

## Superornatiremidae fam. nov. (Copepoda: Harpacticoida): An enigmatic family from North Atlantic anchihaline caves\*

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**SUMMARY:** A new family Superornatiremidae is described from 7 inland marine caves of Bermuda and from Jameos del Agua Cave, a sea water-flooded Holocene lava tube on Lanzarote in the Canary Islands. The family is proposed to accommodate three new genera, *Superornatiremis*, *Neoechinophora* and *Intercrusia*, and six new species: *S. mysticus*, *N. fosshageni*, *N. daltonae*, *N. jaumei*, *N. karaytugi* and *I. problematica*. The major diagnostic character is the unique leg 1 which exhibits supernumerary elements on the proximal and middle exopod segments and the middle and distal endopod segments. The increase of armature elements is regarded as a secondary phenomenon in copepod evolution and not as the result of character reversal. Other unique characters comprise the presence of an epicopulatory flap closing off the copulatory pore, the laterally displaced female gonopores and the paired copulatory ducts, the modified trilobate proximal endite of the maxilla, the fused labrum and labium (derived from the fused paragnaths) forming a well developed oral cone, the modified endopod of leg 2 and the transformation of the distal inner seta of P2-P3 enp-3 into a spine. The family is further characterized by the complete lack of sexual dimorphism on the swimming legs. The three genera can be differentiated primarily by the combination of P1 armature, structure of the outer exopod spines of P1, genital field morphology and segmentation of the male P5. The problematic status of *Intercrusia* is discussed. The new family is placed in the tisburyid complex of families and seems to occupy an intermediate position between the two free-living tisburyid subfamilies Tisbinae and Idyanthinae. The biogeography of the family is briefly discussed.

**Key words:** Copepoda, Harpacticoida, Superornatiremidae fam. nov., *Superornatiremis* gen. nov., *Neoechinophora* gen. nov., *Intercrusia* gen. nov., anchihaline caves, North Atlantic.

**RESUMEN:** SUPERORNATIREMIDAE FAM. NOV. (COPEPODA: HARPACTICOIDA): UNA FAMILIA ENIGMÁTICA DE CUEVAS ANQUIHALINAS DEL ATLÁNTICO NORTE. – Se describe una nueva familia de copépodos harpacticoides, Superornatiremidae, a partir de material procedente de 7 cuevas anquihalinas de Bermuda y de los Jameos del Agua, un tubo volcánico de edad holocena sumergido en el mar y situado en Lanzarote, islas Canarias. La familia está integrada por 3 géneros nuevos, *Superornatiremis*, *Neoechinophora* y *Intercrusia*, y 6 especies nuevas: *S. mysticus*, *N. fosshageni*, *N. daltonae*, *N. jaumei*, *N. karaytugi* y *I. problematica*. El carácter diagnóstico principal de la familia reside en el primer apéndice torácico, que exhibe elementos supernumerarios sobre los segmentos proximal y medio del exópodo, y sobre los segmentos medio y distal del endópodo. El incremento del número de elementos en la armadura de estos segmentos se interpreta como un fenómeno secundario en la evolución de los copépodos y no como resultado de una reversión de carácter. Otras características únicas comprenden la presencia de una pestaña epicopulatoria cerrando el poro copulador, los gonóforos femeninos desplazados lateralmente, y los conductos copuladores pareados, el endito proximal de la maxila modificado en forma de estructura trilobulada, el labrum y labium fusionados (este último derivado de la fusión de los paragnatos) formando un cono oral bien desarrollado, y la modificación del endópodo del segundo apéndice torácico y la transformación de la seta distal interna del enp-3 de P2-P3 en una espina. La familia se caracteriza además por la total ausencia de dimorfismo sexual en las patas natatorias. Los tres géneros se pueden diferenciar primariamente por la combinación de la armadura de la P1, la estructura de las espinas externas del exópodo de P1, la morfológica del campo genital y la segmentación de la P5 del macho. Se discute el estatus problemático de *Intercrusia*. La nueva familia se sitúa dentro del complejo tisburyomorfo de familias y parece ocupar una posición intermedia entre las dos subfamilias de tisburyidos de vida libre Tisbinae y Idyanthinae. Se discute brevemente la biogeografía de la familia.

**Palabras clave:** Copepoda, Harpacticoida, Superornatiremidae fam. nov., *Superornatiremis* gen. nov., *Neoechinophora* gen. nov., *Intercrusia* gen. nov., cuevas anquihalinas, Atlántico norte.

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## INTRODUCTION

Recent exploration and mapping of underwater caves, primarily utilizing advanced cave diving techniques, has produced a distinctive cavernicolous invertebrate fauna exhibiting an unexpectedly high diversity and endemism. The initial discoveries of high taxonomic and evolutionary significance such as the Remipedia, a new class of Crustacea first recorded from the Bahamas and Canary Islands, and the Mictacea, a new order of Peracarida from Bermuda, have aroused interest in anchihaline caves considerably. Set against a phylogenetic background, anchihaline caves and flooded lava tubes, along with the deep-sea hyperbenthic habitat, hydrothermal vents and cold seeps can be regarded as "hot spots" on the Earth's surface (Huys and Boxshall, 1991).

Investigation of caves has revealed many of the most primitive copepods in the orders Platycopioidea, Calanoidea and Misophrioida (e.g. Barr, 1984; Boxshall and Iliffe, 1986, 1987, 1990; Fosshagen and Iliffe, 1985, 1988, 1989, 1991, 1994). Although studies of anchihaline cave copepods were initially directed towards sites in the North Atlantic, recent exploration of similar habitats in the Indo-Pacific (e.g. Fosshagen and Iliffe, 1989; Boxshall and Iliffe, 1990; Ohtsuka *et al.*, 1993) and the Western Mediterranean (Jaume and Boxshall, 1995a-b, 1996a-c, in press) have revealed equally interesting discoveries.

The harpacticoid fauna of anchihaline caves is poorly known. Sket and Iliffe (1980), who provided preliminary findings on the cave fauna of Bermuda, list *Paramphiascella robinsoni* (A. Scott) (Diosaccidae) and an unidentified species of Laophontidae from the Walsingham Caves (Walsingham, Walsingham Sink, Corset and Roadside Caves). Huys (1988) described a new family Rotundiclepeiidae from Cueva del Agua in Tenerife and Boxshall and Huys (1989) presented a cursory note on two unidentified harpacticoid hosts of the tantulocarid *Stygotantulus stocki* Boxshall and Huys, collected in an anchihaline lava pool near Playa de Montana Bermeja on Lanzarote.

Examination of a series of samples collected from various caves on Bermuda by Drs A. Fosshagen and J.H. Stock, and from Jameos del Agua Cave on Lanzarote by Prof. H. Wilkens resulted in the discovery of three new genera *Intercrusia*, *Superornatiremis* and *Neoechinophora* belonging to a new family Superornatiremidae. The latter two generic names and the family name have been cited by Huys and Boxshall (1991) and Huys *et al.* (1996). Huys

and Boxshall (1991) figured the first swimming leg of two undescribed species *S. mysticus* and *N. fossahageni*. The former was also illustrated by Huys *et al.* (1996) who provided a figure of the male P5 of *Superornatiremis* sp. These taxa were merely proposed as intentional *nomina nuda* without any proper diagnoses and consequently are not available. In order to avoid further nomenclatural confusion and instability both names are formally made available herein for the same taxonomic concept. Hence, they will take authorship and date from the current act of establishment, not from their earlier publication (Huys and Boxshall, 1991) as *nomina nuda*.

## METHODS

Specimens were dissected in lactic acid and the dissected parts were placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). All drawings have been prepared using a camera lucida on a Leitz Dialux or Zeiss Axioskop microscope equipped with differential interference contrast.

Females and males of *Neoechinophora daltonae* sp. nov. were examined with a Hitachi S-800 scanning electron microscope. Specimens were prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter-coated with palladium.

The descriptive terminology applied to segmentation and setation of body appendages is adopted from Huys and Boxshall (1991). Abbreviations used in the text and figures are: ae, aesthetasc; P1 - P6, first to sixth thoracopods; exp, exopod; enp, endopod; exp(enp)-1(-2, -3), to denote the proximal (middle, distal) segment of a ramus.

Type material and additional specimens were deposited in the collection of the Zoology Department, The Natural History Museum, London.

With the exception of two samples collected by J.H. Stock in Bermuda and one sample obtained by H. Wilkens in Lanzarote, the material described herein was collected by Audun Fosshagen (occasionally in collaboration with T.M. Iliffe).

## RESULTS

### **Superornatiremidae Fam. Nov.**

Diagnosis: Harpacticoida. Body elongate cyclopidiform. First pedigerous somite fused to cephalosome.

Rostrum weakly developed, largely incorporated into cephalothorax, fused at base. Female genital double-somite with dorsal and ventrolateral hyaline frill marking original segmentation. Anal operculum weakly developed, rounded, spinulose; pseudoperculum absent. Caudal rami cylindrical, variable in length, with 7 setae (seta IV-V well developed, spinulose). Sexual dimorphism in antennule, P5, P6, abdominal ornamentation and in genital segmentation.

Antennule slender, without projections; segment 1 of ♀ distinctly shorter than segment 2; 9-segmented in ♀, with aesthetasc on segment 4 and acrothek on apical segment; 11-segmented and haplocer in ♂, none of segments swollen (geniculation between segments 8 and 9; 3 segments distal to geniculation), with aesthetasc on segments 4 and 6, and acrothek on segment 11; homology of male antennular segmentation: I, II, III-VIII, IX-XII, XIII, XIV-XVII, XVIII, XIX-XX, XXI-XXIII, XXIV-XXV, XXVI-XXVIII. Antenna with allobasis bearing abexopodal seta and 2- to 4-segmented exopod with ancestral formula [2,1,1,1-2]; endopod with 7 distal elements (1 subapical seta, 5 geniculate setae + 1 basally plumose seta) and 3 setae (1 geniculate) laterally. Labrum strongly developed triangular lobe, partly fused to labium (derived by median fusion of paragnaths) forming distinct oral cone. Mandible with elongate stylet-like gnathobase; biramous palp consisting of bisetose basis, 1-segmented endopod with 3-4 setae and 4-segmented exopod with formula [1,1,1,1-2]; basis with modified lash-like seta. Maxillule with elongate arthrite (1 element fused at base); coxal endite with 6 elements; exopod enlarged cylindrical segment with 4 setae; endopod minute, trisetose; basis bearing 2 distinct endites with 3 and 2 elements. Maxillary syncoxa with 2 widely separated endites, proximal endite trilobate with medially directed barbed lobe; endopod completely incorporated into allobasis. Maxilliped subchelate with unarmed syncoxa; basis with 0-1 seta; endopod an elongate segment drawn out into long subdistal claw bearing 3 accessory elements and forming apical pedestal with 2 geniculate setae.

P1 exopod 3-segmented; exp-1 without inner seta but with 3 outer spines, exp-2 with 2 outer spines; exopod with total of 6-7 elements (1 geniculate). P1 endopod 3-segmented, prehensile; with enp-1 bearing inner seta and enp-2 bearing 1-2 outer elements; enp-3 with total of 7 elements. P2-P4 with outer seta on basis, 3-segmented exopods and endopods (except sometimes P2 endopod); P2 endopod modified with elongate enp-1. Spine- and seta formulae as follows (asterisk indicating variable count):

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;*	0-1;*-1;2,2,3
P2	0-0	1-0	1-1;I-1;III,1+1,2	0-1;(0-2;1,2,I+1)
P3	0-0	1-0	1-1;I-1;III,1+1,*	0-1;0-1;1,2,I+2
P4	0-0	1-0	1-1;I-1;III,1+1,*	0-1;0-1;I,1+1,1

P1 exp-3 with 6 or 7 elements; P1 enp-2 with 1 or 2 outer elements; P3-P4 exp-3 with 2 or 3 inner setae. Distal inner seta of P2-P3 enp-3 modified into pinnate spine.

P5 of both sexes laterally displaced, with separate exopod and baseoendopod; in ♀ with baseoendopod partly incorporated into somite, endopodal lobe vestigial with 1 or 2 setae, exopod 1-segmented with 4-5 setae; in ♀ baseoendopod largely defined at base, endopodal lobe vestigial with 1 seta or completely absent, exopod 1- (with 4 setae) or 2-segmented (formula [1,3]).

Female gonopores separate, laterally displaced and each covered laterally by vestigial P6 bearing 2 setae; midventral copulatory pore single, of variable size, largely or partly covered by hyaline epicopulatory flap derived from cuticle outgrowth anterior to gonopores; paired copulatory ducts leading to median seminal receptacle. Number of egg-sacs unconfirmed.

Male sixth pair of legs asymmetrical, with 3 setae/spines each.

Anchihaline caves, freelifving.

Type genus: *Superornatiremis* gen. nov.

Other genera: *Neoechinophora* gen. nov., *Inter-crusia* gen. nov.

### *Neoechinophora* gen. nov.

Diagnosis: Superornatiremidae. Maxilliped with 0-1 seta on basis. Outer spines of P1 exopodal segments without subterminal tubular extensions. P1 exp-3 with 6 elements. P1 enp-2 with 1 outer element. Armature formula of P1-P4 as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;6	0-1;I-1;2,2,3
P2	0-0	1-0	1-1;I-1;III,1+1,2	0 - 1 : ( 0 - 2;1,2,I+1)
P3	0-0	1-0	1-1;I-1;III,1+1,[2-3]	0-1;0-1;1,2,I+2
P4	0-0	1-0	1-1;I-1;III,1+1,[2-3]	0-1;0-1;I,1+1,1

P5 ♀ with 4-5 setae on exopod and 1-2 on endopodal lobe of baseopod. P5 ♂ without endopodal lobe; exopod 2-segmented with 1 outer seta on exp-1 and an apical pinnate spine flanked by 2 setae on exp-2. Copulatory pore large, epicopulatory flap broadly rounded. P6 ♂ with inner pinnate spine, long middle seta and medium long outer seta. Anterior half of ♀ genital double-somite without paired dorsolateral tufts of long setules. Caudal rami variable in size.

Type species: *Neoechinophora fosshageni* gen. et sp. nov.

Other species: *N. daltonae* sp. nov., *N. jaumei* sp. nov., *N. karaytugi* sp. nov.

Etymology: The genus name is derived from the Greek *neos*, meaning new, *echinos*, meaning spine, and *pherein*, meaning to carry, and alludes to the presence of novel armature elements on leg 1. The type species is named for its collector, Dr Audun Fosshagen (University of Bergen) who also collected most other material of the genus. It is with pleasure and encouragement that I dedicate the other species to three young, dynamic and enthusiastic copepodologists based at or affiliated with the Crustacea Research Group in The Natural History Museum: Sophie Conroy-Dalton, Damia Jaume (IMEDEA (CSIC), Palma de Mallorca) and Süphan Karaytug.

#### *Neoechinophora fosshageni* sp. nov.

Material examined: Holotype ♀ (dissected on 6 slides; reg. no. 1996.1204); paratypes are 1 ♂ dissected on 7 slides and 2 ♀♀, 9 ♂♂ in alcohol (reg. nos 1996.1205-1215); collected in Roadside Cave, Bermuda; leg. A. Fosshagen; 18 September 1984; collected with fine mesh dip net from the water column at 0-1 m depths.

Additional material: (a) 1 ♀, 2 ♂♂ from Roadside Cave, Bermuda; leg. A. Fosshagen; 27 September 1984; collected with plankton net (mesh size 93 µm) from the water column at 0-5 m depths; (b) 3 ♀♀, 1 ♂ from Tucker's Town Cave, Bermuda; leg. A. Fosshagen; 10 September 1984; collected with fine mesh dip net from the water column at 0-1 m depths.

Roadside Cave (Hamilton Parish) is a small isolated limestone cave located on the northern edge of the Walsingham area at about 110 m from the nearest shore at Harrington Sound. It has no visible connection with the sea or other caves and the absence of currents in the cave indicates a distant relationship with the sea. Roadside Cave consists of a small entrance into a single room containing a saltwater-filled fissure about 8 m long by 1 m wide and 6 m deep. The bottom consists of bare breakdown rubble. The tidal range (in percentage of open water) and the tidal lag (in minutes) are 57 and 80, respectively. The water is very clear and has a salinity ranging between 30.2‰ at the surface and 31.8‰ at 1

m depth (Kornicker and Iliffe, 1989) although surface salinity varies with changes in rainfall. Roadside Cave is the type locality for two platycopioids, *Antrisocopia prehensilis* Fosshagen (in Fosshagen and Iliffe (1985)) and *Nanocopia minuta* Fosshagen (in Fosshagen and Iliffe (1988)). The misophrioid *Speleophria bivexilla* Boxshall and Iliffe has also been described from this locality (Boxshall and Iliffe, 1986) and specimens of the calanoid *Paracyclops naessi* Fosshagen were recorded by Fosshagen and Iliffe (1986). *Ridgewayia marki* Esterly is one of the most abundant calanoids in Roadside Cave (Fosshagen, pers. commn). Other harpacticoids co-occurring with *N. fosshageni* include various Ameiridae and Diosaccidae, a new representative of the Rotundiclepeidae (Huys, 1988) and *Laophontella* sp. (Tetragonicipitidae).

Tucker's Town Cave (St. George's Parish) is located at the southwestern corner of Castle Harbor on the Tucker's Town peninsula. The cave is about 125 m away from the sea but since no water currents are noted it presumably lacks a direct connection with the sea. Tucker's Town Cave contains a steep entrance shaft reaching a large underwater sand-floored chamber with a maximum depth of 24 m. Salinity ranges between 21.4‰ at the surface and 28.6‰ at 1 m depth (Kornicker and Iliffe, 1989). A complete description of the cave is given in Hart and Manning (1981). Fosshagen and Iliffe (1985) reported *Paracyclops naessi* in small numbers.

#### Description:

Female (Figs. 1-5): Total body length 510 µm measured from tip of rostrum to posterior margin of caudal rami. Largest width 145 µm measured at anterior margin of P2-bearing somite.

Body elongate cycloform (Fig. 1A), with distinct demarcation between prosome and urosome. Integument smooth, not strongly chitinized. Hyaline frill of cephalothorax and body somites plain and smooth (Figs. 1A; 5A-C). Cephalothorax and somites bearing P2-P4 without surface ornamentation (Fig. 1A) except for integumental sensilla. Genital double-somite elongate, completely fused (Figs. 5-C); original segmentation marked by transverse surface frill dorsolaterally (Fig. 5B) and dorsally (Fig. 5A) but not by internal chitinous ribs. Second abdominal somite (Fig. 5C) with midventral and paired lateroventral rows of fine spinules. Third abdominal somite without ornamentation. Anal somite with median longitudinal reinforcement in posterior half (Figs. 5A, C); with paired ventral and lateroventral rows of coarse

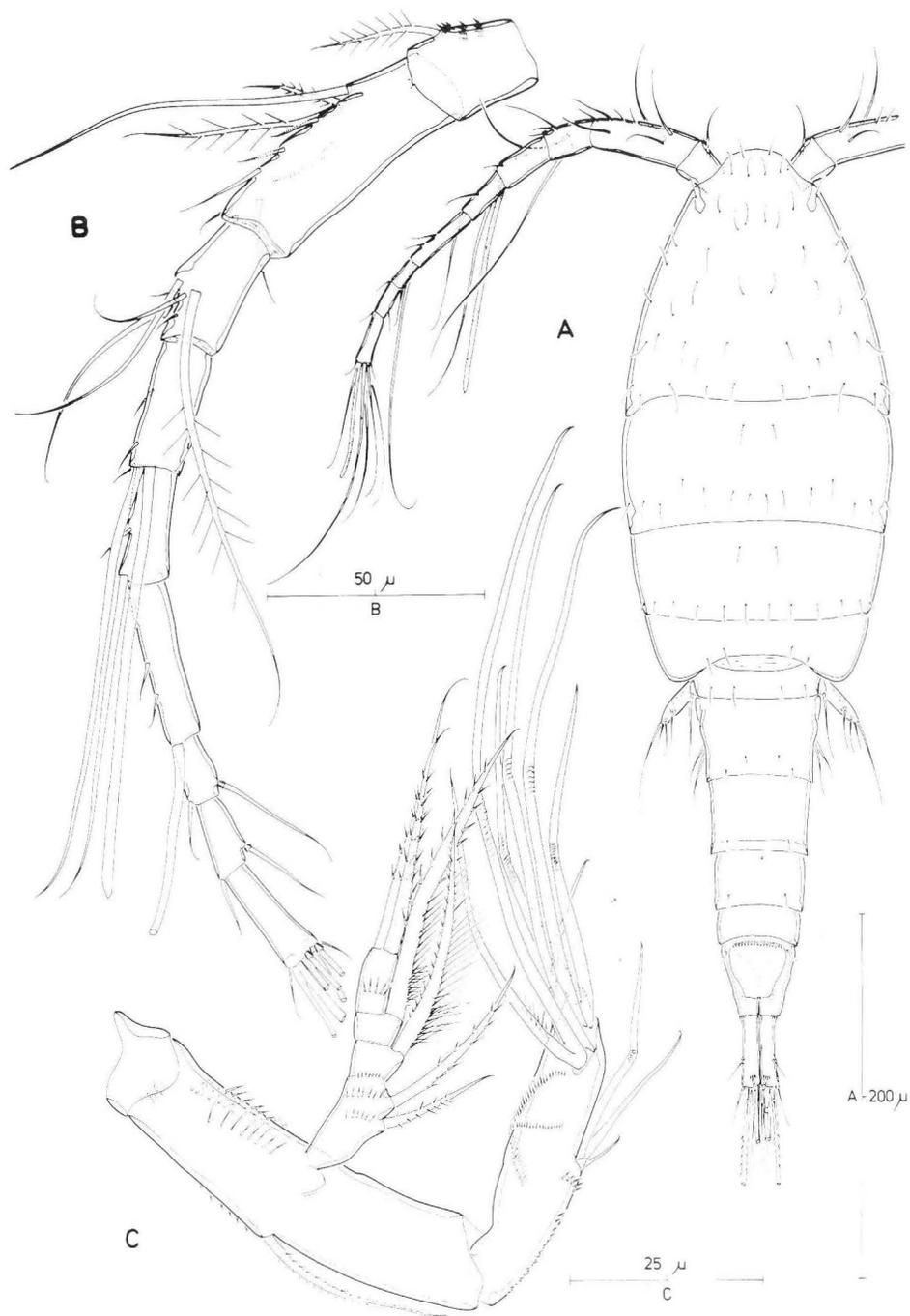


FIG. 1. — *Neoechinophora fosshageni* sp. nov.: A. Habitus ♀, dorsal; B. Antennule ♀, ventral; C. Antenna.

spinules anteriorly; fine spinules present around ventral, lateral and laterodorsal hind margin; anal operculum weakly developed, slightly rounded, with coarse spinules; anal opening large; anal sensilla positioned far anteriorly; paired secretory pores present lateroventrally and posterodorsally near margin of anal opening. Caudal rami (Figs. 5A-C) elongate, slightly widening posteriorly, 3.85 times as long as average width; spinules present around ventral hind margin

and around bases of setae I, II and VII; with 3 secretory pores and 7 setae: seta I relatively short, displaced to ventral position; seta II arising from point at two-thirds distance from anterior margin, smooth; seta III smooth; setae IV and V strongly developed and multipinnate, seta V longer than body; seta VI very long and smooth, partially fused to inner distal margin of caudal ramus; seta VII triarticulate at base and located near posterior margin of ramus.

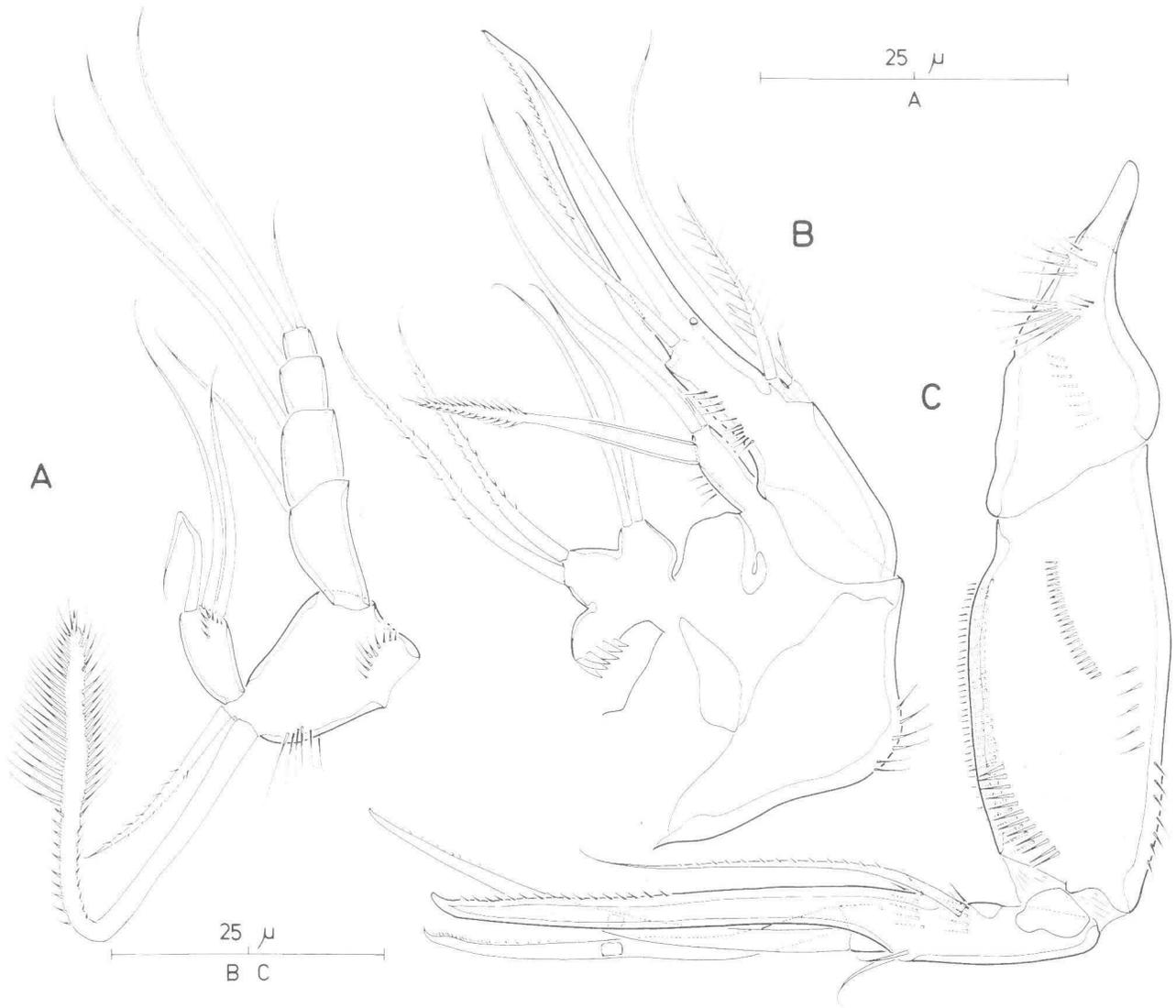


FIG. 2. – *Neoechinophora fosshageni* sp. nov.: A. Mandibular palp; B. Maxilla; C. Maxilliped.

Rostrum as in ♂ (Fig. 6A; see also Fig. 1A) largely incorporated into cephalothorax, not demarcated at base; with 2 dorsal sensilla apically, tube pore not observed.

Antennule (Fig. 1B) elongate and slender, 9-segmented. Segment 1 with 3 anterior spinule rows. Segment 2 longest. Armature formula: 1-[1 pinnate], 2-[2 pinnate + 7 bare], 3-[1 pinnate + 6 bare], 4-[4+ae], 5-[2], 6-[3], 7-[2], 8-[2], 9-[6 + acrothek]. Apical acrothek consisting of short aesthetasc and basally fused seta. Very long setae present on segments 2-6 and 9. Aesthetasc on segment 4 not fused to seta. Proportional lengths of antennular segments (measured along non-setiferous posterior margin): 8.7:21.5:10.5:11.5:10.1:14.7:6.0:6.8:10.2.

Antenna (Fig. 1C): Coxa minute, with short spinule row. Basis and proximal endopod segment completely fused forming allobasis; original segmentation not marked by surface sutures or transverse ribs; with 3 spinule rows in basal half as illustrated in Fig. 1C. Endopod with 2 surface frills subdistally; lateral armature consisting of 1 geniculate seta and 2 bare setae (1 very short); apical armature consisting of 1 subdistal seta and 5 geniculate setae, with longest one fused basally to slender seta bearing proximal row of fine spinules. Exopod 4-segmented (Fig. 1C); armature formula [2.1.1.2]; exp-1 elongate, with 3 fine spinule rows; exp-2 and -3 with setae having basal tuft of setules and bearing spinules as in Fig. 1C; exp-4 with spinule row.

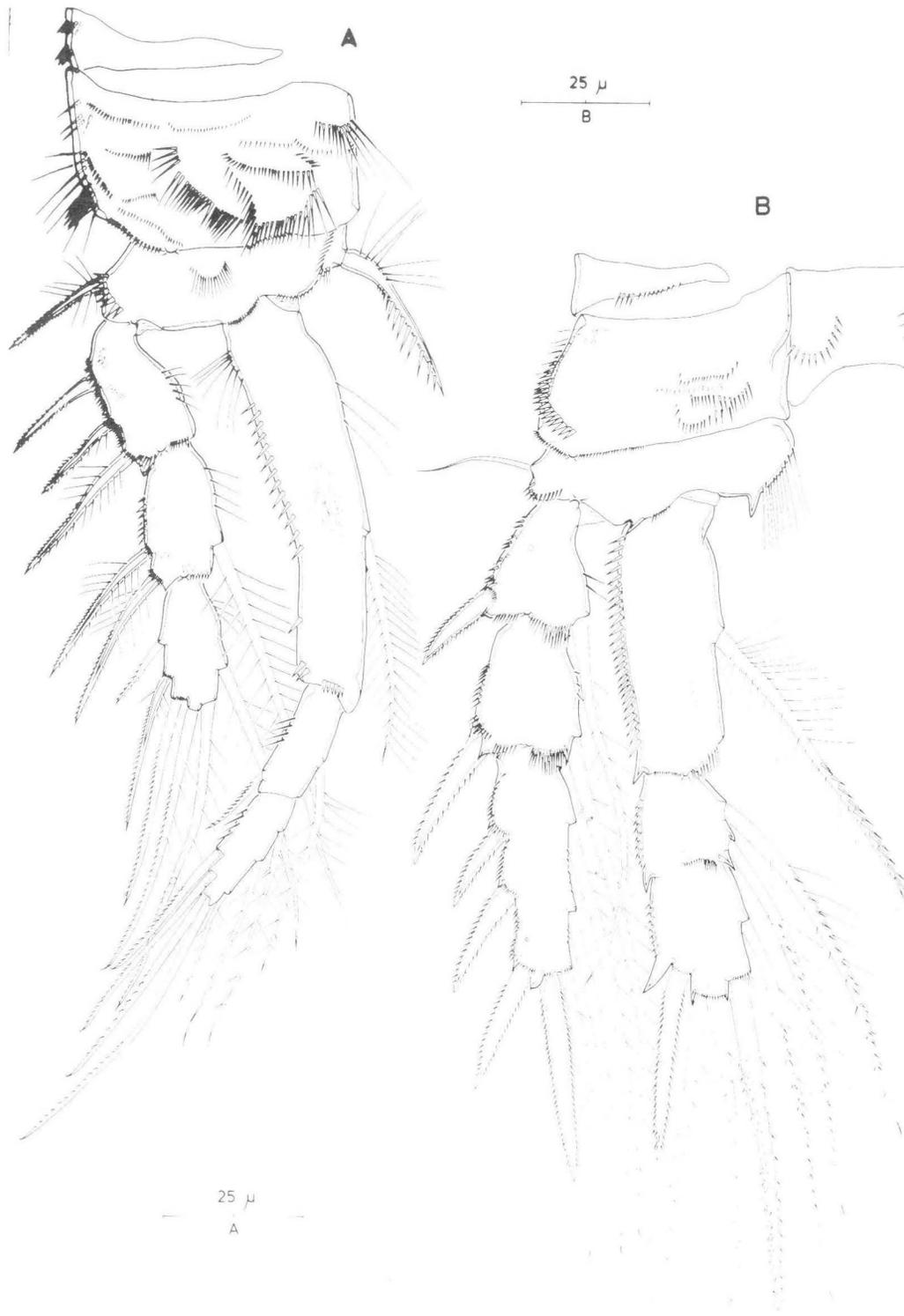


FIG. 3. — *Neoechinophora fosshageni* sp. nov.: A. P1, anterior; B. P2, anterior.

Mandible: Gnathobase stylet-like, with few fine teeth ventrally and 1 slender pinnate seta dorsally. Palp (Fig. 2A) biramous. Basis with 2 spinule rows and 2 setae at inner distal corner (outer one bipinnate, inner one modified, swollen, typically recur-

ved, with densely set long setules in distal half). Endopod 1-segmented, with 1 short and 2 long basally fused setae. Exopod 4-segmented, segments decreasing in size apically; armature formula [1,1,1,2].

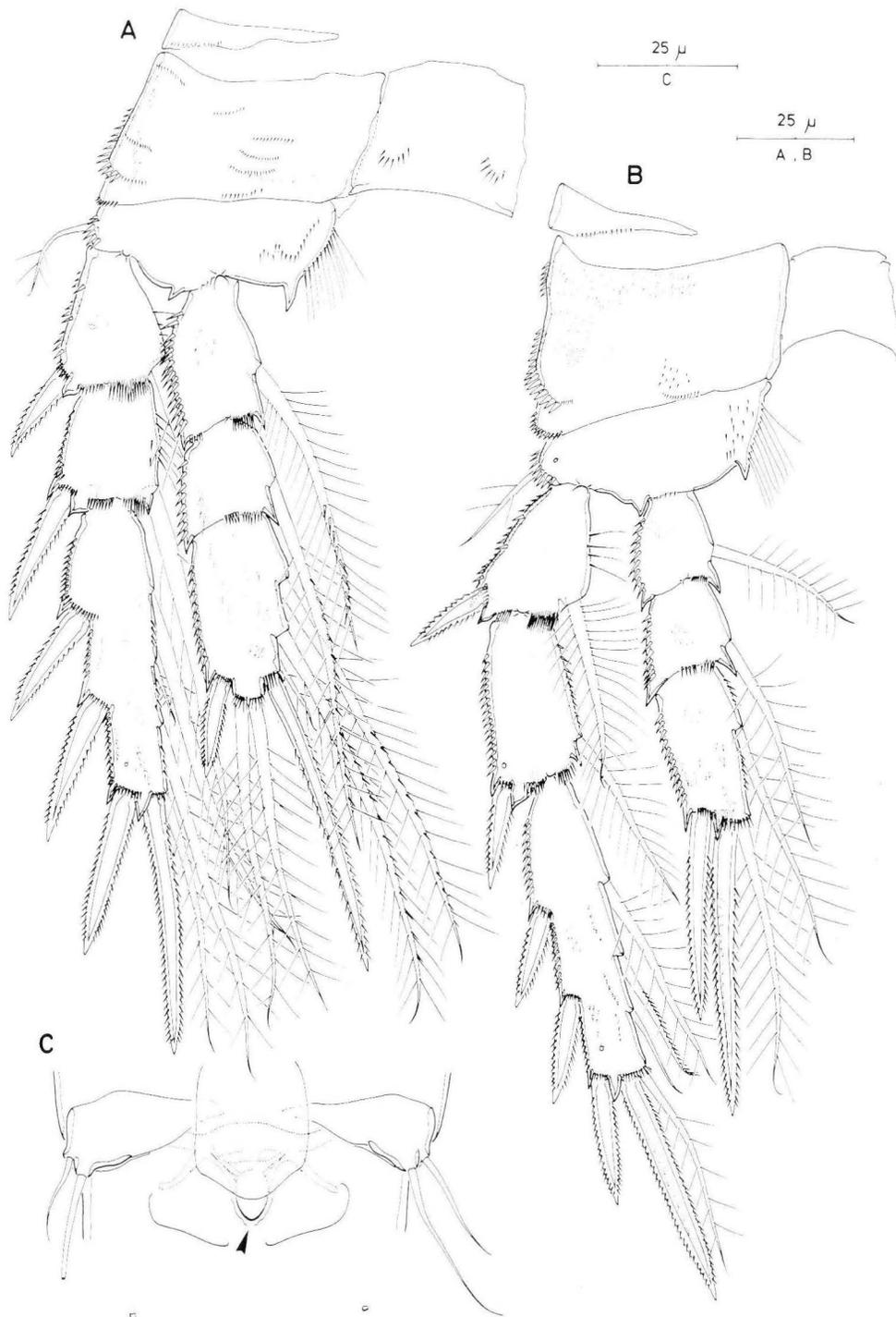


FIG. 4. – *Neoechinophora fosshageni* sp. nov.: A. P3, anterior; B. P4, anterior; C. Genital field ♀ (copulatory pore arrowed).

Maxillule exactly as in *N. daltonae* (Figs. 9B-C).

Maxilla (Fig. 2B): Syncoxa with 2 well developed, widely separated endites; proximal endite of distinctive shape, trilobate: proximal lobe directed adaxially, with 6 overlapping, barb-like spinules along dorsal margin; middle lobe with 2 long bipinnate setae; distal lobe with 2 bare setae; distal endite with

1 apically serrate, 1 long naked and 1 vestigial seta. Allobasis drawn out into long claw bearing fine spinules towards the tip; with 1 pinnate and 1 smooth seta at base. Endopod incorporated into allobasis, represented by membranous area with 1 plumose, 1 long and 1 vestigial bare setae. Fine spinules present along medial margins of allobasis and distal endite.

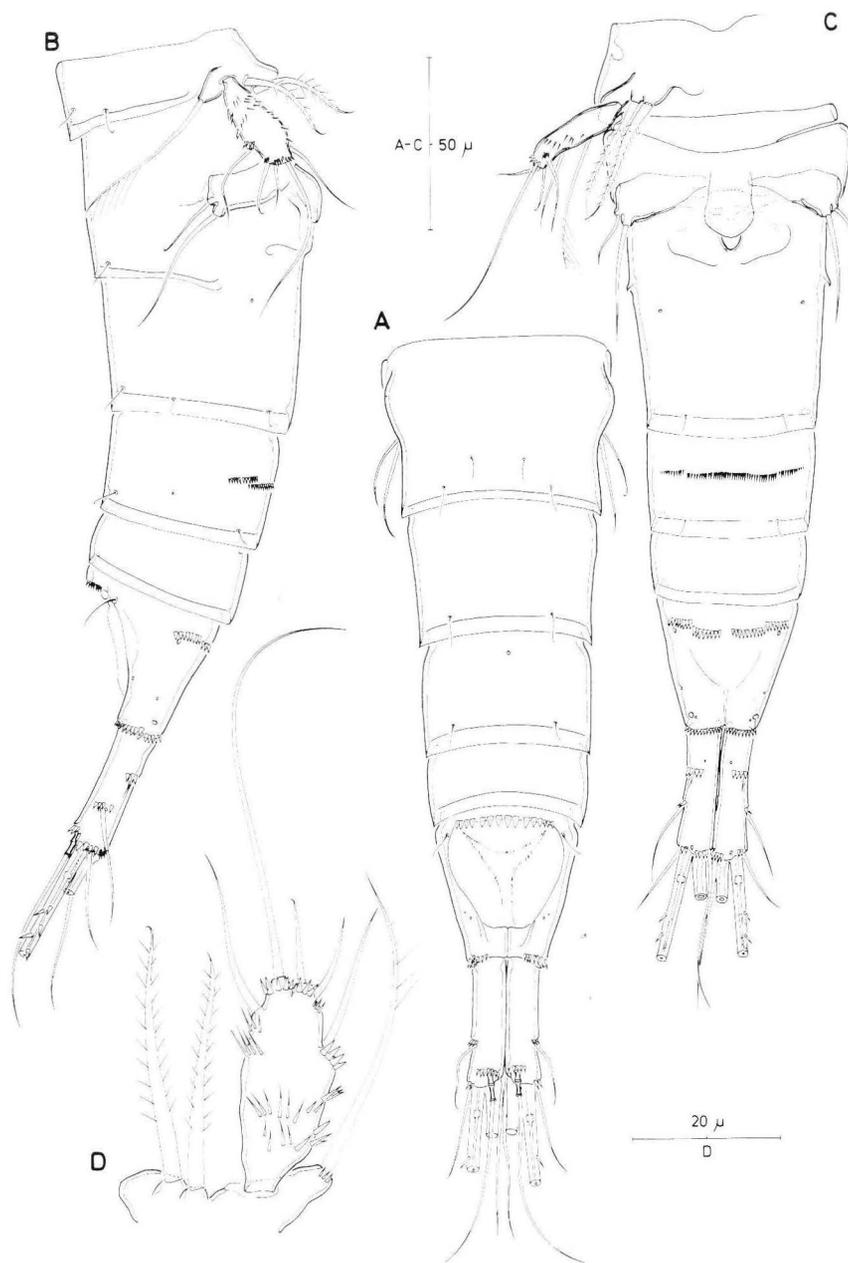


FIG. 5. – *Neoechinophora fosshageni* sp. nov.: A. Urosome ♀ (excluding P5-bearing somite), dorsal; B. Urosome ♀, lateral; C. Urosome ♀, ventral; D. P5 ♀, anterior.

Maxilliped subchelate (Fig. 2C): Syncoxa with spinule rows on anterior and posterior surface as figured. Basis without seta; with 5 rows of fine spinules. Endopod represented by elongate segment drawn out subdistally into long pinnate claw accompanied at base by 2 short outer setae and 1 long pinnate seta along the medial margin; distal portion of endopod forming cylindrical pedestal with 2 juxtaposed, geniculate setae.

P1 (Fig. 3A) with well developed praecoxa. Intercoxal sclerite without spinule rows. Coxa with complex pattern of spinules and long setules as figu-

red. Basis with bipinnate outer seta bearing fine setules in proximal third; inner spine curved, with fine setules along inner and coarse spinules along outer margin. Exopod with slender outer spines, some with long setules proximally; exp-2 with long plumose inner seta; exp-3 with 2 outer pinnate spines, 2 pinnate setae, 1 geniculate and 1 plumose seta. Enp-1 with outer spinule row discontinuous; inner seta arising from point at two-thirds distance from proximal margin; posterior setule patch located proximal to insertion point of inner seta. Enp-2 and -3 elongate and slender.

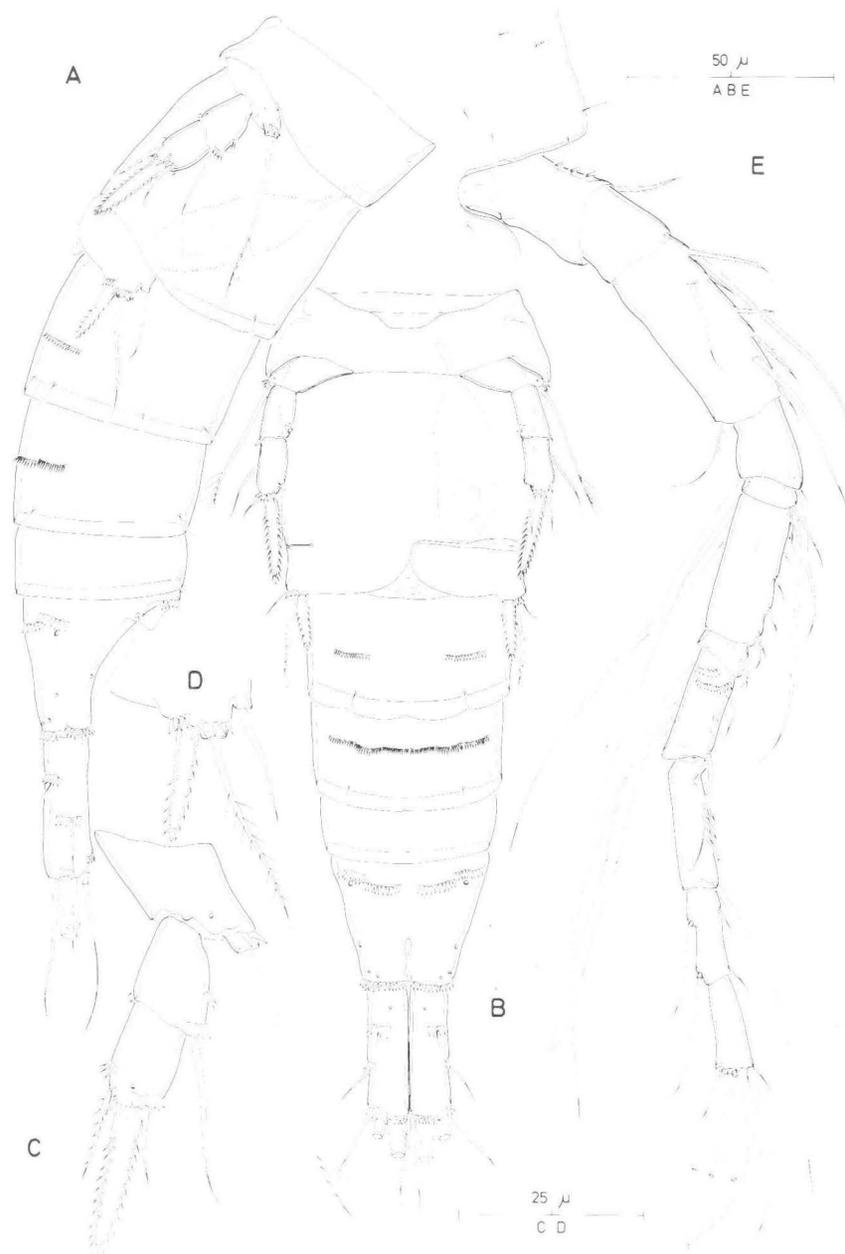


FIG. 6. – *Neoechinophora fosshageni* sp. nov.: A. Urosome ♂, lateral; B. Same, ventral; C. P5 ♂, anterior; D. P6 armature ♂; E. Antennule and rostrum ♂, dorsal.

P2-P4 (Figs. 3B; 4A-B) with 3-segmented rami (except P2 endopod); endopod slightly longer (P2) or distinctly shorter (P3-P4) than exopod. Inner margin of bases with long setules and produced into spinous process. Outer basal seta smooth (P2) or sparsely plumose (P3-P4). All exopod and endopod segments with fine spinules along outer margins and around bases of outer and distal armature elements; frills between segments well developed. Exp-3 as long or longer than exp-1 and -2 combined. Anterior face of segments without surface ornamentation but with scattered spinules on posterior face as figured.

P2 (Fig. 3B): Intercoxal sclerite with anterior spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Endopod 2-segmented with incomplete frill and marginal processes marking fusion plane between enp-2 and enp-3. Enp-1 elongate, longer than distal segment; inner seta plumose with coarse spinules along distal inner margin. Distal compound segment with 3 tripinnate inner setae, 1 tripinnate inner spine, 2 plumose setae distally and long pinnate spine at outer distal corner; outer subdistal corner produced into long recurved spinous process.

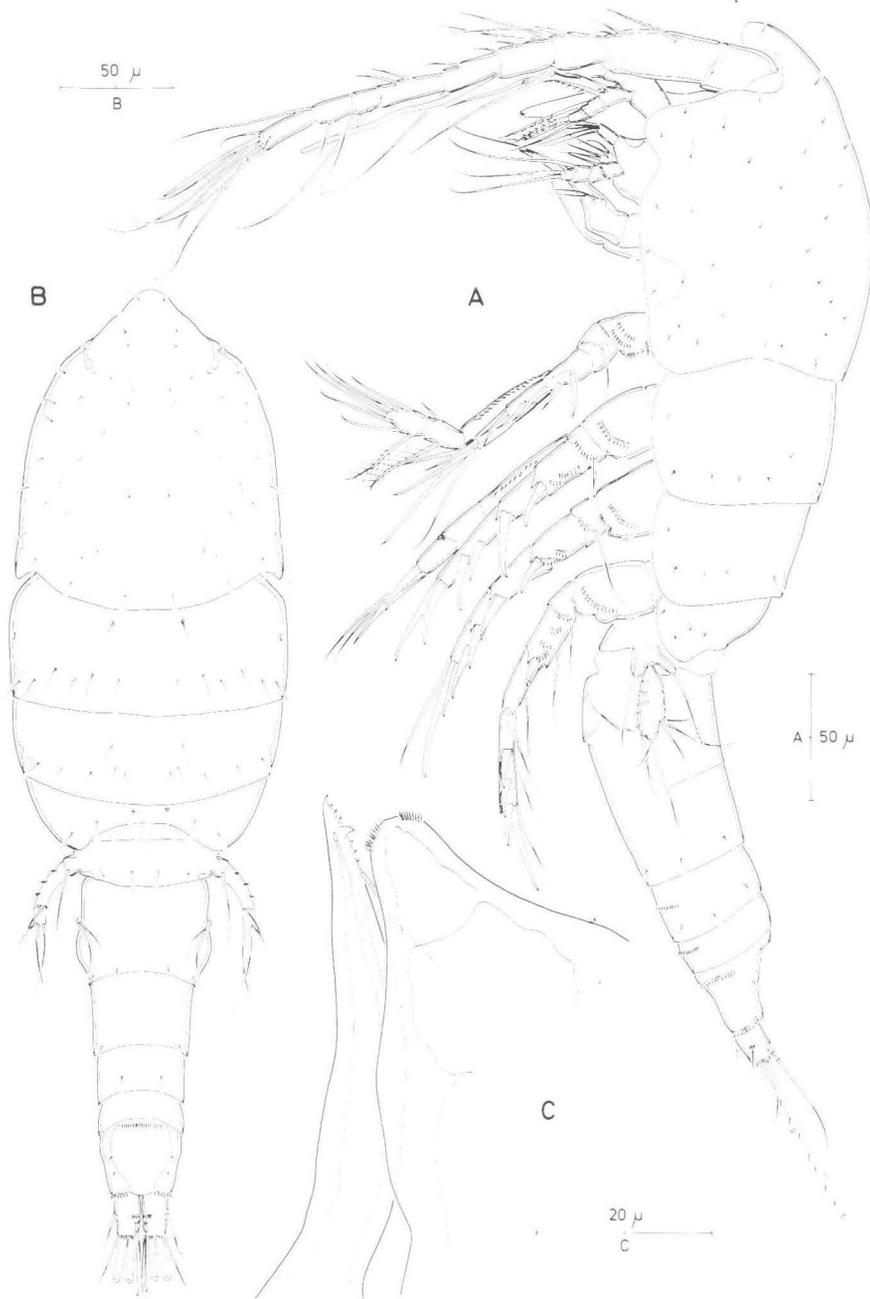


FIG. 7. — *Neoechinophora daltonae* sp. nov.: A. Habitus ♀, lateral; B. Same (antennules omitted), dorsal; C. Labrum and left mandibular gnathobase, anterior.

P3 (Fig. 4A): Intercoxal sclerite with anterior spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Exp-3 with vestigial middle inner seta. Endopod 3-segmented but articulation between middle and distal segment without condyle or arthroial membrane and therefore possibly not functional. Inner seta of enp-1 plumose with coarse spinules along distal inner margin. Enp-3 with 2 tripinnate inner setae, 1 bipinnate inner spine, 2 plumose setae distally and pinnate spine at outer distal corner.

P4 (Fig. 4B): Intercoxal sclerite without ornamentation. Inner margin armature of exp-3 consisting of proximal plumose seta, short unipinnate middle seta and short smooth distal seta. Endopod 3-segmented, distinctly shorter than exopod. Inner seta of enp-1 plumose without coarse spinules along distal inner margin. Enp-3 with 1 plumose inner seta, 1 plumose seta and 1 long spine apically and long pinnate spine at outer distal corner. Outer distal spine of exp-3 and enp-3 tripinnate.



FIG. 8. — *Neoechinophora daltonae* sp. nov.: A. Antennule ♀, ventral; B. Antenna; C. Free antennary endopod, lateral; D. Maxilla (recurved process on proximal endite arrowed); E. Maxillary allobasis, lateral.

Armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;6	0-1;I-1;2,2,3
P2	0-0	1-0	I-1;I-1;III,I+1,2	0-1;[0-2;1,2,I+1]
P3	0-0	1-0	I-1;I-1;III,I+1,3	0-1;0-1;I,2,I+2
P4	0-0	1-0	I-1;I-1;III,I+1,3	0-1;0-1;I,I+1,1

P5 (Fig. 5D) biramous: Baseoendopod incorporated into somite; represented by outer lobe bearing basal sparsely plumose seta, and vestigial endopodal lobe carrying 2 strong bipinnate setae. Exopod somewhat oval-shaped; 2.3 times as long as maximum width; anterior surface with several spinule rows as figured; spinules also present around bases of apical and outer elements; armature consisting of 1 inner, 1 long apical and 3 outer bare setae.

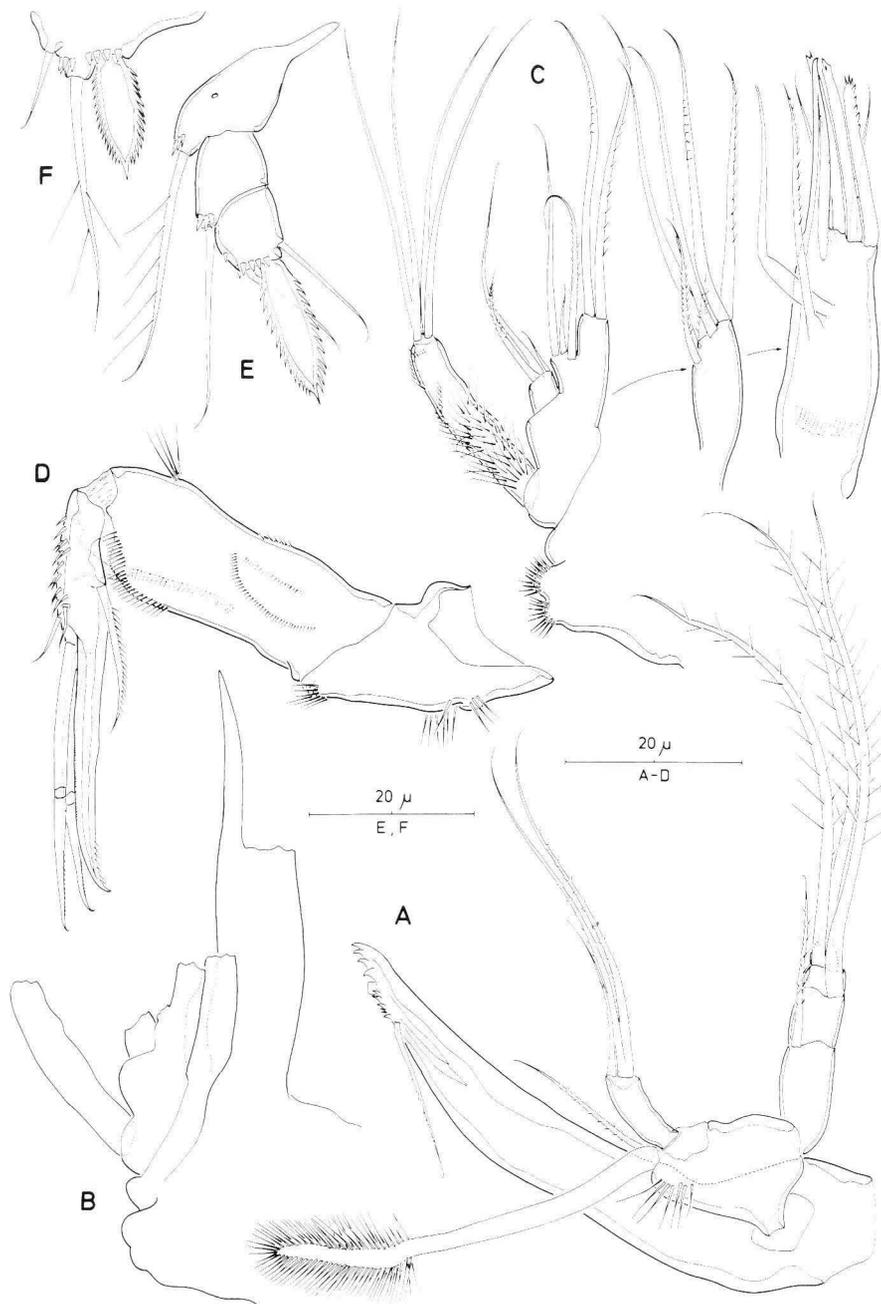


FIG. 9. — *Neoechinophora daltonae* sp. nov.: A. Mandible; B. Contours of maxilla; C. Maxilla, with disarticulated coxal endite and praecoxal arthrite, anterior; D. Maxilliped; E. P5 ♂, anterior; F. P6 armature ♂.

Genital field positioned in anterior third of genital double-somite (Fig. 5C). Gonopores paired, laterally displaced, separated (Fig. 4C); each covered by genital operculum derived from vestigial sixth legs. P6 with 1 short outer and 1 long inner bare seta. Copulatory pore large (arrowed in Fig. 4C), covered anteriorly by broadly rounded hyaline epicopulatory flap derived from an outgrowth of the ventral somite wall; leading via paired chitinized copulatory ducts to median transversely elongated

seminal receptacle. Paired secretory pores present ventrally at about halfway the double-somite length (Fig. 5C).

Egg sac(s) not observed.

Male (Fig. 6): Smaller than female; total body length 480  $\mu\text{m}$  measured from tip of rostrum to posterior margin of caudal rami. Sexual dimorphism in body size, antennule, P5, P6, genital segmentation and abdominal ornamentation.

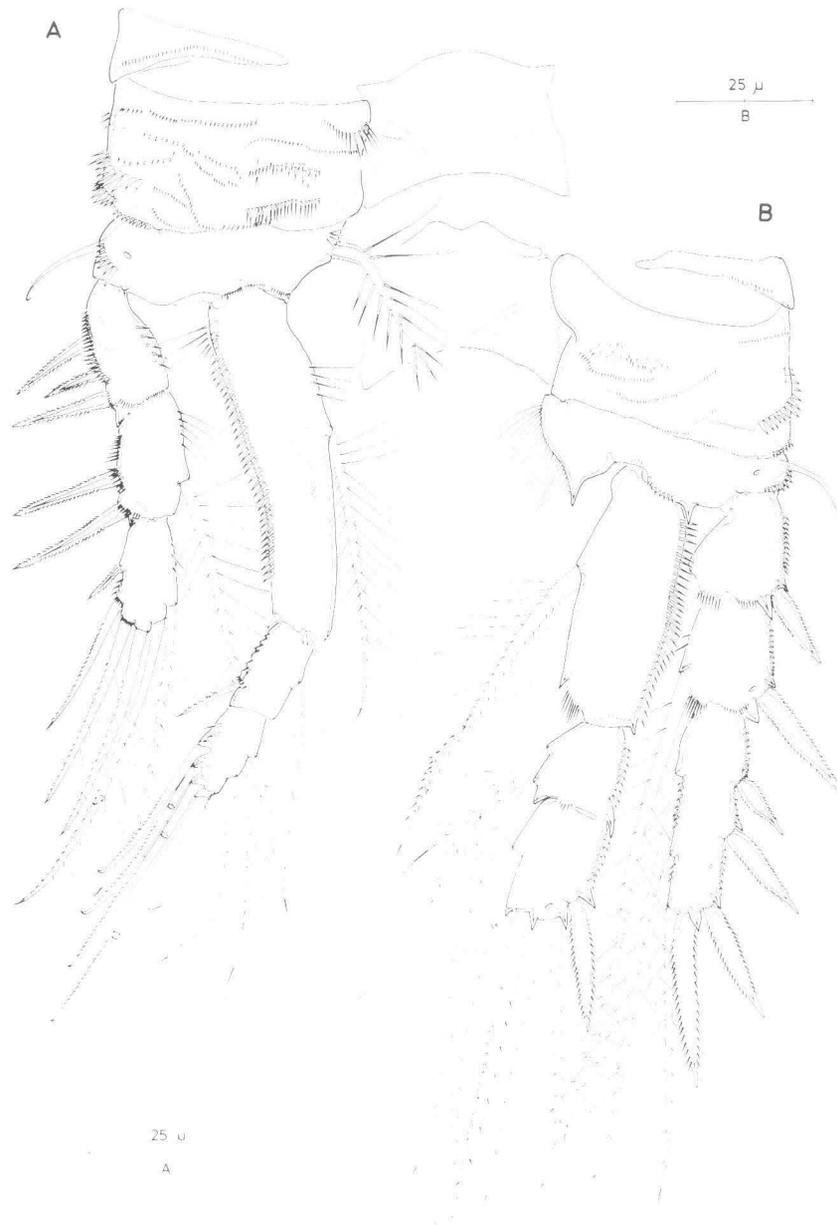


Fig. 10. – *Neocchinophora daltonae* sp. nov.: A. P1, anterior; B. P2, anterior.

Antennule (Fig. 6E) slender, 11-segmented and haplocer; geniculation between segments 8 and 9; segment 2 longest; segment 5 represented by U-shaped sclerite; with long aesthetasc on segments 4 and 6, and as part of apical acrothek on segment 11. Segment 1 with 3 anterior spinule rows. Segment 8 with 2 spinule combs on dorsal surface. Segments around geniculation with 2 and 3 modified, fused elements, respectively. Armature formula: 1-[1 pinnate], 2-[1], 3-[4 pinnate + 4], 4-[6 + ae], 5-[2], 6-[7 + ae], 7-[2], 8-[2 + 2 modified], 9-[1 + 3 modified], 10-[4], [6 + acrothek]. Apical acrothek consisting of short aesthetasc and basally fused seta.

P5 (Fig. 6A-C) uniramous, displaced to ventrolateral position. Baseoendopod with sparsely plumose outer basal seta. Exopod 2-segmented; exp-1 with slender outer seta; exp-2 with strong pinnate spine apically flanked by short bare seta at the inner corner and bipinnate seta the outer subdistal corner. Anterior secretory pores present on baseoendopod and exp-2. Endopodal lobe completely absent.

Sixth pair of legs asymmetrical (Fig. 6B), one member fused to somite leaving minute suture, other (functional member) articulating. P6 armature consisting of inner bipinnate spine, long middle plumose seta and short naked outer seta.

Spermatophore 55  $\mu\text{m}$ .

First abdominal (postgenital) somite with paired spinule rows ventrally.

Variability: None observed.

Remark: *N. fosshageni* differs from the other species in the genus by the long caudal rami, the reduction of the middle inner seta of P3 exp-3, and the absence of a ventral spinule row on the penultimate somite of the female.

### *Neoechinophora daltonae* sp. nov.

Material examined: Holotype ♀ (dissected on 8 slides; reg. no. 1996.1216); paratypes are 1 ♂ dissected on 6 slides and 6 ♀♀, 2 ♂♂ in alcohol (reg. nos 1996.1217-1224); collected in Christie's Cave, Bermuda; leg. A. Fosshagen; 30 August 1984; collected with fine mesh dip net from the water column at 4 m depth.

Additional material: (a) 1 ♀, 1 ♂, 1 cop V ♀; collected in Tucker's Town Cave, Bermuda; leg. A. Fosshagen; 10 September 1984; collected with fine mesh dip net from the water column at 0-1 m depths; (b) 1 ♀, 2 ♂♂; collected in Walsingham Cave, Bermuda; leg. J. H. Stock; 01 October 1984; collected with hand held net.

Christie's Cave (Hamilton Parish) contains a clear pool just inside a collapse cave entrance. Although located within 30 m of Castle Harbor, the cave is apparently well isolated from direct contact with open waters. The pool has a maximum depth of 8 m and a salinity ranging from 6.9‰ at the surface to 19.5‰ at 1 m depth (Kornicker and Iliffe, 1989). Christie's Cave is the type locality of *Erebonectes nesioticus* and one of the six caves where *Paracyclops naessi* has been recorded (Fosshagen and Iliffe, 1985). Other harpacticoids co-occurring with *N. daltonae* include various Diosaccidae, Thalestridae, Ameiridae and an undescribed species of *Diarthrodelta* (Paramesochridae).

Walsingham Cave (Hamilton Parish) forms part of the complex northern Walsingham Cave System which is possibly hydrologically connected with the back sections of the Palm Cave System. All caves are characterized by large underwater stalactites and stalagmites deposited during low sea stands in the Pleistocene. The main water flow through the cave system is apparently from Castle Harbor through Walsingham and Deep Blue Caves. Walsingham Cave, situated 150 m from the coast, consists of a long surface pool at the base of a small rocky cliff. The pool which is partially exposed to daylight interconnects with Deep Blue Cave via extensive underwater fissures and several air-filled breakdown chambers leading back into total darkness. The cave has a maximum depth of 20 m and the salinity ranges from 18.9‰ taken at the surface to 32.6‰ at 1 m depth (Kornicker and Iliffe, 1989). The cyclopoid *Speleoithona bermudensis* Rocha and Iliffe was des-

cribed from this locality as well as from Bee Pit Cave by Rocha and Iliffe (1993). These authors also recorded *Halicyclops ytororoma* Lotufo and Rocha which was originally described from a sandy beach in Brazil. Fosshagen (pers. commn) also found the calanoid *Miostephos leamingtonensis* Yeatman, first described from the dark region of Leamington Cave on Bermuda (Yeatman, 1980). Other harpacticoids co-occurring with *N. daltonae* include *Hypalocleodes* sp. (*Argestidae incertae sedis*), various Laophontidae, Thalestridae and Tisbidae, and a new species of *Zosime* (Tisbidae).

### Description:

Female (Figs. 7-8; 9A-D; 10-12; 14A; 15; 16A-B): Total body length 420  $\mu\text{m}$  measured from tip of rostrum to posterior margin of caudal rami. Largest width 125  $\mu\text{m}$  measured halfway P2-bearing somite.

Body elongate cyclopiform (Figs. 7A-B) but somewhat more robust than *N. fosshageni*. Hyaline frill of cephalothorax and body somites plain and smooth (Figs. 7A-B; 12A-C). Genital double-somite elongate, completely fused, with ventrolateral bulges in anterior half (Figs. 12A-C); original segmentation marked by transverse surface frill dorsolaterally (Fig. 12B) and dorsally (Fig. 12C) but not by internal chitinous ribs. Second abdominal somite (Fig. 12A) with ventral row of spinules which are coarser than in *N. fosshageni*. Third abdominal somite with midventral spinule row (Fig. 12A). Anal somite (Figs. 12A-C) with paired ventral and ventrolateral rows of coarse spinules anteriorly; additional spinules present around ventral, lateral and laterodorsal hind margin; anal operculum weakly developed, slightly rounded, with very fine spinules; anal opening large; anal sensilla positioned halfway the somite length; paired secretory pores present lateroventrally and posterodorsally near margin of anal opening. Caudal rami (Figs. 12A-C) short, about 1.5 times as long as average width; spinules present around ventral hind margin and around bases of setae I-III and VII; with 3 secretory pores and 7 setae; arrangement (Fig. 13D) and form of setae as in type species.

Rostrum (Fig. 11A) more pronounced than in type species (compare Figs. 1A and 7B); triangular; with 2 minute dorsal sensilla apically, tube pore not observed.

Antennule (Fig. 8A) elongate and slender, 9-segmented. Segment 1 with 3 anterior spinule rows. Segment 2 longest. Armature formula: 1-[1 pinnate], 2-[5 pinnate + 4], 3-[1 pinnate + 7], 4-[4+ae], 5-[2],

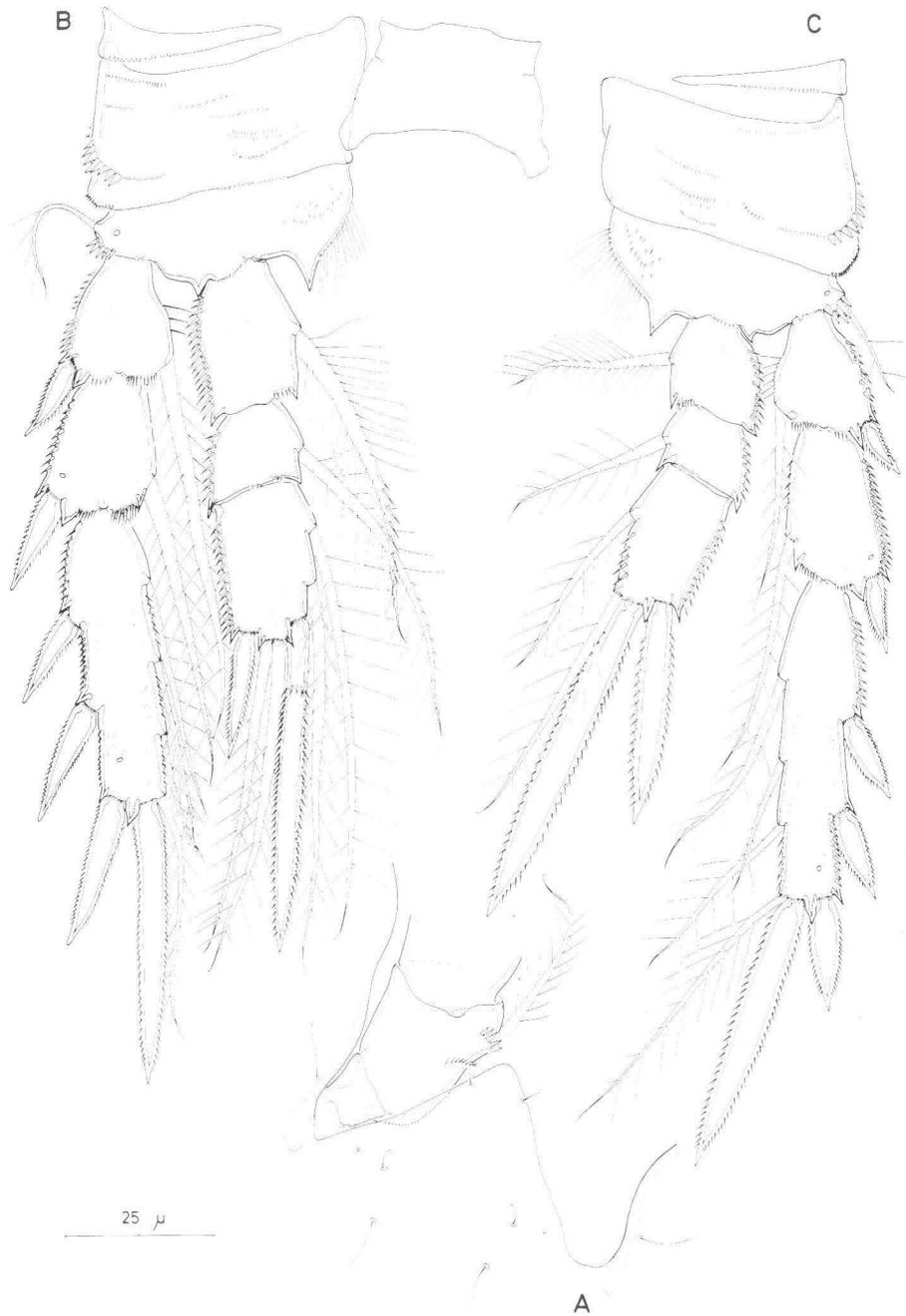


FIG. 11. – *Neoechinophora daltonae* sp. nov.: A. Rostrum and left first antennular segment ♀, dorsal; B. P3, anterior; C. P4, anterior.

6-[3], 7-[2], 8-[2], 9-[6 + acrothek]. Apical acrothek consisting of short aesthetasc and basally fused seta. Aesthetasc on segment 4 not fused to seta. Proportional lengths of antennular segments (measured along non-setiferous posterior margin): 9.6:17.7:11.2:12.2:11.2:13.2:6.1:7.6:11.2.

Antenna (Figs. 8B-C): Coxa minute, bare. Basis and proximal endopod segment completely fused forming allobasis; original segmentation marked by

transverse chitinous rib along abexopodal margin; with 1 spinule row in basal half. Endopod with 2 surface frills subdistally; armature of endopod as in type species. Exopod 3-segmented; armature formula [2,2,2]; exp-1 elongate; exp-2 compound, derived by fusion of segment 2 and 3 expressed in *N. fossage-mi*, original segmentation marked by incomplete surface suture; setae of exp-2 with basal tuft of setules and bearing spinules as in Fig. 8B; exp-3 narrow.

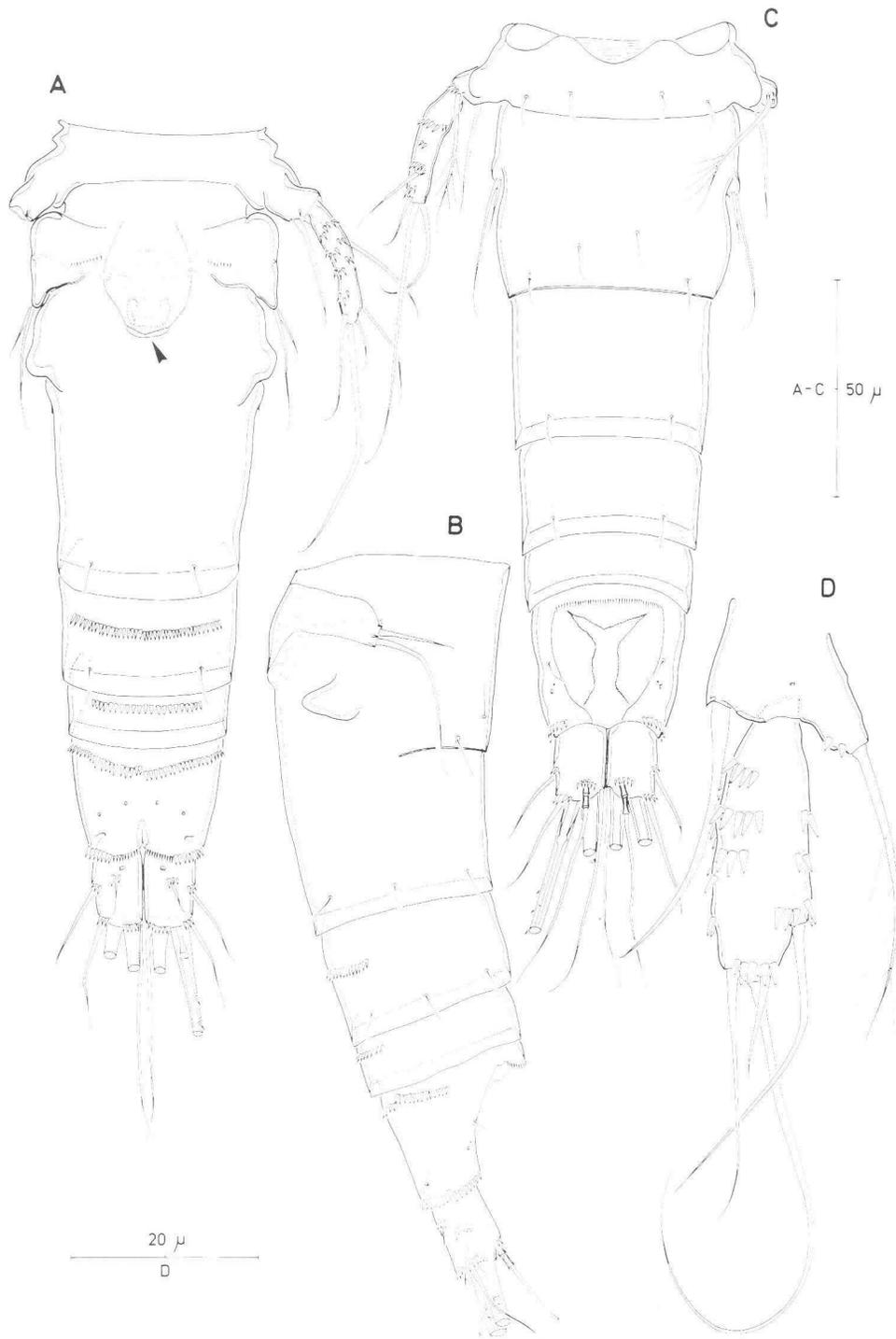


FIG. 12. — *Neoechinophora daltonae* sp. nov.: A. Urosome ♀, ventral (copulatory pore arrowed); B. Urosome ♀ (P5-bearing somite omitted), lateral; C. Urosome ♀, dorsal; D. P5 ♀, anterior.

Labrum (Figs. 7C; 14A; 15A-B): Strongly developed, triangular, tapering towards apical process with spinules.

Mandible (Fig. 9A): Gnathobase stylet-like (Fig. 7C), with few fine teeth ventrally and 1 slender pinnate seta dorsally. Basis with 1 spinule row and 2

setae at inner distal corner (outer one bipinnate, inner one modified, swollen, with densely set long setules in distal third). Endopod 1-segmented, with 1 short and 2 long basally fused setae. Exopod 4-segmented, segments decreasing in size apically; armature formula [1,1,1,1].

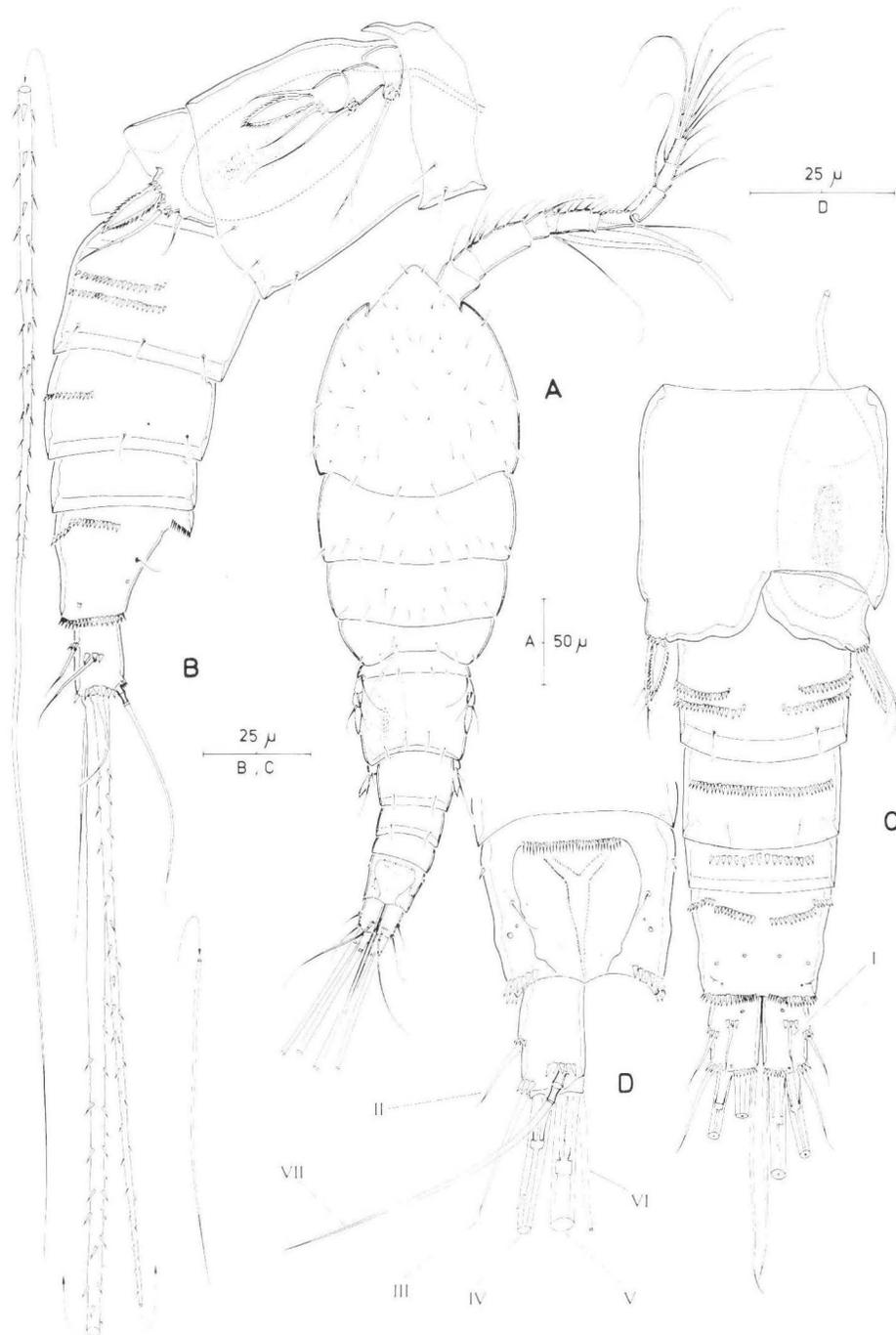


FIG. 13. — *Neoechinophora daltonae* sp. nov.: A. Habitus ♂ (left antennule omitted), dorsal; B. Urosome ♂, lateral; C. Urosome ♂ (excluding P5-bearing somite), ventral; D. Anal somite and left caudal ramus, dorsal.

Maxillule (Figs. 9B-C) with protopodal segments partly fused and closely adpressed. Praecoxa with elongate, narrow arthrite produced into spinous process at distal outer corner (= incorporated spine) and bearing 3 spiniform and 4 setiform elements, all closely adpressed (Fig. 15C); with 2 tubular seta anteriorly and proximal spinule row posteriorly; outer margin of syncoxa with spinulose bulges. Coxa with

cylindrical endite bearing 2 pinnate setae subdistally and apical armature consisting of 1 geniculate, 1 pinnate and 2 bare setae. Basis with 2 widely separated endites; proximal endite with 3 setae, distal endite with 1 geniculate and 1 pinnate seta. Exopod very large cylindrical segment, covered with patch of fine setules and 2 spinule rows; with 4 bare setae apically. Endopod a small segment with 3 setae (1 minute).

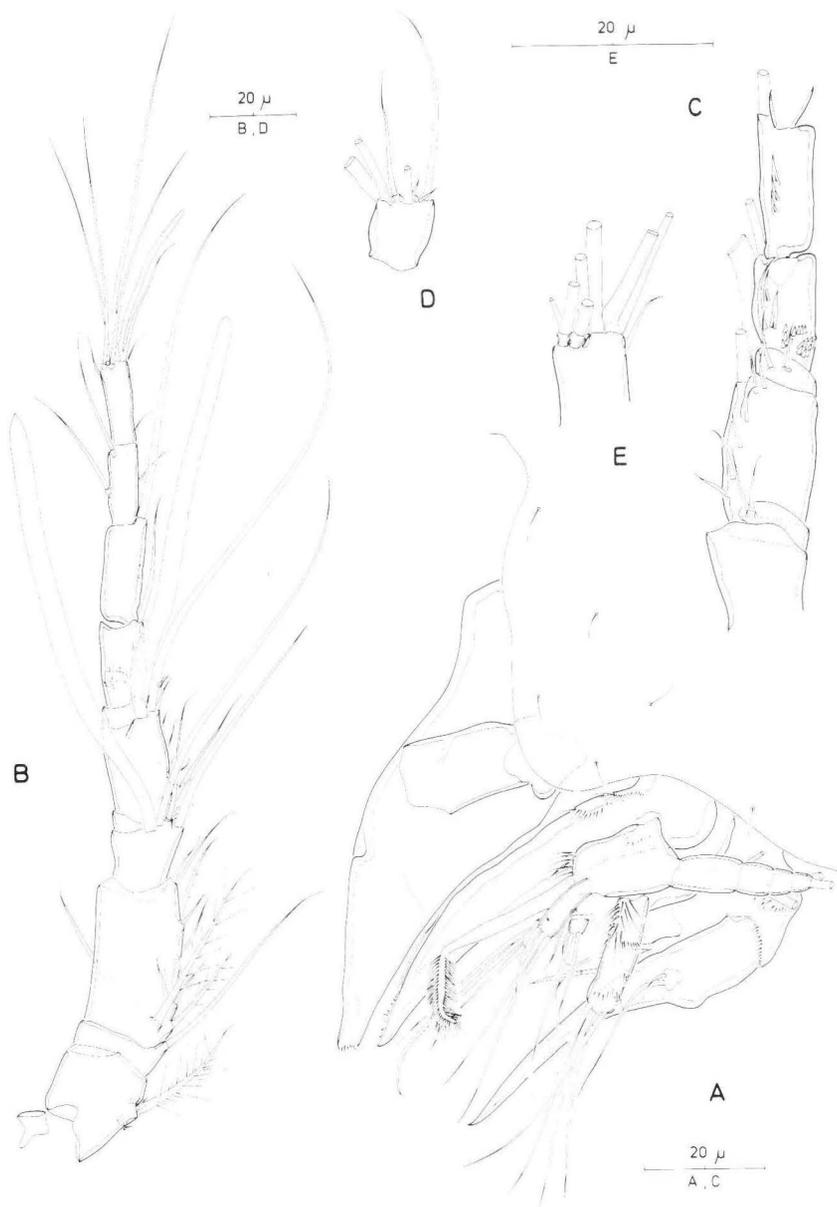


FIG. 14. – *Neoechinophora daltonae* sp. nov.: A. Labrum, mandible, maxillule and maxilla shown *in situ*, lateral; B. Antennule ♂, ventral; C. Antennular segments 5-9 ♂, anterior; D. Antennular segment 4 ♂, anterior; E. Apex of antennular segment 11 ♂, ventral.

Maxilla (Fig. 8D): as in type species except for proximal endite on syncoxa which has an acutely recurved proximal lobe (arrowed in Fig. 8D) without distinct barb-like spinules.

Maxilliped (Fig. 9D): as in type species apart from slight differences in ornamentation of syncoxa and basis and in proportional length of the endopodal claw.

P1 (Fig. 10A): with well developed praecoxa. Intercoxal sclerite without spinule rows. Coxa with complex pattern of spinules and setules different from that in *N. fosshageni*; significant differences

found in length, shape and distribution of individual ornamentation elements. Basis with smooth outer seta; inner spine curved, with fine setules along entire inner margin and spinules (longer and finer than in type species) along outer margin. Exopod with outer spines shorter and less slender than in type species, none with long setules proximally. Enp-1 with continuous outer spinule row; inner seta arising from point at 2/5 distance from proximal margin; posterior setule patch primarily located distal to insertion point of inner seta. Enp-2 and -3 markedly shorter than in type species.

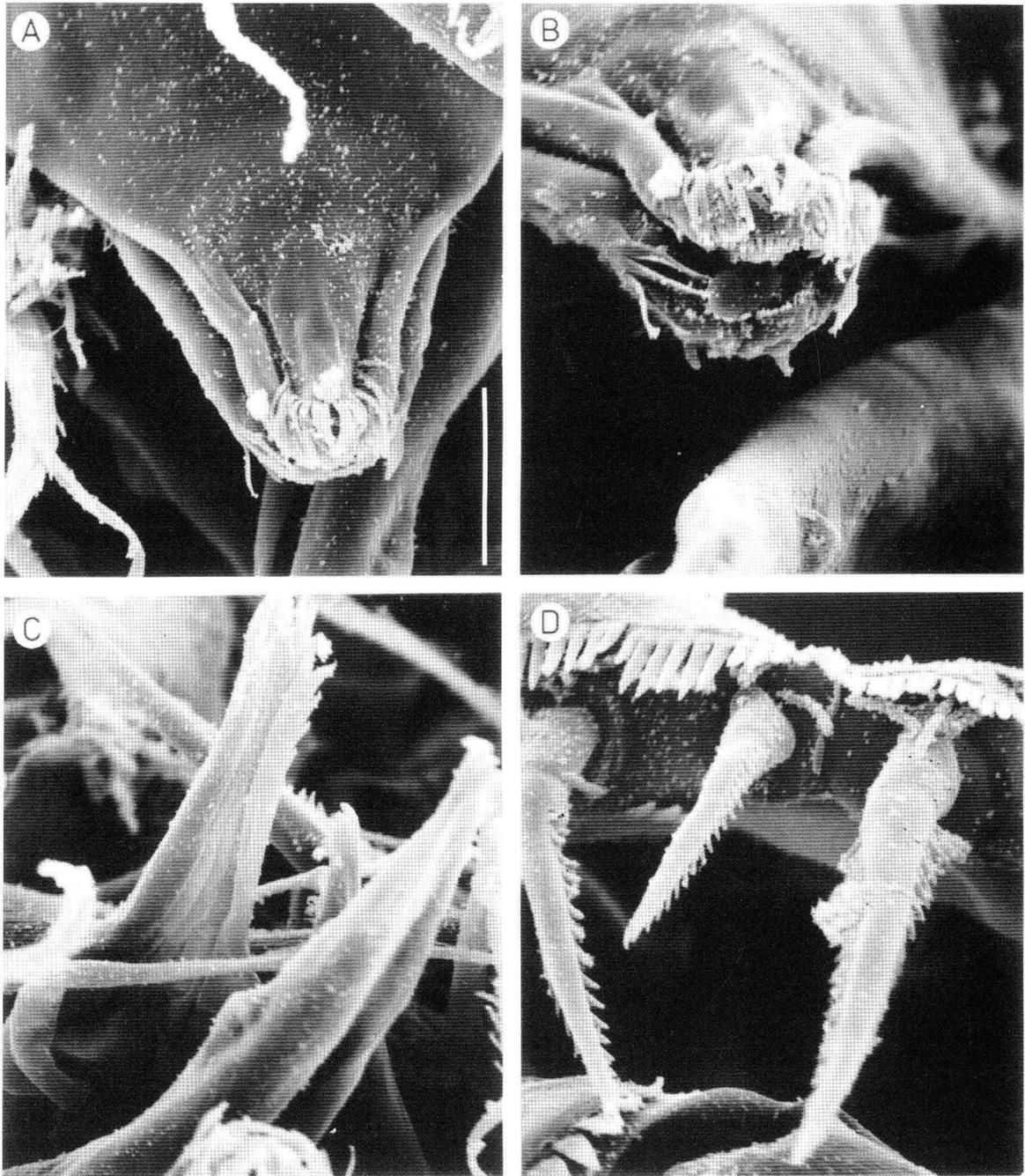


FIG. 15. – *Neoechinophora daltonae* sp. nov., SEM micrographs: A. Distal part of labrum overlying labium, anterior; B. Distal tip of labium and labrum, showing apical opening to oral cone; C. Praecoxal arthrite of maxillule, anterior; D. Exopodal spines of P1 exp-1, lateral. Scale bars (length indicated in A) are: 6  $\mu$ m (A, C), 4.3  $\mu$ m (B, D).

P2-P4 (Figs. 10B; 11B,C): with 3-segmented rami (except P2 endopod). Inner margin of bases with long setules and produced into spinous process. Outer basal seta smooth (P2) or sparsely plumose (P3-P4). Outer exopodal spines typically with naked constricted apex.

P2 (Fig. 10B): Intercoxal sclerite without spinule rows. Exp-1 with posterior vent pore associated

with coarse spinules. Endopod 2-segmented with incomplete frill and marginal processes marking fusion plane between enp-2 and enp-3. Distal compound segment with 3 sparsely plumose inner setae, 1 bipinnate inner spine, 2 plumose setae distally and long pinnate spine at outer distal corner; outer subdistal corner produced into short spike-like process.

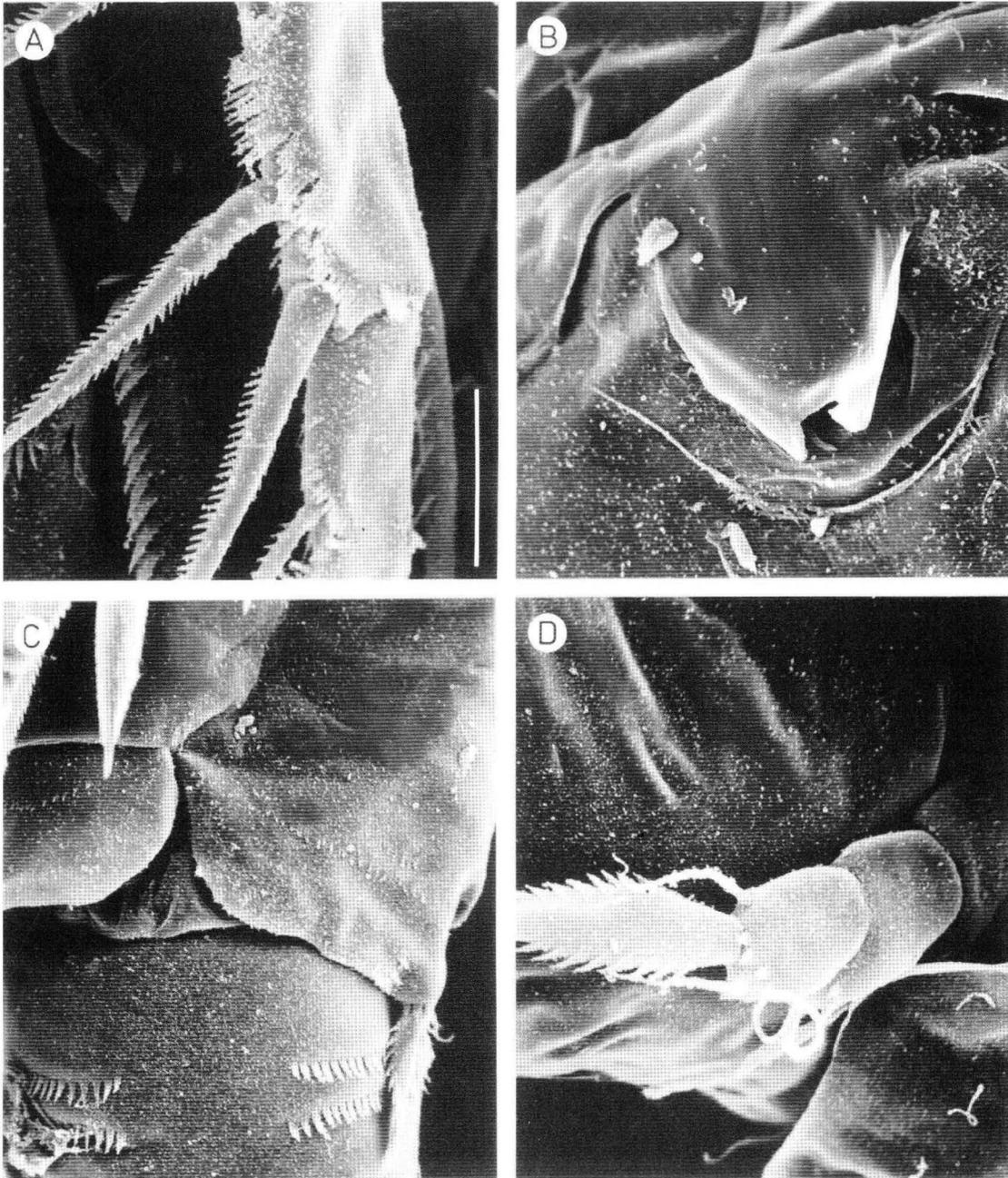


FIG. 16. — *Neoechinophora daltonae* sp. nov., SEM micrographs: A. Exopodal spines of P1 exp-2, lateral; B. Epicopulatory flap overlying copulatory pore; C. P6 ♂; D. Left P5 ♂. Scale bars (length indicated in A): 7.5  $\mu$ m (A, B), 15  $\mu$ m (C), 10  $\mu$ m (D).

P3 (Fig. 11B): Intercoxal sclerite without spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Exp-3 with 3 inner setae successively decreasing in length, none strongly developed as proximal and distal inner setae of *N. fosshageni*. Endopod 3-segmented but articulation between middle and distal segment without distinct condyle or arthrodial membrane and therefore possibly not functional; endopod (particularly enp-3) markedly shorter than in type species. Inner setae of enp-3 plu-

mose; distal inner spine more swollen than in type species and typically with few anterior surface spinules at 1/5 distance from the base.

P4 (Fig. 11C): Intercoxal sclerite without ornamentation. Spines of exopod and enp-3 markedly swollen. Inner margin armature of exp-3 consisting of bipinnate middle seta flanked by longer, plumose, proximal and distal setae. Enp-3 shorter than in type species. Outer distal spine of exp-3 and enp-3 bipinnate.

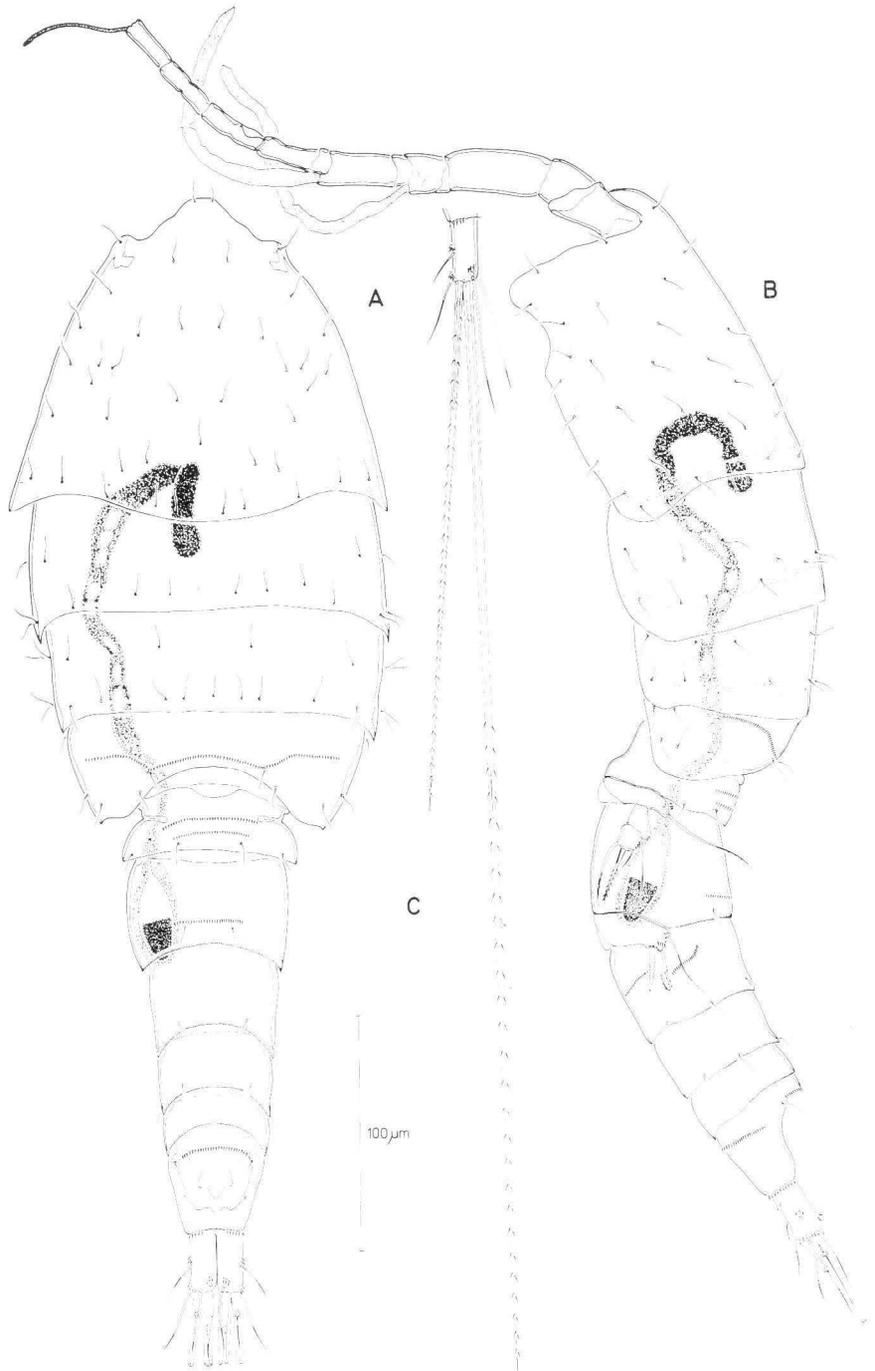


FIG. 17. — *Neoechinophora jaumei* sp. nov.: A. Habitus ♂, dorsal; B. Same, lateral; C. Left caudal ramus, dorsal.

Armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1:6	0-1:I-1;2,2,3
P2	0-0	1-0	1-1;I-1;III,1+1,2	0-1:[0-2:I,2,1+1]
P3	0-0	1-0	1-1;I-1;III,1+1,3	0-1:0-1:I,2,1+2
P4	0-0	1-0	1-1;I-1;III,1+1,3	0-1:0-1:I,1+1,1

P5 (Fig. 12D) biramous: Baseoendopod incorporated into somite (Figs. 12A, C); with outer lobe bearing basal, sparsely plumose, seta, and 1 inner, finely pinnate seta representing endopodal lobe. Exopod elongate oval-shaped; nearly 3 times as long as maximum width; anterior surface with several spinule rows as figured; spinules also present around bases of apical and outer elements; armature consisting of 1 inner, 1 long apical and 2 outer bare setae.

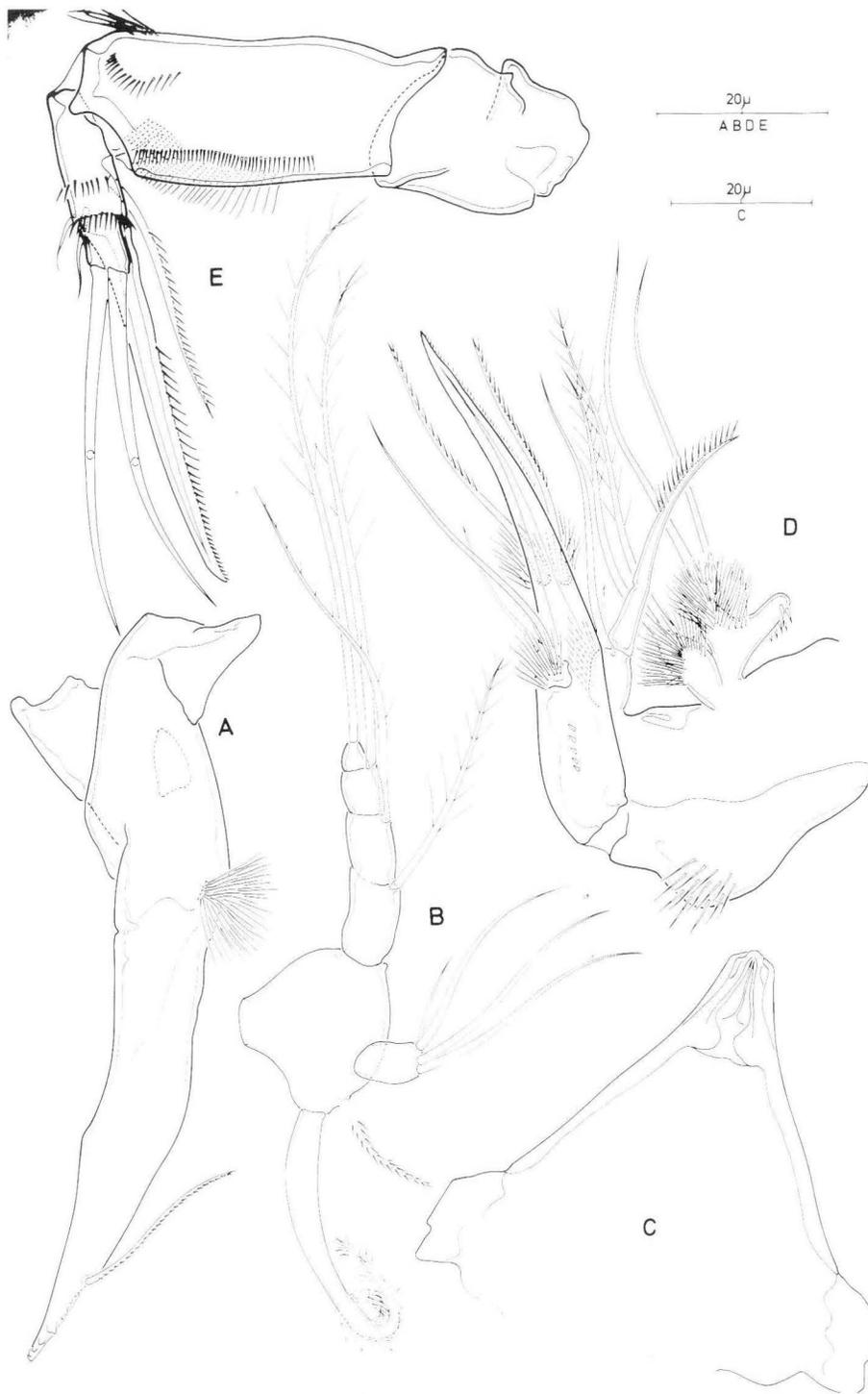


FIG. 18. - *Neoechinophora jaumei* sp. nov.: A. Mandibular gnathobase; B. Mandibular palp; C. Labrum; D. Maxilla; E. Maxilliped.

Genital field positioned in anterior third of genital double-somite (Fig. 12A). Gonopores paired, laterally displaced, entirely separated (Fig. 12A; 16B); each covered by genital operculum derived from vestigial sixth legs. P6 with 1 short outer seta, 1 long inner bare seta and fine row of spinules. Copulatory pore large (arrowed in Fig. 12A), largely

concealed beneath broadly rounded hyaline epicopulatory flap derived from an outgrowth of the ventral somite wall (Fig. 16B); distal margin of flap slightly bilobed; copulatory pore leading via paired chitinized copulatory ducts to median transversely elongated seminal receptacle.

Egg sac(s) not observed.

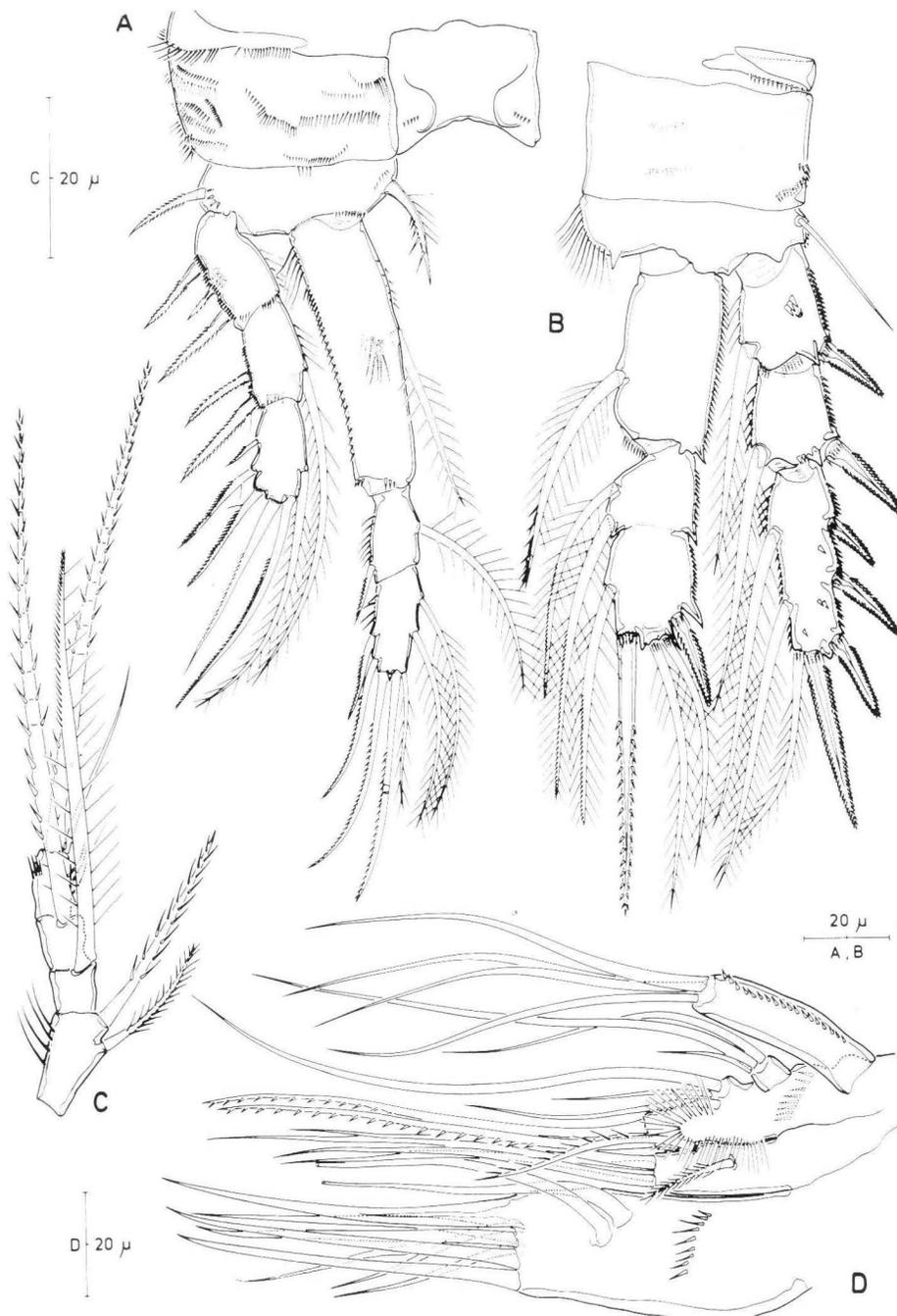


FIG. 19. – *Neoechinophora jaumei* sp. nov.: A. P1, anterior; B. P2, posterior; C. Antennary exopod; D. Maxillule, anterior.

Male (Figs. 9E-F; 13; 14B-E; 16C-D): Smaller than female; total body length 400  $\mu\text{m}$  measured from tip of rostrum to posterior margin of caudal rami. Sexual dimorphism in body size, antennule, P5, P6, genital segmentation and abdominal ornamentation.

Antennule (Figs. 14B-E): slender, 11-segmented and haplocer; geniculation between segments 8 and 9; segment 2 longest; segment 5 represented by U-shaped sclerite (Fig. 14C); with long aesthetasc on

segments 4 and 6, and as part of apical acrothek on segment 11. Segment 1 with 3 anterior spinule rows. Segment 8 with 2 spinule combs on dorsal surface. Segments around geniculation with 2 and 3 modified, fused elements, respectively (Fig. 14C). Armature formula: 1-[1 pinnate], 2-[1], 3-[3 pinnate + 7], 4-[6 + ae], 5-[2], 6-[7 + ae], 7-[2], 8-[2 + 2 modified], 9-[1 + 3 modified], 10-[4], [6 + acrothek]. Apical acrothek consisting of short aesthetasc and basally fused seta.

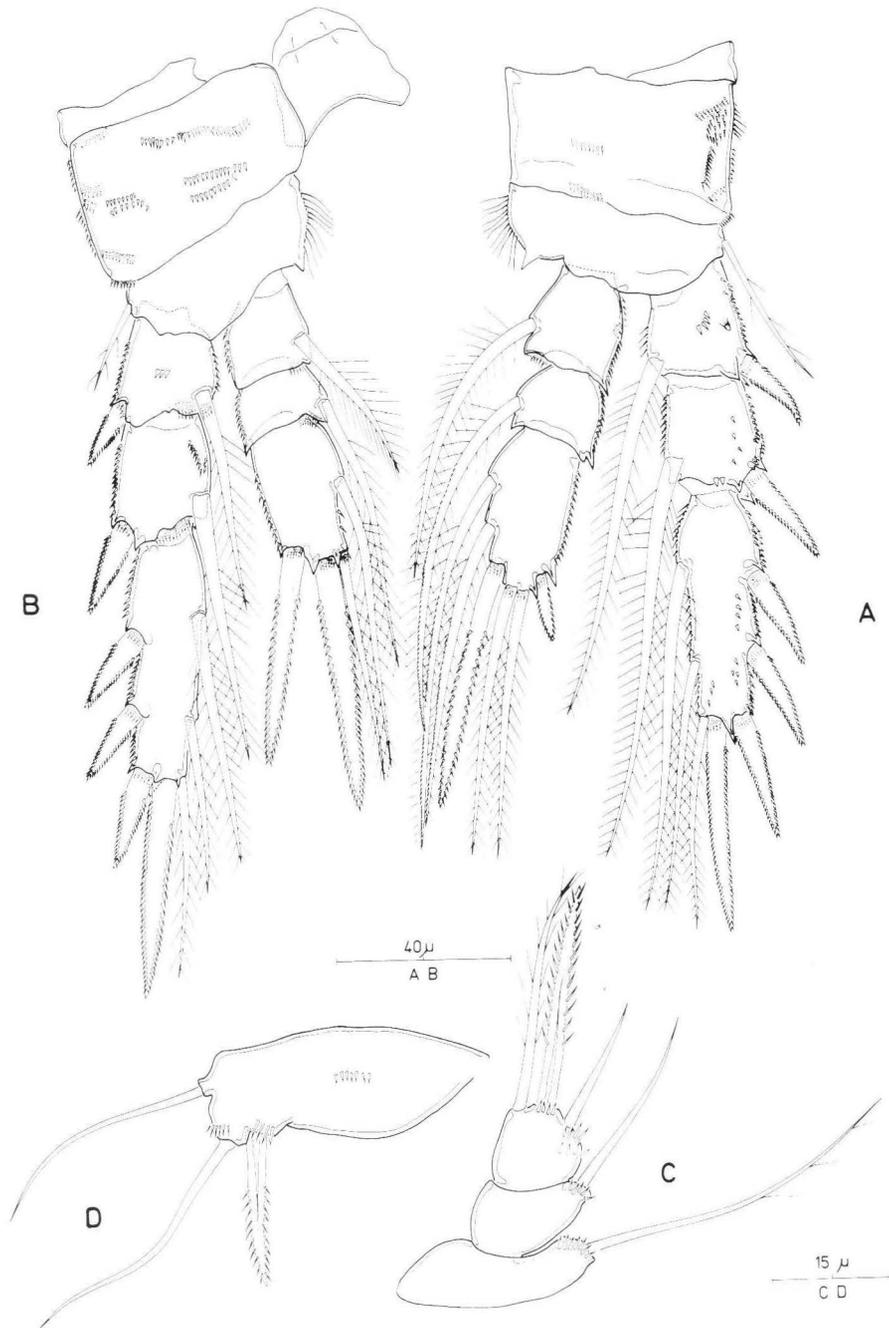


FIG. 20. – *Neoechinophora jaumei* sp. nov.: A. P3, posterior; B. P4, posterior; C. P5 ♂; D. P6 armature ♂.

P5 (Figs. 9E; 16D): uniramous, displaced to ventrolateral position (Fig. 13B). Baseopod with sparsely plumose outer basal seta. Exopod 2-segmented; exp-1 with slender outer seta; exp-2 with short, swollen spine with serrate margins, flanked by short bare seta at either side. Anterior secretory pore present on baseopod. Endopodal lobe completely absent.

Sixth pair of legs asymmetrical (Figs. 13C; 16C), one member fused to somite leaving minute suture,

other (functional member) articulating. P6 armature consisting of swollen, inner serrate spine, long middle plumose seta and short naked outer seta. Both members with diminutive spinule row on anterior surface (Fig. 16C; not discernible using DIC).

Spermatophore 57  $\mu\text{m}$ .

First abdominal (postgenital) somite with double row of paired spinule combs ventrally (Figs. 13B-C). Caudal rami slightly longer than in ♀.

Variability: None observed.

Remark: The fifth legs of both sexes serve to distinguish this species from its congeners. The female P5 is unique in the combination of only 4 elements on the exopod and only 1 on the endopodal lobe. The spine on the male P5 (and P6) is typically stubby, swollen and serrate. An obscure character that proved constant in all specimens examined is the presence of a cluster of anterior surface spinules at 1/5 distance from the base of the distal inner spine of P3 enp-3 (Fig. 11B).

*Neoechinophora jaumei* sp. nov.

Material examined: Holotype ♂ dissected on 6 slides (reg. no. 1996.1225); collected in Deep Blue Cave, Bermuda; leg. A. Fosshagen; depth ca 15 m; 03 September 1984. Paratype ♂ dissected on 6 slides (reg. no. 1996. 1226); collected in Roadside Cave, Bermuda; leg. A. Fosshagen; 27 September 1984; collected with plankton net (mesh size 93 µm) from the water column at 0-5 m depths.

Deep Blue Cave (Hamilton Parish) is a segment of the Walsingham Cave System and contains one of the largest underwater cave chambers in Bermuda. The shaded open pool is situated at the base of a rocky cliff and contains marine algae including *Caulerpa* and crustose corallines. It leads to lightless submerged chambers down to a depth of 23 m. According to Kornicker and Iliffe (1989) salinity varies from 27.2‰ at the surface to 35.3‰ at 1 m depth. Deep Blue Cave is the type locality of the cyclopoid *Halicyclops bowmani* Rocha and Iliffe.

Description:

Female unknown.

Male (Figs. 17-21): Total body length 475 µm measured from tip of rostrum to posterior margin of caudal rami. Largest width 160 µm measured at rear margin of cephalothorax.

Body: elongate cycloform (Figs. 17A-B) but more robust than preceding species. Hyaline frill of cephalothorax and pedigerous somites plain and smooth, that of abdominal somites serrate and with fine striations (Figs. 21B-C). Fine spinule rows present dorsally on somites bearing P4-P6 (Figs. 17A-B). First abdominal somite (Figs. 21B-C) with paired ventral and lateral rows of spinules. Second and third abdominal somites without spinule rows. Anal somite (Figs. 21B-C) with paired ventral rows of fine spinules anteriorly; additional spinules present around ventral, lateral and laterodorsal hind margin; anal operculum weakly developed, slightly rounded,

with fine spinules; anal opening large; anal sensilla positioned far anteriorly; paired secretory pores present lateroventrally and posterodorsally near margin of anal opening. Caudal rami (Figs. 21B-C) medium long, about 2.2 times as long as average width; spinules present around ventral hind margin and around bases of setae I-III and VII; with 3 secretory pores and 7 setae: arrangement (Figs. 17A; 21B) and form of setae as in type species.

Rostrum (Figs. 17A-B): more pronounced than in type species (compare Figs. 1A and 17A); rounded anteriorly; with 2 minute dorsal sensilla apically, tube pore not observed.

Antennule (Figs. 21A): slender, 11-segmented and haplocer; geniculation between segments 8 and 9; segment 2 longest; segment 5 represented by U-shaped sclerite; with long aesthetasc on segments 4 and 6, and as part of apical acrothek on segment 11. Segment 1 with 3 anterior spinule rows. Segment 8 with 2 spinule combs on dorsal surface. Segments around geniculation with 2 and 3 modified, fused elements, respectively. Armature formula: 1-[1 pinnate], 2-[1 pinnate], 3-[7 pinnate + 2], 4-[2 pinnate + 4 + ae], 5-[2], 6-[6 pinnate + 1 + ae], 7-[2 pinnate], 8-[1 pinnate + 1 + 2 modified], 9-[1 + 3 modified], 10-[4], [6 + acrothek]. Apical acrothek consisting of short aesthetasc and basally fused seta. Segment 10 with dorsal membranous insert.

Antenna (Figs. 19C; 21D): Coxa with 1 spinule row. Basis and proximal endopod segment completely fused forming allobasis (Fig. 21D); no traces discernible of original segmentation; with 4 spinule rows. Endopod with armature and ornamentation as in type species. Exopod indistinctly 4-segmented (Fig. 19C); armature formula [2.(1,1),2]; exp-1 elongate, with long setules; exp-2 partly fused to exp-3, original segmentation marked by transverse surface suture; exp-3 with long pinnate seta and short bare seta.

Labrum (Fig. 18C): as in type species.

Mandible: Gnathobase stylet-like (Fig. 18A), with few fine teeth ventrally and 1 slender pinnate seta dorsally; tuft of long setules present near articulation with palp. Palp (Fig. 18B) with 4 setae on endopod; exopod armature formula [1,1,1,1].

Maxillule (Fig. 19D): as in *N. daltonae* except for slight differences in setal lengths and distribution of spinule/setule rows on coxa, basis and exopod.

Maxilla (Fig. 18D): similar to that of type species except for proximal endite on syncoxa which has dense tufts of long setules on middle and distal lobes and 6 barb-like spinules on proximal lobe; endopod with 2 well developed setae.

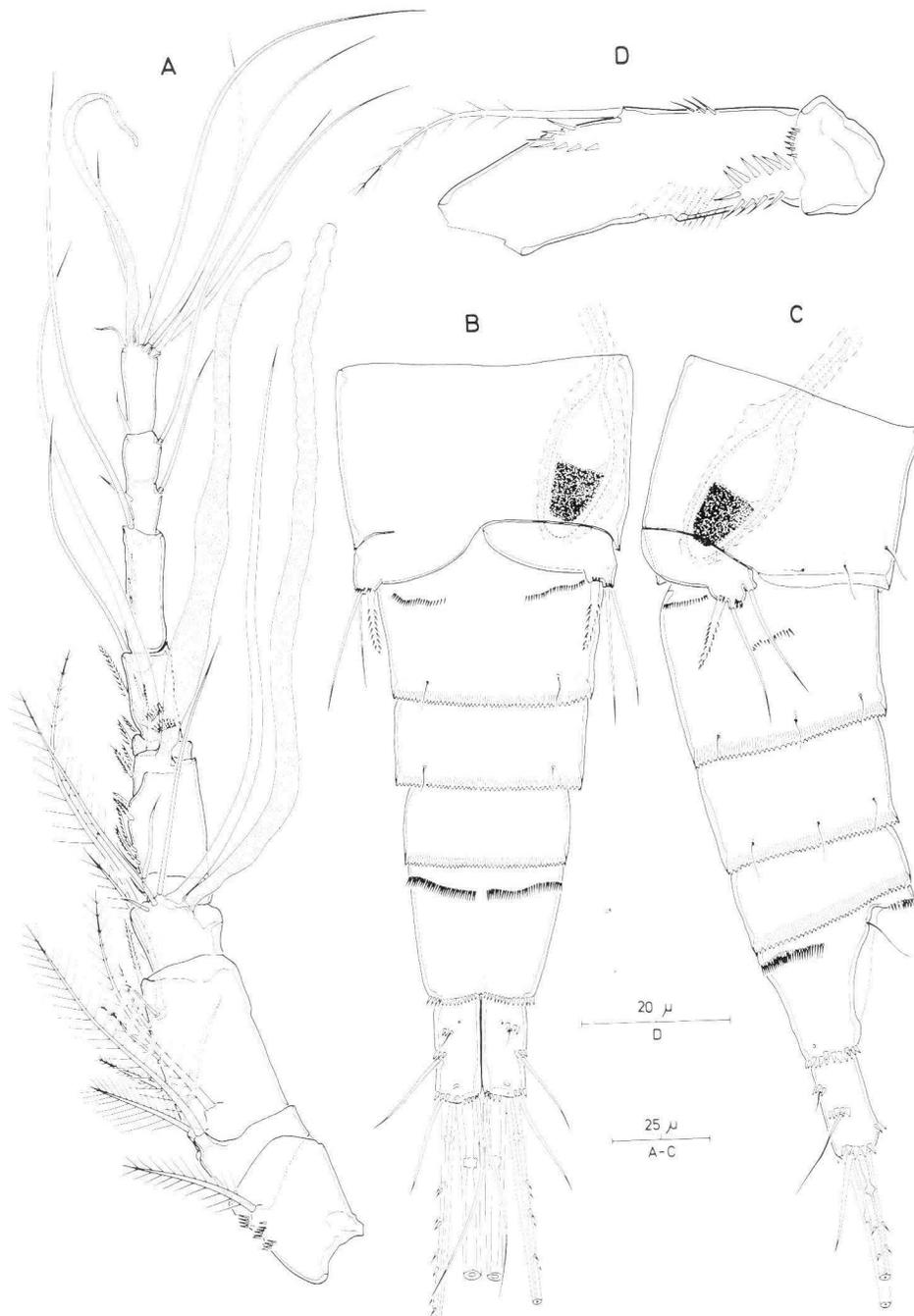


FIG. 21. — *Neoechinophora jaumei* sp. nov.: A. Antennule ♂, ventral; B. Urosome ♂ (excluding P5-bearing somite), ventral; C. Same, lateral; D. Antennary allobasis.

Maxilliped (Fig. 18E): as in type species apart from slight differences in ornamentation of syncoxa and basis and in proportional length of the endopodal claw.

P1 (Fig. 19A): with well developed praecoxa. Intercoxal sclerite with minute spinule rows. Coxa with complex pattern of spinules and setules different from that in *N. fossahageni*; significant differences found in length, shape and distribution of individual ornamentation elements. Basis with bipinnate

outer seta; inner spine curved, with fine setules along middle inner margin and few spinules along outer margin. Exopod with bipinnate outer spines, some of exp-2 and -3 with few long setules proximally; spines of exp-2 shorter and less slender than in type species; middle outer spine of exp-1 very short. Enp-1 with continuous outer spinule row; inner seta located slightly proximal to mid-point of inner margin; posterior setule patch located at level of inner seta. Enp-2 and -3 markedly shorter than in type species.

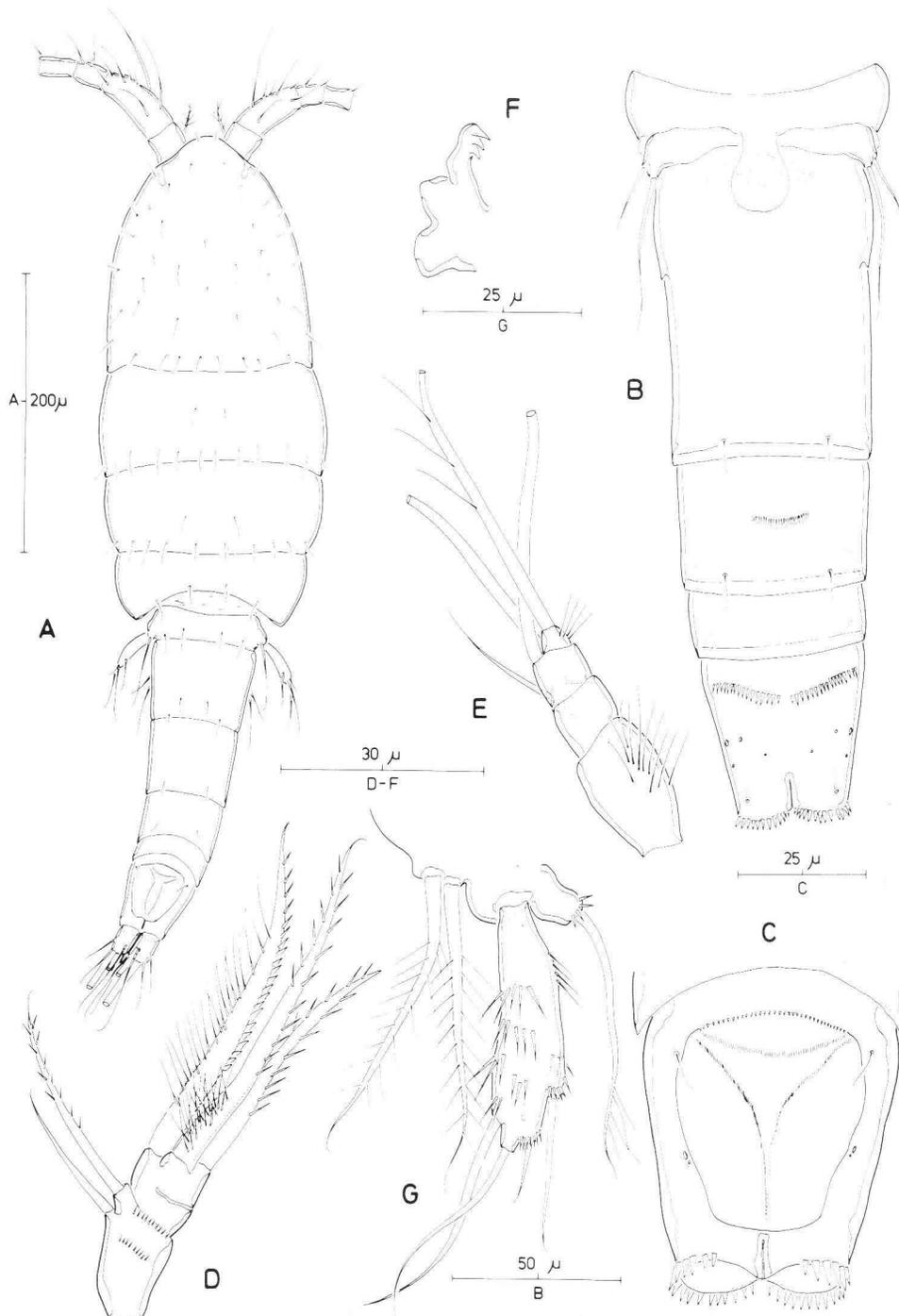


FIG. 22. – *Neoechinophora karaytugi* sp. nov.: A. Habitus ♀, dorsal; B. Urosome (excluding P5-bearing somite and caudal rami) ♀, ventral; C. Anal somite, dorsal; D. Antennary exopod; E. Mandibular exopod; F. Contours of proximal endite of maxillary syncoxa; G. P5 ♀, anterior.

P2-P4 (Figs. 19B; 20A-B): with 3-segmented rami (except P2 endopod). Inner margin of bases with long setules and produced into spinous process. Outer basal seta smooth (P2) or sparsely plumose (P3-P4).

P2 (Fig. 19B): Intercoxal sclerite without spinule rows. Exp-1 with posterior vent pore associated with

coarse spinules. Endopod 2-segmented with incomplete frill and marginal processes marking fusion plane between enp-2 and enp-3. Distal compound segment with 3 tripinnate inner setae, 1 bipinnate inner spine, 2 plumose setae distally and pinnate spine at outer distal corner; outer subdistal corner produced into distinct spinous process.

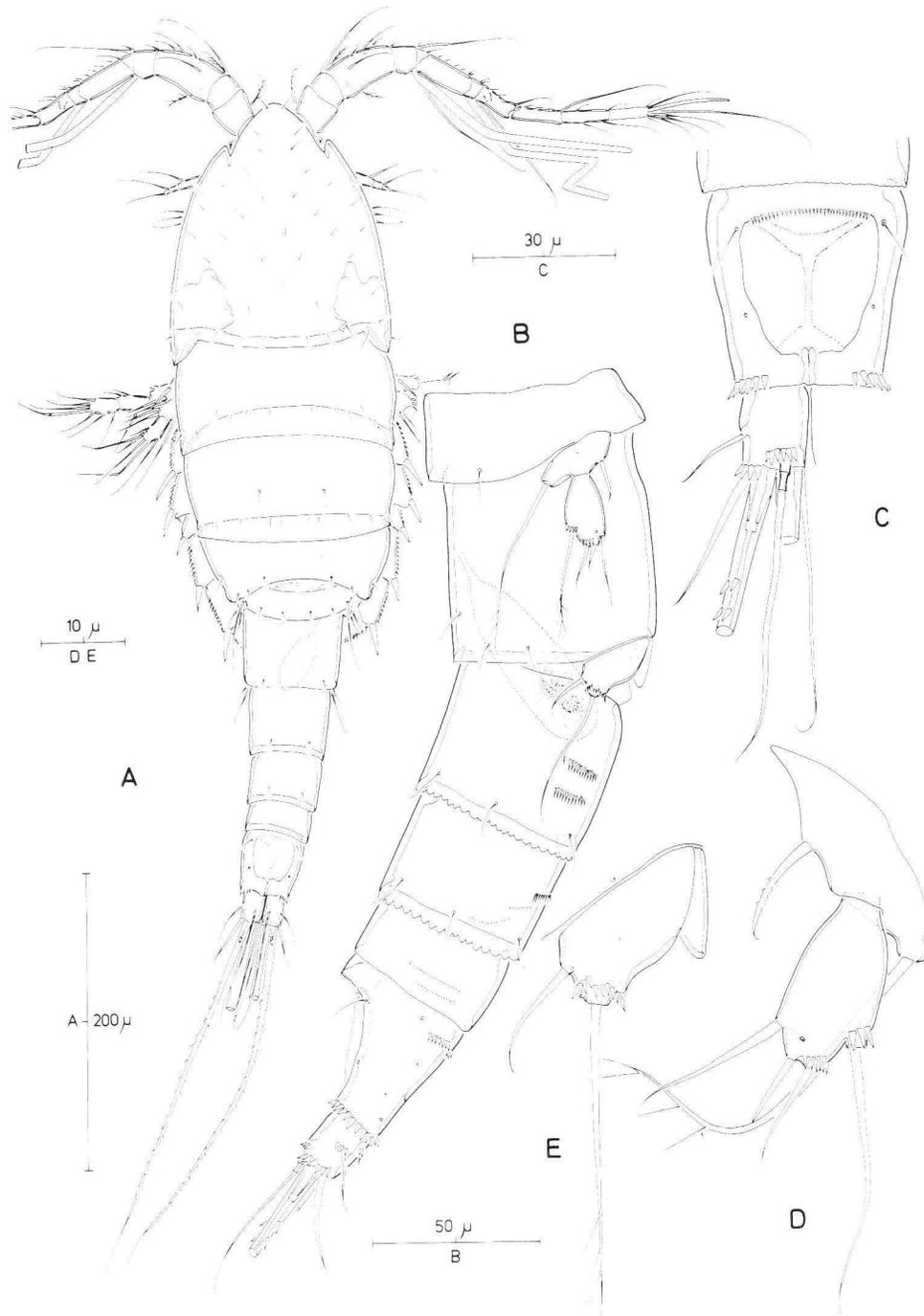


FIG. 23. — *Superornatiremis mysticus* sp. nov.: A. Habitus ♂, dorsal; B. Urosome ♂, lateral; C. Anal somite and left caudal ramus, dorsal; D. P5 ♂, anterior; E. Right P6 ♂, anterior.

P3 (Fig. 20A): Intercoxal sclerite without spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Exp-3 with 2 inner plumose setae, strongly developed as in *N. fosshageni*. Endopod 3-segmented but articulation between middle and distal segment without distinct condyle or arthroal membrane; endopod (particularly enp-3) markedly shorter

than in type species. Inner setae of enp-2 and enp-3 tripinnate.

P4 (Fig. 20B): Intercoxal sclerite without ornamentation. Spines of exopod and enp-3 markedly swollen. Inner margin armature of exp-3 consisting of 2 plumose setae. Enp-3 shorter than in type species. Outer distal spine of exp-3 and enp-3 bipinnate.

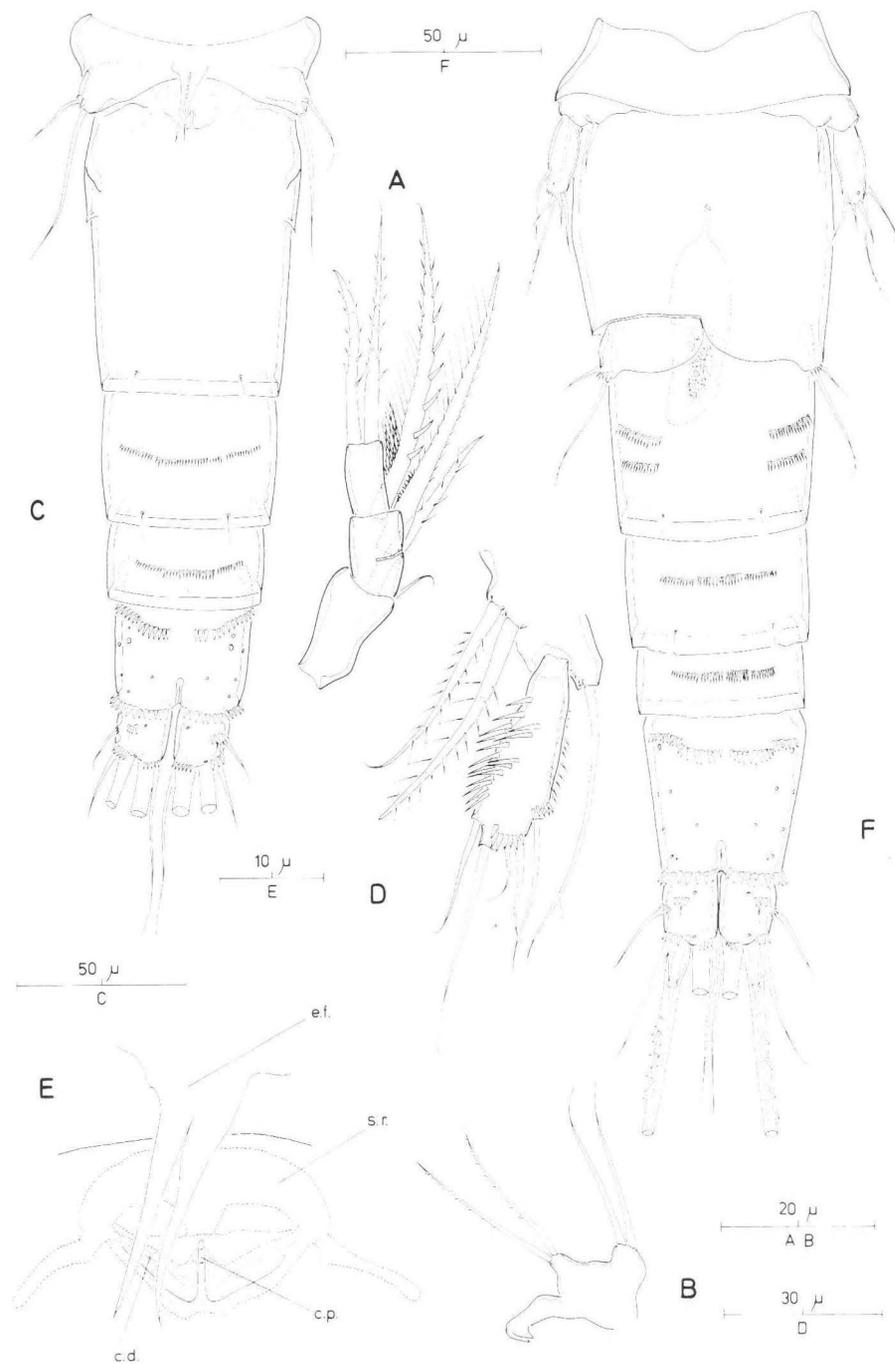


FIG. 24. – *Superornatiremis mysticus* sp. nov.: A. Antennary exopod; B. Proximal endite of maxillary syncoxa; C. Urosome (excluding P5-bearing somite) ♀, ventral; D. P5 ♀, anterior; E. Genital field ♀ (c.d.: copulatory duct; c.p.: copulatory pore; e.f.: epicopulatory flap; s.r.: seminal receptacle); F. Urosome ♂, ventral.

Armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;6	0-1;I-1;2,2,3
P2	0-0	1-0	I-1;I-1;III,1+1,2	0-1;[0-2;1,2,I+1]
P3	0-0	1-0	I-1;I-1;III,1+1,2	0-1;0-1;I,2,I+2
P4	0-0	1-0	I-1;I-1;III,1+1,2	0-1;0-1;I,1+1,1

P5 (Figs. 20C): uniramous, displaced to ventrolateral position (Fig. 17B). Baseoendopod with sparsely plumose outer basal seta. Exopod 2-segmented; exp-1 with slender outer seta; exp-2 with long bipinnate spine, flanked by long inner plumose seta and short bare outer seta. Endopodal lobe completely absent.

Sixth pair of legs asymmetrical (Fig. 21B), one member fused to somite leaving short surface suture, other (functional member) articulating. P6 armature (Fig. 20D) consisting of bipinnate inner spine and long middle and outer naked outer setae. Both members with fine spinules on anterior surface and around bases of middle and inner elements.

Spermatophore 40  $\mu\text{m}$ .

Remark: *N. jaumei* can be readily distinguished from its congeners by the presence of only 2 inner setae on the distal exopod segment of P3 and P4.

### *Neoechinophora karaytugi* sp. nov.

Material examined: Holotype ♀ dissected on 8 slides (reg. no. 1996.1228); collected in Jameos del Agua, Lanzarote, Canary Islands; leg. H. Wilkens; 16 March 1986.

The Cueva de los Verdes-Jameos del Agua system, formed by eruptions of the volcano Monte Corona during the Holocene, is with its total length of more than 8 km one of the world's longest lava tubes (Wilkens and Parzefall, 1974). The Jameos del Agua Cave is an anchihaline lava tube which begins on land at the base of the volcano, extends 6 km to the coast as an unbranching passage and continues as a flooded extension for at least 1600 m away from the island beneath the seafloor (at least 53 m deep). Except for some 100 m at the two entrances the cave is in total darkness. The water is very clear and is swept in the lava tube by moderate reversing currents producing a tidal range of ca 2 m in inland cave pools. The salinity approaches that of the open sea. Jameos del Agua is the type-locality of the arietellid calanoid *Paramisophria reducta* described by Ohtsuka *et al.* (1993), and of several misophrioids described by Boxshall and Iliffe (1987): *Expansophria dimorpha*, *Palpophria aestheta* and *Dimisophria cavernicola*. Although the holotype is partly damaged, the zoogeographical significance of its discovery in the Canary Islands is such that we regard its description justified.

#### Description:

Female (Fig. 22): Total body length 600  $\mu\text{m}$  measured from tip of rostrum to posterior margin of caudal rami. Largest width 165  $\mu\text{m}$  measured halfway P2-bearing somite.

Body elongate cycloform (Figs. 22A): Hyaline frill of cephalothorax and body somites plain and smooth (Figs. 22A-B). Genital double-somite elongate, completely fused; without ventrolateral bulges in anterior half (Fig. 22B); original segmentation marked by

transverse surface frill dorsolaterally and dorsally (Fig. 22A) but not by internal chitinous ribs. Second abdominal somite (Fig. 22B) with midventral row of tiny spinules. Third abdominal somite without spinule rows. Anal somite (Figs. 22B-C) with paired ventral rows of coarse spinules anteriorly; additional spinules present around ventral, lateral and laterodorsal hind margin; anal operculum weakly developed, slightly rounded, with diminutive spinules; anal opening large; anal sensilla positioned far anteriorly; paired secretory pores present lateroventrally and posterodorsally near margin of anal opening. Caudal rami (Fig. 22A) short, about 1.4 times as long as average width; spinules present around ventral hind margin and around bases of setae I-III and VII; with 3 secretory pores and 7 setae; arrangement and form of setae as in type species.

Rostrum, antennules, maxillules and maxillipeds: as in type species.

Antennary exopod (Fig. 22D): 2-segmented; armature formula [2,3]; exp-1 elongate, with 2 spinule rows, 1 bare and 1 pinnate seta; exp-2 compound, derived by fusion of segments 2-4 expressed in *N. fosshageni*, original segmentation partly marked by incomplete surface suture; lateral setae of exp-2 with basal tuft of setules and bearing spinules as in Fig. 22D.

Mandibular exopod (Fig. 22E): 4-segmented; segments decreasing in size apically; armature formula [1,1,1,1]; segments 1 and 4 with long setules.

Maxilla: as in type species except for proximal endite on syncoxa (Fig. 22F) which has 3 barb-like spinules on the proximal lobe.

P1-P4 incomplete; P3-P4 exp-3 with 3 setae along inner margin.

P5 (Fig. 22G) biramous: Baseoendopod incorporated into somite; with outer lobe bearing basal, sparsely plumose, seta, and 2 inner, plumose setae representing endopodal lobe. Exopod elongate oval-shaped, slender; about 3.3 times as long as maximum width; anterior surface with several spinule rows as figured; spinules also present around bases of outer elements; armature consisting of 1 inner, 1 apical and 2 outer bare setae.

Genital field positioned in anterior third of genital double-somite (Fig. 22B). Gonopores paired, laterally displaced, entirely separated; each covered by P6 with 1 short outer seta and 1 long inner bare seta. Copulatory pore large, largely concealed beneath broadly rounded hyaline epicopulatory flap derived from an outgrowth of the ventral somite wall; copulatory pore leading via paired chitinized copulatory ducts to median transversely elongated seminal receptacle.

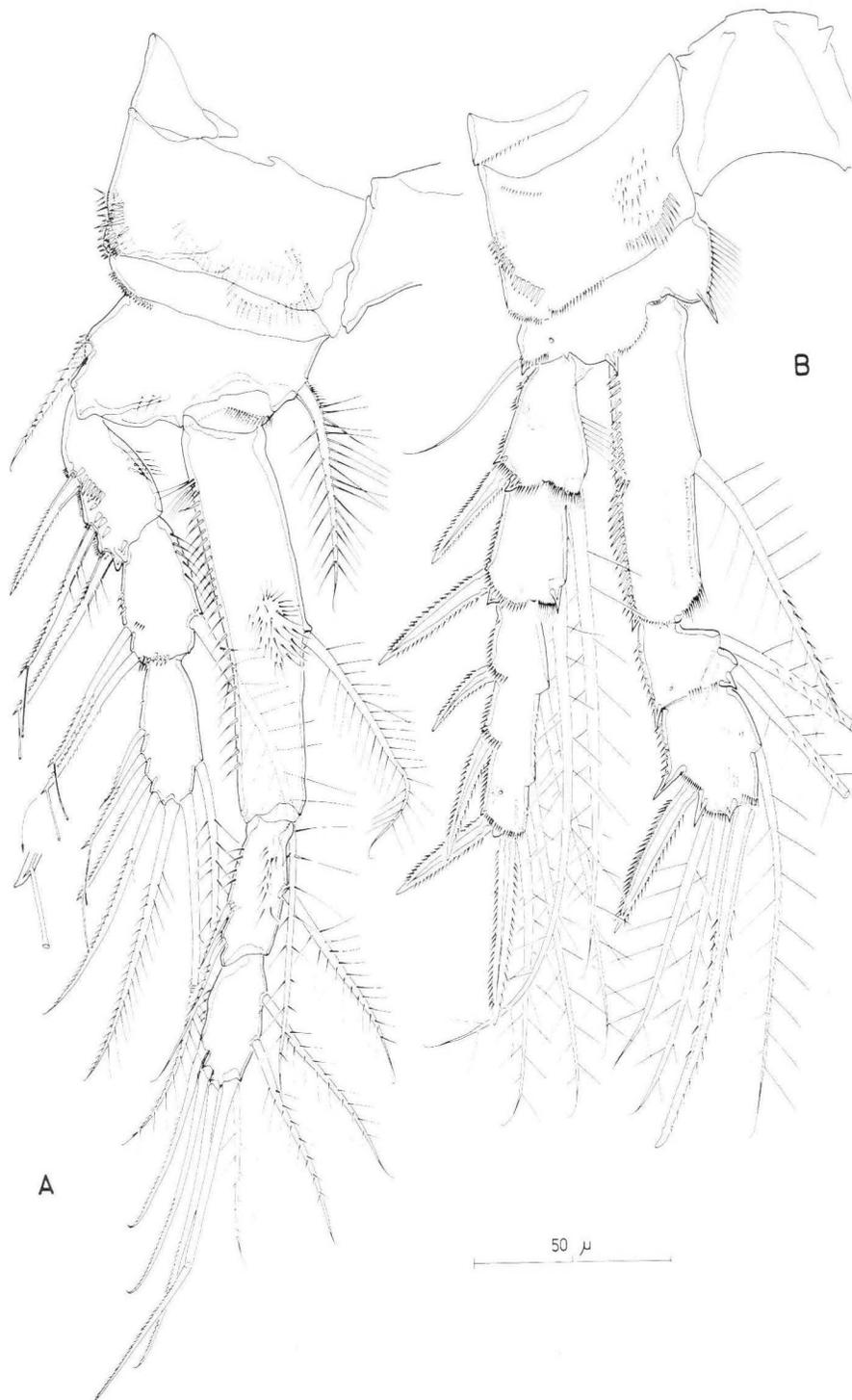


FIG. 25. – *Superornatiremis mysticus* sp. nov.: A. P1, posterior; B. P2, anterior.

Egg sac(s) not observed.

Male unknown.

A complete description of the species was impossible with the only damaged specimen available,

however several characters justify its establishment as a distinct species: (a) 2-segmented antennary exopod; (b) P5 ♀ with combination of 4 setae on exopod and 2 on endopodal lobe; (c) presence of diminutive spinules on anal operculum; (d) spinulation pattern on abdomen.

### *Superornatiremis* gen. nov.

Diagnosis: Superornatiremidae. Maxilliped with 1 seta on basis. Outer spines of P1 exopodal segments with subterminal tubular extensions. P1 enp-2 with 2 outer elements. Armature formula of P1-P4 as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;6	0-1;II-1;2,2,3
P2	0-0	1-0	I-1;I-1;III.I+1,2	0-1;(0-2;I.2.I+1)
P3	0-0	1-0	1-1;I-1;III.I+1,3	0-1;0-1;I.2.I+2
P4	0-0	1-0	1-1;I-1;III.I+1,3	0-1;0-1;I.I+1,1

P5 ♀ with 5 setae on exopod and 2 on endopodal lobe of baseopod. P5 ♂ with 1 seta on endopodal lobe; exopod 1-segmented with 4 setae/spines. Copulatory pore small, epicopulatory flap deeply incised, bifid. P6 ♂ with reduced inner element, long middle seta and medium long outer seta. Anterior half of ♀ genital double-somite without paired dorsolateral tufts of long setules. Caudal rami short.

Type and only species: *Superornatiremis mysticus* gen. et sp. nov.

Etymology: The genus name is derived from the Latin *super* (meaning over), *ornatus* (meaning furnished, adorned, provided) and *remus* (meaning oar), and refers to the presence of supernumerary armature elements on both rami of leg 1. The trivial name is derived from the Latin *mysticus*, relating to mysteries, mystic.

#### *Superornatiremis mysticus* gen. et sp. nov.

Material examined: Holotype ♂ dissected on 7 slides (reg. no. 1996. 1197); paratypes are 1 ♀ dissected on slides and 4 ♀♀ in alcohol (reg. nos 1996. 1198-1203); collected in Walsingham Cave, Bermuda with plankton net; depth 5 m; leg. J.H. Stock; 01 October 1984.

Additional material: 1 damaged ♂ from Devonshire Cave, Bermuda (12 September 1984), 1 damaged Cop V ♀ from Fern Sink Cave, Bermuda (24 July 1984); leg. A. Fosshagen.

Fern Sink Cave (Hamilton Parish) is part of an arm of the Walsingham System that is much more isolated from the sea and shows no apparent water currents. It consists of pool in total darkness which inclines steeply down a breakdown slope to the main level of the cave at 18 m depth. The maximum depth recorded is 24 m and the salinity ranges from 18.0‰ taken at the surface to 26.7‰ at 1 m depth (Kornicker and Iliffe, 1989). No copepods have thus far been identified from this cave.

Devonshire Cave (Devonshire Parish) located on the east coast is only remotely connected with the sea. It is situated ca 50 m from the coast and has clear water. Devonshire Cave is the type locality of the pseudocyclopiid *Paracyclopia naessi* where it occurs in high abundance. Fosshagen and Iliffe (1985) also described the primitive calanoid *Erebonectes nesioticus* Fosshagen from this locality.

#### Description:

Female (Figs. 24A-E; 25, 26): Total body length 580 µm measured from tip of rostrum to posterior margin of caudal rami. Largest width 160 µm measured at posterior margin of cephalothorax.

Body elongate cycloform, with distinct demarcation between prosome and urosome. Integument smooth, not strongly chitinized. Hyaline frill of cephalothorax and body somites plain and smooth. Cephalothorax and somites bearing P2-P4 without surface ornamentation except for integumental sensilla. Genital double-somite elongate, completely fused (Fig. 24C); original segmentation marked by transverse surface frill dorsolaterally and dorsally but not by internal chitinous ribs. Second and third abdominal somites (Fig. 24C) with midventral and paired lateroventral rows of fine spinules. Anal somite (Figs. 23C; 24C) with paired ventral and lateroventral rows of coarse spinules anteriorly; fine spinules present around ventral, lateral and laterodorsal hind margin; anal operculum weakly developed, slightly rounded, with fine spinules; anal opening large; anal sensilla positioned far anteriorly; paired secretory pores present lateroventrally and posterodorsally near margin of anal opening. Caudal rami (Figs. 23C; 24C) slightly longer than wide; spinules present around ventral hind margin and around bases of setae I, III and VII; with 3 secretory pores and 7 setae: seta I relatively short, displaced to ventral position; seta II arising from mid-point of outer margin, smooth; seta III smooth; setae IV and V strongly developed and multipinnate; seta VI very long and smooth, partially fused to inner distal margin of caudal ramus; seta VII triarticulate at base and located near posterior margin of ramus.

Rostrum: as in ♂ (Fig. 23A), well developed, not demarcated at base; with 2 dorsal sensilla apically, tube pore not observed.

Antennule: elongate and slender, 9-segmented; armature as in *N. fosshageni*.

Antennary: endopod with general ornamentation and armature as in *Neoechinophora* species. Exopod (Fig. 24A) 3-segmented; armature formula

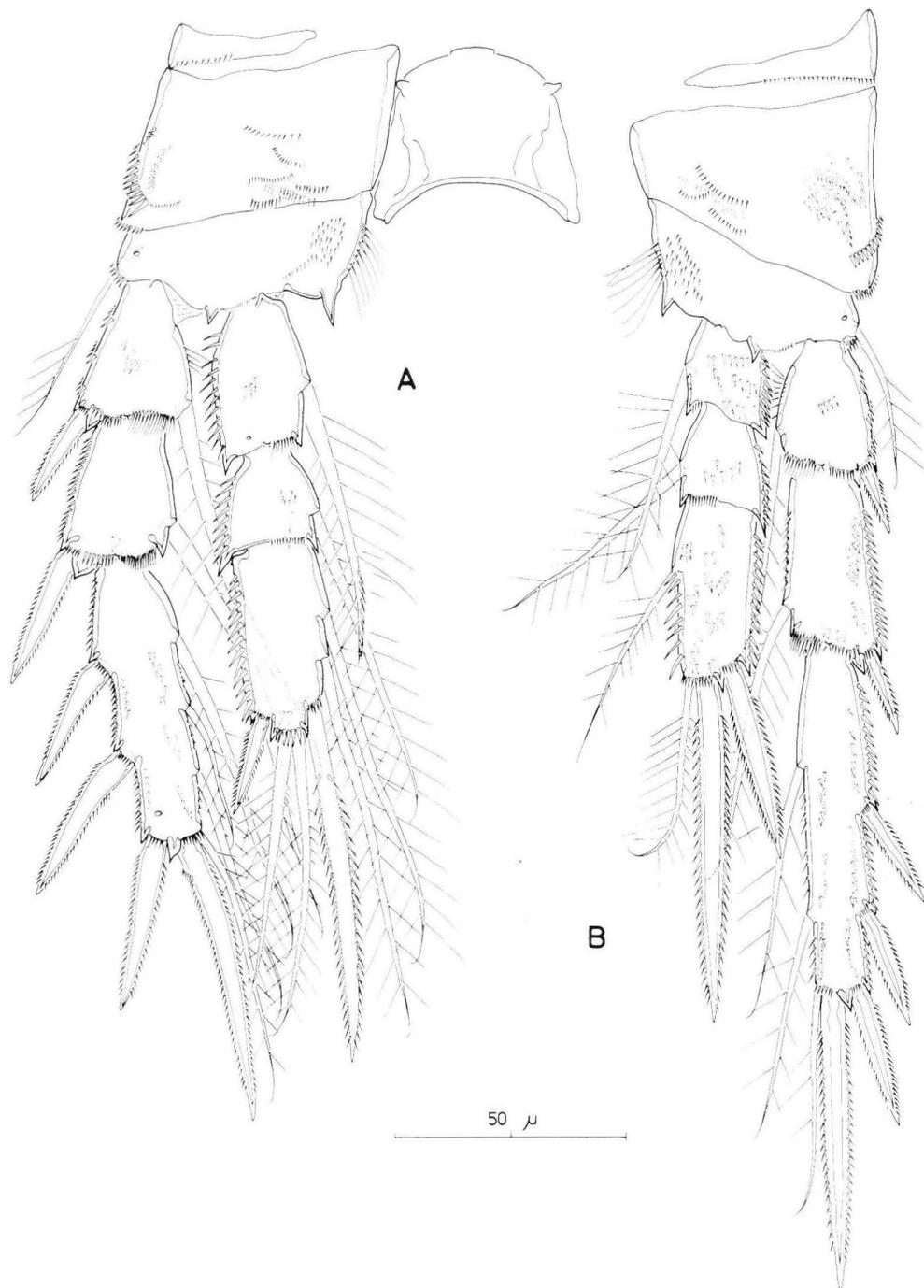


FIG. 26. – *Superornatiremis mysticus* sp. nov.: A. P3, anterior; B. P4, anterior.

[2,2,2]; exp-1 elongate, with 1 short naked seta and 1 bipinnate seta; exp-2 compound, derived from fusion of ancestral exp-2 and -3, original segmentation marked by surface suture, setae having basal tuft of setules and bearing spinules as in Fig. 24A; exp-3 elongate.

Mandible: as in *N. daltonae*. Gnathobase stylet-like but slightly less slender than in *Neoechino-*

*phora*. Exopod 4-segmented; armature formula [1,1,1,1].

Maxillule: exactly as in *N. daltonae*.

Maxilla: as in *N. daltonae* except for proximal lobe of trilobate endite of syncoxa with 2 barb-like extensions along dorsal margin.

Maxilliped: as in *N. daltonae*; basis with seta.

P1 (Fig. 25A): with well developed praecoxa.

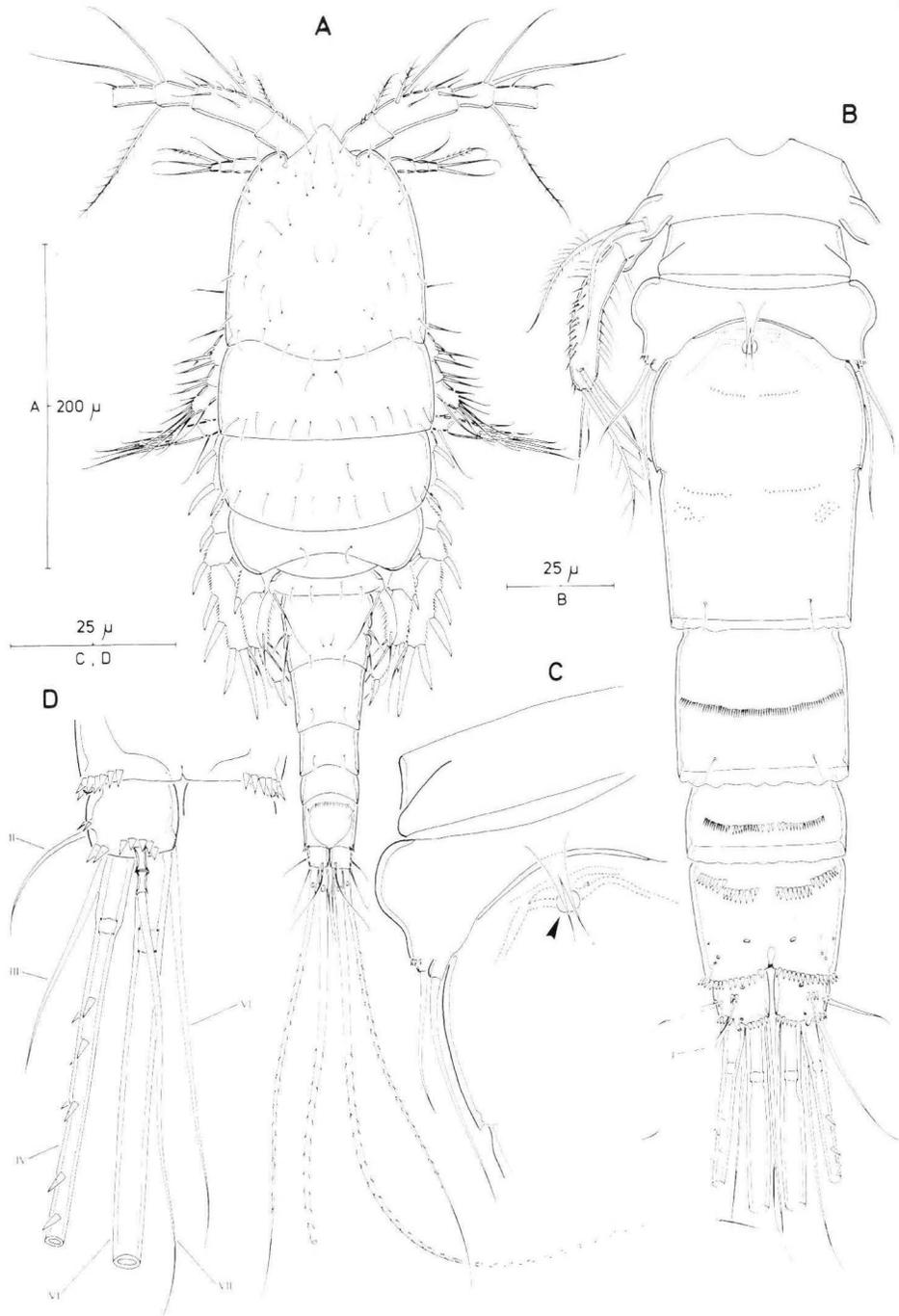


FIG. 27. — *Intercrusia problematica* sp. nov.: A. Habitus ♀, dorsal (distal segments of antennules omitted); B. Urosome ♀, ventral; C. Genital field ♀ (copulatory pore arrowed); D. Left caudal ramus, dorsal.

Intercoxal sclerite without spinule rows. Coxa with complex pattern of spinules and long setules as figured. Basis with bipinnate outer bipinnate seta; inner spine curved, with fine spinules proximally and long setules along both inner and outer margins. Exopod with slender outer spines, some with long setules proximally, all (except proximal one of exp-1 and exp-3) with long subapical tubulat

extensions (see inset); exp-2 with long plumose inner seta; exp-3 with 7 slender elements. Enp-1 with outer spinule row continuous; inner seta arising from point slight distal to mid-point of margin; posterior setule patch located at level of inner seta. Enp-2 and -3 elongate and slender; enp-2 with 2 outer setae; enp-3 with 1 geniculate and 6 simple elements.

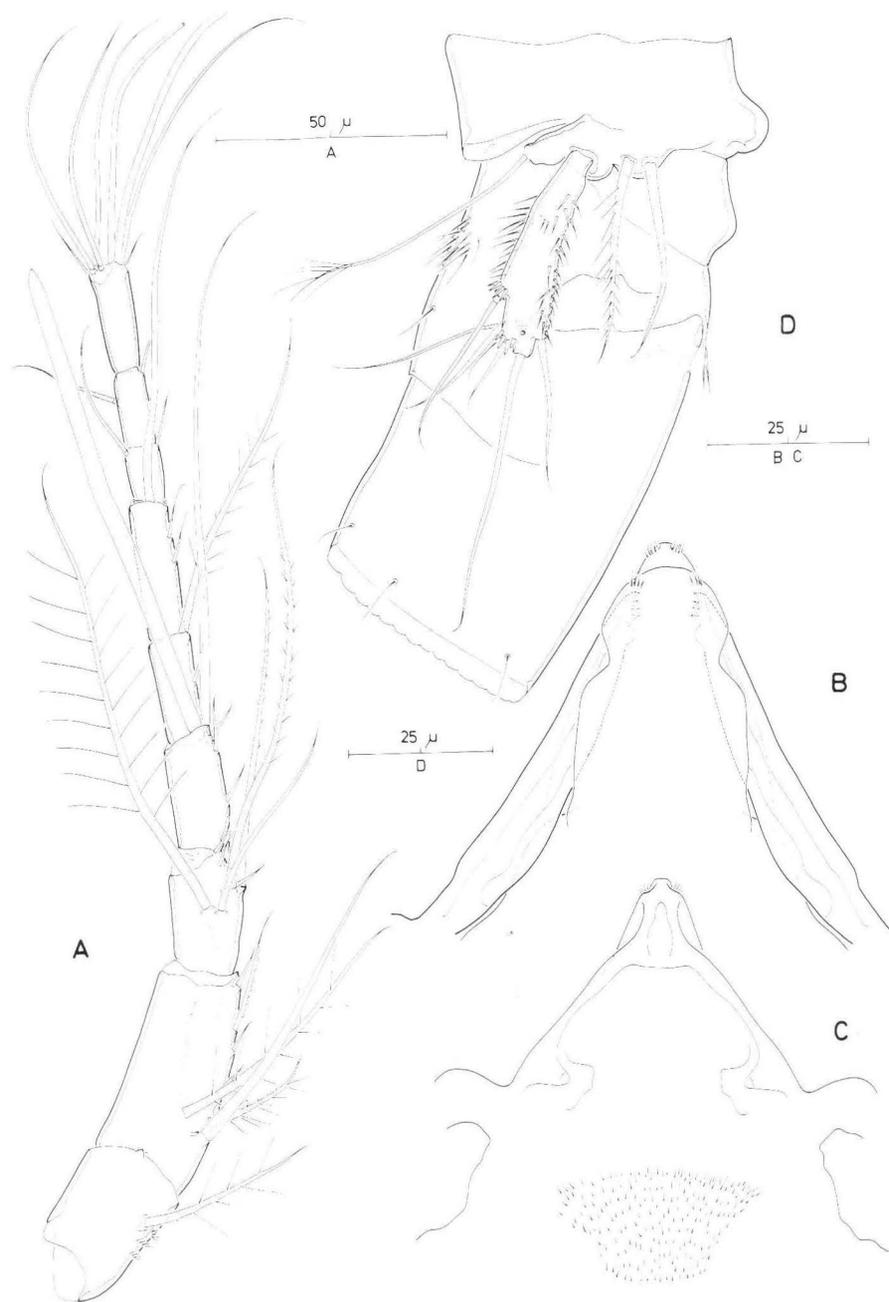


FIG. 28. — *Intercusia problematica* sp. nov.: A. Antennule ♀, ventral; B. Labium (superimposed on mandibular gnathobases and labrum), posterior; C. Labrum, anterior; D. P5-bearing and genital double-somites, lateral.

P2-P4 (Figs. 25B; 26A-B) with 3-segmented rami (except P2 endopod). Inner margin of bases with long setules and produced into pointed process. Outer basal seta smooth (P2) or sparsely plumose (P3-P4). All exopod and endopod segments with fine spinules along outer margins and around bases of outer and distal armature elements; frills between segments well developed. Exp-3 as long or longer than exp-1 and -2 combined. Anterior face of segments without surface ornamentation

but with scattered spinules on posterior face as figured.

P2 (Fig. 25B). Intercoxal sclerite without anterior spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Endopod 2-segmented with incomplete frill and marginal processes marking fusion plane between enp-2 and enp-3. Enp-1 elongate, longer than distal segment; inner seta plumose with coarse spinules along distal inner margin. Distal compound segment with 3 tripinnate inner setae, 1

tripinnate inner spine, 2 plumose setae distally and long pinnate spine at outer distal corner; outer sub-distal corner produced into long spike-like process.

P3 (Fig. 26A). Intercoxal sclerite with anterior spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Exp-3 with short middle inner seta. Endopod 3-segmented but articulation between middle and distal segment without condyle or arthrodial membrane and therefore possibly not functional. Inner seta of enp-1 plumose with coarse spinules along distal inner margin. Enp-3 with 2 plumose inner setae, 1 bipinnate inner spine, 2 plumose setae distally and pinnate spine at outer distal corner.

P4 (Fig. 26B). Intercoxal sclerite without ornamentation. Inner margin of exp-3 with 2 plumose setae. Endopod 3-segmented, distinctly shorter than exopod. Inner seta of enp-1 plumose without coarse spinules along distal inner margin. Enp-3 with 1 plumose inner seta, 1 plumose seta and 1 long, swollen spine apically and long pinnate spine at outer distal corner. Outer distal spine of exp-3 and enp-3 bipinnate.

Armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;7	0-1;II-1;2,2,3
P2	0-0	1-0	I-1;I-1;III,I+1,2	0-1;[0-2;I,2,I+1]
P3	0-0	1-0	I-1;I-1;III,I+1,3	0-1;0-1;I,2,I+2
P4	0-0	1-0	I-1;I-1;III,I+1,2	0-1;0-1;I,I+1,1

P5 (Fig. 24D) biramous. Baseoendopod incorporated into somite; represented by outer lobe bearing basal sparsely plumose seta, and vestigial endopodal lobe carrying 2 strong bipinnate setae. Exopod tapering proximally; 2.85 times as long as maximum width; anterior surface with several spinule rows as figured; spinules also present around bases of apical and outer elements; armature consisting of 1 inner, 1 long apical and 3 outer bare setae.

Genital field positioned in anterior third of genital double-somite (Fig. 24C). Gonopores paired, laterally displaced, separated; each covered by genital operculum derived from vestigial sixth legs. P6 with 1 short outer and 1 long inner bare seta. Copulatory pore small, circular, located in slit-like depression, covered anteriorly by deeply incised, narrow hyaline epicopulatory flap derived from an outgrowth of the ventral somite wall; leading via paired chitinized copulatory ducts to median transversely elongated seminal receptacle.

Egg sac(s) not observed.

Male (Figs. 23; 24F). Smaller than female; total body length 555  $\mu\text{m}$  measured from tip of rostrum to posterior margin of caudal rami. Sexual dimorphism in body size, antennule, P5, P6, genital segmentation and abdominal ornamentation. Hyaline frills of abdominal somites slightly undulated (Fig. 23B).

Antennule slender, 11-segmented and haplocer; geniculation between segments 8 and 9; armature as in *N. fosshageni*.

P5 (Fig. 23B, D) uniramous, displaced to ventrolateral position (Fig. 24F). Baseoendopod with naked outer basal seta and curved bipinnate inner seta representing endopodal lobe. Exopod 1-segmented, more or less oval-shaped; with 4 naked setae, apical one shortest, outer ones with spinules around base. Anterior and posterior secretory pore present on exopod.

Sixth pair of legs asymmetrical (Figs. 23B, E; 24F), one member fused to somite, other (functional member) articulating. P6 armature consisting of inner vestigial element, long middle sparsely plumose seta and short naked outer seta.

Spermatophore 55  $\mu\text{m}$ .

First abdominal (postgenital) somite with double row of paired spinule combs ventrally.

Remarks: *Superornatiremis* differs from *Neoechinophora* in the presence of 2 outer setae on P1 enp-2, and 7 elements on P1 exp-3, the 1-segmented exopod in the male P5, the reduction of the inner element on the male sixth legs, the presence of subapical tubular extensions on the outer spines of P1 and the bifid structure of the epicopulatory flap. It is noted here that the distal inner seta of P1 enp-3 was overlooked in the illustration of the P1 of *S. mysticus* presented by Huys and Boxshall (1991).

### *Intercrusia* gen. nov.

Diagnosis: Superornatiremidae. Maxilliped with 1 seta on basis. Outer spines of P1 exopodal segments with subterminal tubular extensions. P1 exp-3 with 7 elements P1 enp-2 with 1 outer element. Armature formula of P1-P4 as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;7	0-1;I-1;2,2,3
P2	0-0	1-0	I-1;I-1;III,I+1,2	0-1;(0-2;I,2,I+1)
P3	0-0	1-0	I-1;I-1;III,I+1,3	0-1;0-1;I,2,I+2
P4	0-0	1-0	I-1;I-1;III,I+1,3	0-1;0-1;I,I+1,1

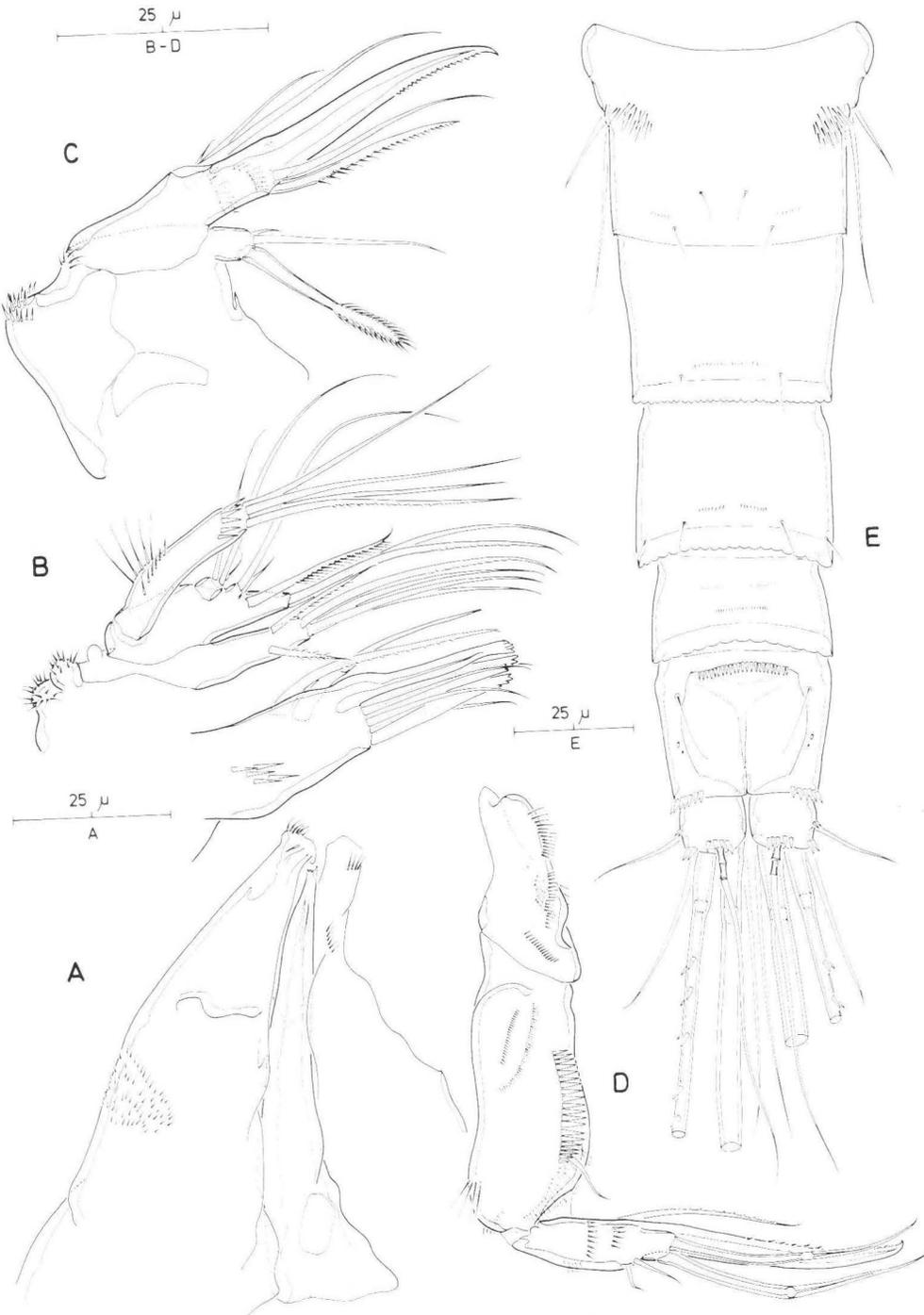


FIG. 29. — *Intercrusia problematica* sp. nov.: A. Labrum, mandibular gnathobase (insertion area of palp stippled) and labium, lateral; B. Maxillule (with arthrite disarticulated), posterior; C. Maxilla; D. Maxilliped; E. Urosome ♀ (excluding P5-bearing somite), dorsal.

P5 ♀ with 5 setae on exopod and 2 on endopodal lobe of baseopod. Copulatory pore small, epicopulatory flap deeply incised, bifid. Anterior half of ♀ genital double-somite with paired dorsolateral tufts of long setules. Caudal rami wider than long. Male unknown.

Type and only species: *Intercrusia problematica*

gen. et sp. nov.

Etymology: The generic name is derived from the Latin *inter*, meaning between, and *crus*, meaning leg, and alludes to the intermediate position between *Superornatiremis* and *Neoechinophora*. The trivial name refers to the problematic position of the species.

### *Intercrusia problematica* sp. nov.

Material examined. - 1 ♀ dissected on 8 slides (reg. no. 1996.1229); collected in Deep Blue Hole to Walsingham Cave; leg. A. Fosshagen; 08 September 1984.

#### Description:

Female (Figs. 27-31). Total body length 460 µm measured from tip of rostrum to posterior margin of caudal rami. Largest width 135 µm measured at posterior margin of P2-bearing somite.

Body elongate cycloform (Fig. 27A), with distinct demarcation between prosome and urosome. Integument smooth, not strongly chitinized. Hyaline frill of cephalothorax and body somites plain and smooth except for slightly undulate frill of genital double-somite and abdominal somites (Figs. 27B; 28D; 29E). Cephalothorax and somites bearing P2-P4 without surface ornamentation (Fig. 1A) except for integumental sensilla. Genital double-somite elongate, completely fused (Figs. 27B; 28D; 29E); original segmentation marked by transverse surface frill dorsolaterally (Fig. 28D) and dorsally (Fig. 29E) but not by internal chitinous ribs; with paired laterodorsal tufts of long setules in anterior half (Figs. 28D; 29E); ventral surface with pattern of minute spinules (Fig. 27B). Dorsal surface of genital double-somite and postgenital somites with rows of minute spinules as in Fig. 29E. Second and third abdominal somites (Fig. 27B) with ventral row of fine spinules. Anal somite with paired ventral and lateroventral rows of coarse spinules anteriorly; coarse spinules present around ventral, lateral and laterodorsal hind margin; anal operculum weakly developed, slightly rounded, with fine spinules; anal opening large; anal sensilla very long, positioned far anteriorly (Fig. 29E); paired secretory pores present ventrally, lateroventrally and posterodorsally near margin of anal opening. Caudal rami (Figs. 27B, D) short, wider than long; spinules present around ventral hind margin and around bases of setae I-III and VII; with 7 setae: seta I relatively short, displaced to ventral position; seta II arising from mid-point of ramus length, smooth; seta III smooth; setae IV and V strongly developed and multipinnate; seta VI long and smooth, partially fused to inner distal margin of caudal ramus; seta VII triarticulate at base and located near posterior margin of ramus.

Rostrum (Fig. 27A) triangular, rounded anteriorly, demarcated at base; with 2 dorsal sensilla apically, tube pore not observed.

Antennule (Fig. 28A) elongate and slender, 9-segmented. Segment 1 with 3 anterior spinule rows.

Segment 2 longest. Armature formula: 1-[1 pinnate], 2-[3 pinnate + 6], 3-[3 pinnate + 4], 4-[4+ae], 5-[1 pinnate + 1], 6-[3], 7-[2], 8-[2], 9-[6 + acrothek]. Apical acrothek consisting of short aesthetasc and basally fused seta. Long setae present on segments 2-6 and 9. Aesthetasc on segment 4 not fused to seta. Proportional lengths of antennular segments (measured along non-setiferous posterior margin): 8.5:19.6:11.1:10.5:10.5:15.1:5.5:8.1:11.1.

Antenna (Fig. 31A). Coxa minute, with short spinule row. Basis and proximal endopod segment completely fused forming allobasis; original segmentation not marked by surface sutures or transverse ribs; with 3 spinule rows as illustrated in Fig. 31A. Endopodal armature as in *N. fosshageni*. Exopod 3-segmented (Fig. 1C); armature formula [2,2,2]; exp-1 elongate, with 3 fine spinule rows; exp-2 compound, derived by fusion of segments 2 and 3 expressed in *N. fosshageni*, original segmentation marked by incomplete suture lines, setae having basal tuft of setules and bearing spinules as in Fig. 31A; exp-3 with spinule row.

Labrum (Figs. 28C; 29A) triangular, with anterior patch of fine spinules proximally; apex with few spinules.

Mandible. Gnathobase stylet-like (Figs. 28B; 29A), with few fine teeth ventrally and 1 slender pinnate seta dorsally. Palp (Fig. 31B) biramous. Basis with few spinules and 2 setae at inner distal corner (outer one minute and slender, inner one modified, swollen, typically recurved, with densely set long setules in distal half). Endopod 1-segmented, with 1 short and 2 long pinnate setae. Exopod 4-segmented, armature formula [1,1,1,1].

Labium (Figs. 28B; 29A) a membranous lobe derived by fusion of paired paragnaths; closely adpressed to labrum forming oral cone; with few spinules around tip.

Maxillule (Fig. 29B). Praecoxa with elongate, narrow arthrite produced into spinous process at distal outer corner (= incorporated spine) and bearing 3 spiniform and 4 setiform elements, all closely adpressed; with 2 tubular seta anteriorly and proximal spinule patch posteriorly; outer margin of syncoxa with 2 spinulose bulges. Coxa with cylindrical endite bearing 2 pinnate setae subdistally and apical armature consisting of 1 geniculate and 3 bare setae. Basis with 2 widely separated endites; proximal endite with 1 minute, 1 bare and 1 pinnate seta, distal endite with 1 geniculate and 1 bare seta. Exopod very large cylindrical segment, with spinule rows as figured in Fig. 29B; with 4 setae apically. Endopod a small segment with 3 setae (1 minute).

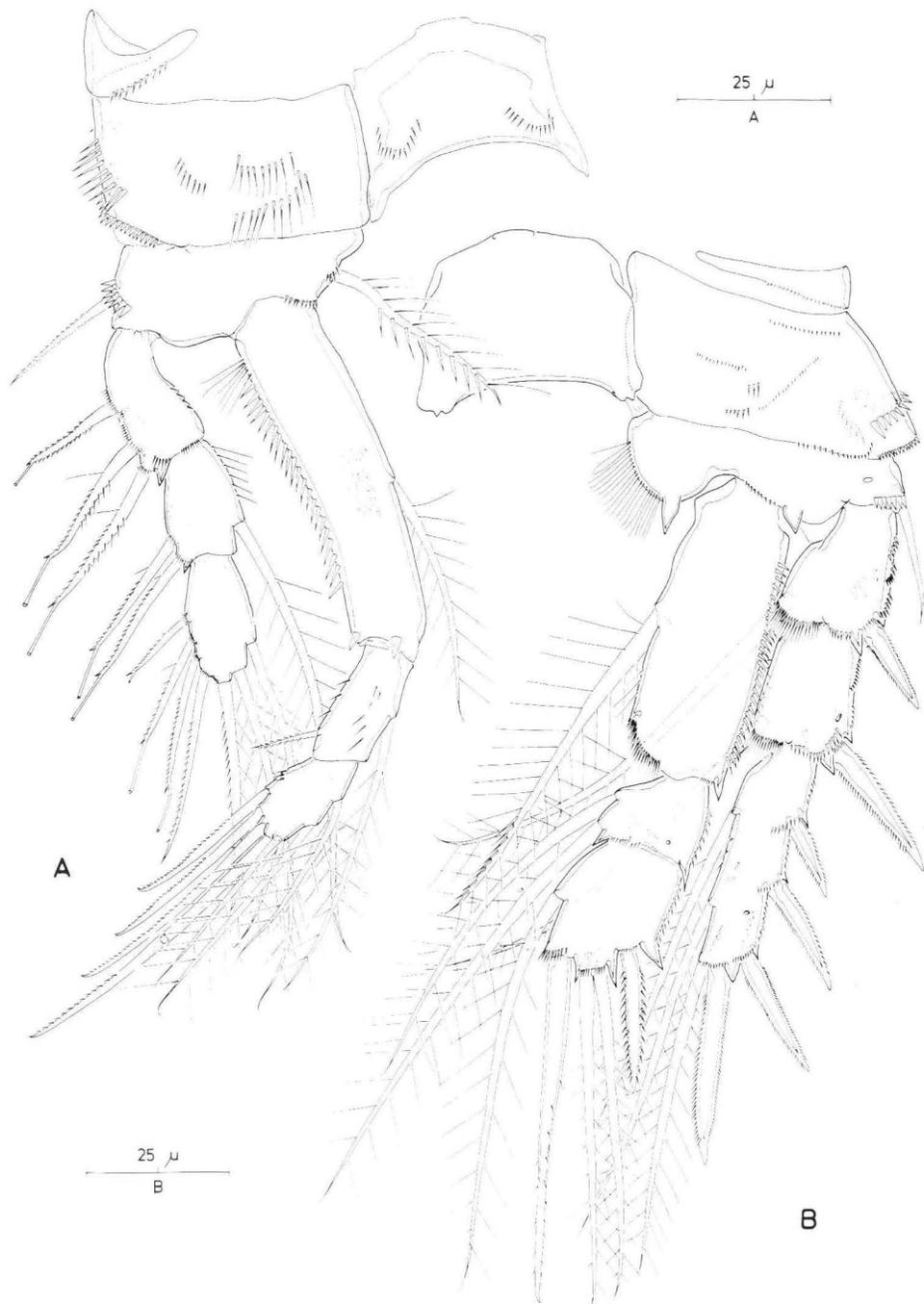


FIG. 30. – *Intercrusia problematica* sp. nov.: A. P1, anterior; B. P2, anterior.

Maxilla (Fig. 29C). Syncoxa with 1 well developed endite with 1 apically serrate, 1 long naked and 1 vestigial seta. Allobasis drawn out into long claw bearing fine spinules towards the tip; with 1 pinnate and 1 smooth seta at base. Endopod incorporated into allobasis, represented by membranous area with 1 plumose, 1 long and 1 vestigial bare seta. Fine spinules present on allobasis and along outer margin of syncoxa.

Maxilliped subchelate (Fig. 29D). Syncoxa and basis with complex pattern of spinule rows on anterior and posterior surfaces as figured. Basis with short naked seta. Endopod represented by elongate segment drawn out subdistally into long pinnate claw accompanied at base by 2 short outer setae and 1 long pinnate seta along the medial margin; distal portion of endopod forming cylindrical pedestal with 2 juxtaposed, geniculate setae.

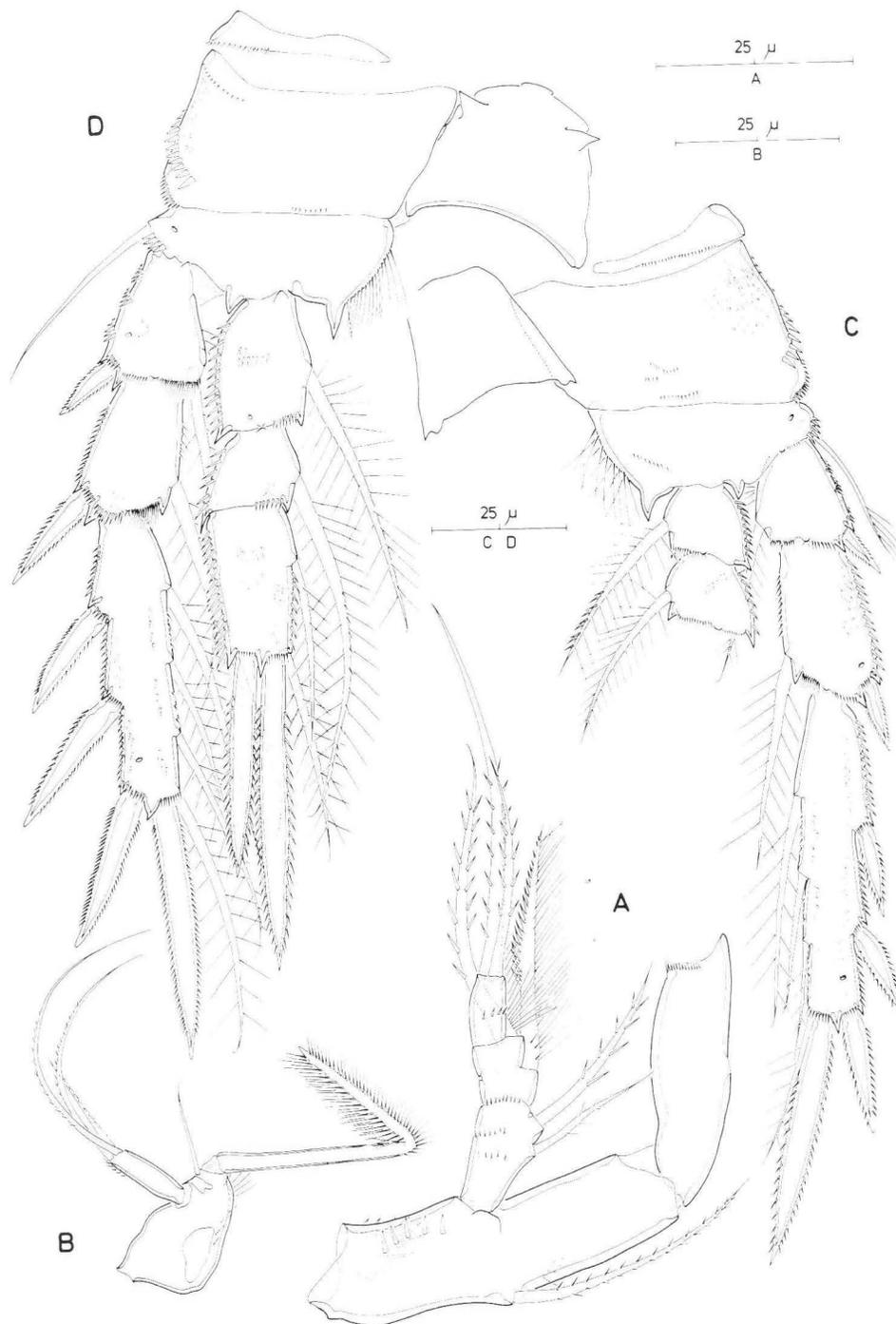


FIG. 31. — *Intercrusia problematica* sp. nov.: A. Antenna (coxa and armature of endopod omitted); B. Mandibular palp (exopod omitted, indicated by stippled area); C. P3, anterior (enp-3 omitted); D. P4, anterior.

P1 (Fig. 30A) with well developed praecoxa. Intercoxal sclerite with spinule rows. Coxa with complex pattern of spinules and long setules as figured. Basis with bipinnate outer seta bearing; inner spine slightly curved, with fine setules along inner and coarse spinules along outer margin. Exopod with slender outer spines, some with long setules

proximally and except for distalmost of exp-3 all with long subapical tubular extensions; exp-2 with long plumose inner seta; exp-3 with 5 slender spines and 2 plumose setae. Enp-1 with continuous outer spinule row; inner seta arising from point slightly distal to midpoint of inner margin; posterior setule patch located at insertion level of inner seta.

P2-P4 (Figs. 30B; 31C-D) with 3-segmented rami (except P2 endopod); endopod slightly longer (P2) or distinctly shorter (P3-P4) than exopod. Inner margin of bases with long setules and produced into spinous process. Outer basal seta smooth (P2, P4) or sparsely plumose (P3). All exopod and endopod segments with fine spinules along outer margins and around bases of outer and distal armature elements; frills between segments well developed. Exopodal spines finely pinnate Exp-3 as long or longer than exp-1 and -2 combined. Anterior face of segments with virtually no surface ornamentation but with scattered spinules on posterior face as figured.

P2 (Fig. 30B). Intercoxal sclerite without anterior spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Endopod 2-segmented with incomplete frill, anterior furrow and marginal processes marking fusion plane between enp-2 and enp-3. Enp-1 elongate, longer than distal segment; inner seta plumose with spinules along distal inner margin. Distal compound segment with 3 plumose inner setae, 1 bipinnate inner spine, 2 plumose setae distally and pinnate spine at outer distal corner; outer subdistal corner produced into recurved spinous process.

P3 (Fig. 31C). Intercoxal sclerite without anterior spinule rows. Exp-1 with posterior vent pore associated with coarse spinules. Exp-3 with 3 inner plumose setae decreasing in size distally. Endopod 3-segmented; enp-1 inner seta plumose with spinules along distal inner margin.

P4 (Fig. 31D). Intercoxal sclerite without ornamentation. Inner margin armature of exp-3 consisting of 3 plumose setae. Endopod 3-segmented, distinctly shorter than exopod. Inner seta of enp-1 plumose without coarse spinules along distal inner margin. Enp-3 with 1 plumose inner seta, 1 plumose seta and 1 long spine apically and long pinnate spine at outer distal corner; spines of enp-3 markedly swollen.

Armature formula as follows:

Leg	Coxa	Basis	Exopod	Endopod
P1	0-0	1-1	III-0;II-1;7	0-1;I-1;2,2,3
P2	0-0	1-0	1-1;I-1;III.I+1,2	0-1;[0-2;1,2,I+1]
P3	0-0	1-0	1-1;I-1;III.I+1,3	0-1;0-1;1,2,I+2
P4	0-0	1-0	1-1;I-1;III.I+1,3	0-1;0-1;I,I+1,1

P5 (Fig. 28D) biramous. Baseoendopod incorporated into somite; represented by outer lobe bearing basal sparsely plumose seta, and vestigial endopodal lobe carrying 2 pinnate setae. Exopod elongate; about 4 times as long as maximum width; anterior

surface with several spinule rows as figured; spinules also present around bases of apical and outer elements; armature consisting of 1 inner, 1 long apical and 3 outer bare setae.

Genital field positioned in anterior third of genital double-somite (Fig. 27B). Gonopores paired, laterally displaced, separated (Fig. 27C); each covered by genital operculum derived from vestigial sixth legs. P6 with 1 long inner and 1 shorter outer bare seta. Copulatory pore small and circular (arrowed in Fig. 27C), covered anteriorly by narrow, deeply incised, hyaline epicopulatory flap derived from an outgrowth of the ventral somite wall; leading via paired chitinized copulatory ducts to median transversely elongated seminal receptacle.

Egg sac(s) not observed.

Male unknown.

Remarks: Species of Superornatiremidae are extremely conservative morphologically. The stunning similarity between species and even genera reminds of the sibling species problem encountered in the genus *Tisbe* Lilljeborg in the Tisbidae (Volkmann-Rocco, 1971) - a closely related family. Males of *Neoechinophora* and *Superornatiremis* can be readily distinguished by the segmentation and shape of the fifth leg, but only relatively few characters can be applied to separate the corresponding females (\*except for the number of elements on the distal exopod segment of P1). In the absence of the male, the taxonomic position of *I. problematica* is therefore difficult to assess. It is similar to species belonging to *Neoechinophora* in the presence of only 1 outer element on the middle endopod segment of P1, however in all other aspects it is more closely related to *Superornatiremis*. This is illustrated by the shape of the epicopulatory flap, the presence of subapical tubular extensions on the exopodal spines of leg 1, and the very short caudal rami. The first two characters are particularly constant in all 4 species of *Neoechinophora* described thus far and inclusion of *I. problematica* on the sole basis of P1 endopod setation would unnecessarily blur the generic boundaries of this genus. The alternative option is to include *I. problematica* in *Superornatiremis* but this would remove the presence of 2 outer spines on P1 enp-2 as a diagnostic character of this genus. The discovery of a second as yet undescribed species of *Superornatiremis* in the Mediterranean, however, revealed this feature to be constant. Inclusion of *I. problematica* as a terminal branch in *Superornatiremis* as a result of character reversal on P1 enp-2 is

regarded unlikely (see discussion). Pending the discovery of the male the species is provisionally placed in a genus by itself which holds an intermediate position between *Neoechinophora* and *Superornatiremis*.

The presence of only one endite on the maxillary syncoxa of *I. problematica* (Fig. 29C) is probably an artefact arising from imperfect dissection. The membranous area corresponding with the position of the proximal trilobate endite in other genera was slightly folded on both sides making it impossible to decide whether a scar was present or not. In the light of the tremendous consistency in mouthpart structure observed in the family the absence of this endite would require confirmation and consequently this feature has not been used in the generic diagnosis nor in the key to genera below.

A unique character of *I. problematica* is the presence of paired dorsolateral tufts on the genital double-somite of the female.

#### KEY TO GENERA

1. P1 exp-3 with 7 elements; P1 outer spines with subapical tubular extensions; epicopulatory flap deeply incised and bifid.....2.
- P1 exp-3 with 6 element; P1 outer spines without subapical tubular extensions; epicopulatory flap broadly rounded, not incised; P5 ♂ without endopodal lobe, with 2-segmented exopod; P1 enp-2 with 1 outer element.....*Neoechinophora* gen. nov.
2. P1 enp-2 with 2 outer elements; P5 ♂ with endopodal lobe represented by 1 seta, with 1-segmented exopod  
    *Superornatiremis* gen. nov.
- P1 enp-2 with 1 outer element; P5 ♂ unknown.....*Intercrusia* gen. nov.

#### DISCUSSION

##### Morphology

The Superornatiremidae exhibit the most remarkable P1 in the whole of the Copepoda. All three genera possess several atypical setation elements on both rami of the first swimming legs. The proximal exopodal segment bears 3 spines on the outer margin and the middle segment bears 2 outer spines. Either 1 (*Neoechinophora*, *Intercrusia*) or 2 (*Superornatiremis*) setae are present on the outer margin of the middle endopodal segment and 2 setae are present on the outer margin of the distal endopodal segment.

No other copepods display more than 2 spines on the outer margin of exp-1 or more than 1 spine on the outer margin of exp-2. No other copepods possess any armature elements at all on the outer margin of enp-2 and no other copepods possess more than 1 seta on the outer margin of the distal exopodal segment of the first swimming leg. Huys and Boxshall (1991) regarded all of these supernumerary elements as novel. Within the Harpacticoida secondary multiplication of armature elements is further only known for three species of the interstitial genus *Scottopsyllus* Kunz (Paramesochridae). In *S. robertsoni* (T. and A. Scott), *S. pararobertsoni* Lang and *S. langi* Mielke a total of 5 setae is present at the inner angle of the basis of the first swimming leg. An apparently similar condition exists in the cyclopinid *Muceddina multispinosa* Jaume and Boxshall, however, scrupulous examination of the extra elements revealed that they are spinous outgrowths of the inner basal margin and thus forming part of the ornamentation rather than the armature (Jaume and Boxshall, 1996b). There is no doubt that the supernumerary spines in Superornatiremidae represent genuine armature elements. For example, the three outer spines on exp-1 are morphologically identical in so far that it is impossible to identify the homologue of the single outer spine found on this segment in other harpacticoids. Each is articulated at the base (Fig. 15D) inserting into a hole passing through the integument, each has a hollow axial core and all are surrounded at the base by spinules and are indistinguishable in their ornamentation, even not in *Superornatiremis* and *Intercrusia* where the spines are equipped with subapical tubular extensions.

Huys and Boxshall (1991) pointed out the uncertainty about the swimming leg spine and seta formula attributed to the exopods of P2-P5 of the ancestral copepod. In Platycopeioida 2 outer spines are found on the proximal exopod segment on legs 2 to 5 of *Platycopeia* Sars and *Antriscopia* Fosshagen but only on legs 2 and 3 of *Nanocopia* Fosshagen. Application of the general oligomerization principle would imply that the 2-spined condition is the plesiomorphic state which is retained only in platycopoids and that the 1-spined condition is apomorphic for all other copepods. There are several reports in the literature (T. Scott, 1894; Fosshagen and Iliffe, 1985; Ohtsuka *et al.*, 1994) of aberrant calanoids exhibiting 2 outer spines on the first exopodal segment. The fact that it is the same segment on the same leg which carries the extra spine in *Pseudocyclopia crassicornis* T. Scott, *Paracyclopia*

*naessi* and *Crassarietellus huysi* Ohtsuka, Boxshall and Roe and that all of these species belong to primitive families, Pseudocyclopiidae and Arietellidae, is remarkable. A possible explanation could be that the plesiomorphic 2-spined state retained from the ancestral copepod stock is the result of a developmental process that has persisted only in the Platycopeioida but was genetically repressed in the calanoid (or possibly neocopepodan) ancestor and only accidentally expressed in aberrant specimens. This hypothesis is not in conflict with the oligomerization principle but would require tremendous elaboration to explain the origin of the superornatiremid armature formula. The Superornatiremidae is a relatively highly advanced family in the harpacticoids and the increase in number of elements is - in the absence of similar evidence in other copepods, aberrant or normal - regarded as a secondary phenomenon. The exopodal formula is constant within the family but the number of outer elements on P1 enp-2 is either 1 or 2. The polarity in character state change is impossible to assess and examination of the only copepodid V of *N. daltonae* proved uninformative since it had already the full complement of elements. It is assumed here that the 2-spined condition in *Superornatiremis* is the apomorphic state, i.e. the superornatiremid ancestor had only 1 outer spine on this segment and a further extra element was added in this genus. Evidence for the more advanced position of *Superornatiremis* is also apparent in the structure of the male P5 and the modification of the supernumerary spines on the P1 exopod. It is on the basis of this assumption that *I. problematica* is maintained as the type species of a transitional but distinct genus rather than as an advanced species of *Superornatiremis* which during the evolution of the genus has secondarily lost the extra outer spine on P1 enp-2. The discovery of the unknown male of *I. problematica* will shed more light on the real taxonomic status of this species.

The female genital field is highly distinctive in superornatiremids. The paired gonopores are separate and typically displaced to a ventrolateral position so that the armature of the vestigial sixth legs is visible in dorsal aspect. The copulatory pore leads via short paired copulatory ducts to a median seminal receptacle which is transversely elongate. In all species the copulatory pore is partly or almost completely concealed under a hyaline extension of the ventral body wall, the epicopulatory flap. The flap originates anterior to the level of the gonopores and extends posteriorly into a semicircular or W-shaped membranous plate. The flap is highly transparent,

usually being closely adpressed to the somite wall, and can only be discerned using differential interference contrast microscopy. Huys (1990) discussed the presence of similar structures overlying the copulatory pore of female Hamondiidae and Ambunguipedidae. The genital complex in these families has a distinctly swollen, ovoid structure, located midventrally in a pronounced depression of the genital double-somite and overlying the anterior half of the minute copulatory pore. This epicopulatory bulb is partly covered by a small medially incised epicopulatory plate and probably serves as a surface against which the anterior face of the spermatophore is cemented during copulation (Huys, 1990). It is unlikely that the epicopulatory flap in superornatiremids serves such a purpose. In other tsiidimorph families the gonopores are not laterally displaced but are medially fused forming a common transverse genital slit, the copulatory pore is not concealed beneath a flap and leads via a single duct to the seminal receptacle.

As far as can be ascertained from the published anatomical information, Superornatiremidae are unique among harpacticoids by the presence of a genuine oral cone. The possession of a stylet-like mandible typically contained within an oral cone formed by the labrum and the medially fused paragnaths (the labium) is a diagnostic ordinal character for the Siphonostomatoida (Boxshall, 1986; Huys and Boxshall, 1991). The oral cone in the Superornatiremidae is derived in the same way and is very similar to that of *Asterocheres*, a primitive representative of the Siphonostomatoida (see Boxshall, 1990 for description). It comprises an anterior lip (labrum) and a posterior lip (labium; derived from the fused paired paragnaths) which are produced together into a tapering conical structure that opens distally (Fig. 15B). The labrum is broad at the base, which usually has an anterior patch of spinules (Fig. 28C), and tapers into an apical process which is fringed with apical spinules (Fig. 15A). The labium is narrower and closely adpressed to the posterior face of the labrum (Fig. 28B). The mandibles are stylet-like (particularly in *Neoechinophora* and *Intercrusia*) and enter the oral cone laterally via the slits between the labrum and the labium (Figs. 28B; 29A). They are guided by weakly developed ridges of the labrum and labium which are discernible from the outside of these lips (Figs. 28B; 29A). Both lips are held together along their lengths by partial fusion of the inner sides below the point of entrance of the gnathobases (Fig. 29A). The biramous mandibular palp is laterally directed and pos-

sesses a large modified seta on the basis which is typically recurved midway its axis (Figs. 2A; 18B; 31B) and presumably performs a sensory role. In whole specimens the maxillules and maxillae are also closely associated with the oral cone (Fig. 19A). The close similarity in oral cone morphology between the Superornatiremidae and primitive siphonostome families such as the Asterocheridae and Dirivultidae is clearly the result of convergence but might suggest a similar feeding mode. Marcotte (1977) described the functional morphology and feeding behaviour of *Tisbe furcata* (Baird) in great detail but overlooked or did not consider the paragnaths in his study. It is possible that the labium (if present) in *Tisbe* and related genera is closely adpressed to the labrum and therefore remained unnoticed thus far in taxonomic descriptions. In *Tisbe* the labrum, mandibular gnathobases and maxillules are elongated and project ventrally as a conical structure which resembles the oral cone in primitive siphonostomatoids. It was this similarity that led Marcotte (1986) to suggest that the Siphonostomatoida probably evolved directly from a *Tisbe*-like harpacticoid ancestor. Such an evolutionary scenario is highly unlikely (Huys and Boxshall, 1991), however, it is possible that the oral cone is a synapomorphy linking the Superornatiremidae to the Tisbinae. Confirmation of the labium in the more primitive bathypelagic genera such as *Bathyidia* Farran and *Volkmannia* Boxshall is required first before such a relationship can be corroborated. It is noteworthy that one of the tisbidimorph branches has led to the Cholidiinae, a subfamily of harpacticoid genera all associated with deep-sea octopuses. It is one of the few lineages in the Harpacticoida that can be regarded as truly parasitic and coincidentally has evolved from a *Tisbe*-like ancestor. The Rotundiclipeidae, also described from anchihaline caves, display a similar arrangement of the mouthparts, have stylet-like mandibles and a labrum that closely resembles the tisbidimorph one in form and shape. The phylogenetic position of the Rotundiclipeidae, currently accommodated in the Cervinioidea (Huys, 1988), might well need reconsideration in the light of the present findings.

### Phylogenetic considerations

Superornatiremids exhibit few primitive characters. Noteworthy are the complete absence of sexual dimorphism on the swimming legs and the 2-segmented P5 exopod retained in the males of *Neoechinophora* (unknown in *Interkrusia*). The lat-

ter character is of particular interest since very few families have retained traces of exopodal segmentation in the male fifth legs. A 3-segmented exopod is exhibited by species of the genera *Eucanuella* T. Scott (Cerviniidae) and *Parastenhelia* Thompson and A. Scott (Parastenheliidae). The further derived 2-segmented condition is found in some Neobradyidae and various representatives of *Idyanthe* Sars (Tisbidae), *Chappuisius* Kiefer (Chappuisiidae), *Tetragoniceps* Brady and *Paraschizopera* Wells (Tetragonicipitidae).

Unique apomorphies for the new family are (1) the medial fusion of the paired paragnaths forming a labium and the presence of an oral cone (possibly shared with the Tisbinae), (2) the modified trilobate proximal endite of the maxillary syncoxa which is provided with a medially directed barbed lobe, (3) the supernumerary armature elements of P1, (4) modification of P2 endopod into a possibly prehensile ramus, (5) transformation of the distal inner seta of P2-P3 enp-3 into a pinnate spine [a similar modification is found on the P2 of *Tachidiopsis cyclopoidea* Sars], (6) presence of epicopulatory flap, (7) paired copulatory ducts and laterally displaced gonopores.

The general body shape, detailed structure of the mouthparts and the morphology of the fifth and sixth legs clearly indicate an affinity with the tisbidimorph families. Several of these families, including the Tisbidae are in an urgent need of revision. A phylogenetic analysis of the Tisboidea (Tisbidimorpha *sensu* Lang (1948)) is beyond the scope of this paper and will have to await the description of another anchihaline family with tisbidimorph affinities discovered in Belize (Huys and Iliffe, in prep.). It is clear however, that the Superornatiremidae occupy an intermediate position between the two free-living tisbid subfamilies, Tisbinae and Idyanthinae, suggesting that the latter should be attributed familial status.

### Biogeographical notes

The Superornatiremidae, with records in Bermuda and the Canary Islands, is another example to be added to the long list of stygobiont taxa assuming a covariant Amphi-Atlantic distribution pattern. This "generalized tract" (*sensu* Croizat) is reinforced by several unpublished records of the family from Belize and the Bahamas (Eleuthera) based on material collected by T.M. Iliffe (Huys and Iliffe, in prep.). Moreover, the recent discovery of Superornatiremidae in the Balearic Islands (D.

Jaume, pers. comm) gives evidence of an Amphiatlantic/Mediterranean distribution pattern as found for various other stygobionts such as *Stygiomysis* (Mysidacea) and *Pseudoniphargus* (Amphipoda), and the copepod genera *Speleophriopsis* Jaume and Boxshall and *Exumella* Fosshagen (Stock, 1993; Jaume and Boxshall, 1995b, 1996c). Examination of extensive collections from different cave types on various Indo-Pacific oceanic island groups such as Hawaii, the Philippines and the Palau archipelago failed to produce any superornatiremids. It is therefore likely that the family is absent from the Indo Pacific and does not assume a circum-tropical distribution, i.e. in the entire region of the former Tethys Sea.

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## REFERENCES

- Barr, D.J. – 1984. *Enantiosis cavernicola*, a new genus and species of demersal copepod (Calanoida: Epacteriscidae) from San Salvador Island, Bahamas. *Proc. Biol. Soc. Wash.*, 97: 160-166.
- Boxshall, G.A. – 1986. Phylogeny of Mormonilloida and Siphonostomatoida. *Syllogeus*, 58: 173-176.
- Boxshall, G.A. – 1990. The skeletomusculature of siphonostomatoid copepods, with an analysis of adaptive radiation in structure of the oral cone. *Phil. Trans. R. Soc. London*, B328: 167-212.
- Boxshall, G.A. and R. Huys. – 1989. New tantulocarid, *Srygotantulus stocki*, parasitic on harpacticoid copepods, with an analysis of the phylogenetic relationships within the Maxillopoda. *J. Crust. Biol.*, 9(1): 126-140.
- Boxshall, G.A. and T.M. Iliffe. – 1986. New cave-dwelling misophrioids (Crustacea: Copepoda) from Bermuda. *Sarsia*, 71: 55-64.
- Boxshall, G.A. and T.M. Iliffe. – 1987. Three new genera and five new species of misophrioid copepods (Crustacea) from anchialine caves on Indo-West Pacific and North Atlantic Islands. *Zool. J. Linn. Soc.*, 91: 223-252.
- Boxshall, G.A. and T.M. Iliffe. – 1990. Three new species of misophrioid copepods from oceanic islands. *J. nat. Hist.*, 24: 595-613.
- Fosshagen, A. and T.M. Iliffe. – 1985. Two new genera of Calanoida and a new order of Copepoda, Platycopioida, from marine caves on Bermuda. *Sarsia*, 70: 345-358.
- Fosshagen, A. and T.M. Iliffe. – 1988. A new genus of Platycopioida (Copepoda) from a marine cave on Bermuda. *Hydrobiologia*, 167/168: 357-361.
- Fosshagen, A. and T.M. Iliffe. – 1989. *Boholina*, a new genus (Copepoda: Calanoida) with two new species from an anchialine cave in the Philippines. *Sarsia*, 74: 201-208.
- Fosshagen, A. and T.M. Iliffe. – 1991. A new genus of calanoid copepod from an anchialine cave in Belize. In: Uye, S.-i., S. Nishida and J.-s. Ho (eds.): *Proceedings of the Fourth International Conference on Copepoda, Karuizawa, Japan, 16-20 September 1990*, *Bull. Plankton Soc. Japan, Spec. Vol. (1991)*, pp. 339-346.
- Fosshagen, A. and T.M. Iliffe. – 1994. A new species of *Erebionectes* (Copepoda, Calanoida) from marine caves on Caicos Islands, West Indies. *Hydrobiologia*, 292/293: 17-22.
- Hart, C.W.Jr. and R.B. Manning – 1981. The cavernicolous caridean shrimps of Bermuda (Alpheidae, Hippolytidae and Atyidae). *J. Crust. Biol.*, 1: 441-456.
- Huys, R. – 1988. Rotundilipeidae fam. nov. (Copepoda, Harpacticoida) from an anchialine cave on Tenerife, Canary Islands. *Stygofauna of the Canary Islands*, 10. *Stygologia*, 4: 42-63.
- Huys, R. – 1990. A new harpacticoid copepod family collected from Australian sponges and the status of the subfamily Rhynchothalestrinae Lang. *Zool. J. Linn. Soc.*, 99: 51-115.
- Huys, R. and G.A. Boxshall. – 1991. *Copepod Evolution*, pp. 468. The Ray Society, London.
- Huys, R., J.M. Gee, C.G. Moore and R. Hamond. – 1996. *Marine and Brackish Water Harpacticoid Copepods: Part I*. Synopses of the British Fauna (New Series), No. 51. Field Studies Council.
- Jaume, D. and G.A. Boxshall. – 1995a. *Stygocyclopiopsis balearica*, a new genus and species of calanoid copepod (Pseudocyclopiidae) from anchialine caves in the Balearic Islands (Mediterranean). *Sarsia*, 80: 213-222.
- Jaume, D. and G.A. Boxshall. – 1995b. A new species of *Exumella* (Copepoda: Calanoida: Ridgewayiidae) from anchialine caves in the Mediterranean. *Sarsia*, 80: 93-105.
- Jaume, D. and G.A. Boxshall. – 1996a. A new genus and two new species of cave-dwelling misophrioid copepods from the Balearic Islands (Mediterranean). *J. nat. Hist.*, 30: 989-1006.
- Jaume, D. and G.A. Boxshall. – 1996b. Two new genera of cyclopinid copepods (Crustacea) from anchialine caves on western Mediterranean and eastern Atlantic islands. *Zool. J. Linn. Soc.*, 117: 283-304.
- Jaume, D. and G.A. Boxshall. – 1996c. The persistence of an ancient marine fauna in Mediterranean waters: new evidence from misophrioid copepods living in anchialine caves. *J. nat. Hist.*, 30: 1583-1595.
- Jaume, D. and G.A. Boxshall. – in press. Two new genera of cyclopinid copepods (Cyclopoida: Cyclopinidae) from anchialine caves of the Canary and Balearic Islands, with a key to genera of the family. *Zool. J. Linn. Soc.*, in press.
- Kornicker, L.S. and T.M. Iliffe. – 1989. Ostracoda (Myodocopina, Cladocopina, Halocypridina) mainly from anchialine caves in Bermuda. *Smiths. Contr. Zool.*, 475: i-iv, 1-88.
- Lang, K. – 1948. *Monographie der Harpacticiden*, pp. 1682. Håkan Ohlsson, Lund.
- Marcotte, B.M. – 1977. An introduction to the architecture and kinematics of harpacticoid (Copepoda) feeding: *Tisbe furcata* (Baird, 1837). *Mikrofauna Meeresboden*, 61: 183-196.
- Marcotte, B.M. – 1986. Phylogeny of the Copepoda Harpacticoida. *Syllogeus*, 58: 186-190.
- Ohtsuka, S., G.A. Boxshall and H.S.J. Roe. – 1994. Phylogenetic relationships between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera. *Bull. nat. Hist. Mus. Lond. (Zool.)*, 60: 105-172.
- Ohtsuka, S., A. Fosshagen and T.M. Iliffe. – 1993. Two new species of *Paramisophria* (Copepoda, Calanoida, Arietellidae) from anchialine caves on the Canary and Galapagos Islands. *Sarsia*, 78: 57-67.
- Rocha, C.E.F. da and T.M. Iliffe. – 1993. New cyclopoids (Copepoda) from anchialine caves in Bermuda. *Sarsia*, 78: 43-56.
- Scott, T. – 1894. Report on Entomostraca from the Gulf of Guinea. *Trans. Linn. Soc. London*, ser. 2, 6: 1-161.
- Sket, B. and T.M. Iliffe. – 1980. Cave fauna of Bermuda. *Int. Rev. ges. Hydrobiol.*, 65: 871-882.
- Stock, J.H. – 1993. Some remarkable distribution patterns in stygobiont Amphipoda. *J. nat. Hist.*, 27: 807-819.
- Volkman-Rocco, B. – 1971. Some critical remarks on the taxonomy of *Tisbe* (Copepoda, Harpacticoida). *Crustaceana*, 21: 127-132.
- Wilkens, H. and J. Parzefall. – 1974. Die Ökologie der Jameos del Agua (Lanzarote). Zur Entwicklung limnischer Höhlentiere aus marinen Vorfahren. *Ann. Spéléol.*, 29: 419-434.
- Yeatman, H.C. – 1980. *Miostephus leamingtonensis*, a new species of copepod from Bermuda. *J. Tenn. Acad. Sci.*, 55: 20-21.

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