NOTES ON SOME POLYZOA WITH CONICAL ZOARIA

by

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Résumé

Cinq espèces de Bryozoaires, dont trois sont connues pour être normalement encroûtantes, produisent des zoaria coniques, libres quand elles croissent sur un fond marin sableux, vaseux ou coquillier. Les zoaria de quatre de ces espèces ont incorporé pendant leur croissance divers organismes de la surface du fond à leurs surfaces basales. Ces organismes comprennent diverses espèces de Bryozoaires et les concavités basales des colonies ont été elles-mêmes colonisées secondairement par une croissance épizoïque comprenant d'autres Bryozoaires. L'apparition de ces formes a été analysée. La faune de Bryozoaires associée aux fonds vaseux et sableux est discutée et une estimation faite de la fréquence des espèces libres de la « faune des sables » dans de tels habitats.

INTRODUCTION

Study of Polyzoa with conical zoaria associated with sandy or muddy sea-bottoms has included examination of colonies of species not usually adapted to life in this type of habitat. The specimens, the majority of which is dry, are preserved in the British Museum (Natural History); they are referred to by their registered numbers, e.g. 1892.1.28...

The following measurements have been made; where possible the dimensions given are the average of 20 measurements; the range is also given.

Lz = length of zooecium
Lo = length of orifice
Lfo = length of fertile orifice
Lov = length of ovicell
Lav = length of avicularium
Lm = length of mandible
Lvav = length of vicarious avicularium

Lvm = length of vicarious mandible
lz = width of zooecium
lo = width of orifice
lfo = width of fertile orifice
lov = width of ovicell
lvav = width of vicarious avicularium
lvm = width of vicarious mandible

The specimens, belonging to 5 species, were collected from the Holothuria Bank, off Cape Talbot, N.W. Australia, and from Tsu Sima (or Tsos Sima), Korea Strait, S. Japan. Colonies of 4 of the species have been briefly discussed by Hastings (1932) and by Harmer (1957:1009), and these have the following characters in common. The zoaria are large, shallow, hollow cones, with an average diameter of 30 mm., completely free-living and without rootlets or other means of attachment. Each originates on the convex side of a shell or a conical Polyzoan colony. The zoaria have developed radially, the zooecia eventually growing away from the original substrate and becoming a discoid lamina. As they have grown, the basal calcification of the colonies has incorporated objects lying upon the surface of the sea bottom, which have thus been preserved virtually *in situ* (see pl. I, 1,3). Analysis of the fauna of the basal concavities of the colonies has yielded evidence as to the nature of the sea-bottom, and an estimate of the frequency, distribution and form of the other species of Polyzoa present. The larvae of both Polyzoa and other animals have successfully colonized the basal surface of the colonies, and their occurrence has also been examined.

The fifth species (see p. 442), also has a conical zoarium, but is small and not concave basally. It exhibits adaptation of the zoarium to life in a sandy or muddy habitat, but has no incorporated or epizoic species on the basal surface.

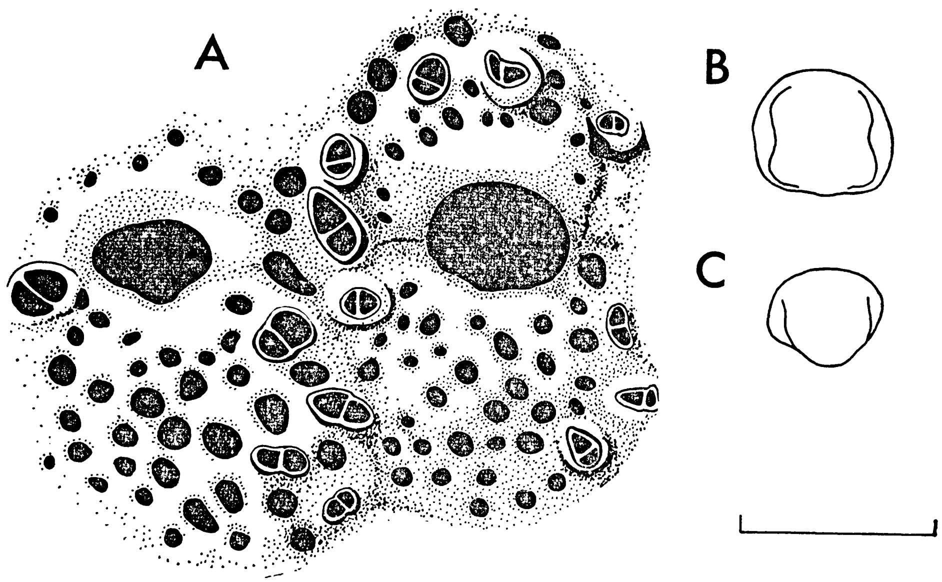
SYSTEMATIC SECTION

Calyptotheca Harmer, 1957: 1008.

Zooecia and ovicells uniformly porous. Zooecia with sinuate, dimorphic orifices. Pore-chambers present. Avicularia present, sometimes large and vicarious. Ovicells hyperstomial, large, closed by the operculum.

Conical, free-living colonies are already known in *Calyptotheca*. Harmer (1957:1014, 1015) described *C. orbiculata* and *C. circularis*, both of which originated encrusting small shell fragments (0.45 mm. and 0.7 mm. in diameter respectively). These differ from 4 of the species described below in their smaller, flatter zoaria (4-9 mm. in diameter), and from all 5 species in their lack of plurilaminar growth. Both have calcareous projections from the basal walls of the zooecia, which in *C. circularis* had uncalcified rootlets attached (cf. *Celleporaria descostilsii* and *C. aperta*, p. 442). *C. circularis* was one of the 6 free-living, conical species (belonging to 5 distinct genera), which occurred in a group of "Siboga" Stations in the Java Sea (Stns. 318-321), where the sea-bottom was "fine yellowish-grey or grey mud". Harmer (1957:649) discussed the correlation of this type of habitat with the occurrence of conical, free-living zoaria.

Vicarious avicularia are absent in *C. circularis*, but one is present in specimen 182A, of *C. orbiculata* (Stn. 260, Kei Is). Although Harmer mentioned the avicularium in his key to the species of *Calyptotheca* (1957:1010), he did not describe it when defining and discussing *C. orbiculata*. The frontal wall is porous, the basal wall thick, and the interior of the avicularium chamber is obscure, but it is possible to see that a reduced polypide is present. The mandible is short, with a pair of outwardly curved sclerites (see text-fig. 2 D). The occlusor muscles are inserted basally and proximally. Harmer also described (p. 1011), but did not name, a species of *Calyptotheca* with vicarious avicularia, which was similar to *C. capitifera.* The mandibular sclerites of the vicarious avicularia of *C. capitifera* curve inwardly, those of the unnamed species curve outwardly, like those of *C. orbiculata* and *C. conica,* see below. The avicularia of *C. capitifera* have no polypides, but these are present in both the unnamed species and *C. conica.* The occlusor muscles in the unnamed species differ from all the others in that they are inserted distally, not proximally. Similar vicarious avicularia are found in some species of *Schizomavella* described by Harmer (1957:1029), see p. 440.



TEXT-FIG. 1
Calyptotheca conica n. sp.

A. Zooecia and ovicell, treated with eau de javel showing sutural avicularia. 1892.1.28.76A.
B. Operculum of fertile zooecium. 1892.1.28.76C.
C. Operculum of autozooecium. 1892.1.1.28.76C.
Scale = 0.20 mm.

Calyptotheca conica n. sp.

(Pl. I, 1-3; text-fig. 1 A-C, 2 A-C)

Described in the discussion of *Schizoporella furcata* Busk by Hastings, 1932:422 and Harmer, 1957:1009.

Holotype, 1892.1.28.76A, Holothuria Bank, N.W. Australia, 15-32 fath., Basset-Smith Coll.

Paratypes, 1892.1.28.76B, C, D, E, F, H, as above.

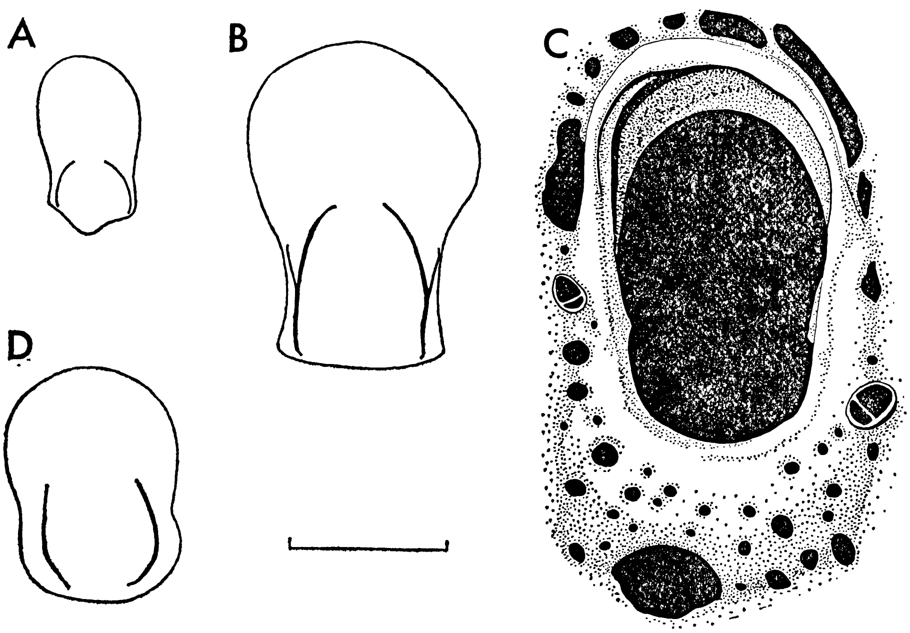
Zoarium a hollow cone. Basal surface with hollow, hooked processes. Zooecial orifices with a broad sinus. Fertile orifices considerably larger. Small, paired, oral avicularia and sutural avicularia present. Vicarious avicularia long, very large, with frontal pores. Mandibles spathulate. Occlusor muscles very long, inserted proximally. Polypide present.

DIMENSIONS

	Specimens A - F and H	Specimen G
Lz	= 0.35-0.55 mm., av. 0.42 mm.	0.40-0.55 mm, av. 0.47 mm.
lz	= 0.23-0.38 mm., av. 0.30 mm.	0.25-0.40 mm., av. 0.33 mm.
Lo	= 0.09-0.11 mm., av. 0.10 mm.	0.10-0.12 mm., av. 0.11 mm.
lo	= 0.10-0.13 mm., av. 0.12 mm.	0.10-0.11 mm., av. 0.11 mm.
Lfo	= 0.10-0.12 mm., av. 0.11 mm.	0.14-0.15 mm., av. 0.14 mm.
lfo	= 0.14-0.16 mm., av. 0.15 mm.	0.14-0.15 mm., av. 0.15 mm.
Lov	= 0.30-0.36 mm., av. 0.34 mm.	0.32-0.40 mm., av. 0.38 mm.
lov	= 0.31-0.35 mm., av. 0.34 mm.	0.35-0.41 mm., av. 0.38 mm.
Lav	= 0.06-0.08 mm., av. 0.07 mm.	0.07-0.10 mm., av. 0.09 mm.
Lm	= 0.02-0.04 mm., av. 0.03 mm.	0.05-0.06 mm., av. 0.06 mm.
Lvav	= 0.70-0.83 mm., av. 0.74 mm.	0.48-0.57 mm., av. 0.52 mm.
lvav	= 0.35-0.50 mm., av. 0.42 mm.	0.36-0.47 mm., av. 0.42 mm.
Lvm	= 0.50-0.53 mm., av. 0.52 mm.	0.19-0.23 mm., av. 0.21 mm.
lvm	= 0.25-0.50 mm., av. 0.36 mm.	0.09-0.12 mm., av. 0.10 mm.

C. conica differs from both *C. furcata* and *C. wasinensis,* the most closely related forms, in that it has smaller zooecia, and the orifices, both of the fertile and infertile zooecia, differ in shape and proportion from those of the other 2 species. The form of the colony, and the presence of vicarious avicularia, may not be important differences (see p. 450).

Each colony primarily encrusts the convex side of a small shell or conical Polyzoan. From this focus the zooecia have budded radially. On the frontal surface there is plurilaminar growth over the central ancestrular area. Elsewhere, groups of plurilaminar zooecia on the frontal surface are often associated with the incor-



TEXT-FIG. 2

Calyptotheca conica n. sp. and *C. orbiculata* Harmer.

A-C. *C. conica.* A. Small mandible of vicarious avicularium. 1892.1.28.76G.
B. Large mandible of vicarious avicularium. 1892.1.28.76C.
C. Vicarious avicularium, treated with eau de javel. 1892.1.28.76C.
D. *C. orbiculata.* Mandible of vicarious avicularium. Siboga 182A.
Scale = 0.20 mm.

poration of large fragments on the basal side. These plurilaminar areas frequently include vicarious avicularia, and the orientation of the zooecia is random.

The calcareous hooks on the basal surface of the zooecia are hollow outgrowths of the basal wall (see pl. I, 2); and cf. *Celleporaria aperta,* p. 442. They are strongly curved, and closed at the tip. Even in specimen 76H, which is the only zoarium preserved in alcohol, there is no trace of rootlets.

Ovicells are present in all the colonies, but in 76F alone, they appear to be associated in groups near the vicarious avicularia.

The vicarious avicularia are frequently longer than the zooecia (even in specimen 76G, see below). A polypide is present, and the mandible is variously spathulate, sometime being very widely expanded distally.

Colony 76G shows small but consistent variations from the others. Generally the dimensions of each measured character are larger than in the other specimens (see above). The fertile orifices are longer, and the sutural avicularia larger and far more numerous. The vicarious avicularia are also more numerous, occurring in a ratio of 1:16 zooecia, in comparison with a ratio of 1:82 zooecia in the other colonies. However, the mandibles are much smaller (see text-fig. 2 A), and not expanded distally.

Calyptotheca parcimunita Harmer.

Calyptotheca parcimunita Harmer, 1957:1015, pl. 65, figs. 12,13.

Type, "Siboga" Stn. 60,303, W. Timor, 0-36 m., 409A.

1862.7.16.69A, Tsu Sima, Korea Strait, 46 fath., Aylen Coll.

Zooecia large. Orifices with a distinct sinus and well-developed condyles. Avicularia small, oral, paired, directed distally. Mandible acute. Ovicells narrower than zooecia. Vicarious avicularia absent.

DIMENSIONS

lz	= 0.55-0.65 mm., av. 0.61 mm.	lo	= 0.35-0.60 mm., av. 0.47 mm.
Lo	= 0.15-0.17 mm., av. 0.16 mm.	Lz	= 0.15-0.19 mm., av. 0.18 mm.
Lfo	= 0.15-0.17 mm., av. 0.16 mm.	lfo	= 0.18-0.20 mm., av. 0.19 mm.
Lov	= 0.35-0.40 mm., av. 0.37 mm.	lov	= 0.35-0.45 mm., av. 0.40 mm.
Lav	= 0.05-0.07 mm., av. 0.06 mm.	Lm	= 0.02-0.04 mm., av. 0.03 mm.

C. parcimunita was originally described as encrusting. The specimen from Tsu Sima agrees well with the type specimen, and both have larger zooecia than the specimens from W. Flores and New Guinea which were included in the species by Harmer.

The orifices are elongated, with well-developed condyles, which are also present in the fertile zooecia. The minute oral avicularia are rare, but they are not plentiful in the type-specimen.

These colonies were mentioned by Hastings (1932:422). It seems very probable that encrusting colonies of *C. parcimunita* occur off S. Japan, but no other specimen of this species has been found in the British Museum.

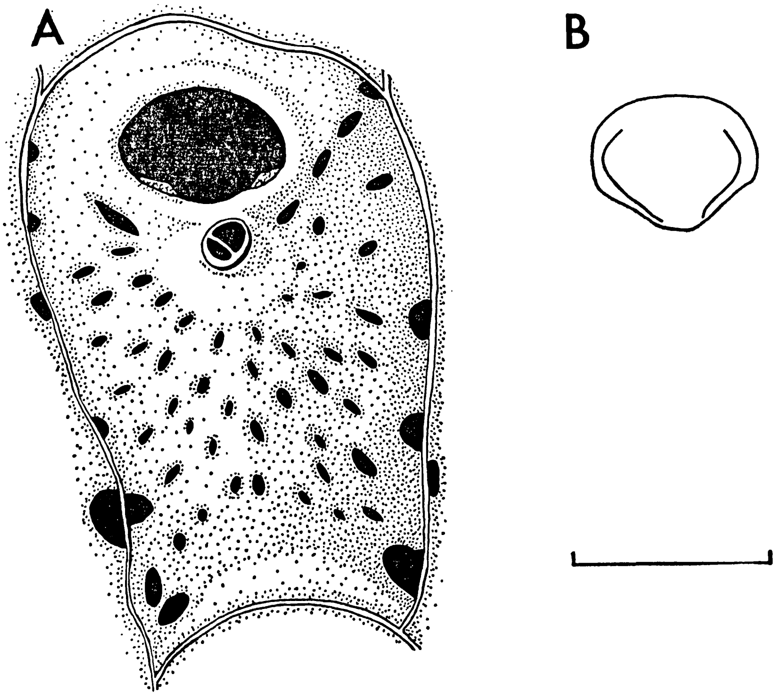
Schizomavella Canu & Bassler, 1917:40.

Zooecia and ovicells porous. Orifice sinuate. Median or submedian avicularium present. Ovicell closed by operculum.

Schizomavella collina n. sp.
(Text-fig. 3 A, B)

Schizomavella sp. Harmer, 1957:1009.

Holotype and only specimen, 1862.7.16.69B, Tsu Sima, Korea Strait, 46 fath., Aylen Coll.



TEXT-FIG. 3
Schizomavella collina n. sp.
A. Zooecium, treated with eau de javel. 1862.7.16.69B.
B. Operculum. 1862.7.16.69B.
Scale = 0.20 mm.

Zoarium free, conical. Zooecia large. Orifice wide, sinus shallow. Suboral avicularium very small, mandible rounded. Ovicells not found.

DIMENSIONS

Lz	= 0.58-0.70 mm., av. 0.66 mm.	lz	= 0.30-0.42 mm., av. 0.38 mm.
Lo	= 0.11-0.12 mm., av. 0.12 mm.	lo	= 0.15-0.17 mm., av. 0.16 mm.
Lav	= 0.05 mm.	Lm	= 0.03 mm.

The zoarium is the same in form as those of *C. conica* and *C. parcimunita* described above.

S. collina is closely reated to *S. inclusa* (Thornely) and to *S.* aff. *inclusa* (see Harmer, 1957:1028, 1029). Both these forms have vicarious avicularia with a rounded, slightly elongated mandible, with outwardly curved sclerites, like those of *Calyptotheca orbiculata* (see above). Neither form has been described with a conical zoarium. *S. collina* has no vicarious avicularia. It differs from *S. inclusa* in its much larger zooecia, and from *S.* aff. *inclusa* in its wider orifices. The suboral avicularium is also smaller, and closer to the orifice in *S. collina,* than in either of the other 2 forms.

Stylopoma Canu and Bassler, 1920:359.

Zooecia and ovicells porous. Orifice with a small sinus. Avicularia present, often vicarious. Ovicells extremely large, obscuring the orifice.

Stylopoma duboisii (Audoin).

Flustra duboisii Audouin, 1826:239; 1828:66, pl. 8, figs. 4^1, 4^2.

Lepralia schizostoma MacGillivray, 1869:135.

Stylopoma schizostoma (MacGillivray) Hastings, 1932:420, text-figs. 8A-F, 9.

Stylopoma duboisii (Audouin) Harmer, 1957:1033, pl. 74, figs. 1-7.

1892.1.28.43, Holothuria Bank, N.W. Australia, 34 fath., Basset-Smith Coll.

The characters of this colony have already been discussed by Hastings (1932) and Harmer (1957).

The zoarium is exactly like those of the other species described above, although the usual form of growth of *S. duboisii* is encrusting and plurilaminar, nodular and massive. The colony originates on the convex side of a zoarium of *Selenaria* (see below). The primary layer is regularly radial in growth, but from the central area and from 4 other foci, secondary layers of zooecia arise in which the orientation is random. Growing between the zooecia on the convex surface are Hydroid stolons, and there are also 3 slits (average length 0.5 mm.), indicating the presence of individuals of an Acrothoracid Cirripede. These commensal Cirripedes have frequently been found inhabiting corals. Recently a species has been discovered associated with several species of Cupuladriidae from west Africa, and another example, in the zoarium of *Selenaria* (from Bass's Straits) is also known (see Cook, 1965 a.). The presence of Acrothoracids implies stability of the host colony, as the long cirri protrude for feeding.

The basal surface of this zoarium of *S. duboisii* is smooth. Some of the zooecia have a slight central protuberance, and there is a white spot, centrally, in each zooecial wall. There are no hooked processes as in *C. conica*. A few ovicells, and 2 large vicarious avicularia with spathulate mandibles, are present. No other specimens of *S. duboisii* from the Holothuria Bank are present in the British Museum.

Celleporaria Lamouroux, 1821 : 43.

Zoarium plurilaminar. Zooecia with a few marginal pores. Orifice not sinuate. Suboral avicularium unilateral, subconical produced into an ascending rostrum. Frontal avicularia present, sometimes gigantic. Ovicell hyperstomial, imperforate, the frontal wall often slightly developed.

Celleporaria aperta (Hincks).

Schizoporella aperta Hincks, 1882:126, pl. 5, fig. 3.

Celleporaria aperta (Hincks) Harmer, 1957:673, pl. 42, figs. 11-13, text-fig. 56.

1892.1.28.104, Holothuria Bank, N.W. Australia, 15 fath., Basset-Smith Coll.

C. aperta is usually an encrusting species. This colony has formed a free-living, conical zoarium 7.5 mm. in diameter. It is circular and the basal side is flat, and almost smooth. It shows that the primary growth was from a central ancestrula surrounded by 5 zooecia. A secondary layer has grown over the primary layer, and can be seen, from a concentric ring of zooecial outlines on the basal side, to have regularly extended beyond it. In both layers, the budding is regularly radial, although the zooecia appear quite randomly orientated on the convex, frontal side of the colony.

The basal walls in the ancestrular region are wanting, as is the original substrate upon which the larve settled. The area presumably once covered by the substrate is small, 0.6 mm. in diameter, unlike the original substrates of the conical colonies described above. Harmer (1957:685) described a similar, free-living, conical colony of *Celleporaria descostilsii* (Audouin), from the Siboga Stn. 321, in the Java Sea (see p. 436). The basal walls of this colony had openings, one of which bore a rootlet. Most of the zooecia of this colony of *C. aperta* also have a pore, or a short, open prominence, in the basal wall. No rootlets have been seen, but it seems probable that they

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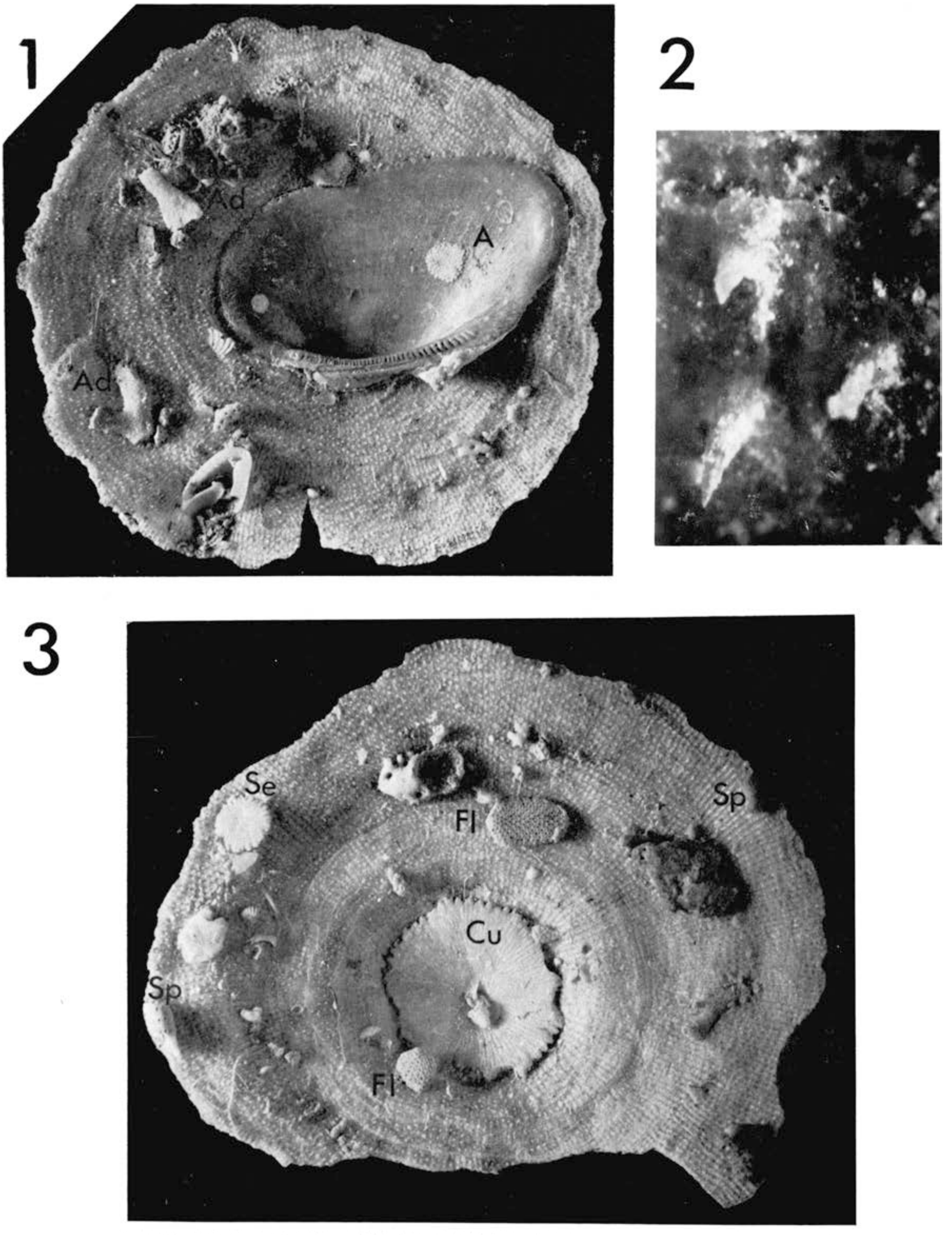
PLATE I

Basal surface of *Calyptotheca conica* n. sp.

1. Specimen 1892.1.28.76B. Showing original substrate, a shell, encrusted by a very young colony of *Adeonella* sp. (A). Incorporated by the basal surface during growth are fragments of 2 colonies of *Adeonella platalea* (*Ad*). (x 2.)
2. As above, basal, calcareous hooked processes. (x 100.)
3. Specimen 1892.1.28.76D. Showing original substrate, a zoarium of *Cupuladria guineensis* (*Cu*). Incorporated by the basal lamina are colonies of *Selenaria maculata* (*Se*), *Spiroporina ? vertebralis* (*Sp*), and *Flabellopora umbonata* (*Fl*) (x 2.4).



P.L. Cook. PLATE I

were once present. *C. descostilsii* has well-developed avicularia, which are generally common in *Celleporaria;* those in this colony of *C. aperta* are not especially large, prominent or frequent. No other specimens of *C. aperta* from the Holothuria Bank are present in the British Museum.

ANALYSIS OF THE ASSOCIATED POLYZOAN FAUNA

The species of Polyzoa found on the basal surface of the colonies of *Calyptotheca conica, C. parcimunita, Schizomavella collina* and *Stylopoma duboisii* comprise 3 elements.

The first group consists of species upon which the larvae initially settled. Initial settlement has been consistently upon a convex surface, not smaller than 4 mm. in diameter (cf. *C. aperta,* above, and Lagaaij, 1963:181). When this original substrate is a Polyzoan, it is always the zoarium of a free-living, conical species, specially adapted to life in a sandy or muddy habitat.

The second group consists both of colonies of similar species, and of fragments of erect species, which have been incorporated, as they lay on the surface of the sea-bottom, by the basal walls of the zooecia of the colonies as they grew.

The third group consists of epizoic species, whose larvae have successfully settled upon the basal side of the large conical colonies. These species include both encrusting and erect forms. The basal central concavities of these conical zoaria are high, that of 1892.1.28. 76A, the highest, being estimated as 22 mm. above the surface of the sea-bottom. This has allowed free growth of young, erect colonies of *Reteporella* on 76C (see below).

Encrusting, epizoic species are frequently found within the basal concavities of large, domed colonies of *Cupuladria* and *Discoporella* Osburn (1914:190) first described *Beania cupulariensis* as consistently associated with *Cupuladria,* the colonies loosely encrusting the basal side. Colonies of *C. multispinata* from South Africa have been seen, encrusted basally with Sponges and worm-tubes, among which are attached small bivalve Mollusca and egg sacs of various, unknown organisms. Similar epizoic species are associated with *C. canariensis* and *Discoporella umbellata* colonies from West Africa (see Cook, 1965 b.).

Colonies of Cupuladriidae are maintained in a position slightly above the sea-bottom by their peripheral vibracular setae (see Cook, 1963), and this presumably allows the entry of larvae into the basal concavities. The colonies from Africa were alive when collected, polypides being present, so that the epizoic forms are not the result of settlement after death, when the setae were no longer active.

Details of the colonies and the associated species are summarized below. The size of the colony and the type of substrate from which it originates are given, followed by a list of the forms primarily incorporated by the basal surface during its growth. The secondary, epizoic species are then listed. The number of colonies, or fragments of colonies, if more than one, is given in parentheses after each name.

Calyptotheca conica, 1892.1.28.76A-H.

A. Segment 40 mm. across, complete zoarium with an estimated diameter of 70 mm.

Originating on the outer, convex side of a bivalve shell, diameter 10 mm.

Incorporated forms : *Selenaria maculata, Conescharellina crassa, Flabellopora umbonata ; Cellaria ? punctata, Adeonella platalea, Spiroporina ? vertebralis.* Foraminifera, shell fragments and small stones.

Epizoic forms: *Mucropetraliella thenardii, Cribrilaria radiata, Aetea truncata, Tubulipora pulcherrima;* Cyclostomata.

B. Colony diameter 42 mm. (see pl. I, 1).

Originating on the outer, convex side of a bivalve shell, measuring 25 mm × 15 mm.

Incorporated forms: *Spiroporina* sp., *Adeonella platalea* (2), *"Retepora"* sp., and 4 fragments of erect Polyzoa. Shell fragments.

Epizoic forms: *Adeonella* sp. Sponge.

C. Colony diameter 38 mm.

Original substrate hidden by a mass of calcareous debris; the central plurilaminar growth on the upper side is very marked. The mass includes *Cabera* sp., *"Retepora"* sp., Cyclostomata, Foraminifera and small shells.

Incorporated forms: *Spiroporina ? vertebralis,* erect Polyzoa (2). Foraminifera.

Epizoic forms: *Smittipora cordiformis, Cribrilaria radiata, Parasmittina tropica, Reteporella ? graeffi* (2).

D. Nearly complete colony, diameter 40 mm. (see pl. I, 3).

Originating on the convex surface of *Cupuladria guineensis,* diameter 10 mm.

Incorporated forms: *Selenaria maculata, Flabellopora umbonata* (2), *"Retepora"* sp., *Spiroporina ? vertebralis* (2). Foraminifera, small stones, average diameter 5 mm.

Epizoic forms: *Aetea truncata.*

E. Segment 29 mm. across, complete zoarium with an estimated diameter of 55 mm.

Originating on the convex surface of *Selenaria* sp., diameter 4 mm.

Incorporated forms: *Selenaria* sp., *Conescharellina symmetrica; Adeonella* sp., *Cleidochasma* sp. *Caberea* sp., erect Polyzoa (2). Worm tube, small shell fragments.

Epizoic forms: *Aetea truncata.*

F. Colony diameter 26 mm.

Originating on the outer, convex side of a bivalve shell, diameter 6 mm.

Incorporated forms: *"Retepora"* sp., Cyclostomata. Worm tube, small shell fragments.

G. Colony diameter 17 mm.

Originating on the convex surface of *Selenaria maculata* diameter 5 mm. The growing edge of a colony of another (unidentified) species of Polyzoan can be seen to have encrusted the *Selenaria* before establishment of the colony of *Calyptotheca.*

Incorporated forms: Erect Polyzoa, small shell fragments.

H. 2 fragments, the larger with an estimated diameter of 35 mm. when complete.

Original substrate hidden by a mass of calcareous debris.

Incorporated forms: *Adeonella* sp., *"Retepora"* sp. Shells and stones, average diameter 4 mm.

Epizoic forms: *Aetea truncata.* Foraminifera, Sponge (2), bivalve Mollusca (4).

Calyptotheca parcimunita, 1862.7.16.69A.

2 colonies, diameter 17 and 22 mm.

Originating on the outer convex side of shells, average diameter 13 mm.

Epizoic forms: *Escharina pesanseris* and *Tubulipora pulcherrima* (growing on the shells).

Schizomavella collina, 1862.7.16.69B.

Colony diameter 17 mm.

Originating on the outer, convex side of a shell, diameter 6 mm.

Incorporated forms: Small stones.

Epizoic forms: *Aetea* sp.

Stylopoma duboisii, 1892.1.28.43.

Colony diameter 19 mm.

Originating on the convex side of *Selenaria maculata* diameter 4 mm.

Incorporated forms: Echinoderm spines and small shell fragments.

Epizoic forms: Cyclostomata. Foraminifera, Hydroid and worm tubes.

Inhabited by Acrothoracid Cirripedes (see p. 441).

NOTES ON SOME OF THE INCORPORATED AND SETTLED SPECIES

I. Incorporated, free-living, conical zoaria associated with sandy or muddy sea-bottoms.

Selenaria maculata Busk, 1854.

This species has been reported from the Australian region, and the British Museum possesses several other specimens from N.W. Australia, including one from the Holothuria Bank (36 fath., 1937.12. 28.1, Basset-Smith Coll.). 4 of the 6 colonies listed above, including those which are the original substrates, were incorporated with the basal side downwards. It is reasonable to assume that, as in the Cupuladriidae, this is the normal position of the living colony, but as none of these zoaria have any chitinous parts, they were probably dead when incorporated (see pl. I, 3). The 2 colonies listed as *Selenaria* sp., which probably belong to *S. maculata,* are worn, and cannot with certainty be referred to that species.

Cupuladria guineensis (Busk, 1854).

C. guineensis has a large distribution in the western Pacific, from the Philippines to S. Australia. There are 4 other specimens from the Holothuria Bank in the British Museum (36 fath., 1892.1.28.45pt., 34 fath., presumably the same haul as *S. duboisii,* above; 1892.1.28.125, Basset-Smith Coll.; and 1891.12.12.1-4). The colony encrusted by *C. conica* has no chitinous parts visible, but it was in the normal, live position when incorporated. The basal sectors are of the smooth, almost square type, with pores at the base of pits (see Cook, 1965 a; and pl. I, 3).

Conescharellina symmetrica Harmer, 1957, and *C. crassa* (Tenison-Woods, 1880)

These species are generally distributed in the Australasian and Malaysian regions (see Harmer, 1957). There is one other specimen of *C. crassa* from the Holothuria Bank in the British Museum (36 fath., 1892.1.28.45pt., cf. *C. guineensis* above). The colonies have been incorporated lying on one side, neither rootlets nor chitinous parts are present.

Flabellopora umbonata (Haswell, 1880).

Distributed from the Philippines to Australia (see Harmer, 1957:751). These colonies are not complete. They have been incorporated lying on one side; no chitinous parts or rootlets are present (see pl. I, 3).

2. Incorporated species with erect zoaria.

Cellaria ?punctata (Busk, 1852, part).

Distribution, Indian Ocean, W. Pacific, Australasia.

The single, small fragment of an internode has neither avicularia nor ovicells. It is quadriserial, and the zooecia have the "conspicuous, longitudinal cryptocyst ridge" described by Harmer (1926:338), as being characteristic of the species.

Spiroporina ?vertebralis Stoliczka, 1865.

Distribution, Pacific and Indian Oceans. There is a specimen in the British Museum from the Holothuria Bank (1892.1.28.78, Basset-Smith Coll.). These fragments are too worn for certain identification, but possess axial kenozooecia and numerous zooecia per whorl. They therefore agree with the characters of *S. vertebralis* as given by Harmer (1957:846) (see pl. I, 3).

Adeonella ?platalea Busk, 1854.

Distribution, Indian Ocean and Philippines to S. Australia.

There is a specimen in the British Museum from the Holothuria Bank (34 fath., 1892.1.28.83, Basset-Smith Coll.). These fragments are worn, but appear to have the characters of typical *A. platalea* (Section 1, see Harmer, 1957:809) (see pl. I, 1).

3. Epizoic, secondarily settled species, both erect and encrusting.

Aetea truncata (Landsborough) Harmer 1926.

Distribution, China Sea, Malaysia, Indian Ocean.

These specimens have the erect part of the zooecia ("peristome") straight and punctate, as described by Harmer (1926:196). These parts are proportionately stouter and shorter in European specimens, which, if the genus is revised, may be considered to be distinct.

The encrusting parts of the zooecia grow between the hooked calcareous basal processes of the colonies of *C. conica*. They are presumably what Harmer (1957:1009) described as "the minute zooecia of a *Hippothoa*". Erect "peristomes" are present on 1892.1.28.76. A, D, E and H.

The unnamed *Aetea* encrusting *S. collina* is worn, only the encrusting parts of the zooecia remaining.

Smittipora cordiformis Harmer 1926.

Distribution, Indian Ocean and Philippines to N.W. Australia. The colony comprises about 150 zooecia, the opercula and many of the mandibles are present. The opesiular indentations are very small, and the avicularian rachis is toothed along its entire length, as described by Harmer (1926:260).

Cribrilaria radiata (Moll, 1803).

Generally distributed in warm waters (see Harmer, 1926:476). The colony on 1892.1.28.760 has about 100 zooecia, that on 76A, about 40; both colonies have ovicells. Chitinous parts and well-developed oral spines are present.

Mucropetraliella thenardii (Audouin, 1826, 1828).

Distribution, Red Sea, Indian Ocean, and W. Pacific from Japan to Australia. The zooecia are long and narrow, with a long suboral mucro. The ovicells are small, as described by Harmer (1957:714). The colony comprises about 120 zooecia. It has branched into 3 lobes. The ovicells and long oral spines are present undamaged. Opercula are present in many zooecia, and, where the frontal walls are broken, the underlying frontal membrane can be seen.

Escharina pesanseris (Smitt, 1873).

Generally distributed in warm waters (see Harmer, 1957:998). 2 worn colonies are present, one of 12, and the other of 30 zooecia. The ancestrulae and several ovicells are present.

Parasmittina tropica (Waters, 1909).

Distribution, Red Sea to S. Africa, and Philippines to Australia. The colony is fairly large, growing over the mass of calcareous debris. Ovicells, and the characteristics long, narrow avicularia are present (see Harmer, 1957:934).

Adeonella sp.

This young colony encrusts the inner, concave surface of the shell in 1892.1.28.76B (see pl. I, 1). It comprises the ancestrula and about 100 zooecia. A fairly large avicularium is present on most zooecia, directed distally across the proximal side of the orifice in a similar manner to that of *Reptadeonella plagiopora* (Busk), see

Harmer, 1957:815. This species has a spiramen, however, not an ascopore, and the zooecia are much smaller than those of *R. plagiopora*. It may be a very young stage of *A. platalea* (see above).

Reteporella graeffi Kirchenpauer, (1869).

Distributed in the W. Pacific and Indian Oceans. The 2 colonies are very young, but agree well with Harmer's description (1934:573) of this species. Both arise from an encrusting base. The long oral spines are present and undamaged.

Tubulipora pulcherrima

Distribution, W. Pacific and Indian Oceans. There is a specimen from the Holothuria Bank in the British Museum (15 fath., 1892.1.28.121 pt. Basset-Smith Coll.). The colony encrusting 1892.1.28.76A has an ancestrula and approximately 40 zooecia. It divides into 2 lobes, one of which has become erect, supported by 2 long rooting processes, as described by Harmer (1915:131). No ovicells are present. The colony on 1892.7.16.69A may belong to this species. It is partially obscured, as it grows between the basal lamina of the colony of *Calyptotheca* and the shell upon which the colony originates. The zooecia are similar to those of *T. pulcherrima,* and short, rooting processes are present.

NOTES ON CONICAL ZOARIA AND SANDY OR MUDDY SEA-BOTTOMS

Polyzoan colonies are usually encrusting, or erect, with an encrusting base, their larvae having settled upon a solid, stable substrate. Where the sea-bottom consists of sand or mud, it is unsuitable for the normal growth of Polyzoa, unless they are specially adapted or have a rooting system capable of anchoring the rest of the colony above the surface of the sea-bottom.

Certain groups of species are particularly adapted to sandy or muddy habitats, and in fact, are almost confined to them. These "sand fauna" species are not all closely related, but all have a conical shape, the zooecial orifices opening upon the convex surface. The mode of life of most of the species is unknown, but living colonies belonging to the Cupuladriidae have been observed (see Marcus & Marcus, 1962, and Cook, 1963). Similar zoarial orientation is probably normal in the free-living Mamilloporidae, Selenariidae, Anoteroporidae and Actisecidae. The Conescharellinidae, which also have conical colonies, appear to be attached above the sea-bottom by rootlets (see Harmer, 1957:725), who also noted (p. 860) that the occurrence of species of Bifaxariidae, which have a well-developed rooting system, was correlated with muddy bottoms at great depth. Harmer had previously (1934:532) discussed the occurrence of Reteporidae from the Indo-Pacific region, where mud and sand is frequent. He concluded that deep, muddy sea-bottoms were unsuitable for such erect species. He noted, however, that where sand or some "other firmer substance" was present, Reteporidae were found.

The principal characters of the muddy or sandy habitat are instability and the constant deposition of particles from the upper layers of water. The effects of instability are lessened by the conical habit common to all free-living zoaria. The Cupuladriidae increase their basal area by means of the peripheral setae (see Cook, 1963). The frictional nature of the basal surface of *Calyptotheca conica* may be increased by the hooked basal processes, but there are no processes in *C. parcimunita, Schizomavella collina* or *Stylopoma duboisii* (see above). Deposits are cleared from the frontal surface of the colony in the Cupuladriidae by the frontal vibracular setae (see Marcus & Marcus, 1962, and Cook, 1963). Large avicularia or vibracula are common in nearly all free-living, conical colonies, e.g. *Lunulites, Selenaria* and *Anoteropera.* Although they may not have the exactly the same function as in the Cupuladriidae; it seems very probable that it is connected with the clearing of deposits from the surface. Large, vicarious avicularia occur in some of the encrusting species of *Calyptotheca* and *Schizomavella,* but are absent in *C. parcimunita* and *S. collina.* In these conical zoaria, the presence or absence of vicarious avicularia is thus not specifically connected with either habit or habitat. The adaptation to a conical form of zoarium in *C. parcimunita* and *Stylopoma duboisii* is also not in itself of specific importance, and the discovery of further material of both *Calyptotheca conica* and *Schizomavella collina* might well show that their more usual form of colony is also both encrusting or erect.

The sea-bottom of the Holothuria Bank and the S. Korea Strait, is sand mud and shell (see Admiralty Charts for Australia, Northern Portion, 1934, and for the China Sea, 1887). Even without such available information, the nature of the sea-bottom may be inferred from the Polyzoan fauna.

For example, a fine specimen of *Adeona foliacea* Lamouroux (Holothuria Bank, 24 fath., 1892.1.28.91), over 150 mm. high, is in the British Museum. Unlike the labels of other specimens from the Basset-Smith Collection, the label of this specimen specifically mentions a sea-bottom of "mud, sand and shell". A well-developed rooting system is present (see Harmer, 1957:789, 796), and adhering to it are sand grains and a shell fragment 8 mm. in diameter. Other specimens, of *Lanceopora* spp. (Holothuria Bank, 15 fath., 1892.1.28.40 and 24-34 fath., 1965.2.2.1; and Tsu Sima, 46 fath., 1862.7.16.90), are also attached by rootlets, and are forms associated with muddy and sandy habitats (see Harmer, 1957:985).

A high proportion of free-living conical species may be expected in collections from such habitats. The British Museum possesses over 200 specimens of these species from N.W. Australia, including the Holothuria Bank. Some specimens, notably those of *Cupuladria guineensis, Selenaria maculata* and *Conescharellina crassa,* were from the same, or very similar depths, and may have been from the same hauls, as the conical colonies of *Calyptotheca conica* and *Stylopoma duboisii.* They were alive when collected, chitinous parts and polypides being present. The specimens of the same species incorporated by the growth of the conical colonies were dead, but it appears that they were also a normal, living component of the fauna.

No other free-living conical zoaria are present from Tsu Sima. Although the sea-bottom is suitable, the winter temperature is almost certainly too low for the typically tropical and subtropical conical genera of the W. Pacific. Lagaaij (1963) has shown that *Cupuladria canariensis* is limited to a distribution represented by a minimum surface temperature of 14°C. Records of *C. guineensis, Selenaria* and *Conescharellina* spp. appear to be restricted to a distribution represented by a minimum surface temperature of not less than 10°C.

Encrusting or erect species without rootlets would not be expected to be part of the Polyzoan fauna of a sandy or muddy habitat, but there are specimens in the British Museum of such species from both the Holothuria Bank and Tsu Sima. The erect species incorporated by the growth of the conical zoaria were worn, and dead, but the other specimens in the British Museum have chitinous parts intact and were probably alive when collected. Those from the Holothuria Bank include several specimens of *Adeonella platalea* and *"Retepora"* spp. The zoaria are large (average height 60 mm.), and all arise from an encrusting, tubular base, growing round algal and Gorgonid stems. The broken ends of erect, tubular colonies of *Parasmittina* sp. (very similar to *P. raigii* (Audouin), see Harmer, 1957:938), show that the original substrate was an alga (S. Korea Strait, 50 fath., 1862.7.16.100). The branching tubes, which have expanded, unilamellar growing edges, average 40 mm. in height. Massive, plurilaminar colonies of the same species, from Tsu Sima (46 fath., 1862.7.16.60), also have a tubular core, and probably had a similar substrate. Many of the other species from Tsu Sima are encrusting, but their substrates, like those of *C. parcimunita* and *S. collina,* consist of single valves of small bivalve shells, not larger than 15 mm. in diameter. Specimens of, for example, *Celleporina radiata* (Ortmann) and *Celleporaria columnaris* (Busk) (Tsu Sima, 4 fath., 1862.7.16.71), arise as small, rounded, columnar masses, 10 mm. in diameter, from the convex side of the shells.

At moderate depths, a sea-bottom of mixed sand, mud and shells appears to be particularly favourable to the growth of Polyzoa. The "Siboga" stations richest in Polyzoa were: Stn. 77, Borneo Bank (59 m., fine, grey, coral sand), Stn. 164, New Guinea (32 m., sand, small stones, shell) and Stn. 273, Aru Is. (13 m., sand, shell), see Harmer, 1915:168-9 and 1957:650. At Stn. 273, both *Adeonella platalea* and *Spiroporina vertebralis* (see p. 447) were present with the erect, rooted "sand fauna" species, *Adeona foliacea. S. vertebralis* was, in fact, present at all 3 stations, and Harmer (1957:850) described the initial stages, encrusting *Amathia,* a Ctenostome which is usually found arising from other erect forms, for example Polyzoa, Gorgonids or Algae. Station 77 also included the conical "sand fauna" species, *Actisecos pulcher, Cyttaridium pulcherrimum, Anoteropora magicapitata* and *Cleidochasma mirabile* (see Harmer, 1957:650). The fragments of *Adeonella* and *Spiroporina* incorporated by the growth of the conical colonies were dead but it is apparently also possible for these forms to be coexistent with typically "sand fauna" species.

None of the erect or encrusting species found epizoic on the colonies is known to possess a planktotrophic larva, and it may be presumed, that as most of the species are known to have ovicells, that the larvae are lecithotrophic. Their free-swimming life is necessarily short, and thus the colonies from which they were liberated were probably fairly close to the conical colonies for successful settlement to have been possible (see Ryland, 1963:50). The larvae may, of course, have been liberated from breeding colonies which were themselves encrusting the basal side of other conical colonies.

CONCLUSIONS

1. The remarkable feature of the adaptation of 5 species (belonging to 4 genera) of Polyzoa, to a basically unsuitable habitat, is that the form of zoarium each produced is of conical shape. This is similar to that shared by the various genera specifically adapted to, and often confined to, sandy or muddy sea-bottoms.

2. Possible inferences may be made as to the habitat from an examination of these zoaria. The shape, and free-living habit indicate an unstable, sandy or muddy sea-bottom. The original substrate of 4 of the species show the presence of small shells and of typically "sand fauna" Polyzoa. The epizoic species growing secondarily on the hollow basal side of these colonies, show that both erect and encrusting species were probably part of the surrounding fauna, although not necessarily living directly on the sea-bottom. These inferences have been supported by study of other specimens from the same localities.

Thus the Polyzoan fauna of a sea-bottom which consists of sand, mud or shell (or a mixture of all three) may be expected to comprise:

a. Conical, free-living colonies specifically adapted to life on the surface of the sea-bottom, with or without the anchorage of rootlets (e.g. *Cupuladria, Selenaria* and *Conescharellina*).
b. Colonies with erect branches, anchored by rootlets (e.g. *Adeona, Lanceopora*).
c. Colonies incidentally adapted, with a conical form, with or without rootlets (e.g. *Calyptotheca parcimunita, Celleporaria aperta* and *C. descostilsii*).
d. Colonies secondarily associated, living above the sea-bottom, encrusting Polyzoa, algae, Gorgonids, etc., which are capable of directly colonising the sand or mud (e.g. *Adeonella, "Retepora"* and *Parasmittina*). These last may be regarded as an extension of the fauna of neighbouring areas, where the sea-bottom is of a harder nature.

It is interesting that the occurrence of these 4 types of colony may be inferred from examination of the basal incorporated and epizoic species of the adapted, conical zoaria. Although the dominant type of zoarium in any fauna is correlated with available substrate, the factors controlling the limits of distribution of Polyzoan species may be the inter-related effects of depth and temperature, available oxygen and calcium carbonate, rather than and overall character of the sea-bottom (see Böggild, 1916; Harmer, 1934:534 and Lagaaij, 1963). The adaptability of Polyzoa is such, that a small proportion of larvae appear to settle successfully, an to produce adult, breeding colonies, even where the character of the sea-bottom would seem to be unsuitable, and the availability of a stable substrate is reduced.

3. An estimate may be made of the frequency and distribution of free-living conical colonies on the sea-bottom in sandy or muddy habitats. The total basal surface area of the 12 colonies described above (excluding that of *C. aperta*), was approximately 6,000 sq. mm. 12 colonies of typically "sand fauna" species were either settled upon initially or later incorporated. This total includes the zoaria of *Flabellopora* and *Conescharellina*. The possible frequency of all these colonies is thus 2,000 per sq. metre. This figure is of the same order as the estimate of 2,500-3,000 given by Marcus & Marcus (1962:283), for colonies of Cupuladriidae from S. America. The volumetric estimate for Madeiran Cupuladriidae given by Cook (1963:409), if expressed in this form, gives a figure of approximately 2,200 colonies per sq. metre.

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Summary

5 species, 3 of which are known to be usually encrusting, have produced free-living, conical zoaria when growing over a sea-bottom of sand, mud and shell. The zoaria of 4 of these species have incorporated various organisms from the surface of the sea-bottom into their basal surfaces during growth. These include species of Polyzoa, and the hollow, basal concavities of the colonies have been secondarily colonized by epizoic growth, including other species of Polyzoa. The occurrence of these forms has been analysed. The Polyzoan fauna associated with sandy or muddy sea-bottoms is discussed, and an estimate is made of the frequency of free-living "sand fauna" species in such habitats.

Zusammenfassung

Fünf Arten von Bryozoen, von denen drei normalerweise krustenbildend sind, bilden freilebende, konische Zoarien, wenn sie auf einem aus Sand, Schlamm und Muschelschalen zusammengesetzten Meeresboden wachsen. Die Zoarien von vier dieser Arten schliessen während ihres Wachstums in ihren basalen Oberflächen verschiedene von der Meeresbodenoberfläche stammende Organismen ein. Es handelt sich unter anderem um Bryozoen und die basalen Körperhöhlen der Kolonien sind sekundär durch epizoisches Wachstum kolonisiert worden, das andere Bryozoenarten einschliesst. Das Auftreten dieser Formen ist analysiert worden. Die Bryozoenfauna der Sand- oder Schlammmeeresböden wird diskutiert und die Frequenz der freilebenden « Sandfauna »-Arten in solchen Biotopen wird geschätzt.

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