963; D.G.G.; calcareous-siliceous ooze with few discoasters; abundant, slightly corroded Radiolaria.

330 6°07′ S., 56°38′ E., 2,674 m; SEALARK 175, 6 Nov. 1905; B.M. (M7482); silty, clayey, calcareous ooze with few siliceous microfossils, except for many sponge spicules; abundant, well-preserved Radiolaria.

*330 6°39′ S., 54°16′ E., 3,822 m, top of core; DISCOVERY 5180, 6 Oct. 1963; D.G.G.; calcareous-siliceous ooze; abundant, well-preserved Radiolaria.

*330 9°49′ S., 56°29′ E., 3,890 m, 2–5 cm; LSDH 18G, 20 Oct. 1962; S.I.O.; calcareous-siliceous ooze with few discoasters; abundant, well-preserved Radiolaria.

331 1°41′ S., 42°13′ E., 2,259 m, top of core; DISCOVERY 5144, 17 Sept. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria.

331 1°42′ S., 42°15′ E., 2,084 m, top of core; DISCOVERY 5201, 21 Oct. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria.

331 2°24′ S., 43°24′ E., 3,557 m, top of core; DISCOVERY 5149, 19 Sept. 1963; D.G.G.; calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

331 2°32′ S., 44°56′ E., 4,170 m, top of core; DISCOVERY 5152, 20 Sept. 1963; D.G.G.; calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

*331 2°34′ S., 44°53′ E., 4,151 m, top of core; DISCOVERY 5194, 15 Oct. 1963; D.G.G.; calcareous-siliceous ooze; abundant, well-preserved Radiolaria.

331 2°48′ S., 47°03′ E., 4,810 m, top of core; DISCOVERY 5155, 21 Sept. 1963; D.G.G.; calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

331 2°51′ S., 47°01′ E., 4,810 m, top of core; DISCOVERY 5190, 13 Oct. 1963; D.G.G.; calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

331 3°30′ S., 49°40′ E., 5,047 m, top of core; DISCOVERY 5160, 23 Sept. 1963; D.G.G.; calcareous ooze with few siliceous microfossils; few, corroded Radiolaria.

331 3°31′ S., 48°23′ E., 4,910 m, top of core; DISCOVERY 5204, 28 Oct. 1963; D.G.G.; calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

*361 11°38′ S., 109°33′ E., 4,612 m, 1–4 cm; MSN 34G, 8 Nov. 1960; S.I.O.; silty, siliceous-calcareous ooze; abundant, well-preserved Radiolaria.

*361 12°22′ S., 101°25′ E., 4,771 m, 0–2 cm; MSN 39G, 21 Nov. 1960; S.I.O.; siliceous-calcareous ooze with few discoasters; abundant, well-preserved Radiolaria.

*362 10°30′ S., 99°00′ E., 5,461 m, 0–2 cm; MSN 40G*a*, 22 Nov. 1960; S.I.O.; silty (partly pyroclastic), siliceous ooze; abundant, well-preserved Radiolaria.

*362 11°30′ S., 94°41′ E., 5,554 m, 5.5–7 cm; MSN 42G, 24 Nov. 1960; S.I.O.; clayey, silty, siliceous ooze; abundant, well-preserved Radiolaria.

362 18°11′ S., 99°24′ E., 5,759 m, 0–2 cm; VEMA 19–158, 21 July 1963; L.G.O.; radiolarian clay with many volcanic shards; few, corroded Radiolaria.

*363 12°44′ S., 82°01′ E., 5,138 m, 0–2 cm; VEMA 19–168, 29 July 1963; L.G.O.; clayey, silty (partly pyroclastic), siliceous ooze; abundant, slightly corroded Radiolaria.

Marsden Square

*363 18°13′ S., 86°43′ E., 4,500 m, 3–4 cm; MSN 46G, 28 Nov. 1960; S.I.O.; clayey, silty (partly pyroclastic), calcareous-siliceous ooze with many discoasters and few zeolites; abundant, well-preserved Radiolaria.

*364 12°58′ S., 75°01′ E., 5,226 m, 0–3 cm; MSN 50G, 1 Dec. 1960; S.I.O.; siliceous ooze; abundant, well-preserved Radiolaria.

*365 14°39′ S., 63°49′ E., approximately 3,658 m, top of core; OWEN CA, 17 Feb. 1962; D.G.G.; clayey, calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria.

*365 17°48′ S., 62°40′ E., 3,738 m, 3.5–7 cm; MSN 55G, 6 Dec. 1960; S.I.O.; calcareous ooze with few discoasters and few siliceous microfossils; abundant, well-preserved Radiolaria.

366 19°11′ S., 59°16′ E., 4,042 m; EGERIA 19, 3 Nov. 1887; B.M. (M3790); clayey, calcareous ooze with few siliceous microfossils; few, slightly corroded Radiolaria.

396 27°10′ S., 111°43′ E., 2,279 m; PENGUIN 8, 16 Apr. 1891; B.M. (M5245); clayey, calcareous ooze with few siliceous microfossils; moderately abundant, well-preserved Radiolaria.

397 27°59′ S., 108°40′ E., 5,147 m, 0–2 cm; VEMA 18–214, 9 July 1962; L.G.O.; silty clay with many sponge spicules; Radiolaria absent.

398 25°46′ S., 95°58′ E., 4,967 m, 0–2 cm; VEMA 18–210, 5 July 1962; L.G.O.; clay; Radiolaria very rare.

398 28°53′ S., 92°50′ E., 3,879 m, 0–2 cm; VEMA 16–94, 11 Feb. 1960; L.G.O.; clayey, silty, calcareous ooze with few discoasters; Radiolaria very rare.

399 25°29′ S., 85°09′ E., 4,547 m, 0–2 cm; VEMA 18–206, 2 July 1962; L.G.O.; slightly zeolitic, coccolith-discoaster ooze; Radiolaria very rare.

400 20°42′ S., 73°10′ E., 4,228 m; EGERIA 13, 27 Oct. 1887; B.M. (M3784); clayey, calcareous ooze with few siliceous microfossils; moderately abundant, well-preserved Radiolaria.

400 24°12′ S., 76°59′ E., 4,262 m, 0–2 cm; VEMA 18–204, 29 June 1962; L.G.O.; slightly zeolitic. calcareous, silty, clay; Radiolaria very rare.

400 29°45′ S., 79°34′ E., 3,938 m, 0–2 cm; VEMA 16–84, 4 Feb. 1960; L.G.O.; clayey, calcareous ooze with few discoasters; Radiolaria absent.

*401 21°02′ S., 65°56′ E., 3,654 m, 0–2 cm; VEMA 18–201, 25 June 1962; L.G.O.; clayey, calcareous ooze with few discoasters and few siliceous microfossils; abundant, corroded Radiolaria.

*402 22°02′ S., 57°33′ E., 4,770 m, 2–4 cm; LSDA 119G, 31 Oct. 1962; S.I.O.; silty (partly pyroclastic), calcareous clay with few siliceous microfossils; abundant, well-preserved Radiolaria.

*402 24°30′ S., 57°29′ E., 4,990 m, 1–2 cm; LSDA 120G*b*, 1 Nov. 1962; S.I.O.; clay with many siliceous microfossils; abundant, well-preserved Radiolaria.

402 24°56′ S., 51°20′ E., approximately 5,512 m, 0–2 cm; VEMA 14–85, 2 May 1958; L.G.O.; silty, calcareous clay; Radiolaria very rare.

402 29°56′ S., 54°06′ E., 4,228 m; EGERIA 22, 16 Nov. 1887; B.M. (M3793); clayey, calcareous ooze; few, well-preserved Radiolaria.

403 28°26′ S., 43°47′ E., 3,637 m, 0–2 cm; VEMA 14–81, 29 Apr. 1958; L.G.O.; clayey, calcareous ooze with many sponge spicules; rare, well-preserved Radiolaria.

403 29°22′ S., 40°07′ E., 4,883 m, 0–2 cm; VEMA 14–79, 27 Apr. 1958; L.G.O.; clayey silt; Radiolaria absent.

404 23°22′ S., 38°51′ E., 3,092 m, top of core; VEMA 19–214, 6 Sept. 1963; L.G.O.; clayey, silty, calcareous ooze with few siliceous microfossils; few, well-preserved Radiolaria.

404 29°50′ S., 37°14′ E., 4,984 m, 0–2 cm; VEMA 14–78, 26 Apr. 1958; L.G.O.; clayey, calcareous silt with few sponge spicules; Radiolaria absent.

432 30°34′ S., 112°58′ E., 5,075 m; PENGUIN 3, 15 Apr. 1891; B.M. (M5240); clayey, silty, calcareous ooze with few siliceous microfossils, except for many sponge spicules; few well-preserved Radiolaria.

Marsden Square

433 36°08′ S., 106°13′ E., 6,077 m, 0–2 cm; VEMA 16–98, 19 Feb. 1960; L.G.O.; clayey silt with many sponge spicules; very rare, well-preserved Radiolaria (probably lower Eocene).

*433 39°24′ S., 101°06′ E., 4,534 m; EGERIA 39, 10 Dec. 1887; B.M. (M3807); clayey, calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria.

434 31°32′ S., 99°15′ E., 2,418 m, 0–2 cm; VEMA 16–96, 14 Feb. 1960; L.G.O.; clayey, silty, calcareous ooze with few discoasters; Radiolaria very rare.

435 33°23′ S., 89°08′ E., 3,506 m, 0–2 cm; VEMA 16–91, 9 Feb. 1960; L.G.O.; clayey, calcareous ooze; Radiolaria very rare.

435 38°32′ S., 82°01′ E., 3,440 m; EGERIA 35, 2 Dec. 1887; B.M. (M3804); clayey, calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria.

436 30°38′ S., 70°07′ E., 4,051 m, 0–2 cm; VEMA 16–81, 1 Feb. 1960; L.G.O.; clayey, calcareous ooze; Radiolaria absent.

436 32°20′ S., 72°38′ E., 4,224 m, 2–4 cm; MSN 60G, 18 Dec. 1960; S.I.O.; calcareous ooze with few siliceous microfossils; moderately abundant, well-preserved Radiolaria.

*436 37°44′ S., 71°42′ E., 4,286 m, 3–6 cm; MSN 61G, 20 Dec. 1960; S.I.O.; calcareous-siliceous ooze; abundant, well-preserved Radiolaria (generally thin-walled).

*436 38°24′ S., 78°40′ E., 2,271 m; EGERIA 34, 1 Dec. 1887; B.M. (M3803); clayey, calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria (generally thin-walled).

436 38°31′ S., 76°45′ E., 2,687 m; EGERIA 33, 30 Nov. 1887; B.M. (M3802); clayey, calcareous ooze with few siliceous microfossils; abundant, well-preserved Radiolaria.

*437 32°44′ S., 62°24′ E., 4,780 m, 0–2 cm; LSDA 124G, 5 Nov. 1962; S.I.O.; siliceous-calcareous ooze; abundant, well-preserved Radiolaria.

*437 33°14′ S., 61°43′ E., 4,800 m, 0–2 cm; LSDA 125G, 5 Nov. 1962; S.I.O.; siliceous-calcareous ooze; abundant, well-preserved Radiolaria.

*437 38°06′ S., 67°09′ E., 4,532 m; EGERIA 31, 27 Nov. 1887; B.M. (M3801); clayey, calcareous-siliceous ooze with few discoasters; abundant, corroded Radiolaria (generally thin-walled).

438 36°25′ S., 52°49′ E., 3,001 m; EGERIA 27, 21 Nov. 1887; B.M. (M3798); calcareous ooze with few siliceous microfossils; few, well-preserved Radiolaria.

438 37°23′ S., 56°43′ E., 4,590 m; EGERIA 29, 23 Nov. 1887; B.M. (M3800); clayey, siliceous-calcareous ooze; abundant, corroded Radiolaria.

439 32°26′ S., 46°34′ E., 2,946 m, 0–2 cm; VEMA 18–191, 12 June 1962; L.G.O.; clayey, calcareous ooze; Radiolaria very rare.

439 37°09′ S., 43°30′ E., 3,643 m, 0–2 cm; VEMA 16–67, 11 Jan. 1960; L.G.O.; clayey, calcareous ooze; rare, well-preserved Radiolaria.

440 38°20′ S., 33°55′ E., 3,680 m, 0–2 cm; VEMA 18–187, 8 June 1962; L.G.O.; clayey, calcareous ooze with few discoasters; Radiolaria absent.

*441 32°50′ S., 29°23′ E., 3,018 m; SERPENT (?) 9, 28 May 1868; B.M. (M7736); clayey, silty, calcareous ooze with few siliceous microfossils, except for many sponge spicules; abundant, well-preserved Radiolaria.

*472 42°01′ S., 71°00′ E., 4,152 m, 2–6 cm; MSN 62G*a*, 21 Dec. 1960; S.I.O.; clayey, silty, siliceous-calcareous ooze with few discoasters; abundant, well-preserved Radiolaria.

472 43°44′ S., 75°33′ E., 3,434 m; VALDIVIA 162, 1 Jan. 1899; B.M. (M8765); clayey, silty, calcareous ooze with few siliceous microfossils; few, well-preserved Radiolaria.

*472 44°38′ S., 70°58′ E., 4,980 m, 0–4 cm; LSDA 128G, 13 Nov. 1962; S.I.O.; silty, calcareous-siliceous ooze; abundant, well-preserved Radiolaria.

475 40°24′ S., 49°49′ E., 3,914 m; WATERWITCH 91, 22 Jan. 1895; B.M. (M8780); clayey, calcareous-siliceous ooze; abundant, slightly corroded Radiolaria.

477 40°14′ S., 25°15′ E., 2,772 m, 0–2 cm; VEMA 16–55, 30 Dec. 1959; L.G.O.; clayey, calcareous ooze; Radiolaria very rare.

Distribution of Sediment Types and Radiolaria

Bezrukov (1964) presented the most comprehensive map of distribution of sediment types in the Indian Ocean which has yet been published. A similar map (fig. 1*a*), based on qualitative analyses of smear slides of 87 sediment samples, was compiled independently during the present study and is in good agreement with that of Bezrukov.

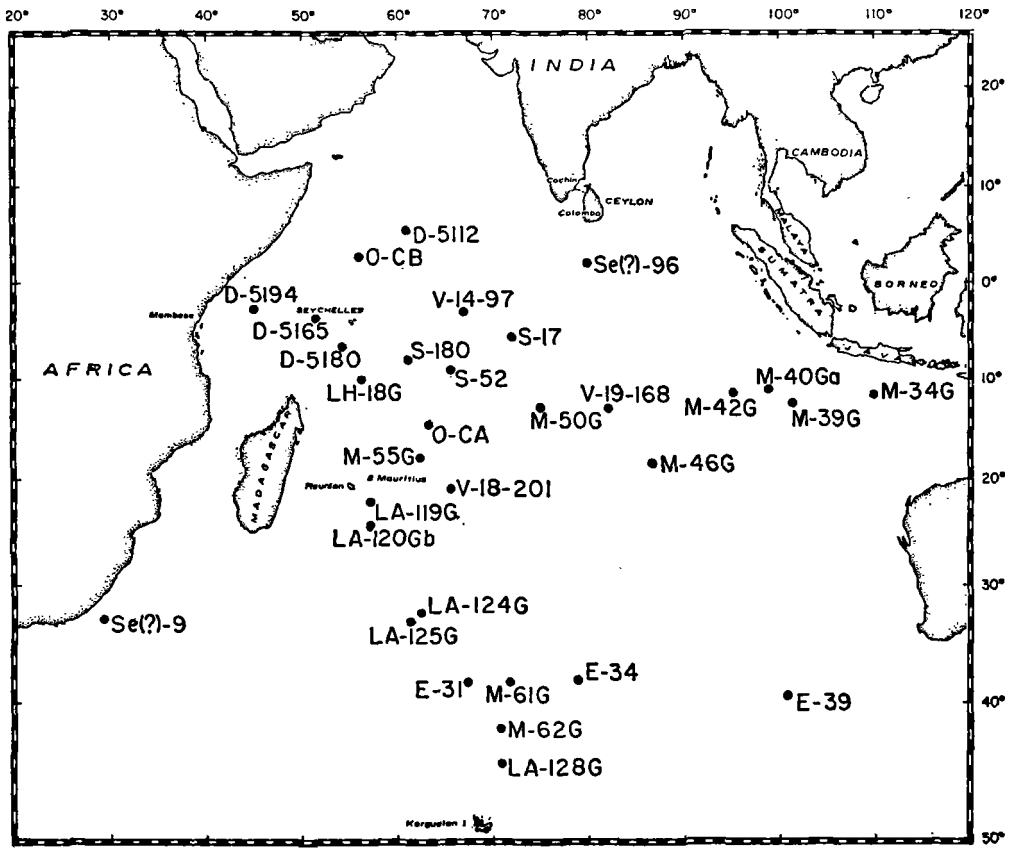

Fig. 1. Chart showing locations and numbers of samples used for radiolarian counts. D = "Discovery"; E = "Egeria"; LA = "Lusiad-Argo"; LH = "Lusiad-Horizon"; M = "Monsoon"; O = "Owen"; S = "Sealark"; Se(?) = "Serpent" (?); V = "Vema."

Siliceous-calcareous oozes extend in a broad band across the equatorial Indian Ocean. East of about 75°E. (from 10°S. to 15°S.), sediments are highly siliceous; Radiolaria are particularly abundant and well preserved. West of 75°E., sediments become increasingly calcareous, although Radiolaria are still abundant. At 65°E. calcareous-siliceous sediments extend from 21°–22°S. to 6°–7°N. Sampling is insufficient to allow extension west of 55°E. of the southern boundary of this band. North of Madagascar (Malagasy), calcareous-siliceous sediments extend to the African coast.

Decreased productivity results in decreased rates of sediment accumulation, and hence Radiolaria deposited in areas of low productivity are exposed to bottom waters for some time and thus tend to dissolve. This effect has been observed in

the western Pacific (Riedel, personal communication). In the Somali Basin, partially dissolved Radiolaria were found in most of the samples examined, but in those nearest the African coast (from depths less than 3,700 m) the Radiolaria were uncorroded. This suggests a general decrease in productivity in the western

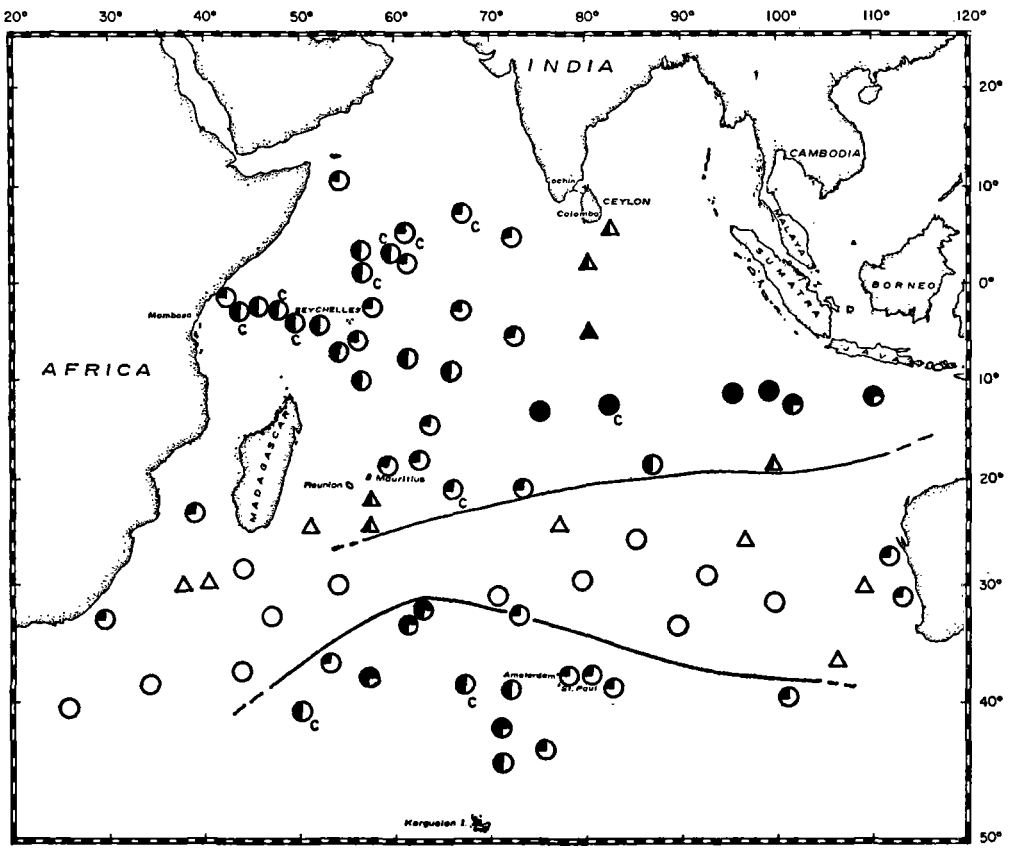

Fig. 1*a*. Distribution of sediment types in the Indian Ocean: *Circle* = calcareous; *quarter-filled circle* = calcareous ooze with few siliceous microfossils; *half-filled circle* = calcareous-siliceous ooze; *three-quarter-filled circle* = siliceous-calcareous ooze; *filled circle* = siliceous ooze; *half-filled triangle* = clay or silt with few siliceous microfossils; *triangle* = clay or silt; c = corroded Radiolaria; solid lines denote boundaries between described areas, based on present sampling and on the work of Bezrukov (1964).

Indian Ocean, except for a narrow belt along the African coast where nutrients are brought to the surface by upwelling of the Somali current (Stommel and Wooster, 1965).

South of the equatorial band of siliceous-calcareous and calcareous-siliceous oozes lies a band, corresponding to the subtropical anticyclonic gyre, of calcareous oozes and red clays which are essentially barren of Radiolaria. Present sampling suggests that this band is continuous across the entire ocean. In the eastern Indian Ocean, calcareous oozes and red clays extend from about 18° S. to 38° S. The band is constricted at about 65° E. to 21°–22° S. to 31° S., and there are indications that a moderate number of Radiolaria occur within the band at about 60°–65° E. (in the region of the southwest limb of the Mid-Ocean Ridge). West of 65° E., the

southern boundary turns southward, but the northern boundary cannot be delineated west of 55° E. on the basis of present sampling.

South of this band to 45° S. (most-southern latitude sampled), calcareous-siliceous oozes reappear and Radiolaria are again abundant and well preserved, particularly between 60° E. and 85° E., although the faunal assemblage is distinct from that of low latitudes (cf. p. 90). Preservation and/or the original structure of the Radiolaria is also rather different. Skeletons are generally thinner and more delicate, becoming quite difficult to see in Canada balsam.

Sediment types and radiolarian distribution south of 45° S. are discussed by Hays (1964).

TAXONOMY

Introduction

Only a small proportion of the radiolarian species present in Recent Indian Ocean sediments have been described herein. In selecting species for detailed study, the relative importance of a number of factors had to be considered, and a balance achieved between them. The abundance of a species, the ease with which it might be recognized by subsequent workers, and the present degree of understanding of the group to which it belongs had to be taken into account. Some groups, such as the Liosphaerida, are not well known and have, therefore, been avoided until a study of the group as a whole can be made. Those species showing an obvious distributional pattern, and particularly those confined to either low or middle latitudes, were favored.

A number of complex taxonomic problems have arisen during this study, and all but a few have been resolved. Some groups (e.g., the Panartida) appear to require a major taxonomic revision, involving research beyond the scope of this paper. In such cases conservative synonymies and partial taxonomic solutions have been made. Comments on individual problems are made in the "discussion" of each species description.

Generic synonymies include: (1) reference to original description; (2) reference to genus by Haeckel (1887); and (3) name used by Campbell (1954) if different from that used by Haeckel (1887). Specific synonymies include all references which contribute to the description of the species and its synonyms.

The catalogue of previously recorded occurrences is thought to be fairly complete. The locality designated by Haeckel as "Indian Ocean, Zanzibar, depth 2,200 fathoms (Pullen)" is the same as Ehrenberg's Indian Ocean location (i.e., 5°37′ S., 61°33′ E.). The material was collected in 1859 by James Hiltons, while serving under Captain Pullen of H.M.S. *Cyclops*. Haeckel received Indian Ocean plankton samples from Captain Heinrich Rabbe of the German ship *Joseph Hayden*. In these samples Radiolaria were found to be most abundant east of Madagascar (Malagasy) and around the Cocos Islands. Exact locations and depths for these samples were not recorded by Haeckel.

Dimensions are based on at least twenty specimens of each species. Photographed specimens are located according to sample and slide number, England Finder coordinates, and Sedgwick Museum reference number.

Topotypic material has been deposited in the Sedgwick Museum, Downing Street, Cambridge, England.

Gross Classification of Described Species

Haeckel (1881) erected a radiolarian classification based largely upon the geometry of their skeletons. Although this system is, as Haeckel himself recognized, largely artificial, and although, in some cases, it violates rules of nomenclature, it has provided a satisfactory and workable system suitable for modification to a more natural classification. Since a revision of Haeckel's classification is presently in progress (Riedel, personal communication), and since most of the literature uses the Haeckelian system, it seems advisable to continue using Haeckel's suprageneric names for the time being. Suprageneric revisions by Campbell (1954) and Loeblich and Tappan (1961) are included for the sake of completeness.

LEGION: Spumellaria (Spumellina in Campbell, 1954)
ORDER: Sphaerellaria (Sphaerellari in Campbell, 1954)
SUBORDER: Sphaeroidea (Liosphaericae in Campbell, 1954; emended to Ethmosphaeracea by Loeblich and Tappan, 1961)
FAMILY: Collosphaerida (Collosphaeridae in Campbell, 1954)
SPECIES: *Polysolenia spinosa* (Haeckel), 1862
Polysolenia flammabunda (Haeckel), 1887
Polysolenia lappacea (Haeckel), 1887
Siphonosphaera polysiphonia Haeckel, 1887
Disolenia quadrata (Ehrenberg), 1872
Disolenia zanguebarica (Ehrenberg), 1872
Otosphaera auriculata Haeckel, 1887
Otosphaera polymorpha Haeckel, 1887
FAMILY: Stylosphaerida (Stylosphaeridae in Campbell, 1954)
SPECIES: *Saturnalis circularis* Haeckel, 1887
FAMILY: Astrosphaerida (Astrosphaeridae in Campbell, 1954; emended to Actinommidae by Loeblich and Tappan, 1961)
SPECIES: *Actinomma antarcticum* (Haeckel), 1887
Actinomma medianum n sp.
Actinomma arcadophorum Haeckel, 1887
SUBORDER: Prunoidea (Ellipsidiicae in Campbell, 1954; emended to Sponguracea by Loeblich and Tappan, 1961)
FAMILY: Panartida (Panartidae in Campbell, 1954)
SPECIES: *Panartus tetrathalamus* Haeckel, 1887
SUBORDER: Discoidea (Cenodiscicae in Campbell, 1954; emended to Coccodiscacea by Loeblich and Tappan, 1961)
FAMILY: Phacodiscida (Phacodiscidae in Campbell, 1954)
SPECIES: *Heliodiscus asteriscus* Haeckel, 1887
Heliodiscus echiniscus Haeckel, 1887
FAMILY: Porodiscida (Euchitoniidae in Campbell, 1954)
SPECIES: *Amphirhopalum ypsilon* Haeckel, 1887
*Euchitonia müller*i Haeckel, 1862
Euchitonia elegans (Ehrenberg), 1872
FAMILY: Spongodiscida (Spongodiscidae in Campbell, 1954)
SPECIES: *Spongaster tetras tetras* Ehrenberg, 1860
Spongaster tetras irregularis n. subsp.
LEGION: Nassellaria (Nassellina in Campbell, 1954)
ORDER: Plectellaria (Plectellari in Campbell, 1954)
SUBORDER: Stephoidea (Stephaniicae in Campbell, 1954; emended to Acanthodesmiacae by Loeblich and Tappan, 1961)
FAMILY: Cyrtostephanidae (The inclusion of the following species in the family

Cyrtostephanidae, proposed by Popofsky (1913, p. 288), is a departure from Haeckel's classification. Haeckel placed the genus *Amphispyris* in the family Androspyrida [Androspyridae in Campbell, 1954].)

SPECIES: *Amphispyris reticulata* (Ehrenberg), 1872
Amphispyris costata Haeckel, 1887

ORDER: Cyrtellaria (Cyrtellari in Campbell, 1954)
SUBORDER: Spyroidea (Triospyridicae in Campbell, 1954)
FAMILY: Zygospyrida (Triospyridae in Campbell, 1954)
SPECIES: *Triceraspyris damaecornis* Haeckel, 1887
Ceratospyris sp.
SUBORDER: Botryodea (Cannobotrydicae in Campbell, 1954)
FAMILY: Lithobotryida (Glycobotrydidae in Campbell, 1954)
SPECIES: *Centrobotrys thermophila* Petrushevskaya, 1965
FAMILY: Pylobotryida (Pylobotrydidae in Campbell, 1954)
SPECIES: *Botryocyrtis scutum* (Harting), 1863
SUBORDER: Cyrtoidea (Archipiliicae in Campbell, 1954)
SUPERFAMILY: Dicyrtida (Sethopiliilae in Campbell, 1954)
FAMILY: Tripocyrtida (Sethopiliidae in Campbell, 1954)
SPECIES: *Lithopera bacca* Ehrenberg, 1872
FAMILY: Anthocyrtida (Sethophormididae in Campbell, 1954; emended to Sethophatnidae by Loeblich and Tappan, 1961)
SPECIES: *Anthocyrtidium ophirense* (Ehrenberg), 1872
Anthocyrtidium zanguebaricum (Ehrenberg), 1872
FAMILY: Sethocyrtida (Lophophaenidae in Campbell, 1954)
SPECIES: *Cornutella profunda* Ehrenberg, 1854
Dictyocryphalus papillosus (Ehrenberg), 1872
SUPERFAMILY: Tricyrtida (Theopiliilae in Campbell, 1954)
FAMILY: Podocyrtida (Theopiliidae in Campbell, 1954)
SPECIES: *Dictyophimus crisiae* Ehrenberg, 1854
Pterocanium praetextum praetextum (Ehrenberg), 1872
Pterocanium praetextum eucolpum Haeckel, 1887
Pterocanium trilobum (Haeckel), 1861
FAMILY: Theocyrtida (Theocorythidae in Campbell, 1954)
SPECIES: *Theoconus hertwigii* (Haeckel), 1887
Lamprocyclas maritalis martitalis Haeckel, 1887
Lamprocyclas maritalis polypora n. subsp.
Theocorythium trachelium dianae (Haeckel), 1887
Theocorythium trachelium trachelium (Ehrenberg), 1872
SUPERFAMILY: Stichocyrtida (Triacartilae in Campbell, 1954; emended to Stichoperilae by Loeblich and Tappan, 1961)
FAMILY: Lithocampida (Stichocorythidae in Campbell, 1954)
SPECIES: *Eucyrtidium acuminatum* (Ehrenberg), 1844
Eucyrtidium hexagonatum Haeckel, 1887
Siphocampe corbula (Harting), 1863
Lithocampe sp.
Spirocyrtis scalaris Haeckel, 1887

Descriptions of Species

Suborder SPHAEROIDEA Haeckel, 1878

Genus *Polysolenia* Ehrenberg *sens. emend.*

Polysolenia Ehrenberg, 1872*a*, p. 318.
Acrosphaera Haeckel, 1887, p. 99.
Choenicosphaerium Haeckel, 1887, p. 103. Proposed as a subgenus of *Choenicosphaera* Haeckel, 1887.

Collosphaeridae with simple shells, the outer surface of which is covered with radial, irregularly scattered spines arising either singly or as a corona from pore margins, or from between the pores, or in any combination of these positions. The definition of this genus is emended herein to include forms having: (1) coronas of spines as well as single ones; and (2) spines arising from pore margins as well as from between pores.

Polysolenia spinosa (Haeckel)

(Pl. 1, fig. 1)

1860*b* *Collosphaera spinosa* Haeckel, Monatsber., for 1860, p. 845.
1862 *Collosphaera spinosa* Haeckel, Monogr. d. Radiol., p. 536, pl. 34, figs. 12, 13.
1871 *Collosphaera spinosa* Haeckel.—Cienkowski, Archiv. f. mikrosk. Anat., vol. 7, p. 374, pl. 29, figs. 7–17.
1885 *Acrosphaera spinosa* (Haeckel).—Brandt, Fauna und Flora des Golfes von Neapel; Die Koloniebildenden Radiolarien (Sphaerozoëen), p. 263, pl. 2, fig. 4.
1887 *Acrosphaera echinoides* Haeckel, "Chall." Rept., p. 100, pl. 8, fig. 1.
1887 *Acrosphaera spinosa* (Haeckel), *ibid.*, p. 100.
1917 *Acrosphaera spinosa* (Haeckel).—Popofsky, Deutsche Südpolar-Exped., vol. 16 (Zool. vol. 8), p. 253, text figs. 14–16 (*partim*).

Description.—Shell thin-walled, smooth, spherical, with numerous, irregularly scattered, subcircular pores of variable size, 1–4 times as broad as the bars. Short spines, usually mounted on conical elevations, project randomly over the shell surface, either singly from pore margins or from between the pores. Spines are usually broadly conical, but may be quite sharp; often they are fenestrate near the shell and sometimes arise from a cluster of small pores rather than from a single pore. Probably these pore clusters form when a single pore is divided by a growing spine.

Dimensions.—Diameter of shell 81–164μ (usually 81–128μ).

Occurrences previously recorded.—Haeckel (1862)—Messina.

Brandt (1881)—*C. spinosa,* Gulf of Naples.

Brandt (1885)—*A. spinosa,* Gulf of Naples.

Haeckel (1887)—*A. echinoides,* southeast corner of the Pacific, Valparaiso, "Challenger" Station 298 (34°07′ S., 73°56′ W., surface); *A. spinosa,* Mediterranian, Messina, Canary Islands.

Popofsky (1917)—Deutsche Südpolar-Expedition, Atlantic Ocean, 6 October 1901 (4°35′ S., 16°48′ W.); Indian Ocean, 2 May 1903 (32°57′ S., 73°50′ E., surface), 6 May 1903 (27°48′ S., 68°06′ E., surface), 8 May 1903 (27°04′ S., 64°40′ E., surface), 22 May 1903 (27°01′ S., 46°16′ E., surface), 26 May 1903 (28°43′ S., 39°24′ E.).

Indian Ocean occurrences (fig. 2).—*P. spinosa* is sparsely distributed in both low and middle latitudes. It forms a high percentage (17%) of the described population in a sample near the African coast (SERPENT [?] 9); and in two samples near the southern limit of tropical radiolarian distribution (VEMA 18–201, 21°02′ S.; and LSDA 119G, 22°02′ S.) the species constitutes 12 percent and 10 percent respectively of the described population.

Discussion.—According to Haeckel (1887) the major difference between *Acrosphaera echinoides* and *Acrosphaera spinosa* is that on the former the spines are straight and radial, while on the latter they are oblique and curved. This distinc-

tion, however, appears to be neither pronounced nor even constant within a single specimen. Hence, *A. echinoides* and *A. spinosa* are considered conspecific.

Popofsky (1917) included *Choenicosphaera flammabunda* and *Choenicosphaera nassiterna* in his synonymy of *A. spinosa*. *C. flammabunda* is thought by the pres-

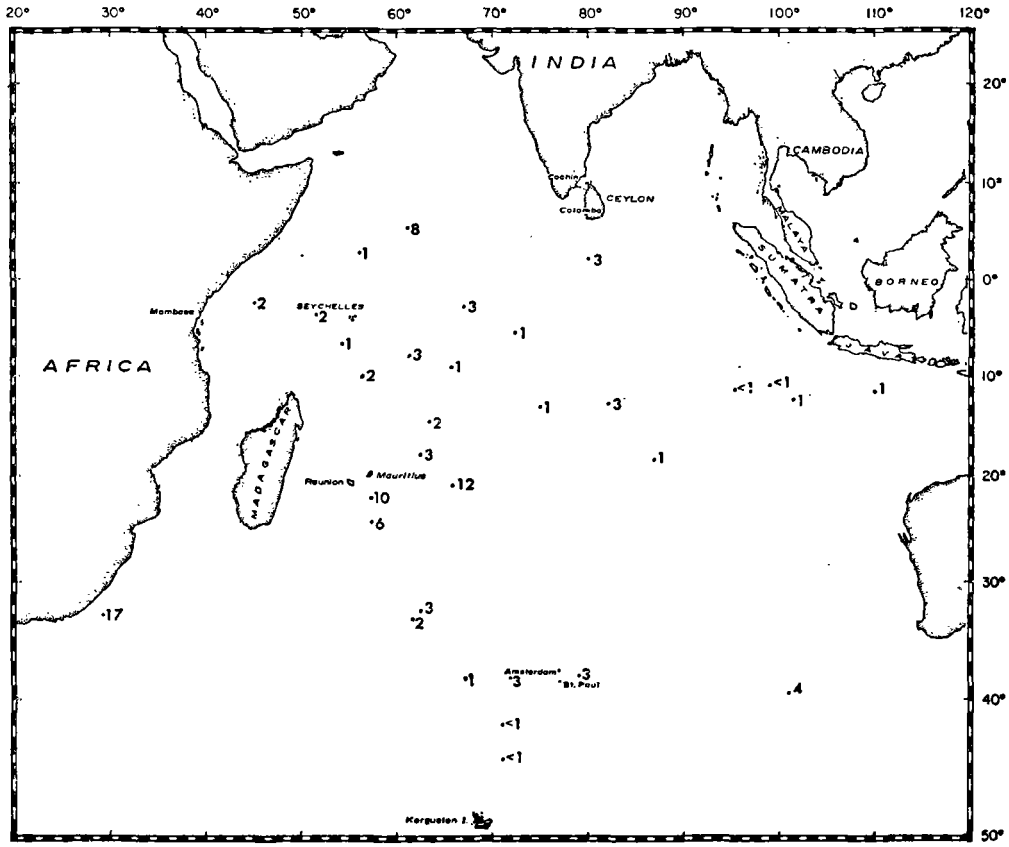

Fig. 2. Distribution of *Polysolenia spinosa*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

ent author to be taxonomically distinct from *P. spinosa* (see description below). No forms having spine coronas as regular as those figured for *C. nassiterna* Haeckel have been observed in Indian Ocean sediments. The reference by Popofsky to Hilmers (1906) could not be checked.

Polysolenia flammabunda (Haeckel)

(Pl. 1, fig. 2)

1887 *Choenicosphaera flammabunda* Haeckel, "Chall." Rept. p. 103, pl. 8, fig. 5.

1917 *Acrosphaera spinosa* Haeckel.—Popofsky, Deutsche Südpolar-Exped., vol. 16 (Zool. vol. 8), p. 253, text figs. 14–16 (*partim*).

Description.—Similar to *Polysolenia spinosa* (p. 14), but with larger pores having a corona of up to 5 flat or conical spines. Single spines are also present on the margins of smaller pores, or may arise from pore clusters, or from between pores. Spines are narrower basally and generally longer than those of *P. spinosa*.

Dimensions.—Diameter of shell 81–136μ.

Occurrences previously recorded.—Haeckel (1887—Central area of the Tropical Pacific, "Challenger" Stations 266 (11°07′ N., 152°03′ W.) to 272 (3°48′ S., 152°56′ W.), depths 4,435 m to 5,349 m.

Popofsky (1917)—as for *P. spinosa* (p. 14).

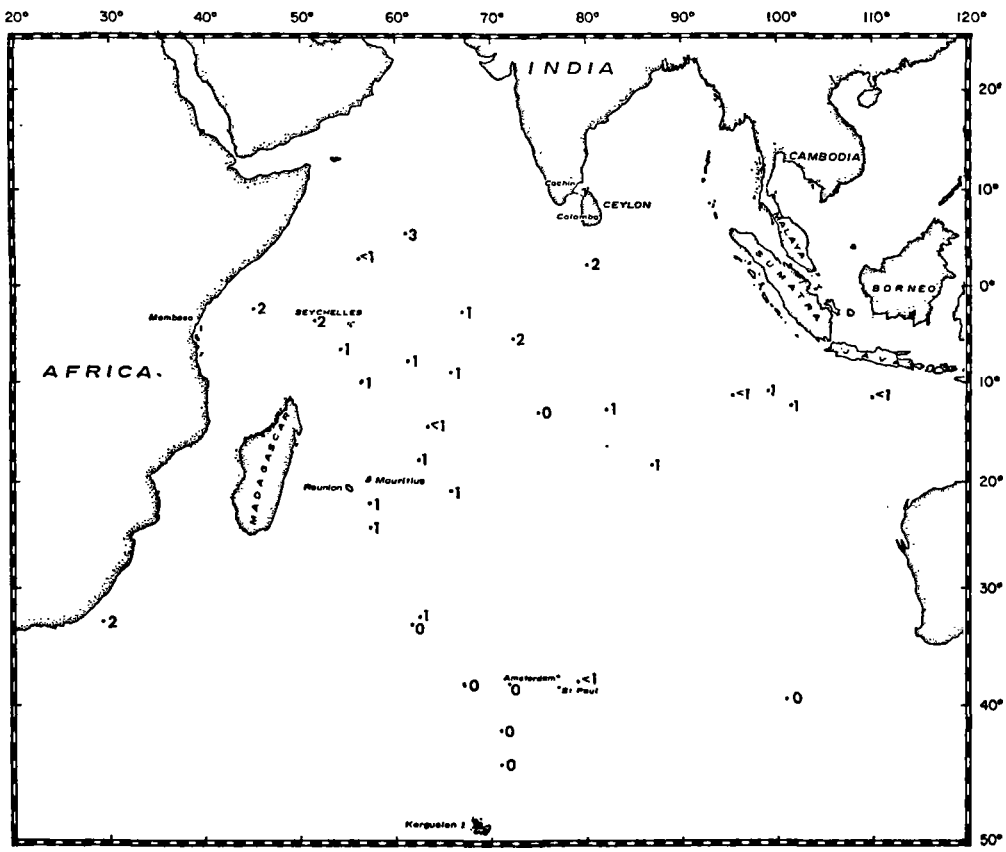

Fig. 3. Distribution of *Polysolenia flammabunda.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Indian Ocean occurrences (fig. 3).—*P. flammabunda* never constitutes more than 3 percent of the described population. In low latitudes it usually forms about 1 percent and in middle latitudes it is practically absent.

Discussion.—Popofsky (1917) synonymized *C. flammabunda* Haeckel and *Acrosphaera spinosa* Haeckel. However, it is thought by the present author that forms having single spines on the pore margins (cf. *P. spinosa,* p. 14) and those having coronas of spines are sufficiently different as to require specific distinction. Forms having regular spine coronas (e.g., *C. nassiterna*) have not been observed in Indian Ocean sediments.

Polysolenia lappacea (Haeckel)

(Pl. 1, fig. 3*a*, 3*b*)

1887 *Xanthiosphaera lappacea* Haeckel, "Chall." Rept., p. 120, pl. 8, figs. 10, 11.

1917 *Acrosphaera lappacea* (Haeckel).—Popofsky, Deutsche Südpolar-Exped., vol. 16 (Zool. vol. 8), p. 258, text fig. 21.

Description.—Similar to *Polysolenia spinosa* (p. 14), but spines are often curved. At different distances from the shell some spines are joined by broad lateral branches which form an irregular and incomplete outer mesh.

Dimensions.—Diameter of shell 81–109μ.

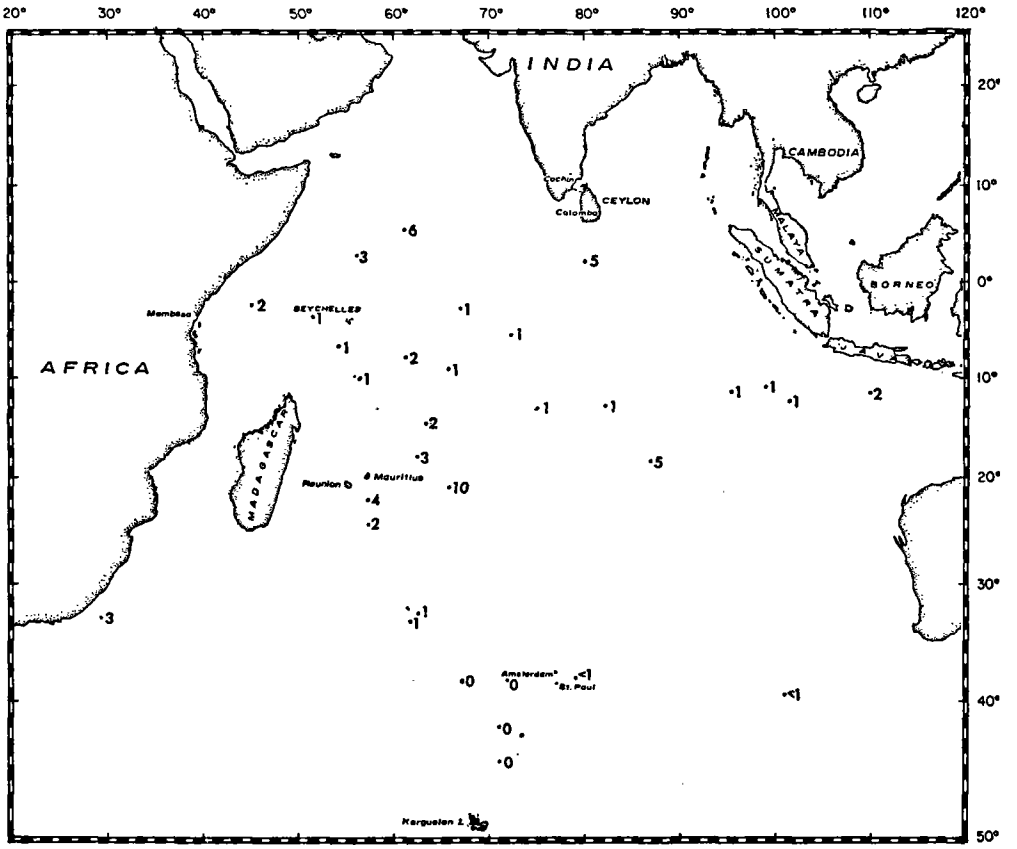

Fig. 4. Distribution of *Polysolenia lappacea*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Occurrences previously recorded.—Haeckel (1887)—Central area of the tropical Pacific, "Challenger" Stations 263 (17°33′ N., 153°36′ W.) to 274 (7°25′ S., 152°15′ W.), depths 4,298 m to 5,486 m.

Popofsky (1917)—Deutsche Südpolar-Expedition, southern Indian Ocean, 6 May 1903 (27°48′ S., 68°06′ E., surface), 22 May 1903 (27°01′ S., 46°16′ E., surface), 26 May 1903 (28°43′ S., 39°24′ E., surface).

Indian Ocean occurrences (fig. 4).—*P. lappacea* is sparsely distributed in low latitudes and is almost entirely absent from middle latitudes. Maximum abundances (6% and 10% of the described population) occur at the northern and southern limits respectively of tropical radiolarian distribution.

Discussion.—The genus *Xanthiosphaera* was defined by Haeckel (1887) as having a "double lattice-shell" with the "surface of the outer shell thorny or spiny." The irregular and incomplete lateral branching of the spines on *X. lappacea* Haeckel hardly constitutes a "lattice-shell." The species has, therefore, been transferred to the genus *Polysolenia* Ehrenberg (= *Acrosphaera* Haeckel).

Since Hilmers (1906) could not be obtained, Popofsky's (1917) reference to *Acrosphaera lappacea* Hilmers could not be checked.

Genus *Siphonosphaera* Müller

Siphonosphaera Müller, 1858*a*, p. 59; Haeckel, 1887, p. 104.

Siphonosphaera polysiphonia Haeckel

(Pl. 1, figs. 4*a*, 4*b*)

1887 *Siphonosphaera polysiphonia* Haeckel, "Chall." Rept., p. 106.

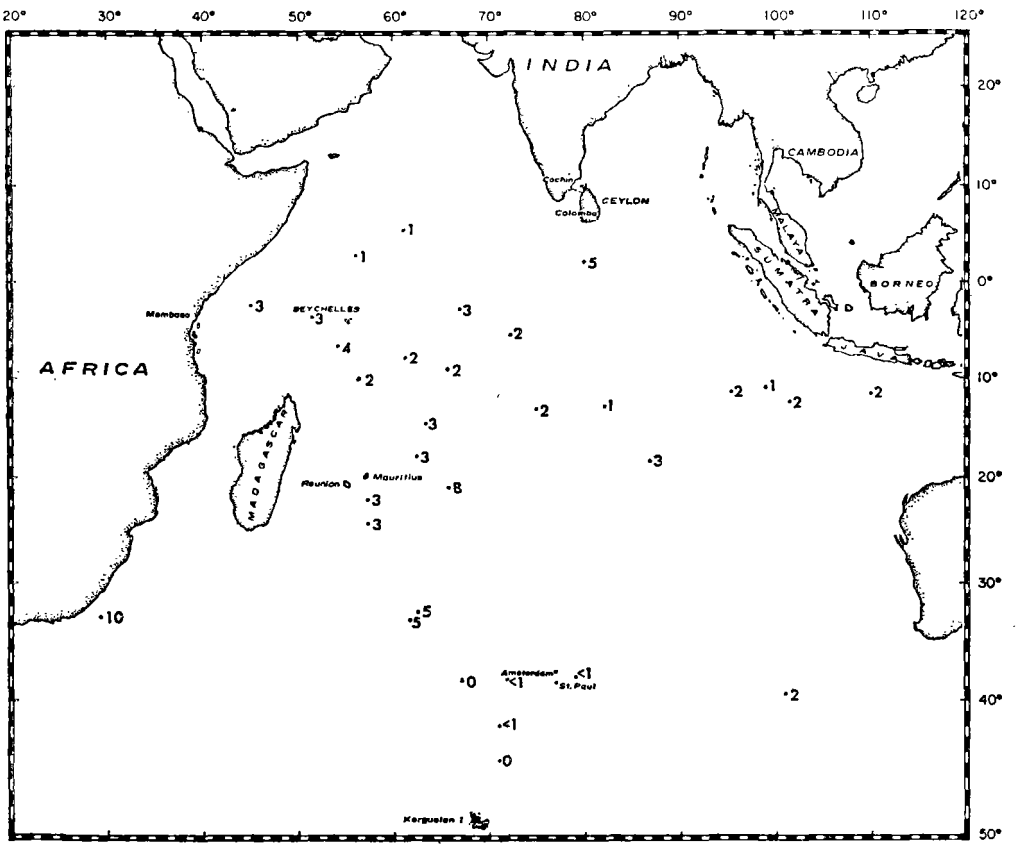

Fig. 5. Distribution of *Siphonosphaera polysiphonia*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Description.—Shell spherical, rather thick-walled with somewhat rough or pitted surface and numerous small subcircular pores, irregularly scattered. Four to ten poreless tubules, thin-walled, cylindrical, having no definite arrangement. Tubules usually as long as broad, about 0.2 shell radius, but may be longer, up to 0.25 shell radius; smoothly truncated tangentially, or sometimes obliquely to the sphere.

Dimensions.—Diameter of shell 81–119μ. Maximum length of tubules 9–27μ; their maximum breadth 9–18μ.

Occurrences previously recorded.—Haeckel (1887)—Tropical and subtropical parts of the western Atlantic, coast of Brazil, etc. (Rabbe).

Indian Ocean occurrences (fig. 5).—*S. polysiphonia* is rather sparsely distributed in low latitudes and is practically absent from middle latitude samples. Maximum abundance occurs in a sample near Africa (SERPENT [?] 9, 10% of the described population).

Discussion.—Haeckel described, but did not figure, *Siphonosphaera polysiphonia.* However, as nearly as one can tell from his description, the species described herein is identical to *S. polysiphonia,* although Haeckel's specimens were generally rather smaller. Haeckel found the species to be present in tropical and subtropical Atlantic samples. A similar distribution has been found in the Indian Ocean.

Genus *Disolenia* Ehrenberg

Disolenia Ehrenberg, 1860*a*, p. 831; Campbell, 1954, p. D52.
Solenosphaera Haeckel, 1887, p. 112.

Haeckel (1887) synonymized Ehrenberg's (1860) genera *Disolenia, Trisolenia, Tetrasolenia, Pentasolenia,* and *Polysolenia* under the name *Solenosphaera.* The name *Disolenia,* however, has priority, as recognized by Campbell (1954).

Disolenia quadrata (Ehrenberg)

(Pl. 1, fig. 5)

1872*a* *Tetrasolenia quadrata* Ehrenberg, Monatsber., for 1872, p. 320.
1872*b* *Tetrasolenia quadrata* Ehrenberg, Abh., for 1872, p. 301, pl. x, fig. 20.
1887 *Solenosphaera variabilis* Haeckel, "Chall." Rept., p. 113.
1887 *Solenosphaera pandora* Haeckel, *ibid.*, p. 113, pl. 7, figs. 10, 11.
1953 ?*Solenosphaera variabilis* Haeckel.—Riedel, Jour. Paleont., vol. 27, no. 6, p. 808, pl. 84, fig. 8.

Description.—Shell smooth, thin-walled, subspherical, with numerous small irregular pores having no definite arrangement. Pored tubules, 3–8 (usually 5), approximately as long as broad or longer, 0.2–0.3 shell diameter. Tubules cylindrical or subcylindrical, sometimes slightly expanded distally; outer apertures truncated, smooth.

Dimensions.—Diameter of shell 63–90μ. Maximum length of tubules 18–36μ; their maximum breadth 18–27μ.

Occurrences previously recorded.—Ehrenberg (1872*a, b*)—Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Haeckel (1887)—*S. variabilis,* central area of the tropical Pacific, "Challenger" Stations 270 (2°34′ N., 149°09′ W.), 271 (0°33′ S., 151°34′ W.), 272 (3°48′ S., 152°56′ W.), depths 4,435 m to 5,349 m; *S. pandora,* central area of the tropical Pacific, "Challenger" Stations 266 (11°07′ N., 152°03′ W.) to 274 (7°25′ S., 152°15′ W.), depths 4,298 m to 5,349 m.

Riedel (1953)—Series 8, sample no. 78 (First Netherlands Timor Expedition), from near Bebalain, Rotti (late Tertiary, approximately Pliocene).

Indian Ocean occurrences (fig. 6).—*D. quadrata* is sparsely distributed in the eastern tropics, but increases in abundance (up to 6% of the described population) west of 75° E. The species is absent from middle latitude samples.

Discussion.—Haeckel (1887) synonymized *Tetrasolenia quadrata* Ehrenberg with his *Solenosphaera variabilis.* The older specific name, *quadrata,* should have been retained and is, therefore, reestablished herein.

S. variabilis and *S. pandora* were originally distinguished on the basis of size and number of pores and tubules. However, observations indicate that these criteria fall within the limits of intraspecific variation. Although Haeckel's measurements of the diameter and tubule breadth of *S. variabilis* are rather greater than

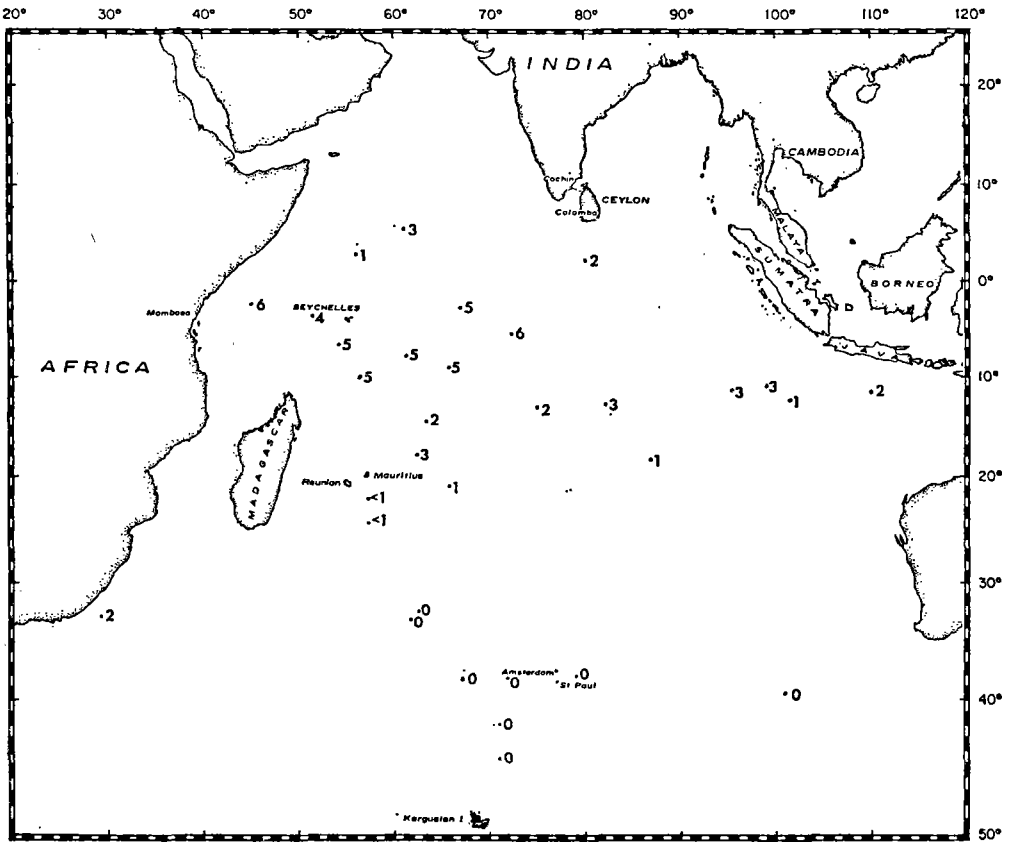

Fig. 6. Distribution of *Disolenia quadrata*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

those found by the author, Ehrenberg's figure of the species leaves no doubt that it is identical with the one described herein.

Disolenia zanguebarica (Ehrenberg)

(Pl. 1, fig. 6)

1872*a* *Trisolenia zanguebarica* Ehrenberg, Monatsber., for 1872, p. 321.
1872*b* *Tetrasolenia venosa* Ehrenberg, Abh., for 1872, p. 301, pl. vii, fig. 22.
1872*b* *Trisolenia zanguebarica* Ehrenberg, *ibid.*, p. 301, pl. x, fig. 11.
1887 *Collosphaera polyhedra* (Ehrenberg).—Haeckel, "Chall." Rept., p. 97.
1887 *Solenosphaera venosa* (Ehrenberg).—Haeckel, *ibid.*, p. 114.
1917 *Solenosphaera zanguebarica* (Ehrenberg).—Popofsky, Deutsche Südpolar-Exped., vol. 16 (Zool. vol. 8), p. 249, text fig. 9.

Description.—Similar to *Disolenia quadrata* (p. 19), but tubules, of which there are 4–6 (usually 5), are broadly conical, narrowing distally; hence, there is no

distinct break in shell contour at the bases of the tubules. Pores rather larger than those of *D. quadrata.*

Dimensions.—Diameter of shell 90–146μ. Breadth of outer aperture of tubules 18–36μ.

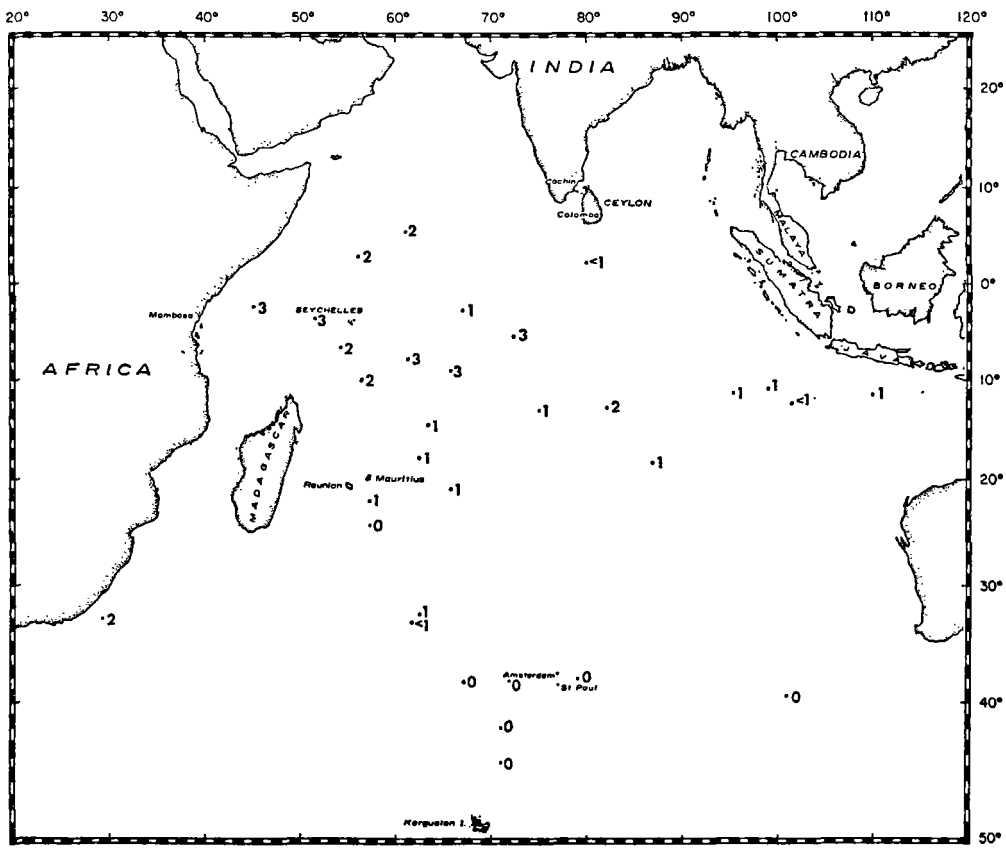

Fig. 7. Distribution of *Disolenia zanguebarica.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Occurrences previously recorded.—Ehrenberg (1860*a*)—*T. venosa,* western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Ehrenberg (1872*a, b*)—*T. zanguebarica,* Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Haeckel (1887)—*C. polyhedra,* tropical zone of the Pacific and the Indian Ocean, "Challenger" Stations 266 (11°07′ N., 152°03′ W.) to 272 (3°48′ S., 152°56′ W.), surface; *S. venosa,* Indian Ocean, Sunda Strait (Rabbe).

Popofsky (1917)—Deutsche Südpolar-Expedition, Indian Ocean, 2 May 1903 (32°57′ S., 73°50′ E., surface), 26 May 1903 (28°43′ S., 39°24′ E., surface); Atlantic Ocean, 5 September 1903 (10°45′ S., 6°23′ W., 400 m).

Indian Ocean occurrences (fig. 7).—*D. zanguebarica* is sparsely distributed in low latitudes and is absent from middle latitude samples. Maximum abundances (up to 3% of the described population) occur in the western tropics.

Discussion.—Ehrenberg (1872*b*, pp. 300–301) referred to a description of

Tetrasolenia venosa published in 1860 (1860*b*, p. 833). However, this description is of the genus *Tetrasolenia;* species of the genus are not mentioned. Both *T. venosa* and *Trisolenia zanguebarica* were figured by Ehrenberg (1872*b*) and appear to be conspecific within the present definition of *Disolenia. T. zanguebarica* was described by Ehrenberg in 1872 (1872*a*). The specific names *venosa* and *zanguebarica* are, therefore, both available for the first time in 1872 and, as far as can be determined, are of eqivalent seniority. Since *T. zanguebarica* was both described and figured, and since its figure is superior to that of *T. venosa,* the name *zanguebarica* has been selected for the species here described as *Disolenia zanguebarica.*

The large openings on *D. zanguebarica* are considered to be tubules rather than large pores, as interpreted by Haeckel (1887), and therefore *Collosphaera polyhedra* can be included in the synonymy.

Hilmers' (1906) synonymy, cited by Popofsky (1917), for *Solenosphaera zanguebarica* could not be examined. However, most of the forms figured by Popofsky appear to be identical with the form described herein as *Disolenia zanguebarica.* The specimen in the upper left-hand corner of text figure 9 may be more closely related to *D. quadrata.*

Genus *Otosphaera* Haeckel *sens. emend.*

Otosphaera Haeckel, 1887, p. 116

Collosphaeridae with simple shells, some of the pores of which are prolonged into simple external radial tubules with fenestrate walls; outer mouth of the tubules armed with a single tooth or spine. The definition of this genus is emended herein to include forms having a spine on the distal end of the tubules.

Otosphaera differs from *Disolenia* Ehrenberg (= *Solenosphaera* Haeckel) by the single tooth or spine on the outer mouth of the tubules, and from *Mazosphaera* Ehrenberg by the fenestration of the walls of the tubules.

Otosphaera auriculata Haeckel

(Pl. 1, fig. 7)

1887 *Otosphaera auriculata* Haeckel, "Chall." Rept., p. 116, pl. 7, fig. 5.

Description.—Shell similar to, but generally rather smaller than, that of *Disolenia quadrata* (p. 19). Two to four tubules, having a length 0.25–0.5 shell diameter. Species distinguished by 1 or 2 spines or a tooth on the outer aperture of each tubule. The spine is a single short solid projection, while the tooth is triangular in outline and bears a large triangular pore.

Dimensions.—Diameter of shell 72–100μ. Maximum length of tubules (including spine or tooth) 9–36μ; their maximum breadth 18–27μ.

Occurrences previously recorded.—Haeckel (1887)—Central tropical Pacific, "Challenger" Stations 268 (7°35′ N., 149°49′ W.) to 272 (3°48′ S., 152°56′ W.), depths 4,435 m to 5,349 m.

Indian Ocean occurrences (fig. 8).—*O. auriculata* is sparsely distributed in the eastern tropics, but increases in abundance (up to 7% of the described population) west of 75° E. The species is absent from middle latitude samples.

Otosphaera polymorpha Haeckel
(Pl. 1, fig. 8)

1887 *Otosphaera polymorpha* Haeckel, "Chall." Rept., p. 116, pl. 7, fig. 6.

Description.—Shell smooth, thin-walled, subspherical, with numerous very small pores, much smaller than the bars. Tubules, 2–5, with rather larger pores, are truncated obliquely, one side prolonged into a prominent acute tooth. Length of tubules, including tooth, 0.25–0.3 shell diameter.

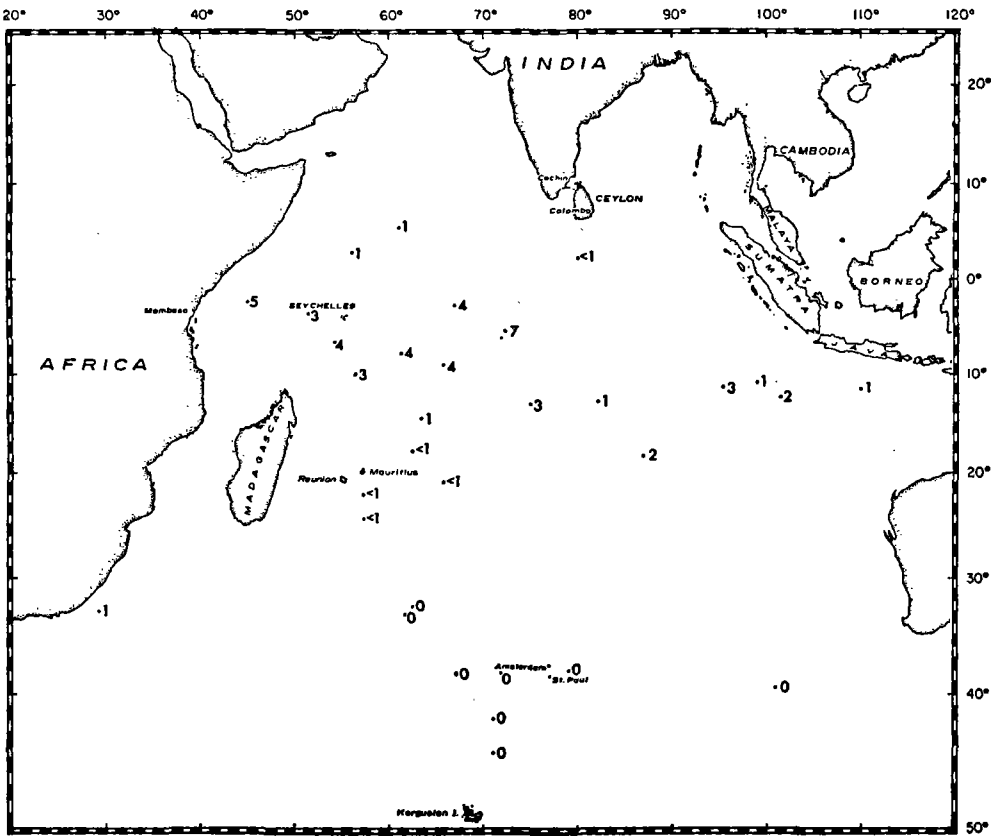

Fig. 8. Distribution of *Otosphaera auriculata.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Dimensions.—Diameter of shell 100–146μ. Maximum length of tubules (including tooth) 18–45μ; their maximum breadth 27–36μ.

Occurrences previously recorded.—Haeckel (1887)—Indian Ocean, east of Madagascar, surface (Rabbe).

Haupt (1905)—Kaiser-Wilhelmsland (North-East New Guinea), probably early Tertiary.

Riedel (1953)—Series 8, sample no. 178 (First Netherlands Timor Expedition) from near Bebalain, Rotti (late Tertiary, approximately Pliocene).

Indian Ocean occurrences (fig. 9).—*O. polymorpha* is very sparsely distributed in low latitudes, never forming more than 1 percent of the described population, and is practically absent from middle latitude samples.

Genus *Saturnalis* Haeckel *sens. emend.*

Saturnalis Haeckel, 1881, p. 450; 1887, p. 131.
Saturnulus Haeckel, 1881, p. 451; 1887, p. 141.

Stylosphaeridae with two concentric lattice spheres and two equal opposite

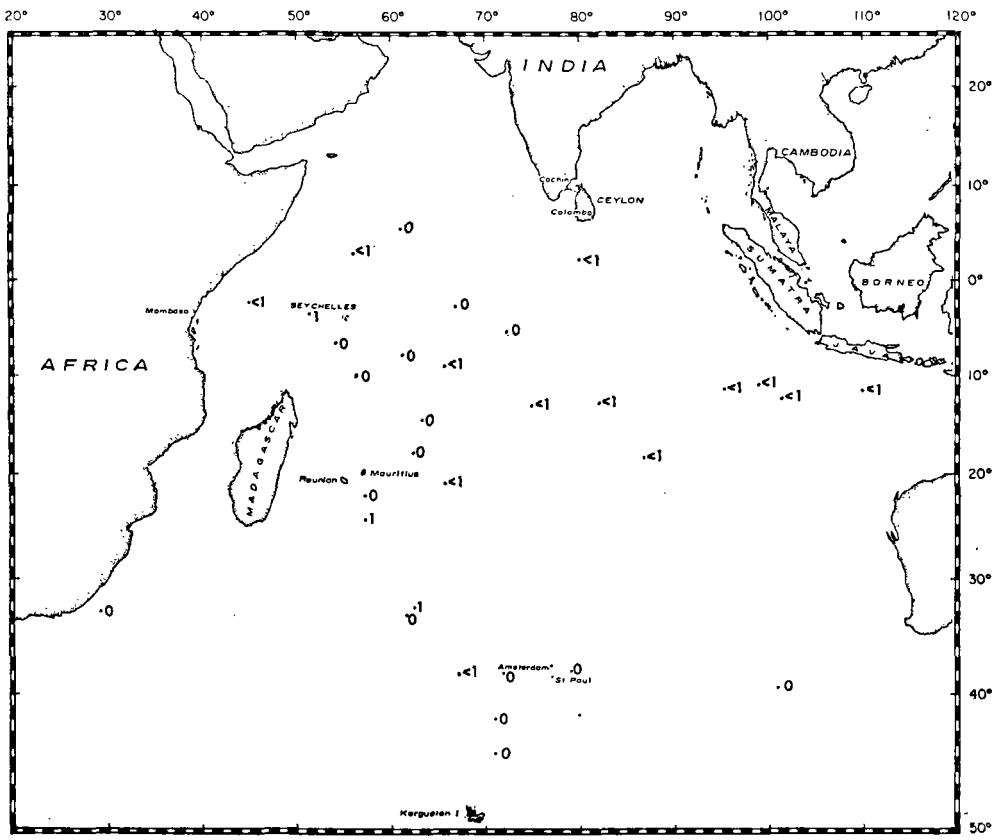

Fig. 9. Distribution of *Otosphaera polymorpha*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

spines, connected at the distal end by a circular or elliptical ring. Type species: *Saturnalis circularis* Haeckel.

According to Haeckel (1887), *Saturnalis* has a single lattice shell and *Saturnulus* a double one. In all other respects the genera are apparently identical. This distinction does not seem well founded, because the medullary shell is very delicate and so may easily be destroyed or not originally developed. Generally, small portions of the two radial beams can be seen even if the medullary shell is absent. Thus, it would appear that two lattice spheres are normally present in completely developed individuals. Since *Saturnalis* is the type genus of the subfamily Saturnalinae, erected by Deflandre (1953), and since it has been used in forming the names of other genera (e.g., *Spongosaturnalis* Campbell and Clark, 1944), *Saturnalis* has been chosen as the name for the revised genus, with *Saturnalis circularis* as the type species.

Saturnalis circularis Haeckel

(Pl. 1, fig. 9)

1887 *Saturnalis circularis* Haeckel, "Chall." Rept., p. 131.
1887 *Saturnalis annularis* Haeckel, *ibid.*, p. 132, pl. 13, fig. 16.

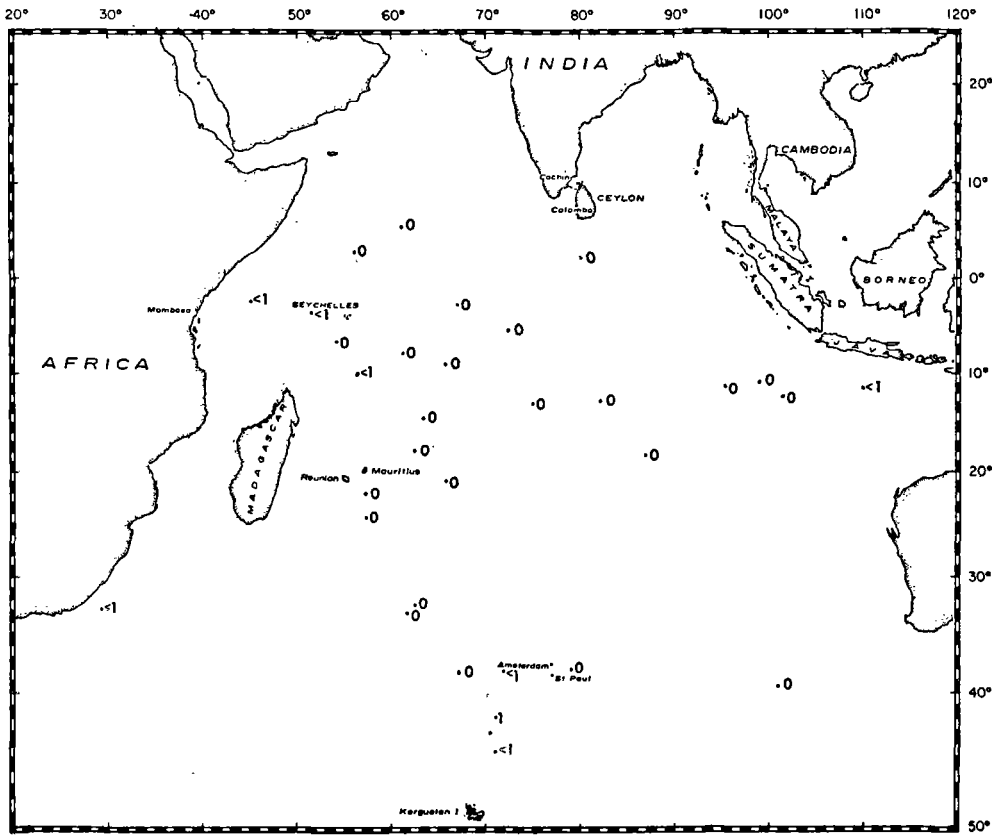

Fig. 10. Distribution of *Saturnalis circularis*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

1887 *Saturnulus circulus* Haeckel, *ibid.*, p. 141.
1887 *Saturnulus annulus* Haeckel, *ibid.*, p. 141.
1887 *Saturnulus ellipticus* Haeckel, *ibid.*, p. 141, pl. 16, fig. 16.
1887 *Saturnulus planetes* Haeckel, *ibid.*, p. 142, pl. 16, fig. 17.
1907 *Saturnulus aureolatus* Haecker, Archiv. f. Protist., vol. 10, p. 121, fig. 6.
1908 *Saturnalis aureolatus* Haecker, Wiss. Ergebn. Deutschen Tiefsee-Exped., vol. 14, p. 443, pl. 84, fig. 581, text fig. 82.
1965 *Saturnalis planetes* Haeckel.—Hays, Biol. of Antarctic Seas II, Antarctic Res. Series 5, p. 167, pl. 1, fig. 5.

Description.—Cortical shell spherical, with circular to subcircular pores, 12–15 on a half-equator; relatively thin wall and somewhat rough surface. Medullary shell usually present, approximately spherical, very delicate, with large angular pores. A narrow radial beam at each pole (present if medullary shell is present) joins with 2 equal and opposite cylindrical or 3-bladed spines connected distally by a smooth, circular to elliptical, 3-bladed ring. Usually, the outer edge of the ring is indented opposite the spines.

Dimensions.—Diameter of cortical shell 72–81μ; of medullary shell 18–27μ. Maximum outside diameter of ring 218–272μ.

Occurrences previously recorded.—Haeckel (1887)—*S. circularis,* South Atlantic, "Challenger" Station 332 (37°29′ S., 27°31′ W., 4,023 m); *S. annularis,* Pacific, central area, "Challenger" Stations 270 (2°34′ N., 149°09′ W.) to 274 (7°25′ S., 152°15′ W.), surface; *S. circulus,* Central Pacific, "Challenger" Station 272 (3°48′ S., 152°56′ W., surface); *S. annulus,* North Pacific, "Challenger" Station 244 (35°22′ N., 169°53′ E., surface); *S. ellipticus,* South Pacific, "Challenger" Station 300 (33°42′ S., 78°18′ W., surface); *S. planetes,* Indian Ocean, Sunda Strait (Rabbe), and "Challenger" Station 200 (6°47′ N., 122°28′ E., surface).

Haecker (1907, 1908)—Deutsche Tiefsee-Expedition Stations 237 (4°45′ S., 48°59′ E., 4,950–4,600m), 268 (9°01′ N., to 12°18′ N., 53°31′ E. to 50°56′ E., 4,800–4,200 m).

Hays (1965)—Quite abundant at depth in cores V16–59 (50°03′ S., 35°11′ E., 4,878 m), V16–60 (50°00′ S., 36°46′ E., 4,581 m), V16–131 (59°20′ S., 117°24′ W., 4,033 m), V16–132 (60°45′ S., 107°29′ W., 4,898 m), V16–57 (45°14′ S., 29°29′ E., 5,289 m), V18–69 (56°33′ S., 81°45′ W., 5,000 m), V17–88 (57°02′ S., 74°29′ W., 4,064 m), V16–66 (42°39′ S., 45°40′ E., 2,996 m); present at depth in cores V16–116 (55°06′ S., 147°29′ E., 3,296 m), V16–130 (59°22′ S., 132°46′ W., 3,910 m).

Indian Ocean occurrences (fig. 10).—*S. circularis* is very sparsely distributed in both low and middle latitudes.

Discussion.—Examination of assemblages from various latitudes has shown that in Quaternary sediments there is only one common species of *Saturnalis* (*S. circularis*). There seems to be no reasonable foundation for the erection of the numerous species described by Haeckel, nor for Haecker's species, *S. aureolatus.*

Genus *Actinomma* Haeckel *sens. emend.*

Actinomma Haeckel, 1860*a*, p. 815; 1887, p. 251.

Actinommidae (cf. Loeblich and Tappan, 1961, p. 222) with one cortical shell and either two medullary shells or one medullary shell and a medullary meshwork. Numerous simple radial spines which may or may not become external. The definition of this genus is emended herein to include forms having (1) a medullary meshwork instead of a true outer medullary shell; and (2) spines projecting beyond the cortical shell.

Actinomma antarcticum (Haeckel)

(Pl. 2, figs. 1*a*–1*d*)

1887 *Spongoplegma antarcticum* Haeckel, "Chall." Rept., p. 90.

1958 *Diploplegma banzare* Riedel, B.A.N.Z. Antarctic Res. Exped. Repts., ser. B, vol. 6, pt. 10, p. 223, pl. 1, figs. 3, 4.

1959 *Cenosphaera antarctica* Nakaseko, Biol. Results, Japanese Antarctic Research Exped. 2, p. 5, pl. i, figs. 3–6.

1959 *Thecosphaera antarctica* Nakaseko, *ibid.*, p. 8, pl. ii, figs. 7, 10*a*, 10*b*.

1965 *Spongoplegma antarcticum* Haeckel.—Hays, Biol. of Antarctic Seas II, Antarctic Res. Series 5, p. 165, pl. 1, fig. 1.

Description.—Cortical shell large, spherical, with a rough surface. Shell thickness varies from a single lattice plate with subcircular to subangular pores of different sizes to a thick spongy meshwork; intervening bars heavy.

Numerous radial beams join the cortical shell to a superficially completely spongy medullary meshwork. However, by breaking open this meshwork a central subspherical shell (cf. pl. 2, figs. 1*c*, 1*d*) having 2.5–3 subcircular pores on a half-equator can be seen.

According to Hays (1965) the medullary meshwork is not always present, but from his extensive examination of Antarctic material he has concluded that forms with and without a central meshwork are conspecific.

Dimensions (according to Hays).—Diameter of cortical shell 225–375μ; of medullary meshwork 100–130μ. Inner medullary capsule approximately one-third the diameter of the medullary meshwork.

Occurrences previously recorded.—Haeckel (1887)—Antarctic Ocean, in large numbers, "Challenger" Station 157 (53°55′ S., 108°35′ E., 3,566 m).

Riedel (1958)—B.A.N.Z.A.R.E. Stations 30 (66°48′ S., 71°24′ E., 540 m), 47 (49°50′ S., 69°33′ E., 150 m), 94 (64°28′ S., 114°59′ E., 1,718 m), 97 (65°10′ S., 108°12′ E., 474 m), 103 (67°03′ S., 74°29′ E., 437 m).

Nakaseko (1959)—*C. antarctica,* Second Japanese Research Expedition Stations 5 (68°17′ S., 31°38′ E., 700 m), 6 (68°17′07″ S., 31°38′ E., 590 m), 8 (68°19′ S., 31°22′ E., 100 m), 9 (68°31′ S., 37°12′ E., 570 m); *T. antarctica,* Second Japanese Antarctic Research Expedition Stations 5 (68°17′ S., 31°38′ E., 700 m), 6 (68°17′07″ S., 31°38′ E., 590 m), 7 (68°19′07″ S., 31°22′ E., 580 m), 9 (68°31′ S., 37°12′ E., 570 m), 10 (68°33′ S., 36°45′ E., 530 m).

Hays (1965, fig. 4)—"One of the most abundant species in the Antarctic fauna."

Discussion.—*Actinomma antarcticum* is one of the most abundant species in Antarctic fauna. However, it occurs in only one sample (LSDA 128G, 53% of the described population) included in the present study. It has been described herein partly because of its close relationship to *Actinomma medianum n. sp.* (p. 27) and *Actinomma arcadophorum* Haeckel (p. 29), and partly because the presence of a central cavity has not formerly been described.

Actinomma medianum n. sp.

(Pl. 2, figs. 2*a*, 2*b*)

1959 *Actinomma capillaceum* Nakaseko, Biol. Results, Japanese Antarctic Research Exped. 2, p. 11, pl. iii, figs. 2*a*, 2*b*.

Description.—Cortical shell a somewhat irregular sphere, thin-walled, with 9–12 subcircular to subangular pores on a half-equator.

Medullary meshwork irregular, more delicate than, but otherwise similar to, that of *Actinomma antarcticum* (p. 26), with an internal shell having 2.5–3 subcircular pores on a half-equator (cf. pl. 2, fig. 2*b*).

Numerous radial beams extend from the outer surface of the medullary meshwork to the cortical shell and sometimes extend externally. Additional, more delicate spines, originating on the cortical surface, are present in some specimens. Occasionally, these spines support a delicate extracortical shell.

Dimensions.—Diameter of cortical shell 164–227μ; of medullary shell 81–100μ. Inner medullary capsule approximately one-third the diameter of the medullary meshwork.

Occurrence previously recorded.—Nakaseko (1959)—Second Japanese Antarctic Research Expedition Station 9 (68°31′ S., 37°12′ E., 570 m).

Indian Ocean occurrences (fig. 11).—*A. medianum* is almost completely absent from low latitudes, but forms 6 percent to 12 percent of the described population

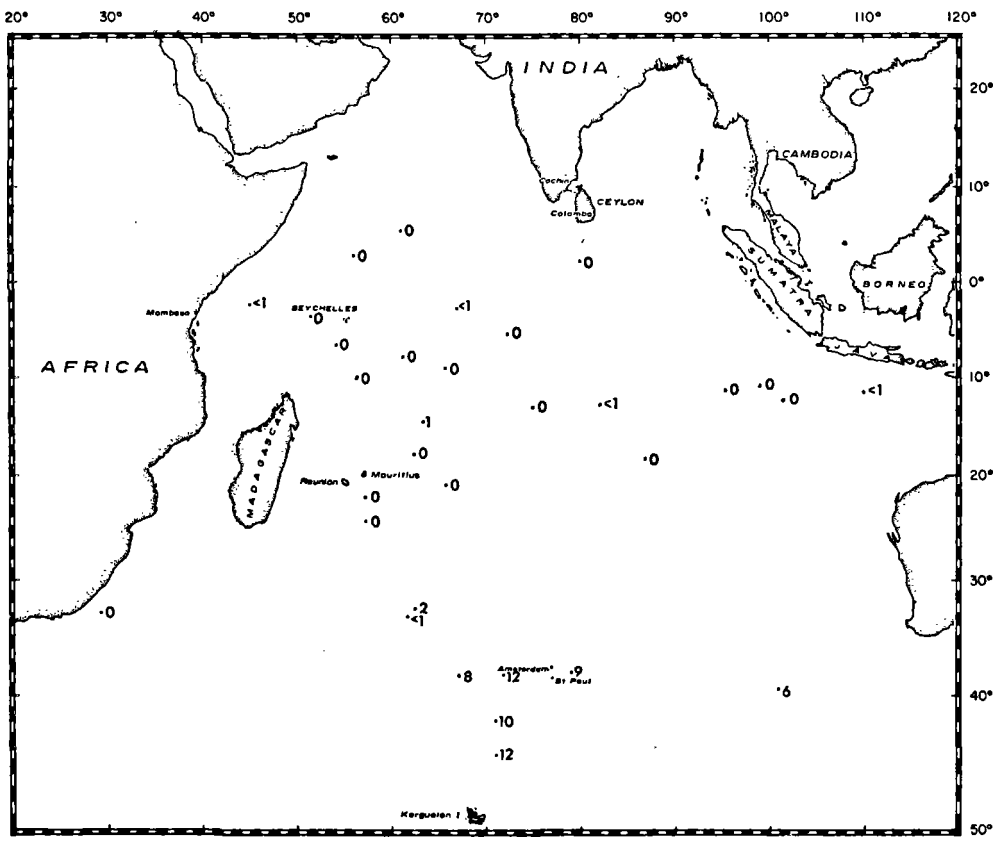

Fig. 11. Distribution of *Actinomma medianum*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

in middle latitude samples. The species is present in high latitudes, but is far outnumbered by *A. antarcticum* (p. 26). *A. medianum* appears to be a reliable and potentially useful member of the middle latitude assemblage. Holotype: LSDA 124G, A-P25/0; Sedgwick Museum No. 856.5.

Discussion.—This species was first described by Nakaseko (1959) as *A. capillaceum*. However, the specific name chosen by Nakaseko is preoccupied by *Actinomma* (*Actinommura*) *capillaceum*. Therefore, according to Article 57(*a*) of the International Code of Zoological Nomenclature, the specific name *capillaceum* is unavailable and cannot be used in the genus *Actinomma*. Although this was brought to the attention of Dr. Nakaseko several months prior to publication, he has not proposed another name. The species must, therefore, be described as new herein. The specific name *medianum* has been selected because the species exhibits characters intermediate between *A. antarcticum* (p. 26) and *A. arcadophorum* (p. 29). It may be distinguished from the former by its simply latticed

cortical shell and more delicate medullary meshwork, and from the latter by its larger cortical pores and heavier medullary meshwork. Distribution of *A. medianum* in the Indian Ocean is also intermediate between that of *A. antarcticum* and *A. arcadophorum*. *A. antarcticum* is found in cold (Antarctic) water, *A.*

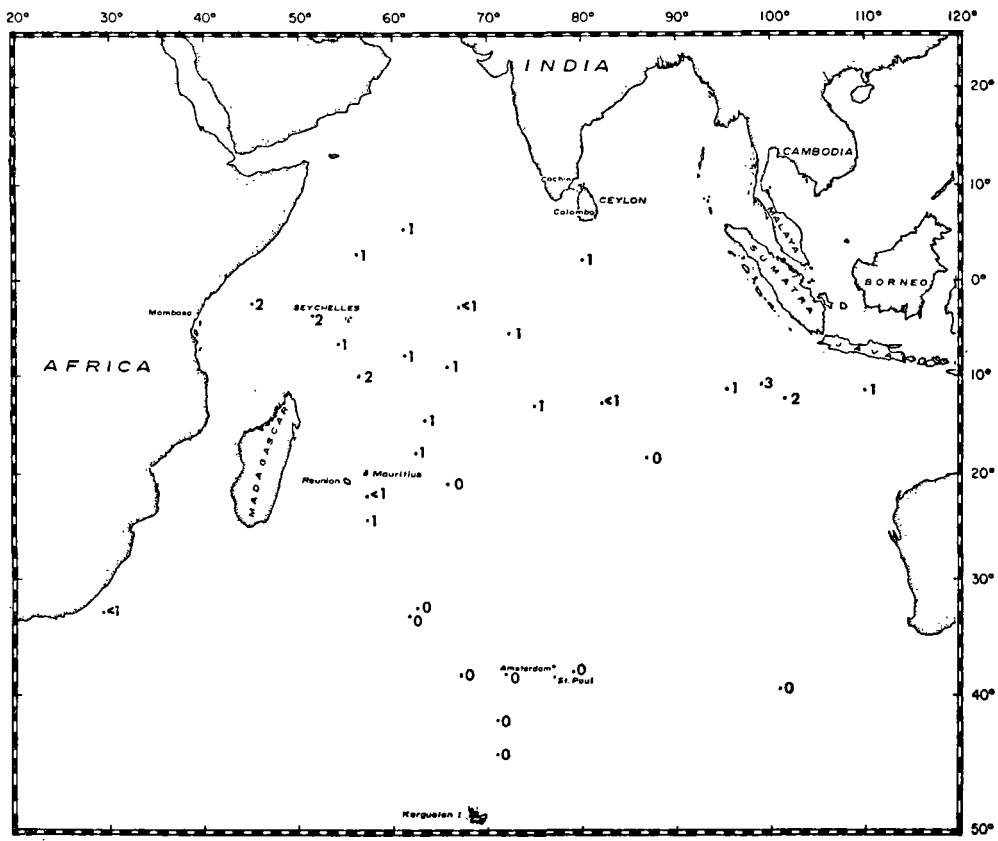

Fig. 12. Distribution of *Actinomma arcadophorum*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

medianum in cool (middle latitude) water, and *A. arcadophorum* in warm (low latitude) water.

Actinomma arcadophorum Haeckel

(Pl. 2, fig. 3)

1887 *Actinomma arcadophorum* Haeckel, "Chall." Rept., p. 255, pl. 29, figs. 7, 8.

Description.—Similar to *Actinomma medianum* (p. 27), but cortical shell is generally larger and much more delicate with many more pores and thinner bars. Radial spines more numerous, occasionally supporting an extracortical shell.

Medullary shell and meshwork as in *A. medianum* and *A. antarcticum* (p. 26), but more delicate.

Dimensions.—Diameter of cortical shell 191–236μ of medullary meshwork 81–100μ. Inner medullary capsule approximately one-third the diameter of the medullary meshwork.

Occurrence previously recorded.—Haeckel (1887)—Central Pacific, "Challenger" Station 266 (11°10′ N., 152°03′ W., surface).

Indian Ocean occurrences (fig. 12).—*A. arcadophorum* is sparsely distributed in low latitudes and does not occur in middle latitude samples. Though rather rare in Recent sediments, it appears to be a useful member of the low latitude assemblage.

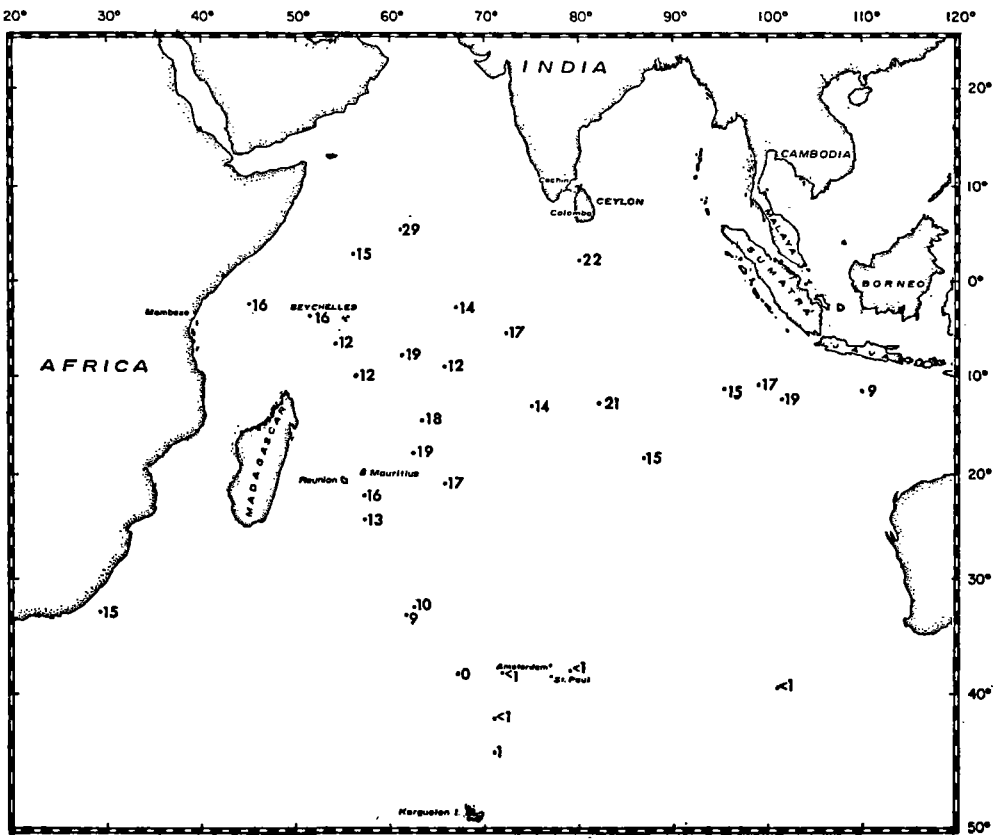

Fig. 13. Distribution of *Panartus tetrathalamus*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Suborder PRUNOIDEA Haeckel, 1883

Genus *Panartus* Haeckel

Panartus Haeckel, 1887, p. 376.

Panartus tetrathalamus Haeckel

(Pl. 2, figs. 4*a*–4*d*)

1887 *Panartus tetrathalamus* Haeckel, "Chall." Rept., p. 378, pl. 40, fig. 3.
1887 *Panartus quadrijugus* Haeckel, *ibid.*, p. 380.
1887 *Peripanartus palliatus* Haeckel, *ibid.*, p. 382.

Description.—Terminology is that proposed by Riedel (1957, p. 76). Cortical twin-shell constricted equatorially, with subcircular to subangular pores, having no definite arrangement, sometimes hexagonally framed; surface usually rough,

spiny. Polar caps, when present, hemispherical to conical, approximately the same breadth as cortical twin-shell, supported by about 12 spines. Caps generally more delicate than twin-shell, with smaller pores and smoother surface. There are approximately equal numbers of specimens with and without single polar caps; rarely, completely or incipiently double-capped specimens are found. A few specimens have a delicate lateral meshwork supported by numerous rods, usually around the twin-shell, but sometimes extending around the caps. There is a tendency for middle latitude forms to develop rather stout unbranched spines, either on the distal ends of the cortical twin-shell or on the polar caps (cf. pl. 2, fig. 4*b*). Such forms are rare in low latitudes.

Outer medullary shell lenticular, inner one spherical; radial beams connect outer medullary to twin-shell at the equatorial constriction.

Dimensions.—Length of cortical twin-shell 90–136μ; of polar caps 36–63μ. Maximum breadth of cortical twin-shell 72–109μ.

Occurrences previously recorded.—Haeckel (1887)—*P. tetrathalamus,* Cosmopolitan: Mediterranean, Atlantic, Pacific, in various depths; *P. quadrijugus,* Cosmopolitan: on the surface of the Atlantic, Indian, and Pacific Oceans; *P. palliatus,* Pacific, central area, "Challenger" Stations 271 (0°33′ S., 151°34′ W., 4,435 m), 272 (3°48′ S., 152°56′ W., 4,755 m).

Riedel (1951*b*)—*P. quadrijugus,* tropical Indian Ocean, Swedish Deep-Sea Expedition Cores (sampled at 1 m intervals) 125 (10°07′ S., 108°56′ E., 6,875 m), 127 (11°07′ S., 103°39′ E., 5,650 m), 128 (11°28′ S., 102°24′ E., 5,170 m), 137 (1°56′ N., 88°12′ E., 4,300 m), 141 (2°18′ N., 76°02′ E., 3,765 m), 142 (0°35′ N., 75°14′ E., 4,050 m), 143 (0°31′ S., 74°33′ E., 3,314 m), 145 (1°20′ S., 68°20′ E., 3,620 m), 147 (1°19′ S., 66°16′ E., 4,380 m), 149 (1°22′ S., 62°38′ E., 4,750 m), 154 (0°23′ S., 54°30′ E., 4,860 m), 155 (4°28′ N., 52°48′ E., 5,117 m).

Riedel (1952)—*P. quadrijugus,* tropical parts of the western Pacific and Indian Oceans, Swedish Deep-Sea Expedition Cores 74 (0°29′ S., 151°33′ W., 4,525 m), 1–2 cm, 87B (2°23′ N., 173°50′ W., 5,560 m), 0–1 cm, 89 (2°48′ S., 178°57′ W., 5,480 m), 0–6 cm, 91B (2°50′ S., 171°18′ E., 4,120 m), 0–1 cm, 95 (0°34′ N., 159°59′ E., 2,880 m), 1–2 cm, 131 (11°10′ S., 96°42′ E., 4,390 m), 0–1 cm, 137 (1°56′ N., 88°12′ E., 4,300 m), 1–1.5 cm, 154 (0°23′ S., 54°30′ E., 4,860 m), 2.5–3 cm.

Indian Ocean occurrences (fig. 13).—*P. tetrathalamus* is abundant in low latitudes, forming up to 29 percent (usually 9% to 22%) of the described population. South of 35° S. only a very few specimens have been observed. The species appears to be a reliable and potentially useful member of the low latitude assemblage.

Discussion.—This species includes forms with and without polar caps, forms with double polar caps, and forms with an "external cortical shell' in the sense of Haeckel (1887, p. 382). It appears that there is only one common species of this general forms in Recent sediments. Proof of this thesis would, however, require extensive observation of material from all oceans, and a gross reclassification of the Panartid group would be necessary. Such a study is beyond the scope of this work.

According to Haeckel (1887), *P. tetrathalamus* and *P. quadrijugus* differ almost entirely by the thorny surface of the latter, and both differ from *P. palliatus* by

the absence of an external cortical shell. These variations are believed by the present author to be intraspecific. Future work will probably reveal other such variations and thus require an expansion of the synonymy of *P. tetrathalamus.*

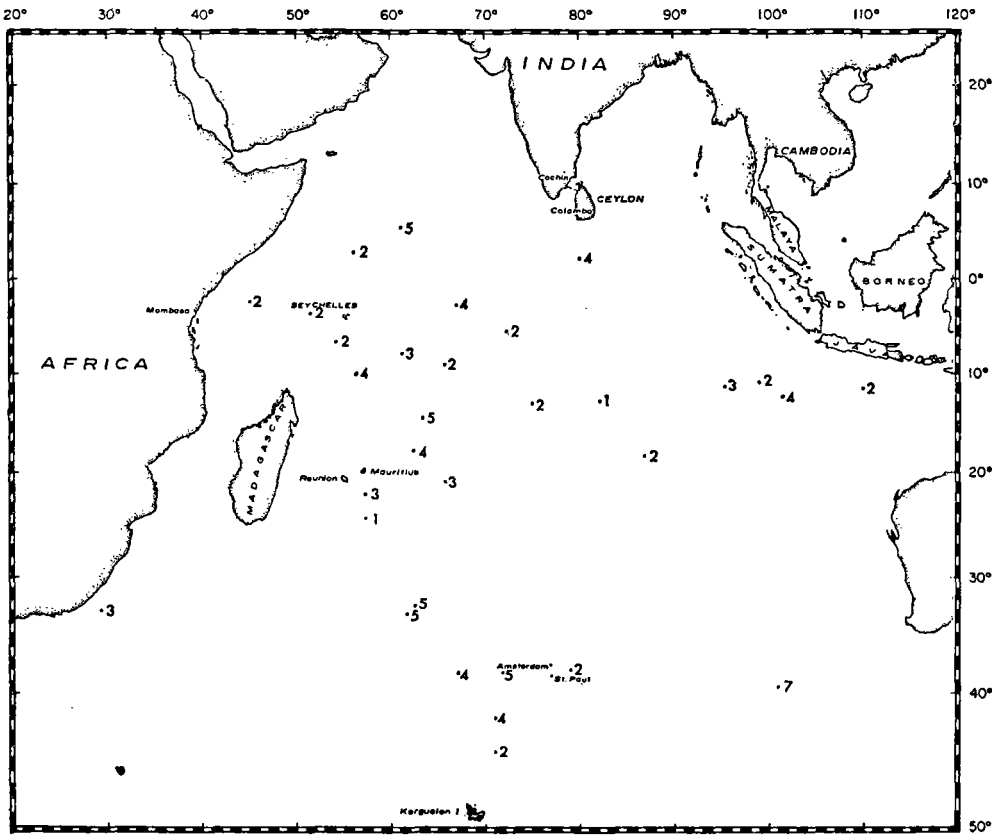

Fig. 14. Distribution of *Heliodiscus asteriscus.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Suborder *DISCOIDEA* Haeckel, 1862

Genus *Heliodiscus* Haeckel *sens. emend.*

Heliodiscus Haeckel, 1862, p. 436; *sens. emend.* Haeckel, 1887, p. 444.

Phacodiscidae with a simple or double medullary shell and with numerous (7 to 20 or more) simple radial spines on the margin of the disc. Spines variable in number and irregularly disposed. The definition of this genus is emended herein to include forms having (1) a double medullary shell; and (2) as few as 7 radial spines.

Heliodiscus asteriscus Haeckel

(Pl. 3, figs. 1*a*, 1*b*)

1887 *Heliodiscus asteriscus* Haeckel, "Chall." Rept., p. 445, pl. 33, fig. 8.

1965 *Heliodiscus asteriscus* Haeckel.—Hays, Biol. of Antarctic Seas II, Antarctic Res. Series 5, p. 171, pl. 3, fig. 7.

Description.—Cortical shell forms a discoidal biconvex lens. Pores circular to

subcircular, sometimes hexagonally framed, fairly regularly arranged over most of the smooth shell surface, but irregular in size, shape, and arrangement near the center of the disc; 7 or 8 (sometimes to 10) pores on a radius.

Medullary shell spherical to ellipsoidal with a diameter approximately 0.3 that of cortical shell. Pores numerous, small, and irregular. Radial beams, 12–16, extend from the medullary shell to the central region of the discoidal surface of the cortical shell. Inner medullary shell delicate, always held eccentrically within outer one by numerous radial beams (cf. pl. 3, fig. 1*b*). Pores large, subcircular, and irregular.

Radial spines 8–12, well developed, straight, 3-bladed near the disc, becoming cylindrical distally, placed more or less regularly around the margin of the cortical shell. Spines up to 0.5 or 0.75 cortical shell diameter; rarely forked. Usually a few short slender marginal by-spines present.

Dimensions.—Diameter of cortical shell 136–191μ; of outer medullary shell 45–63μ; of inner medullary shell approximately 9–18μ.

Occurrences previously recorded.—Haeckel (1887)—Cosmopolitan: Mediterranean (Corfu), Indian Ocean (east of Madagascar), Atlantic, and Pacific, many stations, surface and various depths.

Riedel (1951*b*)—Tropical Indian Ocean, as for *Panartus quadrijugus* (p. 31).

Riedel (1952)—Tropical parts of the western Pacific and Indian Oceans, as for *Panartus quadrijugus* (p. 31).

Riedel (1953)—Series 8, sample no. 178 (First Netherlands Timor Expedition), from near Bebalain, Rotti (late Tertiary, approximately Pliocene).

Hays (1965, fig. 15)—Rarely at the tops of cores from just north of the Polar Front; regularly in core V16–66 (42°39′ S., 45°40′ E., 2,996 m), below 720 cm.

Indian Ocean occurrences (fig. 14).—*H. asteriscus* is found in both low and middle latitudes, forming 1 percent to 7 percent of the described population. It was present in all counted samples.

Discussion.—The most appropriate generic assignment for this species is difficult to determine, because (1) there is some doubt as to which species is most correctly to be regarded as the type species (*H. inchoatus* Rüst, 1885, suggested by Campbell [1954] and *H. phacodiscus* Haeckel, 1861, suggested by Strelkov and Lipman [1959] are both unsatisfactory. The most suitable species for selection as the type is probably *Haliomma sol* Ehrenberg, 1844); and (2) no convincingly thorough descriptions have been published of the type species of *Heliosestrum, Astrosestrum,* and *Astrophacus.*

In view of the wide distribution and abundance of the species here described, and the fact that the only superficially similar form described by Haeckel as being "cosmopolitan" is *Heliodiscus asteriscus,* it seems most convenient to retain that name for the present species, despite the generally larger number of pores which Haeckel described on the cortical shell. In the Indian Ocean material examined, no other closely related form was found to be ubiquitous.

Astrosestrum Haeckel, 1881, is not thought to be cogeneric with *Heliodiscus sens. emend.,* because its type species (*Astrosestrum ephyra* Haeckel, 1887) with broader radial spines is not believed to be related to the genus *Heliodiscus.*

Heliodiscus echiniscus Haeckel

(Pl. 3, figs. 2*a*, 2*b*)

1887 *Heliodiscus echiniscus* Haeckel, "Chall." Rept., p. 448, pl. 34, fig. 5.
1907 *Heliodiscus asteriscoides* Haecker, Archiv. f. Protist., vol. 10, p. 22, fig. 7.
1908 *Heliodiscus asteriscoides* Haecker, Wiss. Ergebn. Deutschen Tiefsee-Exped., vol. 14, p. 444, pl. lxxxiii, figs. 578–580.

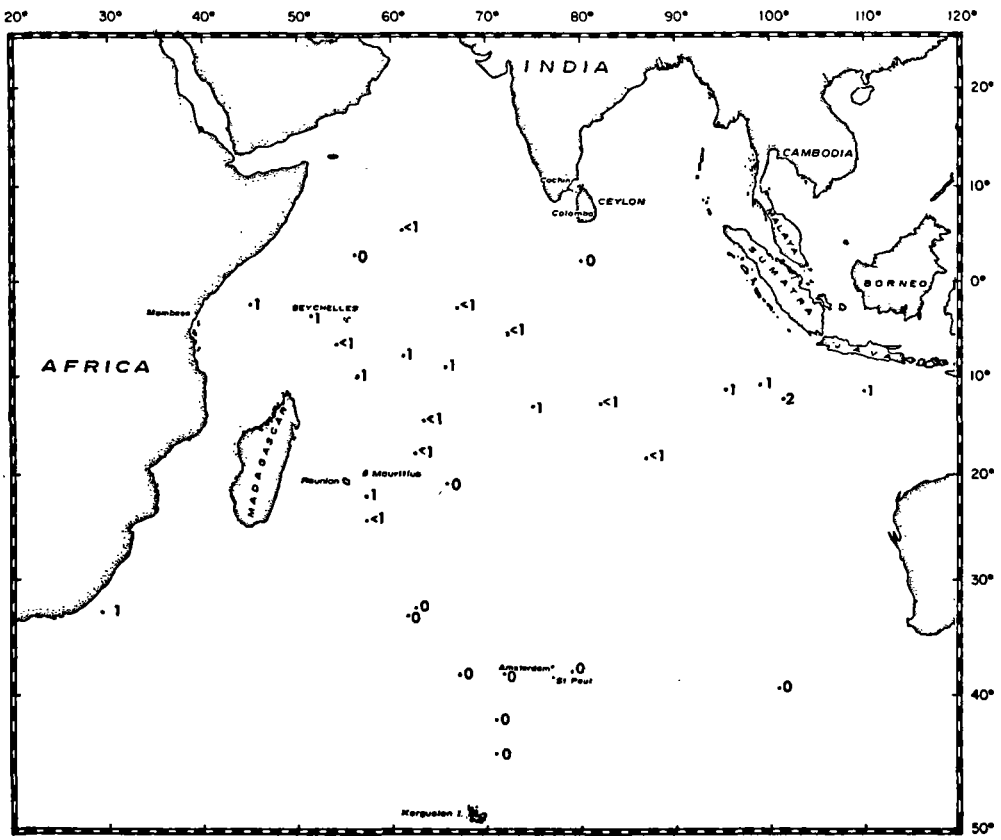

Fig. 15. Distribution of *Heliodiscus echiniscus*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Description.—Similar to *Heliodiscus asteriscus* (p. 32), but with many short slender spines on the discoidal surface of the cortical shell; some are projections of radial beams, others originate on the surface of the cortical shell. Marginal spines conical, more numerous (12 or more) than those of *H. asteriscus*, and generally shorter, 0.25–0.5 the cortical shell diameter. Cortical shell often somewhat distorted; 6–9 (rarely 11) pores on a radius.

Medullary shell similar to that of *H. asteriscus*.

Dimensions.—Diameter of cortical shell 119–173μ; of outer medullary shell 36–54μ; of inner medullary shell approximately 9–18μ.

Occurrences previously recorded.—Haeckel (1887)—Central Pacific, "Challenger" Station 272 (3°48′ S., 152°56′ W., 4,755 m).

Haecker (1907, 1908)—Deutsche Tiefsee-Expedition Stations 88 (31°00′ S.,

7°59′ E., 3,600–3,000 m), 128 (54°30′ S., 3°31′ E., 220–140 m), 221 (4°06′ S., 73°34′ E., 180–145 m), 227 (2°57′ S., 67°59′ E., 1,000–800 m), 229 (2°39′ S., 63°38′ E., 1,000–800 m and 600–400 m), 236 (4°39′ S., 51°17′ E., 180–130 m), 237 (4°45′ S., 48°59′ E., 4,600–4,450 m).

Indian Ocean occurrences (fig. 15).—*H. echiniscus* is sparely distributed in low latitudes, never forming more than 2 percent of the described population. It does not occur in samples from south of 35° S.

Discussion.—The apparently close relationship between this species and *H. asteriscus* has prompted its assignment to the genus *Heliodiscus sens. emend.*

No particularly distinguishing features were described for *H. asteriscoides. H. echiniscus is the only species of Heliodiscus,* having spines on the discoidal surface of the cortical shell, present in sediments examined from the areas of capture of *H. asteriscoides.* Hence, the two species have been synonymized.

Genus *Amphirhopalum* Haeckel *sens. emend.*

Amphirhopalum Haeckel, 1881, p. 460.
Amphirrhopalum Haeckel, 1887, p. 521; Campbell, 1954, p. D86.
Amphicraspedum Haeckel, 1881, p. 460; 1887 p. 522.
Amphicraspedium Haeckel—Campbell, 1954, p. D86 (apparently a typographical error).

Euchitoniidae with two chambered arms, opposite in one axis, with or without a lateral patagium; one arm or both forked at the distal end. Type species: *A. ximorphum* Haeckel (= *A. maclaganium* Haeckel).

Haeckel (1881 and 1887) distinguished *Amphicraspedum* from *Amphirhopalum* by the presence or absence of a patagium. However, specimens lacking a well-developed patagium often have short spines projecting from the main shell. These apparently represent early stages in the development of a patagium. Intermediate stages of patagium formation have also been observed, and hence, it seems reasonable to allow presence or absence of a patagium as an intrageneric and intraspecific variation.

Amphirhopalum ypsilon Haeckel

(Pl. 3, figs. 3*a*–3*d*)

1887 *Amphirhopalum ypsilon* Haeckel, "Chall." Rept., p. 522.
1887 *Amphicraspedum wyvilleanum* Haeckel, *ibid.*, p. 523, pl. 45, fig. 12.

Description.—Shell with 2 opposite, chambered arms, one of which is forked distally. Arms arise from a central structure composed of 2 inner spherical shells and an outer oblate spheroidal shell, all quite smooth and connected by numerous, discontinuous, radial beams. In addition, there is an outer ring of mesh in the plane of the shell which is normally oriented perpendicular to the microscope axis. This orientation makes the central structure appear as a "central, concentrically annulated disc" (cf. Haeckel, 1887, p. 516, Subfamily Euchitonida), because the spheroidal shell has its minor axis along the microscope axis and the external ring, or rings, are in the plane of the slide (cf. pl. 3, figs. 3*c*, 3*d*).

In cross section arms are elliptical with their shortest dimension normally oriented along the microscope axis. Unforked arm is narrow proximally, expands distally to a maximum breadth about two-thirds of the way along its length, then decreases slightly in breadth to a blunt termination. Usually 4–9 distinct chambers,

convex distally, can be seen; however, shell may become spongy over the distal one-third of the arm. Similarly, the forked arm expands distally and branches where its breadth reaches a maximum. Usually 5–9 distinct chambers, including those on the branches, convex distally; chambers on branches sometimes obscured by spongy meshwork.

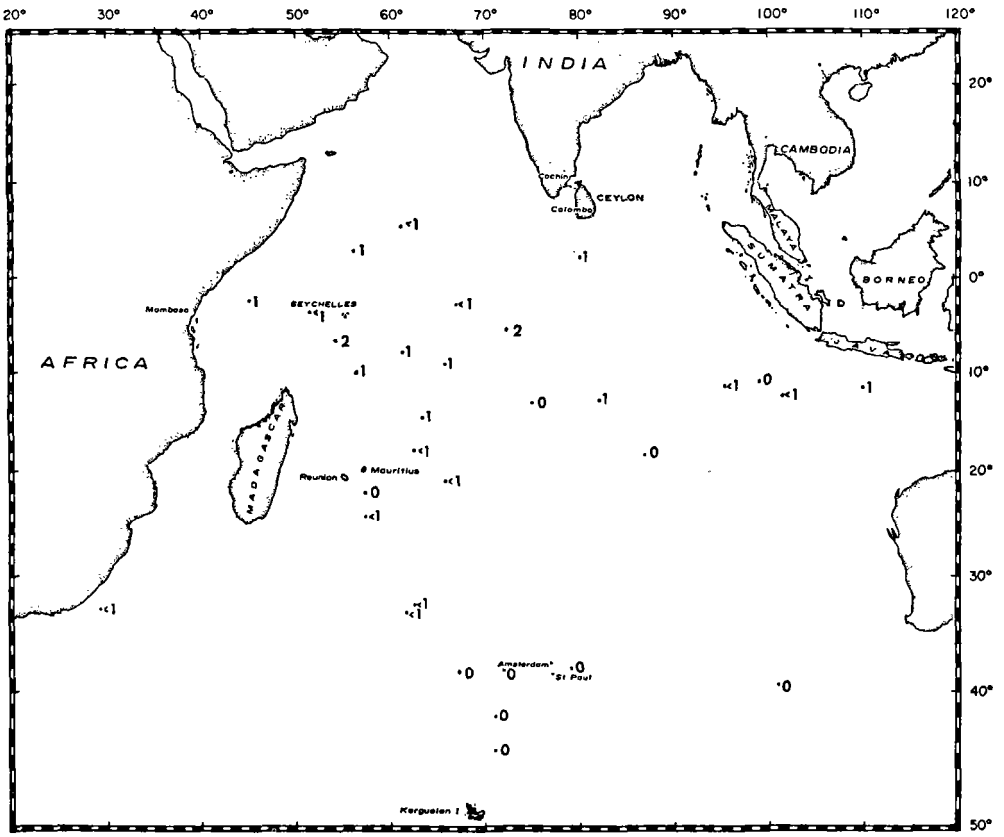

Fig. 16. Distribution of *Amphirhopalum ypsilon*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Internal spines form a basic framework (cf. pl. 3, fig. 3*c*) which is covered by a lattice of small circular to subcircular pores.

In some specimens a patagium is present around the central structure and arms, sometimes with 4 or 5 chambered rows, concave inwards; sometimes simply a spongy mass. It seems probable that a complete patagium (i.e., on a fully developed specimen) might surround the whole basic shell structure, but in all specimens examined the patagium had developed only between the 2 main arms and around the central structure. Patagium generally more delicate than the main shell.

Dimensions.—Total length 236–307μ. Radius of simple arm 119–155μ; of forked arm 119–155μ. Maximum breadth of simple arm 63–119μ; of branches on forked arm 36–63μ.

Occurrences previously recorded.—Haeckel (1887)—*A. ypsilon,* Indian Ocean

(east of Madagascar), surface (Rabbe); *A. wyvilleanum,* South Atlantic, "Challenger" Station 333 (35°36′ S., 21°12′ W., surface).

Indian Ocean occurrences (fig. 16).—*A. ypsilon* is sparsely distributed in low latitudes and is absent from samples south of 35° S. Though rather rare in Recent sediments, it appears to be a useful member of the low latitude assemblage.

Genus *Euchitonia* Ehrenberg *sens. emend.*

Euchitonia Ehrenberg, 1860*b*, p. 831; *sens. emend.* Haeckel, 1887, p. 532.

Euchitoniidae with three simple, undivided, chambered (proximally, at least) arms, with or without terminal spines; triangular shell, bilateral, one unpaired and two paired arms. Patagium may or may not be present. The definition of this genus is emended herein to include forms with and without (1) terminal spines; and (2) a patagium. Type species: *E. mülleri* Haeckel (= *E. furcata* Ehrenberg).

Euchitonia mülleri Haeckel

(Pl. 4, figs. 1*a*, 1*b*)

1862 *Euchitonia mülleri* Haeckel, Monogr. d. Radiol., p. 508, pl. xxx, figs. 5–10.
1872*a* *Euchitonia furcata* Ehrenberg, Monatsber., for 1872, p. 308.
1872*b* *Euchitonia furcata* Ehrenberg, Abh., for 1872, p. 289, pl. IV(iii), fig. 6.
1880 *Euchitonia mülleri* Haeckel.—Stöhr, Palaeontographica, vol. 26, (ser. 3, vol. 2), p. 110, pl. V(XXI), fig. 5.
1887 *Euchitonia furcata* Ehrenberg.—Haeckel, "Chall." Rept., p. 532.
1887 *Euchitonia mülleri* Haeckel, *ibid.*, p. 533.
1912 *Euchitonia mülleri* Haeckel.—Popofsky, Deutsche Südpolar-Exped., vol. 13 (Zool. vol. 5), p. 137, text fig. 54 only.
1912 *Euchitonia aequipondata* Popofsky, *ibid.*, p. 139, pl. vii, figs. 3, 4.
1963 *non Euchitonia mülleri* Haeckel.—Bachmann *et al.*, Mitt. geol. Ges. Wien, vol. 56, pt. 1, p. 136, pl. 11, fig. 62.

Description.—Shell bilaterally symmetrical with 3 arms of approximately equal length, elliptical in cross section. Arms arise from a central structure composed of 2 inner spherical shells and an outer oblate spheroidal shell, all quite smooth and connected by numerous, discontinuous, radial beams. In addition, there is an outer ring of mesh in the plane of the shell which is normally oriented perpendicular to the microscope axis. This central structure is the same as that of *Amphirhopalum ypsilon* (pl. 3, figs. 3*c*, 3*d*).

Arms fairly heavy, increasing in breadth distally and having a blunt or irregularly rounded termination; sometimes with 1–3 slender terminal spines. Proximally arms appear chambered, but a rather dense mesh of subcircular pores generally obscures distal chambers, and gives arms a spongy appearance. Paired arms form the smaller angle opposite odd arm and often curve slightly towards each other.

A patagium may or may not be present. Specimens having a well-developed patagium are rare, and examination of it has not been sufficiently extensive to warrant any general conclusions. Usually, patagium shows partial development or, often, only a few initial branches are present. In other specimens there is no indication of a patagium forming.

Dimensions.—Average length of arms (measured from center of innermost sphere) 164–298μ. Maximum breadth of arms 54–90μ. Angle between paired arms 59°–94°.

Occurrences previously recorded.—Ehrenberg (1860*a*)—*E. furcata,* western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Ehrenberg (1860*b*)—*E. furcata,* North Pacific (California Sea: 20°52′ N., 151°50′ W., 4,755 m).

Stöhr (1880)—Upper Miocene from Grotte, Sicily.

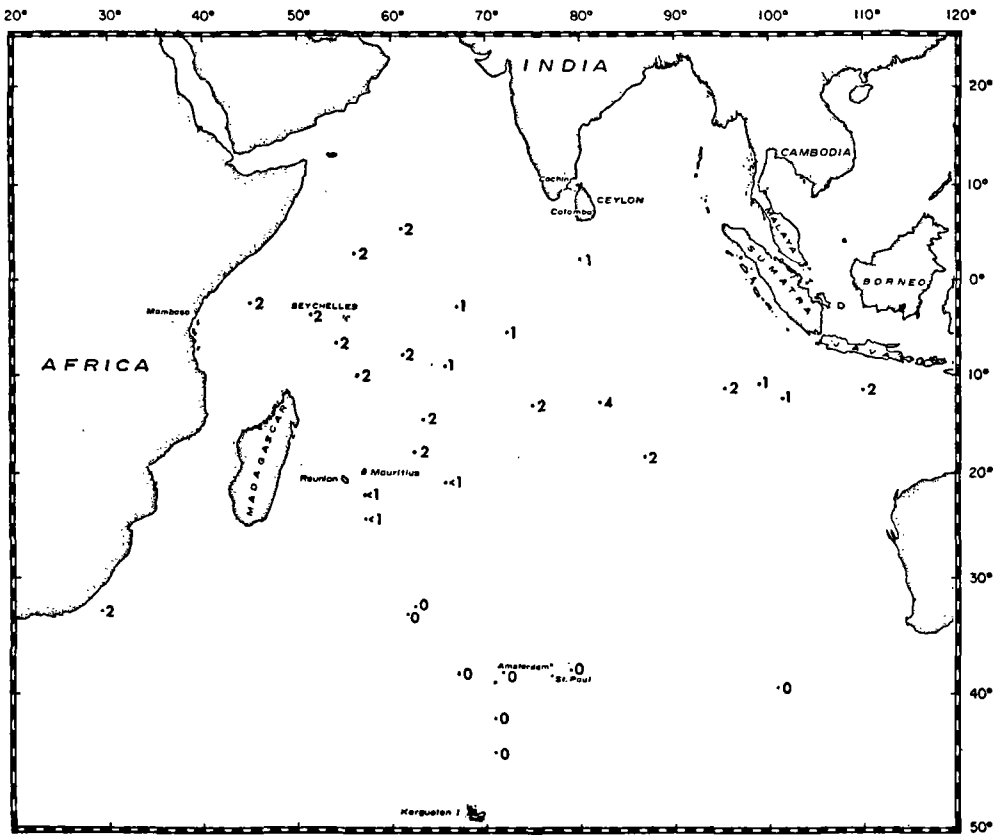

Fig. 17. Distribution of *Euchitonia mülleri.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Haeckel (1887)—*E. mülleri,* cosmopolitan; one of the most common Discoidea in all seas, on the surface as well as at different depths; also fossil in Tertiary rocks of Barbados and Sicily.

Cleve (1902)—*E. mülleri* (incl. *E. ypsiloides*), Malay Archipelago, very rare.

Popofsky (1913)—*E. mülleri,* Deutsche Südpolar-Expedition, 8 August 1903 (30°48′ S., 12°40′ E., 50 m); *E. aequipondata,* 2 June 1903 (33°40′ S., 28°40′ E.), 11 September 1903 (8°08′ S., 13°22′ W., 400 m), 21 September 1903 (0°16′ N., 18°07′ W., 400 m).

Cocco (1905)—*E. mülleri,* Tertiary of Condro, Sicily (questionable since species is unfigured).

Indian Ocean occurrences (fig. 17)—Recognizable specimens of *E. mülleri* are sparsely distributed in low latitudes, and are absent from samples taken south of 35° S. (cf. *E. elegans,* discussion, p. 40).

Discussion.—*Euchitonia ypsiloides* (Haeckel) (1887, p. 536) should, perhaps, be included in the synonymy of *E. mülleri,* but since it was only briefly described by Haeckel and not figured, it has been omitted for the time being. The three specimens described by Popofsky (1912) as *E. aequipondata* are apparently only particularly well-developed examples of *E. mülleri.*

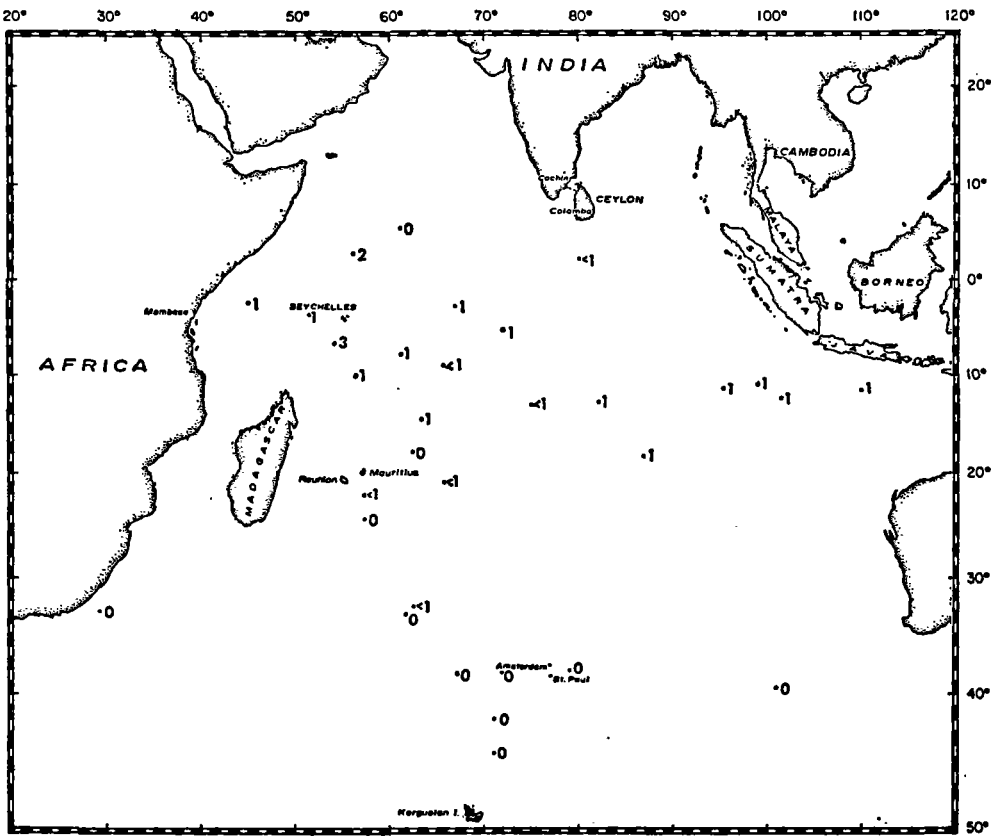

Fig. 18. Distribution of *Euchitonia elegans.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Euchitonia elegans (Ehrenberg)

(Pl. 4, figs. 2*a*, 2*b*)

1872*a* *Pteractis elegans* Ehrenberg, Monatsber., for 1872, p. 319.
1872*b* *Pteractis elegans* Ehrenberg, Abh., for 1872, p. 299, pl. viii, fig. 3.
1887 *Euchitonia elegans* (Ehrenberg).—Haeckel, "Chall." Rept., p. 535.

Description.—Similar to *Euchitonia mülleri* (p. 37), but differing in the shape of its arms. Arms slender, tapering distally, and sometimes terminating in 1 or 2 short, fairly stout spines. Angle between paired arms of *E. elegans* generally smaller than that of *E. mülleri.*

A patagium may or may not be present. When well developed it forms a delicate meshwork around the central structure and between each of the 3 arms (generally less well developed between paired arms). Meshwork forms rows of chambers, convex outwards in larger angles, concave between paired arms, and thickens

towards its outer edge. Sometimes patagium shows partial development or, often, only a few initial branches are present. In other specimens there is no indication of a patagium forming.

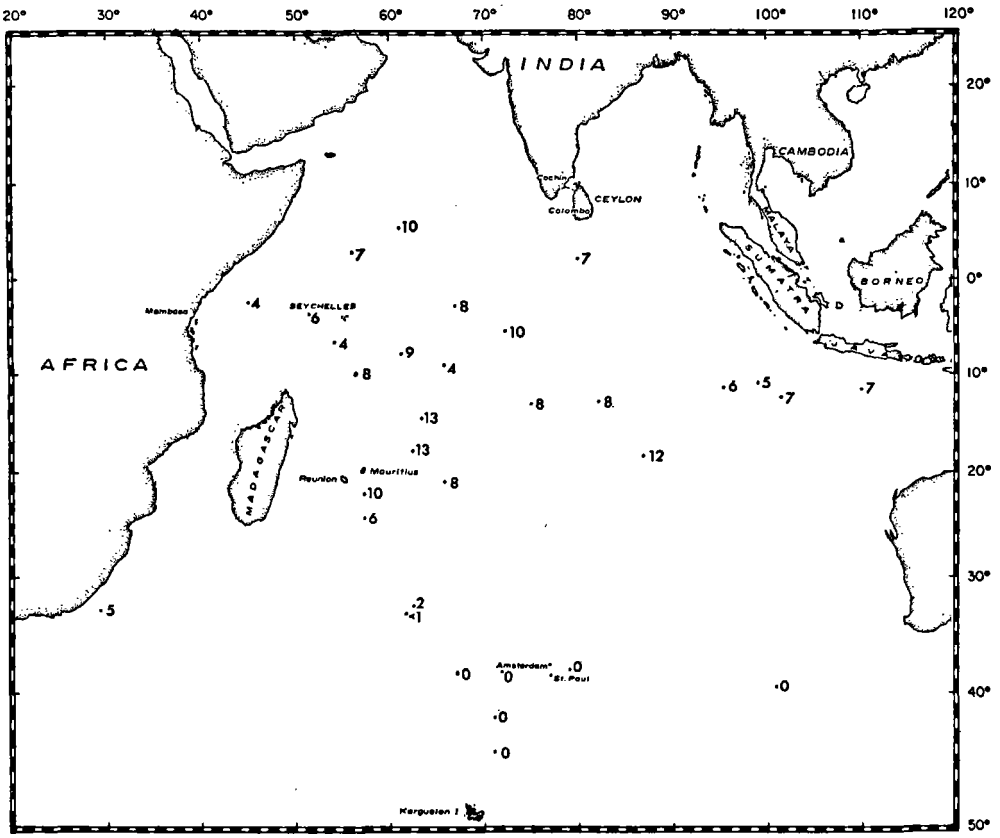

Fig. 19. Distribution of *Euchitonia* sp. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Dimensions.—Average length of arms (measured from center of innermost sphere) 146–289μ (usually 200–289μ). Maximum breadth of arms 36–63μ. Angle between paired arms 54°–75°.

Occurrences previously recorded.—Ehrenberg (1872*a*, *b*)—Western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Cleve (1902)—*E. elegans*, Malay Archipelago, very rare.

Riedel (1951*b*)—Tropical Indian Ocean, as for *Panartus quadrijugus* (p. 31).

Riedel (1952)—Tropical parts of the western Pacific and Indian Oceans, as for *Panartus quadrijugus* (p. 31).

Indian Ocean occurrences (fig. 18).—Recognizable specimens of *E. elegans* are very sparsely distributed in low latitudes and do not occur in middle latitude samples (but see discussion below).

Discussion.—It is usually difficult, if not impossible, to distinguish between *E. elegans* and *E. mülleri*. These species are differentiated by the shape of the arms of fairly complete and well-developed specimens. However, the majority of specimens

found are either broken or not completely developed, making it impossible to identify them to species. One is tempted to make *E. elegans* and *E. mülleri* and the indeterminant forms conspecific, but the difference between end members of

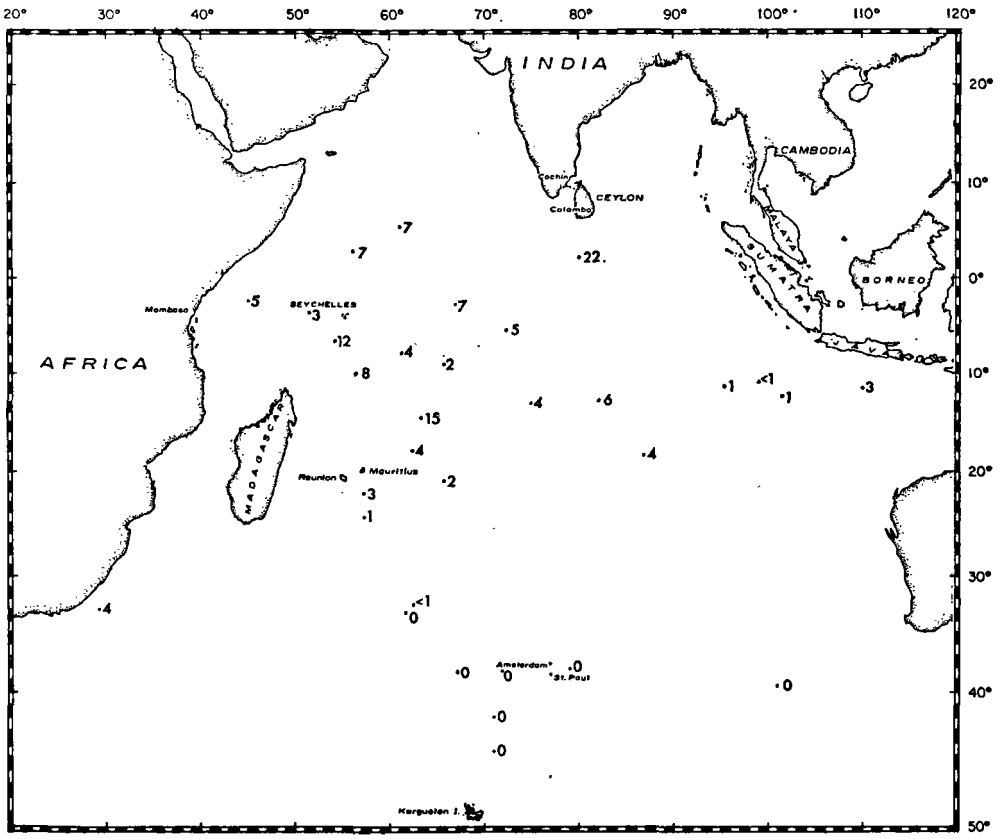

Fig. 20. Distribution of *Spongaster tetras tetras*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

such a series is sufficiently great to indicate that two species are, in fact, involved. Thus, a few specimens definitely belonging to each species and a large number of unidentifiable fragments were present in the samples examined.

Euchitonia sp. (fig. 19) is fairly abundant (4% to 12% of the described population) in low latitudes, but like *E. mülleri* and *E. elegans* it is absent from samples taken south of 35° S. The three forms appear to be reliable and potentially useful members of the low latitude assemblage.

Genus *Spongaster* Ehrenberg

Spongaster Ehrenberg, 1860*b*, p. 833; Haeckel, 1887, p. 596.

Spongaster tetras tetras Ehrenberg

(Pl. 5, figs. 1*a*, 1*b*)

1860*b* *Spongaster tetras* Ehrenberg, Monatsber., for 1860, p. 833; also designated *Spongastrum tetras*, p. 824.

1861*b* *Spongaster tetras* Ehrenberg, Monatsber., for 1861, p. 301.

1862 *Dictyocoryne tetras* Haeckel, Monogr. d. Radiol., p. 469.
1872*b* *Spongaster tetras* Ehrenberg, Abh., for 1872, p. 299, pl. VI (iii), fig. 8.
1887 *Spongaster tetras* Ehrenberg.—Haeckel, "Chall." Rept., p. 597.
1887 *Spongaster quadratus* Haeckel, *ibid.*, p. 597.
1887 *Spongaster pentacyclus* Haeckel, *ibid.*, p. 598.
1912 *Histiastrum quadratum* Popofsky, Deutsche Südpolar-Exped., vol. 13 (Zool. vol. 5), p. 141, pl. vi, fig. 4, text fig. 59.

Description.—Shell is a square with rounded corners. Four spongy, pear-shaped "arms" approximately at right angles, are regularly placed in one plane around 5 concentric lattice spheres (cf. pl. 5, fig. 1*b*). A completely enveloping patagium usually makes the central spheres difficult to see, and, at best, 5 concentric rings can be recognized; the "arms" appear merely as dark patches.

Patagium is, for the most part, a dense irregular spongy meshwork with small subcircular pores, but around the "arms" bars become thicker and 3-bladed. In some specimens radial beams apparently form a basis for the patagium which will then have a radially striated border. Patagium may be depressed slightly around the central structure, but at its periphery its thickness is approximately 0.25 the length of the sides of the square.

Dimensions.—Distance between sides 150–302μ (usually 150–276μ); diagonal 187–369μ (usually 187–316μ).

Occurrences previously recorded.—Ehrenberg (1860*a*)—*S. tetras,* western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Ehrenberg (1860*b*, 1861*b*)—*S. tetras,* North Pacific (California Sea: 20°52′ N., 151°50′ W., 4,755 m).

Ehrenberg (1861*a*)—*S. tetras,* Atlantic Ocean (25°43′20″ N., 80°02′28″ W., 256 m).

Haeckel (1887)—*S. tetras,* cosmopolitan: Atlantic, Indian, Pacific, surface and in various depths; *S. quadratus,* Pacific, central area, "Challenger" Stations 270 (2°34′ N., 149°09′ W.) to 274 (7°25′ S., 152°15′ W.), depths 4,298 m to 5,349 m; *S. pentacyclus,* West Indies, Cuba, surface (Thomson).

Popofsky (1912)—Deutsche Südpolar-Expedition, 6 October 1901 (4°35′ S., 16°48′ W.), 2 June 1903 (33°40′ S., 28°40′ E.), 11 September 1903 (8°08′ S., 13°22′ W., 400 m).

Riedel (1951*b*)—*S. tetras,* tropical Indian Ocean, as for *Panartus quadrijugus* (p. 31).

Riedel (1952)—*S. tetras,* tropical parts of the western Pacific and Indian Oceans, as for *Panartus quadrijugus* (p. 31).

Indian Ocean occurrences (fig. 20).—*S. tetras tetras* is fairly abundant in the western tropics, but decreases in abundance east of 85° E., and is absent from middle latitude samples. It appears to be a reliable and potentially useful member of the low latitude assemblage.

Discussion.—A spongy lattice shell, such as that of *S. tetras tetras,* is so irregular by nature that forms having such a shell structure are frequently quite variable. Haeckel (1887) described the "arms" of *S. pentacyclus* as being dark patches, separated from the central structure by lighter spongy areas. This is a distinction based upon relative heaviness of the spongy lattice and seems inapplicable when

the nature of the shell structure is considered. *S. quadratus* was distinguished by its radially striated border. However, partially striated forms have been observed, thus making the distinction questionable. The clarity with which these striations

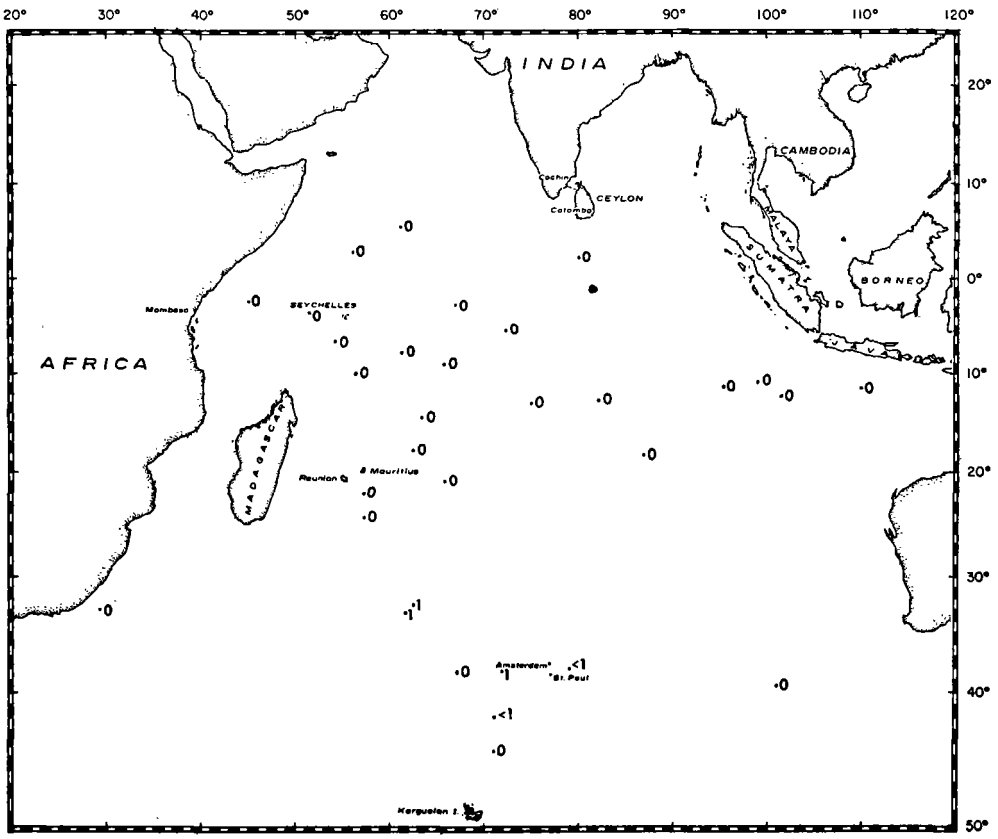

Fig. 21. Distribution of *Spongaster tetras irregularis*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

can be seen depends upon the heaviness of the spongy lattice. The three specimens described by Popofsky (1912) as *Histiastrum quadratum* were apparently particularly spongy examples of *S. tetras tetras*.

Spongaster tetras Ehrenberg *irregularis n. subsp.*

(Pl. 5, fig. 2)

Description.—Shell roughly rectangular, usually irregular, spongy. Basically similar to *Spongaster tetras tetras* (p. 41), with 4 or 5 central concentric lattice spheres, but differing from it by the shape of the patagium and angle between the "arms." "Arms" generally indistinct at 65°–79° to each other, forming an oblique cross; rarely, this angle may be as low as 59° or as high as 84°.

Dimensions.—Length of longer side 136–263μ; of shorter side 100–191μ. Average radius of arms (measured from center of innermost sphere) 80–132μ.

Indian Ocean occurrences (fig. 21).—*S. tetras irregularis* is absent from low

latitudes. In middle latitudes it is sparsely distributed. Though rare in Recent sediments, it appears to be a useful member of the middle latitude assemblage.

Discussion.—Patagium of *S. tetras irregularis* is more irregular in outline than that of either *Spongaster orthogonus* Haeckel, 1861 or *Spongaster scyllaeus*

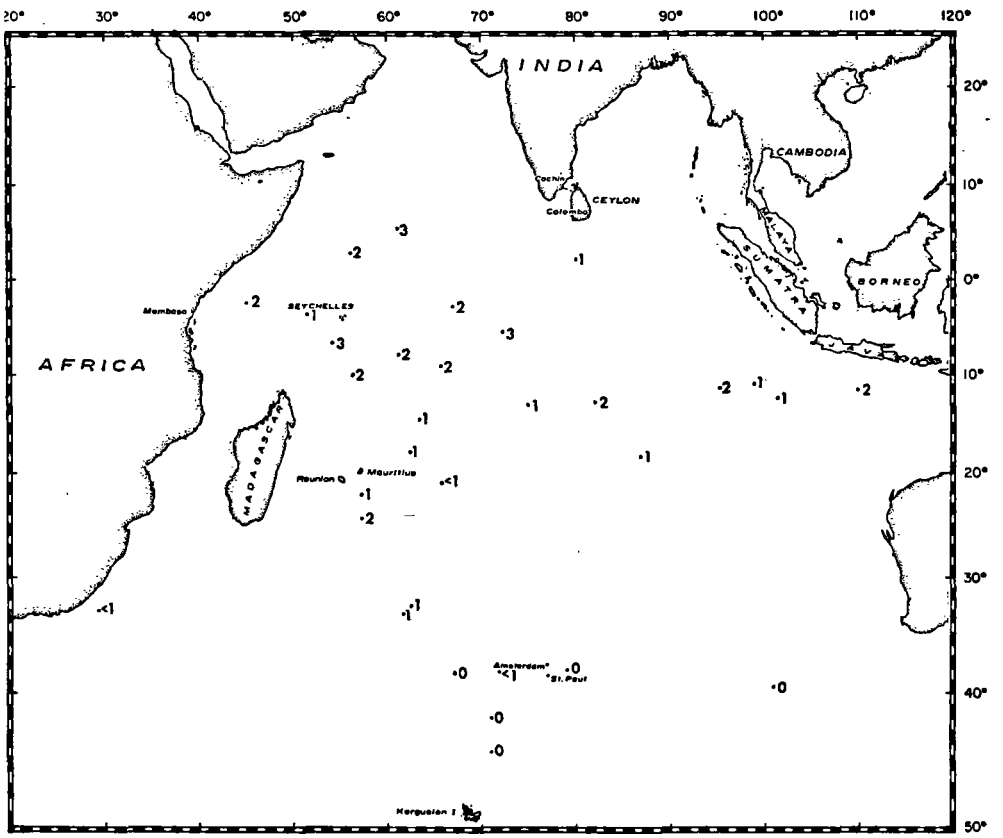

Fig. 22. Distribution of *Amphispyris reticulata.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Haeckel, 1861. Furthermore, according to Haeckel (1887), both these species are found in warm water, whereas *S. tetras irregularis* is found exclusively in middle latitudes (30°–42° S.).

Suborder STEPHOIDEA Haeckel, 1881

Genus *Amphisypris* Haeckel

Amphispyris Haeckel, 1881, p. 444; 1887, p. 1095.

Amphispyris reticulata (Ehrenberg)

(Pl. 5, fig. 3)

1872*a* *Dictyospyris reticulata* Ehrenberg, Monatsber., for 1872, p. 307.
1872*b* *Dictyospyris reticulata* Ehrenberg, Abh., for 1872, p. 289, pl. 10, fig. 19.
1887 *Amphispyris reticulata* (Ehrenberg).—Haeckel, "Chall." Rept., p. 1096.

Description.—Haeckel (1887) described and figured the members of the genus

Amphispyris with a deep "sternal incision" (i.e., basal constriction). However, examination of the sagittal ring has shown that it lies at 90° from the position suggested by Haeckel. The "incision" is, in fact, ventral and the small solid projection protruding into it is the vertical spine. Primary laterals are much reduced and appear as 2 small thorns. Collar pores usually lie in the plane of the slide. Shell is approximately equidimensional in the plane of the collar pores, but is flattened along the direction of the apical spine. Apical horn absent.

Arising from the complete D-shaped sagittal ring are 6 pairs of cylindrical bars, which anastomose laterally and which may give rise to 4 strictures in the otherwise rounded periphery. A cylindrical bar usually stretches across the ventral constriction and makes, with the vertical spine, a B-shaped opening.

Generally, a narrow lateral lattice girdle is present; pores irregular in shape and size, but always smaller than the 14 main pores. Rarely, small, irregular, initial lattice branches occur along the main spines. However, complete infilling of the main pores by latticework has not been observed.

Dimensions.—Maximum shell diameter 128–236μ.

Occurrence previously recorded.—Ehrenberg (1872*a*, *b*)—Indian Ocean (5°37′ S., 61°33′ E., 4,023m).

Indian Ocean occurrences (fig. 22).—*A. reticulata* is sparsely distributed in low latitudes, and is almost entirely absent from middle latitudes. Maximum abundances (up to 3% of the described population) occur in the western tropics.

Discussion.—Ehrenberg's description and illustration of *D. reticulata* are inadequate. However, since he described the species from the Indian Ocean, and since the only similar form commonly found in western tropical Indian Ocean material is the one here described, it seems reasonable to assume that the two forms are conspecific.

It is thought that *A. thorax, A. sternalis,* and possibly *A. toxarium* are also conspecific. However, considering that the Spyroids to which this form is undoubtedly closely related are presently under revision by Robert M. Goll of Ohio State University, a conservative synonymy seems most appropriate at this time.

Amphispyris costata Haeckel

(Pl. 5, fig. 4)

1887 *Amphispyris costata* Haeckel, "Chall." Rept., p. 1097, pl. 83, fig. 3.

Description.—Basically similar to *Amphispyris reticulata* (p. 44). Shell generally smaller, and periphery is rectangular, longer in the direction of the median bar, rather than equidimensional. Sagittal ring structure similar to *A. reticulata,* but with smaller primary laterals and often lacking a ventral crossbar. Lateral lattice girdle broader, with smaller pores than *A. reticulata.* The main pores are often filled or partially filled with irregular latticework, which may extend across the ventral constriction. Incipient infilling of this sort is indicated by small, sometimes stout, by-spines arising from the main bars.

Dimensions.—Maximum length 128–164μ; maximum breadth 90–146μ.

Occurrence previously recorded.—Haeckel (1887)—North Pacific, "Challenger" Station 244 (35°22′ N., 169°53′ E., 5,304 m).

Indian Ocean occurrences (fig. 23).—*A. costata* is very sparsely distributed in low latitudes and is absent from samples taken south of 35° S.

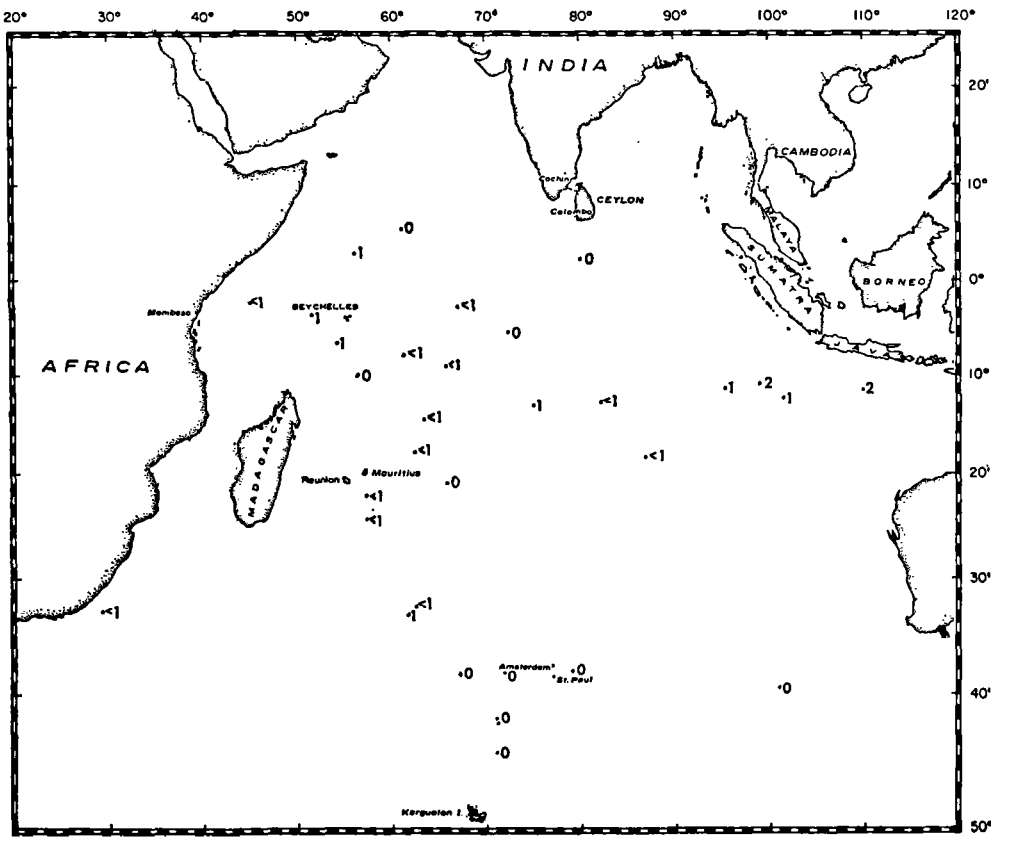

Fig. 23. Distribution of *Amphispyris costata*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Suborder SPYROIDEA Ehrenberg, 1847

Genus *Triceraspyris* Haeckel

Triceraspyris Haeckel, 1881, p. 441; 1887, p. 1029.
Triospyris Haeckel.—Campbell, 1954, p. D112 (cf. Riedel, 1958, p. 230).

Triceraspyris damaecornis Haeckel

(Pl. 5, fig. 5)

1887 *Triceraspyris damaecornis* Haeckel, "Chall." Rept., p. 1032.

Description.—Shell small and broad with slight sagittal constriction. Markedly D-shaped sagittal ring from which a short needle-like apical spine arises subapically; vertical spine thornlike. Basal pores large, 2 cardinal and 2 smaller cervical. Three short, sharply divergent basal feet, 3-bladed in cross section, of approximately equal length, correspond to the primary lateral and dorsal spines; usually with 3 distal branches. On either side of the sagittal ring are large oval to D-shaped pores, bounded by a band, often spiny, which increases in width from a

narrow bar, joined to each side of the basal ring, adjacent to the cardinal pores, to a wide band having unequal subcircular pores in the apical region. Sometimes this widening does not develop fully, and the band remains approximately constant in width, but indications of incipient widening are usually apparent.

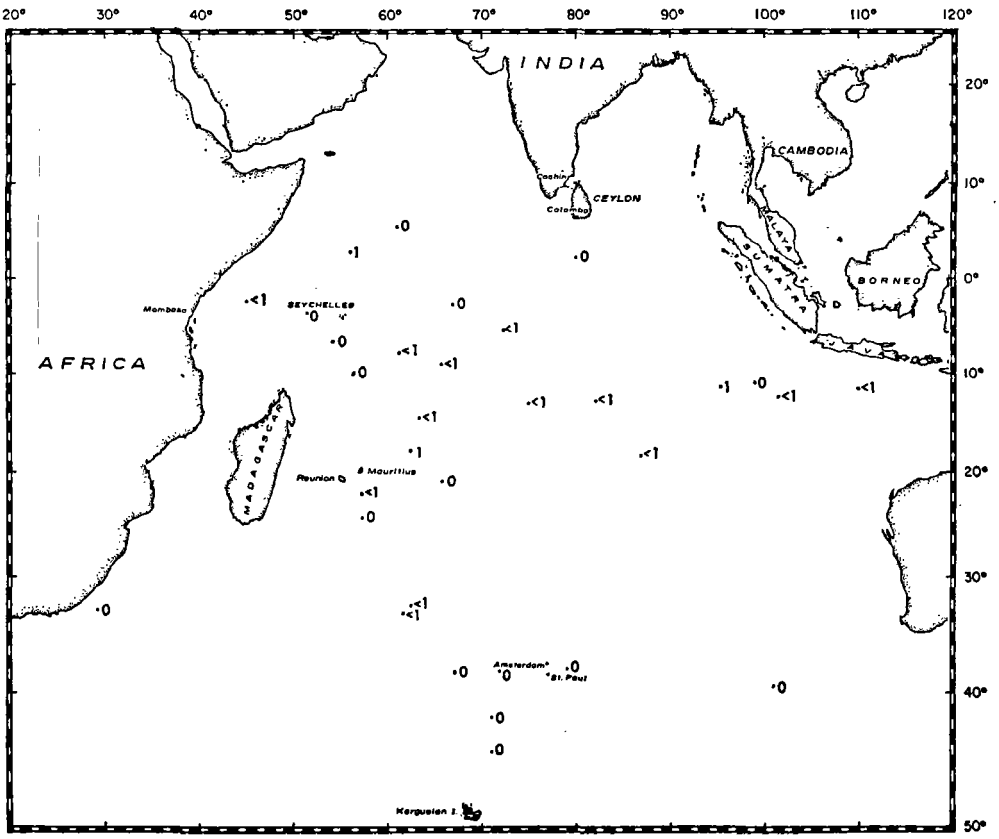

Fig. 24. Distribution of *Triceraspyris damaecornis*. Numbers are percentages of the described, population, based on total counts of 500 specimens in each sample.

Dimensions.—Height of sagittal ring 36–45μ. Maximum breadth of bilocular cephalis 63–81μ. Length of feet 9–18μ.

Occurrence previously recorded.—Haeckel (1887)—South Pacific, "Challenger" Station 295 (38°07′ S., 94°04′ W., 2,743 m).

Indian Ocean occurrences (fig. 24).—*T. damaecornis* is very sparsely distributed in low latitudes and does not occur in samples from south of 35° S.

Discussion.—It is difficult to determine the correct name for this species. A major taxonomic revision of the Spyroids is presently being attempted by Robert M. Goll of Ohio State University, and until this study is completed tentative names must be used. Although *T. damaecornis* is not figured by Haeckel (1887), and topotypic "Challenger" material is unavailable, Haeckel's description of the species closely resembles that of specimens found in the Indian Ocean. Two of the three "horns" described by Haeckel are probably projections from the spiny band and

not true horns, in the sense of being apical or vertical horns. The dimensions given by Haeckel are rather larger than those found herein.

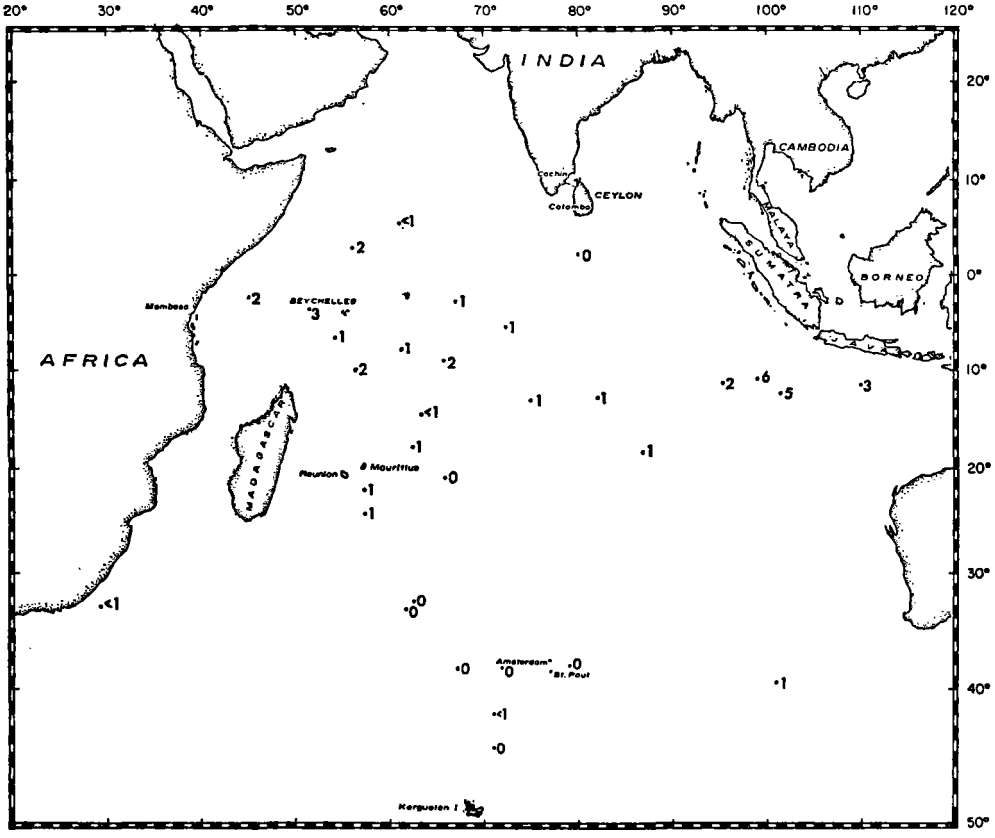

Fig. 25. Distribution of *Ceratospyris* sp. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Genus *Ceratospyris* Ehrenberg

Ceratospyris Ehrenberg, 1847, p. 54; Haeckel, 1887, p. 1066.
Cladospyris Ehrenberg.—Campbell, 1954, p. D114.

Since Haeckel, acting as first reviser, made *Cladospyris* a subgenus of *Ceratospyris,* his decision should be upheld, and the name *Ceratospyris* retained for the genus. Furthermore, the type species, *Cladospyris ramosa,* listed by Campbell (1954) is invalid, since it was not originally included in the genus. The reference to an 1847 description is erroneous. The type species, by monotypy, is *Ceratospyris radicata* Ehrenberg, 1844. This species was listed in Ehrenberg (1847), and in Ehrenberg (1854) it was indicated as synonymous with *Haliomma ? radicatum,* 1844.

Ceratospyris sp.

(Pl. 5, fig. 6)

Description.—Shell formed by straight, 3-bladed skeletal bars which bound large polygonal, or polygonally framed pores. Sagittal constriction pronounced apically,

but barely visible basally. Main pores in pairs, symmetrical about the D-shaped sagittal ring: basally, paired pentagonal cardinal and rhomboidal (2 sides are curved) cervical pores, approximately equal in size; apically, 1 pair of pentagonal pores; dorsally and ventrally, 2 pairs of larger pentagonal, sometimes hexagonal or tetragonal, pores. In all, 7 pore pairs adjacent to sagittal ring. Lateral pores smaller, not constant in size or arrangement.

Apical horn short, needle-like, slightly subapical in position. Numerous straight slender 3-bladed spines, not longer than 0.5 shell height, arise from points of intersection of skeletal bars; 9 similar basal feet up to 0.5 shell length. Three of these feet are extensions of the dorsal and primary lateral spines; the other 6 originate at the angles made by the bars of the cardinal and cervical pores.

Dimensions.—Maximum height 81–119μ; maximum breadth 109–164μ.

Indian Ocean occurrences (fig. 25).—*C.* sp. is sparsely distributed in the western tropics, but forms up to 6 percent of the described population in the eastern tropics. The species is practically absent from middle latitudes.

Discussion.—*C. pentagona* Ehrenberg, *C. allmersii* Haeckel, and *C. mulderi* Haeckel bear a resemblance to the species here described, but none is exactly similar. For example, none is described or illustrated as having nine basal feet. Possibly certain features of these forms were either not seen by Ehrenberg and Haeckel, or were simply omitted from the descriptions. In this group more than most, it is necessary to view specimens from all angles in order to understand their structure completely.

C. allmersii was described from "Challenger" 347 (0°15′ S., 14°25′ W.) material which is now unavailable. A nearby sample (0°49′ S., 14°24′ W.) was examined, but was found to contain no closely related form. *C. mulderi* was described from the Indian Ocean and is probably most like the species described herein. However, it is said to have many more spines and hexagonal, rather than pentagonal or rhomboidal, basal pores. *C. pentagona* was described as cosmopolitan, but it is not possible to determine with confidence the true nature of the species from Ehrenberg's figure (1872*b*). Since the Spyroids are presently under revision, it has been thought best not to assign a specific name to the form here described, but to leave the matter in abeyance.

Suborder BOTRYODEA Haeckel, 1881

Genus *Centrobotrys* Petrushevskaya

Centrobotrys Petrushevskaya, 1965, p. 113.

Centrobotrys thermophila Petrushevskaya

(Pl. 5, fig. 7; fig. 26)

?1913 *Androspyris pithecus* Haeckel.—Popofsky, Deutsche Südpolar-Exped., vol. 14 (Zool. vol. 6), p. 293, pl. xxix, fig. 6.

1913 *Androspyris aptenodytes* Haeckel.—Popofsky, *ibid.*, p. 294, text figs. 17, 18.

1965 *Centrobotrys thermophila* Petrushevskaya, Trudy Zoologicheskogo Inst. (Akad. Nauk SSSR), vol. 35, p. 115.

Description.—Internal cephalic lobe heavy, spherical with small, closely spaced, subcircular pores; surface rough. This lobe is supported above the collar structure

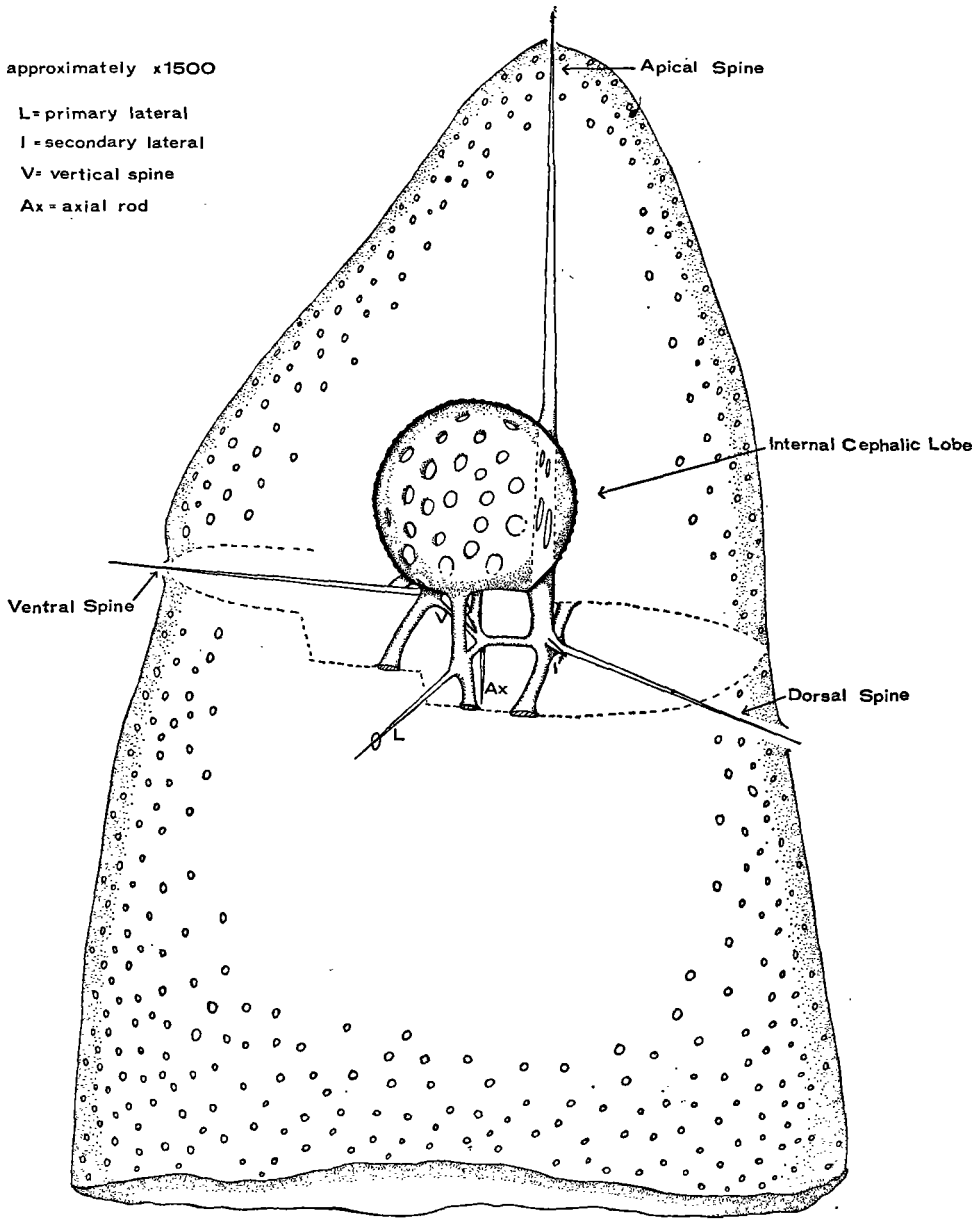

Fig. 26. *Centrobotrys thermophila.*

by 3 stout rods or spines, 2 of which are attached to the primary laterals. The third is part of the apical spine, and originates at one end of the median bar. As it passes through the wall of the cephalic lobe, it is flanked by 2 pairs of pores; it leaves the lobe as a cylindrical, needle-like spine which may or may not pierce the

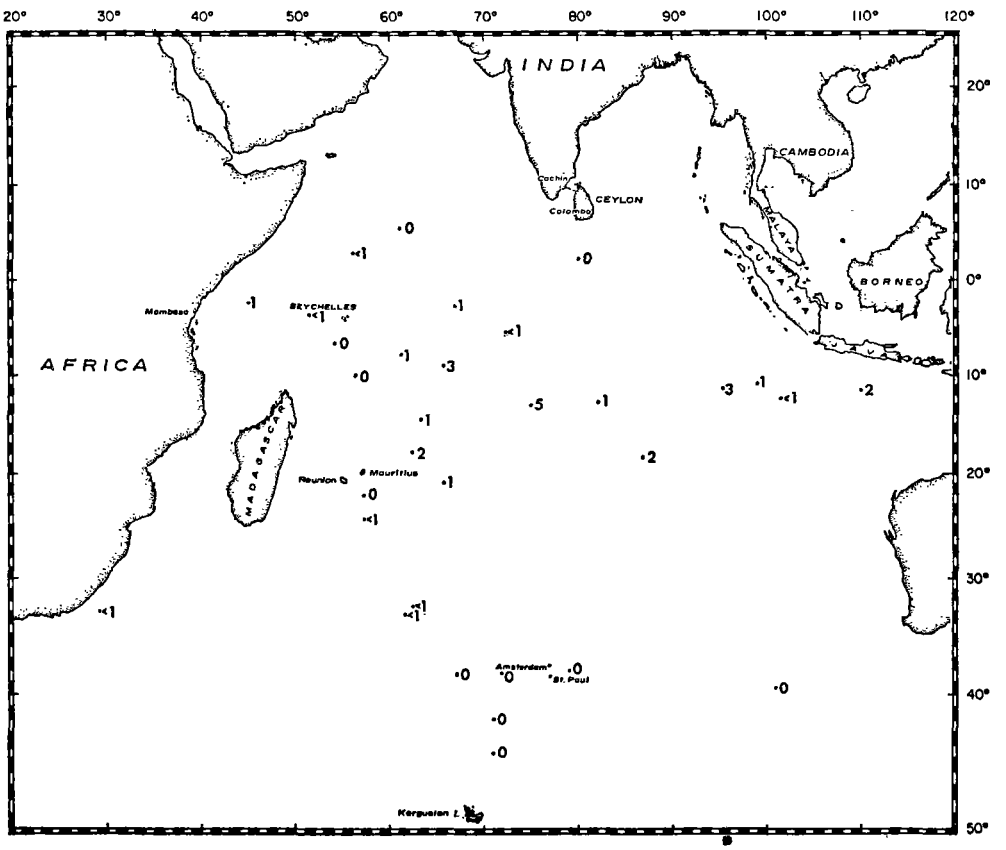

Fig. 27. Distribution of *Centrobotrys thermophila*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

outer cephalic wall. Vertical spine ends as a small thorn in one of the pores of the internal cephalic lobe. Slender, cylindrical primary lateral, dorsal, and ventral spines extend outwards, and usually a little downwards, from the collar structure, often piercing the outer shell. The ventral spine originates near the upper end of the vertical spine. Short secondary laterals and an axial rod are also present. A pair of stout rods extend from either side of the vertical spine to the wall of the outer cephalic shell (fig. 26).

Outer shell approximately triangular in outline, often with a slight collar stricture; elliptical in transverse section. It is thin-walled, hyaline, and smooth with many, irregular scattered, small circular pores. Termination invariably ragged.

Dimensions.—Maximum length 90–128μ. Maximum breadth 63–81μ.

Occurrences previously recorded.—Popofsky (1913)—*A. pithecus,* Deutsche

Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E., 400 m); *A. aptenodytes,* Deutsche Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E., 400 m).

Petrushevskaya (1965)—Indian Ocean.

Indian Ocean occurrences (fig. 27).—*C. thermophila* is rather sparsely distributed in low latitudes and does not occur in samples from middle latitudes. Though rather rare in Recent sediments, it appears to be a useful member of the low latitude assemblage.

Discussion.—The generic and suprageneric placement of this species has been discussed by Petrushevskaya (1965). Certainly *Androspyris aptenodytes* Popofsky (1913) is identical with the species here described. The figured specimen of *Androspyris pithecus* Popofsky (1913) apparently represents a lateral view of the same species, but because it seems unlikely that Popofsky should find four specimens in this orientation, its inclusion in the synonymy of *C. thermophila* is questionable.

The description of the internal structure of *C. thermophila* presented herein differs from that of Petrushevskaya by the presence of two stout rods on either side of a ventral spine, which extends outwards from a point slightly above the collar pores.

Genus *Botryocyrtis* Ehrenberg

Botryocyrtis Ehrenberg, 1860*b*, p. 829; Haeckel, 1887, p. 1120.

Type species: *B. scutum* (Harting) (= *B. serpentis* Ehrenberg).

Botryocyrtis scutum (Harting)

(Pl. 6, figs. 1*a*–1*c*)

1863 *Haliomma scutum* Harting, K. Akad. v. Wetensch., Amsterdam, Verhand., vol. 10, p. 11, pl. 1, fig. 18.

1872*a* *Botryocyrtis Caput Serpentis* Ehrenberg, Monatsber., for 1872, p. 301.

1872*b* *Botryocyrtis Caput serpentis* Ehrenberg, Abh., for 1872, p. 287, pl. x, fig. 21.

1887 *Botryocyrtis serpentis* Ehrenberg.—Haeckel, "Chall." Rept., p. 1120.

1964 *Botryopyle hexapora* Popofsky.—Petrushevskaya, Zoologicheskii zhurnal—Zoological Journal, vol. 43, no. 8, p. 1125, text figs. 4, 5.

1965 *Botryocyrtis caput-serpentis* Ehrenberg.—Petrushevskaya, Trudy Zoologicheskogo Inst. (Akad. Nauk SSSR), vol. 35, p. 102.

Description.—Cephalis tri- or quadrilobate (cf. pl. 6, fig. 1*c*): (1) heavy central lobe (A) directly over collar pores; (2) large lobe (B) on the dorsal side of A; (3) usually indistinct lobe (D) on the ventral side of A; and (4) in many specimens there appears to be a small, inconspicuous lobe (C) beneath and slightly lateral to B. Petrushevskaya (1964) figured this fourth lobe beneath and slightly lateral to lobe D, and in some specimens this appears to be so, but usually lobe C cannot be distinguished either dorsally or ventrally. Possibly the spongy sheath surrounding the entire shell gives the illusion of a fourth lobe. There are 2 large pores at the base of lobe B, leading to the thoracic cavity. Details of the structure of lobes C and D could not be determined. All lobes with numerous small subcircular to subangular pores.

Thorax short, lenticular in cross section, somewhat inflated, with relatively large subangular pores. Lumbar stricture not pronounced externally, but marked internally by a septal ring.

In some specimens there is an abdomen, similar to the thorax, and then a fourth segment of varying length and having smaller pores. In other specimens, the "abdominal segment" is missing, and the small-pored segment adjoins the thorax. Mouth usually wide open or only slightly constricted, with a ragged termination.

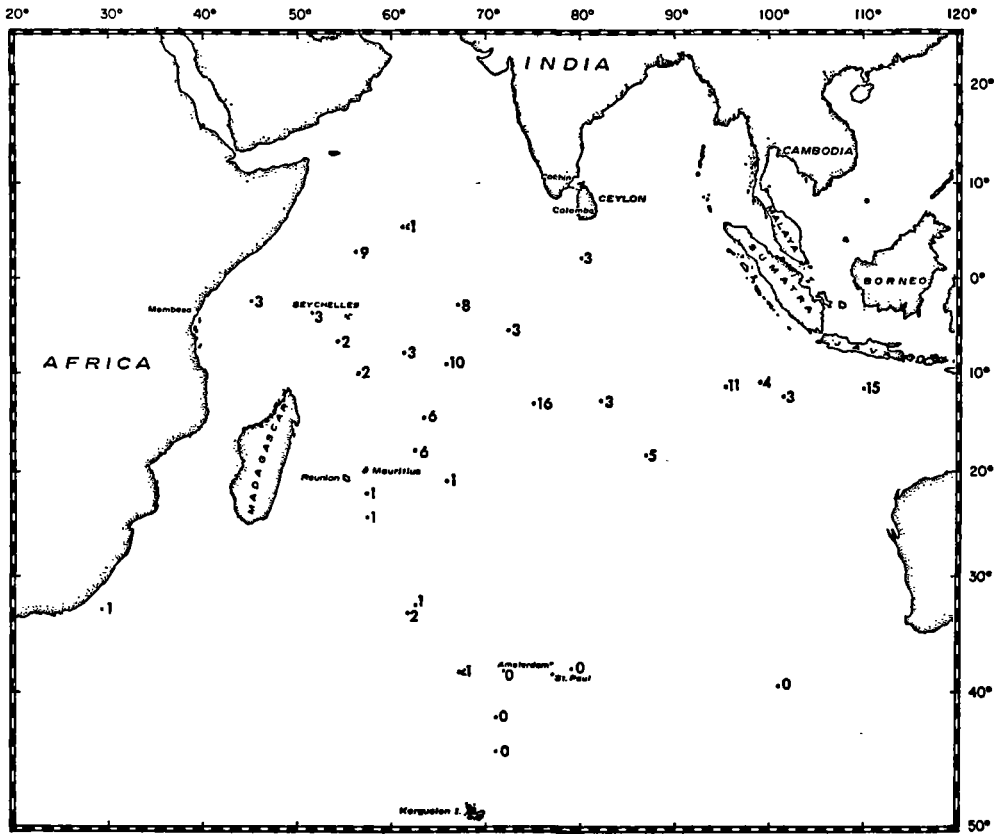

Fig. 28. Distribution of *Botryocyrtis scutum*. Numbers are percentages of the described popluation, based on total counts of 500 specimens in each sample.

Entire shell surrounded by a sheath of spongy material. Particularly spongy specimens have a tubelike protuberance near the lumbar stricture (Petrushevskaya [1964] figured it near the collar stricture), but this feature is not constant, and, therefore, the species is not treated as a tubed Botryoid.

Dimensions.—Total length 81–128μ. Maximum breadth 54–81μ.

Occurrences previously recorded.—Ehrenberg (1860*b*)—*B. caputserpentis*, North Pacific (California Sea: 20°52′ N., 151°50′ W., 4,755 m and 30°51′ N., 130°08′ W., 4,755 m).

Harting (1863)—Banda Sea (4°12′ S., 129°05′ E., 2,195 m).

Ehrenberg (1872*a,b*)—Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Petrushevskaya (1964)—Tropical Indian Ocean.

Indian Ocean occurrences (fig. 28).—*B. scutum* is fairly abundant in low latitudes. South of 20° S. abundances decrease sharply to 1 percent to 2 percent of the described population, and south of 35° S. the species is practically absent. It ap-

pears to be a reliable and potentially useful member of the low latitude assemblage.

Discussion.—Assignment of a specific name to this species poses a difficult taxonomic problem. Ehrenberg (1860*b*) listed two species of *Botryocyrtis, B. Caput serpentis* and *B. Lithobotrys*. In the same paper, the genus *Botryocyrtis* was described, but without an indication that he considered one or the other of the two species then known to him to be more typical. If only one species had been listed, then it would be correct to consider the generic description equivalent to a specific description of the species listed. (This circumstance occurs in the case of *Spongaster tetras* [Ehrenberg, 1860*b*, pp. 824, 833.]) However, since two species were listed, the generic description cannot be considered as a description of either species. Thus, the first valid descriptions of *B. caputserpentis* and *B. lithobotrys* were published by Ehrenberg in 1872*a* (pp. 301, 302). Harting's 1863 description of *Haliomma scutum* (= *B. caputserpentis*) therefore has priority, and the specific name *scutum* has priority over *caputserpentis*.

The species described herein is certainly the same as that described by Petrushevskaya (1964) as *Botryopyle hexapora* Popofsky. However, it is not clear to the present author that the single specimen described by Popofsky as *B. hexapora* is conspecific, and it, therefore, has been omitted from the present synonymy.

Suborder CRYTOIDEA Haeckel, 1862

Superfamily DICYRTIDA Haeckel, 1862

Genus *Lithopera* Ehrenberg *sens. emend.*

Lithopera Ehrenberg, 1847, p. 54; Haeckel, 1887, p. 1233.

Sethopiliidae with three divergent ribs initially enclosed in the cavity of the thorax. Cephalis with or without horn.

The genus *Lithopera* Ehrenberg (1847) was originally described with three divergent ribs enclosed in the thoracic cavity. This structure is present in some specimens of the type species (*Lithopera bacca* Ehrenberg), but longer ribs easily become incorporated distally into the thoracic wall and may even project beyond it to form small wings. Hence, the generic description is emended herein to specify that ribs are only initially enclosed in the thoracic cavity. Inclusion of forms having no cephalic horn was proposed by Popofsky (1913, p. 355), and is supported by the findings of the present author.

Lithopera bacca Ehrenberg

(Pl. 6, fig. 2)

1872*a* *Lithopera bacca* Ehrenberg, Monatsber., for 1872, p. 314.
1872*a* *Lithopera bursella* Ehrenberg, *ibid.*, p. 315.
1872*b* *Lithopera bacca* Ehrenberg, Abh., for 1872, p. 297, pl. viii, fig. 1.
1872*b* *Lithopera bursella* Ehrenberg, *ibid.*, p. 297, pl. x, fig. 4.
1887 *Lithopera bacca* Ehrenberg.—Haeckel, "Chall." Rept., p. 1233.
1887 *Lithopera bursella* Ehrenberg.—Haeckel, *ibid.*, p. 1234.
1913 *Lithopera bacca* Ehrenberg.—Popofsky, Deutsche Südpolar-Exped., vol. 14 (Zool. vol. 6), p. 355, text figs. 61–63.
1913 *Lithopera circopora* Popofsky, *ibid.*, p. 356, text figs. 64–66.

Description.—Cephalis simple, spherical, thick-walled, surface rough with small

subcircular pores; half to two-thirds of cephalis depressed into thorax. Apical horn cylindrical, needle-like, less than or equal to length of cephalis; apical spine free. Dorsal and primary lateral spines extend beyond collar structure. In the region of the collar structure they lie entirely within the thoracic cavity, but very often

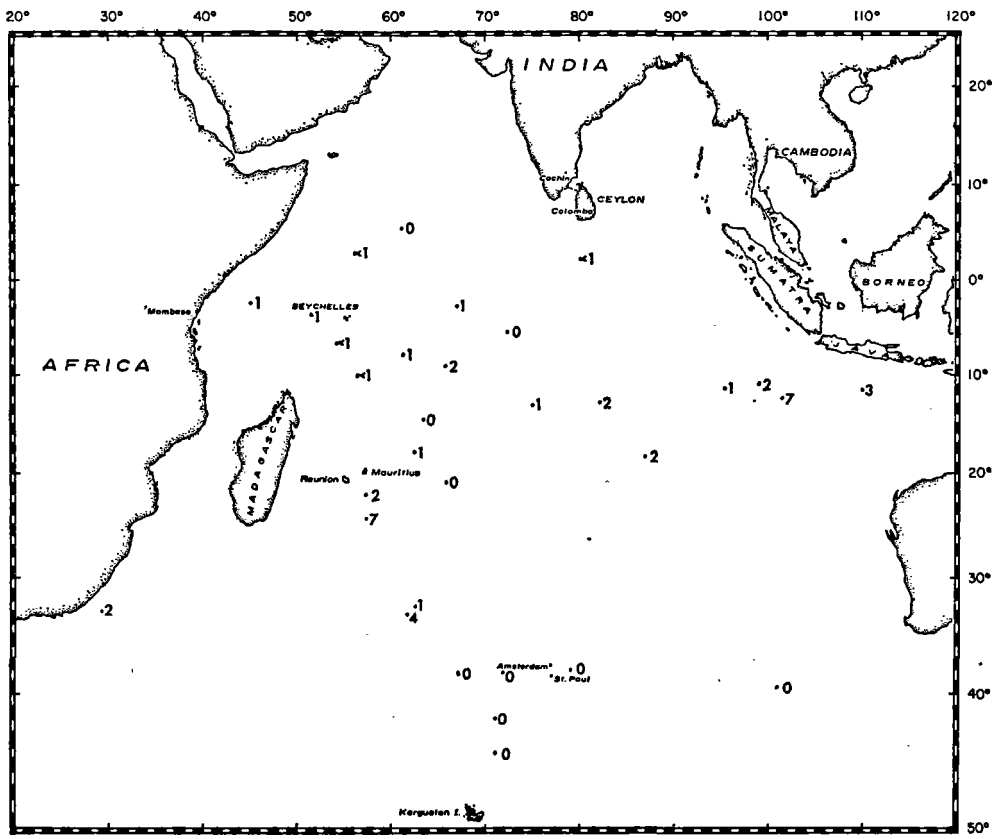

Fig. 29. Distribution of *Lithopera bacca*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

become incorporated distally into the thoracic wall and may even project beyond it to form small wings about a third of the way down the thorax. Rarely, one of these spines forks within the thoracic cavity.

Thorax rather thick-walled, rough, ellipsoidal to subspherical, closed distally. Thoracic pores small, circular to subcircular, sometimes hexagonally framed, arranged in transverse rows.

Dimensions.—Total length (excluding apical horn) 119–136μ. Diameter of cephalis 18–27μ. Length of thorax 100–128μ; breadth 90–109μ.

Occurrences previously recorded.—Ehrenberg (1860*a*)—*L. bacca,* western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Ehrenberg (1860*b*): *L. bacca,* North Pacific (California Sea: 20°52′ N., 151°50′ W., 4,755 m).

Ehrenberg (1872*a, b*)—*L. bursella,* Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Haeckel (1887)—*L. bacca,* tropical Pacific, "Challenger" Stations 200 (6°47′

N., 122°28′ E.), 224 (7°45′ N., 144°20′ E.), 266 (11°07′ N., 152°03′ W.), 271 (0°33′ S., 151°34′ W.), etc., surface; *L. bursella,* Indian Ocean (east of Madagascar), surface (Rabbe).

Popofsky (1913)—*L. bacca,* Deutsche Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E.), 30 August 1901 (33°55′ N., 16°09′ W.), Indian and Atlantic Oceans; *L. circopora,* Deutsche Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E., 400 m).

Indian Ocean occurrences (fig. 29),—*L. bacca* is sparsely distributed in the western tropics, but increases somewhat in abundance in the extreme eastern tropics, and in samples from between 20° and 35° S. (up to 7% of the described population). It does not occur in samples from south of 35° S.

Discussion.—According to Haeckel (1887), *L. bursella* is more slender than *L. bacca* and has smaller pores and thinner bars. Although Haeckel's single measurement of thorax breadth was smaller than any found herein, this character does not seem an appropriate basis for a specific distinction. The distinction based on pore and bar size seems questionable in that *L. bacca* was described as having "small pores and very thin, thread-like bars" (Haeckel, 1887, p. 1233); whereas *L. bursella* was puzzlingly said to have even smaller pores and thinner bars.

Popofsky (1913) erected the species *L. circopora* on the basis of only one complete specimen. The differences between it and *L. bacca* appear to fall within the range of variability of the species, and therefore, the species have been synonymized.

Genus *Anthocyrtidium* Haeckel

Anthocyrtidium Haeckel, 1881, p. 431; 1887, p. 1278.
Anthocyrtissa Haeckel, 1887, p. 1270. Proposed as a subgenus of *Anthocyrtis* Ehrenberg, 1847.

Type species: *A. ophirense* (Ehrenberg) (= *A. cineraria* Haeckel).

Anthocyrtidium ophirense (Ehrenberg)

(Pl. 6, fig. 3)

1872*a* *Anthocyrtis ophirensis* Ehrenberg, Monatsber., for 1872, p. 301.
1872*b* *Anthocyrtis ophirensis* Ehrenberg, Abh., for 1872, p. 285, pl. ix, fig. 13.
1887 *Anthocyrtis ophirensis* Ehrenberg.—Haeckel, "Chall." Rept., p. 1270.
1887 *Anthocyrtidium cineraria* Haeckel, *ibid.*, p. 1278, pl. 62, fig. 16.
1913 *Anthocyrtidium cineraria* Haeckel (?).—Popofsky, Deutsche Südpolar-Expedition, vol. 14 (Zool. vol. 6), p. 370, pl. xxxviii, fig. 1, text fig. 87.
1957 *Anthocyrtidium cineraria* Haeckel.—Riedel, Rep. Swedish Deep-Sea Exped., vol. 6, no. 3, p. 84, pl. 2, figs. 6–9, text fig. 4 (*partim*).

Description.—Riedel (1957, p. 84) synonymized *Anthocyrtidium cineraria* Haeckel and *Sethocyrtis oxycephalis* Haeckel and described what he interpreted to be a single species. The present author does not believe that these species are identical, and consequently 2 separate species, *A. ophirense* (= *A. cineraria*) and *A. zanguebaricum* (= *S. oxycephalis*), are distinguished herein. Riedel's description was based, in part, on Indian Ocean material, and specimens found during the present study agree in most respects with his observations. However, *A. ophirense* has an apical horn which is always longer than the cephalis, and subterminal teeth are almost always well developed. *A. zanguebaricum* has a shorter apical horn, and subterminal teeth are poorly developed or absent (cf. p. 58).

Dimensions.—Length of apical horn 45–90μ; of cephalis 27–36μ; of thorax 81–119μ; of subterminal teeth 9–27μ. Maximum breadth of cephalis about 27μ; of thorax 90–136μ.

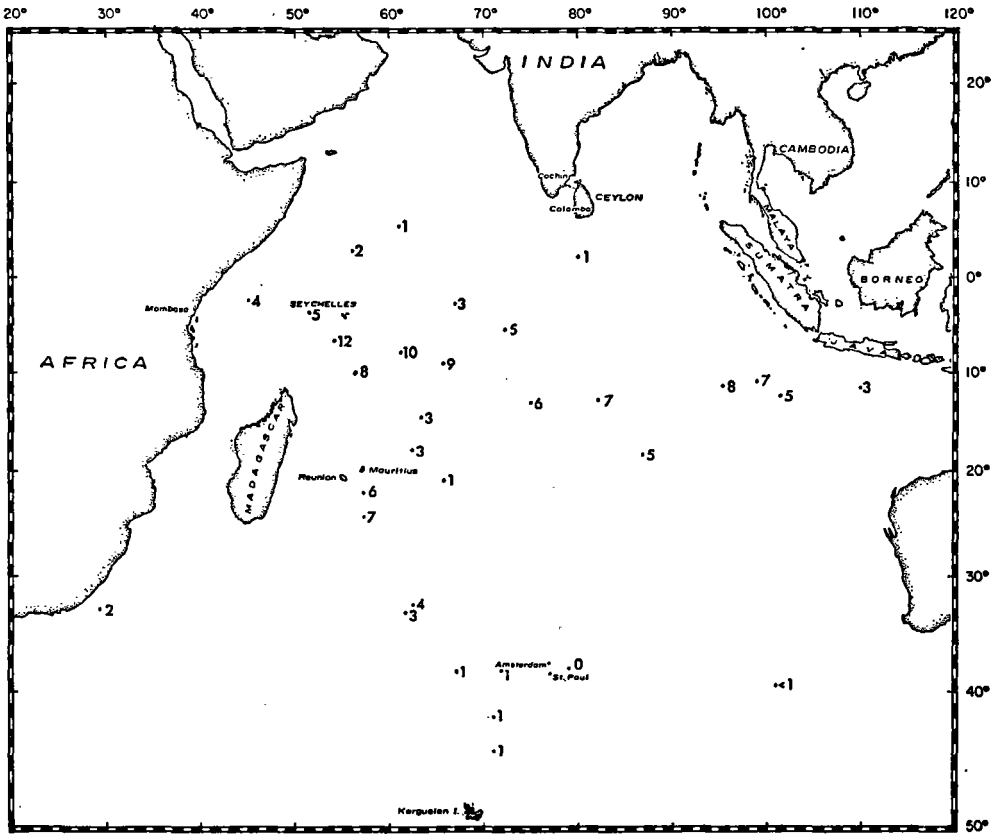

Fig. 30. Distribution of *Anthocyrtidium ophirense*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Occurrences previously recorded.—Ehrenberg (1872*a, b*)—Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Haeckel (1887)—*A. ophirensis,* Indian Ocean (east of Madagascar), surface (Rabbe); *A. cineraria,* Central Pacific, "Challenger" Station 271 (0°33′ S., 151°34′ W., 4,435 m).

Popofsky (1913)—Deutsche Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E., 400 m), 8 August 1903 (30°48′ S., 12°40′ E., 50 m), 20 August 1903 (approximately 25° S., 1° W., 400 m), 26 August 1903 (18°45′ S., 5°07′ W., 200 m), 18 September 1903 (2°32′ S., 16°03′ W., 400 m).

Riedel (1951*b*)—*A. cineraria,* tropical Indian Ocean, as for *Panartus quadrijugus* (p. 31).

Riedel (1952)—*A. cineraria,* tropical parts of the western Pacific and Indian Oceans, as for *Panartus quadrijugus* (p. 31).

Riedel (1957)—Swed. D.-S. Exped. Cores 73B (4°04′ S., 152°53′ W., 5,200 m),

10–39 cm, 73 (4°04′ S., 152°53′ W., 5,200 m), 11.5–848 cm and 1,250 cm, 74 (0°29′ S., 151°33′ E., 4,575 m), 1–1,340 cm, 75 (0°20′ N., 150°36′ W., 4,400 m), 9–820 cm, 76B (3°45′ N., 149°44′ W., 5,155 m), 10–25.5 cm, 76 (3°45′ N., 149°44′ W., 5,155 m), 7.5–509.5 cm, 77B (9°30′ N., 148°40′ W., 5,384 m), 6.5 and 25 cm, 77 (9°30′ N., 148°40′ W., 5,384 m), 10 cm, 83 (8°40′ N., 169°28′ W., 5,456 m), 1 cm, 85B (5°34′ N., 172°12′ W., 5,590 m), 1–9.5 cm and 49 cm, 85 (5°34′ N., 172°12′ W., 5,590 m), 299–930 cm, 87 (2°23′ N., 173°50′ W., 5,560 m), 0–500 cm and 800 cm, 89 (2°48′ S., 178°57′ W., 5,465 m), 0–300 cm, 91 (2°50′ S., 171°18′ E., 4,096 m), 26–210 cm, 93 (1°20′ S., 167°23′ E., 3,942 m), 0.5–1,509 cm.

Indian Ocean occurrences (fig. 30).—*A. ophirense* is abundant in low latitudes, but south of 35° S. it never forms more than 1 percent of the described population. It appears to be a reliable and potentially useful member of the low latitude assemblage.

Discussion.—Ehrenberg's figure of *A. ophirensis,* based on Indian Ocean material, is very similar to *A. cineraria* Haeckel, and it is possible that he overlooked a part of the shell inside the subterminal teeth. Since only one common species of this general form has been found during the present study, it seems reasonable to conclude that *A. ophirensis* and *A. cineraria* are synonymous, and that they rightly belong in the genus *Anthocyrtidium.*

Popofsky (1913) had reservations concerning the forms he described as *A. cineraria,* saying that his specimens had a narrower thorax than had been recorded by Haeckel. This would suggest that they belong to the species *A. zanguebaricum* (Ehrenberg) (p. 58), but his figured specimens appear to be more closely related to *A. ophirense,* and for this reason Popofsky's findings are being included in the notes on this species. It seems probable that he had specimens of both species.

Popofsky (1917) erected the subspecies *A. cineraria brachypes* to embrace the questionable forms of *A. cineraria* he described in 1913. No specimens having dorsal and lateral spines extending through the entire thoracic length have been observed by the present author in Indian Ocean sediments. The subspecies should probably be included in the synonymy of *A. ophirense.*

Anthocyrtidium zanguebaricum (Ehrenberg)

(Pl. 6, fig. 4)

1872*a* *Anthocyrtis zanguebarica* Ehrenberg, Monatsber., for 1872, p. 301.
1872*b* *Anthocyrtis zanguebarica* Ehrenberg, Abh., for 1872, p. 285, pl. ix, fig. 12.
1887 *Anthocyrtium zanguebaricum* (Ehrenberg).—Haeckel, "Chall." Rept., p. 1277.
1887 *Sethocyrtis oxycephalis* Haeckel, *ibid.,* p. 1299, pl. 62, fig. 9.
1917 *Sethoconus trochus* (Ehrenberg).—Popofsky, Deutsche Südpolar-Exped., vol. 16 (Zool. vol. 8), p. 273, text figs. 36, 37.
1957 *Anthocyrtidium cineraria* Haeckel.—Riedel, Rep. Swedish Deep-Sea Exped., vol. 6, no. 3, p. 84 (*partim*).

Description.—Shell rather similar in form to *Anthocyrtidium ophirense* (p. 56). Cephalis lobate as in *A. ophirense,* but apical horn is much shorter, usually about equal in length to the cephalis. Thorax less campanulate, more ovate, and always smaller, both in breadth and length. Subterminal teeth, when present, are poorly developed; terminal teeth may be entirely absent, rudimentary, or in the

form of inconspicuous, small triangular teeth directed either downwards or inwards.

Dimensions.—Length of apical horn 18–36μ; of cephalis 27–36μ; of thorax 63–90μ. Maximum breadth of cephalis 18–27μ; of thorax 63–81μ.

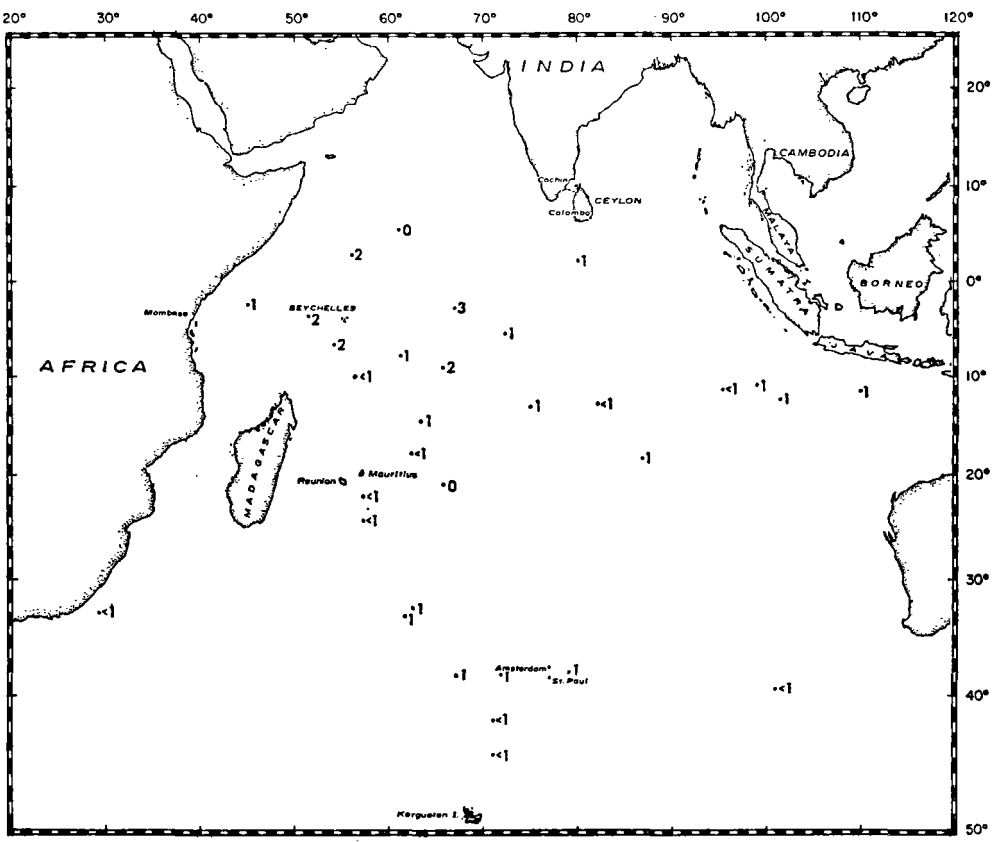

Fig. 31. Distribution of *Anthocyrtidium zanguebaricum*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Occurrences previously recorded.—Ehrenberg (1872*a*, *b*)—Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Haeckel (1887)—Central Pacific, "Challenger" Stations 263 (17°33′ N., 153°36′ W.) to 274 (7°25′ S., 152°15′ W.), depths 4,298 m to 5,486 m.

Popofsky (1917)—Deutsche Südpolar-Expedition, southern Indian and Atlantic Oceans, 15 May 1903 (25°07′ S., 56°07′ E., 400 m), 26 August 1903 (18°45′ S., 5°07′ W.), 11 August 1903 (28°46′ S., 10°17′ E., 200 m), 18 September 1903 (2°32′ S., 16°03′ W., 200 m).

Riedel (1957)—As for *A. ophirense* (p. 56).

Indian Ocean occurrences (fig. 31).—*A. zanguebaricum* is sparsely distributed in both low and middle latitudes. Maximum abundances (up to 3% of the described population) occur in the western tropics.

Discussion.—*A. zanguebaricum* was rather inadequately described and figured by Ehrenberg (1872*a*, *b*) from Indian Ocean material. After the extensive observa-

tions made during the present study, it seems safe to assume that his species and the one described herein are the same. *A. zanguebaricum* is obviously closely related to *A. ophirense,* the type species of the genus *Anthocyrtidium,* and is, therefore, included in that genus.

There is little doubt that *Sethocyrtis oxycephalis* Haeckel is conspecific. Since *S. oxycephalis* is the type species of its genus, and is now regarded as cogeneric with the type species of *Anthocyrtidium,* the two genera become subjective synonyms. However, there are other species which Haeckel placed in the genus *Sethocyrtis,* for example, *S. subacuta* (Ehrenberg) and *S. agamemnonis* Haeckel, which should probably remain generically separated. A new generic name is, therefore, necessary to include those remaining species which conform to the definition of *Sethocyrtis.*

Possibly, the form described by Ehrenberg as *Eucyrtidium pleuracanthus* should be grouped with this species as was suggested by Popofsky (1917). However, since it may have been described from a single specimen (Ehrenberg, 1861*a*, p. 768), and since it was poorly figured (Ehrenberg 1872*b*, pl. vii, fig. 21), the true nature of the form is questionable.

The specimens of *S. trochus* (Ehrenberg) figured by Popofsky (1917) appear to be identical with the forms here described as *A. zanguebaricum.* However, the original figure of *S. trochus* (Ehrenberg, 1872*b*, pl. vii, fig. 17) is poor, making positive identification impossible. The affinity of the forms here described, and those of Popofsky (1917), with *A. zanguebarica* Ehrenberg is more apparent.

Genus *Cornutella* Ehrenberg *sens. emend.*

Cornutella Ehrenberg, 1838, p. 128; Haeckel, 1887, p. 1180.
non Cornutellium Haeckel, 1881, p. 430.
Cornutellium (vel *Ceratarachnium*) Haeckel, 1887, p. 1293. Proposed as a subgenus of *Sethoconus* Haeckel, 1887.
Ceratarachnium Haeckel.—Campbell, 1954, p. D128. Proposed as a subgenus of *Conarachnium* Haeckel, 1881 (= *Sethoconus* Haeckel, 1887).

Lophophaenidae with conical shell, gradually dilated to a wide open mouth. Apex armed with a horn. Cephalis very small, rudimentary, hyaline, without distinct collar septum.

Ehrenberg and Haeckel regarded the members of this genus as monocyrtid. The present author is in agreement with Riedel (1958, p. 232) in thinking that they are probably best regarded as dicyrtid, and the generic definition is thus emended herein. Type species: *C. clathrata* Ehrenberg.

Cornutella profunda Ehrenberg

(Pl. 6, figs. 5*a*–5*c*)

1854*b* *Cornutella clathrata ? β profunda* Ehrenberg, Monatsber., for 1854, p. 241.
1854–56 *Cornutella clathrata β profunda* Ehrenberg, Mikrogeologie, pl. xxxv b, fig. 21.
1856 *Cornutella clathrata β profunda* Ehrenberg.—Bailey, Amer. Jour. Sci. Arts, ser. 2, vol. 22, pl. 1, fig. 23.
1858 *Cornutella profunda* Ehrenberg, Monatsber., for 1858, p. 31.
1862 *Cornutella profunda* Ehrenberg.—Haeckel, Monogr. d. Radiol., p. 284.
1872*a* *Cornutella distenta* Ehrenberg, Monatsber., for 1872, p. 304.

1872*a* *Cornutella longiseta* Ehrenberg, *ibid.*, p. 304.
1872*a* *Cornutella stylophaena* Ehrenberg, *ibid.*, p. 305.
1872*a* *Cornutella trochus* Ehrenberg, *ibid.*, p. 305.
1872*a* *Cornutella tumens* Ehrenberg, *ibid.*, p. 305.
1872*a* *Cornutella verrucosa* Ehrenberg, *ibid.*, p. 305.
1872*b* *Cornutella stylophaena* Ehrenberg., Abh., for 1872, p. 287, pl. VI(iii), fig. 1.
1872*b* *Cornutella distenta* Ehrenberg, *ibid.*, p. 287, pl. VI(iii), fig. 3.
1872*b* *Cornutella tumens* Ehrenberg, *ibid.*, p. 289, pl. VI(iii), fig. 4.
1872*b* *Cornutella trochus* Ehrenberg, *ibid.*, p. 287, pl. ix, fig. 14.
1872*b* *Cornutella longiseta* Ehrenberg, *ibid.*, p. 287, pl. ix, fig. 15.
1872*b* *Cornutella verrucosa* Ehrenberg, *ibid.*, p. 289, pl. ix, fig. 16.
1879 *Cornutella orthoceras* Haeckel, "Atlas, *loc. cit.*" (reference unknown).
1879 *Cornutella bimarginatus* Haeckel, *ibid.*
1887 *Cornutella hexagona* Haeckel, "Chall." Rept., p. 1180, pl. 54, fig. 9.
1887 *Cornutella sethoconus* Haeckel, *ibid.*, p. 1180, pl. 54, fig. 10.
1887 *Cornutella distenta* Ehrenberg.—Haeckel, *ibid.*, p. 1181.
1887 *Cornutella stylophaena* Ehrenberg.—Haeckel, *ibid.*, p. 1182.
1887 *Sethoconus hexagonalis* Haeckel, *ibid.*, p. 1293.
1887 *Sethoconus verrucosus* (Ehrenberg).—Haeckel, *ibid.*, p. 1293.
1887 *Sethoconus orthoceras* (Haeckel), *ibid.*, p. 1294, pl. 54, fig. 11.
1887 *Sethoconus profundus* (Ehrenberg).—Haeckel, *ibid.*, p. 1294.
1887 *Sethoconus longisetus* (Ehrenberg).—Haeckel, *ibid.*, p. 1294.
1887 *Sethoconus bimarginatus* (Haeckel), *ibid.*, p. 1295, pl. 54, fig. 12.
1913 *Cornutella sethoconus* Haeckel.—Popofsky, Deutsche Südpolar-Exped., vol. 14 (Zool. vol. 6), p. 332, text fig. 41.
1958 *Cornutella profunda* Ehrenberg.—Riedel, B.A.N.Z. Antarctic Res. Exped., Repts., ser. B, vol. 6, pt. 10, p. 232, pl. 3, figs. 1, 2.
1963 *Cornutella profunda* Ehrenberg.—Bachmann *et al.*, Mitt. geol. Ges. Wien, vol. 56, pt. 1, p. 134, pl. 8, fig. 43.

Description.—This species was well described by Riedel (1958) in the B.A.N.Z.A.R.E. Reports. Subsequent investigation has substantiated his view that there is only 1 common, widespread species of this general form. Bütschli (1879, p. 1986) believed these forms were derived from Dicyrtida. Although collar pores cannot be seen, it is thought by the present author (in agreement with Riedel, 1958) that the shell should be regarded as dicyrtid.

A sufficient number of specimens, transitional between thin- and thick-walled forms, have been observed to justify regarding all these forms as conspecific. A few specimens, having a particularly large cephalis, have been found. These may constitute a separate species, but too few have been seen to warrant any definite conclusions. These have not been included in the counts for *C. profunda,* nor have rarely occurring curved specimens.

Dimensions.—Length of apical horn up to 72μ (usually up to 27μ); of cephalis 5–9μ; of thorax 105–191μ. Maximum breadth 36–63μ.

These dimensions are in general agreement with those given by Riedel (1958), although the cephalis here is usually smaller, and rarely, the apical horn is much longer.

Occurrences previously recorded.—Ehrenberg 1854*a*, 1854–1856)—*C. clathrata β profunda,* North Atlantic (54°17′ N., 22°33′ W., 3,658 m).

Ehrenberg (1855)—*C. clathrata β profunda,* Coral Sea, 3,933 m.

Bailey (1856)—Sea of Kamchatka.

Ehrenberg (1858)—Mediterranean and Aegean Seas, at depths of 2,012 m, 2,103 m, and 2,963 m.

Ehrenberg (1860*a*)—*C. profunda,* western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Ehrenberg (1860*b*)—*C. profunda,* North Pacific (California Sea: 21° N., 144°25′ W., 4,572 m and 20°52′ N., 151°50′ W., 4,755 m); *C. distenta, C. stylophaena, C. tumens,* North Pacific (California Sea: 20°52′ N., 151°50′ W., 4,755 m).

Ehrenberg (1861*a*)—*C. profunda,* Atlantic Ocean (27°54′ N., 86°15′ W., 2,763 m).

Ehrenberg (1872*a, b*)—*C. longiseta, C. trochus, C. verrucosa,* Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Haeckel (1887)—*C. hexagona,* Central Pacific, "Challenger" Stations 265 (12°42′ N., 152°01′ W.) to 274 (7°25′ S., 152°15′ W.), surface and at different depths; *C. sethoconus,* South Atlantic, "Challenger" Station 332 (37°29′ S., 27°31′ W., 4,023 m; *S. orthoceras,* South Atlantic, "Challenger" Station 325 (36°44′ S., 46°16′ W., surface); *S. profundus,* Cosmopolitan: Mediterranean, Atlantic, Indian, Pacific, at various depths; *S. bimarginatus,* South Pacific, "Challenger" Station 300 (33°42′ S., 78°18′ W., 2,515 m).

Popofsky (1913)—Deutsche Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E., 400 m).

Riedel (1958)—B.A.N.Z.A.R.E Station 94 (64°28′ S., 114°59′ E., 1,718 m).

Bachmann *et al.* (1963)—Miocene ("Badener-Tegel") from Frättingsdorf, North Austria.

Indian Ocean occurrences (fig. 32).—*C. profunda* is rather sparsely distributed (up to 5% of the described population) in low latitudes. In middle latitudes the species is somewhat more abundant, forming up to 9 percent of the described population.

Discussion.—Riedel (1958) tentatively suggested the inclusion of a number of species in the synonymy of *C. profunda.* Since then, additional topotypic material has become available, and inclusion of most of the species he suggested can now be justified.

In two cases original "Challenger" material was examined, namely, "Challenger" 300 (*S. bimarginatus*) and "Challenger" 332 (*C. sethoconus*). *S. orthoceras* was described by Haeckel from "Challenger" 325 (36°44′ S., 46°16′ W.). Material from this station is unavailable, but material from "Vema" 12–52 (39°36′ S., 32°52.5′ W.) was found to contain *C. profunda,* but no other closely related forms.

Ehrenberg described *C. verrucosa, C. longiseta,* and *C. trochus* from the Indian Ocean. The extensive observation of Recent Indian Ocean material during the present study has revealed only one species, namely, *C. profunda.*

Ehrenberg's original material from the North Pacific (20°52′ N., 151°50′ W.) is not available, but examination of sediments from the top of the Scripps Institution of Oceanography core LSDH 98G (19°58′ N., 151°06′ W.) has shown that *C. distenta, C. stylophaena,* and *C. tumens* are conspecific with *C. profunda.*

The only species suggested by Riedel (1958) that has not been included in the present synonymy is *C. trichostyla* Ehrenberg, 1872. This species was figured with

a twisted horn. Since no such form has been seen by the author, its taxonomic position cannot be ascertained.

Possibly *C. clathrata* Ehrenberg (1847 and 1875) should also be synonymized with *C. profunda*. However, it was described from Eocene sediments, and until a

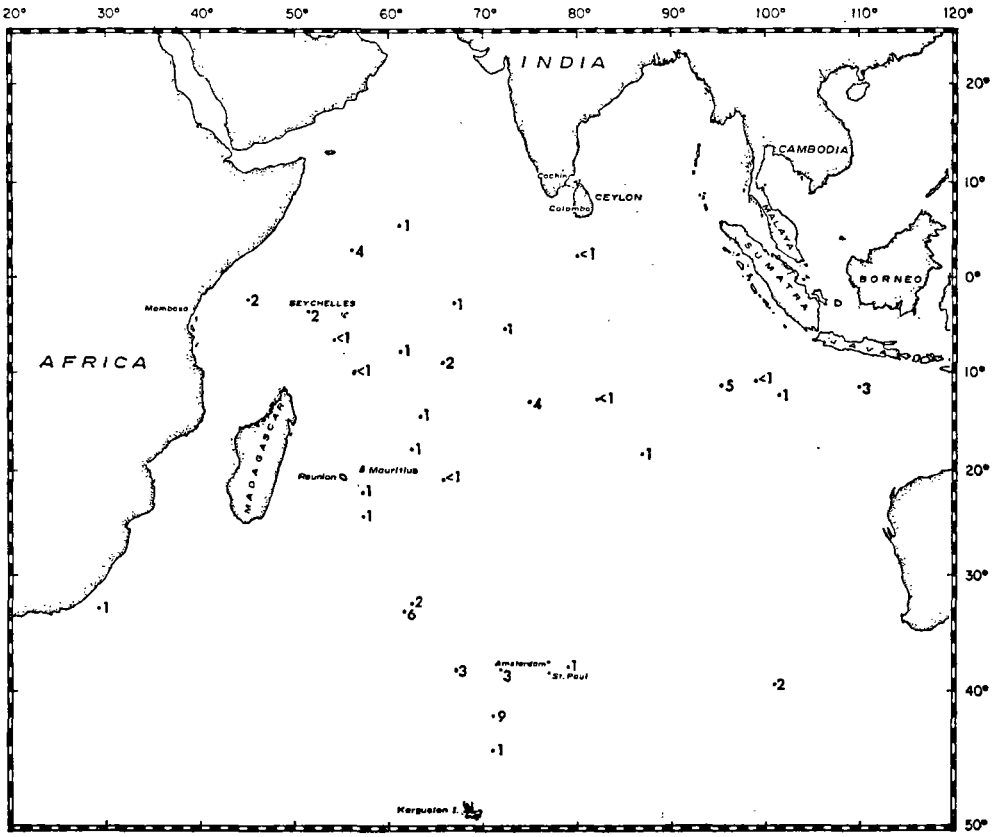

Fig. 32. Distribution of *Cornutella profunda*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

more extensive study of Eocene species can be made, their relationship with Recent forms is uncertain.

Genus *Dictyocryphalus* Haeckel

Dictyocryphalus Haeckel, 1887, p. 1308. Proposed as a subgenus of *Dictyocephalus* Ehrenberg, 1861.

Dictyocephalus Haeckel.—Campbell, 1954, p. D128.

The generic name *Dictyocephalus* Ehrenberg, 1861 was found by Loeblich and Tappan (1961, p. 229) to be a homonym of *Dictyocephalus* Leidy, 1859. The next available valid name is *Dictyocryphalus* Haeckel, 1887.

Dictyocryphalus papillosus (Ehrenberg)

(Pl. 6, fig. 6)

1872*a* *Eucyrtidium papillosum* Ehrenberg, Monatsber., for 1872, p. 310.

1872*b* *Eucyrtidium papillosum* Ehrenberg, Abh., for 1872, p. 293, pl vii, fig. 10.

1880 *Lophophaena amphora* Stöhr, Palaeontographica, vol. 26 (ser. 3, vol. 2), p. 99, pl. iii (19), fig. 18.[1]

1887 *Dictyocephalus australis* Haeckel, "Chall." Rept., p. 1306, pl. 62, fig. 1.

1887 *Dictyocephalus papillosus* (Ehrenberg).—Haeckel, *ibid.*, p. 1307.

1887 *Dictyocephalus tabulatus* Haeckel, *ibid.*, p. 1307.

1958 *Dictyocephalus papillosus* (Ehrenberg).—Riedel, B.A.N.Z. Antarctic Res. Exped., Repts., ser. B, vol. 6, pt. 10, p. 236, pl. 3, fig. 10, text fig. 8.

1963 *non Lophophaena amphora* Stöhr.—Bachmann *et al.*, Mitt. Geol. Ges. Wien, vol. 56, pt. 1, p. 133, pl. 8, fig. 38.

Description.—This species was well described by Riedel (1958). Specimens found in the Indian Ocean are in good agreement with his description and figures, except that the thoracic pores tend to be more regularly arranged than he indicated, and may even form longitudinal rows. However, Riedel was working with very cold water forms, and this probably accounts for their irregularity.

Dimensions.—Length of cephalis 13–18μ; of thorax (including peristome) 63–100μ. Maximum breadth of thorax 45–63μ.

These dimensions are in good agreement with those given by Riedel.

Occurrences previously recorded.—Ehrenberg (1872*a*, *b*)—Western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Stöhr (1880)—Upper Miocene from Grotte, Sicily.

Haeckel (1887)—*D. australis*, east coast of Australia, "Challenger" Station 164 (34°09′ S., 151°55′ E., surface.; *D. tabulatus*, Central Pacific, "Challenger" Station 271 (0°33′ S., 151°34′ E., 4,435 m).

Riedel (1958)—B.A.N.Z.A.R.E. Stations 30 (66°48′ S., 71°24′ E., 540 m), 94 (64°28′ S., 114°59′ E., 1,718 m), 97 (65°10′ S., 108°12′ E., 474 m).

Indian Ocean occurrences (fig. 33).—*D. papillosus* is very sparsely distributed in both low and middle latitudes, never forming more than 1 percent of the described population.

Discussion.—This species has been placed in the genus *Dictyocryphalus* as a matter of convenience. It does not appear to be closely related to the type species [*Cornutella obtusa* Ehrenberg, 1844] of *Dictyocryphalus*, nor has it any readily recognizable relationship to other type species.

Riedel (1958) placed *D. tabulatus* in synonymy with *D. papillosus*, although he was unable to examine material from the type locality ("Challenger" Station 271) of *D. tabulatus*. This material was made available to the author through the kindness of Dr. J. D. H. Wiseman of the British Museum (Natural History), and examination of it has substantiated Riedel's decision. The type locality of *D. australis* is "Challenger" 164. Material from this station has been examined and it now seems reasonable to include *D. australis* in the synonymy. Possibly *D. mediterraneus* should also be placed in synonymy with *D. papillosus*, but samples from its type locality are not presently available for comparison.

Upper Miocene sediments from Sicily have been examined and were found to contain specimens of Stöhr's *Lophophaena amphora*. These are thought to belong to the same species as Recent forms.

[1] Cf. *errata* for this volume; figs. 2 and 3 have been transposed, as have figs. 11 and 18; 18 is the correct figure number for this species.

Superfamily TRICYRTIDA Haeckel

Tricyrtida Haeckel, 1881, p. 426; 1887, p. 1313.
Theopiliilae Haeckel, 1881.—Campbell, 1954, p. D129.

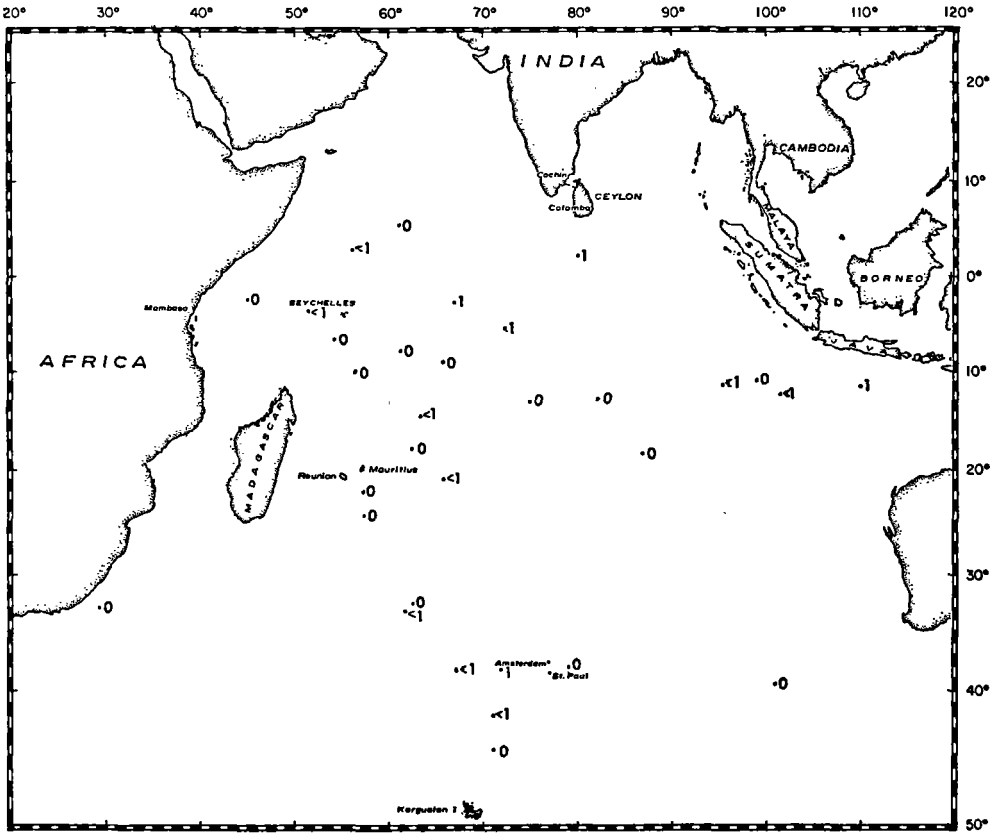

Fig. 33. Distribution of *Dictyocryphalus papillosus*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

In the formal definitions of the families of the Tricyrtida, Haeckel (1887) did not explain clearly his use of the term "radial apophysis," although he did expand his meaning somewhat in notes appended to the definitions. It is proposed herein that the following emendations be made:

Family PODOCYRTIDA Haeckel—Synonymy: Theopilida Haeckel, 1881, p. 435; Theoperida Haeckel, 1881, p. 436; Podocyrtida Haeckel, 1887, p. 1314; Theopiliidae Haeckel, 1881, in Campbell, 1954, p. D130.

Cyrtoidea with a 3-jointed shell, divided by 2 transverse constrictions into cephalis, thorax, and abdomen, and bearing 3 external radial apophyses (either lateral wings or terminal feet). This definition is emended to specify that the radial apophyses be external, in the form of lateral wings or terminal feet.

The family includes the genera *Dictyophimus* (p. 66), formerly regarded as a dicyrtid, and *Pterocanium* (p. 68).

Family PHORMOCYRTIDA Haeckel—Synonymy: Theophormida Haeckel, 1881, p. 436;

Theophaenida Haeckel, 1881, p. 437; Phormocyrtida Haeckel, 1881, p. 1365; Theophormididae Haeckel, 1881, in Campbell, 1954, p. D132.

Cyrtoidea with a 3-jointed shell, divided by 2 transverse constrictions into cephalis, thorax, and abdomen, with numerous, 4–9, radial ribs or external apophyses obviously aligned with extant or former ribs. This definition is emended to specify that the numerous apophyses be either radial ribs, or external projections of extant or former ribs.

Family THEOCYRTIDA Haeckel—Synonymy: Theocorida Haeckel, 1881, p. 434; Theocapsida Haeckel, 1881, p. 436; Theocyrtida Haeckel, 1887, p. 1395; Theocorythidae Haeckel, 1881, in Campbell, 1954, p. D134.

Cyrtoidea with a 3-jointed shell, divided by 2 transverse constrictions into cephalis, thorax, and abdomen, without external radial apophyses, but often (at least) having ribs incorporated in the thoracic wall. This definition is emended to specify that, although external radial apophyses are absent, radial ribs may be incorporated in the thoracic wall.

The family includes the genera *Theoconus* (p. 73), *Lamprocyclas* (p. 74), formerly in the family Phormocyrtida, and *Theocorythium* (p. 77).

Genus *Dictyophimus* Ehrenberg *sens. emend.*

Dictyophimus Ehrenberg, 1847, p. 54, Haeckel, 1887, p. 1195.

Theopiliidae with 3 complete thoracic ribs, prolonged into 3 solid divergent wings. Cephalis with an apical horn. Members of this genus are regarded herein as tricyrtid. Haeckel and Ehrenberg thought them to be dicyrtid. Type species: *Dictyophimus crisiae* Ehrenberg, 1854.

Dictyophimus crisiae Ehrenberg

(Pl. 6, figs. 7*a*, 7*b*)

1854*b* *Dictyophimus crisiae* Ehrenberg, Monatsber., for 1854, p. 241.
1872*a* *Lychnocanium arabicum* Ehrenberg, Monatsber., for 1872, p. 316.
1872*b* *Lychnocanium arabicum* Ehrenberg, Abh., for 1872, p. 297, pl. x, fig. 3.
1887 *Dictyophimus arabicus* (Ehrenberg).—Haeckel, "Chall." Rept., p. 1198.

Description.—Cephalis hemispherical with small closely spaced pores or pits (probably representing infilled pores). Inside cephalis, both apical and vertical spines are free of the shell wall. Externally, apical spine forms a cylindroconical horn which may be up to 3 times the length of the cephalis; vertical spine forms a short, much more delicate horn. In some specimens the dorsal spine is also external, and usually additional by-spines occur on the cephalis and upper thorax. Collar stricture indistinct.

Thorax conical, rather thick-walled, with large subcircular to subangular pores increasing in size distally; bars relatively narrow. Strong thoracic ribs become external just above the lumbar stricture and are prolonged into 3 solid cylindrical or 3-bladed wings as long to 3 times as long as thorax, tapering to a point distally. Wings diverge freely, forming an extension of the conic line of the thorax.

Abdomen thinner-walled, cylindrical, varying in state of development, and having pores similar to those on thorax. No definite termination.

Dimensions.—Length of apical horn 18–72μ; of cephalis 18–27μ; of thorax 45–63μ; of abdomen up to 81μ. Maximum breadth of cephalis 23–32μ; of thorax 63–100μ.

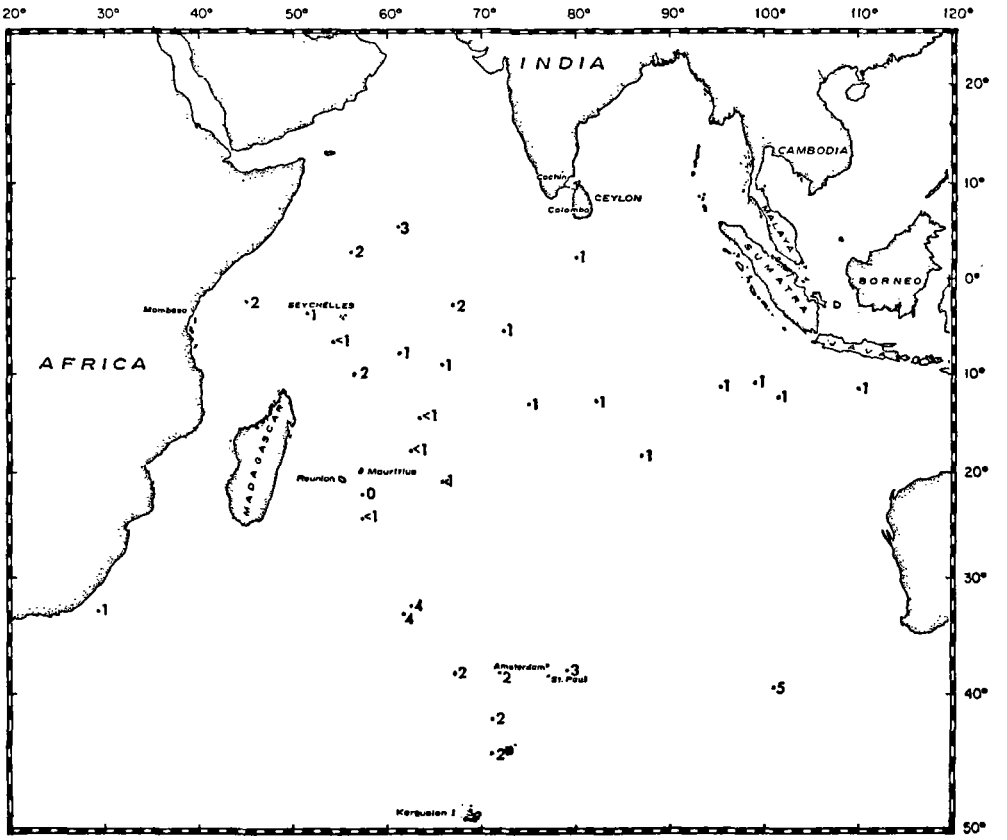

Fig. 34. Distribution of *Dictyophimus crisiae*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Occurrences previously recorded.—Ehrenberg (1854*a*)—Atlantic Ocean, from between 37°05′ N. to 54°17′ N. and 7°08′ W. to 50°05′45″ W., depth from 134 to 3,658 m.

Ehrenberg (1872*a*, *b*)—Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Indian Ocean occurrences (fig. 34).—*D. crisiae* is sparsely distributed in both low and middle latitudes, being slightly more abundant in the latter (up to 5% of the described population).

Discussion.—This species is basically similar to figured species of *Dictyophimus*. According to Campbell's designation (1954), *Lychnocanium lucerna* Ehrenberg, 1847[1] (= *Dictyophimus lucerna*) is the type species of the genus *Dictyophimus*. However, to satisfy Article 69(a) of the International Code of Zoological Nomenclature, the type species of a genus for which no type was originally indicated must be chosen from those species first subsequently referred to the genus. The first such

[1] Campbell has erroneously given the date of this species as 1854. It is, however, figured by Ehrenberg (1847) in a single unnumbered plate.

reference was to *D. ? tethyis* and *D. crisiae* which were described, but not figured, in Ehrenberg (1854*b*). Since *D. ? tethyis* was questioned, *D. crisiae* becomes, by monotypy, the correct type species for the genus *Dictyophimus*. The species was not listed by Haeckel (1887).

Although Ehrenberg did not give the exact location at which he found *D. crisiae*, the paper in which it was described was based on eight samples (listed on p. 60 of the same volume of the Monatsberichte, for 1854) lying between 37°05′ N. and 54°17′ N. and between 7°08′ W. and 50°05′45″ W. Material examined from within this area contains specimens identical to those described herein from the Indian Ocean. Hence, the name *D. crisiae* has been given to the species.

Probably, *D. lucerna* does not belong in the genus *Dictyophimus sens. emend.*, but further work will have to be done to establish its correct taxonomic position.

Possibly, *D. longipipes* Haeckel (1887) and *D. triserratus* Haeckel (1887) should be included in the present synonymy. According to Haeckel, *D. longipipes* is present in "Challenger" 300, but examination of material from this station, which is poor in Radiolaria, failed to reveal any form resembling Haeckel's figure. *D. triserratus* was described from "Challenger" 274 (7°25′ S., 152°15′ W.). Material from this station is unavailable, but a nearby Scripps Institution of Oceanography sample, AMPH 111PG (6°46′ S., 153°49′ W.), was examined and no form quite so thorny as *D. triserratus* could be found, although *D. crisiae* was present.

Lychnocanium arabicum was described by Ehrenberg (1872*a*, *b*) from the Indian Ocean. Since only one species of this general form has been observed in Indian Ocean sediments during this study, it seems reasonable to include *L. arabicum* in the present synonymy.

Genus *Pterocanium* Ehrenberg

Pterocanium Ehrenberg, 1847, p. 54; Haeckel, 1887, p. 1328.

Pterocanium praetextum praetextum (Ehrenberg)

(Pl. 7, fig. 1)

1872*a* *Lychnocanium praetextum* Ehrenberg, Monastber., for 1872, p. 316.
1872*b* *Lychnocanium praetextum* Ehrenberg, Abh., for 1872, p. 297, pl. x, fig. 2.
1887 *Pterocanium virgineum* Haeckel, "Chall." Rept., p. 1330, pl. 73, fig. 6.
1887 *Pterocanium praetextum* (Ehrenberg).—Haeckel, *ibid.*, p. 1330.
1957 *Pterocanium praetextum* (Ehrenberg).—Riedel, Rep. Swedish Deep-Sea Exped., vol. 6, no. 3, p. 86, pl. 3, figs. 1–3.

Description.—Specimens examined by the author are identical with those described by Riedel (1957). A feature not previously described, however, is that inside the cephalis both apical and vertical spines are free of the shell wall. Externally, the apical spine forms a strong cylindroconical horn; the vertical spine, a short, very much more delicate horn. On a few specimens additional by-spines occur on the cephalis and upper thorax.

Dimensions.—Length of apical horn 27–54μ; of cephalis 18μ; of thorax 45–54μ; of abdomen up to 72μ; of feet 72–155μ. Breadth of cephalis 18–27μ; of thorax 63–90μ.

These dimensions are in good agreement with those given by Riedel.

Occurrences previously recorded.—Ehrenberg (1861*a*)—*L. praetextum,* Atlantic Ocean (25°37′40″ N., 80°01′05″E., 353 m).

Ehrenberg (1872*a, b*)—Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Haeckel (1887)—*P. virgineum,* Central Pacific, "Challenger" Station 271 (0°33′ S., 151°34′ W., 4,435 m); *P. praetextum,* Indian Ocean, Ceylon.

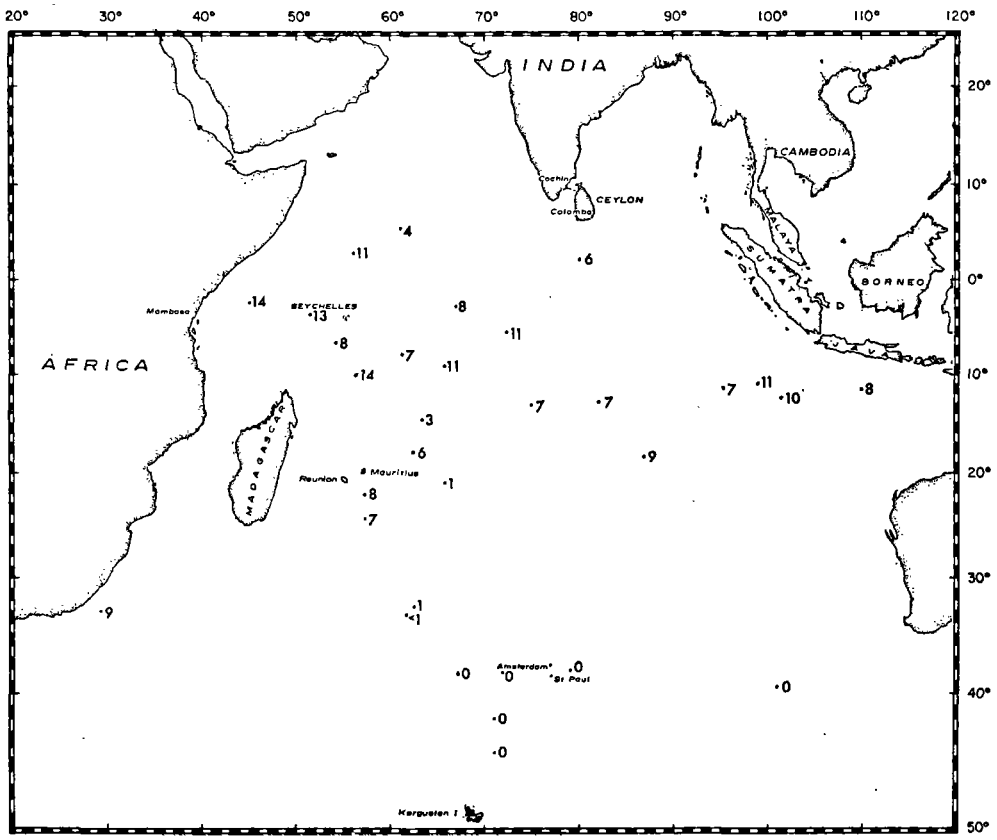

Fig. 35. Distribution of *Pterocanium praetextum praetextum.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Cleve (1902)—*P. praetextum,* Malay Archipelago, Timor; very rare.

Cleve (1904)—*P. praetextum,* Arabian Sea (15° N., 52° E.); 1 specimen.

Riedel (1953)—*P. praetextum,* Series 8, sample no. 178 (First Netherlands Timor Expedition), from near Bebalain, Rotti (late Tertiary, approximately Pliocene).

Riedel (1957)—Swed. D.-S. Exped. Cores 73B (4°04′ S., 152°53′ W., 5,200 m), 10–39 cm, 73 (4°04′ S., 152°53′ W., 5,200 m), 11.5–450 cm (sporadically), 74 (0°29′ S., 151°33′ W., 4,575 m), 1–1,340 cm, 75 (0°20′ N., 150°36′ W., 4,400 m), 9–820 cm, 76B (3°45′ N., 149°44′ W., 5,155 m), 10–20 cm, 76 (3°45′ N., 149°44′ W., 5,155 m), 8 cm, 77B (9°30′ N., 148°40′ W., 5,384 m), 6.5 and 25 cm, 77 (9°30′ N., 148°40′ W., 5,384 m), 10 cm, 83 (8°40′ N., 169°28′ W., 5,456 m), 1 cm, 85B (5°34′ N., 172°12′ W., 5,590 m). 1–9.5, 49, and 79 cm, 87 (2°23′ N., 173°50′ W., 5,560 m), 0–30 cm, 89 (2°48′ S., 178°57′ W., 5,465 m), 0–300 cm, 91 (2°50′ S.,

171°18′ E., 4,096 m), 26–210 cm, 93 (1°20′ S., 167°23′ E., 3,942 m), 0.5–1,509 cm.

Indian Ocean occurrences (fig. 35).—*P. praetextum praetextum* is abundant (3% to 14% of the described population) in low latitudes, but does not occur in samples from south of 35° S. It appears to be a reliable and potentially useful member of the low latitude assemblage.

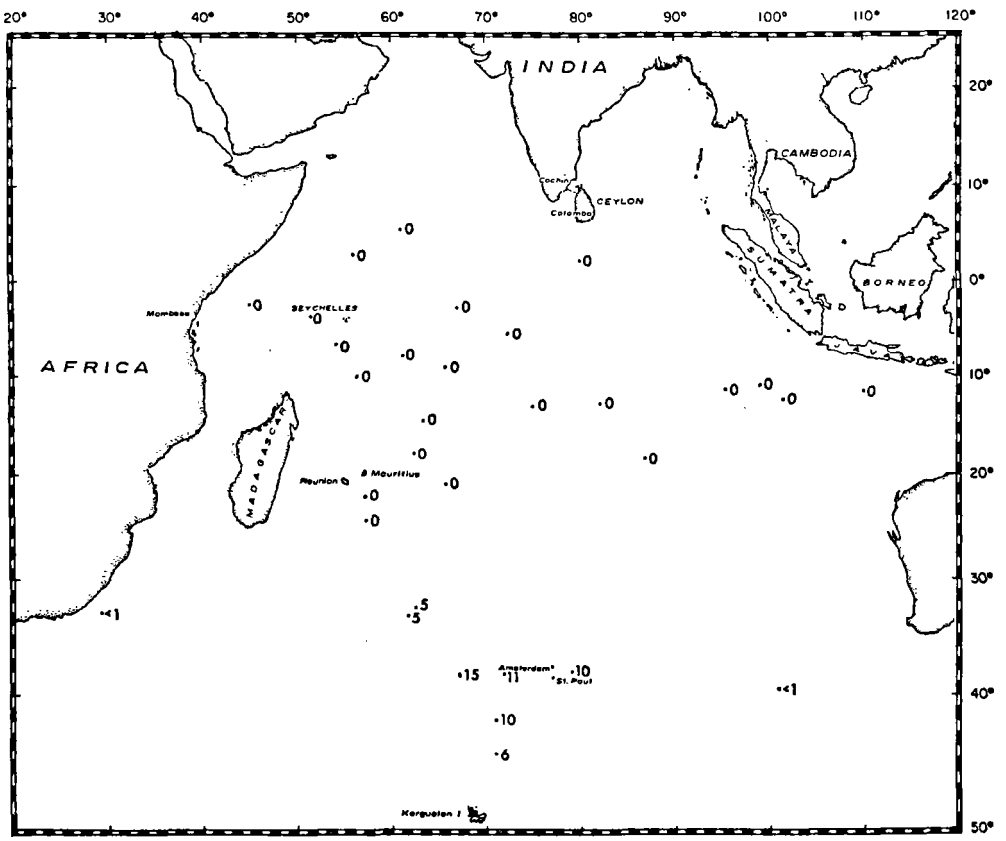

Fig. 36. Distribution of *Pterocanium praetextum eucolpum*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Pterocanium praetextum (Ehrenberg) *eucolpum* Haeckel

(Pl. 7, fig. 2)

1887 *Pterocanium eucolpum* Haeckel, "Chall." Rept., p. 1322, pl. 73, fig. 4.

Description.—Similar to *Pterocanium praetextum praetextum* (p. 68), but differing from it in the following respects: (1) thorax more rounded, less like a biretta; (2) apical horn 3-bladed; (3) abdomen usually less well developed; and (4) shell generally thinner.

P. praetextum eucolpum is found only in middle latitudes (30°–45° S.) and seems to be the cool water form of *P. praetextum praetextum* which is found exclusively in warm water areas.

Dimensions.—Length of apical horn 18–45μ of cephalis 18–27μ; of thorax 36–

63μ; of abdomen up to 54μ; of feet 72–136μ. Breadth of cephalis 18–27μ; of thorax 72–90μ.

Occurrence previously recorded.—Haeckel (1887)—North Pacific, "Challenger" Station 244 (35°22′ N., 169°53′ E., 5,340 m).

Indian Ocean occurrences (fig. 36).—*P. praetextum eucolpum* is abundant (5% to 15% of the described population) south of 35° S., but does not occur in low latitude samples. It appears to be a reliable and potentially useful member of the middle latitude assemblage.

Discussion.—The figure of *Pterocanium eucolpum* in Haeckel (1887) is not exactly like the subspecies here described. However, in material examined by the present author from "Challenger" Station 244, where Haeckel observed *P. eucolpum,* the only closely related form found was this subspecies. It can probably be safely assumed that what Haeckel described and figured is the same as the Indian Ocean middle latitude form. Hence, *eucolpum* is retained as the subspecific name.

Pterocanium trilobum (Haeckel)

(Pl. 7, figs. 3*a*, 3*b*)

1860*b* *Dictyopodium trilobum* Haeckel, Monatsber., for 1860, p. 839.
1862 *Dictyopodium trilobum* Haeckel, Monogr. d. Radiol., p. 340, pl. viii, figs. 6–10.
1887 *Pterocanium trilobum* (Haeckel), "Chall.." Rept., p. 1333.
1913 *Pterocanium trilobum* (Haeckel).—Popofsky, Deutsche Südpolar-Exped., vol. 14 (Zool. vol. 6), p. 390, text figs. 104–109.
1965 *Pterocanium trilobum* (Haeckel).—Hays, Biol. of Antarctic Seas II, Antarctic Res. Series 5, p. 177, pl. iii, fig. 10.

Description.—Cephalis small, spherical with closely spaced pores, or pits (probably representing infilled pores), and bearing a stout conical apical horn approximately twice its length. Apical and vertical spines free within cephalis; both project to form external horns, the vertical horn being shorter and very much more delicate than the apical. Sometimes additional by-spines form on both cephalis and thorax.

Thorax is an inflated tetrahedron with circular to subcircular pores, arranged in longitudinal rows. Thoracic ribs strong, becoming stout 3-bladed feet, latticed proximally and tapering to a point distally. Feet are divergent, convex outwards, as long to half again as long as thorax.

Only traces of an abdomen are preserved. In most specimens a few lattice bars are present, and these seem to form a single row of large pores adjacent to the thorax, and sometimes one large pore bordering on the proximal end of the feet. The rest of the abdomen has smaller pores and apparently hangs free of the feet.

Dimensions.—Length of apical horn 27–54μ; of cephalis 18–27μ; of thorax 63–100μ; of feet 90–173μ. Maximum breadth of cephalis 23–27μ; or thorax 90–136μ.

Occurrences previously recorded.—Haeckel (1887)—Mediterranean, Messina, surface.

Popofsky (1913)—"Challenger" Expedition, cosmopolitan, Pacific and Atlantic Oceans, many stations, surface. (This occurrence is apparently erroneously recorded.) Deutsche Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E., 400 m), 2 June 1903 (33°40′ S., 28°40′ E.), 11 August 1903 (28°46′ S., 10°17′ E.,

200 m), 18 September 1903 (2°32′ S., 16°03′ W., 400 m), 21 September 1903 (0°16′ N., 18°07′ W., 400 m), 13 October 1903 (20°41′ N., 31°53′ W., 200 m).

Hays (1965)—Rarely at the tops of cores just north of the Polar Front; at depth in cores V16–59 (50°03′ S., 35°11′ E., 4,878 m), V16–60 (50°00′ S., 36°46′ E., 4,581 m), V16–131 (59°20′ S., 117°24′ W., 4,033 m), V16–132 (60°45′ S., 107°29′ W., 4,898 m), V16–57 (45°14′ S., 29°29′ E., 5,289 m), V18–69 (56°33′ S., 81°45′ W., 5,000 m), V16–116 (55°06′ S., 147°29′ E., 3,296 m), V17–88 (57°02′ S., 74°29′ W., 4,064 m), V16–66 (42°39′ S., 45°40′ E., 2,996 m).

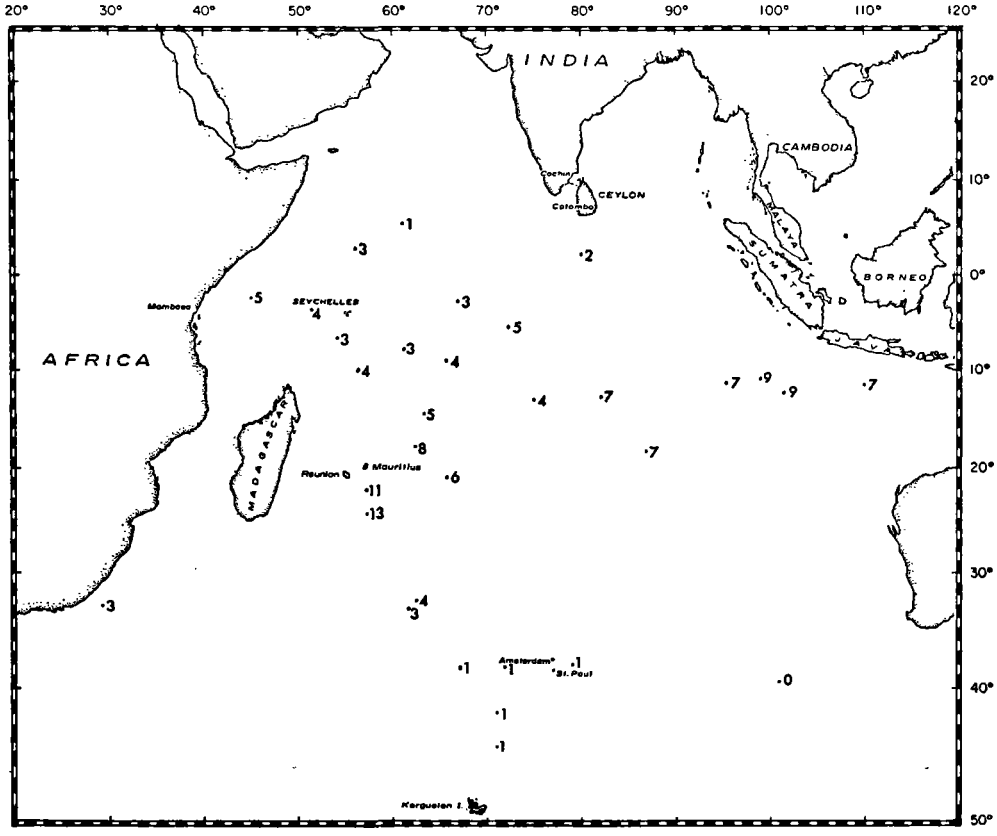

Fig. 37. Distribution of *Pterocanium trilobum*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Indian Ocean occurrences (fig. 37).—*P. trilobum* is fairly abundant (1% to 13% of the described population) in low latitudes, but south of 35° S. it never forms more than 1 percent of the described population. It appears to be a reliable and potentially useful member of the low latitude assemblage.

Discussion.—Possibly *P. tricolpum* Haeckel (1887) should be synonymized with *P. trilobum*. However, neither Haeckel's description nor his figure of the species is sufficiently definitive to warrant formal grouping. The species might equally well be synonymized with *P. praetextum praetextum* (p. 68). It is also probable that *P. polypylum* Popofsky (1913) should be made equivalent to *P. tricolpum*, but conclusive evidence for this is lacking.

Genus *Theoconus* Haeckel

Theoconus Haeckel, 1887, p. 1399.

Theoconus hertwigii (Haeckel)

(Pl. 6, figs. 4*a*, 4*b*)

1887 *Eucyrtidium hertwigii* Haeckel, "Chall." Rept., p. 1491, pl. 80, fig. 12.

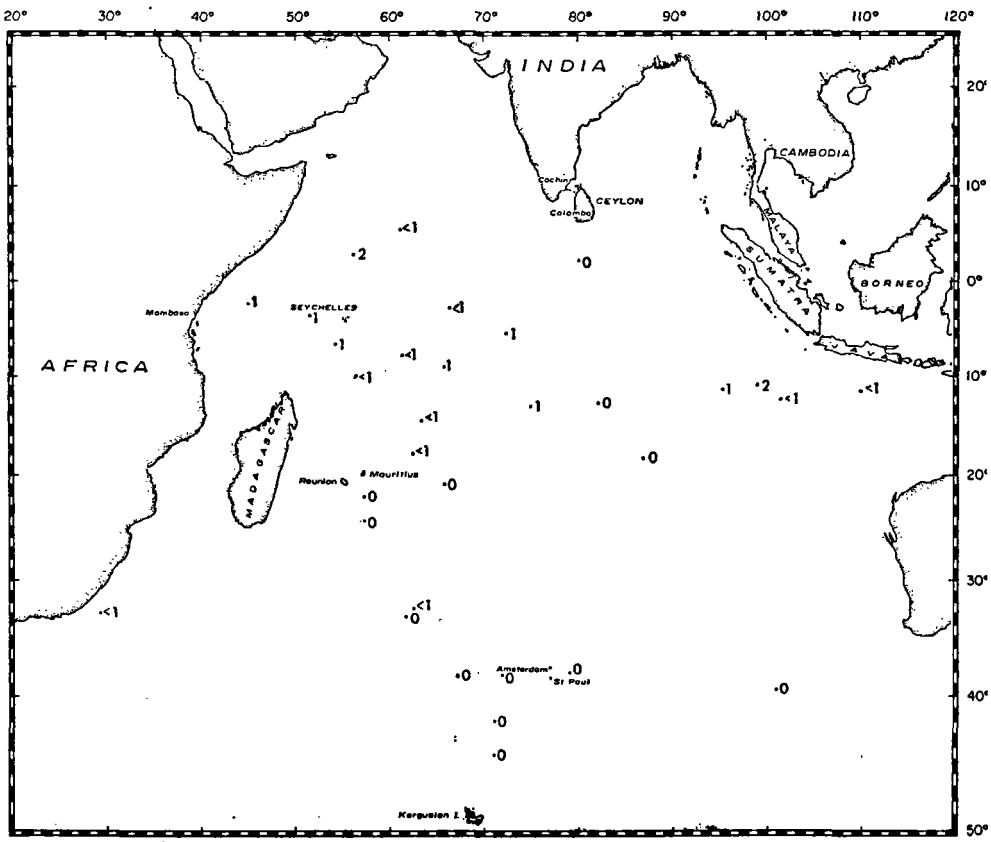

Fig. 38. Distribution of *Theoconus hertwigii*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Description.—Shell conical to ovate, thin-walled, smooth except for longitudinal ridges at irregular intervals. Cephalis trilocular with numerous subcircular pores, heavier than rest of shell. Stout 3-bladed apical horn usually about the same length or a little longer than cephalis. Primary lateral and dorsal spines aligned with three ribs in the thoracic wall.

Thorax campanulate with subcircular to circular pores arranged in longitudinal rows. Lumbar stricture distinct. Abdomen broader than thorax, but with similar pores. In complete specimens abdomen slightly constricted distally with a smooth termination, but most specimens are incomplete.

Both thorax and abdomen ornamented by poreless ridges which run more or less

longitudinally, irregularly spaced and not necessarily continuous for entire shell length. On the thorax some of the ridges frequently bear 1 or 2 small spines.

Dimensions.—Total length (excluding apical horn) 119–191μ. Length of apical horn 9–45μ; of cephalis 23–32μ; of thorax 45–63μ; of abdomen up to 109μ. Maximum breadth of cephalis 27–32μ; of thorax 81–100μ; of abdomen 100–136μ.

Occurrence previously recorded.—Haeckel (1887)—Central Pacific, "Challenger" Station 271 (0°33′ S., 151°34′ W., 4,435 m).

Indian Ocean occurrences (fig. 38)—*T. hertwigii* is very sparsely distributed in low latitudes, and does not occur in samples from south of 35° S.

Discussion.—Haeckel (1887) described this form as four-segmented. From examination of topotypic ("Challenger" 271) and Indian Ocean material, it appears that the species here described is the only ridged form of this type and is always three-segmented. It has, therefore, been transferred to the Tricyrtida, and appears to be most closely related to members of the genus *Theoconus*.

Genus *Lamprocyclas* Haeckel *sens. emend.*

Lamprocyclas Haeckel, 1881, p. 434; 1887, p. 1390.

Theocorythidae with double corona of solid terminal teeth around the mouth. Thoracic ribs present. The definition of this genus is emended herein to include forms having thoracic ribs. The distal projections of members of this genus are regarded as teeth rather than radial apophyses. Hence, the genus belongs to the family Theocorythidae, not Theophormidae (cf. pp. 65–66 herein).

Lamprocyclas maritalis maritalis Haeckel

(Pl. 7, fig. 5)

1887 *Lamprocyclas maritalis* Haeckel, "Chall." Rept., p. 1390, pl. 74, figs. 13, 14.
1907 *Lamprocyclas maritalis* Haeckel.—Haecker, Archiv. f. Protist., vol. 10, p. 126, fig. 12.
1908 *Lamprocyclas maritalis* Haeckel.—Haecker, Wiss. Ergebn. Deutschen Tiefsee-Exped., vol. 14, p. 455, pl. lxxxv, fig. 594.
1965 *Lamprocyclas maritalis* Haeckel.—Hays, Biol. of Antarctic Seas II, Antarctic Res. Series 5, p. 180, pl. 3, fig. ii (*partim*).

Description.—Shell campanulate, usually thick-walled, and generally with a rather rough surface. Cephalis elongate, trilocular, the 2 secondary lobes beneath and somewhat lateral to the larger primary lobe (cf. pl. 7, fig. 7). Pores numerous, subcircular; apical horn stout, 3-bladed, 2 or 3 times cephalic length. Primary lateral and dorsal spines continue as ribs in the thoracic wall for about half its length; rarely, these project from the thorax, forming small wings. Collar stricture not pronounced.

Thorax cupola-shaped (conical above, inflated below) with hexagonally framed circular to subcircular pores, arranged in longitudinal rows and increasing slightly in size distally; 9–11 across the widest part of the segment.

Lumbar stricture distinct and marked internally by a septal ring. Abdomen cylindrical, inflated. Pores hexagonally framed, circular to subcircular, arranged in longitudinal rows; larger than thoracic pores, 9–10 on a half-equator, 3–5 in a vertical series.

Peristome well differentiated, poreless, sometimes with up to 12 triangular lamel-

lar teeth arising from its lower edge, but often teeth are rudimentary or absent. Subterminal teeth, on the abdomen just above the peristome, are conical or thorn-like, divergent, and usually better developed than terminal teeth.

Dimensions.—Total length (excluding apical horn) 119–173μ. Length of cephalis 27–36μ; of thorax 45–63μ; of abdomen (excluding peristome) 45–72μ. Maximum breadth of thorax 81–90μ; of abdomen 100–128μ.

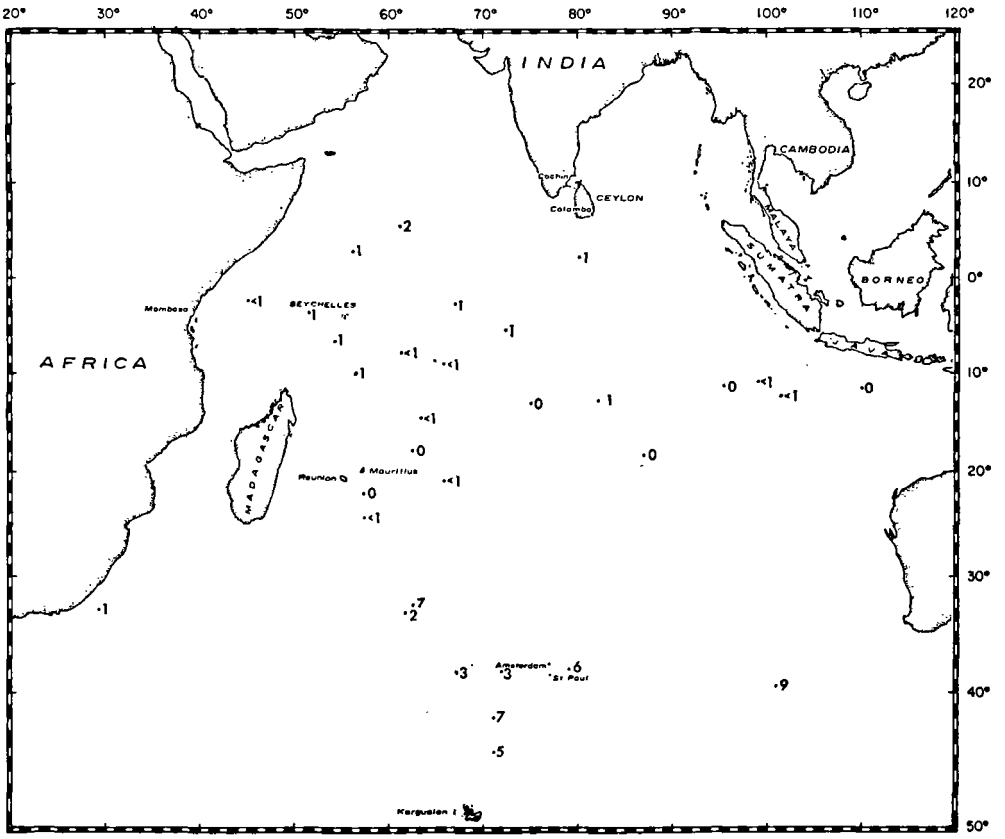

Fig. 39. Distribution of *Lamprocyclas maritalis maritalis*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Occurrences previously recorded.—Haeckel (1887)—Central Pacific, "Challenger" Station 272 (3°48′ S., 152°56′ W., 4,755 m).

Haecker (1907)—Deutsche Tiefsee-Expedition, Stations 227 (2°57′ N., 67°59′ E., 600–400 m), 229 (2°39′ N., 63°38′ E., 1,600–1,400 m), 237 (4°45′ S., 48°59′ E., 4,950–4,600 m).

Haecker (1908)—Deutsche Tiefsee-Expedition Stations 237 (4°45′ S., 48°59′ E., 4,950–4,600 m), 239 (5°39′ S., 43°39′ E., 40–25 m), 268 (9°01′ N. to 12°18′ N., 53°31′ E. to 50°56′ E., 4,800–4,200 m).

Hays (1965, fig. 10)—"Its occurrence seems to be restricted to the cores in the warmest waters" north of the South Polar Front; at depth in cores V16–66 (42°39′ S., 45°40′ E., 2,996 m), V17–88 (57°02′ S., 74°29′ W., 4,064 m).

Indian Ocean occurrences (fig. 39).—*L. maritalis maritalis* is very sparsely dis-

tributed in low latitudes, but is fairly abundant (3% to 9% of the described population) south of 35° S. (cf. *L. maritalis polypora*, discussion, p. 77).

Discussion.—Hays (1965) apparently called all specimens of this general form *L. maritalis*. Two subspecies of this species have been distinguished herein, that is,

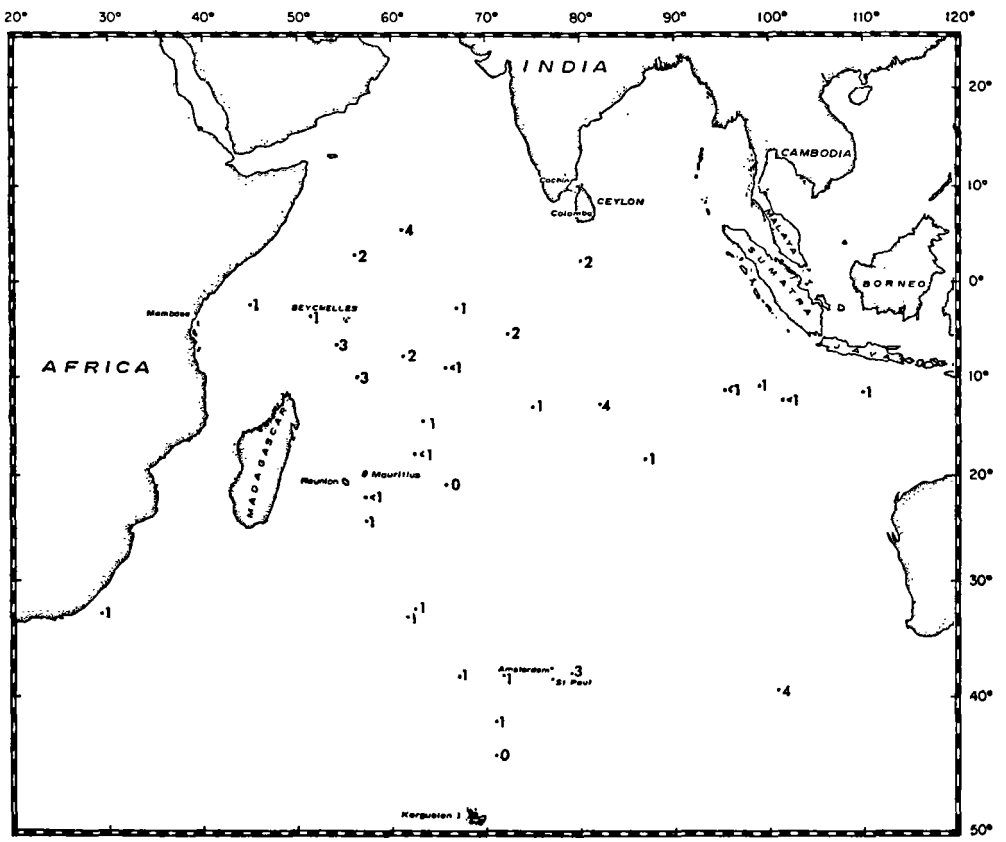

Fig. 40. Distribution of *Lamprocyclas maritalis polypora*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

L. maritalis maritalis and *L. maritalis polypora* (p. 76). Hays' description is probably based on numerous specimens of *L. maritalis maritalis* and rare specimens of *L. maritalis polypora*.

Lamprocyclas maritalis Haeckel *polypora n. subsp.*

(Pl. 7, fig. 6)

Description.—Similar to *Lamprocyclas maritalis maritalis* (p. 74), but with a greater number abdominal pores (11–14 on a half-equator, 4–6 in a vertical series), and shell usually thinner-walled and more delicate. Abdomen tends to expand a little distally, thus becoming truncate conical rather than cylindrical.

Dimensions.—Total length (excluding apical horn) 128–164μ. Length of cephalis 27–36μ; of thorax 45–63μ; of abdomen (excluding peristome) 45–72μ. Maximum breadth of thorax 81–100μ; of abdomen 119–136μ.

Indian Ocean occurrences (fig. 40).—*L. maritalis polypora* is rare in both low

and middle latitudes, occurring in somewhat greater numbers (up to 4% of the described population) in the former (but see discussion below). Holotype: MSN 39G, A-J41/1; Sedgwick Museum No. 846.4.

Discussion.—Distinctions between *L. maritalis maritalis* and *L. maritalis polypora* might seem rather artificial, but they form a useful division insofar as there seems to be a correlation of the two forms with latitude. Both subspecies are found in low and middle latitudes, but in middle latitudes *L. maritalis maritalis* is fairly abundant and *L. maritalis polypora* is rare, and in low latitudes both subspecies are rather rare but *L. maritalis polypora* is relatively more abundant.

Genus *Theocorythium* Haeckel

Theocorythium Haeckel, 1887, p. 1416. Proposed as a subgenus of *Theocorys* Haeckel, 1881.

Theocorythidae with a two-part cephalis: (1) upper sphere; and (2) one or two lobes either directly beneath or slightly lateral to the upper sphere. Single apical horn. Abdomen subcylindrical with numerous terminal teeth and sometimes with subterminal teeth scattered irregularly over the distal half of the abdomen.

The cephalic lobes form a "neck" structure between the upper cephalis and the thorax, which is peculiar to this genus. In addition, the genus differs from *Lamprocyclas* in that the shell is basically cylindrical; rather than conical, and subterminal teeth, when present, never form a regular corona. The collar stricture or "neck" is more pronounced than that of *Theocyrtis*. Type species: *Theocorythium trachelium dianae* (Haeckel).

Theocorythium trachelium (Ehrenberg) *dianae* (Haeckel)

(Pl. 8, figs. 1*a*, 1*b*; pl. 9, figs. 1*a*, 1*b*)

1887 *Theocorys dianae* Haeckel, "Chall." Rept., p. 1416, pl. 69, fig. 11.

1900 *Theocyrtis aculeata* Cleve, K. svenska VetenskAkad., Handl., vol. 34, no. 1, p. 12, pl. iv, fig. 11.

1965 *Calocyclas amicae* Haeckel.—Hays, Biol. of Antarctic Seas II, Antarctic Res. Series 5, p. 178, pl. 3, fig. 9.

Description.—Shell quite smooth and rather thin-walled. Cephalis trilocular, the paired lobes beneath and slightly lateral to the larger unpaired lobe. Apical horn 3-bladed, 1 or 2 times cephalic length. Primary lateral and dorsal spines continue as ribs in the thoracic wall for about half its length, but in none of the specimens examined did these ribs become external. Secondary laterals present.

Thorax inflated conical with circular to subcircular pores, hexagonally framed, arranged in longitudinal rows, 10–13 on a half-equator, 6–9 in a vertical series. Pronounced lumbar stricture.

Abdomen elongated, basically cylindrical, but expanding a little distally; sometimes slightly inflated. Pores similar in size, shape, and arrangement to those of the thorax, 12–15 on a half-equator, 8–17 in a vertical series.

Slight, but sharp, terminal constriction with a poreless peristome and up to 8 triangular terminal teeth. Usually, conical subterminal teeth are present, near the mouth and scattered irregularly over the distal half of the abdomen. Sometimes terminal teeth absent, but a poreless, often poorly developed, peristome is always present.

Dimensions.—Total length (excluding apical horn and terminal teeth) 128–227μ (usually 155–227μ). Length of cephalis 27–36μ; of thorax 45–54μ; of abdomen (excluding terminal teeth) 45–146μ (usually 81–100μ). Maximum breadth of cephalis 18–36μ; of thorax 63–81μ; of abdomen 72–109μ.

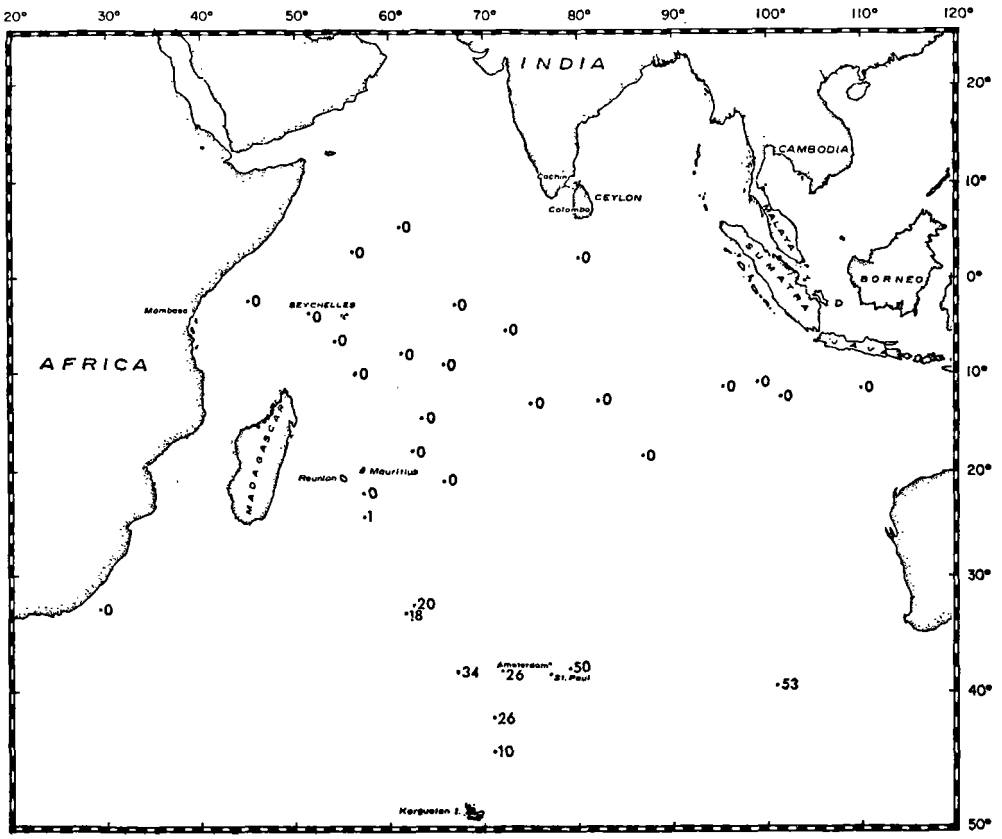

Fig. 41. Distribution of *Theocorythium trachelium dianae*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Occurrences previously recorded.—Haeckel (1887)—North Pacific, "Challenger" Station 253 (38°09′ N., 156°25′ W., surface).

Cleve (1900)—Atlantic Ocean, between 56° N., 17° W., and 48° N., 29° W.

Hays (1965, fig. 11)—An important element in several cores from the Indian Ocean, about 10° north of the Polar Front.

Indian Ocean occurrences (fig. 41).—*T. trachelium dianae* is absent in low latitudes, but south of 30° S. it is abundant in all samples, except one near the African coast (SERPENT [?] 9) which contains a warm water fauna. It appears to be a reliable and potentially useful member of the middle latitude assemblage.

Discussion.—*T. trachelium dianae* differs from *T. trachelium trachelium* (p. 79) in the following respects: (1) cephalis forms a less distinct "neck," thus making the collar stricture less pronounced; (2) thorax is "inflated conical" rather than "cupola-shaped" and is rather smaller; and (3) abdomen expands distally and may be slightly inflated, and is thus broader than the thorax, whereas

in *T. trachelium trachelium* the abdomen is approximately cylindrical and about the same breadth as the thorax.

Theocyrtis aculeata was described by Cleve from the North Atlantic. Material from near the areas of capture reported by Cleve was found to contain specimens identical to *T. trachelium dianae* from the Indian Ocean. *T. aculeata* has, therefore, been placed in synonymy.

Hays (1965) did not distinguish between *Theocorythium trachelium trachelium* (p. 79) and *T. trachelium dianae,* but included both subspecies in his concept of *C. amicae;* nor did he differentiate between *Pterocanium praetextum praetextum* (p. 68) and *P. praetextum eucolpum* (p. 70). The association he observed in Indian Ocean cores just north of the Polar Front was probably that of a middle latitude, not a tropical, assemblage, that is, *T. trachelium dianae, P. praetextum eucolpum* and a few specimens of *A. ophirense.*

Theocorythium trachelium trachelium (Ehrenberg)

(Pl. 8, fig. 2; pl. 9, fig. 2)

1872*a* *Eucyrtidium trachelius* Ehrenberg, Monatsber., for 1872, p. 312.
1872*b* *Eucyrtidium trachelius* Ehrenberg, Abh., for 1872, p. 293, pl. vii, fig. 8.
1887 *Calocyclas amicae* Haeckel, "Chall." Rept., p. 1382, pl. 74, fig. 2.
1887 *Calocyclas vestalis* Haeckel, *ibid.,* p. 1382, pl. 74, fig. 3.
1887 *Theocyrtis trachelius* (Ehrenberg).—Haeckel, *ibid.,* p. 1405.

Description.—Shell rather rough and thick-walled. Cephalis in 2 parts: (1) spherical portion, with circular to subcircular pores, bearing a 3-bladed apical horn, 1 or 2 times its length; and (2) "neck," separated from the first part by an internal ringlike ledge, pores similar but larger and in 2 transverse rows, shell a little heavier. This "neck" is apparently homologous with the paired lobes of a trilocular cephalis in which the lobes are directly beneath the larger unpaired lobe. Collar structure at the base of the "neck." Apical spine incorported in the cephalic wall (both spherical and "neck" parts). A short vertical spine meets the shell wall about midway up the "neck." Primary lateral and dorsal spines continue as ribs in the thoracic wall for about half its length; sometimes these project, or are external, forming small wings.

Thorax large, distinctly cupola-shaped (conical above, expanded below) with hexagonally framed, circular to subcircular pores, closely spaced, quincuncially arranged and aligned longitudinally, 12–15 on a half-equator, 8–10 in a vertical series. Pronounced lumbar stricture.

Abdomen usually elongated, cylindrical or with a slight medial constriction. Pores similar in size, shape, and arrangement to those of the thorax, 12–15 on a half-equator, 8–14 in a vertical series.

Slight terminal constriction usually with 4–6 triangular lamellar teeth. Some specimens have similar subterminal teeth near the mouth or scattered irregularly over the distal half of the abdomen. In most specimens a peristome is either absent or only poorly developed, but a few have a well-differentiated poreless peristome.

Dimensions.—Total length (excluding apical horn and terminal teeth) 146–209μ. Length of cephalis 27–36μ; of thorax 45–72μ; of abdomen (excluding terminal teeth) 54–109μ. Maximum breadth of cephalis 27–36μ; of thorax 81–100μ; of abdomen 72–100μ.

Occurrences previously recorded.—Ehrenberg (1860*a*)—*E. trachelius,* western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Ehrenberg (1860*b*)—*E. trachelius,* North Pacific (California Sea: 20°52′ N., 151°50′ W., 4,755 m).

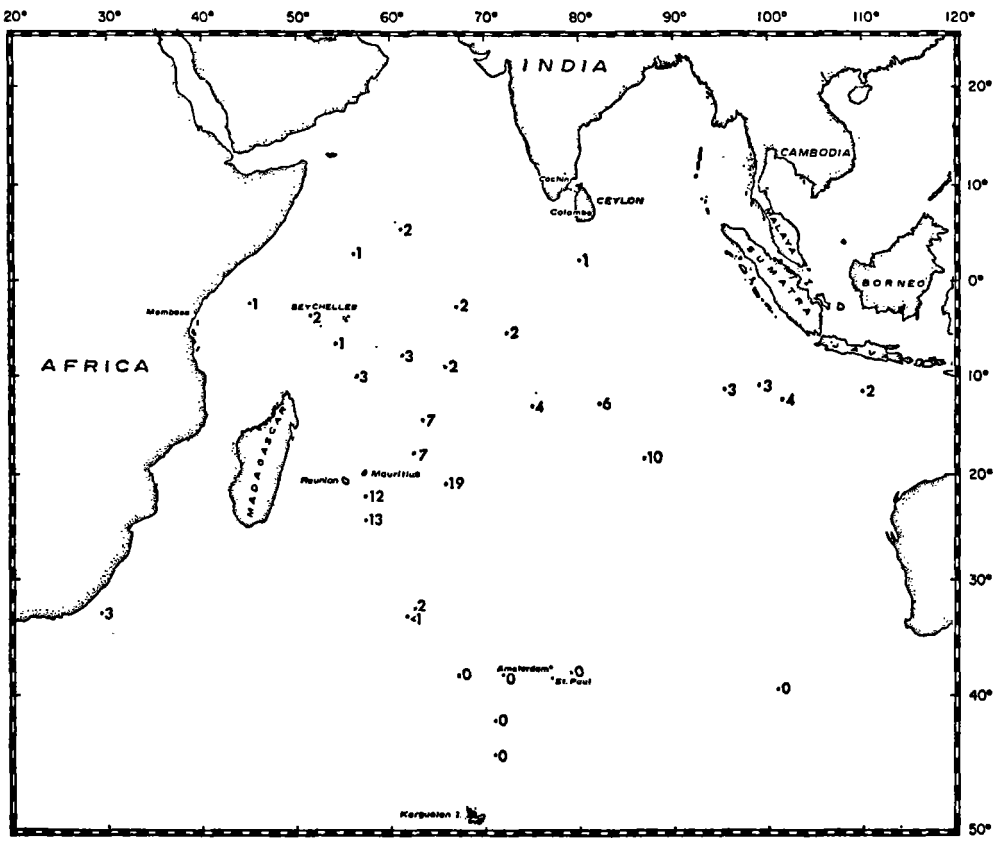

Fig. 42. Distribution of *Theocorythium trachelium trachelium.* Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Haeckel (1887)—*C. amicae,* North Pacific, "Challenger" Station 253 (38°09′ N., 156°25′ W., 5,715 m); *C. vestalis,* Central Pacific, "Challenger" Station 271 (0°33′ S., 151°34′ W., 4,435 m); *T. trachelius,* tropical Pacific, many "Challenger" Stations: 200 (6°47′ N., 122°28′ E.), 224 (7°45′ N., 144°20′ E.), 271 (0°33′ S., 151°34′ W.), etc., surface and in various depths.

Riedel (1951*b*)—*C. amicae,* tropical Indian Ocean, as for *Panartus quadrijugus* (p. 31).

Riedel (1952)—*C. amicae,* tropical parts of the western Pacific and Indian Oceans, as for *Panartus quadrijugus* (p. 31).

Indian Ocean occurrences (fig. 42).—*T. trachelium trachelium* is fairly abundant in low latitudes, but does not occur in samples from south of 35° S. It appears to be a reliable and potentially useful member of the low latitude assemblage.

Discussion.—This form and its close relative, *T. trachelium dianae* (p. 77), belong to the family Theocyrtida because of the presence of three radial apophyses

or ribs either in the thoracic wall, or sometimes projecting slightly from it. True external radial apophyses are absent (cf. p. 66).

The differences noted by Haeckel between *C. amicae* and *C. vestalis* are all relatively minor and within the limits of intraspecific variation; for example, relative segment sizes, length of apical horn, number of teeth, etc. Judging from Haeckel's figures, the species appear to be identical. The type locality of *C. amicae* is "Challenger" 253. Material from this station has been examined and was found to contain *T. trachelium dianae,* and not *T. trachelium trachelium.* However, judging from Haeckel's (1887) description and figure, *C. amicae* seems to be more closely related to *T. trachelium trachelium,* and has therefore been included in the synonymy of this species.

Ehrenberg's original description of *E. trachelius,* based on a single, apparently incomplete, specimen, is inadequate. However, his figure of the species suggests that it should be included in the present synonymy. Haeckel's subsequent amplified description (not figured) seems sufficiently similar to allow for this inclusion, and the specific name *trachelius* is retained.

Superfamily STICHOCYRTIDA Haeckel, 1862

Genus *Eucyrtidium* Ehrenberg *sens. emend.*

Eucyrtidium Ehrenberg, 1847, p. 54; Haeckel, 1887, p. 1487.

Stichocorythidae with ovate or spindle-shaped shell, the mouth of which is constricted and, rarely, may be prolonged into an irregular, short, terminal tube. Tube much less well developed than that of the genus *Eusyringium.* The definition of this genus is emended herein to include forms having a short terminal tube.

Eucyrtidium acuminatum (Ehrenberg)

(Pl. 8, figs. 3*a*, 3*b*)

1844 *Lithocampe acuminata* Ehrenberg, Monatsber., for 1844, p. 84.
1847 *Eucyrtidium acuminatum* (Ehrenberg), Monatsber., for 1848, p. 43.
1854–56 *Eucyrtidium acuminatum* (Ehrenberg), Mikrogeologie, pl. XXII, fig. 27.
1862 *Eucyrtidium acuminatum* (Ehrenberg).—Haeckel, Monogr. d. Radiol., p. 326.
1880 *Eucyrtidium acuminatum* (Ehrenberg).—Stöhr, Palaeontographica, vol. 26, (ser. 3, vol. 2), p. 104, pl. IV, fig. 6.
1887 *Eucyrtidium acuminatum* (Ehrenberg).—Haeckel, "Chall." Rept., p. 1488.
1913 *Eucyrtidium acuminatum* (Ehrenberg).—Popofsky, Deutsche Südpolar-Exped., vol. 14 (Zool. vol. 6), p. 406, text fig. 127.
1965 *Stichopilium annulatum* Popofsky.—Hays, Biol. of Antarctic Seas II, Antarctic Res. Series 5, p. 181, pl. 3, fig. 6.

Description.—Cephalis simple, spherical, with numerous small subcircular pores. Short conical apical horn usually present. Primary lateral and dorsal spines continue as ribs in the thoracic wall for its entire length; rarely, these become external, forming wings. Collar stricture indistinct.

Thorax small, conical, sometimes slightly inflated; thick-walled, with subcircular pores aligned approximately longitudinally. Lumbar stricture not indented externally.

Abdomen and 4–5 post-abdominal segments, thick-walled, of approximately equal length, expanding distally to a maximum breadth at about the third post-

abdominal segment; then, in complete specimens, narrowing to a quite constricted mouth. No peristome or terminal teeth but, rarely, with a short cylindrical terminal tube. Pores small, subcircular, aligned longitudinally, 4–6 per segment in a vertical series. Final segments may become irregular.

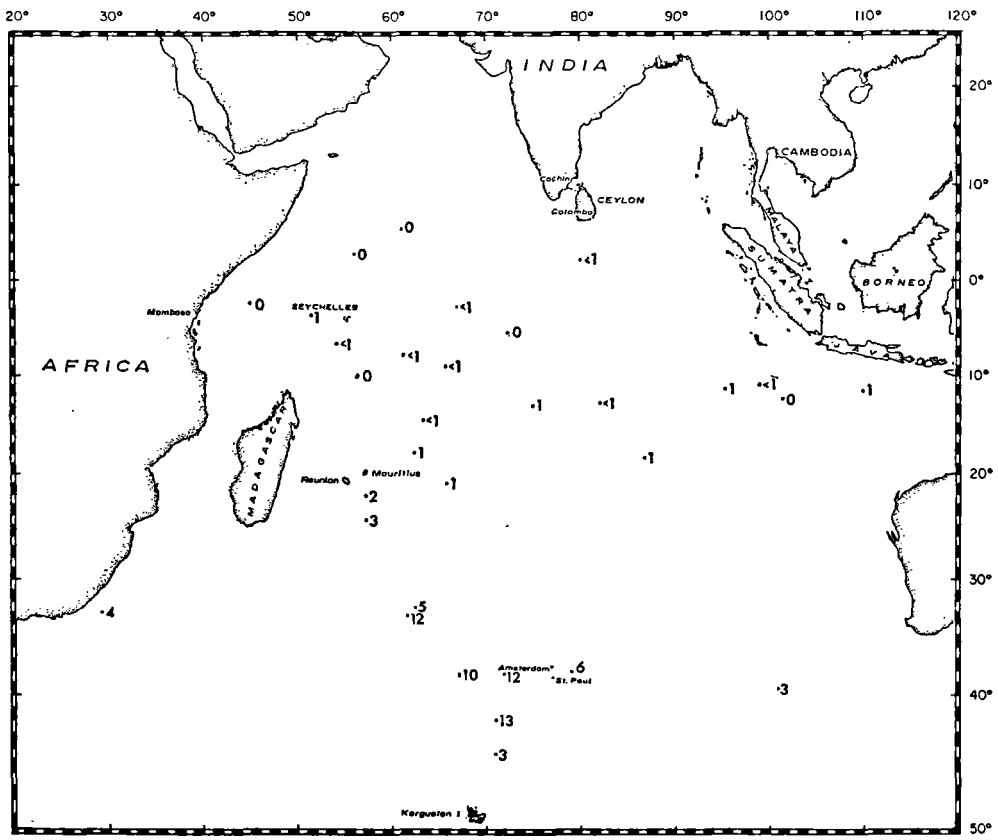

Fig. 43. Distribution of *Eucyrtidium acuminatum*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Dimensions.—Total length 119–182μ. Diameter of cephalis 9–13μ. Length of thorax 9–18μ. Maximum breadth 63–81μ.

Occurrences previously recorded.—Ehrenberg (1844, 1854–1856)—Miocene from Caltanisetta, Sicily.

Ehrenberg (1847)—?Sediments from Barbados.

Ehrenberg (1854*a*)—*E. acuminatum,* North Atlantic (47°38′ N., 7°08′ W., 3,293 m).

Ehrenberg (1860*a*)—*E. acuminatum,* western tropical Pacific (Philippine Sea: 18°03′ N., 129°11′ E., 6,066 m).

Ehrenberg (1872*b*)—*E. acuminatum,* Indian Ocean (5°37′ S., 61°33′ E., 4,023 m).

Stöhr (1880)—Upper Miocene from Grotte, Sicily.

Sequenza (1880)—*E. acuminatum,* Pliocene from the Province of Reggio, Calabria, Italy.

Poposky (1913)—Deutsche Südpolar-Expedition, 26 August 1903 (18°45′ S., 5°07′ W., 200 m), 1 September 1903 (St. Helena), 45 m.

Hays (1965, fig. 12)—"In cores raised from beneath the warmest surface waters" just north of the Polar Front; below 760 cm in core V16–66 (42°39′ S., 45°40′ E., 2,996 m).

Indian Ocean occurrences (fig. 43).—*E. acuminatum* is very sparsely distributed in low latitudes, but is abundant (up to 13% of the described population) in middle latitudes. It appears to be a reliable and potentially useful member of the middle latitude assemblage.

Discussion.—There are forms found in Recent Indian Ocean sediments that are somewhat similar to *E. acuminatum,* but have a larger thorax, and pores in transverse rows. These are considered to be a different species, probably closely related to or the same as *Stichopilium annulatum* Popofsky. Hays' (1965) figured specimen of what he called *S. annulatum* is identical to those forms described herein as *E. acuminatum;* the thorax is small and pores are in longitudinal rows. His description is, therefore, included in the present synonymy.

The shape of some specimens of *E. acuminatum* approaches that of *E. hexagonatum* (p. 83). However, *E. acuminatum* may be distinguished from *E. hexagonatum* by the shape of its thorax and by the smooth contour between thorax and abdomen. The thorax of *E. hexagonatum* is inflated annular, and there is a sharp change in contour at the lumbar stricture. *E. hexagonatum* is limited in distribution to low latitudes, whereas *E. acuminatum* is found mainly in middle latitudes and only rarely in the tropics.

Specimens seen by the author in Miocene samples from Sicily appear to be conspecific with Recent forms.

Müller (1858) described a form which he called *Lithocampe tropeziana* [= *Eucyrtidium tropezianum* (Müller) in Haeckel, 1887] from the Mediterranean. It appears from Müller's figure that he did not see the cephalic structure clearly. The general shape of the figured specimen is, however, similar to that of *E. acuminatum.* Possibly *E. tropezianum* should be included in the present synonymy, but since no topotypic material is available, the question is left in abeyance.

Eucyrtidium hexagonatum Haeckel

(Pl. 8, figs. 4*a*, 4*b*)

1887 *Eucyrtidium hexagonatum* Haeckel, "Chall." Rept., p. 1489, pl. 80, fig. 11.

Description.—Cephalis simple, spherical, with numerous subcircular pores and an erect, or sometimes oblique, needle-like apical horn supported by 3 membranous buttresses; length of horn 1 or 2 times diameter of cephalis. Apical spine free. Cephalis usually depressed into thorax; median bar and vertical spine form a V. Primary lateral and dorsal spines continue as ribs in the thoracic wall, giving the segment a 3-lobed appearance from some angles, and then continue on in the abdominal wall for almost its entire length. Rarely, 1 or more of these ribs becomes external, forming small latticed wings.

Thorax small, inflated annular with rough surface and rather thick wall. Thoracic pores subcircular, usually irregularly arranged, but sometimes in longitudinal rows. Lumbar stricture distinct.

Abdomen and up to 5 post-abdominal segments, thin-walled, smooth; they expand distally, reaching a maximum breadth at about the second or third post-abdominal segment, and then constrict slightly. Most specimens are broken off at this point, and thus appear to have a wide mouth, very slightly constricted; however, in relatively rare complete specimens, narrowing continues and a short cylindrical pored terminal tube is formed. Pores circular to subcircular, arranged in longitudinal rows, but may be irregular in the final 2 or 3 segments.

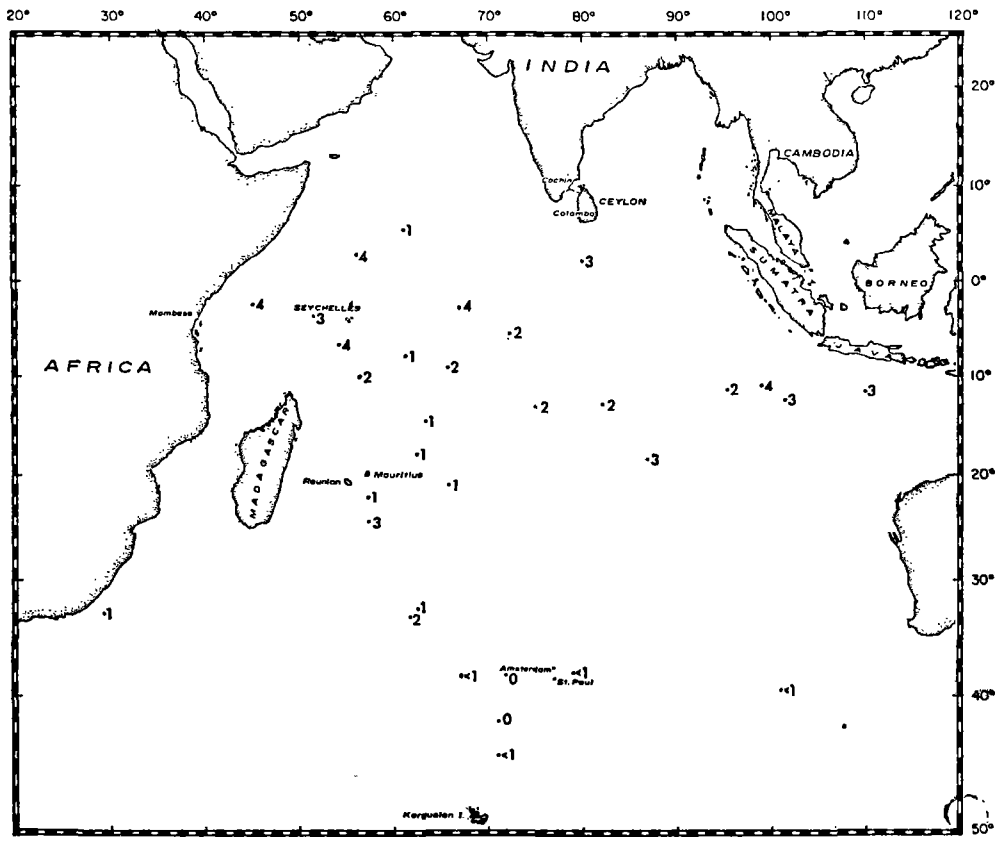

Fig. 44. Distribution of *Eucyrtidium hexagonatum*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

Dimensions.—Total length (excluding apical horn) 146–209μ. Diameter of cephalis 9–18μ. Length of thorax 9–18μ. Breadth of thorax 27–36μ; maximum breadth 72–128μ.

Occurrences previously recorded.—Haeckel (1887)—Central Pacific, Challenger Stations 266 (11°07′ N., 152°03′ W.) to 272 (3°48′ S., 152°56′ W.), depths 4,435 m to 5,349 m.

Indian Ocean occurrences (fig. 44)—*E. hexagonatum* is rather sparsely distributed in low latitudes (1% to 4% of the described population), and is practically absent in middle latitudes. Though rather rare in Recent sediments, it appears to be a useful member of the low latitude assemblage.

Discussion.—*E. hexagonatum* may be distinguished from *E. cienkowskii* Haeckel

by its smaller thorax. *E. cienkowskii* is found in Miocene sediments and, rarely, has been observed in Recent middle latitude sediments from the Indian Ocean.

Genus *Siphocampe* Haeckel

Siphocampe, Haeckel, 1881, p. 438; 1887, p. 1499.
Siphocampium Haeckel.—Campbell, 1954, p. D141.

Although Campbell (1954, p. D141) changed the name of this genus to *Siphocampium*, apparently because of page precedence in Haeckel (1881), the name *Siphocampe* is here retained because of the preference shown it by Haeckel (1887) acting as first reviser.

Siphocampe corbula (Harting)

(Pl. 8, fig. 5; pl. 9, fig. 3)

1863 *Lithocampe corbula* Harting, K. Akad. v. Wetensch., Amsterdam, Verhand., vol. 10, p. 12, pl. 1, fig. 21.
1887 *Tricolocampe polyzona* Haeckel, "Chall." Rept., p. 1412, pl. 66, fig. 19.
1887 *Tricolocampe stenozona* Haeckel, *ibid.*, p. 1413, pl. 66, fig. 20.
1953 *Tricolocampe ? polyzona* Haeckel.—Riedel, Jour. Paleont., vol. 27, no. 6, p. 812, pl. 85, fig. 1.

Description.—Shell thin-walled, smooth, subcylindrical, consisting of 4 segments of which the fourth is the broadest. Cephalis approximately spherical with a well-developed, poreless, lateral tubule which curves downwards so as to lie close to the thorax (cf. pl. 9, fig. 3); numerous subcircular pores; no apical horn. Collar stricture indistinct.

Thorax short, truncate conical, with circular to subcircular pores arranged approximately in transverse rows. Lumbar and post-lumbar strictures distinct.

Abdomen annular, somewhat longer than thorax. Pores small, subcircular to squarish, arranged in 5–8 regular closely spaced transverse rows.

Fourth segment 2–4 times as long as abdomen; pores similar in size and shape to those on abdomen, in 9–17 transverse rows. Segment tapers slightly distally and ends in a generally poreless peristome. Termination smooth.

Dimensions.—Total length 119–173μ. Length of cephalis 9–18μ; of thorax 9–23μ; of abdomen 18–27μ; of fourth segment 54–109μ. Maximum breadth 54–81μ.

Occurrences previously recorded.—Harting (1863)—Banda Sea (4°12′ S., 129°05′ E., 2,195 m).

Haeckel (1887)—*T. polyzona*, Central Pacific, "Challenger" Stations 266 (11°07′ N., 152°03′ W.) to 272 (3°48′ S., 152°56′ W.), depths 4,435 m to 5,349 m, also fossil in the Nicobars and in Barbados; *T. stenozona*, North Pacific, "Challenger" Station 256 (30°22′ N., 154°56′ W., 5,395 m).

Riedel (1951*b*)—*T. polyzona*, tropical Indian Ocean, as for *Panartus quadrijugus* (p. 31).

Riedel (1952)—*T. polyzona*, tropical parts of the western Pacific and Indian Oceans, as for *Panartus quadrijugus* (p. 31).

Riedel (1953)—Series 8, sample no. 178 (First Netherlands Timor Expedition), from near Bebalain, Rotti (late Tertiary, approximately Pliocene).

Indian Ocean occurrences (fig. 45).—*S. corbula* is sparsely distributed in both low and middle latitudes, occurring in somewhat greater numbers (up to 3% of the described population) in the former.

Discussion.—The form described and figured by Harting (1863) as *Lithocampe corbula* appears to be identical with the one described herein from the Indian Ocean, although he did not observe the lateral cephalic tube.

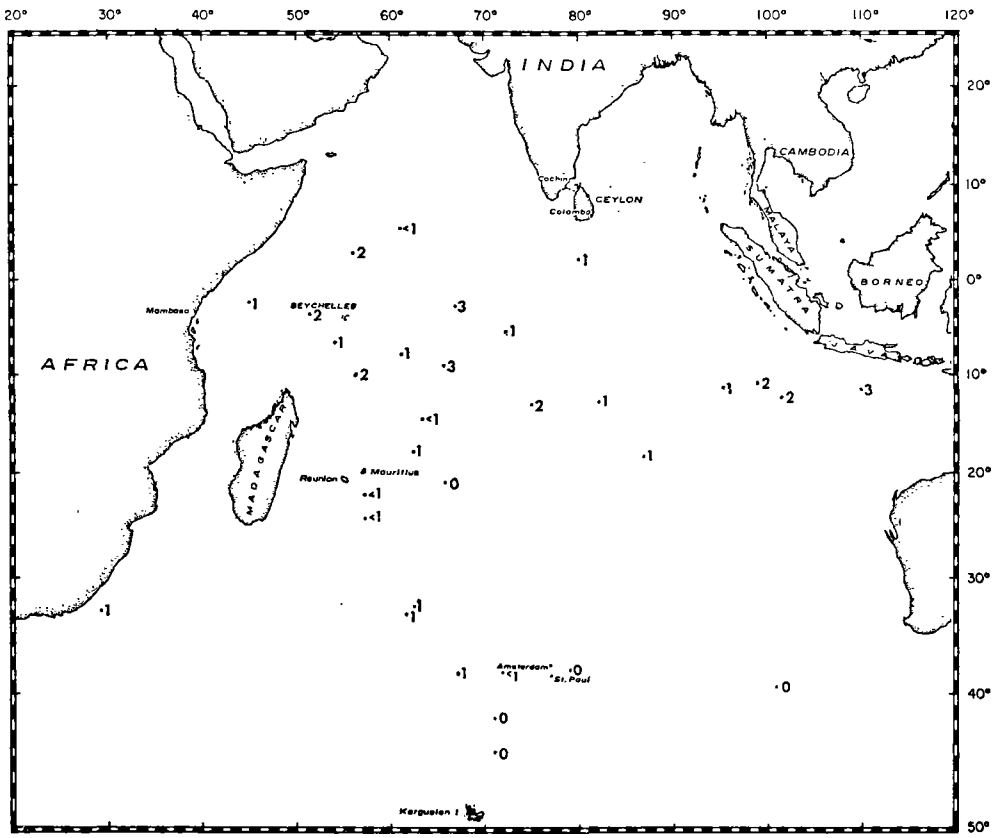

Fig. 45. Distribution of *Siphocampe corbula*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

The type species (*Dictyomitra ehrenbergi* Zittel) of *Theocampe* may possess a cephalic tube, and, therefore, Burma's (1959) suggestion that *Tricolocampe polyzona* and *Tricolocampe stenozona* be placed in the genus *Theocampe* may be justified on the basis of cephalic structure. However, *Siphocampe* is the only genus presently defined as having a cephalic tube, and it seems most convenient to use it for forms bearing this structure. Unfortunately, the true nature of the type species of *Siphocampe* (*S. accrescens* Rüst from the Jurassic of Switzerland) is questionable: the presence of a cephalic tube is doubtful and the mouth is apparently not constricted.

Material from the type localities of *T. polyzona* has been examined and was found to contain specimens of *S. corbula*. Topotypic material for *T. stenozona* is unavailable. However, the differences, cited by Haeckel (1887), between *T. polyzona* and *T. stenozona* are ones of proportion and probably due to individual variation. It seems reasonable to assume, therefore, that these species are identical with each other and with the one here described, and that Haeckel failed to dis-

tinguish the cephalis and cephalic tube. This oversight is quite understandable, especially when viewing specimens from the side of the cephalis away from the cephalic tube.

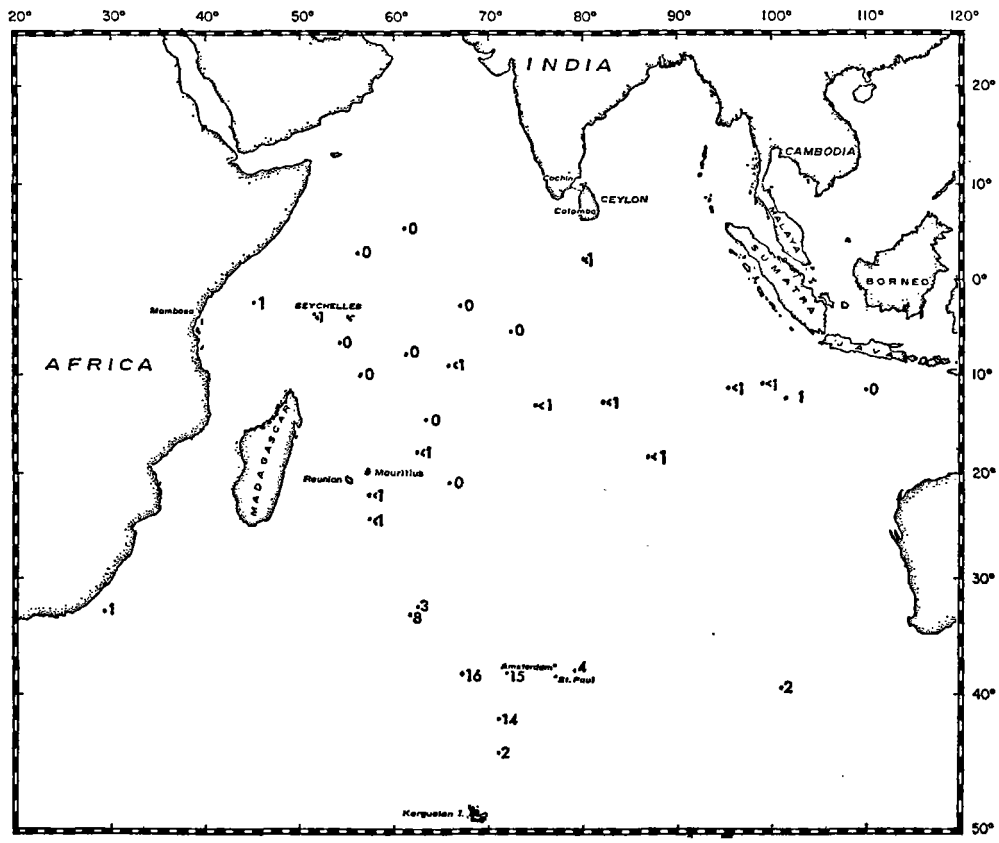

Fig. 46. Distribution of *Lithocampe* sp. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

The function of the cephalic tube is not known. Haeckel (1887, p. 1499) suggested that "it probably serves for the emission of a bunch of pseudopodia." Whatever its function, it does seem that forms possessing this peculiar and distinctive structure must be closely related.

Genus *Lithocampe* Ehrenberg

Lithocampe Ehrenberg, 1838, p. 128; *sens. emend.* Haeckel, 1887, p. 1501.

Lithocampe sp.

(Pl. 8, figs. 6*a*, 6*b*)

Description.—Subcylindrical shell, rather rough and thick-walled, consisting of 5–8 segments. Cephalis simple, approximately hemispherical, with subcircular pores and a short needle-like apical horn. Collar stricture indistinct. Median bar and vertical spine form a V; primary lateral and dorsal spines continue as ribs in the thoracic wall almost to the lumbar stricture.

Thorax conical, usually longer than, but sometimes of the same length as, subsequent segments. Pores subcircular, arranged in transverse rows. Lumbar stricture not pronounced.

Post-thoracic segments cylindrical, of approximately equal length (final segment often longer), each with 4–6 transverse rows of subcircular pores, 9–12 on a half-equator. In complete specimens the last segment narrows sharply to form a constricted mouth. However, the final 1 or 2 segments are often irregular; incomplete specimens in which the shell mouth is ragged and wide open are common.

Dimensions.—Total length 128–218μ. Maximum breadth 54–72μ.

Indian Ocean occurrences (fig. 46).—*L.* sp. is sparsely distributed in low latitudes, but is abundant (2% to 16% of the described population) south of 30° S. It appears to be a reliable and potentially useful member of the middle latitude assemblage.

Discussion.—No specific name has been assigned to this species because of the present uncertainty regarding the many closely related forms of this type known to exist. A detailed study of these forms, from both the Tertiary and Quaternary, must be made before a coherent and workable taxonomy can be formulated.

Genus *Spirocyrtis* Haeckel

Spirocyrtis Haeckel, 1881, p. 438; 1887, p. 1508.

The genus *Spirocyrtis* was formally defined as having spirally arranged constrictions (Haeckel, 1887). This appears to be an unsuitable criterion for generic distinction, since spirality is a variable property of a number of obviously unrelated forms. Bütschli (1889, p. 1995) questioned the presence of true spiral constrictions in the genus. The type species of *Spirocyrtis* is *S. scalaris,* which was originally described by Haeckel (1887) as having spirally arranged constrictions on the shell. Popofsky (1913) included in *S. scalaris* forms with a spiral constriction and those with the usual ring arrangement, saying that the change from one to the other is a simple one. This seems a reasonable assumption. None of the specimens examined from the Indian Ocean was found to have a spiral constriction.

If spirality is ignored, the generic definition of *Spirocyrtis* (*Spirocyrtidium*) becomes formally equivalent to *Lithostrobus* Bütschli, 1882, and *Spirocyrtis* (*Spirocyrtoma*) becomes very similar to *Eucyrtidium* Haeckel *sens. emend.* herein (p. 81). However, the distinctive cephalic structure (cf. pl. 9, fig. 4) of *S. scalaris* certainly places it in a separate genus. *Spirocyrtis* is, therefore, retained and should be used for forms bearing the kind of cephalic tube found in *S. scalaris.*

Spirocyrtis scalaris Haeckel

(Pl. 8, fig. 7; pl. 9, fig. 4)

1887 *Spirocyrtis scalaris* Haeckel, "Chall." Rept., p. 1509, pl. 76, fig. 14.
1913 *Spirocyrtis scalaris* Haeckel.—Popofsky, Deutsche Südpolar-Exped., vol. 14 (Zool. vol. 6), p. 406, text figs. 128–130.

Description.—Shell smooth, thin-walled, conical or subconical with the terminal portion approximately cylindrical; 6–10 segments. Cephalis hemispherical with

numerous subcircular pores. Apical spine free; apical horn short, straight, supported by 3 thin weblike membranes stretching from the horn to the top of the cephalis and giving the horn a triangular outline. On the side of the cephalis away from the apical horn is a large tube, thin-walled, wide open, and usually duck-

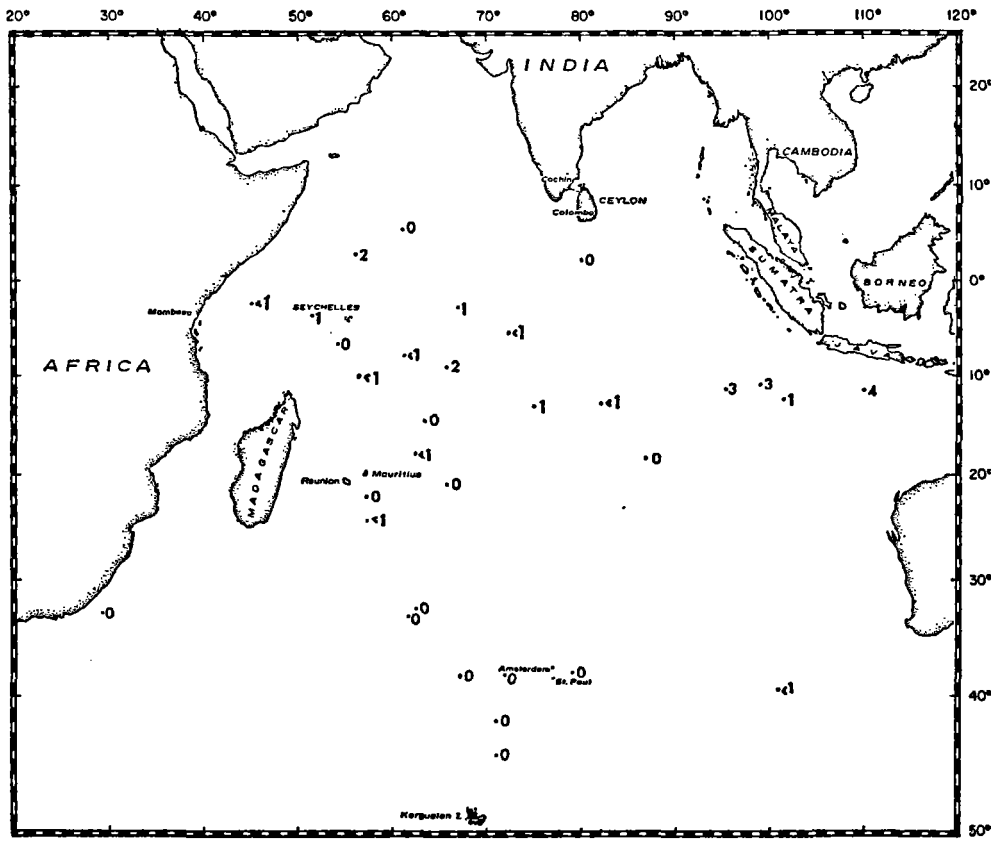

Fig. 47. Distribution of *Spirocyrtis scalaris*. Numbers are percentages of the described population, based on total counts of 500 specimens in each sample.

billed. The vertical spine and 2 spines perpendicular to it form a cross at the cephalic end of the tube. Median bar and proximal end of vertical spine form a V; both primary and secondary laterals present, the former continuing as ribs in the thoracic wall.

Collar stricture indistinct, the cephalis being depressed into the thorax. Thorax and abdomen rounded; lumbar stricture not pronounced. Subsequent segments vary in length, are cylindrical (sometimes with a medial constriction), and form a characteristic steplike profile. All have square to rectangular pores arranged in transverse rows, 2–6 per segment. Shell mouth wide open with no definite terminal structure.

Dimensions.—Total length (excluding apical horn) 109–182μ. Maximum breadth 63–128μ.

Occurrences previously recorded.—Haeckel (1887)—Central Pacific, "Challenger" Stations 271 (0°33′ S., 151°34′ W., 4,435 m), 272 (3°48′ S., 152°56′ W.,

4,755 m), 273 (5°11′ S., 152°56′ W., 4,298 m), 274 (7°25′ S., 152°15′ W., 5,029 m).

Popofsky (1913)—Deutsche Südpolar-Expedition, 15 May 1903 (25°07′ S., 56°07′ E., 400 m), 11 August 1903 (28°46′ S., 10°17′ E., 200 m), 7 September 1903 (9°38′ S., 8°56′ W., 400 m), 21 September 1903 (0°16′ N., 18°07′ W., 400 m).

Indian Ocean occurrences (fig. 47).—*S. scalaris* is sparsely distributed in low latitudes, and is practically absent south of 30° S. Maximum abundances (up to 4% of the described population) occur in the eastern tropics.

Discussion.—Except for two spines branching off the vertical spine, the characteristic spine framework described by Popofsky (1913) could not be seen.

Haeckel (1887) described two or three apical horns; Popofsky (1913) described two. It seems likely that the cephalic tube was thought by them to be an apical horn. A third cephalic projection has never been observed by the present author.

DISTRIBUTION OF DESCRIBED SPECIES

Recent Indian Ocean Sediments

Tropical and Antarctic radiolarian faunas have previously been observed to differ markedly (Riedel, 1958). Hays (1965) observed and described a striking change in fossil radiolarian assemblages across the Polar Front. Now, in the Indian Ocean at least, a middle latitude assemblage can be recognized. Although many of the species described herein are found in both low and middle latitudes, a sufficient number are restricted in their distribution to allow distinction between low and middle latitude assemblages. The boundary between these faunas is at about 30°–35° S. in the Indian Ocean. Two samples (LSDA 124G and LSDA 125G), at about 32°44′ S. and 33°14′ S. respectively, have a mixed low and middle latitude assemblage, and one sample (Serpent [?] 9) near the African coast at 35°50′ S. has an assemblage tending to resemble that characteristic of low latitudes.

A frequency distribution chart is given in table 1 (p. 91). Calculations are based on 29 samples having distinct low or middle latitude radiolarian assemblages. The three samples in which a mixed assemblage occurs are omitted. Occurrences of less than 1 percent are considered as 1 percent. Species are ranked according to decreasing values of the differences (δ) between the product of distribution frequency (DF)[1] and mean occurrences in low latitudes, and that in middle latitudes. Those species having high positive values are regarded as the most reliable members of the low latitude assemblage, and those having high negative values the most reliable members of the middle latitude assemblage.

While individual numbers derived in this way are useful, they could be distorted by even one anomalous occurrence, which might reflect any of a large number of poorly understood physical and biological factors. Therefore, conclusions should not be drawn from the distributions of individual species, but rather from consideration of the entire radiolarian assemblage. Factors, which cannot be numerically evaluated, must also be taken into consideration. For instance, *A. arcadophorum. A. ypsilon,* and *C. thermophila* are thought by the author to be more useful in delineating a low latitude assemblage than their numerical ranking would indicate. These species are easily recognizable forms which can be identified

[1] $\text{DF}\ (\%) = \frac{\text{Number of low (middle) lattitude samples in which the species is found}}{\text{Total number of low (middle) latitude samples}} \times 100$

TABLE 1

FREQUENCY DISTRIBUTION CHART, BASED ON 29 INDIAN OCEAN SAMPLES HAVING DISTINCT LOW OR MIDDLE LATITUDE RADIOLARIAN ASSEMBLAGES

Species	Low latitude			Middle latitude			δ = (Low latitude frequency × mean) − (middle latitude frequency × mean)
	Distribution frequency (%)	Mean occurrence	Frequency (%) × mean	Distribution frequency (%)	Mean occurrence	Frequency (%) × mean	
P. tetrathalamus	100	16.39	1639	83	0.83	69	+1570
P. praetextum praetextum	100	8.30	830	0	0	0	+ 830
Euchitonia sp.	100	7.82	782	0	0	0	+ 782
S. tetras tetras	100	5.52	552	0	0	0	+ 552
B. scutum	100	5.17	517	17	0.17	3	+ 514
P. trilobum	100	5.65	565	83	0.83	69	+ 496
T. trachelium trachelium	100	4.78	478	0	0	0	+ 478
A. ophirense	100	5.26	526	83	0.83	69	+ 457
D. quadrata	100	3.04	304	0	0	0	+ 304
O. auriculata	100	2.39	239	0	0	0	+ 239
P. lappacea	100	2.47	247	33	0.33	11	+ 238
S. polysiphonia	100	2.65	265	67	0.83	57	+ 208
E. hexagonatum	100	2.43	243	67	0.67	45	+ 198
A. reticulata	100	1.70	170	17	0.17	3	+ 167
D. zanguebarica	96	1.61	155	0	0	0	+ 155
Ceratospyris sp.	91	1.70	155	33	0.33	11	+ 144
A. arcadophorum	91	1.57	143	0	0	0	+ 143
L. bacca	83	1.65	137	0	0	0	+ 137
S. corbula	96	1.49	143	33	0.33	11	+ 132
P. flammabunda	96	1.22	117	17	0.17	3	+ 114
C. thermophila	78	1.26	98	0	0	0	+ 98
P. spinosa	100	3.00	300	100	2.16	216	+ 84
H. echiniscus	87	0.91	79	0	0	0	+ 79
A. ypsilon	83	0.91	76	0	0	0	+ 76
S. scalaris	70	1.09	76	17	0.17	3	+ 73
A. costata	78	0.87	68	0	0	0	+ 68
T. hertwigii	74	0.83	61	0	0	0	+ 61
T. damaecornis	61	0.61	37	0	0	0	+ 37
O. polymorpha	61	0.61	37	17	0.17	3	+ 34
L. maritalis polypora	96	1.57	151	83	1.67	139	+ 12
A. zanguebaricum	91	1.17	106	100	1	100	+ 6
D. papillosus	43	0.43	18	50	0.50	25	− 7
S. circularis	17	0.17	3	50	0.50	25	− 22
S. tetras irregularis	0	0	0	50	0.50	25	− 25
H. asteriscus	100	2.78	278	100	3.83	383	− 105
D. crisiae	96	1.22	117	100	2.67	267	− 150
C. profunda	100	1.65	165	100	3.17	317	− 152
L. maritalis maritalis	74	0.78	58	100	5.50	550	− 492
E. acuminatum	74	0.87	64	100	7.83	783	− 719
Lithocampe sp.	57	0.57	32	100	7.83	783	− 751
P. praetextum eucolpum	0	0	0	100	8.83	883	− 883
A. medianum	22	0.22	5	100	9.50	950	− 945
T. trachelium dianae	4	0.04	0.2	100	33.17	3317	−3317

from fragments, but such fragments could not be included in species counts. Had they been included, low latitude occurrence values would have been higher, but middle latitudes are devoid even of fragments.

L. maritalis polypora and *E. hexagonatum* are also more useful than their ranking would indicate. The abundance of these species relative to that of their close, middle latitude, relatives, *L. maritalis maritalis* and *E. acuminatum,* is often a valuable contribution to the overall picture of a low latitude assemblage. Similarly, the relative abundances of *S. tetras irregularis* and *S. tetras tetras* contribute to the middle latitude assemblage picture.

Potential Use in Quaternary Stratigraphy

Recognition of low, middle, and high (Riedel, 1958; Hays, 1965) latitude assemblages provides a useful tool for studying Quaternary stratigraphy (Phleger, Parker, and Peirson, 1953; Ericson and Wollin, 1964). If most of the radiolarians considered here live in the upper few hundred meters of the water column, and if temperature (and its corollary effects) is indeed the principal factor controlling the distribution of these assemblages, then it should now be possible, on the basis of a study of core material, to detect shifts in near-surface water masses during the Pleistocene. Hopefully, the Radiolaria in cores will show an alternation between low and middle latitude assemblages. Such sequences, correlated with similar foraminiferal series, would allow the extension of this kind of Pleistocene stratigraphy into noncalcareous pelagic sediments. Even in calcareous sediments the addition of a number of radiolarian species to those species of foraminifera used stratigraphically would strengthen ecological interpretations.

CONCLUSIONS

During this study, the areas in which Radiolaria are found in Recent Indian Ocean sediments have been determined and described. Two areas in which Radiolaria are abundant have been delineated: (1) a low (10° N. to approximately 20° S.) latitude belt; and (2) a middle (35° S. to 45° S.) latitude belt. These are separated by an area, corresponding to the subtropical anticyclonic gyre, which is essentially barren of Radiolaria.

Detailed examination of the faunas in the areas of high radiolarian abundance has revealed two distinct assemblages: (1) a low latitude assemblage composed of twelve of the described species; and (2) a middle latitude assemblage made up of seven of the described species. The recognition of low, middle, and high latitude assemblages is a potenitally useful tool in the interpretation of Quaternary stratigraphy from deep-sea core material.

In Atlantic Ocean sediments it has been found that the radiolarian fauna is generally poorer than in those of the Indian Ocean. However, Radiolaria do occur in some abundance equatorially (10° N.–10° S.), in middle northern (35°–45° N.) latitudes, and in middle southern (25°–40° S.) latitudes. A preliminary examination of nine samples from these areas has shown that, in general, species restricted to low or middle latitudes in the Indian Ocean are similarly restricted in the Atlantic.

APPENDIX

Radiolaria in Pelagic Sediments from the Atlantic Ocean

Although the taxonomic part of this paper is confined to Indian Ocean fauna, some preliminary work has been carried out on Atlantic Ocean samples. Strewn slides of fifty-five samples of Recent Atlantic Ocean sediments, from between 60° N. and 40° S., were prepared and examined. Using these data (p. 94) and previously published information (p. 3), a chart showing radiolarian distribution in the Atlantic has been compiled (fig. 48). It was found that Radiolaria are generally less abundant in Atlantic sediments than in either Indian or Pacific Ocean sediments. The most prolific assemblages occur:

1. along the equator and in the Guinea Basin, northward to the Cape Verde Islands;
2. in the North Atlantic between 35° and 45° N., east of 30° W. (abundances are irregular in this area);
3. in the South Atlantic, south of 25° S.

More extensive sampling will undoubtedly define these regions more accurately. It must be emphasized that the present survey is purely a preliminary one.

Even the most prolific Atlantic samples are poor in comparison with most tropical Indian Ocean samples. This apparently results from generally lower concentrations of phosphate-phosphorous in the Atlantic and consequently smaller zooplankton volumes. There are large areas of the Atlantic having very low rates of biological production. In addition, the concentration of silica in Atlantic Ocean waters is markedly lower than in the Indian Ocean (Sverdrup, Johnson, and Fleming, 1942, pp. 244–245).

Three samples from the North Atlantic, three from the equatorial Atlantic, and three from the South Atlantic (samples marked with an asterisk, pp. 94–96) were examined in detail to determine if typically low or middle latitude Indian Ocean species are present and similarly distributed in the Atlantic.

The following species with restricted ranges in the Indian Ocean were found too rarely in the Atlantic samples examined to provide convincing distributional patterns:

Actinomma arcadophorum
Spongaster tetras irregularis
Theocorythium trachelium trachelium
Eucyrtidium hexagonatum

In northern middle latitudes (45°, 42°, and 41° N.) the following species, largely confined to middle latitudes in the Indian Ocean, were found to be similarly restricted in the Atlantic:

Actinomma medianum
Lamprocyclas maritalis maritalis
Theocorythium trachelium dianae
Eucyrtidium acuminatum
Lithocampe sp. (at 45° and 42° N.)

Pterocanium praetextum eucolpum was absent from the northern latitude samples examined.

In the southern latitude (30°, 31°, and 37° S.) samples examined, the following species characteristic of the Indian Ocean middle latitude assemblage were found:

Pterocanium praetextum eucolpum (at 31° and 37° S.)
Lamprocyclas maritalis maritalis
Theocorythium trachelium dianae
Eucyrtidium acuminatum
Lithocampe sp. (at 31° and 37° S.)

Actinomma medianum was too rare to give a recognizable distributional pattern.

The following species, largely confined to low latitudes in the Indian Ocean, were similarly restricted in the Atlantic:

Euchitonia sp. (including *E. mülleri* and *E. elegans*)
Spongaster tetras tetras
Pterocanium praetextum praetextum
Lamprocyclas maritalis polypora (relative to *L. maritalis maritalis*)

Panartus tetrathalamus ranged as far south as 31° S., thus giving a low latitude aspect to the sample at 31° S., which otherwise has a typically middle latitude assemblage. The assemblage at 29° S. is regarded as a mixed low and middle latitude fauna.

With the few exceptions noted, those species described herein as characteristic of the low or middle latitude assemblage in the Indian Ocean appear to be similarly distributed in the Atlantic Ocean.

Atlantic Ocean Sample Descriptions, showing Radiolarian Abundances

Marsden Square

*3 0°30′ N., 25°38′ W., 3,620 m, 0–1 cm; SDSE[1] 242; abundant, well-preserved Radiolaria.

3 2°06′ N., 20°07′ W., 5,056 m, 0–1 cm; SDSE 236; abundant, well-preserved Radiolaria.

3 9°29′ N., 28°00′ W., 5,580 m; GOLDFINCH 178, 26 May 1903; B.M. (M4630); abundant, well-preserved Radiolaria.

*4 0°48′ N., 31°28′ W., 3,210 m, 1–2 cm; SDSE 246; abundant, well-preserved Radiolaria.

38 11°35′ N, 17°51′ W., 3,072 m; SERPENT (?) 106, 4 June 1869; B.M. (M9533); Radiolaria absent.

39 15°53′ N., 25°27′ W., 4,280 m, 0–1 cm; SDSE 228; moderately abundant, well-preserved Radiolaria.

40 12°03′ N., 34°12′ W., 6,025 m; METEOR 305*b*, 29 April 1927; B.M. (1959, 436[5]); moderately abundant, well-preserved Radiolaria.

42 12°54′ N., 52°55′ W., 5,128 m, 0–1 cm; SDSE 261; moderately abundant, slightly corroded Radiolaria.

44 16°19′ N., 70°29′ W., 4,049 m; MUTINE 46, 1 Jan. 1914; B.M. (D9.38); moderately abundant, well-preserved Radiolaria.

74 29°55′ N., 17°32′ W., 4,310 m, 0.5–2 cm; SDSE 215; moderately abundant, well-preserved Radiolaria.

75 approximately 27°10′ N., 21°04′ W., 4,603 m, 10 cm; DISCOVERY II 4790, 4 Feb. 1962; D.G.G.; Radiolaria very rare.

75 approximately 28°58′ N., 25°27′ W., 5,333 m, 5 cm; DISCOVERY II 4774, 17 Jan. 1962; D.G.G.; Radiolaria very rare.

77 29°35′ N., 42°33′ W., 2,820 m; VIDAL 6, 7 July 1960; B.M. (1960, 501 [2]); moderately abundant, well-preserved Radiolaria.

[1] SDSE = Swedish Deep-Sea Expedition, samples kindly supplied by Dr. B. Kullenberg, via W. R. Riedel.

Marsden Square

78 21°05′ N., 58°50′ W., 5,596 m (B.M.) or 5,962 m (Murray and Chumley, 1924); RAMBLER 5, 1 March 1898; B.M. (M7384); Radiolaria very rare.

79 20°00′ N., 60°02′ W., 5,069 m; ORMONDE, 18 May 1926; B.M. (D23.22); Radiolaria very rare.

110 32°59′ N., (B.M.) or 32°51′ N. (Murray and Chumley, 1924), 12°53′ W., 3,831 m; DACIA 147, 6 (?) Oct. 1883; B.M. (M3576); Radiolaria rare.

111 36°53′ N., (B.M.) or 35°53′ N. (Murray and Chumley, 1924), 29°47′ W., 3,233 m; MICHAEL SARS 56, 10–11 June 1910; B.M. (M9732); abundant, well-preserved Radiolaria.

113 34°54′ N., 44°20′ W., 4,281 m, 3.5–4 cm; SDSE 281; abundant, well-preserved Radiolaria.

114 33°07′ N., 52°14′ W., 5,651 m; RAMBLER 34, 29 Nov. 1898; B.M. (M7392); Radiolaria very rare.

145 47°54′ N., 9°56′ W., 3,164 m; BRITANNIA 471, 31 July 1899; B.M. (M1573); Radiolaria rare.

146 42°55′ N., 11°18′ W., 2,266 m, top of core; DISCOVERY II 3802, 17 July 1958; D.G.G.; Radiolaria rare.

*146 45°17′ N., 11°22′ W., 4,078 m, top of core; DISCOVERY II 4289, 8 April 1960; D.G.G.; abundant, well-preserved Radiolaria.

147 41°35′ N., 29°37′ W., 1,995 m, 0–1 cm; SDSE 290; moderately abundant, well-preserved Radiolaria.

*147 42°27′ N., 21°08′ W., 3,736 m, 4.5–5.5 cm; SDSE 296; abundant, well-preserved Radiolaria.

147 45°07′ N., 25°22′ W., depth unknown, top of core; DISCOVERY II 4532, 8 Sept. 1960; D.G.G.; moderately abundant, well-preserved Radiolaria.

*148 41°12′ N., 31°30′ W., 2,640 m, 0–1 cm; SDSE 289; abundant, well-preserved Radiolaria.

148 41°19′ N., 38°56′ W., 4,998 m; BRITANNIA 212, 29 June 1899; B.M. (M1348); Radiolaria rare.

149 42°39′ N., 49°48′ W., 2,103 m; SERPENT (?) 13, 11 May 1869; B.M. (M9112); few, well-preserved Radiolaria.

150 42°45′ N., 51°13′ W., 1,280 m; SERPENT (?) 12, 10 May 1869; B.M. (M9111); few, well-preserved Radiolaria.

182 50°13′ N., 11°23′ W., 1,257 m; MICHAEL SARS 93, 25 July 1910; B.M. (M9738); Radiolaria very rare.

183 50°06′ N., 21°54′ W., 3,694 m; CHALLENGER, 16 Sept. 1953; B.M. (1954, 41[16]); Radiolaria very rare.

184 50°03′ N., 30°51′ W., 2,884 m; FARADAY 59, 19 June 1903; B.M. (M4520); moderately abundant, well-preserved Radiolaria.

300 4°42′ S., 7°08′ W., 4,252 m; GAZELLE 29, 24 Aug. 1874; B.M. (M4580); abundant, well-preserved Radioalria.

301 0°01′ S., 13°04′ W., 4,568 m; BUCCANEER 409, 11 March 1886; B.M. (M3435); abundant, well-preserved Radiolaria.

*301 0°49′ S., 14°24′ W., 3,830 m; BUCCANEER 401, 8 March 1886; B.M. (M3433); abundant, well-preserved Radiolaria.

302 6°20′ S., 29°26′ W., 5,082 m; EGERIA 5, 10 March 1897; B.M. (M4311); Radiolaria very rare.

303 0°23′ S., 38°59′ W., 4,376 m; MUTINE 22, 11 Dec. 1913; B.M. (D9.15); few, slightly corroded Radiolaria.

334 5°55′ S., 10°04′ E., 2,994 m; BUCCANEER 382, 19 Feb. 1886; B.M. (M3422); Radiolaria rare.

335 5°48′ S., 6°50′ E., 4,641 m; BUCCANEER 384, 21 Feb. 1886; B.M. (M3424); Radiolaria very rare.

336 19°23′ S., 1°44′ W., 5,121 m; SERPENT (?) 5, 6 July 1868; B.M. (M7745); Radiolaria absent.

Marsden Square

337 12°46′ S., 18°40′ W., (B.M.) or 18°36′ W., (Murray and Chumley, 1924), 4,627 m; SEINE 27, 21 Nov. 1889; B.M. (M7584); Radiolaria rare.

338 14°17′ S., 20°11′ W., 4,899 m; SEINE 29, 21 Nov. 1889; B.M. (M7586); Radiolaria very rare.

*372 29°42′ S., 7°20′ W., 4,152 m, 0–2 cm; LSDA 167G, 11 June 1963; S.I.O.; abundant, well-preserved Radiolaria.

373 24°03′ S., 15°33′ W., 4,045 m, 0–2 cm; LSDA 178G, 19 June 1963; S.I.O.; abundant, well-preserved Radiolaria.

373 29°52′ S., 15°30′ W., 3,405 m; LSDA 175V, 14 June 1963; S.I.O.; abundant, well-preserved Radiolaria.

374 20°41′ S., 27°17′ W., 5,194 m; SEINE 38, 25 Nov. 1889; B.M. (M7593); Radiolaria very rare.

375 26°30′ S., 34°51′ W., 4,481 m; SEINE 47, 28 Nov. 1889; B.M. (M7601); Radiolaria very rare.

406 28°44′ S., 12°26′ E., 3,877 m; SERPENT 104, 17 May 1869; B.M. (M9531); abundant, well-preserved Radiolaria.

407 20°20′ S., 4°35′ E., 5,230 m; SERPENT 105, 22 May 1869; B.M. (M9532); moderately abundant, corroded Radiolaria.

408 35°40′ S., 5°01′ W., 3,552 m; QUEST 15, 6 June 1922; B.M. (D2.24); few, corroded Radiolaria

*410 37°29′ S., 27°31′ W., 4,023 m; CHALLENGER 332, 10 Mar. 1876; B.M. (M404); abundant, well-preserved Radiolaria.

411 39°36′ S., 32°53′ W., 4,883 m, 2–5 cm; VEMA 12–52, L.G.O.; moderately abundant, well-preserved Radiolaria.

412 30°17′ S., 40°27′ W., 3,753 m; SEINE 53A, 30 Nov. 1889; B.M. (M7605); Radiolaria absent.

*443 31°20′ S., 1°55′ E., 4,190 m, 0–2 cm; LSDA 163G, 8–9 June 1963; S.I.O.; abundant, well-preserved Radiolaria.

443 31°30′ S., 3°23′ E., 4,945 m; WATERWITCH 82, 1894; B.M. (1949, 1[52]); few, well-preserved Radiolaria (some admixed Tertiary, ?Eocene).

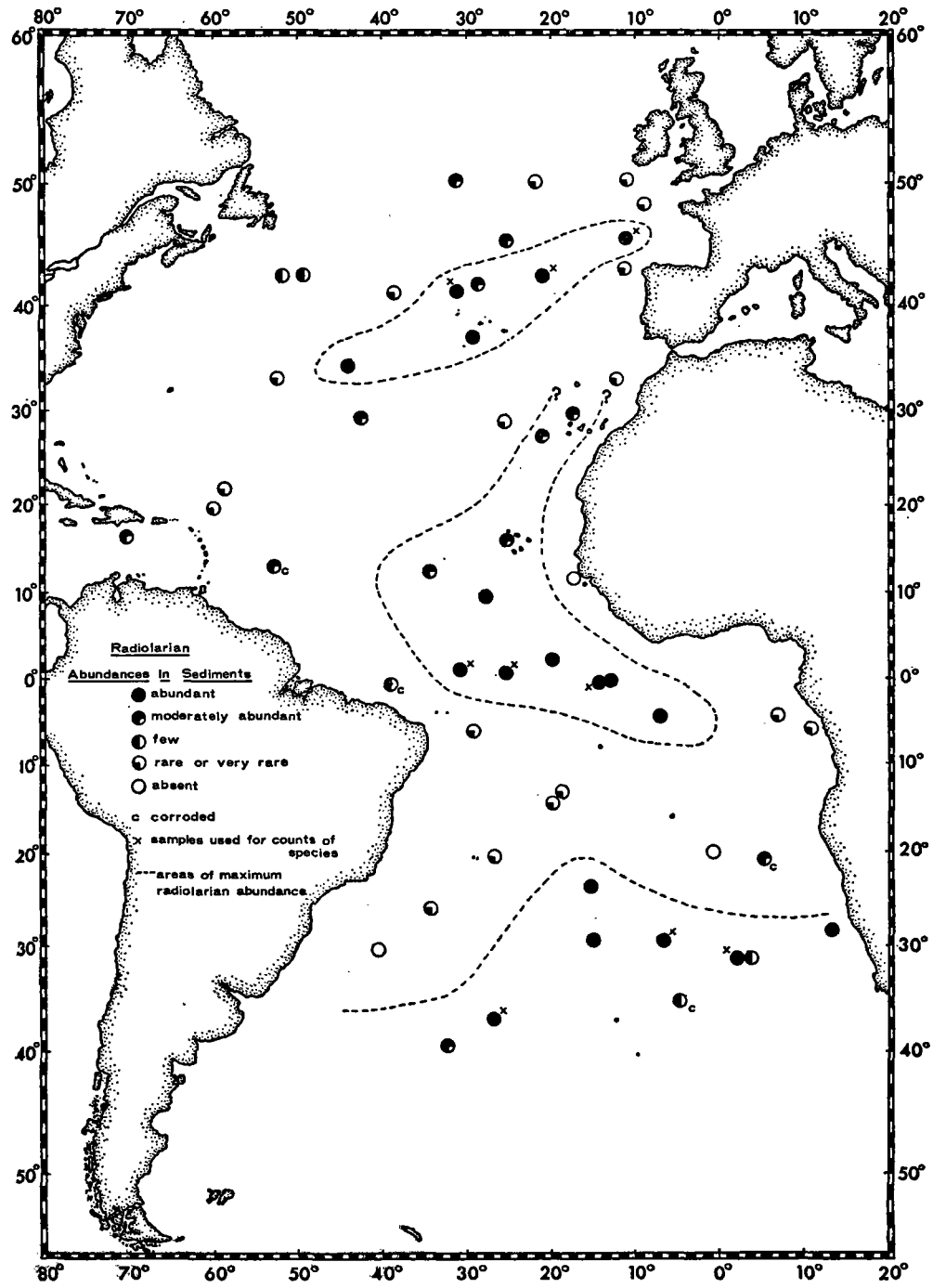
80° 70° 60° 50° 40° 30° 20° 10° 0° 10° 20°
60° 50° 40° 30° 20° 10° 0° 10° 20° 30° 40° 50°
Radiolarian
Abundances In Sediments
abundant
moderately abundant
few
rare or very rare
absent
c corroded
x samples used for counts of species
areas of maximum radiolarian abundance

Fig. 48.

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Explanatory Note

There has been some confusion regarding the correct dates of publication of Ehrenberg's papers. All but one (the Mikrogoelogie, 1854–1856) of Ehrenberg's radiolarian papers were first made public when he read them before the Akademie der Wissenschaften. Sometime after these readings an unbound (soft cover) report of the proceedings of the meeting was distributed. The date of this distribution legally constitutes the date of publication of the paper (cf. International Code of Zoological Nomenclature, Article 8). Proceedings from all meetings held in a particular year were bound and published the following year. This date has often been mistakenly used as the correct year of publication. It would probably be safe to assume that the unbound copy of a paper read early in the year was distributed during the same year, but papers read in November or December may well have not been distributed until the following year. Without examining the soft covers, the correct dates of publication are questionable. Unfortunately, these soft covers are not usually included in the sets of bound volumes found in most libraries. However, some do exist in the sets housed at the University Library (U. L.) and Philosophical Library (Cambridge). The author has thus been able to ascertain the correct dates of publication for four of Ehrenberg's papers. These findings are summarized below. Where proof is lacking, the dates used by Haeckel (1887) are retained herein, and are the year in which the paper was first read.

Similarly, dates of publication for four radiolarian papers by J. Müller were ascertained. Although these papers are not directly involved in the present investigation, their correct dates of publication are included below.

Date read	*Title*	*Journal*	*Date of soft cover issue*
11 Feb. 1847 (Ehrenberg)	Ueber die Mikroscopichen Kieselschaligen Polycystinen . . . von Barbados	Monatsber. Jahrg. 1847, pp. 40–60	1847 (U. L.)
4 Jan. 1858 (Ehrenberg)	Kurze Characteristik der 9 neuen Genera und der 105 neuen Species . . .	Monatsber. Jahrg. 1858, pp. 10–41	1858 (Philos. Lib.)
25 April 1872 (Ehrenberg)	Mikrogeologische Studien als Zusammenfassung . . . der Meeres-Tiefgrunde . . .	Monatsber. Jahrg. 1872, pp. 265–322	1872 (Philos. Lib.)
30 Jan. 1873 (Ehrenberg)	Grossere Felsproben des Polycystinen-Mergels von Barbados	Monatsber. Jahrg. 1873, pp. 213–263	1873 (Philos. Lib.)
19 April 1855 (Müller)	Ueber Sphaerozoum und Thalassicolla	Monatsber. Jahrg. 1855, pp. 229–253	1855 (Philos. Lib.)
5 Nov. 1855 (Müller)	Ueber die im Hafen von Messina beobachteten Polycystinen . . .	Monatsber. Jahrg. 1855, pp. 671–674	1855 (Philos. Lib.)

13 Nov. 1856 (Müller)	Ueber die Thalassicollen, Polycystinen und Acanthometren des Mittelmeeres	Monatsber. Jahrg. 1856, pp. 474–503	1857 (Philos. Lib.)
11 Feb. 1858 (Müller)	Einiger neuen bei St. Tropez am Mittelmeer ... Polycystinen ...	Monatsber. Jahrg. 1858, pp. 154–155	1858 (Philos. Lib.)

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PLATES

PLATE 1

Fig. 1. *Polysolenia spinosa* (Haeckel), ×233, MSN 34G, A-W26/4; Sedgwick Museum No. 843.5.

Fig. 2. *Polysolenia flammabunda* (Haeckel), ×233, DISCOVERY 5194, C-V39/4; Sedgwick Museum No. 862.3.

Fig. 3*a*. *Polysolenia lappacea* (Haeckel), ×233, focused on perimeter, DISCOVERY 5194, C-U33/0; Sedgwick Museum No. 862.2.

Fig. 3*b*. *Polysolenia lappacea* (Haeckel), ×233, focused on surface, DISCOVERY 5194, C-U33/0; Sedgwick Museum No. 862.2.

Fig. 4*a*. *Siphonosphaera polysiphonia* Haeckel, ×233, focused on surface, MSN 39G, A-B30/3; Sedgwick Museum No. 846.1.

Fig. 4*b*. *Siphonosphaera polysiphonia* Haeckel, ×233, focused on perimeter, MSN 39G, A-B30/3; Sedgwick Museum No. 846.1.

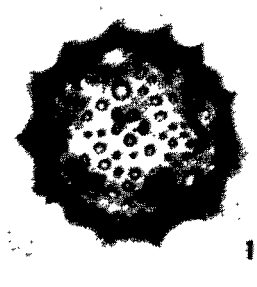
Fig. 5. *Disolenia quadrata* (Ehrenberg), ×233, MSN 39G, B-H42/1; Sedgwick Museum No. 847.1.

Fig. 6. *Disolenia zanguebarica* (Ehrenberg), ×233, DISCOVERY 5194, A-K28/0; Sedgwick Museum No. 860.2.

Fig. 7. *Otosphaera auriculata* Haeckel, ×233, MSN 34G, B-U36/4; Sedgwick Museum No. 844.5.

Fig. 8. *Otosphaera polymorpha* Haeckel, ×233, LSDA 124G, A-R32/0; Sedgwick Museum No. 856.6.

Fig. 9. *Saturnalis circularis* Haeckel, ×233, DISCOVERY 5194, D-J33/1; Sedgwick Museum No. 863.3.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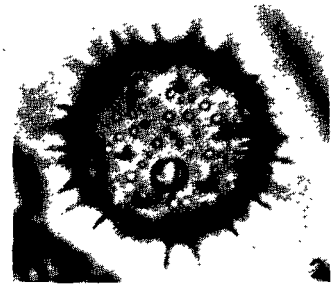
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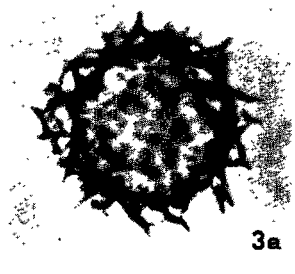
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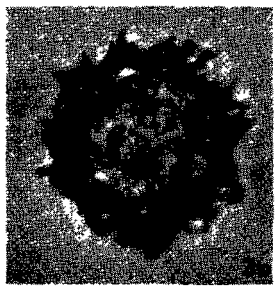
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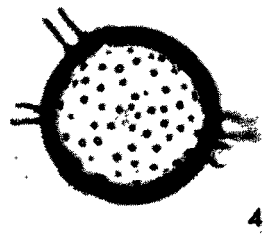
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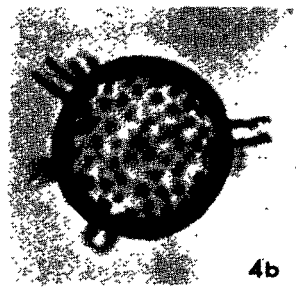
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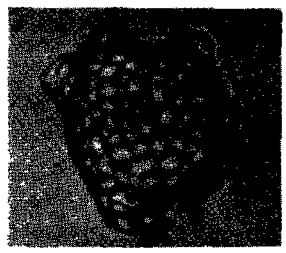
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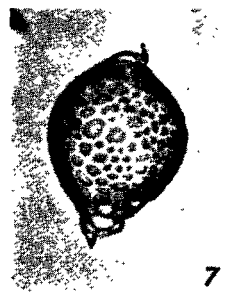
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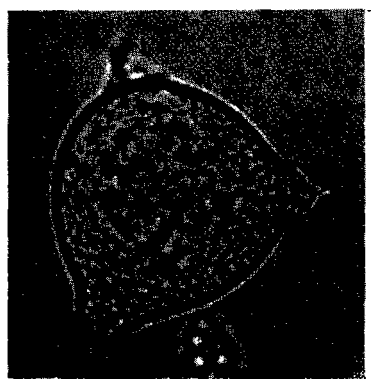
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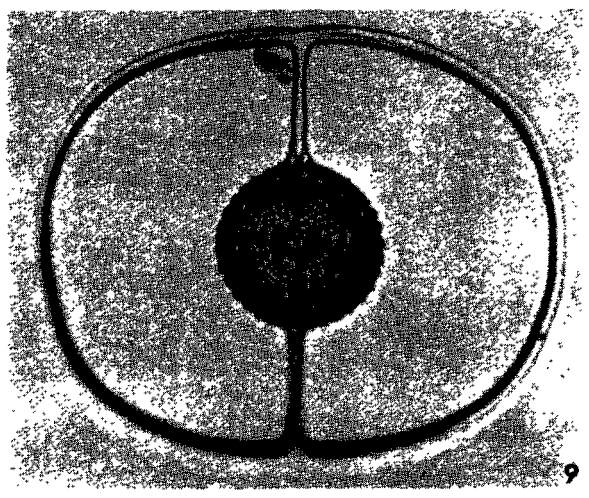
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PLATE 2

Fig. 1*a*. *Actinomma antarcticum* (Haeckel), ×150, focused on surface, no medullary shell or meshwork, LSDA 128G, D-Q36/0; Sedgwick Museum No. 859.2.

Fig. 1*b*. *Actinomma antarcticum* (Haeckel), ×150, focused to show presence of medullary shell and meshwork, LSDA 128G, D-O35/4; Sedgwick Museum No. 859.1.

Fig. 1*c*. *Actinomma antarcticum* (Haeckel), approximately ×108, medullary shell and meshwork of broken specimen, photographed in a wet preparation using Polaroid film.

Fig. 1*d*. *Actinomma antarcticum* (Haeckel), approximately ×108, medullary shell of broken specimen, photographed in a wet preparation using Polaroid film.

Fig. 2*a*. *Actinomma medianum n. sp.*, ×233, holotype, LSDA 124G, A-P25/0; Sedgwick Museum No. 856.5.

Fig. 2*b*. *Actinomma medianum n. sp.*, approximately ×108, medullary shell and meshwork of broken specimen, photographed in a wet preparation using Polaroid film.

Fig. 3. *Actinomma arcadophorum* Haeckel, ×233, MSN 39G, B-Y40/4, Sedgwick Museum No. 847.7.

Fig. 4*a*. *Panartus tetrathalamus* Haeckel, ×233, without polar caps, MSN 39G, B-W27/3; Sedgwick Museum No. 847.6.

Fig. 4*b*. *Panartus tetrathalamus* Haeckel, ×233, with single polar caps bearing prominent spines, LSDA 124G, A-K34/4; Sedgwick Museum No. 856.4.

Fig. 4*c*. *Panartus tetrathalamus* Haeckel, ×233, with single polar caps, MSN 39G, B-Z39/2; Sedgwick Museum No. 847.8.

Fig. 4*d*. *Panartus tetrathalamus* Haeckel, ×233, with single polar caps and lateral meshwork, VEMA 19-168, A-C43/3; Sedgwick Museum No. 864.1.

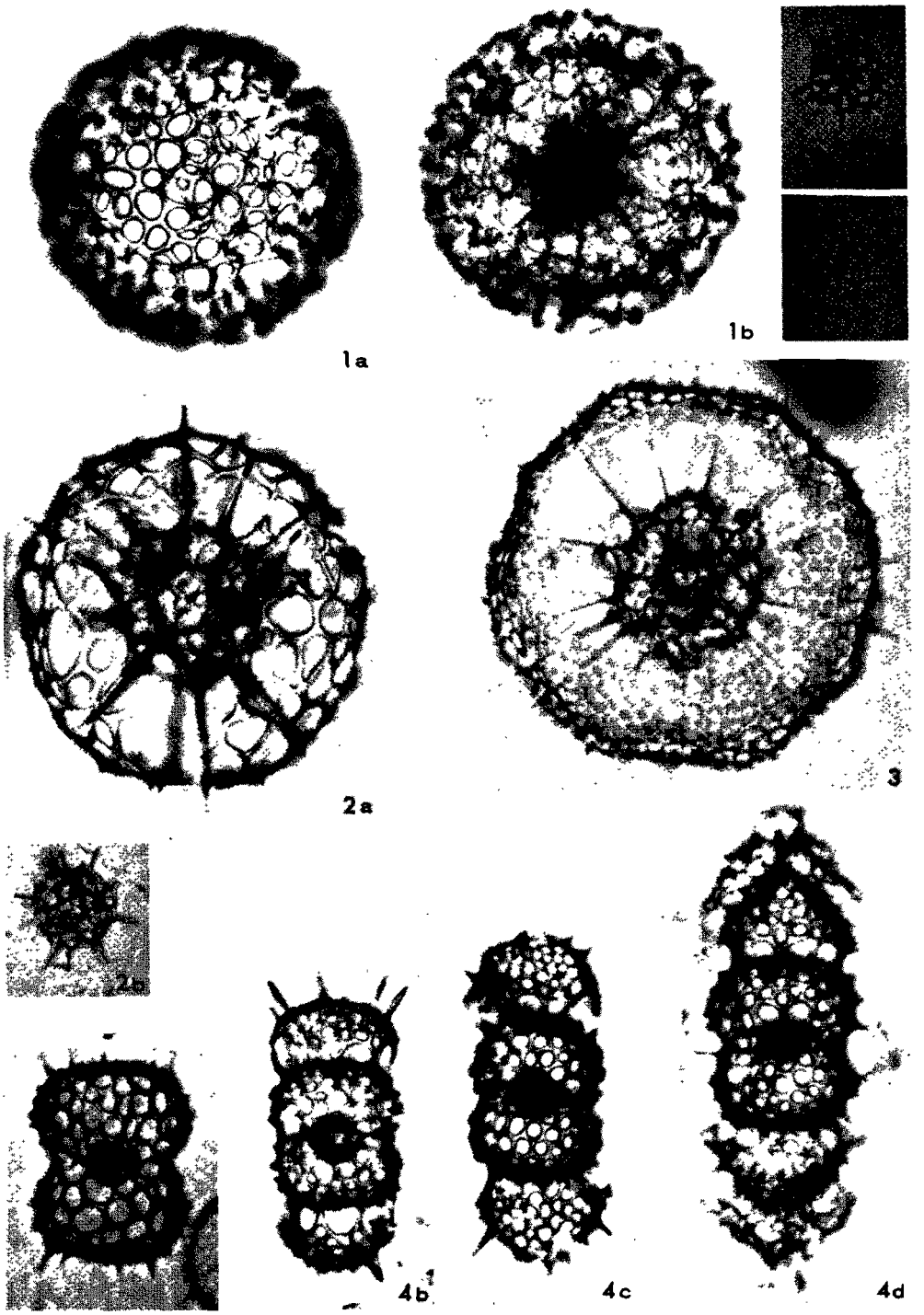

1a
1b
2a
3
4b
4c
4d

PLATE 3

Fig. 1*a*. *Heliodiscus asteriscus* Haeckel, ×150, DISCOVERY 5194, A-H24/4; Sedgwick Museum No. 860.1.

Fig. 1*b*. *Heliodiscus asteriscus* Haeckel, approximately ×333, inner medullary shell of broken specimen, photographed in a wet preparation.

Fig. 2*a*. *Heliodiscus echiniscus* Haeckel, ×150, DISCOVERY 5194, D-K37/0; Sedgwick Museum No. 863.4.

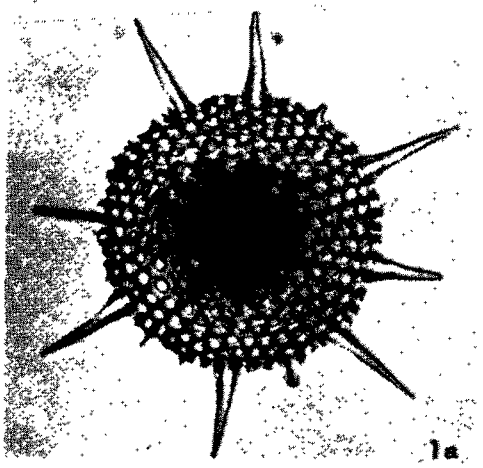
Fig. 2*b*. *Heliodiscus echiniscus* Haeckel, ×150, MSN 39G, D-S37/2; Sedgwick Museum No. 849.1.

Fig. 3*a*. *Amphirhopalum ypsilon* Haeckel, ×233, with patagium, DISCOVERY 5194, C-X34/0; Sedgwick Museum No. 862.4.

Fig. 3*b*. *Amphirhopalum ypsilon* Haeckel, ×233, without patagium, MSN 34G, B-Q43/0; Sedgwick Museum No. 844.3.

Fig. 3*c*. *Amphirhopalum ypsilon* Haeckel, approximately ×383, central structure: A = spheres; B = oblate spheroid; C = ring; D = arm, showing basic framework.

Fig. 3*d*. *Amphirhopalum ypsilon* Haeckel, approximately ×383, central structure viewed at right angles to fig. 3*c*; symbols as for fig. 3*c*.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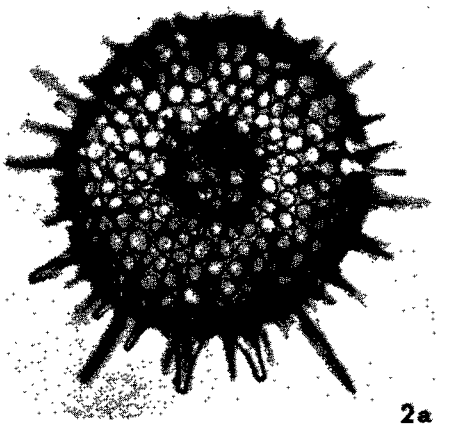
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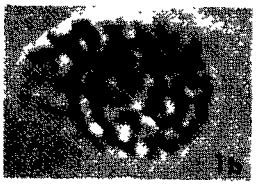
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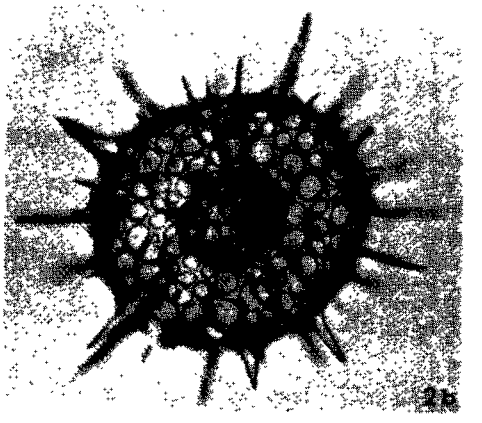
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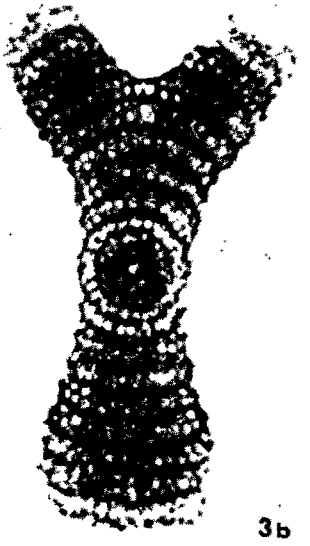
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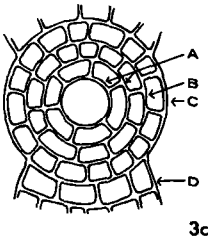

A
B
C
D
3c

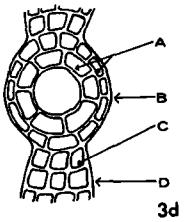

A
B
C
D
3d

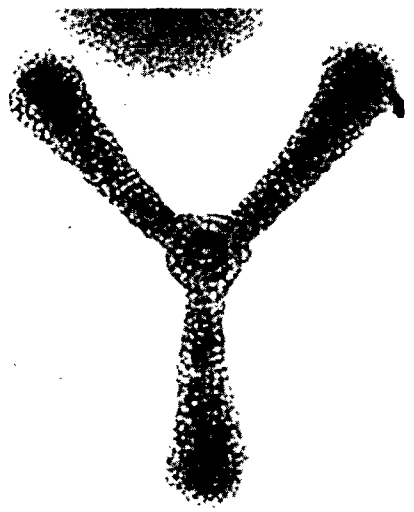
PLATE 4

Fig. 1*a*. *Euchitonia mülleri* Haeckel, ×150, without patagium, MSN 34G, B-V35/1; Sedgwick Museum No. 844.7.

Fig. 1*b*. *Euchitonia mülleri* Haeckel, ×150, with patagium, MSN 39G, B-N41/2; Sedgwick Museum No. 847.2.

Fig. 2*a*. *Euchitonia elegans* (Ehrenberg), ×150, without patagium, DISCOVERY 5194, D-K38/0; Sedgwick Museum No. 863.5.

Fig. 2*b*. *Euchitonia elegans* (Ehrenberg), ×150, with patagium, DISCOVERY 5194, D-J33/0; Sedgwick Museum No. 863.2.



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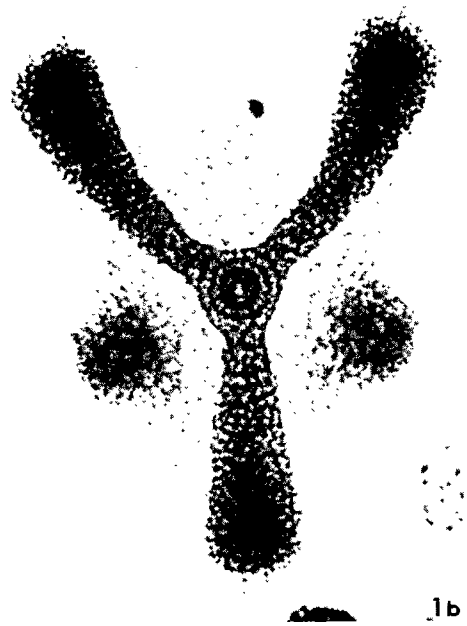

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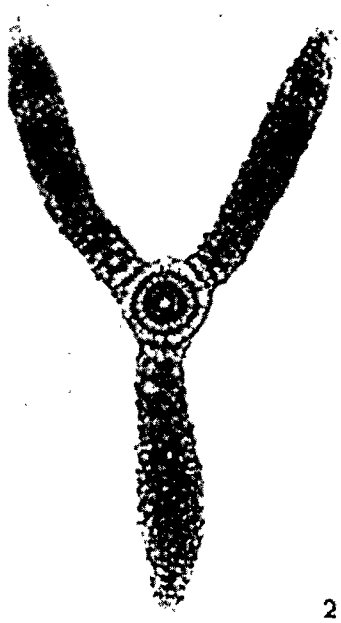

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2b

PLATE 5

Fig. 1*a*. *Spongaster tetras tetras* Ehrenberg, ×233, MSN 34G, A-T43/4; Sedgwick Museum No. 843.4.

Fig. 1*b* *Spongaster tetras tetras* Ehrenberg, ×233, cross section of ground specimen.

Fig. 2. *Spongaster tetras* Ehrenberg *irregularis n. subsp.*, ×233, holotype, LSDA 124G, A-K31/0; Sedgwick Museum No. 856.2.

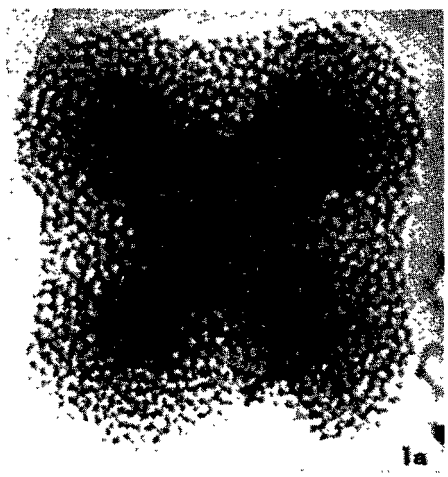
Fig. 3. *Amphispyris reticulata* (Ehrenberg), ×233, DISCOVERY 5194, D-H32/0; Sedgwick Museum No. 863.1.

Fig. 4. *Amphispyris costata* Haeckel, ×233, MSN 34G, B-B32/0; Sedgwick Museum No. 844.1.

Fig. 5. *Triceraspyris damaecornis* Haeckel, ×233, MSN 34G, A-R32/4; Sedgwick Museum No. 843.3.

Fig. 6. *Ceratospyris* sp., ×233, DISCOVERY 5194, C-D23/3; Sedgwick Museum No. 862.1.

Fig. 7. *Centrobotrys thermophila* Petrushevskaya, ×233, MSN 40G*a*, B-X42/0; Sedgwick Museum No. 850.3.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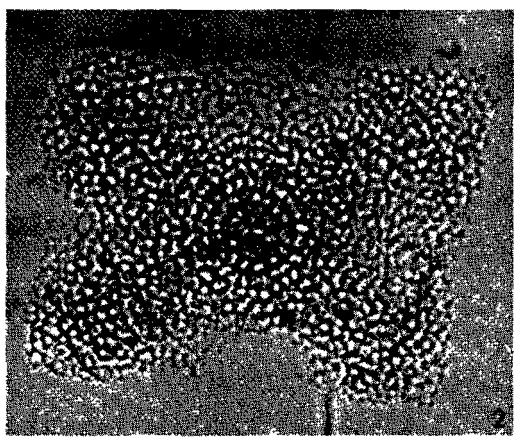
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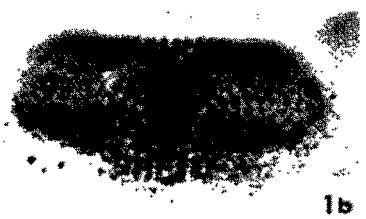
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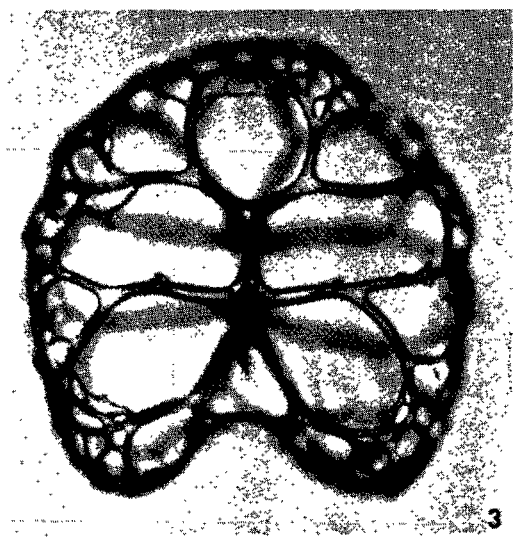
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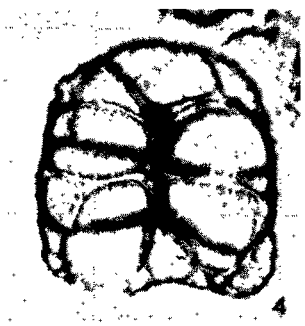
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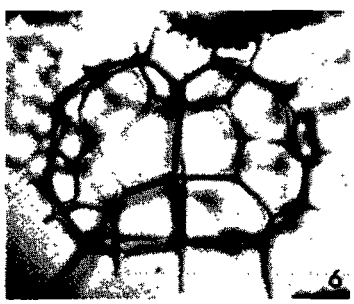
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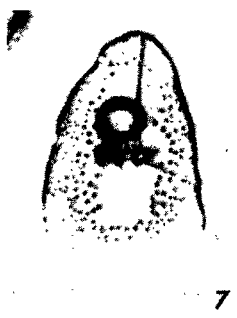
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PLATE 6

Fig. 1*a*. *Botryocyrtis scutum* (Harting), ×233, with one post-thoracic segment, DISCOVERY 5194, B-K29/1; Sedgwick Museum No. 861.1.

Fig. 1*b*. *Botryocyrtis scutum* (Harting), ×233, with two post-thoracic segments, MSN 40G*a*, C-R29/3; Sedgwick Museum No. 851.1.

Fig. 1*c*. *Botryocyrtis scutum* (Harting), approximately ×580, cephalic structure.

Fig. 2. *Lithopera bacca* Ehrenberg, ×233, MSN 39G, A-C34/2; Sedgwick Museum No. 846.2.

Fig. 3. *Anthocyrtidium ophirense* (Ehrenberg), ×233, VEMA 19–168, B-R39/3; Sedgwick Museum No. 865.1.

Fig. 4. *Anthocyrtidium zanguebaricum* (Ehrenberg), ×233, MSN 34G, B-S44/2; Sedgwick Museum No. 844.4.

Fig. 5*a*. *Cornutella profunda* Ehrenberg, ×233, MSN 34G, A-K28/1; Sedgwick Museum No. 843.1.

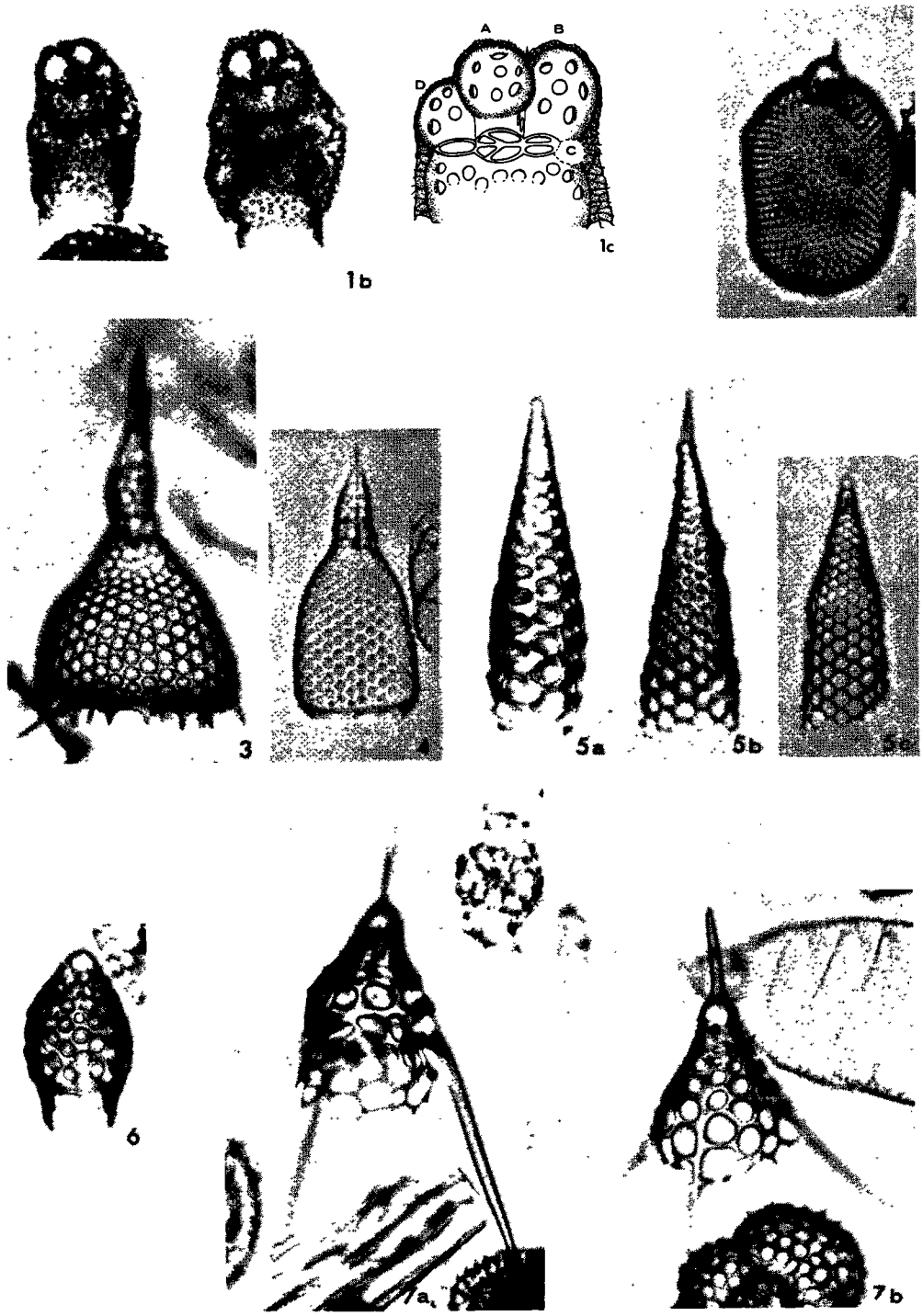
Fig. 5*b*. *Cornutella profunda* Ehrenberg, ×233, MSN 34G, B-D30/2; Sedgwick Museum No. 844.2.

Fig. 5*c*. *Cornutella profunda* Ehrenberg, ×233, MSN 34G, B-U38/0; Sedgwick Museum No. 844.6.

Fig. 6. *Dictyocryphalus papillosus* (Ehrenberg), ×233, MSN 34G, B-V44/2; Sedgwick Museum No. 844.8.

Fig. 7*a*. *Dictyophimus crisiae* Ehrenberg, ×233, MSN 39G, B-T45/1; Sedgwick Museum No. 847.5.

Fig. 7*b*. *Dictyophimus crisiae* Ehrenberg, ×233, MSN 39G, B-Q44/3; Sedgwick Museum No. 847.3.


A
B
D
C
1b
1c
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5a
5b
5c
6
7a
7b

PLATE 7

Fig. 1. *Pterocanium praetextum praetextum* (Ehrenberg), ×233, MSN 39G, B-Q46/0; Sedgwick Museum No. 847.4.

Fig. 2. *Pterocanium praetextum* (Ehrenberg) *eucolpum* Haeckel, ×233, MSN 61G, D-L41/1; Sedgwick Museum No. 855.1.

Fig. 3*a*. *Pterocanium trilobum* (Haeckel), ×233, LSDA 124G, B-S22/2; Sedgwick Museum No. 857.1.

Fig. 3*b*. *Pterocanium trilobum* (Haeckel), ×233, MSN 34G, C-V42/2; Sedgwick Museum No. 845.1.

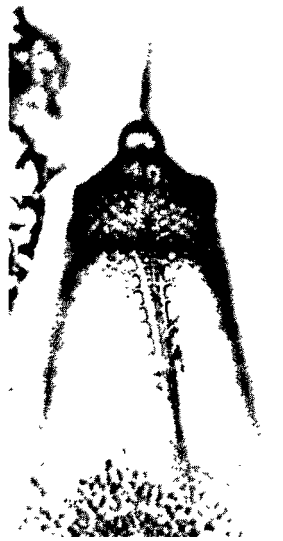
Fig. 4*a*. *Theoconus hertwigii* (Haeckel), ×233, DISCOVERY 5194, A-N25/0; Sedgwick Museum No. 860.3.

Fig. 4*b*. *Theoconus hertwigii* (Haeckel), approximately ×580, internal cephalic structure; D = dorsal spine, L = primary lateral spine, V = vertical spine.

Fig. 5. *Lamprocyclas maritalis maritalis* Haeckel, ×233, MSN 40G*a*, B-G24/3; Sedgwick Museum No. 850.2.

Fig. 6. *Lamprocyclas maritalis* Haeckel *polypora n. subsp.*, ×233, holotype, MSN 39G, A-J41/1; Sedgwick Museum No. 846.4.

Fig. 7. *Lamprocyclas*, approximately ×580, internal cephalic structure, D = dorsal spine, L = primary lateral spine, V = vertical spine.



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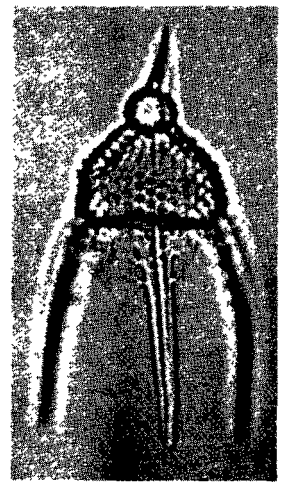

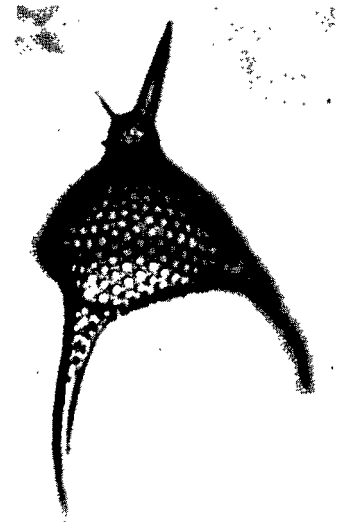

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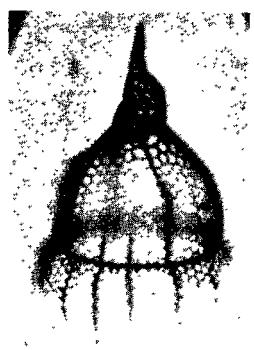

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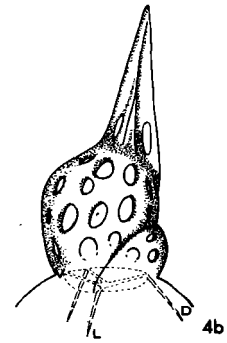

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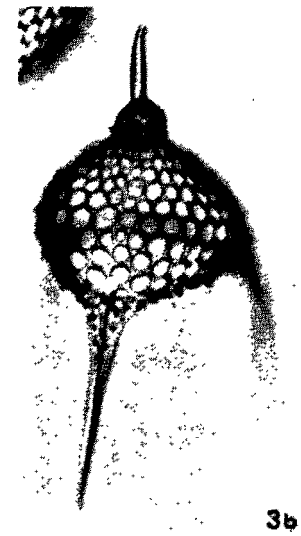

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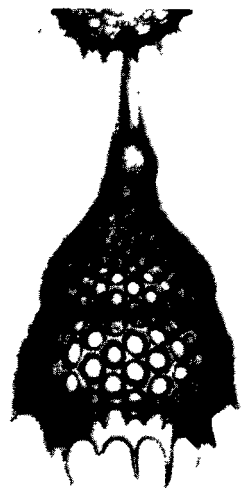

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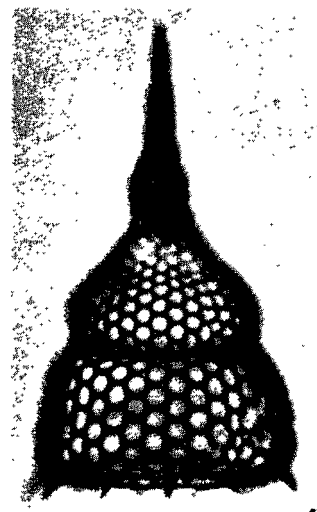

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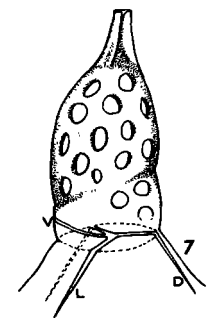


7

PLATE 8

Fig. 1*a*. *Theocorythium trachelium* (Ehrenberg) *dianae* (Haeckel), ×233, LSDA 124G, A-S32/0; Sedgwick Museum No. 856.7.

Fig. 1*b*. *Theocorythium trachelium* (Ehrenberg) *dianae* (Haeckel), ×233, MSN 61G, B-W21/2; Sedgwick Museum No. 853.2.

Fig. 2. *Theocorythium trachelium trachelium* (Ehrenberg), ×233, MSN 40G*a*, C-T26/4; Sedgwick Museum No. 851.2.

Fig. 3*a*. *Eucyrtidium acuminatum* (Ehrenberg), ×233, mouth constricted, LSDA 124G, A-K32/2; Sedgwick Museum No. 856.3.

Fig. 3*b*. *Eucyrtidium acuminatum* (Ehrenberg), ×233, mouth wide open, MSN 61G, A-S29/3; Sedgwick Museum No. 852.1.

Fig. 4*a*. *Eucyrtidium hexagonatum* Haeckel, ×233, mouth constricted, MSN 39G, A-J33/2; Sedgwick Museum No. 846.3.

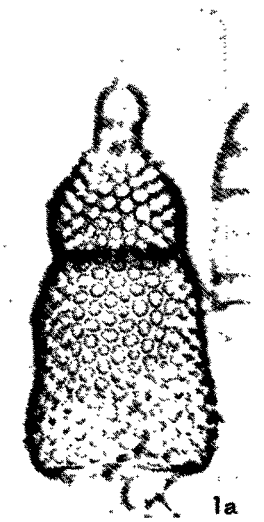
Fig. 4*b*. *Eucyrtidium hexagonatum* Haeckel, ×233, mouth wide open, MSN 34G, A-N30/3; Sedgwick Museum No. 843.2.

Fig. 5. *Siphocampe corbula* (Harting), ×233, MSN 40G*a*, B-E23/0; Sedgwick Museum No. 850.1.

Fig. 6*a*. *Lithocampe* sp., ×233, mouth constricted, LSDA 124G, A-F26/0; Sedgwick Museum No. 856.1.

Fig. 6*b*. *Lithocampe* sp., ×233, mouth wide open, MSN 61G, B-F37/1; Sedgwick Museum No. 853.1.

Fig. 7. *Spirocyrtis scalaris* Haeckel, ×233, MSN 34G, A-X28/2; Sedgwick Museum No. 843.6.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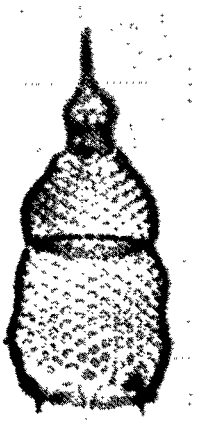
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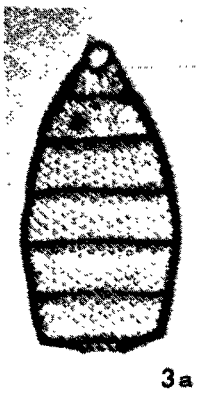
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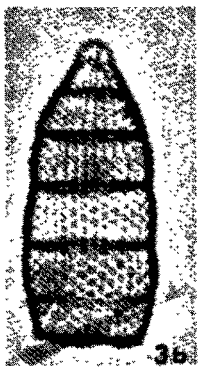
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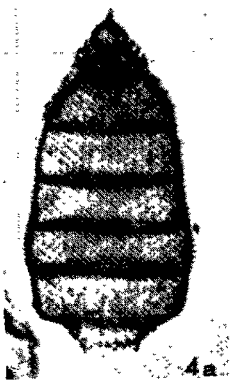
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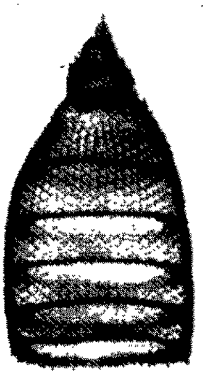
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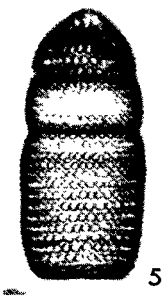
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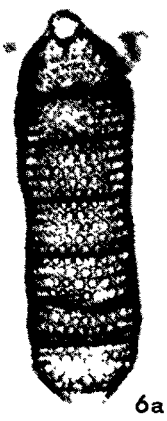
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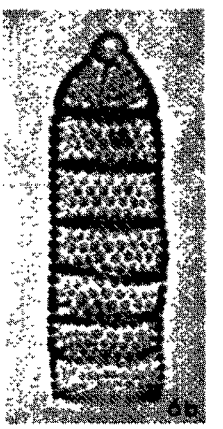
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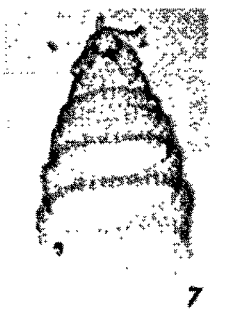
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PLATE 9

Fig. 1*a*. *Theocorythium trachelium* (Ehrenberg) *dianae* (Haeckel), approximately ×580, internal cephalic structure.

Fig. 1*b*. *Theocorythium trachelium* (Ehrenberg) *dianae* (Haeckel), approximately ×580, cephalis viewed at right angles to fig. 1*a*, from the right.

Fig. 2. *Theocorythium trachelium trachelium* (Ehrenberg), approximately ×580, internal cephalic structure.

Fig. 3. *Siphocampe corbula* (Harting), approximately ×580, internal cephalic structure and cephalic tube.

Fig. 4. *Spirocyrtis scalaris* Haeckel, approximately ×580, internal cephalic structure and cephalic tube.

Key to Symbols

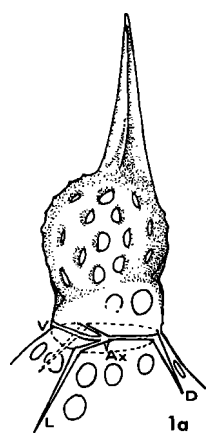
L = primary lateral spine or thoracic extension of it

l = secondary lateral spine

D = dorsal spine

V = vertical spine

Ax = axial rod



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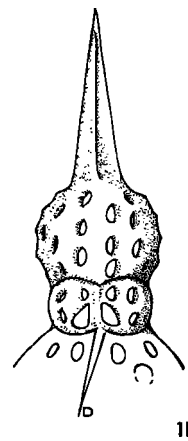

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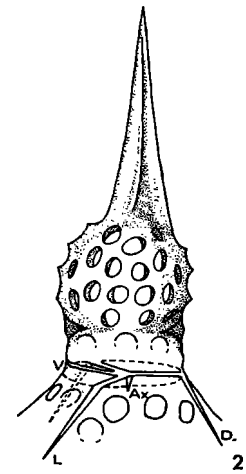

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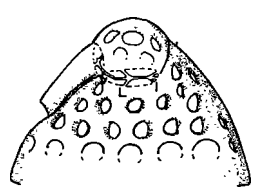

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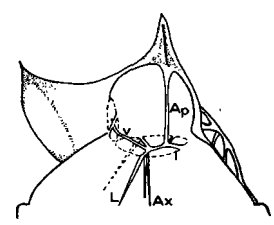

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HYDROIDS FROM THE SOUTH-WEST INDIAN OCEAN

By

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(With 6 figures in the text)

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INTRODUCTION

This paper deals with an assortment of Indian Ocean hydroids from the area east of South Africa and south of Madagascar. With the exception of a small collection from Walter's Shoal all are from depths greater than 300 m. and are thus over the edge of the Continental Shelf, the margin of which is located at 150–300 m. Thus, although some of the stations are situated less than 30 nautical miles off the coast where it shelves steeply, the fauna cannot strictly be included in that of South Africa.

The material from Walter's Shoal is a shallow-water fauna dredged from 38 to 46 m., but, since Walter's Shoal is situated over 420 nautical miles from Madagascar and over 600 nautical miles from Africa, its fauna cannot be included in that of either country.

It was felt that the material from the whole of this area might conveniently be described together.

The material comes from two sources. Those samples bearing the prefixes ABD and WSS were collected by the R/V *Anton Bruun* during her seventh cruise in the International Indian Ocean Expedition in 1964. A final cruise report of the expedition was published by the U.S. Program in Biology, I.I.O.E., in 1965, to which body I am indebted for the opportunity of examining the material.

Material bearing the prefix AFR is part of a collection in the Zoology Department, University of Cape Town, and was collected in 1961 by the government research vessel *Africana II* belonging to the Division of Sea Fisheries, Department of Commerce and Industries.

The position of the collecting stations is roughly indicated on the accompanying sketch-map (fig. 1), and the complete data given in the station list which follows.

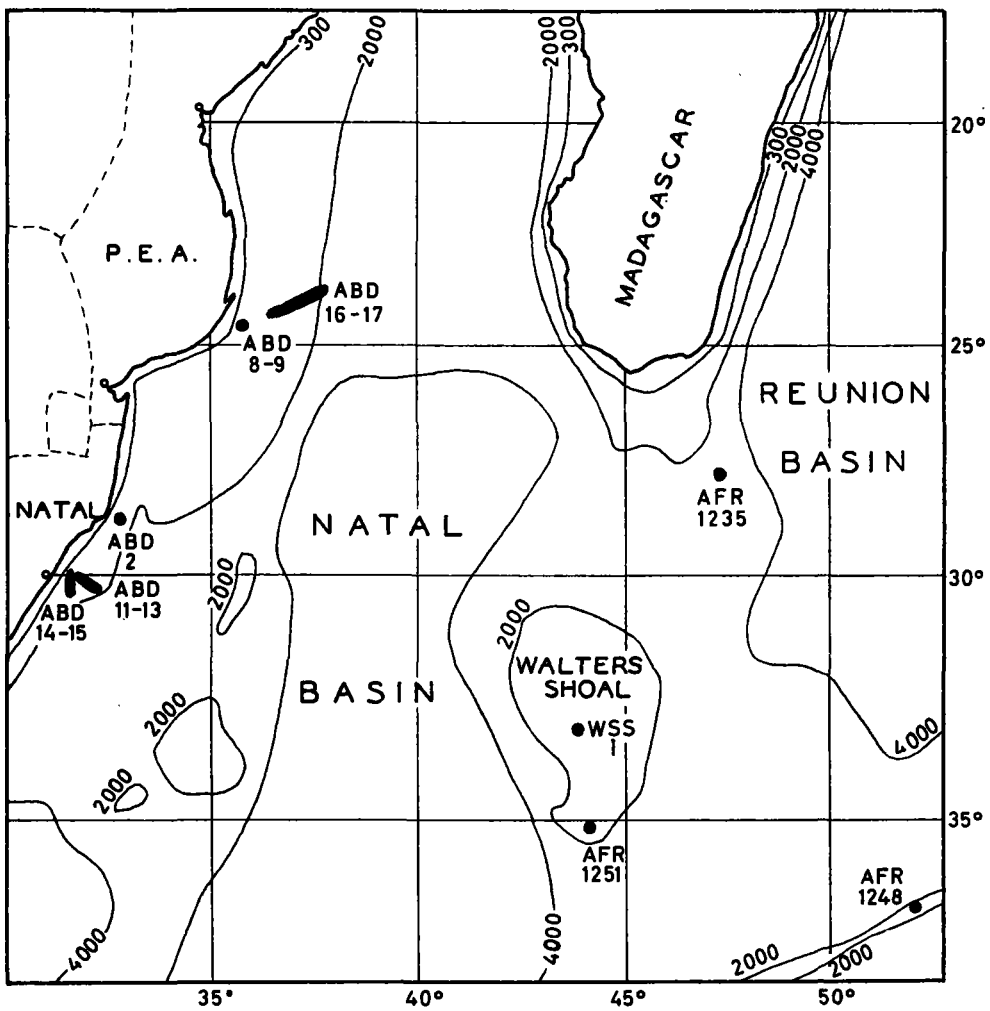

Fig. 1

Sketch-map of the area under consideration showing the approximate positions of the different collecting stations. The reference numbers are the same as those used in the station list. Depths in metres.

In the systematic section the full synonymy is not quoted in every case, but instead a number of references from which such can be obtained.

STATION LIST

U.C.T. cat. no.	Date	Position	Depth (m.)	Bottom	*Anton Bruun* stat. no.
ABD 2	31/7/64	28°43'S/32°38'E	1207	R	359C
ABD 8–9	18/8/64	24°40'S/35°28'E	347	sh. S.	370G
ABD 11	7/9/64	30°12'S/32°01'E	1360	Gl. Oz.	389C
ABD 12	7/9/64	30°09'S/31°37'E	930	s. M. Cl.	389E
ABD 13	8/9/64	29°57'S/31°31'E	700	Gl. Oz.	389G
ABD 14	8/9/64	29°45'S/31°40'E	440	h. S.	390C
ABD 15	8/9/64	29°42'S/31°38'E	350	s. M.	390E
ABD 16	17/8/64	23°48'S/37°45'E	2200	Gl. Oz.	369C
ABD 17	17/8/64	24°04'S/36°15'E	1610	Gl. Oz.	369F
WSS 1	30/8/64	33°13'S/43°51'E	38–46	Calc. Algae	381A–C
AFR 1235	22/6/61	27°48'S/47°19'E	875		
AFR 1248	9/7/61	36°48'S/52°08'E	400		
AFR 1251	11/7/61	35°03'S/44°12'E	600		

LIST OF SPECIES

Family **Campanulinidae**

Stegopoma fastigiatum (Alder)

Family **Lafoeidae**

Acryptolaria conferta australis (Ritchie)
Acryptolaria crassicaulis (Allman)
Acryptolaria rectangularis (Jarvis)
Filellum serratum (Clarke)
Lafoea fruticosa (M. Sars)
Zygophylax armata (Ritchie)

Family **Syntheciidae**

Hincksella echinocarpa (Allman)
Hincksella indiana n.sp.

Family **Sertulariidae**

Salacia ?desmoides (Torrey)
Sertularella arbuscula (Lamouroux)
Sertularella mediterranea Hartlaub
Sertularella megista Stechow
Sertularella polyzonias (Linnaeus)
Sertularella xantha Stechow
Symplectoscyphus ?amphoriferus (Allman)
Symplectoscyphus paulensis Stechow

Family **Plumulariidae**

Kirchenpaueria triangulata Totton
Nemertesia ramosa Lamouroux
Plumularia antonbruuni n.sp.
Plumularia setacea (Linnaeus)
Cladocarpus distomus Clarke
Halicornaria gracilicaulis (Jäderholm)

SYSTEMATIC ACCOUNT

Family **Campanulinidae**

Stegopoma fastigiatum (Alder, 1860)

Stegopoma fastigiata: Millard, 1958: 175.
Stegopoma fastigiatum: Ralph, 1957: 850, fig. 8 n–o. Vervoort, 1959: 234, fig. 10.

Records. ABD 9F (epizootic on *Zygophylax armata*).
Remarks. This species has already been reported from the area, from 333 m. off the coast of Natal (Millard, 1958).

Family **Lafoeidae**

Acryptolaria conferta australis (Ritchie, 1911)

Cryptolaria conferta var. *australis* Ritchie, 1911: 826, pl. 84 (fig. 2), pl. 87 (fig. 1).
Acryptolaria conferta var. *australis:* Totton, 1930: 163, fig. 19 c–e. Ralph, 1958: 315, fig. 4 a–g.
Acryptolaria conferta australis: Millard, 1964: 9, fig. 1 D, F, G.

Records. ABD 9G, 15B.
Description. One colony (ABD 9G) reaching a height of 3·7 cm. and fairly regularly branched, a branch arising next to every third hydrotheca. Hydrothecae with a rather greater proportion of their height adnate than usual (0·59 to 0·88), especially on the thicker parts of the stem and branches. Margins practically parallel to axis of stem.

The other colony (ABD 15B) a single, little-branched stem 5·3 cm. high, with hydrothecae similar to those previously described (Millard, 1964).

Acryptolaria crassicaulis (Allman, 1888)
Fig. 2A

Cryptolaria crassicaulis Allman, 1888: 41, pl. 19 (figs. 3, 3a). Ritchie, 1911: 828–830, pl. 87 (fig. 4). Stechow, 1913: 113, figs. 86, 87.
Cryptolaria crassicaulis, var. *dimorpha* Ritchie, 1911: 830, pl. 87 (figs. 5, 6). Jarvis, 1922: 335.

Records. AFR 1248A.
Description. A single fascicled stem 4·7 cm. in height, giving off a number of branches in a roughly alternate manner.

Hydrotheca adnate for about half height, with base very slightly above top of adnate part of preceding one, with diameter at margin approximately three times that at base. Margin very slightly everted.

Coppiniae absent.

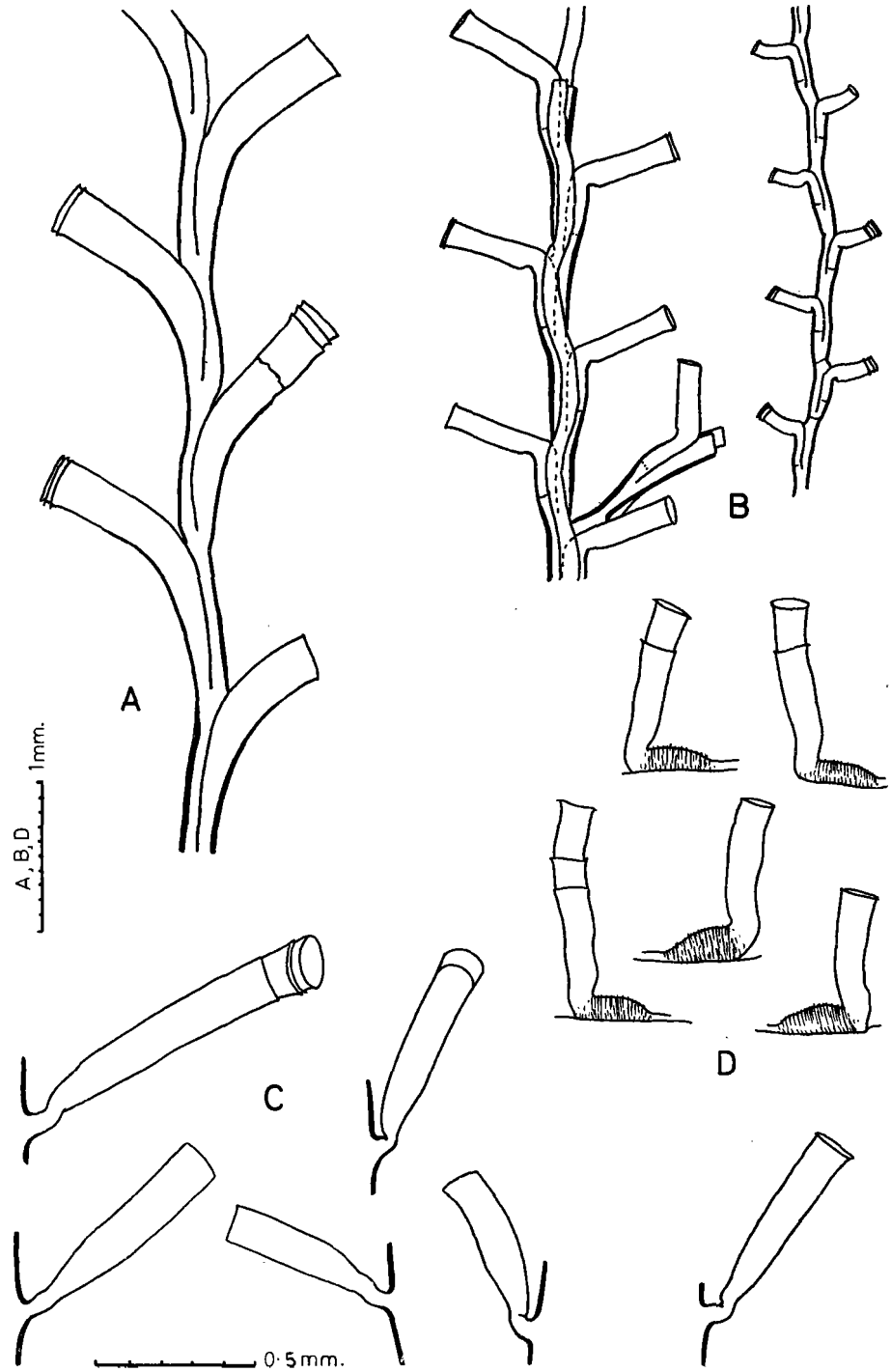

Fig. 2. Lafoeidae.

A. *Acryptolaria crassicaulis* (Allman).
B. *Acryptolaria rectangularis* (Jarvis) from ABD 15P (left) and AFR 1251D (right).
C. Various hydrothecae of *Lafoea fruticosa* (M. Sars).
D. *Filellum serratum* (Clarke) from ABD 9E.

Measurements (mm.)

Hydrotheca, length of adnate part	0·79–1·01
length of free part	0·69–1·18
adnate part/total length	0·40–0·59
diameter at base	0·09–0·13
diameter at margin	0·31–0·39
base/margin	0·29–0·38

Remarks. As the ability to produce solitary hydrothecae is a feature common to many, and possibly all, Lafoeidae, it is not necessary to retain Ritchie's variety *dimorpha.*

Acryptolaria rectangularis (Jarvis, 1922)
Fig. 2B

Cryptolaria rectangularis Jarvis, 1922: 335, pl. 24 (fig. 3).

Records. ABD 15P. AFR 1251D.

Description. Two small and probably young colonies reaching a maximum height of 1·1 cm. Stems unbranched or giving off a few irregular branches. Proximal parts of stem and branches fascicled.

Hydrotheca tubular, adnate for about ½ to ⅔ height, then free and directed sharply outwards. Free part forming an angle of 70–75° with stem, with free part of adcauline wall straight, or slightly concave and recurved towards distal end of stem, with a distinct notch on abcauline wall at point of divergence from stem. Diaphragm present or absent. Margin even and often regenerated. No nematophores.

Gonophores absent.

Measurements (mm.)

	AFR 1251D	ABD 15P
Hydrotheca, adnate part (adcauline)	0·24–0·40	0·52–0·59
free part (adcauline)	0·15–0·29	0·52–0·72
adnate part/total length	0·48–0·71	0·43–0·52
diameter at margin	0·10–0·12	0·18–0·23

Remarks. This material strongly resembles *Cryptolaria angulata* Bale, 1914, except for the absence of a 'boss' or perisarcal thickening on the adcauline wall of the hydrotheca just below the bend. It was mainly on the absence of this boss that Jarvis established the species *rectangularis.*

The two samples have hydrothecae of very different sizes, though the proportions are similar.

In the nature of the diaphragm the species is intermediate between the genera *Acryptolaria* and *Cryptolaria.* In the youngest parts of the colony the diaphragm is either completely absent or is represented by a ring of raised tubercles where the base of the hydranth is attached, but in older parts the tubercles become thickened processes which are attached to one another around the circumference by a thin chitinous shelf, thus forming a definite diaphragm.

This is not visible as a joint on the outer surface of the hydrotheca. The species has been included in the genus *Acryptolaria* mainly on the absence of nematophores.

Filellum serratum (Clarke, 1879)
Fig. 2D

Lafoëa serrata Clarke, 1879: 242, pl. 4 (fig. 25).
Reticularia serrata: Ralph, 1958: 312, fig. 2j, 3a.

Records. ABD 9E. WSS 1R.

Description. Two colonies differing in dimensions and proportions, though both with the adherent part of the hydrotheca sculptured externally by 30–40 delicate perisarcal ridges.

ABD 9E (from 347 m.) epizootic on *Nemertesia ramosa*; hydrothecae large, adnate for about $\frac{1}{3}$–$\frac{1}{2}$ length, free part bent out at right angles.

WSS 1R (from shallower water: 38–46 m.) epizootic on *Plumularia setacea*; hydrotheca small, adnate for $\frac{1}{2}$–$\frac{3}{4}$ length, free part bent out at angle of 60–70°.

Measurements (mm.)

	ABD 9E	WSS 1R
Hydrotheca, length of adnate part	0·48–0·67	0·22–0·47
length of free part (without reduplications)	0·60–1·32	0·12–0·26
adnate part/total length	0·29–0·50	0·52–0·76
diameter at margin	0·22–0·30	0·11–0·14

Remarks. Although these two samples differ greatly in dimensions, they have been included in the same species. The measurements of the smaller form agree with those given by Ralph from New Zealand.

Lafoea fruticosa (M. Sars, 1851)
Fig. 2C

Lafoea fruticosa: Stechow, 1925: 456, fig. 24B. Totton, 1930: 157, fig. 13. Naumov, 1960: 275, fig. 164. Millard, 1964: 14, fig. 3.

Records. ABD 9H.

Description. A young colony with solitary hydrothecae and unbranched stems reaching 0·8 cm. Stems weakly fascicled in basal region.

Hydrothecae long and slender, forming an angle of 40–60° with stem, with adcauline wall very slightly convex. Pedicel with double twist.

Coppinia absent.

Measurements (mm.)

Hydrotheca + pedicel, height	0·52–0·91
Hydrotheca, diameter at margin	0·11–0·17
Hydrotheca + pedicel/diameter	3·71–6·07

Remarks. In general appearance this material differs from that recorded from South Africa (Millard, 1964) in its longer and more slender hydrothecae which

show no sign of a double curvature. In most cases the total length of the hydrotheca plus pedicel is over five times the diameter at the margin. Yet on the same stem are shorter hydrothecae resembling some of those figured in 1964.

The colony strongly resembles Alder's figure of *Lafoea gracillima* (1856, pl. 14, fig. 6), except that the pedicels are not quite so long. However, from the literature I can find no satisfactory means of distinguishing *L. gracillima* from *L. fruticosa*. Totton, who figures both, is himself in doubt and Naumov has united the two species.

Zygophylax armata (Ritchie, 1907)

Brucella armata Ritchie, 1907: 533, pl. 2 (fig. 2–2c).
Zygophylax armata: Millard, 1964: 18, fig. 4G.

Records. ABD 8D, 14V.

Description. Two rather straggling, sterile colonies reaching 4·2 and 3·1 cm. in height respectively.

Family **Syntheciidae**

Hincksella echinocarpa (Allman, 1888)
Fig. 3 A–C

Sertularia echinocarpa Allman, 1888: 57, pl. 28 (figs. 1, 1a).

Records. ABD 16A, 17A.

Description. Altogether six rooted stems, of which the longest is 9·0 cm., and many incomplete stems and fragments.

Rootstock in the form of a branching system for penetration of a soft substratum; consisting of a number of fascicled 'roots' arising at the same level from the base of the stem, these subdividing a number of times and finally producing very delicate unfascicled 'rootlets'.

Stem comparatively flexuous and unable to support itself out of fluid; slightly geniculate; unsegmented; fascicled for most of its length but unfascicled in distal region; the central axial tube giving rise to alternate hydrothecae and alternate hydrocladia. Hydrocladia normally arising immediately below every third hydrotheca; long (reaching 4 cm.); flexuous; the two rows in one plane at origin, but due to flexibility producing an irregular effect; rarely rebranching. Each hydrocladium separated from stem by a distinct oblique joint and thereafter unsegmented except for an occasional transverse node immediately above a hydrotheca; bearing alternate hydrothecae.

Hydrotheca tubular, adnate for less than half adcauline height; then straight or curved very slightly outwards. Free part of adcauline wall straight or slightly convex. Margin untoothed, not everted, facing outwards and upwards, forming an angle of 30–40° with hydrocladium. Two distinct oval areas closed over by thin perisarc present in the perisarc immediately below the base of each hydrotheca.

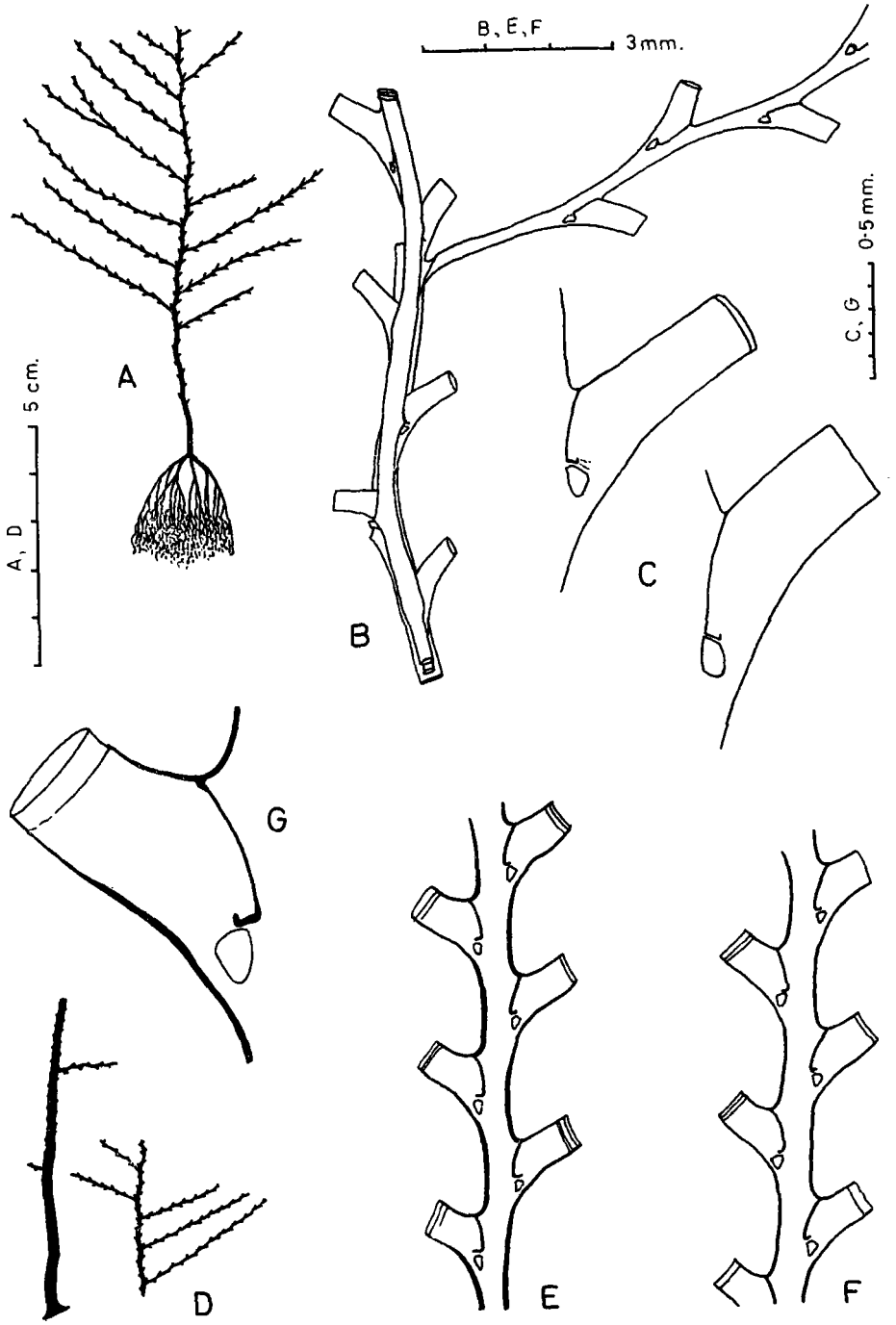

Fig. 3. *Hincksella*.

A–C. *Hincksella echinocarpa* (Allman) from ABD 16A. A, a whole stem; B, a portion of a fascicled stem showing origin of hydrocladium; C, two hydrothecae from different stems.

D–G. *Hincksella indiana*, n.sp., from the holotype. D, two portions of the stem; E and F, old and young portions of hydrocladia respectively; G, a hydrotheca.

Gonophores absent, but presumably emerging through the oval areas mentioned above.

Measurements (mm.)

Hydrotheca, length abcauline (approximate only)	0·85–1·05
length adcauline, adnate part	0·36–0·57
length adcauline, free part	0.60–0·83
adnate part/adcauline length	0·30–0·48
diameter at mouth	0·31–0·45

Remarks. This species is known only from Allman's original material from Kerguelen Island in the southern Indian Ocean. Unfortunately it was not redescribed by Billard in his revision of the British Museum hydroids in 1910. The form of the colony in the present material bears a striking resemblance to Allman's diagram though the individual dimensions are a little less. Other resemblances include the absence of regular segmentation, the shape of the hydrotheca and the presence of the oval areas below the hydrothecae. Allman did not mention nodes at the origins of the hydrocladia, nor did he describe the rootstock. Gonothecae are necessary for final confirmation of the identification.

Closely related is *H. cylindrica* (Bale, 1888), which is a smaller species with an unfascicled stem and without the characteristic oval areas. Possible synonyms of the latter are *H. alternans* (Allman, 1888) and *H. halecina* (Torrey, 1902), both of which bear gonophores from within the hydrothecae. *H. formosa* (Fewkes, 1881) is unfascicled and has hydrothecae of quite different proportions.

Hincksella indiana n. sp.

Fig. 3 D–G

Types and records. Holotype: AFR 1235A (South African Museum registered number SAMH 1646). Other records: AFR 1248C.

Description of holotype. A stiff fascicled stem in three separate portions, together reaching about 13·5 cm., and a number of separated hydrocladia. Rootstock disc-shaped and flattened below, presumably attached to a hard substratum. Stem unsegmented; strongly fascicled at base and consisting of a central hydrotheca- and hydrocladia-bearing tube covered by 8–9 peripheral tubes, the latter gradually decreasing in number towards the distal end, which is unfascicled.

Hydrocladia stiff, alternate, with the two rows in one plane (though most are detached); arising below every third hydrotheca; reaching a maximum length of 4·8 cm.; unfascicled; separated from stem by a partial or complete oblique joint and thereafter unsegmented; with only very rarely a faint oblique or transverse node (probably the result of regeneration).

Hydrothecae alternate on stem and hydrocladia, with the two rows in one plane; large; adnate for over half adcauline length; tubular, with the free part curved towards the adcauline side and with concave adcauline wall. Margin

circular and untoothed, often regenerated. Two distinct oval windows present in the perisarc below the base of each hydrotheca; these are closed by thin membrane only and not by perisarc as in *H. echinocarpa*.

Gonophores absent, but presumably emerging through the oval windows mentioned above.

Measurements (mm., without regenerations)

Hydrotheca, length abcauline (approximate only)	0·66–0·80
length adcauline, adnate part	0·60–0·73
length adcauline, free part	0·30–0·48
adnate part/adcauline length	0·56–0·70
diameter at margin	0·48–0·57

Remarks. This species has certain resemblances to *H. echinocarpa* (Allman, 1888) and *H. formosa* (Fewkes, 1881). It differs from the former in its thicker perisarc and more rigid hydrocladia, in the greater length of the adnate part of the hydrotheca and in the concave adcauline wall; from the latter it differs in the absence of segmentation and in the plane of the hydropore, which is at right angles to the stem or hydrocladial axis rather than approximately parallel to it (cp. Vervoort, 1959, fig. 29).

Family **Sertulariidae**

Salacia ?desmoides (Torrey, 1902)

Fig. 4 A–C

Sertularia desmoides: Nutting, 1904: 56, pl. 3 (figs. 1–3). Fraser, 1937: 161, pl. 37 (fig. 194).
Salacia desmoides: Billard, 1924: 66. Billard, 1925: 207.

Records. WSS 1S.

Description. A small colony of ten unbranched stems reaching a maximum height of 0·6 cm. Hydrorhiza creeping, unsegmented. Stem bearing up to nine pairs of hydrothecae, which are generally, but not always, separated by strongly oblique nodes resembling hinge-joints. Thecal pairs well spaced and always separated by a distance greater than their length. Members of a pair of hydrothecae in contact with one another on anterior surface of stem, free behind.

Hydrotheca adnate to stem for over half adcauline length, widening from base to top of adnate part, then curved outwards and narrowing again to margin. Margin facing outwards and downwards, untoothed. Orifice roughly in the shape of an inverted triangle. Operculum of one large abcauline valve.

Gonophores absent.

Measurements (mm.)

Internode length (where nodes are present)	0·55–0·75
diameter	0·06–0·08
Hydrotheca, length abcauline	0·17–0·21
length adcauline, contiguous part	0·14–0·18

length adcauline, adnate part	0·22–0·26
length adcauline, free part	0·13–0·18
adnate part/total length	0·56–0·65
diameter (vertical) at margin	0·10–0·12

Remarks. There is nothing in the published descriptions to exclude this material from being a young colony of *S. desmoides*, a species known from the Pacific coast of North America. Fraser's material, reported from a number of localities, appears to have somewhat larger dimensions. A greater variety of material and gonophores are necessary for final identification.

Sertularella arbuscula (Lamouroux, 1816)

Sertularella arbuscula: Millard, 1957: 208, fig. 10B, 11C. Millard, 1958: 188. Millard, 1964: 37.

Records. WSS 1N.

Description. A richly branched colony with a strongly fascicled stem 4·8 cm. in length. Hydrothecae closely set and smaller than is normal for the species (abcauline length 0·34–0·40 mm.), but typical in shape. Internal teeth five in number: one large abcauline, two slightly smaller latero-adcauline and two minute latero-abcauline.

Gonothecae abundant, male, smaller than normal (length, mature, 1·54–1·90 mm.), annulated in distal half.

Remarks. This material resembles the common form of *S. arbuscula*, as it is known from South Africa, in the form of the colony and shape of the hydrotheca, but differs in the smaller dimensions of the hydrotheca and gonotheca and in the annulations present on the latter. However, since annulated gonothecae are known to occur in the species (Millard, 1958 and 1964) it is not possible to differentiate the material on these grounds. The gonotheca is similar in appearance to that illustrated by Warren (1908, fig. 6B).

Sertularella mediterranea Hartlaub, 1901

Sertularella mediterranea: Millard, 1957: 215, figs. 10E, 11B.

Records. WSS 1Q.

Description. A small infertile colony reaching a maximum height of 1·6 cm.

Sertularella megista Stechow, 1923
Fig. 4D

Sertularella megista: Millard, 1957: 217, figs. 10L, 11J. Millard, 1964: 45 (synonymy).
Sertularella sp.: Millard, 1958: 192 (PF 12456E).

Records. ABD 8B.

Description. A single unfascicled, unbranched stem 9·8 cm. in height.

Hydrotheca similar to that previously described for this common species, except that the free part is much elongated and exceeds the adnate part in length. Free part of both adcauline and abcauline walls straight or nearly so.

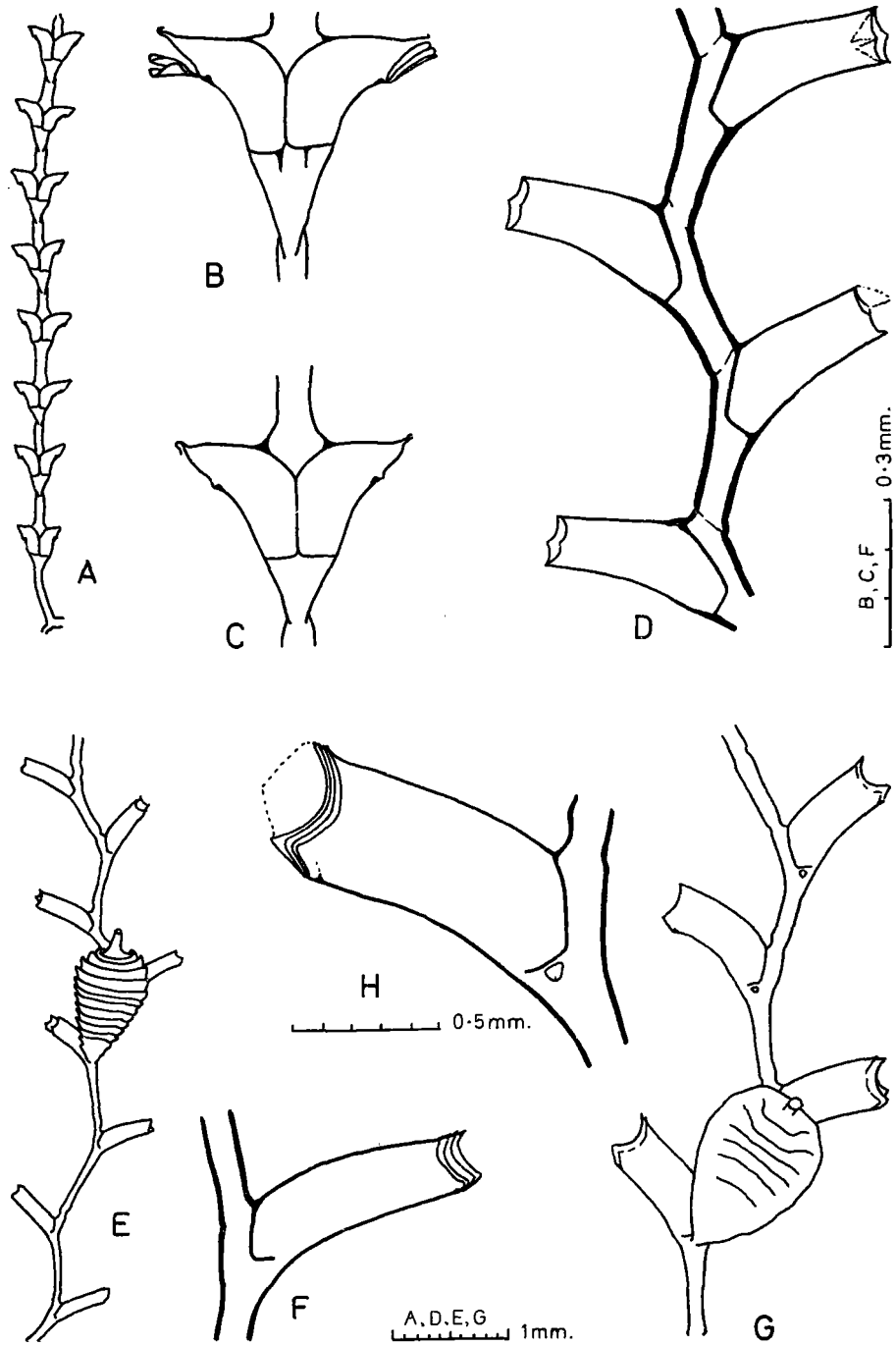

Fig. 4. Sertulariidae.

A–C. *Salacia ?desmoides* (Torrey).
D. *Sertularella megista* Stechow.
E–F. *Symplectoscyphus ?amphoriferus* (Allman).
G–H. *Symplectoscyphus paulensis* Stechow, from ABD 8C.

Measurements (mm.)

Internode length	1·21–1·61
diameter across node	0·42–0·50
Hydrotheca, length abcauline	1·39–1·58
length adcauline, adnate part	0·65–0·75
length adcauline, free part	1·03–1·28
adnate part/adcauline length	0·34–0·42
diameter at mouth	0·48–0·56

Remarks. This material cannot be considered as specifically distinct from *S. megista* since intermediate colonies have been found (chiefly from the Natal coast) with all intergradations in measurements. It should rather be regarded as a form with especially produced hydrothecae. It is similar to the material recorded as *Sertularella* sp. (Millard, 1958), which is now included as a synonym.

The specimen bears a superficial resemblance to *S. polyzonias* var. *gigantea* Hincks, 1874, reported by Stechow (1925, fig. 6) from Plettenberg Bay, which may eventually prove to be a synonym. At present *S. megista* can be readily distinguished by the marked angle in the adcauline thecal wall and the less turgid hydrothecae.

Sertularella polyzonias (Linnaeus, 1758)

Sertularella polyzonias: Millard, 1957: 217, figs. 10J, 11H. Millard, 1958: 191.

Records. WSS 1P.

Description. Colony bearing gonophores and reaching a maximum height of 1·6 cm.

Sertularella xantha Stechow, 1923

Sertularella xantha: Stechow, 1925: 472, fig. 32. Millard, 1957: 218, figs. 10K, 11I.

Records. ABD 15A.

Description. A typical, though sterile, stem 8·5 cm. in length. Rootstock branching and fibrous for penetration of a soft substratum.

Symplectoscyphus ?amphoriferus (Allman, 1877)

Fig. 4 E, F

Sertularella amphorifera Allman, 1877: 22, pl. 15 (figs. 8–10). Nutting, 1904: 88, pl. 20 (figs. 1–2). Billard, 1906: 183.

Records. AFR 1248 IIQ.

Description. A small colony of about ten unbranched and unfascicled stems reaching a maximum height of 1·1 cm. Stem distinctly geniculate in distal part, more or less straight in proximal part, with very slender internodes and indistinct nodes.

Hydrotheca deep and slender, standing well away from stem, adnate for about ¼ adcauline length, then curved gently outwards and narrowing very slightly to margin. Margin with three teeth (one adcauline and two lateral), often regenerated.

Gonotheca arising below hydrotheca, pear-shaped, tapering evenly to base, with a terminal aperture at the end of a slender neck, with 13 well-marked, crested, transverse annulations. One gonotheca present (sex not determinable) and scars of two others.

Measurements (mm., without regenerations)

Internode length	0·60–0·84
Hydrotheca, length abcauline (approximate)	0·35–0·45
length adcauline, adnate part	0·12–0·14
length adcauline, free part	0·34–0·46
adnate part/adcauline length	0·21–0·28
diameter at margin	0·12–0·15
Gonotheca, length	1·19
maximum diameter	0·65

Remarks. This material is assigned to *S. amphoriferus* mainly on the gonotheca, which Billard states may be less elongated and with a shorter neck than that figured by Allman. However, since the species is known only from the North Atlantic, there is some doubt as to the identification. There are also some minor differences in the trophosome, namely

(i) The lack of any sign of branching, though this may be a juvenile character.

(ii) A smaller proportion of the hydrotheca adnate to the stem than generally indicated.

(iii) The detailed measurements, which are all less than those given by Billard.

The shape of the hydrotheca is most like that figured by Nutting, though the internodes are longer and more slender.

The material also shows resemblances to *S. plectilis* (Hickson and Gravely, 1907) from the Antarctic, but the gonothecae are very different.

Symplectoscyphus paulensis Stechow, 1923

Fig. 4 G, H

Symplectoscyphus paulensis: Stechow, 1925: 467, fig. 28.

Records. ABD 8C, 14B. AFR 1248 IIN.

Description. Small, and probably young, colonies reaching a maximum height of 4·7 cm. Hydrorhiza creeping. Most stems unfascicled and unbranched, though two are lightly fascicled at base and several have one or two branches or stumps thereof. Branches arising below hydrothecae and forming a wide angle with stem. The two rows of hydrothecae and branches in one plane. Stem and branches markedly geniculate in younger parts, practically straight in older parts. Nodes only faintly indicated. Internodes slender.

Hydrotheca large, tubular and not narrowing towards margin, curved slightly outwards, adnate for a third or less of adcauline length. Margin sometimes with thickened rim, with three well-marked teeth, one adcauline and two lateral. Consecutive hydrothecae separated by a distance approximately equal to abcauline thecal length. Below each hydrotheca a pair of oval fenestrae

closed by thin perisarc, through which the gonophores emerge and through which the tubes of the fascicled stem communicate.

A single gonotheca present (on ABD 8C), with about five light corrugations around distal half, with a slender terminal neck which is slightly everted at margin.

Measurements (mm.)

	ABD 8C	AFR 1248 IIN
Internode length	0·96–1·48	1·16–1·36
Hydrotheca, length abcauline (approximate)	0·71–0·91	0·64–0·87
length adcauline, adnate part	0·34–0·39	0·22–0·28
length adcauline, free part	0·76–0·92	0·72–1·00
adnate part/adcauline length	0·27–0·34	0·19–0·27
diameter at margin	0·38–0·44	0·34–0·42
Gonotheca, length	1·47	
maximum diameter	1·05	

Remarks. S. paulensis has been reported only once, by Stechow from St. Paul in the southern Indian Ocean. His material was sterile.

Stechow states that the discovery of intermediate forms may prove that *S. paulensis* is a form of *S. columnarius* (Briggs, 1914). However, instead of bridging the gap, the present material emphasizes the differences between the two. *S. paulensis* differs from *S. columnarius* in the following features:

(i) The well-separated hydrothecae.

(ii) The narrower hydrothecae (diameter at margin in present material 0·34–0·44 mm., Stechow's material 0·46, *S. columnarius* (from Ralph, 1961*a*) 0·40–0·60 mm.).

(iii) The smaller proportion of the adnate part of the adcauline thecal wall (adnate part/adcauline length 0·19–0·34 in present material, 0·34–0·40 in Stechow's material, 0·43–0·5+ in *S. columnarius*).

(iv) The smaller gonotheca with less definite annulations.

This material is also very close to *S. tropica* (Hartlaub, 1900) from the Pacific.

S. paulensis differs from *S. amphoriferus* in the larger size, different appearance of the gonotheca and different shape of the hydrotheca.

Family **Plumulariidae**

Kirchenpaueria triangulata (Totton, 1930)

Plumularia triangulata Totton, 1930: 225, fig. 61. Ralph, 1961*b*: 41, fig. 5 f–g.
Kirchenpaueria triangulata: Millard, 1962: 292, fig. 6 E–J.

Records. ABD 2C, 15S.

Description. The first sample with pinnate stems without rootstock, reaching a maximum height of 1·6 cm. Male gonophores present.

The second sample epizootic on *Halicornaria gracilicaulis* and including

both simple and pinnate stems, the latter reaching a maximum height of 2·2 cm. No gonophores present.

Structural details as in previous descriptions. In the second sample (ABD 15S) stem nodes visible only in the extreme distal region and in many hydrocladia the node between the apophysis and the first thecate internode missing.

Nemertesia ramosa Lamouroux, 1816

Nemertesia ramosa: Millard, 1962: 299, fig. 7 A–D.

Records. ABD 8A, 13F, 15Q.

Description. Colonies provided with branching rootstock for penetration of a soft substratum. Stems reaching a maximum height of 21·7 cm., some with gonophores.

Plumularia antonbruuni n. sp.

Fig. 5

Holotype. ABD 14C (South African Museum registered number: SAMH 1647).

Description. Four stems, reaching a maximum height of 5·1 cm. Hydrorhiza of branching, filamentous rootlets for penetration of a soft substratum.

Stem unfascicled, unbranched, bearing alternate hydrocladia, the two rows in one plane. Segmentation not present in lower region, indistinct in upper region. Where demarcated each internode bears one hydrocladium from an apophysis at the distal end. No internodal septa. Apophysis with a distinct mamelon on upper surface. Cauline nematothecae: one on each internode, midway along its length, on opposite side to apophysis; two on each apophysis, one on each side of, and slightly proximal to, the mamelon.

Hydrocladium with one athecate internode, sometimes followed by long thecate internodes only, but often with intermediate athecate internodes present, especially towards the distal end. First internode very short, without nematotheca, with one internodal septum in central region. Thecate internode with two internodal septa, one near proximal end and one near distal end, with 0–3 median inferior nematothecae, one pair of laterals overtopping the thecal margin and sometimes one median superior. Athecate intermediate internode, when present, with two internodal septa, one proximal and one distal, and 0–2 median nematothecae. When no athecate internodes occur the hydrotheca is seated in the distal half of the thecate internode and there are generally two median inferior nematothecae. Athecate internodes, when they occur, appear to be formed by cutting off the proximal end of a thecate internode together with one or more of the median inferior nematothecae. The following thecate internode is shorter, with the hydrotheca seated more or less in the centre and and there is generally only one median inferior nematotheca. However, many variations occur.

Hydrotheca completely adnate, with more or less straight abcauline wall and distinctly convex adcauline wall. Width at margin slightly exceeding depth.

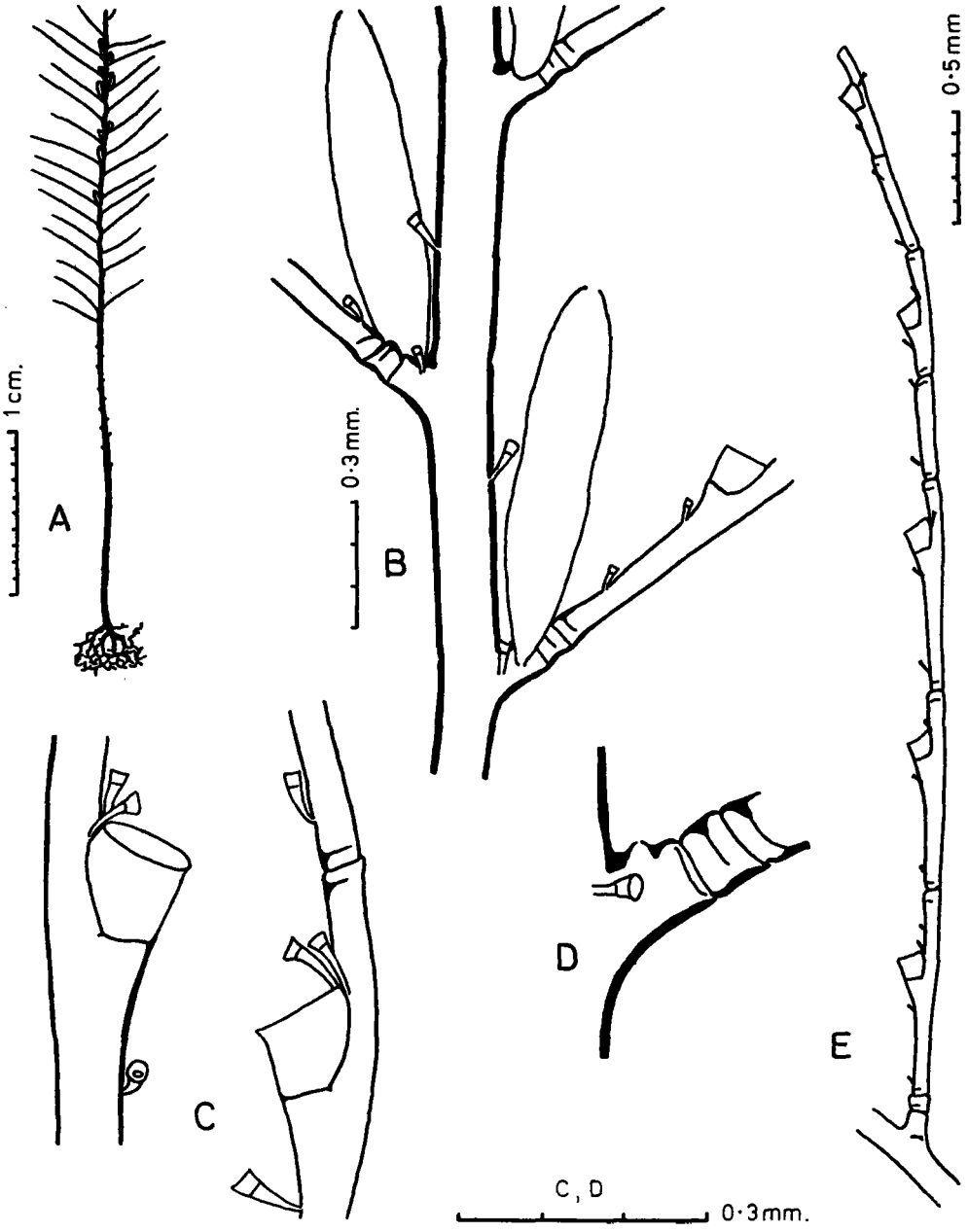

Fig. 5. *Plumularia antonbruuni* n.sp.

A. A whole stem.
B. A portion of the stem showing cauline nematothecae and gonothecae.
C. Portions of hydrocladia with hydrothecae.
D. The origin of a hydrocladium.
E. A single complete hydrocladium.

Nematothecae all two-chambered and movable, laterals slightly shorter than hydrothecae.

Gonothecae (male) borne on hydrocladial apophyses, one or two to each, smooth, elongated, with terminal aperture, held at a small angle (10–15°) to stem.

Measurements (mm.)

Stem internode, length	0·63–0·70
diameter at node	0·13–0·17
Hydrocladium, first athecate internode, length	0·06–0·11
normal thecate internode, length	0·85–0·95
diameter near centre	0·06–0·08
athecate internode, other than first, length	0·38–0·66
Hydrotheca, depth abcauline	0·08–0·10
diameter at margin	0·11–0·12
Gonotheca, length	0·82–0·92
maximum diameter	0·20–0·27
Lateral nematotheca, length	0·07–0·09

Remarks. Although I am reluctant to create a new species in a genus which is already so richly represented there is no other species with quite the same assortment of characters. *P. antonbruuni* is close to *P. diploptera* Totton, 1930, differing from it in the fact that athecate intermediate internodes are normally absent, in its much longer internodes and in the absence of a subthecal internodal septum.

It is also close to *P. ventriculiformis* Marktanner, 1890, differing from it in the presence of a short athecate internode at the base of the hydrocladium and in the presence of only one hydrocladium to a stem internode. It resembles it in the sporadic occurrence of athecate intermediate internodes in the distal parts of the hydrocladium, but in *P. ventriculiformis* these seem to be cut off from the distal ends of the internodes. The two species differ in the shape of the gonotheca.

It is closest of all to *P. orientalis* Billard, 1913, differing only in its larger size, in the usual absence of intermediate athecate internodes and in the presence of cauline nematothecae on the main axis of the stem. The hydrothecae are also a little deeper. The gonothecae of *P. orientalis* are unknown.

Closely related to *P. orientalis* are *P. delicata* Nutting, 1905, and *P. milleri* Nutting, 1905. In these the gonothecae of the former are relatively short and fat while those of the latter are held at right angles to the stem.

Plumularia setacea (Linnaeus, 1758)

Plumularia setacea: Hincks, 1868: 296, pl. 66 (fig. 1). Millard, 1962: 301.

Records. WSS 1L.

Description. A rich colony of numerous fertile stems reaching a maximum height of 6·8 cm.

Cladocarpus distomus Clarke, 1907
Fig. 6

Cladocarpus distomus Clarke, 1907: 17, pl. 14. Stechow, 1925: 506, fig. 47.
Cladocarpus sibogae: Billard, 1913: 71, fig. 57, 58, pl. 4 (fig. 39). Billard, 1918: 25.
Cladocarpella multiseptata Bale, 1915: 304, pl. 47 (figs. 1–5). Bale, 1919: 356.
?Cladocarpus bathyzonatus Ritchie, 1911: 861, pl. 89 (figs. 2, 6–11).
?Cladocarpus multiapertus: Billard, 1913: 73, fig. 59.
?Cladocarpus alatus Jarvis, 1922: 351, fig. 2, pl. 26 (fig. 25).
?Cladocarpus plumularioides Jarvis, 1922: 352, fig. 3.

Records. ABD 11A, 12F, 13E, 16B, 17B.

Description of typical form. Hydrorhiza forming a branching and filamentous rootstock penetrating up to 2·5 cm. into the bottom ooze. The first rootlets arise from the peripheral tubes of what would normally be considered stem and from here on the tubes continue to separate and subdivide until the final ramifications are only 0·15 mm. in diameter.

Stem reaching a maximum height of 9·7 cm., weakly fascicled in basal region; the principal tube always exposed on anterior surface and divided very irregularly by distinct oblique nodes, sometimes with a group of three or four of the latter close together below the level of the first hydrocladium and thereafter isolated ones at more distant, but irregular, intervals. Principal tube giving rise to alternate hydrocladia in its distal part and bearing a row of fairly regularly spaced cauline nematothecae on anterior surface. Of the latter there are 2–12 between the origins of two consecutive hydrocladia, of which one is always axillary.

Hydrocladium bearing up to 23 thecate internodes separated by oblique nodes. Internodal septa variable in number: one below level of median inferior nematotheca, 1–11 behind the hydrotheca and 0–7 above it. Each internode bearing, in addition to the hydrotheca, one median inferior nematotheca which is quite free from the hydrotheca, one pair of laterals and one to three (usually one) median superior nematothecae.

Hydrotheca deep, expanding towards margin, which is perpendicular to hydrocladium. Those hydrothecae at distal end of hydrocladium deeper than those at proximal end. A delicate shelf arising from adcauline side near base and overarching the hydropore. Margin with one median abcauline tooth.

Median nematotheca with a terminal aperture in the form of a narrow transverse slit, which may be subdivided into two parts, and a rounded opening on upper surface near base.

Lateral nematotheca applied to margin of hydrotheca and extending round it usually as far as the median tooth, though sometimes terminating before this; with numerous distal apertures, of which the first is generally raised slightly above the level of the others.

Phylactocarps arising from bases of thecate internodes, as many as six to a hydrocladium, each consisting of 3–6 internodes bearing two nematothecae each. Gonotheca borne on basal phylactocarpal internode, elongate, with a broad distal aperture.

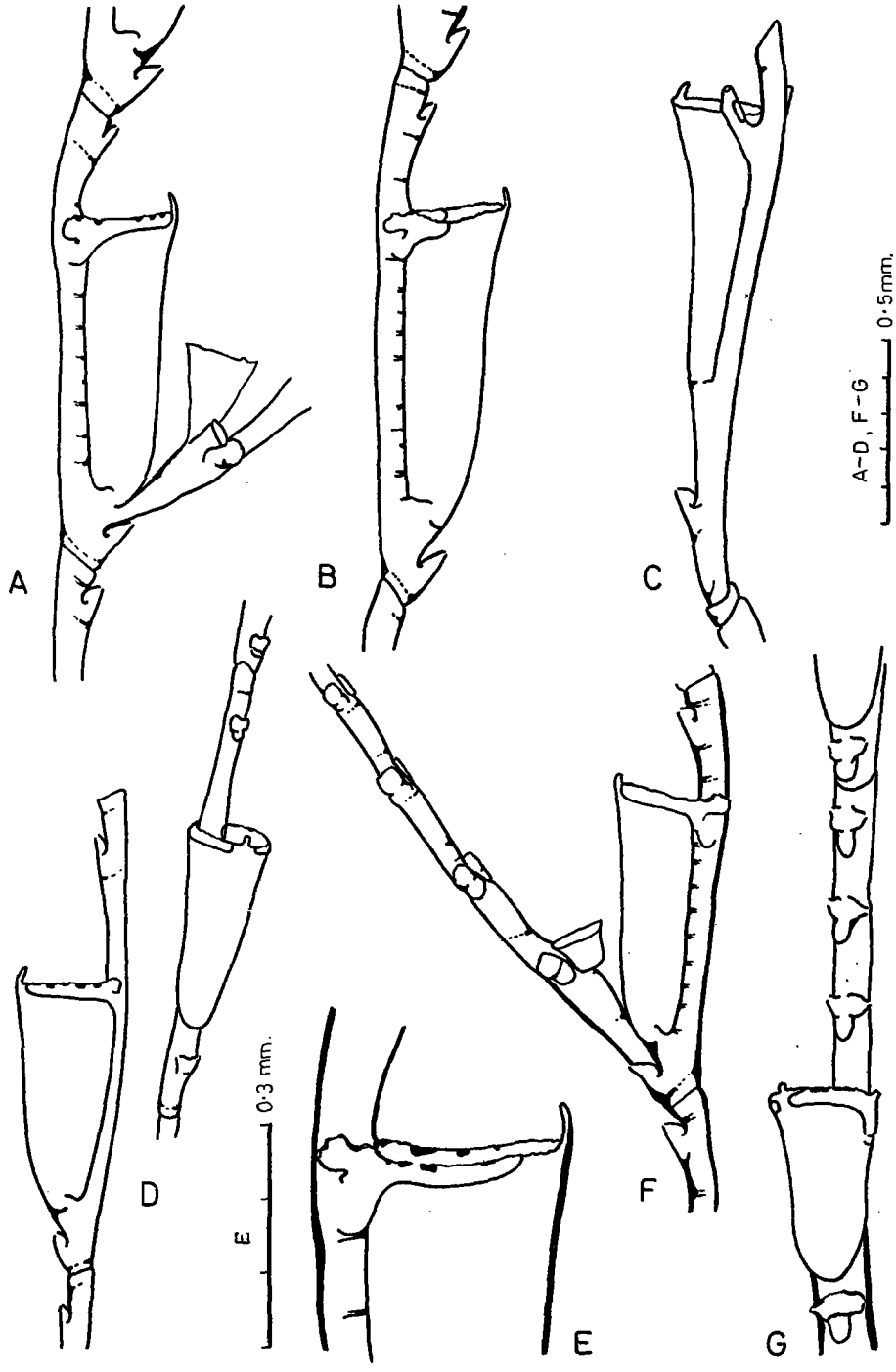

Fig. 6. *Cladocarpus distomus* Clarke.

A–D. Hydrothecae from different colonies. A and B from ABD 13E, C from ABD 16B, D from ABD 11A.
E. Part of a hydrotheca showing the lateral nematotheca from ABD 13E.
F–G. Diagrams from Stechow's slides from Valdivia stations 258 and 264 respectively.
(A and F show portions of phylactocarps)

Measurements (mm.)

	ABD 16B	ABD (rest)	Stechow's material	
			Vald. 258	Vald. 264
Distance between 2 consecutive hydrocladia	1·69–2·87	0·81–1·19		
Hydrocladium, internode length	1·55–1·60	1·14–1·52	1·11–1·38	1·08–1·17
Hydrotheca, depth including median tooth	0·83–1·01	0·51–0·92	0·53–0·83	0·65–0·79
diameter at margin	0·26	0·21–0·29	0·20–0·27	0·24–0·26
Gonotheca, height		1·40–1·50	1·08–1·12	
maximum diameter		0·32–0·36	0·34–0·38	

Remarks. One of the samples, ABD 16B, shows certain divergences from the above description. It consists of a single stem 3·5 cm. in height, with rootstock, but with only two imperfect hydrocladia remaining. The stem has no oblique joints, but a few irregular and indistinct transverse nodes in the distal region. The hydrocladial internodes are long, especially in their proximal regions, so that the median inferior nematotheca is well separated from the hydrotheca. The superior median nematotheca is missing on those hydrocladia which remain and the lateral nematothecae have only one terminal aperture each and do not extend round the lateral margin of the hydrotheca.

The remaining samples are identical with Stechow's material from East Africa described in 1925 and attributed to *C. distomus*. This was established by comparison with Stechow's slides from Valdivia stations 258 and 264 kindly loaned to me by the Munich Museum. The 'Verdoppelung des Thekenrandes' described and figured by Stechow is none other than the extension of the lateral nematotheca as in the present material. Measurements of Stechow's specimens, taken by myself, are included above for comparison.

Stechow has included two other species under the synonymy of *C. distomus*, namely *C. sibogae* Billard, 1911, and *C. multiseptatus* (Bale, 1915). Also closely related are *C. bathyzonatus* Ritchie, 1911, *C. multiapertus* Billard, 1911, *C. alatus* Jarvis, 1922 and *C. plumularioides* Jarvis, 1922. These species appear to differ in certain features such as the number of internodal septa, number of cauline nematothecae, presence or absence of superior median nematothecae, the structure of the lateral nematothecae, etc.

The number of internodal septa has been recognised as being of little systematic value and has been shown to be variable in *C. multiseptatus* by Bale in 1919, in *C. sibogae* by Billard in 1913 and in the Valdivia material by Stechow

in 1925. The number of cauline nematothecae between two consecutive hydrocladia is equally unreliable as it can vary within a single colony.

A superior median nematotheca is present in the type material of *C. distomus*, in Stechow's Valdivia material and in *C. plumularioides*, but absent in all other species. In this collection it is absent in ABD 16B but present in the other samples. In Stechow's material the number varies from one to three depending on the length of the internode. It is probable that this also is a variable character.

The nematothecae of all the species listed are similar in that they possess a circular lateral aperture and a narrow slit-like terminal aperture which has a tendency for subdivision. The latter tendency is particularly marked in the lateral nematothecae where, of the species listed above, one terminal aperture is described for *C. distomus* (type material), *C. sibogae*, *C. multiseptatus* and *C. plumularioides*, two for *C. multiapertus*, one to three in *C. bathyzonatus* and many in *C. alatus*. Stechow's Valdivia material was shown by examination to have many, as does the present material, excepting ABD 16B where there is only one. In the most extreme examples the lateral nematotheca extends right round the margin of the hydrotheca to the median abcauline tooth. Ritchie has shown that the number of terminal apertures may vary from one to three in *C. bathyzonatus*, and Jarvis has remarked on variation in the number in *C. alatus*. In the present material and in Stechow's material a similar variation occurs within a colony, so that some nematothecae are like those of *C. bathyzonatus* and some like those of *C. alatus*.

Apparently the number of terminal apertures in the median nematothecae is also variable in *C. bathyzonatus* where Ritchie describes one or two, and in *C. multiapertus* where Billard describes one, two, or three.

It is probable, therefore, that all these records should be included in one very variable species, namely *C. distomus* Clarke, occurring in deepish tropical or subtropical waters all round the globe. As such, the recorded distribution would include the Eastern Pacific, East Africa, the East Indies and Australia. The rootstock appears to be similar in those records where it is described and is adapted for obtaining a foothold in a muddy or sandy bottom.

Halicornaria gracilicaulis (Jäderholm, 1903)

Lytocarpus gracilicaulis Jäderholm, 1903: 299, pl. 14 (figs. 3–4).
Halicornaria gracilicaulis: Billard, 1907: 364, fig. 12, pl. 25 (fig. 7). Billard, 1913: 63. Millard, 1958: 219, fig. 15 I, J.

Records. ABD 15R.

Description. A single young stem, 3·9 cm. in total height. About 1·5 cm. of this represents a rootstock and apparently penetrates into mud. It consists of numerous and sometimes branching rootlets arising from the central fascicled axis at irregular levels. Stem fascicled except for the distal region, unbranched, bearing no pinnae but alternate hydrocladia with a maximum of six hydrothecae each.

Hydrocladia with internodal septa poorly developed and internodes rather long and slender.

Hydrothecae very similar to those illustrated by Billard, 1907, and differing from those previously illustrated (Millard, 1958) in their greater length.

Gonophores absent.

Discussion

The hydroid fauna of the deeper waters of the Indian Ocean is at present very poorly known. A total of 18 species is recorded here from depths of over 300 m., of which two are new: *Hincksella indiana* and *Plumularia antonbruuni*. Of the remainder, 6 are cosmopolitan (*Stegopoma fastigiatum*, *Acryptolaria conferta*, *A. crassicaulis*, *Filellum serratum*, *Lafoea fruticosa* and *Nemertesia ramosa*), 6 have affinities in the southern oceans (*Zygophylax armata*: Gough Island, South Africa; *Hincksella echinocarpa*: Kergeulen Island; *Sertularella megista*: South Africa, possibly Antarctic; *S. xantha*: South Africa; *Symplectoscyphus paulensis*: St. Paul; *Kirchenpaueria triangulata*: New Zealand, South Africa), 3 have tropical or subtropical affinities (*Acryptolaria rectangularis*: tropical East Africa; *Cladocarpus distomus*: Eastern Pacific, East Indies, North Australia, East Africa; *Halicornaria gracilicaulis*: Eastern Pacific, East Indies, Indian Ocean, Natal) and one is known only from the North Atlantic (*Symplectoscyphus amphoriferus*).

Seven species are recorded from the shallower water of Walter's Shoal, of which four are cosmopolitan (*Filellum serratum*, *Sertularella mediterranea*, *S. polyzonias* and *Plumularia setacea*), one occurs in South Africa (*Sertularella megista*), one in the southern oceans extending into the tropics (*Sertularella arbuscula*: Australia, tropical East Africa, South Africa, South Atlantic) and one is known only from the North Pacific (*Salacia desmoides*).

It is interesting that a number of species can adapt themselves to life in deeper waters by the development of a fibrous, branching rootstock suitable for penetrating and supporting the colony in the soft substratum which is normally encountered. Six species show this characteristic, namely *Hincksella echinocarpa*, *Sertularella xantha*, *Nemertesia ramosa*, *Plumularia antonbruuni*, *Cladocarpus distomus* and *Halicornaria gracilicaulis*. Some of these at least can also produce the normal flattened hydrorhiza on a hard substratum.

Summary

A total of 23 species of hydroids is recorded from the Indian Ocean in the area east of South Africa and south of Madagascar. Some of these were collected by the R/V *Anton Bruun* during the International Indian Ocean Expedition in 1964 and some by the R/V *Africana II* in 1961. Descriptions and diagrams are included for the lesser known species. Two new species are described

and illustrated, namely *Hincksella indiana* and *Plumularia antonbruuni*. The geographical distribution of the species is briefly discussed.

Acknowledgements

The Author wishes to acknowledge with thanks the loan of Stechow's slides of *Cladocarpus distomus* from the Zoologische Sammlung des bayerischen Staates, Munich. Acknowledgements are also due to the Editorial Board of the University of Cape Town and to the Council for Scientific and Industrial Research for financial aid in publication. The holotypes of the new species will be deposited in the South African Museum.

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CHARACTERISTICS OF A MARINE VIBRIO-BACTERIOPHAGE SYSTEM

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During the eighth cruise of the R/V Anton Bruun as part of the International Indian Ocean Expedition, fifteen deep bottom mud samples were obtained and subsequently screened for bacteriophages using bacteria from these muds as host. Only one of the mud samples, obtained at station 418 (05°10'S:41°40'E) from a depth of greater than 3000 meters, where the temperature is 1°C, showed plaque formation and this against bacteria isolated from the same mud.

Information on marine phage is relatively scant. In 1947 Kriss and Rukina obtained phage plaques from several water and mud samples collected in the Black Sea. Spencer (1955, 1960) obtained seven bacteriophages active on four genera of Gram negative bacteria from the North Sea and subsequently he (1963) showed them to be inactivated after exposure to a temperature of 55°C for one hour. These phages were active at temperatures of 0-20°C but frequently not at 30°C or above, Wiebe and Liston (1964) isolated, from marine mud, a bacteriophage active against a pseudomonad. The phage produced maximum lysis between 5-12°C and developed under a pressure of 90 atmospheres. Chen *et al.* (1966) reported the base-ratio and serological relationships of two marine *Cytophaga* phage. Valentine *et al.* (1966) using electron microscopy with negative staining techniques showed one of these phages to have a unique triangular tipped tail. Chaina (1965) tested 629 bacterial cultures and bacteriophages obtained from the Indian Ocean and North Sea waters and found 10 cultures sensitive to phage. Smith and Krueger (1954) reported on a *Vibrio* bacteriophage isolated from marine mud in San Francisco Bay.

MATERIALS AND METHODS. — *Medium.* — The medium (M2) contained 5 gms peptone and 0.5 gms yeast extract in a liter of artificial sea water (Aquarium Systems Inc.). Noble Agar (Difco) was added at 1.5 percent concentration for a solid medium.

Titrations. — Bacteriophages were titrated using the double agar technique of Adams (1959) and incubated at 18°C. Dilutions were made in sterile artificial sea water. Indicator bacteria were subcultured from a turbid 6°C culture and grown 4 to 6 hours at 30°C prior to use. Counts of viable bacteria were made following the standard pour plate technique using sea water as diluent.

Adsorption. — Bacteriophage and host were inoculated into M2 media simultaneously and 5 ml portions passed through a 0.22 micron filter (Millipore) at indicated times. Each filtrate was then titered for bacteriophage by the above method.

Biochemical Tests. — Characterization of the host was done using standard methods (Society of American Bacteriologists, 1957). Oxidase activity was examined by flooding colonies on M2 agar plates with a 1 percent aqueous solution of p-aminodimethylanaline oxalate (Difco) and observing the change in colony color to maroon and black. All media were made with artificial sea water. The antibacterial compound pteridine 0/129 (Shewan, Hodgekiss, and Liston, 1954) was prepared as a saturated solution in distilled water and applied to sterilized filter paper discs. Glucose metabolism was examined using the method of Hugh and Leifson (1953).

Electron Microscopy. — Phage were obtained from plates showing confluent lysis, purified by differential centrifugation, and resuspended in 1 percent ammonium acetate. These preparations titered 10^9 pfu/ml and were negatively stained using 2 percent phosphotungistic acid in a 0.2 percent sucrose solution at a pH of 7.0 (Yamamoto and Anderson, 1961).

RESULTS. — *Growth.* — The initial mud culture filtrate had a titer of 90 plaque forming units (pfu)/ml. Four tubes with 10 mls of M2 medium were inoculated with the host bacteria. Two of these were simultaneously inoculated with the phage-containing filtrate. The other two were inoculated with the phage-containing filtrate after 4 hours of bacterial growth. All cultures were incubated at 25°C. Four hours later chloroform was added to all four tubes and they were titered for phage. Only the tubes where phage was inoculated simultaneously showed plaque formation. The phage titered 3×10^2 pfu/ml.

In a typical growth experiment two flasks containing 500 ml of M2 medium were inoculated with host bacteria. Phage was added simultaneously to one of the flasks to give a final concentration of 3×10^3 pfu/ml and both were then incubated at 25°C. The results are shown in Figure 1A. Both phage and bacterial host multiplied in the flask containing phage and host; the bacteria in this flask showed the same rate of growth as in the flask without phage. Phage was subsequently added at a final concentration of 8×10^4 pfu/ml to this second flask containing only bacteria after this initial growth period. Incubation of the second flask was continued for 90 minutes, after which chloroform was added and the culture titered for phage. There were 18×10^4 pfu/ml at this time indicating no significant increase in phage under these conditions. Figure 1B shows the results of a similar experiment where growth of both phage and host was delayed for one hour after inoculation. Figure 1C and 1D show the results of a similar experiment at 18°C and 6°C. At this lowered tem-

perature it is apparent that the bacterial population declines as the phage grow.

PHAGE CHARACTERISTICS. — Figure 2 shows the typical plaques produced by this phage. Both large and small plaques occur routinely in plating experiments, similar to the plaques reported for another marine *Vibrio* (Smith and Krueger, 1954). Single plaque isolation from both large and small plaques yielded mixed plaques upon replating. Figure 3 shows the phage morphology as revealed by negative staining technique. The head is hexagonal and approximately 60 mμ in diameter. The tail is apparently too small to be resolved in these preparations.

Host Characteristics. — The host is a monotrichous polarly flagellated *Vibrio* sp. sensitive to pterdine 0/129 (Shewan, Hodgkiss, and Liston, 1954). Biochemical results are identical to *Vibrio marinopraesens*, ZoBell and Upham (1944), except that it does not hydrolyze starch (Table 1). It is not hemolytic on blood agar containing 3 percent sodium chloride. It does not grow in nutrient broth without sea water. It grows in 2 days on nutrient agar. However, subculture on nutrient agar does not decrease the time necessary for visable colony formation. It is not luminescent in M2 medium and does not digest agar.

Phage Specificity and Lysogeny. — The phage suspension was tested against 31 strains of sea water requiring Gram (—) rods including hemolytic and luminescent strains isolated from fish, water and mud in the Indian Ocean, all of which were sensitive to pteridine 0/129. No plaques were obtained using the double agar technique. Eight strains of marine *Pseudomonas* sp. showing an oxidative Hugh-Leifson glucose reaction were also not sensitive to the phage when tested in the same manner.

Host bacterial cultures grown at 6°C, 18°C, 25°C, and 30°C were individually tested for evidence of lysogeny by plating 0.5 ml of each with 0.5 ml of a susceptible indicator strain using the double agar technique of Adams (1959). No plaques were produced. The indicator strain alone did not produce plaques thus ruling out pseudolysogeny.

Temperature Effects. — The host will grow within the range of 6°C to 30°C; however, the phage will not produce plaques at 30°C. Simultaneous phage titrations at 6°C and 25°C show no difference in plaque count. A phage suspension containing 21×10^4 pfu/ml was placed in a water bath at 50°C. A titration after 15 minutes showed no plaques at a 10^2 dilution indicating inactivation at this temperature comparable with the results of other workers for marine phage (Spencer, 1963).

During early work with this system, host bacteria used as indicator strains were subcultured at 25°C and on 3 separate occasions lost their susceptibility with time to the phage. After the first such experience, incubation of all titrations was done at 18°C. The susceptibility of host bacteria to phage was tested by subculturing from a 6°C culture to a 6°C, 18°C and 30°C culture for use as indicator. The young 30°C indicator culture routinely gave the best lawn and plaque counts when incubated with phage at 18°C.

Adsorption. — Table 2 shows the results of phage adsorption to host at 6°C and 25°C. At 25°C there was no adsorption whereas at 6°C there was 98 percent adsorption within 15 minutes.

pH Inactivation. — As shown in Table 3, low temperature protects against phage inactivation caused by decreasing pH.

Host Inhibition. — The loss of phage when added to the host in logarithm phase of growth suggested

Table 1. Biochemical characteristics of phage host.

Test	Result	Test	Result
glucose		blood agar	growth no hemolysis
aerobic	acid, no gas		
anaerobic	acid, no gas	lysine decarboxylase	(−)
lactose	(−)	oxidase	(−)
xylose	(−)	catalase	(−)
arabinose	(−)	pteridine 0/129	sensitive
starch	(−)	pencillin 2 units	sensitive
nitrate reduction	(−)	erythromycin 2 mcg	sensitive
indol	(−)	chloromycetin 5 mcg	sensitive
gelatin	(+)	tetracycline 5 mcg	resistant
casein	(−)		
H_2S	(+)		

the possibility of an anti-phage agent. The filtrate passing a 0.22 μ millipore filter from a 24 hour culture was collected. Phage was added to 5 mls of this filtrate and also to 5 mls of the filtrate that had been heated to 100°C for 5 minutes. The results in Table 4 indicate a significant reduction in phage caused by the filtrate.

Table 2. Effect of temperature on phage adsorption.

Time (minutes)	Pharge titer* 6°C (Host 7 × 10^7)	25°C (Host 22 × 10^7)
0	1 × 10^4	9 × 10^3
10	———	8 × 10^3
15	2 × 10^2	———
20	———	14 × 10^3
30	2 × 10^2	9 × 10^3
60	3 × 10^3	9 × 10^3
120	15 × 10^3	11 × 10^3

*pfu/ml

Purification of Phage. — Six liters of host and phage were grown at 25°C for 9½ hours. Chloroform was added and after centrifugation at 3000 RPM the supernatant yielded a titer of 10^7 pfu/ml. After treatment with saturated ammonium sulfate and clarification 30 mls was obtained that titered approximately 10^{10} pfu/ml. Desalting wih Sephadex 25 and high speed centrifugation yielded 1 ml that titred 9.4×10^{11} pfu/ml.

Table 3. Effect of temperature on pH inactivation of phage.

6°C pH	6°C titer*	25°C pH	25°C titer
7.2	8 × 10^7	7.5	3 × 10^7
4.4	5 × 10^7	4.9	5 × 10^7
3.2	3 × 10^6	3.8	3 × 10^5
2.5	1 × 10^2	3.2	1 × 10^2

*pf/ml

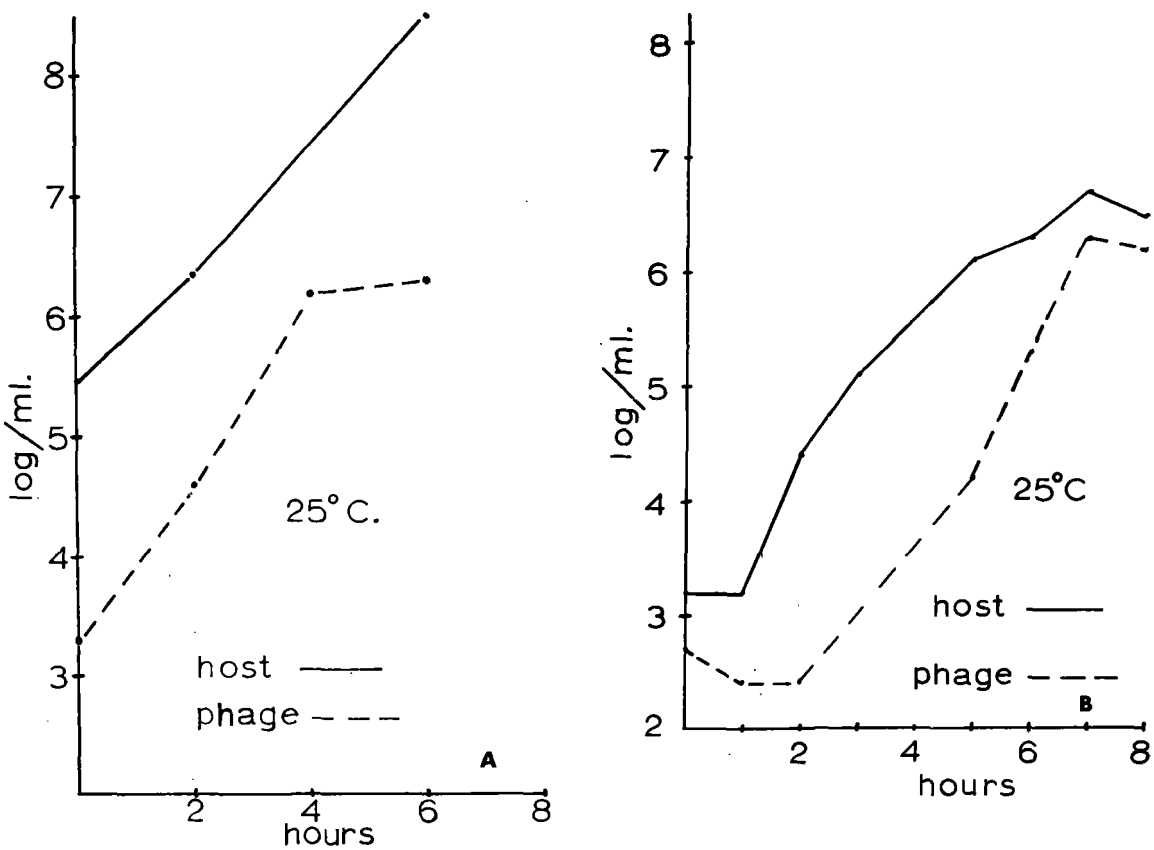


Figure 1.—Growth curves of phage and host at 25°C (A,B) 18°C (C) and 6°C (D).

DISCUSSION. — Of all reported marine phage, only two (Smith and Krueger, 1954; Spencer, 1955) have been grown and purified to the extent necessary for electron microscopic observation. Unlike the *Vibrio* phage previously reported, this phage does not adsorb at 30°C nor was any evidence of lysogeny found. Smith and Krueger (1954) apparently obtained phage titers of 10^{10} pfu/ml without difficulty and reported the phage to have typical phage morphology when examined by electron microscopy. Our phage gives a maximum crude lysate titer of 10^7 pfu/ml.

The phage isolated in this work differs from typical phage in several significant characteristics. (1) It reproduces "symbiotically" with the host over the logarithmic phase of host growth and only during this period. (2) It routinely produces plaques of two sizes. (3) Adsorption of the phage occurs readily at 6°C but is variable with time at 25°C. The second characteristic was also reported for the *Vibrio* phage isolated by Smith and Krueger (1954).

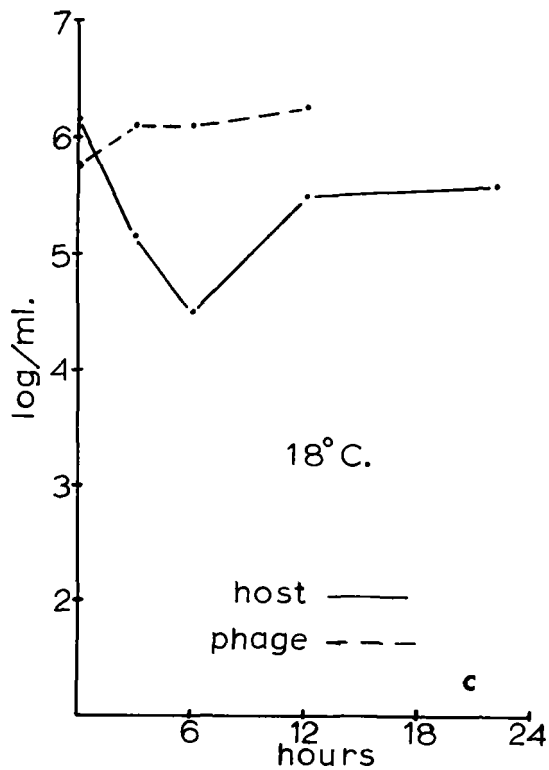
Table 4. Effect of bacterial filtrate on phage.

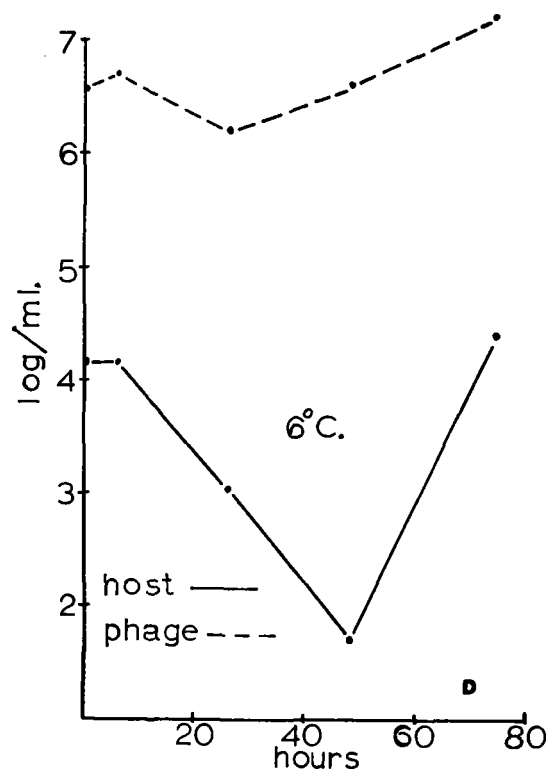
Time (minutes)	Phage titer	
	Filtrate tube	Heated control
0	1.8×10^6	1.8×10^6
5	2×10^4	4.6×10^5
20	6×10^4	9.8×10^5
40	$< 10^4$	5.8×10^5
60	$< 10^4$	10×10^5

The combination of enhanced adsorption, lysis of host cells, and resistance to low pH inactivation at lower temperatures suggest a low optimum functional temperature commensurate with its source of isolation.

The apparent uniqueness of this phage can perhaps be interpreted in terms of its host. *Vibrio* sp. are reported to have 2 or more morphological stages and Hallock (1959) has related this in one case to growth conditions. The relationship however of these stages is by no means clear. The host *Vibrio* sp. in this study occurs primarly in the rod form however coccoid elements have been observed and seem to show a higher incidence at 30°C than at lower temperatures. Preliminary attempts to separate these stages or to correlate them with phage activity have been unsuccessful to date.

The "symbiotic" growth of the phage may be the preferential growth of the phage on one form of the host while another form is resistant. This resistant form apparently predominates in 25°C cultures accounting for variable or delayed adsorption of the





phage (Fig. 1A, 1B). It further causes the continual increase in turbidity and combined with the anti-phage factor produced effectively reduces viable phage.

At 30°C the cells are all resistant to the phage and hence no plaques are found. However a 30°C culture becomes sensitive when subcultured and grown at 18°C. At 6°C the susceptible form predominates but growth of it is retarded at the low temperature. At 18°C there is a mixture of both forms with the susceptibles being in adequate numbers for routine work.

The anti-phage agent produced in old cultures of the host as well as the varied susceptability of host stages may account for the relative lack of isolation of *Vibrio* phages by previous workers.

The bactera host phage system has been deposited with the American Type Culture Collection, Rockville, Md. (Host: ATCC 19648; Phage: 19648-B).

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The collection cruise of the R/V Anton Bruun was supported by the National Science Foundation.

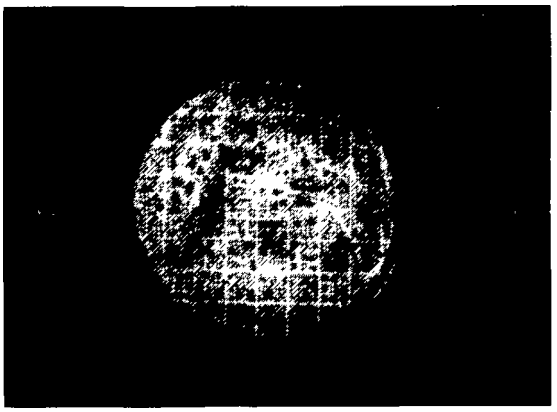

Figure 2.—Plaque size variability characteristic of the phage.

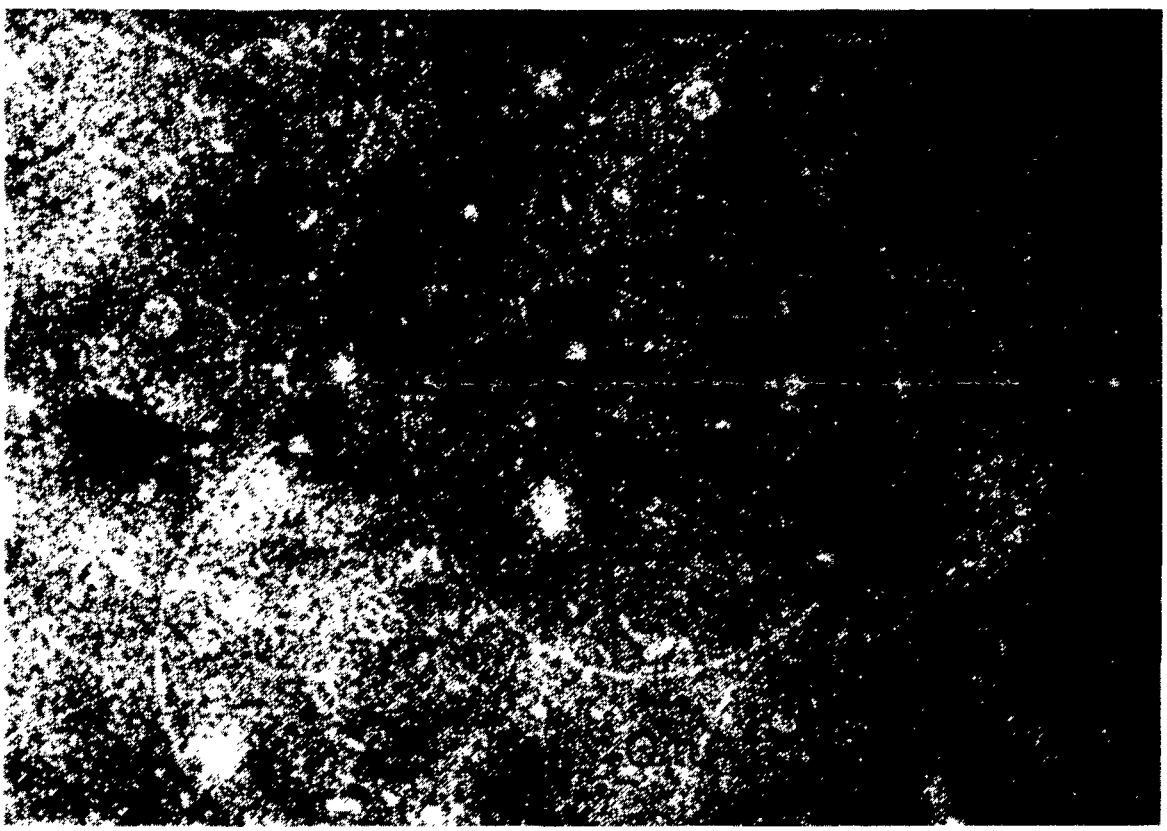

Figure 3.—Morphology of *Vibrio* bacteriophage.

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LICHOMOLGID COPEPODS (CYCLOPOIDA) ASSOCIATED WITH CORALS IN MADAGASCAR

ARTHUR G. HUMES[1,2] AND JU-SHEY HO[1]

INTRODUCTION

Seven species of lichomolgid copepods are known to be associated with madreporarian corals in the region of Nosy Bé, Madagascar. These are *Lichomolgus actinophorus*, *Lichomolgus compositus*, and *Monomolgus unihastatus*, all described by Humes and Frost (1964); *Kombia angulata* Humes, 1962 (see below for a discussion of its familial position); and *Monomolgus psammocorae*, *Rhynchomolgus corallophilus*, and *Lichomolgus rhadinus*, all described by Humes and Ho (1967a). This paper deals with seven new species of *Lichomolgus* and three new lichomolgid genera, each with a single new species, collected from corals at Nosy Bé in 1960 and 1963–64.

All collections were made by A. G. Humes, those in 1960 during an expedition sponsored by the Academy of Natural Sciences of Philadelphia, and those in 1963–64 as part of the U.S. Program in Biology of the International Indian Ocean Expedition. Type material has been deposited in the United States National Museum. Other specimens of certain species have been placed in the Museum of Comparative Zoology.

The study of the specimens has been aided by grants (GB-1809 and GB-5838) from the National Science Foundation of the United States.

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

The measurement of the length of the body has been made in all cases from specimens in lactic acid and does not include the setae on the caudal rami. In the spine and setal formulas of legs 1–4 the Roman numerals indicate spines and the Arabic numerals represent setae. The lengths of the segments of the first antenna have been measured along their posterior non-setiferous margins.

The abbreviations used are: A_1= first antenna, A_2 = second antenna, MD = mandible, P = paragnath, MX_1 = first maxilla, MX_2 = second maxilla, MXPD = maxilliped, and P_1 = leg 1.

We are greatly indebted to Dr. Donald F. Squires of the United States National Museum for the identification of the corals collected in 1960, and to Dr. Michel Pichon, then at the Centre d'Océanographie et des Pêches at Nosy Bé, for the determinations of those collected in 1963–64.

The new copepods described in this paper comprise the following:

1) *Lichomolgus campulus* n. sp. from *Alveopora* sp.
2) *Lichomolgus digitatus* n. sp. from *Goniopora* sp.

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3) *Lichomolgus prolixipes* n. sp. from *Porites* sp. cf. *P. andrewsi* Vaughan, *Porites* sp. cf. *P. nigrescens* Dana, and *Porites* (s. g. *Synaraea*) sp.
4) *Lichomolgus arcuatipes* n. sp. from *Acropora palifera* (Lamarck)
5) *Lichomolgus lobophorus* n. sp. from *Acropora scherzeriana* Brueggemann, *Acropora* sp., and *Acropora cytherea* Dana
6) *Lichomolgus geminus* n. sp. from *Stylophora pistillata* (Esper), *Stylophora mordax* (Dana), and *Acropora* sp.
7) *Lichomolgus crassus* n. sp. from *Stylophora pistillata* (Esper), *Stylophora mordax* (Dana), and *Acropora* sp.
8) *Prionomolgus lanceolatus* n. gen., n. sp. from *Pachyseris speciosa* (Dana)
9) *Haplomolgus montiporae* n. gen., n. sp. from *Montipora sinensis* Bernard, *Montipora* sp., and *Montipora* sp. cf. *M. stellata* Bernard
10) *Ravahina tumida* n. gen., n. sp. from *Porites* sp. cf. *P. andrewsi* Vaughan

The following represent new host records:

1) *Lichomolgus actinophorus* Humes and Frost, 1964, from *Pavona danai* (M. Edwards and Haime), *Pavona* ? *venusta* (Dana), and *Pavona danai* or *P. angularis* (Klunzinger)
2) *Lichomolgus compositus* Humes and Frost, 1964, from *Seriatopora octoptera* Ehrenberg and *Seriatopora* sp.
3) *Monomolgus unihastatus* Humes and Frost, 1964, from *Porites* sp. cf. *P. nigrescens* Dana
4) *Kombia angulata* Humes, 1962, from *Porites* (s. g. *Synaraea*) sp., *Porites* (young colony), and *Porites* sp. cf. *P. nigrescens* Dana

SYSTEMATIC DESCRIPTION

LICHOMOLGIDAE Kossmann, 1877
LICHOMOLGUS Thorell, 1860

Lichomolgus campulus n. sp.
Figs. 1–24

Type material.—31 females, 32 males, and 2 copepodids from *Alveopora* sp. in a depth of 3.5 m, Nosy N'Tangam, on the western side of Nosy Bé, Madagascar. Collected October 23, 1964. Holotype female, allotype, and 50 paratypes (25 females and 25 males) deposited in the United States National Museum, Washington; the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Fig. 1) moderately slender. Length 1.21 mm (1.15–1.26 mm) and greatest width 0.45 mm (0.43–0.47 mm), based on 10 specimens. Ratio of length to width of prosome 1.63:1. Epimeral areas of metasomal segments formed as in figure.

Segment of leg 5 (Fig. 2) 65 × 200 μ. Between this segment and genital segment a short weak ventral intersegmental sclerite. Genital segment broadened anteriorly and narrowed posteriorly, with slight lateral indentations, wider than long, its greatest dimensions being 180 × 224 μ. Areas of attachment of egg sacs located dorsally, each area (Fig. 3) with two small setae 6 and 10 μ long with a spinelike process between them. Three postgenital segments 86 × 107, 70 × 92, and 78 × 83 μ from anterior to posterior. Anal segment with a row of minute spinules along its posteroventral margin on each side.

Caudal ramus (Fig. 4) elongated, 105 × 33 μ, about 3.2 times longer than wide. Outer lateral seta 64 μ, outermost terminal seta 45 μ, innermost terminal seta 62 μ. Two long median terminal setae 260 μ (inner) and 150 μ (outer). Dorsal pedicellate seta 58 μ. All setae naked. Dorsal surface of ramus with a few minute hairs.

Dorsal surface of prosome and urosome with a few minute hairs as in Figure 1;

ventral surface of urosome almost entirely lacking ornamentation. Ratio of length of prosome to that of urosome 1.59:1.

Egg sac unknown.

Rostral area (Fig. 5) poorly developed, without a definite posteroventral margin.

First antenna (Fig. 6) slender, 370 μ long, and 7-segmented, with a sclerite on third segment suggesting an intercalary segment. Lengths of segments: 33 (78 μ along anterior margin), 133, 32, 43, 39, 28, and 19 μ, respectively. Formula for armature: 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in many other species of *Lichomolgus*. All setae naked.

Second antenna (Fig. 7) slender and 4-segmented. Penultimate segment 60 μ along outer edge, last segment 39 μ along outer edge and 20 μ along inner edge. Armature: 1, 1, 3, I. All setae small and naked; terminal claw 41 μ along its axis and rather sinuous.

Labrum (Fig. 8) with two posteroventral lobes.

Mandible (Fig. 9) with proximal region separated into two parts by a constriction. Region beyond constriction having on its convex side a row of small spinules and a prominent elongated posteriorly directed process; on its concave side two lobes each with a row of larger spinules. Flagellum elongated with lateral spinules. Paragnath (Fig. 10) a small lobe with a few hairs. First maxilla (Fig. 11) with three terminal elements, two of them broad and hyaline. Second maxilla (Fig. 12) 2-segmented. First segment large and unornamented. Second segment small, having proximally on its outer (ventral) margin a minute setule only 1.5 μ long followed by a naked seta and on its inner (dorsal) margin a barbed seta; terminal lash with a row of prominent spinules. Maxilliped (Fig. 13) moderately slender and 3-segmented; first segment unarmed, second with two very unequal inner naked setae, and third with a naked seta and a barbed seta, and terminating in a spiniform process with lateral spinules which bears a small setiform element on its outer surface.

Area between maxillipeds and first pair of legs (Fig. 5) not protuberant; a sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 14, 15, 16, and 17) with trimerous rami, except for endopod of leg 4 which is 2-segmented. Armature as follows:

P_1	protopod 0–1; 1–0	exp I–0; I–1; III, I, 4 end 0–1; 0–1; I, 5
P_2	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 3
P_3	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 2
P_4	protopod 0–1; 1–0	exp I–0; I–1; II, I, 5 end 0–1; II

Inner seta on coxa of leg 4 somewhat smaller than in legs 1–3, with shorter lateral hairs. Hairs on inner margin of basis present in legs 1–3 but absent in leg 4. Endopod of leg 4 (Fig. 17) with hairs along outer margins of both segments. First segment 22 × 23 μ, its plumose inner seta 39 μ long. Second segment somewhat bottle-shaped, 35 × 20 μ in greatest dimensions, with two terminal unequal barbed spines 13 μ (outer) and 36 μ (inner) in length.

Leg 5 (Fig. 18) with an elongated free segment, 34 × 13 μ, without a basal expansion. Two terminal naked setae, outer 33 μ, inner 36 μ long. Seta on body near free segment 44 μ and naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 3).

Color in life in transmitted light slightly opaque, eye red.

Male.—Body (Fig. 19) moderately slender as in female. Length 1.11 mm (1.04–1.17 mm) and greatest width 0.39 mm (0.38–0.40 mm), based on 10 specimens. Ratio of length to width of prosome 1.40:1.

Segment of leg 5 (Fig. 20) 36 × 169 μ ventrally, 52 × 169 μ dorsally. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment rather quadrate in dorsal view, 208 × 242 μ, wider than long. Four postgenital seg-

ments 43 × 84, 46 × 80, 39 × 70, and 66 × 73 μ from anterior to posterior.

Caudal ramus resembling that of female, though smaller, 90 × 28 μ.

Dorsal and ventral surfaces of body ornamented with a few minute hairs as in female. Ratio of length of prosome to that of urosome 1.20:1.

Rostral area like that of female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4 (their positions indicated by small arrows in Figure 6), so that formula is 4, 13 + 2 aesthetes, 6, 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All aesthetes a little longer than in female. Second antenna (Fig. 21) resembling that of female, but inner surface of second segment with short spinelike bosses; third segment with a few similar bosses and with three elements, two hyaline and obtuse, the other setiform.

Labrum, mandible, paragnath, first maxilla, and second maxilla resembling those in female. Maxilliped (Fig. 22) slender and 4-segmented, assuming that the proximal part of the claw represents a fourth segment. First segment unarmed, second with two setae and two rows of spinules on inner surface, third small and unarmed. Claw only slightly recurved, 151 μ along its axis (including terminal lamella), with faint indication of division midway; proximally with two unequal naked setae, distal half of longer one hyaline and blunt.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 as in female.

Leg 5 (Fig. 23) with a short free segment, 15 × 9 μ, its terminal setae being 24 and 33 μ in length.

Leg 6 (Fig. 24) consisting of a posteroventral flap on genital segment, bearing two small naked setae about 20 μ long.

Spermatophore not observed.

Color in life in transmitted light similar to female.

Etymology.—The specific name *campulus*, from καμπύλος = bent, refers to the sinuous nature of the claw on the second antenna.

Comparison with related species.—The presence of a prominent elongated process on the basal part of the mandible distinguishes this species from most other species of *Lichomolgus*. Only six other species (among the seventy or more described in the genus) have a process which is at all comparable. *L. actinophorus* Humes and Frost, 1964, has an elongated posteriorly directed process on the mandible, but this process is more pointed and dentiform than in the new species. Furthermore, *L. actinophorus* has a setiferous spherical process on the second maxilla, distinguishing it from *L. campulus*. *L. decorus* Humes and Frost, 1964, has an anteriorly directed toothlike process on the mandible and the formula for the last segment of the exopod of leg 4 is III, I, 5. In *L. organicus* Humes and Ho, 1967b, and *L. conjunctus* Humes and Ho, 1967b, there is a posteriorly directed toothlike process on the mandible, the caudal ramus is not more than 1.5 times longer than wide, and there are two claws on the second antenna. *L. protulae* Stock, 1959, has an anteriorly directed tooth on the mandible, greatly elongated caudal rami, and several claws on the second antenna. *L. rhadinus* Humes and Ho, 1967a, has a process on the mandible rather similar to that in *L. campulus*, but the two species may readily be distinguished. The female of *L. rhadinus* has an inner basal expansion on the elongated (about 5:1) free segment of leg 5 and the genital segment is rather abruptly indented posteriorly on both sides in dorsal view. The male of *L. rhadinus* has a much shorter caudal ramus (28 × 18 μ), its leg 1 shows sexual dimorphism (the last segment being I, I, 4 instead of I, 5 as in the female), and the genital segment is longer than wide. In spite of these clear differences, *L. campulus* seems to be more closely related to *L. rhadinus* than to any other species.

There are eight species of *Lichomolgus*

in which the form of the mandible, being unknown, can not be compared with that of the new species. (Thompson and A. Scott, 1903, did not describe the mandible of their *Lichomolgus gigas*, but stated, p. 280, that the "mouth organs . . . nearly resemble *L. simplex*.") All eight, however, possess characters which distinguish them from *L. campulus*. Thus, *L. dentipes* Thompson and A. Scott, 1903, and *L. rigidus* (Ummerkutty, 1962) have the formula for the last segment of the exopod of leg 4 as III, I, 5; *L. gigas* Thompson and A. Scott, 1903, is much larger (female 2 mm, male 1.4 mm); *L. longipes* (Sewell, 1949), *L. rotundus* Sewell, 1949, *L. tenuicornis* Brady, 1910, and *L. vagans* Gurney, 1927, have two claws on the last segment of the second antenna; and *L. elegans* Thompson and A. Scott, 1903, has the caudal ramus about as broad as long.

Lichomologus digitatus n. sp.

Figs. 25–52

Type material.—9 females, 4 males, and 2 immature specimens from *Goniopora* sp. in a depth of 2 m, west of Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected April 10, 1964. Holotype female, allotype, and 9 paratypes (7 females and 2 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Female.—Body (Fig. 25) with prosome moderately broadened. Length 1.89 mm (1.73–2.00 mm) and greatest width 0.70 mm (0.66–0.73 mm), based on 9 specimens. Ratio of length to width of prosome 1.49:1. Epimeral areas of metasomal segments as in figure.

Segment of leg 5 (Fig. 26) 83 × 255 μ. Between this segment and genital segment a weak ventral intersegmental sclerite. Genital segment broadened anteriorly and tapered posteriorly, wider than long, 253 × 290 μ in greatest dimensions. Areas of attachment of egg sacs located dorsally, each area (Fig. 27) with two small setae (7 and 10 μ long) and a small spinelike process. Three postgenital segments 82 × 122, 55 × 107, and 101 × 104 μ from anterior to posterior. Spinules on posteroventral margin of anal segment very few in number and minute.

Caudal ramus (Fig. 28) elongated, 220 × 36 μ, about 6.1 times longer than wide. Setae relatively short and naked. Outer lateral seta 33 μ, outermost terminal seta 28 μ, innermost terminal seta 33 μ. Two long median terminal setae 172 μ (inner) and 133 μ (outer). Dorsal pedicellate seta very short, 14 μ. Dorsal surface of ramus with refractile points. A minute spinule 5 μ long on proximal outer margin of ramus.

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with scattered refractile points and small hairs as in Figure 25. Ratio of length of prosome to that of urosome 1.37:1.

Egg sac unknown.

Rostral area (Fig. 29) weakly developed.

First antenna (Fig. 30) slender, 390 μ long, segmented and armed as in the previous species. Lengths of segments: 40 (68 μ along anterior margin), 120, 28, 55, 57, 39, and 24 μ respectively. All setae naked.

Second antenna (Fig. 31) 4-segmented, with two proximal segments stouter than in *L. campulus*. Penultimate segment 66 μ along outer edge, last segment 44 μ along outer edge and 31 μ along inner edge. A sclerotized bar running diagonally across outer surface of last segment. Armature: 1, 1, 3, I + 3 minute setules. All setae small and naked; terminal claw 29 μ along its axis and not recurved.

Labrum (Fig. 32) with two posteroventral lobes.

Mandible (Fig. 33) more massive than in *L. campulus*, with a less prominent constriction in proximal region. On convex side a short row of spinules (apparently not always present) and two unequal digitiform hyaline processes, followed by a long row of spinules. Concave margin beyond constriction with two prominent lobes armed with spinules. Flagellum

elongated with lateral spinules. Paragnath (Fig. 34) a small lobe with hairs. First maxilla (Fig. 35) with four lamellate elements and a patch of minute spinules. Second maxilla (Fig. 36) 2-segmented, first segment large and unornamented. Second segment with a small setuliform process on its proximal outer (ventral) margin, a lamellate seta on its anterior surface, and a seta with a striated membranous lamella on its inner (dorsal) margin; terminal lash with a row of spinules. Maxilliped (Fig. 37) stout and 3-segmented; first segment unarmed; second with two naked inner setae and an outer patch of spinules; and third with a slender seta, a spine, and a terminal spiniform process, all naked.

Area between maxillipeds and first pair of legs (Fig. 38) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 39, 40, 41, and 42) segmented as in the previous species, with same spine and setal formula. Leg 4 with inner seta on coxa naked and 31 μ long; hairs present on inner margin of basis. Endopod of leg 4 with hairs along inner margins of both segments. First segment 34 × 30 μ, its plumose inner seta 73 μ long. Second segment 70 × 28 μ in greatest dimensions, with its two terminal unequal fringed spines 37 μ (outer) and 74 μ (inner) in length.

Leg 5 (Fig. 43) with a moderately elongated free segment, 36 × 17 μ in greatest dimensions, without a basal expansion. Two unequal naked terminal setae 20 and 39 μ. Seta on body near free segment 36 μ. All setae naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 27).

Color in life in transmitted light translucid, eye dark red.

Male.—Body (Fig. 44) with prosome moderately broadened as in female. Length 1.55 mm (1.48–1.62 mm) and greatest width 0.54 mm (0.52–0.59 mm), based on 4 specimens. Ratio of length to width of prosome 1.38:1.

Segment of leg 5 (Fig. 45) 52 × 177 μ ventrally, 60 × 177 μ dorsally. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment subquadrate in dorsal view, 275 × 290 μ, a little wider than long. Four postgenital segments 52 × 91, 55 × 90, 39 × 83, and 79 × 83 μ from anterior to posterior.

Caudal ramus resembling that of female, but shorter, 166 × 39 μ, about 4.3 times longer than wide.

Dorsal and ventral surfaces of body ornamented with scattered refractile points and small hairs (Fig. 44) as in female. Ratio of length of prosome to that of urosome 1.06:1.

Rostral area as in female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4, so that formula is same as for male of *L. campulus*. Second antenna (Fig. 46) resembling that of female, but inner surface of second segment with sclerotized spinelike knobs.

Labrum, mandible, paragnath, first maxilla, and second maxilla like those in female. (Mandibles in single male dissected lacking short row of spinules near digitiform processes.) Maxilliped (Fig. 47) slender and 4-segmented, assuming that the proximal part of the claw represents a fourth segment. First segment unarmed, second with two barbed setae and a row of spinules on inner surface, third small and unarmed. Claw recurved, 270 μ along its axis (including terminal lamella), with slight evidence of division midway; proximally with two very unequal setae, the longer one bent and having fine lateral spinules in its distal half.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 as in female, except for sexual dimorphism on last segment of endopod of leg 1 (Fig. 48), where formula is I, I, 4, instead of I, 5 as in female.

Leg 5 (Fig. 49) with free segment more slender than in female, 31 × 9 μ, its two terminal naked setae 27 and 40 μ in length.

Leg 6 (Fig. 50) a posteroventral flap on

genital segment, bearing two small naked setae about 23 μ long.

Spermatophore not observed.

Color in life as in female.

Etymology.—The specific name *digitatus*, from Latin = having fingers, alludes to the small fingerlike processes on the mandible.

Notes on copepods from Porites, closely resembling L. digitatus.—Six females and five males which differ slightly from *L. digitatus* in the proportions of certain parts were recovered from a piece of a massive colony of *Porites* sp. in 1 m, at Ampora, Nosy Bé, October 22, 1964.

One female measures 1.94 × 0.72 mm. The genital segment is slightly larger, 275 × 352 μ. The caudal ramus (Fig. 51) is relatively a little longer, 286 × 42 μ, or 6.8 times longer than wide. The endopod of leg 4 (Fig. 52) is longer, the first segment 50 × 34 μ with its inner seta 110 μ, the second segment 92 × 25 μ with its two terminal spines 44 and 94 μ. The free segment of leg 5 is a little longer, 46 × 19 μ.

One male measures 1.76 × 0.60 mm. The genital segment is larger and slightly wider, 341 × 400 μ. The caudal ramus is relatively longer, 247 × 39 μ, or 6.33 times longer than wide. The claw on the maxilliped is relatively longer, 335 μ. The second segment of the endopod of leg 4 is 88 × 28 μ. The free segment of leg 5 is 44 × 14 μ.

In other respects, such as details of the armature and ornamentation, these copepods from *Porites* are identical with *L. digitatus*. The differences mentioned above, concerning chiefly proportions and based on very few specimens, probably should not be considered at present to be of specific or even subspecific rank. Perhaps the future study of a large series of these copepods from both *Porites* and *Goniopora* would clarify the significance of such proportional differences.

Comparison with related species.—There are fifteen species already described in the genus *Lichomolgus* which have the combination of one claw (often with other small elements) on the second antenna and the formula II, I, 5 on the last segment of the exopod of leg 4, thus resembling the new species. These are: *L. actinophorus* Humes and Frost, 1964, *L. anomalus* A. Scott, 1909, *L. arcanus* Humes and Cressey, 1958, *L. asaphidis* Humes, 1959, *L. campulus*, *L. chamarum* Humes, in press, *L. compositus* Humes and Frost, 1964, *L. elongatus* Buchholz, 1869, *L. gigas* Thompson and A. Scott, 1903, *L. inflatus* Tanaka, 1961, *L. politus* Humes and Ho, 1967*d*, *L. rhadinus* Humes and Ho, 1967a, *L. simulans* Humes and Ho, 1967*d*, *L. spondyli* Yamaguti, 1936, and *L. trochi* Canu, 1899. In only one of these, *L. gigas*, does the mandible resemble that of *L. digitatus* in apparently having two small digitiform processes on the convex side. (Although Thompson and A. Scott did not describe the mouthparts of *L. gigas* in detail, they stated, p. 280, that they nearly resemble those of *L. simplex*, in which the mandible has two "small corner filaments," illustrated on their pl. XV, fig. 30). However, the shape of the genital segment in the female, the relative size of leg 5 in the female, and the relative sizes of segments 3 and 4 of the second antenna (the fourth much longer than the third) distinguish this Ceylonese species from *L. digitatus*.

L. elegans Thompson and A. Scott, 1903, of which only the female is known, has only one claw on the second antenna, but the formula for the last segment of the exopod of leg 4 is unknown. However, this species may be easily distinguished from the new species by its very short caudal ramus, which is about as broad as long, and by the notched genital segment.

Lichomolgus prolixipes n. sp.
Figs. 53–78

Type material.—4 females and 3 males from *Porites* sp. cf. *P. andrewsi* Vaughan in a depth of 3 m, Pte. de Tafondro, Nosy Bé, Madagascar. Collected September 28, 1960. (This is the same colony of coral from which the types of *Monomolgus unihastatus* Humes and Frost, 1964, were col-

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lected.) Holotype female, allotype, and 2 paratypes (one female and one male) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens.—From *Porites* sp. cf. *P. andrewsi*: 4 females in 0.5 m, at the point north of the village of Madirokely, Nosy Bé, October 24, 1960. From *Porites* sp. cf. *P. nigrescens* Dana: 2 females in 1 m, Pte. de Tafondro, Nosy Bé, September 19, 1963. From *Porites* (s. g. *Synaraea*) sp.: 3 females in 1 m, Pte. Lokobe, Nosy Bé, November 20, 1963; 4 females and 2 males in 1–2 m, Ankify, on the mainland of Madagascar, near Nosy Bé, December 30, 1963.

Female.—Body (Fig. 53) with rather slender prosome, cephalosome somewhat pointed anteriorly. Length 1.11 mm (1.05–1.15 mm) and greatest width 0.47 mm (0.46–0.47 mm), based on 4 specimens. Ratio of length to width of prosome 1.41:1. Epimeral areas of metasomal segments as in figure.

Segment of leg 5 (Fig. 54) 58 × 156 μ. Between this segment and genital segment a very weakly developed ventral intersegmental sclerite. Genital segment 177 μ in length, broadened in its anterior two-thirds (156 μ wide) but constricted in its posterior third (88 μ wide). Areas of attachment of egg sacs situated dorsally, each area (Fig. 55) with two small setae (anterior seta held erect and not measured, posterior seta 17 μ in length) and a small spinous process. Three postgenital segments 49 × 75, 43 × 72, and 69 × 72 μ from anterior to posterior. A row of minute spinules on posteroventral margin of anal segment.

Caudal ramus (Fig. 57) moderately elongated, 77 × 29 μ, 2.65 times longer than wide. Setae longer than in preceding species and naked except for the two long setae. Outer lateral seta 85 μ, outermost terminal seta 117 μ, innermost terminal seta 112 μ. Two long median terminal setae 390 μ (inner) and 275 μ (outer), with their edges in midregion roughened to suggest presence of extremely short lateral barbules, but these not clearly visible under oil immersion. Dorsal pedicellate seta relatively short, 50 μ. Dorsal surface of ramus with a few small hairs. No spinule seen on proximal outer margin of ramus.

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with few scattered hairs and refractile points as in Figures 53 and 54. Ratio of length of prosome to that of urosome 1.57:1.

Egg sac (Fig. 57) relatively small, 385 × 220 μ in lateral view, containing about nine eggs, each approximately 112 μ in diameter.

Rostral area (Fig. 58) weakly developed.

First antenna (Fig. 59) slender, 341 μ long, segmented and armed as in previous two species. Lengths of segments: 28 (50 μ along anterior margin), 113, 28, 62, 40, 30, and 18 μ, respectively. All setae naked.

Second antenna (Fig. 60) 4-segmented, more slender than in *L. digitatus*. Penultimate segment 40 μ along outer edge, last segment 37 μ along outer edge and 21 μ along inner edge. Armature: 1, 1, 3, I. Setae small and naked. Apparently no setules near base of terminal claw, which is recurved and 42 μ along its axis.

Labrum (Fig. 61) with two posteroventral lobes of somewhat irregular outline and with hyaline medial margins.

Mandible (Fig. 62) resembling that of *L. digitatus*, with two similar digitiform processes on convex edge, but without spinules near the processes and with flagellum a little shorter. Paragnath (Fig. 63) a small lobe with hairs. First maxilla (Fig. 64) with three terminal elements and a lateral fringe. Second maxilla (Fig. 65) resembling that of *L. digitatus*, but second segment with process on proximal outer (ventral) margin broad and hyaline and seta on inner (dorsal) margin with hyaline lamellae. Maxilliped (Fig. 66) 3-segmented; first segment unarmed; second with two very unequal naked setae and lacking outer patch of spinules seen in previous species; third with two unequal naked setae and

a short terminal finely barbed spiniform process.

Area between maxillipeds and first pair of legs (Fig. 58) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 67, 68, 69, and 70) segmented as in previous two species, with same spine and setal formula. Leg 4 with inner seta on coxa minute and naked, 5 μ long; hairs present on inner margin of basis. Endopod of leg 4 with hairs along outer margins of both segments. First segment 26 × 20 μ in greatest dimensions, its plumose inner seta relatively short, 30 μ. Second segment 44 × 18 μ, with its two terminal fringed spines 31 μ (outer) and 41 μ (inner) in length.

Leg 5 (Fig. 71) with slightly recurved free segment greatly elongated, 203 × 30 μ, or 6.76 times longer than wide, reaching a little beyond posterior end of genital segment. Very small spinules along outer surface. Two naked terminal setae 80 μ (outer) and 100 μ (inner) in length; seta on body near free segment 65 μ long (a row of minute spinules near insertion of this seta).

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 55).

Color in life in transmitted light translucid to opaque, eye red.

Male.—Body (Fig. 72) with prosome more slender than in female, cephalosome more rounded anteriorly. Length 0.82 mm (0.80–0.85 mm) and greatest width 0 30 mm (0.28–0.31 mm), based on 3 specimens. Ratio of length to width of prosome 1.65:1.

Segment of leg 5 (Fig. 73) 39 × 90 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment longer than wide, 165 × 138 μ. Four postgenital segments 24 × 56, 26 × 53, 19 × 51, and 33 × 53 μ from anterior to posterior.

Caudal ramus resembling that of female, but shorter, 46 × 23 μ, or 2 times longer than wide.

Dorsal and ventral surfaces of body ornamented as in female with a few hairs and refractile points (Figs. 72 and 73). Ratio of length of prosome to that of urosome 1.43:1.

Rostral area as in female.

First antenna segmented and armed as in female, but two long aesthetes added on segment 2 and one on segment 4 (see Figure 72), so that formula is same as for males of previous two species. Second antenna (Fig. 74) resembling that of female, but having small spinelike knobs along inner surface of second segment.

Labrum, mandible, paragnath, first maxilla, and second maxilla similar to those in female. Maxilliped (Fig. 75) slender, segmented and armed as in *L. digitatus*; spinules on inner surface of second segment longer than in that species, and claw 172 μ along its axis.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 as in female, except for leg 1 which shows sexual dimorphism in last segment of endopod; formula here being I, I, 4 (Fig. 76), instead of I, 5 as in female.

Leg 5 (Fig. 77) with free segment much shorter than in female, 35 × 10 μ, its two terminal setae 60 μ (outer) and 68 μ (inner), and seta on body adjacent to free segment 58 μ. All setae naked as in female.

Leg 6 (Fig. 78) a posteroventral flap on genital segment, bearing two small naked setae 41 μ and 28 μ in length.

Spermatophore not seen.

Color in life as in female.

Etymology.—The specific name *prolixipes*, from Latin *prolixus* = long, and *pes* = foot, refers to the unusually long fifth legs in the female.

Comparison with related species.—*L. prolixipes* and *L. digitatus* show several features in common which indicate their close relationship. In both, the mandible has similar digitiform processes, the second antenna has a single claw, the formula for the last segment of the exopod of leg 4 is II, I, 5, and there is similar sexual dimor-

phism in the last segment of the endopod of leg 1 (female I, 5, male I, I, 4).

The new species may be readily distinguished from *L. digitatus*, however, by its smaller size, its shorter caudal rami, the shape of the genital segment, and the form of leg 5.

The distinctions made above in comparing *L. digitatus* with other species of *Lichomolgus* (which have the combination of one claw on the second antenna and the formula II, I, 5 on the last segment of the exopod of leg 4) apply also to *L. prolixipes*.

Lichomolgus arcuatipes n. sp.
Figs. 79–104

Type material.—137 females, 111 males, and 13 immature specimens from *Acropora palifera* (Lamarck) in a depth of 2 m, Tany Kely, a small island to the south of Nosy Bé, Madagascar. Collected August 22, 1963. Holotype female, allotype, and 90 paratypes (50 females and 40 males) deposited in the United States National Museum, the same number of paratypes in the Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Acropora palifera*).—84 females, 32 males, and 9 immature specimens in 2 m, Tany Kely, October 3, 1963; 61 females, 39 males, and 1 immature specimen in 0.5 m, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, June 21, 1963.

Female.—Body (Fig. 79) with rather broadened prosome. Length 1.06 mm (1.01–1.11 mm) and greatest width 0.40 mm (0.38–0.41 mm), based on 10 specimens. Ratio of length to width of prosome 1.34:1. Epimeral areas of metasomal segments as in figure.

Segment of leg 5 (Fig. 80) 57 × 208 μ. Between this segment and genital segment no clearly defined ventral intersegmental sclerite. Genital segment subquadrate, 133 × 159 μ, a little wider than long, in dorsal view broadest in its anterior fourth and tapering slightly posteriorly. Areas of attachment of egg sacs located dorsally, each area (Fig. 81) with two small setae about 6 μ long. Three postgenital segments 75 × 89, 66 × 58, and 62 × 48 μ from anterior to posterior. A row of minute spinules along posteroventral border of anal segment.

Caudal ramus (Fig. 82) elongated, 130 × 18 μ, 7.2 times longer than wide. Certain setae with lateral spinules as in figure. Outer lateral seta 60 μ, outermost terminal seta 64 μ, innermost terminal seta 86 μ. Two long median terminal setae 180 μ (inner) and 117 μ (outer). Dorsal pedicellate seta 75 μ. Dorsal surface of ramus with a few small hairs, ventral surface with sclerotized knobs. No spinule seen on proximal outer margin of ramus.

Dorsal surfaces of prosome and urosome with scattered hairs and refractile points, ventral surface of urosome with refractile knobs (as on this surface of caudal ramus). Ratio of length of prosome to that of urosome 1.30:1.

Egg sac (Fig. 79) small, globular, 198 × 187 μ in dorsal view, containing usually 3 eggs (sometimes only 2) flattened against each other.

Rostral area (Fig. 83) not well developed, with refractile knobs.

First antenna (Fig. 84) slender, 278 μ long, segmented and armed as in previous three species. Lengths of segments: 21 (44 μ along anterior edge), 83, 23, 50, 39, 22, and 17 μ, respectively. All setae naked. A group of surficial sclerotizations on proximal dorsal surface of second segment.

Second antenna (Fig. 85). 3-segmented, last two segments being fused, with only a slight break in sclerotization of outer wall indicating bipartite nature. Armature: 1, 1, 2 + I. Last segment (fusion of original segments 3 and 4) with two minute spiniform projections, perhaps representing remnants of two of the three setae often present here in *Lichomolgus*. Terminal claw straight, about 20 μ long, apparently lacking an actual articulation with segment, no small elements near base of claw. With

scalelike knobs on antero-outer surface of second segment.

Labrum (Fig. 86) similar in general form to that of the previous species.

Mandible (Fig. 87) resembling that of *L. digitatus*, but distal convex margin produced, forming two lobes, proximal one with four slender digitiform processes, distal one broadly triangular. Paragnath (Fig. 88) a small lobe with hairs. First maxilla (Fig. 89) with three terminal elements. Second maxilla (Fig. 90) resembling that of the previous species, but element on proximal outer (ventral) margin a slender setule. Maxilliped (Fig. 91) slender, 3-segmented; first segment unarmed; second with two very unequal naked setae; third with two small naked elements and a short barbed terminal spiniform process.

Area between maxillipeds and first pair of legs (Fig. 92) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 93, 94, 95, and 96) segmented as in previous three species, with same spine and setal formula. Outer spines of exopods with either smooth or serrate lamellae, those of leg 1 as in Figure 93, those of legs 2 and 3 as in Figure 94, and those of leg 4 as in Figure 95. Leg 4 with inner coxal seta short, 16 μ, with a few lateral hairs proximally; hairs present on inner margin of basis. Endopod of leg 4 with hairs along outer margins of both segments and along inner distal margin of second segment. First segment 29×22 μ, with plumose inner seta 40 μ. Second segment 58×20 μ (greatest dimensions) with its two terminal fringed spines 39 μ (outer) and 47 μ (inner) in length.

Leg 5 (Fig. 97) with free segment elongated and strongly arched, with its tip extending dorsally over genital segment (as in Figure 80); dimensions about 117×24 μ, with inner surface slightly concave and outer surface convex and ornamented with short broad spinules. Two terminal naked setae 28 μ (outer) and 87 μ (inner). Naked seta on body near free segment 83 μ. A row of spinules on body near insertion of free segment.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 81).

Color in life in transmitted light translucid to opaque, eye red, egg sacs gray.

Male.—Body (Fig. 98) with rather broadened prosome as in female. Length 1.23 mm (1.15–1.28 mm) and greatest width 0.40 mm (0.39–0.43 mm), based on 10 specimens. Ratio of length to width of prosome 1.42:1.

Segment of leg 5 (Fig. 99) 55×153 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment quadrate, 208×200 μ. Four postgenital segments 65×81, 68×70, 62×60, and 78×60 μ, from anterior to posterior.

Caudal ramus resembling that of female, but larger in absolute dimensions, 161×24 μ, ratio of length to width a little less, 6.7:1.

Dorsal and ventral surfaces of body ornamented as in female. Ratio of length of prosome to that of urosome 0.88:1, urosome being a little longer than prosome.

Rostral area as in female.

First antenna segmented and armed as in female, but two long aesthetes added on segment 2 and one on segment 4 (see Figure 98), so that formula is same as for males of previous three species. Second segment with surficial sclerotizations as in female. Second antenna (Fig. 100) resembling that of female, but with inner margin of second segment somewhat irregular with two protuberances bearing scalelike knobs. Claw a little shorter and stouter than in female.

Labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 101) slender, segmented and armed as in the previous species; prominent spinules in two rows on inner surface of second segment. Claw 234 μ along its axis.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 resembling those in female, with similar segmentation and with same spine and setal formula, except for last segment of endopod of leg 1 (Fig. 102) where armature is I, I, 4, instead of I, 5 as in female. Outer spines (except first and last) on exopod of leg 2 showing finely serrated proximal lamellae (instead of smooth as in female); outer terminal spine on endopod of this leg with its outer lamella serrated instead of smooth.

Leg 5 (Fig. 103) with elongated straight free segment, 48 × 12 μ, without surficial ornamentation and much smaller than in female. Two terminal setae 34 μ (outer) and 13 μ (inner), and seta on body near free segment 60 μ. All setae naked.

Leg 6 (Fig. 104) a posteroventral flap on genital segment, bearing two small naked setae 17 and 23 μ in length.

Spermatophore not seen.

Color in life as in female.

Etymology.—The specific name *arcuatipes*, from Latin *arcuatus* = bent in the form of a bow, arched, and *pes* = foot, refers to the form of the fifth legs in the female.

Comparison with related species.—From those species of *Lichomolgus* having one claw on the second antenna and the formula II, I, 5 on the last segment of the exopod of leg 4 (see list above under *L. digitatus*), *L. arcuatipes* may be distinguished by the two lobes on the convex margin of the mandible, one with four slender digitiform processes, the other broadly triangular. These features are not present in any of the fifteen species listed above or in either *L. digitatus* or *L. prolixipes.*

Only one other species of *Lichomolgus*, *L. compositus* Humes and Frost, 1964, has a 3-segmented second antenna, but this species is unlike *L. arcuatipes* in such features as the number of eggs in the egg sac, the nature of the setae on the caudal rami, the surficial ornamentation of the second segment of the first antenna, the armature of the second maxilla, the nature of the outer spines on the exopods of legs 1–4, and the form and ornamentation of leg 5.

L. elegans Thompson and A. Scott, 1903, has one claw on the second antenna, but the formula for the last segment of the exopod of leg 4 is unknown. This species, however, has a very short caudal ramus, about as broad as long, and an elongated notched genital segment, thus distinguishing it from *L. arcuatipes.*

Lichomolgus lobophorus n. sp.
Figs. 105–133

Type material.—21 females, 15 males, and 2 immature specimens from *Acropora scherzeriana* Brueggemann in a depth of 1 m, Pte. Lokobe, Nosy Bé, Madagascar. Collected October 25, 1960. Holotype female, allotype, and 30 paratypes (18 females and 12 males) deposited in the United States National Museum, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Acropora* sp.: 12 females and 20 males in 1 m, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, September 17, 1963; 27 females, 19 males, and 1 immature specimen in 0.5 m, Ambariobe, October 20, 1963. From *Acropora cytherea* Dana: 14 females and 6 males in 1 m, Andilana (sometimes spelled Andilah), Nosy Bé, September 4, 1960.

Female.—Body (Fig. 105) with moderately broadened prosome. Length 1.27 mm (1.21–1.36 mm) and greatest width 0.50 mm (0.47–0.52 mm), based on 10 specimens. Ratio of length to width of prosome 1.44:1. Epimeral areas of metasomal segments expanded as in figure.

Segment of leg 5 (Fig. 106) 104 × 280 μ. Between this segment and genital segment a faint indication of an intersegmental sclerite ventrally. Genital segment rectangular, a little longer than wide, its lateral margins slightly indented in dorsal view. Length 247 μ, width in anterior half 234 μ and in posterior half 228 μ. Areas of attachment of egg sacs situated dorsally, each area

(Fig. 107) with two small naked setae about 7 μ long separated by a minute spinous process; adjacent area with hyaline setules. Three postgenital segments (Fig. 108) 120 × 164, 70 × 107, and 114 × 91 μ, measured dorsally, from anterior to posterior. First postgenital segment asymmetrical in lateral view (Fig. 109), extended ventrally and posteriorly as a prominent broad lobe underlying part of next segment (cf. Figure 108); ventral length of segment including lobe 169 μ. A row of minute spinules along outer posterior border of anal segment.

Caudal ramus (Fig. 110) elongated, 180 × 29 μ, 6.2 times longer than wide. Certain setae with lateral spinules as in figure. Outer lateral seta 73 μ, outermost terminal seta 65 μ, innermost terminal seta 73 μ. Two long median terminal setae 95 μ (inner) and 83 μ (outer). Dorsal pedicellate seta 55 μ. Dorsal and ventral surfaces of ramus with hairs and refractile areas (which appear to be minute depressions in the cuticula rather than knobs). No spinule seen on proximal outer margin of ramus.

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with a few hairs and numerous refractile areas (apparently slight depressions in the cuticula). Ratio of length of prosome to that of urosome 1.42:1.

Egg sac (Figs. 105 and 111) small, globular, 237 × 195 μ in dorsal view, containing 6–7 eggs of somewhat irregular shape.

Rostral area (Fig. 112) not well developed, but covered anteriorly with refractile points.

First antenna (Fig. 113) slender, 376 μ long, segmented and armed as in previous four species. Lengths of segments: 31 (55μ along anterior edge), 136, 28, 62, 46, 28, and 21 μ, respectively. All setae naked.

Second antenna (Fig. 114) 3-segmented, last two segments having been fused, as in *L. arcuatipes*, but fusion even more complete, without an interruption in sclerotization of outer wall and without a trace of three setae usually seen on penultimate segment in *Lichomolgus*. Armature: 1, 1 (very small), I. Terminal claw straight, about 20 μ long, without definite articulation with segment; no minute elements near base of claw. Antero-outer surface of second segment with refractile areas (which, like those on body surface, seem to be slight depressions in the cuticula rather than knobs).

Labrum (Fig. 115) with two lobes more pointed than in previous species.

Mandible (Fig. 116) closely resembling that of *L. arcuatipes*. Paragnath (Fig. 117) a small hairy lobe. First maxilla (Fig. 118) with three terminal elements. Second maxilla (Fig. 119) and maxilliped (Fig. 120) much like those of *L. arcuatipes*.

Area between maxillipeds and first pair of legs (Fig. 121) not protuberant; sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 122, 123, 124, and 125) segmented as in previous four species, with same spine and setal formula. Inner coxal seta of leg 4 moderately long, 41 μ, and haired; basis of this leg with hairs on inner margin. Endopod of leg 4 resembling that of *L. arcuatipes*. First segment 36 × 30 μ, with its plumose inner seta 69 μ. Second segment attenuated distally, 81 × 28 μ (greatest dimensions), with its two terminal fringed spines 50 μ (outer) and 57 μ (inner) in length.

Leg 5 (Fig. 126) with free segment elongated and arched (but less strongly so than in the previous species), dimensions about 200 × 35 μ, with outer convex surface ornamented with short stout spinules. Two terminal naked setae 38 μ (outer) and 75 μ (inner). Naked seta on body near free segment 90 μ. A row of spinules on body near insertion of free segment.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 107).

Color in life in transmitted light slightly amber, eye red, egg sacs gray.

Male.—Body (Fig. 127) with moderately broadened prosome. Length 1.15 mm

(1.11–1.19 mm) and greatest width 0.39 mm (0.37–0.39 mm), based on 10 specimens. Ratio of length to width of prosome 1.40:1.

Segment of leg 5 (Fig. 128) 65 × 166 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment quadrate, 260 × 270 μ, only a little wider than long. Four postgenital segments 78 × 112, 65 × 81, 50 × 72, and 90 × 71 μ, measured dorsally, from anterior to posterior. Second postgenital segment with a prominent broad posteroventral lobe as in female.

Caudal ramus resembling that of female, but shorter, 164 × 29 μ, 5.7 times longer than wide.

Dorsal and ventral surfaces of body ornamented as in female. Ratio of length of prosome to that of urosome 1.0:1.

Rostral area as in female.

First antenna segmented and armed as in female, but two long aesthetes added on segment 2 and one on segment 4 (see Figure 127), so that formula is same as for males of previous four species. Second antenna (Fig. 129) resembling that of female, but small knobs along inner margin of second segment proximal to minute setule.

Labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 130) rather closely resembling that of *L. arcuatipes*. Claw 330 μ along its axis.

Area between maxillipeds and first pair of legs like that of female.

Legs 1–4 resembling those of female, except formula for last segment of endopod of leg 1 (Fig. 131) which is I, I, 4, instead of I, 5 as in female.

Leg 5 (Fig. 132) with elongated straight free segment, 68 × 19 μ (greatest dimensions), with small spinules on outer surface. Two terminal setae 40 μ (outer) and 17 μ (inner), and seta on body near free segment 63 μ. All setae naked.

Leg 6 (Fig. 133) with two small naked setae 18 and 20 μ long.

Spermatophore not seen.

Color in life in transmitted light somewhat more amber than in female, eye red.

Etymology.—The specific name *lobophorus*, from λοβός = a lobe and φορέω = to bear or carry, alludes to the prominent posteroventral lobe on the first postgenital segment in the female (second in male).

Comparison with related species.—The prominent posteroventral lobe on the first postgenital segment of the female (and on the second postgenital segment of the male) distinguishes this species from all other known species of *Lichomolgus*.

By its 3-segmented second antenna (rather than 4-segmented), *L. lobophorus* differs from all species in the genus except *L. compositus* Humes and Frost, 1964, and *L. arcuatipes*. *L. compositus*, though showing a generally similar body form, is unlike the new species in the nature of the setae on the caudal rami, the details of the armature of segment 3 of the second antenna, the form of the mandible (lacking inner digitiform processes), the armature of the second maxilla, and the form of leg 5.

L. lobophorus, being similar to *L. arcuatipes* in many ways (particularly in the form of the mandible), is apparently closely related to it. However, *L. lobophorus* may be distinguished from *L. arcuatipes* by the posteroventral lobe on the postgenital region and by other details such as the number of eggs in the egg sac, the surficial ornamentation of the second segment of the first antenna, the form of the labral lobes, the nature of the outer spines on the exopods of legs 1–4, and the form and ornamentation of leg 5.

Lichomolgus geminus n. sp.

Figs. 134–150

Type material.—141 females and 102 males from *Stylophora pistillata* (Esper) in a depth of 0.5 m, Navetsy, Nosy Bé, Madagascar. Collected September 24, 1964. Holotype female, allotype, and 145 paratypes (90 females and 55 males) deposited in the United States National Museum, 45 paratypes (25 females and 20 males) in the

Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 15 females and 7 males in 0.2 m, Ambariobe, a small island almost between Nosy Komba and Nosy Bé, June 21, 1963; 9 females and 7 males in 0.5 m, Ambariobe, July 21, 1963; 36 females, 16 males, and 1 copepodid in 0.5 m, Ambariobe, August 4, 1963; 27 females and 21 males in 3 m, Ambariobe, August 13, 1963; 18 females and 8 males in 0.5 m, Ambariobe, October 6, 1963; and 2 females and 1 male in 0.5 m, west of Pte. Mahatsinjo, Nosy Bé, January 31, 1964. From *Stylophora mordax* (Dana): 21 females, 7 males, and 1 copepodid in 2 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, October 1, 1963. From *Acropora* sp.: 32 females and 6 males in 2 m, Pte. Lokobe, Nosy Bé, August 16, 1960.

Female.—Body form (Fig. 134) resembling that of *L. compositus* Humes and Frost, 1964. Length 1.59 mm (1.56–1.61 mm) and greatest width 0.58 mm (0.57–0.59 mm), based on 10 specimens. Ratio of length to width of prosome 1.38:1.

Segment of leg 5 (Fig. 135) 83 × 202 μ. Genital segment 146 × 138 μ, very similar in form to that of *L. compositus*. Areas of attachment of egg sacs dorsolaterally placed, each area (Fig. 136) with two very small setae (4 μ long) and a minute process. Three postgenital segments 125 × 138, 107 × 117, and 88 × 100 μ from anterior to posterior.

Caudal ramus (Fig. 137) greatly elongated, 265 × 29 μ (width taken at middle), tapering slightly distally, 9.1 times longer than wide. Setae short and naked, resembling those of *L. compositus*. Outer lateral seta 50 μ, outermost terminal seta 53 μ, innermost terminal seta 55 μ. Two median terminal setae broadened and hyaline, 68 μ (outer) and 75 μ (inner) in length. Dorsal pedicellate seta 34 μ. Both dorsal and ventral surfaces of ramus with minute hairs. No setule seen on proximal outer margin of ramus.

Egg sac (Fig. 138) small, globular, 244 × 212 μ in dorsal view, containing usually 4 eggs (sometimes 5).

Dorsal surface of prosome and dorsal and ventral surfaces of urosome with a few small hairs. Ratio of length of prosome to that of urosome 1.14:1. (In life the urosome may form a Z-shaped flexure, with the genital segment drawn forward under the metasome and the postgenital segments retained in line with the prosome.)

Rostral area with many long setules as in *L. compositus*.

First antenna segmented and armed as in *L. compositus*, first segment having only a single seta. Lengths of segments: 75 (88 μ along anterior edge), 101, 42, 59, 48, 34, and 25 μ, respectively.

Second antenna, labrum, mandible, paragnath, first maxilla, second maxilla, maxilliped, region between maxillipeds and first leg, leg 1, leg 2, and leg 3 like those of *L. compositus*.

Leg 4 (Fig. 139) segmented and armed as in *L. compositus*, last segment of exopod with the formula II, I, 5. Inner coxal seta naked and 22 μ long. Endopod somewhat longer than in that species; first segment 39 × 32 μ, with its plumose inner seta 65 μ; second segment 99 × 23 μ (length including terminal processes of 5 μ and width taken at widest point), narrowest width 12.5 μ, two terminal fringed spines 40 μ (outer) and 74 μ (inner) in length.

Leg 5 (Fig. 140) with free segment slender and arched, 147 × 14 μ (width taken at narrowest point at junction of first and second thirds), without fine ornamentation. Two terminal setae 26 μ (outer) and 88 μ (inner). Seta on body near insertion of free segment 35 μ. All setae naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 136).

Color in life in transmitted light translucid, eye red, egg sacs light gray.

Male.—Body form (Fig. 141) like that of *L. compositus*. Length 1.49 mm (1.42–

1.55 mm) and greatest width 0.50 mm (0.48–0.51 mm), based on 10 specimens. Ratio of length to width of prosome 1.32:1.

Segment of leg 5 (Fig. 142) 55 × 161 μ. Genital segment 208 × 280 μ, wider than long. Four postgenital segments 57 × 94, 86 × 86, 73 × 82, and 78 × 86 μ from anterior to posterior. Caudal ramus (Fig. 153) similar to that in *L. compositus*, but longer, 229 × 31 μ, 7.4 times longer than wide.

Rostral area, first antenna (with aesthetes arranged as 0, 2, 0, 1, 1, 1, and 1), second antenna, labrum, mandible, paragnath, first maxilla, second maxilla, maxilliped (claw 305 μ along its axis), region between maxillipeds and first leg, and leg 1 (with last segment of endopod having one serrated spine, one setiform spine, and four setae) resembling those of *L. compositus*.

Exopods of legs 2, 3, and 4 as in *L. compositus*. Endopod of leg 2 with outer terminal spine on last segment (Fig. 144) modified as shown in detail in Figure 145. Endopod of leg 3 with outer terminal spine on last segment (Fig. 146) shorter than that in *L. compositus*, but not as greatly modified as in preceding leg. Endopod of leg 4 (Fig. 147) elongated; first segment 39 × 33 μ, with its plumose seta 77 μ; second segment 111 × 27 μ (length including terminal processes of 5 μ and width taken at widest point), narrowest width 12.5 μ, two terminal fringed spines 43 μ (outer) and 79 μ (inner) in length.

Leg 5 (Fig. 148) with elongated rectangular free segment 50 × 12.5 μ, unornamented, its two naked terminal setae 28 μ (outer) and 34 μ (inner) in length.

Leg 6 (Fig. 149) the usual posteroventral flap on genital segment, bearing two small naked setae 23 and 19 μ in length.

Spermatophore (Fig. 150), attached to female, oval, 174 × 107 μ (not including the short neck).

Color in life as in female.

Etymology.—The specific name *geminus*, from Latin = twin-born or similar, refers to the close similarity of this species to *L. compositus*.

Comparison with related species.—*L. geminus* shows three features which in combination serve to distinguish it from all species of *Lichomolgus* except *L. compositus* Humes and Frost, 1964 (associated with the coral *Seriatopora subseriata* Ehrenberg in Madagascar). These are: the presence of only a single seta on segment 1 of the first antenna, a 3-segmented second antenna, and the two short broad hyaline setae on the caudal ramus. *L. lobophorus* and *L. arcuatipes* both have a 3-segmented second antenna, but differ from the new species in having four setae on segment 1 of the first antenna, and in having relatively unmodified setae on the caudal ramus.

L. geminus appears to be very closely related to *L. compositus*, the two species showing striking similarities. There exist, however, several significant differences which are sufficiently important in our opinion to warrant considering these copepods from *Stylophora* as representing a distinct species. In *L. geminus* the endopod of leg 4 is relatively more slender than in *L. compositus*, the free segment of leg 5 in the female is more slender, the caudal ramus is longer and more slender (9.1:1 in the female, 7.4:1 in the male), the egg sac is globular with 4–5 eggs (7 eggs in *L. compositus*), and there is sexual dimorphism in the outer terminal spine on the last segment of the endopods of legs 2 and 3 in the male.

Lichomolgus crassus n. sp.

Figs. 151–182

Type material.—54 females and 27 males from *Stylophora pistillata* (Esper) in a depth of 0.5 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, Madagascar. Collected August 4, 1963. Holotype female, allotype, and 61 paratypes (41 females and 20 males) deposited in the United States National Museum, 14 paratypes (10 females and 4 males) in the

Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 1 female and 5 males in 0.2 m, Ambariobe, June 21, 1963; 3 males in 0.5 m, Ambariobe, July 21, 1963; 1 female and 16 males in 0.5 m, Ambariobe, August 13, 1963; 1 female and 10 males in 0.5 m, Ambariobe, October 6, 1963; 3 males in 0.5 m, west of Pte. Mahatsinjo, Nosy Bé, January 31, 1964; and 1 female and 33 males in 0.5 m, Navetsy, Nosy Bé, September 24, 1964. From *Stylophora mordax* (Dana): 33 males in 2 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, October 1, 1963. From *Acropora* sp.: 15 males in 2 m, Pte. Lokobe, Nosy Bé, August 16, 1960.

Female.—Body (Figs. 151 and 152) with broadened and thickened prosome; urosome slender and in life folded under metasome with only postgenital segments visible in dorsal view. Length 1.38 mm (1.32–1.44 mm) and greatest width 0.66 mm (0.60–0.72 mm), based on 10 specimens. Greatest dorsoventral thickness 0.48 mm. Segment of leg 1 clearly set off from head; epimeral areas of metasomal segments as in figures. Ratio of length to width of prosome 1.07:1.

Segment of leg 5 (Fig. 153) 96 × 257 μ. Genital segment (Fig. 153) rather narrow, wider in its anterior third (156 μ) than in its posterior two-thirds (127 μ); its dorsal length (95 μ) much shorter than its ventral length (195 μ). Areas of attachment of egg sacs located dorsolaterally, each area (Fig. 154) with two minute setae about 6 μ in length with a spiniform process between them. First postgenital segment (Fig. 155) shorter dorsally (60 μ) than ventrally (112 μ) and 117 μ wide; second 83 × 96 μ, and third 78 × 98 μ (this last segment apparently without a row of spinules along posteroventral margin).

Caudal ramus (Fig. 156) moderately elongated, 112 × 39 μ, 2.87 times longer than wide. Setae relatively short and naked. Outer lateral seta 41 μ, outermost terminal seta 50 μ, innermost terminal seta 46 μ. Two median terminal setae broadened, 68 μ (outer) and 73 μ (inner) in length. Dorsal pedicellate seta 30 μ. Both dorsal and ventral surfaces of ramus with a few minute hairs and refractile points. No setule seen on proximal outer margin of ramus.

Egg sac unkown.

Dorsal surface of prosome with many refractile points. Dorsal and ventral surfaces of urosome with a few hairs and refractile points. Ratio of length of prosome to that of urosome difficult to establish because of flexure of urosome, but estimated to be about 1.5:1.

Rostral area (Fig. 157) with many hyaline setules. On ventral surface of head a sclerotized ridge extending from insertion of first antenna diagonally toward posterolateral corners of head region.

First antenna (Fig. 158) segmented and armed as in *L. compositus* and *L. geminus*, first segment having only a single seta (in one female first segment of one antenna had an extra seta). Lengths of segments: 66 (84 μ along anterior edge), 70, 40, 35, 42, 21, and 19 μ respectively. All setae short and naked.

Second antenna (Fig. 159) 3-segmented as in *L. compositus*, *L. arcuatipes*, *L. lobophorus*, and *L. geminus*, the dual nature of the slender third segment (formed by fusion of original segments 3 and 4) indicated by three small obtuse hyaline elements (representing the usual three setae on penultimate segment in *Lichomolgus*). Armature: 1, 1, 3 + I + 2 small obtuse elements. Terminal claw short (25 μ along its axis) and reflexed.

Labrum (Fig. 160) with a few hyaline setules, its posteroventral margin bilobed.

Mandible (Fig. 161) resembling that of *L. compositus* and *L. geminus*. Paragnath (Fig. 162) a small somewhat pointed lobe with hairs. First maxilla (Fig. 163), with four elements, second maxilla (Fig. 164), and maxilliped (Fig. 165), resembling those of *L. compositus* and *L. geminus*.

Area between maxillipeds and first pair

of legs (Fig. 166) not protuberant; sclerotized line between bases of maxillipeds not complete.

Legs 1–4 (Figs. 167, 168, 169, and 170) segmented as in previous six species, with same spine and setal formula. Inner coxal seta of leg 4 short, 22 μ in length, and naked; basis of this leg with hairs on inner margin. Spines on exopod of leg 1 lamellate, with short proximal spinules and terminal flagella; these spines on legs 2–4 with smooth lamellae. Endopod of leg 4 moderately elongated. First segment 28 × 24 μ, with its plumose inner seta 40 μ. Second segment 57 × 22 μ (greatest dimensions), its terminal spines naked with obtuse tips, outer 33 μ, inner 56 μ in length.

Leg 5 (Fig. 171) with elongated free segment 88 × 14 μ, only slightly arched and without fine ornamentation. Two terminal setae 24 μ (outer) and 60 μ (inner). Seta on body near insertion of free segment 23 μ. All setae naked.

Leg 6 probably represented by the two small elements near attachment of egg sac (see Figure 154).

Color in life in transmitted light translucid to opaque, reddish amber areas at bases of first antennae and external to insertions of legs, eye red.

Male.—Body (Fig. 172) with prosome less broadened and thickened than in female; urosome not folded under metasome, but extended in a more usual position. Length 1.23 mm (1.20–1.25 mm) and greatest width 0.51 mm (0.50–0.51 mm), based on 10 specimens. Ratio of length to width of prosome 1.2:1.

Segment of leg 5 (Fig. 173) 68 × 168 μ. Genital segment 177 × 224 μ, wider than long, with rounded lateral margins. Four postgenital segments 44 × 91, 64 × 85, 70 × 74, and 65 × 75 μ from anterior to posterior.

Caudal ramus (Fig. 174) similar to that of female, but longer, 149 × 29 μ, 5.13 times longer than wide.

Rostral area as in female.

First antenna (Fig. 175) segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4, so that formula is same as for males of *L. compositus* and *L. geminus*.

Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla resembling those of female. Maxilliped (Fig. 176) segmented and armed as in previous species. Claw 145 μ along its axis (including lamella), showing a distinct line of division about midway, and having hyaline serrations along concave margin.

Area between maxillipeds and first pair of legs like that of female.

Legs 1–4 with same spine and setal formula as in female. Leg 1 (Fig. 177) with spines on exopod and single spine on endopod much more strongly barbed than in female. Legs 2 and 3 with spines on exopods moderately barbed, those on endopod of leg 2 as in Figure 178, and on endopod of leg 3 as in Figure 179. Leg 4 with spines on exopod slightly barbed. Endopod (Fig. 180) longer than in female; first segment 30 × 31 μ, with its plumose inner seta 58 μ; second segment 75 × 25 μ, more attenuated than in female, with its two terminal spines 37 μ (outer) and 66 μ (inner) in length.

Leg 5 (Fig. 181) with straight and moderately short free segment, 35 × 10 μ, without fine ornamentation. Two terminal naked setae 23 and 37 μ long.

Leg 6 (Fig. 182) a posteroventral flap on genital segment, bearing two small naked setae 20 and 17 μ in length.

Spermatophore seen only partly developed inside body of male (Fig. 182).

Color in life resembling that of female.

Etymology.—The specific name *crassus*, from Latin = thick or solid, alludes to the broadened and thickened prosome.

Comparison with related species.—*L. crassus* may be distinguished from all but four species of *Lichomolgus* by its 3-segmented second antenna (resulting from a fusion of segments 3 and 4). These four species are: *L. compositus* Humes and Frost, 1964, *L. arcuatipes*, *L. lobophorus*, and *L. geminus*. Two of these, *L. arcuatipes* and *L. lobophorus*, differ from the

new species in having four setae (instead of one) on the first segment of the first antenna and in having four small fingerlike processes on the basal part of the mandible. The other two, *L. compositus* and *L. geminus*, differ in showing sexual dimorphism in the formula for leg 1 (last segment of endopod I, 5 in the female, I, I, 4 in the male) and in having a less broadened prosome (ratio of length to width in female of *L. compositus* 1.27:1, in *L. geminus* 1.38:1).

On the basis of several points of similarity in *L. crassus*, *L. compositus*, and *L. geminus*, such as the setulose rostral area, the single seta on the first segment of the first antenna, the structure of the mandible, and the two broadened and relatively short terminal setae on the caudal ramus, these three species appear to be closely related.

Lichomolgus actinophorus Humes and Frost, 1964

This species has been previously reported (Humes and Frost, 1964) from *Pavona angulata* Klunzinger and *Pavona cactus* (Forskål) in Madagascar. New host records are:

1) From *Pavona danai* (Milne Edwards and Haime): 31 females and 29 males in 10 cm, Ambariobe, near Nosy Bé, October 6, 1963; 189 females and 193 males in 10 cm, Boloboxo, Nosy Faly, east of Nosy Bé, August 10, 1964.

2) From *Pavona danai* or *Pavona angularis* (Klunzinger): 111 females and 87 males in 1 m, Ambariobe, September 6, 1963. Identification of host uncertain.

3) From *Pavona*? *venusta* (Dana): 28 females and 22 males in 1 m, Ambariobe, September 17, 1963.

Lichomolgus compositus Humes and Frost, 1964

This species has been known only from *Seriatopora subseriata* Ehrenberg in Madagascar (Humes and Frost, 1964). It is now reported as follows:

1) From *Seriatopora octoptera* Ehrenberg: 14 females and 2 males in 2 m, Pte. Ambarionaomby, Nosy Komba, August 18, 1960.

2) From *Seriatopora* sp.: 8 females and 2 males in 1 m, Pte. Ambarionaomby, January 12, 1964.

Monomolgus unihastatus Humes and Frost, 1964

This lichomolgid has been reported only from *Porites* sp. cf. *P. andrewsi* Vaughan in Madagascar (Humes and Frost, 1964). It is now recorded from *Porites* sp. cf. *P. nigrescens* Dana (111 females and 93 males in 1 m, Pte. de Tafondro, Nosy Bé, September 19, 1963).

Kombia angulata Humes, 1962

This copepod has been previously known only from *Psammocora* sp. in Madagascar (Humes, 1962). New host records are:

1) From *Porites* (s. g. *Synaraea*) sp.: 19 females and 43 males in 1 m, Pte. Ambarionaomby, Nosy Komba, November 28, 1963; 28 females and 28 males in 1 m, Pte. Lokobe, Nosy Bé, November 29, 1963; 6 females and 32 males in 2 m, northern end of Nosy Sakatia, an island close to the western shore of Nosy Bé, August 19, 1963; 4 females in 1 m, Ambariobe, near Nosy Bé, September 17, 1963; 10 females and 14 males in 2 m, northern end of Nosy Sakatia, September 18, 1963; 8 females and 10 males in 1 m, Pte. de Tafondro, Nosy Bé, October 2, 1963; 102 females and 153 males in 1 m, Pte. Lokobe, November 30, 1963; and 7 females and 8 males in 1–2 m, Ankify, on the mainland of Madagascar, near Nosy Komba, December 30, 1963.

2) From *Porites* sp. cf. *P. nigrescens* Dana: 1 female and 1 male in 1 m, Pte. de Tafondro, September 19, 1963.

3) From *Porites*, young colony: 3 females and 5 males in 1 m, Pte. de Tafondro, September 19, 1963.

Although Humes (1962) indicated that the genus *Kombia* should probably be placed in the Xarifiidae, it would now seem

that *Kombia* belongs instead to the Lichomolgidae. The discovery of certain new genera of the Lichomolgidae since 1962 has widened our concept of the family. The mouthparts of *Kombia* are essentially lichomolgid in form, though the flagellum of the mandible is relatively short compared to most other genera. A somewhat similar short flagellum is present in other lichomolgids, for example, *Monomolgus unihastatus* Humes and Frost, 1964, and *Rhynchomolgus corallophilus* Humes and Ho, 1967a. The tendency in *Kombia* toward reduction of legs 1–5, beginning at the posterior end of the series, is seen also in *Rhynchomolgus* (where it is even more strongly expressed). Since the limits of the Lichomolgidae, as we see them, now include such transformed genera as *Rhynchomolgus,* it does not seem inconsistent to include *Kombia* in this family.

PRIONOMOLGUS n. gen.

Type and only known species: *Prionomolgus lanceolatus* n. sp.

Body cyclopoid. Segment of leg 1 in female separated from head by a dorsal and lateral furrow, in male lacking this separation. Urosome 5-segmented in female, 6-segmented in male. Caudal ramus with six setae. First antenna 7-segmented, with lichomolgid setation. Second antenna 3-segmented. Mouthparts lichomolgid. Mandible with proximal region having two strongly serrated lobes on concave edge; flagellum relatively short. Paragnath a small nearly naked lobe. First maxilla with three setae. Second maxilla 2-segmented. Maxilliped in female 3-segmented, in male 4-segmented (fourth segment probably forming part of terminal claw).

Legs 1–4 with 3-segmented rami, except for endopod of leg 4 which is 2-segmented. Leg 1 in male showing sexual dimorphism, formula for last segment of endopod being I, I, 4, instead of I, 5 as in female. Endopod of leg 4 with formula 0–1; I. Leg 5 with free segment bearing two terminal setae.

Other features as in the species described below.

Associated with madreporarian corals.

Gender masculine.

Etymology.—The generic name is a combination of πρίων = a saw (alluding to the serrated lobes on the mandible) and μολγός = a sack made of leather.

Prionomolgus lanceolatus n. gen., n. sp. Figs. 183–210

Type material.—31 females, 67 males, and 23 copepodids from *Pachyseris speciosa* (Dana) in a depth of 3 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Madagascar. Collected September 3, 1963. Holotype female, allotype, and 79 paratypes (25 females and 54 males) deposited in the United States National Museum, 13 paratypes (3 females and 10 males) in the Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens (all from *Pachyseris speciosa* in 2 m, Ambariotsimaramara, an islet on the southern shore of Nosy Bé, between Pte. Mahatsinjo and Ampombilava).—6 females, 9 males, and 4 copepodids, October 18, 1963; 2 females and 1 male, June 12, 1964.

Female.—Body (Fig. 183) with flattened and broadened prosome. Length 1.36 mm (1.26–1.42 mm) and greatest width 0.85 mm (0.77–0.91 mm), based on 10 specimens. Ratio of length to width of prosome about 1:1. Segment of leg 1 separated from head dorsally and laterally by a furrow. Epimeral areas of segments of legs 1–3 expanded, those of segment of leg 4 short and pointed.

Segment of leg 5 (Fig. 184) 55 × 263 μ. Between this segment and genital segment no ventral intersegmental sclerite discernible. Genital segment broadened in its anterior fourth and tapered posteriorly, its greatest dimensions being 166 × 245 μ, wider than long. Areas of attachment of egg sacs situated dorsolaterally, each area (Fig. 185) with two minute setae 5 μ in

length. Three postgenital segments 83 × 92, 68 × 88, and 78 × 90 μ from anterior to posterior. Anal segment with a row of minute spinules along its posteroventral margin on each side and two short rows of similar spinules posterodorsally near insertion of ramus (see Figure 186).

Caudal ramus (Fig. 186) moderately elongated, 100 × 39 μ, 2.56 times longer than wide. Outer lateral seta 100 μ and naked, outermost terminal seta 105 μ with a few proximal hairs, innermost terminal seta 113 μ with proximal hairs. Two long median terminal setae 340 μ (inner) and 230 μ (outer), both with very short barbules along their midregions. Dorsal pedicellate seta short, 40 μ, and haired. Dorsal and ventral surfaces of ramus with short hairs and refractile points.

Dorsal surface of prosome with many refractile points and a few hairs; dorsal and ventral surfaces of urosome with a few refractile points. Ratio of length of prosome to that of urosome 1.84:1.

Egg sac (Fig. 187) oval, 363 × 242 μ, containing about 15 eggs, each 94–104 μ in diameter.

Rostral area (Fig. 188) weakly developed, without a definite posteroventral margin.

First antenna (Fig. 189) slender, 376 μ long, and 7-segmented, with a sclerite on third segment suggesting an intercalary segment. Lengths of segments: 42 (86 μ along anterior margin), 141, 26, 42, 39, 27, and 15 μ respectively. Formula for armature: 4, 13 (5 + 2 + 6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in many species of *Lichomolgus*. Several setae on last three segments distally haired as in figure.

Second antenna (Fig. 190) slender and 3-segmented, the last segment representing the fusion of two original segments (dual nature of this segment indicated by presence of three small setae corresponding to those usually found on segment 3 in other lichomolgids). Armature: 1, 1, 3 + I + 1 small hyaline element. Terminal claw short, about 24 μ along its axis.

Labrum (Fig. 191) with two posteroventral lobes having broad medial hyaline margins.

Mandible (Fig. 192) with proximal region separated into two parts by a constriction. Distal area beyond constriction having on its convex side a short row of spinules followed by a triangular process and then by a row of small spinules; on its concave side two lobes with strongly serrated margins. Flagellum relatively short with lateral serrations. Paragnath (Fig. 193) a small lobe, naked except for a single small setule. First maxilla (Fig. 194) having three elements with serrated flanges. Second maxilla (Fig. 195) 2-segmented. First segment unarmed. Second segment with its outer (ventral) margin bearing a minute proximal spinule and a distal spinulose seta, with its inner (dorsal) margin carrying a blunt seta with hyaline lamellae; terminal lash with long proximal spinules and distal serrations. Maxilliped (Fig. 196) 3-segmented; first segment unarmed, second with two sparsely barbed inner setae, and third with two setae (one small and naked, the other larger and barbed) and terminating in a slender barbed spiniform process.

Area between maxillipeds and first pair of legs (Fig. 188) not protuberant; a sclerotized line between bases of maxillipeds.

Legs 1–4 (Figs. 197, 198, 199, and 200) with trimerous rami, except for endopod of leg 4 which is 2-segmented. Armature as follows:

P_1	protopod 0–1; 1–0	exp I–0; I–1; III, I, 4 end 0–1; 0–1; I, 5
P_2	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 3
P_3	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 2
P_4	protopod 0–1; 1–0	exp I–0; I–1; II, 1, 5 end 0–1; I

Inner coxal seta long and haired in legs 1–3, but in leg 4 only 6 μ long and naked. Hairs on inner margin of basis in all four legs. Outer spines on exopod of leg 1 with

coarsely spinulose lamellae and having flagella; those of legs 2–4 with finely spinulose lamellae and without flagella. Endopod of leg 4 (Fig. 201) with hairs along outer margins of both segments. First segment 22 × 14 μ (greatest dimensions), its plumose inner seta 56 μ long. Second segment 26 × 9 μ (greatest dimensions), somewhat narrowed distally, its single terminal spine 33 μ long with narrow hyaline lamellae.

Leg 5 (Fig. 202) having a moderately elongated free segment 84 μ long, 25 μ wide at the level of proximal inner expansion and 17 μ wide halfway from the outer marginal notch to the end. Two terminal naked setae 60 and 77 μ in length. Outer surface of segment with small spinules. Seta on body near free segment 77 μ long and naked; a row of spinules near this seta.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 185).

Color in life in transmitted light translucid, eye dark red, egg sacs gray.

Male.—Body (Fig. 203) with broad flattened prosome nearly as in female. Length 1.04 mm (0.99–1.08 mm) and greatest width 0.53 mm (0.49–0.55 mm), based on 10 specimens. Ratio of length to width of prosome 1.12:1. Segment of leg 1 not separated from head by a furrow. Epimeral areas of metasomal segments as in female.

Segment of leg 5 (Fig. 204) 26 × 172 μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment broader than long, 208 × 270 μ, its lateral borders sclerotized and rounded anteriorly but hyaline and crenated posteriorly. Four postgenital segments 36 × 70, 42 × 67, 40 × 63, and 61 × 67 μ from anterior to posterior.

Caudal ramus resembling that of female, but smaller, 88 × 31 μ, with hairs on setae fewer than in female (see Figure 204).

Dorsal and ventral surfaces of body ornamented as in female. Ratio of length of prosome to that of urosome 1.33:1.

Rostral area like that of female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4, so that formula is 4, 13 + 2 aesthetes, 6, 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 205) slender and 4-segmented, assuming that the proximal part of claw represents a fourth segment. First segment unarmed, second with two naked setae and two rows of spinules on its inner surface, third small and unarmed. Claw elongated, slender, and recurved, 196 μ along its axis (including terminal lamella), with weak indication of division about midway; proximally with two unequal setae, the smaller seta naked, the larger with distal spinules.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented and armed as in female, except for last segment of endopod of leg 1 where formula is I, I, 4 (Fig. 206), instead of I, 5 as in female. Endopod of leg 4 (Fig. 207) with second segment relatively shorter than in female; first segment 15 × 11 μ, with its plumose inner seta 41 μ, and second segment 17.5 × 8 μ, with its terminal spine 28 μ.

Leg 5 (Fig. 208) with free segment 42 × 9 μ, lacking an inner proximal expansion, with outer marginal notch less evident than in female, and with fewer outer spinules than in opposite sex. Two terminal setae 28 and 48 μ; seta on body near insertion of free segment 56 μ.

Leg 6 (Fig. 209) consisting of a posteroventral flap on genital segment, bearing two slender naked setae 33 and 38 μ long.

Spermatophore (Fig. 210), attached to female in a pair, about 200 × 95 μ (not including the neck).

Color in life similar to that of female.

Etymology.—The specific name *lanceolatus*, from the Latin word *lanceola* = a small lance, refers to the single terminal spine on the endopod of leg 4.

Comparison with other lichomolgids.—In the Lichomolgidae eight genera have a 2-segmented endopod in leg 4. These are: *Lichomolgus* Thorell, 1860, *Epimolgus* Bocquet and Stock, 1956, *Gelastomolgus* Humes, in press, *Indomolgus* Humes and Ho, 1967c, *Lichomolgides* Gotto, 1954, *Monomolgus* Humes and Frost, 1964, *Nasomolgus* Sewell, 1949, and *Stellicola* Kossmann, 1877. (*Macrochiron* Brady, 1872, has a 1-segmented endopod which may be partially divided.) Of these only *Gelastomolgus* has the formula for the endopod of leg 4 as 0–1; 1, thus resembling *P. lanceolatus*.

The new genus and species differs, however, from *Gelastomolgus spondyli* Humes, in press, in several important respects. In *G. spondyli* the body form is rather modified from the usual cyclopoid type, the second antenna is 4-segmented, the mandible has a broad elongated blade and lacks serrated lobes, the maxilliped of the female is apparently 2-segmented and much modified, and leg 1 has the same formula in both sexes.

The mandible of *P. lanceolatus*, although basically lichomolgid in form, differs from that in all other genera in the family. In no other genus do the two lobes on the concave side of the basal part of the mandible possess strongly serrated margins; in those genera where such lobes occur they are ornamented with spinules or hairs.

Since there seems to be no known genus in the Lichomolgidae which could receive the new species from *Pachyseris* without radically broadening the generic concept, we have concluded that the species represents a new genus, basing our judgment primarily on the nature of the mandible and the form and armature of the endopod of leg 4.

HAPLOMOLGUS n. gen.

Type and only known species: *Haplomolgus montiporae* n. sp.

Body cyclopoid. Segment of leg 1 fused with head. Urosome 5-segmented in female, 6-segmented in male. Caudal ramus with six setae. First antenna 7-segmented, with lichomolgid setation. Second antenna 4-segmented. Mouthparts lichomolgid.

Legs 1–4 with 3-segmented rami, except for endopod of leg 4 which is composed of a single unarmed segment, often bearing a small rounded terminal lobe. Leg 5 with a large free segment armed with two terminal setae.

Other features as in the species described below.

Associated with madreporarian corals.

Etymology.—The generic name is a combination of ἁπλόος = single (alluding to the 1-segmented unarmed endopod of leg 4) and μολγός = a sack made of leather. Gender masculine.

Haplomolgus montiporae n. gen., n. sp.

Figs. 211–240

Type material.—147 females and 81 males from *Montipora sinensis* Bernard in a depth of 1 m, Nosy Taolankena, a small island on the northwestern side of Nosy Bé, Madagascar. Collected November 15, 1963. Holotype female, allotype, and 140 paratypes (90 females and 50 males) deposited in the United States National Museum, 45 paratypes (30 females and 15 males) in the Museum of Comparative Zoology, and the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Montipora* sp.: 58 females and 19 males in 1 m, west of Pte. de Tafondro, Nosy Bé, December 3, 1963; 165 females and 66 males in 3 m, western side of Nosy Komba, near Nosy Bé, October 19, 1964. From *Montipora* sp. cf. *M. stellata* Bernard: 27 females and 12 males in 2 m, Ampombilava, Nosy Bé, September 26, 1964.

Female.—Body (Fig. 211) rather slender, with prosome moderately thickened dorsoventrally. Length 0.86 mm (0.83–0.89 mm) and greatest width 0.27 mm (0.26–0.29 mm), based on 10 specimens. Ratio of length to width of prosome 1.5:1. Segment of leg 1 not separated from head. Epimeral areas

of metasomal segments only moderately expanded.

Segment of leg 5 (Fig. 212) 101 × 146 μ. Genital segment 112 × 96 μ, only a little longer than wide and slightly wider in its anterior half than posteriorly. Areas of attachment of egg sacs located dorsally, each area (Fig. 213) with two small setae 4 μ long. Three postgenital segments (Fig. 214) 65 × 65, 78 × 55, and 37 × 55 μ from anterior to posterior, the middle segment being the longest. Edge of anal operculum with a row of minute spinules.

Caudal ramus (Fig. 215) moderately elongated, 48 × 21 μ, about 2.3 times longer than wide. Outer lateral seta 54 μ, outermost terminal seta 58 μ, innermost terminal seta 77 μ. Two long median terminal setae 218 μ (inner) and 156 μ (outer). Dorsal pedicellate seta 73 μ. All setae naked. A few hairs on dorsal surface of ramus.

Dorsal surface of prosome and urosome with a few hairs. Ratio of length of prosome to that of urosome 1.21:1.

Egg sac (Fig. 211) approximately 215 × 133 μ, containing two large eggs 107–133 μ in diameter.

Rostrum (Fig. 216) well formed, extending as a tongue-shaped raised area between bases of antennae. Between rostrum and labrum a small raised keel-like area.

First antenna (Fig. 217) slender, 203 μ long, and 7-segmented. Lengths of segments: 17 (35 μ along anterior margin), 64, 18, 19, 30, 22, and 15 μ respectively. Formula for armature: 4, 13 (5 + 2 +6), 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete, as in many lichomolgids. All setae naked.

Second antenna (Fig. 218) 4-segmented. Armature: 1, 1, 3, I. Last segment 28 μ along outer side, 15 μ along inner side. Terminal claw 23 μ along its axis.

Labrum (Figs. 216 and 219) with its free edge having two widely divergent narrow lobes. Immediately dorsal to posteromedian area of labrum two pairs of small spiniform processes.

Mandible (Fig. 220) with an unusually slender proximal part and broadened distal part, the two areas separated by a constricted neck. Distal part bearing on its convex side a large pointed posteriorly directed process (partly hyaline) followed by a row of small serrations, and on its concave side two lobes, each with a row of slender and slightly obtuse spinules. Flagellum moderately long, with lateral spinules distally. Paragnath (Fig. 221) a small lobe with a few hairs. First maxilla (Fig. 222) a single segment with four elements, three finely spinulose setae and a smaller naked seta. Second maxilla (Fig. 223) 2-segmented. First segment with a minute spinule. Second segment bearing on its outer (ventral) margin a minute proximal spinule and a distal lamellate seta and on its inner (dorsal) margin a seta with a row of minute spinules; terminal lash with a row of dentiform spinules becoming more slender distally. Maxilliped (Fig. 224) 3-segmented; first segment unarmed, second with two very unequal setae, and third with two setae (one large and barbed, the other small and naked) and terminating in a barbed spiniform process.

Area between maxillipeds and first pair of legs not protuberant and formed as in Figure 216. Immediately anterior to this area and between second maxillae a median minutely setose lobe.

Legs 1–4 (Figs. 225, 226, 227, and 228) with trimerous rami, except for endopod of leg 4 which has only a single segment. Armature as follows:

P_1	protopod 0–1; 1–0	exp I–0; I–1; III, I, 4 end 0–1; 0–1; I, 5
P_2	protopod 0–1; 1–0	exp I–0; I–1; III, I, 5 end 0–1; 0–2; I, II, 3
P_3	protopod 0–1; 1–0	exp I–0; I–1; II, I, 5 end 0–1; 0–2; II, 2
P_4	protopod 0–1; 1–0	exp I–0; I–1; II, I, 5 end 0

Inner coxal seta long and haired in legs 1–3, but in leg 4 only 7 μ long and naked. Hairs on inner margin of basis in all four legs. Endopod of leg 3 (Fig. 227) with last segment having formula of II, 2, in-

stead of I, II, 2 as often seen in other lichomolgid genera. Endopod of leg 4 (Fig. 229) a single small unarmed segment 17 × 9 μ, bearing a few outer hairs. Often on this endopod a small distal hyaline lobe is present (Figs. 230 and 231), probably not representing a segment.

Leg 5 (Fig. 232) with a broad free segment 85 × 40 μ, its inner surface slightly concave, and armed with two terminal naked setae 39 and 44 μ long. Between these two setae a patch of minute spinules. Seta on body near free segment 46 μ and naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 213).

Color in life in transmitted light slightly amber, eye red, egg sacs grayish black.

Male.—Body (Fig. 233) resembling in general form that of female. Length 0.87 mm (0.81–0.90 mm) and greatest width 0.28 mm (0.27–0.29 mm), based on 10 specimens. Ratio of length to width of prosome 1.43:1. Segment of leg 1 fused with head. Epimeral areas of metasomal segments as in female.

Segment of leg 5 (Fig. 234) 49 × 112 μ. Genital segment 169 × 156 μ, only slightly longer than wide, its lateral borders gently rounded in dorsal view. Four postgenital segments 44 × 56, 53 × 51, 63 × 48, and 34 × 51 μ from anterior to posterior, the next to the last segment being the longest, as in the female.

Caudal ramus resembling that of female, 43 × 22 μ.

Dorsal surface of body ornamented much like that of female. Ratio of length of prosome to that of urosome 1:1.

Rostrum similar to that of female.

First antenna segmented and armed as in female, but two aesthetes added on segment 2 and one on segment 4 (their positions indicated by arrows in Figure 217), so that formula is 4, 13 + 2 aesthetes, 6, 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 235) slender and 4-segmented, assuming that the proximal part of claw represents a fourth segment. First segment unarmed, second with two naked setae and two rows of spinules on its inner surface, third small and unarmed. Claw long, slender, and recurved, 156 μ along its axis, with weak indication of division about midway. Proximal part of claw with two unequal setae, the smaller seta naked, the larger with distal spinules; terminal lamella long and narrow.

Area between maxillipeds and first pair of legs as in female. Small median lobe between second maxillae as in that sex.

Legs 1–4 segmented and armed as in female, but slight sexual dimorphism in endopods of legs 1–3. Endopod of leg 1 (Fig. 236) with third segment relatively longer than in female and with outermost seta short (less than length of segment). Endopod of leg 2 (Fig. 237) with third segment broader, two terminal spiniform processes longer, and inner terminal spine relatively shorter than in female. Endopod of leg 3 (Fig. 238) with third segment relatively shorter and broader than in female. Endopod of leg 4 as in female. Outer seta on basis of leg 1 with proximal lateral hairs.

Leg 5 (Fig. 239) with free segment smaller and narrower than in female, 24 × 11 μ, its two terminal setae 11 and 28 μ long. Three small patches of minute spinules as indicated in figure. Seta on body near base of free segment 60 μ long. All setae naked.

Leg 6 (Fig. 240) a posteroventral flap on genital segment, bearing two naked setae 31 and 38 μ long.

Spermatophore not observed.

Color in life as in female.

Etymology.—The specific name *montiporae* is based on the generic name of the host.

Comparison with other lichomolgids.—We interpret the endopod of leg 4 of *Haplomolgus* as being 1-segmented, though the presence in some specimens of a small hya-

line terminal lobe might suggest a reduced second segment. This lobe is not always present, however. In three females and one male it was seen on both endopods, in five females and five males on only one endopod, and in two females and one male it was absent.

There are five lichomolgid genera in which the endopod of leg 4 is 1-segmented, namely, *Kelleria* Gurney, 1927, *Lichomolgella* Sars, 1918, *Octopicola* Humes, 1957, *Paramacrochiron* Sewell, 1949, and *Pseudanthessius* Claus, 1889. In these, however, the endopod is elongated and always provided with setae or spines, while in *Haplomolgus* the endopod is rather oval and unarmed (the few minute hairs along the outer margin being regarded as ornamentation rather than as armature). The mandible in these five genera does not have the large pointed posteriorly directed process seen in *Haplomolgus*.

In *Heteranthessius* T. Scott, 1903, the endopod of leg 4 is reduced to a minute knob, leg 5 is rudimentary with only two setae, and the mandible lacks the large process characteristic of *Haplomolgus*.

On the basis of the nature of the endopod of leg 4 the new genus appears to occupy a position between the group of five genera mentioned above and *Heteranthessius*. The unarmed 1-segmented endopod of leg 4 serves to distinguish *Haplomolgus* from all other lichomolgid genera known to us.

RAVAHINA n. gen.

Type and only known species: *Ravahina tumida* n. sp.

Female.—Body transformed, with swollen prosome. Segment of leg 1 weakly delimited from head. Urosome 5-segmented. Caudal ramus with six elements. First antenna 7-segmented. Second antenna 4-segmented. Mouthparts lichomolgid. Mandible with a small terminal spiniform process apparently representing a much reduced flagellum. First maxilla with three elements. Second maxilla 2-segmented. Maxilliped 3-segmented.

Legs 1 and 2 with 3-segmented rami; legs 3 and 4 with 3-segmented exopods but endopods represented only by a small unsegmented knoblike process. Leg 5 with free segment bearing two terminal setae.

Other features as in the species described below.

Associated with madreporarian corals.

Male.—Unknown.

Etymology.—The generic name is formed from Ravahiny, the name of a queen of the Sakalava, who reigned at Majunga in Madagascar about 1800. Gender feminine.

Ravahina tumida n. gen., n. sp.
Figs. 241–259

Type material.—2 females from *Porites* sp. cf. *P. andrewsi* Vaughan in a depth of 2 m, Pte. Lokobe, Nosy Bé, Madagascar. Collected September 2, 1960. One of these females is the holotype, the other (dissected) a paratype. Also one paratypic female and one immature specimen from *Porites* sp. cf. *P. andrewsi* in 3 m, Pte. de Tafondro, Nosy Bé (about five kilometers east of Pte. Lokobe). Collected September 28, 1960. Holotype and one paratype deposited in the United States National Museum, dissected paratype and immature specimen in the collection of A. G. Humes.

Other specimen.—1 female from *Porites* sp. cf. *P. andrewsi* in 2 m, Pte. de Tafondro, August 29, 1960.

Female.—Body (Figs. 241 and 242) with expanded and swollen prosome. Urosome relatively slender and sometimes contracted. Dimensions of two uncontracted specimens 1.97 × 1.15 mm and 1.67 × 1.10 mm. Ratio of length to width of prosome about 1.1:1. Segment of leg 1 weakly delimited from head.

Segment of leg 5 (Fig. 243) 91 × 363 μ. Genital segment broad, 173 × 363 μ, with rounded lateral borders in dorsal view. Areas of attachment of egg sacs located dorsally, each area (Fig. 244) with two minute setae 3 μ long. Three postgenital

segments 70 × 213, 73 × 180, and 104 × 208 μ from anterior to posterior, the last segment expanded in its posterior two-thirds.

Caudal ramus (Fig. 245) moderately elongated, 159 × 65 μ in greatest dimensions, about 2.45 times longer than wide. All setae naked and all spiniform except dorsal pedicellate seta which is slender and 34 μ long. Outer lateral seta 32 μ, outermost terminal seta 28 μ, innermost terminal seta 18 μ, and two median terminal setae 47 μ (inner) and 33 μ (outer). A few small hyaline setules on dorsal surface of ramus.

Dorsal surface of prosome with minute refractile irregularities (Fig. 246) in the cuticula. Dorsal and ventral surfaces of urosome almost entirely lacking ornamentation. Ratio of length of prosome to that of urosome 1.85:1.

Egg sac unknown.

Rostral area (Fig. 247) weakly developed.

First antenna (Fig. 248) slender, 393 μ long, and 7-segmented. Lengths of segments: 24 (64 μ along anterior edge), 106, 38, 44, 65, 40, and 36 μ respectively. Formula for armature: 3, 14 (6 + 8), 5, 4, 5, 2 + 1 aesthete, and 7 + 1 aesthete. All setae naked.

Second antenna (Fig. 249) 4-segmented. Last segment 77 μ along outer edge, 44 μ along inner edge. Armature: 1, 1, 3, 6 + I. Terminal claw 46 μ along its axis; adjacent long seta (jointed and somewhat spiniform) 56 μ.

Labrum (Fig. 250) with two slightly truncated posteroventral lobes.

Mandible (Fig. 251) with distal part (beyond slight constriction) bladelike, its convex side with two small surficial lobes and a distal marginal serrated fringe, its concave edge with a row of prominent spines. Tip of mandible forming a small spiniform process, perhaps representing the flagellum usually present in lichomolgids. Paragnath not observed. First maxilla (Fig. 252) a small lobe with three terminal elements. Second maxilla (Fig. 253) 2-segmented. First segment unarmed. Second segment with a minute proximal setule on its outer (ventral) margin, a naked seta on its distal anterior surface, and a strongly spinulose distal area on its inner (dorsal) margin, the segment terminating in a lash (apparently only partially articulated with the segment) bearing a row of strong spines. Maxilliped (Fig. 254) 3-segmented; first segment unarmed, second with two very unequal naked setae, and third with two barbed spines (the distal one possibly lacking an articulation and thus being a process rather than a spine) and two small naked setae.

Area between maxillipeds and first pair of legs not protuberant. Without sclerotization between bases of maxillipeds.

Leg 1 (Fig. 255) and leg 2 (Fig. 256) with 3-segmented rami, leg 3 (Fig. 257) and leg 4 (Fig. 258) with 3-segmented exopods but endopods reduced to a small process. Armature as follows:

P_1	protopod 0–0; 1–0	exp I–(1); I–1; II, II, 2	end 0–0; 0–0; I, 2
P_2	protopod 0–0; 1–0	exp I–(2); I–1; II, II, 1	end 0–0; 0–1; II
P_3	protopod 0–0; 1–0	exp I–0; I–1; II, II, 1	end –
P_4	protopod 0–0; 1–0	exp I–0; I–1; II, II	end –

All four legs without inner coxal seta and without inner marginal hairs on basis. First segment of exopod of leg 1 with an inner setule (probably to be considered as ornamentation rather than as a part of the armature); two such setules in leg 2, but these setules absent in legs 3 and 4. Both first and second segments of endopod of leg 1 and first segment of endopod of leg 2 lacking the inner seta usually seen in lichomolgids. Endopod of legs 3 and 4 consisting of a small knoblike unornamented and unsegmented process lacking a definite articulation with the basis. Intercoxal plates in all four legs wide and short as in leg 1.

Leg 5 (Fig. 259) with a moderately elongated free segment, 73 × 30 μ, of somewhat irregular outline. Two terminal naked

setae 36 and 19 μ in length. Seta on body near free segment 34 μ and naked.

Leg 6 probably represented by the two setae near attachment of egg sac (see Figure 244).

Color in life in transmitted light somewhat opaque, eye red.

Male.—Unknown.

Etymology.—The specific name *tumida,* from Latin = swollen, refers to the tumid prosome.

Comparison with other lichomolgids.—*Ravahina tumida* apparently belongs to the family Lichomolgidae. Its mandible lacks the long flagellum characteristic of many lichomolgid genera, but shows a small terminal spiniform process which may represent a very reduced flagellum. (Reduction of the flagellum to a lesser extent is seen in lichomolgids such as *Monomolgus unihastatus* Humes and Frost, 1964, *Kombia angulata* Humes, 1962, and *Rhynchomolgus corallophilus* Humes and Ho, 1967a.) The other mouthparts are essentially lichomolgid in their form.

The first antenna and legs 1–4 have an armature somewhat different from that in many lichomolgid genera. However, in certain transformed lichomolgid genera such as *Kombia* Humes, 1962, *Heteranthessius* T. Scott, 1903, *Rhynchomolgus* Humes and Ho, 1967a, and *Temnomolgus* Humes and Ho, 1967c, the armature of these appendages may not conform to the more "typical" arrangement seen in untransformed lichomolgids (for example, *Lichomolgus* Thorell, 1860).

Evidence for placing *Ravahina* in the Lichomolgidae would be more conclusive if the structure of the male were known. On the basis of our knowledge of the female, however, we think that the new genus should be provisionally considered as belonging to the Lichomolgidae.

KEY TO THE SEVENTEEN GENERA OF LICHOMOLGIDAE KNOWN FROM THE VICINITY OF NOSY BÉ, MADAGASCAR

1. Legs 1 and 2 with both rami 3-segmented 2
   Legs 1 and 2 with one or both rami reduced to two segments 13
2. Leg 3 with both rami 3-segmented 3
   Leg 3 with one or both rami reduced 15
3. Leg 4 with endopod 3-segmented 4
   Leg 4 with endopod of one or two segments 5
4. Second antenna with claw on third segment; on holothurians ..... *Scambicornus* Heegaard, 1944
   Second antenna with terminal claws on fourth segment; in mantle cavity of pelecypods ..... *Modiolicola* Aurivillius, 1882
5. Leg 4 with endopod 2-segmented, with a distinct line of segmentation between the segments 6
   Leg 4 with endopod 1-segmented 16
6. Second antenna 3-segmented 7
   Second antenna 4-segmented 9
7. Second segment of endopod of leg 4 with two elements; third and fourth segments of second antenna fused to form an apparent single segment; on corals ..... *Lichomolgus* Thorell, 1860 (in part)
   Second segment of endopod of leg 4 with one or three elements 8
8. Mandible with proximal region having two outer serrated lobes; second antenna with a single terminal claw; second segment of endopod of leg 4 with a single spine; on corals ..... *Prionomolgus* n. gen.
   Mandible with proximal region having a row of setae or spines; second antenna with 1, 2, or 3 terminal claws; second segment of endopod of leg 4 with three elements; on asteroids ..... *Stellicola* Kossmann, 1877
9. Endopod of leg 4 with a single element on second segment 10
   Endopod of leg 4 with more than one element on second segment 11
10. First segment of endopod of leg 4 with an inner seta; body rather transformed; in mantle cavity of pelecypods ..... *Gelastomolgus* Humes (in press)
    First segment of endopod of leg 4 unarmed; body typically cyclopoid; on corals ..... *Monomolgus* Humes and Frost, 1964
11. Endopod of leg 4 with two elements on second segment 12
    Endopod of leg 4 with four or five elements (spines or setae) on last segment, formula variable; in zoanthids ..... *Indomolgus* Humes and Ho, 1967c
12. With a pair of setae on anterior part of labrum; maxilliped in female with a long slender last segment; on polychaetes ..... *Nasomolgus* Sewell, 1949
    Without a pair of setae on labrum; maxilliped in female with short last segment; in mantle cavity of pelecypods, on sea anemones, corals, alcyonarians, zoan-

thids, nudibranchs ..... *Lichomolgus* Thorell, 1860 (in part)

13. Both rami of legs 1 and 2 two-segmented; in corals ..... *Rhynchomolgus* Humes and Ho, 1967a
    In legs 1 and 2 exopods 3-segmented, endopods 2-segmented 14
14. Endopod of leg 3 and entire leg 4 absent; in corals ..... *Kombia* Humes, 1962
    Endopod of leg 3 present; leg 4 with 3-segmented rami; on holothurians ..... males of *Scambicornus* Heegaard, 1944
15. Leg 3 with 3-segmented exopod, endopod a small process; in corals ..... females of *Ravahina* n. gen.
    Leg 3 represented only by two setae; in zoanthids ..... *Temnomolgus* Humes and Ho, 1967c
16. Leg 5 with a distinct segment 17
    Leg 5 without a distinct segment; on echinoids, polychaetes ..... *Pseudanthessius* Claus, 1889
17. Second antenna 3-segmented, with large terminal denticulated claw and sometimes an unguiform seta; on hydroids ..... *Macrochiron* Brady, 1872
    Second antenna 4-segmented 18
18. Last segment of second antenna with four claws; endopod of leg 4 with three elements; on cephalopods ..... *Octopicola* Humes, 1957
    Last segment of second antenna with one claw; endopod of leg 4 unarmed; on corals ..... *Haplomolgus* n. gen.

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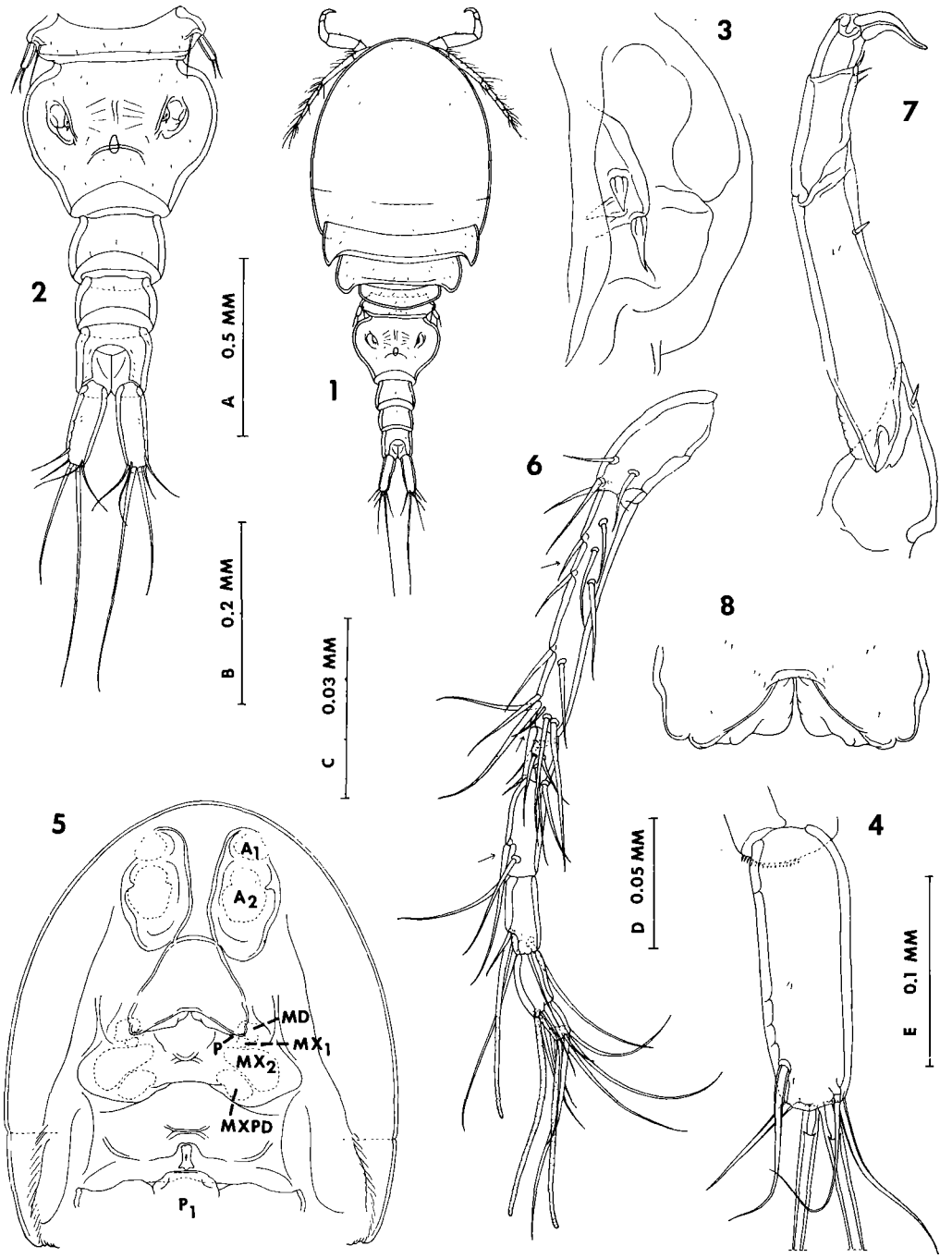
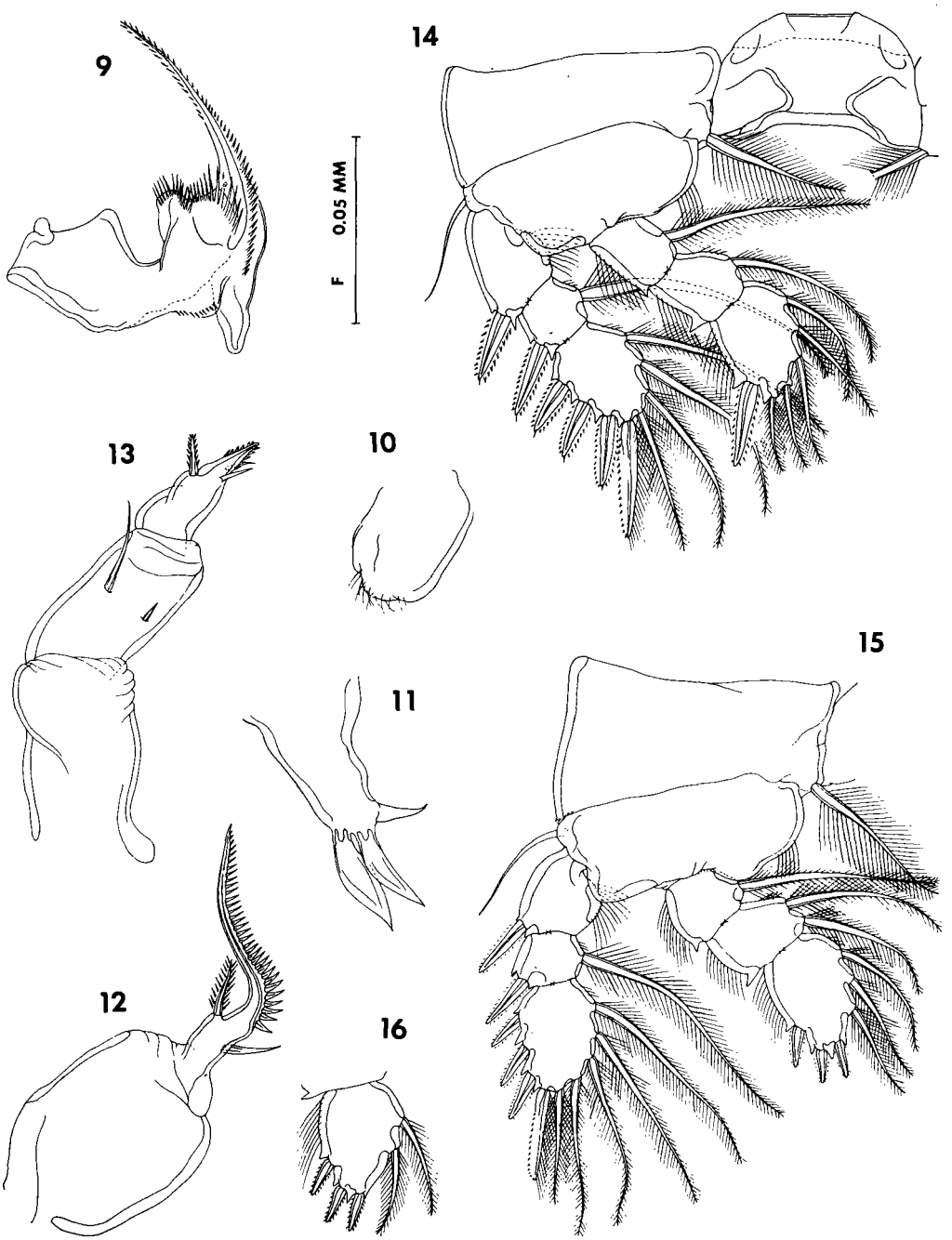
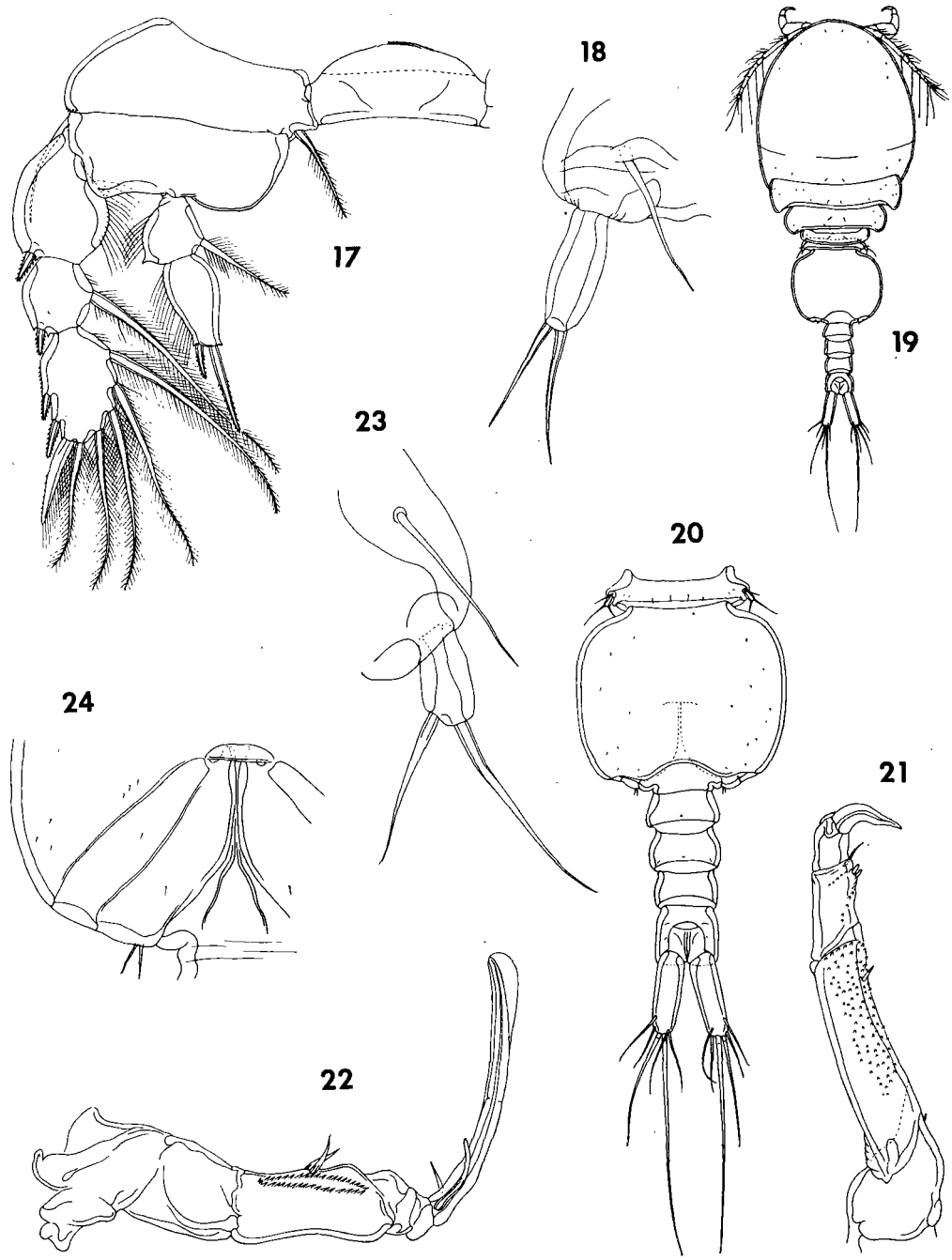


Figures 1–8. *Lichomolgus campulus* n. sp., female. 1, body, dorsal (A); 2, urosome, dorsal (B); 3, area of attachment of egg sac, dorsal (C); 4, caudal ramus, dorsal (D); 5, cephalosome, ventral (B); 6, first antenna, with arrows indicating positions of aesthetes in male, anterodorsal (E); 7, second antenna, outer (E); 8, labrum, ventral (E).

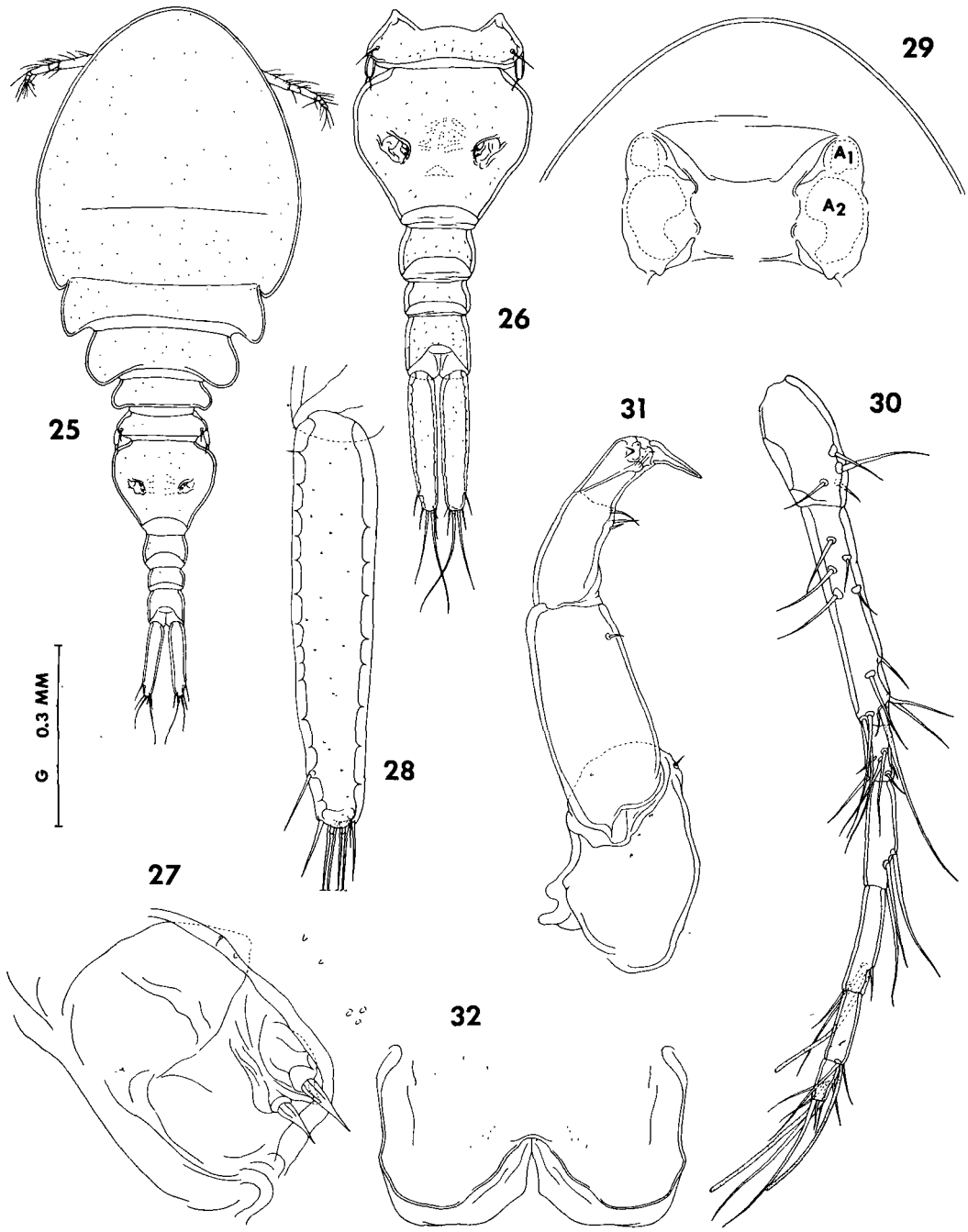


Figures 9–16. *Lichomolgus campulus* n. sp., female (continued). 9, mandible, posterior (F); 10, paragnath, anterior (F); 11, first maxilla, anterior (F); 12, second maxilla, posterior (D); 13, maxilliped, inner (F); 14, leg 1 and intercoxal plate, anterior (D); 15, leg 2, anterior (D); 16, last segment of endopod of leg 3, anterior (D).

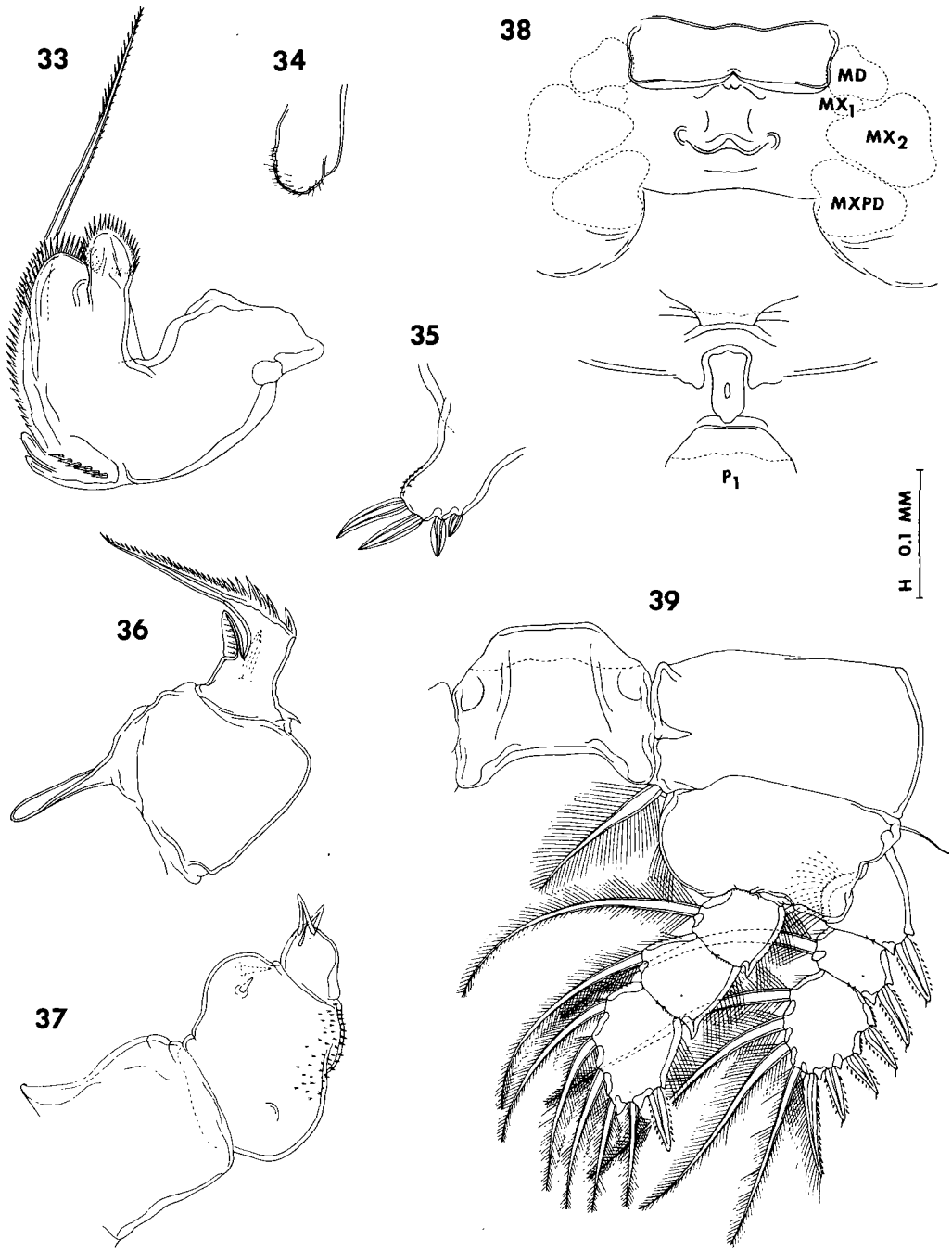


Figures 17–18. *Lichomolgus campulus* n. sp., female (continued). 17, leg 4 and intercoxal plate, anterior (D); 18, leg 5, dorsal (F).

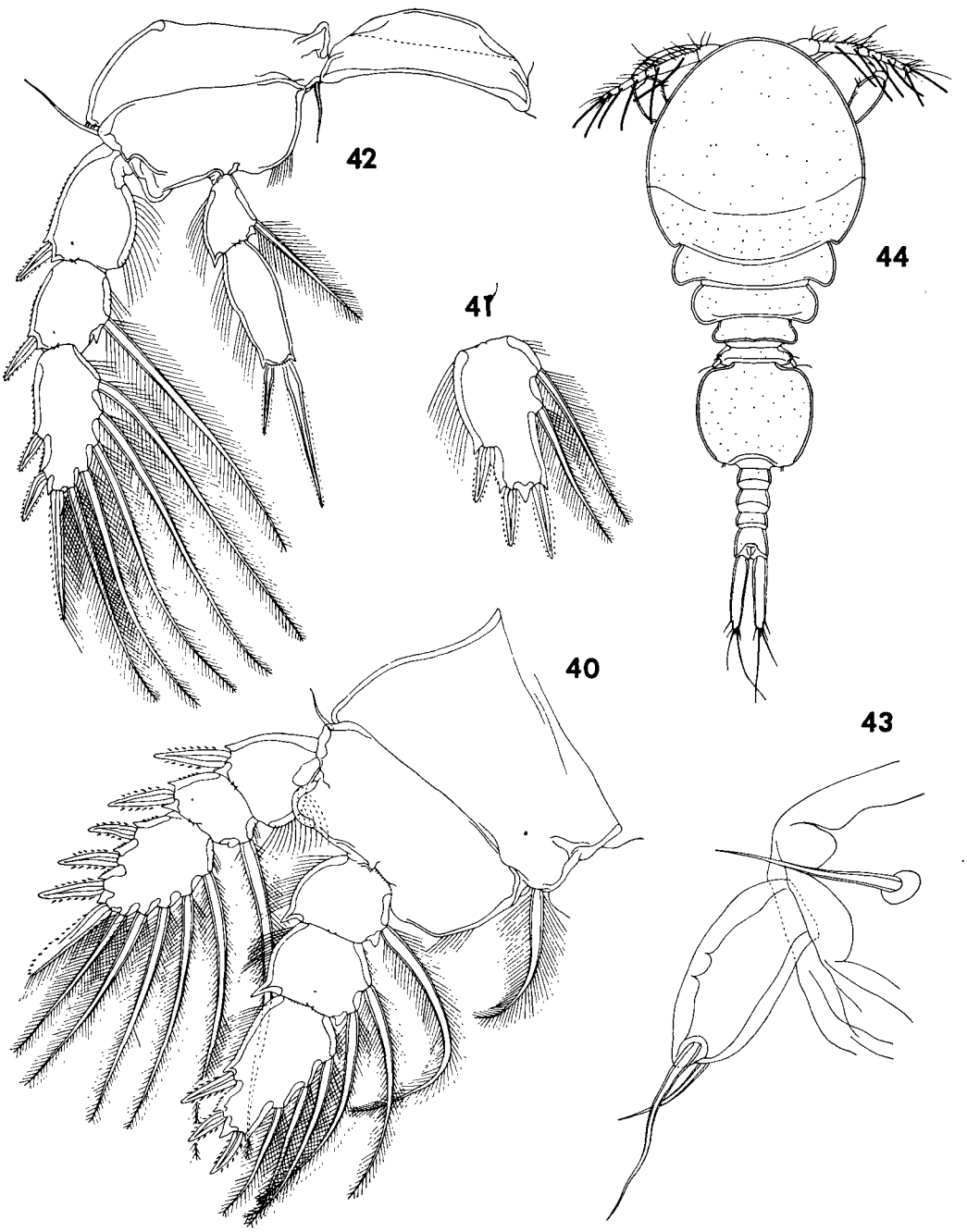
Figures 19–24. *Lichomolgus campulus* n. sp., male. 19, body, dorsal (A); 20, urosome, dorsal (B); 21, second antenna, outer (E); 22, maxilliped, inner (E); 23, leg 5, posterodorsal (G); 24, leg 6, ventral (E).



Figures 25–32. *Lichomolgus digitatus* n. sp., female. 25, body, dorsal (A); 26, urosome, dorsal (G); 27, area of attachment of egg sac, dorsal (C); 28, caudal ramus, dorsal (E); 29, rostral area, ventral (B); 30, first antenna, anterodorsal (E); 31, second antenna, outer (E); 32, labrum, ventral (E).

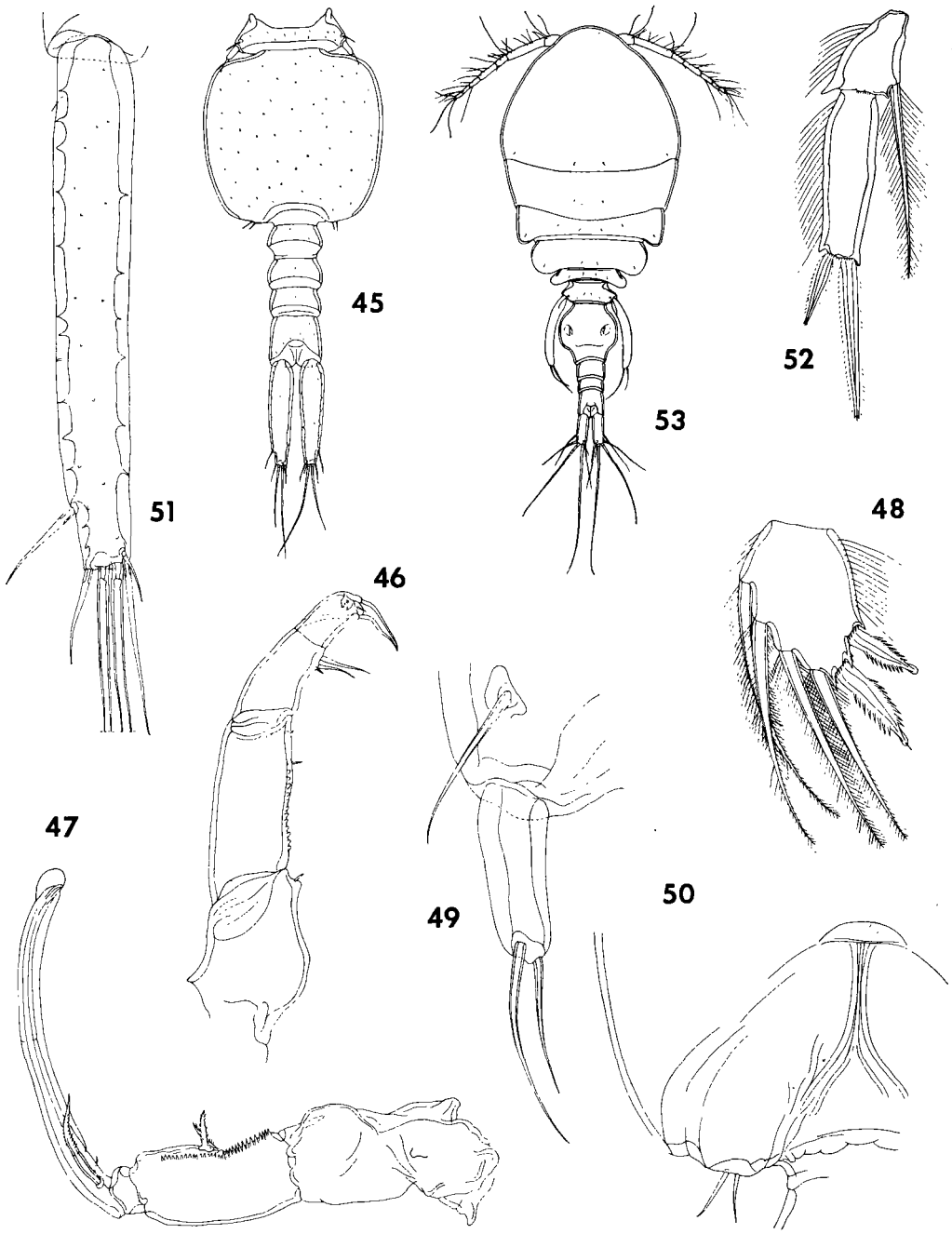


Figures 33–39. *Lichomolgus digitatus* n. sp., female (continued). 33, mandible, posterior (D); 34, paragnath, ventral (D); 35, first maxilla, ventral (D); 36, second maxilla, posterior (E); 37, maxilliped, anterior (D); 38, oral and postoral areas, with edge of labrum turned ventrally, ventral (H); 39, leg 1 and intercoxal plate, anterior (E).



Figures 40–43. *Lichomolgus digitatus* n. sp., female (continued). 40, leg 2, anterior (E); 41, last segment of endopod of leg 3, anterior (E); 42, leg 4 and intercoxal plate, anterior (E); 43, leg 5, dorsal (C).

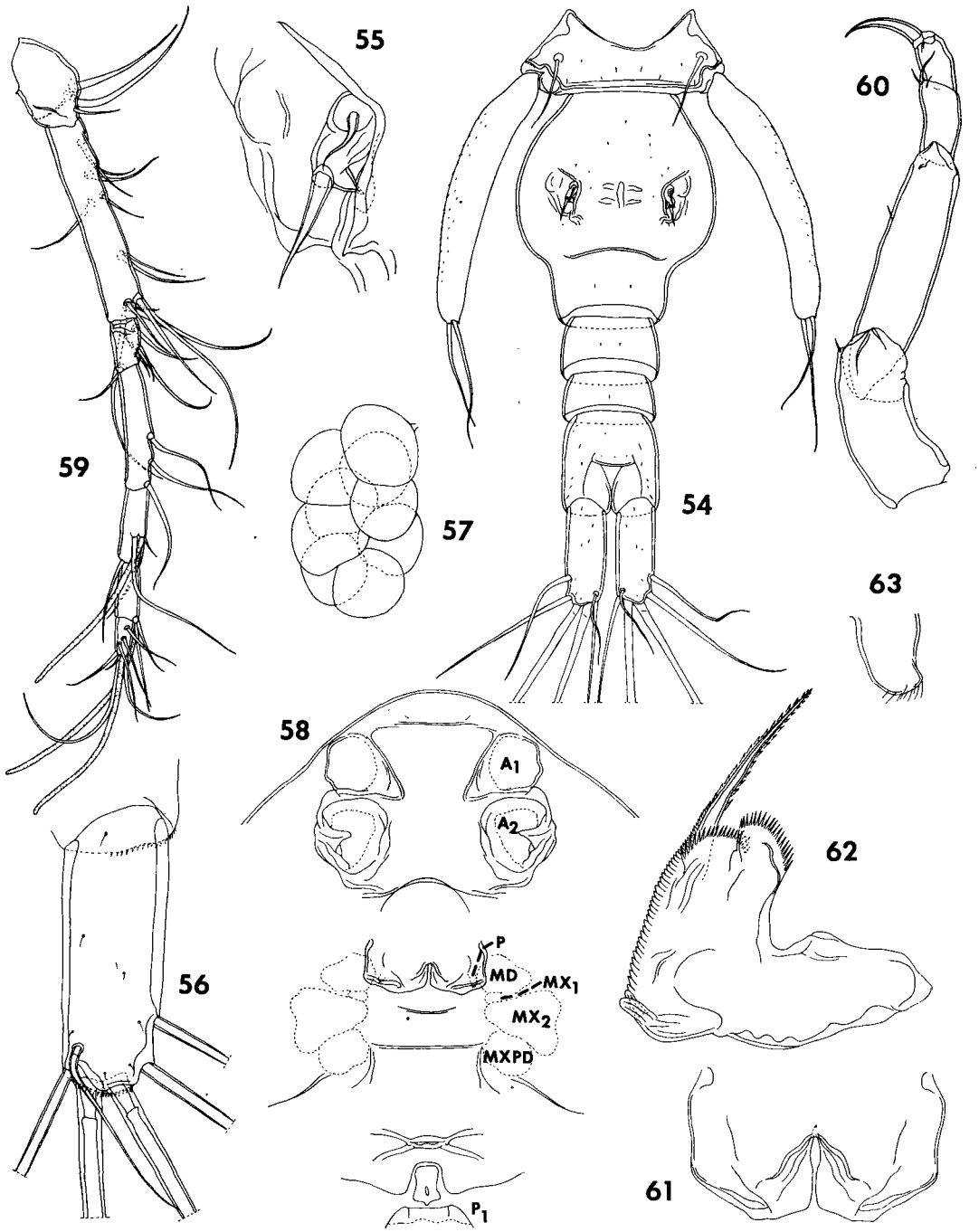
Figure 44. *Lichomolgus digitatus* n. sp., male. 44, body, dorsal (A).



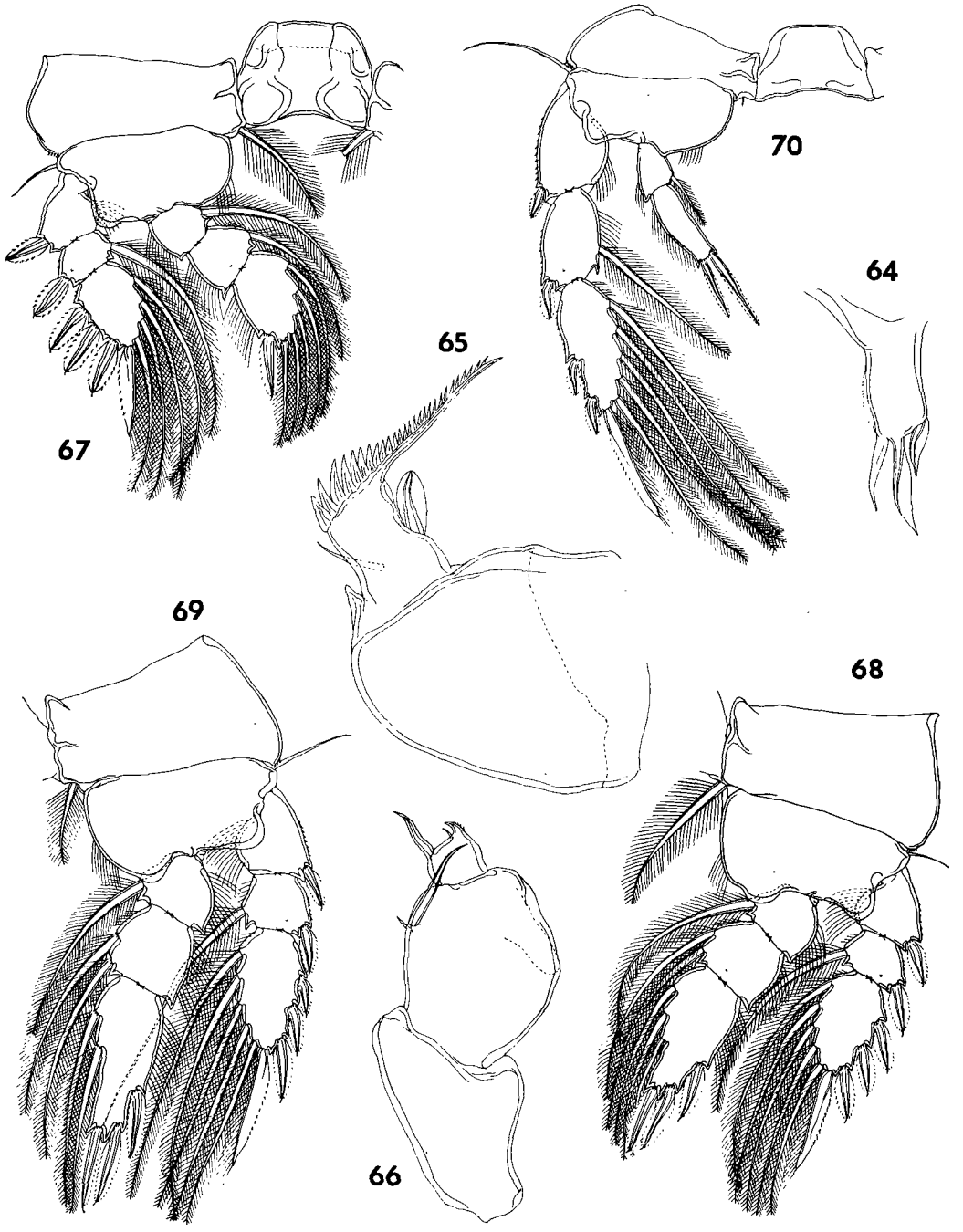
Figures 45–50. *Lichomolgus digitatus* n. sp., male (continued). 45, urosome, dorsal (G); 46, second antenna, inner (E); 47, maxilliped, inner (H); 48, last segment of endopod of leg 1, anterior (D); 49, leg 5, dorsal (C); 50, leg 6, ventral (E).

Figures 51–52. *Lichomolgus digitatus* n. sp., female, from *Porites*. 51, caudal ramus, dorsal (E); 52, endopod of leg 4, anterior (E).

Figure 53. *Lichomolgus prolixipes* n. sp., female. 53, body, dorsal (A).



Figures 54–63. *Lichomolgus prolixipes* n. sp., female (continued). 54, urosome, dorsal (G); 55, area of attachment of egg sac, dorsal (C); 56, caudal ramus, dorsal (F); 57, egg sac, lateral (G); 58, rostral, oral, and postoral areas, ventral (H); 59, first antenna, posteroventral (E); 60, second antenna, inner (E); 61, labrum, ventral (D); 62, mandible, posterior (F); 63, paragnath, ventral (F).



Figures 64–70. *Lichomologus prolixipes* n. sp., female (continued). 64, first maxilla, anterior (F); 65, second maxilla, posterior (F); 66, maxilliped, posterointernal (F); 67, leg 1 and intercoxal plate, anterior (E); 68, leg 2, anterior (E); 69, leg 3, anterior (E); 70, leg 4 and intercoxal plate, anterior (E).

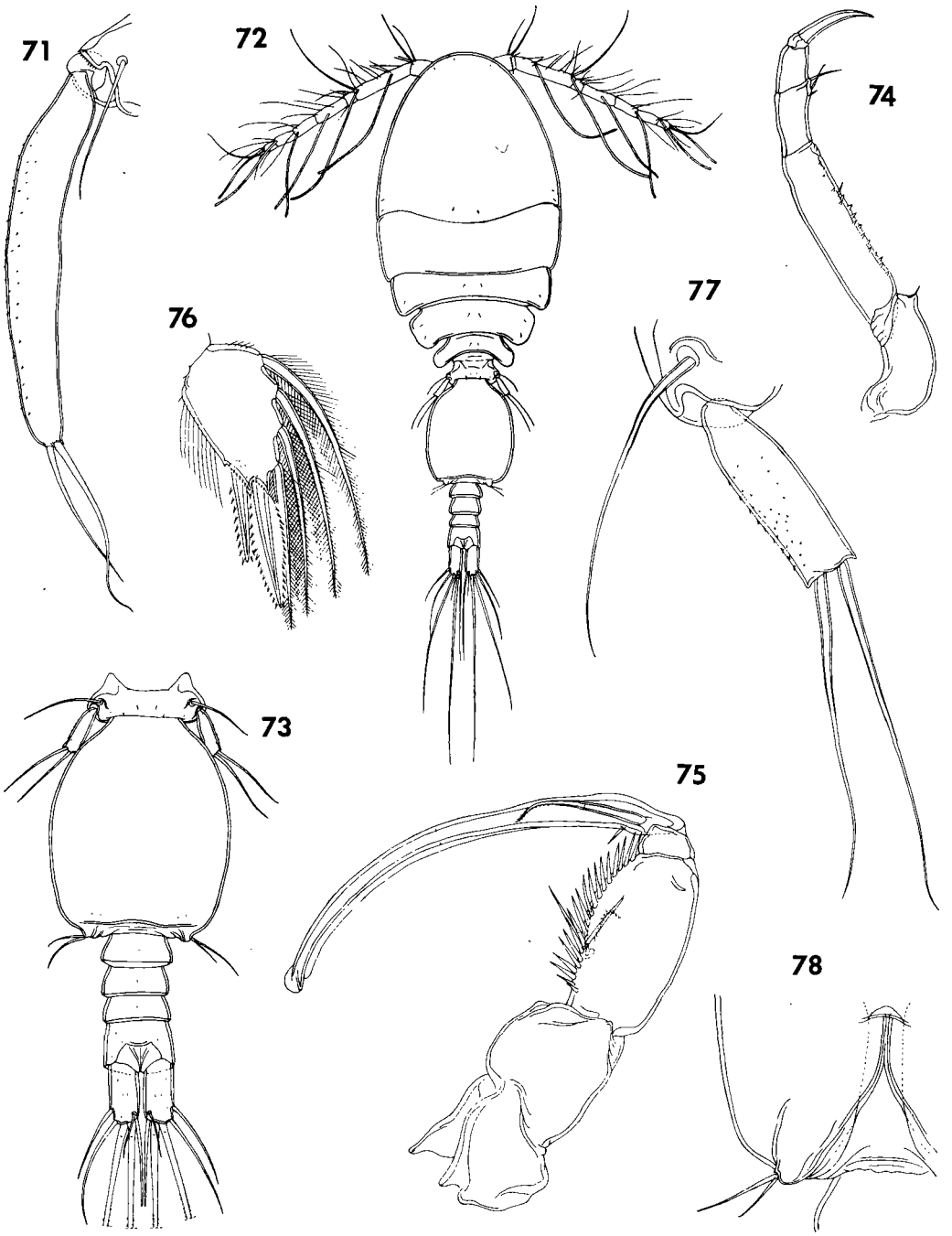
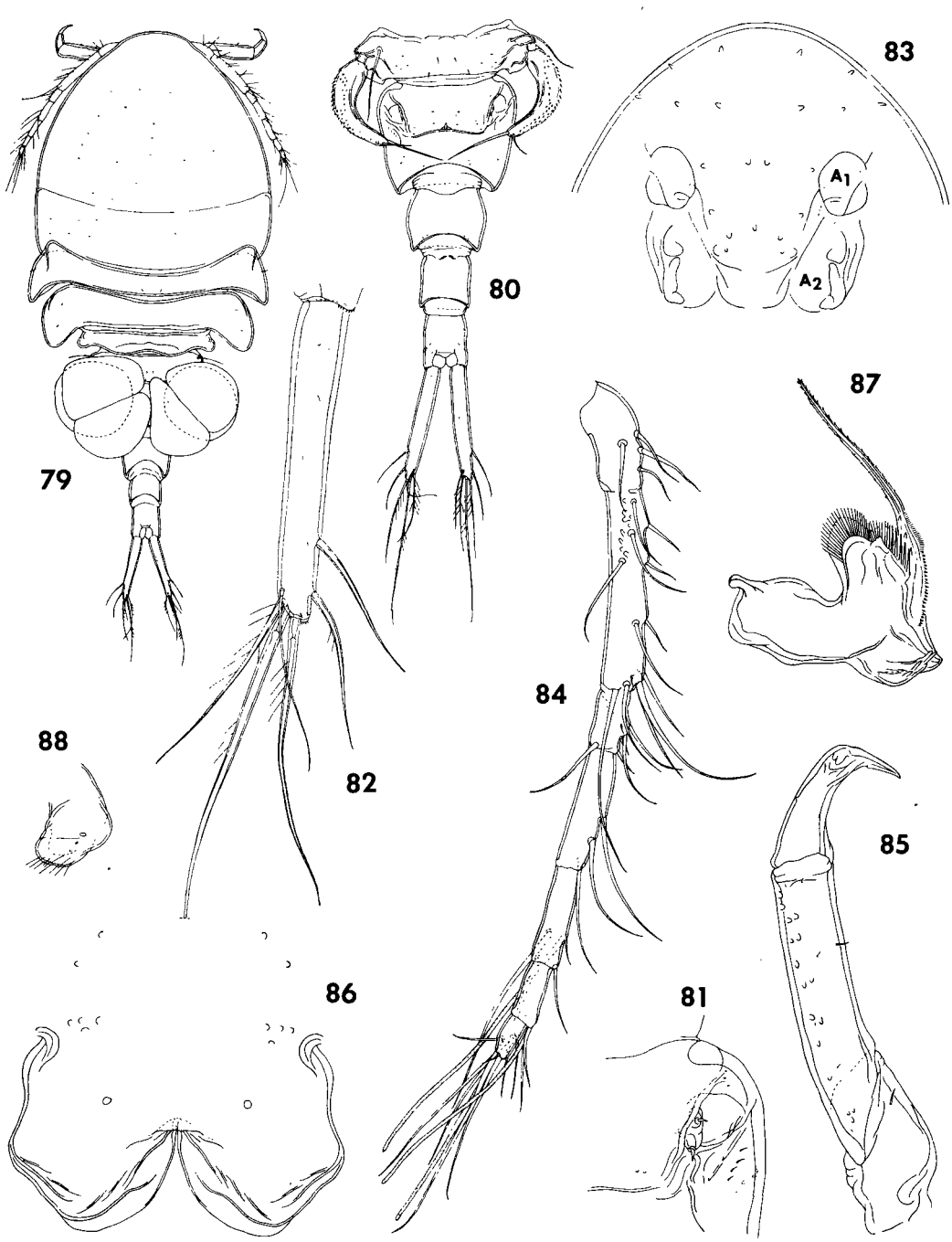
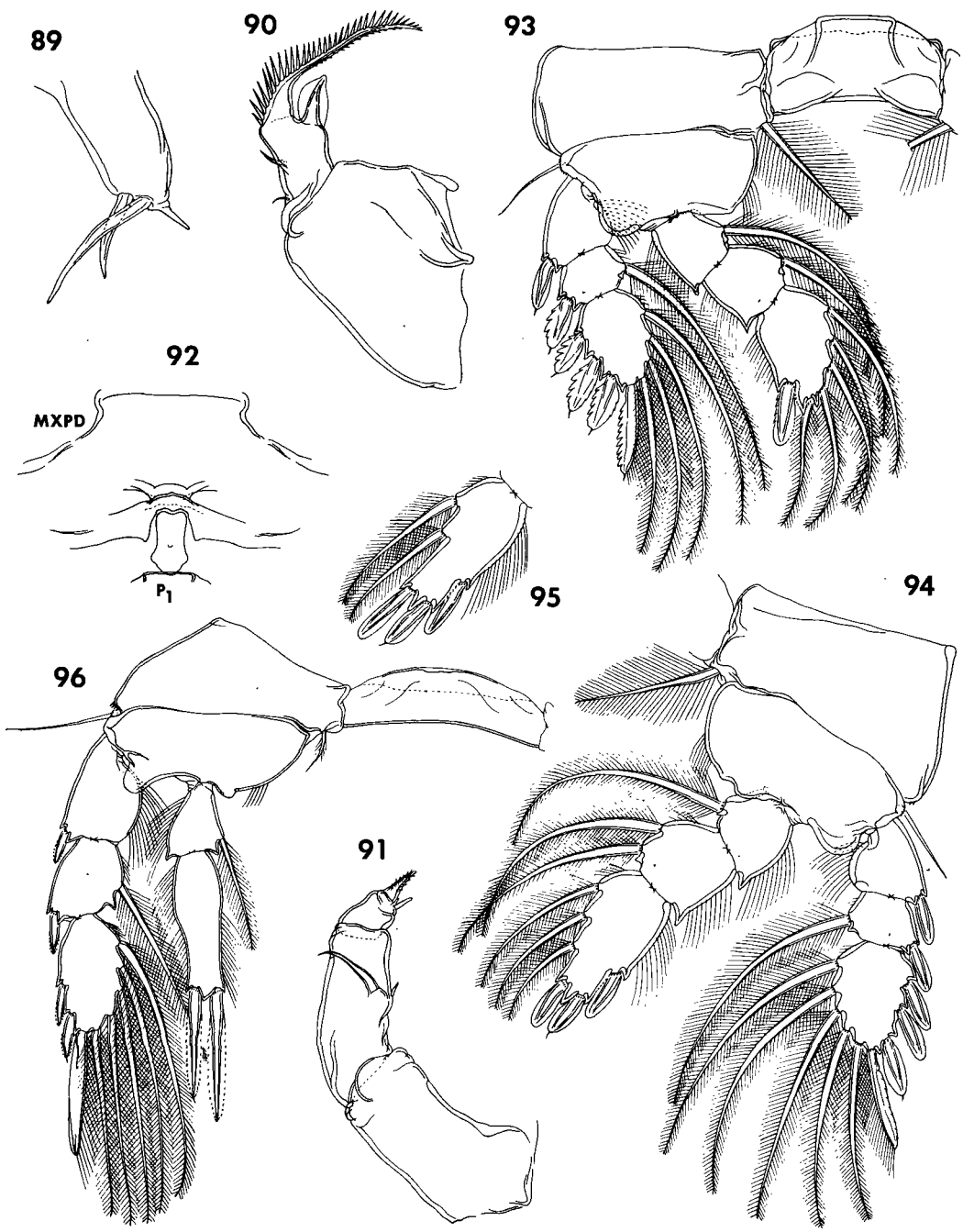


Figure 71. *Lichomolgus prolixipes* n. sp., female (continued). 71, leg 5, dorsal (E).

Figures 72–78. *Lichomolgus prolixipes* n. sp., male. 72, body, dorsal (G); 73, urosome, dorsal (H); 74, second antenna, inner (E); 75, maxilliped, inner (D); 76, last segment of endopod of leg 1, anterior (F); 77, leg 5, dorsal (C); 78, leg 6, ventral (D).



Figures 79–88. *Lichomolgus arcuatipes* n. sp., female. 79, body, dorsal (G); 80, urosome, dorsal (B); 81, area of attachment of egg sac, dorsal (D); 82, caudal ramus, dorsal (D); 83, rostral area, ventral (H); 84, first antenna, dorsal (D); 85, second antenna, outer (D); 86, labrum, ventral (F); 87, mandible, posterior (F); 88, paragnath, ventral (C).



Figures 89–96. *Lichomolgus arcuatipes* n. sp., female (continued). 89, first maxilla, posterior (C); 90, second maxilla, anterior (F); 91, maxilliped, posterior (F); 92, postoral area, ventral (E); 93, leg 1 and intercoxal plate, anterior (D); 94, leg 2, anterior (D); 95, last segment of endopod of leg 3, anterior (D); 96, leg 4 and intercoxal plate, anterior (D).

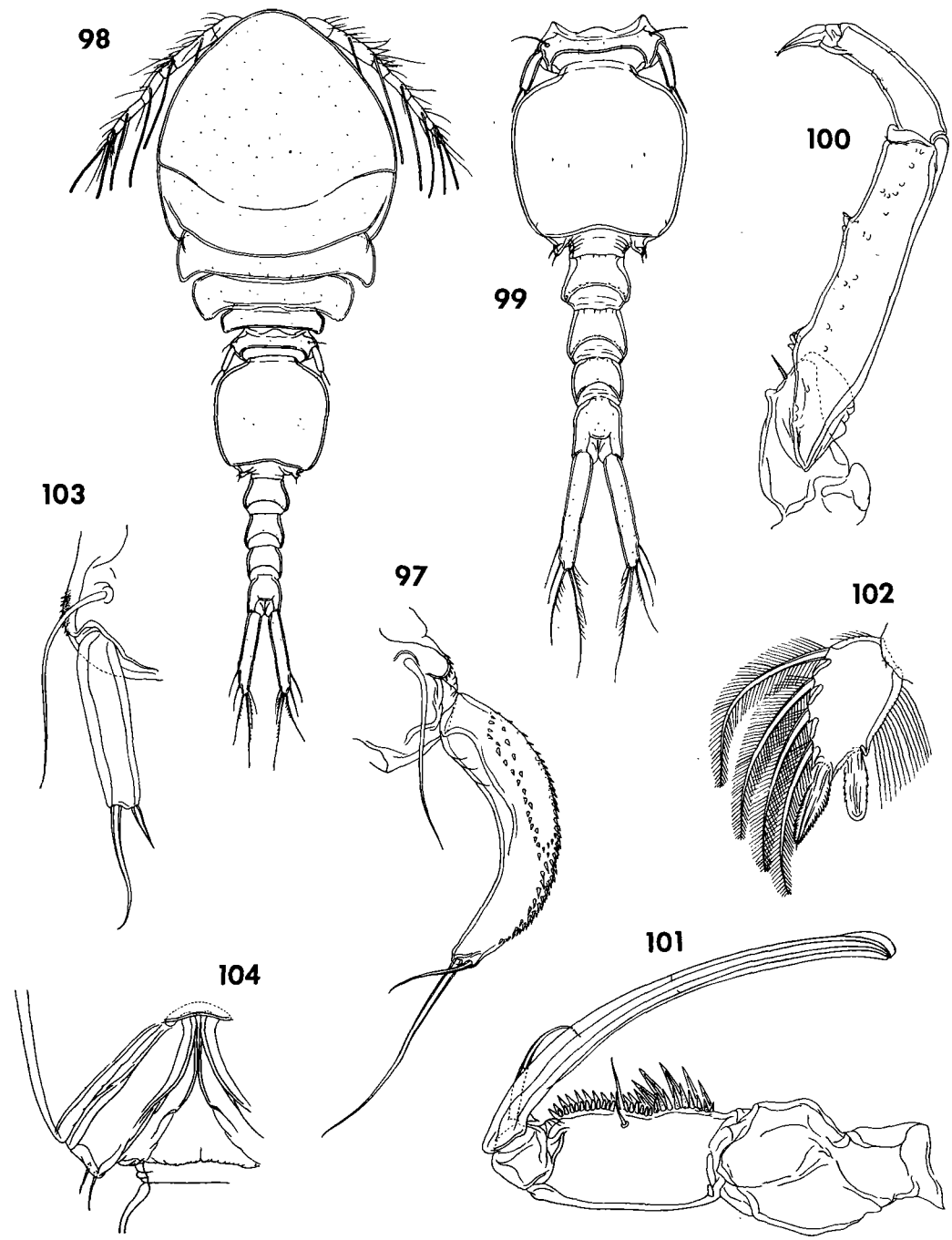
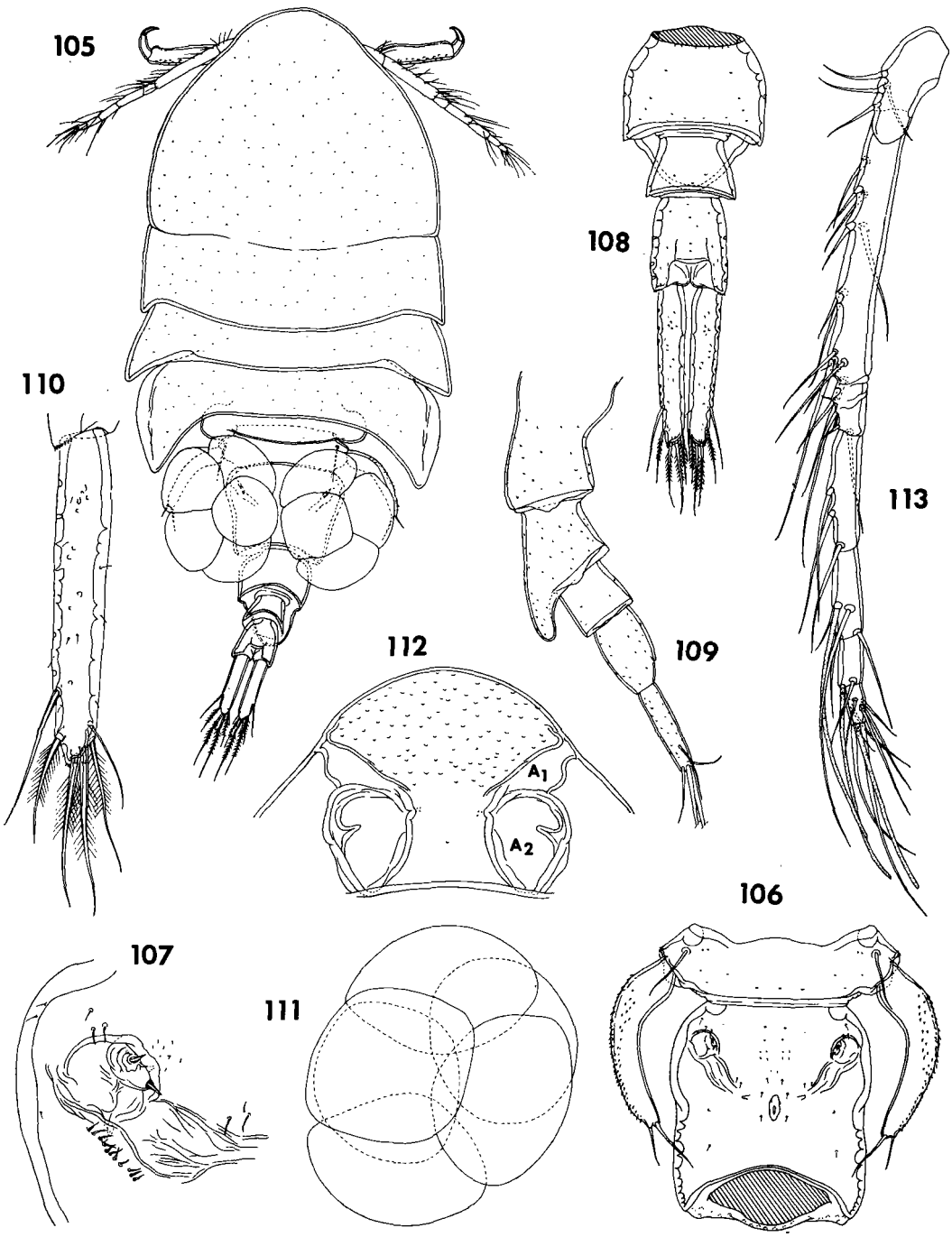
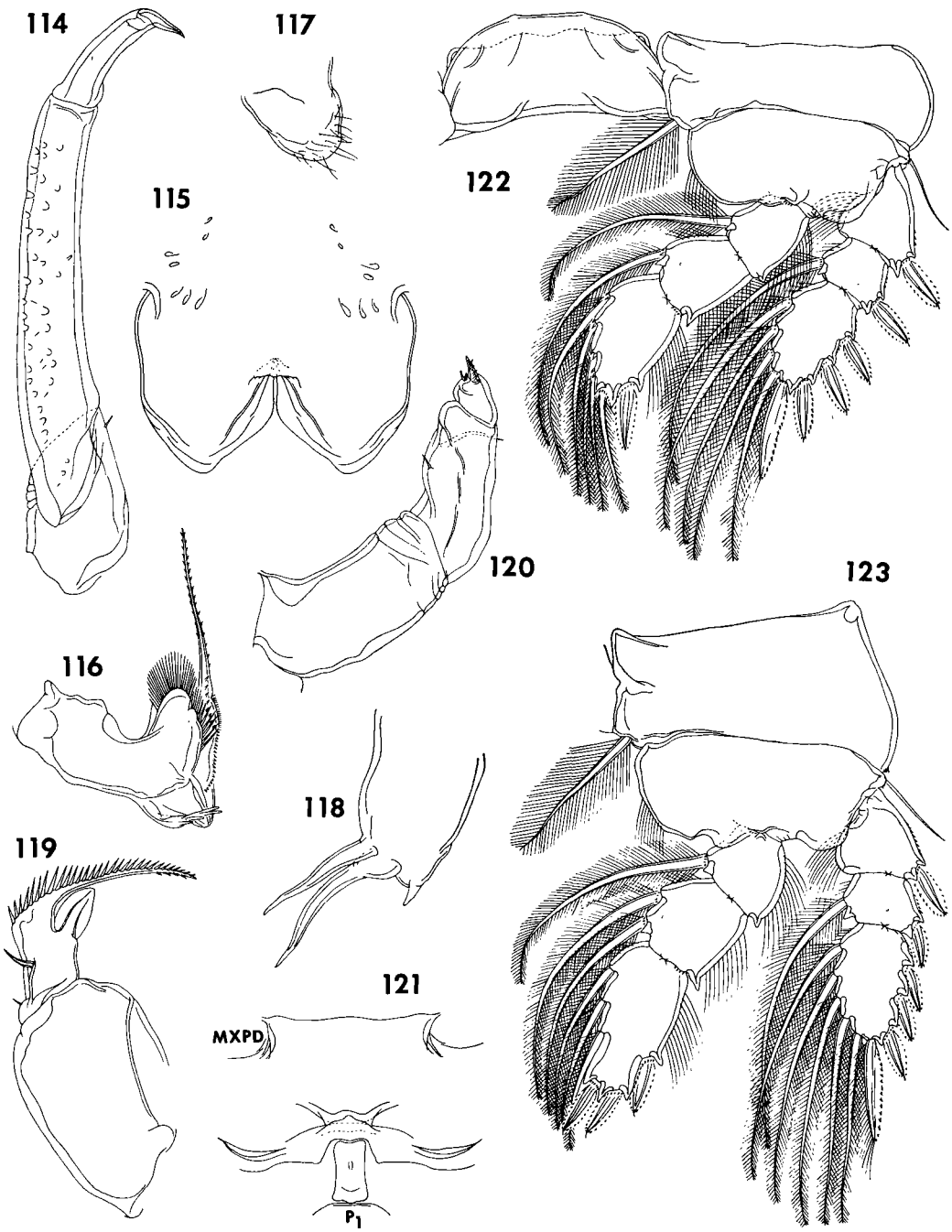


Figure 97. *Lichomolgus arcuatipes* n. sp., female (continued). 97, leg 5, dorsal (D).

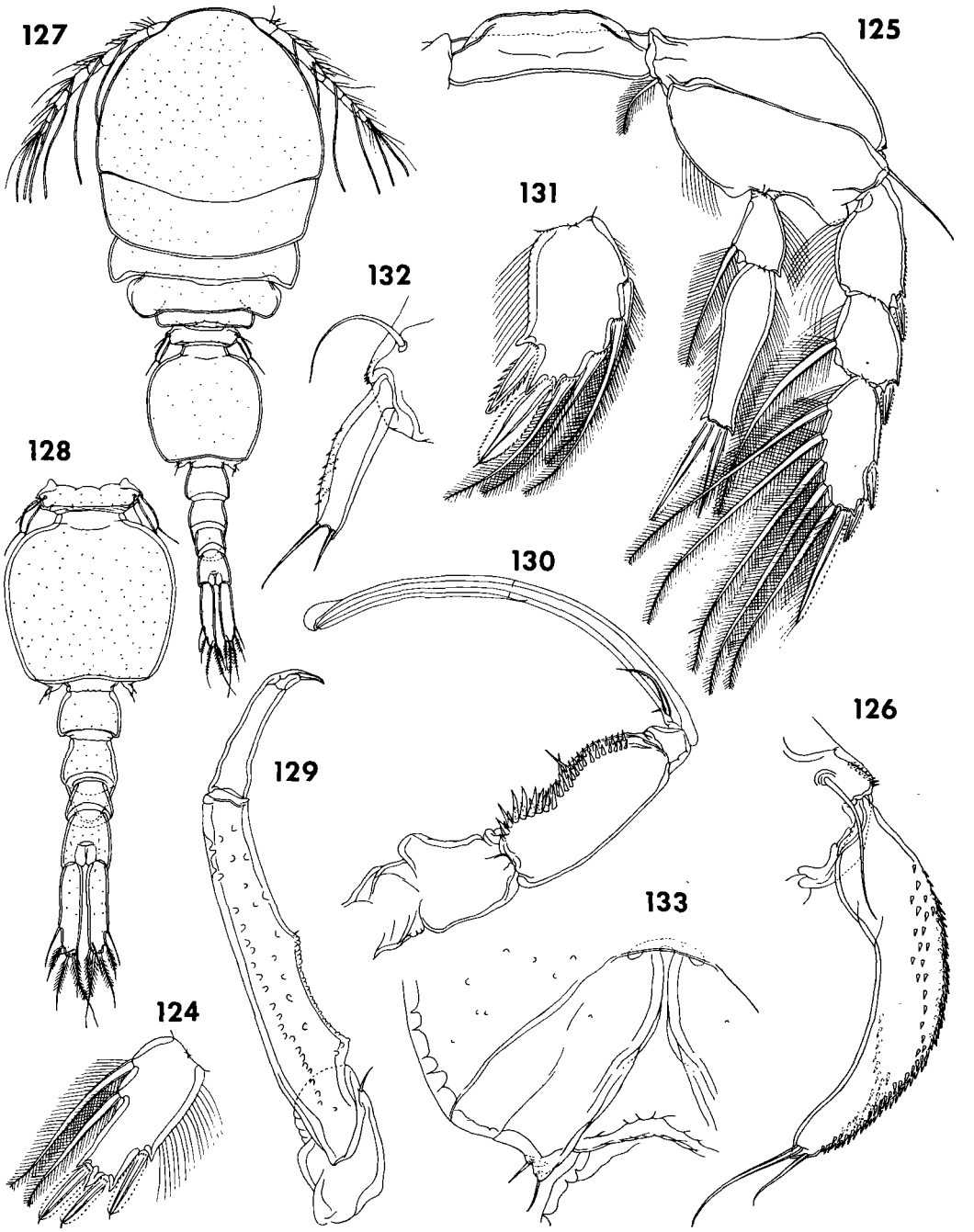
Figures 98–104. *Lichomolgus arcuatipes* n. sp., male. 98, body, dorsal (G); 99, urosome, dorsal (B); 100, second antenna, outer (D); 101, maxilliped, outer (E); 102, last segment of endopod of leg 1, anterior (D); 103, leg 5, dorsal (F); 104, leg 6, ventral (E).



Figures 105–113. *Lichomolgus lobophorus* n. sp., female. 105, body, dorsal (G); 106, segment of leg 5 and genital segment, dorsal (B); 107, area of attachment of egg sac, dorsolateral (D); 108, postgenital segments and caudal rami, dorsal (B); 109, part of urosome, lateral (B); 110, caudal ramus, dorsal (E); 111, egg sac, dorsal (H); 112, rostral area, ventral (H); 113, first antenna, ventral (E).

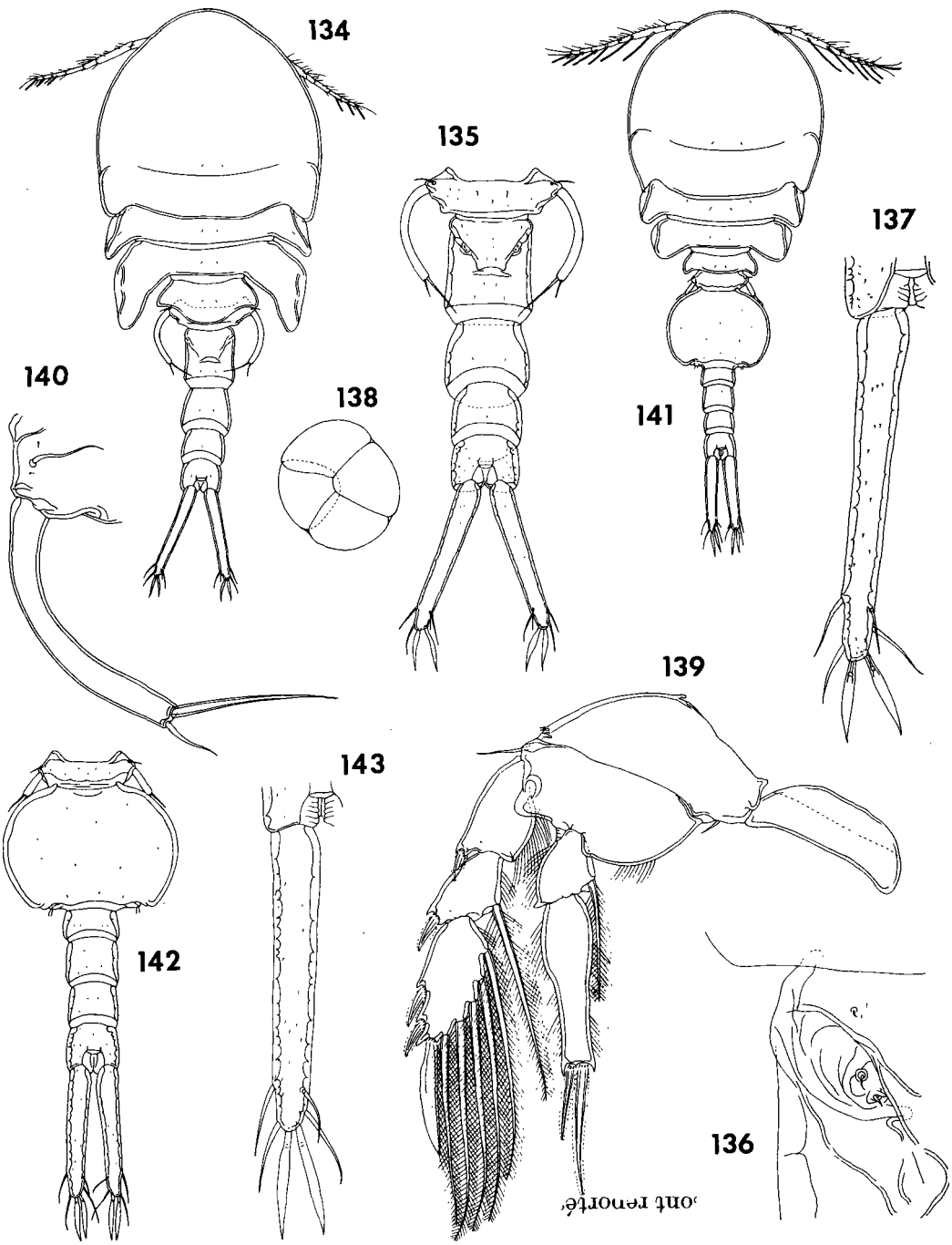


Figures 114–123. *Lichomolgus lobophorus* n. sp., female (continued). 114, second antenna, outer (E); 115, labrum, ventral (D); 116, mandible, posterior (D); 117, paragnath, ventral (C); 118, first maxilla, posterior (C); 119, second maxilla, posterior, (D); 120, maxilliped, anterior (D); 121, postoral area, ventral (H); 122, leg 1 and intercoxal plate, anterior (E); 123, leg 2, anterior (E).



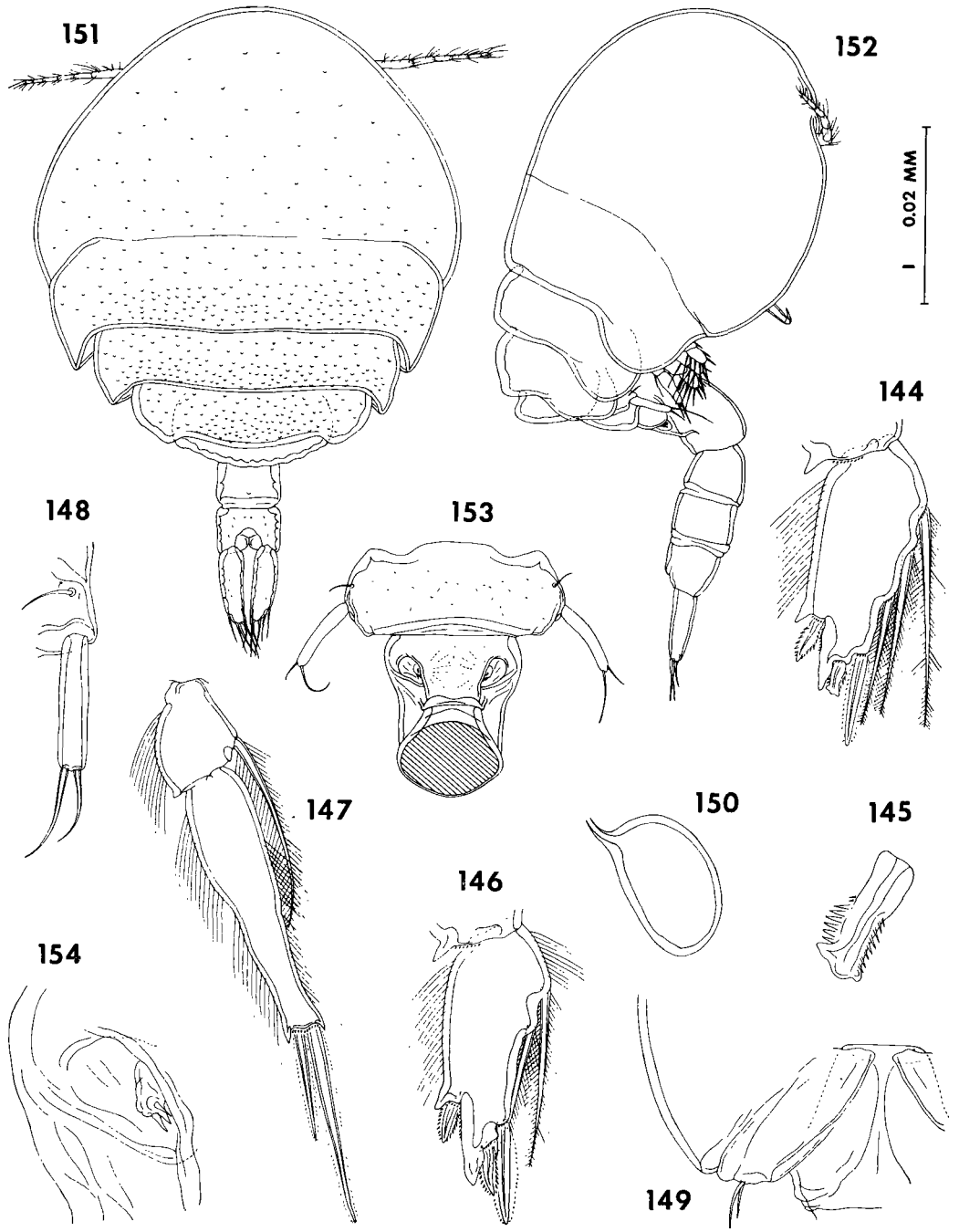
Figures 124–126. *Lichomolgus lobophorus* n. sp., female (continued). 124, last segment of endopod of leg 3, anterior (E); 125, leg 4 and intercoxal plate, anterior (E); 126, leg 5, dorsal (E).

Figures 127–133. *Lichomolgus lobophorus* n. sp., male. 127, body, dorsal (G); 128, urosome, dorsal (B); 129, second antenna, outer (E); 130, maxilliped, inner (H); 131, last segment of endopod of leg 1, anterior (D); 132, leg 5, dorsal (D); 133, leg 6, ventral (E).



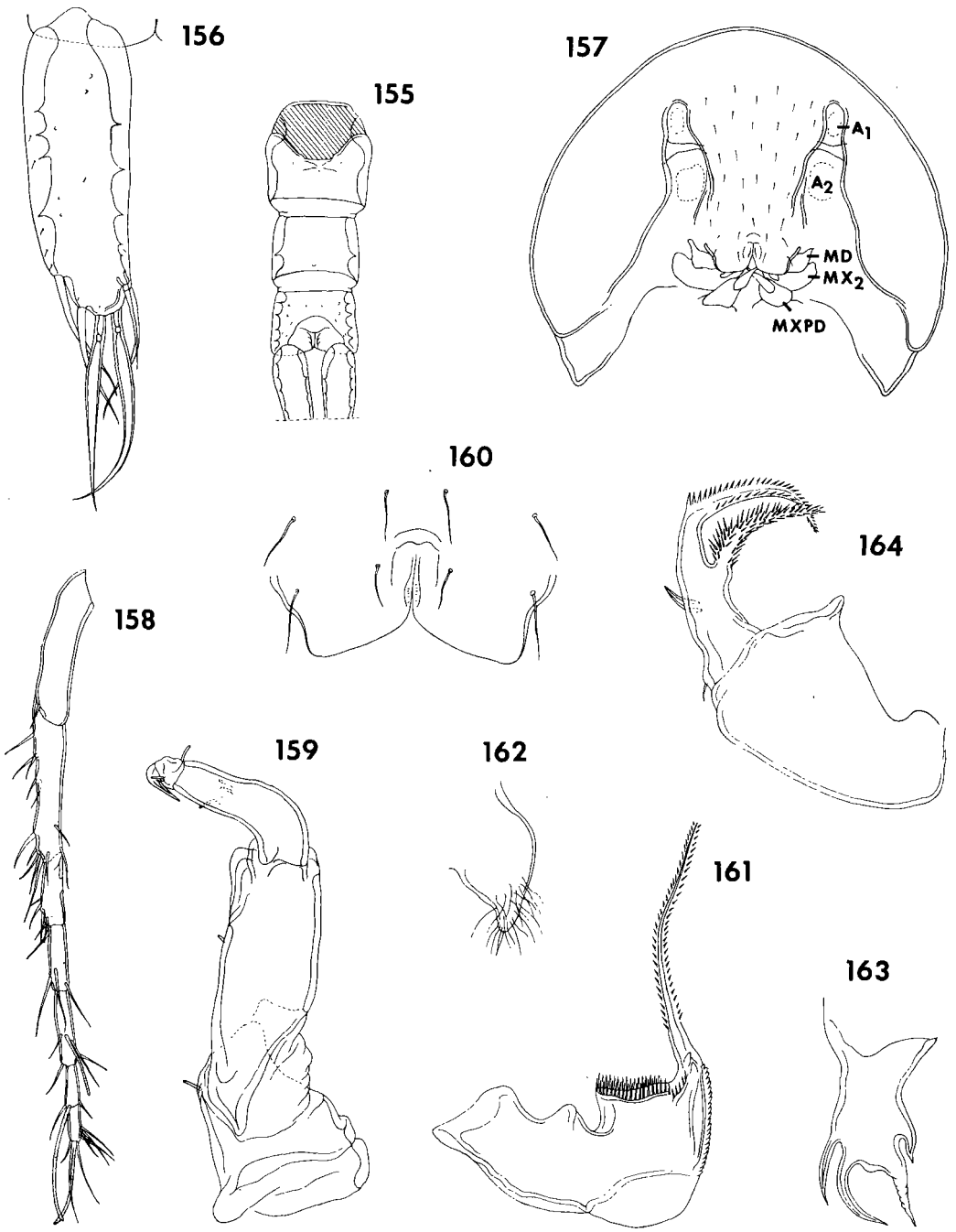
Figures 134–140. *Lichomolgus geminus* n. sp., female. 134, body, dorsal (A); 135, urosome, dorsal (G); 136, area of attachment of egg sac, dorsal (F); 137, caudal ramus, dorsal (H); 138, egg sac, dorsal (G); 139, leg 4 and intercoxal plate, anterior (E); 140, leg 5, dorsal (E).

Figures 141–143. *Lichomolgus geminus* n. sp., male. 141, body, dorsal (A); 142, urosome, dorsal (G); 143, caudal ramus, dorsal (H).

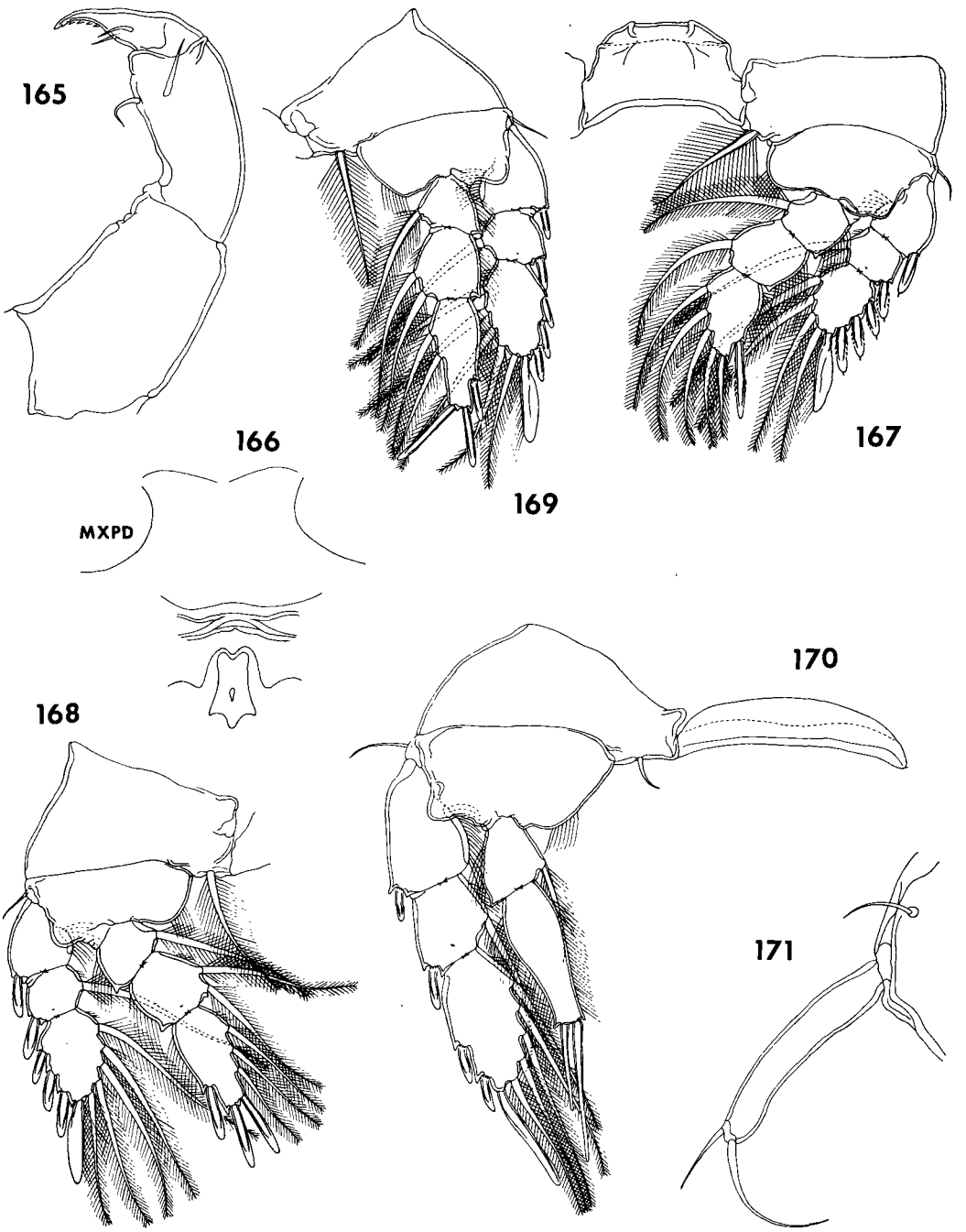


Figures 144–150. *Lichomolgus geminus* n. sp., male (continued). 144, last segment of endopod of leg 2, anterior (D); 145, middle distal spine on last segment of endopod of leg 2, anterior (I); 146, last segment of endopod of leg 3, anterior (D); 147, endopod of leg 4, anterior (D); 148, leg 5, dorsal (D); 149, leg 6, ventral (E); 150, spermatophore, attached to female, dorsal (B).

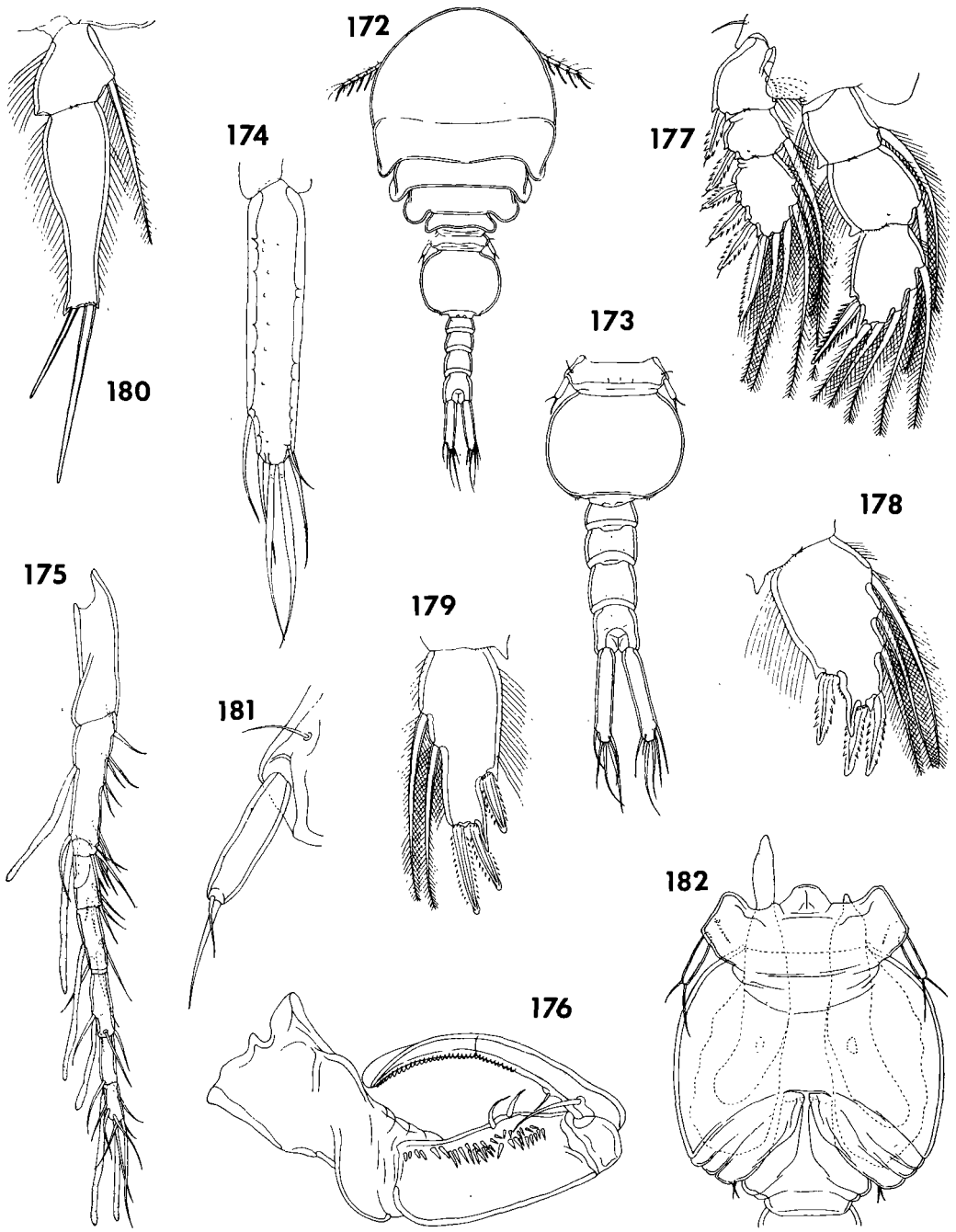
Figures 151–154. *Lichomolgus crassus* n. sp., female. 151, body, dorsal (G); 152, body, lateral (G); 153, segment of leg 5 and genital segment, dorsal (B); 154, area of attachment of egg sac, dorsal (F).



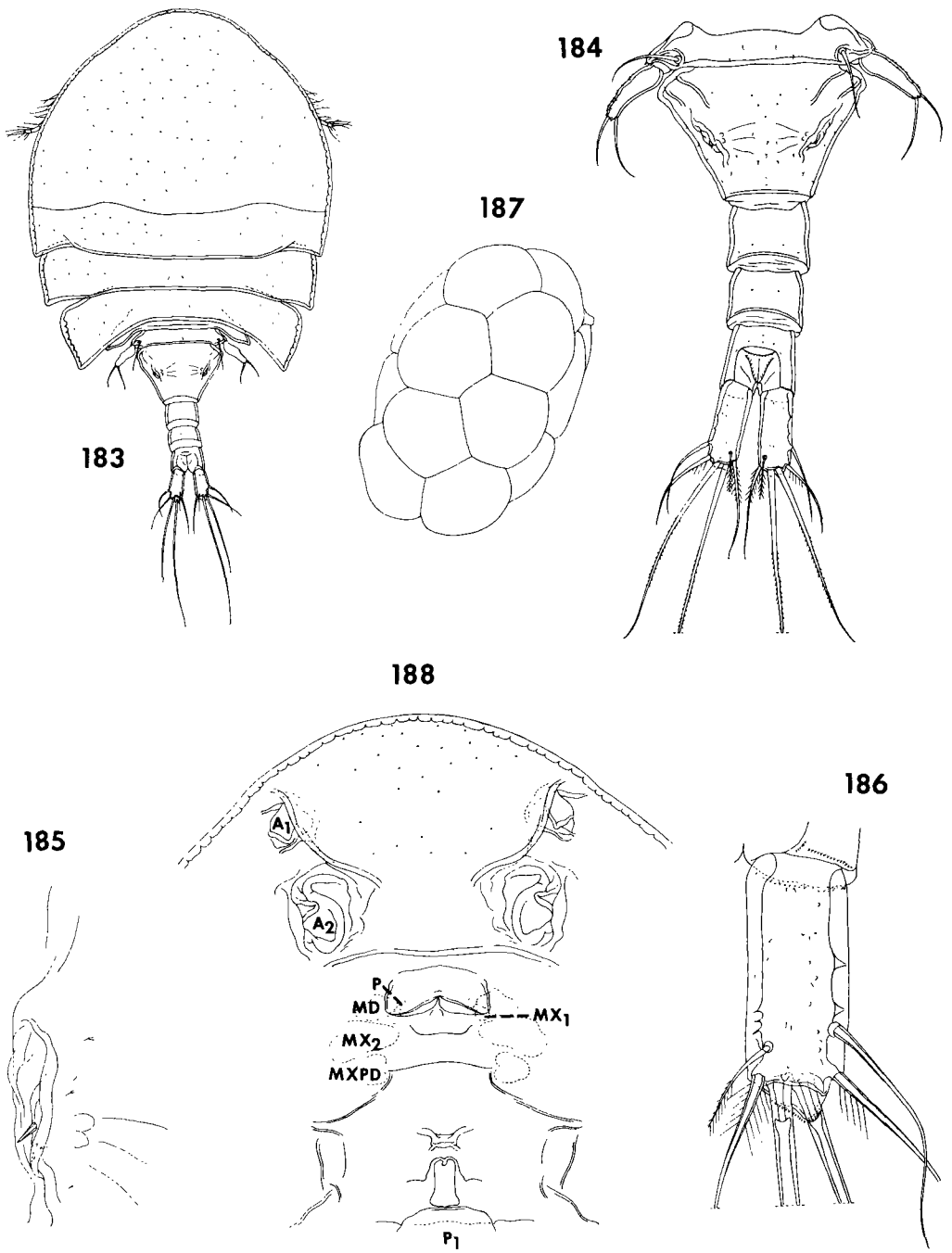
Figures 155–164. *Lichomolgus crassus* n. sp., female (continued). 155, postgenital segments, dorsal (B); 156, caudal ramus, dorsal (D); 157, anterior part of cephalosome, ventral (G); 158, first antenna, dorsal (E); 159, second antenna, outer (E); 160, labrum, ventral (E); 161, mandible, posterior (D); 162, paragnath, posterior (C); 163, first maxilla, anterior (D); 164, second maxilla, anterior (D).



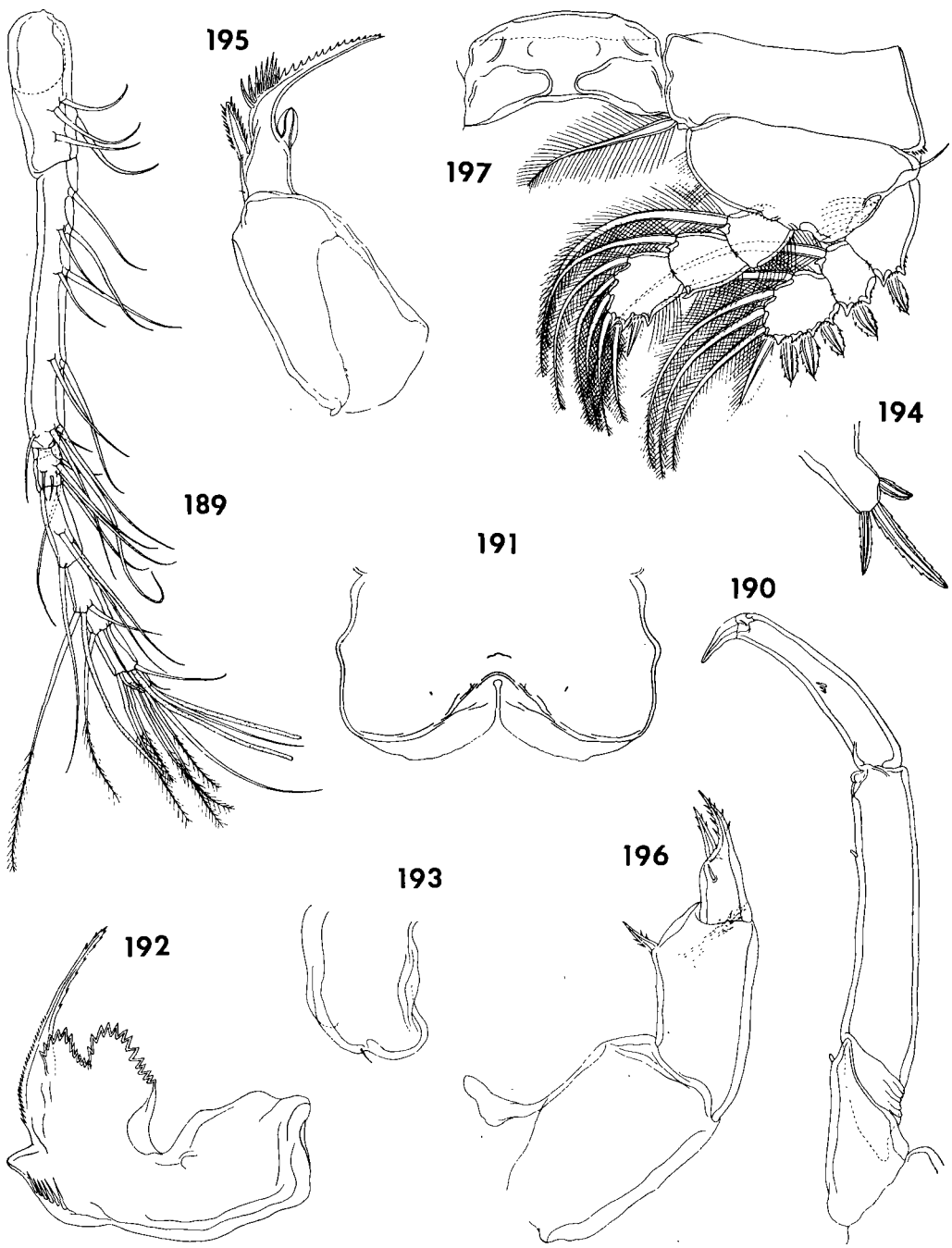
Figures 165–171. *Lichomologus crassus* n. sp., female (continued). 165, maxilliped, inner (D); 166, postoral area, ventral (E); 167, leg 1 and intercoxal plate, anterior (E); 168, leg 2, anterior (E); 169, leg 3, anterior (E); 170, leg 4 and intercoxal plate, anterior (D); 171, leg 5, dorsal (D).



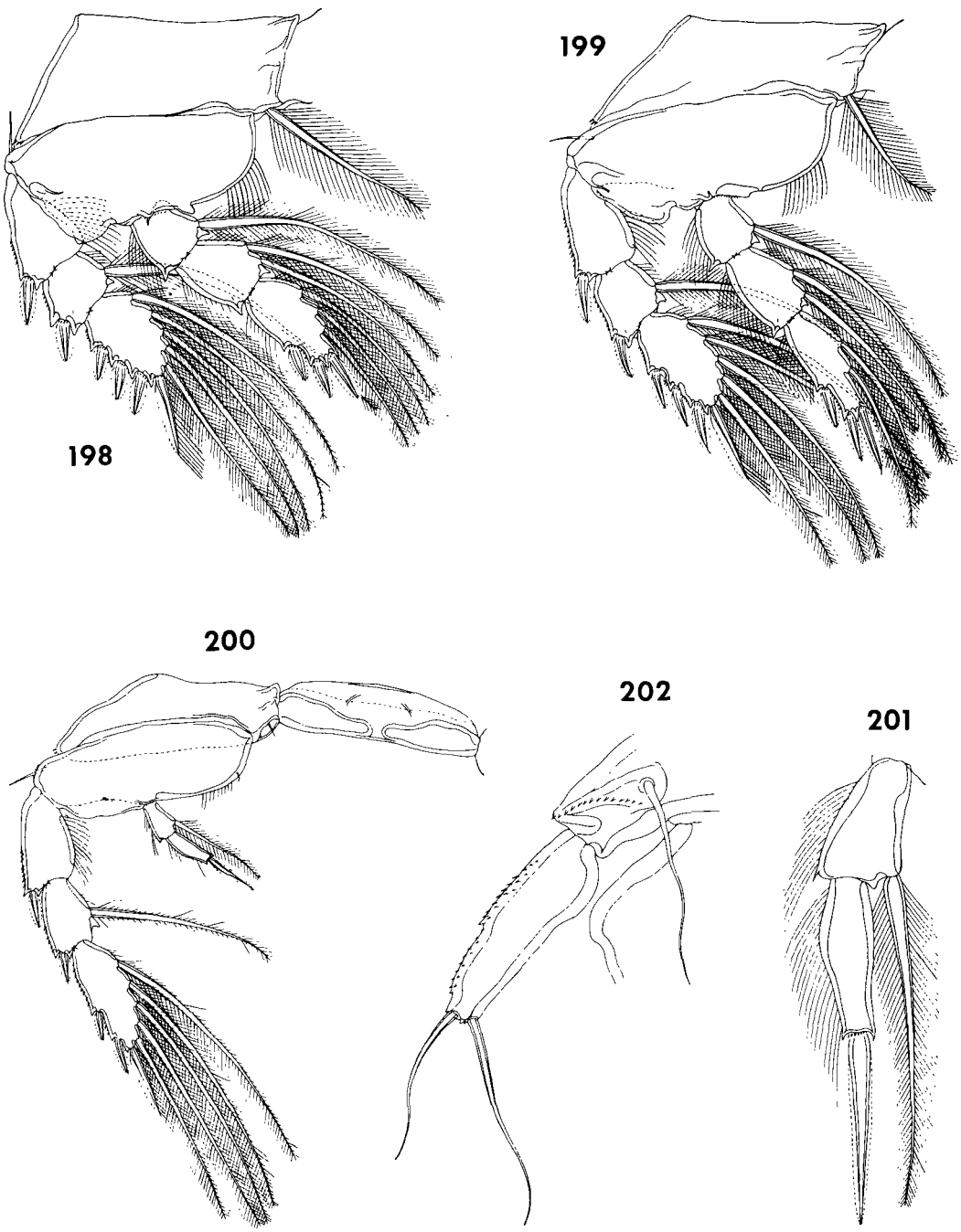
Figures 172–182. *Lichomolgus crassus* n. sp., male. 172, body, dorsal (A); 173, urosome, dorsal (G); 174, caudal ramus, dorsal (E); 175, first antenna, ventral (E); 176, maxilliped, inner (E); 177, leg 1, anterior (E); 178, last segment of endopod of leg 2, anterior (D); 179, last segment of endopod of leg 3, anterior (D); 180, endopod of leg 4, anterior (D); 181, leg 5, dorsal (F); 182, segment of leg 5 and genital segment, ventral (H).



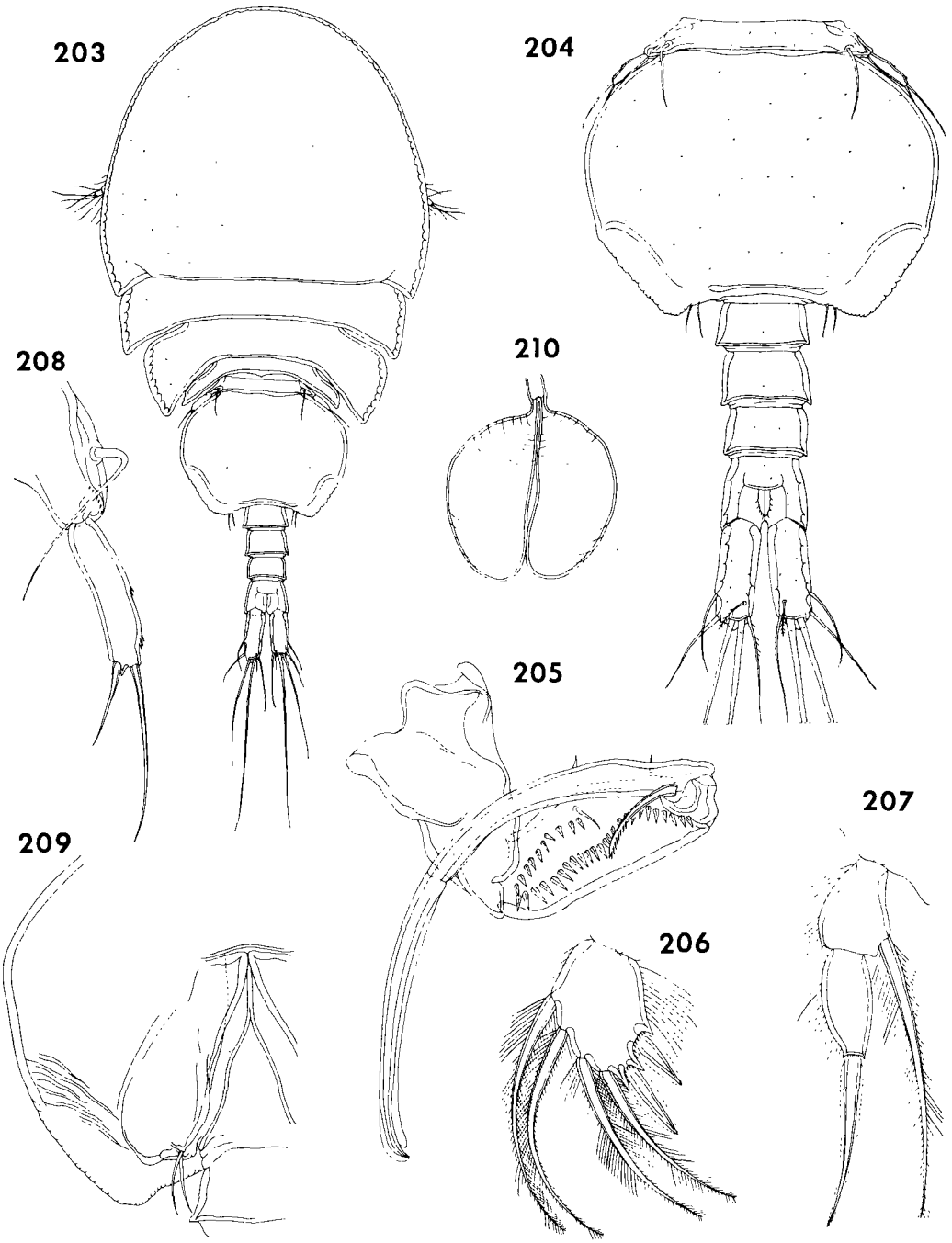
Figures 183–188. *Prionomolgus lanceolatus* n. gen., n. sp., female. 183, body, dorsal (A); 184, urosome, dorsal (B); 185, area of attachment of egg sac, dorsal (F); 186, caudal ramus, dorsal (D); 187, egg sac, ventral (B); 188, cephalosome, ventral (B).



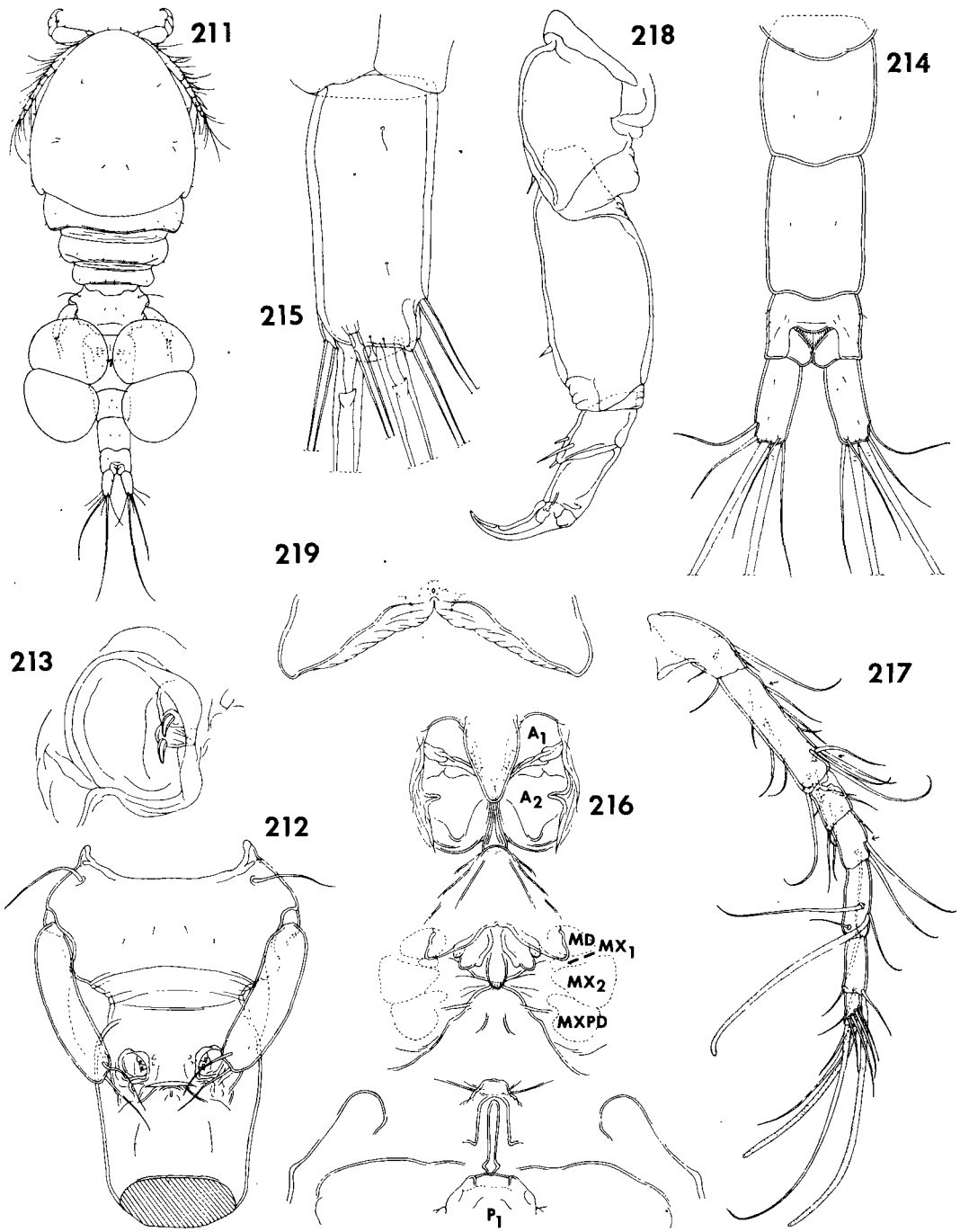
Figures 189–197. *Prionomolgus lanceolatus* n. gen., n. sp., female (continued). 189, first antenna, dorsal (E); 190, second antenna, posterior (E); 191, labrum, ventral (D); 192, mandible, posterior (F); 193, paragnath, posterior (I); 194, first maxilla, posterior (F); 195, second maxilla, anterior (D); 196, maxilliped, outer (F); 197, leg 1 and intercoxal plate, anterior (E).



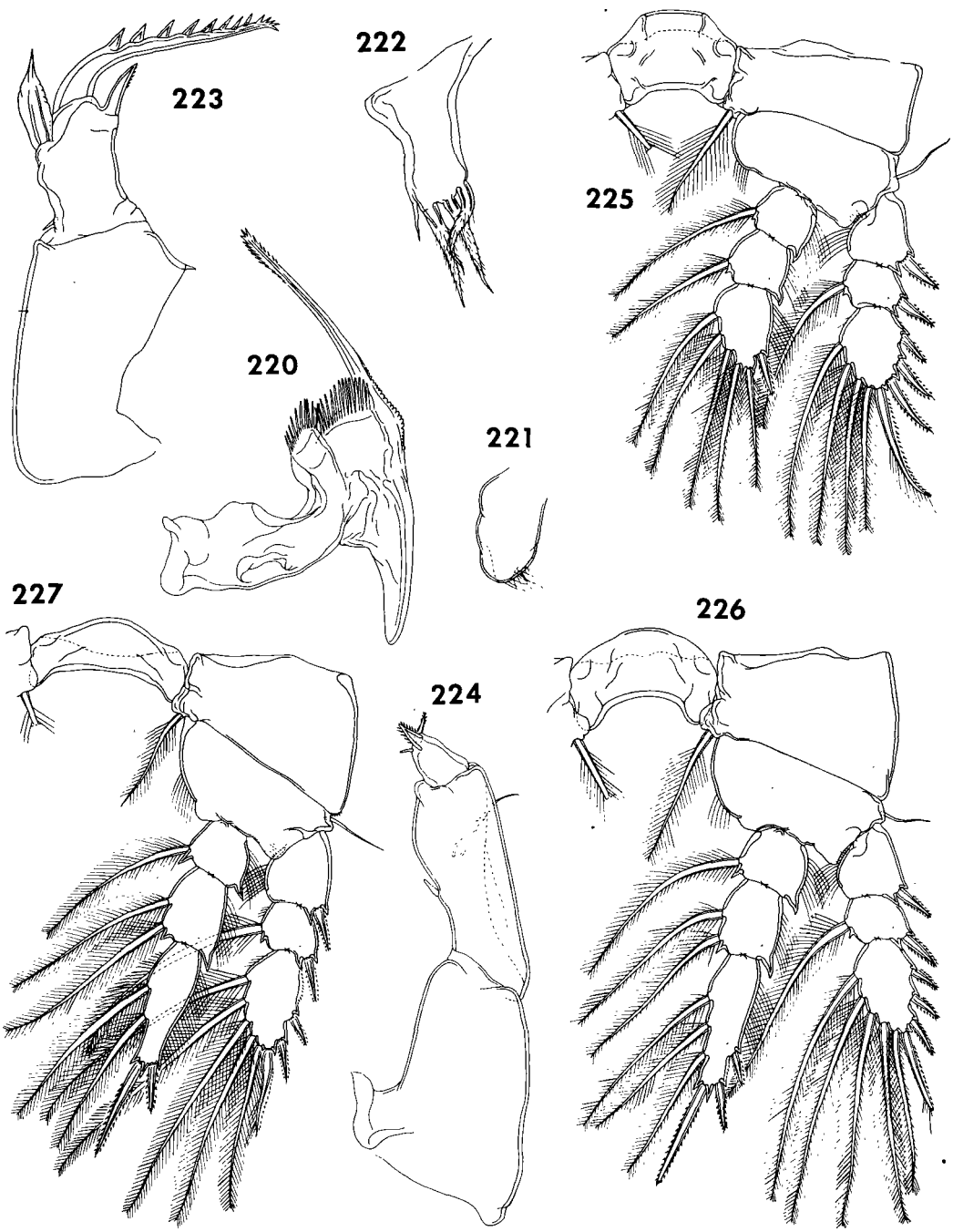
Figures 198–202. *Prionomolgus lanceolatus* n. gen., n. sp., female (continued). 198, leg 2, anterior (E); 199, leg 3, anterior (E); 200, leg 4 and intercoxal plate, anterior (E); 201, endopod of leg 4, anterior (C); 202, leg 5, dorsal (D).



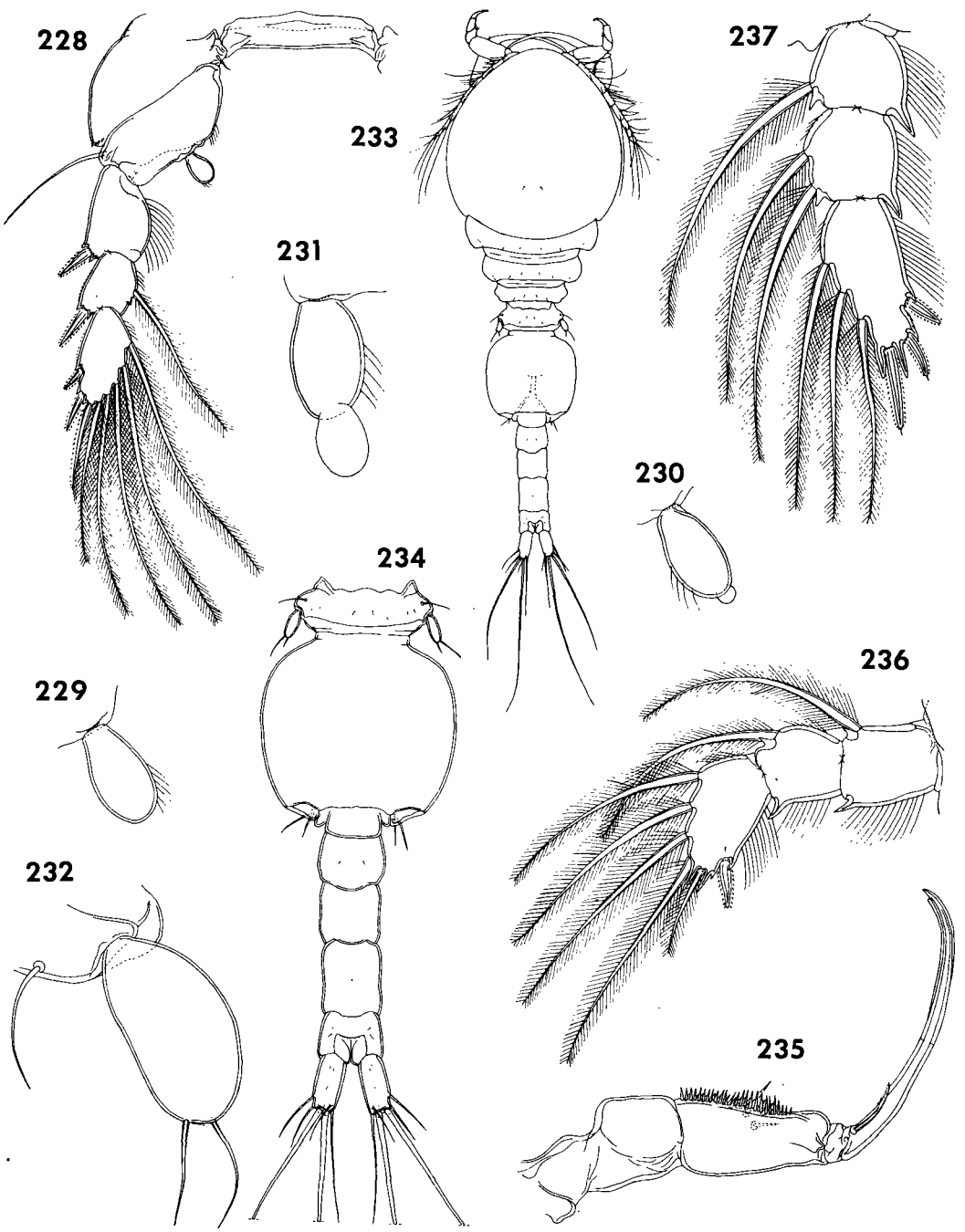
Figures 203–210. *Prionomolgus lanceolatus* n. gen., n. sp., male. 203, body, dorsal (G); 204, urosome, dorsal (H); 205, maxilliped, anterointernal (D); 206, last segment of endopod of leg 1, anterior (F); 207, endopod of leg 4, anterior (C); 208, leg 5, dorsal (F); 209, leg 6, ventral (E); 210, spermatophores, attached to female, lateral (B).



Figures 211–219. *Haplomolgus montiporae* n. gen., n. sp., female. 211, body, dorsal (G); 212, segment of leg 5 and genital segment, dorsal (E); 213, area of attachment of egg sac, dorsal (I); 214, postgenital segments and caudal rami, dorsal (E); 215, caudal ramus, dorsal (C); 216, rostral, oral, and postoral areas, ventral (E); 217, first antenna, with arrows indicating positions of aesthetes in male, posteroventral (D); 218, second antenna, inner (F); 219, edge of labrum, ventral (F).

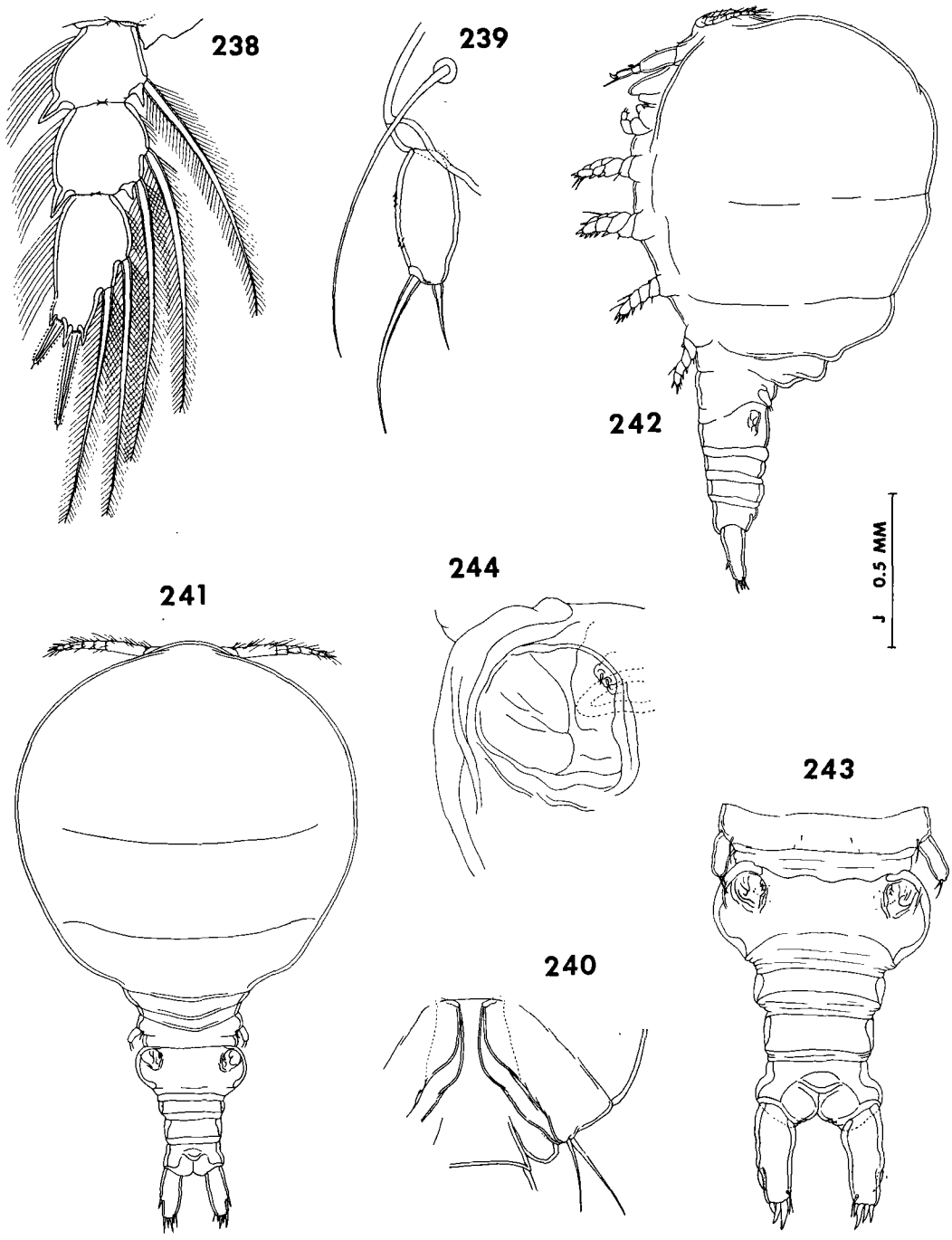


Figures 220–227. *Haplomolgus montiporae* n. gen., n. sp., female (continued). 220, mandible, posterior (C); 221, paragnath, posterior (C); 222, first maxilla, posterior (C); 223, second maxilla, posterior (C); 224, maxilliped, anterior (C); 225, leg 1 and intercoxal plate, anterior (D); 226, leg 2 and intercoxal plate, anterior (D); 227, leg 3 and intercoxal plate, anterior (D).



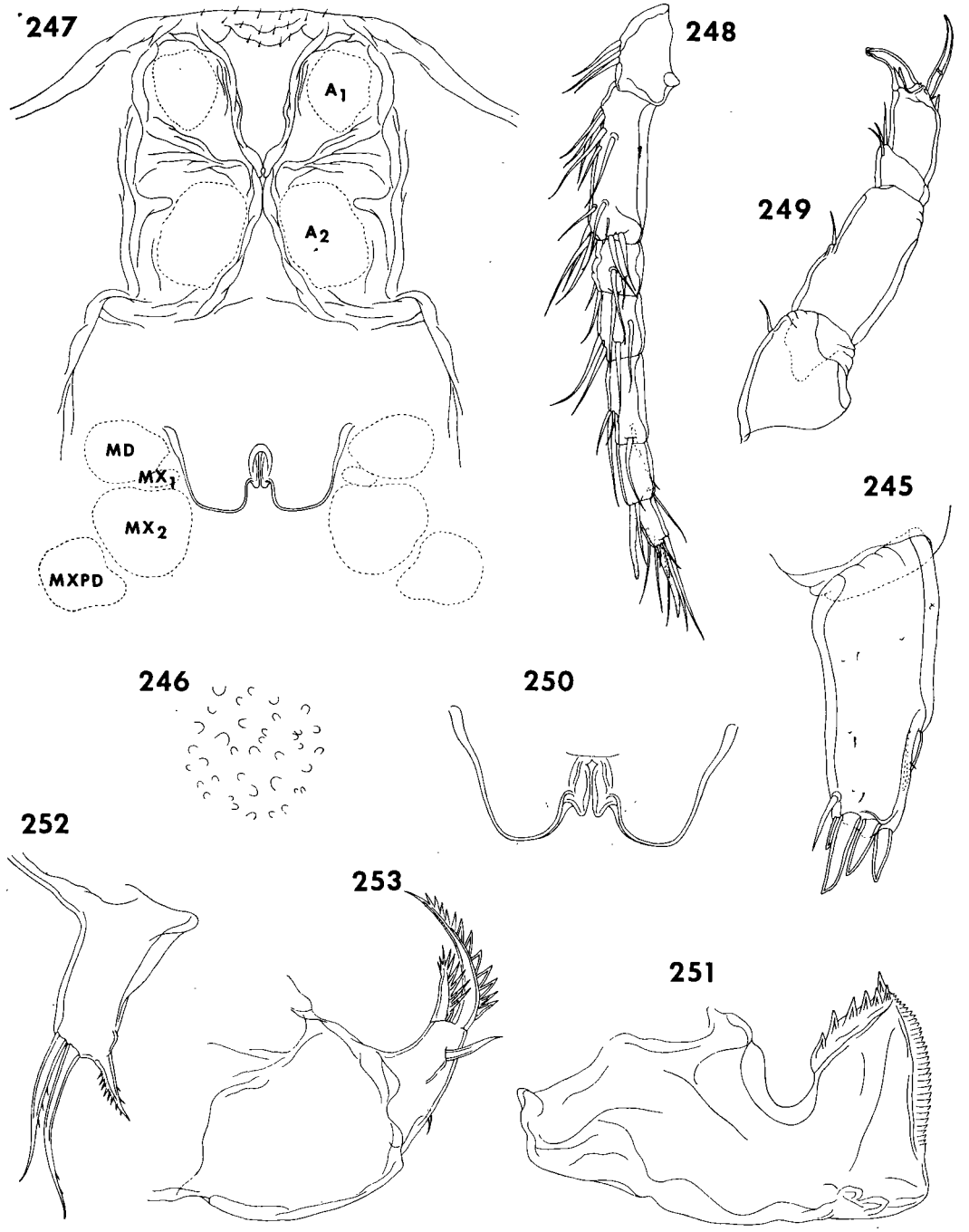
Figures 228–232. *Haplomolgus montiporae* n. gen., n. sp., female (continued). 228, leg 4 and intercoxal plate, anterior (D); 229, endopod of leg 4, anterior (C); 230, endopod of leg 4, anterior (C); 231, endopod of leg 4, anterior (C); 232, leg 5, lateroventral (D).

Figures 233–237. *Haplomolgus montiporae* n. gen., n. sp., male. 233, body, dorsal (G); 234, urosome, dorsal (H); 235, maxilliped, inner (E); 236, endopod of leg 1, anterior (F); 237, endopod of leg 2, anterior (F).

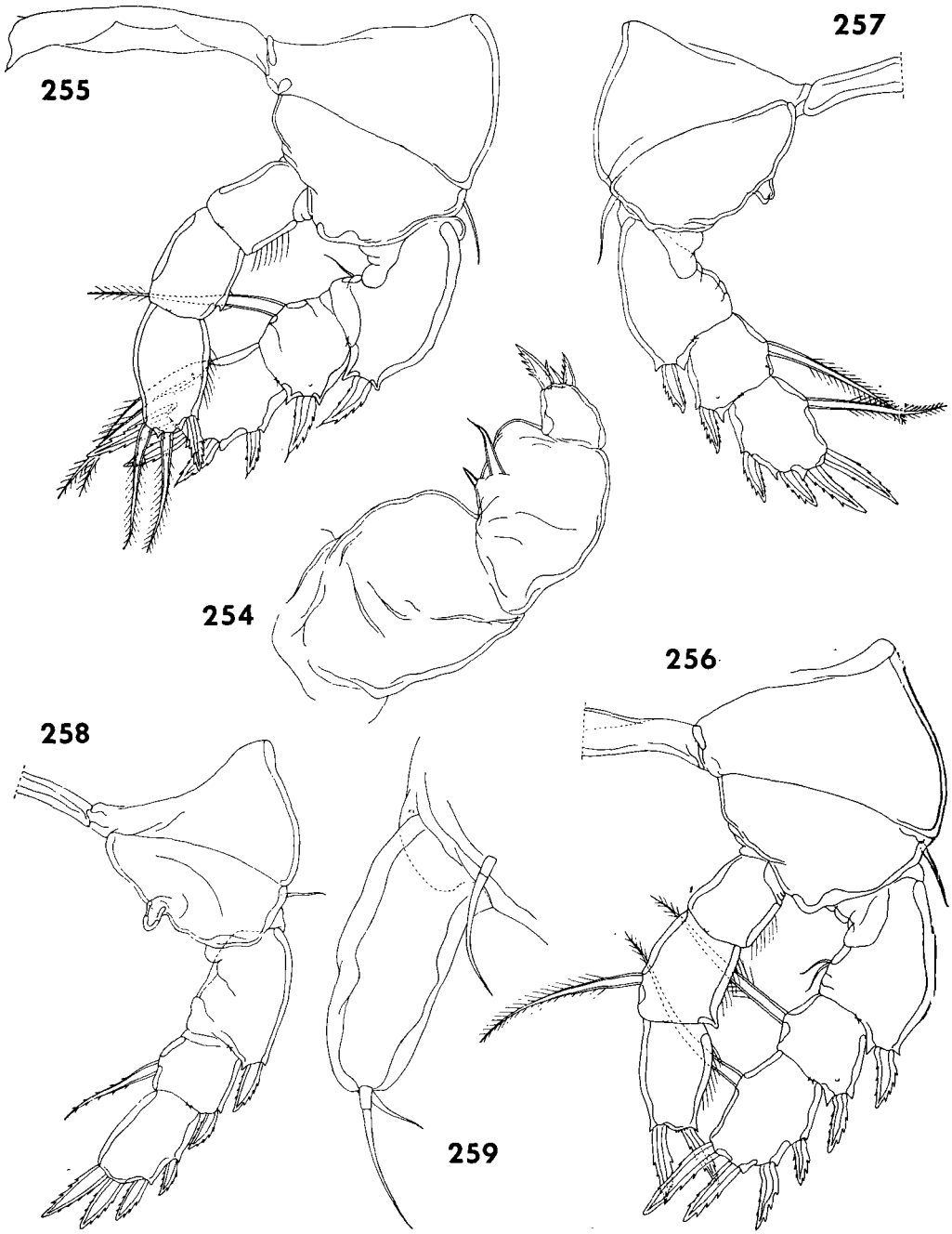


Figures 238–240. *Haplomolgus montiporae* n. gen., n. sp., male (continued). 238, endopod of leg 3, anterior (F); 239, leg 5, dorsal (C); 240, leg 6, ventral (D).

Figures 241–244. *Ravahina tumida* n. gen., n. sp., female. 241, body, dorsal (J); 242, body, lateral (J); 243, urosome, dorsal (G); 244, area of attachment of egg sac, dorsal (D).



Figures 245–253. *Ravahina tumida* n. gen., n. sp., female (continued). 245, caudal ramus, dorsal (E); 246, portion of dorsal surface of segment of leg 1 showing irregular surface of cuticula, dorsal (F); 247, rostral and oral areas, ventral (H); 248, first antenna, anterodorsal (H); 249, second antenna, anterior (H); 250, labrum, ventral (E); 251, mandible, posterior (F); 252, first maxilla, posterior (F); 253, second maxilla, anterior (D).



Figures 254–259. Ravahina tumida n. gen., n. sp., female (continued). 254, maxilliped, anterior (D); 255, leg 1 and intercoxal plate, anterior (E); 256, leg 2, anterior (E); 257, leg 3, anterior (E); 258, leg 4, anterior (E); 259, leg 5, dorsal (F).

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XARIFIID COPEPODS (CYCLOPOIDA) PARASITIC IN CORALS IN MADAGASCAR

ARTHUR G. HUMES[1 2] AND JU-SHEY HO[1]

INTRODUCTION

The family Xarifiidae at present contains only the genus *Xarifia* Humes, 1960. (The genus *Kombia* Humes, 1962, assigned tentatively to this family, belongs more probably to the Lichomolgidae, as pointed out by Humes and Ho, 1968.) Two species, *X. maldivensis* and *X. fimbriata,* were described by Humes (1960) from corals in the Maldive Islands. Nine species are known from corals in the region of Nosy Bé, Madagascar. These are *X. gerlachi, X. longipes, X. dispar, X. reducta, X. serrata, X. tenuis, X. infrequens,* and *X. comata,* all described by Humes (1962), and *X. diminuta* Humes and Ho (1967). This paper deals with nine new species of *Xarifia* and two new species belonging to a new xarifiid genus, collected from corals in the vicinity of Nosy Bé during 1960 and 1963–64.

All collections were made by A. G. Humes, those in 1960 during an expedition of the Academy of Natural Sciences of Philadelphia, and those in 1963–64 as part of the U.S. Program in Biology of the International Indian Ocean Expedition. Type material has been deposited in the United States National Museum. Specimens of several of the new species have been placed in the Museum of Comparative Zoology.

[1] Boston University, Boston, Massachusetts.
[2] Associate in Marine Invertebrates, Museum of Comparative Zoology.

The study of the specimens has been aided by grants (GB-1809 and GB-5838) from the National Science Foundation of the United States.

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

The measurement of the length of the body has been made in all cases from specimens in lactic acid and does not include the setae on the caudal rami. In the spine and setal formulas of legs 1–4 the Roman numerals indicate spines and the Arabic numerals represent setae.

The abbreviations used are: A_1 = first antenna, A_2 = second antenna, MD = mandible, P = paragnath, MX_1 = first maxilla, MX_2 = second maxilla, P_1 = leg 1.

We thank Dr. Donald F. Squires of the United States National Museum for the identifications of corals collected in 1960, and Dr. Michel Pichon, then at the Centre O.R.S.T.O.M. de Nosy Bé, for the determinations of those collected in 1963–64.

The new copepods described in this paper comprise the following:

1) *Xarifia lamellispinosa* n. sp.
   from *Pachyseris speciosa* (Dana)
2) *Xarifia exigua* n. sp.
   from *Pachyseris speciosa* (Dana)
3) *Xarifia decorata* n. sp.
   from *Stylophora pistillata* (Esper)
   and *Stylophora mordax* (Dana)

4) *Xarifia lissa* n. sp.
from *Stylophora pistillata* (Esper) and *Stylophora mordax* (Dana)

5) *Xarifia obesa* n. sp.
from *Pocillopora verrucosa* (Ellis and Solander), *Pocillopora* sp. cf. *P. verrucosa* (E. and S.), and *Pocillopora danae* Verrill

6) *Xarifia brevicauda* n. sp.
from *Alveopora* sp.

7) *Xarifia temnura* n. sp.
from *Montipora sinensis* Bernard

8) *Xarifia anomala* n. sp.
from *Acropora palifera* (Lamarck)

9) *Xarifia hamata* n. sp.
from *Turbinaria* sp.

10) *Orstomella faviae* n. gen., n. sp.
from *Favia* sp.

11) *Orstomella lobophylliae* n. gen., n. sp.
from *Lobophyllia costata* (Dana) and *Lobophyllia corymbosa* (Forskål)

The following represent new host records:

1) *Xarifia dispar* Humes, 1962
from *Echinopora lamellosa* (Esper) and *Echinopora gemmacea* (Lamarck)

2) *Xarifia serrata* Humes, 1962
from *Pocillopora bulbosa* Ehrenberg

KEYS TO THE SPECIES OF THE GENUS *XARIFIA*

Females

1. Endopods of legs 1–4 one-segmented 2
   Endopods of legs 1–4 two-segmented 13
2. Region dorsal to fifth legs with two or three processes 3
   Region dorsal to fifth legs without processes (or at most a median transverse ridge as in *X. serrata*) 10
3. Region dorsal to fifth legs with two processes 4
   Region dorsal to fifth legs with three processes 5
4. Leg 5 with a small free segment (24 × 9 μ); outer element on second segment of exopods of legs 1–4 a seta rather than a spine; body unusually stout, about 4 times longer than wide ..... *obesa*
   Leg 5 without a free segment and represented only by three setae; second segment of exopods of legs 1–4 outwardly unarmed; body elongated and slender, 6.7 times longer than wide ..... *fimbriata*
5. Three processes above fifth legs about equal in length 6
   Two lateral processes distinctly shorter than median process 9
6. Processes short; caudal ramus small and indistinctly set off from anal segment ..... *gerlachi*
   Processes elongated; caudal ramus distinctly set off from anal segment 7
7. Two small lobes between processes; outer element on second segment of exopod of legs 1–4 a seta ..... *maldivensis*
   Without knobs between processes; outer element on second segment of exopod of legs 1–4 a spine 8
8. Three processes about equal in length; length of body 0.75 mm ..... *exigua*
   Middle process a little shorter than other two; length of body 1.48 mm ..... *longipes*
9. Caudal ramus about 9 times longer than wide; first segment of exopod of legs 1–4 without an outer spine, but instead only a minute spiniform projection ..... *tenuis*
   Caudal ramus about 4 times longer than wide; first segment of exopod of legs 1–4 with a distinct (though small) spine ..... *infrequens*
10. Body about 10 times longer than wide; caudal ramus fused with anal segment; postgenital segments fused into a single small segment ..... *temnura*
    Body about 6–7 times longer than wide; caudal ramus distinct; postgenital segments not unusually reduced 11
11. Second segment of exopods of legs 1–4 with only a small outer knob; region dorsal to fifth legs not projected ..... *reducta*
    Second segment of exopods of legs 1–4 unarmed; region dorsal to fifth legs projected to form a slight transverse ridge 12
12. Leg 5 122 μ long; blade of mandible with small spinules; endopod of leg 2 with two terminal setae ..... *serrata*
    Leg 5 72 μ long; blade of mandible with strong teeth; endopod of leg 2 with three terminal setae ..... *lissa*
13. Second segment of exopod of legs 1–4 unarmed ..... *comata*
    Second segment of exopod of legs 1–4 with either a spine or a seta 14
14. First and second segments of exopods of legs 1–4 similarly armed with a slender outer spine (almost setiform) ..... *dispar*
    These segments not so armed 15

15. First and second segments of exopods of legs 1–4 with a strong outer spine 16
    These segments not so armed (second segment with a small outer spine or a seta) 19
16. Endopod of leg 3 with a terminal seta; length of body 1.90 mm .... *lamellispinosa*
    Endopod of leg 3 unarmed; length of body 1.27 mm or less 17
17. Endopod of leg 1 unarmed; endopod of leg 2 with three terminal setae .. *anomala*
    Endopods of legs 1 and 2 with two terminal setae 18
18. Endopod of leg 4 with two terminal setae; length of body 0.98 mm ..... *diminuta*
    Endopod of leg 4 unarmed; length of body 1.27 mm ..... *brevicauda*
19. First segment of exopods of legs 1–4 with a strong outer spine; second segment of exopod of leg 1 with a small outer spine, in legs 2–4 with a seta; endopods of legs 1–4 with terminal setae .. *decorata*
    First segment of exopods of legs 1–4 with a strong outer spine; second segment of these exopods with a seta; endopod of leg 2 with a seta and a clawlike spine, endopods of legs 3 and 4 with only a clawlike spine ..... *hamata*

Males

1. Endopods of legs 1–4 one-segmented 2
   Endopods of legs 1–4 two-segmented 13
2. First and second segments of exopod of leg 1 with a distinct outer spine 3
   Both of these segments or only second segment lacking such a spine 6
3. Caudal ramus small and completely or partially fused with anal segment 4
   Caudal ramus more prominent and distinct from anal segment 5
4. Body about 7 times longer than wide; blade of mandible with spinules; second segment of exopods of legs 2–4 with an outer spine ..... *gerlachi*
   Body about 10 times longer than wide; blade of mandible smooth; second segment of exopods of legs 2–4 unarmed ..... *temnura*
5. Terminal setae on endopods of legs 1–4 arranged as 2, 1, 1, 1; length of body, 1.43 mm ..... *longipes*
   Terminal setae on endopods of legs 1–4 arranged as 2, 2, 1, 1; length of body 0.80 mm ..... *exigua*
6. Second segment of exopod of leg 1 with an outer seta 7
   Second segment of exopod of leg 1 unarmed (or at most with only a small outer knob as in *X. reducta*) 8
7. Body unusually stout, about 4 times longer than wide ..... *obesa*
   Body more slender, a little more than 6 times longer than wide ..... *maldivensis*
8. First segment of exopod of leg 1 without a distinct element, having only a minute outer process ..... *tenuis*
   First segment of exopod of leg 1 with a distinct outer element 9
9. First segment of exopod of leg 1 with an outer spine 10
   First segment of exopod of leg 1 with an outer seta ..... *fimbriata*
10. Second segment of exopod of leg 1 with a small outer knob or hyaline seta 11
    Second segment of exopod of leg 1 unarmed 12
11. Second segment of exopod of leg 1 with a small outer knob; concave surface of claw of maxilliped with a row of about twelve long spinules ..... *reducta*
    Second segment of exopod of leg 1 with a small hyaline seta; concave surface of claw of maxilliped serrated ..... *lissa*
12. Concave margin of claw of maxilliped with irregular rounded serrations; body about 8 times longer than wide .... *serrata*
    Concave margin of claw of maxilliped distally with a few minute teeth; body about 11 times longer than wide ..... *infrequens*
13. Second segment of exopods of legs 1–4 unarmed ..... *comata*
    Second segment of exopods of legs 1–4 with a spine or seta 14
14. Second segment of exopods of legs 1–4 with an outer seta; second segment of endopod of leg 2 with a seta and a clawlike spine ..... *hamata*
    Second segment of exopod of leg 1 with an outer spine; without a clawlike spine on second segment of endopod of leg 2 15
15. Second segment of exopods of legs 2–4 with an outer seta ..... *decorata*
    Second segment of exopods of legs 2–4 with an outer spine 16
16. Spines on first two segments of exopods of legs 1–4 slender, almost setiform .... *dispar*
    Spines on these segments clearly spiniform rather than setiform 17
17. With a terminal seta on endopod of leg 3, formula for terminal elements on endopods of legs 1–4 being 2, 2, 1, 1 ..... *lamellispinosa*
    Without a terminal seta on endopod of leg 3 18
18. Without terminal setae on endopod of leg 1, formula for terminal elements of endopods of legs 1–4 being 0, 3, 0, 0 .... *anomala*

With two terminal setae on endopod of leg 1 19

19. Without terminal setae on endopod of leg 4, formula for terminal elements on endopods of legs 1–4 being 2, 2, 0, 0; postgenital region shortened with segments fused; concave margin of claw of maxilliped with a serrated excrescence ..... *brevicauda*

With two terminal setae on endopod of leg 4, formula for terminal elements on endopods of legs 1–4 being 2, 2, 0, 2; postgenital region not shortened; concave margin of claw of maxilliped without a serrated excrescence ..... *diminuta*

SYSTEMATIC DESCRIPTION

XARIFIIDAE Humes, 1960

XARIFIA Humes, 1960

Xarifia lamellispinosa n. sp.
Figs. 1–22

Type material.—13 females and 14 males from a colony of *Pachyseris speciosa* (Dana) in a depth of 2 m, Ambariotsimaramara, off Ampombilava, Nosy Bé, Madagascar. Collected June 12, 1964. Holotype female, allotype, and 21 paratypes (10 females and 11 males) deposited in the United States National Museum, Washington; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens (all from *Pachyseris speciosa*).—3 females and 11 males in 3 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, September 3, 1963; 1 male in 2 m, Ambariotsimaramara, off Ampombilava, Nosy Bé, October 18, 1963.

Female.—Body (Figs. 1 and 2) slender, about 7 times longer than wide. Length 1.90 mm (1.84–2.00 mm) and greatest width 0.27 mm (0.26–0.27 mm), based on 10 specimens. Segmentation not well defined externally. Region dorsal to fifth legs bearing three long posteriorly directed processes, the median one slightly shorter than the lateral ones. Genital and postgenital segments together a little less than one-fourth of total body length. Areas of attachment of egg sacs located dorsally (Fig. 3). Caudal ramus (Fig. 4) about 51 × 28 μ in greatest dimensions, a little less than 2 times longer than wide; with four short naked setae (one outer and subterminal, the others terminal) and surficial hairs. Egg sac (Fig. 3) 340 μ in length, containing five eggs (except in one female where the sac on one side had only four), each egg about 109 μ in average diameter.

Rostral area a rounded lobe between bases of first antennae and covered with short hairs (Fig. 5). First antenna (Fig. 6) short (about 60 μ in length without setae) and apparently 3-segmented. With numerous naked setae, the armature being 3, 22 + 1 aesthete, and 9 + 2 aesthetes. Second antenna (Fig. 7) 4-segmented, the formula being 1, 1, 2, and I, 1. Recurved claw and seta on last segment both 17 μ long.

Labrum (Fig. 8) with trilobate free margin, the middle lobe slightly indented. Mandible (Fig. 9) with blade having four teeth and a recurved tip. Paragnath absent. First maxilla (Fig. 10) a small lobe with two naked setae. Second maxilla (Fig. 11) probably 2-segmented, second segment bearing two unequal inner setae and a distal lamellate expansion with a terminal knob. Maxilliped (Fig. 12) apparently 3-segmented, first segment with an outer lobate expansion, second segment bearing two inner setae and a lobate expansion, third segment with two small spiniform elements and terminating in a short claw. Relationships of head appendages as in Figure 13.

Legs 2–4 with general form and segmentation like that of leg 1 (Fig. 14), exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_1	protopod 0–0; 1–0	exp I–0; I–0; I, 3	end 0–0; 2
P_2	protopod 0–0; 1–0	exp I–0; I–0; I, 2	end 0–0; 2
P_3 and P_4	protopod 0–0; 1–0	exp I–0; I–0; I, 2	end 0–0; 1

In all four legs posterior surface of protopod with a patch of hairs and basis with an outer naked seta. Exopods with stout spines recurved posteriorly and bearing

conspicuous lamellae (Figs. 14, 15, and 16); three slender setae at inner base of terminal spine in leg 1, two such setae in legs 2, 3, and 4. Endopods with few hairs on outer margins of both segments, and with two terminal setae in legs 1 and 2 but only one such seta in legs 3 and 4. Leg 4 (not drawn) armed as in leg 3. Intercoxal plate V-shaped in leg 1, less so in succeeding legs.

Leg 5 (Fig. 17) elongated and slender, with its free segment not clearly delimited from body. Segment about 110 μ in length and tapered distally, with two unequal terminal naked setae 11 and 37 μ long. A slender seta arising from body wall dorsal to base of segment. Leg 6 absent.

Color in life in transmitted light slightly brownish, eye red.

Male.—Body (Figs. 18 and 19) slender, almost as long as female. Length 1.83 mm (1.76–1.87 mm) and greatest width 0.22 mm (0.19–0.24 mm), based on 10 specimens. Without external segmentation. Caudal ramus about 34 × 25 μ, weakly set off from anal segment (Fig. 20).

Rostral area as in female. First antenna like that of female, but with four aesthetes, one being added on midanterior margin of middle segment. Second antenna, labrum, mandible, first maxilla, and second maxilla resembling those in female. Paragnath absent. Maxilliped (Fig. 21) 4-segmented. First segment short and unarmed. Second large and swollen with two inner setae. Third very short and unarmed. Fourth segment forming a terminal claw 57 μ along its axis, with a prominent conical process on its inner concave margin and trifurcated at its tip, bearing two proximal unequal setae (one sclerotized basally but hyaline and obtuse distally, the other hyaline throughout).

Legs 1–4 as in female, with same spine and setal formula. Leg 5 (Fig. 22) having its small free segment (12 × 8 μ) not distinctly delimited from body and bearing two unequal terminal naked setae 14 and 31 μ long. Leg 6 (Fig. 20) represented by a posteroventral flap on genital segment bearing two small setae.

Spermatophore not observed.

Color as in female.

Etymology.—The specific name *lamellispinosa* is a combination of the Latin words *lamella* = a lamella, and *spinosus* = having spines, in allusion to the conspicuous lamellae on the spines of the exopods of legs 1–4.

Comparison with related species.—Only three of the eleven known species in the genus *Xarifia* resemble the new species in having three long processes dorsal to the fifth legs in the female, in having an elongated leg 5 in the female, and in having 2-segmented endopods in legs 1–4. These are *X. dispar* Humes, 1962, *X. comata* Humes, 1962, and *X. diminuta* Humes and Ho, 1967. From each of these *X. lamellispinosa* may be readily distinguished. *X. dispar* has a slender, almost straight spine instead of a stout recurved spine on the first and second segments of the exopods of legs 1–4. *X. comata* lacks a spine on the second segment of these legs, and has two terminal setae on the endopod of leg 3. *X. diminuta* lacks setae on this endopod, and the mandible has a smooth blade without teeth. Furthermore, *X. lamellispinosa* is considerably larger than these three species, with its size range not overlapping any of them.

Xarifia exigua n. sp.
Figs. 23–43

Type material.—21 females and 28 males from a colony of *Pachyseris speciosa* (Dana) in a depth of 2 m, Ambariotsimaramara, off Ampombilava, Nosy Bé, Madagascar. Collected October 18, 1963. (One male of *X. lamellispinosa* also was washed from this colony.) Holotype female, allotype, and 39 paratypes (16 females and 23 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Figs. 23 and 24) slender, about 7.5 times longer than wide.

Length 0.75 mm (0.71–0.80 mm) and greatest width 0.10 mm (0.10–0.11 mm), based on 10 specimens. External segmentation not well defined. Region dorsal to fifth legs bearing three long posteriorly directed processes of about equal length. Genital and postgenital segments together about one-fourth of total body length. Areas of attachment of egg sacs situated dorsally (Fig. 25). Caudal ramus (Fig. 26) 41 × 11 μ, about 4 times longer than wide, with the usual four setae, all relatively long and slender. Egg sac unknown.

Rostral area rounded (Fig. 27). First antenna (Fig. 27) short, about 50 μ in length, and apparently 3-segmented. Armature: 3, 22 + 1 aesthete, and 9 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 28) 4-segmented, with formula same as in previous species. Slender claw and adjacent seta on last segment both 18 μ long.

Labrum (Fig. 29) with trilobate free margin, slightly indented medially. Mandible (Fig. 30) with smooth pointed blade. Paragnath absent. First maxilla (Fig. 31) the usual small lobe with two naked setae. Second maxilla (Fig. 32) 2-segmented, resembling that of *X. diminuta*, second segment having two unequal inner setae and a terminal lamellate process. Maxilliped (Fig. 33) probably 3-segmented, but segmentation obscure. Region of second segment with two inner setae and a lobate expansion; that of third segment with two minute elements and lacking a claw. Relationships of head appendages as in Figure 34.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 35), exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_1 and P_2	protopod	0–0; 1–0	exp I–0; I–0; I, 2
			end 2
P_3 and P_4	protopod	0–0; 1–0	exp I–0; I–0; I, 2
			end 1

In all four legs, basis with an outer naked seta. Exopod spines rather long and slender, not strongly recurved. Small spiniform process near base of spine on first exopod segment. Endopods consisting of a single segment provided on outer margin with a proximal setule followed by a row of hairs. Endopods of legs 1 and 2 with two terminal setae, those of legs 3 (Fig. 36) and 4 with a single such seta. Intercoxal plate of leg 1 rather wide (Fig. 35), those of succeeding legs narrower.

Leg 5 (Fig. 37) elongated and slender, with free segment weakly delimited from body. Segment about 100 μ long and tapered distally, the two terminal setae 13 and 24 μ in length. Leg 6 absent.

Color in life in transmitted light pale brownish, eye red.

Male.—Body (Figs. 38 and 39) slender, about as long as female. Length 0.80 mm (0.76–0.85 mm) and greatest width 0.10 mm (0.10–0.10 mm), based on 10 specimens. Without external segmentation. Caudal ramus (Fig. 40) smaller than in female, 19 × 10 μ.

Rostral area as in female. First antenna resembling that of female, but with an additional aesthete on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla like those in female. Paragnath absent. Maxilliped (Fig. 41) segmented and armed as in previous species. Second segment with two inner setae. Fourth segment forming a claw 31 μ along its axis, with a conical process on its inner concave margin and bifurcated at its tip (in one male trifurcated on one maxilliped), bearing the usual two unequal proximal setae.

Legs 1–4 as in female, with same spine and setal formula. Leg 5 (Fig. 42) with a small segment not well delimited from body and bearing two unequal setae. Leg 6 (Fig. 43) the usual posteroventral flap on genital segment with two setae.

Spermatophore not observed.

Color as in female.

Etymology.—The specific name *exigua*, from Latin = small in size, refers to the small size of this species, the smallest of any species of *Xarifia* thus far described.

Comparison with related species.—There are eight known species of *Xarifia* in which the endopods of legs 1–4 are 1-segmented, thus resembling *X. exigua*. These are *X. maldivensis* Humes, 1960, *X. fimbriata* Humes, 1960, *X. gerlachi* Humes, 1962, *X. longipes* Humes, 1962, *X. reducta* Humes, 1962, *X. serrata* Humes, 1962, *X. tenuis* Humes, 1962, and *X. infrequens* Humes, 1962. In only two of these, *X. gerlachi* and and *X. longipes*, does the second exopod segment of legs 1–4 bear a spine, as in the new species; in the others there may be a seta, a small knob, or no element at all. *X. exigua* may be readily distinguished from *X. gerlachi* which has three short processes above the fifth legs in the female and a larger size (female 2.04 mm, male 0.89 mm), and from *X. longipes* which has three very long processes (the middle one slightly shorter than the others) dorsal to the fifth legs in the female, relatively very long caudal rami, and a larger size (female 1.48 mm, male 1.43 mm).

Xarifia decorata n. sp.

Figs. 44–69

Type material.—30 females and 22 males from several colonies of *Stylophora pistillata* (Esper) in a depth of 0.5 m, Navetsy, Nosy Bé, Madagascar. Collected September 24, 1964. Holotype female, allotype, and 38 paratypes (22 females and 16 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 19 females and 14 males in 0.5 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, August 4, 1963; 14 females and 12 males in 3 m, Ambariobe, August 13, 1963; 5 females and 10 males in 0.5 m, Ambariobe, October 6, 1963; and 1 male in 0.5 m, west of Pte. Mahatsinjo, Nosy Bé, January 31, 1964. From *Stylophora mordax* (Dana): 4 females in 2 m, Pte. Ambarionaomby, Nosy Komba, October 1, 1963.

Female.—Body (Figs. 44 and 45) slender, about 6.8 times longer than wide. Length 1.49 mm (1.45–1.53 mm) and greatest width 0.22 mm (0.21–0.22 mm), based on 10 specimens. External segmentation poorly defined. Region dorsal to fifth legs bearing three long slender posteriorly directed processes (Fig. 46) of about equal length (220 μ). (In one female carrying a spermatophore these processes were shorter, about 165 μ, and not as slender.) Genital and postgenital segments together a little less than one-fourth of total body length. Areas of attachment of egg sacs located dorsally. Caudal ramus (Fig. 47) elongated, 88 × 19 μ, about 4.6 times longer than wide, and arched dorsally as in Figure 46; bearing one outer subterminal seta and four terminal setae, all relatively short and naked. Egg sac (Fig. 45) containing 2, 3, or 4 eggs in a row, each egg about 122 × 166 μ. Surface of body covered with fine setules as in Figure 46.

Rostral area (Fig. 48) forming a tongue-shaped lobe bearing setules between bases of antennae and projecting a little beyond anterior margin of head in dorsal view (Fig. 49). First antenna (Fig. 50) short, about 54 μ, and apparently 3-segmented, though second and third segments show partial division. Armature: 3, 22 + 1 aesthete, and 9 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 51) 4-segmented and armed as in two previous species. Terminal claw very slender, 13 μ long, and seta adjacent to it 18 μ.

Labrum (Fig. 52) not trilobed, but indented medially. Mandible (Fig. 53) with smooth pointed blade. Paragnath absent. First maxilla (Fig. 54) the usual small lobe with two naked setae. Second maxilla (Fig. 55) 2-segmented, second segment bearing two unequal hyaline setae and projected terminally to form a broad lamellate lobe with hyaline margins. Maxilliped (Fig. 56) with obscure segmentation, region of second segment bearing two small inner setae and two lobate expansions, that of third segment forming two spinelike processes.

Relationships of head appendages as in Figure 57.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 58), exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_1	protopod 0–0; 1–0	exp	I–0; I–0; I, 3
		end	0–0; 3
P_2	protopod 0–0; 1–0	exp	I–0; 1–0; I, 2
		end	0–0; 3
P_3 and P_4	protopod 0–0; 1–0	exp	I–0; 1–0; I, 2
		end	0–0; 1

In all four legs, basis with an outer naked seta and inner group of long setules. Second segment of exopod of leg 1 with a small outer spine; in legs 2 (Fig. 59), 3, and 4 this spine replaced by a small hyaline seta. Inner margins of exopod segments with long hairlike setules. Endopods of all four legs with similar setules on both margins of first segment and on outer margin of second segment. Legs 1 (Fig. 58) and 2 with three terminal setae on endopod; legs 3 (Fig. 60) and 4 with a single such seta. Intercoxal plate of leg 1 narrow and U-shaped (Fig. 58), those of succeeding legs much narrower and V-shaped.

Leg 5 (Fig. 61) elongated and tapered distally, the free segment about 150 μ long and fused with body, the two terminal setae 35 and 37 μ in length. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish brown, eye red.

Male.—Body (Figs. 62 and 63) slender, a little shorter than female. Length 1.27 mm (1.25–1.28 mm) and greatest width 0.17 mm (0.16–0.17 mm), based on 10 specimens. Only slight indication of external segmentation. Caudal ramus (Fig. 64) much shorter than that of female, 24 × 14 μ. Body surface with fewer and less conspicuous setules than in female.

Rostral area like that of female. First antenna similar to that of female, but with an additional aesthete on second segment. Second antenna as in female. Labrum (Fig. 65) resembling that of female, but with outer corners projected. Mandible, first maxilla, and second maxilla like those of female. Paragnath absent. Maxilliped (Fig. 66) segmented and armed as in two previous species. Second segment with two inner setae. Fourth segment forming proximal part of claw and bearing two unequal setae. Claw 67 μ along its axis, showing a line of partial division about midway; its inner concave margin with a row of dentiform spinules and its tip bifurcated.

Legs 1–4 as in female, with same spine and setal formula. Leg 5 (Fig. 67) reduced to a slight ridge bearing two setae 22 and 24 μ in length, with a third seta arising from the body nearby. Leg 6 (Fig. 68) the usual posteroventral flap on genital segment with two setae.

Spermatophore (Fig. 69), attached to female, elongated, 277 × 55 μ, not including the short neck.

Color as in female.

Etymology.—The specific name *decorata*, from Latin = decorated, alludes to the many setules on the body surface and on legs 1–4.

Comparison with related species.—Like *X. dispar* Humes, 1962, *X. comata* Humes, 1962, *X. diminuta* Humes and Ho, 1967, and *X. lamellispinosa*, *X. decorata* has 2-segmented endopods in legs 1–4. The new species may, however, be readily distinguished from each of these four species by the nature of the outer elements on the first and second segments of the exopods of legs 1–4. These segments in *X. dispar* bear a slender spine. In *X. comata* the first segment has a minute spine and the second is unarmed. In *X. diminuta* and *X. lamellispinosa* both segments bear a well developed stout spine. Furthermore, in none of the four species does the claw of the male maxilliped have an inner row of dentiform spinules, as in the new species.

Xarifia lissa n. sp.

Figs. 70–90

Type material.—9 females and 12 males from *Stylophora pistillata* (Esper) in depth of 0.5 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, Madagascar. Collected August 4, 1963. (Nine-

teen females and 14 males of *X. decorata* were also recovered from this colony.) Holotype female, allotype, and 15 paratypes (6 females and 9 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimens.—From *Stylophora pistillata*: 2 females and 1 male in 3 m, Ambariobe, August 13, 1963; 7 females and 6 males in 0.5 m, Ambariobe, October 6, 1963. From *Stylophora mordax* (Dana): 2 females and 1 male in 2 m, Pte. Ambarionaomby, Nosy Komba, October 1, 1963.

Female.—Body (Figs. 70 and 71) moderately slender, about 6 times longer than wide. Length 1.40 mm (1.36–1.50 mm) and greatest width 0.23 mm (0.20–0.25 mm), based on 7 specimens. External segmentation weakly defined. Region dorsal to fifth legs smooth, without processes, in lateral view (Fig. 72) raised dorsally. Genital and postgenital segments together about one-fifth of total body length. Areas of attachment of egg sacs located dorsolaterally (Fig. 72). Caudal ramus (Fig. 73) moderately elongated, 41 × 19 μ (width taken at middle), about twice as long as wide; armed with a subterminal outer seta and four terminal setae, one of them very short. Egg sac (Fig. 71) containing 2 or 3 eggs in a row, eggs somewhat variable in size, distalmost egg in figure 174 × 104 μ. Surface of body with scattered short hairs.

Rostral area as in *X. decorata*. First antenna (Fig. 74) 3-segmented and short, about 45 μ in length. Armature: 3, 18 + 1 aesthete, and 6 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 75) 4-segmented and armed as in three previous species. Terminal claw relatively short, 8 μ, and adjacent seta long, 25 μ.

Labrum (Fig. 76) trilobed, the middle lobe much expanded and not indented medially. Mandible (Fig. 77) with its blade having three relatively large inner teeth, two smaller outer teeth, and a recurved tip. Paragnath absent. First maxilla (Fig. 78) a small lobe with two setae. Second maxilla (Fig. 79) 2-segmented, second segment bearing two unequal elements but lacking a lamellate process. Maxilliped (Fig. 80) probably 3-segmented, but segmentation obscure. Region of second segment bearing two small setae, that of third segment unarmed except for a conical terminal process. Relationships of head appendages as in Figure 81.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 82), exopods 3-segmented, endopods 1-segmented. Spine and setal formula as follows:

P_1 and P_2	protopod 0–0; 1–0	exp	I–0; 0–0; I, 2
		end	3
P_3 and P_4	protopod 0–0; 1–0	exp	I–0; 0–0; I, 2
		end	1

In all four legs, basis with an outer naked seta and an inner group of small setules. Second segment of exopods unarmed (Fig. 82). Endopods of legs 1 and 2 with three terminal setae, endopod of legs 3 (Fig. 83) and 4 with a single such seta. Intercoxal plates in all four legs very narrow and V-shaped.

Leg 5 (Fig. 84) moderately elongated and tapered distally, the free segment partially fused with body and about 72 μ in length. Two terminal setae offset on end of leg, unequal, 24 and 35 μ long. Seta on body near free segment short. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish brown, eye red.

Male.—Body (Figs. 85 and 86) elongated and slender, only a little shorter than female. Length 1.32 mm (1.24–1.40 mm) and greatest width 0.16 mm (0.15–0.16 mm), based on 10 specimens. External segmentation weakly developed. Caudal ramus similar to that of female but smaller, 34 × 14 μ. Body surface with fewer small hairs than in female.

Rostral area like that of female. First antenna (Fig. 87) resembling that of female, but an aesthete added on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla as in female. Paragnath absent. Maxilliped (Fig.

88) segmented and armed as in three previous species. Second segment with two inner setae. Fourth segment forming proximal part of claw, bearing two unequal setae. Claw 63 μ along its axis, with its inner concave margin serrated and its tip bifurcated.

Legs 1–4 segmented as in female. Armature as in female except for second exopod segment of leg 1 where there is a small outer hyaline seta (Fig. 89). This seta absent on legs 2–4.

Leg 5 reduced to 3 setae as in *X. decorata*, without a free segment. Leg 6 (Fig. 90) the usual posteroventral flap on genital segment with two setae.

Spermatophore (seen only inside male, as in Figure 86) elongated.

Color in life as in female.

Etymology.—The specific name *lissa*, from the Greek word λισσός = smooth or bare, refers to the absence of processes on the region dorsal to the fifth legs in the female.

Comparison with related species.—Only two other described species of *Xarifia* lack processes on the region dorsal to the fifth legs in the female. These are *X. reducta* Humes, 1962, and *X. serrata* Humes, 1962. *X. reducta* is smaller (female 1.06 mm, male 0.91 mm), the second exopod segment of legs 1–4 bears a small knob, and the male maxilliped is slender, with the claw bearing a row of dentiform spinules. *X. serrata* has a relatively longer leg 5 in the female, the blade of the mandible bears several small spinules, the maxilliped of the female bears on the third segment a terminal seta and an elongated blunt process and a minute subterminal process, the claw of the male maxilliped has larger serrations, and the second exopod segment of leg 1 in the male is unarmed. The new species thus appears to be close to *X. serrata*, but differs from it in the several respects mentioned.

Xarifia obesa n. sp.
Figs. 91–113

Type material.—8 females and 10 males from *Pocillopora verrucosa* (Ellis and Solander) in 2 m, west of Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected November 2, 1960. (*X. comata* Humes and *X. serrata* Humes were also collected from this colony of coral.) Holotype female, allotype, and 12 paratypes (5 females and 7 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Other specimens.—From *Pocillopora verrucosa*: 1 female, 2 males, and 1 immature specimen in 2 m, Pte. Mahatsinjo, October 26, 1960. From *Pocillopora* sp. cf. *P. verrucosa*: 9 females, 7 males, and 2 immature specimens in 2 m, west of Pte. Mahatsinjo, October 18, 1960. From *Pocillopora danae* Verrill: 3 females, 2 males, and 1 immature specimen in 6 m, Tany Kely, a small island to the south of Nosy Bé, December 28, 1963.

Female.—Body (Figs. 91 and 92) stouter than in other species of *Xarifia*, about 4 times longer than wide. Length 1.34 mm (1.21–1.48 mm) and greatest width 0.34 mm (0.29–0.35 mm), based on 8 specimens. External segmentation indicated by slight swellings. Region dorsal to fifth legs on each side with a posteriorly directed process. Genital and postgenital segments together about one-third of total body length. Areas of attachment of egg sacs located dorsolaterally (Fig. 93). Egg sac (Fig. 94) about 300 × 240 μ, containing seven eggs in a cluster, each egg about 130 μ in diameter. Caudal ramus (Fig. 95) about 70 μ long and fused with body, rather pointed, with its small spherical tip set off from the proximal part. Armed with an outer marginal seta and three terminal setae, all naked. Body surface with a few small hairs.

Rostral area (Fig. 96) somewhat quadrate, with broadly rounded posterior margin. First antenna (Fig. 97) 3-segmented and short, about 40 μ in length. Armature: 3, 17 + 1 aesthete, and 4 + 2 aesthetes, all setae hyaline and naked. Second antenna (Fig. 98) 3-segmented, the last two seg-

ments being fused. Armature as in previous four species; terminal claw strongly recurved, about 20 μ along its axis, and adjacent seta 16 μ.

Labrum (Fig. 99) with projected corners. Mandible (Fig. 100) with two rows of spinules on blade. Paragnath not seen. First maxilla (Fig. 101) a small lobe with two unequal naked setae. Second maxilla (Fig. 102) globose and highly modified, without definite segmentation, the region of second segment indicated by a pair of small setae and a more distal seta and minute process. Maxilliped (Fig. 103) probably 3-segmented, with two small setae on region of second segment, and two processes and a small seta on third segment. Relationships of head appendages as in Figure 104.

Legs 2–4 with general form and segmentation as in leg 1 (Fig. 105), exopods 3-segmented, endopods 1-segmented. Spine and setal formula as follows:

P_1 and P_2	protopod 0–0;	1–0 exp end 3	I–0; 1–0; I, 2
P_3 and P_4	protopod 0–0;	1–0 exp end 1	I–0; 1–0; I, 2

In all four legs, basis with an outer seta. Second segment of exopods with a small hyaline seta instead of a recurved spine, as in Figure 105. Endopods of legs 1 (Fig. 105) and 2 with three terminal setae, endopods of legs 3 (Fig. 106) and 4 with a single such seta. Intercoxal plate of leg 1 wide and not indented, those of succeeding legs narrower.

Leg 5 (Fig. 107) relatively small (cf. Figs. 91 and 93), about 24×9 μ (width taken at middle), with two terminal setae 18 and 22 μ long. Leg 6 absent.

Color in life in transmitted light opaque, intestine greenish with red globules, eye red, egg sacs tinged with red.

Male.—Body (Figs. 108 and 109) stouter than in other species, approximately 4 times longer than wide, and only a little shorter than female. Length 1.21 mm (1.14–1.30 mm) and greatest width 0.29 mm (0.26–0.31 mm), based on 10 specimens. External segmentation weakly developed. Caudal ramus similar to that of female but shorter, 55 μ in length.

Rostral area as in female. First antenna like that of female, but an additional aesthete on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla as in female. Paragnath not seen. Maxilliped (Fig. 110) segmented and armed as in four previous species. Second segment with two inner setae. Fourth segment forming proximal part of claw, bearing two setae, one proximal and the other near middle of concave margin. Distal part of this margin slightly serrated and tip of claw minutely trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 111) reduced to a small lobe with two terminal setae and an adjacent seta arising from body. Leg 6 (Figs. 112 and 113) the usual posteroventral flap on genital segment with two setae.

Spermatophore (seen only inside male, as in Figure 109) elongated.

Color in life as in female.

Etymology.—The specific name *obesa*, from Latin = fat or swollen, alludes to the unusually stout body.

Comparison with related species.—*X. fimbriata* Humes, 1960, is the only other species of *Xarifia* which has in the female two long processes dorsal to the fifth legs. This species may be easily separated from *X. obesa*, however, by its fifth legs which lack a distinct segment. From all species in the genus *X. obesa* may be distinguished by its stout body and the unique form of its caudal ramus.

Xarifia brevicauda n. sp.
Figs. 114–132

Type material.—5 females and 1 male from *Alveopora* sp. in 3.5 m, Nosy N'Tangam, on the western side of Nosy Bé, Madagascar. Collected October 23, 1964. Holotype female, allotype, and 3 paratypic females deposited in the United States National Museum; the remaining paratypic female (dissected) in the collection of A. G. Humes.

Female.—Body (Figs. 114 and 115) moderately slender, about 5.5 times longer than wide. Length 1.27 mm (1.23–1.35 mm) and greatest width 0.23 mm (0.22–0.23 mm), based on 5 specimens. External segmentation weakly indicated. Region dorsal to fifth legs with three nearly equal long posteriorly directed processes. Genital and postgenital segments fused (Fig. 116), form a short "tail," shield-shaped in dorsal view and only about one-sixth of total body length. Areas of attachment of egg sacs situated dorsally. Each sac (Fig. 115) 230×140 μ, containing two eggs, each about 140×120 μ. Caudal ramus (Fig. 117) elongated, 62×23 μ, with one outer marginal and four terminal setae. Body surface with a few scattered small hairs.

Rostral area (Fig. 118) tongue-shaped and rounded. First antenna (Fig. 119) 4-segmented (the third segment in other species being here divided into two segments) and elongated, about 75 μ in length. Setae long and naked. Armature: 3, 22 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. Second antenna (Fig. 120) slender, 4-segmented, and armed as in previous five species. Terminal claw 28 μ long and slender, adjacent seta 18 μ; two setules near base of claw.

Labrum (Fig. 121) projected posteriorly at both free corners. Mandible (Fig. 121) with a pointed smooth blade. Paragnath not seen. First maxilla (Fig. 121) a small lobe with two setae. Second maxilla (Fig. 121) 2-segmented, second segment with two setae and a terminal lamellate expansion. Maxilliped (Fig. 122) probably 3-segmented. First segment with an outer distal expansion. Second segment with two inner setae and two expansions, one inner and the other distal. Third segment with a small lobe and a short terminal claw. Relationships of head appendages as in Figure 123.

Legs 1–4 with 3-segmented exopods and 2-segmented endopods. Spine and setal formula as follows:

P_1 and P_2 protopod	0–0; 1–0	exp	I–0; I–0; I, 3
		end	0–0; 2
P_3 and P_4 protopod	0–0; 1–0	exp	I–0; I–0; I, 2
		end	0–0; 0

In all four legs, basis with an outer seta and an inner group of hairs. Terminal claw on exopods unusually long, nearly as long as second and third segments combined. Endopods of legs 1 (Fig. 124) and 2 with second segment truncated terminally and bearing two setae; endopods of legs 3 (Fig. 125) and 4 with second segment rounded and without setae. In endopods of all four legs inner margin of first segment with hairs; outer margins of both segments with slender setules. Intercoxal plate of leg 1 broadly U-shaped, those of succeeding legs narrower.

Leg 5 (Fig. 126) elongated, 138 μ long, tapered distally, and bearing two unequal terminal setae 17 and 34 μ in length. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish orange, eye red, egg sacs dark gray.

Male.—The description of the male which follows is based on a single specimen, the allotype, which was studied in lactic acid without dissection.

Body (Figs. 127 and 128) moderately slender, about 8 times longer than wide, longer than female. Length 1.51 mm and greatest width 0.18 mm. External segmentation only weakly indicated. Caudal ramus (Fig. 129) minute, 20×13 μ, with four setae. Genital and postgenital segments together about one-fifth of total body length.

Rostral area as in female. First antenna like that of female but with an aesthete added on second segment. Second antenna, labrum, mandible, first maxilla, and second maxilla as in female. Paragnath not seen. Maxilliped (Fig. 130) segmented and armed as in five previous species. Second segment with two inner setae. Claw 62 μ along its axis, armed with the usual two setae. Concave inner proximal margin with a rounded serrated excrescence and tip of claw trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 131) minute, with only

a slight ridge bearing two setae representing the free segment. Leg 6 (Fig. 132) the usual posteroventral flap on genital segment bearing two setae.

Spermatophore not seen.

Color in life as in female.

Etymology.—The specific name *brevicauda*, from the Latin words *brevis* = short, and *cauda* = tail, refers to the unusually short genital and postgenital area.

Comparison with related species.—*X. brevicauda* may be distinguished from all previously described species in the genus by its abbreviated genital and postgenital region and by the serrated excrescence on the claw of the male maxilliped. Apart from these distinctions it may further be separated from those species having 2-segmented endopods in legs 1–4 (*X. dispar* Humes, 1962, *X. comata* Humes, 1962, *X. diminuta* Humes and Ho, 1967, *X. lamellispinosa*, and *X. decorata*) by the nature of the three outer spines on the exopods of legs 1–4 (the two proximal spines being short, the terminal spine longer than the last segment of the exopod).

Xarifia temnura n. sp.

Figs. 133–153

Type material.—12 females and 4 males from *Montipora sinensis* Bernard in a depth of 1 m, Nosy Taolankena, a small island on the northwestern side of Nosy Bé, Madagascar. Collected November 15, 1963. Holotype female, allotype, and 11 paratypes (8 females and 2 males) deposited in the United States National Museum; the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Figs. 133 and 134) elongated and very slender, about 10 times longer than wide. Length 1.52 mm (1.47–1.65 mm) and greatest width 0.15 mm (0.14–0.15 mm), based on 10 specimens. External segmentation lacking. Region dorsal to fifth legs smooth, without processes. Area bearing these legs turned ventrally (Fig. 135) toward sites of attachment of egg sacs and partially overlapping these regions of attachment laterally, thus producing a truncated appearance. Postgenital segments completely fused into a single body region which is relatively minute (52 μ along its dorsal surface and 83 μ along its ventral surface, not including the caudal rami). This "tail" region, together with the caudal rami, only about one-thirteenth of total body length. Caudal ramus (Fig. 136) fused with anal segment, lobate, 28 μ long with four short naked setae. Egg sac (Fig. 133) elongated, with 3 or 4 eggs in a row. In the female figured, right sac 430 μ long with middle egg 140 × 114 μ, left sac 506 μ long with penultimate egg 130 × 125 μ. Body surface with very few small hairs.

Rostral area (Fig. 139) weakly developed. First antenna (Fig. 137) 3-segmented and very short, about 23 μ long. Setae hyaline and naked. Armature: 3, 15 + 1 aesthete, and 6 + 2 aesthetes (though setae so densely arranged that it is difficult to count exact number). Second antenna (Fig. 138) 4-segmented and armed as in six previous species. Terminal claw transformed to a relatively long spine (28 μ in length); adjacent seta short (4 μ) and spiniform. A few small spines on anterior edge of second and third segments.

Labrum (Fig. 139) very slightly trilobed. Mandible (Fig. 140) with a pointed smooth blade. Paragnath (Fig. 139) consisting of a very small lobe with a few minute hairs. First maxilla (Fig. 141) a minute lobe with two naked setae. Second maxilla (Fig. 142) 2-segmented, second segment bearing two minute setae and a terminal clawlike spine. Maxilliped (Fig. 143) highly modified, with two inner setae on second segment and two smaller setae on what is probably the third segment. Relationships of head appendages as in Figure 139.

Legs 1–4 small, exopod of leg 1 (Fig. 144) 3-segmented, exopods of legs 2 (Fig. 146), 3, and 4 probably 3-segmented, but second and third segments of these legs without distinct line of separation; endo-

pods of all four legs 1-segmented. Spine and setal formula as follows:

P_1	protopod	0–0;	1–0
	exp	I–0;	I–0; I, 3
	end	1	
P_2	protopod	0–0;	1–0
	exp	I–0;	0–0; I, 3
	end	1	
P_3 and P_4	protopod	0–0;	1–0
	exp	I–0;	0–0; I, 2
	end	0	

In all four legs, basis with an outer seta. Endopods of legs 1 (Fig. 145) and 2 (Fig. 146) with a single terminal seta; endopods of legs 3 (Fig. 147) and 4 without a seta. In all four endopods outer margin with numerous slender setules. Intercoxal plate of leg 1 U-shaped, becoming narrower in succeeding legs.

Leg 5 (Figs. 135 and 148) minute, located dorsolaterally above truncated region. Free segment reduced to a small lobe about 5 μ in length bearing two setae. Leg 6 absent.

Color in life in transmitted light opaque, intestine reddish brown, eye red, egg sacs reddish brown.

Male.—Body (Figs. 149 and 150) very slender, about 10.5 times longer than wide. Length 1.46 mm (1.43–1.50 mm) and greatest width 0.14 mm (0.13–0.15 mm), based on 4 specimens. External segmentation weakly indicated. Caudal ramus (Fig. 151) minute, 13 μ long, fused with anal segment and bearing four setae; the two rami rather divergent. Genital and postgenital segments together about one-third of total body length. Body surface with very few scattered small hairs.

Rostral area as in female. First antenna like that of female but an aesthete added on second segment. Second antenna as in female. Labrum (Fig. 152) resembling that of female but with posterior margin having a pair of small teeth medially and a small tooth at each corner. Mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (Fig. 153) segmented and armed as in six previous species. Second segment with two inner setae. Claw 42 μ along its axis, armed with two setae. Concave margin proximally with a rather triangular serrated process; tip of claw trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 150) very reduced, consisting only of three small setae, as in *X. lissa*. Leg 6 (Fig. 150) a posteroventral flap on genital segment bearing two small setae.

Spermatophore (seen only inside male, as in Figure 149) elongated.

Color in life as in female.

Etymology.—The specific name *temnura*, from the Greek words τέμνω = cut off and ὀυρά = tail, refers to the truncated appearance of the posterior part of the body.

Comparison with related species.—The females of *X. temnura* may be recognized by the unique truncated posterior region and the very small postgenital area. In only three other species does the female lack processes on the region dorsal to the fifth legs. These are *X. reducta* Humes, 1962, *X. serrata* Humes, 1962, and *X. lissa*. All differ from *X. temnura*, however, in the body being much stouter (6–7 times longer than wide) and in the much longer fifth legs (*X. reducta* = 34 μ, *X. serrata* = 122 μ, and *X. lissa* = 72 μ). The male of *X. temnura* differs from all other species having 1-segmented endopods on legs 1–4 in the nature of the claw of the maxilliped and in the form of the caudal ramus.

Xarifia anomala n. sp.
Figs. 154–173

Type material.—2 females and 3 males from *Acropora palifera* (Lamarck) in a depth of 2 m, Tany Kely, a small island to the south of Nosy Bé, Madagascar. Collected October 3, 1963. Holotype female, allotype, and 1 male paratype deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Female.—Body (Figs. 154 and 155) moderately slender, about 7.8 times longer than wide. Length 1.25 mm (1.25–1.26 mm) and greatest width 0.16 mm (0.16–0.17 mm), based on 2 specimens. External segmentation very weakly indicated. Re-

gion dorsal to fifth legs with three moderately long posteriorly directed processes, all nearly equal in length. Genital and postgenital region recurved in specimens in alcohol, with caudal rami turned dorsally (Fig. 156), this entire region comprising about one-fifth of total body length. Areas of attachment of egg sacs located dorsolaterally. Egg sac unknown. Caudal ramus (Fig. 157) elongated, 52 × 15 μ, with one outer marginal and four terminal naked setae. Body surface with a few scattered small hairs.

Rostral area forming a prominent rounded lobe (Fig. 161), similar to that of male (Fig. 168). First antenna small, about 33 μ in length, probably 3-segmented, though last two segments seem partially divided; similar to that of male (Fig. 168). Armature: 3, 22 (no aesthete visible here), and 9 + 2 aesthetes. Second antenna (Fig. 158) 4-segmented and armed as in previous seven species. Terminal claw recurved and slender, 10 μ long, with adjacent seta 19 μ in length.

Labrum of a form similar to that of male (Fig. 169). Mandible a smooth attenuated recurved blade as in male (Fig. 170). Paragnath an obscure minute smooth prominence near inner base of first maxilla. First maxilla (Fig. 159) a small lobe with two setae and a small spinous process. Second maxilla 2-segmented, second segment with two small setae and an elongated lamellate expansion, as in male (Fig. 171). Maxilliped (Fig. 160) probably 3-segmented. First segment with a well sclerotized almost hooklike lobe on distal outer surface. Second segment with two inner setae. Third segment with a spiniform process and a terminal lamellate element. Relationships of head appendages as in Fig. 161.

Legs 1–4 with 3-segmented exopods and 2-segmented endopods. Spine and setal formula as follows:

P_1 protopod	0–0; 1–0	exp	I–0; I–0; I, 3
		end	0–0; 0
P_2 protopod	0–0; 1–0	exp	I–0; I–0; I, 2
		end	0–0; 3
P_3 and P_4 protopod	0–0; 1–0	exp	I–0; I–0; I, 2
		end	0–0; 0

In all four legs intercoxal plates narrow and V-shaped; basis with an outer seta and an inner group of hairs. Claws on exopods with short but conspicuous terminal lamellae. Second segment of endopod of leg 1 (Fig. 162) without terminal setae (though slender setules occur along outer margin of segment). Second segment of endopod of leg 2 (Fig. 163) with three terminal setae. Legs 3 and 4 resembling in general structure first two legs, but second endopod segment without terminal setae.

Leg 5 (Fig. 164) elongated, about 100 μ in length, tapered distally, with two unequal terminal setae 13 and 23 μ long. Leg 6 absent.

Color in life unknown.

Male.—Body (Figs. 165 and 166) fairly slender, about 9 times longer than wide. Length 1.21 mm (1.15–1.25 mm) and greatest width 0.13 mm (0.12–0.14 mm), based on 3 specimens. External segmentation very weak. Genital and postgenital segments together about one-fourth of total body length. Caudal ramus (Fig. 167) reduced to five setae arising directly from anal segment.

Rostral area and first antenna (Fig. 168) like those in female, as far as could be determined. (The presence of an extra aesthete in the male, as often found in this genus, could not be established.) Second antenna as in female. Labrum (Fig. 169), mandible (Fig. 170), paragnath, first maxilla, and second maxilla (Fig. 171) resembling those of female. Maxilliped (Fig. 172) segmented and armed as in seven previous species. Second segment with two unequal inner setae. Claw 28 μ along its axis, armed with two setae. Concave margin with a few spinules and tip of claw trifurcated.

Legs 1–4 segmented and armed as in female. Leg 5 (Fig. 173) consisting of three small setae, arising from body wall and without a free segment. Leg 6 (Fig. 173) the usual posteroventral flap on genital segment with two small setae.

Spermatophore seen only inside body of male, as in Figure 173.

Color in life unknown.

Etymology.—The specific name *anomala*, from ἀνώμαλος = uneven or unequal, refers to the peculiar formula for the terminal armature of the endopods of legs 1–4.

Comparison with related species.—*X. anomala* may be distinguished from the six already described species of *Xarifia* which have 2-segmented endopods on legs 1–4 by the absence of terminal setae on the endopod of its first leg and by the extreme sexual dimorphism in the caudal ramus. Three of these six species, *X. dispar* Humes, 1962, *X. comata* Humes, 1962, and *X. decorata*, have the outer spine on the second segment of the exopod of leg 1 reduced or absent, thus further separating them from the new species. Of the remaining three species, *X. brevicauda* has a shorter postgenital region, *X. lamellispinosa* has a short stout claw on the second antenna and a toothed mandible, and *X. diminuta* Humes and Ho, 1967, has relatively short stout spines on the exopods of legs 1–4.

Xarifia hamata n. sp.

Figs. 174–194

Type material.—64 females and 16 males from *Turbinaria* sp. (tabulate group, near *T. elegans* Bernard but not this species) in a depth of 2 m, Nosy Taolankena, a small island off the northwestern shore of Nosy Bé, Madagascar. Collected November 15, 1963. Holotype female, allotype, and 58 paratypes (45 females and 13 males) deposited in the United States National Museum; 11 paratypic females in the Museum of Comparative Zoology; and the remaining paratypes in the collection of A. G. Humes.

Female.—Body (Figs. 174 and 175) moderately slender, about 6.3 times longer than wide. Length 1.38 mm (1.29–1.42 mm) and greatest width 0.22 mm (0.21–0.22 mm), based on 10 specimens. External segmentation weakly indicated, except in a few specimens where postgenital segments are more clearly delimited (Fig. 176). Region dorsal to fifth legs with three moderately long posteriorly directed processes, all nearly equal in length. Genital and postgenital region short and held at a slight angle to main body axis, this region comprising about one-seventh of total body length. Areas of attachment of egg sacs situated dorsolaterally. Egg sac (Fig. 175) about 374 × 198 μ, containing usually 5, but sometimes 6 eggs, each about 115 μ in diameter. Caudal ramus (Fig. 177) not clearly delimited from anal segment, approximately 41 × 17 μ (width taken at middle), with a strong outer marginal seta and four more slender terminal setae. All setae naked. Dorsal surface of ramus with a few hairs. Body surface ornamented with very few minute hairs.

Rostral area resembling that of *X. lamellispinosa*. First antenna (Fig. 178) small, about 55 μ in length, apparently 3-segmented, though second and third segments show partial division. Armature: 3, 22 + 1 aesthete, and 9 + 2 aesthetes. Second antenna (Fig. 179) 4-segmented and armed as in eight previous species. Last segment terminally with a slender claw 13 μ long, a seta 19 μ, a small setule, and a minute spinous process.

Labrum (Fig. 180) with trilobate free margin. Mandible (Fig. 181) with a sinuous smooth attenuated blade. Paragnath a small lobe with a few hairs, similar to that shown for the male in Figure 193. First maxilla (Fig. 182) with two naked setae and a spinous process. Second maxilla (Fig. 183) 2-segmented, second segment elongated with two proximal inner setae and a third seta near its obtuse hyaline tip. Maxilliped (Fig. 184) 3-segmented, second segment with two inner setae, third with two inner setae and terminating in a clawlike process. Relationships of head appendages as in Figure 185.

Legs 1–4 with similar form and segmentation, exopods 3-segmented, endopods 2-segmented. Spine and setal formula as follows:

P_1	protopod	0–0; 1–0	exp I–0; 1–0; I, 3
			end 0–0; 2
P_2	protopod	0–0; 1–0	exp I–0; 1–0; I, 3
			end 0–0; 1, I
P_3 and P_4	protopod	0–0; 1–0	exp I–0; 1–0; I, 2
			end 0–0; I

First segment of exopod of all four legs with a spiniform process at base of outer spine; second segment of these exopods with an outer seta instead of a spine. In all four legs inner margins of first and second segments of exopods and outer margins of both segments of endopods with long hairs. Terminal segment of endopod of leg 1 with two setae (Fig. 186), of leg 2 with an outer seta and an inner clawlike spine (Fig. 187), and of legs 3 and 4 with a single clawlike spine (Fig. 188). Leg 4 (not drawn) similar to leg 3. Intercoxal plates roughly V-shaped in all four legs.

Leg 5 (Fig. 189) moderately elongated, about 58 μ long, tapered distally, with two unequal terminal setae 24 and 32 μ long. Leg 6 absent.

Color in life in transmitted light slightly brownish, intestine reddish brown, eye red, egg sacs reddish brown to dark grayish black.

Male.—Body (Figs. 190 and 191) slender, about 9.1 times longer than wide. Length 1.28 mm (1.15–1.56 mm) and greatest width 0.14 mm (0.13–0.14 mm), based on 10 specimens. External segmentation weakly defined except in some specimens in postgenital area (Fig. 192). Genital and postgenital segments together less than one-third of total body length. Caudal ramus similar to that of female but smaller and relatively broader, 25×13 μ.

Rostral area as in female. First antenna like that of female, but with four aesthetes, one being added on midanterior margin of middle segment. Second antenna as in female. Labrum resembling that of female but with a minute toothlike process on corners of outer lobes. Mandible, paragnath (Fig. 193), first maxilla, and second maxilla as in female. Maxilliped (Fig. 194) segmented and armed as in eight previous species. Second segment with two inner setae. Claw 40 μ along its axis, armed with two setae. Concave margin with a few minute serrations near distal seta.

Legs 1–4 segmented and armed as in female. Leg 5 without a free segment, consisting of three small setae, two of them arising from a very slight ridge (Fig. 192). Leg 6 the usual posteroventral flap on genital segment bearing two small setae (Fig. 192).

Spermatophore seen only inside body of male, as in Figure 192.

Color in life resembling that of female.

Etymology.—The specific name *hamata*, from Latin = provided with hooks, refers to the clawlike spines on the endopods of legs 2–4.

Comparison with related species.—*X. hamata* may be distinguished from all other nineteen species in the genus by the combination of the following three characters: the endopods in all four legs 2-segmented, the endopods of legs 3 and 4 with a clawlike terminal spine, and the exopods of all four legs with a spinal armature of I, 1, I. The presence of a clawlike spine on the second segment of the endopod in legs 2–4 is sufficient to separate the new species from all others in the genus (where the endopods either bear setae or are unarmed, though they may be ornamented with slender setules or hairs).

Xarifia dispar Humes, 1962

This species has been previously recorded only from *Echinopora carduus* Klunzinger in Madagascar. It is now reported from two new hosts as follows:

1) from *Echinopora gemmacea* (Lamarck): 3 females and 7 males in 2 m, northern end of Nosy Sakatia, off the western side of Nosy Bé, Madagascar, September 18, 1963; 6 females and 3 males in 1 m, Pte. de Tafondro, Nosy Bé, September 21, 1963.

2) from *Echinopora lamellosa* (Esper): 6 females and 7 males in 1 m, Pte. Ambar-

ionaomby, Nosy Komba, near Nosy Bé, June 24, 1963.

The specimens from the two new hosts agree in all significant features with paratypic specimens. Although in the original description paragnaths were said to be absent, we have found both in paratypic specimens and in the new material two small elongated lobes which are clearly paragnaths.

Xarifia serrata Humes, 1962

The type specimens of this species were taken by Humes (1962) in Madagascar from *Pocillopora damicornis* Dana. He found other specimens on *Seriatopora subseriata* Ehrenberg and *Pocillopora verrucosa* (Ellis and Solander). The species was again reported from *Seriatopora subseriata* by Humes and Frost (1964).

We have now recovered it from a new host, *Pocillopora bulbosa* Ehrenberg, from which 29 females and 34 males were taken in 10 cm at Ankify, on the mainland of Madagascar opposite Nosy Komba, June 11, 1964. These specimens agree completely with paratypic material.

ORSTOMELLA n. gen.

Type species.—*Orstomella faviae* n. sp.

Female.—Body elongated, slender, with indistinct segmentation. Region dorsal to fifth legs without processes. Rostral area weakly developed. Caudal ramus with a few short terminal setae.

First antenna 6-segmented, first segment with an anterior process, remaining segments with numerous short setae. Second antenna 3-segmented, terminal segment (with slight indication of division into two segments) bearing two unequal elements.

Labrum with widely separated lobes. Mandible and paragnath absent. First maxilla with three elements. Second maxilla 2-segmented. Maxilliped 3-segmented.

Legs 1 and 2 with 2-segmented exopods and endopods. Legs 3 and 4 with 2-segmented exopods, but endopods absent. Leg 5 a ridge with three setae. Leg 6 absent.

Male.—Resembling female with following exceptions. First antenna with four aesthetes. Lateral margins of labral lobes with crenated depressions. First maxilla with two elements. Maxilliped probably 4-segmented, claw short. Leg 6 a posteroventral flap with two very small setae.

Living in polyps of madreporarian corals.

Gender feminine.

Etymology.—The name *Orstomella* is formed from ORSTOM, the abbreviation for the Office de la Recherche Scientifique et Technique Outre-Mer, the organization of the French Government which operates the Centre O.R.S.T.O.M. (formerly the Centre d'Océanographie et des Pèches) at Nosy Bé, Madagascar, and which has aided in so many ways the field work in connection with this study.

Orstomella faviae n. sp.

Figs. 195–219

Type material.—11 females, 8 males, and 4 copepodids from two colonies of *Favia* sp. in a depth of 2 m, west of Pte. Mahatsinjo, Nosy Bé, Madagascar. Collected April 10, 1964. Holotype female, allotype, and 12 paratypes (7 females and 5 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Female.—Body (Figs. 195 and 196) elongated and slender, about 6.4 times longer than wide, slightly thickened dorsoventrally in prosomal region, with indistinct segmentation and lacking fine ornamentation. Length 2.19 mm (2.10–2.26 mm) and greatest width 0.34 mm (0.32–0.36 mm), based on 10 specimens. Region dorsal to fifth legs without processes. Genital and postgenital segments together about one-third of total body length. Genital segment (Fig. 197) bipartite, the anterior third narrow (78 × 179 μ) with areas of attachment of egg sacs dorsolateral in position, the posterior two-thirds broader (177 × 198 μ). Three postgenital segments 133 × 180, 55 × 144, and 107 × 122 μ from anterior to posterior. Last segment with a prominent anal

operculum. Caudal ramus (Fig. 198) moderately elongated, 80 × 26 μ, about 3 times longer than wide; bearing terminally a seta 20 μ and a minute spinule 3 μ long, and having on its proximal outer margin a hyaline setule 6 μ long. Egg sac unknown.

Rostral area (Fig. 199) weakly developed. First antenna (Fig. 199) short, about 80 μ in length, and 6-segmented, bearing numerous short setae which are sclerotized proximally but hyaline distally with somewhat obtuse tips. Lengths of segments (measured along their posterior non-setiferous margins) 15, 24, 14, 9, 9, and 8 μ respectively. First segment with an anterior process (probably not a true element, since it has no articulation). Formula for armature: 0, 3, 6, 4, 3, 6. A few minute spinules on surface of segments. Second antenna (Fig. 200) 3-segmented, about 44 μ long without setae; first segment wide with an anteroventral jointed seta 16 μ long; second segment elongated, slender, and unarmed; third segment also elongated and slender, with slight indication of division and bearing terminally a jointed seta 15 μ and a short spine 5 μ long.

Labrum (Fig. 201) with two lobes widely separated and both bearing a surficial seta; other fine ornamentation as indicated in figure. Mandible and paragnath absent. First maxilla (Fig. 202) a small lobe with three distally hyaline elements, two of them bipartite as shown in figure. Second maxilla (Fig. 203) 2-segmented, first segment large and unarmed, second small, bearing two hyaline obtuse elements and a spinous process and prolonged terminally as a rather obtuse process with hyaline border (cf. Figures 203 and 204). Maxilliped (Fig. 205) apparently 3-segmented; first segment unarmed; second segment indistinctly separated from third and bearing two short elements, one straight, the other recurved; third segment small, armed with one hyaline obtuse element and having a terminal prolongation with hyaline lamellae. Labrum and mouthparts situated close together (Fig. 206) with a small median ventral lobe (see Figure 201) between the second maxillae and maxillipeds.

Leg 1 (Fig. 207) and leg 2 with 2-segmented exopods and endopods. Leg 3 (Fig. 209) and leg 4 with 2-segmented exopods, but without endopods. Spine and setal formula as follows:

P_1 and P_2	protopod	0–0; 1–0	exp I–0; (I), I
			end 0–0; 1
P_3 and P_4	protopod	0–0; 1–0	exp I–0; I, I
			end –

Low median ventral protuberances in front and behind first three pairs of legs (seen in lateral view in Figure 196).

In leg 1, first segment of exopod with a small outer spine, second segment with a minute outer spine (or spinous process ?) and a terminal clawlike spine which is swollen on its concave edge (Fig. 208). Endopod with first segment unarmed, second segment with a single partly hyaline and obtusely tipped terminal seta and a small hyaline lobe. Leg 2 similar to leg 1.

In leg 3 both segments of exopod with a small outer spine and second segment with terminal clawlike spine having hyaline lamellae (cf. Figures 209 and 210). Endopod absent. Leg 4 similar to leg 3.

Leg 5 (Fig. 211) consisting of a low slightly sclerotized ridge with three obtuse and mostly hyaline setae 9, 13, and 8 μ in length. Position of this leg as in Figure 196.

Leg 6 absent.

Color in life in transmitted light bright red, with eye darker red.

Male.—Body (Figs. 212 and 213) resembling that of female, about 7.6 times longer than wide. Length 2.12 mm (1.99–2.24 mm) and greatest width 0.28 mm (0.23–0.34 mm), based on 8 specimens. Genital and postgenital segments together about one-third of total body length. Genital segment (Fig. 214) wider than long, 138 × 256 μ. Four postgenital segments 185 × 216, 143 × 190, 65 × 143, and 104 × 122 μ from anterior to posterior. Caudal ramus as in female, but slightly longer, 91 × 23 μ, with the large terminal seta 23 μ long.

Rostral area as in female. First antenna

(Fig. 215) segmented and armed as in female, except for three aesthetes being added on segment 3 and one aesthete on segment 4, making the formula 0, 3, 6 + 3 aesthetes, 4 + 1 aesthete, 3, and 6. Second antenna as in female.

Labrum (Fig. 216) with two lobes smaller than in female and having lateral depressions with well sclerotized crenated edges. Mandible and paragnath absent. First maxilla (Fig. 217) a small lobe with only two elements. Second maxilla as in female. Maxilliped (Figs. 218 and 219) probably 4-segmented, but segmentation obscure. First segment unarmed, second large with two inner hyaline setae, third small and unarmed. Fourth segment forming a short terminal blunt claw 19 μ in length bearing two unequal elements. Relationships of mouthparts as in female.

Legs 1–4 as in female.

Leg 5 similar to that of female.

Leg 6 (Fig. 214) consisting of a posteroventral flap on genital segment bearing two minute setae 8 and 6 μ long.

Spermatophore seen only inside body of male, as in Figure 213.

Color in life as in female.

Etymology.—The specific name *faviae* is derived from the generic name of the host.

Orstomella lobophylliae n. sp.
Figs. 220–239

Type material.—10 females and 16 males from *Lobophyllia costata* (Dana) in a depth of 6–8 m, Ambariobe, a small island nearly between Nosy Komba and Nosy Bé, Madagascar. Collected December 28, 1963. Holotype female, allotype, and 20 paratypes (7 females and 13 males) deposited in the United States National Museum; the remaining paratypes (dissected) in the collection of A. G. Humes.

Other specimen.—1 female from *Lobophyllia corymbosa* (Forskål) in 1 m, Ambariobe, January 13, 1964.

Female.—Body (Figs. 220 and 221) in general appearance similar to preceding species, but much smaller, about 5.5 times longer than wide. Length 1.20 mm (1.23–1.39 mm) and greatest width 0.22 mm (0.17–0.24 mm), based on 9 specimens. Region dorsal to fifth legs without processes. Genital and postgenital segments together about four-tenths of total body length. Genital segment (Fig. 222) bipartite, the anterior half 70 × 140 μ, relatively not as narrow as in preceding species, with areas of attachment of egg sacs lateral in position; the posterior half 101 × 127 μ. Three postgenital segments 90 × 102, 40 × 80, and 44 × 78 μ from anterior to posterior. Last segment with a prominent anal operculum. Caudal ramus (Fig. 223) short, 26 × 15 μ, nearly two times longer than wide, bearing terminally two setae 18 and 11 μ and a minute spinule 3 μ long, and having on its proximal outer margin a hyaline setule 10 μ long. Egg sac unknown.

Rostral area (Fig. 224) not well developed. First antenna (Fig. 224) short, about 84 μ in length, and 6-segmented, bearing numerous short hyaline setae. Lengths of segments (measured along their posterior non-setiferous margins) 20, 24, 11, 10, 9, and 9 μ, respectively. First segment having an anterior process with recurved tip. Two setae on segment 2 and one on segment 3 modified, without evident articulation and with terminal flagella. Formula for armature: 0, 3, 6, 4, 3, 6. A few minute setules on surface of segments. Second antenna (Fig. 225) 3-segmented, short, only 27 μ long without the setae; first two segments unarmed, third segment (showing slight indication of division) with terminally a jointed seta 15 μ and a short spine 6 μ.

Labrum (Fig. 226) resembling that of previous species, but two lobes smaller. Mandible and paragnath absent. First maxilla (Fig. 227) similar to preceding species, with three terminal elements, but the two bipartite elements attenuated. Second maxilla (Fig. 228) similar to preceding species, but terminal prolongation of second segment setiform. Maxilliped (Fig. 229) resembling that of *O. faviae*. Labrum and

mouthparts held close together as in that species.

Leg 1 (Fig. 230) and leg 2 with 2-segmented exopods and endopods. Leg 3 (Fig. 231) and leg 4 with 2-segmented exopods, but without endopods. Spine and setal formula as follows:

P_1 and P_2	protopod	0–0; 1–0	exp	I–0; (I), 1; I, 1
			end	0–0; 1
P_3 and P_4	protopod	0–0; 1–0	exp	I–0; I, I
			end	–

Low median ventral protuberances in front and behind first three pairs of legs (Fig. 221) as in *O. faviae*.

In leg 1 first segment of exopod with a small outer spine, second segment with a minute outer spine (or spinous process ?), a minute spinule, a terminal clawlike spine, and an inner setule. Endopod with first segment unarmed, second segment bearing a terminal seta, with nearby on anterior surface a minute setule and a small patch of denticles. Leg 2 similar to leg 1.

In leg 3 both segments of exopod with a small outer spine, and second segment with clawlike terminal spine having hyaline lamellae. Endopod absent. Leg 4 like leg 3, but second segment with minute outer spine smaller (Fig. 232).

Leg 5 (Fig. 233) consisting of a low ridge with three setae 10, 12, and 9 μ long, more attenuated than in *O. faviae*.

Leg 6 absent.

Color in life in transmitted light bright red, with eye darker red.

Male.—Body (Figs. 234 and 235) similar to that of the female, about 7 times longer than wide. Length 1.30 mm (1.20–1.45 mm) and greatest width 0.19 mm (0.16–0.23 mm), based on 10 specimens. Genital and postgenital segments together (Fig. 236) about one-third of total body length. Caudal ramus as in female but slightly larger, 29 × 16.5 μ.

Rostral area as in female. First antenna similar to that of female, but with four aesthetes added as in male of preceding species. Second antenna as in female.

Labrum (Fig. 237) with both lobes having a lateral depression with crenated edges. Mandible and paragnath absent. First maxilla (Fig. 238) with only two elements. Second maxilla as in female. Maxilliped (Fig. 239) resembling that of *O. faviae*, the terminal claw 17 μ long. Relationships of mouthparts as in female.

Legs 1–4 as in female.

Leg 5 similar to that of female.

Leg 6 (Fig. 236) a posteroventral flap on genital segment bearing two minute setae about 3 μ in length.

Spermatophore seen only inside body of male, as in Figure 235.

Color in life as in female.

Etymology.—The specific name *lobophylliae* is derived from the generic name of the host.

Comparison with the type species.—*Orstomella lobophylliae* differs in significant respects from *O. faviae*. It is much smaller (female 1.20, male 1.30 mm) than that species (female 2.19, male 2.12 mm). The caudal ramus of the female is shorter (26 × 15 μ, or about 2:1) than in *O. faviae* (80 × 26 μ, or about 3:1). There are three modified flagellated setae on the first antenna, while in *O. faviae* all the setae are similar. The first segment of the second antenna is unarmed, while in *O. faviae* this segment bears a jointed seta. In leg 5 the three setae are obtuse, but in *O. faviae* they are attenuated. Other minor differences exist in the armature of the mouthparts and in legs 1–4.

Relationship of ORSTOMELLA *with the hosts.*—Both *O. faviae* and *O. lobophylliae* evidently live in the polyps of the corals. Specimens were recovered in the sediment obtained after allowing the corals to remain overnight in alcoholized sea water (containing about 5 percent ethyl alcohol). They were never found after rinsing the freshly collected corals for only a few minutes. The copepods apparently are stimulated by the weak alcohol to emerge from the polyps, when they fall to the bottom of the container. Since the copepods are unable to swim, they are unable to regain

their positions in the coral after the effects of the alcohol diminish.

The taxonomic position of ORSTOMELLA.— In its elongated body form and its close association with corals, the genus *Orstomella* is suggestive of the genus *Xarifia* Humes, 1960.

There are, however, several important features which distinguish the two genera. In *Orstomella* the processes dorsal to the fifth legs in the female, characteristic of most *Xarifia*, are absent; the first antenna is clearly 6-segmented, instead of 3-segmented (with in some species a partial division of segments 2 and 3) as in *Xarifia*; the second antenna is 3-segmented (with slight indication of partial division of segment 3), instead of 4-segmented (3-segmented in *X. obesa* and a few others); the labrum shows marked sexual dimorphism, instead of weak dimorphism or none in *Xarifia*; the mandible and paragnath are absent, while in *Xarifia* there is a mandible in all species and a paragnath in some; the exopods of legs 1–4 are 2-segmented, instead of 3-segmented in *Xarifia*; and the endopods of legs 3 and 4 are absent, but present in *Xarifia*.

These differences might be regarded as sufficiently fundamental to justify placing *Orstomella* in a separate family. When, however, the range of variation within the genus *Xarifia* is considered, and the tendencies toward simplification and reduction exhibited by *Orstomella* are kept in mind, it seems unlikely to us that *Orstomella* truly represents a familial divergence. In certain species of *Xarifia*, for example, there are no processes dorsal to the fifth legs in the female, the second antenna is 3-segmented, the labrum shows weak sexual dimorphism, the mandible is reduced to a very minute blade, the paragnath may be absent, and the exopods of legs 1–4, though 3-segmented, may show a marked reduction of the second segment. The differences in the segmentation of the first antenna (6-segmented in *Orstomella*, 3-segmented with sometimes partial division of segments 2 and 3 in *Xarifia*) and the nature of the endopods of legs 3 and 4 (absent in *Orstomella*, 1- or 2-segmented in *Xarifia*) seem to be intrafamilial features. Differences of a similar degree exist within other poecilostome families, for example, the Lichomolgidae. The absence of a mandible in *Orstomella*, while of fundamental importance, may simply represent an extreme in intrafamilial reduction, a strong tendency toward reduction of this appendage being already seen in certain *Xarifia*.

For these reasons we place *Orstomella* provisionally in the Xarifiidae, along with the genus *Xarifia*. The study of further collections of related copepods from corals would undoubtedly clarify the relationships of these two genera.

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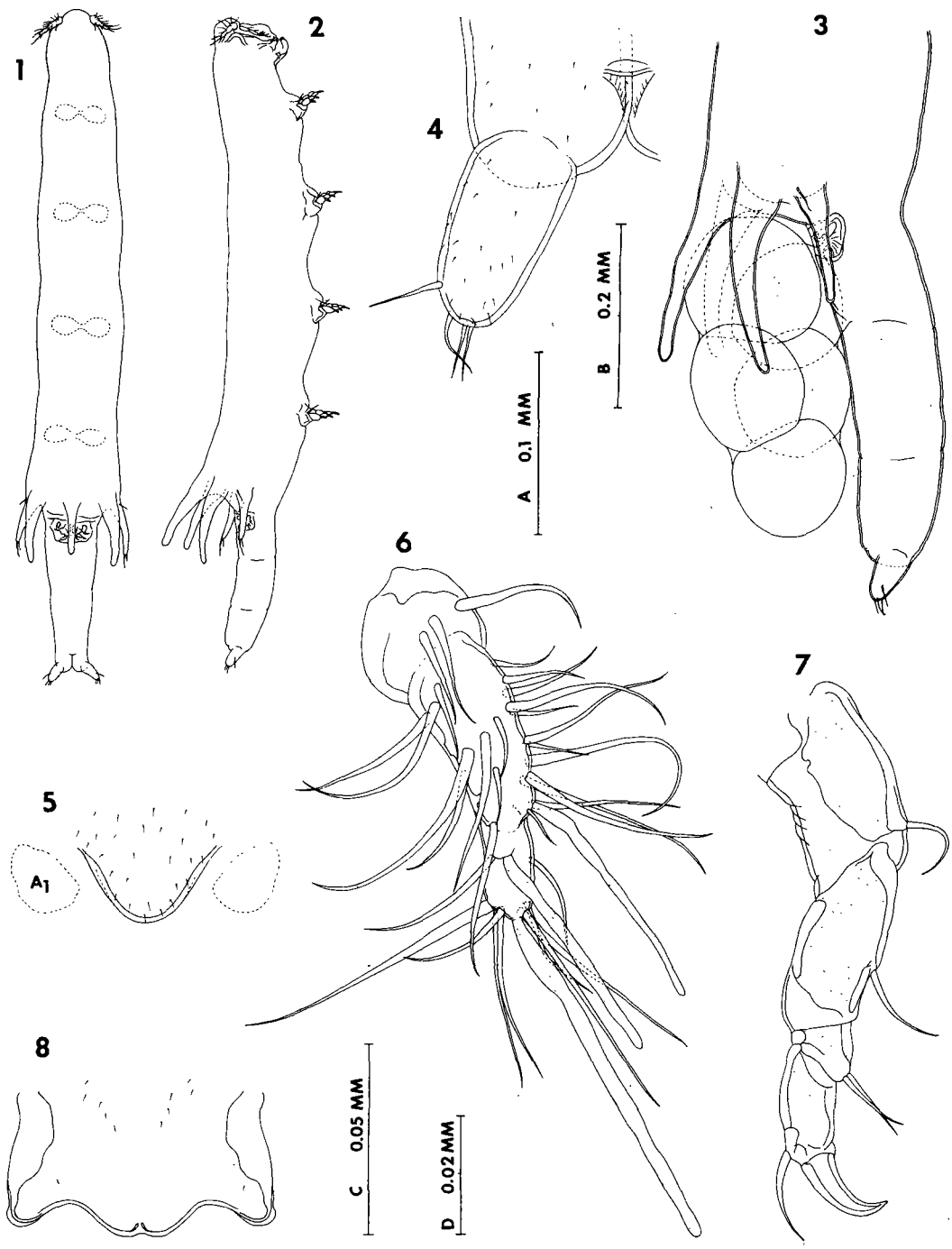
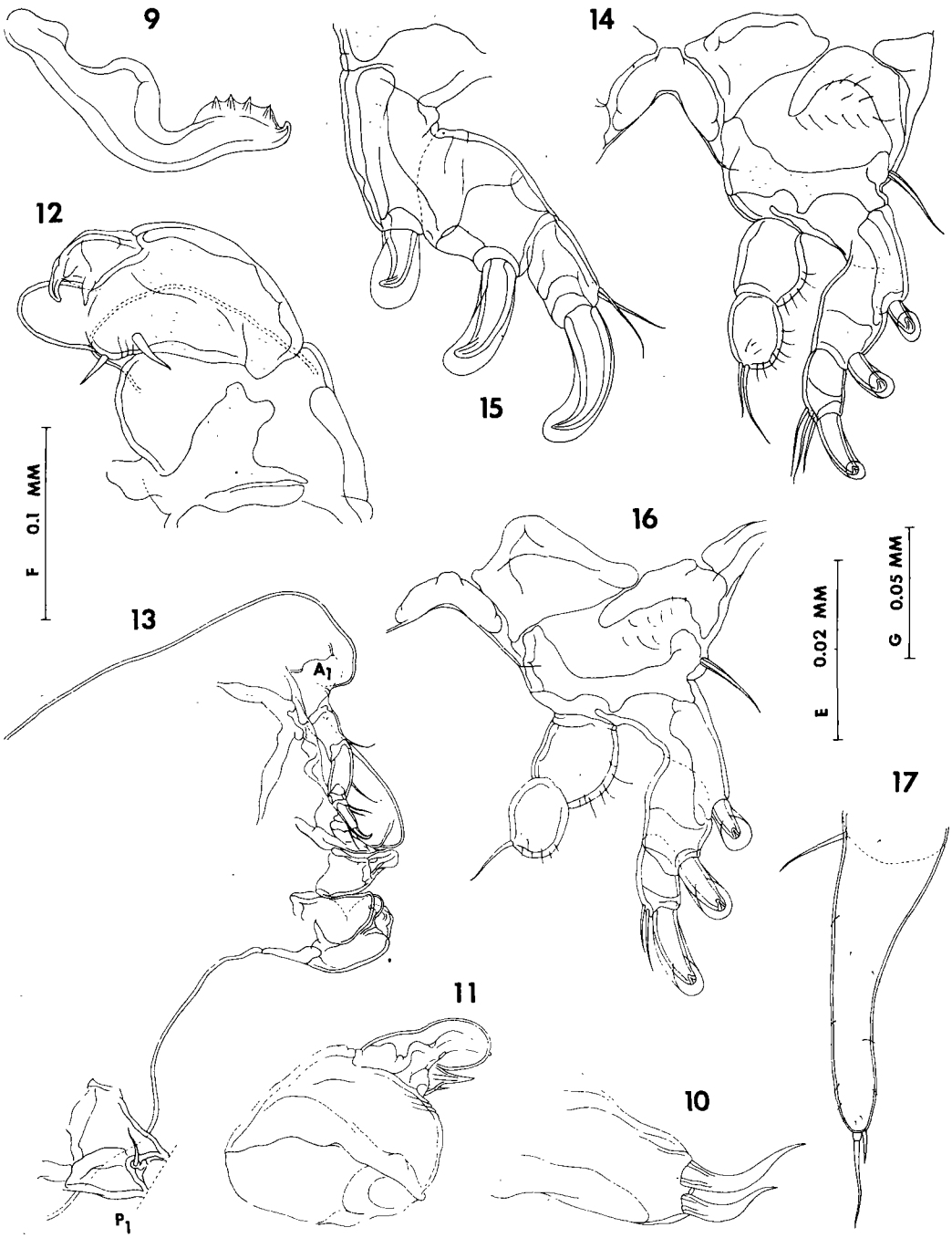
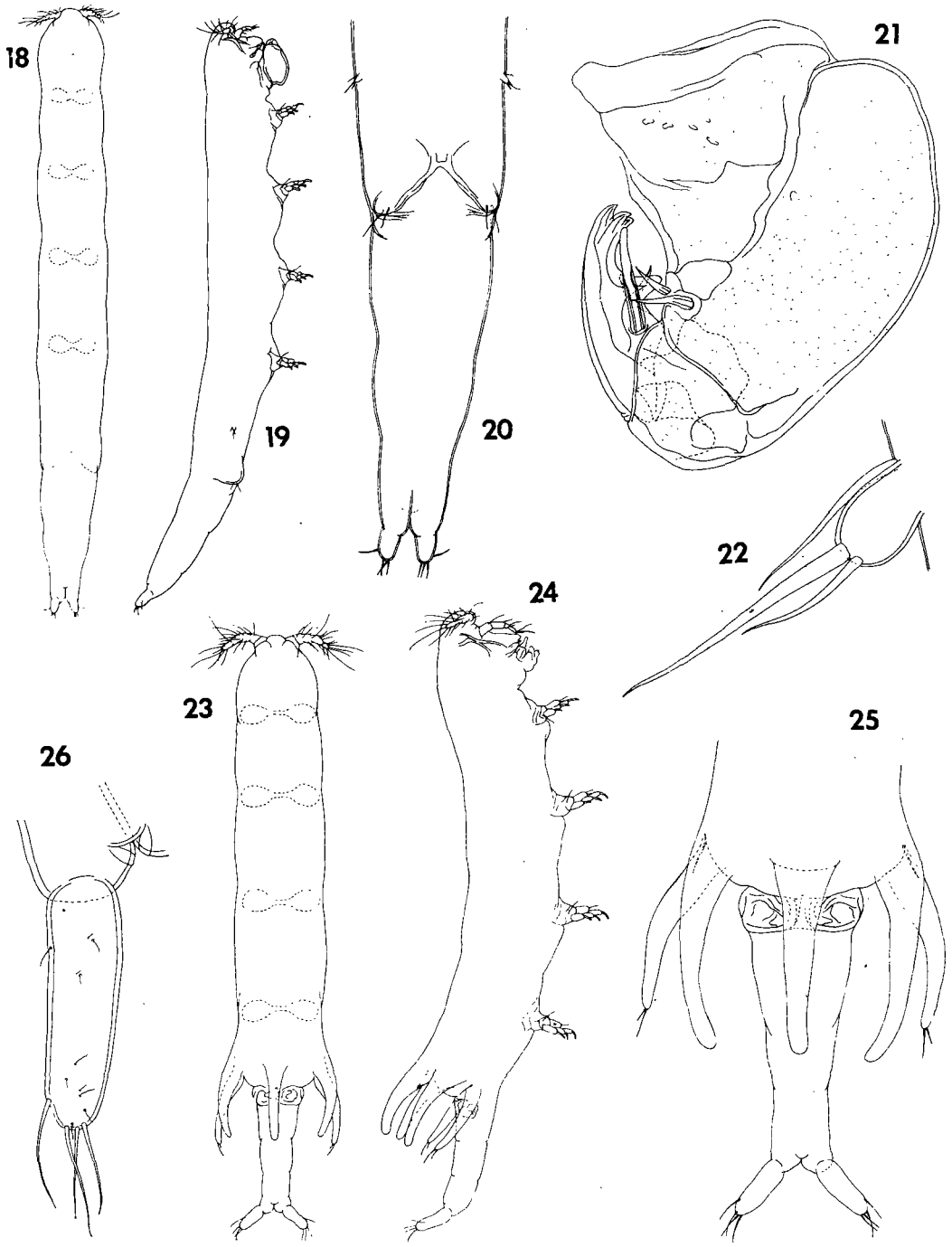


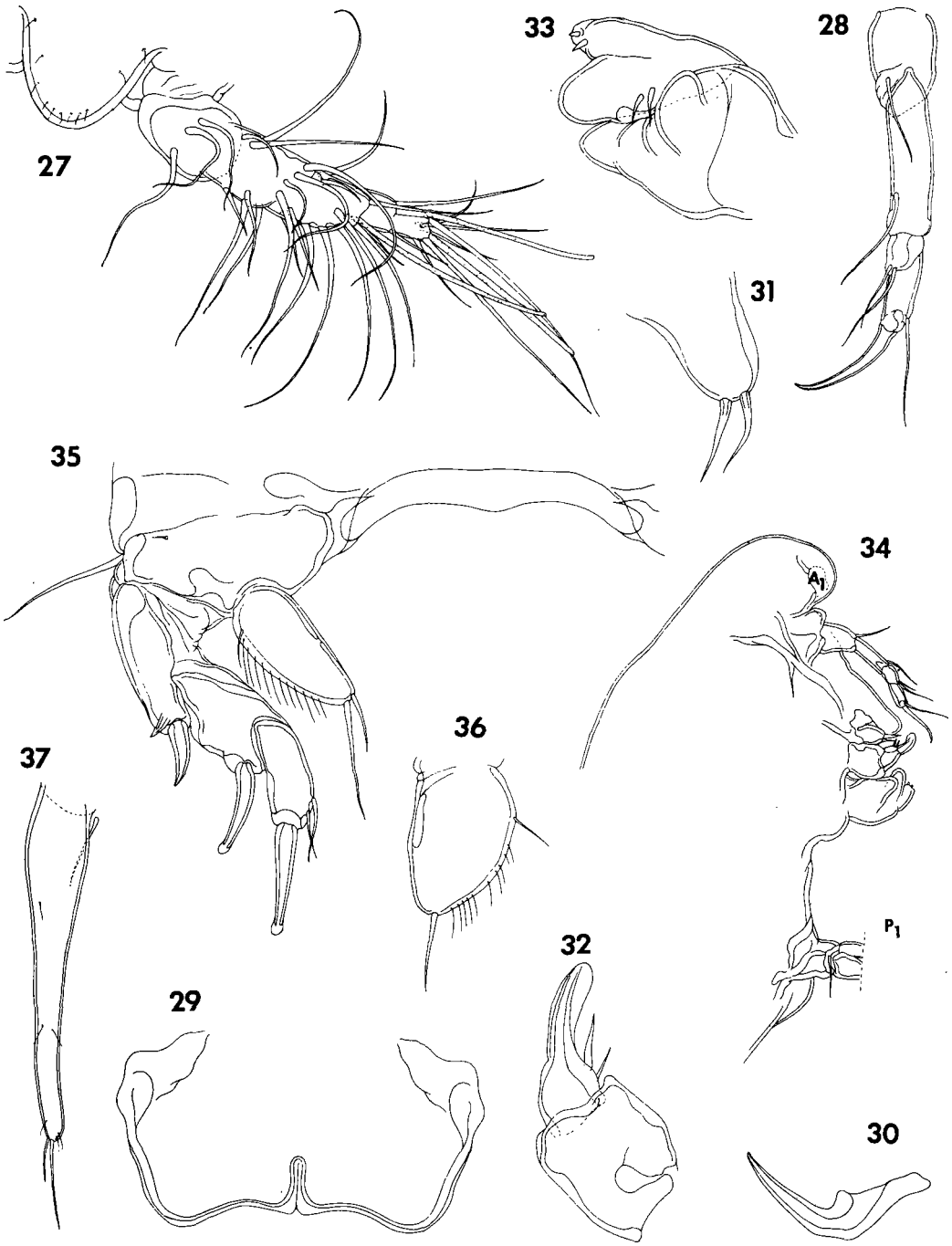
Figures 1–8. *Xarifia lamellispinosa* n. sp., female. 1, body, dorsal (A); 2, body, lateral (A); 3, posterior part of body and egg sac, lateral (B); 4, caudal ramus, dorsal (C); 5, rostrum, ventral (C); 6, first antenna, anterodorsal (D); 7, second antenna, ventral (D); 8, labrum, ventral (C).



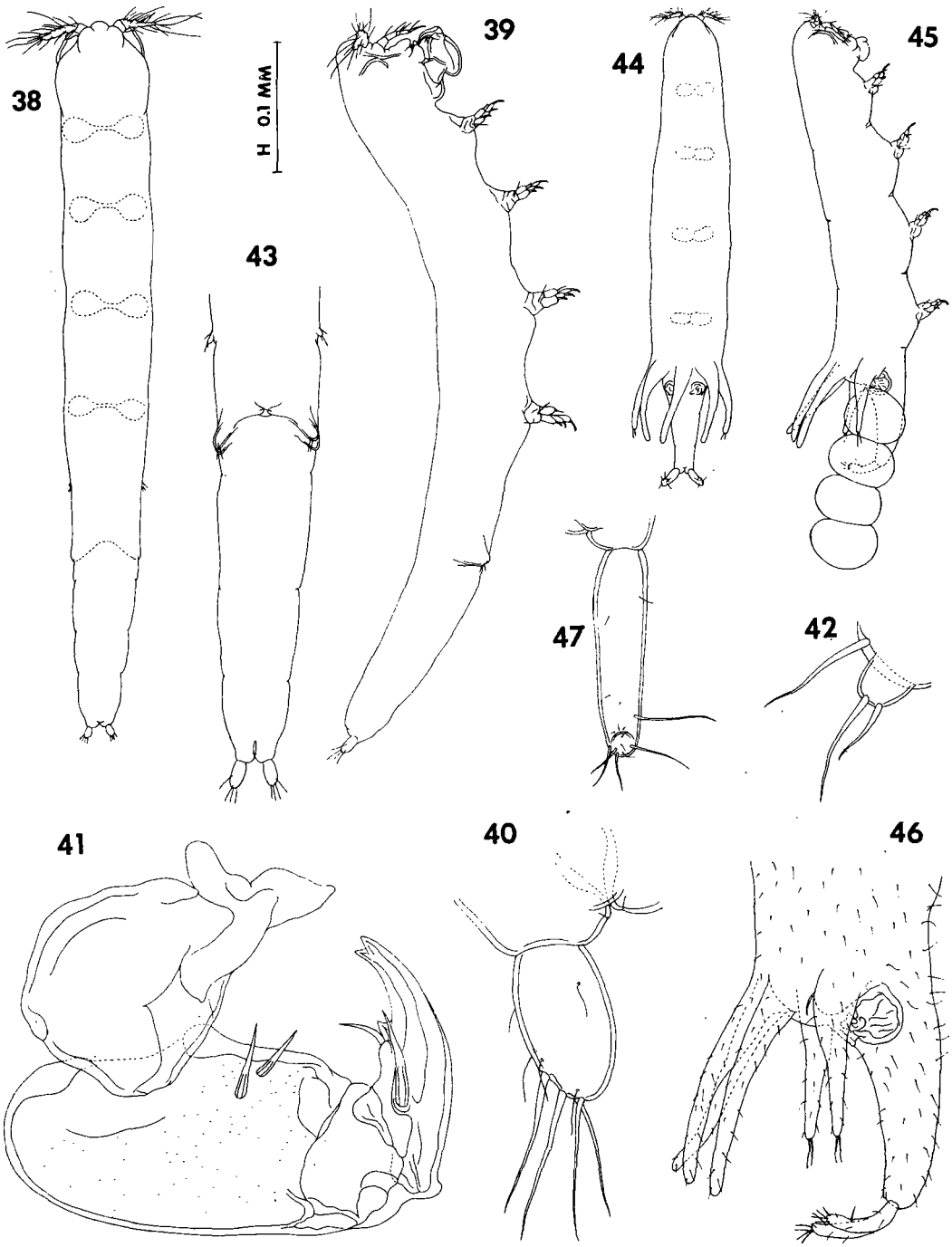
Figures 9–17. *Xarifia lamellispinosa* n. sp., female (continued). 9, mandible, dorsal (E); 10, first maxilla, dorsal (C); 11, second maxilla, anterior (D); 12, maxilliped, inner (D); 13, anterior part of body, lateral (F); 14, leg 1 and intercoxal plate, posterior (C); 15, exopod of leg 2, posterior (D); 16, leg 3 and intercoxal plate, posterior (C); 17, leg 5, lateral (G).



Figures 18–22. *Xarifia lamellispinosa* n. sp., male. 18, body, dorsal (A); 19, body, lateral (A); 20, urosome, ventral (B); 21, maxilliped, medial (C); 22, leg 5, ventral (E).
Figures 23–26. *Xarifia exigua* n. sp., female. 23, body, dorsal (B); 24, body, lateral (B); 25, urosome, dorsal (F); 26, caudal ramus, dorsal (D).

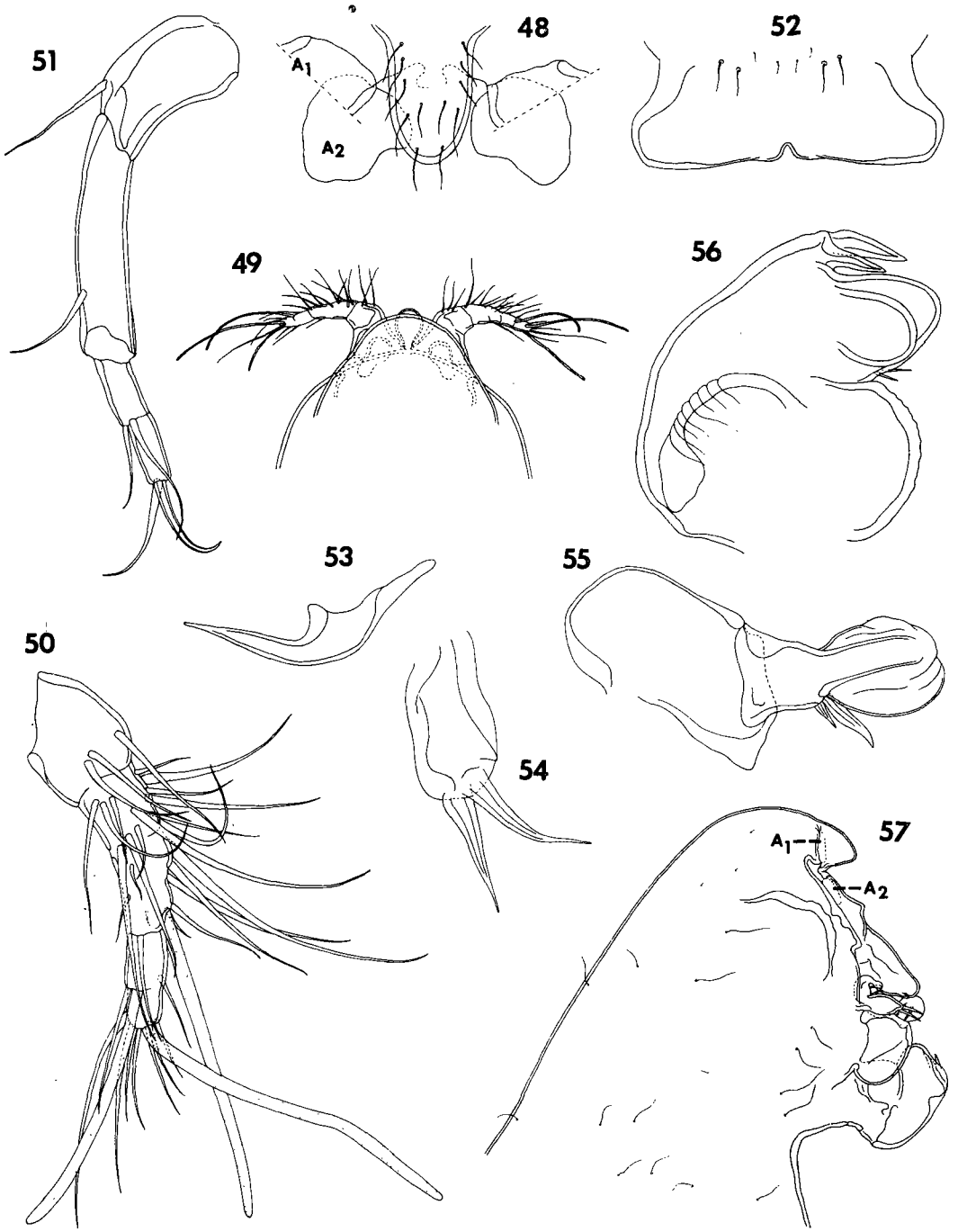


Figures 27–37. *Xarifia exigua* n. sp., female (continued). 27, rostrum and first antenna, anteroventral (D); 28, second antenna, ventral (D); 29, labrum, anteroventral (C); 30, mandible, anteroventral (E); 31, first maxilla, anteroventral (E); 32, second maxilla, anteroventral (E); 33, maxilliped, inner (E); 34, anterior part of body, lateral (G); 35, leg 1 and intercoxal plate, anterior (E); 36, endopod of leg 3, anterior (E); 37, leg 5, lateral (C).

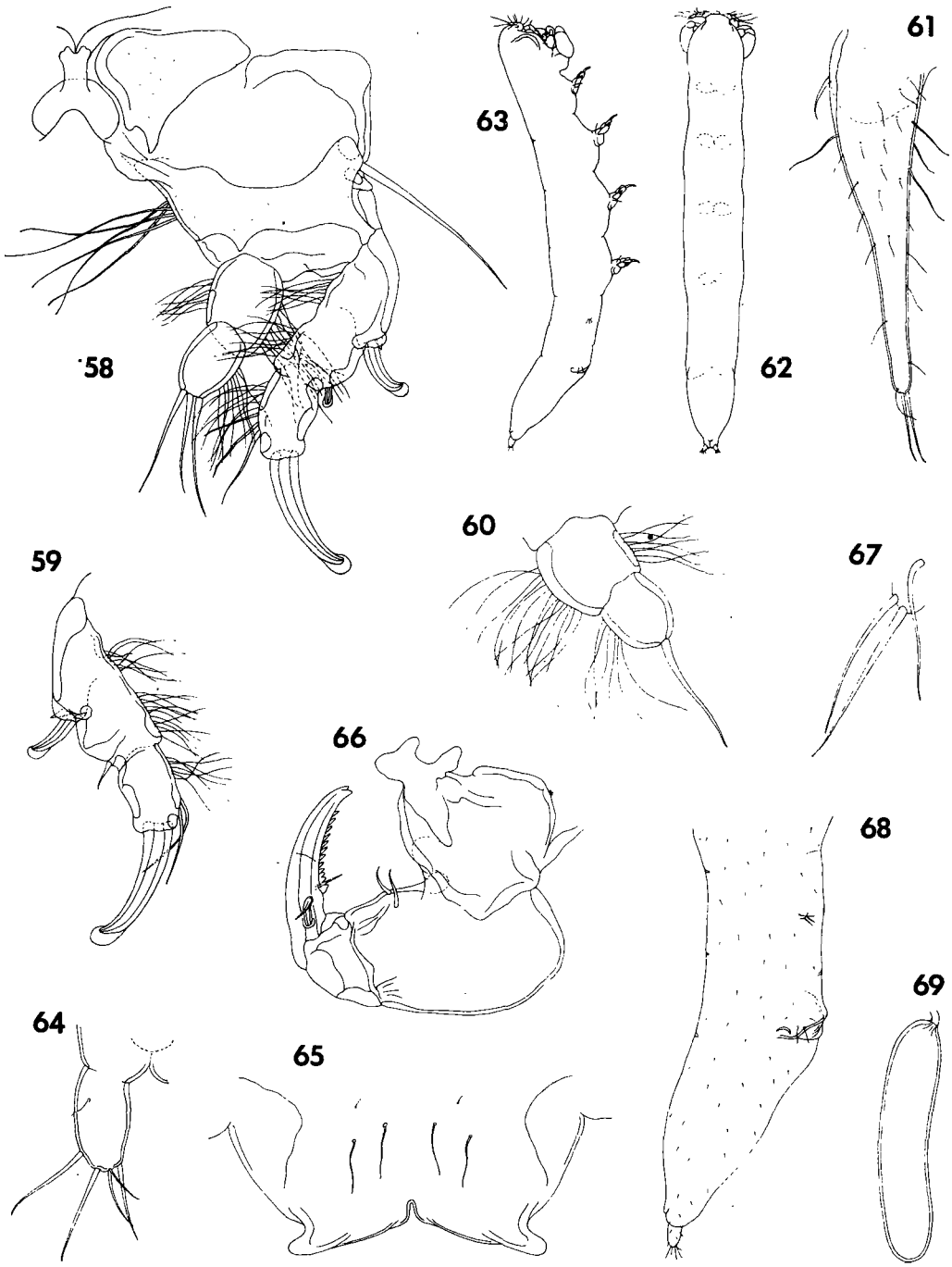


Figures 38–43. *Xarifia exigua* n. sp., male. 38, body, dorsal (B); 39, body, lateral (B); 40, caudal ramus, dorsal (E); 41, maxilliped, inner (E); 42, leg 5, lateral (E); 43, urosome, ventral (H).

Figures 44–47. *Xarifia decorata* n. sp., female. 44, body, dorsal (A); 45, body, lateral (A); 46, urosome, lateral (B); 47, caudal ramus, dorsal (G).

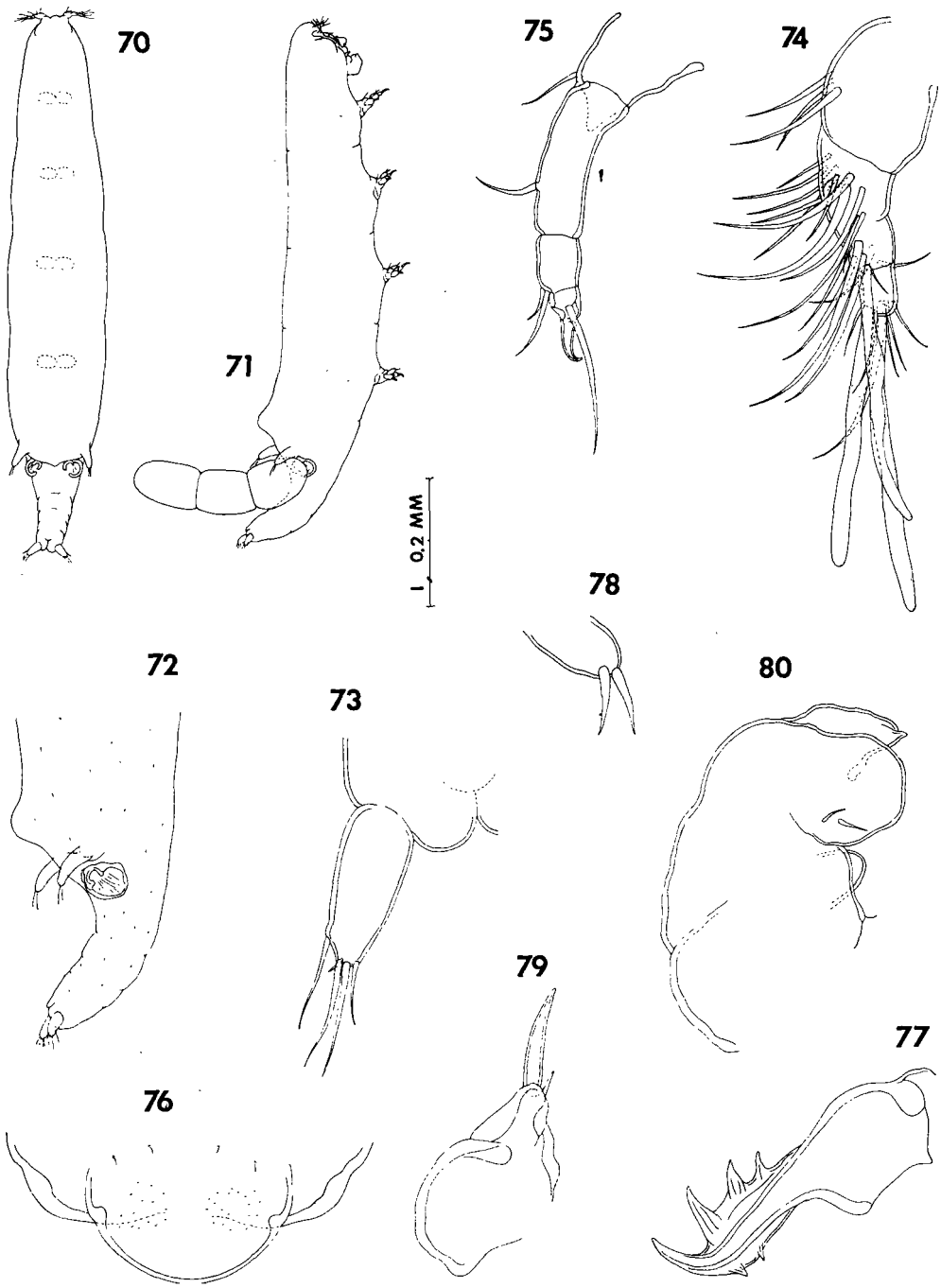


Figures 48–57. *Xarifia decorata* n. sp., female (continued). 48, rostral area, anteroventral (D); 49, anterior end of body, dorsal (F); 50, first antenna, ventral (D); 51, second antenna, ventral (D); 52, labrum, ventral (D); 53, mandible, ventral (E); 54, first maxilla, ventral (E); 55, second maxilla, ventral (D); 56, maxilliped, inner (D); 57, anterior part of body, lateral (F).

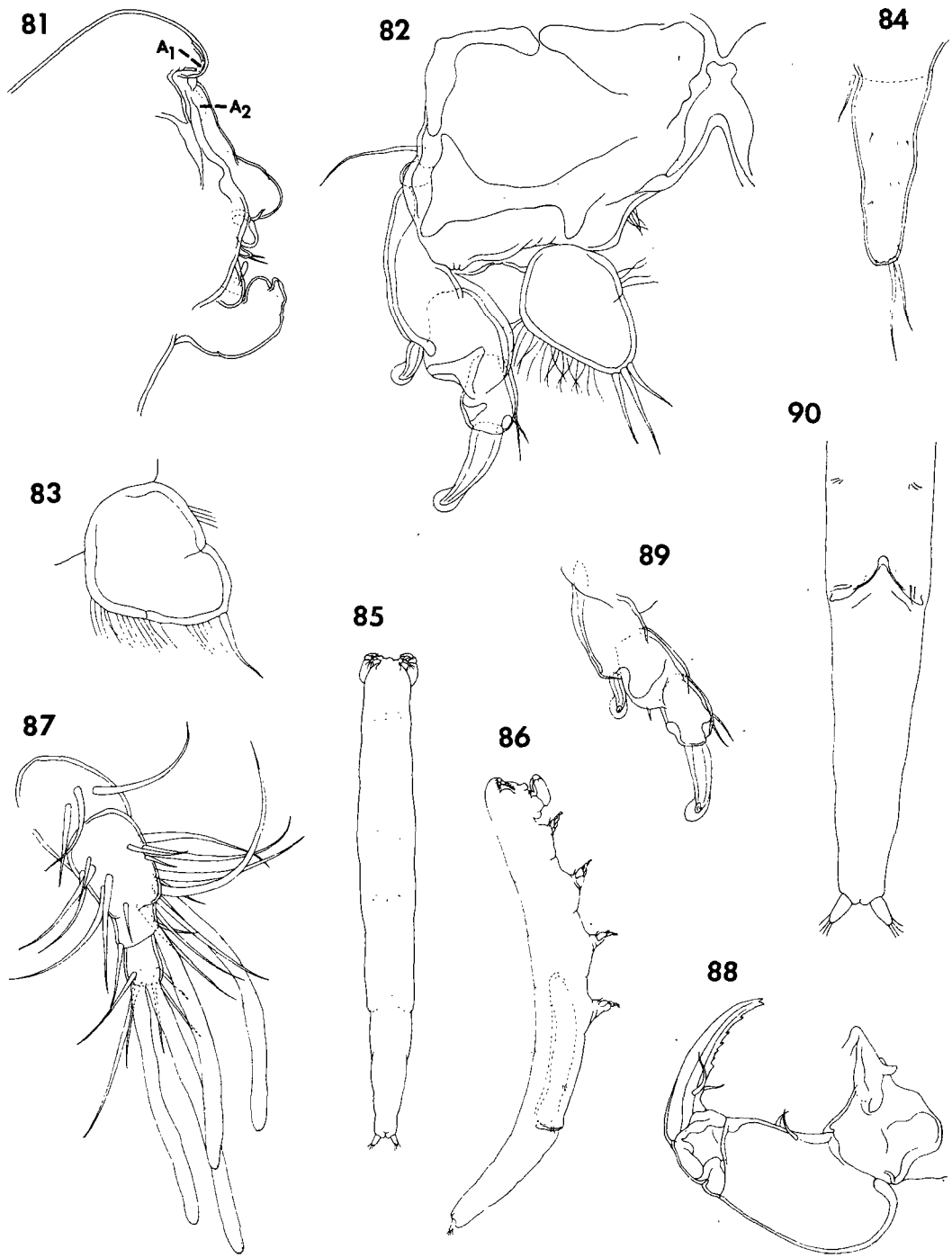


Figures 58–61. *Xarifia decorata* n. sp., female (continued). 58, leg 1 and intercoxal plate, posterior (D); 59, exopod of leg 2, posterior (D); 60, endopod of leg 3, posterior (D); 61, leg 5, lateral (F).

Figures 62–69. *Xarifia decorata* n. sp., male. 62, body, dorsal (A); 63, body, lateral (A); 64, caudal ramus, ventral (C); 65, labrum, ventral (D); 66, maxilliped, inner (G); 67, leg 5, lateral (D); 68, urosome, lateral (B); 69, spermatophore, attached to female, lateral (B).

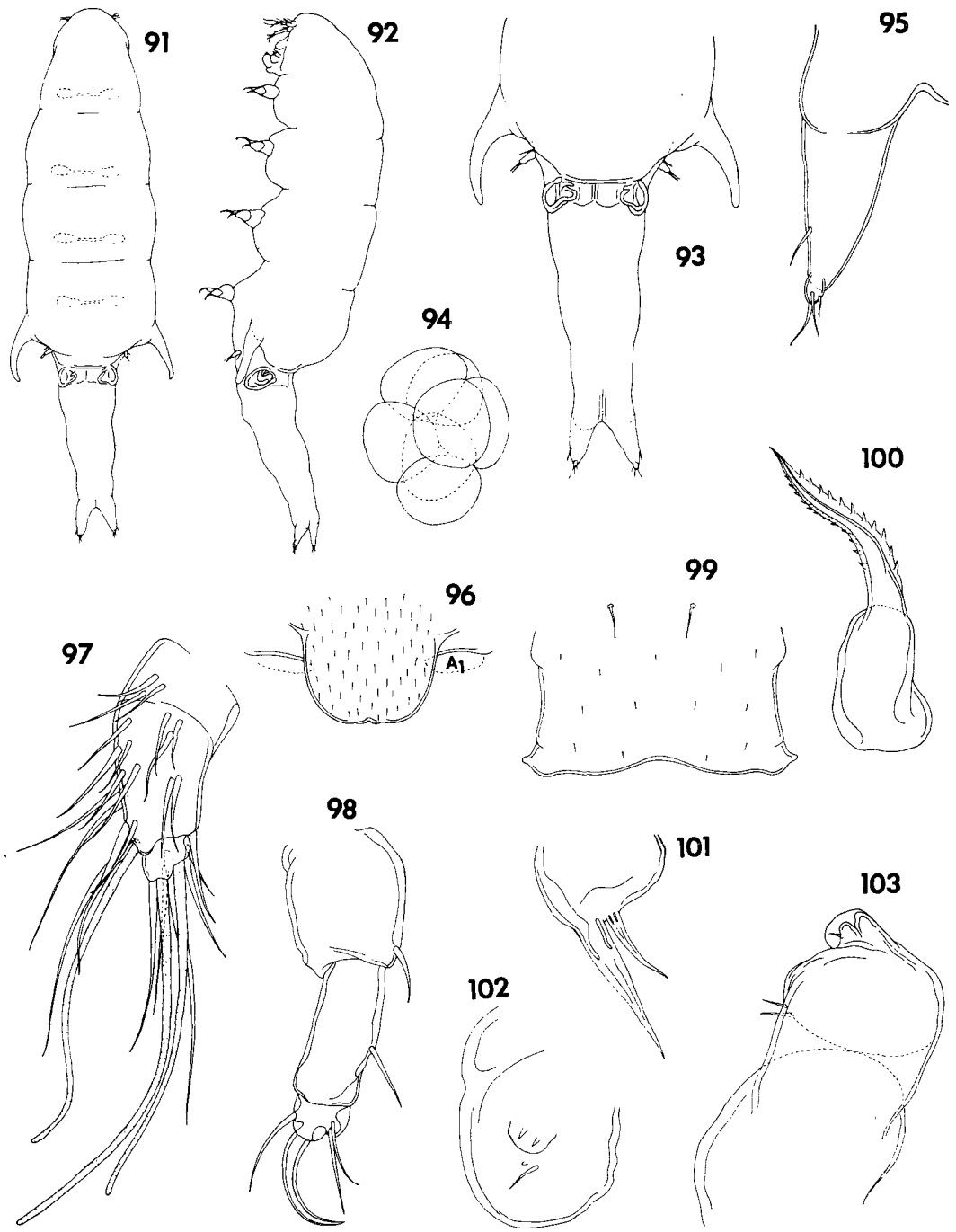


Figures 70–80. *Xarifia lissa* n sp., female. 70, body, dorsal (A); 71, body, lateral (A); 72, urosome, lateral (I); 73, caudal ramus, ventral (C); 74, first antenna, dorsal (D); 75, second antenna, ventral (D); 76, labrum, ventral (D); 77, mandible, ventral (E); 78, first maxilla, ventral (E); 79, second maxilla, ventral (E); 80, maxilliped, inner (D).

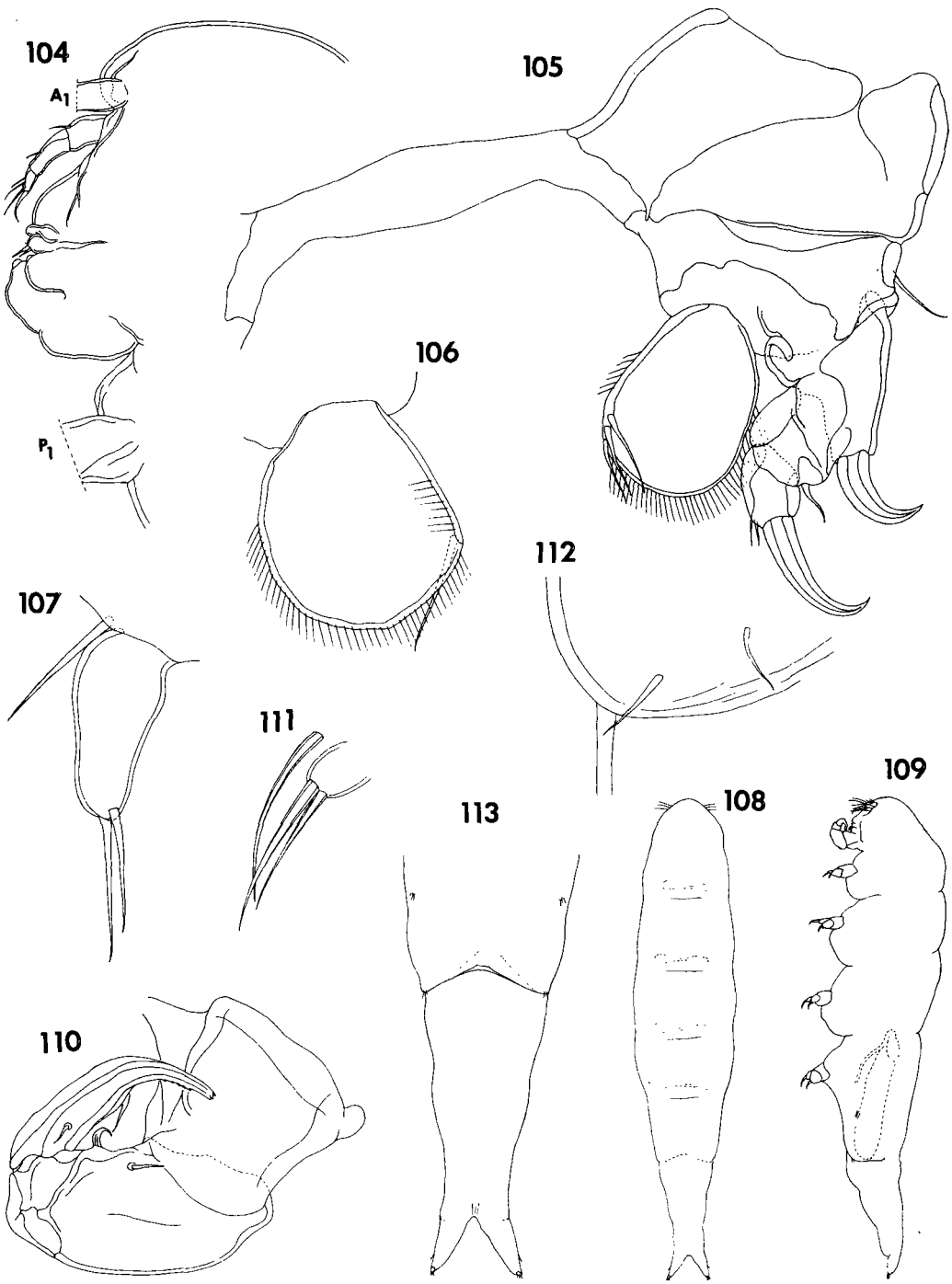


Figures 81–84. *Xarifia lissa* n. sp., female (continued). 81, anterior part of body, lateral (F); 82, leg 1 and intercoxal plate, posterior (D); 83, endopod of leg 3, posterior (D); 84, leg 5, lateral (G).

Figures 85–90. *Xarifia lissa* n. sp., male. 85, body, dorsal (A); 86, body, lateral (A); 87, first antenna, anteroventral (D); 88, maxilliped, inner (G); 89, exopod of leg 1, posterior (D); 90, urosome, ventral (B).

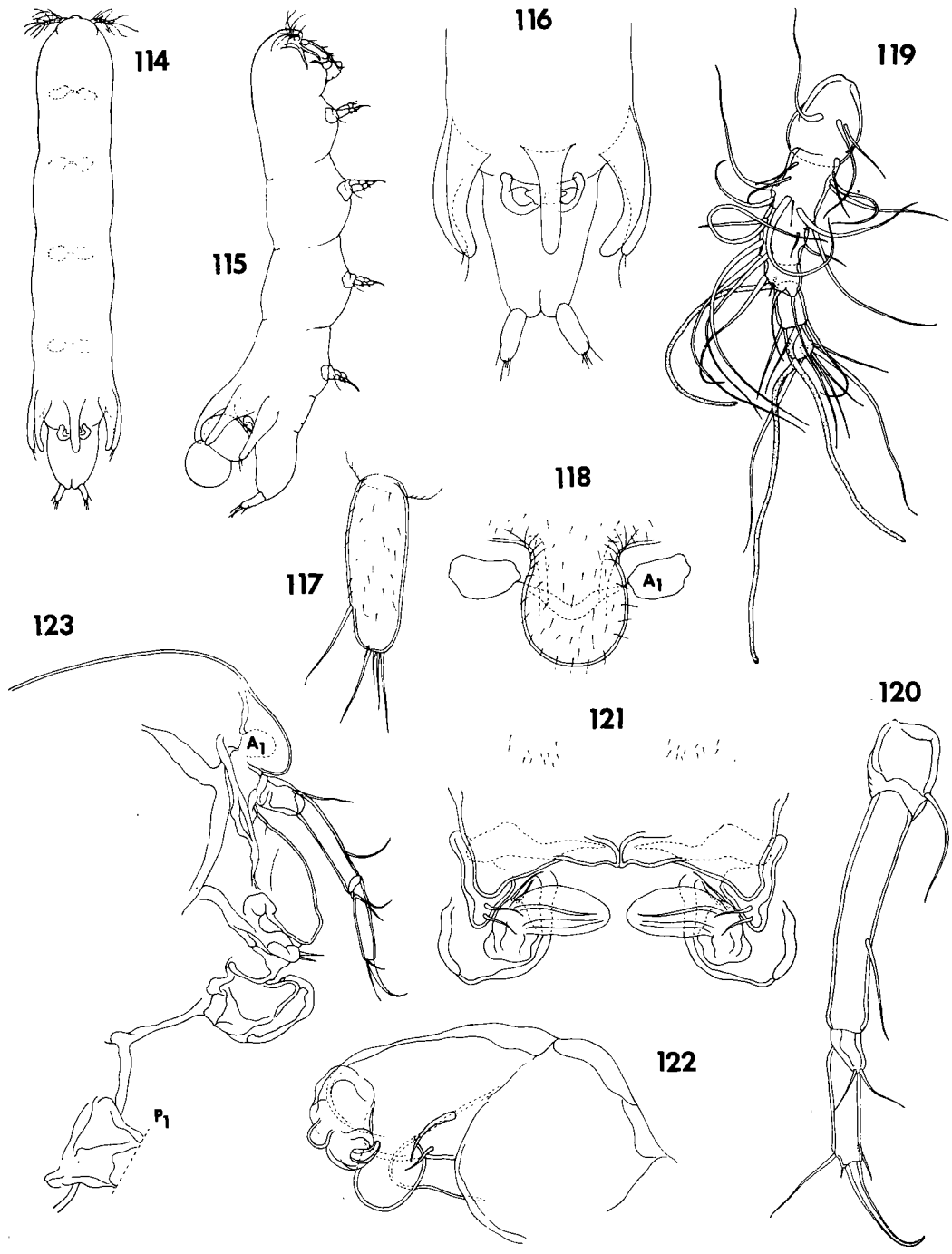


Figures 91–103. *Xarifia obesa* n. sp., female. 91, body, dorsal (A); 92, body, lateral (A); 93, urosome, dorsal (I); 94, egg sac, dorsal (I); 95, caudal ramus, dorsal (G); 96, rostrum, anteroventral (C); 97, first antenna, anterior (D); 98, second antenna, anteroventral (D); 99, labrum, ventral (C); 100, mandible, ventral (E); 101, first maxilla, ventral (E); 102, second maxilla, ventral (E); 103, maxilliped, outer (D).

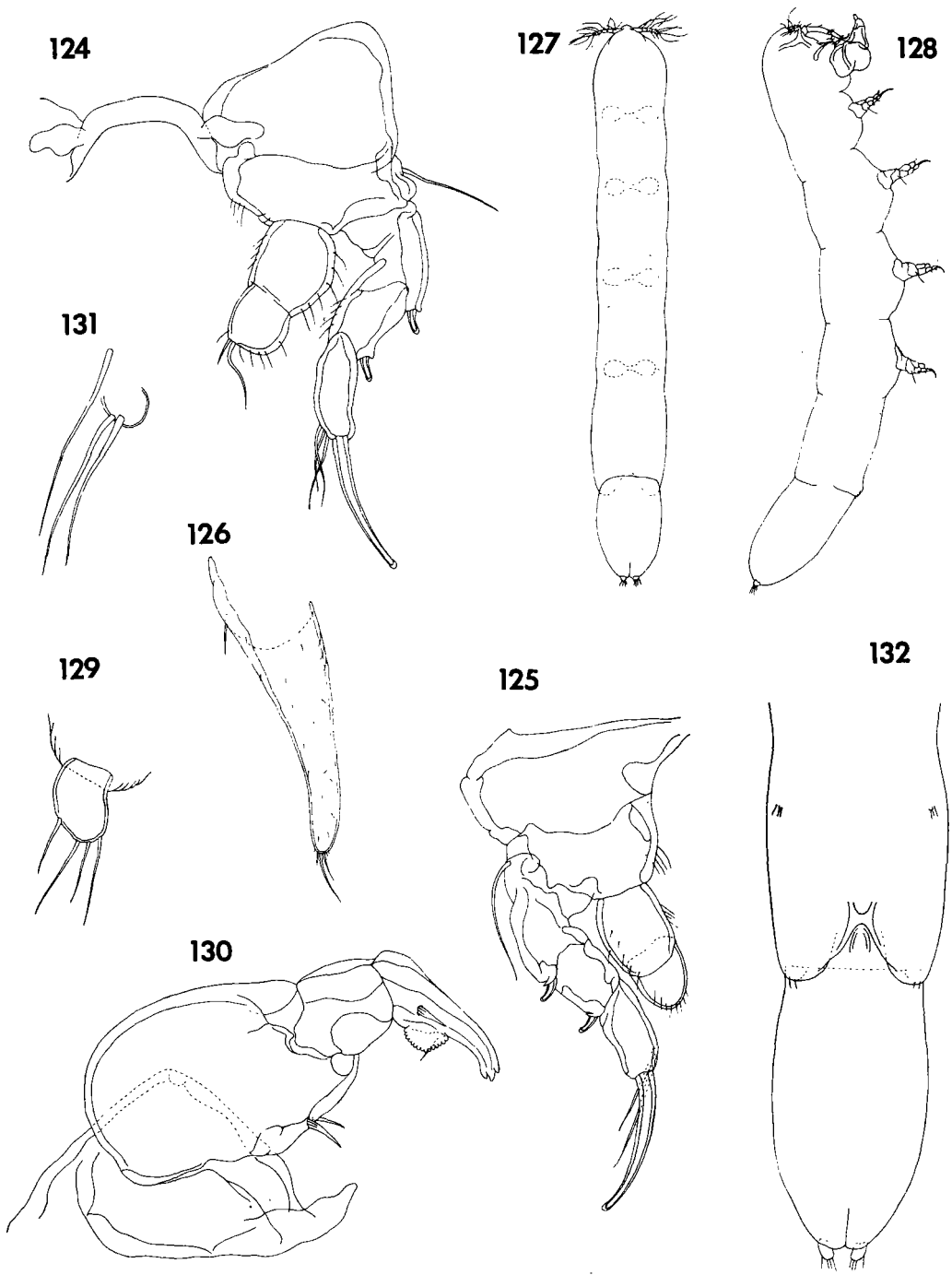


Figures 104–107. Xarifia obesa n. sp., female (continued). 104, anterior part of body, lateral (F); 105, leg 1 and intercoxal plate, posterior (D); 106, endopod of leg 3, anterior (D); 107, leg 5, ventral (D).

Figures 108–113. *Xarifia obesa* n. sp., male. 108, body, dorsal (A); 109, body, lateral (A); 110, maxilliped, inner (C); 111, leg 5, ventral (E); 112, leg 6, ventral (E); 113, urosome, ventral (B).

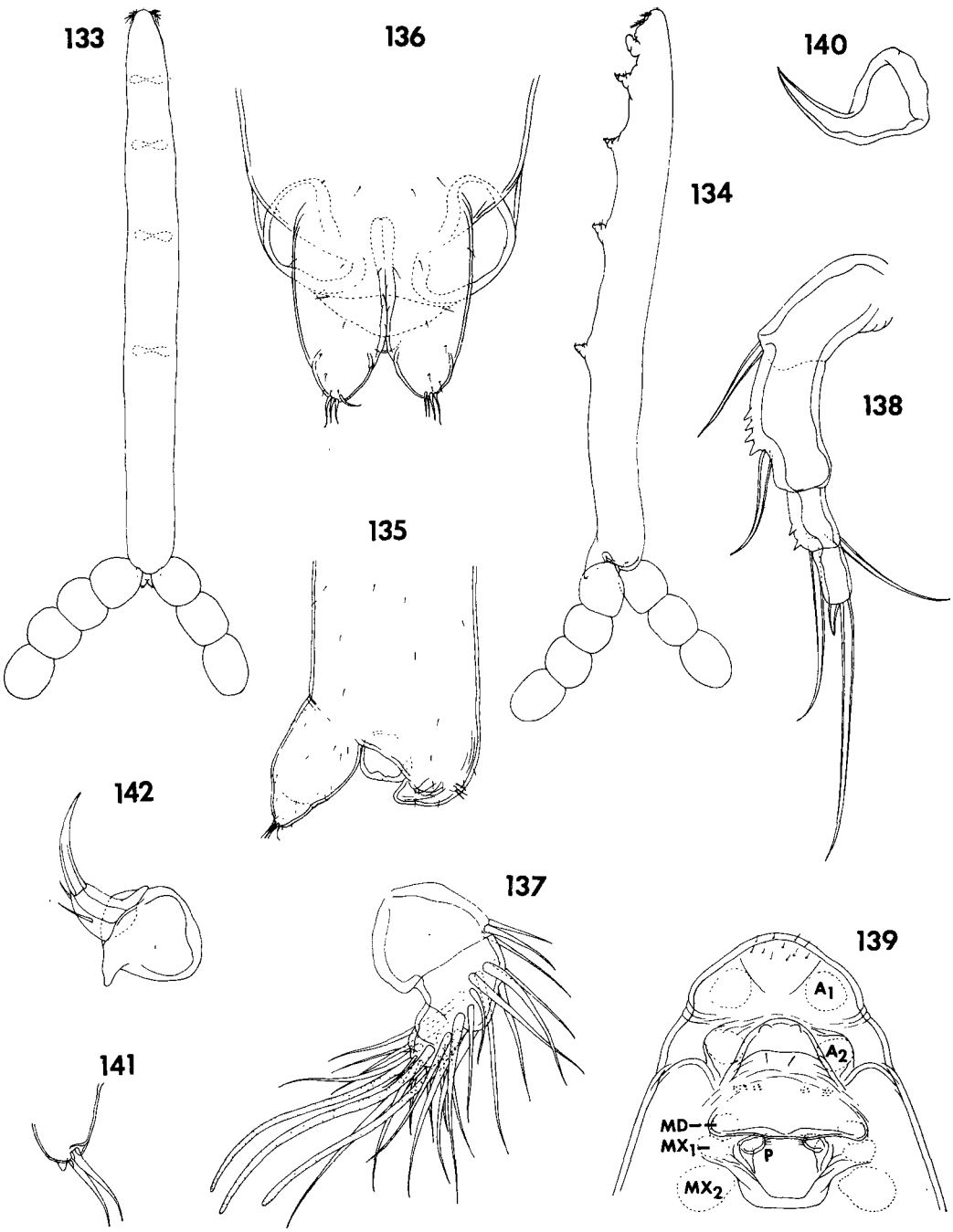


Figures 114–123. *Xarifia brevicauda* n. sp., female. 114, body, dorsal (A); 115, body, lateral (A); 116, urosome, dorsal (B); 117, caudal ramus, dorsal (G); 118, rostral area, anteroventral (C); 119, first antenna, anteroventral (C); 120, second antenna, ventral (C); 121, labrum and mouthparts, anteroventral (C); 122, maxilliped, inner (D); 123, anterior part of body, lateral (F).

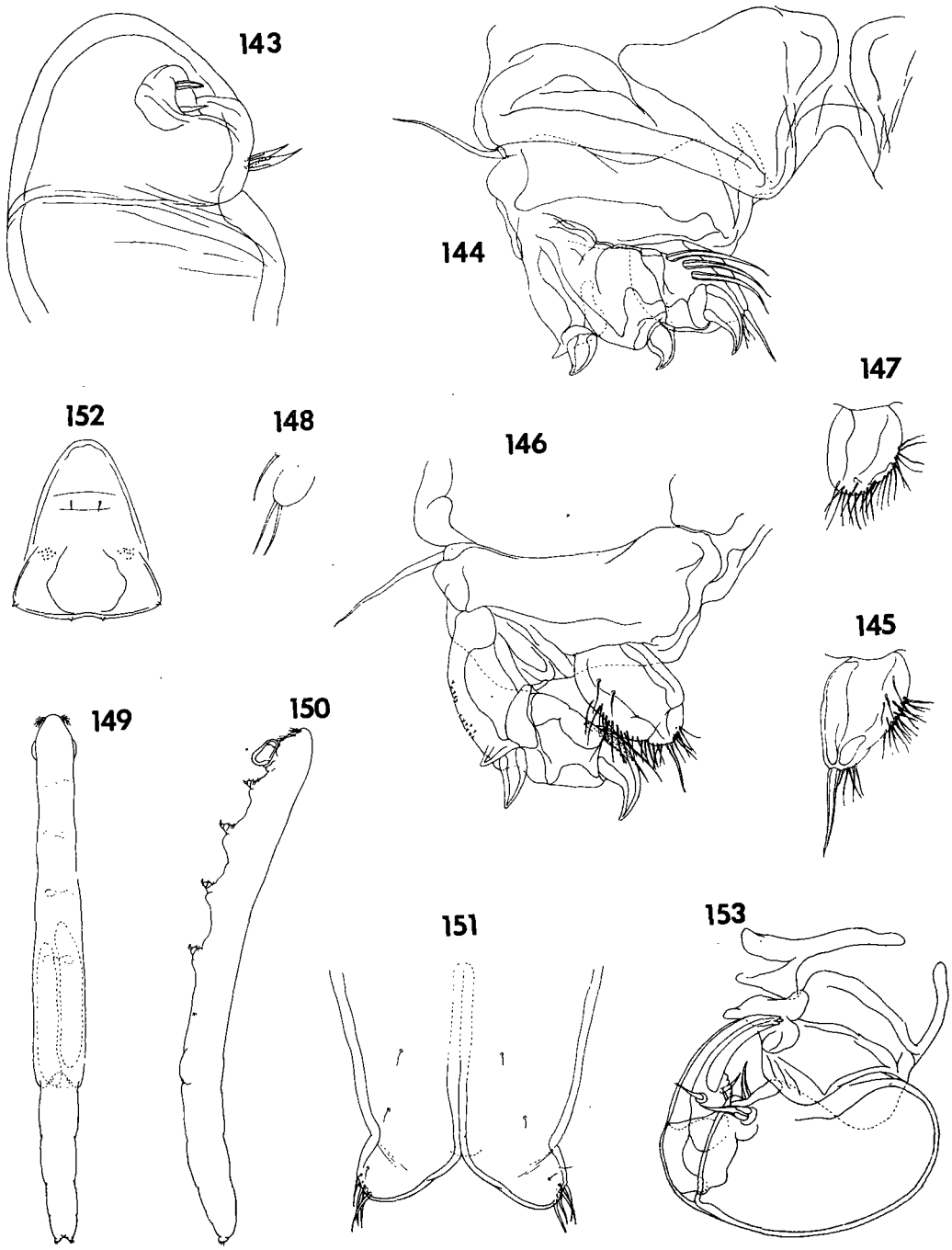


Figures 124–126. *Xarifia brevicauda* n. sp., female (continued). 124, leg 1 and intercoxal plate, anterior (C); 125, leg 3, anterolateral (C); 126, leg 5, lateral (F).

Figures 127–132. *Xarifia brevicauda* n. sp., male. 127, body, dorsal (A); 128, body, lateral (A); 129, caudal ramus, dorsal (C); 130, maxilliped, ventrointernal (G); 131, leg 5, lateral (E); 132, urosome, ventral (B).

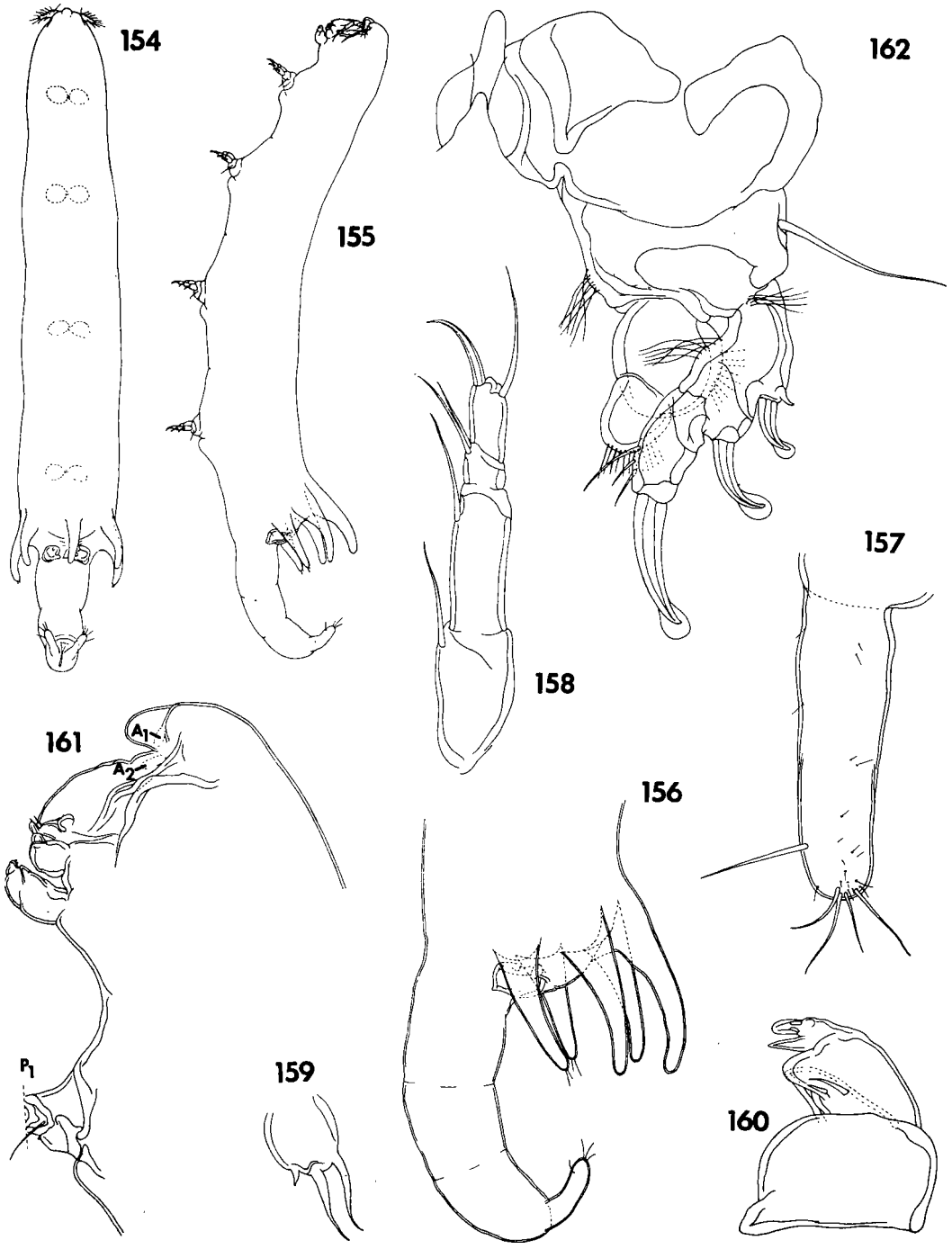


Figures 133–142. *Xarifia temnura* n. sp., female. 133, body, dorsal (A); 134, body, lateral (A); 135, urosome, lateral (H); 136, urosome, ventral (G); 137, first antenna, ventrointernal (E); 138, second antenna, ventrointernal (E); 139, anterior part of body, ventral (C); 140, mandible, ventral (E); 141, first maxilla, ventral (E); 142, second maxilla, posterointernal (E).

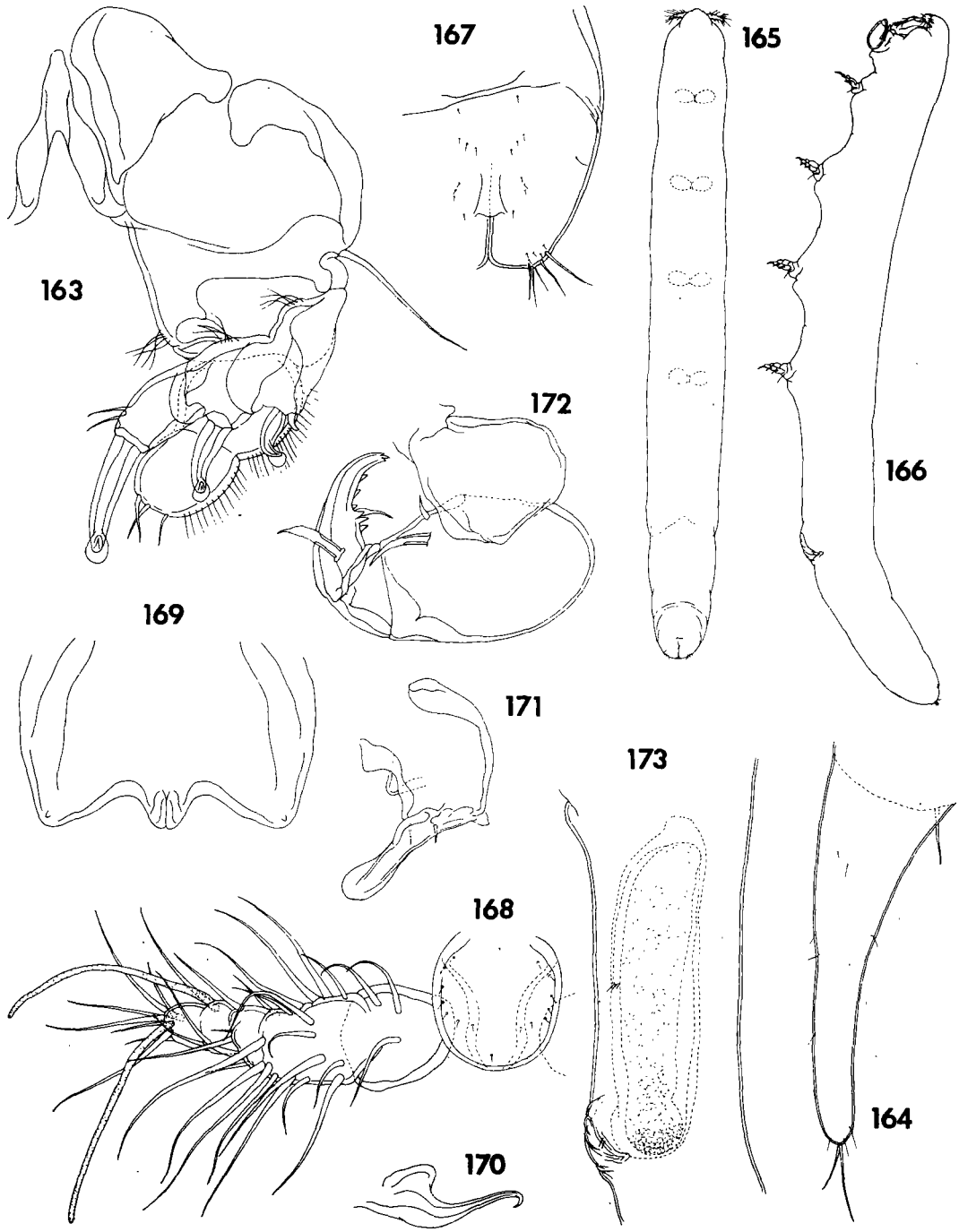


Figures 143–148. *Xarifia temnura n. sp., female* (continued). 143, maxilliped, inner (E); 144, leg 1 and intercoxal plate, posterior (E); 145, endopod of leg 1, anterior (E); 146, leg 2, anterior (E); 147, endopod of leg 3, anterior (E); 148, leg 5, lateral (D).

Figures 149–153. *Xarifia temnura* n. sp., male. 149, body, dorsal (A); 150, body, lateral (A); 151, posterior part of body, ventral (C); 152, labrum, ventral (C); 153, maxilliped, inner (C).

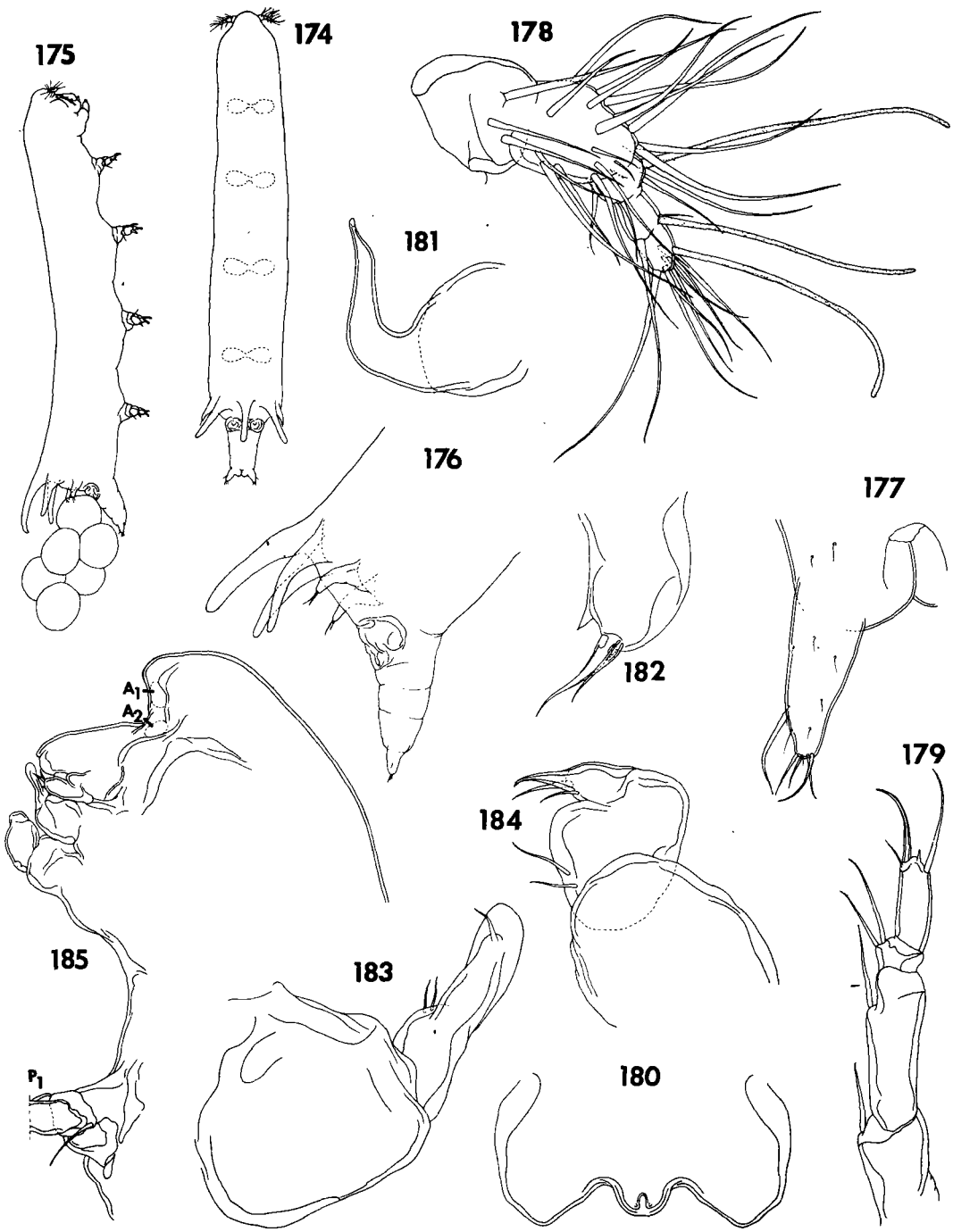


Figures 154–162. *Xarifia anomala* n. sp., female. 154, body, dorsal (I); 155, body, lateral (I); 156, urosome, lateral (H); 157, caudal ramus, dorsal (D); 158, second antenna, ventral (E); 159, first maxilla, posterior (E); 160, maxilliped, inner (E); 161, anterior part of body, lateral (G); 162, leg 1 and intercoxal plate, posterior (E).

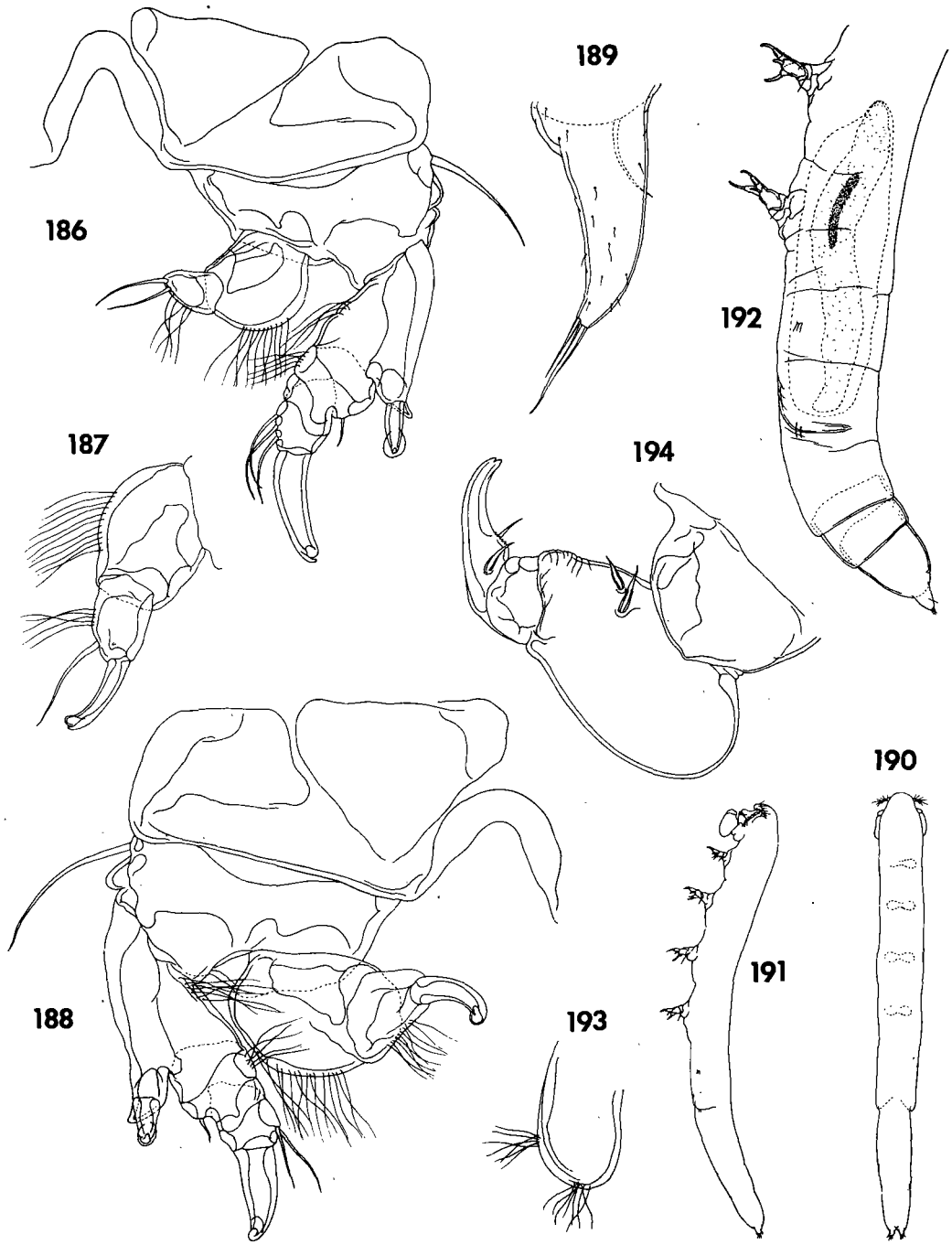


Figures 163–164. *Xarifia anomala* n. sp., female (continued). 163, leg 2 and intercoxal plate, posterior (E); 164, leg 5, lateral (C).

Figures 165–173. *Xarifia anomala* n. sp., male. 165, body, dorsal (I); 166, body, lateral (I); 167, caudal ramus, dorsal (C); 168, rostrum and first antenna, ventral (E); 169, labrum, ventral (E); 170, mandible, ventral (E); 171, second maxilla, anteroexternal (E); 172, maxilliped, medial (D); 173, portion of urosome showing leg 5, leg 6, and position of spermatophore, lateral (H).

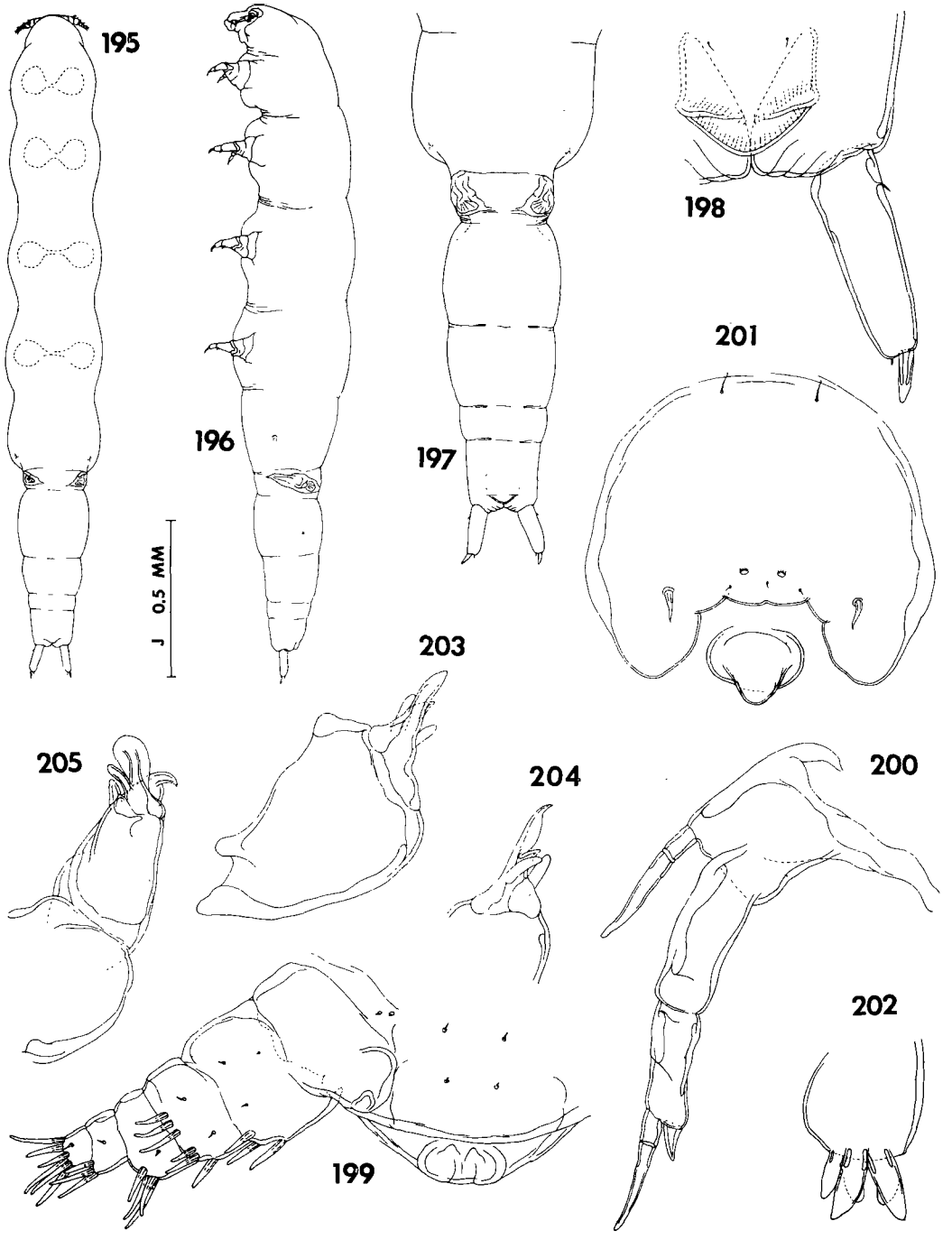


Figures 174–185. *Xarifia hamata* n. sp., female. 174, body, dorsal (A); 175, body, lateral (A); 176, urosome, lateral (B); 177, caudal ramus, dorsal (C); 178, first antenna, anterodorsal (D); 179, second antenna, ventral (D); 180, labrum, ventral (D); 181, mandible, ventral (E); 182, first maxilla, posterior (E); 183, second maxilla, posterior (E); 184, maxilliped, posterointernal (D); 185, anterior part of body, lateral (F).

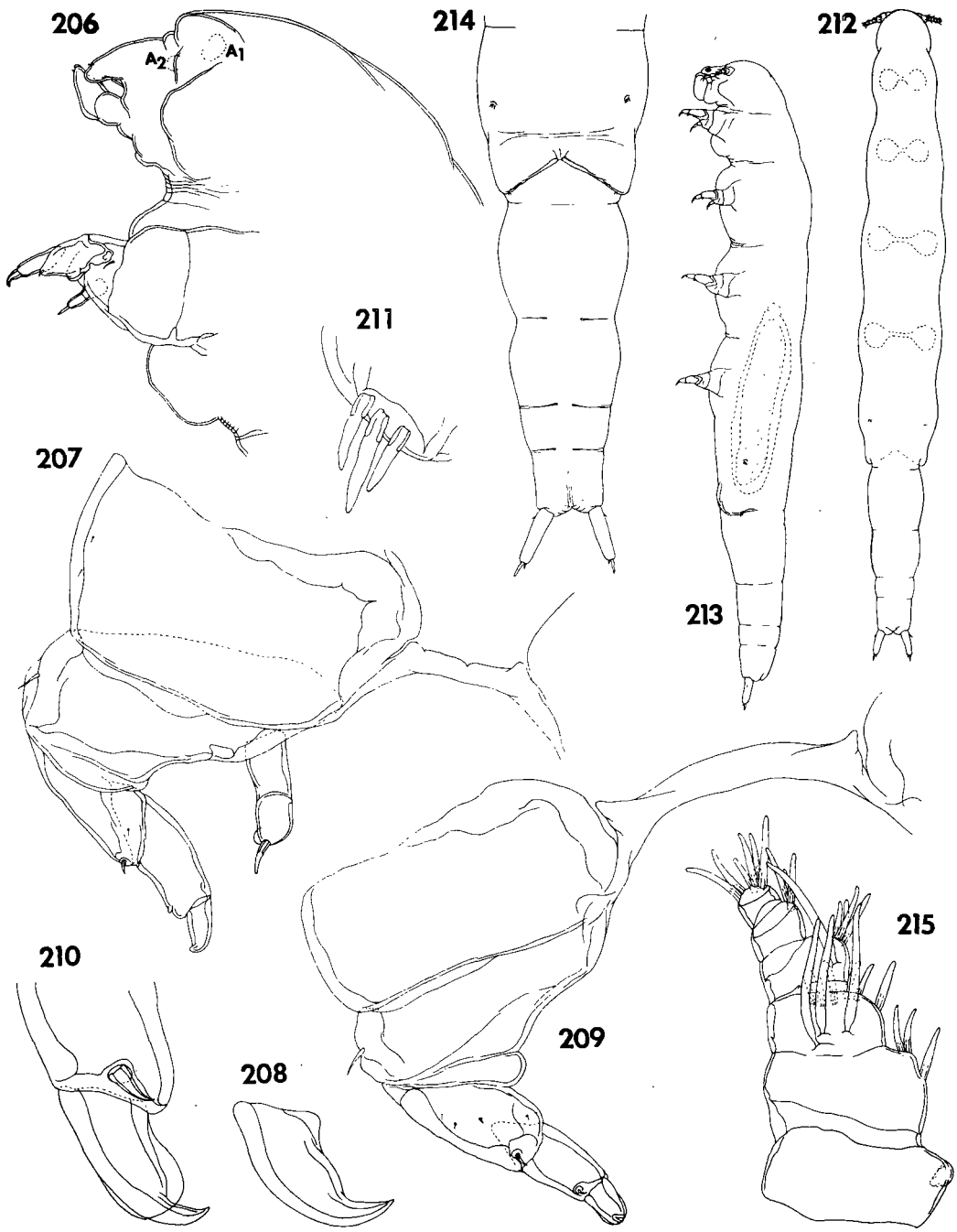


Figures 186–189. *Xarifia hamata* n. sp., female (continued). 186, leg 1 and intercoxal plate, posterior (D); 187, endopod of leg 2, posterior (D); 188, leg 3 and intercoxal plate, posterior (D); 189, leg 5, lateral (C).

Figures 190–194. *Xarifia hamata* n. sp., male. 190, body, dorsal (A); 191, body, lateral (A); 192, posterior part of body, lateral (B); 193, paragnath, ventral (E); 194, maxilliped, inner (C).

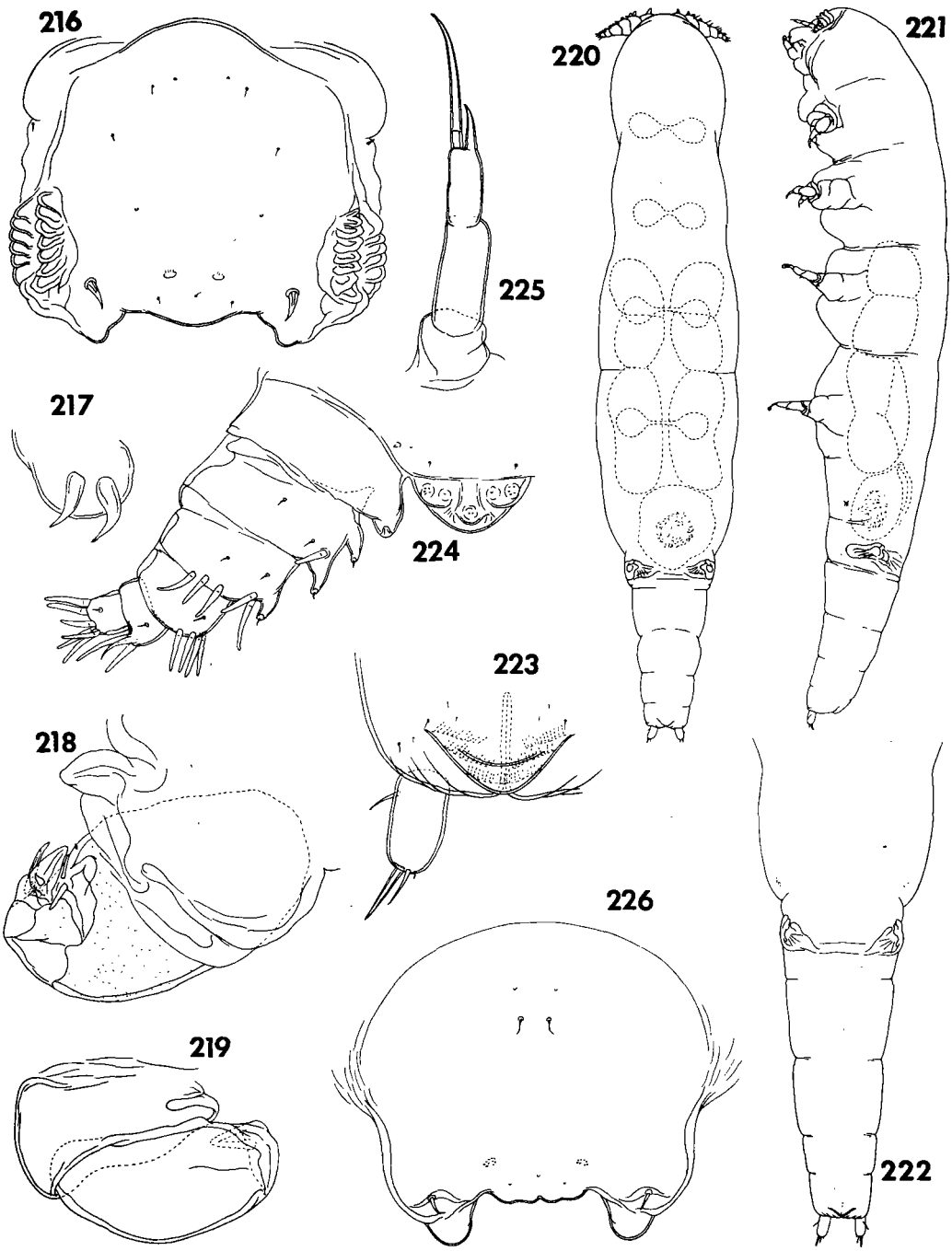


Figures 195–205. *Orstomella faviae* n. gen., n. sp., female. 195, body, dorsal (J); 196, body, lateral (J); 197, urosome, dorsal (I); 198, caudal ramus, dorsal (G); 199, rostral area and first antenna, anterior (C); 200, second antenna, outer (E); 201, labrum and median prominence behind second maxillae, anteroventral (D); 202, first maxilla, anteroventral (E); 203, second maxilla, anteroventral (E); 204, terminal portion of second maxilla, posterior (E); 205, maxilliped, anteroventral (D).

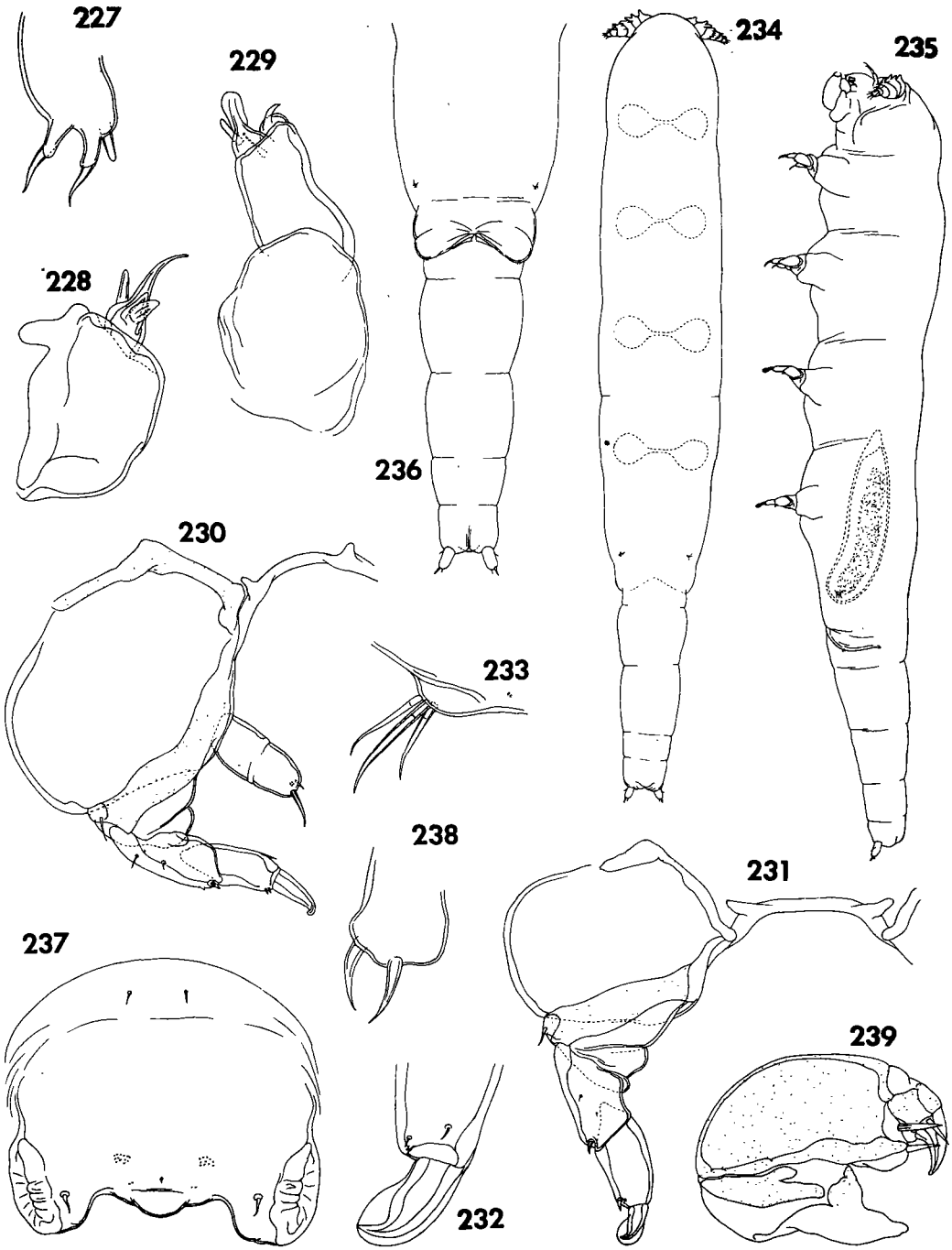


Figures 206–211. *Orstomella faviae* n. gen., n. sp., female (continued). 206, anterior part of body, lateral (H); 207, leg 1 and intercoxal plate, posterior (C); 208, terminal spine on exopod of leg 1, outer (E); 209, leg 3 and intercoxal plate, posterior (C); 210, terminal portion of exopod of leg 3, lateral (E); 211, leg 5, ventral (E).

Figures 212–215. *Orstomella faviae* n. gen., n. sp., male. 212, body, dorsal (J); 213, body, lateral (J); 214, urosome, ventral (I); 215, first antenna, posterior (C).



Figures 216–219. *Orstomella faviae* n. gen., n. sp., male (continued). 216, labrum, anteroventral (D); 217, first maxilla, anteroventral (E); 218, maxilliped, anterointernal (C); 219, maxilliped, outer (G).
Figures 220–226. *Orstomella lobophylliae* n. gen., n. sp., female. 220, body, dorsal (I); 221, body, lateral (I); 222, urosome, dorsal (B); 223, caudal ramus, dorsal (C); 224, rostral area and first antenna, anteroventral (C); 225, second antenna, anteroventral (E); 226, labrum, anterior (D).



Figures 227–233. *Orstomella lobophylliae* n. gen., n. sp., female (continued). 227, first maxilla, ventrointernal (E) 228, second maxilla, ventrointernal (E); 229, maxilliped, outer (D); 230, leg 1 and intercoxal plate, posterior (C); 231, leg 3 and intercoxal plate, posterior (C); 232, terminal portion of exopod of leg 4, lateral (E); 233, leg 5, ventral (E). *Figures 234–239. Orstomella lobophylliae* n. gen., n. sp., *male. 234, body, dorsal (I); 235, body, lateral (I); 236,* urosome, ventral (B); 237, labrum, anteroventral (D); 238, first maxilla, outer (E); 239, maxilliped, inner (C).

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TAXONOMY AND POSTEMBRYONIC DEVELOPMENT OF THE CRYPTORHAGAE, A NEW SUBORDER FOR THE MESOPSAMMIC KINORHYNCH GENUS *CATERIA*

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ABSTRACT: The taxonomic status of the genus *Cateria* Gerlach is discussed and a new suborder, Cryptorhagae, established. *Cateria styx* Gerlach is redescribed on the basis of new topotype-material and a lectotype and paralectotype are designated. The postembryonic life history of *Echinoderes bookhouti* Higgins and homalorhagid kinorhynchs is compared with that of *C. styx*. *Habroderella orientalis* Kirsteuer and *Hapaloderes manglaris* Kirsteuer are synonymized with *Echinoderes caribiensis* Kirsteuer. *Cateria gerlachi* is described as a new species from Waltair, India. The phylogenetic relationships of the kinorhynch taxa are discussed.

The phylum Kinorhyncha consists of fewer than 100 described species which, although not often encountered, are a very common member of the marine meiobenthic community. Until 1954, when Prof. Dr. S. A. Gerlach discovered *Cateria styx* Gerlach, 1956, in samples of intertidal mesopsammon from a beach at Macaé, Brazil, the known habitat of kinorhynchs was restricted to subtidal marine sediments.

Occasionally, the cyclorhagid genus *Echinoderes* has been found in samples of beach interstitial fauna (Renaud-Debyser, 1963). In such instances, however, it is more reasonable to assume that the kinorhynch has been washed into the beach from its subtidal habitat than to assume that the former habitat is its normal one. Nonetheless, finding a new taxon of kinorhynch in a marine beach must not have been entirely unexpected considering the major taxonomic discoveries made through studies of this unique environment during the past 30 years.

Within a year after Gerlach described *Cateria styx* from his 15 specimens, six more were reported from a similar habitat at Lobito, Angola by Delamare-Deboutteville (1957).

Although many investigations of the interstitial fauna of marine beaches continued, five years elapsed before Ganapati & Rao (1962) reported kinorhynchs from the beaches of the Bay of Bengal at Waltair, India. In 1964, I was privileged to observe the specimens collected by Ganapati & Rao and to collect additional specimens from their site. At this time, Dr. Rao was preparing his thesis manuscript and suggested that the species of *Cateria* found locally was not conspecific with *C. styx*. However, because of certain problems caused by insufficient original material and subsequent description, the final assignment of the Indian species was to *Cateria styx* (Rao & Ganapati, 1966).

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[1] I should like to express special thanks to Drs. Howard L. Sanders and Robert R. Hessler, Woods Hole Oceanographic Institution, for their assistance and comradeship during the better part of a two-month collecting trip to India, and to the National Science Foundation, sponsor of the U. S. Program in Biology of the International Indian Ocean Expedition. Additional thanks are due Prof. Dr. P. N. Ganapati, Andhra University, and his former student, Dr. G. C. Rao, Zoological Survey of India, discoverers of the new species described in this paper, who generously provided specimens and facilities; Prof. Dr. S. A. Gerlach, Institut für Meeresforschung, Bremerhaven, for his syntype-material of *Cateria styx*; Miss Janice Czikowsky and Miss Maxine McGinty, my research assistants, for their contributions to this research; to the people of Macaé, Brazil, who cordially received me and generously aided in the collection of *Cateria styx*; and to John C. Boykin, University of Washington, for his helpful criticism of the manuscript and contribution to certain morphological details. This study was supported by the National Science Foundation, grant GB 3069, which is gratefully acknowledged.

Seven additional specimens of *Cateria styx* were collected near Ubatuba, Brazil in September 1964, by Dr. Howard Sanders who sent them to me for examination. Unfortunately, the condition of these specimens would not provide sufficient information for an adequate comparison of the type-species with the specimens from India. Similarly, the two existing syntypes of *Cateria styx*, generously provided me by Prof. Dr. Gerlach, were in a condition which could not resolve the problem. In May 1967, after several days of sampling in the vicinity of Gerlach's type-locality, I was able to collect ample topotype material for the study that follows.

Discussion of Classification

The first attempt to subdivide the Kinorhyncha was made by Reinhard (1887) who also originated the phylum name, a replacement for several previous names, more notably its most common synonym, Echinoderida. At the time of Reinhard's work only the genus *Echinoderes* had been described (Claparède, 1863), but Reinhard found that the existing species could be divided into three groups on the basis of their caudal spines. Consequently, Reinhard's "Monocerca" included the species with a single spine on the terminal segment, the "Bicerca" with two such spines, and the "Acerca" without caudal spines. None of these groups was given a designated taxonomic rank.

Zelinka (1896) found Reinhard's system of classification inadequate and proposed two orders based upon the morphology of the closing mechanism associated with the retraction of the head; these were the orders Cyclorhagae and Homalorhagae. In the later work, Zelinka expanded his classification and added a third order, Conchorhagae (Zelinka, 1907). However, in his monograph (Zelinka, 1928) all three orders were reduced to subordinal rank.

The first comprehensive discussion of Zelinka's classification was written by Lang (1949). Lang considered the suborders Cyclorhagae and Conchorhagae so closely related that he united them under a single suborder, the Heterorhagae, and retained the suborder Homalorhagae for the remaining taxa. Although Lang's formation of two major taxa may be well-founded, there is no necessity for creating a new name; therefore, I have rejected the name Heterorhagae (Higgins, 1964) and consider the phylum Kinorhyncha as consisting of two orders: Cyclorhagida (Zelinka, 1896) Higgins, 1964, and Homalorhagida (Zelinka, 1896) Chitwood, 1958. Chitwood (1958) considered these taxa classes as well as orders.

Methods

Samples of sand from the mid-tide zone of the beach at depths of 10–60 cm were placed in a container with sufficient seawater to thoroughly agitate the samples. While most of the interstitial material was still in suspension the seawater was poured through a fine mesh net (51 μ). After repeating this process several times, the material collected in the net was washed into a vial and preserved with 5–7% formalin. Although there are several methods for extracting interstitial fauna from sand (Delamare-Debouteville, 1960; Uhlig, 1964, 1965), the method used in this study is recommended where a simple field procedure is necessary.

An alcohol solution of rose bengal stain was added to the sample in order to facilitate sorting. Specimens were transferred to a glycerin alcohol solution which was evaporated to a glycerin medium. Each specimen was individually mounted in a modified Hoyer's medium (50% less chloral hydrate) between two cover glasses and sealed. The cover glasses were placed in an aluminum slide binder which permitted examination of either surface of the specimen.

Because of the necessity for introducing some new terminology in the descriptions which follow, most of the terms used are shown in the illustration of *Cateria*

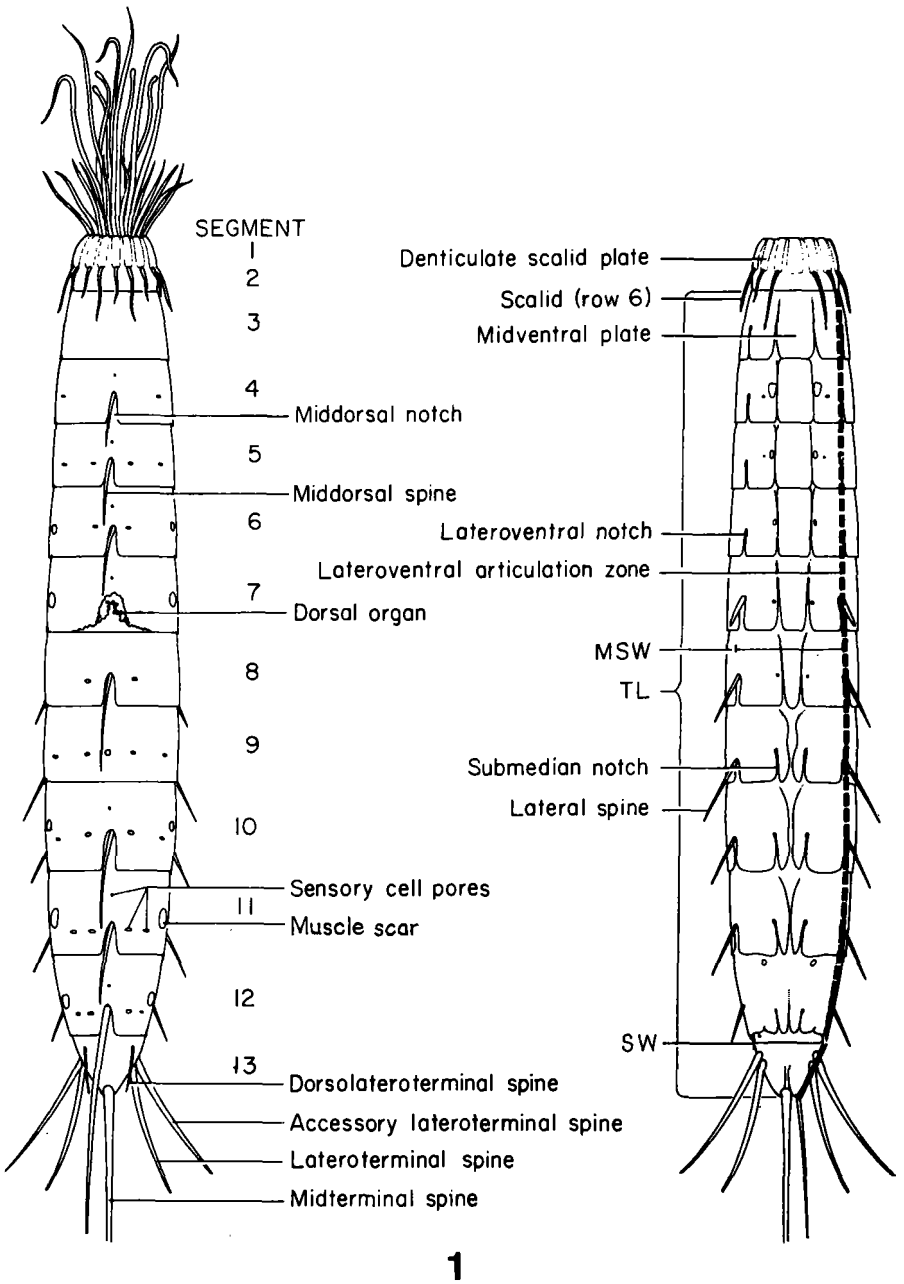


FIG. 1. Representative *Cateria*, indicating terms used in descriptions.

styx in Figure 1. The various measurements (all in microns) and abbreviations used in the descriptions are explained as follows:

Total length (TL) is measured on the midline, from the anterior margin of segment 3 (the first trunk segment) to the posterior margin of segment 13, exclusive of spines. Maximum sternal width (MSW) is measured at the anteroventral margin of the widest pair of ventrolateral or sternal plates as first encountered

in measuring each segment from anterior to posterior. Sternal width at segment 12 (SW) or standard width is measured at the anteroventral margin of the twelfth ventrolateral plates.

Mid-dorsal spines (D) are numbered by segment and their cumulative mean length (DM) calculated. Lateral spines (L) are numbered by segment. Measurements are given for the laterotermínal spines (LTS), laterotermínal accessory spines (LTAS), dorsolaterotermínal spines (DLTS), and midterminal spine (MTS). Because a given juvenile stage may have a mid-dorsal spine so near the terminus that it might be considered the functional midterminal spine, the term posteriormost terminal spine (PTS) is introduced (Table III) to facilitate discussion of the life history stages.

Various indices using the above measurements are indicated by the relative abbreviations separated by a slant (/) and are calculated by dividing the first measurement by the second.

Key to the Adults of the Kinorhynch Genera

1. First trunk segment entire, bivalvate, or without lateroventral articulation; rounded or oval in cross-section; lateral dorsal and terminal spines usually well-developed ..... order Cyclorhagida 3
   First trunk segment with single, strongly-arched dorsal plate, single midventral plate, and two lateroventral plates; with distinct lateroventral articulation; trunk spines, if present, restricted to laterotermínal spines ..... order Homalorhagida 2; family Pycnophyidae
2(1). With two laterotermínal spines ..... *Pycnophyes*
   Without laterotermínal spines ..... *Trachydemus*
3(1). Closing apparatus consisting of 14–16 distinct placids or neck plates; first trunk segment entire, without denticles ..... suborder Cyclorhagae 4
   Closing apparatus not apparent; head with long flexible scalids; without lateroventral articulation; midterminal spine nearly equal to or longer than trunk length; living in psammolittoral of beaches ..... Cryptorhagae, new suborder; family Cateriidae; *Cateria*
4(3). First and second trunk segments consisting of closed rings; midterminal spine absent; laterotermínal spines prominent ..... family Echinoderidae; *Echinoderes*
   Second trunk segment with two lateroventral plates; midterminal spine present ..... family Centroderidae 5
5(4). Lateral spines generally robust, present only on few segments .. *Centroderes*
   Lateral spines narrow, present on all or nearly all segments, lateral spines often accompanied by flattened, apiculate adhesive tubes, lateral spines of first trunk segment often very long ..... *Campyloderes*

Order Cyclorhagida (Zelinka, 1896) Higgins, 1964

Cyclorhagae Zelinka, 1896, p. 197.
Conchorhagae Zelinka, 1907, p. 135 (part).
Heterorhagae Lang, 1949, p. 8.
Heterohaga Gerlach, 1956, p. 124.

DIAGNOSIS: Kinorhyncha with trichoscalids, 10, 6, or lacking, or 13–14 unmodified homologous scalids; trunk segments round to oval in cross-section; protonephridia each with single ligament; gonopores lateral between segments 12–13; pharynx musculature forming closed ring; oblique muscles in segments 3-, or 4–10, or absent; armor joints, if present, consisting of dorsal acetabulum and ventral condyle; variously provided with lateral, mid-dorsal, and midterminal

spines; surface of trunk segments commonly covered with minute hairs or denticles, arranged in distinctive patterns.

DISCUSSION: The tendency for trichoscalids to be few or otherwise modified, even absent, is associated with a corresponding decrease in the prominence of placids. In general, although the trunk is round to oval in cross-section, the dorsal portion may approach a vaulted cross-sectional appearance. The presence of lateral, mid-dorsal, and midterminal spines is important. Lateral and midterminal spines are present in all postembryonic cyclorhagid stages. A midterminal spine is present in the juvenile and adult stages of all genera except *Echinoderes*.

Cryptorhagae n. suborder

Conchorhagata Gerlach, 1956, p. 124 (part).

DIAGOSIS: Cyclorhagida with nine 3-segmented oral styles; six rows of flexible scalids on head, succeeding rows with 20, 10, 10, 20, 10 (or 5), 13–14 scalids; sixth row with undifferentiated scalids, homologous to trichoscalids of other taxa but without cuticular ringing or hairs, each centered on posteromedial border of a plate of minute denticles; 14 placids present but poorly developed.

First trunk segment (third body segment) circular or nearly so in cross-section, with single dorsal plate continuing ventrally to meet a single midventral plate; lateroventral articulation evidenced by lateroventral notches at the posterior margin of the dorsal plate and slight increase or change in denticulation pattern more anteriorly; segment surface with denticulations, posteriorly directed, distinctly patterned and more pronounced near the anterior margin of the segment, diminishing posteriorly, tending to be replaced by cuticular striations.

Second through sixth trunk segments similar to first but with lateroventral areas more distinctly incised or notched at lateroventral articulation zone; midventral plates narrowing, barely indicated on segment 9; segments 9–12 without midventral plates, lateroventral notches and articulation zones more evident; submedial notch developed on either side of ventral midline.

Mid-dorsal spines on segments 4, 5, 6, 8, 10, 11, and 12; lateral spines on segments 7–12; laterotermínal accessory, laterotermínal, and midterminal spines on segment 13; midterminal spine elongate, usually equal to or longer than the trunk length; mid-dorsal spine of segment 12 and midterminal spine of segment 13 with slight constriction in diameter about one-third posteriorly, anterior portion randomly cross-striated; eversible back organ present mid-dorsally between segments 7–8.

Family Cateriidae Gerlach, 1956

DIAGNOSIS: Same as for suborder.

Cateria Gerlach, 1956

TYPE-SPECIES: *Cateria styx* Gerlach, 1956.
DIAGNOSIS: Same as for family.

Cateria styx Gerlach, 1956
Figures 2–9, 14–19

LECTOTYPE: Specimen of undetermined sex, TL 450 μ; beach near Macaé, Brazil, in sand, 40–90 cm deep, 3–6 m from sea; 26 October 1954; S. A. Gerlach, col.; Gerlach syntype No. 529 (Fig. 9), hereby designated lectotype; USNM 36125.

PARALECTOTYPE: Specimen of undetermined sex, broken, TL ca. 450 μ; data as in lectotype; Gerlach syntype No. 107, hereby designated paralectotype; USNM 36126.

TOPOTYPES: 10 adults, sex undetermined, TL 452–537 μ; Caveleiro Beach, ca. 3 km south of Macaé, Brazil (lat. 22° 23′ S; long. 41° 46′ W), ca. 3 m below high tide zone, 20–50 cm deep in medium sand; 29 May 1967; R. P. Higgins, col.; Higgins No. RH 61; 2 topotype adults, RH 61.1 (Figs. 2–5, 14–19) and RH 61.3, USNM 36123–36124. 140 juveniles, TL 140–441 μ; same data; Higgins collection.

OTHER MATERIAL: 7 specimens, poor condition, sex and stage undetermined; Toninhas Beach, Ubatuba, Brazil (lat. 23° 57′ S, long. 45° 06′ W); 22 September 1964; H. L. Sanders, col.; Higgins No. K-98; Higgins collection.

REDESCRIPTION: Topotypic adults of undetermined sex (Figs. 2–5, 14–19) TL 452–537 μ; MSW-8 69–87 μ; SW 53–70 μ; SW/TL 0.11–0.13.

First segment (head) with nine 3-segmented oral styles, ca. 50 μ long, surrounding mouth cone; six rows of flexible scalids, first row with 20 narrow scalids, length ca. 70 μ, second row with 10 narrow scalids, length ca. 65 μ, third row with 10 thick, very long scalids, 6 ca. 140 μ long and 4, clubbed distally, ca. 100 μ long, fourth row with 20 scalids, 52 μ long, fifth row with 10 scalids, ca. 45 μ long; sixth row homologous to trichoscalid row of other taxa, with 13 unmodified scalids, each centered on posteromedial border of a plate of minute denticles except for midventral plate where scalid is lacking, scalid length, beginning with mid-dorsal scalid, alternating short, ca. 20 μ, and long, ca. 30–40 μ.

Second segment (neck) with poorly developed placids (neck plates).

Third segment (first trunk segment) circular in cross-section, single dorsal plate continuing ventromedially to meet single midventral plate; lateroventral margin of dorsal plate deeply incised or notched for about half the segment length, lateroventral notch in line with lateroventral articulation zone of other suborders; midventral plate ca. 20 μ wide at anterior margin where it is not well set off from the dorsal plate, slightly narrower at posterior margin; denticulation in 10–11 rows, followed by minute striations on dorsal surface, striations appear to be continuous with denticulation pattern, pattern (Figs. 2, 14) noticeably interrupted at mid-dorsal anterior margin for about four rows in width and nine rows posterior, submedial interruptions of equal magnitude on either side of mid-dorsal interruption.

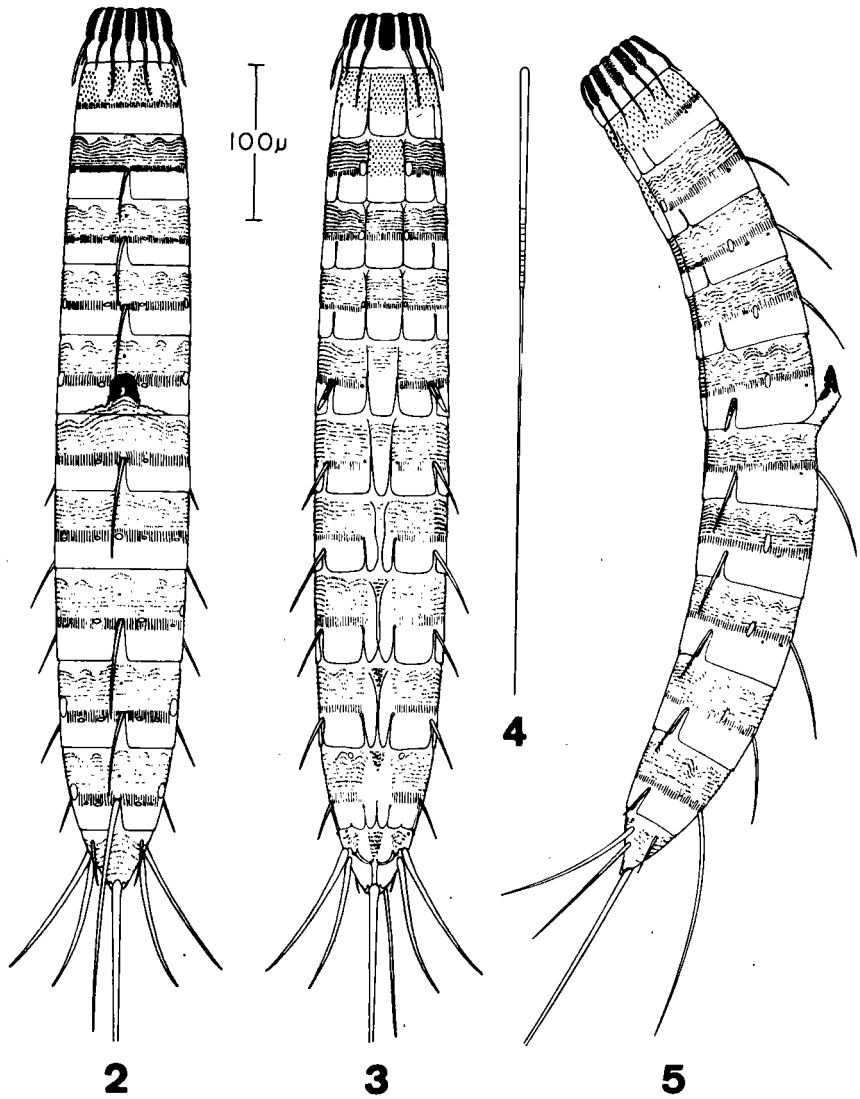
Fourth segment similar to third; mid-dorsal notch at posterior margin extending to center of segment and including mid-dorsal spine at distal limit; ventrolateral notch more prominent than on segment 3; small sensory cell pore slightly anterior to mid-dorsal spine, lateral to mid-dorsal spine, and submedially near ventromedial margin of dorsal plate; larger patches, of similar optical density and presumably muscle scars, at ventromedial margin of dorsal plate; fourth segment densely denticulated except for midventral plate, denticulation forming eight–nine distinct horizontal rows (Figs. 2, 3, 5, 14, 15), except for midventral plate, posteriormost row blends into striations.

Fifth segment similar to fourth; midventral plate narrower, additional sensory pore on dorsal surface, lateral to mid-dorsal spine, muscle scar dorsolaterally situated.

Sixth segment similar to fifth; midventral plate narrower, muscle scar at ventromedial margin of dorsal plate smaller, mid-dorsal sensory cell pore absent.

Seventh segment similar to sixth; midventral plate narrower, particularly at posterior margin, with less denticulation, only six–seven rows which narrow posteriorly; laterodorsal muscle scar enlarged; mid-dorsal spine absent; dorsal organ visible at posteromedial margin; short, thick, lateral spine within distal limits of lateroventral notch, no evidence of adhesive gland at base, with hollow internal structure as illustrated (Fig. 17); ventromedial muscle scar now replaced by sensory cell pore.

Eighth segment similar to sixth; mid-dorsal spine present, midventral plate narrower than that of segment 7; dorsolateral muscle scar absent; lateral spine



FIGS. 2–5. *Cateria styx* Gerlach, topotype. **2.** Dorsal view, head slightly retracted, anterior five scalid rows not illustrated. **3.** Ventral view. **4.** Midterminal spine. **5.** Lateral view.

narrow, elongate; dorsal organ mid-dorsally at anterior margin, everted or withdrawn at mid-dorsal junction of segments 7–8.

Ninth segment similar to eighth; mid-dorsal spine absent, sensory cell pore in its place; dorsolateral muscle scar present; midventral plate evidenced only by small triangular denticulation areas near anteromedial border; ventromedial margins of dorsal plate nearly joined; submedian notch present, extending anteriorly to include sensory cell pore at its distal limit.

Tenth and eleventh segments similar to ninth; both mid-dorsal and lateral spines present.

Twelfth segment similar to tenth and eleventh segments; mid-dorsal spine more elongate; anterior two-thirds of ventromedial margins of dorsal plate fused;

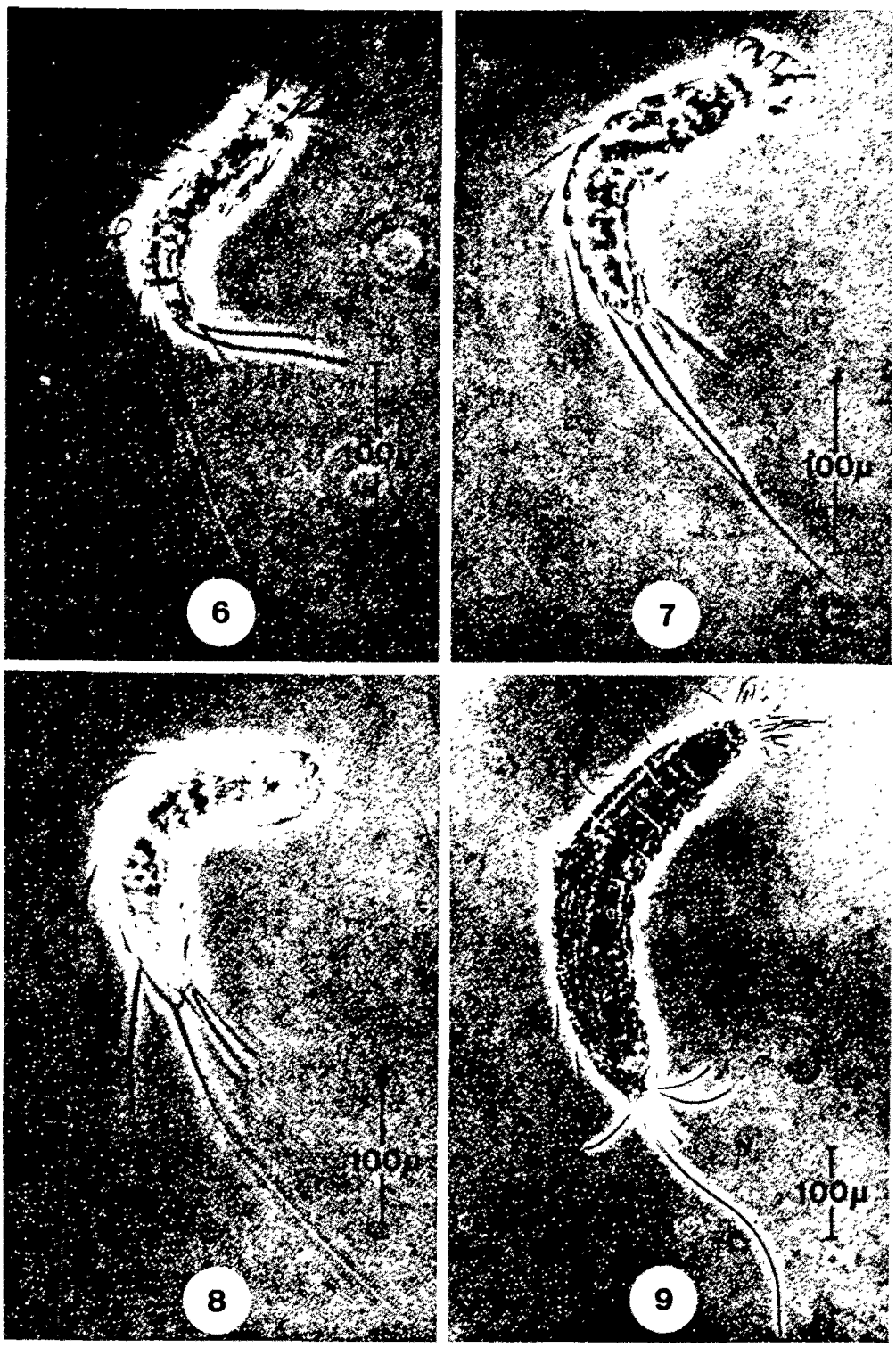

100μ
6
100μ
7
100μ
8
100μ
9

TABLE I
Measurements (μ) and indices for *Cateria styx* adults

Measurement or index	Number of measurements	Range	Mean	Standard error
TL	10	452–537	500	9.55
SW	5	50–70	62	2.86
SW/TL	5	0.11–0.13	0.12	—
MSW	4	69–87	81	3.14
DM	2	41–46	44	2.57
DM/TL	2	0.08–0.10	0.09	0.014
LTS	10	81–104	90	1.94
LTS/TL	10	0.16–0.20	0.18	0.003
LTAS	10	88–112	98	2.13
LTAS/LTS	10	0.94–1.18	1.08	0.02
MTS	1	418	—	—
MTS/TL	1	0.93	—	—

midventral triangular denticulation patch near anterior margin; intermediate ventral notch barely indicated lateral to submarginal notch; muscle scars at anterior margin of ventrolateral denticulation.

Thirteenth or terminal segment without mid-dorsal spine; midterminal spine (Fig. 4) extending posteriorly, nearly equal to trunk length, constricting in diameter ca. one-third posterior, anterior portion randomly cross-striated; laterolateral and laterolateral accessory spines robust, nearly equal in length, slightly recurved; small, narrow dorsolateral spine on either side of dorsal midline; ventral fusion as in segment 12; anterior triangular patch of denticulation at ventral midline, lateral patches of denticulation, each with sensory cell pore near anterolateral margin.

Meristic data for adult specimens is shown in Table I and selected adult and juvenile data is shown in Table II.

DISCUSSION: Recognition of the adult is difficult unless mature eggs and sperm are present. Where reproduction is seasonal, as it seems to be in the case of *Cateria styx*, and where sexually dimorphic characters are not evidenced, other morphological criteria must be used to identify the adult stage. In the present study, ten of the 150 specimens were considered adult. Since the adult kinorhynch does not molt, the length of the largest specimen actively molting at the time of collection provides an arbitrary point of limitation. In this collection, the trunk length of the largest molting specimen was 442 μ. This evidence supported by a single male 452 μ long, with mature sperm, and the adult size range reported by Gerlach (1956), was used to establish 450 μ as an arbitrary lower limit of adult size (Table II).

Because of the fragile nature of the spines, particularly those of the adult, careful observation is necessary to determine whether a spine is missing or broken at or near the base when reporting the presence or absence of the spine. Similarly, the meristic data must be recorded for unbroken spines only. Phase microscopy is essential.

The exoskeletal denticulation appears to be constant in its pattern, although the number of rows vary slightly and blend into striations posteriorly on a given segment. Although the denticulation is always prominent, the striation is highly variable from one specimen to another.

←

FIGS. 6–9. *Cateria styx*. **6.** Lateral view, 11-segmented stage (J-1). **7.** Lateral view, 12-segmented stage (J-2). **8.** Lateral view, 12-segmented stage molting. **9.** Lateral view, adult, lectotype.

TABLE II
Measurements (μ) and indices for selected specimens of *Cateria styx*

Stage →	J-1	J-2	J-2*	J-3	J-4	J-5	Adult[1]	Adult[2]	Adult[3]	Adult[4]
Segments →	11	12	12	13	13	13	13	13	13	13
TL	140	192	237	280	362	407	450	452	497	537
D-4	50	53	57	56	31	36	35	36	34	38
D-5	56	63	67	60	34	42	40	41	39	42
D-6	71	64	70	30	48	45	40	44	38	46
D-organ	–	–	–	–	+	+	+	+	+	+
D-8	60	64	76	65	46	56	58	57	45	59
D-10	64	64	64	62	59	59	65	59	53	64
D-11	216	74	62	62	55	53	55	41	36	57
D-12		244	218	160	134	155	160	broken	132	153
DM	86	89	88	71	58	64	65		54	66
L-7	——— not measured for juvenile series ———						30	22	20	22
L-8							36	36	34	38
L-9							45	52	43	46
L-10							34	36	31	38
L-11							35	34	34	38
L-12							29	30	28	broken
LTS	35	50	71	67	90	87	85	92	81	94
LTAS	104	78	81	62	92	94	100	101	88	102
DLTS							18	29	absent	34
MTS		271	292	broken	384	367	420	418	broken	broken
PTS/TL	1.54	1.41	1.23	—	1.06	0.90	0.93	0.93	—	—

* Specimen molting.
[1] Gerlach (1956, p. 121).
[2–4] Author's lower, middle, and upper size limit examples.

Postembryonic stages

Although the postembryonic life history of the Kinorhyncha is better known than the embryonic development, large gaps of information exist in most genera. The cyclorhagid life history is based presently on studies of the genus *Echinoderes* and a brief review follows in order to better explain the juvenile developmental series in *Cateria styx*.

After a poorly-known series of non-motile stages, considered embryonic by Nyholm (1947a,b), an 11-segmented juvenile is the first of the motile stages. The first three or four stages of *Echinoderes* possess a midterminal spine of considerable prominence. Unfortunately, Zelinka (1907) established genera on the basis of recognizable juvenile stages as well as the adult stages; these first stages in the life history of *Echinoderes* were assigned to the genus *Habroderes* or *Habroderella,* also invalid names. As unfortunate as the original use of such names is the continuance of their use in recent literature; consequently, *Habroderella orientalis* Kirsteuer, 1963 and *Hapaloderes manglaris* Kirsteuer, 1963 are invalid as junior synonyms of *Echinoderes caribiensis* Kirsteuer, 1963.

The example used to illustrate the sequence of events in the postembryonic development of *Echinoderes* is *E. bookhouti* Higgins, 1964. It is of particular importance to note the history of the mid-dorsal spines and spine of the terminal segment in the recognition of the various stages.

The first juvenile stage is 11-segmented and is ca. 122 μ long compared with the adult length of 357 μ. Mid-dorsal spines of the first stage are present on segments 6–10, all are relatively long compared with trunk length and are progressively longer posteriorly. In addition to the laterotermina and laterotermina accessory spines, which will be ignored for discussion purposes, there is a single midterminal spine, longer than any of the mid-dorsal spines that preceed it. The relative length of the mid-dorsal and midterminal spines will decrease with each molt.

The first molt increases the length of the animal and establishes the areas of the terminal segment (segment 11) where the following molt will result in a 12-segmented juvenile of slightly increased length and mid-dorsal spines on segments 6–11. The mid-dorsal spine of the eleventh segment in this new stage is the former midterminal spine moved anterior by the development of the segment. Essentially, the same process occurs when this 12-segmented stage molts to form the 13-segmented stage. Upon reaching the 13-segmented stage, no more segments will be formed; the adult segmentation has been attained. In the first of the 13-segmented juveniles, mid-dorsal spines are present on segments 6–12 with a midterminal spine on segment 13.

Although the next molt does not add a segment, the anterior progression of the midterminal spine to a mid-dorsal spine now takes a different perspective and the resulting juvenile lacks the midterminal spine. Consequently, the "*Centropsis*" or "*Hapaloderes*" phase has changed to the "*Habroderes*" or "*Habroderella*" phase.

This new phase of *Echinoderes* may appear to have a midterminal spine, but careful observation will show that this impression is created by an elongate mid-dorsal spine on segment 12. The next molt forms a juvenile with mid-dorsal spines on segments 6–11; the twelfth mid-dorsal spine is lost, just as the midterminal spine was lost previously. At the final molt, the mid-dorsal spine on segment 11 will disappear, the molting will cease, the definitive adult stage will be established with its typical sequence of mid-dorsal spines on segments 6–10. Gonopores and other sexually dimorphic characteristics are established in the adult stage. Adhesive tubes develop and the chitinous exoskeleton of the adult thickens and "tans."

Analysis of the 140 juvenile specimens of *Cateria styx* revealed a single 11-segmented stage (Fig. 6), 140 μ long, arbitrarily assigned to J-1 (Table II). In addition, there were two 12-segmented specimens; one 192 μ long (Fig. 7) and another 237 μ long, in the process of molting (Fig. 8). The two 12-segmented specimens were arbitrarily assigned to J-2. The smallest of the 13-segmented stages measured the same as the J-2 molt, but a single specimen, 280 μ long, provided more complete meristic data and arbitrarily was selected to represent the J-3 stage in Table II.

As shown in Table II and Figures 6 and 7, the eleventh dorsal spine of J-1 is the functional or posteriormost terminal spine. Upon molting to the J-2 stage with 12 segments, both a mid-dorsal spine and a midterminal spine develop on what appears to be just the twelfth segment. An intermediate stage, where the twelfth mid-dorsal spine is the functional or posteriormost terminal spine, might exist but was not evidenced in this study.

Through the J-2 stage, the D-12 spine has been exceptionally long and prominent as have been D-4, 5, and 6. The J-3 stage, other than for its increased length and reduction in the length of D-6 and D-12, is similar to the prior stage. Indeed, the first three juvenile stages of *Cateria styx* are not only distinctive by their mid-dorsal and terminal spines, but also by the prominently enlarged denticles which are more spinose than in the later stages, including the adult. Apparently, the adult number of denticle rows are present in these juveniles, but the denticles are more evenly spread over the entire segment rather than being restricted to the anterior portion as in the later stages.

In addition, the first three juvenile stages have a distinctive posterior row of hairs at the margin of each segment. The relationship of these hairs to the striate pattern observed in the later stages is unknown; the exact nature of the striations is limited by the optical resolution of the microscope—it is possible that this striation includes hairs or hair-like cuticular processes. In addition to the marginal hairs noted in the first three juvenile stages, a small mid-dorsal seta was

noted at the posterior margin of segment 3 of the J-2 specimen. This seta, ca. 20 μ long, was not visible in the other juveniles, although the hairs of the posterior border near the mid-dorsal spines tend to be more elongate. Another significant characteristic of the first three juvenile stages of *Cateria styx* is the lack of a dorsal organ between the seventh and eighth segments.

A major change is evident upon the molt of the J-3 stage. If there is merit in the suggestion that a stage is missing between J-1 and J-2, and four juvenile stages exist in the early development of *Cateria styx,* it appears that the J-1 through J-3 series, with or without the postulated missing stage, is equivalent to the *"Centropsis"* or *"Hapaloderes"* phase of *Echinoderes.*

Most of the specimens were assigned to stages J-4 and J-5. The lower limit of the J-4 stage was arbitrarily established at 350 μ since a single specimen morphologically similar to the J-3 stage was molting at this length. A specimen 362 μ was selected to represent the J-4 stage (Table II). The J-5 stage is represented in Table II by an individual 407 μ long; two molting specimens measured 429 μ and 442 μ, therefore, the upper limit of the J-5 stage was assumed to be 442 μ. Because of the characteristics already noted in the definition of the adult, any specimen exceeding 442 μ was considered adult. The first specimen exceeding this limit measured 452 μ and was distinguishable as a male by the presence of sperm.

In summary, there is an early motile stage of *Cateria styx,* ca. 140 μ long, that has only 11 segments, mid-dorsal spines on segments 4, 5, 6, 8, and 10 which are significantly longer than the late juvenile stages or the adult, a mid-dorsal spine on segment 11 which is the functional terminal spine, denticles more spinose and much larger than in the late juvenile stages or the adult and which are not restricted to the anterior portion of the segment, a posterior marginal row of hairs, and no dorsal organ between segments 7 and 8.

A second juvenile stage, between 192–237 μ long, has similar spine-length characteristics but has the adult number of spines, similar spinose denticulation and marginal hair row, and lacks a dorsal organ.

The third juvenile stage, ca. 280 μ long, is similar to the prior stage but the mid-dorsal spines on segments 6 and 12 are shorter, more similar to the length in the remaining juvenile stages and the adult.

The fourth and fifth juvenile stages assume the adult characteristics, except for their length and sexual maturity.

The posteriormost terminal spine of the developmental stages shows a progressively smaller proportional length (PTS/TL) and the laterotermínal and laterotermínal accessory spines increase in size during the postembryonic development of *Cateria styx.*

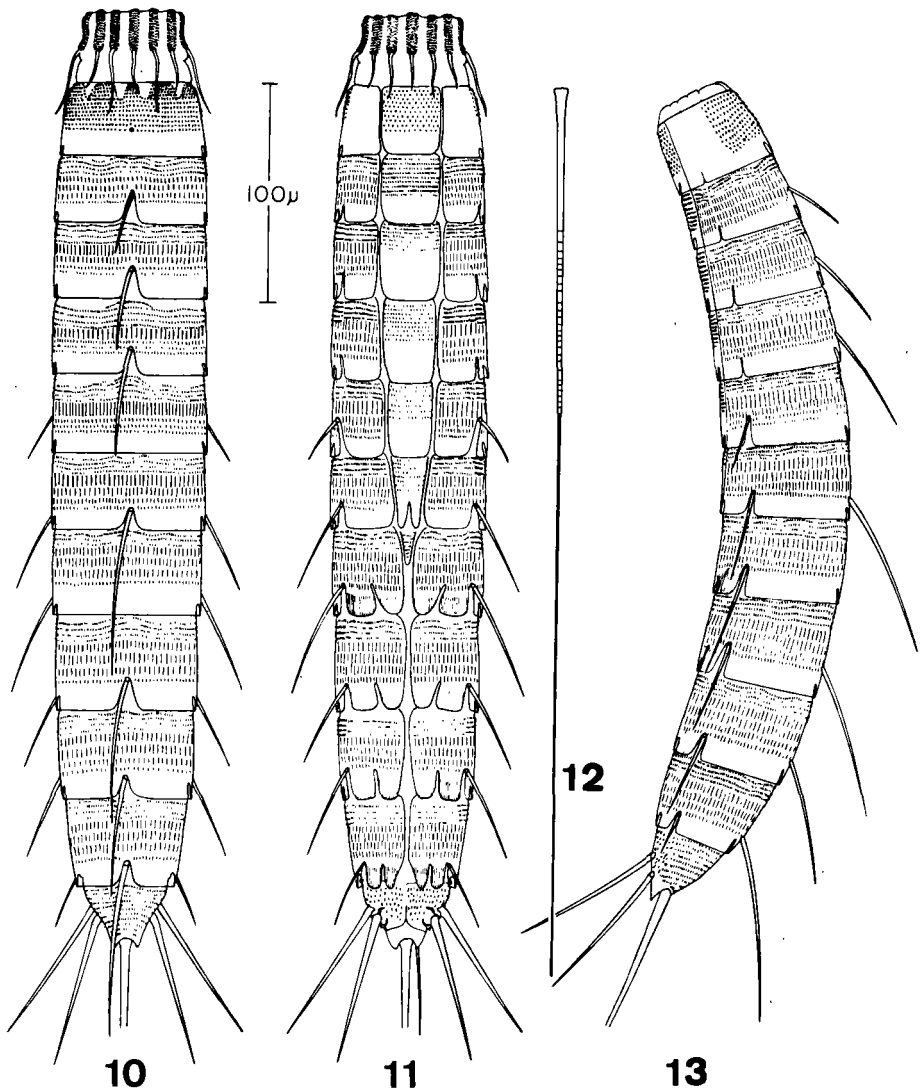
Cateria gerlachi n. sp.
Figures 10–13, 20–25

HOLOTYPE: Adult of undetermined sex, TL 384 μ; beach near Waltair, India (lat. 17° 50′ N, long. 83° 15′ E), in sand, 20–60 cm deep, midtide zone; September 1964; G. C. Rao, col.; Higgins No. K 99.16; USNM 36127.

PARATYPES: 16 adults of undetermined sex, TL 356–463 μ; data as in holotype except for RH 39–40 series, col. 28–29 March 1964; Higgins Nos. K 99 and RH 39–40; Higgins collection.

DESCRIPTION: Holotype adult of undetermined sex (Figs. 10–13, 20–25), TL 384 μ; MSW-6 76 μ; SW 41 μ; SW/TL 0.11.

First segment with nine three-segmented oral styles surrounding mouth cone; six rows of flexible scalids, formula: 20, 10, 10, 20, 5, 14, sixth row with undifferentiated scalids, homologs of trichoscalids, nearly equal in length, each centered on posteromedial border of plate of minute denticles.

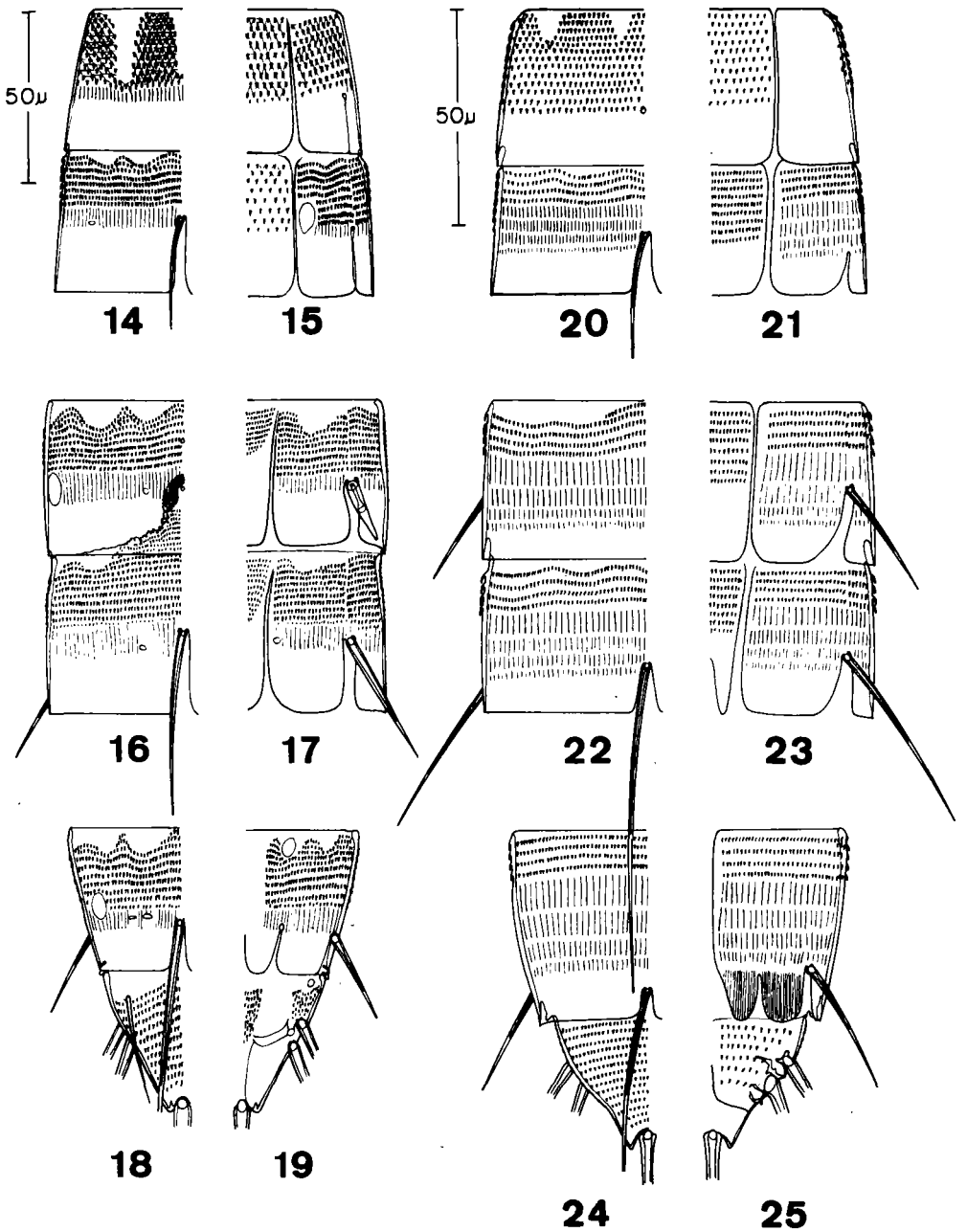


FIGS. 10–13. *Cateria gerlachi*, n. sp., holotype. **10.** Dorsal view, head slightly retracted, anterior five scalid rows not illustrated. **11.** Ventral view. **12.** Midterminal spine. **13.** Lateral view.

Second segment (neck) with poorly developed plates.

Third segment (first trunk segment) circular in cross-section, single dorsal plate continuing ventromedially to meet single midventral plate; lateroventral margin of dorsal plate incised or notched for ca. one-fourth the segment length, lateroventral notch in line with lateroventral articulation zone of other suborders; midventral plate ca. 22 μ wide at anterior margin, entirely set off from dorsal plate, slightly narrower at posterior margin; denticulation in nine rows, not followed by striations, pattern (Figs. 10, 20) noticeably interrupted on either side of midline and again more laterally, denticulation apparently absent lateroventrally, present but less dense on midventral plate.

Fourth segment similar to third; mid-dorsal notch at posterior margin extending to center of segment and including mid-dorsal spine, 29 μ long, at distal



FIGS. 14–19. *Cateria styx*, topotype. **14.** Dorsal view, lateral half, segments 3–4. **15.** Ventral view, lateral half, segments 3–4. **16.** Dorsal view, lateral half, segments 7–8. **17.** Ventral view, lateral half, segments 7–8. **18.** Dorsal view, lateral half, segments 12–13. **19.** Ventral view, lateral half, segments 12–13. FIGS. 20–25. *Cateria gerlachi*, n. sp., holotype. **20.** Dorsal view, lateral half, segments 3–4. **21.** Ventral view, lateral half, segments 3–4. **22.** Dorsal view, lateral half, segments 7–8. **23.** Ventral view, lateral half, segments 7–8. **24.** Dorsal view, lateral half, segments 12–13. **25.** Ventral view, lateral half, segments 12–13.

TABLE III
Measurements (μ) and indices for *Cateria gerlachi* adults

Measurement or index	Number of measurements	Range	Mean	Standard error
TL	17	356–463	419	8.2
SW	2	41–42	41.5	0.71
SW/TL	2	0.01–0.11	0.105	—
MSW	2	74–76	75	1.41
DM	3	64–78	72	2.94
DM/TL	3	0.16–0.18	0.17	0.41
LTS	17	62–102	88	2.55
LTS/TL	17	0.17–0.24	0.21	0.42
LTAS	17	70–98	85	1.85
LTAS/LTS	17	0.91–1.31	0.98	0.76
MTS	13	396–507	450	11.71
MTS/TL	13	0.91–1.22	1.08	8.33

limit; ventrolateral notch more prominent than on segment 3; sensory cell pores probably present but not noted; fourth segment densely denticulated, including midventral plate, denticulation in four rows except for nine rows on midventral plate; except for midventral plate, posteriormost row blends into striations.

Fifth segment similar to fourth; midventral plate narrower, midventral spine 37 μ long.

Sixth segment similar to fifth; midventral plate narrower, lateroventral notch more prominent; mid-dorsal spine 49 μ long.

Seventh segment similar to sixth; midventral plate slightly narrower, with less denticulation; mid-dorsal spine absent; dorsal organ absent; elongate, thin, lateroventral spine present within distal limits of lateroventral notch, 24 μ long (Fig. 23), adhesive or mucous gland at base.

Eighth segment similar to sixth; mid-dorsal spine present, 76 μ long; midventral plate narrower than that of segment 7, posterior margin with deep median notch; lateral spine 42 μ long; dorsal organ absent.

Ninth segment similar to eighth; mid-dorsal spine absent; midventral plate triangular, small, at anterior half of segment; ventromedial margins of dorsal plate nearly joined; submedian notch present; posterior border of ventral surface with distinct, very closely spaced striations; lateral spine 54 μ long.

Tenth, eleventh, and twelfth segments similar to ninth; midventral plate not present or indicated by denticulation; posterior border of ventral surface with distinct, very closely spaced striations; posteromedial margins of dorsal plate diverging from ventral midline; D-10 68 μ, D-11 56 μ, D-12 82 μ; L-10 42 μ, L-11 42 μ, L-12 28 μ.

Thirteenth or terminal segment without mid-dorsal spine; midterminal spine (Fig. 12) 441 μ extending posteriorly, constricting in diameter ca. one-third posterior, anterior portion randomly cross-striated; laterolateral spine 71 μ long; laterolateral accessory spine 70 μ long; dorsolateral spine absent; anterior half of ventromedial margins of dorsal plate fused; dorsal surface evenly denticulate over entire surface, ventral surface less densely denticulate.

Meristic data for adult specimens is shown in Table III and selected adult and juvenile data is shown in Table IV.

ETYMOLOGY: This species is named for Prof. Dr. S. A. Gerlach who discovered and described the first species of *Cateria*. This name was originally suggested by Dr. G. C. Rao.

DISCUSSION: The most prominent of the unique features of *Cateria gerlachi* are the lack of a dorsal organ between the seventh and eighth segments and the significantly long mid-dorsal and lateral spines. These characteristics are

TABLE IV
Measurements (μ) and indices for selected specimens of *Cateria gerlachi*

Stage → / Segments →	J-4 13	J-5 13	Adult[1] 13	Adult[2] 13	Adult[3] 13	Adult[4] 13
TL	260	305	356	407	463	480–530
D-4	34	31	34	33	39	40
D-5	42	40	39	53	56	48
D-6	48	57	42	75	70	60
D-8	73	86	76	99	broken	72
D-10	59	50	59	87	87	68
D-11	56	59	48	71	78	84
D-12	154*	86	broken	99	98	120
DM	67	59	—	74	—	71
L-7	– not measured –		47	22	broken	24
L-8			50	broken	56	80
L-9			67	72	81	74
L-10			39	53	59	66
L-11			45	51	50	56
L-12			20	36	36	48
LTS	62	73	76	97	92	98
LTAS	62	64	78	88	98	—
MTS	broken	418	396	497	474	436
PTS/TL	—	1.37	1.11	1.22	1.02	—

* Not an average measurement, other examples D-12 were between 80–102.
[1-3] Author's lower, middle, and upper size limit examples.
[4] Rao & Ganapati (1966).

obvious under low magnification and readily distinguish this species from *C. styx*.

Although the mean total length for adult *C. gerlachi* is less than that of *C. styx*, the recent paper by Rao & Ganapati (1966) reports a size range more nearly that of the latter species. The total length of the adult may vary with ecological conditions and should not be considered as an important taxonomic character. The slightly shorter midterminal spine in *C. styx* may be significant.

In comparing other measurements and indices (Tables I–IV), very few are of significance. The absence of a dorsolateral terminal spine in *C. gerlachi* is of questionable importance since it was not always observable in *C. styx* and possibly might be a sexually dimorphic character. The morphology of the seventh lateral spine of the two species is significantly different. The L-7 of *C. styx* is short and blunt and that of *C. gerlachi* elongate and pointed.

The presence of 14 equally long scalids (homologs of trichoscalids) in the sixth row of *C. gerlachi* differs from the 13 alternate long and short scalids in the sixth row of *C. styx* where the midventral scalid is missing.

The pattern of denticulation of *C. gerlachi* differs from that of *C. styx*. This is particularly evident on the first trunk segment where the dorsal surface of *C. gerlachi* has four shallow interruptions of the denticulation, a submedian and lateral interruption on either side of the midline, and *C. styx* has three deep interruptions, a mid-dorsal and two lateral interruptions. The lateroventral surface of *C. gerlachi* is without denticulation or is very difficult to observe as opposed to that of *C. styx*. The denticulation of the anterior portions of the trunk segments in *C. gerlachi* occur in four rows followed by extensive striation; in *C. styx* eight–nine rows of denticulations followed by striation are present.

The midventral plate of segment 8 in *C. gerlachi* is notched medially and entire in *C. styx*. The ventral aspect of this same segment shows a triangular remnant of the midventral plate in *C. gerlachi* which is evidenced only by a patch of denticulation in *C. styx*. In the latter species, this denticulation pattern is repeated throughout the remaining segments but is absent in *C. gerlachi*.

The posteromedial margins of the dorsal plates diverge more at the ventral midline in *C. gerlachi* than in *C. styx* and in the former species, the posteroventral borders of segments 9–12 are distinctly striated. The pattern of denticulation of the anteroventral thirteenth segment in *C. gerlachi* is nearly uniform as opposed to the midventral and lateroventral denticulate patches in *C. styx*.

Relationships to Other Kinorhynch Taxa

A discussion of the phylogenetic relationships within the phylum Kinorhyncha necessitates a review of juvenile characteristics. As in many instances, the evolution of the Kinorhyncha seems to have followed a pattern of developmental divergence through neoteny.

Juvenile characters include: (1) a poorly developed cuticle, usually hyaline rather than chitin "tanned"; (2) spinose to denticulate cuticular marking, rather than hairs or pores which communicate with the underlying cells; (3) incomplete or poorly developed segmental or plate articulation, particularly lateroventrally; (4) presence of midterminal spine, laterotermínal and laterotermínal accessory spines, and extensive mid-dorsal and lateral spines; absence of sexually dimorphic characteristics, including various spines, certain adhesive tubes, and functional gonopores.

Within the two orders of Kinorhyncha the most advanced genera (non-juvenile) are *Echinoderes* within the Cyclorhagida and *Pycnophyes* or *Trachydemus*, the only two genera of the Homalorhagida. All three genera have a thick, chitinous, usually yellow-brown cuticle as adults. Generally, the cuticle is covered by a pattern of hairs in *Echinoderes* and is distinctly porous in the homalorhagid genera. Although there are ordinal differences between the ball and socket joints, the articulation of plates is well-developed in all three genera.

The midterminal spine is present only in the early juvenile development of both *Echinoderes* and *Pycnophyes* and is barely indicated in the early stages of *Trachydemus* (Higgins, 1962). Laterotermínal spines are present in the adults of both *Echinoderes* and *Pycnophyes*, but are absent in *Trachydemus*; laterotermínal accessory spines are only in the adult of *Echinoderes*. The dorsal and lateral spines commonly present in *Echinoderes* are evidenced only in the juvenile stages of the homalorhagids. Gonopores occur laterally between the last two segments in *Echinoderes*, adhesive tubes on the fourth ventrolateral plates of both males and females, and males are distinguished by penile spines and modified laterotermínal spines. The gonopores of the homalorhagid genera occur ventrolaterally on the anterior margin of the terminal segment, adhesive tubes on the ventrolateral plates of segment 4 are in the male only, penile spines are present in the male.

With this pattern established, a progressively more juvenile-like adult occurs in the sequence: *Echinoderes—Campyloderes—Centroderes—Semnoderes—Cateria*. The homalorhagid genera have a third dimensional relationship with *Echinoderes* and a relationship with both the *Semnoderes* and *Cateria*, as will be discussed later.

The first two trunk segments of *Echinoderes* are closed rings, only the first trunk segment of *Campyloderes* is a closed ring and in *Centroderes* there is evidence of lateroventral articulation in the first trunk segment; these three genera are in the suborder Cyclorhagae. The suborder Conchorhagae with its genus *Semnoderes* has only the midventral articulation which has extended mid-dorsally as well, forming a bivalved closing apparatus aided by poorly developed placids.

In discussing the relationships of *Cateria* to the other kinorhynch taxa, it is obvious that the early juvenile stages bear a distinct relationship with both cyclorhagid (*Echinoderes*) and homalorhagid (*Pycnophyes*) orders. The occur-

rence of 14 placids is a characteristic in common with most cyclorhagids, the fact that they are nearly indistinguishable except in sections is a feature more like the Conchorhagae, just as there is similarity in scalid flexibility, at least in the anterior-most scalids of *Semnoderes pacificus* Higgins, 1967. Additionally, although the sixth row of scalids is modified in *Cateria,* there is an equal number of trichoscalids in this same row in *Semnoderes pacificus,* a characteristic shared between these two cyclorhagid genera and the other Homalorhagida.

Finally, a relationship between *Cateria* and the homalorhagids can be seen in the presence of a midventral plate, particularly well-developed in the first trunk segment of both taxa but not repeated throughout the major portion of the trunk in the homalorhagids as it is in *Cateria.* With the lateroventral articulation evidenced in *Cateria,* the ventral aspect bears a close similarity to that of the first trunk segment in the homalorhagids.

Therefore, the relationships between the Cryptorhagae and Conchorhagae, initially pointed out by Gerlach (1956), seem obvious, as are certain similarities between *Cateria* and the homalorhagid taxa. It would appear, consequently, that the Cryptorhagae, so named for the obscure nature of their placids, may be as well named relative to both its phylogenetic position within the phylum Kinorhyncha and its subterranean habitat so obviously pointed out in the name of the type-species, *Cateria styx.*

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TWO NEW COPEPODS (CYCLOPOIDA, LICHOMOLGIDAE) FROM MARINE PELECYPODS IN MADAGASCAR

BY

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During a search for copepods associated with marine invertebrates at Nosy Bé, in northwestern Madagascar, in 1960 and 1963-64, two new copepods were discovered in the mantle cavity of *Spondylus varians* Sowerby and *Chama iostoma* Conrad. These copepods, described below, comprise a new lichomolgid genus and species and a new species of the large genus *Lichomolgus*.

The field work in 1960 was carried out while the author was a member of an expedition sent to Madagascar by the Academy of Natural Sciences of Philadelphia, and that in 1963-64 was done as part of the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the material has been aided by a grant (GB-1809) from the National Science Foundation of the U.S.

I wish to thank Dr. William J. Clench of the Museum of Comparative Zoology, Harvard University, for the identifications of the pelecypods, and Dr. Jan H. Stock of the Zoölogisch Museum, Amsterdam, for the collection of some of the *Spondylus* during Scuba diving. I also wish to acknowledge the assistance to the field work given by the staff at the Centre d'Océanographie et des Pêches at Nosy Bé.

Gelastomolgus n. gen.

Body of a modified cyclopoid form, female with the prosome pointed anteriorly and broadened posteriorly, male with the prosome rounded anteriorly and narrowed posteriorly. Segment of leg 4 in the female with a pair of ventrolateral lobes. Segment of leg 1 separated dorsally and laterally from the head by a furrow. Urosome 5-segmented in the female, 6-segmented in the male. First antenna 7-segmented. Second antenna 4-segmented (though the first and second segments may be indistinctly separated). Mandible with a relatively broad elongated blade rather abruptly attenuated distally. Paragnath a minute spinulose lobe. First maxilla a small lobe with three setae. Second maxilla 2-segmented. Maxilliped in the female apparently 2-segmented, in the male 4-segmented, the fourth segment probably forming part of the terminal claw.

Legs 1 to 3 with trimerous rami. Leg 4 with a 3-segmented exopod and a 2-segmented endopod, the first segment of the endopod bearing an inner distal seta and the second segment a single terminal seta. Leg 5 with a single free segment bearing two terminal setae.

Other features as in the species described below.

Living in the mantle cavity of *Spondylus*.

Type and only known species: *Gelastomolgus spondyli* n. sp.

The generic name is a combination of γελαστός = laughable, laughed at, referring to the fancied clownish appearance of the body, and μολγός = a sack made of leather.

Gelastomolgus spondyli n. sp. (figs. 1-36)

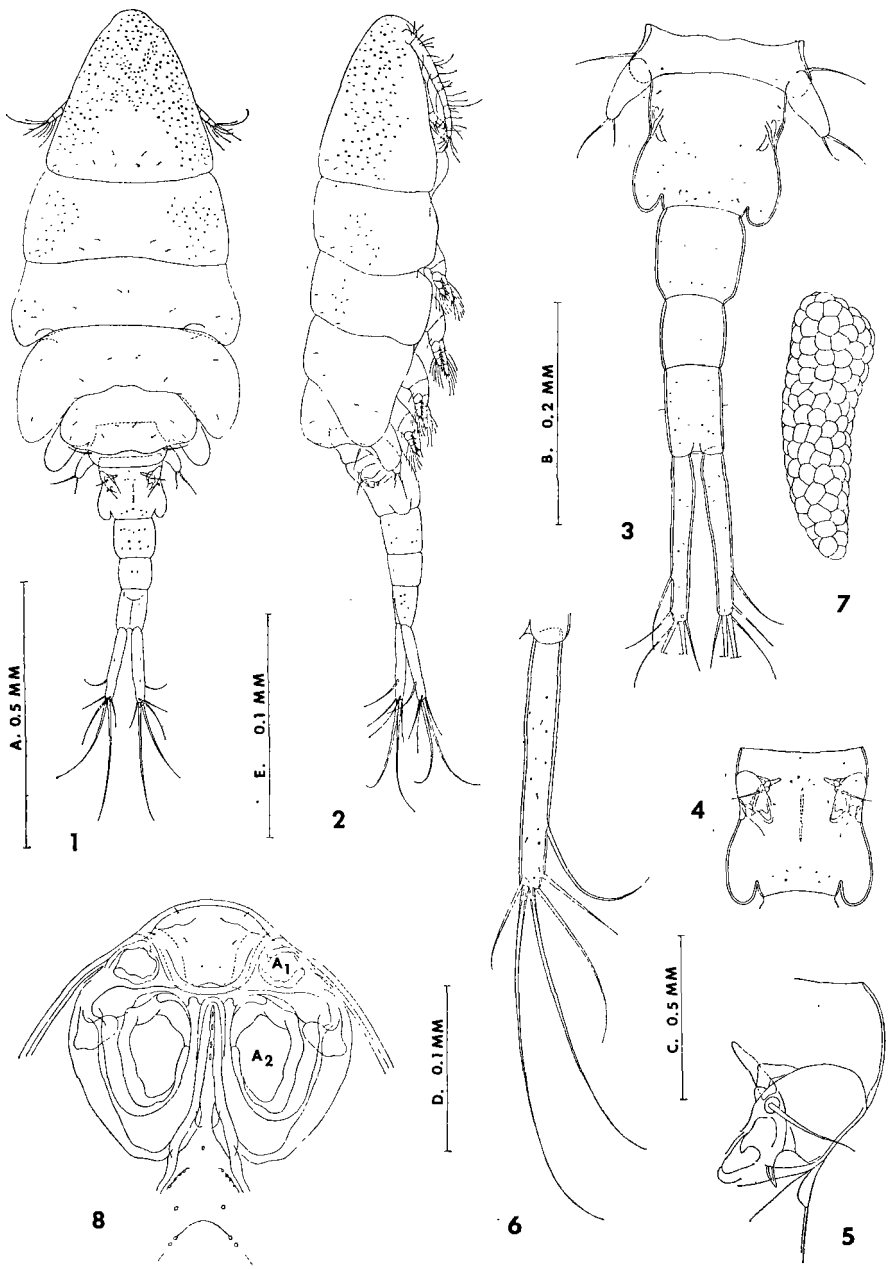
Type material. — 51 ♀♀ and 85 ♂♂ from the mantle cavity of one pelecypod, *Spondylus varians* Sowerby, obtained by Scuba diving in 20 m at Tany Kely, a small island to the south of Nosy Bé, Madagascar. Collected December 20, 1963. Holotype ♀, allotype, and 52 paratypes (16 ♀♀, 36 ♂♂) deposited in the United States National Museum, Washington; 25 paratypes (10 ♀♀, 15 ♂♂) in the Zoölogisch Museum, Amsterdam, and in the Museum of Comparative Zoology, Harvard University, Cambridge; and the remaining paratypes in the collection of the author.

Other specimens (all from *Spondylus varians*). — 3 ♀♀ from 1 host in 10 m at Pte. Lokobe, Nosy Bé, December 18, 1963; 1 ♀ from 1 host in 20 m at Tany Kely, December 20, 1963; 1 ♀ from 1 host in 14 m at Tany Kely, December 23, 1963; and 6 ♀♀ from 1 host in 20 m at Tany Kely, August 24, 1964.

Female. — The body (figs. 1, 2) has a prosome which is pointed anteriorly and broadened posteriorly, the urosome being much more slender. The length (excluding the setae on the caudal rami) is 1.16 mm (1.12-1.21 mm) and the greatest width is 0.36 mm (0.34-0.37 mm), based on 10 specimens. The ratio of the length to the width of the prosome is 1.9 : 1. The segment of leg 1 is separated dorsally and laterally from the head by a well-defined furrow; the epimera of this segment are not expanded. The epimera of the segment of leg 2 are slightly expanded in dorsal view, those of the segment of leg 3 form large posterolateral wings embracing the narrower segment of leg 4. The latter segment is only slightly expanded laterally, but bears a pair of prominent fingerlike ventrolateral lobes arising near the bases of the fourth legs.

The segment of leg 5 is short ventrally but longer dorsally (compare figs. 1 and 3), so that (at least in alcoholized specimens) the urosome is held at a slight angle to the prosome. The genital segment (figs. 3, 4) is 138 μ long including the posterior lobes. The anterior half (123 μ wide) is separated by slight lateral indentations from the posterior half (133 μ wide), which bears a pair of posteriorly directed lateral lobes (see fig. 2). The egg sacs are attached dorsolaterally on the anterior half and each attachment area (fig. 5) bears a naked seta 39 μ long and a naked spine 7 μ long. The three postgenital segments are 75 × 76, 55 × 60, and 75 × 52 μ from anterior to posterior. The anal segment bears a pair of minute lateral hairs 6 μ long.

The caudal ramus (fig. 6), inserted dorsally on the anal segment, is long and slender, 153 × 20 μ in greatest dimensions, or about 7.7 times longer than wide. The marginal setae (beginning with the outer lateral seta which is inserted 114 μ from the base) are 83, 53, 187, 216, and 47 μ in length; the pedicellate dorsal



Figs. 1-8. *Gelastomolgus spondyli* n. gen., n. sp., female. 1, dorsal (A); 2, lateral (A); 3, urosome, ventral (B); 4, genital segment, dorsal (B); 5, area of attachment of egg sac, dorsal (C); 6, caudal ramus, ventral (D); 7. egg sac, dorsal (A); 8, rostral area, ventral (E).

seta is 109 μ long. All six setae are naked. The dorsal and ventral surfaces of the ramus bear a few refractile points and hairs.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear minute hairs (sensilla) and refractile points. The ratio of the length of the prosome to that of the urosome is about 1.6 : 1.

The elongated egg sacs, tapered posteriorly and reaching to the distal ends of the caudal rami, are held in alcoholized specimens parallel to the urosome. Each egg sac (fig. 7) measures approximately 484 $\times$ 184 μ, and contains numerous eggs about 38 μ in diameter.

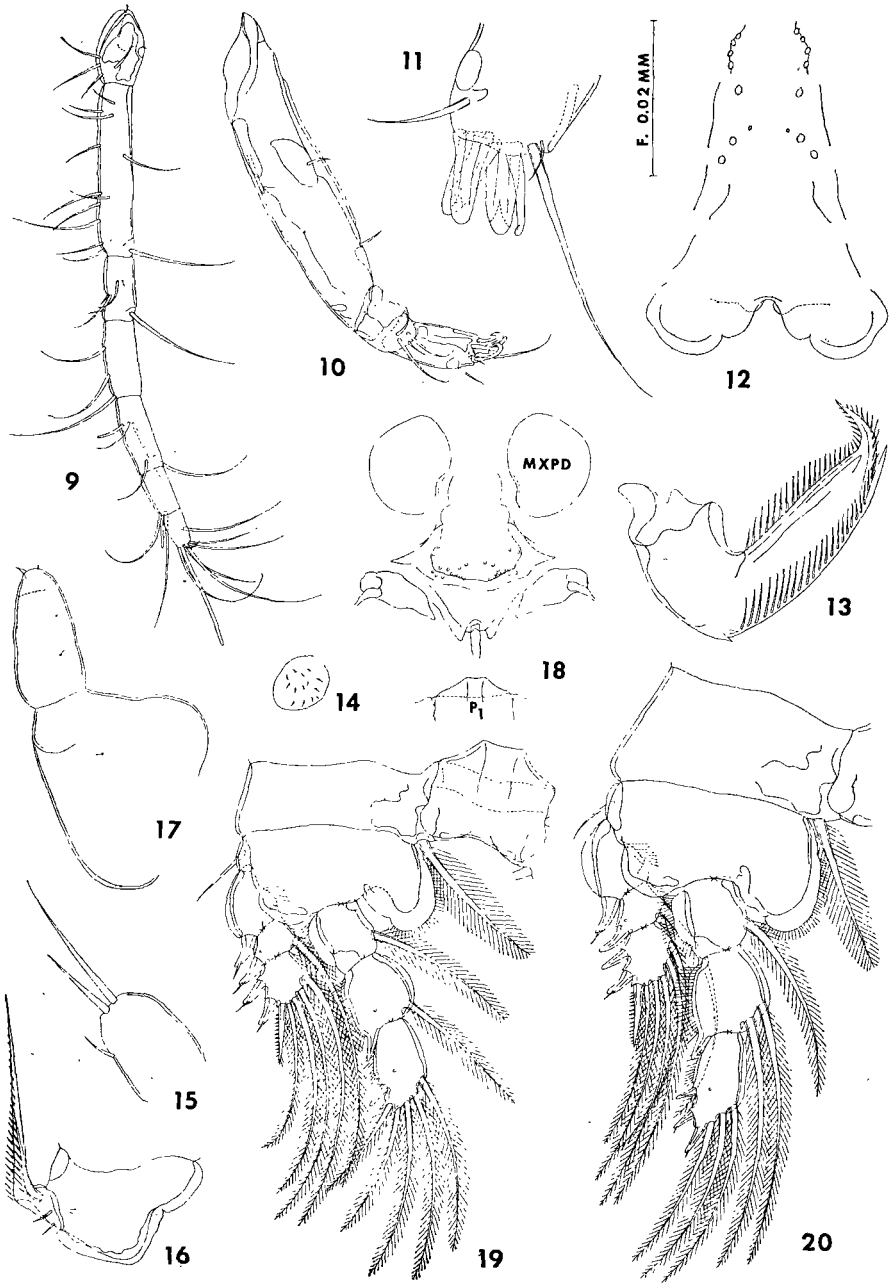
The rostral area (fig. 8) is broadly rounded. Between the well-sclerotized insertions of the second antennae there are two sclerotized longitudinal bars.

The first antenna (fig. 9) is 7-segmented and weakly sclerotized, with a narrow hyaline flange along the anterior setiferous margin of most of the segments. The lengths of the segments (measured along their posterior non-setiferous margins) are: 19 (31 μ along the anterior margin), 71, 27, 32, 32, 20, and 14 μ from proximal to distal. The formula for the armature is: 4, 12, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All the setae are naked. (The boundaries between the segments are sometimes obscure).

The second antenna (fig. 10) is apparently 4-segmented, though the articulation between the first two segments is not very distinct. The last segment measures about 40 $\times$ 17 μ. Each of the first two segments bears a hyaline seta, the third segment has four slender setae, and the fourth segment bears three terminal recurved claws 12 μ long, a blunt rather hyaline spine with a slightly recurved tip, and three adjacent setae, one of them much longer (about 36 μ) than the others (fig. 11). All the setae are naked. In contrast to the first antenna, the second antenna is well-sclerotized.

The labrum (fig. 12) is rather weakly defined anteriorly and its two posteroventral lobes, indented medially, have hyaline margins.

The mandible (fig. 13) has a relatively broad elongated blade rather abruptly attenuated distally and bearing a row of spinules on both concave and convex margins. Toward the distal end of the blade there is a well-sclerotized marginal spinous process on the convex margin and a short spinous projection on the anterior surface; at the base of the blade on the convex margin there are two small spinous processes, one hyaline, the other sclerotized. The entire mandible is about 40 μ long. The paragnath (fig. 14), located medially to the base of the first maxilla. is a minute rounded lobe 8 μ long, bearing slender spinules. The first maxilla (fig. 15) is a small lobe bearing three naked setae, two terminal and one subterminal. The second maxilla (fig. 16) is 2-segmented, the first segment bearing a hyaline flange along the convex margin and a small sclerotized process on the distal anterior surface; the second segment is attenuated to form a long reflexed spinelike process with spinules along one edge and bears two small naked hyaline setae and a large seta with spinules along one margin. The maxilliped (fig. 17) is weakly sclerotized and apparently 2-segmented, though creases in the cuticula



Figs. 9-20. *Gelastomolgus spondyli* n. gen., n. sp., female (continued). 9, first antenna, postero-inner (E); 10, second antenna, dorsolateral (E); 11, tip of second antenna, ventrolateral (F); 12, labrum, ventral (C); 13, mandible, anterior (F); 14, paragnath, ventral (F); 15, first maxilla, ventral (F); 16, second maxilla, inner (C); 17, maxilliped, ventral (C); 18, area between maxillipeds and first pair of legs, ventral (D); 19, leg 1, anterior (E); 20, leg 2, anterior (E).

suggest possible further segmentation. The first segment is broad and weakly set off from the body; the second is elongated with two small hyaline unequal processes at its tip.

The area between the maxillipeds and the first pair of legs (fig. 18) shows a slightly protuberant area with numerous refractile knobs.

Legs 1 to 4 (figs. 19, 20, 21, 22) have trimerous rami except for the endopod of leg 4 which is 2-segmented. The armature of the legs is as follows (the Roman numerals indicating spines, the Arabic numerals setae):

P_1	protopod	0-1;	1-0	exp	I-0;	I-1;	II, I, 4
				end	0-1;	0-1;	I, 5
P_2	protopod	0-1;	1-0	exp	I-0;	I-1;	II, I, 5
				end	0-1;	0-2;	II, I, 3
P_3	protopod	0-1;	1-0	exp	I-0;	I-1;	II, I, 5
				end	0-1;	0-2;	II, I, 2
P_4	protopod	0-1;	1-0	exp	I-0;	I-1;	II, I, 5
				end	0-1;	1	

The margins of the coxa, basis, and segments of the rami in all four legs bear hyaline flanges as indicated in the figures. In leg 1 all four outer spines on the exopod are naked and bear subterminal flagella; in legs 2 to 4 only the proximal and distal of these spines have such flagella. In legs 2 and 3 the distal two spines on the endopod have flagella. In leg 4 the first segment of the endopod (fig. 23) is 28 × 32 μ (including the flanges) and bears an inner distal feathered seta 97 μ long. The second segment is somewhat tapered distally, its greatest dimensions being 48 × 28 μ (including the flanges); its outer margin shows a strong indentation two-thirds of the distance from the base; the segment has a single terminal seta 33 μ long with a sclerotized basal fourth and a more hyaline distal part bearing very narrow flanges.

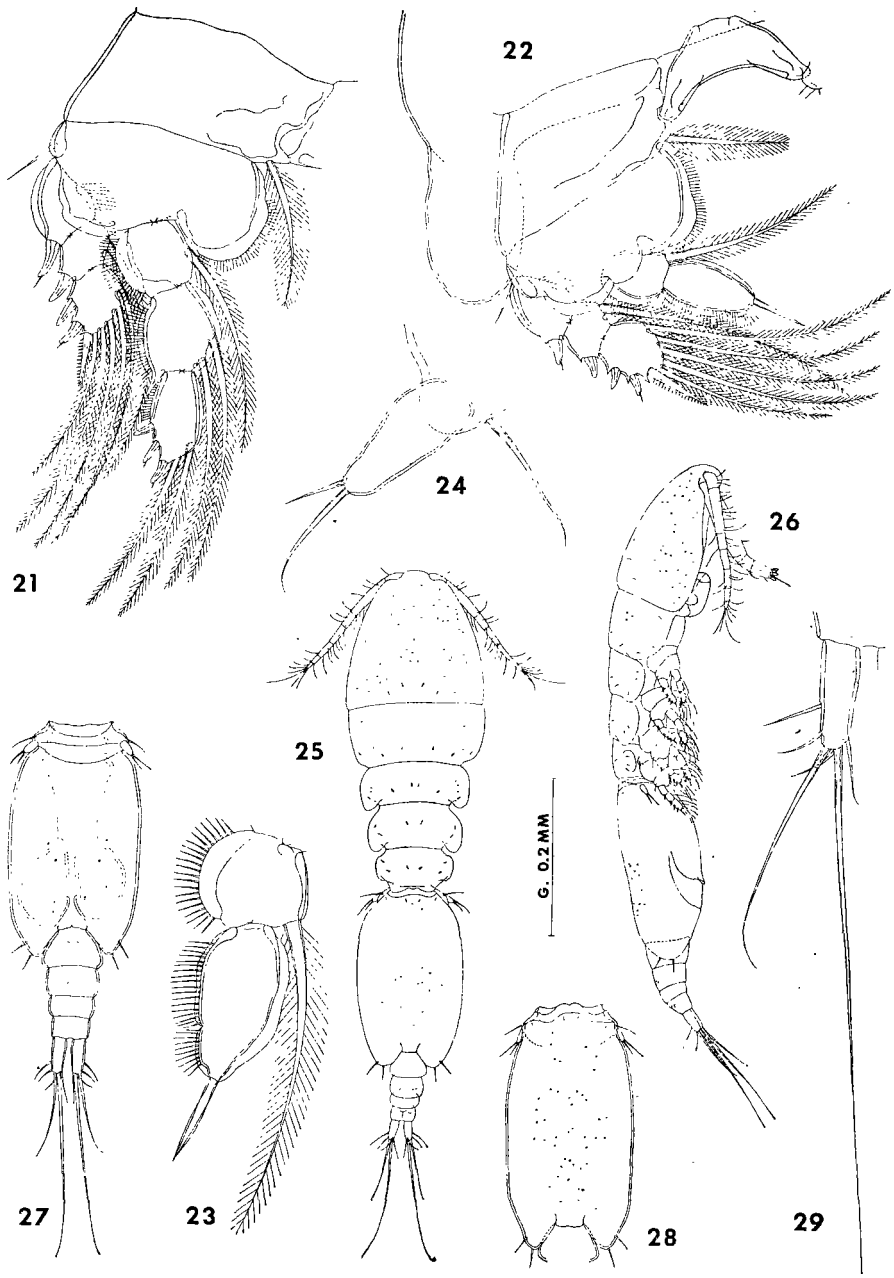
Leg 5 (fig. 24) has a moderately elongated and somewhat tapered free segment 68 × 26 μ in greatest dimensions, which is inserted ventrally on the body segment. It bears terminally a small spiniform process and two naked setae, the outer 54 μ and the inner 26μ in length. The seta on the body segment near the insertion of the free segment is naked and 69 μ long.

Leg 6 is probably represented by the seta and spine near the attachment of the egg sac (see fig. 5).

The color in life in transmitted light is opaque, the eye red, the ovaries yellowish brown, the egg sacs dark gray.

Male. — The body (figs. 25, 26) is much smaller than in the female and has a very different appearance, the prosome being rounded rather than pointed anteriorly and narrowed rather than broadened posteriorly. The length (not including the setae on the caudal rami) is 0.59 mm (0.56-0.63 mm) and the greatest width 0.14 mm (0.13-0.15 mm), based on 10 specimens. The ratio of the length of the prosome to its width is about 2.3 : 1. The segments of legs 2 to 4 are relatively narrow with their epimera expanded as illustrated in the figures.

The segment of leg 5 (figs. 27, 28) is evident in ventral view, but dorsally this segment is indistinctly set off from the genital segment and shows a prominent transverse sclerotized bar. The genital segment is elongated, 179 μ (in-



Figs. 21-24. *Gelastomolgus spondyli* n. gen., n. sp., female (continued). 21, leg 3, anterior (E); 22, leg 4 and adjacent process, anterior (E); 23, endopod of leg 4, anterior (C); 24, leg 5, ventral (E). 25-29. *Gelastomolgus spondyli* n. gen., n. sp., male. 25, dorsal (G); 26, lateral (G); 27, urosome, ventral (B); 28, genital segment, dorsal (B); 29, caudal ramus, ventral (C).

cluding the posterior lobes) × 114 μ in dorsal view. The four postgenital segments are 31 × 53, 26 × 45, 17 × 40, and 19 × 33 μ from anterior to posterior.

The caudal ramus (fig. 29), inserted terminally on the anal segment, is much shorter than in the female, 32 × 12 μ in greatest dimensions, the ratio of length to width being 2.7 : 1. The two long terminal setae are 78 μ (outer) and 156 μ (inner) in length.

The dorsal surface of the prosome and the dorsal and ventral surfaces of the urosome bear minute hairs and refractile points. The ratio of the length of the prosome to that of the urosome is 1.26 : 1.

The rostral area (fig. 30) resembles generally that of the female, with minor differences in the sclerotization.

The first antenna, second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla are much like those of the female. The maxilliped (fig. 31) is 4-segmented (assuming that the proximal part of the claw represents the fourth segment). The first segment is unarmed except for a sharp spiniform process on the inner distal surface. The elongated second segment bears two small naked setae (5 and 8 μ in length) and a long patch of spinules. The small third segment is unarmed. The terminal recurved claw, 55 μ in length along its axis, has about halfway along its length a small swelling on the concave side and a slight evidence of division on its convex side. Terminally the claw is minutely bifurcated. Along its concave edge there is a narrow fringe interrupted at the swelling. Basally the claw bears on its antero-inner surface a prominent seta 20 μ long and on its postero-outer surface a small seta 5 μ long, both of these setae being naked.

The area between the maxillipeds and the first pair of legs lacks the protuberance with refractile knobs seen in the female; the sclerotized areas posterior to this are less strongly developed; there is a line connecting the bases of the maxillipeds.

Legs 1 to 4 resemble in general those of the female, with the same segmentation and armature. The intercoxal plates are relatively shorter and broader (figs. 32 and 33) than in the female. The spines on both rami have lateral spinules and the subterminal flagella are relatively longer than in the female (see fig. 34).

Leg 5 (fig. 35) has a relatively shorter (13 × 6.5 μ) and more symmetrical free segment than in the female.

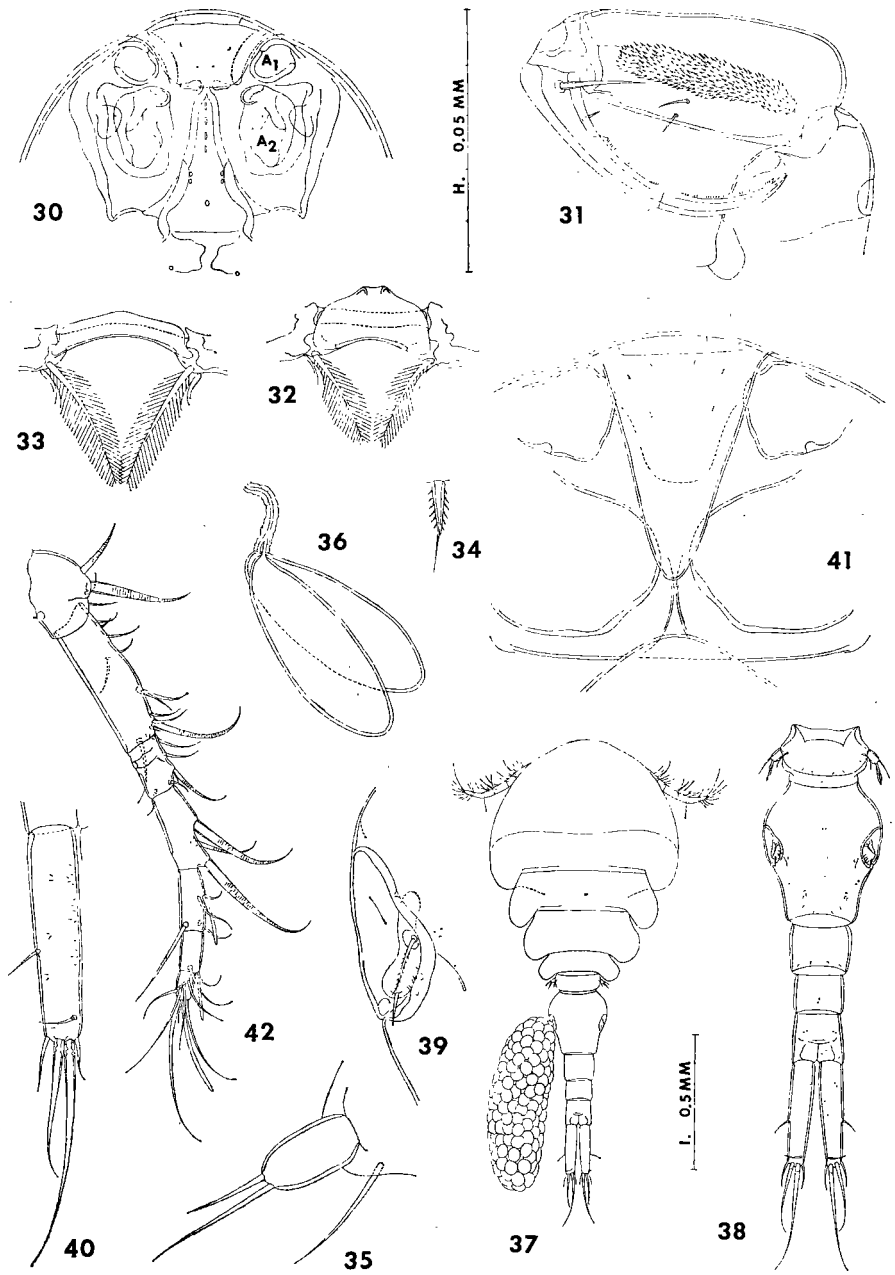
Leg 6 (fig. 27) consists of a slightly developed ventrolateral flap on the posterior part of the genital segment and bears two naked setae about 20 μ long.

Spermatophores (fig. 36) with a common stalk were observed attached to only one female. Each spermatophore is about 187 × 68 μ.

The color in life in transmitted light resembles that of the female.

The specific name *spondyli* is taken from the generic name of the host.

Taxonomic position of the new genus. — In spite of its modified body form, *Gelastomolgus* shows certain features (for example, the nature of the mandible and the structure of the endopod of leg 4) which place it in the family Lichomol-



Figs. 30-36. *Gelastomolgus spondyli* n. gen., n. sp., male (continued). 30, rostral area, ventral (C); 31, maxilliped, antero-inner (H); 32, intercoxal plate of leg 1, anterior (C); 33, intercoxal plate of leg 4, anterior (C); 34, middle spine on third segment of exopod of leg 1, anterior (F); 35, leg 5, ventral (F); 36, spermatophores, attached to female, ventral (B).

Figs. 37-42. *Lichomolgus chamarum* n. sp., female. 37, dorsal (I); 38, urosome, dorsal (A); 39, area of attachment of egg sac, dorsal (E); 40, caudal ramus, dorsal (B); 41, rostral area, ventral (D); 42, first antenna, ventral (B).

gidae. Within that assemblage of more than 25 genera the new genus seems to be closest to *Monomolgus* Humes & Frost, 1964, which is associated with the coral *Porites*. *Monomolgus,* however, has the formula for the endopod of leg 4 of 0-0; I, instead of 0-1; 1, as in *Gelastomolgus*. Other features, such as the body form, the differences in the number of spines on the last segments of the exopods of legs 1 to 4, the terminal armature of the second antenna, etc., further separate these two genera.

Lichomolgus chamarum n. sp. (figs. 37-64)

Type material. — 9 ♀♀ and 5 ♂♂ from the mantle cavity of 40 pelecypods, *Chama iostoma* Conrad, attached to intertidal rocks at Ambariobe, a small island between Nosy Komba and Nosy Bé, Madagascar. Collected August 6, 1960. Holotype ♀, allotype, and 8 paratypes (6 ♀♀, 2 ♂♂) deposited in the United States National Museum, Washington, and the remaining paratypes (dissected) in the collection of the author.

Other specimens (all from *Chama iostoma* collected intertidally). — 4 ♀♀ and 5 ♂♂ from 31 hosts at Pte. Lokobe, Nosy Bé, August 12, 1960; 5 ♀♀ and 5 ♂♂ from 38 hosts at Pte. Lokobe, August 22, 1960; 3 ♀♀ and 1 ♂ from 35 hosts at Ambariobe, October 10, 1960; and 4 ♀♀, 4 ♂♂, and 1 immature from 25 hosts at Pte. Lokobe, November 1, 1960.

Female. — The body (fig. 37) is moderately thickened dorsoventrally. The broad prosome is rounded anteriorly and the urosome is relatively long and slender. The length (excluding the setae on the caudal rami) is 1.66 mm (1.57-1.70 mm) and the greatest width is 0.70 mm (0.64-0.74 mm), based on 10 specimens (the holotype, 8 paratypes, and 1 specimen from Pte. Lokobe, August 22, 1960). The ratio of the length of the prosome to its width is 1.24 : 1. The segment of leg 1 is clearly separated from the head by a dorsal furrow. The epimera of the segments of legs 1 to 4 are rounded as in the figure.

The segment of leg 5 is about 96 × 174 μ. Between this segment and the genital segment there is ventrally a very short weakly developed intersegmental sclerite. The genital segment (fig. 38) is elongated (254 μ in length), somewhat swollen laterally in its anterior two-thirds (217 μ wide) and constricted in its posterior third (130 μ wide). The egg sacs are attached dorsolaterally just in front of the middle of the segment. Each attachment area (fig. 39) bears two setae (one 25 μ long with short lateral spinules, the other 12 μ and naked) and two spiniform processes about 6 μ long. The three postgenital segments are 91 × 109, 68 × 91, and 91 × 92 μ from anterior to posterior.

The caudal ramus (fig. 40) is elongated, its greatest dimensions being 185 × 42 μ, or 4.4 times longer than wide. The outer lateral seta, situated 104 μ from the base of the ramus, is 32 μ long, the outermost terminal seta 47 μ, the innermost terminal seta 41 μ, the two long median terminal setae 122 μ (outer) and 198 μ (inner), and the pedicellate dorsal seta 30 μ. All the setae are naked. The

dorsal and ventral surfaces of the ramus bear a few minute refractile points and hairs.

The dorsal surface of the prosome appears to lack fine ornamentation. The dorsal and ventral surfaces of the urosome bear refractile points and minute hairs. The ratio of the length of the prosome to that of the urosome is 1.16 : 1.

The egg sacs are elongated and held, in the single ovigerous alcoholized female observed, nearly parallel to the urosome, extending just beyond the tips of the caudal rami. Each egg sac (fig. 37) measures about 770 × 242 μ, and contains many eggs about 52 μ in diameter.

The rostrum (fig. 41) is well-developed, forming a long triangular posteriorly directed beak which extends between the bases of the second antennae. It bears a few hairs on its anterior surface.

The first antenna (fig. 42) is 7-segmented, with the third segment showing ventrally a small sclerite which may represent an intercalary segment. The lengths of the segments (measured along their posterior non-setiferous margins) are: 26 (75 μ along the anterior margin), 112, 50, 66, 53, 34, and 26 μ from proximal to distal. The formula for the armature is: 4, 13, 6, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. All the setae are naked.

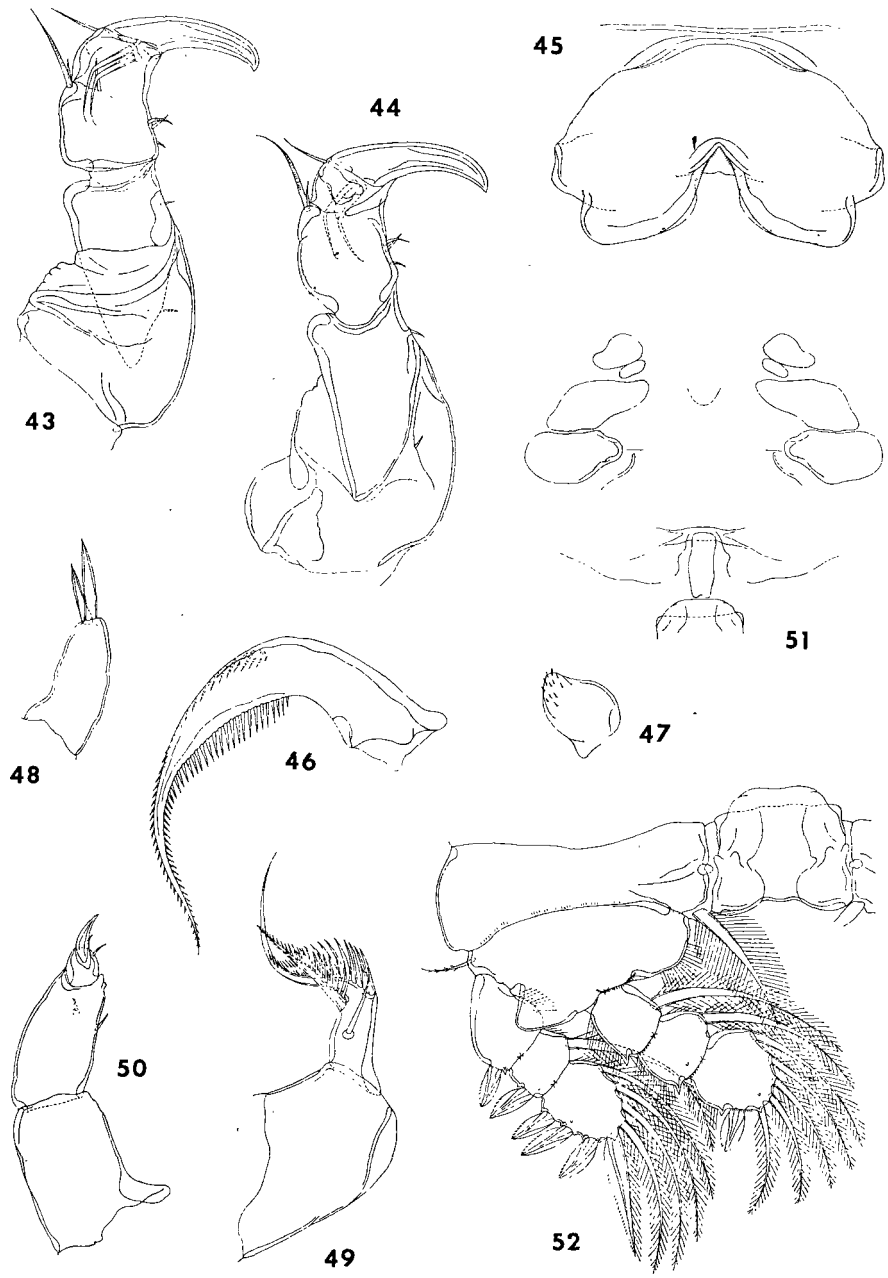
The second antenna (figs. 43, 44) is apparently 4-segmented, though the articulation between the third and fourth segments is obscure. Each of the first two segments bears a minute seta 8 μ long. The third segment bears three small inner setae. The fourth segment bears seven elements: three proximal setae, three distal setae (two of them geniculate), and a large recurved terminal claw 90 μ in length (measured along its axis). All the setae are naked.

The labrum (fig. 45) is bounded anteriorly by a crescentic ridge and its two posteroventrally directed lobes are divergent with rather hyaline margins.

The mandible (fig. 46) has a slender base and a long attenuated lash with spinules along both edges. The paragnath (fig. 47) is a small lobe with a few spinules. The first maxilla (fig. 48) is an elongated lobe armed with two terminal setae having slight flanges. The second maxilla (fig. 49) is 2-segmented; the first segment is unarmed but has an outer hyaline lamella; the second segment, bearing a naked surficial seta and a strong seta with prominent spinules along one edge, is attenuated to form a recurved lash armed with large spinules along one margin. The maxilliped (fig. 50) is 3-segmented, the first segment unarmed, the second segment with two small naked setae, and the small third segment with two small naked setae and a terminal clawlike spine.

On the postoral area (fig. 51), posterior to the lingual region and between the second maxillae, there is a small sclerotized protuberance. The region between the maxillipeds and the first pair of legs is not protuberant, and there appears to be no connecting line between the bases of the maxillipeds.

Legs 1 to 4 (figs. 52, 53, 54, 55) have 3-segmented rami except for the endopod of leg 4 which is 2-segmented. The armature of the legs is as follows (the Roman numerals indicating spines, the Arabic numerals setae):



Figs. 43-52. *Lichomolgus chamarum* n. sp., female (continued). 43, second antenna, postero-inner (D); 44, second antenna, antero-outer (D); 45, labrum, ventral (E); 46, mandible, posterior (C); 47, paragnath, ventral (C); 48, first maxilla, anterior (C); 49, second maxilla, inner (C); 50, maxilliped, anterior (E); 51, postoral area, ventral (B); 52, leg 1, anterior (D).

P_1	protopod	0-1;	1-0	exp	I-0;	I-1;	III, I, 4
				end	0-1;	0-1;	I, 5
P_2	protopod	0-1;	1-0	exp	I-0;	I-1;	III, I, 5
				end	0-1;	0-2;	II, I, 3
P_3	protopod	0-1;	1-0	exp	I-0;	I-1;	III, I, 5
				end	0-1;	0-2;	II, I, 2
P_4	protopod	0-1;	1-0	exp	I-0;	I-1;	II, I, 5
				end	0-1;	II	

The inner seta on the coxa of legs 1 to 3 is large and feathered, but in leg 4 this seta is short (33 μ) and naked. The spines on all four legs have wide hyaline flanges which are coarsely serrate in leg 1 and less so in the remaining three legs. The endopod of leg 4 is shorter than the exopod. Its first segment is 41 $\times$ 40 μ with an inner distal seta 57 μ long. Its second segment is elongated, 95 $\times$ 37 μ in greatest dimensions, and somewhat irregular in outline; the inner margin is smooth, the outer margin often bears a minute spiniform process interrupting the rows of hairs, and the terminal margin bears a row of minute spinules and two unequal spines 43 μ (outer) and 56 μ (inner) in length. There is some variation in the form of this endopod as indicated in fig. 56 (drawn from a different female than in fig. 55), where the first segment is 44 $\times$ 37 μ with its seta 47 μ, the second segment is 109 $\times$ 32 μ, without a spiniform process on the outer margin and with the two terminal spines 36 μ (outer) and 51 μ (inner).

Leg 5 (fig. 57) has a minute free segment 24 $\times$ 18 μ bearing terminally a naked seta 34 μ long and a spine 37 μ long with hyaline flanges.

Leg 6 is probably represented by the two setae near the attachment of the egg sac (see fig. 39).

The color in life in transmitted light is slightly opaque, the eye red, the egg sacs gray.

Male. — The body (fig. 58) resembles in general form that of the female. The length (without the setae on the caudal rami) is 1.34 mm (1.22-1.41 mm) and the greatest width is 0.48 mm (0.46-0.54 mm), based on 10 specimens (the allotype, 3 paratypes, 5 specimens from Pte. Lokobe, August 12, 1960, and 1 specimen from Pte. Lokobe, August 22, 1960). The ratio of the length of the prosome to its width is 1.52 : 1.

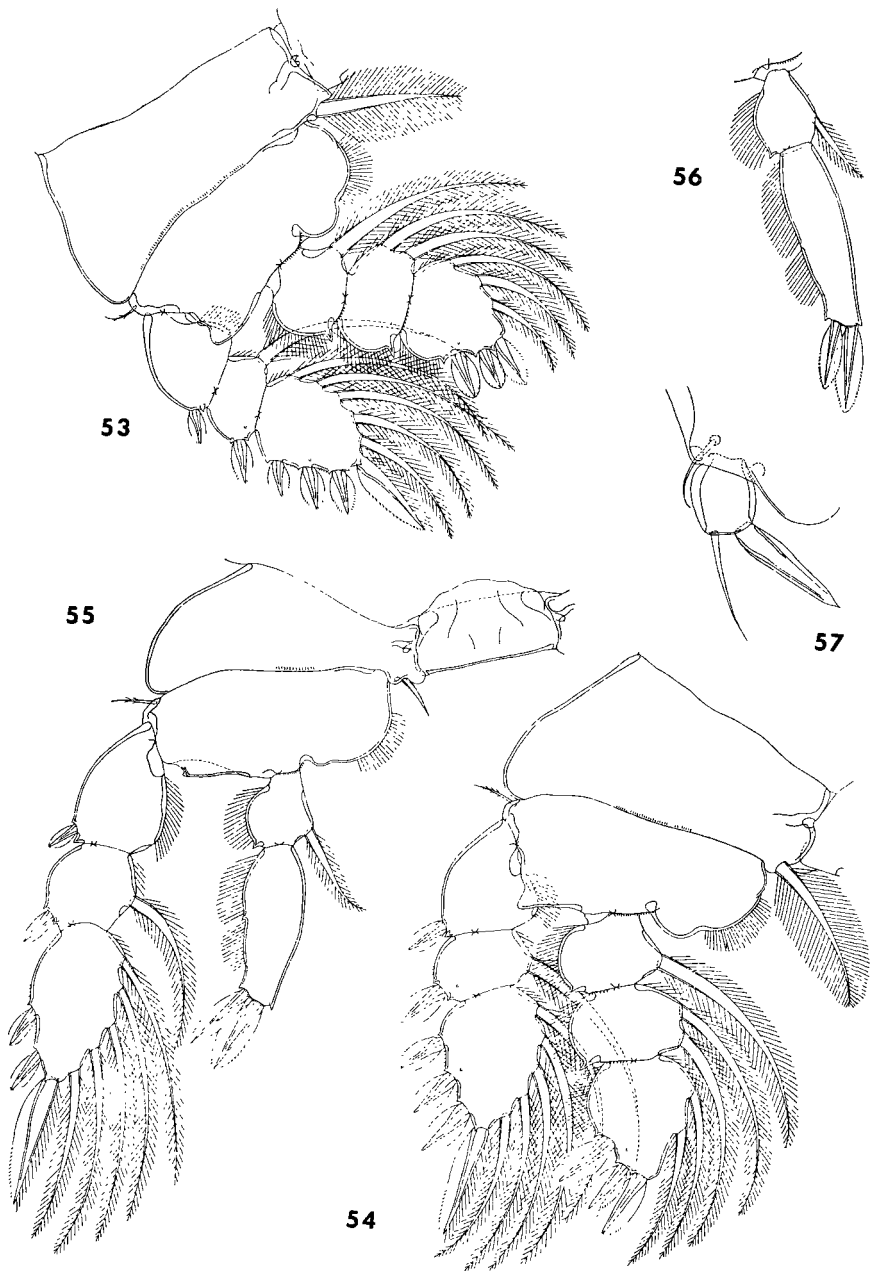
The segment of leg 5 is 47 $\times$ 140 μ. Between this segment and the genital segment there seems to be no ventral intersegmental sclerite. The genital segment (fig. 59) in dorsal view is quadrate, 270 $\times$ 270 μ, with somewhat rounded margins. There is a rather prominent transverse dorsal sclerite near the posterior border of the genital segment. The four postgenital segments are 73 $\times$ 101, 70 $\times$ 91, 58 $\times$ 81, and 73 $\times$ 78 μ from anterior to posterior.

The caudal ramus is like that in the female, with similar proportions.

The ratio of the length of the prosome to that of the urosome is 1.06 : 1.

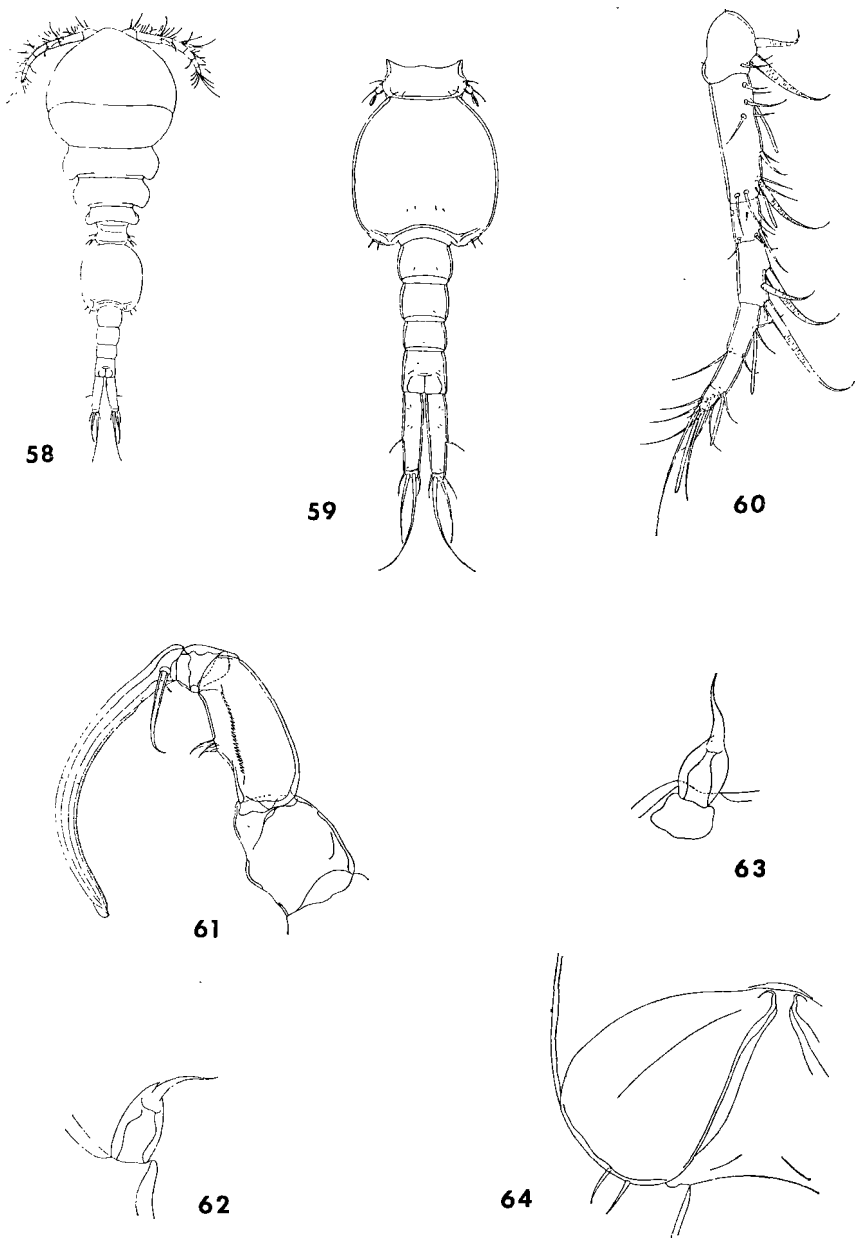
The rostrum resembles that of the female.

The first antenna (fig. 60) is like that of the female except for the addition of three aesthetes. The segments (measured as before) are: 18 (50 μ along the anterior edge), 99, 35, 50, 44, 30, and 21 μ. The formula for the armature is: 4, 13 + 2 aesthetes, 6, 3 + 1 aesthete, 4 + 1 aesthete, 2 + 1 aesthete, and 7 + 1 aesthete. The second antenna, labrum, mandible, paragnath, first maxilla,



Figs. 53-57. *Lichomolgus chamarum* n. sp., female (continued). 53, leg 2, anterior (D); 54, leg 3, anterior (D); 55, leg 4, anterior (D); 56, endopod of leg 4, anterior (D); 57, leg 5, ventral (C).

and second maxilla are like those in the female. The maxilliped (fig. 61) is 4-segmented (assuming that the proximal half of the claw represents the fourth segment). The first segment is unarmed. The relatively slender second segment bears an axial row of blunt spinules on its inner surface; on its antero-inner side



Figs. 58-64. *Lichomolgus chamarum* n. sp., male. 58, dorsal (I); 59, urosome, dorsal (A); 60, first antenna, dorsal (B); 61, maxilliped, inner (D); 62, swollen seta on second segment of maxilliped, posterior (F); 63, same, outer (F); 64, leg 6, ventral (D).

there are two modified naked setae, one relatively slender, the other stout and well-sclerotized proximally and slender and hyaline distally (as in figs. 62 and 63). The postoral area resembles that in the female, except that the small protuberance between the second maxillae appears to be lacking and there is a line connecting the bases of the maxillipeds.

Legs 1 to 4 are similar to those in the female, with the same spine and setal formula. Leg 5 also resembles that of the opposite sex.

Leg 6 (fig. 64) consists of a posteroventral flap on the posterior part of the genital segment, bearing two slender naked setae 25 μ in length.

Spermatophores were not observed.

The color in life resembles that of the female.

The specific name *chamarum* is formed from "chamae" [Latin = gaping cockles], the apparent origin of *Chama,* the generic name of the host.

Comparison with related species. — Four species of *Lichomolgus,* all from pelecypods, have certain characters in common with *L. chamarum* and may be regarded as closely related to this species. They are: *L. arcanus* Humes & Cressey, 1958, from *Arca senilis* L., *Ostrea tulipa* Lamarck, and *Pitar tumens* Gmelin in Senegal; *L. asaphidis* Humes, 1959, from *Asaphis rugosa* Lamarck and *Standella solanderi* Gray in Madagascar; *L. inflatus* Tanaka, 1961, from *Paphia* in Japan; and *L. spondyli* Yamaguti, 1936, from *Spondylus japonicus* Kuroda in Japan (of which only the female is known). In the following features these species are very similar to *L. chamarum*: the general appearance of the body, the form of the second antenna with its single claw, the slender mandible, the first maxilla with two setae, the form of the second maxilla, the armature of legs 1 to 4 (there apparently is a seta on the last segment of the exopod of the second leg omitted from Yamaguti's drawing, pl. 13 fig. 81, of *L. spondyli*), the minute fifth leg, and the shape of the genital segment in the female.

L. arcanus differs from *L. chamarum* in its smaller size (♀ 1.07 mm (1.02-1.13 mm) × 0.43 mm (0.38-0.48 mm), measurements which were inadvertently omitted from the original description, ♂ 0.91 mm), in having a broadly rounded rostrum, in having the caudal ramus 3.47 : 1 with certain setae bearing lateral hairs, in its shorter egg sac with fewer eggs, and in showing sexual dimorphism in the armature of the third segment of the endopod of leg 2.

L. asaphidis differs in its smaller size (♀ 1.32, ♂ 1.03 mm), its broadly rounded and slightly triangular rostrum, in the caudal ramus being 5.7 : 1 with certain setae haired, and in showing sexual dimorphism in the armature of the third segment of the endopod of leg 2.

L. inflatus differs in its smaller size (♀ 1.30, ♂ 0.96 mm), in its rostrum being narrowly rounded posteriorly and not as elongated, in the caudal ramus being a little more than 5 : 1 with certain setae haired, and in the male maxilliped having on its second segment a patch of spinules instead of a row.

L. spondyli differs in its bluntly pointed rostrum, in the caudal ramus being about 3.3 : 1 with the inner long terminal seta much longer than the outer, in the endopod of leg 4 having terminally a seta and a spine (see Yamaguti's pl. 13 fig. 83) instead of two spines, and in the free segment of leg 5 having two spiniform setae.

L. chamarum may be most readily separated from these related species by its elongated pointed rostrum.

EXPLANATION OF THE FIGURES

All the figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn.

RÉSUMÉ

Description de deux espèces de Copépodes de la famille des Lichomolgidae, toutes deux associées à des Pélécypodes provenant de Nosi Bé, Madagascar. Les deux espèces sont *Gelastomolgus spondyli* n. gen., n. sp. (hôte *Spondylus varians*) et *Lichomolgus chamarum* n. sp. (hôte *Chama iostoma*).

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Cyclopoid Copepods of the Genus *Lichomolgus* Associated with Octocorals of the Family Nephtheidae in Madagascar

By Arthur G. Humes and Ju-Shey Ho [1]

Only one lichomolgid copepod, *Lichomolgus spinulifer* Humes and Frost, 1964, has been reported as an associate of nephtheid octocorals in Madagascar, where it lives on *Lemnalia* sp. This paper deals with six new species of *Lichomolgus* and with *L. spinulifer* washed from various species of Nephtheidae in the region of Nosy Bé in northwestern Madagascar.

All collections were made by A. G. Humes, those in 1960 during an expedition sponsored by the Academy of Natural Sciences of Philadelphia, and those in 1963–64 as part of the U.S. Program in Biology of the International Indian Ocean Expedition.

The study of the specimens has been aided by a grant (GB–5838) from the National Science Foundation of the United States.

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The abbreviations used are: A_1=first antenna, A_2=second antenna, L=labrum, MXPD=maxilliped, and P_1=leg 1.

All descriptions are based on type material. The measurements of the length of the body have been made in all cases from specimens in

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lactic acid and do not include the setae on the caudal rami. The lengths of the segments of the first antenna have been measured along their posterior nonsetiferous margins.

We are indebted to Mme. A. Tixier-Durivault of the Muséum National d'Histoire Naturelle, Paris, for the identifications of the octocorals collected in 1960, and to Dr. J. Verseveldt, Zwolle, The Netherlands, for the determinations of those collected in 1963–64.

The new copepods described in this paper comprise the following:

1. *Lichomolgus varirostratus*, new species—from *Dendronephthya mucronata* (Pütter), *D. regia* Verseveldt, *D. stocki* Verseveldt, and *D. köllikeri* Kükenthal.
2. *Lichomolgus exilipes*, new species—from the same four species of *Dendronephthya*.
3. *Lichomolgus gentilis*, new species—from *Dendronephthya mucronata* (Pütter), *D. stocki* Verseveldt, *D. köllikeri* Kükenthal, *Stereonephthya acaulis* Verseveldt, and *S. papyracea* Kükenthal.
4. *Lichomolgus fissisetiger*, new species—from *Stereonephthya acaulis* Verseveldt, *S. papyracea* Kükenthal, and *Lemnalia elegans* (May).
5. *Lichomolgus cuneipes*, new species—from *Stereonephthya acaulis* Verseveldt.
6. *Lichomolgus aculeatus*, new species—from *Nephthea aberrans* Verseveldt, *N. sphaerophora* Kükenthal, *N. crassa* Kükenthal, *N. tixierae* Verseveldt, and *Litophyton arboreum* Forskål.

The following new hosts are recorded for *Lichomolgus spinulifer* Humes and Frost, 1964:

Lemnalia flava May, *L. elegans* (May), *L. amabilis* Tixier-Durivault, *L. africana* (May), and *Paralemnalia thyrsoides* (Ehrenberg).

Family LICHOMOLGIDAE Kossmann, 1877

Genus *Lichomolgus* Thorell, 1860

Lichomolgus varirostratus, new species

FIGURES 1–31

TYPE MATERIAL.—133 ♀♀, 95 ♂♂, and 7 copepodids from a colony of *Dendronephthya mucronata* (Pütter), in 4 m, on the northeastern coast of Antany Mora, Isles Radama, Madagascar, 14°06′10″ S, 47°45′10″ E, collected Sept. 30, 1964. Holotype ♀, allotype, and 85 paratypes (50 ♀♀ and 35 ♂♂) deposited in the United States National Museum, the same number of paratypes in the Zoölogisch Museum,

Amsterdam, and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS.—From *Dendronephthya mucronata:* 168 ♀♀ and 118 ♂♂ from 6 colonies, in 1 m, off Ampombilava, Nosy Bé, Madagascar, Sept. 26, 1964; 7 ♀♀ and 8 ♂♂ from 1 colony, in 1 m, Tany Kely, a small island south of Nosy Bé, June 23, 1963; 38 ♀♀, 36 ♂♂, and 4 copepodids from 1 colony, in 2 m, northern end of Nosy Sakatia, near Nosy Bé, Aug. 19, 1963; and 3 ♀♀ and 1 ♂ from 1 colony, in 20 m, Tany Kely, Dec. 20, 1963. From *Dendronephthya regia* Verseveldt: 5 ♀♀ and 1 ♂ from 1 colony, in 40 m, Banc de Cinq Mètres, west of Nosy Bé, at about 13°23′39″ S, 48°04′00″ E, Aug. 19, 1964. From *Dendronephthya stocki* Verseveldt: 3 ♀♀ from 1 colony, in 20 m, Tany Kely, Dec. 20, 1963, and 4 ♀♀ and 2 ♂♂ from 1 colony, in 40 m, Banc de Cinq Mètres, Aug. 19, 1964. From *Dendronephthya köllikeri* Kükenthal: 3 ♀♀ and 9 ♂♂ from 1 colony, in 8 m, Nosy Ovy, Isles Radama, 13°59′ S, 47°46.5′ E, Sept. 30, 1964.

FEMALE.—Body (fig. 1) with moderately broad prosome. Length 0.83 mm (0.77–0.90 mm) and greatest width (near middle of cephalosome) 0.47 mm (0.43–0.49 mm), based on 10 specimens. Ratio of length to width of prosome 1.24:1. Segment of first leg separated dorsally and laterally from head by a transverse furrow; lateral areas of this segment rounded posteriorly and not expanded. Lateral areas of segment bearing leg 2 expanded, those of segment of leg 3 expanded and slightly truncated, and those of segment of leg 4 small and rounded.

Segment of leg 5 (fig. 2) about twice as wide as long, 65μ x 120μ. Ventrally between this segment and genital segment a slight intersegmental sclerite. Genital segment (fig. 2) a little longer than wide, 138μ x 118μ, in dorsal view expanded in its midregion, anterior and posterior to which the segment is constricted (anterior constricted area set off ventrally from rest of segment by a weak transverse line). Areas of attachment of egg sacs situated dorsolaterally on posterior part of expanded area. Each area (fig. 3) with 2 naked spiniform setae, both about 11μ in length, and a prominent unguiform process. Three postgenital segments 36μ x 68μ, 26μ x 63μ, and 50μ x 62μ, from anterior to posterior.

Caudal ramus (fig. 4) about as long as wide, its greatest dimensions being 25μ x 28μ when measured dorsally and 29μ x 28μ when measured ventrally. Of the usual 6 setae, outer lateral seta 48μ long, pedicellate dorsal seta 26μ, outermost distal seta 73μ, innermost distal seta 122μ, and the 2 long median terminal setae 208μ (outer) and 290μ (inner) and both inserted between dorsal (unornamented) and ventral (with marginal rows of spinules) flaps. All these setae naked except

innermost distal one, which has a row of hairs along inner edge. A few surficial hairs on ramus.

Dorsal surface of prosome and urosome with minute hairs. Ratio of length of prosome to that of urosome 1.9:1.

Most ovigerous females observed carrying clusters of eggs, as in figure 1, rather than complete sacs; egg sacs delicate and easily broken in preserved specimens. One of the few intact egg sacs (fig. 5) 473μ x 180μ, elongated, reaching nearly to ends of ramal setae, with each egg about 50μ–55μ in diameter.

Rostral area (fig. 6) broadly rounded posteroventrally.

First antenna (fig. 7) 7-segmented, 360μ in length, with third segment showing ventrally a proximal sclerotized area suggesting an intercalary segment. Lengths of segments: 39μ (66μ along anterior margin), 98μ, 26μ, 50μ, 54μ, 37μ, and 28μ respectively. Formula for armature: 4, 13, 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All setae naked except for 2 delicately plumose on last segment.

Second antenna (fig. 8) 4-segmented, with last segment moderately elongated, 91μ along its outer edge, 52μ along its inner edge, and 26μ wide. Each of first 2 segments with a small inner seta and surficial spinules as indicated in the figure, third segment with 3 setae (2 subequal and much longer than third), and last segment with 7 elements: 5 short hyaline elements and 2 long slightly unequal recurved claws 101μ and 91μ (measured along greatest axis). All setae naked.

Labrum (fig. 9) with 2 relatively short broadly rounded posteroventral lobes.

Mandible (fig. 10) with basal region distal to constriction bearing on its convex margin a row of spinules followed by a serrated fringe and on its concave margin a row of slender spinules; flagellum elongated with lateral spinules. Paragnath (fig. 11) a small hairy lobe. First maxilla (fig. 12) an elongated segment bearing 3 terminal setae. Second maxilla (fig. 13) 2-segmented, large first segment unarmed, second segment with a small setule on proximal outer margin, a surficial posterior seta barbed along one edge, an inner distal spine with prominent lateral spinules, and the segment produced distally to form a lash with dentiform spines along one edge proximally and fine bilateral spinulation distally. Maxilliped (fig. 14) 3-segmented, first segment with surficial spinules, second with 2 unequal barbed setae and an inner marginal row of small spinules, and third with 2 terminal spiniform barbed setae (producing a bifurcated appearance) and a naked setule. (Articulations of these 2 setae obscure, with inner one perhaps a process rather than an actual seta.)

Area between maxillipeds and first pair of legs (fig. 15) not protuberant; a sclerotized line between bases of maxillipeds.

Legs 1–4 (figs. 16–19) with trimerous rami except for 2-segmented endopod of leg 4. Armature of legs as follows (Roman numerals =spines, Arabic numerals=setae):

P_1	protopod	0–1	1–0	exp	I–0	I–1	III,I,4
				end	0–1	0–1	I,5
P_2	protopod	0–1	1–0	exp	I–0	I–1	III,I,5
				end	0–1	0–2	I,II,3
P_3	protopod	0–1	1–0	exp	I–0	I–1	III,I,5
				end	0–1	0–2	I,II,2
P_4	protopod	0–1	1–0	exp	I–0	I–1	II,I,5
				end	0–I	II	

Inner seta on coxa of legs 1–3 long and plumose, but in leg 4 very short (8μ) and naked. Row of hairs present on inner margin of basis in all 4 legs. In leg 1 spinules along proximal margins of outer spines of exopod more prominent than those on distal margins. Endopod of leg 4 shorter than exopod. First segment 49μ x 34μ (including terminal spinous processes) bearing a distal inner barbed spine 32μ long instead of a seta. Second segment 75μ x 29μ (including processes) bearing 2 terminal unequal barbed spines 29μ (outer) and 51μ (inner). Both segments with outer margins haired, and second segment with short hairs along proximal inner margin and a row of minute spinules near insertions of terminal spines.

Leg 5 (fig. 20) with free segment elongated and slightly arcuate, 120μ x 36μ in greatest dimensions, but wider proximally than distally; outer convex surface covered with pointed scales (fig. 21); bearing 2 terminal naked setae 42μ and 65μ in length. Naked seta on body near free segment 52μ, with a group of spinules near its insertion.

Leg 6 probably represented by the 2 spiniform elements near areas of attachment of each egg sac (see fig. 3).

Color in life in transmitted light slightly opaque; eye red, ovary and egg sacs gray.

MALE.—Body (fig. 22) resembling in general form that of female. Length 0.73 mm (0.69–0.75 mm) and greatest width 0.32 mm (0.29–0.33 mm), based on 10 specimens. Ratio of length to width of prosome 1.37:1.

Segment of leg 5 (fig. 23) 41μ x 72μ. Genital segment about as long as wide, 169μ x 160μ, in dorsal view with its lateral borders rounded. No intersegmental sclerite ventrally between these 2 segments. Four postgenital segments 22μ x 52μ, 21μ x 48μ, 14μ x 45μ, and 33μ x 48μ respectively.

Caudal ramus (fig. 23) relatively slightly longer than in female, 24μ x 22μ when measured dorsally, 27μ x 22μ when measured ventrally. Innermost terminal seta with row of hairlike spinules along both margins proximally.

Surface of prosome and urosome with minute hairs as in female. Ratio of length of prosome to that of urosome 1.48:1.

Rostral area (fig. 24) angular, with a minute median posteroventral knob.

First antenna resembling that of female but with 2 aesthetes about 100μ long added on segment 2 and another such aesthete on segment 4 (at points indicated by arrows in fig. 7), so that formula is 4, 13+2 aesthetes, 6, 3+1 aesthete, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. Second antenna (fig. 25) resembling that of female, but last segment relatively longer, 99μ along outer edge, 68μ along inner edge, and 21μ wide.

Labrum, mandible, paragnath, first maxilla, and second maxilla like those in female. Maxilliped (fig. 26) slender and 4-segmented (assuming that proximal part of claw represents fourth segment). First segment unornamented. Second segment bearing on medial surface 2 naked setae and 3 rows of spinules, a single row extending the length of segment, other 2 rows close together and restricted to region distal to setae. Third segment very small and unarmed. Claw slender, 185μ long (measured along its axis), with narrow terminal lamella, slight fringe along its distal concave surface, and 2 very unequal setae near its base, one on postero-inner surface 86μ long and finely barbed at its tip, other on anterior surface only 5μ and naked. Claw showing a suggestion of division about midway.

Area between maxillipeds and first pair of legs resembling that of female.

Legs 1–4 segmented as in female and with same spine and setal formula, except for endopod of leg 1 (fig. 27), which has arrangement of 0–1; 0–1; I,I,4. This endopod geniculate, with second and third segments set at an angle to one another. First two segments without outer distal spinous processes. Third segment elongated, nearly as long as first two combined; with 2 terminal spines having strong lateral spinules; a prominent minutely spinose process near insertion of inner of these spines. Last segment of endopod of leg 2 (fig. 28) with 2 of terminal spinous processes larger than in female and bearing numerous minute spines. Legs 3 and 4 like those in female.

Leg 5 (fig. 29) with elongated slender straight free segment, 33μ x 9μ, with nearly parallel sides in dorsal view, bearing a few surficial scales and 2 terminal elements, an outer naked seta 30μ long and an inner spiniform seta 20μ long with coarse short lateral spines. No spinules on body near insertion of free segment.

Leg 6 (fig. 30) a posterolateral flap on ventral surface of genital segment bearing 2 naked setae 22μ and 27μ long.

Spermatophore (fig. 31), attached to female, elongated, 172μ x 78μ without neck. Spermatophores readily extruded from male when placed in lactic acid, as shown in figure 30.

Color in life resembling that of female.

ETYMOLOGY.—The specific name *varirostratus*, from Latin *varius*=different and *rostratus*=furnished with a beak, alludes to the different shape of the rostrum in the two sexes of this species.

COMPARISON WITH RELATED SPECIES.—Two features of *L. varirostratus* serve to distinguish it from all other known species in the genus, namely, the presence of a spine instead of a seta on the first segment of the endopod of leg 4 and the two unusually long terminal claws on the second antenna. In only one other species, *L. anomalus* A. Scott, 1909, does the endopod of leg 4 appear to have the formula 0–I, II (based on Scott's fig. 15, pl. LXVII); the usual formula in *Lichomolgus* is 0–1, II. Scott's species differs from the new species, however, in having only one claw on the second antenna. The general structure of the endopod in leg 1 of the male of *L. varirostratus* resembles rather closely that of *L. anomalus*. Scott noted that this geniculate form "is quite distinct from what is usually found in males of this genus."

Two unusually long terminal claws occur on the second antenna in four species—*L. canui* Sars, 1917; *L. ieversi* Thompson and A. Scott, 1903; *L. marginatus* Thorell, 1860; and *L. tenuicornis* Brady, 1910—but in all of these species the formula for the endopod of leg 4 is 0–1, II, thus readily separating them from the new species from Madagascar.

Lichomolgus exilipes, new species

FIGURES 32–55

TYPE MATERIAL.—31 ♀♀ and 18 ♂♂ from a colony of *Dendronephthya mucronata* (Pütter), in 4 m, on the northeastern coast of Antany Mora, Isles Radama, Madagascar, 14°06′10″S, 47°45′10″E, collected Sept. 30, 1964. Holotype ♀, allotype, and 35 paratypes (25 ♀♀ and 10 ♂♂) deposited in the United States National Museum, and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS.—From *Dendronephthya mucronata:* 15 ♀♀ and 8 ♂♂ from 6 colonies, in 1 m, off Ampombilava, Nosy Bé, Madagascar, Sept. 26, 1964, and 6 ♂♂ from 1 colony, in 1 m, Tany Kely, a small island south of Nosy Bé, June 23, 1963. From *Dendronephthya regia* Verseveldt: 2 ♀♀ from 1 colony, in 40 m, Banc de Cinq Mètres, west of Nosy Bé, at about 13°23′30″S, 48°04′00″E, Aug. 19, 1964. From *Dendronephthya stocki* Verseveldt: 1 ♀ and 6 ♂♂ from 1 colony,

in 40 m, Banc de Cinq Mètres, Aug. 19, 1964. From *Dendronephthya köllikeri* Kükenthal: 7 ♀♀ and 12 ♂♂ from 1 colony, in 8 m, Nosy Ovy, Isles Radama, 13°59'S, 47°46.5'E, Sept. 30, 1964.

FEMALE.—Body (fig. 32) a little less broadened than in *L. varirostratus*. Length 0.99 mm (0.91–1.09 mm) and greatest width 0.50 mm (0.46–0.52 mm), based on 10 specimens. Ratio of length to width of prosome 1.3:1. Segment of first leg separated dorsally and laterally from head by a furrow. Lateral areas of segments of legs 1–4 shaped as in figure.

Segment of leg 5 measuring 73μ x 151μ. Between this segment and genital segment a slight ventral intersegmental sclerite. Genital segment (fig. 33) slightly longer than wide, 172μ x 156μ, in dorsal view constricted anteriorly and posteriorly but expanded in midregion. A pair of crescentic sclerotized ridges on anterior dorsal surface. Areas of attachment of egg sacs located dorsolaterally at level of expanded part of segment. Each area (fig. 34) bearing 2 naked setae 11μ and 20μ in length, with a small digitiform process between them. Three postgenital segments 34μ x 81μ, 23μ x 68μ, and 34μ x 70μ, from anterior to posterior.

Caudal ramus (fig. 35) only slightly longer than wide, its greatest dimensions being 30μ x 25μ when measured dorsally and 33μ x 25μ when measured ventrally. Outer lateral seta 109μ and naked, pedicellate dorsal seta 22μ and naked, outermost distal seta 180μ and naked, innermost distal seta 283μ with inner lateral spinules, and the 2 long median terminal setae 418μ (outer) and 550μ (inner), both inserted between dorsal (unornamented) and ventral (with marginal row of spinules) flaps, and bearing lateral spinules in their midregions. A delicate setule on proximal outer edge of ramus, and a few surficial hairs dorsally.

Dorsal surface of prosome and urosome with minute hairs. Ratio of length of prosome to that of urosome 2.24:1.

Egg sacs in most ovigerous females observed broken, as in figure 32. One intact egg sac measuring 430μ x 176μ, elongated, reaching well beyond ends of caudal rami, and containing many small eggs, each about 40μ in diameter.

Rostral area (fig. 36) linguiform, rounded posteroventrally.

First antenna (fig. 37) resembling in general form that of *L. varirostratus*, with same segmentation and formula for armature, but longer, 480μ. Lengths of segments: 36μ (77μ along anterior margin), 133μ, 32μ, 70μ, 75μ, 56μ, and 36μ respectively. All setae naked.

Second antenna (fig. 38) also resembling that of *L. varirostratus*, with similar segmentation and armature. Last segment 135μ along its outer edge, 86μ along its inner edge, and 31μ wide. Three setae on

third segment 42μ, 21μ, and 42μ from proximal to distal, with distalmost spiniform and minutely barbed along one edge. Both claws about 135μ in length.

Labrum (fig. 39) with 2 posteroventral lobes less broadly rounded than in *L. varirostratus*.

Mandible (fig. 40) resembling that of *L. varirostratus*, but with distinct constriction separating basal region into two parts, convex margin of distal part bearing spinules and projected distally as a short blunt process. Paragnath a small lobe bearing hairs. First maxilla (fig. 41) bearing a small subterminal element in addition to 3 terminal ones. Second maxilla (fig. 42) and maxilliped (fig. 43) segmented and armed as in *L. varirostratus*, but slight differences in ornamentation of elements as shown in figures.

Area between maxillipeds and first pair of legs (fig. 44) not protuberant; a sclerotized line between bases of maxillipeds.

Legs 1–4 (figs. 45–48) segmented as in *L. varirostratus*, with same spine and setal formula. Inner seta on coxa of leg 4 short (12μ) and naked. Inner margin of basis of leg 4 without hairs. In leg 1 spinules along proximal margins of outer spines of exopod longer and coarser than those on distal margins. Endopod of leg 4 only slightly shorter than exopod. First segment 56μ x 35μ (including terminal spinous processes), bearing an inner distal minutely barbed spine 43μ long. Second segment 111μ x 30μ (greatest dimensions including processes), bearing 2 terminal barbed spines 39μ (outer) and 77μ (inner); a few minute spinules along inner margin of segment.

Leg 5 (fig. 49) with free segment much elongated, slender, and slightly arcuate, 172μ x 23μ (width 35μ at level of proximal inner expansion). Outer convex surface bearing pointed scales. Two terminal naked setae 122μ and 190μ in length. Naked seta on body near free segment 55μ, with a few minute spinules not far from its insertion.

Leg 6 probably represented by the 2 setae near areas of attachment of each egg sac (see fig. 34).

Color in life in transmitted light as in *L. varirostratus*.

MALE.—Body (fig. 50) resembling that of female in general form. Length 0.78 mm (0.73–0.81 mm) and greatest width 0.34 mm (0.30–0.36 mm), based on 10 specimens. Ratio of length to width of prosome 1.4:1.

Segment of leg 5 measuring 36μ x 101μ. Genital segment (fig. 51) about as long as wide, 221μ x 216μ. No ventral intersegmental sclerite between these segments. Four postgenital segments 22μ x 56μ, 17μ x 55μ, 11μ x 51μ, and 24μ x 56μ respectively.

Caudal ramus (fig. 51) somewhat shorter than in female, 22μ x 24μ dorsally, 23μ x 24μ ventrally. Innermost terminal seta with row of

spinules on both sides. Outermost terminal seta with inner spinules proximally.

Surfaces of prosome and urosome with minute hairs as in female. Ratio of length of prosome to that of urosome 1.43:1.

Rostral area as in female.

First antenna resembling that of female, but with 2 long aesthetes added on second segment and another aesthete on fourth segment, so that formula is same as for male of *L. varirostratus*.

Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla similar to those in female. Maxilliped (fig. 52) less slender than in *L. varirostratus*, but segmented and armed similarly. Claw slender and 170μ along its axis; proximal region of claw slightly swollen and faintly striated.

Area between maxilliped and first pair of legs as in female.

Legs 1–4 segmented as in *L. varirostratus*, with spine and setal formula as in male of that species. Endopod of leg 1 (fig. 53) slightly geniculate. Third segment elongated, with outer terminal spine straight, having lateral spinules and hyaline tip, inner terminal spine bent, with strong spinules along its inner distal edge; spinous process between these 2 spines enlarged and finely spinose. No obvious sexual dimorphism in legs 2–4.

Leg 5 (fig. 54) with a very elongated slender straight free segment, 55μ x 11μ, bearing on its outer surface a few scales and terminally an outer naked seta 56μ long and an inner spine 29μ long with short lateral spinules. No spinules on body near insertion of free segment.

Leg 6 similar to that in *L. varirostratus*, with 2 naked setae 41μ and 78μ in length.

Spermatophore (fig. 55), attached to female, elongated, 174μ x 91μ, not including neck.

Color in life as in *L. varirostratus*.

ETYMOLOGY.—The specific name *exilipes*, from Latin *exilis*=slender and *pes*=foot, refers to the elongated slender form of leg 5 in both sexes of this species.

COMPARISON WITH RELATED SPECIES.—Like *L. varirostratus*, this species may be distinguished from all other known species in the genus on the basis of a combination of two characters: the spine (instead of a seta) on the first segment of the endopod of leg 4 and the two unusually long terminal claws on the second antenna.

Lichomolgus exilipes may readily be separated from *L. varirostratus* by the form of the rostrum, the presence of lateral spinules on the two long setae on the caudal rami, the form of the fifth legs and the genital segment in the female, and the structure of the two spines on the last segment of the endopod of leg 1 in the male.

Lichomolgus gentilis, new species

FIGURES 56–69

TYPE MATERIAL.—20 ♀♀ and 28 ♂♂ from a colony of *Dendronephthya mucronata* (Pütter), in 4 m, on the northeastern coast of Antany Mora, Isles Radama, Madagascar, 14°06′10″S, 47°45′10″E, collected Sept. 30, 1964. Holotype ♀, allotype, and 36 paratypes (14 ♀♀ and 22 ♂♂) deposited in the United States National Museum and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS.—From *Dendronephthya mucronata:* 4 ♀♀ from 6 colonies, in 1 m, off Ampombilava, Nosy Bé, Madagascar, Sept. 26, 1964; 10 ♀♀ and 19 ♂♂ from 1 colony, in 1 m, Tany Kely, a small island south of Nosy Bé, June 23, 1963; 2 ♀♀ from 1 colony, in 2 m, northern end of Nosy Sakatia, near Nosy Bé, Aug. 19, 1963; and 2 ♀♀ and 1 ♂ from 1 colony, in 20 m, Tany Kely, Dec. 20, 1963. From *Dendronephthya köllikeri* Kükenthal: 15 ♀♀ and 19 ♂♂ from 1 colony, in 8 m, Nosy Ovy, Isles Radama, 13°59′S, 47°46.5′E, Sept. 30, 1964. From *Dendronephthya stocki* Verseveldt: 1 ♂ from 1 colony, in 20 m, Tany Kely, Dec. 20, 1963. From *Stereonephthya acaulis* Verseveldt: 1 ♀, 2 ♂♂, and 45 copepodids from 1 colony, in 20 m, Tany Kely, Dec. 20, 1963; 5 ♀♀, 22 ♂♂, and 1 copepodid from 1 colony, in 10 m, Tany Kely, Aug. 21, 1964; 11 ♀♀ and 8 ♂♂ from 1 colony, in 1 m, off Ampombilava, Nosy Bé, Sept. 26, 1964; and 15 ♀♀, 9 ♂♂, and 1 copepodid from 1 colony, in 2 m, Andraikarekabe, Nosy Komba, near Nosy Bé, Oct. 9, 1964. From *Stereonephthya papyracea* Kükenthal: 39 ♀♀ and 52 ♂♂ from 1 colony, in 6 m, Tany Kely, Aug. 26, 1963.

FEMALE.—Body (fig. 56) with moderately broad prosome. Length 0.91 mm (0.82–1.03 mm) and greatest width 0.47 mm (0.45–0.49 mm), based on 10 specimens. Ratio of length to width of prosome 1.28:1.

Segment of leg 5 measuring 52μ x 159μ. Between this segment and genital segment no ventral intersegmental sclerite visible. Genital segment (fig. 57) nearly as long as wide, 148μ x 159μ, in dorsal view expanded in its anterior three-fourths but constricted posteriorly. Areas of attachment of egg sacs located dorsolaterally on posterior part of expanded region. Each area (fig. 58) with a slender naked seta 13μ long, a spiniform unilaterally barbed seta 18μ long, and an adjacent slender setiform process. Three postgenital segments 26μ x 86μ, 20μ x 82μ, and 25μ x 77μ from anterior to posterior.

Caudal ramus (fig. 57) a little shorter than wide, its greatest dimensions being 25μ x 32μ when measured dorsally and 27μ x 32μ when measured ventrally. Outer lateral seta 143μ long and naked, pedicellate dorsal seta 39μ and naked, outermost distal seta 235μ and naked, innermost distal seta 352μ with row of spinules along inner edge, and the 2 long median terminal setae 517μ (outer) and 583μ (inner), both inserted between dorsal (unornamented) and

ventral (with marginal row of spinules) flaps, and both with strong coarse lateral spinules in midregion (these spinules much stronger than in *L. exilipes*).

Ratio of length of prosome to that of urosome 2.5:1.

Most ovigerous females observed carrying only clusters of eggs as in figure 56. One of few intact egg sacs measuring 462μ x 198μ, elongated oval, reaching far beyond caudal rami, with each egg about 44μ in diameter.

Rostral area and first antenna (453μ long) resembling those of *L. exilipes*. Second antenna (fig. 59) formed in general like that of *L. exilipes*, but 3 elements on third segment 35μ, 24μ, and 25μ from proximal to distal. Last segment 130μ along its outer edge, 83μ along its inner edge, and 31μ wide. Two terminal claws different in form and length, one being slender and 143μ along its axis, other stout and 127μ. (Apparently some variation in lengths of claws, with one female 153μ and 117μ on one side and 146μ and 130μ on other. In one female from *Stereonephthya acaulis* 120μ and 99μ, and in another 125μ and 107μ. In all cases, however, longer claw slender, shorter one stout.)

Labrum as in *L. exilipes*. Mandible (fig. 60) without blunt process on convex margin of basal region as in *L. exilipes*. Paragnath, first maxilla, and second maxilla similar to those in *L. exilipes*. Maxilliped (fig. 61) differing only slightly from that species.

Area between maxillipeds and first pair of legs not protuberant, with a sclerotized line connecting bases of maxillipeds.

Legs 1–4 segmented as in 2 previous species, with same spine and setal formula. Inner seta on coxa of leg 4 short (10μ) and naked. Inner margin of basis of leg 4 without hairs. In leg 1 (fig. 62) and leg 2 spinules along proximal margins of outer spines of exopod longer and stouter than those on distal margins. Endopod of leg 4 (fig. 63) shorter than exopod. First segment 55μ x 34μ (including terminal spinous processes), bearing an inner distal finely barbed spine 35μ long. Second segment 99μ x 34μ (greatest dimensions including processes), bearing 2 terminal spines, outer 44μ and finely barbed, inner 79μ with lateral spinules; a row of long hairs along proximal two-thirds of inner margin of segment.

Leg 5 (fig. 64) with elongated free segment, 143μ x 20μ (width taken at level of proximal inner expansion). Outer convex surface with pointed scales. Two terminal naked setae 99μ and 148μ in length. Seta on body near insertion of free segment 40μ long and slightly plumose; a few small spinules near this seta.

Leg 6 probably represented by the 2 setae near areas of attachment of each egg sac (see fig. 58).

Color in life in transmitted light as in 2 previous species.

MALE.—Body (fig. 65) resembling that of female in general aspect. Length 0.72 mm (0.69–0.77 mm) and greatest width 0.34 mm (0.32–0.36 mm), based on 10 specimens. Ratio of length to width of prosome 1.36:1.

Segment of leg 5 measuring 39μ x 104μ. Genital segment (fig. 66) as long as wide, 200μ x 203μ. No ventral intersegmental sclerite between these segments. Four postgenital segments 15μ x 61μ, 17μ x 57μ, 12μ x 56μ, and 22μ x 58μ respectively.

Caudal ramus as in female, but proportions slightly different, 20μ x 24μ dorsally, 27μ x 24μ ventrally. As in *L. exilipes*, outermost terminal seta with inner spinules proximally and innermost terminal seta with row of spinules on both sides.

Ratio of length of prosome to that of urosome 1.7:1.

Rostral area as in female. First antenna similar to that of female, but with 3 aesthetes added (length of proximalmost=130μ) so that formula is same as for males of 2 previous species. Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla like those of female. Maxilliped (fig. 67) with general form similar to *L. exilipes*, but ornamentation of major setae slightly different. Claw slender and 172μ along its axis.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented as in 2 previous species, with spine and setal formula as in males of those species. Endopod of leg 1 (fig. 68) only slightly geniculate. Third segment moderately elongated, with outer terminal spine straight, having lateral spinules and small hyaline tip, inner terminal spine slightly bent (not as strongly so as in *L. exilipes*) with moderately strong spinules along its inner distal edge; spinous process between these 2 spines as in *L. exilipes*. No obvious sexual dimorphism in legs 2–4, except that endopod of leg 4 (fig. 69) has slightly different proportions: first segment 33μ x 25μ, with spine 25μ, second segment 70μ x 22μ (more elongated than in female, ratio 3.2:1 instead of 2.9:1 as in that sex), with 2 terminal spines 31μ and 61μ.

Leg 5 (fig. 66) with elongated free segment, 57μ x 11μ, without pronounced proximal inner expansion, bearing on its outer surface a few scales and terminally an outer naked seta 71μ and an inner barbed spine 19μ. No spinules on body near insertion of free segment.

Leg 6 similar to those in 2 previous species, with 2 naked setae 50μ and 82μ in length.

Spermatophore, attached to female, as in *L. exilipes*.

Color in life as in 2 previous species.

ETYMOLOGY.—The specific name *gentilis*, from Latin=belonging to the same gens or clan, alludes to the close relationship of this species with *L. exilipes*.

COMPARISON WITH RELATED SPECIES.—Like *L. varirostratus* and *L. exilipes* this species may be distinguished from all other members of the genus by the combination of two characters: the spine (instead of a seta) on the first segment of the endopod of leg 4 and the two unusually long terminal claws on the second antenna.

Lichomolgus gentilis may be readily separated from *L. varirostratus* by the form of the rostrum, the presence of lateral spinules on the two long setae on the caudal rami, the form of the genital segment in the female, and the structure of the two spines on the last segment of the endopod of leg 1 in the male.

From *L. exilipes* the new species may be separated by the coarser lateral spinules on the two long setae on the caudal rami, the more unequal nature of the two claws on the second antenna, the lack of a blunt process on the inner margin of the mandible, and the form of the fifth legs and the genital segment in the female.

Lichomolgus fissisetiger, new species

FIGURES 70–83

TYPE MATERIAL.—24 ♀♀ and 20 ♂♂ from a colony of *Stereonephthya acaulis* Verseveldt, in 2 m, Ambafaho, Nosy Bé, Madagascar, collected Sept. 25, 1964. Holotype ♀, allotype, and 34 paratypes (18 ♀♀ and 16 ♂♂) deposited in the United States National Museum, and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS.—From *Stereonephthya acaulis:* 45 ♀♀ and 89 ♂♂ from 1 colony, in 10 m, Tany Kely, a small island south of Nosy Bé, Aug. 21, 1964; 22 ♀♀, 9 ♂♂, and 2 copepodids from 1 colony, in 1 m, off Ampombilava, Nosy Bé, Sept. 26, 1964; and 9 ♀♀ and 16 ♂♂ from 1 colony, in 2 m, Andraikarekabe, Nosy Komba, near Nosy Bé, Oct. 9, 1964. From *Stereonephthya papyracea* Kükenthal: 53 ♀♀, 80 ♂♂, and 92 copepodids from 1 colony, in 6 m, Tany Kely, Aug. 26, 1963. From *Lemnalia elegans* (May): 3 ♀♀ from 1 colony, in 1 m, Pte. Lokobe, Nosy Bé, Oct. 16, 1960.

FEMALE.—Body (fig. 70) similar to that of *L. exilipes* and *L. gentilis.* Length 0.99 mm (0.92–1.03 mm) and greatest width 0.49 mm (0.46–0.51 mm), based on 10 specimens. Ratio of length to width of prosome 1.5:1.

Segment of leg 5 measuring 65μ x 143μ. Between this segment and genital segment a small ventral intersegmental sclerite. Genital segment (fig. 71) slightly shorter than wide, 127μ x 143μ, in dorsal view with its lateral borders rounded. Areas of attachment of egg sacs located almost laterally (only slightly dorsally) in posterior half of segment. Each area (fig. 72) with 2 small naked setae about 11μ long and an adjacent small unguiform process. Three postgenital segments 26μ x 82μ, 21μ x 73μ, and 26μ x 70μ from anterior to posterior.

Caudal ramus (fig. 73) shorter than wide, its greatest dimensions being 20μ x 28μ when measured dorsally, 21μ x 28μ when measured ventrally. Outer lateral seta 83μ long and naked, pedicellate dorsal seta 25μ and naked, outermost distal seta 117μ with proximal inner spinules, innermost distal seta 208μ with spinules along both sides, and the 2 long median terminal setae 440μ (outer) and 590μ (inner), both inserted between dorsal (unornamented) and ventral (with marginal row of spinules) flaps, and both with lateral spinules in midregion (these spinules not as strong as in *L. gentilis*, and more like those of *L. exilipes*).

Ratio of length of prosome to that of urosome 2.9:1.

Egg-sac (fig. 70) 550μ x 209μ, elongated, reaching far beyond ends of caudal rami, containing many eggs, each about 45μ in diameter.

Rostral area and first antenna (428μ long) similar to those of *L. exilipes* and *L. gentilis*. Second antenna (fig. 74) resembling that of *L. gentilis*, but differing in details. Three naked elements on third segment 35μ, 21μ, and 20μ in length from proximal to distal. Last segment 94μ along outer margin, 60μ along inner margin, and 25μ wide. Two terminal claws unequal, not as long as in *L. gentilis*, one 92μ along its axis and slender, the other 77μ and stouter.

Labrum as in *L. exilipes* and *L. gentilis*. Mandible (fig. 75) similar to that in *L. gentilis*, but showing an even more pronounced constriction of basal region. Paragnath and first maxilla as in *L. exilipes* and *L. gentilis*. Second maxilla (fig. 76) resembling *L. exilipes* and *L. gentilis*, but spinulation of lash and distal seta slightly different. Maxilliped as in *L. exilipes* and *L. gentilis*.

Area between maxillipeds and first pair of legs not protuberant, with a sclerotized line between bases of maxillipeds.

Legs 1–4 segmented as in 3 previous species, with same spine and setal formula. Leg 1 similar to that of *L. exilipes* and *L. gentilis*. Legs 2 and 3 like those of *L. exilipes*. Leg 4 (fig. 77) resembling that of *L. gentilis*. Endopod shorter than exopod. First segment 42μ x 32μ (including terminal spinous processes), with inner distal minutely barbed spine 31μ long. Second segment 90μ x 29μ (greatest dimensions including processes), outer terminal spine 34μ with finely barbed fringe, inner 72μ with more coarsely spinulose fringe. Proximal inner margin of this segment with row of very short spinules.

Leg 5 (fig. 78) with elongated free segment having prominent inner basal expansion. Greatest length 148μ, width 42μ at expansion, 23μ immediately distal to expansion, and 16μ near tip. Outer surface with narrow scalelike spines. Two terminal naked setae 72μ and 110μ (the latter with a narrow membrane in its midregion). Seta on body near insertion of free segment about 50μ long and slightly plumose; a few small spinules near this seta.

Leg 6 probably represented by the 2 setae near areas of attachment of each egg sac (see fig. 72).

Color in life in transmitted light somewhat opaque, eye red, ovary dark gray, egg sacs gray.

MALE.—Body (fig. 79) resembling that of female in general form. Length 0.78 mm (0.74–0.81 mm) and greatest width 0.29 mm (0.27–0.30 mm), based on 10 specimens. Ratio of length to width of prosome 1.48:1.

Segment of leg 5 measuring 36μ x 91μ. Genital segment (fig. 80) as long as wide, 185μ x 185μ. No ventral intersegmental sclerite between these segments. Four postgenital segments 17μ x 50μ, 14μ x 52μ, 12μ x 50μ, and 19μ x 52μ respectively.

Caudal ramus resembling that of female but smaller, 14μ x 22μ dorsally, 18μ x 22μ ventrally.

Ratio of length of prosome to that of urosome 1.62:1.

Rostral area as in female. First antenna similar to that of female, but with 3 aesthetes added as in 3 previous species, so that formula is same as for those males. Aesthetes much longer than in preceding species, proximalmost one 240μ in length. Second antenna, labrum, mandible, paragnath, first maxilla, and second maxilla like those in female. Maxilliped resembling in general form that of *L. gentilis*, but one of setae on inner surface of second segment terminating in several pointed spiniform elements (fig. 81). Claw 133μ in length (measured along its axis).

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented as in 3 previous species, with spine and setal formula as in those males. Endopod of leg 1 (fig. 82) only slightly geniculate. Third segment resembling that of *L. gentilis*. Legs 2–4 as in female.

Leg 5 (see fig. 80) resembling that of *L. exilipes*, with free segment 52μ x 9μ, terminally with inner spine 18μ and barbed, outer seta 68μ and naked.

Leg 6 (fig. 83) similar to that in 3 preceding species, with 2 naked setae 44μ and 66μ in length.

Spermatophore not observed.

Color in life in transmitted light more translucid than in female, eye red, genital segment hyaline.

ETYMOLOGY.—The specific name *fissisetiger*, from Latin *fissus*=split and *setiger*=bearing a seta, refers to the nature of the seta on the second segment of the maxilliped in the male of this species.

COMPARISON WITH RELATED SPECIES.—Like the three preceding species *L. fissisetiger* may be distinguished from all other members of the genus by the combination of two characters: the spine (instead

of a seta) on the first segment of the endopod of leg 4 and the two unusually long terminal claws on the second antenna.

Lichomolgus fissisetiger may be separated from *L. varirostratus* by the form of the rostrum, the presence of lateral spinules on the two long setae of the caudal rami, the form of the genital segment and leg 5 in the female, the long aesthetes on the first antenna of the male, and the structure of the two spines on the last segment of the endopod of leg 1 in the male.

It may be distinguished from *L. exilipes* by the form of the genital segment and leg 5 in the female, the more unequal nature of the two claws on the second antenna, the lack of a blunt process on the inner margin of the mandible, the peculiar split seta on the second segment of the maxilliped in the male, and the long aesthetes on the first antenna of the male.

From *L. gentilis* the new species may be distinguished by the form of the genital segment and leg 5 in the female, the pronounced constriction of the basal region of the mandible, the split seta on the second segment of the maxilliped in the male, and the long aesthetes on the first antenna of the male.

Lichomolgus cuneipes, new species

FIGURES 84–96

TYPE MATERIAL.—39 ♀♀ and 18 ♂♂ from a colony of *Stereonephthya acaulis* Verseveldt, in 1 m, off Ampombilava, Nosy Bé, Madagascar, collected Sept. 26, 1964. Holotype ♀, allotype, and 46 paratypes (32 ♀♀ and 14 ♂♂) deposited in the United States National Museum, and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS (all from *Stereonephthya acaulis*).—6 ♀♀ and 3 ♂♂ from 1 colony, in 2 m, Ambafaho, Nosy Bé, Sept. 25, 1964; 9 ♀♀ and 10 ♂♂ from 1 colony, in 10 m, Tany Kely, a small island south of Nosy Bé, Aug. 21, 1964; and 11 ♀♀ and 9 ♂♂ from 1 colony, in 2 m, Andraikarekabe, Nosy Komba, near Nosy Bé, Oct. 9, 1964.

FEMALE.—Body (fig. 84) resembling that of *L. fissisetiger*. Length 0.94 mm (0.89–0.98 mm) and greatest width 0.48 mm (0.45–0.49 mm), based on 10 specimens. Ratio of length to width of prosome 1.56:1.

Segment of leg 5 measuring 65μ x 138μ. Between this segment and genital segment a small ventral intersegmental sclerite. Genital segment (fig. 85) about as long as wide, 125μ x 120μ, in dorsal view with its lateral borders somewhat irregular. Areas of attachment of egg sacs located dorsolaterally in middle of segment. Each area (fig. 86) with 2 small naked setae about 8μ long with a pointed sclerotized process between them. Three postgenital segments 26μ x 75μ, 21μ x 71μ, and 26μ x 71μ from anterior to posterior.

Caudal ramus (fig. 87) shorter than wide, its greatest dimensions being 22μ x 30μ when measured dorsally, 24μ x 30μ when measured ventrally. Outer lateral seta 75μ long, pedicellate dorsal seta 28μ, outermost distal seta 112μ, innermost distal seta 203μ, and the 2 long median terminal setae 380μ (outer) and 495μ (inner), both inserted between dorsal and ventral flaps as in previous species. All setae naked.

Ratio of length of prosome to that of urosome 2.78:1.

Egg sac (fig. 84) 462μ x 187μ, elongated, reaching far beyond ends of caudal rami, containing many eggs, each about 45μ in diameter.

Rostral area (fig. 88) broadly rounded posteroventrally.

First antenna (410μ long) similar to that of *L. exilipes*, the segments 31μ (61μ along anterior edge), 133μ, 28μ, 57μ, 56μ, 42μ, and 32μ in length respectively. Second antenna (fig. 89) with 4 segments having same formula for armature as in previous species. Three elements on third segment consisting of 2 naked setae 22μ and 23μ and a spiniform seta 11μ long and very finely spinulose. Last segment 74μ along outer margin, 40μ along inner margin, and 22μ wide. Two terminal claws not as long as in 4 previous species and unequal, one being 46μ and slender, other 43μ and much stouter.

Labrum as in *L. exilipes*. Mandible as in *L. fissisetiger*. Paragnath and first maxilla as in *L. exilipes*. Second maxilla (fig. 90) resembling in general form that of *L. fissisetiger*, but 4–5 central teeth on lash much stouter than others. Maxilliped much like that of *L. gentilis*.

Area between maxillipeds and first pair of legs not protuberant, with a sclerotized line between bases of maxillipeds.

Legs 1–4 segmented as in 4 previous species, with same spine and setal formula. Legs 1–3 closely resembling those of *L. exilipes*. Leg 4 (fig. 91) with endopod shorter than exopod, its first segment 41μ x 28μ (including terminal spinous processes) with inner distal finely barbed spine 30μ, second segment 90μ x 24μ (greatest dimensions including processes), outer terminal spine 29μ with finely barbed margins, inner 63μ with coarsely barbed fringe on outer margin and very slightly barbed fringe on inner margin. Inner margin of this segment with very short spinules.

Leg 5 (fig. 92) with elongated free segment having a prominent inner basal expansion directed distally. (Shape of this expansion varying somewhat in different individuals, as in figures 93 and 94.) Length of segment 134μ, width at expansion 40μ, width just distal to expansion 26μ. Outer surface with narrow scalelike spines. Two terminal setae 70μ and 88μ (the latter with a narrow membrane as in *L. fissisetiger*). Seta on body near insertion of segment about 40μ long and slightly plumose; a few small spinules near this seta.

Leg 6 probably represented by the 2 setae near areas of attachment of each egg sac (see fig. 86).

Color in life in transmitted light as in *L. fissisetiger*.

MALE.—Body (fig. 95) resembling that of *L. fissisetiger*. Length 0.73 mm (0.69–0.77 mm) and greatest width 0.26 mm (0.22–0.28 mm), based on 10 specimens. Ratio of length to width of prosome 1.73:1.

Segment of leg 5 measuring 34μ x 81μ. Genital segment (fig. 96) about as long as wide, 169μ x 164μ. No ventral intersegmental sclerite between these segments. Four postgenital segments 16μ x 46μ, 16μ x 45μ, 13μ x 44μ, and 18μ x 47μ respectively.

Caudal ramus similar to that of female but smaller, 17μ x 22μ dorsally, 19μ x 22μ ventrally.

Ratio of length of prosome to that of urosome 1.7:1.

Rostral area as in female. First antenna similar to that of female, but with 3 aesthetes added as in 4 previous species, so that formula is same as for those males. Aesthetes long as in *L. fissisetiger*, proximalmost 200μ in length. Second antenna like that of female, but with a few small spinules along inner margins of first, second, and fourth segments.

Labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped as in *L. gentilis*, with claw 146μ in length (measured along its axis).

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented as in 4 previous species, with spine and setal formula as in those males. Endopod of leg 1 as in *L. fissisetiger*. Legs 2–4 as in female.

Leg 5 as in *L. exilipes*, with free segment 51μ x 8μ, its seta 53μ and its spine 19μ in length.

Leg 6 similar to that of *L. fissisetiger*, with 2 naked setae 26μ and 53μ long.

Spermatophore not observed.

Color in life as in female.

ETYMOLOGY.—The specific name *cuneipes*, from Latin *cuneus*=a wedge and *pes*=a foot, alludes to the wedgelike form of the inner basal expansion of leg 5 in the female of this species.

COMPARISON WITH RELATED SPECIES.—*Lichomolgus cuneipes* may be differentiated from all other previously known species in the genus by the combination of two characters: the spine (instead of a seta) on the first segment of the endopod of leg 4 and the second antenna bearing terminally two claws and five small hyaline elements.

Lichomolgus cuneipes may be separated from all four species described above by the shorter and more unequal two claws on the

second antenna, by the nature of the teeth on the lash of the second maxilla, and by the form of the fifth legs in the female.

Lichomolgus aculeatus, new species

FIGURES 97–113

TYPE MATERIAL.—69 ♀♀, 116 ♂♂, and 39 copepodids from a colony of *Nephthea aberrans* Verseveldt, in 10 m, Tany Kely, a small island south of Nosy Bé, Madagascar, collected Aug. 21, 1964. Holotype ♀, allotype, and 154 paratypes (54 ♀♀ and 100 ♂♂) deposited in the United States National Museum, 20 paratypes (10 ♀♀ and 10 ♂♂) in the Zoölogisch Museum, Amsterdam, and the remaining paratypes in the collection of A. G. Humes.

OTHER SPECIMENS.—From *Nephthea sphaerophora* Kükenthal: 33 ♀♀, 17 ♂♂, and 11 copepodids from 1 colony, in 3 m, Pte. Lokobe, Nosy Bé, Oct. 16, 1960. From *Nephthea crassa* Kükenthal: 27 ♀♀, 46 ♂♂, and 33 copepodids from 1 colony, in 2 m, Pte. Mahatsinjo, Nosy Bé, Aug. 8, 1960; 51 ♀♀ and 97 ♂♂ from 1 colony, in 2 m, Tany Kely, Aug. 26, 1960. From *Nephthea tixierae* Verseveldt: 70 ♀♀, 92 ♂♂, and 100 copepodids from 1 colony, in 8 m, Nosy Ovy, Isles Radama, 13°59′S, 47°46.5′E, Sept. 30, 1964. From *Litophyton arboreum* Forskål: 189 ♀♀ and 47 ♂♂ from 1 colony, in 3 m, Andraikarekabe, western shore of Nosy Komba, near Nosy Bé, Oct. 9, 1964.

FEMALE.—Body (fig. 97) with moderately broad prosome. Length 1.26 mm (1.21–1.32 mm) and greatest width 0.57 mm (0.55–0.59 mm), based on 10 specimens. Segment of leg 1 separated from head by a distinct furrow. Epimeral areas of segments of legs 2 and 3 angular. Ratio of length to width of prosome 1.49:1.

Segment of leg 5 measuring 83μ x 190μ. Between this segment and genital segment no ventral intersegmental sclerite. Genital segment (fig. 98) longer than wide, 221μ x 195μ, its lateral areas not expanded. Areas of attachment of egg sacs situated dorsally near middle of segment. Each area with 2 minute naked setae. Three postgenital segments 75μ x 127μ, 44μ x 107μ, and 39μ x 110μ from anterior to posterior.

Caudal ramus (fig. 99) about 2.2 times longer than wide, 100μ x 48μ when measured dorsally, 110μ x 48μ when measured ventrally. Outer lateral seta 122μ long and naked; all other setae with prominent lateral spinules. Pedicellate dorsal seta 55μ, outermost distal seta 148μ, innermost distal seta 161μ, and the 2 long median terminal setae 213μ (outer) and 230μ (inner), both inserted between dorsal and ventral flanges bearing marginal spinules. Dorsal surface of ramus with fine ornamentation as in figure.

Ratio of length of prosome to that of urosome 1.7:1.

Egg sac (fig. 97) approximately 380μ x 200μ, reaching to insertion of caudal ramus, containing 8–11 eggs, each about 100μ in diameter.

Rostral area broadly rounded posteroventrally.

First antenna (433μ long) similar to that of *L. spinulifer* Humes and Frost, 1964, except that all setae are naked; segments 29μ (68μ along anterior edge), 125μ, 31μ, 64μ, 68μ, 46μ, and 31μ respectively. Second antenna (fig. 100) with 4 segments having same formula for armature as in previous species. Three elements on third segment consisting of 2 naked setae 49μ and 40μ and a spiniform seta 35μ barbed along one edge. Last segment 109μ along outer margin, 73μ along inner margin, and 30μ wide. Two terminal claws elongated, slender, and nearly equal, 140μ and 133μ.

Labrum (fig. 101) with 2 posteroventral lobes. Mandible (fig. 102) similar to that of *L. spinulifer*, but with a pointed prominence on its convex margin distal to proximal spinules. Paragnath and first maxilla as in *L. spinulifer*. Second maxilla (fig. 103) similar to *L. spinulifer*, but with first segment broadened so that convex margin of appendage is angular; long spinules on proximal edge of distalmost seta on second segment; small setule on proximal outer area of second segment (as in *L. spinulifer*). Maxilliped (fig. 104) resembling that of *L. spinulifer*, but differing in fine ornamentation; small seta on third segment (as in *L. spinulifer*).

Area between maxillipeds and first pair of legs as in *L. spinulifer*, with a sclerotized line between bases of maxillipeds as in that species.

Legs 1–4 segmented as in 5 previous species, with same spine and setal formula, and closely resembling those of *L. spinulifer*. Endopod of leg 4 (fig. 105) only slightly shorter than exopod, its first segment 55μ x 42μ (including terminal spinous processes) with an inner distal plumose seta 104μ long, second segment 125μ x 35μ (greatest dimensions including processes), outer terminal spine 25μ and finely barbed, inner 78μ with a finely serrated fringe. Outer margin of second segment with row of spinules (lacking distinct articulations) and inner margin smooth, as in *L. spinulifer*.

Leg 5 (fig. 106) similar to that of *L. spinulifer*, elongated free segment having a small proximal inner expansion. Length of segment 151μ, width at expansion 49μ, width near tip 16μ. Outer surface with scalelike spines. Two terminal naked setae 39μ and 88μ. Seta on body near insertion of segment 45μ and naked.

Leg 6 probably represented by the 2 setae near areas of attachment of egg sac.

Color in life in transmitted light opaque, eye red, ovary gray, egg sacs reddish gray.

MALE.—Body (fig. 107) resembling in general form that of female. Length 1.01 mm (0.96–1.07 mm) and greatest width 0.36 mm (0.35–

0.36 mm), based on 10 specimens. Ratio of length to width of prosome 1.56:1.

Segment of leg 5 measuring 44μ x 107μ. Genital segment (fig. 108) somewhat longer than wide, 239μ x 213μ. No ventral intersegmental sclerite between these segments. Four postgenital segments 26μ x 65μ, 23μ x 65μ, 18μ x 63μ, and 23μ x 70μ respectively.

Caudal ramus similar to that of female, 83μ x 39μ dorsally, 85μ x 39μ ventrally.

Ratio of length of prosome to that of urosome 1.45:1.

Rostral area as in female. First antenna similar to that of female, but with 3 aesthetes added as in 5 previous species, so that formula is same as for those males; aesthetes resembling those of *L. spinulifer*. Second antenna (fig. 109) resembling that of female, but with prominent spinules on inner margins of first 2 segments and small spinules added on segments 3 and 4 as in figure.

Labrum, mandible, paragnath, first maxilla, and second maxilla as in female. Maxilliped (fig. 110) resembling that of *L. spinulifer*, with claw 224μ along its axis.

Area between maxillipeds and first pair of legs as in female.

Legs 1–4 segmented as in 5 previous species, with spine and setal formula as in those males. Endopod of leg 1 (fig. 111) with long terminal spine recurved and concave inwardly, bearing 2 rows of strong spinules: outer spine short and differentially barbed on its 2 margins. Legs 2–4 as in female.

Leg 5 (fig. 112) with free segment 55μ x 10μ (extremes in 4 males 53μ–59μ x 9μ–11μ), its seta 44μ and naked, its spine 20μ with an outer fringe; seta on body near insertion of free segment 35μ and naked.

Leg 6 similar to that of *L. spinulifer*, the 2 small naked setae about 8μ long.

Spermatophore (fig. 113), attached to female, elongated, 195μ x 83μ, not including neck.

Color in life as in female.

ETYMOLOGY.—The specific name *aculeatus*, from Latin=provided with prickles, refers to the nature of the terminal spine on the endopod of leg 1 in the male of this species.

COMPARISON WITH RELATED SPECIES.—*Lichomolgus aculeatus* differs from all five species described above in having a seta (instead of a spine) on the first segment of the endopod of leg 4. The new species appears to be closely related to *L. spinulifer* Humes and Frost, 1964, from *Lemnalia* sp. at Nosy Bé, yet differs from it in several significant features: the relatively shorter caudal ramus (2.2:1, instead of 3.3:1 as in *L. spinulifer*), the long terminal claws on the second antenna, the small pointed process on the convex side of the mandible,

and the concave spinulose spine on the last segment of the endopod in the male.

Lichomolgus spinulifer Humes and Frost, 1964

This species has been previously recorded from *Lemnalia* sp. at Nosy Bé, Madagascar (Humes and Frost, 1964).

NEW HOST RECORDS.—From *Lemnalia flava* May: 211 ♀♀, 133 ♂♂, and 26 copepodids from 1 colony, in 1 m, Pte. Ambarionaomby, Nosy Komba, near Nosy Bé, Dec. 14, 1963. From *Lemnalia elegans* (May): 815 ♀♀, 1018 ♂♂, and 230 copepodids from several colonies, in 15 cm, Boloboxo, Nosy Faly, east of Nosy Bé, May 13, 1964. From *Lemnalia amabilis* Tixier-Durivault: 22 ♀♀, 26 ♂♂, and 15 copepodids from 1 colony, in 3 m, Pte. Ambarionaomby, Nosy Komba, Oct. 3, 1960. From *Lemnalia africana* (May): 59 ♀♀, 55 ♂♂, and 3 copepodids from 1 colony, in 2 m, Pte. Ambarionaomby, Nosy Komba, Sept. 27, 1964. From *Paralemnalia thyrsoides* (Ehrenberg): 60 ♀♀, 62 ♂♂, and 12 copepodids from 1 colony, in 3 m, Antsamantsara, northwest of Madirokely, Nosy Bé, Sept. 20, 1964.

These specimens conform completely with paratypes of *L. spinulifer*. The figures of Humes and Frost (1964) should be modified in certain details as follows: in their figures 142 and 160 of the second antenna, another minute element is present near the bases of the two terminal claws, making five such elements in all; in their figure 147 of the female second maxilla, there is a small seta on the proximal outer area of the second segment, and the distalmost seta on this segment has a few minute inner spinules near its tip; in their figure 148 of the female maxilliped, a small seta is present near the two terminal elements; and in their figures 151–154 (female) and 162 (male) of legs 1–4, the outer distal corner of the coxa bears a few small spinules.

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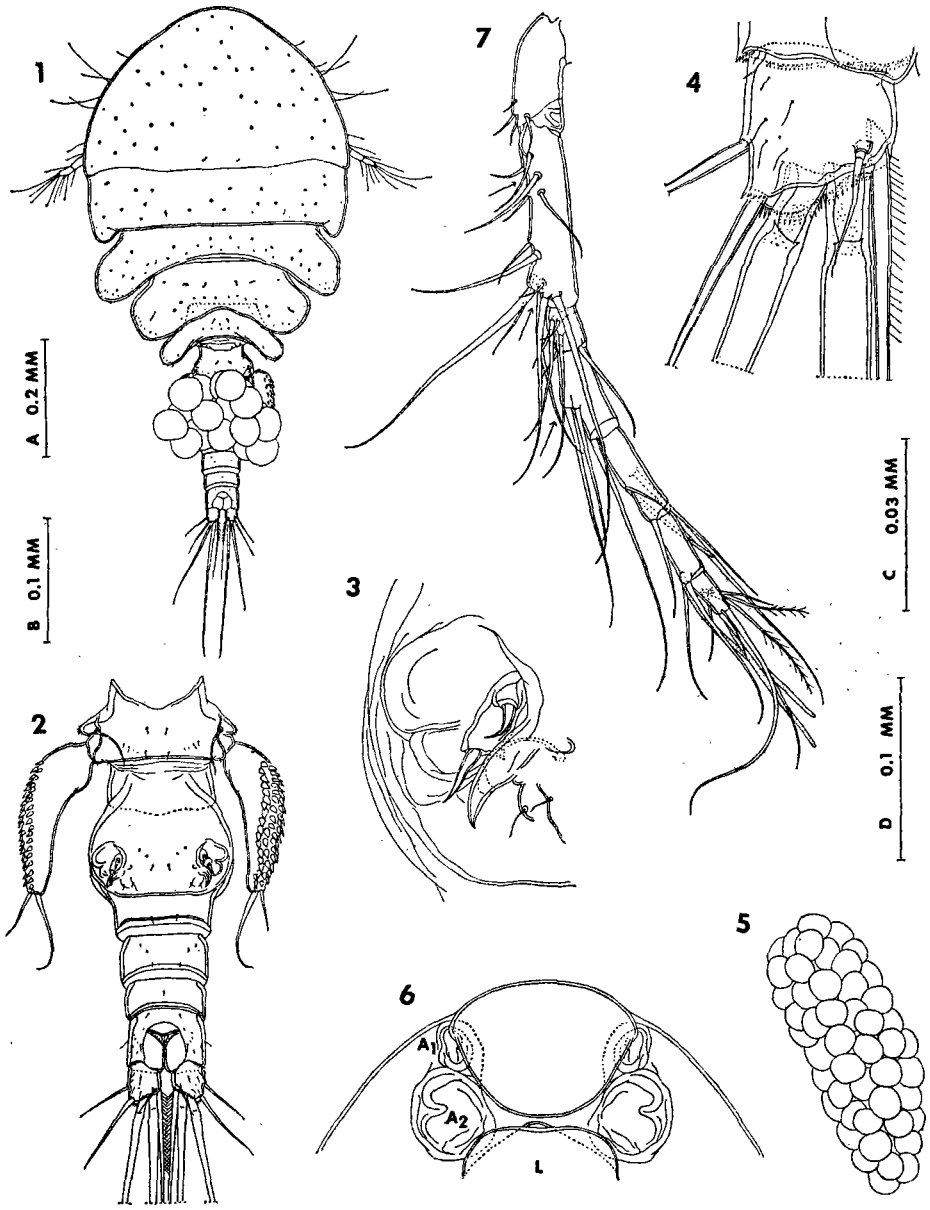
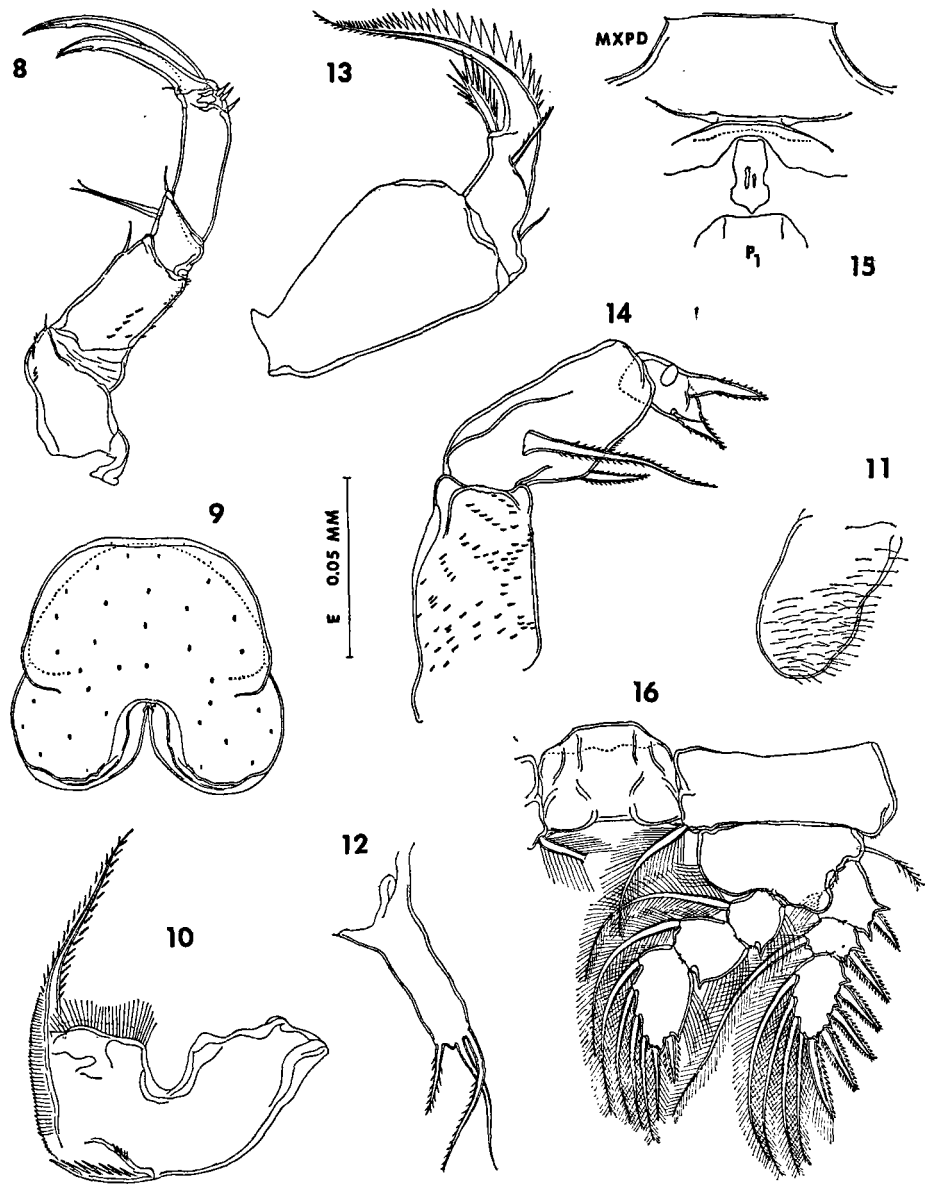
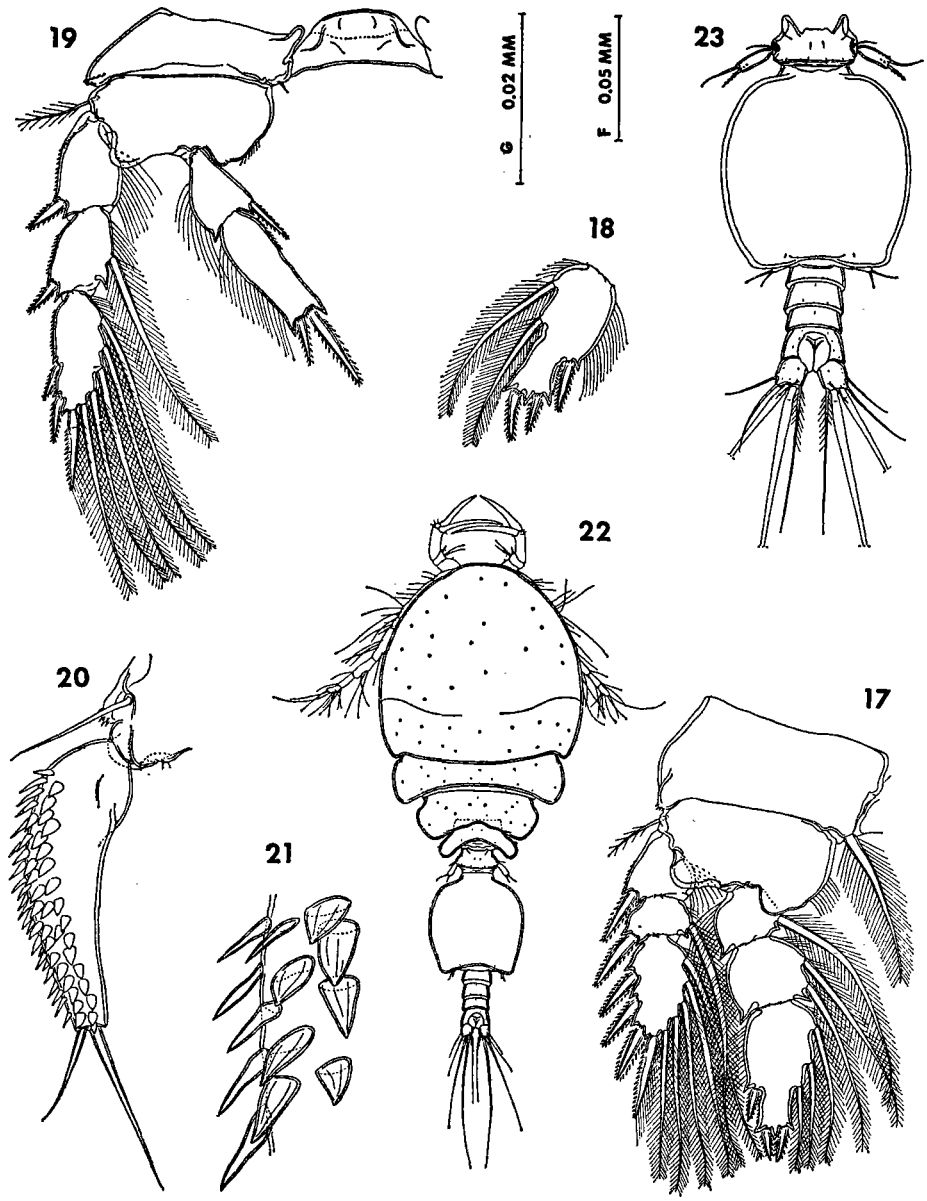


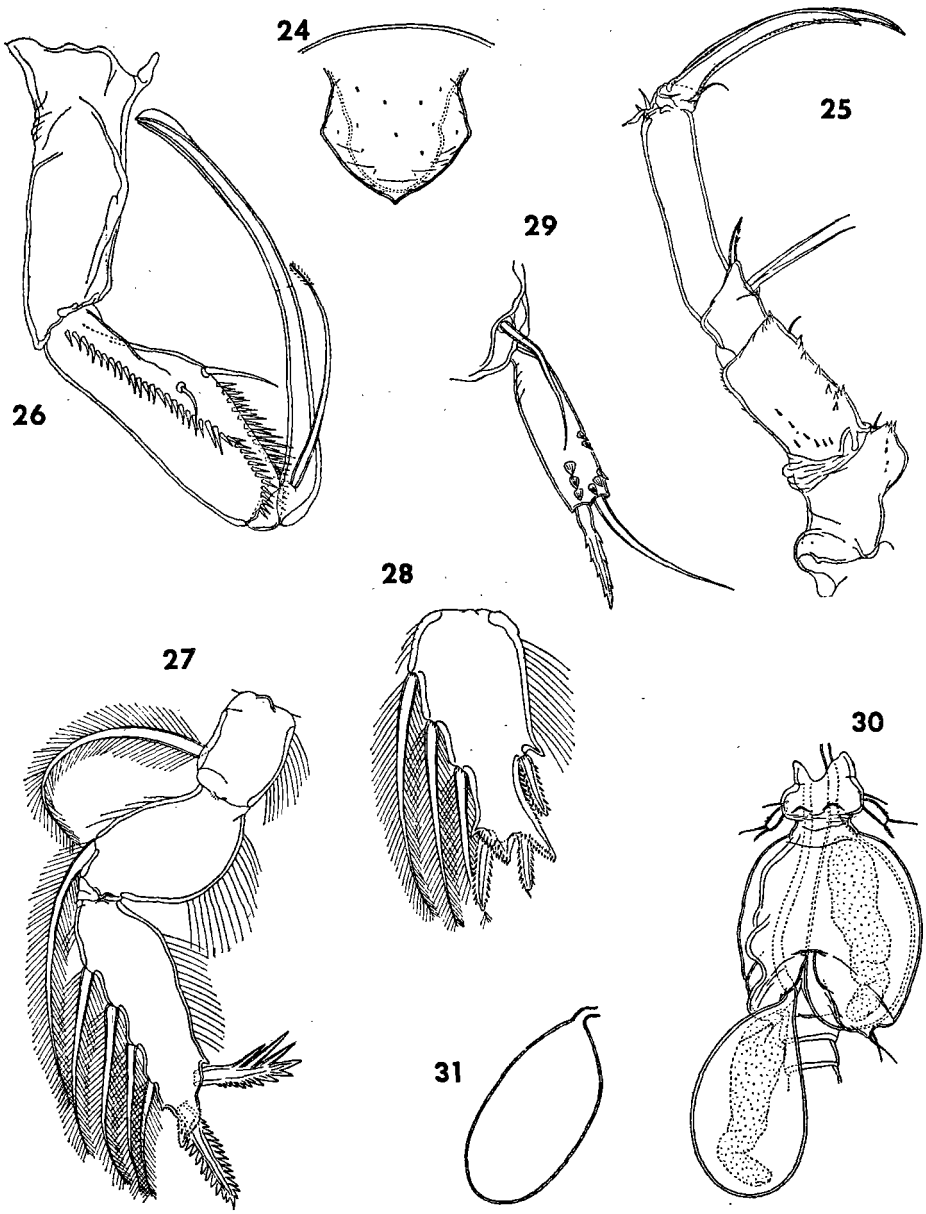
FIGURES 1–7.—*Lichomolgus varirostratus*, new species, female: 1, body, dorsal (A); 2, urosome, dorsal (B); 3, area of attachment of egg sac, dorsal (C); 4, caudal ramus, dorsal (C); 5, egg sac, dorsal (A); 6, rostral area, anteroventral (B); 7, first antenna, dorsal (D).



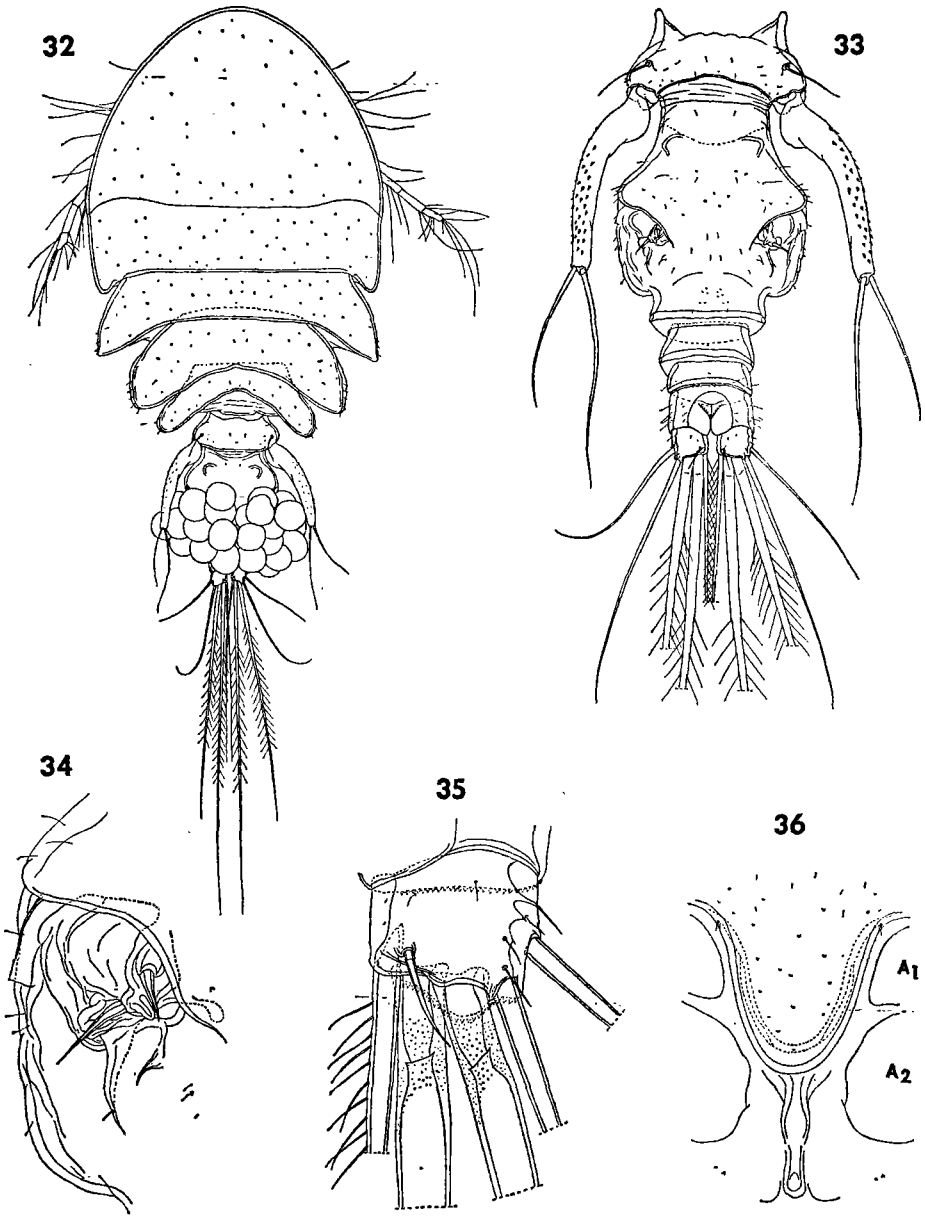
FIGURES 8–16.—*Lichomolgus varirostratus*, new species, female: 8, second antenna, anterior (inner) (D); 9, labrum, ventral (D); 10, mandible, posterior (E); 11, paragnath, ventro-inner (C); 12, first maxilla, anterior (E); 13, second maxilla, posterior (E); 14, maxilliped, postero-inner (E); 15, area between maxillipeds and first pair of legs, ventral (D); 16, leg 1 and intercoxal plate, anterior (D).



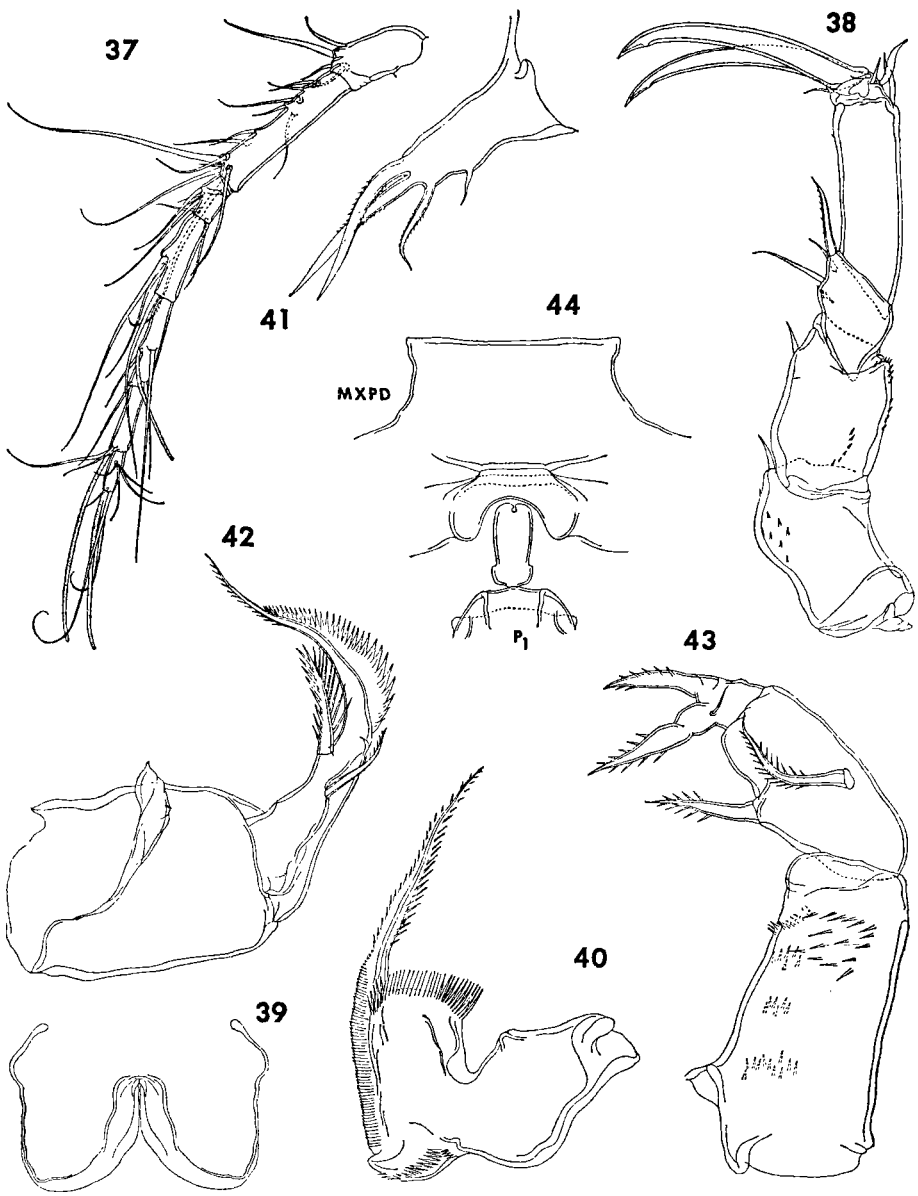
FIGURES 17–23.—*Lichomolgus varirostratus*, new species, female: 17, leg 2, anterior (D); 18, last segment of endopod of leg 3, anterior (D); 19, leg 4 and intercoxal plate, anterior (D); 20, leg 5, dorsal (F); 21, scalelike spines on leg 5, dorso-outer (G). Male: 22, body, dorsal (A); 23, urosome, dorsal (B).



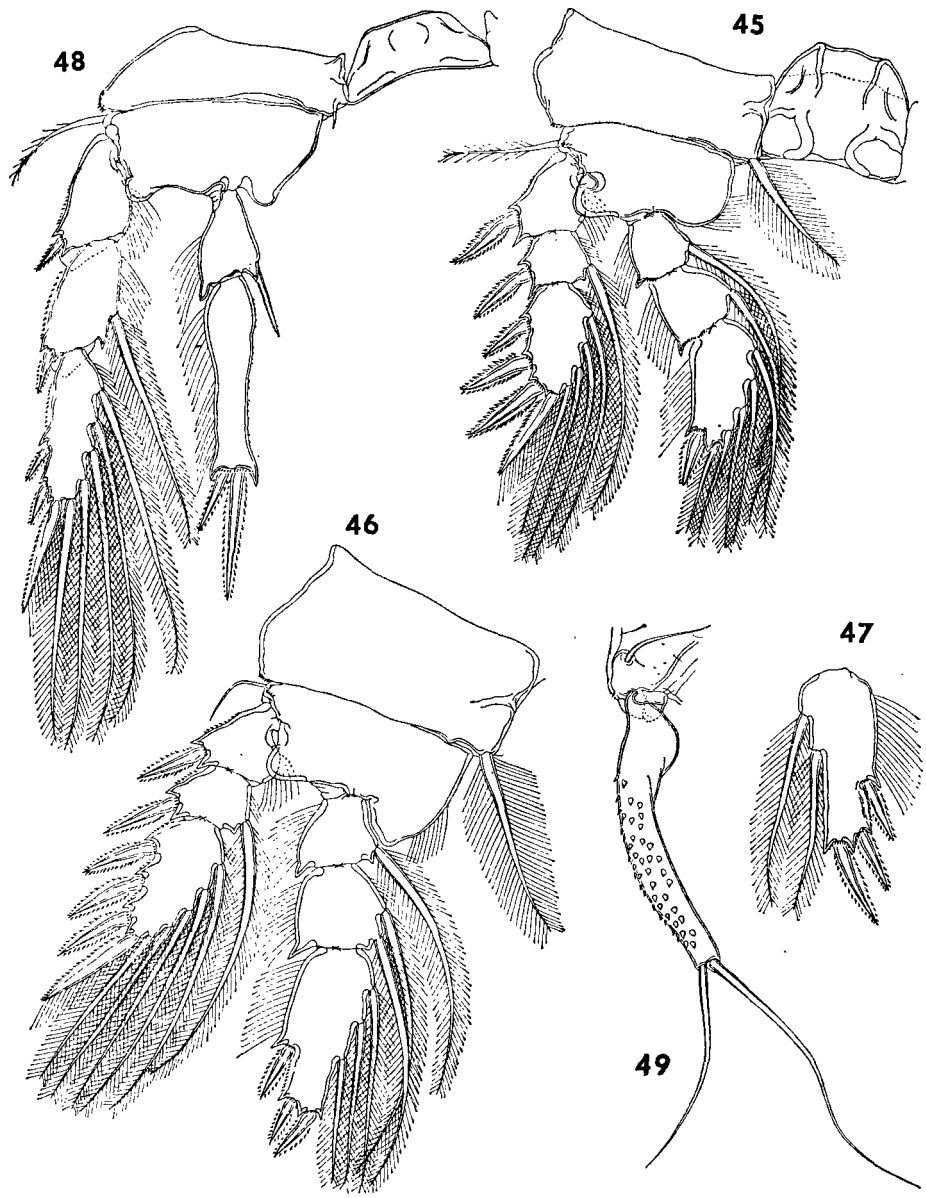
FIGURES 24–31.—*Lichomolgus varirostratus*, new species, male: 24, rostral area, ventral (D); 25, second antenna, anterior (inner) (F); 26, maxilliped, postero-inner (F); 27, endopod of leg 1, anterior (E); 28, last segment of endopod of leg 2, anterior (E); 29, leg 5, dorsal (C); 30, anterior part of urosome, showing extrusion of spermatophore in lactic acid, ventral (B); 31, spermatophore, attached to female, lateral (B).



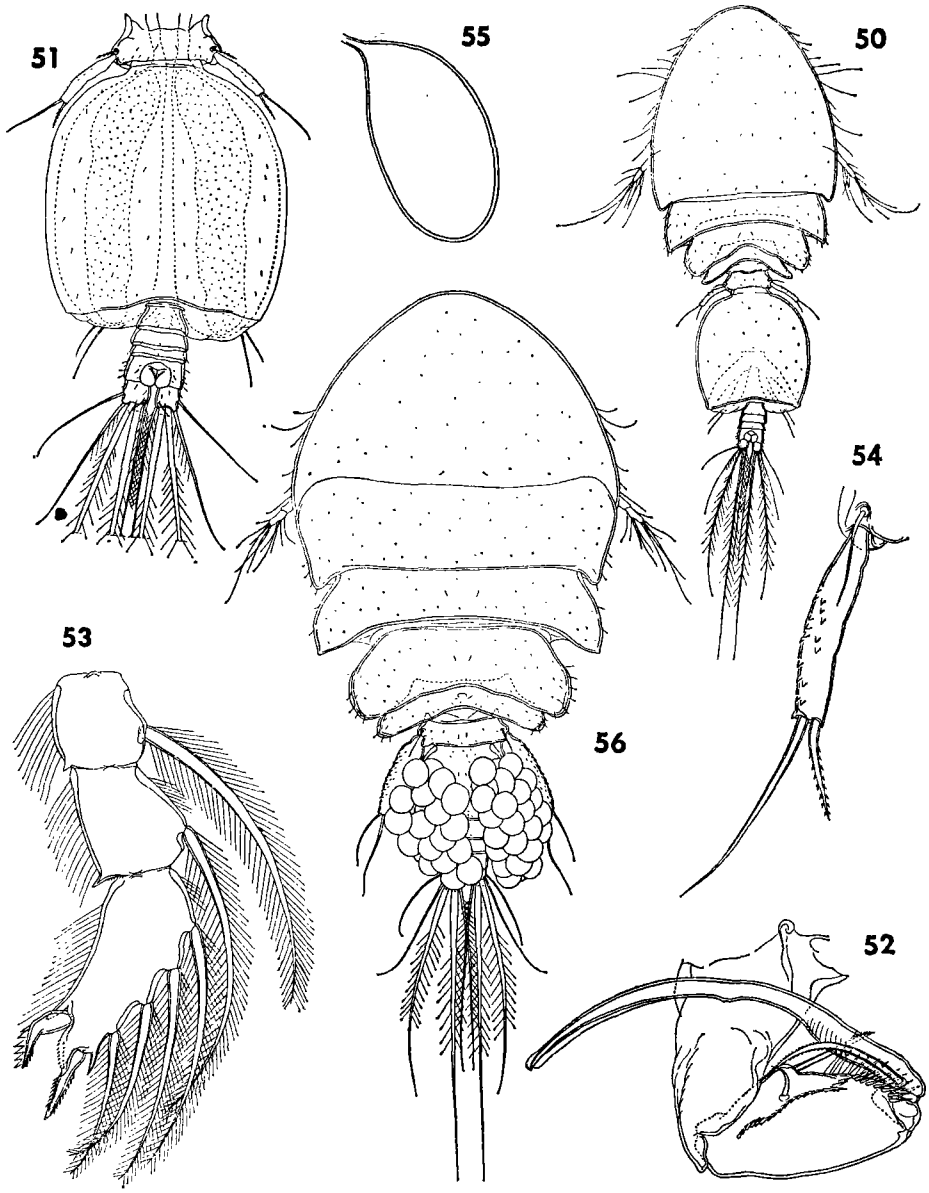
FIGURES 32–36.—*Lichomolgus exilipes*, new species, female: 32, body, dorsal (A); 33, urosome, dorsal (B); 34, area of attachment of egg sac, dorsal (E); 35, caudal ramus, dorsal (C); 36, rostral area, ventral (D).



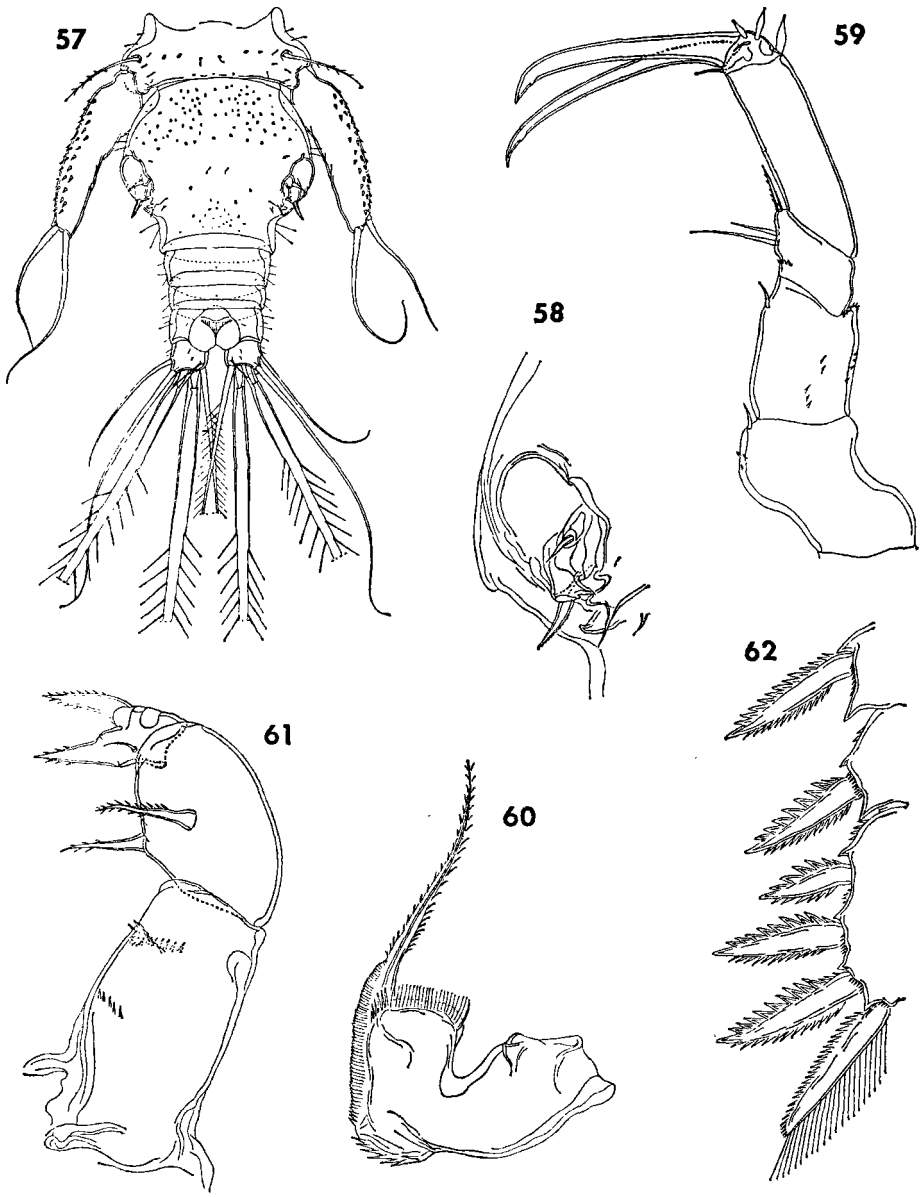
FIGURES 37–44.—*Lichomolgus exilipes*, new species, female: 37, first antenna, ventral (B); 38, second antenna, anterior (inner) (D); 39, labrum, ventral (F); 40, mandible, posterior (E); 41, first maxilla, posterior (E); 42, second maxilla, postero-inner (E); 43, maxilliped, postero-inner (E); 44, area between maxillipeds and first pair of legs, ventral (D).



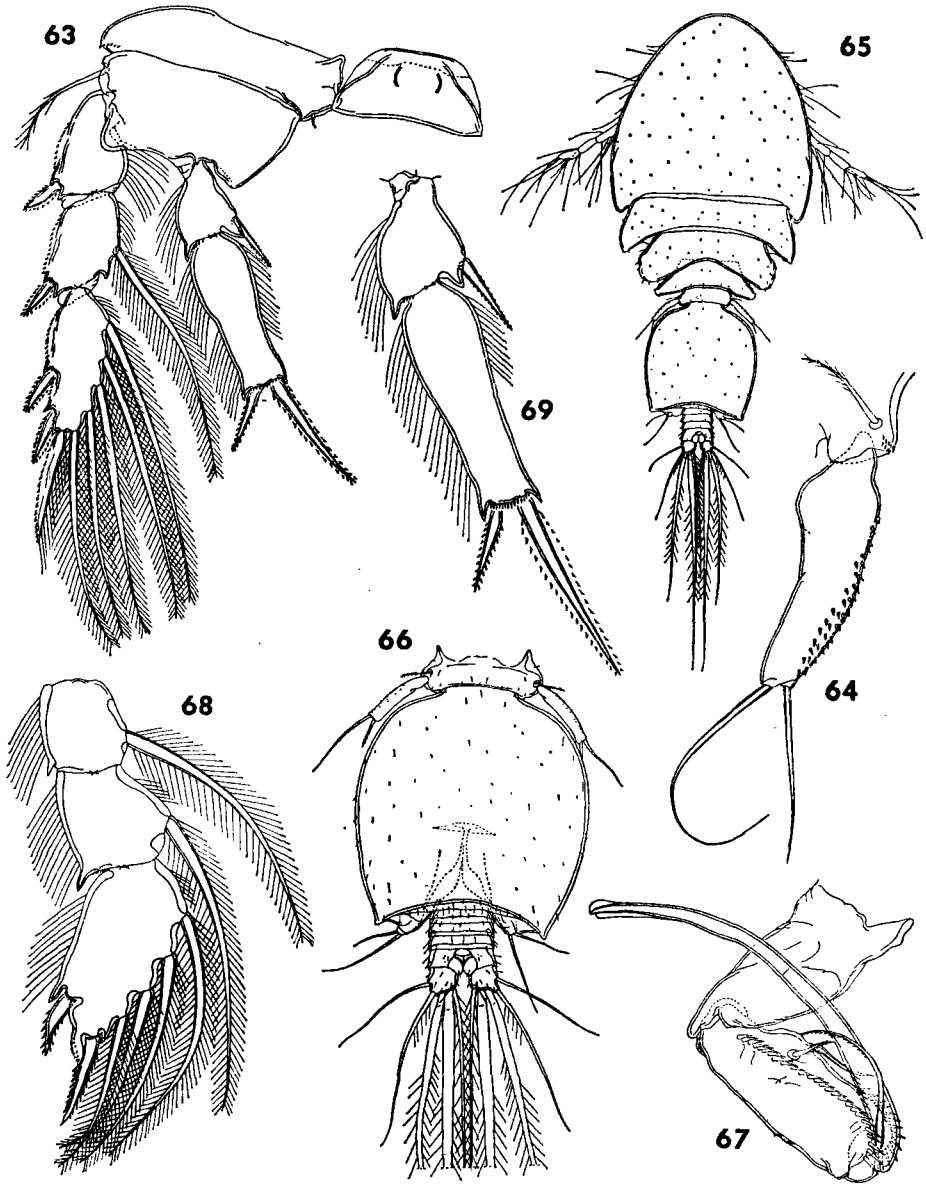
FIGURES 45–49.—*Lichomolgus exilipes*, new species, female: 45, leg 1 and intercoxal plate, anterior (D); 46, leg 2, anterior (D); 47, last segment of endopod of leg 3, anterior (D); 48, leg 4 and intercoxal plate, anterior (D); 49, leg 5, dorsal (D).



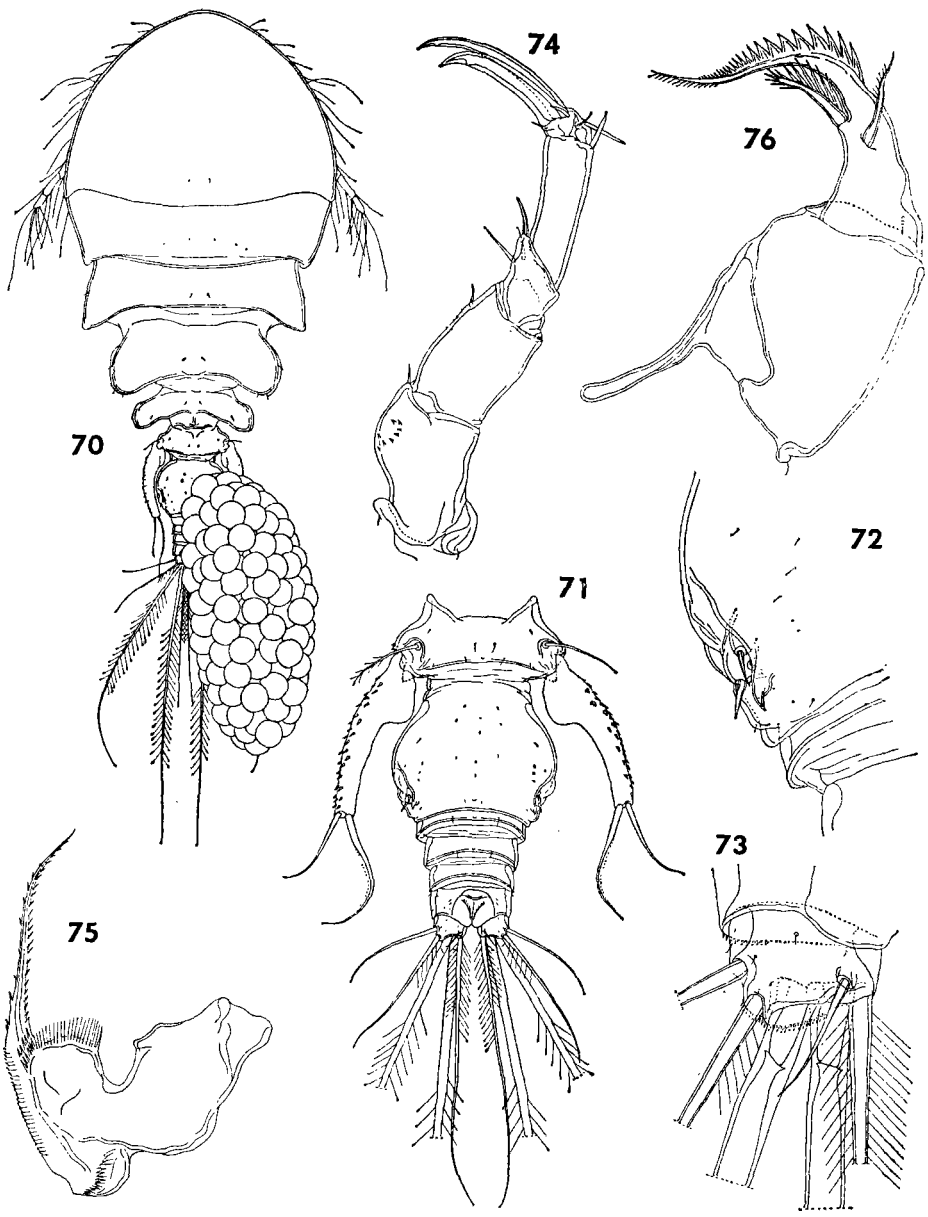
FIGURES 50–56.—*Lichomolgus exilipes*, new species, male: 50, body, dorsal (A); 51, urosome, dorsal (B); 52, maxilliped, postero-inner (F); 53, endopod of leg 1, anterior (E); 54, leg 5, dorsal (E); 55, spermatophore, attached to female, dorsal (B). *Lichomolgus gentilis*, new species, female: 56, body, dorsal (A).



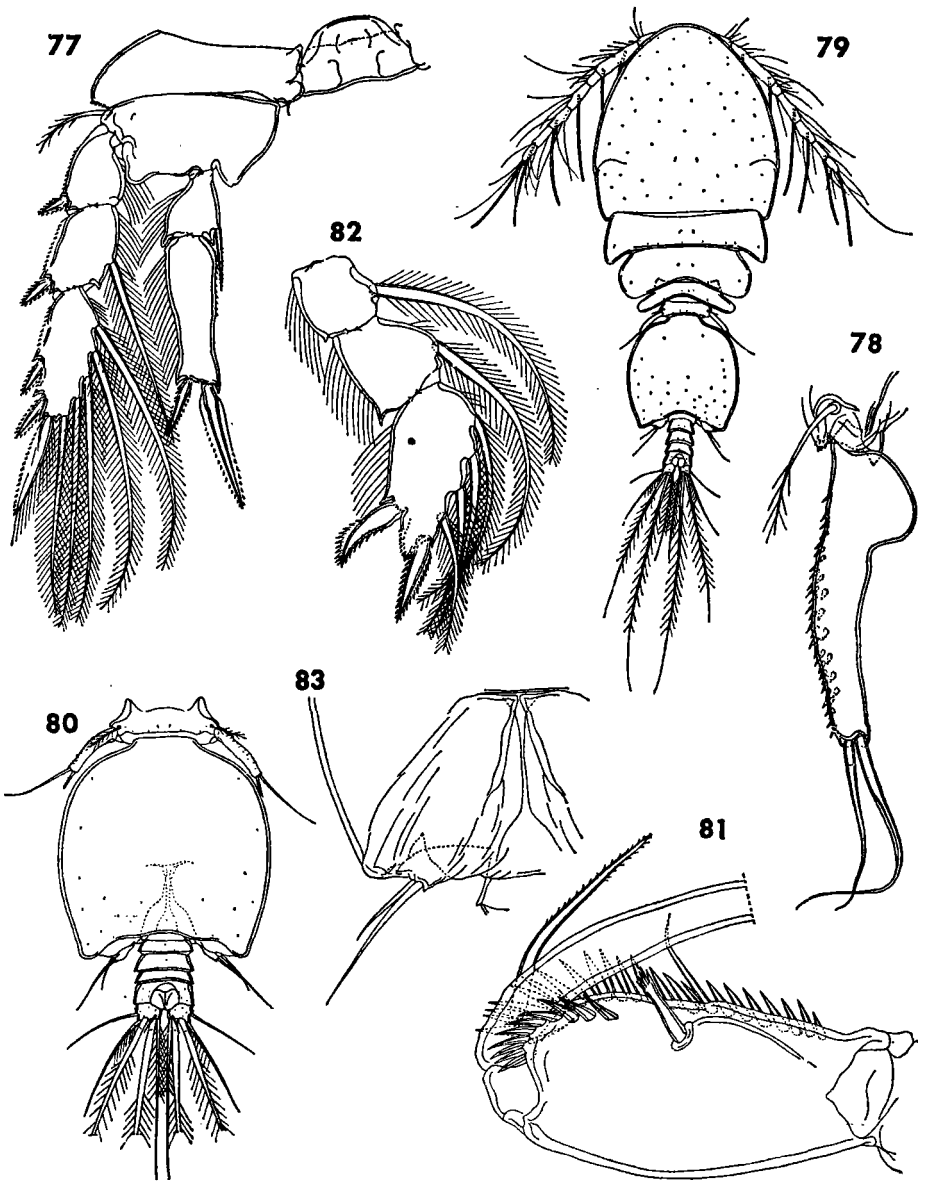
FIGURES 57–62.—*Lichomolgus gentilis*, new species, female: 57, urosome, dorsal (B); 58, area of attachment of egg sac, dorsal (E); 59, second antenna, anterior (inner) (D); 60, mandible, posterior (E); 61, maxilliped, postero-inner (E); 62, spines on exopod of leg 1, anterior (E).



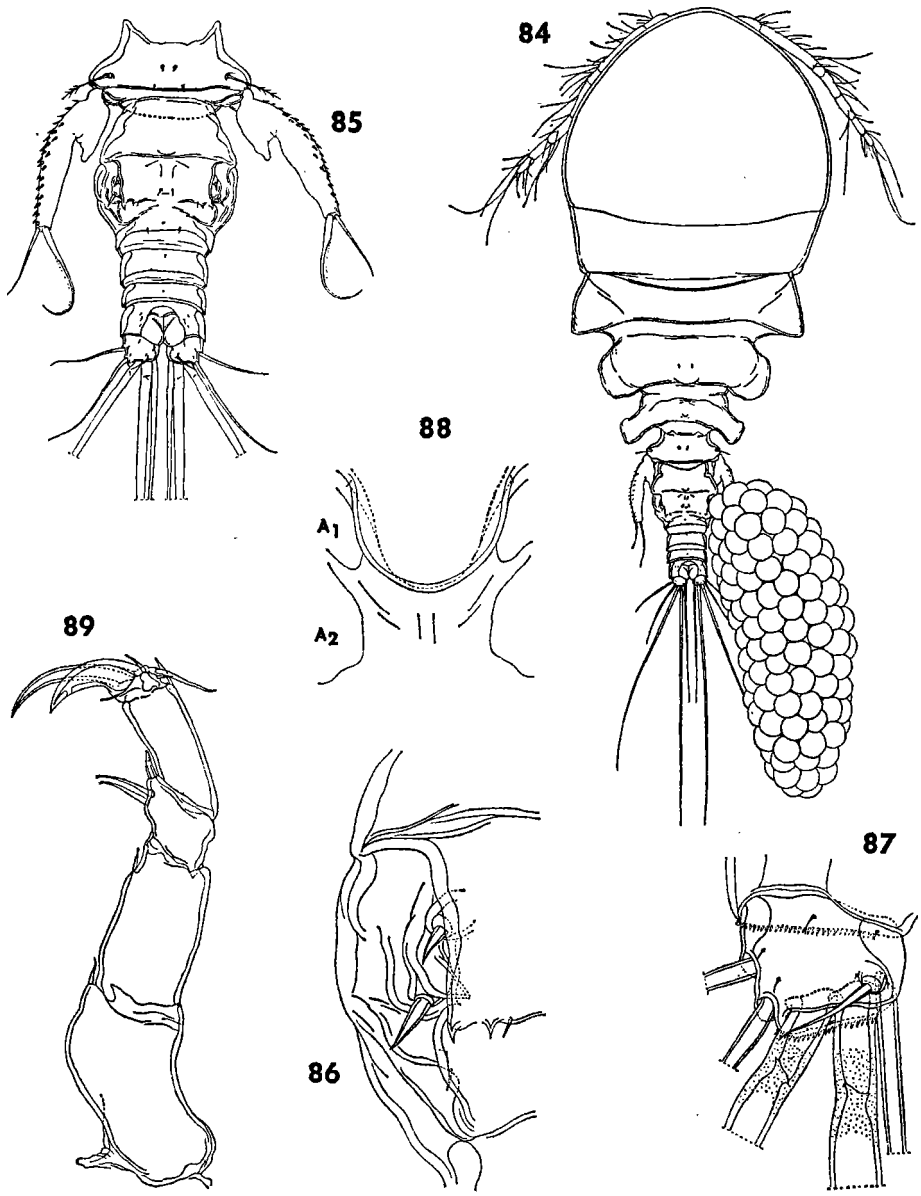
FIGURES 63–69.—*Lichomolgus gentilis*, new species, female: 63, leg 4 and intercoxal plate, anterior (D); 64, leg 5, dorsal (D). Male: 65, body, dorsal (A); 66, urosome, dorsal (B); 67, maxilliped, postero-inner (F); 68, endopod of leg 1, anterior (E); 69, endopod of leg 4, anterior (E).



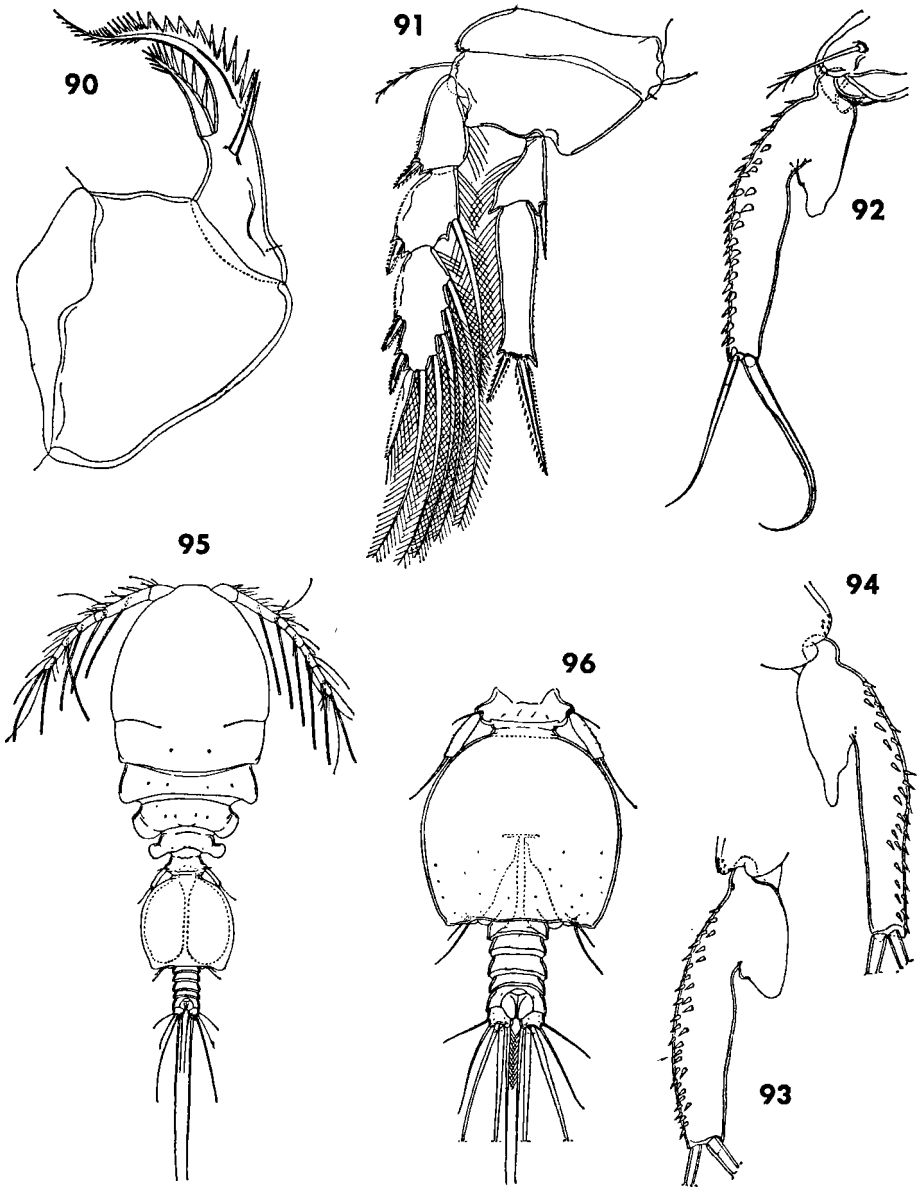
FIGURES 70–76.—*Lichomolgus fissisetiger*, new species, female: 70, body, dorsal (A); 71, urosome, dorsal (B); 72, area of attachment of egg sac, dorsal (E); 73, caudal ramus, dorsal (C); 74, second antenna, anterior (inner) (D); 75, mandible, posterior (E); 76, second maxilla, posterior (E).



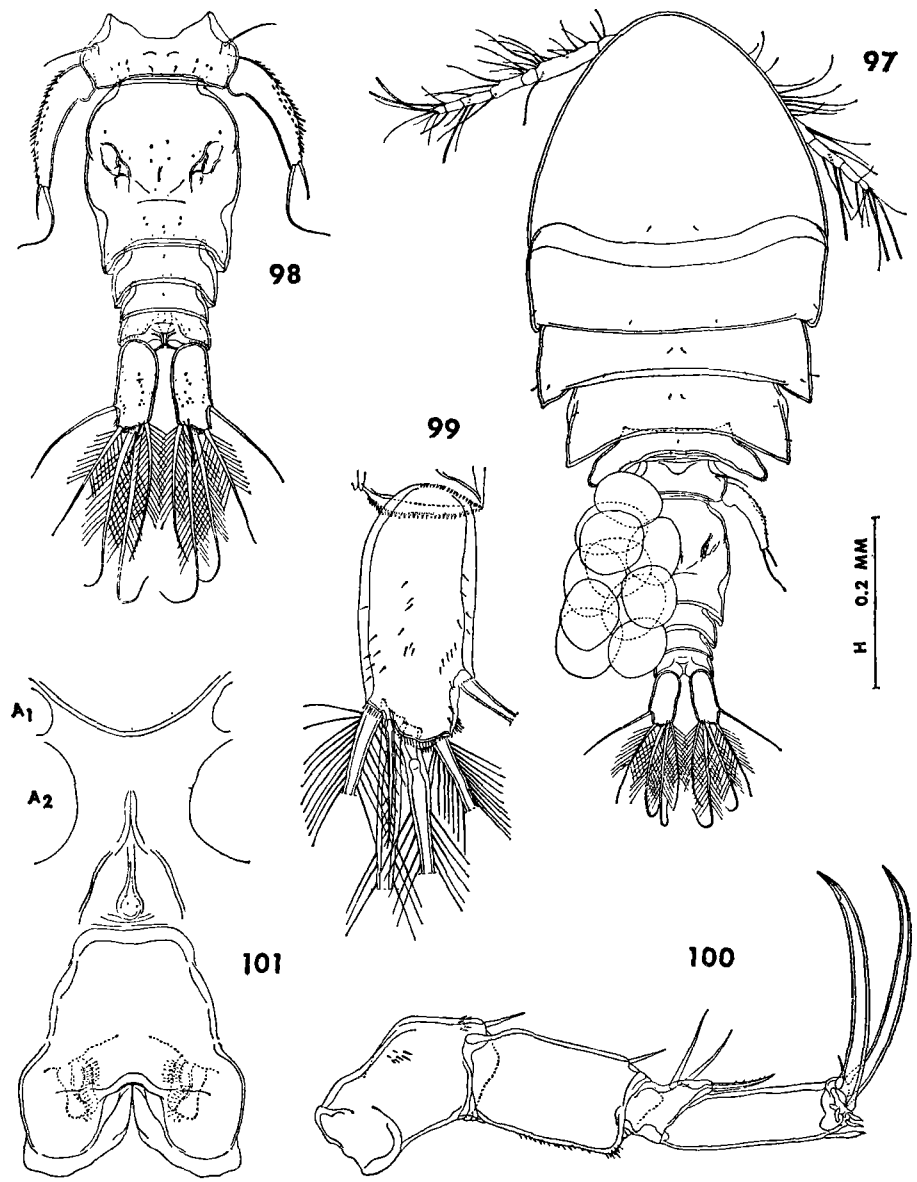
FIGURES 77–83.—*Lichomolgus fissisetiger*, new species, female: 77, leg 4 and intercoxal plate, anterior (D); 78, leg 5, dorsal (F). Male: 79, body, dorsal (A); 80, urosome, dorsal (B); 81, maxilliped, second and third segments and proximal part of claw, ventro-outer (C); 82, endopod of leg 1, anterior (E); 83, leg 6, ventral (F).



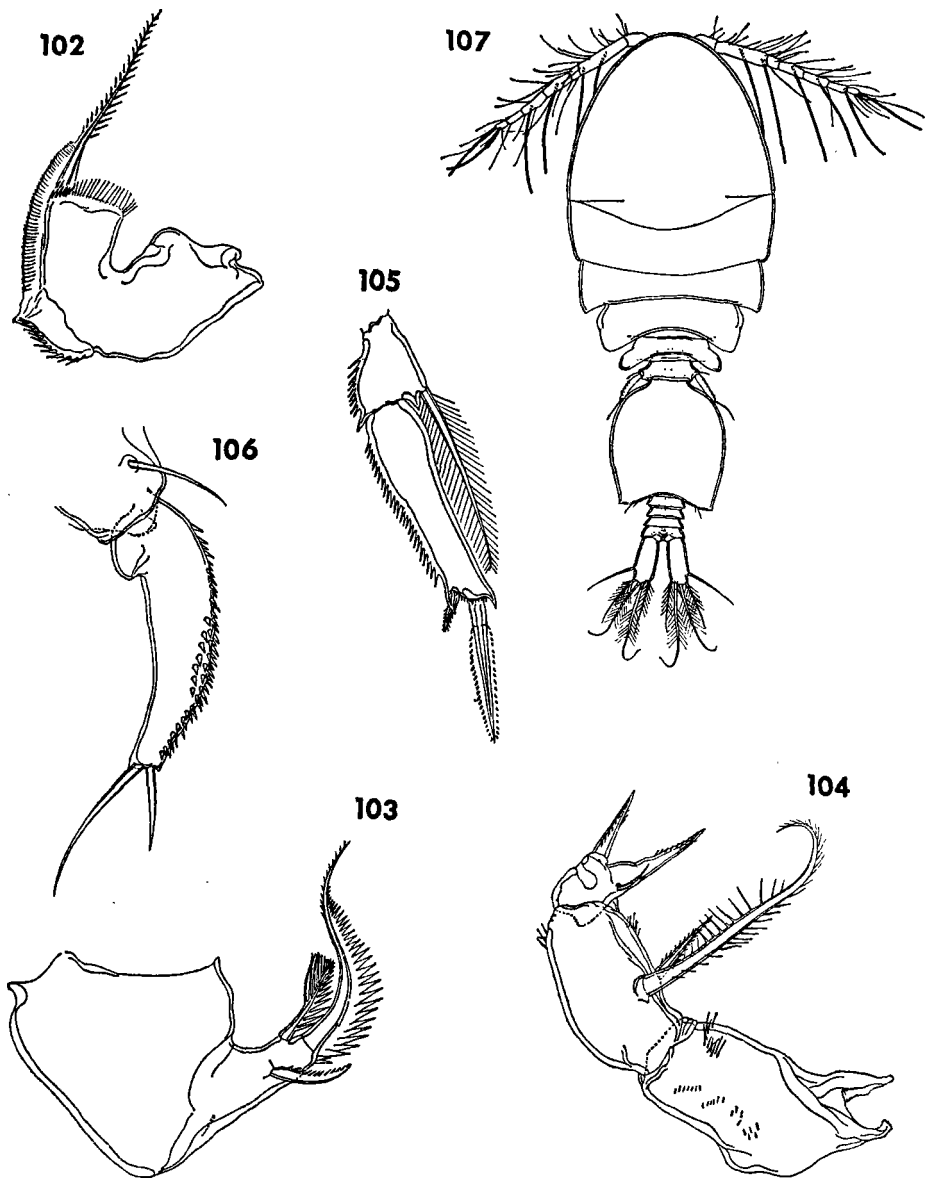
FIGURES 84–89.—*Lichomolgus cuneipes*, new species, female: 84, body, dorsal (A); 85, urosome, dorsal (B); 86, area of attachment of egg sac, dorsal (C); 87, caudal ramus, dorsal (C); 88, rostral area, ventral (D); 89, second antenna, anterior (inner) (F).



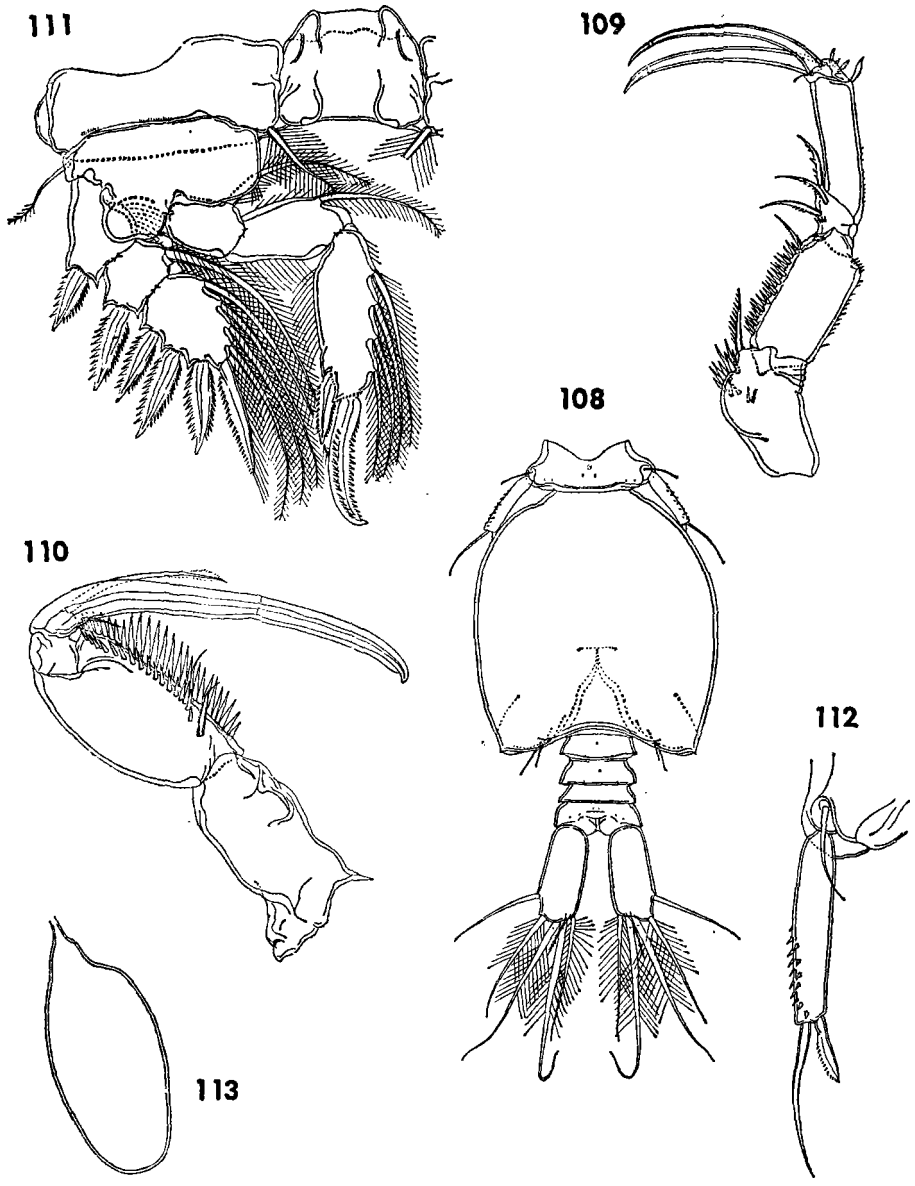
FIGURES 90–96.—*Lichomolgus cuneipes*, new species, female: 90, second maxilla, postero-inner (E); 91, leg 4, anterior (D); 92, leg 5, dorsal (F); 93, free segment of leg 5, dorsal (F); 94, free segment of leg 5, dorsal (F). Male: 95, body, dorsal (A); 96, urosome, dorsal (B).



FIGURES 97–101.—*Lichomolgus aculeatus*, new species, female: 97, body, dorsal (A); 98, urosome, dorsal (H); 99, caudal ramus, dorsal (F); 100, second antenna, anterior (inner) (D); 101, rostral area and labrum, ventral (D).



FIGURES 102–107.—*Lichomolgus aculeatus*, new species, female: 102, mandible, posterior (F); 103, second maxilla, posterior (F); 104, maxilliped, posterior (F); 105, endopod of leg 4, anterior (D); 106, leg 5, dorsal (D). Male: 107, body, dorsal (A).



FIGURES 108–113.—*Lichomolgus aculeatus*, new species, male: 108, urosome, dorsal (B); 109, second antenna, posterior (outer) (D); 110, maxilliped, ventro-outer (D); 111, leg 1 and intercoxal plate, anterior (F); 112, leg 5, dorsal (E); 113, spermatophore, attached to female, ventral (B).

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A. SOURNIA

Muséum national d'histoire naturelle, Paris

Variations saisonnières et nycthémérales du phytoplancton marin et de la production primaire dans une baie tropicale, à Nosy-Bé (Madagascar)

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I. Introduction

On a étudié en trois stations les éléments suivants: température, salinité, oxygène dissous, composition taxinomique du phytoplancton, pigments photosynthétiques, et production primaire in situ par les deux méthodes de l'oxygène et du carbone 14. Le rôle des facteurs climatiques et océanographiques (principalement: vents, pluie, marée) est examiné, ainsi que diverses relations entre le milieu, les aspects quantitatif et qualitatif de la biomasse, et la productivité.

Je dois une profonde reconnaissance à la direction de l'Office de la recherche scientifique et technique outre-mer (O.R.S.T.O.M.), qui a bien voulu m'accueillir pendant dix-huit mois au Centre d'Océanographie de Nossi-Bé. De plus, je suis redevable au personnel technique de ce Centre: 1) de tous les dosages de salinité et d'oxygène dissous, 2) des données „brutes" relatives aux conditions générales de la climatologie et de l'hydrologie, 3) enfin, de l'exécution d'une partie des figures (fig. 1—5, 10, 20, 21, et 27).

Mes remerciements vont aussi à l' „International Agency for ^{14}C determination" (Copenhague) grâce à laquelle j'ai pu pratiquer la méthode du carbone 14.

1. Buts et limites du présent travail

Seront ici étudiés les aspects quantitatif et écologique du phytoplancton et de la production primaire dans une petite baie tropicale.

Des quatre dimensions de l'espace océanographique, on envisagera principalement dans ce travail la quatrième, à savoir le Temps. En effet, eu égard à son exiguité, le secteur étudié peut être assimilé à un point littoral: les variations géographiques ne s'y manifestent que par l'éloignement relatif — toujours réduit — par rapport à la côte (on verra toutefois que l'effet de la marée transpose dans le temps ce facteur); d'autre part, la turbulence des eaux, liée à la faible profondeur de la baie, relègue au second plan les variations bathymétriques. Restent donc les variations temporelles, que j'étudierai tout d'abord sous leur forme saisonnière, puis nycthémérale.

Dans ce cadre, j'aborderai chaque fois que possible le problème des corrélations entre biomasse (composition taxinomique, pigments photosynthétiques) et productivité (assimilation de carbone, production d'oxygène).

Dernières limitations du sujet: aucune donnée, malheureusement, relative aux teneurs en sels minéraux et en oligo-éléments, et l'influence de celles-ci sur le développement du phytoplancton; enfin, aucune mesure absolue des conditions d'éclairement.

Tel qu'ainsi délimité, ce sujet a précédemment donné lieu à une courte note préliminaire (SOURNIA, 1965a). D'autre part, dans cinq publications antérieures, je me suis efforcé de traiter les aspects qualitatif et taxinomique du microplancton dans le canal de Mozambique: diatomées (s. presse, a), *Ceratium* (1966b et s. presse, b), divers genres de Péridiniens „rares ou mal connus" (1967), enfin *Trichodesmium* (s. presse, c). Je me reporterai donc tacitement, pour les questions de Systématique, à l'une ou l'autre de ces références.

Quelques définitions doivent préalablement être précisées: les diverses épithètes désignant les variations temporelles du plancton sont en effet très souvent confondues. D'où les acceptions suivantes (cf. SOURNIA & FRONTIER, s. presse) pour les principales variations: annuelles (annual) = d'une année à l'autre, et non: au cours d'une année; saisonnières (seasonal) = d'une saison à l'autre; mensuelles (monthly) = d'un mois à l'autre; hebdomadaires (weekly) = d'une semaine à l'autre; journalières ou quotidiennes (daily) = d'un jour à l'autre; nycthémérales (nycthemeral, diel) = dans l'intervalle de 24 heures, en rapport avec l'alternance jour/nuit. Enfin, on ne parlera de variations diurnes (diurnal) que par opposition à des variations nocturnes (nocturnal).

D'autre part, au sujet de l'emploi des mots „production" et „productivité", je me réfère à WOOD (1965, p. 79).

2. Travaux antérieurs dans la région étudiée

La phytoplanctologie est une science multiple: relativement ancienne, si l'on pense aux „micrographes" et aux diatomistes du siècle dernier; relativement jeune, sous son aspect écologique, et plus jeune encore lorsqu'on traite des problèmes de productivité: dans ce domaine, les premières estimations datent de 1922 (ATKINS) et 1927 (GAARDER & GRAN), et la méthode maintenant classique du carbone 14 ne remonte qu'à 1951 (STEEMANN NIELSEN).

Devant l'ampleur et la diversité du sujet, je limiterai au canal de Mozambique la mise à jour des connaissances qui se doit de figurer dans toute introduction, et reviendrai point par point, dans le cours de ce travail, sur les diverses données mondiales.

Les recherches relatives au phytoplancton et à la productivité primaire peuvent le plus souvent être réparties en deux catégories, à la fois méthodologiques et biogéographiques: d'une part, les expéditions océanographiques, qui explorent essentiellement le domaine „océanique", et ceci, pourrait-on dire, „avec des bottes de sept lieues". D'autre part, les travaux locaux, réalisés au voisinage de laboratoires côtiers au moyen de petites embar-

cations, et souvent plus étendus dans le temps. Cette distinction est particulièrement nette dans le cas du canal de Mozambique.

Expéditions océanographiques: Je ne les reporte que pour mémoire, puisque leur intérêt est ici secondaire, et que, d'autre part, je serai amené à y revenir dans une publication ultérieure (voir plus bas):

„Valdivia", 1898—1899: cf. KARSTEN (1907).
„Gauss", 1902—1903: cf. HEIDEN & KOLBE (1928).
„Dana", 1928—1930: cf. STEEMANN NIELSEN (1939).
„Discovery II", 1930—1935: cf. HENDEY (1937).

Ces quatre expéditions, dont les deux premières ont seulement effleuré au sud et au nord la région étudiée, ont uniquement donné lieu à des travaux de Systématique (répartitions écologiques incluses). De toute autre nature est la cinquième: celle de la „Galathea" (1950—1952) au cours de laquelle STEEMANN NIELSEN (1952) a inauguré la méthode du carbone 14. Une sixième croisière, toute récente, est celle de l'„Anton Bruun" (1964) à laquelle il m'a été donné de participer; je compte en publier ultérieurement certains résultats, qui s'ajouteront à ceux de RYTHER, HALL et al. (1966) et de SOURNIA (1967b).

Mentionnons enfin que les croisières du „Cdt Robert-Giraud" (1957, 1960, 1962) ont été exclusivement vouées à l'océanographie physique (MÉNACHÉ, 1961, 1963).

Travaux côtiers: Ils nous intéressent en premier lieu, et seront de ce fait examinés et discutés dans la suite de la présente étude. Dans l'ordre chronologique, citons tout d'abord un travail taxinomique de SILVA (1956) portant sur une série d'échantillons prélevés en divers points de la côte du Mozambique, puis une étude qualitative et quantitative (comptages par sédimentation) du même auteur (1960) relative au phytoplancton d'Inhaca, échelonnée sur deux mois, et comportant quelques données sur les variations nycthémérales. Pour la région de Zanzibar, BALLANTINE (1961) a donné une étude qualitative limitée aux Péridiniens. Enfin, deux travaux effectués à Tuléar en 1962, mais publiés tardivement, portent, l'un sur la composition qualitative et quantitative du phytoplancton (TRAVERS, 1965), l'autre sur l'hydrologie et la productivité du même secteur (MAESTRINI & PIZARRO, 1966).

A Nossi-Bé même, diverses données recueillies par le personnel technique du Centre d'Océanographie ont été synthétisées par ANGOT (1964a—b, 1965a—b) et ANGOT & GÉRARD (1967). Etant donné leur intérêt immédiat, ces travaux seront analysés point par point dans le cours de la présente étude.

3. Conditions océanographiques générales

L'île de Nossi-Bé (ou Nosy-Bé) s'élève sur le plateau continental de la côte nord-ouest de Madagascar, à la latitude 13°20′ sud (fig. 1). Les études géomorphologiques de GUILCHER (1956) et de BATTISTINI (1956) font ressortir l'originalité de cette région de Madagascar: côte particulièrement découpée, plateau continental relativement large, apports fluviatiles importants, et active sédimentation dans les baies, favorisant le développement des mangroves.

Courants: Les connaissances sont actuellement très peu avancées dans ce domaine. Il faut, ici comme dans toute la partie nord de l'océan indien, réserver une large part aux variations saisonnières. Les eaux superficielles sont d'origine équatoriale, mais probablement multiple (courants équatoriaux, eaux de la mer d'Arabie); la circulation des eaux intermédiaires et profondes, mal connue dans le canal de Mozambique (cf. TCHERNIA et al.; 1951; MÉNACHÉ, 1961; ZAKLINSKII, 1963), est pratiquement ignorée dans la région qui nous intéresse. Notons que l'étude des populations zooplanctoniques (FRONTIER, comm. pers.) indique une dérive continue vers le large en saison des pluies, et un mouvement inverse discontinu pendant la saison sèche.

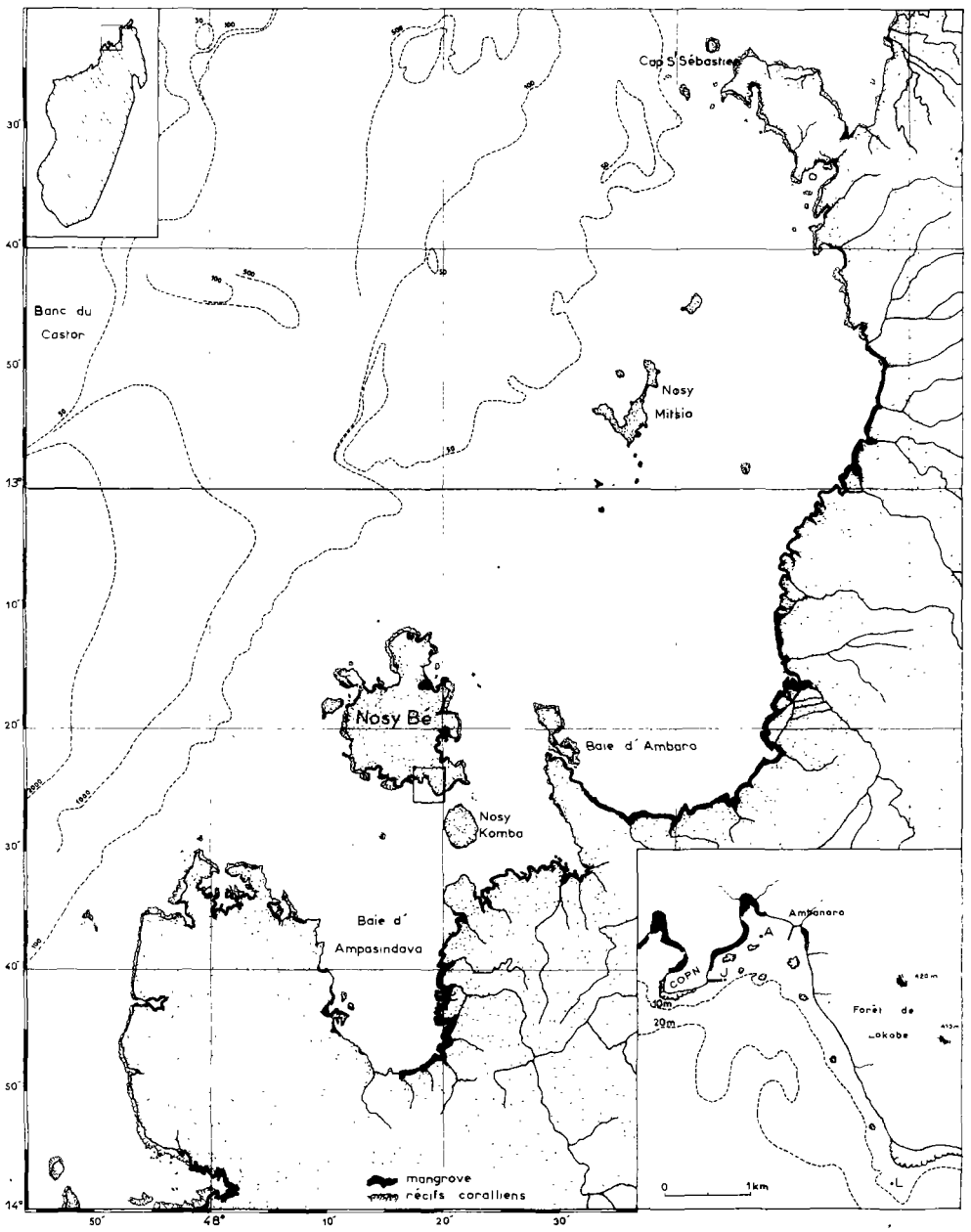


Fig. 1. Région de Nossi-Bé. En bas et à droite: baie d'Ambanoro, et emplacement des trois stations L, A et J. (COPN: Centre d'océanographie et des pêches de Nossi-Bé, O.R.S.T.O.M.)

Marée: Le marnage est assez élevé sur la côte nord-ouest de Madagascar. A Nossi-Bé même, les marées se caractérisent ainsi:

— type „semi-diurne",

— légère inégalité des deux ondes quotidiennes,

— amplitude élevée, mais variant notablement entre vive-eau (V.E.) et morte-eau (M.E.), les niveaux de la pleine mer étant respectivement: V.E. 4 m, M.E. 2,6 m (niveau moyen: 2,22 m).

— une période de 15 à 17 jours sépare deux passages successifs au même niveau et à la même heure. D'autre part, l'heure de la pleine-mer survient plus fréquement aux environs du lever et du coucher du soleil.

Les courants de marée sont donc très variables suivant l'heure et le jour (voir: mesures nycthémérales).

Turbidité; *houle*: La turbidité est très variable, dans cette région, selon le lieu et la saison. Les apports terrigènes, en saison des pluies, peuvent réduire de façon considérable la transparence des eaux.

Nossi-Bé se trouve dans un „*angle mort*" de la côte, à l'abri de la houle océanique; seule est observable, pendant la saison chaude, une légère houle du nord-ouest. Les houles locales prédominent, principalement celle qu'engendre la brise de mer.

4. Climatologie annuelle

Dans le nord–ouest de Madagascar règne un climat tropical d'alizés et de moussons. L'année se divise essentiellement en deux saisons:

— été austral, d'octobre à avril: saison chaude et humide;

— hiver austral, de mai à septembre: saison fraîche et sèche.

Les vents: Le régime des vents (fig. 2), très complexe dans cette région, résulte de trois composantes.

1 — Alizé: L'alizé austral souffle du sud-est sur Madagascar; humide sur la côte est, il se dessèche progressivement en traversant la Grande île. Il ne parvient que difficilement à Nossi-Bé même, ayant pour cela à franchir ou contourner les massifs montagneux du nord malgache.

2 — Moussons: Ces vents saisonniers soufflent, dans l'océan indien, du sud-ouest de mai à septembre, et du nord-est d'octobre à avril. Sur le continent asiatique, ils déterminent respectivement la mousson humide et la mousson sèche. Au sud de l'équateur, leur action se manifeste surtout par le renforcement ou l'affaiblissement de l'alizé. Dans le nord du canal de Mozambique:

— d'octobre à avril, la mousson du nord-est franchit l'équateur, s'incurve alors sous l'effet de la rotation terrestre, et souffle du secteur O.-N.O. dans le canal de Mozambique. Ce vent, que l'on a appelé „mousson du Mozambique", n'est autre, pour certains auteurs, que l'alizé septentrional ayant franchi l'équateur. Il est, quoi qu'il en soit, opposé à l'alizé austral, lequel s'en trouve considérablement diminué pendant cette saison.

— de mai à septembre règne ce que l'on peut appeler la „mousson virtuelle du sud-ouest", qui représente surtout le retour de l'alizé austral: entraîné dans le mouvement général vers le nord, ce dernier franchit l'équateur pour se joindre à la mousson du sud-ouest dans l'hémisphère nord. Pendant cette saison prédominent donc dans le canal de Mozambique des vents de secteur S.E., toutefois peu ressentis localement à Nossi-Bé.

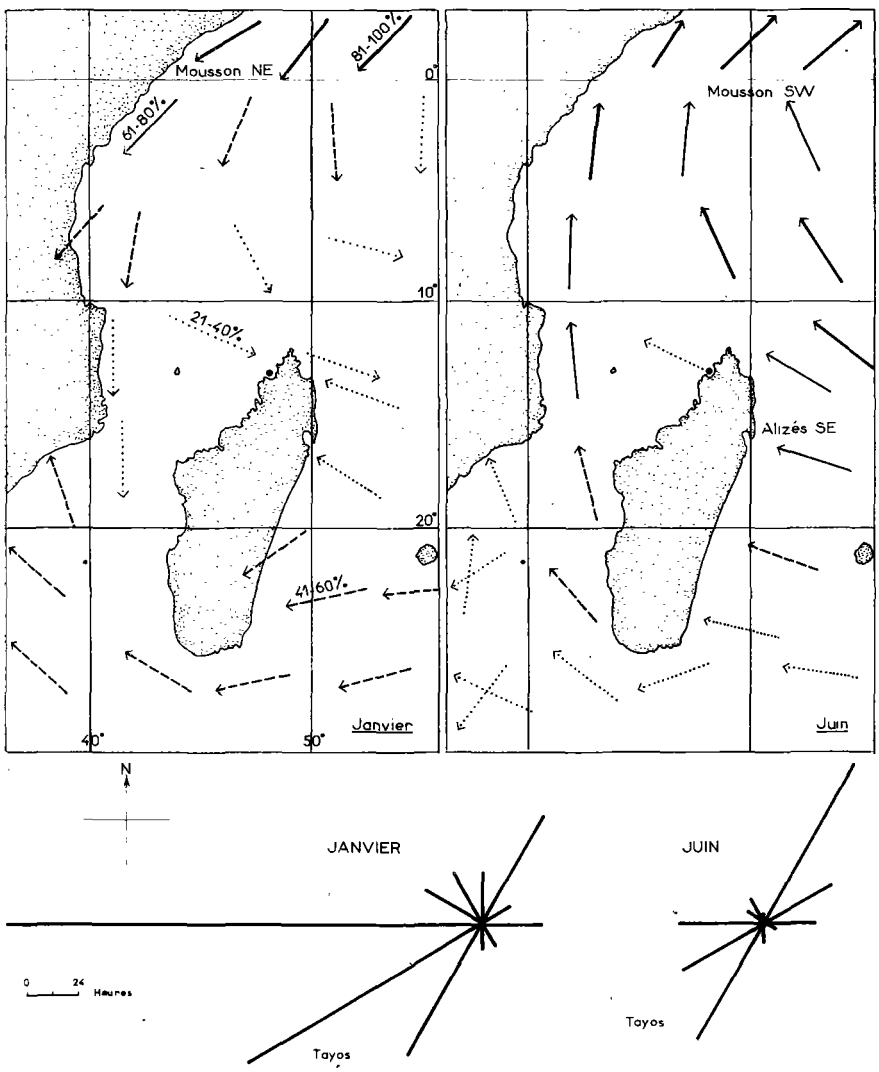


Fig. 2. En haut: régime général des vents, d'après les Monthly meteorological charts. En bas: régime local, d'après les totaux mensuels aimablement communiqués par la Station météorologique de Fascène, à Nossi-Bé

3 — Vents solaires: Ce sont, d'une part la brise de mer (localement appelée „tayo") de secteur O. mais variable (N.O.–S.O.), d'autre part, la brise de terre (ou „varatrasy") de direction opposée.

Régime régional et régime local: La figure 2 permet de comparer, au cours de deux mois opposés, le régime régional des vents au régime local à Nossi-Bé. Les particularités du climat local sont principalement dues au fait que, comme on l'a vu, Nossi-Bé se trouve „sous le vent" par rapport à l'alizé; cette situation favorise également la formation de dépression entre Nossi-Bé et les massifs montagneux du nord de Madagascar, et, par suite, de précipitations hivernales. Les vents solaires locaux exercent à Nossi-Bé une importance particulière; sui-

vant le cas, ils s'ajouteront ou s'opposeront aux vents régionaux, le tayo renforçant par exemple la mousson en saison chaude.

Facteurs climatiques divers: Les moyennes de la température de l'air pendant la période étudiée sont reportées sur la figure 3. Comme il convient en milieu tropical, ces températures sont élevées (moyenne: 26°) et l'amplitude des variations saisonnières est faible. Notons qu'en été les valeurs plafonnent, ou tendent à diminuer légèrement; dans l'ensemble, cette saison paraît plus longue que l'hiver.

Le total annuel des pluies est élevé: 2,25 m. La plus grande partie de ces précipitations survient entre décembre et mars. Il faut cependant noter, en dehors de la saison chaude, une „micro-saison" humide en août (localement appelée „pluie des mangues").

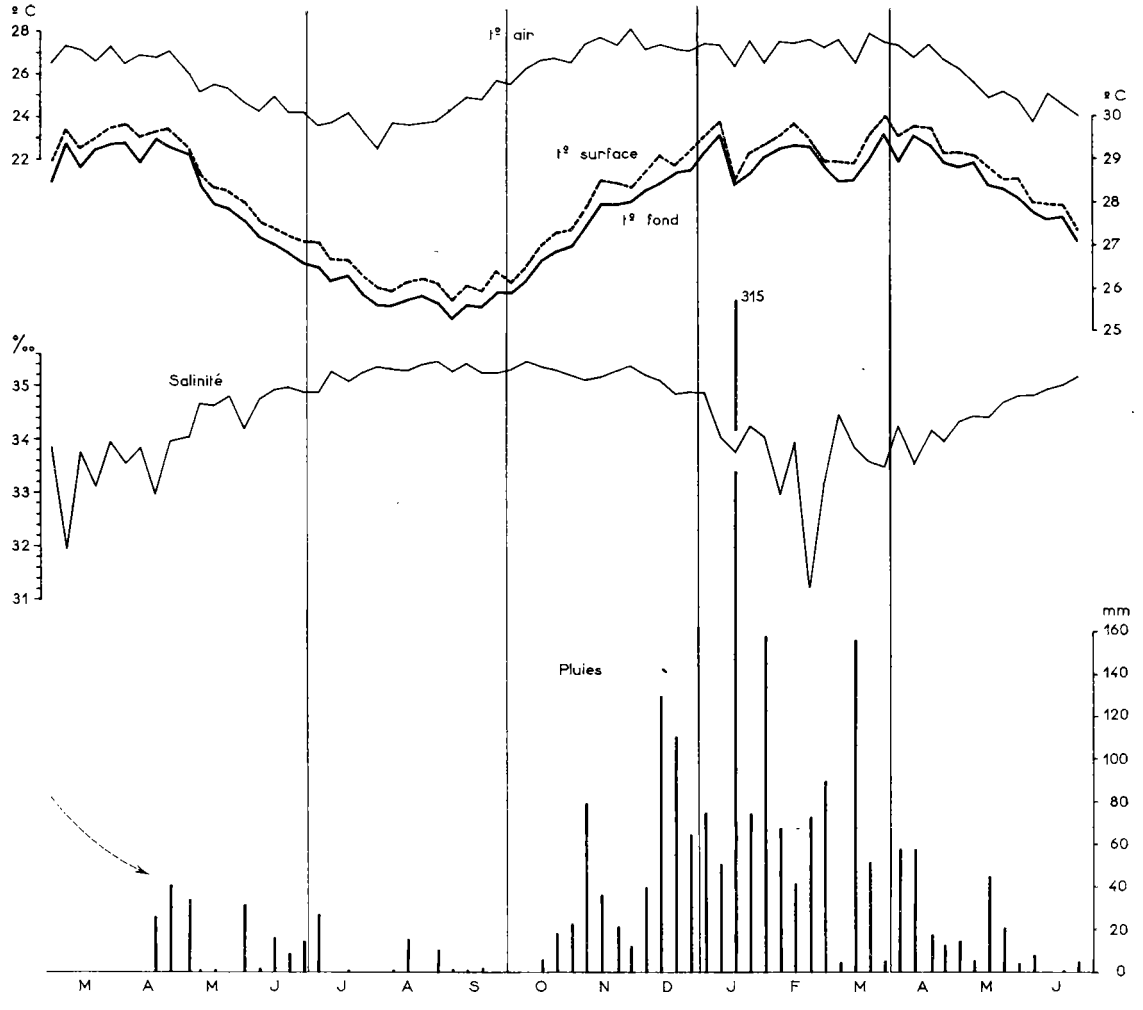


Fig. 3. Hydrologie et climatologie annuelles à Nossi-Bé. Moyennes hebdomadaires (deux mesures par jour); pour les pluies, totaux hebdomadaires. Température de l'eau et salinité mesurées en surface à l'extrémité de la jetée du Centre océanographique (station J). Les données pluviométriques des premiers mois font malheureusement défaut

La pression barométrique est maximale en hiver, minimale en été (fig. 4).

L'état hygrométrique, voisin de la saturation en saison chaude, est minimum en saison fraîche. Le maximum secondaire d'août, correspondant à la „pluie des mangues", est bien accusé (fig. 4).

La nébulosité n'a pu être évaluée que de façon approchée, par la méthode visuelle; d'autre part, l'ensoleillement a été mesuré au moyen d'un héliographe CAMPBELL. Les variations saisonnières de ces deux facteurs (fig. 4) sont telles que l'intensité lumineuse est notablement plus forte en hiver qu'en été.

II. Variations saisonnières

1. Méthodes

a) Définition des trois stations

Les trois cartes de la figure 1 indiquent la position de l'île de Nossi-Bé par rapport à la côte nord-ouest de Madagascar, ainsi que la situation dans Nossi-Bé de la baie étudiée.

Celle-ci, que l'on peut appeler soit „baie d'Ambanoro", soit „baie du Centre océanographique" puisque ce dernier s'élève sur sa rive ouest, est largement ouverte au sud, et caractérise assez bien les conditions littorales générales de cette

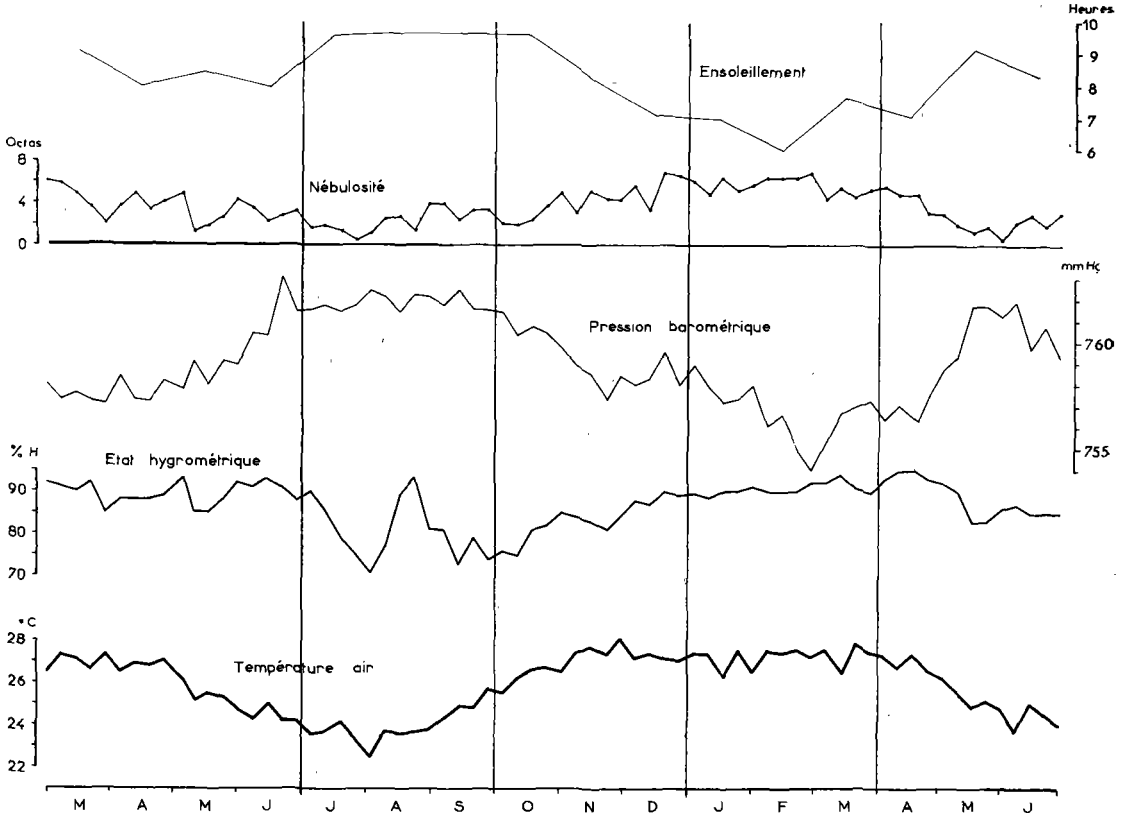


Fig. 4. Climatologie annuelle à Nossi-Bé. Ensoleillement: totaux mensuels aimablement communiqués par la Station météorologique de Fascène. Autres facteurs: moyennes hebdomadaires (deux mesures par jour) d'après les relevés du Centre océanographique

région de Madagascar: apports d'eaux douces et mangrove dans la partie la plus côtière (Ambanoro), et récifs coralliens vers l'extérieur (pointe de Lokobé). Aussi deux points extrêmes ont-ils été choisis pour les travaux de routine:

— Station L: à l'ouverture de la baie. Eaux claires; profondeur 8 m, fond de coraux,

— Station A: au fond de la baie. Eaux turbides (voisinage de la mangrove); profondeur 4 m.

Ces deux stations ont été occupées une fois par semaine de février 1963 à juin 1964: prélèvements en canot automobile, à une profondeur unique, sub-superficielle (1 m), au moyen d'une bouteille Van Dorn de 6 litres. Les deux prélèvements étaient fractionnés en sous-échantillons destinés aux mesures suivantes: salinité; comptage au microscope inversé; productivité par la méthode du ^{14}C et, accessoirement, par celle de l'oxygène; extraction des pigments photosynthétiques. Des récoltes au filet ont été également effectuées aux deux stations.

De plus, en vue d'éliminer d'éventuelles erreurs systématiques causées par le délai de temps séparant les deux prélèvements (environ 15 min), une troisième station a été utilisée de juin 1963 à juin 1964, à l'extrémité même de la jetée du Centre océanographique; le niveau choisi était là aussi de 1 m. Cette station, que j'appellerai ici „J", est étudiée quotidiennement — à quelques interruptions près — depuis 1955 par les techniciens du Centre océanographique, et a fourni matière aux publications de GÉRARD (1964) et ANGOT & GÉRARD (1967) analysées plus loin.

b) Comptages au microscope inversé

Méthode d'UTERMÖHL (1931a, b) appliquée au milieu marin par STEEMANN NIELSEN (1933) et développée par divers auteurs (voir détails et critiques in HOLMES & WIDRIG, 1956; LUND et al., 1958; UTERMÖHL, 1958; PAASCHE, 1960).

Fixation: Solution de lugol et d'acétate de sodium, définie par UTERMÖHL (1958) et dont TRAVERS (1962) reproduit la composition: IK: 10 g; I: 5 g; CH_3COONa: 5 g; H_2O: 70 cc.

Agitation: Il est nécessaire, avant de remplir la cuve de sédimentation, d'agiter l'échantillon d'une manière constante et, du moins, selon un temps constant (par exemple: 3 min). Cette précaution a son importance, puisque le remplissage de la cuve constitue, dans cette méthode, la seconde possibilité d'erreur d'échantillonnage (la première résidant dans le prélèvement à la mer).

Sédimentation: Cuves Zeiss de 100 cc; dans les cas de fortes concentrations planctoniques, cuves de 50 ou 25 cc.

La durée de la sédimentation a été fixée à 24 heures. En effet, de l'avis général, un temps plus court est probablement insuffisant; d'autre part, il m'est apparu inutile de prolonger ce délai au delà de 24 heures: s'il est vrai que le contenu figuré de l'eau de mer (seston) ne sédimente pas en totalité au fond de la cuve (voir plus bas), j'ai pu cependant m'assurer que le taux de sédimentation ne s'améliore pas au bout de 48 heures, ni même de six jours. Il faut admettre que les diverses forces physiques ont atteint dans la cuve, au bout de 24 heures, un équilibre définitif.

Comptage: Selon la taille et l'abondance des organismes, ceux-ci sont dénombrés dans tout le champ de la cuve, ou une partie seulement de celle-ci. Dans les cas de proliférations de certaines espèces, on n'examinait qu'une fraction restreinte du champ, par exemple deux bandes diamétrales perpendiculaires.

Précision et limites: Tout d'abord, comme on l'a évoqué plus haut, il faut supposer que certains organismes échappent à la sédimentation, demeurant adhérents aux parois latérales ou au couvercle de la cuve. Quelques précisions sur ce sujet souvent délaissé:

j'ai pu constater que ces organismes appartiennent principalement au genre *Chaetoceros*, quelquefois *Trichodesmium*, et que l'erreur introduite ne dépasse pas 15%.

Eu égard au faible volume d'eau de mer mis en jeu, cette méthode convient mal au dénombrement des organismes rares ou peu nombreux. Cette réserve concerne particulièrement le microplancton, dont on sait qu'il peut ne compter, en certains lieux ou en certaines périodes, que quelques individus par litre d'eau de mer. Dans ce cas, il n'est d'aucun recours de doubler ou même quintupler le volume de l'échantillon par une sédimentation préalable: une autre méthode doit être recherchée, qui permette de traiter un volume d'eau bien plus considérable (cf. prélèvement par pompage, centrifugation . . .).

Comme on le verra plus loin, les récoltes au filet permettent de remédier dans une large mesure à cette déficience.

Impliquant l'observation d'un matériel fixé, la méthode du microscope inversé convient mal à l'étude des petites formes fragiles dépourvues de squelette externe. Cette réserve concerne principalement le nannoplancton, constitué en grande partie de petits Flagellés nus: partiellement détruits par la fixation, ceux-ci sont très difficilement dénombrables, plus difficilement encore identifiables. Aussi, en matière de nannoplancton, me suis-je limité à un comptage approximatif global d'un ensemble de Péridiniens relativement reconnaissables, appartenant principalement aux genres: *Exuviaella*, *Prorocentrum*, *Amphidinium*, *Gymnodinium* et *Gyrodinium*, ainsi que quelques Phytoflagellés indéterminés.

c) Récoltes au filet

Petit filet de surface, conforme au modèle de Trégouboff & Rose (1957, pl. 1, fig. 1); diamètre 25 cm, longueur 80 cm; nylon n° 17 (Tripette & Renaud, Paris), vide de maille de 50 μ environ.

Récoltes aux stations L et A, à la profondeur de 1 m, pendant 10 à 15 min. Fixation: lugol ou formol; occasionnellement, le matériel était acheminé non fixé au laboratoire, pour étude in vivo.

d) Pigments photosynthétiques

Méthode de Richards & Thompson (1952), modifiée par Creitz & Richards (1955) et Parsons & Strickland (1963). La technique adoptée suit en général les recommandations récemment publiées par le S.C.O.R. (Anonyme, 1966).

Filtration: au laboratoire, après un délai de 30 à 50 minutes (selon la station) après le prélèvement.

Volume filtré: sauf très rares exceptions: 2 litres aux stations L et A, 3 l à la station J (Pour la station A en effet, un volume de 2 l représente souvent le maximum filtrable, en raison de la turbidité des eaux. En vue d'une comparaison plus étroite entre les deux stations L et A, un volume égal a été utilisé dans les deux cas, bien que les eaux fussent toujours plus claires en L).

Temps de filtration: de 5 à 15 min.

Matériel utilisé: filtres Millipore HA, 47 mm ∅. Pompe aspirante-refoulante Millipore (vide: 68 cm Hg).

Une pincée de poudre de CO_3Mg était déposée sur chaque filtre au début de l'opération.

Dessication: dans une enceinte à silicagel, à l'obscurité et à la température ambiante, pendant 24 heures.

Extraction: le lendemain de la filtration. Mise en solution de chaque filtre dans 5 cc d'acétone à 90% bidistillée, pendant 24 heures et à l'obscurité. Les extraits étaient agités à plusieurs reprises au cours de ce temps. Je n'ai donc pas procédé au broyage des filtres, à l'encontre des recommandations actuelles du S.C.O.R.

Centrifugation: à 5.000 tours/min, pendant 10 min.

Mesures des densités optiques: Spectrophotomètre Beckman D. U. Cuves de quartz de 1 cm. Lectures aux longueurs d'onde suivantes, et dans l'ordre suivant: 750, 665, 645, 630, 510, 480 et 430 mμ. Témoin: acétone bidistillée, à 90%, contenant en solution un iltre Millipore vierge.

Correction de turbidité: soit k la densité optique lue à la longueur d'onde 750 mμ. On retranche: k aux valeurs lues à 665, 645 et 630 mμ, 1,5 k aux valeurs lues à 510 mμ, et 2 k aux valeurs lues à 480 et 430 mμ.

Calcul des concentrations: selon les formules de PARSONS & STRICKLAND (ibid.), qui me semblent, pour les raisons mêmes invoquées par ces auteurs, préférables aux formules originelles de RICHARD & THOMPSON (ibid.). Notons que la troisième et dernière solution proposée (Anonyme, 1966) diffère très peu de celle de PARSONS & STRICKLAND. De plus, le rapport des densités optiques à 430 et à 665 mμ (MARGALEF, 1960) a été calculé pour tous les échantillons.

e) Production primaire par la méthode du ^{14}C

Méthode de STEEMANN NIELSEN (1951b) développée par le même auteur (1952, 1954, 1958, 1964, 1965) et STEEMANN NIELSEN & JENSEN (1957), STRICKLAND (1960), BROUARDEL & RINCK (1963), HERRERA & MARGALEF (1966) etc. Matériel provenant en partie de l',,International Agency for ^{14}C determination", Charlottenlund (Danemark). Cette méthode a été employée in situ.

Expérimentation

Inoculation: bouteilles „claires" et „noires" en pyrex, de 265 cc, lavées entre chaque expérience avec un détergent faible. Ampoules de 4 μC. Inoculation à raison d'une ampoule par flacon, soit 4 μC pour 265 cc; cette concentration, dictée par des raisons d'économie, peut paraître faible: à Tuléar, MAESTRINI & PIZARRO (1966) ont employé 10 μC par flacon de 100 cc, et d'autre part, à bord de l' „Anton Bruun" (RYTHER, HALL et al., 1966) le taux utilisé était de 10 μC pour 125 cc. Cependant la présente concentration est suffisante, à condition de filtrer la totalité de l'échantillon, en raison des productivités relativement élevées du secteur littoral étudié; les expériences suivantes le confirment: à plusieurs reprises, à partir d'un même prélèvement, trois flacons ont été respectivement inoculés avec 1, 2 et 3 ampoules; la radioactivité des filtres est approximativement proportionnelle au nombre d'ampoules introduites.

Incubation: toutes les mesures ont été effectuées in situ à l'extrémité de la jetée du Centre, et à la profondeur 1 m, identique à celle des prélèvements. Les bouteilles étaient accrochées à un flotteur, celui-ci suspendu à un tangon et manoeuvrable de la jetée par un jeu de poulies: par ce moyen, les flacons étaient maintenus à distance de l'ombre de la jetée, et accessibles à toute heure de la marée. L'exposition durait quatre heures; de façon à respecter les variations saisonnières de la déclinaison solaire, elle ne commençait pas à heure fixe mais, par simple convention, une heure après le lever du soleil. Les conditions d'éclairement au milieu de la matinée sont le plus souvent sub-optimales (cf. p. 54).

Filtration: dispositif de filtration par pression (STEEMANN NIELSEN, 1958, fig. 1), fabriqué par l'Intern. Agency.

Filtres: Membranfilter (Göttingen), 35 mm ⌀, Gr. 2, porosité 0,6 μ. Notons que ces filtres sont d'emploi beaucoup moins aisé que les membranes Millipore, car plus fragiles et se gondolant après séchage.

Serre-filtres et supports de filtres: de fabrication artisanale, sur les modèles de BROUARDEL & RINCK (1963, fig. 8–10).

Après la filtration, les membranes sont séchées dans une enceinte à silicagel, puis lavées comme suit: exposition aux vapeurs d'HCl fumant pendant 15 minutes, puis passage en enceinte à chaux sodée pendant 10 heures.

Calcul du taux de production

Concentration de l'eau de mer en CO_2: déterminé à l'aide des tables de BUCH (in HARVEY, 1960), en fonction de la température et de la salinité; à défaut de mesures du pH, j'ai supposé celui-ci constant et égal à 8,2.

Mesure de la radioactivité du filtre: Compteur „Saphymo", équipé d'un tube Geiger à fenêtre terminale mince, Tracerlab TGC 2. Le nombre de coups/min. est donné par la moyenne de deux comptages successifs de 15 min. chacun, après déduction de l'acti-

vité de fond (background) — celle-ci mesurée au début et à la fin de chaque série de comptages.

Evaluation de la radioactivité de l'ampoule: par défaut de matériel, je n'ai pu dresser à Nossi-Bé la courbe d'étalonnage de la solution radioactive fournie par l'Intern. Agency. Aussi ai-je adressé à cette dernière, après comptage, les 200 premiers filtres obtenus au cours du cycle annuel, et étalonné par ce moyen l'installation de Nossi-Bé. Le rendement de cette dernière était d'ailleurs testé régulièrement au moyen d'un filtre-étalon, et n'a pas varié pendant les 18 mois de mon séjour.

C'est après avoir pratiquement terminé le présent travail que j'ai eu connaissance de l'importante modification apportée par STEEMANN NIELSEN (1965) à l'évaluation de la radioactivité des ampoules. Toutes les données qui suivent (taux de production et rapports production/pigment) sont donc passibles de la correction proposée par cet auteur, c'est à dire à majorer de „31%", mais la comparaison avec tous les travaux cités reste inchangée.

Expression des résultats

Dans les premiers mois de cette étude, j'ai utilisé en parallèle pour chaque station un flacon „clair" et un flacon „noir"; mais devant la régularité de la fixation de carbone à l'obscurité (cf. p. 35), je n'ai plus maintenu ce procédé que pour la station J. Aucune correction n'a été appliquée concernant le recyclage et la discrimination $^{12}C/^{14}C$.

Sauf indication contraire, les résultats se rapportent donc à l'assimilation apparente de carbone dans les bouteilles claires, et mesurent selon la terminologie de BROUARDEL & RINCK (ibid.) la „production nette apparente de la communauté zoo + phytoplancton".

f) Production primaire par la méthode de l'oxygène

Cette question a été abordée sous deux aspects:

— variations saisonnières de la concentration d'oxygène dissous in situ: cette méthode s'est ici révélée inutilisable (cf. p. 16).

— variations expérimentales, au cours d'une période d'incubation en flacon clos, selon le principe de GAARDER & GRAN (1927), MARSHALL & ORR (1928), etc. (voir aspects méthodologiques récents in SMAYDA, 1957; PRATT & BERKSON, 1959; STRICKLAND, 1960; PATTEN et al., 1964; TEIXEIRA et al., 1965a). Ces expériences ont été conduites parallèlement aux mesures par le ^{14}C, et avec des flacons clairs identiques, mais pendant six mois seulement (de décembre 1963 à juin 1964): deux sous-échantillons supplémentaires étaient constitués à partir du prélèvement à la station J (à l'exclusion des stations L et A, par crainte des délais de transport); l'un d'eux était traité immédiatement, l'autre était accroché au flotteur, aux côtés du flacon à ^{14}C et, comme ce dernier, traité après quatre heures d'exposition.

Etant donné que je n'ai pas utilisé de bouteilles „noires", les résultats exprimés se rapportent à la production nette.

Les dosages étaient effectués par la méthode de WINKLER, et les pourcentages de saturation calculés, en fonction des température et salinité ambiantes, d'après les tables de FOX (in HARVEY, 1960) ou les nomogrammes de KALLE (1939). Au sujet de la validité des tables de FOX, voir TRUESDALE et al. (1955), RICHARDS & CORWIN (1956), RICHARDS (1957, 1965) et le travail tout récent de GREEN & CARRIT (1967).

2. *Hydrologie annuelle*

a) Température et salinité

Le cycle annuel de la température et de la salinité à la station J est représenté sur les figures 3 (moyennes hebdomadaires) et 5 (mesures hebdomadaires). Il suit, avec un décalage de quelques semaines, le cycle climatique précédemment décrit:

— A la saison climatique fraîche (mai—septembre) correspond une saison hydrologique (juin—novembre) aux eaux relativement froides (26—27°) et de salinité relativement élevée (35,2—35,4‰).

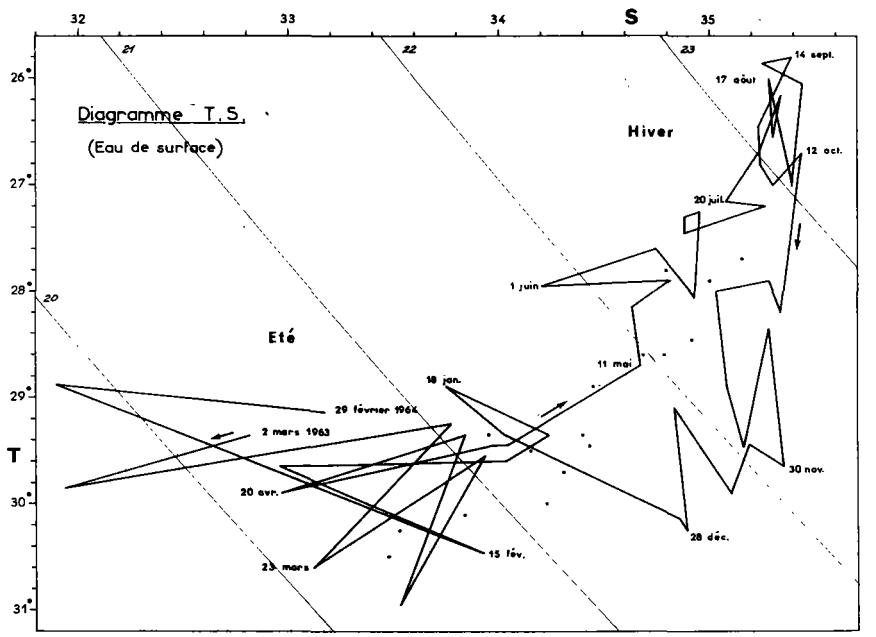


Fig. 5. Diagramme T–S. Mesures hebdomadaires, de mars 1963 à juin 1964 (station J, eau de surface). La ligne brisée forme un cycle de 12 mois; les points isolés représentent le reste des mesures. Chaque valeur représente la moyenne de deux mesures effectuées l'une à basse mer, l'autre à pleine mer, ceci pour annuler l'influence éventuelle de la marée. (Cette figure a été antérieurement publiée dans une note préliminaire: SOURNIA, 1965a)

— A la saison des pluies (octobre—avril) correspond une saison hydrologique (décembre—mai) aux eaux chaudes (29—30°) et peu salées (32—34‰).

Pendant cette seconde période, les températures et, surtout, les salinités présentent des variations secondaires accusées. Par opposition, les caractéristiques hivernales apparaissent homogènes.

L'écart thermique annuel est réduit (4 ou 5 °C); par contre, l'écart annuel des salinités est relativement beaucoup plus important (de l'ordre de 4‰); si l'on ramène les variations de salinité à des taux de dilution, comme le fait MÉNACHÉ (1957), et que l'on considère la valeur 35‰ comme „normale", une salinité de 31‰ représente une dilution de $\frac{35-31}{35} = 11{,}4\%$ d'eau douce. Encore les données ici exposées ne repésentent-elles que des moyennes (fig. 3: moyennes hebdomadaires, à raison de 2 mesures par jour; fig. 5: moyennes de deux mesures effectuées le même jour, à intervalles hebdomadaires). De plus, comme on le verra plus loin, la dilution était souvent supérieure au fond de la baie (station A).

Telles sont les grandes lignes de l'hydrologie annuelle, en accord d'ailleurs avec les observations antérieures de MÉNACHÉ (ibid.) pour la période 1955—56, et de GÉRARD (1964) pour la période 1956—62. Trois remarques de détail sont à ajouter:

1 — Les légères précipitations estivales („pluie des mangues", p. 8) ne semblent pas retentir sur l'hydrologie.

2 — On a vu (p. 8) que la température de l'air plafonne ou diminue légèrement au milieu de l'été (janvier—mars). A cette époque, la température de l'eau révèle, d'après mes données, deux minima secondaires (ces deux accidents se fondent en un seul sur les graphiques de MÉNACHÉ et de GÉRARD (ibid.), dont les échelles de temps sont différentes). Ces chutes de température sont à peu près simultanées aux minima annuels de la salinité et, comme ceux-ci, liées aux chutes de pluie estivales; toutefois, l'enchaînement des phénomènes est difficile à retracer, du fait de la brutalité et de l'irrégularité des précipitations.

3 — Le décalage entre les variations du climat et celles du milieu marin peut être attribué à une triple cause: 1) Décalage entre le réchauffement annuel de l'air et le début des précipitations: celles-ci surviennent lorsque la température de l'air a presque atteint son maximum, 2) Inertie thermique de l'eau de mer par rapport à l'air, 3) Délai entre la chute des pluies et la diminution de la salinité, ce que l'on pourrait appeler „inertie saline".

Un effet remarquable de cette situation réside dans le retard de la salinité sur la température de l'eau de mer aux environs de décembre (fig. 5): salinité encore élevée, température déjà presque à son maximum.

b) Oxygène dissous

Le cycle annuel de l'oxygène dissous a antérieurement été étudié par GÉRARD (1964) dans la baie d'Ambanoro, et par ANGOT (1965a) dans la région avoisinante. Ces deux auteurs concluent à un maximum hivernal et un minimum estival (ce dernier simultané, pour GÉRARD, aux chutes de pluies); mais il ne s'agit là que de valeurs absolues (concentrations en ml/l) et non de valeurs relatives (pourcentages de saturation). GÉRARD donne cependant ces derniers chiffres en annexe, mais ne discute que les premiers. Dans leur ensemble, les interprétations des deux auteurs négligent les conditions physiques de solubilité du gaz étudié:

— la solubilité est inversement fonction de la température et de la salinité du milieu,

— de ces deux facteurs, le premier exerce l'effet le plus important: dans le cas de variations opposées de la température et de la salinité (ce qui est le cas de l'hydrologie annuelle à Nossi-Bé), le rôle de la température prédomine.

Le problème de l'oxygène dissous nous intéresse principalement ici par ses incidences biologiques; celles-ci ne peuvent être évaluées qu'après élimination des causes physiques mentionnées ci-dessus, c'est à dire après calcul des concentrations en termes de pourcentages de saturation.

Traitement des données: Je disposais pour cette étude des mesures de routine du Centre océanographique, à savoir deux mesures quotidiennes, à pleine mer et basse mer (station J, eau de surface). De façon à éliminer les variations dans le temps autres que saisonnières, c'est à dire les variations liées à la hauteur de la marée et à l'heure du jour (qui seront abordées p. 51), j'ai procédé comme suit: les mesures ont été groupées en intervalles (de 10 à 14 jours) séparant deux passages consécutifs de la pleine mer vers 12 h (le choix de cette heure n'est pas tout à fait arbitraire, puisqu'il correspond localement au jour du minimum de morte-eau). Pour chaque „cycle" de la marée ainsi délimité, la teneur moyenne en oxygène dissous a été retenue.

Les résultats sont reportés sur la figure 6. Il apparaît que:

(a) Les teneurs brutes en oxygène dissous (courbe 1) suivent un cycle annuel: maximum hivernal, minimum estival. Ce cycle comporte, en été, d'importantes variations secondaires.

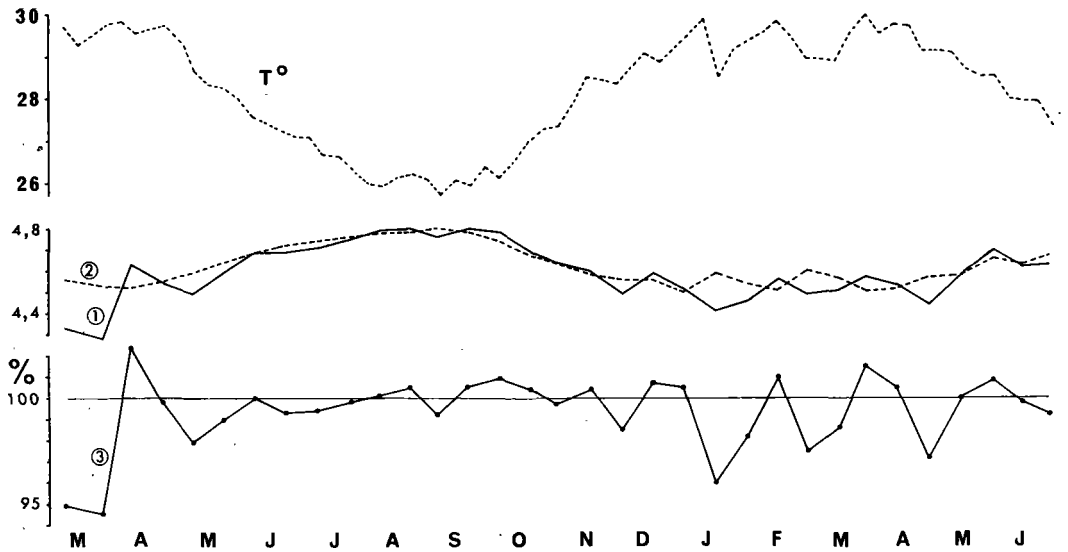


Fig. 6. Cycle annuel de l'oxygène dissous (station J, eau de surface). T°: température (d'après les données de la fig. 3). 1: concentrations brutes mesurées (ml/l). 2: taux de saturation, calculés d'après les températures et salinités correspondantes (ml/l). 3: concentrations relatives, en pourcentages de saturation: quotient de (1) par (2)

(b) Le taux de saturation théorique (courbe 2), calculé d'après les températures et salinités ambiantes, suit un cycle annuel inverse de celui de la température (et parallèle à celui de la salinité, comme annoncé plus haut). A noter les maxima secondaires, en saison des pluies, liés aux minima secondaires de la température.

(c) Les deux cycles 1 et 2 sont, dans une large mesure, parallèles, mais plusieurs divergences se manifestent en été.

(d) Exprimées en pourcentages de saturation (courbe 3), les teneurs en oxygène dissous ne montrent pas de variations saisonnières, mais seulement une notable instabilité estivale. L'on peut dire que ces pourcentages sont, tout au long de l'année, voisins de la saturation, mais présentent plusieurs „anomalies négatives".

(e) Ces anomalies sont principalement estivales. Elles coïncident avec les maxima secondaires du taux de saturation théorique, c'est à dire avec les minima secondaires de la température (et de la salinité) et, en dernière analyse, avec les chutes de pluies. D'autre part, une anomalie est également observable en hiver (début septembre), et peut elle aussi être reliée aux précipitations — quoique faibles — qui surviennent à cette époque.

(f) La sursaturation est fréquente tout au long de l'année (plus fréquente qu'il ne paraît sur le graphique, puisque celui-ci reporte des valeurs moyennes).

Conclusions et discussion

A l'inverse des teneurs absolues, les teneurs relatives en oxygène dissous ne présentent pas de variations saisonnières. Elles sont tout au long de l'année voisines de la saturation, ce qui laisse penser à une intense activité photosynthétique, mais montrent des accidents négatifs simultanés aux chutes de pluies.

Le cycle annuel de l'oxygène dissous semble donc ici de nature essentiellement physico-chimique, et non biologique. On verra qu'il en va différemment des

variations nycthémérales (p. 51), ainsi que des mesures expérimentales en flacon clos (p. 35).

Par anticipation sur la suite du présent travail: si l'on envisage isolément chacun des aspects du développement annuel du phytoplancton, aucun de ceux-ci ne peut être mis en parallèle avec le cycle des teneurs relatives en oxygène; les quelques corrélations observables ne sont que partielles et, d'ailleurs, souvent contradictoires. Une conclusion identique peut être tirée de plusieurs travaux relatifs à diverses zones tropicales littorales ou néritiques: Grande Barrière australienne (ORR, 1933, et cf. MARSHALL & ORR, 1933); côte occidentale des Indes SUBRAHMANYAN, 1959b); golfe du Mexique (MC FARLAND, 1963). Un cycle (annuel est cependant observable au large des côtes du Kénya (NEWELL, 1959).

On sait qu'en milieu tempéré les phénomènes saisonniers sont mieux tranchés, et qu'une corrélation est fréquente entre les taux d'oxygène et les poussées phytoplanctoniques, d'où la possibilité d'une évaluation de la production primaire annuelle (MARSHALL & ORR, 1927; GRAN, 1929; COOPER, 1933; SEIWELL, 1935; BRAARUD & BURSA, 1939; RILEY, 1941a—b, 1952, 1956; REDFIELD, 1948; RILEY & CONOVER, 1956; HALIM, 1960); cependant, même dans les eaux tempérées, cette corrélation n'est pas de règle, et les facteurs physiques peuvent prédominer, comme il ressort des travaux de BRAARUD & KLEM (1931), DAKIN & COLEFAX (1935), PHIFER & THOMPSON (1937).

La complexité des variations saisonnières de l'oxygène dissous tient au grand nombre de facteurs physico-chimiques et biologiques impliqués, ainsi qu'aux difficultés d'évaluation des échanges entre mer et atmosphère d'une part, et entre couche euphotique, eaux sous-jacentes et sédiments d'autre part.

Cette complexité se trouve décuplée dans les régions tropicales littorales (telles que la baie ici étudiée) par suite du haut niveau de productivité, de l'important mixage des eaux, et de la rapidité générale des processus biologiques et biochimiques. Notons que, dans le cas présent, la coïncidence remarquable entre précipitations et teneurs minimales en oxygène reste à expliquer: la cause réelle peut en effet être de nature biologique aussi bien que physique, puisque les chutes de pluies sont généralement accompagnées de proliférations de la Cyanophyte *Trichodesmium* (la présence de ces algues est également invoquée par MC FARLAND (ibid.), mais en sens opposé, pour rendre compte des cas de sursaturation).

3. Composition taxinomique du phytoplancton

a) Microplancton et nannoplancton

La distinction entre ces deux groupes apparaît ici comme fondamentale. D'ailleurs, bien que délicate et imprécise, cette discrimination basée sur le mode de récoltes, donc empirique, n'est pas pour autant arbitraire. Plusieurs caractères distinctifs étaient évidents à Nossi-Bé, et sont reportés dans le tableau I.

Bien que les acceptions les plus diverses aient été données aux mots „microplancton" et „nannoplancton", la limite de taille entre les deux groupes est généralement fixée à 50 μ, sans doute parce que cette dimension correspond au vide de maille des filets les plus fins. Il est cependant d'observation courante que la taille minimum des planctontes récoltés au filet est nettement inférieure à l'ouverture de maille employée; d'autre part, la plus grande partie des cellules qui échappent au filet sont de dimensions inférieures à 15 μ (RILEY et al., 1949; RILEY, 1957; YENTSCH & RYTHER, 1959; HULBURT et. al., 1960). Finalement,

Tableau I — Caractères distinctifs du microplancton et du nannoplancton à Nossi-Bé

	Microplancton	Nannoplancton
Mode de récolte:	Filet ou sédimentation.	Exclu (par définition) des récoltes au filet.
Conditions d'observation; identification:	L'état du matériel permet une identification relativement aisée (difficultés confinées à certains genres, tels que *Chaetoceros*).	Matériel lésé par la fixation, en grande partie non identifiable (nécessiterait techniques particulières).
Précision du comptage:	Incertitudes seulement inhérentes à la distribution *in situ* et au mode d'échantillonnage. Toutefois, la méthode perd toute précision dans le cas de populations très pauvres.	Pour la raison ci-dessus, comptage toujours partiel et très incertain.
Groupe numériquement dominant:	Diatomées.	Péridiniens nus et autres Flagellés.
Groupes d'importance numérique secondaire:	— Cyanophytes (*Trichodesmium*) — Péridiniens cuirassés, et quelques formes nues.	— Protistes divers — Quelques Diatomées — Quelques Péridiniens cuirassés.
Abondance numérique et variations saisonnières:	Très variable, de ε à 200000 cell./l; le plus souvent, moins de 10000. Des phases „subdésertiques".	Variations relativement peu importantes. Toujours plus de 50000 cell./l.

la récente classification limnologique de DUSSART (1966) semble devoir être étendue à l'océanographie:

— microplancton = au dessus de 20 μ,

— nannoplancton[1]) = au dessous de 20 μ, incluant, sauf précision supplémentaire, l'ultranannoplancton (moins de 2 μ).

Notons que la limite de 20 μ correspond approximativement, pour le plancton marin, à la taille minimum des Diatomées et à la taille maximum des Flagellés nus: ceci du moins si l'on considère les deux groupes dans leur ensemble, car les exceptions ne sont pas rares.

Concernant le nannoplancton, je n'ai que peu à ajouter aux caractères généraux exposés dans le tableau I, du fait de l'imprécision de mes comptages (cf. p. 11). Signalons du moins l'apparente diminution du nombre de cellules lors des poussées massives de microplancton — mais il peut s'agir là d'un défaut d'évaluation. Par contre, la comparaison des prélèvements effectués chaque semaine aux trois stations et examinés simultanément est beaucoup plus sûre,

[1]) Le terme d'„hekistoplankton" introduit par COLE (1952) semble n'avoir rencontré que peu de succès, et a d'ailleurs été employé dans des sens différents; son étymologie est en outre ambiguë, puisque ἥκιστος (très faible, très petit) peut être pris pour ἧκιστος (très lent).

et montre que les concentrations sont plus élevées en A qu'en L (cf. p. 41), les concentrations à la station J étant en général intermédiaires.

Le rôle du nannoplancton sera évoqué à nouveau en conclusion de l'étude du cycle annuel (p. 39). Tout le reste du présent chapitre concerne exclusivement le microplancton.

b) Aspect qualitatif et quantitatif

A défaut d'une méthode universelle qui permettrait d'identifier et de dénombrer tous les organismes phytoplanctoniques, du plus gros au plus petit et du plus abondant au plus rare, j'ai utilisé en parallèle les deux méthodes du filet et de la sédimentation:

— la méthode du filet, dont on trouvera les critiques récentes in BRAARUD (1958), YENTSCH & RYTHER (1959), TRAVERS (1962) et GRALL & JACQUES (1964), n'est assurément pas propre à fournir un échantillonnage quantitatif, mais permet de connaître la composition relative des populations, sous réserve d'une certaine sélectivité au sein même du microplancton (YENTSCH & RYTHER, ibid.). Les proportions des divers organismes, ramenées en pourcentages de n individus observés, peuvent être qualifiées de „semi-quantitatives" (cf. fig. 8: les 5 graphiques supérieurs).

— les comptages au microscope inversé (fig. 7, et graphique inférieur de la fig. 8) fournissent des valeurs absolues, mais, à la différence des récoltes au filet, perdent leur signification dans les cas de populations numériquement très pauvres.

c) Inventaire qualitatif

Le détail en est donné dans le tableau II; celui-ci est lui-même résumé, pour ce qui est des répartitions mondiales, dans le tableau III. La prédominance des Diatomées sur les Péridiniens est manifeste. On peut également opposer le cosmopolitisme des premières à la thermophilie générale des seconds. Dans les deux groupes, un très faible pourcentage de taxons sont confinés à l'océan indien ou à l'indo-pacifique. Enfin, la plus grande partie des microplanctontes ici reportés étaient déjà connus dans le canal de Mozambique (SILVA, 1956, 1960; BALLANTINE, 1961; TRAVERS, 1965) et dans diverses zones néritiques de l'océan indien. Pour plus de détails biogéographiques sur cet inventaire, je me permets de renvoyer à mes trois travaux antérieurs (1967, et s. presse a—b).

J'ai utilisé dans les tableaux II et III les termes classiques d',,océanique" et de „néritique"; une vue d'ensemble sur la bibliographie mondiale montre que la distinction est souvent évidente, bien que les critères en soient controversés — ce que dit WOOD (1964, p. 499) en d'autres termes. En accord avec ce dernier auteur, je pense que les expressions „paractique" et „anoictique" créées par SMAYDA (1958) sont superflues; quant à la troisième, „adiaphorique", on peut la traduire très simplement par „indifférent". Ceci étant, il apparaît que, dans le secteur étudié, les espèces néritiques et indifférentes l'emportent en nombre sur les espèces océaniques (ce qui se traduit essentiellement par la prépondérance des Diatomées sur les Péridiniens). De plus, à ce point de vue, une différence saisonnière se manifeste: les espèces océaniques sont proportionnellement plus nombreuses en hiver qu'en été.

Nous sommes donc ici en présence d'une microflore inter-tropicale ou subtropicale, principalement néritique et, dans la mesure où cette délimitation peut être appliquée au phytoplancton marin, indo-pacifique.

Tableau II — Inventaire du microplancton

Répartition mondiale (première colonne)

C: cosmopolite
TT: tropicale – tempérée
IT: inter-tropicale
IP: indo-pacifique
OI: océan indien
O: océanique
N: néritique

Récoltes personnelles à Nosy-Bé (seconde colonne)

Fréquence: E: estivale
H: hivernale
P: pérennante
F: fortuite

Abondance maximale:

5: Espèce présente dans les échantillons „filet" et dans les échantillons „Utermöhl"; relativement très abondante (plus de 10000 cellules/l)
4: Id., abondante (de 500 à 10000 cell./l)
3: Id., rare (de 20 à 500 cell./l)
2: Espèce seulement récoltée au filet, donc très rare
1: Id., extrêmement rare

*: taxons faisant l'objet de nouvelles combinaisons *in* SOURNIA (s. presse a)

				Diatomées Centriques
C	N	F	1–2	*Paralia sulcata* (EHR.) CLEVE
IT?	O?	P–E	2–3	*Stephanopyxis palmeriana* (GREV.) GRUNOW
C	N	F	4	*Skeletonema costatum* (GREV.) CLEVE
C?	O?	F	1	*Thalassiosira subtilis* (OSTENF.) GRAN
C		F	1–2	*Coscinodiscus excentricus* EHR.
C		F	1	*Coscinodiscus lineatus* EHR.
C		F	1	*Coscinodiscus marginatus* EHR.
C	O?	F	1–2	*Coscinodiscus radiatus* EHR.
?		F	1	*Coscinodiscus Thorii* PAVILLARD
IT		F	1	*Coscinodiscus jonesianus* (GREV.) OSTENF.
IT?	O	E?	1	*Coscinodiscus nobilis* GRUNOW
?		F	1	*C. centralis* var. *pacificus* GRAN & ANGST
OI		E	2	*C. gigas* var. *praetextus* (JANISCH) HUSTEDT
OI?		P	2	*C. Janischii* var. *arafurensis* GRUNOW
?		P	2	*Coscinodiscus incertus* KARSTEN*
IT	O	P–E	3	*Planktoniella sol* (WALLICH) SCHÜTT
C	N	F	1	*Actinoptychus senarius* (EHR.) EHR.
C	N	F	1	*Actinoptychus splendens* (SHADB.) RALFS in PRITCH.
OI	N?	F	1	*Actinoptychus trilingulatus* (BRIGHTW.) RALFS in PRITCH.
TT	O	F	1	*Asterolampra marylandica* EHR.
TT?	O?	F	1	*Asterolampra Van-Heurckii* BRUN
TT	O?	F	1	*Asterolampra Grevillei* (WALLICH) GREVILLE
C	O?	P	1–2	*Asteromphalus heptactis* (BREB.) RALFS in PRITCH.
TT	N?	F	1–2	*Asteromphalus flabellatus* (BREB.) GREVILLE
?		F	1	*Asteromphalus roperianus* (GREV.) RALFS in PRITCH.
IT	O	F	1	*Gossleriella tropica* SCHÜTT
C	N	F	1	*Actinocyclus octonarius* EHR. var. *octonarius*
IT?	N?	F	1	*Chrysanthemodiscus floriatus* MANN emend. TAKANO
C	O	F–H	1–2	*Corethron criophilum* CASTRACANE
C?		P	3	*Lauderia annulata* CLEVE
C?	N?	F	1	*Schroederella delicatula* (PERAG.) PAVILLARD*
?		F	1	*Dactyliosolen antarcticus* CASTRACANE
TT		P–H	1	*Dactyliosolen mediterraneus* PERAGALLO
C	N	P	3	*Leptocylindrus danicus* CLEVE
C?	N?	F	3	*Leptocylindrus minimus* GRAN

Tableau II (suite)

C	N	P—E	4	*Guinardia flaccida* (Castr.) Peragallo
C	N	F	3	*Rhizosolenia fragilissima* Bergon
TT	N	F	3	*Rhizosolenia cylindrus* Cleve
TT	O	P—E	3	*Rhizosolenia Bergonii* Peragallo
?		F	1	*Rhizosolenia obtusa* Hensen
C	N	F—E	4	*Rhizosolenia Stolterfothii* Peragallo
TT	O	P—E	3	*Rhizosolenia robusta* Norman in Pritchard
TT	N?	F	3	*R. imbricata* Brightwell var. *imbricata*
C	N?	P	4	*R. imbricata* var. *Shrubsolei* (Cleve) Schröder
C	O	P	3	*R. styliformis* Brightwell var. *styliformis*
IT?	O	E	1	*R. styliformis* var. *latissima* Brightw. ex Ostenf.
?	O?	H	4	*R. styliformis* var. *longispina* Hustedt in Schmidt
C	N	P—H	4	*Rhizosolenia setigera* Brightwell
?	N?	F	3	*Rhizosolenia pungens* Cleve-Euler
IT?		P	3	*Rhizosolenia crassispina* Schröder
C	O	P	3	*R. hebetata* f. *semispina* (Hensen) Gran
TT	O	P	4	*Rhizosolenia calcar-avis* Schultze
IT		F	2	*Rhizosolenia cochlea* Brun
TT?	O?	P—E	4	*Rhizosolenia alata* Brightw. f. *alata*
TT?	O?	P—E	5	*R. alata* f. *gracillima* (Cleve) Gran
TT?	O?	E	4	*R. alata* f. *indica* (Peragallo) Gran
IT	O	F	1	*Rhizosolenia Castracanei* Peragallo
IP	O?	F	3	*Rhizosolenia Clevei* Ostenfeld
IT	N?	E	3	*Rhizosolenia hyalina* Ostenfeld
TT	O?	H	3	*Bacteriastrum delicatulum* Cleve
TT?	N?	F	3	*Bacteriastrum hyalinum* Lauder
IP?	O?	F	2	*Bacteriastrum varians* Lauder
TT	O?	F—H	3	*Bacteriastrum elongatum* Cleve
TT?		F	1	*Bacteriastrum minus* Karsten
TT	O?	F	1	*Bacteriastrum elegans* Pavillard
IT		H	2	*Bacteriastrum comosum* Pavillard
IP		F	1—2	*Chaetoceros denticulatum* Lauder
TT	O	F	1	*C. atlanticum* var. *neapolitanum* (Schr.) Hustedt
TT	O	E	3	*Chaetoceros coarctatum* Lauder
TT	O	F	1	*Chaetoceros tetrastichon* Cleve
TT?	O	F	1	*Chaetoceros Dadayi* Pavillard
C	N	E	2	*Chaetoceros danicum* Cleve
TT		F	1	*Chaetoceros rostratum* Lauder
C	O	P	3	*Chaetoceros peruvianum* Brightwell
C	O	F	3	*Chaetoceros decipiens* Cleve
TT	N	P	3	*Chaetoceros lorenzianum* Grunow
TT	N	F	1	*Chaetoceros Lauderi* Ralfs in Lauder
C	N	P—E	4	*Chaetoceros compressum* Lauder
C?	N	F	1	*Chaetoceros didymum* Ehr. var. *didymum*
TT	N	H	1	*C. didymum* var. *protuberans* (Lauder) Gran & Yendo
C	N	E	3	*Chaetoceros affine* Lauder
TT	N	H	5	*Chaetoceros laciniosum* Schütt
C?	N	P—H	5	*Chaetoceros pelagicum* Cleve
TT	N	F	4	*Chaetoceros breve* Schütt
TT	N	F	3	*Chaetoceros diversum* Cleve
IP	N	F	1	*Chaetoceros laeve* Leuduger-Fortmorel
TT	O	H	5	*Chaetoceros messanense* Castracane
C	N	P—H	4	*Chaetoceros curvisetum* Cleve

Tableau II (suite)

TT ?	N	P	3	*Chaetoceros pseudocurvisetum* MANGIN
C	N	H	5	*Chaetoceros tortissimum* GRAN
C	N	F	1–2	*Eucampia zodiacus* EHR.
IT ?	N ?	E	1–2	*Eucampia cornuta* (CLEVE) GRUNOW in VAN HEURCK
TT ?	O ?	P	3	*Climacodium frauenfeldianum* GRUNOW
TT	N ?	F	1	*Streptotheca Tamesis* SHRUBSOLE
TT	N	F	1	*Bellerochea malleus* (BRIGHTW.) VAN HEURCK f. *malleus*
TT	N	F	1	*B. malleus* f. *biangulata* (PERAG.) HUSTEDT
IT	N	H	1	*Ditylum sol* (GRUNOW in VAN HEURCK) DE-TONI
TT	N	F	1	*Triceratium favus* EHR.
TT	N	P	2	*Triceratium shadboltianum* GREVILLE
TT	N	F	1	*Triceratium formosum* BRIGHTWELL f. *formosum* *T. formosum* f. *quadrangulare* (GREV.) HUSTEDT *T. formosum* f. *quinquelobatum* (GREV.) HUSTEDT
C	N	F	1	*Triceratium alternans* BAILEY
TT ?		H	2	*Biddulphia pelagica* SCHRÖDER*
TT	N	P	1	*Biddulphia pulchella* GRAY
IT	N	F	1	*Biddulphia tridens* (EHR.) EHR.
TT	N	E	2	*Biddulphia sinensis* GREVILLE
TT	O ?	F	2	*Biddulphia mobiliensis* (BAIL.) GRUN. in VAN HEURCK
C	N	F	1	*Biddulphia aurita* (LYNGBYE) BREB.
IT	N	F	1	*Biddulphia membranacea* CLEVE
TT ?		F	1	*Biddulphia schroederiana* SCHUSSNIG
IT ?	N	H	1–2	*Isthmia minima* HARVEY & BAILEY
IT ?	N	F	1	*I. enervis* var. *japonica* CASTRACANE*
C	N	P	3	*Cerataulina pelagica* (CLEVE) HENDEY
TT	N	F	1	*Hemiaulus Hauckii* GRUNOW in VAN HEURCK
IT	N	F	2	*Hemiaulus sinensis* GREVILLE
OI		P	3	*Hemiaulus indicus* KARSTEN
IT		P	3	*Hemiaulus membranaceus* CLEVE
C	O ?	F	1	*Hemidiscus cuneiformis* WALLICH
IT	O ?	H	1	*Hemidiscus hardmanianus* (GREVILLE) MANN
				Diatomées pennées
C	N	P	1	*Rhabdonema adriaticum* KÜTZING
C ?	N	P	1	*Striatella unipunctata* (LYNGBYE) AGARDH
C		F	1	*Striatella delicatula* (KÜTZ.) GRUNOW in VAN HEURCK
C	N	F	1	*Grammatophora marina* (LYNGBYE) KÜTZING
IT	N	F	1	*Grammatophora undulata* EHR.
?	N	F	1	*Licmophora remulus* GRUNOW
C	N	F	1	*Licmophora flabellata* AGARDH
C	N	F	1	*Licmophora Lyngbyei* (KÜTZ.) GRUNOW in VAN HEURCK
C	N	F	1–2	*Licmophora grandis* (KÜTZ.) GRUNOW in VAN HEURCK
OI ?	N	F	1	*Licmophora Aurivillii* CLEVE
TT ?	N	F	1	*Climacosphenia elongata* BAILEY*
TT	N	P	2	*Climacosphenia moniligera* EHR.
C	N	E	1	*Fragilaria crotonensis* KITTON
OI ?		P	2	*Fragilaria Aurivillii* CLEVE
TT	N	F	1	*Synedra hennedyana* GREGORY
TT	N	F	1	*Synedra undulata* (BAILEY) GREGORY
?		F	1	*Synedra rostrata* (HANTZSCH) HUSTEDT in SCHMIDT*
C	N	P	3	*Thalassionema nitzschioides* GRUNOW ex HUSTEDT
C	O	H	1	*Thalassiothrix longissima* CLEVE & GRUNOW
C		P	4	*Thalassiothrix Frauenfeldii* GRUNOW

Tableau (II suite)

IT ?	O ?	H	1	*Thalassiothrix mediterranea* PAVILLARD
?		H	1	*Thalassiothrix delicatula* CUPP
?		F	1	*Asterionella Bleakeleyi* SMITH
TT	N	P–H	4	*Asterionella notata* GRUNOW in VAN HEURCK
C	N	F	2	*Asterionella japonica* CLEVE in CLEVE & MÖLLER
C ?	N	F	1	*Campyloneis Grevillei* (SMITH) GRUNOW
C	N	F	1	*Achnanthes longipes* AGARDH
IT ?		F	1	*Mastogloia rostrata* (WALLICH) HUSTEDT
TT	N	P–E	2–3	*Stauroneis membranacea* (CLEVE) HUSTEDT
?		P	3	*Navicula Wawrikae* HUSTEDT
TT	N	F	1	*Gyrosigma balticum* (EHR.) CLEVE
C	N	F	1	*Pleurosigma elongatum* SMITH
C	N	F	1	*Pleurosigma Normanii* RALFS in PRITCHARD
?		P–H	1–2	*Pleurosigma directum* GRUNOW
C	N	F	1	*Amphora* cf. *ostrearia* BREB. in KÜTZING
?		F	1	*Amphora* cf. *decussata* GRUNOW
C	N	P	1	*Bacillaria paxillifer* (MÜLLER) HENDEY
C	N	P	3	*Nitzschia closterium* (EHR.) SMITH
C	N	F	1	*Nitzschia spathulata* BREB. ex SMITH
C ?	N	F	1	*Nitzschia longissima* (BREB. in KÜTZ.) RALFS in PRITCH.
C	N	P	4	*Nitzschia* cf. *seriata* CLEVE
OI		F	1	*Campylodiscus biangulatus* GREVILLE
C	N	F	1	*Campylodiscus clypeus* EHR.
				Péridiniens
TT	O	F	1	*Phalacroma argus* STEIN
TT	O	F	1	*Phalacroma cuneus* SCHÜTT
TT	O	F	1	*Phalacroma doryphorum* STEIN
IT	O	F	1	*Dinophysis Schuettii* MURRAY & WHITTING
TT	O	F	1	*Dinophysis caudata* SAVILLE-KENT
IP ?	O	E ?	2	*Dinophysis miles* CLEVE
				Ornithocercus magnificus STEIN emend. SCHÜTT
				Ornithocercus quadratus SCHÜTT
IT	O	P–H	1	*Ornithocercus splendidus* SCHÜTT
				Ornithocercus Steinii SCHÜTT emend. KOF. & SKOGSB.
				Ornithocercus Thumii (SCHMIDT) KOF. & SKOGSB.
TT	O	P	1–2	*Pyrophacus horlogium* STEIN
TT	O	F	1	*Peridinium globulus* STEIN
TT		F	1	*Peridinium Steinii* JÖRG.
TT		F	1	*Peridinium diabolus* CLEVE
C		F	1	*Peridinium conicum* (GRAN) OSTENF. & SCHMIDT
C		F	1	*Peridinium depressum* BAILEY
C		F	1	*Peridinium oceanicum* VANHÖFFEN
				Peridinium spp.
TT	O	H	1	*Gonyaulax Kofoidii* PAVILLARD
IT	O	H ?	1	*Gonyaulax pacifica* KOFOID
?		F	1	*Gonyaulax conjuncta* WOOD
TT		F	1	*Ceratium candelabrum* (EHR.) STEIN var. *candelabrum*
TT		F	1	*C. candelabrum* var. *depressum* (POUCHET) JÖRG.
TT		F	1	*C. candelabrum* (EHR.) STEIN „*candelabrum — depressum*“
C		P	1	*Ceratium furca* (EHR.) CLAP. & LACHM. var. *furca*
TT		P	1–2	*C. furca* var. *eugrammum* (EHR.) SCHILLER
C		P	1	*C. furca* (EHR.) CLAP. & LACHM. „*furca — eugrammum*“
TT		H ?	1	*Ceratium pentagonum* var. *tenerum* JÖRG.

Tableau II (fin)

C		F	1	*C. pentagonum* GOURRET „*robustum — tenerum*"
IT	O ?	F	1	*Ceratium teres* KOFOID
IT		H	1	*Ceratium Kofoidii* JÖRG.
?		F	1	*Ceratium minutum* JÖRG.
C		P	1	*Ceratium fusus* (EHR.) DUJARDIN var. *fusus*
TT		P	2	*Ceratium fusus* var. *seta* (EHR.) SOURNIA
C		P	1	*Ceratium fusus* (EHR.) DUJ. „*fusus — seta*"
TT		F	1	*Ceratium extensum* (GOURRET) CLEVE
IT	O	F	1	*Ceratium longirostrum* GOURRET
IT	O	F	1	*Ceratium falcatum* (KOFOID) JÖRG.
TT		P	1—2	*Ceratium tripos* var. *atlanticum* OSTENFELD
IT	O	H	1	*C. tripos* var. *pulchellum* (SCHRÖDER) LOPEZ
TT		H ?	1	*C. tripos* (MÜLLER) NITZSCH „*atlanticum — pulchellum*"
IT		F	1	*Ceratium breve* var. *parallelum* (SCHMIDT) JÖRG.
IT	N ?	P ?	1	*C. breve* var. *Schmidtii* (JÖRG.) SOURNIA
IT		F	1	*C. breve* (OSTF. & SCHM.) SCHR. „*parallelum — Schmidtii*"
TT		F	1	*Ceratium arietinum* CLEVE var. *arietinum*
IT	O ?	F	1	*Ceratium symetricum* PAV. var. *symetricum*
IT	O ?	F	1	*C. symetricum* var. *coarctatum* (PAV.) GRAHAM & BRON.
IT	O ?	F	1	*C. symetricum* var. *orthoceras* (JÖRG.) GRAHAM & BRON.
TT		F	1	*Ceratium azoricum* CLEVE
IT	O	F	1	*Ceratium euarcuatum* JÖRG.
TT		P ?	1	*Ceratium declinatum* f. *normale* JÖRG.
IT	O	F	1	*Ceratium contortum* var. *Karstenii* (PAV.) SOURNIA
IP	N ?	F	1	*Ceratium dens* OSTENFELD & SCHMIDT
IT	O	E ?	1	*Ceratium macroceros* var. *gallicum* (KOF.) SOURNIA
IP ?		F	1	*Ceratium deflexum* (KOFOID) JÖRG.
TT		P	2	*Ceratium massiliense* (GOURRET) JÖRG. var. *massiliense*
TT ?		F	1	*C. massiliense* var. *protuberans* (KARSTEN) JÖRG.
TT	O	F	1	*Ceratium carriense* GOURRET var. *carriense*
IT	O	F	1	*C. carriense* var. *volans* (CLEVE) JÖRG.
IT		P	2	*Ceratium trichoceros* (EHR.) KOFOID
TT	O	F	1	*Ceratium contrarium* (GOURRET) PAVILLARD
IT		F	1	*Ceratium horridum* var. *buceros* (ZACH.) SOURNIA
TT		F	1	*C. horridum* (CLEVE) GRAN „*horridum — buceros*"
TT		F	1	*Goniodoma polyedricum* (POUCHET) JÖRG.
TT		H	1—2	*Ceratocorys horrida* STEIN
IT	O	F	1	*Ceratocorys Gourretii* PAULSEN
TT	O	F	1	*Podolampas bipes* STEIN
TT	O	F	1	*Podolampas elegans* SCHÜTT
TT	O	F	1	*Podolampas palmipes* STEIN
TT	O	F	1	*Podolampas spinifera* OKAMURA
TT ?		F	1	*Pyrocystis fusiformis* WYV. THOMSON ex MURRAY
?		F	1	*Pyrocystis lunula* (SCHÜTT) SCHÜTT

d) Variations quantitatives

Comme indiqué plus haut (tableau I), les variations quantitatives du microplancton sont considérables et brutales. Les trois groupes essentiels sont, par ordre d'importance décroissante: Diatomées, *Trichodesmium*, Péridiniens.

Tableau III — Composition qualitative du microplancton (résumé du tableau II)

Répartition mondiale	Total des taxons	
	Diatomées	Péridiniens
Cosmopolite	60	8
Tempérée-tropicale	53	33
Inter-tropicale	24	25
Indo-pacifique	4	3
Océan indien	7	0
Inconnue	15	3
TOTAL	163	72
„Océanique"	41	33
„Néritique"	87	2
„Indifférente" ou inconnue	35	37

Une remarque préalable: la comparaison des trois stations est difficile, car les différences observées semblent comprises dans l'intervalle d'incertitude de l'échantillonnage et du comptage. Il est seulement évident que le nombre de cellules par litre est de façon générale plus élevé à l'ouverture de la baie (station L) que sur le littoral (stations A et J).

(1) — Diatomées

Au sujet des variations du nombre total de cellules (fig. 8), il est difficile de parler de cycle annuel, puisque diverses poussées s'échelonnent tout au long de l'année, les plus importantes toutefois survenant au milieu de l'été et au milieu de l'hiver. Par contre, au niveau générique, les phénomènes sont bien tranchés, et le sont plus encore au niveau des espèces.

Deux genres sont dominants, *Chaetoceros* et *Rhizosolenia*, suivis de loin par *Bacteriastrum*, *Nitzschia*, *Guinardia*, *Thalassiothrix*, *Skeletonema* et *Asterionella*. Nous examinerons de plus près le cas des deux premiers, ainsi que celui de *Guinardia*, jugé, parmi le second groupe, particulièrement intéressant. Pour les autres genres cités, ainsi que pour les divers taxons purement mineurs, les fréquences et abondances sont indiquées approximativement dans le tableau II.

Chaetoceros: D'après les pourcentages observés dans les récoltes au filet (fig. 8), ce genre est pérennant. Les comptages au microscope inversé (fig. 7) montrent par contre que les poussées importantes sont purement hivernales; les circonstances hydrologiques de ces maxima annuels, reportés sur un diagramme T–S (fig. 9), révèlent une sténohalinité et une eurythermie marquées.

Au niveau spécifique, les poussées en question sont essentiellement dues à *C. pelagicum*, *C. laciniosum*, *C. messanense* et *C. tortissimum*. D'autre part, quelques espèces sont nettement estivales, mais d'importance numérique négligeable: *C. coarctatum*, *C. compressum*, *C. affine* et *C. danicum*.

L'extrême rareté des spores de résistance dans les eaux étudiées mérite d'être signalée; pratiquement ces formations n'ont été observées que chez *C. compressum*.

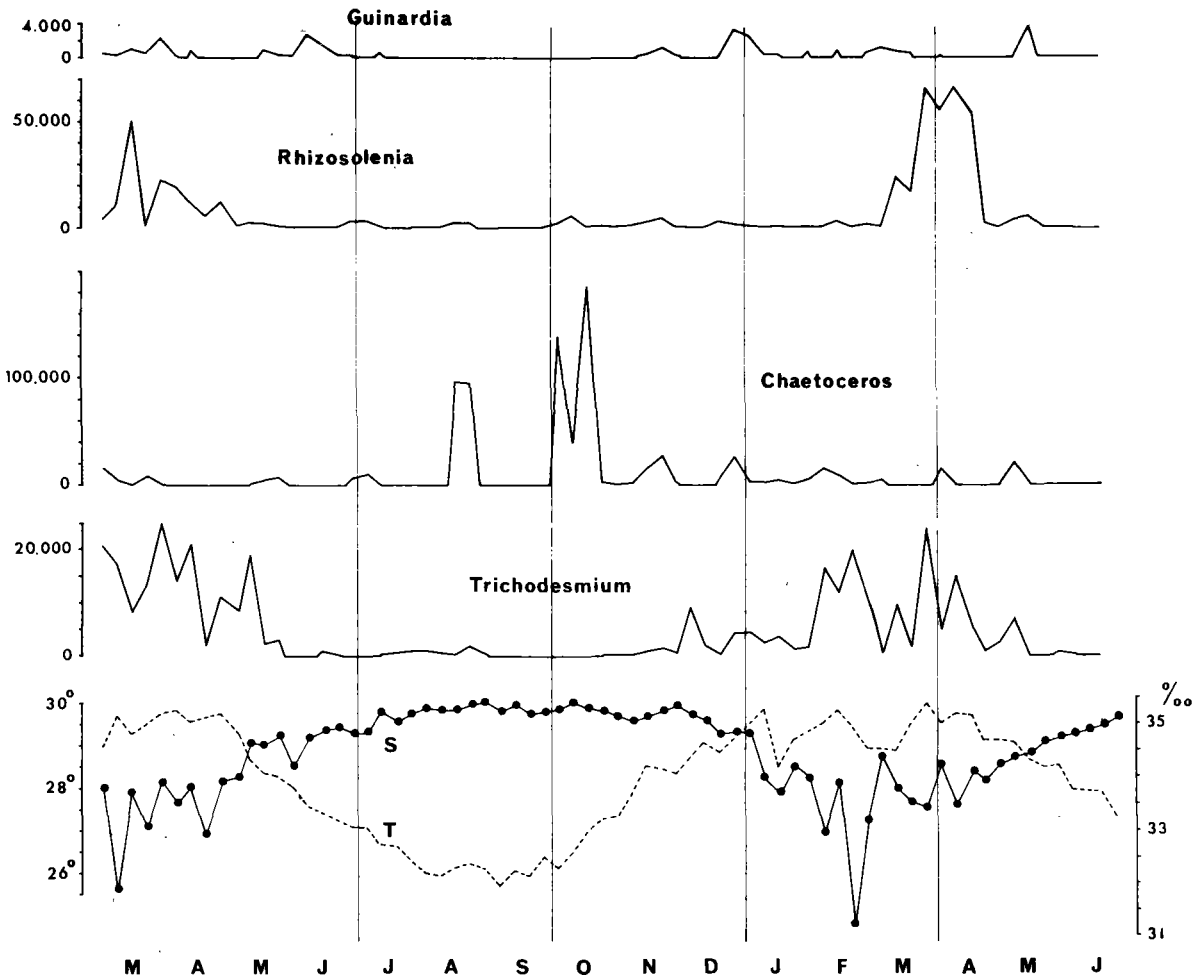


Fig. 7. Comptages au microscope inversé (station L, profondeur: 1 m). Pour *Guinardia*, *Rhizosolenia* et *Chaetoceros*: nombres de cellules par litre. Pour *Trichodesmium*: nombres de filaments par litre. En bas: moyennes hebdomadaires des températures et salinités (d'après les données de la fig. 3)

Rhizosolenia: Comme dans le cas précédent, les valeurs relatives (fig. 8) montrent que ce genre est pérennant, avec toutefois un maximum estival marqué. Par contre, d'après les chiffres absolus (fig. 7), les poussées importantes apparaissent nettement limitées à la saison chaude et, plus précisément (diagramme T–S, fig. 9), liées à des conditions hydrologiques bien définies: température comprise entre 29° et 30°, salinités voisines de 34‰.

Ces poussées estivales sont exclusivement le fait de *R. alata* (dont la forme *gracillima* est dominante). Cette espèce, pérennante, est également responsable du maximum secondaire observé à la fin d'octobre (fig. 8) dans les récoltes au filet, mais ce maximum n'est que relatif, et imperceptible du point de vue quantitatif (fig. 7). La préférence des faibles salinités chez cette *Rhizosolenia* confirme

les données de HULBURT & RODMAN (1963). Chez *R. alata*, les auxospores ont été observées par deux fois en quantités notables: début avril 1963 et début mai 1964, c'est à dire dans les deux cas, à la fin du „bloom" annuel de cette Diatomée.

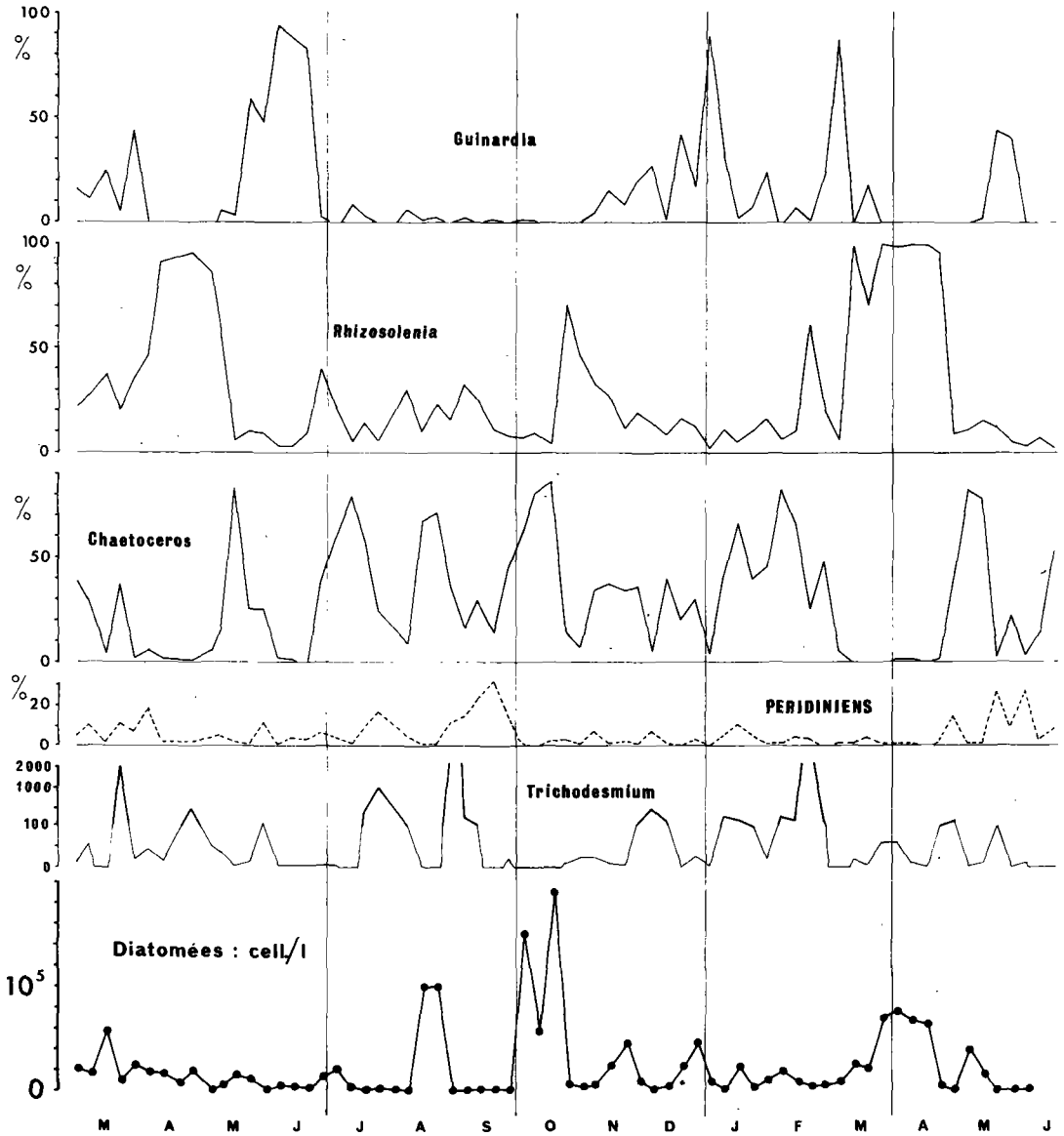


Fig. 8. Station L. Pour les cinq graphiques supérieurs: récoltes au filet. *Guinardia*, *Rhizosolenia*, *Chaetoceros* et Péridiniens: pourcentages par rapport au total „Diatomées + Péridiniens". *Trichodesmium* (échelle arithmétique en deux parties): nombres de filaments pour 100 cellules de „Diatomées + Péridiniens".
En bas: total Diatomées, d'après les comptages au microscope inversé

Les autres espèces montrent des variations saisonnières plus ou moins définies, indiquées dans le tableau II, mais ne jouent un rôle quantitatif que tout à fait secondaire.

La Cyanophycée endophyte *Richelia intracellularis* est pérennante à Nossi-Bé, mais exclusivement inféodée à 3 espèces: *R. cylindrus*, *R. styliformis* var. *longispina* et *R. Clevei*. En dehors du genre *Rhizosolenia*, cette Cyanophycée n'a été observée que chez *Chaetoceros compressum*, cette fois à l'état d'épiphyte.

Guinardia: L'unique espèce récoltée à Nossi-Bé, *G. flaccida*, n'est que semi-pérennante dans les récoltes au filet (fig. 8), puisqu'absente pendant les deux mois d'avril 1963 et 1964 et, d'autre part, très rare ou absente pendant la saison fraîche. Par ailleurs, les comptages par sédimentation (fig. 7) montrent plusieurs poussées, de peu d'importance, au début et à la fin de l'été, dans des conditions hydrologiques intermédiaires entre les exigences précédemment observées chez *Chaetoceros* et *Rhizosolenia*: à la différence de ces deux genres, *Guinardia* est largement eurytherme et relativement euryhaline (fig. 9).

(2) — Péridiniens

Comme indiqué dans le tableau II, les Péridiniens microplanctoniques sont numériquement très rares, si bien que la méthode quantitative ici utilisée, à savoir celle d'UTERMÖHL, ne permet pas d'en évaluer les variations absolues. On ne peut donc utiliser dans ce cas que les résultats des pêches au filet.

Les données semi-quantitatives ainsi obtenues (fig. 8) montrent que les Péridiniens sont bien diversifiés, mais que leur pourcentage reste toujours minoritaire et qu'il est maximum dans l'intervalle des poussées de Diatomées; les variations saisonnières de ce pourcentage sont peu évidentes: il semble seulement que le maximum annuel est hivernal, et le minimum estival. Au niveau générique, on observe que les *Ceratium* sont plus nombreux en hiver. Au niveau spécifique enfin, une certaine discrimination saisonnière apparaît: une douzaine d'espèces sont hivernales, et deux seulement estivales (tableau II); en d'autres termes: les Péridiniens sont mieux diversifiés en hiver.

Aucun phénomène d',,eaux rouges" imputable à des Péridiniens n'a été observé durant l'intervalle de temps étudié.

(3) — Trichodesmium[1])

L'abondance relative de ce genre (récoltes au filet) est reportée sur la figure 8 en nombre de filaments pour 100 cellules de Diatomées et de Péridiniens. On voit que le genre est presque pérennant et que, dans l'intervalle des poussées de Diatomées, son importance devient proportionnellement considérable.

Les quantités absolues, exprimées en nombre de filaments par litre (fig. 7), montrent au contraire une alternance saisonnière caractérisée par un maximum estival: le diagramme T–S correspondant (fig. 9) indique des températures élevées, et une euryhalinité complète.

Les plus importantes poussées déterminent de véritables phénomènes d',,eaux rouges", la couleur de la mer devenant — plus exactement — jaune pailleté.

[1]) Note sur épreuves: Dans un travail postérieur à celui-ci, je tente de montrer que les *Trichodesmium* ne peuvent être génériquement séparés des *Oscillatoria*, et que ce dernier nom doit prévaloir (SOURNIA, s. presse, c).

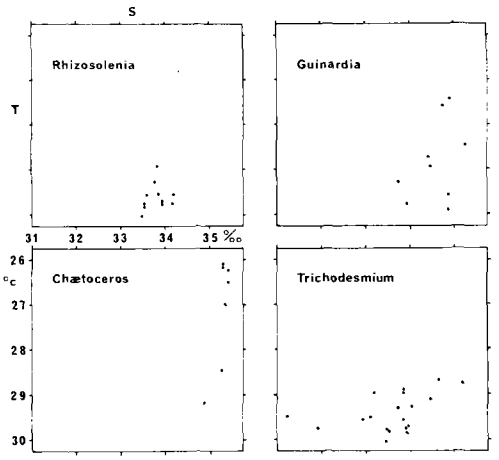


Fig. 9. Station L. Conditions hydrologiques des principales poussées microplanctoniques, reportées sur quatre diagrammes T–S identiques. *Rhizosolenia*: >10000 cell./l. *Guinardia*: >1000 cell./l. *Chaetoceros*: >25000 cell./l. *Trichodesmium*: >8000 filaments/l.

e) Remarques et conclusions

La prédominance des Diatomées sur les Péridiniens, qualitativement évidente, devient presque totale sur le plan quantitatif. Les valeurs numériques peuvent être comparées à diverses observations dans l'océan indien: elles sont du même ordre de grandeur que celles recueillies par TRAVERS (1965) au cours d'un séjour de six semaines à Tuléar; elles sont légèrement inférieures aux concentrations reportées par SILVA (1960) au cours d'un travail de même durée sur la côte du Mozambique. Enfin ces chiffres sont considérablement plus faibles que ceux donnés par SUBRAHMANYAN (1959a) pour la côte occidentale des Indes de 1949 à 1954; toutefois cet auteur insiste sur l'exceptionnelle richesse des eaux étudiées.

On peut ici reconnaître, parmi les Diatomées, une vingtaine d',,espèces de masse", responsables des poussées importantes (voir tableau II: groupes 4 et 5 dans la colonne ,,abondance maximum"). Le tableau IV permet d'en comparer la liste à diverses données analogues obtenues au cours de cycles annuels sur la côte des Indes (SUBRAHMANYAN & SARMA, 1960) et sous diverses latitudes tropicales ou tempérées . Les coïncidences sont nombreuses.

Dans l'intervalle des poussées de Diatomées et de *Trichodesmium*, le microplancton peut être qualifié de sub-désertique, alors que la quantité de nannoplancton conserve tout au long de l'année un niveau élevé.

Le modèle des successions phytoplanctoniques défini par MARGALEF (1958) peut difficilement être appliqué ici: du fait d'une situation tout à fait littorale, de la soudaineté des variations du milieu en été, enfin, comme on le verra plus loin, d'un taux élevé de productivité, un grand nombre de poussées et de successions prennent place dans le cours de l'année; dans ces conditions, il semble bien qu'un ythme hebdomadaire pour les mesures de routine est insuffisant et ne peut endre compte du détail des phénomènes.

Toutefois, les poussées de Diatomées et de Cyanophycées peuvent être réparties en deux groupes: l'un estival (*Rhizosolenia, Guinardia, Trichodesmium*), l'autre hivernal (*Chaetoceros*):

— dans le premier cas, la cause des proliférations microplanctoniques tient apparemment aux chutes de pluies (draînage d'éléments nutritifs) mais peut-être aussi à la force des vents de secteur sud-ouest (brassage des eaux). Les espèces qui dominent alors sont euryhalines (*Trichodesmium*, fig. 9), ou relativement tolérantes vis à vis de la salinité (*Rhizosolenia*, *Guinardia*, même fig.).

— le mécanisme des poussées hivernales est moins clair: un nouveau brassage s'effectuerait sous l'influence d'arrivée d'eaux du large (voir: courants, p. 4), celles-ci rendant compte de la présence d'un nombre relativement important d'espèces océaniques (voir plus haut: inventaire qualitatif). La possibilité d'un up-welling hivernal, dû à l'alizé du sud-est, n'est d'ailleurs pas exclue. Les *Chaetoceros* qui prolifèrent alors sont eurythermes mais nettement sténohalins (fig. 9).

On peut rapprocher ces conditions de celles décrites par MARSHALL (1933): dans la région de la Grande Barrière, les fluctuations saisonnières dépendent essentiellement de la force des vents. Les observations de SUBRAHMANYAN (1959a—b) se rapprochent plus encore du cas présent: sur la côte des Indes, les poussées annuelles maximales surviennent au cours de la mousson humide, mais des vents importants provoquent, pendant la saison opposée, des poussées secondaires. Notons bien qu'à Nossi-Bé les pluies sont estivales, tandis qu'elles ont lieu en saison fraîche sur la côte des Indes. Le rôle de la température, invoqué par SUBRAHMANYAN (1959b) n'est donc nullement déterminant.

4. Pigments photosynthétiques

a) Valeurs absolues

Les teneurs en pigments sont dans l'ensemble élevées, ce qui surprendrait dans un milieu tropical autre que purement côtier. MAESTRINI & PIZARRO (1966) observent d'ailleurs dans le lagon de Tuléar des valeurs du même ordre; par contre, au large de Nossi-Bé les concentrations mesurées au cours de la croisière de l',,Anton Bruun" étaient nettement plus faibles (Anonyme, 1965: stations 412 à 414), comme il convient en milieu ,,océanique".

Les caroténoides constituent ici le groupe le plus important: de 0,20 à 1,30 MSPU/m³ (station J); viennent ensuite les chlorophylles *a* et *c*, toutes deux variant entre 0,20 et 0,95 mg/m³; les concentrations en chlorophylle *b* sont les plus faibles: de 0,05 à 0,28 mg/m³.

Dans les quatre cas, à la station J (fig. 10), les variations sont très accidentées. La chlorophylle *b* ne présente pas de fluctuations autres qu'hebdomadaires; par contre les trois autres pigments montrent l'alternance saisonnière suivante:

— de septembre à janvier: valeurs annuelles minimales. A supposer qu'elle soit liée au cycle hydrologique, cette période est donc en retard de trois mois sur l'hiver hydrologique tel que défini p. 13.

— de février à septembre: teneurs plus élevées ou maximales, mais particulièrement accidentées (cette instabilité pouvant être rapprochée de celle des salinités pendant cette période).

Aux stations L et A, les phénomènes sont identiques, aussi seules les concentrations en chlorophylle *a* ont-elles été représentées sur la figure 18. Les variations sont toutefois beaucoup plus accidentées en A qu'en L, la station J apparaissant, de ce point de vue, intermédiaire entre les deux autres; ainsi l'alternance saisonnière décrite à la station J est-elle moins marquée en A et plus évidente en L.

Tableau IV. Diatomées dominantes à Nosy-Bé et en diverses régions du globe, au cours d'un cycle annuel.

Espèces dominantes à Nosy-Bé	Côte occidentale des Indes	Mer des Sargasses	Méditerranée (Marseille)	Manche (Roscoff)	Atlantique nord-ouest (Région de Long Island Sound)		
	Subrahmanyan & Sarma (1960)	Riley (1957)	Travers (1962)	Grall & Jacques (1964)	Riley (1952)	Conover (1956)	Smayda (1957)
Skeletonema costatum	+	.	+	+	+	+	+
Guinardia flaccida	+	.	.	+	+	+	.
Rhizosolenia Stolterfothii	+	+	.	+	.	.	.
R. imbricata var. *Shrubsolei*	.	.	.	+	.	.	.
R. styliformis var. *longispina*	.	?	.	.	.	.	.
Rhizosolenia setigera	.	.	.	.	.	.	.
Rhizosolenia calcar-avis	.	+	.	.	.	.	.
Rhizosolenia alata	+	+	.	.	.	.	.
Chaetoceros compressum	+	.	+	.	+	+	.
Chaetoceros laciniosum	+	?	.	.	.	.	.
Chaetoceros pelagicum	+	.	.	.	.	.	.
Chaetoceros breve	+	?	.	.	.	.	.
Chaetoceros messanense	.	+	.	.	.	.	.
Chaetoceros curvisetum	+	.	+	.	+	+	+
Chaetoceros tortissimum	.	.	.	.	.	+	.
Thalassiothrix Frauenfeldii	+	+	.	.	.	.	.
Asterionella notata	.	.	.	.	.	.	.
Nitzschia seriata	+	.	+	+	+	.	+
Nombre total d'espèces dominantes mentionnées (A Nosy-Bé: 18)	29	26	5	11	14	30	9

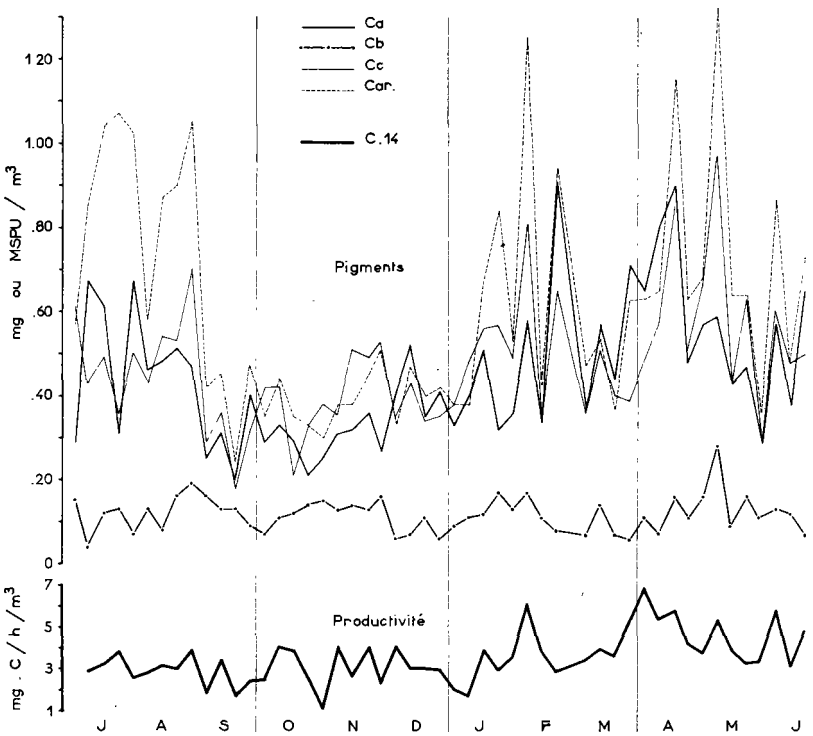


Fig. 10. Station J. Valeurs hebdomadaires des concentrations en pigments (chlorophylles *a*, *b* et *c*, et caroténoides) et de la production primaire in situ. (Cette figure a été antérieurement publiée dans une note préliminaire: SOURNIA, 1965a)

b) Relations inter-pigmentaires

Les mesures portées sur la figure 10 ont été reproduites différemment, après élimination du facteur „temps", sur la figure 11: en abcisses, teneurs en chlorophylle *a*; en ordonnées, concentrations correspondantes des trois autres pigments. En ce qui concerne la chlorophylle *b*, il est probable que les valeurs mesurées sont comprises dans l'intervalle des erreurs méthodologiques, et que les résultats ne sont pas significatifs (points dispersés parallèlement aux abcisses). On décèle par contre entre les chlorophylles *a* et *c* une corrélation positive, très hautement significative (probabilité 0,001; $r = 0{,}59$) selon l'expression linéaire:

$$C_c = 0{,}53\ C_a + 0{,}24\ .$$

Les caroténoides présentent une corrélation non moins significative ($r = 0{,}65$) d'équation:

$$\text{Car.} = 1{,}04\ C_a + 0{,}15\ .$$

(L'on s'est bien entendu assuré préalablement que les répartitions des quatre séries de valeurs peuvent être supposées normales).

Les rapports suivants ont été calculés: chlorophylles *a*/*b*, chlorophylles *a*/*c*, chlorophylle *a*/caroténoides, enfin rapport des densités optiques 430/665 mμ (MARGALEF, 1960): aucun d'eux ne présente de variations saisonnières certaines; mais par ailleurs, abstraction faite du facteur „temps", ces rapports se révèlent

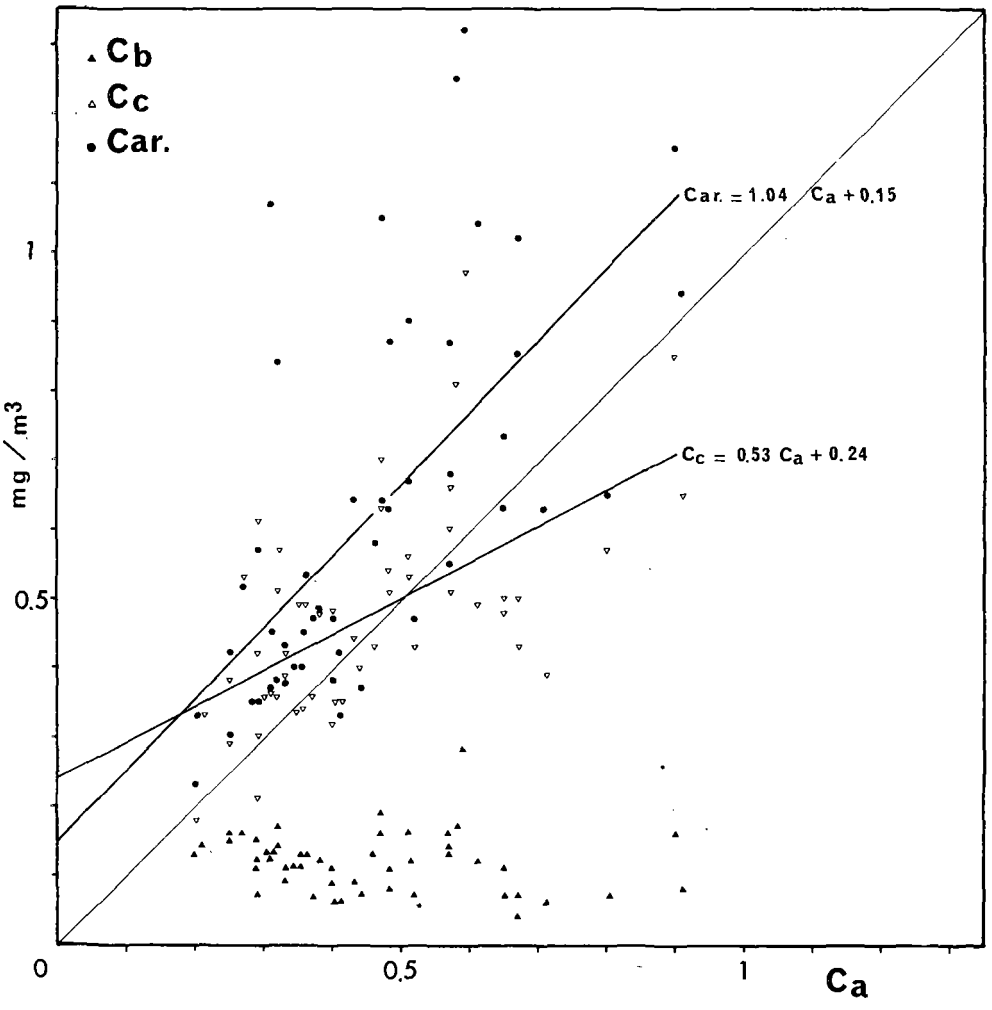


Fig. 11. Concentrations en chlorophylles *b* et *c*, et en caroténoides, en fonction des concentrations en chlorophylle *a* (station J)

mutuellement liés par diverses relations internes, comme l'ont montré MARGALEF (ibid., 1961a, 1963) et MARGALEF et al. (1959):

Un premier exemple en est donné sur la figure 12: relation inverse entre les rapports „chlorophylles *a*/*c*" et „densités optiques 430/665". Ayant vérifié que les deux variables peuvent être supposées normalement distribuées, l'on peut établir comme suit la droite de régression arithmétique:

$$C_a/C_c = -0{,}18\ (\text{D } 430/665) + 1{,}64\ .$$

(Avec $r = -0{,}525$; probabilité $<0{,}001$)

Une telle équation linéaire est assurément approchée; est-elle en fait du type allométrique comme MARGALEF (supra) l'a montré pour diverses relations interpigmentaires? On ne peut l'assurer, puisqu'un calcul identique effectué sur les

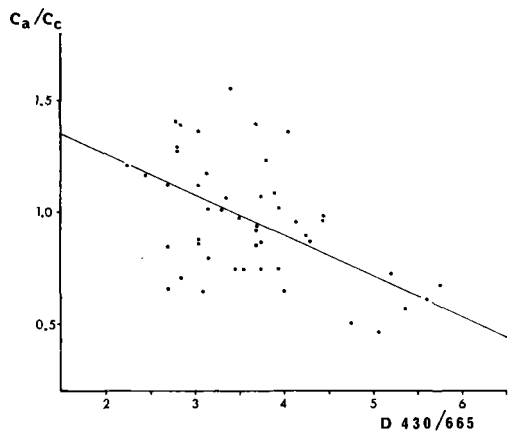


Fig. 12. Rapport des concentrations en chlorophylles *a* et *c*, en fonction du rapport des densités optiques à 430 et 665 mμ (station J)

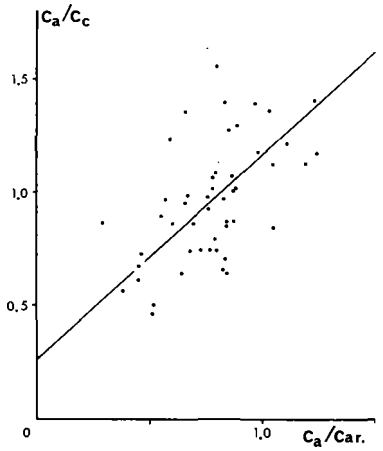


Fig. 13. Rapport des concentrations en chlorophylles *a* et *c*, en fonction du rapport des concentrations en chlorophylle *a* et en caroténoides (station J)

logarithmes des mêmes données conduit à l'équation:

$$\text{Log}\,(C_a/C_c) = -0{,}72\ \text{Log}\,(\text{D}\ 430/665) + 0{,}36\ .$$

Soit $C_a/C_c = (\text{D}\ 430/665)^{-0{,}72} \times 2{,}32$, pour un coefficient de corrélation identique, $r = -0{,}533$.

La corrélation entre les rapports „chlorophylles *a*/*c*" et „chlor. *a*/caroténoides" a été étudiée de la même manière. La relation linéaire est la suivante (fig. 13):

$$C_a/C_c = 0{,}90\ (C_a/\text{Car.}) + 0{,}26, \quad \text{avec} \quad r = 0{,}632\ .$$

On observe par ailleurs entre les logarithmes la relation suivante:

$$\text{Log}\,(C_a/C_c) = 0{,}56\ \text{Log}\,(C_a/\text{Car.}) + 0{,}38\ .$$

Soit $C_a/C_c = (C_a/\text{Car.})^{0{,}56} \times 2{,}39$ avec un coefficient de corrélation légèrement inférieur, $r = 0{,}574$: dans le présent cas, une corrélation allométrique est donc moins probable que la simple relation linéaire.

5. Production primaire

a) Mesures par le carbone-14

Le cycle annuel à la station J (fig. 10) montre, comme dans le cas des pigments, une évolution annuelle très accidentée; on ne peut parler d'alternance saisonnière que dans le sens suivant: les valeurs annuelles minimales surviennent entre septembre et début janvier, et les valeurs maximales pendant le reste de l'année.

Cette alternance disparaît presque entièrement à la station L, et complètement à la station A (fig. 18). Comme celles des pigments, les valeurs de la productivité sont plus élevées, et leurs fluctuations plus accidentées en A qu'en L.

Il faut ici faire une réserve sur la validité des mesures aux stations L et A: pour celles-ci en effet, le délai de temps écoulé entre le prélèvement et l'inoculation (environ 25 minutes pour L et 5 minutes pour A) pouvait faire craindre une erreur méthodologique. D'où

l'établissement, malheureusement tardif, de la station J (voir p. 10 et fig. 1). Diverses expériences en parallèle ont donc été effectuées dans le but d'évaluer cette incertitude. Leur conclusion est qu'un délai de 25 minutes entraîne une réduction de la productivité variant de 0 à 35%. Dans le cas de la station A, c'est à dire d'un délai de 5 minutes, la différence n'est pas décelable.

On peut donc attribuer à cette erreur méthodologique l'irrégularité des valeurs mesurées à la station L. La moyenne de celles-ci serait de plus à majorer de 20% environ.

Le haut niveau général des productivités peut s'expliquer par la situation littorale du secteur étudié. Mes chiffres sont d'ailleurs du même ordre que ceux de MAESTRINI & PIZARRO (1966) pour le lagon de Tuléar (toutefois, les expériences de ces deux auteurs se sont déroulées en lumière artificielle). Par ailleurs, des mesures in situ ont été effectuées au large de Nossi-Bé au cours des croisières de la „Galathea" (STEEMANN NIELSEN & JENSEN, 1957) et de l'„Anton Bruun" (Anonyme, 1965; RYTHER et al., 1966); les productivités mesurées sont naturellement beaucoup plus faibles, puisque relatives au domaine océanique; elles sont respectivement de 0,13 g carbone/m²/jour (station „Galathea" n° 218) et de 0,32—1,25—0,77, mêmes unités (stations „Anton Bruun" n° 412—413—414).

L'assimilation de carbone dans les bouteilles noires ne représente tout au long de l'année qu'un faible pourcentage (1 à 2%) de l'assimilation photosynthétique. Les méthodes de travail utilisées ne me permettaient pas d'évaluer avec précision d'éventuelles variations saisonnières ou locales; aussi ce phénomène sera-t-il laissé de côté.

Par ailleurs, les conditions d'éclairement n'ont été mesurées chaque semaine que de façon très approchée (nébulosité „à l'oeil nu"). C'est probablement pour cette raison que je ne puis observer de relation, à l'échelle annuelle, entre éclairement et production primaire; on verra par contre plus loin (p. 54) que cette relation est évidente à l'échelle des variations diurnes.

b) Comparaison avec les mesures par l'oxygène

Comme on l'a vu plus haut (p. 16), le taux relatif d'oxygène dissous in situ ne présente pas de variations saisonnières, et ne peut donc prêter à une estimation de la productivité annuelle. D'autre part, les variations nycthémérales seront étudiées plus loin (p. 50). Examinons ici les résultats des expériences effectuées parallèlement aux mesures par le carbone 14, de décembre 1963 à juin 1964 (méthodologie: p. 13). Les deux séries de valeurs sont reportées sur la figure 14: au cours des premières semaines, l'assimilation de carbone étant relativement faible, la corrélation avec le dégagement d'oxygène est peu apparente; ce dernier présente d'ailleurs quelques valeurs nulles ou négatives. A

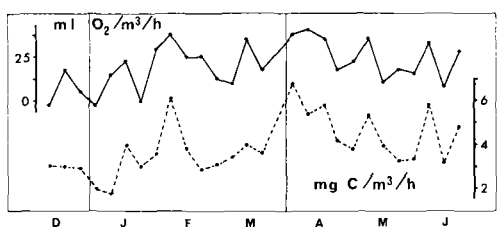


Fig. 14. Mesures en parallèle de la production primaire in situ: dégagement d'oxygène et assimilation de carbone (station J, de décembre 1963 à juin 1964). Il s'agit dans les deux cas de la production nette, telle que mesurée dans les bouteilles „claires".

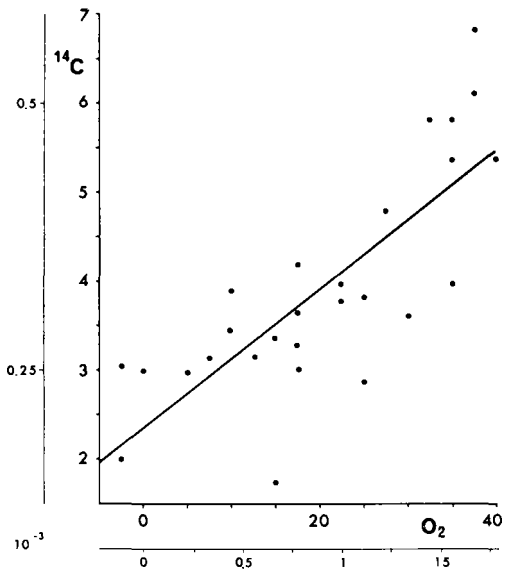


Fig. 15. Corrélation entre les deux séries de mesures de la figure 14. Echelles intérieures: mg carbone et ml oxygène par m³ et par heure. Echelles extérieures: quantités équivalentes en molécules-grammes $\times 10^{-3}$

partir de la fin de janvier, et jusqu'à juin, la productivité étant plus élevée, le parallélisme est évident entre les deux courbes. La corrélation, reportée sur la figure 15, est très hautement significative (probabilité $<0{,}001$, avec $r = 0{,}78$); la droite de régression a pour équation:

$$^{14}C = 0{,}078\ O_2 + 2{,}35 \quad \text{(unités: mg carbone et ml oxygène/m}^3\text{/h)}\ .$$

Les valeurs moyennes de la production mesurée par les deux méthodes pendant ces six mois sont de 20,18 ml oxygène et 3,92 mg carbone/m³/h; soit respectivement 0,901 $\times 10^{-3}$ molécules-grammes et 0,327 $\times 10^{-3}$ atomes-grammes. D'où le quotient photosynthétique apparent de 2,76. La signification de cette valeur sera examinée en conclusion de la présente étude (p. 62); cependant trois remarques peuvent être faites ici:

(1) A propos du rapport $^{14}C/O_2$, notons qu'il serait sans intérêt de l'évaluer par extrapolation sur la droite précédemment définie (pour $O_2 = 22400$, soit 1 mole, $^{14}C = 0{,}15$ mole) car, d'après ce que l'on sait de la validité comparée des deux méthodes (références ci-dessous, § 3), la relation n'est vraisemblablement pas linéaire dans un tel intervalle de valeurs.

(2) Les mesures de production par la méthode de l'oxygène utilisent traditionnellement des temps d'incubation prolongés: trois jours à l'origine (GRAN, 1927; GAARDER & GRAN, 1927), le plus souvent 24 heures ou davantage (RILEY, 1938, 1941a; STEEMANN NIELSEN, 1951a; WILLIAMS & MURDOCH, 1966). Or l'importance des phénomènes secondaires affectant ces résultats a souvent été signalée (STEEMANN NIELSEN, 1952; PRATT & BERKSON, 1959, etc.). Il faut donc remarquer que les présentes mesures sont parfaitement cohérentes, bien qu'effectuées dans les conditions naturelles d'éclairement et pendant des temps d'exposition réduits (4 heures); d'ailleurs, des durées de 2 heures ont même été

pratiquées avec succès, in situ, par RYTHER, YENTSCH et al. (1958) et OCCHIPINTI et al. (1961).

(3) La comparaison des deux méthodes a été le plus souvent établie sur cultures et en éclairage artificiel (RYTHER, 1955, 1956b—c; RYTHER & VACCARO, 1954; RYTHER & YENTSCH, 1958; MCALLISTER, 1961). Néanmoins, mes observations in situ vérifient l'opinion générale selon laquelle les deux méthodes sont susceptibles de fournir des résultats „comparables" dans le cas de milieux eutrophiques en éclairement sub-optimal.

6. Corrélations entre biomasse et productivité

Nous avons examiné plus haut quelques corrélations internes entre divers pigments chlorophylliens, ainsi que la relation entre les mesures de production par les deux méthodes de l'oxygène et du carbone 14. Nous pouvons maintenant passer à l'étude comparée des teneurs en chlorophylle *a* (ce pigment étant considéré comme le plus représentatif) et des productivités, étude qui aboutira à une nouvelle corrélation statistiquement très significative. On verra ensuite, par contre, que dès que la composition taxinomique du plancton entre en jeu, il n'est plus question que de vagues analogies: les causes de ce phénomène seront discutées en conclusion de ce chapitre („rôle du nannoplancton").

a) Production primaire et chlorophylle *a*

Ces deux séries de valeurs, observées parallèlement en fonction du temps (fig. 10 ou 16) suggèrent une corrélation positive, qui devient évidente sur le graphique de la figure 17. L'équation de la droite de régression s'écrit:

$$^{14}C = 3{,}76\ C_a + 1{,}82 \quad \text{(Probabilité: 0,01; } r = 0{,}38)\ .$$

Unités: ^{14}C = production nette in situ, mg carbone/m³/h;

C_a = chlorophylle *a*, mg/m³.

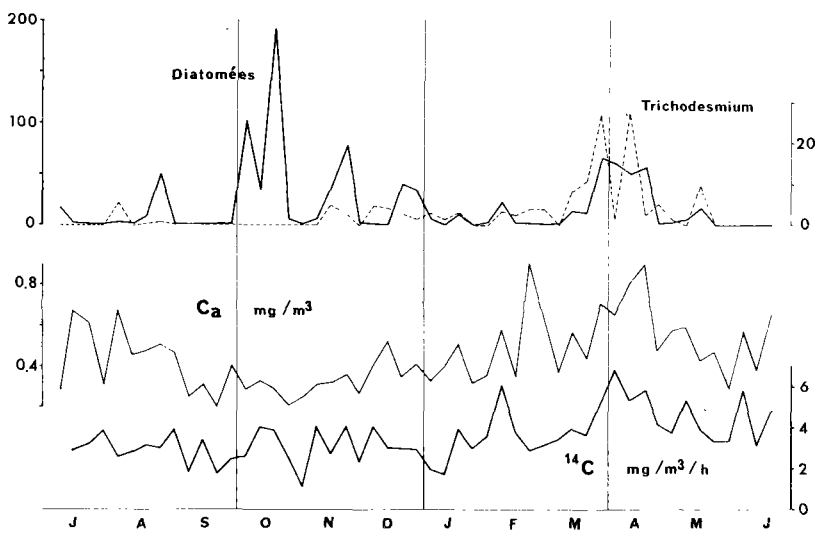


Fig. 16. Comparaison de la biomasse et de la production à la station J. Diatomées (milliers de cell./l), *Trichodesmium* (milliers de filaments/l), chlorophylle *a*, et production nette in situ

Par extrapolation, on obtient la valeur suivante de la production pour une unité de pigment: 5,58 mg carbone/h/mg chlorophylle *a*. Par ailleurs, le rapport des deux valeurs moyennes ($^{14}C = 3{,}51$; $C_a = 0{,}45$) est de 7,80[1]).

Dans les eaux étudiées, le rapport „assimilation de carbone/chlor. *a*" (mêmes unités) varie de 3,2 à 13,3 (station J), et ne présente pas de variations saisonnières, à l'encontre des observations de MENZEL & RYTHER (1961) dans la mer des Sargasses, de STELLE & BAIRD (1961) en mer du Nord et d'ANDERSON (1964) sur la côte occidentale des USA; d'autre part, ce rapport suit davantage les variations des productivités que celles des concentrations en pigment.

Cette question sera reprise en conclusion du présent travail (p. 64).

Notons que les mesures de productivité effectuées pendant les six derniers mois par la méthode de l'oxygène conduisent elles aussi à une corrélation positive avec les teneurs en chlorophylle *a*:

$$O_2 = 42{,}64\ C_a - 1{,}88 \quad \text{(Probabilité: 0,001; } r = 0{,}57) .$$

Unités: O_2 = production nette in situ, ml oxygène/m³/h;

C_a = chlorophylle *a*, mg/m³.

En supposant le quotient photosynthétique égal à 1,25 (RYTHER, 1956b; MCALLISTER et al., 1964), cette équation conduit aux valeurs de 17,47 (par extrapolation) ou 16,72 (moyennes) mg de carbone/h/mg chlor. *a*.

b) Incertitudes sur la composition taxinomique

Reprenons la figure 17: les principales poussées microplanctoniques ont été indiquées par l'initiale du nom du genre; les points dépourvus de lettre désignent les mesures dans lesquelles le microplancton ne joue qu'un rôle quantitatif très réduit (ou pratiquement nul). Il apparaît alors que les points représentatifs des trois genres sont relativement groupés, et correspondent à trois niveaux de productivité différents, mais qu'ils s'intègrent de façon homogène au reste des mesures, à l'exception peut-être de *Rhizosolenia*. Ainsi, la relation entre production et chlorophylle *a* semble-t-elle constante ou, du moins, indépendante de la composition taxinomique du plancton (rappelons que les expériences en cause se sont déroulées in situ en éclairement sub-optimal).

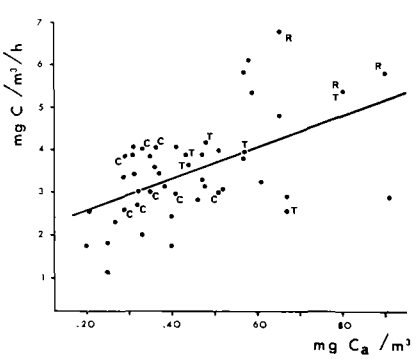


Fig. 17. Corrélation entre biomasse et production, d'après les données de la figure 16. Les poussées majeures du microplancton sont indiquées par les initiales R, C, (*Rhizosolenia*, *Chaetoceros*: >30000 cell./l) et T (*Trichodesmium*: >5000 filaments/l).

[1]) Dans la bibliographie, le rapport en question est parfois exprimé, de façon assez hasardeuse, par extrapolation sur la droite de régression (SHIMADA, 1958); il est le plus souvent donné sous la forme du simple rapport des mesures ou des moyennes de celles-ci. La signification mathématique étant différente dans les deux cas, le procédé utilisé devrait être précisé par les auteurs.

Le même graphique montre que, dans l'ensemble, les points „à microplancton" et les points „sans microplancton" voisinent sans discrimination possible. Dans le même sens, la figure 16 prouve que pigments et production ne sont pas affectés par les phases d'extinction du microplancton.

Dans le détail, aucune corrélation sûre n'apparaît entre l'évolution globale du microplancton, ou celle d'un genre particulier, et les variations des pigments photosynthétiques et de la production; quelques analogies sont observables (fig. 16), mais les contradictions sont aussi nombreuses (signalons toutefois un fait, bien connu depuis MARGALEF (1960, etc.): le rapport des densités optiques à 430 et 665 mμ, compris ici entre les valeurs extrêmes 2 et 6, descend aux environs de 3 lors des poussées de Diatomées).

On peut donc dire, devant cet apparent désordre, que l'essentiel nous échappe en ce qui concerne la composition taxinomique sous son aspect quantitatif. Ceci tient à trois causes possibles:

(1) erreurs d'échantillonnage, et imprécision du comptage. (Voir: méthodologie, p. 11).

(2) défaut d'évaluation de la biomasse: selon divers auteurs, en effet, l'évaluation quantitative de la composition du phytoplancton en termes de nombre de cellules par volume d'eau de mer est défectueuse, ou même constituerait le plus incertain des critères utilisables (RILEY, 1941 b). Cette pratique, la plus répandue car la plus simple, devrait-elle être abandonnée au profit d'une évaluation du volume total des cellules (HARVEY, 1950), ou mieux encore, de leur surface totale (PAASCHE, 1960) ? Dans un récent et remarquable travail sur ce problème, SMAYDA (1965) a repris l'ancienne notion de volume plasmatique de LOHMANN (1908).

(3) un troisième point, eu égard à son importance, justifie un paragraphe particulier:

c) Rôle du nannoplancton

L'importance et les variations du nannoplancton n'ont été évaluées dans cette étude que de façon très approchée (cf. p. 11). Or le rôle quantitatif de cette catégorie d'organismes est actuellement clairement démontré. Suggéré par la théorie, sur la considération du cycle annuel des divers éléments minéraux (ATKINS, 1945), il a été ensuite prouvé expérimentalement sous ses divers aspects:

(1) par comptage direct des organismes (RILEY, 1957; HULBURT et al., 1960; TEIXEIRA & KUTNER, 1963; WOOD, 1963a). Le rôle particulier de certaines espèces a été d'autre part étudié par PARKE, 1949 (six espèces nouvelles de Flagellés), KNIGHT-JONES & WALNE, 1951 (*Chromulina*), COLLIER & MURPHY, 1962 (*Chaetoceros*), etc.

(2) par le dosage des pigments chlorophylliens (RILEY, 1938, 1941a; MILLER et al., 1953).

(3) par la méthode du carbone 14 (STEEMANN NIELSEN & JENSEN, 1957; MCALLISTER et al., 1960; HOLMES & ANDERSON, 1963; SAIJO, 1964; ANDERSON, 1965).

(4) par le dosage du carbone organique (MULLIN, 1965).

(5) par l'emploi simultané des méthodes 1 et 2 (RILEY et al., 1949; WOOD & DAVIS, 1956), 1 et 3 (TEIXEIRA, 1963), 2 et 3 (SAIJO & TAKESUE, 1965), enfin 1, 2 et 3 (YENTSCH & RYTHER, 1959). S'ajoute à cette longue énumération le

travail de WILLIAMS & MURDOCH (1966) basé sur des comptages de cellules, des analyses de pigments et des mesures de production par la méthode de l'oxygène.

Toutes ces recherches attestent l'importance quantitative souvent prépondérante du nannoplancton, ce que confirment mes observations à Nossi-Bé: dans la baie étudiée, le nannoplancton représente pendant la plus grande partie de l'année, à défaut de microplancton, l'essentiel de la biomasse et de la production primaire.

On a fait allusion plus haut (p. 11) aux difficultés pratiques d'étude et de dénombrement des nannoplanctontes: il faut constater en effet, et déplorer, que, parmi toutes les techniques de „routine" utilisées dans les recherches sur le phytoplancton (techniques microscopiques, biochimiques, physiologiques . . .) les moyens d'étude du nannoplancton sont de loin les moins développés.

7. Comparaison des stations L et A

Laissant de côté la station J, en quelque sorte intermédiaire entre les deux autres et occupée pendant 12 mois seulement, comparons maintenant les résultats obtenus aux deux stations extrêmes L (ouverture de la baie) et A (au fond de la baie) de mars 1963 à juin 1964.

Les salinités hebdomadaires (fig. 18) présentent deux types d'écarts dans le

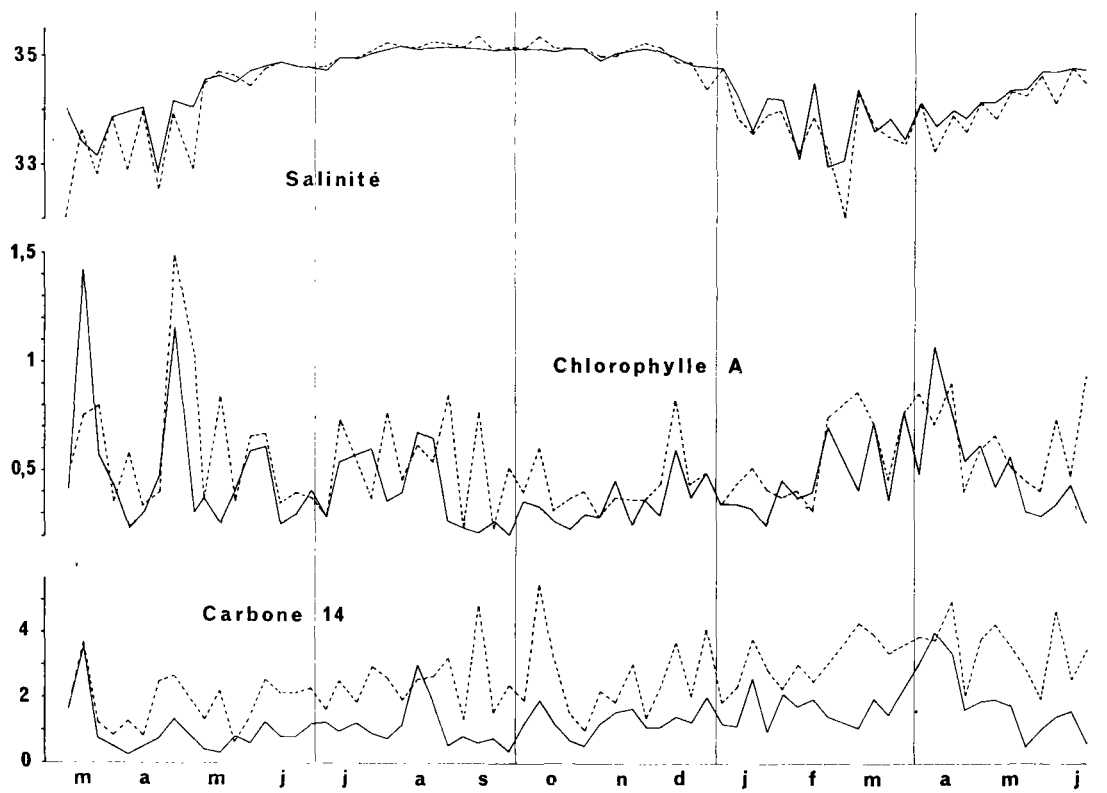


Fig. 18. Comparaison des stations L, à l'ouverture de la baie (trait continu) et A, au fond de la baie (tireté). Chlorophylle *a* en mg/m³, et production en mg carbone/m³/heure

cours de l'année: en saison humide, la station A tend à être dessalée par rapport à l'autre, du fait de l'influence plus proche des eaux douces terrigènes; en saison sèche par contre, les salinités en A peuvent être légèrement excédentaires, par suite d'une évaporation plus intense. Cependant, cette inversion saisonnière n'a pas révélé de corrélation avec le développement planctonique.

Les principaux aspects quantitatifs du phytoplancton sont reportés sur le tableau V sous forme de moyennes annuelles. Les méthodes statistiques permettent de définir dans chaque cas la signification de la différence observée entre les deux stations (probabilité pour que les deux moyennes soient tirées de „populations" différentes). Sur les neuf caractères étudiés, quatre seulement montrent des différences significatives; en d'autres termes, seules apparaissent comme fondamentalement différentes à l'échelle annuelle: les concentrations en chlorophylle *a*, les quantités de nannoplancton (malgré l'imprécision des comptages), les taux de fixation du carbone 14, enfin les rapports des densités optiques à 430 et 665 mμ. Sous les trois premiers aspects, la station A, la plus littorale, est la plus productive; la différence significative observée entre les rapports D 430/665 confirme cette discrimination (cf. MARGALEF, 1960, 1963, etc.).

Dans le détail, et non plus à l'échelle annuelle, les deux stations semblent affectées de différences périodiques, apparemment hebdomadaires (fig. 18): il était tout indiqué de rechercher là une corrélation possible avec le phénomène de la marée, qui présente à Nossi-Bé, entre autres périodes, un rythme de 15 à 17 jours (cf. p. 6). Une première approche révèle alors que les écarts entre les deux stations (salinité, chlorophylle *a*, carbone 14, et nannoplancton) tendent à une relation inverse avec la hauteur de la marée; la relation est plus évidente

Tableau V. Valeurs moyennes entre mars 1963 et juin 1964 des principaux caractères étudiés, et signification statistique des différences observées entre les deux stations

	Station A (la plus littorale)		Station L („océanique")	ε		Degré de signification
Chlorophylle *a* mg/m³	0,55	>	0,45	2,61	→	<0,01
Chlorophylle *b* mg/m³	0,19	>	0,18	0,67		différence non significative
Chlorophylle *c* mg/m³	0,71	>	0,67	0,75		
Caroténoides MSPU/m³	0,94	>	0,90	0,36		
D 430/665 mμ	4,30	<	5,08	2,15	→	0,03
Production nette mg C/m³/h	2,63	>	1,34[1])	7,75	→	≃ 0
Diatomées cell./l	17200	<	22000	0,74		différence non significative
Trichodesmium filaments/l	2400	<	3300	1,00		
Nannoplancton cell./l	86000	>	64000	4,78	→	≃ 0

[1]) Moyenne probablement supérieure de 20% environ (voir p. 35).

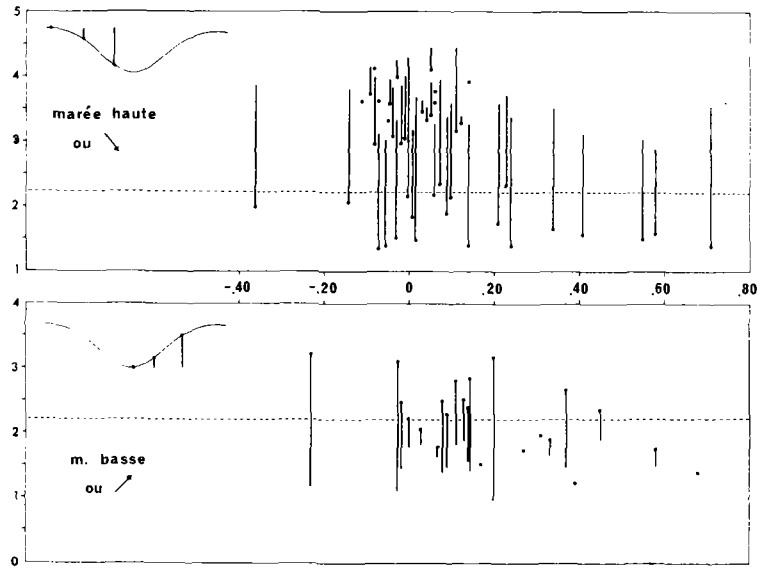


Fig. 19. Ecart des teneurs en chlorophylle *a* aux deux stations L et A (différence algébrique A—L, en abcisses), en fonction de la hauteur de la marée (en ordonnées). Tireté: niveau moyen de la mer. Points isolés: prélèvements effectués à l'heure précise de la pleine mer ou de la basse mer. Segments: prélèvements effectués lors d'un niveau intermédiaire; dans ce cas, l'extrémité libre du segment indique la hauteur de la pleine mer ou de la basse mer précédente

si l'on évalue le niveau instantané en fonction de la hauteur de la pleine mer ou de la basse mer précédente. D'où l'essai suivant de représentation graphique:

Le cas de la chlorophylle *a* a été pris à titre d'exemple (fig. 19). Pour plus de clarté, on a réparti les données en deux groupes: marée haute ou descendante, marée basse ou montante; le fait que les mesures soient plus nombreuses dans le premier cas traduit simplement le rythme propre de la marée: à l'heure du prélèvement (environ 07.00) celle-ci est plus souvent haute que basse (cf. p. 6).

— graphique supérieur: les marées hautes (points, ou segments courts) correspondent aux plus faibles écarts en pigment; les écarts les plus importants surviennent pour les niveaux les plus éloignés de la marée haute.

— le graphique inférieur complète le précédent: les écarts les plus forts correspondent principalement aux basses mers.

Je n'ai pu par ailleurs établir de distinction entre les périodes de morte-eau et de vive-eau.

Ces phénomènes sont à rapprocher du fait que les teneurs en matières organiques, mesurées par l'absorption de l'ultraviolet, sont à la station A plus élevées à marée basse qu'à marée haute (SOURNIA, 1965b).

On peut donc dire que la marée a pour effet d'amplifier périodiquement les différences physico-chimiques et biologiques entre les deux stations: en A, les eaux de marée basse sont relativement plus „littorales", donc plus productives, et les eaux de marée haute relativement plus „océaniques", alors que cette distinction ne se manifeste pas à la station L, plus éloignée de la côte.

III. Variations nycthémérales

1. Introduction

La connaissance des variations nycthémérales du phytoplancton, sous leurs aspects qualitatifs et quantitatifs, demeure actuellement fragmentaire, et les données disponibles sont parfois contradictoires. Les difficultés sont ici de double nature: pratiques tout d'abord, puisque l'expérimentation doit fournir un grand nombre de mesures dans un intervalle de temps réduit (trop de „cycles" ont été établis sur la base de quelques mesures seulement); de ce point de vue, le progrès des techniques devrait permettre de réaliser plus souvent des enregistrements continus, du moins pour les variables physico-chimiques (cf. TEAL & KANWISHER, 1966; SCHRAMM, 1966; KINSEY, 1967), probablement bientôt aussi pour les paramètres phytoplanctoniques eux-mêmes (MARGALEF, 1966). Les difficultés théoriques, d'autre part, tiennent elles-mêmes en deux points principaux: 1) Lorsque la précision des mesures entre en compétition avec l'amplitude des variations, une étude méthodologique et statistique serait seule apte à décider de la signification des résultats: certains auteurs avouent leur incertitude (RYTHER et al., 1961; MCALLISTER, 1963), mais la plupart passent outre. 2) La multiplicité des causes possibles rend délicate l'interprétation des phénomènes.

Un bref historique peut être tracé ici en trois points, le cas des eaux douces étant laissé de côté (voir à ce sujet VERDUIN, 1957; OHLE, 1958; ICHIMURA, 1960):

— l'usage le plus ancien est celui des comptages directs au microscope, qui dans certains cas ont pu être reliés, du moins partiellement, au rythme de la marée (ALLEN, 1923, 1927; MÖBERG, 1927; RANGARAJAN, 1959; TEIXEIRA & KUTNER, 1963) ou aux variations de la salinité (RYTHER et al., 1958; TEIXEIRA & KUTNER, loc. cit.; ANGOT & GÉRARD, 1967). Un rythme solaire est fréquemment observé (SILVA, 1956; WOOD, 1963a, 1964; WOOD & CORCORAN, 1966); en rapport avec ce phénomène, la possibilité de migrations verticales a été prouvée chez certaines espèces de Péridiniens (HASLE, 1950, 1954; SWEENEY & HASTINGS, 1958; SOLI, 1966) *ainsi que chez une Diatomée* (HARDY, 1935).

— les variations nycthémérales du milieu physico-chimique sont connues de longue date: LEGENDRE (1909) cite deux travaux effectués en 1844 et 1846 par dosage eudiométrique de l'oxygène (voir aussi JACOBSEN, 1912; MCCLENDON, 1918; ORR & MOORHOUSE, 1933, etc.). La mesure de l'activité photosynthétique à partir des variations in situ de l'oxygène dissous semble remonter à PÜTTER (1924). Cette méthode a été développée par divers auteurs (voir références des travaux russes in WINBERG, 1958), particulièrement par ODUM (1956) et ODUM & HOSKIN (1958).

— ce que l'on pourrait appeler „l'ère moderne de la phytoplanctologie" (1952: avènement simultané de la méthode spectrophotométrique de RICHARDS & THOMPSON, et de la méthode du carbone-14 de STEEMANN NIELSEN) a donné lieu à diverses recherches sur les variations de la biomasse et de la productivité; ces travaux sont reportés dans le tableau VI, et seront discutés dans la suite de cette étude.

Au total, les données actuelles sur les variations de la composition taxinomique ne prêtent qu'à une seule généralisation: cellules souvent plus nombreuses le jour que la nuit. D'autre part, la capacité photosynthétique (production horaire en éclairage artificiel constant) montre presque constamment un maximum au début du jour et un minimum au début de la nuit: ce résultat a été du moins obtenu par la méthode du ^{14}C (DOTY & OGURI, 1957; YENTSCH & RYTHER, 1957; SHIMADA, 1958; MCALLISTER, loc. cit., DOTY et al., 1963) celle de l'oxygène ayant conduit à un schéma légèrement différent (LORENZEN, 1963). Les données relatives aux concentrations en pigments sont par contre purement contra-

Tableau VI. Principales recherches récentes sur les variations nycthémérales de la biomasse phytoplanctonique, de la production primaire et du milieu (voir autres références dans le texte). L'ordre est chronologique. Les parenthèses indiquent des mesures accessoires (non nycthémérales). Les indications de latitude (première colonne) facilitent le rapprochement, éventuel avec la théorie de Doty (loc. cit.)

AUTEURS	Comptage des cellules	Pigments chlorophylliens	Production en flacon clos		Oxygène in situ	Energie lumineuse	Divers
			^{14}C	O_2			
Doty & Oguri (1957) Pacifique équatorial	·	·	Incubateur	·	·	·	·
Yentsch & Ryther (1957) Woods Hole, 42° N	·	+	Incubateur	·	·	(+)	·
Yentsch & Scagel (1958) Friday Harbor, 49° N	+	+	·	·	(+)	+	PO_4
Ryther et al. (1958) Long Island, 41° N	+	+	·	in situ	+	+	PO_4, NO_3, pH
Shimada (1958) I. Clarion, 18°N	·	+	Incubateur	·	·	·	·
Odum & Hoskin (1958) Texas, Antilles . . .	·	·	·	+	+	·	·
Doty (1959) (Compilation)	·	·	Incubateur	·	·	·	·
Humphrey (1960) Sydney, 34° S	·	+	·	·	·	·	·
Ryther et al. (1961) Bermudes, 32° N	·	+	„simulated in situ“	·	·	+	PO_4, NO_3, NO_2 Zooplancton
Ryther & Menzel (1961) Atlantique, 16—32 ° N	·	+	„simulated“ in situ”	·	·	+	·

Angot (1961) Pacifique, 22° S	·	+	Incubateur et in situ	·	(+)	+	·
Occhipinti et al. (1961) Sao Paulo, 25 ° S	+	+	·	in situ	·	+	PO_4, pH, marée
Jones (1963) Miami, 25 °N	·	·	·	in situ	+	+	·
Lorenzen (1963) Long Island, 41° N	?	+	·	Incubateur	·	+	PO_4, NO_3
Mc Allister (1963) Pacifique, 50° N	·	+	Incubateur	·	·	·	·
Alexander & Corcoran (1963) Floride, 26—28° N	·	+	·	·	·	·	PO_4, σ t
Goering et al., 1964 Bermudes, 32° N.	·	+	Incubateur	·	·	·	Assimilation de NH_4 et NO_3
Wood & Corcoran (1966) Stations diverses	+	+	·	·	·	·	D.S.L., „grazing“
Angot & Gérard (1967) Nosy-Bé, 13° S	+	+	in situ	·	+	+	·
Observations personelles Nosy-Bé, 13 °S	+	+	in situ	·	+	approxi-mative	Courants, marée

dictoires: il apparait seulement que la synthèse de la chlorophylle est inhibée par les forts éclairements.

Outre les phénomènes, les mécanismes nycthéméraux eux aussi restent à définir et prêtent parfois à controverse: en particulier, les relations exactes entre lumière, pigments et photosynthèse sont confuses, car il est délicat de „distinguer les causes des effets" (YENTSCH & RYTHER, 1958). Les mesures de production se heurtent de plus à la difficulté d'évaluer les taux respectifs de la respiration diurne et nocturne. D'autre part, il n'est nullement prouvé que les variations de l'activité photosynthétique soient dues à celles du nombre de cellules chlorophylliennes (contra WOOD & CORCORAN, loc. cit.), ou de la quantité même de chlorophylle dans les cellules: au contraire, comme j'ai pu le montrer tout récemment (1967b), les variations propres de la capacité photosynthétique de la chlorophylle *a* jouent dans ces phénomènes un rôle fondamental. Enfin, l'effet de „broutage" a été invoqué par la théorie (STEEMANN NIELSEN & JORGENSEN, 1962; MCALLISTER, loc. cit.) et vérifié de façon approchée (WOOD & CORCORAN, loc. cit.), mais reste à évaluer quantitativement.

2. Méthodes

Mes résultats tiennent ici en huit séries d'observations de 24 à 38 heures chacune, échelonnées tous les 2 ou 3 mois entre avril 1963 et juin 1964: s'y ajoutent occasionnellement les mesures quotidiennes effectuées à la station J par le personnel technique du Centre d'Océanographie, et aimablement communiquées par celui-ci.

Sur le plan technique, ces huit séries ne sont pas homogènes, car l'expérimentation a été amplifiée de l'une à l'autre, dans le but d'augmenter le nombre et la diversité des mesures; ainsi:

— en avril 1963: 8 prélèvements en 24 heures, à une profondeur unique (1 m) avec les mesures suivantes: température, salinité, comptages au microscope inversé, et analyse des pigments photosynthétiques,

— en avril 1964: 26 prélèvements en 38 heures, à deux niveau (1 et 7 m), avec trois mesures supplémentaires: oxygène dissous, photométrie sommaire, et production par le carbone 14.

Pour l'essentiel, les méthodes sont celles précédemment décrites dans l'étude du cycle annuel; je ne signalerai donc que les différences et les aspects nouveaux.

a) Stations

Les huit séries d'observations, que je désigne chronologiquement de I à VIII, peuvent être groupées comme suit:

— I (2 avril 63), station J. Seule des huit séries, celle-ci ne comporte ni „O_2", ni „^{14}C". Cette „opération préliminaire" s'est trouvée coïncider avec une prolifération brutale de *Trichodesmium* (cf. SOURNIA, 1965b, et s. presse, c).

— II (29 mai) et III (3 juin), station J. Ces deux journées rapprochées ont été choisies de façon à tester l'influence de la marée (heures des PM et BM opposées dans les deux cas). Malheureusement les conditions météorologiques ont également différé puisqu'on avait: en II, ciel couvert (nébulosité moyenne 5/8) et pluvieux (total des pluies: 16,4 mm), en III, ciel clair (1/8) et précipitations négligeables (0,6 mm).

— IV (ler sept.), V (10 nov.), VI (10 févr. 64) et VII (12—13 avril). Dans le but d'étudier les variations selon la profondeur, la station J a été abandonnée: les mesures ont été effectuées à bord du navire de recherches du Centre, l' „Ambariaka", mouillé à 200 mètres de la

station J, sur un fond de 9 mètres. Un second niveau (7 m) a ainsi pu être ajouté au niveau subsuperficiel (1 m) utilisé dans les séries I—III ainsi qu'au cours du cycle annuel.

— VIII (2 juin 64). L'objet de cette dernière série était l'étude des variations nycthémérales aux deux stations L et A, dont on a examiné plus haut les variations saisonnières (p. 40). Les prélèvements ont donc été effectués à l'aide d'un canot automobile rapide (Zodiac), un minutage constant étant respecté entre les prises d'eau aux deux stations et le traitement des divers échantillons; le navire „Ambariaka", au mouillage comme précédemment, servait de base d'opérations.

b) Rythme des mesures

Les mesures couvrent des intervalles de 24 heures (I et VIII), 30 heures (II à VI) ou 38 heures (VII). Le rythme des mesures était le plus souvent de trois heures; pendant le jour, cet intervalle était légèrement augmenté ou diminué, selon la saison. en fonction du cycle solaire: de cette façon les expériences par le ^{14}C débutaient toujours au lever du soleil et se terminaient au coucher. D'autre part, lors de la série VII, un rythme de 1 h 30 a été suivi pour les mesures hydrologiques.

Un problème pratique est de concilier les exigences respectives des cycles nycthéméraux du phytoplancton et du phytoplanctologiste . . .: la solution la plus avantageuse semble bien celle réalisée en VII: *mesures réparties — en plus grand nombre possible — entre* le lever du soleil et le crépuscule du jour suivant.

c) Pigments photosynthétiques; carbone 14

Au sujet des pigments photosynthétiques , une seule modification à la méthode décrite au début de ce travail (p. 11): pour les séries IV à VIII, la filtration a pu être effectuée sur place, c'est à dire à bord de l',,Ambariaka", avec le même dispositif „Millipore" (la pompe étant alimentée par un groupe électrogène); le délai de transport au laboratoire est donc dans ce cas supprimé.

Les mesures de production se sont ici encore déroulées in situ; pour les séries II et III (station J), une seule modification au processus hebdomadaire (cf. p. 12): les échantillons étaient exposés par paires pendant trois et six heures, et non pendant une période unique de 4 heures. Pour les séries IV à VIII („Ambariaka") un filin était attaché au flotteur de façon à exposer les échantillons de 7 mètres à leur niveau d'origine; l'ensemble était maintenu à l'écart de l'ombre du bateau.

d) Mesures diverses

Lors des séries VI et VII, les courants ont été suivis, à la profondeur 4 m, au moyen d'un courantomètre EKMAN; les mesures, de 8 min. chacune, étaient espacées à des intervalles de 45 min. environ.

La pénétration de la lumière a été évaluée au moyen du disque de Secchi (IV à VIII). La nébulosité a été notée „à l'oeil nu" en octas. Enfin, l'énergie lumineuse n'a pu être mesurée que de façon approchée et relative, au moyen d'une cellule photoélectrique dirigée vers un écran blanc, celui-ci orienté perpendiculairement à la direction du soleil; le procédé employé ayant quelque peu varié d'une série à l'autre, les résultats obtenus aux diverses époques de l'année ne sont pas quantitativement comparables (les résultats relatifs à la nébulosité sont bien entendu comparables, mais moins précis).

3. Conditions hydrologiques

a) Température et salinité en surface

Sur ces deux points mes observations confirment ou complètent celles de MÉNACHÉ (1957), GÉRARD (1964) et ANGOT & GÉRARD (1967).

Aux différentes périodes de l'année, les variations nycthémérales de la température décrivent un cycle identique: maximum vers 15 h, minimum à la fin de la nuit, et amplitude, relativement constante, comprise entre 1° et 1°, 5.

Par contre, l'évolution des salinités diffère selon la saison: de manière générale les valeurs sont plus fortes le soir que le matin, par suite de l'évaporation diurne et du caractère essentiellement nocturne des précipitations (écart moyen de juillet 1963 à juin 1964, pour 300 mesures: 0,8‰); cependant, l'amplitude de cette variation est souvent réduite en hiver, tandis qu'elle est plus considérable — mais très variable — en été: pendant cette dernière saison, le sens de la variation peut d'ailleurs être inversé (MÉNACHÉ, GÉRARD, loc. cit.) à la suite de pluies diurnes.

Au sujet de l'influence possible de la marée sur la salinité, il semble que l'alternance „pleine mer-basse mer" soit sans effet à la station J (au sujet de la station A, voir p. 41); on peut penser que, si un tel rythme existe, il est masqué par les variations précédentes. Cependant la marée exerce, selon ANGOT & GÉRARD (loc. cit.) une action à longue période: ces deux auteurs ont en effet décelé en avril 1965 une corrélation entre salinité journalière moyenne et hauteur de la pleine mer le même jour; il s'agit dans ce cas d'un rythme „morte eau — vive eau", dont la période est de 14 jours environ. Ce phénomène reste à généraliser pour les différentes saisons.

b) Diagrammes T–S en surface et en profondeur

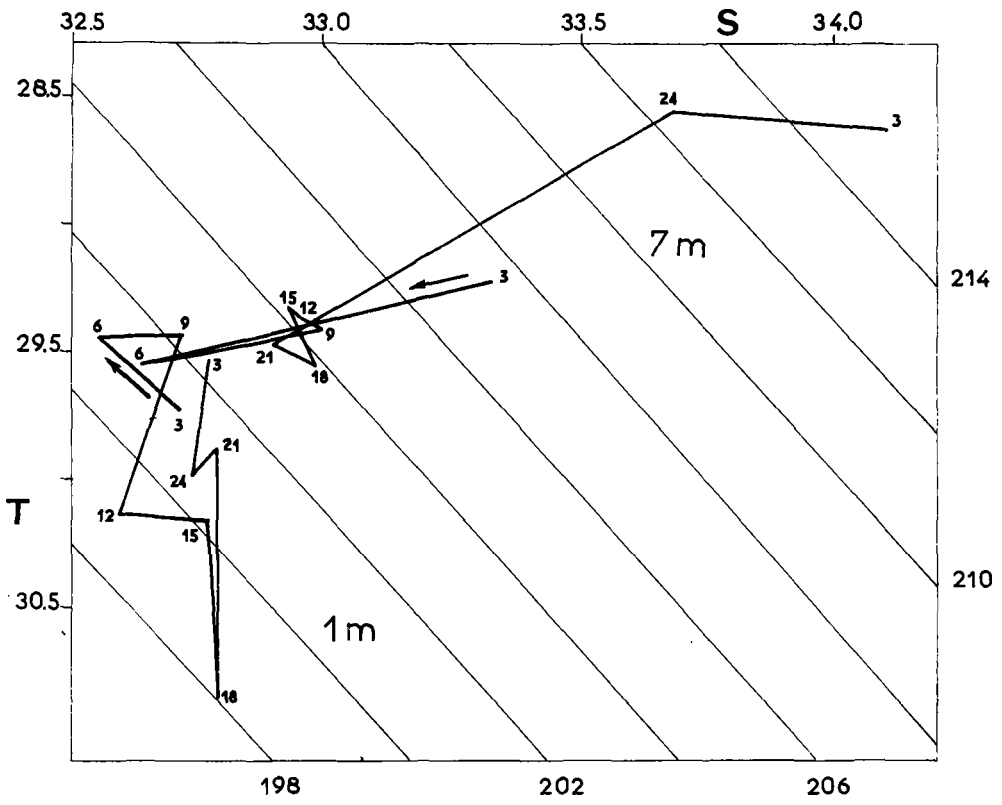
Les séries IV à VII, comportant des mesures parallèles à 1 et 7 mètres, permettent de comparer l'évolution nycthémérale de la température et de la salinité aux deux niveaux. Les phénomènes peuvent être représentés sur des diagrammes T–S, dont un exemple est donné sur la figure 20 (partie supérieure).

Malgré des différences de détail dans les quatre cas étudiés, il apparaît clairement que les cycles des températures et salinités sont différents aux deux profondeurs. De façon générale, les variations de température sont plus importantes à 1 m, et les variations de salinité beaucoup plus considérables à 7 mètres. En outre, la différence entre les densités aux deux profondeurs n'est pas constante: ceci apparaît plus nettement si l'on joint deux par deux les points correspondants à une même heure (fig. 20, partie inférieure); dans le cas ici étudié (série VI) les deux couches d'eau sont homogènes à 6 et 9 h, puis le sont de moins en moins jusqu'à 18 h; on observe une nouvelle homogénéité à 21 h; la stratification est enfin maximale à 24 et 3 heures. Les séries IV et V montraient un cycle analogue, à cette différence que la stratification croissait régulièrement de 11 à 2 h 30.

Dans le cas de mesures s'étendant sur plus de 24 heures, la représentation graphique sur un diagramme T–S devient confuse. Aussi ai-je procédé différemment pour la série VII (fig. 21): un changement d'axes permet d'introduire une nouvelle dimension, le temps. Ce graphique a donc été construit en deux étapes:

— Diagramme T–S identique à celui de la figure 20; les points représentatifs des mêmes heures sont joints deux à deux par un segment. Notons que, dans l'intervalle relativement réduit des deux variables, les isopycnes peuvent être assimilées à des droites.
— Changement d'axes: les nouvelles ordonnées indiquent les densités, les nouvelles abcisses les temps. Les axes des températures et des salinités demeurent perpendiculaires entre eux,

Fig. 20. Diagrammes T–S (20 févr. 1964). Variations nycthémérales de la température et de la salinité à deux profondeurs. En haut: les deux séries de mesures (à noter que la constance des deux caractéristiques entre 9 et 21 hau niveau 7 m n'a pas été retrouvée aux autres périodes de l'année). En bas: on a joint par des segments les prélèvements simultanés aux deux profondeurs. Les nombres indiquent les heures des prélèvements


32.5
33.0
33.5
S
34.0
28.5
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30.5
T
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210
198
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3
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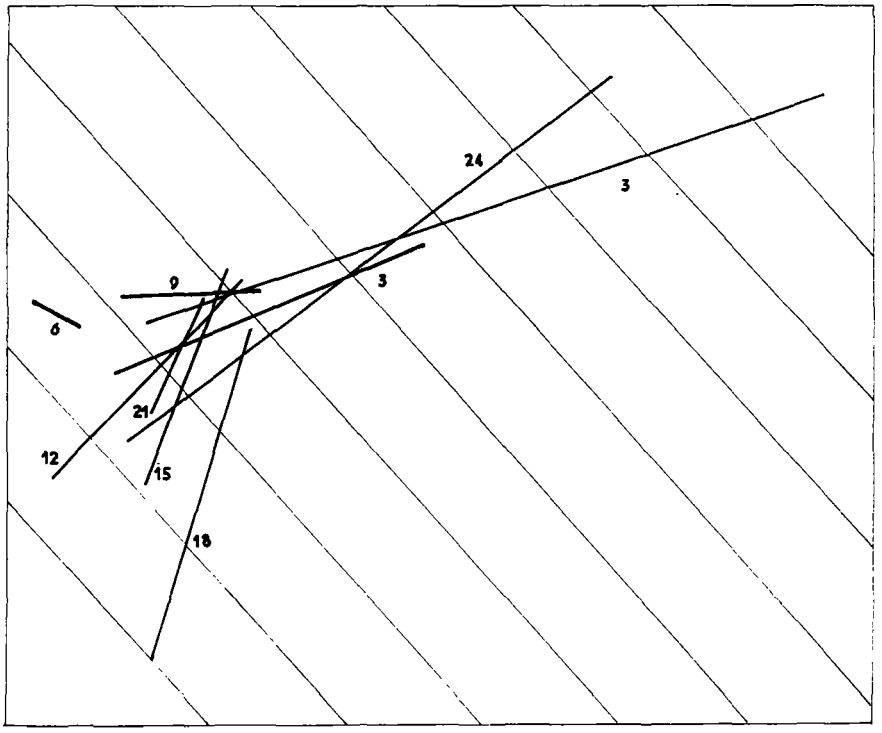
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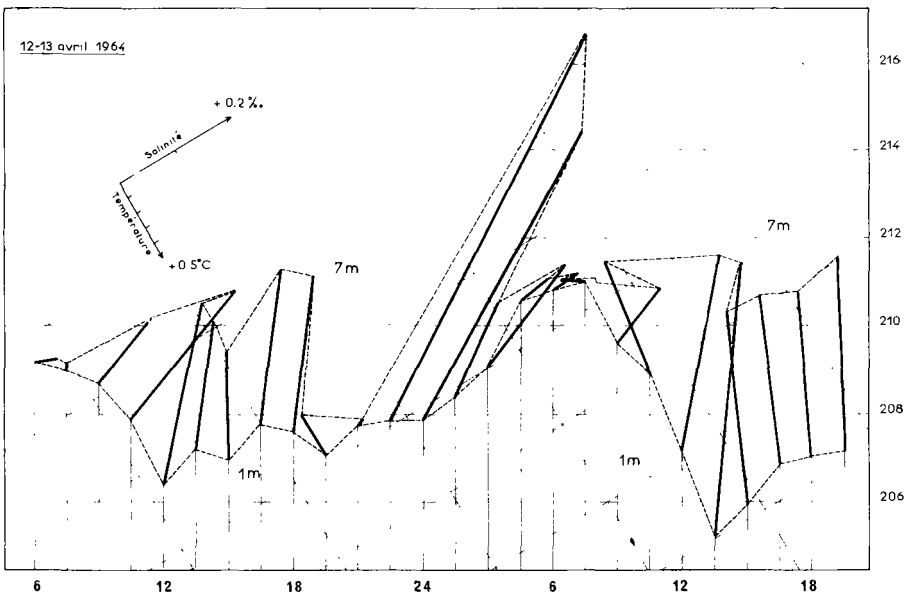

Fig. 21. Variations nycthémérales de la température et de la salinité les 12 et 13 avril 1964 aux deux niveaux 1 et 7 m. Pour la construction, voir p. 48

mais deviennent obliques par rapport aux nouvelles coordonnées. Les segments du diagramme précédent sont alors reportés sur celui-ci; on prend comme origine pour chacun d'eux, par convention, le point „1m", et l'on espace les segments dans l'ordre chronologique par rapport à l'axe des temps; on respecte bien entendu pour chaque segment sa position et sa direction par rapport aux isopycnes.

Sur un tel diagramme, les valeurs des températures et salinités ne sont plus que relatives, mais permettent de comparer les deux extrémités „1 m" et „7 m" d'un même segment. Au total, cinq dimensions sont représentées: densité, temps, température, salinité et profondeur. De plus l'homogénéité des deux couches d'eau est optiquement mise en évidence par la longueur et la direction des segments; enfin l'inclinaison de ces segments sur les axes des températures ou sur ceux des salinités ajoute une nouvelle information.[1])

En conclusion de ce paragraphe: l'homogénéité des eaux aux deux niveaux ("surface": 1 m; "profondeur": 7 m) présente un maximum à l'aube, et parfois un maximum secondaire au crépuscule; la stratification est importante au milieu de la journée et, surtout, au milieu de la nuit.

c) Oxygène dissous

GÉRARD (1964) et ANGOT & GÉRARD (1967) ont précédemment montré que les teneurs en oxygène dissous (concentrations brutes et pourcentages de saturation) sont, dans la baie étudiée, plus fortes le soir que le matin. La seconde publication décrit en outre les variations horaires tout au long du mois d'avril 1965 ainsi que les moyennes horaires pour ce mois.

J'ajoute à ces données la preuve de l'influence de la marée: les pourcentages de saturation observés aux différentes heures de la journée, à marée haute et à marée basse, pendant douze mois, permettent de tracer les deux courbes de la

[1]) Note sur épreuves: Je remarque, mais trop tard, que le graphique aurait gagné à être inversé verticalement: „1 m" au dessus de „7 m", et densités croissant vers le bas . . .

figure 22; on remarque que les différences dues à la marée, bien qu'évidentes, n'ont qu'une importance secondaire par rapport à l'amplitude des variations diurnes; celle-ci est par ailleurs bien supérieure aux écarts observés dans le cours du cycle annuel (cf. p. 16).

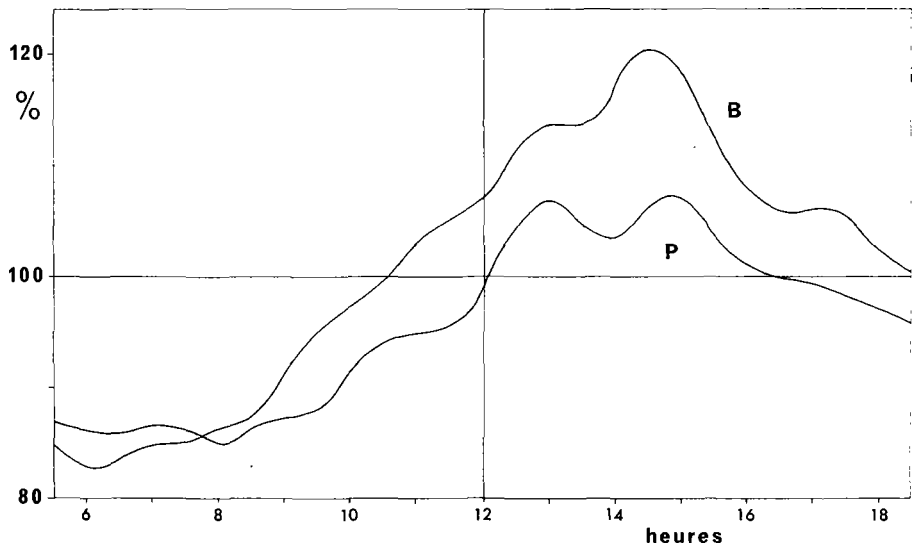

Fig. 22. Variations diurnes du pourcentage de saturation en oxygène dissous (station J, eau de surface). B: basse mer, P: pleine mer. Chaque courbe représente la régression continue de 298 mesures, de juillet 1963 à juin 1964 (mesures quotidiennes, sauf jour fériés)

D'autre part, les mesures obtenues lors des séries II à VII sont reportées sur la figure 24, et seront discutées p. 55.

d) Courantométrie sommaire

Les mesures effectuées en période de vive-eau (série VII: PM = 4,35 m; BM = 0,39) et au voisinage de la morte-eau (VI: PM = 3,52; BM = 1,31) permettent, malgré quelques défauts de fonctionnement de l'appareil, de conclure aux points suivants:

Un courant portant à l'ouest — quelquefois au N ou au NO — est observé aux heures voisines de la marée haute. Son intensité est directement proportionnelle à la hauteur de la pleine mer, ce qui apparaît de deux manières: 1) vitesse différente pour les deux phases „semi-diurnes" (celles-ci légèrement inégales, comme on l'a vu p. 6), 2) vitesse différente en morte-eau (de 0,2 à 0,5 noeuds) et en vive-eau (jusqu'à 0,9 noeuds).

Outre ce courant de marée, on note un mouvement constant, de l'ordre de 0,1 noeud, mais dont la direction n'a pu être précisée.

e) Transparence des eaux

Le disque de Secchi est visible jusqu'au fond (9 m) ou au voisinage du fond jusqu'aux environs de 13 heures; après quoi la limite de visibilité remonte généralement jusque vers 7 m. Ce phénomène ne semble pas lié au rythme de la marée, et, d'autre part, ne peut pas être simplement assimilé à la variation diurne de l'éclairement solaire.

4. Biomasse phytoplanctonique

Au sujet des variations de la composition taxinomique du phytoplancton et de celles des pigments photosynthétiques, mes résultats sont très limités. La méthodologie suivie s'avère en effet défaillante sur trois points:

— l'étendue des mesures (24 ou 30 heures, en une occasion 38 h) semble insuffisante; plusieurs journées consécutives auraient dû être suivies à chaque période de l'année.

— le rythme des mesures (3 h) est trop lâche. Remarquons qu'un rythme nycthéméral de trois heures, appliqué au cycle annuel, correspondrait à des intervalles de six semaines; inversement, le rythme hebdomadaire utilisé au cours du cycle annuel conduirait, pour le cycle nycthéméral, à des intervalles de 30 minutes ... Je pense donc qu'un rythme horaire serait plus approprié.

— la précision des mesures, et surtout les incertitudes d'échantillonnage, jouent certainement un rôle capital, que je n'ai pas évalué. Notons que, dans l'étude des variations nycthémérales, on aborde en quelque sorte le problème de la „microdistribution dans le temps", et que celui-ci implique la connaissance de la microdistribution dans l'espace.

a) Nannoplancton

Malgré les incertitudes d'identification et de comptage, ce groupe a montré un caractère constant à travers les sept séries de mesures: le nombre de cellules passe environ du simple au double entre 6 et 9 heures. Ce phénomène est indépendant du cycle de la marée, puisque les fluctuations observées sur les séries II et III sont parallèles; il semble plutôt lié aux conditions lumineuses: on note en ce sens que, dans le cas de la série V, le nombre de cellules a crû régulièrement jusqu'à 15 heures, mais que ce jour là la nébulosité était, exceptionnellement, très élevée (de 6/8 à 8/8) jusqu'à 14 heures. Par ailleurs, cet accroissement affecte essentiellement la couche supérieure (1 m) sans qu'un phénomène inverse soit observé à 7 m; aussi s'agit-il d'une multiplication cellulaire (ou d'une diminution du taux de „sinking" ou de „grazing") plutôt que d'une migration verticale. On peut rapprocher ce fait du rythme observé par SWEENEY & HASTINGS (1958) sur *Gonyaulax polyedra* en culture.

Cette multiplication matinale constitue le seul évènement „important" du cycle nycthéméral: le reste de la journée ainsi que la nuit présentent des fluctuations irrégulières dont je ne puis rien généraliser.

b) Microplancton

A la différence du groupe précédent, la composition du microplancton varie considérablement selon la période de l'année (cf. p. 25); ainsi chacune des séries d'observations nycthémérales présente-t-elle un cas particulier qui ne peut guère être comparé aux autres:

— séries II et III (29 mai et 3 juin 63): Diatomées assez diversifiées mais rares (de 150 à 1400 cellules/l). Péridiniens (genre unique: *Ceratium*) très rares (moins de 100 cellules/l). *Trichodesmium* rare (de 50 à 750 filaments/l).

— série IV (1er sept.): Diatomées très rares (moins de 300). Péridiniens comme précédemment. *Trichodesmium* très rare (moins de 100). Il s'agit donc ici d'une phase à microplancton „désertique".

— série V (10 nov.): Diatomées abondantes (de 6000 à 40000), *Chaetoceros* dominant. Péridiniens absents. *Trichodesmium* très rare.

— série VI (10 févr. 64): Diatomées assez abondantes (de 500 à 6000), *Chaetoceros* dominant. Péridiniens (*Ceratium*) très rares. *Trichodesmium* rare.

— série VII (12—13 avril): Diatomées abondantes (de 20000 à 50000), *Rhizosolenia alata* dominant. Péridiniens assez diversifiés mais rares. *Trichodesmium* relativement abondant (de 500 à 2000).

— série VIII (2 juin 64): Microplancton „désertique", comme en IV.

Le rôle de la marée a pu être mis en évidence lors des séries II et III: les fluctuations sont manifestement opposées dans les deux cas, traduisant un maximum du nombre de Diatomées et de Cyanophycées aux heures de basse-mer. Mais ce schéma n'est qu'hypothétique car les mesures suivantes (IV à VII) ne l'ont ni vérifié ni démenti.

Une certaine périodicité est parfois observée, au cours d'une même série, dans l'abondance des espèces (cf. SILVA, 1960) mais sur ce point les différentes séries sont contradictoires. Pour l'ensemble du microplancton, je ne puis déceler d'heure d'abondance ou de déclin, ni de discrimination entre le jour et la nuit (contra WOOD, 1963b, 1964, et WOOD & CORCORAN, 1966).

c) Pigments photosynthétiques

Seule l'étude de la chlorophylle *a* conduit à des résultats généralisables, à savoir: pour une période de 24 heures, les concentrations maximales sont observées pendant le jour, les concentrations minimales pendant la nuit.

Au cours de la phase diurne, l'évolution des pigments dépend manifestement des conditions lumineuses: l'accroissement est interrompu au milieu de la journée dans le cas d'un éclairement intense (série III) alors qu'il est régulier jusqu'au soir lors d'un éclairement réduit (V).

Les fluctuations nycthémérales présentent en outre des accidents (variations „en dents de scie": série VI) visiblement dues à une insuffisance méthodologique, ainsi que des „anomalies" telles que maxima secondaires nocturnes (IV et VII).

Ces résultats confirment ceux de ANGOT & GÉRARD (1967); la courbe moyenne donnée par ces auteurs pour une période de 30 jours possède en effet un maximum vers 10 h et un minimum nocturne (loc. cit., fig. 4), mais, dans le détail des courbes nycthémérales, ce schéma est loin d'être constant (ibid., pl. 8).

Quant aux rapports inter-pigmentaires, s'ils présentent, indépendamment de l'heure du prélèvement, des relations mutuelles semblables à celles qui ont été examinées plus haut (p. 32) dans l'étude du cycle annuel, par contre leurs variations nycthémérales sont indistinctes: ce point est en contradiction avec RYTHER, YENTSCH et al. (1958) et YENTSCH & SCAGEL (1958), qui observent une relation entre intensité lumineuse et rapport „chlorophylle *a*/caroténoides" (toutefois les données de ces auteurs s'appliquent à des eaux extrêmement productives).

5. Production primaire

a) Mesures par le carbone 14

Deux remarques préliminaires:

1) Au sujet de l'assimilation de carbone à l'obscurité: la précision de mes mesures ne permet pas de reconnaître de variations entre les diverses heures de la journée (séries II à VII), pas plus qu'entre le jour et la nuit (séries II—III).

2) Au sujet de la durée des incubations: la comparaison des périodes d'exposition de 3 et de 6 heures montre que la production mesurée pendant une période de 6 heures n'est pas significativement différente de la somme des productions mesurées pendant les deux périodes de 3 heures correspondantes. Ceci montre non seulement que les durées de 3 et 6 heures ont la même signification méthodologique, mais aussi que le rôle d'un éventuel transport des populations in situ est nul dans les intervalles de temps mis en jeu.

Dans ces conditions, on n'examinera ci-dessous que les données relatives à la fixation de carbone dans les bouteilles claires, mesurée in situ à raison de quatre incubations de trois heures pour chaque journée solaire.

Ces résultats sont reportés sur la figure 24 sous forme de diagrammes. D'après ces mêmes données, les rapports des productions à 1 et 7 m, pour les séries IV à VII, ont été calculés et sont représentés sur la figure 23 en regard des conditions lumineuses (rappelons que celles-ci n'ont été mesurées que de façon relative, sans permettre de comparaison entre les diverses séries).

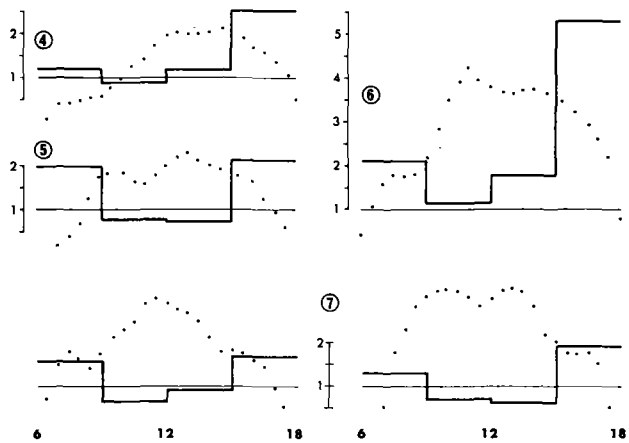

Fig. 23. Assimilation nette de carbone mesurée in situ pendant le jour, à 1 m et à 7 m: rapport (1)/(7). Pour chaque journée solaire, quatre périodes d'exposition consécutives, de trois heures chacune. Les courbes reproduisent les variations diurnes de l'éclairement, mesuré en unités arbitraires toutes les 30 minutes environ

Une dissymétrie apparaît entre les deux moitiés de la journée: les productions sont en général plus élevées l'après-midi que le matin (fig. 24): la cause peut en être attribuée aux conditions d'éclairement, qui présentent une inégalité de même sens (fig. 23).

De façon générale, la production primaire est plus élevée à 1 m qu'à 7 m aux heures d'éclairement réduit (de 6 à 9 h et de 15 à 18 h), et ce rapport est inverse au milieu du jour (de 9 à 15 h). On peut donc parler d'inhibition lumineuse en surface, sans pouvoir assurer toutefois que l'excès de lumière est la cause *directe* de la diminution de l'activité photosynthétique. Rappelons que les mesures hebdomadaires qui constituent le cycle annuel étudié précédemment étaient effectuées au milieu de la matinée, et se déroulaient donc dans des conditions probablement „sub-optimales".

Les différents contours des diagrammes de la production diurne peuvent tous être étroitement rapprochés des courbes de luminosité correspondantes (fig. 23).

b) Variations du taux d'oxygène in situ

Les variations du taux d'oxygène dissous (exprimé en pourcentages de saturation) sont reportées sur la figure 24. Les concentrations sont minimales le matin vers 6 heures et maximales le soir vers 18 h; le maximum diurne se traduit par une légère sursaturation au niveau 1 m, mais la saturation est exceptionnellement atteinte à 7 m (une importante sursaturation en fin de journée était de règle au niveau 0 m: cf. fig. 22). D'autre part, la phase diurne présente deux types distincts: l'accroissement est continu (II à VI), ou interrompu par des minima secondaires (VII).

Facteurs physiques:: Le calcul de la productivité à partir des variations du taux d'oxygène in situ suppose l'évaluation des échanges latéraux et verticaux (MIYAKE, 1948; SUGIURA, 1953, 1956; ODUM, 1956; KOHN & HELFRICH, 1957; ODUM & HOSKIN, 1958), évaluation possible dans des milieux bien définis, plus aisée en conditions artificielles, et le plus souvent incertaine en mer. Dans le cas présent cette question est trop complexe pour être traitée par quelques formules théoriques:

— on ne peut nullement admettre a priori que le taux de diffusion verticale est constant dans l'intervalle de 24 heures. Au contraire, l'étude des conditions hydrologiques (p. 48) a mis en évidence les variations nycthémérales de la stratification des eaux.

— l'intensité des échanges avec l'atmosphère varie certainement dans le cours de 24 heures, ne serait-ce que par suite de l'alternance des vents solaires (p. 7).

— les transports latéraux varient en direction et en intensité, en relation avec les courants de marée (cf. p. 51).

Dans ces conditions, une seule correction physique peut être appliquée avec efficacité: l'évaluation du taux de saturation en fonction de la température et de la salinité ambiantes.

Facteurs biologiques: La signification biologique de ces variations in situ est elle-même très complexe puisque celles-ci mettent en jeu l'ensemble des communautés végétales et animales, planctoniques ou non, du domaine étudié, et que le métabolisme nycthéméral de ces diverses communautés est très mal connu (un des problèmes essentiels est celui des variations nycthémérales des échanges respiratoires).

Aussi, dans le but d'une comparaison avec les mesures effectuées pendant le jour par la méthode du ^{14}C, on peut ne considérer qu'un aspect de la question, et voir dans l'accroissement diurne apparent du taux d'oxygène dissous une valeur approchée de la production nette pendant le jour.

Calcul de l'accroissement diurne apparent: La seule correction ici appliquée est relative au taux de saturation théorique. L'accroissement diurne ainsi mesuré est „apparent" puisqu'il ne tient pas compte des échanges physiques latéraux et verticaux; mais cette valeur, corrigée en fonction des température et salinité ambiantes, me semble plus représentative que la simple différence des concentrations absolues utilisée par exemple par RYTHER, YENTSCH et al. (1958).

Soit d O_2 = accroissement diurne apparent in situ,

m = minimum diurne (ml/l): mesuré le matin à l'heure où le pourcentage de saturation est minimum, c'est à dire vers 6 heures (exceptionnellement: 9 h),

m' = concentration théorique à saturation (ml/l), calculée d'après les température et salinité du prélèvement ci-dessus,

M et M' = mêmes caractéristiques pour le maximum diurne mesuré le soir, à l'heure où le pourcentage de saturation est maximum, c'est à dire vers 18 heures (exceptionnellement: 15 h),

d O_2 = accroissement mesuré — accroissement des taux de saturation,

$$= (M - m) - (M' - m') = (M - M') - (m - m') .$$

Dans le cas d'une courbe diurne discontinue (fig. 24: série VII), je procède de façon identique, en considérant les accroissements successifs: d O_2 = somme des accroissements mesurés — somme des accroissements calculés.

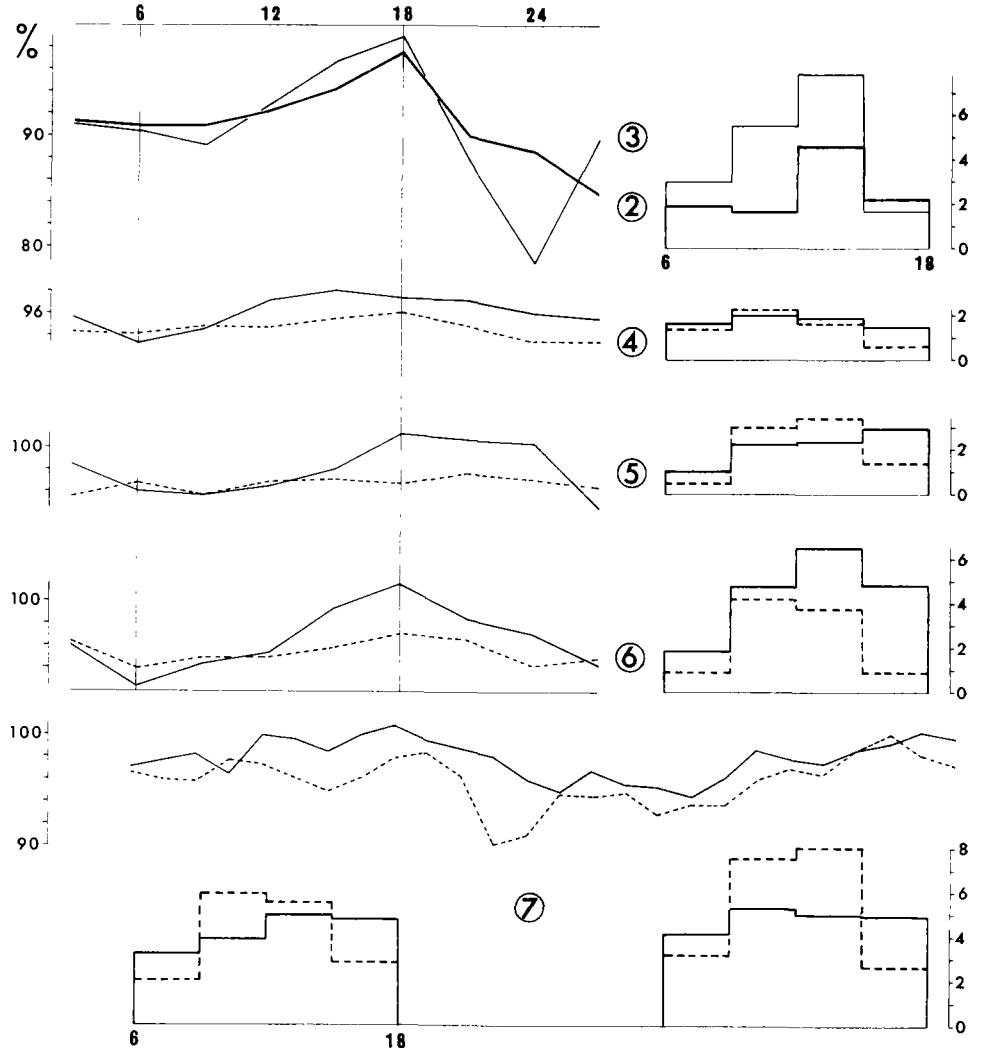

Fig. 24. Consommation de carbone et production d'oxygène. A gauche: variations nycthémérales in situ du pourcentage de saturation en oxygène dissous, pendant 24 heures (séries II à VI) ou 38 heures (série VII). A droite, et en bas: assimilation diurne de carbone (mg C/m³/h). Trait continu pour le niveau 1 m, tireté pour le niveau 7 m

c) Comparaison des deux méthodes

La figure 24 suggère que l'amplitude des variations nycthémérales du taux d'oxygène pourrait être proportionnelle aux productions mesurées par la méthode du carbone 14. Il existe effectivement une corrélation entre d O_2 et l'assimilation de carbone pendant une même journée (fig. 25); de plus les phénomènes sont différents aux deux niveaux étudiés:

— pour les 7 paires de données relatives au niveau 1 m, on peut établir l'équation: $^{14}C = 0{,}149\ d\ O_2 - 7{,}36$, avec $r = 0{,}80$ (probabilité: 0,02).

Unités: ^{14}C = total de l'assimilation nette mesurée au cours des 4 périodes d'incubation de 3 heures, en mg carbone/m³/12 heures, et d O_2 = ml oxygène/m³/12 heures.

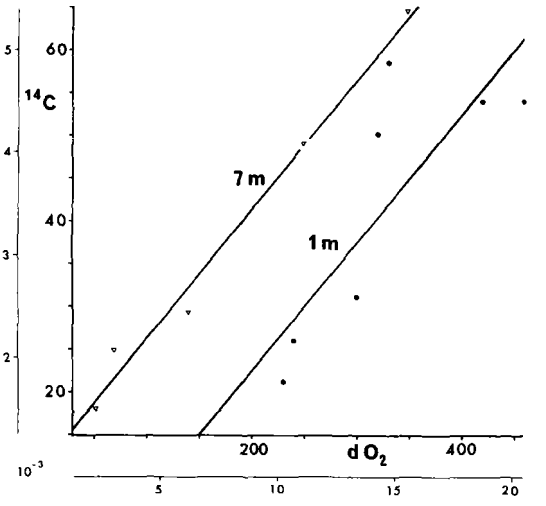

Fig. 25. Consommation de carbone et production d'oxygène. d O_2: accroissement diurne apparent du taux d'oxygène dissous in situ. ^{14}C: fixation nette de carbone pendant les journées solaires correspondantes.
Echelles intérieures: mg carbone et ml oxygène/m^3/12 heures. Echelles extérieures: molécules-grammes $\times 10^{-3}$

Les valeurs moyennes sont de 42,02 mg carbone et 331,40 ml oxygène, soit respectivement $3{,}50 \times 10^{-3}$ atomes-grammes et $14{,}79 \times 10^{-3}$ mol.-grammes; d'où le quotient photosynthétique apparent de 4,22.

— au niveau 7 m, où l'amplitude des variations en oxygène est généralement plus faible (fig. 24), les 5 paires de données conduisent à l'équation:

$$^{14}C = 0{,}150 \text{ d } O_2 + 11{,}25, \text{ avec } r = 0{,}99 \text{ (probabilité: 0,001)} .$$

La moyenne des mesures donne pour quotient photosynthétique: 2,49.

Ces résultats seront comparés plus loin (p. 62) à ceux des mesures hebdomadaires.

6. Rapport production/chlorophylle

La relation entre fixation de carbone et chlorophylle *a* présente deux aspects distincts:

Moyennes diurnes:

Entre les moyennes des concentrations diurnes en pigment et les moyennes de la production diurne existe une corrélation très hautement significative (fig. 26) d'équation:

$$^{14}C = 5{,}60\ C_a + 0{,}72, \text{ avec } r = 0{,}839 \text{ (probabilité: 0,001)} .$$

Unités: ^{14}C = production primaire diurne in situ (moyenne de 12 heures), en mg carbone/m^3/h. C_a = chlorophylle *a* (moyenne des 5 mesures diurnes) en mg/m^3.

On obtient par extrapolation la valeur de 6,32 mg carbone/m^3/h pour 1 mg de chlor. *a*; la moyenne des mesures donne par ailleurs le chiffre de 7,14. Ces résultats diffèrent peu de ceux obtenus au cours du cycle annuel (p. 38). Deux remarques:

— comme dans le cas du cycle annuel, le rapport production/chlorophylle apparaît indépendant de la composition taxinomique du plancton; celle-ci est en effet rappelée sur la figure 26: les initiales R et C indiquent la prédominance du microplancton (R pour *Rhizosolenia*, série VII, C pour *Chaetoceros*, série V) tandis que les points dépourvus de lettre reportent les cas de dominance plus ou moins complète du nannoplancton.

— une discrimination entre les niveaux 1 et 7 m est peu probable.

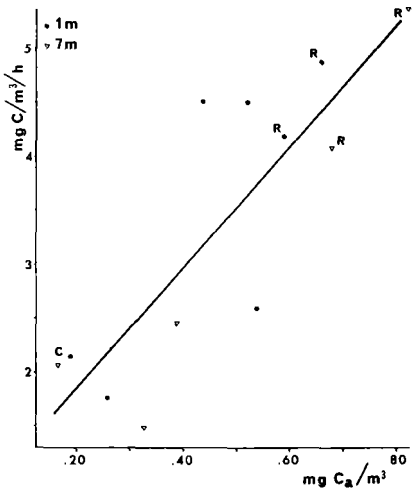

Fig. 26. Corrélation entre production et pigment. ^{14}C: production moyenne in situ pendant les 12 heures de jour (mg carbone/m³/h), C_a: moyenne des 5 mesures diurnes de la chlorophylle *a* (mg/m³). R: *Rhizosolenia alata* dominant. C: *Chaetoceros* dominant

Variations diurnes:

Cette corrélation disparaît totalement lorsque l'on compare d'une part les productions mesurées pendant chaque période d'incubation, d'autre part les teneurs en chlorophylle *a* au début de chaque période. Le rapport „production/pigment" varie en effet considérablement selon l'heure de la journée; dans ces fluctuations, le rôle des deux facteurs est inégal: l'amplitude des variations diurnes est bien plus forte dans le cas de la productivité que dans celui de la chlorophylle, si bien que le rapport des deux variables suit pratiquement le taux de fixation du carbone.

Bien que les mesures des concentrations en pigment soient probablement moins précises que celles de la production, on doit conclure que le rôle de l'énergie lumineuse affecte bien davantage l'intensité photosynthétique que les teneurs en chlorophylle.

7. Comparaison des stations L et A

Les variations nycthémérales reportées précédemment ont été observées à l'extrémité de la jetée du Centre océanographique (station J) ou au voisinage de cette station („Ambariaka"); il convient donc de comparer, comme dans le cas du cycle annuel, deux points opposés de la baie: les stations L et A (voir p. 10 et fig. 1). J'ai dans ce but effectué une série de mesures simultanées aux deux stations (série VIII), dont les résultats sont les suivants:

Température et salinité: Les deux diagrammes T–S (fig. 27, à gauche) diffèrent l'un de l'autre par l'amplitude des variations, celle-ci étant considérablement plus élevée en A (au fond de la baie) qu'en L (ouverture de la baie). La comparaison des prélèvements effectués aux mêmes heures (même fig., à droite) montre que les différences de densité entre les deux stations suivent un cycle nycthéméral, avec maximum au milieu de l'après-midi et minimum nocturne.

Composition taxinomique: Trois échantillons ayant été perdus, je n'ose tracer de courbes nycthémérales ... Cependant le microplancton, quoique „désertique" (de 50 à 600 cell./l) est, dans tous les échantillons examinés, plus abondant en L qu'en A; inversement, le nombre de cellules nannoplanctoniques (de 40000 à 110000 cell./l) est en moyenne deux fois plus élevé en A qu'en L.

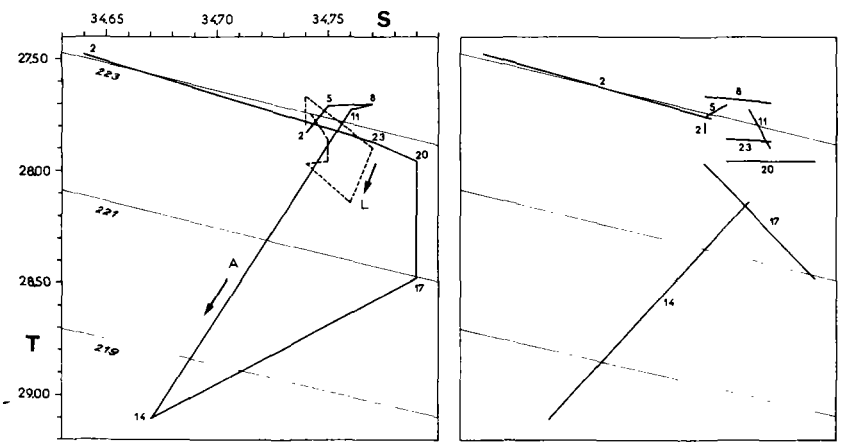

Fig. 27. Diagrammes T–S (2 juin 1964). Variations nycthémérales des températures et salinités aux deux stations L (ouverture de la baie) et A (au fond de la baie). A gauche: les deux séries de mesures. A droite: on a réuni par des segments les prélèvements simultanés aux deux stations. Les nombres indiquent les heures des prélèvements

Pigments chlorophylliens: Pour la chlorophylle *a*, le maximum nycthéméral survient dans les deux cas à 18 heures (fig. 28); les deux courbes diffèrent par la présence d'une dépression à 12 h en A. Les teneurs moyennes en chlorophylle *a* pour la période de 24 heures sont respectivement: 0,52 mg/m³ en A et 0,30 en L.

Production primaire: Les deux diagrammes de la fixation diurne de carbone évoluent parallèlement (fig. 28), donc manifestent une même réponse aux variations des conditions d'éclairement (rappelons que les incubations avaient lieu in situ au milieu de la baie pour les deux séries de prélèvements). Les productivités sont tout au long du jour plus élevées à la station A, les moyennes diurnes étant respectivement de 4,97 mg carbone/m³/h en A, et 2,58 en L.

L'écart diurne des pourcentages de saturation en oxygène dissous (fig. 28) indique également une plus forte activité photosynthétique à la station A.

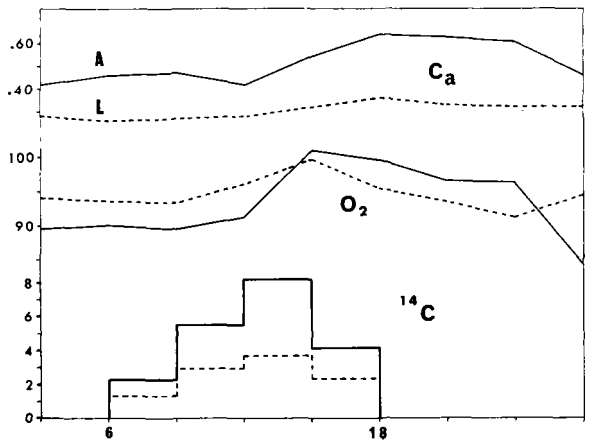

Fig. 28. Variations nycthémérales aux stations L et A. C_a: chlorophylle *a* (mg/m³). O_2: pourcentage de saturation en oxygène dissous. ^{14}C: production in situ (mg carbone/m³/h). Niveau des prélèvements dans les deux cas: 1 m

Ces divers résultats ne portent que sur une série de mesures nycthémérales: plusieurs séries identiques auraient été nécessaires pour tester d'éventuelles différences dans les rapports productivité/biomasse, ainsi que le rôle possible de la marée.

IV. Quelques remarques et conclusions

1. Caractéristiques du cycle annuel

Avant de conclure sur les aspects caractéristiques du cycle annuel dans la baie étudiée, notons que les points de comparaison sont très rares dans l'océan indien. Pratiquement, les seules observations disponibles sont celles de SUBRAHMANYAN (1958—1960) et SUBRAHMANYAN & SARMA (1960), mais leur intérêt est considérable puisqu'elles reposent sur six années consécutives et comportent une étude détaillée des facteurs physico-chimiques (toutefois ces deux auteurs n'ont pas effectué de mesures de la production primaire). Les divers travaux d'ANGOT et de GÉRARD, auxquels j'ai fait de fréquentes allusions, demeurent, du point de vue annuel, fragmentaires. Le schéma d'un cycle annuel du phytoplancton au large du Kénya donné par NEWELL (1959) repose en fait essentiellement sur des observations hydrologiques. Signalons enfin diverses données planctologiques ou hydrologiques aux confins de l'océan indien: DAKIN & COLEFAX (1935), WICKSTEAD (1961) et WOOD (1964, V).

A la différence des conditions reportées par SUBRAHMANYAN (loc. cit.), mais en accord avec de nombreuses observations dans le monde (réf. p. 39), la biomasse est ici essentiellement nannoplanctonique. Bien qu'évaluée approximativement, l'abondance du nannoplancton paraît considérablement plus constante tout au long de l'année que celle du microplancton, comme l'ont montré en d'autres régions RILEY, 1957 (mer des Sargasses, lat. 35° N), SMAYDA, 1957 et YENTSCH & RYTHER, 1959 (côte Est des U.S.A., lat. 41° 30′ N) et HASLE & SMAYDA, 1960 (Oslo, lat. 60° N). Par ailleurs le microplancton, souvent „subdésertique", subit d'importantes variations quantitatives que l'on peut appeler saisonnières puisqu'elles se répartissent principalement en deux groupes estival et hivernal; dans ces deux cas, les facteurs météorologiques (vents et pluies) semblent déterminants, sous la forme d'apport ou de renouvellement des éléments nutritifs (cf. MARSHALL, 1933; SUBRAHMANYAN, 1959b—c). Outre ces variations quantitatives, le microplancton présente une alternance saisonnière plus nette encore sur le plan qualitatif: cependant, sous ces deux aspects, l'évolution du microplancton n'a été suivie que pendant 16 mois: la généralisation nécessiterait une étude sur plusieurs années consécutives[1]).

L'alternance saisonnière est seulement grossière au niveau des pigments chlorophylliens, et moins claire encore pour ce qui est de la fixation de carbone in situ. Dans les deux cas le cycle annuel se définit ainsi: les valeurs annuelles minimales sont observées entre septembre et janvier, et les valeurs maximales surviennent dans le cours du reste de l'année; les variations sont considérablement plus accidentées pendant cette seconde période. Le déterminisme de cette alternance

[1]) Au sujet de la reproductibilité des cycles annuels successifs, l'expérience acquise par ALLEN sur les côtes de Californie fait conclure à cet auteur:" . . . our records show no two years alike (. . .). With nearly twenty years of daily observations behind me, I find it amusing when I see an account of the work of some student of nature who has learned the normal routine of life in a larger or smaller space on sea or land by an intensive study conducted through a few weeks or months or even years (. . .)". (ALLEN, 1940, p. 580).

n'est pas évident, puisque: 1) celle-ci ne peut être expliquée par les variations de la composition du microplancton (il faut peut-être penser alors à un défaut d'évaluation des variations du nannoplancton), 2) la période „hivernale" définie ci-dessus (septembre–janvier) débute en fait à la fin de la saison fraîche, et serait donc en retard de trois mois environ sur l'hiver hydrologique.

Dans ces conditions, la présente étude révèle deux défauts — et suggère deux améliorations:

— l'évaluation précise, quantitative et qualitative, du nannoplancton revêt un intérêt capital.

— dans un milieu tropical littoral tel que celui examiné ici, l'homogénéité relative des températures annuelles s'oppose au caractère brutal et irrégulier des deux facteurs climatiques essentiels: vents et pluies. Pour ces deux raisons, et aussi du fait de l'influence multi-périodique de la marée, les phénomènes biologiques doivent être suivis „de très près" dans le temps. Un rythme de mesures hebdomadaire — tel qu'ici employé — est très probablement insuffisant pour rendre compte des détails dans l'enchaînement et l'interaction des causes et des effets. D'où l'intérêt de mesures journalières, telles qu'effectuées par KRISHNAMURTHY (1962), ANGOT & GÉRARD (1967) pendant des périodes d'un mois, et qui devraient être répétées aux diverses saisons (ou mieux tout au long de l'année ...).

2. Amplitudes comparées des variations saisonnières et nycthémérales

Le tableau VII permet de comparer, pour les principaux facteurs étudiés, les amplitudes respectives des variations saisonnières et nycthémérales, telles que définies dans le cours de ce travail.

Cette récapitulation fait conclure à l'importance des variations nycthémérales, trop souvent négligée dans les recherches océanographiques.

Tableau VII. — Amplitudes comparées des variations saisonnières et nycthémérales pour les principaux facteurs étudiés. A noter que les deux séries ne sont pas équivalentes: un cycle annuel d'une part, moyennes pour sept cycles nycthéméraux d'autre part

Variations	saisonnières	nycthémérales
Température	26–31°	amplitude: 1 à 1,5°
Salinité	32–35,5‰	amplitude: 0 à 5‰
Oxygène (% saturation)	95–102% („accidentelles")	85–110% („systématiques")
Microplancton (cell./l)	ε–200000	du simple au double
Nannoplancton (cell./l)	50000–130000 (?)	45000–110000 (?)
Chlorophylle *a* (mg/m³)	0,20–0,95	du simple au double
D 430/665 mμ	2–6	3–7
Production nette (mg C/m³/h)	1–7	1–5
Production/chlor. *a* (mg C/h/mg C_a)	3–13	4–12

3. Assimilation de carbone et production d'oxygène

Rappelons les résultats des deux séries de mesures en parallèle, les unes hebdomadaires (cf. p. 36), les autres nycthémérales (p. 57), tout en précisant que les

deux séries ne sont pas équivalentes puisque les mesures ne sont pas en nombre égal et qu'elles ne couvrent pas les mêmes périodes de l'année (dans le premier cas: 27 mesures à la profondeur 1 m, entre décembre 1963 et juin 1964; dans le second cas: 7 mesures aux deux profondeurs 1 et 7 m, à différentes saisons).

— L'exposition en parallèle de deux bouteilles claires in situ au milieu de la matinée, l'une des bouteilles étant destinée à la mesure de l'assimilation de carbone, l'autre à la mesure du dégagement d'oxygène, conduit à une corrélation positive (p. 36 et fig. 15) selon l'équation:

$$^{14}C = 0{,}078\ O_2 + 2{,}35 \qquad (1)$$

Unités: mg carbone et ml oxygène/m³/h).

Les valeurs moyennes, exprimées en molécules-grammes, donnent un quotient photosynthétique apparent $Q = 2{,}76$.

— Une corrélation positive est également observée entre l'accroissement diurne apparent du taux d'oxygène in situ et l'assimilation diurne de carbone en bouteilles claires exposées in situ (p. 57 et fig. 25). L'équation diffère aux deux niveaux étudiés:

$$\text{A 1 m: } ^{14}C = 0{,}149\ d\ O_2 - 7{,}36 \quad \text{avec} \quad Q = 4{,}22 \qquad (2)$$

$$\text{A 7 m: } ^{14}C = 0{,}150\ d\ O_2 + 11{,}25 \quad \text{avec} \quad Q = 2{,}49 \qquad (3)$$

(Unités: mg carbone et ml oxygène /m³/12 h).

A propos de l'équation (1)

Cette équation remet en jeu le problème de la validité comparée des deux méthodes de l'oxygène et du ^{14}C. Il faut ici faire état de la correction de 31% proposée par STEEMANN NIELSEN (1965) pour les résultats fournis par la seconde méthode; le quotient apparent, calculé d'après les expériences parallèles en bouteilles claires, passe alors de 2,76 à 2,11. Reste encore à expliquer cette différence du simple au double entre les deux évaluations.

A ce sujet, rappelons que le quotient photosynthétique, dans les conditions naturelles de développement du phytoplancton marin, n'est pas égal mais sensiblement supérieur à l'unité: RYTHER (1956b) et MCALLISTER et al. (1964) proposent la valeur moyenne de 1,25. Au reste, le rapport ici observé vérifie l'opinion courante: du fait qu'une fraction plus ou moins importante du carbone dégagé par la respiration est „recyclé" par la photosynthèse, préférentiellement au carbone extérieur, la méthode du ^{14}C fournit une évaluation intermédiaire entre la production nette et la production brute, souvent plus proche de la première (RYTHER, 1955, 1956b—c; STRICKLAND, 1960. Voir aussi MC ALLISTER, 1961 et STEEMANN NIELSEN, 1964). Il faut par ailleurs envisager une excrétion de ^{14}C à l'état dissous (réf. in STRICKLAND, 1965 p. 524), ainsi que, d'autre part, la possibilité d'assimilation de carbone non marqué (MCALLISTER et al. 1961).

Comparaison des équations (2) et (1)

L'interprétation de l'équation (2) est plus complexe. L'assimilation du carbone a été mesurée de la même manière qu'en (1), mais l'accroissement d'oxygène a été obtenu in situ: il résulte donc non seulement du métabolisme du plancton, mais encore de celui des autres communautés animales et végétales, et dépend en outre, dans un rapport qui n'a pu être évalué, des échanges physiques latéraux et verticaux.

Le quotient photosynthétique apparent correspondant à l'équation (2) est de 4,22 contre 2,76 dans le cas précédent. Les quantités de carbone pouvant

être supposées équivalentes, il reste que l'accroissement d'oxygène est 1,5 fois plus élevé in situ que dans les bouteilles claires. On peut envisager trois principales explications de ce phénomène: 1) défaut d'évaluation des conditions physiques de la distribution du gaz in situ, 2) réduction de l'activité photosynthétique, ou augmentation de l'intensité respiratoire, dans les communautés (essentiellement: phytoplancton et bactéries) enfermées dans les bouteilles, 3) rôle des communautés non planctoniques, principalement de la flore benthique (mais ce facteur semble jouer en sens inverse: voir plus bas).

Les points de comparaison sont rares dans la bibliographie. GRAN (1927) note que les productions mesurées dans les bouteilles sont 4 fois supérieures aux mesures in situ, mais les techniques utilisées par cet auteur sont contestables et, du moins, diffèrent des miennes sur de nombreux points. Plus récemment, ODUM & HOSKIN (1958) montrent que la méthode in situ („diurnal curve method"[1]) donne en général des valeurs plus élevées que la méthode des bouteilles, particulièrement dans le cas de zones littorales à importante végétation benthique; voir dans le même sens OHLE, 1958 (eaux douces).

Comparaison des équations (2) et (3)

Le quotient moyen est nettement plus faible à 7 m (2,49) qu' à 1 m (4,22). Les méthodes étant les mêmes dans les deux cas, ce fait peut être dû principalement:

— à des différences entre les conditions physiques de la distribution de l'oxygène aux deux niveaux,

— à l'utilisation d'oxygène par le zooplancton (plus abondant en profondeur pendant le jour), ou par les communautés benthiques.

4. Rapport production/chlorophylle

Les évaluations du rapport „production/chlorophylle *a*" sont très nombreuses dans la bibliographie, et la question est d'une telle ampleur que j'hésite à l'aborder ici. . .

ODUM et al. (1958) donnent une longue énumération de travaux relatifs aux milieux aquatiques et terrestres les plus divers (il s'agit là du rapport „mg oxygène/h/mg chlorophylle *a*"). Pour le phytoplancton marin dans les conditions optimales d'éclairement, RYTHER & YENTSCH (1957) et STRICKLAND (1960) acceptent les valeurs moyennes respectives de 3,7 et 4 mg carbone/h/mg chlor. *a*, basées presque exclusivement sur l'emploi de la méthode de l'oxygène. On trouvera dans CURL & SMALL (1965) quelques références récentes relatives à la méthode du ^{14}C, auxquelles il faut ajouter plusieurs travaux cités ci-dessous.

Entre ces diverses données, toute comparaison est délicate, car elle implique que les résultats ont été obtenus dans des conditions expérimentales identiques, ce qui est en fait exceptionnel: éclairement in situ ou artificiel, populations naturelles ou cultures pures, milieu enrichi ou non, etc.; plus particulièrement, on ne peut a priori accepter comme équivalents les résultats des deux méthodes de l'oxygène et du carbone 14, puisque les phénomènes étudiés ne sont pas exactement les mêmes dans les deux cas. Enfin, lorsque deux travaux se réfèrent à la même méthode, on doit encore s'assurer que les détails de l'expérimentation sont semblables: ces „détails" sont de particulière importance dans le cas de la méthode du ^{14}C (cf. STEEMANN NIELSEN, 1965).

Dans ces conditions, on ne peut s'étonner que, dans l'état actuel des connaissances, „there is no constant value for carbon assimilation per unit chlorophyll *a* at optimal light intensity for all the oceans during all seasons" (CURL & SMALL, ibid., p. 71) . . . Le contraire serait plus étonnant.

[1]) Il s'agit en fait (cf. p. 3) d'une „ nycthemeral curve method ".

Rappelons que divers facteurs écologiques, outre l'énergie lumineuse, sont susceptibles d'affecter ce rapport: teneur en sels nutritifs (McALLISTER et al., 1964; CURL & SMALL, ibid.), latitude (STEEMANN NIELSEN & HANSEN, 1959), caractère „pélagique" ou „littoral" (ICHIMURA & SAIJO, 1959), température (WILLIAMS & MURDOCH, 1966).

J'ai exposé précédemment les variations hebdomadaires (p. 37) et diurnes (p. 57) du rapport en question. Quelques conclusions peuvent en être tirées ici:

Les mesures hebdomadaires effectuées à heure fixe (p. 37 et fig. 17) ainsi que les moyennes diurnes obtenues lors des séries de mesures nycthémérales (p. 57 et fig. 26) ont révélé une corrélation positive entre production primaire et chlorophylle *a*. Les rapports à l'unité sont très voisins dans les deux cas, et les droites de régression sont du même type que celles données par SHIMADA (1958), ANDERSON (1964), ANDERSON & BANSE (1965) et ANGOT & GÉRARD (1967).

De plus, le rapport $^{14}C/C_a$ ne présente pas ici de variations saisonnières, et semble indépendant de la composition taxinomique du phytoplancton: ce point confirme les expériences en culture de RYTHER (1956b), mais contredit les résultats de SAIJO & TAKESUE (1965), puisque ces deux auteurs, procédant à des filtrations différentielles, ont montré que le rapport étudié est inversement proportionnel à la taille des organismes.

Les mesures hebdomadaires semblent indiquer que le rapport $^{14}C/C_a$ est plus étroitement soumis aux variations de la productivité qu'à celles du pigment; il en est probablement de même dans le cas du cycle annuel décrit par CURL & SMALL (ibid.). Ce phénomène est beaucoup plus net pour les variations diurnes: le rapport $^{14}C/C_a$ suit pratiquement, aux différentes heures du jour, les variations de la production primaire; une semblable conclusion est à tirer du cycle nycthéméral observé par McALLISTER (1963); par ailleurs, comme le montrent HASTINGS et al. (1961), le cycle de la capacité photosynthétique chez *Gonyaulax polyedra* en culture artificielle n'est pas accompagné de variations significatives des teneurs en pigments. Voir aussi le rythme nycthéméral du rapport $^{14}C/C_a$ récemment décrit par SOURNIA (1967b).

Dans le même sens, citons deux travaux basés non plus sur la méthode du radiocarbone, mais sur celle de l'oxygène: les variations saisonnières du rapport „photosynthèse brute/chlorophylle *a*" étudiées par WILLIAMS & MURDOCH (1966) sont parallèles à celles du premier terme et inverses de celles du second, et la corrélation entre productivité et pigment est négative. D'autre part, les variations diurnes décrites par OCCHIPINTI et al. (1961) semblent elles aussi parallèles aux fluctuations de la productivité.

Finalement, il est probable que, dans de nombreux cas, les variations du rapport „production/chlorophylle" reportées dans la bibliographie reflètent simplement celles de la production; en d'autres termes, que les variations de l'activité photosynthétique sont, dans une large mesure, indépendantes de celles des teneurs en pigment.

5. *Variations locales; rôle de la marée*

Les deux stations opposées dans la baie, A (au fond de la baie, à proximité de la mangrove) et L (à l'ouverture de la baie, sur fond de coraux) peuvent être respectivement qualifiées, l'une par rapport à l'autre, de „littorale" et d'„océanique". Les résultats des quelques mesures nycthémérales aux deux stations (p. 59) confirment ceux des mesures hebdomadaires (p. 41).

La station „littorale" est la plus productive, la plus riche en nannoplancton, la plus pauvre en microplancton, et possède, d'après les moyennes annuelles du tableau V, le rapport „production/pigment" le plus élevé. En cette station, l'amplitude des diverses variations hydrologiques et planctologiques, tant hebdomadaires que nycthémérales, est plus forte qu'à la station „océanique".

Une discrimination identique peut être établie entre les eaux de marée basse et celles de marée haute, les premières étant plus „littorales", les secondes plus „océaniques". Le rôle de la marée est évident à la station A et incertain à la station L; par ailleurs, il se manifeste à la station J (en quelque sorte intermédiaire entre les deux autres) par le fait que les pourcentages de saturation en oxygène dissous sont plus élevés à basse mer.

Mentionnons ici quelques travaux relatifs à l'influence de la marée: dans une zone de mangrove, TEIXEIRA & KUTNER (1963) observent que le nombre de cellules (principalement nannoplanctoniques) est inversement fonction de la salinité et de la hauteur de la marée; toutefois, une erreur systématique liée au cycle nycthéméral peut être invoquée, puisque ces deux auteurs ont réparti ainsi leurs prélèvements: 5 à basse mer . . . vers 8 heures, et 5 à pleine mer . . . vers 14 h. Par ailleurs, la production primaire a été reconnue plus élevée à marée basse qu'à marée haute par VATOVA, 1961 (méthode du carbone 14) et par WILLIAMS & MURDOCH, 1962 (méthode de l'oxygène).

V. Résumé

1. L'écart saisonnier des températures étant peu important à la latitude envisagée (lat. 13° sud), les facteurs écologiques dominants du cycle annuel sont les vents et les pluies, qui divisent l'année en deux saisons: été austral, pluvieux (mousson N.E.) et hiver austral, sec (mousson S.O.); du point de vue hydrologique on distingue deux saisons, l'une estivale (décembre à mai) à faibles salinités, l'autre hivernale (juin à novembre) à salinités plus élevées.

2. Les variations saisonnières du taux d'oxygène dissous sont de nature essentiellement physique, et non biologique.

3. Le nannoplancton constitue tout au long de l'année l'essentiel de la biomasse; malheureusement, ce groupe n'a pu être ici étudié que de façon très sommaire.

4. Le microplancton par contre, souvent „sub-désertique", montre d'importantes variations saisonnières, tant qualitatives que quantitatives. Son inventaire compte 236 taxons, dont 163 Diatomées, 72 Péridiniens, et la Cyanophycée *Oscillatoria* (= *Trichodesmium*); on peut en extraire une liste de 18 Diatomées qui constituent, avec *Oscillatoria*, les espèces „dominantes", c'est à dire responsables des poussées quantitatives.

5. Les teneurs en pigments et les valeurs de la production sont élevées et subissent des variations hebdomadaires très accidentées; les variations saisonnières de ces deux facteurs sont confuses.

6. Les mesures parallèles de l'assimilation de carbone et de la production d'oxygène in situ en bouteilles claires conduisent à une corrélation positive.

7. Le rapport production/biomasse, sous la forme „assimilation de carbone in situ/chlorophylle *a*" ne montre pas de variations saisonnières; ses variations hebdomadaires suivent davantage celles du premier terme que celles du second, et ses variations diurnes (c. à d. à différentes heures de la journée) suivent étroitement celles de la production primaire; enfin, ce rapport semble indépendant de la composition taxinomique du phytoplancton.

8. La compréhension synthétique des diverses relations entre production et biomasse nécessiterait une évaluation précise du nannoplancton, dont le rôle est essentiel.

9. Au fond de la baie (eaux „littorales") le microplancton est plus rare, le nannoplancton plus abondant, la production primaire et la concentration en pigments sont plus élevées qu'à l'ouverture de la baie (eaux relativement „océaniques").

10. Une discrimination identique à la précédente peut être établie en fonction de la hauteur de la marée: les eaux de basse-mer sont plus „littorales", les eaux de pleine-mer relativement plus „océaniques".

11. Une brève mise à jour de la question des variations nycthémérales est présentée.

12. Les diagrammes T–S obtenus aux deux profondeurs 1 et 7 m mettent en évidence une variation nycthémérale dans la stratification des eaux.

13. L'accroissement diurne du taux d'oxygène in situ donne lieu à une évaluation de la production nette pendant le jour. Les valeurs ainsi obtenues montrent une corrélation positive avec le taux de fixation diurne du carbone 14 dans les bouteilles claires. On en tire un quotient photosynthétique apparent qui est deux fois supérieur environ à celui obtenu en (6).

14. Quelques données sommaires sur les variations nycthémérales du phytoplancton sont exposées: pour la chlorophylle *a*, on observe en général un maximum diurne et un minimum nocturne; les valeurs diurnes varient selon les conditions lumineuses. Le nannoplancton se multiplie activement vers 9 heures dans les eaux superficielles. La production primaire est sous la dépendance étroite de l'éclairement, une „inhibition" en surface étant de règle dans le milieu de la journée.

15. La comparaison, pour les principaux facteurs étudiés, des amplitudes respectives des variations saisonnières et nycthémérales montre que, dans l'ensemble, les deux rythmes sont d'importance égale.

Summary

1. As seasonal variations of temperature are reduced at the latitude here considered (lat. 13° S.), the main ecological factors in the annual cycle are winds and rain, both dividing year into two seasons: a rainy austral summer (NE monsoon) and a dry austral winter (SW monsoon). From the hydrological point of view, two seasons are distinguished: winter (December to May) with low salinities, summer (June to November) with higher salinities.

2. Background for seasonal variations in oxygen content is physical rather than biological.

3. Nannoplankton makes up the main constituent of biomass throughout the year; unfortunately the author could only obtain a rough estimate of this group.

4. On the other hand, microplankton concentrations are often very low. Quantitative and qualitative variations of this group along the year are evident. 163 Diatoms and 72 Dinoflagellates have been recorded. 18 Diatoms and the Cyanophyta *Oscillatoria* (= *Trichodesmium*) are listed as "dominant" species, i.e. responsible for mass developments.

5. Pigment concentration and primary production are high; they both show sharp weekly fluctuations, but seasonal variations are rather obscure.

6. A positive correlation is observed between carbon assimilation and oxygen production from parallel in situ measurements in light bottles.

7. Production/biomass ratio, expressed as "in situ carbon assimilation/chlorophyll *a*" is not season dependent; its weekly variations rather follow production than pigment values; its diurnal variations (i.e.: at various times during daylight) are strictly submitted to production variations. This ratio seems independent of species composition.

8. A comprehensive study of the various production/biomass relations would require an exact estimate of nannoplankton, the significance of which is essential.

9. At the inshore end of the bay ("littoral" waters), microplankton is less abundant, nannoplankton is more abundant, and production and pigments values are higher than at the mouth of the bay (more "oceanic" waters).

10. A similar distinction can be based upon tidal rhythm, low tide waters being more "littoral", and high tide waters relatively more "oceanic".

11. A short review of nycthemeral (diel) studies is presented.

12. T–S diagrams from 1 and 7 m depths indicate a nycthemeral cycle in water stratification.

13. Diurnal increase of in situ oxygen content is used to an estimation of net primary production during daylight. A positive correlation is observed between these values and the assimilation rates of 14-carbon in light bottles. Thus an apparent photosynthetic quotient is obtained which is twofold higher than the number measured in (6).

14. A few data on nycthemeral variations of phytoplankton are given: Chlorophyll *a* shows generally a diurnal maximum and a nocturnal minimum, and diurnal variations are dependent upon light intensity. Multiplication of nannoplankton cells occurs in surface waters at about 0900. Primary production is strictly controlled by light intensity, surface "inhibition" being frequent in the middle of the day.

15. Amplitudes of seasonal and nycthemeral variations are compared under their various aspects: it appears that both rhythms have a similar importance.

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Quelques nouvelles données sur le phytoplancton marin et la production primaire à Tuléar (Madagascar)

par

A. SOURNIA[1]

(avec 1 fig.)

La présente note fait suite et apporte quelques compléments à deux travaux antérieurs dans les mêmes eaux:

– D'une part, celui de TRAVERS & TRAVERS (1965): étude qualitative et quantitative du phytoplancton sous l'aspect taxinomique, en août et septembre 1962.

– D'autre part, celui de MAESTRINI & PIZARRO (1966): hydrologie, pénétration de la lumière, pigments photosynthétiques et mesure de la production primaire par le ^{14}C, en juillet et août 1962.

Mes propres données ont été recueillies entre le 25 août et le 5 septembre 1964 aux stations définies par les auteurs précédents: de part et d'autre du Grand Récif et dans la baie de Saint-Augustin. L'aspect taxinomique mis à part (voir réf. plus bas), le nombre trop restreint de mes prélèvements ne me permet que quelques remarques générales, auxquelles j'ajouterai cependant le détail d'une étude nycthémérale.

Les moyennes des températures et salinités de surface aux diverses stations sont de 22°C et 35,30 ‰, l'une et l'autre très peu différentes des valeurs correspondantes indiquées par MAESTRINI & PIZARRO. D'autre part, la température moyenne des observations de TRAVERS & TRAVERS – que je calcule d'après les données de ces

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auteurs – est de 24°C: il s'ensuit que mes récoltes seraient légèrement plus „hivernales" que celles de ces deux auteurs[1].

Inventaire qualitatif des diatomées et des dinoflagellés

Travers & Travers, qui ont effectué des prélèvements d'eau de mer à diverses profondeurs et des traits de filet horizontaux et verticaux, donnent une liste de 113 Diatomées, 130 Dinoflagellés, 69 Tintinnides, et mentionnent plusieurs Coccolithophorides et Silicoflagellés, ainsi que la Xanthophycée *Halosphaera*. J'ai pour ma part prélevé de l'eau à différents niveaux et procédé seulement à des traits de filet horizontaux, et me suis limité à l'identification des Diatomées et des Dinoflagellés.

Il semble dès lors intéressant de comparer sur ces deux points les deux inventaires, obtenus à deux années d'intervalle mais sensiblement à la même saison, par des auteurs différents et dans une région peu connue: de tels relevés sont en effet rares sur les côtes de l'Océan indien, les plus notoires étant ceux de Subrahmanyan (1958) et Silva (1956, 1960); rappelons également l'existence, pour l'ensemble de l'Océan indien, des deux „check-lists" de Wood (1963 *a*—*b*).

Il sera tenu compte ici de diverses innovations taxinomiques que j'ai récemment proposées pour les Diatomées (s. presse, *a*), les *Ceratium* (1966 et s. presse, *b*) et divers Dinoflagellés (1967): je me permets donc de renvoyer à ces travaux pour toute précision nomenclaturale ou bibliographique.

Le nouvel inventaire (voir tableau) compte 152 taxons de Diatomées et 156 de Péridiniens, le genre *Ceratium* représentant à lui seul près de la moitié (70) du second groupe. Au total donc 308 taxons, dont 162 sont communs aux deux séries de récoltes, 83 sont seulement reportés par Travers & Travers, et 63 seulement par moi-même.

Du point de vue des innovations, une seule espèce nouvelle pour la science, appartenant au genre *Licmosphenia*, a été décrite à Tuléar (Sournia, s. presse, *a*), mais par ailleurs 20 taxons sont nouveaux pour l'Océan indien.

Sous l'aspect biogéographique, la présente liste peut être décomposée en plusieurs catégories, bien que les connaissances actuelles sur la distribution mondiale du phytoplancton réservent une assez large incertitude, tant sur l'extension de chaque espèce que sur le bien-fondé des subdivisions. . . Nos 308 taxons se répartissent approximative-

[1] Au sujet des méthodes utilisées, je ne citerai ici que leur principe, et reporte pour les détails à une étude plus étendue (Sournia, s. presse, *c*).

ment comme suit:
- répartition mondiale cosmopolite (c) : 62
- zones tropicales et tempérées des trois océans (tt) : 118
- zone intertropicale (it) : 81
- Indo-pacifique (ip) ou Océan indien (oi) : 10
- mers froides (f) : 6
- répartition inconnue (taxons indéterminés ou mal connus) : 31.

La somme des trois premiers termes fait apparaître que 261 taxons sur 308 sont susceptibles d'être rencontrés sous les latitudes tropicales des trois océans. Ceci se justifie par la situation géographique de Tuléar (lat. 23° 20′ Sud) et, d'autre part, donne une nouvelle démonstration – si besoin était – du cosmopolitisme du phytoplancton marin.

Cependant, 10 taxons sont ici provisoirement donnés comme „indo-pacifiques" ou confinés à l'Océan indien, ce qui pose à nouveau le problème de la discrimination entre flores planctoniques atlantique et indo-pacifique. A ce sujet, il semble bien que le nombre d'espèces réputées endémiques de l'une ou l'autre province diminue de jour en jour; j'ai ainsi récemment indiqué (s. presse, *b*) que le genre *Ceratium* ne compte plus qu'une seule espèce „atlantique", d'ailleurs mal connue, et 7 espèces „indo-pacifiques" dont 4 également incertaines. L'avenir, sous la forme de nouvelles données ou d'une mise à jour des connaissances mondiales, confirmera t-il ou non l'existence de cette frontière géographique pour le phytoplancton?

Notons enfin la présence à Tuléar de six formes supposées psychrophiles et qui n'y ont été récoltées, à l'exception de *Pleurosigma directum*, que par TRAVERS & TRAVERS. Ce fait, à rapprocher de l'existence simultanée de plusieurs espèces de Copépodes relativement psychrophiles dans le zooplancton (GAUDY, s. presse, et comm. pers.) permet de croire à un apport d'eaux australes – ou profondes – à l'époque considérée.

LÉGENDE DU TABLEAU

Récoltes (première colonne):

T: TRAVERS & TRAVERS, 1965 (*: sous un synonyme)
S: le présent auteur (incl. SOURNIA, s. presse, *a—c*)
! : taxon nouveau pour l'Océan indien.

Répartition mondiale (seconde colonne):

c : cosmopolite	ip: Indo-pacifique
tt: tempérée – tropicale	oi: Océan indien
it: intertropicale	f : mers froides

***: *nov. sp.* ou *nov. comb., in* SOURNIA, s. presse, a, b.

S		*Achnanthes* sp.
T	?	*Asterionella Bleakeleyi* SMITH
T	c	*Asterionella japonica* CLEVE *in* CLEVE & MÖLLER
T S	tt	*Asterionella notata* GRUNOW *in* VAN HEURCK
T	tt	*Asterolampra Grevillei* (WALLICH) GREVILLE
T S	tt	*Asterolampra marylandica* EHR.
T	tt	*Asteromphalus arachne* (BREB.) RALFS *in* PRITCHARD
T S	tt	*Asteromphalus flabellatus* (BREB.) GREVILLE
T	c	*Asteromphalus heptactis* (BREB.) RALFS *in* PRITCHARD
T	f?	*Asteromphalus Hookeri* EHR.
T* S	c	*Bacillaria paxillifer* (MÜLLER) HENDEY
T S	it	*Bacteriastrum comosum* PAVILL.
T S	tt	*Bacteriastrum delicatulum* CLEVE
T S	tt	*Bacteriastrum elegans* PAVILL.
T	tt	*Bacteriastrum elongatum* CLEVE
T S	tt ?	*Bacteriastrum hyalinum* LAUDER
T S	ip ?	*Bacteriastrum varians* LAUDER
S	it	*Biddulphia membranacea* CLEVE
T S	tt	*Biddulphia mobiliensis* (BAILEY) GRUNOW *in* VAN HEURCK
! S	tt ?	*Biddulphia pelagica* SCHRÖDER***
T S	tt	*Biddulphia pulchella* GRAY
S	c	*Biddulphia rhombus* (EHR.) SMITH
! T	tt ?	*Biddulphia schroederiana* (SCHRÖDER) SCHUSSNIG
T S	tt	*Biddulphia sinensis* GREVILLE
T* S	it	*Biddulphia tridens* (EHR.) EHRENBERG
S	c	*Campylodiscus clypeus* (EHR.) EHRENBERG
T	tt ?	*Campylodiscus decorus* BREB.
T* S	c	*Cerataulina pelagica* (CLEVE) HENDEY
T S	c	*Chaetoceros affine* LAUDER
T	c ?	*Chaetoceros anastomosans* GRUNOW *in* VAN HEURCK
T	c ?	*Chaetoceros atlanticum* CL. var. *atlanticum*
T	?	*Chaetoceros atlanticum* f. *audax* GRAN
T S	tt	*Chaetoceros atlanticum* var. *neapolitanum* (SCHR.) HUST.
S	it ?	*Chaetoceros atlanticum* var. *skeleton* (SCHÜTT) HUST.
T S	tt	*Chaetoceros coarctatum* LAUDER
T S	c	*Chaetoceros compressum* LAUDER

T	f	*Chaetoceros convolutum* CASTRACANE
T S	c	*Chaetoceros curvisetum* CLEVE
S ?	c	*Chaetoceros danicum* CLEVE
T S	c	*Chaetoceros decipiens* CLEVE
T	f	*Chaetoceros dichaeta* EHR.
T S	tt	*Chaetoceros diversum* CLEVE
S	tt	*Chaetoceros laciniosum* SCHÜTT
T S	tt	*Chaetoceros lorenzianum* GRUNOW
T S	tt	*Chaetoceros messanense* CASTRACANE
S	c ?	*Chaetoceros pelagicum* CLEVE
T	f ?	*Chaetoceros pendulum* KARSTEN
T S	c	*Chaetoceros peruvianum* BRIGHTW.
S	tt ?	*Chaetoceros pseudocurvisetum* MANGIN
T	tt	*Chaetoceros tetrastichon* CLEVE
S	c	*Chaetoceros tortissimum* GRAN
! T* S	it ?	*Chrysanthemodiscus floriatus* MANN *emend.* TAKANO
T S	tt	*Climacodium frauenfeldianum* GRUNOW
T S	tt	*Climacosphenia moniligera* EHR.
T* S	c	*Corethron criophilum* CASTRACANE
T	?	*Coscinodiscus denarius* SCHMIDT
T S	c	*Coscinodiscus excentricus* EHR. var. *excentricus*
T	c ?	*Coscinodiscus excentricus* var. *fasciculatus* HUSTEDT
S	?	*Coscinodiscus incertus* KARSTEN***
S	oi ?	*Coscinodiscus Janischii* var. *arafurensis* GRUNOW
T S	c	*Coscinodiscus lineatus* EHR.
T	c	*Coscinodiscus nodulifer* SCHMIDT
S	?	*Coscinodiscus Normanii* GREGORY *in* GREV.
T S	c	*Coscinodiscus oculus-iridis* EHR. var. *oculus- iridis*
T	?	*Coscinodiscus perforatus* var. *Pavillardii* (FORTI) HUSTEDT
T S	c	*Coscinodiscus radiatus* EHR.
S	?	*Coscinodiscus Thorii* PAVILLARD
T S	tt	*Dactyliosolen mediterraneus* PERAGALLO
T S	it	*Ditylum sol* (V. HEURCK)DE-TONI
S	it ?	*Eucampia cornuta* (CLEVE) GRUNOW *in* VAN HEURCK
S	oi ?	*Fragilaria Aurivillii* CLEVE
T		*Fragilaria* sp.
S		*Fragilaria* sp.
T S	it	*Gossleriella tropica* SCHÜTT
S	c	*Grammatophora marina* (LYNGBYE) KÜTZING
T		*Grammatophora* cf. *oceanica* EHR.

T S	c	*Guinardia flaccida* (CASTR.) PERAGALLO
T	tt	*Gyrosigma balticum* (EHR.) RABENH.
T S	tt	*Hemiaulus Hauckii* GRUNOW *in* VAN HEURCK
S	oi	*Hemiaulus indicus* KARSTEN
T S	it	*Hemiaulus membranaceus* CLEVE
T S	it	*Hemiaulus sinensis* GREVILLE
T	c	*Hemidiscus cuneiformis* WALLICH
T	c ?	*Isthmia enervis* EHRENBERG
S	it ?	*Isthmia minima* HARVEY & BAILEY
S	c ?	*Lauderia annulata* CLEVE
T S	c	*Leptocylindrus danicus* CLEVE
S	oi ?	*Licmophora Aurivillii* CLEVE
T	?	*Licmophora Ehrenbergii* var. *ovata* (SMITH) PERAGALLO
S	c	*Licmophora flabellata* (GREVILLE) AGARDH
T* S	c	*Licmophora Lyngbyei* (KÜTZ.) GRUNOW *in* VAN HEURCK
T S	tt ?	*Licmophora remulus* GRUNOW
T		„*Licmophora* sp. (*Jamaji*)"
T		*Licmophora* sp.
S		*Licmosphenia* (nov. sp.)***
T S	tt	*Lithodesmium undulatum* EHRENBERG
T S	c	*Navicula lyra* EHRENBERG
! T S	?	*Navicula Wawrikae* HUSTEDT
T		*Navicula* sp.
T S	c	*Nitzschia closterium* (EHR.) SMITH
T	c ?	*Nitzschia delicatissima* CLEVE
T S	c ?	*Nitzschia longissima* (BREBISSON *in* KÜTZ.) RALFS *in* PRITCH.
T S	c	*Nitzschia seriata* CLEVE
T S	it	*Planktoniella sol* (WALLICH) SCHÜTT
S	f ?	*Pleurosigma directum* GRUNOW
S	c	*Pleurosigma Normanii* RALFS *in* PRITCHARD
T		*Pleurosigma* sp.
T	tt	*Podocystis spathulata* (SHADBOLT) VAN HEURCK
! T	c	*Podosira Montagnei* KÜTZING
T S	c	*Rhabdonema adriaticum* KÜTZING
S	it	*Rhabdonema punctatum* (HARVEY & BAILEY) STODDER *ex* BOYER
T* S	tt ?	*Rhizosolenia alata* BRIGHTWELL f. *alata*
! S	?	*Rhizosolenia alata* f. *curvirostris* GRAN
T S	tt ?	*Rhizosolenia alata* f. *gracillima* (CLEVE) GRAN
T S	tt ?	*Rhizosolenia alata* f. *indica* (PERAG.) GRAN
T S	tt	*Rhizosolenia Bergonii* PERAG.

T S	tt	*Rhizosolenia calcar-avis* SCHULTZE
T S	it	*Rhizosolenia Castracanei* PERAGALLO
T	tt	*Rhizosolenia cylindrus* CLEVE
T S	c	*Rhizosolenia hebetata* f. *semispina* (HENSEN) GRAN
T S	tt	*Rhizosolenia imbricata* BRIGHTW. var. *imbricata*
T S	c	*Rhizosolenia imbricata* var. *Shrubsolei* (CL.) SCHRÖDER
! T S	?	*Rhizosolenia pungens* CLEVE-EULER
T S	tt	*Rhizosolenia robusta* NORMAN *in* PRITCHARD
T S	c	*Rhizosolenia setigera* BRIGHTWELL
T S	c	*Rhizosolenia Stolterfothii* PERAGALLO
T S	?	*Rhizosolenia styliformis* var. *longispina* HUST. *in* SCHMIDT
T S	c	*Rhizosolenia styliformis* BRIGHTWELL var. *styliformis*
T* S	tt	*Rhizosolenia Temperei* var. *acuminata* PERAGALLO
S	c	*Roperia tessellata* (ROPER) GRUNOW *in* VAN HEURCK
T S	c ?	*Schroederella delicatula* (PERAG.) PAVILL. var. *delicatula*
S	c ?	*Schroederella Schroederi* (BERGON) PAVILLARD***
T S	c	*Skeletonema costatum* (GREV.) CLEVE
! T	tt ?	*Stictodiscus parallelus* var. *balearicus* GRUNOW *in* SCHMIDT
S	tt	*Streptotheca Tamesis* SHRUBSOLE
T S	c	*Striatella unipunctata* (LYNGBYE) AGARDH
S	tt	*Synedra hennedyana* GREGORY
T S	tt	*Synedra undulata* (BAILEY) GREGORY
T	tt	*Synedrosphenia gomphonema* (JANISCH & RABENHORST) HUSTEDT
T S	c	*Thalassionema nitzschioides* GRUNOW *ex* HUSTEDT
S	?	*Thalassiothrix delicatula* CUPP
T S	c	*Thalassiothrix Frauenfeldii* GRUNOW
T	tt	*Triceratium balearicum* CLEVE & GRUNOW f. *balearicum*
T	tt	*Triceratium balearicum* f. *quadratum* HUSTEDT
S	tt ?	*Triceratium Broeckii* LEUD.-FORT.
S	it	*Triceratium contortum* SHADBOLT
T S	tt	*Triceratium favus* EHRENBERG
T S	tt	*Triceratium formosum* BRIGHTWELL f. *formosum*
S	tt	*Triceratium formosum* f. *quadrangulare* (GREV.) HUST.

T S	tt	*Triceratium formosum* f. *quinquelobatum* (GREV.) HUST.
S	tt	*Triceratium reticulum* EHRENBERG
T S	tt	*Triceratium shadboltianum* GREVILLE

DINOFLAGELLÉS

T S	it	*Amphisolenia bidentata* SCHRÖDER
S	it ?	*Amphisolenia Lemmermannii* KOFOID
T	ip	*Amphisolenia palaeotheroides* KOFOID
S	it	*Amphisolenia Schauinslandii* LEMMERMANN
T S	it	*Amphisolenia thrinax* SCHÜTT
! T		*Cenchridium* sp.
T* S	tt	*Ceratium arietinum* CLEVE var. *arietinum*
T* S	it	*Ceratium arietinum* var. *gracilentum* (JÖRG.) SOURNIA
T	it	*Ceratium axiale* KOFOID
S	tt	*Ceratium azoricum* CLEVE
T S	it	*Ceratium belone* CLEVE
T	it	*Ceratium Bigelowii* KOFOID
T* S	it	*Ceratium breve* var. *parallelum* (SCHM.) JÖRG.
T*? S	tt	*Ceratium candelabrum* (EHR.) STEIN var. *candelabrum*
T*? S	tt	*Ceratium candelabrum* var. *depressum* (POUCHET) JÖRG.
T*? S	tt	*Ceratium candelabrum* (EHR.) STEIN „*candelabrum-depressum*"
T S	tt	*Ceratium carriense* GOURRET var. *carriense*
T S	it	*Ceratium carriense* var. *volans* (CLEVE) JÖRG.
T S	it	*Ceratium cephalotum* (LEMM.) JÖRG.
T	it ?	*Ceratium concilians* JÖRG.
T*? S	it	*Ceratium contortum* (GOURRET) CLEVE var. *contortum*
T* S	it	*Ceratium contortum* var. *Karstenii* (PAV.) SOURNIA
S	it	*Ceratium contortum* var. *longinum* (KARSTEN) SOURNIA
T*? S	it	*Ceratium contortum* (GOURRET) CL. „*contortum-Karstenii*"
S	tt	*Ceratium contortum* (GOURRET) CL. „*contortum-robustum*"
T* S	tt	*Ceratium contrarium* (GOURRET) PAVILLARD
T*	tt	*Ceratium declinatum* (KARSTEN) JÖRG. f. *declinatum*

T	tt	*Ceratium declinatum* var. *majus* JÖRGENSEN
S	tt	*Ceratium declinatum* f. *normale* JÖRGENSEN
T S	ip ?	*Ceratium deflexum* (KOFOID) JÖRGENSEN
T S	it	*Ceratium euarcuatum* JÖRGENSEN
T S	tt	*Ceratium extensum* (GOURRET) CL.
T	tt ?	*Ceratium falcatiforme* JÖRGENSEN
T*? S	tt	*Ceratium furca* var. *eugrammum* (EHR.) SCHILLER
T*? S	c	*Ceratium furca* (EHRENBERG) CLAP. & LACHM. var. *furca*
T*? S	c	*Ceratium furca* (EHR.) CLAP. & LACHM. „*furca-eugrammum*"
T*? S	c	*Ceratium fusus* (EHRENBERG) DUJ. var. *fusus*
T*? S	tt	*Ceratium fusus* var. *seta* (EHRENBERG) SOURNIA
T*? S	c	*Ceratium fusus* (EHRENBERG) DUJ. „*fusus-seta*"
T S	it	*Ceratium geniculatum* (LEMM.) CLEVE
T* S	it	*Ceratium gibberum* var. *dispar* (POUCHET) SOURNIA
T S	tt	*Ceratium gravidum* GOURRET
S	tt	*Ceratium hexacanthum* GOURRET
T	tt ?	*Ceratium hexacanthum* var. *contortum* LEMMERMANN
T*	it	*Ceratium horridum* var. *buceros* (ZACH.) SOURNIA
S	c	*Ceratium horridum* (CL.) GRAN var. *horridum*
T* S	tt	*Ceratium horridum* (CL.) GRAN „*horridum-buceros*"
T S	it	*Ceratium incisum* (KARSTEN) JÖRGENSEN
T	it	*Ceratium inflatum* (KOFOID) JÖRGENSEN
T S	it	*Ceratium Kofoidii* JÖRGENSEN
T S	it	*Ceratium limulus* (GOURRET *ex* POUCHET) GOURRET
T S	it	*Ceratium longirostrum* GOURRET
T	it	*Ceratium lunula* (SCHIMPER *ex* KARSTEN) JÖRGENSEN
T*? S	it	*Ceratium macroceros* var. *gallicum* (KOF.) SOURNIA
T	f ?	*Ceratium massiliense* f. *armatum* (KARSTEN) JÖRGENSEN
T* S	tt	*Ceratium massiliense* (GOURRET) JÖRG. var. *massiliense*
S	tt ?	*Ceratium massiliense* var. *protuberans* (KARST.) JÖRGENSEN
T S	tt	*Ceratium pentagonum* var. *tenerum* JÖRGENSEN

T* S	c	*Ceratium pentagonum* GOURRET *„robustum-tenerum"*
T* S	it	*Ceratium platycorne* DADAY var. *platycorne*
S	tt ?	*Ceratium porrectum* (KARST.) JÖRGENSEN
T	it	*Ceratium praelongum* (LEMMERMANN) KOFOID *ex* JÖRGENSEN
T S	tt	*Ceratium ranipes* CLEVE
T* S	tt	*Ceratium symetricum* var. *coarctatum* (PAV.) GRAH. & BRON.
T? S	tt	*Ceratium symetricum* var. *orthoceras* (JÖRG.) GRAH. & BRON.
T? S	tt	*Ceratium symetricum* PAVILLARD var. *symetricum*
T S	it	*Ceratium teres* KOFOID
T S	it	*Ceratium trichoceros* (EHR.) KOFOID
T S	tt	*Ceratium tripos* var. *atlanticum* OSTENFELD
! S	?	– f. *neglectum* (OSTENF.) PAULSEN
T S	it	*Ceratium tripos* var. *pulchellum* (SCHRÖDER) LOPEZ
T* S	tt	*Ceratium tripos* (MÜLLER) NITZSCH *„atlanticum-pulchellum"*
T S	it	*Ceratium vultur* f. *japonicum* (SCHRÖDER) WOOD
S	it	*Ceratium vultur* f. *recurvum* (JÖRG.) SCHILLER
T S	it	*Ceratium vultur* var. *sumatranum* (KARSTEN) STEEMANN NIELSEN
S	it	*Ceratium vultur* CLEVE f. *vultur*
T S	it	*Ceratocorys armata* (SCHÜTT) KOFOID
T S	it	*Ceratocorys Gourretii* PAULSEN
T S	tt	*Ceratocorys horrida* STEIN var. *horrida*
T S	it	*Ceratocorys horrida* var. *extensa* PAVILLARD
! T	?	*Ceratocorys magna* KOFOID
T S	tt	*Dinophysis caudata* SAV.-KENT
T S	tt	*Dinophysis hastata* STEIN
T S	ip	*Dinophysis miles* CLEVE
T	tt	*Dinophysis ovum* SCHÜTT
T S	tt	*Dinophysis tripos* GOURRET
S	tt	*Dinophysis uracantha* STEIN
T	oi ?	*Exuviaella lenticulata* MATZ.
T S	tt	*Goniodoma polyedricum* (POUCHET) JÖRGENSEN
S	tt	*Gonyaulax birostris* STEIN
S	?	*Gonyaulax* cf. *conjuncta* WOOD
T S	it	*Gonyaulax glyptorhynchus* MURRAY & WHITTING
S	tt	*Gonyaulax Kofoidii* PAVILL.
T S	it	*Gonyaulax pacifica* KOFOID
T	tt	*Gonyaulax polygramma* STEIN

	T	tt	*Gonyaulax Scrippsae* KOFOID
	T	it	*Histioneis dolon* MURRAY & WHITTING
!	T	it ?	*Histioneis pulchra* KOFOID
	S		*Histioneis* sp.
	T	it	*Ornithocercus heteroporus* KOFOID
	T S	tt	*Ornithocercus magnificus* STEIN *em.* SCHÜTT
	T S	tt ?	*Ornithocercus quadratus* f. *assimilis* (JÖRG.) KOF. & SKOGSBERG
	T	tt ?	*Ornithocercus quadratus* f. *intermedius* KOF. & SKOGSBERG
	T S	tt ?	*Ornithocercus quadratus* SCHÜTT f. *quadratus*
	T S	tt	*Ornithocercus splendidus* SCHÜTT
	T S	tt	*Ornithocercus Steinii* SCHÜTT *em.* KOFOID & SKOGSBERG
	T S	tt	*Ornithocercus Thumii* (SCHMIDT) KOFOID & SKOGSBERG
	T	it ?	*Oxytoxum compressum* KOFOID
	T	it	*Oxytoxum elegans* PAVILLARD
	T	it	*Oxytoxum Milneri* MURRAY & WHITTING
	T S	it	*Oxytoxum scolopax* STEIN
	T	it ?	*Parahistioneis crateriformis* (STEIN) KOF. & SKOGSBERG
!	T	ip ?	*Parahistioneis paraformis* KOFOID & SKOGSBERG
	T	tt	*Peridinium Brochii* KOFOID & SWEZY
	T S	c	*Peridinium conicum* (GRAN) OSTENF. & SCHMIDT
	T	tt	*Peridinium crassipes* KOFOID
	S	c	*Peridinium depressum* BAILEY
	T S	tt	*Peridinium diabolus* CLEVE
	T S	tt	*Peridinium divergens* EHR.
	T	it	*Peridinium elegans* CLEVE
	T	it	*Peridinium fatulipes* KOFOID
	T S	tt	*Peridinium globulus* var. *quarnerense* SCHRÖDER
	T	it	*Peridinium grande* KOFOID
!	T	?	*Peridinium minusculum* PAVILLARD
	T S	c	*Peridinium oceanicum* VANH.
	T	c ?	*Peridinium solidicorne* MANGIN
	T*	tt	*Peridinium sphaericum* OKAMURA
	T	it	*Peridinium Steinii* var. *mediterraneum* KOFOID
	T S	tt	*Peridinium Steinii* JÖRG. var. *Steinii*
!	T	it ?	*Phalacroma apicatum* KOFOID & SKOGSBERG
	T S	tt	*Phalacroma argus* STEIN
	S	tt	*Phalacroma circumsutum* KARST.
	T S	tt	*Phalacroma cuneus* SCHÜTT
	T S	tt	*Phalacroma doryphorum* STEIN

	T	tt	*Phalacroma ovum* SCHÜTT
	T	tt	*Phalacroma parvulum* (SCHÜTT) JÖRGENSEN
	T S	tt	*Phalacroma rapa* STEIN
	T S	tt	*Podolampas bipes* STEIN
	T S	tt	*Podolampas elegans* SCHÜTT
	S	tt	*Podolampas palmipes* STEIN
	T S	tt	*Podolampas spinifera* OKAMURA
	S	it ?	*Prorocentrum gracile* SCHÜTT
!	T	?	*Prorocentrum Hentschelii* SCHILLER
	T S	c	*Prorocentrum micans* EHR.
	T	it ?	*Pyrocystis elegans* PAVILL.
	T S	it ?	*Pyrocystis fusiformis* WYV.-THOMSON *ex* MURRAY
!	T S	it ?	*Pyrocystis Gerbaultii* PAVILL.
	T	it ?	*Pyrocystis hamulus* CLEVE
	T	it ?	*Pyrocystis lanceolata* SCHRÖDER
	S	c ?	*Pyrocystis lunula* (SCHÜTT) SCHÜTT
	T	it ?	*Pyrocystis obtusa* PAVILL.
	T S	it ?	*Pyrocystis robusta* KOFOID
	T S	tt	*Pyrophacus horlogium* STEIN
	T* S	it ?	*Spiraulax Kofoidii* GRAHAM
!	S	it	*Triposolenia depressa* KOFOID
!	S	it	*Triposolenia truncata* KOFOID

COMPOSITION TAXINOMIQUE QUANTITATIVE

Mes comptages par la méthode d'UTERMÖHL indiquent une extrême pauvreté numérique du microplancton: quelques centaines à quelques milliers de cellules par litre (principalement: *Asterionella, Nitzschia, Thalassiothrix, Chaetoceros*). L'essentiel de la biomasse est constitué par les Flagellés et divers Protistes nannoplanctoniques que je n'ai pas tenté de dénombrer, la méthode par sédimentation se prêtant particulièrement mal à cette étude.

Les résultats de TRAVERS & TRAVERS se trouvent donc ici confirmés: grande diversité mais rareté numérique du microplancton, importance quantitative du nannoplancton (une situation semblable est fréquente au cours d'un cycle annuel sur la côte nord-ouest de Madagascar: SOURNIA, s. presse, *c*); une différence cependant: les deux auteurs cités notent „un accroissement sensible de la densité des populations dans les derniers prélèvements", ce qui peut s'expliquer par le fait que, comme on l'a indiqué plus haut, l'époque des récoltes diffère légèrement dans les deux cas.

Par ailleurs, TRAVERS & TRAVERS soulèvent un problème général des plus inquiétants, celui de la fixation et de la conservation des

échantillons. Ces auteurs montrent notamment que le nombre de cellules décroît considérablement dans les bouteilles examinées cinq mois après le prélèvement. Y a t-il destruction, ou simplement adhésion du phytoplancton contre les parois des récipients? Cette question attend encore un traitement méthodologique serré, qui permettrait de définir l'action des divers fixateurs, du transport des échantillons, de la nature des bouteilles, et de la durée de conservation.

Pigments photosynthétiques

Sur ce point, les techniques suivies tant par Maestrini & Pizarro que par moi-même laissent un certain doute sur la valeur des résultats: en l'absence de spectrophotomètre à Tuléar, les échantillons ont dû être conservés plusieurs semaines (à l'obscurité et, dans la mesure du possible, à basse température) avant l'analyse, celle-ci réalisée à Marseille dans le premier cas, à Nossi-Bé (Madagascar) dans l'autre . . . Le principe de la méthode est toutefois le même (Richards & Thompson), à cette différence que j'ai préféré pour ma part l'emploi des formules de Parsons & Strickland (1963); par ailleurs, mes prélèvements sont beaucoup moins nombreux que ceux de Maestrini & Pizarro, et ne concernent que les eaux de surface.

La moyenne de mes 26 mesures s'établit ainsi: chlorophylles *a*, *b* et *c*, respectivement 0,35, 0,19 et 0,69 mg/m^3; caroténoides 1,12 MSPU/m^3. Le rapport moyen des densités optiques à 430 et 665 mμ est de 8,1.

Production primaire

Maestrini & Pizarro ont effectué de nombreuses expériences par a méthode du carbone 14, à diverses profondeurs et en deux stations, tandis que je ne dispose que de quatre mesures sub-superficielles (1 m) en une station unique (celle-ci dans la rade, à 300 m au nord de la jetée, sur un fond de 10 m). Soulignons de plus deux différences méthodologiques:

M. & P.: radioactivité introduite = 10 microcuries par flacon de 100 cc. Exposition en incubateur (env. 17.000 lux) pendant 6 à 8 heures.

S. : 4 μC par flacon de 265 cc. Exposition *in situ* pendant trois heures (de 08.00 à 11.00 h locales).

Dans les deux cas, les résultats sont passibles de la correction récente de Steemann Nielsen (1965).

En termes d'assimilation nette, mes résultats sont de 0,65, 0,81,

1,47 et 3,28 mg carbone/m³/h, soit une moyenne de 1,55. (L'absorption moyenne à l'obscurité était de 2,6 %). Cette production est nettement inférieure à celle mesurée par MAESTRINI & PIZARRO dans la rade au voisinage du récif.

Les mêmes mesures, rapportées aux concentrations correspondantes en chlorophylle *a*, donnent une moyenne de 4,15 mg carbone/m³/h/mg chlor. *a*.

CYCLE NYCTHÉMÉRAL

A la station définie dans le paragraphe précédent, j'ai effectué une série de 13 mesures, séparées par des intervalles de trois heures, et couvrant une durée de 36 heures (Ier sept. à l'aube 2 sept. au coucher); la profondeur des prélèvements était là aussi de 1 m. Les principaux résultats sont reportés sur la figure 1.

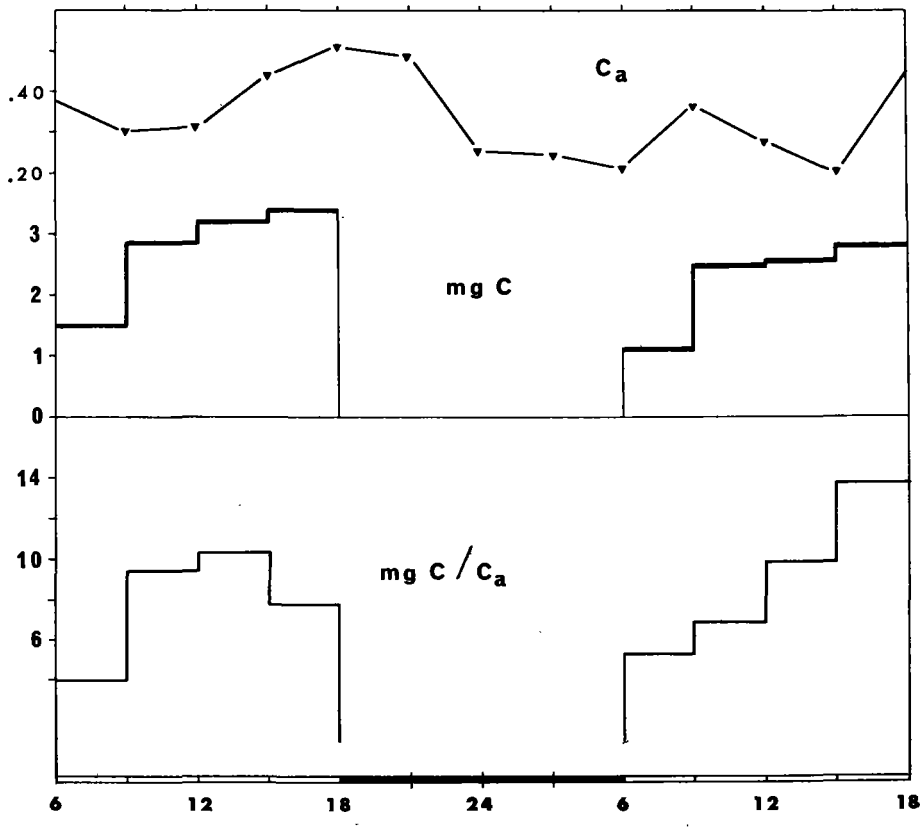

Figure 1 - Variations nycthémérales.
C_a: concentration en chlorophylle *a*, mg/m³.
mgC: production nette de carbone *in situ*, mg/m³/heure.
mg C/C_a: production nette par unité de pigment: mg/m³/h/mg chlor. *a*.

Les températures extrêmes ont été de 21,74 et 23,92° C: cette amplitude est voisine de celle généralement observée plus au nord à Madagascar (ANGOT & GÉRARD, 1966; SOURNIA, s. presse, *c*) D'autre part, les salinités ont varié entre 35,24 et 35,64 ‰, les deux valeurs les plus élevées étant concomitantes de la marée basse – ce qui ne peut suffire à établir une relation significative entre les deux phénomènes.

Les variations des concentrations en chlorophylle *a*, les plus remarquables parmi celles des pigments photosynthétiques, affectent un maximum en fin de journée et au début de la nuit; l'„accident" survenant le second jour à 09.00 h doit être rapproché du fait que, aux environs de cette heure, le ciel était très couvert (nébulosité 7/8) alors qu'il est demeuré clair pendant tout le reste des observations. Dans son ensemble, ce schéma nycthéméral diffère sensiblement de ceux obtenus à Nossi-Bé (réf. ci-dessus), mais l'on ne peut, en l'absence de mesures photométriques dans le cas présent, pousser plus loin la comparaison.

Le rapport „chlorophylle *a* / caroténoides", pas plus que celui des densités optiques 430/665 mμ, ne montre de variations significatives.

La production primaire, mesurée comme indiqué plus haut, croît assez régulièrement du matin au soir au cours des deux journées étudiées. Les deux moyennes diurnes de la photosynthèse nette sont de 2,73 et 2,24 mg carbone/m^3/h. On peut ici encore exprimer l'assimilation de carbone en fonction de la teneur en chlorophylle *a* mesurée au début de chaque exposition; le rapport „production/biomasse" ainsi calculé atteint son maximum au milieu ou à la fin de la journée, et les moyennes diurnes deviennent respectivement 7,85 et 8,39 mg carbone/m^3/h/mg chlor. *a*.

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SUMMARY

A list of 152 Diatoms and 158 Dinoflagellates is given and its biogeographic composition is discussed. Some quantitative data are presented: cells counts after sedimentation, spectrophotometric determination of plant pigments, and *in situ* primary production

measurement using 14-C method. A nycthemeral study, carried out during 30 hours, shows that chlorophyll *a* values are highest between 15.00 and 21.00, and that photosynthesis increases from morning to evening.

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La Cyanophycée Oscillatoria (=Trichodesmium) dans le plancton marin:

Taxinomie, et observations dans le Canal de Mozambique

Par A. SOURNIA[1])

Avec planches 1 (1)–2 (2)

SOMMAIRE – Le nom d'*Oscillatoria* doit être substitué à celui de *Trichodesmium*. Les espèces planctoniques marines responsables de phénomènes d'«eaux rouges» semblent au nombre de quatre : *O. Thiebautii* (GOM. ex GOM.) GEITLER, *O. Hildebrandtii* (GOM.) GEITLER, *O. erythraea* (EHR. ex GOM.) GEITLER, et *O. contorta* (WILLE in SCHÜTT) comb. nov. Dans le Canal de Mozambique, seules les deux premières espèces ont été récoltées, et s'y révèlent respectivement néritique et océanique.

ABSTRACT – The name *Oscillatoria* must prevail over *Trichodesmium*. There seem to be in marine plankton four species which can give rise to «red water» phenomena : *O. Thiebautii* (GOM. ex GOM.) GEITLER, *O. Hildebrandtii* (GOM.) GEITLER, *O. erythraea* (EHR. ex GOM.) GEITLER, and *O. contorta* (WILLE in SCHÜTT) comb. nov. In the Mozambique Channel, the first two species only have been collected, and were respectively neritic and oceanic.

Les cas de prolifération d'une Cyanophycée dans le plancton des mers chaudes sont connus de longue date (voir historique in EHRENBERG, 1830; MONTAGNE, 1844; DARESTE, 1855; WILLE, 1904) et posent d'intéressants problèmes, tant algologiques qu'océanographiques:

– Mode de vie : ces organismes sont-ils purement planctoniques, ou possèdent-ils un stade benthique comme on l'a affirmé assez gratuitement (WILLE, 1903), et comme l'aurait prouvé FELDMANN (1932)?

– Phénomènes d' «eaux rouges» : déterminisme et dynamique de ces poussées massives, et leur rôle dans l'économie des mers. Divers mécanismes ont été invoqués pour rendre compte des cas de toxicité, ceux-ci principalement observés sur les côtes de l'Inde (réf. in BRON-

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GERSMA-SANDERS, 1957 ; DESIKACHARY, 1959), exceptionnellement ailleurs (MOHLER, 1941 ; BAAS BECKING, 1951) ; outre la faune marine, les populations humaines peuvent elles aussi être affectées par ces pullulations, comme l'ont montré tout récemment SATO *et al.* (1966).

– Fixation d'azote moléculaire : cette possibilité, connue chez plusieurs Cyanophycées d'eau douce, a été démontrée chez «*Trichodesmium*» par DUGDALE *et al.* (1961, 1964) et GOERING *et al.* (1966), ainsi que chez deux autres genres marins isolés en cultures pures (STEWART, 1962). L'interrelation de ce processus avec la photosynthèse, étudiée sur une *Anabaena* dulçaquicole par FOGG & THAN-TUN (1960) reste à définir dans le cas présent (cf. MENZEL, 1962).

Cependant, l'aspect taxinomique se trouve singulièrement négligé dans les recherches récentes : il est le plus souvent question de « *Trichodesmium* sp. » et, lorsqu'un nom spécifique est avancé, il apparaît le plus souvent fondé sur des caractères macroscopiques douteux – alors que la détermination des espèces repose essentiellement, comme on le verra plus loin, sur l'examen microscopique.

Oscillatoria ou Trichodesmium ?

Le genre *Trichodesmium* a été créé par EHRENBERG (1830) sous la diagnose suivante : « *Trichodesmium erythraeum* : *Char. gen. Fila septata fasciculata nec oscillantia, fasciculi discreti muco involuti sociales libere natantes.* » On peut considérer que ce genre a été validé par GOMONT (1892), puisque le Code de nomenclature (LANJOUW *et al.*, 1966) adopte cette date, relativement tardive, comme point de départ de la taxinomie des Nostocacées Homocystées. Citons pour mémoire les synonymes postérieurs : *Xanthotrichum* et *Heliotrichum* (WILLE in SCHÜTT, 1892), *Skujaella* (DE-TONI, 1938) et peut-être *Pelagothrix* (SCHMIDT, in OSTENFELD & SCHMIDT, 1901).

Les affinités entre *Oscillatoria* et *Trichodesmium* sont si étroites que GEITLER (1932) a pris l'initiative de réunir les deux genres sous le premier nom, prioritaire ; toutefois, le même auteur réhabilite ultérieurement (1942) le second nom, «aus praktischen Gründen». Citons également FRÉMY (1934) : «Le genre *Trichodesmium* ne diffère guère du genre *Oscillatoria* que par le mode de vie des espèces qu'il comprend. »

En fait, aucun caractère ne peut à lui seul assurer l'autonomie générique des *Trichodesmium* :

– Habitat : si l'on peut décider avec GEITLER (1942) que *Trichodesmium* est un genre exclusivement marin, en transférant l'espèce *T. lacustre* (? = *T. ivanoffianum*) dans le genre voisin (GEITLER, 1925), il demeure bien par contre que les *Oscillatoria* peuplent les deux

milieux marin et dulçaquicole, et possèdent également dans le second des représentants planctoniques responsables de «fleurs d'eau» (*O. planctonica*, *O. Tanganyikae*, *O. rubescens*, *O. prolifera*, *O. Agardhii*, etc.).

– Colonies: l'agrégation des filaments, par production d'une très fine enveloppe mucilagineuse, sous forme de gerbes ou de paquets de formes diverses, n'est pas particulière aux *Trichodesmium* (cf. : les trois dernières Oscillaires citées ci-dessus, ainsi que *O. lacustris*, *O. deflexa*, et aussi le genre *Phormidium*). Ce caractère lui-même n'est d'ailleurs probablement pas essentiel : j'ai du moins pu observer que «*T. Thiebautii*» se présente souvent à l'état de filaments solitaires (voir plus bas : Canal de Mozambique) ; de plus, si l'on admet l'existence d'une phase benthique sédentaire, l'association des trichomes en colonies planctoniques ne prend plus qu'une signification taxinomique purement accessoire.

– Mobilité : ce troisième et dernier critère est peut-être le plus significatif, bien que les travaux récents n'en fassent plus mention. Ehrenberg (*ibid.*) indique en effet «*fila... nec oscillantia*», ce que confirme Collingwood (1868), tandis que Montagne (1844), n'ayant pu observer de matériel vivant, souligne l'intérêt d'une preuve définitive. Or cette «preuve négative», qui ne semble d'ailleurs guère avoir été recherchée depuis le siècle dernier, serait infirmée par Margalef (comm. pers.) qui a pu noter, encore que rarement, «de très légers mouvements» chez «*Trichodesmium*». Il est par ailleurs permis de douter de l'identité des espèces observées par Ehrenberg et par Collingwood (probablement «*T. erythraeum*» et «*T. Hildebrandtii*» à l'état de pullulation). La mobilité reste donc à rechercher systématiquement, notamment chez les formes solitaires. Rappelons enfin que le mouvement oscillatoire, s'il est fréquent dans le genre *Oscillatoria*, n'est cependant pas évident chez toutes les espèces, ce qui diminue notablement l'importance taxinomique de ce caractère.

Il apparaît donc, en l'absence d'un critère décisif, et dans l'attente d'une éventuelle révision du genre *Oscillatoria* (et des genres voisins ?) que ce dernier nom doit être substitué à celui de *Trichodesmium*. La «raison de commodité» ne peut plus guère prévaloir, dès lors que Geitler (1932) a créé les nouvelles combinaisons nécessaires.

Détermination des espèces

Les espèces planctoniques marines susceptibles de donner lieu à des phénomènes d'«eaux rouges», et qui seules font l'objet de la présente note, sont en nombre réduit : 3 à 5, selon les auteurs des principales

monographies (GOMONT, 1892 ; WILLE, 1903 et 1904 ; FORTI, 1907 ; GEITLER, 1932 et 1942; FRÉMY, 1934; DESIKACHARY, 1959). Je reprends ici la conception de WILLE (1903), à quelques modifications près.

Dans l'identification de ces espèces, une importance excessive est souvent accordée aux caractères macroscopiques, principalement à la couleur : encore faut-il ici distinguer entre (1) couleur de la mer, dans les cas d'«eaux rouges», (2) couleur des colonies, isolées par exemple dans un bocal, (3) couleur des filaments examinés au microscope – à l'état frais, ou fixés –, (4) enfin, couleur des exsiccata dans les herbiers... Il n'est nullement assuré qu'aucun de ces aspects possède une valeur spécifique, car l'état physiologique semble déterminant (ainsi, la couleur rouge est-elle souvent attribuée à un état de décomposition). Cette question ne pourra être résolue à l'avenir que sur la foi de déterminations microscopiques sûres. L'odeur de la mer, dans certains cas de pullulations, est plus aléatoire encore.

La forme des colonies, caractère «semi-macroscopique» assez stable, ne peut cependant à elle seule assurer la détermination spécifique. Je modifie donc comme suit la clé dichotomique établie par WILLE (1903) :

– Filaments non comprimés au niveau des cloisons intercellulaires :
  + Diamètre : 3–16 μ (souvent <10 μ). Cellules subquadratiques ou plus hautes que larges ..... *O. Thiebautii*
  + Diamètre : 13–22 μ. Cellules plus larges que hautes .... *O. Hildebrandtii*
– Filaments comprimés au niveau des cloisons intercellulaires :
  + Diamètre : 7–12 μ. Filaments rectilignes ..... *O. erythraea*
  + Diamètre : >16 μ. Filaments flexueux ou spiralés ..... *O. contorta*

OSCILLATORIA THIEBAUTII (GOMONT ex GOMONT) GEITLER

Fig. 1–2

GOMONT, 1890, p. 356 : «*T. Thiebautii spec. nov.*» (sans descr. ni fig.) ; 1892 p. 197, pl. 6, fig. 2–4. GEITLER, 1932, p. 967, fig. 617 c–d.
= *Trichodesmium Thiebautii* GOMONT ex GOMONT
GOMONT, *loc. cit.* WILLE, 1903, 1904. FORTI, 1907. OKAMURA, 1907. FRÉMY, 1934. GEITLER, 1942. DESIKACHARY, 1959.
= *Heliotrichum radians* WILLE in SCHÜTT
SCHÜTT, 1892, p. 277, fig. 87–88.
= *Skujaella Thiebautii* (GOMONT ex GOMONT) DE-TONI
DE-TONI, 1939, p. 292. UMEZAKI, 1961.
= *Trichodesmium tenue* WILLE
WILLE, 1904, p. 61, pl. I, fig. 24–27. FORTI, 1907. FRÉMY, 1934. GEITLER, 1942

L'autonomie de «*Trichodesmium tenue*», mise en doute par la plupart des auteurs – dont WILLE lui-même – me paraît insoutenable après étude de mes récoltes personnelles (voir plus bas). Il convient donc

d'élargir la diagnose d'*O. Thiebautii*, qui devient de ce fait la plus variable des quatre espèces étudiées :

Filaments plus ou moins flexueux, solitaires ou réunis en paquets de taille variable (jusqu'à 6 mm.) ; dans ce dernier cas, les filaments sont soit entrecroisés, soit rayonnants, soit – plus rarement – parallèles. Diamètre des filaments très variable, de 3 à 16 μ, le plus souvent < 10 μ. Cellules parfois subquadratiques, souvent plus hautes que larges, le rapport hauteur/diamètre étant assez variable dans un même filament ; chez les formes très fines, de diamètre 3–7 μ (= « *Trichodesmium tenue* »), les cellules sont toujours plus hautes que larges, et leurs parois sont relativement épaisses. Filaments non comprimés au niveau des cloisons transversales. Cellule terminale de forme variable : rétrécie ou élargie vers l'apex, ou isodiamétrique.

Morphologiquement la plus variable, cette espèce est également la plus commune des quatre : d'origine elle aussi tropicale, mais plus eurytherme, elle s'étend ainsi largement sous les latitudes tempérées de l'Atlantique nord (Cleve, 1900; Ostenfeld, cité in Wille, 1903; Farran, 1932).

OSCILLATORIA HILDEBRANDTII (Gomont) Geitler
Fig. 3

Gomont, 1892, p. 197, pl. 6, fig. 1. Geitler, 1932, p. 968.
= *Trichodesmium Hildebrandtii* Gomont
Gomont, *loc. cit.* Forti, 1907. Desikachary, 1959.
= *Trichodesmium Ehrenbergii* f. *indicum* Hauck
Hauck, 1888, p. 93.
= *Trichodesmium indicum* (Hauck) Lemmermann
Lemmermann, 1899, p. 395. Lemmermann, 1902, 1906.
= *Trichodesmium Hildebrandtii* f. *atlanticum* Reinsch
Reinsch, 1904, p. 536, fig. 1–3.
= *Skujaella Hildebrandtii* (Gomont) De-Toni
De-Toni, 1939, p. 292. Umezaki, 1961.

Filaments rectilignes ou seulement très légèrement flexueux ; stades solitaires exceptionnels : filaments habituellement coloniaux, parallèles, formant des « fagots » de 2 à 5 mm. de longueur. Diamètre des filaments compris entre 13 et 22 μ (? 10–20 selon Umezaki). Cellules toujours plus larges que hautes (rapport diamètre/hauteur : de 2 à 4). Filaments non comprimés au niveau des cloisons transversales. Cellule terminale sub-hémisphérique.

Espèce intertropicale, répartie de façon très sporadique dans les trois océans.

OSCILLATORIA ERYTHRAEA (Ehr. ex Gomont) Geitler
Fig. 4–5

Ehrenberg, 1830, p. 506. Gomont, 1892, p. 196, pl. 5, fig. 27–30. Geitler, 1932, p. 968, fig. 617 a–b.
= *Trichodesmium erythraeum* Ehrenberg ex Gomont
Ehrenberg, Gomont, *loc. cit.* Lemmermann, 1899, 1906. Ostenfeld & Schmidt, 1901. Wille, 1903, *vix* 1904 (confusion partielle avec *O. Hildebrandtii* ?). Forti, 1907. Okamura, 1907 (fig. douteuses). Frémy, 1934. Geitler, 1942. Desikachary, 1959.
= *Skujaella erythraea* (Ehrenberg ex Gomont) De-Toni
De-Toni, 1938, 1 (5), n° 477. De-Toni, 1939.
? = *Trichodesmium Hindsii* Montagne
Montagne, 1844, p. 360, pl. 10, fig. d. Kützing, 1845.
? = *Trichodesmium Ehrenbergii* Montagne
Montagne, 1844, p. 360, pl. 10, fig. a–c, e–i. Kützing, 1845.
? = *Trichodesmium erythraeum* var. *Hindsii* (Montagne) Wille in Schütt
Schütt, 1892, p. 277, fig. 85.

Filaments sub-rectilignes, exceptionnellement isolés, réunis d'ordinaire parallèlement en paquets de couleur pourpre (?) et dont la taille n'excède pas 1 mm. Diamètre des filaments compris entre 7 et 12 μ, «plus rarement 21 μ» (?) selon Gomont ; cellules sub-quadratiques ou plus larges que hautes (rapport diamètre/hauteur : de 1 à 3). Filaments comprimés au niveau des cloisons transversales, et rétrécis aux extrémités. Coiffe bien visible? (Frémy : «déprimée-conique ou convexe»).

Espèce tropicale et subtropicale, assez mal connue : en tant qu'espèce-type du «genre» *Trichodesmium*, elle a pu souvent être hâtivement nommée et ainsi souffrir en quelque sorte de sa célébrité...

OSCILLATORIA CONTORTA (Wille in Schütt) nov. comb.
Fig. 6–7

Schütt, 1892, p. 277, fig. 86 : «*Xanthotrichum contortum*».
= *Trichodesmium contortum* (Wille in Schütt) Wille
Wille, 1903, p. 18, fig. 14, *et* 1904, p. 63, pl. 1, fig. 10–11, 38. Lemmermann, 1906, *non* 1899 *nec* 1902. Forti, 1907. Frémy, 1934. Geitler, 1942.
= *Skujaella contorta* (Wille in Schütt) De-Toni
De-Toni, 1939, p. 291.

Filaments extrêmement flexueux ou spiralés, réunis en colonies de grande taille (jusqu'à 1 cm.), en partie enroulés ensemble comme les fibres d'un câble, et couleur jaune paille (?). Diamètre des filaments : 16–25 μ ou davantage, jusqu'à 52 μ (?). Cellules sub-quadratiques ou plus larges que hautes (rapport diamètre/hauteur : 1 à 8). Filaments

comprimés au niveau des cloisons transversales, et très légèrement rétrécis aux extrémités. Cellule terminale : à décrire.

Atlantique nord-ouest (WILLE) ; la présence d'*O. contorta* dans les autres océans est douteuse.

Bien qu'entourée d'incertitudes, la diagnose de cette espèce n'autorise son identification à aucune des trois précédentes.

Canal de Mozambique

Mes observations personnelles dans cette région tiennent en trois séries de récoltes qualitatives (filet) et quantitatives (comptages par sédimentation), reportées sur la planche 2:

– Nossi-Bé (N) : prélèvements hebdomadaires, échelonnés sur 18 mois, dans un secteur purement côtier (cf. SOURNIA, s. pr.).

– Tuléar (T) : divers prélèvements côtiers ou à peu de distance de la côte.

– Croisière n°8 de l'«ANTON BRUUN» (cf. : Anonyme, 1965) selon l'itinéraire Durban (D) – Beira (B) – Nossi-Bé (N) – Mombasa (M).

Deux des quatre espèces précédentes, *O. Thiebautii* et *O. Hildebrandtii*, étaient représentées, et conduisent aux remarques suivantes :

Morphologie :

O. Thiebautii, de couleur jaune (sous le microscope) et se maintenant telle dans les échantillons formolés, possède le plus souvent un diamètre de 7 à 9 μ et des cellules subquadratiques ou légèrement plus hautes que larges : c'est sous cette forme (fig. 1) que l'algue donne lieu à des poussées massives – celles-ci de couleur jaune-pailleté, à l'œil nu. On rencontre en outre (fig. 2) des filaments plus étroits (3–7 μ), à cellules nettement (2–4 fois) plus hautes que larges (= «*T. tenue*») : toujours rares et isolés, ces filaments semblent figurer un état physiologique déficient, sinon une forme de résistance.

O. Hildebrandtii, beaucoup plus rare il est vrai, présente un type constant : diamètre 16–18 μ, cellules 3–4 fois plus larges que hautes, filaments de couleur verte ou vert-jaune sous le microscope, la couleur de la mer étant elle-même difficilement définissable («sciure de bois»...).

De plus, le contenu cytoplasmique est ordinairement concentré chez *O. Thiebautii* contre les cloisons transversales, tandis qu'il se condense autour de l'axe du filament chez *O. Hildebrandtii*.

Ecologie :

O. Thiebautii, seule espèce récoltée à Nossi-Bé, y est pratiquement pérennante tout au long du cycle annuel, mais ses poussées numériques

et les productions d'«eaux rouges» sont exclusivement estivales (SOURNIA, s. pr.), c'est à dire liées aux conditions hydrologiques suivantes : salinité 32–34‰, température 29–30°C (l'écart thermique annuel étant faible, ce second facteur semble ici secondaire). Lors d'une prolifération spectaculaire à la fin de l'été 1963–64, il a été observé (SOURNIA, 1965) que la teneur en matières organiques, mesurée par l'absorption spectrophotométrique de l'ultraviolet, est plus élevée dans la zone d'«eau rouge» que dans les eaux voisines.

A Tuléar (salinités et températures moyennes : 35,30‰ et 22°C), *O. Thiebautii* n'était représentée qu'en très faibles quantités.

Au cours de la croisière de l'«ANTON BRUUN», j'ai rencontré cette espèce à la presque totalité des stations, le plus souvent en quantités négligeables ; cependant, en quelques stations – néritiques – on dénombrait quelques centaines ou quelques milliers de filaments par litre.

En conclusion[2]), *O. Thiebautii* se présente, dans le Canal de Mozambique, comme une espèce relativement eurytherme (23–30°C) et euryhaline (31–35,5‰) mais préférentiellement néritique, son abondance étant approximativement fonction inverse de la salinité.

La seconde espèce, *O. Hildebrandtii*, n'a été récoltée qu'en quelques stations océaniques ou de salinité supérieure à 35,5‰, principalement au large du Cap Saint-André (pl. 2 : A), c'est à dire aux lieux mêmes de la découverte originelle de HILDEBRANDT : cette espèce formait là, sur une distance de 30 milles, des traînées ou nappes de formes diverses et essentiellement superficielles (jusqu'à 400.000 filaments/litre en surface, moins de 5.000 à 1 m., et quelques centaines au plus dans les prélèvements plus profonds).

Les exigences écologiques d'*O. Hildebrandtii*, à la différence du cas précédent, sont donc étroitement définies : cette espèce, nettement sténohaline dans le canal de Mozambique, semble donc océanique. On voit du moins que les distributions des deux *Oscillatoria* dans cette région sont opposées. Ces données contredisent celles de MARGALEF (s. pr.) relatives à la mer des Antilles, où l'on ne décèle pas de différence écologique marquée entre les deux espèces ; d'après le même auteur (comm. pers.), *O. Thiebautii* et *O. Hildebrandtii* pourraient ne représenter que deux morphoses d'une seule «espèce, au sens large», différant l'une de l'autre par leur diamètre. Souhaitons que cette contradiction inspire de nouvelles recherches.

[2]) On peut ajouter aux observations précédentes le fait suivant : à l'Ile Maurice, où j'ai effectué quelques récoltes côtières en septembre 1964 (salinité : 34 ‰, température : 24°C), la seule espèce présente était encore *O. Thiebautii*.

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LEGENDES DES PLANCHES 1 (1)–2 (2)

PLANCHE 1 (1)

Fig. 1–2 : *Oscillatoria Thiebautii* (GOM. ex GOM.) GEITLER. – Fig. 3 : *O. Hildebrandtii* (GOM.) GEITLER. L'échelle, commune aux trois figures, est de 10 µ. – Fig. 4–5 : *Oscillatoria erythraea* (EHR. ex GOM.) GEITLER, d'après FRÉMY, 1934. – Fig. 6–7 : *O. contorta* (WILLE in SCHÜTT) nov. comb., d'après WILLE, 1904. (Fig. 4–5 : × 500 ; fig. 6 : × 125 ; fig. 7 : × 380).

PLANCHE 2 (2)

Récoltes personnelles dans le Canal de Mozambique.

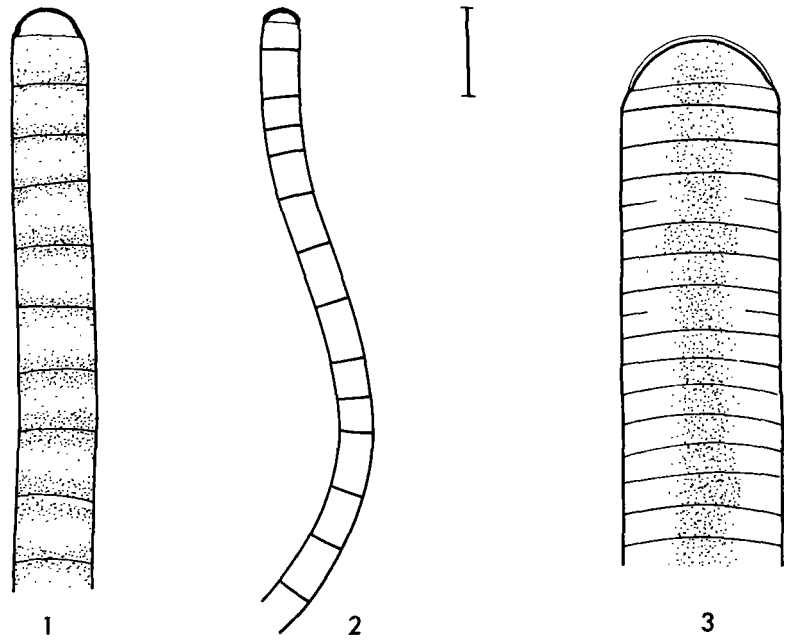
ADDENDUM

Peu de temps après avoir corrigé les épreuves de cette note, je prends connaissance du travail de FRÉMY (1941), «Revision du Genre *Skujaella* J. DE TONI (= *Trichodesmium* EHR. et Auct.) "in : Le Botaniste, Paris, 31 (1–2), pp. 3–19. Je sollicite l'indulgence du lecteur devant cette importante lacune bibliographique, que je m'efforce de combler dans les quelques lignes suivantes.

FRÉMY (ibid.) traite rapidement le problème générique ; il distingue les *Oscillatoria* (dulçaquicoles) des *Skujaella* (marins), mais n'apporte à cette question aucun élément nouveau. (Rappelons que, si la distinction est justifiée, le nom légal du genre marin est *Trichodesmium*, «nomen conservandum» in LANJOUW et al., 1966).

Au niveau spécifique, par contre, la conception de cet auteur est inédite autant que révolutionnaire : FRÉMY discute et élimine successivement les caractères donnés jusqu'alors comme distinctifs (constriction des filaments, épaisseur et hauteur relative des cellules, dimensions et forme des colonies) et conclut à une espèce unique... en laquelle il reconnaît cependant trois formes, ce qui tempère singulièrement la portée de ses conclusions.

Cette conception monospécifique me semble prématurée : outre que les déductions de FRÉMY sont quelque peu hâtives, les Cyanophycées ici étudiées demeurent insuffisamment connues ; les critères morphologiques — que j'ai tenté de redéfinir dans la présente note – ne peuvent être invalidés a priori, au vu des confusions et contradictions qui parsèment la littérature. A. S.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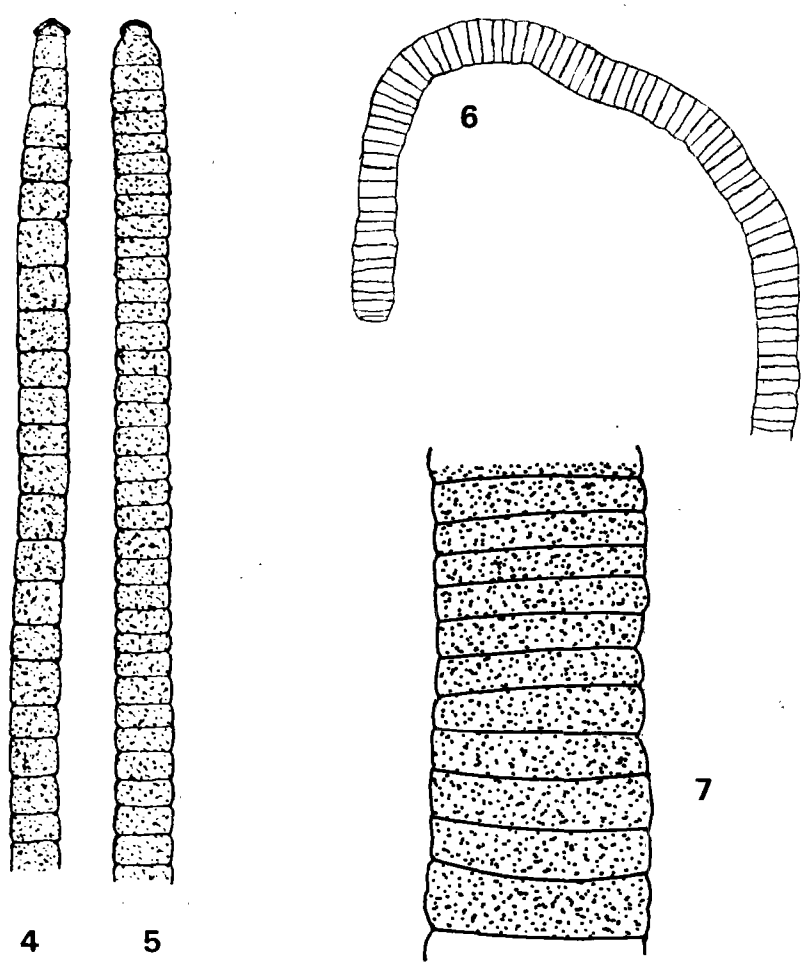
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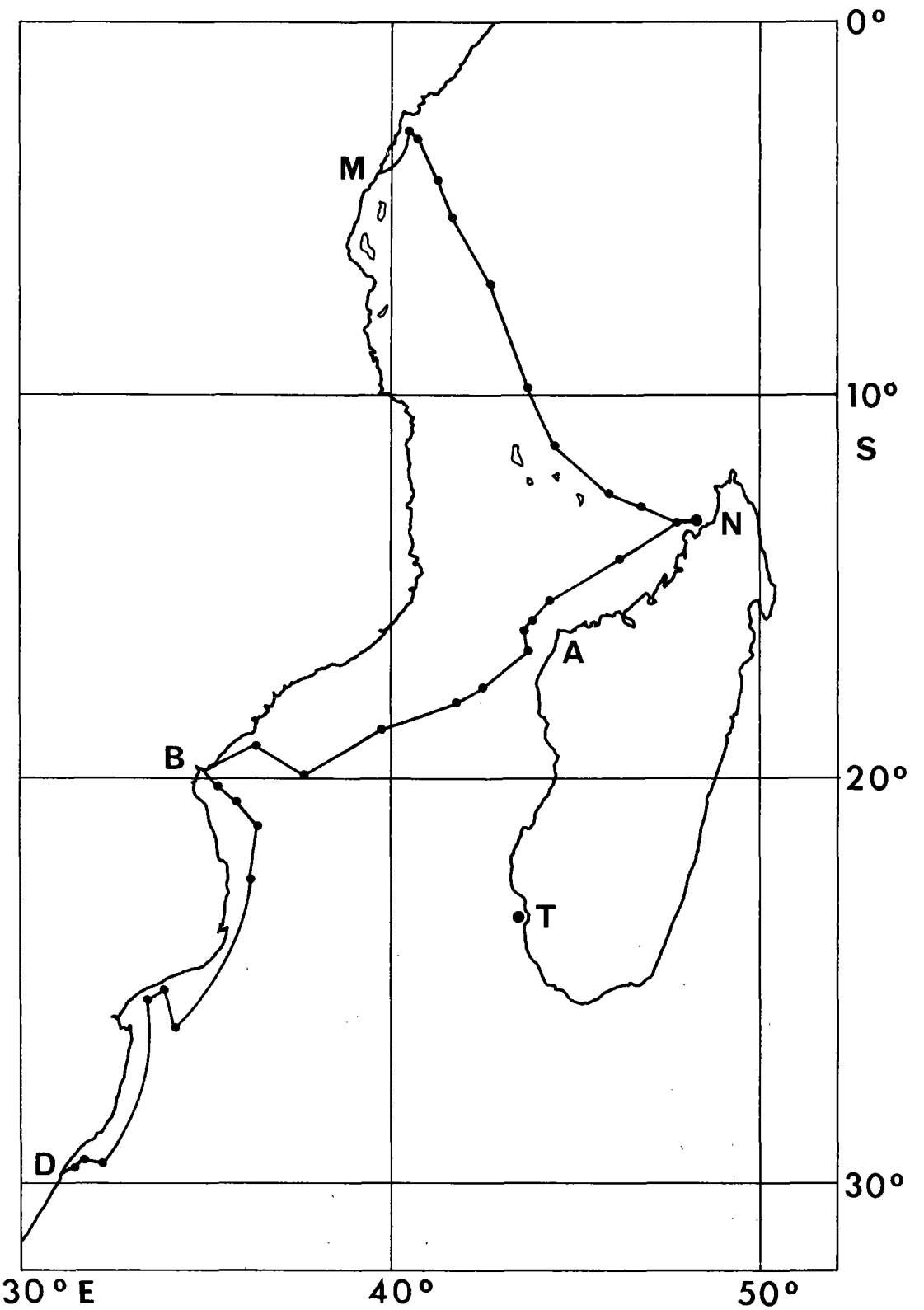
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Part II

Physical oceanography and marine meteorology

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В. Г. Нейман, Б. Н. Филюшкин,
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СТРУКТУРА И ЦИРКУЛЯЦИЯ ВОД ВОСТОЧНОЙ ЧАСТИ ИНДИЙСКОГО ОКЕАНА В ПЕРИОД ЛЕТНЕГО МУССОНА

Индийский океан до сих пор остается наименее изученным в гидрологическом отношении, несмотря на то, что с каждым годом он привлекает все большее число исследователей. Если, например, в северной части Тихого океана в настоящее время количество океанографических станций измеряется десятками тысяч, то во всем Индийском океане таких станций едва ли можно насчитать несколько тысяч. Подавляющее большинство экспедиций, работавших здесь в разные годы, проводило свои наблюдения в зимний сезон северного полушария.

Материалы 35-го рейса и/с «Витязь», проходившего в восточной части Индийского океана в июле — октябре 1962 г., по существу явились первым значительным вкладом в исследование гидрологических условий океана в период летнего муссона. В течение указанного рейса проведены комплексные океанографические наблюдения на 120 станциях, расположение которых показано в работе [1]. Основная часть гидрологических работ выполнена на меридиальных разрезах по 77°, 84°, 91°30′ в. д., а также на разрезах через Бенгальский залив и от западной оконечности о-ва Ява к Австралии. Направление разрезов было выбрано с таким расчетом, чтобы они пересекали под прямым углом систему основных течений в экваториальной и тропической зонах океана.

Гидрологические работы в 35-м рейсе и/с «Витязь» заключались в определении температуры и солености на стандартных горизонтах во всей толще вод, измерении скорости и направления течений, вертикальном зондаже температуры в верхнем слое океана. Наблюдения над течениями производились на якорных буйковых станциях в слое 0—2500 *м*. В связи с плохими погодными условиями и большим комплексом работ наблюдения над течениями удалось провести лишь на 17 станциях.

В настоящей работе дается анализ гидрологических условий в восточной части Индийского океана. При этом использованы материалы только одного указанного рейса, поскольку, как нам кажется, его данные достаточно хорошо отражают гидрологическую ситуацию, характерную для периода установившегося летнего муссона.

НЕКОТОРЫЕ СВЕДЕНИЯ О ПОЛЕ ВЕТРА

Известно, что ветер является одним из важнейших факторов, определяющих характер гидрологического режима бассейнов. Поэтому, прежде чем приступить к анализу гидрологических материалов, остановимся, хотя бы кратко, на основных особенностях поля ветра над северо-во-

сточной частью Индийского океана. С этой целью мы построили схему ветрового поля, на которой в виде векторов-стрелок показан среднесуточный ветер по данным срочных судовых метеонаблюдений в 35-м рейсе и/с «Витязь» (рис. 1) [1]. Эта схема довольно условна, так как основана на материалах несинхронной съемки, занявшей достаточно продолжительное время.

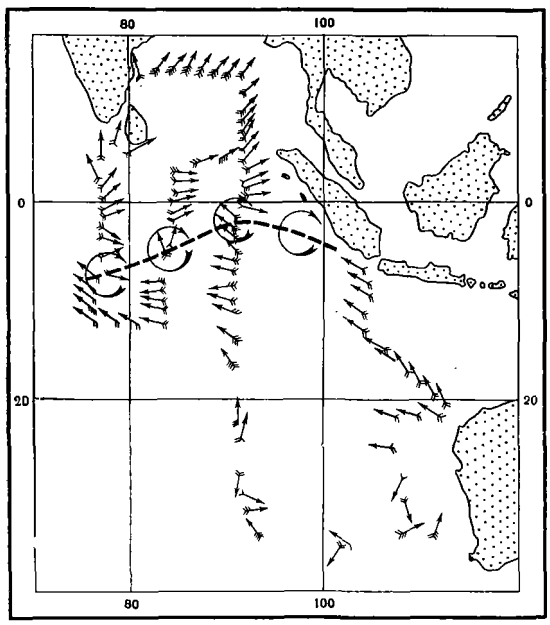

Рис. 1. Поле ветра в период наблюдений

Относительная устойчивость ветра пассатной и муссонной зон в сезонном масштабе дает возможность использовать полученные результаты для оценки пространственных изменений ветрового поля, пренебрегая его изменчивостью во времени. Конечно, данное положение не может быть в равной степени применено к переходным между основными зонами периодам, в течение которых в муссонной зоне происходит перестройка барической структуры.

Сравнение рис. 1 со среднемноголетними характеристиками поля ветра для соответствующего сезона [2, 3] выявляет их общее подобие. Это позволяет сделать важный вывод о том, что работа 35-го рейса и/с «Витязь» протекала в период установившегося летнего муссона. Нужно, однако, отметить, что поле ветра в июле — октябре 1962 г. имело и существенные особенности.

Одна из них — аномальное смещение в сторону экватора северной границы пассатной зоны. Наиболее значительный сдвиг к северу отмечался в центральной части района, где смена пассатного ветра на муссонный наблюдалась в непосредственной близости от экватора.

Вторая характерная особенность поля ветра — наличие обширной области с неустойчивой циркуляцией между 20 и 35° ю. ш. На рис. 1 ветровые векторы в этой области имеют самые различные направления, среди которых очень трудно определить преобладающее.

На границе между пассатной и муссонной зонами существует положительный вихрь касательного напряжения ветра, который получает свое отражение в гидросфере, соответствуя зоне экваториальной дивергенции между Пассатным и Муссонным течениями, о чем будет сказано ниже.

ОСНОВНЫЕ ОСОБЕННОСТИ ПОЛЯ ТЕМПЕРАТУРЫ

Для анализа пространственного распределения температуры в рассматриваемом районе построены соответствующие карты для горизонтов 50 и 500 *м*. На рис. 2 видно, что в поверхностном слое в районе экватора выделяется обширная расширяющаяся к востоку зона наиболее высокой температуры воды (28°). К югу от экватора наблюдается равномерное понижение температуры с увеличением широты, что свидетельствует об

[1] Данные о среднесуточных векторах любезно предоставлены А. В. Фомичевым.

отсутствии заметной меридиональной адвекции тепла в верхних горизонтах в центральной части района. Поскольку процессы, формирующие температурное поле в Бенгальском заливе, находятся под значительным влиянием материка, горизонтальное распределение температуры к северу от экватора имеет более сложный характер. По мере продвижения к северу температура воды в поверхностном слое вначале понижается до 25°, а затем вновь возрастает до 27—28°. К югу от экватора характерное зональное распределение температуры нарушается лишь в западной части района на 3—7° с. ш., где отмечается пятно относительно холодной воды. Подобная картина наблюдается и в период зимнего муссона [4]. Эта аномалия в поле температуры, по-видимому, связана с подъемом вод в зоне дивергенции между Муссонным и Пассатным течениями.

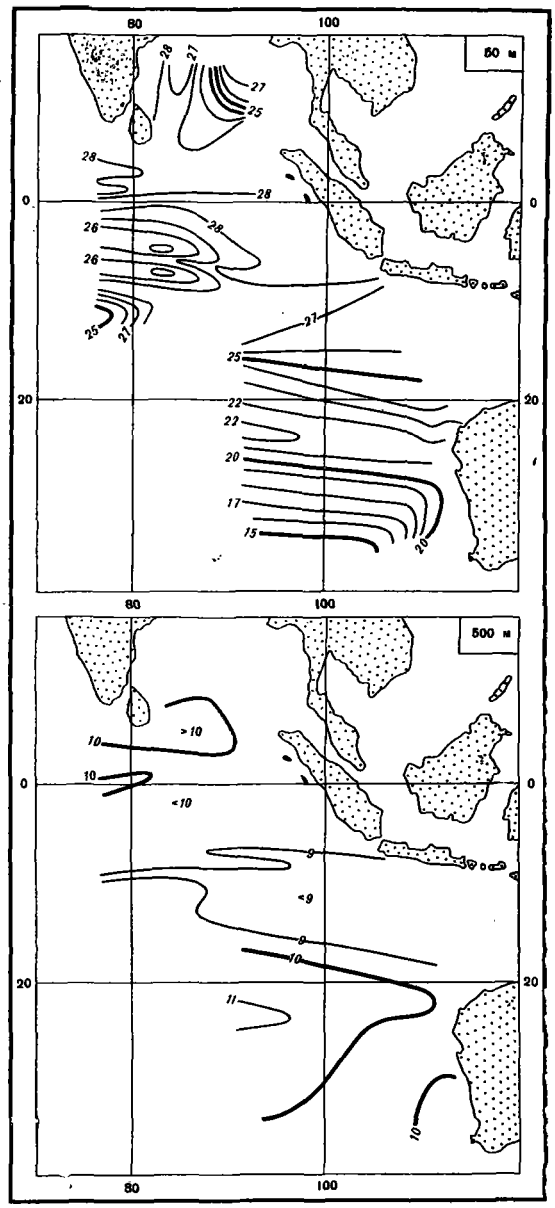

Рис. 2—3. Распределение температуры на горизонтах 50 и 500 *м*

Числа на рисунке означают температуру

Распределение температуры на горизонте 500 *м* (рис. 3) характеризуется относительной однородностью. Во всей северо-восточной части океана температура воды на этом уровне 9—11°. Сравнение данных рис. 3 с данными для зимнего периода показывает, что сезонное перераспределение тепла в экваториальной и тропической зонах, связанное с изменением системы циркуляции, не приводит к сколько-нибудь заметной перестройке в поле температуры на горизонте 500 *м*.

Рассмотрим теперь вертикальное распределение температуры на примере разреза по 91° в. д. (рис. 4). Этот разрез подразделяется на две основные части в соответствии с особенностями вертикальной термоструктуры. С 30 по 17° ю. ш. наблюдается типичное для средних широт изменение температуры с глубиной в зимний период южного полушария: в верхних горизонтах отчетливо выражен изотермический слой, слой

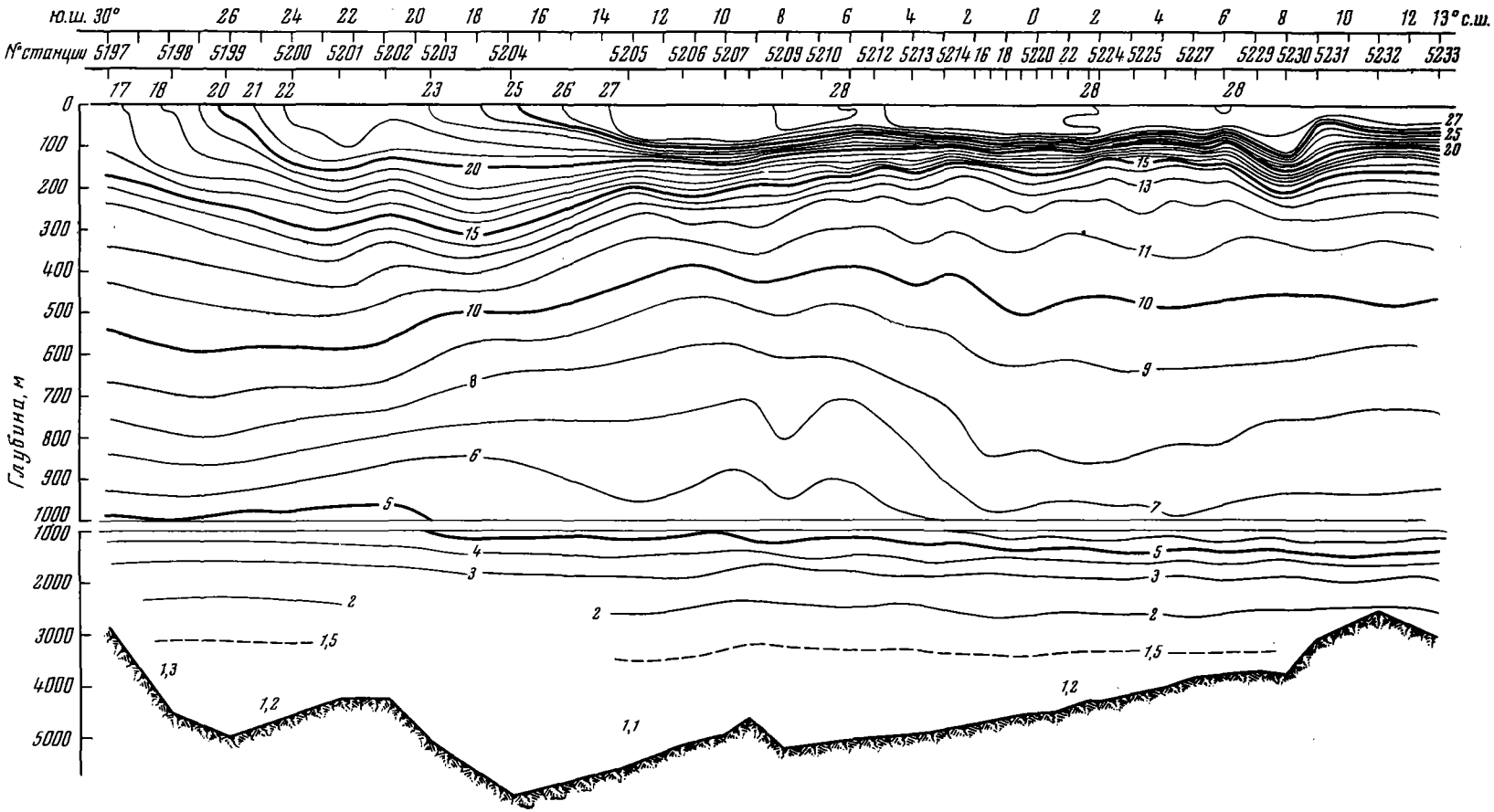

Рис. 4. Распределение температуры воды на разрезе по 91° в. д

Обозначения те же, что на рис. 2

скачка ниже него выражен слабо. Такая структура объясняется опусканием вод, вызванным конвергенцией чисто дрейфовых течений, а также сильно развитым конвективным перемешиванием. Только этим, пожалуй, и можно объяснить, почему в южной части разреза на глубинах 300—600 *м* вода теплее, чем в районе, расположенном ближе к экватору.

Вертикальное распределение температуры в северной части разреза имеет несколько иной характер на всем пространстве от 17° ю. ш. до 13° с. ш. Наиболее теплые (28°) поверхностные воды отделены от промежуточных резко выраженным слоем скачка температуры. В глубинных слоях северной части разреза поле температуры, по всей вероятности, не испытывает существенных изменений даже от года к году. Так, сопоставление разреза, выполненного и/с «Витязь», с двумя разрезами по 90° в. д., выполненными «Дискавери II» 20—30 июля 1950 г. и 9—19 октября 1951 г., а также с разрезом по тому же меридиану, выполненным д/э «Обь» 21 апреля — 6 мая 1957 г. [4], показало, что ниже 500 *м* термические условия были идентичны. При рассмотрении этих материалов можно заметить, что положение изотерм вдоль меридиана на разрезах в слое 300—1000 *м* испытывает периодические колебания относительно некоторого среднего значения. Волнообразные, как бы вторичные изгибы изотерм в общем незначительны и, по всей вероятности, объясняются недостаточно точным приведением горизонтов. Кроме того, растянутые по времени наблюдения на разрезах могли быть проведены в различные фазы внутренних волновых движений в океане, которые и отражаются на наших графиках.

Как правило, вертикальная термоструктура воды в океане характеризуется наличием поверхностного изотермического слоя с вертикальными градиентами меньше 0,01° С/*м*, который сменяется слоем с максимальными градиентами — слоем скачка температуры. Ниже него происходит плавное уменьшение температуры почти до постоянного ее значения на больших глубинах.

Таким образом, при анализе кривых вертикального распределения температуры в большинстве случаев можно однозначно выделить слой ее наибольших вертикальных градиентов.

Существование слоя скачка температуры в значительной мере определяет положение и интенсивность слоя скачка плотности, и поэтому его изучение представляется важным. Слой скачка температуры характеризуется следующими тремя параметрами: H_0 — нижняя граница изотермического слоя, одновременно являющаяся верхней границей слоя скачка; $H_н$ — нижняя граница слоя скачка и величина вертикального градиента температуры в слое скачка ($H_с$) [5]. Для определения этих параметров нами использованы материалы всех гидрологических станций 35-го рейса и/с «Витязь» и на основе полученных данных построены карты распределения указанных величин.

На рис. 5 видно, что в области к югу от 20° ю. ш. существует хорошо заметный верхний однородный слой, средняя толщина которого равняется 100—120 *м*.

В сложном вертикальном профиле различается несколько очень слабо выраженных слоев скачка температуры со средними значениями градиентов в них порядка 0,02—0,04°С/*м*.

Значительная термическая однородность вод по вертикали в этой области объясняется тем, что в августе — зимнем месяце южного полушария — здесь определенно сказывается зимнее охлаждение поверхностных вод, в результате чего слой скачка температуры размывается [5]. Кроме того, в этой области располагается северная периферия зоны субтропической конвергенции, в которой отмечается опускание вод в поверхностном слое.

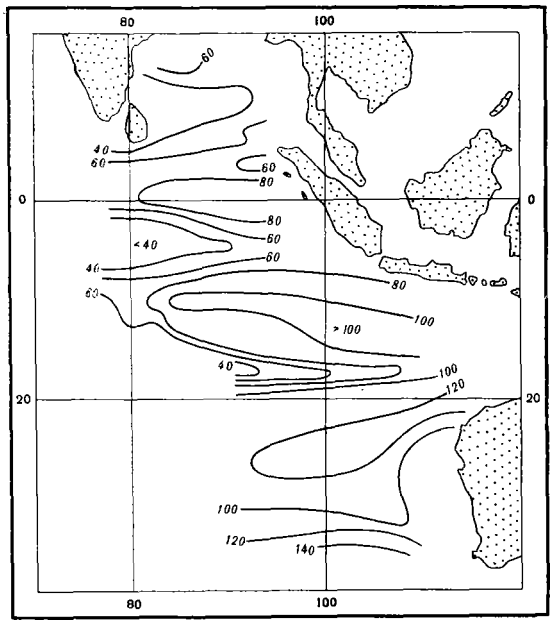

Рис. 5. Топография нижней границы изотермического слоя

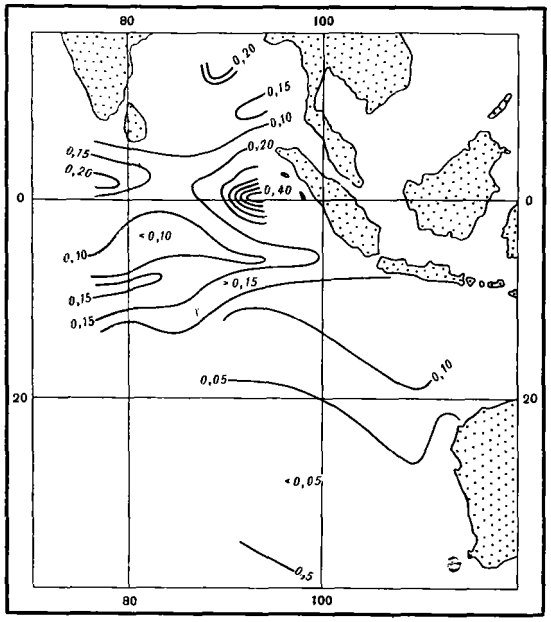

Рис. 6. Значение вертикального градиента в слое скачка температуры

Значительно больший интерес представляет экваториальная область. Наличие здесь сильных и устойчивых течений не позволяет успешно использовать для расчета элементов слоя скачка теоретические модели, применимые для средних широт. Непосредственно на экваторе формула для H_0 вообще не применима, так как во все расчеты по этой формуле входит параметр Кориолиса.

На карте глубины изотермического слоя (см. рис. 5) можно видеть, что изменения H_0 происходят преимущественно в меридиональном направлении. Чередование ложбин и гребней дает возможность выделить на этой карте широтные зоны, в которых изменение H_0 имеет различный характер.

Вполне вероятно, что глубина изотермического слоя зависит от поперечной циркуляции, возникающей в любом горизонтальном потоке. Поэтому широтный гребень, располагающийся в среднем на 3° ю. ш. с незначительным смещением к югу в восточной части района, указывает на наличие здесь зоны подъема вод. Аналогичная зона четко выделяется на 17° ю. ш. Исходя из тех же соображений, можно предположить, что широтная ложбина, располагающаяся в среднем на 10° ю. ш., соответствует зоне опускания. С меньшей уверенностью, из-за ограниченного числа наблюдений, нами выделяется зона подъема вод севернее экватора — от южной оконечности о-ва Цейлон к 10° с. ш. на меридиане 91° в. д.

Сравнение карты, приведенной на рис. 5, со схемой геострофических течений (см. рис. 11), построенной независимо от первой, выявляет их заметное совпадение. Все зоны вертикальных движений, выделяемые по топографии глубины изотермического слоя, совпадают с зонами раздела течений. Таким образом, когда топография H_0 аналогична схеме дина-

мических горизонталей в поверхностном слое, можно даже сформулировать простое правило: если встать лицом по течению, то глубина изотермического слоя будет увеличиваться влево в южном полушарии и вправо в северном. К подобным выводам пришел и Дефант [6], который проанализировал топографию однородного слоя для экваториальных районов Атлантического океана.

Это совпадение для тропических и экваториальных районов объясняется двумя причинами. Во-первых, в резко стратифицированной по температуре воде существуют два практически однородных слоя — поверхностный и глубинный. Во-вторых, здесь имеется установившаяся система градиентных течений. Тогда положение границы раздела может быть определено из уравнения Маргулиса, поскольку оно выведено для двухслойной модели моря с градиентными течениями при отсутствии трения.

На рис. 6 показана величина вертикальных градиентов температуры в слое скачка. Нетрудно заметить, что здесь изменение интенсивности слоя скачка в зависимости от широты в общих чертах сходно с подобным изменением, например в Тихом океане [5]. Слой скачка температуры в экваториальном районе имеет значительную толщину, превышающую в среднем 100 *м* (см. рис. 5). Распределение этого элемента зонально.

Принято считать, что в зоне дивергенции слой скачка температуры расположен близко к поверхности, резко выражен и имеет небольшую толщину, тогда как в зоне конвергенции наблюдается обратная картина. На рис. 5, 6 видно, что в данном случае положение верхней границы слоя соответствует этому утверждению, а распределение интенсивности слоя скачка температуры иногда противоречит ему.

ПОЛЕ СОЛЕНОСТИ И ВЕРТИКАЛЬНАЯ СТРУКТУРА ВОД

Распределение солености в Индийском океане имеет ряд существенных особенностей. Вода северной части бассейна, расположенной в областях, где испарение превышает осадки, обладает высокой соленостью. В северо-восточной части — Бенгальском заливе и в районе Малайского архипелага — выпадает много осадков, пресная составляющая водного баланса положительна, в результате чего воды этой части океана относительно распреснены. Иллюстрацией к сказанному служит карта для горизонта 50 *м* (рис. 7). Здесь следует отметить наличие языка вод пониженной солености, вытянутого в западном направлении вдоль параллели 10° ю. ш., который по своему происхождению связан с районом Тиморского моря. К югу от этой зоны располагается область тропических вод высокой солености — 35,8‰. На глубине 500 *м* (рис. 8) всю северную часть рассматриваемого района вплоть до экватора занимает вода с высокой соленостью (35‰), проникающая в Бенгальский залив из Аравийского моря [7].

К югу от экватора в горизонтальном поле солености на глубине 500 *м* много общих черт с ее распределением в поверхностном слое.

Распределение солености по вертикали отличается большей сложностью по сравнению с распределением температуры. В северной части разреза по 91°31′ (рис. 9) существует тонкий, порядка 100 *м*, распресненный слой, отделенный от промежуточных, более соленых (35‰) вод резко выраженным слоем скачка солености. Интересно отметить, что промежуточные воды, наблюдаемые вдоль всего разреза, в районе 8—12° ю. ш. имеют область разрыва, характеризующуюся пониженной соленостью почти во всей вертикальной толще. Глубинные слои океана повсеместно заполнены водами со значениями порядка 34,7‰, по всей вероятности антарктического происхождения.

Для выделения основных типов структуры вод в период летнего муссона нами использовался анализ *TS*-кривых и графиков вертикального распределения солености. Поскольку мы ограничиваемся в основном рас-

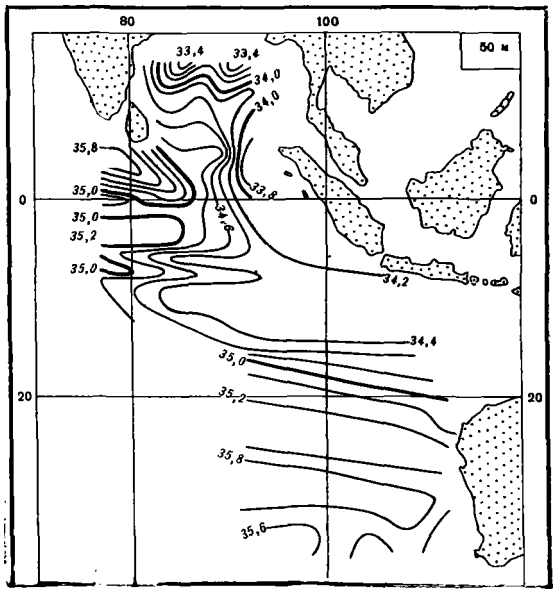

Рис. 7. Распределение солености воды на горизонте 50 *м*

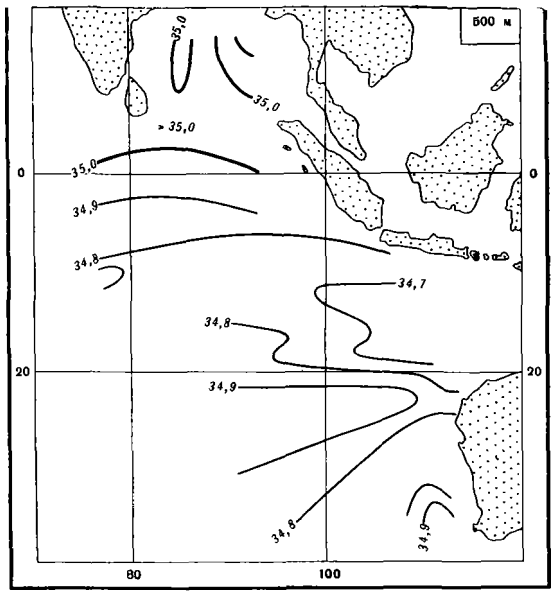

Рис. 8. Распределение солености воды на горизонте 500 *м*

смотрением гидрологических характеристик в верхнем 100-метровом слое, то можно считать, что метод *TS*-кривых дает достоверные результаты.

Термохалинные соотношения показывают, что южная часть разреза по 91°30′ в. д. находится в области интенсивных вертикальных движений вод, являющейся периферией зоны субтропической конвергенции. Здесь происходит значительное осолонение поверхностных вод в результате интенсивного испарения и выпадения незначительного количества осадков в году.

На рис. 10 приведены *TS*-кривые, построенные по данным нескольких станций и отражающие структуру вод этой области.

TS-кривая ст. 5198 характеризуется отсутствием слоя скачка. Вероятное опускание вод с поверхности формирует слой с постоянными градиентами температуры и солености до глубины порядка 600 *м*, который представлен на графике. На глубине примерно 1000 *м* располагается ядро антарктической промежуточной воды пониженной солености. *TS*-диаграмма соседней более северной ст. 5199 является показателем вод переходного типа, а уже на следующей ст. 5200 мы видим ярко выраженную структуру южнотропической области. Опустившиеся в зоне субтропической конвергенции поверхностные воды распространяются к северу в виде подповерхностного слоя повышенной солености (35,5—35,8‰) на глубине 100—300 *м*. Антарктическая промежуточная вода минимальной солености (34,3‰) занимает слой от 900 до 1500 *м*. По существу структура вод тропической части Индийского океана является характерной для вод южных тропиков всего Мирового океана [8].

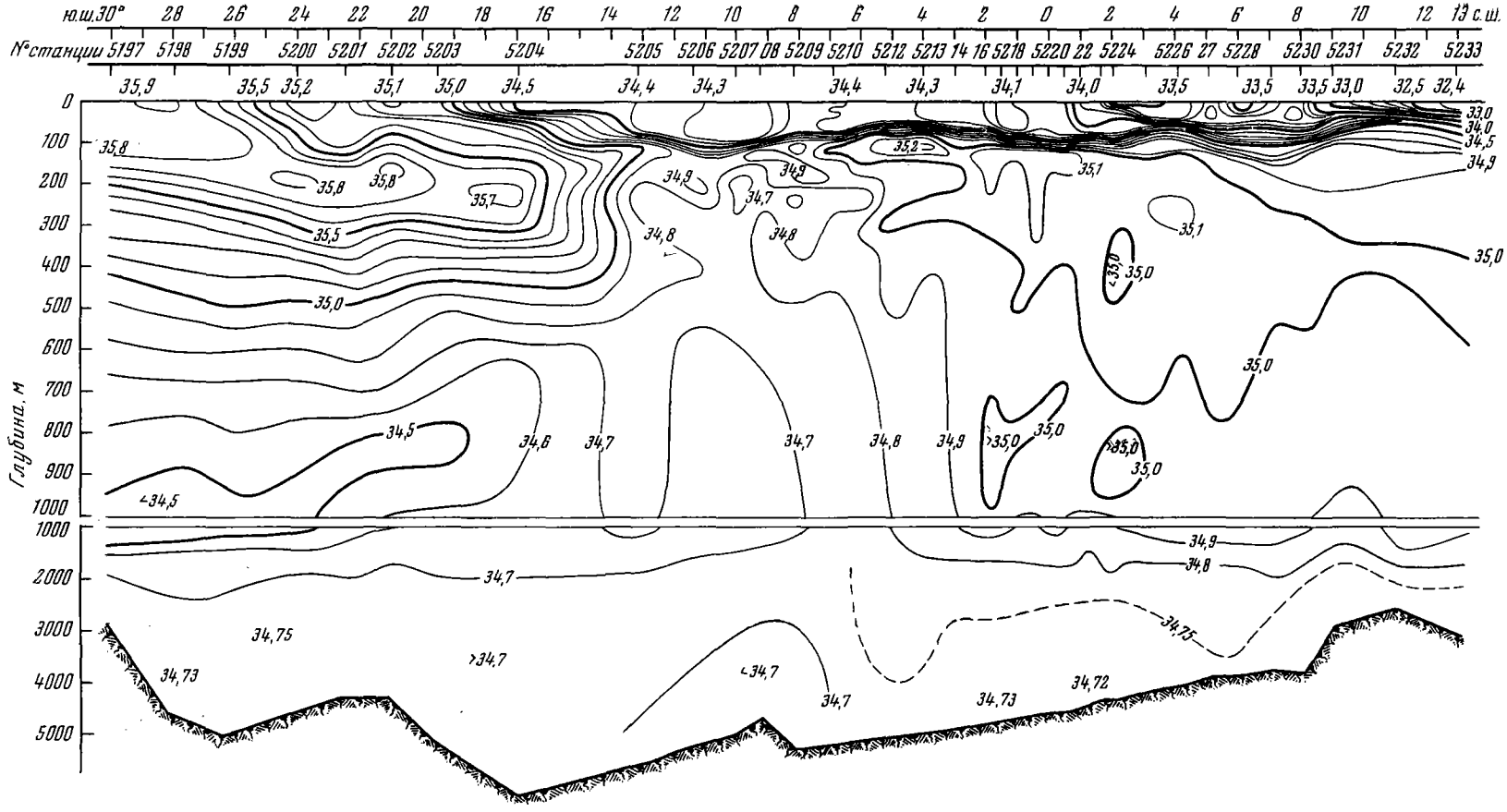

Рис. 9. Распределение солености воды на разрезе по 91° в. д.

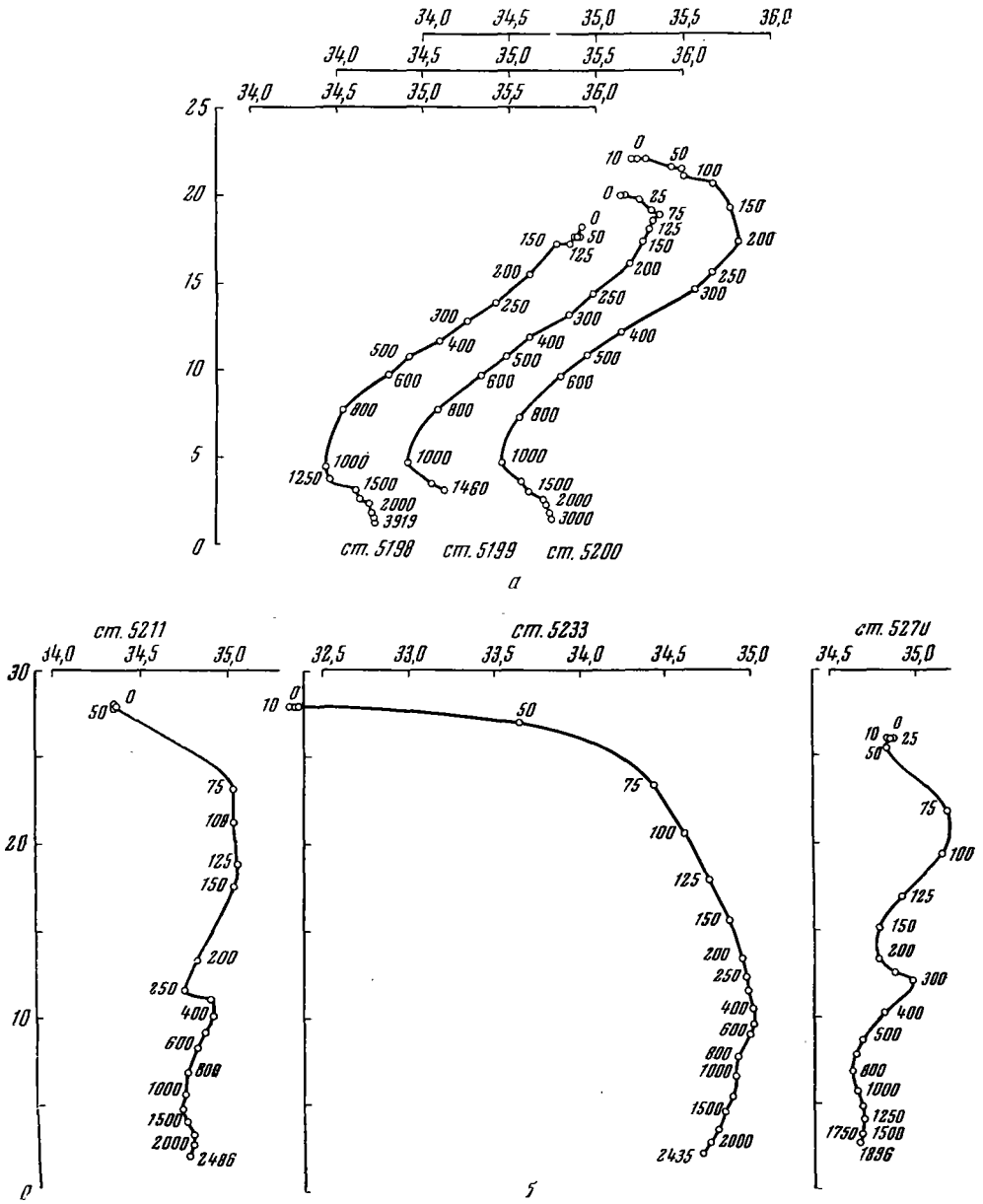

Рис. 10. *TS*-кривые

На разрезе по 91° эта структура прослеживается вплоть до 10—12° ю. ш. При этом ее северной границей является промежуточная зона, проходящая в широтном направлении через весь Индийский океан. Эта зона, делящая восточную часть океана на две большие области с различным термохалинным строением, неоднократно обнаруживалась и в прежних экспедициях. Сама по себе она может рассматриваться отдельно как область особой сложной гидрологической структуры.

В течение 35-го рейса и/с «Витязь» промежуточная зона была пересечена 4 раза от 106 до 77° в. д. При анализе материалов наблюдений в качестве критерия для определения ее ширины нами взято расстояние

между северной границей распространения подповерхностного слоя повышенной солености и южной границей вод, происхождение которых связано с районом Аравийского моря (условно изохалина 35‰). На границах этих слоев существуют большие градиенты солености, которые четко выделяются на разрезе. Ширина промежуточной зоны уменьшается от 300 до 100 миль с востока на запад и увеличивается с глубиной. Сложность структуры вод этой зоны хорошо отражается на *TS*-кривых ст. 5211 и ст. 5270 (см. рис. 10). На графиках можно выделить несколько максимумов солености, основные из которых располагаются на глубине около 100 и 300 *м*.

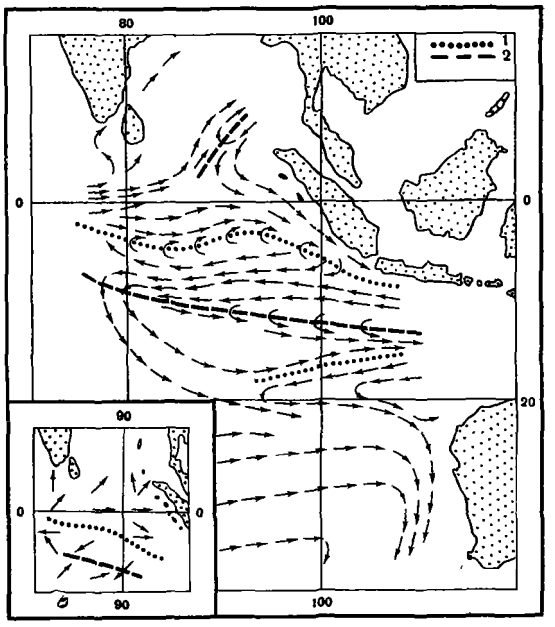

Рис. 11. Схема циркуляции на горизонте 50 *м*

1 — зона дивергенции; *2* — зона конвергенции: на вставке — суммарные течения

Аналогичное вертикальное распределение солености наблюдалось и в 31-м рейсе и/с «Витязь» [9], но несколько севернее.

Происхождение двух главных максимумов солености при этом связывалось с проникновением вод Аравийского моря, образующихся в результате смешения вод Красного моря, залива Оман, Аденского залива и Аравийского моря. Столь сложный генезис вод Аравийского моря определяет и их весьма сложную термохалинную структуру. Однако, проникая в восточную часть Индийского океана, эти воды благодаря интенсивному перемешиванию приобретают характер четко выраженной водной массы с незначительными градиентами температуры и солености. Весьма вероятно, что в формировании минимума солености между двумя указанными максимумами в пределах промежуточной зоны немаловажную роль играют воды пониженной солености, переносимые Пассатным течением из австралийско-азиатского района. Это предположение достаточно подтверждается схемой циркуляции вод в исследуемой области (рис. 11).

Как уже упоминалось, структура вод к северу от промежуточной зоны определяется проникновением сюда высокосоленых вод из Аравийского моря. Благодаря тому, что в период летнего муссона восточный перенос является преобладающим в северных широтах, почти вся толща океана в экваториальном районе занята водами высокой солености, за исключением самых поверхностных горизонтов. Типичная для этого района *TS*-кривая ст. 5233 (рис. 10) указывает на значительные вертикальные градиенты солености в верхнем 100—125-метровом слое. Ниже максимума, расположенного, как правило, на глубине 125 *м*, значения солености постепенно убывают в направлении дна. Однако, как это наблюдалось и в предыдущих рейсах [9], нами было отмечено проникновение антарктической промежуточной воды севернее промежуточной зоны. Минимум солености на *TS*-кривой ст. 5211 (см. рис. 10), расположенной севернее промежуточной зоны, по-видимому, имеет антарктическое происхождение.

Таким образом, предварительный анализ термохалинной структуры вод в период летнего муссона показывает, что:

1. для всего района в целом характерно зональное распределение термохалинных характеристик и лишь в прибрежных районах наблюдается отклонение от зональности под влиянием материка;

2. восточная часть Индийского океана пересекается промежуточной зоной, которая разделяет ее на два больших района, резко различающихся по структуре вод:

а) район южных тропиков с типичной для тропической части Мирового океана структурой вод и б) район к северу от промежуточной зоны, структура вод которого определяется главным образом проникновением сюда вод Аравийского моря.

ЦИРКУЛЯЦИЯ ВОД

Результаты инструментальных наблюдений над течениями, выполненных в 35-м рейсе и/с «Витязь» на 17 станциях, дают сведения о скорости и направлении потоков лишь в отдельных далеко отстоящих одна от другой точках. К сожалению, эти данные настолько отрывочны, что по ним трудно судить о динамике вод всей восточной части океана. Поэтому наряду с материалами непосредственных наблюдений для более полного представления о системе циркуляции вод в период летнего муссона построены схемы геострофических течений на изобарических поверхностях, рассчитанные по наблюденному полю плотности. Для динамических расчетов в качестве нулевой поверхности мы выбрали изобарическую поверхность 2000 *дбар*. Основанием для такого выбора послужил анализ кривых разности динамических глубин «стандартных» изобарических поверхностей по методу Дефанта [6].

Результаты наблюдений над течениями на горизонтах 2000—2500 *м* показывают, что в восточной части Индийского океана на глубине выбранной нами отсчетной поверхности существуют слабые течения преобладающего западного направления. Более того, на нескольких станциях среднесуточные векторы скорости на глубине 2000 *м* имели величину, сравнимую с точностью измерений. Таким образом, можно считать, что схемы течений, о которых пойдет речь, с достаточной достоверностью отражают характерные черты системы геострофической циркуляции, несмотря на то, что динамические расчеты проведены относительно нулевой поверхности, которая не является горизонтальной.

В качестве основы для анализа системы циркуляции вод в поверхностном слое мы взяли карту динамической топографии изобарической поверхности 50—2000 *дбар* и на ее основе построили схему течений на этом горизонте.

В восточной части океана выделяются три основные циркуляционные зоны (см. рис. 11).

Муссонное, или Северное экваториальное течение занимает обширную область севернее 3—5° ю. ш., являясь самым значительным по скорости потоком в рассматриваемой области. Результаты непосредственных измерений показывают, что стрежень Муссонного течения находится в районе экватора, по крайней мере между 70 и 90° в. д. Сгущение изолиний динамических высот южнее Цейлона прослеживается именно там, где были измерены максимальные скорости Муссонного течения. Меридиональный горизонтальный градиент плотности по обе стороны от экватора имеет различные знаки, благодаря чему геострофическое течение во всей приэкваториальной зоне как в южном, так и в северном полушарии направлено на восток. Муссонное течение в основном имеет характер зонального потока и лишь севернее 4—5° с. ш. в нем начинают преобладать меридиональные компоненты. Система дви-

жения вод Бенгальского залива и Андаманского моря ввиду малого количества данных слабо отражена на схемах. Однако общая тенденция в направлении течений и распределении термохалинных характеристик указывает на существование меридионального обмена между Бенгальским заливом и прилежащей областью океана.

При этом вынос распресненных вод из Бенгальского залива происходит преимущественно вдоль его восточного побережья. В то же время отличающиеся повышенной соленостью воды аравийского происхождения проникают далеко на север вдоль западного побережья залива.

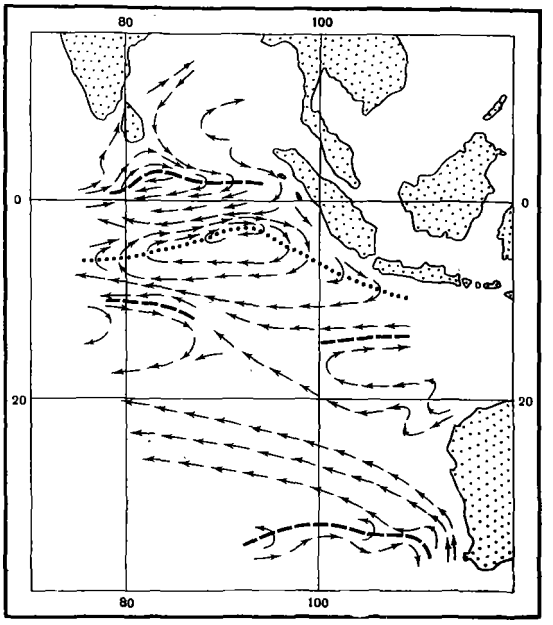

Рис. 12. Схема циркуляции на горизонте 500 м
Обозначения те же, что на рис. 11

Как видно на рис. 12, Пассатное течение представлено на карте северной частью большого антициклонального круговорота, ось которого проходит по 8—12° ю. ш. Этот круговорот не получил отражения на известных картах течений [10, 11], на что обратил внимание Виртки [12], обработавший материал австралийских экспедиций на «Диамантине».

Поскольку зональные геострофические течения бездивергентны, по одним нашим картам нельзя определить характер вертикальных движений на границах между потоками различного направления. Дополнительный анализ данных непосредственных наблюдений над течениями и ветром, а также карты распределения основных характеристик изотермического слоя показывают, что северная граница Пассатного течения представляет собой зону дивергенций, совпадающую с положением зоны положительного вихря ветра в приводном слое атмосферы.

Подобным же образом можно определить, что на южной периферии Пассатного течения, которое ограничивается зональной осью отмеченного выше круговорота, имеет место конвергенция горизонтальных потоков, приводящая к опусканию вод в поверхностных слоях океана. К сожалению, количество инструментальных наблюдений над течениями, выполненных южнее 10° ю. ш., настолько мало, что определить по ним роль геострофической компоненты в суммарном течении не представляется возможным.

По-видимому, циркуляция вод в районе южнее 10° ю. ш. не обладает той устойчивостью во времени, которая наблюдается в Пассатном и Муссонном течениях. Согласно имеющимся данным [11, 7], летом в северном полушарии в восточной части океана в зоне между 10—15 и 40° ю. ш. существует пояс пониженного давления, где постоянно формируются глубокие подвижные циклоны. Неустойчивость ветрового поля в этой зоне отражена и на карте (см. рис. 1), построенной по данным срочных судовых наблюдений в 35-м рейсе и/с «Витязь». Совершенно очевидно, что поле плотности здесь не успевает перестраиваться в соответствии с часто изменяющейся синоптической ситуацией и в каждый момент лишь косвенно отражает результирующее влияние ветра за

предыдущий неопределенно длительный промежуток времени. Поэтому район южнее 10° ю. ш. мы сочли возможным лишь условно назвать зоной слабых течений восточных румбов.

Как и следовало ожидать, геострофическая компонента суммарного течения в этой зоне даже в поверхностных горизонтах очень мала и, как правило, не превышает 10—15 *см/сек*. Линии тока в зоне слабых течений расположены почти точно вдоль параллелей, что свидетельствует об отсутствии заметного меридионального переноса. Исключение составляет район мористее западного побережья Австралии. Здесь под влиянием материка зональный поток изменяет свое направление и резко поворачивает к югу. Скорость течения при этом значительно увеличивается и в районе 30° ю. ш., по данным расчетов, достигает 30 *см/сек*.

Таким образом, материалы наблюдений показывают, что Западно-Австралийское течение в поверхностных слоях океана подвержено сезонной изменчивости. Если зимой северного полушария оно направлено на север, то летом это течение идет на юг, перенося теплые воды из тропической зоны в более высокие широты. Адвекция тепла Западно-Австралийским течением приводит к заметному нарушению широтной зональности в горизонтальном распределении температуры и появлению области с аномально высокими ее значениями западнее австралийского материка.

Для анализа глубинной циркуляции вод в рассматриваемом районе нами построены схемы течений на нескольких изобарических поверхностях, расположенных выше 2000 *м*. Результаты динамических расчетов, относящиеся к глубинным слоям, казалось бы, должны более правильно отражать реальную циркуляцию, чем подобные расчеты для поверхностных горизонтов. Однако по мере приближения к условной нулевой поверхности возрастает и относительная величина погрешности в определении динамических высот за счет негоризонтальности истинной нулевой поверхности. Другими словами, достоверность схем геострофических течений на изобарических поверхностях, достаточно близких к отсчетной поверхности, вызывает большое сомнение потому, что скорость течения на этих поверхностях имеет порядок, близкий к величине скорости на поверхности отсчета, которой мы пренебрегаем. Это общее соображение подтверждается и результатами инструментальных измерений течений на ряде буйковых станций. Поэтому мы ограничиваемся рассмотрением одной лишь схемы геострофической циркуляции на поверхности 500 *дбар*. Скорость течения на этой поверхности достаточно велика, условный выбор отсчетной поверхности не должен вносить значительных искажений в ее топографию.

Представление о вертикальной структуре течения дает разрез изотах по 77° в. д., пересекающий практически под прямым углом основные потоки в поверхностных и глубинных горизонтах.

Распределение скорости течения в районе экватора построено на разрезе по данным непосредственных наблюдений [13], так как динамический метод здесь не применим. В работе [13] показано, что в экваториальной зоне от 3° ю. ш. до 3° с. ш. Муссонное течение захватывает лишь верхний слой океана. Под основным стрежнем Муссонного потока имеет место мощное противотечение, распространяющееся на значительную глубину. Ядро глубинного экваториального противотечения располагается на глубине 700—800 *м*, при этом максимальная его скорость равняется примерно 60 *см/сек*. На рис. 12 видно, что даже на значительной глубине зональный перенос является преобладающим. При этом в отличие от поверхностных слоев зональные течения на глубине 500 *дбар* во всей области к югу от экватора имеют преимущественно западное направление. Лишь к северу от 2—3° с. ш. течение восточных румбов сохраняет свое направление до глубины отсчетной поверхности.

Таким образом, результаты динамических расчетов свидетельствуют о том, что в бароклинном слое восточной части Индийского океана летом северного полушария почти повсеместно, за исключением района Бенгальского залива и пассатной зоны, существует двухслойная горизонтальная циркуляция. Характерно, что и в районе к западу от Австралии движение вод на горизонте 500 *дбар* также имеет противоположное по отношению к поверхностному течению направление. По всей вероятности, через эту область происходит адвективный обмен между водами центральной части Индийского океана и субантарктической зоной, поскольку здесь во всей толще меридиональная компонента движения наиболее значительна. Совпадение наших данных с результатами изопикнического анализа [12] говорит о том, что в районе Западно-Австралийского течения на промежуточных глубинах адвекция субантарктических вод является стационарной по крайней мере во время одного сезона. Схемы течений показывают, что меридиональный перенос здесь наиболее выражен в относительно узкой вытянутой вдоль материка области. К западу от 112° в. д. величина меридиональной компоненты течения постепенно уменьшается и движение вод приобретает почти зональный характер.

ЗОНЫ РАЗДЕЛА ДИНАМИЧЕСКИХ И ТЕРМОХАЛИННЫХ СТРУКТУР

Понятие «гидрологический фронт», в отличие от фронта метеорологического, всякий раз нуждается в уточнении, поскольку во многих работах оно нередко имеет принципиально различное толкование. Едва ли всегда можно считать правильным встречающееся отождествление фронтов с зонами максимальных скоростей или районами дивергенций и конвергенций течений. Такое отождествление допустимо лишь в отдельных частях Мирового океана, обладающих определенными специфическими чертами гидрологического режима [14]. В общем случае гидрологическим фронтом можно называть относительно узкую зону, характеризующуюся наиболее значительными поперечными горизонтальными градиентами физико-химических элементов и разделяющую области с различными гидрологическими структурами. Таким образом, в пределах области с одной и той же структурой водных масс могут существовать несколько зон дивергенций и конвергенций, которые являются зонами раздела элементов циркуляционных систем [15].

При анализе расчетных схем течений для различных горизонтов в исследуемом районе удается однозначно выделить зоны смены направления течений, положение которых, как правило, совпадает с данными инструментальных наблюдений, позволяющими, кроме того, определить знак дивергенции горизонтальных потоков. Что же представляют собой эти зоны в динамическом отношении?

На схеме геострофической циркуляции на поверхности мы видим, что к югу от экватора зоны смены знака течений проходят по центральным областям отдельных, относительно замкнутых круговоротов. В этих областях горизонтальная составляющая скорости течения невелика и неопределенна по направлению, а вертикальная составляющая, по всей вероятности, достигает наибольшей величины. Интенсификация вертикальных движений в центральных областях отмеченных круговоротов отражается на элементах термоструктуры верхнего слоя воды. Например, карта толщины поверхностного изотермического слоя (H_0) позволяет наметить области подъема и опускания вод, полностью совпадающие с зонами дивергенции и конвергенции, которые определяются по схемам циркуляции.

Изменение температуры в промежуточных слоях часто имеет весьма сложный характер и выделить по ней зоны подъема или опускания с такой же определенностью, как это удается при анализе положения нижней границы поверхностного изотермического слоя, не представляется возможным. В равной степени это относится и к распределению солености.

Совместный анализ схем геострофических течений и элементов поверхностного изотермического слоя позволяет выделить следующие основные зоны восточной части Индийского океана в системе движения вод:

1) зона конвергенции между ветвью циркуляционной системы Бенгальского залива и Муссонным течением;

2) зона дивергенции между Муссонным и Пассатным течениями;

3) зона конвергенции на южной периферии Пассатного течения;

4) зона дивергенции на северной границе круговорота, расположенного северо-западнее Австралии.

Все эти зоны раздела динамических структур расположены в районах севернее 15° ю. ш., т. е. в той области, где они пересечены тремя основными разрезами 35-го рейса и/с «Витязь». Южнее этой широты количество данных незначительно, поэтому совместный анализ схем геострофических течений и карт элементов изотермического слоя затруднителен. Однако и здесь можно выделить зону конвергенции с нисходящими вертикальными движениями вод к югу от 30° ю. ш. На поверхности эта зона намечается лишь по увеличению глубины нижней границы изотермического слоя и по общей тенденции хода изолиний солености на разрезе по 91° в. д. На глубине 500 *м* зона конвергенции совпадает с границей между течениями противоположных направлений. Нужно отметить, что в данном случае увеличение толщины изотермического слоя не является достаточным основанием для определения зоны конвергенции, поскольку опускание поверхностных вод в этом районе может быть результатом зимнего охлаждения.

Вследствие значительного изменения системы горизонтальной циркуляции, по мере увеличения глубины, положение зон раздела динамических структур на горизонте 500 *м* существенно отличается от поверхностного слоя. Относительно неизменными остаются лишь зона дивергенции между южной ветвью муссонного потока и пассатным течением, направление которых мало изменяется с глубиной, и зона конвергенции в районе 12—15° ю. ш. на южной периферии Пассатного течения. Нужно отметить при этом, что определение знака вертикальных движений в зонах смены направления течений на глубине 500 *м* на основе наших материалов довольно затруднительно. На рис. 12 показаны границы между основными течениями на горизонте 500 *м*, причем знак дивергенции на этих границах определен приближенно по некоторым данным инструментальных наблюдений и по аналогии с классификацией подобных зон в поверхностном слое.

Исходя из подразделения всей восточной части океана на три области, резко различающиеся по своей термохалинной структуре, нами выделяются две основные фронтальные зоны. Их положение определяет зональные границы промежуточной области, расположенной между экваториальным и тропическим районами Индийского океана, о чем говорилось выше. Идущая в широтном направлении северная фронтальная зона располагается примерно на 7—8° ю. ш. в стрежне Пассатного течения на границе двух противоположно направленных региональных циркуляционных систем. Вторая, более южная зона, также имеющая относительно зональный характер, находится в области слабых течений восточного направления, проходя примерно вдоль 14—15° ю. ш.

Следует отметить, что подразделение восточной части океана на две обширные области с различной термохалинной структурой сохраняется в течение всего года. Это может объясняться тем, что, несмотря на значительные сезонные изменения в системе циркуляции вод в муссонной области, в районе отмеченных фронтальных зон поле течений в поверхностном слое остается относительно стационарным в течение года [10, 11]. В некоторых работах [9, 7] зоне раздела тропической и экваториальной структур водных масс, представляющей собой значительную по площади зональную область со специфическими термохалинными характеристиками, неправильно придается значение единой фронтальной зоны. Относительно низкая соленость во всей вертикальной толще вод промежуточной области не позволяет отождествлять ее с зоной трансформации — обязательным признаком фронтального раздела. К сожалению, приходится, однако, признать, что любой анализ зон раздела динамических и термохалинных структур, основанный на материалах стандартных гидрологических съемок, пока еще далек от совершенства. Решение этого важного в практическом и научном отношении вопроса требует дальнейших усилий по проведению специальных наблюдений. В связи со сложностью массовых наблюдений над течениями особенно следует обратить внимание на подробное изучение термической структуры поверхностных вод при помощи различных зондов, которые позволяют определить характерные особенности динамики вод рассматриваемого района и выделить основные зоны вертикальных движений в тропических и экваториальных районах океана.

ABSTRACT

Hydrographic data carried out on board r/v «Vitjaz» in July — October 1962 were analyzed. It is shown that the current pattern is connected with monsoon and trade winds and determines the main features of distribution of hydrological elements.

On base of dynamical computations it is concluded that the water circulation in baroclinic layer of the ocean corresponds to two-layer model.

It is noted that the topography of the upper isotermal layer is in well agreement with the dynamical topography of ocean surface. Zones of divergences and convergences as well as the boundaries of the regions with different hydrological structure are determined.

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ГИДРОЛОГИЧЕСКИЕ УСЛОВИЯ В КРАСНОМ МОРЕ И АДЕНСКОМ ЗАЛИВЕ ПО НАБЛЮДЕНИЯМ Э/С «АКАДЕМИК А. КОВАЛЕВСКИЙ»

Гидрологический режим Красного моря и Аденского залива изучен значительно меньше по сравнению со Средиземным морем. Только в течение последнего десятилетия, в связи с общим развитием океанографических исследований и, в частности, с международными работами по изучению тропических морей и Индийского океана, начались систематические океанографические работы в этих районах.

Относительно полные гидрологические данные в Красном море и Аденском заливе были получены в экспедициях John Murray в сентябре 1933 г., в мае 1934 г. [1, 2] и в египетской — в северной части Красного моря [3]. Более ранние экспедиции (Natterer [4], Pola [5], Vercelly [6, 7], Picotti [8]) носили преимущественно рекогносцировочный характер. Эпизодические наблюдения на отдельных станциях в Красном море и Аденском заливе в разные годы были выполнены э/с «Albatros», «Snellius», «Discovery II» и шведской глубоководной экспедицией [9].

Более подробные исследования в Красном море и Аденском заливе проведены в период Международного геофизического года американскими научно-исследовательскими судами «Atlantic» (рейс 242) и «Vema», сделавшими здесь в мае-июне 1958 г. около 50 глубоководных гидрологических станций [10].

Начало широкого океанографического изучения Красного моря и Аденского залива советскими исследователями было положено экспедицией Гидрометеослужбы СССР на э/с «А. И. Воейков» [11], сделавшем в сентябре1959 г. десять глубоководных станций на оси впадины Красного моря, две станции в Баб-эль-Мандебском проливе и шесть — вдоль продольной оси Аденского залива. На тех же станциях были проведены повторные наблюдения на э/с «Ю. М. Шокальский» в начале июля 1960 г. [12].

Комплексные гидрологические и биологические исследования Красного моря и Аденского залива были начаты Институтом биологии южных морей АН УССР в декабре-январе 1961/62 г., и были повторены по той же программе в октябре-ноябре 1963 г. Во время этих экспедиций в Красном море выполнено 50 стандартных и 4 суточных станции с наблюдениями над температурой, соленостью, кислородом, фосфатами и полным комплексом биологических наблюдений. Из 50 стандартных станций 15 сделаны в январе 1962 г. и 35 в октябре и в начале ноября 1963 г.

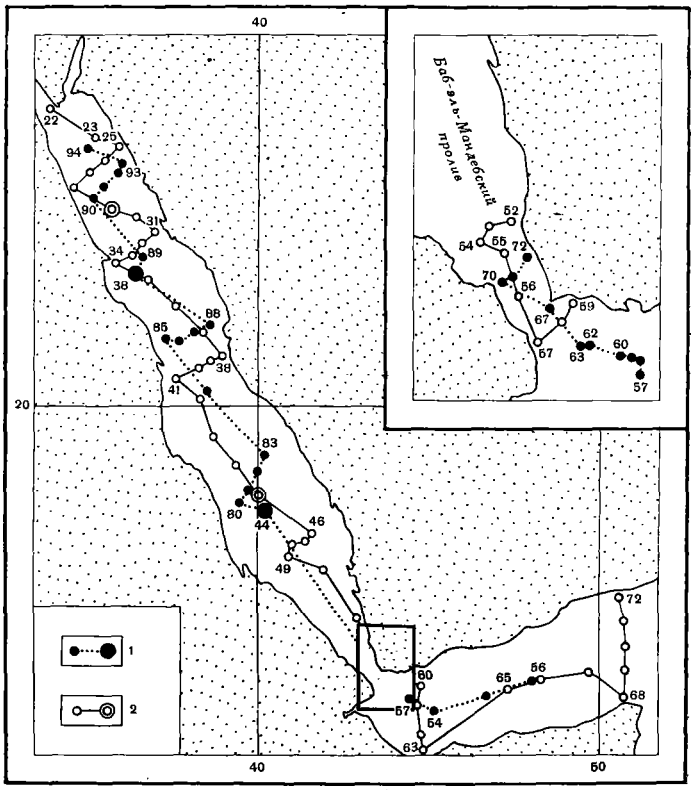

Рис. 1. Схема расположения гидрологических станций, выполненных на *э/с* «Академик А. Ковалевский» в декабре 1961 — 1962 гг. и октябре-ноябре 1963 г.

1 — сут. ст 3.XII 1961 г.— 3.II 1962 г.; *2* — сут. ст. 28.X — 12.XI 1963 г.

Были проведены отдельные наблюдения над течениями в Баб-эль-Мандебском проливе на пяти якорных станциях. Три из них были расположены в самой мелководной части со стороны Красного моря (Томсон считает, что этот мелководный район определяет водообмен через пролив), две станции — вблизи пролива со стороны Аденского залива. В самой узкой части пролива течение из-за интенсивного движения судов не измерялось. Стандартных гидрологических станций в Баб-эль-Мандебском проливе и на предпроливном участке Аденского залива было сделано 15, из них 7 — в январе 1962 г. и 8 — в начале ноября 1963 г. В открытой части Аденского залива было сделано 25 гидрологических станций, 7 из них — в январе 1962 г. и 18 — в ноябре 1963 г. Схема расположения гидрологических станций, выполненных э/с «Академик А. Ковалевский» зимой 1961/62 г. и поздней осенью 1963 г., представлена на рис. 1.

В течение 1963 г. в Красном море и Аденском заливе работало поисковое судно «Владимир Воробьев» [13] Азово-Черноморского института рыбного хозяйства и океанографии. Наряду с поисковыми работами проводились океанологические наблюдения.

Таким образом, к настоящему времени накопилось значительное количество океанографических данных по Красному морю и Аденскому заливу, позволяющих глубже раскрыть особенности режима этих бассейнов и их влияние на формирование промежуточных слоев Индийского океана.

Основная задача гидрологических исследований Красного моря и Аденского залива, производимых Институтом биологии южных морей АН УССР, состояла в получении гидрологического фона, необходимого

для изучения биологической структуры и продуктивности этих морей. Наряду с характеристикой условий обитания растительного и животного планктона, гидрологические наблюдения, выполненные в осенний и зимний периоды, позволяют осветить некоторые вопросы гидрологии этих бассейнов: 1) состояние водных масс, их устойчивость в период зимнего охлаждения и формирования глубинных вод; 2) поступление и трансформация аденских вод в Красном море и красноморских вод в Аденском заливе в период охлаждения, поскольку зимних наблюдений немного; 3) сбор дополнительных сведений по водообмену через Суэцкий канал и Баб-эль-Мандебский пролив; 4) уточнение роли водообмена через пролив в формировании гидрологического режима этих бассейнов.

СУЭЦКИЙ КАНАЛ

Длина Суэцкого канала составляет примерно 150 *км*, его ширина 130 *м* и глубина 13 *м*. В средней части канал проходит через ряд соленых озер, наибольшие из которых Большое и Малое Горькие озера. Высокая соленость озер (44—48‰) обусловливается отсутствием притока пресных вод, малым выпаданием осадков, интенсивным испарением с поверхности озер и вымыванием солей из грунта. Воды канала, проходя через озера, значительно осолоняются, поэтому их соленость оказывается намного выше солености прилегающих к каналу районов Средиземного и Красного морей.

Осолоняющее воздействие озер дает возможность по характеру распределения солености вдоль канала установить господствующий в период наблюдения перенос воды через канал. В целях выяснения направления движения воды по каналу, по ходу движения судна в Красное море и на обратном пути каждые полчаса проводились наблюдения за температурой и соленостью поверхностной воды. По пути в Красное море 10—11 октября 1963 г. было проведено 90 поверхностных наблюдений, на обратном пути 30 ноября — 54 наблюдения.

В октябре соленость воды в Суэцком канале резко увеличивалась с севера на юг. Так, вблизи внешнего мола Порт-Саида она составляла 33,08‰, на расстоянии 6,7 *км* от Средиземного моря — 37,01‰, а в 13,5 *км* от него соленость поверхностной воды увеличилась до 44,00‰. Максимальная соленость на поверхности наблюдалась в северной части Большого Горького озера — 48,00‰. В южной части озера максимальная соленость была 45,18‰. В этом районе корабль стоял на якоре в течение пяти часов. Во время стоянки проводились ежечасные наблюдения в поверхностном слое воды за температурой и соленостью, а также была выполнена одна гидрологическая станция. При 9-метровой общей глубине места проведены наблюдения на 0,3, 5 и 8,75 *м*; прослеживались существенные изменения солености как во времени в поверхностном слое — от 45,18 до 44,48‰, так и по вертикали — от 44,67 на поверхности до 47,88‰ на глубине 8,75 *м*.

В Малом Горьком озере соленость на поверхности была на 3,0‰ ниже, чем в Большом Горьком озере, т. е. 45,02‰. При выходе из Малого Горького озера соленость быстро уменьшалась до 43,38‰ на расстоянии 5,5 *км* от озера и до 42,65‰ на выходе в Суэцкий канал.

Температура воды по каналу изменялась незначительно: в октябре от 27,1°, в северном конце канала до 26,0°— в южном, в последних числах ноября 1963 г. на концах канала температура была соответственно 21,4—21,0°, в средней части 20,3—20,8°. В осенний период плотность воды в канале была на 2,82 условных единицы больше, чем в северном районе Красного моря. Поэтому при отливе, когда воды из канала попадают в Красное море, они опускаются в природные горизонты, и во время следующего прилива в канал поступает поверхностная вода Красного моря.

Соленость воды в канале в конце ноября 1963 г. была значительно меньше, чем в первой половине октября того же года, и меньше, чем в июле 1960 г. Так, максимальная соленость в северной части Большого Горького озера в июле составляла 45,67‰, в то время как в начале октября она достигала 48,00‰. Напротив, в северном конце канала соленость на поверхности несколько превышала норму октября: в 6,1 *км* от Средиземного моря она была 39,94‰ вместо 37,01‰, а вблизи внешнего мола Порт-Саида — 36,85‰ вместо 33,08‰, наблюдавшейся в октябре.

Более плавное увеличение солености в южном конце канала и более резкое в северном указывает на течение из Красного моря в Средиземное. При этом, исходя из распределения солености вдоль канала, течение в конце ноября было более сильным. Вместе с тем по величине наклона бакенов в ноябре течение в северной половине канала было слабее, чем в южной его половине. Ослабление течения в северном конце канала, вероятно, обусловлено не только усилением северо-западного ветра, начавшегося с середины канала, но и приливом.

Как известно, амплитуда колебания приливного уровня в Порт-Саиде составляет всего 15—40 *см*, в то время как в Суэце она достигает величины 1,6—2,0 *м*, т. е. на концах канала происходят значительные колебания уровня. Приливы в Красном море имеют преимущественно полусуточный характер. Поэтому в Суэцком канале течение 2 раза в сутки меняет свое направление, причем северные течения более интенсивны, так как средний уровень Красного моря, как указывают Кларк и Гохар [14], выше Средиземного. Кроме того, течение в канале зависит от прилива, от силы и направления ветра и от разности плотностей в озерах и в прилегающих участках Красного и Средиземного морей. А. М. Муромцев [15] считает, что на положение уровня у северного входа в канал (залив Диба) решающее влияние оказывает сток Нила, паводковые воды которого занимают прибрежное мелководье и повышают уровень у северного входа в канал, создавая сильное распреснение в этом районе. Такие условия А. М. Муромцевым были отмечены в сентябре 1959 г. [11], когда в канале наблюдалось южное течение. В начале июля 1960 г. течение в канале было северным [12].

Ветровые колебания уровня у северного входа в канал оказывают существенное влияние на направление и скорость течения. Сильные ветры северной четверти являются нагонными для присуэцкого района Средиземного моря, ветры южной четверти — сгонными. Однако направление и скорость течения в канале в конкретный момент, как уже отмечалось, определяются и фазой прилива.

СУЭЦКИЙ ЗАЛИВ

На юге канал входит в Суэцкую бухту, расположенную в северо-восточной части Суэцкого залива. Последний представляет собой узкий мелководный и очень вытянутый в направлении с юго-юго-востока на северо-северо-запад залив. Его длина равна примерно 325 *км*, ширина сужается с юго-востока на северо-запад от 46 до 15 *км*, максимальная глубина 80 *м*. Гидрологический режим залива определяется географическим положением, малыми глубинами, отсутствием пресного стока, большим испарением, водообменом с солеными озерами через Суэцкий канал и водообменом с северным районом Красного моря. Минимальная температура отмечается в феврале (18,0—18,5°), максимальная — в августе-сентябре (26,5—28,5°).

Соленость в Суэцком заливе, по наблюдениям э/с «Академик А. Ковалевский», в первой половине октября 1963 г. заметно уменьшалась по

направлению с севера на юг от 42,63 до 40,89‰, а в конце ноября — 42,25 до 40,27‰, т. е. соленость поверхностных вод в ноябре была на 0,4—0,6‰ меньше, чем в октябре. что, вероятно, связано с усилением оттока поверхностных вод залива через Суэцкий канал в Средиземное море. Устойчивый ветер северо-восточного направления в ноябре 1963 г. в Аденском заливе и юго-восточного в южной части Красного моря сопровождался увеличением притока аденских вод в Красное море и повышением его уровня, что в свою очередь вызвало усиление течения из Красного моря в Средиземное.

Температура воды на поверхности в Суэцком заливе увеличивалась с севера на юг от 26 до 28° в начале октября и от 21,8 до 25,3° в конце ноября. За 49 суток температура в северном районе залива понизилась на 4,2°, а в южном — на 1,5°. Кроме того, во время стоянки корабля на якоре на расстоянии километра от волнореза были проведены две серии наблюдений на горизонтах 0, 3 и 6 *м* при общей глубине места 6,5 *м*. По всей глубине температуры и соленость были почти однородны (21,8—21,0° и 42,38—42,45‰). Отмеченное спустя 3 часа изменение солености на 0,24‰ как на поверхности, так и на глубине определяется приливным течением.

КРАСНОЕ МОРЕ

Красное море располагается между Аравийским полуостровом и северо-восточным берегом Африки. Оно вытянуто с юго-юго-востока на северо-северо-запад от 12°40′ до 30° с. ш. Длина его равна 1932 *км*, наибольшая ширина 305 *км*. Площадь поверхности моря составляет 450 тыс. *км*^{2}, объем — 251 тыс. *км*^{3}. За пределами узкой материковой отмели со множеством коралловых рифов отмечаются глубины до 700 *м*. Вдоль большой оси Красного моря простирается ложбина, глубина которой в отдельных местах превышает 2000 *м*. Наибольшая глубина 2604 *м* располагается почти в центральной части моря. Большие глубины разделяются поднятием дна до 900 *м* на широте примерно 23° 30′. На юге перед Баб-эль-Мандебским проливом глубоководная ложбина замыкается поднятием дна до 125 *м*. На севере поднятие дна (до 300 *м*) отделяет Красное море от глубоководного залива Акаба.

Гидрологический режим Красного моря формируется под влиянием жаркого и сухого климата и водообмена с соседними морями. На юге через Баб-эль-Мандебский пролив, площадь сечения которого в самом узком месте равна 2,72 *км*^{2}, осуществляется водообмен с Аденским заливом, на севере через Суэцкий канал Красное море соединяется с солеными озерами и Средиземным морем.

Баб-эль-Мандебский пролив играет в режиме Красного моря такую же роль, какую Гибралтарский пролив играет в режиме Средиземного. Через него поступают менее соленые воды Аденского залива (36,51‰), компенсируя потерю воды на испарение и отток соленых более плотных вод придонным течением пролива. На малых глубинах порога (125 *м*) перед Баб-эль-Мандебским проливом водообмен между Красным морем и Аденским заливом ограничен лишь верхними слоями. Глубинные воды Аденского залива с низкой температурой и соленостью в Красное море не проникают, и режим глубинных вод Красного моря определяется только условиями зимнего конвекционного перемешивания в северной части моря. Поэтому вся глубинная часть Красного моря заполнена водой с очень высокой температурой (21°,5) и соленостью (40,5‰). Ни в одном из других морей Мирового океана на соответствующих глубинах таких высоких значений температур и солености не встречается.

Входящие в море менее соленые аденские воды распресняют поверхностные слои Красного моря. Аденские воды под воздействием

разности уровней постепенно перемещаются на север. Однако это движение распресненных вод на север несколько затушевывается ветровыми и приливными течениями.

Ветер над Красным морем имеет хорошо выраженный муссонный характер, поэтому и ветровое течение меняется с сезонной периодичностью. В летний период (с мая по сентябрь) над Красным морем господствуют ветры северо-северо-западных направлений, кроме того, в поверхностном слое с направлением ветра совпадает горизонтальный градиент солености и плотности. Поэтому поверхностное течение, прижимаясь к африканскому берегу, направлено на юг при незначительном противотечении вдоль восточного берега.

Потеря воды на испарение и отток поверхностных вод с севера на юг под воздействием ветра, вероятно, компенсируется движением вод промежуточного слоя (200—500 *м*) в обратном направлении, т. е. с юга на север. Такая схема течения налагает отпечаток на вертикальное и горизонтально распределения температуры, солености, кислорода и других гидрологических и гидрохимических характеристик.

В зимний период (с октября по апрель) над северной половиной Красного моря господствуют те же северо-северо-западные ветры, южная же половина моря (примерно до широты 20°) находится под воздействием юго-юго-восточных ветров. В это время года система течений в Красном море более сложная. В поверхностном слое под действием преобладающих ветров, вероятно, возникают два циклонических круговорота в северном и южном районах моря с границей между ними на широте 22—25°. Можно полагать, что более сильное течение в северной половине моря будет наблюдаться у африканского берега, в южной — у аравийского. В соответствии с этим под влиянием поперечной составляющей течения на севере скопление поверхностных вод будет у африканского берега, на юге — у аравийского.

Распределение температуры и солености вдоль Красного моря тесно связано с поступлением менее соленых аденских вод, их трансформацией и распределением в зависимости от течения. Толщина слоя распресненных вод не остается постоянной как по площади, так и во времени. По направлению с юга на север она уменьшается от 100—125 *м* на юге до 50—60 *м* в средней части моря. На севере (ст. 27, 28) аденская вода прослеживалась по промежуточному минимуму солености на глубине 50—75 *м*, подобно тому как атлантическая вода — в восточной половине Средиземного моря.

По пути движения с юга на север аденские воды осолоняются за счет интенсивного испарения и перемешивания с более солеными поверхностными водами северного района Красного моря. Кроме того, некоторое влияние на повышение солености поверхностных вод оказывает водообмен между морем и более солеными заливами Суэцким и Акабо. Соленые воды, поступающие из заливов, прослеживались в середине октября в северном районе моря в виде небольшой прослойки, вклинившейся в распресненные аденские воды (ст. 27—29, 33). В декабре и январе 1961—1962 гг. небольшой слой воды с несколько повышенной температурой и соленостью отмечался также и в южном районе моря (ст. 44 и 82). Вертикальное распределение температуры, солености и *TS*-диаграммы для этих станций даны на рис. 2. Толщина слоя более соленых вод была небольшой, однако она довольно устойчиво сохранялась и прослеживалась в декабре-январе 1961—1962 гг. и в октябре 1963 г.

В теплую половину года осолоненные воды высокой температуры растекаются по промежуточному слою от 25 до 75 *м*, в зависимости от их плотности и характера течений. В холодное время года температура воды в наиболее северных районах моря (заливы Суэцкий и Акабо) понижается до 18,5—21,0° при солености 41—42‰. Поскольку плотность вод

в заливах на две-три условные единицы больше плотности поверхностных вод Красного моря, то они, попадая в море, заглубляются. По пути движения они перемешиваются с менее соленой и более теплой красноморской водой, усиливая процесс образования глубинной воды с температурой 21,68—21,80° и соленостью 40,5—40,6‰.

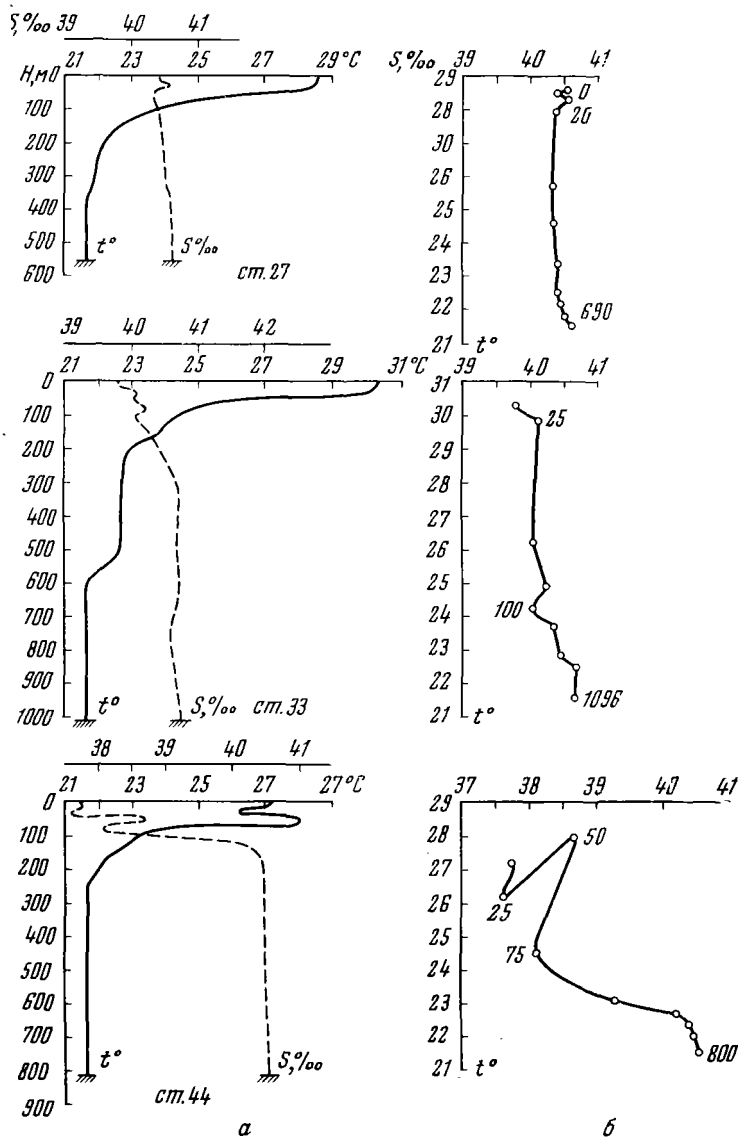

Рис. 2. Вертикальное распределение температуры, солености (*а*) и *TS*-кривые (*б*) для северного района Красного моря

В Красном море в октябре 1963 г. более высокая температура воды отмечалась в его средней части (31,6—32,4°), а по направлению к северу и к югу температура уменьшалась до 28,0°. Соленость воды на поверхности моря уменьшалась по направлению с севера на юг с 40,48‰ (ст. 27) до 36,51‰ в Баб-эль-Мандебском проливе. В январе 1962 г. температура в поверхностном слое понизилась в северном районе моря до 22,64°, в южном — до 26,50°. Соленость с севера на юг уменьшалась от 40,52 до 36,13‰.

Вертикальное распределение температуры и солености на поперечных разрезах для северного, среднего и южного районов Красного моря по наблюдениям э/с «Академик А. Ковалевский» в октябре 1963 г. и январе 1962 г. дано на рис. 3 и 4. Отмечается заметное различие не только в абсолютных величинах температуры и солености, но и в распределении

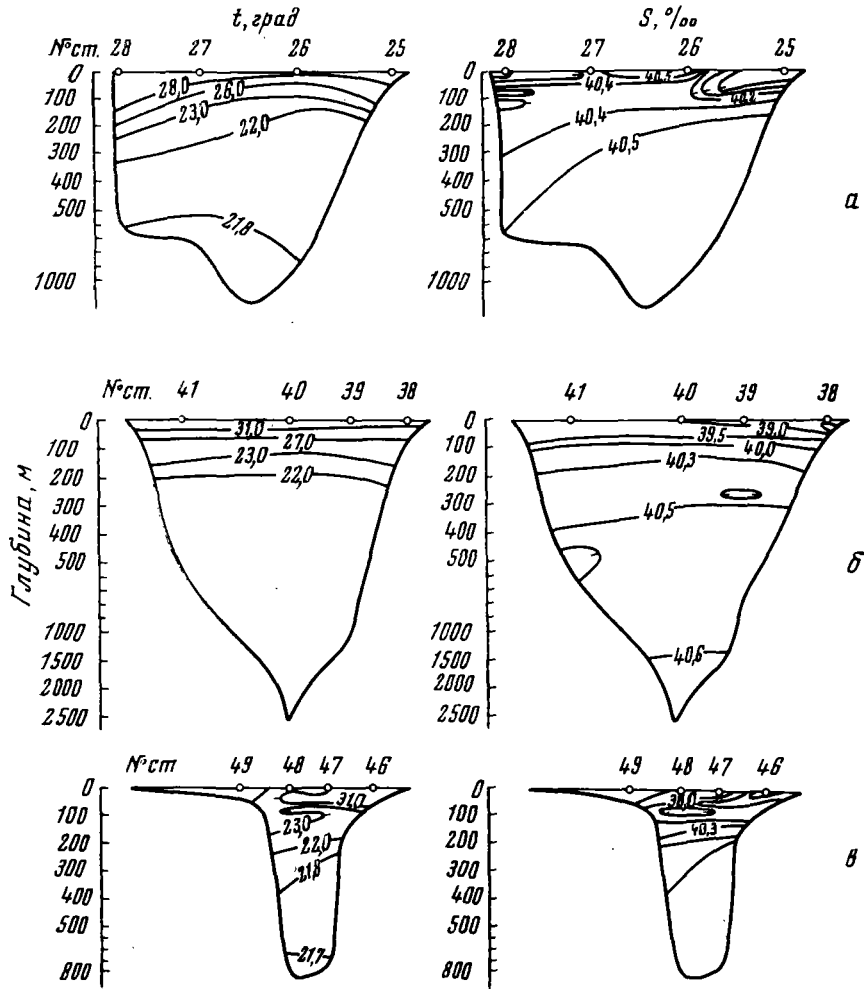

Рис. 3. Вертикальное распределение температуры, солености на поперечных разрезах северного (*а*), среднего (*б*) и южного (*в*) районов Красного моря (октябрь 1963 г.)

этих характеристик на поперечных сечениях. Так, на северном (рис. 3, *а*) наиболее теплые и распресненные воды располагались у аравийского берега как в октябре 1963 г., так и в январе 1962 г. Однако в октябре отмечалось большее распреснение по сравнению с январем 1962 г. (39,84 и 40,34‰ соответственно). Воды с пониженной соленостью в обоих случаях отмечались по всему поперечному сечению. Только в октябре у аравийского берега распресненные воды располагались в поверхностном слое, по направлению к западу они опустились до 80 *м*, в то время как в январе 1962 г. минимальные солености отмечались по всему сечению в поверхностном слое. Температура воды на поверхности по направлению к западному берегу в октябре и январе понижалась с 29,8 до 28,5° и с 23,03 до 22,42°.

В средней части моря в октябре изотермы и изохалины располагались по всему сечению почти горизонтально. В январе 1962 г. температура от восточного берега к западному уменьшилась (от 25,24 до 24,46°), а соленость в этом же направлении увеличилась (с 39,13 до 39,76‰). В ходе изолиний отмечался изгиб, характерный для циклонической системы течений, с центром, расположенным, по-видимому, ближе к африканскому берегу (ст. 86).

Южные поперечные разрезы расположены на разных расстояниях от Баб-эль-Мандебского пролива (в октябре — 44 *км*, в январе — 72 *км*).

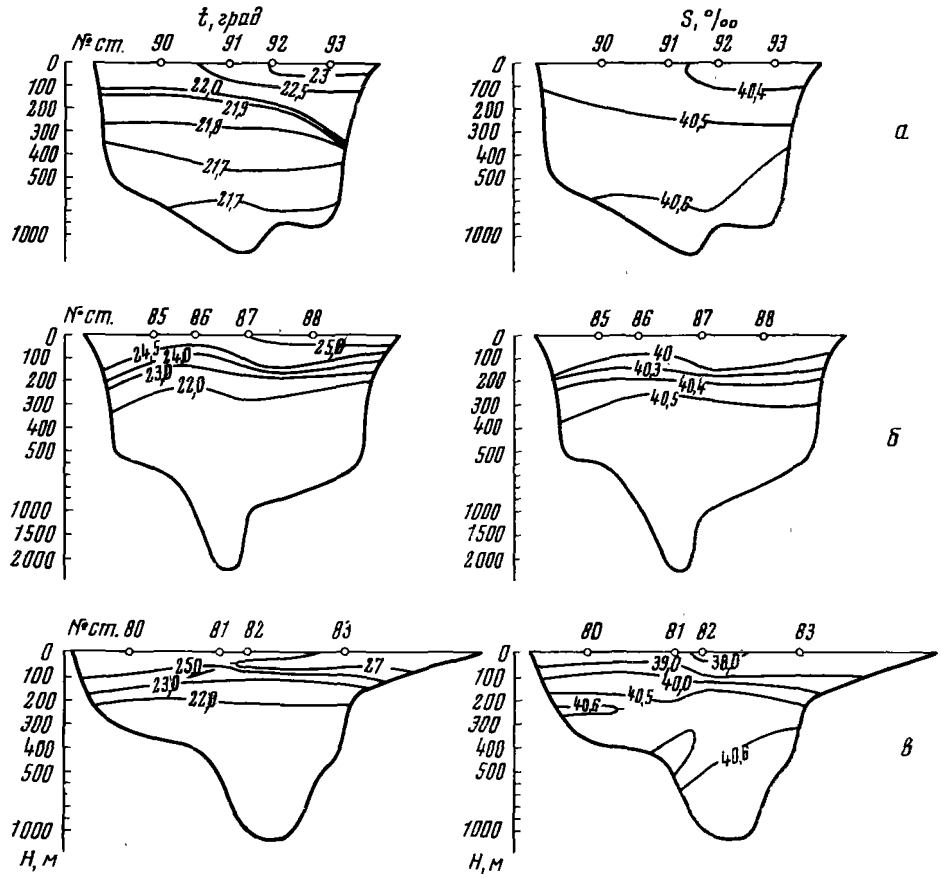

Рис. 4. Вертикальное распределение температуры, солености на поперечных разрезах северного (*а*), среднего (*б*) и южного (*в*) районов Красного моря (январь 1962 г.)

Наибольшее распреснение (37,22‰) отмечалось в октябре у африканского берега и в январе (38,30‰) — у аравийского. Более высокие температуры — 31,84 и 27,13° — в обоих случаях наблюдались у аравийского берега, что указывает на перемещение аденских вод вдоль восточного берега.

Ход изолиний в верхних слоях различен. В октябре отмечалась значительная переслоенность вод по температуре и солености, указывающая на довольно сложную систему течений в этот период. Минимальные значения указанных характеристик (21,46° и 36,92‰) наблюдались на глубине 90 *м*; на глубине 50 *м* температура и соленость соответственно повышаются (31,49° и 38,17‰), а в поверхностном слое вновь понижаются (30,5° и 37,53‰).

Распресненные и относительно холодные воды промежуточного слоя принадлежат промежуточным водам Аденского залива. Они могут поступать в Красное море, вероятно, только при сильных северо-северо-западных ветрах, при которых на юге Красного моря создается нагон поверхностных вод и отток их в Аденский залив. Тот же ветер в предпроливном участке Аденского залива вызывает сгон поверхностных вод и подъем более глубинных, поэтому создаются условия для проникновения в Красное море распресненных, более холодных и богатых питательными солями аденских вод. Эти воды, двигаясь на север, постепенно опускаются благодаря уплотнению при смешении их с солеными и теплыми красноморскими водами [16].

Проникновение аденских вод на глубину 250—400 *м* ранее исследователями не отмечалось. Во время экспедиций на э/с «Академик А. Ковалевский» аденские воды прослеживались по понижению солености и температуры не только в южном районе моря, но и на севере (рис. 5). Возможно, обилие планктонных организмов в этих слоях, на которое указывал Кусто, и повышение количества геторотрофных бактерий, по данным М. Н. Лебедевой [17] для зимы 1962 г., связаны с поступлением в промежуточные слои аденских вод, более богатых фосфатами. Опускание аденских вод на эти глубины возможно только при сильных северо-северо-западных ветрах, когда в вершине Аденского залива наблюдается сгон поверхностных вод и подъем глубинных. В такие моменты в Красное море поступают воды промежуточного слоя Аденского залива (с глубины 100—150 *м*) с несколько пониженной температурой и соленостью, но с более высоким содержанием биогенных солей. Они опускаются в соответствии с их плотностью на глубины с 250 до 400 *м*. Некоторое распреснение промежуточных слоев отмечалось на глубинах от 90 до 250—400 *м* как в январе 1962 г., так и в октябре 1963 г. не только в южном, но в центральном и даже северном районах Красного моря. Так, в декабре-январе 1961—1962 гг. аденские воды прослеживались в южном и северном районах Красного моря на глубинах 300—400 *м* (ст. 38, 81), в октябре 1963 г. — в южном и центральном районах на глубине 90—300 *м* (ст. 39, 48).

Теплые и соленые воды северного района Красного моря, перемещаясь к югу, в зависимости от величины солености и температуры, растекаются по поверхности менее соленых аденских вод или погружаются в промежуточные слои в соответствии с их плотностью. Так, на самом южном разрезе (ст. 46—49) в октябре 1963 г. они заглублялись до 80 *м* у западного берега.

Изменение температуры по вертикали характеризуется довольно монотонным убыванием с 28—32° на поверхности до 22,5—23,0° на глубине 100—150 *м*. Глубже 250—300 *м* температура по всей толще воды остается по существу одинаковой — 21,6—21°,7, с небольшим повышением глубже 1000 *м* за счет адиабатического нагрева.

В вертикальном распределении солености характерным является резкое нарастание солености на глубине 90—125 *м* в зоне смешения аденских вод с красноморскими. В южной части моря, куда непрерывно поступают аденские воды с меньшей соленостью, отмечается наиболее резкий скачок плотности, что затрудняет обмен поверхностных вод с промежуточными слоями. По направлению на север, по мере увеличения солености в поверхностном слое, градиент плотности в слое смешения аденских вод с красноморскими уменьшается, а следовательно, увеличивается вертикальное перемешивание.

В октябре 1963 г. в северном районе Красного моря наблюдалась однородность в вертикальном распределении солености, что создавало благоприятные условия для перемешивания при незначительном понижении температуры воды на поверхности. В январе 1962 г. плотность воды в

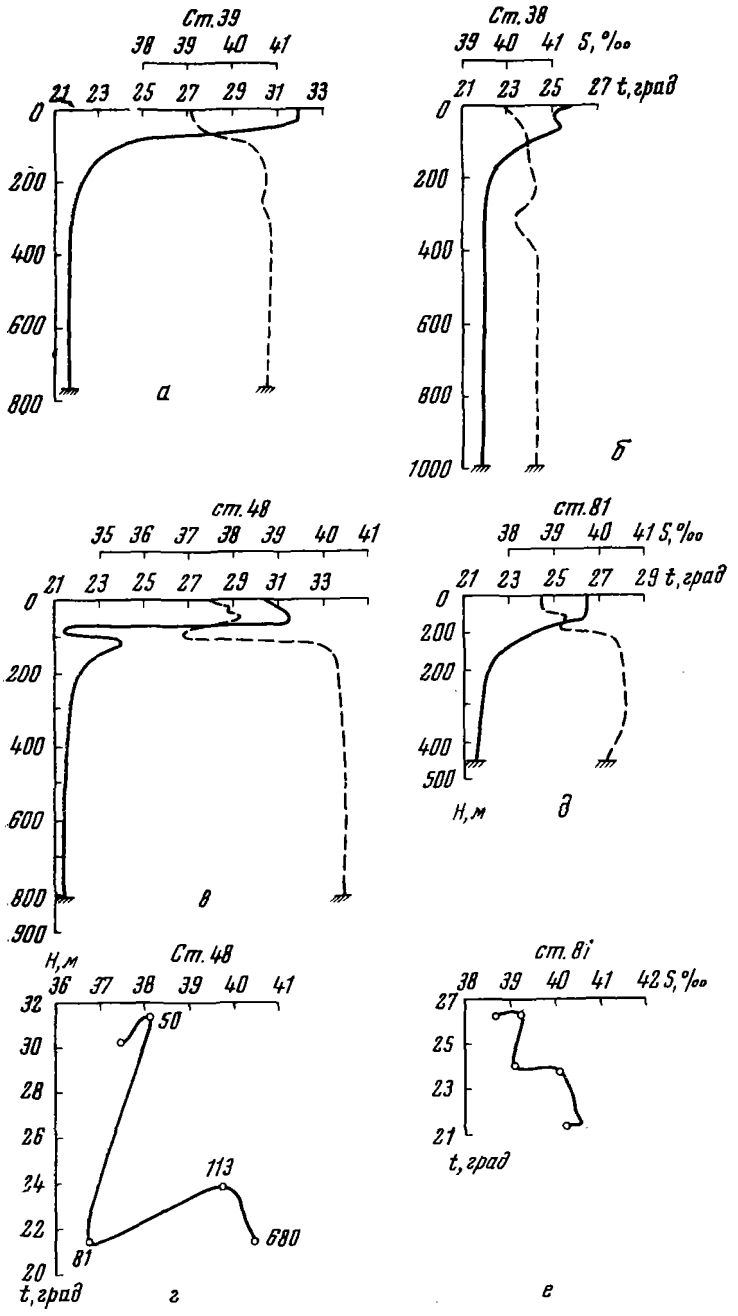

Рис. 5. Вертикальное распределение температуры, солености и TS-кривые

а, б — в средней части Красного моря; *в—е* — в южной части

северном районе моря была близка к плотности глубинных вод Красного моря (28, 26 условных единиц). В этих условиях достаточно понижения температуры воды в поверхностном слое на 1°, чтобы вызвать ее перемешивание в этом районе до дна. Кроме того, в зимнее время из Суэцкого залива и залива Акабо поступают более холодные и соленые воды, которые ускоряют процесс перемешивания и формирования глубинных вод Красного моря. В конце ноября 1963 г. плотность вод Суэцкого залива (30,08 условных единиц) превышала таковую красноморской в северном районе моря на 1,8 условных единиц. Эти воды, попадая в Красное море в холодное время года, когда их температура несколько ниже, чем в северном районе Красного моря, заглубляются и, перемешиваясь с более теплой красноморской водой, ускоряют начало формирования глубинных вод.

Наличие значительного градиента плотности на глубинах 90—125 *м* затрудняет перемешивание верхнего 100—150-метрового слоя воды с нижележащими водами. Поскольку скачок плотности расположен глубже зоны фотосинтеза, а в слое скачка резко снижается вертикальное перемешивание, то естественно затрудняется подача кислорода из продуцируемого слоя в более глубокие горизонты.

Многие исследователи указывают на существование в Красном море минимума кислорода в промежуточном слое (300—500 *м*), причем его количество в этом слое увеличивается по направлению с юга на север. В работах А. М. Муромцева [11, 12] также указывается на наличие слоя минимума кислорода и на увеличение его содержания от 0,54—0,70 *мл/л* у Баб-эль-Мандебского пролива до 0,80—1,34 *мл/л* в северной части Красного моря. Это увеличение кислорода Муромцев связывает с промежуточным северным течением, компенсирующим отток на юг глубинных вод, формирующихся на севере. Однако само движение промежуточных вод на север еще не объясняет возрастания кислорода в водах этого течения, поскольку время пребывания их в промежуточных слоях возрастает по направлению движения, т. е. с юга на север. На наш взгляд, увеличение кислорода в промежуточном слое определяется не фактом самого течения, а тем, что на севере наблюдается уменьшение градиента плотности на стыке поверхностных и промежуточных вод, что сопровождается более интенсивным их перемешиванием по вертикали, а следовательно, и поступлением кислорода из зоны фотосинтеза в глубины моря.

Относительно малые величины кислорода (3,96—3,98 *мл/л*) в поверхностном слое Красного моря обусловлены высокой температурой и соленостью, уменьшающей растворимость кислорода морской водой. Вследствие этого увеличивается отдача избытка кислорода, продуцируемого планктоном, в атмосферу.

Значительное содержание кислорода (свыше 2,0 *мл/л*) на глубинах более 800 *м* указывает на довольно быстрое обновление глубинных вод Красного моря. Промежуточные воды (на глубине 250—500 *м*) обновляются значительно медленнее: здесь содержание кислорода уменьшается до 0,52 и 0,90 *мл/л* соответственно в южной и средней частях моря и до 1,30 *мл/л* в его северной части. Однако отмеченное А. М. Муромцевым [11] значительное увеличение солености во всей толще вод Красного моря в течение нескольких месяцев нам представляется недостаточно убедительным. Так, если допустить, что соленость в толще вод Красного моря с июня 1958 г. [10] по сентябрь 1959 г. [11] изменилась с 40,5—40,6 до 42,13—42,37 ‰, то это означает, что за зиму 1958/59 г. произошло почти полное обновление глубинных вод Красного моря. То же самое должно было произойти с сентября 1959 по июль 1960 г., когда соленость вновь уменьшилась с 42,13—42,37 до 40,40—40,53 ‰. Однако А. М. Муромцев [11] считает возможным такое быстрое обновление глу-

бинных вод за счет исключительно высокого испарения с поверхности моря в 1959 г.

Поскольку величина осадков и речного стока для Красного моря очень мала, то потеря воды на испарение восполняется в основном поступлением менее соленых вод из Аденского залива. Если допустить, что из Красного моря соленые воды в 1959 г. через пролив совсем не вытекали, а из Аденского залива поступило лишь то количество воды, которое потеряно на испарение (1869 *км*^{3}), то и в этом случае соленость вод Красного моря не могла бы увеличиться на 1,63—1,77‰, как это видно из уравнения солевого баланса. Если за начальную величину принять соленость 40,5‰, наблюдавшуюся в июле 1958 г. Нейманом и Мак Гиллом [10], то уравнение солевого баланса без учета стока в Аденский залив запишется в виде

$$VS_{58} + Q_{59}S_A = VS_{59};\ S_{59} = \frac{VS_{58} + Q_{59}S_A}{V},$$

где V — объем вод Красного моря; Q_{59} — величина испарения за год в *км*^{3}; S_{58}, S_{59}, S_A — соленость вод Красного моря по наблюдениям в 1958, 1959 гг. и поступающей воды из Аденского залива. В данном уравнении не учитывается потеря солей на водообмен с Аденским заливом, хотя известно, что сток красноморских вод в Аденский залив довольно значительный. Красноморские воды прослеживаются не только по всему Аденскому заливу, но и в Индийском океане, где они формируют особую промежуточную водную массу.

Даже такой грубый подсчет показывает, что соленость Красного моря могла бы повыситься при данном испарении всего на 0,2‰, т. е. была бы равна 40,7‰.

Повышение солености вод Красного моря до 42,25‰ (при том же допущении — отсутствии оттока красноморских вод в Аденский залив) могло бы произойти лишь при увеличении испарения до 26,8 *м/год*. Если же учесть двухсторонний водообмен через Баб-эль-Мандебский пролив, при котором часть солей Красного моря выносится в Аденский залив, то испарение должно было быть еще большим.

Таким образом, «осолонение» Красного моря в 1959 г. могло бы произойти только за счет невероятно большого испарения (до 13 560 *км*^{3}/*год*) и полного перемешивания во всей толще вод Красного моря в зиму 1958/59 г. Очевидно, при таком интенсивном перемешивании не сохранилось бы промежуточного слоя с минимальным содержанием кислорода. «Опреснение» вод Красного моря, отмечаемое с сентября 1959 г. по июль 1960 г., напротив, могло произойти только за счет невероятно большого увеличения водообмена с Аденским заливом, когда в течение десяти месяцев воды Красного моря должны были на 90% обновиться. Даже довольно грубый подсчет показывает, что Баб-эль-Мандебский пролив с поперечным сечением в 2,72 *км*^{2} не в состоянии пропустить объем воды (в оба направления), более чем в 1,5 раза превышающий объем вод Красного моря. Выполненные расчеты показывают, что соленость, полученная э/с «А. И. Воейков» в 1959 г., завышена примерно на 1,6—1,8‰.

Изменение солености от года к году, несомненно, существует в связи с циклическими колебаниями атмосферной циркуляции, приходом солнечной радиации, осадков и водообмена через Баб-эль-Мандебский пролив. Однако эти изменения в глубинной толще вод любого моря, в том числе и Красного, могут сказаться лишь по истечении довольно длительного периода времени, соизмеримого с продолжительностью многолетних циклов изменения. Верхние горизонты подвержены более быстрому изменению. В сезонном аспекте они связаны с изменением погодных условий и сезонными колебаниями водообмена через Баб-эль-Ман-

Таблица 1

Сезонные изменения температуры, солености и условной плотности вод Красного моря по наблюдениям экспедиций 1960, 1962 и 1963 гг.

H, м	Лето			Осень			Зима		
Серерная часть									
	«Ю. М. Шокальский» 6. VII 1960 г. φ=27°12′ с. ш. λ=34°36′ в. д.			«Академик А. Ковалевский» 12. X 1963 г. φ=27°07′ с. ш. λ=35°08′9 в. д.			«Академик А. Ковалевский» 27—28.I 1962 г. φ=26°54,2′с. ш. λ=34°56′0 в. д.		
	$t°$	S, ‰	σ_t	$t°$	S, ‰	σ_t	$t°$	S, ‰	σ_t
0	26,6	40,57	27,11	29,36	40,20	25,88	22,64	40,52	28,26
50	23,91	40,42	27,72	27,21	40,26	26,65	22,41	40,49	28,29
100	22,30	40,37	28,12	23,50	40,34	27,82	22,12	40,50	28,29
500	21,74	40,50	28,48	21,70	40,60	28,56	21,68	40,62	28,58
	700 м			800 м					
1000	21,70	40,53	28,50	21,71	40,64	28,58	21,72	40,62	28,56
Средняя часть									
	7. VII 1960 г. φ=23°10′ λ=37°06′			29. X 1963 г. φ=21°57,5′ λ=38°14,3′			23. I 1962 г. φ=22°21′ λ=38°27,9′		
0	28,86	39,79	25,63	30,92	39,50	24,82	25,24	39,13	26,42
50	26,44	39,74	26,52	29,03	39,47	25,48	24,88	39,60	26,96
100	23,56	40,20	27,72	24,19	40,15	27,43	24,92	39,78	26,98
500	21,68	40,53	28,27	21,68	40,55	28,65	21,66	40,53	28,62
				950 м			829 м		
1000				21,76	40,59	28,54	21,71	40,57	28,67
Южная часть									
	9. VII 1960 г. φ=17°39′ λ=40°10′			29. X 1963 г. φ=17°32′ λ=40°02′			20. I 1962 г. φ=18°08′ λ=39°51,7′		
0	31,84	37,01	22,73	31,32	38,60	24,02	26,50	37,64	24,89
50	26,06	37,47	24,90	30,38	38,77	24,44	27,40	38,47	25,23
100	24,46	39,52	26,91	23,73	40,01	27,53	23,62	39,70	27,34
500	21,70	40,30	28,32	21,64	40,61	28,56	21,62	40,57	28,56
	829 м						850 м		
700	21,68	40,30	28,33	21,72	40,56	28,53	21,72	40,58	28,53

дебский пролив. В табл. 1 приведены значения температуры, солености и плотности воды в разные сезоны, выполненные судами «Ю. М. Шокальский» и «Академик А. Ковалевский». Температура в поверхностном слое в северном районе моря изменялась от 22,64° в январе 1962 г. до 29,36° в октябре 1963 г. Минимальная температура наблюдениями не захвачена, однако, судя по температуре воды в основной толще моря, она не может быть выше 21,5°.

БАБ-ЭЛЬ-МАНДЕБСКИЙ ПРОЛИВ

Водообмен через Баб-эль-Мандебский пролив играет важную роль в режиме как Красного моря, так и Аденского залива. Однако количественной характеристики водообмена не имеется до последнего времени. Данные по вертикальному распределению температуры и солености в проливе и единичные наблюдения над течением дают лишь качественную характеристику водообмена. Примерная количественная характеристика водообмена через Баб-эль-Мандебский пролив была нами

Таблица 2

Величины расходов красноморского и аденского течений в Баб-эль-Мандебском проливе

Величина испарения с поверхности Красного моря			Водообмен через пролив, *км³/год*			Средняя скорость течения в проливе, *м/сек*	% ежегодного обновления вод Красного моря
слой за сутки, *см*	слой за год, *м*	за год со всей поверхности моря, *км³*	расход красноморских вод	расход аденских вод	суммарный по всему течению		
0,96 *	3,5	1574	9461—12614	15768	28382	0,33	6,3
0,73	2,66	1197	21850	23047	44897	0,52	8,9

* Данные Большой советской энциклопедии [18].

получена косвенным методом, исходя из уравнения установившегося солевого и водного баланса Красного моря и средней величины испарения с поверхности моря (табл. 2). В уравнении не учитывались осадки и материковый сток, поскольку для Красного моря они очень малы и существенной роли в режиме моря не играют. Величина испарения взята средняя из наблюдений в сентябре 1959 г. на э/с «А. И. Воейков» и в июле 1960 г. на э/с «Ю. М. Шокальский». Для сравнения в табл. 2 приведены величины испарения и расходов красноморского и аденского течений в проливе, заимствованные из Большой советской энциклопедии [18].

Количество вод, вытекающих из Красного моря в Аденский залив, равно 21850 *км³/год*, приток аденских вод — 23047. Полученные нами величины водообмена через Баб-эль-Мандебский пролив в 1,5 раза больше приведенных в энциклопедии. Средняя скорость для всего живого сечения пролива, полученная также косвенным методом, равна 0,52 *м/сек*. Однако в действительности скорости течения весьма не постоянны. Они значительно колеблются как по величине, так и по направлению. Течения в проливе имеют сложный характер, поскольку приливные колебания уровня в Красном море, Баб-эль-Мандебском проливе и Аденском заливе по периоду и по амплитуде не одинаковы. Поэтому в зависимости от соотношения фаз изменяется разность уровней на концах пролива и течение испытывает значительные колебания. При определенном сочетании максимумов и минимумов уровней скорости течения достигают больших значений (1,5—2,0 *м/сек*). В отдельные моменты на непродолжительное время оно почти совсем затухает. Например, на якорной станции 53, расположенной в районе порога со стороны Красного моря, в 13 час. 50 мин. течение, направленное в Красное море, было настолько сильное, что сносило опускаемые батометры на угол более 60°. Но спустя два часа угол наклона троса уменьшился до 30°, измеренная скорость течения была 0,92 *м/сек*, а еще через полтора часа планктонная сетка шла почти вертикально.

Наблюдения над течением проводились лишь на шести стандартных станциях. Они выполнялись с корабля морскими вертушками. Корабль стоял на одном якоре, вытравленном на утроенную глубину станции. Полученные данные не позволяют рассчитать величины расходов верхнего и нижнего течений, поскольку в этом районе отмечаются значительные приливы. Они характеризуют течение лишь для конкретного отрезка времени. На рис. 6 дается годограф скоростей на ст. 53, расположенной в районе возвышения дна перед проливом со стороны Красного моря. Там же нанесено распределение температуры и солености. Направление течения хорошо прослеживается по распределению солености по вертикали. Верхнее течение (толщина слоя 0—75 *м*) направлено в сторону Красного моря. Нижнее, охватывающее слой от 100 *м* и до дна

(200 *м*) — из Красного моря в Аденский залив. Максимальная скорость (0,92—0,90 *м/сек*) в верхнем слое отмечалась на глубине 10 *м*, в нижнем — на 150 *м*. Вдоль аравийского побережья течение было направлено на север (глубина в месте наблюдения 24 *м*, $V=0{,}22$ *м/сек*), у африканского — на юг. Поскольку в проливе отмечаются значительные приливные течения, а наблюдения проводились в разное время (на ст. 52 в 8—9 час., на ст. 53 в 16—17 и на ст. 54 — в 23—24 час. 6 ноября 1963 г.), т. е. в разные моменты прилива, то не представляется возможным определить расходы красноморских и аденских вод.

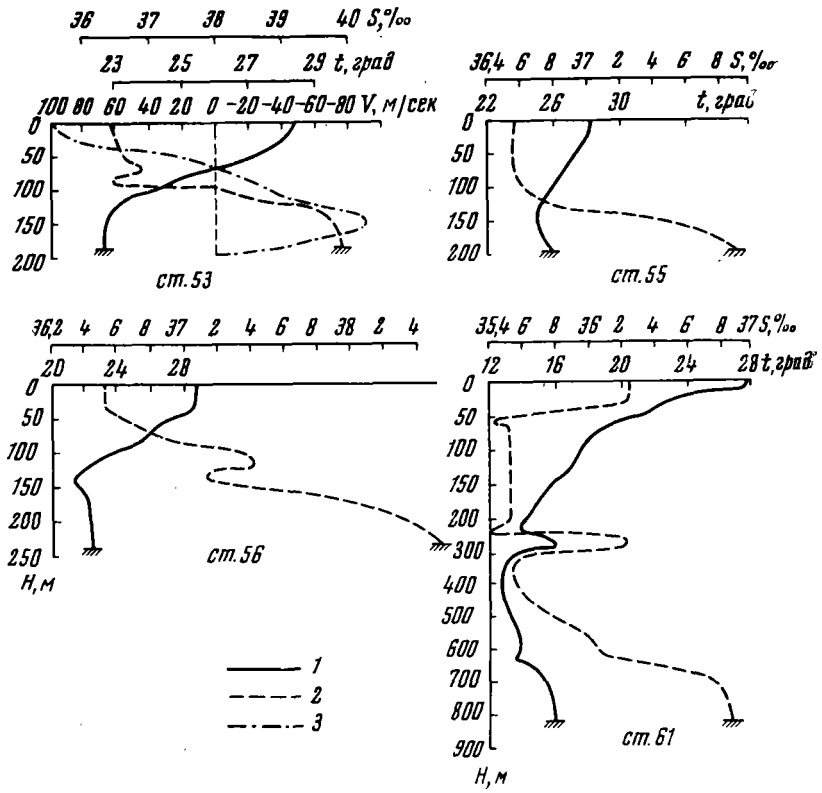

Рис 6. Вертикальное распределение температуры, солености и скорости течения на станциях, расположенных перед проливом (ст. 53, 55), в проливе (ст. 56) и на выходе из пролива в Аденский залив (ст. 61)

1 — температура; *2* — соленость; *3* — скорость

Как известно, течение в проливе зависит не только от разности уровней между Аденским заливом и Красным морем, но и от разности плотностей их вод, от направления и силы ветра и от фазы прилива. Для получения истинной характеристики течения и водообмена через пролив необходимы стационарные наблюдения продолжительностью не менее 15 суток, да к тому же выполненные в разные сезоны: при устойчивых северо-северо-западных ветрах — летом, юго-юго-восточных — зимой, а также в переходные периоды.

Как следует из данных вертикального распределения температуры и солености (рис. 6), на ст. 53 хорошо выражены две водные массы: в верхней 100-метровой толще располагаются аденские воды ($t=28{,}6°$ и $S=36{,}47‰$) и в придонном слое — красноморские воды ($t=22{,}62°$ и $S=39{,}84‰$). Смена течений совпадает с границей раздела водных масс.

В самой узкой части пролива (ст. 56) наблюдается переслоенность водных масс с относительным максимумом и минимумом солености на глубинах 120 и 135 *м*, что, вероятно, связано со слоистой структурой течения.

АДЕНСКИЙ ЗАЛИВ

Гидрологический режим Аденского залива формируется под воздействием свободного водообмена с Аравийским морем и водообмена с Красным морем, ограниченного небольшой глубиной порога (125 *м*), а также определяется большим приходом солнечной радиации, интенсивным испарением и муссонным режимом ветра.

Большие глубины залива на выходе в Аравийское море обеспечивают хороший водообмен с океаном, поэтому гидрологические характеристики глубинных вод не отличаются от океанских на соответствующих горизонтах. Поверхностные воды залива по своим характеристикам близки к североаравийской поверхностной воде, поскольку они в основном из нее формируются. В период зимнего муссона поверхностные воды северо-западного района Аравийского моря интенсивно поступают в Аденский залив. Здесь аравийские воды несколько трансформируются под влиянием интенсивного испарения и смешения с поверхностной красноморской водой, поступающей в залив в период летнего муссона. Толщина поверхностного слоя небольшая и в зависимости от течения меняется от 10—25 до 75—100 *м*.

Температура и соленость в поверхностном слое залива повышается по направлению с востока на запад: в январе от 24,70 до 25,98° и от 35,89 до 36,10‰, в ноябре — от 25,98 до 28,80° и от 35,56 до 36,51‰. Это объясняется испарением и процессами смешения с красноморской водой. В поперечном направлении залива распределение температуры и солености в поверхностном слое зависит от ветра и господствующей системы течения. Зимой при устойчивом северо-восточном и восточном ветрах в заливе устанавливается циклоническая система течения, которая характеризуется господствующим переносом вод с Аравийского моря в Аденский залив вдоль аравийского побережья [13]. В этот период более высокая соленость отмечается у африканского побережья, а повышенные температуры — у аравийского. Наиболее низкие температуры (23,6°) отмечались у юго-восточного побережья залива, где при восточных и северо-восточных ветрах наблюдается сгон поверхностных и подъем промежуточных вод с более низкой температурой и высоким содержанием питательных солей (в частности фосфатов) до 58—60 *мг/м*³ Р (по данным М. А. Добржанской).

Летом при господствующих западном и юго-западном ветрах в Аденском заливе усиливается течение вдоль африканского берега и ослабевает у противоположного аравийского. Такая система течений приводит к нагонному эффекту и скоплению на юге залива поверхностных, относительно теплых и соленых вод. У северо-западного побережья залива при указанных ветрах наблюдается сгон поверхностных и подъем глубинных вод. Поэтому в летнее время в этом районе, наряду с некоторым понижением температуры и солености, наблюдается повышение содержания биогенных солей, поскольку промежуточные воды на глубине 150—200 *м* ими более богаты.

В ноябре 1963 г. ветровой режим зимнего сезона еще не установился, вследствие чего в западной половине залива сохранилось летнее распределение, т. е. более теплые и соленые воды располагались у африканского берега. Так, по 45 меридиану температура и соленость по направлению с севера на юг повышались от 27,6 до 28,7° и от 35,84 до 36,51‰ соответственно. По 52 меридиану распределение гидрологических характеристик в поверхностном слое было несколько иное.

Максимальная температура и соленость (29,8° и 36,42‰) отмечалась на ст. 69, расположенной в 93 *км* к северу от африканского побережья. По направлению к югу и северу от этой станции температура и соленость уменьшались.

Скопление более теплой и соленой воды в районе ст. 69 и значительное понижение температуры на крайней южной станции с характерным вогнутым строением изолиний дают основание предположить образование в юго-восточном районе залива (в переходный сезон) области антициклонического течения. На динамической карте, построенной Серым и Химица по зимним наблюдениям [13], антициклоническое завихрение течения отмечалось несколько восточнее — на шельфе о-ва Сокотра.

Распределение температуры и солености по вертикали в Аденском заливе совершенно отличается от красноморского. Здесь нет той однородности и исключительно высокой температуры и солености, которая наблюдается в глубинной толще вод Красного моря. В Аденском заливе отмечается понижение температуры и некоторое уменьшение солености с глубиной — от 28,14 — 24,70° и 36,53—35,89‰ на поверхности до 2,82° и 34,79‰ на глубине 2340 *м*. Особенностью вертикального распределения гидрологических характеристик является значительная переслоенность его вод по температуре и солености. Такое строение вод Аденского залива определяется водообменом через Баб-эль-Мандебский пролив. Несмотря на ограниченность водообмена с Красным морем, поступление красноморских вод оказывает существенное влияние на формирование промежуточных вод залива, поскольку их температура и соленость значительно превышают эти характеристики в Аденском заливе.

Вертикальное распределение гидрологических характеристик в Аденском заливе тесно связано с количеством красноморских вод, поступающих в залив, и глубиной их погружения, т. е. начальной плотностью этих вод. Кроме того, распределение температуры и солености в толще вод залива зависит от интенсивности водообмена с Аравийским морем, т. е. скорости обновления промежуточных вод пониженной солености.

Вертикальное распределение температуры и солености на поперечных разрезах близ Баб-эль-Мандебского пролива (на меридиане 45 и 51) дано на рис. 7 и 8. На первом разрезе, расположенном вблизи пролива (рис. 7, *а* и 8, *а*), трансформированные красноморские воды прослеживались в придонном слое на глубине 250—350 *м*. Они имели относительно невысокую температуру и соленость (16,0° и 37,49‰) и, вероятно, образовались в период сгонов в вершине залива, когда красноморские воды, проходя через пролив, уже значительно перемешались с холодными водами Аденского залива.

В западной части залива (рис. 7, *б* и 8, *б*) разрез расположен примерно на расстоянии 130 *км* от пролива, красноморские воды прослеживались двумя слоями с максимумом солености 36,24 и 36,84‰ на глубине 288 и 800 *м* соответственно и с относительным минимумом солености 35,52‰ — на глубине 370 *м*. Распределение красноморской воды по разрезу неравномерное: с более мощным придонным слоем и небольшим промежуточным. В обоих случаях максимальная концентрация красноморских вод располагалась в северной части разреза.

На восточном разрезе на траверзе м. Рас-Алула (рис. 7, *в* и 8, *в*) красноморская вода прослеживалась в виде 4-х слоев с относительными максимумами солености на глубинах: 75—100 *м*, 200, 500 и 800 *м* (35, 65, 35,71, 35,87 и 35,81‰ соответственно) и минимумами — на 40, 150, 300, 600—700 *м* (35,37‰, 35,44, 35,40 и 35,64‰). На разрезах хорошо прослеживается переслоенность вод по температуре и солености. Ход изохалин указывает на довольно сложную систему течений. Наибольшее количество красноморских вод расположено в южной части разреза —

у африканского берега. По направлению на север они растекаются и образуют несколько языков. Глубина погружения трансформированной красноморской воды и ее распределение по поперечным сечениям связано с начальной плотностью и системой течения в заливе. Некоторое усложнение в конфигурации изотерм и изохалин возможно и за счет приливных колебаний, поскольку наблюдения проводились в разные

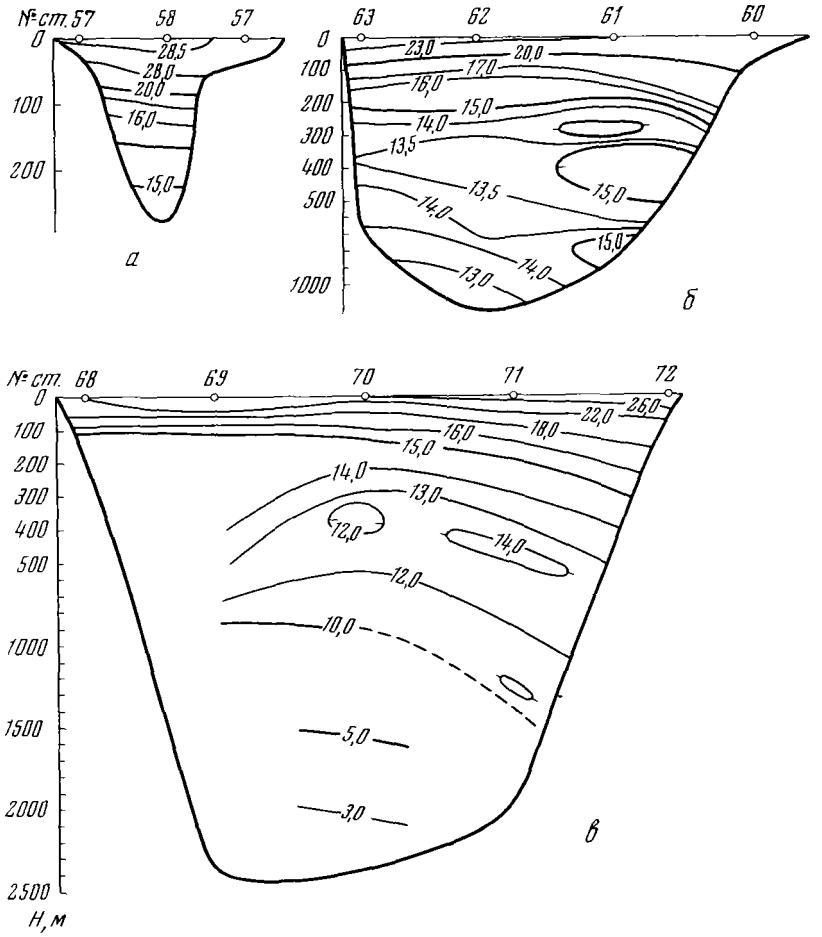

Рис. 7. Вертикальное распределение температуры на поперечных разрезах в Аденском заливе

а — вблизи пролива; *б* — по 45 меридиану; *в* — по 51 меридиану

фазы прилива. Однако значительная переслоенность вод отмечалась также и на отдельных станциях при одновременном наблюдении на 15 горизонтах. Это подтверждает существование значительной переслоенности вод Аденского залива и непостоянства в расположении слоев разной солености, что определяется системой течения.

Для выявления изменчивости характеристик водных масс в слоях максимума и минимума солености были построены *TS*-кривые вдоль залива на разных расстояниях от его вершины (рис. 9), по наблюдениям в январе 1962 и ноябре 1963 г., Красноморские воды прослеживались в обоих рейсах вдоль всего Аденского залива. Глубина их залегания от станции к станции колебалась, однако в общем она увеличивалась по направлению к выходу из залива. Также не оставалось постоянным и количество слоев с относительным максимумом и минимумом солености.

Красноморские воды поступают в Аденский залив на глубине 200 *м*, где они имеют значительно большую соленость и температуру по сравнению с аденской водой на этих горизонтах. Поэтому, вначале они быстро погружаются до глубин 300—800 *м*. По мере движения на восток они перемешиваются с относительно холодной и менее соленой промежуточной водой Аденского залива, вследствие чего их температура и соленость понижаются.

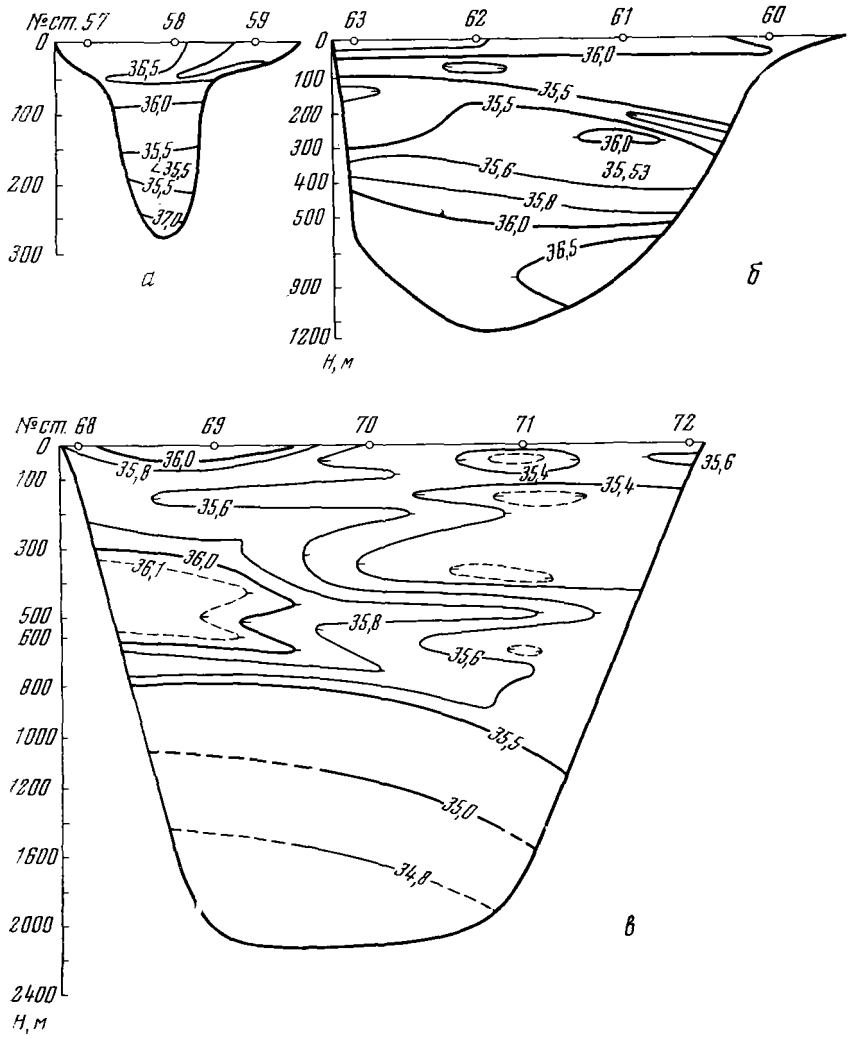

Рис. 8. Вертикальное распределение солености на поперечных разрезах в Аденском заливе

а — западный; *б* — центральный; *в* — восточный

Напротив, промежуточные воды с пониженной соленостью поступают в Аденский залив из Аравийского моря. Поскольку они движутся в Аденском заливе несколькими слоями и перемешиваются с солеными водами красноморского происхождения, то их характеристики также меняются по мере приближения к вершине залива. Гидрологические характеристики трансформированных красноморских вод и промежуточных аденских вод с пониженной соленостью меняются как в пространстве, так и во времени, поскольку меняется интенсивность водообмена

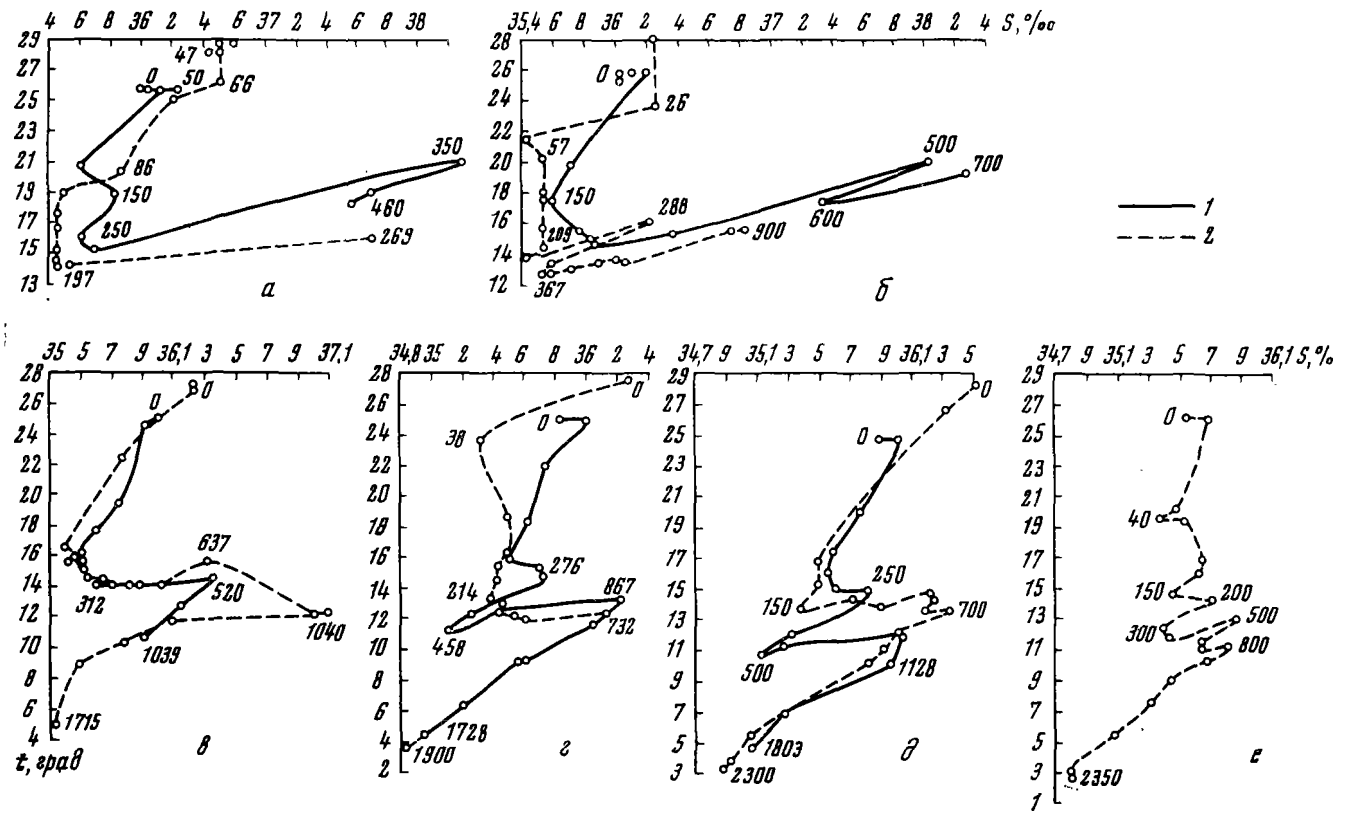

Рис. 9: *TS*-кривые, характерные для Аденского залива, по наблюдениям январе 1962 г. (*1*) и ноябре 1963 г. (*2*)

а — ст. 58 и 60; *б* — ст. 57 и 61; *в* — ст. 55 и 65; *г* — ст. 56 и 66; *д* — ст. 56 и 67; *е* — ст. 70

с соседними морями. Поэтому изменения характеристик могут быть косвенным показателем интенсивности водообмена как с Красным морем, так и с Аравийским.

По наблюдениям в январе 1962 и в ноябре 1963 г. заметны различия как в характере распределения красноморских вод вдоль продольной оси Аденского залива, так и в величинах температуры и солености. В январе 1962 г. гидрологические характеристики трансформированной красноморской воды и промежуточного минимума солености были несколько выше по сравнению с ноябрем 1963 г. (табл. 3).

Промежуточные воды пониженной солености в Аденском заливе не представляют единого слоя. Гидрологические характеристики их определяются глубиной расположения трансформированной красноморской воды. Если красноморская вода прослеживается на глубине 200—300 *м*, воды верхнего слоя пониженной солености характеризуются температурой 14—18° и соленостью 35,37—35,60‰. В том случае, когда трансформированные красноморские воды погружаются на большие глубины (от 750 до 1100—1200 *м*), воды промежуточного минимума солености характеризуются более низкой температурой и соленостью (10,7—12,4° и 35,12—35,40‰). В зависимости от глубины залегания красноморских вод и степени их смешения с холодными и менее солеными водами Аденского залива меняются и гидрологические характеристики промежуточных вод пониженной солености.

Малые глубины Баб-эль-Мандебского пролива ограничивают водообмен между Красным морем и Аденским заливом лишь водами верхних слоев. В этих условиях возрастает роль сгонно-нагонной циркуляции на предпроливных участках Красного моря и Аденского залива в водообмене через пролив. Сгоны и нагоны оказывают существенное влияние как на величину расходов, так и на океанографические характеристики вод нижнего течения красноморских и верхнего — аденских вод.

В период летнего муссона при сильных северных и северо-западных ветрах в южном районе Красного моря наблюдается нагон. При этом по направлению к проливу происходит утолщение поверхностного слоя, значительно разбавленного аденской водой. Нижним течением в таком случае выносятся воды высокой температуры и относительно пониженной солености. Обычно в это время в Аденском заливе наблюдаются юго-западные и западные ветры, при которых в предпроливном участке залива происходит сгон поверхностных вод и подъем глубинных. Поэтому промежуточным течением пролива, направленным в Красное море, выносятся более глубинные воды Аденского залива, поднявшиеся в результате сгона в приповерхностные горизонты. Они имеют несколько пониженную температуру и соленость и относительно высокое содержание фосфатов. В таких случаях воды нижнего течения, несущего в основном поверхностные красноморские воды, соприкасаются и перемешиваются с относительно холодными аденскими водами промежуточного течения. Поэтому в Аденский залив красноморские воды поступают с несколько пониженной температурой и соленостью.

При северо-восточных ветрах (зимний муссон) происходит нагон поверхностных вод к вершине залива, а в южном районе Красного моря, вследствие господства юго-юго-восточных ветров, отмечается сгон. Последний сопровождается подъемом глубинных вод в районе порога и перетеканием их через мелководье. Поэтому при сгонах в южном районе Красного моря нижним течением захватываются относительно глубинные красноморские воды высокой солености и относительно пониженной температуры (40,0‰ и 22,0°). В этих случаях более соленые красноморские воды соприкасаются и смешиваются в проливе с теплыми поверхностными водами Аденского залива, поэтому в залив будут поступать красноморские воды относительно более высокой температуры

Таблица 3

Гидрологические характеристики промежуточных слоев максимума и минимума солености в Аденском заливе

Январь 1962 г.							Ноябрь 1963 г.						
Слои min$S$				Слои max$S$			Слои min$S$				Слои max$S$		
км	H, м	$t°$	S, ‰	H, м	$t°$	S, ‰	км	H, м	$t°$	S, ‰	H, м	$t°$	S, ‰
48	147	16,45	35,66	123	21,5	36,22	26	90	17,74	35,44	250	16,02	37,49
85	125	20,64	35,61	—	—	—	156	57	21,38	35,44	288	14,95	36,88
85	200	16,04	35,62	350	20,94	38,07	156	232	13,62	35,40	800	15,49	36,84
93	125	20,64	35,61	—	—	—	418	57	16,6	35,41	1040	12,40	37,10
93	250	15,28	35,64	400	20,03	37,09	511	38	21,63	36,35	80	16,3	35,51
111	200	15,67	35,54	500	19,75	37,95	511	214	13,40	35,40	732	13,84	36,48
130	150	17,43	35,59	700	19,25	38,22	667	150	13,73	35,37	500	14,26	36,24
222	210	15,79	35,61	735	12,81	36,44	667	—	—	—	700	13,53	36,33
352	104	19,28	35,15	518	14,59	36,37	778	40	19,56	35,37	200	14,30	35,71
467	500	10,7	35,13	904	12,03	36,03	778	150	14,60	35,44	500	12,97	35,87
—	—	—	—	—	—	—	778	300	12,37	35,40	800	11,20	35,81

и солености по сравнению с летним периодом. Воды нижнего течения по плотности значительно выше аденских на глубине их втекания, вследствие чего они погружаются на большие глубины в соответствии с их плотностью. Смешение их по пути движения с холодными и менее солеными водами Аденского залива приводит к уплотнению и дальнейшему заглублению. Кроме того, сгоны сопровождаются подъемом глубинных вод, более богатых питательными солями, что оказывает благотворное влияние на распределение и развитие растительного и животного планктона, что в свою очередь определяет районы промыслового скопления рыбы.

В Аденском заливе преобладают два господствующих направления ветра. Летом, с июня по сентябрь, повторяемость западных и юго-западных ветров составляет 78—89% [19] зимой, с ноября по апрель, повторяемость восточных и северо-восточных достигает 75—85%. Переходными месяцами в смене указанных направлений ветра являются май и сентябрь, октябрь. Устойчивые по направлению ветры создают определенные районы подъема глубинных вод, где на продолжительное время создаются благоприятные условия для биологической жизни. Так, для периода зимнего муссона устойчивым районом сгона и обогащения является юго-восточное побережье Аденского залива (м. Гвардафуй). Для летнего сезона таким районом является северо-западное побережье залива в районе Адена. Данные поисковых работ на э/с «Владимир Воробьев» [13] указывают на образование устойчивых скоплений ставриды в летнее время в районе шельфа у Адена. В зимний период промысловые скопления некоторых рыб отмечаются в районе о-ва Сокотра.

ABSTRACT

This report gives a hydrological characteristic of the Red Sea and also of the Channel and Gulf of Suez, Bab-el-Mandeb and the Gulf of Aden in autumn and winter seasons according to the observations of the research ship «Academik A. Kovalevsky» in December — January of 1961/62 and in October — November of 1963.

This paper considers the influence of the exchange of water through the Bab-el-Mandeb on the formation of hydrological conditions of the Red Sea and those of the intermediate layer of high salinity waters in the Gulf of Aden. It points out that the waters of the Gulf of Aden enter not

only the surface horizons of the Red Sea but as well the intermediate layers — from 90—100 m to 300—400 m. It is supposed that this is the cause for a richer life in these depths.

The author defines more exactly the influence of monsoons and the effect of the «piling-up» and «upwelling» circulation in the regions stretched before the Strait of Bab-el-Mandeb and in the Northern area of the Red Sea upon the exchange of water through the Strait and the Channel of Suez.

The author also examines the conditions of formation of steady areas of upwelling and the enrichment of the upper layers with the nutritions in the Gulf of Aden. It is shown that the areas of this kind are: in summer — the North — West coast of the gulf (the area of Aden), and in winter — the South — East (the area of cape Guardafui). A richer development of life is characteristic of these areas.

The author examines the distribution of the Red Sea waters in the Gulf of Aden (according to the T° and S‰ data). It has been found out that characteristic of the Red Sea waters distribution change according to the temperature and salinity value, and the rate of motion and mixing with the waters of the intermediate layer of the Gulf of Aden.

The paper shows the mechanism of the Red Sea water masses formation and estimates the values of the salinity — water balance in this formation. It calculates the rate of discharge of the upper and lower currents in the Strait by the equation of the salinity balance and the data from literature on the Red Sea deep waters salinity for 1958, 1959 and 1960.

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О «ЗАДЕРЖИВАЮЩИХ СЛОЯХ» В НИЖНЕЙ ТРОПОСФЕРЕ НАД ИНДИЙСКИМ ОКЕАНОМ

Под «задерживающими слоями» в данной работе понимаются слои температурной инверсии, изотермии и слои резкого уменьшения градиента температуры (больше чем на 0,2°/100 *м*) на высотах до 3—3,5 *км*. О пассатной инверсии над Атлантическим и Тихим океанами опубликован целый ряд обстоятельных работ [1—6], в которых рассматриваются вопросы географического расположения задерживающих слоев, вскрывается их влияние на формирование погоды в данных районах, а также высказываются некоторые соображения о причинах образования; сведения о задерживающих слоях над Индийским океаном до последнего времени оставались поразительно скудными, а имеющиеся данные носят весьма отрывочный характер.

Лишь работа французского метеоролога Эмона [6] непосредственно посвящена температурной инверсии над Индийским океаном. В ней автор использовал аэрологические наблюдения на трех станциях — Диего-Суарес, Тюлеар (обе на Мадагаскаре) и на о-ве Маврикия,— выполненные метеорологической службой британских ВВС за три года (1945—1947 гг.). Для этих станций подсчитана повторяемость появления инверсии, высота ее основания, мощность, перепад температуры. Интересным оказался сезонный ход повторяемости инверсии: в зимний период (с мая по ноябрь) на всех станциях она очень велика, достигая временами 100%, в летний же период (с декабря по апрель) наблюдается резкое уменьшение повторяемости. Вопрос о причинах появления задерживающих слоев над Индийским океаном в работе Эмона не рассматривается.

Некоторые отрывочные сведения о температурной инверсии над Индийским океаном есть также в работе Р. Ф. Усманова [7], описавшего меридиональный аэрологический разрез в западной части Индийского океана по наблюдениям в первом рейсе д/э «Обь», в работе С. П. Хромова [8] по материалам второго рейса д/э «Обь», а также в статье В. Г. Снопкова [9] по материалам 33 рейса и/с «Витязь».

В настоящей работе на основании имеющихся материалов сделана попытка дать достаточно полное описание задерживающих слоев над Индийским океаном. Для этой цели используются данные 31, 33 и 35 рейсов и/с «Витязь» и двух рейсов д/э «Обь» в 1956 и 1957 гг. [10].

Учитывая, что от зимы к лету над северной частью Индийского океана осуществляется коренная перестройка атмосферной циркуляции (смена муссонов), мы нашли целесообразным провести исследования отдельно для периода зимнего северо-восточного (ноябрь—март) и летнего юго-западного (май—сентябрь) муссона. Для более детального, например помесячного, исследования инверсионных слоев в настоящее

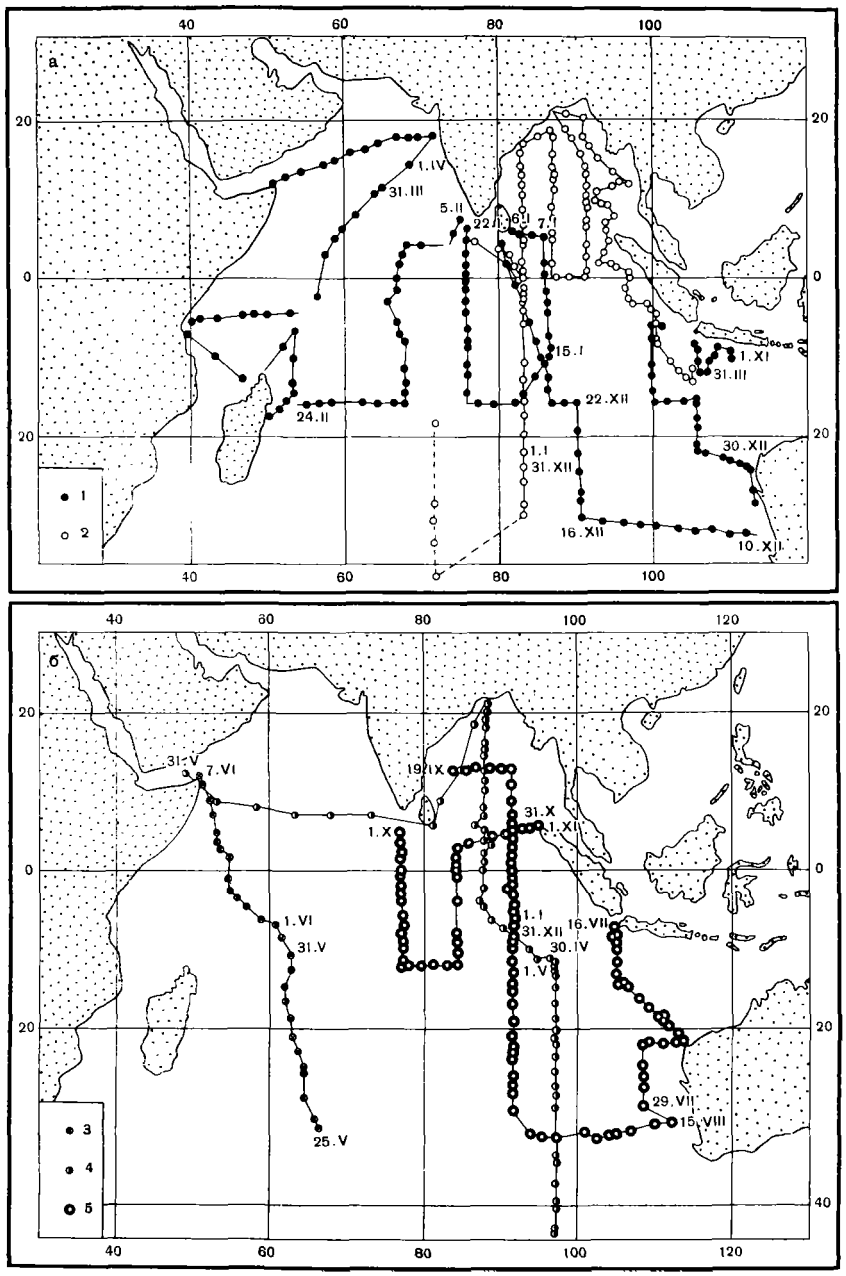

Рис. 1. Маршруты экспедиций

а — период зимнего муссона; *б* — период летнего муссона. *1* — 31 рейс и/с «Витязь» в 1959/60 г.; *2* — 33 рейс и/с «Витязь» в 1960/61 г.; *3* — д/э «Обь» в 1956 г.; *4* — д/э «Обь» в 1957 г.; *5* — 35 рейс и/с «Витязь» в 1962 г.

время данных совершенно недостаточно. В соответствии с этим все наблюдения делились на две части: наблюдения 31 и 33 рейсов и/с «Витязь» были отнесены к периоду северо-восточного муссона, а остальные — к периоду юго-западного муссона. К сожалению, в силу некоторых обстоятельств нам не удалось воспользоваться частью наблюдений 33 рейса и/с «Витязь», выполненных в Аравийском море.

Наблюдения в переходные месяцы также относились к одному из этих периодов (в зависимости от конкретной обстановки, наблюдавшейся в соответствующем году). При этом в тексте сделаны специальные оговорки относительно возможной нехарактерности этих наблюдений для основных периодов.

Схемы маршрутов с указанием места и месяца проведения аэрологических наблюдений приведены на рис. 1.

Исходя из установленной в последнее время большой изменчивости атмосферной циркуляции в тропиках [3] и данных наблюдений на пространственно-временных разрезах, где каждое наблюдение является оторванным от остальных по времени и в пространстве, полученную картину распределения задерживающих слоев над Индийским океаном в целом нельзя отождествлять со средним многолетним климатологическим распределением. Лишь в отдельных случаях, когда в результате анализа для этого были получены достаточные основания, мы считали возможным подчеркнуть режимность выявленного характера распределения инверсионных задерживающих слоев в тех или иных районах океана.

О ПРИЧИНАХ ОБРАЗОВАНИЯ СЛОЯ ИНВЕРСИЙ В ТРОПИЧЕСКИХ ШИРОТАХ

Первые наблюдения над пассатной инверсией, как известно, были сделаны в 1854 г. английским астрономом Пиацци-Смитом при восхождении на пик Тенериф (Азорские острова). Заметив, что быстрый рост температуры воздуха с высотой наблюдается выше верхних границ облаков, Пиацци-Смит решил, что подобное распределение температуры объясняется радиационным охлаждением поверхности облаков. Дальнейшие исследования показали, однако, несостоятельность такого заключения. Оказалось, как пишет Риль, температура у основания инверсии приблизительно соответствует температуре у поверхности моря; это значит, что частицы воздуха, поднимающиеся от поверхности, достигают нижней границы инверсии с температурой, которая не очень отличается от их первоначальной. Именно теплота и сухость воздуха в слое инверсии и над ним выражает аномальность режима инверсии.

Обстоятельное объяснение причин образования пассатной инверсии дал Фиккер [1], проанализировав аэрологические наблюдения в Атлантическом океане, выполненные во время экспедиции «Метеора» (1926—1927 гг.). Фиккер строил свое объяснение, опираясь на представление о циркуляции в тропиках в виде замкнутого меридионального гадлеевского кольца (пассат — антипассат). По мысли Фиккера, часть воздуха, приносимого антипассатом из экваториальных широт в тропики, опускается на полярной стороне тропического пояса высокого давления и по мере обратного движения к экватору по приземной траектории успевает, смешавшись с воздухом умеренных широт, существенно охладиться и увлажниться. В связи с этим другая часть воздуха, которая адиабатически опускается на экваториальной стороне антициклонического пояса и также включается в пассатный поток к экватору, оказывается теплее и суше первой. Таким образом, создается устойчивый инверсионный слой в одном и том же пассатном потоке. Направление движения в верхней и нижней ветвях пассата отличаются лишь на начальном отрезке пути, когда ветры в нижней ветви дуют с северо-востока (северное полуша-

рие), а в верхней — с северо-запада. В дальнейшем, по мере движения к экватору ветры обеих ветвей пассата становятся северо-восточными.

Наименьшие высоты нижней границы слоя инверсии в Атлантическом океане (500 *м*) наблюдались, по данным э/с «Метеор», у западных берегов Африки на 20—25° северной и южной широт. Это обстоятельство Фиккер объяснял возникновением приземных инверсий над холодными (Канарским и Гвинейским) течениями и превращением их в высотные при поступлении воздуха на более теплую подстилающую поверхность. Эти процессы, по мнению Фиккера, нарушали общую систему пассатных инверсий, связанных с оседанием воздуха в тропиках, а в конечном счете и приводили к наблюдаемому снижению нижней границы слоя инверсии у западных берегов Африки.

Разрушение инверсий, которое наблюдалось в приэкваториальных широтах, Фиккер связывал с мощной свободной конвенцией, развивающейся в этих районах из-за разности температуры вода — воздух.

Объяснение образования пассатной инверсии, данное Фиккером, в последующие годы претерпело некоторые изменения, связанные с уточнением наших понятий об атмосферной циркуляции.

Как показал целый ряд наблюдений, в тропиках не отмечается устойчивая меридиональная циркуляция с антипассатом, по Гадлею. Такое замкнутое кольцо получается лишь в среднем многолетнем при осреднении по целому полушарию [11]. В отдельные же периоды в тропиках могут наблюдаться весьма разнообразные картины высотных потоков, никак не укладывающиеся в простую схему гадлеевской циркуляции [12][1]. В связи с этим в последних работах [3, 14] слово «антипассат» исчезло из параграфов, посвященных пассатной инверсии. Ее образование, как и у Фиккера, объясняется адиабатическим нагреванием при оседании воздуха в областях высокого давления, однако источники воздуха, прибывающего на место осевшего, могут быть различными.

Характерное распределение температуры и относительной влажности с высотой, при котором до слоя инверсии влажность почти не изменяется и иногда даже растет с высотой, а в слое инверсии резко уменьшается, при обоих вариантах объяснения причин образования пассатной инверсии остаются одинаковыми.

Для того чтобы происходило оседание воздуха, а следовательно, и образование инверсии в нижней тропосфере (1—3 *км*), необходимо наличие в этом месте дивергенции приземной скорости ветра. Чем больше дивергенция, тем интенсивнее должно быть оседание воздуха. Области дивергенции приземного ветра, как известно, характерны для антициклональных образований.

Однако районы максимальных значений дивергенции приземной скорости ветра, как это показано в [15], не совпадают с центрами антициклонов или осями гребней. И поэтому распределение инверсионных слоев над океаном следует сопоставлять с распределением дивергенции скорости ветра, а не с полем давления.

Приземные инверсии над холодными течениями, которым Фиккер отводил большую роль, в Индийском океане, имеют, видимо, более ограниченное значение, поскольку большие инверсионные разности температуры вода — воздух наблюдаются здесь лишь в очень небольших районах (Сомалийское течение, северный и западный районы Бенгальского залива) и то только в течение летних месяцев [16]. Зато инверсии, близкие к фронтальным, образованные двумя потоками разного происхожде-

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[1] Интересный результат получен Рилем [12] и Кришнамурти [13]. Они установили, что замкнутое кольцо циркуляции получается в тропиках в отдельные периоды, если рассматривать циркуляцию не относительно меридианов и параллелей, а относительно оси субтропического струйного течения.

Повторяемость различных видов задерживающих слоев над северной частью Индийского океана

Месяц	Инверсия		Изотермия		Резкое уменьшение температурного градиента		Отсутствие «задерживающих слоев»		Сумма наблюдений	
	число наблюдений	%	число наблюдений	%	число наблюдений	%	число наблюдений	%	число наблюдений	%
Январь	1	1,5	8	12,3	34	52,4	22	33,8	65	100
Февраль	—	0	5	9,3	33	61,1	16	29,6	54	100
Март	—	0	5	8,6	29	49,1	25	42,3	59	100
Апрель	10	28,6	14	40,0	11	31,4	—	0	35	100
Май	8	16,6	10	20,8	17	35,5	13	27,1	48	100
Июнь	2	13,3	3	20,0	8	53,4	2	13,3	15	100
Июль	9	34,6	13	50,0	2	7,7	2	7,7	26	100
Август	4	14,8	16	59,3	3	11,1	4	14,8	27	100
Сентябрь	—	0	9	36,0	6	24,0	10	40,0	25	100
Октябрь	—	0	13	35,1	4	10,8	20	54,1	37	100
Ноябрь	13	46,4	8	28,6	4	14,3	3	10,7	28	100
Декабрь	15	35,7	16	38,1	6	14,3	5	11,9	42	100
Всего	62	13,4	120	26,2	157	34,1	122	26,3	461	100

ния, которые Фиккер в своей работе не рассматривал, здесь имеют большое распространение. Подробнее об этом будет сказано при рассмотрении летней инверсии в Бенгальском заливе.

Следует сказать несколько слов о причинах разрушения инверсионных слоев. Как известно, в настоящее время большая роль в формировании приэкваториальной циркуляции отводится не свободной термической конвекции на термическом экваторе, а динамическим факторам, в частности, барическим градиентам в субтропических максимумах высокого давления. В месте встречи пассатных ветров северного и южного полушарий, обусловленных этими градиентами, образуется зона внутритропической конвергенции с неизбежными восходящими в ней потоками. Поэтому нам кажется, что, кроме возможного влияния термической конвекции, большую роль в разрушении инверсионных слоев следует отводить именно вынужденной конвекции, обусловленной конвергенцией пассатов северного и южного полушарий. Фиккер вообще уделил недостаточное внимание тем районам, где отсутствовала пассатная инверсия. Он считает, что в приэкваториальных широтах наблюдений до большой высоты было мало, а в тех, которые все же имелись, лишь в очень редких случаях обнаруживался слабый задерживающий слой. Тем не менее он посчитал возможным проинтерполировать характеристики инверсионных слоев (мощность, высоту основания и т. д.) через весь океан, не делая никаких разрывов. При этом оказалась невыявленной зона внутритропической конвергенции, одним из отличительных признаков которой является отсутствие инверсионных слоев. Картина циркуляции в тропиках тем самым, на наш взгляд, оказалась существенно обедненной. В настоящей работе мы сделали попытку исправить этот недостаток.

ХАРАКТЕРИСТИКА ЗАДЕРЖИВАЮЩИХ СЛОЕВ ПО СЕЗОНАМ

Для характеристики задерживающих слоев над северной частью Индийского океана, нами были использованы данные 461 аэрологического наблюдения, проведенных в различные годы и месяцы почти над

всеми районами океана. Распределение различных видов задерживающих слоев по месяцам приведено в таблице. В 339 случаях (73,7%) в различные месяцы наблюдалась температурная инверсия, изотермия или резкое уменьшение температурного градиента. При этом наибольшей повторяемостью (34,1%) обладает резкое уменьшение температурного градиента. Повторяемость изотермии (26,2%) несколько меньше, чем повторяемость уменьшения градиента. Наиболее часто этот вид задерживающих слоев встречается летом. Повторяемость температурной инверсии, по сравнению с другими видами задерживающих слоев, значительно меньше (13,4%). Отсутствие задерживающих слоев, по использованным нами данным, наблюдалось в 121 случае, что составляет 26,3%.

Из таблицы видно, что задерживающие слои над Индийским океаном получают наибольшее развитие с апреля по август, что соответствует периоду летнего муссона (зимний период в южном полушарии). Задерживающие слои в этот период характеризуются преобладанием изотермии или слоев с малыми градиентами температуры. Инверсия в чистом виде встречается сравнительно редко (лишь в 33 случаях, что составляет 7,1% от общего числа наблюдений). Но ввиду того, что наблюдения распределены неравномерно по акватории океана и проводились в различное время, годовой ход интенсивности развития задерживающих слоев в отдельных районах океана (например, у Австралии) может существенно изменяться.

ПЕРИОД ЗИМНЕГО МУССОНА

Как видно из рис. 1, больше всего наблюдений проведено в восточной и центральной частях океана, в западной же части их проводилось очень мало. По срокам проведения наиболее удачно наблюдения распределились в центральном районе, где все наблюдения 31-го и 33-го рейсов «Витязя» приходятся на декабрь, январь и февраль. Наблюдения, выполненные в восточной части Бенгальского залива, относятся к марту; наблюдения в Аравийском море — к апрелю, а наблюдения между Австралией и Явой — к ноябрю и марту. Для наблюдений, выполненных в последних трех районах, следует иметь в виду возможную нехарактерность их для периода зимнего муссона.

Распределение основных характеристик задерживающих слоев над Индийским океаном приводится на рис. 2.

Рассматривая его, легко заметить существенное отличие полученной картины от карт, помещенных в работе Фиккера. Как видно из рис. 2, *а*, здесь, в отличие от результатов Фиккера, через весь океан тянется довольно широкая (до 10°) зона отсутствия задерживающих слоев, в которой до значительных высот наблюдается равномерное падение температуры с высотой ($\gamma = 0{,}7 \div 0{,}8°/100$).

Есть основания полагать, что сам факт наличия этой зоны, а в некоторой степени и выявленное согласно нашим данным расположение являются характерной чертой метеорологического режима тропической части Индийского океана, а не эпизодическим явлением, относящимся лишь ко времени наблюдений и/с «Витязь». В этой связи укажем лишь на одно обстоятельство. Согласно нашим данным, в феврале и марте зона отсутствия инверсий захватила северную часть о-ва Мадагаскар. По исследованиям Эмона, в эти месяцы инверсия отсутствовала и в 1945—1947 гг. Забегая вперед, укажем, что в период летнего муссона зона отсутствия инверсии, по нашим данным, сместилась на 10—15° к северу, а в районе Мадагаскара появились задерживающие слои. Данные Эмона подтверждают факт образования инверсии на Мадагаскаре в этот период времени. Короче говоря, полученная нами картина согласуется с

результатами предыдущих исследований, что свидетельствует о сравнительной устойчивости выявленных особенностей в распределении задерживающих слоев.

Дальнейший анализ проводился нами по отдельным районам океана с юга на север и с востока на запад, в соответствии примерно с маршрутом и/с «Витязь» в 31-м рейсе.

Из рис. 2, *а* видно, что в районе океана, расположенном к югу от зоны отсутствия задерживающих слоев, отмечается наибольшее число случаев с чисто инверсионным распределением температуры, особенно на востоке района. Градиент температуры в слоях инверсии ни в одном случае не превышал 1°/100 *м*. В восточной части района наблюдается наименьшая мощность инверсионного слоя (<500 *м*) и относительно небольшая высота его нижней границы. По направлению к западу и к северо-западу инверсии сменяются изотермией и слоями резкого уменьшения градиента, одновременно увеличивается мощность задерживающего слоя (рис. 2, *б*) и повышается нижняя граница слоя.

Относительная влажность воздуха в этом районе под задерживающим слоем, как правило, с высотой не изменялась, или же несколько увеличивалась (от 70—75% до 80—85%). В слое инверсии наблюдалось уменьшение относительной влажности на 20—25%.

Просмотр синоптических карт, составленных в 31-м и 33-м рейсах и/с «Витязь», показал, что над всей центральной частью рассматриваемого района в это время располагался Южно-Индийский антициклон, который занимал примерно свое среднее положение, указанное в работе [17], а на востоке района между Австралией и Индонезией — отрог этого антициклона, также отмеченный на картах Стехновского. Циклоническая деятельность развивалась над Австралией. Влияние одного из Австралийских циклонов, по всей видимости, сказалось на вертикальном распределении температуры воздуха на станциях, выполненных вблизи западного побережья Австралии, где, как можно видеть на рис. 2, *а, б*, несколько увеличилась мощность задерживающего слоя и поднялась его нижняя граница.

Приземный ветер на всем пути следования и/с «Витязь» в этом районе, как правило, был восточным или юго-восточным. Западные направления отмечались лишь у берегов Австралии, где сказывалось влияние австралийских циклонов. Шаропилотные наблюдения проводились здесь всего семь раз. Из них в трех случаях в задерживающих слоях не наблюдалось никаких изменений в направлении или скорости ветра, по сравнению с выше или ниже лежащими уровнями; в четырех же случаях такие изменения были обнаружены. При этом ниже задерживающего слоя ветер был юго-восточным, в слое он сменялся северо-восточным, выше он опять становился юго-восточным.

Все четыре случая относятся к району южнее Явы, где ветры с северной составляющей должны быть, по-видимому, теплее, чем ветры с южной составляющей. Не исключена возможность, что к югу от Явы определенную роль в образовании инверсий играют потоки воздуха различного происхождения. Эта догадка нуждается, конечно, в проверке на базе более обширного материала наблюдений.

Что касается задерживающих слоев во всей остальной части рассматриваемого района, то, на наш взгляд, они определенно являются инверсиями оседания. Об этом свидетельствует характерное для инверсий оседания изменение с высотой температуры и влажности воздуха. Существенным фактором является то, что задерживающие слои располагаются в области высокого давления. Кроме того, распределение инверсий хорошо согласуется с распределением дивергенции скорости приземного ветра [18] и, следовательно, с вертикальными потоками воздуха. Так, на востоке района, где наблюдается резкая инверсия, дивергенция

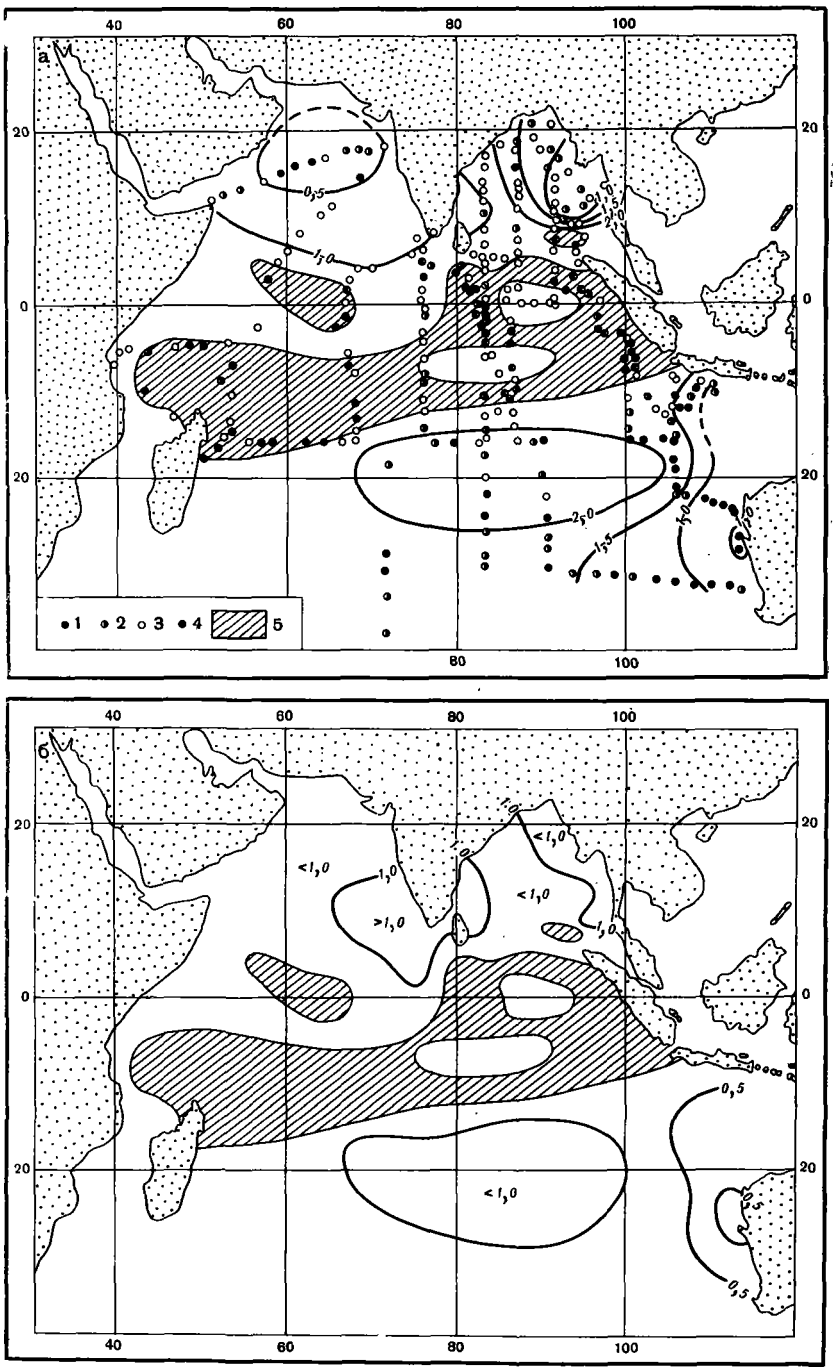
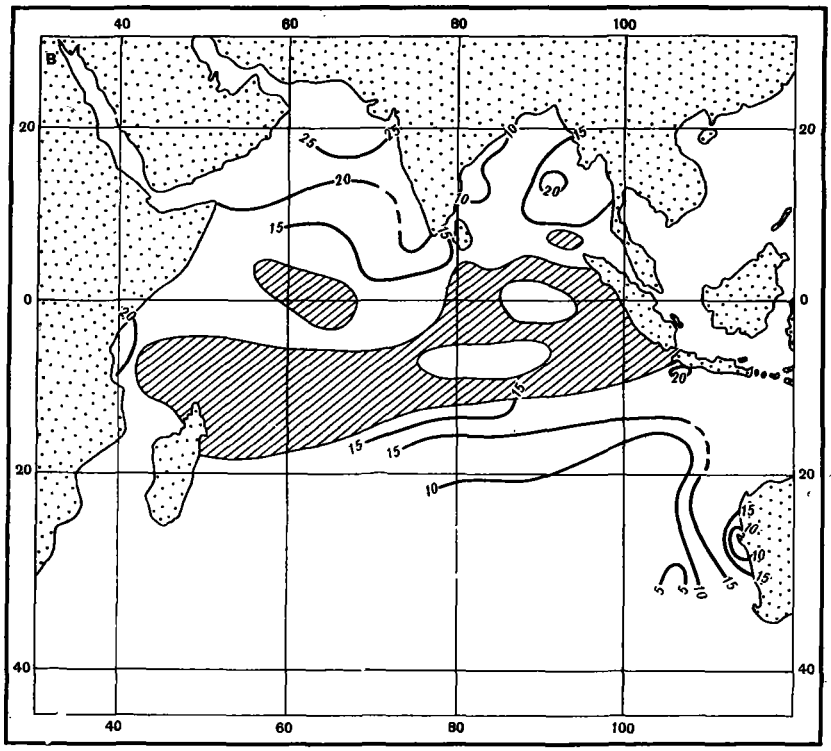


Рис. 2 (стр. 76—77). Характеристики задерживающих слоев в период зимнего муссона

а — высота нижней границы задерживающих слоев (в *км*); *б* — мощность (в *км*); *в* — температура нижней границы; *г* — уменьшение относительной влажности в задерживающих слоях (в %). *1* — инверсия; *2* — изотермия; *3* — резкое уменьшение температурного градиента; *4* — отсутствие задерживающего слоя; *5* — зона отсутствия задерживающих слоев


B'
40
60
80
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20
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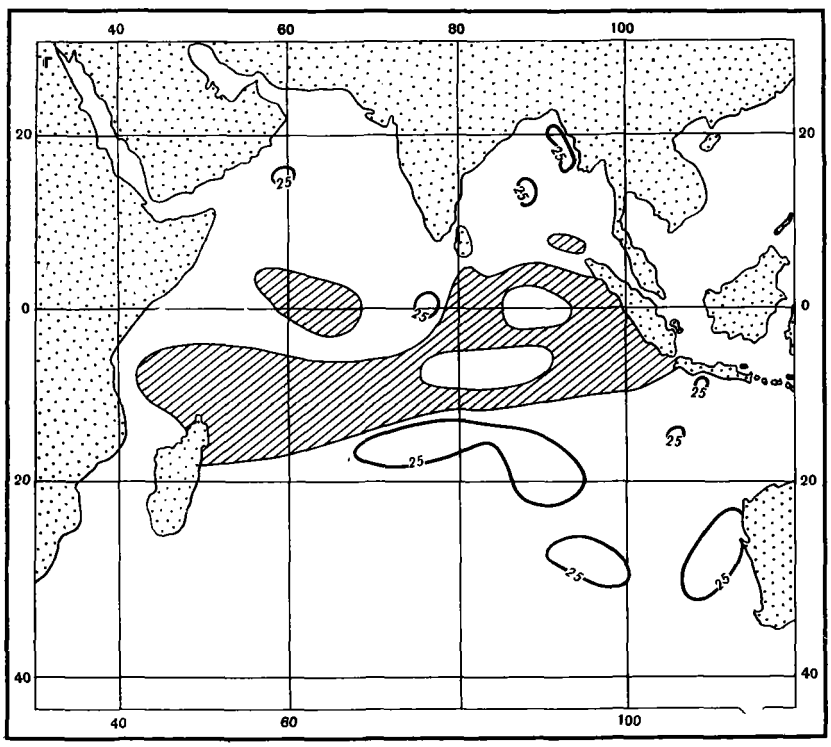
10
5


40
60
80
100
20
0
20
40
25

скорости ветра в январе оказывается наибольшей; к западу, где инверсия ослабляется, уменьшается и дивергенция скорости ветра.

Карты дивергенции скорости ветра были построены по средним многолетним данным, и поэтому указанное совпадение свидетельствует о близости полученной картины распределения задерживающих слоев в данном районе к средним многолетним условиям.

Севернее рассмотренного района располагается зона отсутствия задерживающих слоев. При подходе к ней обычно наблюдалось постепенное изменение вертикального распределения температуры и влажности: постепенно увеличивалась высота нижней границы слоя, ослабевали инверсионные градиенты в задерживающих слоях. Окончательное исчезновение задерживающего слоя в нижних 3—3,5 *км* обычно происходило в то время, когда, судя по ряду признаков (сдвиг ветра, мощная облачность, осадки, большая влажность), судно оказывалось в зоне внутритропической конвергенции. В 31-м рейсе и/с «Витязь» при движении на север отсутствие задерживающего слоя было отмечено 25 декабря. В отчете синоптика этого рейса Ю. Завернина написано следующее «25 декабря на 10°30′ ю. ш. была пересечена зона тропической конвергенции[1]. При ее пересечении (хотя в поле ветра она выражена очень четко) значительной облачности не наблюдалось. Дожди были только кратковременными, ливневыми. Основное ухудшение погоды наблюдалось в зоне северной конвергенции...». В 33-м рейсе зондирование не обнаруживало задерживающего слоя на 10°42′ ю. ш. В отчете синоптика 33-го рейса В. Г. Снопкова читаем «6 и 7 января 1961 г. на 10°42′ ю. ш. выполнялась суточная станция. В это время на этой широте находился тропический фронт. В связи с этим наблюдалось развитие облачности до 10 баллов. За 6 и 7 января выпало около 10 *мм* осадков. При этом ветер был от 4 до 5 *м/сек* и дальнейшего усиления его не наблюдалось. 12 января вблизи экватора «Витязь» пересек северную зону тропической конвергенции, что сопровождалось увеличением облачности, выпадением осадков и поворотом ветра с западного на северо-восточное».

Учитывая сказанное, видимо, можно считать, что отсутствие задерживающих слоев в приэкваториальном районе является неплохим индикатором зоны внутритропической конвергенции (если поблизости нет каких-либо самостоятельных депрессий, не связанных с этой зоной), поскольку он отмечает вхождение в зону даже в тех случаях, когда некоторые из характерных признаков границ зоны внутритропической конвергенции (усиление ветра, мощная облачность) отсутствуют.

Как видно из рис. 2, *а*, в восточной части заштрихованной зоны имеется два разрыва. Происхождение более южного из них, на наш взгляд, связано с миграциями зоны внутритропической конвергенции, которые могут быть весьма значительными. Некоторым показателем смещения зоны внутритропической конвергенции могут быть, например, данные об изменении положения изобары 1010 *мб* на каком-либо из подходящих меридианов.

Для меридиана 71° в. д. с 1 по 11 января 1961 г. было получено соответственно следующее положение изобары: 9, 16, 19, 15, 16, 13, 12, 15, 6, 11, 12 ю. ш.

Эти данные приведены в отчете 31-го рейса и/с «Витязь».

Таким образом, в период с 8 по 9 января изобара 1010 *мб* сместилась к северу до 6° ю. ш. Можно предположить, что соответствующим образом к северу сместилась и зона внутритропической конвергенции.

[1] В данном случае под тропической конвергенцией и тропическим фронтом понимается южная граница, а под северной конвергенцией — северная граница зоны внутритропической конвергенции в нашем понимании. Дискуссию о терминологии можно найти в работе [19].

Так, вечером 8 января «Витязь», находясь на широте 6°, оказался южнее зоны внутритропической конвергенции. Здесь опять наблюдался задерживающий слой. На следующий день «Витязь», идя на север, снова вышел в зону внутритропической конвергенции, и задерживающий слой пропал.

Очень интересно было выяснить условия образования задерживающего слоя в районе экватора, между 85 и 95° в. д., где и/с «Витязь» работало с 9 по 11 февраля 1961 г. В это время здесь наблюдалась сплошная кучевая облачность (высота основания 1000 *м*) и западный приземный ветер. Шаропилотные наблюдения, к сожалению, не проводились. Судя по синоптическим картам, составленным в рейсе, вдоль экватора в это время располагался слабый гребень, к северу и к югу от которого находились области более низкого давления (на 1 *мб* ниже, чем в гребне). Этот гребень, а вернее связанная с ним вертикальная циркуляция (оседание), по-видимому, и обусловила образование задерживающего слоя.

Насколько закономерно образование задерживающего слоя в этом районе? Карты дивергенции скорости ветра, построенные по данным, осредненным для пятиградусных «квадратов», являются недостаточно детальными для анализа явления, наблюдающегося в узкой приэкваториальной зоне. Все же на январской карте дивергенции в этом месте можно заметить небольшое пятно положительной дивергенции скорости ветра (нисходящие потоки), к северу и к югу от которого знак дивергенции меняется на обратный. Небольшой гребень в этом месте показан также на январской карте среднего многолетнего давления, составленной недавно Вейкманом [20], т. е. можно говорить о режимности задерживающих слоев у экватора на востоке Индийского океана.

Заметим, что в период летнего муссона в этом месте также были обнаружены задерживающие слои, причем более резкие (изотермия) и по более полным данным.

Как видим, в восточной части Индийского океана, так же как это раньше было обнаружено в Тихом океане, происходит раздвоение зоны отсутствия задерживающих слоев, а следовательно, и зоны внутритропической конвергенции.

Нам известны две гипотезы, объясняющие раздвоение зоны внутритропической конвергенции в приэкваториальном районе; гипотеза Флетчера [21] и гипотеза Россби [22].

Флетчер объясняет раздвоение экваториальной зоны затишья термическими причинами, полагая, что «испарение, охлаждение воздуха и уменьшение инсоляции под облачным покровом первоначального единого экваториального пояса должны привести к изменению знака термических сил и создает холодный источник и нисходящее движение ниже первичного облачного покрова». Россби, изложив вначале свою точку зрения на происхождение экваториальных восточных ветров, затем пишет: «Повсюду, за исключением ближайшей окрестности экватора, такой пояс восточных ветров должен подвергаться действию сил Кориолиса, направленных к полюсу. Вследствие существования двух поясов восходящего движения (по одному с каждой стороны от экватора) и соответствующих меридиональных циркуляций для сохранения динамического равновесия должны иметь место градиенты давления, направленные на высоких уровнях к экватору. Таким образом, мы приходим к гораздо более сложным моделям ячеек для экваториальной области, до некоторой степени напоминающим модели, предложенные Флетчером для объяснения двойной экваториальной зоны затишья: но происхождение и положение этих новых «колес» циркуляции являются следствием скорее динамических, чем термических причин».

Как видим, объяснения Россби и Флетчера в корне различны.

Однако следствия из их рассуждений, касающиеся вертикальной циркуляции у экватора, а следовательно, и вертикального распределения температуры и влажности, почти одинаковы. По любой из этих гипотез может возникать инверсия оседания, правда, по мнению Россби, который учитывает силу Корнолиса, она возникает строго на экваторе, по Флетчеру же — она может оказаться и в стороне от экватора.

Поскольку в нашем случае задерживающий слой наблюдался на экваторе, решить, какая из гипотез более справедлива, невозможно.

Заканчивая обсуждение приэкваториального разрыва зоны, стоит отметить, что если бы мы, следуя Фиккеру, не выделяли зону отсутствия задерживающих слоев, то нам бы вообще не удалось подметить своеобразие этого приэкваториального района.

Конфигурация северной границы зоны отсутствия задерживающих слоев оказалась несколько сложнее, чем южной. Это можно объяснить тем, что и поле давления на севере было сложнее, чем на юге. Здесь чаще наблюдались отдельные депрессии, иногда связанные с зоной конвергенции (а иногда и не связанные), в которых, так же как и в зоне, отсутствовали задерживающие слои. На наших картах (рис. 2, *а*) отражены все случаи, когда отсутствовали задерживающие слои независимо от того, наблюдалось ли это в зоне внутритропической конвергенции или в отдельной депрессии. Видимо, в силу этого обстоятельства, общая картина и получилась не очень гладкой.

В Бенгальском заливе наблюдения производились в феврале и марте 1961 г. Как видим, из рис. 2, инверсий в чистом виде здесь нет. Имеются лишь случаи с изотермией и с резким уменьшением градиентов температур. На восточной стороне залива случаев с изотермией больше и основания задерживающих слоев расположены ниже, чем на западной стороне. На синоптических картах за этот период над заливом обычно располагался слабый антициклон или гребень давления с Индокитая, а над восточной Индией — небольшие депрессии. Так распределение задерживающих слоев согласуется с полем давления. Тот факт, что на средних многолетних картах дивергенции скорости ветра этот район характеризуется ее положительными значениями, говорит о режимности задерживающих слоев в Бенгальском заливе. В этом районе было выполнено пять шаропилотных наблюдений. В трех случаях приземный северо-западный ветер в задерживающем слое сменился на юго-западный; в одном — северо-восточный на юго-западный; и еще в одном — никакого изменения ветра в задерживающем слое не произошло. Что можно сказать о таком результате? Естественно предположить, что более южные и более западные ветры должны здесь приносить с собой более теплый воздух, чем ветры северные и восточные. Возможно, смена ветров в значительной степени способствует созданию задерживающего слоя. Однако для каких-либо определенных выводов нужны, конечно, более обширные материалы наблюдений.

О распределении задерживающих слоев над западной примадагаскарской частью Индийского океана в начале статьи мы уже немного говорили. Следует заметить, что интенсивность процессов дивергенции в этом районе, по-видимому, существенно ослаблена по сравнению с восточным районом, поскольку здесь не наблюдалось ни одного случая чистой инверсии и даже изотермии.

Положение зоны отсутствия задерживающих слоев здесь соответствует среднему многолетнему январскому положению зоны внутритропической конвергенции [23, 3, 20]. К северу от основной зоны намечается вторая полоса отсутствия задерживающих слоев, однако наблюдений здесь очень мало, и ее положение, конечно, малонадежно.

Наконец, очень низкие и довольно интенсивные задерживающие слои наблюдались в апреле 1960 г. в Аравийском море. В это время

здесь стояла ясная и сухая погода. Над районом плавания почти все время располагался антициклон (с одной-двумя замкнутыми изобарами через 2,5 *мбар*) или гребень высокого давления с Аравийского полуострова. Приземный ветер был различным в зависимости от того, в каком секторе антициклона или гребня проводились наблюдения. Ветер на высотах измерялся три раза. Во всех трех случаях в задерживающем слое наблюдался поворот ветра к более южному (13 апреля — у земли с ССЗ на СЗ, 14-го — с З на Ю и 16-го — с В на ВЮВ).

Судя по средним многолетним картам давления Вейкмана, существование антициклона над Аравийским морем в апреле является обычным состоянием. На апрельской карте дивергенции результирующего ветра над Аравийским морем располагается область положительной дивергенции. Все это тоже говорит о режимности задерживающих слоев в этом районе.

ПЕРИОД ЛЕТНЕГО МУССОНА

Как уже отмечалось, располагая разновременными наблюдениями, мы можем характеризовать задерживающие слои над различными районами океана только в определенный период, когда были произведены эти наблюдения. Но это в большей степени относится к западной части океана, так как в восточной, особенно в приэкваториальных районах, наблюдения в различных рейсах охватывают почти все месяцы исследуемого периода.

В период летнего муссона термический экватор располагается в северном полушарии. Перемещается к северу и полярный фронт в южной части океана. Соответственно этому барические центры действия атмосферы занимают наиболее северное положение.

Значительный сезонный ход намечается и в положении зоны внутритропической конвергенции. Уже упоминаемые ранее карты дивергенции показывают, что зона конвергенции смещается к северу, при этом в западном районе это смещение достигает 10—15° широты. К тому же субтропический пояс повышенного давления в южной части океана не представляет собой единого целого, а имеет ряд замкнутых областей. Области антициклогенеза расположены, например, над западной частью океана и над Австралией. Именно в западной части и у берегов Австралии наблюдается некоторое увеличение числа инверсий (рис. 3, *а*).

Над остальными районами океана преобладает более слабое оседание и образование изотермии или слоев с резким уменьшением градиента температуры.

По обе стороны от экватора примерно с 12° ю. ш. до 2° ю. ш. и от 0—3° с. ш. до 5° с. ш. на западе и 11° с. ш. на востоке (рис. 3) расположены две зоны с отсутствием задерживающих слоев. Западная и восточная границы южной зоны ввиду отсутствия наблюдений проведены нами весьма приблизительно. Именно в этих зонах сосредоточено основное число наблюдений, которые показывают отсутствие задерживающих слоев (42 из 51 в данный период). Зоны отсутствия задерживающих слоев соответствуют зоне внутритропической конвергенции.

Однако у экватора эта зона прерывается полосой с хорошо выраженными задерживающими слоями в виде изотермии и резкого уменьшения градиента.

Наличие задерживающих слоев у экватора может быть объяснено лишь устойчивой зоной дивергенции в этом районе, так как наблюдения проводились на четырех разрезах, выполнеиных в различное время. Наблюдения в 35 рейсе и/с «Витязь» указывают на дивергенцию приземного ветра у экватора, а аэрологические данные подтверждают этот вывод (рис. 4).

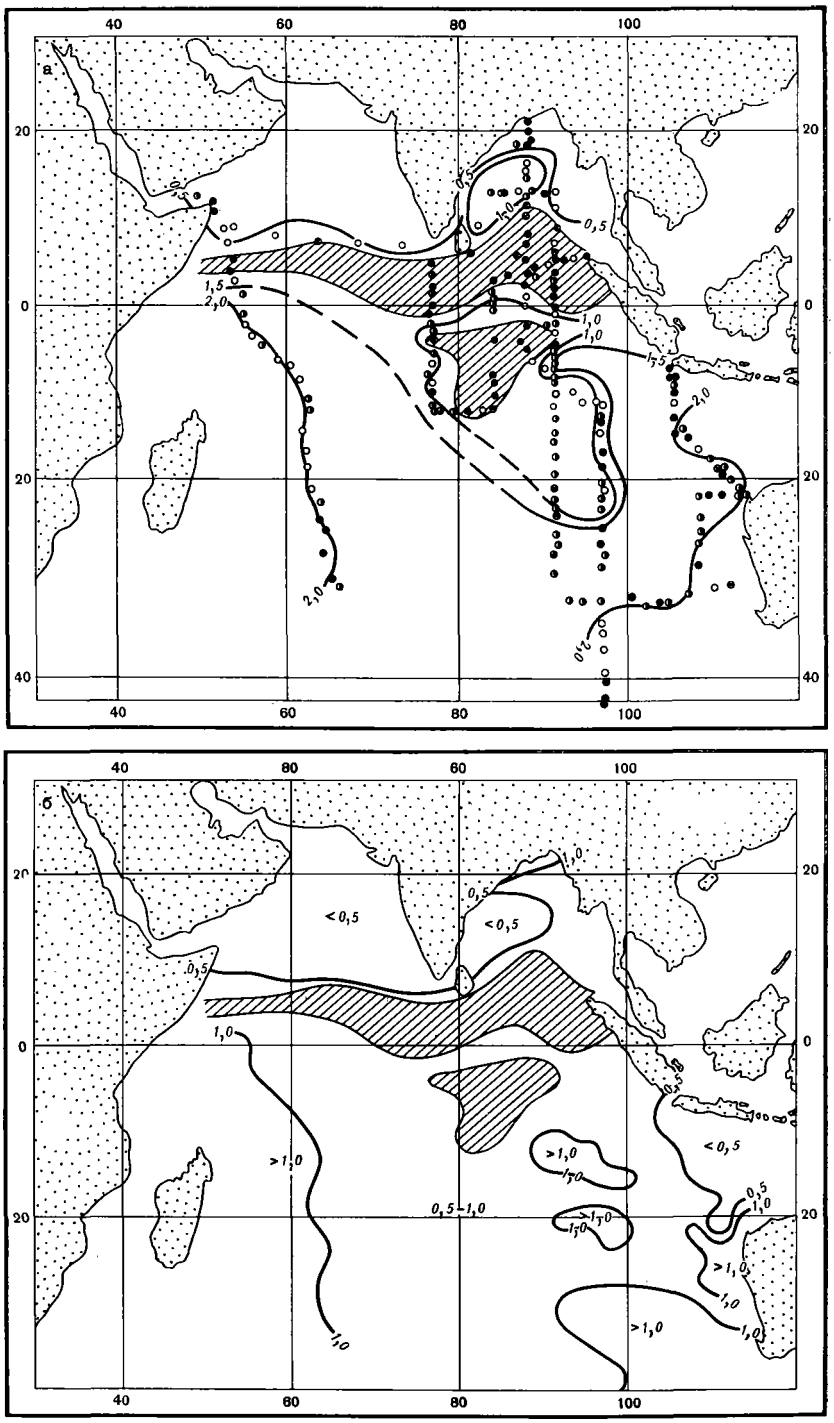
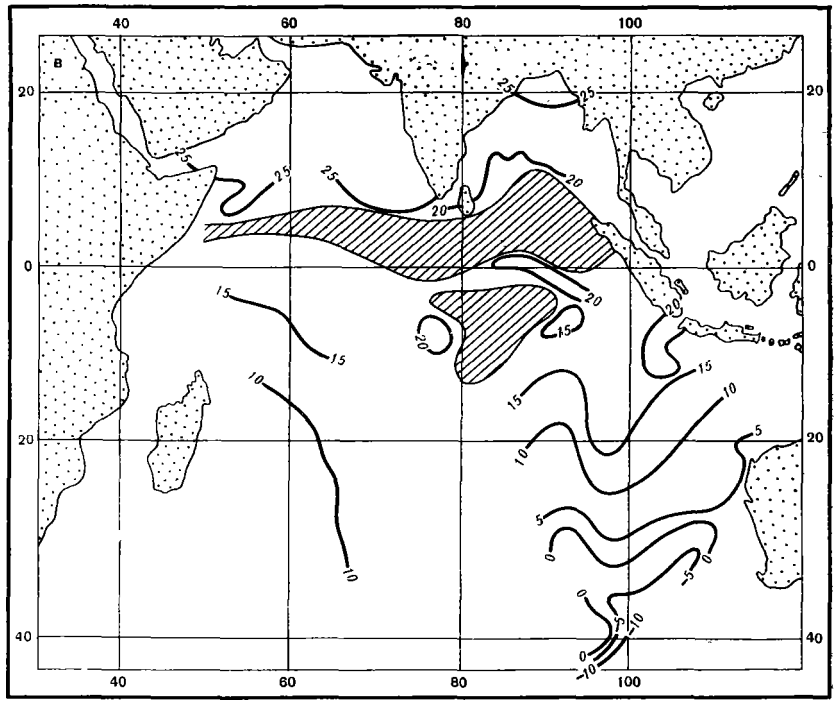
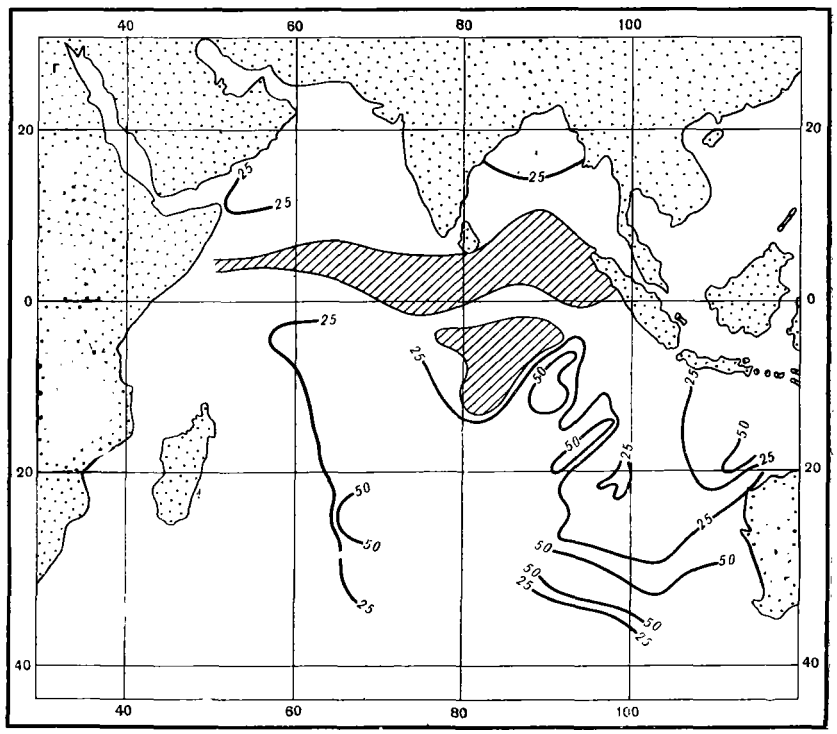


Рис. 3 (стр. 82—83). Характеристики задерживающих слоев в период летнего муссона

Обозначения те же, что на рис. 2


40
60
80
100
20
0
20
40
В
25
20
15
10
5
0
-5
-10


40
60
80
100
20
0
20
40
Г
25
50

По данным Верплоха [24], в Индийском океане в летний период на экваторе расположен небольшой гребень повышенного давления, а его расчеты дивергенции по одноградусным квадратам указывают на наличие у экватора узкой полосы дивергенции. К северу и югу от нее расположены зоны конвергенции. Эти расчеты были проведены по многолетним данным. Следовательно, мы можем говорить о режимности указанного явления.

Наличие задерживающих слоев в Бенгальском заливе отмечено по наблюдениям на и/с «Витязь» в октябре 1962 г., на д/э «Обь» в мае 1957 г. Высота нижней границы задерживающих слоев была порядка

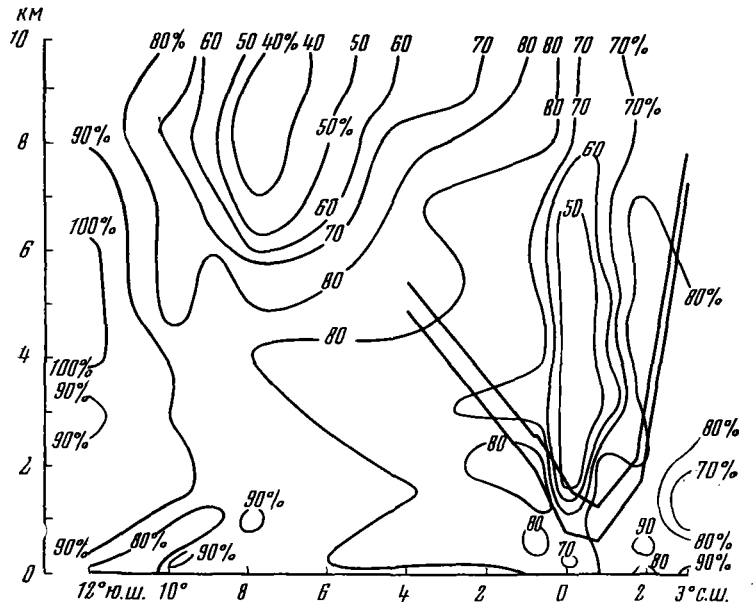


Рис. 4. Вертикальное распределение относительной влажности (в %) на разрезе по 84° в. д. (по данным 35-го рейса и/с «Витязь», с 19 по 27 октября 1962 г.)

1000 *м*, а к северу она уменьшалась до 500 *м* и даже ниже. В устье Ганга, по данным С. П. Хромова [8], инверсия 14 мая 1957 г. распространялась от поверхности моря до 230 *м*, над нею же до 1220 *м* была изотермия.

При этом разность температур вода — воздух к северу от 17° с. ш. была отрицательной и воздух почти во все сроки наблюдений был теплее воды (иногда до 1°, а в среднем на 0°,4). Очевидно это является причиной образования приземной инверсии в северном районе Бенгальского залива. Но задерживающие слои всех трех видов наблюдаются уже с 11° с. ш. Причина их образования, на наш взгляд, возможно объясняется ветровым режимом в этом районе.

В нижних слоях примерно до 1000—1500 *м*, по данным Вагнера и Рамакришнана [25, 26], преобладает южный и юго-западный перенос относительно теплого и влажного воздуха с океана. В более высоких слоях господствует западный перенос прогретого и сухого континентального воздуха из Индии. Это может приводить к образованию задерживающих слоев. На рис. 3, *а* показана высота нижней границы задерживающих слоев.

Высота основания задерживающих слоев в Индийском океана в этот период отличается от той картины, которую Фиккер дал для Атланти-

ческого океана. Наибольшие высоты характерны для юго-восточного района океана. Нижняя граница задерживающих слоев расположена здесь на высоте примерно 2000 *м*.

В западном районе основание задерживающих слоев отмечается на высоте около 2000 *м*, но данных для более точного анализа недостаточно. По сведениям Эмона, высота основания инверсии на Мадагаскаре и о-ве Маврикия в период с апреля по октябрь колеблется в пределах 2—3,5 тыс. *м*. В центральных областях океана высота нижнего основания задерживающих слоев понижается до 1,5—1,0 тыс. *м*. В районе экватора задерживающие слои расположены на высоте 600—1000 *м*, а к северу и югу (к границам зоны отсутствия задерживающих слоев) их основание повышается до 2000—4000 *м*. В Бенгальском заливе основание слоев расположено, как уже упоминалось, на высоте около 1000 *м*. В северной части Бенгальского залива и в Аравийском море высота опускается до 500 *м* и ниже. Это, очевидно, связано с уже упоминавшейся приземной инверсией, т. е. образованием задерживающих слоев у подстилающей поверхности.

Мощность задерживающих слоев (рис. 3, *б*) находится в соответствии с высотой их нижней границы, т. е. чем выше основание, тем больше мощность. В восточном районе океана мощность слоя увеличивается до 1000 *м* и более. В западном районе, по сведениям Эмона, мощность инверсии изменяется в пределах 400—800 *м*. По данным д/э «Обь», в некоторых местах она достигает величины до 1000—1200 *м*.

В центральных районах океана мощность задерживающих слоев изменяется в широких пределах от 500 до 1000 *м*. В районе экватора мощность задерживающих слоев — от 500 до 700 *м*, к границам она уменьшается до 440—500 *м*. В Бенгальском заливе мощность слоев колеблется до 500 *м*, а в северной части увеличивается до 700—1000 *м*. В Аравийском море мощность приземных задерживающих слоев невелика и колеблется от 90 до 500 *м*. В зависимости от широты места и высоты основания слоя находится температура его нижней границы (рис. 3, *в*). В восточном районе, находящемся в наибольшем удалении от экватора, высокие задерживающие слои характеризуются наиболее низкой температурой нижней границы. Она изменяется от —10 до +10°.

Температура нижней границы задерживающих слоев в западном районе около 10°, но для более подробной характеристики данных недостаточно, то же самое можно сказать и о центральных районах океанов.

К северу от 10° ю. ш. температура изменяется от 12—15° до 20—22°.

В Бенгальском заливе температура нижней границы задерживающих слоев колеблется от 20 до 30°.

На рис. 3, *г* представлено уменьшение относительной влажности в задерживающих слоях в период летнего муссона. Максимальное уменьшение относительной влажности (на 50—70%) отмечается в восточном районе океана, где располагаются наиболее мощные и высокие задерживающие слои.

Еще один район с большим уменьшением влажности располагается к северо-западу от Австралии. В центральных областях океана относительная влажность уменьшается в пределах до 50%. Но к востоку и северу (в приэкваториальной области) происходит резкое падение перепада влажности до 7—20%.

Такие же значения наблюдаются севернее зоны отсутствия задерживающих слоев, за исключением северного района Бенгальского залива, где падение влажности выражается величинами от 25 до 46%, и западного района Аравийского моря, где было отмечено уменьшение влажности на 26%.

ВЫВОДЫ

1. В отличие от карт Фиккера для Атлантического океана, на картах для Индийского океана, по нашим данным, в приэкваториальных районах отмечается широкая зона отсутствия задерживающих слоев, связанная с зоной внутритропической конвергенции. Эта зона существует во все сезоны.

2. Зона внутритропической конвергенции испытывает значительные сезонные смещения. В соответствии с этим происходят сезонные смещения зоны отсутствия задерживающих слоев.

В период летнего муссона она расположена на 10—15° севернее своего положения в период зимнего муссона.

3. В период летнего и зимнего муссонов в восточной части Индийского океана у экватора располагается сравнительно узкая полоса дивергенции воздушных потоков. Это приводит к образованию полосы с задерживающими слоями внутри зоны отсутствия задерживающих слоев. Наличие задерживающих слоев у экватора при отсутствии других данных может служить косвенным признаком дивергенции воздушных потоков в этом месте.

4. В результате большого числа фактических наблюдений были отмечены значительные суточные колебания в положении границ зоны внутритропической конвергенции. Можно предположить, что зона отсутствия задерживающих слоев также испытывает значительные суточные колебания, в результате чего границы этой зоны, где происходит постоянная перестройка задерживающих слоев, выражена недостаточно четко.

5. Причины образования задерживающих слоев в различных районах океана различны. В основном их образование связано с крупномасштабным оседанием в антициклонах или в пассатной зоне.

В Бенгальском заливе в период летнего муссона задерживающие слои образуются в результате смены воздушных потоков на высоте около 1000 *м*.

В северной части Бенгальского залива, в Персидском заливе и Аравийском море задерживающие слои могут образовываться в результате приземной инверсии температуры, вызванной отрицательной разностью температур вода — воздух.

Для более обстоятельного и детального изучения вопроса о зоне внутритропической конвергенции, о задерживающих слоях и причинах их образования необходимы данные ветрового зондирования, но эти исследования в настоящее время на и/с «Витязь» не проводятся.

ABSTRACT

Using the aerological data of the five Indian Ocean surveys (three on the «Vitjaz» and two on the «Ob») the maps of some features of the inversion layers in the lower troposphere are constructed for the Indian Ocean tropical part in the summer and winter monsoon. The cause of the arising of the inversion layers and its relation to the region of the surface winds divergence and convergence are discussed. The results are compared with those received for the Atlantic and Pacific Ocean by other authors.

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Calculation of Turbulent Fluxes by Integral Methods[1]

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ABSTRACT

Aircraft and dropsonde measurements of humidity and wind velocity over the Indian Ocean during the winter monsoon season have been used to calculate the horizontal flux of water vapor and the rate of evaporation from the water surface. Calculations of evaporation over areas several hundred kilometers on a side are compared with calculations made at a point from buoy measurements of the vertical profiles of wind velocity, humidity and temperature. Using direct measurements of differences in horizontal flux, large errors occurred in three of nine cases; these discrepancies may be traced to changes in the wind field which occurred during the flights of the observing aircraft. Using values of horizontal flux divergence estimated from the heat flux equation, the two independent methods agree in sign and in approximate magnitude. The results are also compared with a small sample of aircraft measurements of the covariance of vertical velocity and absolute humidity. Individual values of covariance taken over 1-min periods vary widely in sign and magnitude, but average values agree in sign and approximate magnitude with results using the other methods.

Further comparisons of the integral, covariance and profile methods for calculating vertical fluxes in the boundary layer are proposed, and suggestions are made for coping with more complex situations.

1. Introduction

The problem of specifying boundary layer fluxes with reasonable accuracy and detail is among the most important and the most difficult encountered in meteorology; important, because large-scale predictions beyond a few days depend critically on this information; difficult, because the fluxes must be described on time and space scales which are compatible with the large-scale prediction model. This means that average values of the vertical fluxes of water vapor, heat and momentum in the boundary layer must be determined on scales of, let us say, 500 km in space and 12 hr in time. One will want to be able to relate these large-scale average fluxes to gross properties of the atmosphere and ocean near the surface, probably measured at a single point; for example, the average wind speed, temperature and humidity at a certain height, surface temperature, and some property of the wave spectrum. To do this requires an extensive series of observations designed to compare vertical fluxes measured at a point or over limited areas with large-scale averages. It is important that methods be used which are independent in either basic principle or in technique of measurement and data reduction, or preferably, in both.

Boundary layer fluxes may be measured using the following more or less independent methods.

a) The flux of water vapor (or enthalpy, or horizontal momentum) near the interface may be determined directly from the covariance of vertical velocity and absolute humidity (or temperature, or horizontal velocity).

b) The conservation equations for water vapor (enthalpy, momentum) may be formulated so as to express boundary layer flux as a function of observable differential or integral terms (the so-called budget method).

c) Observations of equilibrium vertical profiles of horizontal velocity and humidity (temperature, horizontal velocity) may be used to calculate vertical fluxes through the aerodynamic or profile theory.

d) The turbulent transfer coefficients and the vertical fluxes may be calculated through the use of Kolmogoroff's law which relates the energy spectrum and wave number in the inertial subrange.

Methods a) and b) above provide direct and essentially independent measurements of vertical flux, whereas c) and d) require assumptions which, especially over water surfaces, remain subjects of active inquiry. Methods a), c) and d) are applied a few meters above the interface where it is reasonable to assume steady state in time and space, even though on the scale appropriate to method b) the fluxes may vary in space and time. For discussion of these matters and of the covariance method, see Lumley and Panofsky (1964).

Each of the methods listed has its inherent difficulties and limitations; consequently, rather special circumstances and careful planning are needed in order to carry out a program of comparative observations. In the following we describe a pilot project, as simple as possible commensurate with the objective, which

[1] Contribution No. 136, Department of Atmospheric Sciences, University of Washington.

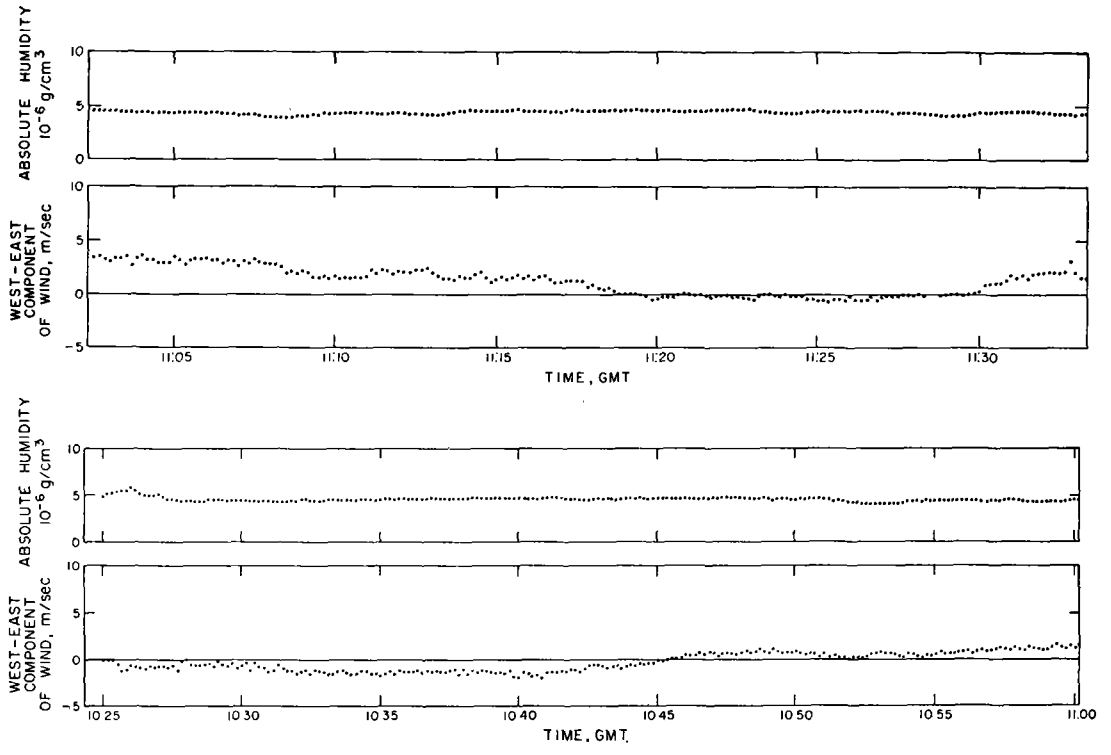

FIG. 1a. Time series of the west-east wind component and absolute humidity at 1.3 km taken on two successive traverses of the observing area, 17 February 1964.

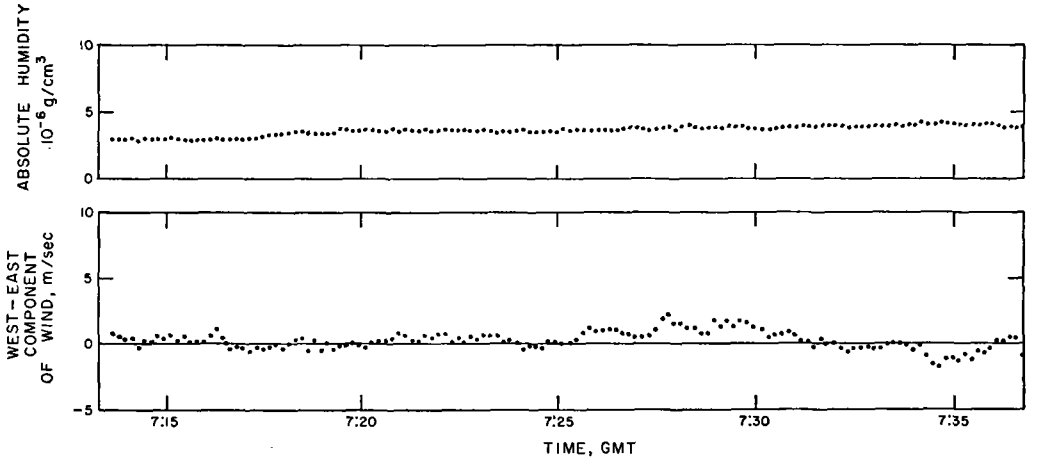

FIG. 1b. Time series of west-east wind component and absolute humidity at 0.5 km taken along the east side of the observing area, 25 February 1964.

was planned initially by the Meteorology Working Group for the Indian Ocean Expedition (Fleagle *et al.*, 1961). The intention was to carry out compatible flux measurements over the ocean by the conservation, covariance and profile methods.

Water vapor flux was considered of greatest importance because over the ocean the energy associated with evaporation usually dominates the enthalpy transfer. The opportunity afforded by the Indian Ocean Expedition was considered especially valuable because during the winter monsoon season 1) the velocity field over the Arabian Sea is likely to be

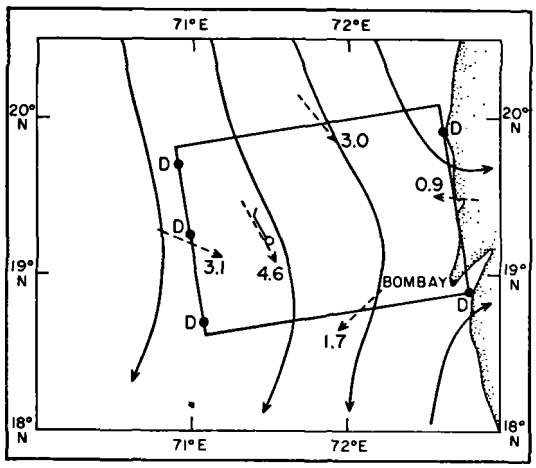

FIG. 2a. Surface streamlines at 1030 and upper winds for 1249 to 1407 local time, 17 February 1964. Dashed arrows represent mean winds at 1.26 km in m sec^{-1}. D's represent dropsondes.

uniform and steady over large areas, 2) the rate of evaporation is likely to be large, and 3) condensation and precipitation are not important. These three conditions are uniquely favorable for a first test of the integral method.

In the following we examine, using the data and experience gained in the pilot project, the potentialities and limitations of integral methods for estimating the rate of evaporation from extensive water surfaces. For reasons of expediency profile measurements have been used as the primary basis of comparison. In addition, scattered values of covariance obtained by the Woods Hole aircraft at heights ranging from 200 to 500 m provide an independent comparison.

2. Design of experiment

In the absence of condensation or evaporation the specific humidity of an element of air is changed only by diffusion across its boundaries. For an open system fixed with respect to the earth's surface, this leads to the conservation statement

$$\int_\tau \frac{\partial \rho_v}{\partial t} d\tau + \int_\tau \nabla \cdot \rho_v \mathbf{V} d\tau = \int_\tau D\nabla^2 q d\tau, \qquad (1)$$

where ρ = air density, $\mathbf{V}$ = velocity, q = specific humidity, τ = volume, D = molecular diffusivity of water vapor, ρ_v = water vapor density (ρq), and where $\nabla\cdot$ is the three dimensional divergence operator, and ∇^2 is the three dimensional Laplacian operator. In the more general case in which condensation and precipitation are included, additional terms must be added to the left side of Eq. (1). These may be written $(dm_w/dt)+P$ where m_w represents the mass of liquid water and ice within the volume of integration and P represents the rate of precipitation over the area. Upon expanding and introducing the divergence theorem, the following alternate forms of Eq. (1) may be written as

$$\int_\tau \frac{\partial \rho_v}{\partial t} d\tau + \int_\sigma \rho_v \mathbf{V}_n d\sigma = D \int_\sigma (\nabla q)_n d\sigma, \qquad (2)$$

$$\int_\tau \frac{\partial \rho_v}{\partial t} d\tau + \int_\tau \rho_v \nabla \cdot \mathbf{V}_h d\tau + \int_\tau \mathbf{V}_h \cdot \nabla \rho_v d\tau + \int_\tau \frac{\partial (\rho_v w)}{\partial z} d\tau = D \int_\sigma (\nabla q)_n d\sigma, \qquad (3)$$

where σ represents surface area, w represents vertical

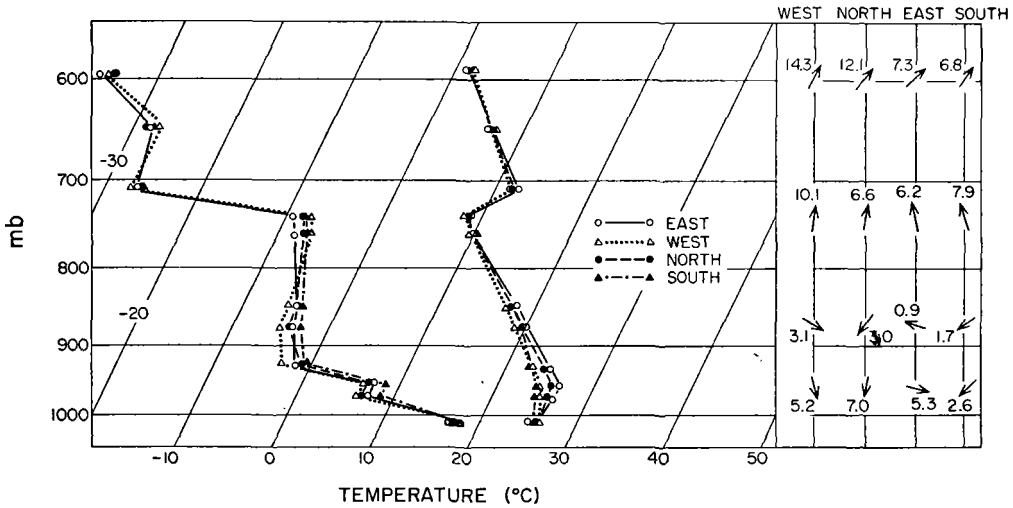

FIG. 2b. Composite temperature and dew-point profiles for 17 February 1964. Arrows represent mean aircraft winds in m sec^{-1}.

velocity, the subscript n indicates the outwardly directed normal component of the vector on the surface, and the subscript h indicates the horizontal component.

The molecular flux terms on the right side of Eqs. (2) and (3) are negligible except for the ocean boundary. If the lower boundary is taken a meter or so above the ocean, molecular flux may be neglected compared to the vertical turbulent flux $\rho_v w$ which emerges from the left side of Eqs. (2) and (3). Then, upon separating the surface integrals into a vertical wall area A and a horizontal cross-sectional area A_h, the two equations become

$$\int_\tau \frac{\partial \rho_v}{\partial t} d\tau + \int_A \rho_v V_{hn} d\sigma + \int_{A_h} (\rho_v w)_{z_2} d\sigma = \int_{A_h} (\rho_v w)_{z_1} d\sigma \equiv \frac{F_E A_h}{L}, \quad (4)$$

$$\int_\tau \frac{\partial \rho_v}{\partial t} d\tau + \int_\tau \rho_v \nabla \cdot \mathbf{V}_h d\tau + \int_\tau \mathbf{V}_h \cdot \nabla \rho_v d\tau + \int_{A_h} (\rho_v w)_{z_2} d\sigma = \int_{A_h} (\rho_v w)_{z_1} d\sigma \equiv \frac{F_E A_h}{L}, \quad (5)$$

where z_2 is the height of the upper horizontal boundary, z_1 the height of flux measurement near the ocean surface, L the latent heat of vaporization, F_E the average upward flux of latent heat at the ocean surface, and the averaging overbars are omitted.

Eq. (5), which separates explicitly the effects of divergence and advection, requires evaluation of volume integrals, whereas Eq. (4) requires primarily evaluation of surface integrals. Surface integrals are inherently easier to measure than are volume integrals, so that Eq. (4) has an advantage over (5). However, cases arise in the experiments described here, especially due to change in the velocity field during the course of the aircraft observations, in which the horizontal velocity divergence cannot be directly determined from the velocity field (the *kinematic method*). In these cases it is useful to separate the vapor advection, which can be measured directly with reasonable accuracy, from the divergence.

The divergence may be estimated independently using the following adaptation of the *adiabatic method* [Panofsky (1951) having described both the kinematic

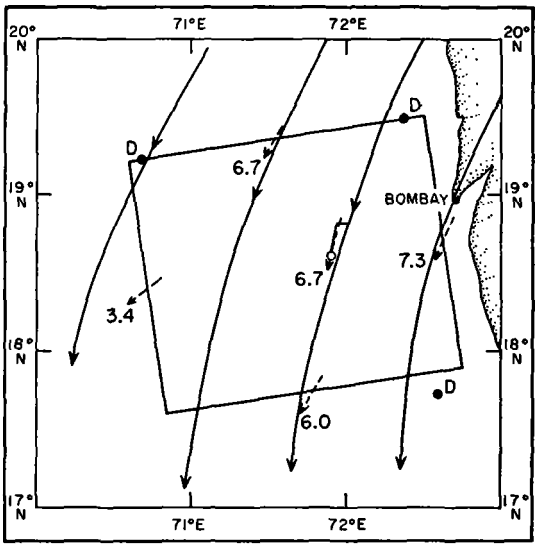

FIG. 3a. Surface streamlines at 1030 and upper winds for 1046 to 1240 local time, 24 February 1964. Dashed arrows represent mean winds at 0.50 km in m sec^{-1}. D's represent dropsondes with no humidity records.

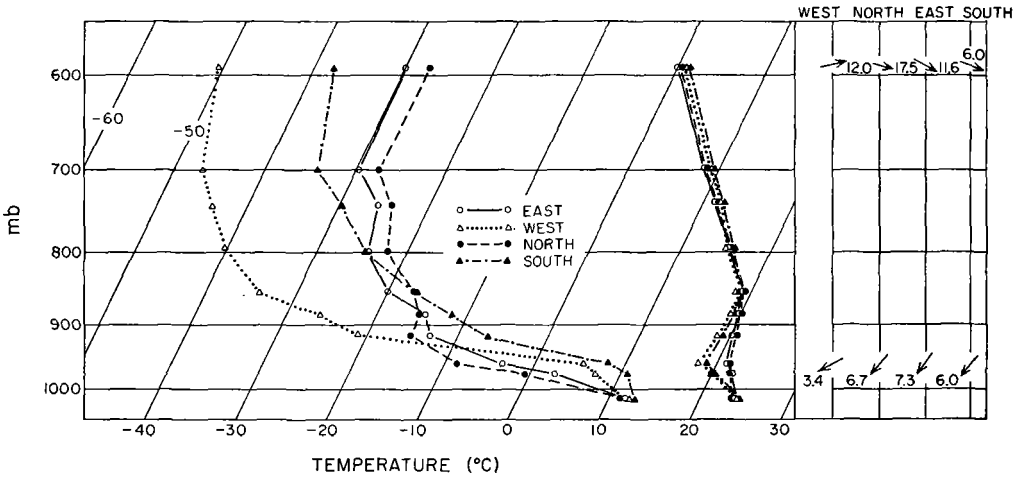

FIG. 3b. Composite temperature and dew-point profiles for 24 February 1964. Arrows represent mean aircraft winds in m sec^{-1}.

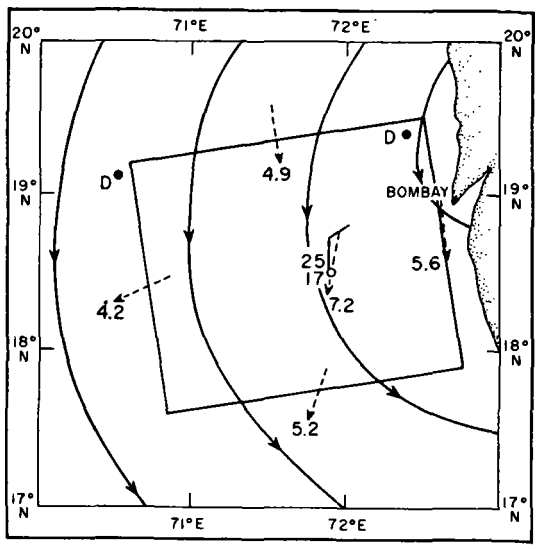

FIG. 4a. Surface streamlines at 1030 and upper winds for 1058 to 1252 local time, 25 February 1964. Dashed arrows on side represent mean winds at 0.50 km in m sec^{-1}. D's represent dropsondes with no humidity record.

and adiabatic methods]. The potential temperature is expressed by $\theta(x,y,z,t)=\theta_0(x,y,t)+\theta^*(x,y,z,t)+\theta'(x,y,z,t)$ where θ_0 represents the time mean at the top of the layer, θ^* the difference between the time mean and θ_0, and θ' the fluctuation. Using this expansion, the adiabatic form of the first law of thermodynamics may be written as

$$\frac{\partial\theta}{\partial t}+\mathbf{V}_h\cdot\nabla\theta+\frac{\partial(\theta^*w)}{\partial z}+\frac{\partial(\theta'w)}{\partial z}-(\theta^*+\theta')\frac{\partial w}{\partial z}=0. \quad (6)$$

Upon introducing the equation of continuity in the last term of Eq. (6), integrating over volume, and averaging over time, we obtain

$$\int_\tau\frac{\partial\bar{\theta}}{\partial t}d\tau+\int_\tau\overline{\mathbf{V}_h\cdot\nabla\theta}d\tau+\int\overline{\theta^*\nabla_h\cdot\mathbf{V}}d\tau-\int\frac{gw\theta^*}{RT}d\tau$$
$$=\int_{A_h}\overline{(\theta^*w)_{z_1}}d\sigma-\int_{A_h}\overline{(\theta^*w)_{z_2}}d\sigma+\int_{A_h}\overline{(\theta'w)_{z_1}}d\sigma$$
$$-\int_{A_h}\overline{(\theta'w)_{z_2}}d\sigma. \quad (7)$$

The last term on the left, which arises from the compressibility term in the equation of continuity, is at least an order of magnitude less than the leading terms and is neglected. The first two terms on the right are separately zero, the first because the mean w is negligible at z_1 (a meter or so above the sea), the second because, by definition, $\theta^*\equiv 0$ at z_2. The last two terms on the right are proportional to the turbulent heat flux at z_1 and z_2, respectively. The MENTOR profile results show that the turbulent flux term at z_1 is typically a fraction of the advection term ($\sim 1/5$); therefore, the difference between the heat flux terms, which is still smaller, may be neglected. It follows that for layers of the order of a kilometer in thickness the mean divergence may be expressed by

$$\nabla_h\cdot\mathbf{V}=-\frac{\dfrac{\partial\theta}{\partial t}+\mathbf{V}_h\cdot\nabla\theta}{\theta^*}, \quad (8)$$

where the overbars have been omitted.

Errors due to approximations are expected to be of the order of 10%, which is comparable to the effects

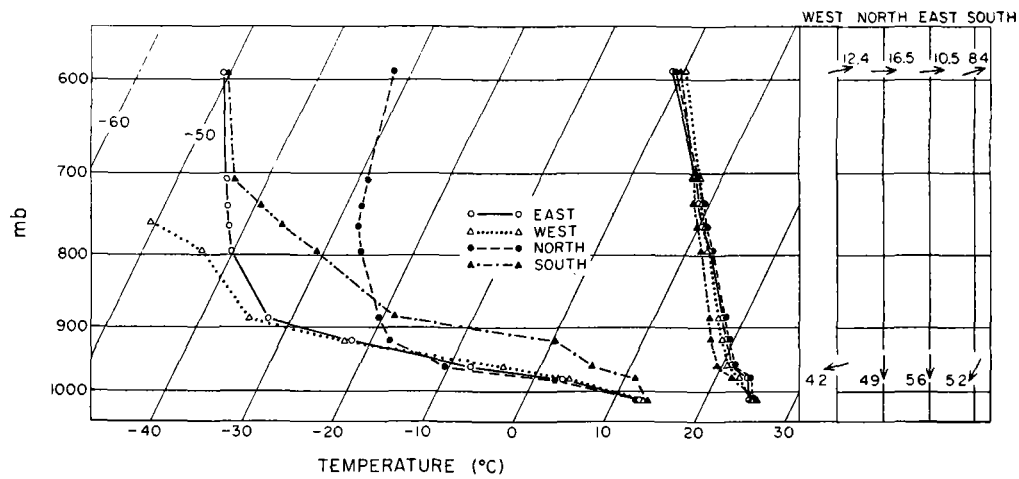

FIG. 4b. Composite temperature and dew-point profiles for 25 February 1964. Arrows represent mean aircraft winds in m sec^{-1}.

of instrumental errors (indicated in Tables 2–8) and is probably smaller than the errors resulting from inadequate data.

Eq. (8) may be used serially to calculate the mean divergence for layers extending from the sea surface to z_2, sea surface to z_3, etc., taking care to redefine θ^* each time. From this series of means it is a simple matter to calculate the mean divergence for the separate layers, z_2 to z_3, etc. The calculated divergences then are substituted into Eq. (5).

For the cases discussed here separate calculations have been made using Eqs. (4) and (5). The former implies direct measurement of horizontal velocity divergence by the *kinematic method* using aircraft velocity measurements, while the latter utilizes the *adiabatic method* as expressed in Eq. (8).

Integral equations expressing conservation of water substance have been applied by Riehl and his collaborators (1951) in a series of studies beginning in 1951; they have been reviewed by Malkus (1962). Benton and Estoque (1954) have estimated, using a conservation equation, the rate of evapotranspiration over North America. Recently, Palmén (1963) has applied a similar equation to the evaluation of evaporation from the Baltic Sea. In each of these cases only standard data were available. Vapor flux was averaged over periods of a month or longer, and comparisons were not made using other methods. These studies provide useful information concerning average values of vapor flux over extended areas and periods, but they provide little information about the dependence of evaporation rate on wind speed, static stability, or other gross properties of the atmosphere or the underlying surface. They also indicate that, even in regions of relatively dense networks of stations, routine surface and upper air data are not quite adequate for calculation of average rates of evaporation which are compatible with the synoptic time scale (a day or less).

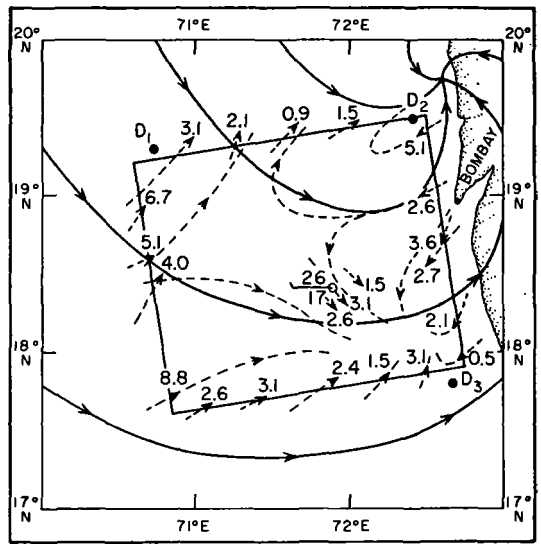

FIG. 5a. Surface streamlines at 1030 and upper winds for 1056 to 1234 local time, 26 February 1964. Dashed arrows represent mean winds at 1.30 km in m sec^{-1}. D's represent dropsondes with no humidity record.

In order to evaluate the surface and volume integrals in Eqs. (4) and (5), the basic observations were planned to be made by two or three instrumented aircraft flying around a closed rectangular course at specified heights. Observations of wind velocity, temperature, and humidity were to be made continuously or at intervals of a few seconds throughout the flights, including ascents and descents. Two aircraft were to fly at the same height on opposite sides of the area,

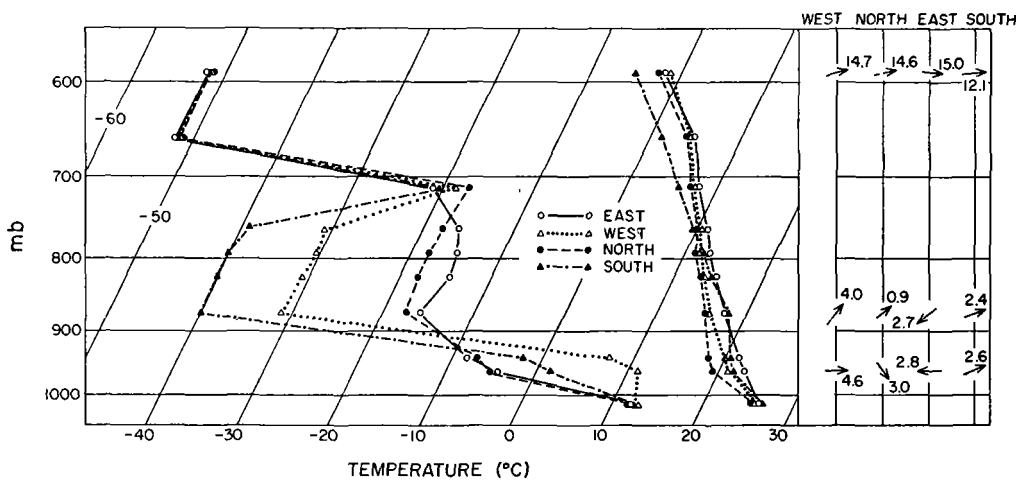

FIG. 5b. Composite temperature and dew-point profiles for 26 February 1964. Arrows represent mean aircraft winds in m sec^{-1}.

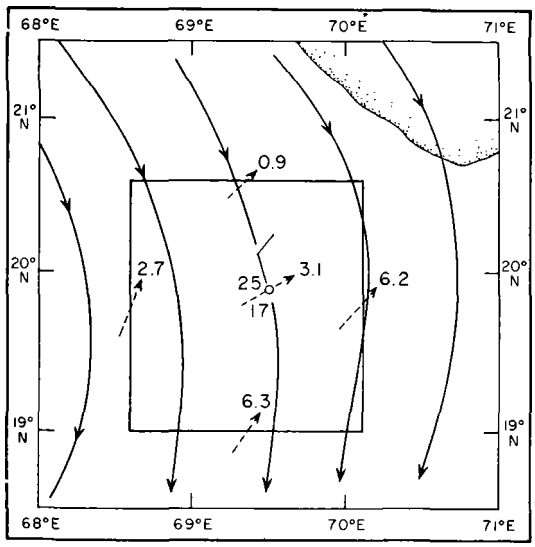

FIG. 6a. Surface streamlines at 1030 and upper winds for 0947 to 1149 local time, 28 February 1964. Dashed arrows represent mean winds at 2.44 km in m sec^{-1}.

so that unambiguous determinations of horizontal divergence could be made. One plane flying at the highest level (~4 km) was planned to launch dropsondes at the maximum rate for which unambiguous records could be obtained (~1 every 15 min). An additional aircraft, equipped for fluctuation measurements, would fly across the enclosed region at low elevation. Each observation was planned to extend over a period of about 2–4 hr and was to coincide with continuous profile observations and fluctuation observations made from an instrumented buoy located near the center of the course.

This scheme for comparison of calculated vertical fluxes provides weak resolution of the integrals in Eqs. (4) and (5), and it relies heavily on conditions being appropriately uniform in space and time. For example, the first terms in Eqs. (4), (5), and (6) require evaluation of a volume integral. It was anticipated that conditions would be near enough to steady state that this integral could be evaluated from overlapping portions of aircraft flights and from surface observations at the MENTOR station, but in certain cases this may not have been justified.

Observations were made during February and March 1964 over the eastern part of the Arabian Sea as shown in Figs. 2–8. Aircraft observations were made by two Weather Bureau DC-6's and the Woods Hole Oceanographic Institution C-54Q. The former

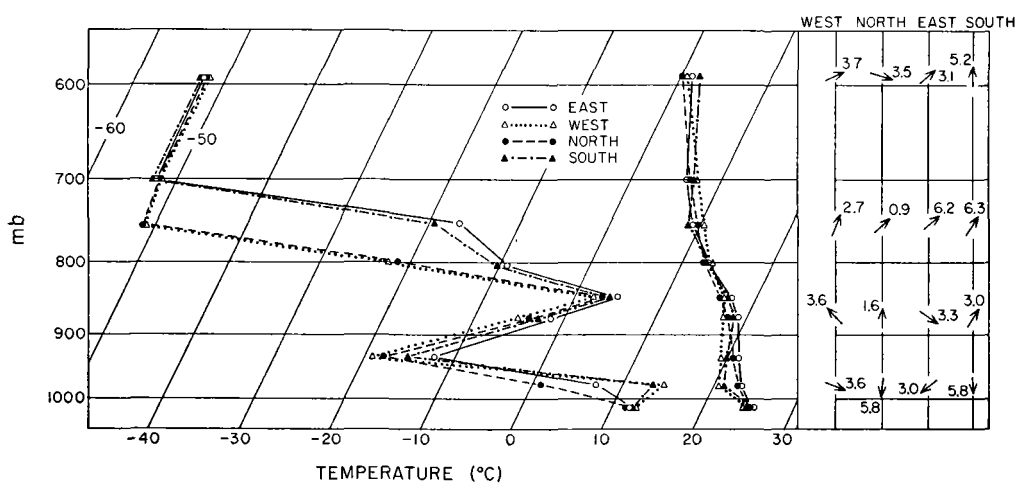

FIG. 6b. Composite temperature and dew-point profiles for 28 February 1964. Arrows represent mean aircraft winds in m sec^{-1}.

TABLE 1. "System accuracies" of aircraft observations.*

Aircraft	Wind speed (m sec^{-1})	Wind direction (degrees)	Temperature (°C)	Specific humidity (gm kg^{-1})	Absolute humidity (gm cm^{-3})	Pressure (mb)
W.B. DC-6	±1.5	$\pm\left[0.4+\frac{77}{V(\text{m sec}^{-1})}\right]$	±0.5	—	$\pm0.05\times10^{-6}$	±0.1
WHOI	±2	similar	±0.5	±0.1	—	±0.5

* Further instrumental details are discussed by Hsueh *et al.* (1966).

were equipped with APN82 Doppler radar systems, vortex thermometers, infrared hygrometers, aneroid barometers and dropsonde systems; the latter was equipped with a similar Doppler radar system, recording thermistor psychrograph, accelerometers, gyroscope and pressure gust anemometer. Wind velocities, temperatures and humidities were recorded on the Weather Bureau aircraft each 10 sec, and on the Woods Hole aircraft average values were recorded at intervals of 2–5 min. Fluctuations are reported by Bunker (1955, 1960, 1963) to be reliably sensed by the Woods Hole aircraft between horizontal dimensions of 20 and 350 m. These measurements have been further discussed by Telford and Warner (1962, 1963).

The "system accuracies" of the sensors, as reported by the Weather Bureau (Reber and Friedman, 1964) and the Woods Hole Oceanographic Institution are summarized in Table 1. Variations in temperature and humidity are presumably sensed more accurately than is indicated in Table 1. Also, errors tend to be approximately constant at a given altitude and air speed, and the random errors in any two instruments are probably not correlated with each other, so that average values of products are not critically affected by the instrument errors. In consequence, instrumental accuracy, while far from ideal, is considered to be adequate for calculation of mean rates of evaporation under the conditions sought for in these experiments. The effects of errors in measurement along single sides of the observational area within the lowest layer of the atmosphere are indicated in Tables 2–8. Arbitrary errors of 1.5 m sec^{-1} in normal wind speed, 0.05×10^{-6} gm cm^{-3} in vapor density, and 0.5C in temperature have been used to compute these estimated uncertainties. Such uncertainties are, of course, possible for any and all sides of the areas and for other layers, but they are likely to be random rather than additive.

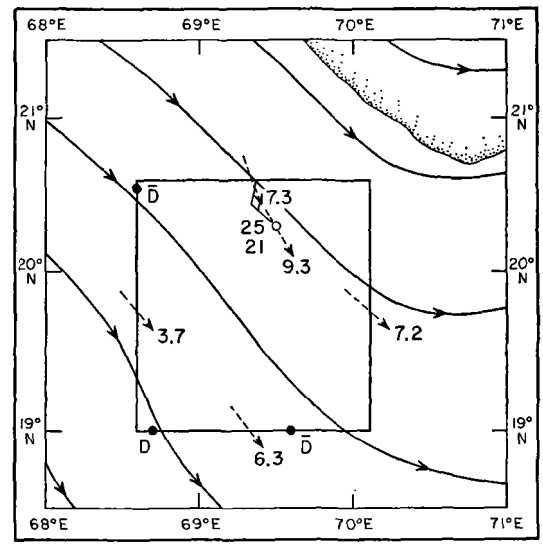

FIG. 7a. Surface streamlines at 1030 and upper winds for 0941 to 1159 local time, 2 March 1964. Dashed arrows represent mean winds at 0.30 km in m sec^{-1}. D's represent dropsondes with humidity records.

In most cases, uncertainties are larger for the lowest layer than for upper layers where vapor density is smaller. These numbers reflect errors of measurement only—uncertainties resulting from inadequate data may be larger.

There is an additional uncertainty which is not indicated in Table 1. Observations at right-angle corners suggest a persistent difference in the recorded wind depending on the heading of the aircraft. This could lead to fictitious normal wind differences along two opposite sides of the flight pattern with consequent fictitious computed values of divergence. In all but

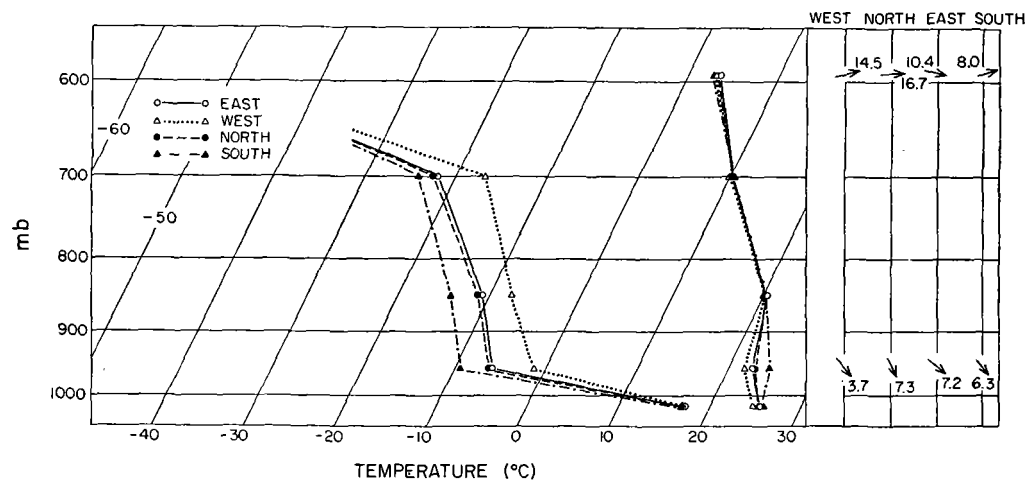

FIG. 7b. Composite temperature and dew-point profiles for 2 March 1964. Arrows represent mean aircraft winds in m sec^{-1}.

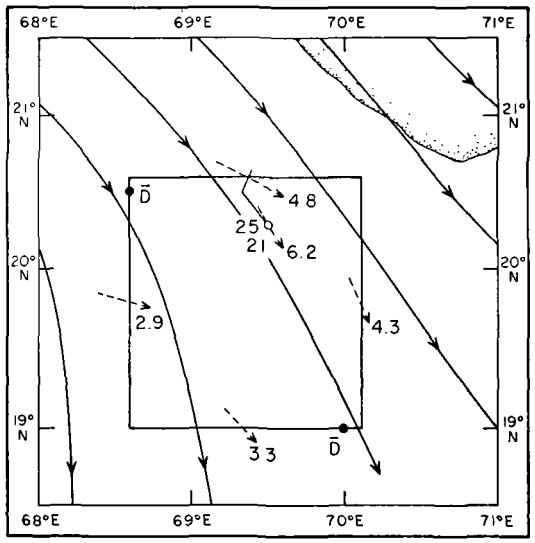

FIG. 8a. Surface streamlines at 1030 and upper winds for 1058 to 1231 local time, 3 March 1964. Dashed arrows represent mean winds at 0.30 km in m sec^{-1}. D's represent dropsondes with humidity records.

one case this error appears to be no greater than 1 m sec^{-1}. On 26 February a change of 4 m sec^{-1} was observed by the aircraft in making one right angle turn; this may account for the erroneous convergence in the horizontal flux computation for that date.

A method for compensating wind differences of this sort has been suggested by the Research Flight Facility in cases where the aircraft makes closed loops at right-angle corners. The assumptions underlying this method of compensation are somewhat arbitrary, so that it would be highly desirable to have a wind measuring system free of this uncertainty.

Instrumental uncertainty for dropsonde temperature is probably comparable to the uncertainty quoted for the aircraft temperature sensor, but dropsonde humidities are likely to be subject to uncertainty an order of magnitude greater than that quoted for the infrared hygrometer. Dropsondes are useful primarily in determining vertical variation of vapor density and temperature, and cannot be used alone for integral calculations of vapor flux.

A total of only 25 dropsondes were launched, and reliable humidity records were obtained for only 16 soundings out of the approximately 65 planned for the 9 periods of observation. Dropsondes were therefore less useful in analysis and calculation than had been planned. Aircraft observations were made regularly at separate heights, so that determination of horizontal divergence is subject to considerable uncertainty beyond that imposed by instrumental capabilities.

Surface observations were made using the University of Washington instrumented buoy MENTOR; the design and instrumentation has been discussed by Badgley *et al.* (1964). Profiles were measured using an automatic, vertically travelling probe on which were mounted a cup anemometer and a thermocouple psychrometer. Fluctuations at 4 m height were measured by cup anemometer, thermocouple psychrometer, and sonic anemometer-thermometer. Observations were recorded on the tending ship OCEAAN on magnetic tape. The profile measurements and calculations are discussed by Miyake *et al*[2].

[2] Miyake, M., F. I. Badgley and R. G. Fleagle, 1966: Capabilities of instrumented buoy (MENTOR) for the measurement of turbulent fluxes over the sea. Paper presented at Amer. Geophys. Union meeting, 22 April, Washington, D. C.

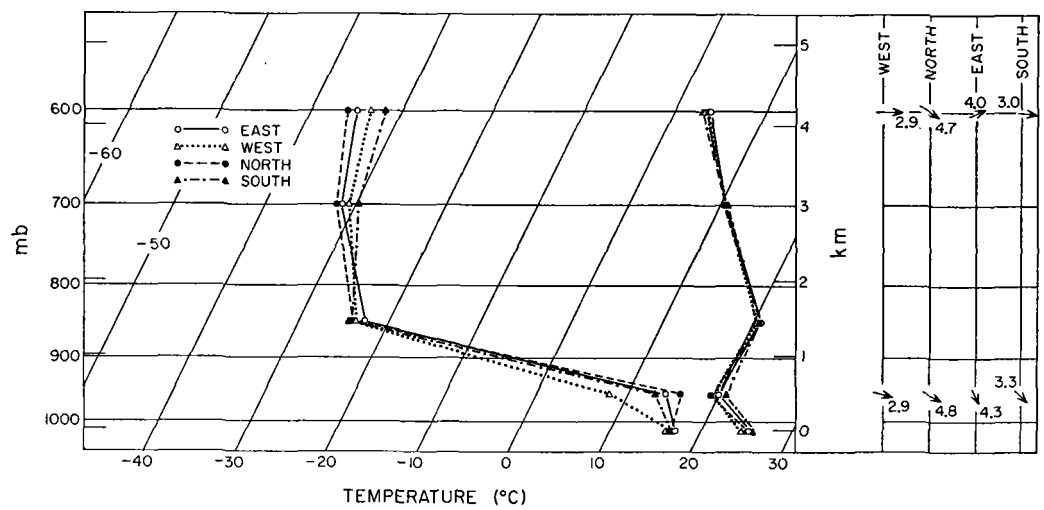

FIG. 8b. Composite temperature and dew-point profiles for 3 March 1964. Arrows represent mean aircraft winds in m sec^{-1}.

The Woods Hole aircraft measurements of vertical flux have been based on averages of 1-min observations. This procedure excludes the flux contributed by eddies larger in horizontal dimension than about 5 km, and little accuracy is claimed for eddies larger than 350 m. Therefore, the aircraft measurements probably underestimate vertical flux. Bunker[3] has discussed these measurements separately.

Pilot balloon observations and surface weather observations were made from the OCEAAN during each observation period. These, together with standard surface and upper air observations in the Indian Ocean area, were utilized as supplements to the aircraft data.

3. Results

Surface integrals along the vertical walls were separated into mean and eddy components. Mean values of wind velocity and humidity were obtained along each leg of the aircraft flights and were carried out objectively by computer. Examples of the aircraft velocity and humidity records are shown in Fig. 1. To determine mean vertical profiles of humidity a more subjective analysis was required. The aircraft ascents and descents, pilot balloons and dropsondes provided the basic shapes of the profiles which were then fitted to the mean values along individual legs of the aircraft flights. MENTOR observations of low-level humidity and velocity were used to extend the profiles to the ocean surface. The horizontal eddy fluxes and the advection were measured directly and objectively from the aircraft records by computer.

[3] Bunker, A. F., 1966: Measurement of the turbulent flux of sensible heat and latent heat over the Indian Ocean. Paper presented at the Conference on Marine Meteorology, 7–9 September, Virginia Beach, Va.

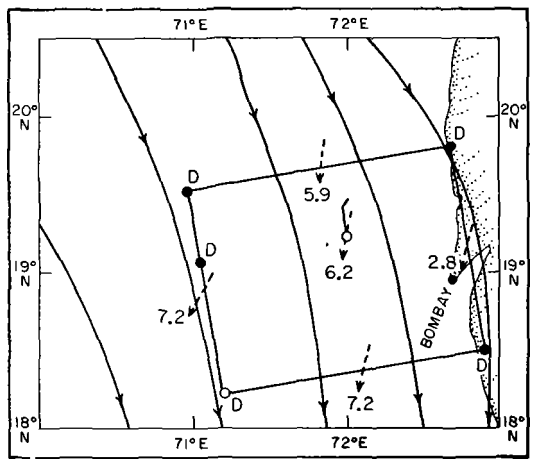

FIG. 9a. Surface streamlines at 1030 and upper winds for 1008 to 1515 local time 4 March 1964. Dashed arrows represent mean winds at about 0.44 km in m sec^{-1}. D's represent dropsondes (open circle without humidity record).

To evaluate vertical velocity at a height z_2 the kinematic method was applied to Eq. (4) and the adiabatic method to Eq. (5). Errors in vertical velocity at z_2 may be large but z_2 has been chosen high enough (and humidities small enough) that vertical transport of water vapor is small. The error in this term is probably no larger than errors in other terms.

The volume integral of the local rate of change of vapor density has been estimated from the change in humidity observed between the overlapping points of the aircraft flights and from the surface observations made at the MENTOR station. This crude evaluation may be marginally satisfactory in most of these cases,

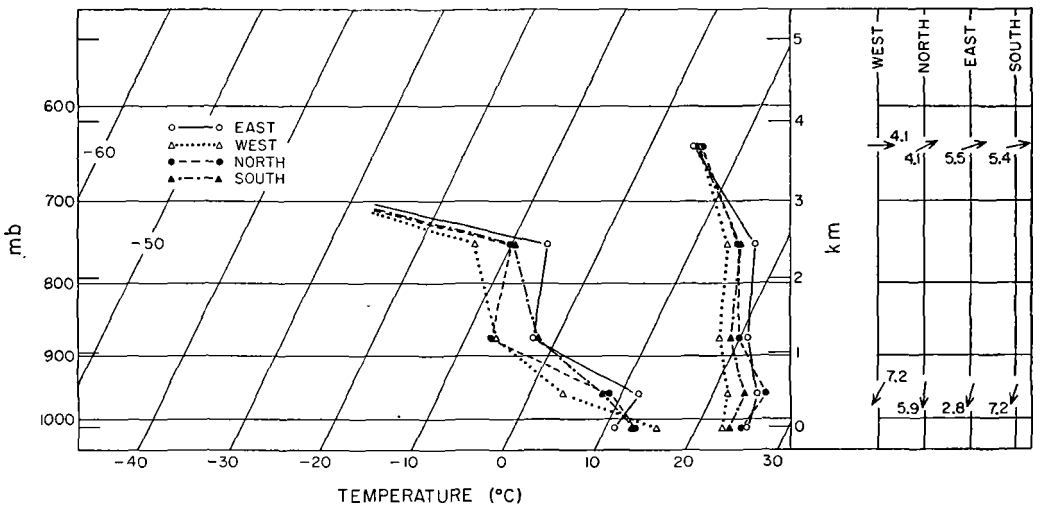

FIG. 9b. Composite temperature and dew-point profiles for 4 March 1964. Arrows represent mean winds in m sec^{-1}.

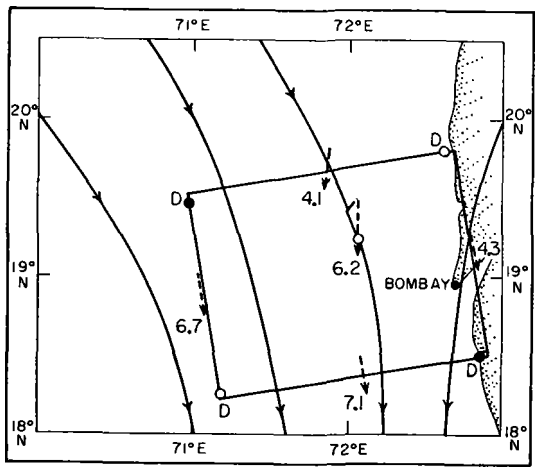

FIG. 10a. Surface streamlines at 1030 and upper winds for 1005 to 1453 local time, 5 March 1964. Dashed arrows represent mean winds at about 0.46 km in m sec^{-1}. D's represent dropsondes (open circles without humidity records).

but in the more general case observations must be designed to adequately measure the volume integral.

Profile calculations of evaporation have been based on the equation

$$F_E = -\frac{\rho k^2 (q_b - q_a)(u_b - u_a)}{\left[\ln \frac{z_b}{z_a}\right]^2} (1-18\ \mathrm{Ri})^{\frac{1}{2}}, \qquad (9)$$

where Ri represents Richardson number, k von Kármán constant, and the subscripts a and b refer to heights above the surface within the equilibrium boundary layer. Eq. (9) follows directly from the assumptions that the coefficients of turbulent transfer of heat and vapor density are equal and that Ri equals height divided by the Monin-Obukov length as suggested independently by Businger (1966). The latter assumption is also used by Pandolfo (1966) and Dyer (private communication). The use of Eq. (9) over a water surface, where prior data are limited, presents additional uncertainties.

Results of the analysis are shown in Figs. 2 through 10 and in Tables 2 through 10. Profile calculations have been carried out by Paulson (1967).

a. 17 February 1964: 1024 to 1425 local time. This experiment was carried out adjacent to the west coast of India. The coastal sea breeze was well developed, making this first case an especially complicated and interesting one. Fig. 2 shows that surface flow over the observational area was generally from the north but that a sharp trough in the streamlines lay along the coast. Skies were clear. The structure of the flow along the coast corresponded closely to observations and numerical models of the sea breeze [see, for example, Fisher (1960, 1961)].

Flow from sea to land prevailed in the lowest kilometer, return flow from land to sea prevailed between about 1 and 2 km, with flow again from sea to land above 2 km. Changes in wind direction amounting to 45° or more occurred at 500 m over periods of about 2 hr as indicated by the Woods Hole aircraft. Thus, there is evidence that the velocity field at low levels was not uniform in time during the period of observation.

Composite temperature and humidity soundings are shown in Fig. 2 separately for the boundaries of the observational area. These are based on aircraft data

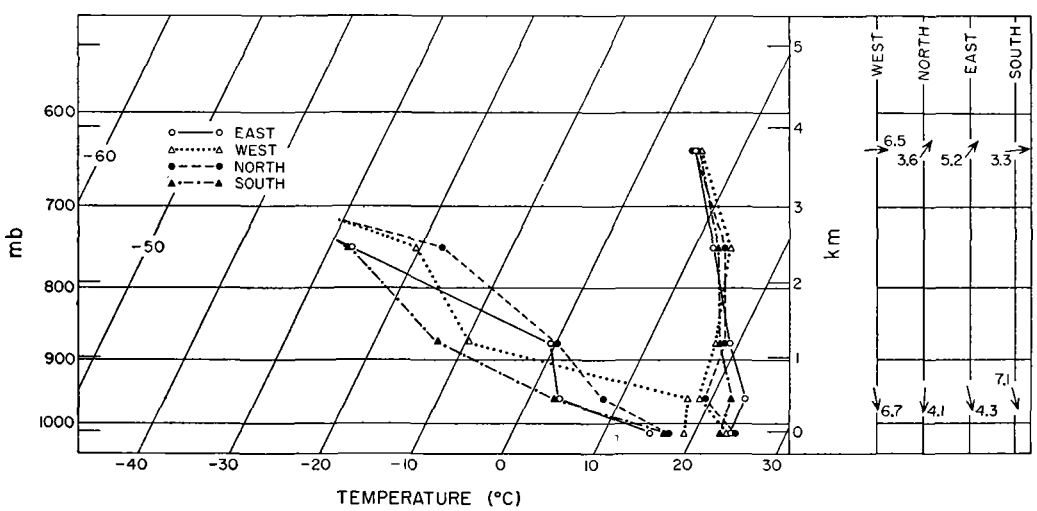

FIG. 10b. Composite temperatures and dew-point profiles for 5 March 1964. Arrows represent mean winds in m sec^{-1}.

TABLE 2. Terms in Eqs. (4) and (5) for 17 February 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 197 km, S-N 138 km.

Layer (km)	Equation (4) Total	Equation (5) Horizontal flux	Equation (5) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	1.43					0.04
2.6–4.6	−0.75	−0.90	0.15	0.15	0.14	0.44
1.3–2.6	−3.00	−3.15	0.15	−0.09	0.40	0.46
0.5–1.3	−2.59	−2.84	0.25	0.15	−0.65	−0.25
0–0.5	0.72	−0.18±1.1*	1.00	0.25±0.02**	−0.69±0.47***	0.56
Total	−4.19	−7.07	1.55	0.46	−0.80	1.25
Mean rate of evaporation:		−39±9 mW cm^{-2}			12±5 mW cm^{-2}	
MENTOR profile result:			14 mW cm^{-2}			

The asterisks indicate the range due to 1.5 m sec^{-1} uncertainty in normal wind velocity (*), 0.05×10^{-6} gm cm^{-3} uncertainty in vapor density (**), and 0.5C uncertainty in temperature (***) along one side through the layer extending from the ocean surface to the top of the first layer.

at four heights and on five successful dropsondes. These soundings reveal that as the air flowed southward it was cooled by the underlying surface and moisture was added to it. A steep gradient of humidity was observed between the surface and 930 mb, with nearly uniform humidity between 930 and 740 mb. Modification was limited to the layer below 750 mb, and greatest modification occurred at 950 mb. Evaluation of the mean rates of evaporation using Eqs. (4) and (5) is summarized in Table 2. Eq. (4) yields downward flux at 39 mW cm^{-2} (equivalent to condensation at the rate of 0.5 mm hr^{-1}), while Eq. (5) yields upward flux at 12 mW cm^{-2}. The observed winds indicate large horizontal velocity convergence throughout the depth of the volume. Convergence of this magnitude, if real, would correspond to strong upward motion and upward transport of water vapor. But the low humidity above 750 mb indicates that strong upward motion was unlikely, and the adiabatic method indicates divergence and downward motion. The rate of evaporation computed from the MENTOR profile observations was 14 mW cm^{-2}, close to the value computed for the whole area from Eq. (5). There is, therefore, strong evidence that the aircraft wind observations in this case were inadequate to define the divergence field.

Fig. 1a shows the fluctuations in the east-west wind component and humidity observed by the aircraft along two traverses through the center of the area at a height of 1.3 km. The runs were made first from east to west and then from west to east. Individual points in the velocity series representing running 20-sec means were recorded each 10 sec. Fluctuations of periods ranging from 10 sec to 30 min or so are recognized; the shift from easterly component to westerly component which occurs halfway along each run probably represents the leading edge of the sea breeze return flow. The mean south-north velocity and the flux computed from the second traverse were each one-third larger than the corresponding values computed from the first traverse. The traverses were made

TABLE 3. Terms in Eqs. (4) and (5) for 24 February 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 197 km, S-N 182 km.

Layer (km)	Equation (4) Total	Equation (5) Horizontal flux	Equation (5) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	0.29					0.19
1.5–4.5	2.47	2.47	0.0	2.56	−0.21	2.35
0.5–1.5	0.77	0.77	0.0	1.06	1.25	2.31
0–0.5	2.52	1.94±1.1*	0.58	2.88±0.03**	−3.42±2.83***	0.04
Total	6.05	5.18	0.58	6.50	−2.38	4.89
Mean rate of evaporation:		42±8 mW cm^{-2}			34±28 mW cm^{-2}	
MENTOR profile result: (6 hr before experiment) 17 mW cm^{-2}						

See footnote Table 2 for explanation of asterisks.

TABLE 4. Terms in Eqs. (4) and (5) for 25 February 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 197 km, N-S 170 km.

Layer (km)	Equation (4) Total	Equation (4) Horizontal flux	Equation (4) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	0.06					0.02
2.4–4.5	0.13	0.13	0.00	0.18	0.01	0.19
0.9–2.4	0.13	0.13	0.00	0.13	−0.06	0.07
0–0.9	2.87	2.67±1.1*	0.20	2.40±0.06**	−0.90±0.33***	1.70
Total	3.19	2.93	0.20	2.71	−0.95	1.98
Mean rate of evaporation:	24±9 mW cm^{-2}				15±3 mW cm^{-2}	
MENTOR profile result:			18 mW cm^{-2}			

See footnote Table 2 for explanation of asterisks.

consecutively, so the time interval between them amounts to only about 30 min. Here is further evidence that in this case representative values of flux divergence could not be obtained using a single aircraft at each height. The fluctuations are large enough to raise serious doubt that representative average velocities could be obtained by single aircraft flights along the sides of the area.

Comparison of the upwind and downwind temperature soundings suggests that the air was cooled from below by contact with the sea surface. The MENTOR profile results yield downward heat flux of 0.8 mW cm^{-2}, less than 10% of the absolute value of latent heat flux.

b. 24 February 1964: 1046 to 1448 local time. In this case a uniform current of dry air 1.5 km deep flowed southwestward over the observation area. Above 1.5 km flow was from the west, but most of the change in humidity and temperature was confined to the lower layer. The composite soundings show clearly the increase in humidity of the 1.5 km layer (6 gm kg^{-1} at 960 mb) as it moved from northeast to southwest. Local changes of temperature for the cases of 24 and 25 February were estimated from the observed changes between the two cases. Table 3 shows that Eq. (4) yields upward energy flux at the rate of 42 mW cm^{-2}, while Eq. (5) gives upward flux of 34 mW cm^{-2} (equivalent to evaporation of 0.5 mm hr^{-1}). The large uncertainty associated with Eq. (5) reflects the near-adiabatic layer between the surface and 0.5 km.

Coincident MENTOR observations were not made, but calculations using profiles made at sunrise (6 hr prior to the aircraft observations) give upward energy flux of 17 mW cm^{-2}.

The composite temperature soundings show a half kilometer superadiabatic layer next to the ocean indicating upward heat flux.

c. 25 February 1964: 1130 to 1530 local time. This case is similar to the 24 February case; flow was generally from the northeast in the lowest kilometer and from the west at higher levels. Vapor density increased along the flow at all levels, especially within the lowest kilometer. The mean vertical flux for the area was computed from (4) as 24 mW cm^{-2} and from

TABLE 5. Terms in Eqs. (4) and (5) for 26 February 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 185 km, S-N 165 km.

Layer (km)	Equation (4) Total	Equation (4) Horizontal flux	Equation (4) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	−0.27					0.03
1.8–4.5	−0.03	−0.03	0.0	1.03	0.01	1.04
0.6–1.8	−3.29	−3.34	0.05	0.05	−0.30	−0.20
0–0.6	−5.58	−5.83±1.2*	0.25	−0.26±0.02**	3.54±1.40***	3.53
Total	−9.17	−9.20	0.30	0.82	3.25	4.40
Mean rate of evaporation:	−72±10 mW cm^{-2}				34±14 mW cm^{-2}	
MENTOR profile result:			17 mW cm^{-2}			

See footnote Table 2 for explanation of asterisks.

TABLE 6. Terms in Eqs. (4) and (5) for 28 February 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 197 km, S-N 138 km.

Layer (km)	Equation (4) Total	Equation (4) Horizontal flux	Equation (5) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	0.0					0.0
2.4–4.3	−0.30	−0.30	0.0	−0.09	0.00	0.09
1.5–2.4	0.58	0.58	0.0	0.07	0.09	0.16
0.7–1.5	1.08	1.08	0.0	−0.09	−0.05	−0.14
0–0.7	−1.30	−1.30±0.8*	0.0	1.82±0.03**	0.66±0.47***	2.48
Total	0.06	0.06	0.0	1.71	0.70	2.41
Mean rate of evaporation:	0.6±9 mW cm^{-2}				24±5 mW cm^{-2}	
MENTOR profile result:			21 mW cm^{-2}			

See footnote Table 2 for explanation of asterisks.

(5) as 15 mW cm^{-2}, with the profile calculation yielding 18 mW cm^{-2}.

Fig. 1b shows the fluctuations in the west-east velocity component and the humidity along the east side of the observation area at a height of 0.5 km. Fluctuations are smaller than those observed on 17 February, and we infer that time changes in velocity field were small enough that single aircraft runs were able to determine average velocities on each side which were reasonably representative of the period of observation.

d. 26 February 1964: 0927 to 1411 local time. This was an especially complex case in which the sea breeze developed during the period of observation over the eastern portion of the area. Aircraft observations were made at 0.4, 1.3 and 4.5 km; pilot balloon observations and surface observations were made at the MENTOR station; and three temperature dropsonde records were obtained. These are sufficient to describe the complexity of the case but not to evaluate the surface vapor flux directly from the aircraft winds. It was during these observations that the 4 m sec^{-1} error in wind velocity was detected at one of the corners. Streamlines at about 1.3 km are shown in Fig. 5; above about 2 km flow was from the west. The soundings show more moisture above 2 km than was observed in earlier cases, and there was a considerable increase in humidity as the air crossed the area from west to east.

Eq. (4) yields strong condensation for this case, whereas Eq. (5) gives upward flux at 34 mW cm^{-2}, and the MENTOR profile calculations show upward flux of 17 mW cm^{-2}. Whereas the reported velocity field indicates low-level convergence, the adiabatic calculation reveals strong divergence. Also, there probably was considerable variation in vapor flux over the area, so that the point measurement may not be representative of the area average.

e. 28 February 1964: 0947 to 1536 local time. This case was characterized by contrasting currents of dry air from the northeast below 1 km and moist air from the southwest above 1 km. The humidity profiles indicate downwind increase in humidity within both currents. For this case the calculated rates of upward

TABLE 7. Terms in Eqs. (4) and (5) for 2 March 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 141 km, N-S 177 km.

Layer (km)	Equation (4) Total	Equation (4) Horizontal flux	Equation (5) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	0.0					0.0
1.5–4.3	0.80	0.80	0.0	1.24	−0.04	1.20
0.3–1.5	−0.19	0.01	−0.20	−0.71	0.11	−0.80
0–0.3	1.01	1.11±1.2*	−0.10	−0.25±0.02**	2.27±0.60***	1.92
Total	1.62	1.92	−0.30	0.28	2.34	2.32
Mean rate of evaporation:	16±12 mW cm^{-2}				23±6 mW cm^{-2}	
MENTOR profile result:			19 mW cm^{-2}			

See footnote Table 2 for explanation of asterisks.

TABLE 8. Terms in Eqs. (4) and (5) for 3 March 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 141 km, S-N 182 km.

Layer (km)	Equation (4) Total	Equation (4) Horizontal flux	Equation (4) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	−0.30					0.04
1.5–4.4	−1.00	−1.00	0.00	−0.90	−0.03	−0.93
0–1.5	3.24	2.94±1.0*	0.30	0.81±0.05**	1.74±0.21***	2.85
Total	1.94	1.94	0.30	−0.09	1.71	1.96
Mean rate of evaporation:	19±10 mW cm^{-2}				19±3 mW cm^{-2}	
MENTOR profile result: (1 hr after end of experiment)		21 mW cm^{-2}				

See footnote Table 2 for explanation of asterisks.

flux were 0.6 mW cm^{-2} from Eq. (4) and 24 mW cm^{-2} from Eq. (5), whereas the MENTOR profile calculations yield 21 mW cm^{-2}.

Aircraft flights were made at four heights, giving reasonably complete definition of the velocity field. However, the aircraft winds indicate very strong convergence in the lowest layer, probably again reflecting time changes during the aircraft flight.

Bunker[3] (1966) has reported aircraft covariance calculations for 11 one-minute runs during the period covered by this case. These eleven minutes provide the most complete sample available for any of the cases. The average upward flux was 17 mW cm^{-2}, compared with 24 mW cm^{-2} computed by the integral methods from Eq. (5) and 21 mW cm^{-2} computed by the profile method.

f. 2 March 1964: 0941 to 1457 local time. This was a relatively simple case in which flow below 2 km was from the northwest and above 2 km was from the southwest. Below 2 km humidity decreased in the downwind direction, but this was more than compensated by horizontal divergence. Above 2 km humidity increased in the downwind direction.

The calculated rate of upward flux shown in Table 7 was 16 mW cm^{-2} from Eq. (4) and 23 mW cm^{-2} from Eq. (5), whereas the profile result was 19 mW cm^{-2}. In this case the wind observed on board OCEAAN and the aircraft winds were especially steady over the period of observation.

g. 3 March 1964: 0552 to 1231 local time. This case was another in which the flow below 2 km was from the northwest while above 2 km flow was from the southwest. The computed rate of upward flux was 19 mW cm^{-2} from Eq. (4) and 19 mW cm^{-2} from Eq. (5). The MENTOR profile result was 21 mW cm^{-2}. Determination of the divergence from Eq. (8) for the adiabatic layer just above the surface is indeterminate, so it was necessary, in this case, to use a layer extending from the surface to 1.5 km.

h. 4 March 1964: 1008 to 1515 local time. In this case the low-level aircraft flight covered only the southern half of the rectangular observational area. It was necessary, therefore, to extrapolate temperatures,

TABLE 9. Terms in Eqs. (4) and (5) for 4 March 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 199 km, N-S 144 km.

Layer (km)	Equation (4) Total	Equation (4) Horizontal flux	Equation (4) Local change	Equation (5) Advection	Equation (5) Divergence	Equation (5) Total
Top surface	−0.14					−0.01
2.56–3.89	0.79	0.94	−0.15	0.60	−0.04	0.41
1.24–2.56	−0.67	−0.62	−0.05	1.04	1.28	2.27
0.44–1.24	0.39	−0.25	0.64	−0.10	−0.98	−0.44
0–0.44	1.24	0.89±0.9*	0.35	−0.18±0.02**	−1.40±0.77***	−1.23
Total	1.61	0.96	0.79	1.36	−1.14	1.00
Mean rate of evaporation:	16±9 mW cm^{-2}				10±8 mW cm^{-2}	
MENTOR profile result: (9 hr after end experiment)			9 mW cm^{-2}			

See footnote Table 2 for explanation of asterisks.

TABLE 10. Terms in Eqs. (4) and (5) for 5 March 1964. Units: 10^9 gm sec^{-1}; area dimensions: W-E 199 km, S-N 182 km.

	Equation (4)		Equation (5)			
Layer (km)	Total	Horizontal flux	Local change	Advection	Divergence	Total
Top surface	−0.08					−0.07
2.56–3.91	−0.07	−0.09	0.16	−0.11	0.03	0.08
1.25–2.56	−1.07	−0.34	−0.73	−0.38	−0.23	−1.34
0.46–1.25	2.31	−0.83	3.14	−1.63	0.99	2.50
0–0.46	2.41	0.41±1.50*	2.00	−0.66±0.02**	−1.35±2.38***	−0.01
Total	3.64	−0.95	4.57	−2.78	−0.56	1.16
Mean rate of evaporation:		36±15 mW cm^{-2}			11±24 mW cm^{-2}	
MENTOR profile result:			9 mW cm^{-2}			

See footnote Table 2 for explanation of asterisks.

humidities and wind velocities to the northern boundary on the basis of observations taken in the southern half of the area. Thus, an additional source of error is present in this case. However, this error may be compensated by the fact that successive flights across the center of the area at the upper level provided more accurate determinations of the local changes of humidity and temperature than had been available for the earlier cases.

Eq. (4) yields an upward flux of 16 mW cm^{-2}, Eq. (5) 10 mW cm^{-2}, and the MENTOR profile result 9 hr later is 9 mW cm^{-2}, smaller than for any of the earlier cases.

i. 5 March 1964: 1005 to 1453 local time. The final case studied is of special interest because aircraft repeated flights through the center at four heights, giving more detail for measurement of local changes than in any other case, and because a pronounced influx of cool, humid air from the northwest occurred during the period of observation. For this reason the soundings shown in Fig. 10b appear erratic, and the measured local changes are very large.

Eq. (4) gives an upward flux of 36 mW cm^{-2}, Eq. (5) 11 mW cm^{-2}, and the MENTOR profile result is 9 mW cm^{-2}. The instrumental uncertainty associated with Eq. (5) is especially large, reflecting the small value of θ^* computed for the lowest layer.

4. Summary of results

Using Eq. (4), which depends critically on kinematic measurement of the horizontal velocity divergence, six of the nine cases agree in sign and approximate magnitude with the MENTOR profile results. In the three cases of poor agreement unreasonably large values of horizontal convergence were indicated by the aircraft winds. These observations were associated with phenomena of a time or space scale smaller than could be properly resolved by the observations.

Using Eqs. (5) and (8), which depends upon the vertical divergence of the vertical heat flux being small, all nine cases agree in sign and approximate magnitude with the MENTOR results. Table 11 shows that the averages of all cases for the two independent methods agree within 25%.

Individual differences may be due to one or more of the following: 1) the difference between a point measurement and a space mean, 2) neglected terms in Eq. (8), 3) errors of observation or of analysis in evaluation

TABLE 11. Evaporation rates (mW cm^{-2}).

Date	V(8m) (m sec^{-1})	ΔT (8m-sfc) (°C)	Integral method Eq. (4)	Integral method Eq. (5)	Profile method
Feb. 17	7.96	+0.05	−39±9	12±5	14
24	6.20	−0.23	42±8	34±28	17*
25	5.45	−0.12	24±9	15± 3	18
26	5.14	−0.34	−72±10	34±14	17
28	5.45	−0.13	0.6±9	24±5	21
Mar. 2	6.87	−0.13	16±12	23±6	19
3	6.35	−0.14	19±10	19±3	21
4	4.45	−0.07	16±9	10±8	9**
5	6.43	−0.20	36±15	11±24	9
Average			6±10	20±11	16
Standard deviation			33	9	4

* 6 hr. earlier.
** 9 hr. later.

of the integrals in Eq. (5), or 4) inaccuracy in the theory underlying Eq. (9).

The standard deviation of the individual profile results was 4 mW cm^{-2}. This represents the combined effects of day-to-day variation in mean vertical flux, shorter period or space variations in vertical flux, unknown errors associated with the theory which underlies Eq. (9), and the sum of instrumental and sampling errors (less than 10% of the flux). The standard deviation of the individual values calculated from Eq. (5) was 9 mW cm^{-2}; this represents the combined effects of day-to-day variation and errors in the integral determinations. The latter, therefore, appears to be at least 5 mW cm^{-2} but probably no greater than 9 mW cm^{-2}. Thus, using Eq. (5) the standard deviation of the errors are estimated to have amounted to 25–45% of the calculated values.

The averages of the estimated instrumental uncertainties associated with Eqs. (4) and (5) are nearly identical, even though Eq. (4) gave large errors in computed flux in at least three cases. This indicates that the accuracy of Eq. (4) is not inherently more limited than is Eq. (5), and that if wind velocities had been measured simultaneously on opposite sides of the area as planned, Eqs. (4) and (5) would probably have yielded comparable results in all cases. Due to the fact that divergence becomes indeterminate for small values of θ^*, the instrumental uncertainties for Eq. (5) may be larger in individual cases than those for Eq. (4).

The aircraft covariance results are tabulated in Table 12. The number of 1-min runs on 17, 26 February and 2, 3, 4 March clearly are inadequate to place any reliance on the values calculated for these individual cases. The average of all 31 runs, on which more reliance may be placed, comes to 12 mW cm^{-2}. This may be compared to 16 mW cm^{-2} calculated for the profile method by weighting according to the number of aircraft runs, and to 20 mW cm^{-2} from the integral method using (5) and (8). The smaller average vertical flux measured by the aircraft appears consistent with the fact that measurements were made several hundred meters above the sea surface and that the eddy spectral range was limited to horizontal dimensions of roughly 20 to 350 m.

These nine cases demonstrate that it is feasible to measure the vertical flux of water vapor from an ocean surface on the synoptic space scale. Conditions for these cases were distinctly favorable; evaporation was rapid, winds were uniform and light, and there were no clouds. Under other conditions measurement may not have been possible. On the other hand, substantial improvements in the observational program can be achieved.

For these cases representing a uniform ocean surface, the space variation of surface vertical flux appears to have been small and unimportant. This is strongly implied by the fact that the day-to-day variation must account for much of the 4 mW cm^{-2} standard deviation (25% of the flux) calculated from profile results. Therefore, profile measurements, when carried out carefully, appear capable of providing reasonably accurate measurements of vertical flux on the synoptic scale.

5. Plans for a second and later experiments

Primary limits to accuracy of the computed evaporation rates have resulted from 1) inadequate data to provide measurements of local rates of change of temperature and vapor density, 2) weak resolution in the vertical, associated especially with lack of data in the first few hundred meters, 3) ambiguity in the horizontal velocity divergence resulting from the time interval between aircraft velocity measurements on opposite sides of the observation area, and 4) possible uncertainty in velocities obtained by Doppler radar.

In future experiments a reliable dropsonde program should be assured. A minimum of eight dropsondes per experiment should be planned, four at the beginning and four at the end of the period of observation at the same points. Aircraft flights should be planned so that two aircraft fly simultaneously on opposite sides of the observation area. Doppler wind measurements on each side of the area should be supplemented by at least one RAWIN to provide a check on the Doppler measurements. Aircraft should fly each leg at least twice in order that local change can be estimated accurately. Surface buoys should be located on the boundaries reporting wind velocity, air temperature, humidity, and the vertical temperature distribution from the surface through the thermocline. Special consideration should be given to measurements of the vertical profiles between the surface and 300 m.

TABLE 12. Comparison of profile, integral, and aircraft covariance results.

Date	No. of runs	Location	Height (m)	Covariance (mW cm^{-2})	Integral method (mW cm^{-2})	Profile method (mW cm^{-2})
Feb. 17	4	West edge	225	−2	12	14
26	4	Southern part	423	4	34	17
28	11	Scattered	224	17	24	21
Mar. 2	2	NW corner	470	1	23	19
3	2	SW corner	415	50	19	21
4	1	Center	460	10	10	9
5	7	Center	240	9	11	9
Weighted average			257	12	20	16

In the experiments described here cases were deliberately selected in which the velocity and humidity fields were expected to be relatively uniform in space and time. Only under these conditions could one expect the coarse resolution described here to yield results which agree in sign and approximate magnitude with independent measurements made at a point. Future experiments should include cases of greater complexity in which an aircraft traversing one side of the closed figure would be expected to encounter substantial fluctuations in velocity, temperature and humidity. One such record, obtained for the case of 17 February 1964, is shown in Fig. 1. To obtain horizontal fluxes which are representative of a period of several hours in these more complicated cases it may be necessary to make multiple traverses along the same path. Cases should be anticipated in which two traverses may be adequate, others in which three or more may be needed, and others in which the needed resolution in time may well be beyond achievable observational capabilities. It should be one of the objectives of future experiments to examine the range of usefulness of integral methods in increasingly complex weather situations. The next experiment probably should be designed for a region of rapid evaporation with clouds of limited vertical extent. In the future, also, plans should include measurement of heat and momentum flux, as well as vapor flux. These will require considerably more accurate measurements of the velocity field than was achieved in this first experiment.

Questions concerning spatial variability of the rate of evaporation can be answered by making simultaneous profile and covariance observations at several (perhaps four) locations within the area of observation. Observations within the inertial subrange also should be made, permitting calculation using the method d) based on Kolmogoroff's law.

The pilot experiment reported here was limited to a single enclosed area, the smallest unit of information attainable by the integral method. Later experiments should be based on an array of buoys and interesecting aircraft flights, thus providing simultaneously several units of information. The spatial continuity achieved in this way will add a new dimension to the study, and at the same time the cost per unit of information should be substantially reduced.

Future experiments should include areas and periods in which condensation within clouds and precipitation are occurring. This will require considerably more elaborate instrumentation including cloud sampling and radar and satellite surveillance. For these more complex situations it is not entirely clear what is the best way to proceed in detail. Therefore, a step-by-step program should be followed, with each experiment carefully chosen to test a crucial problem.

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PROBLEMS OF A MONSOON OCEAN*

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THE International Indian Ocean Expedition lasted 7 years, from 1959 to 1965, involving about 25 nations and 44 research vessels. The Meteorology Programme, concentrated in 1963 and 1964, besides including special experiments, capitalized on and expanded routine meteorological observations made at land stations and from ships and aircraft. Collection, scrutiny and processing of all these data has occupied much of the time at the India Meteorological Department International Meteorological Centre operated from January 1963 to June 1966 in Bombay, and at the Department of Geosciences of the University of Hawaii since mid-1964. Research on the data is sufficiently advanced to justify reporting.

What makes Indian Ocean meteorology unique is the effect of Asia, Africa and Australia on that body of water. North of 10°S and off the coasts of Australia and southern Africa, the low-level atmospheric circulation is monsoonal, possessing a marked annual period. Warm moist winds blow into low pressure over the continents in summer, cool dry winds blow out from high pressure over the continents in winter. Almost all of the southern Indian Ocean is no more monsoonal than the south-east Pacific and so has received relatively little attention from the investigators.

SUMMER MONSOON

Over the continents and adjacent ocean areas, the winter monsoon is predictably fine for weeks on end, whereas during the summer, monsoon rains may fluctuate sharply from one week to the next or between one summer and another. The moist onshore winds are a necessary, but not a sufficient condition for summer rains. Since the summer monsoon is more intense over the Arabian Sea than anywhere else, investigators concentrated research ships and aircraft there and, to a lesser degree, in the Bay of Bengal.

We confirmed that depressions, by increasing convergence in the monsoon current and its speed, enhance rainfall through dynamic and mechanical lifting (Sarker 1966).

Bay of Bengal monsoon. 'Monsoon depressions' bring rain to northern Burma and to eastern and north-eastern India. They may be moderately vigorous, resembling weak typhoons and are best developed near the surface. The average monsoon depression forms over the northern part of the Bay of Bengal and then moves rather slowly west-north-westward along the general line of the Ganges Valley, accompanied by copious rain.

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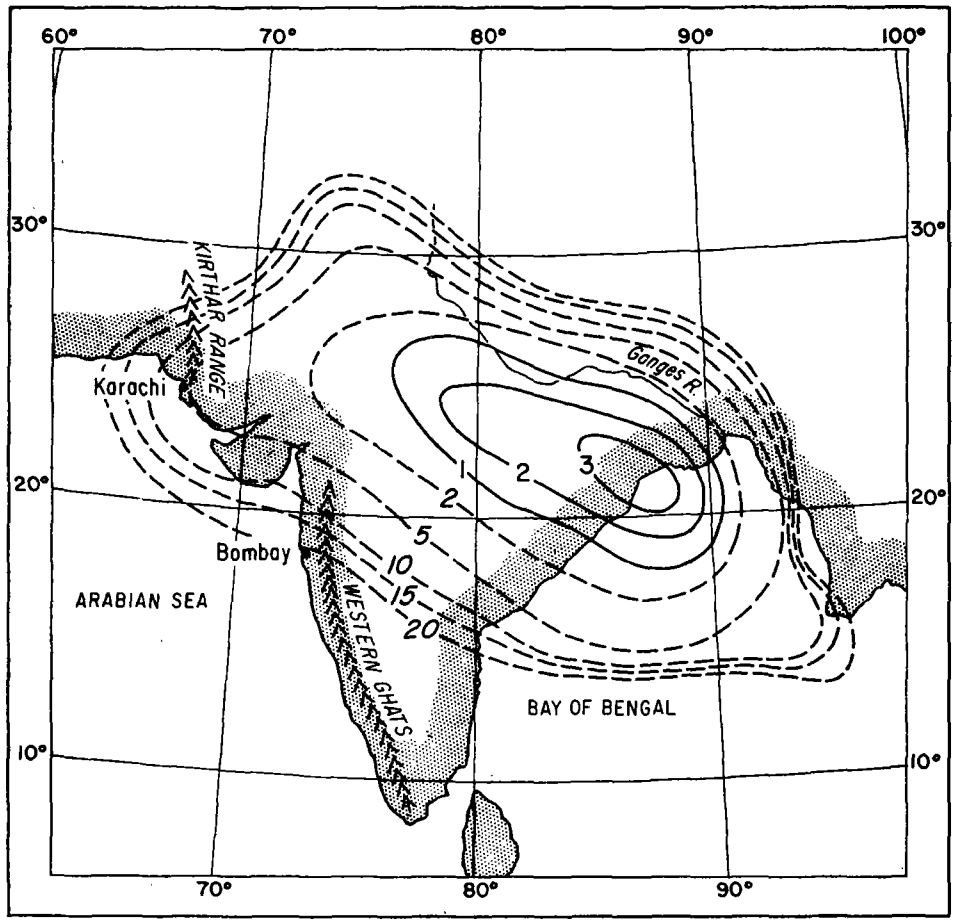

Fig. 1. Mean frequency of surface depression development during summer. Isopleths labelled in times per season (solid) and in years between occurrences (dashed)

Arabian Sea Monsoon. Equally heavy rains fall in the vicinity of Bombay through the agency of subtropical cyclones (Simpson 1952) which usually form, intensify, and decay just off the west coast and are most intense at around 4,500 to 6,000 m above the surface (Miller and Keshavamurthy 1967). Fig. 1 emphasizes the difference between the Bay of Bengal and Arabian Sea regimes, for subtropical circulations seldom extend to the surface.

Subtropical cyclones, the summer surface heat-low of Somalia, Arabia and West Pakistan and the south-west monsoon of the Arabian Sea are complexly linked (Ramage 1966). The heat-low develops first and south-westerlies set in along its southern periphery. Then, after a deep layer of moist air reaches the north-eastern Arabian Sea (usually through the agency of a monsoon depression farther east), export of middle and upper tropospheric cyclonic vorticity from the heat-low triggers a subtropical cyclone. Outflow of subsiding westward-flowing air from the top of the subtropical cyclone and monsoon depressions (1) intensifies the heat-low and consequently the surface south-westerlies, and (2) is reflected in a subsidence inversion and persistently fine

weather over the central and western Arabian Sea (Colon 1964). The sub-tropical cyclone eventally draws in dry air, and dissipates; the rains ease; the heat-low, south-westerlies and subsidence-inversion to the west weaken and a 'break' occurs in the monsoon rains. The model is crude and qualitative, but it can account for the fact that north of Bombay and inland from Karachi, when the onshore surface monsoon flow is strong, near-desert conditions prevail. Less rain falls on the Kirthar Range, directly exposed to the monsoon, than over the Deccan Plateau of central India, lying in the rain shadow of the Western Ghats.

The concept that discontinuities in monsoon weather can be associated with discontinuities in vertical motion and not necessarily with air-mass discontinuities, and that dynamic, rather than advective, processes can adequately account for changes in monsoon weather is beginning to prevail.

Upwelling and weather off Somalia. Oceanographers in IIOE intensively explored offshore from Somalia and Arabia where in summer the strong south-

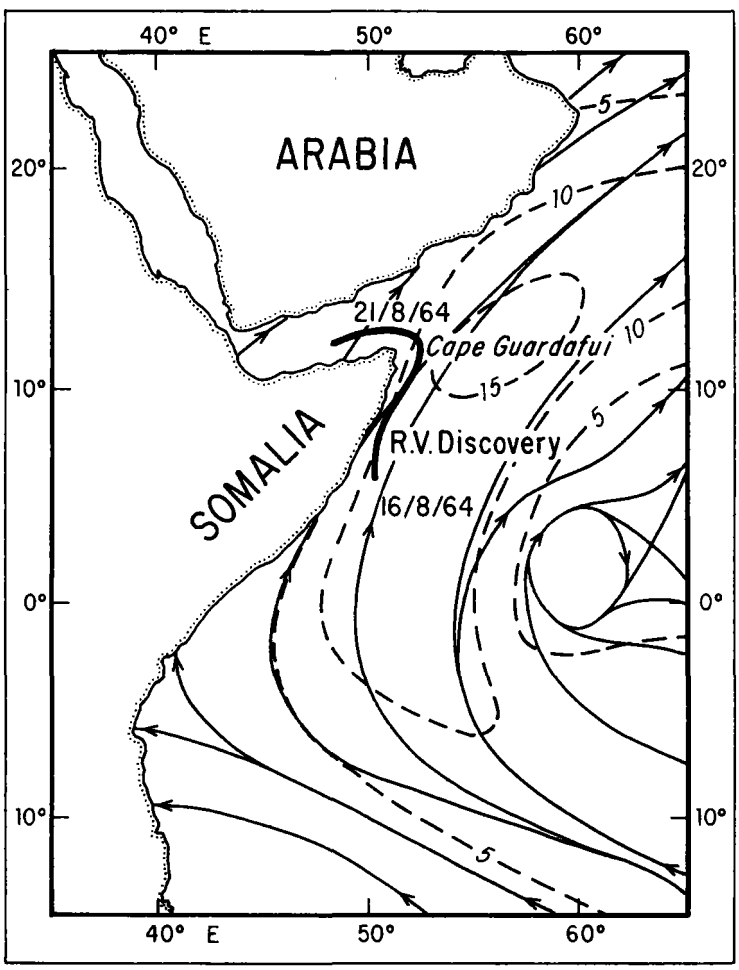

Fig. 2. Kinematic analysis of surface winds for 0600 GMT, 20 August 1964. Streamlines (full line); isotachs in m sec^{-1} (dashed line)

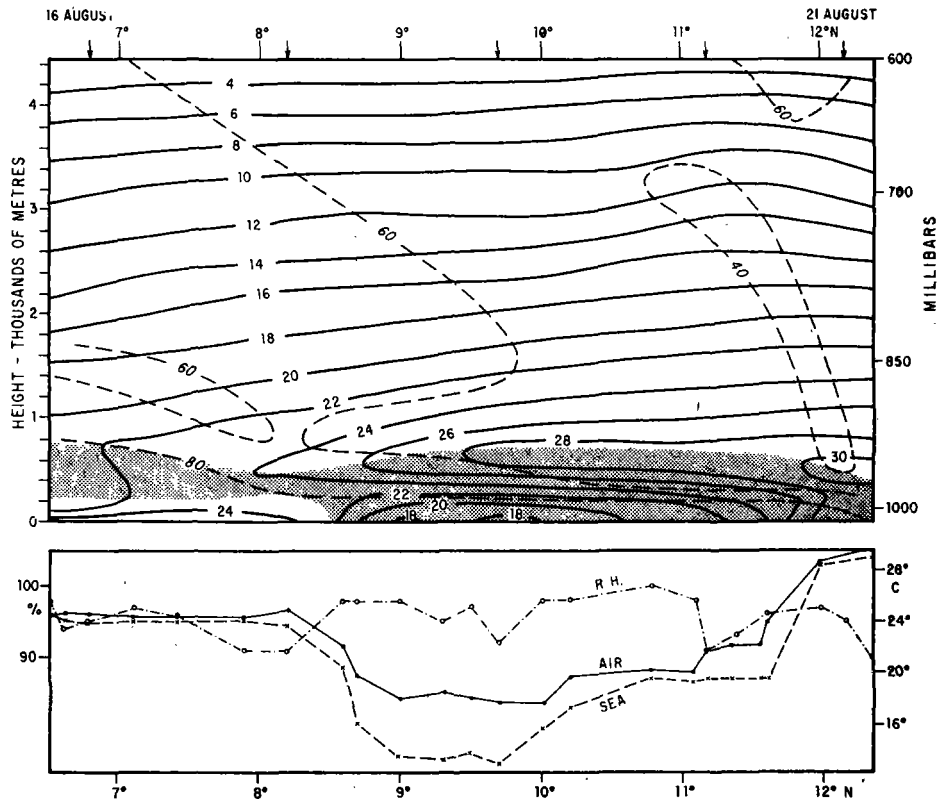

Fig. 3. Analysis of measurements made along about 50°E by R. V. *Discovery* between 16 and 21 August 1964

Upper diagram: Isotherms (full line); relative-humidity isopleths (dashed line); inversion layer (stippled). Arrows denote locations of radiosonde ascents

Lower diagram: Air temperature at deck level (full line); relative humidity at deck level (dot-dashed line); sea-surface temperature (dashed line)

westerlies, by forcing surface waters away from the coast, cause colder water to upwell. The upwelled water cools the adjacent air, producing a local pressure-ridge and a steep thermal gradient. These two effects combine, strengthening the winds by protecting the heat-low from inflowing maritime air, and creating a low-level jet (Bunker 1967).

The research vessel *Discovery* was in the area during the summer of 1964. Observations made from the ship, when combined with an understanding of the tropospheric circulation over the Arabian Sea, help to explain summertime absence of fog. Between 16 and 21 August 1964 *Discovery* sailed northward along about 50°E from 6·5°N to 12·3°N (Fig. 2), making numerous sea-surface and air temperature measurements as well as five aerological soundings (Fig. 3). The synoptic situation, which changed little during this period, is illustrated by the surface analysis for 06 GMT 20 August (Fig. 2). The clouds are typified in the photo taken a few days later from the Woods Hole Oceanographic Institution's research aircraft (Fig. 4 on p. 24).

From 16 to 21 August *Discovery* never recorded more than 10 per cent of

low cloud nor visibility below 10 km. Winds blew persistently from between south and south-west at from 10 to 15 m sec^{-1}, diminishing only after the ship sailed to the lee of Cape Guardafui.

At the outset, air and sea temperatures were the same and a weak inversion extending from about 200 to 800 m inhibited low cloud development. Then when the ship encountered cold water near 8·5°N, the inversion extended to the surface, being itensified both from below and above to greater than 10 deg. C. Although relative humidity of the surface air exceeded 90 per cent, no fog developed, despite the fact that the air moving over the cooling surface had possessed, but 24 hr before, a dew-point 9 deg C higher than the temperature of the upwelled water.

As Emmons and Montgomery (1947) point out, when air is cooled from beneath, not only heat, but also moisture is transported downward to condense on the underlying surface. Thus unless the air is *further cooled* by some independent agency, such as radiation, saturation might never be attained.

Discovery's soundings reveal a rapid decrease in relative humidity accompanied by a slight increase in mixing ratio with height in the inversion, thus confirming the existence of a downward moisture-flux (Roll 1965). The strong surface-winds no doubt facilitated heat and moisture transport, despite the great stability of the air.

A mystery remains—why does fog never form here whereas off California fog frequently occurs under apparently similar conditions? The answer can be found in the character of the summer circulation over the Arabian Sea, as already discussed. As compensation for the great upward motion accompanying the monsoon rains of India, into which the surface south-westerlies feed, convergent easterlies dominate the upper troposphere over the western Arabian Sea north of 7 or 8°N, and in turn cause massive and persistent subsidence. Consequently, warming due to subsidence at the top of the inversion overpowers cooling by both radiation or by upwelled water at the base, a conclusion borne out by the *Discovery* measurements and a possible explanation for the lack of fog. At the inversion top, the temperature at 7°N, south of both the main subsidence and the upwelled water, was 6 deg C below the temperature at 10°N where maximum surface cooling took place.

Cause and effect. For the past 20 years, tropical meteorologists have tried to apply mid-latitude concepts of upper level-troughs and vorticity advection as 'causes' of weather. They have achieved limited success. Plausible climatological evidence that the summertime easterly 'jet' in the high troposphere over southern India was 'caused' by a steepening north-south temperature gradient resulting from release of latent heat through heavy rain over central India led Raman and Ramanathan (1964) to investigate cause and effect on a daily basis. They found a high correlation between heavy monsoon rains over Indo-Pakistan and *subsequent* (several hours) development to the south of a sharply defined jet in the upper tropospheric easterlies. Heavy monsoon rains and *previous* development of a jet to the south were uncorrelated. The easterlies experienced no wave deformations. This result has cleared away

some misconceptions—but has hardly improved the prospects for monsoon rain forecasts!

NEAR-EQUATORIAL TROUGHS

An east-west oriented pressure-trough exists throughout the year in the tropics of each hemisphere. The troughs, separated by persistent equatorial west winds, appear to participate in a double oscillation through the course of the year. In the *summer hemisphere*, the trough lies well away from the equator over the continents (as far as 28° over India) and closer over the oceans. Raman (1968) has discovered a very weak secondary trough close to the equator in the northern hemisphere. One may also exist in the southern hemisphere. As the year progresses from summer to winter, the primary trough weakens and dissipates and the secondary trough becomes predominant. The sequence reverses from winter to summer. This model satisfactorily removes two difficulties inherent in the old concept of a single trough undergoing an annual oscillation between the summer tropics of both hemispheres—frequent, apparently discontinuous latitudinal jumps, and the usual absence of double rainfall maxima between 10° and 25° latitudes. Cyclones of varying intensities frequently develop in the primary summer-hemisphere trough with consequent severe weather. However, depressions may and do develop in the winter-hemisphere trough and although they are generally weak, they may on rare occasions reach hurricane force and cause unexpected widespread damage. It is not particularly uncommon especially in the spring and autumn transition seasons to observe tropical cyclones developing or coexisting on both sides of the equator, more or less at the same time.

Near-coincidence of trough and thermal equator which provides a facile explanation for the trough in the summer hemisphere (the heat low) can certainly not be adduced to account for the trough in the winter hemisphere. Theoretical studies (Gordon 1967; Gordon and Taylor 1968) hint that the steep gradient of the Coriolis force between the parallels of 5° and 10° predisposes the lower troposphere to develop cyclonic vorticity. If this is so then development of a vigorous summer-hemisphere trough in higher latitudes represents a thermally-induced distortion of the norm.

Sadler (1968) shows from weather satellite photographs that near-equatorial troughs are relatively cloud-free except when tropical storms develop in them. However, the troughs lie close to the axes of maximum air temperature and maximum surface heating. It appears then that trough location, even in the winter hemisphere, may be partially under thermal control. Air converging into a trough would ascend, and clouds, rain and occasionally vigorous cyclonic circulations would develop and, by interrupting incoming solar radiation, sharply reduce the surface heating needed to maintain the trough. A new trough would form where insolation was much greater, on the edge of the rain area. Presumably, the trough would tend to re-form towards the sun's zenithal latitude. In the winter hemisphere it should on the average lie equatorward of the rain belt, and in the summer hemisphere, poleward of the rainbelt.

Thus, in the mean, maximum rains and thermal troughs cannot quite coincide (*cf.* Riehl 1954).

AIR-SEA INTERACTION

Measurement. It is a truism that time and space variations in the exchange of heat and moisture between ocean and atmosphere must be accurately measured and explained before we can make real progress in understanding the weather. Thus during IIOE several groups attempted in various ways to determine the exchange.

Most commonly, expedition vessels carried equipment to measure one or more components of the net radiation at the sea surface. Results have not yet been published.

More ambitious programmes carried out on board Japanese and U.S. research vessels included measurements of momentum, moisture and temperature-fluxes, while a University of Washington experiment eliminated the distorting effect of the ship by mounting the instruments on a buoy-supported mast. Takahashi (1967) using shipboard observations made in the south-eastern Indian Ocean, and Badgley and Paulson (1968) presenting mast data obtained in early 1964 off Bombay, agree that profiles resemble those observed above smooth ground.

Estimation. Some investigators applied empirical equations after the fashion of Budyko (1956) to standard marine meteorological observations to determine monthly averages of the heat budget at the ocean surface. Results (Mani, Chacko, Krishnamurthy and Desikan 1967; Miller and Osell 1968) do not differ much from Budyko's except for providing more detail. Colon (1964) showed that the equations give rates of evaporative cooling of the surface waters of the Arabian Sea which are comparable to what is measured by oceanographic soundings. Bhumralkar (1967) used the equations in a detailed study which confirmed earlier ideas that moisture evaporated from the Arabian Sea is insufficient to supply all the summer monsoon rainfall of western India, while Pisharoty (1967) calculated that three times as much water vapour crosses the west coast of India as crosses the equator into the Arabian Sea.

Although useful, the equations suffer from a lack of direct measurements of all the budget components, particularly during periods of strong winds and high seas.

In the monsoon regions, strong winds and cloudy skies reduce summertime heating of the ocean surface whereas light winds and clear skies enhance wintertime heating. Maximum heating occurs in spring and autumn and the annual curve is bimodal.

CLIMATE

As many as possible of the regular and special observations made during IIOE, including satellite cloud (Sadler 1968) and radiation (Allison and Kreins 1967) measurements and air-borne time-lapse movies of clouds (Bunker and

Chaffee 1968)* have been analysed, averaged and compared with long-term means (*cf.* Miller and Jefferies 1967).

Much of the information is being incorporated in a two-volume *Meteorological Atlas*. Projection (Mercator's) and scale (1:40 million) conform to World Meteorological Organization specifications for meteorological atlases.

Volume I (Ramage, Miller and Jefferies 1968) describes the surface climate of the Indian Ocean as determined from 194,000 ship observations made during 1963 and 1964 when Expedition activity was at its height. From the observations, averages—by individual month and by 5-deg latitude-longitude square—of wind, pressure, air- and sea-surface temperatures, vapour pressure, clouds, precipitation, and heat exchange, together with analyses are depicted on 144 charts.

Meteorologists and oceanographers will be able to use the volume as a background to detailed studies, enabling them to relate physical and biological distributions to the monthly climate. Also, by comparing the charts with long-term meteorological atlases, they will be able to determine significant departures from normal.

Volume II (Ramage and Raman 1968), which describes the upper-air climate of the Indian Ocean and its neighbouring continents, incorporates information from before, during and after the Expedition period. Monthly long-term averages of resultant wind, wind steadiness, pressure-height, temperature, and dew-point are presented on two sets of charts—constant pressure level charts for 850, 700, 500, 300, 200 and 100 mb (approximately 1·5, 3·1, 5·8, 9·6, 12·4 and 16·5 km above m.s.l., respectively) covering the area between 45°N and 50°S and 20°E and 155°E, and 45°N to 50°S meridional cross-section charts for the longitudes 30°E, 73°E, 110°E and 140°E. On the constant pressure-level charts, analysis consists of streamlines and isotachs; on the meridional charts isotachs of the zonal wind component and isentropes are shown.

Besides averages computed from sounding-balloon observations, averages of flying-level winds measured from aircraft provide significant detail over the open ocean.

Meteorologists, climatologists and airline operators should be among those finding uses for this volume. From the plotted data they will be able to construct different sets of isopleths.

The atlas compilations, the investigations reported above, and many minor studies have established a firm basis for reinterpreting the climate of the Indian Ocean (Ramage 1968).

Space does not allow me to mention all the meteorological research based on IIOE observations, or stimulated by the Expedition. In emphasizing monsoonal phenomena I have not mentioned some excellent papers on tropical cyclones, published in the *Indian Journal of Meteorology and Geophysics* and an investigation of the complex cycles of diurnal variation over India.

* Many of the movies were made by RAF Transport Command crews flying between Aden and Singapore, via Gan.

CONCLUDING REMARKS

The stimulating association of Indians and Americans in the International Meteorological Centre is reflected in their research efforts and in the healthy differences of opinion engendered by their hypotheses. For various reasons, few meteorologists from other countries could come to work at IMC or have used the readily accessible Expedition data files. The often-voiced hope that practical benefits would accrue from the research is unlikely to be realized unless Indian Ocean meteorological services *evaluate* and then work out ways to *apply* the investigators' findings. Or better still, conduct their own research.

Many problems remain, and the material with which to tackle them is at hand. Opportunity challenges the indigeneous scientists.

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Radiation and Associated Observations Made on Indian Ocean Cruises

I. Cruises during 1962

By E. L. Deacon and J. Stevenson

Division of Meteorological Physics Technical Paper No. 16

Commonwealth Scientific and Industrial
Research Organization, Australia
Melbourne 1968

RADIATION AND ASSOCIATED OBSERVATIONS MADE ON INDIAN OCEAN CRUISES

I. CRUISES DURING 1962

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[*Manuscript received October* 4, 1967]

Summary

Measurements of the global radiation (short-wave and short-wave plus long-wave), sea surface and air temperatures, cloud amount and type, and wind speed, made on two cruises in the Indian Ocean, are tabulated, together with the net radiation income from the sea, which was calculated from these measurements. The results are in accord with the daily average values of the sea albedo by Ter-Markaryants.

I. INTRODUCTION

As a contribution to the meteorological programme of the International Indian Ocean Expedition, radiation and associated observations were made on a number of cruises of H.M.A.S. *Diamantina* and H.M.A.S. *Gascoyne*, two naval frigates fitted with hydrological gear. This report gives the data obtained on the two cruises attended in 1962, one to the Coral Sea (Dm 1/62 from 12th February to 25th March) and the other a south–north–south traverse of the 110°E. meridian (G 4/62 from 19th August to 16th September).

The tracks of the cruises are shown in Figures 1 and 2, which also show the positions of the hydrological stations. The meteorological elements measured were:

Global radiation, short-wave
Global radiation, short-wave plus long-wave
Sea surface temperature
Air temperatures, dry bulb and wet bulb
Cloud amount and type
Wind speed.

From these the net radiation income of the sea surface has been calculated by assuming reflection factors of the sea surface from other work.

II. OBSERVATIONAL METHODS

Global Radiation, Short-wave (I).—The short-wave radiation from Sun and sky incident on a horizontal surface was recorded using a Moll–Gorczynski solarimeter feeding one channel of a self-balancing potentiometer recorder. The solarimeter was

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rigged high above the foredeck so that obstruction to its field of view was negligible except when the shadow of the mast fell upon it. These occasions have been excluded. The solarimeter was set with its receiving surface horizontal before the ship left harbour. The errors introduced, mainly at low elevations of the Sun, by the small changes of trim and heel of the ship at sea were accepted; the different headings of the ship at different times should cause the errors to be random rather than systematic, so that mean values obtained by analysis of the results should be acceptably accurate.

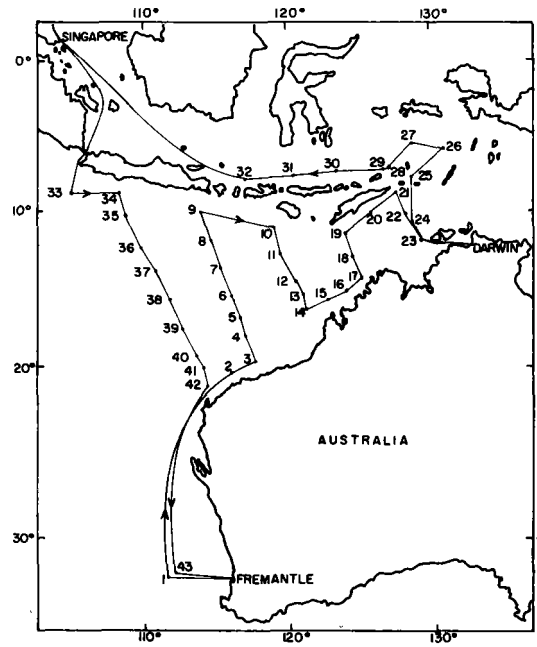

Fig. 1

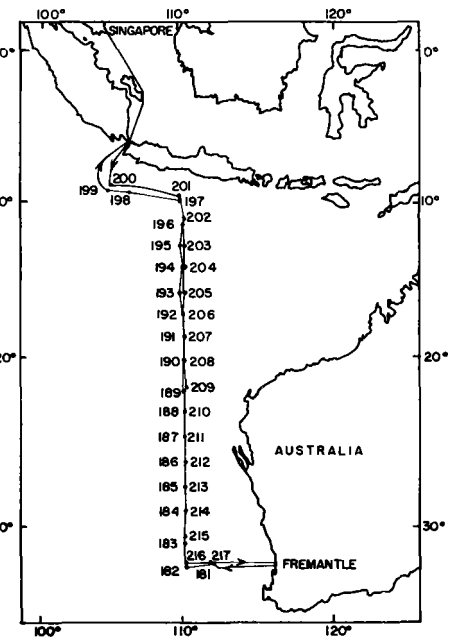

Fig. 2

Fig. 1.—Track chart of cruise Dm 1/62, February 12–March 25, 1962.
Fig. 2.—Track chart of cruise G 4/62, August 19–September 16, 1962.

The solarimeter was calibrated before and after each voyage. The substandard instrument used in calibration was Ångström pyrheliometer No. 502 (short tube type—made in Sweden), which was calibrated by the Swedish Meteorological and Hydrological Institute in 1957. Recalibration in Sweden in 1962 gave a constant 0·65% smaller than the 1957 value.

Global Radiation, Short-wave plus Long-wave (R↓).—This was measured using a polythene-shielded net radiometer (Funk 1959), the lower side of which was enclosed in a blackened cavity. The temperature of the cavity was measured by means of a thermistor. Radiometer and thermistor circuit outputs were applied to another two channels of the recorder. $R\downarrow$ can then be obtained from these recordings, as the radiation incident on the lower surface of the radiometer can be taken to be σT_C^4, where T_C is the cavity temperature (degrees K) and the Stefan–Boltzmann constant $\sigma = 5{\cdot}67 \times 10^{-12}$ W cm^{-2} degK^{-4}. The polythene hemisphere was inspected daily

and cleaned, as was also the solarimeter. The two instruments were mounted about 70 cm apart.

Short-wave calibration of the radiometer before and after the voyage was by a similar method to that used for the solarimeter. In both cases solar radiation on a clear day was used. Long-wave calibration employed a black-body cavity as radiation

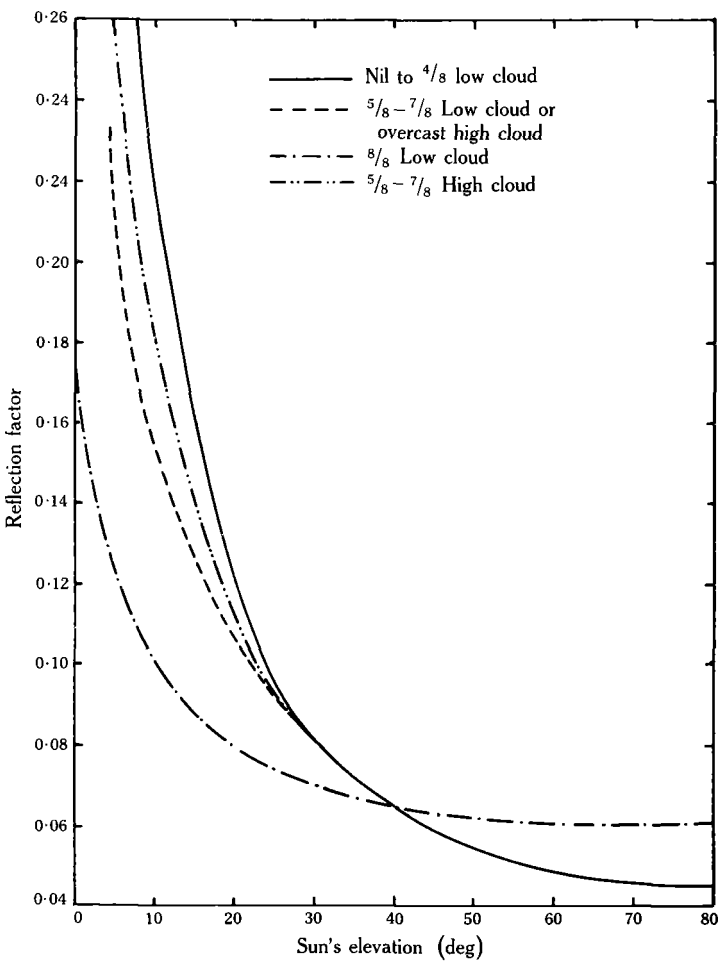

Fig. 3.—Values of the short-wave reflection factor of the sea surface adopted for the calculation of net radiation.

source. The short- and long-wave sensitivities were equal within the limits of the experimental error.

During the voyages checks on the consistency of the two radiometers were obtained on suitable occasions of fairly smooth sea and clear sky by shading both instruments from the direct solar beam. The change in output of the two instruments, converted to mW cm^{-2}, should be the same if they are functioning correctly.

Net Radiation (R_N).—This was calculated from the relationship:

$$R_N = (1-r_L)\,(R\downarrow-\sigma T_S^4)-(r_S-r_e)I, \quad (1)$$

in which r_L = long-wave reflection factor of the sea surface,

r_S = short-wave reflection factor of the sea surface,

T_S = sea surface temperature.

The value of $r_L = 0{\cdot}03$ was adopted and r_S, which depends on state of sky and elevation of the Sun, was taken from Figure 3, which was based on the extensive measurements made at Lake Hefner (U.S. Geological Survey 1954). These values accord quite well with the daily average values of the sea albedo given by Ter-Markaryants (1960). The elevations of the Sun required in applying Figure 3 are given in the tables as they are also useful in analysis of the data.

Sea Surface Temperature.—Sea surface temperatures on station were obtained by a mercury-in-glass thermometer and a sea temperature bucket consisting of a vacuum flask mounted in a protective cylinder. When the ship was cruising between stations, the sea surface temperature was recorded by means of a thermistor temperature element towed in the water surface abreast of the bridge on the port side. Agreement between the two methods was $\pm 0{\cdot}2$°C.

Air Temperatures.—Air temperatures, dry bulb and wet bulb, were obtained using an Assmann psychrometer held over the windward rail of the quarterdeck at a height of 3 m above the sea surface. On station the ship was held either with the wind on the starboard beam or on the stern in the stronger winds. Care was taken to maintain a clean wet-bulb wick and to discard any readings that might have been affected by spray. Generally 10 pairs of readings of the thermometers were obtained during a 10 min observation period and the average taken.

Wind Speed.—Wind speeds are averages over a 10 min period and were obtained using electric contact cup anemometers (Mark III of the British Meteorological Office). Two anemometers were used, one mounted towards the fore part of the vessel and the other near the stern, both at a height of 9 m above water level. On station, the stern anemometer was generally used, and when the vessel was under way the instrument that had the best exposure was selected to obtain an apparent wind speed. On these occasions the apparent wind speed and directions have been corrected for the ship's course and speed. The anemometers were calibrated before each voyage.

III. Results

Table I gives the results of cruise Dm 1/62 and Table 2 those for G 4/62.

Key to Symbols in Column Headings of Tables 1 and 2

T_a = air temperature at a height of 3 m above sea level.
T_w = wet bulb temperature at a height of 3 m above sea level.
T_s = sea surface temperature.
p = atmospheric pressure at sea level.
e_a = water vapour pressure at height 3 m above sea level.
e_s = saturation vapour pressure of sea water at temperature T_s.
I = short-wave solar and sky radiation incident on a horizontal surface.
$R\downarrow$ = global radiation, short-wave plus long-wave, incident on a horizontal surface.
R_N = net radiation income at sea surface.

Ship Time

The ship time in relation to U.T. is as follows:

Table 1: cruise Dm 1/62

Period	13–22 Feb.	23–24 Feb.	2–5 Mar.	6–10 Mar.	15–23 Mar.
Ship time − U.T. (hr)	8	9	9½	8½	7½

Table 2: cruise G 4/62

Period	18–30 Aug.	30 Aug.–15 Sept.	16 Sept.
Ship time − U.T. (hr)	8	7½	8

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TABLE 1

DATA FOR CRUISE Dm 1/62

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind		Temperature			p-1000	T_a-T_s	e_a	e_s	e_s-e_a	Cloud		Sun's Elevn	I	$R\downarrow$	R_N
					Dirn (deg)	Speed (m/s)	T_a (°C)	T_w (°C)	T_s (°C)	(mb)	(°C)	(mb)	(mb)	(mb)	Type	Amount (octes)	(deg)	(mW/cm²)	(mW/cm²)	(mW/cm²)
13 Feb	0800	1	32°02'	111°31'	100	4.4	19.85	14.95	22.10	11.5	-2.25	13.7	26.1	12.4	Sc	4	20	-	-	-
	1100		31°40'	111°35'	070	2.1	20.90	16.85	22.60	11.3	-1.7	16.4	26.9	10.5	CuSc	2	68	-	-	-
	1300		31°23'	111°40'	110	4.1	21.45	16.20	23.00	11.0	-1.55	14.8	27.5	12.7	Cu	Tr	70	110.1	120.3	72.9
	1500		31°02'	111°46'	130	7.7	21.80	17.90	22.80	10.6	-1.0	17.8	27.2	9.4	Sc	Tr	53	91.7	98.6	51.6
	1700		30°50'	111°52'	150	6.1	22.00	18.20	22.40	10.4	-0.4	18.3	27.5	9.2	-	0	28	43.0	45.3	-0.5
14 Feb	0800		27°22'	112°26'	190	11.0	23.65	20.65	24.80	10.3	-1.15	22.3	30.7	8.4	Cu	4	22	-	-	-
	1000		26°47'	112°30'	150	9.2	24.05	20.95	25.05	10.0	-1.0	22.7	31.1	8.4	Cu	1	49	87.9	117.1	68.2
	1200		26°13'	112°34'	180	12.5	24.75	21.65	26.80	9.5	-2.05	23.7	34.5	10.8	Cu	1	73	112.2	143.1	92.7
	1400		25°47'	112°42'	160	10.0	24.85	22.40	26.35	8.7	-1.5	25.4	33.6	8.2	Cu	1	67	104.7	136.0	86.1
	1600		25°25'	112°48'	180	12.6	24.95	22.10	26.25	6.8	-1.3	24.7	33.4	8.7	Cu	Tr	41	69.2	107.6	58.0
	1800		25°02'	112°56'	190	14.8	25.2	22.45	26.45	5.7	-1.25	25.3	33.9	8.6	-	0	15½	18.7	58.9	10.5
15 Feb	0800		22°00'	113°42'	170	7.9	27.25	24.85	26.60	6.7	+0.65	29.8	34.1	4.3	Ac(1)Ci	4	23	28.9	69.6	21.1
	1000		21°46'	113°51'	090	4.1	27.65	24.40	25.65	5.3	2.0	28.3	32.2	3.9	Ci	5	50	69.3	108.7	61.0
	1200		21°32'	114°01'	060	6.2	28.70	24.40	27.00	4.6	1.7	27.6	34.9	7.3	CiCs	7	76	111.1	152.9	101.9
	1400		21°16'	114°22'	070	9.5	28.25	25.25	26.90	3.7	1.35	30.1	34.7	4.6	SoNs	8	66	26.0	70.2	22.8
	1600		21°00'	114°42'	050	7.4	28.70	26.15	29.30	3.4	-0.6	32.2	39.9	7.7	SoNsAc	8	41	20.2	64.6	16.0
	1800		20°44'	115°03'	030	4.6	28.40	25.50	28.55	4.1	-0.15	30.7	38.3	7.6	CuSoNs	8	13	8.7	53.7	6.5
	2215	2	20°12'	115°45'	070	8.1	27.55	25.30	27.80	8.7	-0.25	30.7	36.6	5.9	CuSc	8	-	0	44.8	-1.6
16 Feb	0815	3	19°37'	117°53'	030	4.7	27.45	24.40	28.25	7.2	-0.8	28.5	37.6	9.1	Ci	1	30	44.8	85.7	35.4
	1000		19°32'	117°48'	340	1.9	28.40	24.55	28.20	6.9	+0.2	28.2	37.5	9.3	Ci	1	55	89.6	125.1	74.3
	1200		18°59'	117°37'	340	2.1	28.35	24.55	27.95	6.3	0.4	28.3	36.9	8.6	CuCi	1	79	111.1	145.8	94.5
	1400		18°35'	117°26'	300	1.2	27.85	24.00	28.30	5.6	-0.45	27.2	37.7	10.5	CuCi	Tr	67	98.2	134.6	83.7
	1600		18°11'	117°16'	340	1.5	27.75	24.40	28.55	6.1	-0.8	28.3	38.3	10.0	Cu	1	38	57.8	99.5	48.9
	1735	4	18°00'	117°10'	350	3.9	27.60	24.50	28.80	6.8	-1.2	28.5	38.8	10.2	Cu	1	15	24.6	63.4	12.4
	1852	4	18°00'	117°10'	350	3.7	27.55	24.30	28.60	7.2	-1.05	28.1	38.3	10.2	CuCi	1	-	0	38.2	-6.6
17-18 Feb		No records																		
19 Feb	1630		10°17'	116°00'	280	12.0	25.55	24.55	28.15	8.7	-2.6	30.1	37.4	7.3	SoNs	8	33	2.9	45.4	-1.8
	1800		10°21'	116°26'	270	11.8	25.95	24.75	28.05	8.3	-2.1	30.4	37.2	6.8	SoNs	8	12	2.9	44.5	-1.7
20 Feb	0840	10	10°50'	119°08'	230	5.2	27.50	25.15	28.40	9.3	-0.9	30.3	37.9	7.6	Ci	3	37	59.2	98.4	47.8
	1000		11°06'	119°22'	260	8.1	27.75	25.50	28.25	8.6	-0.5	31.1	37.6	6.5	Cu	3	56	88.1	128.0	77.1
	1200		11°30'	119°26'	240	5.6	28.40	25.60	28.40	8.0	0.0	30.9	37.9	7.0	CuCi	3	87	91.0	129.5	78.8
	1400		11°55'	119°30'	240	8.0	28.35	25.25	28.50	7.8	-0.15	30.0	38.1	8.1	CuSc	6	62	-	-	-
	1723	11	12°26'	119°35'	210	7.75	27.85	24.8	28.10	6.9	-0.25	29.2	37.2	8.0	Sc(1)Ac	8	14	10.1	51.4	4.2
21 Feb	0730	12	14°19'	120°34'	200	4.90	27.90	25.85	28.10	7.3	-0.2	31.9	37.2	5.3	Ac	7	22	26.0	64.2	15.3
	1000		14°43'	120°43'	205	4.40	28.25	26.35	28.10	8.6	+0.15	33.0	37.2	4.2	Ac	6	58	47.7	87.9	39.0
	1200		15°08'	120°52'	185	5.1	28.35	26.15	28.10	7.4	0.25	32.4	37.2	4.8	Cu(1)Ac	3	83	99.6	135.7	84.9
	1335	13	15°22'	121°00'	190	8.6	28.40	26.35	28.20	6.4	0.2	32.9	37.5	4.6	Cu(1)Ac	4	69	96.7	135.3	84.6
	1500		15°33'	121°04'	230	2.8	28.70	26.80	28.50	6.2	0.2	33.9	38.1	4.2	Cu(1)AcCi	5	48	70.7	102.3	51.9
	1630		15°59'	121°11'	230	2.8	28.70	27.05	28.10	5.9	0.6	34.7	37.2	2.5	Ci	4	28	28.9	67.5	18.7
	1800		16°06'	121°18'	200	2.6	28.20	27.00	27.90	6.6	0.3	34.8	36.8	2.0	Ac(1)Ci	3	5	4.3	43.7	-3.5
	1910	14	16°15'	121°24'	210	5.0	28.25	27.05	28.10	7.1	0.15	35.0	37.3	2.3	Ac	2	-	0	38.0	-8.5

22 Feb	0800		15°16'	124°02'	010	3.3	27.90	25.40	28.00	7.2	-0.1	30.7	37.1	6.4	AcAs	8	32	24.5	67.5	19.2
	1000		15°00'	124°13'	Light Airs		28.20	26.05	28.70	6.3	-0.5	32.3	38.6	6.3	Ac	2	60	88.1	125.5	74.6
	1130		14°53'	124°25'	010	3.3	28.50	25.90	29.30	5.6	-0.8	31.7	40.0	8.3	Ac	6	78	86.6	125.1	73.7
	1300		14°37'	124°37'	330	3.5	28.40	25.80	29.60	4.7	-1.2	31.4	40.6	9.2	Ac(2)Ci	6	73	98.2	136.6	83.0
	1430		14°20'	124°48'	090	2.3	29.10	26.25	29.40	4.2	-0.3	32.2	40.2	8.0	AcAs	7	52	53.4	98.8	48.1
	1600		14°10'	125°00'	050	2.4	29.15	26.10	29.00	3.9	+0.15	31.7	39.2	7.5	AcAs	6	30	17.3	59.9	11.5
	1735	17	13°59'	125°15'	020	4.15	28.40	25.90	28.10	4.3	0.3	31.7	37.3	5.6	ScAs	8	7	2.9	45.6	-0.3
	1900		13°45'	125°09'	020	4.1	28.30	25.65	28.30	4.7	0.0	31.1	37.7	6.6	-	3	-	0	40.8	-5.7
23 Feb	0800	19	11°12'	124°08'	110	2.9	28.15	25.95	28.70	6.0	-0.55	32.0	38.5	6.5	Cu(1)Ac	7	32	39	75.6	25.9
	0930		11°06'	124°16'	300	6.1	28.20	26.30	28.90	5.6	-0.7	33.0	39.0	6.0	Cu(3)Ac	4	56	86.7	120.9	69.9
	1100		11°00'	124°30'	300	5.2	28.15	26.10	28.80	5.4	-0.65	33.4	38.8	5.4	Cu(1)AsCi	4	75	101.0	135.1	83.9
	1230		10°51'	124°45'	290	5.9	28.55	26 25	28.95	4.1	-0.40	32.6	39.2	6.6	Cu(3)Ci	4	82	116	148.6	96.7
	1500		10°40'	125°01'	280	4.7	28.80	26.20	29.00	3.9	-0.2	32.3	39.3	7.0	Cu(1)AcCiCs	4	44	63.5	101.9	51.2
	1630		10°28'	125°17'	280	4.8	28.85	26 05	29.45	3.6	-0.6	31.8	40.3	8.5	Cu(2)Ac	6	22	24.5	69.8	18.8
	1800		10°15'	125°40'	280	6.5	28.40	26.25	29.00	4.3	-0.6	32.7	39.3	6.6	Ac	4	-	0	41.5	-5.2
	1908	20	10°00'	125°55'	240	4.75	28.40	26.25	28.75	4.4	-0.35	32.6	38.7	6.1	-	4	-	0	42.1	-4.8
24 Feb	0730	21	9°00'	127°52'	190	3.75	28.40	25.35	28.40	5.6	0.0	30.3	37.9	7.6	AcAs	6	13	13.0	55.2	6.5
	0900		9°03'	127°54'	180	4.0	27.55	24.80	28.30	5.8	-0.75	29.4	37.7	8.3	CuNs(2)AcAs	8	35	34.7	75.8	27.0
	1030		9°18'	128°03'	210	3.8	27.45	25.00	28.30	6.1	-0.85	30.0	37.7	7.7	CuSc(3)AcAs	8	58	43.3	83.7	34.6
	1200		9°34'	128°10'	270	7.7	27.20	25.40	28.55	4.7	-1.35	31.2	38.2	7.0	AcAs	6	80	93.8	130.5	79.3
	1330		9°50'	128°15'	275	7.6	27.90	25.90	28.60	3.9	-0.7	32.0	38.3	6.3	Cu(1)AcAs	7	79	57.8	99.7	50.1
	1515	22	10°07'	128°22'	210	5.65	28.60	26.05	29.00	2.7	-0.4	32.0	39.2	7.2	Cu(1)Ac	6	37	66.4	113.4	62.4
	1730		10°15'	128°33'	230	2.4	28.55	26.10	28.60	3.4	-0.05	32.1	38.3	6.2	Cu	3	19	23.1	63.8	14.1
	1900		10°32'	128°42'	210	3.3	28.30	26.10	28.20	4.2	+0.1	32.3	37.5	5.2	Cu(1)As	3	-	0	41.7	-5.8
2 March	1615	23	11°29'	129°19'	280	8.35	28.75	25.70	29.00	5.4	-0.25	30.9	39.2	8.3	Cu(3)As	6	44	33.9	76.00	26.8
	1840		11°05'	129°12'	285	5.0	28.85	25.60	28.75	7.2	+0.1	30.6	38.8	8.2	Cu(3)As	8	7	2.3	44.60	-1.4
	2150	24	10°31'	128°50'	280	8.15	28.50	25.70	28.35	10.2	0.15	31.1	37.8	6.7	Cu	4	0	0	38.90	-5.6
3 March	0800		8°25'	128°16'	270	4.9	28.40	25.30	28.25	10.7	0.15	30.1	37.6	7.5	Ac	3	14	13.9	55.6	12.0
	0900		8°13'	128°16'	270	8.9	28.70	25.13	28.60	10.9	0.1	29.5	38.3	8.8	AcAs	2	28	44.7	85.1	42.3
	1000		8°04'	128°22'	270	7.5	28.85	25.50	28.35	11.4	0.5	30.3	37.8	7.5	Cu(1)AcAsCi	3	46	70.8	93.4	68.9
	1100		7°54'	128°39'	280	8.1	28.30	25.50	28.20	11.3	0.1	30.7	37.5	6.8	AcAsCi	4	60	64.7	102.3	63.5
	1200		7°54'	128°50'	-	-	28.20	25.50	28.15	11.0	0.05	30.7	37.3	6.6	Ac	3	73	103.2	140.0	101.7
	1300	25	7°45'	128°49'	270	6.3	28.20	25 25	28.10	10.9	0.1	30.1	37.2	7.1	AcAs	5	85	111.0	147.8	108.8
	1400	"	"	"	290	6.75	27.95	25.25	28.05	10.7	-0.1	30.3	37.1	6.8	AcAs(2)Cs	4	74	111.0	144.6	109.4
	1500	"	"	"	290	5.80	28.45	25.25	28.20	8.6	+0.25	30.0	37.2	7.2	Ac(1)CiCs	6	60	90.0	130.8	88.4
	1600	"	"	"	280	6.2	29.05	25.35	28.35	8.0	0.7	29.8	37.8	8.0	Sc	5	47	66.3	104.5	64.7
	1700		7°40'	128°53'	270	6.9	28.90	25.40	28.25	9.4	0.65	30.0	37.6	7.6	CuSc(2)CiCs	4	31	50.9	79.8	48.4
	1800		7°31'	129°03'	275	5.8	28.40	25.40	28.05	11.3	0.35	30.3	37.1	6.8	Ac(2)CiCs	6	17	24.7	65.8	22.1
	1900		7°23'	129°12'	270	6.7	28.00	25.45	28.00	11.7	0.0	30.8	37.0	6.2	Ac(1)Ci	4	-	0	41.0	-5.4
4 March	0500	26	6°02'	130°47'	280	5.45	27.50	25.35	28.05	11.8	-0 55	31.0	37.1	6.1	Ac	3	-	0	43.7	-4.6
	0700	"	"	"	280	6.7	27.75	25.60	28.15	11.5	-0.4	31.5	37.3	5.8	Cu(3)AcAs	8	-	3.1	44.8	-1.7
	0800	26	6°02'	130°47'	280	4.0	28.00	25.40	28.25	11.6	-0.25	30.6	37.6	7.0	CuCb(4)AcAs	8	15	24.3	72.5	21.9
	0900		5°52'	130°39'	285	4.1	28.35	25.45	28.15	11.9	+0.2	30.6	37.4	6.8	Cu(1)AcAs	8	29	43.2	85.3	35.2
	1000		5°49'	130°27'	280	2.3	28.45	25.40	28.25	12.3	0.2	30.3	37.6	7.3	Cu(1)AsCiCs	7	46	77.1	118.9	67.7
	1100		5°46'	130°16'	285	4.5	28.45	24.75	28.05	12.0	0.4	28.7	37.1	8.4	Cu(1)AsCiCs	7	59	47.8	90.6	41.8
	1200		5°42'	130°06'	310	4.1	28.50	24.95	27.95	11.5	0.55	29.1	36.9	7.8	Cu(2)AcAsCiCs	6	73	103.2	139.8	89.0
	1300		5°39'	129°54'	310	4.0	28.45	25.35	28.05	10.4	0.4	30.2	37.1	6.9	Cu(2)AcCiCs	4	84	96.6	146.6	95.0

TABLE 1 (*Continued*)

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind Dirn (deg)	Wind Speed (m/s)	Temperature T_a (°C)	Temperature T_w (°C)	Temperature T_s (°C)	p-1000 (mb)	T_a-T_s (°C)	e_a (mb)	e_s (mb)	e_s-e_a (mb)	Cloud Type	Cloud Amount (octas)	Sun's Elevn (deg)	I (mW/cm²)	$R\downarrow$ (mW/cm²)	R_N (mW/cm²)
4 March	1400		5°36'	129°43'	300	4.0	28.10	25.50	28.55	9.8	-0.45	30.8	38.2	7.4	CuCb(5)Ac	6	75	38.7	85.7	36.8
	1500		5°32'	129°32'	300	4.5	28.35	25.50	28.65	9.1	-0.3	30.6	38.4	7.8	Cu(5)Ac	6	60	108.0	133.4	81.5
	1600		5°31'	129°20'	285	5.6	28.35	25.35	28.55	8.7	-0.2	30.3	38.2	7.9	Cu	3	46	74.0	111.3	60.4
	1700		5°31'	129°08'	300	5.9	28.30	25.25	28.40	8.9	-0.1	30.1	37.9	7.8	Cu	4	32	49.3	93.4	43.0
	1800		5°30'	128°56'	285	4.4	28.50	24.80	28.35	9.2	+0.15	28.8	37.8	9.0	Cu	6	17	26.2	66.3	16.6
	1900	27	5°29'	128°50'	290	7.15	28.00	24.80	28.40	9.5	-0.4	29.1	37.9	8.8	Cu(1)AcAs	3	3	0.7	41.8	- 4.5
	2100	"	5°29'	128°50'	280	6.9	27.75	25.35	28.20	9.4	-0.45	30.7	37.5	6.8	CuSc	3	-	0	40.9	- 5.6
5 March	0800		7°11'	127°19'	260	3.0	27.35	24.85	28.05	10.1	-0.7	29.6	37.1	7.5	As(2)CiCs	3	15	12.3	55.9	7.4
	0900		7°20'	127°09'	-	-	-	-	28.00	10.4	-	-	37.0	-	As(2)CiCs	3	30	49.3	74.8	24.9
	1000		-	-	-	-	-	-	28.15	-	-	-	37.4	-	CiCs	6	44	64.7	102.6	52.3
	1100	28	7°19'	127°11'	270	3.4	27.95	24.7	28.30	11.2	-0.35	28.9	37.7	8.8	CiCs	4	60	80.2	118.4	68.0
	1200	"	7°19'	127°11'	260	5.05	27.95	24.95	28.40	10.5	-0.45	29.5	37.9	8.4	CiCs	6	74	108.0	142.5	91.2
	1300	"	7°19'	127°11'	270	4.20	27.95	25.10	28.50	9.8	-0.55	29.8	38.1	8.3	CiCs	6	86	108.0	147.1	95.7
	1400	"	7°19'	127°11'	270	4.55	28.20	25.05	28.75	9.5	-0.55	29.6	38.7	9.1	CiCs	7	75	81.7	136.8	85.8
	1500	-							28.40						CiCs	5	59	103.3	139.9	88.8
	1610	29	7°21'	126°52'	280	3.7	28.15	25.40	28.60	8.0	-0.45	30.5	38.3	7.8	AcAs(3)CiCs	7	46	78.6	115.8	64.7
	1700	"	7°21'	126°52'	-	-			28.45						CiCs	2	31	27.8	67.95	19.2
	1800	"	7°21'	126°52'	280	5.05	28.35	25.30	28.60	7.0	-0.25	30.2	38.4	8.2	AcAs(1)CiCs	4	17	27.8	68.40	17.9
6 March	0800	30	7°29'	123°27'	150	3.2			27.35						-	0	23	35.5	79.00	29.2
	0830	"	7°29'	123°27'			27.30	24.40	27.80	10.9	-0.5	29.6	36.6	7.0	-	0	31	49.3	88.10	38.0
	0900	"	7°29'	123°27'					27.80						-	0	38	57.0	96.80	46.7
	1000	"	7°29'	123°27'	150	3.75	27.75	24.10	27.95	11.0	-0.2	27.5	36.9	9.4	-	0	53	82.5	120.80	70.2
	1100								28.05						-	0	67	95.6	133.60	83.1
	1200		7°28'	123°15'	250	1.8	28.15	23.90	28.40	9.8	-0.25	26.7	37.9	11.2	-	0	81	104.9	142.50	91.2
	1300								30.10						-	0	81	104.9	141.95	89.6
	1400		7°40'	122°50'	250	1.5	28.50	24.10	30.00	8.4	-1.5	27.0	41.6	14.6	-	0	67	97.1	133.50	81.6
	1500								29.50						-	0	53	83.2	120.0	68.4
	1600		7°50'	122°36'	Calm		28.90	24.30	29.20	7.1	-0.3	27.2	39.7	12.5	-	0	37	59.4	98.35	47.2
	1700								31.00						-	0	22	33.9	75.00	25.1
	1800		7°56'	122°11'	Calm		29.00	24.05		8.0	-0.9	26.5	41.2	14.7	-	0	8	6.9	45.85	- 0.6
7 March	0535	31	7°45'	120°19'	250	3.75	27.55	24.25	28.40	10.6	-0.85	28.0	37.9	9.9	Cu	2	-	0	39.65	- 7.0
	0705	"	7°45'	120°19'	260	3.55	27.35	24.40	28.35	11.0	-1.0	28.5	37.8	9.3	Ci	Tr	7	7.7	45.90	- 0.2
	0900		7°45'	120°14'	260	2.4	27.60	24.70	28.30	11.5	-0.7	29.1	37.7	8.6	Ac	3	36	38.5	79.05	29.7
	1000								28.20						Ac	4	50	78.6	118.50	68.4
	1100		7°46'	120°00'	260	2.9	28.10	24.50	28.70	11.9	-0.6	28.2	38.5	10.3	Ac(1)Cs	2	64	98.6	134.4	83.3
	1200								29.15						Ci	2	78	107.1	143.4	91.6
	1300		7°47'	119°36'	260	1.5	28.15	23.75	30.20	10.3	-2.05	26.4	42.1	15.7	Ci	T_R	83	104.9	141.45	89.0
	1400								30.10						Ci	1	71	101.8	137.80	85.7
	1500		7°49'	119°10'	Calm		28.70	23.85	30.20	9.3	-1.5	26.2	42.2	16.0	Ci	T_R	55	85.6	123.15	71.2
	1600								29.40						AcAs	3	40	67.8	104.8	53.3
	1700		7°52'	118°49'	Calm		28.60	23.75	29.0	8.9	-0.4	26.0	39.2	13.2	AcAs	2	25	43.2	82.2	31.2
	1800								28.75						AcAs	2	10	10.0	51.4	1.8

	1900		7°54'	118°25'	Calm		28.20	24.10	28.75	9.3	-0.55	27.2	38.7	11.5	Cu(2)Ac	3	0	0	43.3	- 2.6
8 March	0300	32	7°57'	117°09'	140	5.86	25.95	24.20	28.50	10.0	-2.55	29.0	38.1	9.1	NsAs	8	0	0	42.9	- 4.0
	0800		7°45'	116°29'	120	2.0	27.90	24.20	28.80	11.0	-0.9	27.7	38.8	11.1	AcAs	6	16	15.4	58.0	9.1
	0900								28.25						Ac	3	31	24.7	67.5	19.0
	1000		7°30'	116°04'	090	2.3	28.20	23.90	28.60	11.7	-0.4	26.7	38.3	11.6	Ac	1	45	77.0	118.1	66.8
	1100								28.80						Ac	3	60	91.0	129.9	78.4
	1200		7°16'	115°38'	060	2.3	28.50	24.20	28.85	11.3	-0.35	27.3	38.9	11.6	Cu(2)Ac	4	74	unst. 95.6	137.9	86.6
	1300								29.15						CuAc	6	85	unst. 84.8	127.7	75.5
	1400		7°02'	115°13'	340	2.2	26.55	23.60	29.00	10.3	-2.45	27.1	39.3	12.2	NsCb(5)AcAs	8	74	unst. 84.8	129.6	77.5
	1500								28.50						CuAc	7	60	32.4	75.6	26.8
	1600		6°48'	114°52'	320	3.8	27.45	24.50	28.55	8.3	-1.1	28.7	38.2	9.5	AcAs	8	46	67.8	105.3	54.8
	1700								28.40						AcAs	7	30	30.8	71.9	23.4
	1800		6°35'	114°28'	300	2.0	27.35	24.40	28.35	7.9	-1.0	28.5	37.80	9.3	AcAs	7	15	11.6	52.6	4.6
9 March	0800		5°07'	111°30'	330	4.2	27.05	24.05	28.10	10.3	-1.05	27.8	37.25	9.4	NsCuCb	6	10	4.6	46.7	- 0.6
	0900								28.00						AcAs	6	26	18.5	62.5	14.3
	1000		5°00'	111°05'	330	3.8	27.40	24.25	28.05	10.7	-0.65	28.1	37.15	9.0	Cu(2)AcCl	6	40	15.4	58.4	11.0
	1100								28.15						AcAs	6	55	55.5	114.3	64.4
	1200		4°53'	110°43'	330	1.3	27.00	24.60	28.25	10.1	-1.25	29.2	37.6	8.4	Cu(2)AcAs	6	69	unst. 81.7	129.7	79.7
	1300								28.35						CuAcAs	4	83	117.2	153.6	103.4
	1400		4°47'	110°18'	300	4.8	27.40	24.80	28.40	9.4	-1.0	29.5	37.9	8.4	Ns(3)CuAc	7	78	-	-	-
	1500								28.60						CuAcAs	6	65	-	139.5	-
	1600		4°42'	110°01'	280	3.2	27.25	25.00	28.90	6.9	-1.65	30.1	39.0	8.9	Cu(2)AcCl	5	50	86.3	123.4	71.9
	1700								28.80						-	-	35	-	71.9	-
	1800		4°36'	109°30'	280	5.0	27.55	25.20	28.75	6.4	-1.2	30.4	38.7	8.3	Cu(1)AsCl	6	21	30.8	71.9	20.4
	1900								28.50						-	-	5	4.6	48.6	1.6
10 March	0800		3°00'	107°18'	330	4.9	27.45	24.70	27.55	9.3	-0.1	29.2	36.0	6.8	Cu	3	7	4.6	47.5	0.1
	0900								27.40						Cu	2	22	30.8	73.5	24.1
	1000		2°39'	107°08'	330	5.6	27.35	25.05	27.60	9.6	-0.25	30.2	36.2	6.0	CuCb	6	37	-	-	-
	1100								27.40						Cu	1	51	80.2	122.6	72.3
	1200		2°12'	107°08'	350	6.2	28.05	24.70	27.80	10.2	+0.25	28.8	36.6	7.8	Cu	4	67	103.3	141.4	90.5
	1300								27.95						Cu	1	82	106.4	141.6	90.6
	1400		1°43'	107°08'	350	5.9	28.05	24.60	27.80	9.1	0.25	28.4	36.6	8.2	Cu	2	87	106.4	144.3	93.3
	1500								27.65						Cu	3	67	-	-	-
	1600		1°15'	107°08'	350	3.1	27.30	24.30	27.65	7.1	-0.35	29.3	36.3	7.0	Cu	2	53	83.2	121.2	70.8
	1700								27.60						Cu	4	39	-	-	-
	1800		0°55'	106°46'	010	3.5	27.20	24.55	27.70	6.4	-0.50	29.0	36.4	7.4	Cu	2	23	37.0	74.9	24.9
11 March	0800		Approaching Singapore Is.				26.80	24.60	27.35	9.8	-0.55	29.4	25.6	6.2	Cu	3	8	24.7	69.4	21.6
15 March	1600		0°54'N	105°08'	135	1.0	27.35	24.45	28.20	8.2	-0.85	28.6	37.5	8.9	Cl	4	37	57.0	97.9	47.6
	1700								28.35						-	-	22	-	90.5	-
	1800		0°33'N	105°27'	135	1.0	27.40	23.90	28.00	8.3	-0.60	27.2	37.0	9.8	Ac	7	8	6.2	49.9	2.4
16 March	0800		2°22'S	107°09'	180	3.8	27.75	24.90	28.40	10.1	-0.65	29.5	37.9	8.4	Cu(1)Ac	7	22	26.2	69.8	20.5
	0900								28.70						-	-	37	63.2	103.8	-
	1000		2°50'	107°17'	160	2.8	27.60	25.20	28.50	11.1	-0.90	28.3	38.1	9.8	Cu	2	52	81.7	121.5	70.6
	1100								28.45						Cu	2	67	97.1	130.7	79.9
	1200		3°21'	107°24'	165	1.0	28.30	24.20	29.55	10.8	-1.25	27.4	40.5	13.1	Cu	1	82	106.4	142.7	90.7
	1300								31.55						Cu	3	82	111.0	149.1	95.6

TABLE 1 (*Continued*)

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind Dirn (deg)	Wind Speed (m/s)	Temperature T_a (°C)	T_w (°C)	T_s (°C)	p-1000 (mb)	T_a-T_s (°C)	e_a (mb)	e_s (mb)	e_s-e_a (mb)	Cloud Type	Cloud Amount (octas)	Sun's Elevn (deg)	I (mW/cm²)	$R\downarrow$ (mW/cm²)	R_N (mW/cm²)
16 March	1400		3°47'	107°12'	210	1.0	29.05	25.15	31.50	7.8	-2.45	29.3	45.3	16.0	Cu	4	67	97.9	136.5	83.5
	1500								30.30						Cu	2	52	91.0	130.3	77.2
	1600		4°14'	107°00'	135	1.0	29.40	25.05	29.95	6.9	-0.55	28.8	41.5	12.7	Cu	3	37	61.6	103.0	51.3
	1700								30.00						Cu	1	22	38.5	80.0	28.2
	1800		4°38'	106°43'	135	2.6	29.35	25.05	30.25	7.3	-0.9	28.8	42.2	13.4	Cu	2	8	4.6	47.2	0.3
17 March	0800		7°22'	105°00'	120	6.7	28.25	25.25	28.70	10.3	-0.45	30.1	38.6	8.5	Cu	4	20	21.6	64.1	14.8
	0900								28.75						Cu	1	35	54.0	91.7	41.3
	1000		7°51'	105°00'	140	6.0	28.70	25.2	28.85	11.2	-0.15	29.6	38.9	9.3	Cu	1	50	77.1	118.0	66.9
	1100								28.65						Cu	Tr	65	95.6	134.7	83.8
	1200		8°19'	105°01'	120	6.8	28.85	24.95	28.75	11.5	+0.1	28.9	38.7	9.8	Cu	2	78	103.3	140.5	89.2
	1300														Cu	2	80	104.8	142.0	90.8
	1400		8°51'	105°01'	125	4.6	29.25	25.10	28.70	8.1	0.55	29.0	38.5	9.5	Cu	2	70	97.9	136.60	85.4
	1500	33	9°00'	105°00'	080	5.50	28.35	25.15	28.80	7.8	-0.45	29.8	38.8	9.0	Cu	3	55	84.0	123.95	74.9
	1630	"	9°00'	105°00'	130	5.75	28.25	25.15	28.70	7.4	-0.45	29.8	38.5	8.7	Cu(1)Ci	3	32	45.5	84.20	34.0
	1800	"	9°00'	105°00'	150	5.7	28.35	25.20	28.55	8.0	-0.2	29.8	38.2	8.4	Cu(1)Ci	3	10	7.7	46.75	1.3
18 March	0800		8°48'	107°46'	060	5.3	28.60	24.70	28.25	10.6	+0.35	28.4	37.6	9.2	Cu	2	24	38.5	79.75	29.3
	0900								28.25						CuCi	3	38	67.8	109.40	58.4
	1000	34	8°54'	108°12'	050	5.95	28.35	24.50	28.80	10.6	-0.45	28.1	38.8	8.7	Cu(2)Ci	3	53	61.6	98.00	49.9
	1100	"	8°54'	108°12'					28.85						Ci	3	68	107.9	147.00	95.3
	1200	"	8°54'	108°12'	030	4.75	28.25	24.75	28.75	10.3	-0.5	28.8	38.6	9.8	Cu(1)Ci	3	78	107.9	146.3	94.7
	1300								28.75						Cu	2	76	107.9	145.45	93.9
	1400		9°14'	108°22'	090	3.5	28.45	25.35	28.95	9.3	-0.5	30.2	39.1	8.9	Cu	2	64	94.0	136.80	85.6
	1500								28.88						Cu	Tr	50	81.0	119.50	68.3
	1600		9°37'	108°35'	110	1.6	28.50	25.10	29.10	8.3	-0.6	29.5	39.5	10.0	Cu	2	36	60.1	100.60	50.4
	1700								29.0						Ac	1	21	32.4	74.30	24.6
	1800		9°51'	108°43'	100	4.1	28.20	25.00	28.80	8.7	-0.6	29.5	38.8	9.3	Cu	Tr	7	3.1	42.85	- 3.3
	2000	35	10°13'	108°46'	130	4.2	28.30	24.60	28.65	10.3	-0.35	28.4	38.5	10.1	Ac	Tr	-	0	39.60	- 7.2
	2100	"	10°13'	108°46'	120	5.05	28.30	24.65	28.65	10.3	-0.35	28.5	38.5	10.0	Ac	Tr	-	0	38.90	- 7.8
	2200	"	10°13'	108°46'	130	4.50	28.20	24.90	28.60	10.8	-0.4	29.2	38.4	9.2	Ac	1	-	0	39.90	- 6.8
19 March	0800		12°00'	109°45'	110	6.2	28.55	25.60	28.25	12.0	+0.3	30.8	37.6	6.8	Cu	4	24	41.6	85.30	34.6
	0900								28.30						Ac	Tr	40	60.1	99.60	49.3
	1010	36	12°10'	109°50'	080	6.65	28.65	26.10	28.50	11.6	0.15	32.1	38.1	6.0	Cu	6	56	89.4	130.95	79.5
	1100	"	12°10'	109°50'					28.70						Cu	2	68	101.7	139.75	88.5
	1200	"	12°10'	109°50'	090	4.90	28.45	25.90	28.55	10.6	-0.1	31.6	38.2	6.6	Cu(2)Ci	3	78	106.4	144.4	93.0
	1300								28.40						Cu(2)Ci	2	76	106.4	143.4	87.6
	1400		12°16'	109°54'	085	3.1	29.00	26.10	29.00	9.6	0.0	31.2	39.3	8.1	Cu(2)Ci	3	63	92.5	131.95	80.8
	1500								28.90						Ci	1	48	78.6	119.70	68.4
	1600		12°28'	110°00'	085	3.0	28.80	25.80	29.00	9.9	-0.2	31.2	39.3	8.1	Cu(1)Ci	4	34	-	-	-
	1700								28.95						Ac	2	19	30.8	76.55	24.9
	1800		12°45'	110°07'	150	3.0	28.60	25.15	28.70	10.2	-0.1	29.6	38.6	9.0	Cu(1)AcCi	4	5	3.1	43.75	- 2.2
	2100	37	13°40'	110°44'	120	7.25	27.60	25.40	28.80	11.8	-1.2	30.9	38.8	7.9	Cu	2	-	0	41.05	- 5.8
	2300	"	13°40'	110°44'	120	7.05	27.75	25.85	28.60	12.2	-0.85	32.5	38.3	5.8	AcAs	4	-	0	41.20	- 5.7

20 March	0800		15°20'	111°40'	130	5.6	28.30	26.05	28.20	12.4	+0.1	32.2	37.5	5.3	Cu(1)AcAs	8	26	27.8	65.85	17.4
	0900								28.50						AcAs	6	41	49.3	91.10	39.3
	1000	38	15°32'	111°40'	140	7.0	28.45	26.05	28.50	13.1	-0.05	32.1	38.1	6.0	AcAs	7	53	58.6	99.70	49.8
	1100	"	15°32'	111°40'					28.70						AcAs	6	67	89.4	123.35	72.3
	1200	"	15°32'	111°40'	135	6.95	28.60	25.95	28.90	12.1	-0.30	31.7	39.0	7.3	As	7	76	69.4	105.65	55.4
	1300								28.60						As	7	73	50.9	93.25	43.8
	1400		15°48'	111°50'	150	6.2	28.75	25.90	28.35	10.8	+0.4	31.4	37.8	6.4	As	7	61	41.6	64.65	34.3
	1500								28.45						As	6	45	32.4	75.20	26.5
	1600		16°00'	111°57'	155	6.3	29.35	25.50	28 55	10.6	0.8	30.0	38.2	8.2	As	7	29	54.0	96.20	44.9
	1700								28.60						AcAs	4	16	12.4	56.80	8.1
	1800		17°12'	112°05'	160	6.3	28.65	25.20	28.65	11.6	0.0	29.7	38.5	8.8	Cu(1)AsCi	5	2	1.5	44.80	- 4.0
	2240	39	17°25'	112°35'	190	7.3	28.30	25.35	28.60	11.9	-0.3	30.3	38.3	8.0	Ac	Tr	-	0	38.85	- 7.8
	2400	"	17°25'	112°35'	190	6.65	28.25	25.05	28.50	12.1	-0.25	29.5	38.1	8.6	Ac	Tr	-	0	38.95	- 7.7
21 March	0800		18°29'	113°27'	170	7.6	28.05	25.20	28.40	12.4	-0.35	30.0	37.9	7.9	-	0	27	43.2	81.80	31.4
	0900								28.60								41	64.8	102.30	51.7
	1100	40	19°11'	113°34'	180	10.5	28.30	24.65	28.75	11.0	-0.45	28.5	38.6	10.2	-	0	66	95.6	134.80	83.7
	1200	"	19°11'	113°34'			28.30	24.75	28.85	10.4	-0.55	28.8	38.9	10.1	-	0	70	100.1	134.05	83.5
	1300								28.60						-	0	66	96.3	134.10	82.9
	1400		19°23'	113°36'	175	6.0	28.10	25.05	28.50	9.6	-0.4	29.7	38.1	8.4	-	0	55	84.0	123.0	72.1
	1500								28.50						-	0	43	67.8	105.75	55.2
	1600		19°35'	113°42'	185	3.8	28.20	25.25	28.55	8.9	-0.35	30.1	38.2	8.1	-	0	29	45.5	84.65	34.0
	1700								28.50						-	0	15	2.0	46.50	- 0.3
	1800	41	20°00'	114°05'	195	9.15	27.95	25.10	28.40	10.2	-0.45	29.9	37.9	8.0	Ci	3	0	0	38.10	- 8.4
22 March	0115	42	21°55'	114°34'	205	10.05	27.20	23.05	27.30	11.5	-0.1	25.3	37.7	12.4	Ac	Tr	0	0	37.50	- 8.3
	0800		22°05'	113°42'	200	6.8	25.10	22.20	26.85	12.4	-1.75	24.7	34.6	9.9	AcAs	3	27	46.3	82.20	32.6
	0900								26.25						Ac	2	40	78.6	110.50	60.4
	1000		22°27'	113°32'	200	5.3	25.15	22.30	26.85	13.0	-1.7	24.9	34.6	9.7	AcAsCiCs	3	51	83.2	119.50	69.6
	1100								26.80						CiCs	2	62	77.0	129.95	80.4
	1200		22°53'	113°25'	195	4.2	25.30	22.36	26.40	12.5	-1.1	25.0	33.7	8.7	Ci	2	68	100.2	134.95	85.2
	1300								26.00						Ac	1	63	94.0	129.95	80.6
	1400		23°17'	113°22'	220	6.1	24.95	22.85	25.20	10.1	-0.25	25.4	31.4	6.0	Ac	Tr	52	81.7	118.10	69.2
	1500								25.50						-	0	42	66.3	104.0	55.0
	1600		23°41'	113°19'	225	4.0	25.00	22.75	24.85	10.9	-0.15	26.11	30.75	4.6	Ac	Tr	28	41.6	82.40	34.3
	1700								25.15						Ac	1	15	20.0	59.00	12.0
	1800		24°03'	113°13'	240	4.0	24.65	22.85	24.60	11.0	0.05	26.57	30.30	3.7	Ac	Tr	1	0	37.95	- 6.3
23 March	0800		27°29'	112°26'	190	1.0	25.20	22.80	25.75	12.3	-0.55	26.25	32.45	6.2	Ci	Tr	25	40.8	78.85	28.1
	0900								25.90						-	0	37	60.1	94.35	45.3
	1000		27°53'	112°21'	290	2.6	25.00	22.95	25.95	12.6	-0.95	26.59	32.80	6.2	AcAs	2	49	77.1	113.45	64.3
	1100								26.00						Ac	3	58	97.1	134.80	85.0
	1200		28°17'	112°15'	270	3.0	24.70	22.65	26.25	12.0	-1.55	26.09	33.40	7.3	Ac(1)Ci	4	63	94.0	130.00	80.6
	1300								24.60						Ac	3	60	87.9	123.35	74.8
	1400		28°41	112°10'	290	2.6	24.55	22.40	24.55	11.4	0.0	25.78	30.25	4.5	AcAs	7	52	-	-	-
	1500								24.30						AcAs	2	41	33.9	70.15	24.0
	1600		29°05'	112°05'	280	2.1	24.35	22.10	24.35	11.2	0.0	25.07	29.85	4.8	AcAs	5	29	26.2	63.85	17.5
	1700								24.70						AcAs	1	15	27.8	62.75	14.6
	1800		29°31'	112°00'	210	4.6	23.40	22.10	24.60	11.5	-1.2	25.71	30.30	4.6	AcAs	7	1	0	37.05	- 7.3
24 March	0510	43	32°00'	111°20'	165	10.4	20.80	18.95	21.70	13.0	-0.9	20.57	25.45	4.9	-	-	0	0	34.75	- 7.8

TABLE 2

DATA FOR CRUISE G 4/62

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind		Temperature								Cloud		Sun's Elevn	I	$R\downarrow$	R_N
					Dirn (deg)	Speed (m/s)	T_a (°C)	T_w (°C)	T_s (°C)	p-1000 (mb)	T_a-T_s (°C)	e_a (mb)	e_s (mb)	e_s-e_a (mb)	Type	Amount (octas)	(deg)	(mW/cm²)	(mW/cm²)	(mW/cm²)
18 Aug	1400		31°55'	115°10'	120	3.0	13.40	8.40	20.15	29.3	-6.75	7.6	23.1	15.5	Cu	1	43	66.0	-	-
	1530		31°55'	115°10'	130	3.7	12.70	8.80	20.00	29.0	-7.30	8.6	22.9	14.3		0	28	44.0	-	-
	1700		31°55'	114°55'	180	3.5	13.70	10.10	20.15	28.8	-6.45	9.9	23.1	13.2		0	10	-	-	-
	1830		31°55'	114°40'	160	3.2	13.85	10.00	19.90	28.7	-6.05	7.6	22.8	15.2		0	-	0	28.6	-12.7
	1930		31°55'	114°30'			-	-									-	0	29.6	-11.7
	2030		31°55'	114°20'	270	1.5	14.65	11.10	19.75	29.5	-5.10	10.8	21.6	10.8		0	-	0	30.7	-11.3
19 Aug	0800	181	31°58'	111°48'	050	7.3	16.55	12.40	19.15	27.6	-2.60	11.5	22.7	11.2	Sc	7	10	17.9	52.0	8.8
	0930	"		"	070	7.7	16.85	13.20	19.50	26.8	-2.65	12.7	22.2	9.5	CuSc	6	29	17.9	52.3	9.5
	1100	"	"	"	040	8.1	17.25	13.20	19.50	26.3	-2.25	12.4	22.2	9.8	CuSc	7	43	24.8	59.6	10.1
	1230	"	"	"	020	8.5	17.30	13.10	19.50	25.7	-2.20	12.2	22.2	10.0	CuSc	6	48	44.0	76.1	32.3
	1400	"	"	"	035	9.0	17.45	13.50	19.55	23.9	-2.10	12.8	22.3	9.5	CuSc	7	43	38.5	68.7	25.1
	1530	"	"	"	025	8.4	17.60	13.35	19.55	23.1	-1.95	13.1	22.3	9.2	CuSc	7	29	16.5	51.4	8.6
	1700	"	"	"	000	7.5	17.70	14.00	19.55	23.3	-1.85	13.4	22.3	8.9	CuSc	6	10	5.5	41.7	-0.7
	1830		31°58'	111°42'	010	7.4	17.80	14.05	19.40	23.7	-1.60	13.5	22.1	8.6	Sc	6	-	0	38.2	-3.3
20 Aug	0800	182	32°08'	110°00'	010	10.0	18.40	15.75	19.50	18.2	-1.10	16.1	22.2	6.1	CuSc	TR	9	11.0	42.7	-1.2
	0930	"	"	"	020	10.2	18.95	15.75	19.55	18.8	-0.60	15.7	22.3	6.6	CuAs	2	28	45.3	77.9	31.2
	1100	"	"	"	015	10.3	18.65	15.55	19.65	18.5	-1.00	15.5	22.4	6.9	Cu(TR)AS	4	42	78.3	103.4	57.1
	1230		32°04'	110°00'	000	6.1	19.30	15.60	19.50	16.8	-0.20	15.4	22.2	6.8	Cu(2)As	8	49	19.2	53.5	6.9
	1400		31°49'	110°00'	340	10.5	19.15	15.80	19.45	15.4	-0.30	15.5	22.1	6.6	AcAs	8	44	33.0	68.2	25.0
	1530		31°34'	110°00'	340	10.6	19.25	15.80	18.90	15.6	+0.35	15.6	21.4	5.8	AcAs	8	31	16.5	52.2	9.9
	1700		31°19'	110°00'	340	9.5	19.00	15.90	18.80	16.6	0.20	15.9	21.3	5.4	AcAs	8	14	5.5	43.5	1.7
	1830		31°03'	110°00'	330	9.5	18.90	16.35	18.70	16.7	0.20	16.8	21.1	4.3	AcAs	8	-	0	38.0	-2.7
	2100	183	30°30'	110°00'	330	8.0	18.70	16.90	18.80	16.7	-0.10	18.0	21.3	3.3	AcAs	4	-	0	38.4	-2.6
	2300	"			330	9.5	19.00	16.85	18.75	18.0	-0.25	17.7	21.2	3.5	AcAs	4	-	0	35.7	-5.2
21 Aug	0800	184	29°00'	110°00'	330	10.0	19.95	17.85	19.25	17.3	0.70	19.0	21.9	2.9	Cu	1	12	16.5	47.6	3.4
	0900	"	"				19.1										24	37.1	69.1	25.5
	1000	"	"	"	310	9.1	20.20	17.70	18.90	17.5	1.30	18.5	21.4	2.9	Cu	TR	35	52.9	85.5	40.8
	1100	"	"	"			19.0										44	65.3	98.1	51.3
	1200	"	"	"	300	11.3	20.30	18.05	18.95	17.1	1.35	19.2	21.5	2.3	CuAc	1	50	77.0	106.8	61.6
	1300						19.9										51	85.2	111.8	66.0
	1400		28°38'	110°00'	310	8.8	21.25	18.95	21.00	16.3	0.25	20.3	24.4	4.1	Cu	2	47	75.6	102.2	56.2
	1500						20.9										39	59.1	87.2	40.8
	1600		28°14'	110°10'	310	9.5	21.60	19.60	21.05	16.9	0.55	21.4	24.5	3.1	CuCb	4	29	41.2	74.8	28.6
	1700								21.20								18	28.9	66.8	20.6
	1800		27°54'	110°00'	320	11.1	21.60	19.60	21.80	17.5	-0.20	21.4	25.6	4.2	Cu	3	5	2.7	41.7	-1.7
	1900								21.80									0	38.1	-4.6
	2000	185	27°30'	110°00'	280	7.8	20.80	19.25	20.40	18.8	0.40	21.2	23.5	2.3	Low	6	-	0	39.7	-2.4
	2100	"	"	"					20.50								-	0	41.1	-1.1
	2200	"	"	"	320	2.4	20.40	19.00	20.25	19.9	0.15	21.0	23.3	2.3	Low	2	-	0	41.6	-0.4
22 Aug	0800	186	26°00'	110°00'	155	4.0	20.40	18.10	20.80	21.9	-0.40	19.2	24.1	4.9	Ac	Tr	13	19.2	52.3	6.8
	0900	"	"	"					21.00								25	38.5	71.9	26.2

	1000	"	"	"	155	4.7	20.20	17.95	21.05	23.1	-0.85	19.0	24.5	5.5	Ac	1	37	58.4	83.0	37.1
	1100	"	"	"					21.20								47	71.5	92.3	46.5
	1200	"	"	"	135	4.2	20.20	18.05	21.20	22.6	-1.00	19.2	24.7	5.5	Ac	1	54	79.0	97.6	51.3
	1300								21.50								56	63.2	88.5	43.4
	1400		25°45'	110°00'	180	3.5	21.35	18.40	21.85	21.7	-0.50	19.1	25.7	6.6	Cu	Tr	52	75.6	95.3	49.5
	1500								21.60								42	63.9	87.2	41.3
	1600		25°21'	110°00'	150	2.8	20.80	18.20	21.60	21.7	-0.80	19.1	25.3	6.2	Ac	1	31	45.4	74.2	28.5
	1700								21.20								18	13.1	51.4	7.4
	1800		24°57'	110°00'	130	2.4	20.85	19.20	21.25	22.1	-0.40	21.1	24.8	3.7	Ac	3	6	3.4	42.3	-1.0
	1900								21.20								-	0	35.4	-6.9
	2000	187	24°30'	110°00'	115	6.3	20.80	19.15	21.20	23.1	-0.40	21.0	24.7	3.7	Low	3	-	0	36.4	-5.7
	2100	"	"	"					21.0								-	0	35.7	-6.5
	2200	"	"	"	080	6.5	20.70	18.90	21.05	23.8	-0.35	20.6	24.5	3.9	Low	1	-	0	35.7	-6.6
23 Aug	0800	188	23°00'	110°00'	095	10.0	21.75	18.70	22.45	22.2	-0.70	19.5	26.6	7.1	Cu	2	12	11.0	47.0	1.9
	0900	"	"	"					22.50								25	44.0	77.8	30.7
	1000	"	"	"	070	10.2	21.85	19.00	22.50	22.9	-0.65	20.0	26.7	6.7	Cu	3	37	63.3	96.6	49.4
	1100	"	"	"					22.60								48	75.6	107.1	60.0
	1200	"	"	"	050	11.0	21.80	18.85	22.65	22.6	-0.85	19.7	26.9	7.2	Cu	3	56	88.0	120.9	73.6
	1300								22.80								57	94.9	125.8	78.1
	1400		22°48'	110°00'	100	6.1	21.95	19.05	22.70	20.7	-0.75	20.0	27.0	7.0	Cu	2	52	85.3	116.3	68.9
	1500								22.70								43	72.9	106.1	57.9
	1600		22°24'	110°00'	090	4.2	21.90	19.20	22.50	19.1	-0.60	20.4	26.70	6.3	Cu	2	31	55.0	89.2	41.9
	1700								22.50								18	34.4	68.7	21.1
	1800		22°00'	110°00'	120	6.2	21.75	19.15	22.65	20.0	-0.90	20.4	26.9	6.5	Ac	Tr	6	5.5	39.7	-4.9
	1900								22.60								-	0	32.9	-10.1
	2000	189	21°30'	110°00'	130	7.9	21.75	19.50	22.95	21.0	-1.20	21.1	27.4	6.3		0	-	0	33.3	-9.8
	2100	"	"	"					23.00								-	0	33.3	-10.0
	2200	"	"	"	120	7.2	21.95	19.60	23.25	20.6	-1.30	21.2	28.0	6.8		0	-	0	33.3	-10.2
24 Aug	0800	190	20°00'	110°00'	080	8.3	22.50	20.40	23.20	20.1	-0.70	22.5	27.9	5.4	Cu	Tr	13	19.3	48.0	1.4
	0900	"	"	"					23.30								26	41.2	76.5	29.3
	1000	"	"	"	075	6.5	22.90	20.20	23.45	21.0	-0.55	21.8	28.3	6.5		0	39	63.2	96.7	48.2
	1100	"	"	"					23.30								50	79.7	110.9	63.3
	1200	"	"	"	100	3.2	23.15	20.35	23.45	19.3	-0.30	22.0	28.3	6.3		0	58	85.9	119.5	72.1
	1300								23.0								60	86.6	120.2	72.7
	1400		19°36'	110°00'	100	8.2	24.00	19.90	24.30	18.5	-0.30	20.4	29.8	9.4		0	54	80.5	113.8	65.9
	1500								24.00								44	68.7	103.1	55.1
	1600		19°12'	110°00'	080	6.8	24.05	20.00	24.65	17.4	-0.60	20.6	30.4	9.8		0	32	48.8	84.8	36.9
	1700								24.30								20	30.3	63.8	16.1
	1800		18°52'	110°00'	100	4.2	23.80	20.80	24.70	17.5	-0.90	22.5	29.4	6.9	Cu	Tr	7	6.2	41.2	-4.3
	1900								23.90								-	0	35.0	-8.8
	2000	191	18°30'	110°00	070	6.0	23.90	20.15	24.20	18.8	-0.30	21.0	29.6	8.6		0	-	0	34.7	-9.2
	2100	"	"	"					24.20								-	0	35.1	-8.8
	2200	"	"	"	040	6.6	23.75	20.40	24.40	18.6	-0.65	21.7	30.0	8.3		0	-	0	35.2	-8.9
25 Aug	0800	192	17°00	110°00	060	6.9	23.95	19.50	24.40	18.6	-0.45	19.6	30.0	10.4	Cu	3	13	15.1	54.9	9.9
	0900	"	"	"					24.40								27	52.2	89.1	40.3
	1000	"	"	"	065	7.1	24.15	19.90	24.45	19.4	-0.30	20.3	30.0	9.7	Cu	2	41	64.6	98.7	50.5
	1100	"	"	"					24.40								52	83.8	123.1	74.6

TABLE 2 (*Continued*)

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind Dirn (deg)	Wind Speed (m/s)	Temperature T_a (°C)	Temperature T_w (°C)	T_s (°C)	p-1000 (mb)	T_a-T_s (°C)	e_a (mb)	e_s (mb)	e_s-e_a (mb)	Cloud Type	Cloud Amount (octas)	Sun's Elevn (deg)	I (mW/cm²)	$R\downarrow$ (mW/cm²)	R_N (mW/cm²)
25 Aug	1200	"	"	"	040	3.4	24.10	20.45	24.65	18.5	-0.55	21.5	30.4	8.9	Cu	1	59	90.7	126.4	75.8
	1300								24.3								60	92.1	127.1	78.6
	1400		16°36'	110°00'	NO OBSERVATIONS POSSIBLE DUE TO NAVAL EXERCISE				24.3								55	83.1	118.4	69.5
	1500								24.5								46	74.2	109.6	61.2
	1600		16°12'	110°00'	080	3.9	24.60	20.70	24.90	15.6	-0.30	21.7	30.8	9.1	Cu	2	34	56.4	96.1	47.5
	1700								25.10								21	34.4	71.8	23.3
	1800		15°48'	110°00'	090	5.1	25.05	21.00	25.10	15.9	-0.05	22.1	31.2	9.1	Cu	2	9	6.9	42.6	0.8
	1900								25.20								-	0	36.1	-8.5
	2000	193	15°33'	110°00'	080	7.1	24.85	20.50	25.30	16.6	-0.45	21.1	31.6	10.5	-	0		0	37.3	-7.5
	2100	"	"	"					25.30									0	36.1	-8.5
	2200	"	"	"	040	6.6	24.85	20.95	25.35	16.3	-0.50	22.1	31.7	9.6	As	3		0	38.3	-6.4
26 Aug	0800	194	14°00'	110°00'	080	9.6	25.30	20.85	25.55	16.0	-0.25	21.6	32.1	10.5	Cu	3	16	23.4	62.4	14.0
	0900	"	"	"					25.60								29	53.6	91.1	41.0
	1000	"	"	"	085	7.1	25.55	20.70	25.55	17.0	0.00	21.1	32.1	11.0	Cu	Tr	41	64.6	102.6	53.5
	1100	"	"	"					25.60								53	77.5	114.1	65.1
	1200	"	"	"	070	7.0	25.25	20.40	25.65	16.2	-0.40	20.6	32.3	11.7	-	0	63	87.2	123.2	74.2
	1300								25.60								65	88.0	125.0	76.1
	1400		13°36'	110°00'	110	6.2	25.35	21.10	25.65	14.3	-0.30	22.1	32.3	10.2	Cu	Tr	58	84.5	121.4	72.5
	1500								25.60								48	71.4	109.7	60.9
	1600		13°12'	110°00'	120	9.1	25.35	21.40	25.80	13.2	-0.45	22.8	32.6	9.8	Cu	1	35	55.7	93.1	44.1
	1700								25.90								22	33.0	72.9	24.2
	1800		12°50'	110°00'	080	7.1	25.50	21.25	25.75	13.7	-0.25	22.3	32.5	10.3	Cu	3	8	4.1	42.3	-3.8
	1900								25.80								-	0	38.3	-6.7
	2000	195	12°34'	110°00'	080	68	25.50	21.25	25.80	15.2	-0.30	22.3	32.6	10.3	Cu	1	-	0	38.3	-6.7
	2100	"	"	"					25.80								-	0	36.8	-8.2
	2200	"	"	"	070	7.2	25.50	21.30	25.90	16.0	-0.40	22.4	32.8	10.4	-	0	-	0	36.9	-8.0
27 Aug	0800	196	11°00'	110°05'	095	7.6	25.60	20.30	25.80	15.4	-0.20	20.2	32.6	12.4	Cu	1	15	22.0	59.8	11.3
	0900	"	"	"					25.70								29	48.8	83.6	34.5
	1000	"	"	"	095	7.4	25.90	20.15	25.90	16.0	0.00	19.6	32.8	13.2	Cu	Tr	43	67.4	99.8	50.7
	1100	"	"	"					25.70								56	82.4	116.0	67.1
	1200	"	"	"	100	7.5	25.55	20.55	26.00	15.9	-0.45	20.8	32.9	12.1	Cu	Tr	66	92.7	126.4	77.5
	1300								25.60								68	101.7	135.8	86.5
	1400		10°36'	110°00'	130	7.7	25.50	20.70	25.95	14.1	-0.45	20.1	32.9	12.8	Cu	1	61	92.0	127.7	78.7
	1500								25.70								49	82.4	120.2	70.8
	1600		10°10'	110°00'	130	7.6	25.55	21.20	26.00	23.4	-0.45	22.2	32.9	10.7	Cu	Tr	35	59.1	96.7	47.6
	1700								25.70								22	38.5	77.2	28.0
	1800		9°50'	110°00'	100	-	25.75	21.40	25.90	13.3	-0.15	22.5	32.8	10.3	Cu	1	8	11.8	49.7	1.7

	1900								25.70								-	0	39.9	-5.1
	2000								25.70								-	0	37.7	-7.3
	2100	197	9°30'	110°00'	130	7.5	25.40	21.90	25.85	15.1	-0.45	23.9	32.7	8.8	Cu	2	-	0	39.2	-5.8
	2200	197	9°30'	110°00'					25.70								-	0	39.8	-5.2
	2300	"	"	"	100	10.2	25.40	22.05	25.85	15.5	-0.45	24.2	32.7	8.5	Cu	1	-	0	38.2	-6.8
28 Aug	0800		9°00'	108°36'	120	5.1	25.30	21.35	25.55	15.5	-0.25	22.7	32.1	9.4	Cu	2	17	23.4	62.5	14.4
	0900								25.30								32	22.0	62.2	15.6
	1000		9°00'	108°24'	110	5.9	25.40	21.05	25.50	17.9	-0.10	21.9	32.0	10.1	Cu(1) AcAs	.7	45	35.7	78.4	31.6
	1100								25.10								59	80.2	111.5	62.8
	1200		9°02'	107°57'	120	5.6	25.65	21.10	25.55	15.3	+0.10	21.9	32.1	10.2	Ac	1	67	90.7	126.1	76.2
	1300								25.20								69	94.1	128.8	80.1
	1400		9°03'	107°32'	120	5.2	25.55	20.80	25.55	13.5	0.00	21.3	32.1	10.8		0	63	88.6	123.5	76.1
	1500								25.10								50	77.0	114.2	65.5
	1600		9°03'	107°09'	120	5.3	25.35	21.45	25.50	13.0	-0.15	22.9	32.0	9.1		0	38	59.0	98.9	50.4
	1700								25.40								24	37.1	75.0	26.5
	1800		9°04'	106°53'	120	-	25.40	22.05	25.85	13.0	-0.45	24.2	32.7	8.5	Cu	1	10	13.8	51.1	3.3
	1900								25.50								-	0	38.0	-6.8
	2000								25.20								-	0	38.1	-6.6
	2100	198	9°07'	106°22'	120	10.0	25.30	22.15	25.45	12.0	-0.15	24.5	31.9	7.4		0	-	0	37.5	-7.2
	2200								25.30								-	0	37.5	-7.3
	2300		9°05'	106°18'	120	11.2	25.35	22.55	25.65	12.3	-0.30	25.4	32.9	7.5	Cu	2	-	0	40.4	-4.5
29 Aug	0800	199	9°00'	105°00'	130	9.1	25.50	22.15	25.95	12.4	-0.45	24.4	32.9	8.5	Cu	2	14	20.0	63.7	15.1
	0900								25.80								27	41.3	80.0	31.2
	1000	"	"	"	090	10.0	25.55	22.15	25.95	12.9	-0.40	24.3	32.9	8.6	Cu	1	44	63.3	101.3	52.6
	1100								25.70								55	84.0	120.4	71.3
	1200	"	"	"	090	8.3	25.55	22.35	26.05	12.1	-0.50	24.8	33.0	8.2	Cu	2	65	92.2	126.6	77.5
	1300								25.80								70	96.3	131.1	81.7
	1400	"	"	"	110	7.7	25.80	22.35	26.05	10.7	-0.25	24.6	33.0	8.4	Cu	1	65	90.8	128.4	79.3
	1500								26.05								54	83.2	121.4	72.0
	1600	"	"	"	100	7.3	25.45	23.05	26.20	9.7	-0.75	26.5	33.4	6.9	Cu	4	42	63.3	102.6	53.6
	1700								25.90								27	45.4	84.2	35.0
	1800	"	"	"	105	7.2	25.65	22.75	26.15	9.6	-0.50	25.7	33.2	7.5	Cu	5	13	11.0	52.2	5.4
	1900								26.0								-	0	40.3	-4.9
	2000								26.1								-	0	39.9	-5.3
30 Aug	0800		6°26'	105°00'	120	3.3	26.05	23.70	26.15	10.0	-2.10	27.7	37.4	9.7	Cu(1) AcAs	8	15	4.1	47.9	-0.8
	0900								27.50											
	1000		6°18'	105°24'	120	5.6	26.70	24.15	28.20	10.7	-1.50	28.4	37.5	9.1	Sc (Hazy)	8	29	20.6	63.1	15.5
	1100								28.00								43	24.8	67.6	19.7
	1200		6°07'	105°42'	180	5.5	27.10	23.85	28.25	11.5	-1.15	27.3	37.6	10.3	Ac (Hazy)	7	57	59.1	97.8	47.9
	1300								28.10								70	66.0	106.9	57.3
																	74	112.5	146.5	94.6

TABLE 2 (*Continued*)

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind Dirn (deg)	Wind Speed (m/s)	Temperature T_a (°C)	Temperature T_w (°C)	Temperature T_s (°C)	p-1000 (mb)	T_a-T_s (°C)	e_a (mb)	e_s (mb)	e_s-e_a (mb)	Cloud Type	Cloud Amount (octas)	Sun's Elevn (deg)	I (mW/cm²)	$R\downarrow$ (mW/cm²)	R_N (mW/cm²)
30 Aug	1400		5°33'	106°01'	160	3.8	28.10	23.35	29.90	9.7	-1.80	25.4	41.3	15.9	As	1	67	90.7	127.7	76.3
	1500								29.80								55	81.1	117.9	66.5
	1600		5°22'	106°12'	080	4.6	28.00	23.75	28.65	7.5	-0.65	26.4	38.5	12.1		0	41	63.9	98.8	48.5
	1700								28.10								27	42.6	78.5	28.5
	1800		5°00'	106°27'	070	5.8	27.35	23.75	28.10	6.9	-0.75	26.8	37.2	10.4		0	12	17.9	53.6	3.9
	1900								27.90									0	39.5	-6.8
31 Aug	0800		2°21'	107°20'	070	3.4	27.05	24.60	27.80	9.9	-0.75	29.3	36.6	7.3		0	24	32.3	72.4	22.7
	0900								27.90								39	52.3	92.8	43.1
	1000		1°55'	107°15'	130	6.8	27.60	24.70	27.80	10.2	-0.20	29.1	36.6	7.5	Cu	1	54	72.9	112.9	62.9
	1100								27.70								67	88.7	128.2	78.1
	1200		1°31'	107°06'	140	6.2	27.80	24.40	28.05	9.0	-0.25	28.3	37.2	8.9	Cu	2	78	77.0	129.9	79.8
	1300								28.00								73	101.7	138.4	87.0
	1400		1°05'	106°58'	160	8.0	28.05	24.25	28.00	7.5	+0.05	27.7	37.0	9.3	CuSc	7	61	77.0	113.1	63.0
	1500								28.00								47	71.5	111.3	60.8
	1600		0°39'	105°50'	160	7.4	28.50	24.75	28.00	7.0	+0.50	28.6	37.0	8.4	CuSc	8	33	50.9	91.3	41.2
	1700								28.00								18	33.0	73.0	22.6
	1800		0°13'	105°48'	160	8.0	28.00	24.45	28.05	6.5	-0.05	28.2	37.2	9.0	CuAcAs	6	4	2.8	42.4	3.4
4 Sept	1700								28.20								22	30.2	RADIOMETER OUT OF ACTION	
	1800		0°30' (N)	105°00'	180	2.1	28.30	24.40	28.20	6.1	+0.10	27.9	37.5	9.6	Ci	3	8	6.2	"	"
5 Sept	0800		1°03' (S)	106°56	150	7.1	27.40	24.30	27.65	9.5	-0.25	28.2	36.3	8.1	Cu	5	26	34.4	"	"
	0900								27.80								40	60.5	"	"
	1000		1°26'	107°04'	140	4.1	27.65	24.15	27.60	9.2	+0.05	27.7	36.2	8.5	Cu	Tr	55	81.1	"	"
	1100								27.30								67	97.6	"	"
	1200		1°48'	107°12'	140	3.7	27.90	24.40	27.85	8.1	+0.05	28.2	36.7	8.5	Cu	1	80	98.3	"	"
	1300								27.90								76	96.2	"	"
	1400		2°09'	107°20'	160	1.0	27.80	24.15	28.25	7.2	-0.45	27.6	37.5	9.9	Cu	2	63	91.4	129.9	79.0
	1500								28.10								47	20.6	64.2	11.7
	1600		2°34'	107°21	160	7.3	28.15	24.75	28.20	5.5	-0.05	28.9	37.5	8.6	Cu(1) Ci HAZY	5	33	41.3	82.2	32.7
	1700								27.40								17	17.9	58.8	10.2
	1800		2°57'	107°22'	160	4.6	28.15	24.25	28.05	6.5	0.10	27.6	37.2	9.6	Cu.Ci	3	5	2.8	42.9	-2.8
6 Sept	0800		5°25'	106°11'	130	3.4	26.80	23.70	28.10	9.2	-1.30	27.2	37.3	10.1	Cu.Ci	2	22	37.1	75.4	25.1
	0900								28.10								36	60.5	95.5	45.1
	1000		5°50'	106°03'	200	1.6	27.45	22.65	28.55	10.2	-1.10	24.2	38.2	14.0		0	51	79.7	113.8	63.2
	1100								27.90								65	90.7	125.3	75.1

	1200		6°09'	105°40'	230	3.3	27.20	23.05	28.30	8.7	-1.10	25.3	37.7	12.4		0	76	95.6	132.0	81.3
	1300								28.10								76	94.8	131.8	81.2
	1400		6°22'	105°15'	190	7.2	26.70	23.60	28.25	7.3	-1.55	27.0	37.5	10.5		0	65	79.7	108.4	58.8
	1500								27.90								51	EXCESSIVE SPRAY FORD.		
	1600		6°36'	104°50'	150	10.0	27.05	23.60	26.65	6.7	0.40	26.8	36.3	9.5		0	36	READINGS IN DOUBT		
	1700								26.90								22	"	" "	
	1800		6°58'	104°52'	130	9.3	25.75	23.00	26.65	7.4	-0.90	26.2	34.2	8.0	Cu	TR	6	"	" "	
7 Sept	0600	200	8°53'	105°03'	100	9.0	24.95	21.70	25.25	10.1	-0.30	23.7	31.5	7.8	Cu	2	-	0	39.5	-5.1
	0700	"							25.10								6	4.1	45.5	0.2
	0800	"	"	"	115	9.0	25.30	22.05	25.25	10.7	0.05	24.3	31.5	7.2	Cu	3	21	13.8	52.3	6.1
	0900								25.10								35	61.2	99.2	49.6
	1000		8°53'	105°15'	110	6.3	25.60	22.10	25.40	11.5	0.20	24.2	31.8	7.6	Cu	1	50	78.4	115.8	66.8
	1100								25.50								63	92.8	127.2	78.2
	1200		8°53'	105°37'	120	5.8	25.60	22.65	25.50	9.9	0.10	25.5	32.0	6.5	Cu	TR	72	97.6	130.9	81.4
	1300								25.50								72	101.8	135.2	85.8
	1400		8°53'	105°59'	120	5.2	25.50	22.70	25.60	8.4	-0.10	25.7	32.2	6.5	Cu	4	63	92.1	123.3	74.5
	1500								25.70								50	75.6	113.7	64.6
	1600		8°53'	106°23'	120	6.2	25.50	22.55	25.70	7.7	-0.20	25.3	32.4	7.1	Cu	3	35	24.8	83.2	35.3
	1700								25.70								21	31.6	68.8	20.2
	1800		8°54'	106°45'	120	6.0	25.45	22.00	25.50	8.9	-0.05	24.1	32.0	7.9	Cu(1) Cl	4	6	4.1	42.8	21.8
8 Sept	0800		9°23'	109°16'	110	5.5	26.00	22.75	25.45	11.7	0.55	25.4	31.9	6.5	Cu	2	26	39.8	81.6	33.3
	0900								25.10								39	66.6	101.4	52.6
	1000		9°26'	109°44'	110	5.0	25.75	23.30	25.40	11.8	0.35	26.9	31.8	4.9	CuNs	6	53	90.7	128.5	76.8
	1100								25.20								65	93.4	131.8	83.0
	1200	201	9°27'	109°49'	130	6.3	26.65	23.35	25.60	10.2	1.05	26.4	32.2	5.8	Cu	1	73	100.3	134.4	85.3
	1300								25.30								69	104.4	139.7	90.4
	1400		9°48'	109°51'	120	5.8	25.35	23.15	25.55	9.5	-0.20	26.8	32.0	5.2	Cu	3	58	86.8	122.2	73.3
	1500								25.10								45	71.4	109.4	60.6
	1600		10°09'	109°53'	120	6.5	25.30	23.20	25.20	8.9	0.10	27.0	31.4	4.4	Cu	2	31	43.9	82.5	35.4
	1700								25.10								16	23.4	-	-
	1800		10°30'	109°56'	130	5.0	25.35	23.10	25.20	10.2	0.15	26.7	31.4	4.7	Ci	2	-	0	40.8	-3.8
	1900								24.90								-	0	39.3	-5.2
	2000								24.90								-	0	39.3	-5.2
	2100	202	10°58'	110°00'	130	5.8	25.15	23.00	25.15	11.8	0.00	26.6	31.3	4.7	-	0	-	0	39.3	-5.3
	2200	"	"	"					25.00								-	0	39.9	-4.7
	2300	"	"	"	110	5.5	25.25	23.20	25.20	9.5	0.05	27.0	31.4	4.4	Cu	1	-	0	40.3	-4.4
9 Sept	0800	203	12°30'	110°00'	130	5.4	25.70	22.45	26.10	14.0	-0.40	24.9	33.1	8.2		0	25	41.9	81.1	32.0
	0900								25.80								39	61.2	99.0	50.1
	1000	"	"	"	135	4.6	26.45	22.75	26.15	14.5	+0.30	25.1	33.2	8.1	Ac	6	53	55.6	96.3	48.7
	1100								25.90								66	57.7	99.5	51.7
	1200	"	"	"	115	4.6	25.85	22.70	26.40	13.5	-0.55	25.4	33.8	8.4	CuAc	TR	73	94.8	129.1	79.8
	1300								26.20								68	96.2	130.5	81.1

TABLE 2 (*Continued*)

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind Dirn (deg)	Wind Speed (m/s)	Temperature T_a (°C)	Temperature T_w (°C)	Temperature T_s (°C)	p-1000 (mb)	T_a-T_s (°C)	e_a (mb)	e_s (mb)	e_s-e_a (mb)	Cloud Type	Cloud Amount (octas)	Sun's Elevn (deg)	I (mW/cm²)	$R\downarrow$ (mW/cm²)	R_N (mW/cm²)
9 Sept	1400		12°45'	110°00'	120	5.9	25.60	22.60	26.40	11.8	-0.80	25.4	33.8	8.4	Cu	TR	58	83.8	120.3	71.3
	1500								26.20								44	67.3	103.2	54.2
	1600		13°10'	110°00'	130	3.8	25.55	22.40	26.40	11.5	-0.85	24.9	33.8	8.9	-	0	30	45.3	81.0	32.3
	1700								26.10								16	24.7	61.3	12.4
	1800		13°35'	110°00'	130	4.2	25.35	21.95	26.25	12.6	-0.90	24.0	33.4	9.4	Cu	1	2	1.4	38.3	-6.3
	1900								25.80								-	0	-	-
	2000	204	14°00'	110°00'	100	5.5	25.15	21.70	25.75	13.4	-0.60	23.6	32.5	8.9	Cu	6	-	0	41.3	-3.7
	2100	"							25.60								-	0	37.6	-7.3
	2200	"	"		130	7.1	25.00	22.30	25.70	12.9	-0.70	25.1	32.4	7.3	Cu	1	-	0	37.8	-7.1
10 Sept	0800	205	15°30'	110°00'	120	2.6	24.15	19.85	25.65	15.0	-1.50	20.2	32.3	12.1	-	0	24	39.8	76.2	27.6
	0900								25.60								39	62.5	97.0	48.5
	1000	"	"	"	085	2.1	24.45	20.65	25.75	15.7	-1.30	21.7	32.5	10.8	-	0	52	79.7	113.7	64.9
	1100								25.50								57	90.7	123.9	74.7
	1200	"	"	"	050	3.7	24.50	20.90	25.90	14.5	-1.40	22.2	32.8	10.6	Cu	TR	69	96.9	130.0	80.2
	1300								25.60								66	101.6	136.7	97.4
	1400				NO OBSERVATIONS DUE TO NAVAL EXERCISE												56	84.5	118.3	69.4
	1500								25.70								44	67.3	101.9	53.1
	1600		16°10'	110°00'	130	3.4	24.80	21.60	25.75	13.4	-0.95	23.6	32.5	8.9	Cu	2	30	44.0	81.5	31.9
	1700								25.40								15	27.5	65.7	16.6
	1800		16°25'	"	130	3.5	24.85	22.00	25.30	14.3	-0.55	24.5	31.6	7.1	CuSc	3	-	0	39.7	-5.0
	1900								25.20								-	0	42.7	-2.0
	2000								25.10								-	0	41.9	-2.8
	2100	206	17°00'	"	110	6.3	24.45	21.85	24.60	16.6	-1.15	24.4	30.3	5.9	CuNs	7	-	0	43.3	-1.2
	2200	"	"	"					24.40								-	0	40.9	-3.4
	2300	"	"	"	110	7.4	24.30	21.80	24.60	16.8	-0.30	24.4	30.3	5.9	Cu	5	-	0	39.8	-4.5
11 Sept	0800	207	18°30'	110°00'	100	7.4	23.10	20.75	24.40	16.4	-1.30	22.9	29.9	7.0	Cu	4	24	41.2	75.8	27.7
	0900								24.40								38	64.6	100.4	51.1
	1000		"	"	105	7.4	23.45	20.55	24.55	17.1	-1.10	22.2	30.2	8.0	Cu	6	51	85.2	119.8	71.1
	1100								24.40								61	96.1	129.9	81.6
	1200		"	"	110	6.3	23.15	20.45	24.60	16.0	-1.45	22.2	30.3	8.1	Cu	3	66	104.4	138.5	89.8
	1300								24.40								63	97.5	130.1	81.6
	1400		18°49'	110°00'	100	9.0	23.60	20.30	24.80	15.1	-1.20	21.7	30.7	9.0	Cu	5	55	87.9	124.2	75.3
	1500								24.20								43	67.3	103.6	55.4
	1600		19°13'	"	110	8.1	23.00	19.50	24.00	14.9	-1.00	22.5	29.2	6.7	CuSc	7	29	19.2	60.3	13.5
	1700								23.80								15	11.0	48.4	3.2
	1800		19°26'	"	150	6.3	22.45	18.95	23.80	16.0	-1.35	20.2	28.9	8.7	Sc	4	-	0	38.3	-5.5
	1900								23.40								-	0	36.8	-6.8
	2000								23.20								-	0	36.8	-6.7

	2100	208	20°00'	110°00'	120	6.1	21.95	18.90	23.10	17.9	-1.15	19.7	27.7	8.0	Cu	2	-	0	37.3	-6.0
	2200								22.90								-	0	38.0	-5.2
	2300	"	"	"	090	4.8	21.80	18 75	23.05	18.1	-1.25	19.5	27.6	8.1	-	0	-	0	36.2	-7.0
12 Sept	0800	209	21°30'	110°00'	120	7.8	21.20	17.45	22.50	18.6	-1.30	17.4	26.7	9.3	-	0	23	38.5	70.9	24.2
	0900								22.30								36	60.5	91.7	48.9
	1000	"	"	"	130	8.6	21.00	17.55	22.35	19.80	-1.35	17.6	26.5	8.9	Cu	2	48	78.3	109.4	61.6
	1100								22.10								57	39.3	121.5	74.1
	1200	"	"	"	155	7.1	21.20	17.30	22.80	19.0	-1.60	17.1	27.2	10.1	-	0	63	94.2	124.4	77.6
	1300								22.80								61	91.4	124.9	74.7
	1400		21°48'	110°00'	NOT POSSIBLE DUE TO MAN-OEUVRING		21.30	17.45	23.30	18.2	-2.00	17.3	28.0	10.7		0	52	79.7	110.3	62.9
	1500								23.20								41	63.9	96.7	49.5
	1600		22°00'	110°00'	130	3.8	21.10	17.20	23.40	17.0	-2.30	16.9	28.2	11.3	Ac	6	27	44.0	75.7	28.3
	1700								23.10								15	22.7	54.6	7.6
	1800		22°24	110°00'	180	4.0	20.95	16.80	22.90	18.3	-1.95	16.3	27.4	11.1	CuAc	TR	-	0	35.3	-8.2
	1900								22.10								-	0	33.1	-9.7
	2000								22.70								-	0	32.9	-10.2
	2100	210	23°00'	110°00'	160	6.8	20.15	16.50	21.80	20.3	-1.65	16.3	25.6	9.3	Cu	TR	-	0	33.1	-9.6
	2200	"	"	"					21.80								-	0	35.6	-7.1
	2300	"	"	"	170	6.4	20.15	16.10	21.85	19.8	-1.70	15.5	25.7	10.2		0	-	0	34.2	-8.4
13 Sept	0800	211	24°29'	110°00'	155	7.7	19.70	14.75	20.80	21.1	-1.10	13.4	24.1	10.7	CuSc	8	22	17.2	55.3	11.8
	0900								20.80								35	28.1	67.0	20.3
	1000	"	"	"	165	6.4	19.95	16.00	20.95	22.1	-1.00	15.5	24.1	8.6	CuAc RAIN IN VIC	7	46	63.2	96.8	48.0
	1100								20.90								55	53.6	88.8	43.6
	1200	"	"	"	170	8.0	20.20	16.65	21.05	21.3	-0.85	16.5	24.4	7.9	CuNs RAIN PROCEEDING	7	59	75.6	108.2	62.3
	1300								20.90								57	90.7	120.0	73.3
	1400		24°48'	110°00'	170	8.2	20.05	15.80	20.95	20.5	-0.90	15.0	24.3	9.3	CuSc	6	49	46.7	85.9	41.0
	1500								20.80								39	42.6	76.3	31.5
	1600		25°12'	110°00'	170	6.6	19.85	15.40	20.85	20.8	-1.00	14.4	24.1	9.7	Ac	4	27	50.9	85.7	39.4
	1700								20.60								14	5.5	42.0	0.5
	1800		25°36	110°00'	160	7.6	19.35	15.15	20.65	21.5	-1.30	13.3	23.9	10.6	Cu	3	-	0	33.6	-8.3
	1900								20.90								-	0	35.1	-7.0
	2000	212	26°00'	110°00'	160	7.6	19.35	15.10	21.50	22.3	-2.15	14.2	25.1	10.9	Sc	4	-	0	35.8	-6.8
	2100	"							21.60								-	0	36.2	-6.4
	2200	"	"	"	160	7.4	19.25	16.15	21.40	22.8	-2.15	16.2	25.0	8.8	Cu	5	-	0	37.0	-5.5
14 Sept	0800	213	27°30'	110°00'	030	6.8	17.65	13.30	19.95	22.4	-2.30	12.3	22.8	10.6	CuSc	7	22	19.3	57.1	13.5
	0900								20.00								35	24.7	60.9	17.5
	1000	"	"	"	080	6.0	18.25	13.95	20.00	22.4	-1.75	13.0	22.9	9.9	CuSc	4	44	82.5	114.2	67.9
	1100								20.00								52	85.2	116.1	70.1

TABLE 2 (*Continued*)

Date 1962	Time	Stn No.	Lat.S.	Long.E.	Wind Dirn (deg)	Wind Speed (m/s)	Temperature T_a (°C)	Temperature T_w (°C)	Temperature T_s (°C)	p-1000 (mb)	T_a-T_s (°C)	e_a (mb)	e_s (mb)	e_s-e_a (mb)	Cloud Type	Cloud Amount (octas)	Sun's Elevn (deg)	I (mW/cm²)	$R\downarrow$ (mW/cm²)	R_N (mW/cm²)
14 Sept	1200	"	"	"	120	4.7	18.50	14.40	20.35	21.7	-1.85	13.3	23.4	10.1	Cu	1	56	90.7	117.9	71.9
	1300								20.30								54	86.6	116.0	70.0
	1400		27°40'	110°00'					20.20								48	81.8	112.0	66.9
	1500								20.40								38	63.2	92.7	48.2
	1600		28°02'	110°00'	150	3.4	18.10	14.00	20.35	19.9	-2.25	13.2	23.4	10.2	Cu	1	27	41.2	66.7	23.3
	1700								20.30								14	10.3	43.4	12.2
	1800		28°26'	110°00'	150	3.1	18.00	13.65	19.80	20.3	-1.80	12.6	22.6	10.0	Cu	5	-	0	36.1	-5.5
	1900								19.80								-	0	32.4	-9.1
	2000								19.60								-	0	35.9	-5.5
	2100	214	29°00'	110°00'	170	2.4	17.50	12.60	19.60	21.1	-2.10	11.2	22.3	11.1	Cu	3	-	0	36.5	-5.1
	2200								19.80								-	0	32.7	-8.8
	2300	"	"	"	180	1.3	17.40	13.05	19.60	20.5	-2.20	12.1	22.3	10.2	Sc	3	-	0	32.5	-5.1
15 Sept	0800	215	30°30'	110°00'	325	3.5	16.60	13.80	18.00	18.2	-1.40	13.9	20.2	6.3	Ac	2	20	35.7	69.3	24.6
	0900								18.00								32	61.9	96.7	51.7
	1000	"	"	"	300	5.1	17.20	13.70	18.10	17.6	-0.90	13.3	20.3	7.0	Cu (4) Ac 2	6	42	66.0	105.4	60.0
	1100								18.50								50	26.1	63.1	20.7
	1200	"	"	"	245	12.3	14.65	13.15	18.60	16.8	-3.95	14.0	21.0	7.0	NS RAIN AT OBS	8	54	38.5	75.8	32.6
	1300								18.80								52	45.4	79.9	36.5
	1400		30°42'	110°00'	160	7.5	16.20	13.10	18.45	16.6	-2.25	13.0	20.8	7.8	CuSc CbNS	7	46	26.1	62.3	19.9
	1500								18.40								35	67.4	98.6	53.3
	1600		31°12'	110°00'	160	8.3	16.20	12.85	17.60	16.8	-1.40	12.5	19.7	7.2	Cu	3	24	39.9	68.6	24.7
	1700								19.00								12	17.9	45.5	39.8
	1800		31°36'	110°00'	150	9.6	15.95	11.70	18.10	17.6	-2.15	10.8	20.3	9.5	Cu	2	-	0	30.4	-10.0
	1900								18.30								-	0	30.4	-10.1
	2000	216	32°00'	110°00'	180	11.3	15.60	12.00	18.35	19.4	-2.75	11.6	20.6	9.0	Cu	2	-	0	29.8	-10.8
	2100								18.40								-	0	33.6	-7.0
	2200	"	"	"	170	10.0	15.60	12.40	18.40	20.0	-2.80	12.2	20.7	8.5	Cu	3	-	0	34.4	-6.3
16 Sept	0800	217	32°00'	111°52'	210	8.7	15.30	11.70	19.45	22.1	-4.15	11.3	22.1	10.8	Sc	7	12	12.4	49.7	6.5
	0900	"							19.60								23	41.3	70.0	24.8
	1000	"	"	"	195	8.4	15.40	11.55	19.65	23.6	-4.25	11.0	22.4	11.4	Cu	3				
	1200		32°00'	112°04'	170	10.1	15.85	12.50	19.90	23.6	-4.05	12.2	22.8	10.6	CuSc	3				
	1400		32°00'	112°24'	160	11.6	16.00	12.65	19.95	22.0	-3.95	12.3	22.8	10.5	Ac	3	RECORDER OUT OF ACTION			
	1600		32°00'	112°44'	160	11.0	15.40	12.35	17.40	22.3	-2.00	12.3	19.5	7.2	CuSc	3				
	1800		32°00'	113°04'	150	9.3	15.65	12.90	18.20	22.7	-2.55	13.0	20.5	7.5	Sc	8				

Part III

Marine geology and geophysics

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The Gulf of Aden

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The details of topography outlined in a new contour chart of the sea floor are related to the geophysical studies made in the Gulf of Aden during the last decade. These studies include magnetic and gravity field, seismic refraction, heat flow and earthquake epicentre measurements. The Gulf is interpreted as a tensional feature involving the separation of the continental blocks of Arabia and Africa and the formation of new oceanic crust in between. The central rough zone is compared with mid-ocean ridges. The matching of pre-Miocene continental geology on either side is discussed in the light of this theory.

Introduction

During the past five years, a renewed interest in the Indian Ocean has taken many oceanographic research ships and survey ships through the Gulf of Aden. Most of these ships are equipped with deep-sea echosounders and the resulting accumulation of soundings has made it possible to prepare a new contour chart of the bathymetry of the Gulf and its eastern extension into the Arabian Sea.

Several of these ships also made measurements of the total intensity of the Earth's magnetic field, of the gravitational field, of heat flow and of the crustal structure in the Gulf of Aden, using seismic refraction techniques. The geophysical data can be examined together with the structural trends indicated by the bathymetry, to find out the geological history of the Gulf and its relation to current trends of thought on continental fracture and drift.

The account given here is the result of a preliminary examination of the data, many of which are still coming in, and some of which are still being collected. The publication of the bathymetric chart covering the Gulf of Aden will have to await the production of a fair copy, but examples of two parts of the chart are shown.

Topography

The main features of the topography in the Gulf of Aden were outlined by Farquharson (1935), following the John Murray expedition and have been later discussed by Stocks (1941, 1944) and Cloos (1942). These authors recognized the northeast–southwest lineation of ridges and valleys in the centre of the Gulf and the similarities between the coastlines of Arabia and Somaliland. However, the mean spacing between echosounding lines available at this time was about 30 miles and much of the data used was derived from earlier spot soundings obtained by weight and wire.

Today much of the Gulf is covered with echosounding lines separated by less than 10 miles, and the improved quality of the records enables a new assessment of the topography to be made. Samples of the newly contoured chart showing the density of tracks are shown in figures 2 and 3.

A problem arises with the correlation of soundings taken in such a comparatively densely sounded area. The navigational accuracy away from the coast depends on the

quality of the horizon for astronomical observations. During parts of the year dust storms, haze and variable refraction lead to errors in fixes that may be 10 miles or more, and horizontal shear in the surface currents can increase the errors in the interpolated track between fixes. Some sounding lines have had to be moved by up to 15 miles to present a consistent picture of the topography. When the navigational errors are comparable to the sounding line spacing, contouring can produce a spuriously complicated picture, which is not improved by additional data.

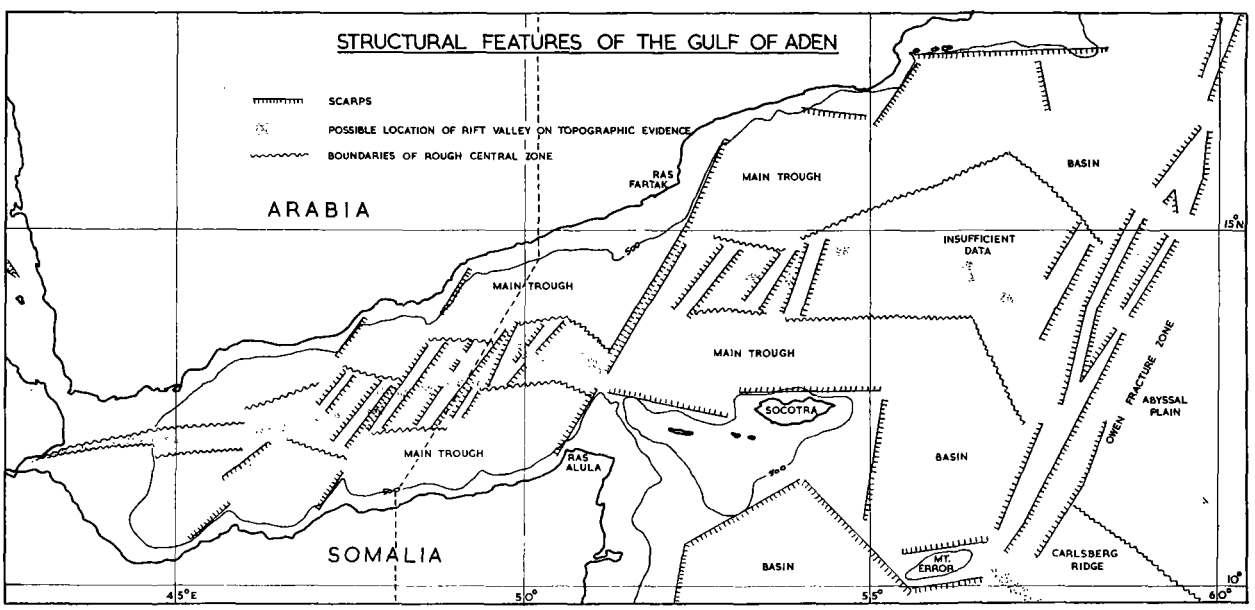

FIGURE 1. Structural features of the Gulf of Aden.
(Dashed line shows position of profile shown in figure 2.)

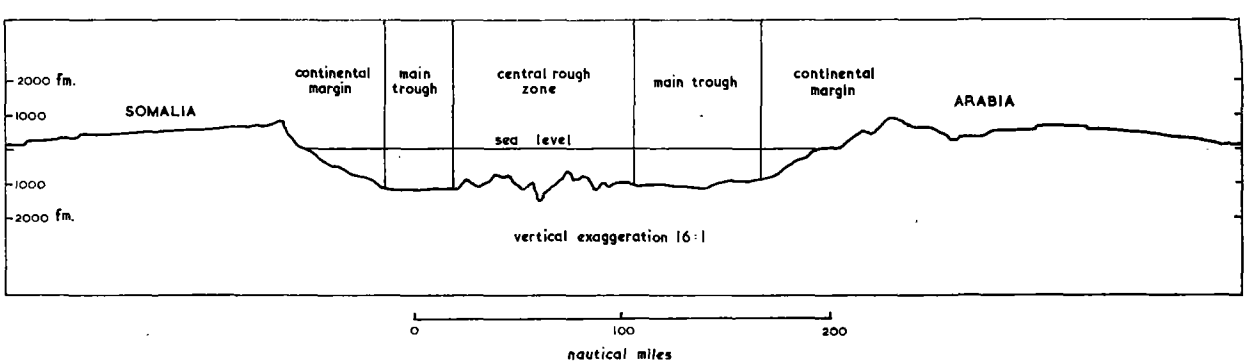

FIGURE 2. Typical topographical profile across the Gulf of Aden.

PHYSIOGRAPHIC ZONES

The main features of the Gulf of Aden deduced from the underwater topography are outlined in figure 1. Three physiographic zones can be recognized; a typical cross-section is shown in figure 2.

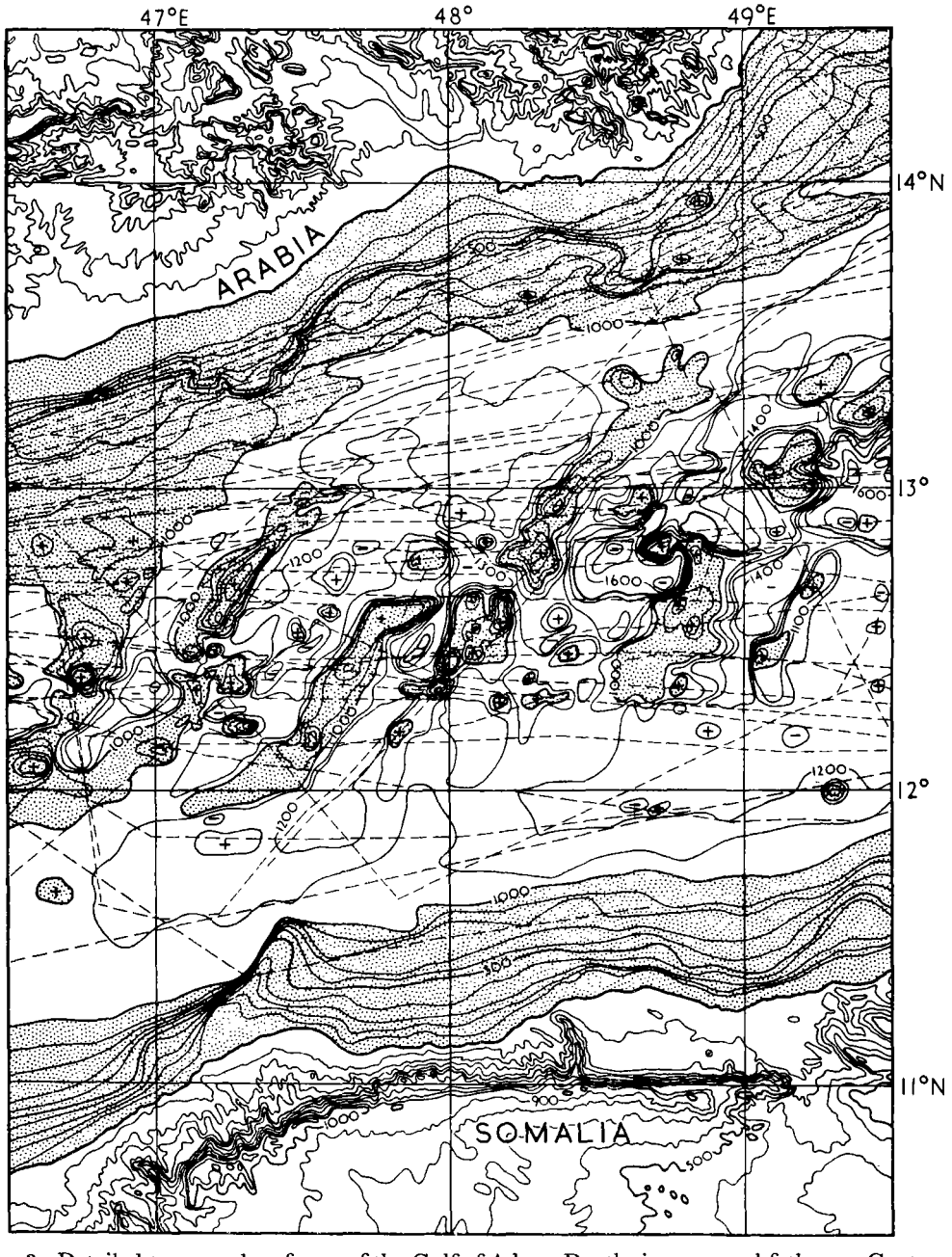

FIGURE 3. Detailed topography of part of the Gulf of Aden. Depths in corrected fathoms. Contour interval on land and sea 100 fm. Stippled area: 0 to 1000 fm. depth. Dashed lines: ship's tracks with sounding data.

Continental margins

The coastlines of Arabia and Somalia consist of a series of capes separated by broad shallow bays. These capes and bays can be correlated across the Gulf and have suggested to many geologists that they once fitted together. However, it is the continental shelf edges which have to be considered in this context.

The continental shelves west of 52° E are narrow and not well delineated by the soundings. The slopes are gentle (1 in 20) and lead smoothly into the sediment-filled basins at the bottom. In many places the slopes are cut with canyons and channels.

However, north and south (respectively) of the capes on the Somalia and Arabian coasts, the continental shelf extends some tens of miles farther out to sea and the slope itself is steepened into a scarp lying along a northeast–southwest axis. On the Somalia coast, the scarps face northwest and on the Arabian coast they face southeast. These linear scarps can be matched in pairs between the north and south coasts of the Gulf and are related to features in the centre of the Gulf.

East of 51° E off the African coast, the continental shelf is well developed and forms the platform out of which rise the islands of Abd Al Kuri, the Brothers and Socotra. The continental slope forming the northern boundary is steep (1 in 5) and has a strike east–west.

Off the Arabian coast between 56 and 58° E, the shelf is well developed, supporting the Kuria Muria Islands, and the south-facing slope is also steep (1 in 2 in places) and strikes east–west. North of the spur of the shelf at 17½° N, 58° E, the continental slope resumes the north-easterly trend that is found off the east coast of Somalia.

The edge of the continental shelf is fairly well defined by the 500 fm. line, except in the western part of the Gulf where the depth of the main trough becomes less than 500 fm. In this region the shelf edge is better located by the 100 fm. line which runs roughly parallel with the coast line.

Main trough

Between the continental slopes on either side, there is the main trough of the Gulf of Aden in the centre of which is a zone of rough topography which forms the third physiographic division. In this paper, the main trough will refer to the fairly flat zone lying between the base of the continental slope and the well-defined edges of the central rough zone.

The depths in the main trough increase steadily from west to east. Between 44 and 46° E, the depth increases from 200 to 1000 fm. Between 46 and 56° E the increase is less rapid from 1000 to 2000 fm. By and large, the line joining equal depths either side of the central rough zone lies parallel to the main northeast–southwest lineations of the Gulf.

The floor of the main trough is sediment covered in most places, gently undulating and cut by occasional channels, but in places there are small abyssal plains.

Between Socotra and the Owen fracture zone, and also south of the spur at 17½° N, 58° E, the main trough widens into flat-bottomed sediment-filled basins bounded to the east by the ridges of the Owen fracture zone. The northerly basin may have connexions with the Arabian abyssal plain through gaps in the ridges.

Central rough zone

Occupying the centre third of the Gulf of Aden is a zone of rough topography whose character changes progressively from west to east, developing from a single valley to a 100-mile wide range of mountains.

In the extreme west, i.e. west of 45° E, the zone is characterized by a single deep valley that runs slightly south of west right into the coast in the Gulf of Tadjura. This valley is in places 500 fm. deeper than the adjacent shelves.

From 45 to 46° E no continuous valley can be seen and the zone is characterized by isolated peaks and ridges.

The greater part of the rough central zone, between 46 and 54° E consists of parallel ridges and valleys trending 030–210°: the distance between crests of ridges is about 30 miles and their relief relative to the valleys is often about 1000 fm. The ridges terminate quite abruptly and the zone is well defined by a line joining these terminations, and enclosing most of the isolated hills.

An important fact regarding the valleys is that they are usually deeper than the adjacent main trough, although there is no barrier preventing them from being filled by sediment from the coast. Indeed one valley (at 13° 15′ N, 49° 00′ E) contains an abyssal plain fed by a canyon from the north. This suggests that the valleys (and hence the ridges) were formed after the greater part of the sediment in the main trough had been laid down.

East of the Alula–Fartak trench (cf. below) the lineation in the central rough zone is still present although less well defined. Between 54 and 57° E, the sounding data is too sparse to establish any lineations. But east of 57° E, the zone runs into the three major ridges forming the central part of the Owen fracture zone (Matthews 1966, this volume, p. 172). The most westerly ridge is terminated within the zone, but the other two form part of a ridge and trough system extending 1500 miles both north and south. The trend of the fracture zone is similar to that of the lineations farther into the Gulf.

The boundaries of the central rough zone indicate that it increases in width from 25 mi. at 44° E to 150 mi. at 57° E. The boundaries also show a series of offsets in a left lateral sense, and these correspond in direction and amplitude to the offsets on the edge of the continental shelves discussed above. Each offset block comprises two ridges and the direction of the offsets is parallel to the ridges.

The most spectacular offset is that at 52° E where the axis of the central rough zone is displaced by 100 mi. The offset is marked by a linear trench 150 mi. long and 10 mi. wide (figure 4). This runs between Ras Alula on the Somalia coast and Ras Fartak on the Arabian coast. It is suggested that the trench be called the Alula–Fartak trench. The maximum recorded depth is 2931 fm. (corrected) and depths greater than 2000 fm. are recorded over 120 mi. of its length. To the west of the trench is a ridge 400 to 500 fm. above the main trough level of 1200 fm. and this extends southward from a bulge in the continental slope. (The bulge is thought to be due to the deltaic accumulation of sediments from the mouth of the Wadi Hadramaut at 51° E, confined to the east by the ridge associated with the Alula–Fartak trench. It is cut with numerous canyons and channels emanating from the mouth of the Wadi.)

The section of the central rough zone between 54 and 57° E resembles in many ways

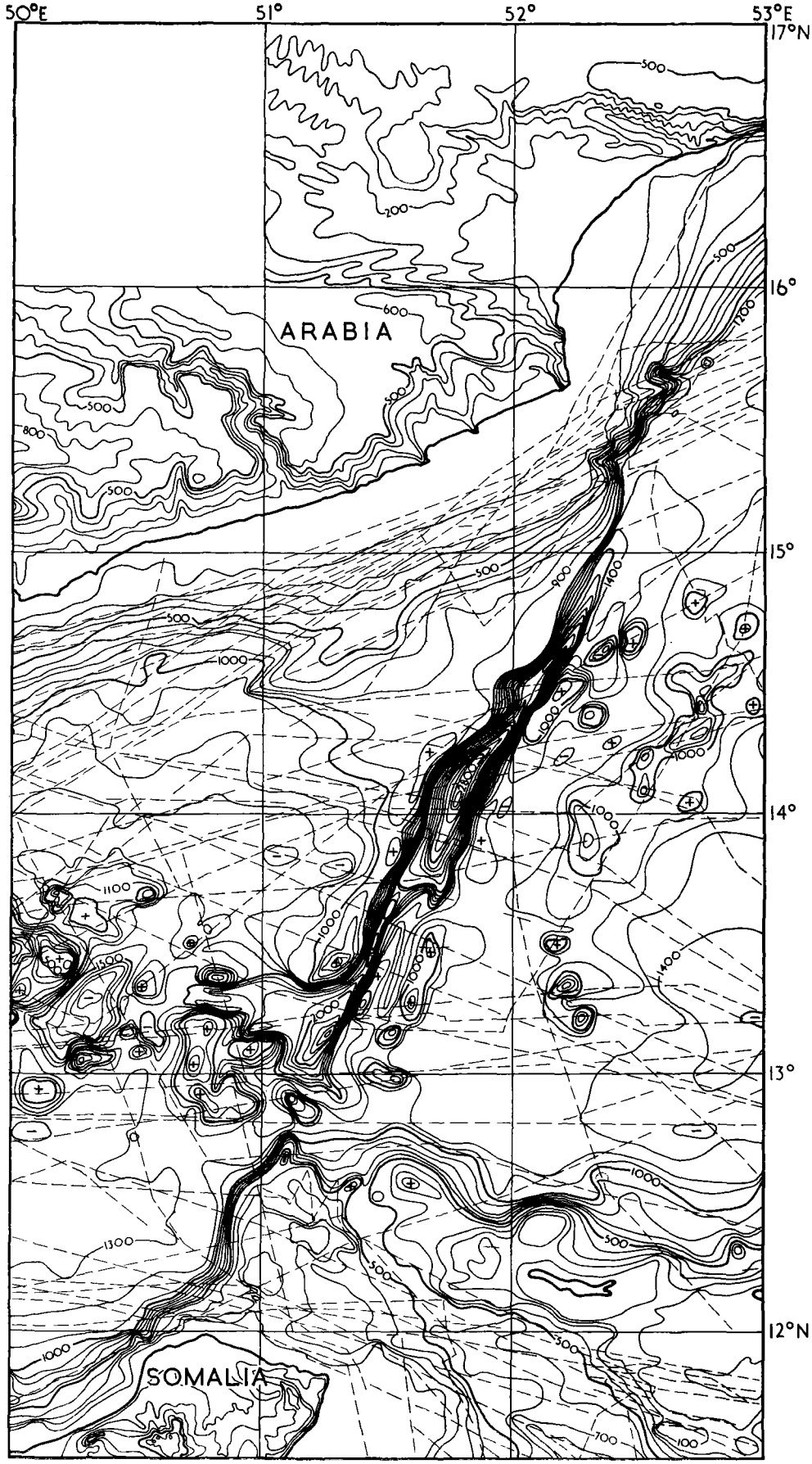

FIGURE 4. Detailed topography of Alula–Fartak trench. Depths in corrected fathoms. Contour interval on land and sea 100 fm.

the northwest end of the Carlsberg Ridge. The scale of the topography, the magnetic anomalies and epicentre belt suggest the Carlsberg Ridge to have been displaced south-westwards by the Owen fracture zone since its formation (Matthews 1963, 1966). It is therefore pertinent to look for a median valley in the central rough zone equivalent to that on the Carlsberg Ridge.

Any section at random across the zone will show one, or perhaps two, deep valleys but, as discussed above, these are alined northeast–southwest not east–west. A median valley is obvious in the extreme west. Between 46 and 55° E, an examination of the topography was made to see if the traces of a median valley could be found superimposed on the linear ridge and valley system. It was found that many ridges were interrupted along their length by a gap, or col, some 500 fm. below the ridge crest (e.g. 12° 40′ N, 48° 15′ E, cf. figure 3). Many of the valleys had an especially deep region (e.g. 12° 50′ N, 48° 35′ E). When connected together such regions show east–west lineations within each offset block and may represent the locus of new fractures (cf. dotted areas in figure 1).

In the eastern region deep soundings have been found on two crossings at 14° 20′ N, 56° 25′ E, but no linear trend has been established.

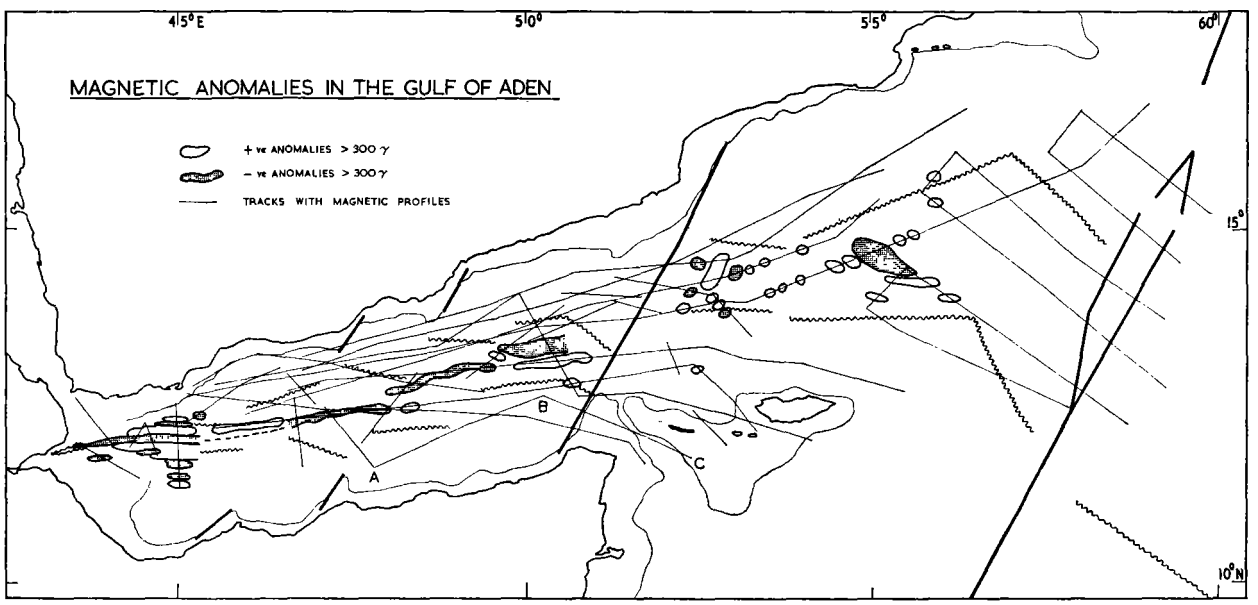

FIGURE 5. Magnetic anomalies.

GEOPHYSICAL DATA

Magnetic field

The position of tracks along which measurements have been made of the total intensity of the earth's magnetic field are shown in figure 5. A regional gradient has been removed from the profiles using a third-order polynomial regional field derived from meaning the data over the northwest Indian Ocean (Admiralty 1963). The resultant anomalies have been plotted and, where the spacing of the data permits, they have been contoured.

The continental shelf, apart from the neighbourhood of Aden where there are extensive volcanics on land, is characterized by a flat magnetic field, anomalies seldom exceeding a few tens γ.

In contrast to this, the anomalies over the main trough are typically $\pm 100\,\gamma$ with wavelengths of the order of 10 mi. These anomalies are reminiscent of those found over the deep ocean basins and are indicative of a rough buried topography of volcanic rocks. A striking example of the contrast with the shelf anomalies is shown on the crossing of the shelf edge 30 mi. north of Ras Alula (figure 6).

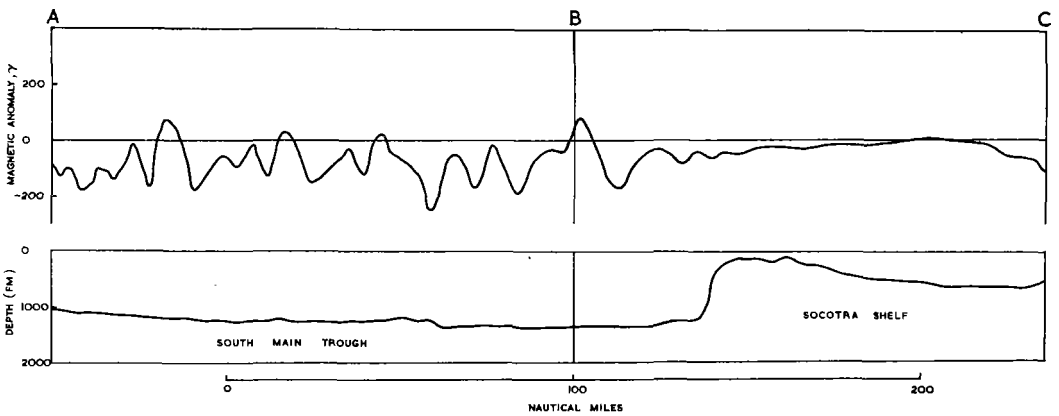

FIGURE 6. Comparison of magnetic anomalies over south main trough and Socotra shelf (position of profile shown in figure 5).

In the central rough zone the magnetic field is extremely disturbed and there are anomalies as high as $\pm 1000\,\gamma$. In figure 5 positive and negative anomalies $> 300\,\gamma$ are shown and it can be seen that these all lie within the central rough zone. (An exception is at the west end of the Gulf where the source of the anomalies is shallow and hence the anomalies are large.) Most crossings in the zone are characterized by a large negative anomaly whose trend can be fairly accurately determined to be east–west.

West of 45° E, the main magnetic anomalies have been interpreted by Girdler & Peter (1960). The large negative anomaly which lies over the rift valley can be accounted for by an intrusive dyke or dyke swarm 4·5 km wide reaching up to the bottom of the valley from about 15 km. The intensity of magnetization is $2{\cdot}5 \times 10^{-3}$ e.m.u./cm^3 and is alined with the present earth's field. Just north of the valley, a positive anomaly is ascribed to a reversely magnetized dyke or dyke swarm 1·2 km wide reaching the surface. The intensity of magnetization is $4{\cdot}0 \times 10^{-3}$ e.m.u./cm^3. The other strips of negative and positive anomalies north and south of the valley may also be attributed to normally and reversely magnetized dykes.

East of 45° E, the east–west lineation of the main negative anomaly can be followed as far as the Alula–Fartak trench, although it is offset with the blocks of the central rough zone. It appears to follow the line suggested by the topography for an incipient median valley. North and south of it there are positive anomalies with similar lineation, although not well defined.

East of the Alula–Fartak trench, the large anomalies are still found although the trends are difficult to establish. At $14\frac{1}{2}°$ N $55\frac{1}{2}°$ E an east–west trend is apparent from the difference of projected wavelength along two courses at right angles. The largest anomaly ($-710\,\gamma$) is found in the centre of the rough zone.

East of 56° E, the magnetic relief dies away rapidly and the Owen fracture zone ridges do not have a clear magnetic signature. However, because of the orientation of tracks, a median magnetic anomaly may exist undetected along the line of earthquake epicentres between 56 and 58° E.

Superimposed on the main median magnetic anomaly are smaller anomalies (of the order of $\pm 100\,\gamma$) that show a certain tendency to be alined with the northeast–southwest ridge and valley structure. These are found throughout the central rough zone and may perhaps be continuous with those found over the smoother main trough. There is, however, no magnetic anomaly associated with the Alula–Fartak trench. Indeed the field over the trench seems abnormally smooth. If the trench is a region of shear in the crust, brecciation, dislocation and low grade metamorphism may reduce the overall magnetic effect of the rocks, as has happened in the Carlsberg ridge (Matthews, Vine & Cann 1965).

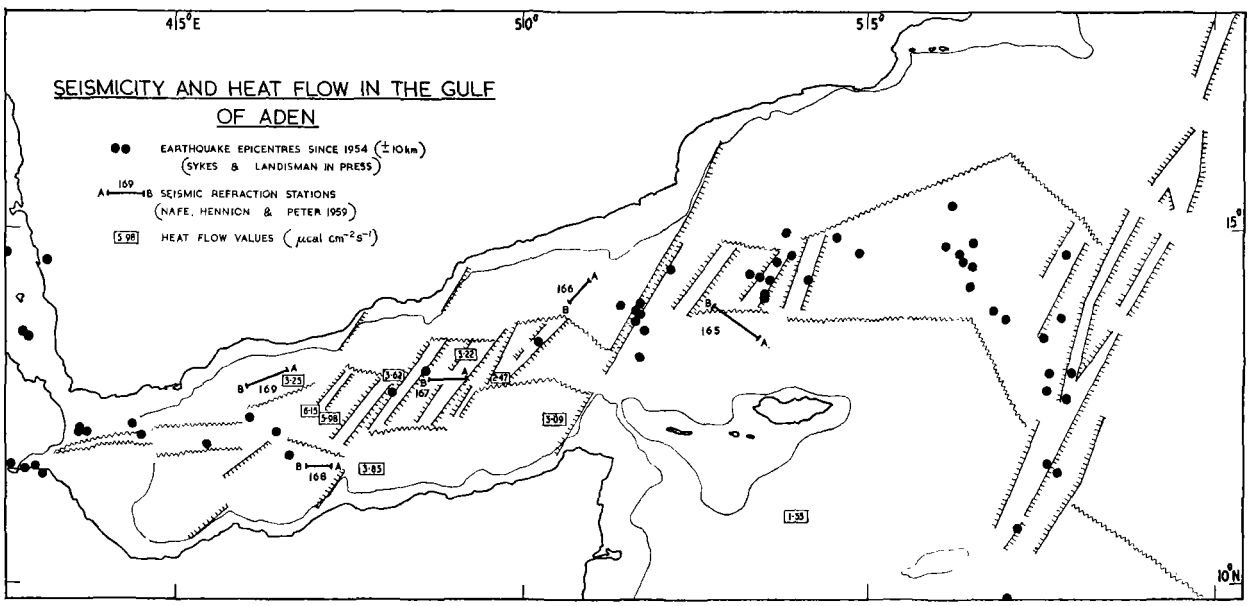

FIGURE 7. Seismicity, seismic refraction stations and heat flow data.

Seismicity and heat flow

A belt of shallow focus earthquakes has long been known to run into the Gulf of Aden. Sykes & Landisman (1964) have relocated epicentres of earthquakes since 1954 to an estimated accuracy of 10 km. These are shown in figure 7, where the size of the dots indicates the accuracy of location. Nearly all epicentres lie within the rough central zone excepting those that are concentrated on the Alula–Fartak trench and on the Owen fracture zone.

Heat-flow measurements made in the Gulf of Aden (figure 5) are all higher than normal ranging from 2·5 to 6·0 μcal cm^{-2} s^{-1} (Herzen 1963; Sclater, p. 271 below). Although the highest values lie within the central zone, the three stations in the main trough also show abnormally high values, suggesting that if the high values are associated with the upward limb of a mantle convection current, then it is wider than the earthquake belt.

Seismic refraction data

In 1958 R.V. *Vema* and R.V. *Atlantis* carried out five seismic refraction stations in the Gulf, two of which lay within the central rough zone and three in the main trough (figure 7). The results were discussed by Nafe, Hennion & Peter (1959), although details of the layering were not published. Table 1 and figure 8 present the data. The structure

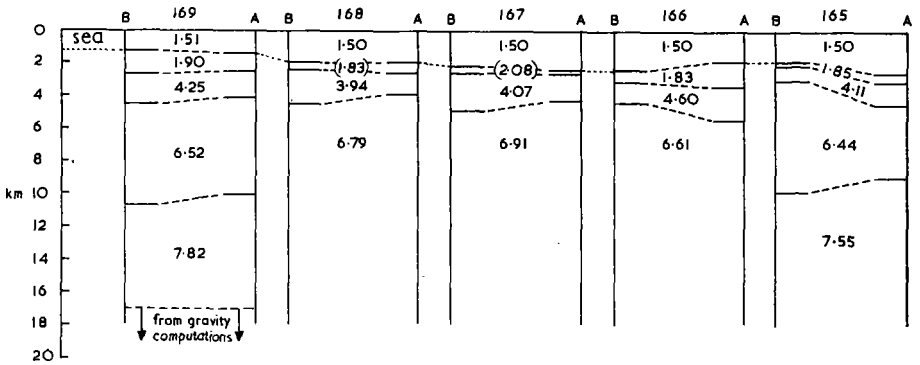

FIGURE 8. Crustal layering obtained by seismic refraction stations of *Vema* and *Atlantis* 1958 (by courtesy of Dr Nafe, Lamont Geological Observatory).

is essentially similar at all five stations although the high velocity (7·7 km/s) layer was observed only at stations 169 and 165. The main crustal layer (6·4 to 6·9 km/s) had a mean thickness of about 6 km, the bottom lying at a depth of 10 km below sea level. This velocity and thickness is comparable to the oceanic crustal layer attributed to basic igneous rocks.

Above these rocks there is a layer with velocities ranging from 3·94 to 4·60 km/s. These fall within the range of velocities for Layer 2 (Raitt 1963), although they are lower than the mean value of 5·07 km/s for all oceans.

The superficial layer of sediments (1·85 km/s) varies in thickness from 1·5 km in the north main trough, to 0·5 km in the south main trough and even less in the central rough zone, as might be expected.

The low value of velocity in the sub-crustal rocks may be due to poor determinations of the velocity. However, if they are typical mantle rocks with appropriate densities, then gravity computations (Nafe *et al.* 1959) suggest a large positive anomaly which is not observed. The transition to mantle rocks could only take place below 17 km below sea level. The 7·7 km/s layer may be similar to the modified mantle rocks found beneath the mid-ocean ridges (Le Pichon *et al.* 1965).

A comparison of crustal structure can be made with that of the Red Sea (Drake & Girdler 1964) where an oceanic section was observed for the central valley, whereas under

the shallower regions of the main trough, velocities of 5·8 km/s were attributed to continental shield rocks. The difference between the crustal structure of the main troughs in the Red Sea and the Gulf of Aden is critical to the interpretation of these features in relation to continental drift movements of Arabia relative to Africa.

TABLE 1. LAYER DETERMINATIONS IN GULF OF ADEN

Vema 14—Atlantis 242 1958 (by courtesy Dr J. E. Nafe, Lamont Geological Observatory).

station no.	station *B*	locations *A*	thickness at *B* (km)	velocity (km/s)	thickness at *A* (km)	comments
165	13° 54′ N, 52° 45′ E	13° 29′ N, 53° 23′ E	1·98	sea 1·50	2·67	high velocity weakly determined
			0·23	1·85	0·55	
			0·85	4·11	1·36	
			6·84	6·44	4·44	
				7·55		
166	13° 58′ N, 50° 36′ E	14° 17′ N, 51° 00′ E	2·48	sea 1·50	2·00	offset assumed 4·6 to 6·6 interface
			0·74	1·83	1·54	
			1·22	4·60	1·95	
				6·61		
167	—	12° 58′ N, 49° 47′ E	2·22	sea 1·50	2·45	( ) assumed velocity and consequent assumed thickness
			(0·40)	(2·08)	(0·28)	
			2·36	4·07	1·64	
				6·91		
168	11° 38′ N, 46° 48′ E	11° 38′ N, 47° 16′ E	1·97	sea 1·50	2·00	( ) assumed velocity and consequent assumed thickness
			(0·44)	(1·83)	(0·61)	
			2·13	3·94	1·53	
				6·79		
169	12° 47′ N, 46° 01′ E	13° 02′ N, 46° 35′ E	1·31	sea 1·51	1·48	high velocity weakly determined
			1·33	1·90	1·12	
			1·85	4·25	1·57	
			6·25	6·52	5·90	
				7·82		

Drake & Girdler allow relative movement of Arabia such that the axial rift represents the amount of new oceanic crust formed and the main trough consists of the down-faulted continental blocks resulting from the collapse of the up-arched Arabian–Nubian shield. Such an interpretation is not possible in the Gulf of Aden where the whole width of the main trough, including the rough central zone, has the characteristic velocities and thicknesses of an oceanic crust, and where the magnetic anomalies indicate extensive emplacement of basic rock. The concentration of earthquake epicentres, high heat flow and the existence of a median valley with associated large magnetic anomalies, in the rough central zone, suggests that this is the presently active region of the creation of new ocean crust whereas the main trough is older and no longer so active.

If this interpretation is accepted, then a reconstruction of the African–Arabian continent must involve the fitting of continental edges along the continental slope, which is fairly represented (except in the extreme west) by the 500 fm. line.

The validity of such a reconstruction rests on the matching of geological features that were formed prior to the relative movement of the continents.

Geological evidence for predrift reconstruction

Simplified geology

A simplified map of the geology of South Arabia and Somalia is shown in figure 9. On the Arabian peninsula the geological features have been taken from Wissman, Rathjens & Kossmat (1942), Beydoun (1960), Geological Map of Africa sheet 3 (U.N.E.S.C.O. 1963)

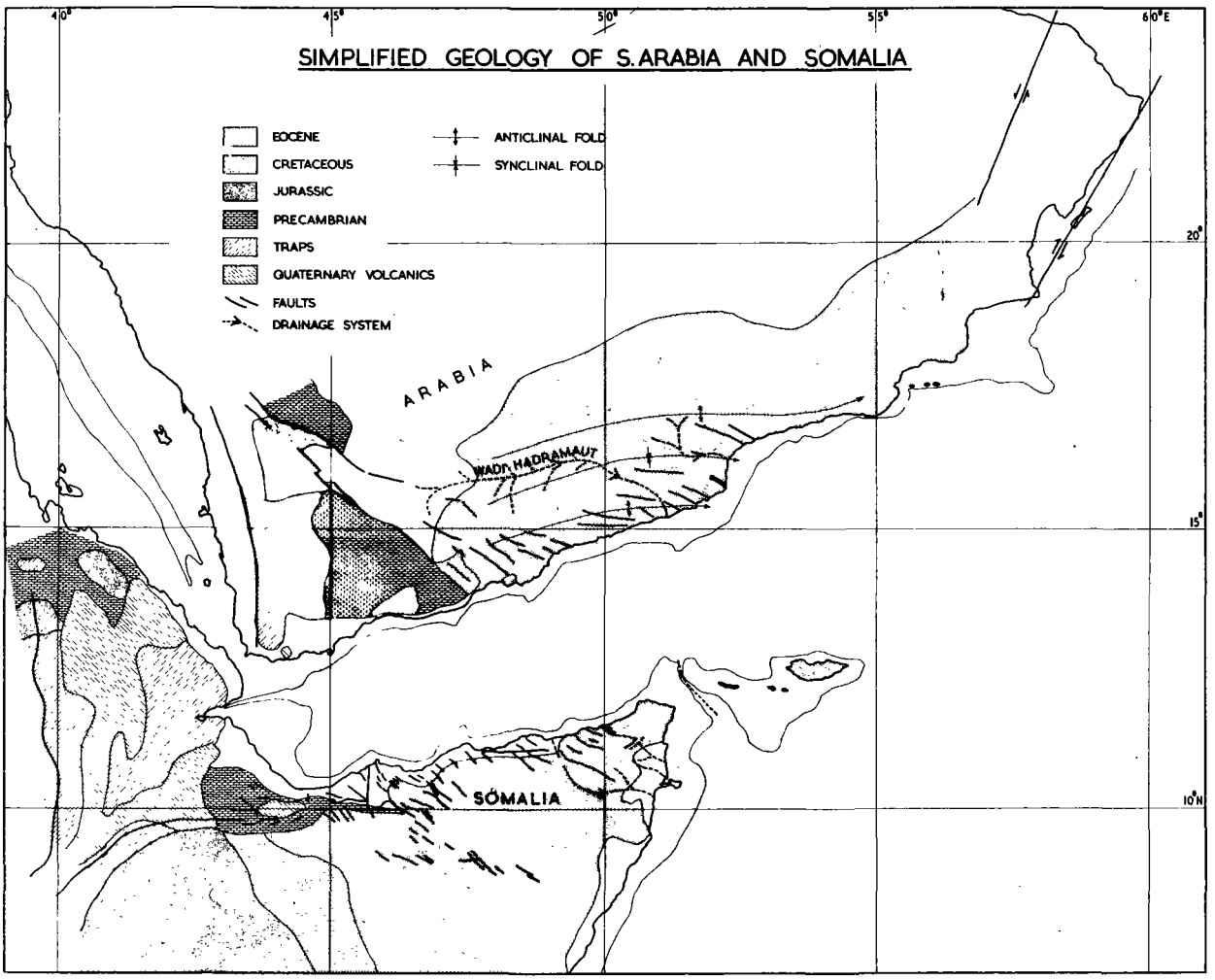

FIGURE 9. Simplified geology of south Arabia and Somalia.

and Geological Map of the Arabian Peninsula (U.S.G.S. and ARAMCO 1963). On the Somali coast data has been drawn from Dainelli (1943), Somaliland Oil Exploration Company (1954) and Geological Map of Africa sheet 6 (U.N.E.S.C.O. 1963).

East of 47° E in Arabia and east of 44° E in Somalia the geology is very similar. Middle to Upper Eocene strata occupy the top of the stratigraphic column underlain by Lower Eocene, Cretaceous and in most places Jurassic beds. These sit unconformably on Precambrian crystalline basement rocks. In Arabia, this sequence is gently folded along an

east–west axis. The North and South Hadramaut arches (along 17 and 15° N) are separated by a synclinal depression which crosses the coast at Qamar Bay (16° 10′ N, 52° 30′ E). 'The south flank of the south arch has collapsed in complex block-faulting in the western part and in more regular E–W and ENE–WSW step faulting to the east, where the blocks are generally tilted southwards' (Beydoun 1960). Beydoun suggests that the Hadramaut arch attained its maximum development in the Upper Eocene after emergence. The folding is truncated obliquely by the coastline between 52 and 55° E.

The Eocene Sea was limited to the west by the uplifted zone now represented by the exposed Precambrian rocks of the Yemen (Wissman *et al.* p. 290, 1942). Along the north-east side of this zone an extensive fault system has been mapped (U.S.G.S. and ARAMCO 1963) running southeast from 17° N, 44° E, to the coast at 14° N, 47½ °E.

In the North Somaliland Plateau the Mesozoic and Lower Tertiary succession is tilted gently upwards to the north but is severely down faulted along an east–west line to produce the Guban Sunklands lying between the coastal mountain range and the coast itself.

Three main trends of faulting have been demonstrated in Somalia (Som. Oil Ex. Co. 1954). 'Red Sea trend' faults are numerous but are concentrated mainly in the region between 45½ and 47½° E where the east–west mountain range is interrupted. A belt of these faults continues southeast across the Nogal region to 8½° N, 48½° E. The Red Sea trend faults are dated by stratigraphic disruptions to be Upper Eocene to Oligocene.

The east–west, or 'Gulf of Aden trend', faults responsible for the north boundary of the main mountain ranges (the Golis Scarp) in Somalia are dated with certainty to have been initiated in early Miocene times (Som. Oil Ex. Co. 1954, p. 35).

The third fault system, with north–south or 'East African trend' is developed only at 45½° E and is thought to be pre-Jurassic, although rejuvenated in the Tertiary.

West of the Eocene plateau in Central Somalia, Cretaceous and Jurassic beds are exposed bounded farther west by the north end of the Rift Valley.

The Precambrian basement is exposed north of the Golis scarp between 43 and 45° E. The northern limit of this exposure is 10° 40′ N. On the Arabian side, Precambrian metamorphics form a large part of the exposed rock between the fault line running northwest–southeast through 15° N, 46° E, and the volcanic rocks of the Yemen.

The greater part of the rocks occupying the Afar triangle, forming the northern part of the African Rift Valley, are Oligocene-Miocene and Quaternary volcanics, although the Danakil mountains at 14° N, 41° E are Jurassic.

Evidence for the start of the tectonic movements that caused the Gulf of Aden come from the dating of the 'Gulf of Aden trend' faults that parallel the Gulf, which have been associated with the uparching and subsequent block faulting of the original graben. These are clearly post-Eocene as Eocene strata are faulted. In Somalia they have been found to be Miocene (Som. Oil Ex. Co. 1954). Girdler (1958) discusses the age of the Red Sea–Rift Valley system and suggests Eocene-Miocene for the main Rift subsidence. Beydoun (1960) recognizes an Oligocene-Miocene marine invasion of the Gulf of Aden trough giving sedimentary sequences which have been subsequently faulted and tilted.

Evidence for pre-drift geological connexions must therefore be sought in pre-Miocene geological features. The evidence can be discussed under three headings: stratigraphic, tectonic and erosional.

Stratigraphic continuity

Figure 10 shows Arabia shifted towards Africa to fit along the 500-fathom contours. This fit was discussed by Wissman *et al.* (1942), but eventually rejected in favour of mainly vertical movements. Such a shift does not overlap exposures of the Precambrian basement but brings them adjacent. The western limit of the Eocene sea is concordant between

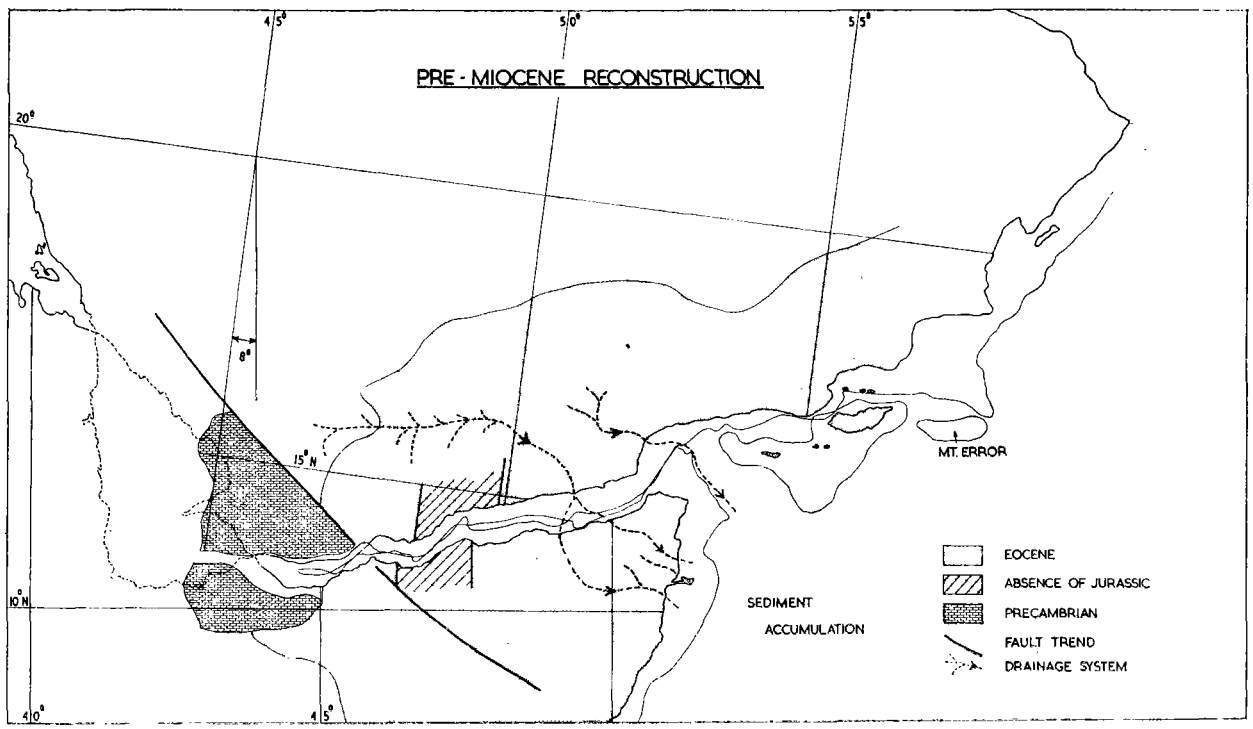

FIGURE 10. Pre-Miocene reconstruction of Gulf of Aden.

Africa and Arabia. The overlap of the Yemen and parts of Ethiopia imply that only parts of these areas can have a continental basement and that the remainder was formed as new crust after drift was initiated. It is suggested that a large part of the Afar triangle represents this new crust, whereas the volcanics of the Yemen were extruded through fractured continental crust which they now cover. The Danakil mountains are interpreted as a continental remnant.

An interesting correlation can be made of the Jurassic strata (figure 11) underlying the Cretaceous and Eocene in Arabia and Somalia. Beydoun (1960) remarks on the block faulting following the Jurassic in Arabia 'resulting in variable elevation and erosion, and in the complete removal of the Jurassic from a broad, elevated feature extending south–north through Mukalla' (p. 144). The axis of this erosion lies along 49½° E. In Somalia a similar uplift and erosion has removed Jurassic strata between 46½ and 47½° E (Som. Oil Ex. Co. 1954) in the Guban. South of the plateau scarp Jurassic rocks are absent between 43 and 47° E. The reconstruction in figure 10 shows how the uplifted and eroded Jurassic beds form a continuous feature across the closed up Gulf.

The reconstruction brings the Socotra shelf with its islands close to the Arabian coast. To fit the steep continental slopes together requires an additional shift of the shelf northeastwards relative to Africa. Socotra then becomes adjacent to the Kuria Muria Islands. A faulted south shore to the latter islands was suggested by Wiseman & Sewell (1937).

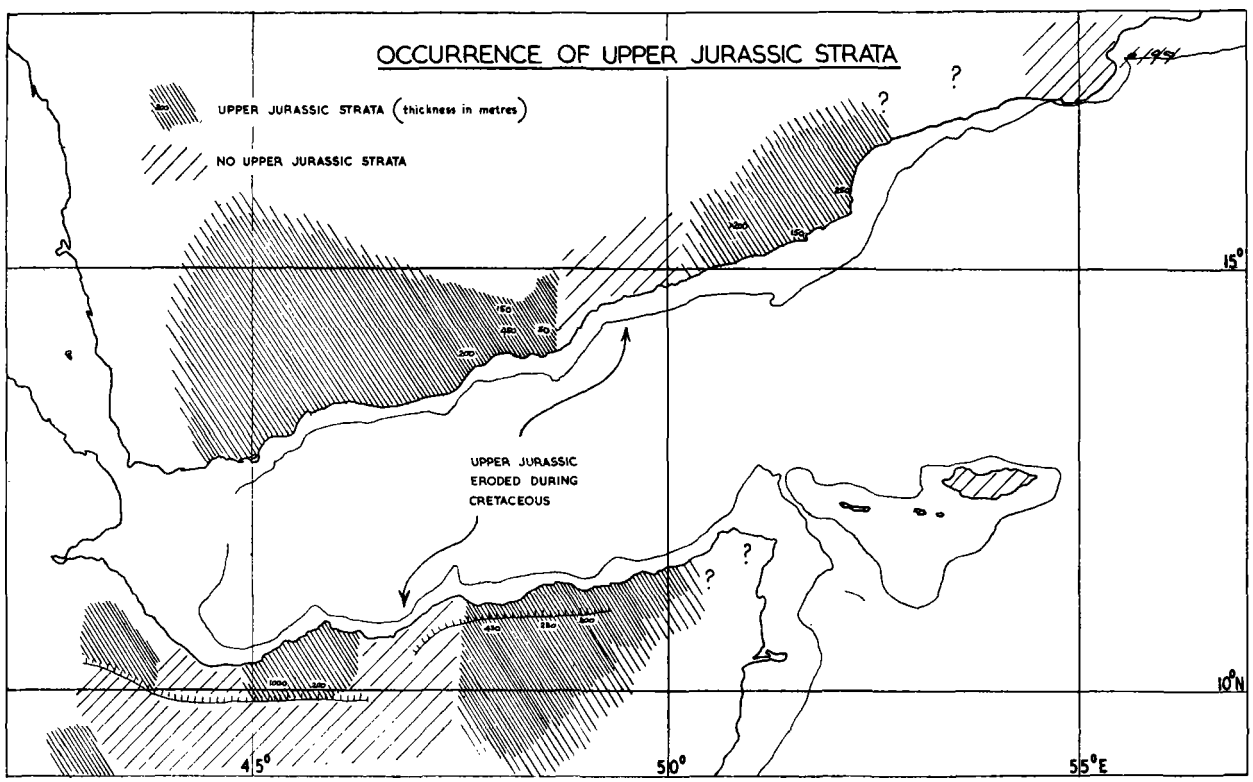

FIGURE 11. Occurrence of Upper Jurassic strata in South Arabia and Somalia.

Reed (1949) describes the islands on the Socotra shelf as fault blocks separated from the mainland in late Tertiary times. Both the Socotran Islands and the Kuria Muria Islands have a stratigraphy similar to that of the adjacent Arabian and Somalia mainland, and are similar to each other. An important aspect of their similarity is the absence of Jurassic rocks. In the case of Socotra, this places limitations on the position along the Arabian coastline where it might have originated.

Mount Error is a flat-topped non-magnetic seamount which is believed to be continental in origin and which now lies in position $10\frac{1}{4}°$ N, 56° E on the extension of the Carlsberg ridge (figure 1). It is discussed elsewhere in relation to the Owen fracture zone (Matthews 1966). Fine grained porcelaneous limestone has been dredged from the top. It is possible that Mount Error was originally part of the continent east of Socotra and fitted against the shelf now in position $17\frac{1}{2}°$ N, 57° E, and that the major tear fault, which displaced the Carlsberg ridge from the mouth of the Gulf of Aden and formed the Owen fracture zone, also moved Mount Error southwards.

Tectonic continuity

The major 'Red Sea trend' fault system in the Yemen and Somalia predates the opening up of the Gulf of Aden. It should therefore be recognizable on both sides. A continuous fault zone running from the Yemen to $8\frac{1}{2}°$ N, $48\frac{1}{2}°$ E can be recognized, although the data is inadequate to be certain about this. On the Arabian coast the faults are east–west at 50° E but turn to WNW–ESE at 52° E where the structures form the high cliffs of Ras Fartak. No detailed information has been found about the possible continuity of these trends across the Horn of Africa. Similarly, the lack of data has not allowed the South Hadramaut arch to be traced across the same region.

The pre-Jurassic north–south fault at $45\frac{1}{2}°$ E on the Somalia coast should be detectable on the Arabian coast at $47\frac{3}{4}°$ E. Although no known fault is mapped there, it coincides with the truncation of the mountains west of the funnel of dune sands extending 30 mi. inland from the coast.

Continuity of erosion features

A major erosional feature such as a river valley formed prior to drift should be able to be traced between the land masses. The Wadi Hadramaut is the dominating erosion feature of the Arabian coast, adjacent to the Gulf. It has been described in detail and its method of formation discussed by Wissman *et al.* (1942). It consists of a narrow and steep-sided canyon some 250 mi. long cut through the almost flat Tertiary and Mesozoic strata of the Hadramaut. Its western end widens into the desert sands of Ramlat as Sab'atayn and to the east it curls south to the Gulf at 51° E. Over half its length it follows more or less along the syncline between the North and South Hadramaut arches but at its eastern end it cuts across the South arch. Since the synclinal folding reached its maximum during the Upper Eocene (Beydoun 1960), the river cutting the canyon must have originated between the emergence of the Middle Eocene strata and the Upper Eocene folding. Wissman describes how the Wadi Hadramaut developed continuously during the recession of the Eocene Sea 'when part of the Yemen was rising up as the lip of an older Red Sea graben but when the Gulf of Aden had not yet made inroads as a graben' (p. 315).

We can therefore look for evidence of the continuity of this feature at about $49\frac{1}{4}°$ E on the Somalia coast. Aerosurvey maps (War Office & Air Ministry 1960) show a large drainage system running south from 10° 50′ N, 49° 15′ E (south of Bender Cassim) and curving towards the east into the Wadi Giahel which reaches the coast at Ras Hafun (10° 30′ N, 51° 00′ E). There is a break in the coastal mountain range near its highest point through which a connexion might be made. An alternative course of the river might have been from Candala (11° 30′ N, 49° 50′ E), eastwards to 50° 20′ E and thence to the coast near 11° N, 51° E along Wadi Giael (not to be confused with Wadi Giahel). The north coast sections of possible old river courses will, of course, have been subsequently reversed and possibly obscured by the faults of the Gulf of Aden formation.

A second drainage system of S. Arabia, Wadi al Jiz, runs into Al Qamar Bay at $16\frac{1}{4}°$ N, $52\frac{1}{4}°$ E. Before the drift, this would have crossed the shelf between Socotra and the Horn of Africa and may be related to the 500 fm. deep channel now found separating the two.

The contours of the North Somali Basin suggest that a large part of the sediment filling it has come from the north. Seismic reflexion profiling has indicated large thicknesses of

sediment; with the present topography of the Gulf of Aden it is difficult to see where such large quantities of sediment have originated, since the Socotran shelf and the Horn of Africa do not seem adequate. Sediment from farther north would be trapped by the Gulf of Aden.

However, in the suggested reconstruction, Wadi Hadramaut and Wadi al Jiz could have carried sediment from a large part of South Arabia and deposited it in the north Somali basin. If this is so, then Tertiary sediments in the basin ought to be quite near to the surface.

Development of the Gulf of Aden

If the reconstruction described above is a true one for pre-Tertiary times, then it should be possible to outline the stage by stage development of the Gulf of Aden on the basis of current ideas about continental margins, continental drift and mid-ocean ridges. The following account is highly speculative and only the initial stages have been geologically dated.

As the Eocene sea receded eastwards and the sediments emerged, synclinal folding started in the Hadramaut reaching its maximum during the Upper Eocene (Beydoun 1960). The uplift of the northern edge of the Somali Plateau was possibly part of this same folding, the whole system being part of the uplifted arch or dome which characterizes the junction between the African Rift Valley, the Red Sea and the Gulf of Aden (Cloos 1942). The Red Sea trend fault system in Somalia developed during this period. The uplift may be associated with the rising limb of mantle convection.

Associated with the arching, either simultaneously as in the case of the African Rift valley, or later (Miocene in Somalia), block faulting took place along the axis of the embryo Gulf, giving rise to the Gulf of Aden fault scarps of Somalia, and the east–west faults of Southern Arabia (figure 12). The graben so formed would then collect sediments from the mountains either side: the river systems would be truncated and trapped, and possibly flow eastwards along the graben towards the sea. This graben is now found as the coastal plains and continental shelves.

At the western end of the Gulf at the junction with the Red Sea, the faulting might have resulted in the extensive lava flows that now cover much of the Yemen and Ethiopia.

The sub-crustal movements also produced forces that both carried the Arabian block north-northeast and rotated it anticlockwise. The down-faulted block yielded along two sets of fracture lines, one set being east–west parallel to the faults on land, the other being northeast–southwest parallel to the continental margin. The line of parting between the two continental blocks ran along both sets of these fractures in an echelon pattern passing between Socotra and the Kuria Muria Islands.

The first phase of the drift of Arabia relative to Africa opened up the main trough of the Gulf of Aden, the movement being shown in figure 13. New crustal material was formed in the Gulf by stretching, fracturing and thinning of the continental crust and by massive intrusion of basaltic dykes, giving it the magnetic properties and structure discussed above. The Aden volcanic rocks may belong to this development. In the Afar triangle, continental fragments remained, surrounded by basaltic material. The movement of the Socotra shelf towards Africa may have taken place at this time.

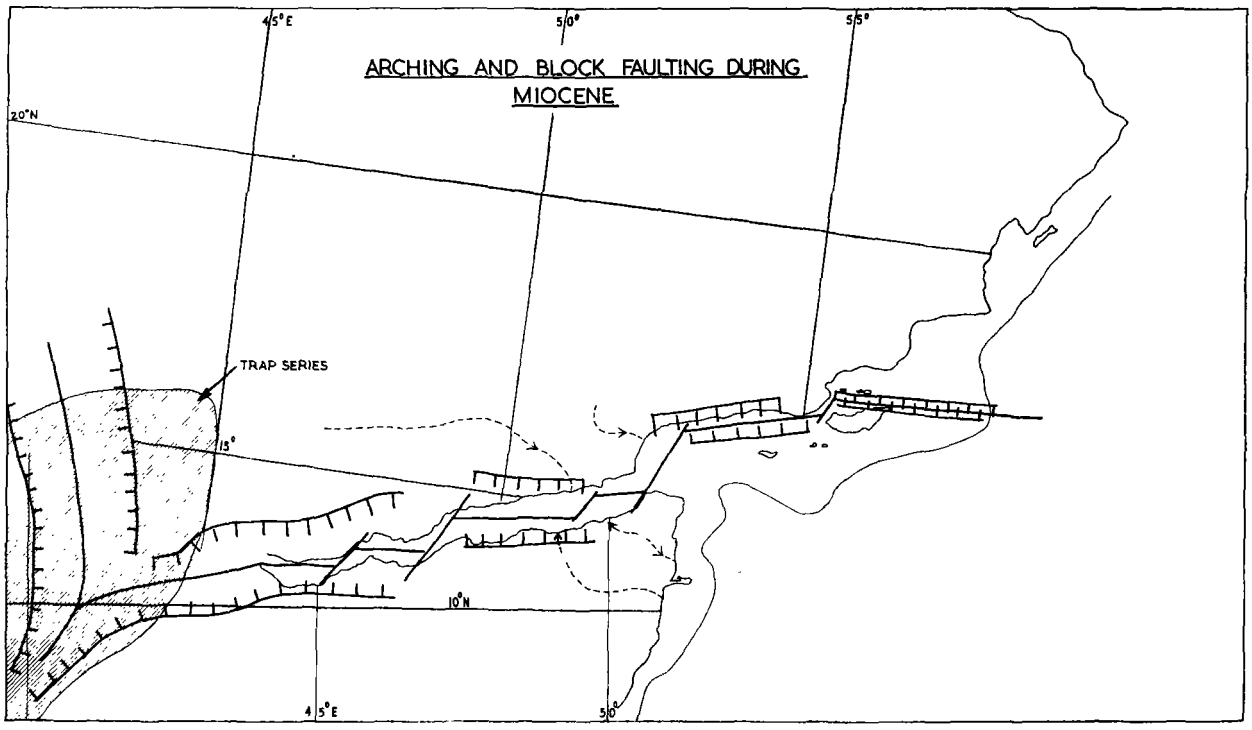

FIGURE 12. Arching and block faulting during Miocene.

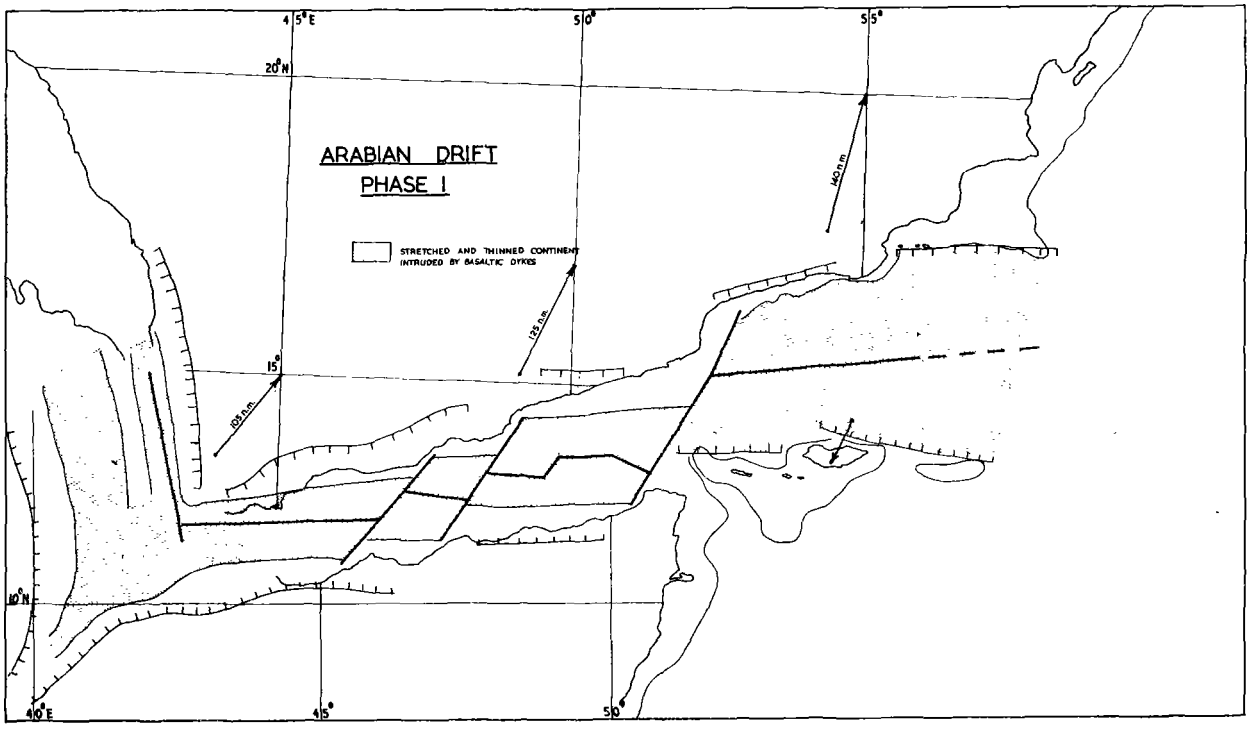

FIGURE 13. Arabian drift, phase 1.

After this first phase, there may have been a period of reduced movement during which the main trough accumulated the 0·5 to 1·5 km of sediment indicated by the seismic refraction data. This would obscure the rugged relief that one would expect from the formation of the new crust. It is unlikely that the sediment was deposited during the second active phase of drift since there are valleys in the central rough zone which have not been filled.

The second phase of the Arabian drift is shown in figure 14. A new line of parting follows the same two sets of preferred fracture lines running along the centre of the now

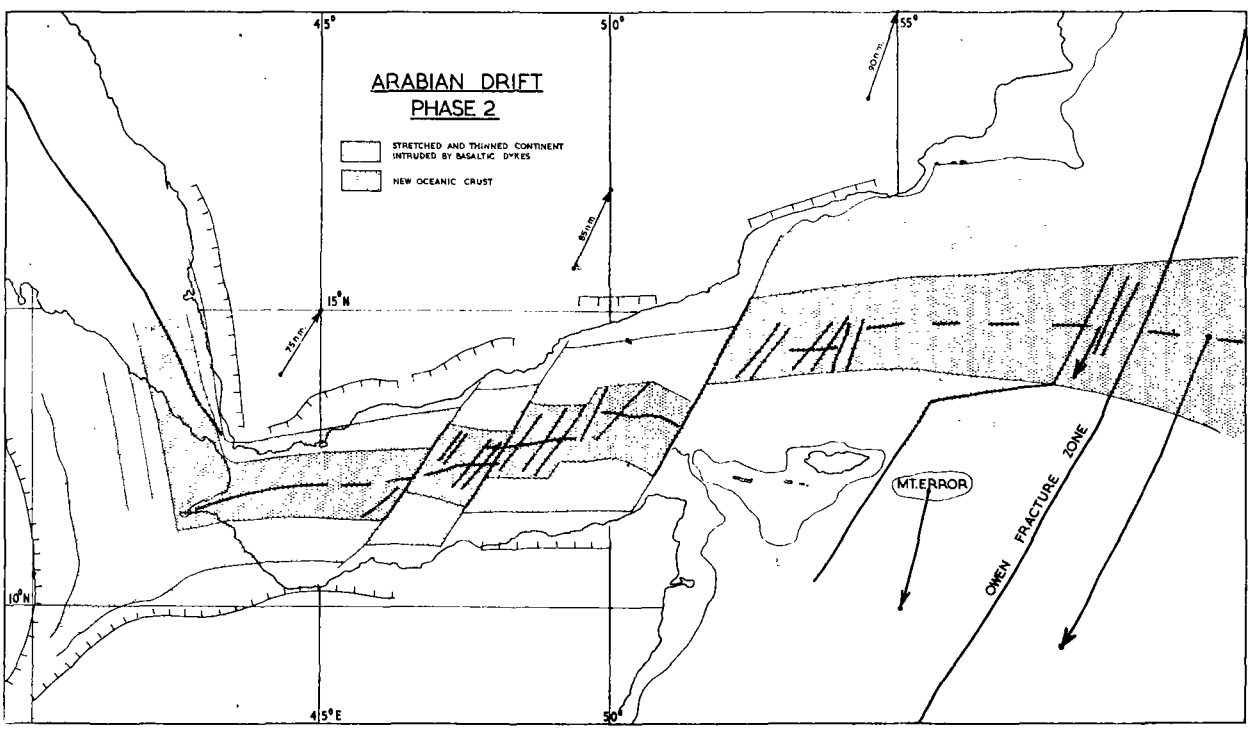

FIGURE 14. Arabian drift, phase 2.

inactive main trough. The movement is in the same direction as before and accompanied by rotation. The resulting new crustal material, perhaps consisting now of basic rocks alone without continental fragments, forms the central rough zone of the Gulf. The northeast–southwest linear features in the zone may be volcanic fissures along lines dictated by the fracture pattern combined with horst and graben structures. This zone extending out into the Arabian Sea develops into the Carlsberg ridge.

The offsets of the blocks forming the central rough zone therefore represent the boundaries of the new crust resulting from the original stepped fracture line, in just the same way as the edges of the continental shelves are offset. The northeast–southwest lines joining these offsets, the biggest being the Alula–Fartak trench, are therefore not tear faults in the usual sense of the word since the surface area on either side is not conserved, although along parts of the line shearing has taken place. This accounts for the fact that no trace of these major lineations can be found on the adjacent continental blocks.

In the final phase, massive crustal movement has displaced the Arabian Sea end of the Carlsberg Ridge south-westwards resulting in the Owen fracture zone (Matthews 1963, 1966) and in the displacement of Mount Error.

Recent activity, indicated by high heat flow and earthquakes, is responsible for the formation of yet another fracture line running down the centre of the rough zone giving rise to the well developed Tadjura rift valley and the embryo median valley farther east. The central rift valley of the southern end of the Red Sea may also belong to this era.

Discussion

The formation of the Gulf of Aden by continental drift of Arabia away from Africa has been long postulated by Wegener (1929) and others in the general break up of Gondwanaland. Wiseman & Sewell (1937) associated the Carlsberg Ridge with the rift structures of Africa and the Red Sea. However, in the extensive German studies of the area, Wissman *et al.* (1942) and more strongly Cloos (1942) consider the drift theory and reject it in favour of a continental horst and graben development arising from extension in a NNW–SSE direction and compression in a NNE–SSW direction. 'The breaking-up of the floor of the Gulf is partly due, then, to the arched extension of the Nubian–Arabian Shield. The general pattern was dictated by the environment of the graben emerging from great depths, but the particular directions of fractures were a consequence of older environmental factors and more recent forces acting in the upper crust at this time' (p. 361). His objections to drift lay in the proximity of Arabia and Africa at the south end of the Red Sea and the continental character of the Danakil Alps. These objections are discussed above. The available geophysical data on the Gulf oppose the view of a continental crust.

The recent swing of opinion in favour of continental drift has revived interest in the relationship of Arabia to Africa. Swartz & Arden (1960) discuss the geological history of the Red Sea in terms of the continental geology of Arabia and Africa and favour a theory in which the Red Sea has been formed by the separation of the two crustal blocks starting in the Lower Eocene at the northern end and continuing through the Middle Eocene and Oligocene. In the Lower Miocene they suggest the breaking away of the Horn of Africa and the formation of the Gulf of Aden. Their reconstruction of the Arabian–African continental block requires the fitting together of the shelves of the two continents and the overlapping of the Yemen on Ethiopia. However, Drake & Girdler (1964) and Girdler (1964) consider geophysical data (seismic, magnetic and gravity) from the Red Sea and conclude that only the 60 km wide central rift valley is new oceanic crust and that the main trough is a down-faulted continental block. This cannot be easily reconciled with the development of the Gulf of Aden outlined above. The key to the problem lies in more detailed information about the crustal structure in the Afar triangle. Drake & Girdler present evidence, from the distribution of magnetic anomalies and of topographic features in the Red Sea and the Gulf of Aden, for the rotation of Arabia relative to Africa of 6 to 9° anticlockwise. Palaeomagnetic data from Aden volcanics (Irving & Tarling 1961) support this view. This is consistent with the rotation required for the theory presented above (8°). However, the two theories differ in the distance of movement of Arabia, i.e. in the choice of a fulcrum about which rotation has taken place. In such discussions,

it is assumed that the continental blocks have moved bodily without change of shape, whereas such distortions are probable in the light of work on continental tectonics.

In east Arabia, the mountain ranges of the Oman have been folded and overthrust during the Miocene-Pliocene (Morton 1959). In the Zagros mountains of Iran, the geological picture is one of thrust from the southwest. These compression features bordering the Persian Gulf are consistent with a northeast movement of Arabia during the late Tertiary.

If it is assumed that the Arabian drift occurred at a uniform rate since the early Miocene, say 20 My ago, and that the mean displacement of the Hadramaut relative to Africa is 210 n.mi. (400 km), then the drift is 2 cm/y. However, if the movement was spasmodic, as has been suggested, higher drift speeds may have occurred for shorter periods.

The ideas outlined in this paper are based on the published data of the land geological history and on the recent geophysical work at sea, much of which has arisen from the International Indian Ocean Expedition. However, a great deal more detailed information on the land geology, in particular the deeper structure revealed by geophysical techniques, lies in the hands of the oil exploration companies. Data from the International Indian Ocean Expedition is still being collected and many critical regions might be examined in the light of the above ideas. Very little is known of the actual rocks of the central rough zone of the Gulf of Aden or of the Owen fracture zone and it is hoped that this paper will stimulate a greater collection of data.

Thanks are due to those laboratories which have allowed me to incorporate unpublished data in this paper. Much of the magnetic data has been obtained and assembled by the Department of Geodesy and Geophysics, Cambridge, from cruises of H.M.S. *Owen*, H.M.S. *Dalrymple* and R.R.S. *Discovery*. This department has also supplied new heat-flow data in the Gulf. Topography and magnetic data have been supplied by Imperial College, London, from H.M.S. *Dalrymple*, by Lamont Geological Observatory, New York, from R.V. *Vema* and Woods Hole Oceanographic Institution, Massachusetts, from R.V. *Chain*. Lamont have kindly supplied further details of seismic refraction stations. Soundings from many other ships have been made available on the collected sounding sheets of the Hydrographer of the Navy, Great Britain.

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THE GULF OF ADEN, IN RELATION TO THE RED SEA AND THE AFAR DEPRESSION OF ETHIOPIA

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Abstract

The mid-ocean ridge system has been suggested as the locus of the generation of new oceanic crust, resulting from the separation of continental blocks. In the NW Indian Ocean, the Carlsberg Ridge meets the Afro-Arabian continental mass at the Gulf of Aden, thereby linking it with the African Rift valley system and the Red Sea.

Some authors have explained the Gulf of Aden as a graben formed by vertical movement only, whereas others have been impressed by the congruity of the coastlines and have suggested predominantly horizontal drift movement of the continental blocks. Recent geophysical evidence in the Gulf of Aden has shown that the crustal structure is more similar to an oceanic than a continental crust, thereby supporting the idea of an origin by continental separation. The evidence may be summarized as follows:

(a) The topography shows a central rough zone running the whole length of the Gulf of Aden, which is associated with an earthquake epicentre belt, high linear magnetic anomalies, and high heat flow. This is a logical continuation of the Carlsberg Ridge.

(b) The crustal structure, determined by seismic refraction stations combined with gravity profiles, is oceanic, except that beneath layer 3, the mantle velocity is low and is associated with low density. The base of this low density layer is 40 km., comparable to that found beneath the mid-Atlantic Ridge.

(c) NE-SW transform faults can be followed across the Gulf and indent the edge of the continental shelf. A good fit is obtained by matching shelf edges at the 500 fm. line, and predrift (i.e. pre Miocene) geological features are continuous across the reassembly.

The suggested reassembly involves superposition of the Yemen on a large part of the Afar depression of Ethiopia in the pre-Miocene, and a large closure of the southern Red Sea. It is suggested that a large part of the Afar depression might be new basaltic crust resulting from the continental split, and that the Danakil Alps are a fragment left between the two separating continents. The reassembly can be tested by palaeomagnetic measurements.

INTRODUCTION

The mid-ocean ridge system is thought by many to be the surface expression of upper mantle movements and, possibly, the locus of generation of new suboceanic crustal material. Where a limb of this system approaches a continental margin, it is important to know the effect it may have on a continental block. The Gulf of Aden, the Red Sea and the Rift valleys of Africa are clearly connected in some way with the Carlsberg Ridge in the NW Indian Ocean (Fig. 1). Matthews (1965) has shown that the Carlsberg Ridge is a typical mid-ocean ridge and that its axis is displaced southeast of Socotra by the Owen fracture zone. A continuation of the ridge further north into the Gulf of Aden has been established on the basis of topography, the earthquake epicentre belt, and magnetic anomalies. Through the Gulf of Aden, therefore, the connection is established with the Red Sea and the African Rift valley system.

However, although the Red Sea, the Gulf of Aden and the African Rift valleys may have been produced by a common subcrustal mechanism, their physical characteristics differ considerably. The Red Sea is flanked on land by high cliffs, now erosional but probably originally fault controlled. The underwater shape of its south end consists of a central axial trough, some 2,000 m deep and 50 km wide, bordered for 150 km on either side by water that commonly is less than 100 m deep. The shallow shelves are dotted with coral reefs and islands, the biggest of which are Dahlak Islands on the west side and Farisan Islands on the east side of the axial trough. Further north the shelves are narrower and are separated from the axial trough by water of intermediate depth.

By contrast, the Gulf of Aden is very much deeper, except at its extreme western end. Recent data obtained during the International Indian Ocean Expedition have enabled the main physiographic features of the Gulf to be outlined and its crustal structure to be determined (Laughton, 1966). Figure 2 shows how the Gulf can be divided, on topographic data, into: (a) continental shelves and slopes; (b) a main trough and basins whose depth increases from about 2,000 m at 46°E to 4,000 m at 56°E; and (c) a central rough zone of echelon ridges and valleys with a relative relief of 2,000 m. At the western end of the Gulf, this zone merges into an E-W trough running into the Gulf of Tadjura in a region where there is little contrast between the continental shelves and the main trough. The central zone shows a series of offsets, the largest of which is between Ras Alula and Ras Fartak at 52°E. These offsets are reflected on the continental margins by offsets of the continental shelf edges. They are examples of "transform faults" recently described by Wilson (1965).

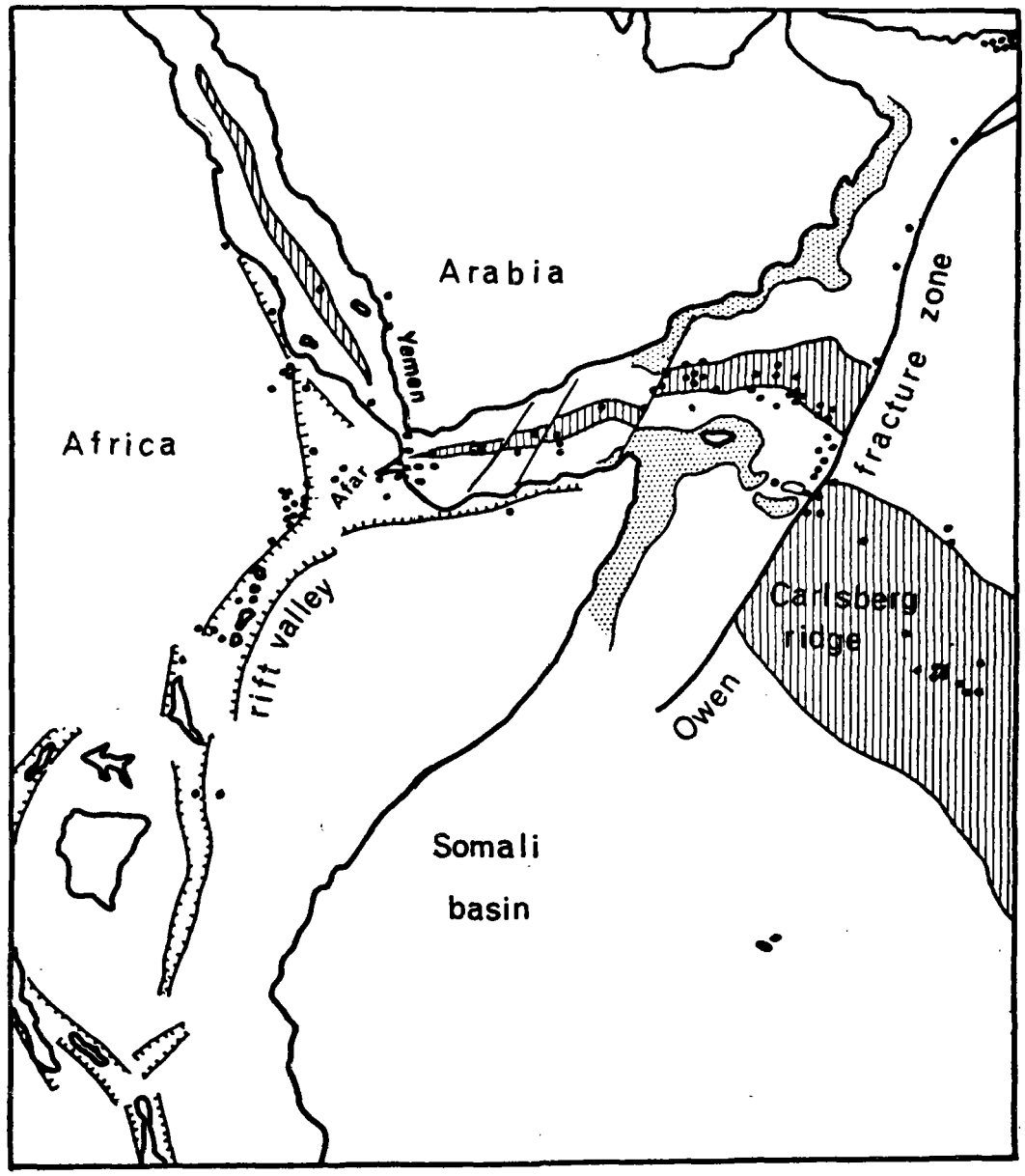

Figure 1. Physiographic sketch map showing relation between the Carlsberg Ridge, the Owen fracture zone and the Gulf of Aden. Dots show shallow earthquake epicentres: shading shows magnetic seamounts of the Carlsberg Ridge, the central rough zone of the Gulf of Aden, and the axial trough of the Red Sea: stippling shows non-magnetic seamounts and continental margin near Socotra.

THE GULF OF ADEN

The geophysical data obtained in the Gulf of Aden suggest that the structure is more similar to an oceanic crust than to a continental crust. These data are described in detail in Laughton (1966) and will only be summarized here.

The central rough zone is in many ways similar to a mid-ocean ridge. Sykes and Landisman (1964) have redetermined the position of recent earthquake epicentres with an accuracy of 10 km; the epicentres all lie within the central rough zone and are particularly concentrated along the Alula-Fartak trench, and along the Tadjura trough. High values of heat flow have been measured right across the Gulf with peak values of 6 microcal/sq cm/sec in the centre (Herzen, 1963; Sclater, 1966). The axis of the central rough zone is marked by relatively large magnetic anomalies (>300 γ) showing an E-W lineation; those at the western end have been described by Girdler and Peter (1960).

All the above types of features are associated with the mid-ocean ridge system. The chief differences lie in the echelon lineation of the ridges in the Gulf, which contrast with the parallel lineations of the Carlsberg ridge; and in the absence of a clear median valley in the Gulf, except at its western end. Transform faults are apparently common in the mid-ocean ridge systems (Wilson, 1965).

In the main troughs on either side of the central zone, there are magnetic anomalies of $\pm$ 100 γ whose trends have not been established. However, they are conspicuously absent on the Socotra shelf, suggesting a difference in basement rock type.

Seismic refraction data have been obtained by Nafe, Hennion and Peter (1959) at five stations distributed along the Gulf in both the main trough and the central rough zone. Two of these stations reached a high velocity layer, and all of them showed a similar structure above it (Fig. 3). Beneath a variable thickness of sediments, there is a layer with velocity 3.9-4.6 km/sec beneath which is a basement showing 6.4-6.9 km/sec. At two stations, the base of the lower layer velocity was determined at about 10 km below sea level, and a high velocity layer of 7.5-7.8 km/sec was found. Nowhere was a granitic-type velocity of 5.6 km/sec found.

The above section is similar to that found under ocean basins but differs in the following respects: (a) the water depth is typically 2 km, not 5 km; and (b) the sub-basement velocity is lower than the usual 8.1 km/sec of the upper mantle.

Continuous gravity profiles through the Gulf of Aden and across the Socotra continental shelf and into the Somali basin have been combined

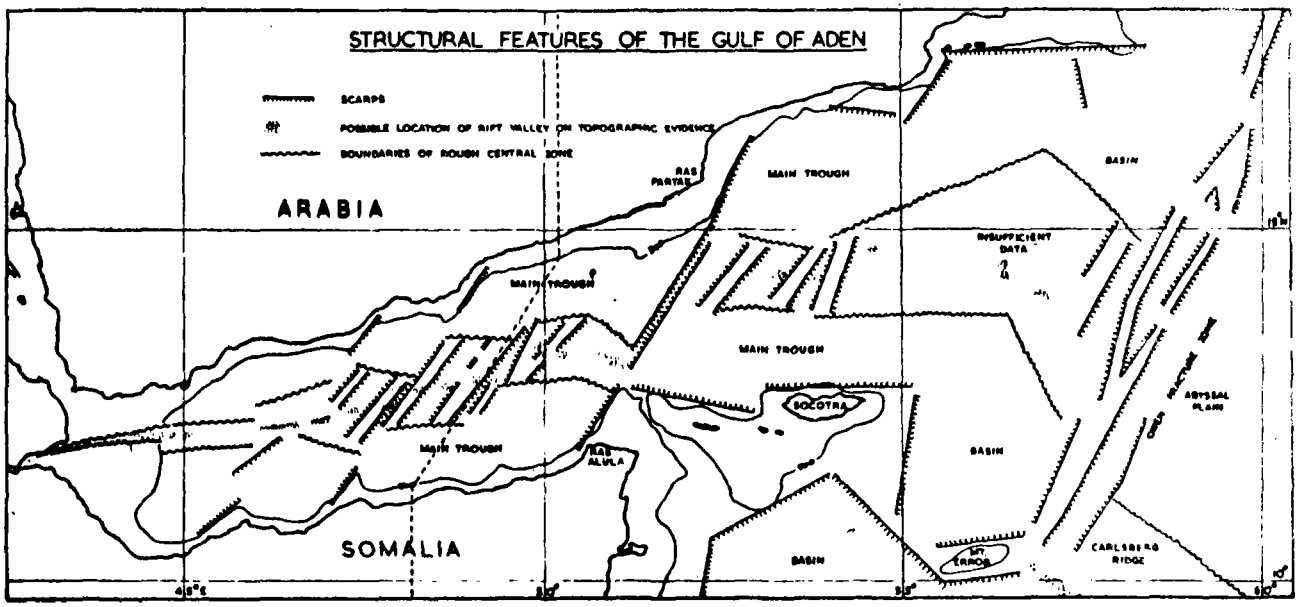

Figure 2. Structural features of the Gulf of Aden (from Laughton 1966).

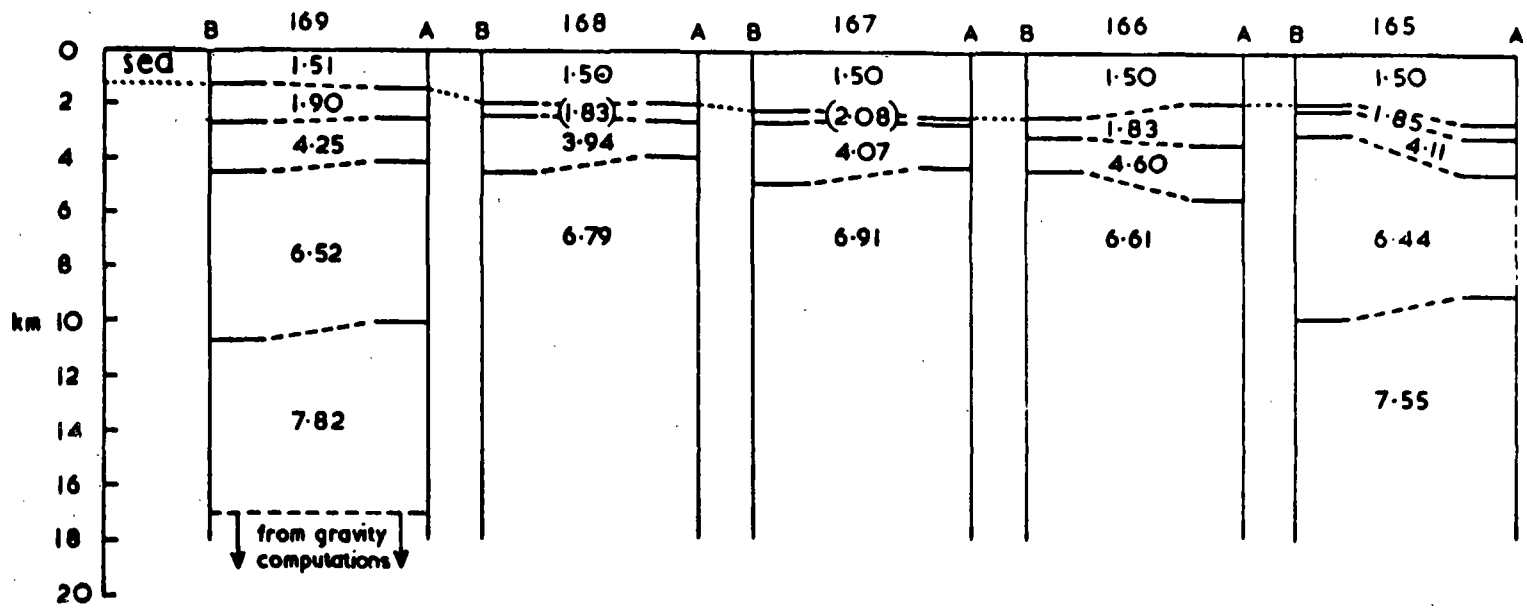

Figure 3. Crustal layering in the Gulf of Aden obtained by seismic refraction stations of VEMA and ATLANTIS 1958 (by courtesy of Dr. Nafe, Lamont Geological Observatory).

with the seismic data to provide additional structural information. Assuming a standard continental section (Worzel and Shurbet, 1955) for the Socotra continental shelf, which is consistent with a typical oceanic section for the N. Somali basin, the gravity data can be used to determine the base of the anomalously low mantle velocity layer below the Gulf (Fig. 4). The depth of 39 km between densities of 3.15 and 3.30 gm/cc is similar to that found beneath the mid-Atlantic ridge (Talwani, Le Pichon and Ewing, 1965), although the latter ridge does not have a 6.7 km/sec layer beneath its crest.

The seismic and gravity data suggest, therefore, that the crust beneath the Gulf of Aden could not have been formed as a downfaulted block of continent unless the entire crust had subsequently been modified in thickness and in physical properties. All the geophysical data point to the conclusion that the Gulf has resulted from the separation of the continental masses of Arabia and Africa and the formation of new oceanic crust from a juvenile and highly active mid-ocean ridge. If such a separation occurred, it must have taken place along the edges of the continental shelves, which can be approximated by the 500 fm (1,000 m) contour. Figure 5 shows the way in which the geological picture can fit across a reconstructed Gulf of Aden, prior to the Miocene.

The fit of the pre-Miocene geology and evidence for the date of separation is discussed in Laughton (1966), but the main features are summarized here:

(a) The congruity of shelf edges and the guide lines of the transform faults allows the position of fit to be well located. The coast-lines approach to within 50-80 km.

(b) There are many similarities between the late Mesozoic and Tertiary succession of sedimentary rocks of Arabia and Somaliland, although the details of the stratigraphy suggest that the two coast-lines were never closely adjacent (Beydoun, 1961). The western boundaries of the Eocene sea match better in this reconstruction than in their present position.

(c) The north and south areas of exposed Precambrian basement in the western part do not overlap.

(d) The major "Red Sea trend" fault system in Yemen and Somalia predates the opening of the Gulf of Aden and can be traced as a more or less continuous band of faults across the closed Gulf.

(e) The Mukalla arch of uplifted and eroded Jurassic sediments (Beydoun, 1960) can be matched in Somalia.

(f) The Wadi Hadramaut in Arabia developed during middle Eocene and should therefore have cut across the reconstructed Gulf. There is evidence of such a cut in the high plateau south of Bender Cassim in

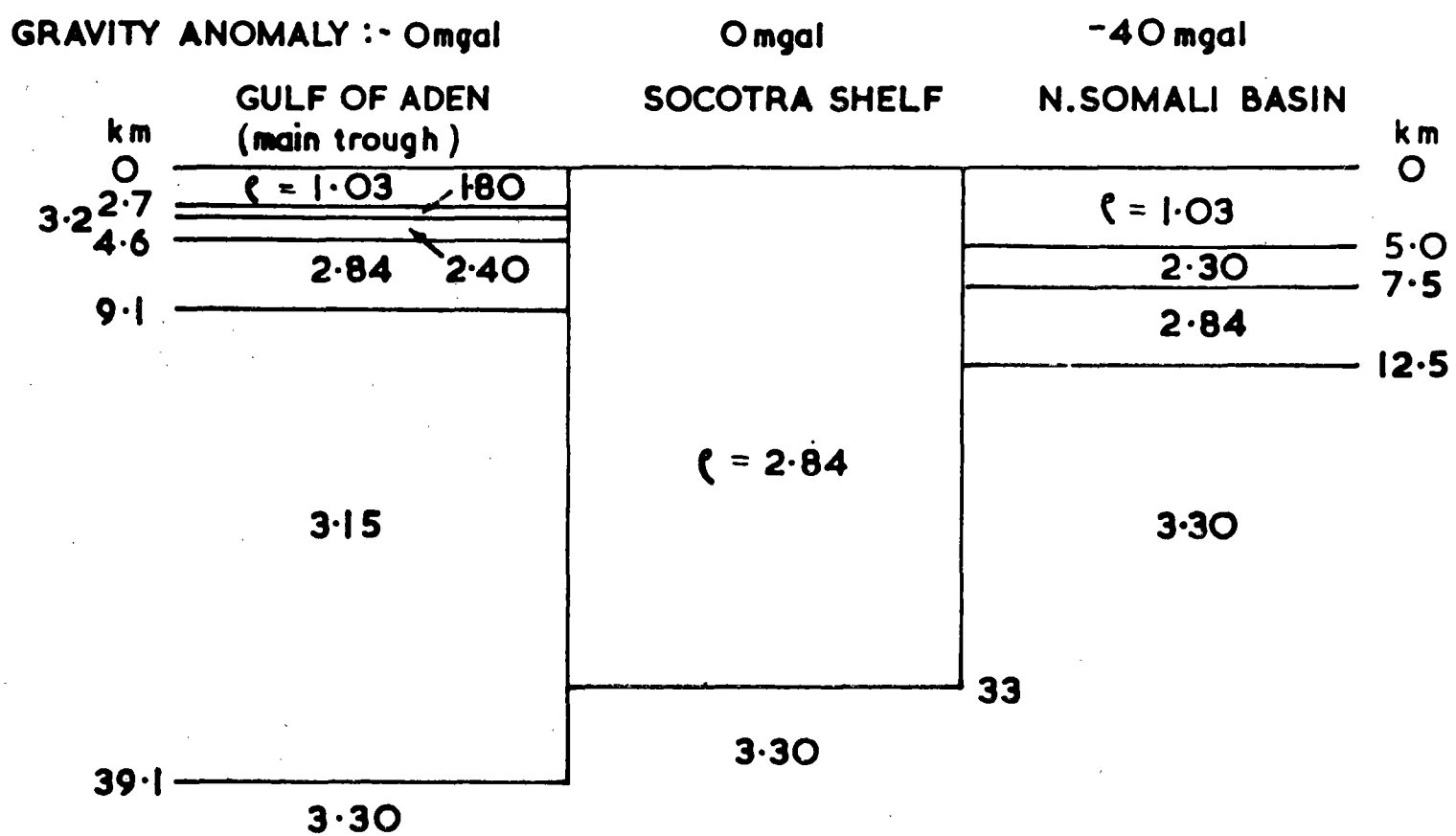

Figure 4. Crustal sections of the Gulf of Aden, the Socotra Shelf and the Somali Basin derived from seismic refraction and gravity data.

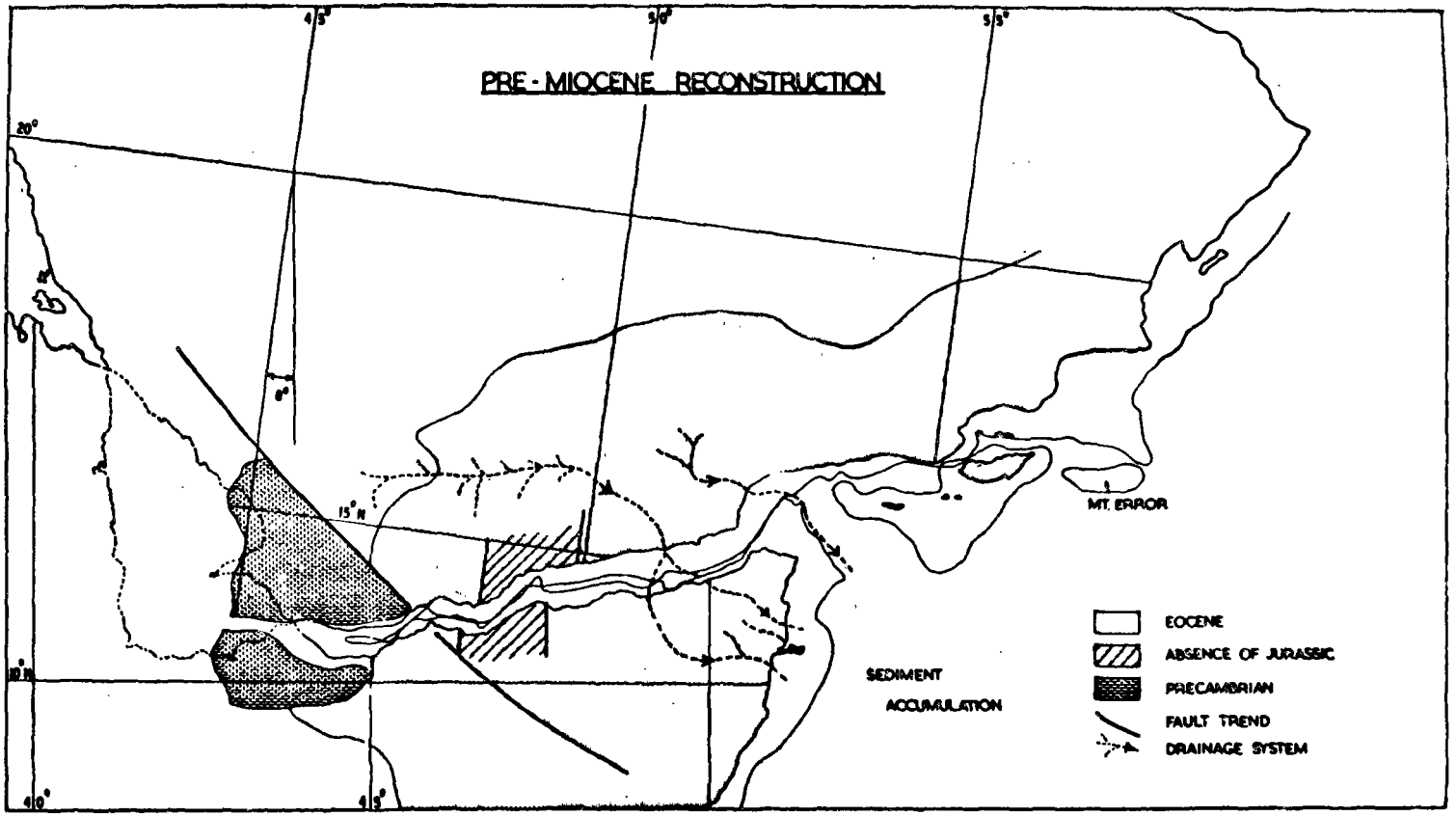

Figure 5. Pre-Miocene reconstruction of the Gulf of Aden (from Laughton 1966).

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Somalia, and of estuarine and lagoonal sediments of Miocene age filling in a long and broad valley reaching up to this cut from the east coast of Somalia near Ras Hafun (Azzaroli, 1958).

This description has taken no account so far of the overlap of the Yemen onto the Afar depression of Ethiopia, the Danakil Alps, or of the results obtained by other workers on the geological development of the Red Sea. The Red Sea will be considered first.

THE RED SEA

Drake and Girdler (1964) have made a geophysical study of the Red Sea, and further geophysical surveys have been made by T.D. Allan of SACLANT, La Spezia (unpublished). These studies include bathymetry, magnetics, gravity and seismic refraction measurements. The axial trough of the Red Sea has a positive Bouguer gravity anomaly and linear magnetic anomalies parallel to its length. The seismic stations may be classed according to their results as: (a) shallow (depth 400 m); (b) deep (depth 1,000 m); and (c) intermediate (depth 400-1,000 m). In the southern part of the Red Sea, there are only shallow and deep stations. The shallow stations were characterized by a basement velocity of 5.6-6.4 km/sec, whereas in the axial trough deep stations, the velocity range was 6.7-7.4 km/sec. Drake and Girdler interpret the geophysical data as indicating that the Red Sea has been formed as a tension feature, the axial trough representing the lateral separation of Arabia and Africa (Fig. 6); beneath the axial trough basic intrusives give rise to its magnetic anomalies and maintain it in isostatic equilibrium (Fig. 7). The shallow and intermediate depths of the remainder of the Red Sea are interpreted as down-faulted and tilted continental blocks covered, first by carbonate sediments and evaporites, and later, by coral and unconsolidated sediments.

The rotation of Arabia relative to Africa implied by the opening of the axial trough about a fulcrum in the Sinai Peninsula is 3-4°, and the opening at 15°N is about 60 km. These figures should be compared with those obtained from the Gulf of Aden, which suggest a rotation of Arabia relative to Africa of 8° about a fulcrum in the Eastern Mediterranean, giving rise to an opening of 250 km at 15°N. If Arabia has moved as a single undistorted block, the data from the Red Sea and the Gulf of Aden are mutually inconsistent and need further examination.

The south end of the Red Sea axial trough tapers to nothing at 14°N, as does the Tadjura trough at the west end of the Gulf of Aden. Both show similar dimensions and are characterized by earthquake activity and strong magnetic anomalies. In Laughton (1966), the suggestion is made that the growth of the Tadjura trough was the last of three phases of movement that tended to separate Arabia and Africa, the first and second phases giving

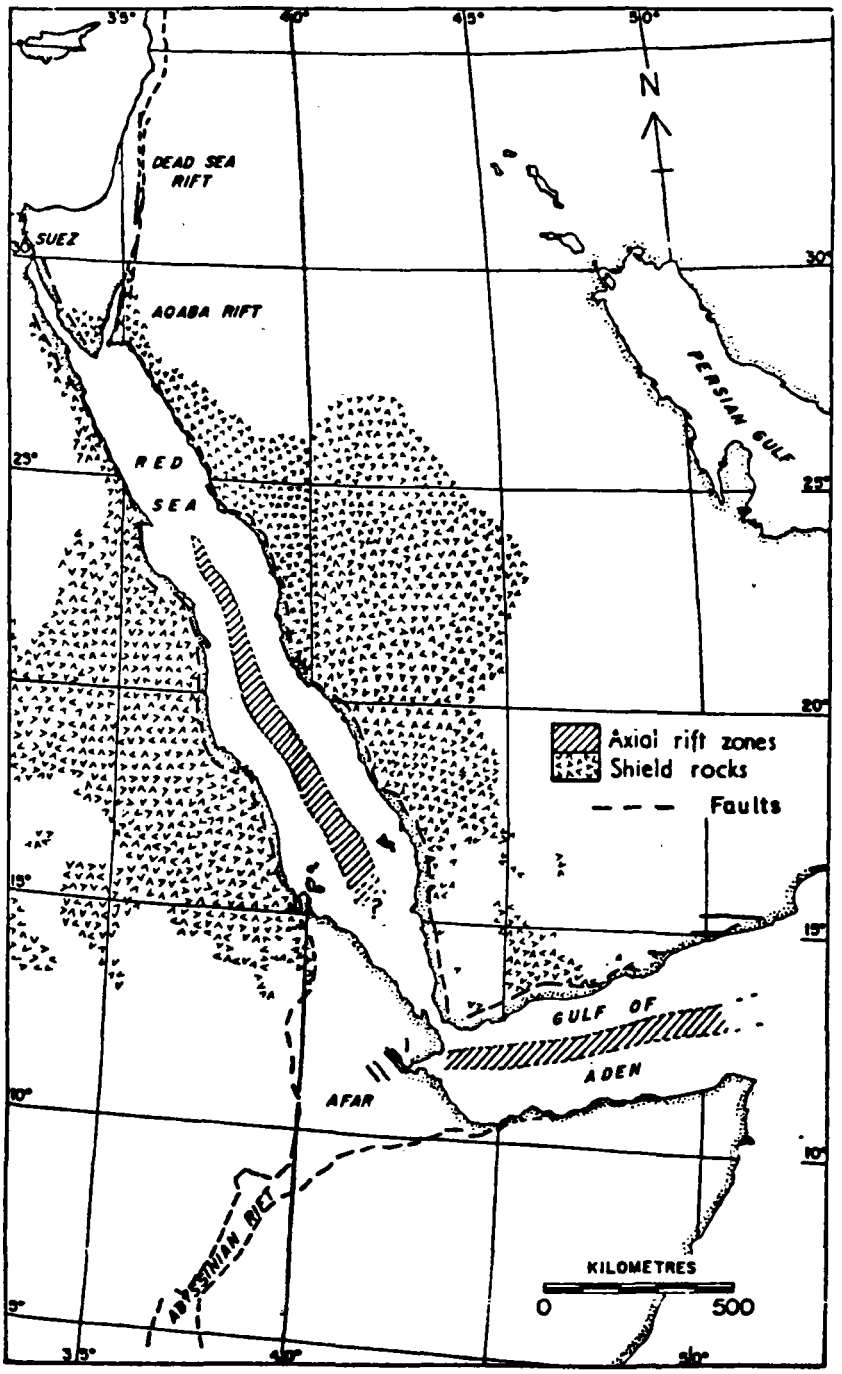

Figure 6. Structural map of the Red Sea area, showing the axial rift valley and region of continental separation (shaded) inferred by Drake and Girdler (from Drake and Girdler 1964).

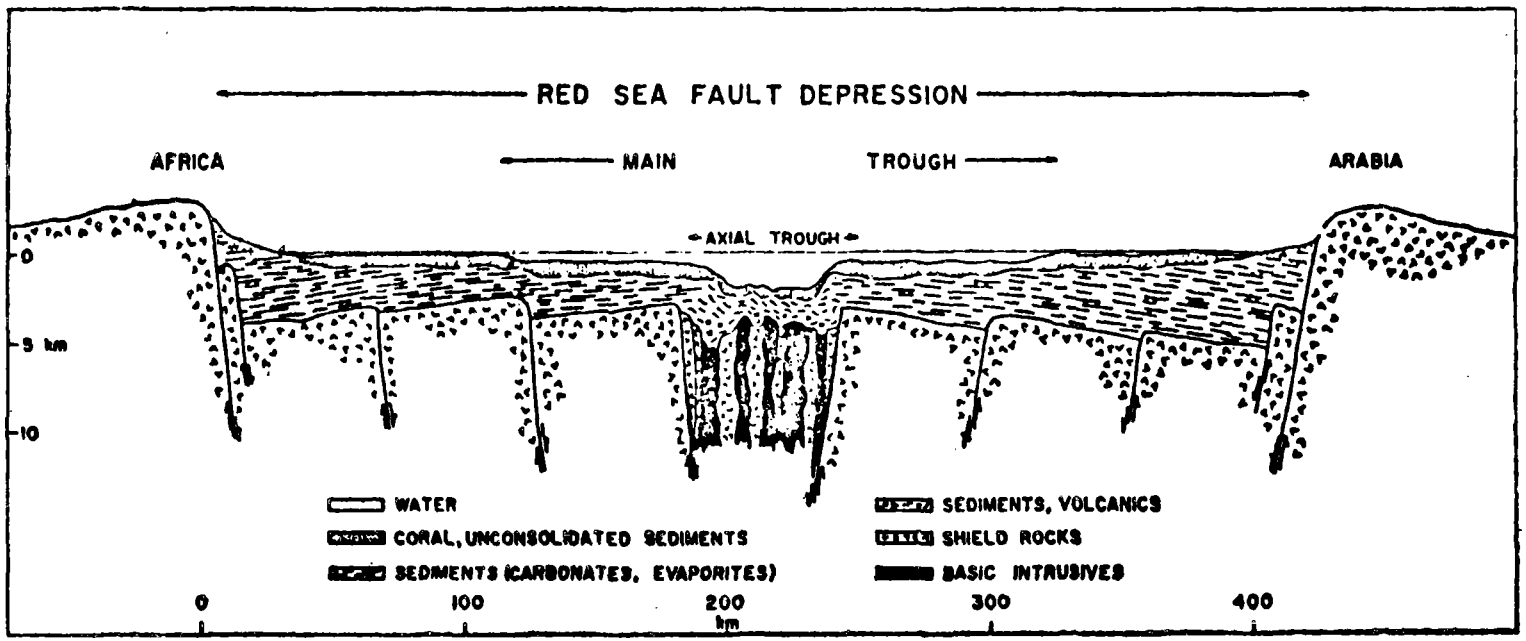

Figure 7. Structural section of the northern part of the Red Sea inferred from geophysical data (from Drake and Girdler 1964).

rise to the main trough and the central rough zone respectively. It is possible that the axial trough of the Red Sea represents a final phase of opening, and that during earlier phases, a large part of the Red Sea (thought by Drake and Girdler to be downfaulted continental crust) was in fact previously formed oceanic crust. The main geophysical arguments against this are the shield-rock velocities obtained for the basement at seismic refraction stations 175, 176 and 177 situated in shallow water to the west of the axial trough in the vicinity of Dahlak Islands. Of the five high velocity lines determined (176 was not reversed), four fall in the range 6.28 to 6.52 km/sec, and at station 175 where 5.64 km/sec was obtained, there was considerable dip. It is possible that these velocities should be attributed to basic rocks rather than shield rocks, or at least to rocks containing substantial proportions of basic intrusions. This would permit a much greater separation than the 60 km suggested by the axial trough.

In the southern part of the Red Sea, the magnetic and gravity fields have not been adequately surveyed on either side of the axial trough owing to the hazards of navigation, and so it is not known whether they are consistent with a 250 km opening at 15°N prior to the formation of the axial trough. If pronounced magnetic anomalies are not found here, their absence could be attributed to a reduction of magnetization by intensive shearing accompanying the separation of the continents.

THE AFAR DEPRESSION, THE DANAKIL ALPS, AND THE YEMEN

The lowland country in the funnel at the north end of the Ethiopian Rift valley has not yet been discussed in the interpretation of either the Red Sea or the Gulf of Aden development. The movement of Arabia deduced from both areas is such that, prior to drift, part of the Yemen was superimposed on what is now emerged land. On the basis of the Red Sea data, the overlap is relatively small, but it is significant because of the high terrain on either side of the Straits of Bab el Mandeb. The Gulf of Aden data indicate that the overlap is large, involving the superposition of the Yemen over a large part of the Afar depression (Fig. 5). The interpretation of the geology and deep structure of this region is therefore crucial to test whether either or neither of the two movements of Arabia postulated above are real. A summary of the geology is presented in Figure 8, based on the Geological Map of Africa (UNESCO, 1963) and on recent work of Mohr (1961).

The Afar depression is bounded on its western side by the great scarp of the Ethiopian Plateau, and on the south by the scarp of the Somali Plateau. On the northeast side lie the Danakil Alps extending from the Gulf of Zula to the Gulf of Tadjura. The most recent work on the geology of Ethiopia (Mohr, 1961) describes the area as follows:

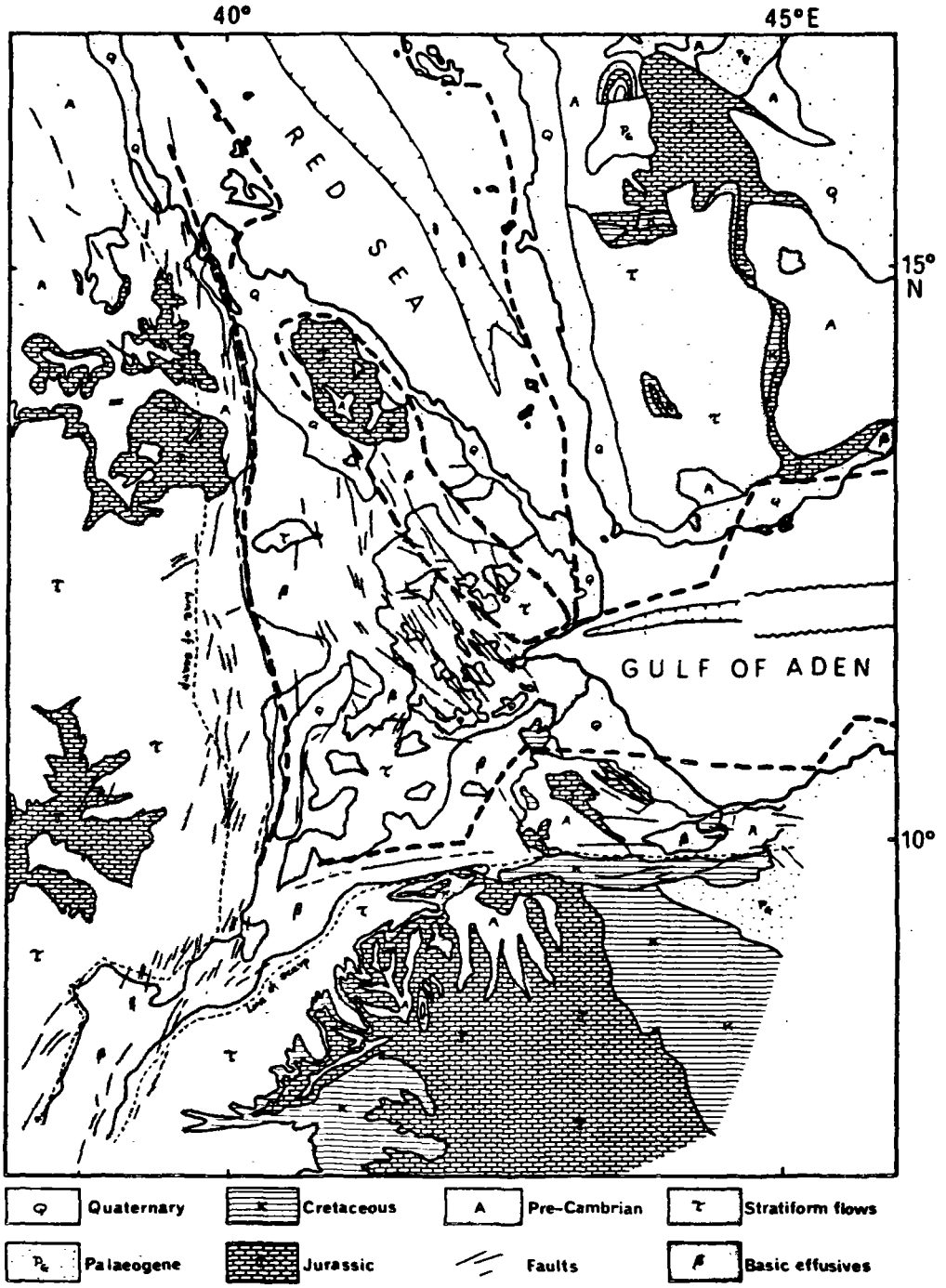

Figure 8. Geological map of the Afar region of Ethiopia based on 1963 edition of the Geological Map of Africa (ASGA-UNESCO) and Mohr (1961). Heavy dashed lines indicate edges of separated continental blocks which are fitted together in Figure 9.

"This immense downfaulted region, much of which lies below sea-level, has a geography and geology which even today are known only in the barest outline, and this is especially true of the inhospitable interior. Almost nothing is known of the faulting of the floor of internal Afar. Around the periphery of the Salt Plain [in the northern apex] faulting is associated with recent outpourings of immense quantities of fissure-basalts which have tended to smooth out any irregularities of the floor surface caused by older faulting.....In Western Afar faulting of the floor trends parallel to the scarp of the Ethiopian Plateau....."

Mohr presents a map of the faults which has been included in Figure 8. Except in the southern part of the area, these converge toward the northern apex. The present positions of the bounding escarpments to the west and south do not represent the major fault lines of the depression but lie some 40-50 km farther out, being the result of erosion of the high plateau country.

The northern end of the Danakil Alps consists of an uplifted horst sloping gently to the sea in a northeast direction and having an extremely denuded scarp on its southwest side overlooking the Salt Plain. The horst consists mainly of Jurassic rocks with patches of exposed Precambrian basement. The southwest-facing scarp of the horst meets the west-bounding scarp of the Afar depression and continues north to form the main western boundary fault zone of the Red Sea near the Gulf of Zula. Mohr believes the Salt Plain to be "the infilled form of a tectonic trough whose faulting, particularly along the eastern margin, is strongly developed and very recent in age".

The Danakil Alps continue southeasterly but consist of immense piles of volcanic rocks perhaps obscuring a continental basement. The mountain range is terminated by the E-W fault of the Gulf of Tadjura.

Within the Afar depression itself, no sedimentary rocks older than Quaternary have been described, most of the area being covered by basic effusives and stratified lava flows.

On the Arabian side of the junction of the Red Sea and the Gulf of Aden in the Yemen, the geological map shows stratified lava flows lying on top of Cretaceous and Jurassic sediments, which in turn rest on a Precambrian basement. It is not clear whether the cliffs behind the coastal plain represent the position of a boundary fault, or whether as in Ethiopia, they have been eroded back from this line. However, there seems little doubt that the Yemen is largely a continental mass connected to the Arabian continent.

Thus, if Arabia has moved, since the Miocene, the distance suggested by the Gulf of Aden data, then the Yemen represents the continental piece that fitted where the Afar depression now is, and a large part of the crust beneath the Afar region must have formed since the drifting occurred.

The absence of any old continental rocks in the area and the immense quantities of basaltic lavas tend to support this idea.

There is, however, the problem of the Danakil Alps which are certainly in part, and possibly completely continental. Figure 9 shows how these might be a fragment of continent which, at one time, was parallel and adjacent to the west bounding fault of the Afar depression. In Figure 9, the fit of the overlap has been determined by the fit of the Gulf of Aden. There is room for the Danakil Alps between the Ethiopian highlands and the Yemen. The Farisan Islands appear between the Dahlak Islands and the Danakil Alps.

As the opening took place, the Danakil Alps were swung anticlockwise, remaining nearly attached to Ethiopia at their northern end and to the Yemen at their southern end. Thus the tapering off of the Red Sea and its axial rift at their south end is compensated by an opening of the Afar depression southwest of the Danakils. The trend of the faults in the Afar is not inconsistent with this idea.

Some predictions based on the above hypothesis, by which it can be checked, are as follows:

(a) The palaeomagnetic directions obtained from, say, the Jurassic rocks, or from pre-Miocene volcanic lavas should give the following rotations relative to Ethiopia: (1) Danakil Alps, 35° anticlockwise; (2) the Yemen, 8° anticlockwise. These rotations could be measured. Irving and Tarling (1961) have already measured an anticlockwise rotation of 6-9° for the Aden volcanics, but these rocks may not be representative of the Arabian continental mass.

(b) The crustal structure beneath the southern end of the Red Sea should be similar to that beneath the Afar depression. In particular, there should be evidence of a pattern of magnetic anomalies in the centre of the Afar depression resembling that over the axial trough of the Red Sea. An aerial magnetic survey could map such a pattern. Gravity and seismic surveys would be needed on land to determine the thickness of the lavas, and to see if they are underlain by shield rocks. The relatively positive Bouguer anomaly found over the northern end of the Ethiopian Rift valley (Girdler, 1958) suggests a considerable thinning of the crust in that area.

(c) The Gulf of Zula and the Salt Plain define one of the major initial fault zones along which separation started. Geophysical data might throw more light on this.

(d) The geometrical operation whereby Arabia is moved as an undeformed unit to close the Red Sea and the Gulf of Aden requires a pivot point somewhere in the Eastern Mediterranean. The opening up of these

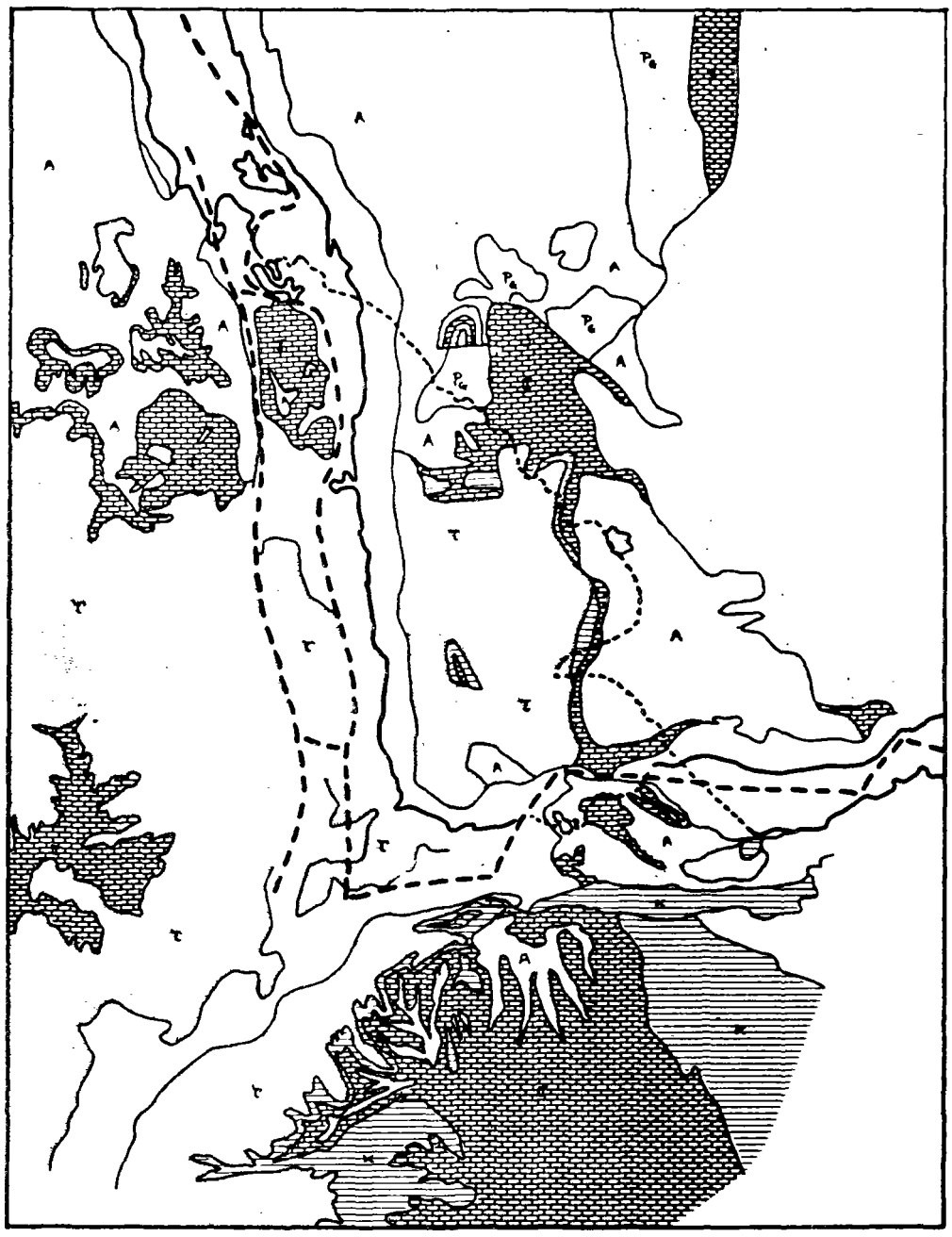

Figure 9. Pre-Miocene reconstruction of the Yemen and Ethiopia. Heavy dashed line indicates line along which separation will take place.

features in this way implies considerable left lateral shear along the Gulf of Aquaba-Dead Sea Rift. Quennel (1958) has described such a shear of 107 km, and this has been further examined by Freund (1965).

In conclusion, the geophysical data obtained from the Gulf of Aden and from the Red Sea both suggest relative horizontal movement between Arabia and Africa, but by different distances and angles. Both involve some overlap of the Yemen onto the Afar depression. The geology of the Afar region and the Danakil Alps can be interpreted to allow the large overlap suggested by the Gulf of Aden data in pre-Miocene times, provided the Danakil Alps can be rotated by 35° during the separation. Considerably more geophysical and geological data are required in this critical area before the problem can be resolved satisfactorily.

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DISCUSSION

Dr. D.C. Krause (U.S.A.)

I find the ideas expressed here very interesting. They can, as a model, be applied to other areas. For example, the Gulf of California bears a lot of similarity except that there is a strong strike-slip component as well, and I think that many of the features in the central Atlantic Basin can also be developed on the same model.

Dr. T.D. Allan (U.S.A.)

I am curious as to the southward extension of the Axial rift zones of the Red Sea. You have ended them with a question mark.

Dr. Laughton

The idea I have is that the separation of the continental crust along the Red Sea is continuous but is nullified at the south end of the sea by the formation of the triangular block of Afar.

Dr. W.F. Whittard (U.K.)

What happens to the seismic structure at the western end of the Gulf of Aden. Does the rift zone bifurcate or change in trend?

Dr. Laughton

The westernmost seismic stations we have are just southeast of Aden. The structure there appears to be similar to all other stations in the Gulf of Aden. There does not seem to be a change in the seismic structure from east to west. Now possibly if we went even further west toward the junction with the Red Sea, and I think this is a particularly critical area to investigate, we may find some transition from oceanic to continental crust. Perhaps this is the region to test Dr. Beloussov's idea of oceanization of continental crust. We do have a transition from oceanic structure up the axis of the Gulf of Aden to something that we believe to be continental, and this transition is not marked by a continental margin as we normally think of continental margins.

Reprinted from *International upper mantle project—The world rift system*, p. 430-439

GRAVITY OVER TRENCHES AND RIFTS[1]

Carl Bowin
Woods Hole Oceanographic Institution

Abstract

Mid-ocean ridges and the deep trenches are the most prominent features of the ocean basins, and both have been explained by investigators as resulting from convection in the mantle. Some aspects of these interpretations are examined. The ridges are in nearly isostatic equilibrium (free-air anomaly values are generally less than 50 mgal), but the trenches have very large negative free-air anomaly values and are considerably out of isostatic equilibrium. The Puerto Rico Trench has the largest free-air anomaly so far measured on the earth's surface (-380 mgal). A comparison of the Gulf of Aqaba, the East African Rifts, the Red Sea, the Gulf of California, and the Cayman Trough is made. Assuming a tensional origin for these features, it is concluded that between 40 and 100 kilometres of separation appear to be necessary before dense substratum begins to rise upward beneath the trough or rift.

INTRODUCTION

Ten to fifteen years ago the deep trenches associated with island arcs were cited as the most dramatic surface expression of convection currents taking place in the mantle of the earth. These trenches, the deepest portions of the world's oceans, and the associated large negative gravity anomalies, were attributed to the effect of compressive forces and the downward pull of the descending part of a convection cell. As parts of the crust were pulled deeper into the earth, they became metamorphosed as a result of the higher temperatures. Isostatic adjustments and erosion after the convection current had ceased, resulted in exposure of a core of metamorphosed rocks.

Investigators pondered what the configuration of these convection cells would be in three dimensions, confined as they are to a rotating spherical shell, and wondered how the arcuate structure of the island arcs and trenches is produced. They further wondered where were the extensional areas which must be associated with the rising limb of the convection cell. Satisfactory answers were not forthcoming and generally only the downward portions of a convection cell were related with a two-dimensional profile to surface geology.

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[1]Contribution No. 1730 of the Woods Hole Oceanographic Institution.

The developing field of oceanography had a great impact on our geological concepts. With the discovery of the gigantic mid-ocean mountain ranges and their central rift valleys, a spectacular tensional feature was located. Soon the crestal portion of the ridge was found to have the highest values of heat flow on earth (excluding possible localized thermal areas associated with hot springs on land), and confirmation that the ridge was indeed the site of the rising limb of a convection cell seemed assured.

Although both depressed (compressional) and tensional areas were then identified, the relating of these two regions to a single convection cell was generally bypassed by the introduction of the concepts of the youthful age of the ocean floor and of sea-floor spreading (Hess, 1962; Dietz, 1962) which appeared to explain the similarity of shape of the South American and African coastlines and the existence of mountain ridges midway between two continental masses. These hypotheses hold that the crust rides passively on top of the horizontal limbs of convection cells and is carried away from the site of upwelling. Thus South America and Africa were originally joined at the present location of the Mid-Atlantic Ridge and were slowly separated by horizontal motion of the underlying limb of the convection cell at a rate of about 1 centimetre per year. To account for the lack of Tertiary and Quaternary deformation along the eastern seaboards of North and South America, these entire continents were assumed to be riding on the back of the Atlantic convection cell. The downward limb of the convection cell was first located on the Pacific coasts of these continents where the present tectonic activity occurs. However, it now appears that the East Pacific Rise and its associated high heat flow impinges on the west coast of North America at the Gulf of California and may continue northward beneath California. Thus this potential site of the downward portion of the Atlantic cell seems eliminated. Where, then, is the downward limb? And where is it on the European and African side of the Atlantic? Apparently it is as difficult to locate as were the tensional areas for the early proponents of the tectogene hypotheses.

Deep trenches and mid-ocean ridges are the most prominent features of the ocean basins. Are their origins related, and are they produced by convection cells? If indeed they are related and produced by the same convection cell, the cell must have a severely contorted shape, confined within a spherical zone of a rotating, gravitating earth. If they are formed by separate convection cells, where are the tensional areas for the "trench cells", and where are the compressional areas for the "rift cells"? Must we choose between these two prominent types of structures, as to which feature may be produced by such cells and attempt to determine a different origin for the other, or should a non-convection origin be sought for both trenches and rifts?

Girdler (1963) concluded that a fifth degree spherical harmonic convection pattern best explains the location of the world rift system. Wilson (1965) has attempted to relate both mid-ocean ridges and mountain ranges to a single world-wide convection cell. Although Wilson's construction seems unsatisfactory in several localities, it is a useful approach. More efforts should be made in this direction, especially to bring into better focus the possible relation of convergent and divergent flow to local intensity of tectonism. Both geological and theoretical approaches should be advanced as, hopefully, they will antagonize each other and eventually converge on the truth.

TRENCHES

The deep-ocean trenches of the world are characterized by very large negative free-air gravity anomalies as first noted by Vening Meinesz for the Java and Puerto Rico Trenches. Over the Puerto Rico Trench the value obtained was -328 mgal. The maximum negative free-air values obtained in the East Indies are as follows: Java Trench, -165 mgal; the deep north of Tanimber Island, -255 mgal; the deep north of western Ceram, -162 mgal; the deep north of Soela Island, -216 mgal; and in the passage northwest of Halmahera, -179 mgal. A gravity survey of the Puerto Rico Trench conducted from R/V CHAIN of the Woods Hole Oceanographic Institution in 1962 located two minima (-330 and -380 mgal) along the axis of the trench. The latter -380 magal value is centred approximately on longitude 66°30'W and is the largest known negative free-air anomaly on the earth's surface (Bowin, in preparation).

In 1947, Lamont Geological Observatory initiated a program of gravity measurements at sea. The locations of several thousand pendulum measurements conducted in submarines during the period 1947 to 1953 is given by Worzel et al. (1955). From these measurements (Worzel, personal communication, 1965), the following maximum negative free-air anomaly values have been determined: Chile-Peru Trench, -223 mgal; Middle America Trench, -102 mgal; Aleutian Trench, -190 mgal; Japan Trench, -311 mgal; Marianas Trench, -250 mgal; North Solomons Trench, -248 mgal; and North New Hebrides Trench, -278 mgal. Submarine pendulum measurements aboard H.M.S. TELEMACHUS in the Tonga-Kermadec area (Talwani et al., 1961) obtained maximum negative free-air anomaly values of -224 mgal over the Tonga Trench and -210 mgal over the Kermadec Trench.

That the deep-sea trenches are not in local isostatic gravity equilibrium is obvious. Isostatic gravity computations (both local and regional for T = 30 km, R = 0 to 232.4 km) show anomalies in the East Indies region greater than -100 mgal (Vening Meinesz, 1948, Plates 1-3). Hayford-Bowie isostatic anomalies (T = 113.7 km) computed for the Puerto Rico

Trench show values of over -200 mgal (de Bruyn, 1951). A contour map of a portion of the Japan Trench (Hayford isostatic anomalies, d = 40 km) was presented by Hess (1948, Fig. 9) from values computed by Heiskanen on data obtained by Matuyama. Anomalies greater than -150 mgal occur over the trench.

The extent to which the trench areas of the world may be in regional adjustment is still to be decided. Talwani (1964) pointed out that the positive gravity anomalies over ridges adjacent to the trenches have been largely ignored in tectonic analyses, and he emphasized that since it is generally accepted that isostatic equilibrium takes place on a regional rather than a local basis, the mass deficit should probably be computed over an area including the trench and the island arc. The only area for which this appears to have been done is the Puerto Rico Trench.

Talwani (1964, Fig. 10) presented a crustal section along longitude 66°30'W across the island arc and trench, and a profile of mass deficiency per unit area for the crustal section. The mass deficit over the trench and a much smaller mass excess over the island clearly demonstrate that there is an over-all mass deficiency in this area.

The free-air anomaly profile across the Aleutian Trench presented by Peter et al. (1965, Fig. 9) at first appeared to indicate that the integrated free-air anomaly across the trench would have a positive value. However, to the south of their profile, positive free-air anomalies of 30 to 40 mgal continue for about 360 kilometres (Peter, personal communication, 1965). This suggests that the observed anomalies should be compared to a regional value of +30 to +40 mgal rather than to zero; if this is done, a negative integrated free-air anomaly value across the trench becomes apparent.

A somewhat similar relationship characterizes the Java Trench. Integration (using a planimeter) along the five regional isostatic anomaly profiles of the Java Trench and across Java and Sumatra presented by Collette (1954, Figs. 4-8) yields positive values (18, 12, 20, 20, and 14 mgal) for all profiles, using zero mgal as a datum. With +20 mgal as a regional datum, as given in Collette's profiles, integration yields a negative value for three of the profiles and positive values for the remaining two (-2, -0.4, +0.4, +8, and -8 mgal, respectively). Free-air anomaly profiles are not presented by Collette, but a similar integration of the free-air anomalies of that region would be interesting for comparison.

It is important to ascertain whether all trench-island arc systems have an over-all average mass deficit, or whether some have an average mass excess. Clearly, if some have a total mass excess, then the convection hypothesis has major difficulties. In any event, knowledge of the

total gravity field of trench-island arc systems is needed to study the total mass balance of these features, and thereby to better interpret their origin.

WORLD RIFT SYSTEM

A world encircling system of mid-ocean ridges was inferred by Ewing and Heezen (1956) from bathymetry and from the coincidence of earthquake epicentres with the crest of the ridge. Menard (1958) pointed out how closely the mid-ocean ridges are located at median distances from continents. Important exceptions are the East Pacific Rise where it impinges on the North American continent near Lower California, and the Carlsberg Ridge where it trends into the Gulf of Aden.

From the gravity measurements of Vening Meinesz (1948) in the North Atlantic, it was determined that the Mid-Atlantic Ridge is characterized by small free-air anomalies of generally less than ±50 mgal. Talwani et al. (1965) showed the results of continuous gravity profiles across the Mid-Atlantic Ridge and the East Pacific Rise. These profiles confirm that the free-air anomalies are close to zero mgal (within ±50 mgal) over the ridges. The Mid-Atlantic Ridge profile (near latitude 32°N) indicates that an integrated free-air anomaly over the ridge would be positive, as also suggested by the data of Vening Meinesz for the area north of about latitude 20°N, but the East Pacific Rise profile suggests that it would integrate to a small negative value. In both cases the mid-ocean ridges appear to have positive anomalies with respect to the surrounding ocean basins.

The small free-air anomaly values over the ridge indicate that the ridge is nearly in isostatic equilibrium, for were the mass composing the ridge not compensated, it would produce a free-air anomaly of over +250 mgal at the crest. Seismic refraction studies (Menard, 1960; Le Pichon et al., 1965) have shown that the crust does not thicken beneath the mid-ocean ridges, and Talwani et al. (1965) have suggested that the isostatic compensation may be achieved by the existence in the ridge area of anomalous low-density mantle material.

As noted previously, the mid-ocean ridge system impinges on a continental mass in two locations: the Gulf of Aden and the Gulf of California. Earthquake epicentres and magnetic anomalies suggest a continuity of structure from the crest of the Carlsberg Ridge into the Gulf of Aden (Matthews, 1963; Sykes and Landisman, 1964). At the west end of the Gulf of Aden the trend of epicentre locations bifurcates, one branch trending northwest along the Red Sea, and the other continuing along the trends of the African Rift valley structures. Structural trends appear again to bifurcate at the north end of the Red Sea, the Gulf of Suez constituting one branch, and the Gulf of Aqaba-Dead Sea-Jordan Valley trend the other branch. On the

basis of structural, gravity, and seismic information, current investigators have generally considered these features to be tensional in origin.

Hamilton (1961) concluded that the Gulf of California was a pull-apart feature and that subcontinental materials had welled up into the rift gap. Heat flow measurements (Menard, 1964, Fig. 6.10; Lee and Uyeda, 1965, Fig. 4) suggest that the Pacific Rise structure continues into the Gulf of California and perhaps northward under California. Thus at both locations where mid-ocean ridges impinge upon continental masses, rift structures occur inland from the continental margin.

Table – Gravity Anomalies and Dimension of Rifts and Possible Rifts

	Maximum Free-Air Anomaly	Maximum Bouguer Anomaly (crustal density = 2.67)	Width km
Gulf of Aqaba (Allan et al., 1964, Fig. 5)	-180	-100	26
East African Rift, Lake Albert (Bullard, 1936, p. 508)	-100	-190 (-50 to -80)	42
Red Sea, at latitude 16°N (Drake and Girdler, 1964)	0 to -40	+120	100
Gulf of California (Harrison and Spiess, 1961; Harrison and Mathur, 1964)	-70	+140	150
Cayman Trough (Data from R/V CHAIN Cruise 46)	-150	+330	220

A summary of gravity anomalies and dimensions of the rifts referred to above are presented in the Table. All are characterized by negative free-air gravity anomalies although the values for the Red Sea do not depart greatly from zero mgal. The Bouguer gravity anomalies, on the other hand, are negative over the Gulf of Aqaba and Lake Albert Rift, and positive over the others. The local Bouguer anomaly (difference between values for the centre and side of the rift) for the Lake Albert Rift was given as -50 mgal by Girdler (1964). A Bouguer gravity map published by the Department of

Mines and Surveys, Uganda, shows an anomaly of about -80 mgal over the Albert Rift, i.e. -210 mgal over the centre and -130 mgal on the Uganda side (Girdler, personal communication, 1965). The negative Bouguer anomalies suggest a mass deficiency beneath the Gulf of Aqaba and East African Rifts, whereas positive Bouguer anomalies and seismic refraction investigations (Drake and Girdler, 1964; Phillips, 1964) show that there is dense material beneath the Red Sea and the Gulf of California. The Bouguer anomaly values are close to zero at the margins of both the Gulf of California and the Red Sea.

From the Table it is clear that as the width of the rift increases, the Bouguer anomalies become increasingly positive. This relationship suggests a common process of development, but interpretation is complicated because these features may be in different stages of development, the intensity of tectonism may be different, and the original crustal thicknesses were probably different. These relations are interpreted to suggest that a certain amount of extension of the crust must take place before denser subcrustal material is able to rise up beneath the centre of the rift. From the information collected in the Table, it appears that when about 40 to 100 kilometres of separation of the earth's crust has occurred subcrustal material has an opportunity to rise to a shallower level and thereby change the gravity characteristics of the central trough.

The Cayman Trough is included in the Table not because it is considered to be part of the world rift system, but to emphasize that its gravity values and dimensions suggest that it may be the result of a tectonic process similar to that producing the other rift features. Bouguer anomalies at the margin of the Cayman Trough are about +95 mgal. Seismic refraction measurements in the Cayman Trough indicate that the mantle rises to about 11 kilometres below sea-level (Ewing et al., 1960) and thus the trough is similar to the Red Sea and Gulf of California in that the increase in positive Bouguer anomaly values over the centre of the trough presumably results from dense crustal or subcrustal material at a shallow level.

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Seismic Refraction Measurements in the Southern Indian Ocean[1]

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Twenty-seven seismic refraction profiles in the southern Indian Ocean are described. They straddle four major physiographic features: Two branches of the mid-ocean ridge system, Broken ridge, and the Ninetyeast ridge. The Réunion and Crozet basins are structurally very similar to the flanks and adjacent basins of the northern mid-Atlantic ridge. North of Amsterdam Island the mantle beneath the crest of mid-ocean ridge has a velocity of 7.61 km/sec; away from the crest the mantle has normal velocity but is exceptionally shallow. Broken ridge has a quasi-continental structure, and Ninetyeast ridge appears to be upfaulted oceanic crust rather than volcanic accumulation. A station in the West Australian basin revealed a shallow, low-velocity mantle.

INTRODUCTION

In November and December 1962 the research ships *Argo* and *Horizon* carried out seismic refraction work in the southern Indian Ocean while on passage between Port Louis, Mauritius, and Fremantle, Western Australia, and between Fremantle and Darwin, North Australia. This investigation was one phase of the geophysical program of Lusiad Expedition and a contribution of the Scripps Institution of Oceanography to the International Indian Ocean Expedition. The results of seismic refraction work done during an earlier phase of Lusiad Expedition in the northwest Indian Ocean have already been published [*Francis and Shor,* 1966]. The stations discussed in the present paper are shown in Figure 1. Twenty-eight receiving positions were occupied, resulting in 24 split profiles and 3 reversed profiles.

GEOGRAPHIC SETTING

The simplified bathymetric chart of the southern Indian Ocean shown in Figure 1 outlines the main topographic features of the sea floor. Three branches of the mid-ocean ridge system meet to form an inverted Y centered at about 25°S, 70°E. A more spectacular feature, narrower than the mid-ocean ridge but generally rising closer to the sea surface, is the strikingly linear Ninetyeast ridge. Near its southern end the large shallow area stretching toward southwest Australia has been termed Broken ridge by *Heezen and Tharp* [1965]. The bank seemingly coming out to meet it from the Australian coast is Naturaliste plateau. These two shallow areas are bounded to the south by the Diamantina fracture zone. The best known and most studied feature in this part of the Indian Ocean is the Indonesian trench, in the northeast corner of the diagram.

Many of the features shown in Figure 1 were delineated for the first time during the International Indian Ocean Expedition. The very generalized contours over most of the area emphasize how little is known even now of its precise topography.

AIMS AND TECHNIQUES

With the exception of the Indonesian trench, which was intensively studied by Scripps' ships during an earlier phase of the International Indian Ocean Expedition [*Raitt and Shor,* 1964], seismic refraction stations in the area of Figure 1 before Lusiad Expedition were few and far between. *Gaskell et al.* [1958] describe five short-range buoy stations between the equator and 10°S, one being of particular interest as it was shot over the Ninetyeast ridge. A normal oceanic crust was found by *Neprochnov* [1962] in the basin west of the Ninetyeast ridge, and *Hawkins et al.* [1965] have described a detailed survey on the continental shelf off the southwest corner of Australia, which attempted to delineate the seaward extent of the Perth basin.

Furthermore, at the time of Lusiad Expedi-

[1] Contribution from the Scripps Institution of Oceanography, University of California, San Diego.

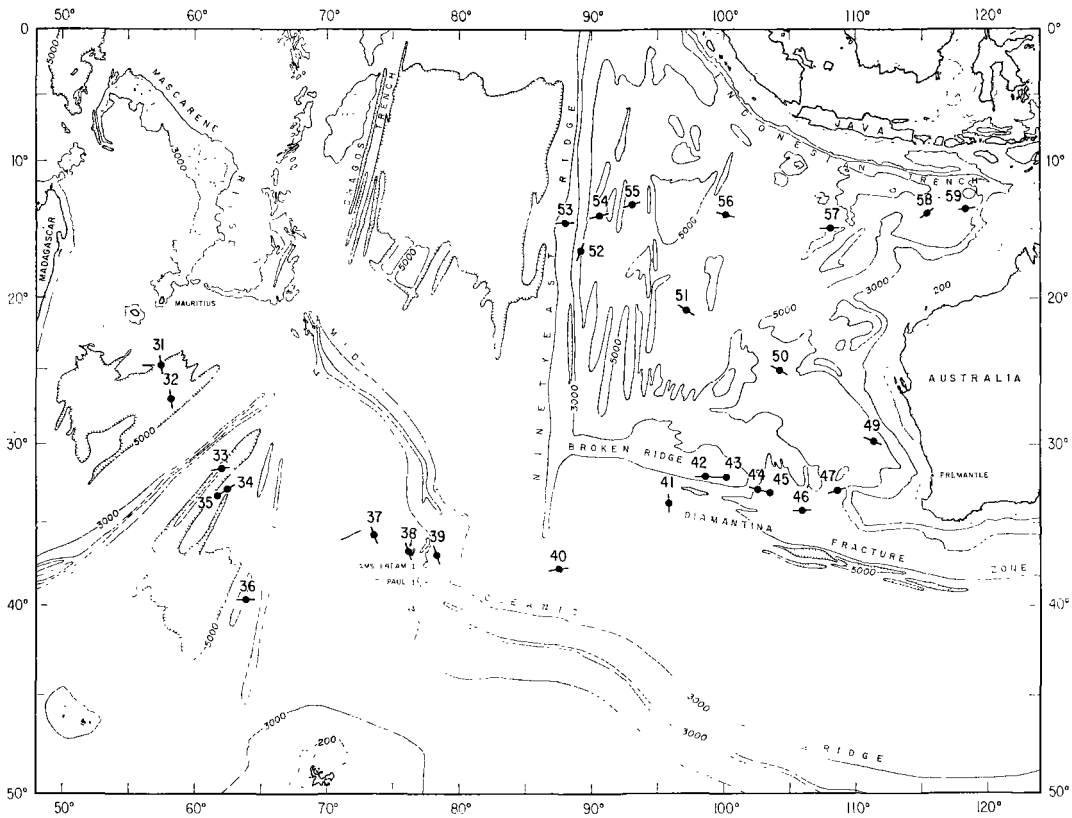


Fig. 1. Stations positions; bathymetry has been compiled from original unpublished charts of R. L. Fisher, the bathymetric sketch accompanying Heezen's physiographic diagram (1965), and the work of *Marova* [1966]. For clarity, only the 200-meter (shown dotted), 3- and 5-km contours have been included.

tion the topography of the sea floor in the area was almost as little known as the nature of the crust. The extent of the Ninetyeast ridge had not been discovered, and the mid-ocean ridge, at least south of the fork, was defined more from earthquake epicenters than from sounding lines. Thus the seismic shooting went hand in hand with bathymetric exploration, and it was not always possible at the time to choose the optimum sites for the profiles. Within these limitations stations have been shot to straddle four of the major topographic features shown in Figure 1: the two southerly branches of the mid-ocean ridge, Broken ridge, and Ninetyeast ridge.

The techniques used are summarized in the previous paper [*Francis and Shor*, 1966] and described in detail by *Raitt* [1956*a*] and *Shor* [1963]. Most of the profiles discussed in this paper were of the 'split' type, in which shots are fired on opposite sides of a single receiving point. A dipping-layer solution can be computed for this type of profile, but it tends to generate meaningless dips since no part of the line is truly reversed. The solutions presented here are average solutions computed, assuming horizontal layering, from an average travel-time plot for the station. This is obtained by averaging the slopes and intercepts of corresponding lines from the two sides, the observed intercepts being weighted by the number of points on their associated lines. Dipping layer solutions are presented, however, for two reversed profiles, though similar arguments about the validity of reversals apply to this type of profile too.

Table 1 summarizes station positions, seismic velocities, and layer thicknesses. Detailed descriptions of the individual profiles and travel-time plots are given in the appendix. The equa-

TABLE 1. Summary of Velocity and Depth Determinations

Station	Location	Mean Water Depth, km	Velocity, km/sec							Thickness, km							Thickness of Crust, km	Depth to *M*, km
			a	*b*	*c*	*d*	*e*	*f*	*g*	*a*	*b*	*c*	*d*	*e*	*f*	*g*		
31	24°34′S, 57°27′E	4.91	2.15*	5.0*	6.69	8.06				0.11	0.7	3.8					4.7	9.6
32	26°56′S, 58°10′E	5.49	2.15*	5.48	6.94	8.12				0.21	1.2	4.1					5.4	10.9
33	31°29′S, 61°52′E	4.33	2.15*	6.24	6.82	8.16				0.31	1.8	3.5					5.6	9.9
34	32°55′S, 62°26′E	4.79	2.15*	5.78	6.77	8.39				0.22	1.2	4.7					6.2	11.0
34	32°55′S, 62°26′E	4.79	2.15*	5.62	6.82	8.30				0.22	1.4	4.0					5.6	10.4
35	33°16′S, 61°43′E	4.85								0.14	1.4	4.3					5.8	10.7
36	39°45′S, 63°58′E	4.99	2.15*	(5.46)†	6.89	8.13				0.12	1.7	2.6					4.4	9.4
37	35°46′S, 73°40′E	4.04	2.15*	5.0*	6.81	7.99				0.26	0.9	2.8					4.0	8.0
38	36°51′S, 76°23′E	3.20	2.15*	4.43	(6.71)	8.23				0.33	1.2	2.4					3.9	7.1
39	37°15′S, 78°31′E	1.90	2.15*	4.52	6.73	7.61				0.37	1.5	6.6					8.5	10.4
40	37°56′S, 87°39′E	3.75	2.15*	4.57	6.71	7.80				0.32	0.5	7.4					8.2	11.9
41	33°48′S, 96°01′E	4.33	2.15*	6.57	7.12	8.06				0.55	1.6	5.0					7.2	11.5
42-in	32°02′S, 98°51′E	1.97	2.15*	(4.80)	(5.60)	(6.07)	(6.78)	(7.77)		0.68	2.1	1.3	2.9	14.6			21.6	23.6
42-out	32°02′S, 98.51′E	1.97	2.15*	4.70‡	5.81‡	6.07*	6.43	7.25	(8.23)	0.60	2.0	0.9	1.7	7.2	5.9		18.3	20.5
43	32°05′S, 100°20′E	2.45																
44	32°45′S, 102°45′E	4.85	2.15*	5.0*	6.26	8.18				0.27	1.0	6.4					7.7	12.5
45	33°01′S, 103°30′E	5.14								0.53	0.8	3.7					5.1	10.2
46	34°11′S, 105°55′E	5.57	2.15*	5.98	6.88	8.24				0.47	1.2	5.2					6.9	12.4
47	32°50′S, 108°41′E	5.35	2.15*	4.66‡	6.70	7.87				0.60	1.1	3.0					4.7	10.0
49	29°42′S, 111°31′E	5.35	2.15*	4.98	6.49	8.28				0.35	1.3	4.3					6.0	11.3
50	25°03′S, 104°12′E	5.10	2.15*	4.86	7.14	8.11				0.07	2.4	2.5					4.9	10.0
51	20°43′S, 97°12′E	5.74	2.15*	4.78	6.74	8.14				0.14	1.4	4.7					6.2	12.0
52	16°25′S, 89°19′E	5.73	2.15*	4.80	6.46	7.94				0.15	0.6	3.5					4.2	10.0
53	14°31′S, 88°02′E	2.71	2.15*	4.67	6.64	7.07‡				0.71	2.2	2.9						
54	13°50′S, 90°48′E	5.00	2.15*	5.38	6.84	(8.57)				0.21	1.4	7.7						
						8.1*						5.6					7.2	12.2
55	13°09′S, 93°13′E	5.22	2.15*	5.09	6.68	(8.07)				0.08	1.2	6.2					7.5	12.7
56	13°50′S, 100°15′E	5.95	2.15*	5.37	6.94	7.67	(8.63)?‡			0.13	1.7	0.9	12.0				2.8 or 14.8	8.7 or 20.7
							8.1*?						7.9				2.8 or 10.7	8.7 or 16.6
57	14°57′S, 108°09′E	5.59	2.15*	5.38	6.51	8.28				0.27	1.3	4.5					6.1	11.6
58	13°47′S, 115°33′E	5.68	2.15*	5.18	7.00	8.23				0.49	2.4	6.1					9.0	14.7
59	13°31′S, 118°26′E	5.67	2.15*	4.89*	6.61	8.09				0.56	0 8	7.0					8.4	14.1

* Assumed velocity.

† Values in parentheses represent velocity from a single run.

‡ See notes on station in appendix.

tions of the least-squares lines also appear on the travel-time plots, together with the standard errors of the intercepts and apparent velocities. The errors in the real velocities are likely to be greater because of geological factors that cannot be taken into account. With the exception of plots of bottom and sub-bottom reflections and close range refracted arrivals for stations 46 and 47, all travel-time plots show refracted arrivals with the delay time in the water removed. Table 2 summarizes the sediment velocities and thicknesses measured from sub-bottom reflections.

Interpretation

Mid-ocean ridge south of Mauritius and adjacent basins. Stations 31 to 36 lie roughly on a line crossing the southwest-trending branch of the mid-ocean ridge. Without exception they yield normal oceanic structures. The receiving position of station 33 was only 185 km from the axis of the ridge (as depicted by *Heezen and Tharp* [1965]); yet, no low mantle velocity was detected. Thus a zone of low mantle velocity must be narrow, if it exists at all, as was found in the case of the Carlsberg ridge further north [*Francis and Shor,* 1966]. An alternative explanation might be that the low velocity is absent altogether because this particular section of mid-ocean ridge is not generating new crust and causing sea floor spreading, as witnessed by the absence of an appreciable central magnetic anomaly [*Vine,* 1966]. Earthquake epicenters are, however, as common and as well aligned on this part of the ridge system as elsewhere [*Stover,* 1966]. A particularly seismic region at about 34°S, 58°E, close to stations 33 and 34, has been studied in some detail by *Benioff* [1955].

Stations 31 and 32 give an average depth to the mantle for the Réunion basin between Mauritius and the mid-ocean ridge of 10.25 km. Similarly, stations 33 to 38 may be considered representative of the Crozet basin south of the fork of the mid-ocean ridge, giving an average depth to the mantle of only 9.0 ± 1.4 km standard deviation (stations 34 and 35 being included as a single profile). The difference between the two basins is probably not significant, but it is fair to conclude that the mantle is shallower in these basins than is usual in oceanic areas. For stations 31 to 38 the average sea depth is 4.54 km, close to the most commonly observed depth [*Menard and Smith,* 1966], but the average crustal thickness is only 4.8 ± 0.8 km standard deviation, in comparison with the average thickness of oceanic crust of about 7 km [*Raitt,* 1963].

Mid-ocean ridge north of Amsterdam and St. Paul islands. Three stations were shot just north of Amsterdam and St. Paul islands. The submarine topography in this area has been studied in detail by *Fisher* [1966]. Figure 2 shows the topographic and seismic profile along the line joining stations 37 and 39. The topography here is derived from one of Fisher's charts. The axis of the ridge, though not obvious on this profile, is conspicuous on Fisher's chart as a north–south median valley just east of Amsterdam and St. Paul. From this it is apparent that station 39 is less than 50 km from the axis. A low mantle velocity is indeed observed. In other respects, however, the structure at station 39 is not typical of the axial region of a mid-ocean ridge. Layer 2 is not unusually thick, and the crustal layer is not thin. Furthermore, the low mantle velocity is found at a depth of 10.4 km, much deeper than is usual for the low velocities beneath mid-ocean ridges [*Menard,* 1964, *Le Pichon et al.,* 1965]. The explanation of this probably lies in the proximity of the large area of shallow water associated with Amsterdam and St. Paul islands.

Stations 37 and 38 are both remarkable in the Mohorovicic discontinuity being very shallow. However, all the velocities observed at these two stations are normal, and the structure is analogous to that at stations close to,

TABLE 2. Sediment Velocities and Thicknesses from Sub-Bottom Reflections

Station	Velocity, km/sec	Thickness, km	Is Reflector Layer 2?*
41	1.78	0.17	No
46	1.61	0.24	No
47	1.40	0.39	Yes (assumed)
51	1.90	0.19	Yes
58	2.98	0.45	No

* In other words, is the first observed refraction velocity tangential to the reflection curve?

but not at, the crest of the East Pacific rise [*Raitt,* 1956*b*], where the crust is thinned and the mantle is shallow but of normal velocity.

Broken ridge and adjacent basins. Stations 42 to 47 lie roughly on a line extending from Broken ridge to the foot of Naturaliste plateau. The seismic results are shown in Figure 3 together with a simplified topographic profile. All these stations lie to the north of the Diamantina fracture zone. The deep-water stations differ as much among themselves as from the single station just south of the fracture zone, number 41, but this does not mean that there is no appreciable structural change across it. Topographically the zone is a much more spectacular feature than the fracture zones of the North Pacific, with water depths varying from less than 2 to more than 7 km. This probably implies a much younger age for the Diamantina fracture zone.

The structure of Broken ridge is the most interesting part of the profile. Some difficulty was found in the interpretation of stations 42 and 43 (see appendix), but the structure obtained for the reversed part of the profile seems most likely. This is almost continental. The velocities 5.81, 6.07 and 6.43 km/sec all fall within the granitic range, and the 7.25 km/sec velocity lying at 14.6 km is at just the depth at which the Conrad discontinuity is sometimes found beneath the continents.

Stations 44 and 45, forming a reversed profile at the foot of Broken ridge, detect the mantle rising from its greater depth beneath the shallower water. The low 'layer 3' velocity (6.26 km/sec) distinguishes this profile from numbers 46 and 47, which have normal crustal velocities. This structure seems to be quite common in the Indian Ocean beneath deep-water areas immediately adjacent to shallow banks, though it is rare as a normal oceanic section. It has been found just west of Maldive ridge [*Francis and Shor,* 1966] and just west of the Seychelles bank [*Francis et al.,* 1966]. (A 'layer 2' overlying the layer of about 6.3 km/sec is difficult to detect and may or may not be present. Similarly a 6.8-km/sec crustal layer underneath may be present but masked on the travel-time plot.) A possible interpretation of the present structure is that it represents an extension of granitic material from Broken ridge. Alternatively, the 6.26-km/sec layer is smooth lava from sea-floor fissure flows [see *Francis and Shor,* 1966, p. 431]. The fact that this structure is not confined to the environs of granitic banks favors the latter interpretation.

The topographic similarity of Broken ridge and Naturaliste plateau is obvious from the profile. A further point of similarity worth mentioning is the shallowness of the mantle at the foot of each bank (at stations 45 and 47). At station 46 the mantle is deeper.

A station over Naturaliste plateau would have been an appropriate end to the profile of Figure 3, but it was not shot. However, *Hawkins et al.* [1965] shot a number of stations over the continental shelf adjacent to Naturaliste plateau. Thirty km west of Cape Naturaliste they detected the Archaean shield with a velocity of about 5.9 km/sec overlain by between 1 and 2 km of sediment. No data are available to show whether Naturaliste bank is merely an extension of the shield material with little sedimentary cover, or a downfaulted block with some sedimentary cover, though the latter is geologically more probable.

Larger scale studies of the West Australian shield were made by *Bolt et al.* [1958], who observed the seismic signals from the 1956 atomic explosions at Maralinga, South Australia. They found $P_1 = 6.03$ km/sec and $P_n = 8.21$ km/sec, detected no intermediate layers, and computed the depth to the Mohorovicic discontinuity to be 36 km.

The almost continental structure beneath Broken ridge and its physiographic similarity to Naturaliste plateau suggest the possibility that the ridge was once a part of the Western Australian shield. If this is so, either the crust has been thinned tectonically or the mantle has risen at the expense of the crust by some process at the Mohovoricic discontinuity. Detailed knowledge of the structure of Naturaliste plateau would throw light on these ideas.

Stations 49, 50, and 51 were widely spaced along the ships' tracks extending in a northwesterly direction from Perth, Western Australia. All reveal normal oceanic structures, though the crustal velocity is rather low at station 49.

Good sub-bottom reflections were the exception rather than the rule at the stations described in this paper. The stations at which

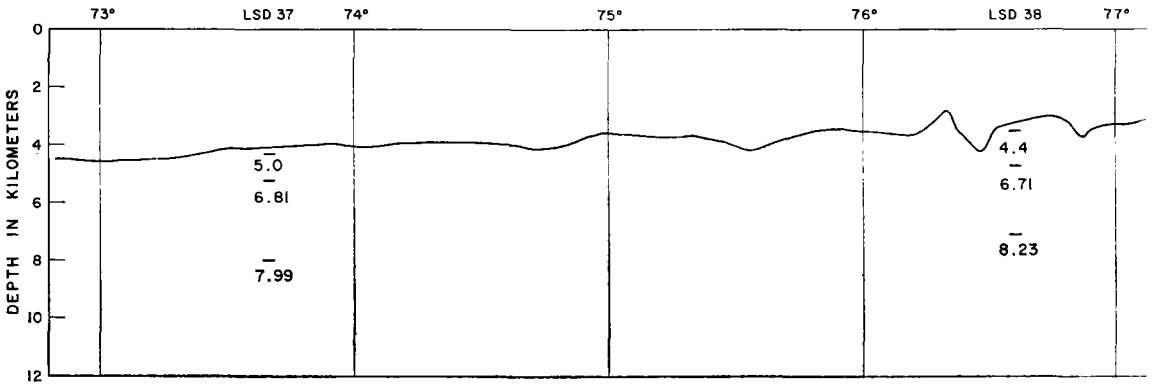


Fig. 2. Topographic and seismic profile on a line through stations 37 and 39. Vertical exaggeration 13:1.

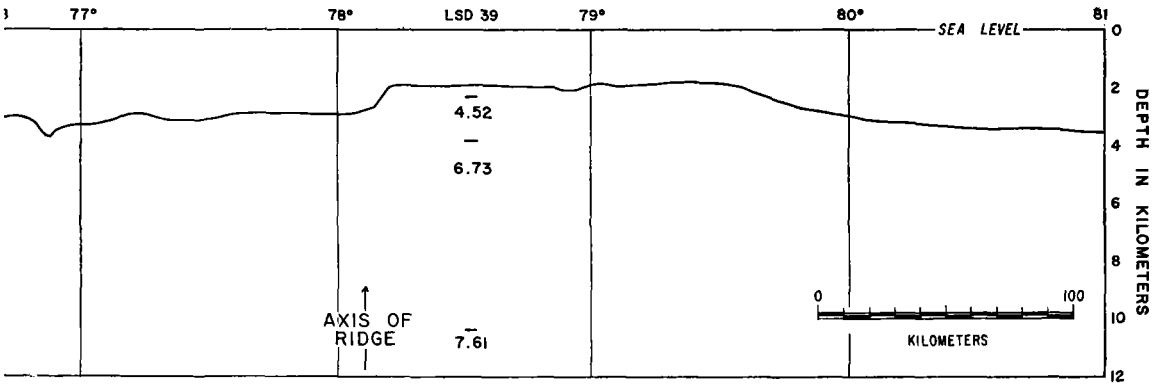
they were observed were, however, nearly all in the West Australian basin and may signify the presence there of an acoustically transparent layer of sediments such as found in other parts of the world by workers from the Lamont Geological Observatory [*Ewing et al.*, 1964; *Ludwig et al.*, 1966]. This is almost certainly the case in the region of stations 46 and 47 (see appendix).

Ninetyeast ridge and adjacent basin. Stations 52 to 59 lie roughly on a line extending east from Ninetyeast ridge at about 15°S latitude. Figure 4 shows the topographic and seismic profile near the ridge. The crustal section of station 52 has been extrapolated into this profile from 250 km to the south. In the topographic profile the eastern (right-hand) hump is the true Ninetyeast ridge. The western hump is a large shoal area, probably of volcanic origin, that impinges on it at about 15°S. The presence of this feature and the large variations of water depth make station 53 difficult to interpret (see appendix). If, however, the 6.64-km/sec boundary represents the top of the oceanic crustal layer, as the velocity would indicate, the second layer is much thinner than the volcanic structures usually beneath oceanic islands. Thus, beneath Eniwetok Atoll in the Pacific, layers with velocities of 4.15 and 5.59 km/sec are about 8 km thick [*Raitt*, 1957], and beneath the Saya de Malha bank in the western Indian Ocean layers of 4.36 and 5.58 km/sec are about 7 km thick [*Shor and Pollard*, 1963]. This suggests that the Ninetyeast ridge is a horst-type feature rather than a volcanic accumulation along a line of weakness in the earth's crust. The large scarps visible on most P.D.R. crossings of the ridge support this interpretation.

Station 52 presents what is perhaps another example of a low crustal velocity adjacent to a shallow area (see above). The depth to the crustal layer is consistently about 6.5 km at stations 52, 54, and 55 but a kilometer shallower beneath the ridge. If the ridge were pushed down to the level of the basins on either side, the 7.07-km/sec boundary would be at the usual depth of the Mohorovicic discontinuity. This leads one to wonder whether, after the elevation of the ridge, the Mohorovoicic discontinuity migrated downward, leaving the higher crustal velocity as a 'fossil' boundary. Such an interpretation requires the Mohorovicic discontinuity to be a phase change.

Heezen and Tharp [1965] classified the Ninetyeast ridge as an aseismic ridge. However, a broad band of earthquake epicenters trending NW–SE intersects the ridge between the equator and 15°S [*Stover*, 1966]. Another trend intersecting the ridge at about 15°S is a line of volcanic activity, which emerges from the Indonesian trench at about 110°E [*Bathymetric Chart of the Indian Ocean*, 1963; *Heezen and Tharp*, 1965]. Cocos-Keeling and Christmas islands fall on this line. The shoal area just west of the Ninetyeast ridge at 15°S forms an extension to this latter trend and is therefore thought to be volcanic.

The remaining stations, 56 to 59, lie in the basin south of the Cocos-Keeling to Christmas trend. Normal oceanic structures are found except at station 56. Here the structure is ex-



ceptional for a deep ocean basin. Various interpretations of the travel-time plot are discussed in the appendix, but it is difficult to escape the conclusion that the crustal layer is thin and a low-velocity mantle (7.67 km/sec) is present beneath only 2.8 km of crust. This is the type of structure found beneath mid-ocean ridges [*Menard*, 1964; *Le Pichon et al.*, 1965]. The fact that station 56 lies on the broad band of earthquakes mentioned above makes the situation more intriguing. No abnormal values of heat flow were observed, however, in this basin, nor does the bathymetry suggest an embryo mid-ocean ridge. Until more data are available it is not possible to conclude whether the structure at station 56 is part of a larger feature or merely a local phenomenon.

Stations 58 and 59 were shot in the small basin between the Indonesian trench and the northwest Australian continental slope. Both show the mantle in this basin to lie about 3 km deeper than the average depth in the much larger Western Australian basin. This deepening is not the result of a thickening of sedimentary layers near the continental slope but is caused by an unusually thick oceanic crust for a deep-water area. The explanation probably lies in the proximity of the Indonesian trench.

General conclusions about the Indian Ocean

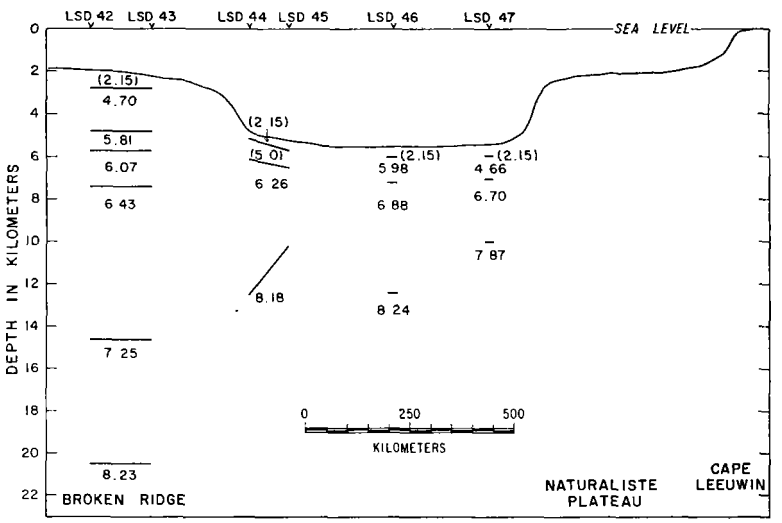


Fig. 3. Seismic sections and simplified topographic profile on a line between station 42 and the southwesterly tip of Australia (Cape Leeuwin). Vertical exaggeration 51:1.

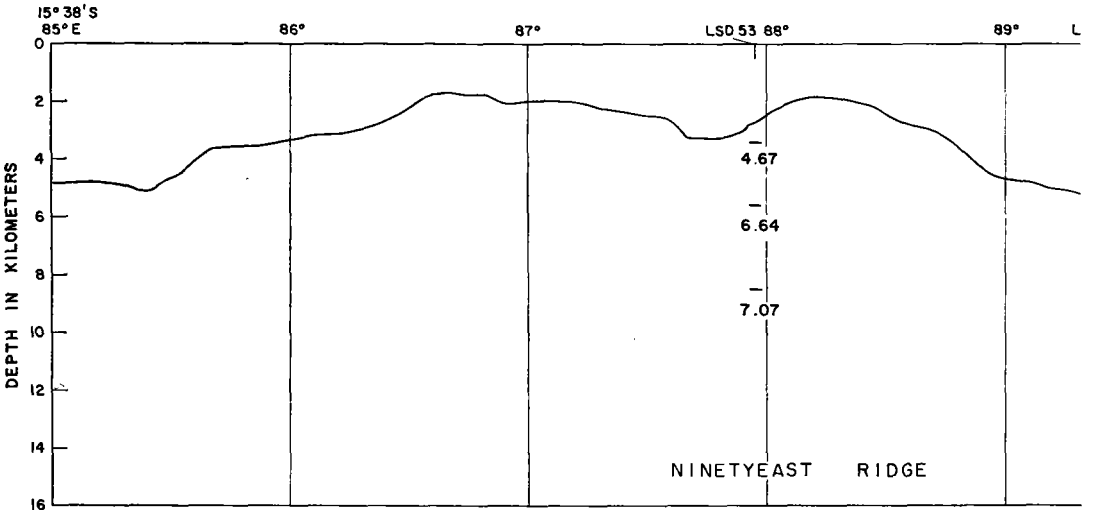


Fig. 4. Topographic and seismic profile on a line across the Ninetyeast ridge. Vertical exaggeration 11.2:1.

crust. Figures 5 and 6 show respectively plots of mantle depth and crustal thickness against water depth for stations at which the crustal thickness exceeded 2 km. The reversed profiles 34, 35 and 44, 45 are represented by average values.

If the oceanic crust is in isostatic equilibrium, simple Airy type compensation, in which an increase in water depth is accompanied by a decrease in crustal thickness, leads to the following expressions for mantle depth and crustal thickness:

$$M = -\frac{(\rho_2 - \rho_1)}{(\rho_3 - \rho_2)}\omega + k$$

$$C = -\frac{(\rho_3 - \rho_1)}{(\rho_3 - \rho_2)}\omega + k$$

where ρ_1, ρ_2, ρ_3 are the densities of the water, crust, and mantle, ω is the water depth, and k is a constant. By definition $M = C + \omega$. Taking $\rho_1 = 1.03$, $\rho_2 = 2.8$, $\rho_3 = 3.3$ gm/cm^3 and for average structure $C = 7$ km when $\omega = 4.5$ km [*Hill,* 1957; *Raitt,* 1963], these expressions become

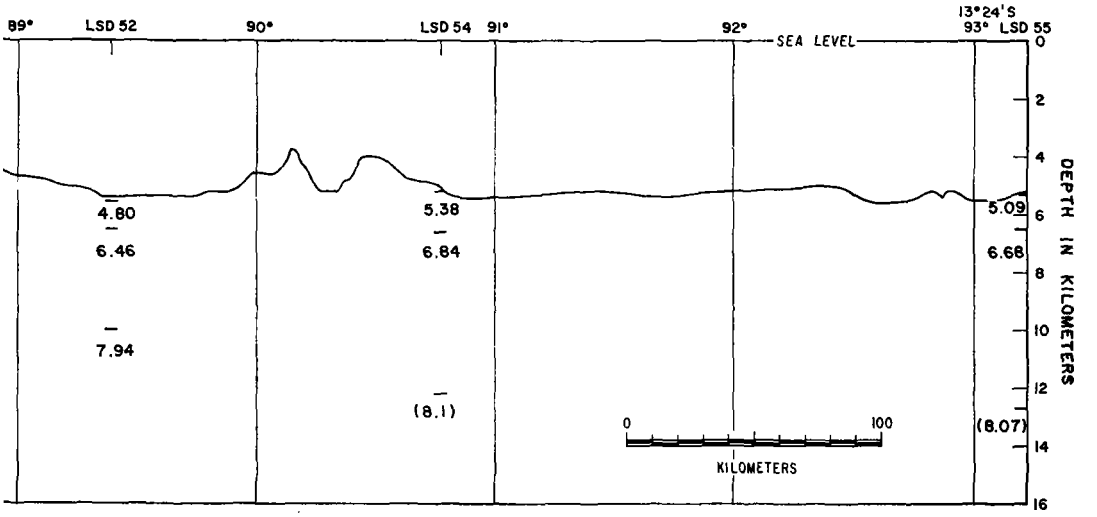
$$M = -3.54\omega + 27.4$$

$$C = -4.54\omega + 27.4$$

They are drawn on the appropriate plots in Figures 5 and 6.

The most remarkable feature of these plots is that the points group according to their geographic distribution. This suggests that the ridge features that have been used to distinguish groups of stations are not merely independent features in a uniform oceanic crust, but to some extent they also are boundaries between different crust/mantle provinces.

Stations 31 to 38 form a particularly interesting group which appears to have no relation at all to the simple isostatic model. On the mantle depth plot the points correlate remarkably closely to a line with a gradient not much greater than unity, whereas the crustal thickness is almost independent of water depth. If these correlations are real, then in the Réunion and Crozet basins the crust is an approximately uniform layer overlying the mantle, and the large-scale topography of the sea floor is just a repetition of that in the Mohorovicic discontinuity. If the area is nevertheless in isostatic equilibrium, this must in large measure be the result of density variations within the mantle. The fact that the mantle/water depth line has a gradient somewhat greater than unity (i.e., there is a correlation between increasing crustal thickness and increasing water depth) may indicate that where the mantle has bulged upward the crust has not only been raised but also thinned slightly by the tensional stresses that the bulging generated.



It should be emphasized that these deductions rely heavily on the points from stations 37 and 38. Stations 31 to 36 group as fairly normal oceanic crust, though the tendency here is still in the direction of thinner crust and shallower water depth when compared with the West Australian basin points (stations 44 to 57). The distributions observed for stations 31 to 38 agree closely, however, with the distributions found from seismic refraction stations over the flanks and adjacent basins of the northern mid-Atlantic ridge [*Le Pichon et al.*, 1965], where mantle depth, crustal thickness, and water depth were found to be related by the expressions:

$$M = 1.86\omega + 1.35$$

$$C = 0.80\omega + 1.20$$

(Le Pichon et al. define crust as the mantle depth less the thickness of the water column and the unconsolidated sediment; here only the water depth is subtracted.) Indeed, the standard deviations of stations 31 to 38 from these two lines are smaller than those found for the Atlantic stations from which they were deduced (0.7 km cf. 1.0 km for the crust; 0.8 km cf. 0.9 km for the mantle depth). These two expressions are shown on the appropriate plots. It may be concluded that Réunion and Crozet basins are geologically very similar to the flanks and adjacent basins of the northern mid-Atlantic ridge.

Stations 44 to 57 present an interesting contrast to stations 31 to 38 (see Figure 6). Whereas stations 31 to 38 spread over a large range of water depth but only a small range of crustal thickness, stations 44 to 57 have only a small range of water depth but are widely spread in crustal thickness. This corresponds more closely to the simple Airy isostatic model. If the water depth corresponding to a crust of 7 km is taken as 5 km, rather than 4.5 km as plotted, the agreement would be quite good. A surprising corollary to this interpretation is that the anomalous shallow mantle of station 56 is in isostatic equilibrium with the remainder of the basin. This result may be entirely fortuitous, however, since the mantle velocity at station 56 is low enough to imply a lower density mantle.

Figure 7 shows histograms of the distribution of seismic velocity, mantle depth, and water depth for the southern Indian Ocean (this paper), the northwest Indian Ocean [*Francis and Shor*, 1966; *Francis et al.*, 1966], the whole of the Indian Ocean (the first two sets combined), and for comparison the Pacific Ocean [from *Raitt and Shor*, 1959]. They complete the comparison started in the earlier paper [*Francis and Shor*, 1966]. One of the tentative conclusions drawn there was that the average subcrustal velocity in the northwest Indian

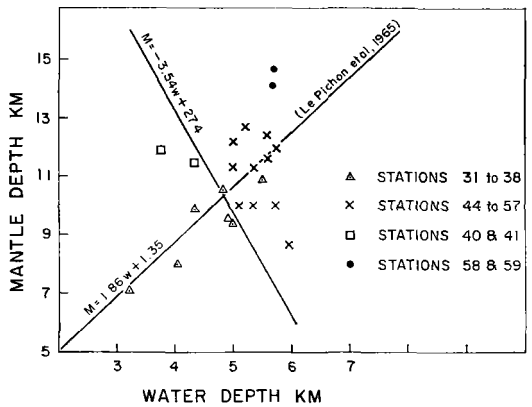


Fig. 5. Plot of depth to mantle against water depth.

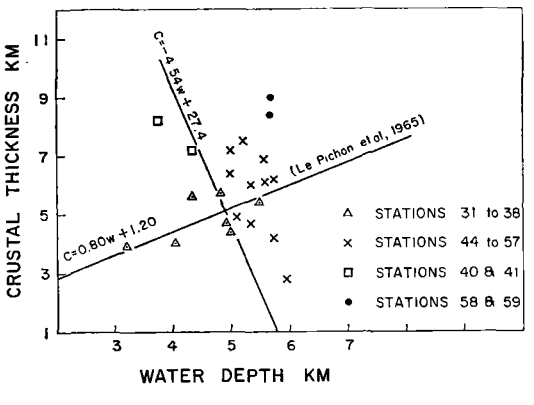


Fig. 6. Plot of thickness of crust (depth to mantle from the sea floor) against water depth.

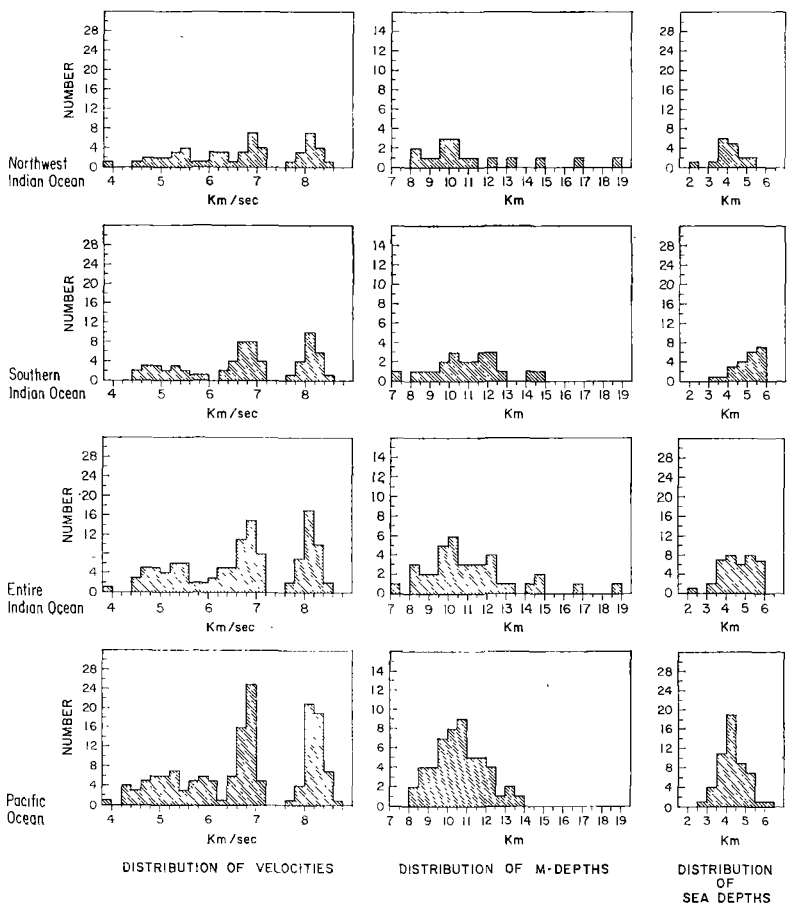


Fig. 7. Histograms of seismic velocity, mantle depth, and sea depth. From top to bottom, for the northwest Indian Ocean, the southern Indian Ocean (this paper), the entire Indian Ocean and the Pacific Ocean. Only stations at which the sea depth exceeds 2 km have been included.

Ocean (8.10 ± 0.19 km/sec standard deviation) was significantly less than the Pacific average (8.20 ± 0.18 km/sec standard deviation). The t distribution shows this with more than 95% confidence, but it was thought that the methods of selection of sites for seismic stations might invalidate the statistical approach. The results of this paper support the conclusion, however. The average mantle velocity for the southern Indian Ocean is 8.11 ± 0.17 km/sec standard deviation and for the whole Indian Ocean is 8.11 ± 0.18 km/sec standard deviation. The close agreement in mean mantle velocity for the two Indian Ocean areas makes the concept of a mean mantle velocity for the Indian Ocean more justifiable.

Appendix

Station 31 was a split profile in approximately 5 km of water. Good agreement between the two halves of the profile results in a typical oceanic section. The layer-2 velocity is assumed through the first observed point on each side; hence, the sediment thickness is poorly determined.

Station 32 was a split profile in just over 5 km of water, in the same basin as station 31. The topography was gentle but for a curious undulation on the outgoing leg. Typical oceanic profile.

Station 33. The receiving position of this station was only 100 nautical miles from the axis of the mid-ocean ridge (as depicted by *Heezen and Tharp* [1965]). Large variations of topography were encountered on the incoming leg, which was closest to the ridge crest. The direction of shooting made an angle of about 30° with the ridge axis. The similarity in apparent velocity between the first two observed lines on the eastern leg could be interpreted as due to a fault in a single refracting boundary. However, a two-layer interpretation is at least as likely and is in better agreement with the incoming profile. The low apparent velocity for the mantle on the western leg might be associated with proximity to the ridge crest, but it is much more likely to be a topographic effect, since the sea depth shoals toward the ridge end of this profile. The mean mantle velocity for the station is normal, as is the whole crustal structure.

Stations 34 and 35 form a split and a reversed profile approximately parallel to the ridge axis and about 180 nautical miles displaced from it. In spite of the proximity of the ridge, the bottom topography is gentle, perhaps because the trends run parallel to it. There is no significant difference between the two interpretations for station 34. The 3.60-km/sec velocity observed on the outgoing leg of station 34 is interpreted as the shear wave from the crustal layer. The ratio 6.55/3.60 = 1.82.

Station 36 was a split profile over undulating topography in the basin between the two branches of the mid-ocean ridge.

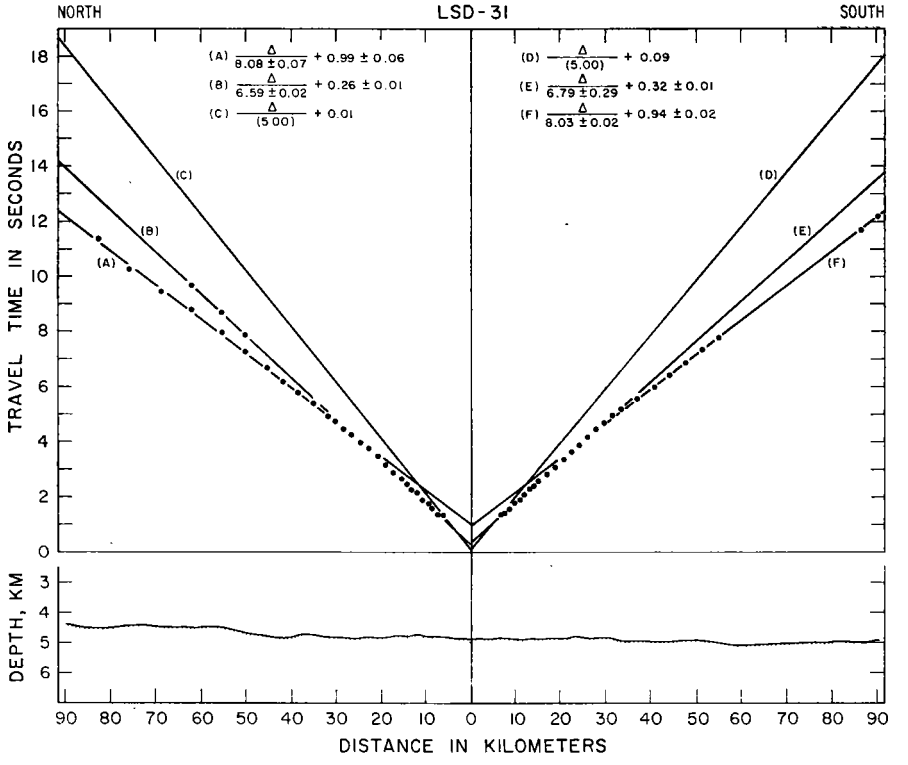
Station 37 was shot in about 4 km of water. The layer-2 velocity is assumed through the first observed point on each side. A normal sequence of velocities is found, but the mantle is unusually shallow.

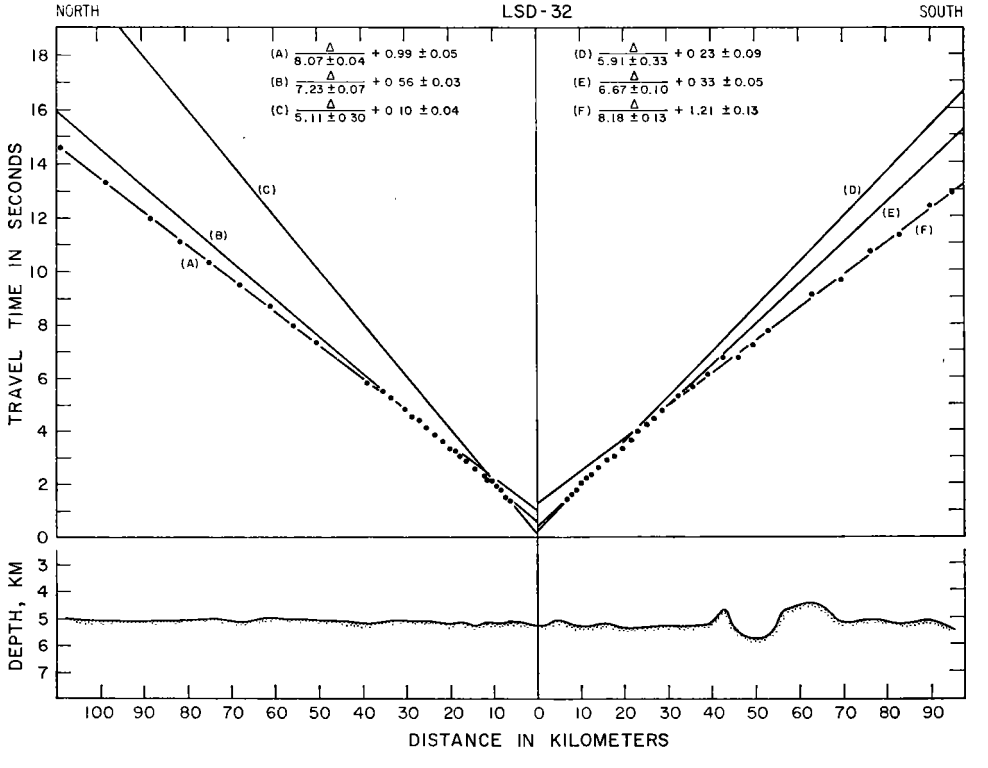
Station 38. This profile was shot over rough topography about 100 nautical miles northwest of Amsterdam Island. The travel time plots are remarkable. Mantle arrivals are observed at 11-km range on the northern and at 18-km range on the southern leg. This and the large variations of water depth make it impossible to determine the velocities and intercepts for shallower layers with much accuracy. A crustal velocity (6.71 km/sec) is observed only on the southern leg and has had to be assumed for the other leg. In spite of these difficulties the agreement between mantle intercepts is good, and the mantle is exceptionally shallow.

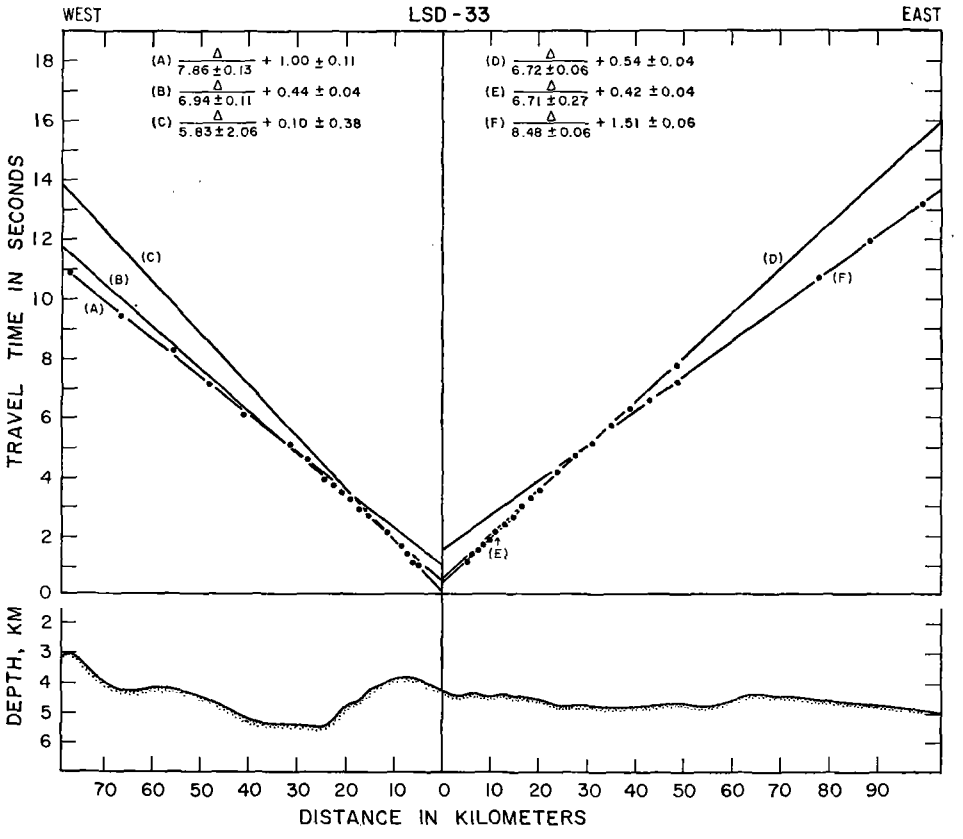
Station 39 was a split profile shot close to the axis of the mid-ocean ridge. Topographic variations along the line were minimized by shooting parallel to this axis. The mantle velocity is low.

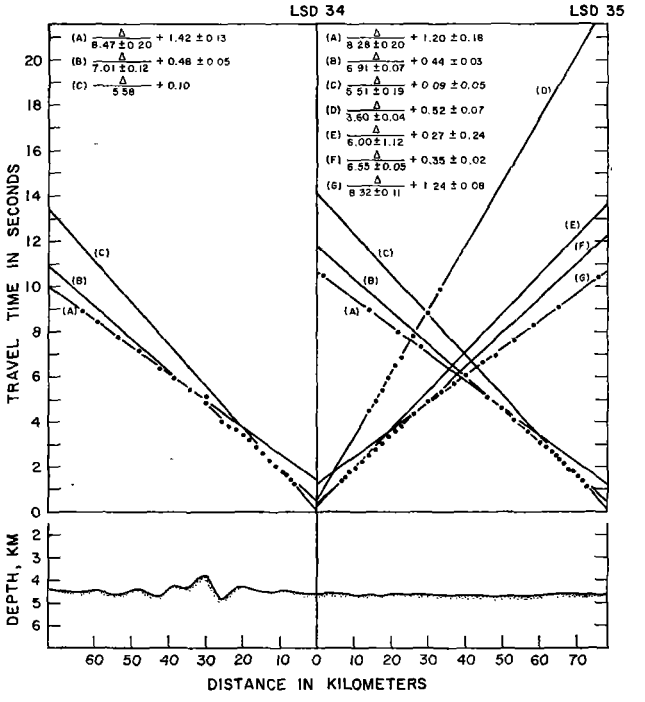
Station 40. The short incoming leg of this profile produced an anomalous velocity, probably because of sub-bottom topography. It has been ignored in the interpretation. The first three points of line B on the eastern leg are in fact sub-bottom reflections. They have been included because the slope of this line was obtained by drawing it through the first refracted point and tangential to the reflections. Line C is of rather dubious value; the three points could lie almost as well on line D.

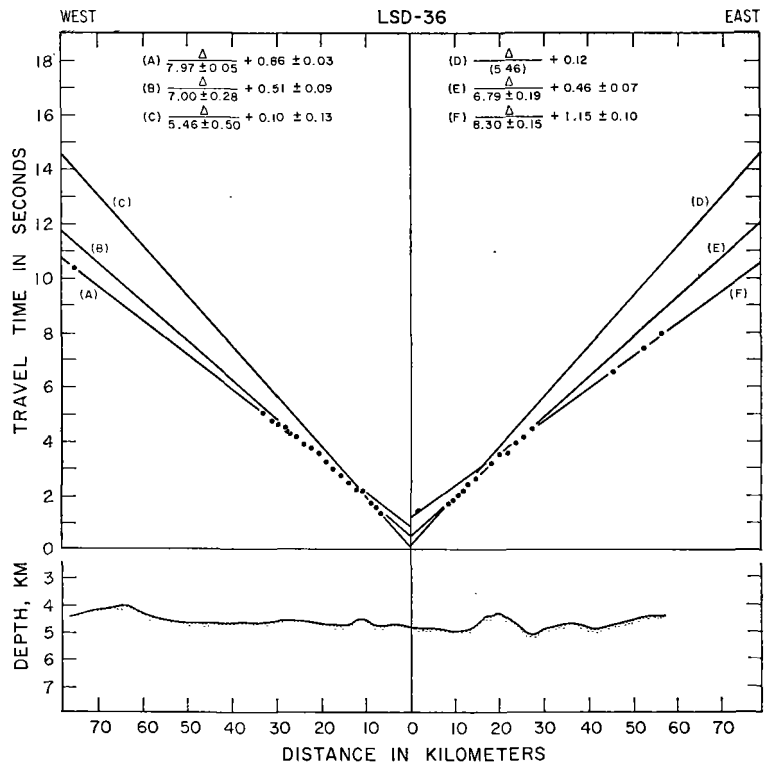
Station 41 was a split profile shot in the basin south of Broken ridge. The agreement between the intercepts from the two sides is good. The high velocity obtained for the second layer

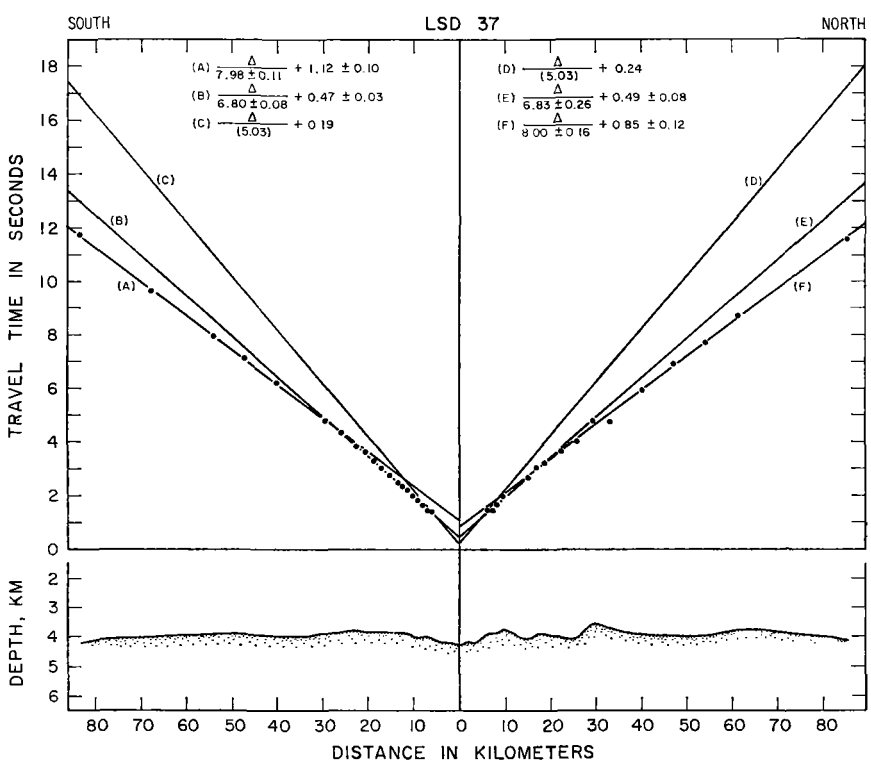

NORTH
LSD-31
SOUTH
(A) Δ/8.08 ±0.07 + 0.99 ± 0.06
(B) Δ/6.59 ±0.02 + 0.26 ± 0.01
(C) Δ/(5.00) + 0.01
(D) Δ/(5.00) + 0.09
(E) Δ/6.79 ±0.29 + 0.32 ± 0.01
(F) Δ/8.03 ±0.02 + 0.94 ± 0.02
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

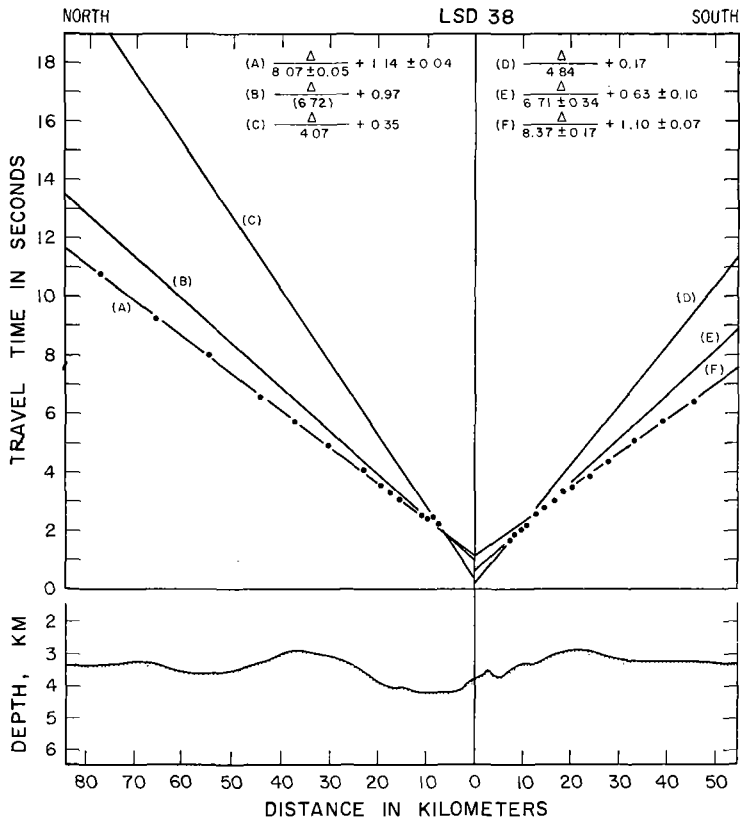

NORTH
LSD-32
SOUTH
(A) Δ/8.07 ±0.04 + 0.99 ± 0.05
(B) Δ/7.23 ±0.07 + 0.56 ± 0.03
(C) Δ/5.11 ±0.30 + 0.10 ± 0.04
(D) Δ/5.91 ±0.33 + 0.23 ± 0.09
(E) Δ/6.67 ±0.10 + 0.33 ± 0.05
(F) Δ/8.18 ±0.13 + 1.21 ± 0.13
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

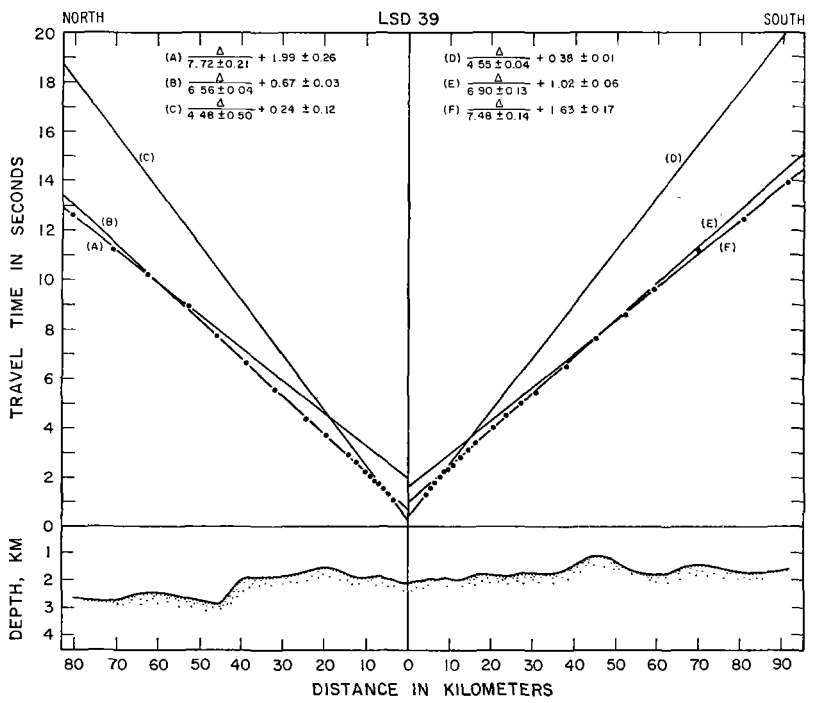

WEST
LSD - 33
EAST
(A) Δ/7.86±0.13 + 1.00 ± 0.11
(B) Δ/6.94±0.11 + 0.44 ± 0.04
(C) Δ/5.83±2.06 + 0.10 ± 0.38
(D) Δ/6.72±0.06 + 0.54 ± 0.04
(E) Δ/6.71±0.27 + 0.42 ± 0.04
(F) Δ/8.48±0.06 + 1.51 ± 0.06
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

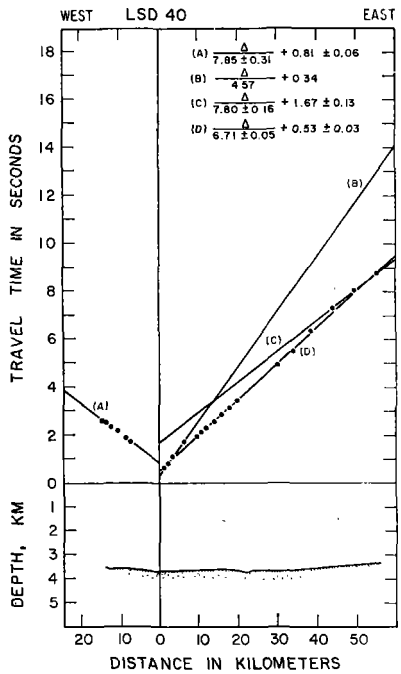

LSD 34
LSD 35
(A) Δ/8.47±0.20 + 1.42 ± 0.13
(B) Δ/7.01±0.12 + 0.48 ± 0.05
(C) Δ/5.58 + 0.10
(A) Δ/8.28±0.20 + 1.20 ± 0.18
(B) Δ/6.91±0.07 + 0.44 ± 0.03
(C) Δ/5.51±0.19 + 0.09 ± 0.05
(D) Δ/3.60±0.04 + 0.52 ± 0.07
(E) Δ/6.00±1.12 + 0.27 ± 0.24
(F) Δ/6.55±0.05 + 0.35 ± 0.02
(G) Δ/8.32±0.11 + 1.24 ± 0.08
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

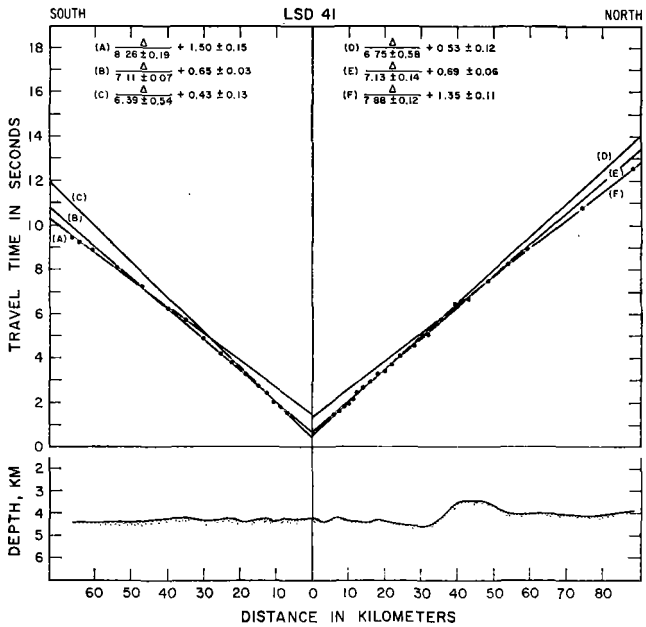

WEST
LSD-36
EAST
(A) Δ/7.97±0.05 + 0.86 ±0.03
(B) Δ/7.00±0.28 + 0.51 ±0.09
(C) Δ/5.46±0.50 + 0.10 ±0.13
(D) Δ/(5.46) + 0.12
(E) Δ/6.79±0.19 + 0.46 ±0.07
(F) Δ/8.30±0.15 + 1.15 ±0.10
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

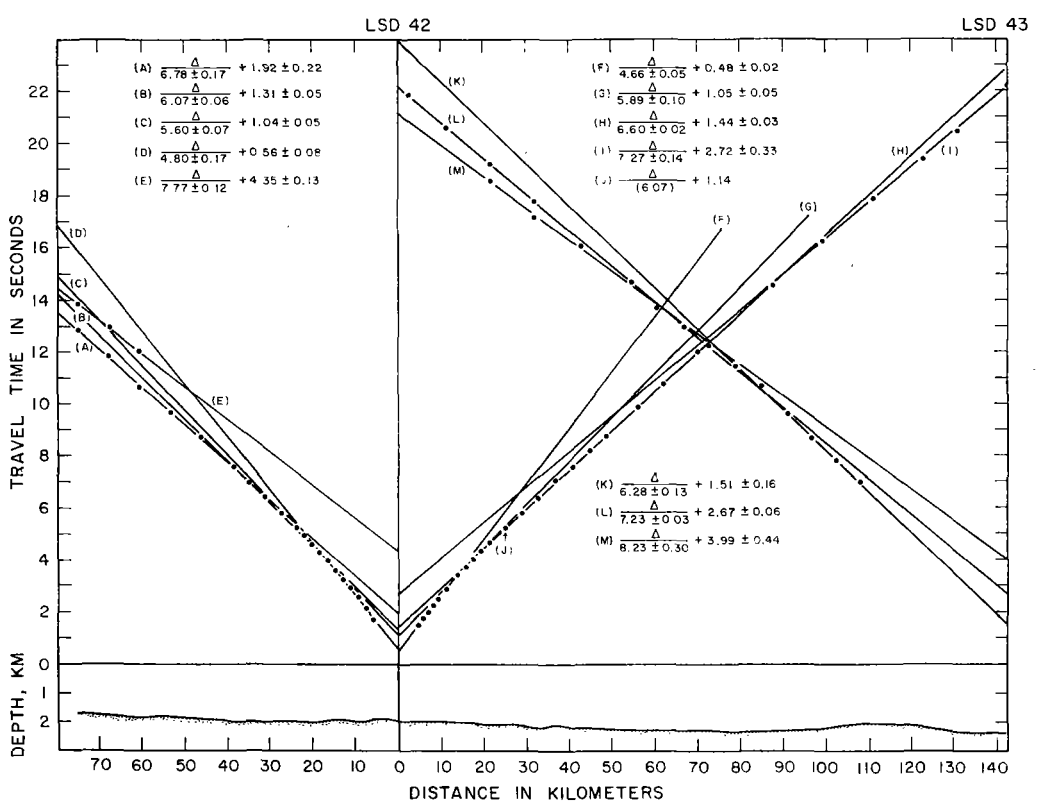

SOUTH
LSD 37
NORTH
(A) Δ/7.98±0.11 + 1.12 ±0.10
(B) Δ/6.80±0.08 + 0.47 ±0.03
(C) Δ/(5.03) + 0.19
(D) Δ/(5.03) + 0.24
(E) Δ/6.83±0.25 + 0.49 ±0.08
(F) Δ/8.00±0.16 + 0.85 ±0.12
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

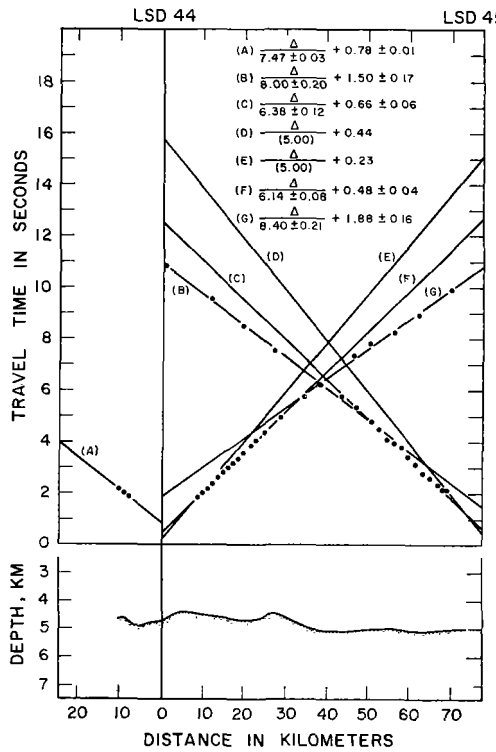

NORTH
LSD 38
SOUTH
(A) Δ/8.07±0.05 + 1.14 ±0.04
(B) Δ/(6.72) + 0.97
(C) Δ/4.07 + 0.35
(D) Δ/4.84 + 0.17
(E) Δ/6.71±0.34 + 0.63 ±0.10
(F) Δ/8.37±0.17 + 1.10 ±0.07
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

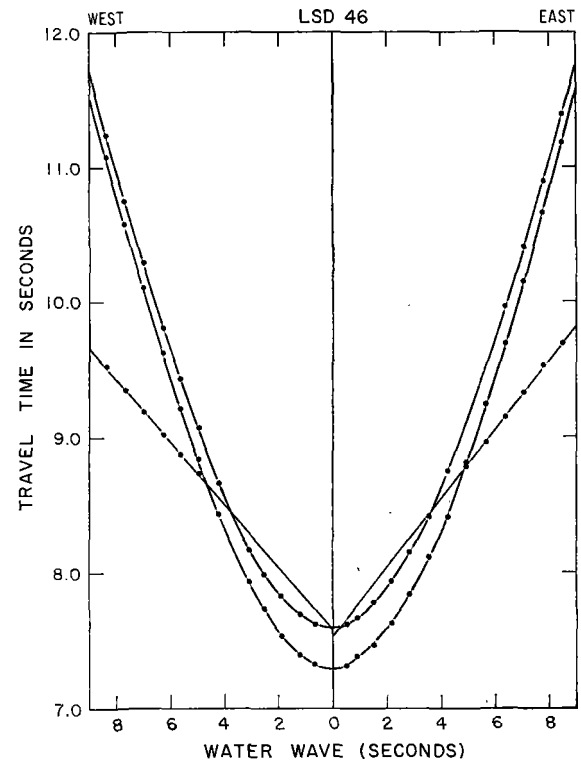

NORTH
LSD 39
SOUTH
(A) Δ/7.72±0.21 + 1.99 ±0.26
(B) Δ/6.56±0.04 + 0.67 ±0.03
(C) Δ/4.48±0.50 + 0.24 ±0.12
(D) Δ/4.55±0.04 + 0.38 ±0.01
(E) Δ/6.90±0.13 + 1.02 ±0.06
(F) Δ/7.48±0.14 + 1.63 ±0.17
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

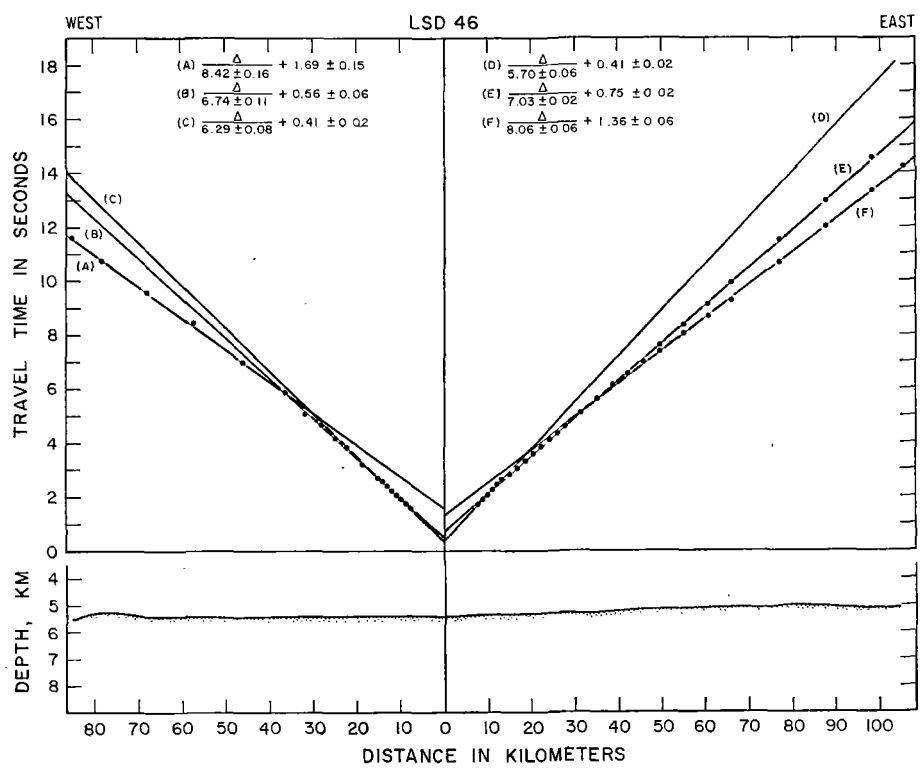

WEST
LSD 40
EAST
(A) Δ/7.85 ± 0.31 + 0.81 ± 0.06
(B) Δ/4.57 + 0.34
(C) Δ/7.80 ± 0.16 + 1.67 ± 0.13
(D) Δ/6.71 ± 0.05 + 0.53 ± 0.03
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

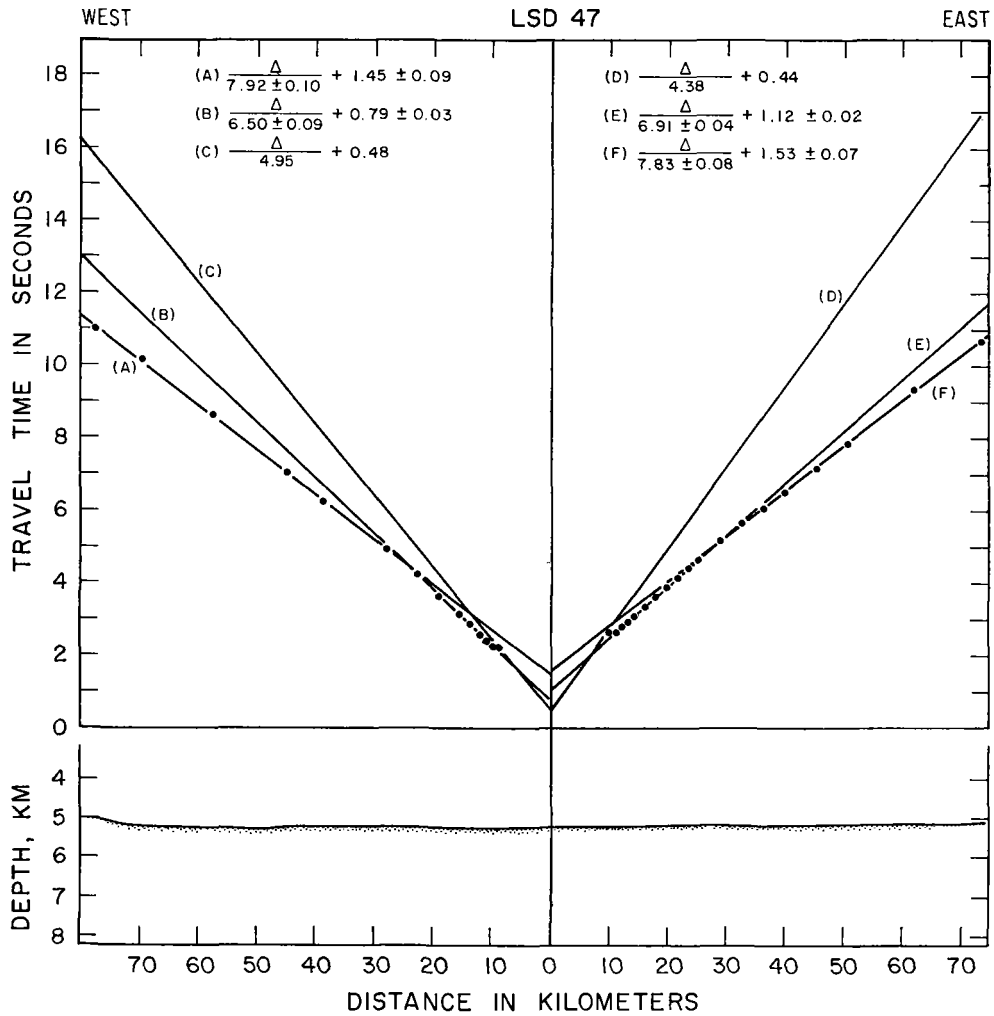

SOUTH
LSD 41
NORTH
(A) Δ/8.26 ± 0.19 + 1.50 ± 0.15
(B) Δ/7.11 ± 0.07 + 0.65 ± 0.03
(C) Δ/6.39 ± 0.54 + 0.43 ± 0.13
(D) Δ/6.75 ± 0.58 + 0.53 ± 0.12
(E) Δ/7.13 ± 0.14 + 0.69 ± 0.06
(F) Δ/7.86 ± 0.12 + 1.35 ± 0.11
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

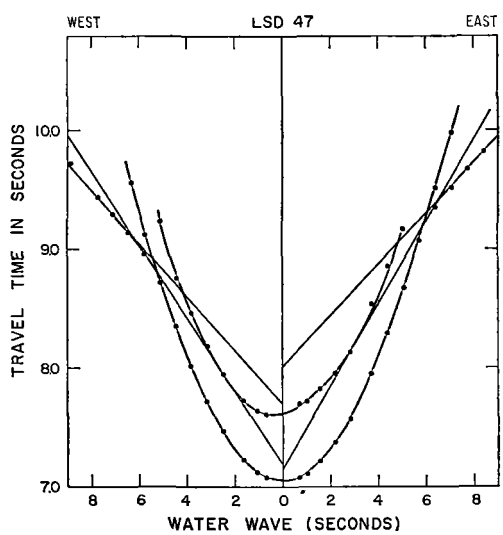

LSD 42
LSD 43
(A) Δ/6.78 ± 0.17 + 1.92 ± 0.22
(B) Δ/6.07 ± 0.06 + 1.31 ± 0.05
(C) Δ/5.60 ± 0.07 + 1.04 ± 0.05
(D) Δ/4.80 ± 0.17 + 0.56 ± 0.08
(E) Δ/7.77 ± 0.12 + 4.35 ± 0.13
(F) Δ/4.66 ± 0.05 + 0.48 ± 0.02
(G) Δ/5.89 ± 0.10 + 1.05 ± 0.05
(H) Δ/6.60 ± 0.02 + 1.44 ± 0.03
(I) Δ/7.27 ± 0.14 + 2.72 ± 0.33
(J) Δ/(6.07) + 1.14
(K) Δ/6.28 ± 0.13 + 1.51 ± 0.16
(L) Δ/7.23 ± 0.03 + 2.67 ± 0.06
(M) Δ/8.23 ± 0.30 + 3.99 ± 0.44
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

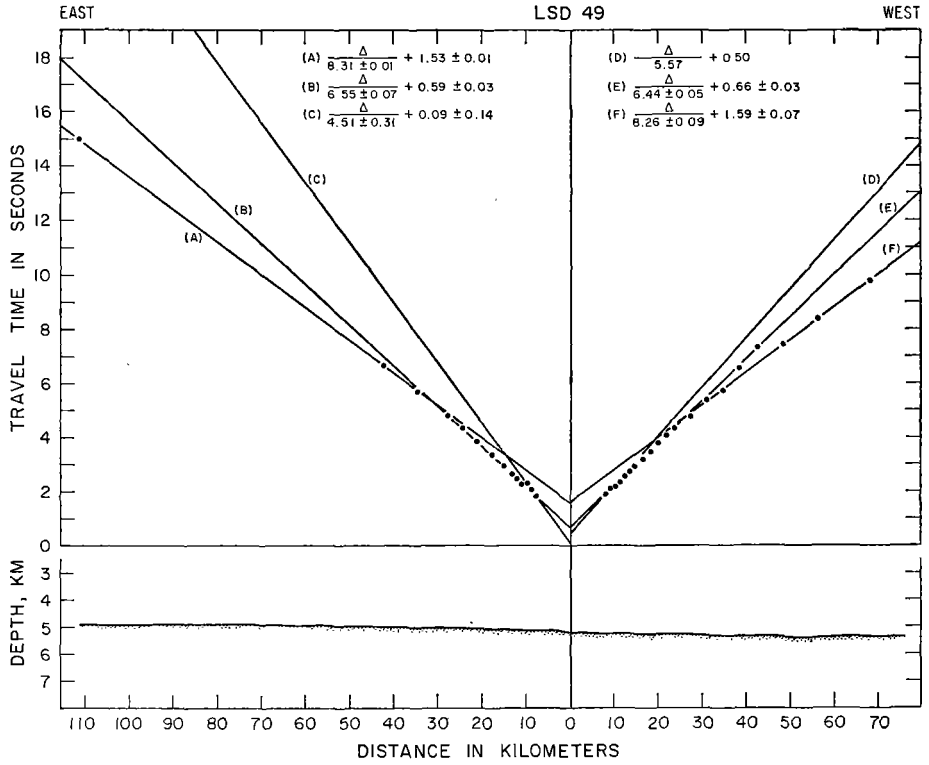

LSD 44
LSD 45
(A) Δ/7.47 ±0.03 + 0.78 ±0.01
(B) Δ/8.00 ±0.20 + 1.50 ±0.17
(C) Δ/6.38 ±0.12 + 0.66 ±0.06
(D) Δ/(5.00) + 0.44
(E) Δ/(5.00) + 0.23
(F) Δ/6.14 ±0.08 + 0.48 ±0.04
(G) Δ/8.40 ±0.21 + 1.88 ±0.16
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

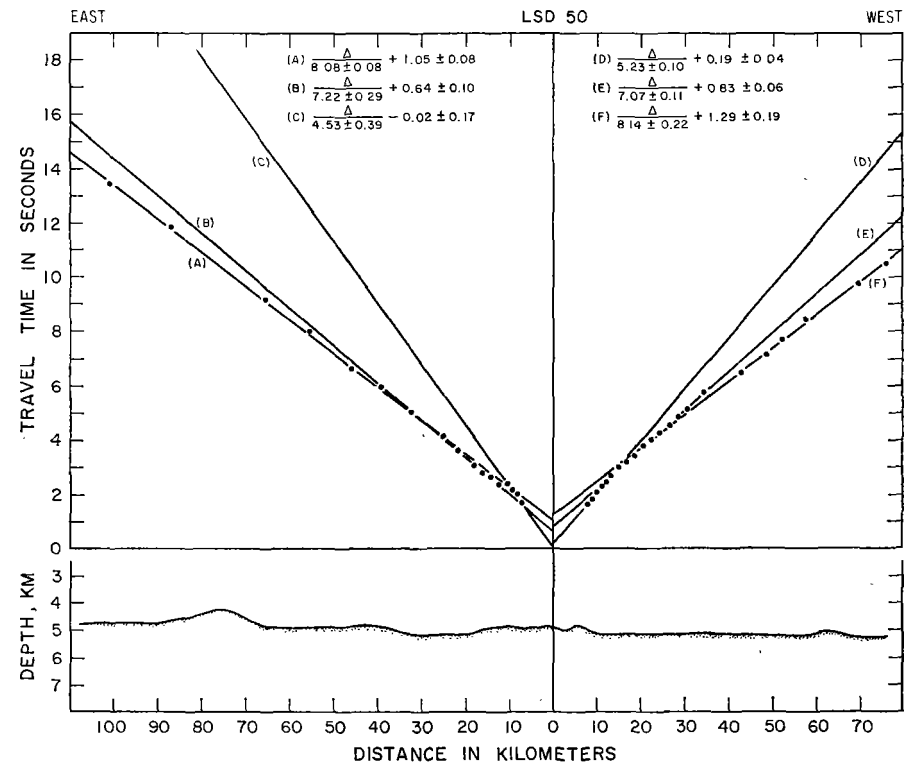

WEST
LSD 46
EAST
TRAVEL TIME IN SECONDS
WATER WAVE (SECONDS)

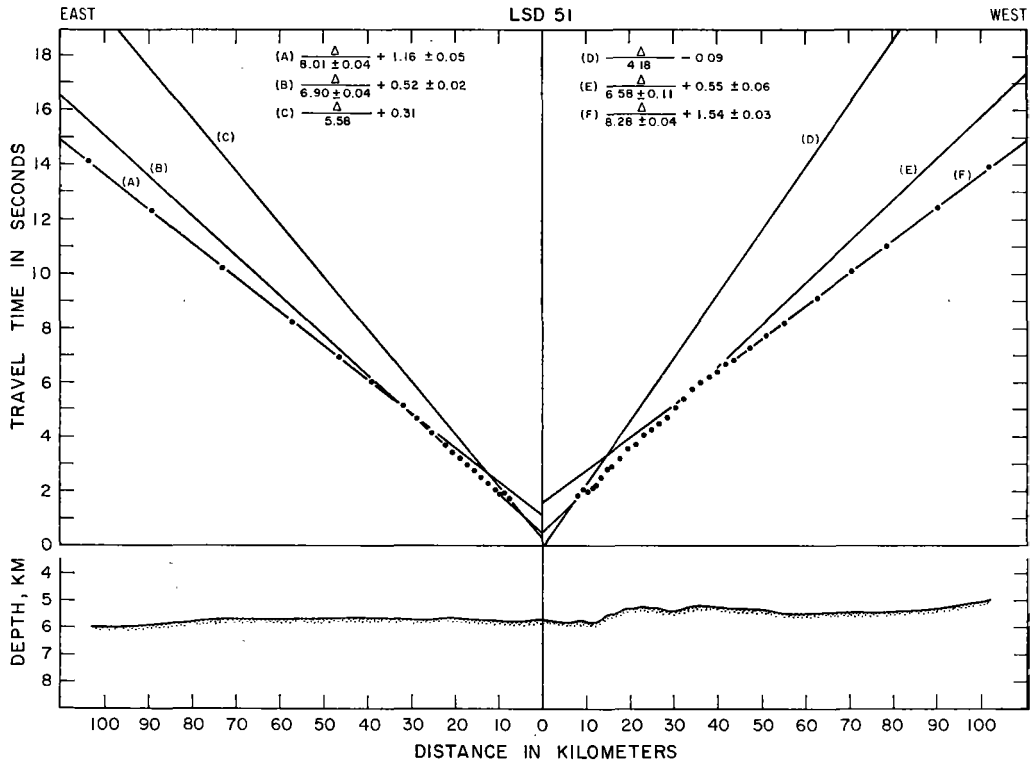

WEST
LSD 46
EAST
(A) Δ/8.42 ±0.16 + 1.69 ±0.15
(B) Δ/6.74 ±0.11 + 0.56 ±0.06
(C) Δ/6.29 ±0.08 + 0.41 ±0.02
(D) Δ/5.70 ±0.06 + 0.41 ±0.02
(E) Δ/7.03 ±0.02 + 0.75 ±0.02
(F) Δ/8.06 ±0.06 + 1.36 ±0.06
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

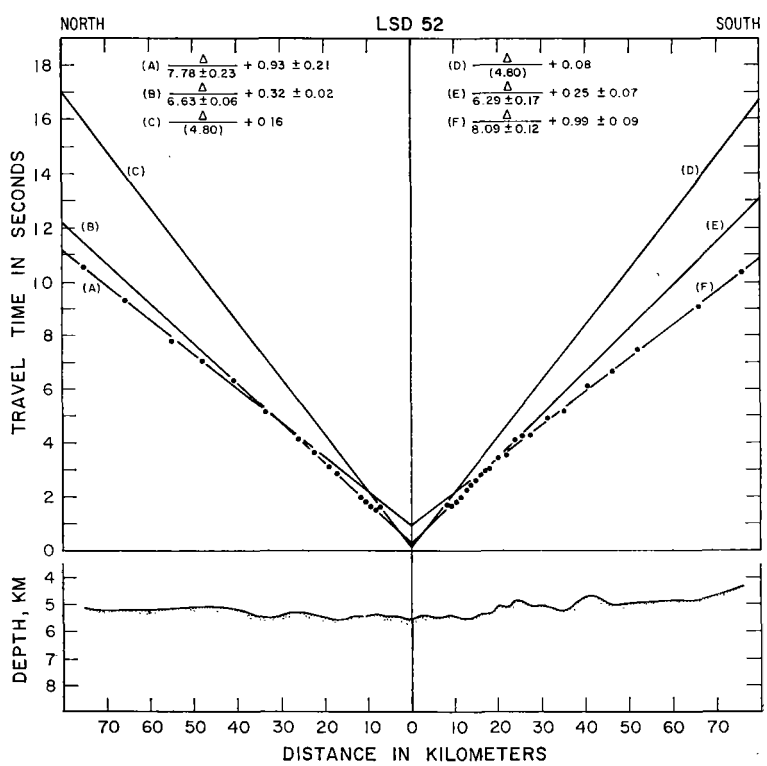

WEST
LSD 47
EAST
(A) Δ/7.92±0.10 + 1.45 ±0.09
(B) Δ/6.50±0.09 + 0.79 ±0.03
(C) Δ/4.95 + 0.48
(D) Δ/4.38 + 0.44
(E) Δ/6.91±0.04 + 1.12 ±0.02
(F) Δ/7.83±0.08 + 1.53 ±0.07
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

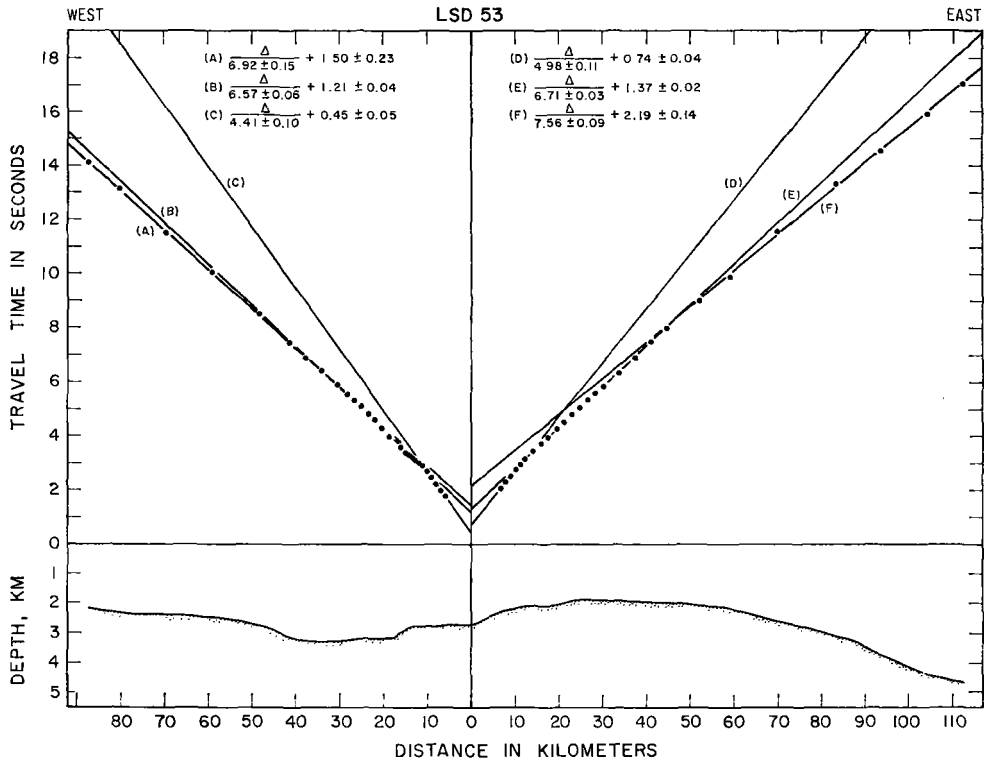

WEST
LSD 47
EAST
TRAVEL TIME IN SECONDS
WATER WAVE (SECONDS)

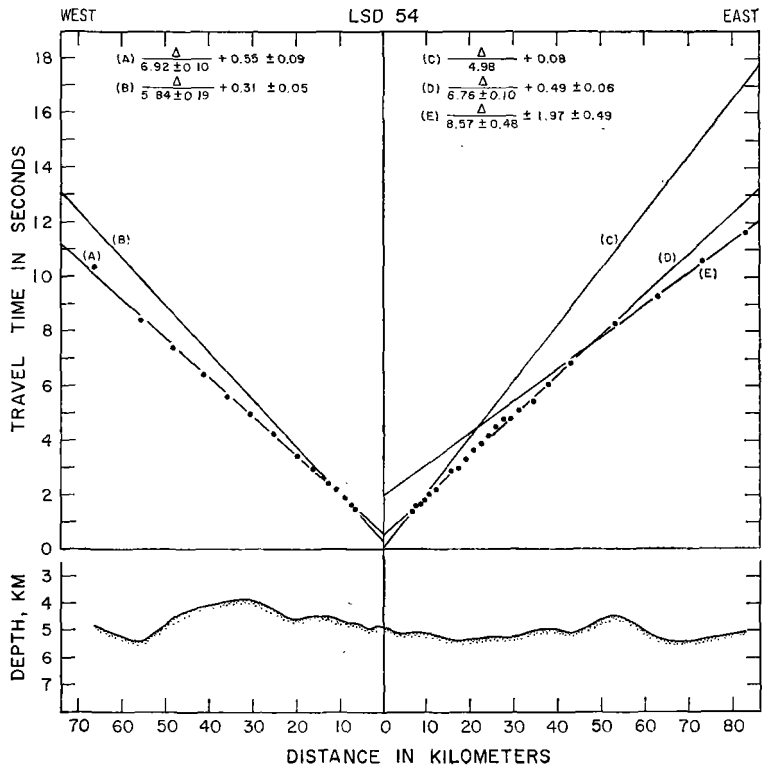

EAST
LSD 49
WEST
(A) Δ/8.31 ±0.01 + 1.53 ±0.01
(B) Δ/6.55 ±0.07 + 0.59 ±0.03
(C) Δ/4.51 ±0.31 + 0.09 ±0.14
(D) Δ/5.57 + 0.50
(E) Δ/6.44 ±0.05 + 0.66 ±0.03
(F) Δ/8.26 ±0.09 + 1.59 ±0.07
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

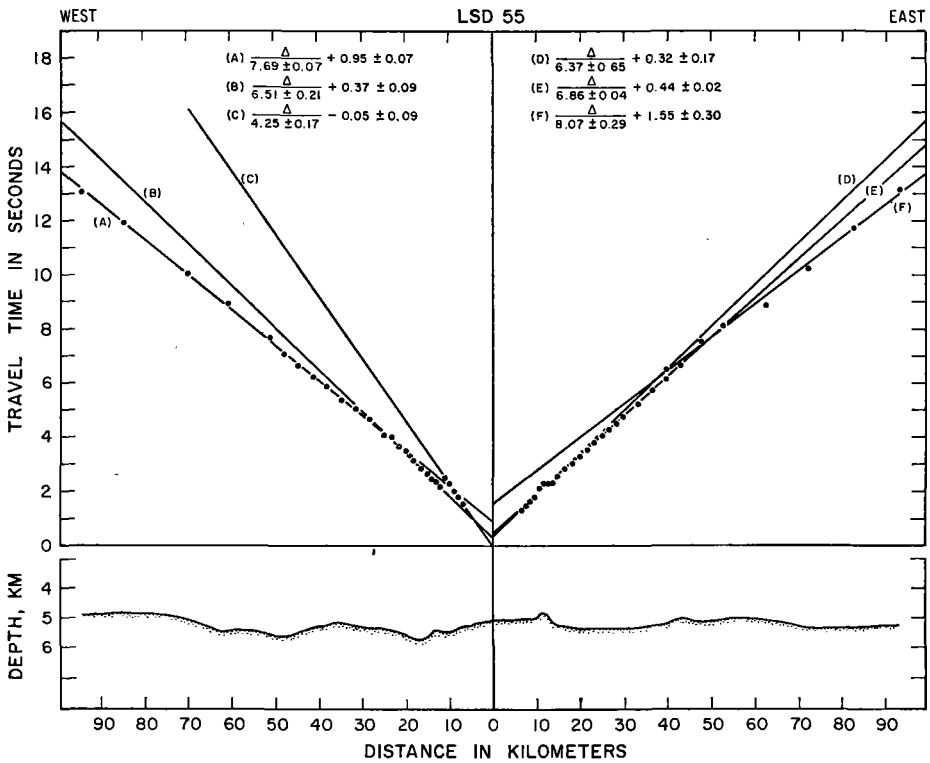

EAST
LSD 50
WEST
(A) Δ/8.08 ±0.08 + 1.05 ±0.08
(B) Δ/7.22 ±0.29 + 0.64 ±0.10
(C) Δ/4.53 ±0.39 − 0.02 ±0.17
(D) Δ/5.23 ±0.10 + 0.19 ±0.04
(E) Δ/7.07 ±0.11 + 0.83 ±0.06
(F) Δ/8.14 ±0.22 + 1.29 ±0.19
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

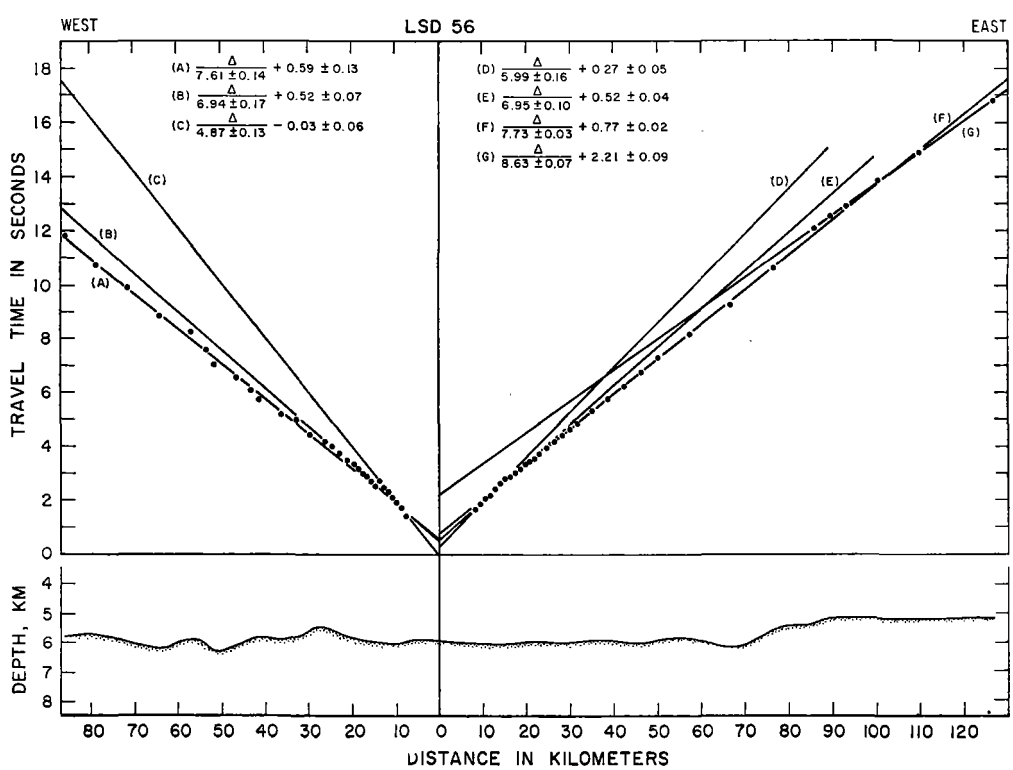

EAST
LSD 51
WEST
(A) Δ/8.01 ±0.04 + 1.16 ±0.05
(B) Δ/6.90 ±0.04 + 0.52 ±0.02
(C) Δ/5.58 + 0.31
(D) Δ/4.18 − 0.09
(E) Δ/6.58 ±0.11 + 0.55 ±0.06
(F) Δ/8.28 ±0.04 + 1.54 ±0.03
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

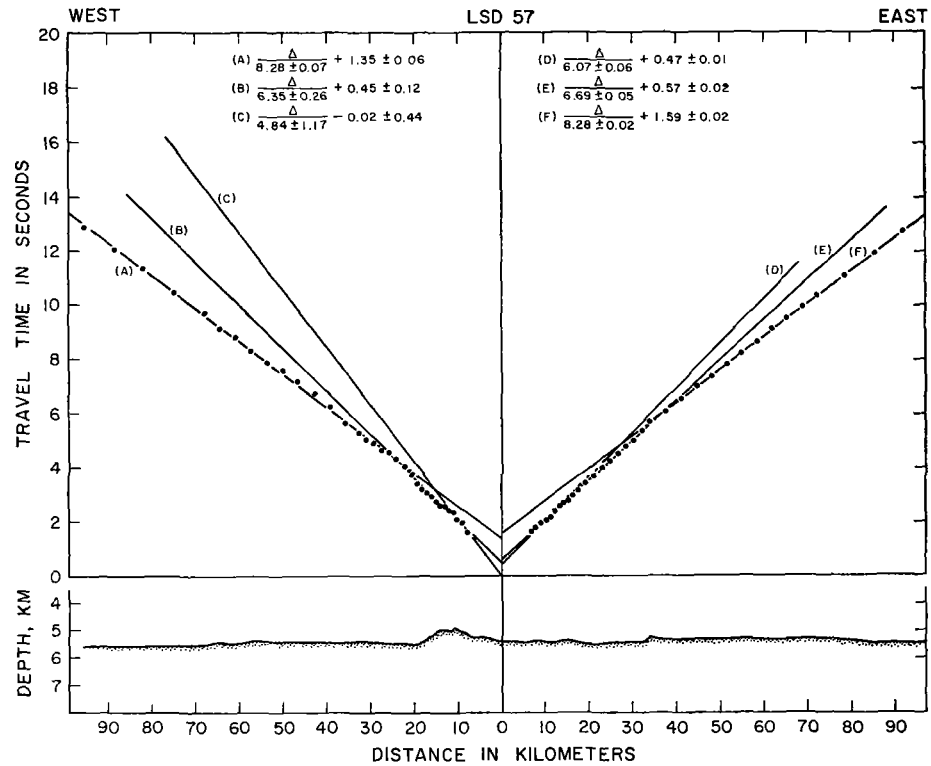

NORTH
LSD 52
SOUTH
(A) Δ/7.78 ±0.23 + 0.93 ±0.21
(B) Δ/6.63 ±0.06 + 0.32 ±0.02
(C) Δ/(4.80) + 0.16
(D) Δ/(4.80) + 0.08
(E) Δ/6.29 ±0.17 + 0.25 ±0.07
(F) Δ/8.09 ±0.12 + 0.99 ±0.09
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

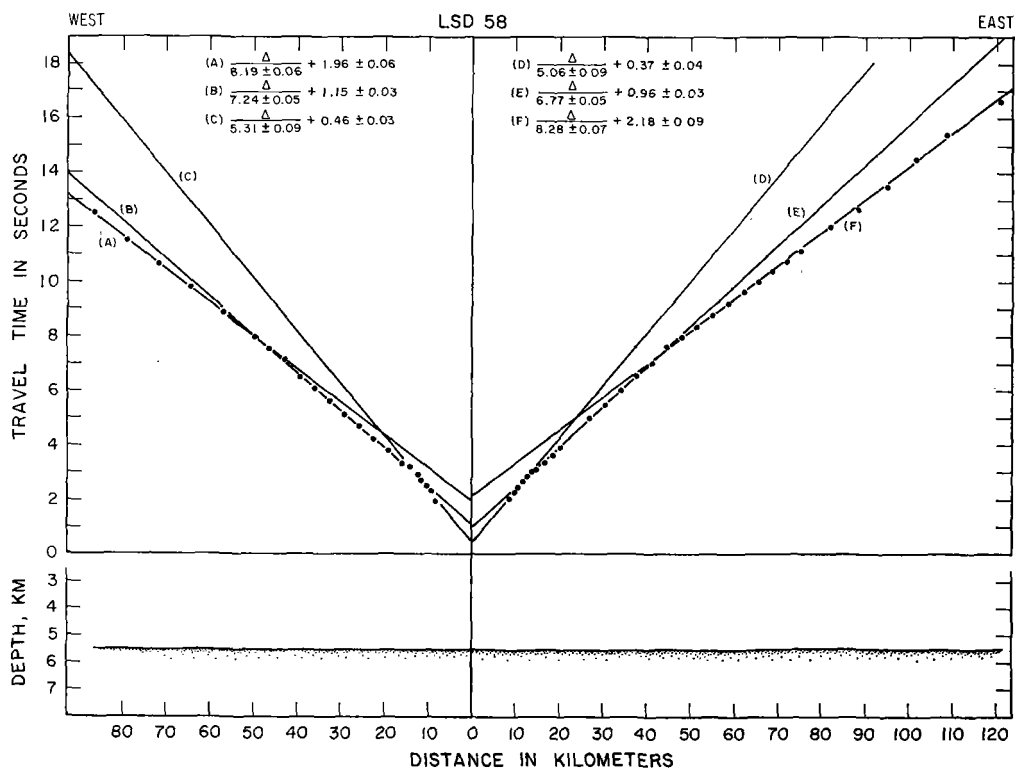

LSD 53
WEST
EAST
(A) Δ/6.92±0.15 + 1.50 ± 0.23
(B) Δ/6.57±0.06 + 1.21 ± 0.04
(C) Δ/4.41±0.10 + 0.45 ± 0.05
(D) Δ/4.98±0.11 + 0.74 ± 0.04
(E) Δ/6.71±0.03 + 1.37 ± 0.02
(F) Δ/7.56±0.09 + 2.19 ± 0.14
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS

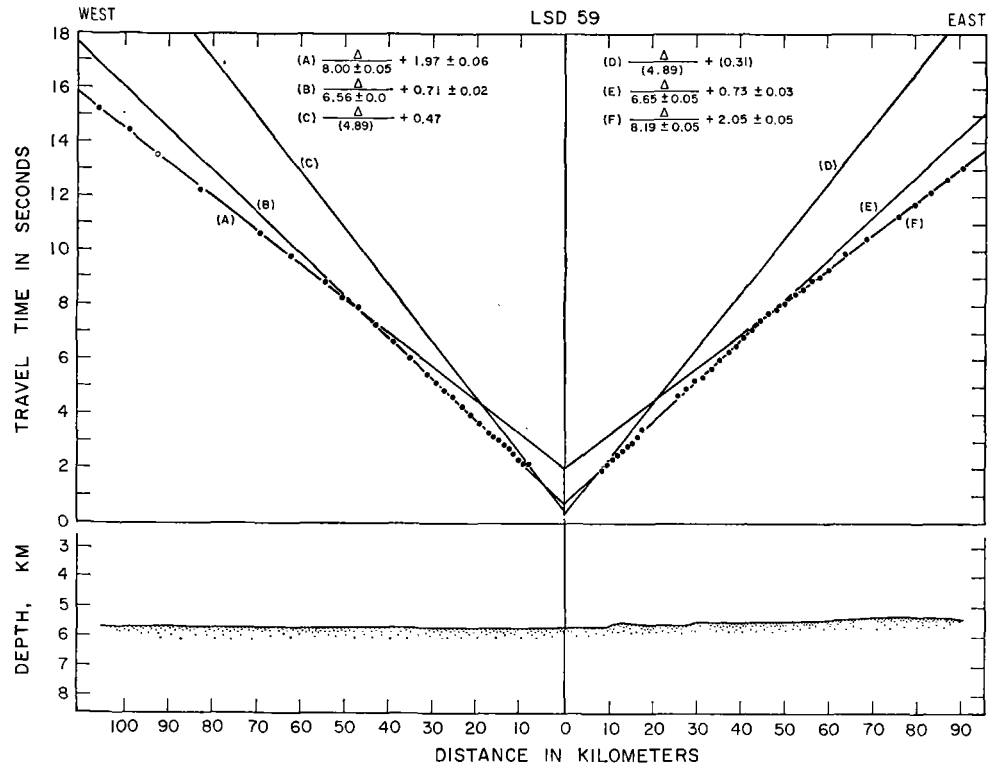

LSD 54
WEST
EAST
(A) Δ/6.92±0.10 + 0.55 ± 0.09
(B) Δ/5.84±0.19 + 0.31 ± 0.05
(C) Δ/4.98 + 0.08
(D) Δ/6.76±0.10 + 0.49 ± 0.06
(E) Δ/8.57±0.48 ± 1.97 ± 0.49
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS


WEST
LSD 55
EAST
(A) Δ/7.69 ±0.07 + 0.95 ±0.07
(B) Δ/6.51 ± 0.21 + 0.37 ±0.09
(C) Δ/4.25 ±0.17 − 0.05 ±0.09
(D) Δ/6.37 ±0 65 + 0.32 ±0.17
(E) Δ/6.86 ±0 04 + 0.44 ±0.02
(F) Δ/8.07 ±0.29 + 1.55 ±0.30
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS


WEST
LSD 56
EAST
(A) Δ/7.61 ±0.14 + 0.59 ±0.13
(B) Δ/6.94 ±0.17 + 0.52 ±0.07
(C) Δ/4.87 ±0.13 − 0.03 ±0.06
(D) Δ/5.99 ±0.16 + 0.27 ±0 05
(E) Δ/6.95 ±0.10 + 0.52 ±0.04
(F) Δ/7.73 ±0.03 + 0.77 ±0.02
(G) Δ/8.63 ±0.07 + 2.21 ±0.09
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS


WEST
LSD 57
EAST
(A) Δ/8.28 ±0.07 + 1.35 ±0.06
(B) Δ/6.35 ±0.26 + 0.45 ±0.12
(C) Δ/4.84 ±1.17 − 0.02 ±0.44
(D) Δ/6.07 ±0.06 + 0.47 ±0.01
(E) Δ/6.69 ±0.05 + 0.57 ±0.02
(F) Δ/8.28 ±0.02 + 1.59 ±0.02
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS


WEST
LSD 58
EAST
(A) Δ/8.19 ±0.06 + 1.96 ±0.06
(B) Δ/7.24 ±0.05 + 1.15 ±0.03
(C) Δ/5.31 ±0.09 + 0.46 ±0.03
(D) Δ/5.06 ±0.09 + 0.37 ±0.04
(E) Δ/6.77 ±0.05 + 0.96 ±0.03
(F) Δ/8.28 ±0.07 + 2.18 ±0.09
TRAVEL TIME IN SECONDS
DEPTH, KM
DISTANCE IN KILOMETERS



might be a topographic effect, since the thickness of the sedimentary layer is excessive for an area completely isolated from terrigenous deposition.

Stations 42 and 43 form a split and a reversed profile over Broken ridge. Water depth was approximately 2 km and the bottom sloped gently eastward along the line of shooting. The interpretation is rather complex. First consider the reversed profile 42 *out* and 43. Shooting on 43 stopped at about 35-km range from the receiving position. Hence the superficial velocities and intercepts for this leg were taken from the split profile 42 *in* and *out*. The following lines were thus assumed: $t = (\Delta/2.15) + 0.0$, $t = (\Delta/4.73) + 0.52$, $t = (\Delta/5.74) + 1.05$, and $t = \Delta/6.07 + 1.28$. The 6.07-km/sec velocity had also to be assumed, and no mantle velocity was observed on 42 *out*. Because of this lack of detail the solution given in Table 1 is the average for the profile. Station 42 *in* presents an enigma. Shooting was carried out only to 75-km range, and thus no 7.2-km/sec velocity could be observed. Mantle arrivals were observed as second arrivals, however, with a velocity of 7.8 km/sec from a range of about 60 km. If the 7.2-km/sec layer, well established on both 42 *out* and 43, is assumed for 42 *in*, the range at which refracted arrivals from the mantle can first appear is about 106 km. With only a 6.8-km/sec crustal layer present, however, this critical range becomes about 63 km. Thus if the 7.8-km/sec line is the result of refracted arrivals from the mantle, no 7.2-km/sec layer can exist beneath 42 *in*.

Stations 44 and 45 form a reversed profile in about 5 km of water just off the eastern flank for Broken ridge. A layer-2 velocity has had to be assumed, and no normal crustal velocity of about 6.8 km/sec is observed. If the 6.8-km/sec velocity is present but masked, the mantle can at most be 0.3 km deeper than in the interpretation shown. The three refracted arrivals on 44 *in* are not considered significant enough to include in the interpretation.

Station 46 was a split profile shot over gently undulating topography in about 5.5 km of water. Excellent sub-bottom reflections were readable to more than 30 km each side of the receiving ship, owing to the poor reflectivity of

the bottom and the acoustical transparency of the sediment layer above the reflector. The sub-bottom reflections were noticeably stronger than the bottom ones on both the low frequency (about 10 cps) and the intermediate frequency (about 50 cps) channels. The P. D. R. record also indicated the low reflectivity of the sea floor. The first observed refracted arrivals came from a layer deeper than that giving the reflections. The interval velocity determined from the reflections, 1.61 km/sec, has a standard error of only 0.04 km/sec, much smaller than is usual for this type of measurement.

Station 47 was a split profile shot over smooth topography in 5.3 km of water. Good sub-bottom reflections were observed, giving an interval velocity of 1.40 ± 0.27 km/sec. The layer-2 velocities, 4.95 and 4.38 km/sec, were obtained by passing a line through the first observed point on each side tangential to the sub-bottom reflection curve. Hence the mean velocity of 4.66 km/sec.

Station 49 was a split profile shot in just over 5 km of water near the foot of the continental slope. In spite of the smoothly sedimented bottom sloping gently seaward, both the sub-bottom reflections and the first observed refracted arrivals showed the subsediment surface to be quite rough. On each side the first observed refracted line was tangential to the sub-bottom reflection curve, but the latter was not consistent enough to yield a sensible interval velocity for the sediment. The only conclusion to be drawn from the reflections is that the sediment thickness varied from about 0.3 km on the eastern side to about 0.45 km on the western side of the receiving position. The intercepts of the crustal and mantle velocities agreed well from one side to another in spite of these superficial differences.

Station 50 was a split profile shot over gently undulating topography in about 5 km of water.

Station 51 was a split profile in 5 to 6 km of water.

Station 52 was shot parallel to the Ninetyeast ridge at the foot of its eastern slopes. Sub-bottom reflections show that the sediment cover is thin, about 0.1 km, but they are insufficient to give a sedimentary velocity. Good agreement is found between the intercepts from each side.

Station 53. This profile was shot over the crest of the Ninetyeast ridge. The widely varying topography presented difficulties. In particular the 7.56-km/sec velocity observed on the outgoing run is radically affected by the topography. The seven shots forming this line were fired in water depths ranging from 2.1 to 4.8 km. Thus the velocity on the water-corrected plot is almost certainly too great, because the deeper the sea floor is the earlier the arrival will be (when the water correction has been made). A topographic correction was made assuming a uniform cover of sediment and the 4.98/6.71-km/sec boundary to be horizontal. This produces a velocity of 7.22 km/sec and an intercept of 1.76 sec—in much closer agreement with the 1.50-sec intercept observed for the equivalent line on the opposite side. These topographically corrected values were used in the average solution. Further topographic corrections were not attempted because of the assumptions involved.

Station 54. A split profile normal to the structure of the ridge over rugged topography to the east. The intercepts of the crustal velocities agree well for the two halves, but a mantle velocity was observed only on the eastern half. The three points on this line hardly determine the velocity well, and a better estimate of depth to mantle probably comes from an 8.1-km/sec line through their center of gravity, which gives an intercept of 1.47 sec. This is computed assuming the average structure for the station above. The minimum intercept, an 8.1-km/sec line, could have on the western side without being observed is 1.94 sec. Thus the mantle is probably at least 3 km deeper on the western than on the eastern side. The mantle shallowing eastward is also suggested by the high apparent velocity on the eastern leg.

Station 55 was another split profile normal to the structure of the ridge in the basin to the east. The layer-2 velocity and sediment thickness are poorly determined. The crustal layer velocity is, however, well determined, with good agreement of the intercepts for incoming and outgoing legs. Unusually large residuals on the mantle lines may indicate large variations in depth to the mantle, since they are larger than the residuals found for shallower layers (except over the small seamount). The 7.69-km/sec line on the western leg is probably bogus. 8.07-km/sec lines forced through the innermost five

and outermost seven points fit quite well with intercepts 1.43 and 1.14 sec, respectively. The mantle depth for the station has been computed with the intercept 1.49 sec, the mean of 1.43 and 1.55 sec.

Station 56 was shot in about 6 km of water southwest of the Cocos Islands. The travel-time plot is remarkable for a deep ocean basin. Apparent velocities of 7.61 and 7.73 km/sec are found for most of the range of each leg. They establish a 7.67-km/sec layer only 2.8 km below the sea floor beneath an unusually thin crustal layer. If the 8.63-km/sec velocity observed on the eastern leg represents the true mantle, it lies at 20.7 km below sea level. If, however, its velocity is the result of local dip, a better estimate of mantle depth for the line is obtained by assuming a velocity of 8.1 km/sec through the center of gravity of the 8.63-km/sec points. This gives an intercept of 1.45 sec and a depth to the 8.1 km/sec layer of 16.6 km. An alternative interpretation is that the 8.63-km/sec velocity is entirely fortuitous and that the points in fact lie on the 7.73-km/sec line. This implies that larger residuals appear on the 7.73-km/sec line than appear earlier, but they are no larger than the residuals for the 7.61-km/sec line on the other side. A point in favor of drawing a separate line through the last six points is the unusually large amplitude of the first arrival at approximately 84 km. This is perhaps because it is close to the range for a critical angle reflection from the boundary giving the 8.63-km/sec velocity. Yet another interpretation, though an improbable one, is that the mantle has normal velocity throughout but changes depth radically along the line. A shallow mantle beneath the receiving position dipping down at between 5° and 7° would give apparent velocities of about 7.7 km/sec. On the eastern leg, the mantle must change its dip at about the halfway mark to slope up toward the end of the line at about 5°. In conclusion, it can be stated with certainty that a velocity of at least 7.67 km/sec is close to the sea floor beneath station 56. This velocity is possibly bounded by a more normal mantle velocity at about 17 km below sea level.

Station 57 was a split profile in 5 to 6 km of water. The layer-2 velocity and hence sediment thickness was poorly determined, partly owing to a small seamount just west of the receiving position.

Stations 58 and 59 were both split profiles in the small, possibly enclosed, basin between the Indonesian trench and the northwest Australian continental slope. The mantle is rather deeper than usual for deep-ocean basins at both stations. The refracted arrivals were insufficient to determine sediment thickness with any confidence, but sub-bottom reflections at both stations showed it to be at least 0.5 km. Only the reflections at station 58 were good enough to give a sediment velocity.

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EVIDENCE FOR TURBIDITE ACCUMULATION IN TRENCHES IN THE INDO-PACIFIC REGION[1]

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SUMMARY

Sedimentary evidence in three cores taken from the Java, Mindanao and Mariana Trenches indicates that the Java and Mindanao Trenches are receiving sediments that are mostly turbidites. The Mariana Trench is receiving mostly pelagic muds with minor, but significant additions of sediments transported by turbidity flows.

INTRODUCTION

In 1964, cores (Fig.1) from the Java, Mindanao and Mariana Trenches, were taken from the ship U.S.C. and G.S. "pioneer" as part of the International Indian Ocean Expedition. The sediments in these cores exhibit unexpected textural and compositional features that indicate they are turbidites.

METHODS

The cores were taken with a large-diameter (3-inch) piston corer operated without a piston deactivator. The lower portions of the cores were disturbed, and were not analyzed. Analyses were performed by the senior author at the Pacific Oceanographic Laboratory (POL), Institute for Oceanography, Environmental Science Services Administration, Seattle, Washington. The upper portions were logged (U. S. DEPARTMENT OF COMMERCE, 1965), analyzed granulometrically, and examined under a stereomicroscope (× 60). A summary of these data is presented in Fig.2, 3 and 4. The cores, both reference and working halves, are stored at POL.

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[1] Contribution No.2, Joint Oceanographic Research Group and Contribution No. 389, Department of Oceanography, University of Washington, Seattle, Wash. (U.S.A.).

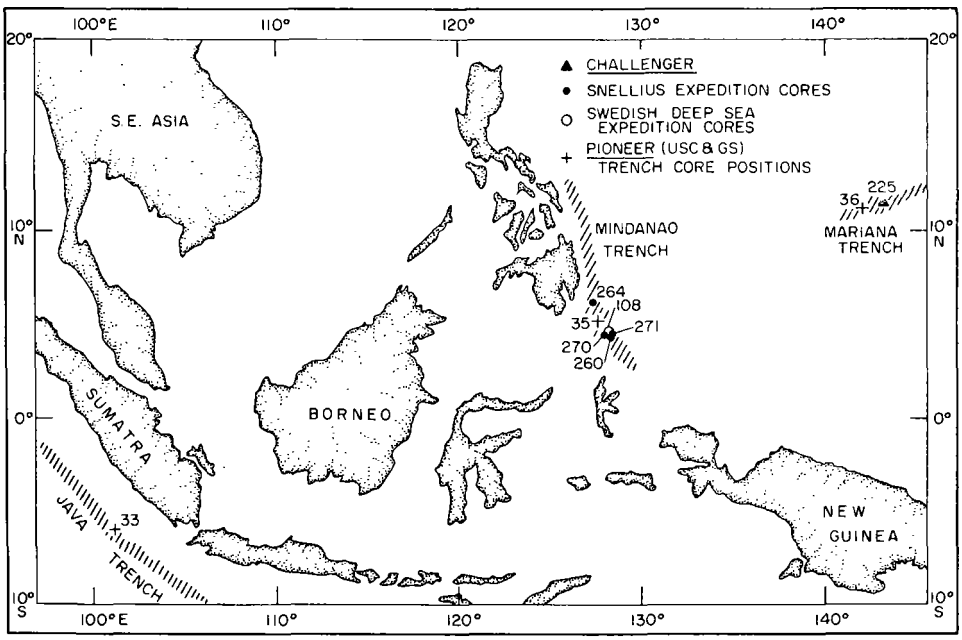


Fig.1. Location of cores taken in the Java, Mindanao and Mariana Trenches.

Features diagnostic of turbidites

Similarity between the sediment properties described on the following pages and the properties of turbidites listed by KUENEN (1964a) is presented as evidence of turbidites in the Indo-Pacific Trench cores.

Maximum grain sizes

The coarsest particles in the trench sediments fall within KUENEN's (1964) size limits. Grain sizes at the first percentile are coarser than very fine sand (4.5 phi) in Java and Mariana Trench sediments, and fine sand (3.5 phi) in Mindanao Trench sediments.

Grading

Pronounced grading occurs in the Java Trench core. A bed grades 2.3 phi units over 10 cm in one case. Less well-defined graded beds occur throughout the core. Size grading was not observed in the sediments in the Mindanao Trench core; however, the contacts between beds of coarse and of fine texture are often transitional over several centimeters. This grading of texture can be considered as graded bedding in this core. In the Mariana Trench core, the size and abundance of mud lumps grades uniformly in beds up to 20 cm thick. There is no corresponding gradation in mean grain size in these sediments.

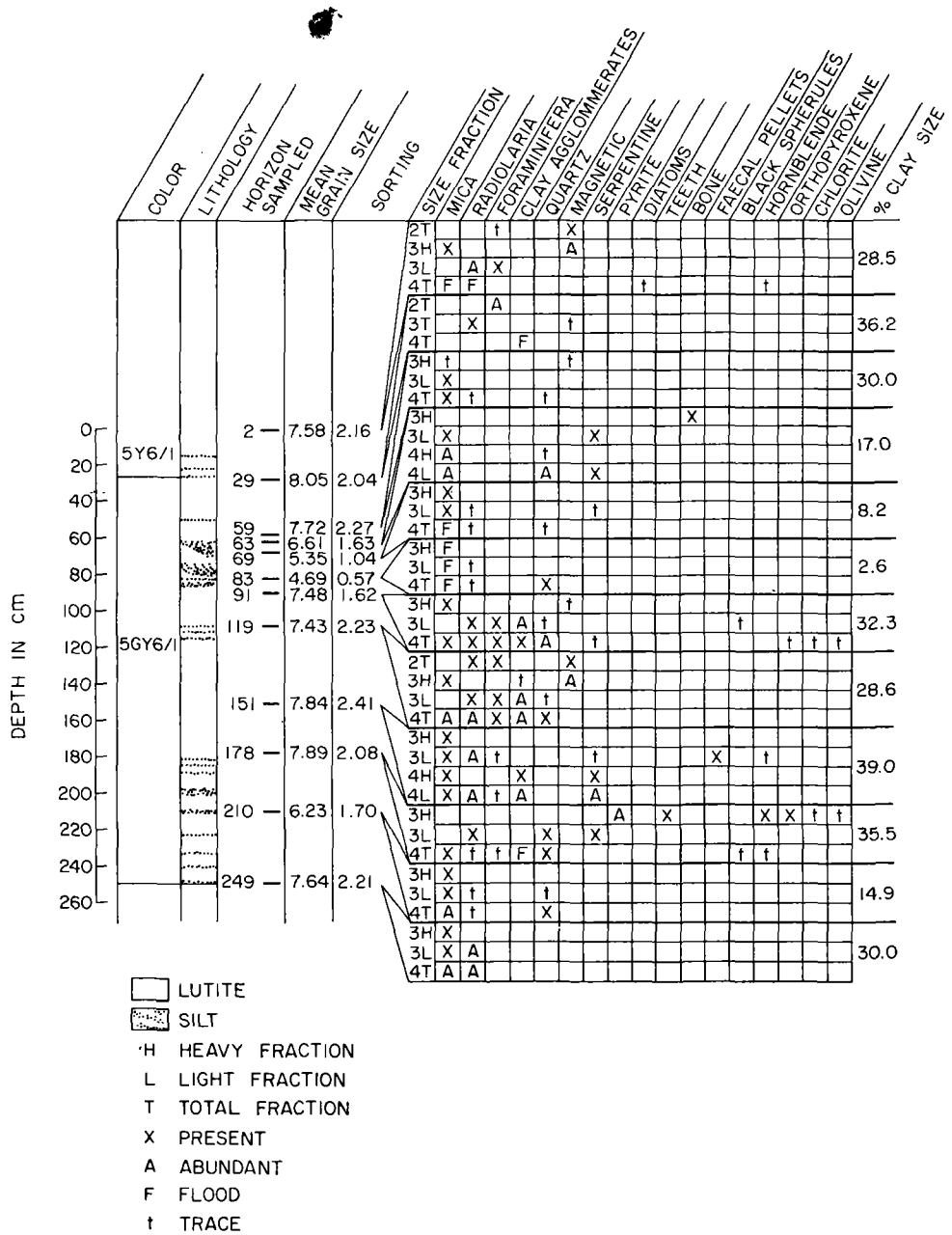


Fig.2. Java Trench core (PI-442-64-33) sediment analysis data. Numerical values in mean grain size, sorting and size fraction columns are in phi units.

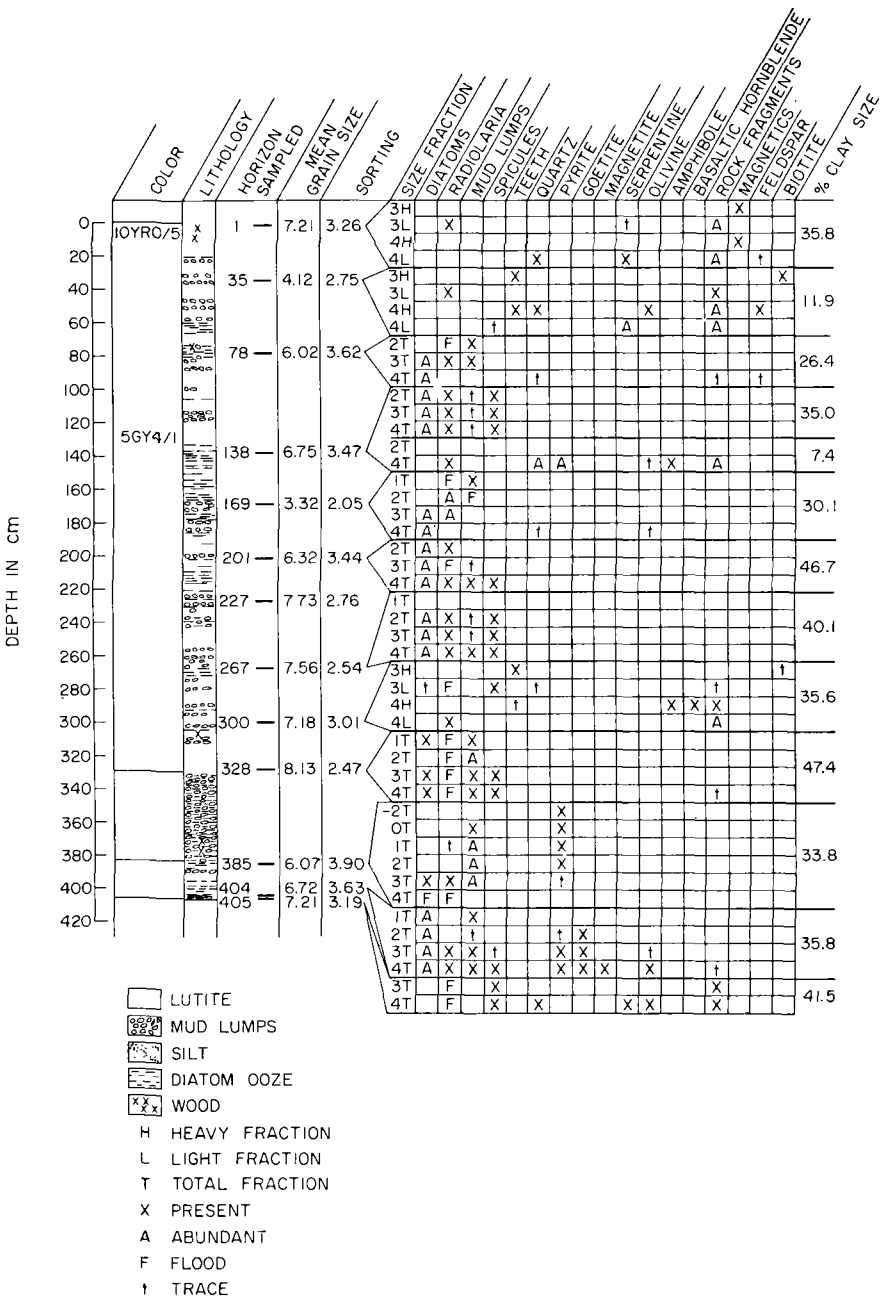


Fig.3. Mindanao Trench core (PI-442-64-35) sediment analysis data. Numerical values in mean size, sorting and size fraction columns are in phi units.

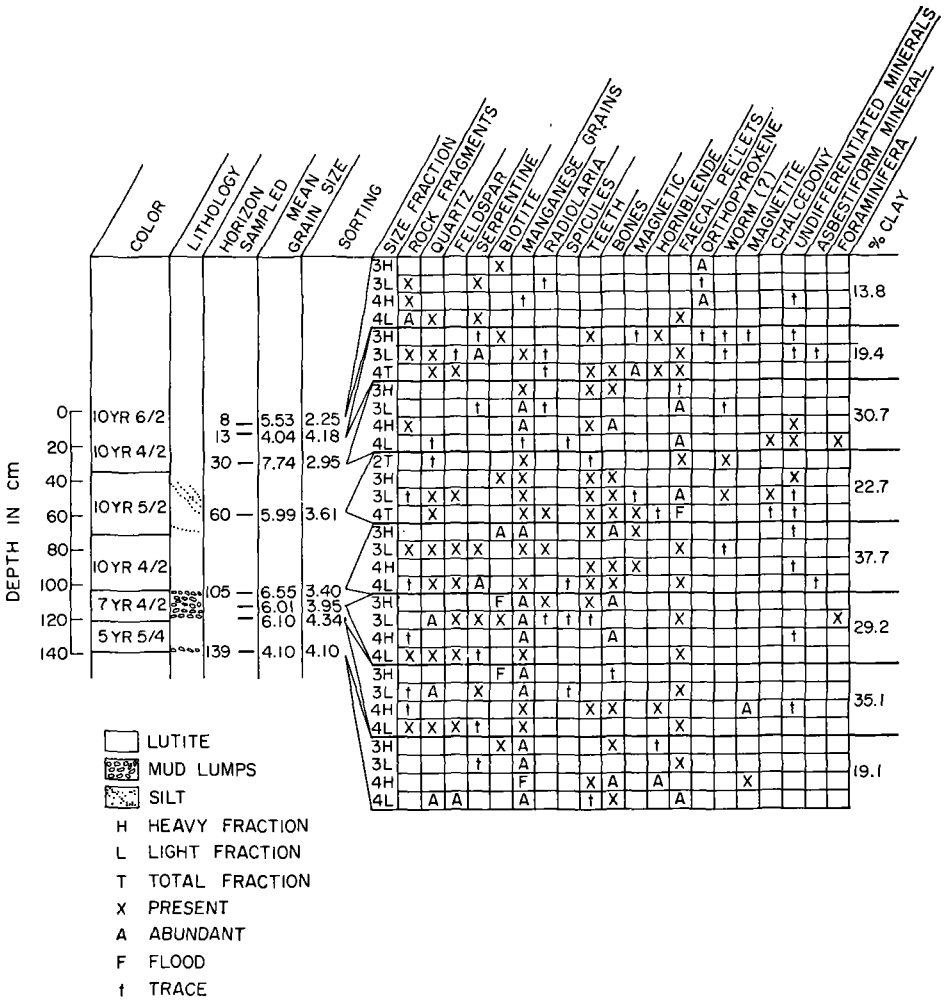


Fig.4. Mariana Trench core (PI-442-64-36) sediment analysis data. Numerical values in mean grain size, sorting and size fraction columns are in phi units.

Sorting

The generally poor sorting in these cores does not agree with the moderate to good sorting cited by KUENEN (1964a, p.10) as typifying deep-sea sands. The disparity probably is caused by excessive amounts of lutite in the trench core sediments.

Inorganic constituents

Beside clay minerals, the most abundant component, trench sediments contain angular quartz, mica, feldspar and pyrite. These are all cited (KUENEN, 1964) as existing in turbidites. These materials are not diagnostic of their depth of original

deposition but the presence of rock fragments and feldspar suggests that the materials have undergone few sedimentary cycles.

Origin and distribution of organic constituents

Organic materials in the trench sediments are mostly the remains of siliceous planktonic organisms. Foraminifera in the Java Trench core occur principally in fine-textured layers. In the Mindanao Trench core, the diatom, *Ethmodiscus rex* (Plate IB, C), occurs only in certain coarse-textured layers (Plate 1A). All other organic remains (Radiolaria, sponge spicules, fish teeth and wood occur in both fine and coarse-textured layers. Fish teeth and fish bone fragments occur throughout the Mariana Trench core, but most of the Radiolaria occur in layers containing abundant mud lumps.

Of all organic constituents in these sediments, the wood is unquestionably of terrestrial origin. Fish bones and sponge spicules might be of neritic origin. It is difficult to interpret the origin of the few tubular, arenaceous Foraminifera found in Java Trench core or of the other organic constituents in the Mindanao and Mariana Trench cores.

Lamination

The sediments from the Java Trench and Mindanao Trench cores are strongly and irregularly laminated. Laminae range in thickness from a few millimeters to as much as 20 cm. Alterations in sediment laminae are marked by changes in color and texture or, in silt streaks, by changes in mean grain size.

Layering in the Mariana Trench core is marked by changes in texture and by subtle changes in color. Textural changes reflect changes in the amounts of mud lumps present in the laminae. The thickness of lamina of lutite is similar to the other trench cores. Silt occurs in streaks about 1 mm thick or layers as much as 20 cm thick.

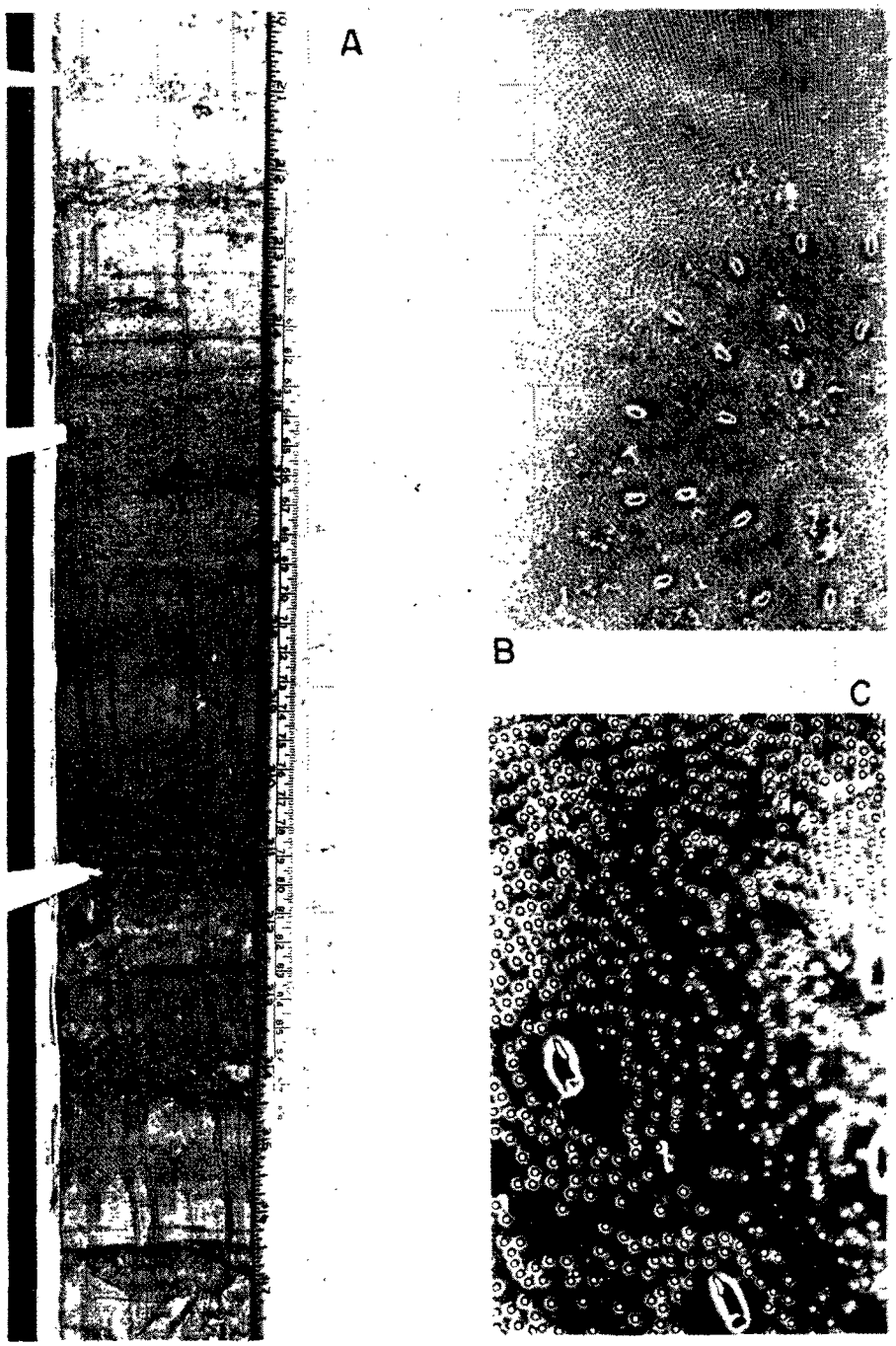
Distorted beds

These are found in the sediments from the Java Trench and Mariana Trench cores. Sediments with contorted bedding lie between layers having normal bedding in the Java Trench core. In the Mariana Trench core there are irregular silty lenses lying about 50° to the core axis. These lenses lie between layers having bedding normal to the core axis.

Ripple lamination

A structure resembling cross-bedding occurs in the core from the Java Trench. Streaks of fine sand, 1–2 cm apart, accentuate bedding surfaces tangential to the underlying layer and truncated by the overlying layer. This structure is about 5 cm thick and may be a portion of a large-scale ripple mark. No ripple marks were found in the other two trench cores.

PLATE I



A. Photograph of a portion of Mindanao Trench sediment core (PI-442-64-35) showing the alternation of lithology. Occurrence of diatom, *Ethmodiscus rex*, in seidment with coarse texture is indicated by white arrow. Mud lump layers occur at 56 cm and at 87 cm.

B. Photomicrographs of central area of *Ethmodiscus rex* from Mindanao Trench core sample, 137–138 cm below sediment surface; × 250 (phase contrast).

C. Photomicrographs of central area of *Ethmodiscus rex* from Mindanao Trench core sample, 137–138 cm below sediment surface; × 770 (phase contrast).

Mud lumps

Mud lumps occur in all three cores. They are about 1 mm in diameter in the Mariana Trench core and about 1 cm in diameter in the Mindanao Trench core (Plate IA). Only a few large (up to 3 cm in diameter) lumps occur in the Java Trench core. The lumps have the same color as the surrounding sediment.

An analysis of mud lumps indicated that they are not aggregations of the surrounding fine-textured sediment. Sand–silt–clay ratios for disaggregated mud lumps are plotted on Fig.5, 6 and 7 as open circles. Ratios for the sediments including mud lumps are plotted as solid circles.

The sediments from the Mindanao Trench core have sand–silt–clay ratios that fall along the dashed line in Fig.6. Because mud lumps fall in the sand size, their removal from the sediment should not affect the silt–clay ratio of the remaining material and the ratio should remain that indicated by the dashed line in Fig.6. Ratios for disaggregated mud lumps do not fall near the dashed line, indicating a silt–clay ratio different from that of the complete sediment.

In the sediments from the Mariana Trench core (Fig.7), there is no linear trend in sand–silt–clay ratios. However, a line drawn through the sand apex and a solid circle intersects the silt–clay axis at a point representing a silt–clay ratio lower than that of the mud lumps removed from that sediment. It appears that these mud lumps are not formed in situ.

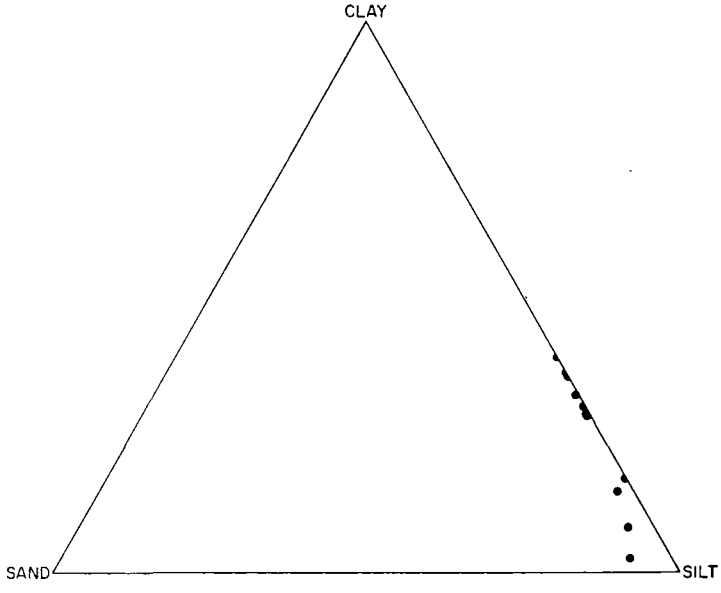


Fig.5. Java Trench core triangular diagram of size components.

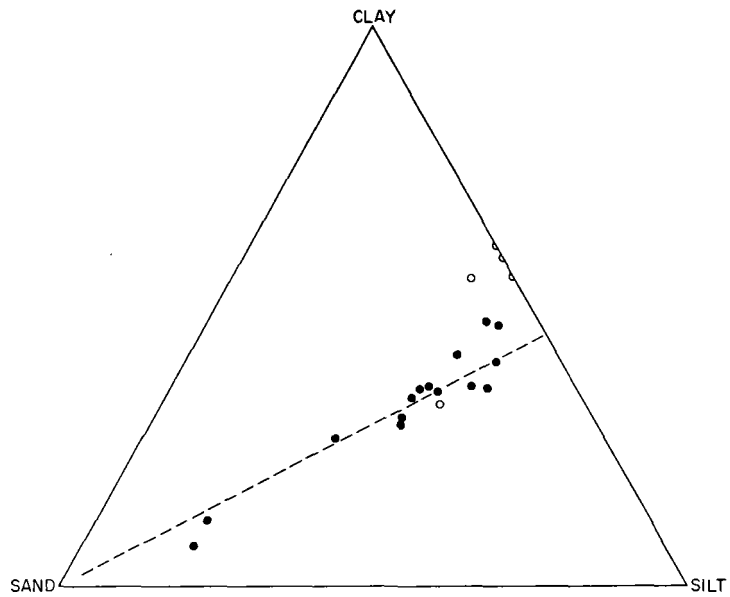


Fig.6. Mindanao Trench core triangular diagram of size components.

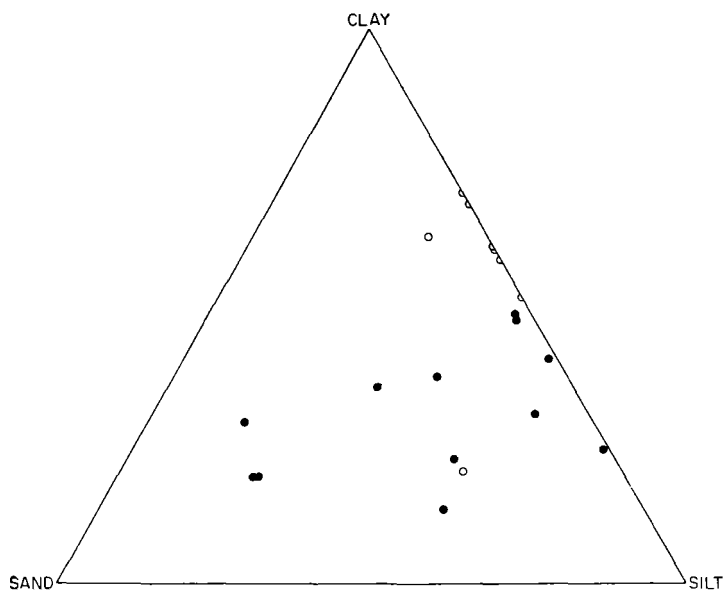


Fig.7. Mariana Trench core triangular diagram of size components.

Thickness

The thickness of sediment layers interpreted as turbidites varies from a few millimeters to about 18 cm. If the entire series of alternating layers in the cores from the Java and Mindanao Trenches represents deposition from a single turbidity flow, then the thickness of the deposits exceeds the lengths of these cores; i.e., 2.5 and 4 m, respectively. In the Mariana Trench core, turbidites are a graded mud lump layer 17 cm thick and possibly streaks of silt less than a millimeter thick.

Contacts

In the Java Trench core most contacts are sharp. In only two cases gradational upper boundaries were observed. The Mindanao Trench core shows sharp contacts with several gradational upper contacts and a few gradational lower contacts. Both contacts are gradational in a few layers. Few distinct contacts appear in the Mariana Trench core; these are sharp rather than gradational.

Burrowing

Evidence of burrowing is restricted to the upper few centimeters of the Java and Mindanao Trench cores and the upper 70 cm of the Mariana Trench core. The Java Trench core shows thin zones of oxidized coloration at 40, 70 and 88 cm. These zones of oxidized sediments represent either pelagic sediments deposited at the top of turbidite accumulations or the oxidized upper portions of individual turbidite layers.

Erosion at lower contacts

Many of the thin layers of sediment in the Java Trench core have thin streaks of coarse mica at their lower contact. In the Mindanao Trench core a few layers have a unit thickness of mud lumps, diatom frustules, or silt streaks at their lower contact. No such feature occurs in the Mariana Trench core. KUENEN (1964b) interprets this feature as a lag deposit resulting from erosion of the underlying layer. Although he refers to erosion of a pelagic layer, one could expect erosion of an underlying turbidite layer if turbidity flows occurred in rapid succession. The only condition is that the underlying layer be uncompacted.

Alternations of layers

There is a contrast in the amount of microorganisms in the layers in the Java Trench core. Layers of fine-textured sediments contain Foraminifera and Radiolaria, whereas coarse-silt layers with coarse texture and containing considerably more mica contain only a trace of these organisms.

The Mindanao Trench core has alternating layering that shows a contrast among three sediment types. Fine-textured sediment layers are rich in Radiolaria, the diatom *Ethmodiscus rex*, and organisms tentatively identified as Foraminifera. Layers rich in clay lumps are free of diatoms and contain only a few Radiolaria. *Ethmodiscus* ooze layers contain a rich microfauna. These ooze layers contain a large amount of Frustules, have a coarse texture, and lack the rock fragments and mineral grains present in fine-textured layers. The sediments in the Mariana Trench core are mainly uniform and finely textured with interbedded, graded layers of mud lumps and streaks and lenses of silt.

Color bands and variegation up to 1 cm thick in the Java and Mindanao Trench cores present striking evidence that a nonuniform environment of deposition exists in these trenches.

Influence of source materials

This influence is striking if the three trench cores are compared. The Java Trench receives sediments rich in mica. The Mindanao Trench receives sediments either rich in clay lumps, silt and terrestrial plant debris, or rich in *Ethmodiscus rex*. Besides pelagic brown mud, the Mariana Trench receives silt and mud lumps. The existence of two ore more sediments in two of these cores indicates that more than one source may supply a single trench even though the diversity of materials may be transported to the site of deposition by a single mechanism; e.g., a turbidity flow.

Influence of distance to source

Of the three trenches studied, the Mariana Trench is the farthest from a major land mass. This is reflected by the preponderance of pelagic sediments and the thinness of the silt layers in the Mariana Trench core. The coarseness of the mud lumps and thickness of the graded mud lump layer in this core suggest that the source of the mud lumps is much closer.

The Mindanao and Java Trenches lie close to major land masses. In the Java Trench core, the layers of coarse mica are thicker (up to 10 cm) and closer together. The interbedded lutite comprises about 80% of the core. The Mindanao Trench core contains still less fine-textured lutite. The Java and Mindanao Trenches lie about the same distance from nearest major land masses, therefore other factors such as frequency or degree of tectonic activity (BEZRUKOV and PETELIN, 1959) and amount of relief and type of drainage of the land masses must exert influences upon the nature of turbidite accumulation that override the influence of distance to source.

Pelagic interbeds

The pelagic sediments in the Mariana Trench core are brown mud (clay) typical of open ocean abyssal regions. The only organic materials found in this

sediment are fish teeth and bones, and possible faecal pellets. The pelagic sediments in the Java Trench core are fine-grained, micaceous, gray–green lutites. The Mindanao Trench core appears to contain few pelagic interbeds. These are fine-grained lutites containing Radiolaria but few or no diatoms.

Slope of bottom

Slopes were not measured in the areas of the three trench cores. It is likely that the slope of some of the bottom of the trenches is less than a degree so that turbidites can accumulate there.

DISCUSSION

The sediments in all three trench cores contain several features typifying turbidites. Although it is not reasonable to identify the sediments in Mariana Trench core as turbidites, the effects of turbidity flows can be recognized in these sediments. The abundance of evidence leaves little doubt that the sediments in the Java and Mindanao Trench cores are turbidite accumulations.

The sediments in the Java Trench core are interpreted as hemipelagic micaceous lutites alternating with graded and ungraded micaceous silts that are introduced by turbidity flows. There is only a single source of sediments, presumably the island of Sumatra. Of the three cores studied, the Java Trench core presents the least complex example of turbidite accumulation.

The turbidite accumulations in the Mindanao Trench core are the most complex. The sediments in this core are interpreted to be a turbidite sequence of lutites containing Radiolaria and diatoms interbedded with terrigenous silts, mud lump accumulations and *Ethmodiscus* ooze. It is possible that the lutite layers are hemipelagic. However, the occurrence of wood fragments in these layers argues against this interpretation. It is more likely that lutite is introduced to the core site by turbidity flows originating close to the coast of Mindanao Island. Mud lumps probably result from mass movement of preexisting sediments from higher portions of the trench. BEZRUKOV (1957) reached the same conclusion regarding the Izdu-Bonin and Mariana Trenches.

Several observations indicate that *Ethmodiscus* frustule fragments are transported to the core site, presumably by turbidity flows. Although the three trenches are located within the biogeographic distribution region of *Ethmodiscus rex* (SEMINA, 1959), the occurrence of *Ethmodiscus* ooze in these cores and in others from the Indo-Pacific region (NEEB, 1943; OLAUSSON, 1960; ZHUZE et al., 1959) is erratic. The ooze occurs in the Mindanao Trench core in irregularly spaced layers between 75 and 328 cm. It is rare in the Java Trench core and is absent from the Mariana Trench core. NEEB (1943) reports no significant amounts of diatoms in cores from the Mindanao Trench taken during the "Snellius" Expedition (Fig.1), but KOLBE (1954) states that

diatom fragments thought to be *Ethmodiscus rex* are found in "nearly all cores and levels of the Equatorial Pacific."

SEMINA (1959) found no close relationship between the presence of *Ethmodiscus rex* in sediments and in the water above. She is inclined to agree with KOLBE (1957), HENDEY (1958) and ZHUZE et al. (1959) that there are other factors, e.g., bottom current, flow of the ooze, or irregular submarine topography, that control the distribution of this diatom ooze on the present-day ocean bottom. RIEDEL (1954) reexamined the Radiolaria assemblage from the original "Challenger" Station 225 (11°24.0'N—143°16.0'E; depth: 4,475 m) and concluded that "There is little doubt that the sediment obtained at "Challenger" Station 225 is an outcrop of Middle Tertiary Radiolarian ooze. The occurrence of *Ethmodiscus rex* in this sediment has no connection with its existence in the overlying water at the present day, but rather means that the diatom lived in that region during Middle Tertiary time." These observations are in accord with the concept that *Ethmodiscus* ooze accumulates within the limits of its biogeographical region but is transported by occasional turbidity flows, so that its distribution on the bottom is patchy and its distribution within bottom sediments is irregular.

The sediments in the Mariana Trench core contain fewer features typical of turbidites than do the sediments in the Java and Mindanao Trench cores. Nevertheless, the features found in the Mariana Trench core, e.g., graded mud lump layers and silt streaks, are just as important because they show that nonpelagic sediments with properties characteristic of turbidites can occur in a trench remote from land and separated from land by several ridges and basins.

It is likely that mud lumps are introduced into the Mariana Trench by mass movement such as sliding or slumping; the dislocation of slightly compacted clay is probably the mechanism whereby the mud lumps are formed. The silt in layers and streaks has been transported from distant terrestrial sources. The mechanisms for the transportation of this material cannot be specified at present.

ACKNOWLEDGEMENTS

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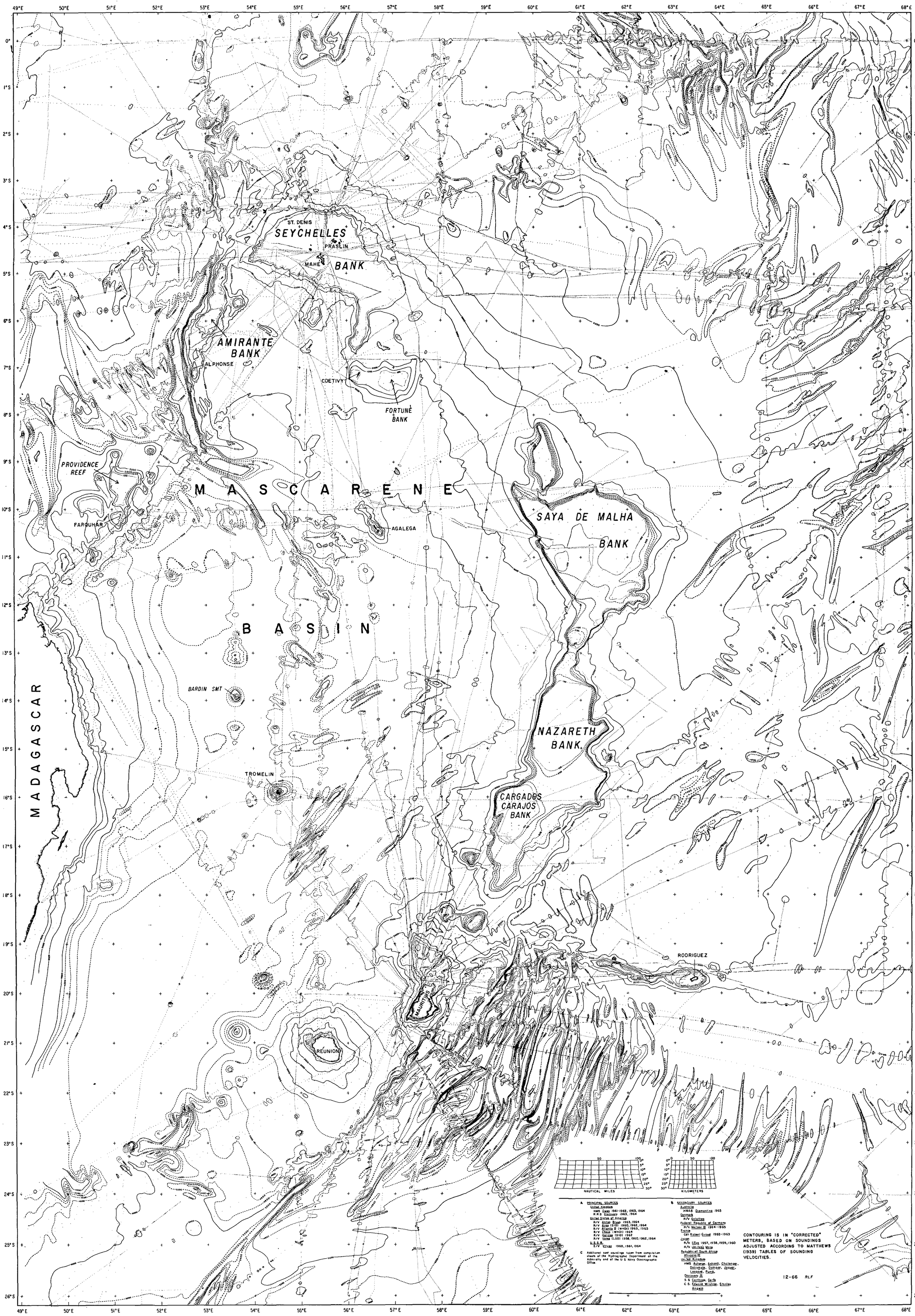

FISHER AND OTHERS, PLATE 1
Geological Society of America Bulletin, volume 78

SUBMARINE TOPOGRAPHY OF THE MASCARENE PLATEAU, THE MASCARENE BASIN, AND PART OF THE MID-INDIAN OCEAN RIDGE

Note: From the Equator to 20°S. the crest of the mid-Indian Ocean Ridge lies between 66° and 68+°E., just inside the eastern border of this chart. Note also that in areas of greater than 4000 m depth a 200-m contour interval was employed.

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Mascarene Plateau, Western Indian Ocean

Abstract: The submarine Mascarene Plateau, lying east and northeast of Madagascar in the west central Indian Ocean, extends as a faulted composite arc for 2300 km, from the Precambrian granitic "microcontinent" of Seychelles Bank southward through the coral–reef–capped volcanic structures (?) of Saya de Malha, Nazareth, and Cargados Carajos banks to the faulted Tertiary–Quaternary oceanic volcanic island Mauritius. Locally the aseismic plateau is buttressed by spurs, is steep-sided and angular in plan, or is extended, disrupted, or offset by cross-faulting.

Other major structural elements in a sector centered on the Mascarene Plateau are: (1) the seismically active Mid-Indian Ocean Ridge and rift zone (including that portion known as the Carlsberg Ridge) between the equator and its bifurcation near 23°S.; (2) the angular and faulted Amirante Trench lying between Seychelles Bank and the Madagascar-Farquhar complex; (3) the east–west late Tertiary–Pleistocene Rodriguez Ridge and its possible extension eastward as a fracture zone offsetting the Mid-Indian Ocean Ridge; (4) the Mauritius Trench, a 1400-km border deep-trending southwest from east of Mauritius to 28°S., 51°E. Irregular topography, attributed to volcanism and block faulting, is strikingly developed southeast of the intersection of Rodriguez Ridge with the Mascarene Plateau. Here linear, slightly sedimented deeps and narrow ridges lie subparallel to Mauritius Trench and to the southwest branch of the Mid-Indian Ocean Ridge.

Except in the northwest sector where northwest and north trends lie within the Agalega–Seychelles–Amirante–Owen Fracture Zone complex, the dominant topographic lineations are northeast to east–northeast. These are displayed by large features such as fractures offsetting the mid-oceanic ridge (for example, Vema Trench), the Mauritius Trench and the linear topography southeast of Mauritius, the apparent offsets of the southern half of the Mascarene Plateau, spurs on the west flank of the mid-oceanic ridge, and the smaller ridges protruding from the sedimented rise and abyssal plain between Tromelin and the Mascarene Plateau. Offsets of the Mascarene Plateau along northeast-trending faults occurred in Tertiary time as adjustments accompanying formation of the Mascarene Basin. Activity on several of these faults has continued where they intersect the crestal portions of the mid-oceanic ridge system, but growth of the exceedingly rough ridge in this region is primarily by addition of igneous material along its axis.

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INTRODUCTION

The Mascarene Plateau forms the foundation for a series of islands and shallow banks that extend in a gentle northwest-to-south crescent across the western tropical Indian Ocean. From north to south, the islands and banks include the Seychelles Archipelago, the Saya de Malha, Nazareth and Cargados Carajos banks, and the island of Mauritius. The plateau is over 2300 km long. It ranges from 100 to nearly 400 km in width at the base and is a major structural element of the Indian Ocean.

Hydrographic surveys of the shallow banks were made from the mid-nineteenth to the early twentieth centuries, but our knowledge of the deeper flanks of the Mascarene Plateau is almost entirely a result of the International Indian Ocean Expedition, 1960–1965. Most of the recent trans-Indian Ocean expeditions have called at Mauritius, and many have visited the Seychelles. Co-ordination of programs of the Expedition has provided a unique concentration of relatively precise topographic data. Slight deviations in the routes of participating oceanographic vessels were made to cover many critical areas. Earlier, precise but localized investigations were made by cable survey and repair ships. Submarine cables operated between Réunion, Mauritius, Rodriguez, and the Seychelles for the past seventy years have frequently failed due to chafing effects of bottom currents on the insular slopes and ridges. Ripple marks, scour, and rock outcrops seen on seafloor photographs taken during the Expedition constitute further evidence of these bottom currents and of movement of detritus that has affected the cables.

Mauritius, Rodriguez, and Réunion, the three Mascarene islands, are wholly volcanic edifices. Documentation for such identification, and for other statements in this introduction, is presented in later sections. Rodriguez is a ridge partially bordered by an emerged coralline platform and surrounded by a 7-to-20-km-wide shelf and fringing reef. Recent potassium-argon dating indicates the rocks exposed on Rodriguez are less than 2 m.y. old. Mauritius, an eroded complex volcanic pile surrounded by a narrow shelf and barrier reefs, appears geomorphically younger but consists largely of volcanic structures of Tertiary age. Réunion bears active volcanoes. Though showing a superficial east-west arrangement athwart the Mascarene Plateau, the three islands are independent topographic entities. Rodriguez lies on the essentially east-west Rodriguez Ridge, which was discovered in 1901 by the cable ship *Anglia* during the laying of the Mauritius–Rodriguez cable. This ridge is a major east-west element which intersects and perhaps crosses the dominant meridional trend of the Mascarene Plateau just north of Mauritius. Mauritius lies on the southern extension of the Mascarene Plateau, and Réunion is a separate volcanic pile 170 km to the southwest.

The Seychelles Islands lie near the northern termination of the Mascarene Plateau. The Seychelles are the only islands rising from the deep-sea floor that are composed of granitic rocks, and recent seismic refraction studies indicate that such granitic material lies beneath most of the wide shelf surrounding and linking the small islands. Radiometric analyses have shown the granites to be Precambrian in age.

The northern portion of the Mascarene Plateau appears "continental," suggesting that the entire shoal structure might be a "microcontinent." However, the Mascarene Islands, which lie near and on the southern termination of the plateau, are composed of "oceanic-type" basalts, while seismic refraction observations on the intervening Saya de Malha Bank indicate a crustal composition intermediate between that of continent and ocean.

Thus the shallow Mascarene Plateau, a topographic entity that is complex from the viewpoints of petrology, age, and crustal structure, constitutes a major structural element of the Indian Ocean and must be considered in a discussion of continental drift or the genesis of the Indian Ocean Basin. The present paper, based primarily on recently available topographic information supplemented by magnetic, seismic, and heat-flow data from the International Indian Ocean Expedition, is an attempt to delineate and interpret structural trends in the west-central Indian Ocean (Fig. 1).

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Names of vessels which provided the primary sounding data employed in the preparation of the bathymetric charts are listed on those figures. In the course of the study, varied information was provided by J. Baissac, M. Talwani, L. B. Slichter, A. R. Miller, C. Bowin, E. T. Bunce, and I. McDougall. Cable repair information was made available by D. Scott, Engineer-in-Chief, Cable and Wireless Ltd. Discussions with D. Matthews, T. W. C.

SUBMARINE TOPOGRAPHY AND ECHO-SOUNDER TAPES NEAR MAURITIUS

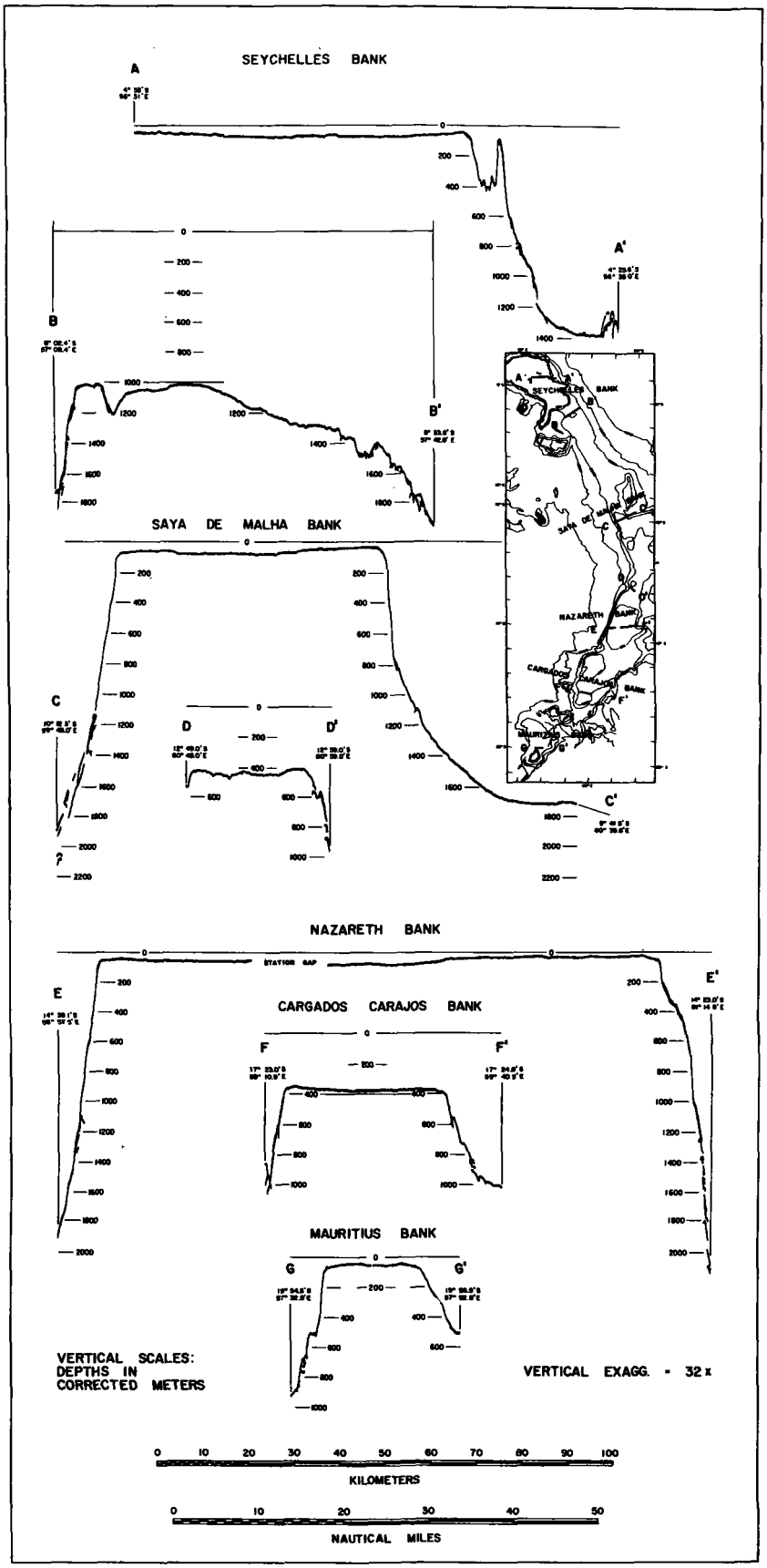


Figure 1. Tracings of Precision Depth Recorder (SIO) and Precision Graphic Recorder (WHOI) crossings of the Mascarene Plateau.

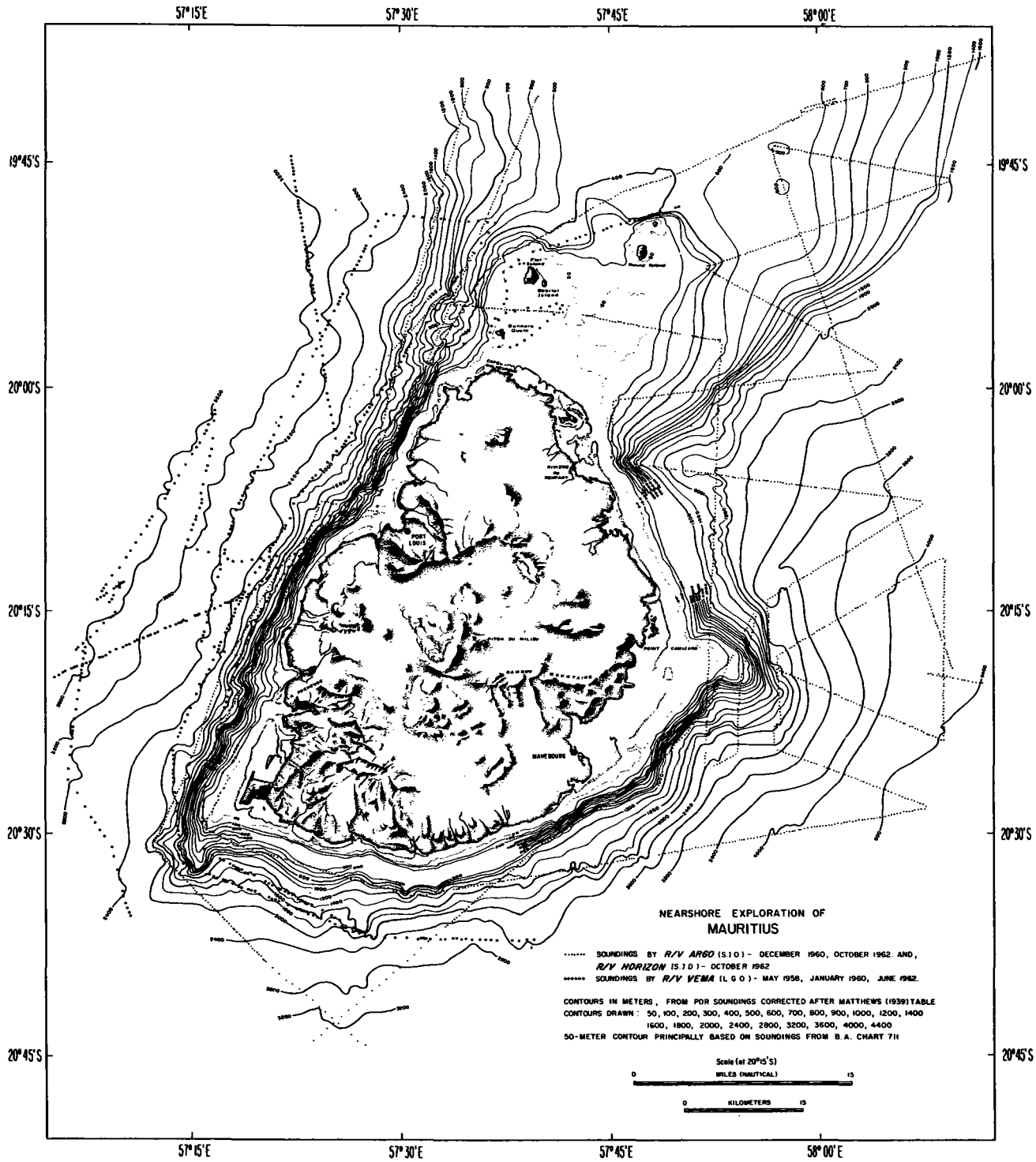


Figure 2. Submarine topography near Mauritius.

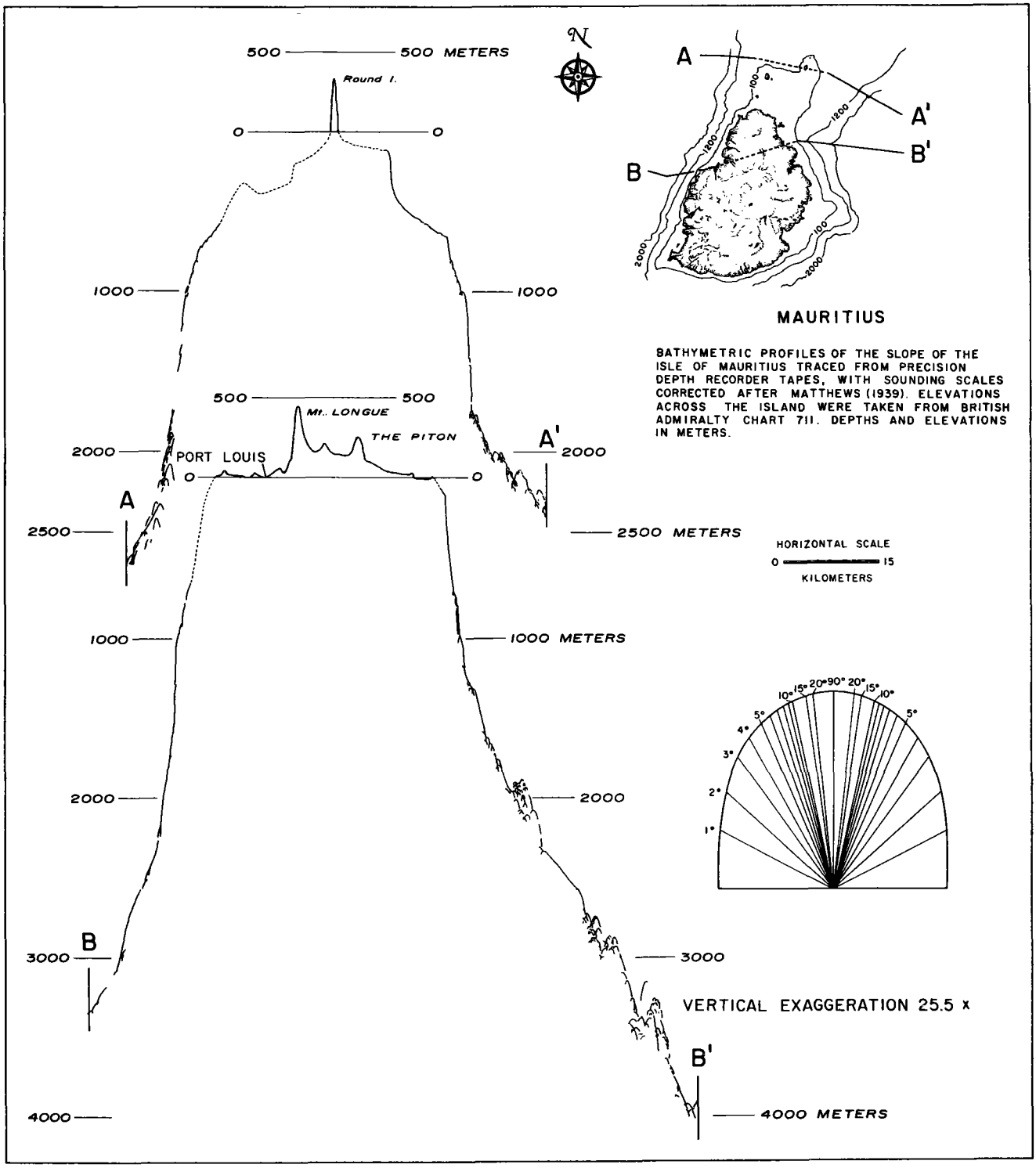


Figure 3. Tracings of Precision Depth Recorder tapes from the insular slopes of Mauritius.

Figure 1. Index map: a portion of the Heezen–Tharp Physiographic Diagram of the Indian Ocean (Geological Society of America, Inc., 1965). Copyright: 1964, Bruce C. Heezen and Marie Tharp. Note: This figure has not been redrawn to incorporate additional data acquired since mid-1964 that have been used in the preparation of the contoured chart, Plate 1.

Hilde, A. S. Laughton, M. N. Hill, A. E. J. Engel, G. G. Shor, J. B. Hersey, J. R. Conolly, H. W. Menard, C. J. Shipek, and M. Langseth are gratefully acknowledged. Illustrations were drafted by D. G. Crouch. This work was supported by the Office of Naval Research of the U. S. Navy, National Science Foundation grants G–22255, GP–5538, GA–580, and the Bell Telephone Laboratories.

PREPARATION OF THE BATHYMETRIC CHARTS

Dots representing all soundings used in constructing Plate 1 and Plate 2, fig. 2, are shown on those plots. Most of the sounding lines were run after 1961 by ships participating in the International Indian Ocean Expedition, 1960–1965. Nearly all of these ships were equipped

with echo-sounders having a recording precision of better than two meters in 5000. Soundings were made at few-second intervals; however, except near shore, the records were read either at fixed intervals (commonly about 1.5 km of track) or at significant inflection points. Except for the detailed surveys (as around Mauritius), soundings were plotted on U. S. Navy Oceanographic Office oceanic plotting sheets (Mercator, 4 inches equal to 1° of longitude) or on 1:1,000,000 Admiralty Mercator plotting sheets. No slope corrections were applied. Little of the exploration occurred within sight or radar range of shore; practically all the ships were dependent on celestial navigation, so their fixes have an accuracy of about ±4 km under good weather conditions. Navigational tracks were corrected aboard ship for drift and speed variations where these were known. Small gaps or large offsets in the sounding tracks occur at sampling stations, during trawling operations, or occasionally when sounding equipment was inoperative. In the final compilation for Plate 1, made on U.S.N.O.O. oceanic-scale plotting sheets, older or less well-controlled tracks were adjusted in position until their soundings made good crossings with the accepted lines; doubtful lines were used in part only, or not at all.

Although the soundings recorded are relatively precise, they are subject to the usual difficulties of interpretation of echo-sounding: side-echo effects, slope corrections, and sweeping of the sound cone as the ship rolls. Nevertheless, in the regions of gentle slope at any depth and on the abyssal plains, the discrepancies in depth at crossings were commonly only 5–30 m. During contouring on steep slopes, especially in ridge areas, the discrepancies accepted were considerably greater. Along the plateau south of Saya de Malha (Pl. 1) and around the Mascarene Islands, the 100-m contour, as well as the 200-m contours down to 1000 m, were drawn in order to indicate the variations in extent, shape, and depth of the shoal features. On Seychelles Bank, on the Amirante Ridge, and on isolated, little-investigated islands such as Tromelin and Agalega, the 1000-m isobath closely follows the 100-m contour; intermediate contours were not drawn. On the chart generally, 1000-m contours were drawn down to 4000 m in order to emphasize general trends shoaler than the deep-sea floor. This procedure necessarily misses much of the relief on the extremely rough median ridge, but all soundings, exaggerated plots of profiles, and the echo-sounder tapes themselves were considered in determining the presence and trend of features such as the "rift valley" commonly found on the mid-oceanic ridge. For areas more than 4000 m in depth, a 200-m interval was employed in an attempt to portray the texture and the structural pattern of the deep-sea floor. The availability of precise soundings in the deeper areas permitted an attempt at correlation of local, narrow, flat-bottomed deeps between adjacent sounding tracks; this method was used most extensively in the southeast and northeast portions of the area shown on Plate 1.

That area west of the Mascarene Plateau–Mauritius Trench (Pl. 1) probably represents the submarine topography fairly accurately. East of these features, especially on the mid-oceanic ridge east of 63° E., the contours shown are very much less definitive.

THE MASCARENE PLATEAU AND THE SURROUNDING SEA FLOOR

In the extended usage in this paper, the Mascarene Plateau includes the Seychelles–Mauritius Ridge (Fairbridge, 1948) and the Mascarene Ridge (Sewell, 1935; Shor and Pollard, 1963) of various authors as well as the "Shoals of Capricorn" picturesquely named by Ommanney (1952). At the 1200-m isobath, the structure stretches from Seychelles Bank southeast and south through 14.5 degrees of latitude to the southern edge of Cargados Carajos Bank. There, two passages more than 2500 m deep separate the northern banks from similar shoals and the high volcanic island of Mauritius. At its base the Mascarene Plateau varies in width from 100 km to nearly 400 km; it is flanked by several spurs, notably just south of the Seychelles (Pl. 1). Despite gaps in continuity, the feature is properly called a plateau rather than a ridge, for it has a characteristically wide and level summit, due to extensive growth of calcareous reef organisms, and rather precipitous flanks down to depths of nearly 2000 m. Plates 1 and 2 show very clearly the extremely steep and linear scarps that bound the plateau and the west side of Mauritius. Although the steep upper flanks of the platforms probably simply reflect the upward growth of coral on a subsiding foundation, many of the steep scarps at greater depth may have a fault origin. Faulting is suggested by the blocky outline and angular intersections of the scarps. However, this oceanic plateau is not marked by current seis-

mic activity and appears to be a relatively stable relict structure, except possibly for differential subsidence or drowning of the banks.

Recent seismic refraction (Shor and Pollard, 1963; Davies and Francis, 1964) and reflection studies (Bunce and others, 1966) and magnetic and gravity observations (Matthews and Davies, 1966) bear out these essentially morphological conclusions. Refraction measurements on Seychelles Bank (Davies and Francis, 1964) indicate a "continental" crust more than 30 km thick. Shor and Pollard (1963) reported that up to several hundred meters of calcareous sediment and coral thicken away from island outcrops of Precambrian granites, and that material with "granitic velocity" underlies a large portion, probably all, of Seychelles Bank. In the deeper portions between Seychelles Bank and Saya de Malha, the shallow crust "is composed of stratified rocks, probably sedimentary. The stratification parallels the sea bottom, slopes seaward on the flanks of the ridge, and is nearly horizontal in the central portion. The magnetic anomalies are generally less than 200 gammas" (Bowin and others, 1965). Refraction work of Shor and Pollard (1963) on Saya de Malha was interpreted as showing lagoonal calcareous material from 200 to 500 m thick overlying coral rock (about 1 km thick) on a base of material displaying seismic velocities (4.4–5.4 km/sec) typical of Pacific volcanic islands. Mantle velocities were not observed, but an "oceanic" crustal layer (velocity from 6.8 to 7.0 km/sec) at depths greater than 8 km was detected. Bowin and others conclude that on Nazareth and Cargados Carajos banks the flat summits are underlain by limestone, although sub-bottom penetration was not observed, and that strong (400 gammas or greater) magnetic anomalies near the western edge of the structure suggest that volcanic rocks underlie a limestone cap. Immediately north of Mauritius several small islands rise from a broad submarine platform. The islands consist of vesicular basalts and dolerites extruded on bedded tuff and agglomerate (Walker and Nicolaysen, 1954); these are vents from which marine erosion has removed the greater part of the original cones. The proportion of coralline material comprising the shoals has not been determined. The limited development of fringing reefs around Mauritius suggests that this bank may well represent a beveled pyroclastic portion of the volcanic pile.

Exploration of the "Shoals of Capricorn" between 8° and 17° S. has been inhibited by the presence there of coralline pinnacles which rise several meters from the flattish summits or even reach sea level as sand cays, as in the southeast quadrant of Cargados Carajos. However, there are at least four passes more than 200 m deep between the banks; one of these, near 9°35′ S., is deeper than 700 m. Just south of the islets of Cargados Carajos, the reef flank drops quite steeply down to a gently-sloping flat area that may be a drowned coralline platform (Pl. 2, fig. 1, F–F′). A deeper crossing just north of Nazareth Bank (D–D′) shows a less regular surface where leveling by coral growth perhaps has not occurred. Profile B–B′ just southeast of Seychelles Bank is similarly rough, with irregular, probably rocky, flanks extending nearly to the 1000 m summit. Two isolated peaks, reaching 25-m depths, lie just southeast of B–B′; Fortune Bank–Coëtivy Island are off the ridge on an east-west spur nearby. Similar shoals, as yet undiscovered, may lie on the 1700–1800-m-deep ridge between 6° and 8° S. In the areas of broadest reef development, as on Seychelles Bank (A–A′), at Saya de Malha Bank (C–C′), and on Nazareth Bank (E–E′), echograms show ramparts from 5 to 40 km wide fringing a central, wide lagoon a few meters deeper or, as on Saya de Malha (Pl. 1), several lagoon systems on a gently tilted base. In these areas the plateau's upper flanks are steep, but apparently rather smooth, down to depths of from 800 to 1200 m. Thicknesses of this magnitude for coral debris or limestone capping are indicated by the seismic results as well. Throughout the length of the structure, the flanks at depths greater than 2000 m are locally irregular but characteristically more gentle in slope than the upper portions.

West of the Mascarene Plateau, there is considerable topographic variation. Northwest of Seychelles Bank, the lower slopes and frontal apron are separated from the Somali Abyssal Plain by a possible southern extension of the Owen Fracture Zone and by the Amirante Trench–Amirante Ridge complex (Fig. 2). South of 9° S., the east–southeast trend of the Amirante Trench is not well established. However, minor topography at the north edge of the Mascarene Basin, as well as the base of Agalega, has a marked northwest trend. Between the Seychelles and the Amirante–Agalega "arc" is a sedimented region of intermediate (3500–4000 m) depth with a few isolated peaks and abyssal hills. Within the sector Agalega–

Fortune Bank–Saya de Malha, the sea floor slopes gently and fairly smoothly southward as an apron, although here, too, small hills protrude. Occurrence of an extensive, thinly sedimented region shoaler than 4000 m between the Amirantes–Agalega trend and the Mascarene Plateau proper suggests the presence there of intermediate crustal structure.

South of 11° S. and east of the Madagascar-Farquhar Islands complex, the sea floor is deep. A very gently sloping apron (at depths of 3500–4000 m) fronts the Mascarene Plateau as far south as 15° S., and a narrow plain about 4300 m deep separates the apron from a zone of abyssal swales and hills (Pl. 1; Fig. 2). The swales show relief of 100 to 400 m and an elongation either somewhat east–west or strongly northeast–southwest, the latter being subparallel to the Mascarene Plateau. The southwest trend is strikingly developed east and southeast of Tromelin Island, where ridges protrude as much as 1400 m above the deep sedimented sea floor (Pl. 1; Fig. 5, upper). Several isolated mountains, of which Tromelin is the largest, occur in this area. West of Tromelin, the gentle swale topography terminates at the eastern boundary of the Malagasy Abyssal Plain, which extends southward to 23° S. The absolute change in depth from the plain to the swale topography is from 100 to 200 m, not sufficient to be clearly identifiable on the contour map. However, on echograms the change is abrupt, from essential flatness to irregular low relief.

From the latitudes of Cargados Carajos to the north end of Mauritius, the west flank of the Mascarene Plateau is irregular in plan and relief, possibly reflecting the intersecting trends of the plateau and the Rodriguez Ridge. However, at Mauritius the west flank is steep, linear, and probably fault-controlled (Pl. 2, fig. 2).

North of the portion of the Mascarene Plateau between Seychelles Bank and Saya de Malha, the east flank drops directly and with no slope reversals into a fringing apron from 4000 to 4100 m deep (Pl. 1). North of 4° S. the flat region deepens northward, to reach 4600 m just south of the equator. A low, generally smooth, northwest-trending rise bearing a few peaks up to 3000 m high is developed near 4° S., 60° E. However, the sea floor generally deepens, as a region of abyssal hills, east to the foothills of the mid-oceanic ridge near 65° E. and northeast to the troughs and ridges bordering the Carlsberg Ridge, the northwest-trending portion of the mid-oceanic ridge.

At approximately 9 to 10° S., a low rise bounding the northern deep area connects Saya de Malha to the mid-oceanic ridge and Vema Trench topography (Heezen and Nafe, 1964). South of these latitudes, the east flank of the Mascarene Plateau steepens and becomes more angular in plan. Some of the scarps, developed to 2000–3000-m depths, strike northeast; the topographic pattern suggests *en echelon* faulting. The plateau may be offset between Nazareth and Cargados Carajos banks, with Nazareth Bank displaced east-northeast relative to Cargados Carajos. Much more exploration is needed, but it appears that between 10° and 19° S. the southern basin is narrow and only locally flat-floored, with elongated fault deeps commonly trending subparallel to Vema Trench, and that near 18° S. hilly topography flanking the mid-oceanic ridge extends westward nearly to the base of the plateau. The generally north-trending Mid-Indian Ocean Ridge and rift valley seem cross-fractured and offset in these latitudes, and ENE. or NE. trends persist on the ridge, and particularly on its western flank, to the equator. The pattern is developed especially well between 3° and 11° S.; a series of spurs and intervening flat-floored troughs extends from near 65° E. to, or beyond, the "crest" of the mid-oceanic ridge. South of Saya de Malha, the trend of the eastern flank of the Mascarene Plateau is similar to that of the mid-oceanic ridge. The most obvious ridge dislocation, right-lateral in sense, occurs at the Vema Trench; this offset seems reflected by the necking and possible displacement of the plateau between Saya de Malha and Nazareth banks. The structural trend may continue west of the plateau in the linear ridges east and southeast of Tromelin.

MASCARENE ISLANDS

Regional Geologic Setting

Geological investigations of nearly all of the islands and islets on and adjacent to the Mascarene Plateau have been carried out and reported recently. Baker (1963) did detailed field work in the Seychelles, Amirante, and Farquhar groups. He described the Precambrian intrusive rocks and basaltic dikes, mostly early Tertiary, of the granitic islands of Seychelles Bank and the surficial calcareous deposits of the low sand cays, atolls, and patch reefs where no basement igneous rocks have been obtained. Wiseman (1936) described an (Eocene–Oligocene?) basaltic agglomerate that was dredged off the southwestern margin of Providence Reef at a depth of 1350 m in 1905. According to Matthews and Davies (1966), magnetic traverses by

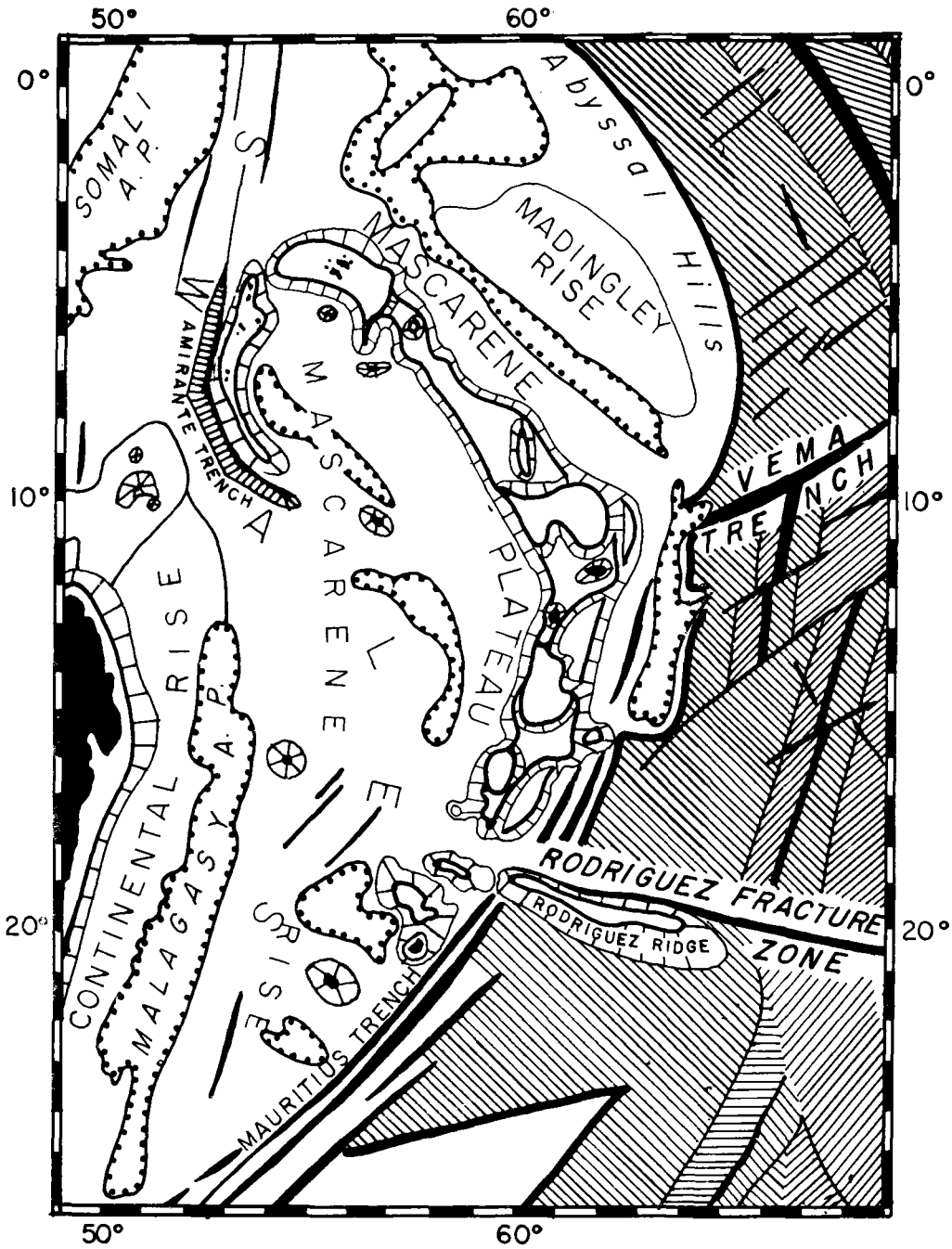


Figure 2. Province chart (partly redrawn from Heezen and Tharp, 1965).

HMS *Owen* in 1961–1962 suggest the presence of basaltic foundations at a depth of less than 1 km beneath the atolls of the Amirante Group. Descriptions of Agalega and the several reefs and islets on Cargados Carajos Bank in nautical publications (*e.g.* Anonymous, 1952) indicate these are composed of beach rock and coralline sand, with no igneous rocks exposed. Saya de Malha and Nazareth banks are wholly submerged; in 1964 the Research Vessel *Chain* dredged one volcanic(?) pebble from the ridge flank northeast of Saya de Malha (Bunce and

others, 1966). West of the Mascarene Plateau, the isolated island of Tromelin and the seamount Bardin (Belousov, 1965) 140 km northwest of Tromelin are volcanic peaks; Soviet workers collected basalt on Tromelin in 1964 (J. Tuzo Wilson, personal commun.).

The Mascarene Islands have been restudied rather intensively. Rodriguez is composed of a uniform series of alkalic olivine basalt flows as the summit of a very large, steep-sided elongated volcanic pile built up from the ocean floor (McDougall and others, 1965). The present emerged portion, which caps an elliptical, beveled submarine platform of more than 10 times greater extent, has undergone little erosion. One flow has been dated at 1.54 ± 0.05 m.y. by the potassium-argon method, and these authors conclude that Rodriguez became extinct in Pliocene-Pleistocene times. A fringing reef well offshore and extensive reef-flats border the southern and western coasts; on the east the fringing reef reaches the shore. Raised beaches have been found, and on the southern and eastern coasts cross-bedded calcarenites, of probable Pleistocene age, occur up to elevations of 62 m above sea level. However, on the evidence of the embayed coastline and fringing reefs, McDougall and others suggest that over-all subsidence has been dominant in the recent history of Rodriguez.

Companion papers by Simpson (1950) and Walker and Nicolaysen (1954) summarize the geology and petrology, respectively, of Mauritius. These authors postulate that sea-floor fissure eruptions, possibly in Cretaceous time, had built up by early Tertiary a pile of massive olivine-rich (picritic) basalt flows, with differentiation to trachytes and phonolitic trachytes that now appear as jointed plugs. The upper portion of this pile may have been removed by explosions or caldera collapse, and the stumps underwent long erosion. A late Tertiary series of somewhat vesicular olivine-bearing tholeiitic flood basalts covered the southwestern part of Mauritius. The final volcanic event was the eruption of vesicular olivine-rich flood basalts from a NNE.-trending group of 25 shield volcanoes. These flows form the present watershed of Mauritius and comprise the small islands to the north. Since the most recent basalts are overlain locally by coral reefs assigned to high Pleistocene sea levels, these authors conclude that volcanism on Mauritius ended more than 100,000 years ago and that eustatic submergences and emergences have been superimposed on a progressive subsidence of the volcanic pile. The present study indicates that the NNE.-trending line of weakness extends at least to 19° S. and may be expressed in the very deep cleft near 19°20′ S., 58° E.

The geology of volcanically active Réunion has been studied most extensively by Lacroix (1936) and, more recently, by Upton and Wadsworth (1965). Drawing on the former author's work, Walker and Nicolaysen (1954) compared the islands of Mauritius and Réunion, finding petrological similarities as well as rather important differences, particularly in the youngest volcanics. The lower (older) part of the Piton des Neiges series on Réunion corresponds petrologically to the oldest rocks on Mauritius. However, intrusions of gabbro, alkali-gabbro and quartz-syenite are found on Réunion; their absence on Mauritius might be due to foundering. The latest lavas of Réunion, such as those from the still-active Piton de la Fournaise, correspond to the Pleistocene flows on Mauritius, except that on Réunion the rocks are variations of tholeiite–picrite basalts of explosive eruption, while on Mauritius the late flows are very uniform vesicular olivine basalts. It may be noted here that while Réunion and Mauritius are separate piles, with deep-sea floor between them, the vents on Réunion have a northwesterly trend, and several well-attested, if isolated, shoal soundings west and north of Réunion indicate that the volcanic activity extends well beyond Réunion.

In all three of the Mascarene Islands, then, the latest volcanics are olivine basalts of oceanic type, dated at Pliocene-Pleistocene on Rodriguez, Pleistocene on Mauritius, and Recent on Réunion. Coral reef occurrences show a similar progression; reefs are extensively developed at Rodriguez, less so at Mauritius, and absent at Réunion.

Submarine Topography of Mauritius

Nearshore exploration of Mauritius clearly reveals the broadly indented lobate eastern slope resulting from volcanic flows and the relatively straight western flank here interpreted as a fault scarp (Pl. 2, fig. 2). On the southern and western coasts the shelf is up to 2 km wide, except for a 5-km southwestern extension of Le Morne Brabant. Off the northern coast a shallow bank extends for 26 km. To the east, the shelf width varies from 3 to 11 km, with the greatest width along the extension of the early volcanic Bambou Mountains. The prin-

cipal shelf break is at 80–90 m (Pl. 2, fig. 1, G–G′), but terraces occur at depths of about 28, 38, and 48 m.

The steep western flank and less regular eastern slope (Pl. 2, fig. 3) both show pinnacles or irregularities at depths greater than 2000 m. At shoaler depths on the east side the echo-sounder return is sharp and discrete, suggesting the presence there of masking lava flows from the most recent volcanoes. One supposed late flow is shown in profile on the upper section (Pl. 2, fig. 3). Inshore lines paralleling the western slope (Fig. 3, 4) show small gullies or can-

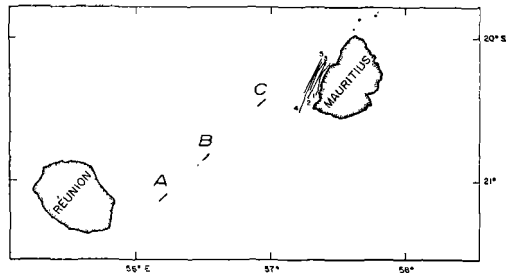


Figure 3. Index map for Figure 4 and Plate 3

yons that have not been traced to the base of the slope. Exploration east of the island has not been done in sufficient detail to determine if canyons occur there. The large re-entrant off Rivière du Rempart (Pl. 2, fig. 2) is a valley between volcanic lobes.

West of Mauritius, at depths greater than 2500–3000 m, an apron extends to the archipelagic plain which lies at 4362 ± 7 m. The surface of this apron (Pl. 3, C) is relatively gentle but shows some low irregularities; Heezen and Tharp (1965) have termed such undulations abyssal swales. East of Mauritius an apron is well developed in the re-entrant near 20° S., but southeast of the island it is sharply terminated by the Mauritius Trench (Pl. 1). Reflection profiles (Fig. 5, upper) show the sediments collected in the deep area east and east-northeast of Mauritius.

Magnetic traverses around Mauritius confirm the conclusion that this island is composed primarily of basic volcanics extruded as flows rather than as ash or pumice; the magnetic traces closely reflect the topographic relief. Gravity measurements made during *Argo* and *Vema* surveys have not been fully interpreted.

Submarine Topography of Réunion

Réunion is the exposed portion of a volcanic pile more than 30,000 km² in area at the 4000-m contour (Pl. 1). Exploration is scanty, but the flanks appear to be unfaulted. Steep upper slopes decrease in gradient at depth to merge with the deep sea floor (Fig. 3; Pl. 3, B, C). A seismic reflection profile crossing the base of the slope east of the island (Fig. 5, lower) does not detect acoustically transparent sediment there on the broad apron. The northern and western flanks are less regular. A north-south sounding profile passing 30 km west of Réunion (Pl. 4, fig. 1, A) crosses a 50-km-wide plateau lying at a depth of 2000–2300 m. Its surface roughness suggests a collapsed crater, a link to the volcanism west of Réunion noted above. Peaks to the west and a large caldera(?) on the submerged flank of Réunion fit very well with a suggestion of Upton and Wadsworth (1965) who studied Réunion itself. They consider that over-all volcanic activity has steadily shifted southeastward from Piton des Neiges. On this assumption, the submerged caldera is older than some of the late Quaternary flows of oceanic basalts from Piton des Neiges. The trend may mark a rift developing on the sea floor in a southeasterly direction, and the possible source of the flood basalts. The trends and extent of the several peaks and deeps from 250 to 450 km southwest of Réunion (Pl. 1), and their relation to the development of the Mascarene Plateau, are not well established.

Neither the faulted Mauritius nor the more extensive Réunion is bordered by a moat. Moats or bordering depressions are variously ascribed to scour, to caldera collapse, or to subsidence due to loading of the oceanic crust by a volcanic pile. In the case of Réunion, at least, the absence of such a feature may be in accord with its relative youth. However, the frequency of cable failures on the lower slopes and northern apron (Fig. 6) indicates that slumping or deposition by turbidity currents or both may have buried the depression; the small peaks between 22° and 23° S. near 55° E. protrude above a sedimented apron.

Rodriguez Ridge

The elliptical shape of Rodriguez and its surrounding platform is continued at depth; that island is the only emergent portion of a narrow, nearly east-west ridge that can be traced westward at least to an intersection with the Mas-

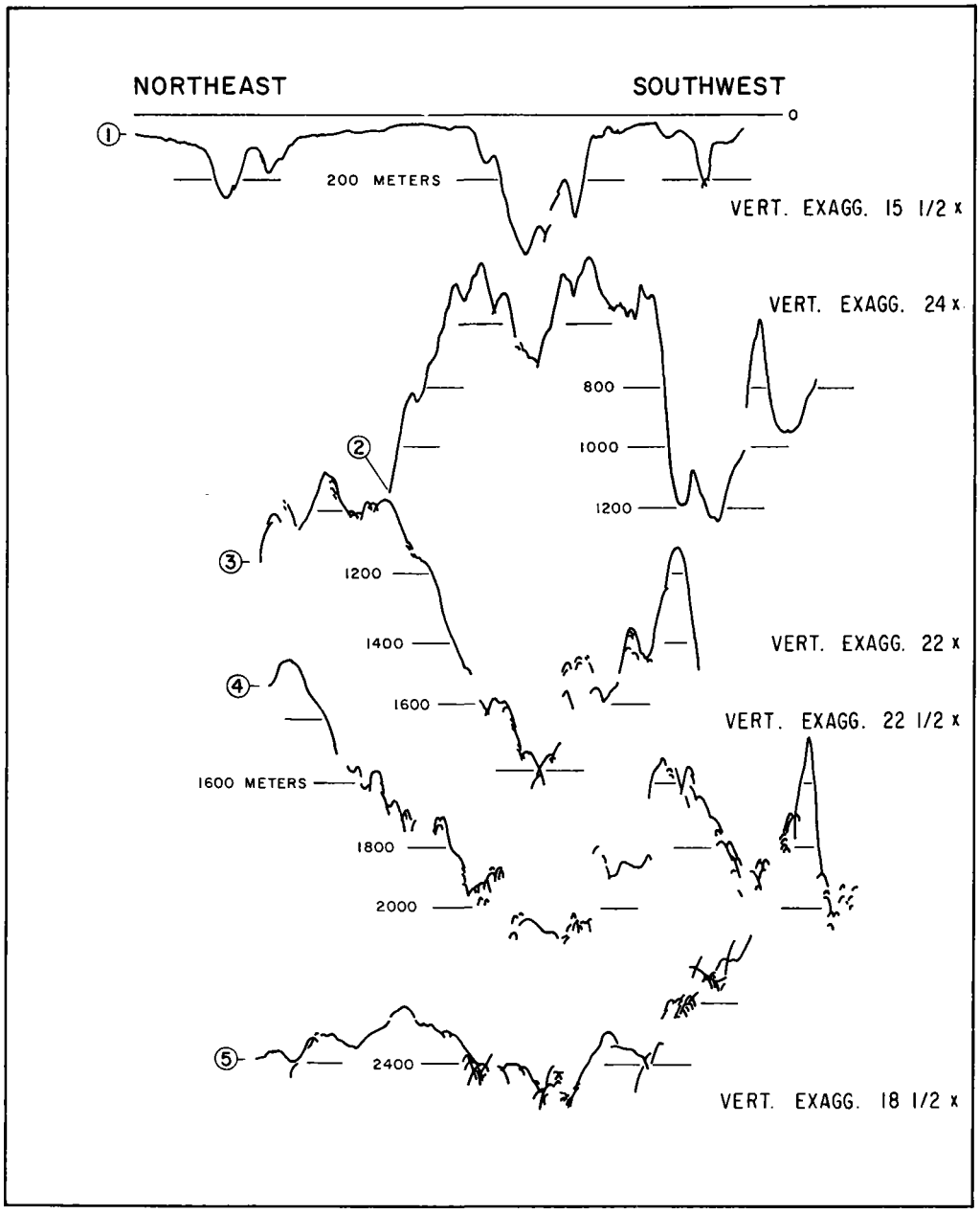
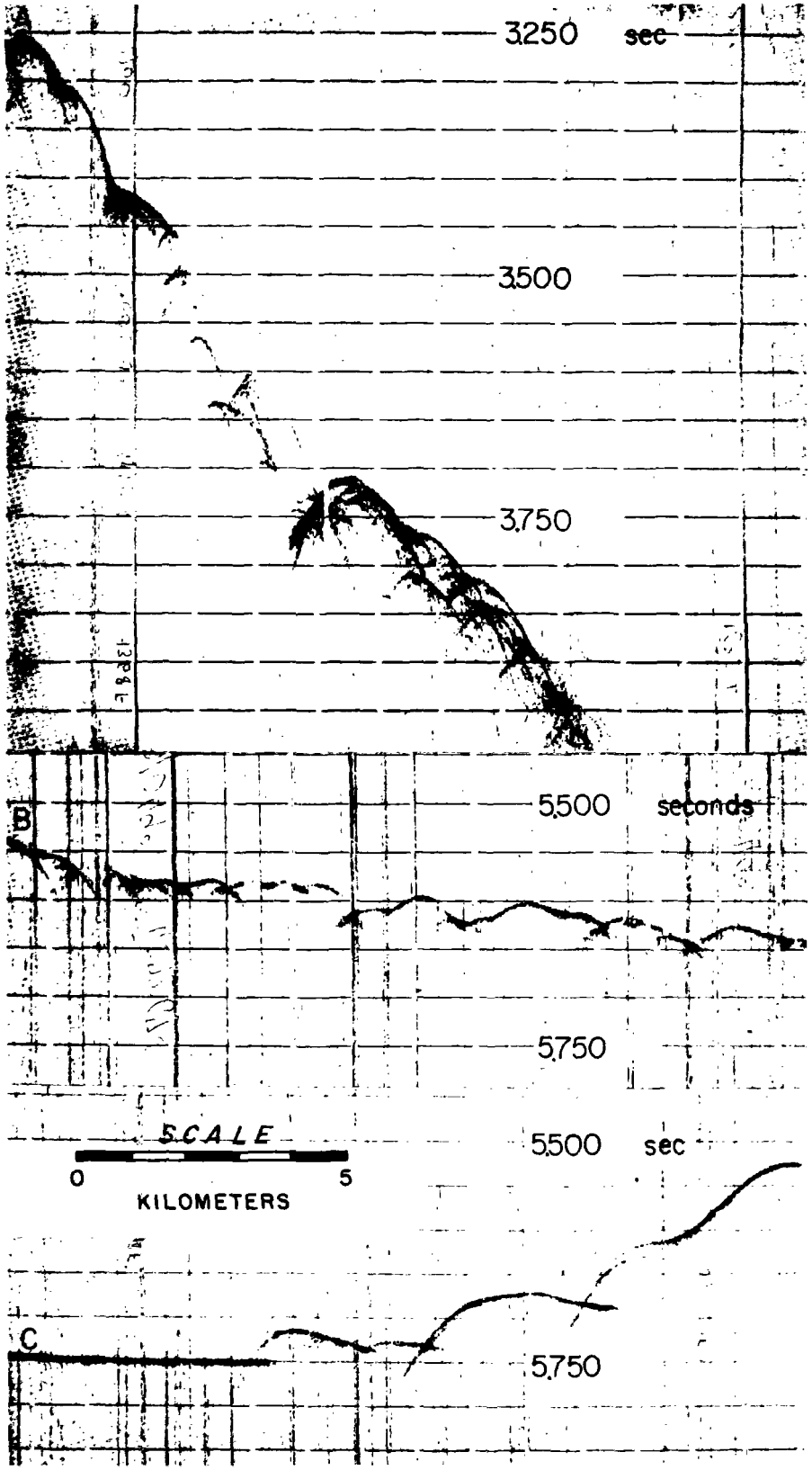
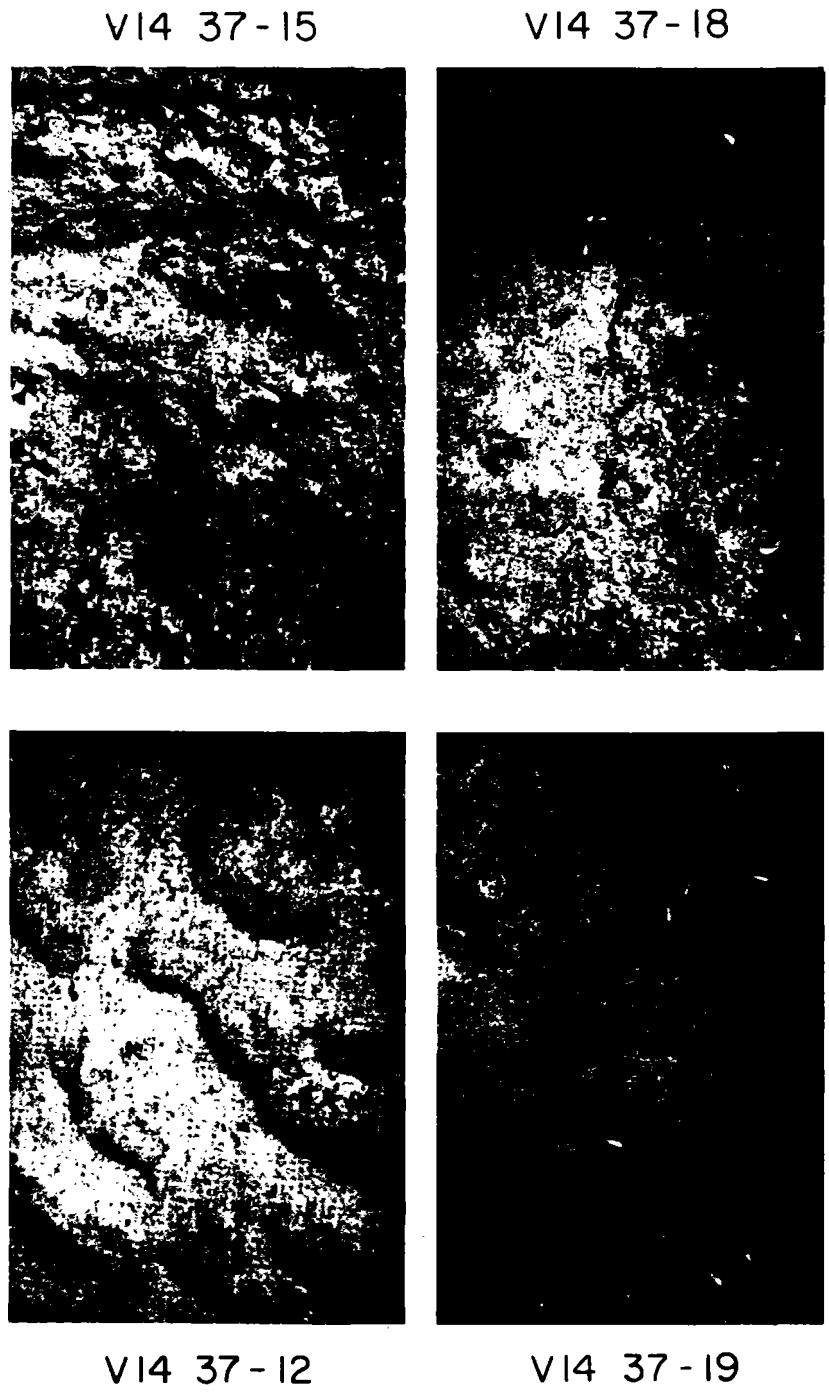


Figure 4. Redrawn sounding traces along the western slope of Mauritius. See Figure 3 for locations of profiles.

carene Plateau (Pl. 1). The two connected shoals between Mauritius and Cargados Carajos, separated from the latter features by passes more than 2500 m deep, apparently belong to this structure rather than to the Mascarene Plateau proper, but the westerly trend does not extend into the Mascarene Basin. The Rodriguez Ridge is most poorly expressed at its intersection with the "Mauritius Trench" near 60° E.; soundings to date indicate that the pass is nearly 4000 m deep and the trench complex may extend as an ill-defined basin adjacent to

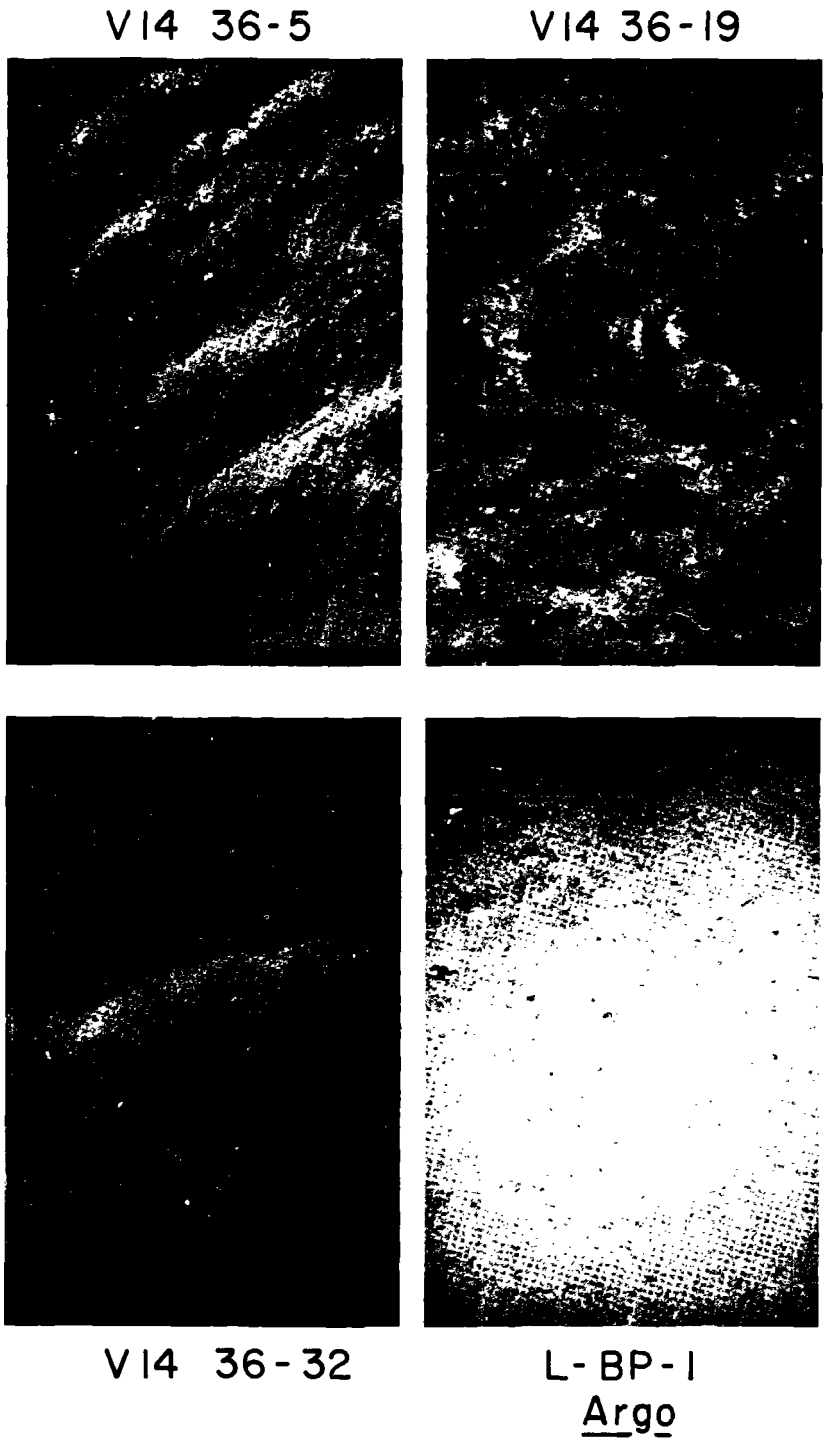


THREE SEGMENTS OF A *VEMA-16* PRECISION DEPTH RECORDER RECORD MADE BETWEEN MAURITIUS AND RÉUNION: A) Insular slope of Réunion. B) Réunion apron. C) Base of slope west of Mauritius. See Figure 3 for location of segments. Vertical scale: reflection time in milliseconds.



BOTTOM PHOTOGRAPHS FROM STATION V14–37

Bottom photographs from station V14–37 (20°12′S., 57°23′E.) on the western flank of Mauritius, at depths of about 800 m (Pl. 4, fig. 2).



BOTTOM PHOTOGRAPHS FROM STATION V14–36 AND LUSIAD BP-1

Bottom photographs from stations V14–36 (23°06′S., 56°43′E., depth 4800 m) and Lusiad BP–1 (24°33′S., 57°29′E., depth 5050 m) on the deep-sea floor south of Mauritius (Pl. 4, fig. 2).

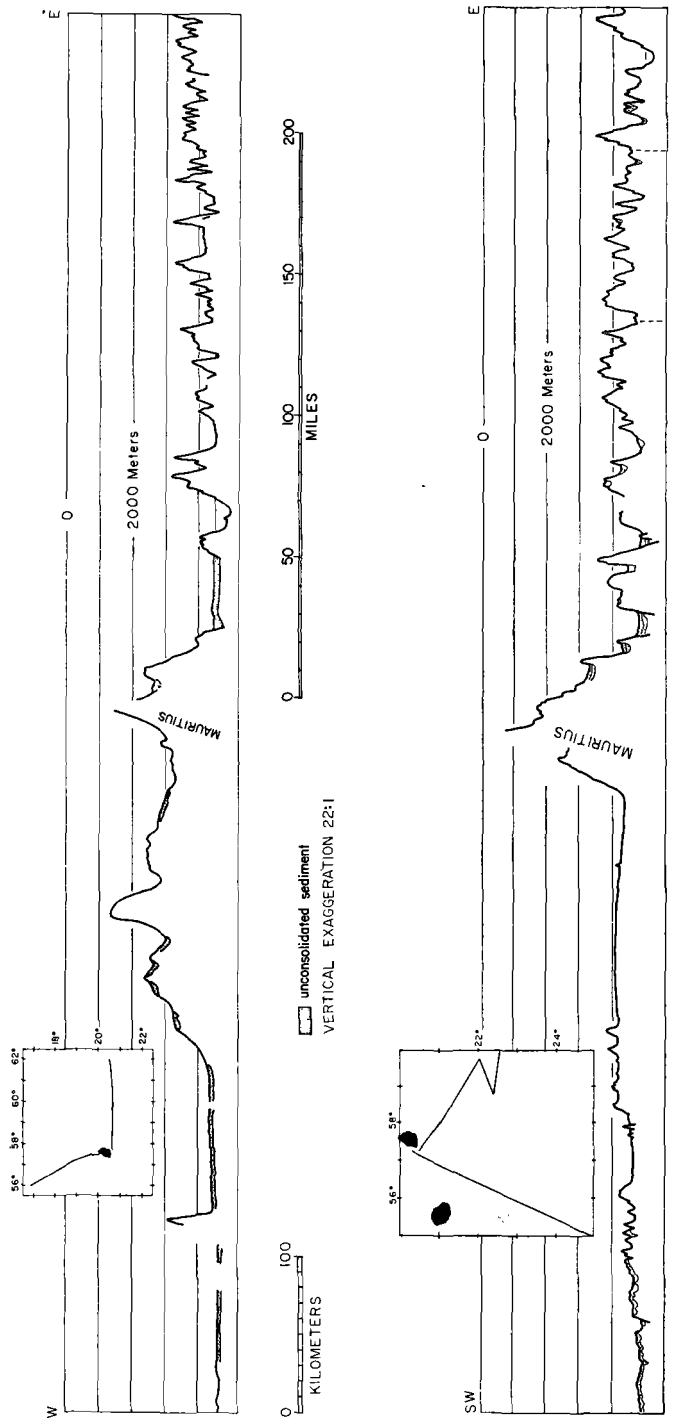


Figure 5. Seismic reflection profiles: upper, *Vema*-18, 1962; lower, *Vema*-20, 1964.

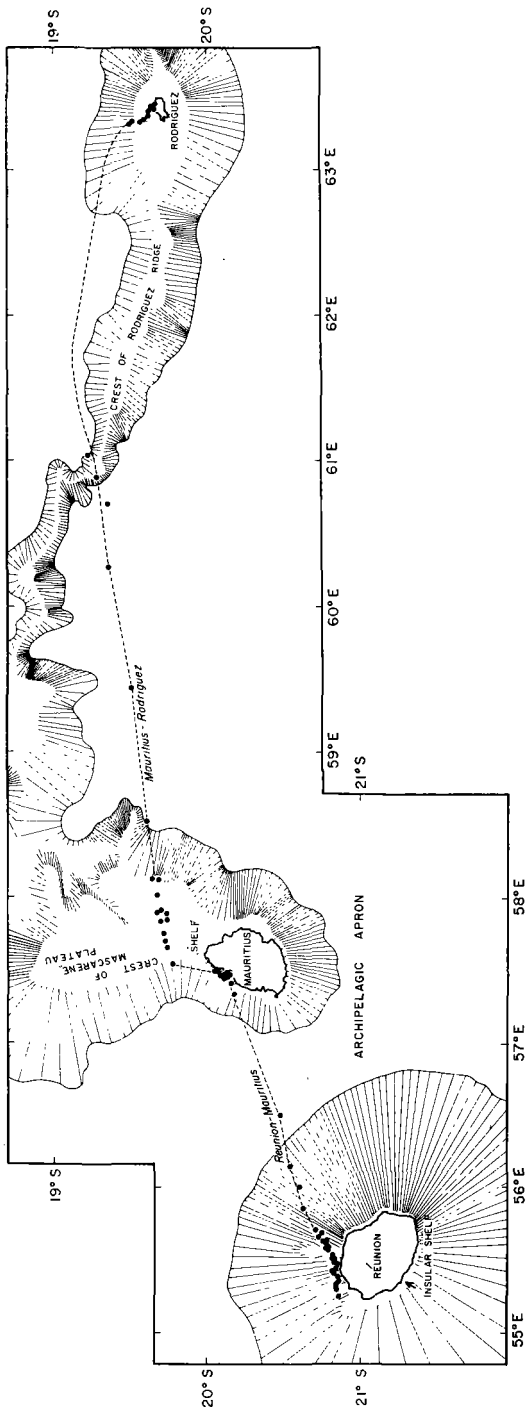


Figure 6. Cable failures between Réunion and Rodriguez since 1901.

Cargados Carajos. The shoalest portions of the ridge are not irregular or conical peaks, but elongated blocks with terraced, reef-flattened summits. Two banks are shallow enough to support living reef-corals. The western portions of the shoals centered at 61°30′ E. and at 62°15′ E. are guyots or drowned atolls, supporting the evidence for subsidence of Rodriguez reported by McDougall and others (1965).

Marked shoals occur as far east as 64° E. and the ridge could continue for several hundred km to the east as a narrow spine, either just north or just south of 20° S. An interpretation by Heezen and Tharp (1965), shown in Figure 2 of this paper, postulates that the Rodriguez Ridge lies on a major fracture zone along which an apparent 300 km left-lateral offset of the axis of the mid-oceanic ridge has occurred. Exploration between 19°–23° S. and 65°–75° E. is insufficient to establish that offset or the exact nature of the intersection of the southeast and southwest branches of the mid-oceanic ridge complex. There are no sounding tracks between 20°–21° S. and 66°–70° S. Less direct evidence than Precision Depth Recorder records—regional level, seismicity and heat flow—suggests, however, that Rodriguez Ridge and its postulated extension eastward as a fracture zone is a major structural discontinuity. First, north of 20° S. there is extensive shoal (<3000 m) development of the north-northeast-trending mid-oceanic ridge (Pl. 1). To the south and east of 21° S., 68°30′ E. a comparable shoal area, and possibly a median valley, trends more nearly north-south for more than 400 km, and farther south bends toward the southeast. The north-south topographic lineations south of the Rodriguez Ridge between the longitudes of Mauritius and Rodriguez are not obvious north of 20°–21° S. Second, north of 20° S. the single mid-oceanic ridge is seismically active (see Gutenberg and Richter, 1954). From 20° S. to the vicinity of Amsterdam–Saint Paul, the southeast branch is much less active. Third, Von Herzen and Vacquier (1966) note that heat-flow values obtained on the crest, flanks, and lower flanks of the mid-oceanic ridge between 11° S. and 28° S. group into two populations. Measurements north of 20°–21° S. characteristically are low; 21 values average 0.6×10^{-6} cals/cm^2/sec. Twelve values south of 21° S. average 2.6×10^{-6} cals/cm^2/sec. Similarly, M. Langseth (personal commun.) found very high values near 22° S. This evidence is suggestive, but not conclusive, relative to a "Rodriguez fracture zone"; however, the association of generally high heat flow with present low seismicity is puzzling.

THE MAURITIUS TRENCH

Southwest of the intersection of the Rodriguez Ridge and the Mascarene Plateau, the smooth slopes of the Mascarene Basin–Mascarene Rise are separated from the irregular sea floor of the Réunion Basin by a deep trough or trench that is clearly tectonic in origin. This feature, which has been traced southwestward for a distance of 1400 km to 28° S., 51° E., is here designated the Mauritius Trench (Pl. 1; Fig. 2). It is distinctively straight, narrow, and flat-floored over much of its length, and thus provides a key base for the very rugged linear pattern to the east.

All bathymetric profiles taken within a sector extending from northeast of Mauritius clockwise to south of that island show extremely irregular topography extending for from 300 to 500 km seaward of Mauritius. Plate 4, figure 3 (see Pl. 4, fig. 2, for locations) was constructed from soundings from several sources; the apparently greater irregularity of the peaks, and flatness of the small deeps along profiles 2, 5, 6, 8, 9, 10, and 13, as contrasted with profiles 1, 3, 4, 11, and 14, are due to closer spacing and greater precision of soundings in the former group. East of 60° E. southeast of Mauritius, the narrow deeps (>5000 m) do not appear; the relief is irregular in the range 3400–4600 m out to the southwest-trending mid-oceanic ridge near 25° S., 66° E.

In a sector south-southeast to south-southwest of Réunion (Pl. 1; Pl. 4, fig. 3: profiles 10–14), the well-defined Mauritius Trench lies north of small linear deeps and several hundred km of deep swale topography within the Réunion Basin. The extremely irregular mid-oceanic ridge is reached near 31° S., 57° E.

The depth of the Mauritius Trench is at least in part a function of the amount of sedimentary fill received from Mauritius and Réunion. Along profile 6, for example, where the trench is 4485 m deep, seismic reflection measurements (Fig. 5, lower) show at least an additional 250–300 m of sediment without the basement being detected. Most of the filling must be due to deposition of sediment transported along the sea floor. Throughout the year, winds and surface currents are westerly; volcanic ejecta from the islands would move toward the Malagasy Abyssal Plain. The greatest depth yet found in the Mauritius Trench, 5810 m, lies between 26° and 28° S., far from emergent volcanoes.

Most extensive fill occurs at the foot of the insular slope of Mauritius, and to the southwest, off Réunion, the amount of filling depends on protection afforded by the narrow ridge on the northwest side of the trench (Pl. 4, fig. 3: profiles 9, 11). However, it is not clear whether or not this portion of the Mauritius Trench predated the formation of the large shield capped by Réunion; bathymetric lines southeast from Réunion to the trench as drawn are lacking. A small depression in the sediment fill near the western side of Mauritius Trench on profiles 6 and 7 (Pl. 4, fig. 3) suggests that here the trench is still subsiding.

Deeper, less-sedimented clefts lie subparallel to Mauritius Trench farther to the east and southeast. One, near 20° S., 60° E. (Pl. 1), is receiving sediment through a gap in the ridge east of Mauritius Trench. The shape of the basement in this ridge-and-trough region is not known, but the over-all pattern suggests splinter faulting—with closely spaced parallel or subparallel faults that extend several tens of kilometers along the strike—coupled with volcanism along the ridges and extension in an easterly or southeasterly direction south of Rodriguez Ridge.

SEDIMENT DISTRIBUTION

Seismic reflection measurements were made by the *Vema* during cruises 18 and 20 (1962 and 1964, respectively). A thickness of 100 m of sediment was detected in the smooth topography to the northwest of Mauritius (Fig. 5, upper). The lack of relief at the base of the zone suggests it is a sediment–sediment boundary rather than a sediment–basement contact. Reflection results gave little indication of the total thickness of sediment in this area. East of Mauritius, beneath the Mauritius Trench, more than 200 m of sediment was observed; here again it is likely that a much greater thickness of sediment than the measurements indicate is present. The smooth archipelagic apron south of Réunion consists of acoustically opaque sediments. One core in the area (Pl. 4, fig. 4: V16–73) is composed entirely of pyroclastic debris.

Sediment cores on the crest of the Mascarene Plateau consist primarily of calcareous lutite (Pl. 4, fig. 4: V14–89, V14–90). Turbidites and volcanic debris are found on the archipelagic aprons (Pl. 4, fig. 4: V16–73, V16–74). Analysis of a pebble from a depth of 500 cm in core V16–73 showed labradorite 45 percent, pyroxene 45 percent, ore 5 percent, and glass 5 percent; the composition is similar to that of the basalts erupted by Piton de Fournaise (D. Ninkovitch, personal commun.). Brown lutite is the type of sediment generally found in the isolated deep ocean basins adjoining the islands (Pl. 4, fig. 4: V16–75, V18–198). Core V16–75 has been dated by the protoactinium–ionium method by T. Ku of Lamont Geological Observatory. He found a rate of sedimentation of 6 mm per 1000 years. From seismic reflection profiles (Fig. 5), the rough topography east of the Mauritius Trench and at the flanks of the mid-Indian Ocean Ridge appears to be nearly devoid of sediment. This is borne out for the most part by bottom sampling and by photographs which reveal frequent outcropping of rock and evidence of deep-sea currents. A short core (Pl. 4, fig. 4: V18–199) was taken on the flank of the Mid-Indian Ocean Ridge. The lower portion of this core consisted almost entirely of irregular fragments of serpentinite. Petrological examination of a sample at 160 cm below the top revealed a composition of serpentine 70 percent, magnetite 25 percent, and iddingsite 5 percent. A sample at 170 cm consisted of serpentine 35 percent, carbonate (magnesite) 35 percent, magnetite 25 percent, and iddingsite 5 percent. The serpentine, magnesite, and iddingsite are products of the alteration of olivine. The primary rock was composed of olivine 75 percent and very fine-grained and dispersed magnetite 25 percent (D. Ninkovitch, personal commun.).

Photographs showing rock outcrops and rippled bottom have been taken on the west flank of Mauritius in depths of about 800 m (Pl. 5). Photographs taken south of Mauritius at a depth of 4800 m show a current-scoured and rippled bottom (Pl. 6: V14–36). Bottom currents producing these features must have a considerable effect on the distribution of sediments. Currents are most active on the steep submarine slopes of the islands and over the shoal portions of the submarine plateaus and ridges, but also act at the base of these elements. The pattern and frequency of failure, mostly through chafe, of submarine telegraph cables between Réunion and Rodriguez (Fig. 6) gives clear evidence of current activity. An undisturbed mud bottom occurs in the swale topography 450 km south of Mauritius (Pl. 6: L-BP-1).

DISCUSSION OF TECTONIC ELEMENTS

The Mascarene Plateau, the Mid-Indian Ocean Ridge, and the Rodriguez Ridge are

VOLCANIC SLOPE ECHO-SOUNDER TRACINGS, INDEX MAP, BATHYMETRIC PROFILES, AND SEDIMENT CORE LOG

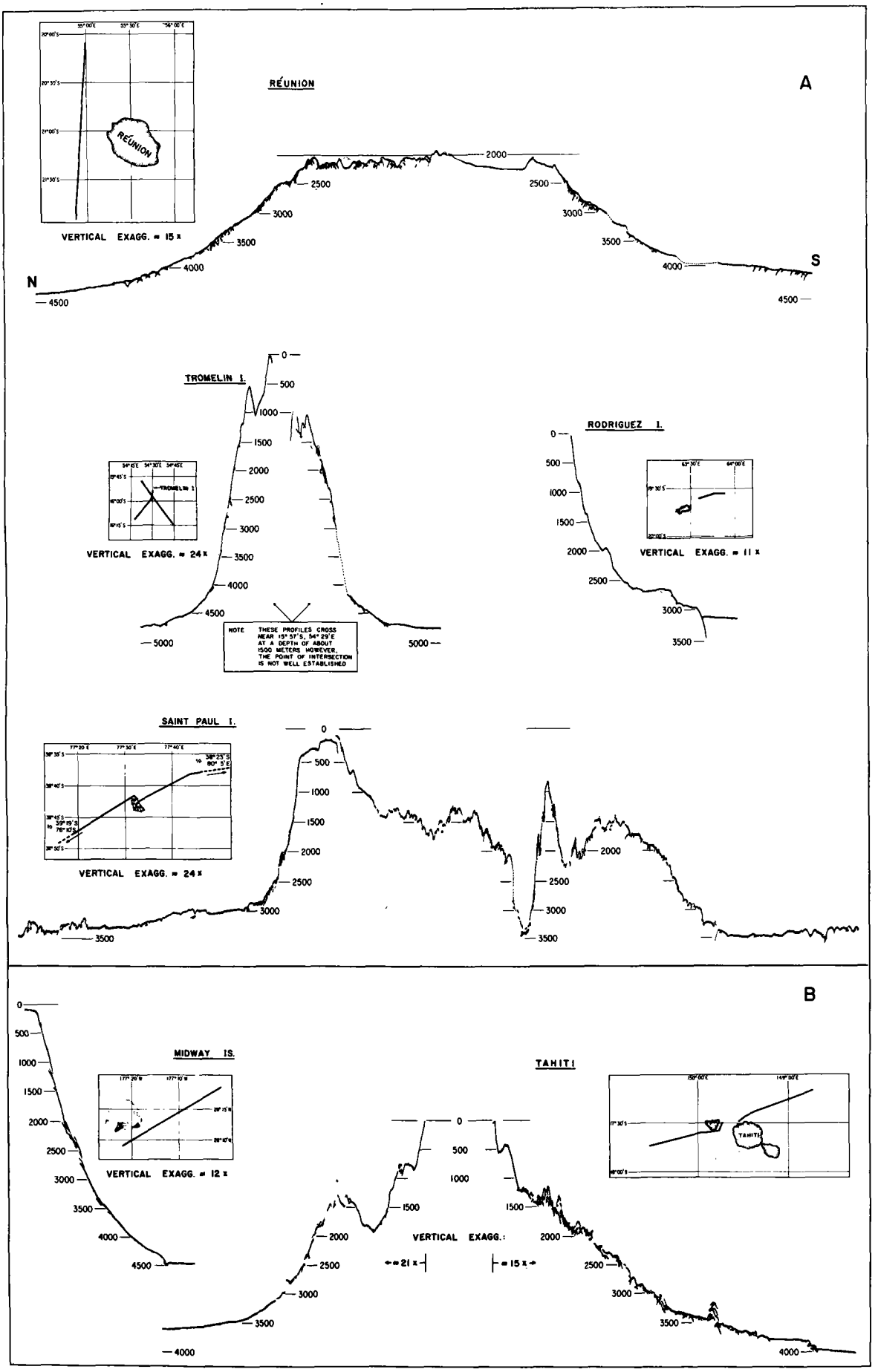


Figure 1. Tracings of Precision Depth Recorder profiles of slopes of volcanic structures.

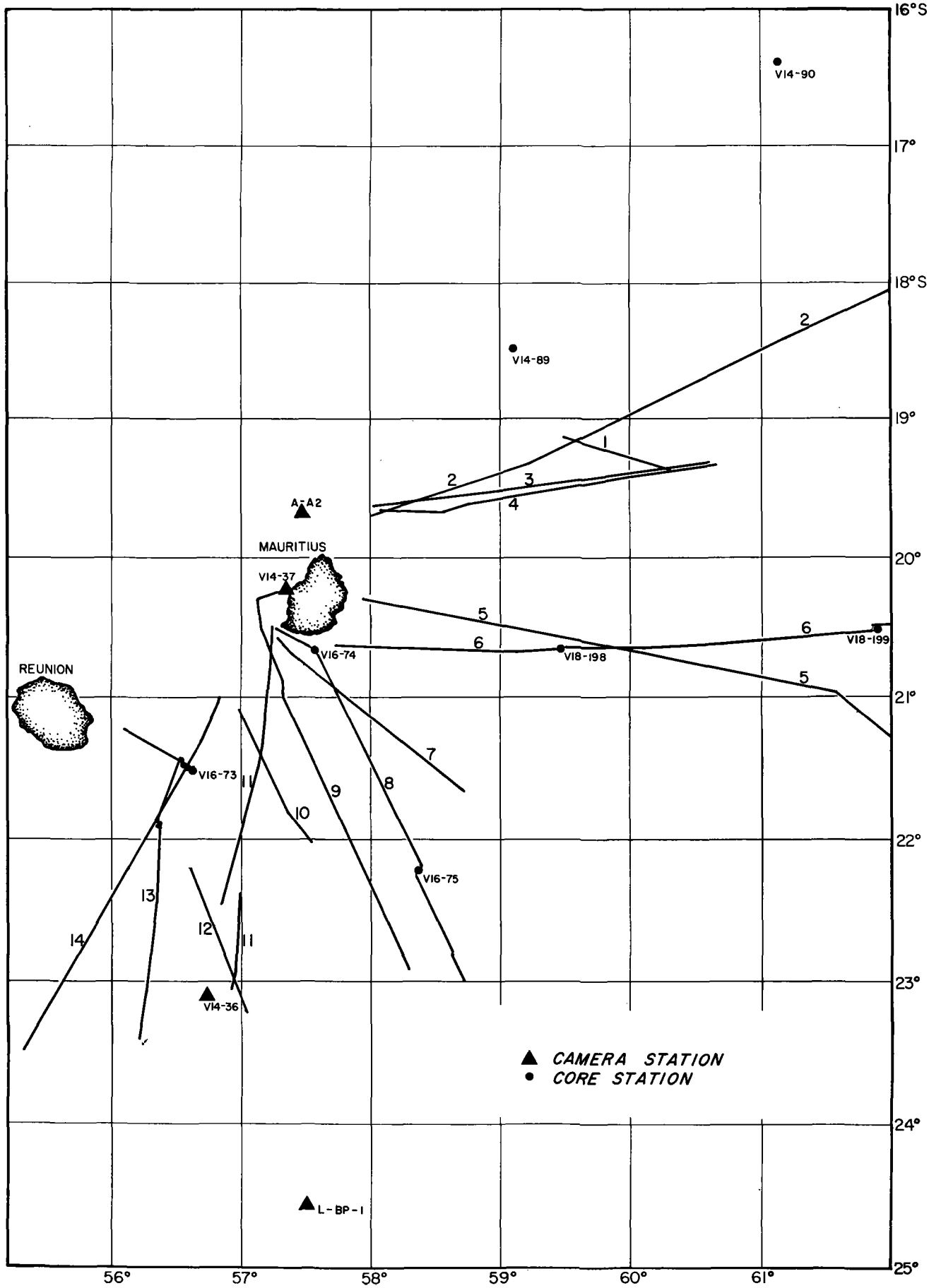


Figure 2. Index map for Plate 4, figs. 3 and 4, and Plates 5 and 6.

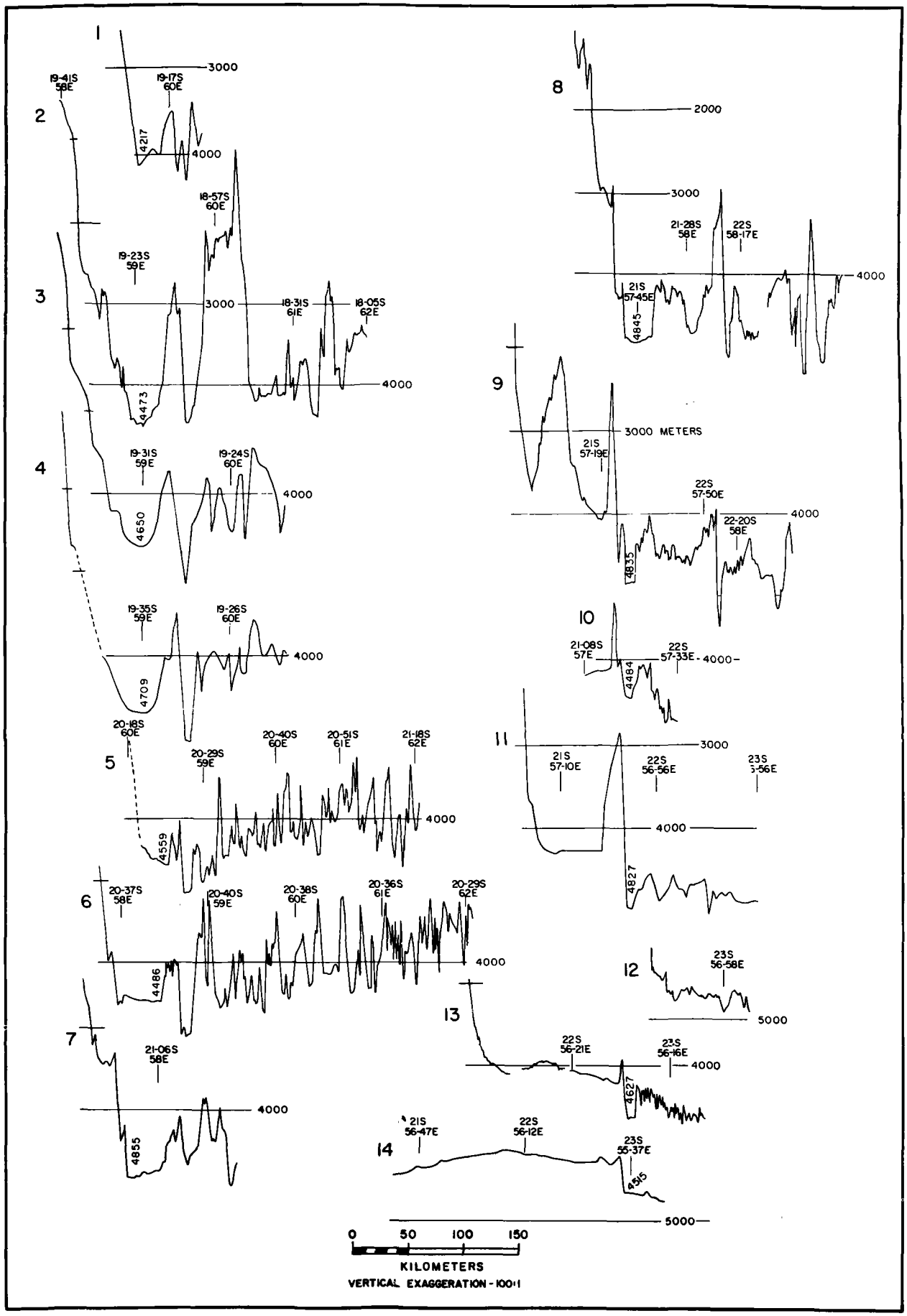


Figure 3. Bathymetric profiles of the Mauritius Trench and rough topography east to south–southwest of Mauritius. See fig. 2 above for location of profiles.

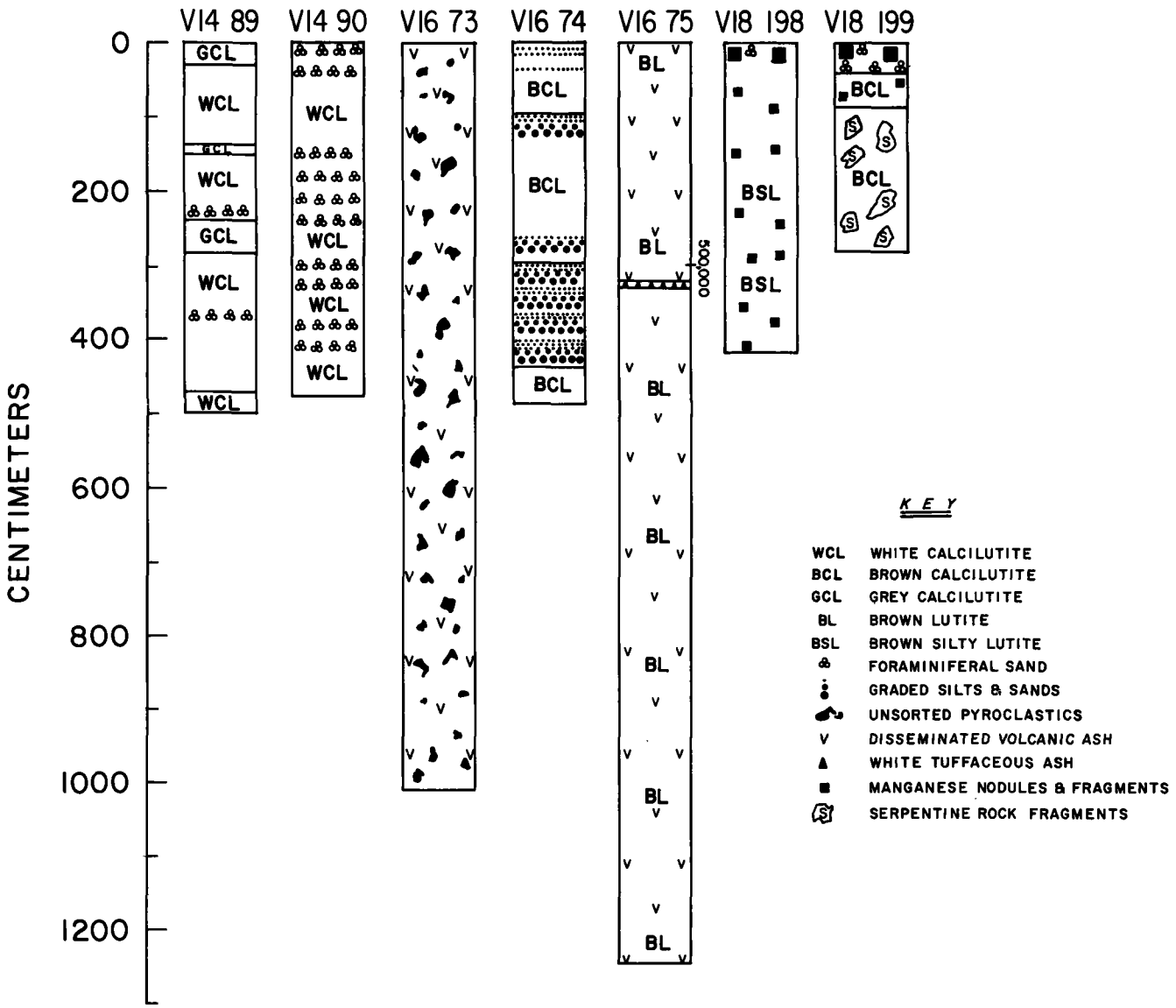


Figure 4. Graphic log of seven LGO sediment cores taken near Mauritius (see fig. 2 above). V14–89: 18°29′S., 59°06′E., depth 2681 m. V14–90: 16°23′S., 61°09′E., depth 3314 m. V16–73: 21°30′S., 56°34′E., depth 4057 m. V16–74: 20°40′S., 57°35′E., depth 2906 m. V16–75: 22°13′S., 58°23′E., depth 4767 m. V18–198: 20°30′S., 59°28′E., depth 4413 m. V18–199: 20°31′S., 61°55′E., depth 3301 m.

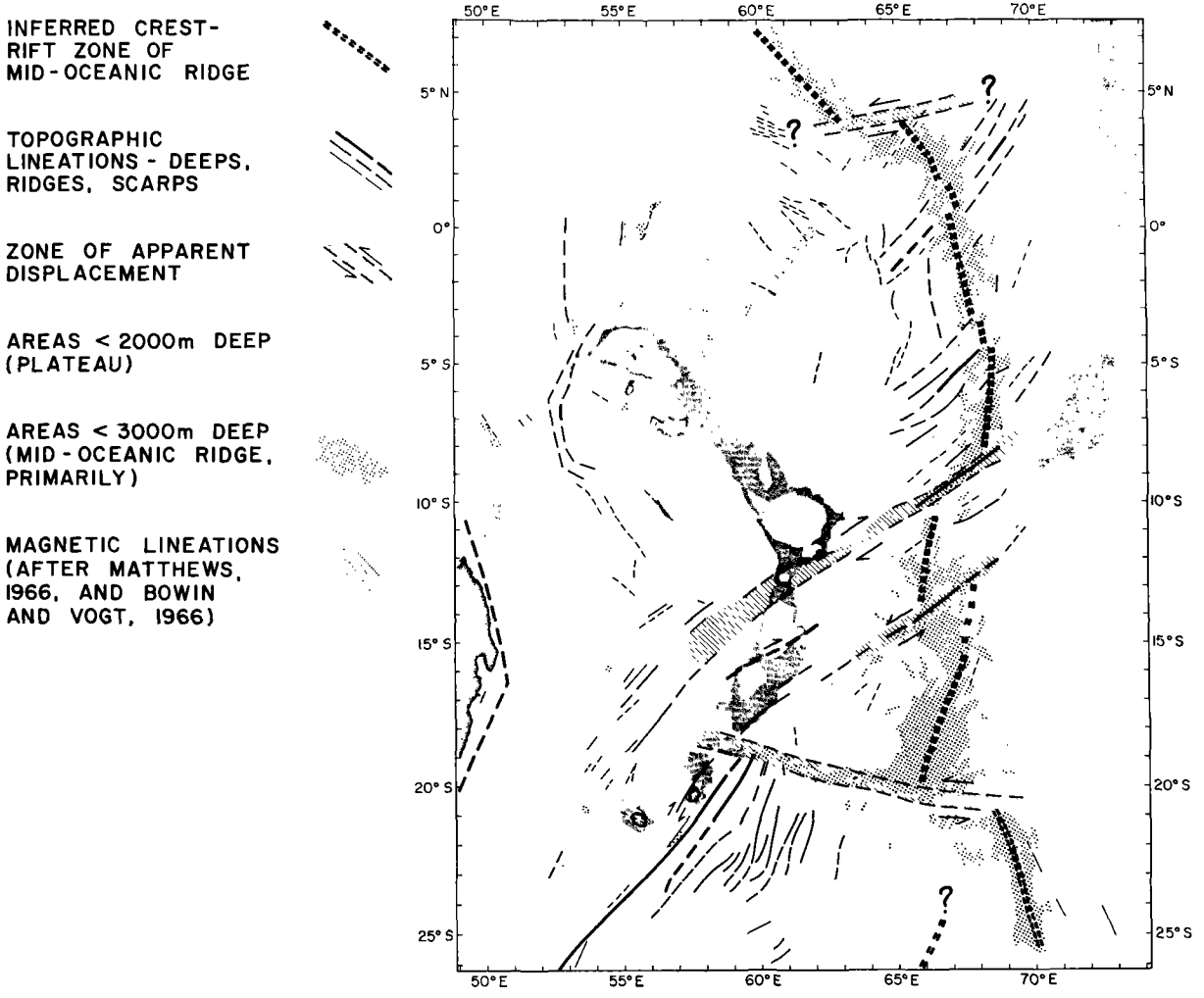


Figure 7. Lineations and inferred structural trends.

discrete but interrelated features differing in age, crustal structure, stage of development, and nature of fracturing. Some of the fault trends can be traced across both the mid-oceanic ridge and the Mascarene Plateau (Fig. 7). The fractures are still active and apparent at the crest of the mid-oceanic ridge, but are inactive and buried beneath the sedimented aprons and plains. The time that has elapsed since the most recent movement along any of the NE.-SW. fractures apparently increases with increasing distance from the crest of the mid-oceanic ridge, but the date at which the Mascarene Plateau was offset cannot yet be determined. This variation in time of activity on single zones also implies that these are not classical strike-slip faults, but that some, at least, are transform faults, belonging to a new class of horizontal shear faults recognized by Wilson (1965 *et seq.*). The Chagos-Laccadive Ridge lies just east and northeast of the region here discussed. It is an aseismic north-south elevation, composed of coral atolls which are underlain by approximately 5 km of material whose compressional wave velocity ranges from 3 to 6 km/sec (interpreted as volcanic rock), and which overlies a thick crustal (6.8 ± km/sec) layer (Francis and Shor, 1966). Topographically similar to the Mascarene Plateau, it has not been appreciably offset by the prevalent northeast-trending fracturing.

Any inferred geologic history for this region must be extremely speculative at this stage of investigation. Nevertheless, a presentation based primarily on topographic evidence, but with the following assumptions, interpretations, or observations, will be made:

(1) Madagascar and Precambrian granitic rocks underlying Seychelles Bank were once joined or close together. A linear fault zone, active since Cretaceous time, lies just seaward of the east coast of Madagascar (Dixey, 1960, after Lemoine) and marks a sharp edge of the Precambrian block.

(2) The presence of basaltic agglomerate of early Tertiary age near Providence Reef, northeast of Madagascar (Wiseman, 1936), implies that initial separation had occurred by that time.

(3) The granitic basement underlying Seychelles Bank is sharply bounded on the eastern and northern sides of that bank (Francis and Shor, 1966; Matthews and Davies, 1966, respectively). Francis and Shor measured a 10-km-thick layer of 6.03 km/sec material from 100 km east of Agalega to the base of the western flank of Saya de Malha Bank, in water depths of from 2800 to 3900 m. It is here assumed that this quasi-continental crust underlies Coëtivy Island-Fortune Bank and extends southeast along the western side of the Mascarene Plateau perhaps as far as Cargados Carajos. West of Seychelles Bank it extends to the east side of the Amirante Ridge.

(4) Three seismic reflection profiles on the deep (1000–2000 m) portion of the Mascarene Plateau between the Seychelles and the northern edge of Saya de Malha Bank show dominantly flat-lying sedimentary beds (limestone?). Similar stratification was observed beneath the 1000–2000-m bench east of Cargados Carajos Bank, but no layering was detected beneath the shoalest and nearly level central portions of that bank, where magnetic anomalies of high amplitude and short wave length suggest the presence of volcanic rocks at shallow depth (Bunce and others, 1966).

(5) The granitic rocks of Seychelles Bank are intruded by early Tertiary basaltic dikes (Baker, 1963) which are expressed by short period high-amplitude anomalies on magnetic profiles recorded in the central portion of the bank (Matthews and Davies, 1966). Similar anomalies are found at Cargados Carajos and occasionally occur along the western flank of the Plateau but are absent from the few profiles run on the other banks (Bunce and others, 1966). From seismic refraction work on Saya de Malha Bank, Shor and Pollard (1963) reported a thick sequence of 4.4 and 5.4 km/sec material beneath from 1200 to 1500 m of calcareous debris and above an "oceanic crustal layer" (6.8–7.0 km/sec) whose upper contact lies from 8 to 9 km beneath sea level. Drawing an analogy to similar velocity-structure at Hawaii and Eniwetok, these authors suggest that the base of the Saya de Malha-Mauritius portion of the Mascarene Plateau was formed by outpourings of lava along a line of weakness in the ocean floor. However, similar velocity-structure was observed in the nonvolcanic Cretaceous and Tertiary limestone-and-marl sequence of the Blake Plateau (Sheridan and others, 1966). Davies and Francis (1964) report that on Seychelles Bank the upper contact of the 6.8–6.9 km/sec layer lies about 15 km below sea level; thus the crust beneath Seychelles Bank has both a continental character and a continental thickness, capped by less than a half kilometer of calcareous debris.

(6) The narrow, linear Rodriguez Ridge was formed by volcanic eruptions that ended, on

Rodriguez, about 1.5 m. y. ago. The age of initial volcanism on this trend is unknown.

It is postulated that late in Mesozoic time a portion of continental crust separated from Madagascar. Subsequently it has moved northeast, relative to Madagascar, a distance of from 1000 to 1200 km. (Alternatively, Madagascar may have moved south-to-southwest.) The extent of the fragment is not specified, but it included at least the present Seychelles Bank-Fortune Bank complex and possibly the entire western flank of the Mascarene Plateau north of Cargados Carajos. Oceanic basaltic material was emplaced between the separated blocks, and now floors the intervening oceanic area. Between Madasgascar and the Seychelles are ridges, peaks, and troughs formed by faulting and volcanism in a tensional environment; the Amirante Ridge and trench are products of this activity, though of more recent development. Their trend may be extended well north of the Seychelles. As a consequence of the disruption, a boundary line of weakness developed in a meridional direction; volcanic rocks now forming much of the Mascarene Plateau from Saya de Malha south to Mauritius were extruded, commencing in Cretaceous(?)-early Tertiary time. Limestone was deposited on the ridge as it neared the sea surface and coralline forms could be supported. Fundamental to this argument is a volcanic base underlying the banks from Cargados Carajos to Saya de Malha; recovery of rock samples by intensive dredging of the steep lower slopes, at depths of from 2000 to 3000 m, may be required to establish this point.

North and northwest topographic trends occur as major elements in the northwest quadrants of Plate 1 and Figure 7, north of a zone extending from Saya de Malha to eastern Madagascar. In the remainder of the area, lineations are considered to mark continuing adjustments of the oceanic crust, with displacement and volcanism in a system of subparallel shears, as a consequence of the separation. From Mauritius north to Saya de Malha Bank, the Mascarene Plateau appears to have been broken by northeast-southwest-trending faults with right-lateral offsets. The most obvious dislocation occurs between Saya de Malha and Nazareth Bank. This faulted zone apparently continues northeast and includes the Vema Trench, where topography and magnetic profiles (Von Herzen and Vacquier, 1966) indicate right-lateral offset of the crest of the mid-oceanic ridge, and southwest along the northeast-trending ridges, probably volcanic, that protrude from the floor of the sedimented Mascarene Basin south of Tromelin Island. Along this trend seismic activity is observed only where the zone crosses the mid-oceanic ridge. This implies that the ridge, rather than the fault zone, is now the active member. It is suggested that the northeast fracture pattern predates the development of the mid-oceanic ridge, although a rough parallelism of the eastern side of the Mascarene Plateau and the crest of the ridge south of 10° S. (from topography, magnetic profiles, and earthquake epicenters) implies that both plateau and ridge have been affected by the major fractures. Further, the transcurrent system has been active at times since initiation of the ridge, for segments of the ridge—if the ridge does represent continuing emplacement of new crust along a zone thousands of kilometers long (see next section)—would not have been born offset. Nevertheless, confinement of recent earthquake activity to the ridge crest, and especially to the areas where the fracture zones cross that crest, suggests ridge-widening and the predominance of transform faulting in the manner proposed by Wilson (1965). On such an assumption, igneous material is being added along the ridge crest; crustal blocks on both sides of a fracture zone are moving away from the crest; actual displacement between crestal segments on the Vema Trench fracture zone, for example, is now opposite to the apparent right-lateral offset; and the Mascarene Plateau, offset earlier, need not be differentially faulted, because movement is limited to portions of the faults lying between crestal segments. Earthquake first-motion studies, such as those of Sykes (1967), of this part of the mid-oceanic ridge system would establish the nature and direction of current faulting; closely spaced magnetic profiles south of 5° N. would test the existence of linear anomalies taken to indicate ridge growth (Vine and Matthews, 1963). Some well-expressed northeast lineations are not apparent where they would intersect the ridge crest, do not offset it, yet continue northeast of the ridge as well (for example, near the equator, Fig. 7).

The Rodriguez Ridge with its extension eastward across the mid-oceanic ridge complex was formed late in Tertiary time, but does not extend west of the Mascarene Plateau. Subsequent to the development of Rodriguez Ridge there has been separation between Mauritius and Cargados Carajos, and right-

lateral offset in the Mauritius block. The most recent lavas on Mauritius, from vents aligned in a NNE. direction, may have been extruded following this adjustment. The northwest-trending branch of the mid-oceanic ridge appears offset by the postulated eastward extension of Rodriguez Ridge. Again, present-day epicenters are confined to the mid-oceanic ridge itself. The southwest-trending branch, which lacks a well-developed crest within the area shown on Plate 1, is the more seismically active at present; its trend, extended, would not join the mid-oceanic ridge crest north of Rodriguez either.

The extremely rough, generally unsedimented, and youthful-appearing topography between the Mauritius Trench and the southwest branch of the mid-oceanic ridge is attributed to faulting and volcanism in a tensional zone on the deep-sea floor bordering the southwest branch of the mid-oceanic ridge. A continuation of this rough zone has not been found north of Rodriguez Ridge west of Rodriguez. Mauritius Trench, a recently active feature, forms a topographic boundary on the west, and may have been the chief locus of crustal dilation and graben formation. Its relief may derive from recent tectonic activity related to flood basalt volcanism at Réunion and Mauritius and to formation of deep irregular basins southwest of Réunion, but its trend, which parallels the mid-oceanic ridge, may be inherited. One core (Pl. 4, fig. 4: V16–75) from this topographically irregular region would, from its length alone, imply sedimentation at least since early Pleistocene time; the upper 25 percent of this 12-m core was deposited in the last 0.5 m.y.

TECTONICS OF THE WEST CENTRAL INDIAN OCEAN

According to recently presented geological-geophysical evidence for sea-floor spreading, the worldwide mid-oceanic ridge has grown wider throughout geologic time (Heezen, 1959). In the area discussed here this growth is manifested by a progressive separation of the Mascarene Plateau and the Chagos-Laccadive Plateau. Such separation is apparently accomplished by addition of crustal material at the crest of the mid-oceanic ridge (Heezen, 1960, 1962; Hess, 1962, 1965; Vine and Matthews, 1963; Vine, 1966). The swale topography which covers large areas south of Réunion and extends through the area west of the Mascarene Plateau from Réunion to the Seychelles probably represents more thickly sedimented and thus relatively old oceanic crust. Similarly, the magnetic lineations north and northeast of the Seychelles (Fig. 7) figured by Matthews (1966) and by Bowin and Vogt (1966) may be due to ridge topography now buried or thickly sedimented. Topographic lineations are not well developed in this portion (Pl. 1). Nearer to and on the Carlsberg Ridge, northwest topographic trends are apparent. A detailed survey of the ridge crest centered on 5° 20′ N., 61° 45′ E. (Matthews and others, 1965) showed that topography and magnetic anomalies there are elongated parallel to the ridge.

The Carlsberg Ridge sector of the mid-oceanic ridge was apparently created by the emplacement of new crust during the separation of the Seychelles granitic block from the Indian subcontinent. The fractures which transect the Carlsberg Ridge are nearly parallel to the NNE.-trending Owen Fracture Zone (Matthews, 1966) near the western termination of the Carlsberg Ridge, but their trend progressively shifts to northeast between the Owen Fracture Zone and the Vema Trench (Heezen and Tharp, 1965, 1966). Throughout the worldwide mid-oceanic ridge system, the crest of the ridge characteristically lies parallel or subparallel to the edges of the bordering continental blocks; this is shown most strikingly in the relatively simpler geometry of the Atlantic. In the more complex tectonic pattern exhibited by the central Indian Ocean floor, this mid-oceanic ridge is neither closely parallel to, nor exactly in a median position between, the major continental blocks of Africa, Australia, Asia, and Antarctica. However, the Carlsberg Ridge sector of the Mid-Indian Ocean Ridge does lie in a median position between, and is parallel to, the margin of the Indian subcontinent on the northeast and the Seychelles granitic block on the southwest. The segment of the Mid-Indian Ocean Ridge between Vema Trench and the Rodriguez Ridge lies in a median position between, and is approximately parallel to, the Saya de Malha-Mauritius portion of the Mascarene Plateau and the extension southward of the Chagos-Laccadive Plateau. Thus, in the central Indian Ocean, these microcontinents bear a close geometrical relation to the mid-oceanic ridge similar to that borne by the major continents bordering the Atlantic. This relation suggests that these microcontinents have acted as "continents" during development of the mid-oceanic ridge in the central Indian Ocean. Their function here as "continents" does not

imply any particular petrologic character of their foundations or help to discriminate between intrusive, extrusive, or sedimentary origins, but may simply reflect their extent and near-continental crustal thickness. However, it does imply that their foundations did exist, in approximately their present form and extent, prior to the birth of the Mid-Indian Ocean Ridge system.

Throughout the world, the mid-oceanic ridge ranges in width from less than 400 km, as in the Norwegian Sea and the Gulf of Aden, to more than 5000 km in the Southeast Pacific. Minor relief of the ridge characteristically consists of subparallel ridges and troughs. Major changes in ridge width tend to occur at fracture zones, which probably mark discontinuities in rate of ridge growth. The 1000-km-wide Carlsberg Ridge may have grown during the same interval as the 300-km-wide section of the Mid-Indian Ocean Ridge lying between Nazareth Bank and Chagos Bank.

Geophysical exploration to supplement and extend the topographic information presented here is required to establish the character of the Mid-Indian Ocean Ridge between fracture zones south of 5° N., and to test the structural pattern here proposed. Well-controlled magnetic surveys, such as that of Matthews and others (1965) on the Carlsberg Ridge, could demonstrate the existence, width, spacing, and amount of offset of the expected northerly lineations on the flanks and in deeper areas alongside the mid-oceanic ridge. The meeting of three active branches of the Mid-Indian Ocean Ridge near Rodriguez Island presents an intriguing tectonic problem; the area is scarcely explored and requires a detailed multiphase survey to establish the ridges' trends, relative stage of development, rate of growth, and the relation of at least the two southern members to each other and to the east-west Rodriguez Ridge.

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Part IV Marine chemistry

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AN INCIDENCE OF VERY HIGH PHOSPHATE CONCENTRATIONS IN THE WATERS AROUND ANDAMAN ISLANDS

In the course of our investigations on the distribution of phosphate in the Bay of Bengal and the Andaman Sea during the Cruises of INS *Kistna* in September, 1963 as part of the Indian Programme of International Indian Ocean Expedition, we encountered abnormally high concentrations of inorganic phosphates in the samples collected from the vicinity of the Andamans. The location of INS *Kistna* stations at which we detected high values of phosphates is given in the figure (Fig. 1). The samples for analysis were obtained from all standard depths from the surface down to 200 metres and estimation of phosphates was done following the method of Robinson and Thompson (1948).[1]

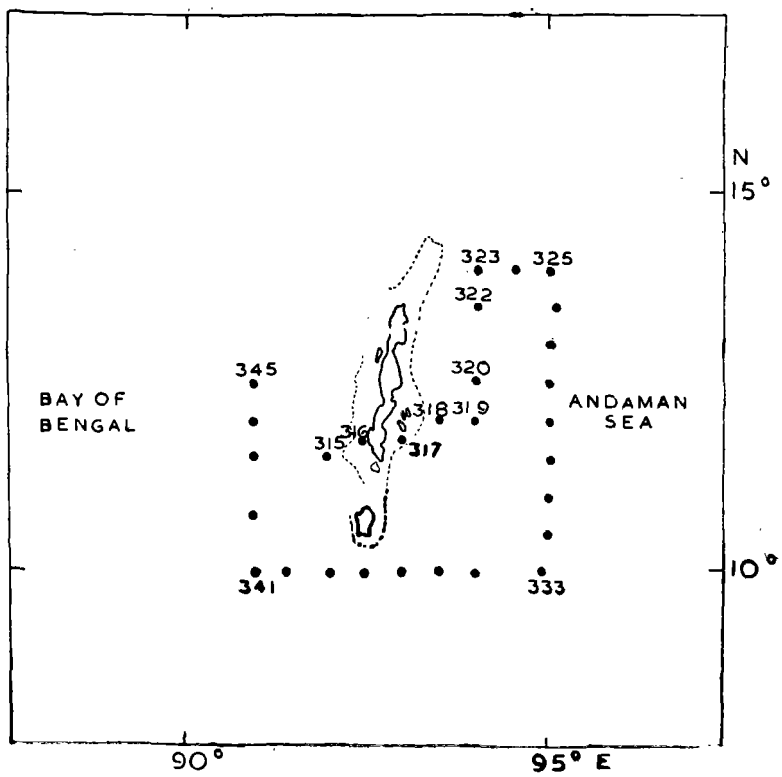

FIG. 1. Map showing INS *Kistna* station locations.

An examination of the results obtained shows the following features, *viz.*, (1) Concentration of phosphates exceeding 12 μg at/L were found at all the depths at the stations close to the coast (315 to 318). At other stations these high concentrations were confined to only a fewer depths at random. (2) The vertical distribution of phosphates in the 200 metre column does not appear to correspond to any regular accepted pattern. (3) All the samples having the abnormally high phosphate concentration were found to be highly turbid and having milky-white appearance. It was suspected that the turbidity might be due to the presence of carbonate but qualitative tests proved negative.

Since this is the first time this type of studies were carried out in this region any explanation for this phenomenon at this stage could at best be considered as purely tentative.

A detailed examination of the general hydrographical features of the Andaman Nicobar regions might however provide some answer to this very interesting phenomenon. We have been examining the possible sources of this abnormally high phosphate waters. It is found that along the western edge of the continental shelf of Andaman Islands which is wider than

the eastern shelf, there are a number of coral banks and as stated by Sewell (1925)[2] during the south-west monsoon period these coral banks are subjected to the effect of rough sea leading to the formation of the large amount of coral detritus. Nair *et al.* (1966)[3] in the course of work in Angria Bank region of the Arabian Sea which also contains several coral banks and islands have come across waters of abnormally high concentration of phosphates. It is therefore suggested that there is some kind of association between the occurrence of coral banks and occurrence of water with abnormal concentration of phosphates. Examining further about the other chemical and bio-chemical factors it has been found (Zernova and Ivannov, 1964)[4] that Andaman Sea is a region of highest production of phytoplankton in the northern Indian Ocean. Tipper (1911)[5] had reported about the occurrence of phosphatic nodules in the shelf regions around Andaman Islands. Sen Gupta and Pylee (1966)[6] have reported a very high specific alkalinity of these waters indicating high calcium content and this factor combined with high phosphate content might explain the turbidity of these waters presumably due to the precipitation of the calcium phosphate. That high calcium content may stimulate the precipitation of phosphorous has also been reported by Bhushinski (1964).[7] It is also possible, as indicated by Emery and Dietz (1950)[8] as a result of their investigations off the California coast, that during certain times of the year the product of calcium and phosphate ions in these waters may exceed the solubility product of tricalcium phosphate thereby giving rise to precipitation of these compounds. We do not have sufficient data to support this view but the possibility of such a precipitation is not ruled out. It is further suggested that more detailed investigations in this area would help in a better understanding of this phenomenon.

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MANGANESE IN THE SHELF SEDIMENTS OFF THE WEST COAST OF INDIA

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As a part of the programme aimed at understanding the nature and distribution of different elements in the marine sediments fringing the west coast of India in relation to their source and environmental factors, the distribution pattern of manganese has been determined and the results of the same are presented in this short note. The locations of the stations from where the sediment samples were collected are given in Fig. 1.

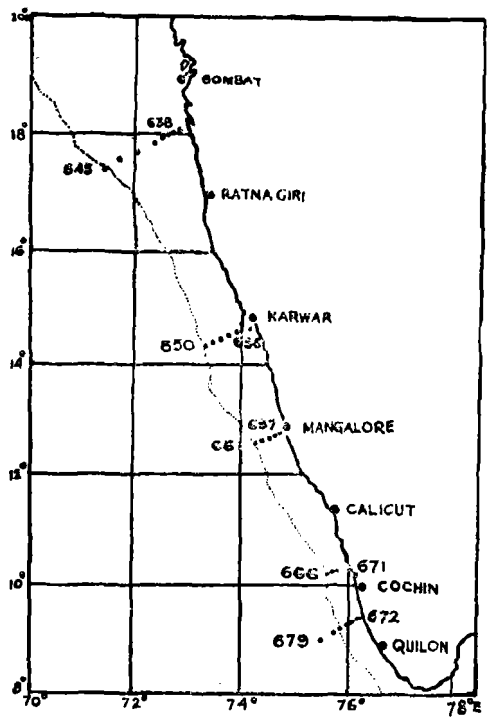
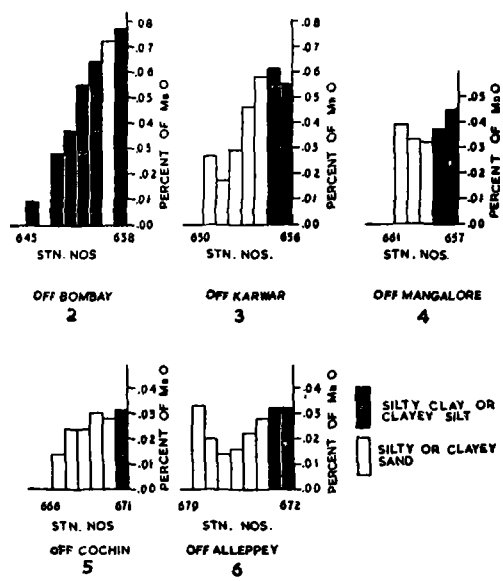


FIG. 1 Map showing the station locations.

In the area under study, the sediments exhibit a well-marked zonation in regard to their distribution in that the inner shelf (upto a depth of about 20 fthm.) is covered by silty clays or clayey silts and this is followed by a zone of silty or clayey sands in the rest of the shelf and slope regions. This is particularly so between Alleppey and Karwar while off the Bombay coast, the shelf, for the greater part, is covered by fine-grained sediments.

Manganese has been determined in these sediments colorimetrically using the method described by Sandell.[1] All the measurements were made on 'UNICAM' spectrophotometer SP 500 at 545 mμ. Although manganese has been estimated in the sediments by the authors on the total sample (including sand fraction) as well as in the silt and clay fraction, for the purpose of this paper, the values obtained in the silt and clay fraction alone are presented in Figs. 2-6 (*not on* carbonate free basis) and it may suffice to add here that the values obtained on the total sample basis are generally found to be less than those obtained in the finer fraction.



FIGS. 2-6. Manganese concentration and texture of the sediments.

An examination of data presented in

Figs. 2-6 reveals the following distribution pattern for the manganese in these sediments:

(*i*) There is a progressive increase in the manganese content of the sediments from south to north.

(*ii*) Along any given section, there is a progressive decrease in the manganese content in a direction seaward and away from the coast and

(iii) Along all the sections except off the Bombay coast, the sediments in the slope region are slightly more enriched in their manganese content than the immediately adjoining sediments in the shelf region.

The manganese content of the deep sea deposits has been attributed to different agencies: volcanic eruption, submarine weathering, chemical precipitation, biological extraction, etc. But in the case of the shelf deposits forming not far away from the land, the source must be found in the adjacent land mass itself. Manganese is carried to the sea both in solution and as a constituent of sedimentary debris (Murata, 1939).[2]

During weathering manganese is dissolved mainly as bicarbonate. Divalent manganese is readily oxidised to quadrivalent state when the waters bearing the manganese come into contact with the atmospheric or dissolved oxygen in the lake waters or the shallow near-shore waters. pH is another important factor controlling the migration of manganese and the colloidal hydroxides of manganese precipitate at pH 6. According to Rankama and Sahama[3] this precipitation takes place mostly in the river waters itself, while some manganese is precipitated in the brackish water areas. Thus what little manganese that is supplied to the sea will be preserved in the sediments as long as they are in contact with oxygenated waters.

The progressive decrease in the manganese content of the sediments in the seaward direction shows that the contribution is practically from land. A consideration of the distribution pattern of the sediments (particularly between Alleppey and Karwar) shows that the inner shelf is characterised by high rates of sedimentation. The sediments in the outer shelf have been described as relict sediments by Nair *et al.*[4] which are characterised by a high content of carbonate. The favourable hydrographic conditions for the deposition of fine-grained sediments in the inner shelf and the adsorption of manganese by these colloidal particles may account for the relatively high manganese observed in the inshore sediments along all the sections. While this is so in any given section, the manganese distribution shows a definite trend in the north-south direction also in that it decreases progressively from north to south. The climatic conditions on land and the hydrographic conditions in the shelf region being similar along the different parts of the west coast of India, the decreasing trend towards the south may have to be attributed to the differences in the rock types present along the different parts of the west coast of India (Deccan traps along the Bombay coast, Granitic rocks along the Mysore coast and the Tertiary and Sub-Recent formations, Peninsular gneissic complex and the Charnockitic rocks along the Kerala coast). The low values of manganese observed in the sediments of the 'Vembanad Lake' in Kerala State and the associated rivers by one of the authors (Murty, unpublished) confirms this surmise.

The sediments in the slope region are slightly enriched in their manganese content than the immediately adjoining sediments in the shelf region, along all the sections except off Bombay. Murty *et al.*[5] have reported high organic matter content in the slope sediments of the area under study and attributed the same to its preservation under a reducing environment. While the low manganese content off the Bombay coast is understandable in view of the fact that part of the manganese precipitated may be redissolved at the bottom under reducing conditions, it is difficult to explain enrichment in the slope sediments of other regions, particularly in view of their similarity in texture as well as composition to the immediately adjoining shelf sediments (silty or clayey sands characterised by high carbonate content). The only possible reason which can be offered is that these slope sediments are characterised by a high content of foraminiferal tests and perhaps manganese has been extracted from the waters by the planktonic foraminifera and preserved in their tests. The possibility of biological extraction of manganese from solution in sea-water involving the ingestion of this element by planktonic foraminifera and retention in their shells has been suggested by Correns[6] and confirmed by Goldberg *et al.*[7] as a mechanism contributing to the process of bringing manganese to the sediments.

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DISTRIBUTION OF TOTAL PHOSPHORUS IN THE SHELF SEDIMENTS OFF THE WEST COAST OF INDIA

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The total phosphorous content in the sediment samples collected from different stations on the continental shelf along five sections normal to the coast near Bombay, Karwar, Mangalore, Cochin and Alleppey has been determined and the distribution studied. The study reveals that the sediments off the Kerala coast are uniformly rich in phosphorus while those off Karwar and Mangalore are relatively poor with those off Bombay coming in between. The distribution of phosphorus in these sediments has been discussed in relation to upwelling and biological productivity.

INTRODUCTION

In a marine environment the productivity depends upon the concentration and distribution of nutrients like phosphates, silicates and nitrates dissolved in water. It is an accepted fact that the bottom sediments, where the regeneration takes place in part, act as reservoirs for these nutrients under favourable circumstances. While considerable work has been done on the distribution of these nutrients in the waters of the Arabian Sea and Bay of Bengal, except for the work done by Seshappa (1953) and Seshappa and Jayaraman (1956) on the sediments in the inshore region off Calicut, practically no information is available on the distribution of phosphorus in the shelf sediments off the east and west coasts of India. Hence bottom samples collected from the continental shelves covering the regions between 'Swatch of no ground' to Karaikal in the Bay of Bengal and between Bombay and Quilon in the Arabian Sea have been analysed for their total phosphorous content and the distribution studied. Some of the results that are brought to light as a result of these studies on the distribution of phosphorus in the Arabian Sea particularly in relation to upwelling and biological productivity are presented here.

FIELD AND LABORATORY PROCEDURES

Samples of bottom sediments from the shelf and slope regions were obtained along five sections (Fig. 1) during the 25th and 26th cruises of I.N.S. *Kistna* using the Phlegar Corer and La Fond-Dietz Snapper. In the region

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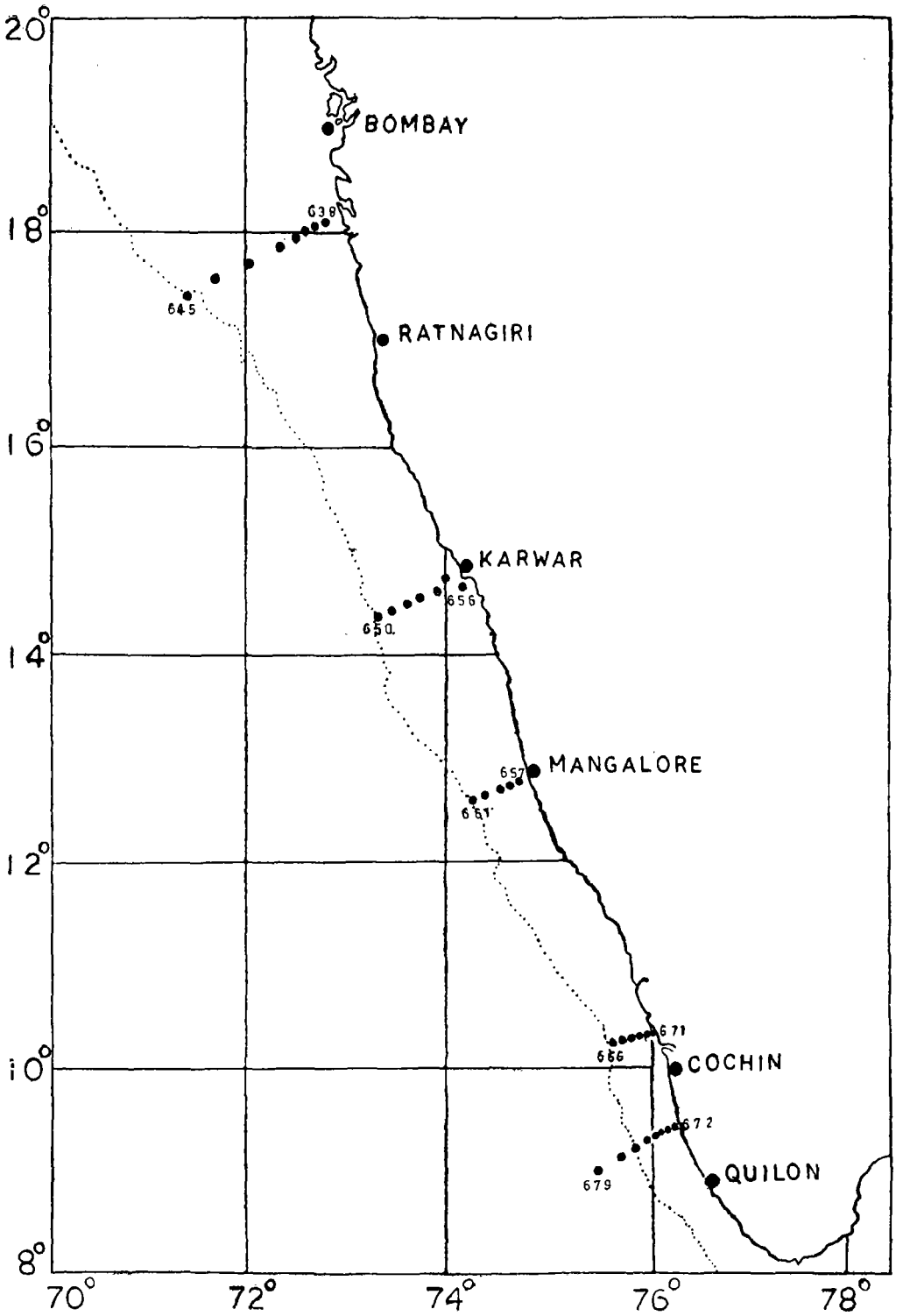

FIG. 1. Map showing the station locations.

under study, the width of the continental shelf is about 90 miles in the north and it gradually narrows down to about 30 to 35 miles in the south. A number of small rivers empty into the sea and their effect on the shelf may be very local. The sediments along the section off Bombay coast range from silty clays to silty sands in the shelf region to clayey silts in the slope region. Along the section off Karwar they range from clayey silt to silty clays and silty sands in the shelf region to clayey sands in the slope region. The sediments along the section off Mangalore range from clayey silts to silty sands. Off Cochin they range from silty clays to silty sands. Along the seetion off 'Ambalapuzha' (about 30 miles north of Quilon) they range from clayey silts to silty clays and silty sands. The samples collected from these five sections represent essentially the upper 12″ to 32″ in the case of core samples and the upper 4″ in the case of the snapper samples.

In the case of the core samples each core was cut into 4″ long bits and from each bit silt and clay fraction was separated from the sand fraction by wet sieving through ASTM Sieve No. 230. In the case of the snapper samples the sample was thoroughly mixed before the silt and clay fraction was separated from the sand fraction. The silt and clay fraction thus separated was dried at about 60° C in a hot air oven and then pulverized. A suitable quantity of the sample was taken and the total phosphorous content determined by the method as described by Rochford (1951). All the measurements were made on the 'Unicam' spectrophotometer at 700 mμ. The total phosphorus estimated here includes different forms of phosphates, viz. interstitial phosphate, adsorbed phosphate, organic phosphate and insoluble inorganic phosphate.

Results

The total phosphorous content has been determined on samples collected from 33 stations distributed over five sections mentioned above. In the case of the core samples depth distribution has been studied. The results obtained are shown in Table I. An analysis of the data shows that the following broad generalizations can be made in regard to the distribution of the total phosphorus in these sediments:

1. The sediments off Cochin and Alleppey coasts are uniformly rich in their total phosphorous content.

2. The sediments off Karwar and Mangalore coasts are uniformly poor in phosphorus.

3. The sediments off Bombay coast are generally richer in phosphorus than those off Karwar and Mangalore but are, with a few exceptions here and there, poorer than those off Cochin and Alleppey.

4. In the case of core samples the total phosphorous content shows no trend with depth.

TABLE I

Sl. No.	Stn. No.	Depth in fathoms	Type of sample	Sediment level in inches	Texture	Total phosphorus in micro-grams per gram of silt
Off Bombay:						
1.	638	13	Corer	0–4	Silty clay	410
				4–8	,,	320
				8–12	,,	340
2.	639	17	Snapper	0–4	Silty sand	390
3.	640	19	Corer	0–4	Sandy clay	400
				4–8	,,	560
				8–12	,,	270
4.	641	19	,,	0–4	Silty clay	740
				4–8	,,	260
				8–12	,,	1,240
				12–16	,,	420
				16–20	,,	520
				20–24	,,	810
				24–28	,,	290
5.	642	26	,,	0–4	,,	1,370
				4–8	,,	540
				8–12	,,	290
				12–16	,,	190
				16–20	,,	520
				20–24	,,	810
				24–28	,,	290
6.	643	38	Snapper	0–4	,,	760
7.	645	250	Corer	0–4	Clayey silt	350
				4–8	,,	620
				8–12	,,	1,430
				12–16	,,	1,400
				16–20	,,	1,540
				20–24	,,	570
				24–28	,,	590
				28–32	,,	810
Off Karwar:						
8.	650	110	,,	0–4	Clayey sand	240
				4–8	,,	260
				8–12	,,	280
				12–16	,,	100
				16–20	,,	180
				20–24	,,	230
				24–28	,,	170
				28–32	,,	220
9.	651	55	,,	0–4	Silty sand	330
				4–8	,,	210
				8–12	,,	200
				12–16	,,	190
				16–20	,,	310

TABLE I—*contd.*

Sl. No.	Stn. No.	Depth in fathoms	Type of sample	Sediment level in inches	Texture	Total phosphorus in micro-grams per gram of silt
10.	652	42	Corer	0–4	Silty sand	240
				4–8	,,	240
				8–12	,,	240
				12–16	,,	160
				16–20	,,	110
11.	653	32	Snapper	0–4	,,	250
12.	654	25	,,	0–4	,,	240
13.	655	12	Corer	0–4	Silty clay	110
				4–8	,,	190
				8–12	,,	130
				12–16	,,	120
14.	656	10	,,	0–4	Clayey silt	130
				4–8	,,	140
				8–12	,,	100
				12–16	,,	160
				16–20	,,	60
				20–24	,,	40
				24–28	,,	70
				28–32	,,	110
Off Mangalore:						
15.	657	10	,,	0–4	,,	180
				4–8	,,	190
				8–12	,,	330
				12–16	,,	280
				16–20	,,	430
16.	658	17	,,	0–4	,,	300
				4–8	,,	180
				8–12	,,	320
				12–16	,,	270
				16–20	,,	240
				20–24	,,	240
				24–28	,,	190
17.	659	23	,,	0–4	Silty sand	140
				4–8	,,	220
				8–12	,,	260
18.	660	43	,,	0–4	Clayey sand	230
				4–8	,,	220
				8–12	,,	260
19.	661	105	,,	0–4	Silty sand	140
				4–8	,,	120
				8–12	,,	90
Off Cochin:						
20.	666	46	Snapper	0–4	,,	1,000
21.	667	32	,,	0–4	,,	900
22.	668	23	,,	0–4	,,	680

TABLE I—*concld.*

Sl. No.	Stn. No.	Depth in fathoms	Type of sample	Sediment level in inches	Texture	Total phosphorus in micrograms per gram of silt
23.	669	17	Snapper	0–4	Silty sand	990
24.	670	14	,,	0–4	,,	1,050
25.	671	13	,,	0–4	Silty clay	730
Off Ambalapuzha:						
26.	673	9	Corer	0–4	Clayey silt	1,322
				4–8	,,	1,115
				8–12	,,	1,221
27.	672	10	,,	0–4	Silty clay	1,137
				4–8	,,	1,410
				8–12	,,	1,010
28.	674	20	,,	0–4	Silty sand	1,979
				4–8	,,	1,054
				8–12	,,	670
				12–16	,,	1,348
29.	675	27	,,	0–4	,,	755
				4–8	,,	1,052
				8–12	,,	620
30.	676	29	Snapper	0–4	,,	521
31.	677	85	,,	0–4	,,	830
32.	678	250	Corer	0–4	,,	578
				4–8	,,	970
				8–12	,,	620
33.	679	370	,,	0–4	,,	860
				4–8	,,	950
				8–12	,,	780

DISCUSSION

The importance of upwelling as a factor giving rise to sediments rich in phosphorus has been well established. The formation of sediments rich in phosphorus on the continental shelves off the coast of Peru, Chile, South-West Africa and North America has been attributed to the phenomenon of upwelling (Dietz *et al.* 1942) followed by a slow rate of deposition of detrital matter. The existence of upwelling on the west coast of India has been brought to light by investigations of several workers (Ramamritham and Jayaraman 1960; Jayaraman and Gogate 1957; Banse 1959; Carruthers *et al.* 1959). The dependence of upwelling and sinking on the coastal currents has been stressed by Varadachari (1961). Investigations by Varadachari and Sharma (1964) on the circulation of surface waters in the North Indian Ocean show that along the different coasts in the area divergence (and hence upwelling) is associated with a

clockwise coastal circulation and convergence with a counter-clockwise circulation and that the coastal circulation is clockwise along the west coast of India from February to September. Departures from this relationship between coastal circulation and the surface divergence may occur during periods of strong on-shore or off-shore winds. Recent investigations by Reddy and Sankaranarayanan (1967) on the distribution of nutrients in the shelf-waters along the west coast of India, covering the region between Ratnagiri and Quilon during the monsoon and post-monsoon periods, reveal two distinct environmental conditions characterized by nutrient deficient layers in the post-monsoon periods and nutrient rich surface layers in the monsoon period. The nutrient levels show a general increasing trend towards the south from Ratnagiri and this distribution has been attributed to upwelling with an increasing trend towards the southern region.

The present investigation reveals that the sediments off the Kerala coast are uniformly rich in phosphorus while the sediments off the Central part of the west coast (Karwar and Mangalore region) are uniformly poor in phosphorus with the sediments off the Bombay coast coming in between. This distribution of total phosphorus in the sediments bears a close correspondence to the distribution of phosphorus in the waters and also to the differences in the abundance of sea fish. Thus the differences found in the concentration of total phosphorus in sediments in the different regions off the west coast of India may perhaps be attributed to the differences in upwelling in the different regions and to the corresponding variations in the levels of biological productivity and the subsequent chain of events of the regenerative phase such as the settling of the organic detritus to the bottom and the bio-diagenetic processes operating at the mud water interface and in the sediments. Another important factor that may have to be considered in regard to the contribution of phosphorus to the sediments is run off from land. Not much work has been done on this coast in this direction but the available information shows that the contribution from run off is negligible (Rao and George 1959).

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Part V

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477. VACELET, J. Descriptions d'éponges pharetronides actuelles des tunnels obscurs sous-récifaux de Tuléar (Madagascar), p. 37-62.
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„METEOR“
FORSCHUNGSERGEBNISSE

Herausgegeben von der Deutschen Forschungsgemeinschaft

Reihe A - No. 1

ALLGEMEINES
PHYSIK UND CHEMIE DES MEERES

Redaktion: G. Dietrich - Kiel
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1. Reisebericht der Indischen Ozean Expedition
mit dem Forschungsschiff „Meteor“ 1964-1965
von Günter Dietrich, Gunther Krause, Eugen Seibold und Kurt Vollbrecht..... Seite 1

2. Struktur des heißen salzreichen Tiefenwassers im zentralen Roten Meer
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3. Trübungsmessungen im Persischen Golf und im Golf von Oman
von Jochen Ziegenbein ..... Seite 59

1966

GEBRÜDER BORNTRAEGER · BERLIN-NIKOLASSEE

Reisebericht der Indischen Ozean Expedition mit dem Forschungsschiff „Meteor" 1964—1965

bearbeitet von

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Institut für Meereskunde der Universität Kiel

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Inhalt

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Report of the Indian Ocean Expedition with R.V. "Meteor" 1964—1965

Summary

I. Preparations for the Indian Ocean Expedition with R. V. "Meteor". The previous history of the International Indian Ocean Expedition and the German participation is described. From the beginning, the German scientists were ready to work in the IIOE. However, for an effective contribution they had no suitable research vessel. First in 1962, all necessary suppositions for the construction of a new ship were given. Therefore construction of "Meteor" as well as the preparations for the first expedition had to be carried out at the same time, hoping the new multipurpose ship under construction would fulfill all requests.

Eleven working groups were interested in the cruise to the Indian Ocean: physical and chemical oceanography, marine meteorology, marine geology, marine geophysics, planktology, marine botany, marine zoology, ichthyology, marine microbiology, and ship building.

71 scientists and 21 technicians were necessary to treat the tasks of the above mentioned branches during the different parts of the cruise. As the ship has only 25 berths for scientists it was necessary to exchange the participants by a carefully designed exchange program.

In brief the programs of the different working groups are described. It was possible to carry out these programs in good conformity with the plans.

II. Cruise Report. The cruise was carried out in 10 parts:

1. Hamburg to Naples 29. 10.—9. 11. 1964
2. Naples to Port Said 11. 11.—17. 11. 1964
3. Port Said to Aden I 18. 11.—26. 11. 1964
4. Aden I to Aden II 28. 11.—14. 12. 1964
5. Aden II to Mombasa 15. 12. 1964—16. 1. 1965
6. Mombasa to Cochin 24. 1.—11. 2. 1965
7. Cochin to Bombay 14. 2.—23. 2. 1965
8. Bombay to Karachi 26. 2.—14. 3. 1965
9. Karachi to Djibouti 14. 3.—23. 4. 1965
10. Djibouti to Hamburg 24. 4.—18. 5. 1965

A map for the whole cruise is to be seen in fig. 1. The location of the sections and stations is represented in 4 special maps: Area round Bab el Mandeb (fig. 2), west side of Arabian Sea (fig. 3), east side of Arabian Sea (fig. 4) and Persian Gulf (fig. 5). In the

Strait of Bab el Mandeb and on the way from Aden to Mombasa, the work was hindered by anomalous strong winds, on the other parts of the cruise the weather conditions were normal.

The main aim of all working groups aboard was to obtain exact measurements and samples, only few evaluation work could be done.

After some measurements in the hot salty water hole and on few stations in the Red Sea, the in- and outflow in the Strait of Bab el Mandeb was investigated by the physical oceanographic group, but also the other groups obtained a lot of measurements and samples in this area. From Aden up to Bombay, the routine program started in which all groups participated in the same measure.

The meteorological program ended in Bombay, oceanographic research was reduced in favour of geophysical investigations which were carried out in a cooperation with the INS "Kistna". From Karachi, the main working groups were represented by geologists and geophysicists. The work was concentrated on the east side of the Persian Gulf.

On the way home, the hot salty water hole was reinvestigated. 58.2 °C were measured in the deepest of three layers.

"Meteor" returned to Hamburg on May 18th, 1965. The whole distance was 24 500 nautical miles. 385 stations were made.

III. List of Members and Institutes which participated in the Expedition. According to the plans, scientists of 11 branches of marine sciences took part in the cruise. From table 1, name of the members, profession and institute are to be seen. In table 2, addresses of the institutes are listed and table 3 contains the names of the crew members.

IV. Station list and maps. Table 4 contains station number, position, depth and the number of measurements carried out with instruments outside the ship on each station. The table is devided into the 10 expedition parts (see Chap. 2).

The instruments in the list are:

Bathysonde	bathysonde; temperature, electrical conductivity, pressure in situ
D-Gerät	transparency-meter
Strommesser	current-shear measurement
O_2-Sonde	oxygen probe
Hydroserie	hydrographic cast
Planktonserie	plankton cast
Multinetz	remote controlled phyto-plankton net
Larvennetz	larvae net
IOS-Netz	IOS standard net
Trawl	trawl
Bodengreifer	bottom grab
Kerngerät	core devices (the sum of the geological devices listed in table 5)
Dredge	dredge

Table 5 completes the station list for parts 9 and 10 of the cruise.

The following instruments are listed:

TS-Sonde	temperature-salinity-recorder
Mikrobiologie-Serie	cast with Zobell samplers
Kastengreifer	push-box sampler
Stoßrohr	gravity corer
Kastenlot 2 m	box corer 2 m
Kastenlot 4 m	box corer 4 m
Kolbenlot	piston corer
Foraminiferen-Lot	small gravity corer
Freefall-Corer	freefall-corer
Fernsehen	deep sea television and photo camera

V. Numbers of observations. In table 5, the total numbers of observations on the 10 parts of the cruise are listed. Fig. 6 shows the working times of the surface data recorders. The recorders and data are:

Tiefseechograph	deep sea echo sounder
Oberflächen-temperatur	surface temperature
Oberflächen-salzgehalt	surface salinity
Oberflächentrübung	surface transparency
Magnetometer	magnetometer
Seegravimeter	sea gravimeter
Meteorologische Daten	meteorological data
Meteorologische Strahlungs-messungen	meteorological radiation measurements
Plankton-registrierung	plankton records
Radioaktivität des Oberflächenwassers	radioactivity of surface water

VI. Brief description of scientific instruments. The instruments mentioned in the station list (table 4 and 5) are briefly described. References for literature and manufacturer of instruments are given.

VII. Photos of scientific instruments. A number of instruments described in chap. VI is illustrated in fig. 7 to fig. 30.

Die Struktur des heißen salzreichen Tiefenwassers im zentralen Roten Meer

von

GUNTHER KRAUSE und JOCHEN ZIEGENBEIN
Institut für Meereskunde der Universität Kiel

The structure of the hot salty deep water in the central Red Sea

Summary

On her cruise to the Indian Ocean, R. V. "Meteor" worked a section through the Red Sea with stations in several deep holes. But only in the "Discovery deep" (St. 28) and in the area of the "Atlantis deep" (St. 384) (fig. 1) hot salty water occured. The upper limits of the abnormal water were indicated by scattering layers (fig. 2). In both holes continuous temperature and transparency measurements were carried out. On station 28 (fig. 4 the temperature rose within a thermocline of 45 m thickness from 21,6 °C to 44,8 °C. On station 384 (fig. 3) 3 layers were observed. The temperature first rose from 21,6 °C to 41,2 °C, then to 57,7 °C and finally to 58,4 °C near the bottom. On both stations the water was very turbid. Some chemical properties of the water are given.

For the explanation of the 3 different layers on station 385 it is suggested that water from different holes flows together and is stratified according to density.

Trübungsmessungen im Persischen Golf und im Golf von Oman

von

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Transparency-measurements in the Persian Gulf and Gulf of Oman

Summary

The results discussed in this paper refer to investigations with a beam transmission meter, which have been carried out during the "Meteor"-expedition in the northern part of the Gulf of Oman and in the eastern part of the Persian Gulf in March and April 1965. The area is a small strip parallel to the Persian coast, 80 km broad and 700 km long, beginning with the Street of Hormuz in the south and ending near the Isle of Khark at 29.5°N. The temperature measurements which have been taken simultaneously with the optical attenuance have been used only in some cases for interpreting the results of the turbidity measurements. As a detailed discussion of the temperature and salinity distribution, which will be written by P. KOSKE e. a., is not yet ready, a comparing interpretation of the results of light attenuance measurements and other hydrographic results cannot be made.

In the area of the Street of Hormuz a relative high turbidity can be observed in the surface layer. This is mainly caused by the high content of biological matter. The high light attenuance found in the bottom layer is significant for the sediment transport by the bottom current which is going southward. Across the continental shelf at a depth of 220 m this bottom current raises and can be observed as a current layer which at a distance of 200 sm off the Strait of Hormuz is still 80 m mighty showing higher turbidity and temperatures being nearly 2 °C higher than the environmental temperatures.

Around the axis of the U-shaped valley, which forms the northeastern deeper part of the Persian Gulf up to the Isle of Khark, very clear water with only a very small content of plankton can be observed. The incoming water of the Gulf of Oman, which in this season is warmer than that of the Persian Gulf decreases its temperature for nearly 2 °C on its way to the North, but still remains very clear. Turbidity only increases near the coast, near the bottom and in the thermoclines. The layer with increased turbidity in the thermocline can be derived from a high content of plankton. In most cases this layer can also be observed as a scattering layer with the echograph. The high turbidity near the bottom and near the coast is mainly caused by mineralogical matter which is whirled up by the bottom current respectively the breakers. Sediment transport occurs in a bottom layer with a thickness of about 25 to 30 m as a function of the bottom current velocity.

„METEOR“
FORSCHUNGSERGEBNISSE

Herausgegeben von der Deutschen Forschungsgemeinschaft

Reihe A - No. 2

ALLGEMEINES

PHYSIK UND CHEMIE DES MEERES

Redaktion: G. Dietrich - Kiel

W. Hansen - Hamburg und J. Joseph - Hamburg

Physikalische und chemische Daten nach Beobachtungen des Forschungsschiffes „Meteor“ im Indischen Ozean 1964/65

von

Günter Dietrich, Walter Düing, Klaus Grasshoff
und Peter H. Koske

1966

GEBRÜDER BORNTRAEGER · BERLIN-NIKOLASSEE

Physikalische und chemische Daten nach Beobachtungen des Forschungsschiffes „Meteor" im Indischen Ozean 1964/65

von

GÜNTER DIETRICH, WALTER DÜING, KLAUS GRASSHOFF und PETER H. KOSKE
Institut für Meereskunde der Universität Kiel

Physical and chemical data according to the observations of R. V. "Meteor" in the Indian Ocean 1964/65

Summary

The present volume gives the observed physical and chemical data obtained by R. V. "Meteor" in the Indian Ocean during her cruise 1964/65. The tables are based on the computations made by the National Oceanographic Data Center (NODC) in Washington. In addition to the normally communicated data, the tables contain four chemical parameters: alkalinity, ammonia, fluoride, and calcium.

„METEOR“
FORSCHUNGSERGEBNISSE

Herausgegeben von der Deutschen Forschungsgemeinschaft

Reihe A - No. 3

ALLGEMEINES
PHYSIK UND CHEMIE DES MEERES

Redaktion: G. Dietrich - Kiel

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1967

GEBRÜDER BORNTRAEGER · BERLIN-NIKOLASSEE

Hydrographische Beobachtungen im Arabischen Meer während der Zeit des Nordostmonsuns 1964/65

von

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Hydrographic observations in the Arabian Sea during the NE-monsun period 1964/65

Summary

In this paper the sections for temperature and salinity are presented, which were obtained during the cruise of R.V. "Meteor" in the Indian Ocean (1964/65).

The hydrographic observations in the Arabian Sea, had the aim to provide information on the influence of the *NE*-monsoon on the distribution of salinity and temperature off the east coast of Africa and off the west coast of India. Special attention was given to the spreading of highly saline water from the Red Sea and the Persian Gulf. The track of the expedition was layed out according to these plans and is presented in figure 1.

The data were collected by means of hydrographic casts with newly developed water bottles, and by means of "in-situ" measurements with the "bathysonde", an instrument for the continuous recording of electrical conductivity, temperature and pressure. This paper only deals with the data of the casts which are presented in a special publication together with the chemical data. The hydrographic conditions off the east coast of Africa are characterised by a rather complicated distribution of salinity within the first 1 000 m of depth with several intermediate maxima and minima (hydrographic sections III—IX). This is due to the spreading of highly saline water mainly from the Red Sea, which can be traced southwards at least as far as 4° N (figure 9).

Similar complicated conditions were found off the west coast of India (sections XI—XVI). Here the cause can be traced back to watermasses from the Persian Gulf.

In depths below 2 000 m the *TS*-relation is virtually the same at both sides of the Arabian Sea.

Ausbreitung und Vermischung des salzreichen Wassers aus dem Roten Meer und aus dem Persischen Golf

von

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und

WOLF-DIETRICH SCHWILL, Deutsches Rechenzentrum, Darmstadt

Spreading and mixing of the highly saline water of the Red Sea and the Persian Gulf

Summary

The present investigation concerns itself with two problems: First it is investigated with the aid of the hydrographic data available until medio 1965 from the Indian Ocean, whether due to the varying actions of the monsoons a large scale seasonal shift in the distribution of the isohalines occurs at the level of intermediate salinity maxima (depth range about from 300 to 800 m). Furthermore it is investigated by means of two theoretical models whether advection or horizontal mixing dominates in the large scale distribution of the salinity in the Arabian Sea.

In the treatment of the first problem, distribution charts for the water from the Read Sea and the Persian Gulf were made with the aid of the core layer method for both monsoon periods. The core layer of Red Sea water lies at about 600 to 800 m depth. The watermasses from the Persian Gulf sink from 200 to 500 m while moving from north to south. In both seasons the observable limit of extension lies at about 3° N. Seasonal variations occur apparently only in the northern part of the basin and at its margins.

The observed distribution of salinity shows at all levels (300, 400, 500, and 600 m) an east-west pattern (fig. 7 to 10). In no case a tongue form appears in the isohalines. The observed distribution is satisfactorily interpreted by means of a model which considers only horizontal mixing and the natural boundary conditions (Dirichlets problem for the rectangle). A further model which includes advective terms does not corroborate the observations.

The investigations lead to the conclusion that the existing stationary distribution of salinity in the central part of the Arabian Sea is maintained essentially by large scale mixing processes. Further theoretical considerations, which are based upon observations at the 800 m level, suggest that the distribution of salinity at the margins of the basin strongly influences the salinity of the inner part. A change in the marginal distribution on the other hand, may be caused by means of horizontal movements of relatively small width. In further investigations on the circulation of the Arabian Sea one has therefore to consider especially the processes at the margins of the basin.

Die Vertikalzirkulation in den küstennahen Gewässern des Arabischen Meeres während der Zeit des Nordostmonsuns

von

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The vertical field of motion at the margins of the Arabian Sea during the NE-monsoon

Summary

Although vertical velocities are very small, they are of great importance with regard to chemical and biological processes in the sea. A study of the circulation phenomena of down- and upward moving water masses is not possible experimentally. Therefore, the vertical velocities were determined by means of a theoretical model using empirical data obtained by R. V. "Meteor" in the Arabian Sea, during the period of the NE-monsoon 1964/65.

Based upon the observed data for the density the physical topography of the sea level was calculated by means of the dynamic method. The wind registrations during the hydrographic stations of R. V. "Meteor" show a very constant wind distribution of the NE-monsoon.

The data of wind distribution, shapes of sea level and pycnocline were used in a simple two dimensional two layer model with two constant densities and two constant vertical eddy coefficients.

The main results are presented in horizontal charts for four levels from 0 to 300 m for the African and for the Indian coast (plate 6 and 7). The charts show alternative strips of weak upward and downward movements parallel to the coast. The width of the strips varies from 30 to 80 km. There are three areas of intensified vertical velocities: south of the island of Socotra (profile III), south of the equator near the coast of Mombasa (profile VIII), and southerly from Karachi (profile XV). These results of stripwise distribution of upward and downward velocities are compared for one case with the distribution of particulate carbon, which shows a similar alternative distribution of minimum and maximum values (plate 8).

Maximum velocities of $2 \cdot 10^{-4}$ cm/sec occur in profile XV, in the layers between 100 and 200 m. On the other profiles velocities are less than 10^{-5} cm/sec.

In all cases it was found that the vertical velocities reach a maximum well below the pycnocline, in order to decrease in either direction.

Hydrographische Beobachtungen auf einem Äquatorschnitt im Indischen Ozean

von

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Hydrographical observations on a transequatorial section in the Indian Ocean

Summary

During the expedition of R.V. "Meteor" in the Indian Ocean the following data were observed on a section from 58° E, 3° S to 58° E, 2° N during the end of january 1965: Temperature and salinity by hydrographic casts as well as by continuous registrations with the bathysonde. In addition, observations of several chemical parameters, and measurements of the meridional and zonal current distribution down to 250 m depth were obtained.

The results indicate no evidence of an eastward directed equatorial undercurrent towards the end of january 1965: On the contrary, we find relatively strong westward directed currents. Chemical data corroborate this fact as there is no similarity with the distribution of oxygen or phosphate on transequatorial sections from the Pacific or the Atlantic Ocean. A weak eastward directed component of current at 3° S indicates the appearance of the equatorial counter-current.

The bathysonde-registrations indicate the existence of at least two characteristic watermasses: Water from the Arabian Sea between 50 to 100 m depth and water from the Red Sea at 700 to 800 m depth.