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# ZOOTAXA

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## **Copepods (Cyclopoida) associated with ascidian hosts: Ascidicolidae, Buproridae, Botryllophilidae, and Enteropsidae, with descriptions of 84 new species**

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**COPEPODS (CYCLOPOIDA) ASSOCIATED WITH ASCIDIAN HOSTS: ASCIDICOLIDAE,  
BUPRORIDAE, BOTRYLLOPHILIDAE, AND ENTEROPSIDAE, WITH DESCRIPTIONS OF 84  
NEW SPECIES**

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## Abstract

The Monniot collection of copepods associated with ascidian hosts was built up over several decades of field collecting and taxonomic research on ascidians by Drs Claude & Françoise Monniot (MNHN, Paris). This paper describes a total of 84 new species of copepods collected from ascidian hosts and five new genera are established. Prior to this study the family Ascidicolidae comprised two genera accommodating five valid species; here we add two new genera, *Hamistyelicola* **gen. nov.** and *Bathycopola* **gen. nov.**, and eight new species in total. The family Buproridae comprised a single genus consisting of three species; here we add a new monotypic genus, *Buprorides* **gen. nov.** The family Botryllophilidae comprised 68 valid species in seven genera and here we add 45 new species; 13 of *Botryllophilus* Hesse, 1864, nine of *Schizoproctus* Aurivillius, 1885, three of *Haplostomides* Chatton & Harant, 1924, 12 of *Haplostoma* Chatton & Harant, 1924, seven of *Haplostomella* Chatton & Harant, 1924 and a single new species of *Haplosaccus* Chatton & Harant, 1924. The Enteropsidae comprised 42 species in five genera and here we add two new genera, *Monnioticopa* **gen. nov.** and *Periboia* **gen. nov.**, plus a total of 30 new species; 15 of *Enterocola* van Beneden, 1860, two of *Enterocolides* Chatton & Harant, 1922, five of *Enteropsis* C.W.S. Aurivillius, 1885, five of *Monnioticopa* **gen. nov.**, two of *Mychophilus* Hesse, 1865, plus the type species of *Periboia* **gen. nov.** Generic diagnoses are provided for all genera represented in the collection. A further 13 known species are also reported and brief supplementary descriptive notes or full redescrptions are provided, as appropriate.

**Keywords:** taxonomy, new species, ascidian hosts, symbiotic copepods

## Introduction

Copepods are common associates of both solitary and colonial ascidians and several families within the order Cyclopoida either exclusively or predominantly use ascidians as hosts (Boxshall & Halsey, 2004). The most species rich family, the Notodelphyidae, and the closely related family Archinotodelphyidae have been the subject of recent major studies (Kim & Boxshall, 2020a, 2020b). Together, these two studies described 15 new species of archinotodelphyids and 178 new species of notodelphyids, all from the Monniot collection of copepods housed at the Museum National d'Histoire Naturelle in Paris. The present account represents the third paper based the Monniot collection. It covers four cyclopoid families, the Ascidicolidae, Botryllophilidae, Buproridae, and Enteropsidae, all of which comprise taxa that are exclusively associated with ascidian hosts. New taxa are described within all of these families.

## Material and Methods

The specimens examined in this study were collected by Claude and Françoise Monniot (Museum National d'Histoire Naturelle, Paris) during several decades of field collecting and distinguished systematic research on ascidians. The copepods were extracted from hosts collected during research campaigns undertaken all over the world and then stored in the MNHN collections. The host ascidians were initially fixed in seawater-formalin, and the copepods, once extracted, were preserved in 70-80% ethanol. Prior to microscopic observation, the copepods were immersed in lactic acid for at least 10 minutes and then dissected. Dissected appendages were observed using the reverse slide method of Humes & Gooding (1964). Drawings were made with the aid of a microscope equipped with a drawing apparatus. Lengths of copepod specimens and measurements of appendages are mostly based on a single dissected specimen of each species. Body lengths were measured along the middle axis of body. The lengths of the appendage segments are given as the average of the longest and shortest margins. Type specimens have been deposited in the Museum National d'Histoire Naturelle, Paris; copepod registration numbers have the prefix MNHN-IU. Host names were provided by Claude and Françoise Monniot and have been cross checked against those in the World Register of Marine Species (WoRMS Editorial Board, 2020). Some individual ascidian hosts are stored in the MNHN, Paris and their registration numbers have the prefix MNHN-IT. The morphological terminology for the copepods follows Huys & Boxshall (1991).

## Systematics

### Family Ascidicolidae Thorell, 1859

**Diagnosis** (female). Body cylindrical. Prosome 5-segmented, consisting of cephalosome and 4-segmented metasome. Urosome 5- or 6-segmented, with 3- or 4-segmented abdomen. Fifth pedigerous somite obscurely defined. Caudal rami usually small, armed with 5 or 6 setae. Rostrum not developed. Antennule small, 5- to 8-segmented; aesthetascs small. Antenna consisting of coxobasis and 2-segmented endopod, or 4-segmented including obscurely defined coxa, basis bearing 1 spine distally; distinct flexure present between basis and first endopodal segment; second endopodal segment bearing terminal claw. Labrum broad, bearing 1 or 2 dentiform processes at posterolateral corners. Mandible consisting of coxa and palp; coxa with well-developed gnathobase bearing irregular denticles on medial margin; palp uniramous, or biramous with well-defined basis, exopod and endopod. Maxillule consisting of precoxa and palp; precoxa bearing 7 to 9 setal elements on arthrite; palp uniramous or biramous; coxal endite present or absent. Maxilla 2- to 4-segmented; syncoxa (first segment) with 2 endites each bearing 1 seta, or 1 endite bearing 2 or 3 setae, or endites absent; basis with strong claw in addition to setae, or with setae only; endopod reduced, 1- or 2-segmented; in *Ascidicola* and *Styelicola* basis and endopod completely fused to form allobasis. Maxilliped unsegmented and unarmed, or armed with 1 to 7 setae. Legs 1-4 broad, biramous; coxa usually lacking inner seta; basis of leg 1 with or without inner distal spine; exopods 2-segmented; endopods mostly 2-segmented. First endopodal segment of legs 1 and 2 always lacking inner seta. Exopods and endopods of legs 1-4 usually armed with spines only. Leg 5 large, lamellate, bearing rudimentary setae, or consisting of lamellate protopod bearing outer distal seta and setiferous exopod. Leg 6 represented by 3 dentiform processes on genital operculum.

**Remarks.** Thorell (1859) first established the Ascidicolinae as a subfamily of the family Notodelphyidae in order to accommodate his new genus *Ascidicola* Thorell, 1859. As highlighted by Illg & Dudley (1980), it was treated both as a subfamily and as a family level taxon throughout the late nineteenth and the twentieth centuries. Its composition has varied over this period but it gradually expanded until it contained a total of seven main component taxa, each of which was recognized as a subfamily of the family Ascidicolidae by Illg & Dudley (1980) in their comprehensive revision. The seven subfamilies were: the Ascidicolinae, Buprorinae Thorell, 1859, Botryllophyliinae Sars, 1921, Enterocolinae Della Valle, 1883, Enterognathinae Illg & Dudley, 1980, Enteropsinae Aurivillius, 1885, and Haplostominae Chatton & Harant, 1924. The Enterognathidae was treated as a separate family by Boxshall & Halsey (2004) and Ohtsuka et al. (2010), and comprises associates of echinoderm and hemichordate hosts. It is not considered further here. Subsequent revision of the remaining six subfamilies resulted in the recognition of four valid family level taxa (see Boxshall & Halsey, 2004).

Illg & Dudley (1980) retained only two genera, *Ascidicola* and *Styelicola* Lützen, 1968, in their subfamily Ascidicolinae which was subsequently returned to family status, as the Ascidicolidae by Boxshall & Halsey (2004). Two new genera *Hamistyelicola* **gen. nov.** and *Bathycopola* **gen. nov.** are added to the family in the present work. All species currently placed in this family were found living in association with solitary ascidians.

In the genera *Styelicola*, *Hamistyelicola* **gen. nov.** and *Bathycopola* **gen. nov.**, leg 5 consists of a lamellate protopod and a small, setiferous distal segment. This distal segment was recognized as the endopod by Lützen (1968) and by Illg & Dudley (1980), but Boxshall & Halsey (2004) re-interpreted it as representing the exopod. The four genera of the Ascidicolidae are distinguishable using the following key.

### Key to genera of the Ascidicolidae

1. Second exopodal segment of legs 2-4 transformed to large hook ..... *Hamistyelicola* **gen. nov.**  
Second exopodal segment of legs 2-4 not transformed ..... 2
2. Caudal ramus armed with spines and setae; maxilla 3- or 4-segmented ..... *Bathycopola* **gen. nov.**  
Caudal ramus armed with setae only; maxilla 2-segmented ..... 3
3. Leg 5 consisting of lamellate protopod and small, setiferous exopod; endopods of legs 1-4 unarmed or armed only with spines; second segment (first endopodal segment) of antenna unarmed ..... *Styelicola*  
Leg 5 consisting only of lamellate protopod; endopods of legs 1-4 with extremely elongate setae; second segment (first endopodal segment) of antenna armed with 1 seta ..... *Ascidicola*

## Genus *Ascidicola* Thorell, 1859

**Diagnosis** (female). Body elongate, cylindrical, with indistinct prosome-urosome division. Prosome 5-segmented, shorter than urosome. Urosome 5-segmented. Ventral spinose pad (remnant of penultimate abdominal somite of copepodid V) present or absent between last 2 abdominal somites. Caudal ramus with 5 or 6 setae. Rostrum not developed. Antennule short, 5-segmented; first segment with 4 or 5 setae. Antenna 3-segmented, consisting of coxobasis and 2-segmented endopod tipped with claw; armed with 1, 1, and 4 to 6 armature elements on first to third segments, respectively. Labrum with pair of tooth-like processes on each posterolateral corner. Mandible consisting of coxa and palp; palp 1-segmented, but articulated from segment-like extension of coxa, armed with 5 setae. Maxillule consisting of precoxa and palp; precoxa with 8 elements on arthrite; palp with 7 or 8 elements. Maxilla consisting of syncoxa and allobasis (fused basis and endopod); syncoxa bearing single endite tipped with 2 setae; allobasis terminated in claw-like process and armed with 7 or 8 setae. Maxilliped unsegmented, armed with 2 to 5 setae. Legs 1-4 biramous with 2-segmented exopods and endopods; inner coxal seta absent; outer seta on basis large. Basis of leg 1 bearing inner distal spine. Inner setae on endopods large, armed as follows: 1 seta on first segment of legs 3 and 4; 1, 3, 3, and 2 setae on second segment of legs 1-4, respectively; setal pattern constant but number of spines on rami variable depending on species. Leg 5 lamellate, covering fifth pedigerous and genital somites, armed with 3 minute, vestigial setae. Leg 6 absent.

**Type species.** *Ascidicola rosea* Thorell, 1859 by original monotypy.

**Remarks.** The genus *Ascidicola* currently comprises only two species, *A. rosea* and *A. secunda* Kim I.H. & Moon, 2011, but in the present work two new species are added. Within the genus, the armature of legs 1-4 seems to be a reliable character for species discrimination, since it appears to be variable between species but consistent within any given species. The four known species can be distinguished using the following key.

### Key to species of *Ascidicola*

1. Second exopodal segment of legs 1 and 2 bearing 7 spines ..... 2  
Second exopodal segment of legs 1 and 2 bearing 5 and 4 spines, respectively ..... 3
2. Second exopodal segment of leg 3 with 6 spines; second endopodal segment of leg 4 with 3 spines; caudal ramus about 3.9 times longer than wide ..... *A. rosea*  
Second exopodal segment of leg 3 with 7 spines; second endopodal segment of leg 4 with 2 spines; caudal ramus about 2.5 times longer than wide ..... *A. antarctica* sp. nov.
3. Second endopodal segment of leg 1 armed with 3 spines; second endopodal segment of leg 3 armed with 2 spines ..... *A. secunda*  
Second endopodal segment of leg 1 armed with 2 spines; second endopodal segment of leg 3 with 3 spines ..... *A. philippinensis* sp. nov.

### *Ascidicola rosea* Thorell, 1859

(Fig. 1)

**Material examined.** 1 ♀ (MNHN-IU-2018-1924) from *Ascidia mentula* Müller, 1776; Kristineberg, Sweden, Monniot coll., 1962.

2 ♀♀ (MNHN-IU-2018-1925) from *Ascidia obliqua* Alder, 1863; Kristineberg, Sweden, Monniot coll., 1962;

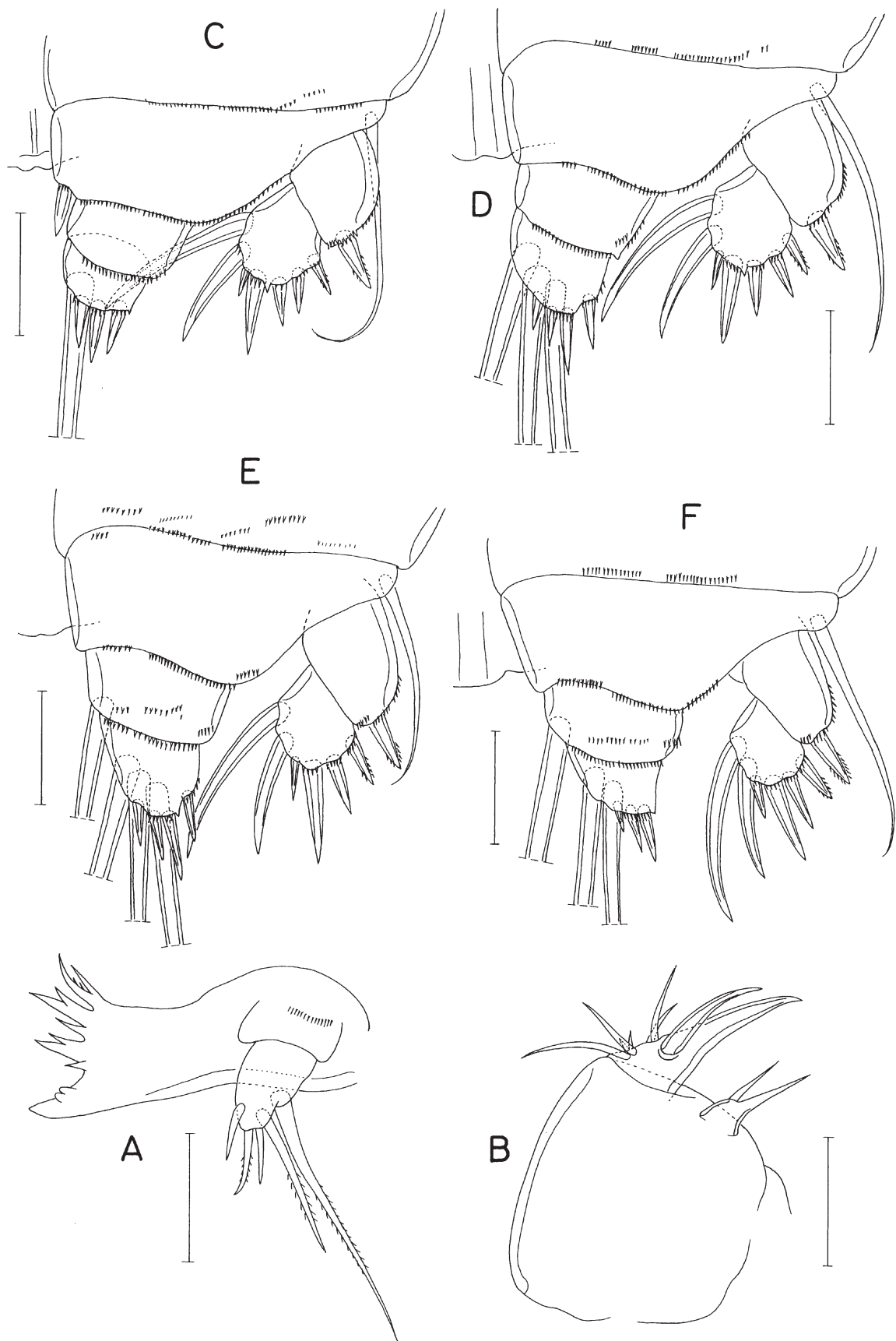
2 ♀♀ (MNHN-IU-2018-1926) from *A. obliqua* Kristineberg, Sweden, Monniot coll., 1962.

3 ♀♀ (MNHN-IU-2018-1927) from *Ascidella aspersa* (Müller, 1776), Banyuls, Mediterranean coast of France;

1 ♀ (MNHN-IU-2018-1928) from *A. aspersa*, North Sea (56°39.9'N, 01°10.1'W), depth 89 m; 1 ♀ (MNHN-IU-2018-1929) from *A. aspersa*, Mediterranean Sea off Corsica, MEDITS 2016 cruise, RV "L'Europe", Stn M16-2 (43°20.98'N, 4°19.64'E), depth 32-33 m, 31 May 2016.

2 ♀♀ (MNHN-IU-2018-1930) from *Ascidella scabra* (Müller, 1776); Kristineberg, Sweden, Monniot coll., 1962.

1 ♀ (MNHN-IU-2018-1931) from *Corella eumyota* Traustedt, 1882; Port Le Havre, Atlantic coast of France, collected by G. Breton, 2008.



**FIG. 1.** *Ascidicola rosea* Thorell, 1859, female. A, mandible; B, maxilla; C, leg 1; D, leg 2; E, leg 3; F, leg 4. Scale bars: 0.05 mm.



2 ♀♀ (MNHN-IU-2018-1932) from *Corella parallelogramma* (Müller, 1776); Kristineberg, Sweden, Monniot coll., 1962.

1 ♀ (MNHN-IU-2018-1933) from *Herdmania momus* (Savigny, 1816); Red Sea, collected in 19<sup>th</sup> Century.

1 ♀ (MNHN-IU-2018-1934) from *Microcosmus claudicans* (Savigny, 1816); Roscoff, Atlantic coast of France, Monniot coll.

8 ♀♀ (MNHN-IU-2018-1935) from *Microcosmus sabatieri* Roule, 1885; Banyuls, Mediterranean coast of France; 25 ♀♀ (MNHN-IU-2018-1936) (1 ♀ dissected and figured) from *M. sabatieri*; Banyuls, Mediterranean coast of France.

8 ♀♀ (MNHN-IU-2018-1937) from *Microcosmus vulgaris* Heller, 1877; Banyuls, Mediterranean coast of France; 1 ♀ (MNHN-IU-2018-1938) from *M. vulgaris*; Naples, Italy.

1 ♀ (MNHN-IU-2018-1939) from *Phallusia mammillata* (Cuvier, 1815); Banyuls, Mediterranean coast of France.

1 ♀ (MNHN-IU-2018-1940) from *Styela canopus* (Savigny, 1816); Mediterranean Sea, Île Grosse, Banyuls, collected by trawl.

**Supplementary description of female.** Body length 3.70 mm. Ventral spinose pad between 2 last abdominal somites variously developed, sometimes absent. Caudal ramus about 3.9 times longer than wide (236×60 µm); armed with 5 setae (1 lateral and 4 distal), lateral seta positioned at 42% of ramus length.

Antennule, antenna, maxillule, and maxilliped as described by Ooishi (2007a). Mandible (Fig. 1A) consisting of coxa and reduced palp; palp 1-segmented, but articulated from unarmed, pedestal-like extension of coxa; free segment of palp armed with 5 setae. Maxilla (Fig. 1B) consisting of syncoxa and allobasis; syncoxa bearing 1 endite tipped with 2 setae; proximal seta on endite not articulated at base; allobasis with unarmed inner margin, terminating in claw-like process; armed with 1 spine on anterior surface plus 6 setae (4 proximal and 2 sub-proximal) on outer (ventral) margin; Leg 6 represented by 2 small setae and 4 small teeth on genital operculum. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0;	1-I	I-0; III, I, III	0-0; 0, III, 1
Leg 2	0-0	1-0	I-0; III, I, III	0-0; I, III, 3
Leg 3	0-0	1-0	I-0; II, I, III	0-1; I, III, 3
Leg 4	0-0	1-0	I-0; II, I, III	0-1; 0, III, 2

**Remarks.** Ooishi (2007a) thoroughly redescribed *Ascidicola rosea*. This distinctive species occurs widely in the North and South Atlantic and along the Pacific coast of North America (Boxshall & Halsey, 2004). Boxshall & Halsey (2004) listed 25 species of solitary ascidians previously recorded as hosts of *A. rosea*. Ooishi (2007a) recorded an additional species, *Ascidia mentula*, as host of this copepod, and here we add three more new host species: *Ascidiella scabra* from the Swedish coast, *Styela canopus* from the Mediterranean, and *Herdmania momus* from the Red Sea. Our observations of the *A. rosea* material listed above revealed a constant armature formula for legs 1-4; no variation was noted either with host or with locality. The identification of all the above specimens was confirmed by *in situ* observation of the leg armature.

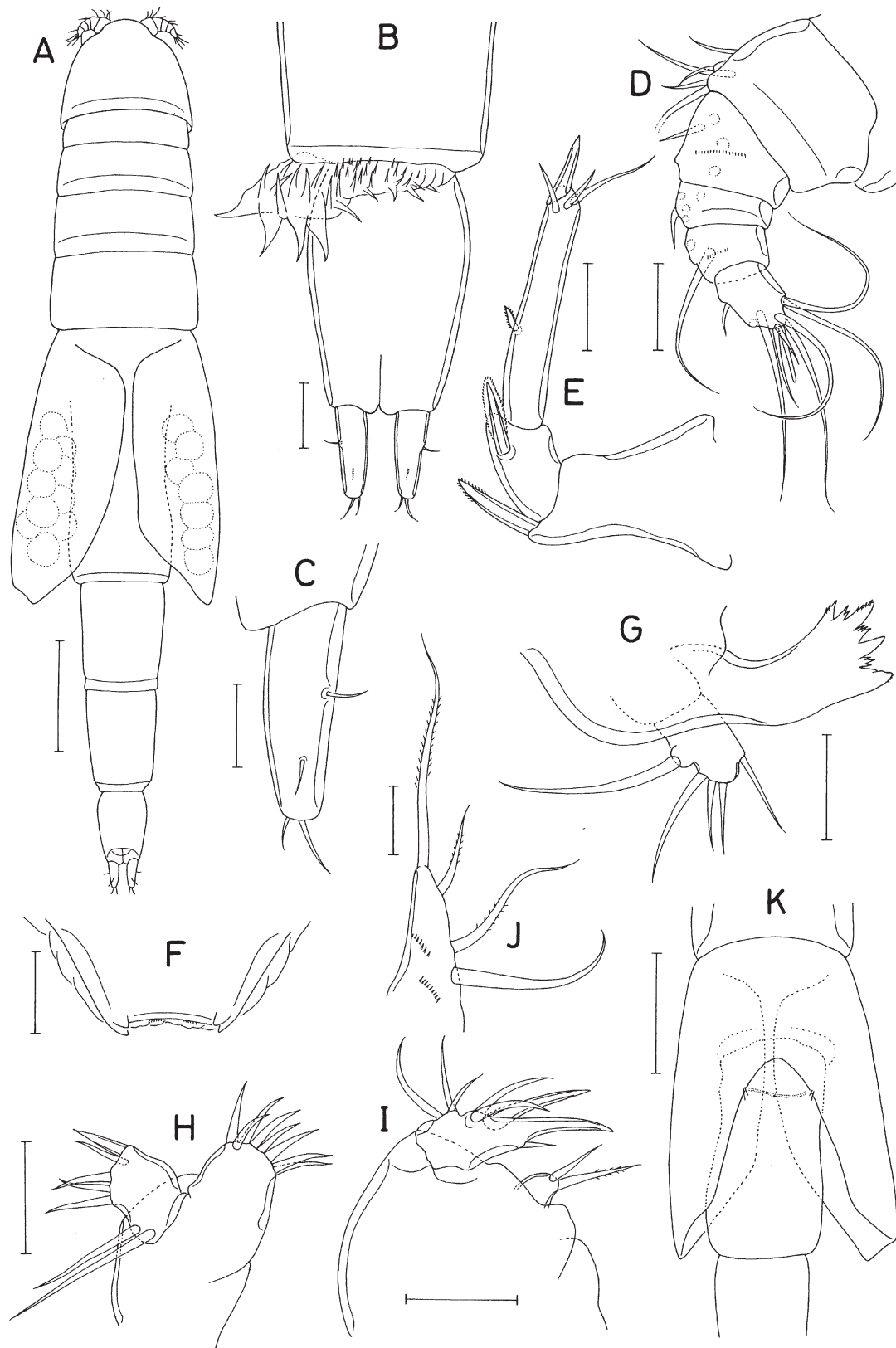
### *Ascidicola secunda* Kim I.H. & Moon, 2011

(Figs. 2, 3)

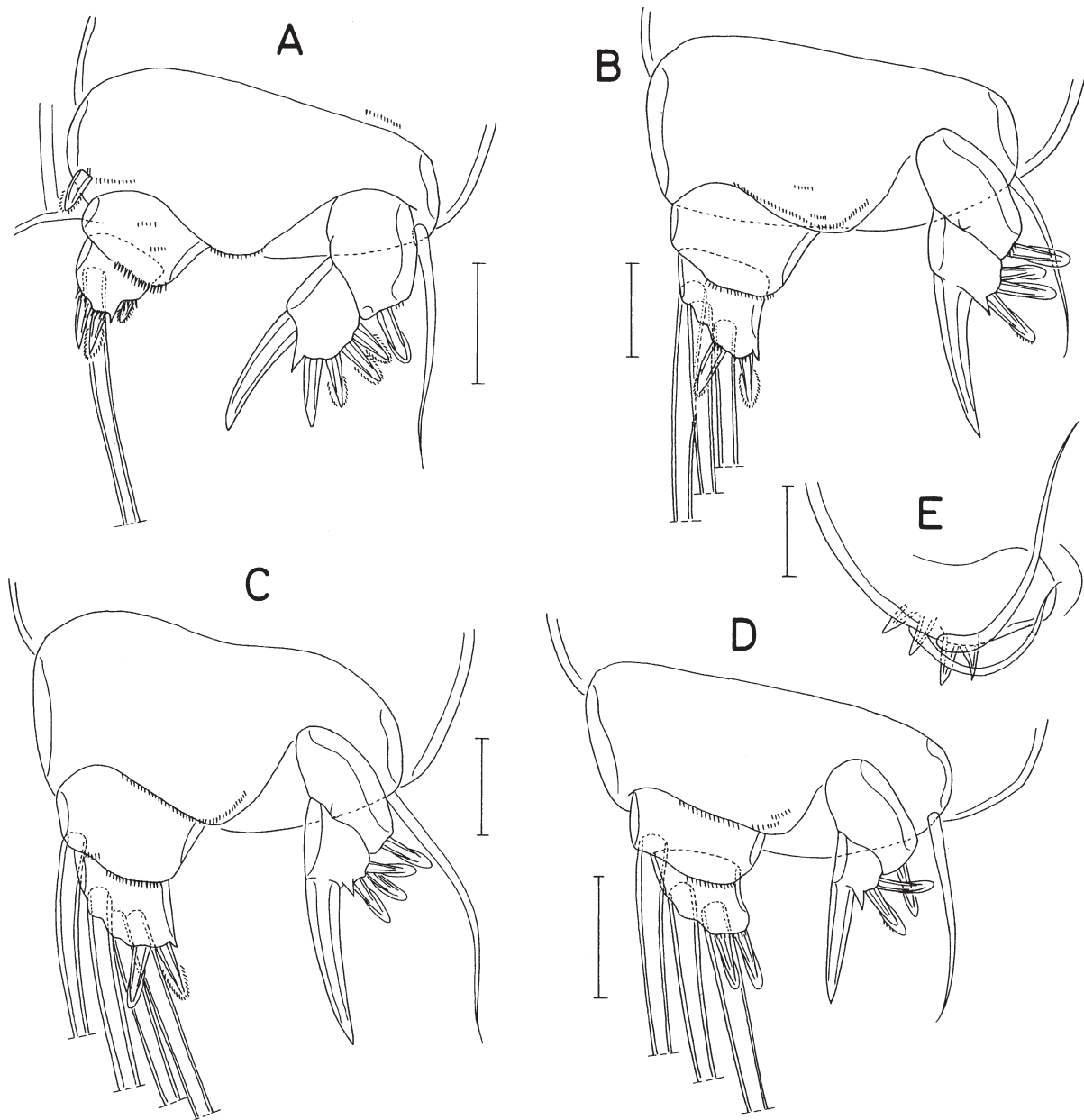
**Material examined.** 1 ♀ (MNHN-IU-2014-17361, dissected) in *Polycarpa papillata* (Sluiter, 1886); New Caledonia.

**Supplementary description of female.** Body (Fig. 2A) elongate, cylindrical, clearly segmented; prosome-urosome division indistinct; body length 3.94 mm. Prosome 1.41 mm long, occupying about 36% of body length, consisting of cephalosome and 4 pedigerous somites. Cephalosome 409×600 µm; pedigerous somites becoming gradually longer and wider from first to fourth. Urosome 5-segmented; fifth pedigerous somite and genital somite obscurely defined from each other; both 950×480 µm. Three free abdominal somites 518×400, 455×318, and 349×236 µm, respectively. Spinose pad ornamented with various sizes of spinules present ventrally between last 2

abdominal somites (Fig. 2B). Anal somite (Fig. 2B) about 1.5 times longer than wide. Caudal ramus (Fig. 2C) 2.82 times longer than wide ( $127 \times 45 \mu\text{m}$ ), 36% as long as anal somite, armed with 1 lateral, 1 subdistal dorsal, and probably 4 distal setae (2 of distal setae missing in Fig. 2A–C); lateral seta positioned at 43% length of caudal ramus.



**FIG. 2.** *Ascidicola secunda* Kim I.H. & Moon, 2011, female. A, habitus, dorsal; B, distal part of urosome, ventral; C, right caudal ramus, dorsal; D, antennule; E, antenna; F, labrum; G, mandible; H, maxillule; I, maxilla; J, maxilliped; K, leg 5 and genital somite, ventral. Scale bars: A, K, 0.5 mm; B, 0.1 mm; C–I, 0.05 mm; J, 0.02 mm.



**FIG. 3.** *Ascidicola secunda* Kim I.H. & Moon, 2011, female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 6. Scale bars: A-D, 0.05 mm; E, 0.02 mm.

Rostrum absent. Antennule (Fig. 2D) short, 184  $\mu\text{m}$  long, curved posteriorly, 5-segmented; first segment bearing 5 setae; numbers of setae on other segments uncertain due to loss of some setae. Antenna (Fig. 2E) 3-segmented, consisting of coxobasis and 2-segmented endopod; coxobasis narrowing distally, armed with 1 spine (52  $\mu\text{m}$  long) distally; short first endopodal segment with 1 spine (45  $\mu\text{m}$  long) subdistally; second endopodal segment elongate, 5.07 times longer than wide (137 $\times$ 27  $\mu\text{m}$ ), armed with 1 small spine (15  $\mu\text{m}$  long) near proximal third and 3 setae subdistally, and terminating in small, straight claw (40  $\mu\text{m}$  long).

Labrum (Fig. 2F) wider than long, fringed with hyaline covering along lateral margin, and with 2 tooth-like processes at each posterolateral corner. Mandible (Fig. 2G) consisting of coxa and palp; coxa with well-developed gnathobase bearing 3 major and 4 minor teeth on medial margin; minor teeth serrate at tip; palp 1-segmented, articulated from pedestal-like extension of coxa, armed with 5 setae (outer proximal seta distinctly larger than other setae). Maxillule (Fig. 1H) consisting of precoxa and palp; precoxa bearing 8 naked setae on arthrite; palp not divided, slightly longer than wide, armed with 7 setae (2 longer outer proximal, 3 subdistal, and 2 distal, with inner distal seta spiniform). Maxilla (Fig. 2I) 2-segmented; broad first segment (syncoxa) with lobate endite tipped with 2

setae; second segment (allobasis) terminating in spiniform process, armed with 1 spine and 5 setae on outer margin and 1 small seta on inner margin. Maxilliped (Fig. 2J) unsegmented, elongate, armed with 4 setae (1 apical and 3 medial), and ornamented with 2 rows of minute spinules.

Legs 1-4 (Fig. 3A-D) biramous with 2-segmented rami; coxa and basis broad; inner coxal seta absent; first exopodal segment lacking inner seta; inner setae on endopods large. Distal spine on second exopodal segment of legs 1-4 claw-like, indistinctly articulated from second exopodal segment. First endopodal segment of legs 3 and 4 bearing inner seta, but that of legs 1 and 2 lacking inner seta. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; IV, I, 0	0-0; I, II, 1
Leg 2	0-0	1-0	I-0; III, I, 0	0-0; 0, II, 3
Leg 3	0-0	1-0	I-0; III, I, 0	0-1; 0, II, 3
Leg 4	0-0	1-0	I-0; II, I, 0	0-1; 0, II, 2

Leg 5 (Fig. 2K) skirt-like, encircling first 2 urosomites, bearing 2 minute vestigial setae on proximal ventral margin (Fig. 2K); left and right legs 5 fused proximally on ventral side but separate dorsally. Leg 6 (Fig. 3E) represented by 2 large setae and 4 spiniform processes on genital operculum.

**Male.** Unknown.

**Remarks.** This species was described from Korean waters (Kim I.H. & Moon, 2011). The caudal ramus of the single female specimen from New Caledonia examined here is distinctly smaller than that of type specimens, only 2.82 times longer than wide ( $127 \times 45 \mu\text{m}$ ) compared to 4.23 times longer than wide ( $338 \times 80 \mu\text{m}$ ) in the type specimens, and 0.36 times as long as anal somite compared to 0.76 times as long in the type material. This difference in the dimension of the caudal ramus is tentatively interpreted here as intraspecific variation because no other significant difference was observed between the types and the New Caledonian material. Material from both locations exhibits the identical armature of the mouthparts and legs 1-4.

***Ascidicola philippinensis* sp. nov.**

(Figs. 4, 5)

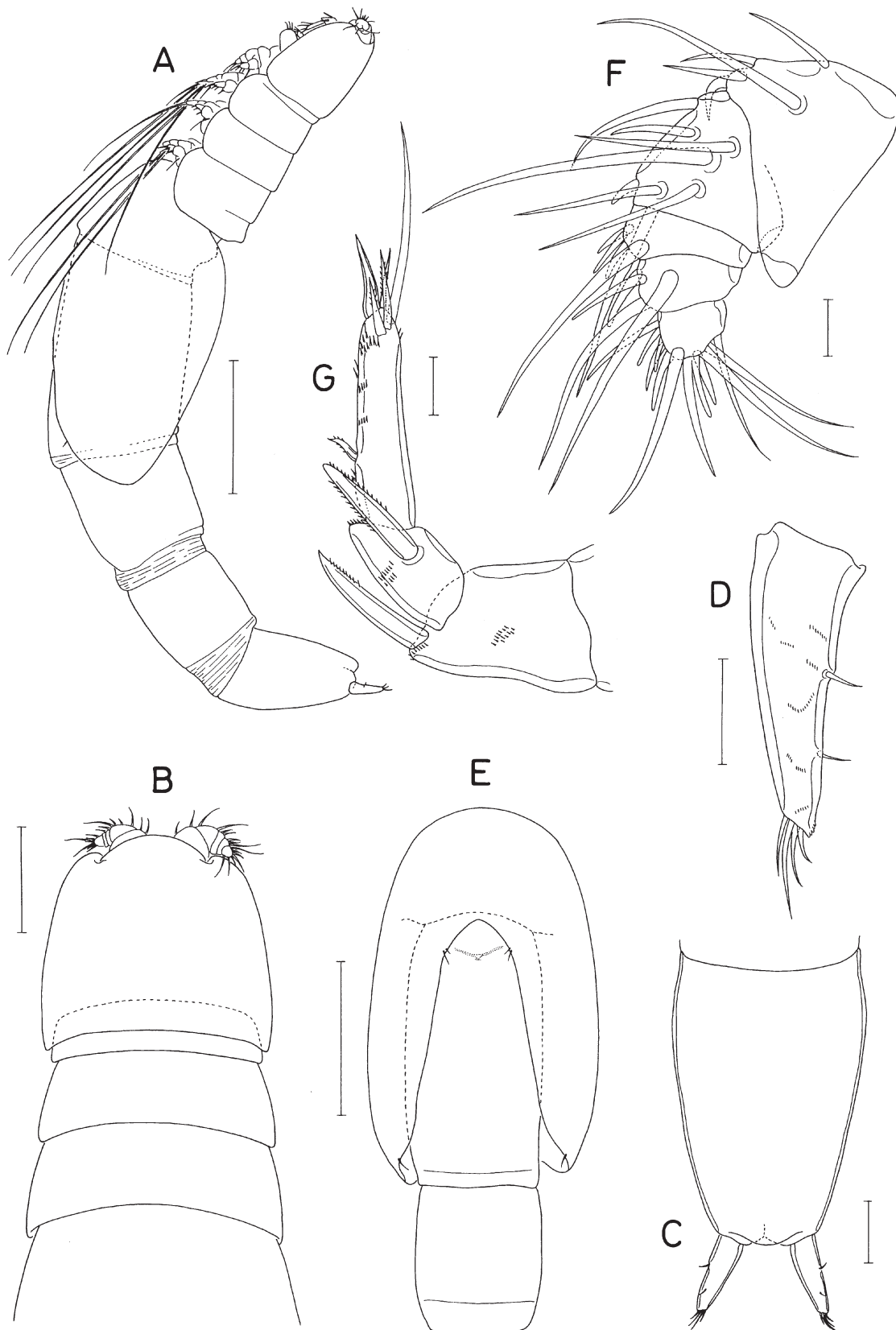
**Type material.** Holotype ♀ (MNHN-IU-2018-1941, dissected and mounted on a slide) from *Pterygascidia longa* (Van Name, 1918); The Philippines, MUSORSTOM 3 cruise, RV “Coriolis”, Stn CP131 (11°27'N, 121°43'E), depth 120-122 m, Bouchet & Triclot-MNHN coll., 05 June 1985.

**Etymology.** The name of this new species is based on the type locality.

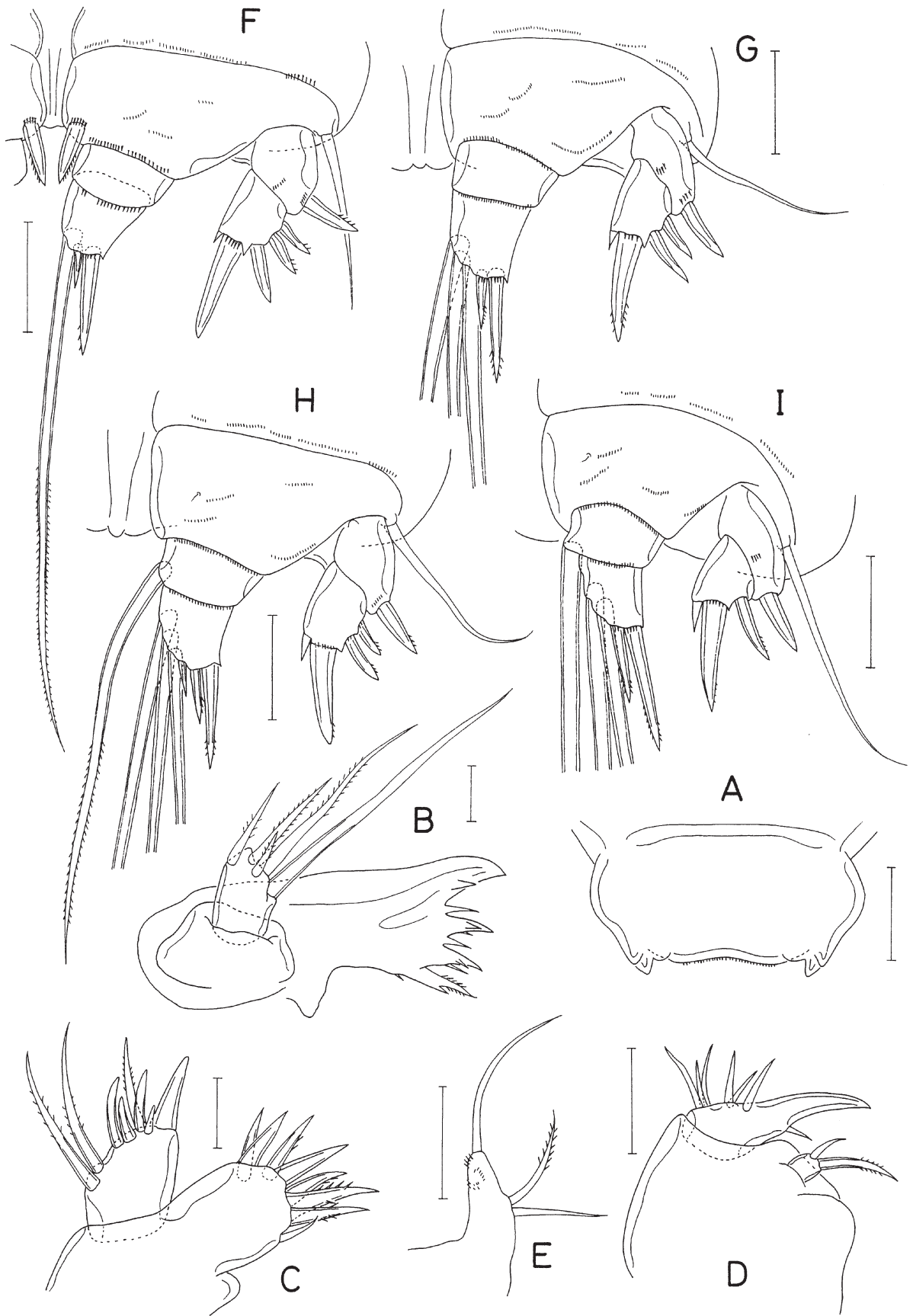
**Description of female.** Body (Fig. 4A) elongate, body shape and segmentation as in type species, *A. rosea*. Body length 3.40 mm. Prosome (Fig. 4B) slightly depressed dorsoventrally, about 1.0 mm long, occupying 29% of body length. Cephalosome  $369 \times 438 \mu\text{m}$ , with rounded anterior margin; first to fourth pedigerous somites  $92 \times 400$ ,  $138 \times 446$ ,  $154 \times 488$ , and  $230 \times 378 \mu\text{m}$ , respectively. Urosome 5-segmented, curved dorsally; genital somite about  $860 \mu\text{m}$  long (average of longer ventral and shorter dorsal margins); copulatory pore positioned on ventral surface at anterior 17% of somite length. First and second abdominal somites  $470$  and  $446 \mu\text{m}$  long, respectively; anal somite (Fig. 4C) slightly tapering, about 1.5 times longer than wide ( $477 \times 315 \mu\text{m}$ ), widest anterior 20% of somite length; anal operculum broad. Spinose pad lacking between second abdominal and anal somites. Caudal ramus (Fig. 4D) tapering, 2.76 times longer than wide ( $149 \times 54 \mu\text{m}$ ), 31% as long as anal somite, armed with 6 small setae and ornamented with several rows of minute spinules; all caudal setae shorter than proximal width of ramus; lateral and subdistal dorsal setae positioned at 42% and 70% of ramus length, respectively.

Rostrum absent. Antennule (Fig. 4F) short,  $138 \mu\text{m}$  long, 5-segmented; all segments wider than long; armature formula 5, 8, 4, 4, and 12; setae naked and of different lengths, some of shorter, blunt setae aesthetasc-like. Antenna (Fig. 4G) 3-segmented, consisting of coxobasis and 2-segmented endopod; coxobasis slightly longer than wide ( $54 \times 46 \mu\text{m}$ ), bearing 1 strong spine ( $50 \mu\text{m}$  long) distally; first endopodal segment  $35 \times 25 \mu\text{m}$ , bearing 1 strong spine ( $46 \mu\text{m}$  long) subdistally; second endopodal segment gradually narrowing distally, 1.90 times long than wide

(78×20 μm), terminating in slender claw (28 μm long); armed with 1 small spine proximally and 4 setae distally (one 73 μm long, much longer than other 3).



**FIG. 4.** *Ascidicola philippinensis* sp. nov., female. A, habitus, left; B, anterior part of prosome, dorsal; C, anal somite and caudal rami, dorsal; D, right caudal ramus, dorsal; E, anterior part of urosome, ventral; F, antennule; G, antenna. Scale bars: A, E, 0.5 mm; B, D, 0.2 mm; C, 0.1 mm; F, G, 0.02 mm.



**FIG. 5.** *Ascidicola philippinensis* sp. nov., female. A, labrum; B, mandible; C, maxillule; D, maxilla; E, maxilliped; F, leg 1; G, leg 2; H, leg 3; I, leg 4. Scale bars: A, D-I, 0.05 mm; B, C, 0.02 mm.

Labrum (Fig. 5A) broad, with 2 dentiform processes at each posterolateral corner and row of minute spinules along posterior margin. Mandible (Fig. 5B) consisting of coxa and palp: coxal gnathobase broadened, medial margin bearing strong tooth distally, 3 larger and 3 smaller teeth; larger teeth bearing 1 or 2 subsidiary denticles; palp 1-segmented, articulated with broad, pedestal-like extension of coxa, armed with 5 unequal setae, largest seta (on medial margin) 110 µm long. Maxillule (Fig. 5C) consisting of precoxa and palp; precoxa with medially extended arthrite bearing 7 spines and 1 small proximal seta; palp distinctly articulated from precoxa, bearing 8 elements (5 unequal spines and 3 setae). Maxilla (Fig. 5D) consisting of syncoxa and allbasis; syncoxa broad, bearing 1 endite tipped with 2 setae (proximal seta larger and spiniform); allbasis terminating in claw-like process, bearing 6 setae on outer margin and 1 small seta on inner margin. Maxilliped (Fig. 5E) slender, digitiform, bearing 1 apical and 2 medial setae; ornamented with fine spinules distally.

Legs 1-4 (Fig. 5F-I) biramous with 2-segmented rami; coxa unarmed; intercoxal sclerite narrow; setae on endopods large and stiff, as usual for genus. Leg 1 with inner distal seta on basis 28 µm long, longer than first endopodal segment. Medial of 2 distal spines on second exopodal segment of legs 1-4 denticle-like, much smaller than outer spine but distinctly articulated at base. First endopodal segment unarmed in legs 1 and 2, but with inner seta in legs 3 and 4. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; III, II, 0	0-0; 0, II, 1
Leg 2	0-0	1-0	I-0; II, II, 0	0-0; 0, II, 3
Leg 3	0-0	1-0	I-0; II, II, 0	0-1; 0, III, 3
Leg 4	0-0	1-0	I-0; I, II, 0	0-1; 0, II, 2

Leg 5 (Fig. 4E) lamellate, encircling fifth pedigerous and genital somites, extending to posterior margin of genital somite, bearing 3 minute setules (2 ventro-proximal and 1 ventro-distal); left and right legs separated from each other on dorsal side, but fused proximally on ventral side. Leg 6 not examined.

**Male.** Unknown.

**Remarks.** *Ascidicola philippinensis* **sp. nov.** differs from *A. rosea*, *A. secunda*, and *A. antarctica* **sp. nov.** described below in having 2 spines + 1 seta on the second endopodal segment of leg 1 (in contrast to 3 spines + 1 seta in all three congeneric species) and 3 spines + 3 setae on the second endopodal segment of leg 3 (in contrast to 2 spines + 3 setae in *A. secunda* and 4 spines + 3 setae in the other two congeners). The numbers of spines on the second exopodal segments of legs 1-4 of the new species are same as in *A. secunda*, but the shape and arrangement of the spines are quite different between the two species: there are fewer spines on the outer margin of the segment in *A. philippinensis* **sp. nov.** and it lacks the small, dentiform inner distal spine that is present on this segment in *A. secunda*. The possession of 3 setae on the maxilliped is an additional difference between *A. philippinensis* **sp. nov.** and both *A. rosea* and *A. secunda* which have 5 and 4 setae, respectively, on the maxilliped.

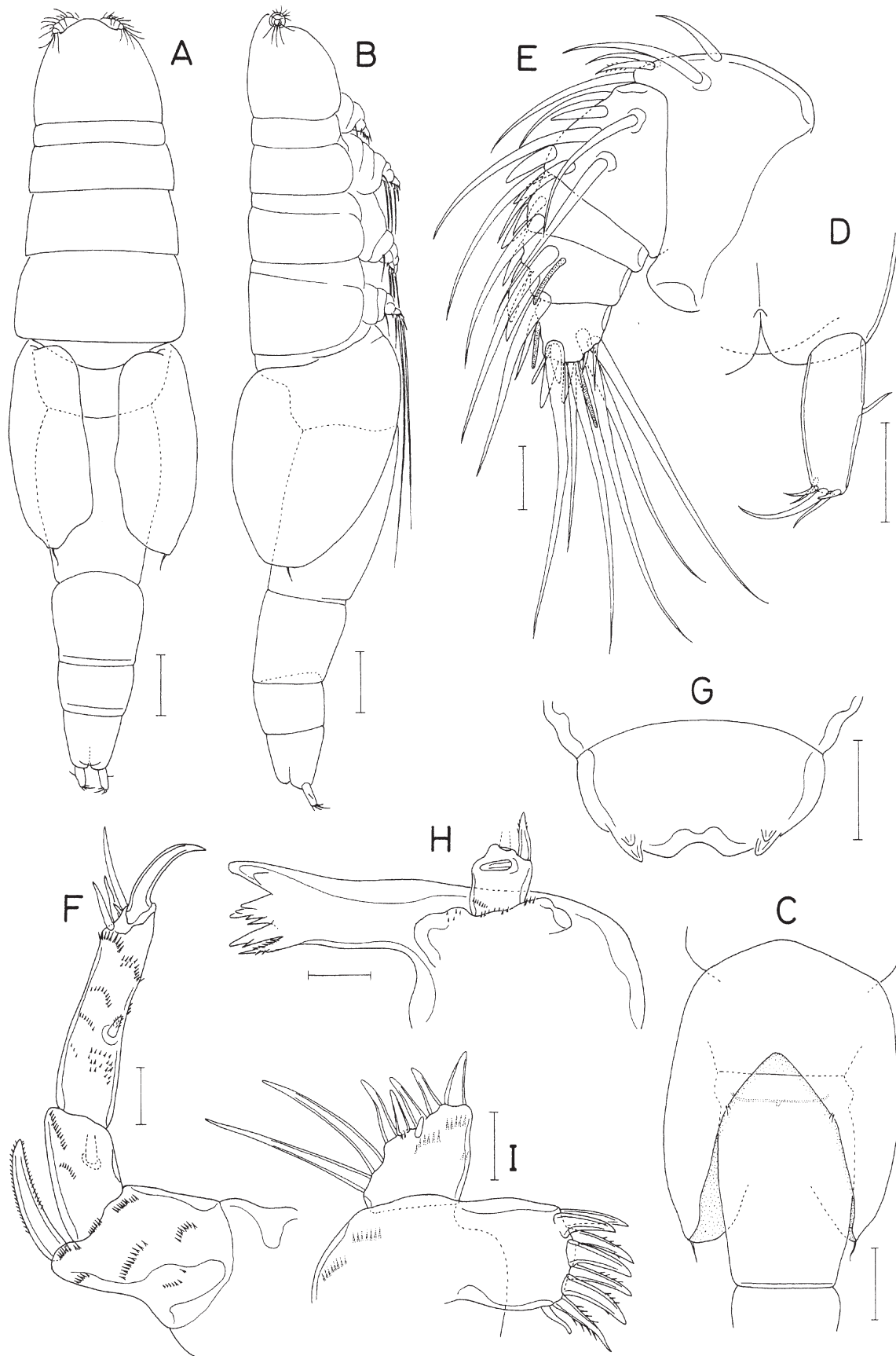
***Ascidicola antarctica* sp. nov.**

(Figs. 6, 7)

**Type material.** Holotype ♀ (MNHN-IU-2018-1942, dissected and mounted on a slide) from *Corella antarctica* Sluiter, 1905; Antarctic Ocean, Eltanin cruise 12, Stn 1078 (61°26'S, 41°55.4'W), depth 604 m, 12 April 1964.

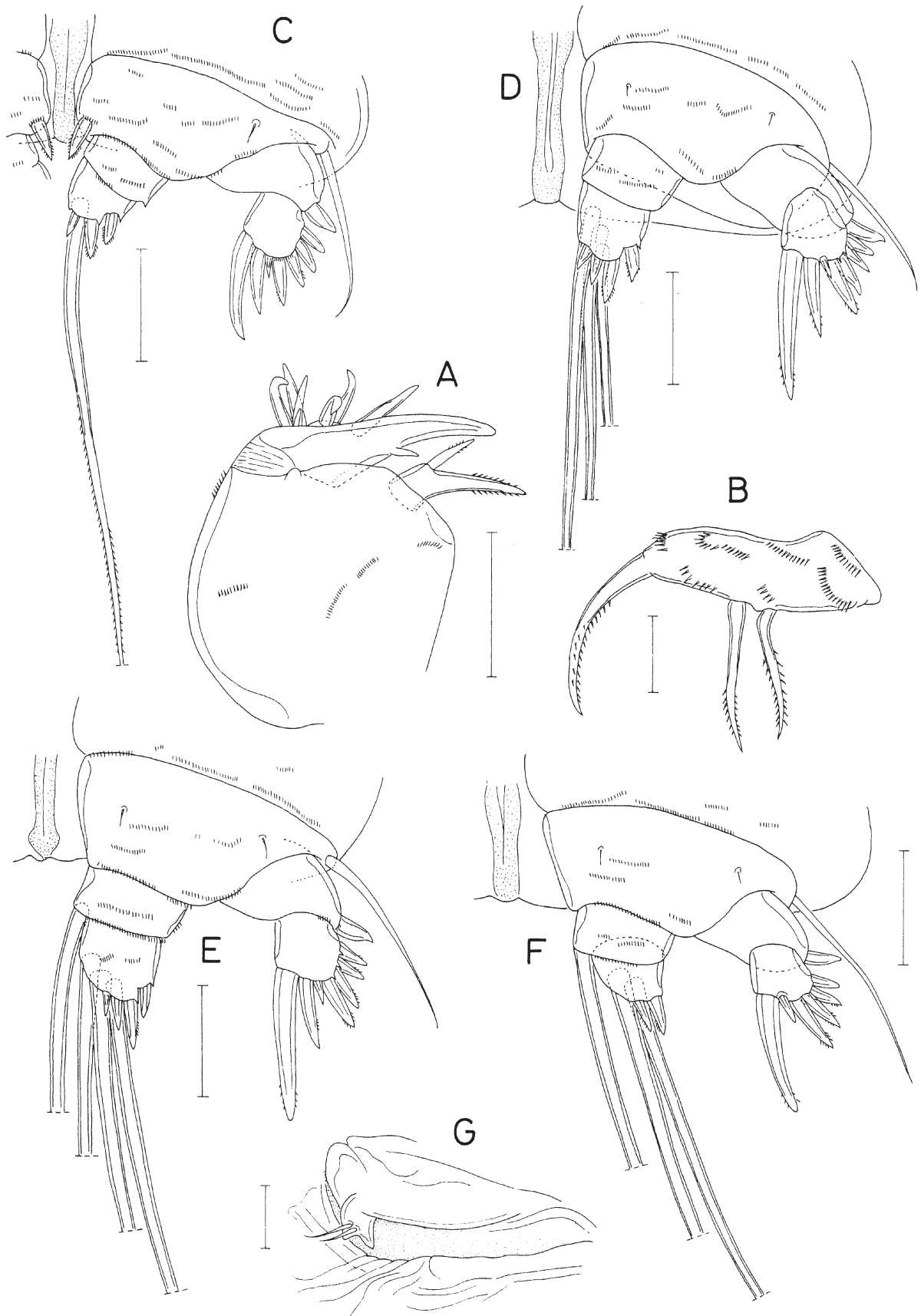
**Etymology.** The name of the new species refers to its distribution in the Antarctic Ocean.

**Description of female.** Body (Fig. 6A, B) elongate, cylindrical, segmented as in congeners. Body length 2.56 mm. Prosome slightly depressed; maximum width 560 µm across fourth pedigerous somite. Prosome 1.08 mm long, occupying 41% of body length, gradually broadening distally; cephalosome 351×425 µm; first to fourth pedigerous somites 68×431, 154×480, 203×505, and 283×560 µm, respectively. Urosome 5-segmented; fifth pedigerous somite about 220×440 µm, genital somite (Fig. 6C) 1.40 times longer than wide (578×412 µm); small copulatory pore visible on proximal ventral surface. Three abdominal somites 265×302, 154×252, and 185×197 µm, respectively; ventral spinose pad absent between last 2 abdominal somites. Caudal ramus (Fig. 6D) 2.53 times longer than wide



**FIG. 6.** *Ascidicola antarctica* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, anterior part of urosome, ventral; D, left caudal ramus, ventral; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule. Scale bars: A-C, 0.2 mm; D, G, 0.05 mm; E, F, H, I, 0.02 mm.





**FIG. 7.** *Ascidicola antarctica* sp. nov., female. A, maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, genital aperture. Scale bars: A, C-F, 0.05 mm; B, G, 0.02 mm.

(81×32 μm), 0.44 times as long as anal somite, with slightly convex inner margin: armed with 6 small setae (1 lateral and 5 distal); lateral seta positioned at 47% of ramus length; largest of distal setae 47 μm long, 0.58 times as long as caudal ramus, all other setae shorter than width of ramus at base.

Rostrum absent. Antennule (Fig. 6E) short, 5-segmented; all segments wider than long; armature formula 5, 8, 5, 5+aesthetasc, and 12+3 aesthetascs; all setae naked; shorter setae usually broadened; aesthetascs small. Antenna (Fig. 6F) 3-segmented, consisting of coxobasis and 2-segmented endopod; basis slightly longer than wide (50×47 μm) armed with 1 large spine (45 μm long) distally and ornamented with several scattered rows of spinules; first endopodal segment about 1.6 times longer than wide (38×24 μm), armed with 1 element (only insertion scar was observed) and 2 rows of spinules; second endopodal segment 3.5 times longer than wide (77×22 μm), terminating in slender claw; armed with 1 stout spiniform seta near middle and 4 unequal setae distally (1 much smaller than other 3), and ornamented with several rows of spinules; terminal claw 38 μm long, half as long as second endopodal segment.

Labrum (Fig. 6G) with concave posterior margin and bearing pair of teeth at each posterolateral corner. Mandible (Fig. 6H) consisting of coxa and palp: coxa with well-developed gnathobase bearing 4 teeth on medial margin; distal 3 teeth bearing 1-4 subsidiary denticles and proximal tooth setiform, weakly pinnate; palp 1-segmented, articulated from broad, pedestal-like extension of coxa; as long as wide, armed with spiniform elements (only 2 spines confirmed; other elements missing). Maxillule (Fig. 6I) consisting of precoxa and unsegmented palp; precoxa bearing 7 spines and 1 proximal seta on arthrite and 2 rows of minute spinules on outer side; palp bearing 7 spiniform elements and 1 minute seta along oblique outer and distal margins, and ornamented with 2 rows of minute spinules subdistally; 2 proximal elements on palp distinctly longer than others. Maxilla (Fig. 7A) consisting of syncoxa and allobasis; syncoxa broad, bearing 1 endite tipped with 1 seta and 1 spine (spine not articulated at base); allobasis drawn out into claw-like process, armed with 7 spiniform setae (grouped as 4, 2, and 1) along outer margin and 1 setiform process on inner margin. Maxilliped (Fig. 7B) 2.4 times longer than wide (58×24 μm), unsegmented, digitiform, ornamented with several rows of fine spinules; armed with 1 apical and 2 medial spinulose setae; apical seta not articulated at base.

Legs 1-4 (Fig. 7C-F) biramous with 2-segmented rami and narrow intercoxal sclerites; coxa lacking inner seta. Leg 1 with inner distal spine on basis 19 μm long, as long as first endopodal segment. Spines on second exopodal segment of legs 1-4 increasingly longer from outer proximal to inner distal, but fifth spine markedly smaller than other spines. Inner setae on endopods elongate and stiff, as usual for genus. First endopodal segment of legs 3 and 4 bearing inner seta, but this seta absent in legs 1 and 2. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; III, I, III	0-0; I II, 1
Leg 2	0-0	1-0	I-0; III, I, III	0-0; I, III, 3
Leg 3	0-0	1-0	I-0; III, I, III	0-1; I, III, 3
Leg 4	0-0	1-0	I-0; III, I, II	0-1; 0, II, 2

Leg 5 (Fig. 6C) lamellate, covering fifth pedigerous and genital somites, not extending to posterior margin of genital somite, bearing 3 minute vestigial setae (2 ventro-proximal and 1 ventro-distal); left and right legs separate from each other on dorsal side, but fused proximally on ventral side. Leg 6 (Fig. 7G) represented by bifurcate process bearing 2 small setae on genital operculum.

**Male.** Unknown.

**Remarks.** The leg armature of *Ascidicola antarctica* **sp. nov.** is similar to that of *A. rosea* except for the second endopodal segment of leg 4, which is armed with 2 spines and 2 setae (compared to 3 spines and 2 setae in *A. rosea*). In the second exopodal segment of legs 1-4 of *A. antarctica* **sp. nov.** the fifth spine is the smallest, but in legs 3 and 4 of *A. rosea* the fourth is the smallest. *Ascidicola antarctica* **sp. nov.** differs from *A. rosea* and *A. secunda* in the dimension of the caudal ramus which is 2.53 times longer than wide, while it is 3.93 times (present study) or about 4 times (Ooishi, 2007a) longer than wide in *A. rosea* and 2.82 times (present study) or 4.60 times (Kim I.H. & Moon, 2011) longer than wide in *A. secunda*.

*Ascidicola antarctica* **sp. nov.** has a similar shape caudal ramus to *A. philippinensis* **sp. nov.** and both new spe-

cies possess the same number of setae (3) on the maxilliped. However, they are easy to distinguish because the setal armature of legs 1-4 is very different.

### Genus *Styelicola* Lützen, 1968

**Diagnosis.** Body flexible with weak exoskeleton. Prosome not segmented or indistinctly segmented, but cephalosome and 4 pedigerous somites discernible by dorsal cephalic shield and 4 dorsal tergites. Urosome shorter than prosome, incompletely segmented. Caudal ramus bearing 6 setae. Rostrum not developed. Antennule 5- to 8-segmented; first segment bearing 2 setae. Antenna 3-segmented; first segment (coxobasis) bearing broad spine distally; second segment (first endopodal segment) unarmed; third segment (second endopodal segment) bearing terminal claw and several small setae. Mandible consisting of coxa with well-developed gnathobase bearing 4 major teeth on medial margin, and 1- or 2-segmented palp. Maxillule consisting of precoxa armed with 7 or 8 elements on arthrite, and 1- or 2-segmented palp bearing 9 to 11 setae. Maxilla consisting of syncoxa and allobasis; syncoxa bearing single endite tipped with 2 setae, or endite absent. Maxilliped lobate, digitiform, and unarmed, or armed with 1 seta distally. Legs 1-4 biramous with 2-segmented rami. Coxa of legs 1-4 unarmed. Basis of leg 1 bearing inner distal spine. Exopods tapering, with small or vestigial outer spines; endopods broad, rounded distally, unarmed or armed with few spines. Leg 5 consisting of lamellate protopod and small, setae-bearing exopod. Leg 6 represented by 3 denticles on genital operculum.

**Type species.** *Styelicola bahusia* Lützen, 1968 by original designation.

**Remarks.** Three species have been assigned to the genus *Styelicola*: *S. bahusia* associated with *Styela sigma* Hartmeyer, 1912 (as *S. atlantica* in the original description) and *Styela gelatinosa* (Traustedt, 1886) from Swedish waters (Lützen, 1968), *Styelicola lighti* Illg & Dudley, 1980 associated with *Hartmeyeria chinensis* Tokioka, 1967 in the China Sea (Illg & Dudley, 1980), and *Styelicola omphalus* Kim I.H., Cruz-Rivera, Sherif, & El-Salmar, 2016 associated with *Phallusia nigra* Savigny, 1816 in the Red Sea (Kim I.H. et al., 2016). In the present account a new species is added to this genus, and *Styelicola lighti* is removed to a new genus.

The absence of any armature element on the first endopodal segment of the antenna seems to be the most outstanding feature of the genus *Styelicola* within the Ascidicolidae. Other features have been considered as distinguishing characters of the genus, including: the body has a weakly sclerotized, soft exoskeleton, the maxilliped is unarmed or armed with a single seta, the armature on the rami of the swimming legs is less well developed than other genera of the family, and the exopods of the swimming legs taper distally while the endopods are very broad and appear lamellate.

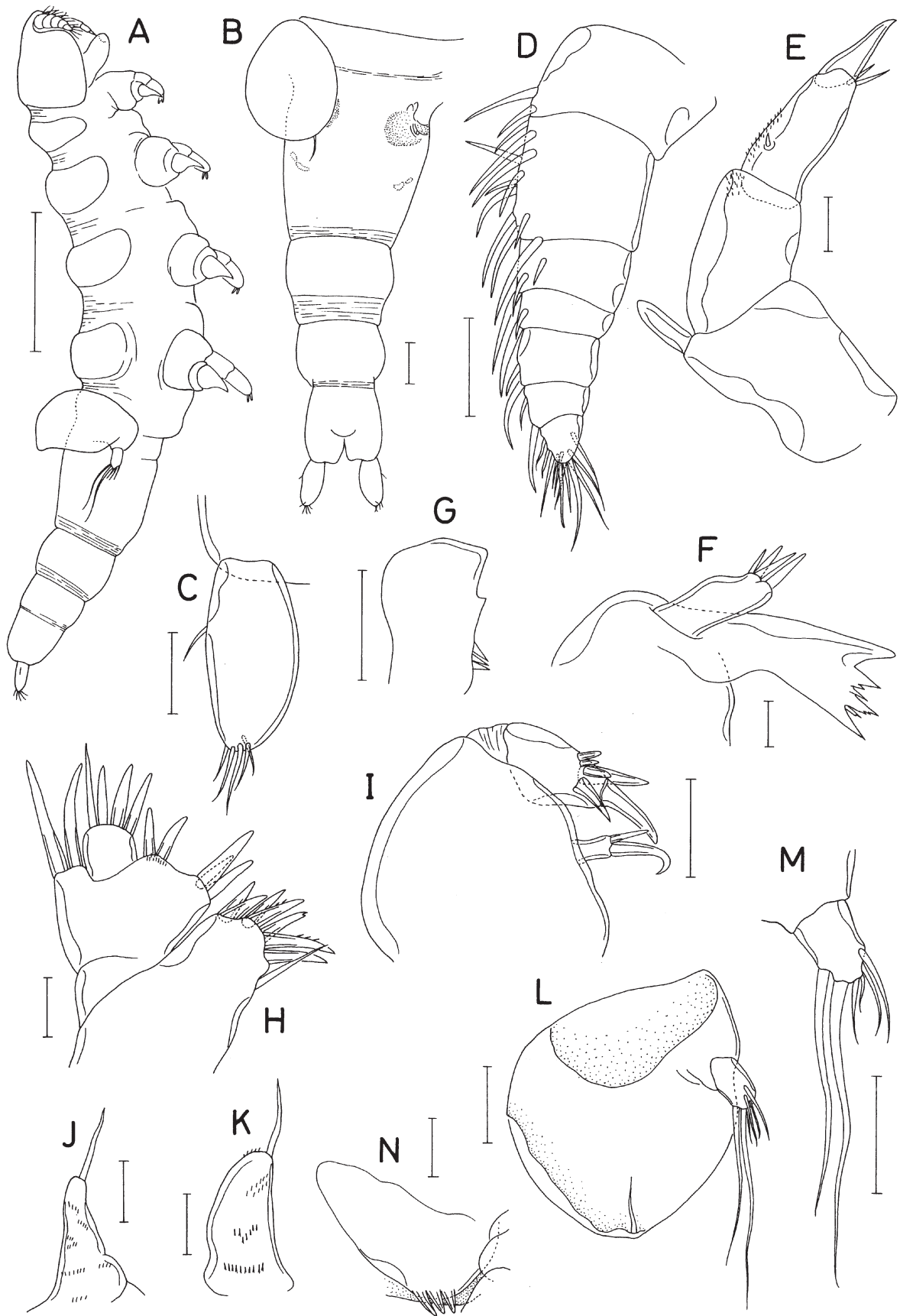
### *Styelicola bahusia* Lützen, 1968

(Figs. 8, 9)

**Material examined.** 1 ♀ (MNHN-IU-2015-7, dissected) in *Styela sigma* Hartmeyer, 1912; off French Guiana, GUYANE 2014 cruise, RV “Hermano Gines”, Stn CP4366 (07°09'N, 53°05'W), depth 300-301 m, MNHN coll., 01 August 2014.

**Description of female.** Body (Fig. 8A) elongate, curved dorsally, with weakly sclerotized, rather soft exoskeleton; body length 2.62 mm. Prosome longer than urosome, slightly depressed, and unsegmented, but cephalosome defined by cephalic shield and 4 pedigerous somites recognizable by weak dorsal tergites. Urosome (Fig. 8B) 5-segmented, gradually narrowing posteriorly. Articulation between fifth pedigerous somite and genital somite obscure; genital somite longer than wide; genital apertures positioned dorsally. Anal somite slightly longer than wide, longer than second abdominal somite, with deep posteromedian incision; anal operculum distinct. Caudal ramus (Fig. 8C) nearly fusiform, 2.09 times longer than wide (117×56 µm), 0.63 times as long as anal somite, with strongly convex inner margin: armed with 6 small setae (1 lateral and 5 distal); lateral seta positioned at 36% of ramus length; all setae naked and shorter than width of ramus.

Rostrum absent. Antennule (Fig. 8D) stout, 228 µm long, 7-segmented, gradually narrowing distally; armature



**FIG. 8.** *Styelicola bahusia* Lützen, 1968, female. A, habitus, right; B, urosome, dorsal; C, right caudal ramus, ventral; D, antennule; E, antenna; F, mandible; G, paragnath; H, maxillule; I, maxilla; J, K, maxilliped; L, leg 5, medial; M, exopod of leg 5; N, genital aperture. Scale bars: A, 0.5 mm; B, L, M, 0.1 mm; C, D, G, I, 0.05 mm; E, F, H, J, K, N, 0.02 mm.

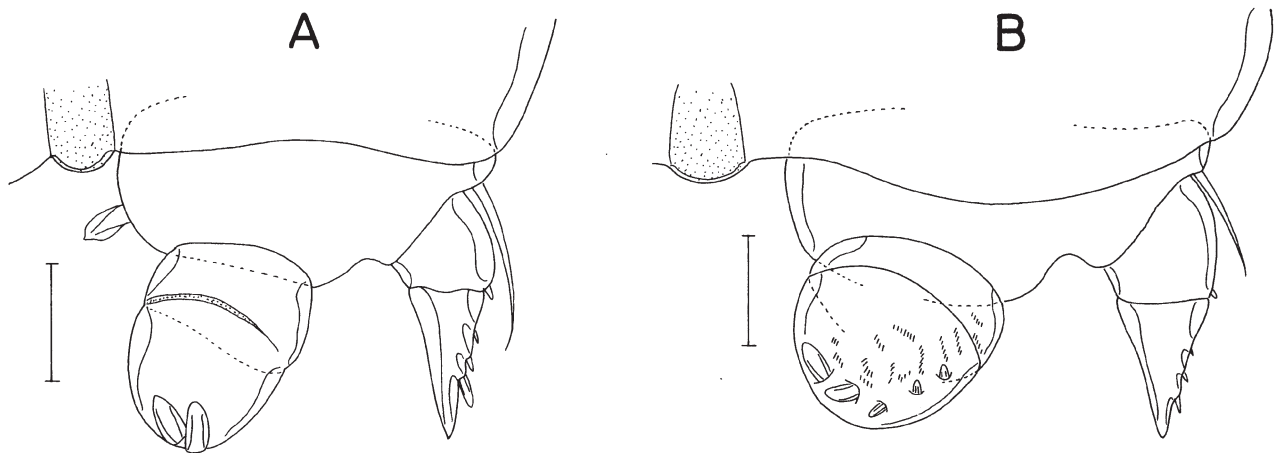


FIG. 9. *Styelicola bahusia* Lützen, 1968, female. A, Leg 1; B, leg 2. Scale bars: 0.05 mm.

formula 2, 11, 3, 2, 2, 2, and 12; setae small and naked; 2 of setae on terminal segment aesthetasc-like. Antenna (Fig. 8E) consisting of coxobasis and 2-segmented endopod; coxobasis broadening distally, longer than wide, armed with 1 broad spine distally: first endopodal segment unarmed, but ornamented with patch of minute spinules near anterodistal corner; second endopodal segment as long as first, bearing 3 small setae (1 proximal and 2 distal) plus acutely pointed claw; ornamented with minute spinules proximally on anterior surface.

Labrum not observed (destroyed). Mandible (Fig. 8F) consisting of coxa and unsegmented palp: coxal gnathobase with 4 major and 3 subsidiary teeth on medial margin; palp about 2.2 times longer than wide, with slightly convex outer margin, armed distally with 4 short setae. Paragnath (Fig. 8G) broadening distally, with 3 setiform elements proximally on medial margin, 1 dentiform process at distal third of medial margin and angular mediiodistal corner. Maxillule (Fig. 8H) consisting of precoxa and palp: precoxal arthrite armed with 7 spines and 1 proximal seta; palp 2-segmented; first segment subdivided proximally, bearing 7 blunt setae (3 proximal and 2 distal setae on medial margin, and 2 longer setae at outer distal corner); second segment (?endopod) quadrate, bearing 4 setae on distal margin. Maxilla (Fig. 8I) consisting of syncoxa and allobasis; syncoxa broad, bearing single endite tipped with 2 unequal setae, both articulated at base; allobasis armed with 6 unequal spiniform elements (largest element distally). Maxilliped (Fig. 8J, K) as digitiform lobe tipped with 1 seta and ornamented with several rows of minute spinules.

Legs 1-4 biramous with 2-segmented rami; coxa lacking inner seta; second exopodal segment conical (Fig. 9A, B). Outer spines on exopods and endopods usually rudimentary. Endopods stout, expanded, with incomplete articulation between segments; distal margin of second segment rounded. Legs 3 and 4 shaped and armed as in leg 2. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; III, 0	0-0; 0, II, 0
Legs 2-4	0-0	1-0	I-0; III, 0	0-0; III, II, 0

Leg 5 (Fig. 8L) 2-segmented, consisting of lamellate protopod and small exopod; protopod  $318 \times 303 \mu\text{m}$ , subcircular, extending to middle of genital somite (Fig. 8B), bearing 1 small seta distally; exopod (Fig. 8M) about 1.3 times longer than wide ( $68 \times 52 \mu\text{m}$ ), inserting on ventral margin of protopod and armed with 6 unequal setae (2 dorsal setae distinctly longer than other 4). Leg 6 (Fig. 8N) represented by 3 spiniform processes on genital operculum

**Male.** Unknown.

**Remarks.** The single female specimen examined here is elongate and contrasts with the body form in the original description of *Styelicola bahusia* by Lützen (1968) who described the female body as short, thick and broad. This difference is almost certainly due to the different methods of specimen preservation: we consider that our specimens became inflated after fixation, whereas the type specimens probably contracted. There are other differences: in the

type specimens the antennule is 8-segmented, the maxillular palp is unsegmented, and the swimming legs have a different armature formula. However, we consider it likely that these differences are artefacts or possibly represent intraspecific variation. The shape of the caudal ramus and the armature of the mandible, maxillule, and maxilliped of our West Atlantic specimen all coincide exactly with the description of the type specimens and, it is on the basis of this evidence that we identify them as *S. bahusia*.

***Styelicola elongata* sp. nov.**

(Figs. 10, 11)

**Type material.** Holotype ♀ (MNHN-IU-2018-1943, dissected and mounted on a slide) from *Polycarpa aurita* (Sluiter, 1890); Plateau des Chesterfield, Coral Sea, west of New Caledonia, CORAIL 2 cruise, R.V. “Coriolis”, Stn CP90 (19°02.8’S, 158°56.3’E), depth 44 – 48 m, B. Richer de Forges-IRD coll., 26 July 1988.

**Etymology.** The name of the new species refers to its elongate body.

**Description of female.** Body (Fig. 10A) elongate, cylindrical, slightly curved ventrally. Body length 6.55 mm; maximum width 0.94 mm across third pedigerous somite. Prosome unsegmented, but cephalosome and four pedigerous somites discernible by constrictions and weak dorsal tergites. Prosome-urosome division obscure; fifth pedigerous somite not articulated from prosome. Urosome indistinctly 6-segmented; articulations between somites represented by constrictions and surface wrinkles. Caudal ramus (Fig. 10B) about 1.5 times longer than wide (89×58 µm), narrowing distally; armed with 6 setae (1 lateral, 1 subdistal, and 4 distal), all naked and less than half width of ramus; lateral seta positioned at 32% of ramus length.

Rostrum absent. Antennule (Fig. 10C) 235 µm long, broad, 1.7 times longer than wide; 5-segmented, second and terminal segments subdivided; armature formula 2, 9, 3, 2, and 12; setae short and naked, some bluntly tipped and aesthetasc-like. Antenna (Fig. 10D) consisting of coxobasis and 2-segmented endopod; coxobasis slightly longer than wide, bearing 1 spiniform seta distally; first endopodal segment as long as coxobasis, unarmed; second endopodal segment as long as first, 2.3 times longer than wide (74×32 µm); armed with 5 small setae (2 proximal and 3 distal) plus small terminal claw (23 µm long).

Labrum (Fig. 10E) broad, narrowing distally, bearing pair of dentiform processes at each posterolateral corner. Mandible (Fig. 10F) consisting of coxa with well-developed gnathobase bearing on medial margin 4 major teeth and 1 or 2 small subsidiary teeth between major teeth, and 2-segmented palp; first segment (fused basis and exopod) with 2 bluntly tipped setae (originally exopodal setae) distally; second segment (endopod) nearly quadrate, with 4 bluntly tipped setae on distal margin. Maxillule (Fig. 10H, I) bilobed: inner lobe (precoxal arthrite) bearing 7 setae; outer lobe (palp) bearing 1 seta subdistally and 8 setae distally (3, 2, and 3 setae on 3 small lobes); all setae on maxillule bluntly tipped and subequal in length. Maxilla (Fig. 10J) consisting of syncoxa and allobasis; syncoxa broad, unarmed, with 1 small pore (opening of maxillary gland) on inner surface; allobasis terminating in spiniform claw, armed with 4 spines (1 on outer margin and 3 on inner margin) near base of terminal claw. Maxilliped (Fig. 10K) as blunt, unarmed digitiform lobe.

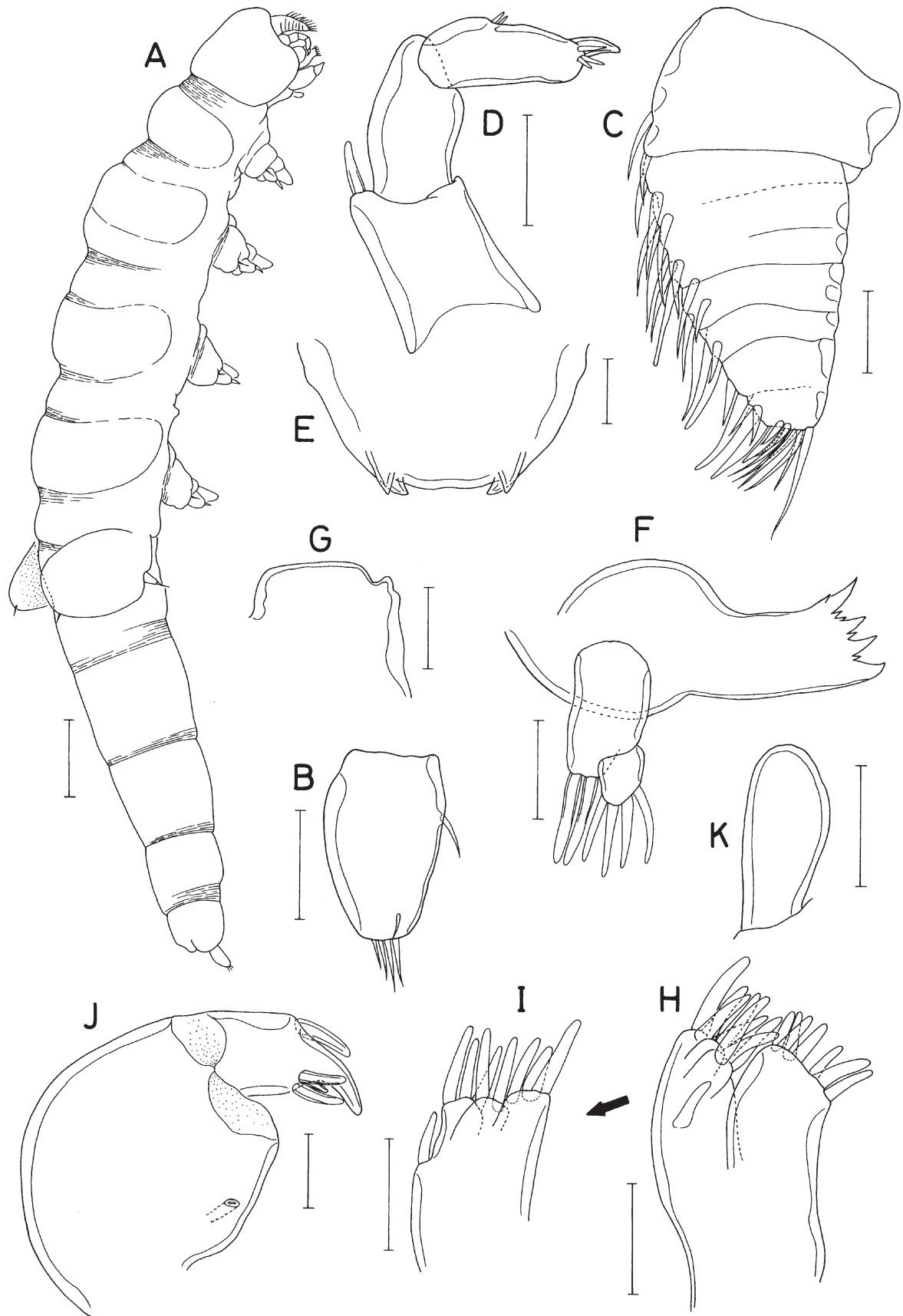
Leg 1 (Fig. 11A) consisting of unarmed coxa, basis bearing outer seta, and 2-segmented exopod and endopod. Outer spines on exopod small, rudimentary. Second exopodal segment tapering and terminating in spiniform process. Endopod broad, both segments unarmed; second segment blunt, with broadly rounded distal margin. Legs 2-4 shaped and armed as in leg 1, but larger than leg 1, increasing in size from leg 2 to leg 4. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Legs 1-4	0-0	1-0	I-0; III, 0	0-0; 0

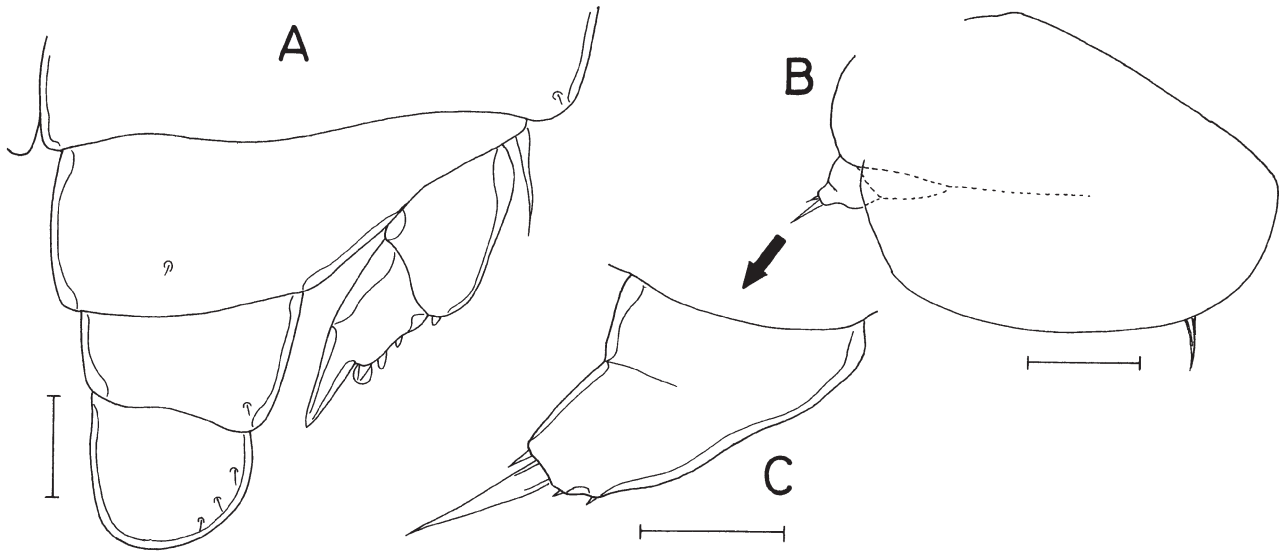
Leg 5 (Fig. 11B) consisting of lamellate protopod and small exopod: protopod 558×818 µm, directed dorsally, bearing 1 small seta dorsodistally; exopod 91×89 µm, inserting on ventral margin of protopod, strongly tapering, partially subdivided on ventral side; armed distally with 1 large and 3 minute setae. Leg 6 not observed.

**Male.** Unknown.

**Remarks.** The distinctive features of *Styelicola elongata* sp. nov. are as follows: (1) the body of the female is large,



**FIG. 10.** *Styelicola elongata* sp. nov., female. A, habitus, right; B, right caudal ramus, dorsal; C, antennule; D, antenna; E, labrum; F, mandible; G, paragnath; H, maxillule; I, palp of maxillule; J, maxilla; K, maxilliped. Scale bars: A, 0.5 mm; B-K, 0.05 mm.



**FIG. 11.** *Styelicola elongata* sp. nov., female. A, leg 1; B, leg 5; C, exopod of leg 5. Scale bars: A, C, 0.05 mm; B, 0.2 mm.

6.55 mm long; (2) the caudal ramus is broad, about 1.5 times longer than wide; (3) the mandibular palp is 2-segmented; (4) the maxilla lacks an endite; (5) the endopods of legs 1-4 are unarmed; and (6) the exopod of leg 5 is distinctly tapering and armed with 1 large and 3 small setae. Character states (4) and (5) are shared with *S. omphalus*, but the others are exhibited exclusively by *S. elongata* sp. nov. In congeners, such as *S. omphalus*, the body is at most 4.35 mm long, the caudal ramus is at least twice as long as wide, the mandibular palp is single-segmented, and the exopod of leg 5 is nearly rectangular and bears 5 or 6 setae.

### ***Hamistyelicola* gen. nov.**

**Diagnosis.** Body slender; prosome-urosome division not distinct. Prosome 5-segmented. Urosome 6-segmented. Spinose pad present ventrally between pre-anal and anal somites. Caudal ramus bearing 6 setae. Rostrum not developed. Antennule 7-segmented. Antenna 3-segmented, bearing terminal claw; all segments armed. Mandible consisting of coxa with well-developed gnathobase bearing 4 major teeth on medial margin, and biramous palp, armed with 6 setae on endopod and 1 seta on tip of small exopod. Maxillule consisting of precoxa and biramous palp; precoxa bearing 7 to 9 setae on arthrite; palp bearing 5 setae on basis, 2 setae on exopod, and 6 setae on endopod; exopod and endopod articulated from or fused with basis. Maxilla 2- or 3-segmented; first segment (syncoxa) with single endite tipped with 3 setae; second segment (allobasis) or second and third segments (basis and endopod) bearing 8 or 9 setae in total, lacking claw. Maxilliped 1 or 2-segmented, armed with 4 or 5 setae. Legs 1-4 broad, biramous with 2-segmented rami; coxa unarmed; basis with large outer seta. Basis of leg 1 bearing inner distal spine. Spines on exopods and endopods distinct. Distal segment of exopod of legs 2-4 transformed to large, powerful hook. Leg 5 consisting of lamellate protopod bearing 1 seta distally and small exopod bearing 6 setae. Leg 6 represented by 3 dentiform processes on genital operculum.

**Type species.** *Hamistyelicola lighti* (Illg & Dudley, 1980) **comb. nov.** (originally as *Styelicola lighti*), by original designation.

**Other included species.** *Hamistyelicola monniotorum* gen. et sp. nov.

**Etymology.** The name is derived from the Latin *ham* (=hooked) and the generic name *Styelicola*. Gender masculine.

**Remarks.** The most outstanding feature of *Hamistyelicola* gen. nov. is the transformation of the second exopodal segment of legs 2-4 into a powerful hook. The discovery of a second species possessing this hook, as in *Styelicola lighti*, leads us to establish a new genus to accommodate both these two species.

Within the family, *Hamistyelicola* gen. nov. appears closer to *Ascidicola* than to *Styelicola* as both genera share the following character states: the first endopodal segment of the antenna bears a seta, the maxilliped is armed with



multiple setae, and the inner spine on the first endopodal segment is present at least in leg 4. The presence of the large conspicuous hook on the exopod of legs 2-4, and the possession of 2-segmented fifth leg are distinctive features separating the new genus from *Ascidicola*.

***Hamistyelicola monniotorum* gen. et sp. nov.**

(Figs. 12, 13)

**Type material.** Holotype ♀ (MNHN-IU-2018-1944, dissected and mounted on a slide) from *Pyura gangelion* (Savigny, 1816); Ibo, Mozambique, AURACEA 1995 cruise, depth 0 - 20 m, Monniot coll., November 1995.

**Etymology.** The name of this new species is dedicated to Drs. Claude and Françoise Monniot who collected the copepod material studied in the present work.

**Description of female.** Body (Fig. 12A) slender, cylindrical, and distinctly segmented. Body length 2.83 mm; maximum body width 500 µm across third pedigerous somite. Prosome consisting of cephalosome and 4 pedigerous somites, occupying 44% of body length. Urosome 6-segmented, but articulation indistinct between fifth pedigerous somite and genital somite. Genital somite much shorter than first abdominal somite; genital aperture positioned dorsally. Four abdominal somites 335×269, 388×246, 299×201, and 132×166 µm, respectively; penultimate abdominal somite ornamented with numerous minute spinules dorsally and ventrally along posterior margin (Fig. 12B). Caudal rami (Fig. 12B) widely separated from each other, slightly divergent; each ramus about 4 times longer than wide (177×44 µm), gradually narrowing distally: armed with 6 small setae; outer and subdistal dorsal setae positioned at 53% and 80% of ramus length, respectively; largest of 4 distal setae 67 µm long, longer than proximal width of ramus, all other setae shorter than proximal width of ramus.

Rostrum absent. Antennule (Fig. 12C) 7-segmented, gradually narrowing distally; armature formula 4, 6, 5, 3, 3, 3, and 9+2 aesthetascs; first segment subdivided on one surface into 2 parts each bearing 2 setae; some of shorter setae on third to fifth segments finely spinulose unilaterally. Antenna (Fig. 12D) 3-segmented, consisting of coxobasis and 2-segmented endopod; coxobasis about twice as long as wide and armed with 1 spine distally (52 µm long); first endopodal segment distinctly shorter than coxobasis, armed with 1 spine (32 µm long) near middle and ornamented with several rows of fine spinules; second endopodal segment 3.0 times longer than wide (75×25 µm), armed with terminal claw, 2 spiniform setae on anterior (inner) margin, and 1 subdistal and 2 distal setae; ornamented with several rows of fine spinules; terminal claw small, less than half length of second endopodal segment.

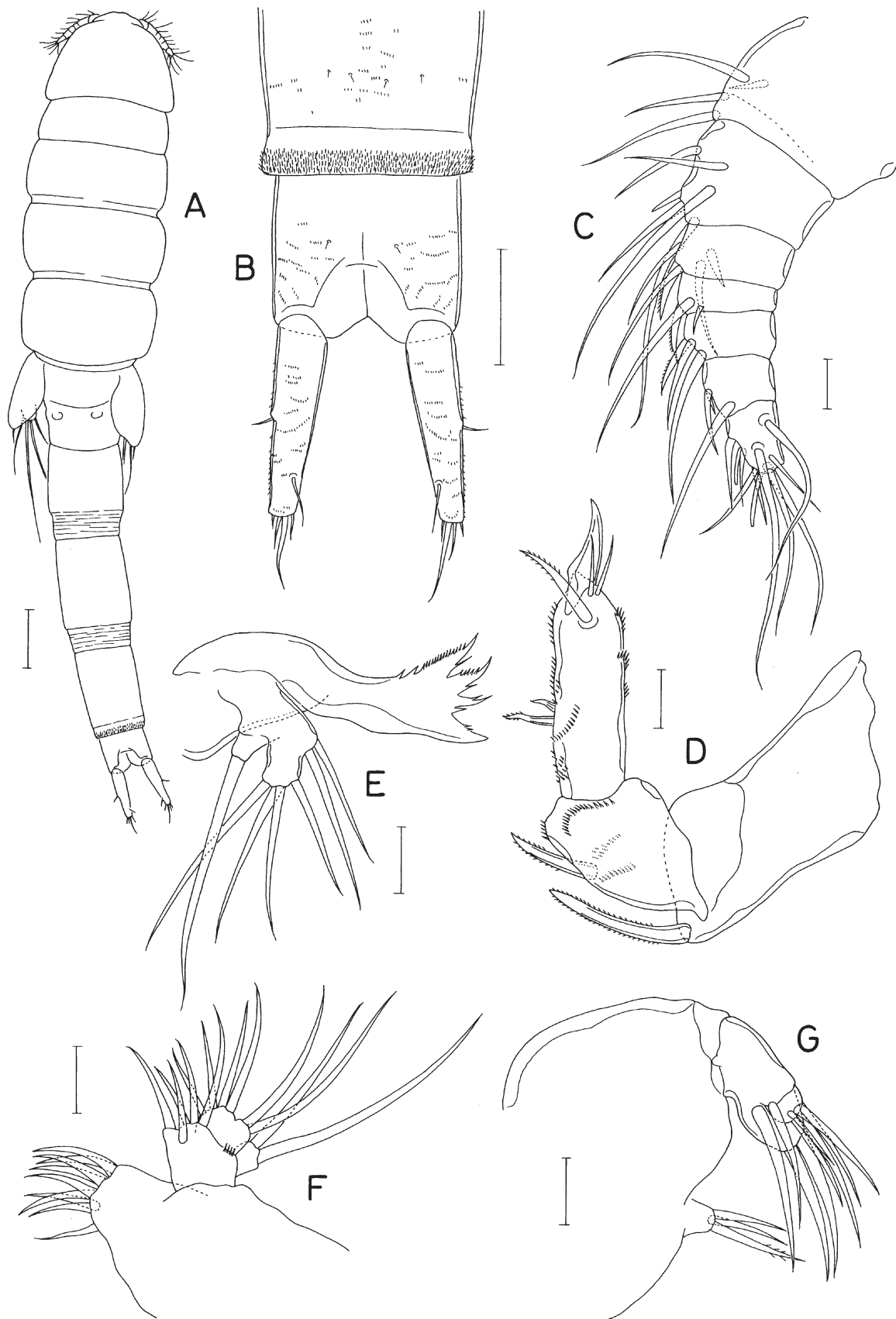
Labrum weak, flexible, easily destroyed. Mandible (Fig. 12E) consisting of coxa and palp; coxal gnathobase bearing 4 major teeth on medial margin and 2 denticles and row of spinules on proximal margin; palp unsegmented, biramous, armed with 1 large seta on tip of small exopod and 6 setae (2 medial and 4 distal) on fused basis + endopod. Maxillule (Fig. 12F) consisting of precoxa bearing 9 setae on arthrite and biramous palp comprising basis and articulating exopod and endopod; armed with 5 setae on basis, 2 setae on exopod, and 6 setae on endopod. Maxilla (Fig. 12G) consisting of syncoxa, basis, and rudimentary endopod; syncoxa broad, bearing 1 endite tipped with 3 setae; basis lacking claw, blunt at tip, bearing 4 setae (2 subdistal and 2 distal); endopod small, with 5 setae. Maxilliped (Fig. 13A) as tapering lobe bearing 5 setae (2 on medial margin and 3 apically).

Legs 1-4 broad, biramous with 2-segmented rami (Fig. 13B-D); coxa lacking inner seta; outer seta on basis large; spines on rami distinct, but setae lacking from both rami of legs 1-4. Second segment of leg 1 endopod (Fig. 13B) quadrilobate along distal margin, all these lobes marginally spinulose. Second (distal) segment of exopod of leg 2-4 transformed to large, powerful hook (Fig. 13C, D). Second endopodal segment of legs 2-4 bearing longitudinal groove receiving exopodal hook and 2 horizontal rows of spinules on posterior surface. First endopodal segment of leg 4 bearing inner spine, but this spine absent in legs 1-3. Armature formula for legs 1-4 as follows:

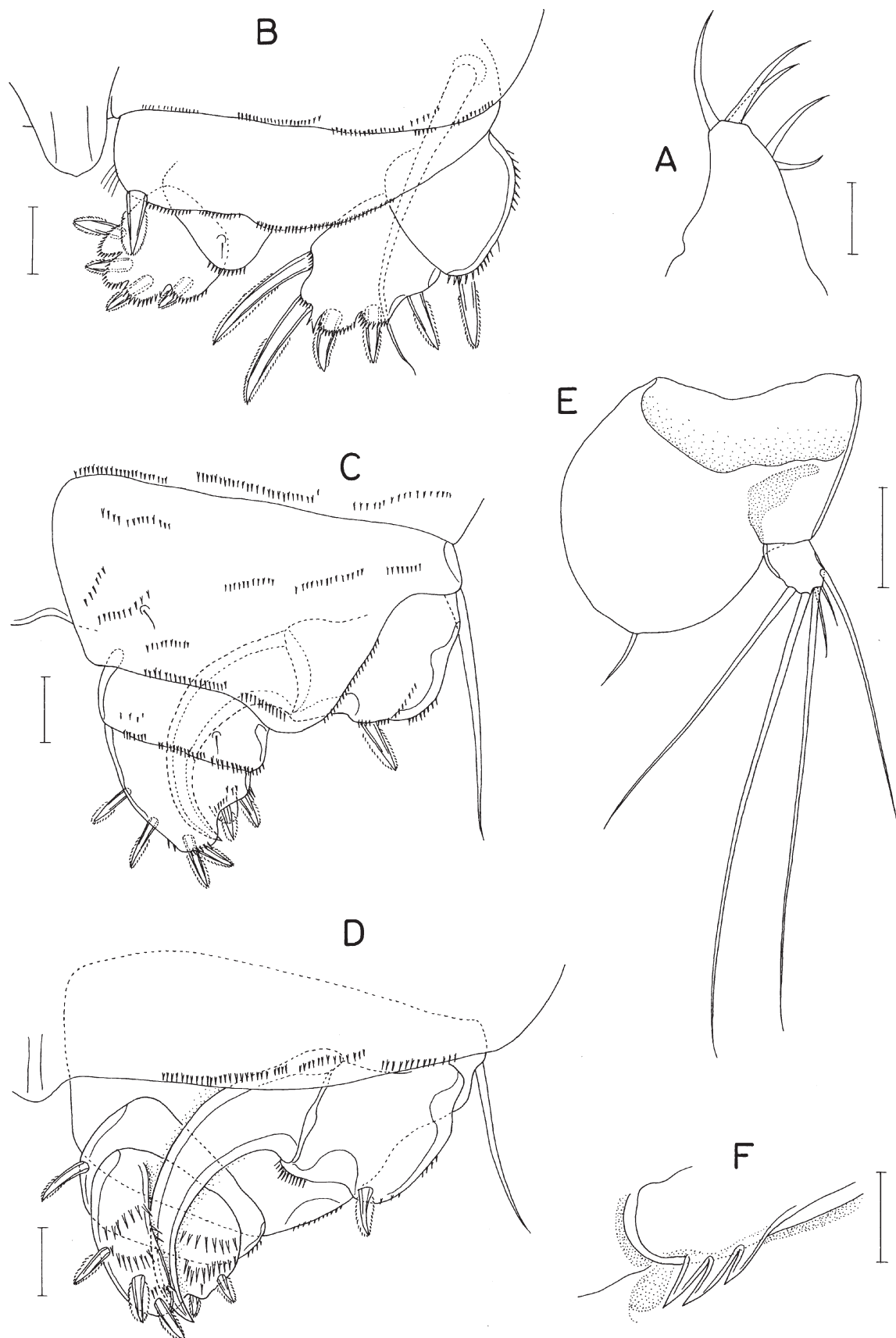
	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; II, I, II	0-0; IV
Legs 2 & 3	0-0	1-0	I-0; hook	0-0; II, II, II
Leg 4	0-0	1-0	I-0; hook	0-1; II, II, I

Leg 5 (Fig. 13E) consisting of protopod and small exopod; protopod lamellate, 252×252 µm, slightly oblong, with 1 seta distally; exopod 1.15 times longer than wide (54×47 µm), bearing 4 large and 2 small setae: lengths of large

setae 280, 457, 485, and 308  $\mu\text{m}$  long, respectively, from ventral to dorsal; 2 small setae 39 and 67  $\mu\text{m}$ . Leg 6 (Fig. 13F) represented by 3 teeth on genital operculum.



**FIG. 12.** *Hamistylelicola monniotorum* gen. et sp. nov., female. A, habitus, dorsal; B, distal part of urosome, dorsal; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla. Scale bars: A, 0.2 mm; B, 0.1 mm; C-G, 0.05 mm.



**FIG. 13.** *Hamistylicola monniotorum* gen. et sp. nov., female. A, maxilliped; B, leg 1; C, leg 2; D, leg 4; E, leg 5; F, genital aperture. Scale bars: A-D, F, 0.02 mm; E, 0.1 mm.

**Male.** Unknown.

**Remarks.** *Hamistylelicola monniotorum* **gen. et sp. nov.** is distinguishable from *H. lighti* (Illg & Dudley, 1980) **comb. nov.** as follows: (1) a small tubercle is present at the distal border of the anal somite (near the base of the caudal ramus), as figured by Illg & Dudley (1980) in the original description of *H. lighti* **comb. nov.**, but is absent in *H. monniotorum* **gen. et sp. nov.**; (2) the exopod and endopod of the maxillule are fused with the basis in *H. lighti*, but distinctly articulated from the basis in *H. monniotorum* **gen. et sp. nov.**; (3) the maxilliped is armed with 4 setae in *H. lighti* **comb. nov.**, but with 5 setae in *H. monniotorum* **gen. et sp. nov.**; (4) the second exopodal segment of leg 1 is armed with 6 spines in *H. lighti* **comb. nov.**, but with 5 spines in *H. monniotorum* **gen. et sp. nov.**; and (5) the first endopodal segment of legs 2 and 3 bears an inner spine in *H. lighti* **comb. nov.**, but this spine is absent in *H. monniotorum* **gen. et sp. nov.**

### ***Bathycopola* gen. nov.**

**Diagnosis.** Body rather stout. Prosome cylindrical, longer than urosome, incompletely 5-segmented; fourth pedigerous somite produced posterodorsally. Urosome 5-segmented; fifth pedigerous somite short, obscurely defined from prosome. Caudal ramus typically small, armed with 3 spines and 3 setae. Rostrum not developed. Antennule 7- or 8-segmented; first segment bearing 2 setae. Antenna 3- or 4-segmented; basis with 1 large spine distally; first endopodal segment with 1 seta on inner margin; second endopodal segment with several setae and slender terminal claw. Labrum bilobed; each lobe bearing 1 or 2 teeth on apex. Mandible consisting of coxa and palp; coxa with well-developed gnathobase bearing 1 tooth and several denticles on medial margin; palp biramous, consisting of basis, exopod and endopod, and armed with 3 setae on basis, 4 setae on exopod, and 5 or 6 setae on endopod. Maxillule consisting of precoxa and palp; precoxa bearing 9 setae on arthrite; palp unsegmented, but divisible into coxal endite bearing 1 seta, basis bearing 6 setae, exopod bearing 2 setae, and endopod bearing 3 to 6 setae. Maxilla consisting of syncoxa, basis, and 1- or 2-segmented endopod; syncoxa bearing 2 endites each tipped with 1 seta; basis with large claw in addition to setae; endopod with 5 or 6 setae. Maxilliped unsegmented with 4 to 7 setae. Legs 1-4 biramous; both rami armed mostly with spines. Exopods 2-segmented; second exopodal segment armed with 6 to 8 armature elements. Endopods 1- or 2-segmented; in 2-segmented condition, first segment lacking inner element and second segment armed with 4 or more armature elements. Leg 5 consisting of lamellate protopod and small exopod bearing 6 setae. Leg 6 represented by 3 spiniform elements on genital operculum

**Type species.** *Bathycopola karubar* **gen. et sp. nov.** by original designation.

**Other included species.** *Bathycopola brevicaudata* **gen. et sp. nov.**, *B. dicarpae* **gen. et sp. nov.**, and *B. setifera* **gen. et sp. nov.**

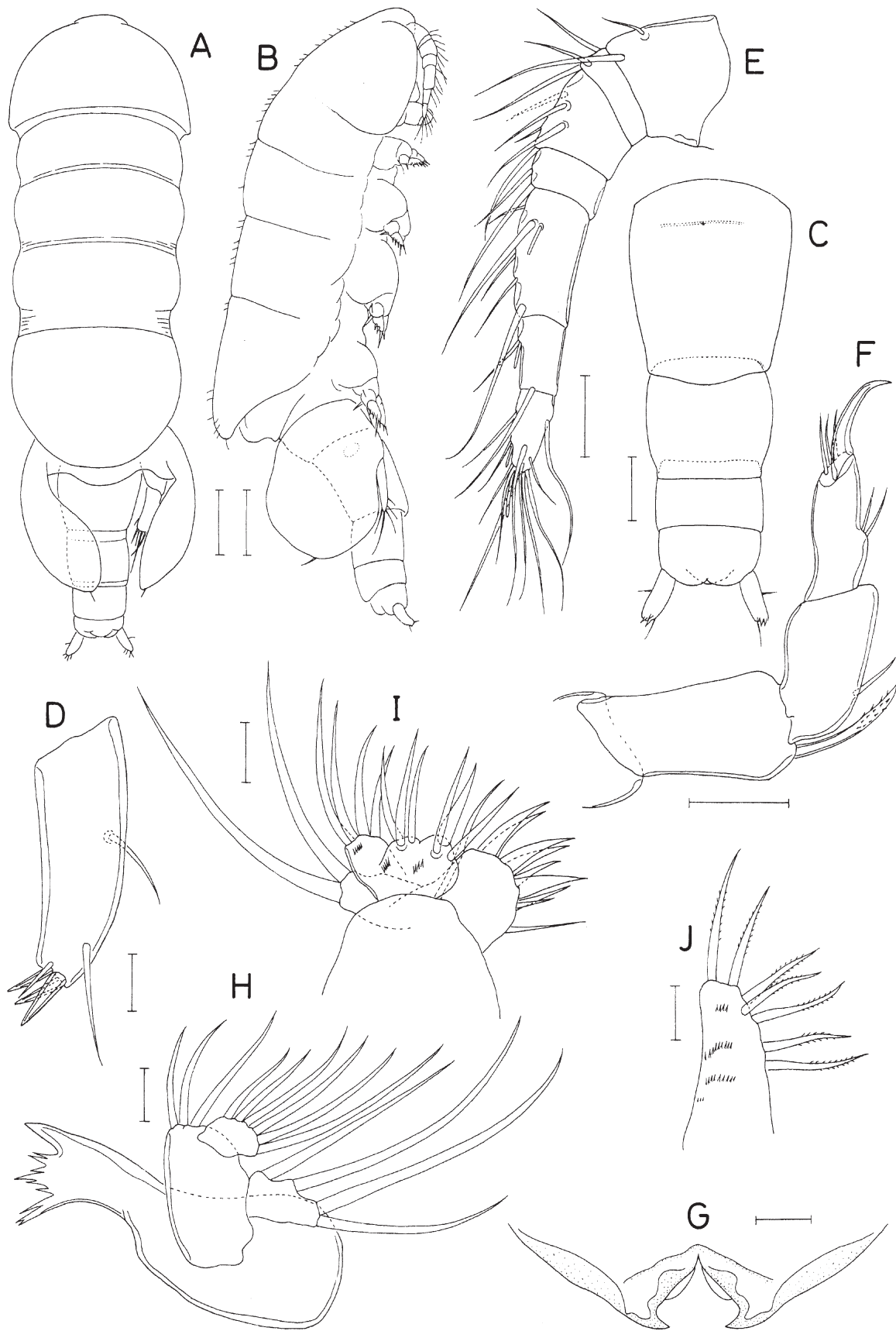
**Etymology.** The name is derived from the Latin *bath* (=deep) and *col* (=dwell), referring to the deep water (603 m to 5124 m) habitats occupied by species of this genus. Gender feminine.

**Remarks.** Four new species are included in *Bathycopola* **gen. nov.** and each is represented by only one or two specimens. One of these species is from the tropical West Pacific, and remaining three are from the Atlantic. They have a rather uniform body form and all possess 3 spines and 3 setae on the caudal ramus. *Bathycopola* **gen. nov.** exhibits some of the most plesiomorphic character traits of any genus within the Ascidiocolidae, in retaining a discrete endopod on the maxilla and in displaying the most complex setation on the mouthparts and swimming legs. All species of the genera *Ascidicola*, *Stylelicola*, and *Hamistylelicola* **gen. nov.** lack the inner seta on the coxa of legs 1-4, but some species of *Bathycopola* **gen. nov.** retain this seta on the posterior swimming legs.

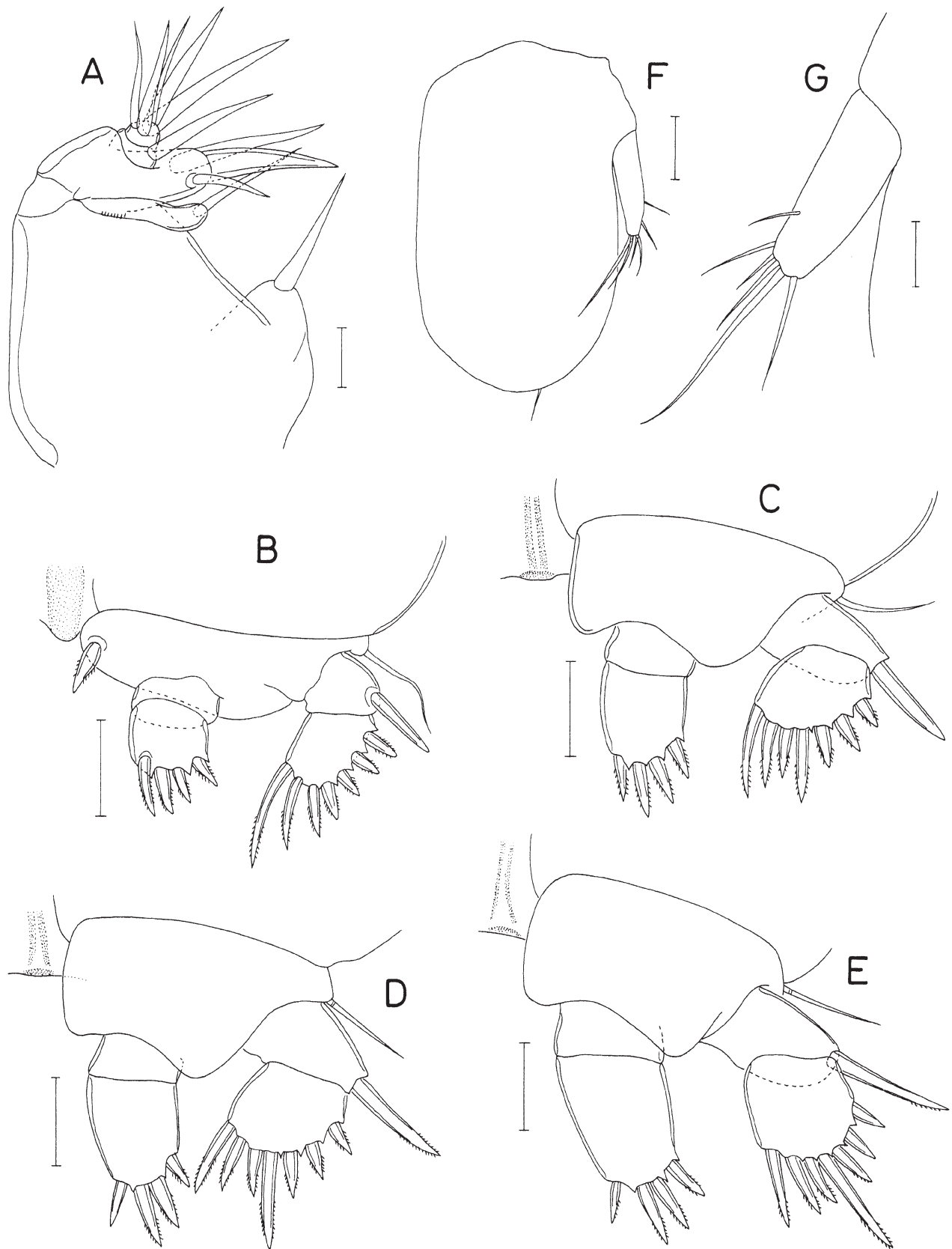
### ***Bathycopola karubar* gen. et sp. nov.**

(Figs. 14, 15)

**Type material.** Holotype ♀ (intact) (MNHN-IU-2018-1945) from *Styela squamosa* Herdman, 1881; off Tanimbar Is., Indonesia KARUBAR Expedition Stn CC57 (08°19'S, 131°53'E), depth 603-620 m, Bouchet, Kastoro & Métivier coll., 31 October 1991. 1 ♀ (dissected paratype, MNHN-IU-2014-17362) in *S. squamosa* (MNHN-IT-2008-8357 = MNHN S1/STY/285), Tanimbar Is., Indonesia, KARUBAR Expedition Stn CP54 (08°21'S, 131°43'E), depth 836-869 m, Bouchet, Kastoro & Métivier coll., 30 October 1991.



**FIG. 14.** *Bathycopola karubar* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genital somite and abdomen, ventral; D, right caudal ramus, ventral; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule; J, maxilliped. Scale bars: A, B, 0.2 mm; C, 0.1 mm; D, G-I, 0.02 mm; E, F, 0.05 mm.



**FIG. 15.** *Bathycopola karubar* **gen. et sp. nov.**, female. A, maxilla; B, leg 1; C, leg 2; D, leg 3; E, leg 4; F, leg 5; G, exopod of leg 5. Scale bars: A, 0.02 mm; B-E, G, 0.05 mm; F, 0.1 mm.

**Etymology.** The specific name refers to the “KARUBAR” Expedition to Indonesia during which the type specimens were collected.

**Description of female.** Body (Fig. 14A, B) stout; body length 1.99 mm; maximum width 567 µm across cephalosome. Prosome cylindrical, consisting of cephalosome and 4 pedigerous somites, with almost parallel margins, distinctly longer than urosome, occupying 65% of total body length. Articulations between pedigerous somites incomplete; tergites weak, sparsely covered with fine setules; tergite of fourth pedigerous somite extended posterodorsally. Urosome 5-segmented, but fifth pedigerous somite obscurely articulated from prosome, directed posteroventrally. Genital somite (Fig. 14C) longer than wide (300×255 µm); gradually narrowing posteriorly, with copulatory pore proximally on ventral surface. Three abdominal somites 182×200, 109×170, and 90×160 µm, respectively; anal operculum distinct, broad. Caudal rami small, extremely widely separated from each other; each ramus (Fig. 14D) 2.68 times longer than wide, slightly curved, narrowing distally; armed with 3 setae (1 lateral, 1 subdistal, and 1 distal), and 3 distal spines; lateral seta positioned at 43% of ramus length; largest of 3 distal spines 24 µm long. Egg sac 745×482 µm, flattened, 2 eggs-thick, containing about 20 eggs; each egg about 160 µm in diameter.

Rostrum represented by blunt anterior prominence of cephalosome. Antennule (Fig. 14 E) slender, 307 µm long, 7-segmented; armature formula 2, 3, 5, 2, 5+aesthetasc, 2+aesthetasc, and 11+2 aesthetascs; setae slender and naked, aesthetascs very small, hardly visible. Antenna (Fig. 14F) 3-segmented, excluding rudimentary coxa; first segment (basis) gradually broadening distally, 1.7 times longer than wide, distally bearing 1 slender spine (63 µm long) ornamented with spinules in distal half; second segment (first endopodal segment) 1.5 times longer than wide, 0.7 times as long as basis, with 1 seta on inner margin; third segment (second endopodal segment) 2.67 times longer than wide (72×27 µm), armed with 2 inner margin setae and 3 distal setae plus slender terminal claw, 0.8 times as long as second endopodal segment.

Labrum (Fig. 14G) much broader than long, strongly tapering, with deep and wide posteromedian incision and medially directed, tooth-like pointed process on each posterolateral apex. Mandible (Fig. 14H) consisting of coxa and palp: medial margin of coxal gnathobase bearing 1 strong distal tooth and several spinule-like denticles along mid-region, and slender, spinulose process proximally; palp biramous, consisting of well-defined basis, exopod, and endopod, armed with 3 setae on basis, 4 setae on exopod, and 6 setae on endopod; all setae naked and distinct. Maxillule (Fig. 14I) consisting of precoxa and palp; precoxa bearing 9 setae on arthrite (5 broad and spiniform); palp trilobate with 2 large setae on outer lobe (representing original exopod), 4 setae on middle lobe (endopod), and 6 setae on medial lobe (basis); 1 seta (original enditic seta of coxa) present between arthrite and medial lobe. Maxilla (Fig. 15A) consisting of syncoxa, basis, and 2-segmented endopod; syncoxa bearing 2 prominent endites, each tipped with 1 seta, distal endite located between syncoxa and basis; basis produced medially, armed with claw plus 2 setae; endopod small, bearing 1 seta on first segment and 5 on second. Maxilliped (Fig. 14J) as unsegmented, digitiform lobe armed with 7 setae (2 apical and 5 on medial margin); ornamented with rows of minute spinules.

Legs 1-4 (Fig. 15B-E) biramous with 2-segmented rami; coxae lacking inner seta. Exopods and endopods armed only with spines, lacking setae. Outer spine on first exopodal segment large, longer than width of segment. First endopodal segment of legs 1-4 lacking inner seta. Exopods of legs 1-4 bearing same armature formula; endopods of legs 1-4 also bearing same armature formula, as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; III, I, III	0-0; I, II, I
Legs 2-4	0-0	1-0	I-0; III, I, III	0-0; I, II, I

Leg 5 (Fig. 15F) consisting of lamellate protopod and small exopod: protopod 550×330 µm, nearly elliptical, extending to posterior margin of first abdominal somite, bearing 1 small seta distally; exopod (Fig. 15G) 2.9 times longer than wide (156×54 µm), slightly tapering, armed with 6 setae (1 on ventral margin, 1 subdistally, and 4 distally). Leg 6 not observed.

**Male.** Unknown.

**Remarks.** The diagnostic features of *Bathycopola karubar* **gen. et sp. nov.** are: (1) the antennule is distinctly 7-segmented; (2) the mandibular palp bears a clearly defined exopod and endopod; (3) the maxilla has a 2-segmented endopod armed with 1 and 5 setae on the first and second segments, respectively; (4) all swimming legs lack the inner seta on the coxa; and (5) all endopods of legs 1-4 are armed with four spines on the distal segment.

***Bathycopola brevicaudata* gen. et sp. nov.**

(Figs. 16, 17)

**Type material.** Holotype ♀ (MNHN-IU-2018-1946, dissected and mounted on a slide) from *Bathystyeloides enderbyanus* (Michaelsen, 1904) (MNHN-IT-2008-1439 = MNHN S1/BAT.B/24); West Atlantic, DEMERABY cruise, RV “Jean Charcot”, Stn CP 08 (10°25.10'N, 46°46.90'W), depth 4850 m, 01 September 1980.

**Etymology.** The name is derived from the Latin *brev* (=short) and *caud* (=the tail), referring to the short urosome of the new species.

**Description of female.** Body (Fig. 16A, B) stout, pupa-shaped. Body length 1.15 mm; maximum width 386 µm across fourth pedigerous somite. Prosome 5-segmented, occupying most of body length; cephalosome 204×364 µm, slightly wider than first and second pedigerous somites; dorsal cephalic shield well-developed. First to third pedigerous somites each bearing thin tergite; tergite of fourth pedigerous somite extended posteriorly, covering most of urosome, with rounded posterior margin in dorsal view (Fig. 16A), but obliquely tapering in lateral view (Fig. 16B). Urosome (Fig. 16C) small, about 355 µm long, gradually narrowing posteriorly, 5-segmented but first segment (fifth pedigerous somite) very short, obscure. Genital somite wider than long, bearing small copulatory pore proximally on ventral surface. Caudal ramus (Fig. 16D) about 2.8 times longer than wide (76×27 µm); armed with 3 spines and 3 setae (1 seta on outer margin, 1 seta on subdistal inner side, and 1 seta and 3 spines distally); outer margin seta longest, half as long as caudal ramus; innermost of 3 distal spines much smaller than other 2.

Rostrum as short, blunt anterior prominence on cephalosome. Antennule (Fig. 16E) slender, 220 µm long, 6-segmented; armature formula 2, 8, 3, 6+aesthetasc, 2+aesthetasc, and 11+2 aesthetascs; second segment subdivided into 3 and 5 setae regions; setae thin and generally long; aesthetascs small, confusable with setae. Antenna (Fig. 16F) 3-segmented, consisting of basis and 2-segmented endopod; basis broadening distally, 59×45 µm, armed with 1 elongate spine (56 µm long) distally and bearing few spinules in distal region; first endopodal segment 55×32 µm with 1 seta on inner margin; second endopodal segment about 2.5 times longer than wide (45×18 µm); armed with 2 middle and 4 distal setae plus slender terminal claw, 0.8 times as long as segment.

Labrum (Fig. 16G) short but broad, with pair of bicuspid processes on posteroventral surface. Mandible (Fig. 16H) consisting of coxa and palp: coxal gnathobase bearing 1 distal tooth and several spinule-like denticles along medial margin; palp biramous, armed with 3 setae on basis, 4 on exopod, and 6 on endopod; endopod articulated from basis but exopod not demarcated from basis; setae on exopod feebly pinnate, other setae naked. Maxillule (Fig. 16I) consisting of precoxa and palp; precoxa bearing 9 setae on arthrite; palp consisting of basis, exopod and endopod; armed with 6 setae on basis, 2 on exopod, and 3 on endopod; exopod and endopod not articulated from basis; 1 additional seta present between arthrite and basis. Maxilla (Fig. 17A) 3-segmented; large syncoxa bearing 2 endites each tipped with 1 seta; basis with claw plus 3 setae; endopod small, bearing 5 setae. Maxilliped (Fig. 17B) as tapering lobe bearing 7 setae and 3 rows of spinules.

Legs 1-4 (Fig. 17C-F) biramous with 2-segmented rami. Inner seta on coxa present only in leg 4. First endopodal segment of legs 1-4 unarmed. In legs 3 and 4, outer spine of first exopodal segment and distal spine of second exopodal segment markedly elongated (longer than exopod). Most of spines on rami spinulose distally. Exopods and endopods of legs 2-4 with same armature formula, as follows:

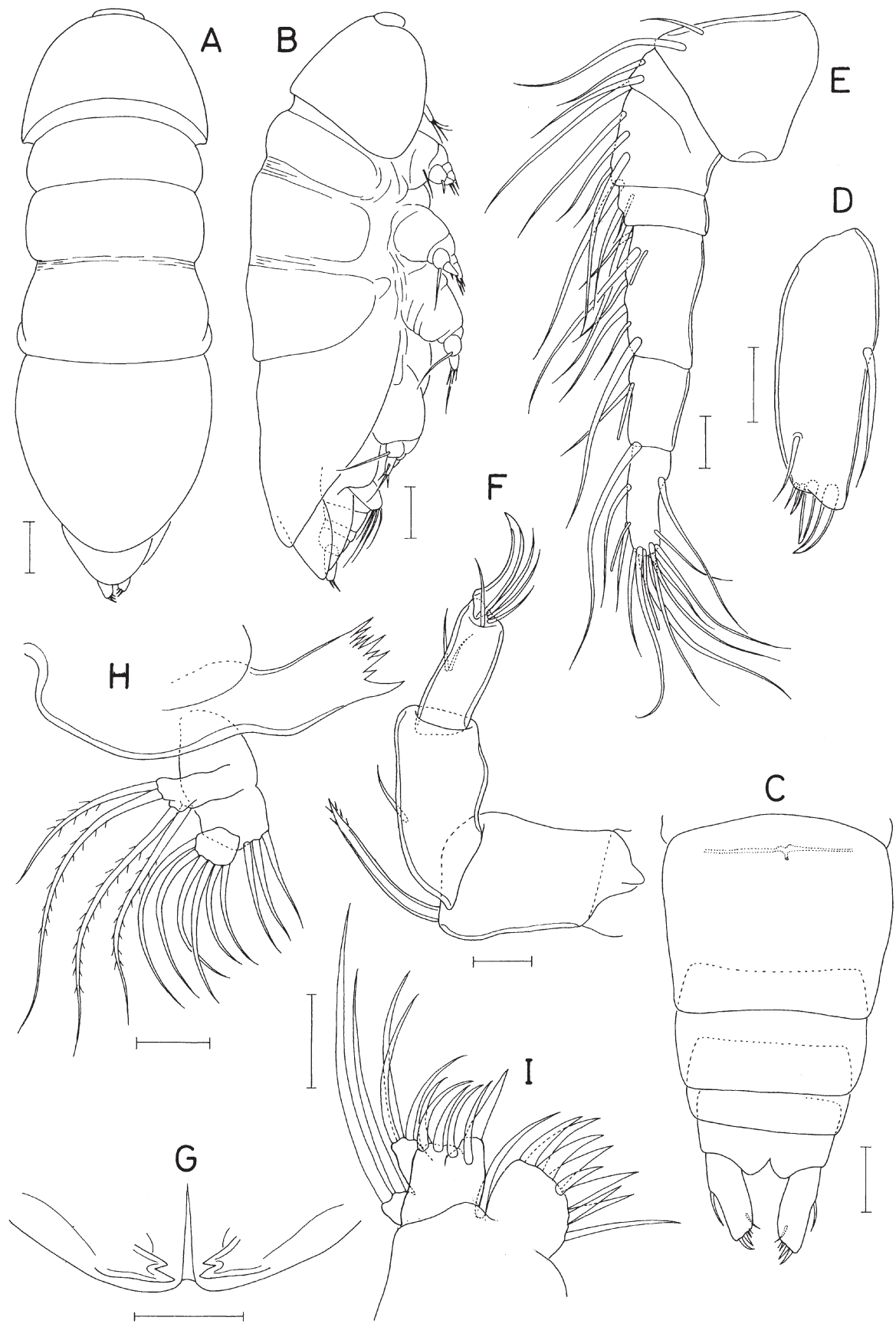
	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; III, I, III	0-0; I, II, I
Legs 2 & 3	0-0	1-0	I-0; III, I, III+1	0-0; I, II, I+1
Leg 4	0-1	1-0	I-0; III, I, III+1	0-0; I, II, I+1

Leg 5 (Fig. 17G) consisting of lamellate protopod and small exopod; protopod as long as urosome, covering almost entire dorsal surface of urosome (Fig. 16A, B), bearing 1 small seta on distal margin; exopod 2.18 times longer than wide (98×45 µm), armed with 6 unequal setae (1 on ventral margin and 5 distally). Leg 6 not examined.

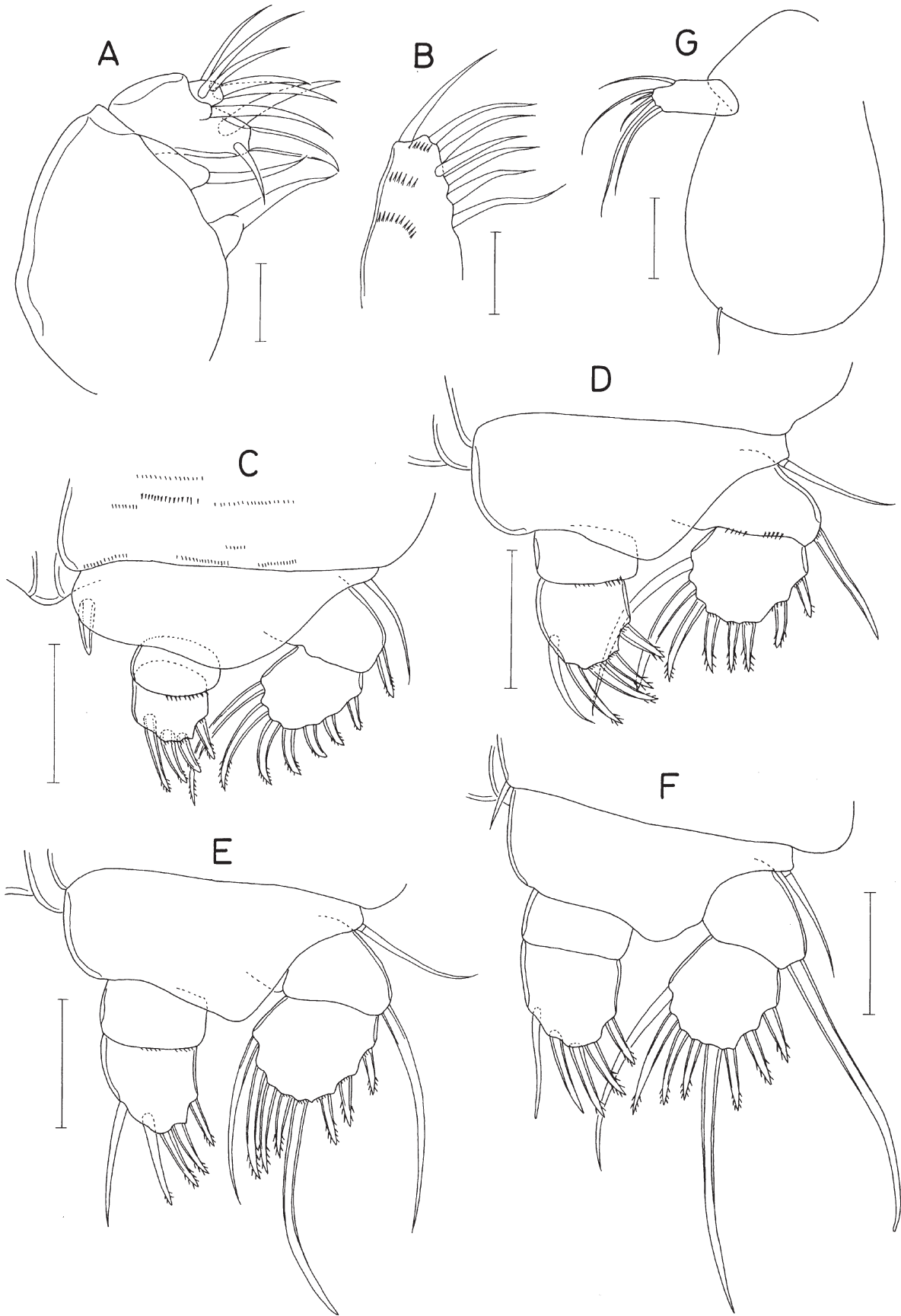
**Male.** Unknown.

**Remarks.** The diagnostic features of *Bathycopola brevicaudata* gen. et sp. nov. are; (1) the dorsal tergite of the fourth pedigerous somite extends posteriorly to cover most of the urosome; (2) the maxillary endopod is 1-segmented and





**FIG. 16.** *Bathycopola brevicaudata* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, right; C, urosome, ventral; D, right caudal ramus, dorsal; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule. Scale bars: A, B, 0.1 mm; C, 0.05 mm; D-I, 0.02 mm.



**FIG. 17.** *Bathycopola brevicaudata* gen. et sp. nov., female. A, maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, leg 5. Scale bars: A, B, 0.02 mm; C-F, 0.05 mm; G, 0.1 mm.

armed with five setae; (3) the second exopodal segments of legs 2-4 are each armed with 7 spines and 1 seta; (4) the second endopodal segments of legs 2-4 are each armed with 4 spines and 1 seta; and (5) the inner coxal seta present only in leg 4. These diagnostic features serve to distinguish the new species from its congeners.

***Bathycopola dicarpae* gen. et sp. nov.**

(Figs. 18, 19)

**Type material.** Holotype ♀ (MNHN-IU-2018-1947, dissected and mounted on a slide) from *Dicarpa lata* Monniot C. & Monniot F., 1976 (MNHN-IT-2008-2786 = MNHN S1/DIC/10); Angola Basin, South Atlantic, Walda cruise, RV “Jean Charcot”, Stn Cy 02 (18°52.1’S, 07°23.1’E), depth 5124 m, 06 June 1971.

**Etymology.** The generic name of the ascidian host, *Dicarpa*, provides the specific name of the new species.

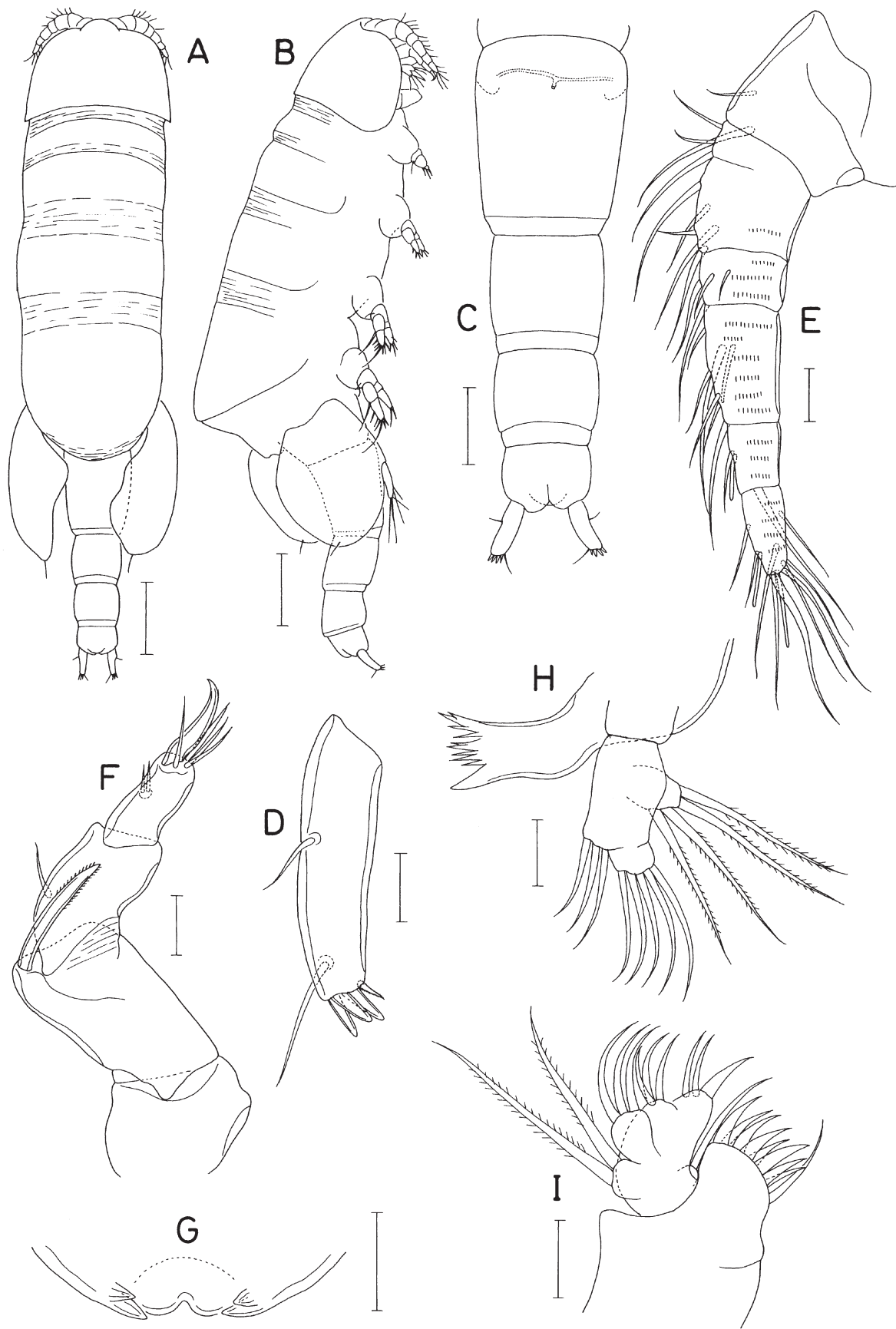
**Description of female.** Body (Fig. 18A, B) narrow; body length 1.88 mm. Prosome cylindrical, unsegmented, 1.24×0.42 mm, occupying 66% of body length, with parallel lateral margins. Cephalic shield distinct; 4 pedigerous somites obscurely discernible by traces of tergites and surface wrinkles. Urosome (Fig. 18C) directed posteroventrally, 5-segmented; first urosomite (fifth pedigerous somite) short, obscure. Genital somite 242×197 µm, bearing small copulatory pore proximally on ventral surface. Three abdominal somites 152×148, 121×136, and 76×115 µm, respectively. Caudal rami widely separated from each other; each ramus (Fig. 18D) about 3.04 times longer than wide (76×25 µm), as long as anal somite; armed with 1 lateral seta, 1 subdistal seta, and 3 spines and 1 seta distally; distal spines shorter than ramus width, longest one 15 µm long, and smallest seta spiniform; subdistal seta 40 µm long, about twice as long as lateral seta; lateral seta positioned at 44% region of ramus length.

Rostrum absent. Antennule (Fig. 18E) slender, about 220 µm long, 6-segmented with second segment subdivided into 3 and 5 setae regions; armature formula 2, 8, 4, 6+aesthetasc. 2+aesthetasc, and 9+2 aesthetascs; second to terminal segments ornamented with 1 to 6 transverse rows of fine spinules. Antenna (Fig. 18F) 4-segmented, consisting of coxa, basis, and 2-segmented endopod; coxa short and unarmed; basis 1.5 times longer than wide (64×41 µm), broadening distally, armed with 1 large spine distally (45 µm long); first endopodal segment 44×28 µm, about 0.7 times as long as basis, bearing 1 seta on inner margin; second endopodal segment twice as long as wide (36×18 µm), shorter than first; armed with 5 setae (2 in middle and 3 distally) plus terminal claw 32 µm long, slightly shorter than second endopodal segment.

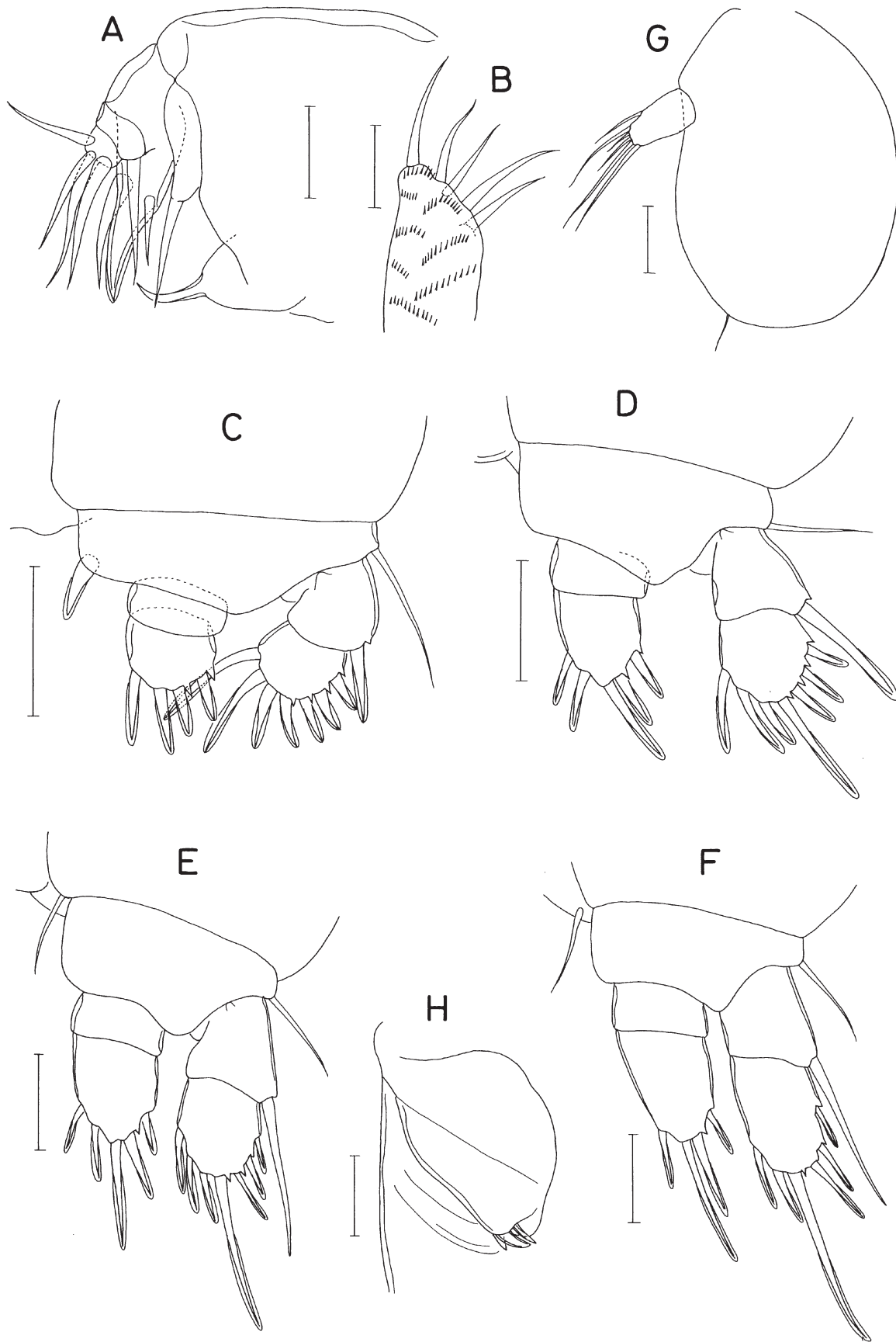
Labrum (Fig. 18G) short and broad, bearing 2 pairs of tooth-like processes, as in preceding species, but with shallow posteromedian incision. Mandible (Fig. 18H) consisting of coxa and palp; medial margin of coxal gnathobase bearing 1 strong tooth distally and several spinules along middle and proximal regions; palp consisting of basis, exopod and endopod; basis with 3 setae mediolaterally; exopod with 4 weakly pinnate setae; endopod incompletely articulated from basis, armed with 5 or 6 setae distally. Maxillule (Fig. 18I) consisting of precoxa bearing 9 setae on arthrite and unsegmented palp, bearing coxal endite, basis, and lobate exopod and endopod; armed with 1 seta on coxal endite, 6 on basis along bilobed medial margin (3 on proximal and 3 on distal lobes), 2 large, weakly pinnate setae on exopod, and 3 on endopod. Maxilla (Fig. 19A) 4-segmented, consisting of syncoxa, basis, and 2-segmented endopod; syncoxa broad, bearing 2 prominent endites each tipped with 1 seta, seta on proximal endite not articulated at base; basis drawn out to robust claw bearing 2 setae near base; endopod small, with 1 and 4 setae on first and second segments, respectively. Maxilliped (Fig. 19B) as spinulose lobe bearing 4 or 5 setae (1 seta positioned at apex).

Legs 1-4 (Fig. 19C-F) biramous with 2-segmented rami. Inner coxal seta absent in legs 1 and 2, but present in legs 3 and 4. Rami of legs 1-4 armed with spines only except first exopodal segment of legs 3 and 4 bearing outer seta, outer spine present on same segment in legs 1 and 2. Distal spine on second exopodal segment of legs 2-4 elongated, about 3 times longer than nearby spines. First endopodal segment of legs 1-4 unarmed. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; III, I, III	0-0; I, II, I
Leg 2	0-0	1-0	I-0; III, I, III	0-0; I, II, II
Leg 3	0-1	1-0	1-0; III, I, III	0-0; I, II, II
Leg 4	0-1	1-0	1-0; III, I, II	0-0; I, II, II



**FIG. 18.** *Bathycopola dicarpae* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, right; C, urosome, ventral; D, right caudal ramus, ventral; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule. Scale bars, A, B, 0.2 mm; C, 0.1 mm; D-I, 0.02 mm.



**FIG. 19.** *Bathycopola dicarpae* gen. et sp. nov., female. A, maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, leg 5; H, genital aperture. Scale bars: A, B, H, 0.02 mm; C-F, 0.05 mm; G, 0.1 mm.

Leg 5 (Fig. 19G) consisting of lamellate protopod and small exopod; protopod  $475 \times 330 \mu\text{m}$ , extending beyond posterior margin of genital somite, bearing 1 thin seta distally; exopod about 1.83 times longer than wide ( $106 \times 58 \mu\text{m}$ ), slightly tapering; armed with 6 setae (1 on subdistal ventral margin and 5 on distal margin). Leg 6 (Fig. 19H) represented by 3 small spiniform elements on genital operculum.

**Male.** Unknown.

**Remarks.** *Bathycopola dicarpae* **gen. et sp. nov.** has a 4-segmented maxilla, and is armed with 7 spines on the second exopodal segment of legs 2 and 3, plus 4 spines on the second endopodal segment of leg 4. These features are shared only with the type species, *B. karubar* **gen. et sp. nov.** However, *B. dicarpae* **gen. et sp. nov.** can be readily distinguished from *B. karubar* **gen. et sp. nov.** by the following character states: (1) the second endopodal segment of the maxilla bears 4 setae in *B. dicarpae* **gen. et sp. nov.** (cf. 5 setae in *B. karubar* **gen. et sp. nov.**); (2) the maxilliped bears 4 or 5 setae (cf. 7 setae); (3) the second endopodal segment of legs 2 and 3 bears 5 spines (cf. 4 spines); (4) the second exopodal segment of leg 4 bears 6 spines (cf. 7 spines); (5) legs 3 and 4 bear an inner seta on the coxa (cf. seta absent in *B. karubar* **gen. et sp. nov.**); and (6) the exopod of leg 5 is about 1.83 times longer than wide (cf. about 2.89 times in *B. karubar* **gen. et sp. nov.**).

### *Bathycopola setifera* **gen. et sp. nov.**

(Figs. 20, 21)

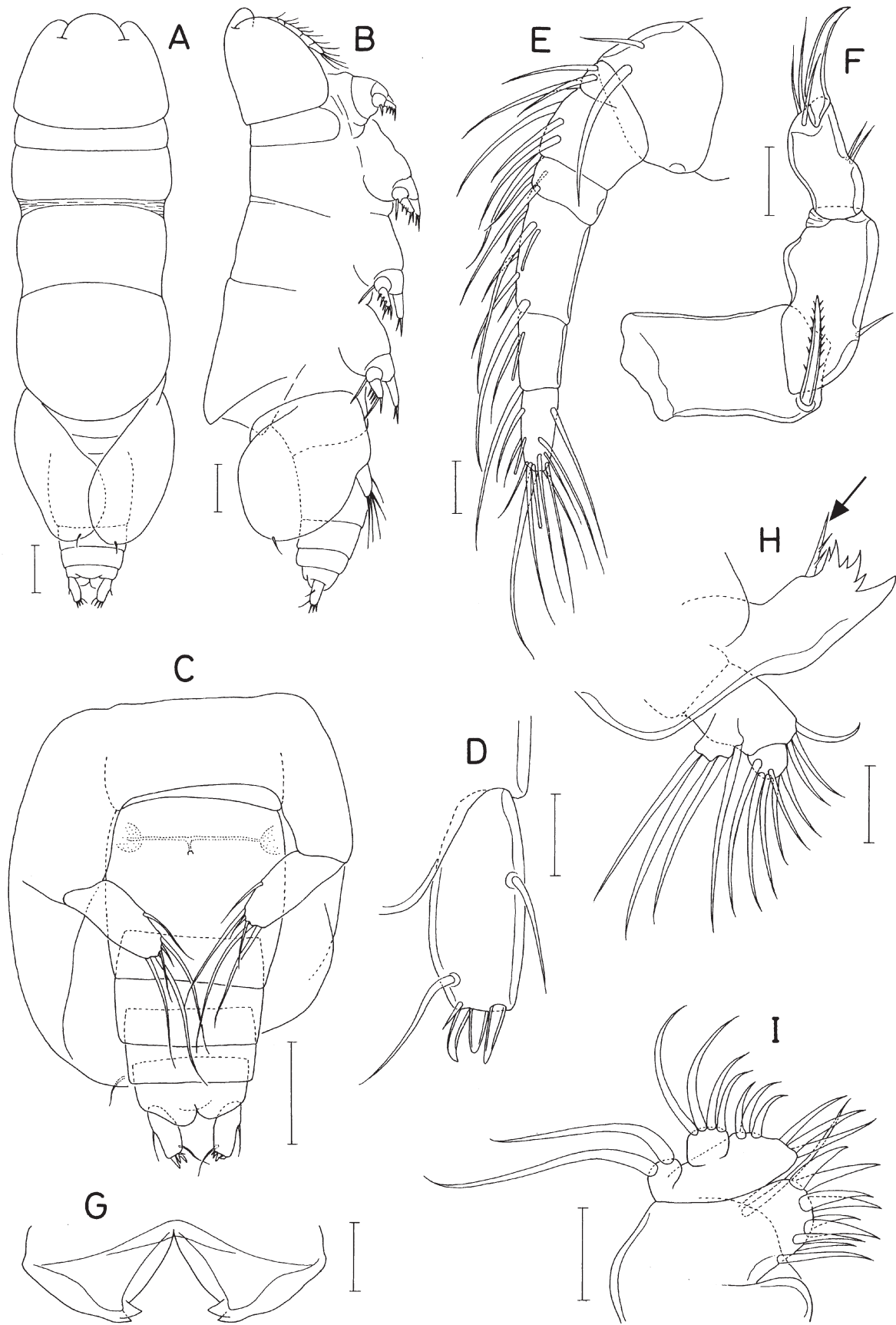
**Type material.** Holotype ♀ (MNHN-IU-2018-1948, dissected and mounted on a slide) from *Cnemidocarpa digonas* Monniot C. & Monniot F., 1968; Bay of Biscay, BIOGAS 3 Expedition, RV “Jean Charcot”, Stn DS45 ( $47^{\circ}33.9'N$ ,  $09^{\circ}38.4'W$ ), depth 4260 m, September 1973.

**Etymology.** The specific name refers to the presence of a seta on the proximal margin of the coxal gnathobase of the mandible.

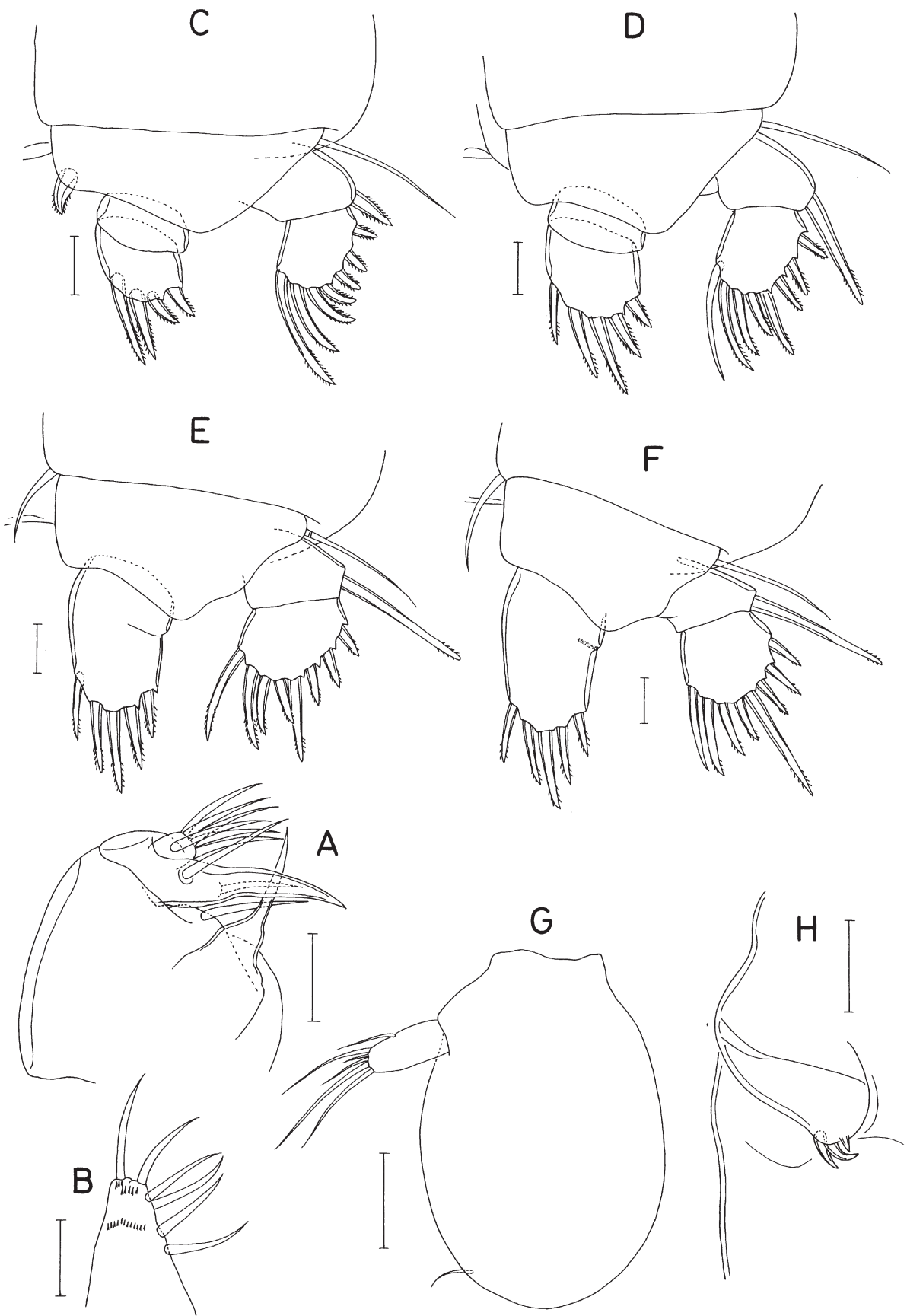
**Description of female.** Body (Fig. 20A, B) narrow, 1.28 mm long. Prosome cylindrical, longer than urosome, consisting of cephalosome and 4 pedigerous somites; maximum width of body  $339 \mu\text{m}$  at level of second pedigerous somite. Pedigerous somites discernible by 3 dorsal suture lines, becoming longer from anterior to posterior; posterodorsal border of fourth pedigerous somite produced posterodorsally, with rounded posterodorsal margin. Urosome (Fig. 20C) 5-segmented; fifth pedigerous somite short, indistinctly demarcated from prosome. Genital somite as long as wide ( $170 \times 170 \mu\text{m}$ ), bearing copulatory pore on ventral surface. Three abdominal somites  $110 \times 143$ ,  $70 \times 127$ , and  $60 \times 110 \mu\text{m}$ , respectively. Caudal ramus (Fig. 20D) about 2.3 times longer than wide ( $55 \times 24 \mu\text{m}$ ), slightly shorter than anal somite, with convex inner margin; armed with 1 lateral seta, 1 inner subdistal seta, and 3 spines plus 1 seta distally; lateral seta positioned at 40% of ramus length; lateral and inner subdistal setae more than half length of ramus; distal spines small, outer spine longest ( $15 \mu\text{m}$ ); small distal seta spiniform.

Rostrum as blunt anterior prominence of cephalosome (Fig. 20A, B). Antennule (Fig. 20E) slender,  $85 \mu\text{m}$  long, 6-segmented; armature formula 2, 7, 3, 6+aesthetasc, 2+aesthetasc, and 11+2 aesthetascs; aesthetascs small and setiform. Antenna (Fig. 20F) 3-segmented, consisting of coxobasis and 2-segmented endopod; coxobasis  $54 \times 33 \mu\text{m}$ , with 1 large, spinulose spine ( $31 \mu\text{m}$  long); first endopodal segment  $44 \times 27 \mu\text{m}$ , with 1 seta on inner margin; second endopodal segment 2.12 times longer than wide ( $36 \times 17 \mu\text{m}$ ); armed with 2 setae in middle of inner margin and 3 setae distally plus terminal claw  $36 \mu\text{m}$  long, as long as second endopodal segment.

Labrum (Fig. 20G) forming 2 tapering posterior lobes, with deep and wide posteromedian incision; both lobes bearing medially facing pair of teeth at apex. Mandible (Fig. 20H) consisting of coxa and palp: coxal gnathobase bearing strong distal tooth and 5 spiniform denticles on medial margin and 1 spinulose seta (arrowed) on proximal margin; palp biramous, bearing 3 setae on mediobasal corner of basis, 4 setae on exopod and 6 setae on endopod; endopod distinctly articulated from basis, but exopod not articulated at base. Maxillule (Fig. 20I) consisting of pre-coxa with 9 setae on arthrite, and biramous palp with 6 setae on medial margin of basis; exopod and endopod lobate, not articulated from basis, bearing 2 and 4 setae, respectively; 1 seta present between basis and arthrite. Maxilla (Fig. 21A) 3-segmented; syncoxa bearing 2 endites, each tipped with 1 seta, seta on proximal endite not articulated at base; basis with strong claw plus 2 setae; endopod small, 1-segmented, with 6 setae (1 inserted in middle of segment). Maxilliped (Fig. 21B) as tapering lobe bearing 6 setae (4 medial and 2 apical) and 2 rows of minute spinules.



**FIG. 20.** *Bathycopola setifera* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, right; C, urosome, ventral; D, right caudal ramus, dorsal; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule. Scale bars: A-C, 0.1 mm; D-I, 0.02 mm.



**FIG. 21.** *Bathycopola setifera* gen. et sp. nov., female. A, maxilla; B, maxilliped; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, leg 5; H, genital aperture. Scale bars: A-F, H, 0.02 mm; G, 0.1 mm.



Legs 1-2 (Fig. 21C-F) biramous with 2-segmented rami; coxa lacking inner seta. Legs 3 and 4 (Fig. 21E, F) with 2-segmented exopods and 1-segmented endopods; coxa of legs 3 and 4 bearing inner seta; endopods subdivided by partial suture line on outer side. Outer spine on first exopodal segment of legs 2-4 elongated. Most of spines on rami of legs 1-4 spinulose distally. Legs 3 and 4 with same armature; armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-I	I-0; III, I, III	0-0; I, II, I
Leg 2	0-0	1-0	I-0; III, I, III+1	0-0; I, II, II
Legs 3 & 4	0-1	1-0	I-0; III, I, IV	I, II, II

Leg 5 (Fig. 21G) consisting of lamellate protopod and small exopod; protopod oval, 375×257 µm, extending beyond distal margin of first abdominal somite, armed with 1 minute seta on ventral side of distal margin; exopod about 2.2 times longer than wide (86×39 µm), bearing 6 unequal setae (1 on ventral margin and 5 on distal margin); left and right legs fused with each other proximally on ventral surface (Fig. 20C). Leg 6 (Fig. 21H) represented by 3 small spines on genital operculum.

**Male.** Unknown.

**Remarks.** In *Bathycopola* **gen. nov.** the leg armature seems to be a robust taxonomic character that can be used to differentiate between species, but *B. setifera* **gen. et sp. nov.** and *B. brevicaudata* **gen. et sp. nov.** have the same armature formula for the rami of legs 2-4. In addition, both species share a 3-segmented maxilla. The major differences between the two species are in the number of setae on the maxillary endopod and the maxilliped, and the presence or absence of the inner coxal seta on leg 3 (Table 1). The segmentation of legs 3 and 4 and the length of some of the exopodal spines on these legs also differ significantly between the two species.

**TABLE 1.** Characteristics of four new species of *Bathycopola* **gen. nov.** Abbreviations: enp = endopod, exp = exopod.

Characters	<i>B. karubar</i> <b>gen. et sp. nov.</b>	<i>B. brevicaudata</i> <b>gen. et sp. nov.</b>	<i>B. dicarpae</i> <b>gen. et sp. nov.</b>	<i>B. setifera</i> <b>gen. et sp. nov.</b>
maxilla enp armature	1, 5	5	1, 4	6
setae on maxilliped	7	7	4 or 5	6
legs 2-4 exp armature	8, 8, 8	9, 9, 9	8, 8, 7	9, 9, 9
legs 2-4 enp armature	4, 4, 4	5, 5, 5	5, 5, 4	5, 5, 5
inner coxal seta	absent	present leg 4	present legs 3-4	present legs 3-4
Distributions (known depths)	Indonesia (603-872 m)	W. Atlantic (4850 m)	S. Atlantic (5124 m)	N. Atlantic (4260 m)

## Family Buproridae Thorell, 1859

**Diagnosis** (female). Body stout, consisting of distinct cephalosome and extremely inflated trunk. Rostrum with rounded apex. Abdomen extremely reduced to short lobe; caudal rami absent. Antennule 3- to 7-segmented; first segment bearing 2 setae. Antenna 3-segmented, with armature formula 1, 4, and 5 or 6. Labrum distinct. Mandible consisting of coxa with well-developed gnathobase and palp with 1 to 3 distal setae, or palp represented by seta. Maxillule consisting of precoxa and palp; precoxa with 6 or 7 spiniform setae on arthrite; palp unsegmented with 4 or 5 setae. Maxilla consisting of syncoxa with 1 large endite tipped with 2 elements, and allobasis with 4 or 5 elements. Maxilliped unsegmented, unarmed or armed with 4 setae. Legs 1-4 biramous with 2-segmented exopods; endopods 1-segmented in *Buprorus* and 2-segmented in *Buprorides* **gen. nov.**; coxa unarmed; basis of leg 1 with or without inner distal element. Leg 5 unsegmented, extending beyond posterior margin of abdomen and armed distally with several setae.

**Remarks.** The family Buproridae was established by Thorell (1859) to accommodate his new monotypic genus, *Buprorus* Thorell, 1859. However, in their comprehensive revision of the family Ascidicolidae, Illg & Dudley (1980) accorded this taxon subfamily status, as the Buprorinae. They considered that the antenna of all the other subfamilies within the ascidicolid series could be derived from a limb exhibiting the basic structure of the antenna in *Buprorus* (Illg & Dudley, 1980). Marchenkov & Boxshall (2002) compared the antennal segmentation patterns across all subfamilies of Ascidicolidae and showed that the ancestral first and second endopodal segments of the antenna are fused in *Buprorus* and the third endopodal segment is free, and that the main flexure plane of the limb lies between the basis and endopod. In contrast, in all of the other subfamilies the third endopodal segment is fused with the second and the main flexure plane of the limb lies between the ancestral first and second endopodal segments. Based primarily on this difference, Marchenkov & Boxshall (2002) treated the Buproridae as a family level taxon.

Until the present account, the Buproridae remained a monotypic family represented only by the genus *Buprorus*. The genus *Buprorus* currently consists of three species: *B. loveni* Thorell, 1859 known from Scandinavian waters and from off Mauritania in the eastern North Atlantic (Thorell, 1859; Marchenkov & Boxshall, 2002) and from the Atlantic coast of America in the western North Atlantic (Dudley & Illg, 1991), *B. nordgaardi* G.O. Sars, 1921 known from Norway (Sars, 1921), and *B. caudatus* Illg & Dudley, 1980 known from southern California on the Pacific coast of America (Illg & Dudley, 1980).

### ***Buprorides* gen. nov.**

**Diagnosis** (female). Cephalosome depressed, subcircular, well-defined from trunk somites by constriction. Urosome wider than long, with small rounded abdomen; caudal rami absent. Rostrum present. Antennule 5-segmented; first segment with 2 setae. Antenna 3-segmented, with 1, 4, and 6 setae on first to third segments, respectively. Labrum broad. Mandible consisting of coxa and 1-segmented palp; coxa with well-developed gnathobase; palp armed with 3 setae distally. Maxillule bilobed; inner lobe (precoxa) with spinulose spines on medial margin; outer lobe (palp) narrower than inner lobe, armed with 4 setae. Maxilla consisting of syncoxa and allobasis; syncoxa broad, with single large mediobasal endite tipped with 2 elements; allobasis with several setae. Maxilliped plate-like, unarmed. Legs 1-4 biramous with 2-segmented rami, armed only with setae; coxa lacking inner seta; intercoxal sclerite not discernible. Basis of leg 1 lacking inner distal element. Leg 5 expanded, lobate, extending over posterior margin of abdomen, armed with 5 naked setae distally.

**Type species.** *Buprorides trilobatus* gen. et sp. nov. by original designation.

**Etymology.** The new genus is named after *Buprorus*, the type genus of the family, and the suffix *-ides*. Gender masculine.

**Remarks.** In all three species of *Buprorus*, the maxilliped is armed with 4 setae and legs 1-4 have single-segmented endopods. *Buprorides* gen. nov. can be distinguished from *Buprorus*, because the maxilliped is unarmed and legs 1-4 have 2-segmented endopods. There are other notable differences between the genera, such as, the possession of 3 setae on the mandibular palp in *Buprorides* gen. nov. compared with 1 or 2 setae in *Buprorus*, and the presence of 6 slender setae on the terminal segment of the antenna rather than 5 setae (some spiniform) in *Buprorus*.

The type species of *Buprorides* gen. nov. and *Buprorus nordgaardi* are associated with compound ascidians, but the other two species of *Buprorus* are associated with solitary ascidians.

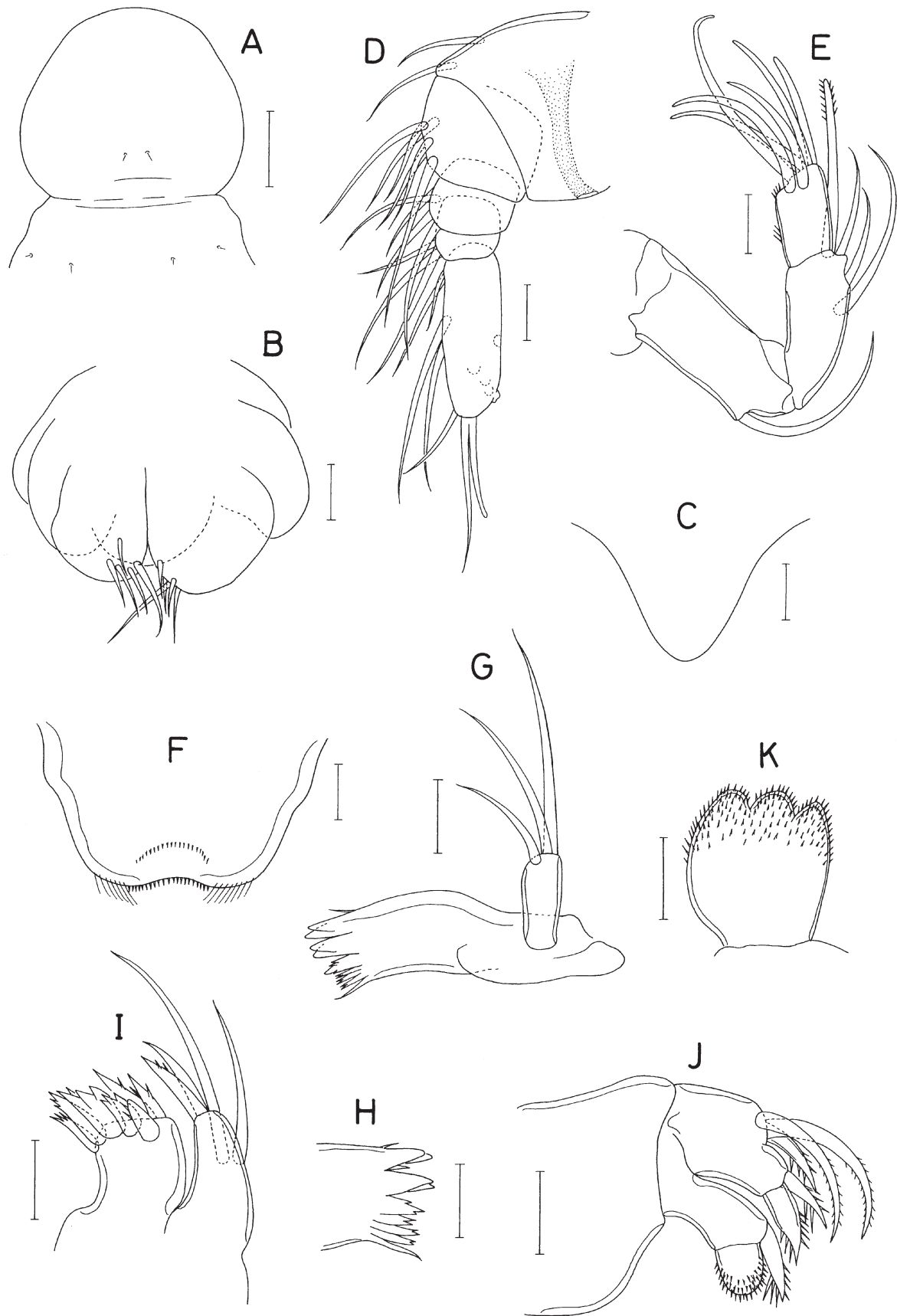
### ***Buprorides trilobatus* gen. et sp. nov.**

(Figs. 22, 23)

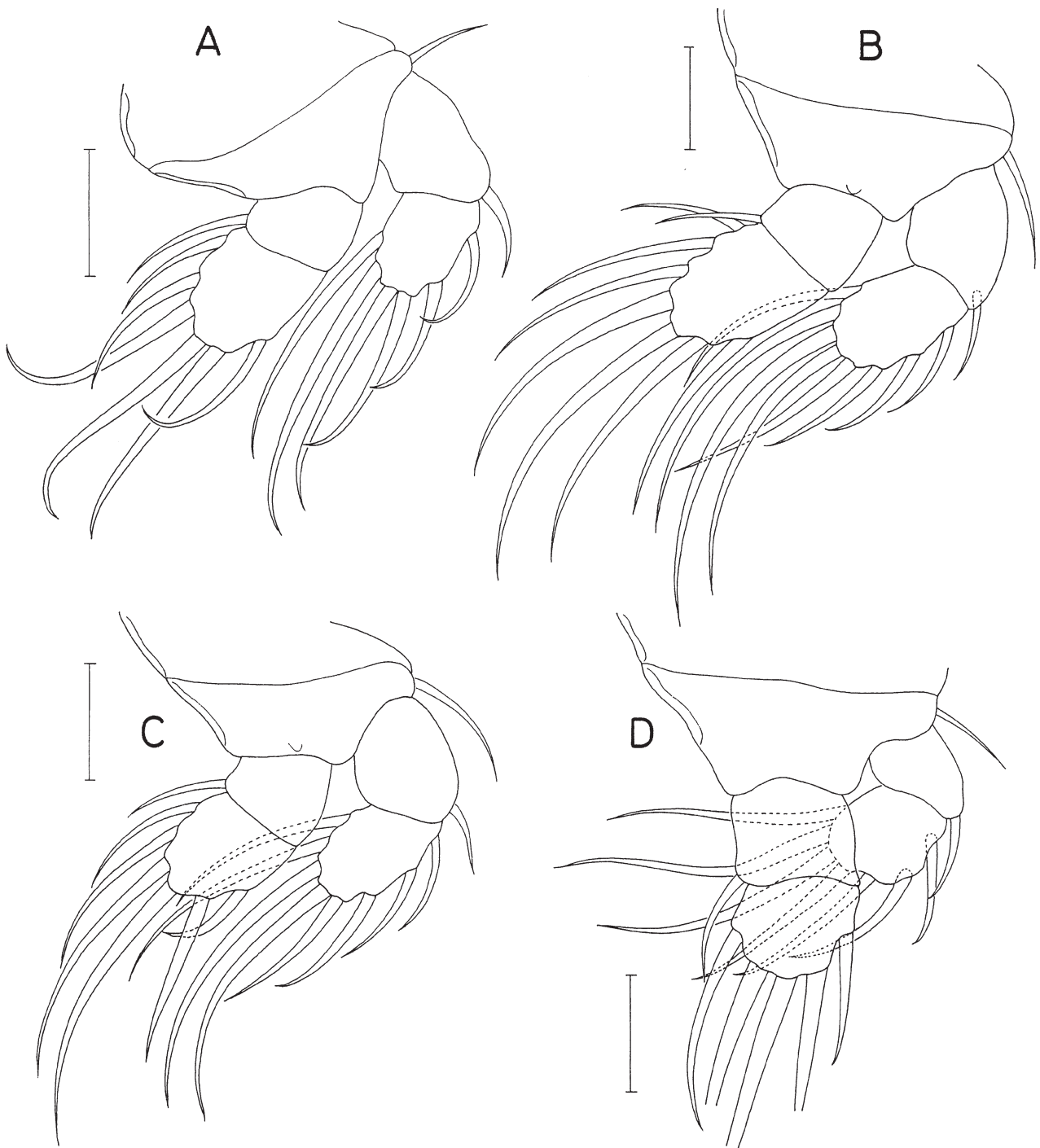
**Type material.** Holotype ♀ (MNHN-IU-2018-1949, damaged, dissected and mounted on a slide) and Paratype ♀ (MNHN-IU-2018-1950, damaged, dissected and mounted on a slide) from unidentified Didemnidae; Mont Jumeaux west, Norfolk Ridge, North of New Caledonia, CHALCAL 2 cruise, RV “Coriolis”, Stn DW79, depth 243 m, Bouchet, Métivier & Richer de Forges-IRD coll., 30 October 1986.

**Etymology.** The specific name refers to the trilobed maxilliped of the new species.

**Description of female.** Body form and size unknown due to damage to specimens. Cephalosome (Fig. 22A) depressed, subcircular, 126×148 µm, well-defined from trunk by deep constriction. Urosome (Fig. 24B) wider than long, constricted anteriorly; abdomen semicircular, unarmed, shorter than leg 5. Caudal rami absent.



**FIG. 22.** *Buprorides trilobatus* gen. et sp. nov., female. A, cephalosome, dorsal; B, urosome; C, rostrum; D, antennule; E, antenna; F, labrum; G, mandible; H, gnathobase of mandibular coxa; I, maxillule; J, maxilla; K, maxilliped. Scale bars: A, 0.05 mm; B-K, 0.01 mm.



**FIG. 23.** *Buprorides trilobatus* gen. et sp. nov., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scale bars: 0.02 mm.

Rostrum (Fig. 22C) strongly tapering, slightly wider than long, rounded apically, not demarcated from cephalosome. Antennule (Fig. 22D) 5-segmented; terminal segment longest; first segment much broader than distal segments, with transverse band of sclerotization, and armed with 2 setae; second to fifth segments armed with 6, 4, 3, and 11+aesthetasc, including insertion scars of setae on terminal segment; all setae naked. Antenna (Fig. 22E) 3-segmented, consisting of basis and 2 endopodal segments, strongly flexed between basis and first endopodal segment; armature formula 1, 4, and 6; basis  $33 \times 13 \mu\text{m}$ ; first and second endopodal segments  $21 \times 11$  and  $15 \times 9 \mu\text{m}$ , respectively: distalmost seta on first endopodal segment larger than proximal 3 setae, bluntly tipped and spinulose distally; all 6 setae on second endopodal segment naked and bluntly tipped.

Labrum (Fig. 22F) wider than long, narrowing distally, with setules laterally on distal margin and 2 rows of

minute spinules: 1 row along concave medial part of distal margin and other row on subdistal medial region of ventral surface. Mandible (Fig. 22G, H) consisting of coxa and 1-segmented palp; coxa with well-developed gnathobase bearing on medial margin 2 bifurcate distal teeth, 1 spinulose tooth, and proximally 3 small bifurcate spinules and 1 setule; distal margin bearing 1 small setule; palp 2.6 times longer than wide (13×5 μm), armed distally with 3 setae of unequal lengths, longest about 2.5 times longer than segment. Maxillule (Fig. 22I) bilobed; inner lobe (precoxa) with 7 thick, spinulose spines on medial margin; outer lobe (palp) narrower than inner lobe, armed with 2 longer subdistal and 2 shorter distal setae. Maxilla (Fig. 22J) consisting of syncoxa and allobasis; syncoxa broad, with 1 large mediodistal endite tipped with massive, spinulose, globular proximal element and 1 broad, spinulose distal seta; allobasis with 3 outer subdistal and 2 distal, spinulose setae (proximal of 2 distal setae broad and spini-form). Maxilliped (Fig. 22K) plate-like, narrowing proximally, trilobed along distal margin, unarmed, but densely ornamented with spinules on distal surface.

Legs 1-4 (Fig. 23A-D) biramous with 2-segmented rami, and armed only with naked setae; coxa lacking inner seta; intercoxal sclerite not discernible. Basis of leg 1 lacking inner distal element. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	1-0; 2, 1, 3	0-1; 1, 2, 3
Legs 2 & 3	0-0	1-0	1-0; 3, 1, 4	0-1; 2, 1, 3
Leg 4	0-0	1-0	1-0; 2, 1, 4	0-1; 1, 2, 2

Leg 5 (Fig. 22B) expanded, lobate, extending beyond posterior margin of abdomen, armed with 5 naked setae on rounded apex. Leg 6 absent.

**Male.** Unknown.

**Remarks.** Unfortunately, the two specimens available in this study were damaged, both with a crushed metasome. Therefore the precise body form and size are unknowable, but all the cephalic appendages and the swimming legs remained virtually intact.

### Family Botryllophilidae Sars, 1921

**Diagnosis.** Female: Body inflated, unsegmented or obscurely segmented, consisting of anterior and posterior parts, without distinct prosome-urosome division. Anterior part of body consisting of cephalosome to fifth pedigerous somites, posterior part consisting of genital somite and abdomen. Abdomen basically 4-segmented but with pattern obscured by additional annulations in some species of *Botryllophilus* and *Schizoproctus*. Caudal ramus armed with 6 armature elements (some represented by claws), or occasionally some lost. Rostrum weak or absent. Antennule short, at most 5-segmented. Antenna uniramous, 2- to 4-segmented, consisting coxa, basis, and 1- or 2-segmented endopod, and armed with up to 8 setal elements (setae or spines); coxa and basis sometimes fused to form coxobasis. Mandible variable, consisting of coxa bearing well-developed gnathobase and setiferous palp in *Botryllophilus* and *Schizoproctus*, but palp absent or consisting of 1- or 2-segmented lobe tipped with 1 or 2 armature elements in other genera. Maxillule consisting of precoxa and palp in *Botryllophilus*, *Schizoproctus* and *Haplostomides*, but absent or represented by small lobe in other genera. Maxilla primitively 3-segmented, armed with up to 10 setae in *Botryllophilus* and *Schizoproctus*, but absent or reduced to 1- or 2-segmented lobe bearing 1 or 2 setae in other genera. Maxilliped 4-segmented, consisting of syncoxa, basis, and 2-segmented endopod plus terminal claw; in *Haplostomella* endopodal segments and terminal claw usually fused to form subchela. Legs 1-4 biramous with 1- or 2-segmented rami; coxa lacking inner element; basis lacking inner distal element in leg 1. Legs 1-4 of *Botryllophilus* usually showing left-right asymmetry. Leg 5 variable, present as digitiform process, lamellate, or represented by small lobe, bearing up to 4 setae. Leg 6 represented by 3 spiniform elements on genital operculum.

Male: Body cycloform with distinct prosome-urosome division. Urosome consisting of fifth pedigerous, genital and 4 abdominal somites. Caudal ramus armed with 6 setae. Antennule 4-segmented, with numerous aesthetascs on proximal segment (antennule of *Haplostomella* 8-segmented, with few aesthetascs on proximal segment). Antenna as in female. Mandible, maxillule and maxilla absent or vestigial. Maxilliped similar to that of female. Legs

1-4 biramous typically with 3-segmented rami, but leg 1 endopod 1- to 3-segmented, with modified setation and leg 4 endopod 2- or 3-segmented. Inner coxal seta present or absent. Basis of leg 1 with or without inner distal element. Leg 5 consisting of outer protopodal seta located laterally on surface of somite and free exopodal segment bearing 2 setae. Leg 6 represented by 2 setae on genital operculum.

**Type genus.** *Schizoproctus* Aurivillius, 1885.

**Other included genera.** *Botryllophilus* Hesse, 1864, *Haplostomides* Chatton & Harant, 1924, *Haplostoma* Chatton & Harant, 1924, *Haplosaccus* Chatton & Harant, 1924, *Haplostomella* Chatton & Harant, 1924, and *Paulillgia* Monniot C., 1982.

**Remarks.** In their revision of the family Ascidicolidae, Illg & Dudley (1980) treated the Botryllophilinae as a subfamily comprising two valid genera, *Botryllophilus* and *Schizoproctus*. They classified it as a *nomen conservandum* and attributed it to Sars (1921). Illg & Dudley (1980) took this action because they recognised that the family name Schizoproctidae Aurivillius, 1885 has priority over the Botryllophilidae Sars, 1921, but the name Schizoproctidae had not been used in the preceding 50 years. However, no formal case was made to the International Commission on Zoological Nomenclature. In continuing to use Botryllophilidae as a conserved name, Boxshall & Halsey (2004) followed Illg & Dudley (1980) in the interests of nomenclatural stability, and we continue this usage here.

Boxshall & Halsey (2004) pointed to a number of synapomorphies between *Botryllophilus* and *Schizoproctus* and the genera *Haplostomides*, *Haplostoma*, *Haplosaccus*, and *Haplostomella* which were placed in the subfamily Haplostominae Chatton & Harant, 1924 by Illg & Dudley (1980). Monniot (1982) subsequently added another genus, *Paulillgia*, to the Haplostominae. Boxshall & Halsey (2004) considered that the synapomorphies, especially those exhibited by the males, constituted strong evidence of a close relationship and they did not adopt the subfamilial division, instead they recognised all seven genera as members of a single family level taxon, for which they used the name Botryllophilidae.

### Genus *Botryllophilus* Hesse, 1864

**Diagnosis** (female). Body usually asymmetrical, consisting of broader anterior part and narrower posterior part. Anterior part consisting of cephalosome and first to fifth pedigerous somites. Posterior part consisting of genital somite and abdomen; abdomen comprising 4 somites in some species, or 5 to 8 annulations in others. Caudal rami short, with 4 claws and 1 or 2 setae; claws curved outwards or ventrally. Rostrum present or absent. Antennule short and broad, 4- or 5-segmented. Antenna consisting of short coxa, basis, and 1- to 3-segmented endopod (endopod mostly 2-segmented), armed with 5 to 8 setae, usually asymmetrical between right and left antennae in form and length of setae. Labrum not specialized. Mandible consisting of coxa and palp; medial margin of coxal gnathobase bearing 3 or 4 teeth distally and spinulose proximal part; palp elongate, unsegmented, typically armed with 9 setae: 3 (exopodal setae) on outer proximal region, 2 in subdistal region, and 4 distally. Maxillule consisting of precoxa with 4 to 7 setae on arthrite, and palp consisting of coxobasis and endopod; coxobasis with 2 setae on medial margin, 3 setae (exopodal setae) on outer margin, and usually with 1 small seta representing epipodite; endopod with 3 setae on distal margin. Maxilla obscurely 2- or 3-segmented, armed with up to 10 setae. Maxilliped consisting of syncoxa, basis, and small 2-segmented endopod with small terminal claw; armed with 0 to 2 setae on syncoxa, 2 setae on basis. Legs 1-4 biramous with at most 2-segmented rami, lacking inner seta on coxa, but with outer seta on basis. Exopods 1 or 2-segmented; endopods occasionally 1-segmented in leg 1, but 2-segmented in legs 2-4. Segmentation of leg rami often incomplete. Basis of leg 1 lacking inner distal element. Each pair of legs 1-4 asymmetrical between right and left sides (except symmetrical in *B. macropus* Canu, 1891). Right exopods usually armed with spines and left exopods with setae. Leg 5 lobate or digitiform, positioned dorsolaterally or laterally on somite; armed with 4 setae; left and right legs widely separated from each other.

**Type species.** *Botryllophilus ruber* Hesse, 1864, by original designation.

**Remarks.** According to Schellenberg (1922), three species in the genus *Botryllophilus* have symmetrical exopods

of legs 1-4: *B. aspinosus* Schellenberg, 1922, *B. macropus* Canu, 1891, and *B. ruber* Hesse, 1864. Of these three, *B. ruber* was redescribed by Ooishi (1999) and was shown to have asymmetrical legs 3 and 4. Ooishi (2014b) re-studied *B. aspinosus* and mentioned that right and left endopods of leg 4 are armed with different numbers of setae (6 and 7, respectively), which means that at least leg 4 of this species is also asymmetrical. Therefore, within the genus *Botryllophilus* the only species that exhibits true symmetry in all pairs of swimming legs is *B. macropus*, as redescribed by Ooishi (1996: 179).

Lang (1948) was of the opinion that the structure and armature of the swimming legs was highly variable in *Botryllophilus* species, and subsequently Stock (1970) refrained from using leg structure for distinguishing between the species he was studying. The variability Lang (1948) mentioned mainly referred to the symmetry and segmentation of legs, and we have been unable to confirm the existence of any infraspecific variability in leg setation with respect to all of the species we have examined in this account, with the exception of *B. norvegicus* in which the exopod of the right leg showed variation in setation. On the evidence available to us, we have found leg setation to be an extremely valuable taxonomic character for the recognition of species of *Botryllophilus*.

Ooishi & Illg (1988) recognized two female morphotypes in *Botryllophilus*: type A, with a 4-segmented abdomen, and type B which has an apparently 5- to 8-segmented abdomen. Huys & Boxshall (1991) suggested the latter condition was the result of secondary annulation and Boxshall & Halsey (2004) considered that the female abdomen was primitively 4-segmented but that this segmentation was obscured by secondary annulations in type B species. Subsequently, Ooishi (2000) divided morphotype A into subgroups I and II, based on leg armature patterns. However, the distinctiveness of these subgroups has been blurred due to the discovery in the present work of several new species that have leg setation patterns that deviate markedly from both of Ooishi's patterns.

*Botryllophilus* currently comprises 19 valid species (Ooishi, 2014d). Thirteen new species are described in the present work. The numbers of armature elements on rami of the right and left legs 1-4 in *Botryllophilus* species are compared in Table 2.

**TABLE 2.** Armature of legs 1-4 in *Botryllophilus* species (four groups with same combination of armature elements shown in bold). Abbreviations: Enp = endopod, Exp = exopod.

Species	Armature of legs 1-4				Source
	Right Exp	Right Enp	Left Exp	Left Enp	
<i>B. macropus</i> Canu, 1891	7-8-9-9	8-8-7-6	7-8-9-9	8-8-7-6	Ooishi (1996)
<i>B. symmetricus</i> Ooishi, 2014	7-6-6-6	8-8-6-6	7-6-6-6	8-9-7-6	Ooishi (2014b)
<i>B. conicus</i> Conradi et al., 1994	7-6-6-6	8-8-7-6	6-5-5-6	7-8-7-6	Conradi et al. (1994)
<i>B. aspinosus</i> Schellenberg, 1922	6-6-?-5	8-8-6-6	6-6-?-5	8-8-6-7	Ooishi (2014b)
<i>B. randalli</i> Stock, 1970	7-6-6-6	8-7-8-6	6-5-5-5	7-9-7-6	Stock (1970)
<i>B. ruber</i> Hesse, 1864	<b>7-6-6-6</b>	<b>8-9-7-6</b>	<b>7-6-6-6</b>	<b>8-9-7-6</b>	Ooishi (1999)
<i>B. dentirostris</i> <b>sp. nov.</b>	<b>7-6-6-6</b>	<b>8-9-7-6</b>	<b>7-6-6-6</b>	<b>8-9-7-6</b>	Present study
<i>B. bermudensis</i> <b>sp. nov.</b>	7-6-6-6	8-9-6-6	7-6-6-6	8-9-7-6	Present study
<i>B. longipes</i> <b>sp. nov.</b>	7-6-6-6	8-9-7-6	7-5-5-5	8-9-7-6	Present study
<i>B. antarcticus</i> <b>sp. nov.</b>	6-5-6-6	8-9-6-5	6-5-5-6	7-8-7-6	Present study
<i>B. guadeloupensis</i> <b>sp. nov.</b>	6-6-6-6	8-9-7-6	5-5-5-5	8-9-7-6	Present study
<i>B. norvegicus</i> Schellenberg, 1921	7-6-6-6*	8-8-6-6	7-6-6-6	8-8-6-6	Ooishi (1996)
<i>B. neapolitanus</i> Ooishi, 2006	<b>7-6-6-5</b>	<b>8-8-6-6</b>	<b>7-6-6-5</b>	<b>8-8-6-6</b>	Ooishi (2006)
<i>B. kozloffii</i> Ooishi, 2014	<b>7-6-6-5</b>	<b>8-8-6-6</b>	<b>7-6-6-5</b>	<b>8-8-6-6</b>	Ooishi (2014c)
<i>B. banyulensis</i> Brément, 1909	6-6-6-5	8-7-6-6	5-5-5-4	8-8-6-6	Ooishi (2006)
<i>B. millari</i> Ooishi, 2014	6-5-5-5	7-7-6-6	6-4-4-5	7-7-6-6	Ooishi (2014c)
<i>B. brevipes</i> Brément, 1909	<b>7-6-6-5</b>	<b>8-8-6-6</b>	<b>6-5-5-4</b>	<b>8-8-6-6</b>	Ooishi (2006)
<i>B. distinctus</i> Ooishi, 2012	<b>7-6-6-5</b>	<b>8-8-6-6</b>	<b>6-5-5-4</b>	<b>8-8-6-6</b>	Ooishi (2012)

...Continued on the next page

**TABLE 2.** (Continued)

Species	Armature of legs 1-4				Source
	Right Exp	Right Enp	Left Exp	Left Enp	
<i>B. tuberculatus</i> <b>sp. nov.</b>	7-6-6-5	8-8-6-6	6-5-5-4	8-8-6-6	Present study
<i>B. stenurosus</i> <b>sp. nov.</b>	7-6-6-5	8-8-6-6	6-5-5-4	8-7-6-6	Present study
<i>B. spinulosus</i> Ooishi, 2012	7-6-6-5	8-8-6-6	6-5-5-5	8-8-6-6	Ooishi (2012)
<i>B. longicaudatus</i> <b>sp. nov.</b>	7-6-6-5	8-8-?-6	6-5-5-5	8-8-6-6	Present study
<i>B. pentachaetus</i> <b>sp. nov.</b>	7-6-6-5	8-7-6-6	7-6-6-5	8-7-6-6	Present study
<i>B. angustus</i> <b>sp. nov.</b>	7-6-6-6	8-8-6-6	6-5-5-4	8-8-6-6	Present study
<i>B. curtipes</i> <b>sp. nov.</b>	7-6-6-4	7-7-6-6	7-5-5-4	8-7-6-6	Present study
<i>B. abbotti</i> Ooishi & Illg, 1989	6-5-5-4	8-7-5-5	5-4-4-3	8-7-5-6	Ooishi & Illg (1989)
<i>B. inaequipes</i> Hansen, 1923	6-5-5-4	8-7-5-5	5-4-4-3	9-7-5-5	Ooishi (2002b)
<i>B. bamfieldensis</i> Ooishi, 2000	6-5-5-4	8-7-5-5	5-4-4-3	8-7-5-5	Ooishi (2000)
<i>B. koreensis</i> Seo & Lee, 1995	6-5-5-4	8-7-5-5	5-4-4-3	8-7-5-5	Seo & Lee (1995)
<i>B. sarsi</i> Ooishi, 2002	6-5-5-4	8-7-5-5	5-4-4-3	8-7-5-5	Ooishi (2002c)
<i>B. coniorhynchus</i> <b>sp. nov.</b>	6-6-6-4	8-8-6-6	5-5-5-4	8-8-6-6	Present study
<i>B. nudisetatus</i> <b>sp. nov.</b>	5-4-3-4	7-7-5-5	5-4-3-3	7-7-5-5	Present study

\*Exopod of right leg 4 of *B. norvegicus* is armed with 6 or 7 spines

***Botryllophilus dentirostris* sp. nov.**

(Figs. 24-26)

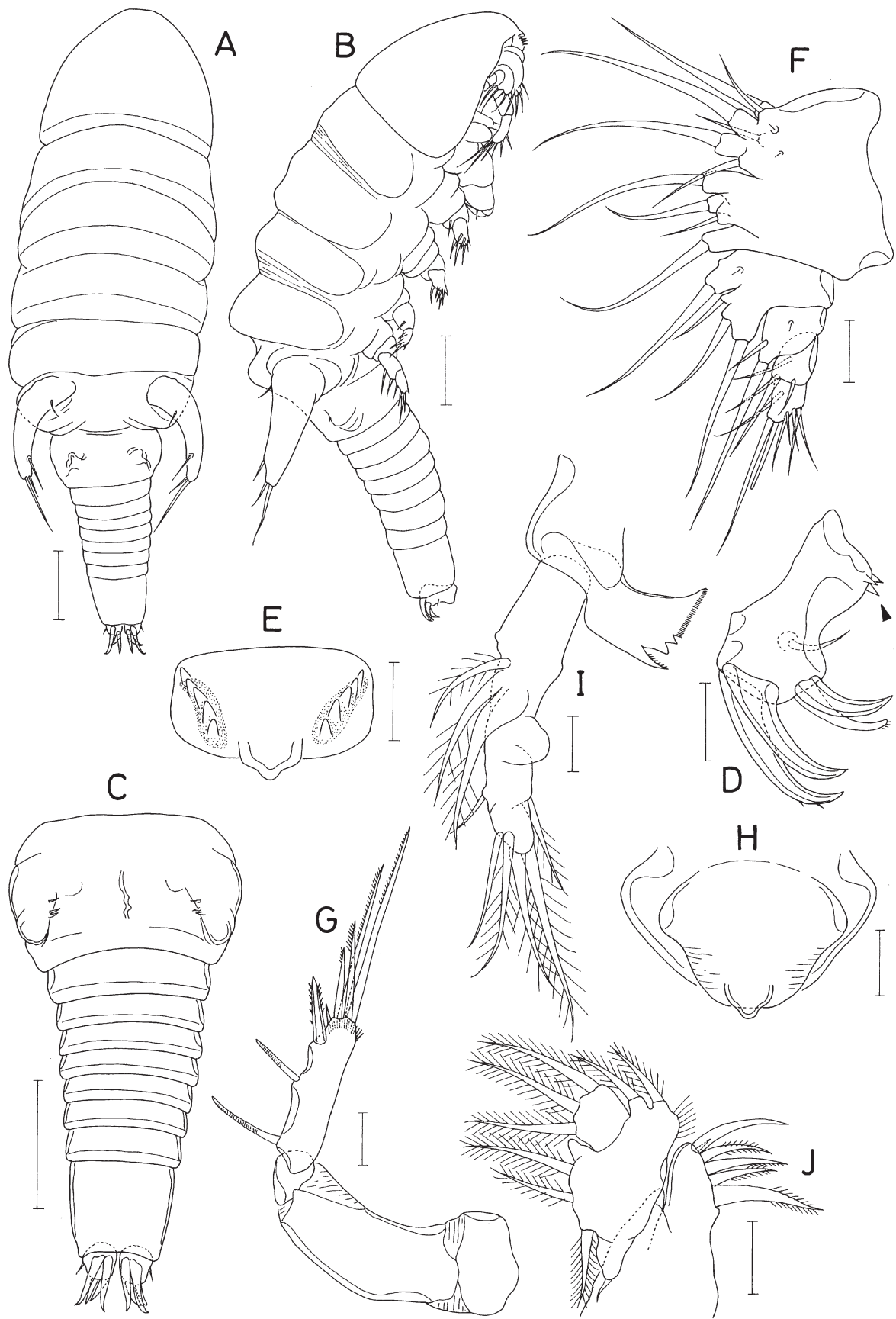
**Type material.** Holotype ♀ (MNHN-IU-2018-1951), 4 ♀♀ paratypes (intact, MNHN-IU-2018-1952) and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17363) from *Eudistoma clarum* (Van Name, 1902) (MNHN-IT-2008-4031 = MNHN A3/EUD/35); Guadeloupe Stn 13, West of l'îlet à Cochons, depth 5-10 m, Monniot coll., 23 December 1980.

**Etymology.** The specific name refers to the presence of rows of denticles on the ventral surface of the rostrum.

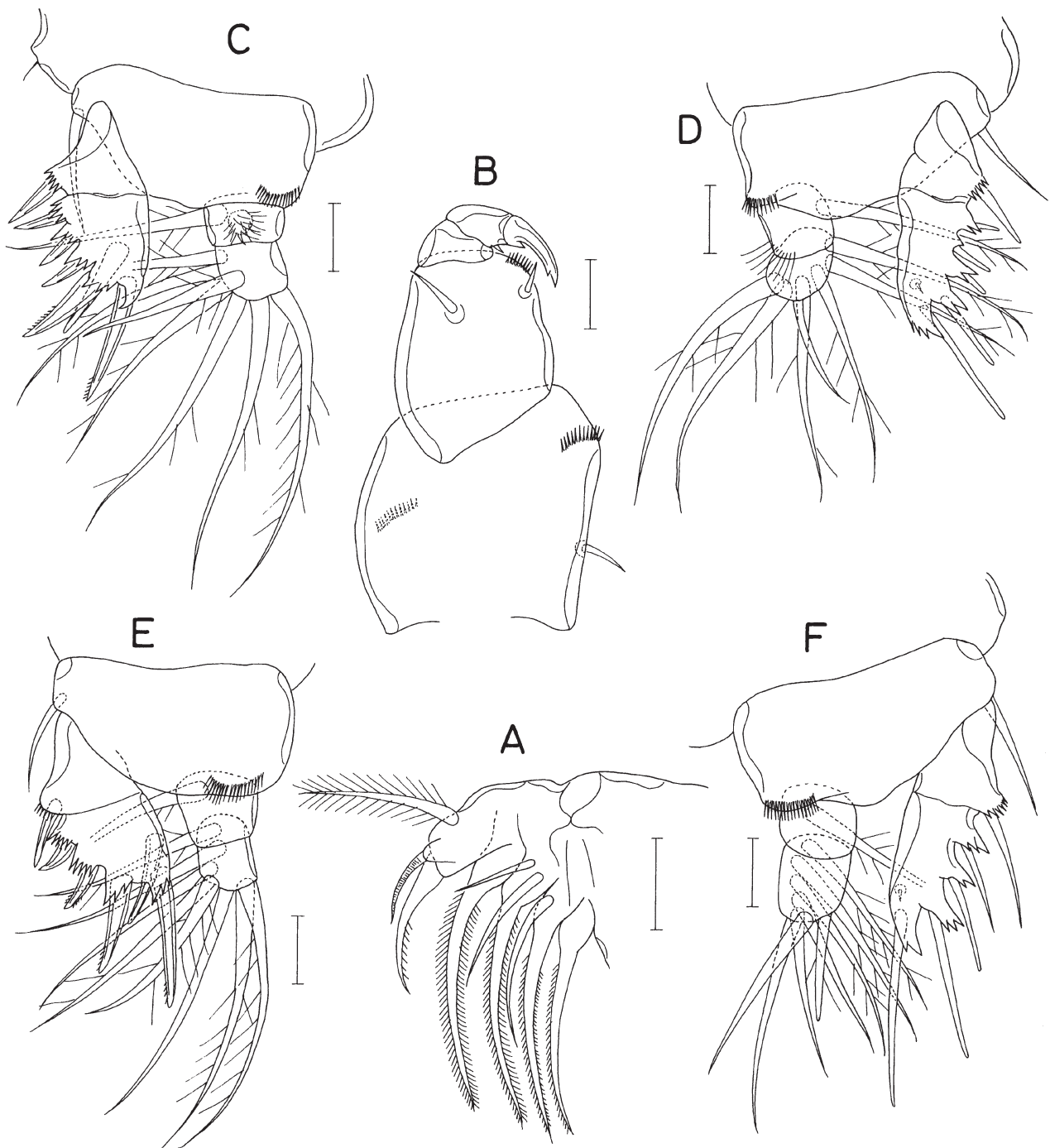
**Description of female.** Body (Fig. 24A, B) with broader anterior and narrower posterior parts, ventrally flexed between two parts. Body length 927 µm in figured specimen; maximum width 290 µm across second pedigerous somite. Anterior part slightly depressed, consisting of cephalosome and first to fifth pedigerous somites, with nearly parallel lateral margins; all somites of anterior part well-defined in dorsal view. Posterior part (Fig. 24C) slightly directed to left or right side, comprising genital somite and abdomen consisting of 8 annulations. Genital somite 110×184 µm, with convex lateral margins; genital areas located dorsally. Abdomen distinctly annulated; anterior 7 annulations much shorter than wide, 164 µm long in total; last annulation (anal somite) 73×82 µm. Caudal ramus (Fig. 24D) armed with 4 claws distally (2 larger inner and 2 smaller outer) and 1 dorsal seta and ornamented with 3 or 4 denticles (indicated by arrowhead in Fig. 24D) at outer proximal corner; one of outer claws blunt, with minute spinules at tip.

Rostrum (Fig. 24E) rectangular, much wider than long, ornamented with oblique rows of 5 denticles ventrally on each side and with lobate tubercles posteromedially. Antennule (Fig. 24F) short and broad, distinctly 5-segmented; distal 3 segments much narrower than proximal 2 segments; armature formula 10 (5 large and 5 small), 4 (2 large and 2 small), 2 (1 large and 1 small), 4, and 7+aesthetasc; all setae naked. Right antenna (Fig. 24G) 4-segmented, consisting of coxa, basis, and 2-segmented endopod; coxa short and unarmed; basis longest segment, unarmed; first endopodal segment short and unarmed; second endopodal segment about 3.6 times longer than wide (64×18 µm), armed with 1 spine and 7 setae; proximal 2 inner setae naked; third inner element (spine) spinulose; innermost distal seta minute; 4 distal setae unequal in length, bearing spinules distally on inner margin. Left antenna with 2 outer distal setae slightly longer than those on right antenna.





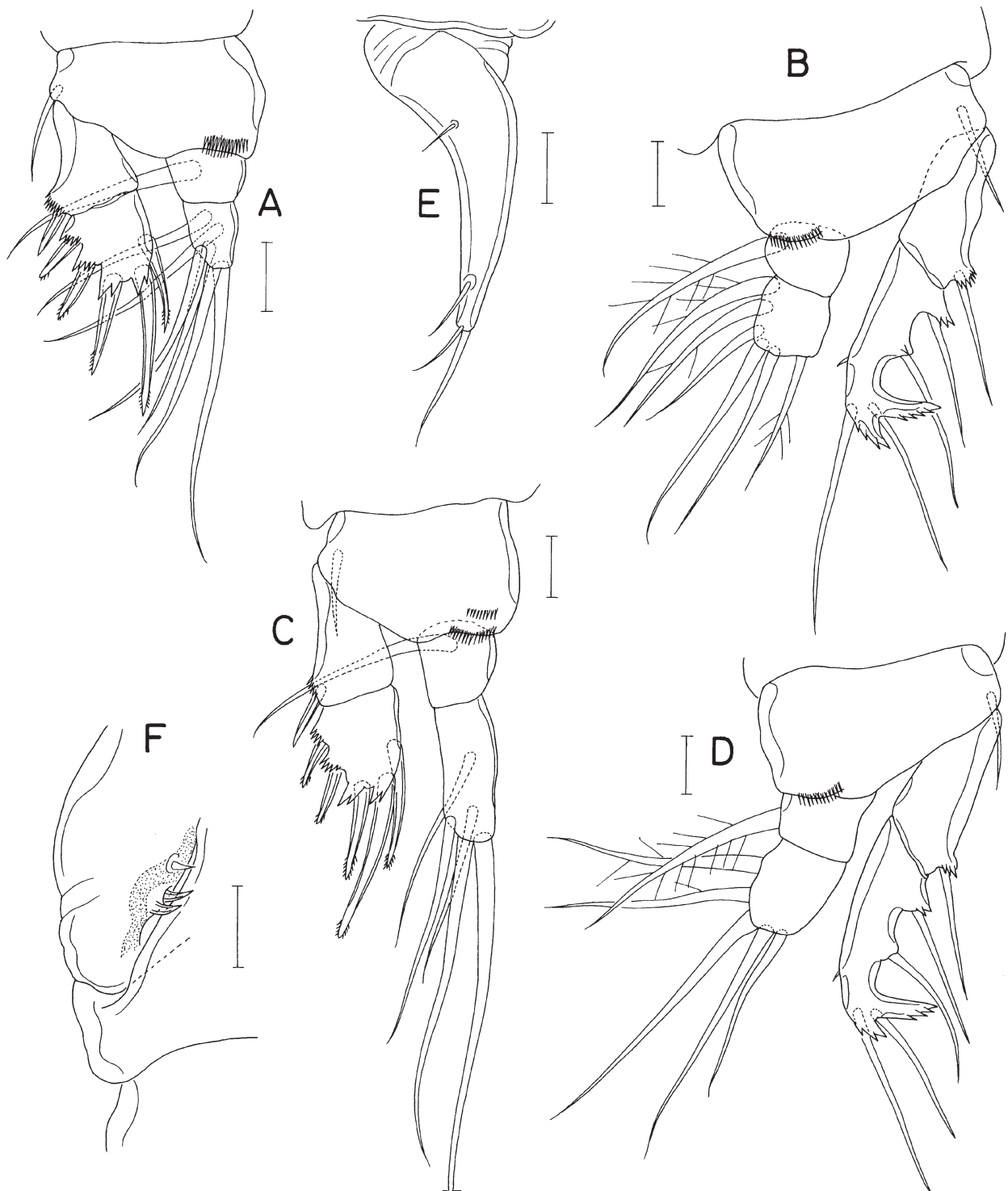
**FIG. 24.** *Botryllophilus dentirostris* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, posterior part of body, dorsal; D, caudal ramus; E, rostrum; F, antennule; G, antenna; H, labrum; I, mandible; J, maxillule. Scale bars: A-C, 0.1 mm; D-J, 0.02 mm.



**FIG. 25.** *Botryllophilus dentirostris* sp. nov., female. A, maxilla; B, maxilliped; C, right leg 1; D, left leg 1; E, right leg 2; F, left leg 2. Scale bars: 0.02 mm.

Labrum (Fig. 24H) subtriangular with well-sclerotized outer margins and soft ventral inflation bearing tapering lobe distally. Mandible (Fig. 24I) consisting of coxa and palp; medial margin of coxal gnathobase bearing 3 teeth distally (distalmost elongate with minute spinules along proximal margin) and finely spinulose proximally; palp unsegmented, with medial inflation near middle, armed with 3 outer setae (exopodal setae) proximally, 2 subdistal setae, and 4 distal setae; small, outer subdistal and outer distal seta naked, other setae pinnate. Maxillule (Fig. 24J) consisting of precoxa and palp; precoxa with 5 distinct setae and 1 minute seta on arthrite; palp consisting of coxobasis and endopod; coxobasis with 2 medial setae, 3 outer setae, 1 seta on epipodite, and 1 outer distal tubercle; endopod well-defined from coxobasis, with 3 setae distally. Maxilla (Fig. 25A) obscurely 2-segmented and armed with 10 setae (6 larger and 4 smaller). Maxilliped (Fig. 25B) 4-segmented; consisting of syncoxa, basis,

and small, 2-segmented endopod bearing terminal claw; syncoxa broad, with 1 small seta on inner margin and 2 rows of fine spinules each on inner distal and outer middle surfaces; basis with 2 small setae subdistally and 1 row of fine spinules mediodistally; first endopodal segment unarmed; second endopodal segment with minute seta on inner margin; terminal claw slender, longer than segment and bearing 2 denticles on inner margin (1 proximally and 1 subdistally).



**FIG. 26.** *Botryllophilus dentirotis* sp. nov., female. A, right leg 3; B, left leg 3; C, right leg 4; D, left leg 4; E, leg 5; F, left genital aperture. Scale bars: A-D, F, 0.02 mm; E, 0.05 mm.

Legs 1-4 (Figs. 25C-F; 26A-D) biramous with 2-segmented rami; each leg asymmetrical between right and left members; coxae lacking inner element, but with row of minute spinules at mediodistal corner; basis with outer seta.

Exopods of swimming legs spinulose along outer margins, mainly near bases of spines and setae; exopods of right swimming legs armed with spines, but endopods of right swimming legs and both rami of left swimming legs armed with setae. First endopodal segment of leg 1 with setulose tubercle on anterior surface. Second exopodal segment of left legs 3 and 4 elongated, hook-like (Fig. 26B, D), with pronounced subdistal process at base of third outer seta. One seta (inner subdistal seta) on second exopodal segment of left swimming legs vestigial. Numbers of spines (Roman numerals) and setae (Arabic numerals) on rami of legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	I; VI	1; 7	1; 5	1; 7
Leg 2	I; V	1; 8	1; 5	1; 8
Leg 3	I; V	1; 6	1; 5	1; 6
Leg 4	I; V	1; 5	1; 5	1; 5

Leg 5 (Fig. 26E) tapering, approximately 210×100 µm, curved, with concave inner margin; armed with 4 naked setae (1 proximal, 1 subdistal, and 2 distal). Leg 6 (Fig. 26F) represented by 2 spinules and 1 setule in genital area.

**Male.** Unknown.

**Remarks.** *Botryllophilus dentirostris* **sp. nov.** shares the same armature formula of legs 1-4 only with *B. ruber*. Both species also share an additional rare feature, i.e., the rami of all the swimming legs are 2-segmented (*B. macropus* is the only other species that shares this feature). *Botryllophilus ruber* was fully redescribed by Ooishi (1999) and, unlike in that species, the second exopodal segment of left legs 3 and 4 of *B. dentirostris* **sp. nov.** is characteristically elongated and hook-like. In *B. ruber*, the rostrum is feeble, tapering, and lacks denticles (cf. rectangular and ornamented with rows of denticles in *B. dentirostris* **sp. nov.**), the maxilla is armed with 8 setae and 1 minute seta (cf. with 10 setae in *B. dentirostris* **sp. nov.**), the inner margin of the second endopodal segment of the antenna bears 3 spines (cf. 2 setae and 1 spine in *B. dentirostris* **sp. nov.**). These differences are sufficient to differentiate between these two species.

### *Botryllophilus bermudensis* **sp. nov.**

(Figs. 27-29)

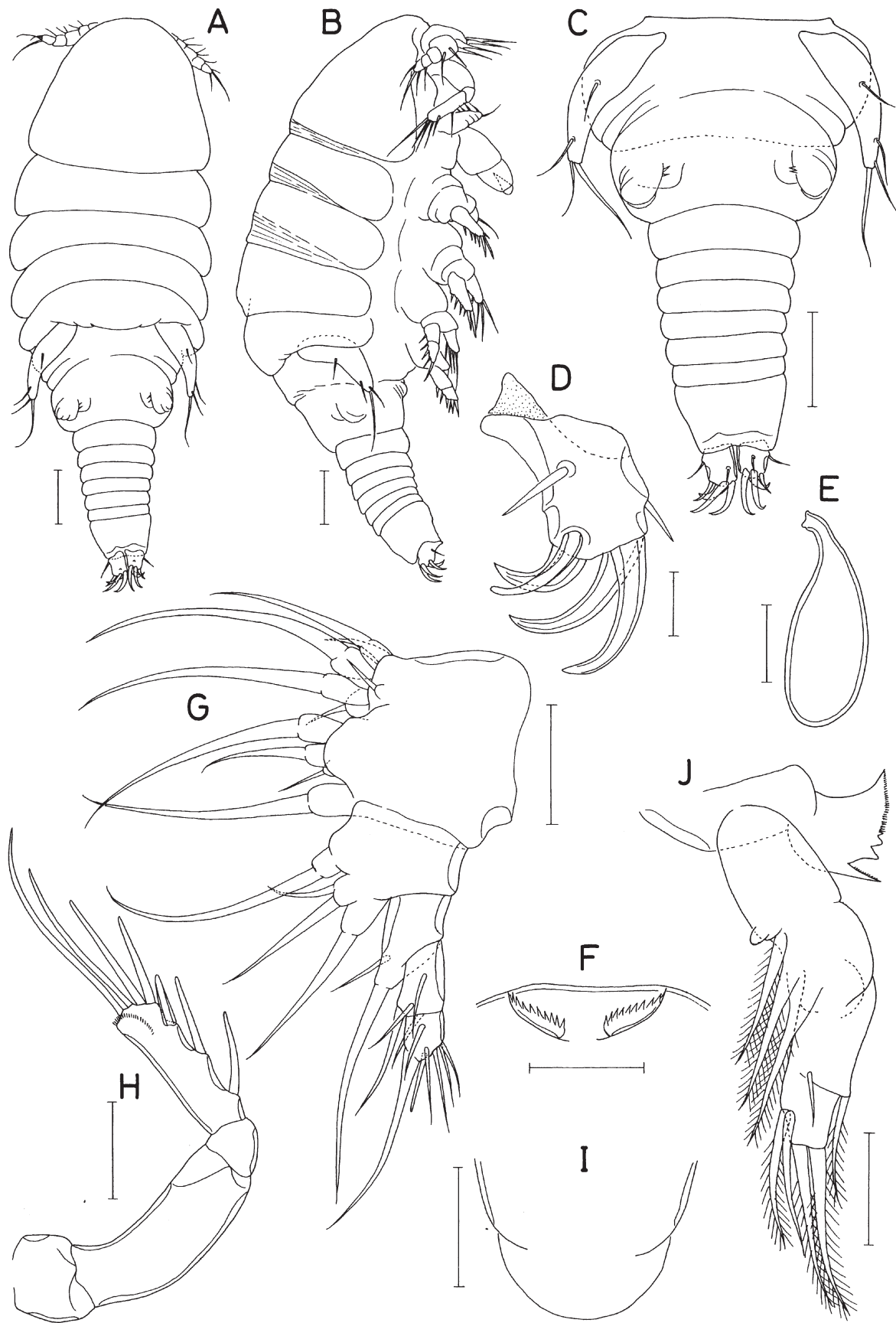
**Type material.** Holotype ♀ (MNHN-IU-2018-1953), 2 ♀♀ paratypes (intact, MNHN-IU-2018-1954), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17364) from *Distaplia bermudensis* Van Name, 1902; Bermuda, Monniot coll., March to May 1970.

**Additional material.** 1 ♀ (MNHN-IU-2018-1955), 1 ♀ (dissected, MNHN-IU-2014-17365) and 1 ♀ (MNHN-IU-2018-1956), all from *D. bermudensis*; Bermuda.

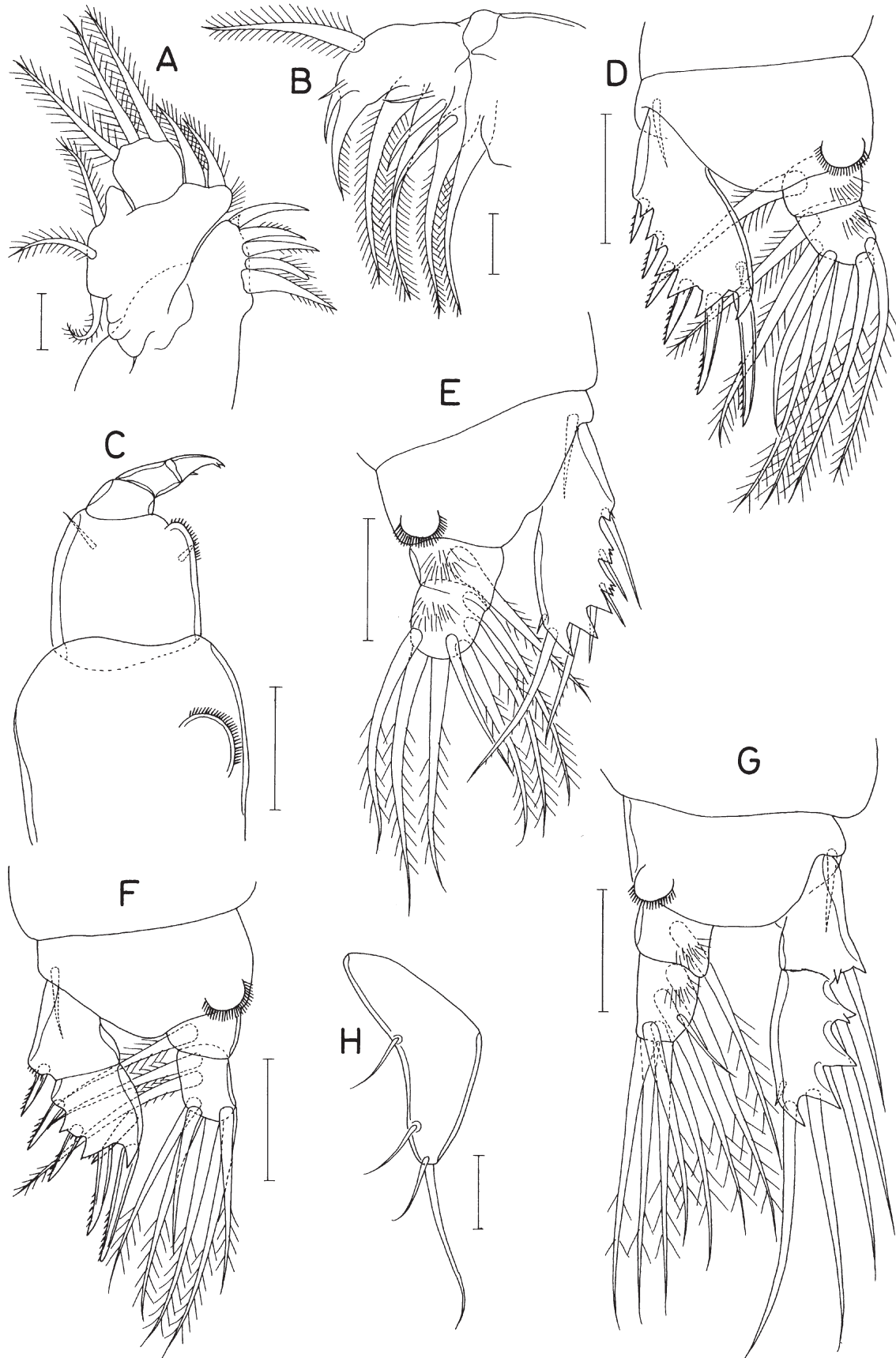
**Etymology.** The new species is named after the type locality, Bermuda.

**Description of female.** Body (Fig. 27A, B) stout, divisible into broader anterior and narrower posterior parts. Body length 1.04 mm; maximum width 382 µm. Anterior part consisting of cephalosome and first to fifth pedigerous somites; each somite well-defined by dorsal and lateral constrictions; first to fourth pedigerous somites each bearing weak dorsal tergite. Posterior part of body comprising genital somite and abdomen consisting of 7 annulations (Fig. 27C). Genital somite 100×228 µm; genital apertures positioned dorsally. First to sixth abdominal annulations much shorter than wide; seventh (anal somite) 70×113 µm, ornamented with scattered fine spinules ventrally. Caudal ramus (Fig. 27D) about 1.7 times longer than wide, armed with 4 claws and 2 setae; outer distal claw bluntly tipped. Spermatophore (Fig. 27E) attached to female 140×52 µm, bulbous.

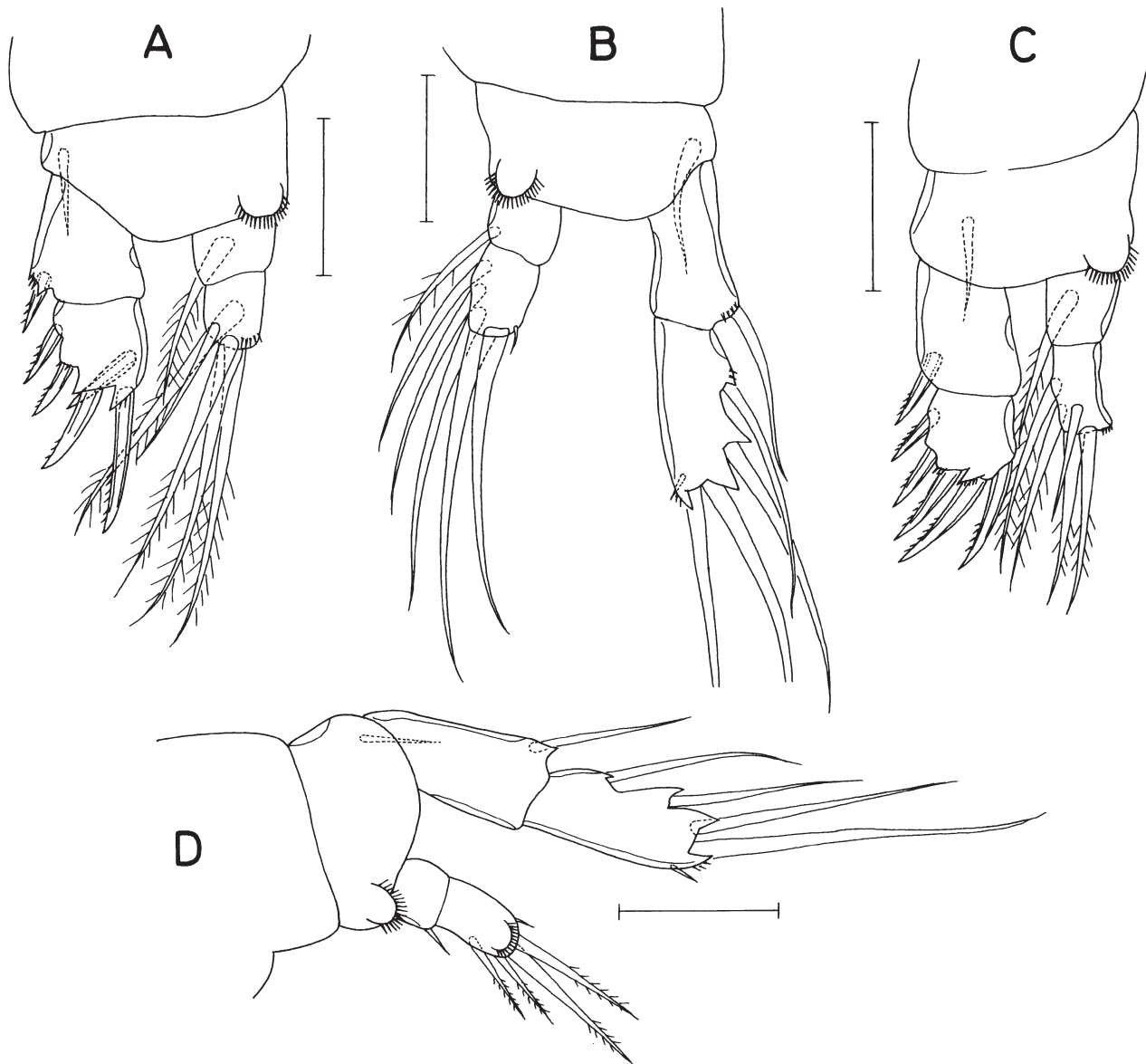
Rostrum absent but pair of comb-like membranes present on ventral surface of rostral area (Fig. 27F). Antennule (Fig. 27G) 172 µm long, 5-segmented; proximal 2 segments distinctly broadened; armature formula 10 (5 large and 5 small), 4 (3 large and 1 small), 2 (1 large and 1 small), 4, and 6+aesthetasc. Left antenna (Fig. 27H) 4-segmented; coxa, basis and first endopodal segment unarmed; second endopodal segment 3.2 times longer than wide (80×25 µm), armed with 6 setae and 1 spine (including 2 setae and 1 spine on inner margin). Right antenna differing slightly from left antenna in bearing 2 slightly shorter outer distal setae. All elements on antenna naked.



**FIG. 27.** *Botryllophilus bermudensis* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, posterior part of body from fifth pedigerous somite, dorsal; D, caudal ramus; E, spermatophore; F, rostral area; G, antennule; H, antenna; I, labrum; J, mandible. Scale bars: A-C, 0.1 mm; D, 0.02 mm; E-J, 0.05 mm.



**FIG. 28.** *Botryllophilus bermudensis* sp. nov., female. A, maxillule; B, maxilla; C, maxilliped; D, right leg 1; E, left leg 1; F, right leg 2; G, left leg 2; H, leg 5. Scale bars: A, B, 0.02 mm; C-H, 0.05 mm.



**FIG. 29.** *Botryllophilus bermudensis* sp. nov., female. A, right leg 3; B, left leg 3; C, right leg 4; D, left leg 4. Scale bars: 0.05 mm.

Labrum (Fig. 27I) simple, unornamented, consisting of thick-walled proximal part and thin-walled, convex distal part. Mandible (Fig. 27J) consisting of coxa and palp; coxa with 3 teeth on gnathobase, distal tooth spiniform, bearing minute spinules along proximal margin; palp elongate, armed with 9 setae arranged as 3, 2 (smaller one naked), 2 (including one naked), and 2; outer margin bearing small tubercle near base of proximalmost seta. Maxillule (Fig. 28A) consisting of precoxa and palp: precoxa with 5 distinct setae (second proximal seta bluntly tipped) and 1 minute seta on arthrite; palp 2-segmented; coxobasis with 2 setae on medial margin, 1 small seta on epipodite, 3 setae on outer margin, and 1 tubercle distally; endopod clearly defined from basis, with 3 setae on distal margin. Maxilla (Fig. 28B) obscurely 2-segmented, with 10 setae, including minute distal seta. Maxilliped (Fig. 28C) 4-segmented; first segment (syncoxa) broad, lacking seta, but with 1 inner, semicircular tubercle bearing row of minute spinules distally; second segment (basis) as long as wide, bearing 2 small setae subdistally and row of minute spinules at inner distal corner; third and fourth segments (first and second endopodal segments) small and unarmed; terminal claw small, bearing 2 minute denticles (proximal and subdistal) on concave inner margin.

Legs 1-4 (Figs. 28D-G, 29A-D) biramous, without inner seta on coxa; basis with outer seta and spinulose inner distal tubercle. Right and left leg 1 with 1-segmented exopod, but all rami of other swimming legs 2-segmented, although articulation incomplete between exopodal segments of left legs 2 and 3. Second exopodal segment of left

legs bearing prominent tooth-like processes along outer margin; inner subdistal seta on this segment minute (Figs. 28E, G, 29B, D). Outer distal seta on second endopodal segment of legs 3 and 4 also minute. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	1; 7	7	1; 7
Leg 2	I; V	1; 8	1; 5	1; 8
Leg 3	I; V	1; 5	1; 5	1; 6
Leg 4	I; V	1; 5	1; 5	1; 5

Leg 5 (Fig. 28H) positioned dorsolaterally (Fig. 27C), about 2.6 times longer than wide, tapering, curved inwards, extending to middle of genital somite; armed with 4 setae (1 proximal, 1 subdistal, and 2 distal). Leg 6 represented by 2 small denticles on genital operculum.

**Male.** Unknown.

**Remarks.** The female of *B. bermudensis* **sp. nov.** possesses an abdomen consisting of 7 annulations and this feature is shared with four previously described species: *B. aspinosus*, *B. randalli* Stock, 1970, *B. conicus* Conradi, López-González & García-Gómez, 1994, and *B. symmetricus* Ooishi, 2014. The abdomen of *B. ruber* may be variable in apparent segmentation, exhibiting between 6 and 8 annulations (Ooishi, 1999). Two of these five species, *B. randalli* and *B. conicus*, are known to have 7 armature elements on the terminal segment of the antenna (Stock, 1970; Conradi et al., 1994), as in *B. bermudensis* **sp. nov.** They may be differentiated from the new species by the different setation of legs, because the right endopod of leg 2 of *B. bermudensis* **sp. nov.** is armed with 9 setae, compared to 7 in *B. randalli* and 8 in *B. conicus*, and the left endopod of leg 1 of *B. bermudensis* **sp. nov.** is armed with 8 setae, compared to 7 in *B. randalli* and *B. conicus*.

### *Botryllophilus longipes* **sp. nov.**

(Figs. 30-32)

**Type material.** Holotype ♀ (MNHN-IU-2018-1957) and 1 ♀ paratype (dissected, MNHN-IU-2014-17366) from *Polyclinum saturnium* Savigny, 1816 (MNHN-IT-2008-7031 = MNHN A1/POL.B/24); Red Sea, Joussaume coll.

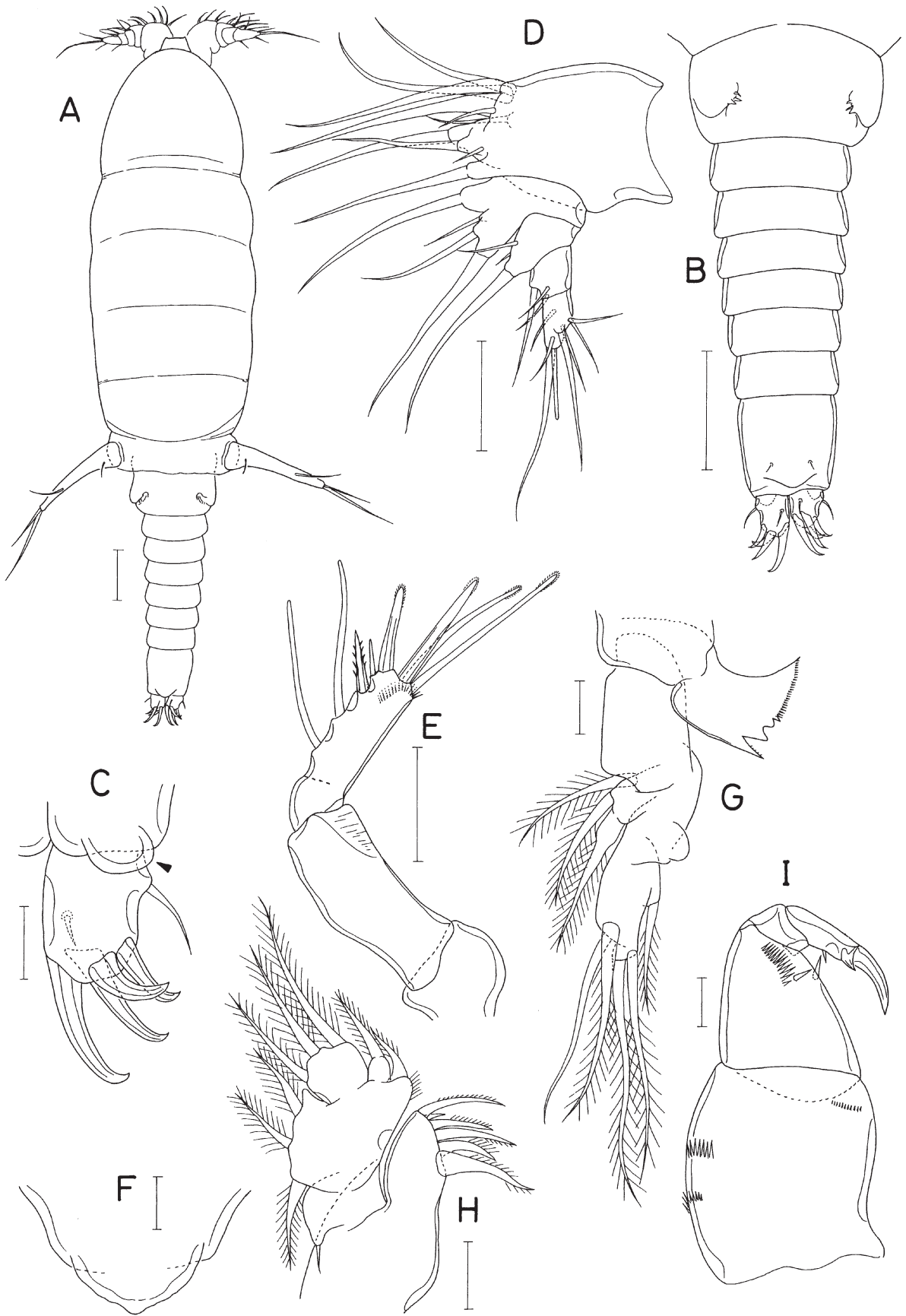
**Additional material.** 1 ♀ (MNHN-IU-2014-17367, dissected) in *Polyclinum macrophyllum* Michaelsen, 1919; New Caledonia, outer Reef, Stn NC 24, depth 38 m, Monniot coll., 19 September 1985.

**Etymology.** The name of the new species refers to its elongate leg 5.

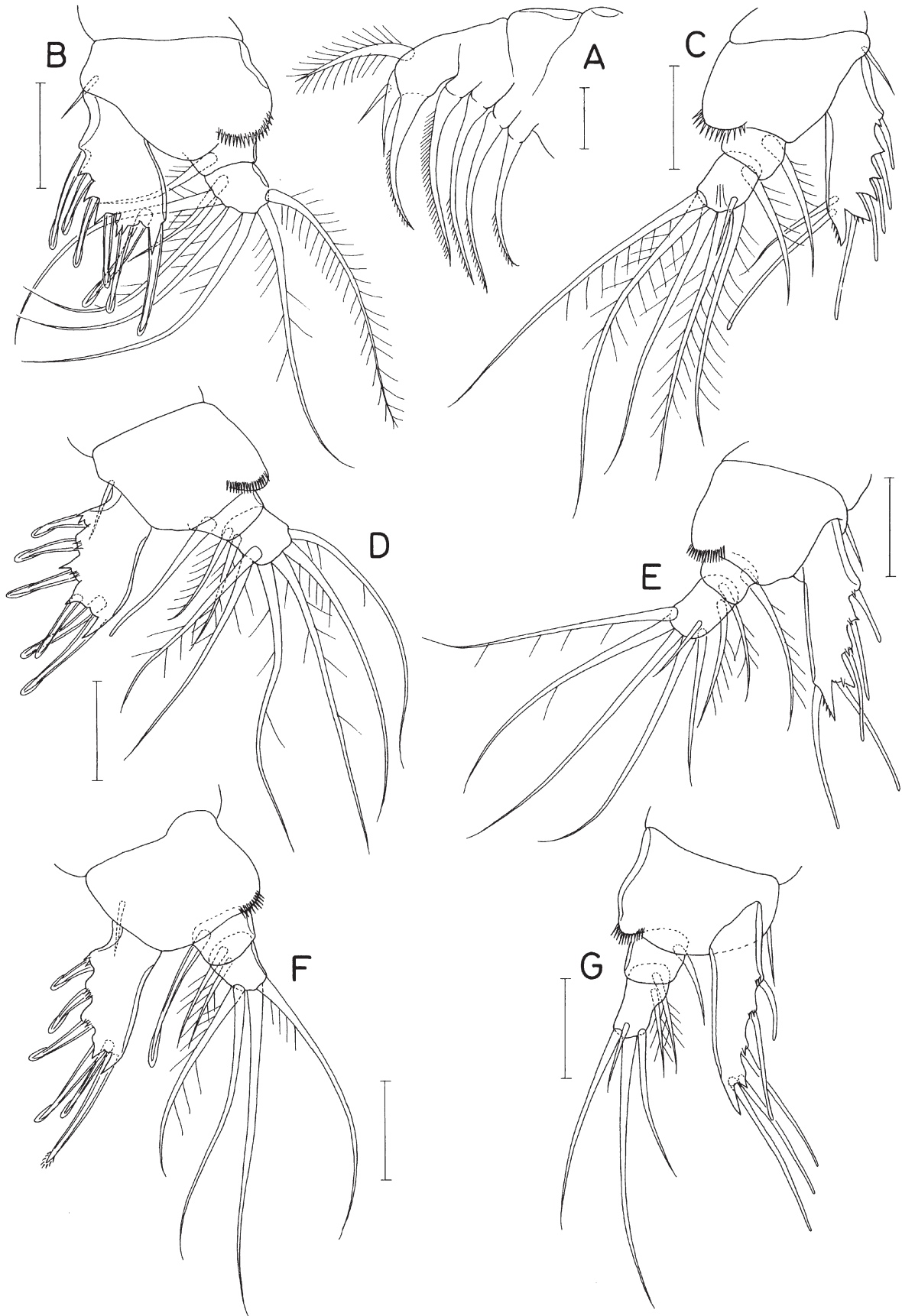
**Description of female.** Body (Fig. 30A) slender, symmetrical, divisible into broader anterior part comprising cephalosome and first to fifth pedigerous somites, and narrower posterior part comprising genital somite and 7 abdominal annulations (Fig. 30B). Body length 1.35 mm; width 335 µm across second pedigerous somite. Cephalosome and first to fourth pedigerous somites defined only by weak constrictions and faint dorsal suture lines. Genital somite 76×164 µm; genital aperture positioned dorsally. Abdomen gradually narrowing posteriorly; 6 anterior abdominal annulations nearly equal in length, much wider than long; seventh (anal somite) 85×84 µm, bearing pair of large tubercles (indicated by arrowhead in Fig. 30C) posteroventrally. Caudal ramus (Fig. 30C) 37×29 µm, armed with 4 strong claws and 2 setae; claws pointed at tip and articulated at base.

Rostrum as anterior process of cephalosome, with truncate anterior margin (Fig. 30A). Antennule (Fig. 30D) short, 5-segmented; first and second segments distinctly broader than distal segments, curved through right angle between first segment and remaining part; armature formula 10, 4, 3, 4, and 7+aesthetasc. Right antenna (Fig. 30E) 3-segmented, consisting of coxa, basis, and unsegmented endopod, but endopod bearing trace of articulation proximally on one surface; coxa and basis unarmed; endopod 71×23 µm, armed with 8 elements consisting of 2 slender proximal setae and 1 spinulose distal spine on inner margin, 1 small innermost distal spine, 2 inner distal spines, and 2 slender outer distal setae; all elements except distal spine on inner margin bluntly tipped; 4 outer distal elements bearing fine spinules distally. Left antenna different from right antenna in having 5 unornamented distal setae, of which 2 outer setae distinctly longer than those of right antenna.

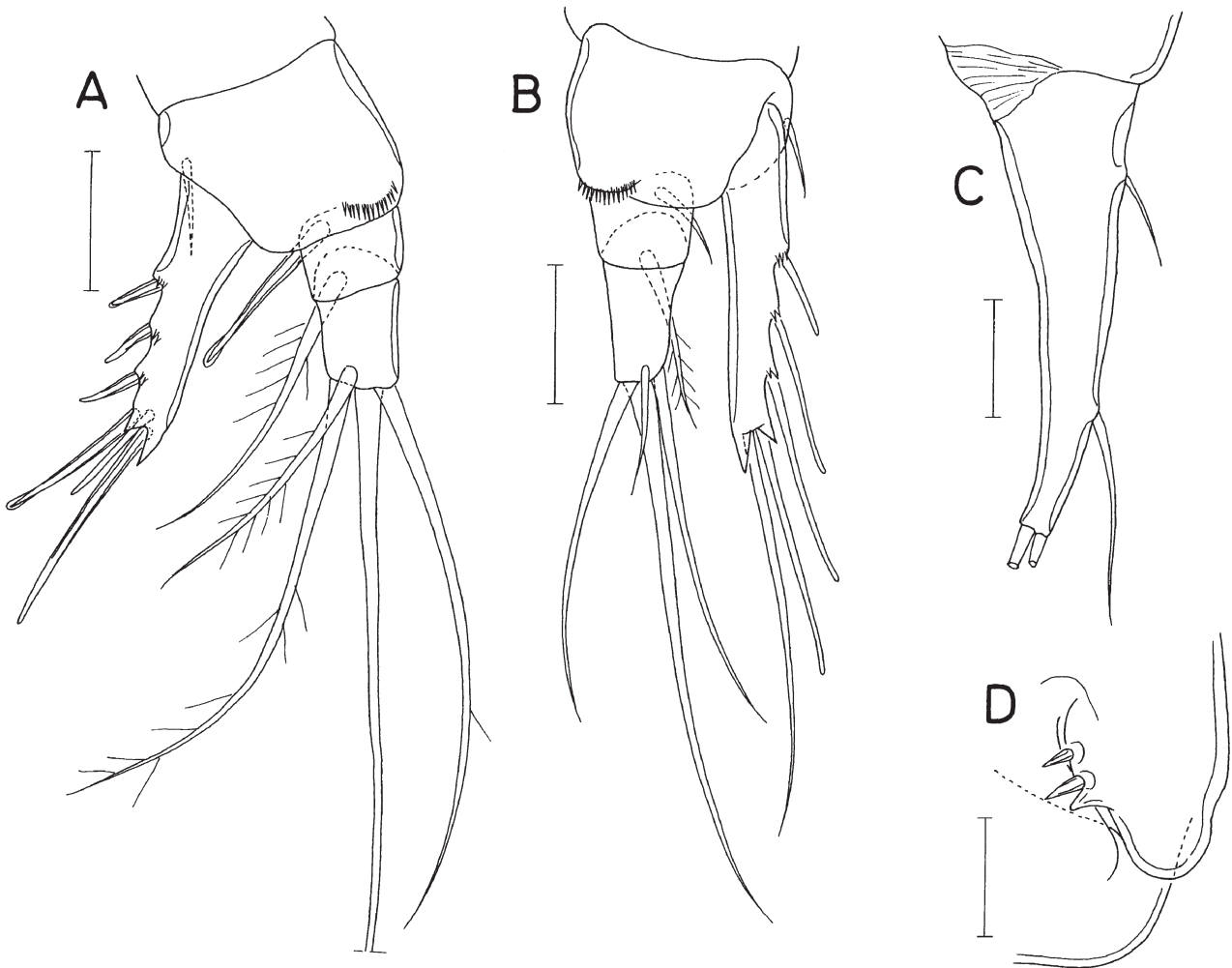




**FIG. 30.** *Botryllophilus longipes* sp. nov., female. A, habitus, dorsal; B, posterior part of body, dorsal; C, left caudal ramus, ventral; D, antennule; E, right antenna; F, labrum; G, mandible; H, maxillule; I, maxilliped. Scale bars: A, B, 0.1 mm; C, F-I, 0.02 mm; D, E, 0.05 mm.



**FIG. 31.** *Botryllophilus longipes* sp. nov., female. A, maxilla; B, right leg 1; C, left leg 1; D, right leg 2; E, left leg 2; F, right leg 3; G, left leg 3. Scale bars: A, 0.02 mm; B-G, 0.05 mm.



**FIG. 32.** *Botryllophilus longipes* sp. nov., female. A, right leg 4; B, left leg 4; C, leg 5; D, right genital aperture, dorsal. Scale bars: A-C, 0.05 mm; D, 0.02 mm.

Labrum (Fig. 30F) strongly tapering, consisting of well-sclerotized proximal part and narrower, fleshy distal part. Mandible (Fig. 30G) bearing 2 teeth on coxal gnathobase and 8 setae on palp arranged as 3, 1, 2, and 2; 1 subdistal seta naked, all others pinnate. Maxillule (Fig. 30H) consisting of precoxa and palp; precoxa bearing 5 distinct setae and 1 minute seta on arthrite; palp consisting of coxa, basis, and endopod; coxa with small naked seta on epipodite; basis with 2 setae on medial margin (distal seta expanded at base), and 3 setae on outer margin; endopod incompletely articulated from basis, armed with 3 setae distally. Maxilla (Fig. 31A) obscurely segmented, armed with 8 setae; 5 medial setae bearing setules (or fine spinules) along their distal margin; 3 distal setae consisting of 2 smaller naked setae and 1 outer pinnate seta. Maxilliped (Fig. 30I) 4-segmented; syncoxa (first segment) unarmed but ornamented with 2 rows of spinules on outer side and 1 row of minute spinules on inner distal surface; basis tapering distally, bearing 2 small setae and 1 longitudinal row of spinules in distal region; first endopodal segment much wider than long, unarmed; second endopodal segment about 2.5 times longer than wide, bearing 1 small seta on inner margin and 1 tooth-like process at inner distal corner; terminal claw smooth, slightly shorter than second endopodal segment.

Legs 1-4 (Figs. 31B-G, 32A, B) biramous with 1-segmented exopods and 2-segmented endopods; coxa lacking inner seta; basis with small outer seta and row of minute spinules at inner distal corner. First endopodal segment of right legs 3 (Fig. 31F) and 4 (Fig. 32A) characteristically bearing elongate spine. Spines on rami of legs 1-4 usually bluntly tipped, with membranous cap at tip. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	1; 7	7	1; 7
Leg 2	VI	1; 8	5	1; 8
Leg 3	VI	1; 6	5	1; 6
Leg 4	VI	1; 5	5	1; 5

Leg 5 (Fig. 32C) elongate, tapering, directed posterolaterally (Fig. 30A), about 3 times longer than wide ( $203 \times 67 \mu\text{m}$ ); armed with 4 setae; proximal and subdistal setae positioned at 22% and 75% of length of leg, respectively. Leg 6 (Fig. 32D) represented by 2 small spines and 1 dentiform process on genial operculum.

**Male.** Unknown.

**Remarks.** Two outstanding features of *B. longipes* **sp. nov.** serve to differentiate it from all of its congeners: 1) the transformation of the seta on the first endopodal segment of right legs 3 and 4 into a spine, and 2) the presence of the pair of large ventrodiscal tubercles on the anal somite. As additional diagnostic features of *B. longipes* **sp. nov.**, the free abdomen comprises 7 well defined annulations and the antenna is armed with 8 setal elements. The latter combination of features is shared with *B. aspinosus*, *B. symmetricus*, and one variety of *B. ruber*. But *B. longipes* **sp. nov.** is readily distinguishable from these three congeners by the above-mentioned outstanding features and by having a different leg setation pattern; for example, the number of setae on the exopod of left leg 2 is 5, rather than 6 as in these three congeners.

***Botryllophilus antarcticus* sp. nov.**

(Figs. 33-35)

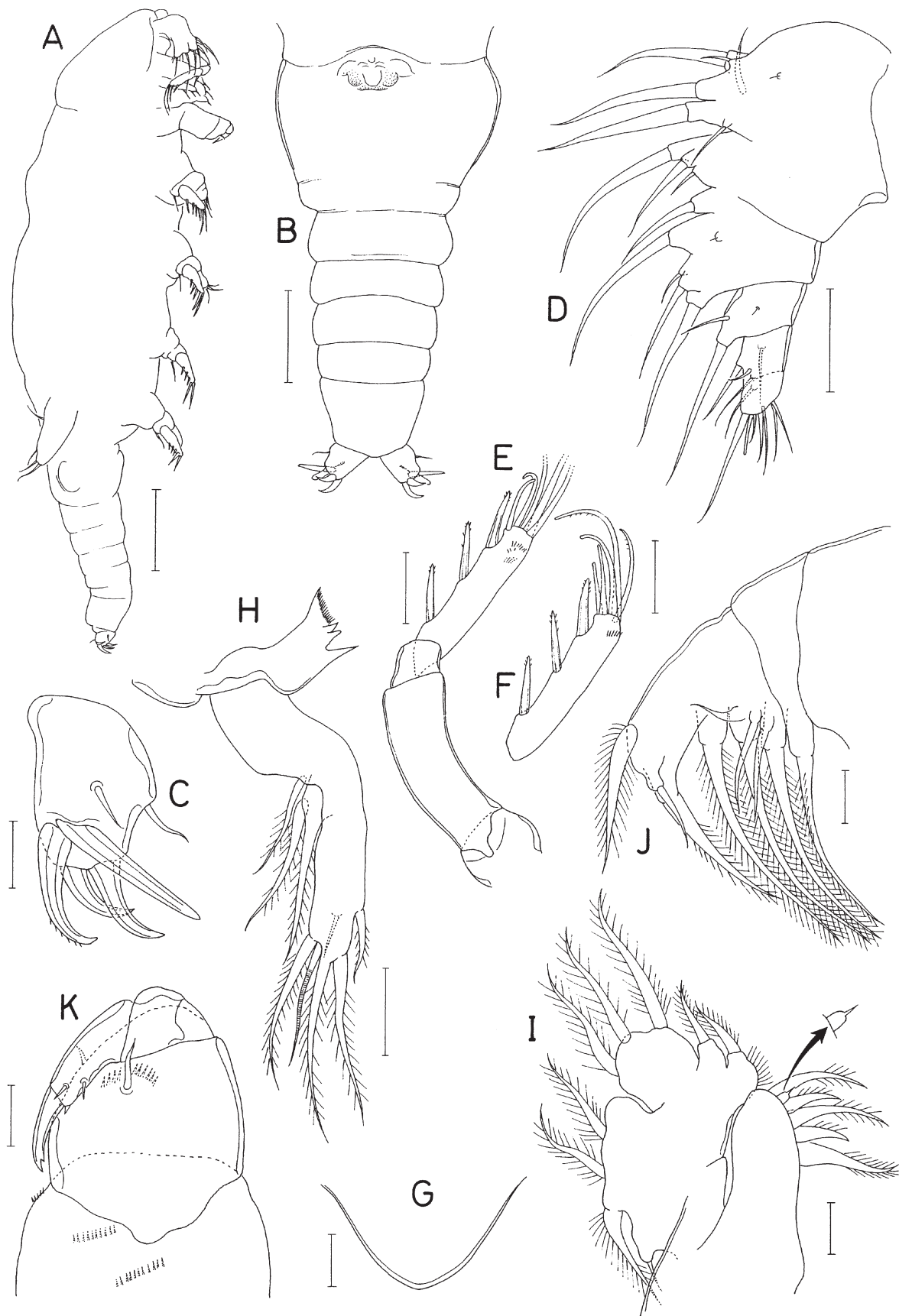
**Type material.** Holotype ♀ (MNHN-IU-2018-1958, dissected and mounted on a slide) from *Aplidium falklandicum* Millar, 1960 (MNHN-IT-2008-386 = MNHN A1/APL.B/532); Antarctic, Terre Adélie, CEAMARC cruise, RV “Aurore Australis”, Stn 18EV479 ( $66^{\circ}10'S$ ,  $139^{\circ}41'E$ ), depth 402-437 m, IPEV-AAD-MNHN coll., 15 January 2008.

**Etymology.** The name of the new species is based on its type locality, the Antarctic.

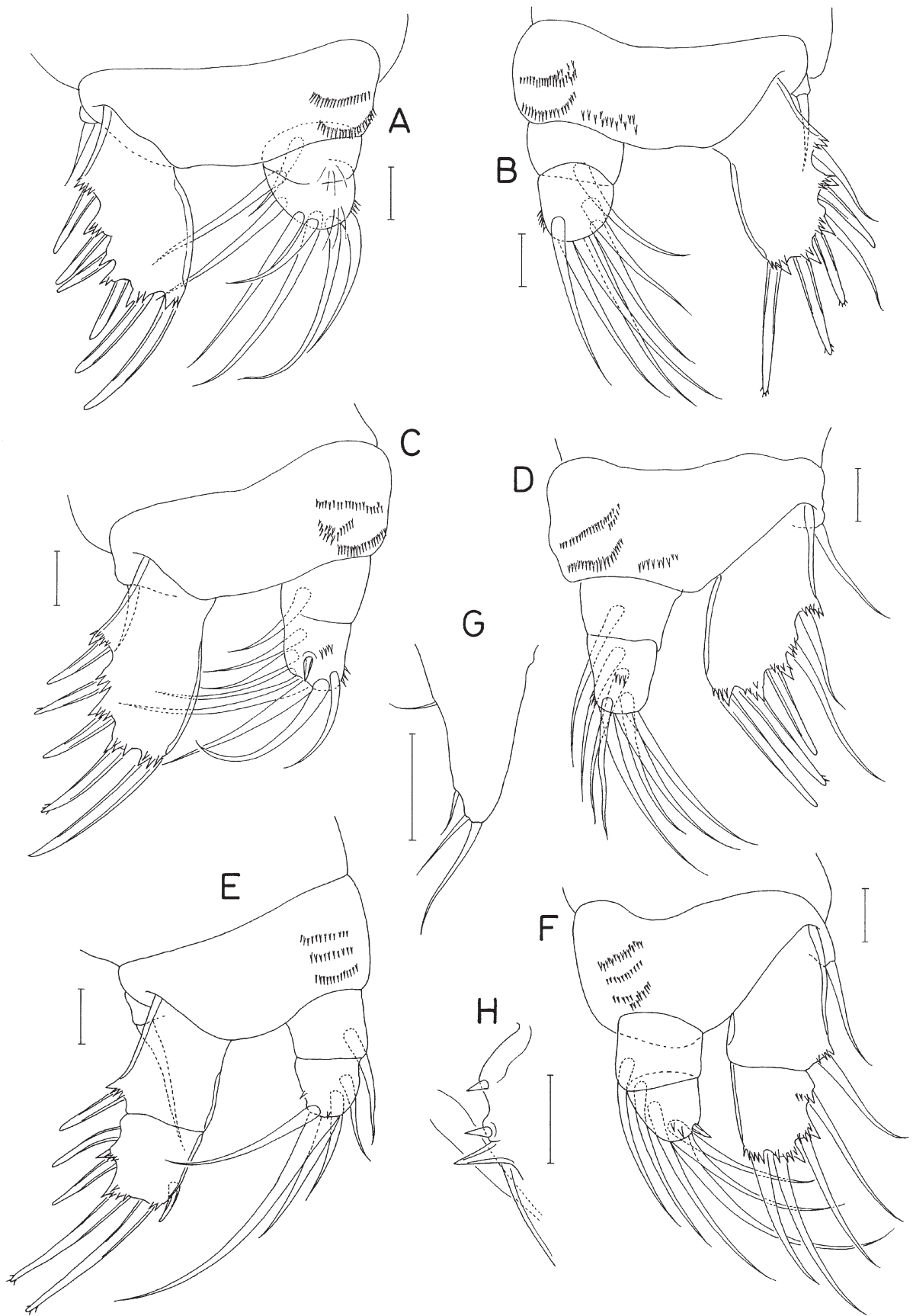
**Description of female.** Body (Fig. 33A) fleshy with thin exoskeleton; length 1.58 mm. Anterior part of body unsegmented; cephalosome recognizable from metasome only by faint dorsal constriction. Narrower posterior part (Fig. 33B) comprising genital somite and abdomen consisting of 5 indistinct annulations. Genital somite  $170 \times 250 \mu\text{m}$ , obscurely defined from fifth pedigerous somite; genital apertures positioned dorsolaterally. Abdomen gradually narrowing posteriorly; first to fourth abdominal annulations subequal in length; fifth (anal somite)  $77 \times 115 \mu\text{m}$ , distinctly wider than long. Caudal rami divergent; each ramus (Fig. 33C) about 1.4 times longer than wide ( $54 \times 38 \mu\text{m}$ ), armed with 4 claws and 2 setae; all caudal claws pointed at tip, longest claw straight,  $48 \mu\text{m}$  long, as long as caudal ramus.

Rostrum absent. Antennule (Fig. 33D) stout,  $195 \mu\text{m}$  long, 4-segmented, but terminal segment subdivided by incomplete suture on one surface; first and second segments expanded, incompletely articulated from each other; armature formula 9, 5, 2, and 11+aesthetasc; all setae naked. Antenna (Fig. 33E, F) 4-segmented; coxa, basis, and first endopodal segment unarmed; second endopodal segment 4.7 times longer than wide, armed with 3 spines on inner margin and 5 setae on distal margin. No difference recognizable between right and left antennae.

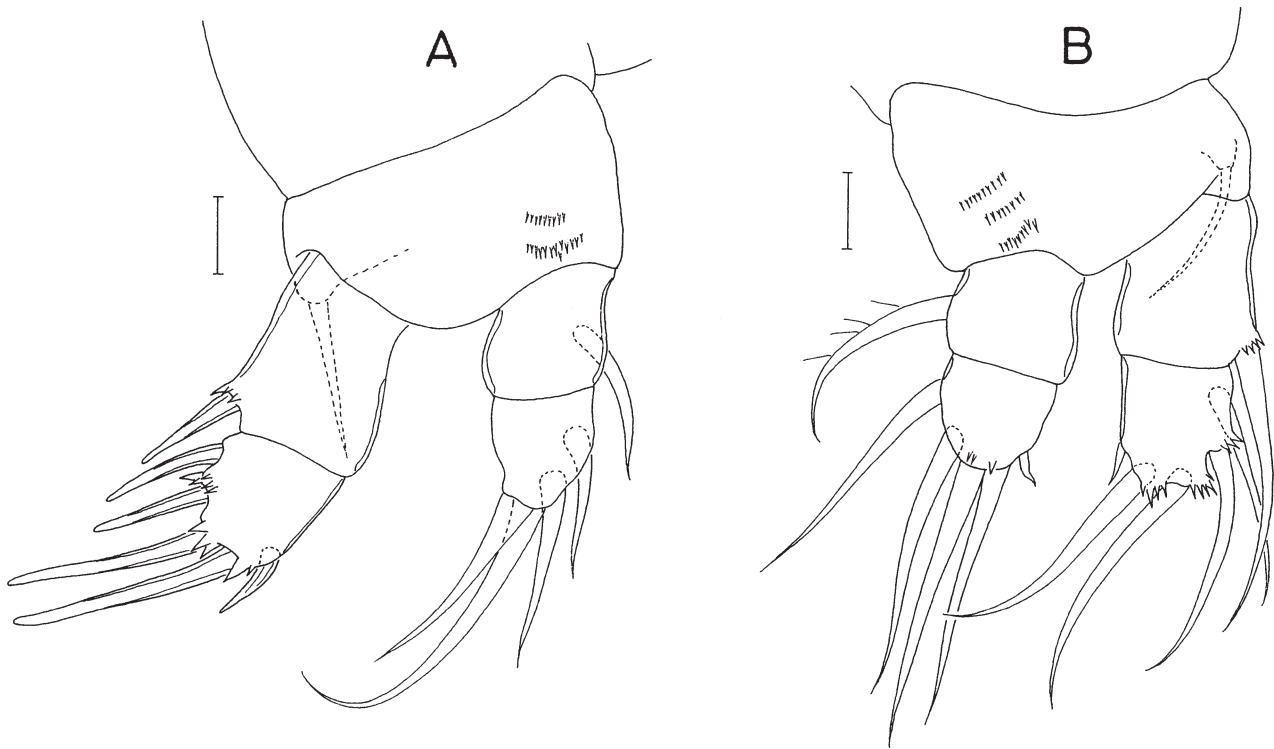
Labrum (Fig. 33G) simple, nearly semicircular. Mandible (Fig. 33H) with 3 teeth on coxal gnathobase; palp with 9 setae, grouped as 3, 2, 2, and 2. Maxillule (Fig. 33I) consisting of precoxa and palp; precoxa with 6 setae on arthrite, minute second distal seta lobate and tipped with setule; palp with 2 setae on medial margin, 3 setae on outer margin, and 1 minute naked seta at outer proximal corner (representing epipodite); endopod not articulated at base, armed with 3 setae on distal margin. Maxilla (Fig. 33J) obscurely segmented, armed with 10 setae (4 small and naked). Maxilliped (Fig. 33K) stout, 4-segmented; syncoxa (first segment) unarmed but with 3 transverse rows of fine spinules; basis (second segment) with 2 unequal setae and 1 transverse row of fine spinules subdistally; first endopodal segment short and unarmed; second endopodal segment about twice as long as wide, armed with 2 small setae subdistally and 1 denticle at inner distal corner; terminal claw about 0.65 times as long as second endopodal segment, bearing 1 denticle subdistally on concave margin.



**FIG. 33.** *Botryllophilus antarcticus* sp. nov., female. A, habitus, right; B, posterior part of body, ventral; C, caudal ramus; D, antennule; E, left antenna; F, second endopodal segment of right antenna; G, labrum; H, mandible; I, maxillule, with inset showing modified seta on precoxa; J, maxilla; K, maxilliped. Scale bars: A, 0.2 mm; B, 0.1 mm; C, G, I-K, 0.02 mm; D-F, H, 0.05 mm.



**FIG. 34.** *Botryllophilus antarcticus* sp. nov., female. A, right leg 1; B, left leg 1; C, right leg 2; D, left leg 2; E, right leg 3; F, left leg 3; G, leg 5; H, leg 6. Scale bars: A-F, H, 0.02 mm; G, 0.1 mm.



**FIG. 35.** *Botryllophilus antarcticus* sp. nov., female. A, right leg 4; B, left leg 4. Scale bars: 0.02 mm.

Legs 1-4 (Figs. 34A-F, 35A, B) biramous, asymmetrical in setation between left and right legs; coxa unarmed: basis with outer seta and 2 or 3 rows of minute spinules on inner side of anterior surface. Exopods of legs 1 and 2 unsegmented, but other rami of swimming legs 2-segmented. Exopods of left legs 1 and 2 (Fig. 34B, D) characteristically with mixture of spines and setae (as figured). Second endopodal segment of right leg 2 (Fig. 34C) and left leg 3 (Fig. 34F) bearing 1 small spine in addition to setae. One seta on second exopodal and endopodal segments of left leg 4 (Fig. 35B) remarkably reduced in size. Almost all setae on legs 1-4 naked. Numbers of spines (Roman numerals) and setae (Arabic numerals) on rami of right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VI	1; 7	IV+2	1; 6
Leg 2	V	1; I+7	III+2	1; 7
Leg 3	I; V	1; 5	1; 4	1; I+5
Leg 4	I; V	1; 4	1; 5	1; 5

Leg 5 (Fig. 34G) evenly tapering, about 1.5 times longer than wide (163×108 µm); armed with 4 setae. Leg 6 (Fig. 34H) represented by 2 spinules and 1 prominent spiniform process on genital operculum.

**Male.** Unknown

**Remarks.** In legs 1-4 of *Botryllophilus* species the exopods of the right legs are typically armed only with spines whereas the exopods of the left legs are typically armed only with setae. One exception to this generalisation is *B. macropus*, in which the right and left legs are symmetrical and the exopods of both right and left legs 1 and 2 are armed with mixture of spines and setae. *Botryllophilus antarcticus* sp. nov. is another species bearing a mixture of spines and setae on the exopods of legs 1 and 2, although it differs from *B. macropus* in the precise armature formula for the swimming legs and in other respects. Other unique features of *B. antarcticus* sp. nov. include the abdomen consisting of 5 annulations, and the combination of the armature on the exopods and endopods of right legs 1-4 which are 6-5-6-6 and 8-9-6-5, respectively. These unique features clearly differentiate *B. antarcticus* sp. nov. from its congeners, and support the establishment of the new species.

***Botryllophilus guadeloupensis* sp. nov.**

(Figs. 36-38)

**Type material.** Holotype ♀ (MNHN-IU-2018-1959), 2 ♀♀ paratypes (intact, MNHN-IU-2018-1960), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17368) from *Leptoclinides latus* Monniot F., 1983; Guadeloupe Stn 83-13, SE of Îlet Fajou, near Passe à Colas, depth 5-20 m, Monniot coll., 29 March 1983.

**Etymology.** The name of the new species is taken from its type locality, Guadeloupe.

**Description of female.** Body (Fig. 36A) small, rather stout, nearly symmetrical; body length 797 µm in largest specimen (dissected), 718 µm in smallest specimen. Broader anterior part of body occupying about 65% of body length, consisting of cephalosome and first to fifth pedigerous somites: first to fourth pedigerous somites each with weakly developed dorsal tergite. Narrower posterior part (Fig. 36B) consisting of genital somite and 7 abdominal annulations (8-annulate abdomen observed in 1 of 5 specimens). Genital somite much wider than long (68×159 µm); genital apertures positioned dorsally. Abdomen gradually narrowing distally: first to sixth abdominal annulations short, 128 µm long in total. Last annulation (anal somite) (Fig. 36C) wider than long (68×82 µm), ornamented with 2 horizontal rows of minute spinules on proximal part of ventral surface. Caudal ramus (Fig. 36D) slightly longer than wide (36×30 µm), armed with 4 claws and 2 setae; outermost claw bluntly tipped and weakly sclerotized.

Rostrum as simple frontal lobe on cephalosome. Antennule short, 4-segmented; armature formula 10, 4, 2, and 11+aesthetasc; terminal segment subdivided by incomplete posterior suture line into proximal region bearing 4 setae and distal region bearing 7 setae plus 1 aesthetasc. Right antenna (Fig. 36F) 3-segmented, consisting of coxa, basis, and 1-segmented endopod; endopod about 4 times longer than wide (64×16 µm), armed with 8 elements consisting of 2 proximal setae plus 1 distal spine on inner margin and 5 unequal setae on distal margin, innermost seta on distal margin minute, setule-like. Left antenna differing from right antenna in having 2 longer outer setae on distal margin of endopodal segment.

Labrum weak, easily destroyed. Mandible (Fig. 36G) bearing 3 teeth on coxal gnathobase; palp as usual for genus, bearing 9 setae arranged as 3, 2, 2, and 2. Maxillule (Fig. 36H) with 5 distinct setae and 1 minute seta on arthrite of precoxa; coxobasis with 2 setae (both with swollen base) on medial margin, 3 setae on outer margin, 1 naked seta at outer proximal corner, and 1 tapering process in outer distal region; endopod distinctly defined from basis and armed with 3 setae. Maxilla (Fig. 36I) indistinctly 2-segmented, with 10 setae. Maxilliped (Fig. 37A) 4-segmented; syncoxa unarmed and unornamented; basis with 2 small, equal setae and 1 row of minute spinules subdistally; first endopodal segment short and unarmed; second endopodal segment about 1.8 times longer than wide, bearing small seta distally on inner margin; terminal claw as long as second endopodal segment, bearing 2 tooth-like processes, 1 proximally and 1 subdistally on inner margin.

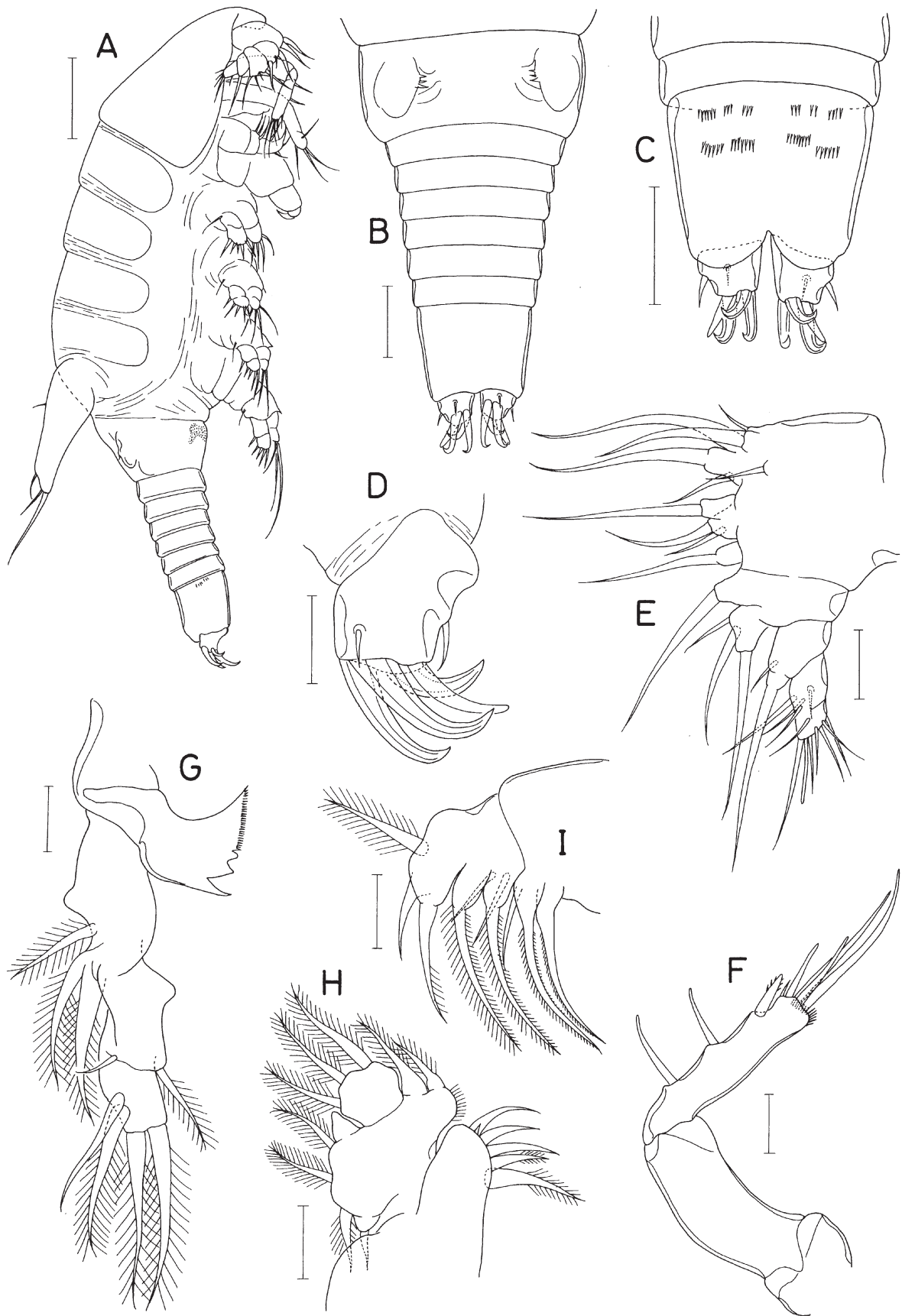
Legs 1-4 (Figs. 37B-E, 38A-D) biramous, asymmetrical. In left leg 4 (Fig. 38D) protopod divided into coxa and basis, but in other legs coxa and basis fused to form unsegmented protopod bearing 1 seta on outer margin and row of spinules at inner distal corner. Exopods 1-segmented in right and left legs 1 and 2, but 2-segmented in endopods and in both rami of legs 3 and 4. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VI	1; 7	5	1; 7
Leg 2	VI	1; 8	5	1; 8
Leg 3	I; V	1; 6	1; 4	1; 6
Leg 4	I; V	1; 5	1; 4	1; 5

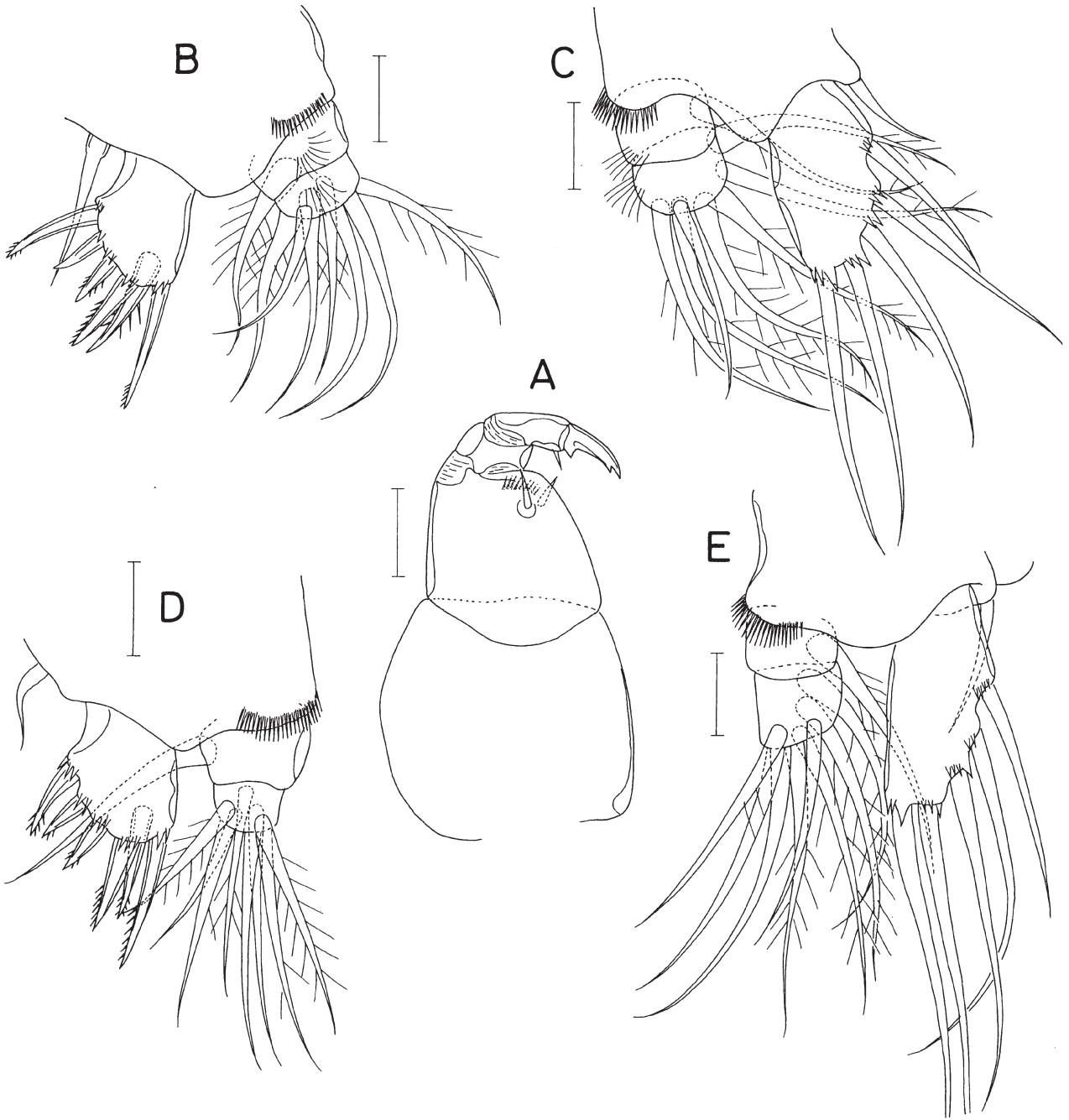
Leg 5 (Fig. 38E) large, extending beyond posterior margin of genital somite, about 2.4 times longer than wide (160×67 µm), evenly tapering, armed with 4 setae. Leg 6 represented by 2 small spinules and 1 spinule-like process on genital operculum.

**Male.** Unknown.

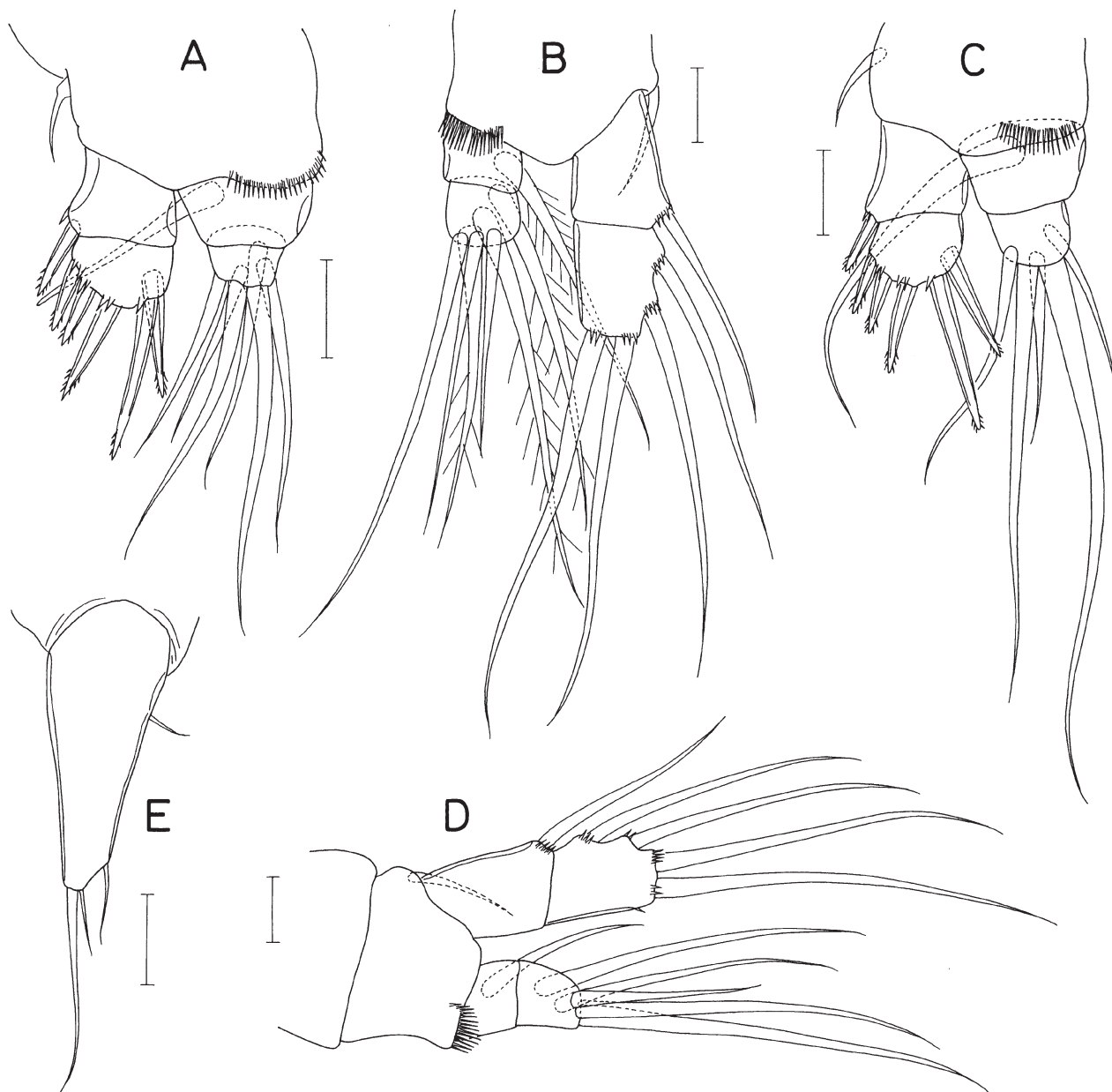




**FIG. 36.** *Botryllophilus guadeloupensis* **sp. nov.**, female. A, habitus, right; B, posterior part of body, dorsal; C, posterior part of abdomen, ventral; D, caudal ramus; E, antennule; F, antenna; G, mandible; H, maxillule; I, maxilla. Scale bars: A, 0.1 mm; B, C, 0.05 mm; D-I, 0.02 mm.



**FIG. 37.** *Botryllophilus guadeloupensis* **sp. nov.**, female. A, maxilliped; B, right leg 1; C, left leg 1; D, right leg 2; E, left leg 2. Scale bars: 0.02 mm.



**FIG. 38.** *Botryllophilus guadeloupensis* **sp. nov.**, female. A, right leg 3; B, left leg 3; C, right leg 4; D, left leg 4; E, leg 5. Scale bars: A-D, 0.02 mm; E, 0.05 mm.

**Remarks.** In *B. guadeloupensis* **sp. nov.** the exopods of right legs 1-4 are armed with 6 spines whereas the exopods of left legs 1-4 are armed with 5 setae. This characteristic leg setation is unique within *Botryllophilus* and typifies the new species. The 3-segmented condition of the antenna (with a 1-segmented endopod) is also a significant feature of *B. guadeloupensis* **sp. nov.**, because it is shared only with *B. norvegicus* (see Ooishi, 1996) and *B. longipes* **sp. nov.**, although the latter two species are not similar to *B. guadeloupensis* **sp. nov.** in female body form, or in the setation patterns of the antenna and swimming legs.

## *Botryllophilus norvegicus* Schellenberg, 1921

(Figs. 39-41)

**Material examined.** 1 ♀ (MNHN-IU-2014-17369, dissected and figured) in *Polycarpa pigmentata* (Herdman, 1906) (MNHN-IT-2008-6635 = MNHN S1/POL.B/405); Boiboiwaga Island, Papua New Guinea, OCDN 5782-T (10°12.26'S, 150°44.75'E), depth 20 m, CRRF coll., 27 May 2008; 1 ♀ (MNHN-IU-2018-1961) in *Polycarpa* sp., Mediterranean coast of Israel; 1 ♀ (MNHN-IU-2018-1962) in *Dendrodoa* sp., Grand Rivière, Atlantic coast of Canada.

**Supplementary description based on female from Papua New Guinea.** Body (Fig. 39A) T-shaped in lateral view, 4.05 mm long in dissected specimen. Broader anterior part of body unsegmented, extremely swollen posterodorsally. Narrower posterior part of body (Fig. 39B) consisting of genital and 4 abdominal somites; genital somite 464×709 µm, with broad tubercle in middle of dorsal surface; genital apertures positioned dorsally. Four abdominal somites gradually narrowing posteriorly. Caudal ramus (Fig. 39C) 267×127 µm, armed with 4 straight, blunt claws and 2 small setae; claws unequal in length, longest claw 152 µm, and second longest claw 70 µm long.

Rostrum absent. Antennule (Fig. 39D) 4-segmented with indistinct articulation between last 2 segments; armature formula 12, 3, 4, and 8; 7 setae on first segment very large, exceeding length of antennule. Antenna consisting of coxa, basis, and 1-segmented endopod; endopod armed with 5 rod-shaped spines on right antenna, but with 5 slender setae on left antenna (Fig. 39E) (2 on inner margin and 3 on distal margin).

Labrum (Fig. 39F) with broad posteromedial lobe and 4 patches of minute spinules along medial surface. Mandible with broadened coxal gnathobase (Fig. 39G) bearing bifurcate distal tooth and 5 small, blunt denticles on medial margin; palp (Fig. 39H) armed with 8 setae arranged as 3, 1, and 4. Maxillule (Fig. 39I) with precoxal arthrite bearing 7 setae including 1 minute seta; palp with 2 setae on medial margin and 3 setae on outer margin of basis region, 1 seta on epipodite; endopod fused with basis, armed with 3 setae on distal margin. Maxilla (Fig. 40A) obscurely segmented, with 11 setae (including 4 small and naked). Maxilliped (Fig. 40B) robust, 4-segmented; syncoxa as long as wide, with protruded outer margin, 2 minute setae on proximal inner margin, and patch of minute spinules at subdistal inner margin; basis with 2 minute inner distal setae; first endopodal segment shorter than wide, unarmed; second endopodal segment with 1 minute seta near middle; terminal claw small, about half as long as second endopodal segment.

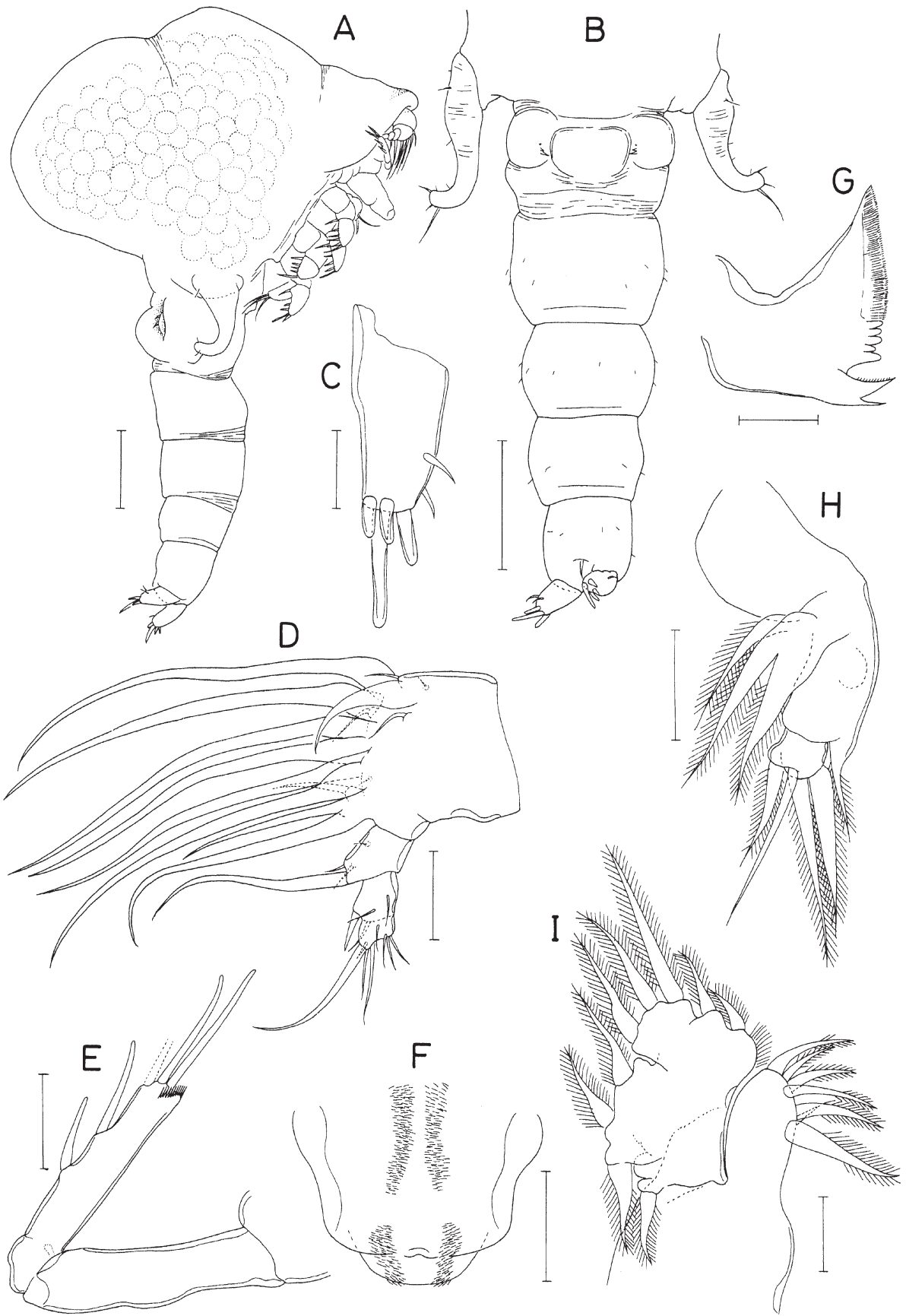
Legs 1-4 (Figs. 40-G, 41A-C) with 1-segmented exopods and 2-segmented endopods; coxa lacking inner seta; basis with small outer seta. Exopod of right leg 1 (Fig. 40C) with 1 inner subdistal seta, in addition to 6 spines. First endopodal segment of right and left leg 1 bearing setulose tubercle on anteromedial surface. Numbers of spines (Roman numerals) and setae (Arabic numerals) on rami of legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VI+1	1; 7	7	1; 7
Leg 2	VI	1; 7	7	1; 7
Leg 3	VI	1; 5	6	1; 5
Leg 4	VII	1; 5	6	1; 5

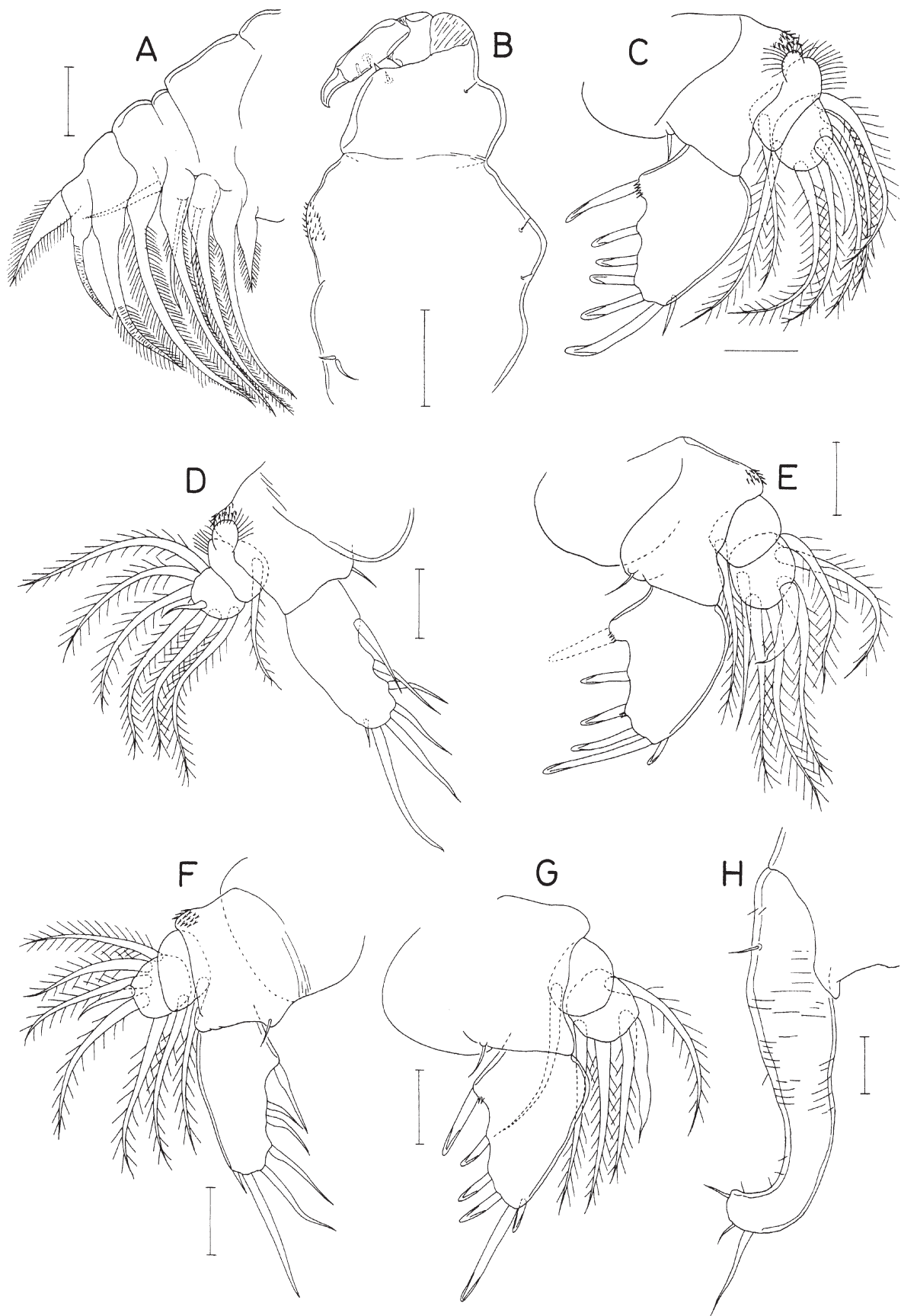
Leg 5 (Fig. 40H) elongate, gradually narrowing distally, with dorsolaterally curved distal part and blunt tip; armed with 4 setae; largest subdistal seta as long as proximal width of leg, other 3 setae minute. Leg 6 represented by 2 small spinules and 1 spiniform process on genital operculum.

**Male.** Unknown.

**Remarks.** *Botryllophilus norvegicus* is known to be widely distributed in the North Atlantic and Arctic Oceans (Dudley & Illg, 1991). In the present study its known distribution is extended to include the Mediterranean Sea and the tropical West Pacific. Ooishi (1996) redescribed this species based on a single female collected in Scotland and mentioned that this species is distinguishable from other “type A” species of the genus primarily by the hump-shaped body and the presence of 5 spines on the antenna. Additional remarkable diagnostic features of this species are as follows: the caudal rami bear straight, rod-shaped claws, leg 5 is curved dorsolaterally, and the antennule bears extremely large setae on the first segment.



**FIG. 39.** *Botryllophilus norvegicus* Schellenberg, 1921, female. A, habitus, right; B, legs 5 and posterior part of body, dorsal; C, caudal ramus; D, antennule; E, left antenna; F, labrum; G, mandibular coxa; H, mandibular palp; I, maxillule. Scale bars: A, B, 0.5 mm; C-F, H, 0.1 mm; G, I, 0.05 mm.



**FIG. 40.** *Botryllophilus norvegicus* Schellenberg, 1921, female. A, maxilla; B, maxilliped; C, right leg 1; D, left leg 1; E, right leg 2; F, left leg 2; G, right leg 3; H, leg 5. Scale bars: A, 0.05 mm; B-H, 0.1 mm.

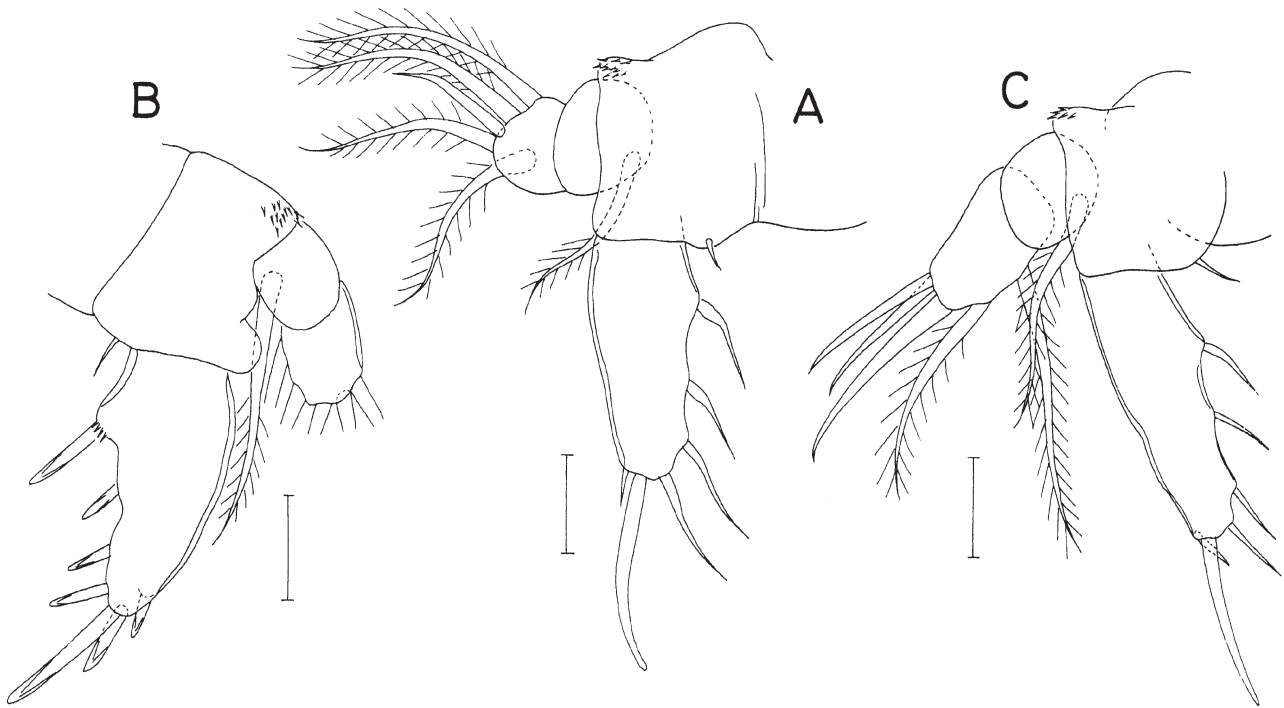


FIG. 41. *Botryllophilus norvegicus* Schellenberg, 1921, female. A, left leg 3; B, right leg 4; C, left leg 4. Scale bars: 0.1 mm.

It is noticeable that *B. norvegicus* displays variation in the setation pattern of the antenna and of the exopods of right leg 1 and right leg 4, as follows: (1) the right antenna is always armed with 5 spines, but left antenna may be armed with 5 spines as in Ooishi's (1996) specimen and our specimen from the Atlantic coast of Canada, or may be armed with 5 setae as in 2 specimens each collected in Papua New Guinea and off the Mediterranean coast of Israel; (2) the exopod of the right leg 4 may be armed with 6 spines as in Ooishi's specimen and our specimen from the Atlantic coast of Canada, or it may be armed with 7 spines as in our specimens from Papua New Guinea and off the Mediterranean coast of Israel; and (3) the exopod of right leg 1 may be armed with 6 spines plus 1 seta, as in Ooishi's specimen and all of our specimens, but Dudley & Illg (1991) figured the exopod as bearing 7 spines (Dudley & Illg, 1991: Fig. 27). The material available for study was limited so the exact nature of this variation cannot yet be determined.

### ***Botryllophilus kozloffii* Ooishi, 2014**

**Material examined.** 1 ♀ (MNHN-IU-2018-1963) in *Clavelina lepadiformis* (Müller, 1776), Île Grande, Atlantic coast of France; 1 ♀ (MNHN-IU-2014-17370, dissected) in *Cystodytes senegalense* Monniot F., 1969, Dakar, Senegal; 3 ♀♀ (MNHN-IU-2018-1964, 1 ♀ dissected) in *Cystodytes roseolus* Hartmeyer, 1912 (MNHN-IT-2008-2602 = MNHN A3/CYS/4), Dakar, Senegal Stn. 17, IFAN coll., 21 January 1941.

**Remarks.** Ooishi (2014c) described this species based on specimens associated with *Clavelina lepadiformis* collected from the Atlantic coast of France. *Cystodytes senegalense* and *C. roseolus* reported above are new host records. Almost all morphological features of our new material agree well with the original description, except for the absence of a pair of setulose lobes on the anteromedial margin of the first endopodal segment of right and left leg 1, which were described and figured in the original description.

This species is very similar to *B. neapolitanus* Ooishi, 2006. Both have the same setation pattern on the antenna and the swimming legs. Ooishi (2014c) listed several differences between the two species, the most easily observed of which appears to be leg 5, which is short and stout in *B. kozloffii* but longer and tapering in *B. neapolitanus*.

***Botryllophilus tuberculatus* sp. nov.**

(Figs. 42-44)

**Type material.** Holotype ♀ (MNHN-IU-2018-1965), ♀ paratype (MNHN-IU-2018-1966), and ♀ paratype (dissected, MNHN-IU-2014-17371) from *Pseudodistoma delicatum* Monniot C., Monniot F., Griffiths & Schleyer, 2001; Sodwana Bay, South Africa, Schleyer coll., 1993.

**Etymology.** The specific name refers to the presence of a pair of posteroventral tubercles on the fifth pedigerous somite.

**Description of female.** Body (Fig. 42A, B) rather stout, slightly asymmetrical, 1.10 mm long in largest dissected specimen. Anterior part of body gradually broadening posteriorly, with distinct cephalic shield and weak lateral constrictions. Fourth and fifth pedigerous somites not defined from each other; leg 5 positioned laterally. Fifth pedigerous somite bearing paired blunt tubercles posteroventrally (indicated by arrowhead in Fig. 42A-C) on both sides. Posterior part of body consisting of genital somite and 4 abdominal somites; 110×190, 75×135, 90×125, 77×113, and 140×98 µm, respectively. Genital somite with densely sclerotized region surrounding copulatory pore on ventral surface; genital apertures positioned dorsally. Anal somite about 1.4 times longer than wide. Caudal ramus (Fig. 42D) about 1.55 times longer than wide (51×33 µm), armed with 4 claws and 2 setae; second inner claw strongly curved, not articulated from ramus; 1 outer claw bluntly tipped, gradually broadening distally, with serrate, membranous cap at tip; 2 caudal setae unequal in length.

Rostrum absent. Antennule (Fig. 42E) short, 169 µm long, 4-segmented, but articulation between first and second segments distinct only on dorsal surface; armature formula 8, 5, 2+aesthetasc, and 11+aesthetasc; 3 larger setae on first, 2 on second, 1 on each of third and apical segments. Left antenna (Fig. 42F) 4-segmented, slender, with unarmed coxa, basis, and first endopodal segment; second endopodal segment 3.4 times longer than wide (55×16 µm), shorter than basis, armed with 7 setae (4 of them shorter and bluntly tipped); longest of distal setae 95 µm long. Second endopodal segment of right antenna (Fig. 42G) longer than that of left antenna, 64×14 µm, armed with 7 spiniform setae bearing blunt, serrate distal tips, all setae at most 50 µm long, shorter than second endopodal segment.

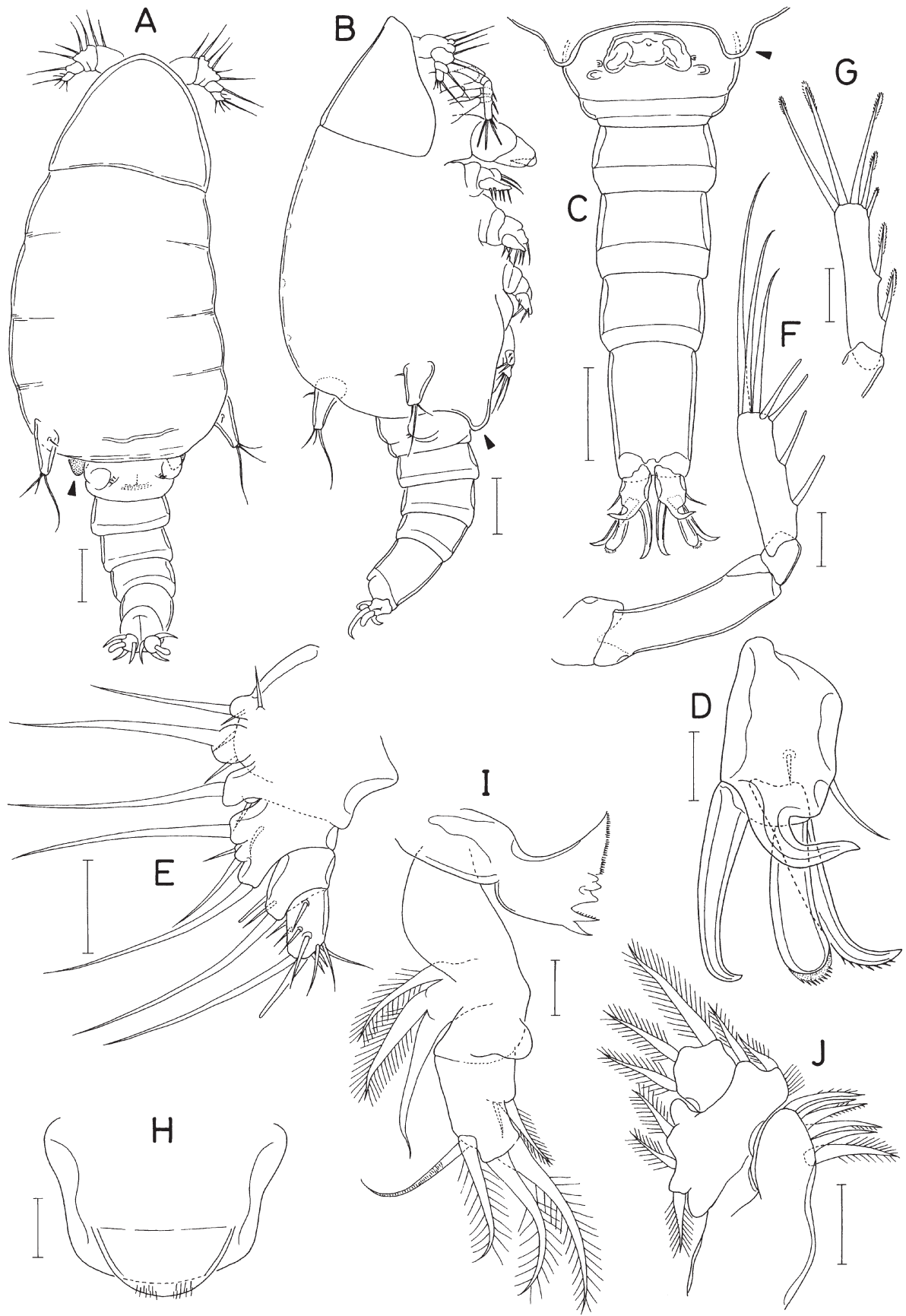
Labrum (Fig. 42H) with thick lateral borders and linguiform posteromedian lobe ornamented with minute setules distally. Mandible (Fig. 42I) bearing bifurcate distal tooth and 3 smaller, blunt teeth on coxal gnathobase; palp bearing blunt tubercle on medial margin and armed with 9 setae arranged as 3, 2, 2, and 2; distal of 3 proximal setae and 1 of subterminal setae naked. Maxillule (Fig. 42J) with 6 distinct setae on precoxal arthrite; coxobasis with 2 setae on medial margin and 3 setae on outer margin, plus outer distal lobe; endopod well-defined from basis, armed with 3 setae. Maxilla (Fig. 43A) indistinctly 3-segmented and armed with 2, 4, and 3 setae on first to third segments, respectively; one of 4 setae on second segment very small. Maxilliped (Fig. 43B) robust, 4-segmented; syncoxa much broader than long, with 2 minute setae on medial margin; basis with 2 minute setae; short first endopodal segment unarmed; second endopodal segment with 2 minute setae (1 subdistal and 1 distal); terminal claw obscurely articulated from second endopodal segment, bearing 2 denticles on inner margin (1 proximal and 1 subdistal).

Legs 1-4 (Figs. 43C-F, 44A-D) biramous, asymmetrical; coxa unarmed; basis with 1 outer seta. Exopods of legs 1-4 unsegmented. Endopod of right leg 1 segmented only on posterior surface. Endopod of left leg 1 unsegmented. Endopods 2-segmented in right and left legs 2-4. Second endopodal segment of right leg 3 with 2 spines and 3 setae (Fig. 44A). Second endopodal segment of left leg 3 with 1 spine and 4 setae. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

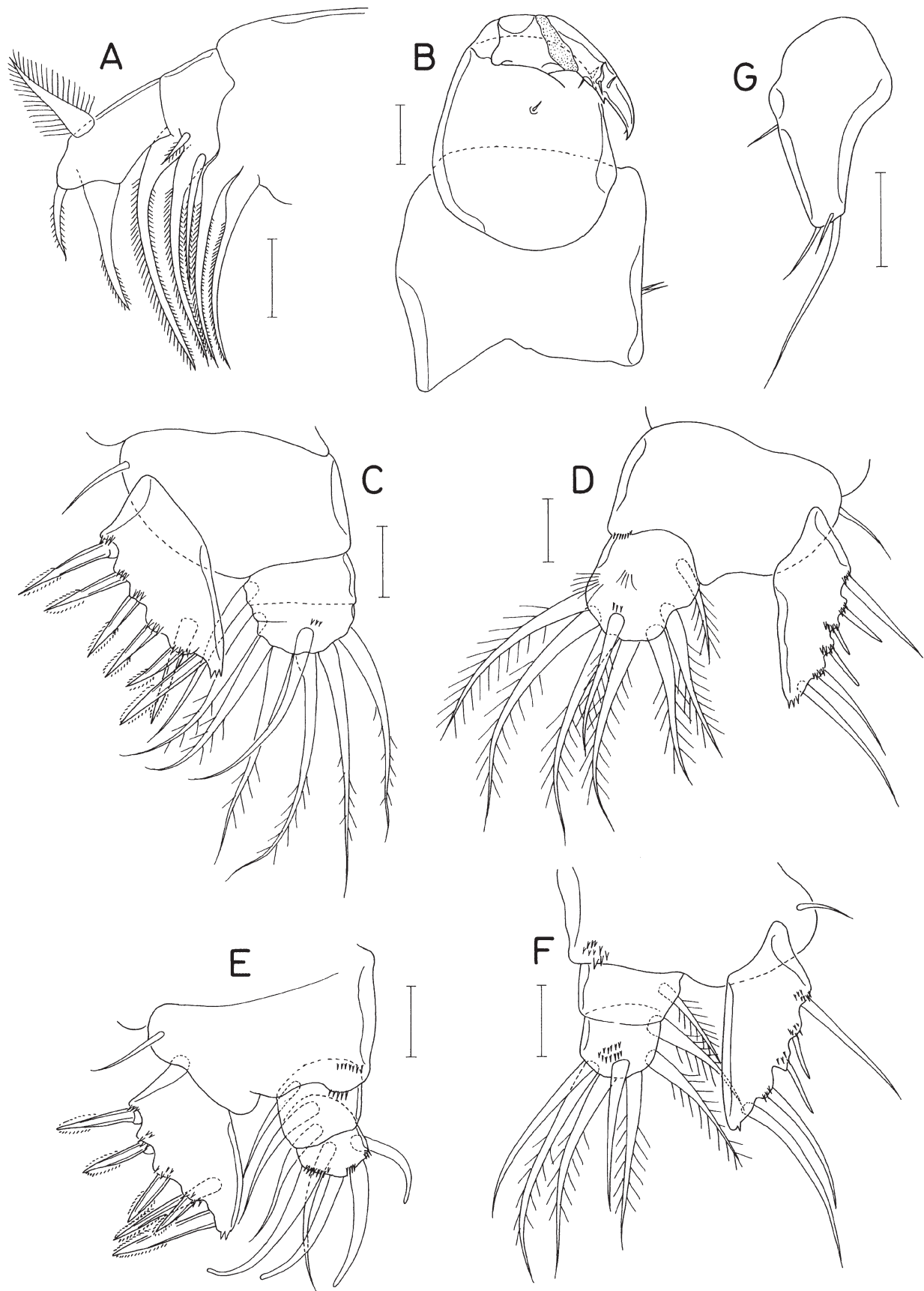
	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	8	6	8
Leg 2	VI	1; 7	5	1; 7
Leg 3	VI	1; II+3	5	1; I+4
Leg 4	V	1; 5	4	1; 5

Leg 5 (Fig. 43G) small, positioned laterally on fifth pedigerous somite, strongly tapering, 113×63 µm, armed with 4 setae (1 on proximal dorsal margin and 3 distal); distal longest seta 100 µm long, slightly shorter than segment. Leg 6 (Fig. 44E) represented by 1 small spine and 1 spiniform process on genital operculum; about 9 small surface tubercles present near leg 6.

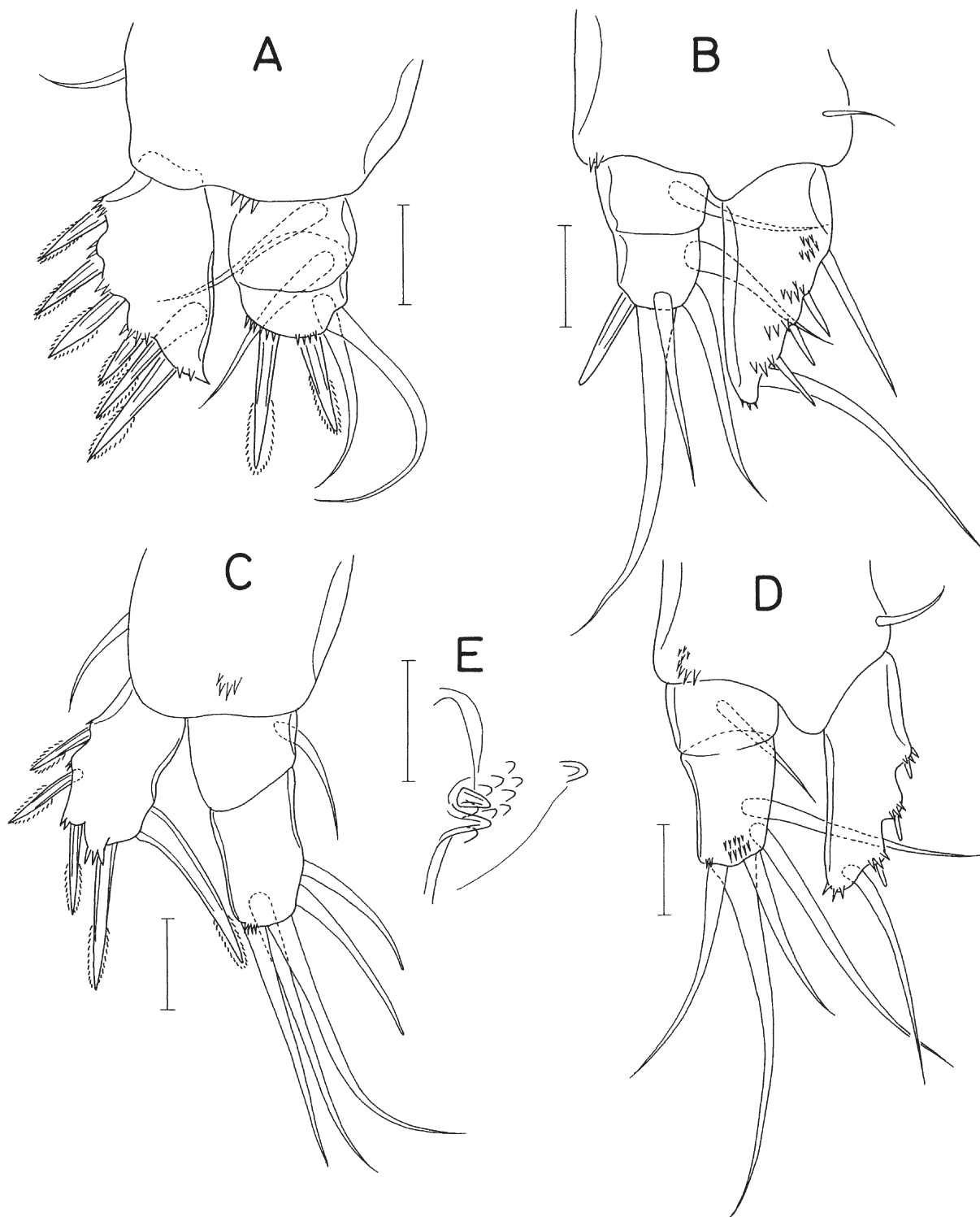




**FIG. 42.** *Botryllophilus tuberculatus* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, posterior part of body, dorsal; D, caudal ramus; E, antennule; F, left antenna; G, second endopodal segment of right antenna; H, labrum; I, mandible; J, maxillule. Scale bars: A-C, 0.1 mm; D, F-J, 0.02 mm; E, 0.05 mm.



**FIG. 43.** *Botryllophilus tuberculatus* sp. nov., female. A, maxilla; B, maxilliped; C, right leg 1; D, left leg 1; E, right leg 2; F, left leg 2; G, leg 5. Scale bars: A-F, 0.02 mm; G, 0.05 mm.



**FIG. 44.** *Botryllophilus tuberculatus* **sp. nov.**, female. A, right leg 3; B, left leg 3; C, right leg 4; D, left leg 4; E, leg 6. Scale bars: 0.02 mm.

**Male.** Unknown.

**Remarks.** *Botryllophilus tuberculatus* **sp. nov.** most closely resembles *B. distinctus* Ooishi, 2012 known as an associate of *Eudistoma* sp. in Madagascar. They have the same number of armature elements on the antenna and on legs 1-4 and have similar setation on the antennule. Distinguishing the new species from *B. distinctus* is easy: *B. tuberculatus* **sp. nov.** possesses a pair of tubercles in the posteroventral region of the fifth pedigerous somite (vs. no

such tubercles present in *B. distinctus*), the exopod of right leg 3 is unsegmented (vs. 2-segmented in *B. distinctus*), the exopod of left leg 4 is short and unsegmented (vs. elongate and 2-segmented in *B. distinctus*), and the second endopodal segment of left leg 3 is armed with 1 spine plus 4 setae (vs. 5 setae only in *B. distinctus*). The differences are sufficient to justify the establishment of a new species.

***Botryllophilus stenurosus* sp. nov.**

(Figs. 45-47)

**Type material.** Holotype ♀ (MNHN-IU-2018-1967), 3 ♀♀ paratypes (intact, MNHN-IU-2018-1968), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17372) from *Exostoma ianthinum* (Sluiter, 1909); Papua New Guinea, south coast near bootless inlet, South Motupore reef, OCDN 1643-I (09°31.81'S, 147°17.05'E), depth 3 m, CRRF coll., 29 October 1992.

**Additional material.** 1 ♀ (MNHN-IU-2014-17373, dissected) from *E. ianthinum*, Papua New Guinea, CRRF coll.

**Etymology.** The specific name is derived from the Greek *sten* (=narrow) and *uro* (=tail), referring to the slender abdomen of the new species.

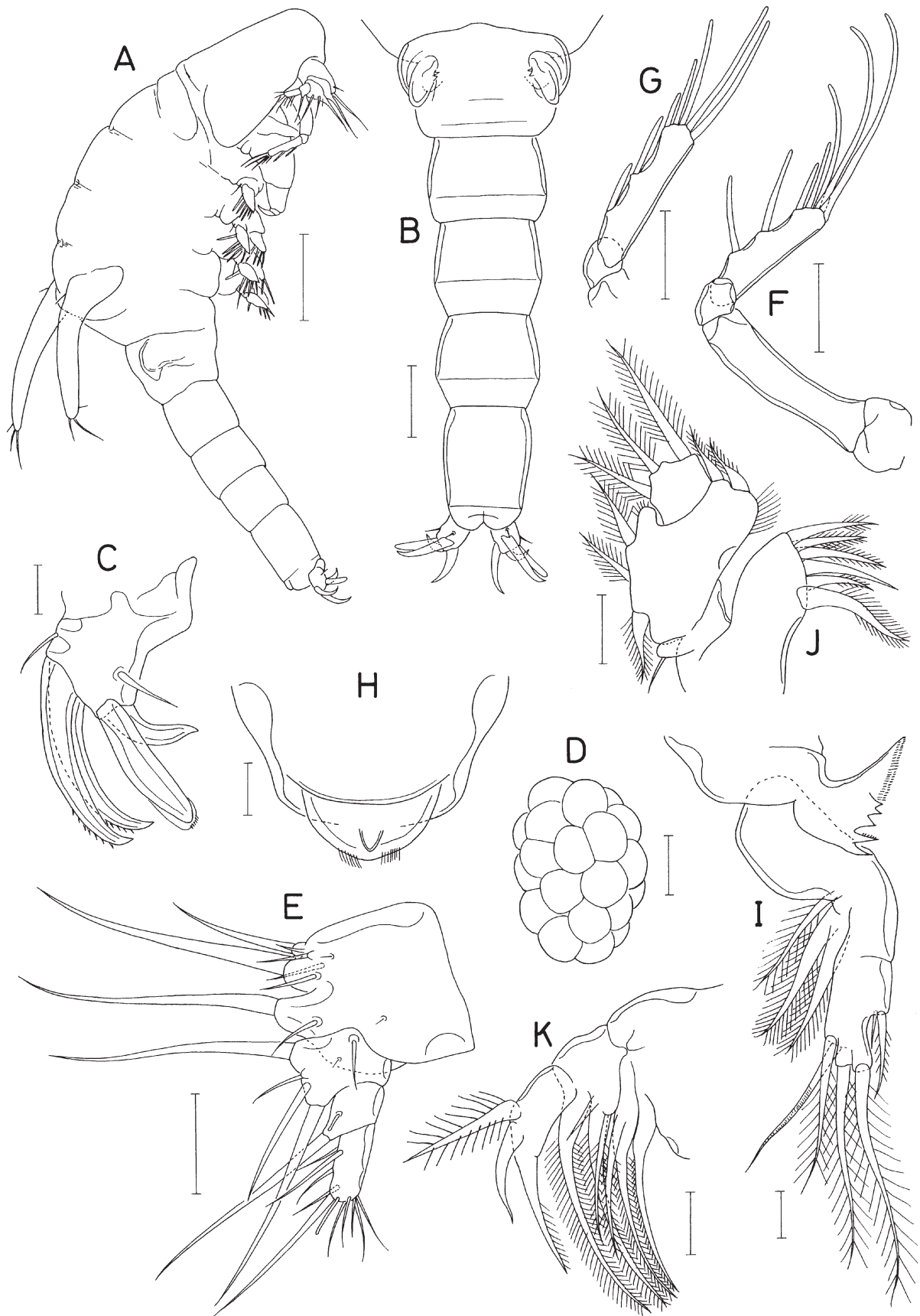
**Description of female.** Body (Fig. 45A) narrow, slightly asymmetrical, arched ventrally; body length 1.50 mm. Anterior part of body gradually broadening posteriorly, unsegmented, but divisible into 5 parts by indistinct cephalic shield and 3 weak dorsolateral constrictions; fourth and fifth pedigerous somites not defined from each other. Leg 5 positioned dorsolaterally. Posterior part of body (Fig. 45B) slender, occupying 45% of body length, consisting of genital somite and abdomen of 4 somites. Genital somite 152×242 µm, narrowing posteriorly; genital apertures positioned dorsally. Abdominal somites 121×167, 133×152, 127×145, and 172×123 µm, respectively. Caudal ramus (Fig. 45C) armed with 4 claws and 2 setae; larger inner distal claws longer than ramus; 1 inner distal claw blunt with membranous tip. Egg sac (Fig. 45D) oval, 640×455 µm; each egg about 160 µm in diameter.

Rostrum absent. Antennule (Fig. 45E) short, 4-segmented; armature formula 8, 5, 1+aesthetasc, and 10+aesthetasc; 2 larger setae on first, 2 on second, and 1 on third segments. Left antenna (Fig. 45F) slender, 4-segmented; proximal 3 segments unarmed; second endopodal segment about 3.4 times longer than wide (79×23 µm), distinctly shorter than basis, armed with 7 bluntly tipped, slender setae, longest outer distal seta 128 µm. Second endopodal segment of right antenna (Fig. 45G) about 4 times longer than wide (91×23 µm), longer than that of left antenna, but with shorter setae, longest second outer distal seta 83 µm.

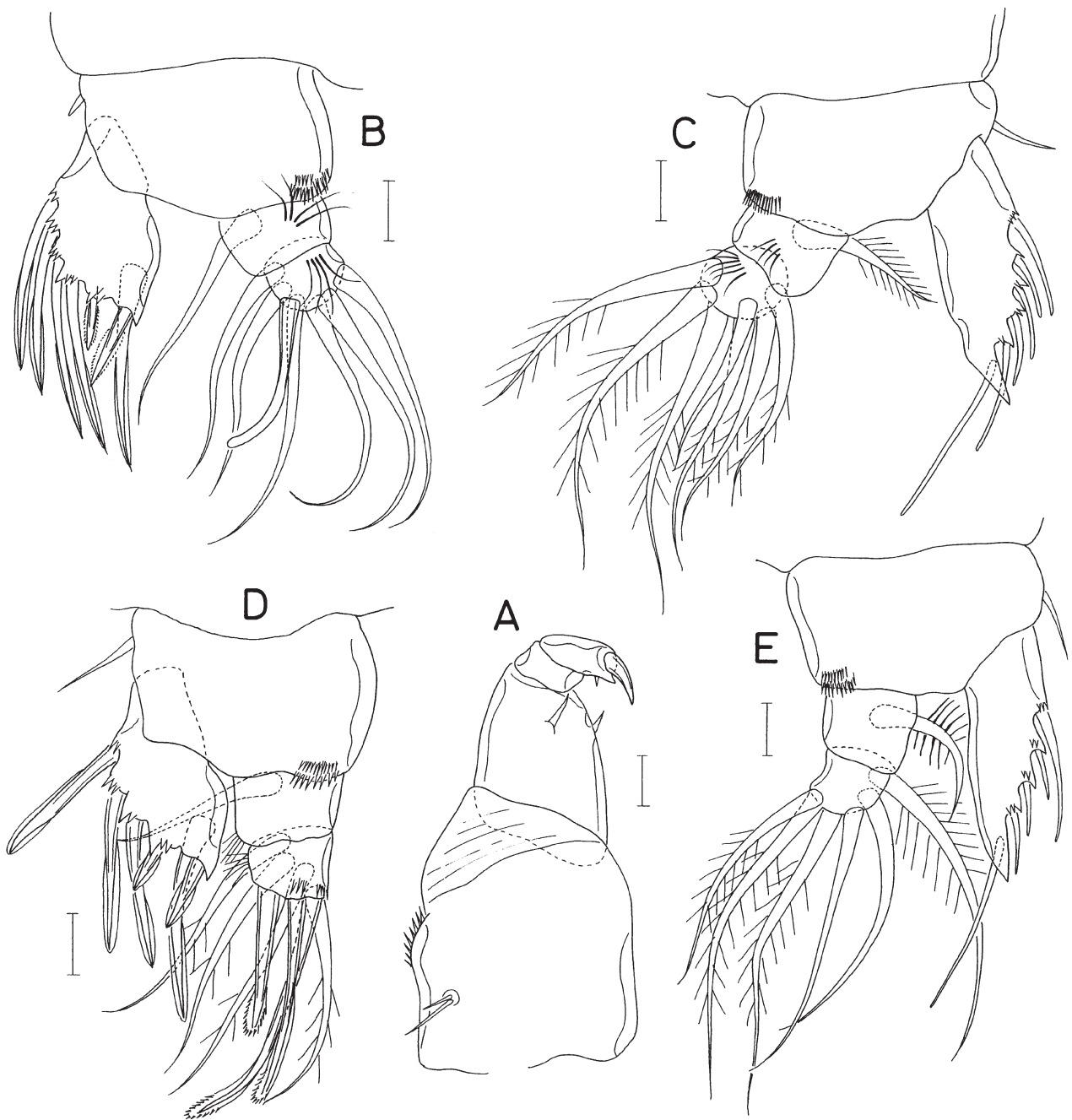
Labrum (Fig. 45H) with thickened lateral borders and linguiform posteromedian lobe bearing small lobe on ventral surface and minute setules on distal margin. Mandible (Fig. 45I) bearing bifurcate distal tooth and 3 smaller teeth on coxal gnathobase; palp with 9 setae arranged as 3, 2 (including 1 minute seta), 2, and 2; distal 2 of 3 outer proximal setae broadened. Maxillule (Fig. 45J) with 6 distinct setae on precoxal arthrite; coxobasis with 1 vestigial seta on epipodite, 2 medial and 3 outer setae on basis region; setulose distal lobe present on basis; endopod distinctly articulated from basis, armed with 3 setae. Maxilla (Fig. 45K) indistinctly 3-segmented with 3, 4, and 3 setae on first to third segments, respectively. Maxilliped (Fig. 46A) relatively narrow, 4-segmented; syncoxa as long as wide, with 2 small setae proximally and row of several spinules near middle of outer surface; basis with 2 small setae; small first endopodal segment unarmed; second segment twice as long as wide, with 1 small seta on inner margin and produced inner distal corner; terminal claw small, shorter than second endopodal segment.

Legs 1-4 (Figs. 46B-E, 47A-D) biramous, asymmetrical; coxa obscure, lacking inner seta; basis with small outer seta, ornamented with patch of spinules at inner distal corner. Exopods of all swimming legs unsegmented, but all endopods distinctly 2-segmented. Second endopodal segment of right legs 2-4 bearing spines in addition to setae. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

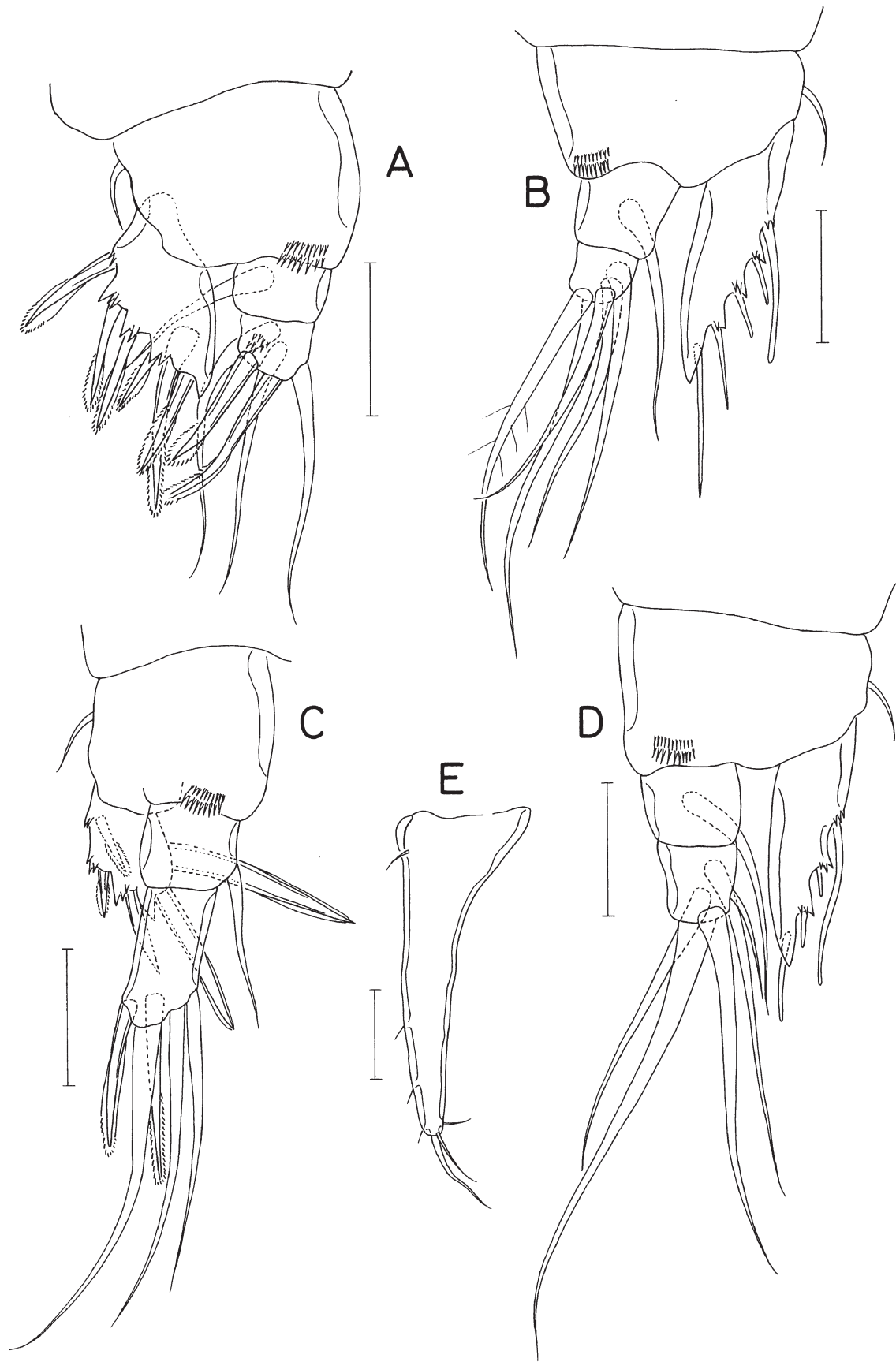
	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	1; 7	6	1; 7
Leg 2	VI	1; III+4	5	1; 6
Leg 3	VI	1; II+3	5	1; 5
Leg 4	V	1; II+3	4	1; 5



**FIG. 45.** *Botryllophilus stenurosus* sp. nov., female. A, habitus, right; B, posterior part of body, dorsal; C, caudal ramus; D, egg sac; E, antennule; F, left antenna; G, distal part of right antenna; H, labrum; I, mandible; J, maxillule; K, maxilla. Scale bars: A, D, 0.2 mm; B, 0.1 mm; C, H-K, 0.02 mm; E, F, G, 0.05 mm.



**FIG. 46.** *Botryllophilus stenurosus* sp. nov., female. A, maxilliped; B, right leg 1; C, left leg 1; D, right leg 2; E, left leg 2. Scale bars: 0.02 mm.



**FIG. 47.** *Botryllophilus stenurosus* **sp. nov.**, female. A, right leg 3; B, left leg 3; C, right leg 4; D, left leg 4; E, leg 5. Scale bars: A-D, 0.05 mm; E, 0.1 mm.

Leg 5 (Fig. 47E) elongate, extending beyond posterior margin of genital somite (Fig. 45A), 2.5 times longer than wide (380×150 µm); armed with 4 setae (3 thin, setule-like); largest distal seta 110 µm long, but shorter than proximal width of leg 5. Leg 6 represented by 1 small spinule and 1 spinule-like process on genital operculum.

**Male.** Unknown.

**Remarks.** Leg 5 is generally large in members of the *Botryllophilus* type B species group but small in members of the type A species group. *Botryllophilus stenurosus* **sp. nov.** belongs to the type A group, but possesses a large leg 5 which seems to be the most salient diagnostic feature of the new species. Within the type A group, *B. abbotti* Ooishi & Illg, 1989 and *B. banyulensis* Brément, 1909 carry a fairly large leg 5, but they differ from *B. stenurosus* **sp. nov.** in having different combinations of armature elements on the swimming legs. For example, *B. abbotti* and *B. banyulensis* each have 6 spines (cf. 7 spines in *B. stenurosus* **sp. nov.**) on the exopod of right leg 1, and 7 setae (cf. 8 setae in *B. stenurosus* **sp. nov.**) on the endopod of right leg 2.

The combination of setal numbers (8-7-6-6) on the endopods of left legs 1-4 of *B. stenurosus* **sp. nov.** is unique within the genus and this feature alone serves to differentiate *B. stenurosus* **sp. nov.** from all of its congeners.

### ***Botryllophilus longicaudatus* sp. nov.**

(Figs. 48-50)

**Type material.** Holotype ♀ (MNHN-IU-2018-1969, dissected and mounted on a slide) from *Sigillina* sp.; Juan de Fuca, MUA 88, Juan de Nova Is., Mozambique Channel, Laboute coll., 02 February 1996.

**Etymology.** The name is a combination of Latin *longus* (=long) and *cauda* (=tail), referring to the relatively long abdomen of the new species.

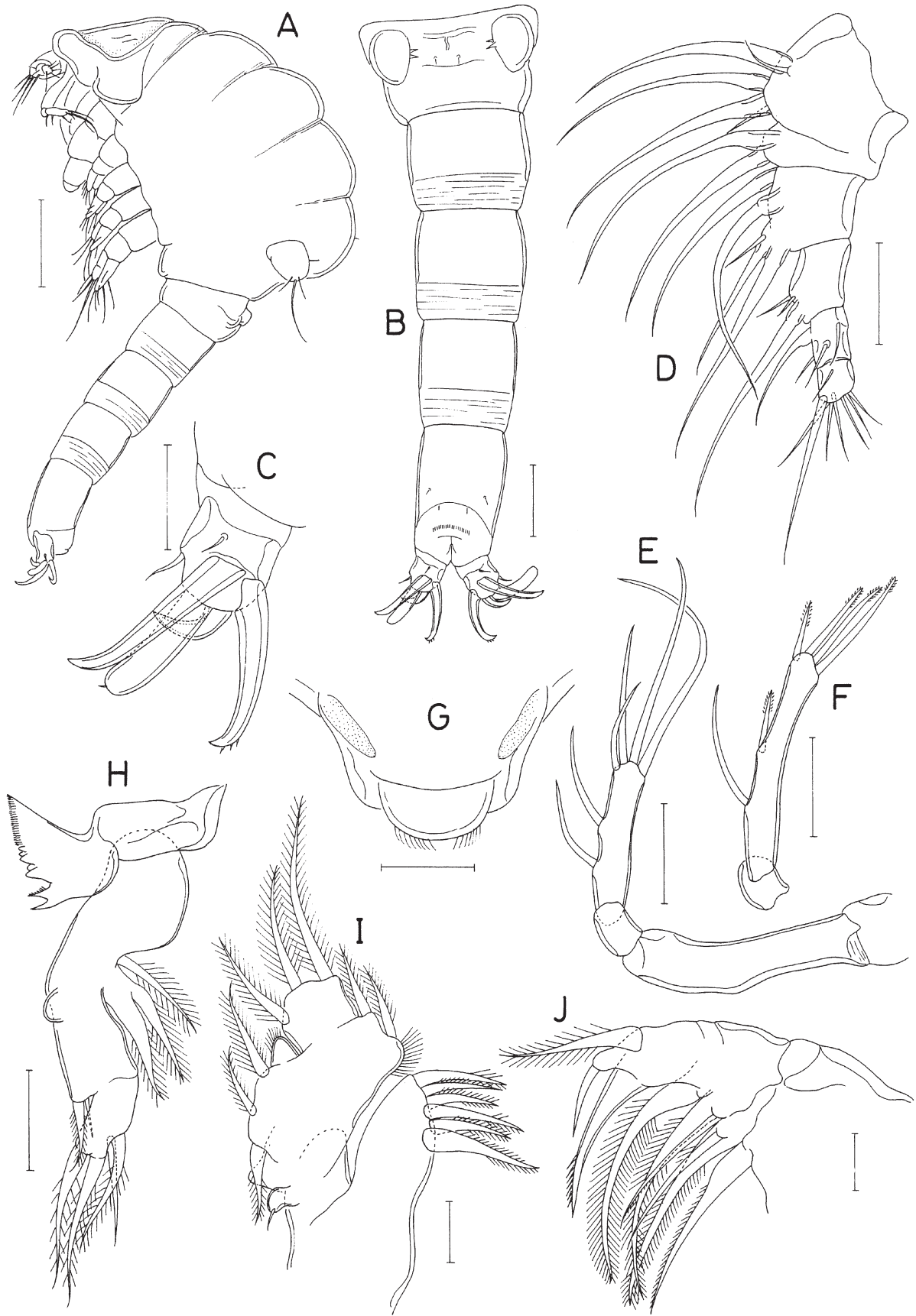
**Description of female.** Body (Fig. 48A) consisting of swollen anterior part and elongate posterior part, with thick exoskeleton; body length 1.45 mm. Anterior part of body expanded dorsally and laterally, with slightly depressed cephalosome and 3 dorsolateral constrictions, without division between fourth and fifth pedigerous somites. Leg 5 positioned laterally. Posterior part of body (Fig. 48B) as long as anterior part; consisting of genital and 4 abdominal somites. Genital somite 148×255 µm; genital apertures large, located dorsally. Four abdominal somites 138×175, 154×157, 151×138, and 200×126 µm, respectively. Caudal ramus (Fig. 48C) short, 51×46 µm, armed with 4 claws and 2 small setae; inner largest claw 92 µm long, much longer than ramus; 2 outer distal claws comprising blunt straight claw (60 µm long) tipped with 1 small setule, and strongly curved short claw (41 µm long).

Rostrum absent. Antennule (Fig. 48D) 187 µm long, not expanded, 5-segmented; articulation between 2 terminal segments incomplete, expressed only on one surface; armature formula 7, 5, 3, 4, and 8; first to third segments with 5, 3, and 1 large setae, respectively. Antenna (Fig. 48E, F) slender, 4-segmented; coxa, basis, and first endopodal segment unarmed; second endopodal segment of left antenna about 4.3 times longer than wide (82×19 µm), armed with 2 inner and 4 distal, attenuate setae. Second endopodal segment of right antenna (Fig. 48F) longer than that of left antenna, 115×18 µm; armed with longer, naked proximal seta and 5 shorter, spiniform setae ornamented with spinules distally.

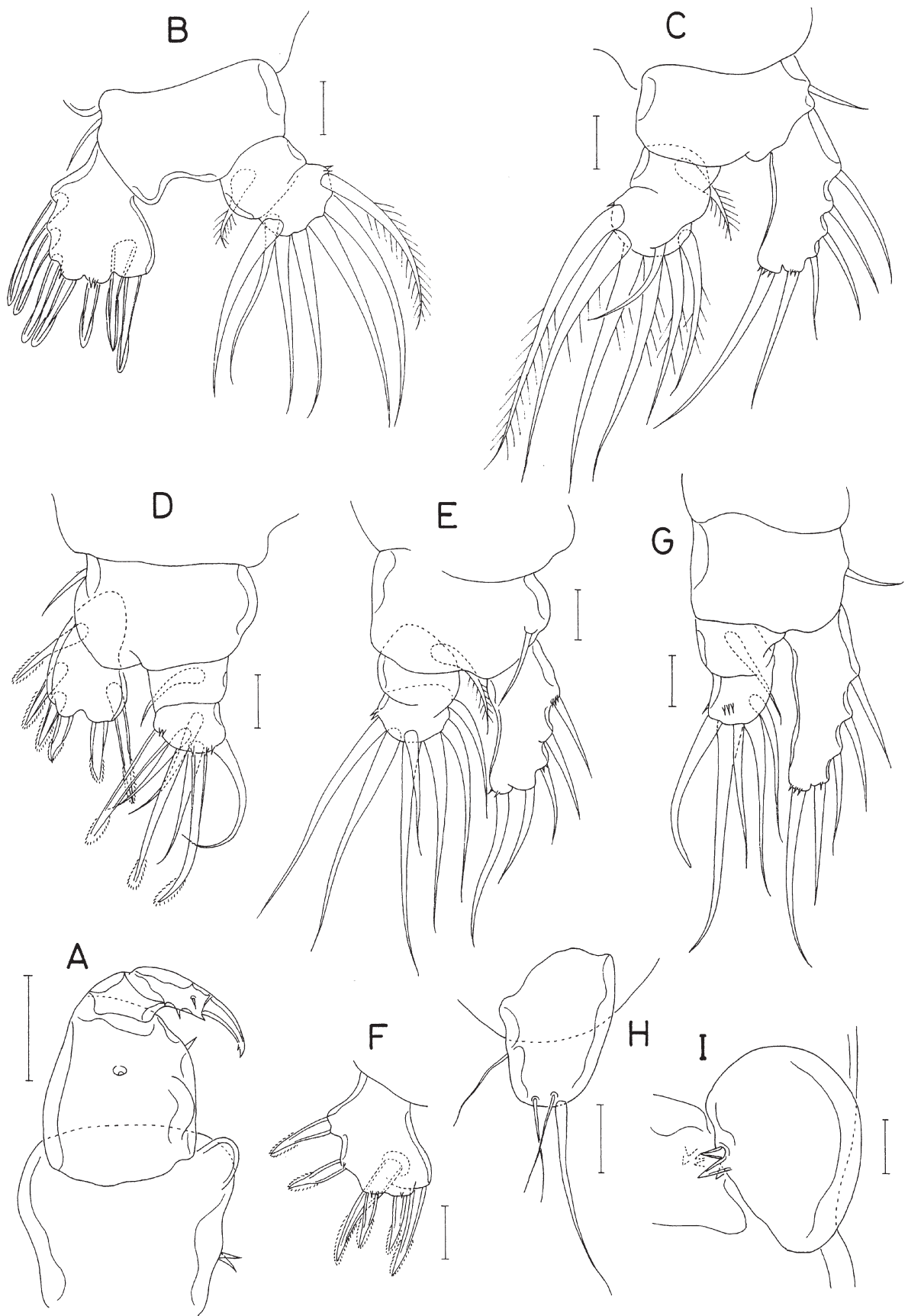
Labrum (Fig. 48G) with broad posteromedian lobe bearing setules along posterior margin. Mandible (Fig. 48H) consisting of coxa and palp; medial margin of coxal gnathobase with bifurcate distal tooth and 4 or 5 smaller, blunt teeth; palp with semicircular tubercle on middle of medial margin and armed with 9 setae arranged as 3, 2, 2, and 2. Maxillule (Fig. 48I) consisting of precoxa and palp; precoxa with 6 distinct setae on arthrite; palp divisible into coxa, basis, and endopod; coxa with small, knob-like epipodite tipped with minute vestigial seta; basis with 2 medial and 3 outer setae and 1 tubercle-like distal process; endopod wider than long, incompletely articulated from basis, armed with 3 setae on distal margin. Maxilla (Fig. 48J) indistinctly 2-segmented with 3 setae on first segment and 6 setae on second, mediobasal seta strong, claw-like. Maxilliped (Fig. 49A) 4-segmented; syncoxa with 2 small setae on medial margin and blunt tubercle at mediobasal corner; basis with 1 small seta; first endopodal segment small, unarmed; second segment with 2 minute setae and 1 inner distal, dentiform process; terminal claw as long as second endopodal segment, bearing small subterminal denticle.

Legs 1-4 (Figs. 49B-G, 50A, B) biramous and asymmetrical, with unsegmented exopods and incompletely 2-segmented endopods (endopod of right leg 3 missing); coxa unarmed; basis with outer seta, but unornamented. First endopodal segment of all swimming legs bearing short seta; second endopodal segment of right leg 2 with 3 spines

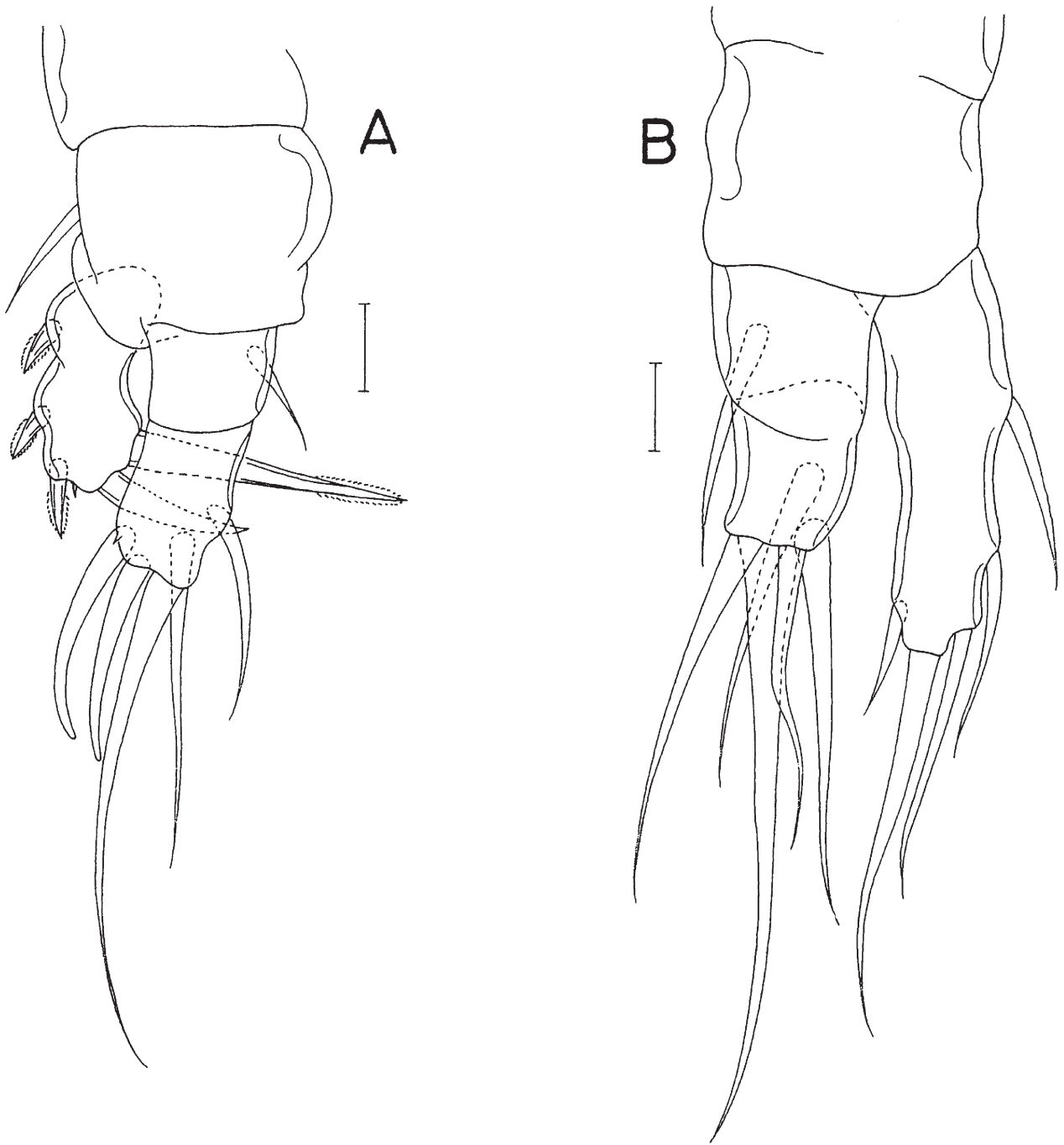




**FIG. 48.** *Botryllophilus longicaudatus* sp. nov., female. A, habitus, left; B, posterior part of body, dorsal; C, caudal ramus; D, antennule; E, left antenna; F, endopod of right antenna; G, labrum; H, mandible; I, maxillule; J, maxilla. Scale bars: A, 0.2 mm; B, 0.1 mm; C-H, 0.05 mm; I, J, 0.02 mm.



**FIG. 49.** *Botryllophilus longicaudatus* sp. nov., female. A, maxilliped; B, right leg 1; C, left leg 1; D, right leg 2; E, left leg 2; F, exopod of right leg 3; G, left leg 3; H, leg 5; I, genital aperture. Scale bars: A, H, 0.05 mm; B-G, 0.02 mm.



**FIG. 50.** *Botryllophilus longicaudatus* sp. nov., female. A, right leg 4; B, left leg 4. Scale bars: 0.02 mm.

and 4 setae; endopods of legs 1 and 4 armed with setae only. Some of setae on endopods of legs 1 and 2 pinnate, other setae naked. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	1; 7	6	1; 7
Leg 2	VI	1; III+4	5	1; 7
Leg 3	VI	(missing)	5	1; 5
Leg 4	V	1; 5	5	1; 5

Leg 5 (Fig. 49H) small, not extending beyond anterior border of genital somite, about 1.4 times longer than wide (117×86 µm) with rounded distal margin; armed with 3 thin shorter setae and 1 large distal seta, longer than leg 5. Leg 6 (Fig. 49I) represented by 1 spinule and 1 spiniform process on genital operculum. Five small papillae present near leg 6.

**Male.** Unknown.

**Remarks.** In having the same combination of armature elements on legs 1, 2 and 4 and on the exopod of right leg 3 (the endopod of right leg 3 is missing in the single available specimen of *B. longicaudatus* **sp. nov.**), *B. longicaudatus* **sp. nov.** is comparable only with *B. spinulosus* Ooishi, 2012. The latter species lives in association with an ascidian of the genus *Synoicum* in Madagascar (Ooishi, 2012). The main differences that serve to distinguish between *B. longicaudatus* **sp. nov.** and *B. spinulosus* are: (1) the anterior part of the body is swollen (cf. narrow in *B. spinulosus*); (2) leg 5 is stout (cf. elongate in *B. spinulosus*); (3) the first segment of the antennule is armed with 5 large and 2 small setae (cf. 2 large and 6 small setae in *B. spinulosus*); (4) the second endopodal segment of right leg 2 is armed with 3 spines and 4 setae (cf. 3 naked and 4 pinnate setae in *B. spinulosus*).

***Botryllophilus pentachaetus* sp. nov.**

(Figs. 51-53)

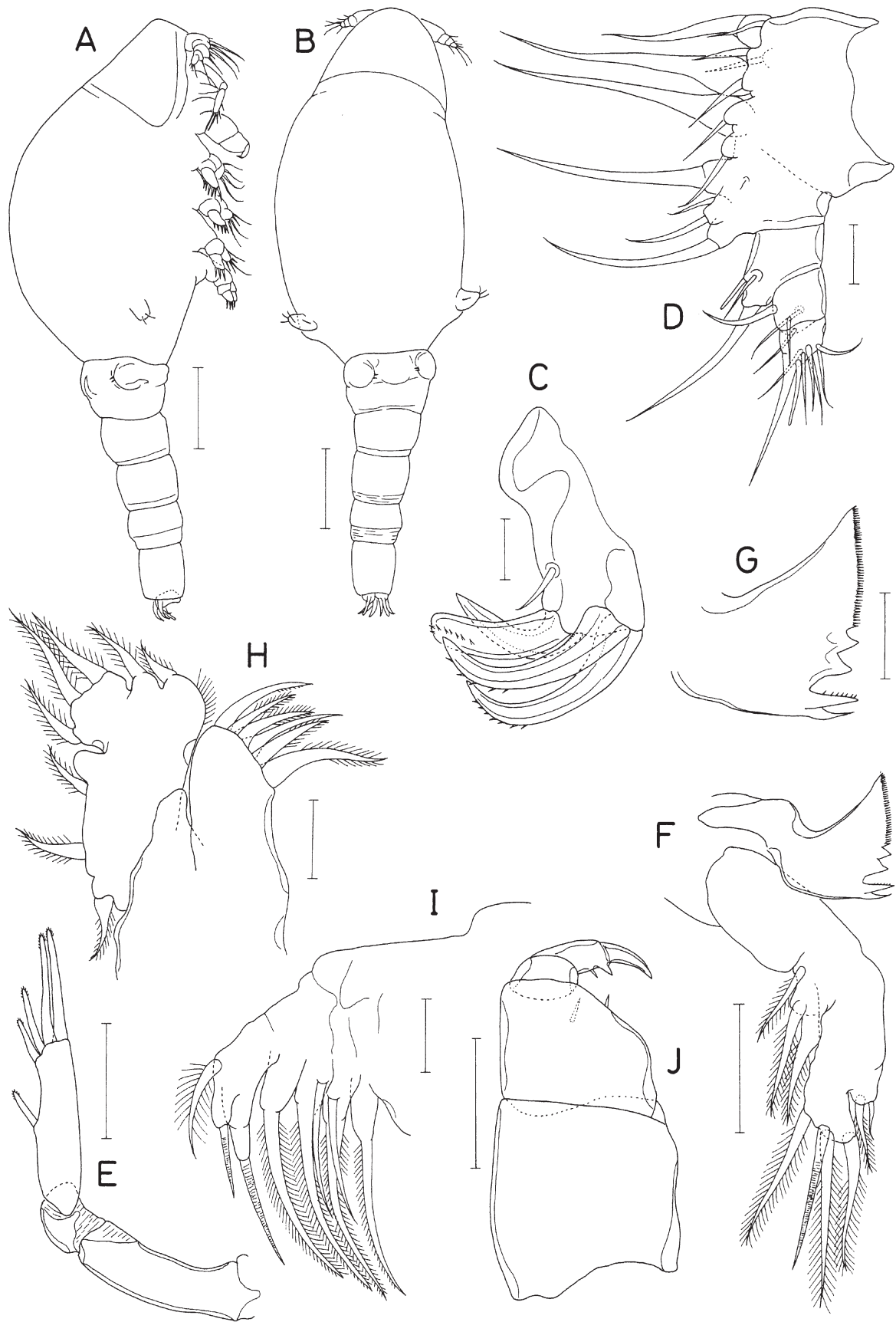
**Type material.** Holotype ♀ (MNHN-IU-2009-5057), 2 ♀♀ paratypes (intact, MNHN-IU-2018-1970) and ♀ paratype (dissected, MNHN-IU-2014-17374) from *Eudistoma viride* Tokioka, 1955 (MNHN-IT-2008-4294 = MNHN A3/EUD/344); Danau A Gam lake mangrove (marine lake), Raja Ampat, West Papua, Indonesia, Stn DAG 043 (00°26.518'N, 130°41.134'E), depth 0.5 m, F. Monniot coll., 23 November 2007.

**Etymology.** The name of the new species is derived from the Greek *pent* (=five) and *chaet* (=a bristle), referring to the presence of five setae on the antenna.

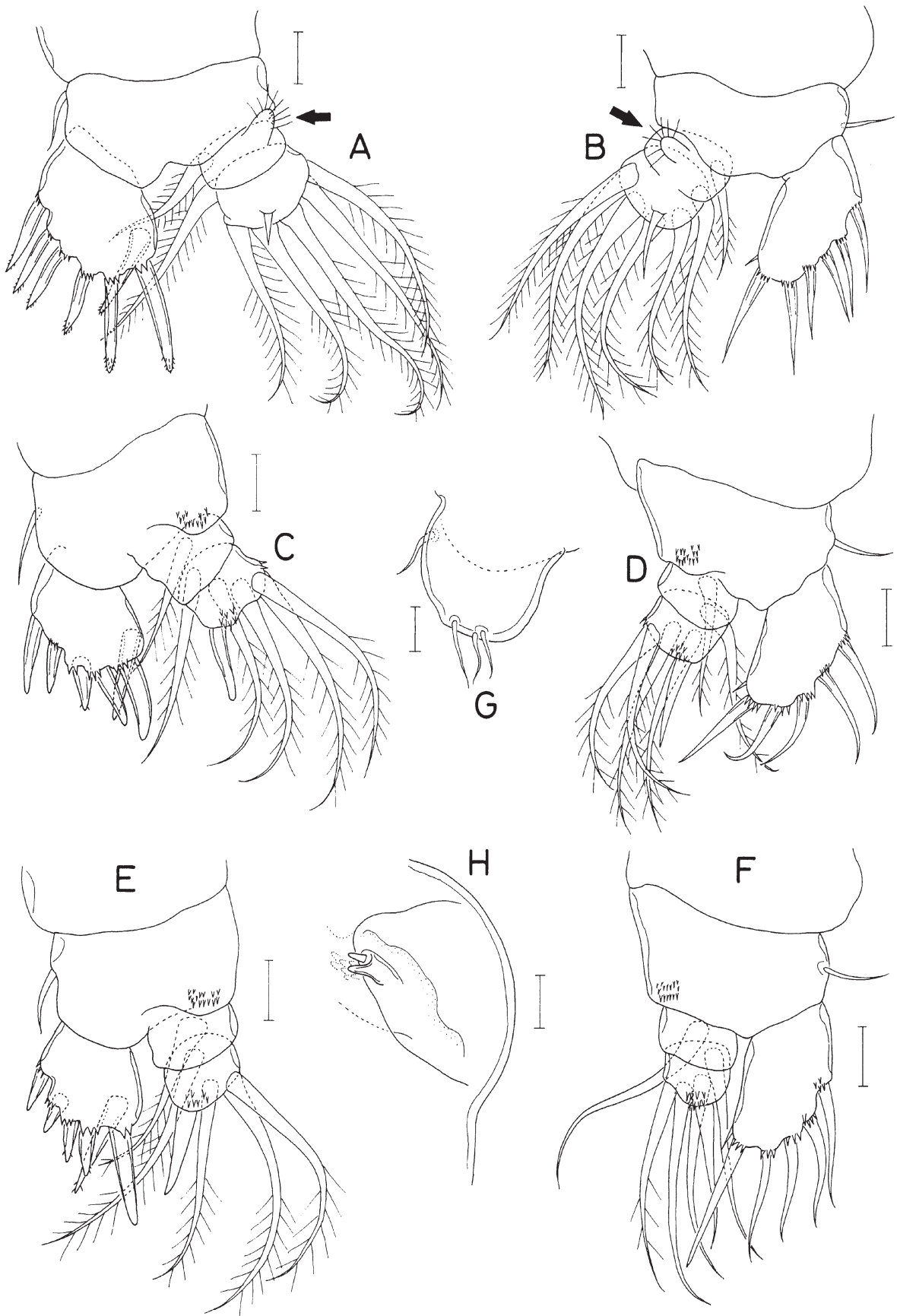
**Description of female.** Body (Fig. 51A, B) slightly asymmetrical, consisting of moderately swollen anterior part and narrower, cylindrical posterior part: body length 1.48 mm in dissected largest specimen and 1.30 mm in smallest specimen. Anterior part of body nearly elliptical, 860×468 µm, roundly expanded dorsally, unsegmented, without any constriction or trace of suture; dorsal cephalic shield distinct. Posterior part of body occupying 43% of total body length, consisting of genital somite and 4 abdominal somites. Genital somite 154×231 µm; genital apertures positioned dorsally. Four abdominal somites 115×173, 119×148, 104×135, and 135×115 µm, respectively. Caudal ramus (Fig. 51C) armed with 4 claws and 1 seta (lacking inner seta); 1 of outer distal claws blunt.

Rostrum absent. Antennule (Fig. 51D) 4-segmented; armature formula 13, 2+aesthetasc, 4, and 7+aesthetasc; first segment subdivided by incomplete suture line on one surface; setae on first segment comprising 5 large and 8 small ones. Right antenna (Fig. 51E) 4-segmented, including obscure coxa; proximal 3 segments unarmed; second endopodal segment 3.6 times longer than wide (69×19 µm), characteristically armed with 5 setae, 1 on inner margin and 4 on distal margin. Left antenna different from right antenna in having shorter second endopodal segment and longer outer distal setae.

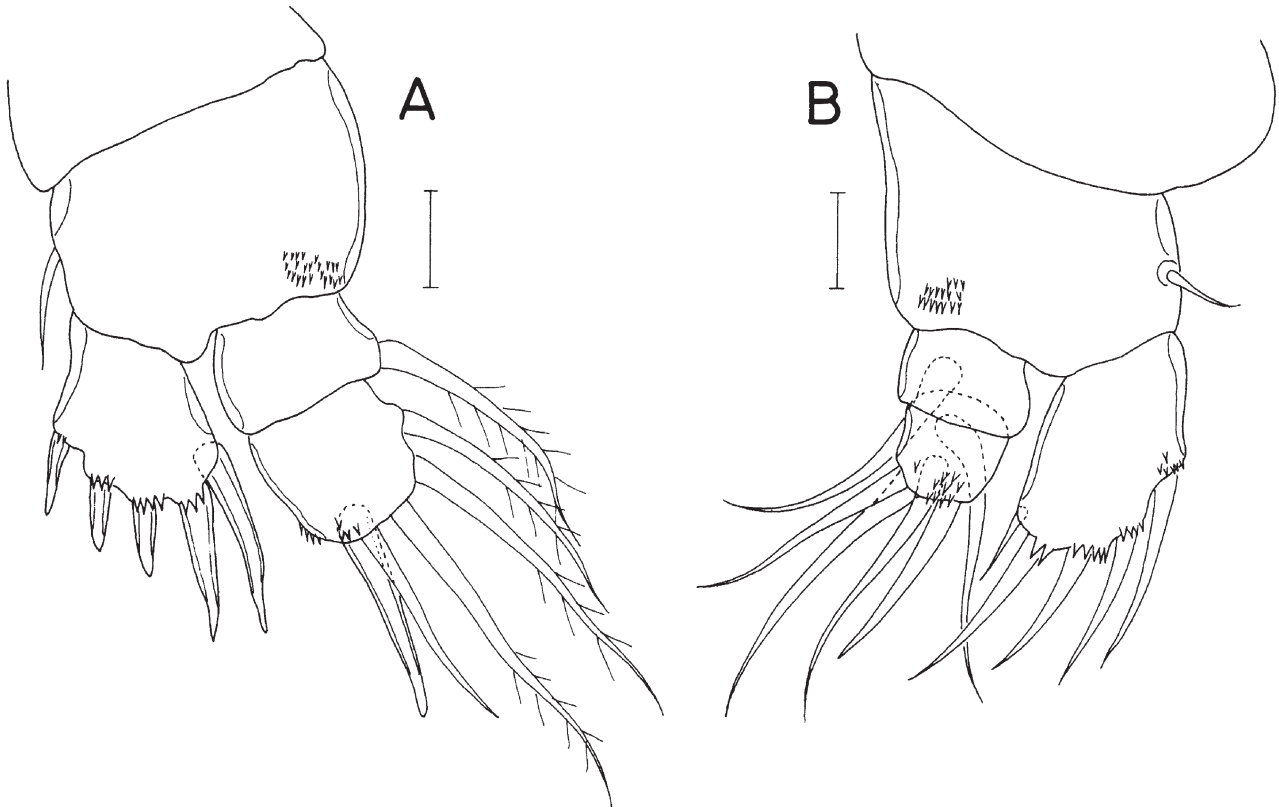
Labrum with broad posteromedian lobe. Mandible (Fig. 51F) with coxal gnathobase (Fig. 51G) bearing 3 teeth, distal tooth bifurcate; palp with 9 setae arranged as 3, 2, and 4. Maxillule (Fig. 51H) consisting of precoxa and unsegmented palp; precoxal arthrite bearing 6 distinct setae; palp bearing 2 medial and 3 outer setae on basis



**FIG. 51.** *Botryllophilus pentachaetus* **sp. nov.**, female. A, habitus, right; B, habitus, dorsal; C, caudal ramus; D, antennule; E, right antenna; F, mandible; G, coxal gnathobase of mandible; H, maxillule; I, maxilla; J, maxilliped. Scale bars: A, B, 0.2 mm; C, D, G-I, 0.02 mm; E, F, J, 0.05 mm.



**FIG. 52.** *Botryllophilus pentachaetus* **sp. nov.**, female. A, right leg 1; B, left leg 1; C, right leg 2; D, left leg 2; E, right leg 3; F, left leg 3; G, leg 5; H, genital aperture. Scale bars: 0.02 mm.



**FIG. 53.** *Botryllophilus pentachaetus* sp. nov., female. A, right leg 4; B, left leg 4. Scale bars: 0.02 mm.

region; endopod completely fused with basis, armed with 3 setae. Maxilla (Fig. 51I) indistinctly 3-segmented with 3 setae on each segment. Maxilliped (Fig. 51J) 4-segmented; broad syncoxa unarmed; basis with 2 small setae; first endopodal segment unarmed; second segment with 1 small seta and 1 tooth-like process on inner margin; terminal claw simple, slightly shorter than second endopodal segment.

Legs 1-4 (Figs. 52A-F, 53A, B) biramous, asymmetrical; with unsegmented exopods and 2-segmented endopods; coxa unarmed; basis with outer seta. Basis of leg 2-4 with patch of spinules at inner distal corner. First endopodal segment of right and left leg 1 bearing setulose tubercle on anterior surface (arrowed in Figs. 52A and B). One of setae on second endopodal segment of right and left leg 1 markedly smaller than other setae on same segment; second endopodal segment of right legs 2-4 with 1 spine in addition to setae. Outer subdistal seta on second endopodal segment of left legs 1-4 small, setule-like. Setal formula for right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	1; 7	7	1; 7
Leg 2	VI	1; I+5	6	1; 6
Leg 3	VI	1; I+4	6	1; 5
Leg 4	V	1; I+4	5	1; 5

Leg 5 (Fig. 52G) very small, lobate, slightly wider than long ( $54 \times 60 \mu\text{m}$ ), armed with 4 small setae (1 proximal and 3 distal) of subequal lengths. Leg 6 (Fig. 52H) represented by 1 spinule and 1 spiniform process on genital operculum.

**Male.** Unknown.

**Remarks.** The most conspicuous diagnostic feature of *B. pentachaetus* sp. nov. is the presence of only 5 setae on the antenna, this feature is shared only with *B. norvegicus* within the genus. *Botryllophilus norvegicus* cannot be confused with *B. pentachaetus* sp. nov. or any other species of *Botryllophilus* as it displays unique features such

as the extremely swollen metasome and the strongly curved leg 5. Another conspicuous feature of *B. pentachaetus* **sp. nov.** is the small size of its leg 5, which is wider than long and comparable only with the smallest known leg 5, in *B. kozloffii*, which is 1.33 times longer than wide (Ooishi, 2014c). The combination of the numbers of armature elements on the rami of legs 1-4 of *B. pentachaetus* **sp. nov.** also is unique within the genus.

***Botryllophilus angustus* sp. nov.**

(Figs. 54-56)

**Type material.** Holotype ♀ (MNHN-IU-2018-1971) and paratype ♀ (dissected, MNHN-IU-2014-17375) from *Eudistoma* sp.; Mabul, Malaysia, OPHG 1067-S (04°14.51'N, 118°37.32'E), depth 5-20 m, CRRF coll., 16 January 2004.

**Etymology.** The name of the new species is derived from the Latin *angust* (=narrow), indicating the narrow body.

**Description of female.** Body (Fig. 54A, B) narrow, consisting of broader anterior and narrower posterior parts; body length 1.45 mm, width 0.33 mm. Cephalosome longer than wide. Anterior part of body gradually broadening posteriorly, unsegmented, but with 4 dorsal traces of articulations. Posterior part of body (Fig. 54C) not articulated from anterior part, consisting of genital and 4 abdominal somites. Genital somite much wider than long, with complicated, densely sclerotized sculpture on ventral surface; genital apertures positioned dorsally. Four abdominal somites clearly defined, 112×154, 127×140, 119×127, and 135×110 µm, respectively. Caudal ramus (Fig. 54D) armed with 4 claws and 1 seta; 1 of 2 outer distal claws massive and blunt, other outer claw not articulated from ramus.

Rostrum absent. Antennule (Fig. 54E) 120 µm long, 4-segmented; first and second segments broadened; armature formula 9 (3 large + 6 small), 4 (2 large + 2 small), 2 (1 large + 1 small), and 12. Left antenna (Fig. 54F) 4-segmented; proximal 3 segments unarmed; terminal segment (second endopodal segment) about 2.7 times longer than wide (59×22 µm), armed with 7 bluntly tipped setae. Terminal segment of right antenna (Fig. 54G) about 3.3 times longer than wide (69×21 µm), longer than that of left antenna; all setae distally capped with finely serrate membrane, 3 outer setae on distal margin shorter than those of left antenna.

Labrum weak, easily destroyed. Mandible (Fig. 54H) consisting of coxa and palp; coxal gnathobase with 4 teeth including 2 distal acutely-pointed, longer teeth; palp with 9 setae arranged as 3, 2, 2, and 2. Maxillule (Fig. 54I) consisting of precoxa and palp; precoxa with 6 distinct setae on arthrite; palp divisible into coxa, basis, and endopod; coxa with 1 vestigial seta on epipodite; basis with 2 setae on medial margin, 3 setae on outer margin, and setulose lobe distally; endopod articulated from basis, distinctly wider than long, armed with 3 setae. Maxilla (Fig. 55A) indistinctly 3-segmented, armed with 3, 4 and 3 setae on first to third segments, respectively. Maxilliped (Fig. 55B) 4-segmented; syncoxa with 2 small setae on inner margin; basis with 1 rudimentary seta on inner margin; first endopodal segment unarmed; second endopodal segment with 1 rudimentary seta on inner margin and 1 minute denticle at inner distal corner; terminal claw small, bearing minute subdistal denticle.

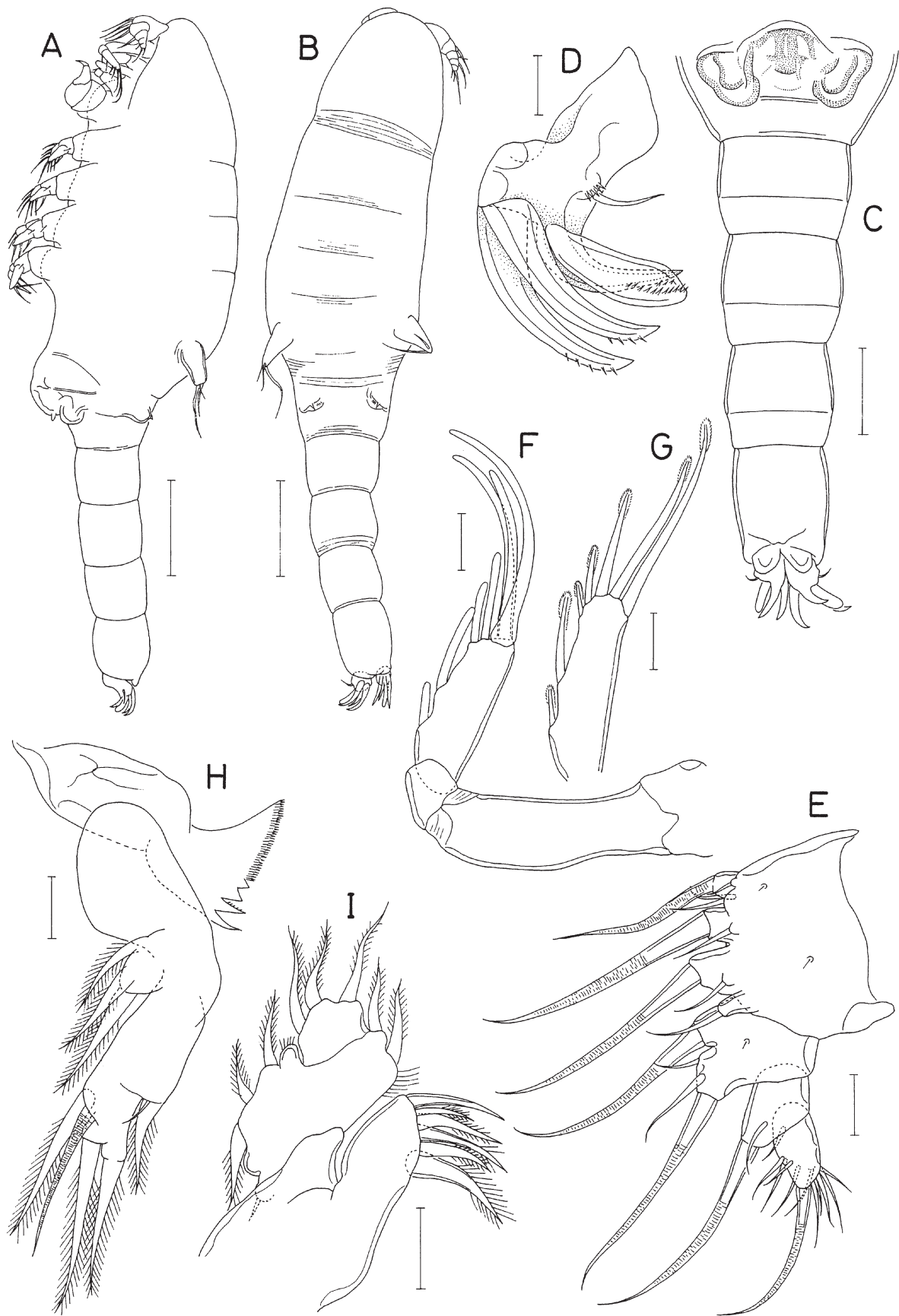
Legs 1-4 (Figs. 55C-F, 56A-D) biramous, asymmetrical, with unsegmented exopods and 2-segmented endopods; coxa unarmed; basis with outer seta and row of spinules at inner distal corner. Second endopodal segment of right legs 2-4 with mix of spines and setae. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	1; 7	6	1; 7
Leg 2	VI	1; III+4	5	1; 7
Leg 3	VI	1; II+3	5	1; 5
Leg 4	VI	1; II+3	4	1; 5

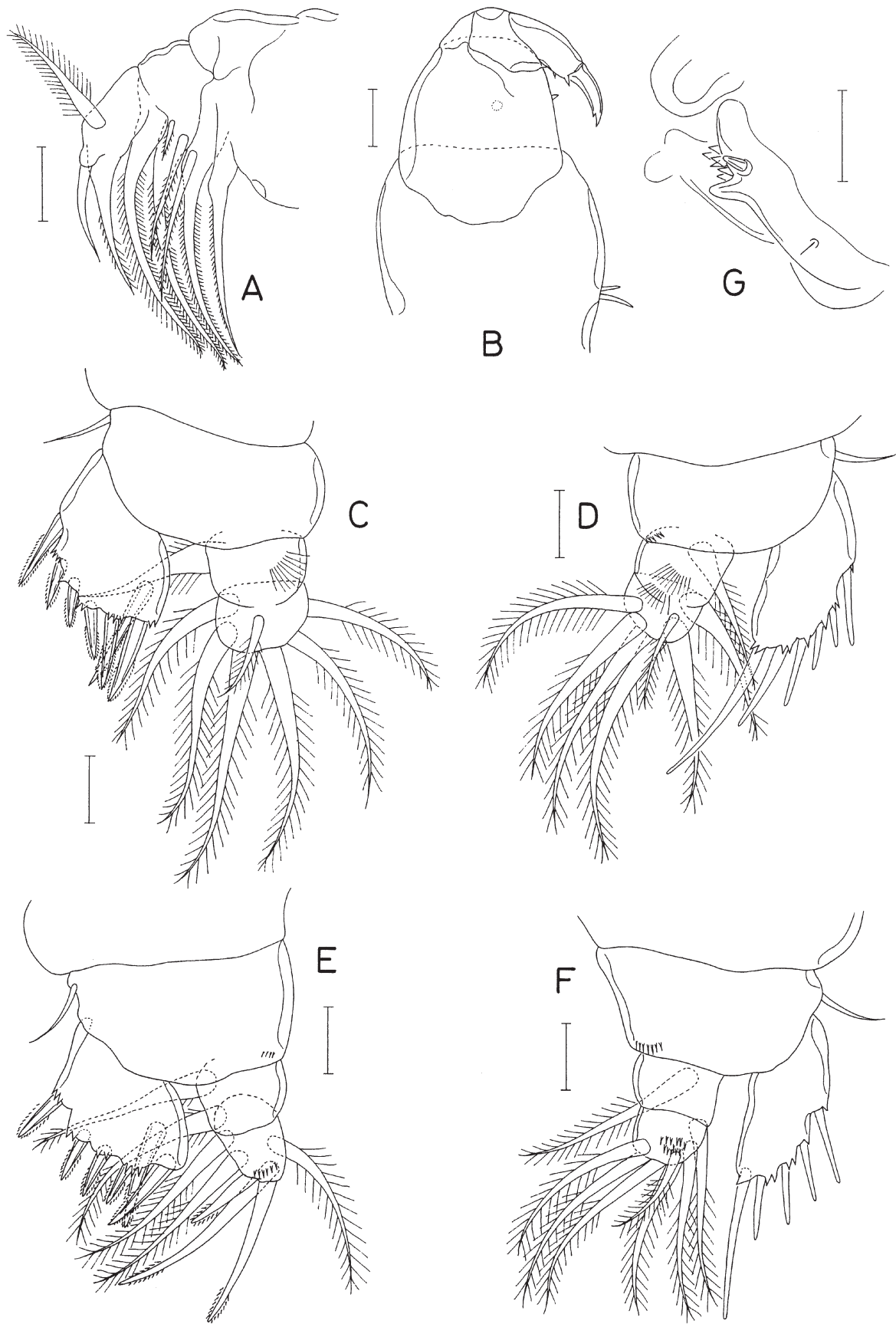
Leg 5 (Fig. 56E, F) small, about 1.4 times longer than wide (86×60 µm), strongly tapering, armed with 4 setae (1 proximal and 3 distal), distal longest seta 114 µm, distinctly longer than segment. Leg 6 (Fig. 55G) represented by 1 spinule and 1 spiniform process on genital operculum; several dentiform elements on surface immediately adjacent to leg 6.

**Male.** Unknown.

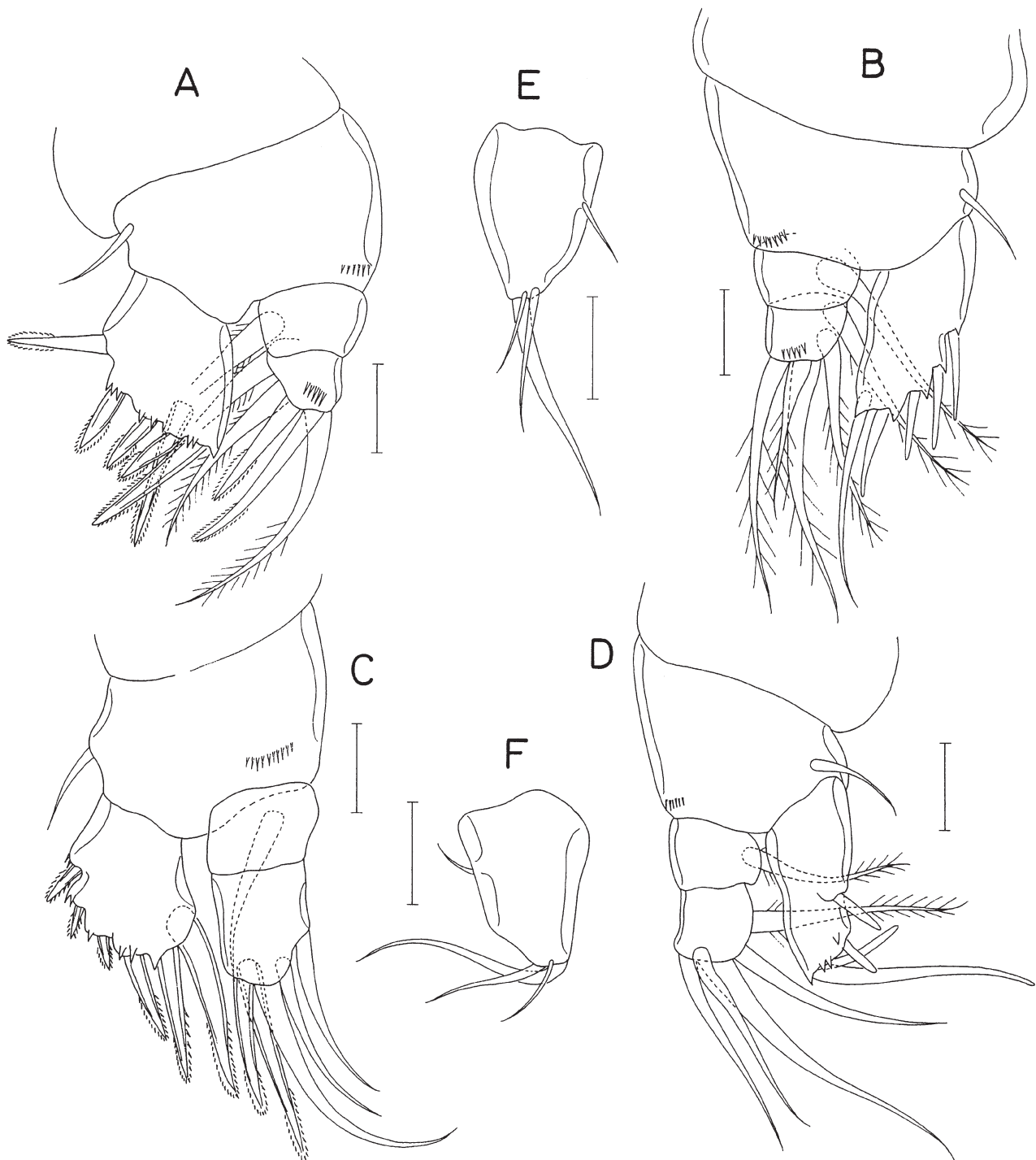




**FIG. 54.** *Botryllophilus angustus* sp. nov., female. A, habitus, left; B, habitus, dorsal; C, posterior part of body, ventral; D, caudal ramus; E, antennule; F, left antenna; G, distal part of right antenna; H, mandible; I, maxillule. Scale bars: A, B, 0.2 mm; C, 0.1 mm; D-I, 0.02 mm.



**FIG. 55.** *Botryllophilus angustus* **sp. nov.**, female. A, maxilla; B, maxilliped; C, right leg 1; D, left leg 1; E, right leg 2; F, left leg 2; G, genital aperture. Scale bars: 0.02 mm.



**FIG. 56.** *Botryllophilus angustus* **sp. nov.**, female. A, right leg 3; B, left leg 3; C, right leg 4; D, left leg 4; E, F, leg 5. Scale bars: A-D, 0.02 mm; E, F, 0.05 mm.

**Remarks.** The exopods of right legs 1-4 of *B. angustus* **sp. nov.** are armed with 7, 6, 6, and 6 armature elements, respectively (the combination 7-6-6-6). This combination is common in members of the type B group (species with 5 or more annulations in the abdomen), but is very rare in members of the type A group, because the exopod of right leg 4 in type A usually bears 4 or 5 spines. In the type A group only two species, *B. norvegicus* and *B. angustus* **sp. nov.**, deviate from this pattern, although in the former species the combination may be either 7-6-6-6 or 7-6-6-7. *Botryllophilus norvegicus* does not require detailed comparison with *B. angustus* **sp. nov.**, because it carries distinctive features, such as the swollen metasome and the elongate and curved leg 5.

In *B. angustus* **sp. nov.** the antenna is armed with 7 setae and leg 5 is very small. Both of these features are

shared with three congeners, *B. distinctus*, *B. millari* Ooishi, 2014, and *B. tuberculatus* **sp. nov.** However, all three of these species bear 5 setae on the second endopodal segment of right leg 4, and differ from *B. angustus* **sp. nov.** which has 2 spines and 3 setae on that segment of right leg 4.

***Botryllophilus curtipes* sp. nov.**

(Figs. 57-59)

**Type material.** Holotype ♀ (MNHN-IU-2018-1972, dissected and mounted on a slide) from *Eudistoma renieri* (Hartmeyer, 1912) (MNHN-IT-2008-4188 = MNHN A3/EUD/281); Ibo Is., Mozambique, AURACEA 1995 cruise, Stn Pl 20, depth 6 m, Monniot coll., 16 November 1995.

**Etymology.** The specific name is from the Latin *curt* (=short) and *pes* (=a foot), referring to the short leg 5.

**Description of female.** Body (Fig. 57A) rather stout, consisting of broader anterior and narrower posterior parts; body length 1.10 mm. Anterior part of body broadening posteriorly, divisible by dorsal and lateral constrictions into cephalosome and 4 pedigerous somites; fifth pedigerous somite 388 µm wide, with convex lateral margins (Fig. 57B). Posterior part of body (Fig. 57B) consisting of genital and 4 abdominal somites, indistinctly defined from fifth pedigerous somite. Genital somite about 117×227 µm; genital apertures located dorsally. Four abdominal somites gradually narrowing posteriorly 89×188, 110×166, 105×141, and 154×114 µm, respectively. Caudal ramus (Fig. 57C) with short inner margin and much longer outer margin, armed with 4 claws and 1 seta; 1 outer distal claw rounded at tip.

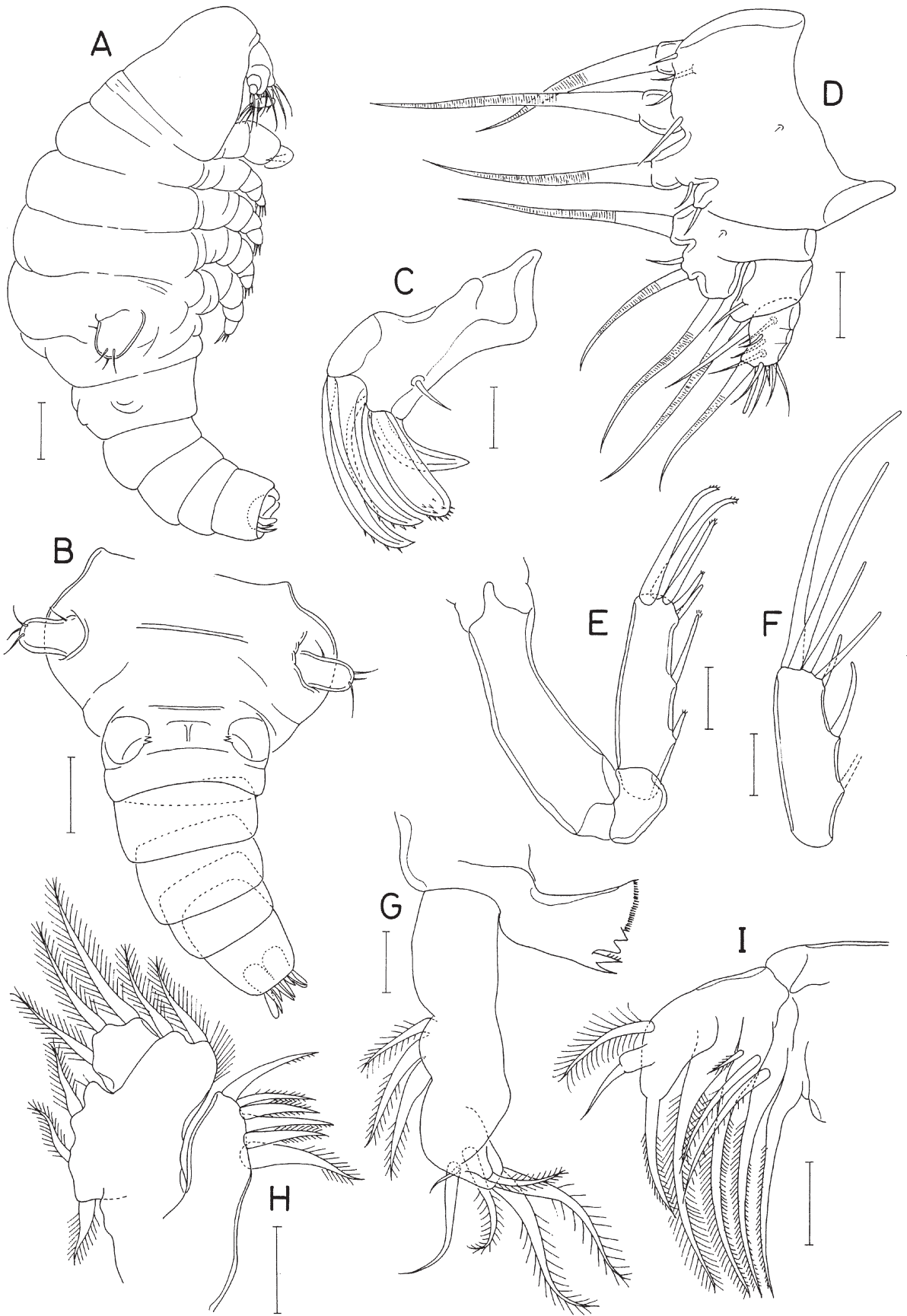
Rostrum absent. Antennule (Fig. 57D) small, 113 µm long, 4-segmented; first and second segments expanded; fourth segment with 2 traces of sutures on posterior side; armature formula 9 (3 large and 6 small), 4 (3 large and 1 small), 2 (1 large and 1 small), and 11+aesthetasc. Antenna (Fig. 57E, F) 4-segmented, including obscure coxa; basis and first endopodal segment unarmed; second endopodal segment of right antenna 3.2 times longer than wide (68×21 µm), armed with 7 setae; all setae shorter than segment, ornamented with several minute spinules at tip (Fig. 57E). Second endopodal segment of left antenna (Fig. 57F) slightly shorter (61×21 µm) than that of right antenna; setae unornamented, 2 outer distal setae 95 and 76 µm long, distinctly longer than segment.

Labrum (Fig. 58A) broad, unornamented, with short posteromedial lobe. Mandible (Fig. 57G) with coxal gnathobase bearing distal bifurcate tooth and 2 short teeth on medial margin; palp with 9 setae, as usual for genus. Maxillule (Fig. 57H) with 6 setae on arthrite of precoxa; palp consisting of coxobasis and endopod; coxobasis with 2 medial and 3 outer setae and weakly pronounced distal lobe; endopod wider than long, distinctly articulated from coxobasis, armed with 3 setae. Maxilla (Fig. 57I) indistinctly 3-segmented with 3, 4, and 3 setae on first to third segments, respectively; distal seta on third segment naked and carried on digitiform process. Maxilliped (Fig. 58B) 4-segmented; syncoxa broad and unarmed; basis with 2 small setae; first endopodal segment unarmed; second segment slightly longer than first, with 1 small seta; terminal claw as long as second endopodal segment, bearing 2 minute denticles (proximal and subdistal).

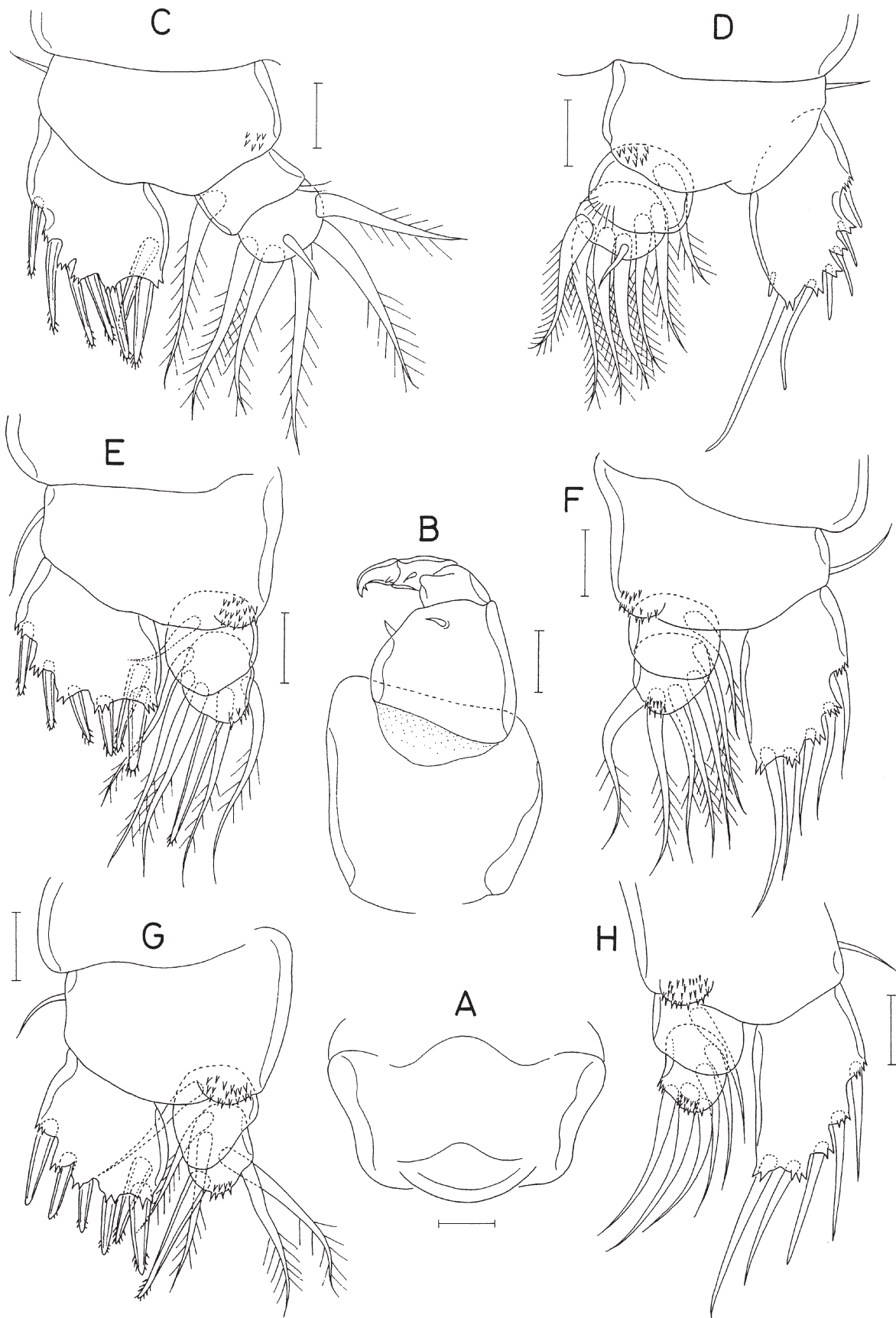
Legs 1-4 (Figs. 58C-H, 59A, B) biramous, asymmetrical, with 1-segmented exopods and 2-segmented endopods; coxa unarmed; basis with 1 seta on outer margin and patch of spinules at inner distal corner. Inner subdistal seta on exopod of left leg 1 rudimentary. One seta on second endopodal segment of left leg 1 small. Second endopodal segment of right legs 2-4 armed with 1 spine in addition to setae. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	VII	1; 6	7	1; 7
Leg 2	VI	1; I+5	5	1; 6
Leg 3	VI	1; I+4	5	1; 5
Leg 4	IV	1; I+4	4	1; 5

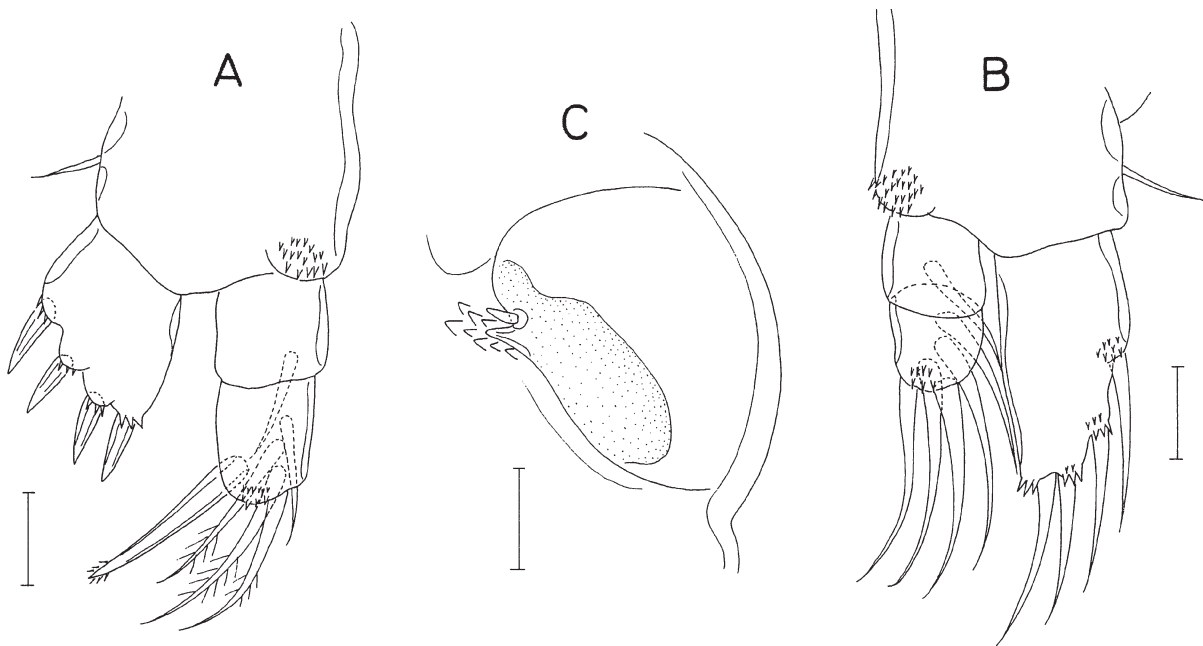
Leg 5 (Fig. 57A, B) small, lobate, about 1.3 times longer than wide (100×77 µm), with rounded distal margin; armed with 1 proximal and 3 distal setae, all small (shorter than leg segment). Leg 6 (Fig. 59C) represented by 1 spinule and 1 spinule-like process on genital operculum; several spinules on surface adjacent to leg 6.



**FIG. 57.** *Botryllophilus curtipes* sp. nov., female. A, habitus, right; B, posterior part of body including fifth pedigerous somite, dorsal; C, caudal ramus; D, antennule; E, right antenna; F, second endopodal segment of left antenna; G, mandible; H, maxillule; I, maxilla. Scale bars: A, B, 0.1 mm; C-I, 0.02 mm.



**FIG. 58.** *Botryllophilus curtipes* sp. nov., female. A, labrum; B, maxilliped; C, right leg 1; D, left leg 1; E, right leg 2; F, left leg 2; G, right leg 3; H, left leg 3. Scale bars: 0.02 mm.



**FIG. 59.** *Botryllophilus curtipes* sp. nov., female. A, right leg 4; B, left leg 4; C, right genital aperture. Scale bars: 0.02 mm.

**Male.** Unknown.

**Remarks.** The combination of armature on the exopods of right legs 1-4 (7-6-6-4) and left legs 1-4 (7-5-5-4) of *B. curtipes* sp. nov. is unique within *Botryllophilus*. The combination of armature on the endopods of the right legs (7-7-6-6) and left legs (8-7-6-6) of *B. curtipes* sp. nov. is also unusual; the former combination is shared only with *B. millari* and the latter combination is shared only with *B. stenurosus* sp. nov. and *B. pentachaetus* sp. nov.

***Botryllophilus coniorhynchus* sp. nov.**

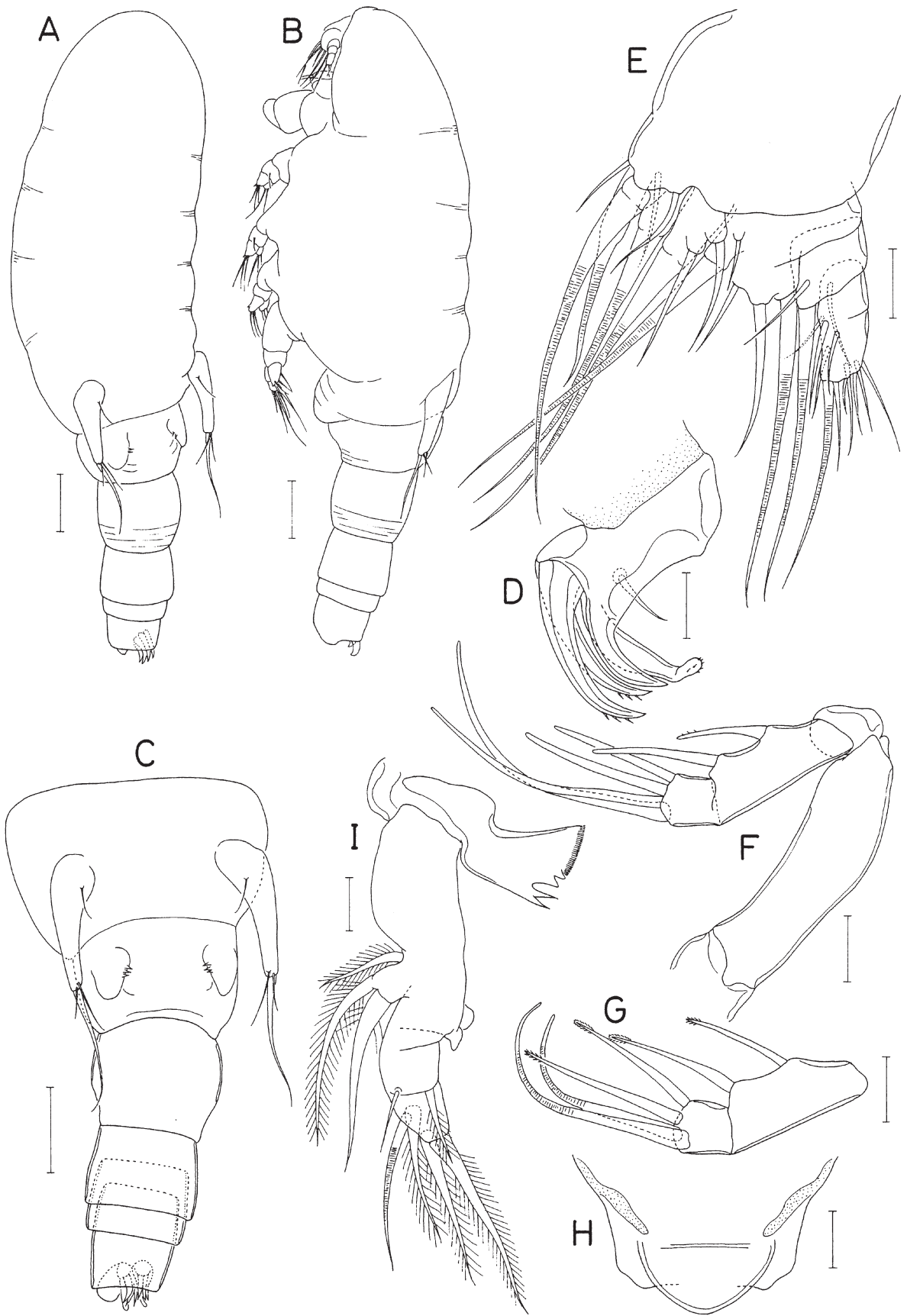
(Figs. 60-62)

**Type material.** Holotype ♀ (MNHN-IU-2018-1973), 3 ♀♀ paratypes (intact, MNHN-IU-2018-1974), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17376) from *Aplidium falklandicum* Millar, 1960 (MNHN-IT-2008-386 = MNHN A1/APL.B/532); Antarctic, Terre Adélie, CEAMARC cruise, RV “Aurore Australis”, Stn 18EV479 (66°10’S, 139°41’E), depth 402-437 m, IPEV-AAD-MNHN coll., 15 January 2008.

**Etymology.** The name of the new species is derived from the Greek *coni* (= a cone) and *rhynch* (= a snout), and refers to the conical rostrum.

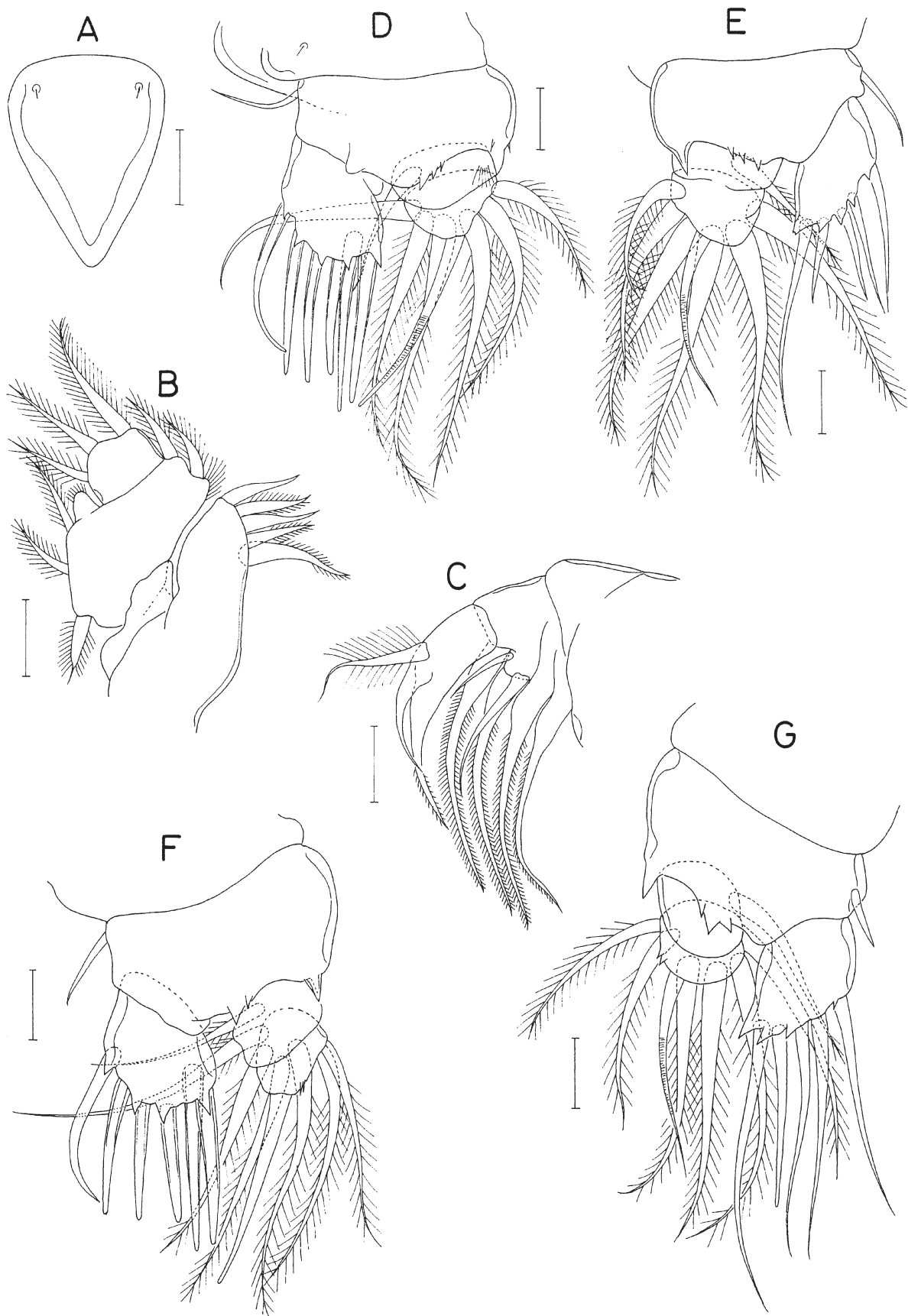
**Description of female.** Body (Fig. 60A, B) asymmetrical, 1.15 mm long. Anterior part of body comprising cephalosome to fifth pedigerous somite, 0.73 mm long, invariably slightly curved to right side, unsegmented but with 4 weak constrictions dorsally and laterally; lateral margins parallel. Body width 0.33 mm across middle of anterior part. Posterior part of body (Fig. 60C) consisting of genital and 4 abdominal somites. Genital apertures positioned dorsally on genital somite. Caudal ramus (Fig. 60D) armed with 4 claws and 1 seta; 1 outer distal claw bluntly tipped, other claw not articulated with ramus.

Rostrum (Fig. 61A) distinct, conical, longer than wide (57×42 µm). Antennule (Fig. 60E) short, about 115 µm long, strongly tapering, with markedly broadened first and second segments; terminal segment subdivided on posterior side; armature formula 9 (3 large and 6 small), 5 (2 large and 3 small), 2 (1 large and 1 small), and 12. Left antenna (Fig. 60F) apparently 5-segmented, consisting of coxa, basis, and 3-segmented endopod; proximal 3 segments unarmed; second endopodal segment (fourth segment) 46×18 µm, with 2 bluntly tipped setae on inner margin; third endopodal segment 17×16 µm, with 4 (2 shorter inner and 2 longer outer) bluntly tipped setae on distal margin. Right antenna similar in size and segmentation to left antenna; 2 setae on second endopodal segment and 2 inner distal setae on third endopodal segment slightly longer than those of left antenna and distally spinulose (Fig. 60G); 2 outer distal setae distinctly shorter than those of left antenna.

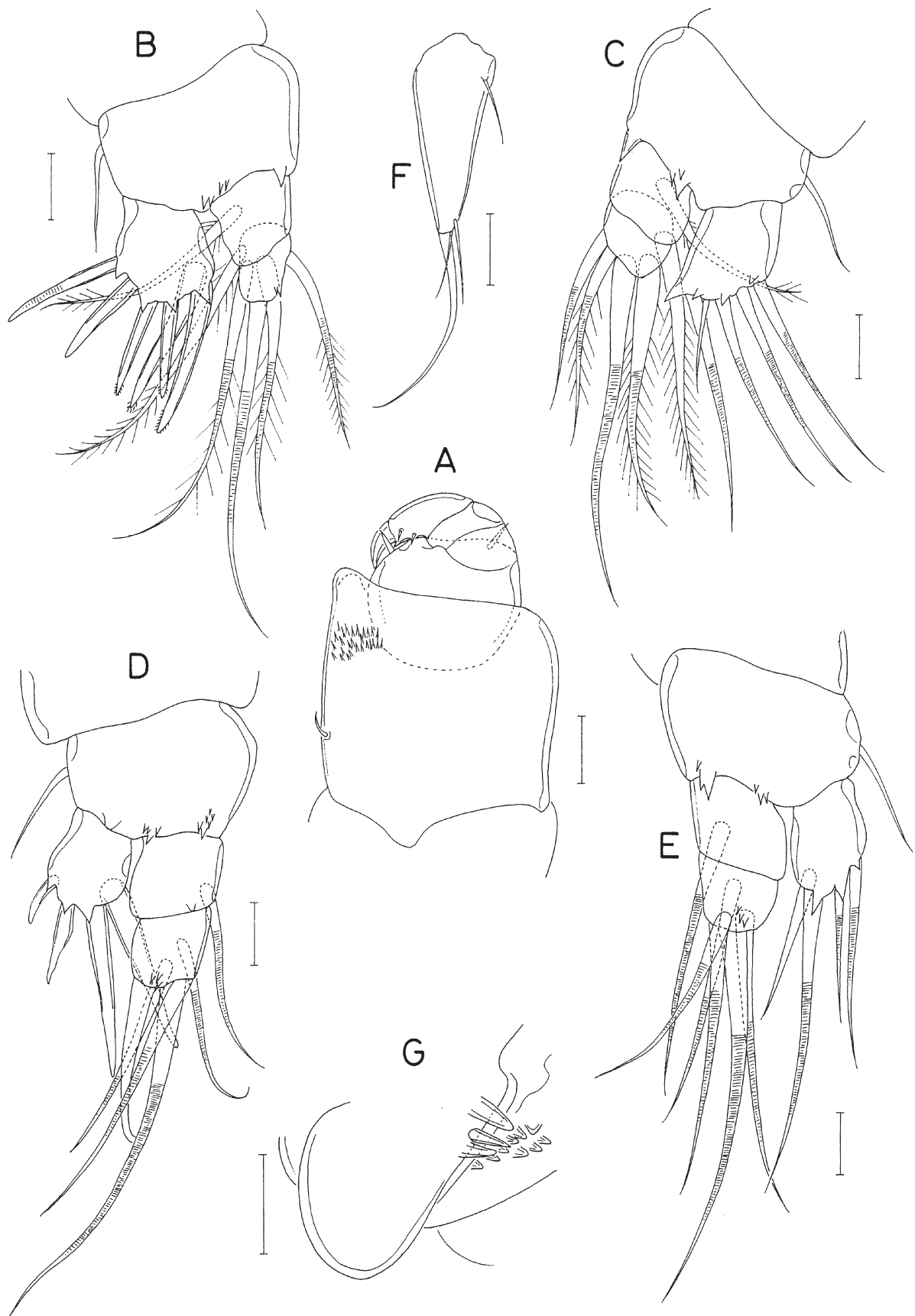


**FIG. 60.** *Botryllophilus coniorhynchus* sp. nov., female. A, habitus, dorsal; B, habitus, left; C, posterior region of body, dorsal; D, caudal ramus; E, antennule; F, left antenna; G, distal part of right antenna; H, labrum; I, mandible. Scale bars: A-C, 0.1 mm; D-I, 0.02 mm.





**FIG. 61.** *Botryllophilus coniorhynchus* sp. nov., female. A, rostrum; B, maxillule; C, maxilla; D, right leg 1; E, left leg 1; F, right leg 2; G, left leg 2. Scale bars: 0.02 mm.



**FIG. 62.** *Botryllophilus coniorhynchus* sp. nov., female. A, maxilliped; B, right leg 3; C, left leg 3; D, right leg 4; E, left leg 4; F, leg 5; G, genital aperture. Scale bars: A-E, G, 0.02 mm; F, 0.05 mm.

Labrum (Fig. 60H) with large, semicircular posteromedian lobe. Mandible (Fig. 60I) with 1 bifurcate tooth and 2 shorter teeth on coxal gnathobase; palp with 2 lobes in middle of inner margin, armed with 9 setae arranged as 3, 2, 2, and 2. Maxillule (Fig. 61B) consisting of precoxa and palp; precoxa with 5 distinct setae on arthrite; palp 3-segmented, consisting of coxa, basis, and endopod; coxa unarmed (lacking seta of epipodite); basis with 2 setae on medial margin, 3 setae on outer margin, and setulose distal lobe; endopod articulated from basis, armed with 3 setae on distal margin. Maxilla (Fig. 61C) indistinctly 3-segmented and armed with 2, 4, and 3 setae on first to third segments, respectively. Maxilliped (Fig. 62A) 4-segmented; syncoxa large, with 1 small seta proximally on inner margin and patch of spinules subdistally on inner side; basis with 2 small isolated setae; short first endopodal segment unarmed; second endopodal segment with 2 small setules and 1 pointed inner distal process; terminal claw small, about half as long as second endopodal segment.

Legs 1-4 (Figs. 61D-G, 62B-E) biramous, with 1-segmented exopods and 2-segmented endopods; coxa unarmed; basis with 1 seta on outer margin. Basis of legs 1-3 with 1 prominent, spiniform process at inner distal corner and 2 to 4 spinules on distal margin near base of endopod; basis of leg 4 with 2 patches of several spinules at each inner distal corner and on distal margin. Spines on exopods of right legs 1-3 elongate. Exopods of right legs 1 and 2 armed with 1 seta (outer proximal element) and 5 spines. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	V+1	1; 7	5	1; 7
Leg 2	V+1	1; 7	5	1; 7
Leg 3	VI	1; 5	5	1; 5
Leg 4	IV	1; 5	4	1; 5

Leg 5 (Fig. 62F) positioned dorsolaterally on fifth pedigerous somite, evenly tapering, 2.4 times longer than wide (140×58 µm), with 1 small seta proximally and 2 small plus 1 larger seta distally; larger distal seta longer than leg (exopodal) segment. Leg 6 (Fig. 62G) represented by 1 spinule and 2 spinule-like processes on genital operculum; 9 small denticle-like elements on surface adjacent to leg 6.

**Male.** Unknown.

**Remarks.** Three outstanding features serve to characterize *B. coniorhynchus* **sp. nov.** as follows: (1) the exopods of right legs 1 and 2 each carry 1 seta in addition to spines; (2) the combination of armature elements on right legs 1-4 is 6-6-6-4, and (3) the endopod of the antenna is apparently 3-segmented, the segmentation has not been recorded previously in *Botryllophilus* and, as it appears incomplete, it may represent a distinct fold in the cuticle rather than a true articulation. The combination of armature elements on the exopods of left legs 1-4 (5-5-5-4) also is unusual, known previously only in *B. banyulensis*.

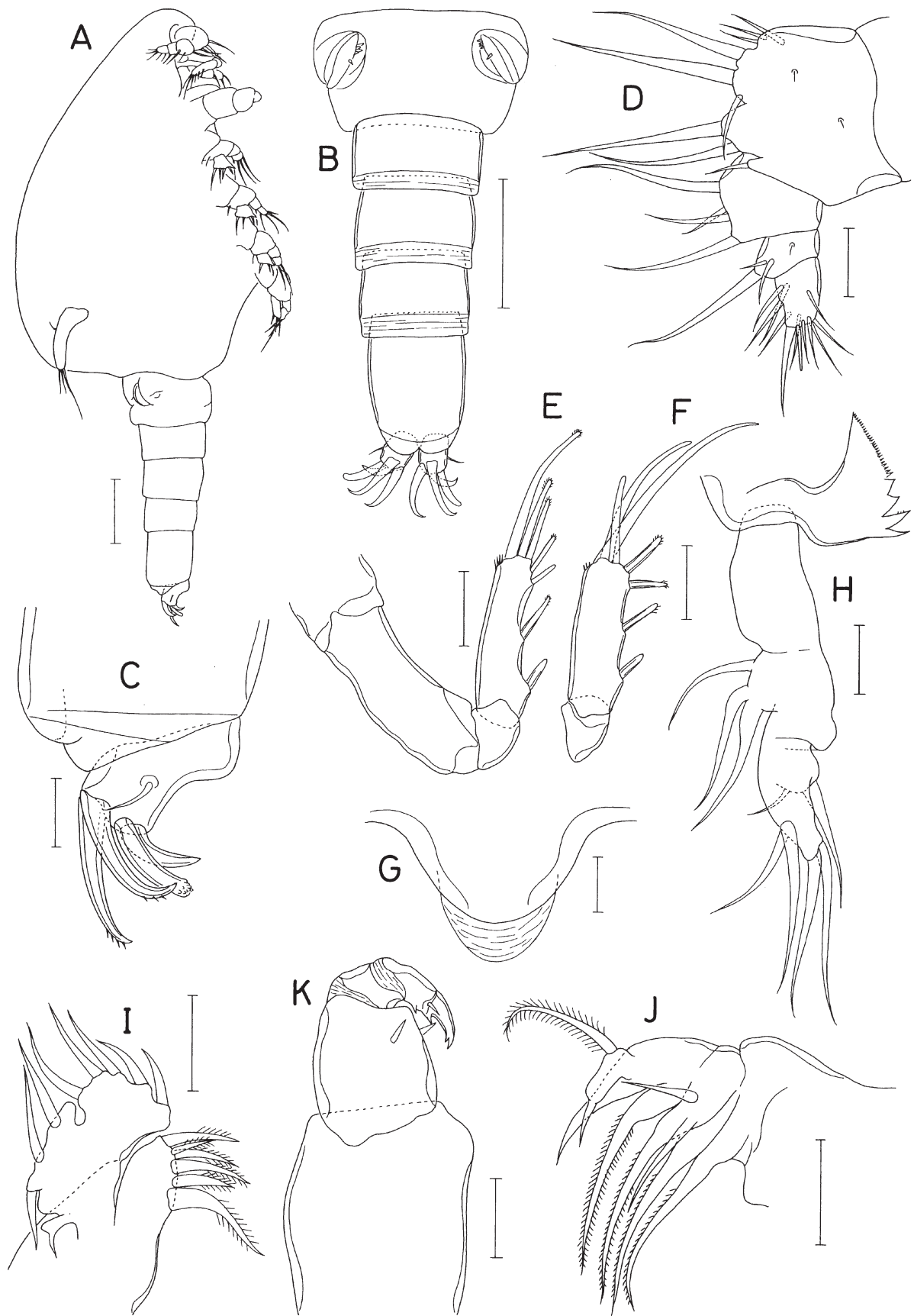
***Botryllophilus nudisetatus* sp. nov.**

(Figs. 63, 64)

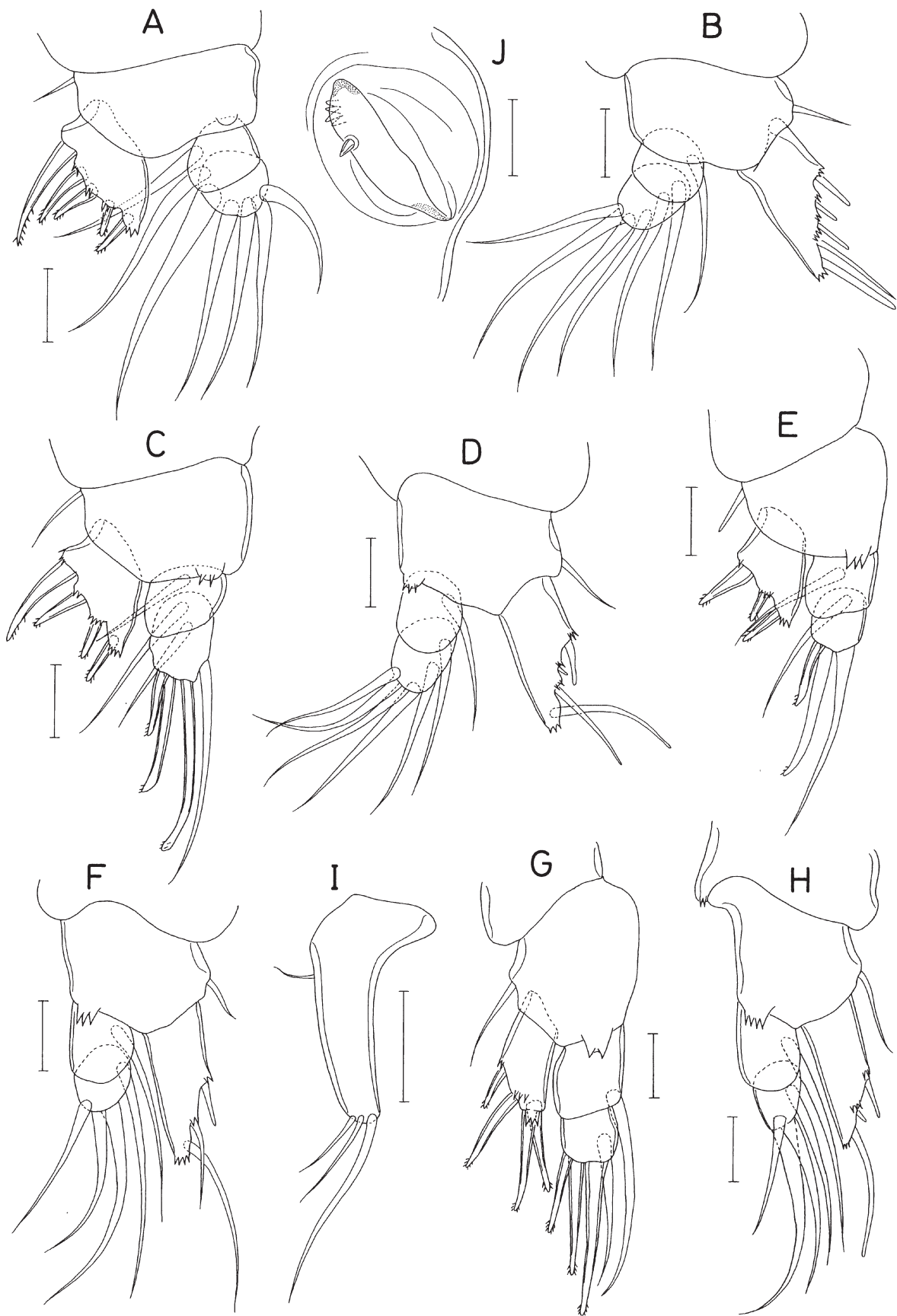
**Type material.** Holotype ♀ (MNHN-IU-2018-1975) and 1 ♀ paratype (dissected, MNHN-IU-2014-17377) from *Eudistoma carolinense* Van Name, 1945 (MNHN-IU-2008-4023 = MNHN A3/EUD/14); Anse de Baille Argent, Guadeloupe Stn 7, Monniot coll., 19 December 1980.

**Etymology.** All setae on legs of *B. nudisetatus* **sp. nov.** are naked, and are alluded to in the name of the new species.

**Description of female.** Body (Fig. 63A) symmetrical, straight, 0.93 mm long. Anterior part of body markedly swollen, unsegmented, without any trace of articulation, 0.38 mm in dorsoventral depth. Posterior part of body (Fig. 63B) clearly defined from anterior part, consisting of genital somite and 4-segmented abdomen. Genital somite 82×165 µm; genital apertures large, positioned dorsally; 4 abdominal somites 58×102, 67×95, 65×85, and 109×76 µm, respectively. Caudal ramus (Fig. 63C) armed with 1 bluntly tipped and 3 pointed claws and 1 seta.



**FIG. 63.** *Botryllophilus nudisetatus* sp. nov., female. A, habitus, right; B, posterior part of body, dorsal; C, caudal ramus; D, antennule; E, right antenna; F, endopod of left antenna; G, labrum; H, mandible; I, maxillule; J, maxilla; K, maxilliped. Scale bars: A, B, 0.1 mm; C-J, 0.02 mm.



**FIG. 64.** *Botryllophilus nudisetatus* sp. nov., female. A, right leg 1; B, left leg 1; C, right leg 2; D, left leg 2; E, right leg 3; F, left leg 3; G, right leg 4; H, left leg 4; I, leg 5; J, genital aperture. Scale bars: A-H, J, 0.02 mm; I, 0.05 mm.

Rostrum absent. Antennule (Fig. 63D) small, 4-segmented; armature formula 9 (4 large and 5 small), 4 (2 large and 2 small), 3 (1 large and 2 small), and 11+aesthetasc. Right antenna (Fig. 63E) consisting of coxa, basis, and 2-segmented endopod; proximal 3 segments unarmed; second endopodal segment about 3.1 times longer than wide ( $47 \times 15 \mu\text{m}$ ), armed with 7 bluntly tipped setae, longest outer distal seta as long as segment, other setae shorter than segment. Second endopodal segment of left antenna (Fig. 63F) slightly shorter than that of right antenna,  $43 \mu\text{m}$  long; 2 outer distal setae distinctly longer than those of right antenna.

Labrum (Fig. 63G) semicircular with large, soft posteromedian lobe. Mandible (Fig. 63H) with bifurcate distal tooth and 2 shorter teeth on coxal gnathobase; palp with 9 naked setae, grouped as 3, 2, 2, and 2. Maxillule (Fig. 63I) consisting of precoxa and unsegmented palp; precoxa with 6 setae on arthrite; palp with 8 setae (2 on medial margin, 3 on outer margin, and 3 on distal margin) plus 1 vestigial seta at outer proximal margin representing epipodite; endopod completely fused with basis. Maxilla (Fig. 63J) indistinctly 3-segmented, with 9 setae arranged as 2, 4, and 3. Maxilliped (Fig. 63K) relatively narrow, 4-segmented; syncoxa slightly longer than wide, unarmed and unornamented; basis with 2 small setae; short first endopodal segment unarmed; second segment with 1 denticle on inner margin and 1 small seta on distal margin; terminal claw as long as second endopodal segment, with 1 proximal and 1 subdistal denticle on inner margin.

Legs 1-4 (Fig. 64A-H) biramous with 1-segmented exopods and 2-segmented endopods; coxa unarmed; basis with 1 seta on outer margin. Basis of legs 2-4 with small inner distal lobe bearing 2-4 spinules. Endopods of right legs 2-4 bearing 3, 1, and 3 spines, respectively. All setae on legs 1-4 naked and all spines with spinulose tip. Exopods of left legs 1, 2, and 4 each with small second outer seta. Numbers of spines (Roman numerals) and setae (Arabic numerals) on right and left legs 1-4 as follows:

	Right exopod	Right endopod	Left exopod	Left endopod
Leg 1	V	1; 6	5	1; 6
Leg 2	IV	1; III+3	4	1; 6
Leg 3	III	1; I+3	3	1; 4
Leg 4	IV	1; III+1	3	1; 4

Leg 5 (Fig. 64I)  $104 \times 58 \mu\text{m}$ , with broadened proximal region, not extending beyond posterior margin of anterior part of body; armed with 4 setae (1 proximal and 3 distal); largest of 3 distal setae as long as leg segment, twice as long as adjacent seta. Leg 6 (Fig. 64J) represented by 1 spinule on genital operculum.

**Male.** Unknown.

**Remarks.** The exopods of right legs 1-3 of *B. nudisetatus* **sp. nov.** are armed with 5, 4, and 3 spines, respectively. Each of these numbers of spines is less than that of any other known species of *Botryllophilus*. The other rami of the swimming legs of this new species are armed with smallest number of armature elements known elsewhere within the genus. This reduced armature of the swimming legs serves to characterize the new species.

### Genus *Schizoproctus* Aurivillius, 1885

**Diagnosis** (female). Body symmetrical, dorsoventrally depressed or laterally compressed, consisting of broader anterior and narrower posterior parts. Anterior part of body segmented or unsegmented; fifth pedigerous somite completely fused with fourth pedigerous somite. Posterior part of body comprising genital somite and abdomen consisting of 3 to 6 somites or annulations; abdomen occasionally unsegmented. Caudal ramus short, armed with 4 or 5 claws and 1 or 2 setae. Rostrum small or absent. Antennule 4- or 5-segmented. Antenna 4-segmented; proximal 3-segments unarmed; terminal segment (second endopodal segment) armed with 8 elements (mostly spines). Labrum not specialized. Mandible, maxillule, and maxilla as in *Botryllophilus*. Maxilliped basically 4-segmented as in *Botryllophilus*, but terminal segment may be fused with terminal claw. Legs 1-4 symmetrical, biramous with 1-segmented rami; coxa unarmed; basis armed with 1 seta on outer margin; exopods armed with 4 to 7 spines along outer and distal margins plus 1 rudimentary inner subdistal seta in some species. Endopods usually shorter than

exopods, and usually armed with setae. Leg 5 elongate or lamellate, with 1 to 4 setae. Leg 6 represented by 1 or 2 spinules and 1 spinule-like process on genital operculum.

**Type species.** *Schizoproctus inflatus* Aurivillius, 1885 by original monotypy.

**Remarks.** According to Illg & Dudley (1980), the genus *Schizoproctus* was a well-established, readily recognizable genus defined from *Botryllophilus* by its broad, lamellate leg 5. This distinction between the two genera, on the basis of the form of leg 5, has become obscured by the discovery of new species in the present account which exhibit a mix of the key morphological features of the two genera.

In three new species to be described below (*S. magnus* **sp. nov.**, *S. bisetatus* **sp. nov.**, and *S. fusiformis* **sp. nov.**), left and right legs 5 are narrow and widely separated from each other, a feature corresponding to *Botryllophilus*. However, the characteristics of left and right legs 1-4 of these three new species differ markedly from those in species of *Botryllophilus*, but are shared with other species of *Schizoproctus*. Comparison of the two genera leads us to redefine both genera. The most robust differences between the two genera seem to lie in the morphology of swimming legs, as follows: (1) both rami of legs 1-4 of *Schizoproctus* are 1-segmented, but at least the endopods of legs 2-4 of *Botryllophilus* species are 2-segmented (in many instances the exopods are also 2-segmented); (2) left and right legs 1-4 of *Schizoproctus* are invariably symmetrical, in contrast to the asymmetry of these legs in *Botryllophilus* (with the exception of *B. macropus* which has symmetrical legs 1-4), with spines on the exopods and setae on the endopods. We consider that these differences are more robust than the difference in the form of leg 5 between these two genera. In addition, the body and the antennae are also typically symmetrical in *Schizoproctus*, unlike those of *Botryllophilus*.

Differences between the two genera are marked in the leg setation of the males, as well. While describing the male of *Haplostoma brevicauda* (Canu, 1886), Ooishi (2004b) mentioned that the males of *Haplostoma* are distinguished from the males of *Botryllophilus* by having fewer spines on the third segment of leg 2 endopod. This segment is armed with 2 spines (occasionally 1 spine) plus 3 setae (formula generally II, 3 but occasionally I, 3) in *Haplostoma* but 3 spines plus 3 setae (formula III, 3) in *Botryllophilus*. The same segment of the leg of the male of *Schizoproctus pinguis* **sp. nov.** described in the present work is armed with 1 spine plus 3 setae (I, 3). The reduction in the number of spines on legs of the male of *Schizoproctus* is not limited to the endopod of leg 2; the armature formula for the third endopodal segment of legs 3 and 4 is I, 2 and I, 4, respectively in *Schizoproctus*, compared to II, 2 and II, 3, respectively, in males of *Botryllophilus abbotti*, *B. ruber*, *B. bamfieldensis*, and *B. banyulensis* (as described by Ooishi & Illg, 1989; Ooishi, 1999; 2000; 2006, respectively). In contrast, the third exopodal segment of legs 2-4 of *S. pinguis* **sp. nov.**, described below, is armed with more spines (IV, 5) than in any of the four known males of *Botryllophilus* species (III, 5).

*Schizoproctus* exhibits a range of different leg armature patterns, according to species (Table 3), which allows for easy differentiation between species.

**TABLE 3.** Armature of caudal ramus and legs 1-5 of *Schizoproctus* species (\* indicates lack of an endopod; Roman numerals indicate spines, Arabic numerals indicate setae)

Species	Caudal ramus	Leg 1		Leg 2		Leg 3		Leg 4		Leg 5
		Exp	Enp	Exp	Enp	Exp	Enp	Exp	Enp	
<i>S. inflatus</i> Aurivillius, 1885	IV	V	IV	V	III,1	V	?	V	III	?
<i>S. vestitus</i> (Sars, 1921)	IV,1	VI	3	VI	2	VI	?	VI	6	1
<i>S. magnus</i> <b>sp. nov.</b>	IV,2	VI,1	8	VI,1	9	VI,1	7	VI,1	7	4
<i>S. bisetatus</i> <b>sp. nov.</b>	V,1	VI,1	8	VI,1	8	VI,1	7	VI,1	7	2
<i>S. fusiformis</i> <b>sp. nov.</b>	IV,1	VI	II	V	II	IV	*	IV	*	4
<i>S. tripartitus</i> <b>sp. nov.</b>	V,1	V,1	6	IV,1	5	IV,1	3	IV,1	2	4
<i>S. frigidus</i> <b>sp. nov.</b>	IV,2	VII	8	VII	8	VII	7	VII	7	1
<i>S. oligomerus</i> <b>sp. nov.</b>	V,1	VI,1	7	VI,1	7	VI,1	6	VI,1	6	2
<i>S. mollis</i> <b>sp. nov.</b>	IV,2	VI	7	VI	6	VI	4	VI	3	2
<i>S. fijiensis</i> <b>sp. nov.</b>	IV,1	VI	8	VI	3	VI	2	VI	2	4
<i>S. pinguis</i> <b>sp. nov.</b>	IV,2	V	8	V	3	V	2	V	2	4

***Schizoproctus magnus* sp. nov.**

(Figs. 65, 66)

**Type material.** Holotype ♀ (MNHN-IU-2018-1976, dissected and mounted on 2 slides) from *Pyura bouvetensis* Michaelsen, 1904 (MNHN-IT-2008-7430 = MNHN S2/PYU/450); Antarctic, Terre Adélie, CEAMARC cruise, RV “Aurore Australis”, Stn 31EV268 (66°35′S, 145°01′E), depth 429-451 m, IPEV-AAD-MNHN coll., 03 January 2008.

**Etymology.** The specific name is derived from the Latin *magn* (=large), referring to the large body size.

**Description of female.** Body (Fig. 65A, B) large, slender, 4.88 mm long; maximum width 1.03 mm. Anterior part of body unsegmented, with weak constriction dorsally and laterally between cephalosome and remaining part; legs 5 directed laterally, perpendicular to body axis. Posterior part of body narrower and slightly shorter than anterior part, not articulated from anterior part, gradually narrowing posteriorly, consisting of genital and abdomen of 6 annulations; annulations indistinct or separated by constrictions. Caudal ramus (Fig. 65C) as long as wide (120×120 µm), armed with 4 claws and 2 small setae; claws shorter than ramus, 2 shorter, outer distal claws bluntly tipped, 1 rudimentary.

Rostrum (Fig. 65D) small, semicircular with rounded apex. Antennule (Fig. 65D) 417 µm long, 5-segmented; armature formula 12, 6, 3, 4, and 7; first segment much broader than other segments; setae small, much shorter than width of first segment. Left antenna (Fig. 65E) 4-segmented; coxa, basis, and first endopodal segment unarmed; second endopodal segment about 3.3 times longer than wide (92×28 µm), slightly shorter than basis, armed with 8 bluntly tipped, smooth setae. Right antenna as for left, but second inner seta on distal margin of second endopodal segment (Fig. 65F) longer than that of left antenna.

Labrum weak, semicircular, with rounded posterior margin. Mandible (Fig. 65G) with 3 teeth on coxal gnathobase, distalmost tooth finely spinulose along proximal margin; palp with 9 setae arranged as 3, 1, 1, 2, and 2. Maxillule (Fig. 65H) consisting of precoxa and palp: precoxa with 7 setae on medial margin and 1 rudimentary seta distally; proximalmost seta specialized, tipped with pinnate setule; palp consisting of coxa, basis, and endopod, with 1 small seta on coxal epipodite, 2 medial and 3 (proximal 1 naked and weak) outer setae on basis; endopod articulated from basis, with 3 setae on distal margin. Maxilla (Fig. 65I) 2-segmented; first segment with 3 setae; second segment with bilobed tubercles on outer margin and 6 setae, distal seta naked and accompanied by minute tubercle (setal vestige) near base. Maxilliped (Fig. 66A) 4-segmented; syncoxa longer than wide, with 2 small setae on inner side; basis much shorter than syncoxa, with 2 small setae; first endopodal segment short and unarmed; second endopodal segment with 1 small seta on inner margin; terminal claw smooth, shorter than second endopodal segment.

Legs 1-4 (Fig. 66B-E) biramous with 1-segmented exopods and endopods; coxa and basis indistinctly defined from or fused with each other; coxa unarmed; coxa of leg 1 with large tubercle on inner side (Fig. 66B). Basis with numerous minute spinules on anterior surface. Legs 1 and 2 with small outer seta on basis, but legs 3 and 4 with unarmed basis. Exopods longer than endopods. Spines on exopods rod-shaped, roundly tipped, gradually becoming longer from proximal to distal, but inner subdistal spine rudimentary. Legs 3 and 4 not different from each other. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	VI, 1	8
Leg 2	0-0	1-0	VI, 1	9
Legs 3 & 4	0-0	0-0	VI, 1	7

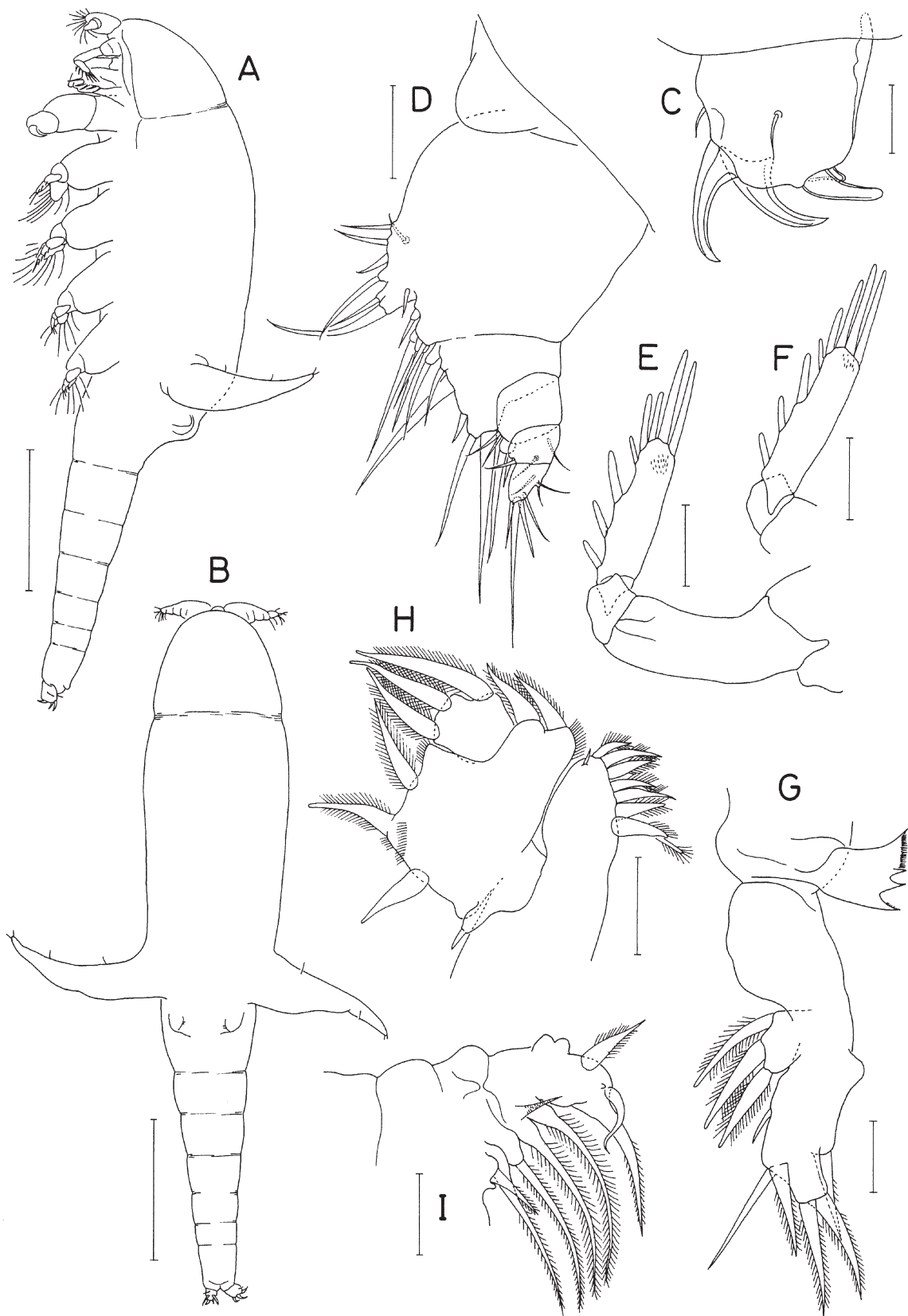
Leg 5 (Fig. 66F) elongate, tapering distally, as long as body width (1.00×0.34 mm), directed dorsolaterally; armed with 4 rudimentary setae (1 at proximal third, 1 at distal third, and 2 distally). Leg 6 (Fig. 66G) represented by 1 spinule, 1 spinule-like process, and 1 small setule on genital operculum.

**Male.** Unknown.

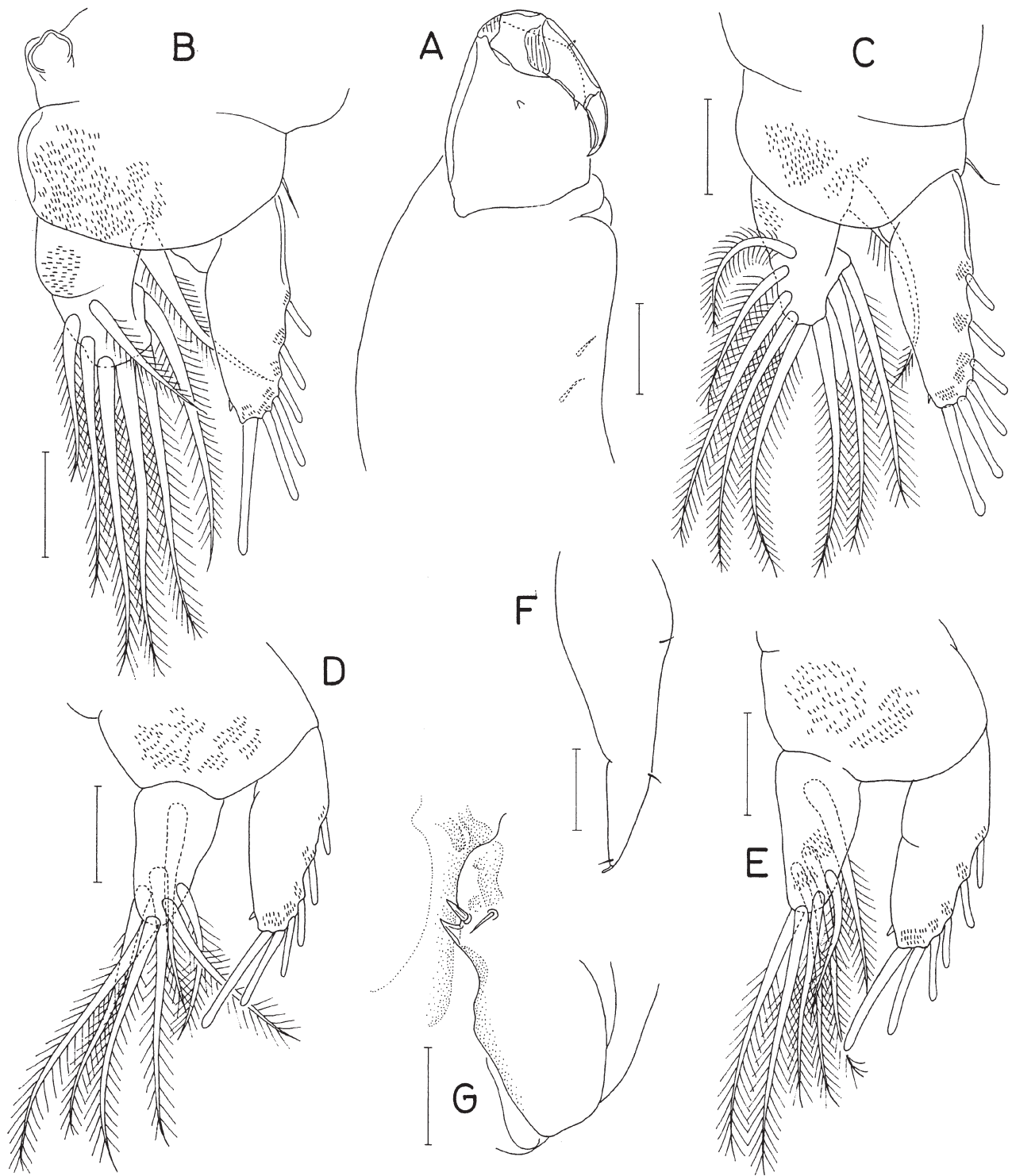
**Remarks.** *Schizoproctus magnus* sp. nov. is readily recognizable by having an abdomen of 6 annulations, although the separation of the annulations is incomplete, and by the characteristic leg 5 which is elongate, tapering, and dor-



solaterally directed. The combination of setal numbers on the endopods of legs 1-4 (8-9-7-7) of the new species is unique within the genus (Table 3).



**FIG. 65.** *Schizoproctus magnus* sp. nov., female. A, habitus, left; B, habitus, dorsal; C, caudal ramus; D, rostrum and antennule; E, left antenna; F, endopod of right antenna; G, mandible; H, maxillule; I, maxilla. Scale bars: A, B, 1 mm; C, E, F, 0.05 mm; D, G-I, 0.1 mm.



**FIG. 66.** *Schizoproctus magnus* sp. nov., female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 4; F, leg 5; G, genital aperture. Scale bars: A-F, 0.1 mm; G, 0.05 mm.

***Schizoproctus bisetatus* sp. nov.**

(Figs. 67, 78)

**Type material.** Holotype ♀ (MNHN-IU-2018-1977, dissected and mounted on a slide) from *Caenagnesia bocki* Årnäck-Christie-Linde, 1938 (MNHN-IT-2008-1840 = MNHN P3/CAE/6); Weddell Sea, EPOS 3 3 cruise, RV “Polarstern”, Stn MG7 (75°05.5'S, 28°01.0'W), depth 462 m, 01 February 1989.

**Etymology.** The name is derived from the Latin *bi* (=two) and *set* (=a bristle), referring to leg 5 of the new species, which is armed with 2 setae.

**Description of female.** Body (Fig. 67A) symmetrical, narrow, 2.90 mm long. Anterior part of body unsegmented; cephalosome defined from metasome by dorsal and lateral constrictions; metasome slightly inflated dorsally with convex dorsal margin in lateral view and narrower posterior part. Legs 4 and 5 positioned on same transverse plane. Posterior part of body (Fig. 67B) slender, consisting of genital somite and 4-segmented abdomen, but articulation incomplete between last 2 somites. Genital somite 394×406 µm; 4 abdominal somites 187×315, 133×300, 188×255, and 242×182 µm, respectively. Caudal ramus (Fig. 67C) as long as wide, ornamented with 2 patches of minute spinules on ventral surface; armed with 5 claws and 1 seta; spine on subdistal inner margin setiform, pale.

Rostrum (Fig. 67D) short, strongly tapering towards rounded apex. Antennule (Fig. 67E) 5-segmented, forming right angle between first and remaining segments; armature formula 13, 5, 3, 4, and 7+aesthetasc; aesthetasc on last segment very small and similar in appearance to smaller setae. Antenna (Fig. 67F) consisting of coxa, basis, and 2-segmented endopod; coxa short and unarmed; basis unarmed but ornamented with 2 patches of minute spinules subdistally; first endopodal segment short and unarmed; second endopodal segment about 3 times longer than wide (121×41 µm), with vestigial suture at distal third: armed with 8 spines (4 on inner margin and 4 on distal margin) and ornamented with 1 patch of minute spinules subdistally; fourth spine on inner margin shortest, and second outer spine on distal margin longest

Labrum (Fig. 67G) small, unornamented, with broad posteromedial lobe. Mandible (Fig. 67H) consisting of coxa and palp; coxal gnathobase with 3 teeth and finely spinulose proximal part on medial margin; palp with 9 setae arranged as 3, 2, 2, and 2. Maxillule (Fig. 67I) consisting of precoxa and palp; precoxa with 8 unequal setae on arthrite (including 2 small distal setae); palp consisting of coxa, basis, and endopod; coxa with 1 minute vestigial seta on epipodite; basis with 2 setae on medial margin, 3 setae on outer margin, and weakly bilobed process distally; endopod incompletely articulated from basis, with 3 setae on distal margin. Maxilla (Fig. 68A) obscurely 2-segmented, with 9 setae. Maxilliped (Fig. 68B) 4-segmented with 2 setae on syncoxa, 2 on basis, and 1 on second endopodal segment; terminal claw as long as second endopodal segment, with 1 denticle proximally on inner margin.

Legs 1-4 biramous with 1-segmented exopods and endopods (Fig. 68C, D), and unarmed coxa. Basis of leg 1 lacking outer seta, but with 2 patches of minute spinules on anterior surface. Basis of leg 2 unornamented, with short, very thin outer seta. Exopods of legs 1-4 armed with 7 spines, but inner subdistal spine rudimentary; ornamented with patch of fine spinules near base of outer and distal spines. Endopod of legs 1 and 2 ornamented with 3 patches of minute spinules on anterior surface. Outer proximal seta on endopod of legs 1 and 2 markedly shorter than other setae. Armature formula for legs 1-4 as follows:

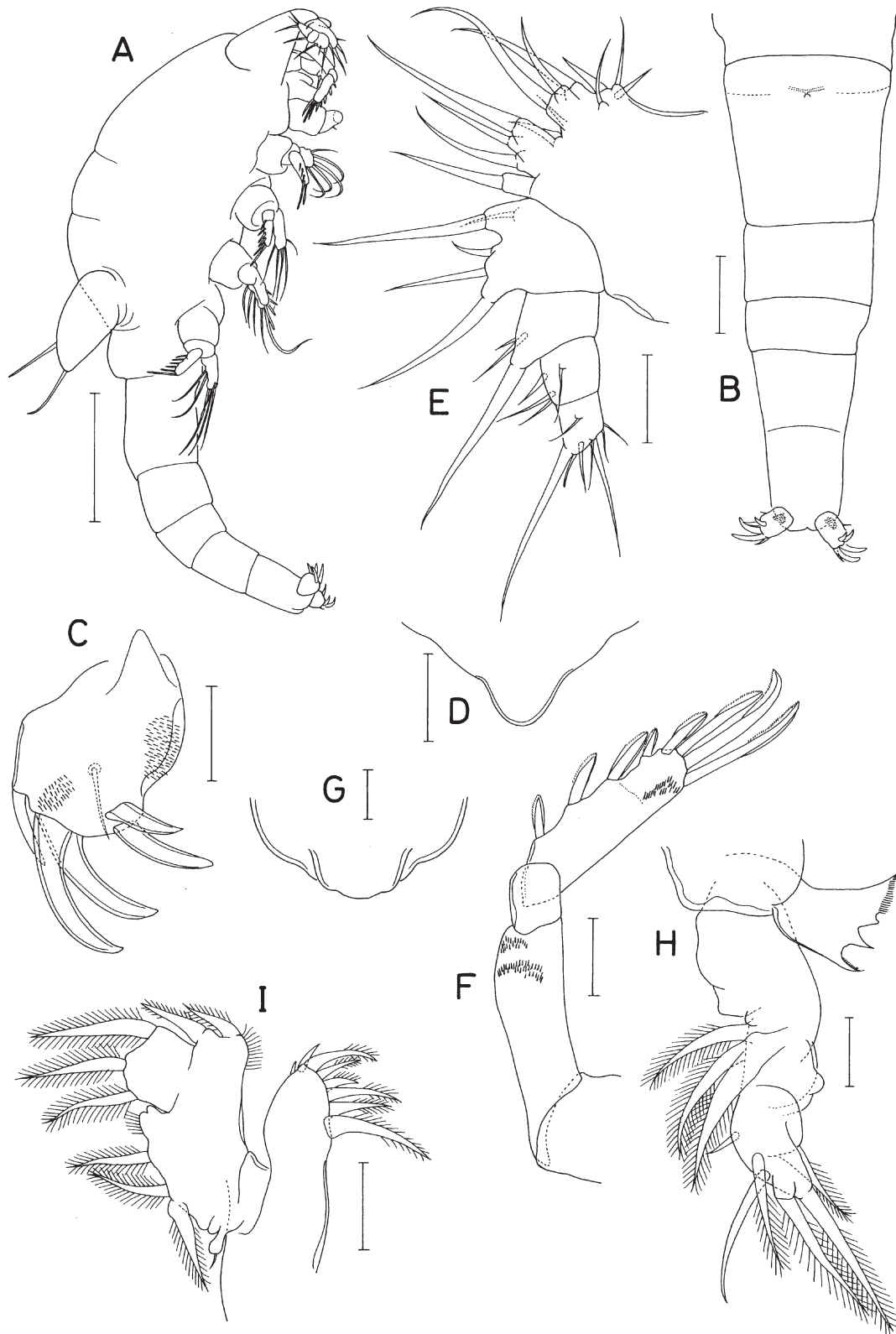
	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	0-0	VI, 1	1, 2, 5
Leg 2	0-0	1-0	VI, 1	1, 2, 5
Legs 3 & 4	0-0	1-0	VI, 1	1, 2, 4

Leg 5 (Fig. 68E) flattened, sub-rectangular, twice as long as wide (500×245 µm), armed with 2 setae on oblique distal margin. Leg 6 not seen.

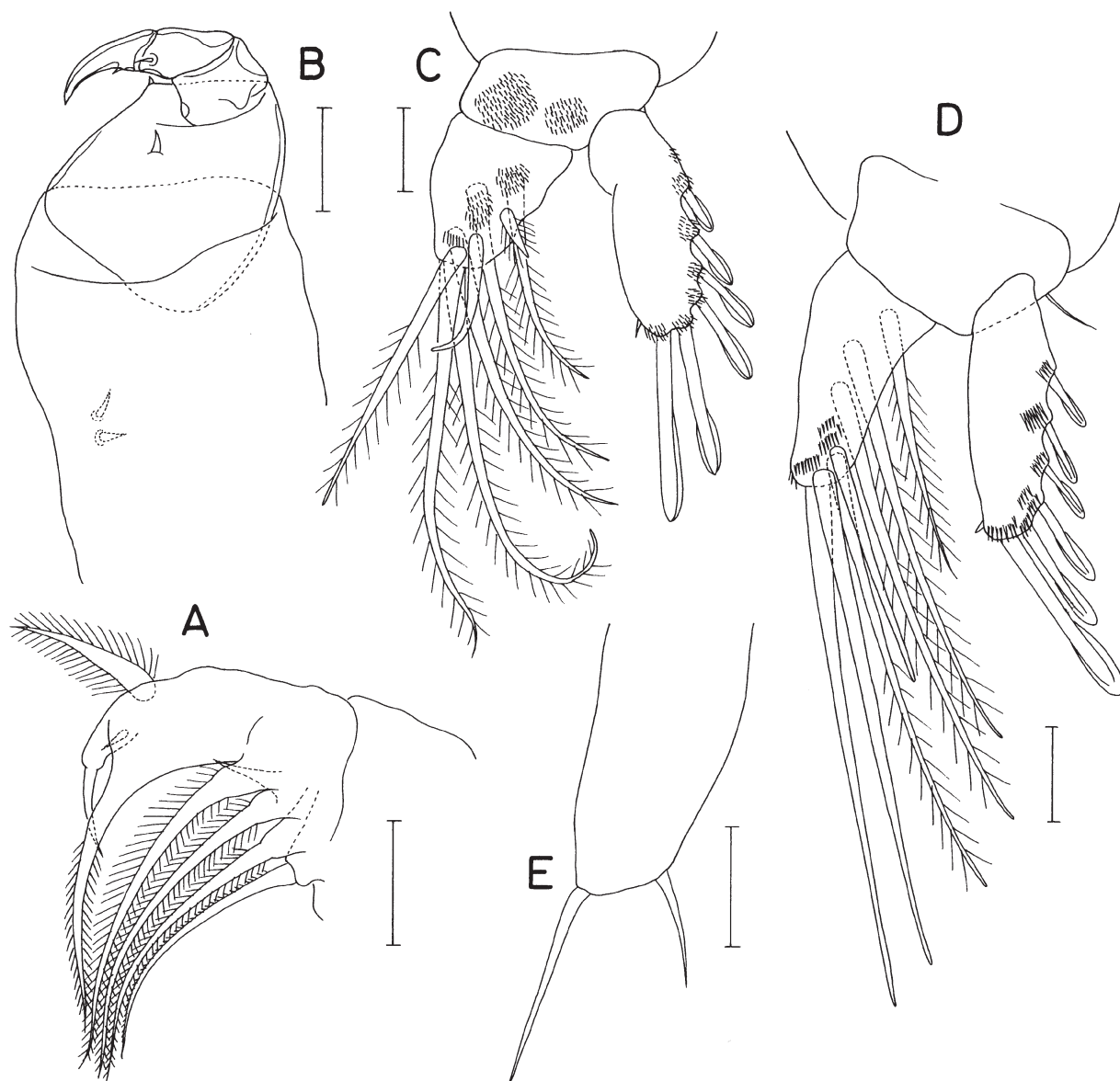
**Male.** Unknown.

**Remarks.** *Schizoproctus bisetatus* sp. nov. is most similar to *S. magnus* sp. nov. because they share the same armature formula of legs 1-4, with the exception only of the endopod of leg 2 which bears 8 setae in *S. bisetatus* sp. nov. compared to 9 setae in *S. magnus* sp. nov. The main differences between these two species are as follows: (1) the abdomen is 4-segmented in *S. bisetatus* sp. nov., but consists of 6 indistinct annulations in *S. magnus* sp. nov.;

(2) the caudal ramus is armed with 5 claws and 1 seta in *S. bisetatus* **sp. nov.**, but with 4 claws and 2 setae in *S. magnus* **sp. nov.**; (3) all setae on the antennule of *S. bisetatus* **sp. nov.** are much shorter than the width of the first segment, whereas some of setae on the antennule of *S. magnus* **sp. nov.** are large, as long as the width of the first segment; and (4) leg 5 is sub-rectangular with 2 distinct setae in *S. bisetatus* **sp. nov.**, but elongate and tapering with 4 rudimentary setae in *S. magnus* **sp. nov.**



**FIG. 67.** *Schizoproctus bisetatus* **sp. nov.**, female. A, habitus, right; B, posterior part of body, ventral; C, caudal ramus; D, rostrum; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule. Scale bars: A, 0.5 mm; B, 0.2 mm; C-F, H, I, 0.05 mm; G, 0.02 mm.



**FIG. 68.** *Schizoproctus bisetatus* sp. nov., female. A, maxilla; B, maxilliped; C, leg 1; D, leg 3; E, leg 5. Scale bars: A-D, 0.05 mm; E, 0.2 mm.

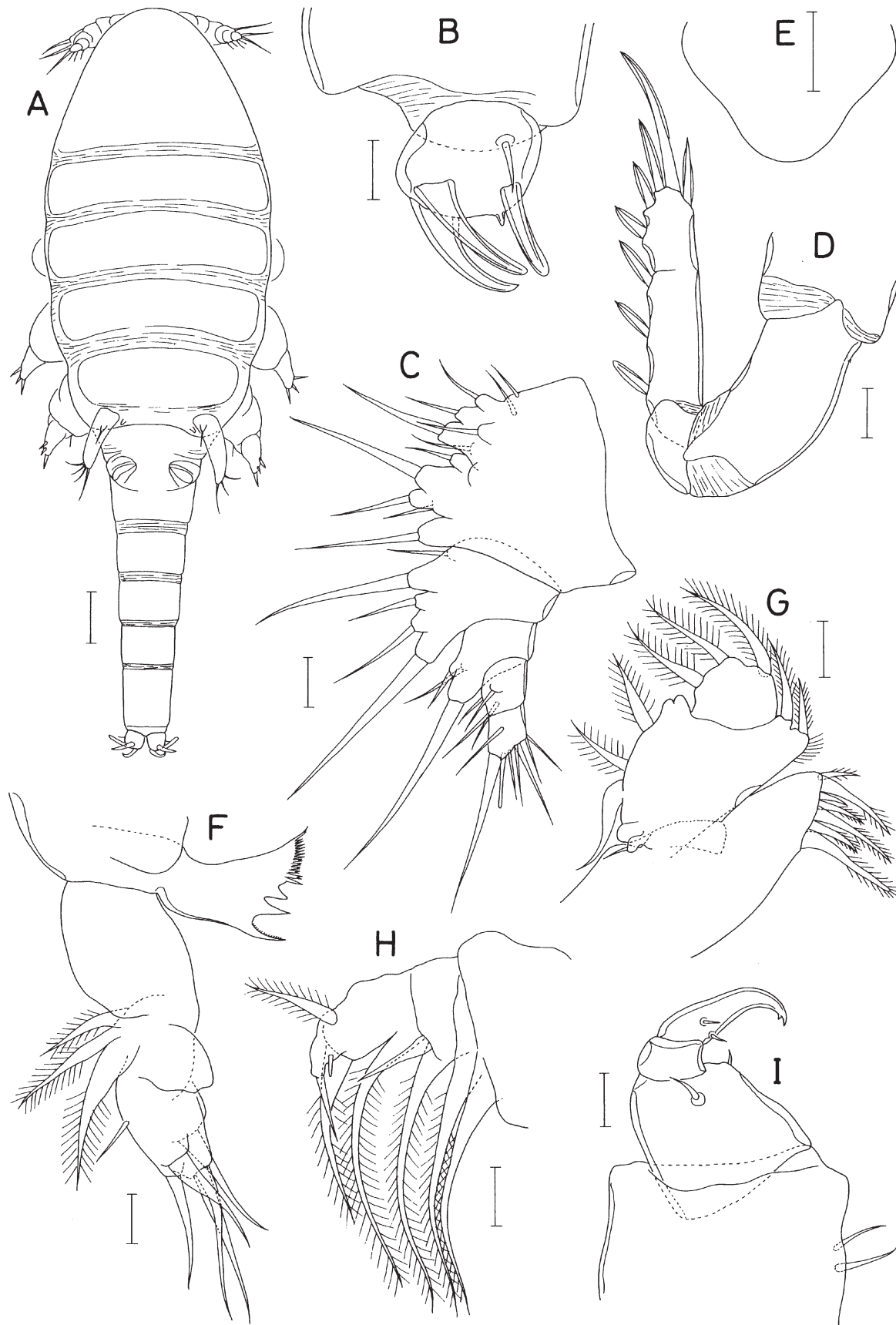
***Schizoproctus fusiformis* sp. nov.**

(Figs. 69, 70)

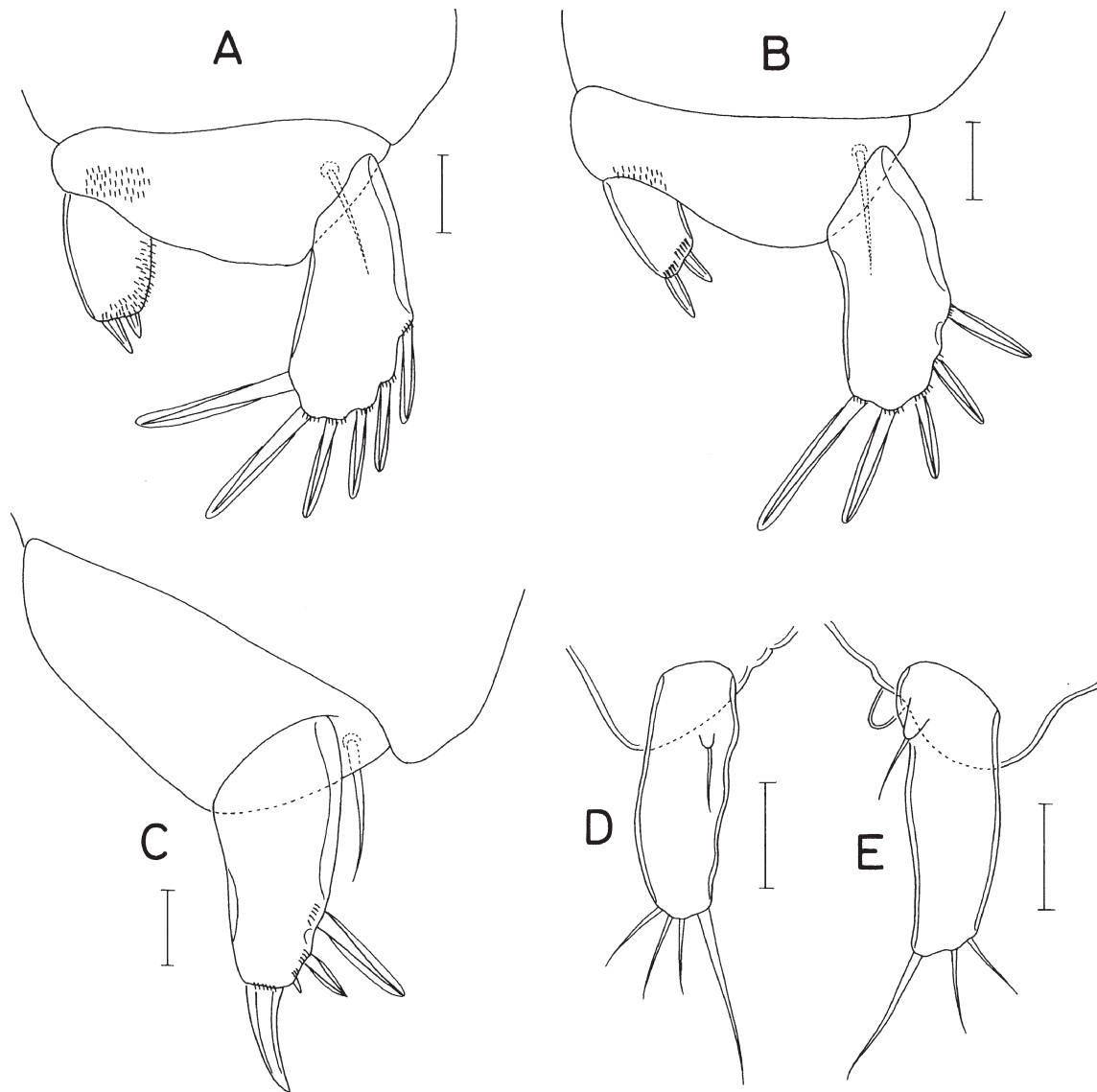
**Type material.** Holotype ♀ (MNHN-IU-2018-1978, dissected and mounted on a slide) from *Polycarpa fibrosa* (Stimpson, 1852); off Tromsø, Norway, NORBI Cruise, RV “Jean Charcot”, Stn CP11 trawl, (69°52’N, 17°08’E), depth 250-300 m, Bouchet & Warén coll., 01 July 1975.

**Etymology.** The specific name refers to the fusiform anterior part of body of the new species.

**Description of female.** Body (Fig. 69A) straight, with fusiform anterior part and narrower posterior part; body length 1.40 mm. Anterior part 800×440 µm, not segmented, but cephalosome and 4 metasomal somites discernible by weak cephalic shield and 4 dorsal tergites. Fifth pedigerous somite not defined from fourth pedigerous somite. Posterior part of body consisting of genital somite and 4-segmented abdomen. Genital somite 250×220 µm, gradually narrowing posteriorly; genital apertures positioned dorsally. Four abdominal somites 82×131, 90×118, 77×105, and 122×98 µm, respectively. Caudal ramus (Fig. 69B) wider than long, armed with 4 spines and 1 seta; outer distal spine very small, nipple-shaped, not articulated from ramus.



**FIG. 69.** *Schizoproctus fusiformis* sp. nov., female. A, habitus, dorsal; B, caudal ramus; C, antennule; D, antenna; E, labrum; F, mandible; G, maxillule; H, maxilla; I, maxilliped. Scale bars: A, 0.1 mm; B-D, F-I, 0.02 mm; E, 0.05 mm.



**FIG. 70.** *Schizoproctus fusiformis* sp. nov., female. A, leg 1; B, leg 2; C, leg 3; D, left leg 5; E, right leg 5. Scale bars: A-C, 0.02 mm; D, E, 0.05 mm.

Rostrum absent. Antennule (Fig. 69C) short, 5-segmented; first segment broad; distal segments gradually narrowing; armature formula 12, 5, 3, 4, and 7+aesthetasc. Antenna (Fig. 69D) 4-segmented; coxa, basis, and first endopodal segment unarmed; second endopodal segment about 4 times longer than wide ( $95 \times 24 \mu\text{m}$ ), with partial subdivision on inner side at distal third; armed with 8 spines (4 on inner margin and 4 on distal margin); spines on inner margin shorter than width of segment; longest second outer spine on distal margin  $65 \mu\text{m}$  long, twice as long as second longest adjacent spine.

Labrum (Fig. 69E) weak, thin-walled, strongly tapering towards rounded distal margin. Mandible (Fig. 69F) with 3 teeth on coxal gnathobase; palp with 9 setae and 1 large medial swelling; 3 outer proximal setae pinnate, but remaining distal setae naked. Maxillule (Fig. 69G) consisting of precoxa and palp; precoxa with 7 setae on arthrite, proximalmost seta bluntly tipped; palp consisting of coxa, basis, and endopod; coxa with vestigial seta on epipodite; basis with 2 setae on medial margin, 3 setae on outer margin (proximal seta naked, others pinnate), and bilobed distal tubercle; endopod distinctly articulated from basis, with 3 setae on distal margin. Maxilla (Fig. 69H) indistinctly 3-segmented with 9 setae (1 distal seta minute). Maxilliped (Fig. 69I) 4-segmented, but second endopodal segment and terminal claw completely fused; syncoxa much broader than long, with 2 setae on inner margin; basis with 2 widely isolated setae; first endopodal segment short and unarmed; terminal segment (fused second endopodal segment and terminal claw) strongly curved, with 2 small setae proximally and 1 small subterminal denticle.

Legs 1 and 2 (Fig. 70A, B) biramous with 1-segmented rami; endopods much smaller than exopods. Legs 3 and 4 uniramous with 1-segmented exopod; endopod lacking; third outer spine rudimentary. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	VI	II
Leg 2	0-0	1-0	V	II
Legs 3 & 4	0-0	1-0	IV	(endopod lacking)

Leg 5 (Fig. 70D, E) 1-segmented, subrectangular: left leg 5 (Fig. 70D) 2.93 times longer than wide (123×42 µm) with 1 proximal and 4 distal setae; right leg 5 (Fig. 70E) 2.96 times longer than wide (142×48 µm), with 1 proximal and 3 distal setae; right leg 5 accompanied by 1 tubercle on fifth pedigerous somite near base of leg segment. Leg 6 not discernible.

**Male.** Unknown.

**Remarks.** All known species of *Schizoproctus* have biramous legs 1-4. Therefore, the possession of uniramous legs 3 and 4, lacking an endopod, in *S. fusiformis* **sp. nov.** serves to distinguish the new species from all congeners. The armature patterns of legs 1 and 2 also are unique within the genus (Table 3). The fusion of the second endopodal segment with the terminal claw in the maxilliped of *S. fusiformis* **sp. nov.** is a notable feature shared with the type species, *S. inflatus*, and with *S. frigidus* **sp. nov.** described below. Other morphological features of these two species also differ from those of *S. fusiformis* **sp. nov.**, such as the broad circular shape of their leg 5.

### *Schizoproctus tripartitus* **sp. nov.**

(Figs. 71, 72)

**Type material.** Holotype ♀ (MNHN-IU-2018-1979) and 1 ♀ paratype (MNHN-IU-2014-17378, dissected) from *Araneum sigma* Monniot C. & Monniot F., 1973 (syntypes: MNHN-IT-2008-821, MNHN-IT-2008-826); NE Atlantic, BIACORES cruise, RV “Jean Charcot”, Stns DS126, CHG245, CHG-F249, depth 3360-4690 m, Boury-Esnault coll., October-November 1971.

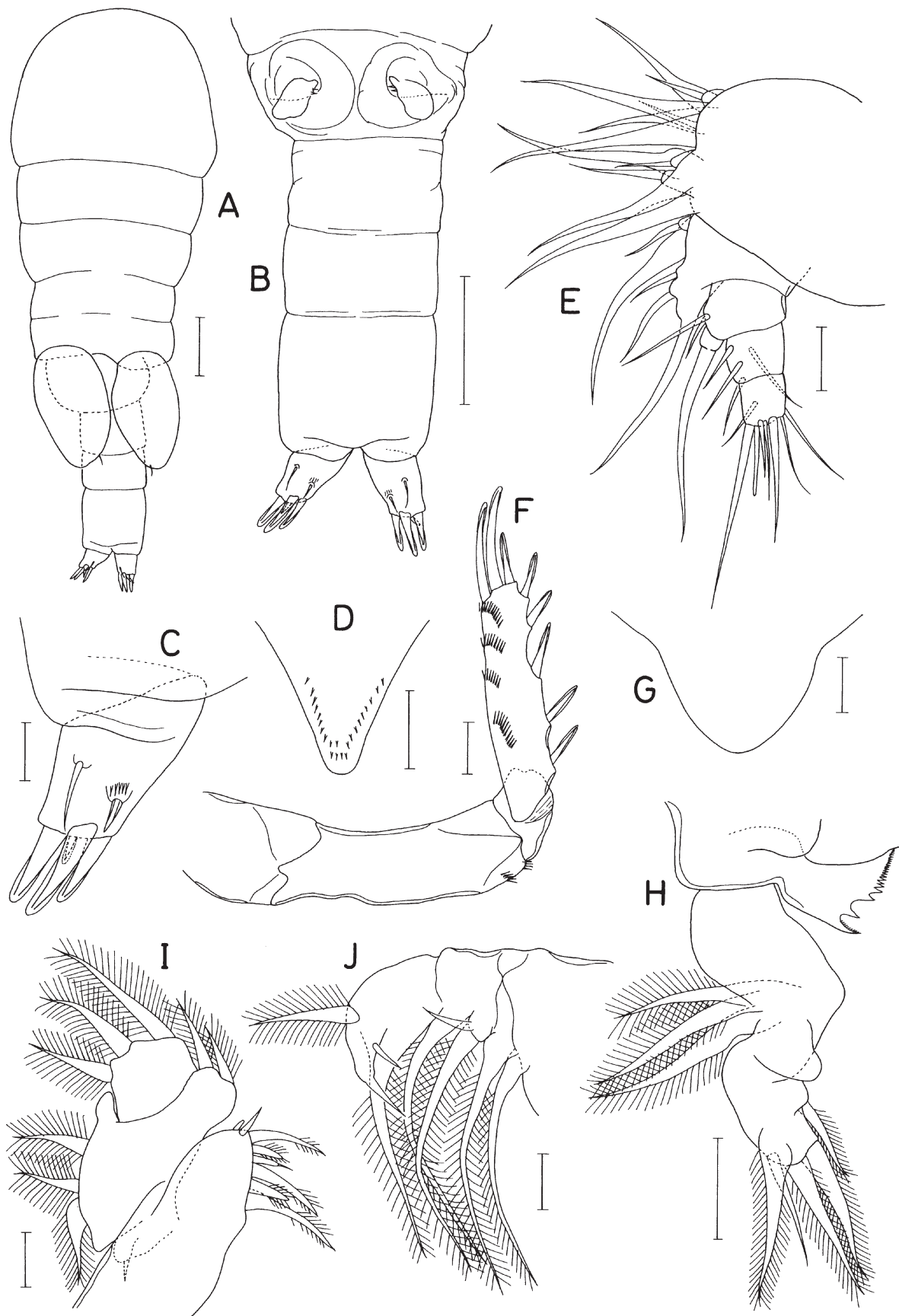
**Etymology.** The name of the new species refers to the 3-segmented abdomen of the female.

**Description of female.** Body (Fig. 71A) slightly dorsoventrally depressed, with thin exoskeleton; body length 0.98 mm; width 0.35 mm across cephalosome. Anterior part of body gradually narrowing posteriorly, consisting of cephalosome and 4 indistinctly separated metasomites; fourth metasomite consisting of completely fused fourth and fifth pedigerous somites. Posterior part of body (Fig. 71B) consisting of genital somite and 3-segmented abdomen. Genital somite about 2.1 times wider than long (82×170 µm), distinctly wider than abdomen; genital apertures large, located dorsally. Abdomen with parallel lateral margins; first to third abdominal somites 73×118, 65×120, and 110×120 µm, respectively. Caudal rami divergent; each ramus (Fig. 71C) about 1.7 times longer than wide (60×36 µm), with shorter outer and longer inner margins; armed with 5 straight claws and 1 seta; inner dorsal claw 12 µm long, accompanied by several spinules near base; lengths of 4 distal claws 27, 37, 28, and 10 µm.

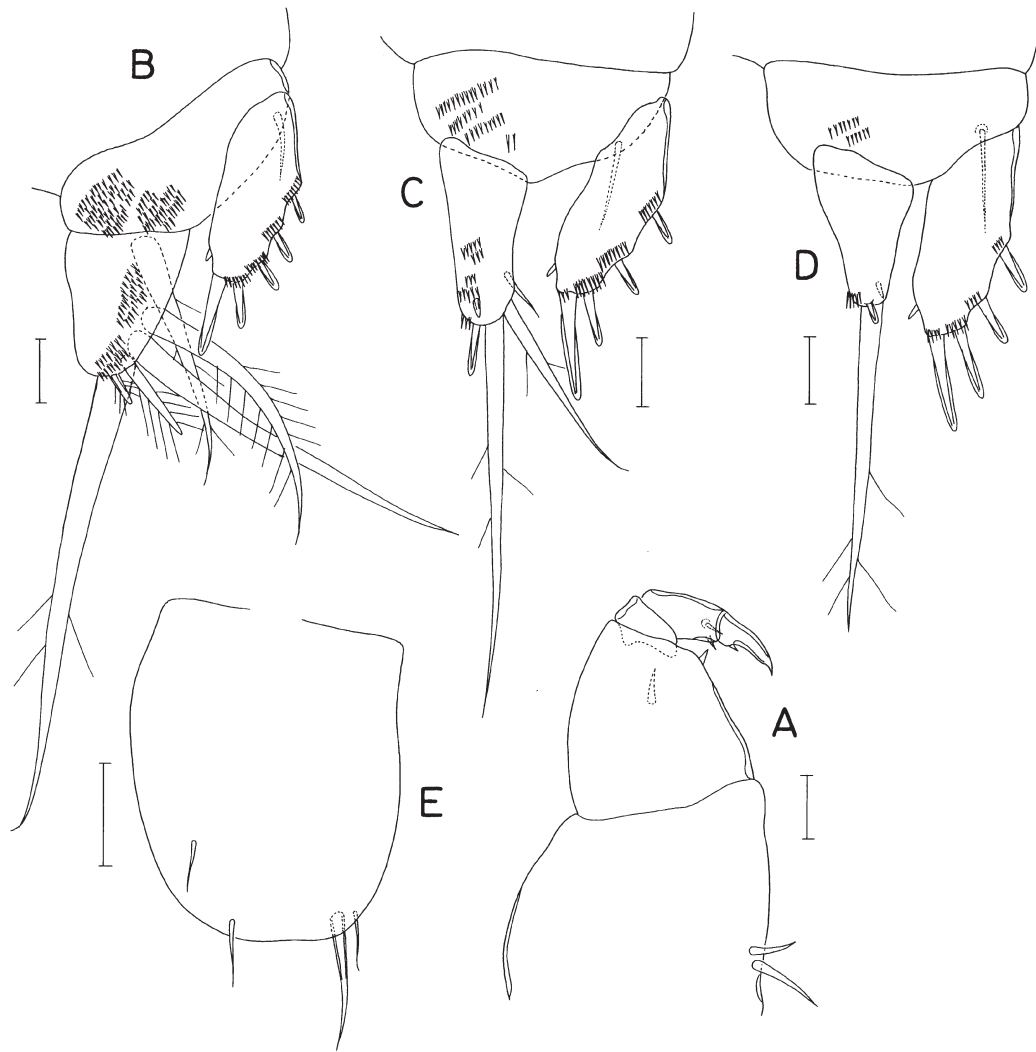
Rostrum (Fig. 71D) strongly tapering towards blunt apex; with rows of fine spinules ventrally along lateral margins. Antennule (Fig. 71E) 5-segmented; first segment extremely inflated; armature formula 11, 5, 3, 4, and 7+aes-thetasc. Antenna (Fig. 71F) consisting of coxa, basis, and 2-segmented endopod; coxa and first endopodal segment unarmed; basis unarmed, but ornamented with 2 rows of fine spinules on inner distal surface; second endopodal segment about 3.2 times longer than wide (77×24 µm) and ornamented with 4 rows of fine spinules; armed with 8 spines (spines on inner margin shorter than width of segment), including 2 outer spines on distal margin longer than segment width, 38 (outer) and 41 µm long (inner).

Labrum (Fig. 71G) weak, flexible, semicircular. Mandible (Fig. 71H) with 4 major teeth on coxal gnathobase; palp with large tubercle near middle and 8 setae arranged as 3, 1, 2, and 2. Maxillule (Fig. 48I) consisting of precoxa and palp; precoxa with 8 unequal setae on arthrite, 2 distal setae rudimentary; palp consisting of coxa, basis, and endopod; armed with 1 vestigial seta on coxal epipodite, 2 medial and 3 outer setae on basis, and 3 setae on endopod;





**FIG. 71.** *Schizoproctus tripartitus* **sp. nov.**, female. A, habitus, dorsal; B, posterior part of body, dorsal; C, caudal ramus; D, rostrum; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule; J, maxilla. Scale bars: A, B, 0.1 mm; C-G, I, J, 0.02 mm; H, 0.05 mm.



**FIG. 72.** *Schizoproctus tripartitus* sp. nov., female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 5. Scale bars: A-D, 0.02 mm; E, 0.05 mm.

digitiform lobe present distally on basis. Maxilla (Fig. 71J) indistinctly 3-segmented, with 2, 3, and 4 setae on first to third segments, respectively. Maxilliped (Fig. 72A) 4-segmented; syncoxa and basis each with 2 small setae; first endopodal segment short and unarmed; second endopodal segment with 2 small setae subdistally; terminal claw shorter than second endopodal segment, with 1 small denticle proximally on inner margin.

Legs 1-4 biramous with 1-segmented rami (Fig. 72B-D); coxa unarmed; basis with outer seta and ornamented with patch of spinules on inner side of anterior surface, this patch of spinules becoming smaller from legs 1 to 4. Distalmost seta on endopod of leg 1 small and spiniform. Distal spines on endopods of legs 2-4 small. Leg 4 similar to leg 3, but endopod bearing only 1 spine and 1 seta. Inner subdistal seta on exopod of legs 1-4 rudimentary. Distal spines on endopod of legs 2 and 3 small. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	V, 1	6
Leg 2	0-0	1-0	IV, 1	II+ 3
Leg 3	0-0	1-0	IV, 1	II+ 1
Leg 4	0-0	1-0	IV, 1	I+ 1

Leg 5 (Fig. 72E) arising on posterodorsal surface of double metasomite (comprising fused fourth and fifth pedigerous somites); roughly quadrate, lamellate, longer than wide (159×130 μm); armed with 4 setae, 1 distinctly larger than other 3. Leg 6 represented by 2 small spinules on genital operculum.

**Male.** Unknown.

**Remarks.** The setal combination on the endopods of legs 1-4 (6-5-3-2) of *S. tripartitus* **sp. nov.** is unique within the genus (see Table 3) and this allows the new species to be distinguished from all of its congeners. The 3-segmented abdomen of *S. tripartitus* **sp. nov.** is a feature shared with *S. vestitus* (Sars, 1921) and *S. mollis* **sp. nov.** described below. These two species are easy to distinguish from *S. tripartitus* **sp. nov.** by the setation of endopods of legs 1-4 (the combination on the endopods of legs 1-4 is 3-2-?-6 in *S. vestitus* (the setation of the endopod of leg 3 is unknown in *S. vestitus*) and 7-6-4-3 in *S. mollis* **sp. nov.**). In addition there are two other significant differences, as follows: (1) the body length is 1.80 mm in *S. vestitus* according to Sars (1921), and 1.94 mm in *S. mollis* **sp. nov.**, in contrast to 0.98 mm in *S. tripartitus* **sp. nov.**, and (2) the exopods of legs 1-4 of *S. vestitus* and *S. mollis* **sp. nov.** are armed with 6 spines each, in contrast to 5 spines plus 1 seta in leg 1 and 4 spines plus 1 seta in legs 2-4 of *S. tripartitus* **sp. nov.**

### *Schizoproctus frigidus* **sp. nov.**

(Figs. 73, 74)

**Type material.** Holotype ♀ (MNHN-IU-2018-1980, dissected and mounted on a slide) from *Corella antarctica* Sluiter, 1905; Antarctic Ocean, Eltanin cruise 12, Stn 1078 (61°26'S, 41°55.4'W), depth 604 m, 12 April 1964.

**Etymology.** The specific name is derived from the Latin *frig* (cold), referring to its discovery in Antarctic waters.

**Description of female.** Body (Fig. 73A) robust, 2.88 mm long. Anterior part of body unsegmented and inflated; cephalosome defined from metasome by faint dorsal constriction. Posterior part of body (Fig. 73B) consisting of genital somite and 4-segmented abdomen. Genital somite much wider than long (205×487 µm) incompletely articulated from first abdominal somite. First and second abdominal somites 354×436 and 230×385 µm, respectively; third and fourth abdominal somites indistinctly articulated from each other, 128×297 and 210×270 µm, respectively. Caudal ramus (Fig. 73C) about 107×135 µm, armed with 4 claws and 2 setae; lengths of claws 58, 76, 50, and 25 µm from inner to outer.

Rostrum (Fig. 73D) broad, steeply tapering towards nipple-shaped, semicircular apex. Antennule (Fig. 73E) 252 µm long and indistinctly 5-segmented; first segment broad, forming right angle with distal 4 segments; 2 distal articulations incomplete; armature formula 11, 6, 3, 2, and 8+aesthetasc. Left antenna (Fig. 73F) consisting of unarmed coxa, basis and unsegmented endopod; endopod 163×65 µm, armed with 8 short setae and with rudimentary suture line subdistally defining proximal 3-setae part and distal 5-setae part; longest distal seta 96 µm. Right antenna segmented and armed as left antenna; endopod (Fig. 73G) 167×65 µm, subdivided by subdistal sclerotization band.

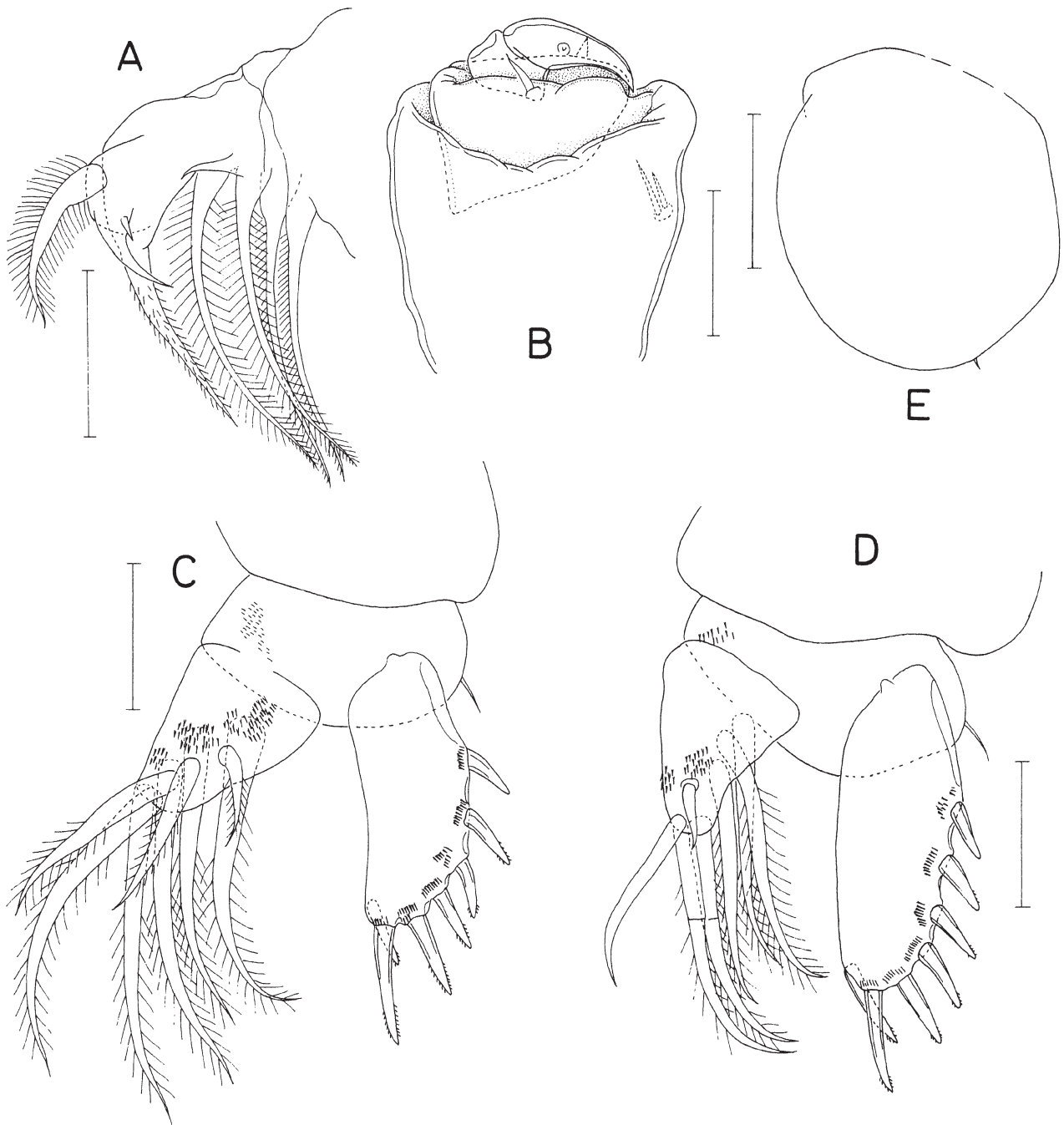
Labrum (Fig. 73H) much broader than long, with large, soft posteromedian protuberance. Mandible (Fig. 73I) as usual for genus, with 3 teeth on coxal gnathobase and 9 setae on palp. Maxillule (Fig. 73J) with 8 setae on arthrite, distal seta rudimentary; palp unsegmented with vestigial seta representing epipodite, 2 setae on medial margin, 3 setae on outer margin, 1 tubercle distally, and 3 setae on endopod; endopod fused with basis. Maxilla (Fig. 74A) 2-segmented with 2 setae on first segment and 7 setae on second. Maxilliped (Fig. 74B) robust, 4-segmented, but second endopodal segment completely fused with terminal claw; syncoxa broadening distally; basis much wider than long, bearing 2 setae; first endopodal segment unarmed; second endopodal segment + terminal claw complex unarmed, with 1 minute papilla at proximal third.

Legs 1-4 biramous with 1-segmented rami; coxa unarmed; basis with small outer seta. Legs 1 (Fig. 74C) and 2 with same armature. Legs 3 (Fig. 74D) and 4 also with same armature. Outer spines on exopods gradually becoming longer from proximal to distal; longest distal spine shorter than width of exopodal segment. Endopods distinctly tapering. Two anterior (ventral) setae on endopod of legs 3 and 4 naked. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Legs 1 & 2	0-0	1-0	VII	8
Legs 3 & 4	0-0	1-0	VII	7



**FIG. 73.** *Schizoproctus frigidus* sp. nov., female. A, habitus, left; B, posterior part of body, dorsal; C, caudal ramus; D, rostrum; E, antennule; F, left antenna; G, distal part of right antenna; H, labrum; I, mandible; J, maxillule; K, genital aperture. Scale bars: A, 0.5 mm; B, 0.2 mm; C, E, J, K, 0.05 mm; D, F-I, 0.1 mm.



**FIG. 74.** *Schizoproctus frigidus* **sp. nov.**, female. A, maxilla; B, maxilliped; C, leg 1; D, leg 3; E, leg 5. Scale bars: A-D, 0.1 mm; E, 0.5 mm.

Leg 5 (Fig. 74E) circular, fleshy, lamellate,  $100 \times 92 \mu\text{m}$ , with 1 rudimentary seta distally. Leg 6 (Fig. 73K) represented by 2 small spinules and 1 spiniform process on genital operculum.

**Male.** Unknown.

**Remarks.** The most distinctive diagnostic feature of *S. frigidus* **sp. nov.** is the presence of 7 spines on the exopods of legs 1-4, because in other species of the genus the maximum number of spines on the exopod of any leg is 6, although several species bear an additional rudimentary seta on the exopod. The armature sequence on the endopods of legs 1-4 (8-8-7-7) is also an outstanding diagnostic feature shared only with *S. bisetatus* **sp. nov.** (Table 3), which differs from *S. frigidus* **sp. nov.** in the presence of 2 setae on the lamellate exopod of leg 5. The fusion of the second

endopodal segment and the terminal claw of the maxilliped of *S. frigidus* **sp. nov.** is an unusual feature within the genus, which is only known in *S. inflatus*, as figured by Sars (1921) and *S. fusiformis* **sp. nov.**

***Schizoproctus oligomerus* sp. nov.**

(Figs. 75, 76)

**Type material.** Holotype ♀ (MNHN-IU-2018-1981, dissected and mounted on a slide) from *Pareugyrioides char-dyi* Monniot C. & Monniot F., 1977; Gulf of Gascogne, BIOGAS 6 cruise, RV “Jean Charcot”, Stn CP10 (47°30'N, 09°04'W), depth 2878 m, Station Marine d'Endoume coll., 21 October 1974.

**Etymology.** The specific name is from Greek *oligo* (=few) and *merous* (=parted), referring to the oligomeric body.

**Description of female.** Body (Fig. 75A) poorly segmented; 2.50 mm long; maximum width 0.81 mm. Anterior part of body divisible by incomplete suture into cephalosome and unsegmented metasome incorporating fifth pedigerous somite. Posterior part of body (Fig. 75B) consisting of genital somite and unsegmented abdomen. Genital somite not articulated from anterior part, much wider than long, 409 µm wide; genital apertures located dorsally. Abdomen distinctly narrower than genital somite, about 800×259 µm, obscurely articulated from genital somite, unsegmented but with 3 indistinct transverse surface wrinkles. Caudal ramus (Fig. 75C) wider than long (98×103 µm), lamellate: armed with 5 spiniform claws and 1 small seta; claws straight, outer 4 claws fringed with narrow membrane along both margins, 67, 121, 150, 112, and 45 µm long from inner (dorsal) to outer (ventral).

Rostrum absent. Antennule (Fig. 75D) short, 5-segmented; first segment markedly broadened; armature formula 12, 5, 2, 4, and 7+aesthetasc; all setae shorter than width of first segment. Antenna (Fig. 75E) 4-segmented, consisting of coxa, basis, and 2-segmented endopod; proximal 3 segments unarmed; second endopodal segment about 3.4 times longer than wide (182×54 µm); armed with 8 spines (4 inner and 4 distal); proximal 2 spines on inner margin shorter than width of segment, all other spines longer than width of segment; second outer spine on distal margin longest, 130 µm.

Labrum (Fig. 75F) wider than long, with large posteromedian protuberance bearing 4 rows of minute spinules on surface. Mandible (Fig. 75G) with 3 teeth on coxal gnathobase; palp with 8 setae. Maxillule (Fig. 75H) with 8 setae (including 2 small distal setae) on precoxal arthrite, 1 small seta on coxal epipodite, 5 setae on basis (2 on medial and 3 on outer margins) and 3 setae on endopod. Maxilla (Fig. 75I) 3-segmented with 2, 3, and 4 setae respectively on first to third segments; 2 of 4 setae on third segment small, setule-like. Maxilliped (Fig. 75J) 4-segmented; syncoxa and basis broad, each with 2 setae; first endopodal segment short and unarmed; second endopodal segment with 2 minute setae; terminal claw longer than second endopodal segment, with 1 small denticle proximally on inner margin.

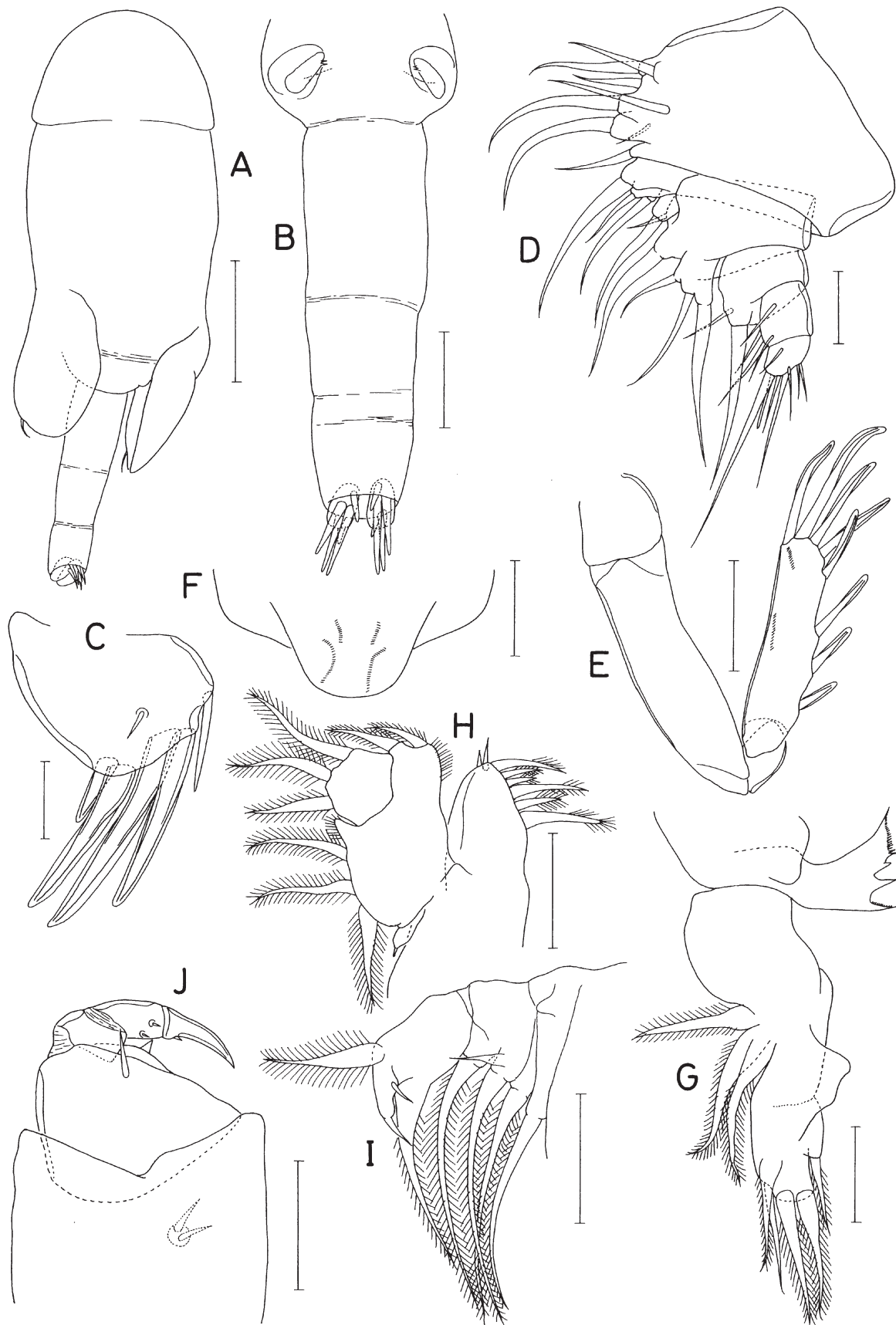
Legs 1-4 biramous with 1-segmented rami (Fig. 76A, B); coxa unarmed; basis with 1 small outer seta and ornamented with inner patch of minute spinules on anterior surface; all exopods with 6 slender spines and 1 rudimentary inner subdistal seta. Distalmost spine on exopods much longer than other spines, at least twice as long as adjacent seta. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Legs 1 & 2	0-0	1-0	VI, 1	7
Legs 3 & 4	0-0	1-0	VI, 1	6

Leg 5 (Fig. 76C) lamellate, about 564×542 µm, with rounded distal margin and 2 small setae distally (1 minute). Leg 6 represented by 1 spinule and 1 spinule-like process on genital operculum.

**Male.** Unknown.

**Remarks.** The diagnostic features of *S. oligomerus* **sp. nov.** include: (1) the abdomen is unsegmented (a unique feature); (2) the caudal ramus is armed with 5 claws and 1 seta (shared only with *S. bisetatus* **sp. nov.** and *S. tripartitus* **sp. nov.**); and (3) the armature of the endopods of legs 1-4 is 7, 7, 6, and 6 setae (a unique combination, see Table 3). The combination of these three features serves to distinguish *S. oligomerus* **sp. nov.** from all congeneric species.



**FIG. 75.** *Schizoproctus oligomerus* sp. nov., female. A, habitus, dorsal; B, posterior part of body, dorsal; C, caudal ramus; D, antennule; E, antenna; F, labrum; G, mandible; H, maxillule; I, maxilla; J, maxilliped. Scale bars: A, 0.5 mm; B, 0.2 mm; C, D, 0.05 mm; E-J, 0.1 mm.

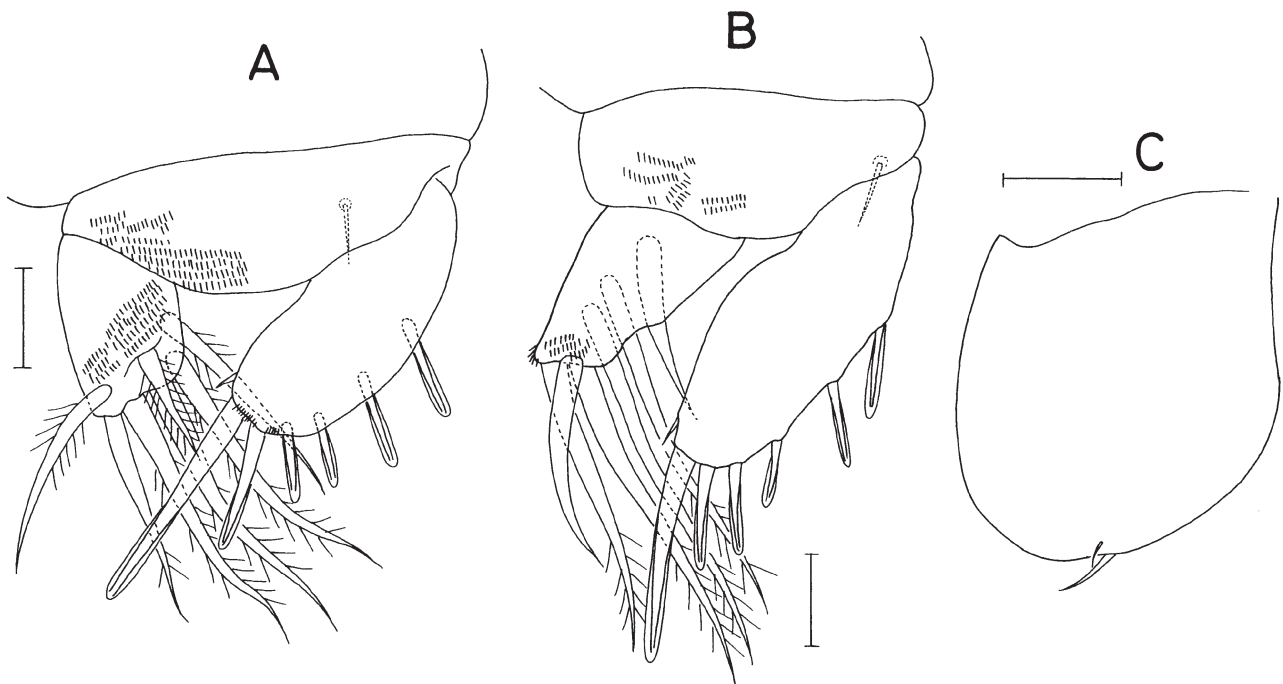


FIG. 76. *Schizoproctus oligomerus* sp. nov., female. A, leg 1; B, leg 3; C, leg 5. Scale bars: A, B, 0.05 mm; C, 0.2 mm.

***Schizoproctus mollis* sp. nov.**

(Figs. 77, 78)

**Type material.** Holotype ♀ (MNHN-IU-2018-1982, dissected and mounted on a slide) from *Ciona intestinalis* (Linnaeus, 1767) (MNHN-IT-2008-1886 = MNHN P1/CIO/24); Locality and date unknown, MNHN-Saint Joseph coll.

**Etymology.** The specific name is from the Latin *moll* (=soft), alluding to the weak exoskeleton of the new species.

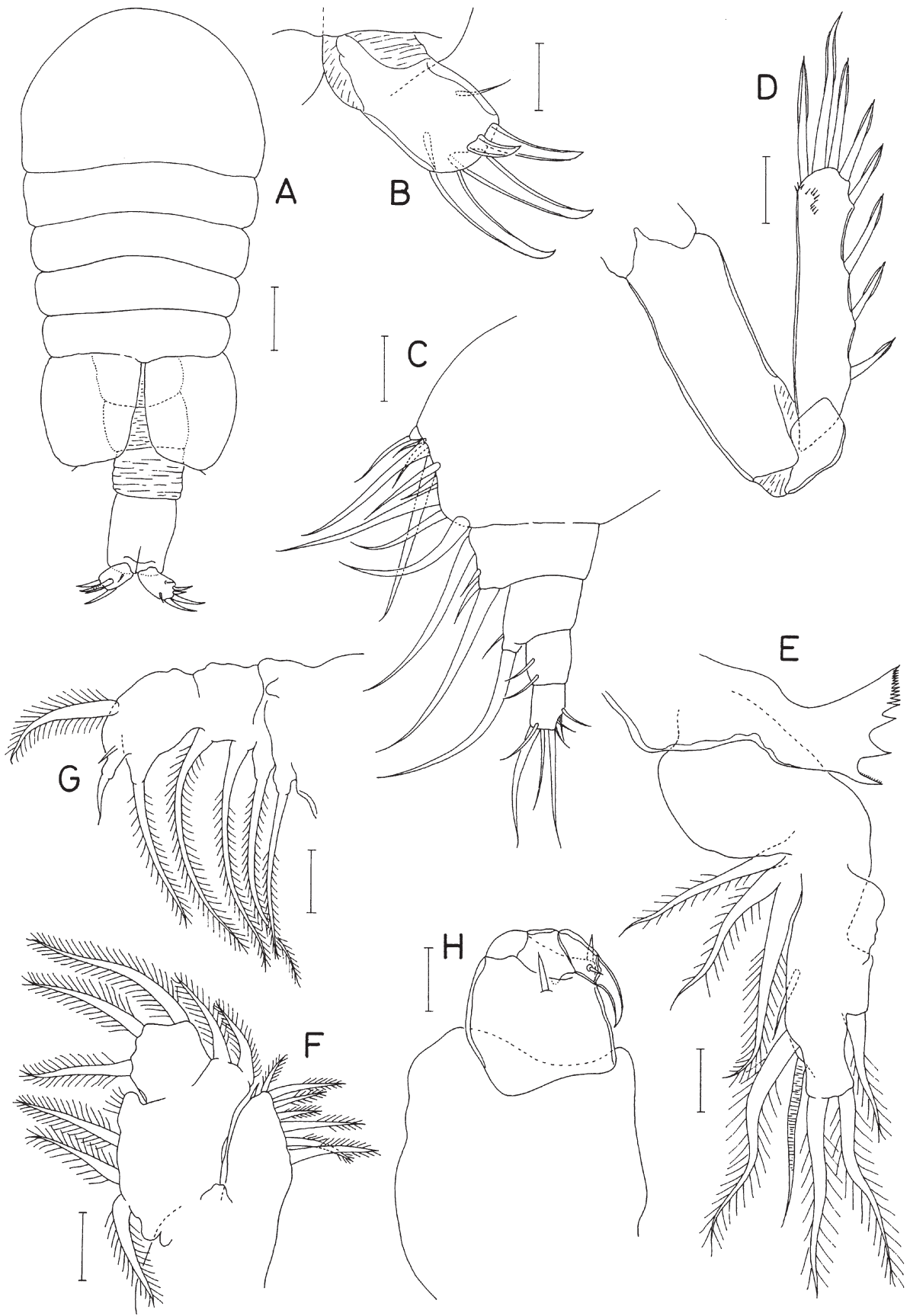
**Description of female.** Body (Fig. 77A) dorsoventrally depressed, with soft exoskeleton; body length 1.94 mm. Anterior part of body gradually narrowing posteriorly, distinctly 5-segmented; last metasomite consisting of fused fourth and fifth pedigerous somites. Cephalosome 519×778 μm, with broadly rounded anterior margin. Posterior part of body consisting of genital somite and 3-segmented abdomen; genital and first 2 abdominal somites extremely soft, flexible. Genital apertures not seen. Caudal rami divergent; each ramus (Fig. 77B) about 130×72 μm, armed with 4 distal claws and 2 setae; lengths of claws 110, 115, 39, and 74 μm, respectively, from inner to outer.

Rostrum small, less than half length of first antennular segment, semicircular, slightly longer than wide. Antennule (Fig. 77C) 5-segmented, evenly tapering; articulation between first 2 segments indistinct; armature formula 10, 4, 2, 2, and 8. Antenna (Fig. 77D) consisting of coxa, basis, and 2-segmented endopod; proximal 3 segments unarmed; second endopodal segment about 4 times longer than wide (185×46 μm), as long as basis; armed with 8 spines; longest second outer spine on distal margin 123 μm long, 0.66 times as long as segment.

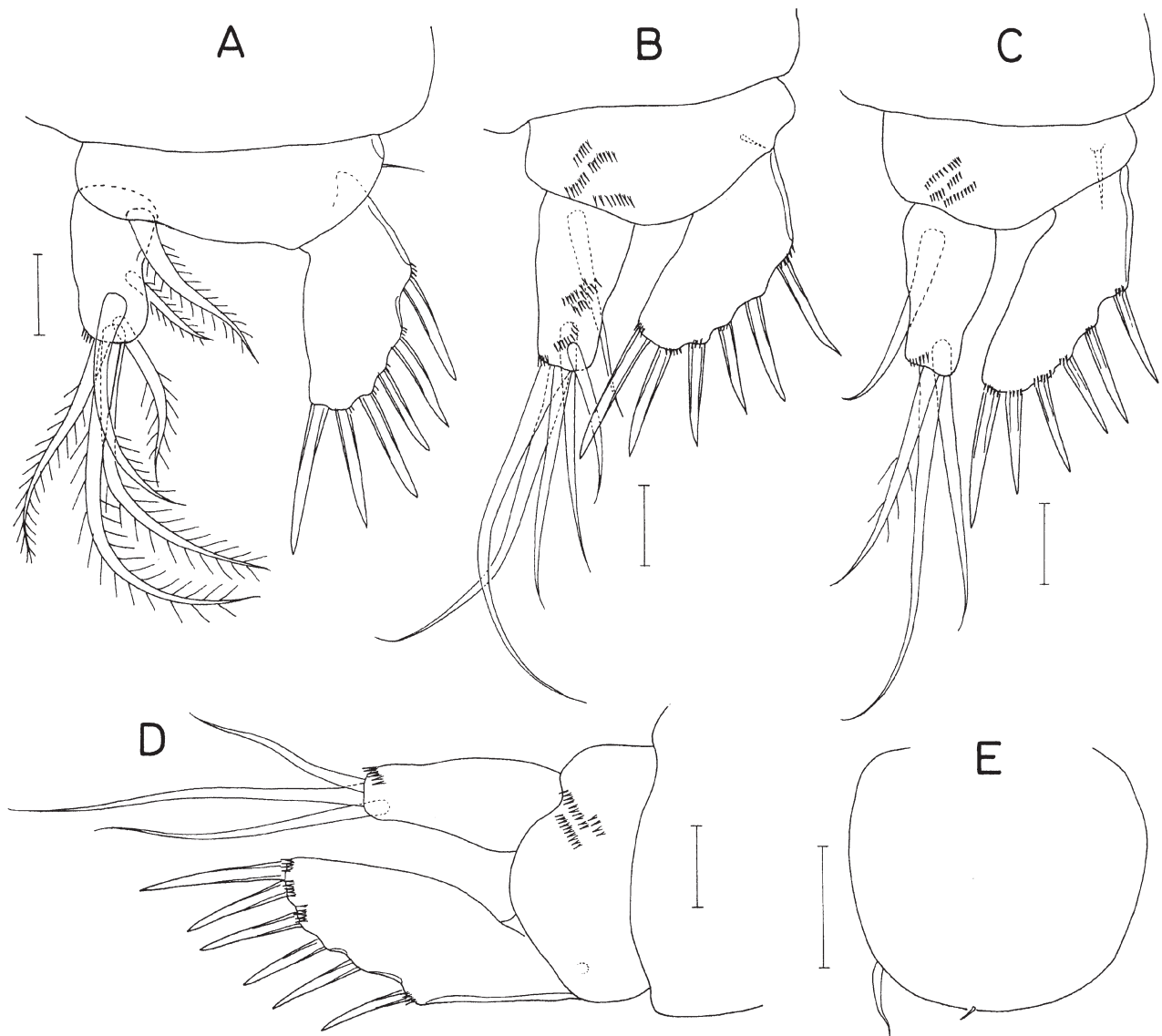
Labrum very weak, flexible. Mandible (Fig. 77E) with 3 teeth on coxal gnathobase; palp with 9 setae arranged as 3, 1, 1, 2, and 2. Maxillule (Fig. 77F) with 8 setae (including minute distalmost seta) on precoxal arthrite, 5 setae (2 inner and 3 outer) on basis, and 3 setae on endopod. Maxilla (Fig. 77G) 3-segmented with incomplete articulation between basis and endopod; armed with 2, 2, and 4 setae on proximal to distal segments. Maxilliped (Fig. 77H) 4-segmented; syncoxa unarmed; basis with 2 setae; first endopodal segment unarmed; second endopodal segment with 1 small seta; terminal claw longer than second endopodal segment.

Legs 1-4 (Fig. 78A-D) biramous with 1-segmented rami; coxa unarmed; basis with small outer seta. Exopods of legs 1-4 each with 6 slender spines. Seven setae on endopod of leg 1 comprising 1 unilaterally pinnate and 6 pinnate setae. Armature formula for legs 1-4 as follows:





**FIG. 77.** *Schizoproctus mollis* sp. nov., female. A, habitus, dorsal; B, caudal ramus; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, maxilliped. Scale bars: A, 0.2 mm; B-H, 0.05 mm.



**FIG. 78.** *Schizoproctus mollis* sp. nov., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: A-D, 0.05 mm; E, 0.2 mm.

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	VI	7
Leg 2	0-0	1-0	VI	6
Leg 3	0-0	1-0	VI	4
Leg 4	0-0	0-0	VI	3

Leg 5 (Fig. 78E) large, lamellate, subcircular, wider than long,  $463 \times 504 \mu\text{m}$ , with 1 seta at outer distal corner and 1 minute setal vestige on middle of distal margin. Leg 6 not seen.

**Male.** Unknown.

**Remarks.** The setation of the endopods of legs 2-4 characterizes *S. mollis* sp. nov. because the pattern of 6, 4, and 3 setae is unique within the genus (Table 3). *Schizoproctus mollis* sp. nov. can be also distinguished from its congeners by the combination of a 3-segmented abdomen (shared only with *S. vestitus* and *S. tripartitus* sp. nov.), the possession of 4 claws and 2 setae on the caudal ramus (compared to 4 claws and 1 seta in *S. vestitus*, and 5 claws and 1 seta in *S. tripartitus* sp. nov.), and by having 2 setae on leg 5 (compared to 1 seta in *S. vestitus* and 4 setae in *S. tripartitus* sp. nov.).

***Schizoproctus fijiensis* sp. nov.**

(Figs. 79, 80)

**Type material.** Holotype ♀ (MNHN-IU-2018-1983, dissected and mounted on a slide) from *Culeolus recumbens* Herdman, 1881 (MNHN-IT-2008-2479 = MNHN S2/CUL/47); Ride de Lau, Fiji, BORDAU 1 cruise, RV “Alis”, Stn CP1415 (16°31'S, 179°00'W), depth 670-682 m, Bouchet, Warén & Richer-IRD coll., 27 February 1999.

**Etymology.** The name of the type locality provides the name of the new species.

**Description of female.** Body (Fig. 79A) dorsoventrally flattened, consisting of broader anterior and narrower posterior parts, with weak exoskeleton. Body length 1.69 mm and maximum width 625 µm across cephalosome. Anterior part distinctly 5-segmented; fifth pedigerous somite completely fused with fourth pedigerous somite. Posterior part of body consisting of genital somite and 4-segmented abdomen. Genital somite much wider than long. Anal somite about 1.4 times longer than wide, twice as long as third abdominal somite. Caudal ramus (Fig. 79B) about 1.3 times longer than wide (81×62 µm), armed with 4 claws and 1 seta, and ornamented with fine spinules ventrally on inner distal surface; lengths of 4 claws 73, 64, 59, and 35 µm from inner to outer, respectively.

Rostrum (Fig. 79C) much wider than long, with rounded apex and ornamented distally with minute spinules on lateral margins. Antennule (Fig. 79D) strongly tapering, 5-segmented, but articulation between first and second segments indistinct; armature formula 12, 5, 2, 3, and 8. Left antenna (Fig. 79E) 4-segmented; proximal 3 segments unarmed; terminal segment (second endopodal segment) as long as basis, armed with 8 spines; 3 proximal inner spines as long as segment width; fourth inner spine smallest; second outer spine on distal margin longest, 89 µm long. Terminal segment of right antenna (Fig. 79F) as long as that of left antenna, but armed with 7 spines (lacking small fourth inner spine of left antenna); longest second outer spine on distal margin 86 µm long.

Labrum (Fig. 79G) weak, flexible, subdivided into wider proximal and thin-walled, semicircular distal parts, with weak dorsal protuberance in middle. Mandible (Fig. 79H) consisting of coxa and palp: coxal gnathobase (Fig. 79I) specialized, with medial margin bearing 9 teeth; distalmost tooth elongate, close to second tooth, thin, bearing fine spinules along proximal margin; second and third distal teeth strong, widely separated from each other; proximal 6 teeth smaller, finely bifid at tip; palp armed with 9 setae arranged as 3, 2, 2, and 2. Maxillule (Fig. 79J) with 8 distinct setae on precoxal arthrite, 1 small seta representing coxal epipodite, 5 setae (2 inner and 3 outer) and prominent distal tubercle on basis, and 3 setae on endopod. Maxilla (Fig. 79K) indistinctly 3-segmented, armed with 3, 3, and 4 setae on first to third segments, respectively; shortest seta on third segment spiniform. Maxilliped (Fig. 80A) robust, consisting of syncoxa, basis, and 2-segmented endopod; syncoxa with 2 large setae on inner side; basis with 2 unequal setae; first endopodal segment short and unarmed; second endopodal segment bearing 2 small setae and 1 spinule; terminal claw completely fused with segment.

Legs 1-3 (Fig. 80B-D) and leg 4 biramous with unsegmented rami; coxa unarmed; basis with small outer seta. Endopods tapering, much smaller than exopods. Exopods of legs 1-4 each armed with 6 distinct spines. Leg 4 armed as in leg 3. All setae on endopods pinnate. Armature formula for legs 1-4 as follows:

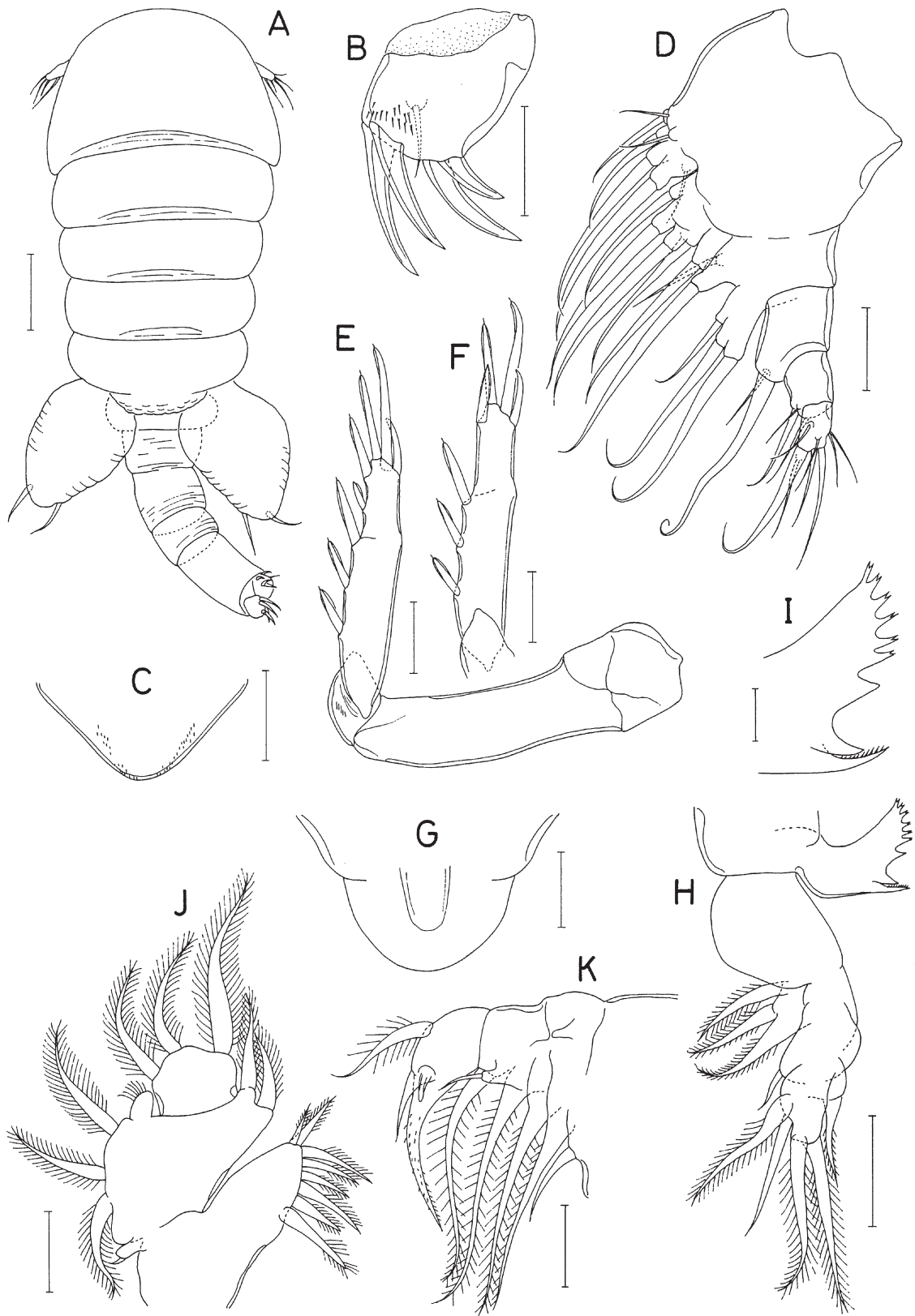
	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	VI	8
Leg 2	0-0	1-0	VI	3
Legs 3 & 4	0-0	1-0	VI	2

Leg 5 (Fig. 80E) fleshy, lamellate, oval, 404×308 µm, with 2 small and 2 larger setae, 3 located distally and 1 on ventral margin. Leg 6 not observed due to damage to genital somite during dissection.

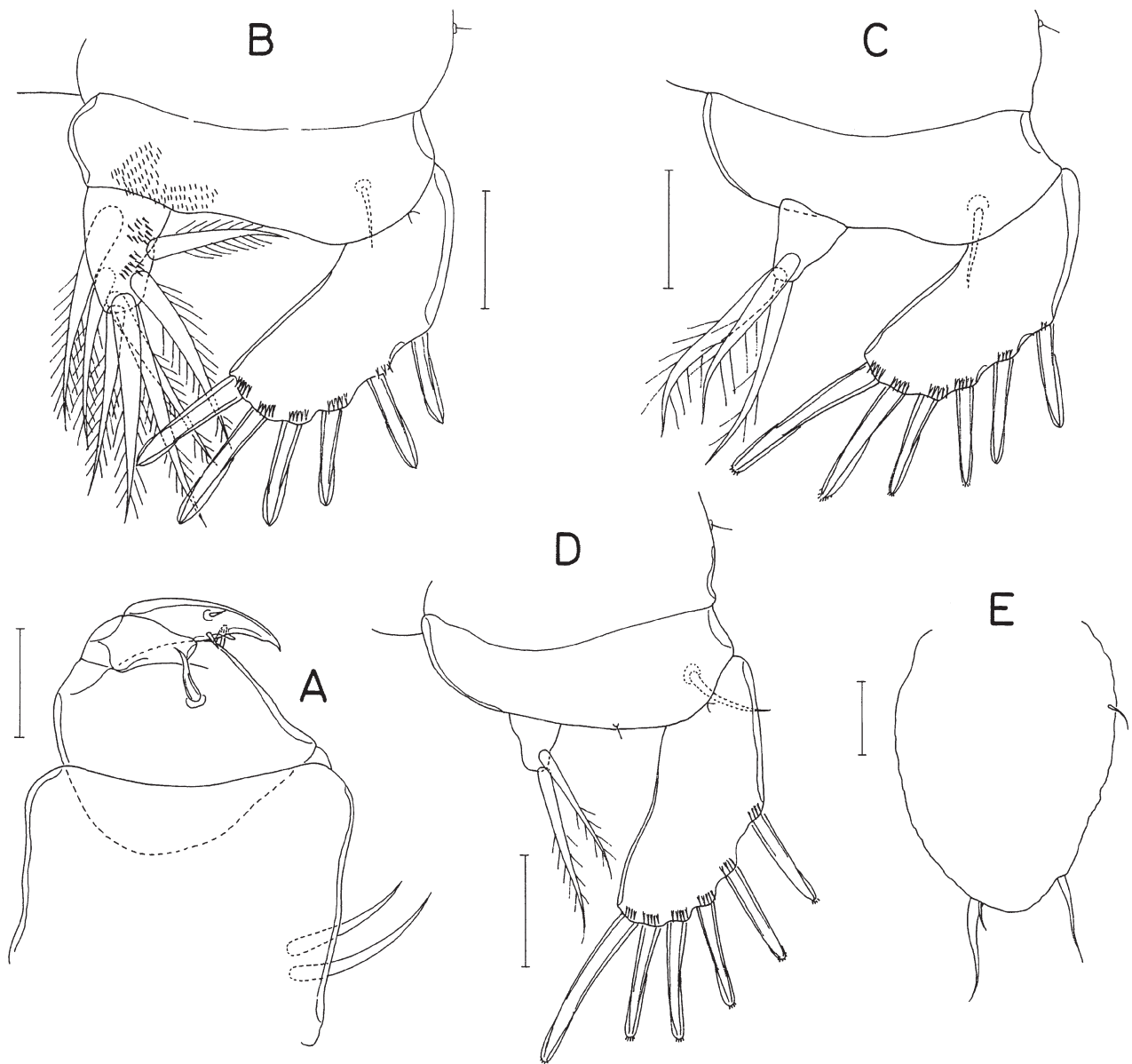
**Male.** Unknown.

**Remarks.** The medial, cutting margin of the coxal gnathobase of the mandible of *Schizoproctus* typically bears 3 or 4 distal teeth and has a pectinate proximal part (carrying an array of fine spinules). In contrast, the medial margin of the coxal gnathobase of *S. fijiensis* sp. nov. is armed with 3 distal teeth and a proximal array of 6 bifid teeth. This specialized form of the coxal gnathobase has not been found previously within the family Botryllophilidae and thus serves to characterize *S. fijiensis* sp. nov. Additional diagnostic features of *S. fijiensis* sp. nov. include, (1) the endopods of legs 2-4 are tapering and much smaller than the exopods; (2) the numbers of setae on the endopods of

legs 1-4 are 8, 3, 2, and 2, respectively, which is a unique combination within the genus; (3) leg 5 is elliptical; and (4) the two setae on the syncoxa (first segment) of the maxilliped are relatively large, half as long as the width of the syncoxa.



**FIG. 79.** *Schizoproctus fijiensis* sp. nov., female. A, habitus, dorsal; B, caudal ramus; C, rostrum; D, antennule; E, left antenna; F, endopod of right antenna; G, labrum; H, mandible; I, coxal gnathobase of mandible; J, maxillule; K, maxilla. Scale bars: A, 0.2 mm; B-F, J, K, 0.05 mm; G, I, 0.02 mm.



**FIG. 80.** *Schizoproctus fijiensis* sp. nov., female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 5. Scale bars: A-D, 0.05 mm; E, 0.1 mm.

***Schizoproctus pinguis* sp. nov.**

(Figs. 81-84)

**Type material.** Holotype ♀ (MNHN-IU-2018-1984), 1 ♀, and 2 ♂♂ intact paratypes (MNHN-IU-2018-1985) and 1 ♀, 1 ♂ paratypes (dissected, MNHN-IU-2014-17379) from *Aplidium hians* (Monniot F. & Gail), 1978 (MNHN-IT-2008-445 = MNHN A1/SID.B/16); East Kerguelen Is., MD04-BENTHOS cruise, R.V. “Marion Dufresne”, Stn CP13 (49°32-33’S, 70°57’E), depth 149-155 m, Boury-Esnault coll., 22 February 1975.

**Etymology.** The name of the new species is derived from the Latin *pingu* meaning “stout” and refers to the stout body of the female.

**Description of female.** Body (Fig. 81A) stout, consisting of broader anterior and narrower posterior parts; body length 1.31 mm and maximum width 464 µm. Anterior part of body unsegmented, with parallel lateral margins and rounded anterior margin, showing vestiges of suture lines on dorsal surface. Fourth and fifth pedigerous somites not defined from each other; legs 4 and 5 positioned in same transverse plane. Posterior part of body (Fig. 81B) distinctly 5-segmented, consisting of genital and 4 abdominal somites. Genital somite about 110×243 µm; genital apertures large, positioned dorsally. Four abdominal somites 68×186, 57×166, 57×157, and 159×141 µm, respectively. Caudal rami divergent; each ramus (Fig. 81C) 77×50 µm, armed with 4 claws and 2 setae; lengths of claws 59, 54, 29, and 26 µm, respectively, from inner to outer.

Rostrum (Fig. 81D) small, semicircular, with 2 patches of spinules on ventral surface. Antennule (Fig. 81E) 5-segmented; first segment expanded, comprising about half length of entire limb; articulation between two terminal segments indistinct; armature formula 13, 4, 3, 4, and 7+aesthetasc. Antenna (Fig. 81F) 4-segmented; coxa, basis, and first endopodal segment unarmed; second endopodal segment 3.3 times longer than wide (100×30 µm), slightly longer than basis; armed with 8 armature elements (6 spines and 2 setae), spines shorter than width of segment; 2 setae (2 outer elements on distal margin) 52 µm long (outermost) and 86 µm.

Labrum (Fig. 81G) strongly tapering towards rounded posterior margin. Mandible (Fig. 81H) with 3 teeth on medial margin of coxal gnathobase; palp with 9 setae, as usual for genus. Maxillule (Fig. 81I) with 7 setae (third distal seta minute) on precoxal arthrite, 1 small seta representing coxal epipodite, 2 medial and 3 outer setae on basis, and 3 setae on endopod. Maxilla (Fig. 81J) 2-segmented; proximal segment with 2 large setae; distal segment with 6 setae, second distal seta vestigial. Maxilliped (Fig. 82A) robust, 4-segmented; syncoxa and basis each with 2 setae; first endopodal segment unarmed; second endopodal segment with 2 small setae subdistally; terminal claw bearing 2 denticles proximally and 2 subdistally.

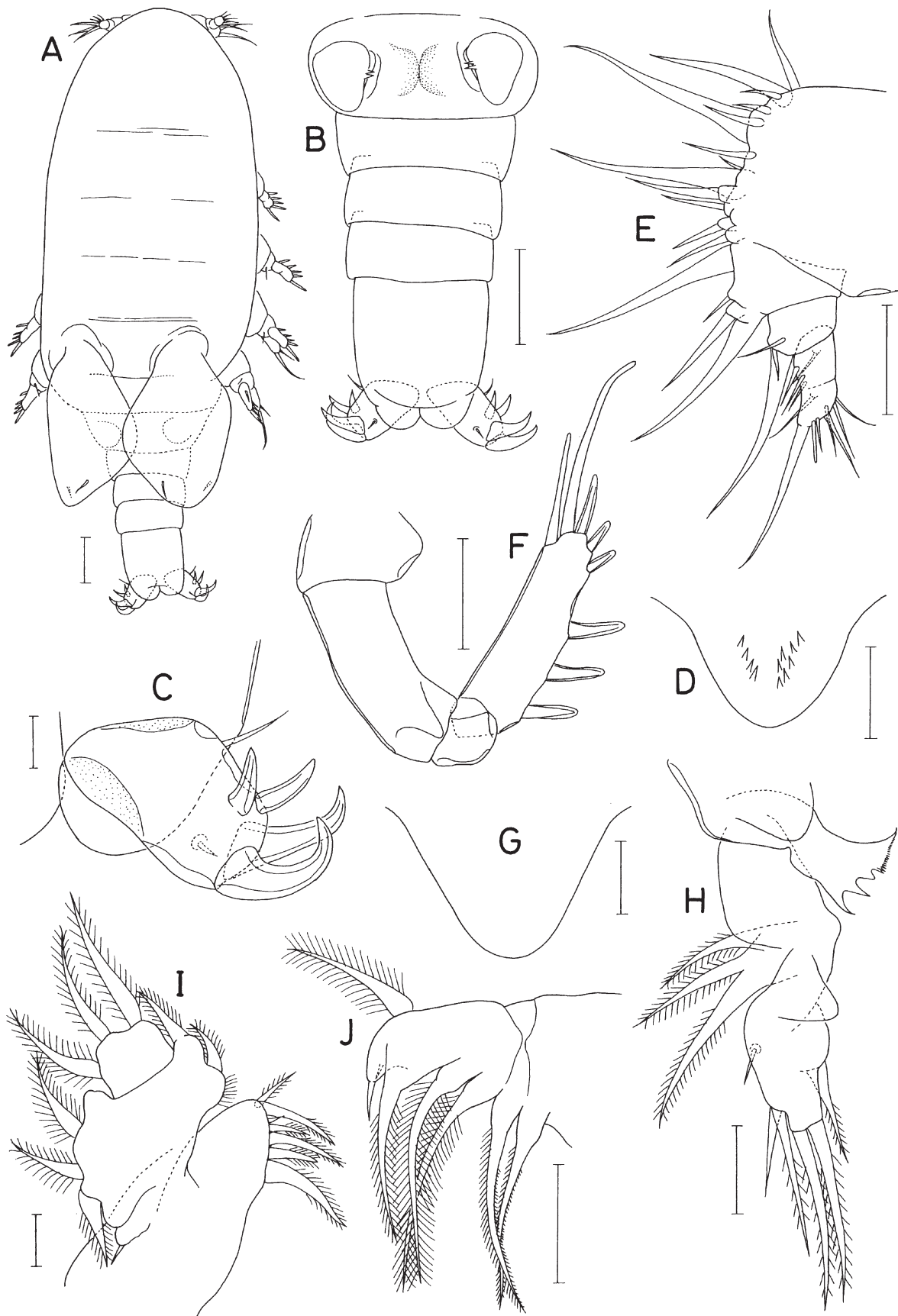
Legs 1-3 (Figs. 82B-D) and leg 4 biramous with unsegmented rami. Leg 1 with defined coxa and basis, but protopod of legs 2-4 not segmented. Exopods and endopods subequal in length. Exopods each armed with 5 spines. All setae on endopods naked. Legs 3 and 4 with same structure. Armature formula for legs 1-4 as follows:

	Protopod	Exopod	Endopod
Leg 1	1-0	V	8
Leg 2	1-0	V	3
Legs 3 & 4	1-0	V	2

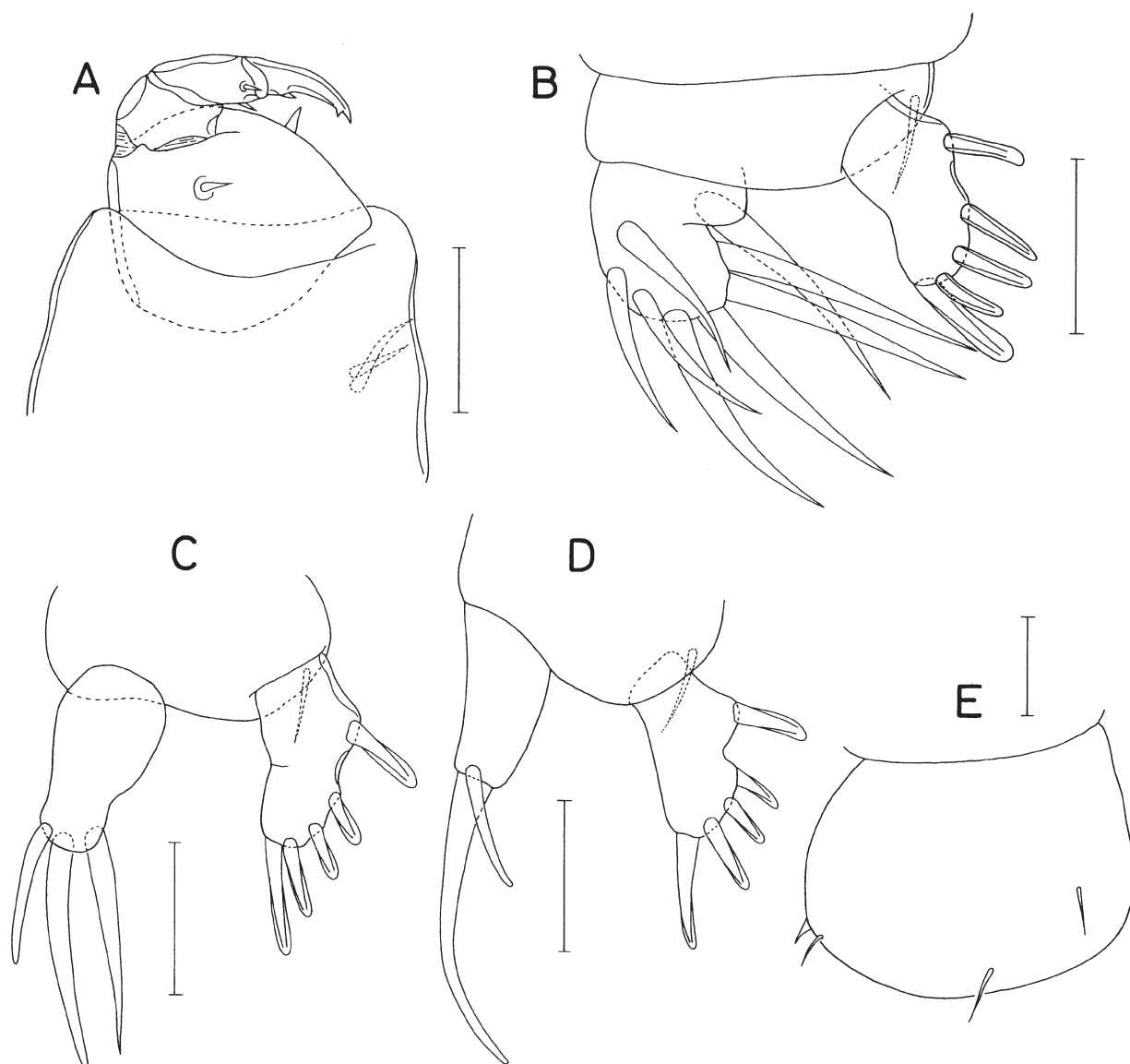
Leg 5 (Fig 82E) inserted into dorsal surface of body, lamellate, wider than long (239×333 µm), armed with 4 small setae, 2 (1 thick and 1 slender) positioned close to each other on ventrodistal margin. Leg 6 represented by 2 spinules on genital operculum.

**Description of male.** Body (Fig. 83A) narrow, distinctly segmented, consisting of well-defined prosome and urosome: body length 797 µm and maximum width 249 µm. Prosome 497 µm long, consisting of cephalothorax and 3 free pedigerous somites. Cephalothorax 278 µm long, with dorsal suture line between cephalosome and first pedigerous somite. Urosome (Fig. 83B) 5-segmented; fifth pedigerous somite 79 µm wide; genital somite 90×89 µm, with well-developed genital opercula. Three abdominal somites 38×58, 27×50, and 73×44 µm, respectively; anal somite with row of minute spinules on ventral surface near base of caudal rami. Caudal ramus 2.6 times longer than wide (52×20 µm); setation uncertain due to damage.

Rostrum narrower than that of female. Antennule (Fig. 83C) 4-segmented; first segment with 5 setae and numerous (more than 130) aesthetascs; second segment with 15 setae or aesthetascs (setae difficult to distinguish from aesthetascs); third segment with 3 setae and 1 broad aesthetasc; terminal segment with 6 setae and 4 aesthetascs (including 2 broad ones). Antenna as in female.



**FIG. 81.** *Schizoproctus pinguis* **sp. nov.**, female. A, habitus, dorsal; B, posterior part of body, dorsal; C, caudal ramus; D, rostrum; E, antennule; F, antenna; G, labrum; H, mandible; I, maxillule; J, maxilla. Scale bars: A, B, 0.1 mm; C, D, I, 0.02 mm; E-H, J, 0.05 mm.



**FIG. 82.** *Schizoproctus pinguis* sp. nov., female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 5. Scale bars: A-D, 0.05 mm; E, 0.1 mm.

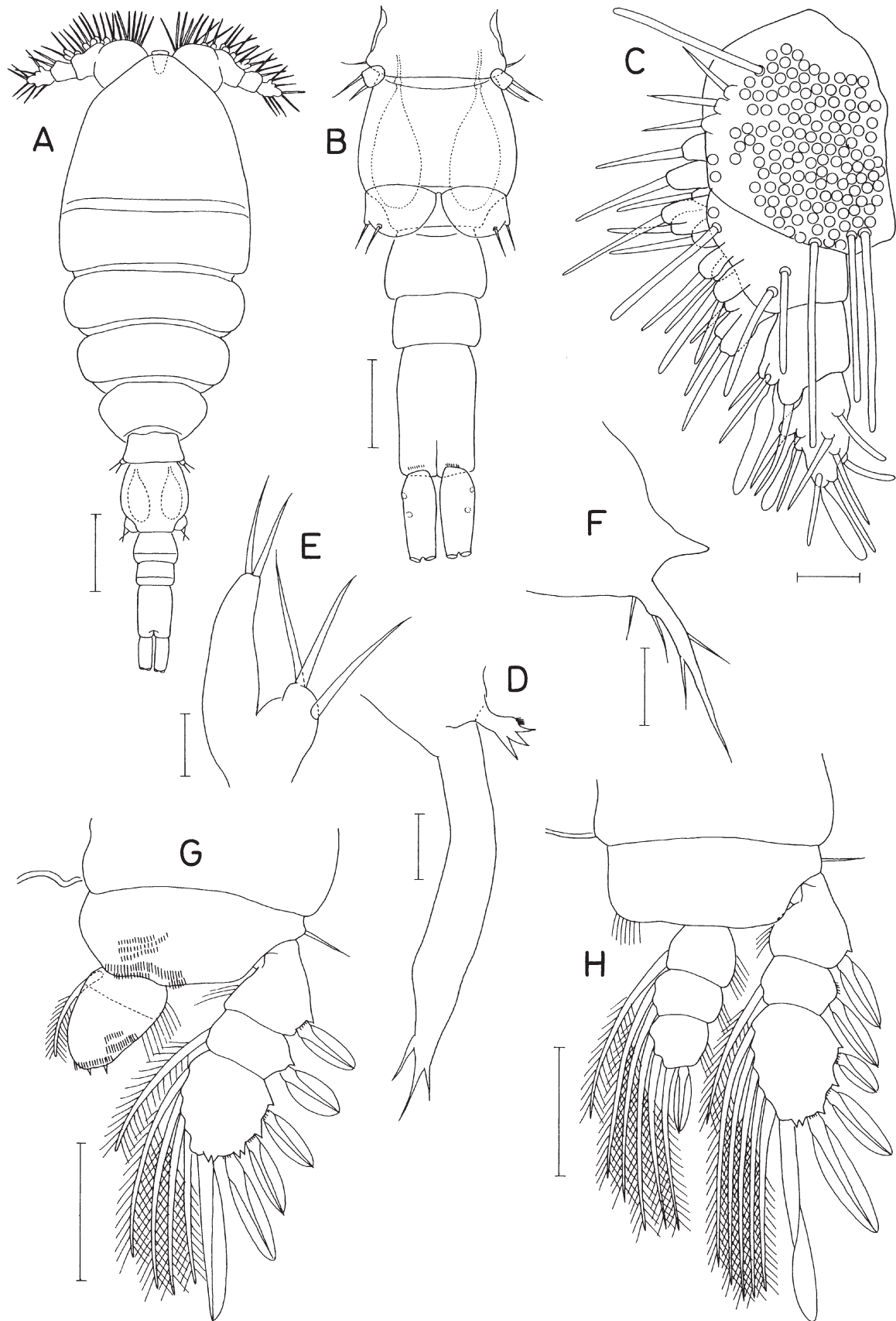
Labrum missing. Mouthparts extremely small, feeble and transparent. Mandible (Fig. 83D) consisting of coxa and palp; coxa small, stellate, bearing 3 teeth and several minute spinules; palp elongate, trifurcate (or with 3 setae) distally. Maxillule (Fig. 83E) bilobed; longer lobe tipped with 2 setae and shorter lobe with 3 setae. Maxilla (Fig. 83F) unequally bilobate, with short tapering lobe and elongated lobe bearing 4 setae and seta-like distal part. Maxilliped as in female but more slender.

Legs 1-4 (Figs. 83G, H, 84A, B) biramous with well-defined coxa and basis. Legs 1 and 2 with unarmed coxa, but coxa of legs 3 and 4 each with inner seta. Basis of legs 1-4 with small outer seta. Exopods 3-segmented in legs 1-4, distinctly longer than endopods. Endopods incompletely 2-segmented (articulation only on posterior surface) in leg 1, 3-segmented in legs 2 and 3, and 2-segmented in leg 4. Distal segment of leg 1 endopod with 2 minute, hardly visible setae. Armature formula for legs 1-4 as follows:

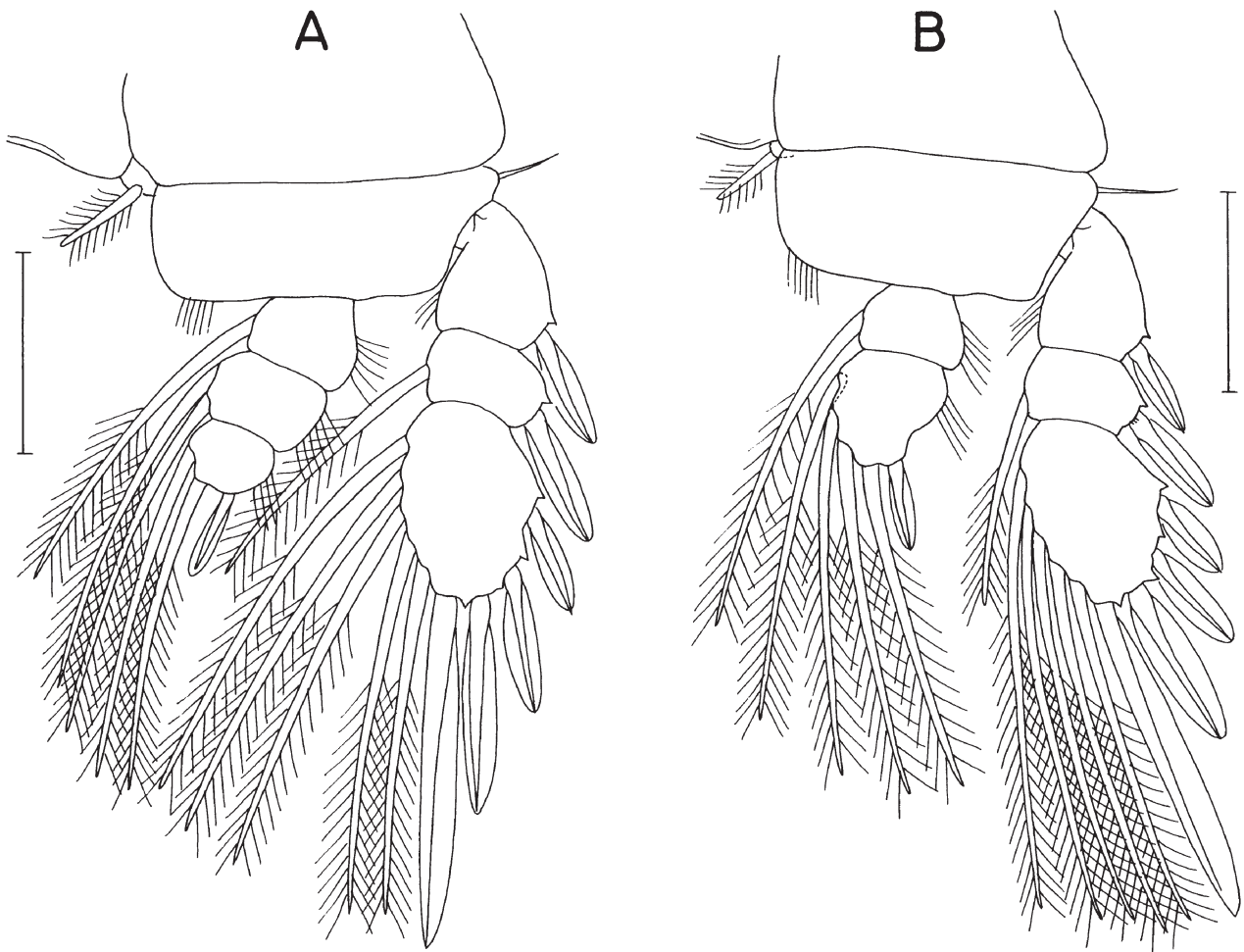
	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	I-0; I-1; III, I, 4	0-1; 2
Leg 2	0-0	1-0	I-0; I-1; III, I, 5	0-1; 0-2; I, 3
Leg 3	0-1	1-0	I-0; I-1; III, I, 5	0-1; 0-2; I, 2
Leg 4	0-1	1-0	I-0; I-1; III, I, 5	0-1; I, 4



Leg 5 (Fig. 83B) consisting of outer seta on fifth pedigerous somite and small, free exopodal segment bearing 2 setae distally. Leg 6 (Fig. 83B) represented by 2 setae on genital operculum



**FIG. 83.** *Schizoproctus pinguis* sp. nov., male. A, habitus, dorsal; B, urosome, ventral; C, antennule; D, mandible; E, maxillule; F, maxilla; G, leg 1; H, leg 2. Scale bars: A, 0.1 mm; B, G, H, 0.05 mm; C, D, F, 0.02 mm; E, 0.1 mm.



**FIG. 84.** *Schizoproctus pinguis* **sp. nov.**, male. A, leg 3; B, leg 4. Scale bars: 0.05 mm.

**Remarks.** *Schizoproctus pinguis* **sp. nov.** resembles *S. fijiensis* **sp. nov.** in sharing the same armature formula (8, 3, 2, and 2) for the endopods of legs 1-4 but differs from the latter in many other respects. For example, the coxal gnathobase of the mandible of *S. pinguis* **sp. nov.** is not specialized as in *S. fijiensis* **sp. nov.**, the exopods of legs 1-4 are armed with 5 spines (cf. 6 spines in *S. fijiensis* **sp. nov.**), and leg 5 is wider than long (cf. longer than wide in *S. fijiensis* **sp. nov.**).

*Schizoproctus pinguis* **sp. nov.** shares some character states with *S. vestitus*, such as the setation of the exopods of legs 1-4, which bear 5 spines in both species. However, *S. vestitus* differs from *S. pinguis* **sp. nov.** in having a larger body, 7 mm long according to Aurivillius (1885) or 6.1 mm according to Sars (1921), a 5-segmented abdomen, and in being armed with spines on the endopods of legs 1, 2, and 4 (leg 3 is unknown).

Numerous diatom frustules were observed in the gut of the examined female specimens of *S. pinguis* **sp. nov.** The atrophied mouthparts of the male suggest that the adult is a non-feeding stage.

### **Genus *Haplostomides* Chatton & Harant, 1924**

**Diagnosis.** Female: Body vermiform, unsegmented or incompletely segmented, indistinctly divisible into cephalosome, metasome, and genitoabdomen. Caudal rami usually fused with abdomen, armed with 1 terminal spine and 1 to 4 setae. Rostrum weakly developed. Antennule small, 1- to 5-segmented. Antenna 2- or 3-segmented; terminal segment (endopod) armed with 2 to 4 spines. Labrum simple. Mandible 1- or 2-segmented, with 2 or 3 setae on distal segment, rarely with 1 seta on proximal segment; mandible with rudimentary gnathobase in some species. Maxillule typically 2-segmented, consisting of precoxa and palp, bearing 2 to 5 setae on medial margin of precoxa

and 4 to 6 setae on palp. Maxilla as small lobe bearing 2 to 4 setae. Maxilliped consisting of coxa, basis, and 2-segmented endopod plus small terminal claw. Legs 1-4 consisting of unsegmented protopod, exopod, and endopod. Protopods with or without outer margin seta. Exopods with 1 seta and 2 to 5 spines; 2 distal spines occasionally fused at base to form bifurcate spine. Endopods lobate, unarmed, sometimes vestigial. Leg 5 reduced to small lobe bearing 2 to 4 setae.

Male (based on *Haplostomides scotti* Chatton & Harant, 1924): Body cycloform, distinctly segmented, consisting of cephalosome, 4-segmented metasome, and 6-segmented urosome. Caudal ramus with 5 setae. Antennule 4-segmented, with numerous aesthetascs on first segment. Antenna 3-segmented, similar to that of female. Mandible, maxillule, and maxilla degenerated. Maxilliped similar to that of female. Legs 1-4 biramous. Leg 1 with 3-segmented exopod and transformed 1-segmented endopod. Legs 2 and 3 with 3-segmented rami. Leg 4 with 3-segmented exopod and 2-segmented endopod. Inner coxal seta absent in legs 1 and 2, but present in legs 3 and 4. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-0	1-0	I-0; I-0; III, I, 4	II, 6
Leg 2	0-0	1-0	I-0; I-1; II, I, 5	0-1; 0-2; 0, II, 3
Leg 3	0-1	1-0	I-0; I-1; II, I, 5	0-1; 0-2; 0, II, 2
Leg 4	0-1	1-0	I-0; I-1; II, I, 5	0-1; 0, II, 3

Leg 5 consisting of obscure protopod bearing 1 seta and free exopodal segment bearing 2 setae. Leg 6 represented by 2 setae on distal margin of genital operculum.

**Type species.** *Haplostomides scotti* Chatton & Harant, 1924, by original designation.

**Remarks.** Marchenkov & Boxshall (2003) mentioned that species of *Haplostomides* differ from one another in details of the antennae, mandibles, maxillules and maxillae, and other limbs have little taxonomic value at the species level. Key character states of the ten known and the three new species described below are summarized in Table 4.

**TABLE 4.** Appendage armature of *Haplostomides* species. (Roman numerals denote spines, Arabic numerals denote setae; abbreviations: exp = exopod).

Species	Caudal ramus	Antenna	Mandible	Maxillule	Maxilla	Legs 1-4 exp
<i>H. amarouci</i> (Blake, 1929)	I+3?	IV	3	5+4	3	IV-III-II-II
<i>H. bellus</i> Ooishi & Illg, 1977	I+2	IV	1+2	5+5	3	IV-III-III-III
<i>H. brementi</i> Chatton & Harant, 1924	I+1	IV	2	3+5	2	IV-III-II-II
<i>H. gottoi</i> Ooishi, 2008	I+2	IV	3	3+6	2	V-IV-III-III
<i>H. hawaiiensis</i> Ooishi, 1994	I+2	II	3	3+4	2	II-II-II-II
<i>H. hibernicus</i> (Scott T. & A. 1895)	I+2	II	3	2+4	2	V-IV-III-III
<i>H. luteolus</i> Ooishi & Illg, 1977	I+2	IV	1+3	5+5	4	IV-III-II-II
<i>H. otagoensis</i> Ooishi, 2001	I+2	IV	3	4+5	1+2	IV-III-II-II
<i>H. sanamyani</i> Marchenkov & Boxshall, 2003	I+3	IV	3	4+5	3	IV-III-II-II
<i>H. scotti</i> Chatton & Harant, 1924	I+4	IV	3	4+5	2	IV-III-III-III
<i>H. similis</i> <b>sp. nov.</b>	I+2	II	3	2+5	2	II-II-II-II
<i>H. bermudensis</i> <b>sp. nov.</b>	I+2	IV	2	3+5	2	II-III-II-II
<i>H. partitus</i> <b>sp. nov.</b>	I+1	IV	2	5	9	II-II-II-II

## *Haplostomides scotti* Chatton & Harant, 1924

(Figs. 85, 86)

**Material examined.** 4 ♀♀ (MNHN-IU-2018-1986, 2 ♀♀ dissected) from *Polychinum aurantium* Milne Edwards, 1841; Saint-Vaast-la-Hougue, Atlantic coast of France, Monniot coll.

**Supplementary redescription of female.** Body (Fig. 85A) maggot-shaped, narrowing anteriorly, consisting of cephalosome, incompletely 5-segmented metasome and 2-segmented genitoabdomen. Body length 1.48 mm; maximum width 0.46 mm (across middle). Anterior half of metasome narrowing anteriorly; cephalosome 150×235 µm, much narrower than first pedigerous somite. Pedigerous somites defined by constrictions. Genitoabdomen (Fig. 85B) distinctly bipartite with parts defined by deep constriction; anterior part strongly tapering posteriorly, subdivided by trace of transverse suture line; posterior part (anal somite) narrowing anteriorly. Caudal ramus (Fig. 85C) conical, not articulated from anal somite, as long as wide, armed with 1 triangular spine distally plus 4 setae (2 outer, 1 dorsal, and 1 inner subdistal); distal spine broader than long.

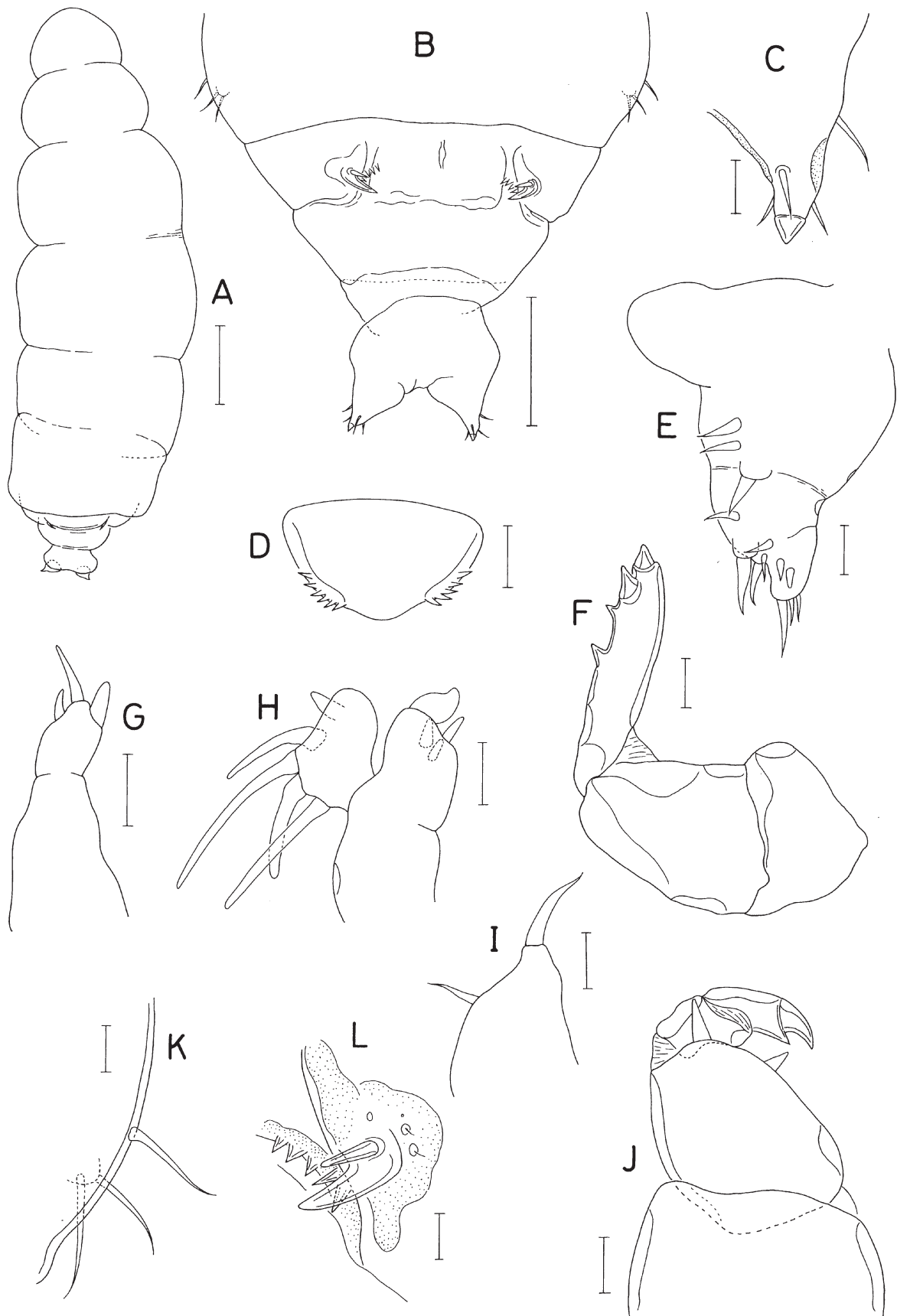
Rostrum (Fig. 85D) wider than long (19×32 µm), nearly triangular, with blunt apex, ornamented with 5 or 6 denticles subdistally on lateral margins. Antennule (Fig. 85E) unsegmented, but with traces of 2 articulations, distinctly tapering, with large protuberance on proximal ventral margin, and armed with 13 small setae (arranged as 3, 3, and 7). Antenna (Fig. 85F) 3-segmented, consisting of coxa, basis, and endopod; coxa and basis unarmed; endopod slightly longer than basis, bearing 4 spines (2 proximal spines smaller, not articulated at base, dentiform).

Labrum small, unornamented, with convex posterior margin. Mandible (Fig. 85G) incompletely 2-segmented, digitiform, with 3 blunt setae on distal segment. Maxillule (Fig. 85H) 2-segmented; proximal segment (precoxa) with 4 blunt setae on mediodistal surface, distalmost seta broad, leaf-like; distal segment (palp) originating on outer margin of proximal segment, broadening distally, bearing 5 bluntly tipped setae of unequal lengths, innermost shortest. Maxilla (Fig. 85I) lobate, tapering distally, with 2 setae (1 lateral and 1 distal). Maxilliped (Fig. 85J) consisting of 4 segments plus terminal claw; first segment (syncoxa) much wider than long, unarmed; second segment (basis) with 1 distal and 1 subdistal setae; third segment unarmed; fourth segment with pointed inner distal corner; terminal claw stout, shorter than fourth segment.

Leg 1 (Fig. 86A) consisting of protopod, exopod, and endopod. Protopod unarmed, with transverse sclerotized band. Exopod armed with 1 seta on outer margin, 2 small spines on subdistal outer margin, and 1 bifurcate spine distally. Endopod prominent, not articulated from protopod, unarmed and unornamented, as long as wide, with rounded distal margin. Leg 2 (Fig. 86B) broader than leg 1. Exopod armed with 1 seta, 1 small spine on subdistal outer margin and bifurcate distal spine. Endopod narrower than that of leg 1. Legs 3 and 4 same as leg 2 in form and armature. Leg 5 (Fig. 85K) consisting of 3 small equal setae on lateral margin of fifth pedigerous somite (2 located on small lobe). Leg 6 (Fig. 85L) represented by 1 spine and 1 larger, spiniform process on genital operculum; 5 tooth-like elements present on surface medial to leg 6.

**Male.** Ooishi (2002a) described the male of this species.

**Remarks.** *Haplostomides scotti*, the type species of the genus and first described by Chatton & Harant (1924b), was redescribed by Ooishi (2002a) on the basis of specimens taken from the *Polychinum aurantium* Milne Edwards, 1841. There are some minor discrepancies between our specimens and Ooishi's redescription. Firstly, Ooishi (2002a) did not figure or mention the presence of denticles on the lateral margins of the rostrum, which are quite distinct in our specimens. Secondly, the setae on the maxillule of our specimens are blunt and the distalmost seta on its proximal segment (precoxa) is broad, leaf-like, but in Ooishi's specimens the setae are generally attenuated and the distalmost seta on the first segment is vestigial. Thirdly, we observed 1 spine and 4 setae on the caudal ramus in our specimens whereas Ooishi described and figured 1 spine and 2 setae on the ramus. Because of the numerous similarities between the two sets of material, we consider that these discrepancies are likely to be due either to the state of the material observed or to variation. The similarities between Ooishi's specimens and ours include: (1) the shape of the genitoabdomen is consistent, i.e., the anterior and posterior parts are clearly demarcated by a deep constriction; (2) they both have a large proximal protuberance on the ventral margin of the antennule; and (3) the distalmost seta on the distal segment (palp) of the maxillule is much smaller than the proximal setae. In addition, both sets of material were found in the same host species, *Polychinum aurantium*, in the Northeast Atlantic.



**FIG. 85.** *Haplostomides scotti* Chatton & Harant, 1924, female. A, habitus, dorsal; B, genitoabdomen, dorsal; C, right caudal ramus, dorsal; D, rostrum; E, antennule; F, antenna; G, mandible; H, maxillule; I, maxilla; J, maxilliped; K, leg 5; L, genital aperture. Scale bars: A, 0.2 mm; B, 0.1 mm; C-L, 0.01 mm.

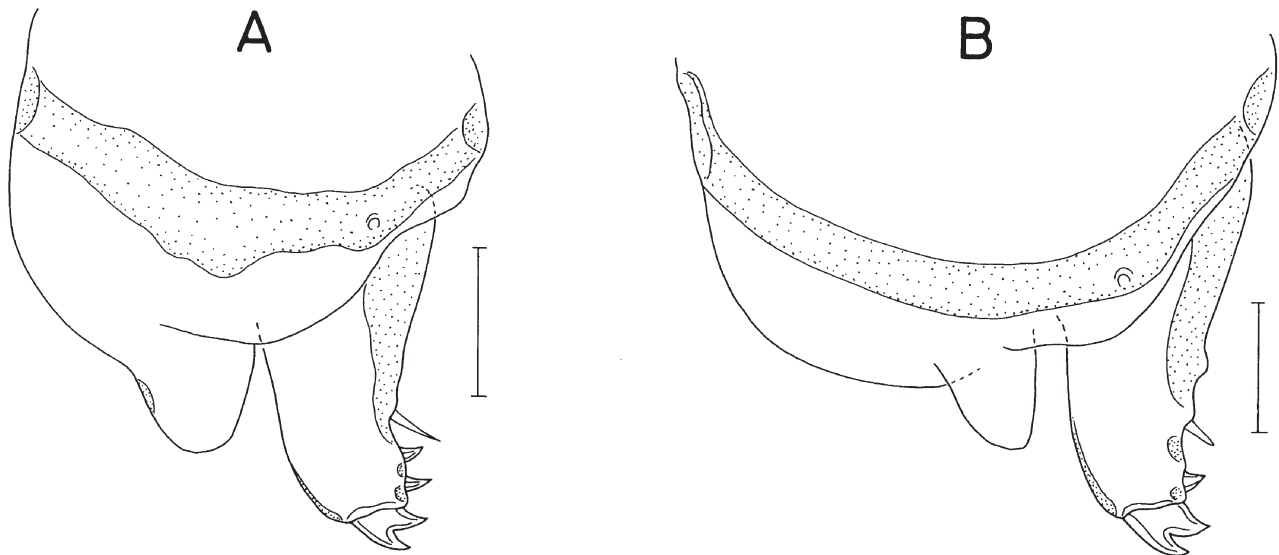


FIG. 86. *Haplostomides scotti* Chatton & Harant, 1924, female. A, leg 1; B, leg 2. Scale bars: 0.02 mm.

***Haplostomides similis* sp. nov.**

(Figs. 87, 88)

**Type material.** Holotype ♀ (MNHN-IU-2018-1987), 5 ♀♀ intact paratypes (MNHN-IU-2018-1988), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17380) from *Polyclinum macrophyllum* Michaelsen, 1919; New Caledonia, Stn NC6, Mont Dore devant Îlet Bailly, depth 0 m, Monniot coll., 20 August 1985.

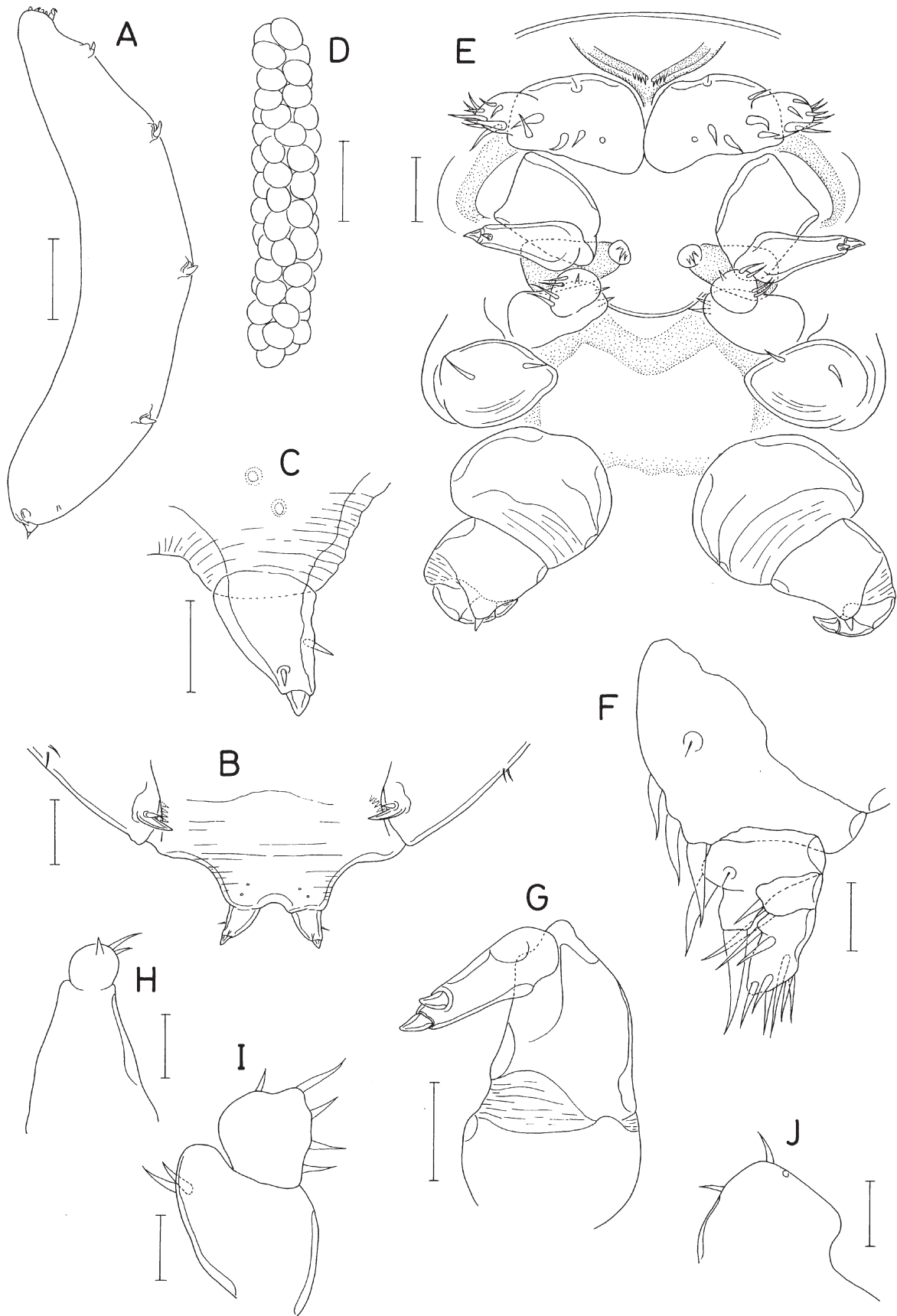
**Etymology.** The name of the new species reflects its close similarity to *H. hawaiiensis* Ooishi, 1994.

**Description of female.** Body (Fig. 87A) maggot-shaped, unsegmented, curved dorsally, gradually narrowing anteriorly. Body size variable; body length 3.53 mm in largest specimen. Legs 1-4 separated by intervals of 620, 870, and 970 µm; leg 4 isolated from posterior border of body by 970 µm. Genitoabdomen (Fig. 87B) very small, much wider than long, not demarcated from metasome. Caudal ramus (Fig. 87C) articulated from genitoabdomen, tapering, about 1.3 times longer than wide (29×22 µm), armed with 1 conical distal spine, 1 subdistal dorsal seta and 1 outer lateral seta. Egg sac (Fig. 87D) containing 3-5 rows of eggs, 2.16×0.43 mm in measured sample; each egg about 170 µm in diameter.

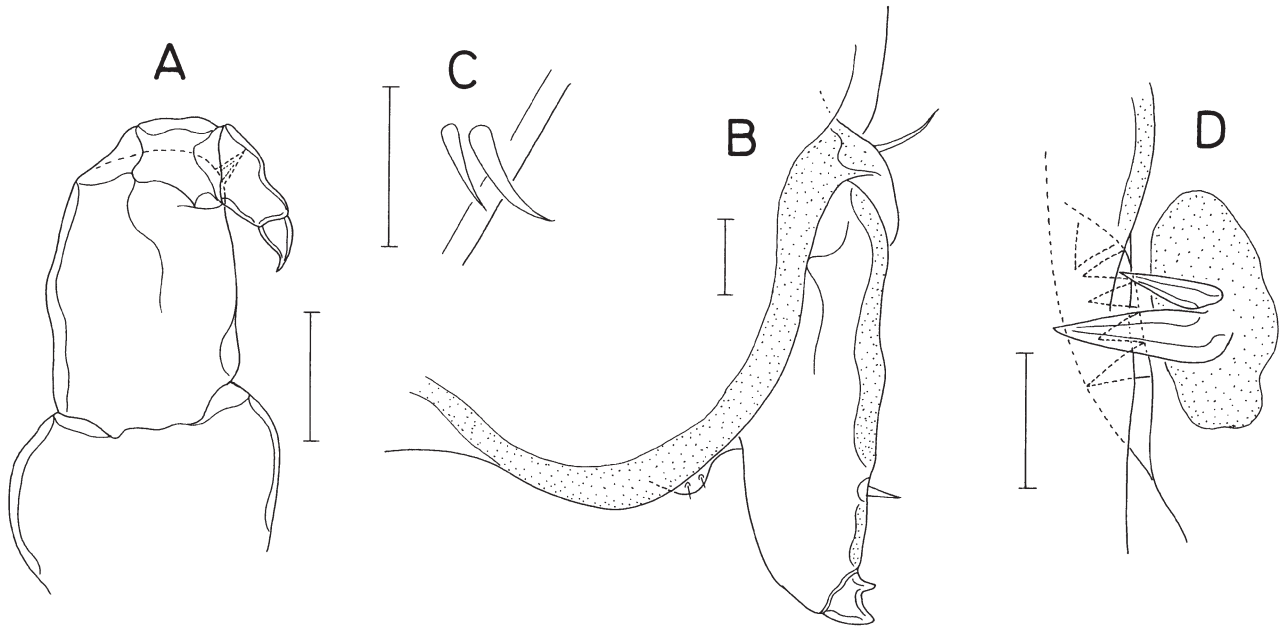
Rostrum absent, but rostral area sclerotized and ornamented with paired rows of 4 minute denticles (Fig. 87E). Antennule (Fig. 87F) indistinctly 4-segmented, with 3, 2, 2, and 8 setae on first to fourth segments, respectively; first segment much broader than distal segments; 2 setae on second segment larger than other setae. Antenna (Fig. 87G) 3-segmented, consisting of broad coxa and basis and narrow endopod; coxa and basis unarmed; endopod shorter than basis, 2.5 times longer than wide (30×12 µm), gradually narrowing distally, armed with distal and subdistal spines, both spines equal in size.

Labrum simple, unornamented, with convex posterior margin (Fig. 87E). Mandible (Fig. 87H) indistinctly 2-segmented; proximal segment tapering distally, unarmed; distal segment circular, much shorter than proximal segment, armed with 3 small setae distally. Maxillule (Fig. 87I) 2-segmented; proximal segment (precoxa) projecting mediolaterally, with 2 equal setae on subdistal medial margin; distal segment (palp) with 5 setae (3 on outer margin and 2 on distal margin). Maxilla (Fig. 85J) lobate with 2 small setae (1 on medial margin and 1 apically). Maxilliped (Fig. 88A) 4-segmented; first segment wider than long, unarmed; second segment with 1 seta at inner distal corner; short third segment unarmed; fourth segment also unarmed; terminal claw small, pointed distally.

Legs 1-4 identical in form and armature (Fig. 88B). Protopod with outer seta. Exopod with 1 subdistal seta and 1 bifurcate distal spine; outer branch of distal spine much smaller than inner branch. Endopod rudimentary, represented by small protuberance bearing 2 minute sensilla. Leg 5 (Fig. 88C) represented by 2 small setae on ventrolateral surface near posterior end of metasomal region (Fig. 87B). Leg 6 (Fig. 88D) probably represented by 2 spiniform elements in genital region accompanied by 5 dentiform elements.



**FIG. 87.** *Haplostomides similis* **sp. nov.**, female. A, habitus, right; B, genitoabdomen, dorsal; C, right caudal ramus, dorsal; D, egg sac; E, cephalic appendages *in situ*, ventral; F, antennule; G, antenna; H, mandible; I, maxillule; J, maxilla. Scale bars: A, D, 0.5 mm; B, 0.05 mm; C, E, G, J, 0.02 mm; F, H, I, 0.01 mm.



**FIG. 88.** *Haplostomides similis* **sp. nov.**, female. A, maxilliped; B, leg 1; C, leg 5; D, genital aperture. Scale bars: 0.02 mm.

**Male.** Unknown.

**Remarks.** According to the keys to species of *Halostomides* provided by Ooishi (1994) and by Marchenkov & Boxshall (2003), *H. similis* **sp. nov.** would be identified as *H. hawaiiensis* Ooishi, 1994, based on the shared possession of 2 spines on the antenna, 3 setae on the mandible, 7 setae on the maxillule, and 2 setae on the maxilla. However, there are several significant differences which confirm the distinct status of *H. similis* **sp. nov.**, as follows: (1) the maxillule of *H. hawaiiensis* bears 3 setae on the proximal segment and 4 setae on the distal segment, whereas the maxillule of *H. similis* **sp. nov.** bears 2 setae on the proximal segment and 5 setae on the distal segment; (2) the exopods of legs 1–4 of *H. similis* **sp. nov.** each bear 2 spines which are fused together at the base thus appearing as a single bifurcate spine, but in *H. hawaiiensis*, the 2 spines are separate; (3) leg 5 of *H. similis* **sp. nov.** is represented by 2 setae, but it consists of 3 setae in *H. hawaiiensis*; and (4) the antennule is 4-segmented in *H. similis* **sp. nov.**, although the segmentation is incomplete, but unsegmented in *H. hawaiiensis*.

*Haplostomides hawaiiensis* was originally described as an associate of *Polyclinum constellatum* Savigny, 1816 at Hawaii (Ooishi, 1994) and it was subsequently reported from the same host, an invasive species in the Gulf of California (Tovar et al., 2010). The new species is associated with *Polyclinum macrophyllum* collected in New Caledonia.

***Haplostomides bermudensis* sp. nov.**

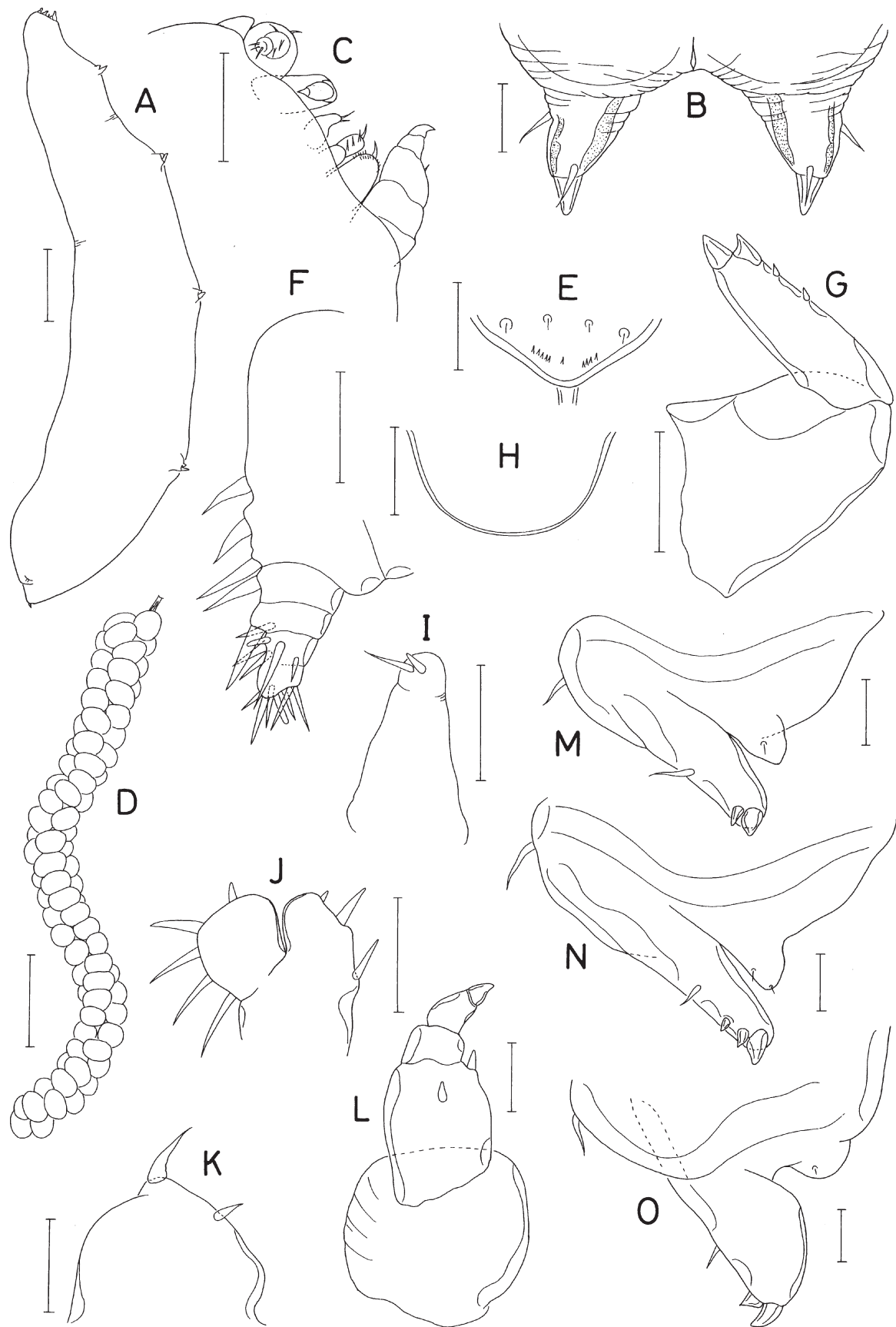
(Fig. 89)

**Type material.** Holotype ♀ (MNHN-IU-2018-1989), 4 ♀♀ paratypes (MNHN-IU-2018-1990), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17381) from *Polyclinum constellatum* Savigny, 1816 (MNHN-IT-2008-6981 = MNHN A1/POL.B/3); St David's I., Bermuda, 1970.

**Etymology.** The new species is named after its type locality.

**Description of female.** Body (Fig. 89A) similar to *H. similis* **sp. nov.** in form, unsegmented, curved dorsally, and narrowing anteriorly. Body length 4.20 mm; maximum width 0.97 mm in posterior quarter. Intervals between first to fourth legs 0.76, 0.98, and 1.21 mm, respectively. Genitoabdomen short, not defined from metasome. Caudal ramus (Fig. 89B) slightly wider than long (25×29 µm), indistinctly defined from genitoabdomen, armed with 1 distal spine and 2 setae (1 at proximal third of outer margin and 1 dorsal, subdistally); distal spine longer than wide (11×8 µm). Egg sac (Fig. 89D) 3.26×0.29 mm, containing 3 or 4 rows of eggs; each egg about 170 µm in diameter.





**FIG. 89.** *Haplostomides bermudensis* **sp. nov.**, female. A, habitus, right; B, caudal rami, dorsal; C, cephalic appendages, right; D, egg sac; E, rostrum; F, antennule; G, antenna; H, labrum; I, mandible; J, maxillule; K, maxilla; L, maxilliped; M, leg 1; N, leg 2; O, leg 3. Scale bars: A, D, 0.5 mm; B, E-O, 0.02 mm; C, 0.05 mm.

Rostrum (Fig. 89C, E) small, much wider than long, ornamented with minute spinules subdistally and 4 minute sensilla proximally. Antennule (Fig. 89F) 4-segmented; armature formula 3, 1, 2, and 10+2 aesthetascs; terminal segment subdivided by partial suture in middle of posterior side into parts bearing 4+aesthetasc and 6+aesthetasc. Antenna (Fig. 89G) 2-segmented; proximal segment (coxobasis) unarmed; distal segment (endopod) with 2 larger distal and 2 very small subdistal spines; all spines articulated at base.

Labrum (Fig. 89H) weak, flexible, unornamented, with broadly convex posterior margin. Mandible (Fig. 89I) digitiform, tapering distally, with slight constriction distally and 2 small setae subapically. Maxillule (Fig. 89J) incompletely 2-segmented; proximal segment (precoxa) with 3 setae (distalmost rudimentary); distal segment (palp) roughly quadrate, with 5 setae (4 outer and 1 distal), distal seta shorter than other 4. Maxilla (Fig. 89K) as broad lobe bearing 1 apical and 1 subapical seta. Maxilliped (Fig. 89L) 4-segmented; first segment broad, unarmed; second segment with 2 small setae; third and fourth segments small, unarmed; terminal claw small, conical, half as long as fourth segment.

Legs 1-4 biramous, consisting of protopod, exopod, and small endopod (Fig. 89M-O). Both rami not articulated from protopod; protopods with outer seta. Exopods of legs 1, 3, and 4 each armed with 1 seta and 2 spines (Fig. 89M, O). Exopod of leg 2 (Fig. 89N) armed with 1 seta and 3 spines. Endopod rather distinct, bearing 1 or 2 sensilla. Endopods of legs 3 and 4 shorter but broader than in legs 1 and 2.

Leg 5 represented by 2 minute setae. Leg 6 represented by 1 spine and 1 spiniform process in genital area, accompanied by 5 internal, tooth-like elements.

**Male.** Unknown.

**Remarks.** In the genus *Haplostomides* the number of armature elements on the exopod of leg 1 is more than or the same as that of leg 2. The exopods of legs 1-4 of *Haplostomides bermudensis* **sp. nov.** are armed with 3, 4, 3, and 3 armature elements, respectively, which is an unusual combination of armature elements that serves to characterize the new species. The maxillule of *H. bermudensis* **sp. nov.** is armed with 3 setae on the proximal segment and 5 setae on the distal segment. This maxillary setation is shared only with *H. brementi* Chatton & Harant, 1924, but further comparison between *H. brementi* and the new species is unnecessary because of the different armature patterns in legs 1-4 of *H. brementi* (5, 4, 3, and 3 according to Ooishi (2008a)).

### *Haplostomides partitus* **sp. nov.**

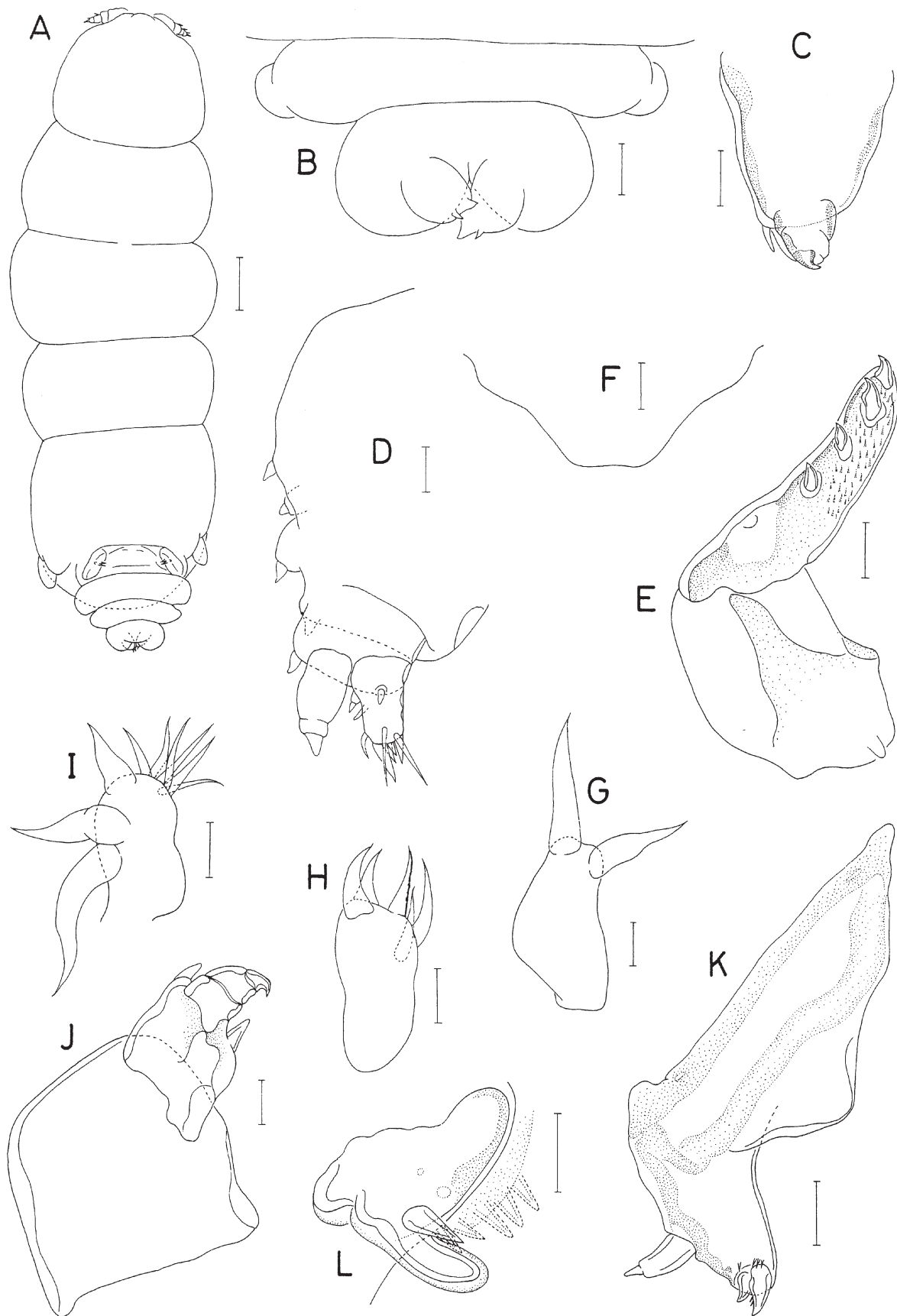
(Fig. 90)

**Type material.** Holotype ♀ (MNHN-IU-2018-1991, dissected and mounted on a slide) from *Aplidium benhami* (Brewin, 1946) (MNHN-IT-2018-19 = MNHN A1/APL.B/547); Madagascar, Îlot des Roches, ATIMO VATAE expedition, Stn TA56 (24°58'S, 47°03'E), depth 1-8 m, MNHN coll., 14 June 2010.

**Etymology.** The name is derived from the Latin *partit* (=divided), referring to the segmented body of the female of the new species.

**Description of female.** Body (Fig. 90A) maggot-shaped, well-segmented, consisting of cephalosome, 4-segmented metasome, and 4-segmented genitoabdomen. Body length 1.15 mm; maximum width 0.37 mm across second pedigerous somite. Body somites clearly defined from one another by deep constrictions and distinct suture lines. Genitoabdomen indistinctly articulated from metasome, consisting of genital somite and 3-segmented abdomen. Genital apertures positioned dorsally. Abdomen strongly tapering. Caudal rami (Fig. 90B) convergent, originating on dorsal surface of anal somite, not articulated from somite; each ramus (Fig. 90C) tapering, longer than wide, divided into larger proximal part bearing 1 seta distally and lobate distal part bearing 1 small, claw-like distal spine.

Rostrum absent. Antennule (Fig. 90D) 3-segmented; first segment expanded, about twice as long as distal part of antennule, armed with 4 small setae; second segment incompletely articulated from first, armed with 1 small and 1 large, extremely expanded seta; third segment armed with 10 setae (3 proximal and 7 distal and subdistal). Antenna (Fig. 90E) 2-segmented, consisting of coxobasis and endopod; coxobasis unarmed; endopod about 3.1 times longer than wide (50×16 µm), longer than coxobasis, armed with 4 claw-like spines, all articulated at base, and ornamented with many minute spinules along outer surface.



**FIG. 90.** *Haplostomides partitus* sp. nov., female. A, habitus, dorsal; B, distal part of genitoabdomen, ventral; C, left caudal ramus, ventral; D, antennule; E, antenna; F, labrum; G, mandible; H, maxillule; I, maxilla; J, maxilliped; K, leg 1; L, genital aperture. Scale bars: A, 0.1 mm; B, K, 0.02 mm; C-J, L, 0.01 mm.

Labrum (Fig. 90F) pale, much wider than long, strongly tapering towards truncate apex. Mandible (Fig. 90G) lobate, with convex medial margin; armed with 2 broad setae distally. Maxillule (Fig. 90H) unsegmented, lobate, armed with 5 broad setae (2 posterodistal, 2 anterodistal, and 1 subdistal). Maxilla (Fig. 90I) also unsegmented and lobate, armed with 9 setae (6 slender and 1 broad setae distally and 2 expanded setae on posterior margin). Maxilliped (Fig. 90J) 4-segmented; first segment much larger than other segments, as long as wide, unarmed; second segment with 2 small, transparent setae (1 mediolateral and 1 outer distal), third and fourth segments small, unarmed, with similar lengths; terminal claw small, with strongly curved, acute tip.

Leg 1 (Fig. 90K) biramous, but both rami not articulated from protopod; protopod unarmed, lacking outer seta; exopod with 1 swollen, transparent seta in middle of outer margin and 2 distal spines of unequal lengths, ornamented with several minute spinules near bases of distal spines; endopod short, broad, appearing as convex inner protuberance on protopod. Legs 2-4 exactly same as leg 1 in form and armature.

Leg 5 as unarmed posterolateral lobe on compound fourth metasomite (Fig. 90A). Leg 6 (Fig. 90L) represented by 1 spine and 1 large, blunt process covered with transparent material. Five dentiform internal elements present near leg 6.

**Male.** Unknown.

**Remarks.** *Haplostomides partitus* **sp. nov.** can be differentiated from its congeners by three diagnostic features, as follows: (1) the maxillule is unsegmented (in all previously known species of the genus the maxillule is 2-segmented, consisting of the proximal precoxa and the distal palp); (2) the maxilla is armed with 9 setae, compared to a maximum of 4 setae in all congeners (as for example in *H. luteolus* Ooishi & Illg, 1977); and (3) the outer seta on the exopod of legs 1-4 is markedly swollen and distinctly broader than the distal spines (another unique feature of the new species).

## Genus *Haplostoma* Canu, 1886

**Diagnosis.** Female: Body eruciform, unsegmented or indistinctly segmented. Genitoabdomen fused with or obscurely defined from metasome. Caudal rami armed with 1 to 6 armature elements (spines plus setae), or occasionally unarmed. Rostrum not developed. Antennule small, 1- to 5-segmented. Antenna 2- or 3-segmented; terminal segment bearing 3 to 5 armature elements (usually 4 spines). Labrum simple or with 2 or 3 pairs of lobes on posterior margin. Mandible absent or small, mostly 1- or 2-segmented, tipped with 1 to 3 setae. Maxillule and maxilla absent. Maxilliped consisting of 4 segments plus terminal claw. Legs 1-4 usually consisting of protopod, exopod and endopod. Protopods unsegmented, with or without outer seta. Exopods with up to 5 armature elements; in some species distal spines fused at base to form bifurcate spine; exopod occasionally with single, claw-like distal element. Endopods represented by inner distal protuberance on protopod, sometimes absent. Leg 5 variously reduced, usually lobate and bearing 1 to 3 small setae. Male: Body cycloform with distinct prosome-urosome division. Prosome consisting of cephalosome and first to fourth pedigerous somites. Urosome 6-segmented. Caudal rami armed with 5 setae. Rostrum not developed. Antennule 4-segmented; first segment bearing numerous aesthetascs. Antenna 3-segmented with 3 or 4 armature elements on terminal segment. Labrum simple. Mandible 1- to 3-segmented, with 1 to 3 setae distally. Maxillule absent. Maxilla as a lobe, unarmed or armed with 1 apical seta. Maxilliped consisting of 4 segments plus terminal claw. Leg 1 with 3-segmented exopod; endopod 1- or 2-segmented, with transformed setal elements. Legs 2 and 3 with 3-segmented rami. Leg 4 with 3-segmented exopod and 2-segmented endopod. First exopodal segment of legs 1-4 lacking inner seta. Leg 5 consisting of 1 lateral seta on fifth pedigerous somite and exopodal segment tipped with 2 setae, Leg 6 represented by 2 setae on genital operculum.

**Type species.** *Haplostoma brevicauda* (Canu, 1886) by original monotypy.

**Remarks.** Ooishi (2009b) recognized 18 species of *Haplostoma* as valid. In seven of these species, which she recognized as “subgroup 2”, the exopods of legs 1-4 are armed only with spines and lack setae (the proximal seta is transformed to a spine). In the present work 12 new species are described, including three belonging to Ooishi’s subgroup 2 and nine placed in subgroup 1.

***Haplostoma rectangulatum* sp. nov.**

(Fig. 91)

**Type material.** Holotype ♀ (MNHN-IU-2009-5230) and 1 ♀ paratype (dissected, MNHN-IU-2014-17382) from *Polysyncraton* sp.; off Libanona, Sud Madagascar, ATIMO VATAE Expedition, Stn TR01 (25°00.25'S, 46°59.4'E), depth 9 m, MNHN coll., 28 April 2010.

**Additional material.** 1 ♀ (MNHN-IU-2009-5232) in *Polysyncraton* sp., Port Dauphin, Madagascar, ATIMO VATAE expedition, Stn TR03 (25°0.08'S, 47°0.01'E), depth 21 m, 29 April 2010.

**Etymology.** The name of the new species refers to its rectangular abdomen.

**Description of female.** Body (Fig. 91A, B) eruciform, cylindrical, slightly curved dorsally, consisting cephalosome, indistinctly 5-segmented metasome, and small 2-segmented genitoabdomen. Body length 940 µm; maximum width 290 µm across fourth pedigerous somite. Cephalosome 175×210 µm, narrower than first pedigerous somite; second to fourth pedigerous somites nearly equal in width, each wider than first. Fourth and fifth pedigerous somites demarcated from each other by dorsal and ventral constrictions. Genitoabdomen (Fig. 91C) small, 105×120 µm, occupying only 11% of body length, consisting of triangular anterior somite bearing genital apertures dorsally, and narrow, rectangular free abdomen (posterior somite); free abdomen clearly defined from anterior somite due to abrupt narrowing, longer than wide (39×27 µm). Caudal rami absent, but 1 caudal seta may be present on postero-lateral corner of free abdomen (Fig. 91D).

Rostrum absent. Antennule (Fig. 91E) as small, unsegmented lobe, 24×17 µm, bearing patch of small spinules (or setae?) on apex. Antenna (Fig. 91F) stout, 3-segmented; first segment broad but very short and unarmed; second segment longest, unarmed; terminal segment slightly longer than wide, armed with 4 bifurcate spines; spines becoming gradually larger from proximal to distal.

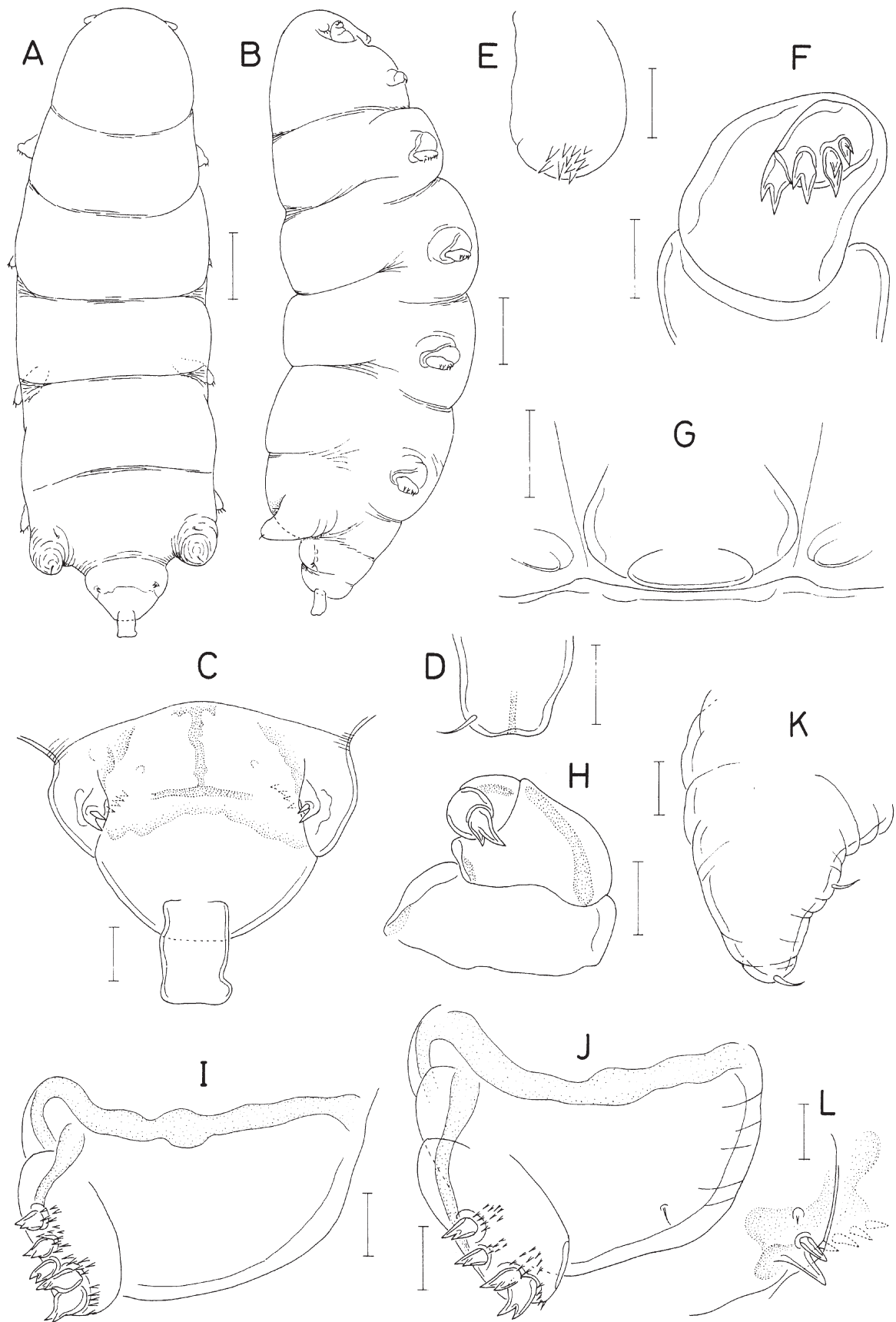
Labrum (Fig. 91G) simple, unornamented, with broad distal lobe. Mandible (Fig. 91G) vestigial, represented by pair of weak unarmed tubercles, located lateral to labrum. Maxillule and maxilla absent. Maxilliped (Fig. 91H) stout, very small, 4-segmented; all segments wider than long; proximal 3 segments unarmed; distal segment bearing unequally bifurcate terminal claw.

Legs 1-4 consisting of protopod and exopod; endopod not discernible; exopods armed only with spines (lacking seta), incompletely articulated from protopod. Exopod of leg 1 (Fig. 91I) armed with 5 bifurcate spines and ornamented with spinules near base of each spine. Leg 4 (Fig. 91J) slightly larger than leg 1, armed with 4 bifurcate spines and ornamented as in leg 1. Legs 2 and 3 same as leg 4 in shape and armature.

Leg 5 (Fig. 91K) as conical fleshy process on fifth pedigerous somite, directed posterodorsally, bearing 2 small setae (1 dorsal and 1 distal). Leg 6 (Fig. 91L) represented by 1 small spine and 1 spiniform process on genital operculum. Four dentiform elements present near leg 6.

**Male.** Unknown.

**Remarks.** Ooishi (2009b) recognized seven species of *Haplostoma* as “subgroup 2”. In one member of this group, *H. bispinosum* Ooishi, 2009, the exopods of legs 1-4 are armed with 5, 4, 5, and 5 spines (5-4-5-5 pattern), respectively. The other six species of this group all display a 5-4-4-4 pattern for legs 1-4, in common with *H. rectangulatum* sp. nov. However, only one of these six species, *H. dudleyae* Ooishi, 1998, is comparable with the new species in having a single caudal seta and a vestigial mandible lacking any setal elements. Ooishi (1998) described *H. dudleyae* on the basis of material from Florida, USA and it has a leg 5 represented only by a pair of setae. In contrast, leg 5 of *H. rectangulatum* sp. nov. is well-developed, being represented by a distinct fleshy process bearing 2 setae. *Haplostoma dudleyae* also has caudal rami, although they are small and lobate, while *H. rectangulatum* sp. nov. lacks defined caudal rami. The latter feature of the new species is unique within the genus. Collectively these differences justify the establishment of the new species.



**FIG. 91.** *Haplostoma rectangulatum* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genitoabdomen, dorsal; D, distal part of abdomen; E, antennule; F, antenna; G, labrum and mandibles; H, maxilliped; I, leg 1; J, leg 2; K, leg 5; L, genital aperture. Scale bars: A, B, 0.1 mm; C, D, G, K, 0.02 mm; E, F, H-J, L, 0.01 mm.

***Haplostoma manadoense* sp. nov.**

(Fig. 92)

**Type material.** Holotype ♀ (MNHN-IU-2018-1992), 3 ♀♀ paratypes (MNHN-IU-2018-1993), and 1 ♀ paratype (dissected, MNHN-IU-2014-17383) from *Eudistoma* sp.; Point called TG Torowitan, North tip of Sulawesi, Indonesia, OCDN 1431-P, Site MANADO 25 (01°45.10'N, 124°58.87'E), depth 5 m, CRRF coll., 21 May 1993.

**Etymology.** The name of the type locality, Manado, is taken for the name of the new species.

**Description of female.** Body (Fig. 92A) eruciform, relatively slender, slightly curved dorsally, consisting of cephalosome, 4-segmented metasome, and 3-segmented genitoabdomen. Body length 1.69 mm; maximum width 350 µm across fourth pedigerous somite; maximum dorsoventral depth 380 µm at fourth pedigerous somite. Cephalosome narrower than metasome, defined from metasome by indistinct articulation. Metasome gradually broadening posteriorly; somites defined from one another by constrictions. Genitoabdomen (Fig. 92B, C) as long as wide (215×220 µm), tapering, consisting of genital and 2 abdominal somites. Genital somite bearing transverse stripe dorsally; genital apertures positioned dorsolaterally. Second abdominal somite distinctly narrower than first. Left and right caudal rami completely fused with each other (Fig. 92D), each bearing 1 conical spine on distal margin and 1 seta on lateral margin.

Rostrum absent. Antennule (Fig. 92E) longer than wide, distinctly 2-segmented, armed with 1 seta distally on proximal segment, and cluster of about 12 setae around apex of segment; all setae short and bluntly tipped. Antenna (Fig. 92G) 2-segmented; proximal segment swollen, unarmed; distal segment about 1.5 times longer than wide, armed with 4 spines, proximal spine minute and simple, 3 distal spines larger and bifurcate.

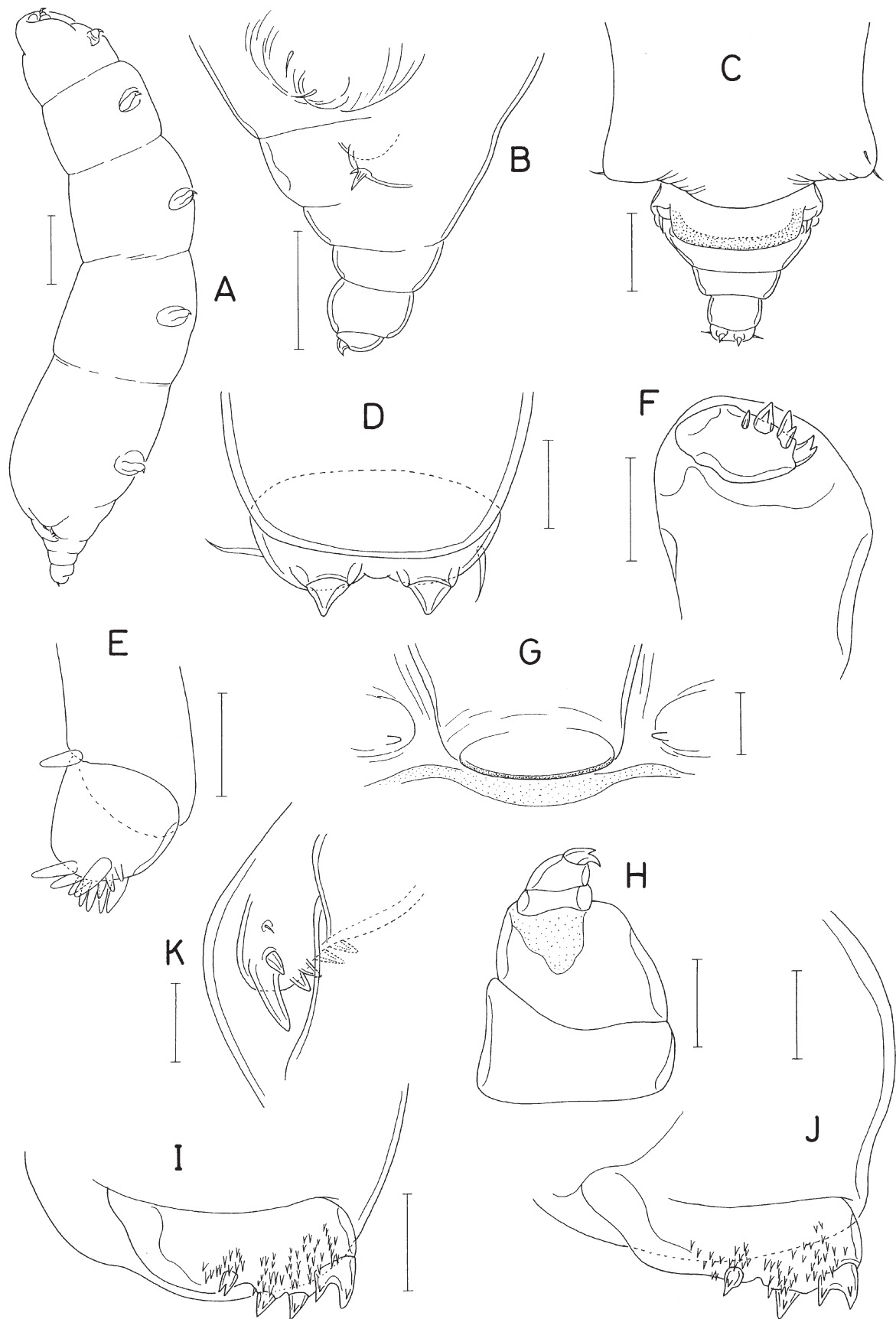
Labrum (Fig. 92G) simple, unornamented with sclerotized posterior margin. Mandible (Fig. 92G) as weak lobe positioned lateral to labrum, each tipped with 1 small, nipple-shaped element. Maxillule and maxilla absent. Maxilliped (Fig. 92H) small, stout, 4-segmented; proximal 3 segments unarmed, each wider than long; terminal segment bearing unequally bifurcate claw.

Legs 1-4 each consisting of protopod and exopod; endopod not discernible. Exopods with short inner margin and much longer outer margin, armed only with spines (lacking seta). Two terminal spines on each exopod fused at base (arising from common base). Leg 1 (Fig. 92I) exopod armed with 5 spines and ornamented with many spinules on anterior surface. Legs 2 (Fig. 92J), 3 and 4 shaped and ornamented as leg 1, but armed with 4 spines (with 2 terminal spines fused at base).

Leg 5 (Fig. 92C) as short, blunt posterolateral tubercle on compound last metasomite bearing 1 or 2 small setae. Leg 6 (Fig. 92K) represented by 1 small spine and 1 spiniform process; 4 dentiform elements on surface adjacent to leg 6.

**Male.** Unknown.

**Remarks.** While describing *Haplostoma junctum* Ooishi, 2009 as an associate of *Eudistoma* sp. in Madagascar, Ooishi (2009b) mentioned that this copepod was the only species of *Haplostoma* to have medially fused caudal rami. *Haplostoma manadoense* sp. nov. is the second species characterised by the possession of medially fused caudal rami and is, therefore, compared in detail with *H. junctum*. The new species differs from *H. junctum* as follows: (1) the fused caudal rami are clearly articulated from the anal somite (cf. indistinctly articulated in *H. junctum*); (2) the caudal rami are armed with 1 spine and 1 seta (cf. armed only with 1 spine in *H. junctum*); (3) the first segment of the antennule is not expanded (cf. markedly expanded in *H. junctum*); (4) the two terminal spines on the exopods of legs 1-4 are fused at base (cf. these spines separate from each other in *H. junctum*); and (5) the mandible is tipped with a rudimentary setal element (cf. tipped with 2 setae in *H. junctum*).



**FIG. 92.** *Haplostoma manadoense* **sp. nov.**, female. A, habitus, right; B, distal part of body, right; C, distal part of body, dorsal; D, anal somite, dorsal; E, antennule; F, antenna; G, labrum and mandibles; H, maxilliped; I, leg 1; J, leg 2; K, genital aperture. Scale bars: A, 0.2 mm; B, C, 0.1 mm; D-K, 0.02 mm.



***Haplostoma gracile* sp. nov.**

(Fig. 93)

**Type material.** Holotype ♀ (MNHN-IU-2018-1994, as a whole mount on a slide) from *Leptoclinides* sp.; New Caledonia, no other collection data.

**Etymology.** The name is derived from the Latin *gracil* (=slender), referring to the elongate, vermiform body of the new species.

**Description of female.** Body (Fig. 93A) extremely elongate, vermiform, straight, consisting of unsegmented trunk and small abdomen. Body 11 times longer than wide; length 3.25 mm and maximum width 286 µm, across region of leg 3. Cephalosome (Fig. 93B) obscurely defined from and narrower than metasome. Intervals between first to fourth legs 409, 614, 764 µm, respectively; distance from leg 4 to posterior tip of urosome 1182 µm. Genital apertures not seen. Abdomen (Fig. 93C) small, slightly longer than wide (116×103 µm), incompletely articulated from metasome, lacking any trace of segmentation, slightly narrowing posteriorly, with convex rear margin. Caudal ramus (Fig. 93C) as small semicircular lobe lacking caudal setae.

Rostrum absent (Fig. 93B). Antennule (Fig. 93D) as transparent lobe, unsegmented and unarmed. Antenna (Fig. 93D) small, indistinctly 2-segmented; proximal segment unarmed, but well-sclerotized; distal segment short, armed with 4 equal, simple spines.

Labrum small, slit-like, unornamented (Fig. 93B). Mandible, maxillule, and maxilla absent. Maxilliped (Fig. 93E, F) short, indistinctly segmented, tipped with small, simple, spiniform claw.

Legs 1-4 adhering closely to ventral surface of metasome, extremely flattened dorsoventrally, not observable in anterior or posterior views; endopods not discernible. Exopods armed only with spines, lacking seta, ornamented with numerous minute spinules. Leg 1 (Fig. 93G) with 5 small bifurcate spines on exopod. Leg 2 (Fig. 93H) with 1 small bifurcate spine on protopod and 4 bifurcate spines on exopod. Leg 3 (Fig. 93I) with 4 bifurcate spines on exopod. Leg 4 armed as in leg 3. Legs 5 and 6 not discernible.

**Male.** Unknown.

**Remarks.** In having 5, 4, 4, and 4 spines, respectively, on the exopods of legs 1-4, *H. gracile* sp. nov. belongs to the so-called subgroup 2 of Ooishi (1998, 2009b). However, detailed comparison with its congeners in the subgroup is unnecessary since it exhibits numerous outstanding features, including: (1) the body is extremely elongate, about 11 times longer than wide; (2) the abdomen is reduced to a small segment; (3) the caudal rami are rudimentary and lack setae; (4) the antennae and legs 1-5 are adpressed to the ventral surface of the body; (5) the mouthparts are represented only by the maxilliped; and (6) leg 5 is absent.

***Haplostoma pingue* sp. nov.**

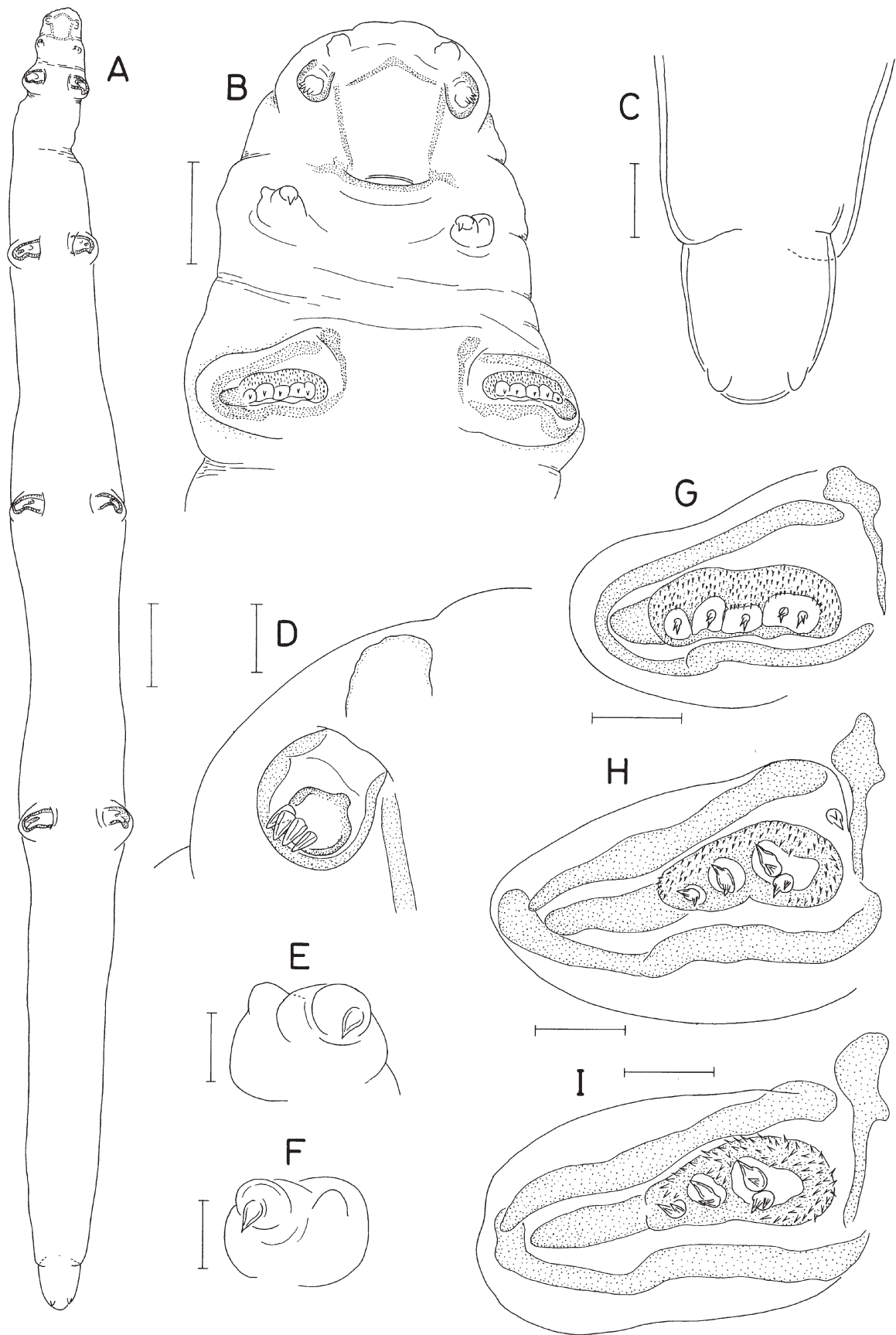
(Figs. 94, 95)

**Type material.** Holotype ♀ (MNHN-IU-2018-1995, dissected and mounted on a slide) from *Trididemnum* sp.; SW Cape, Republic of South Africa, depth 0 m (intertidal), 05 February 1996.

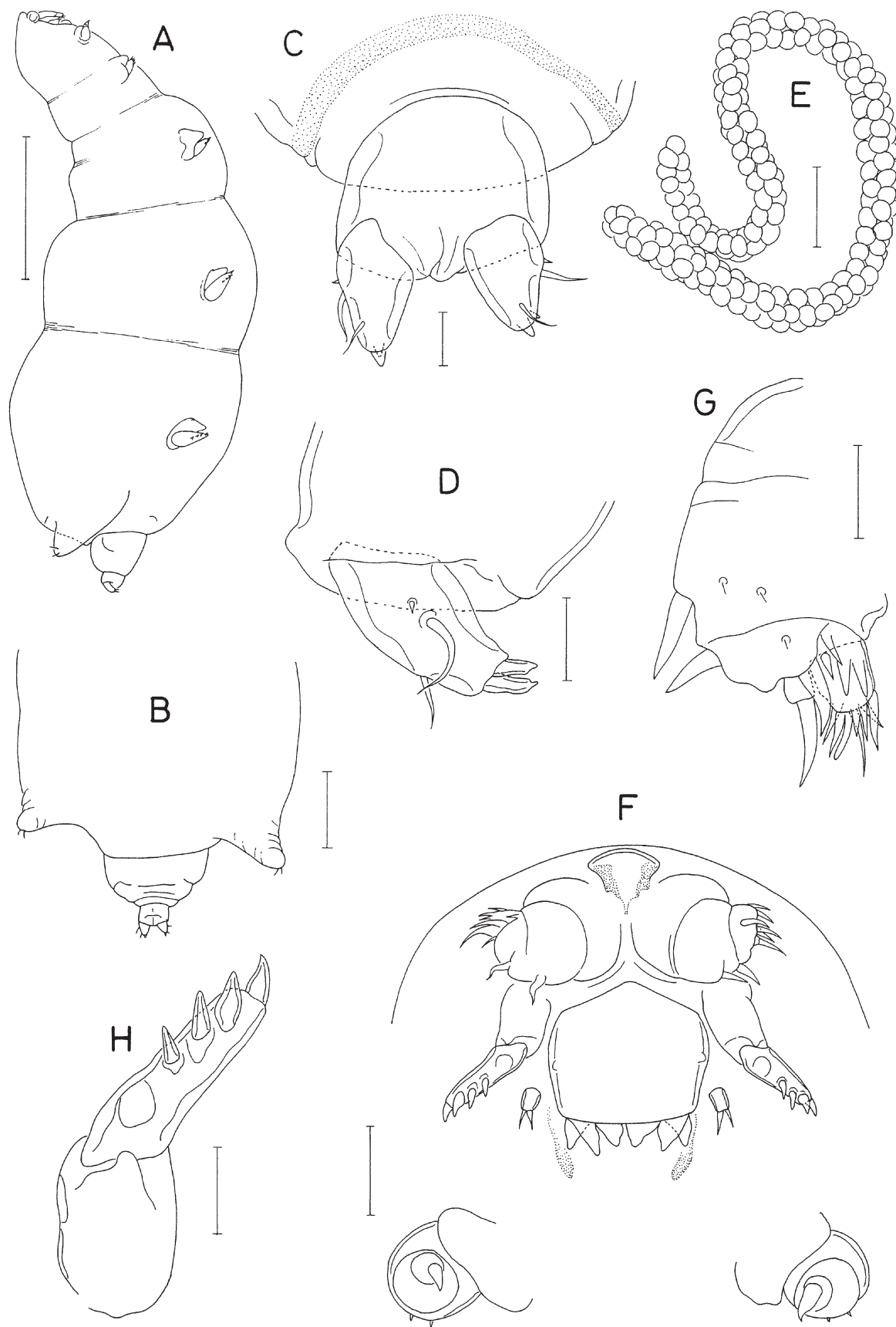
**Etymology.** The specific name is derived from the Latin *pingu* meaning “fatty”, referring to the stout body.

**Description of female.** Body (Fig. 94A) eruciform, slightly curved dorsally, consisting of fleshy anterior part and small genitoabdomen. Body length 2.08 mm; maximum width of body 790 µm across last metasomite. Anterior part of body strongly tapering anteriorly, divisible by constrictions into 5 somites comprising cephalosome and 4 metasomites; last metasomite compound, representing fused fourth and fifth pedigerous somites. Genitoabdomen (Fig. 94B) small, 215×277 µm, occupying about 10% of body length, 2-segmented; anterior somite containing genital apparatus, strongly tapering posteriorly with transverse strip of sclerotization on dorsal surface (Fig. 94C); posterior somite (free abdomen) (Fig. 94C) clearly defined from anterior somite, wider than long. Caudal ramus (Fig. 94C, D) tapering, directed posteroventrally, 1.54 times longer than wide (40×26 µm); armed with 2 distal spines and 1 dorsal plus 2 lateral setae; proximal lateral seta small, spinule-like. Egg sac (Fig. 94E) stringy, 6.28×0.2 µm, much longer than body, containing 4 or 5 rows of eggs.

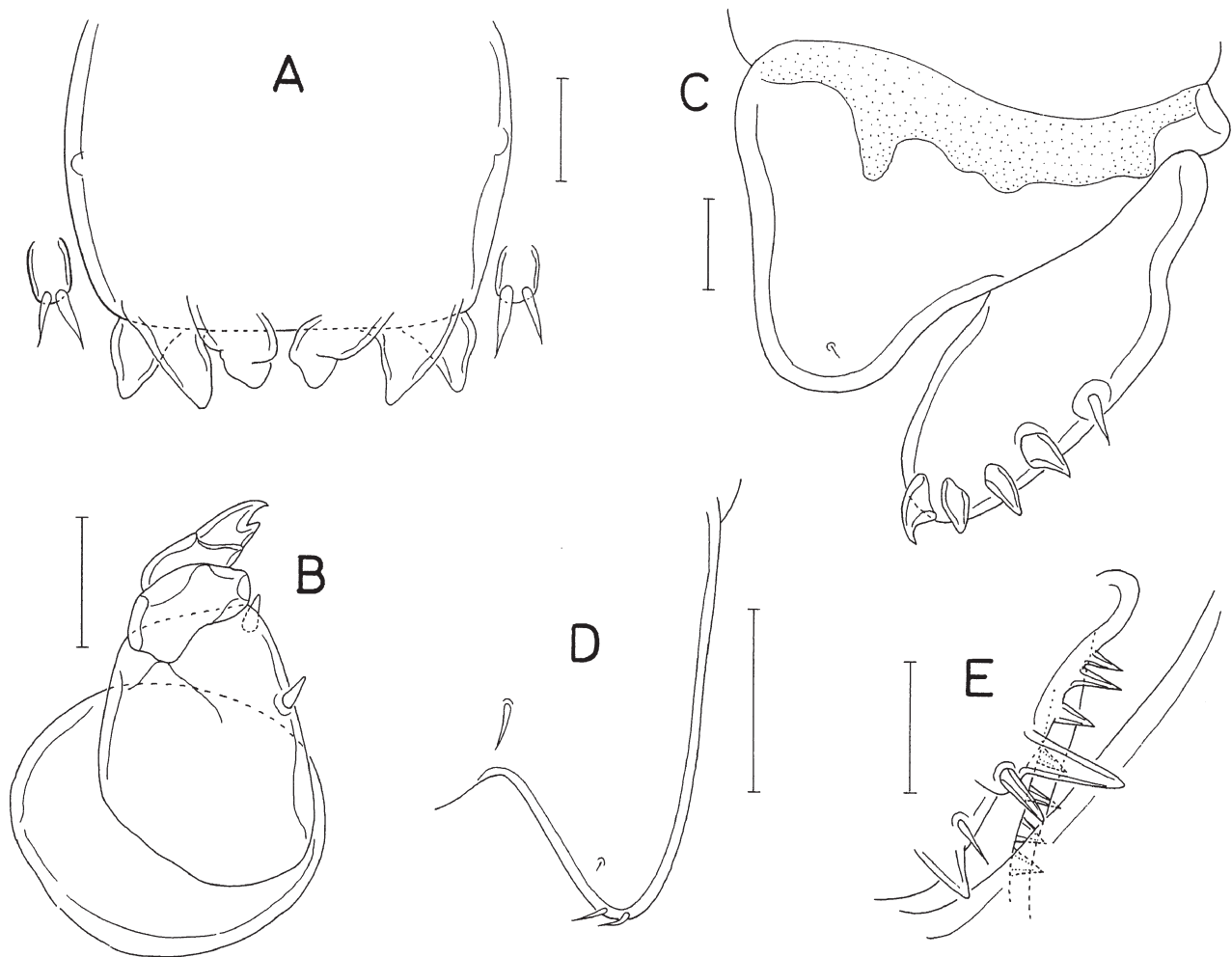
Rostrum (Fig. 94F) as small, sclerotized protuberance. Antennule (Fig. 94G) indistinctly 2-segmented; proximal



**FIG. 93.** *Haplostoma gracile* **sp. nov.**, female. A, habitus, ventral; B, anterior part of body, ventral; D, distal part of body, dorsal; D, antennule and antenna, ventral; E, F, maxillipeds; G, leg 1, ventral; H, leg 2, ventral; I, leg 3, ventral. Scale bars: A, 0.2 mm; B, C, 0.05 mm; D-F, 0.01 mm; G-I, 0.02 mm.



**FIG. 94.** *Haplostoma pingue* sp. nov., female. A, habitus, right; B, posterior end of body, dorsal; C, abdomen, dorsal; D, caudal ramus, lateral; E, egg sac; F, cephalic appendages *in situ*, ventral; G, antennule; H, antenna. Scale bars: A, E, 0.5 mm; B, 0.2 mm; C, D, G, H, 0.02 mm; F, 0.05 mm.



**FIG. 95.** *Haplostoma pingue* sp. nov., female. A, labrum and mandibles; B, maxilliped; C, leg 1; D, leg 5; E, genital aperture. Scale bars: A-C, E, 0.02 mm; D, 0.1 mm.

segment swollen, subdivided by anterior partial suture line, with 4 broad setae (distal seta inserted on lobe); distal segment obscurely articulated from proximal segment, much smaller; armed with 11 setae and 1 aesthetasc. Antenna (Fig. 94H) 2-segmented; proximal segment unarmed; distal segment 1.4 times longer than proximal, armed with 4 simple spines along distal half of segment.

Labrum (Fig. 95A) with 6 tapering lobes along posterior margin; these labral lobes slightly longer than wide, 2 medial lobes each with partial subdivision at distal third; second outer lobes slightly longer than other 4. Mandible (Figs. 94F, 95A) as small lobe tipped with 2 setae; inner seta thicker than outer. Maxillule and maxilla absent. Maxilliped (Fig. 95B) consisting of 4 segments plus terminal claw; first segment much broader than long, unarmed; second segment about 1.3 times longer than wide, bearing 2 equal, small setae on medial side; third and fourth segments short and unarmed; terminal claw stout, unequally bifurcate.

Leg 1 (Fig. 95C) consisting of protopod and exopod; protopod unarmed, with broad inner distal protuberance representing endopod; exopod clearly articulated from protopod, armed with 1 seta and 4 simple spines. Legs 2-4 armed and shaped as in leg 1.

Leg 5 (Fig. 95D) conical, as long as wide, directed posterodorsally, with short dorsal and long ventral margins; armed with 3 small setae (1 proximal and 2 distal). Leg 6 (Fig. 95E) represented by 1 small spine, 1 setule, and 5 (1 larger and 4 smaller) spiniform processes on genital operculum; 4 internal spiniform elements present near leg 6.

**Male.** Unknown.

**Remarks.** *Haplostoma pingue* sp. nov. possesses six large lobes along the posterior margin of the labrum. This

derived feature is shared with *H. banyulensis* (Brément, 1909), *H. eruca* (Norman, 1869), and *H. kimi* Seo & Lee, 2001. The first two of these species were redescribed by Ooishi (2004a) and Ooishi & O'Reilly (2004), respectively. These four species can be readily distinguished from one another by the different armature of the caudal rami; the armature formulae of the caudal rami are: II+3 (2 spines and 3 setae) in *H. pingue* **sp. nov.**, III+2 in *H. banyulensis*, I+2 in *H. kimi*, and II+1 in *H. eruca*. These species also differ in the armature patterns of the exopods of legs 1-4.

The exopods of legs 1-4 of *H. pingue* **sp. nov.** are all armed with 4 spines and 1 seta (the combination 5, 5, 5, and 5). Only *H. ambiguum* Ooishi & Illg, 1977 is known to share this armature combination with *H. pingue* **sp. nov.**, however, *H. ambiguum* differs from *H. pingue* **sp. nov.** in having only 4 weak lobes on the posterior margin of the labrum, 1 spine and 3 setae (formula I+3) on the caudal ramus, an outer seta on the protopod of legs 1-4, and in lacking a free abdomen.

### ***Haplostoma vanuatuense* sp. nov.**

(Fig. 96)

**Type material.** Holotype ♀ (MNHN-IU-2018-1996, dissected and mounted on a slide) from *Rhopalaea desme* Monniot F., 2003 (Type MNHN-IT-2008-7888 = MNHN P1/RHO.A/32); S. Anatom Is., Vanuatu, MUSORSTOM 8 cruise, RV "Alis", Stn CP961 (20°18'S, 169°50'E), depth 100-110 m, Bouchet & Richer de Forges-IRD coll., 21 September 1994.

**Etymology.** The type locality, Vanuatu, provides the name of the new species.

**Description of female.** Body (Fig. 96A, B) eruciform, narrow, slightly curved dorsally: body length 2.43 mm, maximum width 540 µm and maximum dorsoventral depth of 570 µm both at level of second pedigerous somite. Cephalosome and 4 metasomites defined by lateral constrictions; fourth metasomite compound, consisting of fused fourth and fifth pedigerous somites. Genitoabdomen slightly longer than wide (277×270 µm), distinctly 3-segmented, consisting of genital somite and 2-segmented abdomen. Genital somite comprising broad anterior and narrower posterior parts; genital apertures positioned dorsally. Caudal ramus (Fig. 96C) tapering, slightly wider than long (38×40 µm); armed with 1 claw-like distal spine, 1 subdistal seta, and 1 outer seta. Egg sac longer than body, coiled, containing about 5 rows of eggs; each egg about 200 µm in diameter.

Rostrum absent, but rostral area sclerotized (Fig. 96D). Antennule (Fig. 96E) incompletely 2-segmented, armed with 1 seta on proximal segment and 18 setae on distal segment; all setae short and bluntly tipped, except 5 longer, attenuated setae in distal region. Antenna (Fig. 96F) 2-segmented; proximal segment unarmed; distal segment narrower and shorter than proximal segment, 2.6 times longer than wide; armed with 4 simple spines, all articulated at base.

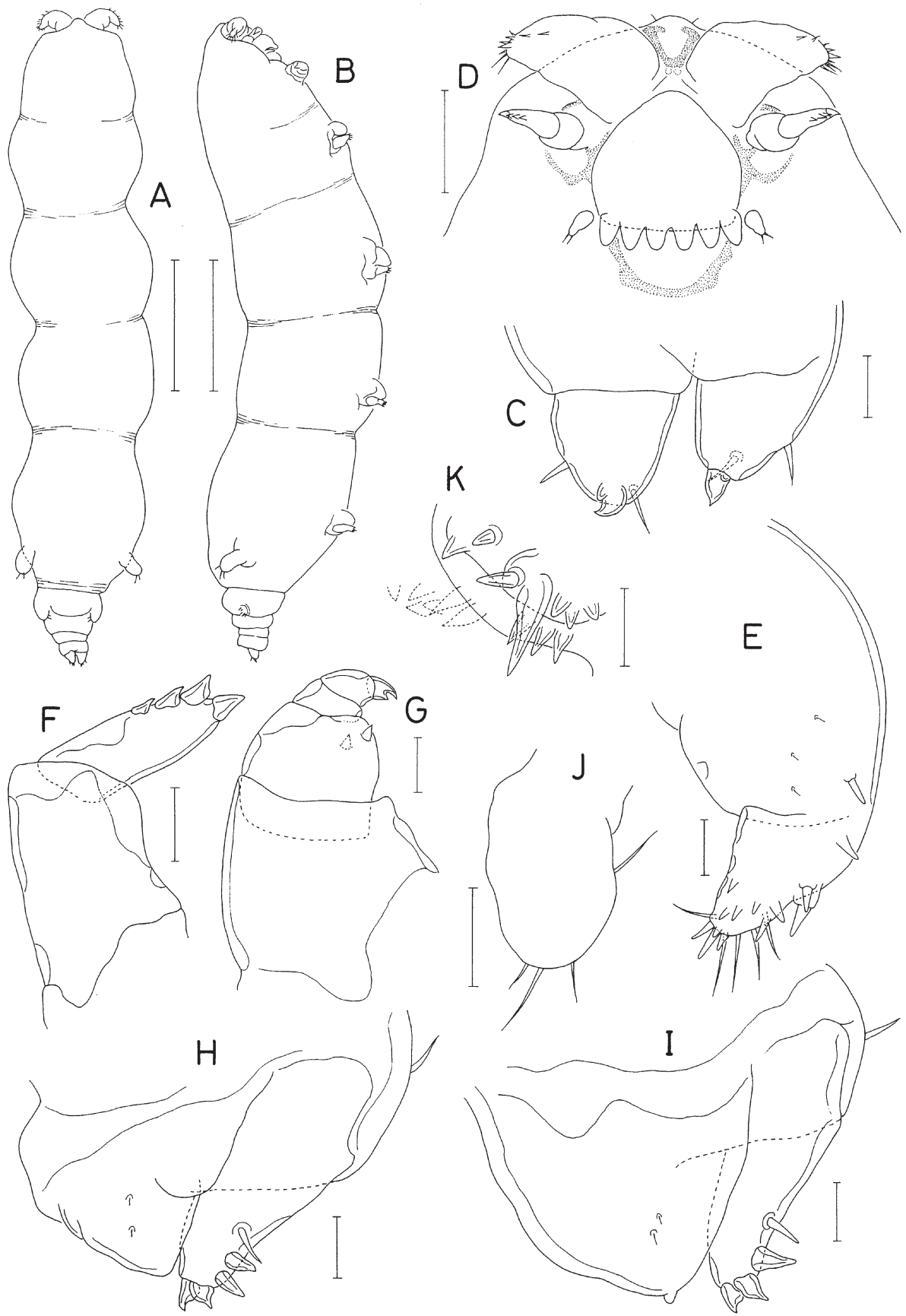
Labrum (Fig. 96D) well-developed, with 6 equal lobes along posterior margin, all of these lobes longer than wide and each with rounded apex. Mandible (Fig. 96D) twice as long as wide (33×16 µm), tapering, with 2 equal setae on apex. Maxillule and maxilla absent. Maxilliped (Fig. 96G) robust, 4-segmented; broad first segment unarmed; second segment bearing broad, short setae; small third and fourth segments unarmed; terminal claw small, bifurcate.

Leg 1 (Fig. 96H) consisting of protopod, exopod and endopod; protopod bearing 1 seta on outer margin; exopod incompletely defined from protopod, armed with 1 seta and 4 simple spines; endopod triangular, not articulated from protopod, shorter than exopod. Leg 2 (Fig. 96I) with 1 seta and 3 spines on exopod; endopod much larger than that of leg 1, as long as exopod, with small nipple-shaped tubercle on apex. Legs 3 and 4 similar to leg 2 in armature and shape, but lacking distal tubercle on endopod.

Leg 5 (Fig. 96J) small but distinct, digitiform, longer than wide (110×67 µm), not articulated at base; rounded distal margin armed with 4 thin setae (1 dorsal and 3 distal). Leg 6 (Fig. 96K) represented by 2 small spines, 1 larger spiniform process, and 7 denticles on genital operculum; 6 other internal denticles visible near leg 6.

**Male.** Unknown.

**Remarks.** *Haplostoma vanuatuense* **sp. nov.** possesses 6 distinct, equal lobes on the posterior margin of the labrum and has a combination of 5, 4, 4, and 4 armature elements on the exopods of legs 1-4. Among previously known species only *H. kimi* Seo & Lee, 2001 recorded from the Sea of Japan (Seo & Lee, 2001) shares both of these features.



**FIG. 96.** *Haplostoma vanuatuense* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, caudal rami, ventral; D, cephalic appendages *in situ*, ventral; E, antennule; F, antenna; G, maxilliped; H, leg 1; I, leg 2; J, leg 5; K, genital aperture. Scale bars: A, B, 0.5 mm; C, E-H, K 0.02 mm; D, J, 0.05 mm.

*Haplostoma kimi* is distinguishable from *H. vanuatuense* **sp. nov.** by three main features: (1) the genitoabdomen is not segmented (cf. 3-segmented in *H. vanuatuense* **sp. nov.**); (2) the outer margins of legs 3 and 4 each bear a large protrusion near the base of the proximal seta (cf. such a protrusion is absent in *H. vanuatuense* **sp. nov.**); and (3) leg 5 is strongly tapering, with 1 proximal and 2 distal setae (cf. digitiform, with 1 proximal and 3 distal setae in *H. vanuatuense* **sp. nov.**). These differences are sufficient to justify the establishment of the new species.

### *Haplostoma laticaudatum* **sp. nov.**

(Figs 97, 98)

**Type material.** Holotype ♀ (MNHN-IU-2018-1997), 1 ♀ paratype (MNHN-IU-2018-1998), and 1 ♀ paratype (dissected MNHN-IU-2014-17384) from *Pseudodistoma cyrnusense* Pérès, 1952; Tunisia, no other collection data.

**Etymology.** The name is derived from the Latin *lat* (=broad) and *cauda* (=the tail), alluding to the broad caudal rami of the new species.

**Description of female.** Body (Fig. 97A, B) eruciform, slightly curved dorsally; body length 1.60 mm, maximum width 424 µm at region of leg 2. Cephalosome (Fig. 97C, D) not defined from first pedigerous somite (Fig. 97A), narrowing anteriorly. Metasomites defined only by constrictions; last metasomite consisting of fused fourth and fifth pedigerous somites. Genitoabdomen (Fig. 97E) consisting of genital somite and 2-segmented abdomen. Genital somite wider than long (118×200 µm), consisting of broader anterior and narrower posterior parts, with dorsal strip connecting paired genital apertures. First and second abdominal somites 27×109 and 55×90 µm, respectively. Caudal ramus (Fig. 97F) triangular, slightly wider than long (36×38 µm); armed with 1 seta on outer margin and 1 unequally bifurcate spine on apex. Egg sac longer than body, containing 2-4 rows of eggs; each egg about 140 µm in diameter.

Rostrum not developed, represented by produced frontal apex of cephalosome (Fig. 97C). Antennule (Fig. 97G) tapering, unsegmented, but with 3 or 4 partial suture lines along posterior side, armed with 16 small setae, fourth proximal seta with swollen base. Antenna (Fig. 97H) 2-segmented; proximal segment unarmed; distal segment as long as proximal, armed with 4 large, conical spines.

Labrum (Fig. 97I) with 6 large, blunt lobes along posterior margin, 2 lateral lobes on each side fused proximally (appearing as 2 bifurcate lobes and 2 simple lobes). Mandible (Fig. 97I) longer than wide, tipped with 1 or 2 small setae. Maxillule and maxilla absent. Maxilliped (Fig. 98A) tapering distally, 4-segmented; first segment unarmed; second segment incompletely articulated from first, slightly wider than long, armed with 2 small setae; third segment unarmed; fourth segment with small denticle at inner distal corner; terminal claw as long as fourth segment, with 1 small denticle proximally on inner margin.

Legs 1-4 consisting of protopod, exopod and endopod; protopods unarmed; exopods incompletely demarcated from protopod; endopods represented by broad protuberance. Exopod of leg 1 (Fig. 98B) armed with 1 seta and 4 simple spines. Exopod of leg 2 (Fig. 98C) armed with 1 seta and 3 simple spines. Legs 3 and 4 armed as leg 2.

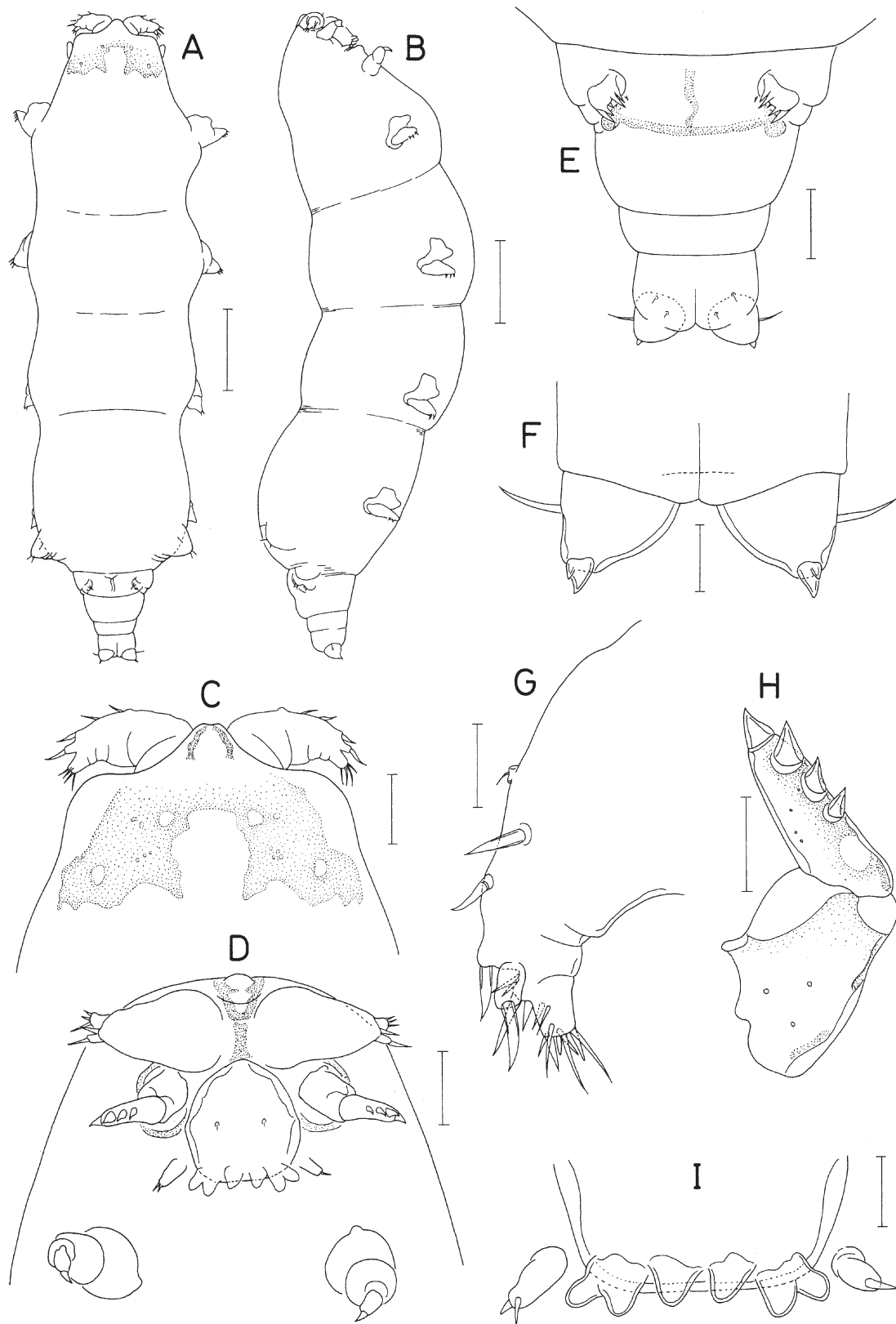
Leg 5 (Fig. 98D) as conical tubercle, wider than long, bearing 1 proximal and 2 distal setae. Leg 6 (Fig. 98E) represented by 1 spinule and 3 spiniform processes on genital operculum; 9 small internal denticles present near leg 6.

**Male.** Unknown.

**Remarks.** Five species of *Haplostoma* are now known to have 6 large lobes along the posterior margin of the labrum, as in *H. laticaudatum* **sp. nov.** They are *H. banyulensis*, *H. kimi*, *H. eruca*, *H. pingue* **sp. nov.**, and *H. vanuatuense* **sp. nov.** Of these species, only in *H. eruca* are the 2 lateral lobes on each side of the labrum fused at base (Ooishi & O'Reilly, 2004) as in *H. laticaudatum* **sp. nov.** *Haplostoma laticaudatum* **sp. nov.** differs from *H. eruca* in having 1 spine plus 1 seta on the caudal ramus (vs. 2 spines and 1 seta in *H. eruca*), 3 spines plus 1 seta on the exopod of legs 3 and 4 (vs. 2 spines plus 1 seta in *H. eruca*), and a small leg 5 (vs. large leg 5, about 1.2 times longer than wide in *H. eruca* according to Ooishi & O'Reilly, 2004).

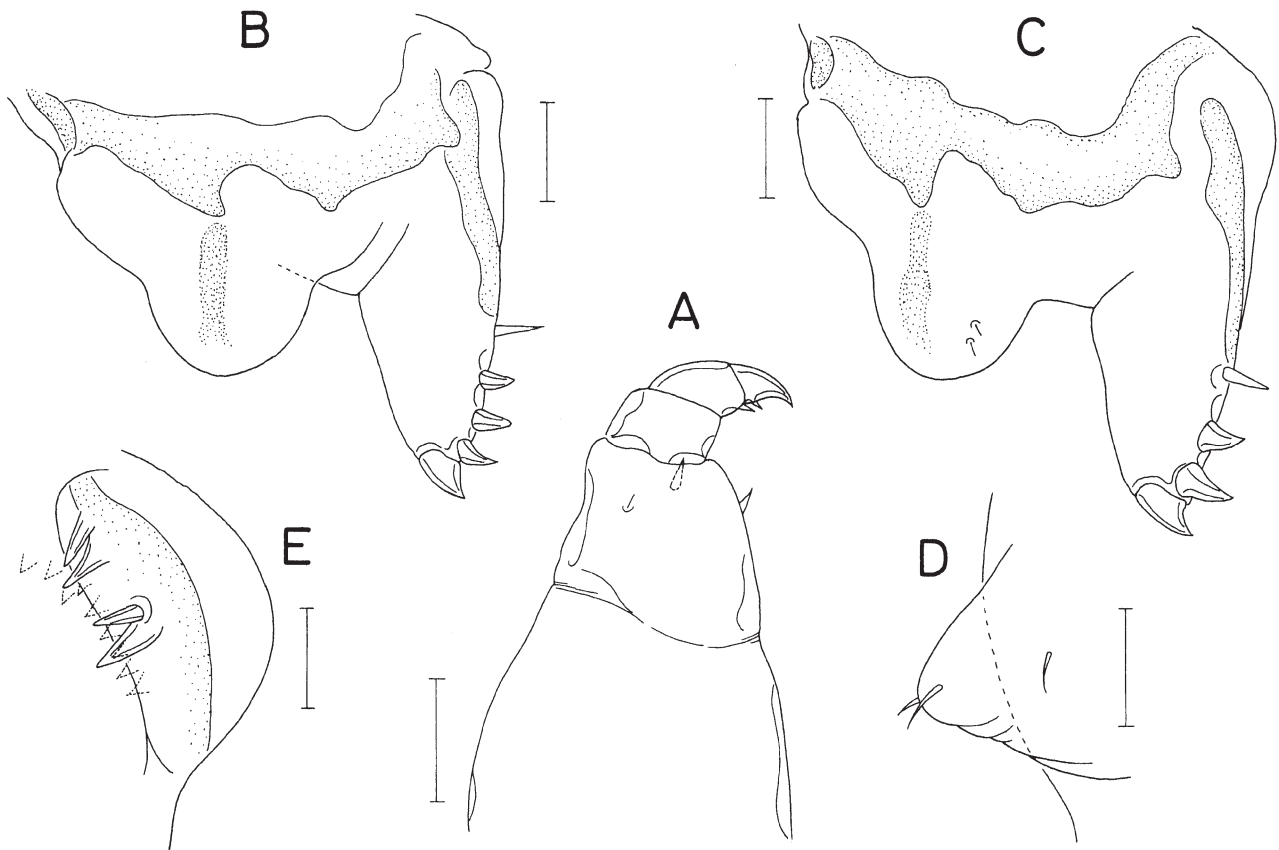
In *H. laticaudatum* **sp. nov.** the exopod of leg 1 is armed with 4 spines plus 1 seta and the exopods of legs 2-4 are each armed with 3 spines plus 1 seta. This combination of armature is shared with *H. brevicauda* (Canu, 1886), *H. kimi*, *H. setiferum* Ooishi & Illg, 1977, and *H. vanuatuense* **sp. nov.**, but, *H. laticaudatum* **sp. nov.** can

be distinguished from these congeners by the different form of the labrum as mentioned above and by the differing armature of caudal ramus, which bears 2 armature elements (1 spine plus 1 seta) in contrast to 3 or more armature elements in these other four congeneric species.



**FIG. 97.** *Haplostoma laticaudatum* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, cephalic region, dorsal; D, cephalic region, ventral; E, genitoabdomen, dorsal; F, caudal rami, ventral; G, antennule; H, antenna; I, labrum and mandibles. Scale bars: A, B, 0.2 mm; C, D, E, 0.05 mm; F-I, 0.02 mm.





**FIG. 98.** *Haplostoma laticaudatum* sp. nov., female. A, maxilliped; B, leg 1; C, leg 2; D, leg 5; E, genital aperture. Scale bars: A-C, E, 0.02 mm; D, 0.05 mm.

***Haplostoma brevicaudum* (Canu, 1886)**

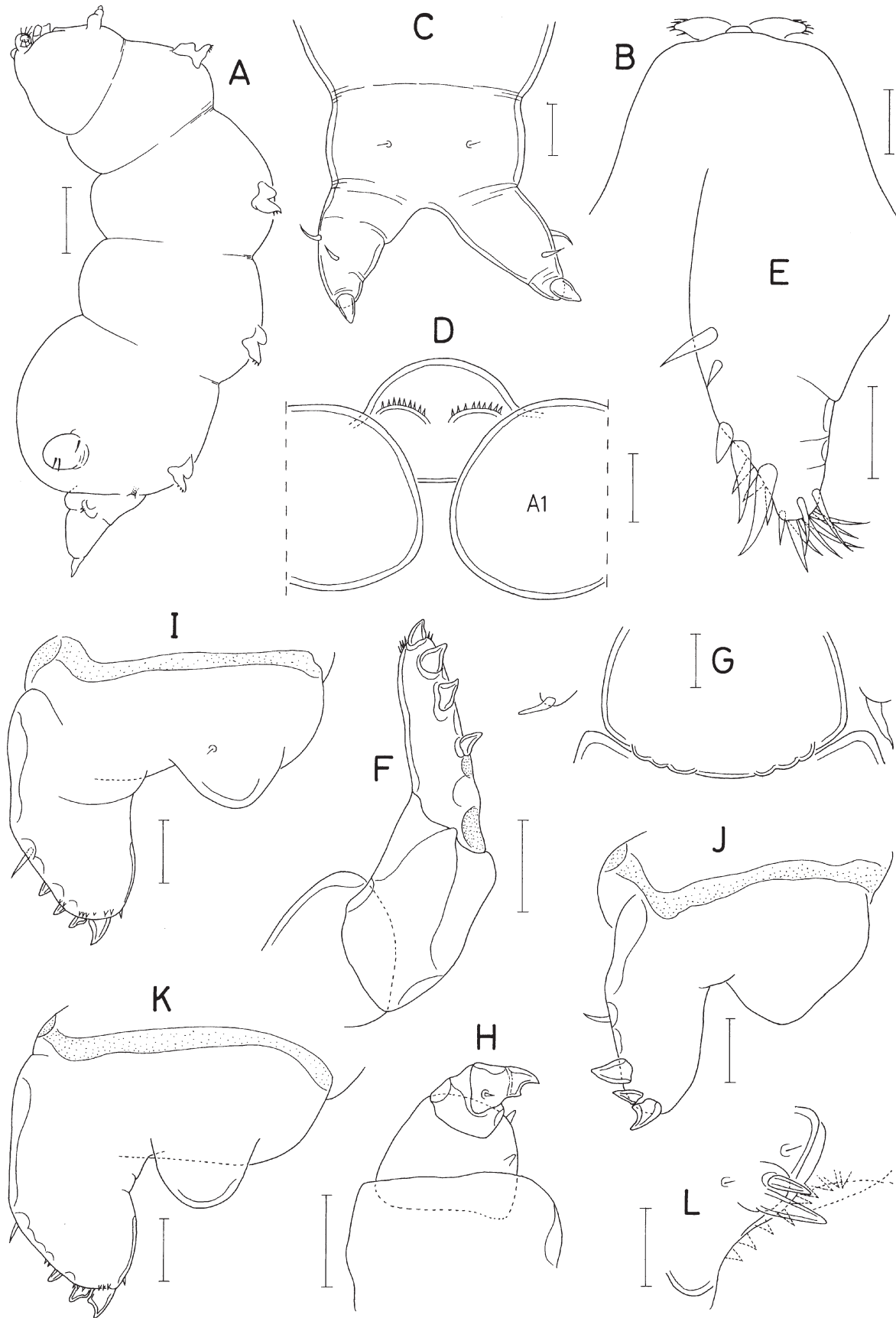
(Fig. 99)

**Material examined.** 3 ♀♀ (MNHN-IU-2018-1999, 1 ♀ dissected) in *Aplidium turbinatum* (Savigny, 1816), Dinard, Atlantic coast of France; 2 ♀♀ (MNHN-IU-2018-2000, 1 ♀ dissected) in *A. turbinatum*, Roscoff, France.

**Supplementary description of female.** Body (Fig. 99) eruciform, fleshy, curved dorsally, consisting of cephalosome, 4-segmented metasome, and 1-segmented genitoabdomen. Body length 1.93 mm. Cephalosome (Fig. 99B) narrowing anteriorly, narrower than metasome, indistinctly defined from first metasomite. Metasome gradually broadening posteriorly, incompletely 4-segmented; last metasomite compound, consisting of fused fourth and fifth pedigerous somites. Genitoabdomen tapering posteriorly, subdivided by weak constriction (Fig. 99C). Caudal ramus (Fig. 99C) tapering, about 1.6 times longer than wide ( $50 \times 31 \mu\text{m}$ ), obscurely defined from genitoabdomen; armed with 1 distal spine and 2 small setae (1 dorsal and 1 on outer margin).

Rostrum (Fig. 99D) as small anterior protuberance of cephalosome, characteristically bearing 2 saw-like transverse rows of denticles. Antennule (Fig. 99E) tapering, unsegmented, but with 3 partial suture lines along posterior side, armed with 17 setae, several on anterior margin broadened. Antenna (Fig. 99F) 3-segmented; first segment (coxa) short and unarmed; second segment (basis) also unarmed; third segment (endopod) slightly longer than second and ornamented with several minute spinules near base of distalmost spine; armed with 4 simple spines, all articulated at base, distalmost spine smaller than second distal spine.

Labrum (Fig. 99G) with convex posterior margin produced into 3 very weak lobes (appearing as wavy portions of posterior margin) on each side. Mandible (Fig. 99G) represented by single seta tipped on small papilla-like lobe. Maxillule and maxilla absent. Maxilliped (Fig. 99H) stout, 4-segmented; first segment much wider than long, unarmed; second segment wider than long, with 2 small setae on medial side; third segment unarmed; fourth segment with 1 minute seta on anterior surface; terminal claw small, with blunt dentiform protuberance proximally on medial margin.



**FIG. 99.** *Haplostoma brevicaudum* (Canu, 1886), female. A, habitus, right; B, cephalic region, dorsal; C, abdomen, dorsal; D, rostral area, ventral (A1 indicating base of antennule); E, antennule; F, antenna; G, labrum and mandibles; H, maxilliped; I, leg 1; J, leg 4; K, leg 2; L, genital aperture. Scale bars: A, 0.1 mm; B, 0.1 mm; C-L, 0.02 mm.

Legs 1-4 consisting of protopod, exopod, and endopod; protopods lacking outer seta; exopods not articulated from protopod; endopods present as semicircular mediolateral protuberance on each protopod. Exopod of leg 1 (Fig. 99I) with 1 seta and 4 spines (3 small and 1 larger distal). Exopod of leg 2 (Fig. 99K) with 1 seta and 3 spines, proximal spine markedly smaller than distal 2. Leg 3 shaped and armed as leg 2. Exopod of leg 4 (Fig. 99J) with same armature formula as in legs 2 and 3, but proximal spine larger than distal.

Leg 5 (Fig. 99A) as blunt tubercle on last metasomite bearing 3 minute setae (1 proximal and 2 distal). Leg 6 (Fig. 99L) represented by 1 spine and 1 spiniform process on genital operculum; 9 dentiform internal elements accompanied with leg 6.

**Male.** Unknown.

**Remarks.** In her redescription of *H. brevicauda*, Ooishi (2004b) mentioned and figured the presence of an outer seta on the protopod of legs 1-4 of this species. Although we failed to observe that seta, we were able to confirm close agreement between Ooishi's redescription and our specimens, including the same combination of the armature on the exopods of leg 1-4, the small, blunt leg 5, the presence of 6 weak lobes on the labrum, the presence of 9 dentiform internal elements near leg 6, and, most of all, the presence of 2 rows of 9 denticles on the ventral surface of the rostrum. On this basis our material from France is identified as conspecific with Ooishi's material. The suffix *-stoma* is neuter so *H. brevicauda* (Canu, 1886) is here amended to *H. brevicaudum* (Canu, 1886).

***Haplostoma depressum* sp. nov.**  
(Figs. 100, 101)

**Type material.** Holotype ♀ (MNHN-IU-2009-5190), 4 ♀♀ paratypes (MNHN-IU-2014-21515), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17385) from *Aplidiopsis pyriformis* (Herdman, 1886); Kerguelen, MD42-SIBEX cruise, RV "Marion Dufresne", Stn 4/CP25 (53°11'S, 74°05'E), depth 285-375 m, MNHN coll., 14 January 1985.

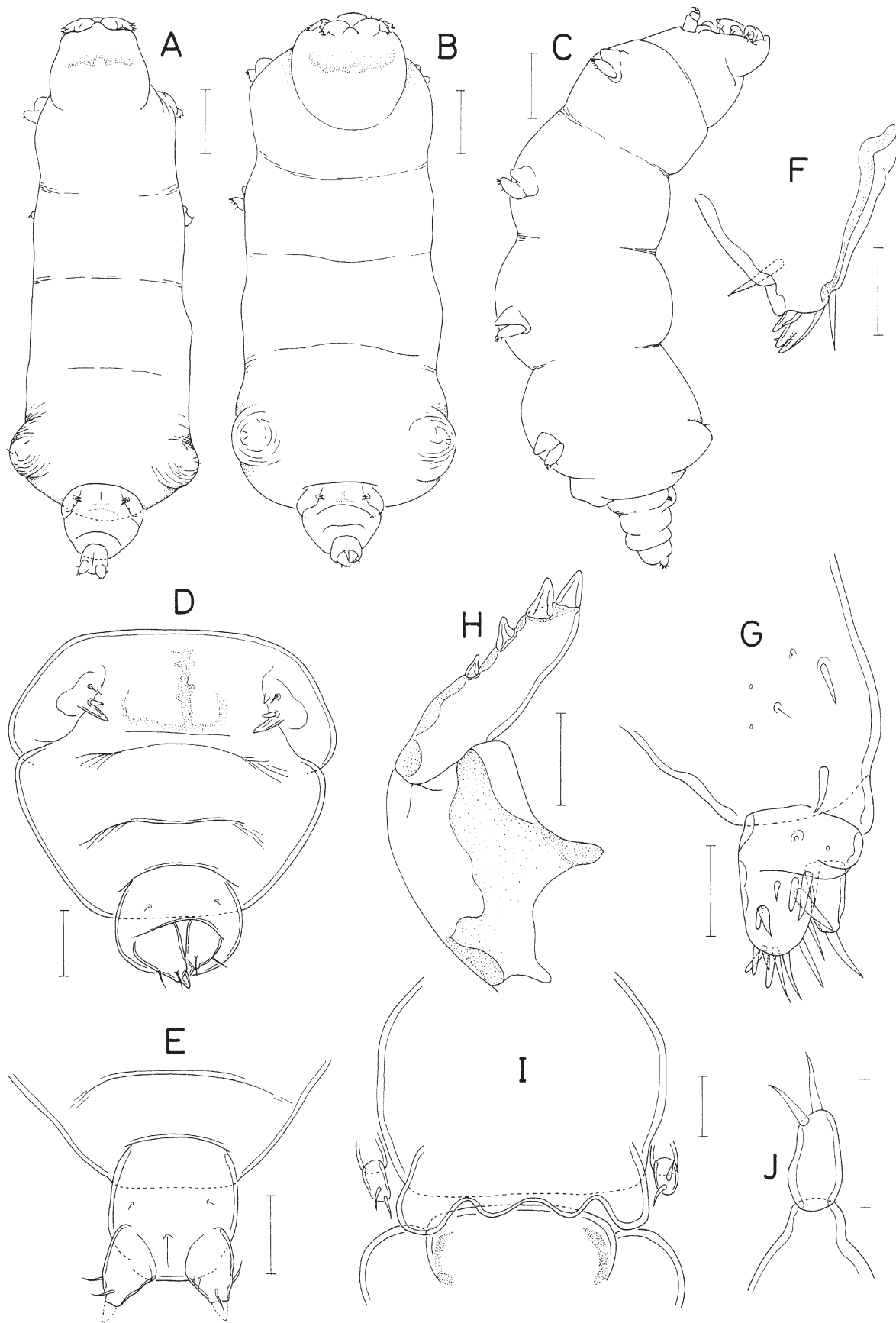
**Additional material.** 4 ♀♀ (MNHN-IU-2014-21516) from *Aplidium fuegiense* Cunningham, 1871; Kerguelen, no other locality data; 7 ♀♀ in *A. pyriformis*, SSE Kerguelen Is., MD04-BENTHOS cruise, R.V. "Marion Dufresne", Stn DC275 (49°58'S, 70°29'E), depth 234 m, Boury-Esnault coll., 15 March 1975.

**Etymology.** The body of the new species is dorsoventrally depressed, hence its name.

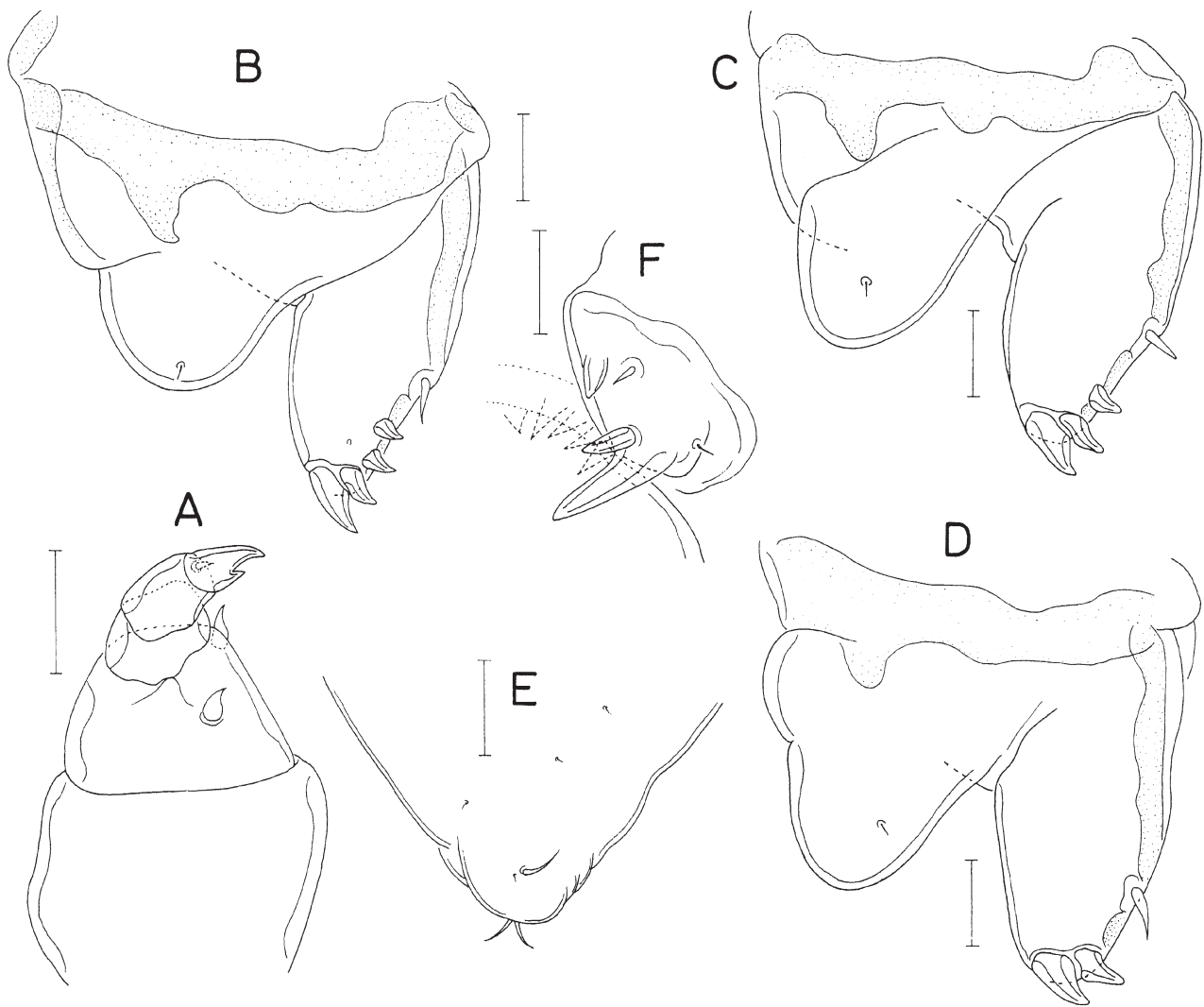
**Description of female.** Body (Fig. 100A-C) eruciform, slightly depressed dorsoventrally, consisting of cephalosome, 4-segmented metasome, and small genitoabdomen. Body length 1.91 mm in dissected specimen (Fig. 100B); maximum width 740 µm across last metasomite and maximum dorsoventral depth 542 µm. Cephalosome distinctly narrower than metasome, metasome gradually broadening posteriorly, obscurely segmented in dorsal and ventral views (Fig. 100A, B), but metasomites distinctly defined by dorsal and ventral constrictions (Fig. 100C). Compound last metasomite consisting of fused fourth and fifth pedigerous somites. Genitoabdomen (Fig. 100D) as long as wide (262×258 µm), 2-segmented; anterior somite subcircular, with traces of 2 suture lines on dorsal surface; small posterior somite (free abdomen) distinctly defined from anterior somite, wider than long in contracted specimen (Fig. 100D), but longer than wide in relaxed specimen (Fig. 100E). Caudal ramus (Fig. 100F) strongly tapering, armed with 2 setae (1 dorsal and 1 on outer margin) and 2 distal spines. Distal spines (ventral and dorsal) on caudal ramus unequal; ventral spine smaller and simple; larger dorsal spine bifurcate, with pointed dorsal and blunt ventral branches; ventral branch invariably ornamented with 1 or 2 minute spinules subdistally.

Rostrum as small, semicircular anterior protuberance on cephalosome. Antennule (Fig. 100G) 3-segmented; articulation incomplete between 2 distal segments; armed with 2, 2, and 13 small setae on first to third segments, respectively; one seta on second segment consisting of extremely swollen proximal half and slender distal half. Antenna (Fig. 100H) 2-segmented; proximal segment unarmed; distal segment 2.6 times longer than wide (43×16 µm), as long as proximal, armed with 4 simple spines, proximal 2 smaller than distal 2; all spines distinctly articulated at base.

Labrum (Fig. 100I) bearing 4 broad lobes on posterior margin, lateral lobes longer, prominent, medial lobes short. Labium well-developed, located posterior to labrum. Mandible (Fig. 100J) distinctly 2-segmented; tapering proximal segment unarmed; distal segment 1.8 times longer than wide, tipped with 2 equal setae. Maxillule and maxilla absent. Maxilliped (Fig. 101A) 4-segmented; broad first segment unarmed; second segment also wider than



**FIG. 100.** *Haplostoma depressum* **sp. nov.**, female. A, B, habitus, dorsal; C, habitus, left; D, genitoabdomen, dorsal; E, abdomen, dorsal; F, right caudal ramus, medial; G, antennule; H, antenna; I, labrum, mandibles, and labium; J, mandible. Scale bars: A-C, 0.2 mm; D, E, 0.05 mm; F-J, 0.02 mm



**FIG. 101.** *Haplostoma depressum* **sp. nov.**, female. A, maxilliped; B, leg 1; C, leg 2; D, leg 3; E, leg 5; F, genital aperture. Scale bars: A-D, F, 0.02 mm; E, 0.05 mm.

long, bearing 2 leaf-like setae; short third segment unarmed; fourth segment with 1 small seta distally; terminal claw unequally bifurcate.

Legs 1-4 each consisting of protopod, exopod, and endopod; protopods lacking outer seta. Exopods incompletely articulated from protopods. Endopods prominent, semicircular, indistinctly defined from protopods. Exopod of leg 1 (Fig. 101B) armed with 1 seta and 4 simple spines, proximal 2 spines smaller than distal 2. Exopod of leg 2 (Fig. 101C) armed with 1 seta and 3 simple spines; spines becoming larger from proximal to distal. Exopod of leg 3 (Fig. 101D) armed with 1 seta and 2 simple spines. Leg 4 shaped and armed as leg 3.

Leg 5 (Fig. 101E) short, wider than long, strongly tapering towards blunt apex; armed with 1 subdistal and 2 distal, small setae. Leg 6 (Fig. 101F) 1 small spine, 2 unequal, spiniform processes, and 1 small setule on genital operculum; 5 internal dentiform elements present near leg 6.

**Male.** Unknown.

**Remarks.** The combination of armature elements on the exopods of legs 1-4 of *H. depressum* **sp. nov.** is 5, 4, 3, and 3, as in *H. albicatum*, *H. dentatum* Ooishi & Illg, 1977, *H. elegans* Ooishi & Illg, 1977, *H. minutum*, and *H. eruca*. *Haplostoma depressum* **sp. nov.** can be clearly distinguished from those five species as well as all other congeners by the three following features: (1) the caudal ramus is armed with 2 spines and 2 setae; (2) the labrum bears 4 lobes on the posterior margin; and (3) the mandible is 2-segmented. Although the second feature is shared with *H.*

*ambiguum*, the 4 lobes on the labrum of the latter species are equally weak, unlike the combination of 2 large lateral and 2 weak medial lobes in the new species.

***Haplostoma fusiforme* sp. nov.**

(Figs. 102, 103)

**Type material.** Holotype ♀ (MNHN-IU-2014-21518) and 1 ♀ paratype (dissected, MNHN-IU-2014-17386) from *Pareugyrioides galatheae* (Millar, 1959) (MNHN-IT-2008-6004 = MNHN S3/PAR.A/11); Kerguelen Is., SW Heard I., MD03-ICTHYO cruise, RV "Marion Dufresne", Stn 12-36-CP08, Bassin de Crozet (55°49.5'S, 69°35.7'E), depth 4200-4225 m, 11 April 1974.

**Etymology.** The name of the new species alludes to its fusiform body.

**Description of female.** Body (Fig. 102A, B) large, fusiform, tapering anteriorly and posteriorly. Body length 3.80 mm and maximum width 1.30 mm in holotype; dissected paratype 3.35 mm long. Cephalosome not defined from first metasomite, but indistinct trace of suture present between them dorsally. Four metasomites distinctly defined by 3 deep constrictions; last metasomite compound, consisting of fused fourth and fifth pedigerous somites, narrowing posteriorly. Genitoabdomen (Fig. 102C) tapering posteriorly, about 500 µm long, occupying about 15% of body length, 2-segmented; anterior somite 1.33 times wider than long, with broad dorsal stripe between genital apertures; genital apertures large, positioned dorsolaterally; posterior somite (free abdomen) about 1.3 times wider than long, half as long as anterior somite. Caudal ramus (Fig. 102D) conical, about 1.47 times longer than wide (91×62 µm), 0.63 times as long as free abdominal somite; armed with 2 small setae (1 subdistal dorsal and 1 on outer margin) and 1 distal spine bearing small subsidiary denticle on outer margin.

Rostrum small, semicircular, unornamented. Antennule (Fig. 102E) incompletely 3-segmented, tapering; armed with 1, 5, and 12 small setae on first to third segments, respectively; second seta of second segment with enlarged base fused to segment. Antenna (Fig. 102F) 3-segmented; first segment (coxa) short and unarmed; second segment (basis) slightly longer than wide, unarmed; third segment (endopod) swollen proximally, narrowing distally; armed with 4 spines, becoming gradually larger from proximal to distal; distal spine bearing 3 or 4 spinules.

Labrum (Fig. 102G) short and broad, with simple convex posterior margin. Mandible (Fig. 102H) elongate, tapering, with 1 distal seta and 1 small subdistal seta. Maxillule and maxilla absent. Maxilliped 4-segmented; first and third segments unarmed; second segment with 2 small setae; fourth segment with 1 small seta distally; terminal claw short, bearing small dentiform process proximally on inner margin.

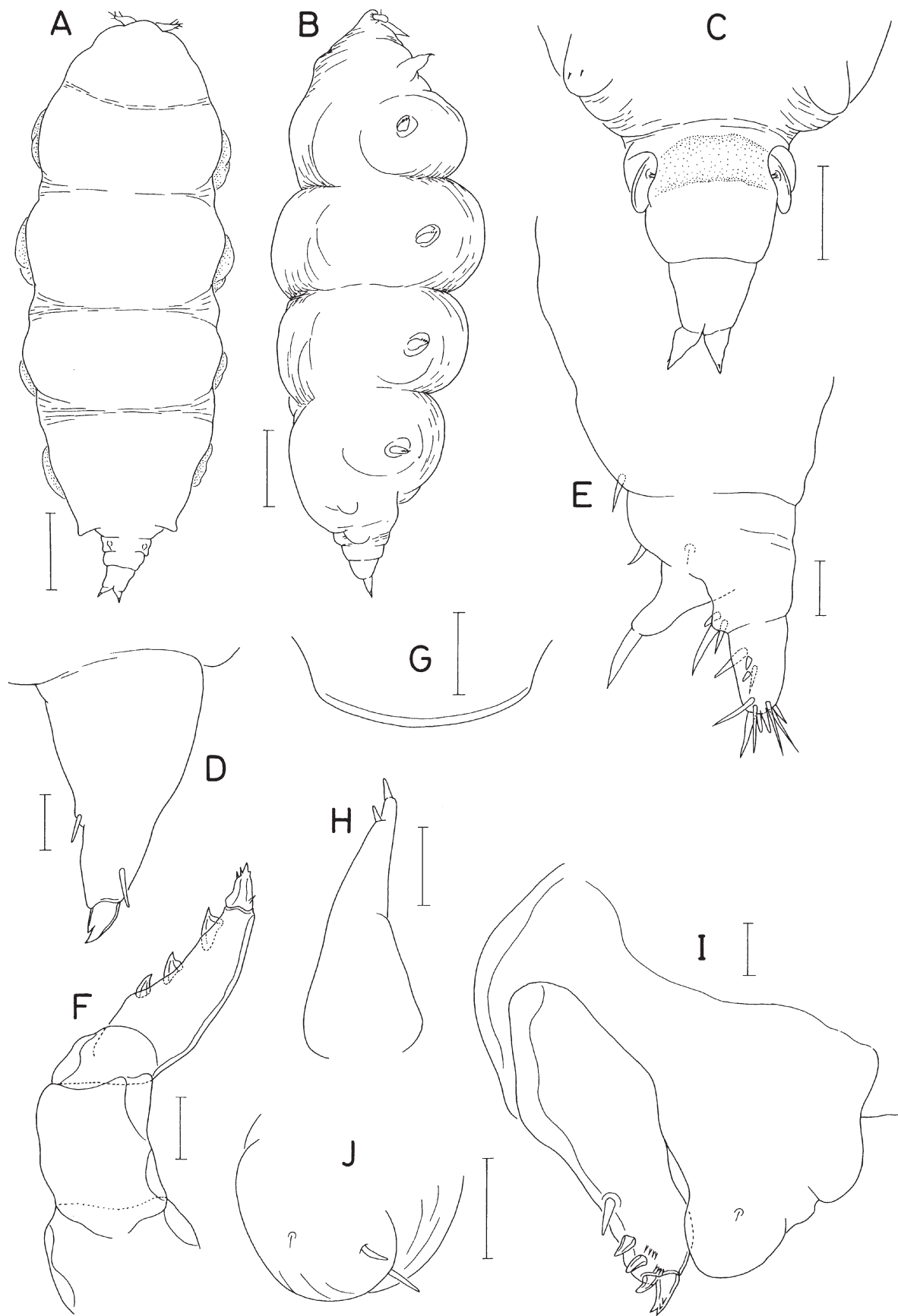
Legs 1-4 each consisting of protopod, exopod, and endopod; protopod lacking outer seta; endopod not clearly defined from protopod, but extending to distal end of exopodal segment. Exopod of leg 1 (Fig. 102I) armed with 1 seta and 4 spines (3 small proximal and 1 larger distal). Exopod of leg 2 (Fig. 103A) armed with 1 seta and 3 spines (2 small proximal and 1 larger distal). Exopod of legs 3 (Fig. 103B) and 4 armed with 1 seta and 2 distal spines. In legs 3 and 4, two distal spines on exopod fused at base. Larger distalmost spine on exopods of legs 1-4 distally trifurcate or quadrifurcate.

Leg 5 (Fig. 102J) small, papilla-like (Fig. 102A, B), bearing 2 minute setae distally. Leg 6 represented by 1 spine and 1 spiniform process (at low magnification).

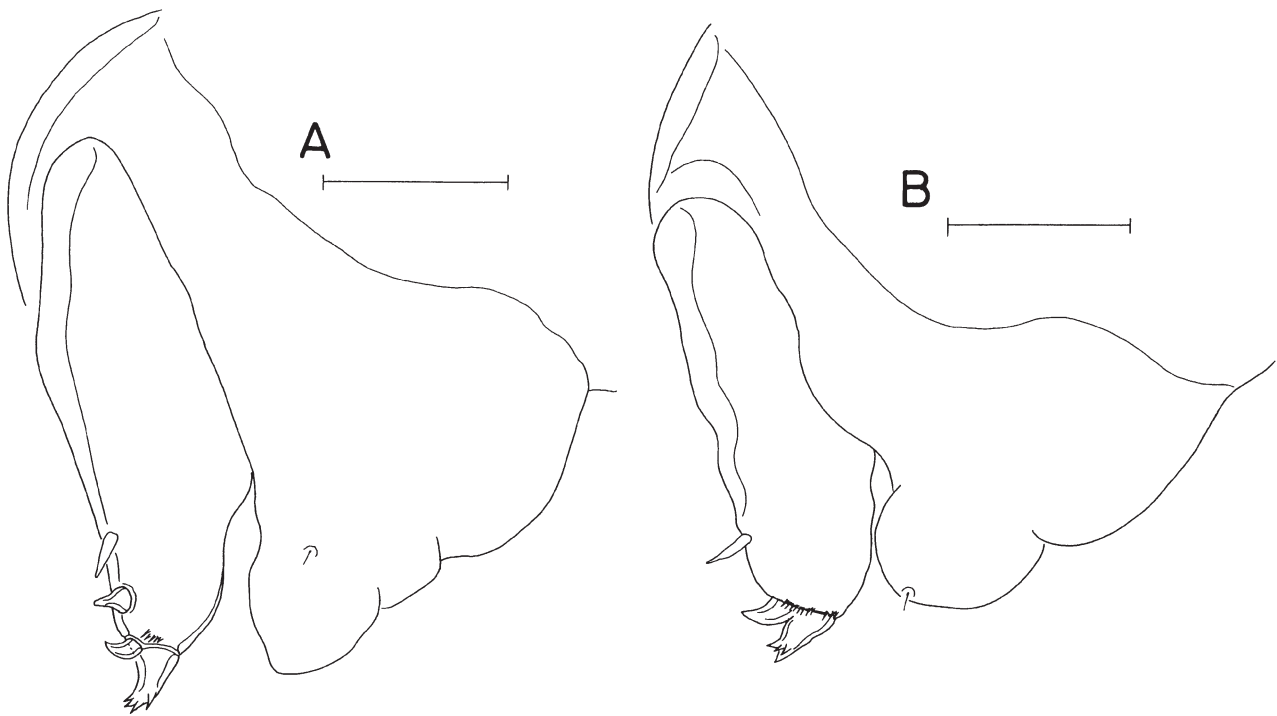
**Male.** Unknown.

**Remarks.** The combination of armature elements on the exopods of legs 1-4 of *H. fusiforme* sp. nov. is 5, 4, 3, and 3. This combination is shared by six other species of *Haplostoma*; *H. albicatum*, *H. dentatum*, *H. elegans*, *H. minutum*, *H. eruca*, and *H. depressum* sp. nov.

*Haplostoma fusiforme* sp. nov. can be distinguished from *H. dentatum*, *H. eruca* and *H. depressum* sp. nov. by the absence of any lobes or processes on the posterior margin of the labrum (cf. 8 pointed lobes in *H. dentatum*, 6 lobes in *H. eruca*, and 4 lobes in *H. depressum* sp. nov.), and from *H. albicatum*, *H. elegans*, and *H. minutum* by the absence of an outer seta on the protopod of legs 1-4. The new species can be differentiated further from *H. albicatum* and *H. minutum* by the narrower caudal ramus which is about 1.5 times longer than wide (cf. wider than long in *H. albicatum* and *H. minutum*) and from *H. elegans* by the possession of 2 setae on the mandible (cf. 3 setae in *H. elegans*).



**FIG. 102.** *Haplostoma fusiforme* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genitoabdomen, dorsal; D, left caudal ramus, outer; E, antennule; F, antenna; G, labrum; H, mandible; I, leg 1; J, leg 5. Scale bars: A, B, 0.5 mm; C, 0.2 mm; D-F, H, I, 0.02 mm; G, J, 0.05 mm.



**FIG. 103.** *Haplostoma fusiforme* sp. nov., female. A, leg 2; B, leg 3. Scale bars: 0.05 mm.

***Haplostoma mammiferum* sp. nov.**

(Fig. 104)

**Type material.** Holotype ♀ (MNHN-IU-2014-21519, dissected and mounted on a slide) from *Leptoclinides* sp.; Papua New Guinea, CRRF coll., 1999.

**Etymology.** The name reflects the presence of a prominent posterodorsal mammiform process on the last metasomite of the female.

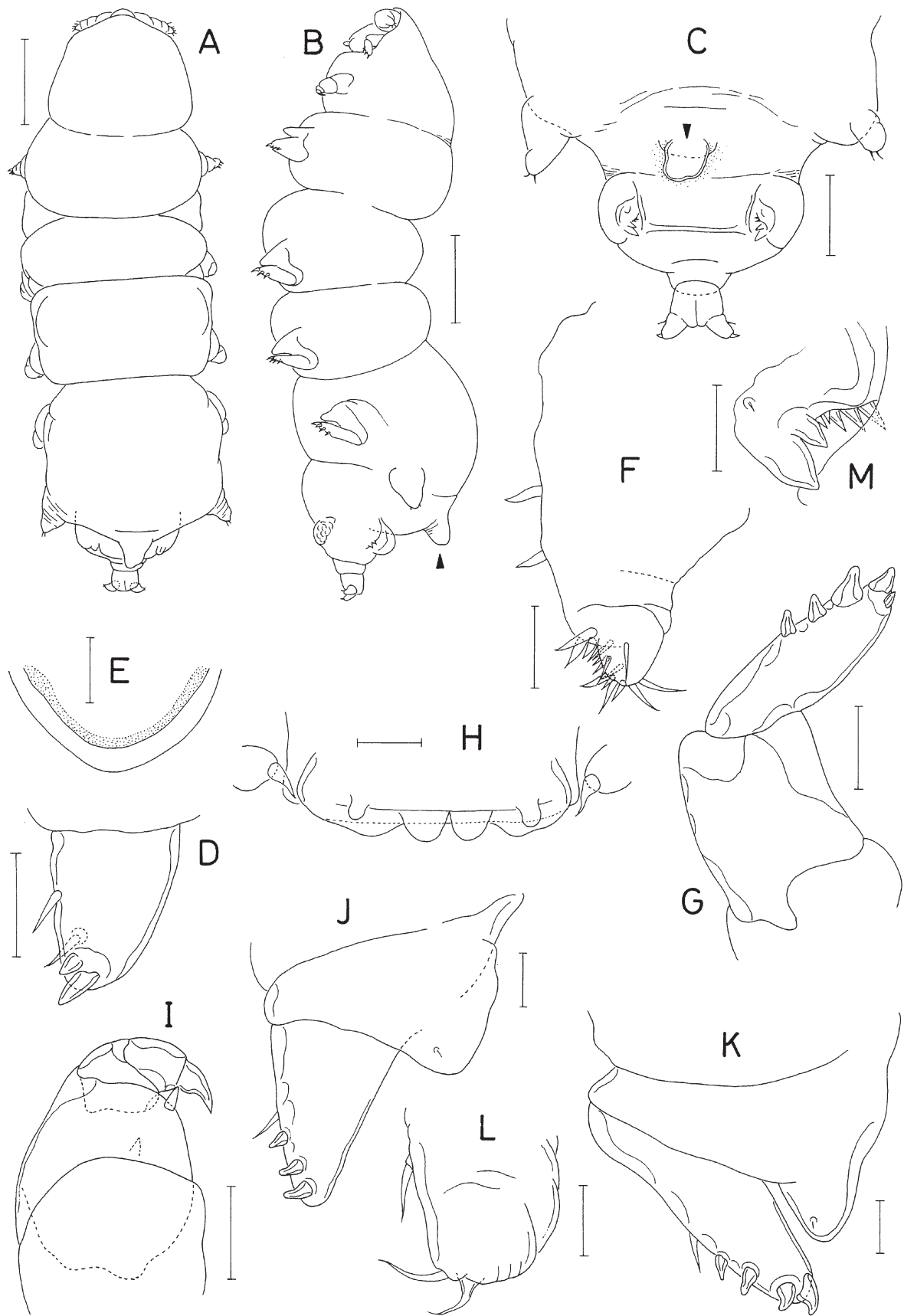
**Description of female.** Body (Fig. 104A, B) eruciform, consisting of cephalosome, 4-segmented metasome, and 2-segmented genitoabdomen. Body length 1.37 mm; maximum width 435 µm across second metasomite. Cephalosome 280×330 µm, narrower than metasome; 4 metasomites distinctly defined by deep constrictions; last metasomite compound, comprising fourth and fifth pedigerous somites, subdivided by ventral constriction, characteristically bearing distinct median tubercle posterodorsally (indicated by arrowhead in Fig. 104B, C). Genitoabdomen (Fig. 104C) small; anterior somite 130×237 µm; genital apertures located dorsally; posterior somite (free abdomen) clearly articulated from anterior somite, 46×62 µm. Caudal ramus (Fig. 104D) about 1.3 times longer than wide (33×25 µm) tapering; armed with 2 equal setae and 2 unequal spines, larger distal spine twice as long as smaller subdistal spine.

Rostrum (Fig. 104E) short, semicircular, fringed with thick, transparent surface layer. Antennule (Fig. 104F) indistinctly 2-segmented; armed with 2 setae on proximal segment and 16 setae on small distal segment; all setae small. Antenna (Fig. 104G) 2-segmented; proximal segment slightly longer than wide, unarmed; distal segment (endopod) about 2.4 times longer than wide (45×19 µm); armed with 5 stout spines (2 distal and 3 on inner margin), third inner margin spine largest and outermost of distal spines smallest.

Labrum (Fig. 104H) with 4 transparent lobes on posterior margin, 2 median lobes larger and semicircular, and 2 lateral lobes smaller, nipple-shaped. Mandible (Fig. 104H) positioned lateral to labrum, as lobe tipped with 1 seta. Maxillule and maxilla absent. Maxilliped (Fig. 104I) robust, 4-segmented; second segment bearing 2 small setae, other segments unarmed; terminal claw unarmed and unornamented.

Leg 1-4 consisting of protopod, exopod, and endopodal protrusion; exopods evenly tapering. Leg 1 (Fig. 104J) exopod armed with 1 seta and 3 small simple spines; endopod much broader than long. Legs 2 and 3 shaped and armed as leg 1. Leg 4 (Fig. 104K) exopod armed with 1 seta and 4 spines; endopod narrower than for legs 1-3.





**FIG. 104.** *Haplostoma mammiferum* sp. nov., female. A, habitus, dorsal; B, habitus, left; C, posterior end of body, dorsal; D, caudal ramus; E, rostrum; F, antennule; G, antenna; H, labrum; I, maxilliped; J, leg 1; K, leg 4; L, leg 5; M, genital aperture. Scale bars: A, B, 0.2 mm; C, 0.1 mm; D-K, M, 0.02 mm; L, 0.05mm.

Leg 5 (Fig. 104L) small, stout, as long as wide, bearing 3 setae (1 proximal and 2 distal). Leg 6 (Fig. 104M) represented by 2 broad, pointed processes and 5 smaller, dentiform elements on genital operculum.

**Male.** Unknown.

**Remarks.** *Haplostoma mammiferum* **sp. nov.** exhibits three unique features, each of which clearly differentiates it from other species, as follows: (1) the last metasomite bears a distinct median tubercle posterodorsally; (2) the labrum bears 4 lobes on the posterior margin, 2 larger median and 2 smaller lateral lobes; and (3) the exopod is armed with 1 seta and 3 spines in legs 1-3, but with 1 seta and 4 spines in leg 4. This last feature is especially remarkable because in legs 1-4 of all previously known species of *Haplostoma*, the numbers of armature elements on the exopods of legs 1 to 4 generally reduce from anterior (leg 1) to posterior (leg 4).

***Haplostoma symbioticum* sp. nov.**

(Figs. 105, 106)

**Type material.** Holotype ♀ (MNHN-IU-2014-21520) and 1 ♀ paratype (MNHN-IU-2014-17387, dissected) from *Leptoclinides* sp. (MNHN-IT-2008-4855 = MNHN A2/LEP/108); Baluan Is., Papua New Guinea, CRCHO 555 (02°32.27'S, 147°17.97'E), depth 15 m, Colin-CRRF coll., 23 June 2003.

**Etymology.** The specific name is derived from the Greek *symbio* (=living together), referring to its co-occurrence together with *H. mammiferum* **sp. nov.** in the same genus of host in the same geographic region.

**Description of female.** Body (Fig. 105A, B) small, slightly dorsoventrally depressed; consisting of cephalosome, 4-segmented metasome, and small genitoabdomen. Body length 723 µm; maximum width 270 µm (across last metasomite). Cephalosome 125×188 µm, narrower than first metasomite; metasome gradually broadening posteriorly; articulations between metasomites incomplete, but each metasomite distinctly defined by constrictions. Compound last metasomite with broad dorsal protrusion in middle (Fig. 105B). Genitoabdomen (Fig. 105C) 146×136 µm, obscurely defined from metasome, indistinctly 2-segmented (Fig. 105D), with short posterior somite (free abdomen). Caudal ramus (Fig. 105D) about 1.6 times longer than wide (34×21 µm), armed with 2 blunt setae (1 dorsal and 1 distal); distal seta specialized (with expanded proximal and slender distal halves), giving caudal ramus apparent 2-segmented condition.

Rostrum (Fig. 105E) as short, convex protrusion. Antennule (Fig. 105F) small, stout, 43 µm long, incompletely 3-segmented; armed with 1, 3, and 4 small setae on first to third segments, respectively. Antenna (Fig. 105G) 3-segmented including short first segment (coxa); second segment as long as wide, unarmed; third segment twice as long as wide (24×12 µm); armed with 3 spines, 2 larger distal spines each bearing 1-3 spinules subdistally.

Labrum (Fig. 105H) broad, with nearly parallel lateral margins, convex posterior margin with slightly angular apex; narrow sclerotization stripe present along posterolateral borders. Mandible, maxillule, and maxilla absent. Maxilliped (Fig. 105I) robust, 3-segmented; first segment much wider than long, unarmed; second segment (basis) wider than long, unarmed, with 1 spinulose tubercle near mediolateral corner; third segment (endopod) short, unarmed; terminal claw stout, with tooth-like process on inner proximal surface.

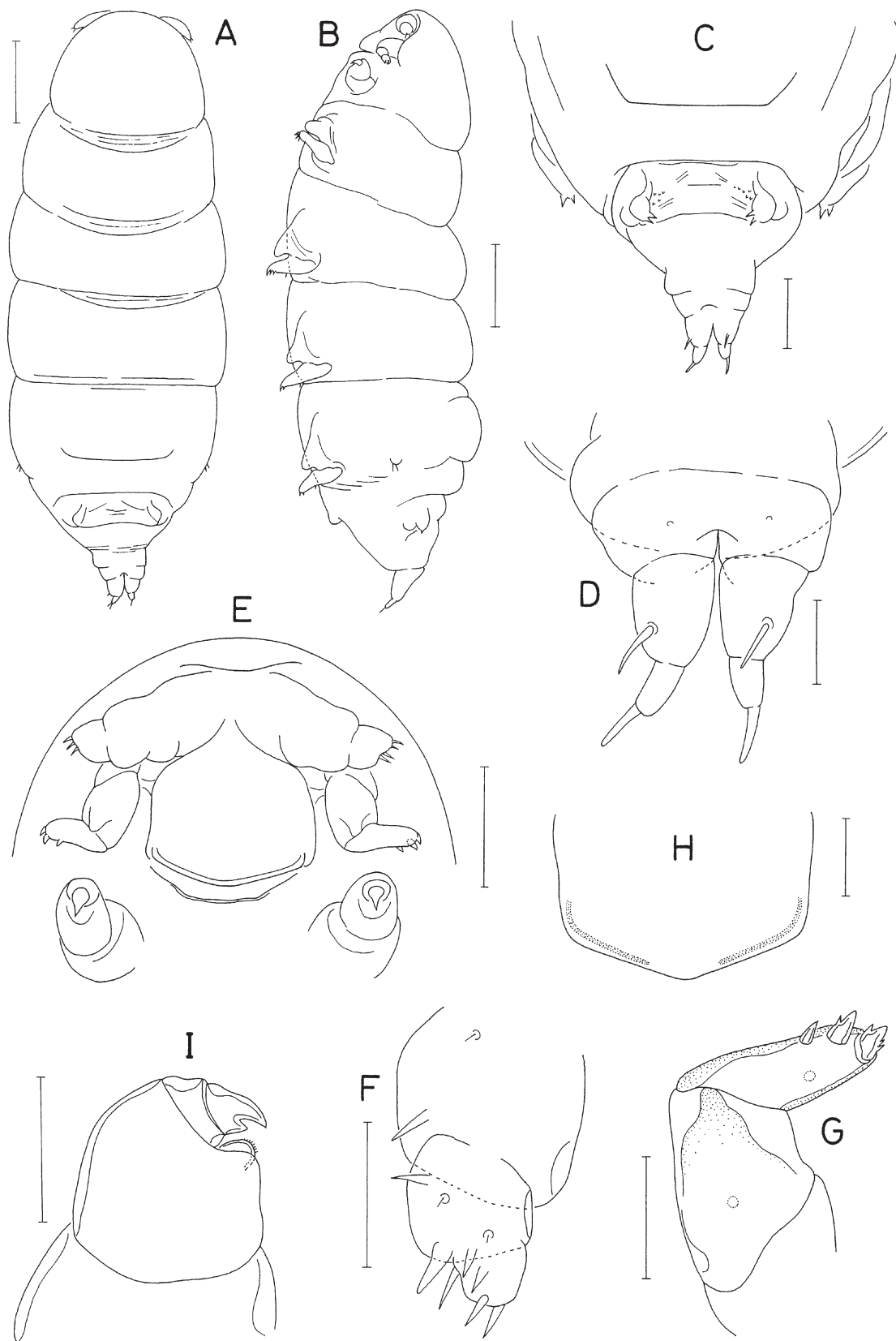
Legs 1-4 (Fig. 106A-D) each consisting of protopod, exopod, and semicircular endopod. Exopods armed with 1 seta plus 4 spines in leg 1, 1 seta plus 3 spines in leg 2, and 1 seta plus 2 spines in legs 3 and 4. Spines on exopods with 1 to several spinules subdistally. Two distal spines on exopods fused at base, appearing as single bifurcate spine. Endopods of legs 1-4 distinct.

Leg 5 (Fig. 106E) as small papilla-like lobe tipped with 2 setae. Leg 6 (Fig. 106F) represented by 2 groups (each group enclosed with hyaline material) of 3 dentiform processes; additional 5 smaller dentiform elements present near leg 6.

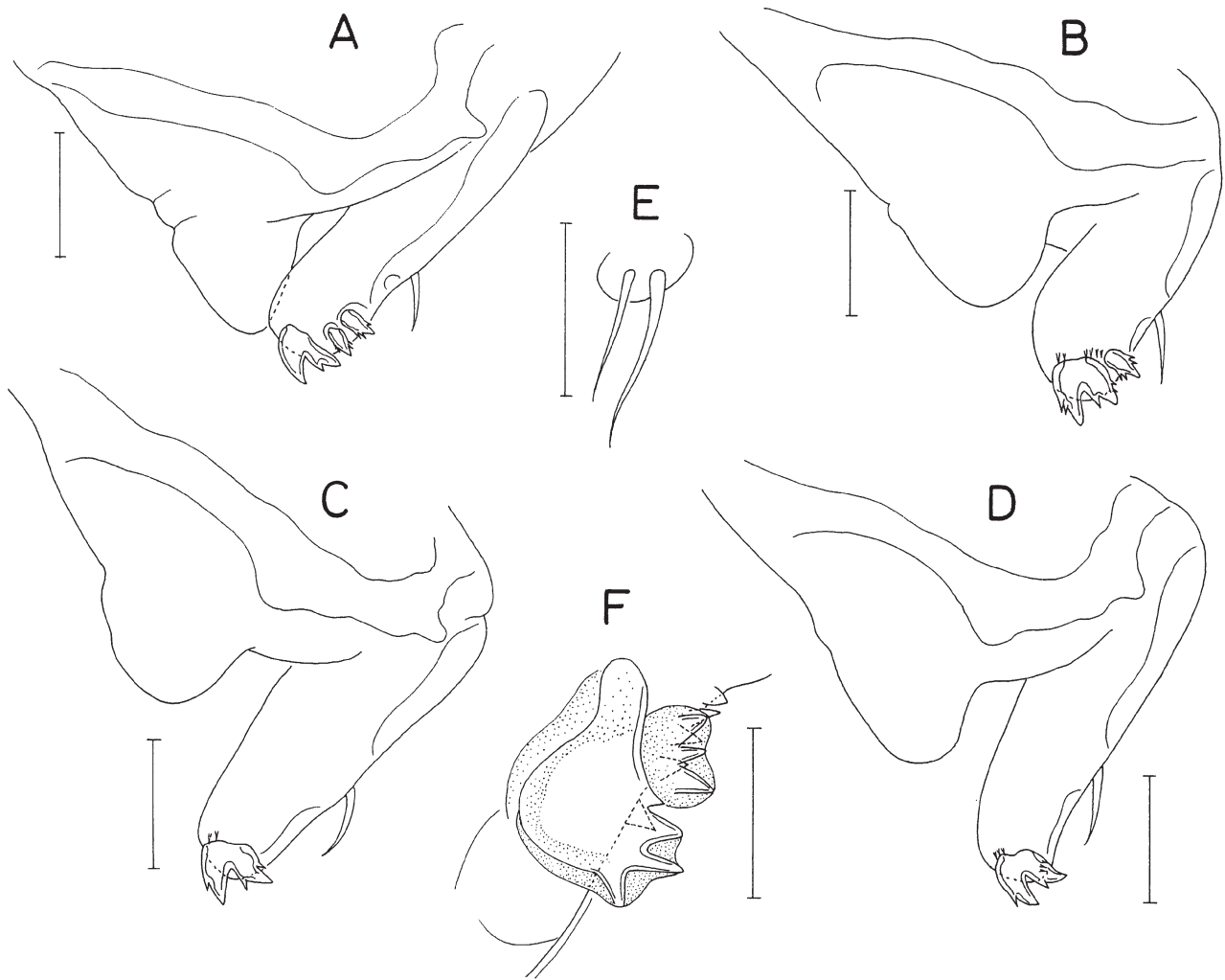
**Male.** Unknown.

**Remarks.** *Haplostoma symbioticum* **sp. nov.** may be differentiated from other congeneric species by the characteristic form and armature of its caudal ramus which bears 1 simple dorsal seta and 1 proximally expanded distal seta. The presence of only 3 spines on the antenna is also an unusual feature within *Haplostoma*, because only *H.*

*gibberum* (Schellenberg, 1922) was recorded as having 3 spines, although the latter species is not similar to the new species in other respects.



**FIG. 105.** *Haplostoma symbioticum* sp. nov., female. A, habitus, dorsal; B, habitus, left; C, genitoabdomen, dorsal; D, abdomen, dorsal; E, cephalic region, ventral; F, antennule; G, antenna; H, labrum; I, maxilliped. Scale bars: A, B, 0.1 mm; C, E, 0.05 mm; D, F-I, 0.02 mm.



**FIG. 106.** *Haplostoma symbioticum* **sp. nov.**, female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5; F, genital aperture. Scale bars: 0.02 mm.

In having a proximal seta on the exopods of legs 1-4, *H. symbioticum* **sp. nov.** belongs to subgroup 1 as defined by Ooishi (2004b). Members of this subgroup generally have simple spines on the exopods of legs 1-4, with the exception of two species, *H. minutum* and *H. setiferum*, described by Ooishi & Illg (1977), both of which have the two terminal spines on the exopods fused at base, thus appearing as one bifurcate spine, as in *H. symbioticum* **sp. nov.** In *H. minutum* and *H. setiferum* the caudal ramus bears 3 or more armature elements, the antenna bears 4 armature elements, and the protopods of legs 1-4 bears an outer seta. These differences serve to distinguish both of them from the new species.

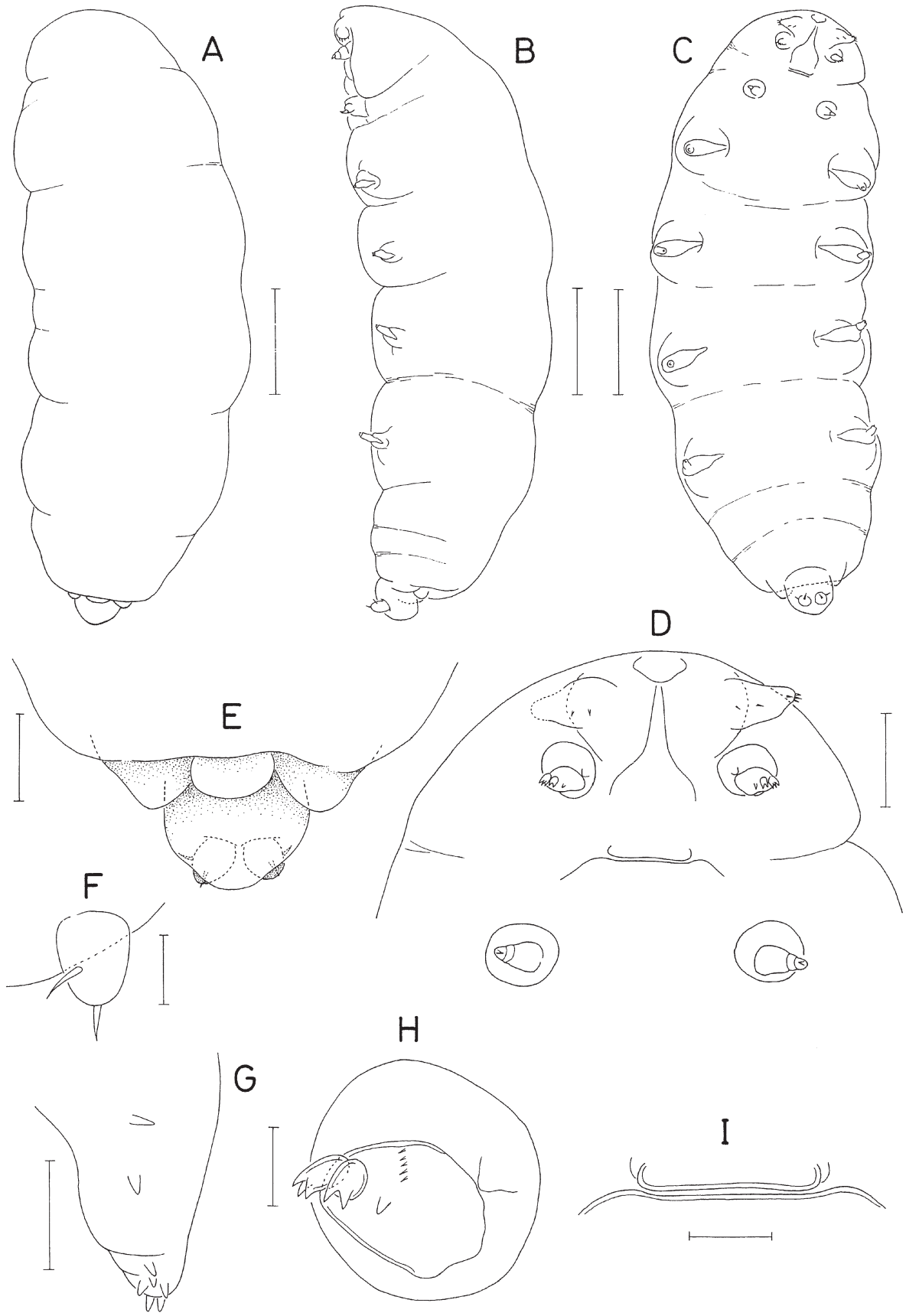
***Haplostoma simplex* sp. nov.**

(Figs. 107, 108)

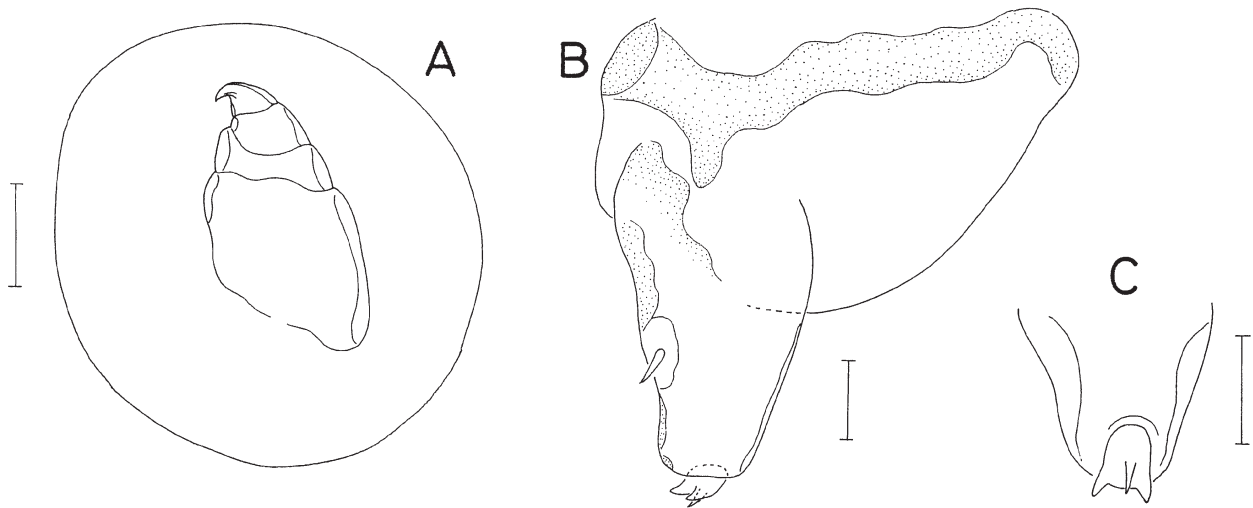
**Type material.** Holotype ♀ (intact, MNHN-IU-2014-21521) from *Citorclinum laboutei* Monniot F. & Millar, 1988; New Caledonia, UA281, depth 33 m, August 1986.

**Etymology.** The name is derived from the Latin *simpl* (=simple), referring to the simplified armature of legs and the loss oral appendages.

**Description of female.** Body (Fig. 107A-C) maggot-shaped, slightly dorsoventrally depressed; body length 1.18 mm, maximum width 427 µm (across second metasomite). Cephalosome (Fig. 107D) indistinctly defined from metasome, narrower than metasome; 4 metasomites defined by weak constrictions. Last metasomite bearing 3 broad



**FIG. 107.** *Haplostoma simplex* sp. nov., female. A, habitus, dorsal; B, habitus, left; C, habitus, ventral; D, cephalosome, ventral; E, genitoabdomen, dorsal; F, right caudal ramus, ventral; G, antennule; H, antenna, distal; I, labrum. Scale bars: A-C, 0.2 mm; D, E, 0.05 mm; F, G, I, 0.02 mm; H, 0.01 mm.



**FIG. 108.** *Haplostoma simplex* sp. nov., female. A, maxilliped; B, leg 1; C, distal part of exopod of leg 1, outer.

lobes along posterodorsal margin. Genitoabdomen (Fig. 107E) small, unsegmented, occupying only about 8% of body length, obscurely defined from metasome; genital apertures not seen, probably concealed by posterodorsal lobes of last metasomite. Caudal rami (Fig. 107F) small, 1.23 times longer than wide ( $27 \times 22 \mu\text{m}$ ), rounded distally, originating on ventral surface of genitoabdomen; armed with 2 small setae (1 outer and 1 distal).

Rostrum (Fig. 107D) small, wider than long, with convex posterior margin. Antennule (Fig. 107G) unsegmented, with partial suture line subdistally, armed with 8 small, blunt setae. Antenna (Fig. 107H) 2-segmented; proximal segment plate-like, broad, short, and unarmed; distal segment with 2 spines (trifurcate distal and bifurcate subdistal), 1 rudimentary seta at distal third, and 1 row of minute spinules near middle.

Labrum (Fig. 107D, I) small, slit-like, unornamented. Mandible, maxillule, and maxilla absent. Maxilliped (Fig. 108A) consisting of 4 segments plus terminal claw; all segments unarmed and unornamented; first segment plate-like, much broader than other segments; terminal claw short, curved.

Leg 1 (Fig. 108B) consisting of protopod and exopod. Protopod lacking outer seta. Exopod tapering, not articulated from protopod, armed with 1 small seta on outer margin and 1 spine distally; distal spine (Fig. 108C) bifurcate, with ventral and dorsal branches, bearing 1 small setule in middle of outer surface. Endopod not defined. Legs 2-4 same as leg 1 in form and armature. Legs 5 and 6 not seen.

**Male.** Unknown.

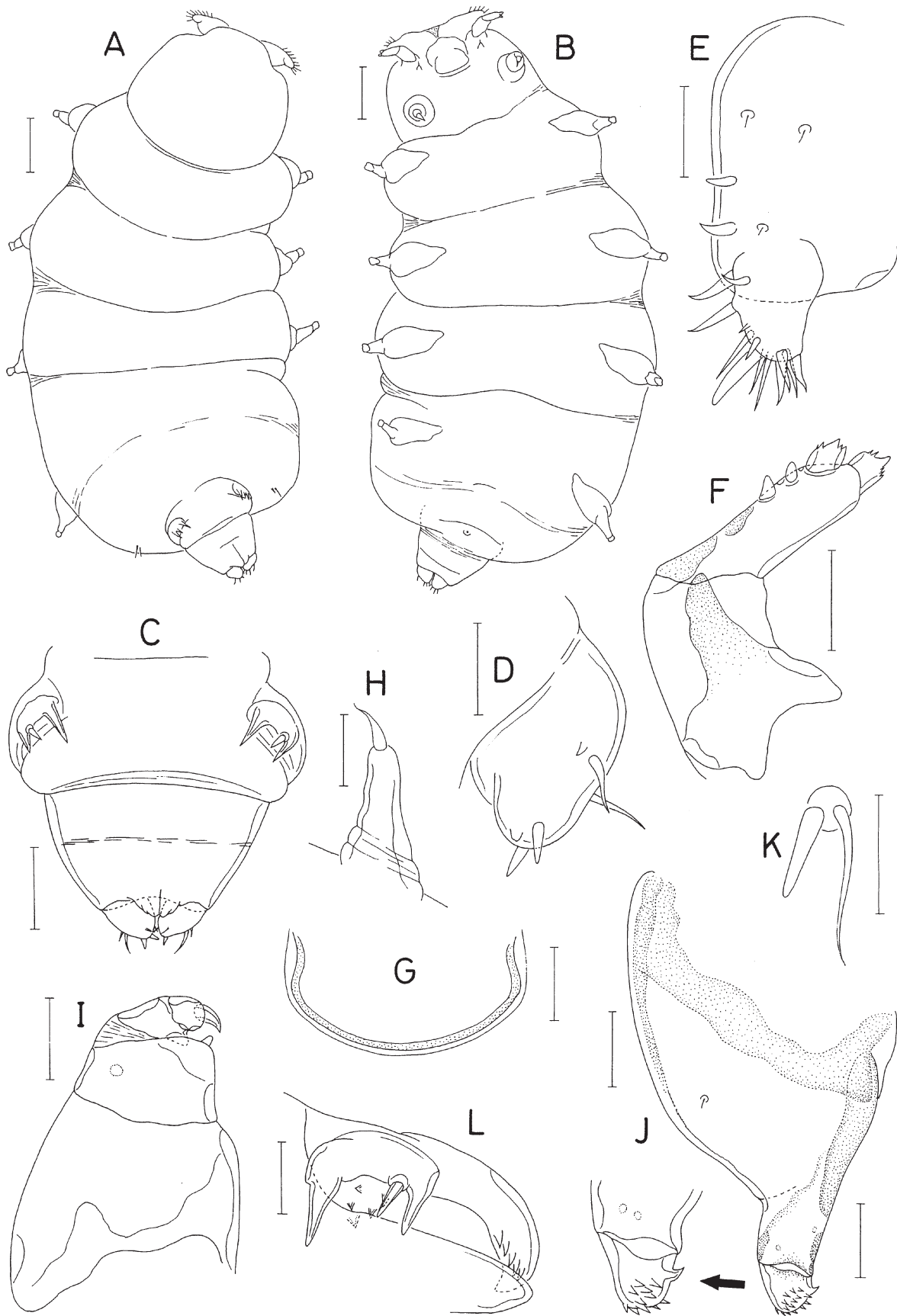
**Remarks.** *Haplostoma simplex* sp. nov. may readily be distinguished from its congeners by the armature of legs 1-4. All of the legs are identical: each has 1 outer seta and 1 distal, bifurcate spine on the exopod. Across all species of *Haplostoma* this is the smallest known number of armature elements on the legs; for example, all other species are known to have at least 4 armature elements on the exopod of leg 1. The distal spine of the exopod of each leg is specialized; it is bifurcate with dorsal and ventral branches (not inner and outer branches as is typical) and it bears a setule on its outer surface.

*Haplostoma simplex* sp. nov. exhibits several other unusual features, including the lack of the mandible and leg 5, the possession of small caudal rami bearing only 2 simple setae, and the presence of 2 spines and 1 rudimentary seta on the antenna.

***Haplostoma pygmaeum* sp. nov.**

(Fig. 109)

**Type material.** Holotype ♀ (MNHN-IU-2014-21522, dissected and mounted on a slide) from *Cystodytes dellechiajei* (Della Valle, 1877); New Caledonia, Récif Neobumki, 1 mile North of passe de Kouaré, Stn NC31, depth 10-40m, Monniot coll., 10 March 1987.



**FIG. 109.** *Haplostoma pygmaeum* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, genitoabdomen, dorsal; D, right caudal ramus, dorsal; E, antennule; F, antenna; G, labrum; H, mandible; I, maxilliped; J, leg 1; K, leg 5; L, genital aperture. Scale bars: A, B, 0.1 mm; C, 0.05 mm; D-G, I-L, 0.02 mm; H, 0.01 mm.

**Etymology.** The name is derived from the Greek *pygm* (=a fist), alluding to the fist-like distal armature on exopods of legs 1-4.

**Description of female.** Body (Fig. 109A, B) eruciform, robust, dorsoventrally depressed, divisible into cephalosome, 4-segmented metasome, and 2-segmented genitoabdomen. Body length 1.10 mm; maximum width 512  $\mu\text{m}$  (across third metasomite). Cephalosome 231 $\times$ 296  $\mu\text{m}$ , clearly defined from and distinctly narrower than first metasomite; metasome gradually broadening posteriorly; 4 metasomites well-defined from one another. Genitoabdomen (Fig. 109C) 172 $\times$ 183  $\mu\text{m}$ ; genital apertures large, positioned dorsolaterally. Abdomen strongly tapering, 1.9 times wider than long. Caudal rami convergent, small; each ramus (Fig. 109D) wider than long (25 $\times$ 28  $\mu\text{m}$ ), armed with 6 setae (2 rudimentary, papilliform).

Rostrum absent. Antennule (Fig. 109E) 2-segmented, 76  $\mu\text{m}$  long; broad proximal segment with 2 setae; narrower distal segment less than half length of proximal segment, armed with 12 setae and 1 aesthetasc. Antenna (Fig. 109F) 2-segmented; proximal segment unarmed; distal segment as long as proximal segment, about 2.6 times longer than wide (37 $\times$ 14  $\mu\text{m}$ ); armed with 4 spines (proximal 2 small and transparent, distal 2 broad, with serrate distal margin).

Labrum (Fig. 109G) with convex posterior margin bearing thin, transparent fringe. Mandible (Fig. 109H) as elongate lobe tipped with 1 small seta. Maxillule and maxilla absent. Maxilliped (Fig. 109I) robust, 4-segmented; first segment broad but unarmed; second segment much wider than long, with 1 small, blunt seta mediolaterally; third and fourth segments small, unarmed; terminal claw small and simple.

Leg 1 (Fig. 109J) consisting of protopod and exopod, but lacking articulation: protopod unarmed; endopod absent. Exopod digitiform, armed distally with subglobular, fist-like element articulated from exopodal segment at base, and bearing 1 small, claw-like process on outer margin and ornamented with about 10 spinules (or denticles) on anterior surface; no seta or spine present on exopod. Legs 2-4 as leg 1 in shape and armature.

Leg 5 (Fig. 109K) located on posteroventral surface of last metasomite; present as small knob tipped with 1 broad, blunt seta and 1 thin, longer seta. Leg 6 (Fig. 109L) represented by 1 small spine and 2 spiniform processes on genital operculum; 5 minute denticles present posterior to leg 6, and row of 5 spinules present lateral to leg 6.

**Male.** Unknown.

**Remarks.** The taxonomic position of *Haplostoma pygmaeum* **sp. nov.** seems to lie close to the boundary between *Haplostoma* and the related genus *Haplosaccus* Chatton & Harant, 1924. In the original description of *Haplosaccus* given by Chatton & Harant (1924c), three characters were highlighted as diagnostic features for the new genus: (1) the caudal rami are extremely reduced; (2) the antenna is armed with a strong distal claw; and (3) the exopods of legs 1-4 have a terminal hook. In retaining distinct caudal rami and in the presence of 4 spines on the last segment of the antenna, the new species seems better placed in *Haplostoma*. The peculiar form of the exopod of legs 1-4, which bears only the fist-like terminal element, is a distinctive autapomorphy of *H. pygmaeum* **sp. nov.** We infer that this exopod is derived from the single spine-bearing type of exopod, as found in *Haplostoma*.

## Genus *Haplosaccus* Chatton & Harant, 1924

**Diagnosis** (female). Body eruciform or vermiform, unsegmented. Genitoabdomen defined by its narrowness; genital apertures positioned dorsolaterally, with copulatory pore on ventral surface. Caudal rami vestigial. Rostrum present or absent. Antennule short, at most 2-segmented, armed with setae. Antenna 2- or 3-segmented; terminal segment armed distally with 1 claw only, or 1 claw plus 1 spine, or 2 spines. Labrum present. Mandible absent, or represented by 1 seta or as digitiform, distally bilobed process. Maxillule and maxilla absent. Maxilliped consisting of 4 segments plus terminal claw. Legs 1-4 same in form and armature, consisting of unarmed protopod plus rami; exopod distally with 1 strong claw or bifurcate spine, with or without 1 seta on outer margin; endopod variably defined. Leg 5 represented by 1 small seta or absent. Leg 6 represented by 1 spine and 1 spiniform process on genital operculum, accompanied with 5 dentiform elements.

**Type species.** *Haplosaccus sacculus* (Chatton & Brément, 1910) (originally as *Aplostoma sacculus*) by original designation.



**Remarks.** The discovery of *Haplosaccus ardius* sp. nov. described below, raises uncertainty about the generic position of *H. elongatus* Ooishi & Illg, 1977. The most important diagnostic features of *Haplosaccus* seem to be the presence of a strong terminal claw on the antenna and on each of the exopods of legs 1-4. The type species *H. sacculus* and *H. ardius* sp. nov. share these features, but *H. elongatus* does not. It seems possible that *H. elongatus* should be transferred to another genus, possibly *Haplostoma*, but this must await re-examination of the type material. The major morphological differences between these three species, their known hosts and their distributions are given in Table 5.

**TABLE 5.** Summary of differences between species of *Haplosaccus*.

Characters	<i>H. sacculus</i> (Chatton & Brément, 1910)	<i>H. elongatus</i> Ooishi & Illg, 1977	<i>H. ardius</i> sp. nov.
antennal armature	1 claw	2 spines	1 claw and 1 spine
mandible	absent	bilobed process	a seta
legs 1-4 exopods	1 claw	bifurcate spine	1 claw + 1 seta
legs 1-4 endopods	absent	vestigial	well-developed
Leg 5	absent	a seta	a seta
Hosts	<i>Diplosoma spongiforme</i> (Giard, 1872)	<i>Aplidium arenatum</i> (Van Name, 1945); <i>A. glabrum</i> (Verrill, 1871)	<i>Didemnum molle</i> (Herdman, 1886)
Distribution	Mediterranean Sea	Northeast Pacific	New Caledonia

***Haplosaccus ardius* sp. nov.**

(Fig. 110)

**Type material.** Holotype ♀ (MNHN-IU-2014-21523), 6 ♀♀ paratypes (MNHN-IU-2014-21524) and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17388) from *Didemnum molle* (Herdman, 1886); near Ouaco, Koumac Sector, New Caledonia, LAGON cruise, RV “Alis”, Stn DW919 (20°52.2’S, 164°25.2’E), depth 17 m, B. Richer de Forges-IRD coll., 26 April 1988.

**Etymology.** The name is derived from the Greek *ard* (=arrowhead), reflecting the arrowhead-like rostrum of the new species.

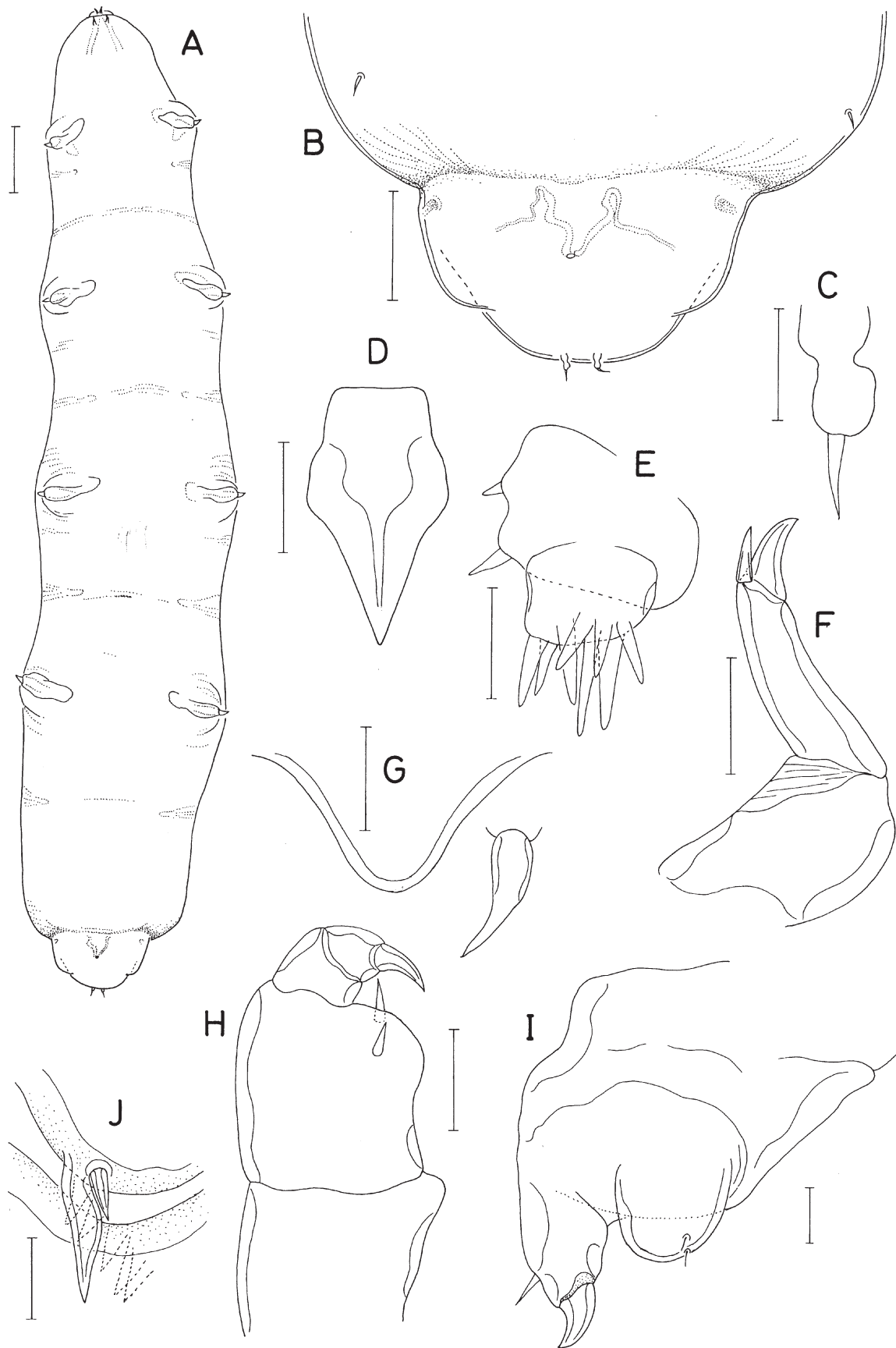
**Description of female.** Body (Fig. 110A) vermiform, unsegmented, gradually narrowing anteriorly; body length 2.96 mm, maximum width 0.64 mm (at level of leg 4). Cephalosome not defined from metasome; 4 metasomes recognizable by weak lateral constrictions. Genitoabdomen (Fig. 110B) 164×297 µm, not articulated from metasome, but defined by abrupt narrowing, unsegmented but divisible into broader anterior two-thirds and narrower posterior third, with convex rear margin. Caudal ramus (Fig. 110C) vestigial, 12×6 µm, constricted in middle, tipped with 1 minute seta. Egg sac containing 10 rows of eggs; each egg about 160 µm in diameter.

Cephalic appendages very small. Rostrum (Fig. 110D) 24×13 µm, minute, but well-sclerotized, arrowhead-shaped with pointed apex. Antennule (Fig. 110E) 19 µm long, shorter than wide, 2-segmented, armed with 2 and 8 setae on first and second segments, respectively. Antenna (Fig. 110F) 2-segmented; proximal segment slightly longer than wide, unarmed; distal segment 2.25 times longer than wide (18×8 µm), armed distally with 1 inner claw and 1 outer spine.

Labrum (Fig. 110G) strongly tapering posteriorly towards rounded apex. Mandible (Fig. 110G) represented by broad seta lateral to labrum. Maxillule and maxilla absent. Maxilliped (Fig. 110H) consisting of 4 segments plus terminal claw; first segment unarmed, second segment as long as wide, with 2 small setae; narrower third and fourth segments unarmed; terminal claw acutely pointed, slightly longer than fourth segment.

Leg 1 (Fig. 110I) consisting of protopod, short exopod and semicircular endopod; protopod lacking outer seta; exopod incompletely defined from protopod, armed with 1 seta on outer margin and strong claw distally; endopod unarmed but with pair of minute sensilla. Legs 2-4 exactly same as leg 1 in shape and armature.

Leg 5 (Fig. 110B) represented by 1 minute seta located ventrolaterally on posterior part of metasome. Leg 6 (Fig. 110J) represented by 1 spine and 1 larger, spiniform process on genital operculum; 5 spiniform internal elements accompanying leg 6.



**FIG. 110.** *Haplosaccus ardius* sp. nov., female. A, habitus, ventral; B, urosome, ventral; C, caudal ramus; D, rostrum; E, antennule; F, antenna; G, labrum and left mandible; H, maxilliped; I, leg 1; J, genital aperture. Scale bars: A, 0.2 mm; B, 0.1 mm; C-J, 0.01 mm.

**Male.** Unknown.

**Remarks.** In having a strong terminal claw on the antenna and on the exopods of legs 1-4, the new species belongs to the genus *Haplosaccus* which currently consists of only two known species, *H. sacculus* and *H. elongatus*. The most significant diagnostic features of *H. ardius* **sp. nov.** are: the antenna is armed terminally with 1 strong claw and 1 spine, and the exopods of legs 1-4 are armed with 1 outer seta and 1 strong terminal claw. These features clearly differentiate the new species from its two congeners (see Table 5 for more detailed comparison).

### Genus *Haplostomella* Chatton & Harant, 1924

**Diagnosis.** Female: Body eruciform or vermiform, usually unsegmented, but occasionally indistinctly divisible into cephalosome, metasome, and genitoabdomen. Cephalosome discernible by weakly developed cephalic shield. Metasome incorporating fifth pedigerous somite, sometimes with lobate dorsolateral folds in same plane as legs 1-5. Genitoabdomen not articulated from metasome, consisting of broad genital and narrow abdominal regions. Genital apertures large, positioned dorsolaterally; genital operculum bearing 3 teeth on inner side of distal border. Caudal rami distinct, armed with up to 5 setae. Rostrum not developed. Antennule small, 1- or incompletely 2-segmented, but exceptionally 4-segmented in *Haplostomella magellanica* (Chatton & Brément, 1910). Antenna basically 3-segmented, with unarmed first segment, 1 seta on second segment, and 3 setae and 1 lobate element on third segment. Labrum broad, simple, or occasionally with lobes on posterior margin. Mandible absent or consisting of lobe tipped with distal element(s); distal element(s) variable with species, either spine, claw, or 1 or 2 setae. Maxillule absent. Maxilla indistinctly 2-segmented; proximal segment unarmed; distal segment with 1 or 2 setae. Maxilliped broad, chelate, and consisting of 2 segments plus terminal claw; proximal segment (syncoxa) unarmed; distal segment (basis) bearing inner distal protrusion and acute spine on anteromedial surface; terminal claw short, directed between distal protrusion and spine of second segment. Legs 1-4 consisting of unsegmented protopod, exopod and endopod; protopod with seta on outer margin; exopod distally bilobed, with sclerotized, claw-like anterior lobe and rounded posterior lobe tipped with 1 setule; endopod not articulated from protopod, unarmed. Ventrolateral surface of body lateral to legs 1-4 sometimes with 1 to 5 tubercles. Leg 5 as small lobe tipped with 2 or 3 setae.

Male: Body cyclopiform, distinctly segmented, clearly divisible into prosome and urosome. Prosome consisting of cephalosome and first to fourth pedigerous somites. Urosome 6-segmented, consisting of fifth pedigerous somite, genital somite, and 4 abdominal somites. Caudal ramus with 6 setae; 2 median terminal setae (setae IV and V) long, fringed with membrane along both margins. Antenna 7- or 8-segmented; proximal segments each with 1 large aesthetasc. Antenna and labrum as in female. Mandible, maxillule, and maxilla vestigial or absent. Maxilliped similar to that of female. Legs 1-4 biramous, consisting of coxa, basis, exopod, and endopod. Setation variable with species: coxa with or without inner seta; basis with outer seta; inner distal element on leg 1 present or absent. Exopod 3-segmented. Endopod 1- to 3-segmented in leg 1, and 3-segmented in legs 2-4. Leg 5 consisting of 1 lateral seta on fifth pedigerous somite and free or lobate exopod tipped with 2 setae. Leg 6 represented by 1 or 2 setal elements on genital operculum

**Type species.** *Haplostomella malacocera* Chatton & Harant, 1924, by original designation.

**Remarks.** Marchenkov & Boxshall (2003) recognised 11 valid species in the genus *Haplostomella*, including their new species, *H. borealis* Marchenkov & Boxshall, 2003. Boxshall & Halsey (2004) regarded *Haplostomella* as the first offshoot within the family Botryllophilidae because its male lacks many of the synapomorphies that are shared by the males of *Botryllophilus*, *Haplostoma* and *Haplostomides*, such as the presence of the rosette of densely packed aesthetascs on the proximal segment of the antennule. The female of *Haplostomella* is distinctive within the family in the form of its antenna, maxilliped, and swimming legs.

## *Haplostomella tuberculata* (Chatton & Harant, 1924)

(Fig. 111)

**Material examined.** 33 ♀♀ (MNHN-IU-2014-21525, 2 ♀♀ dissected) in *Aplidium nordmanni* Milne Edwards, 1841; Greece, Stn 486, Koukouras coll., date unknown.

**Redescription of female.** Body (Fig. 111A) eruciform, consisting of cephalosome, cylindrical metasome, and small genitoabdomen. Body length 2.36 mm, maximum width 545 µm (across anterior third): cephalosome 190×290 µm, incompletely separated from metasome, but distinctly defined by its narrowness. Metasome unsegmented, lacking any constriction, with 5 pairs of small dorsolateral folds (vestiges of tergites), each pair located at level of leg pair (legs 1 to 5). Genitoabdomen (Fig. 111B, C) tapering, unsegmented, not articulated from metasome, occupying about 16% of body length, with narrow posterior half; genital apertures positioned dorsolaterally; genital operculum large, rounded, with 3 strong denticles. Caudal rami (Fig. 111D) incompletely articulated from abdomen, narrowing distally, 2.64 times longer than wide (95×36 µm); armed with 4 distinct setae (3 distal and 1 dorsal) and 1 small setule located midway along outer margin.

Rostrum short with convex posterior margin. Antennule (Fig. 111E) incompletely 2-segmented, about 2.2 times longer than wide, bearing 16 setae; all setae characteristically small, setule-like, subequal in length. Antenna (Fig. 111F) indistinctly 3-segmented and curved ventrally; first segment longest but unarmed; second segment distally bearing 1 small seta and 1 row of several spinules; third segment bearing 1 subdistal and 2 distal, small setae, 1 spinulose lobate process subdistally, and patch of spinules in middle.

Labrum (Fig. 111G) short, unornamented, with broadly convex posterior margin. Mandible (Fig. 111H) 1-segmented, digitiform, with 2 weak swellings on medial margin, and tipped with 1 naked seta. Maxillule absent. Maxilla (Fig. 111I) 1-segmented, with 2 weak swellings on subdistal medial margin, tipped with 1 weakly pinnate seta. Maxilliped (Fig. 111J) robust, consisting of 2 segments plus terminal claw; proximal segment (syncoxa) much broader than long, unarmed; distal segment (basis) as long as wide, bearing 1 spine and 1 spinulose, lobate process at mediolateral corner, and ornamented with numerous minute spinules on outer (ventral) surface; terminal claw pointed distally and directed between mediolateral process and spine of distal segment.

Leg 1 (Fig. 111K) consisting of unsegmented protopod, exopod and endopod. Intercostal plate absent. Protopod broad, with 1 seta on outer margin. Exopod bilobed; anterior lobe claw-like, sclerotized, pointed distally, bearing small, mammiform subdistal process; posterior lobe broader than anterior, rounded distally, tipped with 1 small setule. Unarmed endopod broader than long, broader than exopod, with slightly concave distal margin. Legs 2-4 same as leg 1.

Leg 5 (Fig. 111B, C, L) as small lobe tipped with 3 small, naked setae.

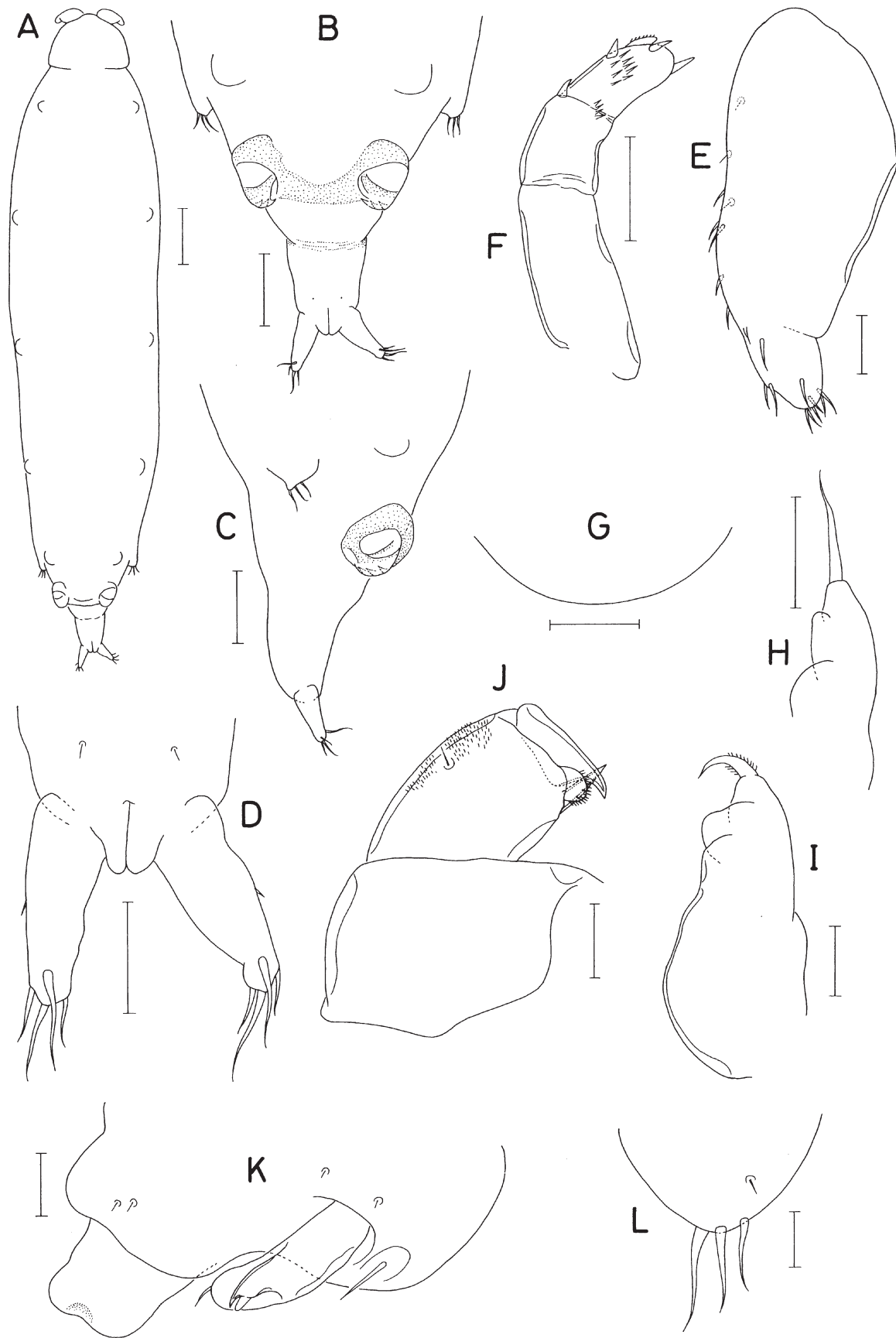
**Male.** Unknown.

**Remarks.** The above specimens are identified as *H. tuberculata* on the basis of the close agreement between these specimens and the original description of this species given by Chatton & Harant (1924a), as follows: (1) the metasome bears 5 pairs of small dorsolateral folds (vestiges of tergites); (2) the form of the genitoabdomen in lateral view is the same as illustrated in the original description; (3) the antennule is incompletely 2-segmented and armed with equally small setae; (4) the caudal ramus bears 4 distal setae; (5) the mandible and maxilla are each tipped with 1 seta; and (6) leg 5 bears 3 setae. Chatton & Harant (1924a) gave a measurement of 1.5 mm for the body length of the type specimens; this is significantly shorter than 2.36 mm for our measured specimen. This length difference can probably be explained by variation in the state of maturity of the material: Chatton & Harant (1924a) mentioned that the type specimens were immature females. In addition, we have observed that females of *Haplostomella* are highly elastic and will swell up gradually when immersed in lactic acid for study.

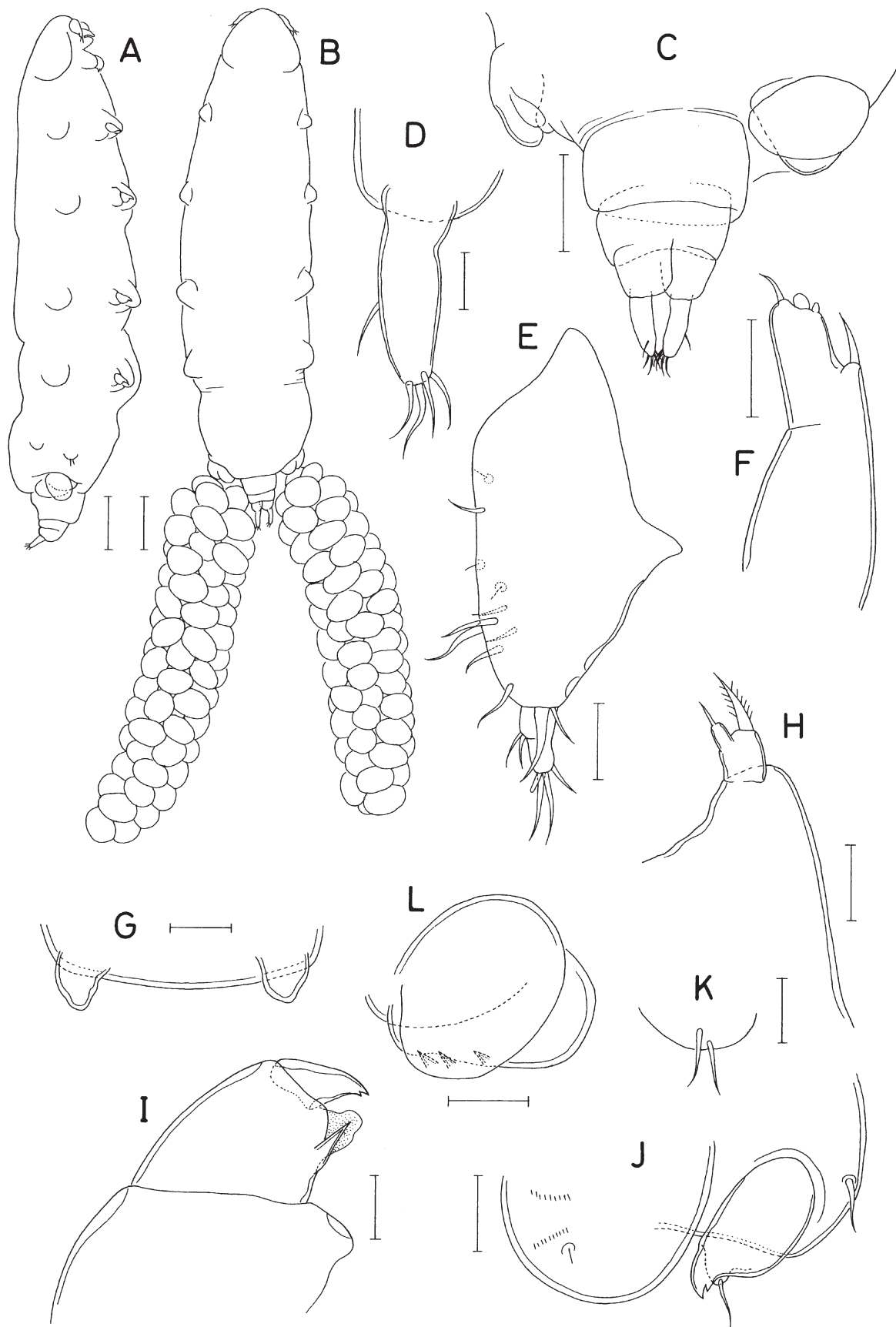
## *Haplostomella bilobata* sp. nov.

(Figs. 112, 113)

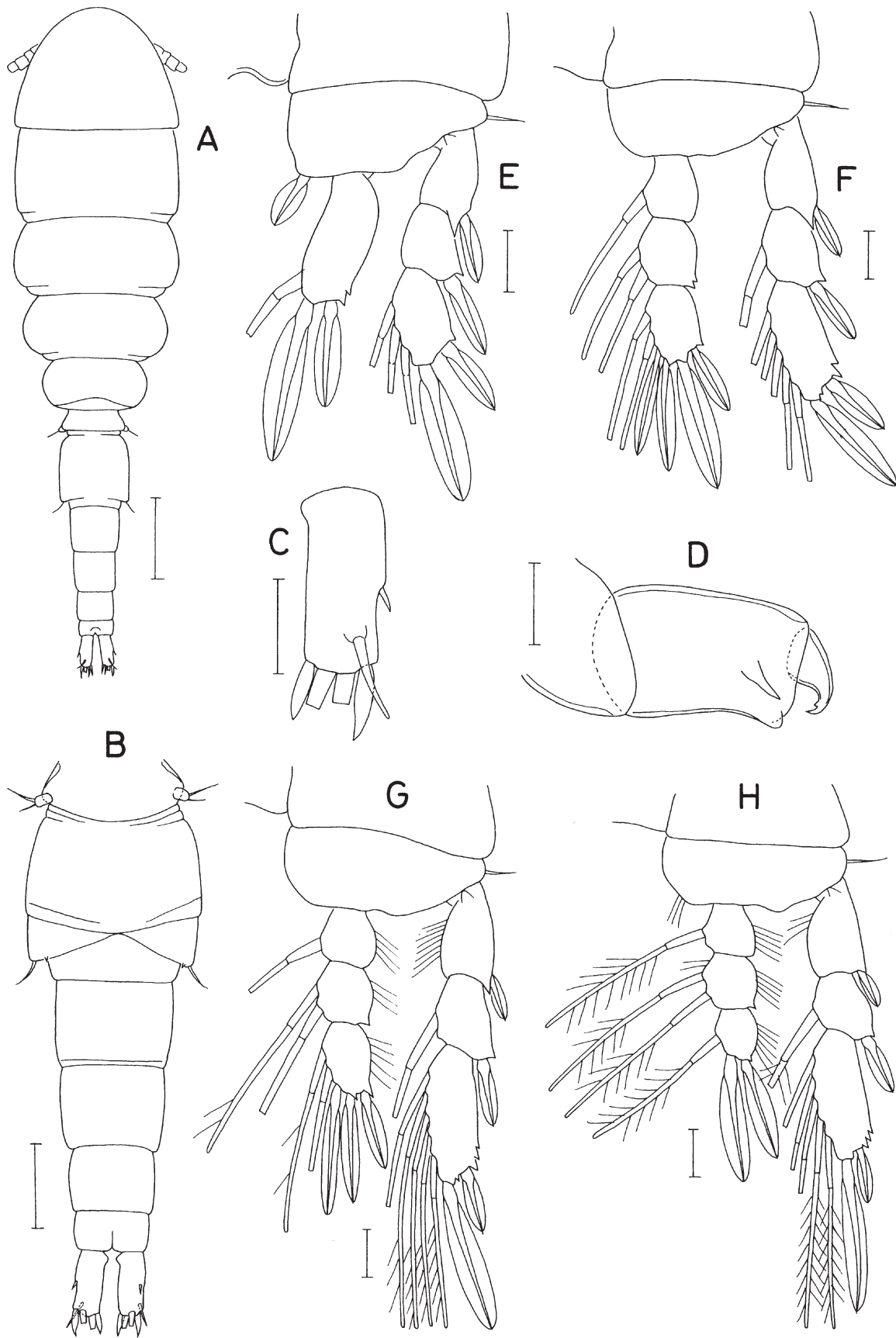
**Type material.** Holotype ♀ (MNHN-IU-2014-21526), 2 ♀♀ paratypes (MNHN-IU-2014-21527), and 2 ♀♀, 1 ♂ paratypes (dissected, MNHN-IU-2014-17389) from *Aplidium* sp.; Kerguelen Islands, no other collection data.



**FIG. 111.** *Haplostomella tuberculata* (Chatton & Harant, 1924), female. A, habitus, dorsal; B, posterior part of body, dorsal; C, posterior part of body, left; D, caudal rami, dorsal; E, antennule; F, antenna; G, labrum; H, mandible; I, maxilla; J, maxilliped; K, leg 1; L, leg 5. Scale bars: A, 0.2 mm; B, C, 0.1 mm; D, 0.05 mm; E-L, 0.02 mm.



**FIG. 112.** *Haplostomella bilobata* sp. nov., female. A, habitus, right; B, habitus, dorsal; C, genitoabdomen, dorsal; D, right caudal ramus, ventral; E, antennule; F, antenna; G, labrum; H, maxilla; I, maxilliped; J, leg 1; K, leg 5; L, genital aperture. Scale bars: A, B, 0.2 mm; C, 0.1 mm; D-K, 0.02 mm; L, 0.05 mm.



**FIG. 113.** *Haplostomella bilobata* sp. nov., male. A, habitus, dorsal; B, urosome, ventral; C, right caudal ramus, dorsal; D, maxilliped; E, leg 1; F, leg 2; G, leg 3; H, leg 4. Scale bars: A, 0.1 mm; B, 0.05; C-H, 0.02 mm.

**Etymology.** The specific name alludes to the presence of a pair of lobes on the labrum of the new species.

**Description of female.** Body (Fig. 112A, B) eruciform, consisting of unsegmented anterior part and short abdomen. Body length 2.04 mm; maximum width 496  $\mu\text{m}$  (across region of leg 4). Anterior half of body slightly tapering anteriorly; cephalosome narrower than metasome, incompletely defined from metasome by posterolateral margins of cephalic shield. Cylindrical metasomal region incorporating leg 5, with 5 pairs of small dorsolateral folds; last pair at level of leg 5 much smaller than anterior 4 pairs. Genital somite completely fused to metasome; paired genital apertures (Fig. 112L) positioned dorsolaterally. Genital operculum bearing 3 teeth inside. Abdomen (Fig. 112C) tapering, 3-segmented, but articulation incomplete between last 2 somites. Caudal ramus (Fig. 112D) about 2.9 times longer than wide (69 $\times$ 24  $\mu\text{m}$ ), slightly longer than anal somite, with 5 subequal, naked setae (1 lateral and 4 distal); lateral seta positioned at 63% of ramus length. Egg sac (Fig. 112B) 1.40 $\times$ 0.34 mm; each egg about 115  $\mu\text{m}$  in diameter.

Rostrum absent. Antennule (Fig. 112E) 100  $\mu\text{m}$  long, 2-segmented; proximal segment with 9 setae; distal segment small, only 17  $\mu\text{m}$  long, subdivided in middle, with 5 setae and 1 short aesthetasc; all setae naked. Antenna (Fig. 112F) indistinctly 2-segmented; proximal segment unarmed; distal segment with 1 seta on inner margin, 1 short, blunt seta plus 1 lobate process subdistally, and tipped with 1 seta.

Labrum (Fig. 112G) short and broad, characteristically with pair of large lobes on posterior margin. Mandible and maxillule absent. Maxilla (Fig. 112H) distinctly 2-segmented; broad proximal segment unarmed; distal segment shorter and narrower than proximal segment, distally armed with 2 setae; outer seta pinnate, small medial seta naked and located on tip of digitiform process of segment. Maxilliped (Fig. 112I) consisting of 2 segments plus terminal claw; proximal segment broad and unarmed; distal segment as long as wide, with short medial margin and longer outer margin, bearing 1 broad, plate-like process and 1 acute spine near mediiodistal corner; terminal claw stout with bicuspid tip.

Leg 1 (Fig. 112J) consisting of protopod, exopod, and endopod; protopod obscurely defined at medial side, with 1 seta on outer margin; exopod distally bilobed, anterior lobe claw-like, with bicuspid tip, posterior lobe tipped with 1 small seta; endopod large, semicircular, more than twice as wide as exopod, and ornamented with rows of minute spinules. Legs 2-4 same as leg 1.

Leg 5 (Fig. 112A, K) as rudimentary lobe tipped with 2 small setae.

**Description of male.** Body (Fig. 113A) narrow, cycloform, clearly segmented, with distinct prosome-urosoma division. Body length 809  $\mu\text{m}$ . Maximum width of body 205  $\mu\text{m}$  across third pedigerous somite. Prosoma consisting of cephalosome and 4 pedigerous somites. Urosoma (Fig. 113B) 6-segmented, consisting of fifth pedigerous somite, genital somite and 4-segmented abdomen. Genital somite as long as wide. Four abdominal somites 50 $\times$ 70, 50 $\times$ 61, 36 $\times$ 50, and 23 $\times$ 43  $\mu\text{m}$ , respectively. Caudal ramus (Fig. 113C) rectangular, 2.24 times longer than wide (38 $\times$ 17  $\mu\text{m}$ ), armed with 6 setae (1 small outer, 1 dorsal, and 4 broad distal).

Rostrum absent. Antennule 7-segmented; armature on segments uncertain due to many setae missing. Antenna as in female. Labrum, mandible, maxillule, and maxilla absent. Maxilliped (Fig. 113D) 2-segmented; proximal segment short and unarmed; distal segment 1.5 times longer than wide, with 1 spine subdistally and 1 small lobe at mediiodistal corner; terminal claw strongly curved, with bicuspid tip.

Legs 1-4 (Fig. 113E-H) biramous, consisting of coxa, basis, exopod, and endopod. Coxa unarmed; basis with outer seta; basis of leg 1 additionally with inner distal spine. Exopods 3-segmented in all swimming legs. Endopods 1-segmented in leg 1, but 3-segmented in legs 2-4. All setae on swimming legs geniculate proximally, and all spines fringed with broad membranes bilaterally. Endopod of leg 1 and third exopodal segment of leg 2 with bicuspid outer distal corner. Third exopodal segment of legs 3 and 4 with tricuspid outer distal corner.

Leg 5 (Fig. 113B) represented by free exopod tipped with 2 unequal setae. Leg 6 represented by 1 seta on distolateral apex of genital operculum.

**Remarks.** Species of *Halostomella* seldom bear any lobes on the labrum in the female. The only known exception is *H. magellanica* (Chatton & Brément, 1910) in which the labrum bears 2 pairs of lobes, as illustrated by Chatton & Brément (1910). Therefore, *H. bilobata* **sp. nov.** can be distinguished from all other species of the genus by the possession of a single pair of lobes on the female labrum. Other diagnostic features of the female of *H. bilobata* **sp. nov.** include: (1) the abdomen is 3-segmented, a feature shared only with *H. australiensis* Gotto, 1970; (2) the antennule is distinctly 2-segmented, which is a unique feature of the new species; (3) the mandible is absent, a fea-



ture shared only with *H. reducta* Ooishi & Illg, 1977; and (4) the maxilla is distinctly 2-segmented and armed with 2 setae on its distal segment, a feature shared only with *H. borealis*. The combination of these diagnostic features serves to characterize the new species.

***Haplostomella uniseriata* sp. nov.**

(Fig. 114)

**Type material.** Holotype ♀ (MNHN-IU-2014-21528) and 1 ♀ paratype (MNHN-IU-2014-17390, dissected) from *Exostoma ianthinum* (Sluiter, 1909); Chuuk Island, OCDN 0900-M (07°25.29'N, 151°49.02'E), depth 4 m, CRRF coll., 11 November 1992.

**Etymology.** The name of the new species refers to the uniseriate arrangement of eggs within its egg sac.

**Description of female.** Body (Fig. 114A) vermiform, cylindrical, curved dorsally, and unsegmented; body length 1.53 mm, maximum width 250 µm. Cephalosome (Fig. 114B) 136×163 µm, narrower than metasomal region, and incompletely defined from metasomal region by posterolateral margins of cephalic shield. Metasomal region bearing 5 pairs of dorsolateral folds at levels of legs 1-5, respectively, last pair smaller than anterior 4 pairs. Genitoabdomen (Fig. 114C) not defined from metasome; genital apertures large, positioned dorsolaterally; genital operculum with 3 teeth distally and 1 small palm-like element bearing 6 digits on ventral side (Fig. 114N). Abdomen (Fig. 114C) not articulated from, but distinctly defined from metasomal region by its narrowness, slightly longer than wide (67×62 µm). Caudal ramus (Fig. 114D) 1.9 times longer than wide (30×16 µm), almost rectangular, armed with 5 naked setae, 1 at middle of outer margin and 4 distally; largest distal seta 28 µm long, about twice as long as other 3. Egg sac (Fig. 114E) 590×155 µm, containing 5 or 6 uniseriate eggs; each egg about 125 µm in diameter.

Rostrum absent. Antennule (Fig. 114F) small, unsegmented, 64 µm long, armed with 7 setae on anterior margin and 6 setae plus 3 short aesthetascs on distal margin; 1 seta on distal margin more than twice length of other setae. Antenna (Fig. 114G) unsegmented, slender, curved, with 1 process-like seta subdistally on inner margin, plus 1 blunt process, 1 spinulose lobe and 1 seta distally.

Labrum (Fig. 114H) simple, semicircular. Mandible (Fig. 114I) unsegmented, lobate, tipped with elongate, acutely pointed spine. Maxilla (Fig. 114J) unsegmented, but consisting of short and broad proximal part and narrow digitiform distal part bearing 1 weakly pinnate seta subdistally. Maxilliped (Fig. 114K) 2-segmented; proximal segment unarmed; distal segment with 1 spine and 1 blunt process mediolaterally; and ornamented with several rows of minute spinules on posterior surface; terminal claw simple.

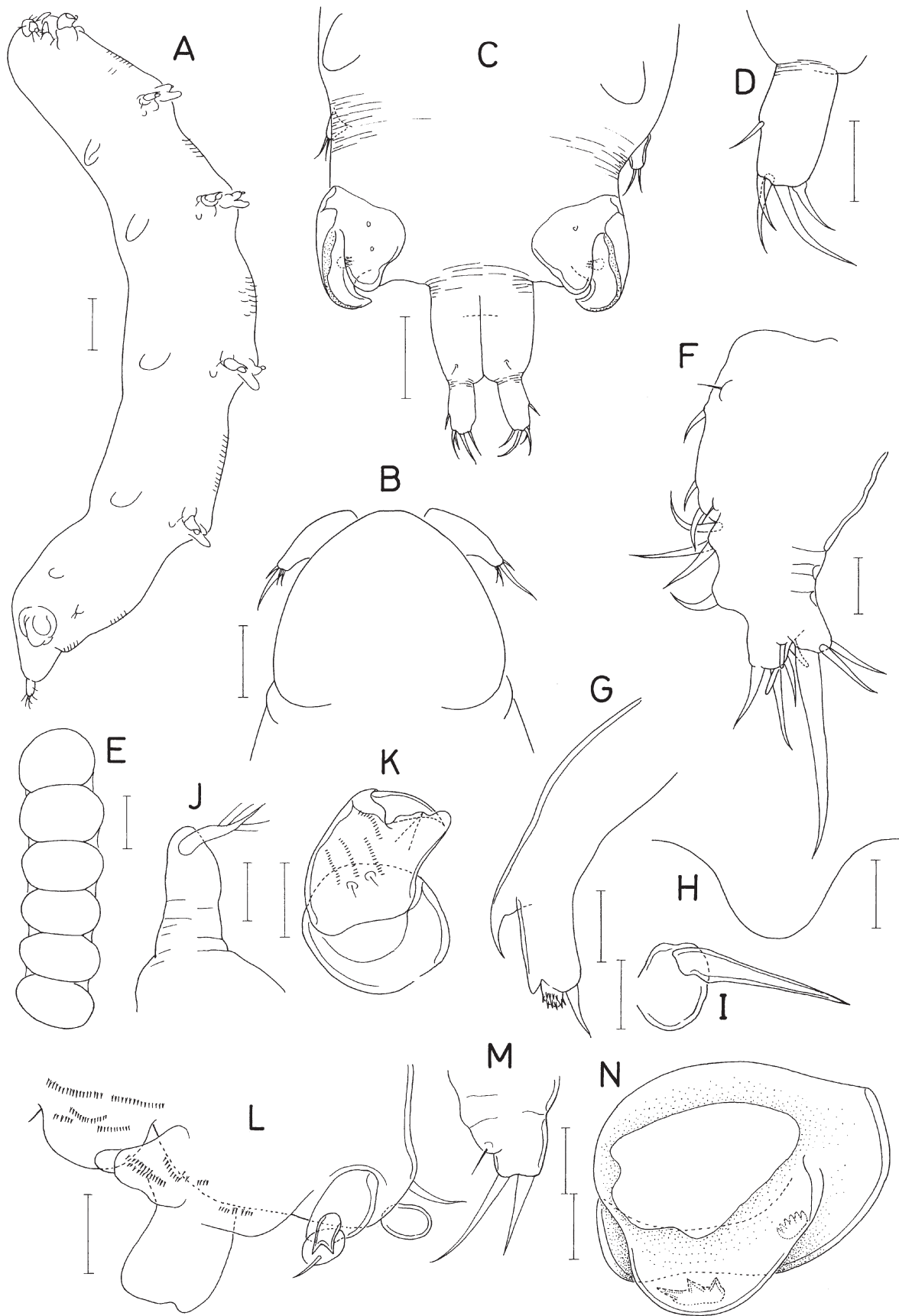
Leg 1 (Fig. 114L) consisting of protopod, exopod, and endopod. Intercoxal plate (Fig. 114L) present between left and right legs, not sclerotized but distinct and broad, ornamented with several rows of minute spinules on anterior surface. Protopod bearing 1 seta on outer margin and 1 tubercle at inner distal corner. Exopod small, distinctly articulated from protopod, and distally bilobed; anterior lobe sclerotized and distally bifurcate; posterior lobe sub-circular, tipped with 1 seta. Endopod well-defined, almost rectangular, longer than wide, with truncate and slightly bilobed distal margin. Legs 2-4 same as leg 1, but distal margin of endopods weakly trilobed. Legs 1-4 accompanied by small tubercle on ventral surface of body just lateral to each leg (Fig. 114A, L).

Leg 5 (Fig. 114M) as small lobe bearing 1 minute seta subdistally and 2 naked setae on distal margin.

**Male.** Unknown.

**Remarks.** The distal armature element on the mandible of *H. uniseriata* sp. nov. is a slender, straight spine by which the new species can be distinguished from its congeners, since in other species of *Haplostomella* the distal element is a robust claw in *H. borealis*; a curved spine in *H. distincta* Ooishi & Illg, 1977 and *H. oceanica* Ooishi & Illg, 1977; a strong, spinulose blade in *H. halocynthiae* (Fukui, 1965); a single seta in *H. dubia* Ooishi & Illg, 1977, *H. magellanica*, *H. malacocera*, and *H. tuberculata*; and it is absent in *H. reducta*. The mandible of *H. australiensis* is unknown, but it has a large body size, 6.5 mm long in the female, a 3-segmented abdomen, and 2 distal setae on the maxilla (Gotto, 1970), which serve to distinguish it from the new species.

Egg sacs are known in only five species of the genus *Haplostomella*, and all of these species have a multiseriata arrangement of eggs. The uniseriate arrangement of eggs in the egg sac of *H. uniseriata* sp. nov. also seems to be an unusual feature within the genus.



**FIG. 114.** *Haplostomella uniseriata* sp. nov., female. A, habitus, right; B, cephalosome, dorsal; C, posterior part of body, dorsal; D, left caudal ramus, dorsal; E, egg sac; F, antennule; G, antenna; H, labrum; I, mandible; J, maxilla; K, maxilliped; L, leg 1; M, leg 5; N, genital aperture. Scale bars: A, E, 0.1 mm; B, C, 0.05 mm; D, K, L, N, 0.02 mm; F-J, M, 0.01 mm.

***Haplostomella ooishiae* sp. nov.**

(Figs. 115, 116)

**Type material.** Holotype ♀ (MNHN-IU-2014-21529), 3 ♀♀ paratypes (MNHN-IU-2014-21530), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17391) from *Aplidium californicum* (Ritter & Forsyth, 1917) (MNHN-IT-2008-242 = MNHN A1/APL.B/200); British Columbia, Canada, Pennachetti coll.

**Etymology.** This new species is named in honor of the late Dr. Shigeo Ooishi, who contributed enormously to the taxonomy of ascidicolous copepods.

**Description of female.** Body (Fig. 115A, B) vermiform, unsegmented, slightly compressed laterally, with 5 pairs of dorsolateral folds at levels of legs 1-5. Body length 2.80 mm; maximum width 0.48 mm (in middle); maximum dorsoventral depth 0.58 mm. Body surface ornamented with numerous rows of fine spinules (Fig. 115C). Cephalosome weakly defined from rest of body by dorsolateral constriction. Posterior third of body straight or curved dorsally, gradually narrowing posteriorly; abdominal part variable in relative length. Genitoabdomen or abdomen not defined. Genital apertures (Fig. 116E) large; genital operculum with 3 small internal teeth distally and row of 6 denticles on ventral side. Caudal rami (Fig. 115C) divergent, nearly rectangular, about 2.35 times longer than wide (54×23 µm); armed with 5 setae (1 on outer margin and 4 distally; outer margin seta shorter than others and positioned at 58% of ramus length).

Rostrum absent. Antennule (Fig. 115D) strongly tapering, 90×48 µm, incompletely 2-segmented; proximal segment with 3 vestigial suture lines along posterior side and armed with 10 setae (including 2 large setae) plus 2 aesthetascs; small distal segment armed with 4 setae, distal seta longer and broader than other 3. Antenna (Fig. 115E) 3-segmented; first segment longest but unarmed; second segment quadrate, incompletely articulated from first, with 1 seta at inner distal corner; third segment distinctly articulated from second, bearing 2 short, nipple-shaped setae, 1 spinulose lobe and 1 naked seta.

Labrum (Fig. 115F) simple, unornamented, with slightly concave posterior margin. Mandible (Fig. 115G) consisting of short segment and whip-like (but not flexible) distal spine. Maxillule absent. Maxilla (Fig. 115H) 2-segmented; proximal segment unarmed; distal segment shorter and narrower than proximal, tipped with 1 weakly pinnate seta. Maxilliped (Fig. 115I, J) 2-segmented; proximal segment much wider than long, unarmed; distal segment slightly longer than wide, with 1 blunt process and 1 pointed spine mediolaterally; terminal claw with bicuspid tip.

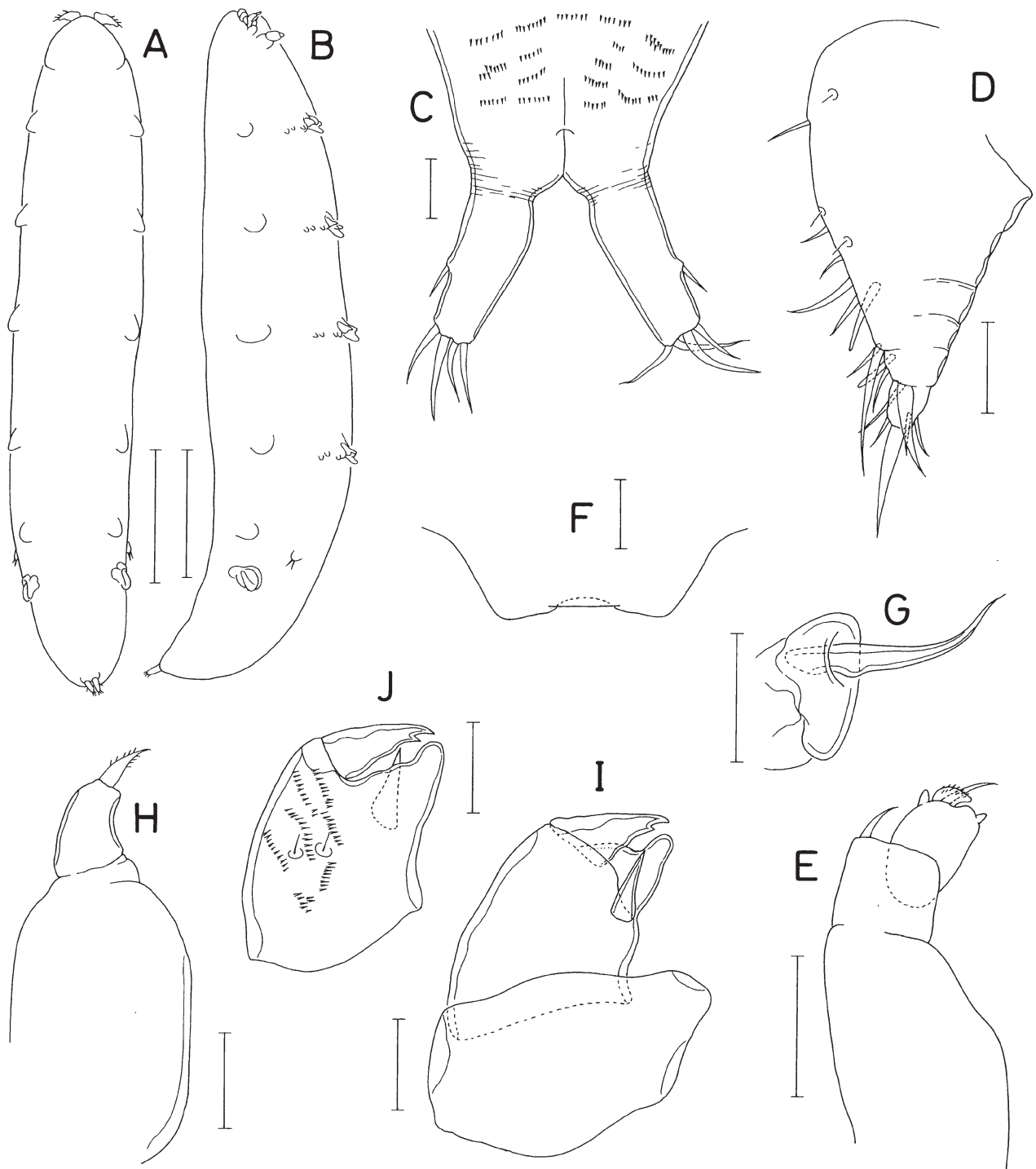
Leg 1 (Fig. 116A) consisting of unsegmented protopod, exopod and endopod. Protopod with seta on outer margin, plus large mediolateral protrusion with bilobed apex. Exopod distally bilobed; anterior lobe claw-like and bicuspid at tip; posterior lobe flexible, unarmed. Endopod longer than wide, distally bilobed. Legs 2 and 3 similar to leg 1, but distal margin of endopod trilobed (Fig. 116B). Leg 4 similar to leg 1, but with 1 seta on tip of posterior lobe of exopod (this seta absent in legs 1-3). Legs 1-4 each accompanied laterally by 2 or 3 tubercles (1 anterior and 2 posterior) on ventral surface of body (Figs. 116A-C), posterior 2 lobes always present, but anterior lobe present or absent, and variable in size.

Leg 5 (Fig. 116D) as small lobe tipped with 2 setae of unequal length.

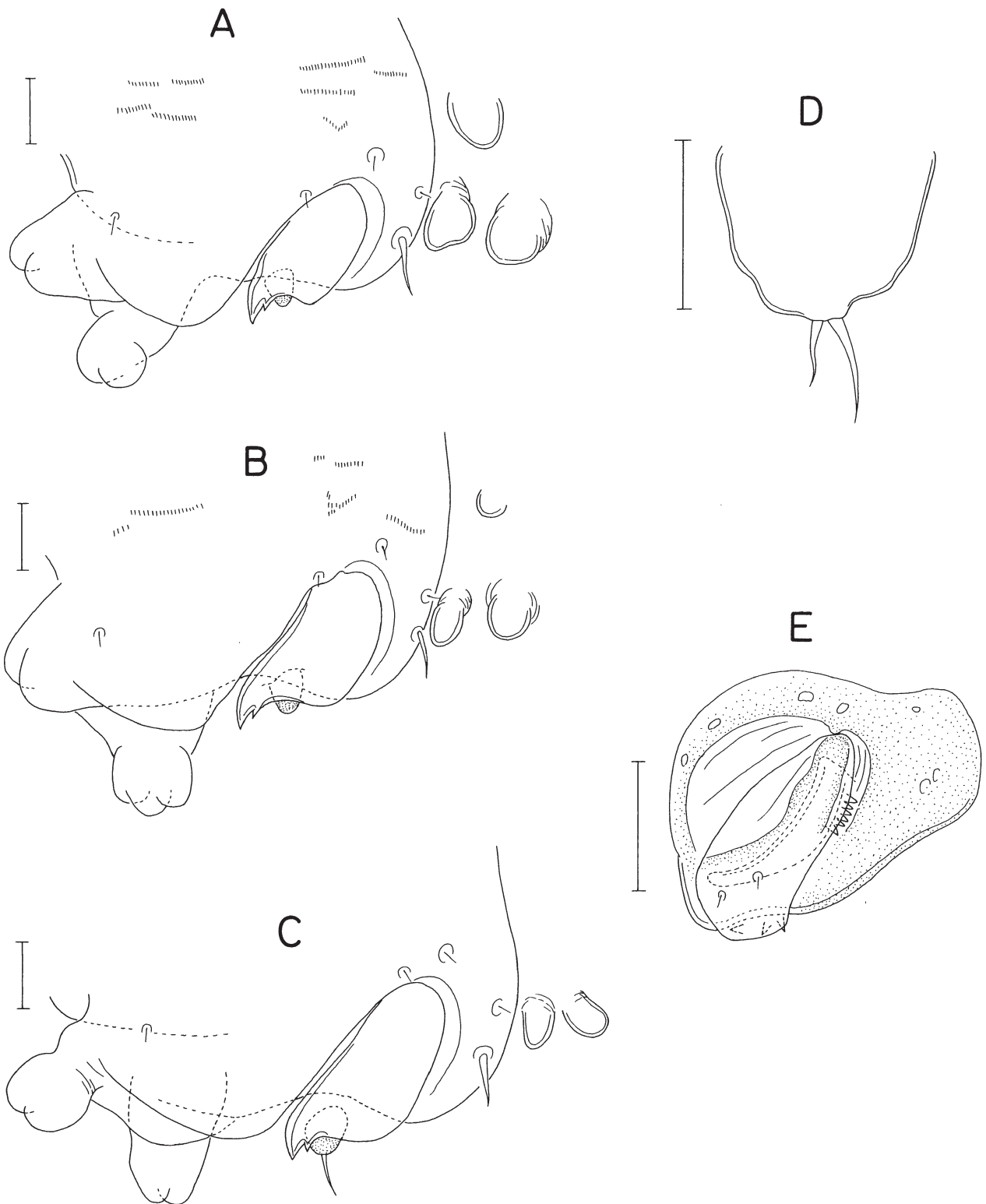
**Male.** Unknown.

**Remarks.** In species of *Haplostomella* the inner distal corner of the protopod of legs 1-4 can be variously protruded, as follows: (1) a large expansion in *H. australiensis*, which Gotto (1970) interpreted as representing an inner lobe of the endopod; (2) a broad protrusion in *H. distincta* Ooishi & Illg, 1977, which was also interpreted as an inner lobe of the endopod by Ooishi & Illg (1977) and by Marchenkov & Boxshall (2003); (3) a bilobed protrusion in *H. malacocera*, which was illustrated by Chatton & Harant (1924a); and (4) a tubercle in *H. uniseriata* sp. nov. In *H. ooishiae* sp. nov. the inner distal corner of the protopod of legs 1-4 bears a large, distally-bilobed protrusion, similar to that of *H. malacocera*. The latter species is known from the Mediterranean and differs from *H. ooishiae* sp. nov. in having a clearly defined abdomen, as illustrated by Chatton & Harant (1924a), a 2-segmented antenna, and no dorsolateral folds on the metasomal region.

The presence in leg 4 only of a distal seta on the posterior lobe of the exopod (the seta is absent in legs 1-3) seems to be the most remarkable distinguishing feature of *H. ooishiae* sp. nov., because all known *Haplostomella* species possess this seta on the posterior lobe of the exopods of legs 1-4. In addition, the shape of the distal spine on the mandible is characteristically distally attenuated, curved, and whip-like, although it is stiff, not flexible.



**FIG. 115.** *Haplostomella ooishiae* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, caudal rami, dorsal; D, antennule; E, antenna; F, labrum; G, mandible; H, maxilla; I, maxilliped, anterior; J, distal segment of maxilliped, posterior. Scale bars: A, B, 0.5 mm; C-J, 0.02 mm.



**FIG. 116.** *Haplostomella ooishiae* sp. nov., female. A, leg 1; B, leg 2; C, leg 4; D, leg 5; E, genital aperture. Scale bars: A-C, 0.02 mm; D, E, 0.05 mm.

***Haplostomella multinodosa* sp. nov.**

(Figs. 117, 118)

**Type material.** Holotype ♀ (MNHN-IU-2014-21531) and 1 ♀ paratype (MNHN-IU-2014-17392, dissected) from *Ritterella rubra* Abbott & Trason, 1968; British Columbia, Canada, seapool rocks (48°49'N, 125°12'15"W), depth 40 m, Pennachetti coll., date unknown.

**Etymology.** The specific name is derived from the Latin *mult* (=many) and *nod* (=swelling), and alludes to the presence of multiple interpodal tubercles associated with legs 1-4.

**Description of female.** Body (Fig. 117A) eruciform, unsegmented, slightly curved dorsally; body length 1.85 mm; maximum width 429 µm (in middle). Anterior part of body tapering anteriorly; cephalosome partially defined by posterolateral margins of cephalic shield. Metasomal region lacking any division, with 5 pairs semicircular dorsolateral folds, each pair located at level of legs 1-5, respectively: last pair of folds smaller than anterior 4 pairs. Genitoabdomen (Fig. 117B) short, occupying less than 20% of body length, unsegmented, not demarcated from metasome, strongly tapering; genital apertures (Fig. 118D) large, positioned dorsolaterally; genital operculum bearing 3 teeth distally and row of 4 denticles on ventral side. Caudal ramus (Fig. 117C) 2.0 times longer than wide (40×20 µm), gradually narrowing distally; armed with 5 setae (1 on outer margin, 1 subdistal dorsal, and 3 distal); seta on outer margin smaller than other caudal setae and positioned at 65% length of ramus. Egg sac (Fig. 117D) about 1.57×0.41 mm, containing multiseriate eggs; each egg about 180 µm in diameter.

Rostrum absent. Antennule (Fig. 117E) about 85 µm long, unsegmented, with traces of 3 weak articulations along posterior side; armed with 15 setae (3 distal setae larger than others). Antenna (Fig. 117F) broad, 3-segmented; first segment unarmed; second segment wider than long, with short outer and longer inner margins, and with 1 seta at inner distal corner; third segment 1.5 times longer than wide, with 1 setiform process, 2 setae (including very small one) and 1 spinulose lobe.

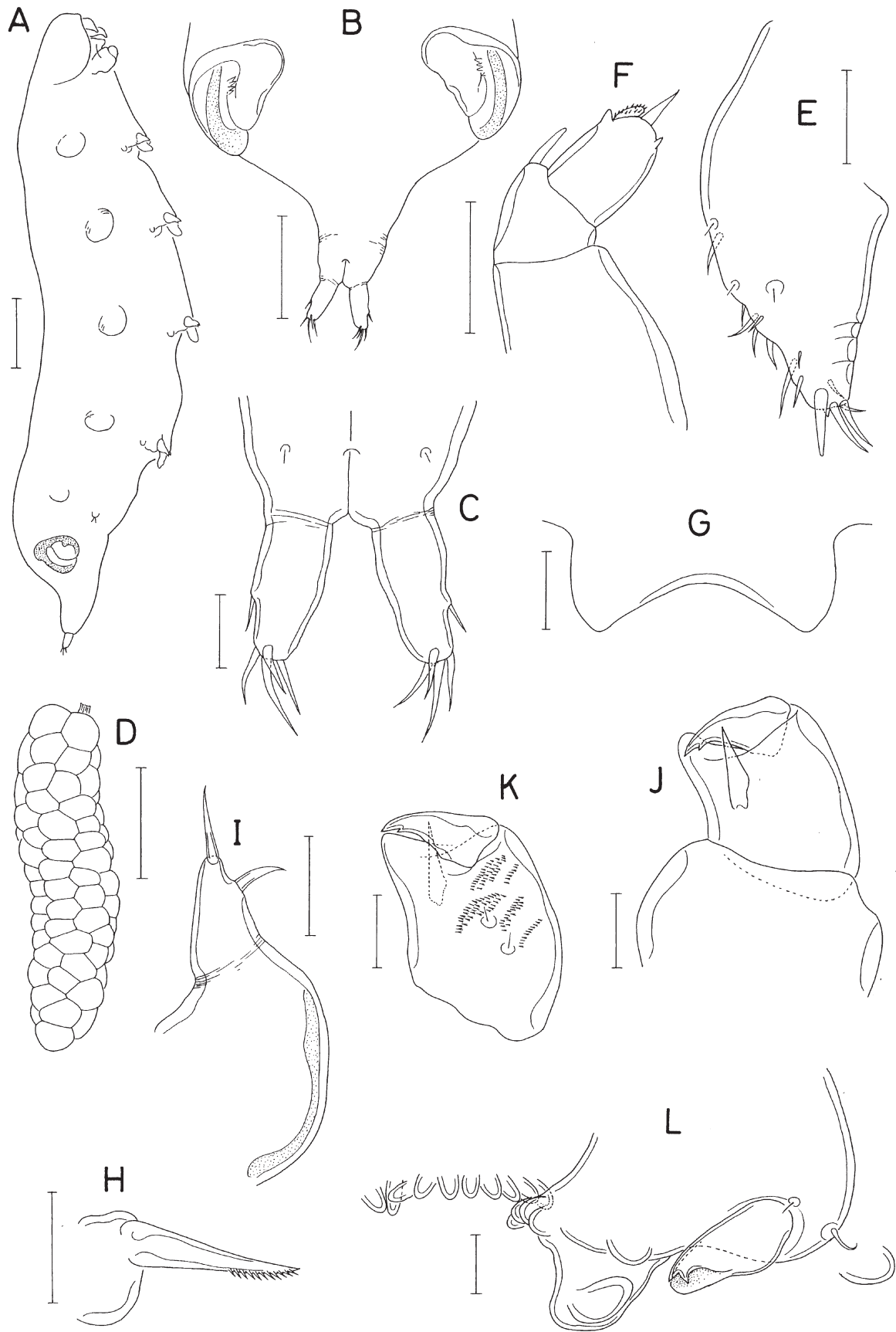
Labrum (Fig. 117G) much wider than long, unornamented, with concave posterior margin. Mandible (Fig. 117H) consisting of segment plus strong, straight distal spine bearing 1 row of spinules distally. Maxillule absent. Maxilla (Fig. 117I) unsegmented, but divisible into broad proximal and narrower distal parts; armed with 2 setae (1 apical and 1 subapical). Maxilliped (Fig. 117J) broad, 2-segmented; proximal segment very broad, unarmed; distal segment with several patches of minute spinules on posterior surface (Fig. 117K), bluntly protruded mediolateral corner, and 1 acutely pointed spine on anteromedial surface; terminal claw with bicuspid tip.

Leg 1 (Fig. 117L) consisting of protopod, exopod, and endopod. Protopod bearing 1 small seta on outer margin, 1 short tubercle on posterior margin between rami, and 4 tubercles at inner distal corner. Exopod with bifurcate anterior lobe and rounded posterior lobe lacking distal seta. Endopod wider than long, with 1 large tubercle on anterior surface. Ventral lateral surface of body lateral to leg 1 bearing 1 tubercle. Ventral surface of body between left and right legs 1 bearing 10 rounded interpodal tubercles (replacing intercoxal plate). Leg 2 (Fig. 118A) similar to leg 1, except bearing 2 distal tubercles on endopod (large outer and small inner). Leg 3 same as leg 2. Leg 4 (Fig. 118B) similar to leg 2, except bearing 9 interpodal tubercles and 2 small tubercles at inner distal corner of endopod.

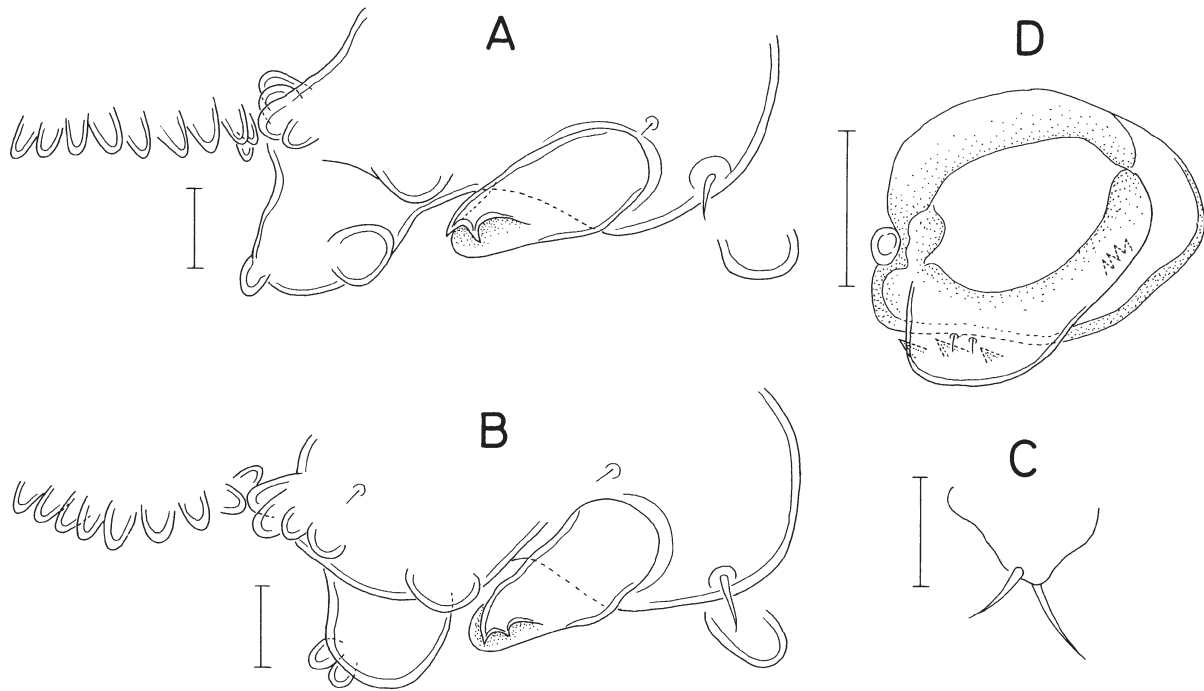
Leg 5 (Fig. 118C) as tapering, rudimentary lobe, wider than long, tipped with 2 small setae.

**Male.** Unknown.

**Remarks.** *Haplostomella multinodosa* sp. nov. is a very distinctive species, readily distinguishable from all of its congeners by the possession of the characteristic, multiple interpodal tubercles between left and right members of legs 1-4 of the female. These can be observed without dissection and it is likely these tubercles are derived from the transformed intercoxal plate. Tubercles are also present at the inner distal corner of protopods (invariably 4) and on the endopods (1 on leg 1 and 2 on legs 2-4). As additional diagnostic features of the new species, the ventral body surface lateral to each of legs 1-4 bears a single tubercle (a feature shared with *H. uniseriata* sp. nov.), the mandible bears a strong spine, and the body is unsegmented, lacking any trace of segmentation.



**FIG. 117.** *Haplostomella multinodosa* sp. nov., female. A, habitus, right; B, genitoabdomen, dorsal; C, caudal rami, dorsal; D, egg sac; E, antennule; F, antenna; G, labrum; H, mandible; I, maxilla; J, maxilliped; K, distal segment of maxilliped, posterior; L, leg 1. Scale bars: A, 0.2 mm; B, 0.1 mm; C, E-L, 0.02 mm; D, 0.5 mm.



**FIG. 118.** *Haplostomella multinodosa* sp. nov., female. A, leg 2; B, leg 4; C, leg 5; D, genital aperture. Scale bars: A-C, 0.02 mm; D, 0.05 mm.

***Haplostomella binodosa* sp. nov.**

(Fig. 119)

**Type material.** Holotype ♀ (MNHN-IU-2014-21532), 5 ♀♀ paratypes (MNHN-IU-2014-21533), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17393) from *Cystodytes roseolus* Hartmeyer, 1912 (MNHN-IT-2008-2602 = MNHN A3/CYS/4); Dakar, Senegal, Stn 17, dredge, I.F.A.N. coll., 21 January 1941.

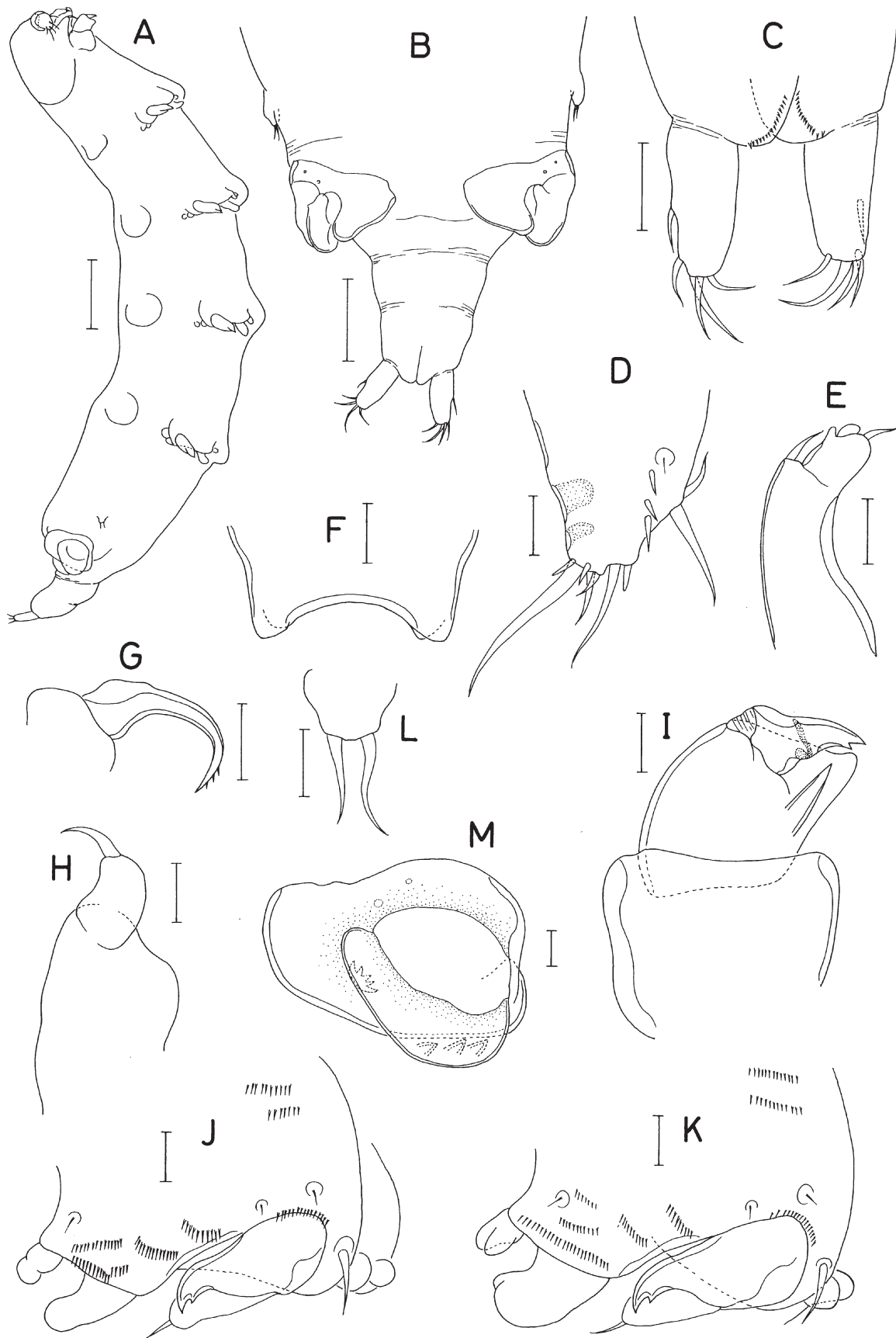
**Etymology.** The specific name is derived from Latin *bi* (=two) and *nodus* (swelling) and refers to the presence of double tubercles on the ventral body surface lateral to legs 1-4.

**Description of female.** Body (Fig. 119A) eruciform, relatively small, curved dorsally, with 4 pairs of dorsolateral folds, 1 each at level of legs 1-4. Body length 1.01 mm; maximum width 0.21 mm. Ventral surface of body bearing 4 short, blunt protrusions, between left and right members of each leg pair (Fig. 119A). Cephalosome defined from metasomal region by posterolateral margins of cephalic shield. Genitoabdomen not defined from metasomal region; genital apertures large, positioned dorsolaterally; genital operculum (Fig. 119M) bearing 3 teeth along distal border and 1 palm-like element on ventral side bearing 5 digits. Abdomen defined from genital region only by weak constriction, unsegmented but with slight constriction in middle; dorsoposterior region of abdomen bearing row of minute spinules on each side of anal slit (Fig. 119C). Caudal ramus (Fig. 119C) about 2.3 times longer than wide ( $36 \times 16 \mu\text{m}$ ), with 1 outer and 4 distal setae; outer seta positioned at 55% of ramus length.

Rostrum absent. Antennule (Fig. 119D) stout, unsegmented, almost as long as wide, with 5 setae (including 1 large seta) on anterior side and 7 setae (including 2 larger setae) on distal margin. Antenna (Fig. 119E) incompletely 2-segmented; proximal segment bearing 1 seta at inner distal corner; distal segment short, slightly longer than wide, with 1 blunt process, 1 leaf-like lobe, and apical seta.

Labrum (Fig. 119F) with concave posterior margin and protruded, unequally bilobed posterolateral corners. Mandible (Fig. 119G) consisting of short, lobate segment and recurved, hook-like distal spine bearing few small spinules distally. Maxillule absent. Maxilla (Fig. 119H) incompletely 2-segmented; broad proximal segment unarmed; narrower distal segment tipped with 1 seta. Maxilliped (Fig. 119I) broad, 2-segmented; proximal segment much broader than long, unarmed; distal segment as long as wide, bearing mediolateral protrusion and medial spine; terminal claw with transverse unsclerotized region in middle, representing trace of articulation between endopod and claw; with bicuspid tip.





**FIG. 119.** *Haplostomella binodosa* sp. nov., female. A, habitus, right; B, genitoabdomen, dorsal; C, caudal rami, dorsal; D, antennule; E, antenna; F, labrum; G, mandible; H, maxilla; I, maxilliped; J, leg 1; K, leg 2; L, leg 5; M, genital aperture. Scale bars: A, 0.1 mm; B, 0.05 mm; C, 0.02 mm; D-M, 0.01 mm.

Leg 1 (Fig. 119J) with broad protopod bearing 1 seta on outer margin, 1 large tubercle at inner distal corner, and several rows of minute spinules on anterior surface. Exopod bilobed; anterior lobe claw-like, bicuspid at tip; posterior lobe tipped with 1 setule. Endopod shorter and narrower than exopod, distinctly articulated from protopod, unornamented, with rounded distal margin. Ventral surface of body lateral to leg 1 bearing 2 globular tubercles. Leg 2 (Fig. 119K) similar to leg 1, but inner distal tubercle on protopod bilobed, and endopod broader and weakly bilobed. Legs 3 and 4 same as leg 2.

Leg 5 (Fig. 119L) rudimentary, as small lobe tipped with 2 setae.

**Male.** Unknown.

**Remarks.** Three major diagnostic features of *H. binodosa* **sp. nov.** differentiate it from its congeners, as follows: (1) the distal element of the mandible is a hook-like, recurved spine; (2) the inner distal corner of the protopod of legs 1-4 bears a tubercle which is simple in leg 1, but bilobed in legs 2-4; and (3) legs 1-4 are accompanied by a pair of tubercles positioned on the ventrolateral surface of body lateral to each leg. The first of these features was previously recorded only in *H. oceanica*. The second feature, the inner distal tubercle or protrusion on the protopod of legs 1-4 has been recorded in several species of *Haplostomella*, but only *H. uniseriata* **sp. nov.** is comparable with *H. binodosa* **sp. nov.** in sharing a small, clearly defined tubercle (in other species the protrusion is large and not clearly defined from the protopod). The third diagnostic feature, the number of tubercle(s) on the ventral surface lateral to legs 1-4 is variable according to species and has been recorded or illustrated as 4 in *H. australiensis*, *H. distincta*, and *H. halocynthiae*; 3 in *H. oceanica*; 2 or 3 in *H. ooishiae* **sp. nov.**, and 1 in *H. uniseriata* **sp. nov.** and *H. multinodosa* **sp. nov.** Therefore, the new species can be distinguished from its congeners by the combination of the above three diagnostic features.

### ***Haplostomella crassa* sp. nov.**

(Fig. 120)

**Type material.** Holotype ♀ (MNHN-IU-2014-21534) and 1 ♀ paratype (MNHN-IU-2014-17394, dissected) from *Synoicum floriferum* Monniot, F. & Monniot, C., 2006 (MNHN-IT-2018-18 = MNHN A1/SYN/116); Sainte Luce, SW Îlot Souillac, Madagascar, ATIMO VATAE expedition, Stn TA36 (24°45'S, 47°12'E), MNHN coll., 04 June 2010.

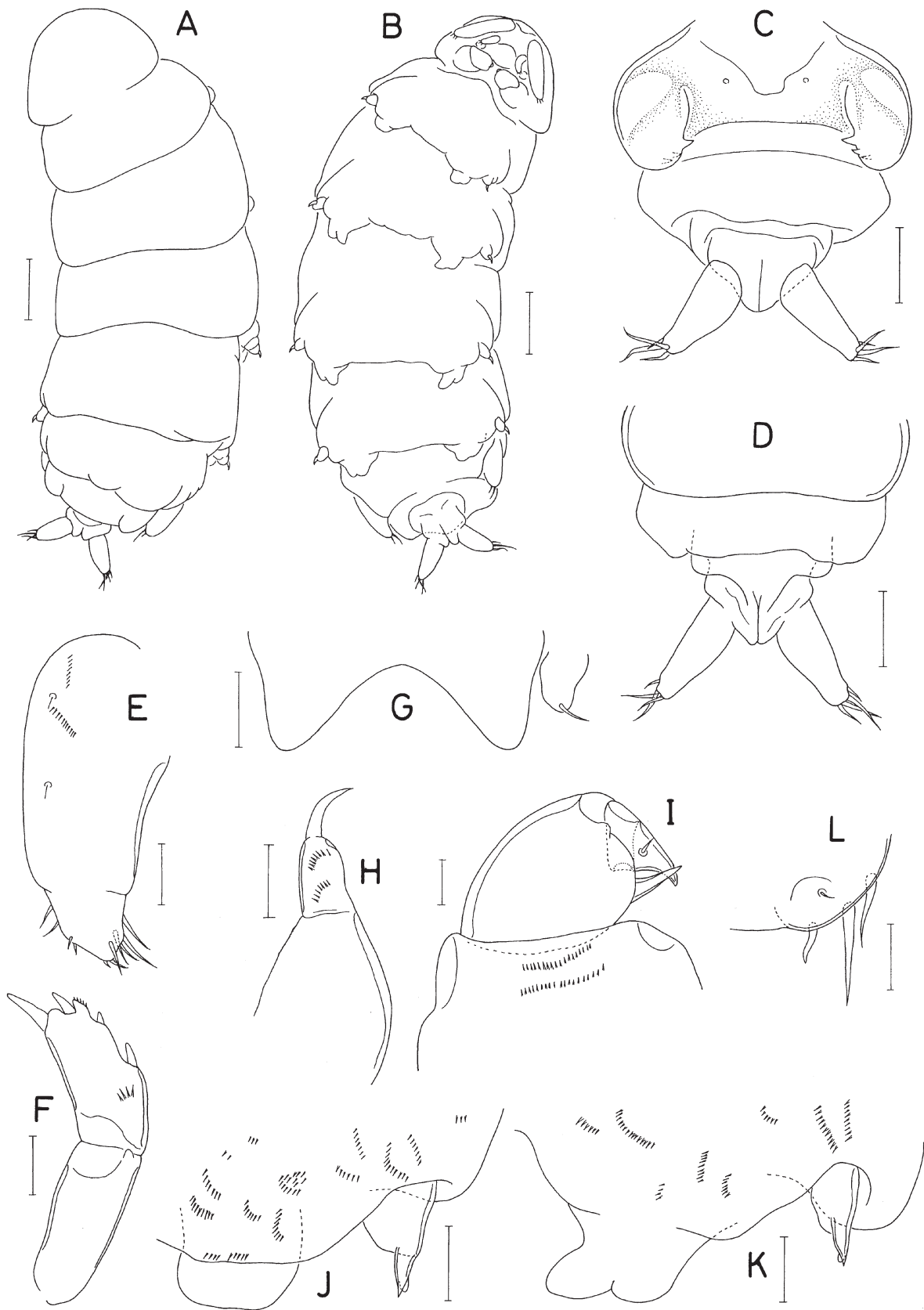
**Etymology.** The specific name is derived from the Latin *crass* (= thick) and alludes to the relatively broad body of the female.

**Description of female.** Body (Fig. 120A, B) eruciform, relatively small and stout, distinctly segmented; body length 957 µm; maximum width 330 µm. Cephalosome nearly triangular, 158×231 µm, incompletely articulated from metasome. First to fifth pedigerous somites well-defined from one another, similar in width. Genitoabdomen (Fig. 120C) distinctly articulated from fifth pedigerous somite, 4-segmented, consisting of genital somite and indistinctly 3-segmented abdomen. Genital somite much wider than long; genital apertures large, positioned dorso-laterally; genital operculum bearing 3 teeth on mediodistal margin. First abdominal somite broad; second and third abdominal somites much narrower than first. Caudal rami (Fig. 120D) divergent, about 2.2 times longer than wide (69×31 µm), bearing 4 small setae distally.

Rostrum absent. Antennule (Fig. 120E) indistinctly 2-segmented, 107 µm long, twice as long as wide; proximal segment unarmed, but ornamented with 2 rows of minute spinules proximally; short distal segment occupying about 20% length of antennule, obscurely articulated from first segment, but defined by abrupt narrowing; armed with 11 slender setae of unequal lengths (4 on anterior margin and 7 on distal and posterior margins). Antenna (Fig. 120F) 2-segmented; proximal segment 28×12 µm, unarmed; distal segment 25×13 µm, slightly shorter than first, bearing 4 setae (2 on inner margin and 2 on distal margin) and 1 lobe bearing minute spinules, and ornamented with short row of spinules proximally.

Labrum (Fig. 120G) with deeply concave posterior margin. Mandible (Fig. 120G) as small lobe tipped with 1 seta. Maxillule absent. Maxilla (Fig. 120H) incompletely 2-segmented; broad proximal segment unarmed; narrow distal segment tipped with 1 naked seta and ornamented with 2 rows of minute spinules. Maxilliped (Fig. 120I) robust, 2-segmented; proximal segment much wider than long, unarmed but ornamented with 2 transverse rows of minute spinules on anterior surface; distal segment bearing medial spine, but lacking mediodistal protrusion;

terminal claw robust, strongly tapering, with trace of suture line at proximal third, 1 small seta in middle of anterior surface; apex of terminal claw simple, not bicuspid.



**FIG. 120.** *Haplostomella crassa* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, genitoabdomen, dorsal; D, abdomen, ventral; E, antennule; F, antenna; G, labrum and left mandible; H, maxilla; I, maxilliped; J, leg 1; K, leg 2; L, leg 5. Scale bars: A, B, 0.1 mm; C, D, 0.05 mm; E, G, H, J-L, 0.02 mm; F, I, 0.01 mm.

Leg 1 (Fig. 120J) consisting of protopod, exopod, and endopod. Protopod short, unarmed, but ornamented with rows of minute spinules on anterior surface. Exopod divisible into broader proximal part and abruptly narrower distal part; distal part distally bilobed, with pointed, spinule-like anterior lobe and rounded posterior lobe lacking seta. Endopod much broader than exopod, truncate, with rounded distal corners. Ventral surface of body lateral to legs 1-4 lacking any tubercles or protrusions. Leg 2 (Fig. 120K) similar to leg 1; exopod same as that of leg 1, but endopod distally bilobed, with inner lobe more prominent than outer lobe. Legs 3 and 4 same as leg 2.

Leg 5 (Fig. 120L) as lobe bearing 3 unequal setae.

**Male.** Unknown.

**Remarks.** The caudal ramus in *Haplostomella* is typically armed with 5 setae. The recorded exceptions to this are: the presence of 4 setae in *H. tuberculata*, although this species has a rudimentary additional seta on the outer margin of the caudal ramus (as redescribed in the present work), 1 in *H. magellanica*, as described by Chatton and Brément (1910), and none in *H. sycozoae* (Salfi, 1926). In having 4 caudal setae, *H. crassa* **sp. nov.** is similar only to *H. tuberculata*. These two species also share the possession of 3 setae on leg 5, a feature shared only with *H. dubia* and *H. biseta* **sp. nov.** described below. However, *H. crassa* **sp. nov.** is readily distinguishable from *H. tuberculata* by its 3-segmented abdomen (vs. abdomen unsegmented in *H. tuberculata*) and a 2-segmented antenna (vs. 3-segmented in *H. tuberculata*), and by the absence of the dorsolateral folds on the metasomal region (vs. the folds are present in *H. tuberculata*).

The small body size (0.96 mm in length) of *H. crassa* **sp. nov.** is noteworthy because it is the smallest species known: the range of known body lengths in *Haplostomella* is from 1.01 mm recorded in the present work for *H. binodosa* **sp. nov.** to 11.7 mm recorded by Kim I.H. (2012) for *H. halocynthiae*.

### ***Haplostomella biseta* sp. nov.**

(Fig. 121)

**Type material.** Holotype ♀ (MNHN-IU-2014-21535), 2 ♀♀ paratypes (MNHN-IU-2014-21536), and 1 ♀ paratype (dissected, MNHN-IU-2014-17395) from *Aplidium falklandicum* Millar, 1960; E. Kerguelen Is., MD04-BENTHOS cruise, R.V. "Marion Dufresne", Stn CP13 (49°32-33'S, 70°57'E), depth 149-155 m, Boury-Esnault coll., 22 February 1975.

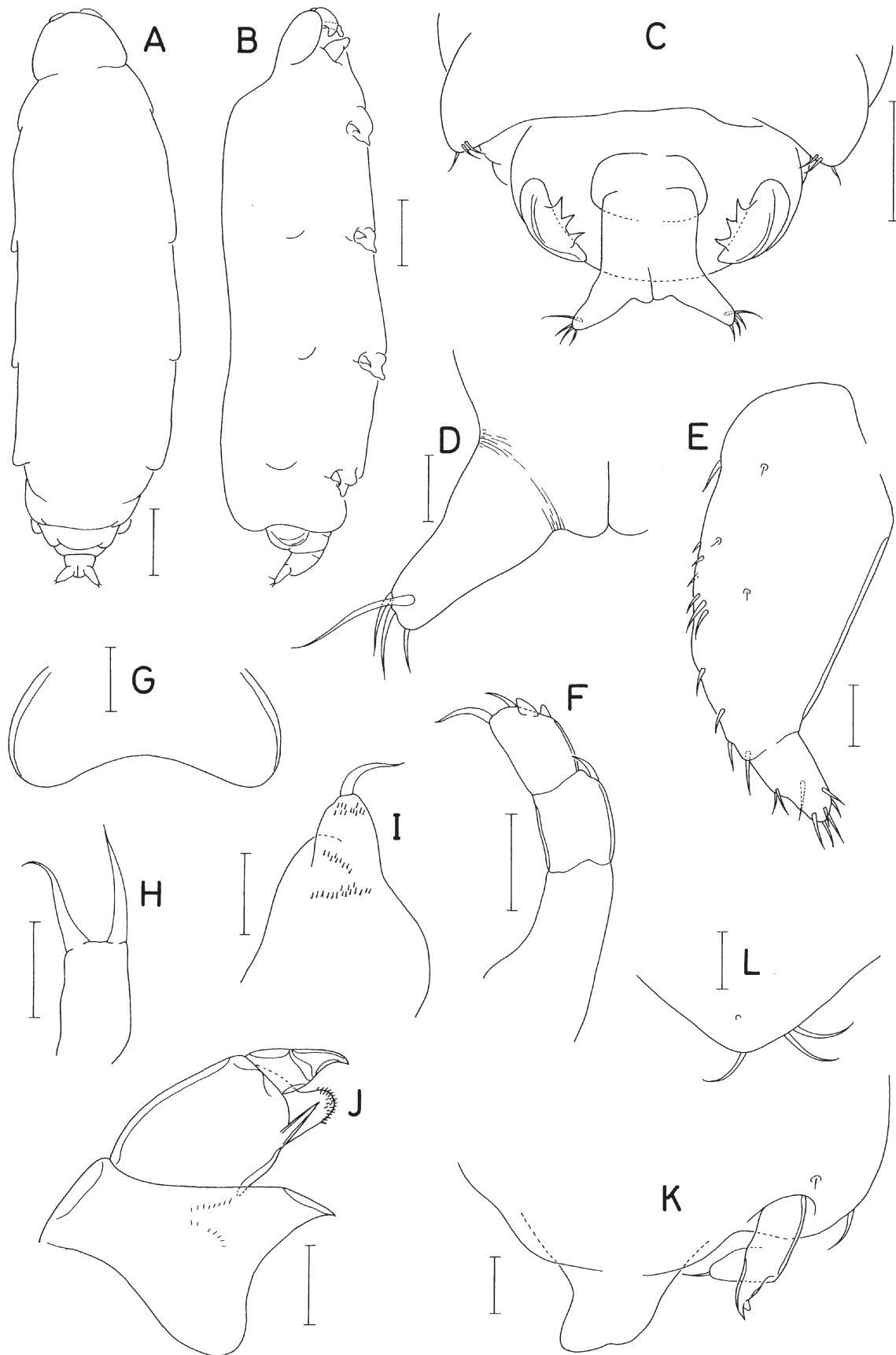
**Additional material.** 3 ♀♀ (MNHN-IU-2014-21537) from *Aplidium circumvolutum* (Sluiter, 1900), NW Kerguelen Is., MD03-ICTHYO cruise, RV "Marion Dufresne", Stn 18-52-CP11, (47°42'S, 68°07'E), depth 243 m, 15 April 1974.

**Etymology.** The specific name refers to the presence of 2 setae on the mandible.

**Description of female.** Body (Fig. 121A, B) cruciform, consisting of cephalosome, metasome, and genitoabdomen. Body length 1.74 mm; maximum width 0.51 mm. Cephalosome incompletely defined from metasome, 190×284 µm, distinctly narrower than metasome, and dorsoventrally depressed. Metasome cylindrical, comprising first to fifth pedigerous somites, unsegmented, without any trace of division, bearing 3 pairs of weak dorsolateral folds, at levels of legs 2-4, respectively (Fig. 121B). Genitoabdomen (Fig. 121C) wider than long, consisting of genital somite and 2-segmented abdomen. Genital somite much wider than long; genital apertures large, positioned dorsolaterally; genital operculum bearing 3 teeth on medial margin. Abdomen clearly defined, much narrower than genital somite; first abdominal somite short; second abdominal somite incompletely articulated from first, as long as wide. Caudal rami widely divergent (Fig. 121C, D), not articulated from somite, narrowing distally, about 1.8 times longer than wide (58×32 µm), armed with 3 distal setae and 1 subdistal, dorsal seta (at least twice as long as other setae).

Rostrum absent. Antennule (Fig. 121E) 150 µm long, 2.4 times longer than wide, 2-segmented; articulation incomplete between segments; proximal segment bearing 11 small setae; distal segment distinctly shorter and narrower than proximal segment, bearing 9 small setae. Antenna (Fig. 121F) 3-segmented; first segment longest, unarmed; second segment slightly longer than wide, with 1 seta at inner distal corner; third segment as long as second, bearing 2 unequal setae distally and 1 small, blunt seta and 1 lobe subdistally.

Labrum (Fig. 121G) simple, with concave posterior margin. Mandible (Fig. 121H) as rectangular lobe bearing



**FIG. 121.** *Haplostomella biseta* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genitoabdomen, ventral; D, left caudal ramus, dorsal; E, antennule; F, antenna; G, labrum; H, mandible; I, maxilla; J, maxilliped; K, leg 1; L, leg 5. Scale bars: A, B, 0.2 mm; C, 0.1 mm; D-L, 0.02 mm.

2 equal setae distally. Maxillule absent. Maxilla unsegmented (Fig. 121I), but divisible into broad proximal part and narrower distal part, bearing 1 seta apically, and ornamented with 3 patches of minute spinules distally. Maxilliped (Fig. 121J) 3-segmented; first segment broad, unarmed; second segment with prominent mediobasal projection bearing minute spinules distally and 1 spine on medial margin; third segment short and narrow, unarmed; terminal claw short and simple.

Leg 1 (Fig. 121K) with broad protopod bearing 1 seta on outer margin; exopod narrow, distally bilobed; anterior lobe claw-like, bearing pale, blunt lobe subdistally; posterior lobe tipped with 1 seta. Endopod wider than exopod, with mediobasal corner protruded. Legs 2-4 same as leg 1, but mediobasal corner of endopod of legs 2 and 3 more prominent than in legs 1 and 4.

Leg 5 (Fig. 121L) short, much broader than long, with 1 apical and 2 subapical setae; all setae equal in length.

**Male.** Unknown.

**Remarks.** The mandible of females of the genera *Haplostomides* and *Haplostoma* is typically armed with 1 to 3 distal setae. In contrast to these two genera, the mandible of female *Haplostomella* is variable in its armature, depending on species; it can be a spine, or a claw, or a seta. In five species of *Haplostomella* the distal element of the female mandible is a seta. These species are *H. dubia*, *H. magellanica*, *H. malacocera*, *H. tuberculata*, and *H. crassa* **sp. nov.** However, no species has hitherto been reported with a pair of setae on the mandible, as in *H. biseta* **sp. nov.** Therefore, the new species can be differentiated from its congeners by the unique setation of its mandible alone.

The combination of three other features also serves to differentiate *H. biseta* **sp. nov.** from its congeners. These are: (1) the caudal ramus is armed with 4 distinct setae (as in *H. tuberculata*), (2) the antennule is 2-segmented (as in *H. bilobata* **sp. nov.** and *H. crassa* **sp. nov.**), and (3) leg 5 is tipped with 3 setae (as in *H. dubia*, *H. tuberculata*, and *H. crassa* **sp. nov.**). No other species share all three of these diagnostic features.

## Family Enteropsidae Aurivillius, 1885

**Diagnosis.** Female: Body eruciform or vermiform, unsegmented or indistinctly segmented, generally lacking prosome-urosome division, consisting of cephalosome, metasomal trunk, and short genitoabdomen. Trunk consisting of first to fifth pedigerous somites. Caudal rami reduced; caudal setae reduced in number or absent. Rostrum absent or weakly developed. Antennule small, at most 4-segmented. Antenna up to 4-segmented, usually 1- or indistinctly 2-segmented, but 3- or 4-segmented in *Monnioticopa* **gen. nov.** and *Periboia* **gen. nov.** Labrum unarmed, or armed with 2 to 8 setiform processes; labrum with setiform palps in *Enterocola* van Beneden, 1860, *Enterocolides* Chatton & Harant, 1922, and *Lequerrea* Chatton & Harant, 1924; palps absent in other genera. Mandible as powerful claw in *Monnioticopa* **gen. nov.** and *Periboia* **gen. nov.**, or setiform element in *Enterocola* and *Enterocolides*, or absent in other genera. Maxillule consisting of precoxa and palp; precoxa bearing up to 3 setae or processes and endite tipped with 1 seta; palp armed with up to 6 setae. Maxilla 2-segmented; proximal segment (syncoxa) unarmed or bearing endite tipped with 1 seta or spiniform element; distal segment (basis) armed with up to 3 setae or processes. Maxilliped absent. Legs 1-4 biramous, consisting of protopod and 1- or 2-segmented rami. Protopods typically 2-segmented; coxa unarmed; basis occasionally with outer seta. Exopods and endopods rudimentary in *Enteropsis* Aurivillius, 1885 and *Mychophilus* Hesse, 1865. Endopods armed distally with 1 or 2 setae in *Enterocola* and *Monnioticopa* **gen. nov.** Endopods of legs 3 and 4, or of all swimming legs, unarmed in *Enterocolides* and *Lequerrea*. Leg 5 absent or represented by large lamellate lobe.

Male: Body cycloform, consisting of 5-segmented prosome and 6-segmented urosome. Prosome comprising cephalosome and first to fourth pedigerous somites. Caudal rami broad, armed with 6 setae. Rostrum well-developed. Antennule 6- or 7-segmented. Antenna of *Enterocola* 3- or 4-segmented, consisting of coxobasis (or coxa and basis) and 2-segmented endopod; coxa and first endopodal segment unarmed; basis with 1 seta; second endopodal segment with 4 or 5 setae plus claw. Antenna of *Mychophilus* reduced, 2-segmented. Labrum rudimentary. Mandible absent or as small, digitiform process. Maxillule 2-segmented, armed with 3 (in *Mychophilus*) or 6 (in *Enterocola*) setae on distal segment. Maxilla lobate, tipped with 1 seta. Maxilliped absent. Legs 1-4 biramous, with 2-segmented protopods. Coxae unarmed. Basis with outer seta; inner distal spine present (in *Enterocola*) or absent (in *Mychophilus*). Leg 1 exopod 2-segmented; other rami 3-segmented in legs 1-4. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-I	I-I (1-0); I, I, 3	0-0; 0-0 (0-1); 1, 2, 2
Leg 2:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-2 (0-1); 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; II, I, 5	0-1; 0-2 (0-1); 1, 2, 3
Leg 4:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 2

Leg 5 represented by 1 lateral seta plus small exopod tipped with 1 seta; or leg 5 represented by 2 isolated setae. Leg 6 absent or represented by 2 setae on genital operculum.

**Type genus.** *Enteropsis* Aurivillius, 1885 by original monotypy.

**Other included genera.** *Mychophilus* Hesse, 1865, *Enterocola* van Beneden, 1860, *Enterocolides* Chatton & Harant, 1922, *Lequerrea* Chatton & Harant, 1922, *Monnioticopa* **gen. nov.**, and *Periboia* **gen. nov.**

**Remarks.** In their revision, Illg & Dudley (1980) recognized two subfamilies of their ascidicolid cluster as especially closely related, the Enteropsinae (comprising *Enteropsis* and *Mychophilus*) and the Enterolinae (comprising *Enterocola*, *Enterocolides*, and *Lequerrea*). All five genera were included in a single family, the Enteropsidae, by Boxshall & Halsey (2004) because of the numerous synapomorphies exhibited, particularly between males of *Mychophilus* and *Enterocola*. The adult male of *Enterocola* had been known since Canu (1892) but the adult male of *Mychophilus* was first described by Gotto et al. (1984) only after Illg & Dudley's landmark study. In the present work two new genera are established and all seven genera can be distinguished using the following key.

#### Key to genera of Enteropsidae (based on females)

1. Leg 5 absent; legs 1-4 with rudimentary rami; mandible absent ..... 2  
 Leg 5 present, lamellate; legs 1-4 with distinct exopods and endopods; mandible present ..... 3
2. Anus positioned on dorsal surface anterior to genital apertures; maxilla lobate ..... *Mychophilus*  
 Anus positioned posterior to genital apertures; maxilla subchelate ..... *Enteropsis*
3. Antenna digitiform, 3- or 4-segmented; labrum without palps; mandible developed as powerful claw ..... 4  
 Antenna lamellate, 1- or 2-segmented; labrum with palps; mandible setiform ..... 5
4. Fifth pedigerous somite well defined from fourth pedigerous somite; caudal rami elongate, unarmed; endopod of legs 1-4 fused with protopod to form unarmed, tapering process ..... *Periboia* **gen. nov.**  
 Fifth pedigerous somite confluent with fourth pedigerous somite; caudal rami broad, with at least 1 distinct seta; endopod of legs 1-4 articulated with protopod and armed distally with 2 setae ..... *Monnioticopa* **gen. nov.**
5. Antennule or antenna absent ..... *Lequerrea*  
 Both antennule and antenna present ..... 6
6. Endopods of legs 1-4 armed distally with 1 or 2 setae ..... *Enterocola*  
 Endopods of legs 3 and 4 or all swimming legs unarmed ..... *Enterocolides*

#### Genus *Enterocola* van Beneden, 1860

**Diagnosis.** Female: Body eruciform, unsegmented or weakly segmented, consisting of cephalosome, metasomal trunk, and genitoabdomen. First to fourth pedigerous somites usually bearing dorsal tergite or dorsolateral tergal folds plus 1 or 2 ventral protrusions between left and right legs. Anal somite with dorsally protruded anal prominence bearing anus. Caudal rami unarmed, or with 1 small seta in some species. Rostrum not developed. Antennule small, typically leaf-like and 1- or 2-segmented; occasionally up to 4-segmented. Antenna lamellate, unsegmented or incompletely 2-segmented, typically with 6 setae, occasionally with 4 or 5 setae. Labrum lamellate with pair of spinulose setiform palps. Mandible spinulose and setiform. Maxillule consisting of precoxa and palp; precoxa with endite tipped with 1 spine or seta; palp palm-shaped, with 5 spines or setae on distal margin and 1 seta on lateral margin. Maxilla massive, 2-segmented; proximal segment (syncoxa) bearing large process or spine on mediodistal endite; distal segment sclerotized, bluntly bifurcate distally, armed with 1 small seta proximally on posterior surface. Maxilliped absent. Legs 1-4 biramous with 2-segmented protopod; protopods usually unarmed. Exopods unsegmented, but occasionally 2-segmented; exopods of legs 1, 2, and 4 tipped with small claw; exopod of leg 3 attenuated. Endopods unsegmented, but occasionally incompletely 2-segmented; typically armed with 2 setae distally (occasionally all or some of legs 1-4 armed with single seta). Leg 5 lamellate, unarmed or with 2 vestigial setae.

Male: Body cycloform with 5-segmented prosome and 6-segmented urosome. Caudal rami broad, 1.2 to 1.5 times longer than wide. Rostrum large, elongate, with bifid apex. Antennule 7-segmented; first segment with 10 to 13 setae. Antenna 3- or 4-segmented, armed with 1 seta on basis and 4 or 5 setae plus claw on terminal (second endopodal) segment. Labrum vestigial. Mandible absent or represented by digitiform process. Maxillule 1- or 2-segmented and armed with 6 setae. Maxilla unsegmented, tipped with seta. Maxilliped absent. Intercoxal plates of swimming legs narrow. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-I	I-0; I, I, 3	0-0; 0-0; 1, 2, 2
Leg 2:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; II, I, 5	0-1; 0-2; 1, 2, 3
Leg 4:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 2

Leg 5 consisting of lateral seta on surface of somite plus small exopod tipped with 1 seta. Leg 6 represented by 2 small setae on genital operculum.

**Type species.** *Enterocola fulgens* van Beneden, 1860 by original designation.

**Remarks.** Ooishi (2010b) synonymized *E. brementi* Illg & Dudley, 2010 with *E. mammiferus* Chatton & Harant, 1922 and later (Ooishi, 2014a) synonymized *E. setiferus* Hansen, 1923 with *Styelicola bahusia* Lützen, 1968 of the family Ascidicolidae. In that study Ooishi recognized 20 valid species in the genus *Enterocola*, including the two new species that she had just described (Ooishi, 2014a). Taxonomic characters are relatively limited in *Enterocola* (Marchenkov & Boxshall, 2005). We consider that the proportional lengths of setae on the antenna and legs 1-4, especially those of leg 1, are useful as morphological characters for distinguishing between species, and it is helpful that the antenna and leg 1 are most frequently illustrated in previous descriptions. On the basis of published figures, we measured the proportional lengths of the setae of these appendages (see Table 6), except for *E. bilamellatus* Sars, 1921 for which leg 1 is unknown.

**TABLE 6.** Summary of key differences between species of *Enterocola*. (= indicates approximate ratio or number)

Species	Characters (see below)										Data source
	1	2	3	4	5	6	7	8	9	10	
<i>E. adnatus</i>	0	2	5	5	V	IV	I	0	1.2	=2	Ooishi (2014a)
<i>E. africanus</i>	>1	pointed	5	6	VI	V	I	2	1.3	1.8	L-G (1993)
<i>E. bilamellatus</i>	=3	4	3?	7	IV	VI	I	2	?	?	Sars (1921)
<i>E. clavelinae</i>	1.29	tapered	9	6	III	II	I	2	1.6	1.0	Present study
<i>E. coniculus</i>	0	2	2	6	V	IV	I	2	0.3	0.3	Ooishi (2014a)
<i>E. dicaudatus</i>	=3	bulbous	4	6	I	VI	V	1	0.3	1.7	M & B (2005)
<i>E. fertilis</i>	=1.5	tapered	3	6	V	VI	I	2	1.5	1.1	I & D (1980)
<i>E. fulgens</i>	2.52	3	3	6	II	V	IV	2	0.7	1.0	Present study
<i>E. gottoi</i>	<1	tapered	=5	6	VI	V	I	2	1.0	1.0	Con. (1992)
<i>E. hessei</i>	2.27	tapered	13	6	VI	V	I	1	1.7	1.2	Present study
<i>E. ianthinus</i>	2.5	2	6	6	VI	V	III	2	1.1	1.0	Ooishi (2014a)
<i>E. laticeps</i>	=2.5	elongate	16	5	V	VI	II	0	0.5	0.8	I & D (1980)
<i>E. mammiferus</i>	>1	leaf-like	4	6	*			2	0.8	1.0	Ooishi (2010b)
<i>E. monnioti</i>	0	2	=2	6	V	III	I	0	0.3	1.0	M & B (2005)
<i>E. ooishiae</i>	=2	elongate	10	6	VI	V	I	2	1.9	1.5	O'Reilly (2008)
<i>E. parapterophorus</i>	2.5	leaf-like	3	5	V	IV	I	1	0.5	1.4	Present study
<i>E. petiti</i>	=1	tapered	2	6	V	VI	I	2	1.4	0.9	I & D (1980)

...Continued on the next page



**TABLE 6.** (Continued)

Species	Characters (see below)										Data source
	1	2	3	4	5	6	7	8	9	10	
<i>E. precarius</i>	=1.5	tapered	=8	6	V	III	I	2	0.8	1.0	I & D (1980)
<i>E. pterophorus</i>	2.03	leaf-like	4/5	6	VI	V	III	0	1.0	1.2	Present study
<i>E. sydnii</i>	=1	tapered	7	6	*			2	0.9	1.3	Ooishi (2011)
<i>E. seticauda</i> <b>sp. nov.</b>	2.02	2	7	6	VI	V	I	2	1.9	1.3	Present study
<i>E. quadriseta</i> <b>sp. nov.</b>	3.17	leaf-like	6	4	IV	III	II	0	0.9	1.2	Present study
<i>E. mabulensis</i> <b>sp. nov.</b>	1.53	leaf-like	5	5	V	IV	**	1	0.6	1.2	Present study
<i>E. robustus</i> <b>sp. nov.</b>	3.00	leaf-like	3	6	VI	V	**	1	0.7	1.3	Present study
<i>E. parvus</i> <b>sp. nov.</b>	2.10	bulbous	3	6	VI	I	**	1	0.8	1.1	Present study
<i>E. tuberculatus</i> <b>sp. nov.</b>	3.2	elongate	5	5	VI	V	III	1	1.3	1.4	Present study
<i>E. australis</i> <b>sp. nov.</b>	2.46	tapered	7	6	VI	V	I	0	1.2	0.7	Present study
<i>E. angustus</i> <b>sp. nov.</b>	1.92	bulbous	5	6	VI	V	**	0	0.8	1.8	Present study
<i>E. sedentarius</i> <b>sp. nov.</b>	1.8	tapered	7	6	VI	V	I	2	2.2	1.1	Present study
<i>E. sulcatus</i> <b>sp. nov.</b>	1.75	tapered	7	6	VI	V	I	2	2.0	1.1	Present study
<i>E. neocaledonicus</i> <b>sp. nov.</b>	2.07	leaf-like	4	6	VI	V	**	1	0.9	1.2	Present study
<i>E. nodulosus</i> <b>sp. nov.</b>	2.63	leaf-like	5	6	VI	V	II	1	1.0	1.1	Present study
<i>E. oligosetosus</i> <b>sp. nov.</b>	1.85	tapered	7	5	V	VI	III	0	1.0	1.4	Present study
<i>E. curticauda</i> <b>sp. nov.</b>	0	tapered	7	5	V	IV	I	0	0.7	1.4	Present study
<i>E. unisetosus</i> <b>sp. nov.</b>	1.1	lobate	1	6	IV	III	VI	0	1.2	-	Present study

**Characters 1-9:** 1, length to width ratio of caudal ramus (0 indicates absence of caudal rami); 2, segments or shape of antennule; 3, number of setae on antennule; 4 number of setae on antenna; 5, longest seta of antenna (\* indicates equal lengths of setae I-VI); 6, second longest seta of antenna; 7, shortest seta of antenna (\*\* indicates two or more setae equal shortest); 8, numbers of ventral interpodal protrusions on fourth pedigerous somite; 9, length ratios of laterodistal seta to endopodal segment in leg 1; 10, length ratios of laterodistal to mediodistal setae on endopod of leg 1.

**Abbreviations for data sources:** I & D: Illg & Dudley; L-G: López-González, Conradi & García-Gómez; M & B: Marchenkov & Boxshall; Con.: Conradi, López-González & García-Gómez.

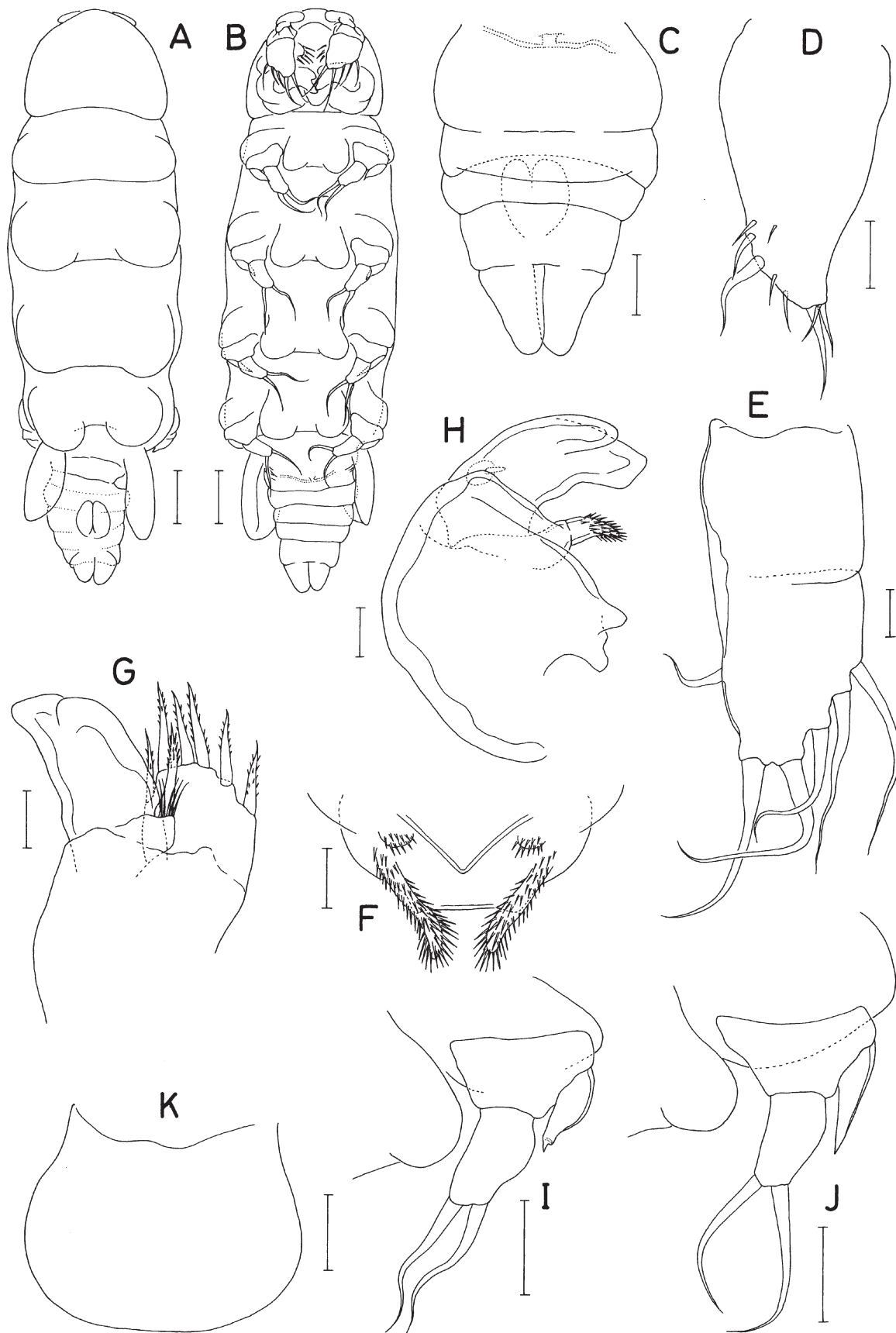
### *Enterocola clavelinae* Chatton & Harant, 1924

(Fig. 122)

**Material examined.** 7 ♀♀ (MNHN-IU-2014-21538, 1 ♀ dissected) in *Pycnoclavella nana* (Lahille, 1890) MNHN-IT-2008-2064; Roscoff, Atlantic coast of France, no other collection data.

**Supplementary description of female.** Body (Fig. 122A, B) eruciform, straight: body length 1.11 mm, maximum width 336 µm (across second pedigerous somite). Cephalosome wider than long, distinctly articulated from metasome. Trunk unsegmented, incorporating fifth pedigerous somite, with 4 distinct dorsal tergites; tergites of second to fourth pedigerous somites bilobed, forming left and right tergal folds (Fig. 122A). First to fourth pedigerous somites each with pair of large interpodal protrusions on ventral surface between left and right legs (Fig. 122B, I, J). Genitoabdomen (Fig. 122C) obscurely 4- or 5-segmented, about half as long as trunk; anal prominence distinct, directed anterodorsally. Caudal rami immediately adjacent to one another, incompletely articulated from anal somite, tapering, about 1.3 times longer than wide (75×58 µm), unarmed, with rounded distal margin.

Rostrum not developed. Antennule (Fig. 122D) narrowing distally, unsegmented, 87×50 µm, armed with 9 small, unequal setae along distal third (5 setule-like). Antenna (Fig. 122E) lamellate, twice as long as wide (145×69 µm), incompletely 2-segmented, with partial articulation on outer (lateral) surface; proximal segment unarmed; distal segment armed with 6 naked setae; medial seta (seta I) shortest, 30 µm long, positioned at midlength of medial margin of distal segment; 5 other setae (setae II-VI) 90, 100, 70, 80, and 82 µm, respectively, from medial to lateral.



**FIG. 122.** *Enterocola clavelinae* Chatton & Harant, 1924, female. A, habitus, dorsal; B, habitus, ventral; C, genitoabdomen, ventral; D, antennule; E, antenna; F, labrum; G, maxillule; H, maxilla; I, leg 1; J, leg 3; K, leg 5. Scale bars: A, B, 0.1 mm; C, I-K, 0.05 mm; D-H, 0.02 mm.

Labrum (Fig. 122F) on ventral surface with triangular, sclerotized elevated area in middle, and small spinulose lobe plus elongate, spinulose palp on each side. Mandible very similar to labral palp, elongate, and densely spinulose. Maxillule (Fig. 122G) consisting of precoxa and palp; precoxa comprising endite bearing 1 spinulose seta and about 5 setules, and highly sclerotized, bifurcate distal part; palp palm-like, armed with 6 spinulose setae. Maxilla (Fig. 122H) 2-segmented; proximal segment (syncoxa) with mediolateral endite bearing thick spinulose element; distal segment distally bifurcate, with small, transparent seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each consisting of 2-segmented protopod and 1-segmented rami; protopods unarmed. Exopods of legs 1, 2 and 3 shorter than endopodal segment, with small claw-like distal tip indistinctly demarcated by rudimentary suture. Exopod of leg 3 evenly tapering (Fig. 122J), slightly longer than endopodal segment, with pointed tip. Leg 1 (Fig. 122I) endopod 1.6 times longer than wide ( $53 \times 33 \mu\text{m}$ ), with convex outer margin; 2 distal setae equal in length,  $83 \mu\text{m}$  long, 1.57 times longer than endopodal segment. Endopods of legs 2-4 similar in dimensions to that of leg 1, but laterodistal seta about 1.9 times longer than endopodal segment and slightly longer than medial seta.

Leg 5 (Fig. 122K) lamellate, distinctly wider than long ( $124 \times 185 \mu\text{m}$ ), unarmed, with concave medial surface.

**Male.** Unknown.

**Remarks.** Chatton & Harant (1924a) originally described this species based on specimens collected on the Atlantic coast of France. Illg & Dudley (1980) redescribed it and recorded Banyuls-sur-Mer on the Mediterranean coast of France as an additional collection locality. The specimens examined in the present work are identified as *E. clavelinae* because the form of the caudal rami, the antennule and antenna, and the proportional lengths of the antennal setae and the setae on legs 1-4 all are in accord with those illustrated by Illg & Dudley (1980). *Pycnoclavella nana* (reported as *Clavelina nana* in the original description) is the only known ascidian host of this copepod.

### ***Enterocola hessei* Chatton & Harant, 1924**

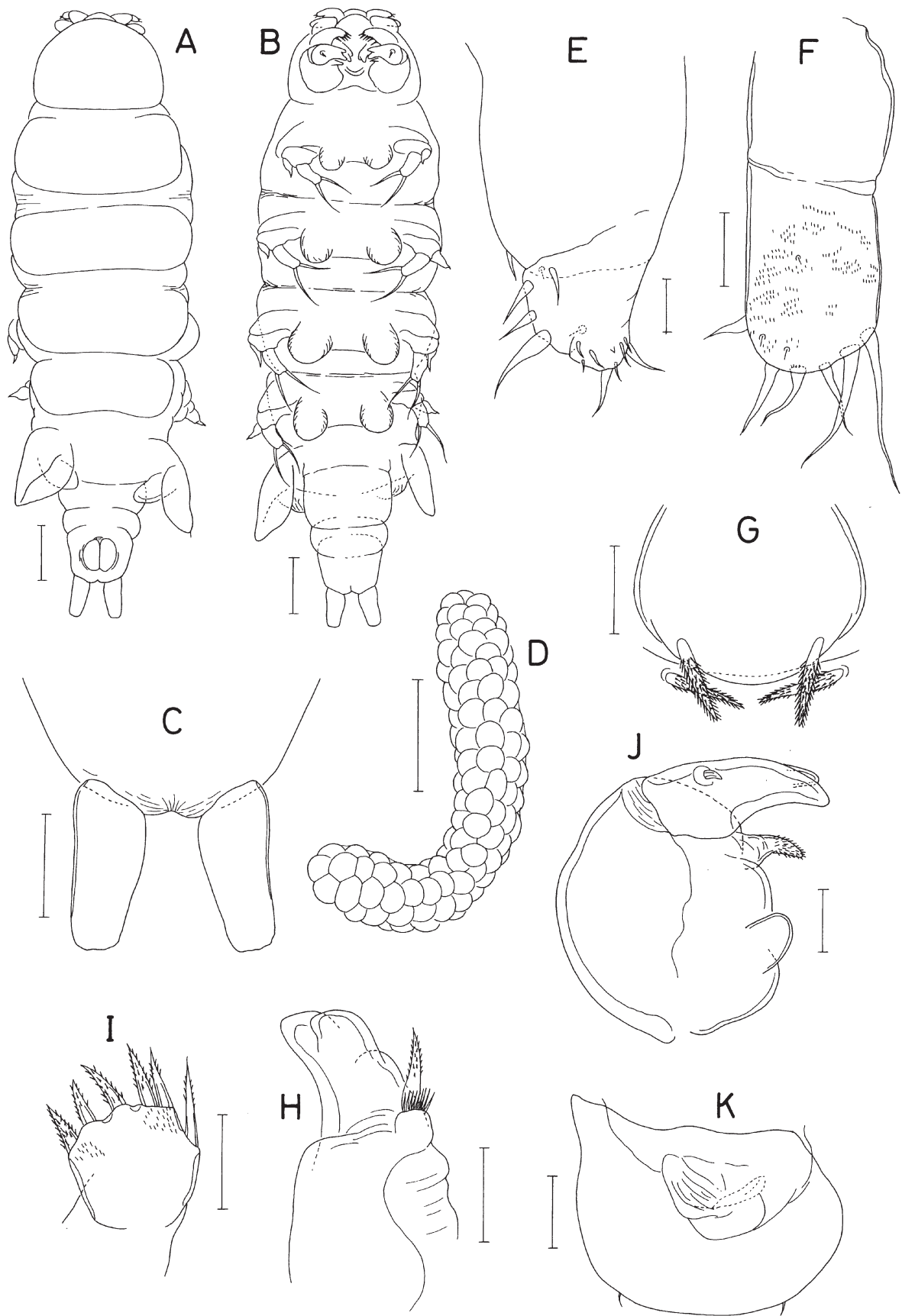
(Figs. 123, 124)

**Material examined.** 3 ♀♀ (MNHN-IU-2014-21539, 1 ♀ dissected) from *Clavelina lepadiformis* (Müller, 1776), Saint-Vaast-la-Hougue, Atlantic coast of France, Monniot coll.; 4 ♀♀ (MNHN-IU-2014-21540) from *C. lepadiformis*, Roscoff, France.

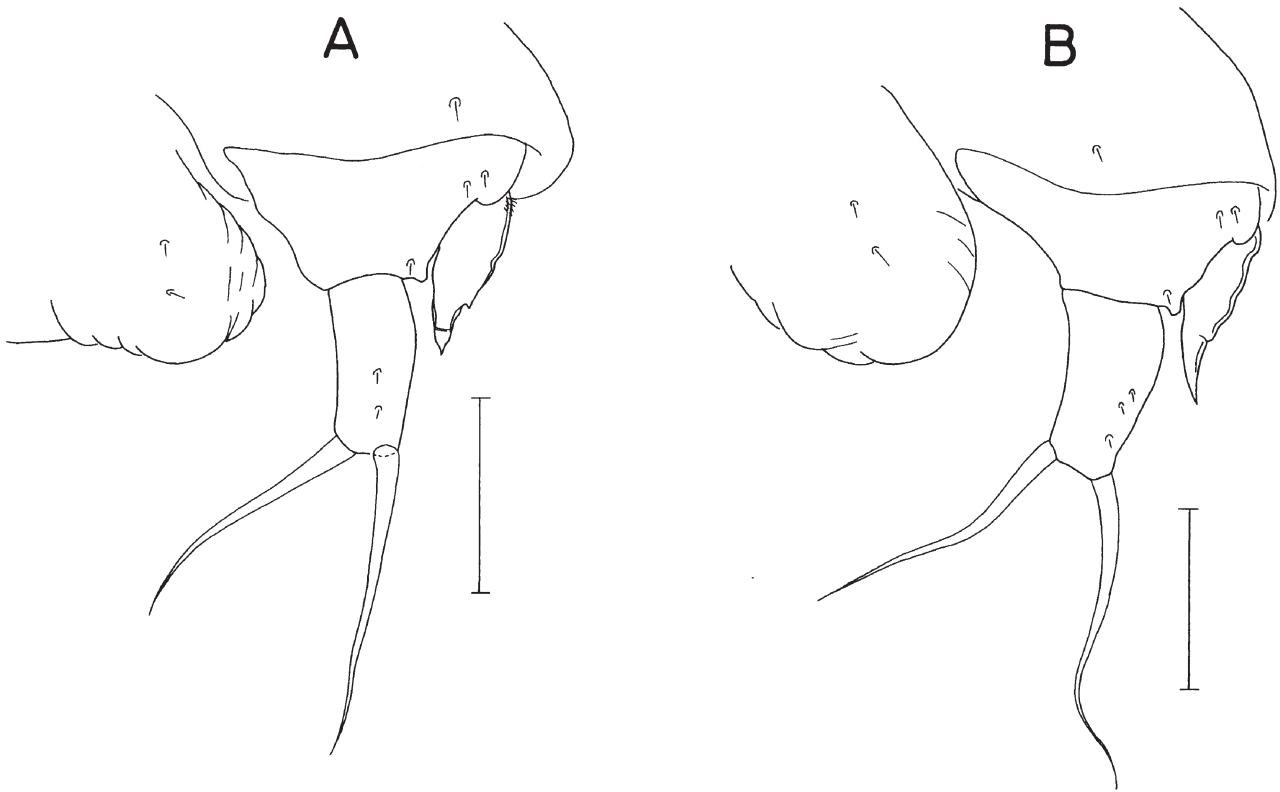
**Supplementary description of female.** Body eruciform, straight, consisting of cephalosome, 5-segmented trunk, and incompletely 3-segmented genitoabdomen. Body length 2.21 mm; maximum width  $664 \mu\text{m}$  (across second pedigerous somite). Cephalosome wider than long. First to fourth pedigerous somites each bearing distinct dorsal tergite; tergites simple, not forming dorsolateral folds; pedigerous somites each bearing pair of large, subglobular interpodal protrusions on ventral surface between left and right legs (Fig. 123B, 124A, B). Fifth pedigerous somite not articulated from fourth pedigerous somite. Anal somite bearing distinct anal prominence dorsally. Caudal rami (Fig. 123C) slightly divergent, well separated from each other, and clearly articulated from anal somite; each ramus sub-rectangular, unarmed, 2.27 times longer than wide ( $159 \times 70 \mu\text{m}$ ), gradually narrowing distally, with longer outer and shorter inner margins. Egg sac (Fig. 123D) L- or C-shaped,  $2.0 \times 0.35 \text{ mm}$  in measured sample, containing numerous eggs; each egg about  $130 \mu\text{m}$  in diameter.

Rostrum absent. Antennule (Fig. 123E) about  $135 \times 83 \mu\text{m}$ , incompletely 2-segmented, gradually narrowing distally; longer proximal segment with 1 small seta distally; distal segment armed with 12 unequal setae and 1 minute spinule, several of distal setae setule-like; longest seta  $30 \mu\text{m}$  long. Antenna (Fig. 123F) about  $245 \times 100 \mu\text{m}$ , indistinctly 2-segmented; shorter proximal segment unarmed and unornamented; longer distal segment with rounded distal margin, ornamented with numerous minute spinules on convex anterior surface, and armed with 6 naked setae of lengths 31, 55, 50, 50, 94, and  $107 \mu\text{m}$ , from medial to lateral (setae I-VI), respectively; shortest medial seta positioned at 80% along medial margin of segment.

Labrum (Fig. 123G) subcircular, smooth, with pair of slender, spinulose palps. Mandible (Fig. 123G) setiform, spinulose, similar to labral palp. Maxillule consisting of precoxa and palp; precoxa (Fig. 123H) with 1 subdistal and 2 distal projections on distal sclerotized part and endite bearing 1 spinulose seta and about 10 thin setules; palm-shaped palp (Fig. 123I) with 6 spinulose setae, 5 on distal and 1 on lateral margins, latter seta longer than distal setae. Maxilla (Fig. 123J) 2-segmented; proximal segment with 1 large smooth tubercle proximally on medial side



**FIG. 123.** *Enterocola hessei* Chatton & Harant, 1924, female. A, habitus, dorsal; B, habitus, ventral; C, caudal rami, ventral; D, egg sac; E, antennule; F, antenna; G, labrum and mandibles; H, precoxa of maxillule; I, palp of maxillule; J, maxilla; K, leg 5. Scale bars: A, B, 0.2 mm; C, K, 0.1 mm; D, 0.5 mm; E, 0.02 mm; F-J, 0.05 mm.



**FIG. 124.** *Enterocola hessei* Chatton & Harant, 1924, female. A, leg 1; B, leg 3. Scale bars: 0.1 mm.

and mediiodistal endite bearing spinulose process; second segment unequally bifurcate distally, armed with 1 small spine proximally on posterior surface. Maxilliped absent.

Legs 1-4 each consisting of 2-segmented protopod and 1-segmented rami; protopods unarmed. Exopods shorter than endopods: exopods of legs 1, 2, and 3 with rudimentary articulation distally; exopod of leg 3 claw-like (Fig. 124B). Endopods each bearing 2 setae on distal margin, lateral seta longer than medial seta in legs 1-4. Endopodal segment  $93 \times 41$ ,  $102 \times 48$ ,  $102 \times 52$ , and  $91 \times 57$   $\mu\text{m}$ , respectively, in legs 1-4. Distal setae of leg 1 (Fig. 124A) endopod 159 (lateral) and 136  $\mu\text{m}$  (medial), therefore, lateral seta about 1.7 times longer than endopodal segment and 1.17 times longer than medial seta. Distal setae of leg 3 endopod 184 (lateral) and 161  $\mu\text{m}$  (medial). Proportional lengths of distal setae of endopods of legs 2 and 4 similar to those of leg 3.

Leg 5 (Fig. 123K) lamellate, smooth, wider than long ( $267 \times 370$   $\mu\text{m}$ ); armed with 2 minute setae, separated by distance of about 230  $\mu\text{m}$ .

**Male.** Unknown.

**Remarks.** In her redescription of this species, Ooishi (2010a) mentioned or illustrated that (1) the ventral surface of the metasome bears 4 prominent pairs of interpodal protrusions, (2) the antennule is armed with 12 setae, (3) leg 1 endopod is 2.3 times longer than wide, and (4) the laterodistal seta of leg 1 endopod is 1.2 times longer than the mediiodistal seta. These features are almost exactly the same as in our specimens. Some discrepancies, such as the slightly longer caudal rami (2.6 times longer than wide) are minor, while others such as the 5-segmented genitoabdomen in Ooishi's specimens, may be due to the reproductive state of the material. Both Ooishi's and our samples of this copepod species were collected from the ascidian *Clavelina lepadiformis* in the vicinity of the type locality.

## *Enterocola pterophorus* Chatton & Brément, 1909

(Figs. 125, 126)

**Material examined.** 6 ♀♀ (MNHN-IU-2014-21541, 2 ♀♀ dissected) in *Trididemnum cereum* (Giard, 1872); Glenan Is., Atlantic coast of France, Lafargue coll., date unknown.

**Supplementary description of female.** Body (Fig. 125A, B) inflated, unsegmented, slightly depressed, and curved dorsally. Body length 1.09 mm in largest specimen; maximum width 445 µm (across region of leg 2). Cephalosome obscurely defined from trunk, much wider than long. Trunk narrowing posteriorly, with 3 pairs of dorsal tergal folds, 1 pair each on second to fourth pedigerous somites; left and right tergal folds separated from each other on second pedigerous somite, but close to each other on third and fourth pedigerous somites. Ventral surface of trunk lacking interpodal protrusions between left and right legs. Genitoabdomen not defined from but distinctly narrower than trunk, lacking any trace of articulation; dorsal anal prominence distinct. Caudal rami (Fig. 125C) about 2.0 times longer than wide (67×33 µm), unarmed, tapering towards blunt apex. Egg sac (Fig. 125D) curved, 505×240 µm; eggs arranged in 3 or 4 rows, each egg about 160 µm in diameter.

Rostrum absent. Antennule (Fig. 125E) 42×27 µm, strongly tapering, with convex anterior margin and straight posterior margin, armed distally with 5 (occasionally 4) setae of subequal lengths. Antenna (Fig. 125F) flattened, indistinctly 2-segmented, 119×57 µm; proximal segment unarmed; distal segment as long as proximal segment, armed with 6 small setae, and ornamented with fine spinules on concave surface; lengths of setae I-VI (medial to lateral setae) 15, 12, 12, 20, 21, and 34 µm, respectively; setae 1-3 curved and stiff.

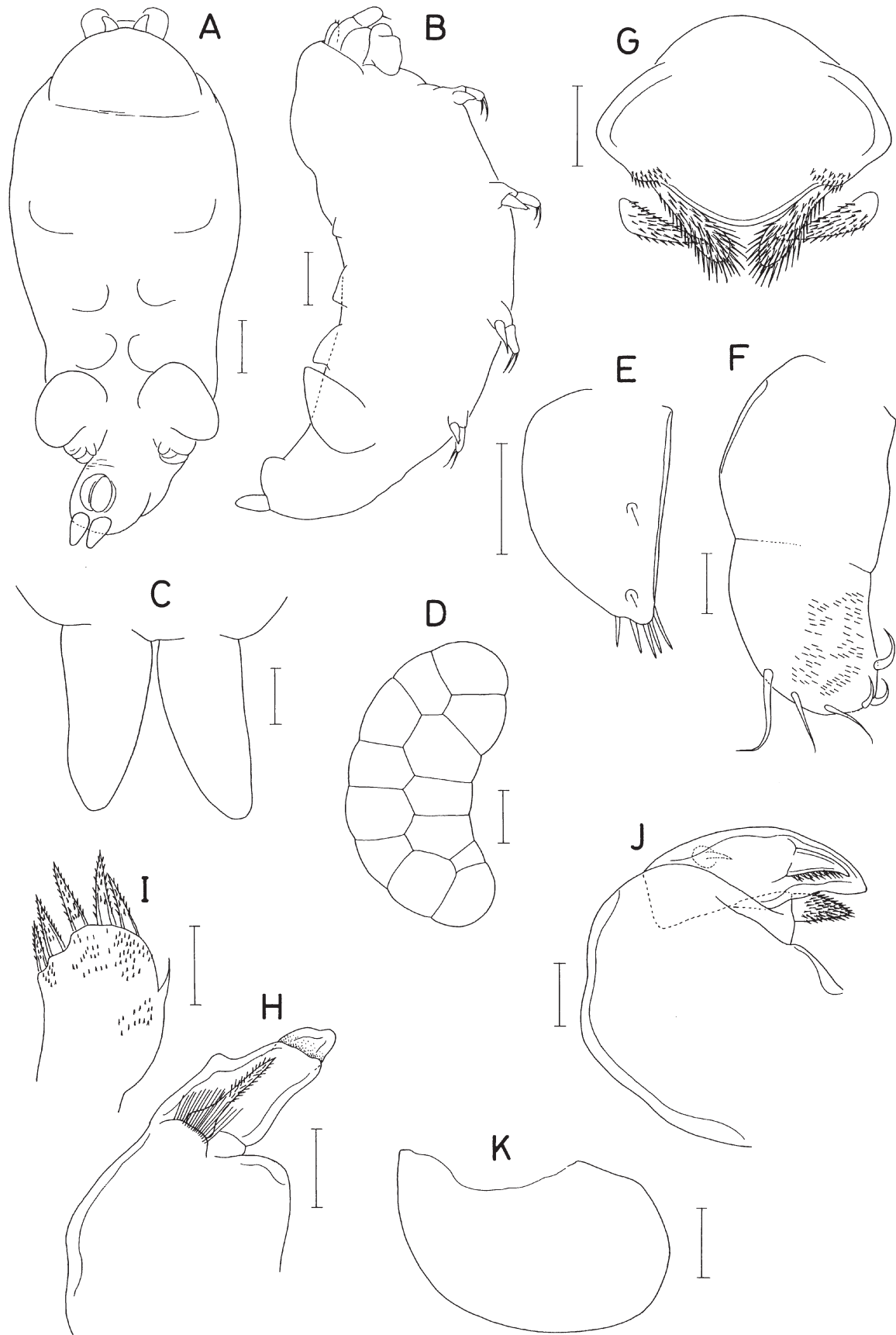
Labrum (Fig. 125G) rhomboidal, bearing pair of palps and patch of spinules near base of palps; palp densely spinulose, club-shaped, gradually thickening distally. Mandible (Fig. 125G) tapering, densely spinulose, slightly shorter than labral palp. Maxillule (Fig. 125H, I) 2-segmented; endite of proximal segment (precoxa) with 1 slender, spinulose seta and more than 20 thin setules; palm-shaped distal segment (palp) with 5 spinulose setae on distal margin and 1 small, naked, setiform process on lateral margin. Maxilla (Fig. 125J) 2-segmented; proximal segment (syncoxa) with mediodistal endite bearing thick, spinulose, spiniform element; distal segment with tapering distal part, with thick subterminal spine bearing several rows of spinules along medial margin, and with 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each with unsegmented protopod and rami (Fig. 126A-C); protopods unarmed. Exopod of leg 3 (Fig. 126B) elongate, longer than endopod, and acutely pointed. Exopods of legs 1, 2, and 3 distinctly shorter than endopod, tipped with small, claw-like process. Endopods of legs 1-4 50×27, 58×29, 54×27, and 46×26 µm, respectively. Lengths of laterodistal and mediodistal setae on endopods: 52 and 45, 45 and 41, 48 and 45, and 50 and 41 µm in legs 1-4, respectively.

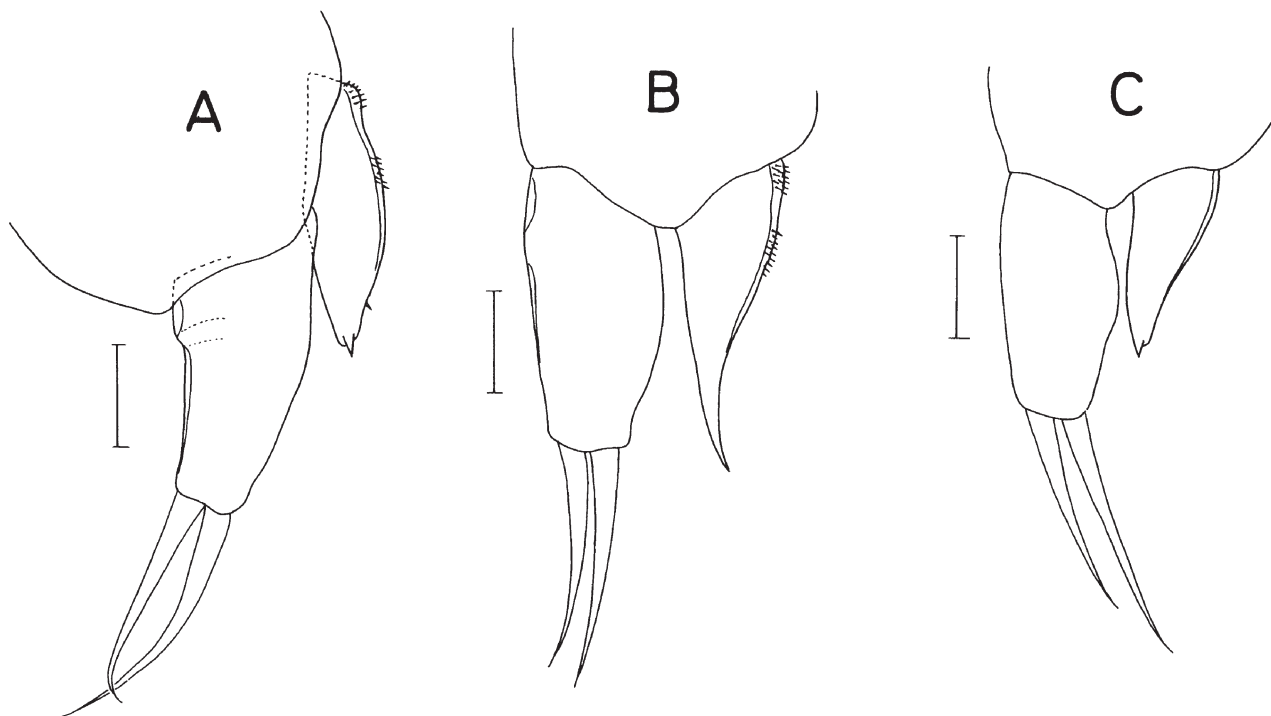
Leg 5 (Fig. 125K) much wider than long (120×205 µm) and unarmed.

**Male.** Unknown.

**Remarks.** *Enterocola pterophorus* was redescribed and illustrated in detail by Illg & Dudley (1980) based on specimens from a variety of different ascidian hosts. Of the copepods they examined, those associated with *Didemnum fulgens* (Milne Edwards, 1841) from the Mediterranean Sea and *Trididemnum tenerum* (Verrill, 1871) from the North East Atlantic displayed the characteristic form and setation of the antennule and antenna, and this was shared with our specimens associated with *Trididemnum cereum* from the North East Atlantic. In this material the antennule tapers and is armed with 3 to 5 small setae distally, and the antenna is armed with 6 small setae (mediodistal 3 strongly curved). In addition to these features, our specimens and those of Illg & Dudley's share an unsegmented genitoabdomen and the absence of the ventral interpodal protrusions between left and right legs. On the basis of the evidence provided by the combination of all these characters, we identified our specimens as *E. pterophorus*.



**FIG. 125.** *Enterocola pterophorus* Chatton & Brément, 1909, female. A, habitus, dorsal; B, habitus, right; C, caudal rami; D, egg sac; E, antennule; F, antenna; G, labrum and mandibles; H, precoxa of maxillule; I, palp of maxillule; J, maxilla; K, leg 5. Scale bars: A, B, D, 0.1 mm; C, E-J, 0.02 mm; K, 0.05 mm.



**FIG. 126.** *Enterocola pterophorus* Chatton & Brément, 1909, female. A, leg 1; B, leg 3; C, leg 4. Scale bars: 0.02 mm.

***Enterocola fulgens* van Beneden, 1860**

(Figs. 127, 128)

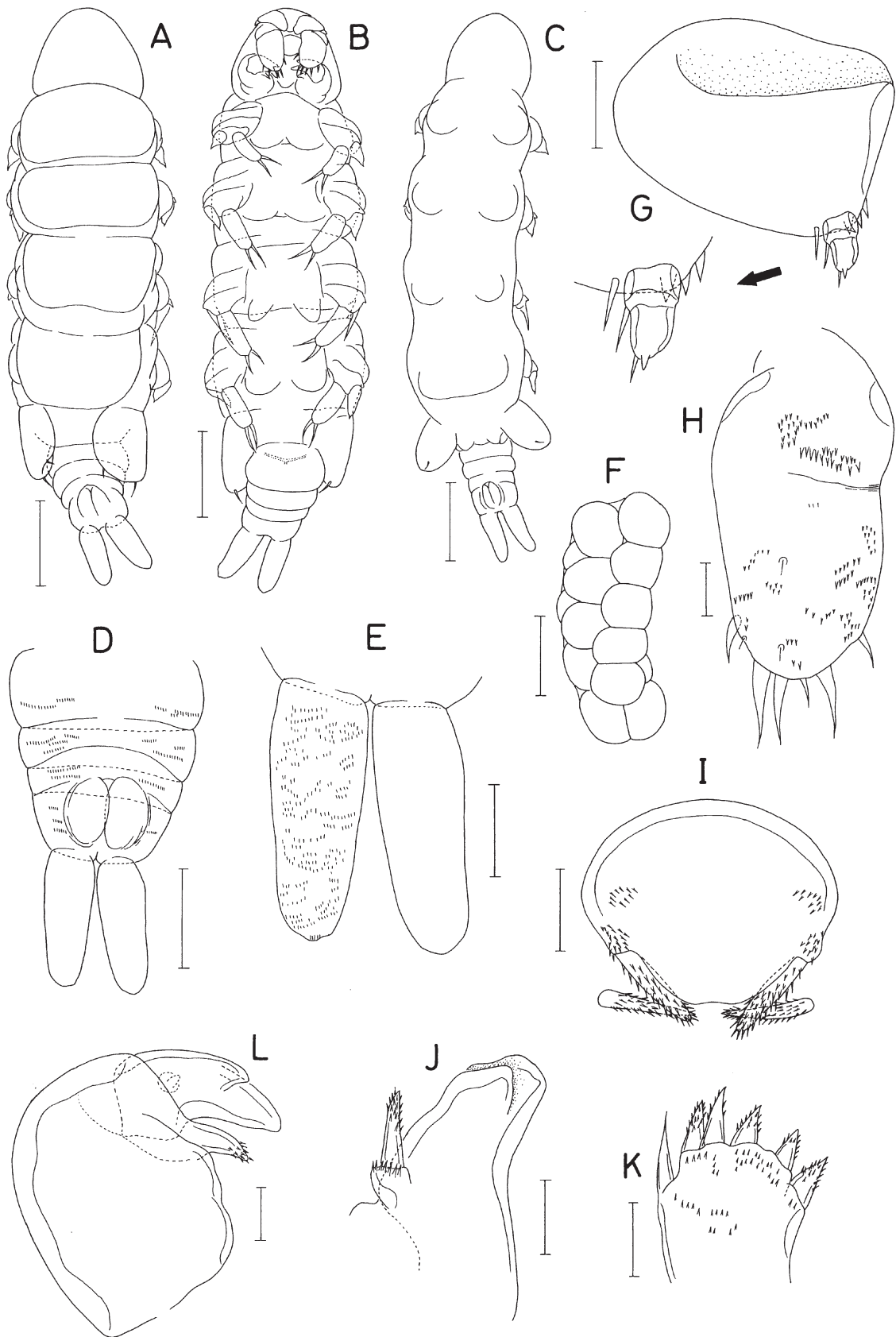
**Material examined.** 9 ♀♀ (MNHN-IU-2014-21542, 2 ♀♀ dissected) from *Polyclinum aurantium* Milne Edwards, 1841; Saint-Vaast-la-Hougue, Atlantic coast of France, Monniot coll., date unknown.

**Supplementary description of female.** Body (Fig. 127A-C) eruciform, cylindrical, consisting of cephalosome, trunk and genitoabdomen. Body length 1.36 mm in dissected specimen; mean body length 1.27 mm (0.98-1.45 mm), based on 7 specimens: maximum width 352 µm (across second pedigerous somite). Cephalosome 1.25 times wider than long, distinctly narrower than trunk, and well-defined from first pedigerous somite. Trunk consisting of first to fifth pedigerous somites, unsegmented or indistinctly segmented; first to fourth pedigerous somites each bearing dorsal tergite and paired ventral interpodal protrusions, these protrusions weak in first and second pedigerous somites, but prominent in third and fourth; in young adult (Fig. 127C) dorsal tergites usually incomplete, forming dorsolateral tergal folds. Genitoabdomen (Fig. 127D) 4-segmented, consisting of genital double-somite and 3 abdominal somites, ornamented with numerous minute spinules on all surfaces; articulations between somites distinct on ventral surface but indistinct dorsally; anal prominence large. Caudal rami (Fig. 127E) unarmed, about 2.5 times longer than wide (136×54 µm), slightly narrowing distally, about twice as long as anal somite, with rounded distal margin; covered with numerous minute spinules.

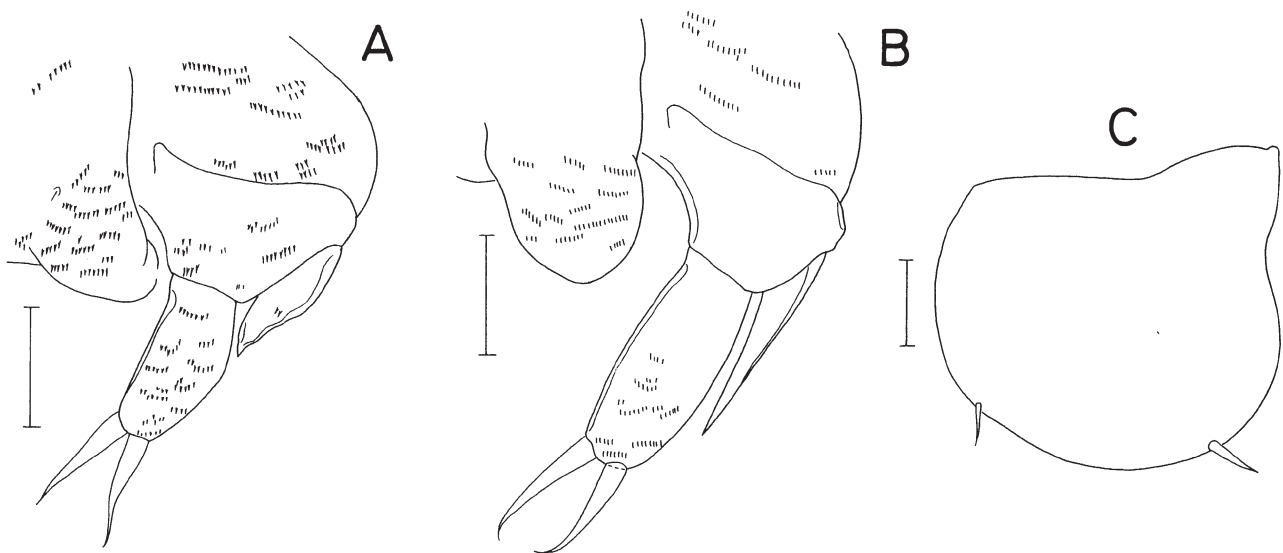
Rostrum absent. Antennule (Fig. 127G) distinctly 3-segmented, consisting of expanded first segment and small distal segments; first segment much wider than long (45×61 µm), with straight, sclerotized anterior margin, strongly protruding posterior margin, armed with 1 small seta distally and ornamented with 2-5 setiform spinules near base of second segment; second segment wider than long (5×8 µm) armed with 1 small seta at posterodistal corner; third segment slightly longer than wide (7×5 µm), armed with 1 seta and 1 setiform process distally. Antenna (Fig. 127H) about 135×68 µm, 2-segmented, but suture line between segments vestigial; proximal segment unarmed, but ornamented with spinules on convex surface; distal segment distinctly longer than proximal segment, armed with 6 small setae and ornamented with scattered spinules on convex surface; lengths of setae I-VI (medial to lateral) 18, 32, 25, 11, 27, and 13 µm, respectively; setae IV and VI markedly smaller than other 4 setae.

Labrum (Fig. 127I) with cylindrical, spinulose palp and 2 patches of spinules on each side; posterior margin projecting, with truncate apex. Mandible (Fig. 127I) spinulose, shorter and more slender than labral palp. Maxillule





**FIG. 127.** *Enterocola fulgens* van Beneden, 1860, female. A, habitus, dorsal; B, habitus, ventral; C, habitus of young adult, dorsal; D, genitoabdomen, dorsal; E, caudal rami, dorsal; F, egg sac; G, antennule, with inset showing detail of distal segments; H, antenna; I, labrum and mandibles; J, precoxa of maxillule; K, palp of maxillule; L, maxilla. Scale bars: A-C, F, 0.2 mm; D, 0.1 mm; E, 0.05 mm; G-L, 0.02 mm.



**FIG. 128.** *Enterocola fulgens* van Beneden, 1860, female. A, leg 1; B, leg 3; C, leg 5. Scale bars: 0.05 mm.

consisting of precoxa (Fig. 127J) and palp (Fig. 127K): precoxa (Fig. 127J) with bluntly bifurcate tip; endite tipped with 1 spinulose spine and about 10 short spinules: palp (Fig. 127K) with 5 stout spinulose spines on distal margin and 1 naked, attenuated spine on lateral margin. Maxilla (Fig. 127L) 2-segmented; proximal segment (syncoxa) with mediolateral endite extending to distally spinulose large process; distal segment with 2 blunt distal projections (shorter anterior and longer posterior), and 1 small, blunt seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each consisting of 2-segmented protopod and 1-segmented rami; protopods unarmed, but ornamented with rows of minute spines. Exopods shorter than endopods (Fig. 128A); exopod of leg 3 acute, spiniform (Fig. 128B). Endopods  $68 \times 33$ ,  $89 \times 38$ ,  $92 \times 39$ , and  $82 \times 38$   $\mu\text{m}$ , respectively, in legs 1-4; each endopod armed with 2 setae distally. Two distal setae on endopods characteristically equal in length, 0.6-0.7 times as long as endopodal segments; lengths of endopodal setae 48, 59, 55, and 55  $\mu\text{m}$ , respectively, in legs 1-4.

Leg 5 (Fig. 128C) wider than long ( $167 \times 196$   $\mu\text{m}$ ), armed with 2 small setae on distal margin separated by distance of 136  $\mu\text{m}$ .

**Male.** See Ooishi (2007b).

**Remarks.** Ooishi (2007b) redescribed this species in detail on the basis of specimens collected from the ascidian *Polyclinum aurantium* at Roscoff. Our examined copepod specimens were associated with the same ascidian host from a nearby geographical locality. *Enterocola fulgens* seems to be a distinctive species due to its characteristic antennule which is distinctly 3-segmented, with the first segment inflated and 2 small distal segments. Nevertheless, we found some differences in details between Ooishi's and our material, as follows: (1) the caudal ramus is 1.6 times longer than wide in Ooishi's material, compared to 2.5 times longer than wide in our material; (2) the antennule is armed with 2, 1, and 3 setae on the first to third segments, compared to the setation 1, 1, and 1 in our material; (3) the setae on the antenna of Ooishi's material are shorter than those of our material; (4) the ventral interpodal protrusions on the first to fourth pedigerous somites of Ooishi's material are obscure, but distinct in our material; and (5) the 2 distal setae on the endopods of legs 1-4 of Ooishi's material are unequal in length, compared to the equal lengths in our material. On the evidence available, we interpret these differences as due to infraspecific variation, at least in part because some of this variability is shown in the illustrations of Illg & Dudley (1980).

Illg & Dudley (1980) recorded variability in the setation of the antenna, noting that either 5 or 6 setae were present. In the 5-setae condition in Illg & Dudley's material, the smallest apical seta (seta IV), which is the most likely to be overlooked, was missing. This variability could not be confirmed in our study or by Ooishi (2007b).

***Enterocola parapterophorus* Marchenkov & Boxshall, 2005**

(Figs. 129, 130)

**Material examined.** 3 ♀♀ (MNHN-IU-2014-21543, 1 ♀ dissected) from *Didemnum* sp. (MNHN-IT-2008-3357 = MNHN A2/DID.C/322); Suez, Ph. Dollfus coll., 22 December 1928.

**Supplementary description of female.** Body (Fig. 129A-C) stout, curved dorsally; body length 873 µm; maximum width 364 µm (across second pedigerous somite). Cephalic shield 164×247 µm, distinctly narrower than trunk, with obscure posterior margin. Trunk unsegmented, but 5 pedigerous somites defined by constrictions; dorsolateral tergal folds absent on first pedigerous somite, but present on second to fourth pedigerous somites. First to fourth pedigerous somites each with single mid-ventral interpodal protrusion between left and right legs, small in first pedigerous somite, but broad in others (Fig. 129C). Genitoabdomen dorsally unsegmented but ventrally 4-segmented. Caudal ramus (Fig. 129D) unarmed, 2.47 times longer than wide (74×30 µm), slightly narrowing distally, with rounded distal margin.

Rostrum absent. Antennule (Fig. 129E) 1.5 times longer than wide (53×35 µm), widest in middle, with protruding posterior margin; armed with 3 small setae distally (setae almost equal, about 9 µm long, but anteriormost thicker than other 2). Antenna (Fig. 129F) 136×64 µm, unsegmented, but with weak wrinkle in middle of lateral side, armed with 5 setae (3 mediodistal and 2 laterodistal), and ornamented with fine spinules just proximal to transverse wrinkle; lengths of setae I-V (medial to lateral) 18, 18, 23, 24, and 28 µm, respectively.

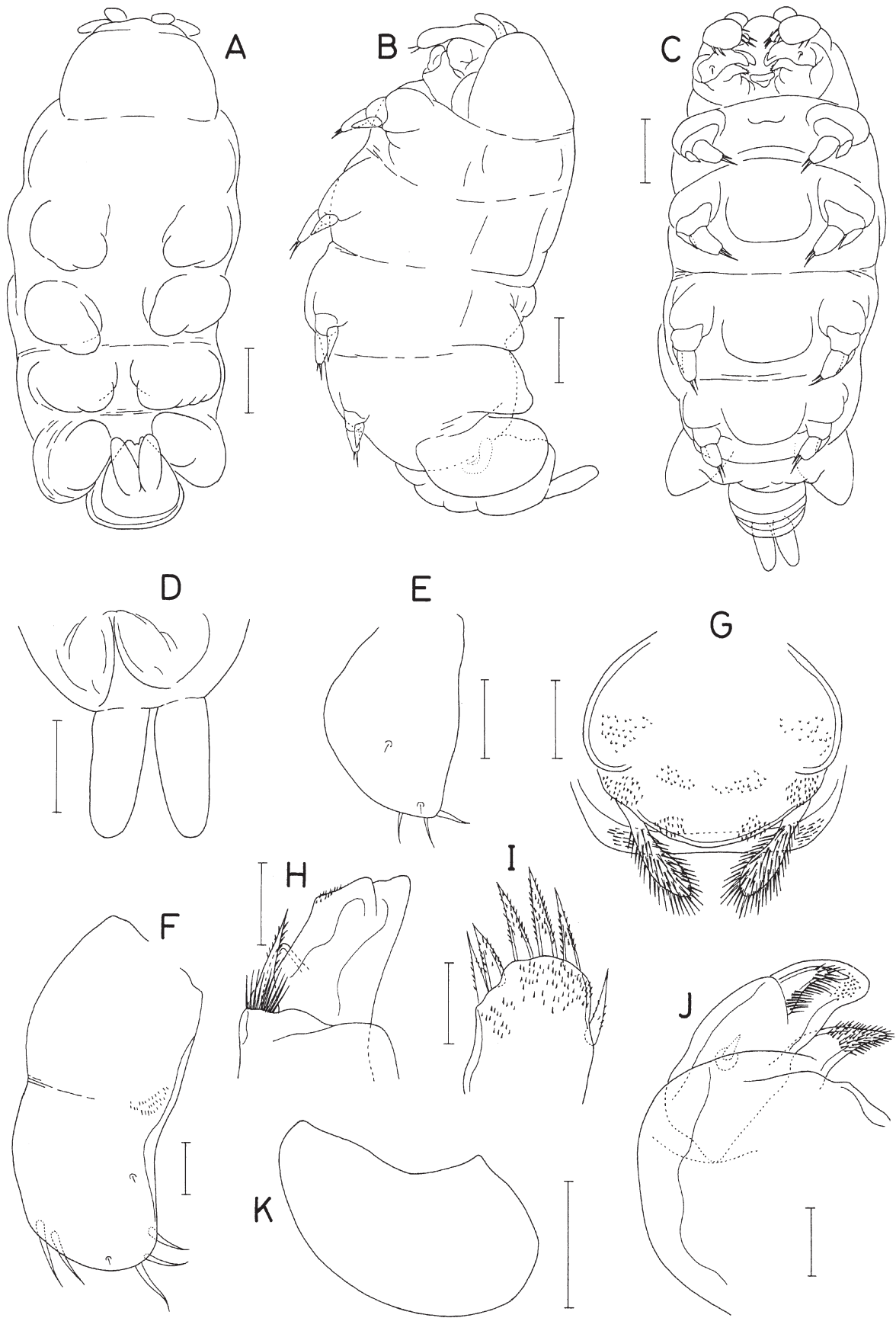
Labrum (Fig. 129G) circular, ornamented with scattered minute spinules on ventral surface; palps slender proximally, moderately expanded distally, covered with stiff, long setules (or setule-like spinules). Mandible narrower than labral palp, gradually narrowing distally. Maxillule consisting of precoxa (Fig. 129H) and palp (Fig. 129I); sclerotized distal part of precoxa bifurcate distally, with 1 tubercle proximally, 1 patch of minute spinules subdistally; endite of precoxa tipped with 1 spinulose seta and more than 10 stiff setules; palp with 6 spinulose, spiniform setae (1 on lateral margin, 3 on distal margin, and 2 near mediodistal corner). Maxilla (Fig. 129J) 2-segmented; proximal segment with large, tapering mediodistal process covered with spinules distally; distal segment bluntly tipped, with 1 setulose spine subdistally and 1 small seta proximally. Maxilliped absent.

Legs 1-4 (Fig. 130A-D) each consisting of 2-segmented protopod and unsegmented rami; protopods unarmed. Exopods bearing patch of minute spinules at proximal part of lateral margin. Exopods of legs 1, 2, and 4 tipped with small cusp and with 1 minute spinule subdistally on lateral margin. Endopods 54×28, 53×26, 49×30, and 36×25 µm, respectively, in legs 1-4. Endopods of legs 3 and 4 with distinctly convex lateral margin. Distal setae on endopods distinctly shorter than the endopodal segments. Lengths of laterodistal and mediodistal setae 27 and 19, 24 and 20, 29 and 17, and 25 and 18 µm, respectively, in legs 1-4.

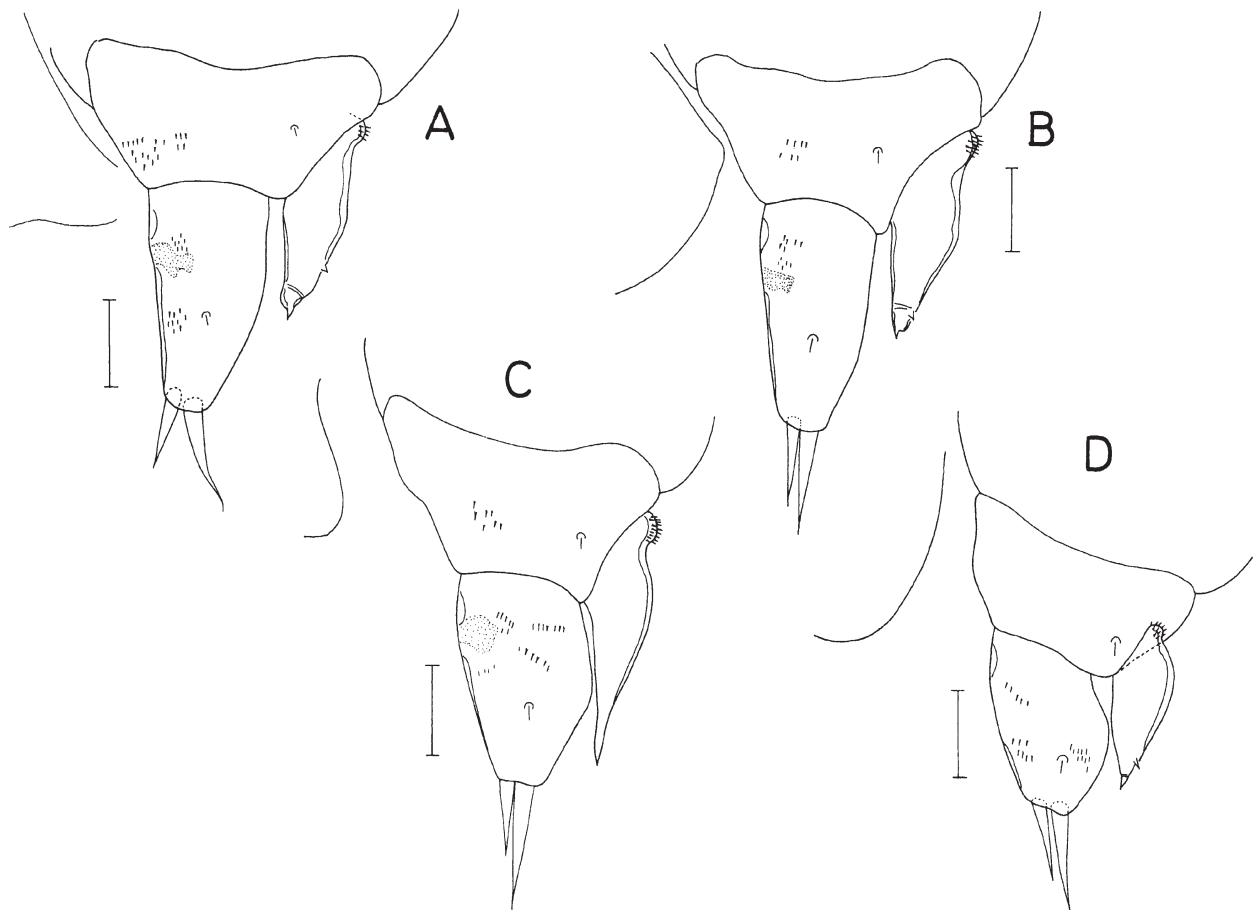
Leg 5 (Fig. 129K) lamelliform, unarmed, obliquely wider than long (113×209 µm).

**Male.** Unknown.

**Remarks.** This species was described as an associate of the ascidian *Didemnum granulatum* Tokioka, 1954 from Djibouti coast of the Red Sea. In the original description of this species Marchenkov & Boxshall (2005) described or illustrated that (1) the second to fourth pedigerous somites have well-developed dorsolateral tergal folds, (2) the caudal rami are about 2.5 times longer than wide, (3) the antennule is armed with 3 or 4 setae distally, (4) the antenna is armed with 5 setae, (5) the distal setae on the endopods of the swimming legs are distinctly shorter than endopodal segments, and (6) the laterodistal seta on the endopods of the swimming legs is distinctly longer than the mediodistal seta. Our specimens from Suez exhibit the above diagnostic features and there are no significant differences from the original description.



**FIG. 129.** *Enterocola parapterophorus* Marchenkov & Boxshall, 2005, female. A, habitus, dorsal; B, habitus left; C, habitus, ventral; D, anal prominence and caudal rami; E, antennule; F, antenna; G, labrum; H, precoxa of maxillule; I, palp of maxillule; J, maxilla; K, leg 5. Scale bars: A-C, K, 0.1 mm; D, 0.05 mm; E-J, 0.02 mm.



**FIG. 130.** *Enterocola parapterophorus* Marchenkov & Boxshall, 2005, female. A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scale bars: 0.02 mm.

***Enterocola seticaudus* sp. nov.**

(Figs. 131-133)

**Type material.** Holotype ♀ (MNHN-IU-2014-21544), 3 ♀♀ paratypes (MNHN-IU-2014-21545), and 1 ♀, 1 ♂ paratypes (dissected, MNHN-IU-2014-17396) from *Pharyngodictyon cauliformis* Monniot C. & Monniot F., 1991 (MNHN-IT-2008-6229 = MNHN A1/PHA/7); New Caledonia, between Île des Pins and Récif S., SMIB 4 cruise, RV “Alis”, Stn DW60 (23°00’S, 167°21.6’E), depth 500 m, B. Richer de Forges-IRD coll., 10 March 1989.

**Etymology.** The specific name refers to the presence of a seta on the caudal rami.

**Description of female.** Body (Fig. 131A, B) eruciform, cylindrical, consisting of cephalosome, trunk, and genitoabdomen. Body length 1.42 mm in dissected largest specimen (other 4 specimens 1.08, 1.32, 1.33, and 1.41 mm); maximum width 370 µm (across fourth pedigerous somite). Cephalosome much wider than long (212×321 µm), defined from trunk by lateral constriction. Trunk unsegmented, gradually broadening posteriorly, with weak constrictions between somites. First to fourth pedigerous somites each with paired dorsolateral tergal folds; these tergal folds variously developed depending on individuals, usually becoming smaller from anterior to posterior. On ventral surface, each pedigerous somite with pair of interpodal protrusions; protrusions becoming larger from anterior to posterior. Genitoabdomen (Fig. 131C) 5-segmented; articulations distinct ventrally, but obscure dorsally; anal prominence distinct. Caudal rami (Fig. 131D) inserted close to each other; each ramus about 2.0 times longer than wide (91×45 µm), gradually narrowing distally, with rounded distal margin, and tipped with 1 small, naked seta 28 µm long.

Rostrum absent. Antennule (Fig. 131E) tapering, 74 µm long, 2-segmented; articulation between segments indistinct, but segments clearly defined by width difference; broad proximal segment 54×48 µm, armed with 4 setae distally; small distal segment 23×15 µm, armed with 3 setae (distal seta larger than others). Antenna (Fig. 131F)

144×68 µm, indistinctly 2-segmented; proximal segment unarmed; distal segment longer than proximal segment, armed with 6 naked setae (1 small medial margin and 5 large on distal margin); lengths of setae I-VI (medial to lateral) 24, 55, 70, 83, 97, and 106 µm, respectively; setae V and VI longer than distal segment; medial seta positioned at about 80% along medial margin of segment.

Labrum (Fig. 131G) sub-rectangular, with patch of spinules on both sides; palp spinulose, curved laterally. Mandible (Fig. 131G) tapering, spinulose, slightly longer than labral palp. Maxillule consisting of precoxa and palp: precoxa (Fig. 131H) distally bilobed and strongly sclerotized, with endite bearing 1 slender, spinulose seta and more than 10 long setules: palp (Fig. 131I) with 5 spinulose, spiniform setae on distal margin and 1 shorter seta on lateral margin. Maxilla (Fig. 131J) 2-segmented; proximal segment with mediobasal endite bearing distally bifurcate and spinulose process; distal segment bluntly bifurcate distally, with 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each with 2-segmented protopod and unsegmented rami (Fig. 131K, L); protopods with 1 small outer seta on basis. Exopods shorter than endopods in legs 1, 2, and 4, but as long as endopod in leg 3. Endopods 53×37, 61×30, 60×34, and 57×36 µm, respectively, in legs 1-4; outer margin of endopods convex. Lengths of laterodistal and mediobasal setae on endopods 106 and 83, 105 and 90, 109 and 85, and 114 and 83 µm, respectively, in legs 1-4. All endopodal setae longer than endopodal segment. Laterodistal seta 1.28 times longer than mediobasal seta in leg 1.

Leg 5 (Fig. 131M) much wider than long (125×216 µm); armed with 2 small setae on distal margin, separated by distance of 148 µm.

**Description of male.** Body (Fig. 132A) cyclopiform, narrow, with distinct prosome-urosome division. Body length 1.24 mm; maximum width 342 µm (across cephalosome). Prosome consisting of cephalosome and first to fourth pedigerous somites. Cephalosome 313 µm long, slightly wider than long, with truncate anterior apex. Fourth pedigerous somite distinctly narrower than anterior somites, with convex lateral margins. Urosome (Fig. 132B) slender, shorter than prosome, consisting of fifth pedigerous somite, genital somite, and 4 abdominal somites. Fifth pedigerous somite 113 µm wide; genital somite 153×112 µm, with well-developed genital opercula ventrally. Four abdominal somites 64×76, 47×71, 45×74, and 29×80 µm, respectively; anal somite shorter than penultimate abdominal somite; anal operculum not seen. Caudal rami (Fig. 132B) broad, 1.18 times longer than wide (45×38 µm), armed with 6 pinnate setae; lateral seta shortest.

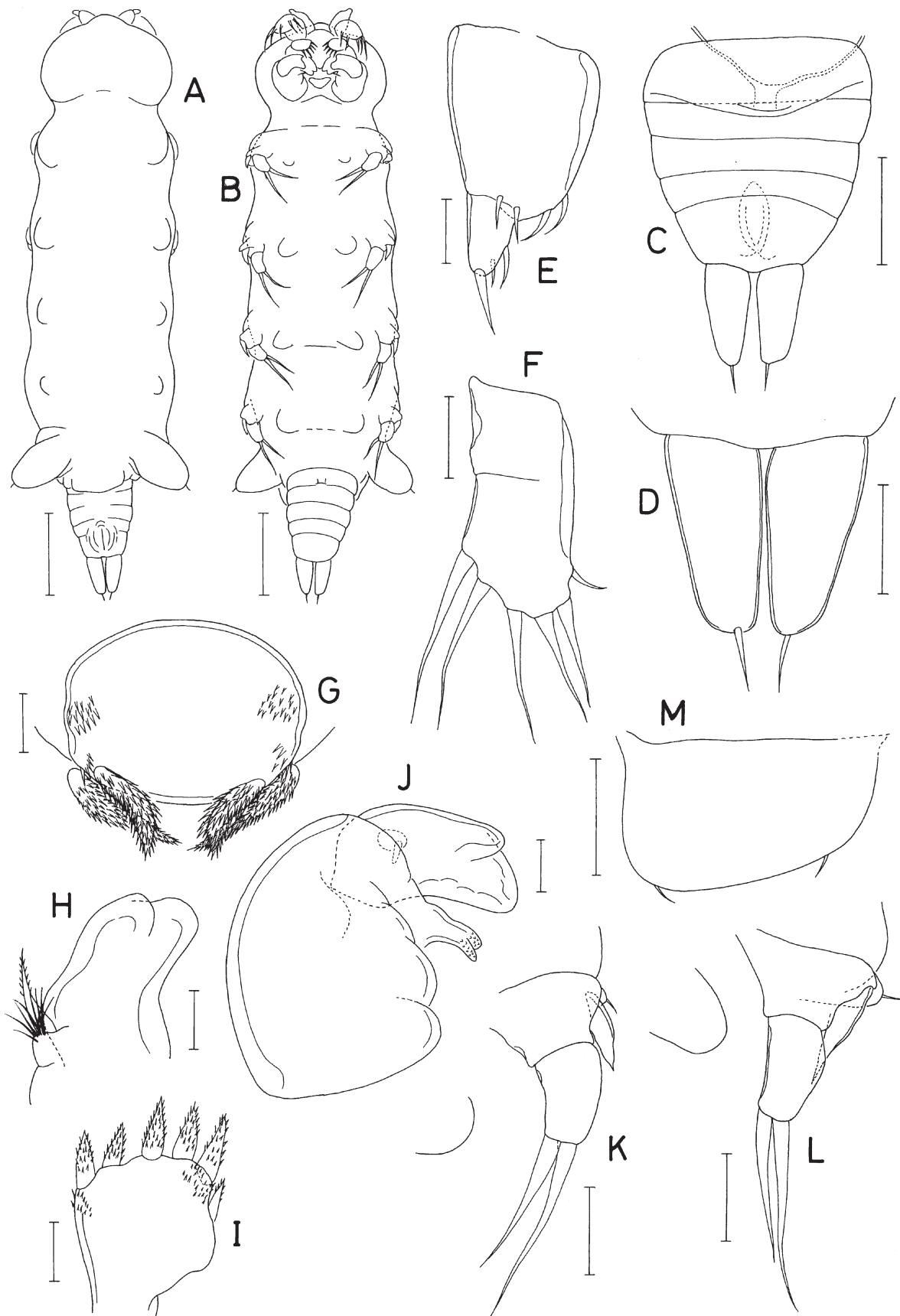
Rostrum (Fig. 132C) large, 151×78 µm, tapering, slightly constricted near proximal third, with minutely bifid apex. Antennule (Fig. 132D) 237 µm long, 7-segmented; first segment broader than other segments; armature formula 12, 2, 3, 0, 2, 1, and 9+aesthetasc; 2 setae on first and 1 on sixth segments pinnate, all other setae naked. Antenna (Fig. 132E) 3-segmented; first segment 82 µm long, armed with 1 naked seta subdistally; second segment as long as first, unarmed, but ornamented with setules along outer margin; third segment about 3.7 times longer than wide (67×18 µm), distinctly narrower than proximal segments, ornamented with setules on proximal outer margin; armed with 5 setae plus claw (29 µm long), subdistal seta 90 µm long, much longer than others.

Labrum (Fig. 132F) very small, but well-sclerotized. Mandible (Fig. 132G) forming unarmed and unornamented digitiform process. Maxillule (Fig. 132H) 2-segmented; broad proximal segment unarmed; distal segment nearly circular, armed with 6 large, pinnate setae. Maxilla (Fig. 130I) lobate, tipped with 1 pinnate seta. Maxilliped absent.

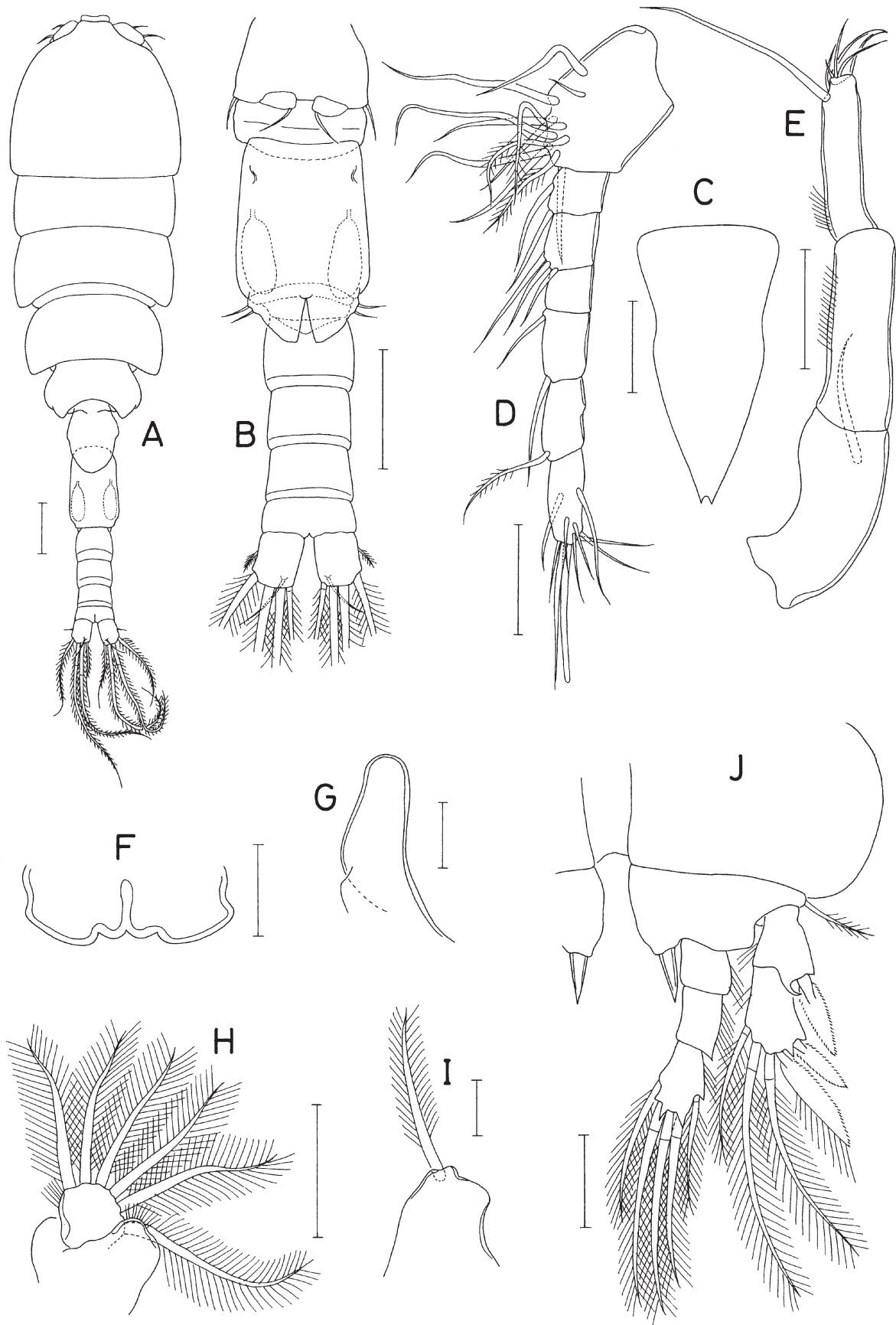
Legs 1-4 (Fig. 132J, 133A-C) biramous, with 2-segmented protopod; coxa unarmed; basis with pinnate outer seta; basis of leg 1 with inner distal spine (27 µm long). Leg 1 with 2-segmented exopod and 3-segmented endopod. Legs 2-4 with 3-segmented exopods and endopods. First and second endopodal segments of leg 1 unarmed. Most setae on exopods and endopods geniculate proximally. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-I	I-0; I, I, 3	0-0; 0-0; 1, 2, 2
Leg 2:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; II, I, 5	0-1; 0-2; 1, 2, 3
Leg 4:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 2

Leg 5 (Fig. 132B) consisting of small lateral seta on somite and small free exopodal segment tipped with 1 small seta. Leg 6 (Fig. 132B) represented by 2 small setae on proximal lateral margin of genital operculum.

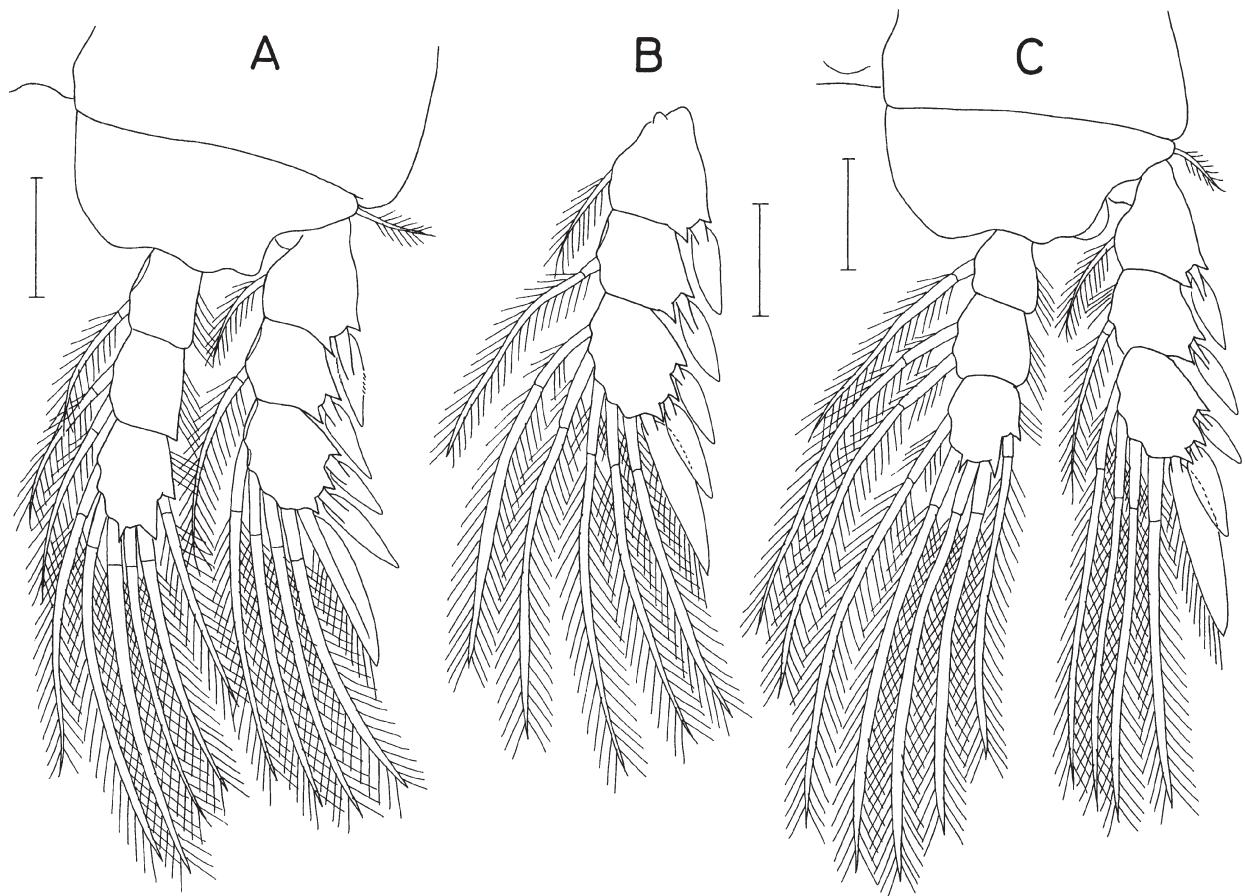


**FIG. 131.** *Enterocola seticaudus* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, genitoabdomen, ventral; D, caudal rami; E, antennule; F, antenna; G, labrum and mandibles; H, precoxa of maxillule; I, palp of maxillule; J, maxilla; K, leg 1; L, leg 3; M, leg 5. Scale bars: A, B, 0.2 mm; C, M, 0.1 mm; D, F, K, L, 0.05 mm; E, G-J, 0.02 mm.



**FIG. 132.** *Enterocola seticaudus* sp. nov., male. A, habitus, dorsal; B, urosome, ventral; C, rostrum; D, antennule; E, antenna; F, labrum; G, mandible; H, maxillule; I, maxilla; J, leg 1. Scale bars: A, B, 0.1 mm; C-E, H, J, 0.05 mm; F, G, I, 0.02 mm.





**FIG. 133.** *Enterocola seticaudus* **sp. nov.**, male. A, leg 2; B, leg 3 exopod; C, leg 4. Scale bars: 0.05 mm.

**Remarks.** The female of *E. seticaudus* **sp. nov.** can be distinguished from existing congeneric species by the unique setation of its antennule and by the presence of a prominent seta on the caudal ramus. The antennule of the new species is 2-segmented with 4 and 3 setae on the proximal and distal segments, respectively. This setation pattern is unique, although the antennular armature of female *E. ianthinus* Illg & Dudley, 1980 is similar, with 4 setae on the proximal but only 2 setae on the distal segment (Ooishi, 2014a). The presence of a caudal seta was recorded in *E. laticeps* Illg & Dudley, 1980 by Illg & Dudley (1980) and in *E. ianthinus* by Ooishi (2014a), but the caudal seta of these two species is very small and spinule-like, unlike *E. seticaudus* **sp. nov.** *Enterocola laticeps* and *E. ianthinus* can be distinguished from the new species by additional differences: *E. laticeps* has 2-segmented rami in legs 1-4 (cf. unsegmented in the new species) and *E. ianthinus* carries 2 almost equal distal setae on the endopods of legs 1-4 (cf. unequal).

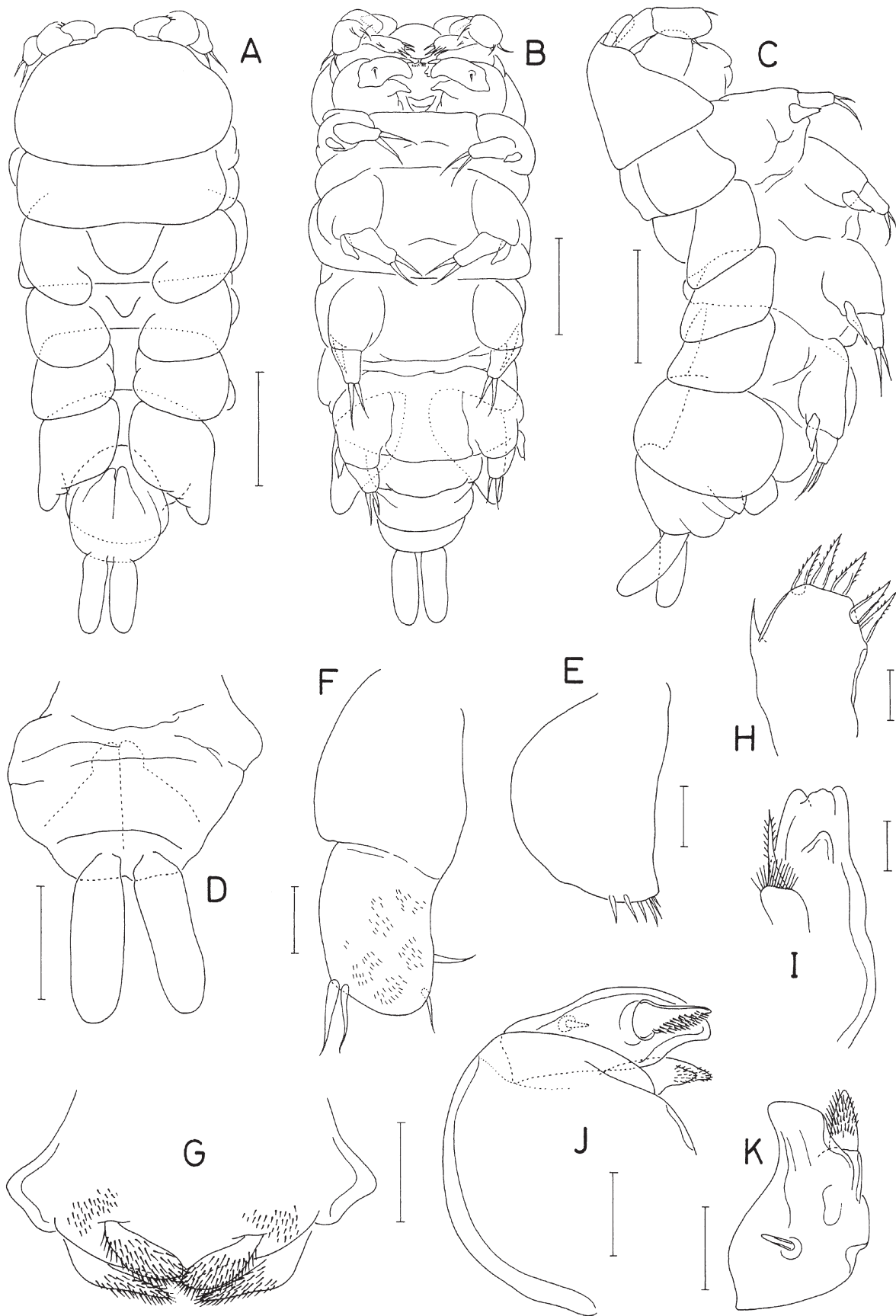
Males of *Enterocola* are known in only four species, *E. fulgens*, *E. fertilis* Illg & Dudley, 1980, *E. gottói* Conradi, López-González & García-Gómez, 1992, and *E. sydnii* Chatton & Harant, 1924 (Ooishi, 2011). The males of all these species exhibit a uniform segmentation and setation pattern in the swimming legs, and in most other appendages. The most notable features of the male of *E. seticaudus* **sp. nov.** are that the terminal segment of the antenna is armed with 5 setae including 1 large subdistal seta (cf. only 4 small setae in the four congeners), and the armature formula of the antennule, which appears to be species-specific in this genus.

***Enterocola quadrisetus* sp. nov.**

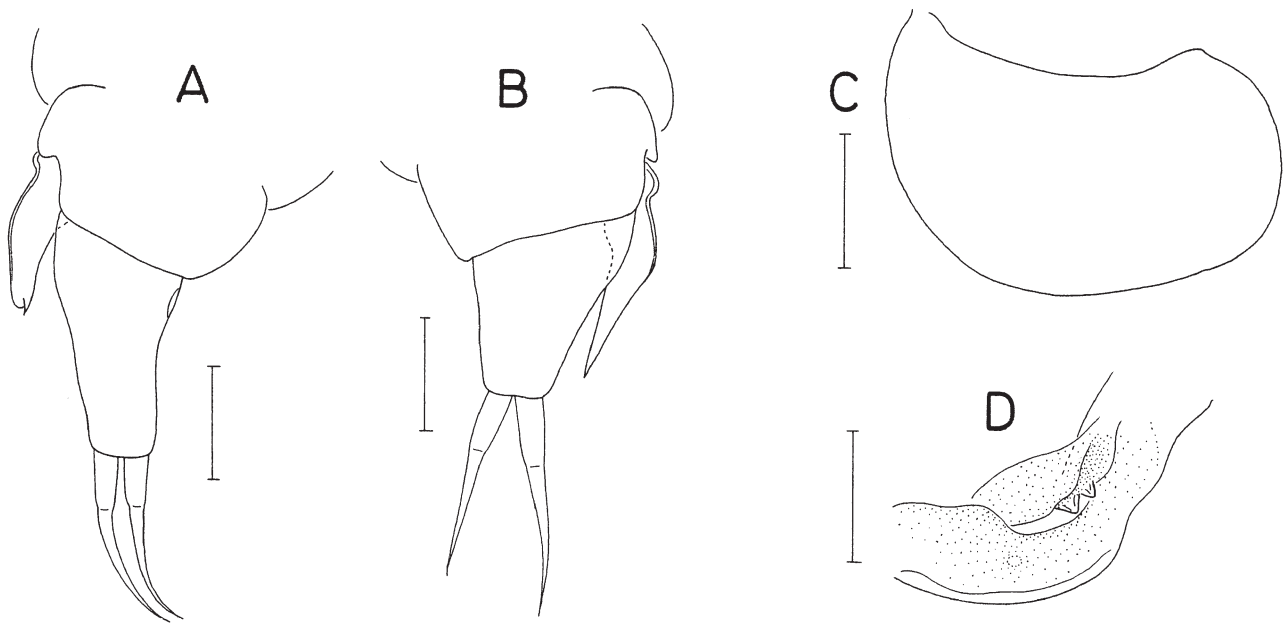
(Figs. 134, 135)

**Type material.** Holotype ♀ (MNHN-IU-2014-21546), 3 ♀♀ paratypes (MNHN-IU-2014-21547), and 1 ♀ paratype (dissected, MNHN-IU-2014-17397) from *Didemnum* sp.; Tulear, Madagascar, depth 15 m.

**Etymology.** The name of the new species refers to the presence of only 4 setae on the female antenna.



**FIG. 134.** *Enterocola quadrisetus* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, genitoabdomen, ventral; E, antennule; F, antenna; G, labrum and mandibles; H, palp of maxillule; I, precoxa of maxillule; J, maxilla; K, distal segment of maxilla. Scale bars: A-C, 0.1 mm; D, 0.05 mm; E, H, I, 0.01 mm; F, G, J, K, 0.02 mm.



**FIG. 135.** *Enterocola quadrisetus* sp. nov., female. A, leg 1; B, leg 3; C, leg 5; D, genital aperture. Scale bars: A, B, D, 0.02 mm; C, 0.05 mm.

**Description of female.** Body (Fig. 134A-C) small, eruciform, curved dorsally, narrowing from anterior to posterior, consisting of cephalosome, 5-segmented trunk, and unsegmented genitoabdomen. Body length of dissected largest specimen 535  $\mu\text{m}$ ; maximum width 192  $\mu\text{m}$  (across cephalosome). Cephalosome 125  $\mu\text{m}$  long, much wider than long. First pedigerous somite bearing simple dorsal tergite; second to fourth pedigerous somites each bearing pair of large dorsolateral tergal folds. Second and third pedigerous somites each bearing 1 tubercle in middle of dorsal surface, large on second pedigerous somite and smaller on third (Fig. 134A). Pedigerous somites lacking ventral interpodal protrusions. Genitoabdomen short, flexible, unsegmented, but with 2 or 3 wrinkles on ventral surface (Fig. 134D); anal prominence distinct. Caudal rami unarmed, incompletely articulated from genitoabdomen, about 3.2 times longer than wide (73 $\times$ 23  $\mu\text{m}$ ) with parallel lateral margins and rounded distal margin.

Rostrum absent. Antennule (Fig. 134E) unsegmented, about 1.5 times longer than wide (37 $\times$ 25  $\mu\text{m}$ ), with inflated, convex posterior margin and nearly straight anterior margin; armed distally with 6 small setae (2 anterodistal setae setule-like). Antenna (Fig. 134F) indistinctly 2-segmented, 2.2 times longer than wide; proximal segment unarmed; distal segment 50 $\times$ 34  $\mu\text{m}$ , slightly shorter than proximal segment, and ornamented with minute spinules; armed with 4 setae, lengths of setae I-IV (medial to distal) 13, 14, 21, and 23  $\mu\text{m}$ , respectively; 2 lateral setae originating close to each other.

Labrum (Fig. 134G) with sclerotized, angularly protruded lateral margins; palp inflated, bulbous, and spinulose. Mandible (Fig. 134G) spinulose, tapering, distinctly narrower than labral palp. Maxillule consisting of precoxa and palp; precoxa (Fig. 134I) with trilobate distal margin, 1 tubercle subdistally, and endite bearing thin, spinulose seta and about 15 thin setules; palp (Fig. 134H) with 5 spines on distal margin plus setiform process on lateral margin. Maxilla (Fig. 134J) 2-segmented; proximal segment with mediolateral endite bearing distally spinulose, bifurcate process; distal segment (Fig. 134K) bluntly tipped, subdistally with 1 stout spine bearing numerous spinules on medial surface and 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 biramous with incompletely 2-segmented protopods and 1-segmented rami (Fig. 135A, B); protopods unarmed. Exopods of legs 1, 2, and 4 tipped with small cusp; exopod of leg 3 attenuated distally (Fig. 135B). Endopods 45 $\times$ 20, 35 $\times$ 24, 30 $\times$ 30, and 38 $\times$ 36  $\mu\text{m}$ , respectively, in legs 1-4. Lengths of laterodistal and mediolateral setae on endopods 39 and 33, 35 and 32, 40 and 34, and 33 and 25  $\mu\text{m}$ , respectively, in legs 1-4.

Leg 5 (Fig. 135C) lamellate, unarmed, wider than long (82 $\times$ 145  $\mu\text{m}$ ). Leg 6 (Fig. 135D) probably represented by 2 small cusps in genital operculum.

**Male.** Unknown.

**Remarks.** The antenna of female *Enterocola* is typically armed with 6 setae, rarely with 5 setae. *Enterocola quadrisetus* **sp. nov.** is the only known species in the genus having only 4 setae on the antenna, which allows the new species to be easily distinguished from all of its congeners. The possession of a dorsal tubercle on the second and third pedigerous somites is another unusual feature of the new species.

***Enterocola mabulensis* sp. nov.**

(Figs. 136, 137)

**Type material.** Holotype ♀ (MNHN-IU-2014-21548), 1 ♀ paratype (MNHN-IU-2014-21549), and 1 ♀ paratype (dissected, MNHN-IU-2014-17398) from *Didemnum* sp.; NW channel running due West from SMART resort, Mabul, Malaysia, ODHG 1301 W, depth 20 m, CRRF coll., 04 July 2004.

**Etymology.** The name of the new species is derived from its type locality, Mabul, Malaysia.

**Description of female.** Body (Fig. 136A-C) unsegmented, narrow, cylindrical, curved dorsally, and slightly compressed laterally. Body length 815 µm in dissected largest specimen; maximum width 230 µm (across fourth pedigerous somite). Cephalosome partially covered by cephalic shield; first pedigerous somite also partially covered with tergite. Second to fourth pedigerous somites each bearing well-developed dorsolateral tergal folds; these tergal folds digitiform, with blunt, posteriorly-directed tip in dorsal view (Fig. 136A) but tapering in lateral view (Fig. 136C). Ventral surface of trunk bearing single interpodal protrusion between left and right members of legs 1-4. Genitoabdomen short, obscurely defined from trunk, lacking any trace of articulation; anal prominence distinct. Caudal rami (Fig. 136D) unarmed, 1.53 times longer than wide (49×32 µm), narrowing distally, with rounded distal margin. Egg sac (Fig. 136E) 519×188 µm, slightly curved, containing 2 or 3 rows of eggs; each egg about 130 µm in diameter.

Rostrum absent. Antennule (Fig. 136F) small, about 1.3 times longer than wide (38×29 µm), widest in proximal third, with straight anterior margin and inflated posterior margin; armed with 5 (1 subdistal and 4 distal) small setae, one distal seta 12 µm long (larger than other setae). Antenna (Fig. 136G) unsegmented, about 115×54 µm, ornamented with minute spinules on convex surface of distal region; armed with 5 minutely spinulose setae, setae at most as long as half width of antenna; lengths of setae I-V: 16, 21, 18, 18, and 27 µm, respectively.

Labrum (Fig. 136H) almost circular in ventral view; palp distally expanded, bulbous, covered with fine spinules. Mandible spinulose, tapering, much narrower than labral palp. Maxillule consisting of precoxa and palp; precoxa (Fig. 136I) with distal sclerotized part with bluntly bifurcate distal margin and 1 prominent tubercle on medial side; endite bearing 1 spiniform naked seta and more than 10 long setules; palp (Fig. 136J) with 6 spinulose setae. Maxilla (Fig. 136K) 2-segmented; proximal segment with mediolateral endite bearing large spinulose process; distal segment with bifurcate distal part, armed subdistally with 1 stout spine bearing numerous spinules on medial surface, plus 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 consisting of unsegmented protopods and unsegmented rami (Fig. 137A-C); protopods unarmed. All exopods shorter than endopods: exopods of legs 1, 2, and 4 tipped with small cusp; exopod of leg 3 attenuated (Fig. 137B). Endopods of legs 1 and 2 subdivided by partial suture line on medial side; endopod of leg 4 with distinctly convex lateral margin. Endopods 42×22, 52×24, 47×22, and 35×22 µm, respectively, in legs 1-4. Laterodistal and mediolateral setae on endopods distinctly shorter than endopodal segments, 27 and 20 µm in leg 1, 25 and 22 µm in leg 2, and 31 and 25 µm in legs 3 and 4.

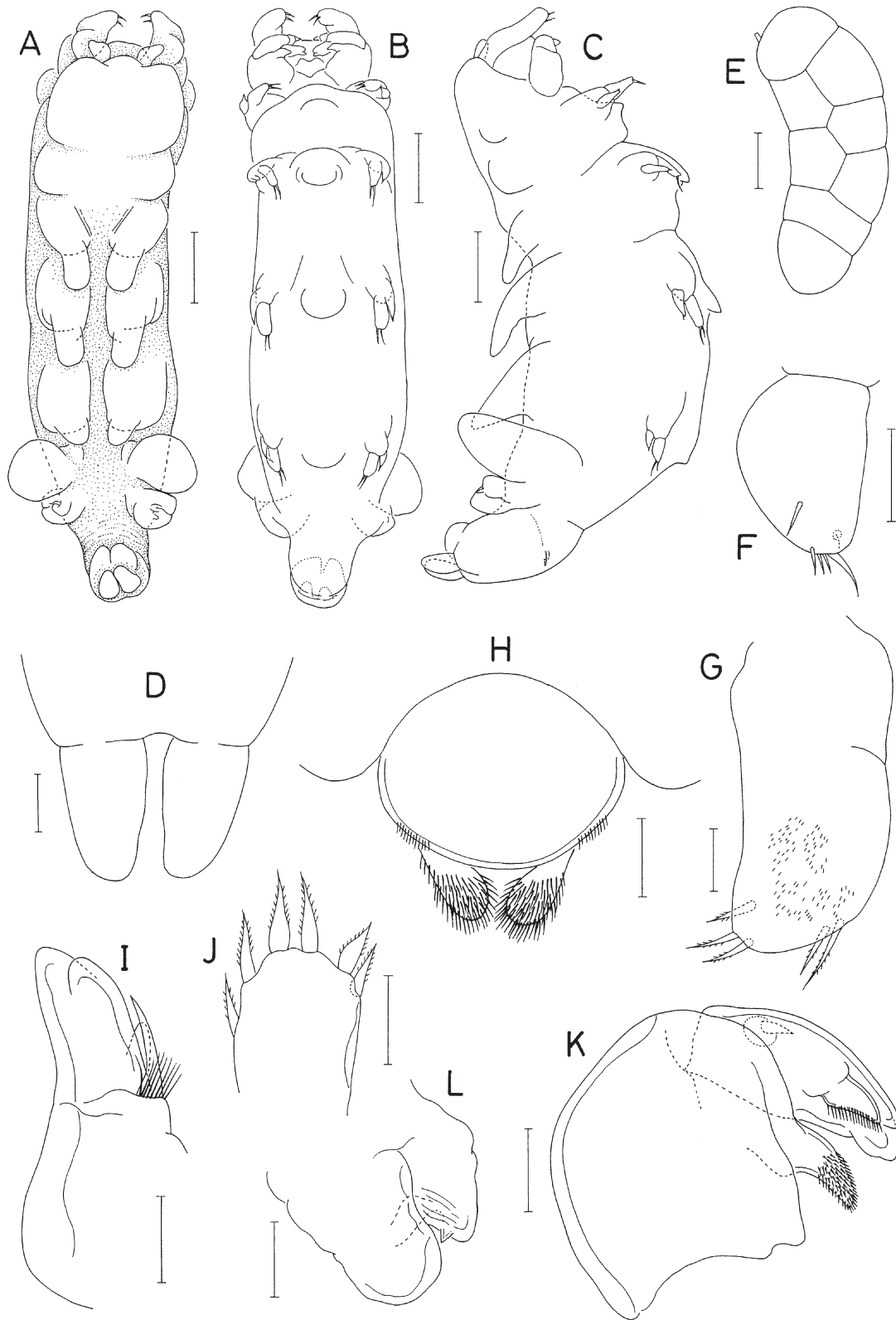
Leg 5 (Fig. 137D) unarmed, oval, 127×125 µm, not widened. Leg 6 probably represented by 1 small cusp in genital area (Fig. 136L).

**Male.** Unknown.

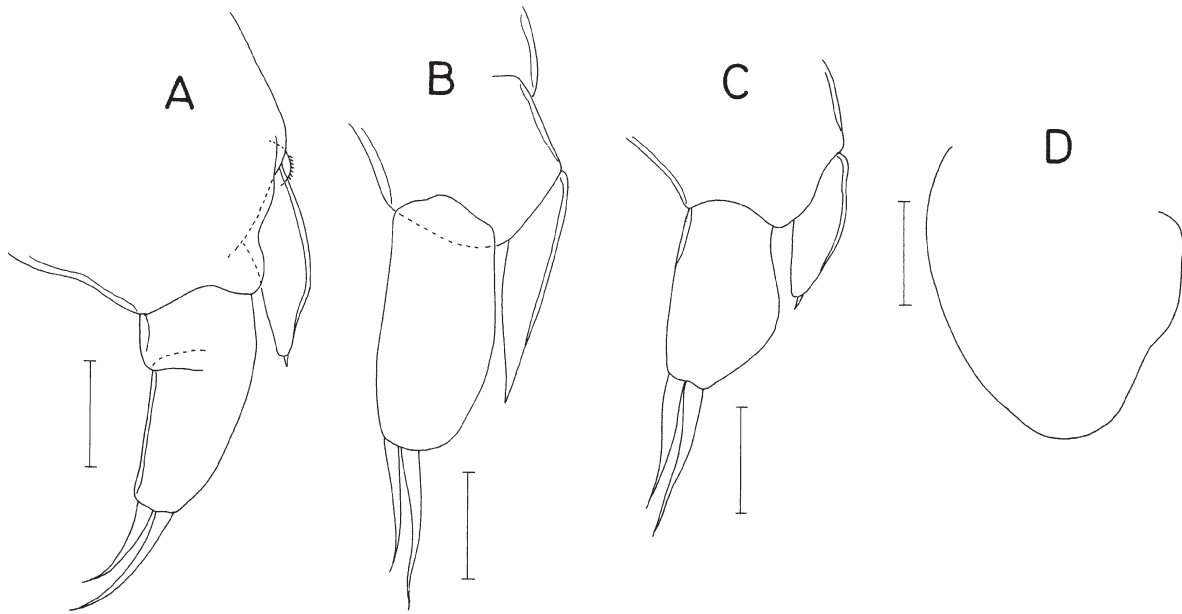
**Remarks.** The antenna of *E. mabulensis* **sp. nov.** is armed with 5 setae, a feature shared with three existing species: *E. adnatus* Ooishi, 2014; *E. laticeps*, and *E. parapterophorus*. These three species can be distinguished from *E. mabulensis* **sp. nov.** by various different features, as follows: *E. adnatus* lacks caudal rami, the antennule is 2-segmented, and the endopodal setae on swimming legs are longer than the endopodal segments (Ooishi, 2014a); *E. laticeps* has caudal rami that are more than twice as long as wide (about 1.5 times longer in *E. mabulensis* **sp. nov.**), the antennule is armed with as many as 16 setae, and both rami of swimming legs are 2-segmented (Illg & Dudley, 1980); finally, in *E. parapterophorus* the caudal rami are more than twice as long as wide, as measured from March-

enkov & Boxshall (2005: Fig. 8g), and the antenna is 2-segmented.

In all species of *Enterocola* for which leg 5 is known, this limb is wider than long. The ovoid form of leg 5 of female *E. mabulensis* sp. nov., which is slightly longer than wide, is unusual for the genus and may also serve to distinguish the new species.



**FIG. 136.** *Enterocola mabulensis* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, caudal rami; E, egg sac; F, antennule; G, antenna; H, labrum; I, precoxal part of maxillule; J, palp of maxillule; K, maxilla; L, genital aperture. Scale bars: A-C, E, 0.01 mm; D, F-L, 0.02 mm.



**FIG. 137.** *Enterocola mabulensis* sp. nov., female. A, leg 1; B, leg 3; C, leg 4; D, leg 5. Scale bars: A-C, 0.02 mm; D, 0.05 mm.

***Enterocola robustus* sp. nov.**

(Figs. 138, 139)

**Type material.** Holotype ♀ (MNHN-IU-2014-21550), 1 ♀ paratype (MNHN-IU-2014-21551), and 1 ♀ paratype (dissected, MNHN-IU-2014-21484) from *Leptoclinides* sp.;

**Type locality.** Maldives, N. Male atoll, 4km NW of Male I., OCDN 5247-N (4°12.88'N, 73°29.27'E), depth 10 m, CRRF coll., 16 September 1997.

**Etymology.** The specific name reflects the robust body.

**Description of female.** Body (Fig. 138A, B) robust, fleshy, curved dorsally; body length 623 µm; maximum width 292 µm (across second pedigerous somite). Cephalosome 131×196 µm, distinctly narrower than trunk, with distinct cephalic shield. First to fourth pedigerous somites defined from one another by lateral constrictions, each somite bearing pair of dorsolateral tergal folds, pair on first pedigerous somite indistinct. First and second pedigerous somites lacking ventral interpodal protrusion; third and fourth pedigerous somites each with single, broad interpodal protrusion (Fig. 139B, C). Genitoabdomen 4-segmented on ventral surface, but lacking traces of segmentation on dorsal surface; anal prominence distinct. Caudal ramus (Fig. 138C) unarmed, distinctly articulated from abdomen, about 3.0 times longer than wide (57×19 µm), slightly broadening distally, with rounded distal margin.

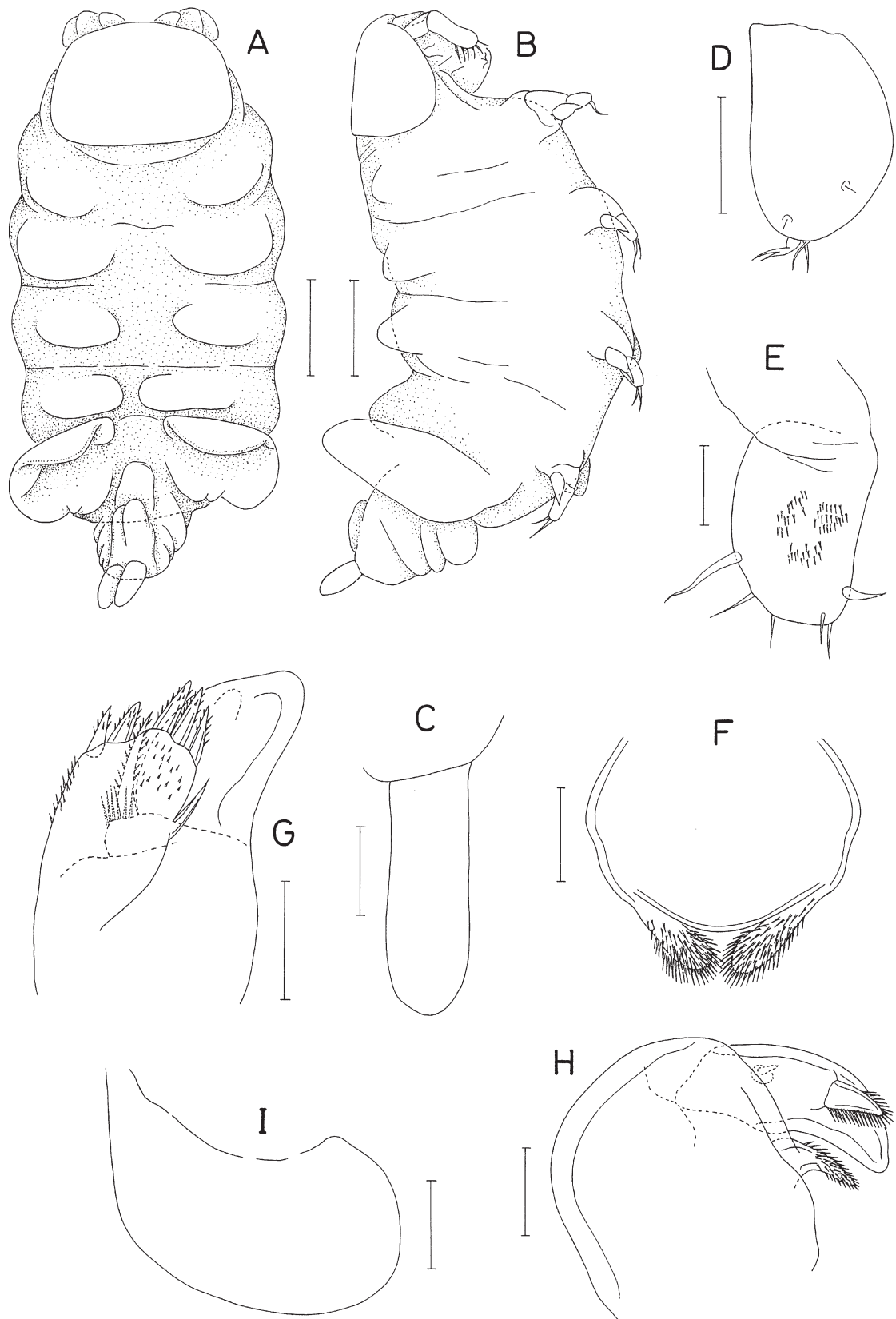
Rostrum absent. Antennule (Fig. 138D) unsegmented, about 1.5 times longer than wide (38×25 µm), widest in middle with convex posterior margin; armed with 3 setae on apex (anteriormost seta thick and bifurcate). Antenna (Fig. 138E) incompletely 2-segmented; shorter proximal segment unarmed; distal segment about 50×34 µm, ornamented with patches of fine spinules on concave surface; armed with 6 setae (I-VI), lengths of setae 13, 9, 8, 8, 16, and 22 µm, respectively; medial seta (seta I) and lateral seta (seta VI) thicker than others.

Labrum (Fig. 138F) sub-circular with spinulose, bulbous palps. Mandible spinulose, narrower than labral palp. Maxillule (Fig. 138G) as usual for genus; endite of precoxa tipped with 1 spinulose seta and several spinules; palp with 5 spinulose spine on distal margin plus 1 naked, slender, spiniform seta on lateral margin. Maxilla (Fig. 138H) also as usual for genus; distal segment subdistally with 1 spinulose, basally articulated spine on anterior surface and 1 rudimentary seta proximally on posterior surface. Maxilliped absent.

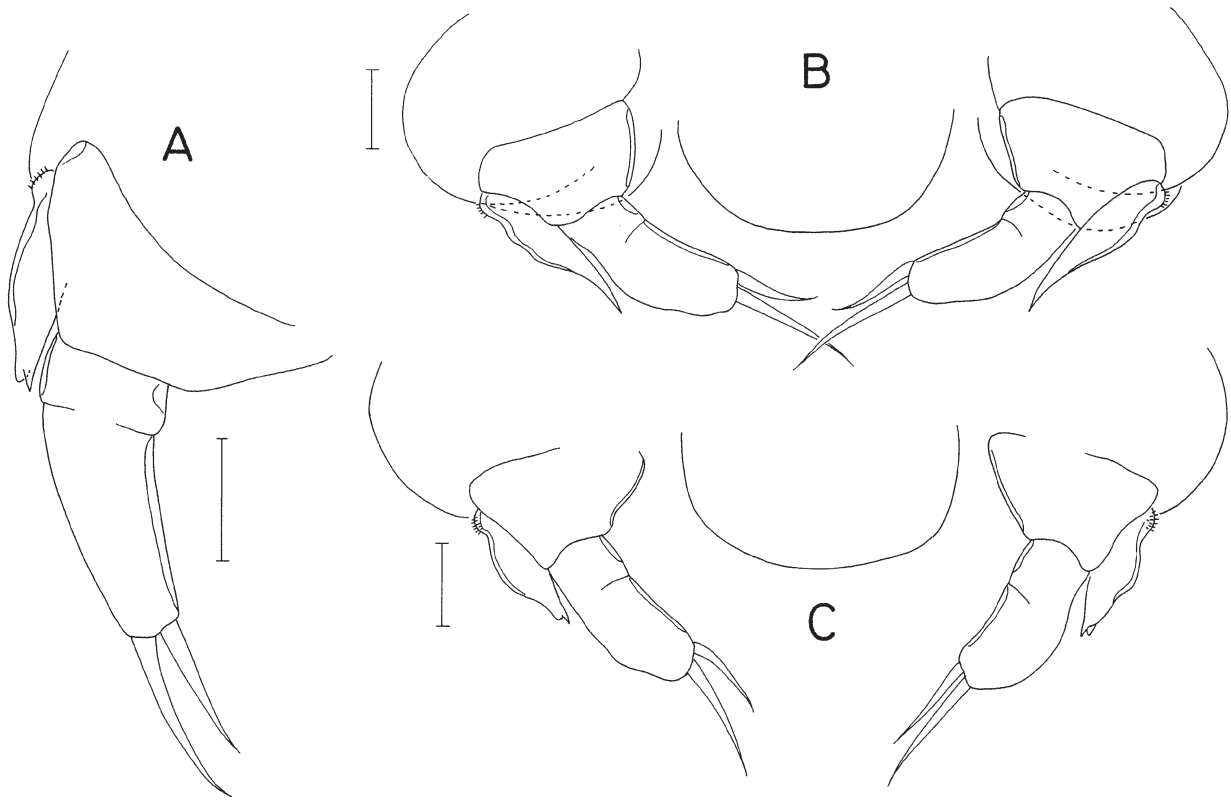
Legs 1-4 biramous with incompletely 2-segmented protopods (Fig. 139A-C); protopods unarmed. Exopods of legs 1, 2, and 4 tipped with small cusp; exopod of leg 3 acutely attenuated (Fig. 139B). Endopods incompletely 2-segmented, armed distally with 2 setae of unequal lengths. Sizes of endopods of legs 1, 3, and 4 (leg 2 pair missing) 46×22, 44×18, and 42×18 µm, respectively. Laterodistal and mediolateral setae on endopods unequal in length

(former at least 1.27 times longer than latter), both shorter than endopodal segments, 31 and 24  $\mu\text{m}$  in leg 1, 35 and 25  $\mu\text{m}$  in leg 3, and 33 and 26  $\mu\text{m}$  in leg 4.

Leg 5 (Fig. 138I) unarmed, obliquely wider than long (94 $\times$ 162  $\mu\text{m}$ ).



**FIG. 138.** *Enterocola robustus* sp. nov., female. A, habitus, dorsal; B, habitus, Right; C, caudal ramus; D, antennule; E, antenna; F, labrum; G, maxillule; H, maxilla; I, leg 5. Scale bars: A, B, 0.1 mm; C-H, 0.02 mm; I, 0.05 mm.



**FIG. 139.** *Enterocola robustus* **sp. nov.**, female. A, leg 1; B, legs 3 and interpodal protrusion; C, legs 4 and interpodal protrusion, Scale bars: 0.02 mm.

**Male.** Unknown.

**Remarks.** The setation of the endopods of the swimming legs of *E. robustus* **sp. nov.** is unusual because: firstly, the laterodistal seta is longer than the mediodistal seta, and secondly, both setae are shorter than endopodal segment. This combination of character states is shared with only five known species, *E. parapterophorus*, *E. mabulensis* **sp. nov.**, *E. quadrisetus* **sp. nov.**, *E. dicaudatus* Marchenkov & Boxshall, 2005, and *E. sydnii*. The first three species can be eliminated from further comparison because they have fewer than 6 setae on the antenna (viz. 5 setae in *E. parapterophorus* and *E. mabulensis* **sp. nov.** and 4 setae in *E. quadrisetus* **sp. nov.**).

*Enterocola sydnii* is currently known from the Northeastern Atlantic and can be distinguished from *E. robustus* **sp. nov.** by its short caudal rami (which are approximately as long as wide), by the possession of 7 setae on the antennule, by having a slender labral palp, and by having paired interpodal protrusions on each of the first to fourth pedigerous somites (Ooishi, 2011). *Enterocola dicaudatus* is known from Tanzania and differs from *E. robustus* **sp. nov.** in having an elongate antenna, a digitiform posteroventral process on the genitoabdomen, and a tapering process at the rear margin of the dorsal cephalic shield (Marchenkov & Boxshall, 2005).

***Enterocola parvus* sp. nov.**

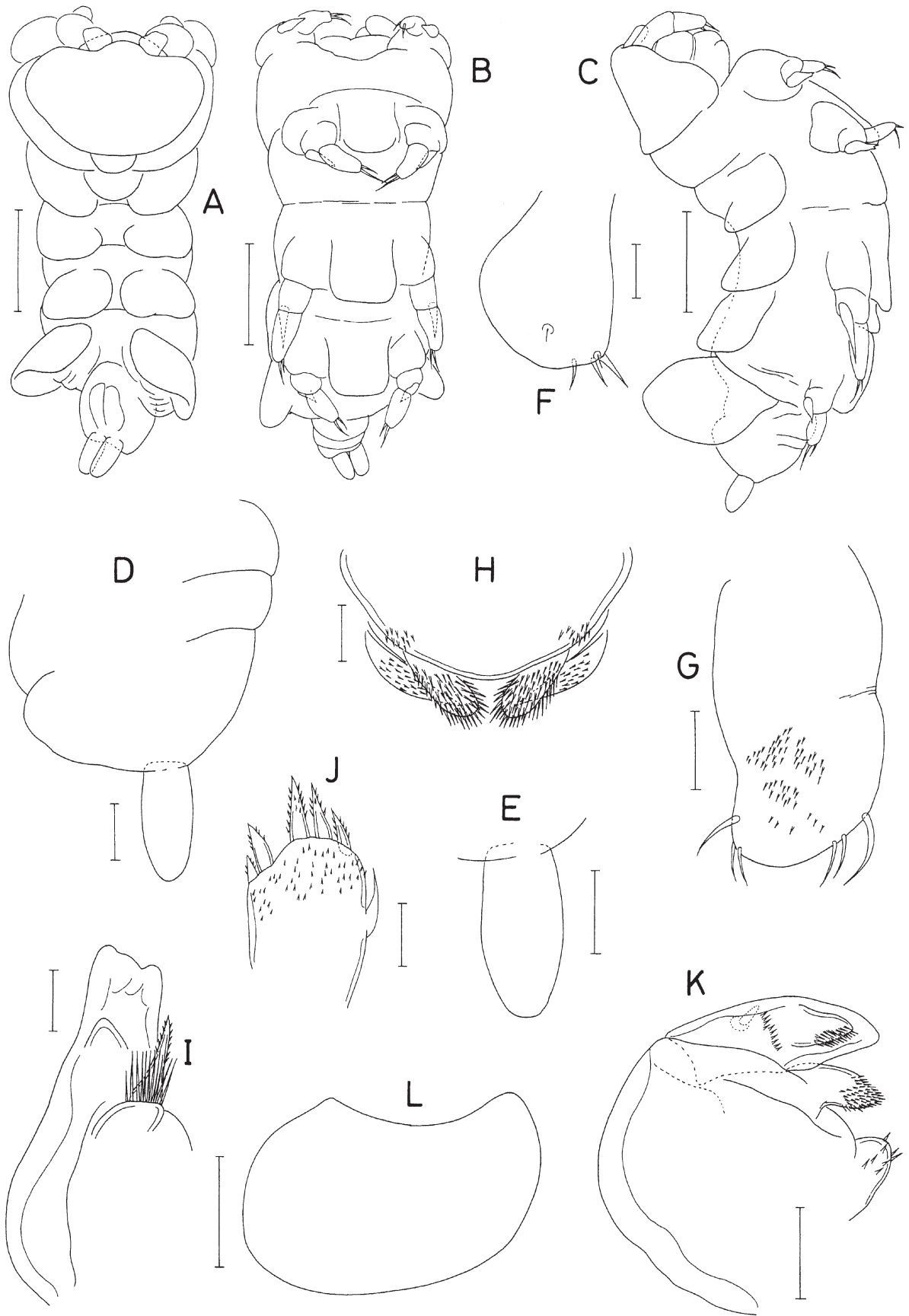
(Figs. 140, 141)

**Type material.** Holotype ♀ (MNHN-IU-2014-21552), 2 ♀♀ paratypes (MNHN-IU-2014-21553), and 1 ♀ paratype (dissected, MNHN-IU-2014-21483) from *Didemnum psammatoedes* (Sluiter, 1895); Iles Mesha, Djibouti, intertidal, Monniot coll., 13 October 1996.

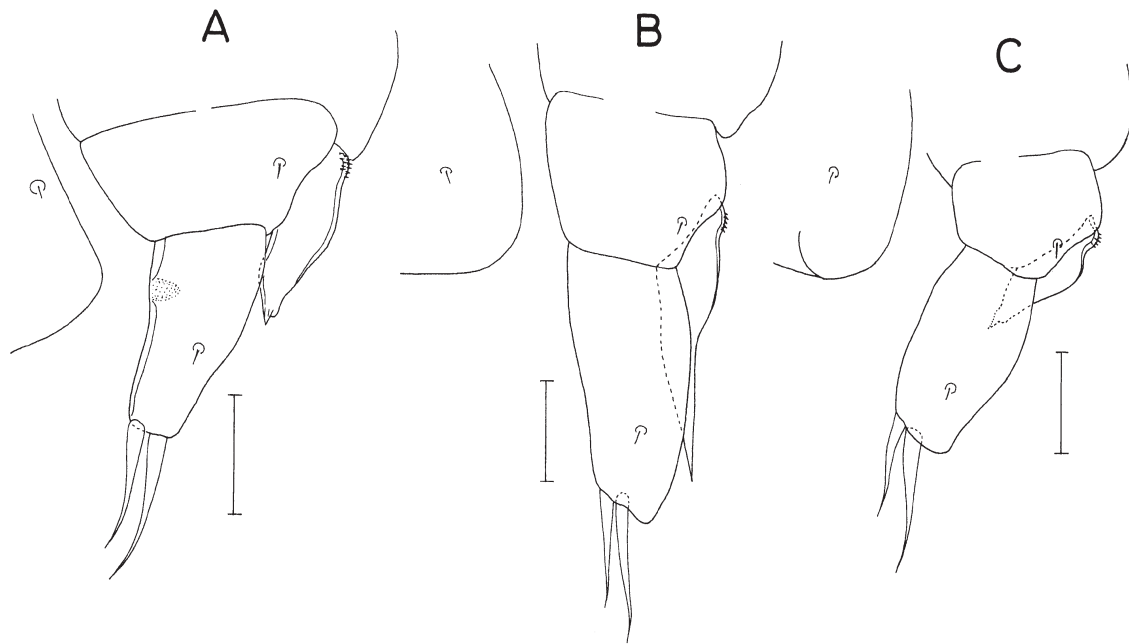
**Etymology.** The specific name is derived from the Latin *parv* (=small), alluding to the small body size of the new species.

**Description of female.** Body (Fig. 140A-C) small, unsegmented, curved dorsally; body length 560 µm; maximum width 200 µm (across cephalosome). Cephalosome partly covered by cephalic shield, wider than trunk, with





**FIG. 140.** *Enterocola parvus* sp. nov., female. A, habitus dorsal; B, habitus, ventral; C, habitus, right; D, genitoabdomen, right; E, caudal ramus; F, antennule; G, antenna; H, labrum and mandibles; I, precoxa of maxillule; J, palp of maxillule; K, maxilla; L, leg 5. Scale bars: A-C, 0.1 mm; D, E, G, K, 0.02 mm; F, H-J, 0.01 mm; L, 0.05 mm.



**FIG. 141.** *Enterocola parvus* sp. nov., female. A, leg 1 and interpodal protrusion; B, leg 3 and interpodal protrusion; C, leg 4 and interpodal protrusion. Scale bars: 0.02 mm.

semicircular median tubercle posterodorsally. First to fourth pedigerous somites each with well-developed dorso-lateral tergal folds (Fig. 140A) and single, broad mid-ventral interpodal protrusion between left and right legs (Fig. 140B). First pedigerous somite with large median tubercle dorsally between left and right tergal folds (Fig. 140A), as on cephalosome but larger. Genitoabdomen (Fig. 140D) short, dorsally unsegmented, but ventrally 3-segmented; anal prominence distinct. Caudal rami unarmed, incompletely articulated from abdomen, originating close to each other; each ramus (Fig. 140E) fusiform, widest in middle, about 2.1 times longer than wide ( $42 \times 20 \mu\text{m}$ ), with rounded distal margin.

Rostrum absent. Antennule (Fig. 140F) bulbous, 1.2 times longer than wide ( $34 \times 28 \mu\text{m}$ ), with narrow proximal part and strongly convex posterior margin; armed with 3 small setae distally. Antenna (Fig. 140G) about twice as long as wide, unsegmented, but with rudimentary partial suture line in middle of lateral margin; ornamented with minute spinules on distal half of concave surface; armed with 6 small setae, at most as long as half width of segment; lengths of setae I-VI (medial to lateral) 15, 11, 11, 13, 12, and  $22 \mu\text{m}$ , respectively; setae II and III, and setae IV and V close to each other.

Labrum (Fig. 140H) with distally expanded, bulbous palps. Mandible (Fig. 140H) tapering, narrower than labral palp. Maxillule consisting of precoxa and palm-shaped palp: precoxa (Fig. 140I) with blunt, sclerotized distal part, 1 tubercle subdistally, and endite near middle; endite tipped with 1 spinulose spine and more than 10 long, stiff setules; palp (Fig. 140J) with 5 spinulose spines on distal margin (medial spine shortest), and 1 naked seta on lateral margin. Maxilla (Fig. 140K) massive, 2-segmented; proximal segment with 1 spinulose tubercle proximally on medial margin and 1 large mediolateral, spinulose process; distal segment bluntly tipped, with subdistal spinulose process, 1 transverse row of minute spinules in middle of anterior surface, and 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each with 2-segmented protopod and unsegmented rami (Fig. 141A-C); protopods unarmed. Exopods of legs 1, 2, and 4 shorter than endopods, tipped with small cusp; exopod of leg 3 as long as endopod (Fig. 141B), acutely attenuated distally. Endopods  $36 \times 18$ ,  $36 \times 21$ ,  $51 \times 23$ , and  $39 \times 21 \mu\text{m}$ , respectively, in legs 1-4. Laterodistal and mediolateral setae on endopods distinctly shorter than endopodal segments, 27 and 24, 25 and 20, 29 and 23, and 28 and  $20 \mu\text{m}$ , respectively, in legs 1-4. Length ratios of laterodistal to mediolateral setae, 1.13, 1.71, 1.26, and 1.40, respectively, in legs 1-4.

Leg 5 (Fig. 140L) unarmed, wider than long ( $82 \times 132 \mu\text{m}$ ).

**Male.** Unknown.

**Remarks.** In *E. parvus* **sp. nov.** the antennule is unsegmented and armed with relatively few setae (less than 5), the antenna is armed with 6 setae, and the distal setae on the endopods of legs 1-4 are distinctly shorter than endopodal segments. This combination of features is shared only with three other species: *E. dicaudatus*, *E. mammiferus*, and *E. robustus* **sp. nov.** These three congeners can be readily distinguished from *E. parvus* **sp. nov.** by distinctive character states. In *E. dicaudatus* the antenna is elongate (with its setae positioned subterminally), the genitoabdomen bears a large ventral process, the cephalic shield carries a posterodorsal process, and the distal setae on the endopods of legs 1-3 are very small (less than one-third of the length of the endopods) (Marchenkov & Boxshall, 2005). In *E. mammiferus* the caudal rami are short (wider than long), the antennule is tapering, the 6 setae on the antenna are subequal in length, and the first to fourth pedigerous somites each bear a pair of ventral interpodal protrusions (Ooishi, 2010b). In *E. robustus* **sp. nov.** the body is robust, the caudal rami are 3 times longer than wide, setae IV and V of the antenna are separated from each other, and the mediiodistal process on the proximal segment of the maxilla is slender.

The presence of the two dorsal tubercles each on the cephalosome and on the first pedigerous somite is a characteristic feature of *E. parvus* **sp. nov.** Similar tubercles are present in *E. quadriseta* **sp. nov.**, but in this species the tubercles are located on the second and third pedigerous somites.

### ***Enterocola tuberculatus* sp. nov.**

(Figs. 142, 143)

**Type material.** Holotype ♀ (MNHN-IU-2014-21554) and 1 ♀ paratype (dissected, MNHN-IU-2014-21472) from *Polysyncraton cerebellum* Monniot F. & Monniot C., 2001 (MNHN-IT-2008-7078 = MNHN A2/POL/96); Papua New Guinea, CRCHO 262, Brooker IIs., Louisiades, Site Brooker CH (11°03.09'S, 152°28.62'E) depth 12 m, CRRF coll., 01 June 1998.

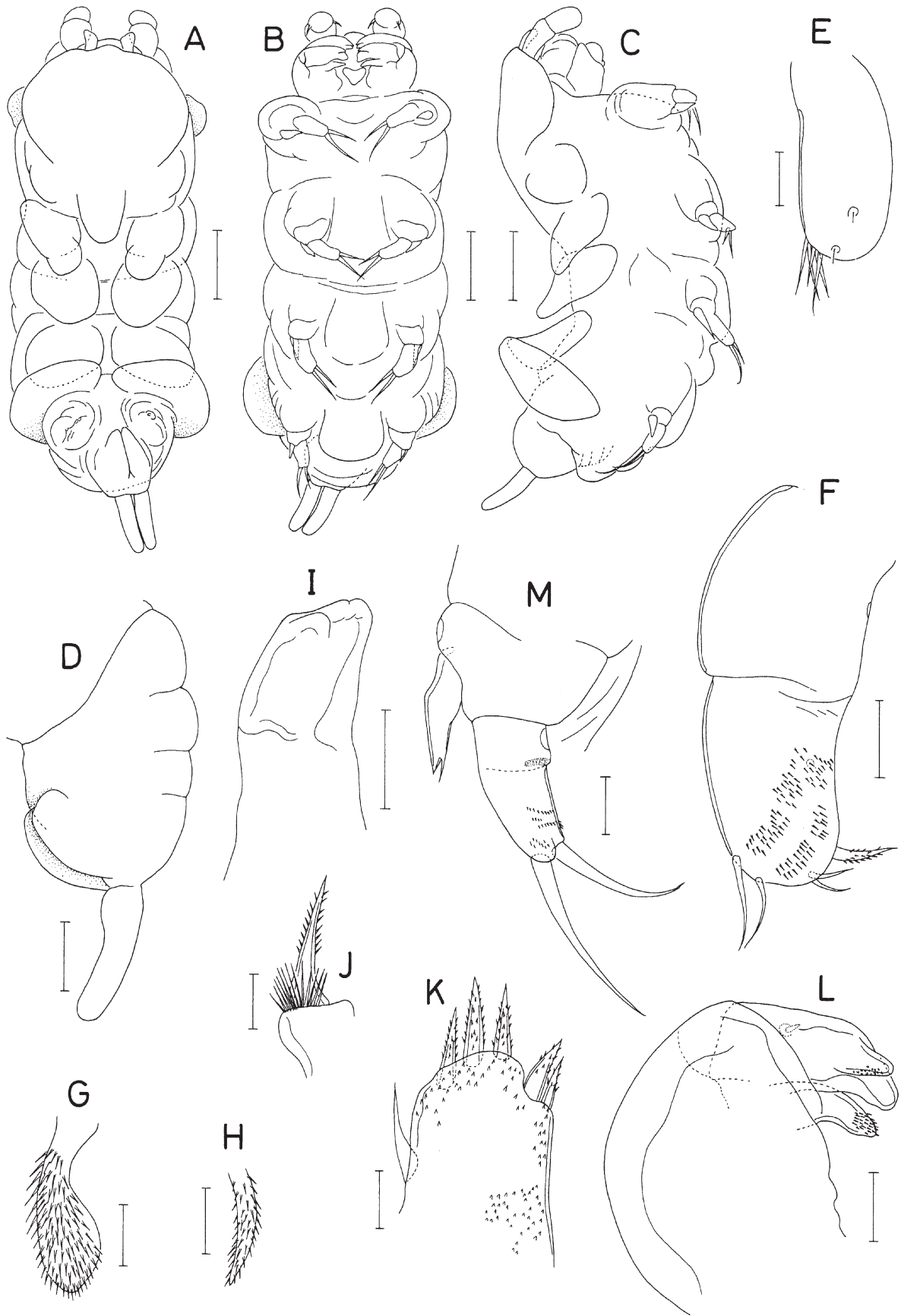
**Etymology.** The specific name alludes to the presence of a large dorsal tubercle on the first pedigerous somite of the new species.

**Description of female.** Body (Fig. 142A-C) eruciform, curved dorsally; body length 760 µm, maximum width 244 µm (across cephalic shield). Cephalic shield with obscure posterior margin. First pedigerous somite with weak tergal folds posterolaterally, but with large mid-dorsal projection (Fig. 142A); second to fourth pedigerous somites each with pair of large, lamellate dorsolateral tergal folds and single, broad ventral interpodal protrusion between left and right legs. Genitoabdomen (Fig. 142D) short, unsegmented dorsally, but 4-segmented ventrally, with distinct anal prominence. Caudal rami elongate, unarmed, originating close to each other; each ramus (Fig. 142D) about 3.5 times longer than wide (102×29 µm), slightly broadened proximally, with rounded distal margin.

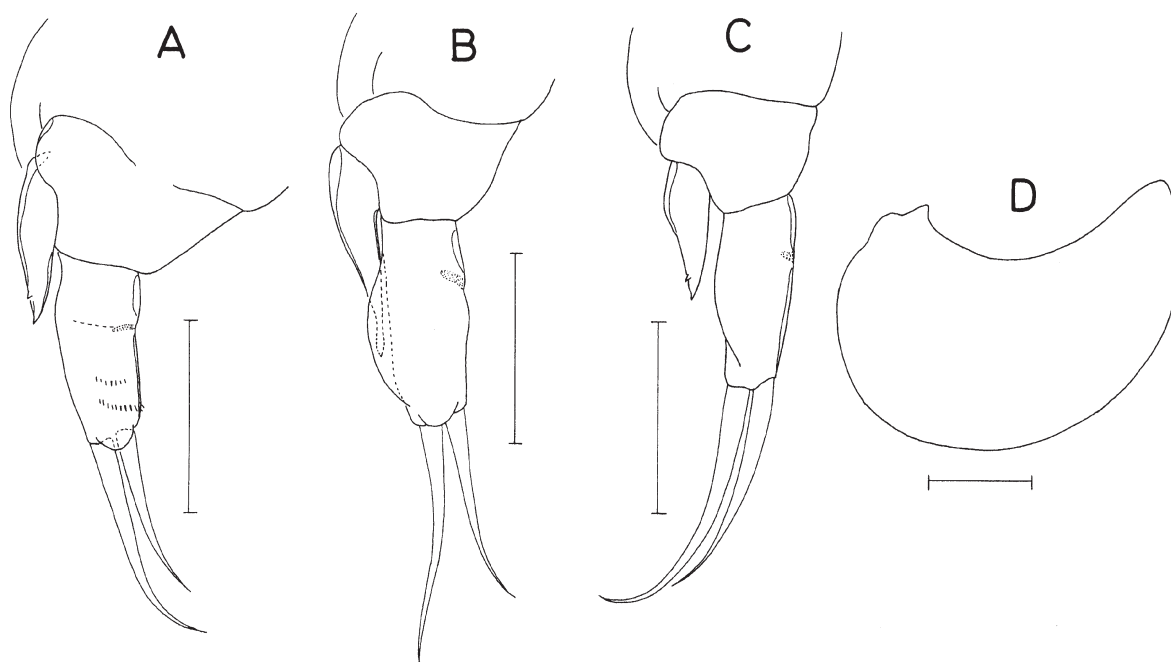
Rostrum absent. Antennule (Fig. 142E) unsegmented, more than twice as long as wide (approximately 39×18 µm), with rounded distal margin, nearly parallel anterior and posterior margins; armed with 5 small setae at antero-distal corner. Antenna (Fig. 142F) incompletely 2-segmented, 2.34 times longer than wide (103×44 µm); proximal segment unarmed; distal segment as long as, but narrower than, proximal segment, and ornamented with fine spinules on concave surface; armed with 5 setae, lengths of setae I-V 17, 12, 12, 17, and 25 µm; medial seta (seta I) spinulose and distinctly thicker than other 4 setae; setae II and III positioned close to each other.

Labrum destroyed; palp (Fig. 142G) spinulose, bulbous, markedly inflated in distal half. Mandible (Fig. 142H) spinulose, slender, much narrower than labral palp. Maxillule as usual for genus; distal sclerotized part of precoxa (Fig. 142I) weakly bilobed; endite of precoxa tipped with 1 spinulose spine and more than 10 stiff setules; palp (Fig. 142K) armed with 5 spines on distal margin and 1 naked seta on lateral margin. Maxilla (Fig. 142L) 2-segmented; proximal segment with unarticulated, spinulose mediiodistal process; distal segment distally bifurcate, with 1 minute seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 (Fig. 142M; 143A-C) each consisting of incompletely 2-segmented protopod and unsegmented rami; protopods unarmed. Exopods of legs 1, 2, and 4 with pointed distal tip and minute cusp subdistally on lateral margin; exopod of leg 3 elongate (Fig. 143B) and thin distally. Endopods 51×35, 48×22, 55×27, and 48×20 µm, respectively, in legs 1-4. Endopods of legs 3 and 4 with convex lateral margin. Lengths of laterodistal and mediiodistal setae on endopods 68 and 49, 59 and 47, 65 and 52, and 68 and 59 µm, respectively, in legs 1-4. Laterodistal setae on endopods longer than endopodal segments, 1.39, 1.26, 1.25, and 1.15 times longer than mediiodistal setae on legs 1-4, respectively. Leg 5 (Fig. 143D) unarmed, wider than long (98×167 µm).



**FIG. 142.** *Enterocola tuberculatus* sp. nov., female. A, habitus dorsal; B, habitus, ventral; C, habitus, right; D, genitoabdomen, right; E, antennule; F, antenna; G, labral palp; H, mandible; I, distal part of maxillular precoxa; J, endite of precoxa of maxillule; K, palp of maxillule; L, maxilla; M, leg 1. Scale bars: A-C, 0.1 mm; D, 0.05 mm; E, G, H, J, K, 0.01 mm; F, I, L, 0.02 mm.



**FIG. 143.** *Enterocola tuberculatus* sp. nov., female. A, leg 2; B, leg 3; C, leg 4; D, leg 5. Scale bars: 0.05 mm.

**Male.** Unknown.

**Remarks.** The most conspicuous feature of *E. tuberculatus* sp. nov. is the presence of a large dorsal tubercle on the first pedigerous somite, which serves to differentiate the new species from its congeners. The presence of any dorsal tubercles or projections has been recorded in only three species: there is a tapering posterior projection on the cephalic shield in *E. dicaudatus* (see Marchenkov & Boxshall, 2005), there are 2 tubercles (one each on the second and third pedigerous somites) in *E. quadrisetus* sp. nov., and 2 tubercles (one each on the cephalosome and first pedigerous somite) in *E. parvus* sp. nov.

The caudal rami of *E. tuberculatus* sp. nov. are elongate, 3.2 times longer than wide. This is another potential diagnostic feature of the new species, because in other species of *Enterocola* the length/width ratio of the caudal rami seldom exceeds 3.0. The exceptions are *E. bilamellatus* Sars, 1921, *E. dicaudatus*, *E. quadrisetus* sp. nov., and *E. robustus* sp. nov. all of which have caudal rami with a length to width ratio of about 3. These four species are easily separated from *E. tuberculatus* sp. nov. by their lack of a dorsal tubercle on the first pedigerous somite.

The antenna of *E. tuberculatus* sp. nov. is armed with 5 setae. This feature is shared with some varieties of *E. fulgens* and by four other species, *E. adnatus*, *E. laticeps*, *E. parapterophorus*, and *E. mabulensis* sp. nov. (Table 6). All of these species also lack any dorsal tubercles or projections.

### *Enterocola australis* sp. nov.

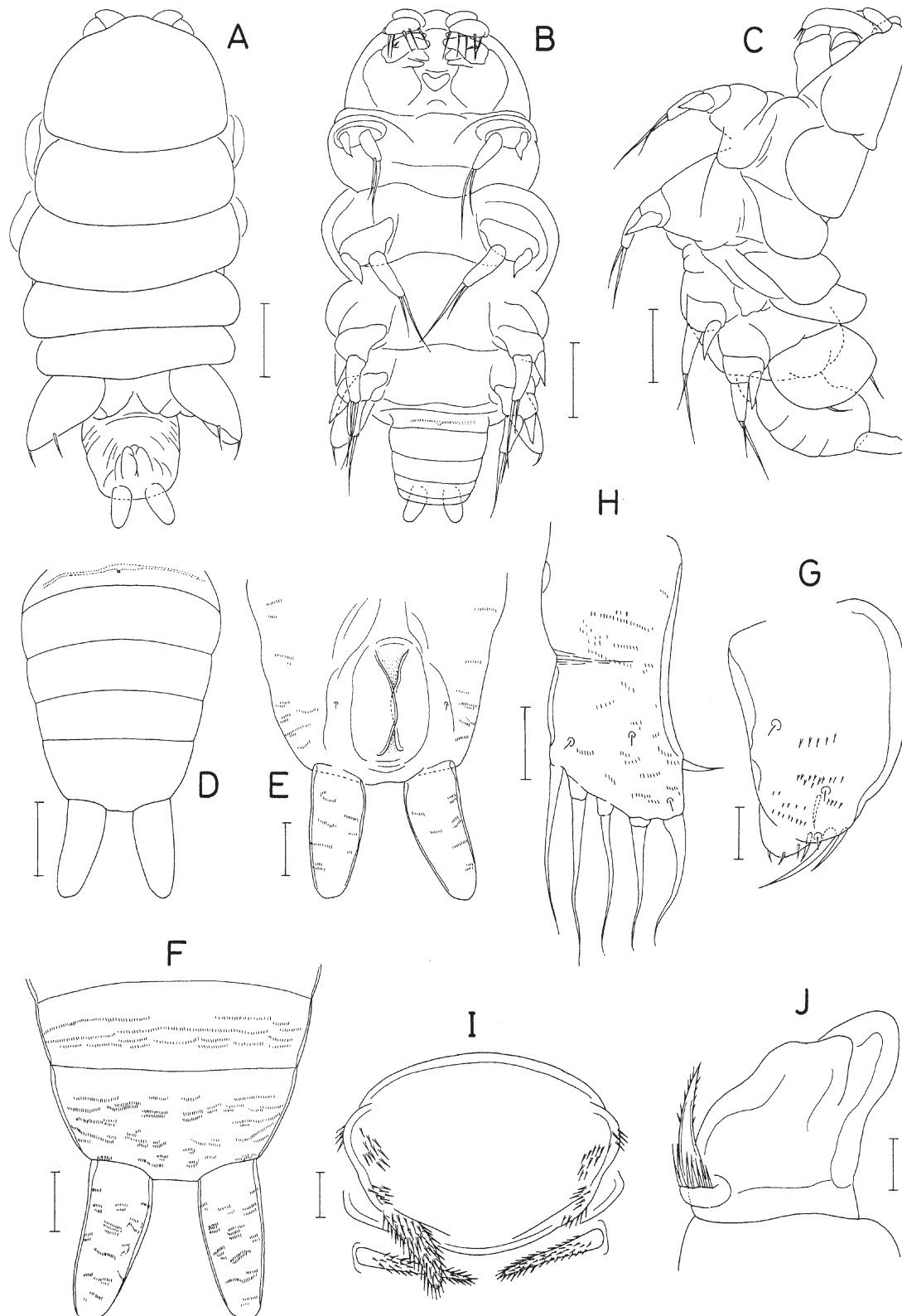
(Figs. 144, 145)

**Type material.** Holotype ♀ (MNHN-IU-2014-21555), 7 ♀♀ paratypes (MNHN-IU-2014-21556), and 1 ♀ paratype (dissected, MNHN-IU-2014-21473) from *Pseudodistoma* sp. (MNHN-IT-2008-7383 = MNHN A1/PSE/45); South Africa, Ouderkraal, SAA 55, depth 8 m, Griffiths coll., 18 August 1994.

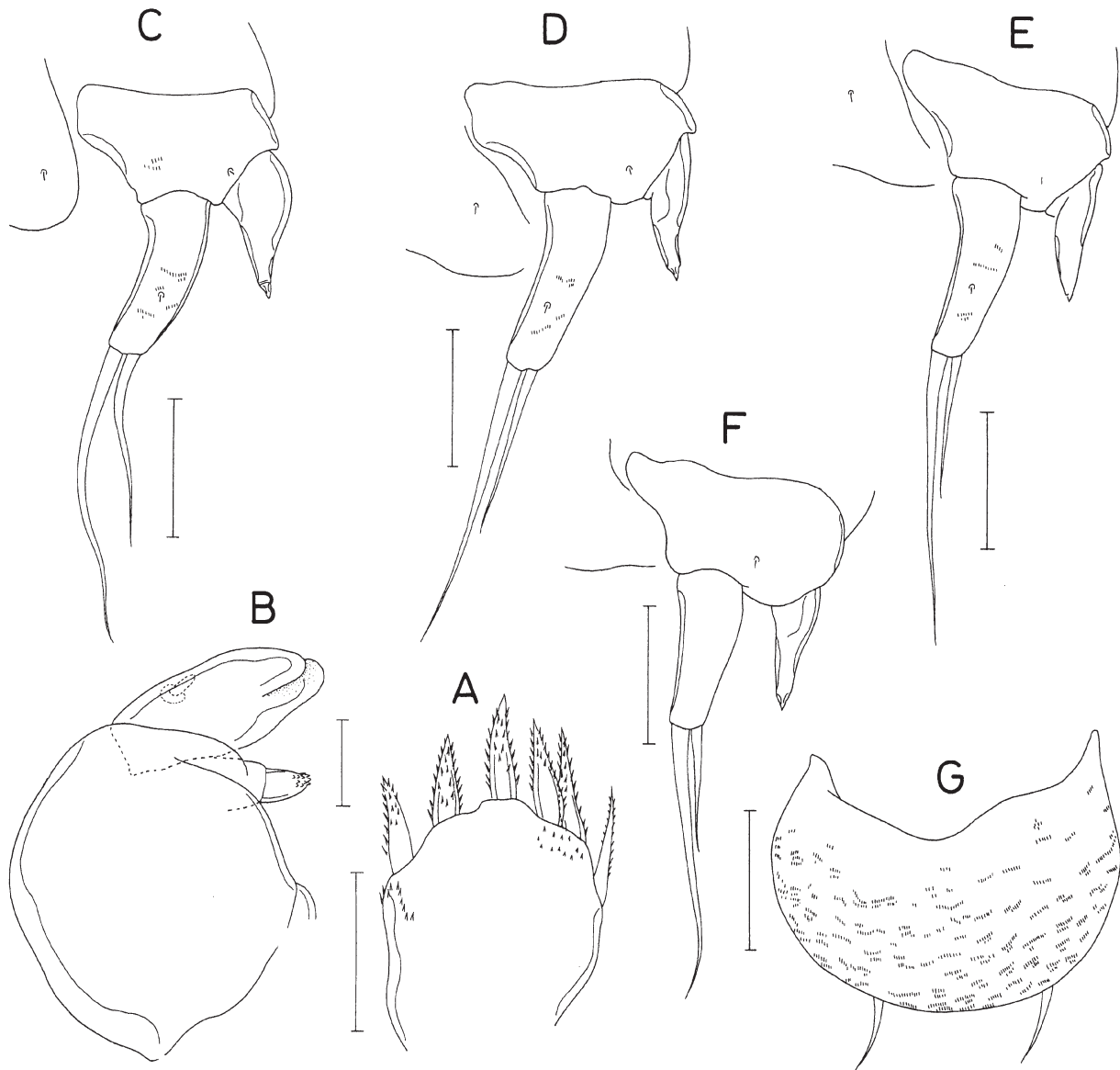
**Etymology.** The specific name is derived from the Latin *austral* (=southern), indicating the location of the type locality in South Africa.

**Description of female.** Body (Fig. 144A-C) eruciform, depressed, curved dorsally; body length 1.45 mm; maximum width 650 µm (across second pedigerous somite). Cephalosome 335×509 µm, well-defined from first pedigerous somite. Trunk distinctly segmented; first to fourth pedigerous somites bearing simple, distinct dorsal tergites, without dorsolateral tergal folds. Ventral interpodal protrusions not developed (Fig. 144B). Genitoabdomen (Fig. 144D) gradually narrowing posteriorly, unsegmented dorsally but 5-segmented ventrally, with many incom-

plete transverse rows of minute spinules (Fig. 144E, F); anal prominence distinct, with large anal opening (Fig. 142E). Caudal rami (Fig. 144D-F) widely separated from each other, slightly divergent, unarmed, about 2.5 times longer than wide ( $133 \times 54 \mu\text{m}$ ), gradually narrowing distally towards rounded distal margin.



**FIG. 144.** *Enterocola australis* sp. nov., female. A, habitus dorsal; B, habitus, ventral; C, habitus, left; D, genitoabdomen, ventral; E, posterior part of genitoabdomen, dorsal; F, posterior part of genitoabdomen, ventral; G, antennule; H, antenna; I, labrum (left palp omitted) and mandibles; J, precoxa of maxillule. Scale bars: A-C, 0.02 mm; D, 0.1 mm; E, F, H, 0.05 mm; G, I, J, 0.02 mm.



**FIG. 145.** *Enterocola australis* sp. nov., female. A, palp of maxillule; B, maxilla; C, leg 1; D, leg 2; E, leg 3; F, leg 4; G, leg 5. Scale bars: A, B, 0.05 mm; C-G, 0.1 mm.

Rostrum absent. Antennule (Fig. 144G) indistinctly 2-segmented, tapering, 1.47 times longer than wide ( $100 \times 68 \mu\text{m}$ ); proximal segment with 4 setae and ornamented with scattered minute spinules distally; distal segment small, semicircular, armed with 3 small, setule-like setae on distal margin. Antenna (Fig. 144H) more than twice as long as wide ( $203 \times 95 \mu\text{m}$ ), obscurely 2-segmented, ornamented with rows of minute spinules on convex surface; proximal segment unarmed; distal segment with 6 naked setae (1 small seta on medial margin and 5 large setae on oblique distal margin); lengths of setae I-VI 27, 93, 93, 109, 125, and  $118 \mu\text{m}$ , respectively; setae III-V geniculate near base; seta I positioned at 70% along medial margin of segment.

Labrum (Fig. 144I) with 3 patches of spinules on each side; palp spinulose, gradually narrowing distally, not expanded. Mandible (Fig. 144I) spinulose, slender, much narrower than labral palp. Maxillular precoxa (Fig. 144J) with bifurcate distal part; endite tipped with 1 spinulose spine and array of several spinules; palp (Fig. 145A) with 6 spinulose elements including slender lateral seta. Maxilla (Fig. 145B) 2-segmented; mediolateral endite on proximal segment bearing thick, basally articulating, spiniform element; distal segment bifurcate, smooth, with 1 small seta proximally. Maxilliped absent.

Legs 1-4 (Fig. 145C-F) each consisting of 2-segmented protopod and 1-segmented rami; protopods unarmed. Exopods distinctly shorter than endopods; exopod of leg 3 not elongated. Endopods slender, more than twice as long

as wide; 125×49, 139×48, 130×50, and 116×48 µm, respectively, in legs 1-4. Lengths of laterodistal and mediodistal setae 143 and 220, 130 and 215, 107 and 214, and 91 and 200 µm, respectively, in legs 1-4. Laterodistal setae much shorter than mediodistal setae.

Leg 5 (Fig. 145G) lamellate, wider than long (127×253 µm), armed with 2 setae (both 56 µm long) on distal margin and ornamented with numerous rows of minute spinules on convex surface; distance between 2 setae 123 µm.

**Male.** Unknown.

**Remarks.** In *E. australis* **sp. nov.** the laterodistal setae on the endopods of legs 1-4 are distinctly shorter than the mediodistal setae, less than 0.7 times as long as the latter. This is a distinctive feature of the new species, considering that the laterodistal setae are typically longer than the mediodistal setae in *Enterocola* species. Only four species, *E. coniculus*, *E. fulgens*, *E. laticeps*, and *E. petiti* Guille, 1964, are known to diverge from this pattern and are compared with the new species in more detail.

Unlike the new species, *E. coniculus* lacks caudal rami (a characteristic feature of this species). In *E. fulgens* the caudal rami are about 1.6 times longer than wide (cf. 2.5 times in the new species), the antennule is 3-segmented (cf. indistinctly 2-segmented), and the distal setae on the endopods of legs 1-4 are much shorter than the endopodal segments (cf. often longer). In *E. laticeps* the antennule is elongate (cf. not elongate in new species), both rami of legs 1-4 are 2-segmented (cf. 1-segmented), and the antenna is armed with 5 setae (cf. 6 setae). Finally, in the redescription of *E. petiti* by Illg & Dudley (1980) the caudal rami are as long as wide (cf. 2.5 times in new species), the first to fourth pedigerous somites bear tergal folds (cf. absent), and the endopodal segments of legs 1-4 are short, only slightly longer than wide (cf. more than twice as long as wide).

Other notable features of *E. australis* **sp. nov.**, are the elongate endopods of legs 1-4 which are more than twice as long as wide, and leg 5 bears relatively large setae.

### ***Enterocola angustus* sp. nov.**

(Figs. 146, 147)

**Type material.** Holotype ♀ (MNHN-IU-2014-21557) and 1 ♀ paratype (dissected, MNHN-IU-2014-21474) from *Didemnum nocturnum* Monniot F. & Monniot C., 1997 (MNHN-IT-2008-3178 =MNHN A2/DID.C/404); Tanzania, Site ZAN 02, Morogo bank reef, 6 miles W of Zanzibar town, OCDN 3563-I (06°11.30'S, 039°07.70'E), depth 21 m, CRRF coll., 19 January 1996.

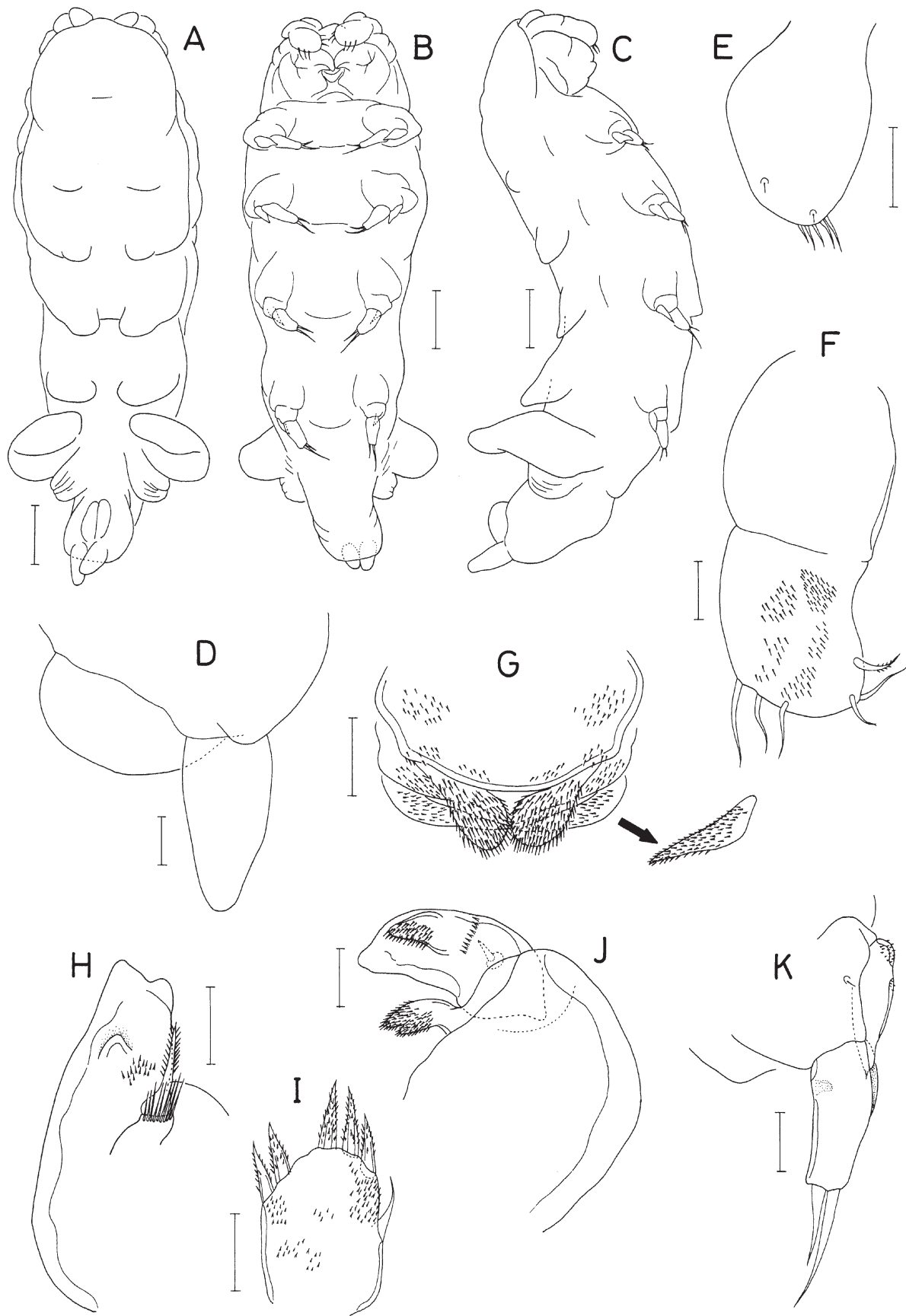
**Etymology.** The name is derived from the Latin *angust* (= narrow), referring to the relatively narrow body of the new species.

**Description of female.** Body (Fig. 146A-C) eruciform, relatively narrow, unsegmented, curved dorsally; body length 1.05 mm; maximum width 316 µm (across second pedigerous somite). Posterior part of body from second pedigerous somite to genitoabdomen gradually narrowing in dorsal and ventral views. Cephalic shield about 175×250 µm, defined from first pedigerous somite only by lateral constrictions, lacking defined posterodorsal margin. Dorsolateral tergal folds small on first pedigerous somite, but prominent in second to fourth pedigerous somites. Third and fourth pedigerous somites each with single, weak ventral interpodal protrusion. Genitoabdomen short, unsegmented; anal prominence (Fig. 146D) well-developed. Caudal ramus (Fig. 146D) tapering, unarmed, about 1.9 times longer than wide (73×38 µm).

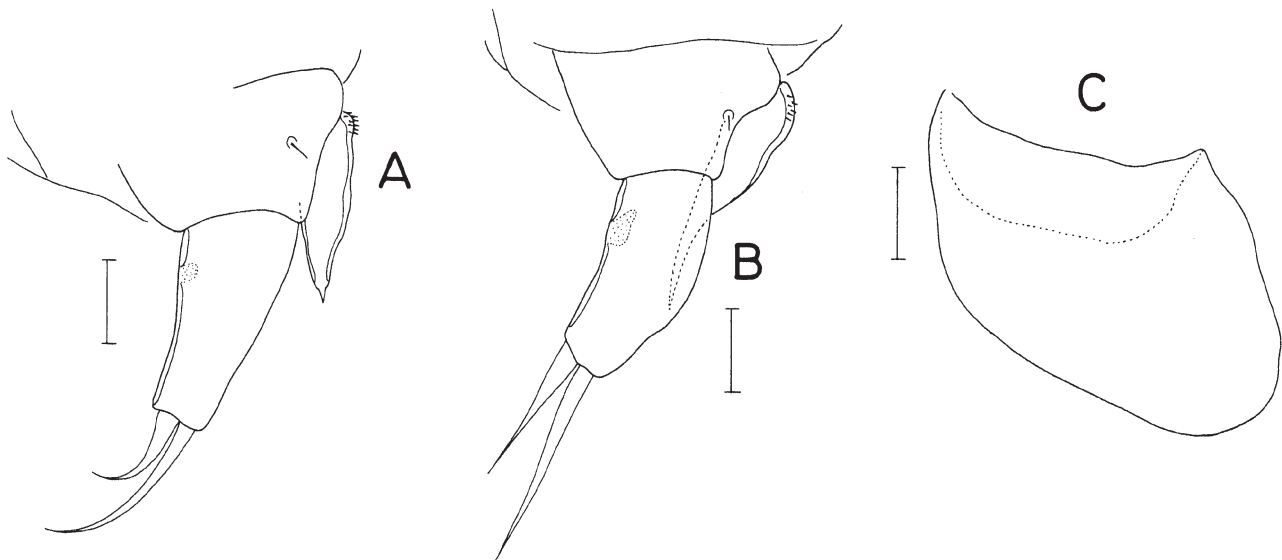
Rostrum absent. Antennule about 1.5 times longer than wide (51×35 µm), bulbous, with narrow proximal part; armed with 5 small setae on apex, longest seta 10 µm. Antenna (Fig. 146F) incompletely 2-segmented, about 2.1 times longer than wide (125×59 µm); proximal segment unarmed, slightly longer than distal segment; distal segment ornamented with minute spinules on concave surface; armed with 6 setae, lengths of setae I-VI (medial to lateral) 18, 19, 14, 21, 22, and 29 µm, respectively; seta I weakly pinnate, positioned at 70% along medial margin of segment; setae II and III close to each other, both widely separated from seta IV.

Labrum (Fig. 146G) with convex posterior margin and markedly inflated, bulbous palps. Mandible (Fig. 146G) tapering, much narrower than labral palp. Maxillule consisting of precoxa and palp; precoxa (Fig. 146H) with endite tipped with 1 spinulose seta and more than 30 thin, stiff setules; distal sclerotized part of precoxa weakly bifurcate,





**FIG. 146.** *Enterocola angustus* **sp. nov.**, female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, anal prominence and caudal ramus, right; E, antennule; F, antenna; G, labrum and mandibles, with inset showing left mandible; H, precoxa of maxillule; I, palp of maxillule; J, maxilla; K, leg 1. Scale bars: A-C, 0.1 mm; D-K, 0.02 mm.



**FIG. 147.** *Enterocola angustus* **sp. nov.**, female. A, leg 2; B, leg 3; C, leg 5. Scale bars: A, B, 0.02 mm; C, 0.05 mm.

with 1 blunt tubercle and 1 patch of minute spinules near middle; palp (Fig. 146I) with 2+3 spines on distal margin and 1 naked seta on lateral margin. Maxilla (Fig. 146J) with bifurcate, spinulose process on endite of proximal segment; distal segment bearing spinulose subdistal process and 1 row of minute spinules on anterior surface; armed with 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each with incompletely 2-segmented protopod and unsegmented rami (Figs. 146K, 147A, B); protopods unarmed. Exopods with proximal patch of spinules on lateral margin. Endopods  $50 \times 21$ ,  $54 \times 26$ ,  $52 \times 24$ , and  $51 \times 20$   $\mu\text{m}$ , respectively, in legs 1-4. Lengths of laterodistal and mediodistal setae 44 and 27, 44 and 25, 50 and 35, and 50 and 30  $\mu\text{m}$ , respectively, in legs 1-4. Length ratios of laterodistal to mediodistal setae on endopods 1.63:1, 1.76:1, 1.43:1, and 1.67:1, respectively, in legs 1-4.

Leg 5 (Fig. 147C) unarmed, obliquely wider than long ( $149 \times 165$   $\mu\text{m}$ ), with expanded dorsodistal corner.

**Male.** Unknown.

**Remarks.** The endopod of leg 1 of *E. angustus* **sp. nov.** carries a laterodistal seta which is distinctly shorter than the endopodal segment, but distinctly longer than the mediodistal seta. Seven species of *Enterocola* share these features with *E. angustus* **sp. nov.**, as follows: *E. parapterophorus*, *E. quadrisetus* **sp. nov.**, *E. mabulensis* **sp. nov.**, *E. dicaudatus*, *E. sydnii*, *E. robustus* **sp. nov.**, and *E. parvus* **sp. nov.**

The first three of these listed species can readily be distinguished by the presence of 4 or 5 setae on the antenna, compared with 6 setae in *E. angustus* **sp. nov.**. There are additional differences, such as the antennule of *E. parapterophorus* is armed with 3 or 4 setae (cf. 5 setae in the new species), the caudal rami of *E. quadrisetus* **sp. nov.** are about 3.2 times longer than wide (cf. 1.9 times), and leg 5 of *E. mabulensis* **sp. nov.** is oval (cf. obliquely wider than long, with expanded dorsodistal corner).

The remaining four congeners can be distinguished from *E. angustus* **sp. nov.** by the following features: in *E. dicaudatus* the cephalic shield bears a posterodorsal process, the caudal rami are elongate (about 3 times longer than wide), and the genitoabdomen bears a large ventral process (Marchenkov & Boxshall, 2005); in *E. sydnii*, the caudal rami are short (as long as wide), the antennule is armed with 7 setae, and the first to fourth pedigerous somites each bear a pair of ventral interpodal protrusions (Ooishi, 2011); in *E. robustus* **sp. nov.** the body is robust, the caudal rami are 3 times longer than wide, the antennule is armed with 3 setae, and the third and fourth pedigerous somites each bear a large interpodal protrusion on the ventral surface, and in *E. parvus* **sp. nov.** the body is small (560  $\mu\text{m}$  long), the first and second pedigerous somites each bear a large dorsal tubercle, the antennule is armed with 3 setae, and the maxilla bears a spinulose tubercle proximally on the medial margin of the proximal segment.

***Enterocola sedentarius* sp. nov.**

(Figs. 148, 149)

**Type material.** Holotype ♀ (MNHN-IU-2014-21558) and 1 ♀ paratype (dissected, MNHN-IU-2014-21475) from *Hypodistoma deerratum* (Sluiter, 1895); Papua New Guinea, CRRF coll.

**Etymology.** The name of the new species reflects its sedentary body form.

**Description of female.** Body (Fig. 148A-C) small, curved dorsally, appearing posteriorly truncated sedentary in lateral view (Fig. 148C). Body length 522 µm; maximum width 230 µm (across second pedigerous somite). Cephalic shield distinct from first pedigerous somite, 133×161 µm. Trunk obscurely segmented (Fig. 148C), but somites distinctly defined by deep lateral constrictions. First to fourth pedigerous somites each with well-developed tergite dorsally; tergite of first pedigerous somite simple, but those of second to fourth pedigerous somites forming paired posterolateral tergal folds (Fig. 148A). First to fourth pedigerous somites each with single mid-ventral interpodal protrusion (Fig. 148B). Genitoabdomen (Fig. 148D) unsegmented, much wider than long in lateral view; anal prominence large (Fig. 148D). Caudal rami (Fig. 148E) originating close to each other, directed ventrally, arising on ventral margin of genitoabdomen (Fig. 148D) but not articulated at base, about 1.8 times longer than wide (25×14 µm); armed with 2 or 3 minute setae. Egg sac containing 5 or 6 eggs; each egg 145 µm in diameter.

Rostrum absent. Antennule (Fig. 148G) 40×25 µm, unsegmented, but distinctly divisible into broad proximal part and short, narrow distal part; proximal part armed with 4 setae distally and 1 small tubercle subdistally; distal part occupying 20% length of antennule, armed with 3 setae on distal margin. Antenna (Fig. 148H) incompletely 2-segmented, about 2.1 times longer than wide; proximal segment unarmed; distal segment armed with 6 large setae, lengths of setae I-VI (medial to lateral) increasing 19, 32, 34, 36, 48, and 61 µm, respectively; setae IV-VI longer than width of segment at tip.

Labrum (Fig. 148I) broad with convex lateral margins, ornamented with patches of minute spinules on ventral surface; palp spinulose, curved laterally, with narrow proximal quarter and moderately expanded distal three-quarters. Mandible spinulose, narrower than labral palp. Precoxa (Fig. 148J) of maxillule with bifurcate apex, and endite bearing slender, spinulose spine and more than 10 thin spinules; palp (Fig. 148K) armed with 6 subequal spinulose spines along convex distal margin. Maxilla (Fig. 148L) 2-segmented; proximal segment bearing 1 smooth tubercle proximally on medial margin and mediiodistal endite tipped with spinulose element; distal segment smooth, tapering, with 1 tubercle on anterior surface and 1 seta on posterior surface. Maxilliped absent.

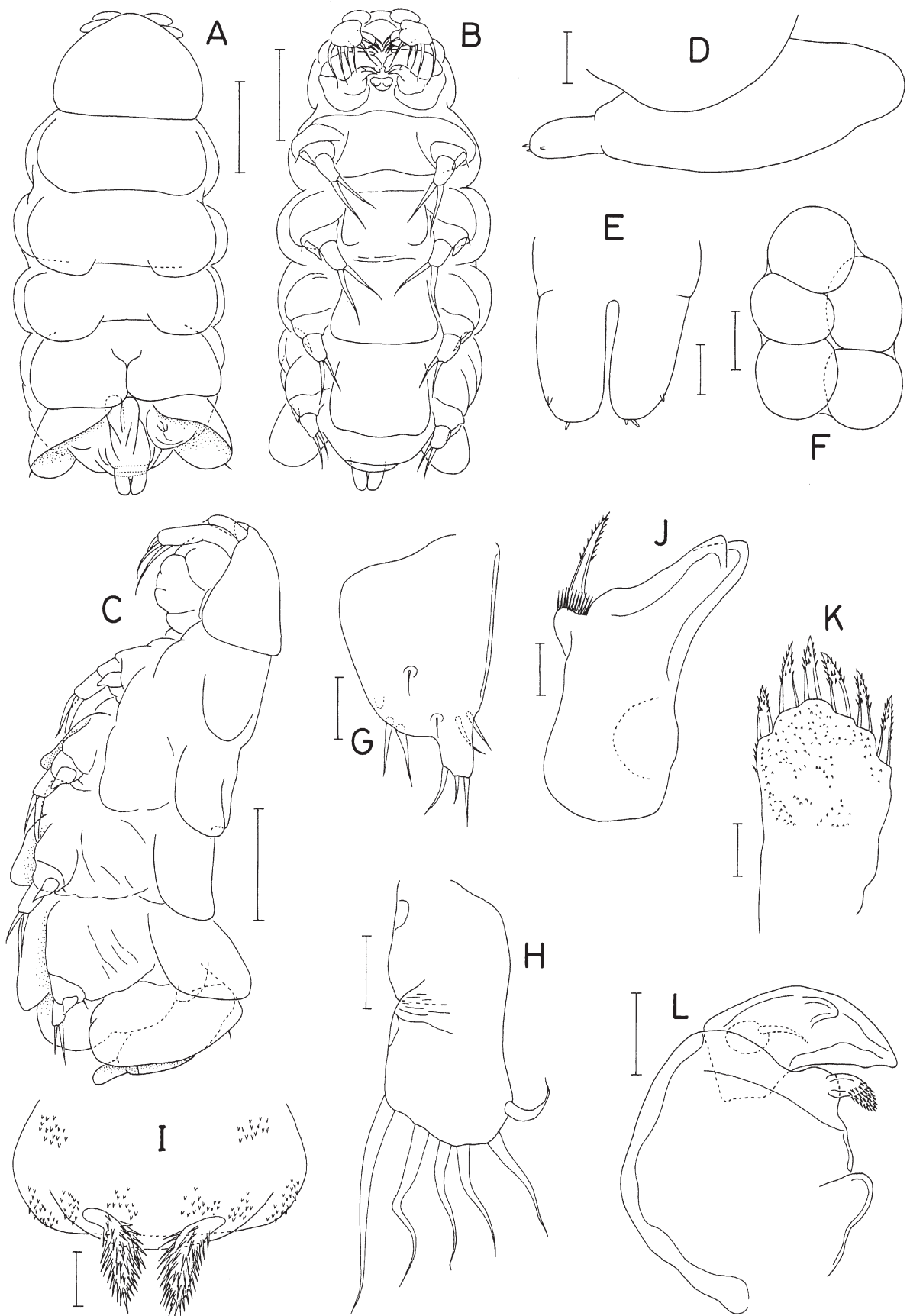
Legs 1-4 each consisting of 2-segmented protopod (coxa and basis) and unsegmented rami (Fig. 149A, B); basis with outer seta. Exopods with proximal patch of spinules on lateral margin. Endopods less than twice as long as wide, 31×21, 31×20, 31×18, and 25×15 µm, respectively, in legs 1-4. Distal setae on endopods distinctly longer than endopodal segments. Laterodistal and mediiodistal setae 67 and 59, 71 and 56, 42 and 42, and 40 and 33 µm, respectively, in legs 1-4. Laterodistal setae distinctly longer than mediiodistal setae in legs 1, 2, and 4, but equal in length in leg 3.

Leg 5 (Fig. 149C) more than twice as wide as long (63×150 µm); armed with 2 minute setae on distal margin; separated by distance of 87 µm.

**Male.** Unknown.

**Remarks.** The posteriorly-truncated body, with its ventrally directed abdomen, is an extraordinary body form for the genus *Enterocola*, and serves to characterize *E. sedentarius* sp. nov. In addition, about half of known congeneric species have a laterodistal seta on the endopod of leg 1 that is as long as or longer than the endopodal segment, but in none of these is the laterodistal seta more than twice as long as the endopodal segment as in *E. sedentarius* sp. nov.

The caudal rami of *E. sedentarius* sp. nov. are armed with 2 or 3 setae. Although the setae are minute, this feature is remarkable because caudal rami of *Enterocola* species that are known to be setiferous, i.e. *E. ianthinus*, *E. laticeps*, and *E. seticaudus* sp. nov., only ever have a single caudal seta. The antennules of *E. sedentarius* sp. nov. are armed with 7 setae (Table 6). This setation is shared with three known species, *E. sydnii*, *E. seticaudus* sp. nov., and *E. australis* sp. nov. but none of these species shares the ventrally-directed abdomen that is diagnostic for *E. sedentarius* sp. nov.



**FIG. 148.** *Enterocola sedentarius* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, left; D, genitoabdomen, left; E, caudal rami; F, egg sac; G, antennule; H, antenna; I, labrum; J, precoxa of maxillule; K, palp of maxillule; L, maxilla. Scale bars: A-C, F, 0.1 mm; D, H, L, 0.02 mm; E, G, I-K, 0.01 mm.

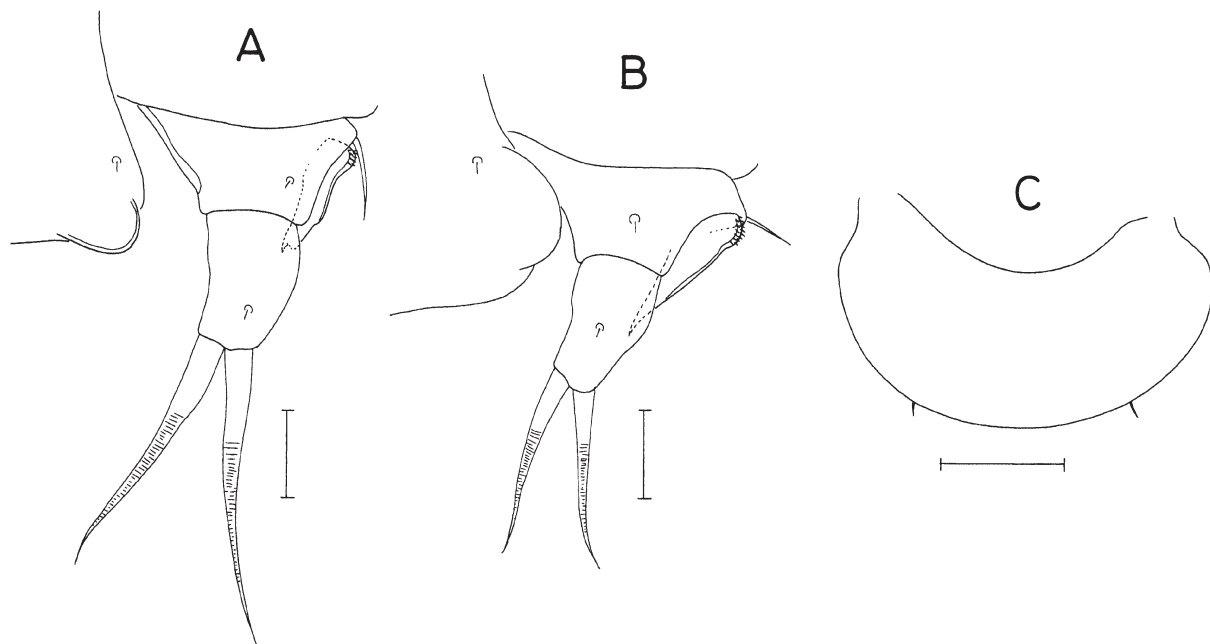


FIG. 149. *Enterocola sedentarius* sp. nov., female. A, leg 1; B, leg 3; C, leg 5. Scale bars: A, B, 0.02 mm; C, 0.05 mm.

***Enterocola sulcatus* sp. nov.**

(Figs. 150, 151)

**Type material.** Holotype ♀ (MNHN-IU-2014-21559) and 1 ♀ paratype (dissected, MNHN-IU-2014-21476) from *Aplidium nadaense* (Nishikawa, 1980) (MNHN-IT-2008-576 = MNHN A1 /APL.B/407); Papua New Guinea, Louisiades Archipelago, Calvados Islands, Channel E of Brooker I., Site Brooker Channel, OCDN 5743-A, (11°03.09'S, 152°28.62'E), depth 7 m, CRRF coll., 01 June 1998.

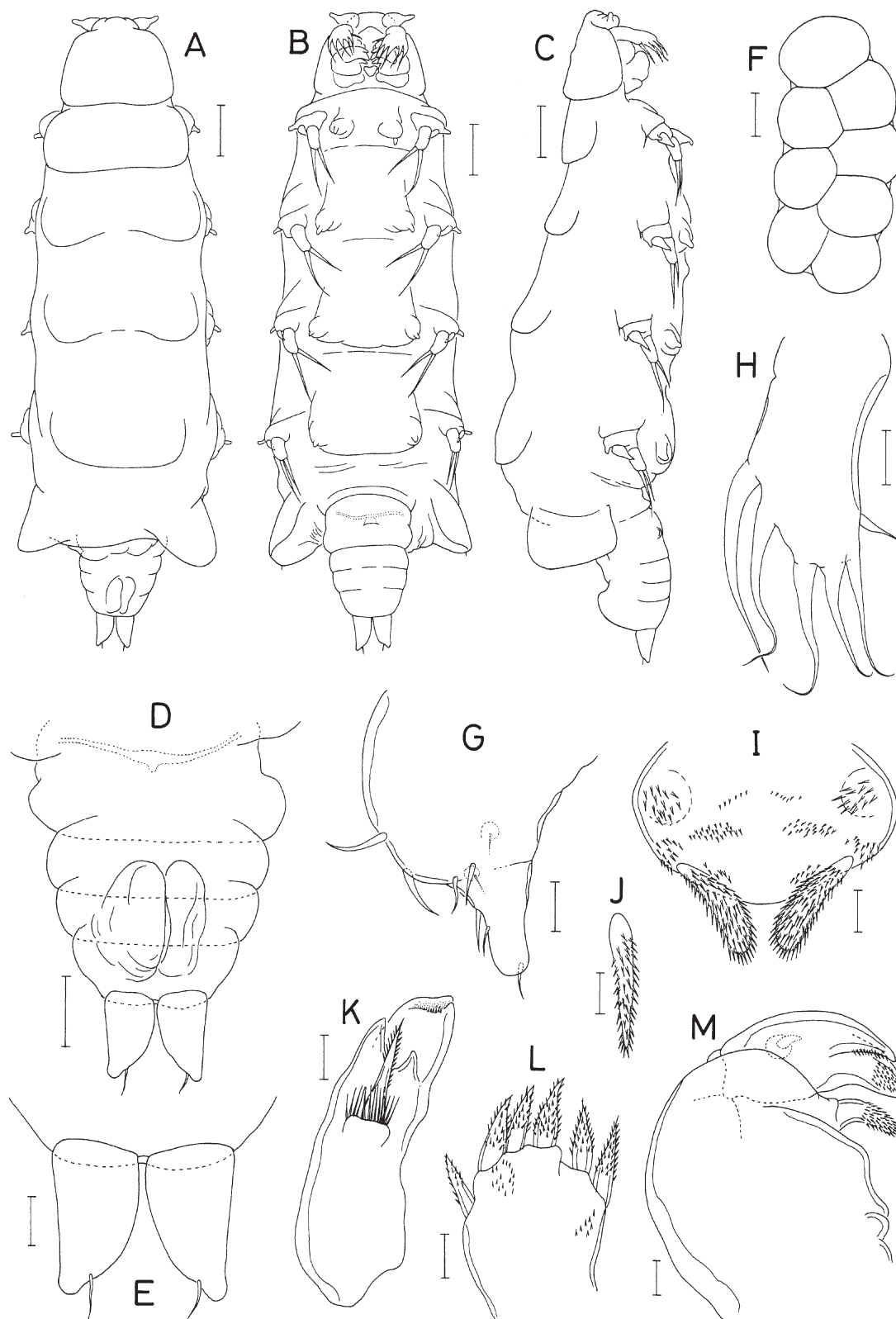
**Etymology.** The name is derived from the Latin *sulc* (=a furrow), alluding to the presence of a longitudinal furrow on the endopods of legs 1-4.

**Description of female.** Body (Fig. 150A-C) eruciform, consisting of cephalosome, trunk, and genitoabdomen. Body length 1.24 mm; maximum width 373 µm (across fourth pedigerous somite). Cephalic shield distinctly narrower than trunk (177×223 µm), with distinct posterior margin. Trunk gradually broadening posteriorly, unsegmented; first to fourth pedigerous somites each bearing dorsal tergite; first pedigerous somite completely covered by tergite, but second to fourth pedigerous somites partly covered by tergite; tergites on second and third pedigerous somites with incomplete posterior margin, thus forming dorsolateral tergal folds. First to fourth pedigerous somites each bearing pair of ventral interpodal protrusions between left and right legs; each protrusion tipped with nipple-shaped knob (Fig. 150B, 151A-D). Genitoabdomen (Fig. 150D) directed slightly posteroventrally (Fig. 150C), dorsally unsegmented, but ventrally 4-segmented; anal prominence large. Caudal rami (Fig. 150E) tapering, 1.75 times longer than wide (63×36 µm), with straight lateral margin, convex medial margin, blunt apex; armed with 1 small seta (19 µm long) subdistally on medial margin. Egg sac containing 6 to 8 eggs in 2 rows; each egg relatively large, about 160 µm in diameter.

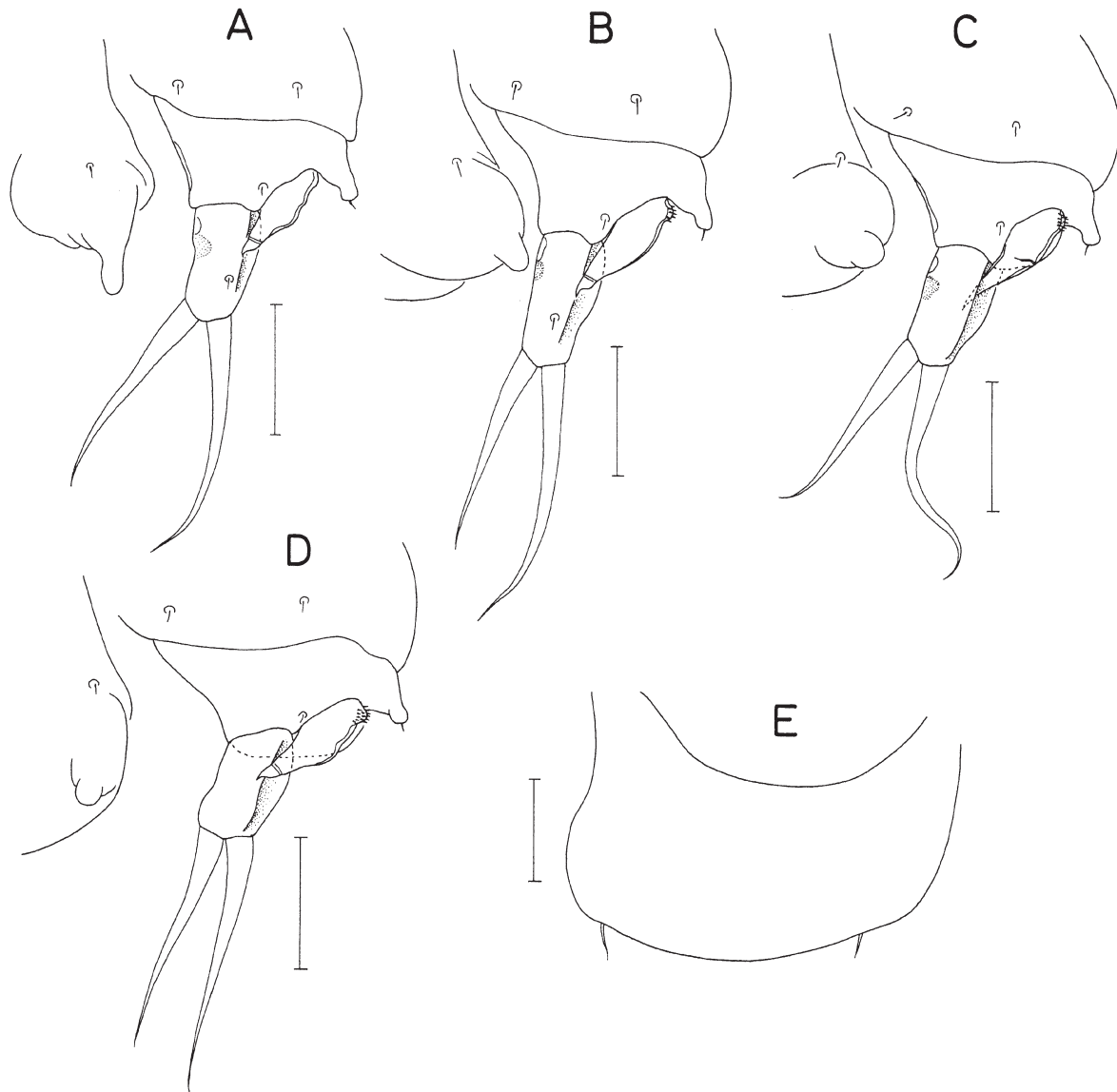
Rostrum absent. Antennule (Fig. 150G) about 58×45 µm, obscurely 2-segmented; proximal segment broad, armed with 4 setae (2 on convex posterior margin and 2 distally); distal segment shorter and much narrower than proximal segment, armed with 3 setae (2 on posterior margin and 1 on apex). Antenna (Fig. 150H) unsegmented, lacking any trace of articulation, approximately 89×41 µm, armed with 6 naked setae (1 on medial margin, 2 on lateral margin and 3 on distal margin); setae II-VI longer than width of segment; lengths of setae I-VI 16, 45, 45, 54, 61, and 75 µm, respectively.

Labrum (Fig. 150I) with patches of spinules on ventral surface; palp densely spinulose, gradually broadening distally. Mandible (Fig. 150J) tapering, spinulose, distinctly narrower than labral palp. Maxillular precoxa (Fig. 150K) with excavated apex, 2 processes subdistally, and endite in middle tipped with 1 spinulose spine and about

15 stiff setules; palp (Fig. 150L) armed with 6 thick spines, 5 on distal margin and 1 on lateral margin. Maxilla (Fig. 150M) 2-segmented; proximal segment bearing 1 small tubercle proximally on medial margin and 1 spinulose, basally articulated element on mediobasal endite; distal segment bifurcate and spinulose distally, with 1 small seta on posterior surface. Maxilliped absent.



**FIG. 150.** *Enterocola sulcatus* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, genitaloabdomen, dorsal; E, caudal rami, dorsal; F, egg sac; G, antennule; H, antenna; I, labrum; J, mandible; K, precoxa of maxillule; L, palp of maxillule; M, maxilla. Scale bars: A-C, F, 0.1 mm; D, 0.05 mm; E, H, 0.02 mm; G, I-M, 0.01 mm.



**FIG. 151.** *Enterocola sulcatus* sp. nov., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: 0.05 mm.

Legs 1-4 (Fig. 151A-D) each consisting of coxa, basis, and unsegmented rami; coxae unarmed; basis characteristically bearing digitiform laterodistal process tipped with minute seta. Exopods of legs 2-4 bearing patch of spinules proximally on lateral margin. Endopods marked by longitudinal furrow along lateral surface, receiving tip of exopods. Sizes of endopods  $46 \times 26$ ,  $52 \times 26$ ,  $48 \times 27$ , and  $46 \times 27$   $\mu\text{m}$ , respectively, in legs 1-4. Laterodistal and mediodistal setae distinctly longer than endopodal segments, setal lengths 94 and 85, 105 and 81, 94 and 81, and 101 and 87  $\mu\text{m}$ , respectively, in legs 1-4. Laterodistal setae 1.1, 1.3, 1.2, and 1.2 times longer than mediodistal setae, respectively, in legs 1-4.

Leg 5 (Fig. 151E) more than twice as wide as long ( $90 \times 188$   $\mu\text{m}$ ), bearing 2 small setae on distal margin, separated by distance of 125  $\mu\text{m}$ .

**Male.** Unknown.

**Remarks.** *Enterocola sulcatus* sp. nov. can be recognized by the following outstanding features: (1) the paired ventral interpodal protrusions on the first to fourth pedigerous somites are tipped with a nipple-shaped knob; (2) in legs 1-4, the basis bears a digitiform laterodistal process; and (3) the endopods of legs 1-4 each bear a longitudinal furrow along the lateral surface. These three features are as yet unknown elsewhere in *Enterocola* and, therefore, serve to characterize the new species.

An additional diagnostic feature of *E. sulcatus* **sp. nov.** is the armature of a single seta on the caudal rami. This feature is shared with three other known species, *E. inathinus*, *E. laticeps*, and *E. seticaudus* **sp. nov.** Of these, *E. seticaudus* **sp. nov.** is the most similar to *E. sulcatus* **sp. nov.** in sharing the same basic body form and the setation patterns of the antennule, antenna, and swimming legs. However, none of these congeners exhibits any of the three features highlighted above. We also note that *E. seticaudus* **sp. nov.** differs from *E. sulcatus* **sp. nov.** in other morphological details, for example, the caudal seta is positioned at apex of the caudal ramus, and the mediiodistal process of first maxillary segment is bifurcate unlike that of *E. sulcatus* **sp. nov.**

***Enterocola neocaledonicus* sp. nov.**

(Fig. 152)

**Type material.** Holotype ♀ (MNHN-IU-2014-21560), 2 ♀♀ paratypes (MNHN-IU-2014-21561), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-21477) from *Didemnum ligulum* Monniot F., 1983; Goelands I., New Caledonia, Stn NC 47, depth 12 m, Thomassin coll., 20 March 1987.

**Additional non-type material.** 10 ♀♀ (MNHN-IU-2014-21562) in *D. ligulum*; anse Vata, Nouméa, New Caledonia, Stn NC 60, depth 0-3m, Monniot coll., 27 March 1987.

**Etymology.** The name of the new species is derived from its type locality, New Caledonia.

**Description of female.** Body (Fig. 152A, B) eruciform, curved dorsally; body length 790 µm in dissected specimen and 556, 691, and 760 µm in 3 other measured specimens; maximum width 260 µm (across first pedigerous somite). Cephalic shield 142×233 µm, with well-defined posterior margin. Trunk unsegmented, gradually narrowing posteriorly; first pedigerous somite bearing dorsal tergite, but second to fourth pedigerous somites bearing well-developed dorsolateral tergal folds. Third pedigerous somite bearing small tubercle mid-dorsally (indicated by arrowhead in Fig. 152A, B) between left and right dorsolateral tergal folds. First to fourth pedigerous somites each with single, ventral interpodal protrusion between left and right legs, weak in first and second pedigerous somites but well-developed in third and fourth pedigerous somites. Genitoabdomen dorsally unsegmented and ventrally 4-segmented; anal somite with distinct anal prominence. Caudal ramus (Fig. 152D) fusiform, unarmed, distinctly articulated from anal somite, about 2.07 times longer than wide (58×28 µm), widest in middle. Egg sac (Fig. 152E) containing 5 or 6 eggs; each egg 138 µm in diameter.

Rostrum absent. Antennule (Fig. 152F) unsegmented, about 1.6 times longer than wide (48×30 µm), with straight anterior margin and strongly protruded posterior margin; armed with 4 small setae on apex (grouped as 2 and 2). Antenna (Fig. 152G) incompletely 2-segmented, about 100 µm long, 52 µm wide; proximal segment unarmed; distal segment as long as proximal segment, ornamented with spinules on concave surface; armed with 6 setae, lengths of setae I-VI (medial to lateral) 14, 15, 11, 15, 20, and 31 µm, respectively; all setae curved medially; 3 medial setae (setae I-III) widely separated from other setae.

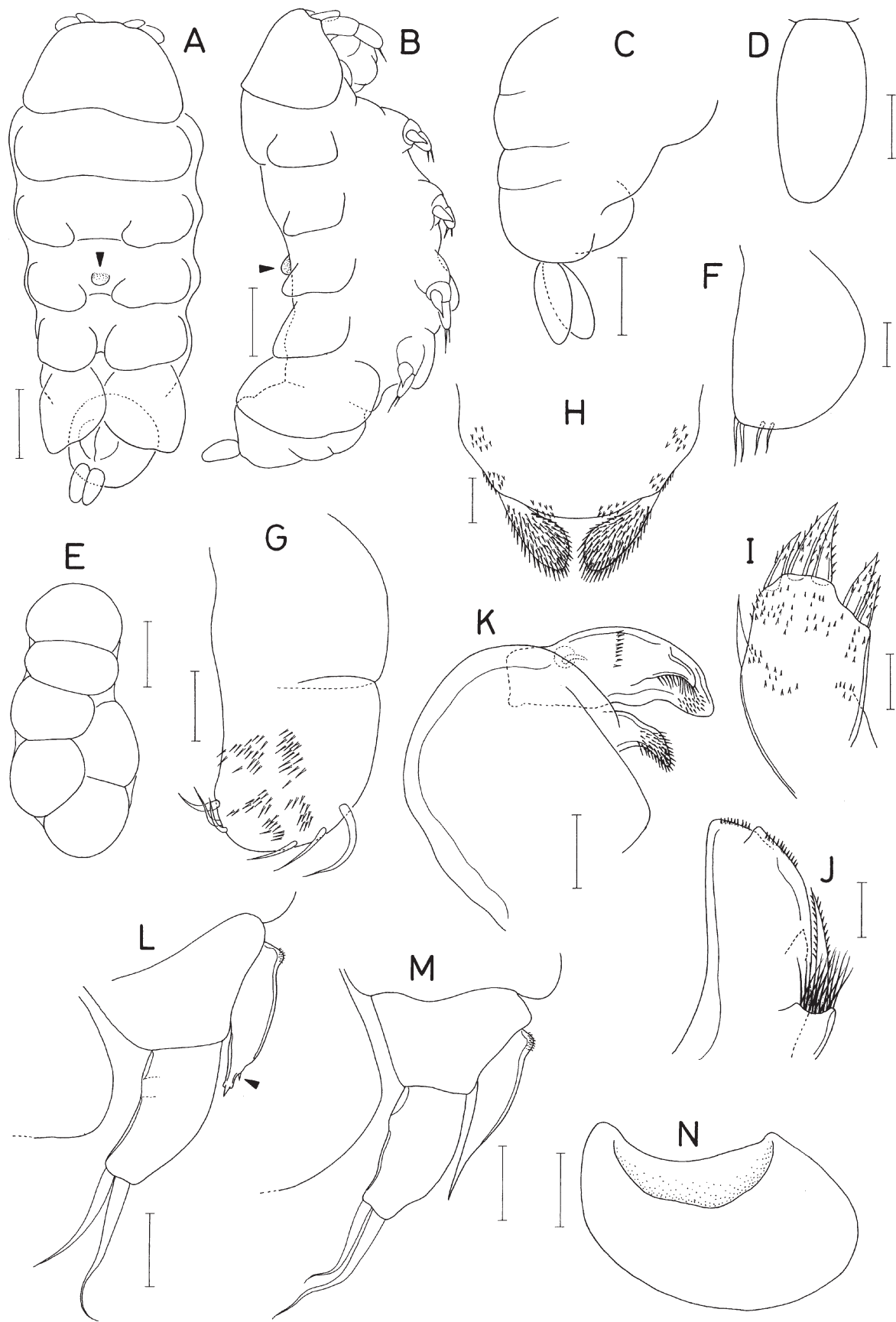
Labrum (Fig. 152H) with 3 small patches of spinules on each side of ventral surface; palp gradually inflating distally. Mandible tapering, less than half as wide as labral palp. Maxillule consisting of precoxa (Fig. 152J) and palp (Fig. 152I); distal sclerotized region of precoxa with 2 small tubercles (subdistal and proximal) and spinule-covered distal margin; endite of precoxa tipped with 1 spinulose spine and more than 20 setules; palp with 5 spines on distal margin and 1 naked seta on lateral margin. Maxilla (Fig. 152K) bearing spinulose process on endite of proximal segment; distal segment with 1 spinulose, spiniform process on subdistal anterior surface, 1 transverse row of minute spinules in middle of anterior surface, and 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each consisting of 2-segmented protopod and unsegmented rami (Fig. 152L, M); protopods unarmed. Exopods bearing patch of minute spinules proximally on lateral margin; exopods of legs 1, 2, and 4 tipped with small cusp; exopods of legs 1 and 2 with minute cusp subdistally on lateral margin (Fig. 152L). Endopods 43×20, 45×20, 40×21, and 33×20 µm, respectively, in legs 1-4. Lengths of laterodistal and mediiodistal setae 38 and 32, 42 and 34, 42 and 31, and 46 and 36 µm, respectively, in legs 1-4.

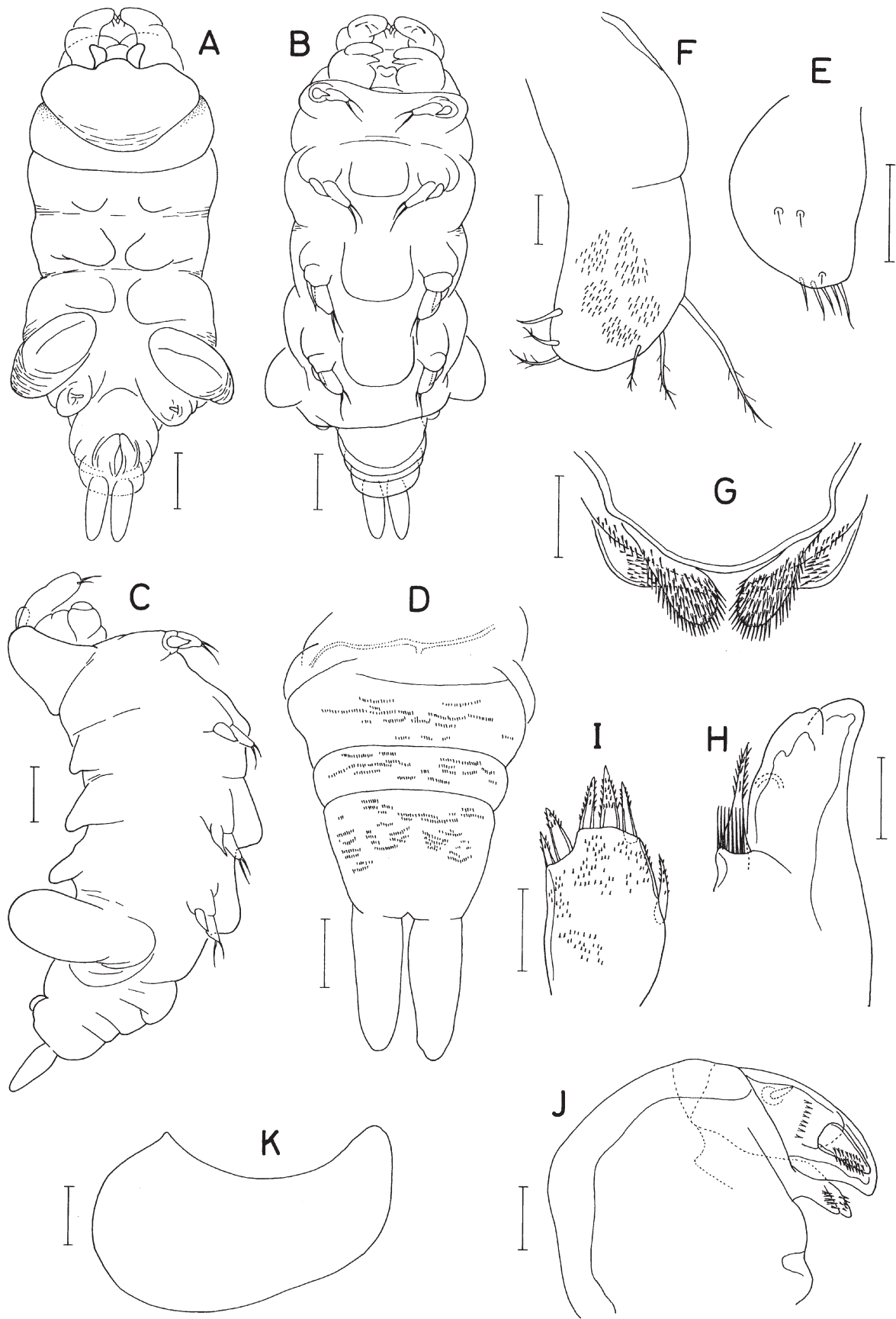
Leg 5 (Fig. 152N) unarmed, wider than long (109×190 µm).

**Male.** Unknown.





**FIG. 152.** *Enterocola neocaledonicus* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genitoabdomen, left; D, caudal ramus; E, egg sac; F, antennule; G, antenna; H, labrum; I, palp of maxillule; J, precoxa of maxillule; K, maxilla; L, leg 1; M, leg 3; N, leg 5. Scale bars: A, B, E, 0.1 mm; C, N, 0.05 mm; D, G, K-M, 0.02 mm; F, H-J, 0.01 mm.



**FIG. 153.** *Enterocola nodulosus* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, genitoabdomen, ventral; E, antennule; F, antenna; G, labrum and mandibles; H, precoxa of maxillule; I, palp of maxillule; J, maxilla; K, leg 5. Scale bars: A-C, 0.1 mm; D, K, 0.05 mm; E-J, 0.02 mm.

**Remarks.** The antennule of *E. neocaledonicus* **sp. nov.** is armed with 4 setae. Similar numbers of setae (3-5 setae) on the antennule are observable in more than 15 known species of *Enterocola* (Table 6). Seven of these species are similar to *E. neocaledonicus* **sp. nov.**, because they share the same unsegmented, bulbous shaped antennule, which is circular or semicircular (D-shaped). These seven species are *E. parapterophorus*, *E. mabulensis* **sp. nov.**, *E. dicaudatus*, *E. mammiferus*, *E. robustus* **sp. nov.**, *E. parvus* **sp. nov.**, and *E. angustus* **sp. nov.** The first two of these, *E. parapterophorus* and *E. mabulensis* **sp. nov.**, can be excluded from further comparison because both have 5 setae on the antenna, whereas *E. neocaledonicus* **sp. nov.** has 6 setae.

The remaining five species can be distinguished from *E. neocaledonicus* **sp. nov.** as follows: *E. dicaudatus* has, unlike *E. neocaledonicus* **sp. nov.**, an elongate antenna and a posterodorsal process on the cephalic shield; *E. mammiferus* has caudal rami which are wider than long (in contrast to about twice as long as wide in *E. neocaledonicus* **sp. nov.**). In *E. robustus* **sp. nov.** there are 3 setae on the antennule, the narrow caudal rami are 3.0 times longer than wide, and the endopods of swimming legs are 2-segmented, although the segmentation is incomplete. *Enterocola parvus* **sp. nov.** differs in having 3 setae on the antennule, a dorsal tubercle on the first and second pedigerous somites, and a spinulose tubercle on the medial margin of the proximal maxillary segment. Finally, *E. angustus* **sp. nov.** has 5 setae on the antennule, tapering caudal rami, and a bifurcate process on the endite of the proximal maxillary segment.

The third pedigerous somite of *E. neocaledonicus* **sp. nov.** bears a small dorsal tubercle, although it is easy to overlook because of its small size. The presence of a dorsal tubercle or process on the cephalic shield or on any pedigerous somites is known for *E. dicaudatus* (on the cephalic shield), *E. quadrisetus* **sp. nov.** (on the second and third pedigerous somites), *E. parvus* **sp. nov.** (on the first and second pedigerous somites), and *E. tuberculatus* **sp. nov.** (on the first pedigerous somite). The presence of a tubercle on the third pedigerous somite only is unique within the genus.

### *Enterocola nodulosus* **sp. nov.**

(Fig. 153, 154)

**Type material.** Holotype ♀ (MNHN-IU-2014-21563, dissected and mounted on a slide) from *Eudistoma* sp.; Indonesia, no other collection data.

**Etymology.** The name of the new species alludes to the presence of a distal nodule on the endopods of the swimming legs.

**Description of female.** Body (Fig. 153A-C) eruciform, curved dorsally; body length 909 µm; maximum width 350 µm (across second pedigerous somite). Cephalosome with convex posterodorsal margin. Trunk unsegmented, but pedigerous somites defined from one another by dorsal and lateral constrictions; second to fourth pedigerous somites each bearing pair of dorsal tergal folds (Fig. 153A, C) and single, large, plate-like ventral interpodal protrusion between left and right legs (Fig. 153B). Genitoabdomen (Fig. 153D) unsegmented dorsally but 4-segmented ventrally; segmentation indistinct between genital and first free abdominal somites. Free abdominal somites covered with ornamentation of minute spinules on all surfaces; anal prominence distinct. Caudal rami (Fig. 153D) straight, incompletely articulated from anal somite, gradually narrowing distally, unarmed, about 2.6 times longer than wide (100×38 µm).

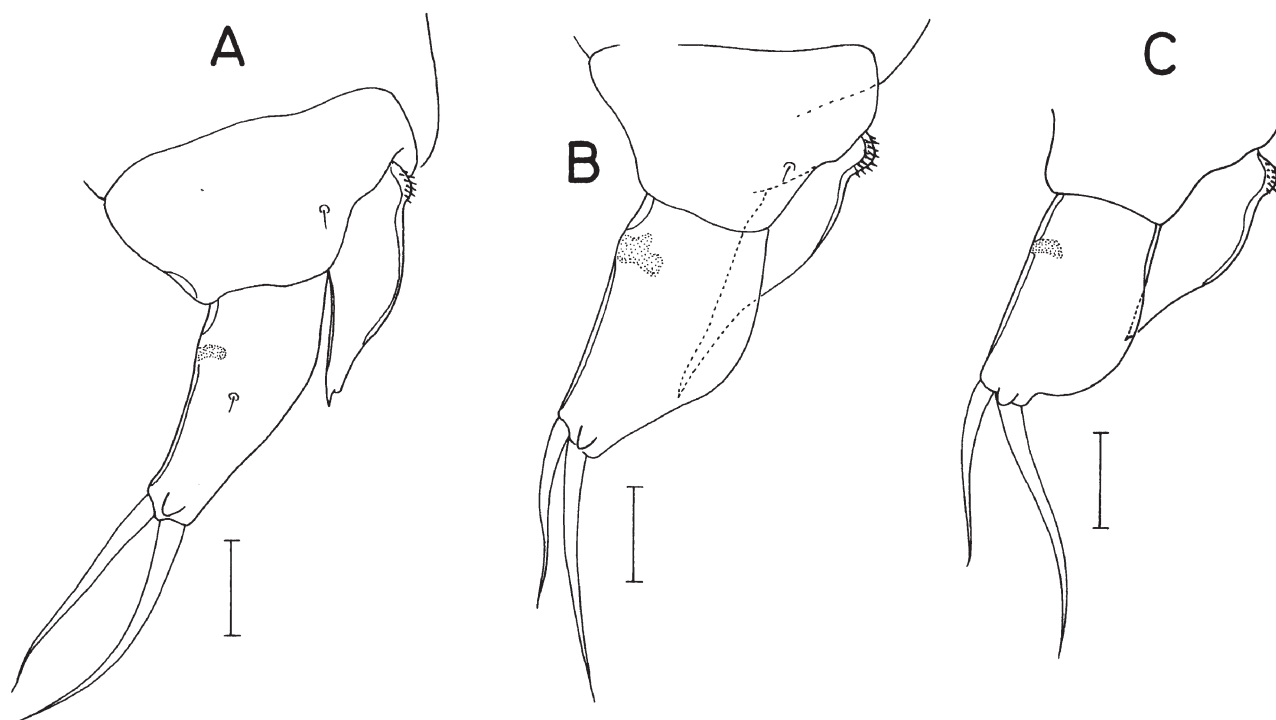
Rostrum absent. Antennule (Fig. 153E) leaf-like, 39×27 µm, inflated posteriorly, with convex posterior margin; armed with 5 small, subequal setae at apex. Antenna (Fig. 153F) about 2.6 times longer than wide, incompletely 2-segmented, slightly curved medially; proximal segment unarmed; distal segment ornamented with minute spinules on convex surface; armed with 6 thin setae, lengths of setae I-VI 20, 18, 23, 19, 32, and 64 µm, respectively; seta I naked, but other 5 setae weakly pinnate; setae I-III widely separated from setae IV-VI.

Labrum (Fig. 153G) with spinulose, distally swollen palps. Mandible (Fig. 153G) spinulose, tapering, narrower than labral palp. Maxillule consisting of precoxa (Fig. 153H) and palm-shaped palp (Fig. 153I); precoxa with bifurcate distal part, 1 small tubercle subdistally, and endite in middle bearing 1 spinulose seta and more than 20 thin spinules; palp with 6 spinulose spines. Maxilla (Fig. 153J) with bifurcate, spinulose mediobasal process on proximal segment; distal segment with 1 robust, basally articulated, spinulose spine subdistally, 1 transverse row of minute spinules on middle of anterior surface, and 1 small seta on posterior surface. Maxilliped absent.

Legs 1-4 each consisting of unarmed, 2-segmented protopod and unsegmented rami. Exopods bearing patch of

spinules proximally on lateral margin (Fig. 154A-C). Endopods armed distally with 2 naked setae and 1 nodule. Sizes of endopods 55×25, 55×24, 55×32, and 48×27 μm, respectively, in legs 1-4; endopods of legs 3 and 4 with markedly protruded lateral margin. Lengths of laterodistal and mediodistal setae 56 and 50, 55 and 43, 55 and 40, and 58 and 39 μm, respectively, in legs 1-4. Laterodistal setae longer than or as long as endopodal segments and about 1.1, 1.3, 1.4, and 1.5 times longer than mediodistal setae in legs 1-4, respectively.

Leg 5 (Fig. 153K) lamellate, unarmed, much wider than long (129×255 μm).



**FIG. 154.** *Enterocola nodulosus* **sp. nov.**, female. A, leg 1; B, leg 3; C, leg 4. Scale bars: 0.02 mm.

**Male.** Unknown.

**Remarks.** *Enterocola nodulosus* **sp. nov.** is characterized by the presence of a nodule (small tubercle) distally on the endopods of swimming legs 1 to 4. In addition, the unsegmented antennule of the new species is inflated and leaf-like. This form of the antennule (bulbous or D-shaped) is shared with ten known species of *Enterocola* (Table 6). Interestingly, in species with this form of antennule, the body is small (mostly less than 1.0 mm long), and the laterodistal setae on the endopods of swimming legs are shorter than endopodal segments but as long as or longer than the mediodistal setae. Six of those species (*E. parapterophorus*, *E. dicaudatus*, *E. quadrisetus* **sp. nov.**, *E. mabulensis* **sp. nov.**, *E. parvus* **sp. nov.**, and *E. neocaledonicus* **sp. nov.**) can be eliminated from further comparison because they have fewer than 6 setae on the antenna (cf. 6 setae in *E. nodulosus* **sp. nov.**), or 1 or 2 dorsal tubercles or processes on the cephalosome or pedigerous somites (cf. lacking in *E. nodulosus* **sp. nov.**).

The remaining four species (*E. mammiferus*, *E. pterophorus*, *E. robustus* **sp. nov.**, and *E. angustus* **sp. nov.**) can be distinguished from the new species as follows: in *E. mammiferus* the caudal rami are wider than long (cf. about 2.6 times longer than wide in *E. nodulosus* **sp. nov.**), the antennule is armed with 4 setae (cf. 5 setae), the 6 setae on the antenna are subequal in length (cf. setae unequal), and the 2 distal setae on the endopods of legs 1-4 are almost equal in length, as described or illustrated by Ooishi (2010b). In *E. pterophorus* (as redescribed above), the ventral interpodal protrusion is absent on the pedigerous somites (cf. present, large in second to fourth pedigerous somites of *E. nodulosus* **sp. nov.**), the lateral seta (seta VI) of the antenna is 34 μm long, distinctly shorter than that of *E. nodulosus* **sp. nov.** (cf. 64 μm long), the labral palp is less expanded, and the mediodistal element of the proximal maxillary segment is articulated at base and simple, not bifurcate. In *E. robustus* **sp. nov.** the antennule is armed with 3 setae (cf. 5 setae in *E. nodulosus* **sp. nov.**), the mediodistal element of the proximal maxillary segment is simple, not bifurcate, the setae on the antenna are shorter, the longest lateral seta (seta VI) is only 22 μm long (cf. 64 μm long), and the distal setae on the endopods of legs 1-4 are distinctly shorter than endopodal segments (cf. the setae

are equal or subequal in length to endopodal segments in *E. nodulosus* **sp. nov.**). Finally, in *E. angustus* **sp. nov.** the caudal rami are strongly tapering and about 1.9 times longer than wide (cf. about 2.6 times longer than wide in *E. nodulosus* **sp. nov.**), the longest lateral seta (seta VI) of the antenna is 29  $\mu\text{m}$  long (cf. 64  $\mu\text{m}$  long), the ventral interpodal protrusions on pedigerous somites are obscure, weakly developed (cf. large and well developed), and the distal setae on the endopods of legs 1-4 are distinctly shorter than endopodal segment (cf. as long as or longer).

***Enterocola oligosetosus* sp. nov.**

(Figs. 155, 156)

**Type material.** Holotype ♀ (MNHN-IU-2014-21564), 3 ♀♀ paratypes (MNHN-IU-2014-21565), and 1 ♀ paratype (dissected, MNHN-IU-2014-21478) from *Didemnum* sp.; Guadeloupe, Îlet aux Pigeons, Stn 20, depth 5-12 m, Monniot coll., 27 December 1980.

**Etymology.** The name of the new species refers to the presence of a single seta on the endopod of leg 4.

**Description of female.** Body (Fig. 155A-C) eruciform, curved dorsally; body length 968  $\mu\text{m}$  in largest dissected specimen; maximum width 386  $\mu\text{m}$  (across second pedigerous somite). Cephalosome clearly defined, 168×263  $\mu\text{m}$ , distinctly narrower than trunk. Trunk inflated, unsegmented, but 4 anterior pedigerous somites defined by lateral constrictions between them; first to third pedigerous somites bearing small dorsolateral tergal folds; fourth pedigerous somite narrower than anterior pedigerous somites, bearing dorsal tergite. Ventral interpodal protrusions absent. Genitoabdomen (Fig. 155D) gradually narrowing posteriorly, 5-segmented; articulations obscure dorsally; articulation between last 2 somites incomplete. Caudal ramus (Fig. 155E) tapering, incompletely articulated from anal somite, about 1.85 times longer than wide (76×41  $\mu\text{m}$ ), blunt distally; armed with 1 weakly pinnate, dorsal seta at 70% of ramus length; seta length 44  $\mu\text{m}$ , more than half length of ramus.

Rostrum absent. Antennule (Fig. 155F) incompletely 2-segmented, about 76×40  $\mu\text{m}$ , with inflated proximal two-thirds and narrow distal third; proximal segment with convex posterior margin armed with 3 setae (1 subdistal and 2 distal); distal segment small, 11×7  $\mu\text{m}$ , rectangular, armed with 4 setae on distal margin. Antenna (Fig. 155G) elongate, about 2.7 times longer than wide (145×54  $\mu\text{m}$ ), unsegmented, and ornamented with several patches of minute spinules on concave surface; armed with 5 unequal setae, lengths of setae (medial to lateral) 19, 9, 9, 45, and 41  $\mu\text{m}$ , respectively; setae II and III small, close to each other and positioned at mediiodistal corner, both setae widely separated from seta I and setae IV and V; seta IV and V distinctly larger than other setae, originating close to each other, positioned at laterodistal corner.

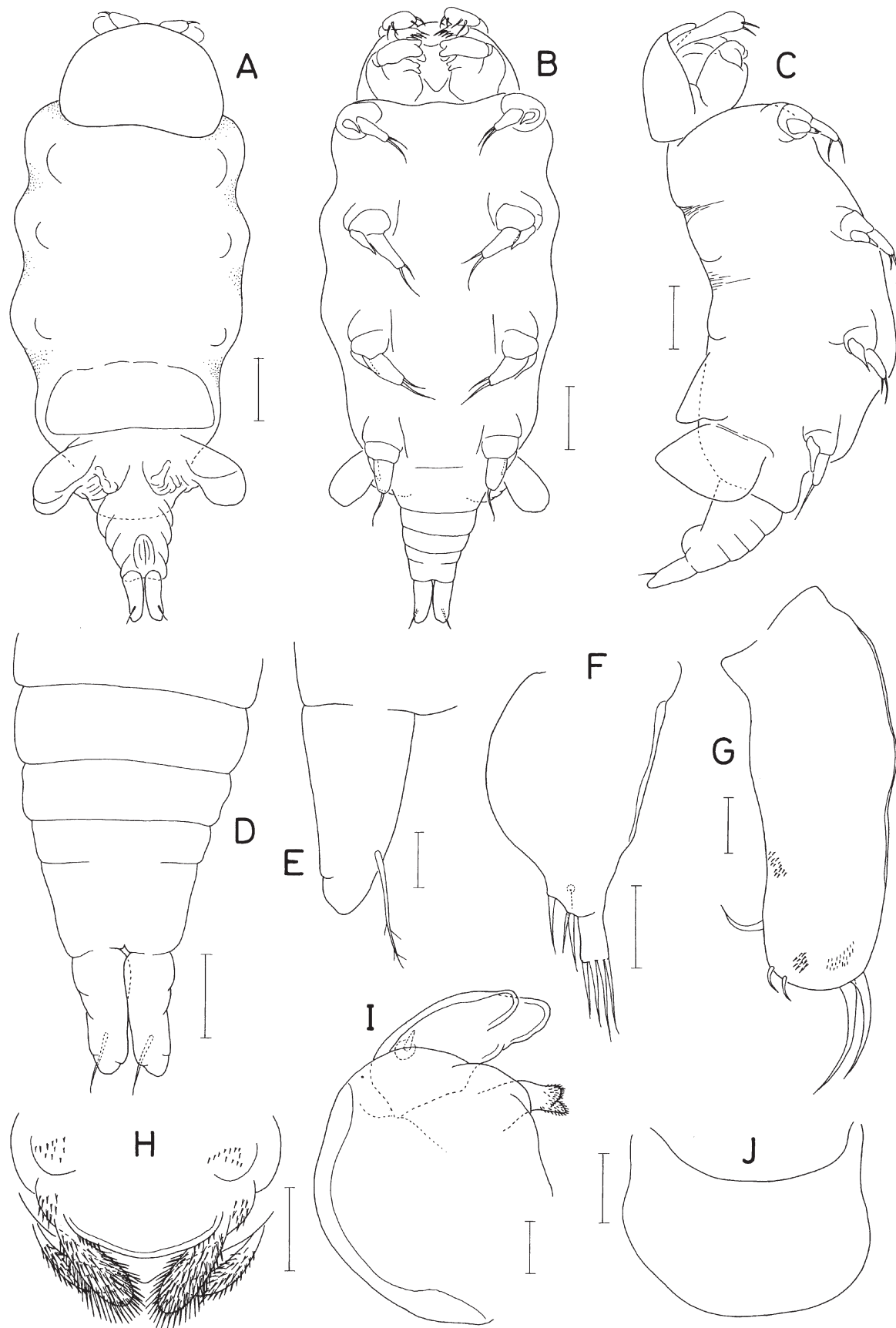
Labrum (Fig. 155H) with 2 patches of minute spinules on each side of ventral surface; palp densely spinulose, gradually expanded distally. Mandible (Fig. 155H) spinulose, about half as wide as labral palp. Maxillule consisting of precoxa (Fig. 156A) and palp (Fig. 156B); precoxa with bifurcate distal part, 1 subdistal tubercle, and endite tipped with 1 seta, (proximally plumose and distally spinulose); palp with 5 spinulose setae on distal margin and 1 naked seta on lateral margin. Maxilla (Fig. 155I) 2-segmented; proximal segment with bifurcate mediiodistal process bearing fine spinules distally; distal segment bifurcate distally, with 1 small seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each consisting of unarmed, 2-segmented protopod and unsegmented rami (Fig. 156C-E). Exopods with 3 patches of minute spinules along lateral margin. Endopods of legs 1-3 armed with 2 setae distally, but endopod of leg 4 armed with 1 seta distally (in 1 of 5 examined specimens, endopods of legs 2-4 armed with 1 seta), all setae weakly pinnate. Endopodal segments 59×30, 64×31, 64×30, and 58×33  $\mu\text{m}$ , respectively, in legs 1-4. Lengths of laterodistal and mediiodistal setae 59 and 42, 66 and 41, and 68 and 41  $\mu\text{m}$ , respectively, in legs 1-3. Length of distal seta on leg 4 endopod 68  $\mu\text{m}$ .

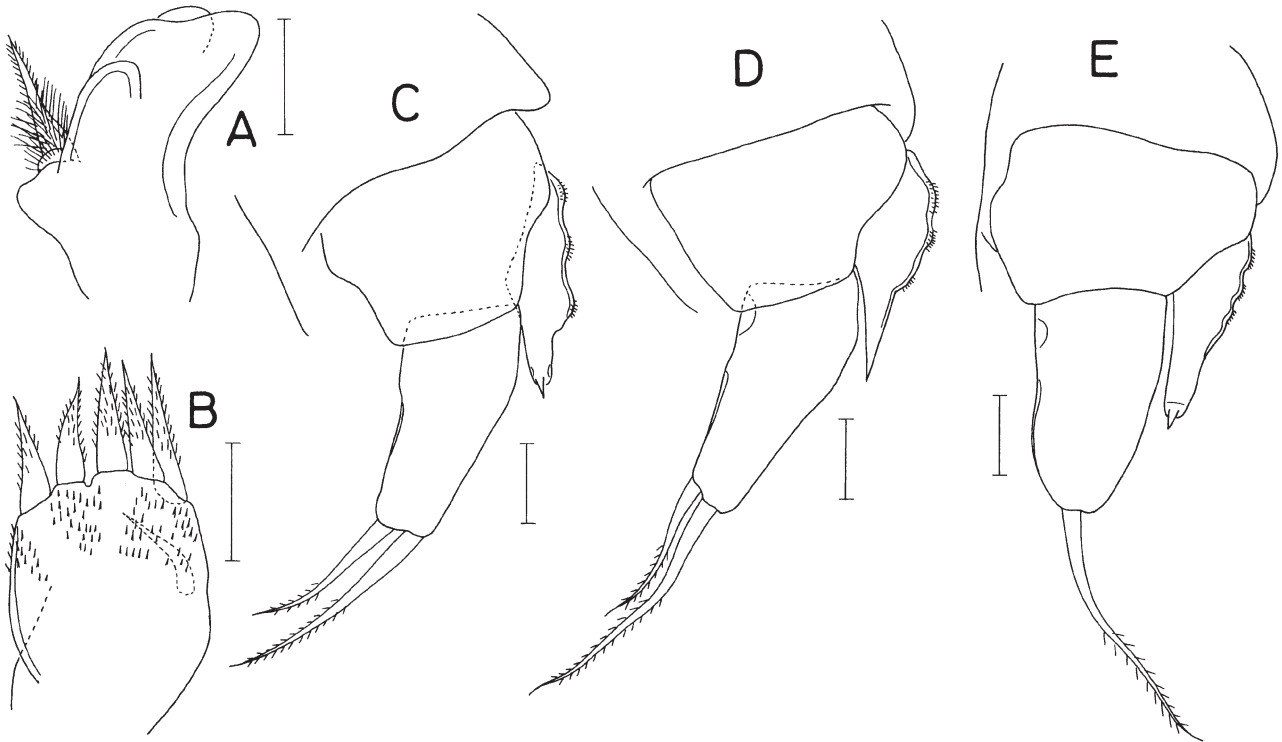
Leg 5 (Fig. 155J) unarmed, wider than long (98×180  $\mu\text{m}$ ).

**Male.** Unknown.

**Remarks.** This new species is very easily distinguishable from all of its congeners by the possession of a single seta on the endopod of leg 4. The combination of three other character states, the caudal ramus is armed with 1 seta, the antenna is elongate and armed with 5 setae, and the distal setae on the endopods of all swimming legs are pinnate, provides additional evidence supporting the establishment of the new species.



**FIG. 155.** *Enterocola oligosetosus* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, genitoabdomen, ventral; E, left caudal ramus, lateral; F, antennule; G, antenna; H, labrum and mandibles; I, maxilla; J, leg 5. Scale bars: A-C, 0.1 mm; D, J, 0.05 mm; E-I, 0.02 mm.



**FIG. 156.** *Enterocola oligosetosus* sp. nov., female. A, precoxa of maxillule; B, palp of maxillule; C, leg 1; D, leg 3; E, leg 4. Scale bars: 0.02 mm.

***Enterocola curticaudus* sp. nov.**  
(Fig. 157)

**Type material.** Holotype ♀ (MNHN-IU-2014-21566), 7 ♀♀ paratypes (MNHN-IU-2014-21567), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-21479) from *Trididemnum* sp.; Florida, United States of America, C. Young coll.

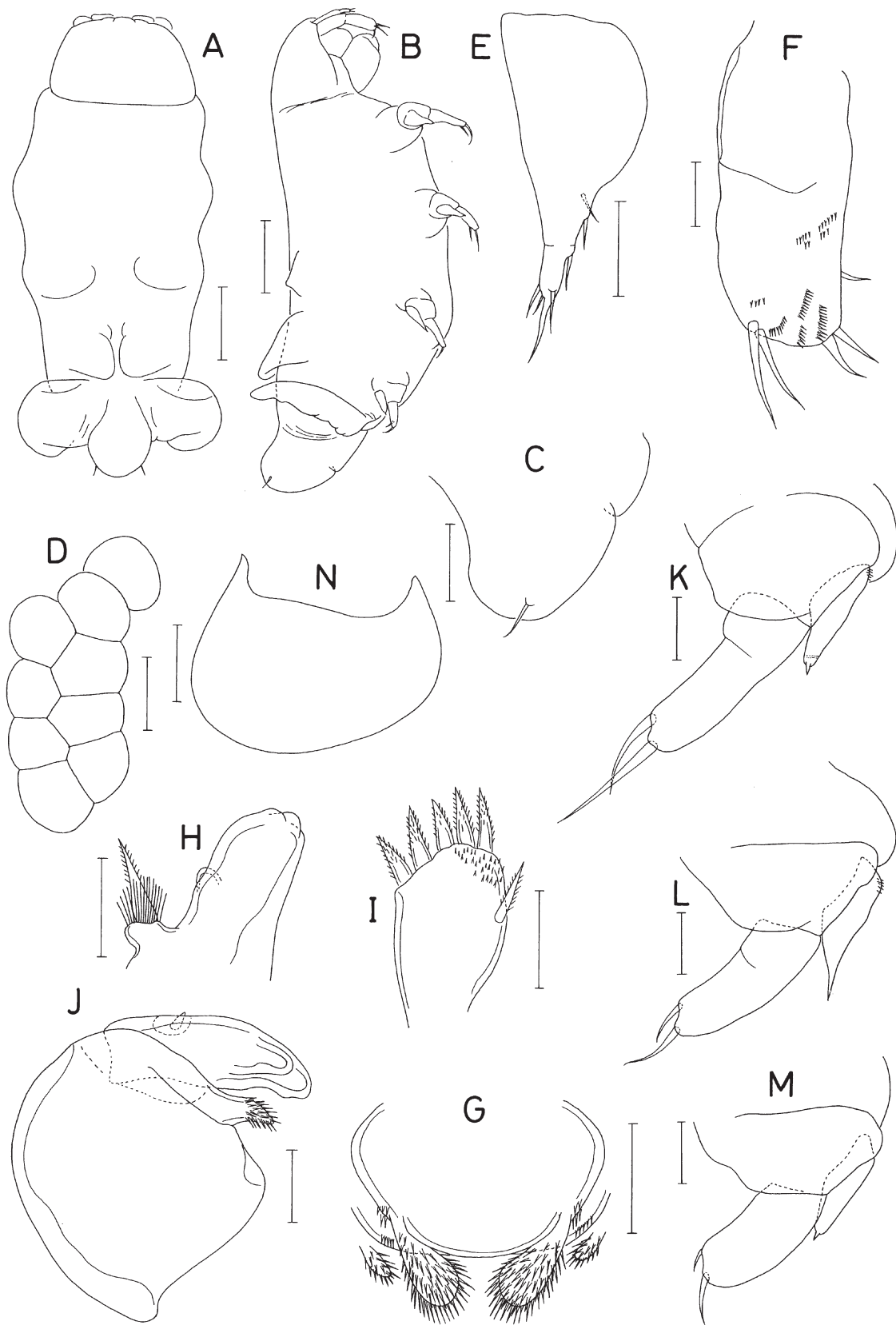
**Etymology.** The specific name of the new species is derived from Latin *curt* (=short) and *caud* (=the tail), referring to its short genitoabdomen.

**Description of female.** Body (Fig. 157A, B) eruciform, slightly curved dorsally; body length 633 µm; maximum width 275 µm (across second pedigerous somite). Cephalosome wider than long (120×200 µm), dorsally well-defined from trunk. Trunk unsegmented, with weak lateral constrictions between somites; third and fourth pedigerous somites with paired tergal folds dorsally. Ventral interpodal protrusions absent between left and right legs. Genitoabdomen (Fig. 157C) short, semicircular, unsegmented, wider than long, lacking anal prominence. Caudal rami not expressed, but pair of small caudal setae (setule-like and 22 µm long) present subdistally on lateral margins of genitoabdomen (Fig. 157C).

Rostrum absent. Antennule (Fig. 157E) obscurely 2-segmented, 60×28 µm, strongly tapering from broad proximal two-thirds towards narrow distal third; proximal segment with 2 small setae on posterior margin; distal segment narrow, about one-third as long as proximal segment, armed with 5 setae, distal seta larger than other setae, but not articulated from segment. Antenna (Fig. 157F) about 2.5 times longer than wide (100×40 µm), indistinctly 2-segmented; proximal segment unarmed; distal segment as long as proximal segment, and ornamented with several rows of minute spinules on concave surface; armed with 5 setae, lengths of setae 9, 16, 16, 28, and 33 µm, respectively; setae II and III positioned at mediiodistal corner, and setae IV and V at laterodistal corner.

Labrum (Fig. 157G) with small patch of spinules near base of palp; palp inflated distally, bulbous. Mandible (Fig. 157G) rudimentary, reduced to small digitiform process, about one-third as long as labral palp. Maxillule as usual for genus; endite of precoxa tipped with 1 spinulose seta and numerous setules (Fig. 157H); palp (Fig. 157I) with 5 spines on distal margin and 1 seta on lateral margin. Maxilla (Fig. 155J) with unarticulated, spinulose

mediodistal process on proximal segment; distal segment bluntly bifurcate and smooth distally, with 1 small seta on posterior surface. Maxilliped absent.



**FIG. 157.** *Enterocola curticaudus* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genitoabdomen, right; D, egg sac; E, antennule; F, antenna; G, labrum and mandibles; H, precox of maxillule; I, palp of maxillule; J, maxilla; K, leg 1; L, leg 3; M, leg 4; N, leg 5. Scale bars: A, B, D, 0.1 mm; C, N, 0.05 mm; E-M, 0.02 mm.



Legs 1-4 biramous, with unarmed, incompletely 2-segmented protopods (Fig. 157K-M). Exopods of legs 1-3 with patch of minute spinules proximally on lateral margin. Endopods 62×25, 57×25, 50×21, and 41×21 µm, respectively, in legs 1-4, incompletely 2-segmented in legs 1-3, but unsegmented in leg 4. Laterodistal and mediodistal setae distinctly shorter than endopodal segments, 41 and 29, 32 and 17, 22 and 15, and 18 and 6 µm, respectively, in legs 1-4, becoming shorter from anterior to posterior legs.

Leg 5 (Fig. 157N) unarmed, lamellate, wider than long (98×162 µm).

**Male.** Unknown.

**Remarks.** The absence of caudal rami is shared with only three known species of *Enterocola*, *E. monnioti*, *E. adnatus*, and *E. coniculus* but the new species can be easily differentiated from these congeners by the presence of a caudal seta, since all of these species lack caudal setae. There are additional differences: *E. monnioti* has 6 setae on the antenna (cf. 5 setae in *E. curticaudus* **sp. nov.**) and a 3-segmented endopod of leg 1 (cf. incompletely 2-segmented); *E. adnatus* has unsegmented endopods of legs 1-3 (cf. incompletely 2-segmented); and *E. coniculus* has 2 setae on the antennule (cf. 5 in *E. curticaudus* **sp. nov.**) and 6 setae on the antenna (cf. 5 setae). These differences are sufficient to distinguish the new species. The mandible of *E. curticaudus* **sp. nov.** is rudimentary, which is an unusual feature within the genus.

### *Enterocola unisetosus* **sp. nov.**

(Figs. 158, 159)

**Type material.** Holotype ♀ (MNHN-IU-2014-21568, dissected and mounted on a slide) from *Polyclinum* sp.; Saldana Bay, South Africa, Monniot coll., 02 August 1996.

**Etymology.** The name is derived from the Latin *uni* (=one) and *set* (=a bristle), referring to the presence of a single seta on the endopods of legs 1-4.

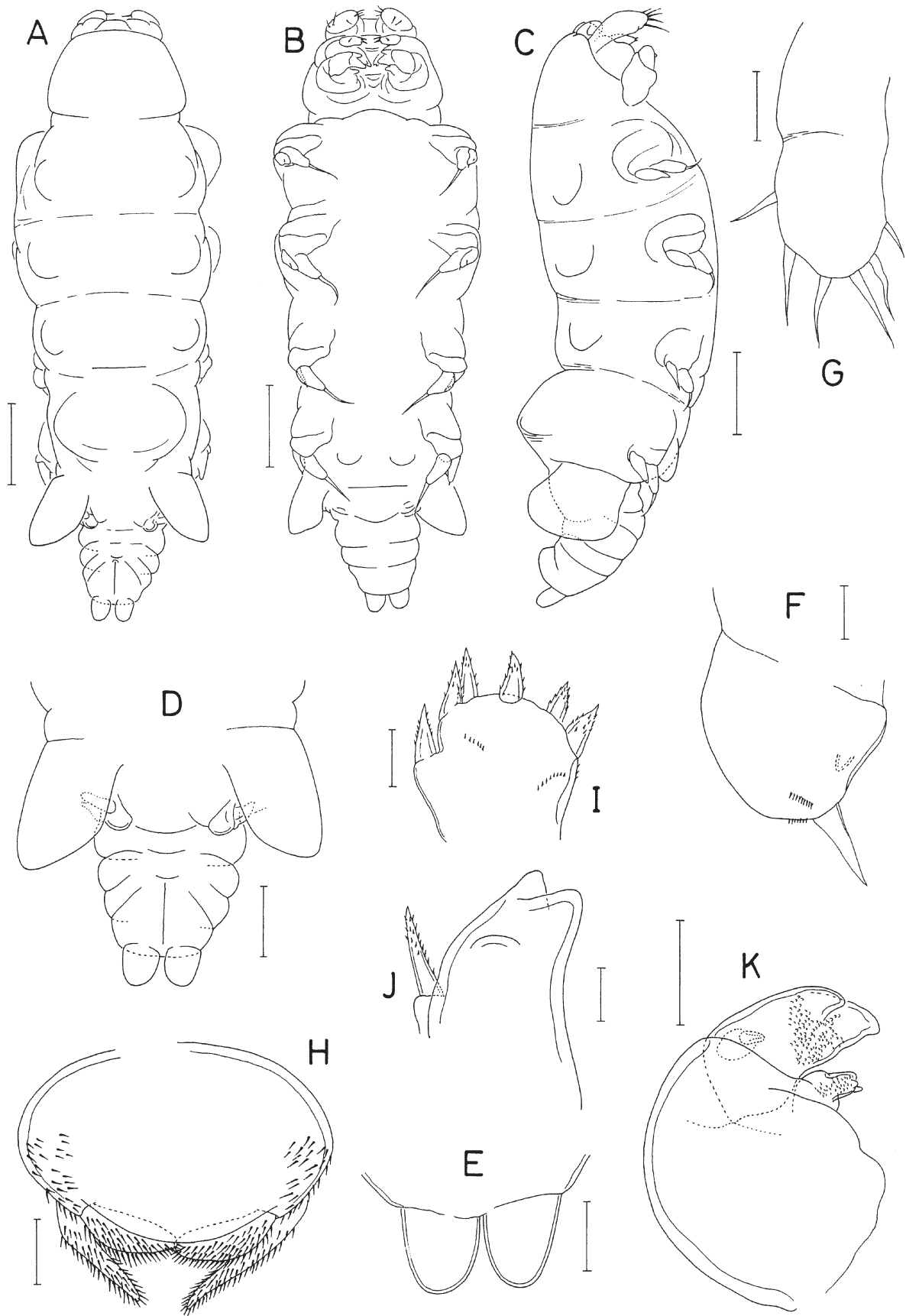
**Description of female.** Body (Fig. 158A-C) eruciform, slightly curved dorsally; body length 1.48 mm; maximum width 480 µm (across second pedigerous somite). Cephalosome 240×338 µm, distinctly narrower than trunk, indistinctly defined from trunk. Trunk unsegmented, but with faint wrinkles dorsally and laterally between somites; first to third pedigerous somites bearing small dorsolateral tergal folds. Fourth pedigerous somite produced dorsally (Fig. 158C), bearing pair of ventral interpodal protrusions (Fig. 158B). Genitoabdomen (Fig. 158D) incompletely 4-segmented; anal prominence obscure. Caudal rami (Fig. 158E) short, 1.07 times longer than wide (61×57 µm), unarmed, with rounded distal margin.

Rostrum absent. Antennule (Fig. 158F) unsegmented, semicircular, wider than long (55×72 µm), armed with 1 small tubercle in middle of posterior side and 1 broad, naked seta (32 µm long) posterodistally; and ornamented with 2 rows of minute spinules distally. Antenna (Fig. 158G) indistinctly 2-segmented; proximal segment unarmed; distal segment armed with 6 setae; lengths of setae I-VI (medial to lateral) 36, 57, 54, 59, 69, and 58 µm, respectively.

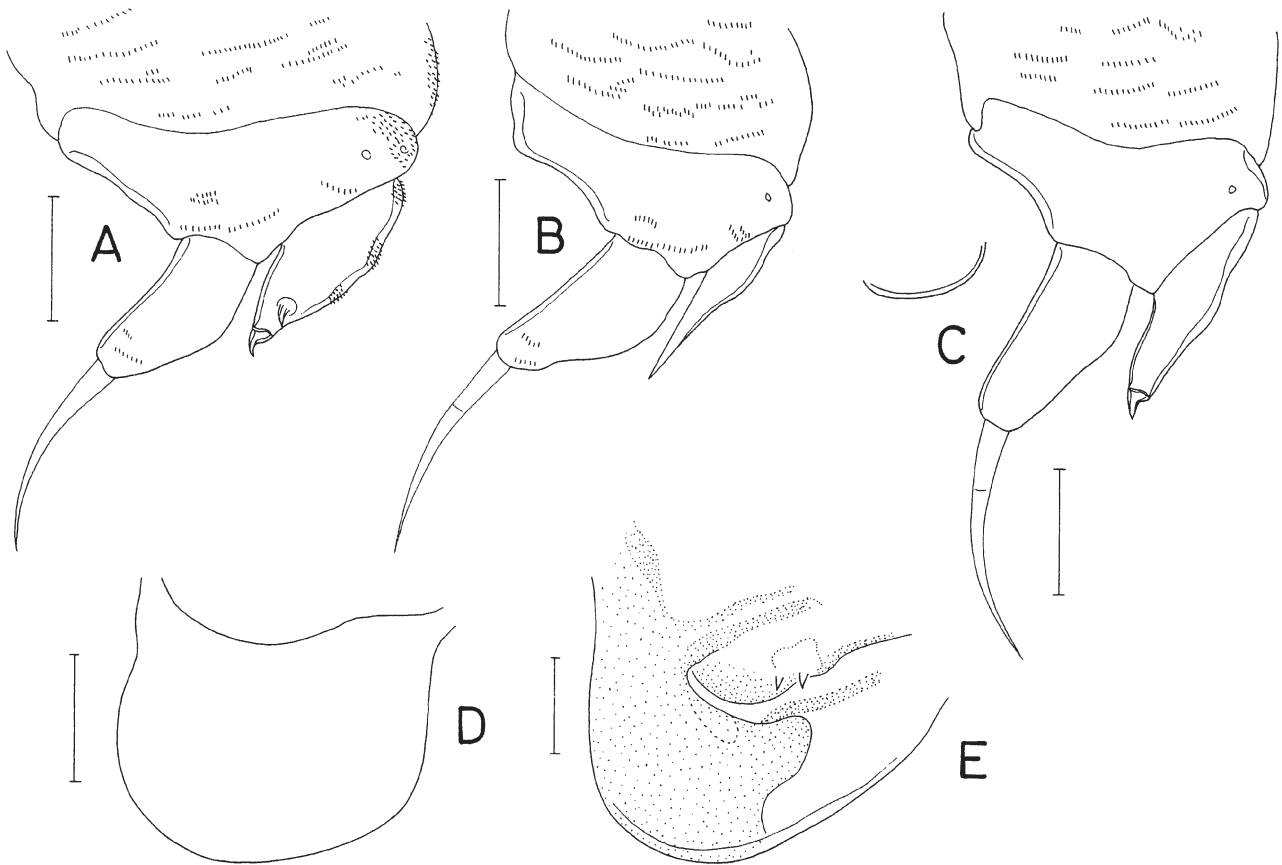
Labrum (Fig. 158H) with scattered spinules on ventrolateral surface; palp spinulose, broad, leaf-like. Mandible (Fig. 158H) spinulose, gradually narrowing distally, narrower but longer than labral palp. Maxillule consisting of precoxa (Fig. 158J) and palp (Fig. 158I); precoxa bifurcate distally, with endite bearing 1 spinulose spine (without tuft of setules or spinules); palp armed with 6 stout, subequal spines (5 on distal margin and 1 on lateral margin). Maxilla (Fig. 158K) 2-segmented; mediodistal process of proximal segment truncate, bearing 2 small tubercles distally, surface covered with granules; distal segment bifurcate distally, with numerous granules on anterior surface and 1 stout seta proximally on posterior surface. Maxilliped absent.

Legs 1-4 each consisting of unarmed, distinctly 2-segmented protopod and unsegmented rami (Fig. 159A-C); protopods ornamented with multiple rows of fine spinules on anterior surface. Exopods of leg 1 and 2 with 2 small claws (distal and subdistal) and 3 patches of minute spinules on lateral margin (Fig. 159A); exopod of leg 3 attenuated, lacking claw or spinules (Fig. 159B); exopod of leg 4 tipped with small claw (Fig. 159C). Endopods of legs 1-4 armed with single seta distally; endopodal segments about twice longer than wide, with convex lateral margin. Setae on endopods about 1.2 times longer than endopodal segment.

Leg 5 (Fig. 159D) unarmed, wider than long (172×246 µm). Leg 6 (Fig. 159E) probably represented by 2 small spinules on genital operculum.



**FIG. 158.** *Enterocola unisetosus* sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, leg 5 and genitoabdomen, dorsal; E, caudal rami; F, antennule; G, antenna; H, labrum and mandibles; I, palp of maxillule; J, precoxa of maxillule; K, maxilla. Scale bars: A-C, 0.2 mm; D, 0.1 mm; E, G, K, 0.05 mm; F, H-J, 0.02 mm.



**FIG. 159.** *Enterocola unisetosus* sp. nov., female. A, leg 1; B, leg 3, C, leg 4; D, leg 5; E, genital aperture. Scale bars: A-C, 0.05 mm; D, 0.1 mm; E, 0.02 mm.

**Male.** Unknown.

**Remarks.** *Enterocola unisetosus* sp. nov. is clearly recognizable by one striking feature: the presence of only a single seta on the endopods of swimming legs 1-4. No other species has 1 seta on all legs. In *E. oligosetosus* sp. nov. the endopod of leg 4 is armed with 1 seta, but legs 1-3 typically have 2 setae. In some other *Enterocola* species, one of the 2 distal setae on the endopods can be reduced to a minute setule-like vestige, such as in legs 3 and 4 of *E. coniculus* and *E. monnioti* (Ooishi, 2014a; Marchenkov & Boxshall, 2005), but in none of these has one of the distal setae been lost from all swimming legs, as in the new species. The leg setation of *E. unisetosus* sp. nov. seems to represent an intermediate condition between the typical *Enterocola* pattern and that of *Enterocolides*, in which the endopods of legs 3 and 4 are unarmed, as redefined in the present work.

### Genus *Enterocolides* Chatton & Harant, 1922

**Diagnosis.** Female: Body form and most morphological features as in *Enterocola*, except as follows: genitoabdomen short, unsegmented, lacking caudal rami. Palp of maxillule lacking lateral seta, or this seta vestigial. Endopods of legs 1 and 2 unarmed or armed with 2 setae distally; endopods of legs 3 and 4 unarmed.

**Type species.** *Enterocolides ecaudatus* Chatton & Harant, 1922 by original designation.

**Remarks.** Until now *Enterocolides* has remained a monotypic genus and its type species was redescribed by Illg & Dudley (1980). In its original description, Chatton & Harant (1922) separated this genus from *Enterocola* by its unsegmented abdomen, the lack of caudal rami, the lack of setae on the endopods of swimming legs, the presence of a supplementary claw on the exopods of legs 1 and 2, and by the dorsal position of the anus. Later authors (Illg & Dudley, 1980; Boxshall & Halsey, 2004) recognized the absence of setae on the endopods of the swimming legs as a key character of *Enterocolides*.

A new species *Enterocolides pacificus* sp. nov. is described below and is placed in *Enterocolides* even though it carries a pair of setae on the endopods of legs 1 and 2. It shares the lobate genitoabdomen lacking caudal rami, the reduction of the lateral seta on the maxillular palp, and the lack of setae on the endopods of legs 3 and 4, with the type species *E. ecaudatus* and, on the balance of evidence available, we therefore place the new species in *Enterocolides* rather than in *Enterocola*.

***Enterocolides pacificus* sp. nov.**

(Figs. 160-162)

**Type material.** Holotype ♀ (MNHN-IU-2014-21569), 3 ♀♀ paratypes (MNHN-IU-2014-21570) and 1 ♀ paratype (dissected, MNHN-IU-2014-21480) from *Leptoclinides* sp. (MNHN-IT-2008-4853 = MNHN A2/LEP/95); Papua New Guinea, SE Normanby Is., Cape Prevost, CRCHO 501, Site PREVOST 2 (12°06.33'S, 150°57.68'E), depth 49 m, CRRF coll., 20 January 2002.

**Additional non-type material.** 11 ♀♀ (MNHN-IU-2014-21571, 2 ♀♀ dissected) from *Atrium marsupialis* Monniot F., 1989 (MNHN-IT-2008-1347 = MNHN A2/ATR/1); New Caledonia, Grande Terre, Ilot Maitre, près de la balise, Stn NC 14, depth 6-9 m, Monniot coll., 11 September 1985; 7 ♀♀ (MNHN-IU-2014-21572, 1 ♀ dissected) from *Trididemnum* sp.; Papua New Guinea, CRCHO 491, Site DUCHEDD IS, off W Normanby I. (09°57.82'S, 150°50.73'E), depth 10 m, CRRF coll., 19 January 2002.

**Etymology.** The name of the new species reflects its distribution (Pacific Ocean), in contrast to the Mediterranean distribution of the type species.

**Description of female.** Body (Fig. 160A, B) cylindrical, unsegmented, curved dorsally. Body length 800 µm; maximum width 315 µm (across second pedigerous somite). Cephalic shield 167×256 µm, slightly narrower than trunk, with incomplete posterior margin. Trunk unsegmented; first to fourth pedigerous somites each bearing large, lamellate tergal folds dorsolaterally. Genitoabdomen (Fig. 160C) short, dorsoventrally deeper than laterally wide, unsegmented, with 2 or 3 faint wrinkles laterally; anal prominence large. Caudal rami and caudal setae absent. Egg sac (Fig. 160D) containing 4-6 eggs; each egg about 167 µm in diameter.

Rostrum absent. Antennule (Fig. 160E) elongate, unsegmented, about 2.3 times longer than wide (70×30 µm), tapering in distal half; armed with 8 small setae, 4 subdistally and 4 on apex. Antenna (Fig. 160F) about 2.0 times longer than wide (127×63 µm), 2-segmented; proximal segment unarmed, but ornamented with posterodistal patch of minute spinules; distal segment narrowing distally, armed with 4 setae (setae II-V) at apex, 1 larger than others; setae I and VI reduced to setule-like vestiges separated from large setae.

Labrum (Fig. 160G) with narrow, spinulose palps. Mandible spinulose, tapering, slightly broader than labral palp. Maxillule consisting of precoxa (Fig. 160H) and palp (Fig. 160I); precoxa bluntly trilobed distally, with endite bearing 1 naked seta and tuft of numerous thin setules; palp with 5 spinulose spines (or spiniform setae) on distal margin and 1 minute vestigial seta on lateral margin. Maxilla (Fig. 160J) 2-segmented; proximal segment with large, spinulose process mediodistally; distal segment unequally bifurcate, unarmed and unornamented. Maxilliped absent.

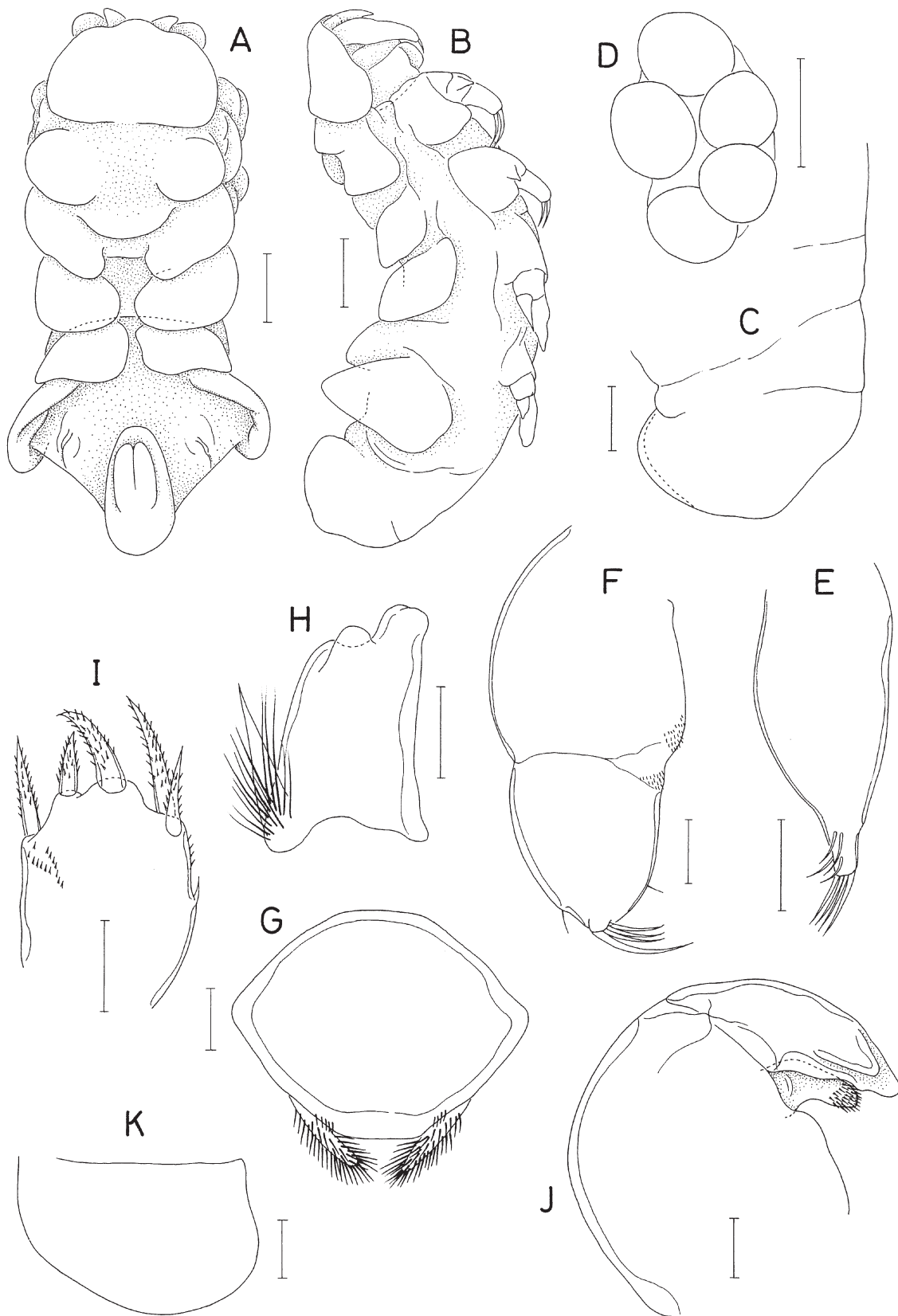
Legs 1-4 each consisting of 2-segmented, unarmed protopod and unsegmented rami (Fig. 161A-C). Exopods of legs 1, 2, and 4 small, much shorter than endopods, unarmed, triangular, pointed distally; exopod of legs 3 attenuated, with acutely pointed tip. Endopods of legs 1 and 2 twice as long as wide, armed with 2 naked setae distally; laterodistal seta 0.7 times as long as endopodal segment, but slightly longer than mediodistal seta. Endopods of legs 3 and 4 unarmed, slightly longer than wide, with rounded distal margin.

Leg 5 (Fig. 160K) lamellate, unarmed, wider than long (130×196 µm).

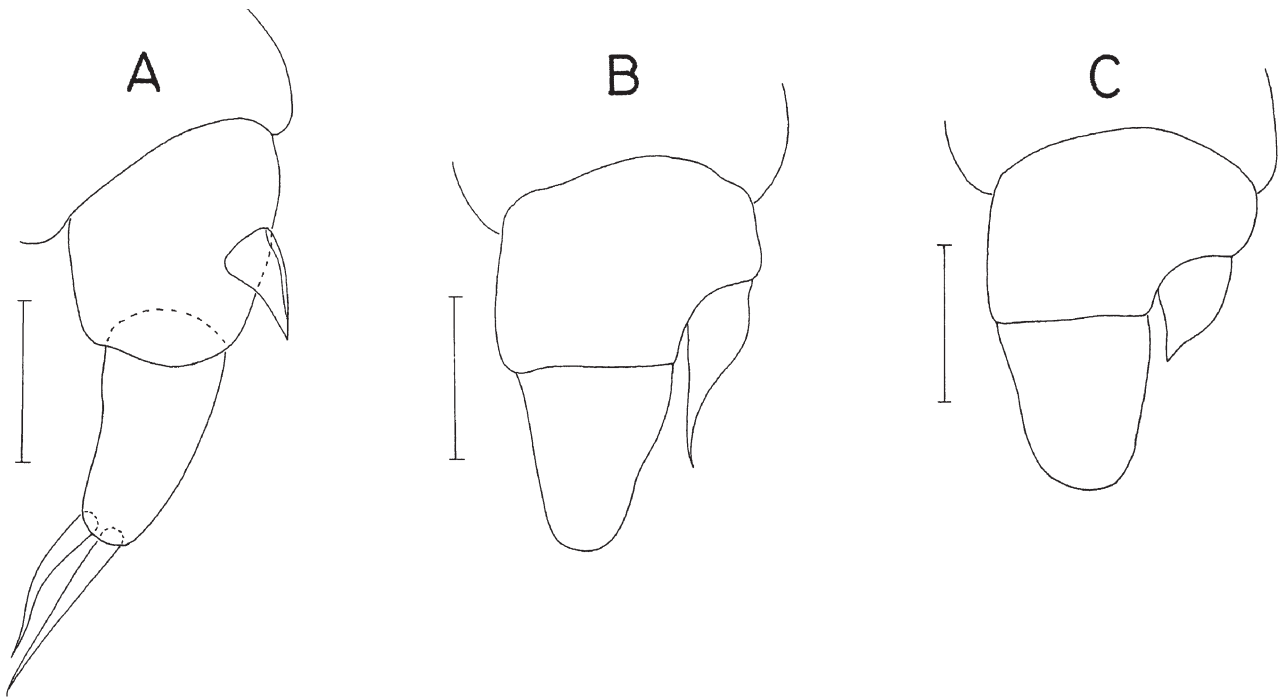
**Comparative description of female associated with *Atrium marsupialis* in New Caledonia (Fig. 162).** Body (Fig. 162A, B) inflated, fleshy; body length 1.03 mm in dissected specimen; mean body length 0.96 mm (0.82-1.11 mm, n=8); maximum width 441 µm (across second pedigerous somite). Cephalic shield much narrower than trunk, with obscure dorsal margin. Dorsolateral tergal folds less developed than those of type specimens. Egg sac containing more than 30 eggs; each egg about 140 µm in diameter, smaller than in type specimens.

Antennule (Fig. 162C) more slender than that of type specimens, armed with 8 small setae. Antenna (Fig. 162D) as that of type specimens in form and armature, but relative lengths of setae slightly different. Labrum (Fig. 162F)

ornamented with several patches of spinules on ventral surface. Mandible (Fig. 162F), maxillule (Fig. 162G, H), and maxilla (Fig. 162I) as in type specimens.



**FIG. 160.** *Enterocolides pacificus* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genitoabdomen, right; D, egg sac; E, antennule; F, antenna; G, labrum; H, precoxa of maxillule; I, palp of maxillule; J, maxilla; K, leg 5. Scale bars: A, B, 0.1 mm; C, K, 0.05 mm; D, 0.2 mm; E-J, 0.02 mm.



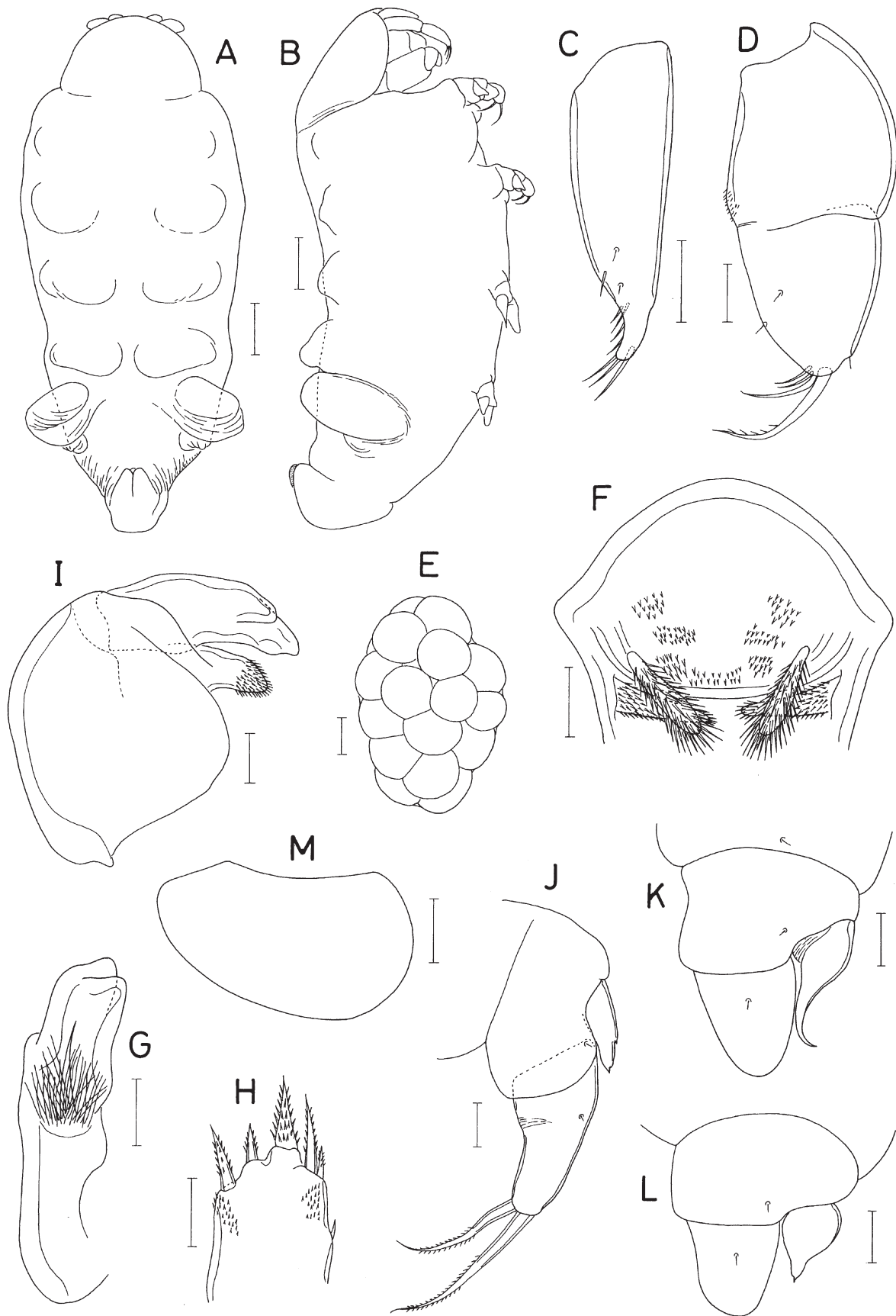
**FIG. 161.** *Enterocolides pacificus* **sp. nov.**, female. A, leg 1; B, leg 3; C, leg 4. Scale bars: 0.05 mm.

Legs 1-4 with same form and setation as in type specimens, but distal setae on endopods of legs 1 and 2 slightly longer and weakly pinnate. Leg 5 (Fig. 162M) 110×204  $\mu$ m.

**Male.** Unknown.

**Remarks.** As illustrated, the type specimens from Papua New Guinea and additional material from New Caledonia exhibit some differences in body form, in the development of the dorsolateral tergal folds on the trunk, the relative lengths of the setae on the antenna and legs 1 and 2, and in the size of the eggs. However, we infer that these differences represent infraspecific variation.

The presence of 2 setae on the endopods of legs 1 and 2 of *E. pacificus* **sp. nov.** is the most marked difference from the type species, *E. ecaudatus*, which lacks endopodal setae on all legs. Other differences include: the presence of well-developed dorsolateral tergal folds on the first to fourth pedigerous somites (cf. these tergal folds lacking in *E. ecaudatus*), the antennule is armed with 8 setae (cf. 2 setae and several spinules in *E. ecaudatus*, according to illustration in Illg & Dudley, 1980), the antenna is 2-segmented and armed with 4 naked setae plus 2 setule-like vestiges (cf. unsegmented and armed with 6 spinulose setae in *E. ecaudatus*), the distal margin of the maxillular palp is armed with 5 setae (cf. 4 setae in *E. ecaudatus*), the lateral margin of the exopods of legs 1, 2, and 4 is smooth (cf. ornamented with a cusp and spinules in *E. ecaudatus*), the distal segment of the maxilla is distally bifurcate and lacks a proximal seta (cf. simple, but with a proximal seta in *E. ecaudatus*), and leg 5 is wider than long and unarmed (cf. longer than wide and armed with a pair of small setae in *E. ecaudatus*).



**FIG. 162.** *Enterocolides pacificus* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, antennule; D, antenna; E, egg sac; F, labrum and mandibles; G, precoxa of maxillule; H, palp of maxillule; I, maxilla; J, leg 1; K, leg 3; L, leg 4; M, leg 5. Scale bars: A, B, E, 0.1 mm; C, D, F-L, 0.02 mm; M, 0.05 mm.

***Enterocolides elongatus* sp. nov.**

(Figs. 163, 164)

**Type material.** Holotype ♀ (MNHN-IU-2014-21573, dissected and mounted on a slide) from *Distaplia* sp.; Red Sea coast of Israel, 1962.

**Etymology.** The name of the new species refers to its elongate body.

**Description of female.** Body (Fig. 163A-C) vermiform, cylindrical, curved dorsally; body length 1.58 mm; maximum width 292 µm (across fourth pedigerous somite). Cephalosome wider than long (154×192 µm), narrower than trunk, indistinctly articulated from trunk. Trunk unsegmented, gradually broadening posteriorly; first to fourth pedigerous somites defined from one another by weak lateral constrictions, each somite with pair of distinct tergal folds dorsolaterally (Fig. 163A) and pair of large, lobate ventral protrusions (Fig. 163B). First and second pedigerous somites ornamented with rows of minute spinules on dorsal surface (Fig. 163A). Genitoabdomen short, slightly longer than wide, unsegmented, not articulated from trunk, with copulatory pore ventrally and small anal prominence dorsally. Caudal rami very small, widely separated from each other; each ramus (Fig. 163D) about 1.8 times longer than wide (33×18 µm), unarmed, with parallel lateral margins and rounded distal margin.

Rostrum not developed. Antennule (Fig. 163E) tapering, about 65 µm long, incompletely 3-segmented, not articulated at base, but with sclerotized band at base; first segment with 1 small seta anterodistally and several blunt spinules in middle; second segment short with 2 setae on anterior margin; third segment with 5 setae, largest terminal seta process-like, not articulated at base. Antenna (Fig. 163F) lamellate, unsegmented, longer than wide, and ornamented with scattered rows of minute spinules on anterior and posterior surfaces; armed with 5 naked setae (4 distal and 1 subdistal).

Labrum (Fig. 163G) with convex posterior margin, ornamented with 3 groups of minute spinules on each side of ventral surface; with pair of narrow, spinulose palps. Mandible small, similar to labral palp. Maxillule (Fig. 163H) biramous, consisting of precoxa and palp; precoxa (Fig. 163I) terminating in spiniform process, with endite tipped with 1 spinulose spine and several spinules encircling spine, and armed with 2 spinulose spines near base of process; palp (Fig. 163J) bearing 4 spinulose spines on distal margin and 1 slender, naked seta on lateral margin. Maxilla (Fig. 163K) 2-segmented; proximal segment with strongly projecting mediobasal corner tipped with robust, spinulose spine; distal segment armed with 2 naked spines (1 distal and 1 subdistal) and 1 strong naked seta on posterior surface. Maxilliped absent.

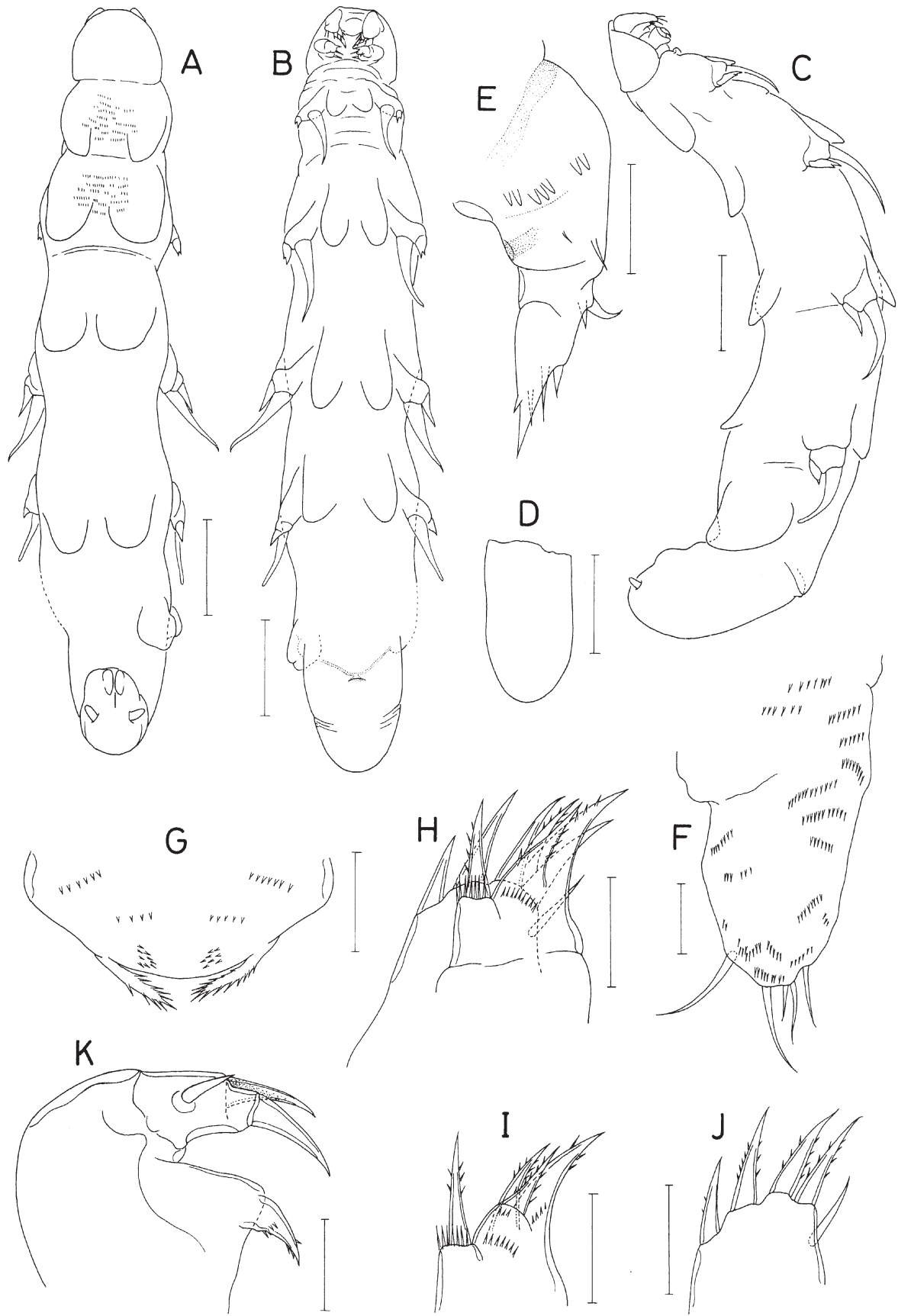
Legs 1-4 (Fig. 164A-D) each consisting of unarmed 2-segmented protopod and unsegmented rami. Proximal segment (coxa) of protopod short, indistinct, ornamented with several rows of minute spinules. Exopods of legs 1 and 2 terminating in spiniform process and 1 small, claw-like spine subdistally on lateral margin. Lengths of exopods 40, 45, 58, and 38 µm, respectively, in legs 1-4; exopod of leg 3 (Fig. 164C) attenuated, acutely pointed distally; exopod of leg 4 tipped with 1 small spine (Fig. 164D). Endopods of legs 1-4 as large, flattened, laterally curved, tapering element, sclerotized along medial margin, acutely pointed distally in legs 1-3, but with blunt tip in leg 4. Sizes of endopods 102×29, 173×33, 179×38, and 147×36 µm, respectively, in legs 1-4.

Leg 5 (Fig. 164E) lamellate, wider than long, with obliquely rounded ventral margin and straight dorsal margin; armed with 2 minute, almost invisible setae.

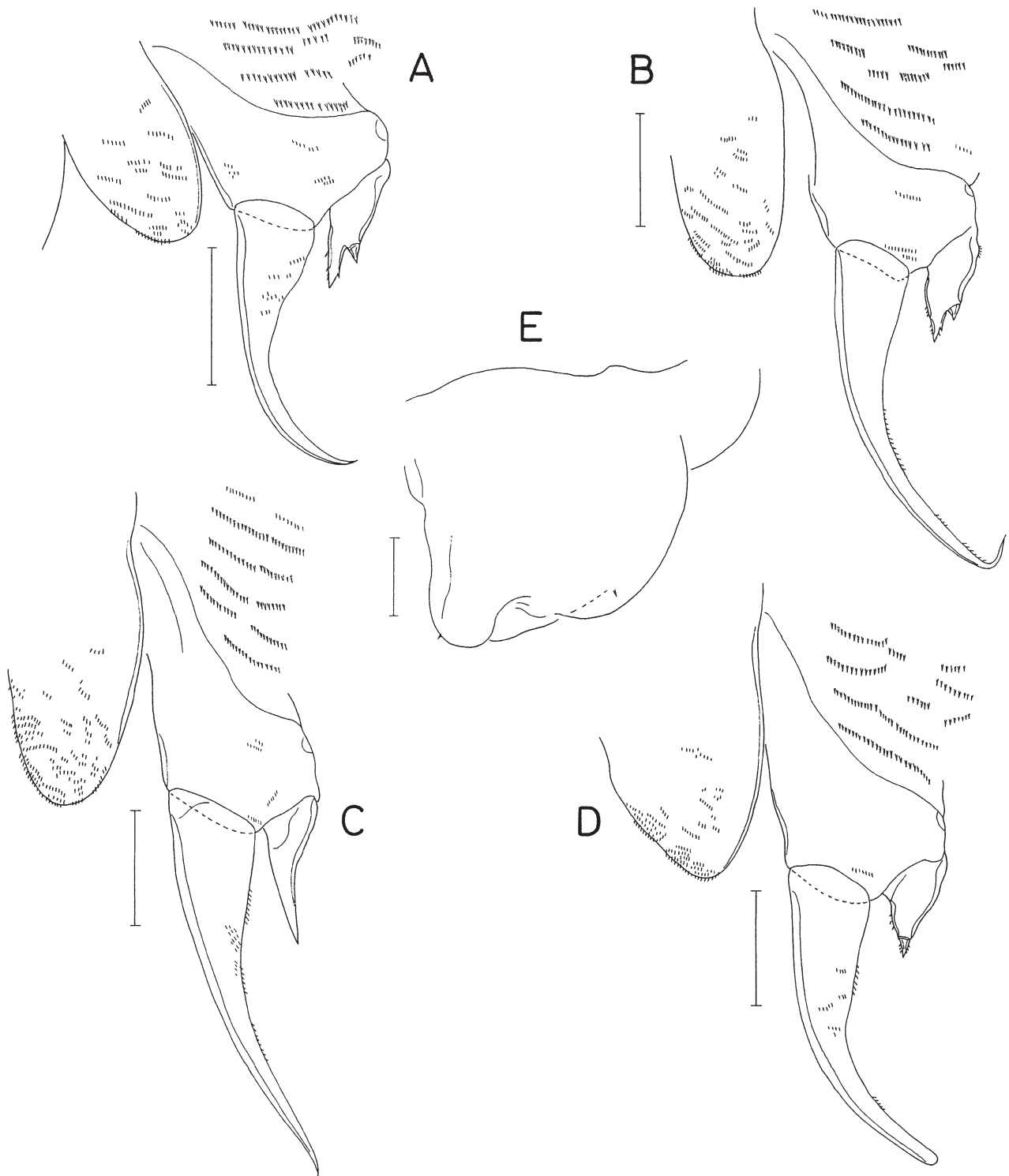
**Male.** Unknown.

**Remarks.** In the possession of distinct rami on the swimming legs, the lamellate antenna and leg 5, and the labrum bearing a pair of palps, *Enterocolides elongatus* sp. nov. belongs to the *Enterocola-Enterocolides-Lequerrea* lineage. Within this small cluster of genera, the new species is included in *Enterocolides* due to the presence of both antennules and antennae, and to the possession of unarmed endopods on swimming legs 1-4. However, the new species differs markedly from its two congeners, *E. ecaudatus* and *E. pacificus* sp. nov. as follows: the endopods of the swimming legs are attenuated and extremely elongated, caudal rami are present (although very small), the first to fourth pedigerous somites bear dorsal tergal folds and ventral interpodal protrusions, and the precoxa of the maxillule and distal segment of the maxilla are armed with spines or spiniform processes. The relatively plesiomorphic condition of the maxillule and maxilla, and the apomorphic state of the swimming legs are the most notable characters defining the new species, but it is clear that the relationships between these genera are in need of further analysis, perhaps when males become known.





**FIG. 163.** *Enterocolides elongatus* sp. nov., female. A, habitus, dorsal (left leg 5 damaged); B, habitus, ventral; C, habitus, right; D, caudal ramus; E, antennule; F, antenna; G, labrum; H, maxillule; I, precoxa of maxillule; J, palp of maxillule; K, maxilla. Scale bars: A-C, 0.2 mm; D-K, 0.02 mm.



**FIG. 164.** *Enterocolides elongatus* sp. nov., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars: 0.05 mm.

***Monniotocopa* gen. nov.**

**Diagnosis.** Female: Body eruciform or vermiform, weakly segmented, consisting of cephalosome, trunk incorporating first to fifth pedigerous somites, and genitoabdomen. Dorsal tergites indistinct or well-developed on first to fourth pedigerous somites. Anal somite bearing distinct anal prominence. Caudal rami broad, flattened, armed with 1 major and several vestigial setae. Rostrum present. Antennule small, 2- to 4-segmented, armed with small setae.

Antenna digitiform, 3- or 4-segmented, unarmed, or almost unarmed. Labrum simple, lacking palps. Mandible modified as powerful claw. Maxillule bilobed; inner lobe (precoxal endite) armed with 0 to 2 setae (or spines) on apex; outer lobe (palp) armed with 1 apical seta. Maxilla bilobate or unilobate, with unsegmented syncoxa; when bilobate, inner lobe (endite of syncoxa) tipped with 1 seta, and outer lobe (basis) armed with 3 setae. Maxilliped absent. Legs 1-4 biramous, each with 2-segmented protopod: coxa unarmed, but expanded and flattened in some species; basis unarmed or armed with outer seta and mediobasal seta in leg 1. Exopods unsegmented or 2-segmented in legs 3 and 4, apically tipped with 1 small claw, and in some species armed with 2 setae on lateral margin. Exopod of leg 3 armed additionally with 1 large spine on lateral margin. Endopods armed distally with 2 setae. Leg 5 lamellate, armed with 2 or 4 minute setae.

Male: unknown.

**Type species.** *Monnioticopa prima* **gen. et sp. nov.** by original designation.

**Etymology.** The new genus is named in honour of Dr. Françoise Monniot, who made it possible for us to study the copepod material she and Claude Monniot collected. Gender feminine.

**Remarks.** *Monnioticopa* **gen. nov.** can be readily differentiated from existing genera in the family Enteropsidae by the following apomorphic character states: (1) the mandible is represented by a strong claw; (2) the antenna is digitiform, 3- or 4-segmented, and unarmed or almost unarmed; (3) the labrum lacks palps (or any processes); and (4) the caudal rami are broad and armed with 1 major plus several vestigial setae. Within the family, *Monnioticopa* **gen. nov.** is most closely related to *Enterocola* with which it shares the possession of biramous swimming legs armed with a pair of setae on the endopods, and the lamellate fifth leg. However, the four apomorphic features of *Monnioticopa* **gen. nov.** listed above are highly significant and ensure that the new genus cannot be confused with *Enterocola* (or any other genera in the Enteropsidae).

#### Key to species of *Monnioticopa* **gen. nov.**

1. Inner lobe of maxillule armed with 2 spines; maxilla unilobate; exopods of legs 1 and 2 armed with claw plus 2 setae. . . . . *M. planicoxa* **gen. et sp. nov.**
2. Inner lobe of maxillule unarmed or armed with 1 seta; maxilla bilobate; exopods of legs 1 and 2 armed with distal claw . . . . . 2
3. Inner lobe of maxillule unarmed; coxae of legs 1-4 with large mediobasal projection . . . . . *M. firma* **gen. et sp. nov.**
4. Inner lobe of maxillule tipped with 1 seta; coxae of legs 1-4 lacking mediobasal projection. . . . . 3
5. Legs 1-4 exopods 2-segmented; first antennular segment with 1 seta; leg 5 proximally narrowed . . . . . *M. minuta* **gen. et sp. nov.**
6. Legs 1-4 exopods 1-segmented; first antennular segment with 2 or more setae; leg 5 not proximally narrowed. . . . . 4
7. First antennular segment with 2 setae; first segment of antenna the longest; all setae on outer lobe of maxilla not transformed . . . . . *M. prima* **gen. et sp. nov.**
8. First antennular segment with 4 setae; terminal segment of antenna the longest; 2 distal setae on outer lobe of maxilla sigmoid . . . . . *M. manadoensis* **gen. et sp. nov.**

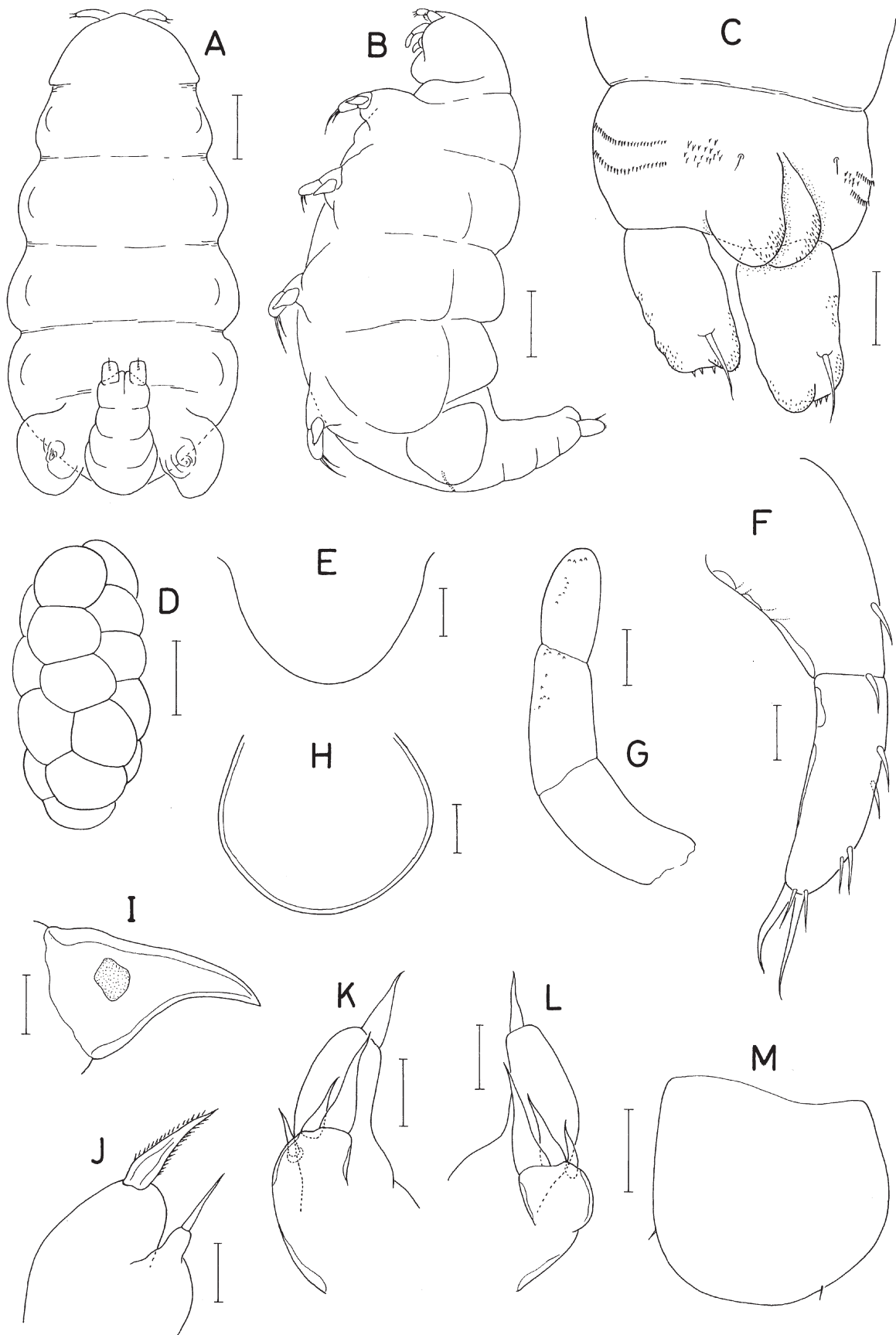
#### *Monnioticopa prima* **gen. et sp. nov.**

(Figs. 165, 166)

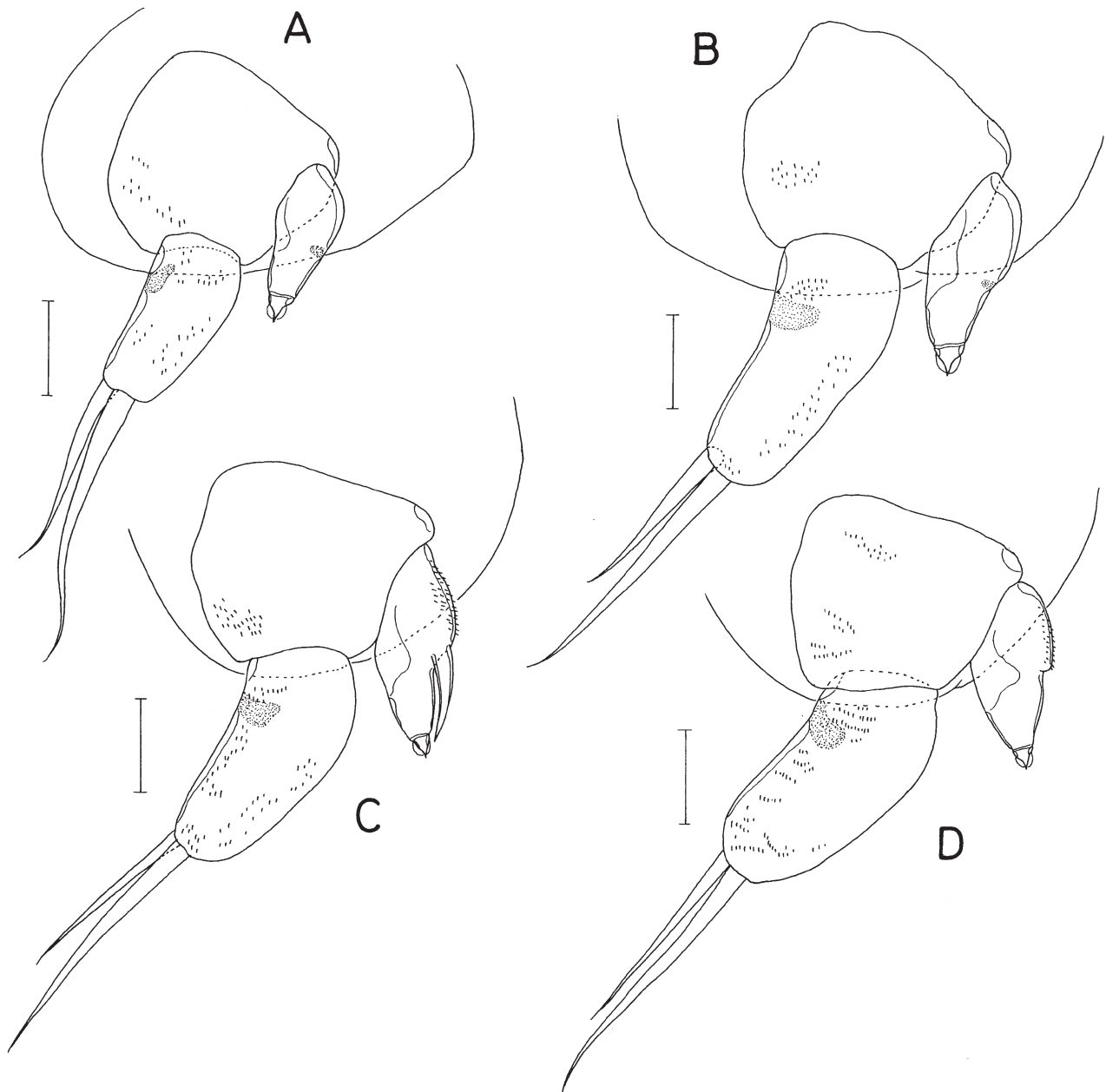
**Type material.** Holotype ♀ (MNHN-IU-2014-21574), 2 ♀♀ paratypes (MNHN-IU-2014-21575), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-21481) from *Cystodytes* sp. (MNHN-IT-2008-2621 = MNHN A3/CYS/135); The Philippines, OCDN 5119-X, (09°31.02'N, 123°40.83'E), depth 10 m, CRRF coll., 15 April 1997.

**Etymology.** The name is derived from the Latin *prim* (=first), indicating that it is first described species in the genus.

**Description of female.** Body (Fig. 165A, B) eruciform, stout; body length 916 µm; maximum width 364 µm (across third pedigerous somite). Cephalosome short, twice as wide as long (113×236 µm), not articulated from trunk, but defined by lateral constrictions. Trunk gradually broadening posteriorly; first to fourth pedigerous somites defined from one another by lateral constrictions and wrinkles; each somite with small, weak dorsolateral tergal folds (Fig. 165A), but lacking ventral interpodal protrusions. Fifth pedigerous somite completely fused with fourth. Genitoabdomen directed dorsally, indistinctly segmented dorsally, but distinctly 4-segmented ventrally. Anal somite



**FIG. 165.** *Monnoticopa prima* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, left; C, anal somite and caudal rami, dorsal; D, egg sac; E, rostrum; F, antennule; G, antenna; H, labrum; I, mandible; J, maxillule; K, L, maxillae; M, leg 5. Scale bars: A, B, D, 0.1 mm; C, 0.02 mm; E-L, 0.01 mm; M, 0.05 mm.



**FIG. 166.** *Monnioticopa prima* gen. et sp. nov., female. A, leg 1; B, leg 2; C, leg 3; D, leg 4. Scale bars: 0.02 mm.

(Fig. 165C) ornamented with 2 to 4 transverse rows of minute spinules on lateral surfaces and patch of minute spinules on each side of anal prominence; anal prominence large, bilobed, with patch of minute spinules near apex of lobes. Caudal ramus (Fig. 165C) rectangular, about 1.5 times longer than wide ( $44 \times 30 \mu\text{m}$ ), with rounded mediolateral protrusion, and ornamented with numerous minute spinules on surfaces of distal two-thirds of ramus; armed with 1 prominent dorsal seta ( $17 \mu\text{m}$  long) at 70% of ramus length and 3 minute, spinule-like setae on distal margin. Egg sac (Fig. 165D)  $396 \times 189 \mu\text{m}$ , fusiform; each egg about  $100 \mu\text{m}$  in diameter.

Rostrum (Fig. 165E) well-developed, semicircular, unornamented. Antennule (Fig. 165F)  $79 \mu\text{m}$  long, narrow, 2-segmented; proximal segment armed with 2 small setae; distal segment slightly longer than proximal segment, armed with 8 setae (4 on anterior margin and 4 on apex), 2 of distal setae distinctly larger than other setae, longest  $20 \mu\text{m}$  long. Antenna (Fig. 165G)  $65 \times 13 \mu\text{m}$ , elongate, digitiform, 3-segmented, unarmed, but ornamented with few minute granules on 2 distal segments; lengths of first to third segments 25, 21, and  $19 \mu\text{m}$ , respectively; third segment blunt with rounded apex.

Labrum (Fig. 165H) simple, subcircular, lacking palp, unornamented. Mandible (Fig. 165I) as massive claw,  $37 \times 24 \mu\text{m}$ , tapering, sclerotized, slightly curved, with subcircular unsclerotized region proximally. Maxillule (Fig.

165J) bilobed; larger inner lobe tipped with broad, spinulose seta; small outer lobe tipped with small, naked seta. Maxilla (Fig. 165K, L) bilobate; longer inner lobe (endite of syncoxa) tipped with 1 broad, naked seta; shorter outer lobe armed with 3 broad, naked setae (2 distal and 1 subdistal) of unequal sizes. Maxilliped absent.

Legs 1-4 (Fig. 166A-D) each consisting of unarmed 2-segmented protopod and unsegmented rami; coxa expanded, plate-like; basis with patches of minute spinules on medial side of anterior surface. Exopods shorter than endopods, tipped with 1 claw-like element and circular membranous element. Exopod of leg 3 armed with 1 elongate, acute spine originating in middle of lateral margin and extending to apex of ramus; exopod of leg 4 with small notch in middle of lateral margin. Endopods armed with 2 naked setae distally and with unsclerotized region at proximal third of medial side. Sizes of endopods  $38 \times 19$ ,  $57 \times 27$ ,  $64 \times 31$ , and  $67 \times 33$   $\mu\text{m}$ , respectively, in legs 1-4. Lengths of laterodistal and mediobasal setae of endopods 62 and 44, 59 and 40, 72 and 50, and 77 and 57  $\mu\text{m}$ , respectively, in legs 1-4.

Leg 5 (Fig. 165M) lamellate, subcircular,  $134 \times 138$   $\mu\text{m}$ , with 2 minute vestigial setae; separated by distance of 100  $\mu\text{m}$ .

**Male.** Unknown.

**Remarks.** The two dissected paratypes revealed no noticeable variation, except in the ornamentation of the anal somite, with 2 transverse rows of minute spinules on lateral surfaces in one specimen, but 4 rows of spinules in another.

***Monnioticopa minuta* gen. et sp. nov.**

(Figs. 167, 168)

**Type material.** Holotype ♀ (MNHN-IU-2014-21576) and paratype ♀ (dissected, MNHN-IU-2014-21482) from *Lissoclinum badium* Monniot F. & Monniot C., 1996 (MNHN-IT-2008-4913); Papua New Guinea, N tip of Normanby I., pinnacle W of Observation Point, CRCHO 516, ( $09^{\circ}44.59'S$ ,  $150^{\circ}43.01'E$ ), depth 36 m, CRRF coll., 16 January 2002.

**Etymology.** The name of the new species refers to its relatively small body.

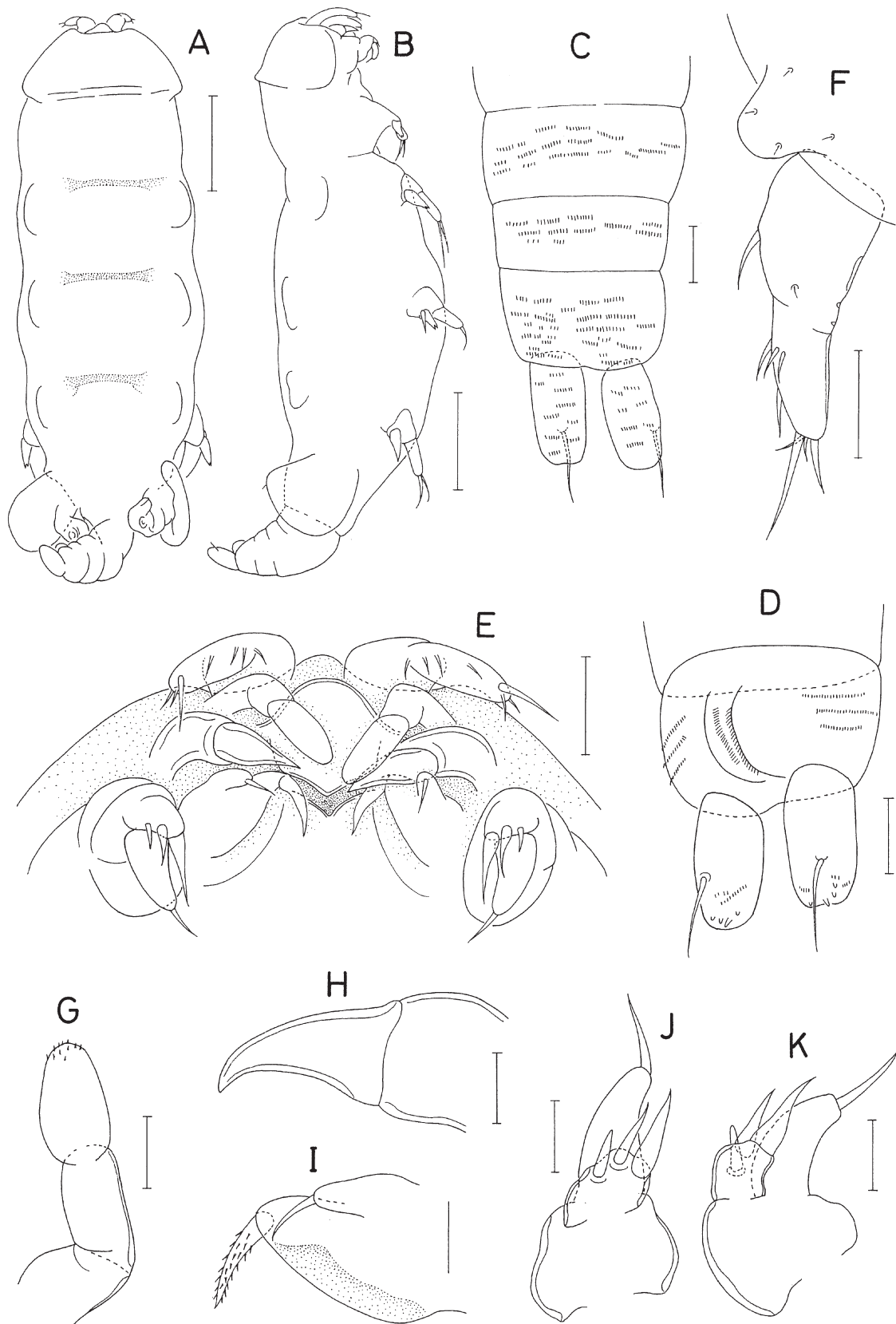
**Description of female.** Body (Fig. 167A, B) relatively small; body length 636  $\mu\text{m}$ ; maximum width 192  $\mu\text{m}$  (across third pedigerous somite). Cephalic shield short, more than twice as wide as long ( $74 \times 164$   $\mu\text{m}$ ), with indistinct posterodorsal margin. Trunk unsegmented with 3 faint transverse sclerotization bands between 4 anterior pedigerous somites; second to fourth pedigerous somites bearing weak tergal folds dorsolaterally, but without ventral interpodal protrusions; fifth pedigerous somite narrower than anterior part of trunk. Genitoabdomen (Fig. 167C) 4-segmented; 3 free abdominal somites  $25 \times 58$ ,  $22 \times 50$ , and  $28 \times 47$   $\mu\text{m}$ , respectively, ornamented with many rows of minute spinules on ventral surface. Anal somite with 3 transverse rows of minute spinules on lateral surfaces; anal prominence distinct, with longitudinal row of minute spinules on each lobe. Caudal ramus (Fig. 167D) nearly rectangular, nearly twice as long as wide ( $37 \times 19$   $\mu\text{m}$ ); ornamented with transverse rows of minute spinules on ventral surface; armed with 1 dorsal seta (25  $\mu\text{m}$  long) at 65% of ramus length, and 4 wart-like, rudimentary setae subdistally on dorsal margin.

Rostrum (Fig. 167F) small, semicircular, bearing pairs of sensilla subdistally and proximally. Antennule (Fig. 167F) 51  $\mu\text{m}$  long, incompletely 2-segmented; proximal segment armed with 1 seta on anterior margin; distal segment narrower and slightly shorter than proximal segment, armed with 8 setae grouped as 3, 1, and distal 4. Antenna (Fig. 167G) elongate, about 42  $\mu\text{m}$  long, digitiform, 3-segmented; distal segment broader than proximal segments, with minute spinules on apical surface.

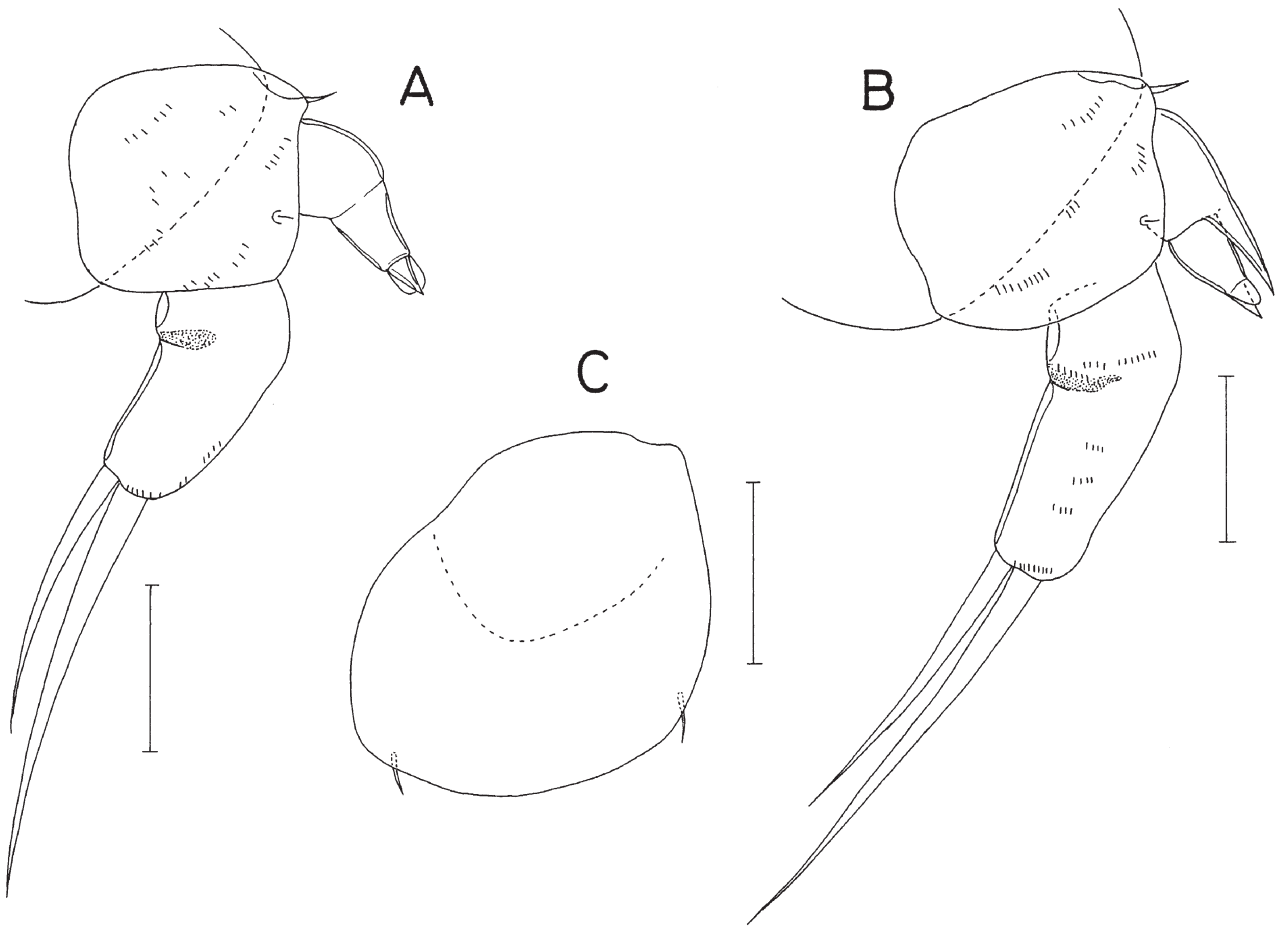
Labrum (Fig. 167E) unornamented; lacking palps. Mandible (Fig. 167H) unsegmented, tipped with powerful claw 25  $\mu\text{m}$  long. Maxillule (Fig. 167I) bilobed; larger inner lobe tipped with spinulose seta and densely pigmented area along medial side; smaller outer lobe tipped with 1 thin, naked seta. Maxilla (Fig. 167J, K) bilobate, with longer inner lobe (endite of syncoxa) tipped with 1 seta; shorter outer lobe with 3 unequal setae (2 distal and 1 subdistal). Maxilliped absent.

Legs 1-4 each consisting of 2-segmented protopod, 2-segmented exopod, and unsegmented endopod; basis with small outer seta. Legs 1, 2, and 4 same in form and armature; distal exopodal segment tipped with small claw and circular element (Fig. 168A). Exopod of leg 3 (Fig. 168B) with large spiniform process on laterodistal margin.

Endopods of legs 1-4 with 2 unequal, naked setae distally; laterodistal seta about 1.5 times longer than mediodistal seta. Mediodistal seta as long as or slightly longer than endopodal segment.



**FIG. 167.** *Monnioticopa minuta* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, right; C, genitoabdomen, ventral; D, anal somite and caudal rami, dorsal; E, cephalic appendages *in situ*, ventral; F, rostrum and antennule; G, antenna; H, mandible; I, maxillule; J, K, maxillae. Scale bars: A, B, 0.1 mm; C-F, 0.02 mm; G-K, 0.01 mm.



**FIG. 168.** *Monnioticopa minuta* gen. et sp. nov., female. A, leg 1; B, leg 3; C, leg 5. Scale bars: A, B, 0.02 mm; C, 0.05 mm.

Leg 5 (Fig. 168C) lamellate, as long as wide ( $100 \times 100 \mu\text{m}$ ), narrowed proximally; armed with 2 small setae on distal margin.

**Male.** Unknown.

**Remarks.** *Monnioticopa minuta* gen. et sp. nov. is distinguishable from the type species of the genus by the following features: (1) the caudal rami are 1.95 times longer than wide (vs. 1.47 times in the type species); (2) the proximal segment of the antennule is armed with 1 seta (vs. 2 setae in the type species); (3) the coxa of the swimming legs is not expanded (vs. expanded, disc-shaped); (4) the basis of swimming legs 1-4 is armed with an outer seta (vs. unarmed in the type species); and (5) leg 5 narrows proximally (vs. not narrowed).

***Monnioticopa firma* gen. et sp. nov.**

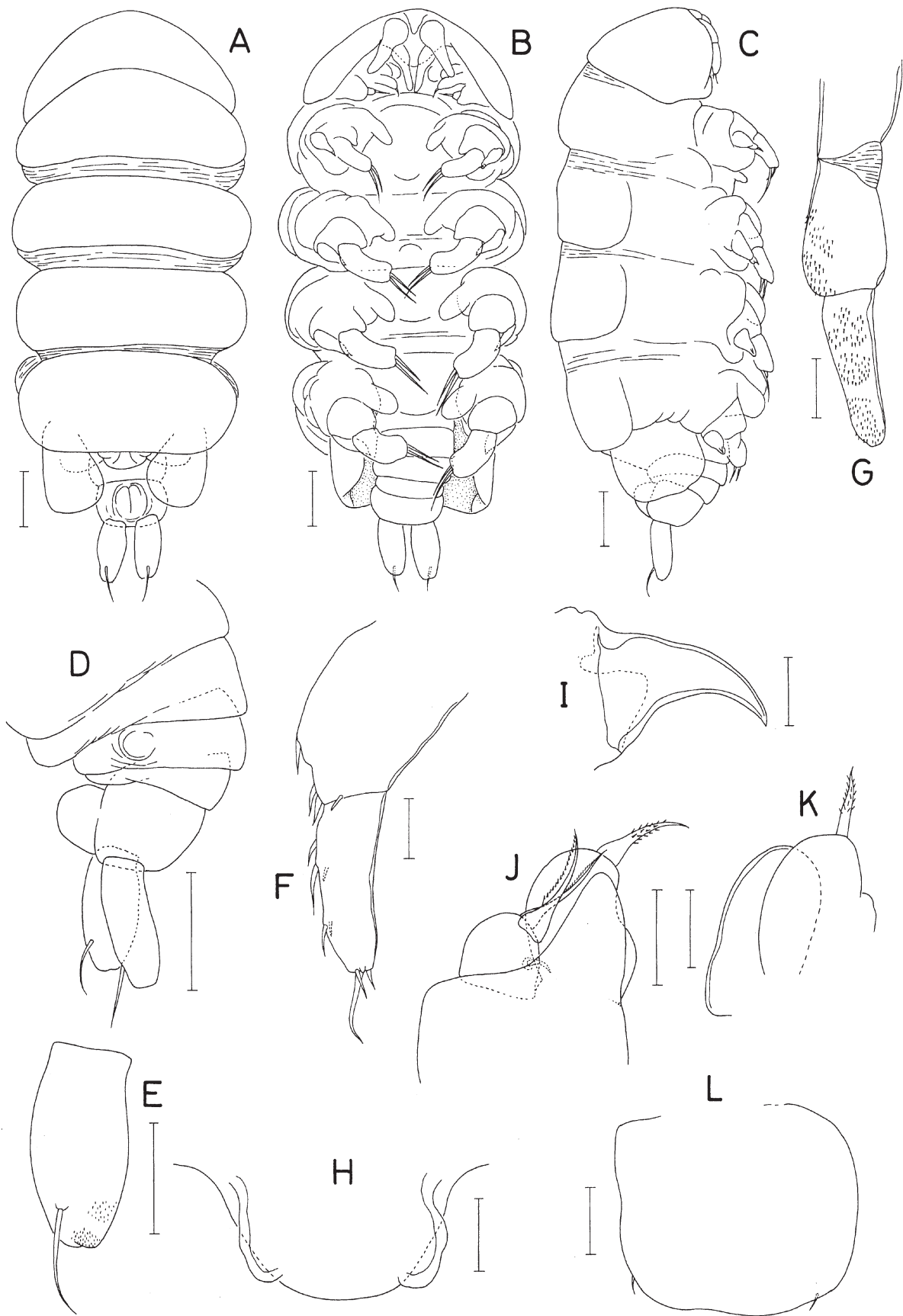
(Figs. 169, 170)

**Type material.** Holotype ♀ (MNHN-IU-2014-21577, dissected and mounted on a slide) from *Pycnoclavella diminuta* (Kott, 1957); Ibo I., Mozambique, AURACEA 1995 cruise, Stn P12, on reef, Monniot coll., 13 November 1995.

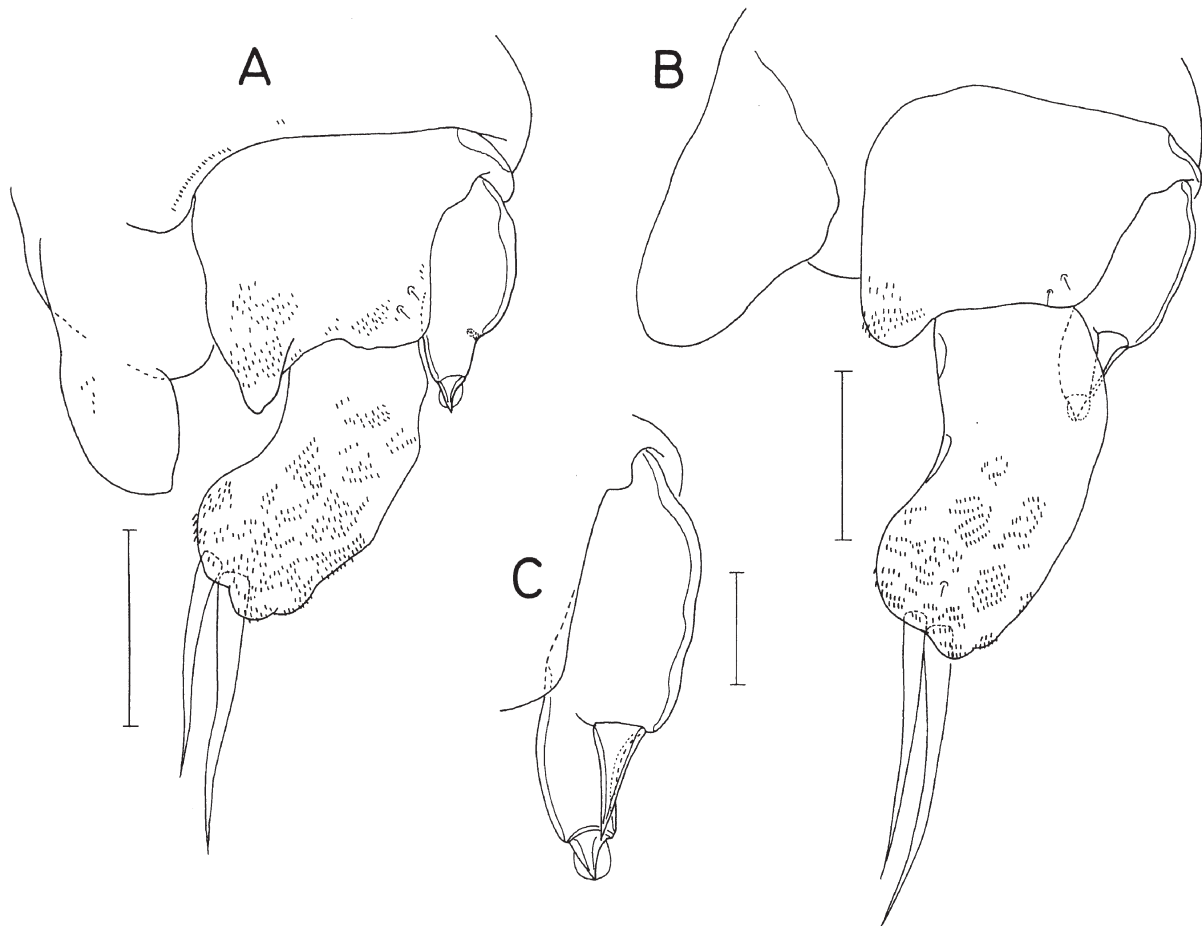
**Etymology.** The name is derived from the Latin *firm* (=strong), reflecting its stout body bearing well-developed tergites on the pedigerous somites.

**Description of female.** Body (Fig. 169A-C) eruciform, robust; body length 1.05 mm; maximum width  $440 \mu\text{m}$  (across second pedigerous somite). Cephalosome clearly defined from trunk, only slightly narrower than first pedigerous somite. First to fourth pedigerous somites distinctly defined from one another, subequal in width, each





**FIG. 169.** *Monniotocopa firma* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, ventral; C, habitus, right; D, genitoabdomen, right; E, left caudal ramus, dorsal; F, antennule; G, antenna; H, labrum; I, mandible; J, maxillule; K, maxilla; L, leg 5. Scale bars: A-D, 0.1 mm; E, L, 0.05 mm; F-K, 0.02 mm.



**FIG. 170.** *Monnioticopa firma* gen. et sp. nov., female. A, leg 1; B, leg 3; C, exopod of leg 3. Scale bars: A, B, 0.05 mm; C, 0.02 mm.

bearing distinct tergite with rounded lateral margins. Genitoabdomen (Fig. 169D) 4-segmented; first free abdominal somite bearing tubercle on lateral surface; anal somite bearing large anal prominence dorsally. Caudal ramus (Fig. 169E) fusiform, longer than anal somite, 2.04 times longer than wide ( $112 \times 55 \mu\text{m}$ ), with weakly bilobed distal margin, and ornamented with 2 patches of minute spinules ventrodistally; armed with 1 large dorsal seta ( $63 \mu\text{m}$  long) at 80% of ramus length.

Rostrum small, tapering towards rounded apex. Antennule (Fig. 169F) 2-segmented,  $123 \mu\text{m}$  long; proximal segment armed with 4 small setae; distal segment narrower but longer than proximal segment; armed with 8 small setae. Antenna (Fig. 169G) elongate, unarmed, distinctly 3-segmented, about  $132 \mu\text{m}$  long; second segment wider than other segments; second and third segments covered with minute spinules; third segment longest, narrower than other segments, gradually narrowing distally.

Labrum (Fig. 169H) unornamented, with sclerotized lateral margins. Mandible (Fig. 169I) as powerful claw, smooth and curved. Maxillule (Fig. 169K) bilobed; inner lobe unarmed; outer lobe tipped with 1 spinulose seta. Maxilla (Fig. 169J) consisting of proximal part plus inner and outer lobes; proximal part with strongly projecting mediodistal corner; longer inner lobe tipped with 1 spinulose seta; shorter outer lobe armed with 2 unilaterally serrate setae distally, and 1 small naked seta at midlength. Maxilliped absent.

Legs 1-4 each consisting of 2-segmented, unarmed protopod and unsegmented rami (Fig. 170A-C); coxa with large mediodistal protrusion (Fig. 170A, B); basis with weak mediodistal protrusion covered with minute spinules. Exopods distinctly shorter than endopods. Exopods of legs 1 and 2 tipped with 1 claw and 1 circular lamella; exopods of leg 3 and 4 additionally with 1 large spine on anterolateral surface at distal two-thirds of ramus length (Fig. 170C). Endopods robust, curved medially, with truncate distal margin, armed with 2 setae distally, and covered with minute spinules. Endopodal segments  $74 \times 36$ ,  $98 \times 45$ ,  $105 \times 49$ , and  $90 \times 49 \mu\text{m}$ , respectively, in legs 1-4. Lengths of laterodistal and mediodistal setae 72 and 55, 78 and 72, 96 and 79, and 102 and 84  $\mu\text{m}$ , respectively, in legs 1-4.

Leg 5 (Fig. 169L) quadrate, slightly wider than long (159×179 µm), covering lateral margin of genitoabdomen; armed with 2 small setae.

**Male.** Unknown.

**Remarks.** *Monnioticopa firma* **gen. et sp. nov.** differs from the two congeners described above as follows: (1) the first segment of the antennule of the new species is armed with 4 setae, compared to 2 setae in *M. prima* **gen. et sp. nov.** and 1 seta in *M. minuta* **gen. et sp. nov.**; (2) the third segment of the antenna is distinctly longer and narrower than the proximal segments, but in the two congeners this segment is not longer or narrower than the proximal segments; (3) the inner lobe of the maxillule is unarmed, compared to bearing 1 seta in the congeners; (4) the proximal part of the maxilla bears a strong mediodistal projection, which is absent in both congeners; (5) the coxa of the swimming legs bears a large mediodistal projection, which is absent in the congeneric species.

***Monnioticopa manadoensis* gen. et sp. nov.**

(Figs. 171, 172)

**Type material.** Holotype ♀ (MNHN-IU-2014-21578, dissected and mounted on a slide) from *Eudistoma incrustatum* Monniot F. & Monniot C., 1996 (MNHN-IT-2008-4103 = MNHN A3/EUD/76); N. Sulawesi, Indonesia, 13MI W of Murex Resort, W of Manado town OCDN 1283-F, Site MANADO 6 (01°23.56'N, 124°32.62'E), depth 43 m, CRRF coll., 10 May 1993.

**Etymology.** The type locality is the source of the name of the new species.

**Description of female.** Body (Fig. 171A, B) eruciform, with soft exoskeleton; body length 1.29 mm; maximum width 382 µm (across second pedigerous somite). Cephalosome short, slightly narrower than first pedigerous somite. Trunk obscurely segmented; first to fourth pedigerous somites defined from one another by lateral constrictions, bearing indistinct dorsal tergites. Genitoabdomen recurved dorsally, 4-segmented; anal somite (Fig. 171C) ornamented with 4 transverse rows of minute spinules on lateral surfaces; anal prominence distinct. Caudal rami (Fig. 171C) rectangular, broad, slightly longer than anal somite, about 1.8 times longer than wide (80×44 µm), ornamented with numerous, minute spinules; armed with 1 large naked seta (38 µm long) positioned at 66% of ramus length plus 3 granule-like vestigial setae subdistally on dorsal surface.

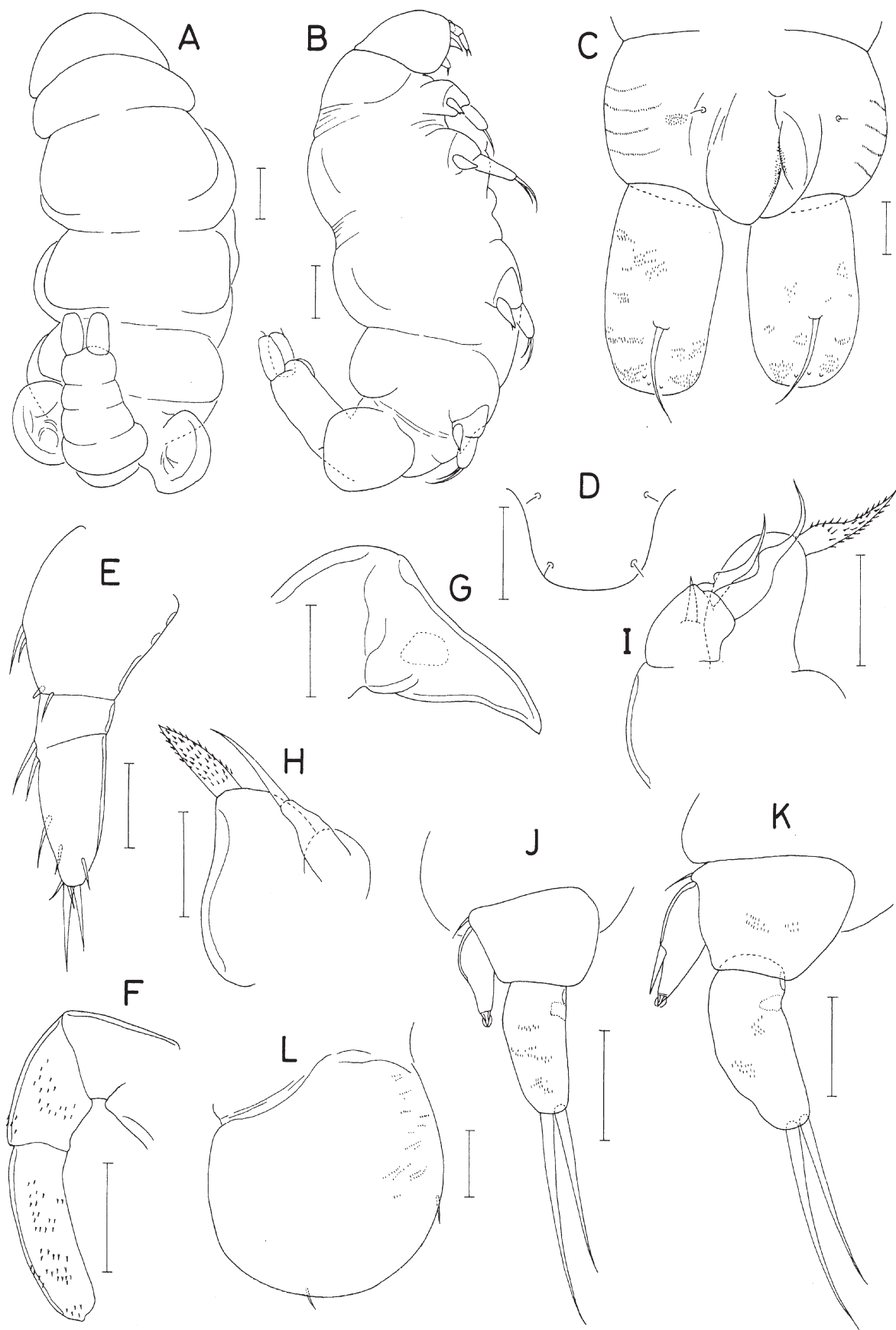
Rostrum (Fig. 171D) small, sub-rectangular, with rounded posterolateral corners. Antennule (Fig. 171E) small, 87 µm long, 3-segmented, articulation between second and third segments incomplete; armed with 4, 1, and 8 small setae on first to third segments, respectively. Antenna (Fig. 172F) about 70 µm long, digitiform, unarmed, 3-segmented with right angle curve between first and second segments; third segment longest, 33 µm long; second and third segments ornamented with scattered spinules.

Labrum semicircular, unarmed and unornamented. Mandible (Fig. 171G) represented by large, powerful claw. Maxillule (Fig. 171H) bilobed; larger inner lobe with 1 broad, spinulose seta apically; outer lobe shorter and narrower than inner, digitiform, tipped with 1 slender, naked seta. Maxilla (Fig. 171I) bilobate, with broad basal part; inner lobe (endite of syncoxa) twice as long as outer lobe, armed with 1 spinulose seta apically; outer lobe armed with 1 small seta at mid-length plus 2 unequal distal setae, both characteristically sigmoid in shape. Maxilliped absent.

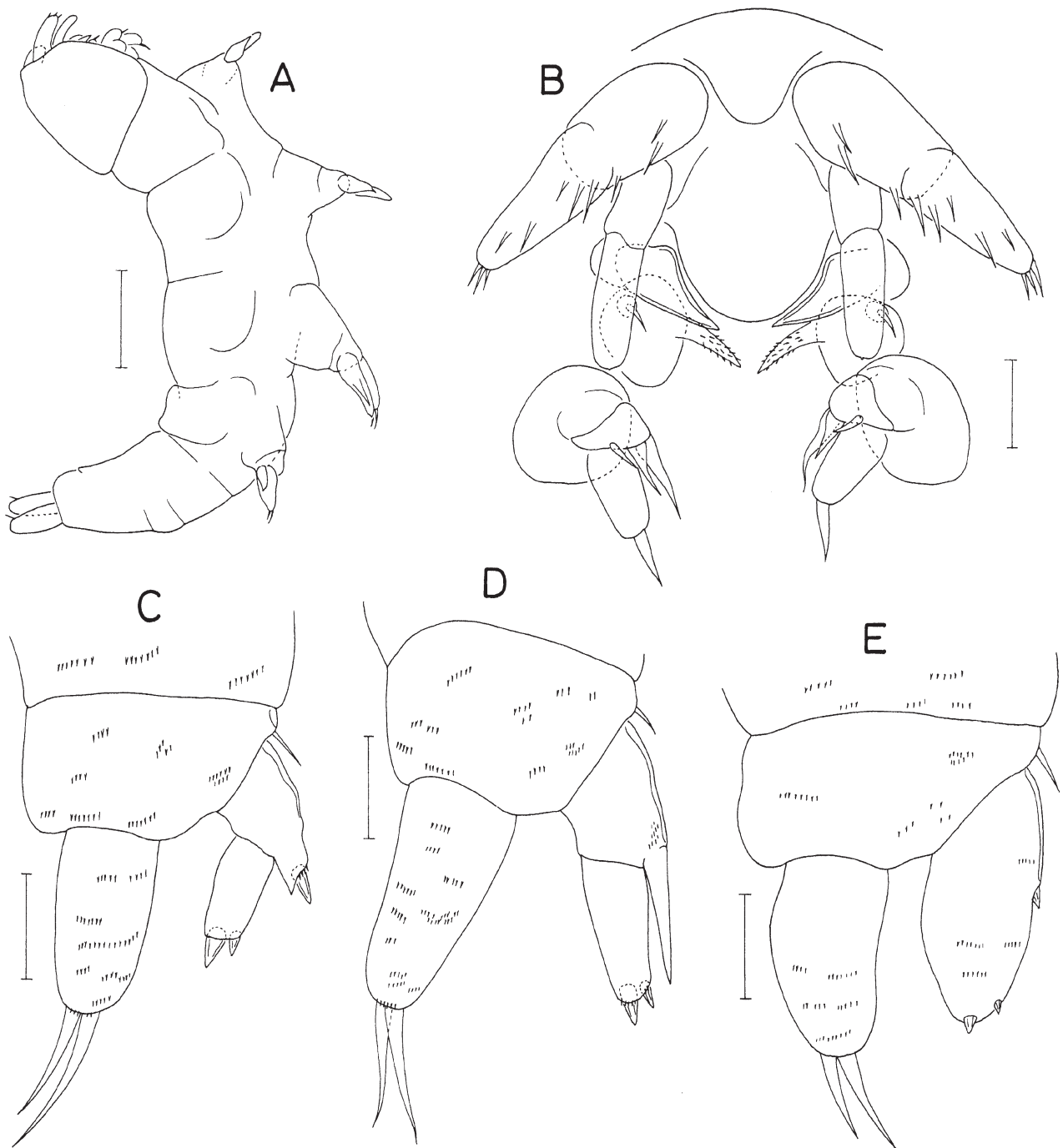
Legs 1-4 each consisting of 2-segmented protopod and unsegmented rami (Fig. 171J, K); basis with small outer seta. Exopods much smaller than endopods, tipped with 1 small claw and 1 small, circular lamella; exopod of leg 3 armed additionally with 1 large spine on lateral margin (Fig. 171K). Endopods 59×29, 86×36, 91×38, and 89×38 µm, respectively, in legs 1-4. Lengths of laterodistal and mediodistal setae on endopods 97 and 83, 105 and 89, 108 and 86, and 109 and 85 µm, respectively, in legs 1-4.

Leg 5 (Fig. 171L) lamellate, nearly circular, as long as wide (172×176 µm), with 2 small setae; distance between setae 118 µm.

**Copepodid juvenile.** Body (Fig. 172A) curved dorsally, consisting of cephalosome, 4-segmented trunk, and indistinctly 3-segmented genitoabdomen. First to fourth pedigerous somites each with faint tergite; fifth pedigerous somite not differentiated. Anal somite ornamented as in adult female. Caudal ramus 2.20 times longer than wide, armed as in adult female.



**FIG. 171.** *Monnioticopa manadoensis* gen. et sp. nov., female. A, habitus, dorsal; B, habitus, right; C, anal somite and caudal rami, dorsal; D, rostrum; E, antennule; F, antenna; G, mandible; H, maxillule; I, maxilla; J, leg 1; K, leg 2; L, leg 5. Scale bars: A, B, 0.1 mm; C-I, 0.02 mm; J-L, 0.05 mm.



**FIG. 172.** *Monnioticopa manadoensis* gen. et sp. nov., copepod juvenile. A, habitus, right; B, cephalic appendages; C, leg 1; D, leg 3; E, leg 4. Scale bars: A, 0.1 mm; B-E, 0.02 mm.

Rostrum (Fig. 172B) semicircular. Antennule 2-segmented, armed with 4 setae on proximal segment and 11 setae on distal segment. Antenna 3-segmented, curved as in adult female, but not ornamented. Labrum (Fig. 172B) semicircular, smooth. Mandible, maxillule, and maxilla as for adult female. Maxilliped absent.

Legs 1-4 biramous with 2-segmented protopods; basis bearing 1 small seta on outer margin. Leg 1 (Fig. 172C) exopod 2-segmented; proximal segment of exopod with projecting laterodistal corner bearing pointed distal process and 1 thick spine; distal segment inserted into medial margin of proximal segment, armed with 2 thick spines distally (medial spine twice as long as lateral); endopodal segment 1.7 times longer than wide, 2 distal setae shorter than segment. Leg 2 same as leg 1. Leg 3 (Fig. 172D) exopod 2-segmented; proximal segment of exopod armed with large spine at laterodistal corner; distal segment armed as in legs 1 and 2, but longer; endopodal segment twice

as long as wide, armed as in legs 1 and 2. Leg 4 (Fig. 172E) exopod unsegmented, armed with 3 small spines, 1 on lateral margin, 1 subdistal, and 1 distal; distal setae on endopodal segment short, less than half length of segment. Leg 5 not differentiated.

**Male.** Unknown.

**Remarks.** *Monnioticopa manadoensis* **gen. et sp. nov.** is distinguishable from its congeners by the possession of the 2 specialized (sigmoid in shape) setae located distally on the outer lobe of the maxilla. In addition, in *M. manadoensis* **gen. et sp. nov.** the first segment of the antennule is armed with 4 setae and the third segment of the antenna is the longest segment. These features of the antennule and antenna are shared only with *M. firma* **gen. et sp. nov.** However, these two species are easy to separate because in *M. firma* **gen. et sp. nov.** the antenna is straight, the first to fourth pedigerous somites each bear a well-developed dorsal tergite, the inner lobe of the maxillule is unarmed, and the coxae of legs 1-4 each bear a large mediolateral projection.

***Monnioticopa planicoxa* gen. et sp. nov.**

(Figs. 173, 174)

**Type material.** Holotype ♀ (MNHN-IU-2014-21579, dissected and mounted on a slide) from *Asajirus* sp.; North of Lubang Island, the Philippines, ESTASE 2 cruise, RV “Jean Charcot”, Stn CP02 (14°05.4'N, 120°02.5'E), depth 2050 m, Métivier coll., 14 November 1984.

**Etymology.** The specific name is derived from the Latin *plan* (=flat) and *coxa*, in reference to the flat, discoid coxa of swimming legs.

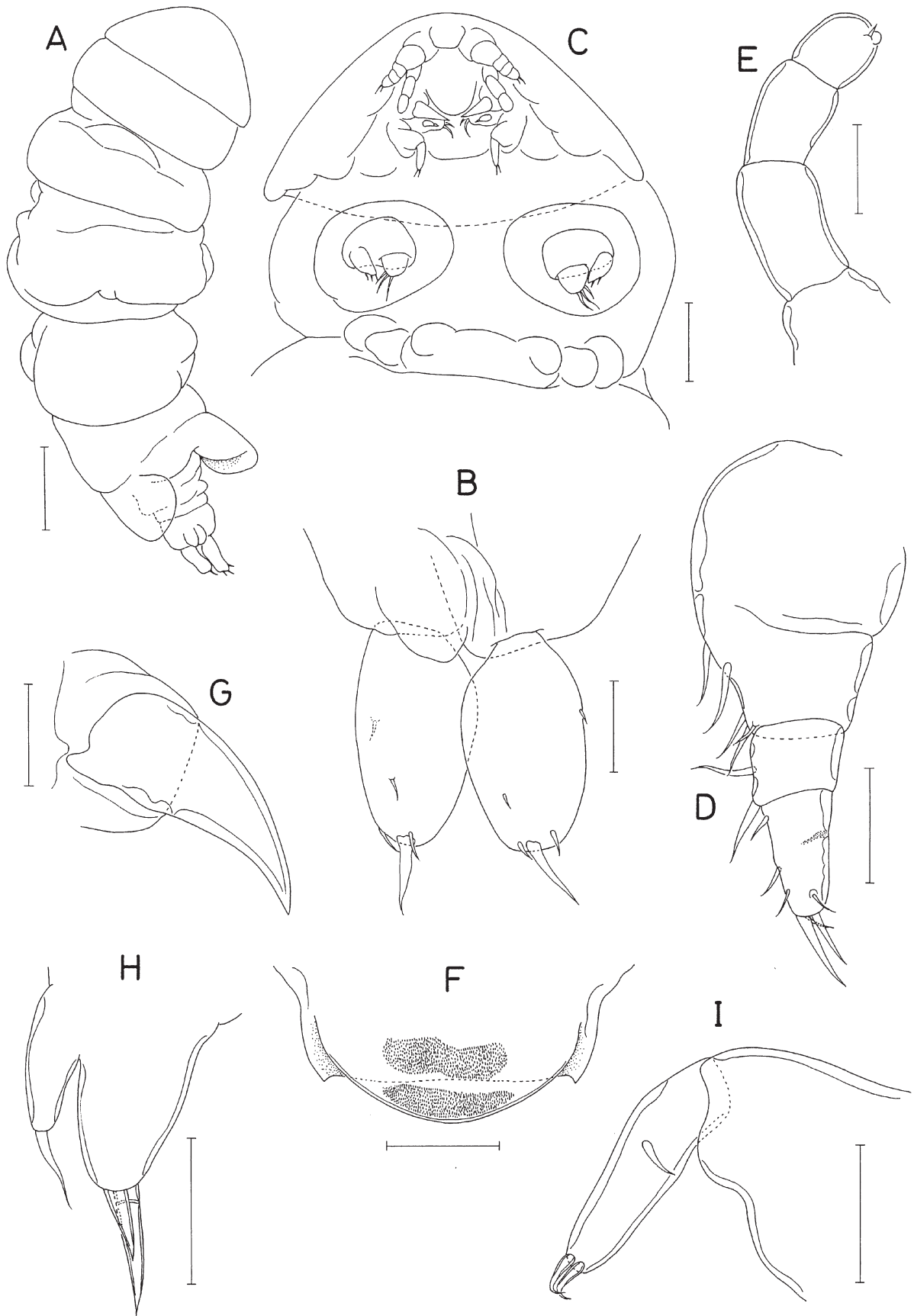
**Description of female.** Body (Fig. 173A) eruciform, with thin exoskeleton, consisting of cephalosome, 5-segmented trunk, and short genitoabdomen. Body length 3.74 mm; maximum width about 1.2 mm (across third pedigerous somite). Cephalosome (Fig. 173C) wider than long (0.49×1.04 mm), with distinct posterodorsal margin, as wide as first pedigerous somite. First to fourth pedigerous somites well-defined from one another, but their tergites obscure or absent; trunk bearing 3 pairs of subcircular tubercles on ventral surface between first and second pedigerous somites (Fig. 173C). Genitoabdomen segmentation uncertain due to post-fixation shrinkage. Caudal rami (Fig. 173B) broad, oval, about 1.8 times longer than wide (243×135 µm), narrow proximally; armed with 1 major and 4 small, setule-like setae; major distal seta 87 µm long, 2 of small setae positioned at 44 and 70% of ramus length, other 2 small setae positioned distally.

Rostrum (Fig. 173C) small. Antennule (Fig. 173D) small, 201 µm long, tapering, 4-segmented, articulation between proximal 2 segments incomplete; armed with 0, 5, 2, and 7 small setae on first to fourth segments, respectively. Antenna (Fig. 173E) 4-segmented, including short first segment; proximal 3 segments unarmed; fourth segment slightly longer than wide, with 1 small seta plus 1 small tubercle distally.

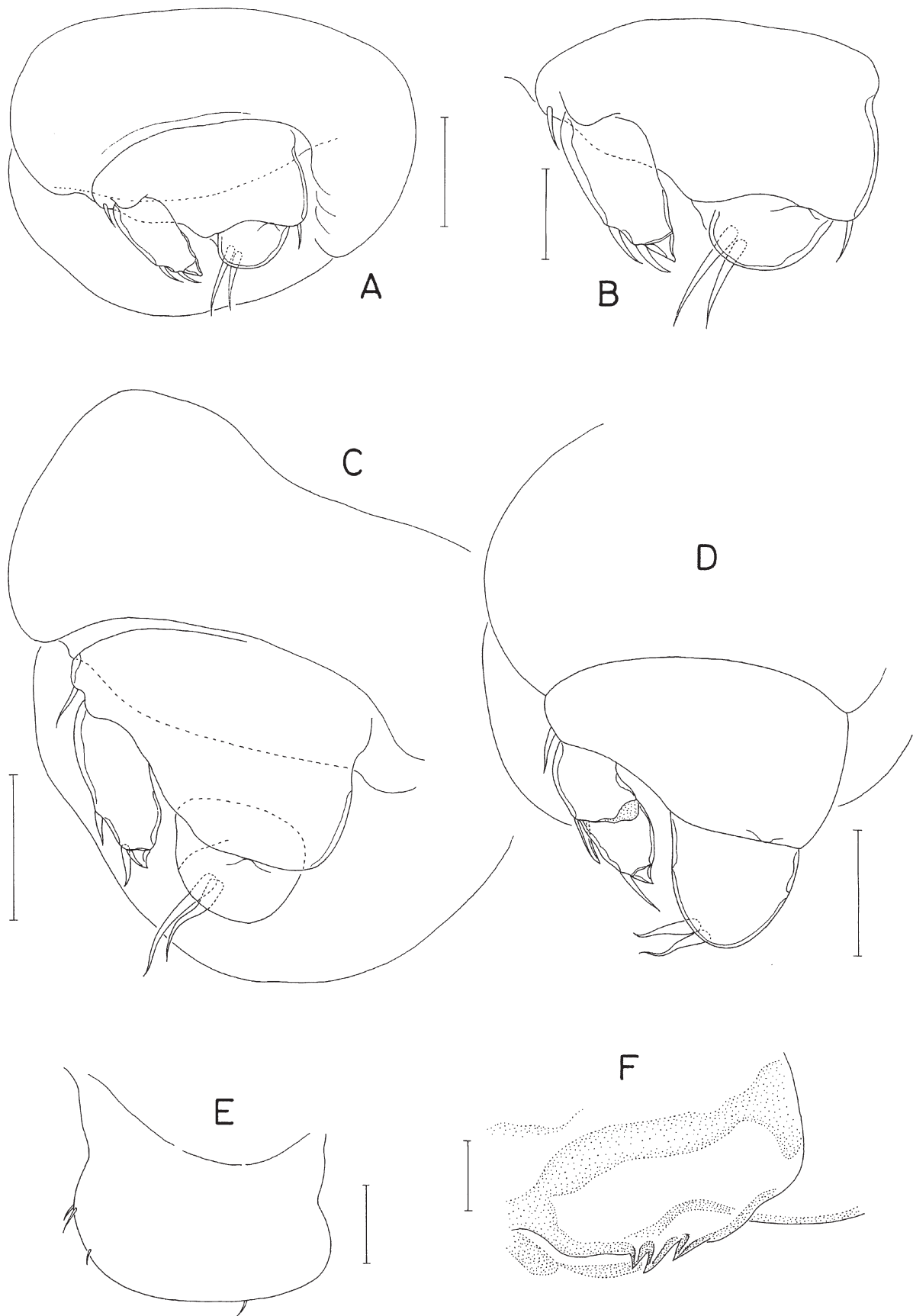
Labrum (Fig. 173F) with convex posterior margin, angular posterolateral corners, and ornamented with 2 patches of minute granules on ventral surface. Mandible (Fig. 173G) represented by weakly curved, powerful claw. Maxillule (Fig. 173H) bilobed; larger inner lobe tipped with 2 unequal, naked spines (45 and 26 µm long, respectively); small outer lobe tipped with 1 naked seta. Maxilla (Fig. 173I) 2-segmented; broad proximal segment unarmed; distal segment slender, 3.35 times longer than wide (87×26 µm), armed with 3 setae (2 distally and 1 at proximal 45% of segment length). Maxilliped absent.

Legs 1-4 biramous, with 2-segmented protopod (Fig. 174A-D); coxa extremely inflated, discoid; basis with small seta on outer margin; leg 1 additionally with inner distal seta (Fig. 174B) on basis. Exopods of legs 1 and 2 unsegmented, armed with 2 setae (1 on lateral margin and 1 at laterodistal corner) and 1 apical, triangular claw. Exopods of leg 3 (Fig. 174D) and leg 4 same in segmentation and armature, 2-segmented; proximal segment with 1 spine at laterodistal corner; distal segment with 1 seta at laterodistal corner and 1 apical, triangular claw. Endopods short, wider than long, armed with 2 naked setae distally; laterodistal seta slightly longer than mediolateral seta in legs 1-3, but almost equal in length in leg 4.

Leg 5 (Fig. 174E) lamellate, wider than long (370×674 µm), slightly narrowed in proximal third; armed with 4 minute setae (2 on medial margin, 1 near mediolateral corner, and 1 on distal margin). Leg 6 (Fig. 174F) probably represented by 3 cusps on genital operculum.



**FIG. 173.** *Monnioticopa planicoxa* gen. et sp. nov., female. A, habitus, dorsal; B, caudal rami, dorsal; C, cephalosome and first pedigerous somite, ventral; D, antennule; E, antenna; F, labrum; G, mandible; H, maxillule; I, maxilla. Scale bars: A, 0.5 mm; B, 0.1 mm; C, 0.2 mm; D-I, 0.05 mm.



**FIG. 174.** *Monniotocopa planicoxa* gen. et sp. nov., female. A, leg 1; B, basis and rami of leg 1; C, leg 2; D, leg 3; E, leg 5; F, genital aperture. Scale bars: A, C, D, 0.1 mm; B, 0.05 mm; E, 0.2 mm; F, 0.02 mm.



**Male.** Unknown.

**Remarks.** *Monnioticopa planicoxa* **gen. et sp. nov.** differs from other species of *Monnioticopa* **gen. nov.** in having a simple maxilla lacking the inner lobe, a 4-segmented antennule, and better developed setation on the exopods of swimming legs. Despite these differences, there are significant synapomorphies that allows the new species to be accommodated in the same genus. These synapomorphies include the claw-like, modified mandible, the 3- or 4-segmented digitiform antenna, the broad caudal rami armed with 1 major and several vestigial setae, and the bilobed maxillule.

It is noticeable that *M. planicoxa* **gen. et sp. nov.** shares with the type species of the genus, the expanded, flattened coxa of the swimming legs, but the scale of the expansion is greater in *M. planicoxa* **gen. et sp. nov.** than in the type species.

### ***Periboia* gen. nov.**

**Diagnosis.** Female. Body vermiform, divisible into prosome consisting of cephalosome and first to fourth pedigerous somites, and urosome comprising fifth pedigerous somite, genital double-somite and unsegmented abdomen. Caudal rami elongate, unarmed. Antennule 2-segmented, armed with few seta. Antenna digitiform, 3-segmented, unarmed. Labrum rudimentary, unarmed and unornamented. Mandible forming powerful claw. Maxillule unsegmented, unequally bilobed, with 2 apical setae on inner lobe and 1 seta on small outer lobe. Maxilla bilobate, with unarmed proximal part; inner lobe (endite of syncoxa) tipped with 1 seta; outer lobe armed with 1 seta on lateral margin and 2 spines distally. Maxilliped absent. Legs 1-4 each consisting of tapering, unsegmented process formed by fusion of protopod and endopod, plus small, lamellate, free exopod. Exopods tipped with small claw, but fused protopod and endopod unarmed. Leg 5 small, lamellate, unarmed.

**Type species.** *Periboia tahitiensis* **gen. et sp. nov.** by original designation.

**Etymology.** In Greek mythology, *Periboia* was a princess of the giants, daughter of the giant king Porphyryon. Gender feminine.

**Remarks.** *Periboia* **gen. nov.** is undoubtedly closely related to *Monnioticopa* **gen. nov.** In both genera, the mandible forms a powerful claw, the antenna is digitiform and distinctly segmented, and the maxillule is bilobed. However, several significant features prevent its type species from being accommodated within *Monnioticopa* **gen. nov.** The most significant diagnostic feature of the new genus is found in the swimming legs, which consist of a small, free exopod and an elongate, unsegmented protopod-endopod complex. Within the Enteropsidae, a similar form of swimming legs is present in *Lequerrea canui* Illg & Dudley, 1980 (Illg & Dudley, 1980), but the genus *Lequerrea* can be clearly differentiated from *Periboia* **gen. nov.** by the lack of antennae and by the structure of the mouthparts.

The body of female *Periboia* **gen. nov.** is clearly divisible into prosome and urosome, and this can be considered as a diagnostic feature of the genus, because the prosome-urosome division is obscured by fusion of the fourth and fifth pedigerous somites in all known species of Enteropsidae. The caudal rami are also distinctive in *Periboia* **gen. nov.**; they are elongate and unarmed, which differs from the broad caudal ramus, uniformly armed with 1 major and several vestigial setae in known species of *Monnioticopa* **gen. nov.**

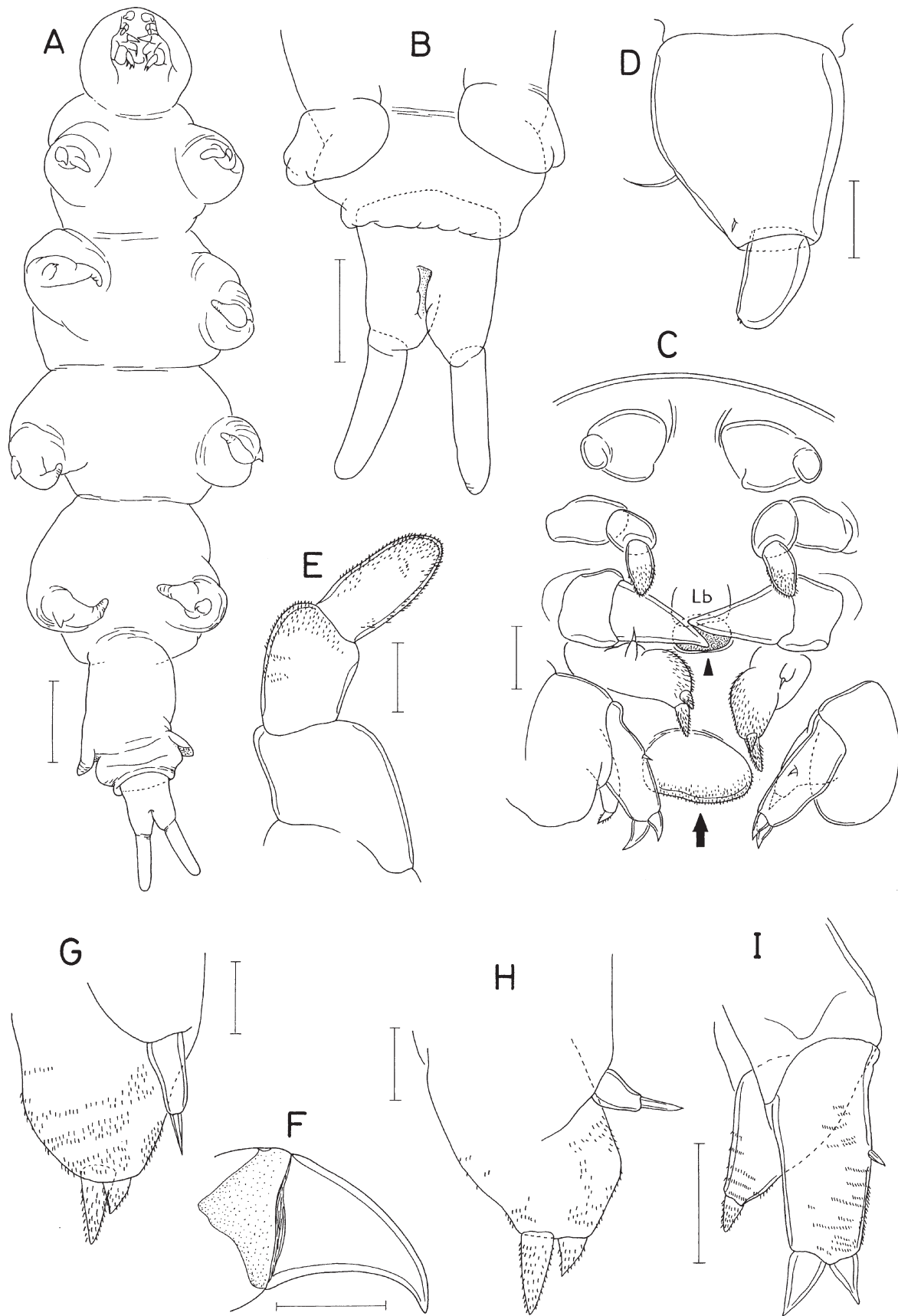
### ***Periboia tahitiensis* gen. et sp. nov.**

(Figs. 175, 176)

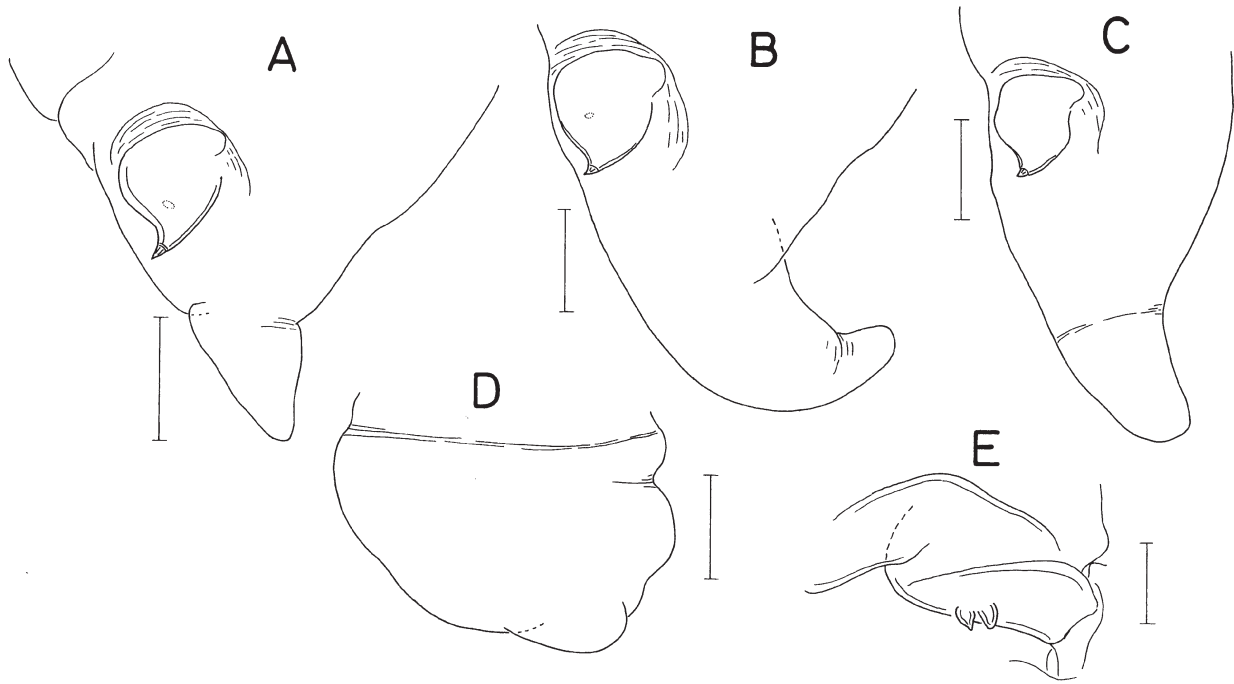
**Type material.** Holotype ♀ (MNHN-IU-2014-21580, dissected and mounted on 2 slides) from *Ascidia archaia* Sluiter, 1890 (MNHN-IT-2008-866 = MNHN P5/ASC.A/166); Tahiti, N. Moorea I., W. Motu d'Irioa, Stn M13, Monniot coll., June 1984.

**Etymology.** The type locality provides the name for the new species.

**Description of female.** Body (Fig. 175A) large, vermiform, divisible into prosome and urosome; body length 11.0 mm; maximum width 2.80 mm (across third pedigerous somite). Prosome consisting of cephalosome and first



**FIG. 175.** *Periboia tahitiensis* gen. et sp. nov., female. A, habitus, ventral; B, leg 5 and genitoabdomen, dorsal; C, cephalic appendages (Lb = labrum), ventral; D, antennule; E, antenna; F, mandible; G, H, maxillule; I, maxilla. Scale bars: A, 1 mm; B, 0.5 mm; C, F, I, 0.1 mm; D, E, G, H, 0.05 mm.



**FIG. 176.** *Periboia tahitiensis* gen. et sp. nov., female. A, leg 1; B, leg 3; C, leg 4; D, leg 5; E, genital aperture. Scale bars: A-D, 0.02 mm; E, 0.05 mm.

to fourth pedigerous somites, incompletely segmented, but clearly defined by deep constrictions between somites. Cephalosome small, circular,  $1.14 \times 1.36$  mm. First to fourth pedigerous somites all similar in length and lacking dorsal tergite. Urosome (Fig. 175B) 3-segmented, consisting of fifth pedigerous somite, genital double-somite, and unsegmented abdomen. Fifth pedigerous somite elongated,  $1.36 \times 1.09$  mm, bearing leg 5 posterolaterally. Genital double-somite obscurely defined from fifth pedigerous somite, wider than long, about  $0.45 \times 1.09$  mm, laterally convex; genital apertures located dorsolaterally, covered by leg 5. Abdomen  $770 \times 710$   $\mu\text{m}$ , lacking anal operculum or anal prominence. Caudal rami (Fig. 175B) elongate, about 3.8 times longer than wide ( $727 \times 190$   $\mu\text{m}$ ), unarmed, with parallel lateral margins, and rounded distal margin.

Rostrum represented by short ridge between antennules (Fig. 175C). Antennule (Fig. 175D) 2-segmented; proximal segment slightly longer than wide ( $139 \times 124$   $\mu\text{m}$ ), narrowing distally, armed with 1 seta on posterior margin and 1 minute setule subdistally; distal segment about 1.7 times longer than wide ( $68 \times 39$   $\mu\text{m}$ ), unarmed. Antenna (Fig. 175E) curved, digitiform, 3-segmented, unarmed; first to third segments  $89 \times 91$ ,  $76 \times 67$ , and  $98 \times 45$   $\mu\text{m}$ , respectively, narrowing from proximal to distal; anterior surface of second and third segments covered with minute spinules.

Labrum (indicated by Lb in Fig. 175C) rudimentary, flexible, not covering any oral appendages. Mouth (indicated by arrowhead in Fig. 175C) visible just posterior to labrum. Mandible (Fig. 175F) positioned lateral to mouth, short, bearing strong claw distally, with dense sclerotized area between proximal part and claw. Maxillule (Fig. 175G, H) bilobed; larger inner lobe with 2 broad, unequal setae apically and ornamented with numerous minute spinules on distal surfaces and setae; small outer lobe digitiform, tipped with 1 spine (or spiniform seta). Maxilla (Fig. 175I) bilobate, with short proximal part; both lobes ornamented with transverse rows of minute spinules; inner lobe (endite of syncoxa) tapering, tipped with 1 broad, spinulose seta; outer lobe longer than inner, rectangular, armed with 1 small spine on outer margin and 2 triangular spines at apex. Ventral surface of cephalosome between left and right maxillae bearing broad, linguiform protuberance (arrowed in Fig. 175C). Maxilliped absent.

Legs 1-4 all same in form and structure (Fig. 176A-C); each leg consisting of small free exopod plus fleshy, tapering, unsegmented process formed by complete fusion of protopod and endopod. Exopods flattened, lamellate, tapering, tipped with small claw (or claw-like process). Legs 2-4 larger than leg 1.

Leg 5 (Fig. 176D) small, lamellate, unarmed, wider than long ( $376 \times 636$   $\mu\text{m}$ ), narrowing distally, and covering only anterior part of genital double-somite. Leg 6 (Fig. 176E) probably represented by 2 small cusps on genital operculum.

**Male.** Unknown.

**Remarks.** This species, with a female body length of 11.0 mm, is the largest known member of the family Enteropsidae.

### Genus *Enteropsis* C.W.S. Aurivillius, 1885

**Diagnosis.** Female: Body eruciform or vermiform, unsegmented or indistinctly segmented, without dorsal tergites. No prosome-urosome division present. Anus positioned posteriorly or on dorsal surface posterior to genital apertures. Caudal rami absent, or reduced and armed with at most 1 seta or spine. Rostrum not developed, usually absent. Antennule small, 1- to 3-segmented, armed with few small setae. Antenna up to 4-segmented, usually 2-segmented; terminal segment forming claw, or tipped with 1 or 2 spines or processes. Labrum unarmed or armed with 2 to 8 processes or setiform elements. Mandible absent. Maxillule bilobed, armed with 1 to 3 (usually 2) apical setae or processes on inner lobe and 0 to 5 (usually 2 or 3) apical setae or processes on outer lobe. Maxilla robust, unguiform, 2-segmented; proximal segment unarmed; distal segment terminating in strong claw, with 1 small seta proximally on posterior surface. Maxilliped absent. Legs 1-4 consisting of 2-segmented, unarmed protopod and rudimentary exopod and endopod; intercoxal plates absent. Leg 5 absent.

Male: Unknown.

**Type species.** *Enteropsis sphinx* Aurivillius, 1885 by original monotypy.

**Remarks.** Copepods of the genus *Enteropsis* are associated with solitary and compound ascidians. Ooishi (2009a) recognized 11 species as valid in *Enteropsis* and Kim I.H. & Moon (2011) subsequently described a new species of this genus. In the present work, we add five additional new species. The major taxonomic characters that can be used to differentiate between these 17 species include the distal armature of the caudal rami, the segmentation and setation of the antennule, the terminal armature of the antenna, the ornamentation of the labrum, and the armature of the maxillule (see Table 7).

**TABLE 7.** Summary of major differences between species of *Enteropsis*. Abbreviations: Atl = antennule, Ant = antenna, CR, caudal ramus, Mxl = maxillule, proc = process.

Species	CR distal armature	Atl segs (setae)	Ant terminal armature	Labrum proc.	Setae on Mxl lobes	
					Inner	Outer
<i>E. abbotti</i> Illg & Dudley, 1980	CR absent	1 (5)	Claw	2	2	2
<i>E. arctica</i> Marchenkov, 1994	Process	1 (ca. 7)	2 setae	6	2	3
<i>E. capitulata</i> Illg & Dudley, 1980	0	2 (6)	2 proc.	5	2	3
<i>E. chattoni</i> Monniot, 1961	Spine	2 (4)	2 proc.	0	2	2
<i>E. fusiformis</i> Ooishi, 2009	CR absent	1 (5)	Claw	6	1	2
<i>E. georgiana</i> Schellenberg, 1922	Process	2 (7)	2 proc.	6	2	3
<i>E. minor</i> Illg & Dudley, 1980	-	1 (5)	Claw	2	2	0
<i>E. nudus</i> Kim I.H. & Moon, 2011	Spine	1 (6)	Claw	0	2	2
<i>E. onychophora</i> Schellenberg, 1922	Seta	1 (?)	Claw	?	2	2
<i>E. roscoffensis</i> Chatton & Brément, 1909	Seta	1 (7)	Claw	6	2	3
<i>E. sphinx</i> Aurivillius, 1885	Spine	2 (ca. 7)	2 spines	8	2	3
<i>E. superba</i> Illg & Dudley, 1980	Spine	2 (10)	2 spines	0	2	3
<i>E. hispida</i> <b>sp. nov.</b>	Seta	1 (8)	Spine	1	2	2
<i>E. elongata</i> <b>sp. nov.</b>	0	1 (7)	0	4	2	1
<i>E. obtusa</i> <b>sp. nov.</b>	0	2 (8)	Claw	3	2	2
<i>E. tromsoensis</i> <b>sp. nov.</b>	Spine	2 (7)	Claw	6	5	3
<i>E. tasmanica</i> <b>sp. nov.</b>	Spine	1 (10)	2 spines	6	2	3

Generic names ending in *-opsis* are feminine so in Table 7 we have amended the following names accordingly: *Enteropsis arcticus* Marchenkov, 1994 becomes *E. arctica*, *E. capitulatus* Illg & Dudley, 1980 becomes *E. capitulata*, *E. georgianus* Schellenberg, 1922 becomes *E. georgiana*, *E. nudus* Kim I.H. & Moon, 2011 becomes *E. nuda*, *E. onychophorus* Schellenberg, 1922 becomes *E. onychophora*, and *E. superbus* Illg & Dudley, 1980 becomes *E. superba*.

***Enteropsis hispida* sp. nov.**

(Figs. 177, 178)

**Type material.** Holotype ♀ (MNHN-IU-2014-21581, dissected and mounted on a slide) from *Aplidium mernoensis* (Brewin, 1956) (MNHN-IT-2008-552 = MNHN A1/APL.B/215); New Caledonia, Stn NC16, platier de l'îlot Maitre, near l'îlot Carnard (under stones and in interstices between corals), depth 3-8 m, Monniot coll., 12 September 1985.

**Etymology.** The name of the new species is derived from the Latin *hispid* (=hairy), referring to its hairy body.

**Description of female.** Body (Fig. 177A, B) eruciform, unsegmented; body length 832 µm, excluding caudal rami; maximum width 216 µm (across second pedigerous somite). Body surface sparsely ornamented with scattered setules (or sensilla) (Fig. 177A, B, C). Cephalosome, first to fourth pedigerous somites, and genitoabdomen defined by weak lateral and ventral constrictions. Cephalosome slightly narrower than first pedigerous somite, semicircular, 164 µm wide, with sclerotized sculpturing dorsally. First to fourth pedigerous somites each with sclerotized sculpturing dorsolaterally, as shown in Fig. 177A and B. Genitoabdomen tapering, short, 116 µm long, without any trace of articulations; genital apertures positioned laterally in middle of genitoabdomen; anal prominence small, but distinct and bilobed. Caudal ramus (Fig. 177C) represented by large, stiff caudal seta, 87 µm long.

Rostrum absent. Antennule (Fig. 177D) small, unsegmented, 2.1 times longer than wide (36×17 µm), slightly narrowing distally; armed with 8 naked setae (1 very small). Antenna (Fig. 177E) very small, 32 µm long, digitiform, 2-segmented; proximal segment unarmed, 16×12 µm; distal segment 16×9 µm, armed with 1 spinulose apical spine (12 µm long) and ornamented with 2 transverse rows of spinules distally.

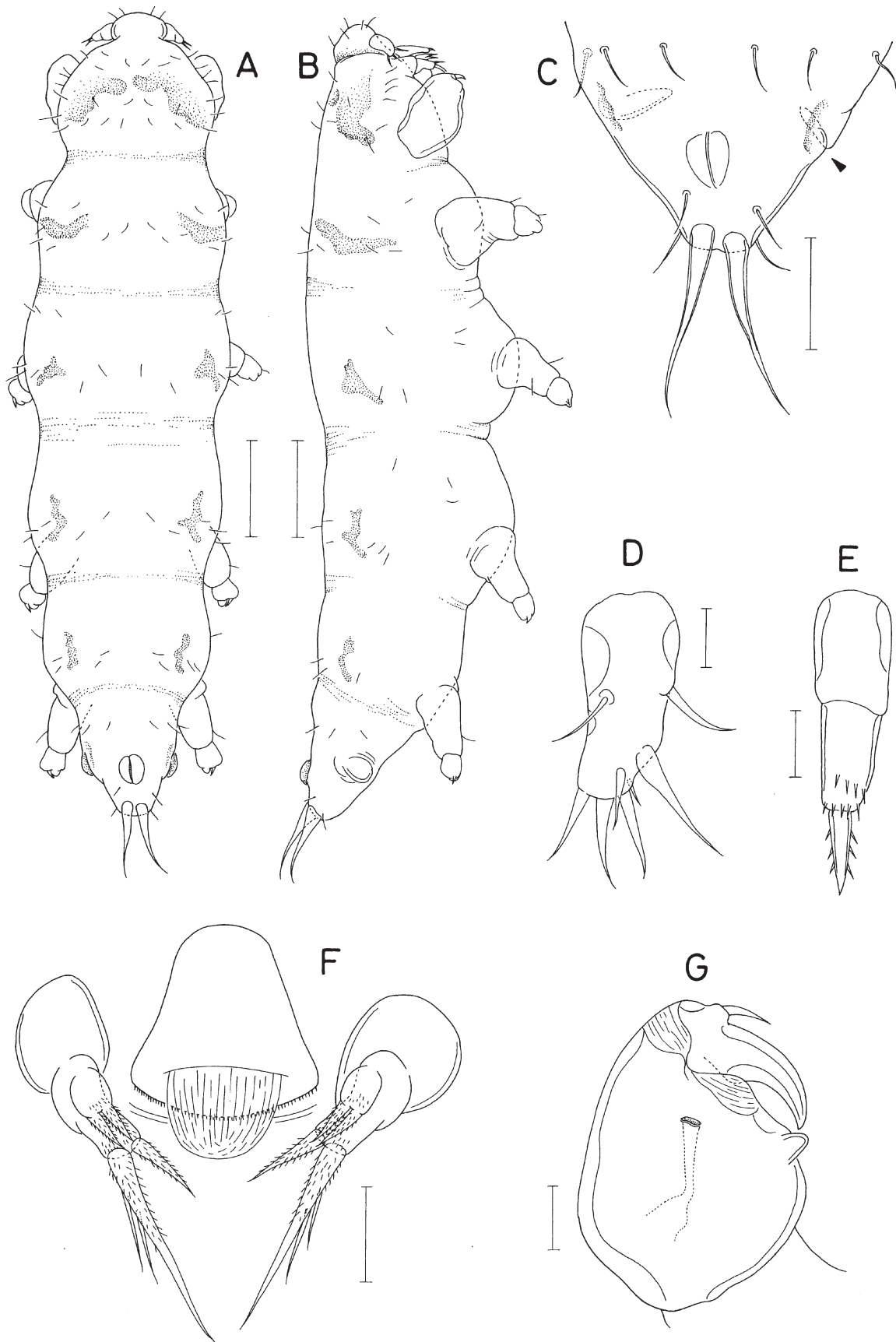
Labrum (Fig. 177F) longer than wide, with finely spinulose, convex posterior margin and 1 large, transparent, linguiform protrusion subdistally on ventral surface. Mandible absent. Maxillule (Fig. 177F) 2-segmented; proximal segment unarmed; distal segment bilobed; larger inner lobe tipped with 2 spinulose setae, larger seta 42 µm long, 2.6 times longer than smaller seta, bearing 2 prominent setules near proximal third; smaller outer lobe tipped with 2 equal, small spinulose setae (about 10 µm). Maxilla (Fig. 177G) 2-segmented, subchelate, robust; proximal segment with 1 tubercle-like process on medial margin, opposing tip of terminal claw of distal segment; with pore of maxillary gland subdistally on posterior surface; distal segment bearing strong, curved terminal claw and 1 proximal seta laterally. Maxilliped absent.

Legs 1-4 (Fig. 178A-C) 2-segmented; proximal segment (coxa) unarmed, ornamented with large setules on ventral surface; numbers of setules 4 in leg 1, 5 in leg 2, and 3 in legs 3 and 4. Distal segment subcircular or subquadrate, tipped with 1 small claw (representing exopod) embedded in transparent covering and with 1 setule near base of claw; endopod absent. Leg 5 absent.

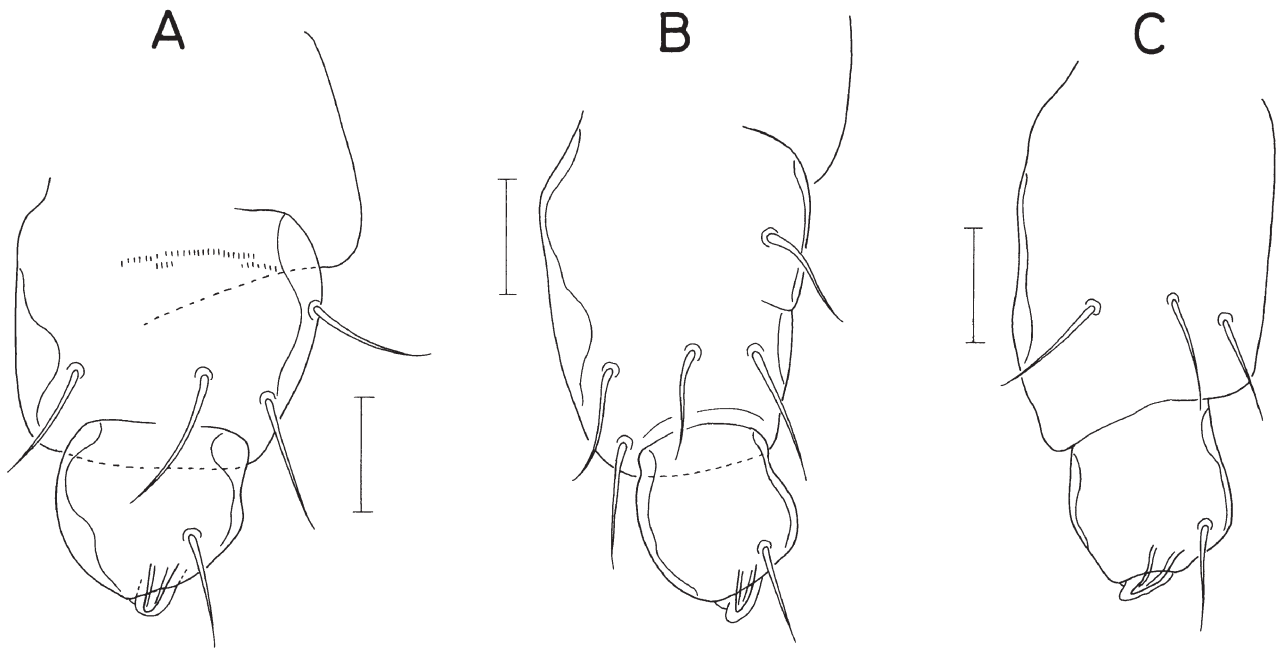
**Male.** Unknown.

**Remarks.** The armature of the labrum seems to be a useful character for distinguishing between species of *Enteropsis*. The armature of the labrum is known for most species of the genus, with the exception of *E. onychophora* Schellenberg, 1922. Schellenberg (1922) described for the labrum as “Oberlippe mit behaarten Borsten” (upper lip with hairy bristles). This indicates that the labrum of *E. onychophora* is armed with 2 or more setiform processes. In the other 11 known species of *Enteropsis* the labrum is unarmed (in three species) or armed with 2 to 8 processes (in the remaining eight species) (Table 7). Therefore, the possession of a single, broadly linguiform process on the labrum is a unique feature of *Enteropsis hispida* sp. nov.

The form and armature of the antenna of *E. hispida* sp. nov. also is characteristic. It is digitiform, 2-segmented, and tipped with a spine, whereas in other known species the antenna is typically broad and its distal segment is unarmed, or transformed to a claw, or armed with 2 spines (or setae). *Enteropsis hispida* sp. nov. can be distinguished by these two diagnostic features, together with its characteristic caudal rami which are each represented by a single large seta.



**FIG. 177.** *Enteropsis hispida* sp. nov., female. A, habitus. Dorsal; B, habitus, right; C, distal part of genitoabdomen, dorsal (arrowhead indicating right genital aperture); D, antennule; E, antenna; F, labrum and maxillules; G, maxilla. Scale bars: A, B, 0.1 mm; C, 0.05 mm; D, E, 0.01 mm; F, G, 0.02 mm.



**FIG. 178.** *Enteropsis hispida* sp. nov., female. A, leg 1; B, leg 2; C, leg 3. Scale bars: 0.02 mm.

***Enteropsis elongata* sp. nov.**

(Figs. 179, 180)

**Type material.** Holotype ♀ (MNHN-IU-2014-21582), 14 ♀♀ paratypes (MNHN-IU-2014-21583), and 2 ♀♀ paratypes (dissected, MNHN-IU-2014-17400) from *Botrylloides niger* Herdman, 1886 (MNHN-IT-2008-1688 = MNHN S1/BOT.A/23); Guadeloupe Stn 13, sand bank west of l'îlet à Cochons, depth 5-10 m, Monniot coll., 23 December 1980.

**Etymology.** The name of the new species reflects its elongate vermiform body.

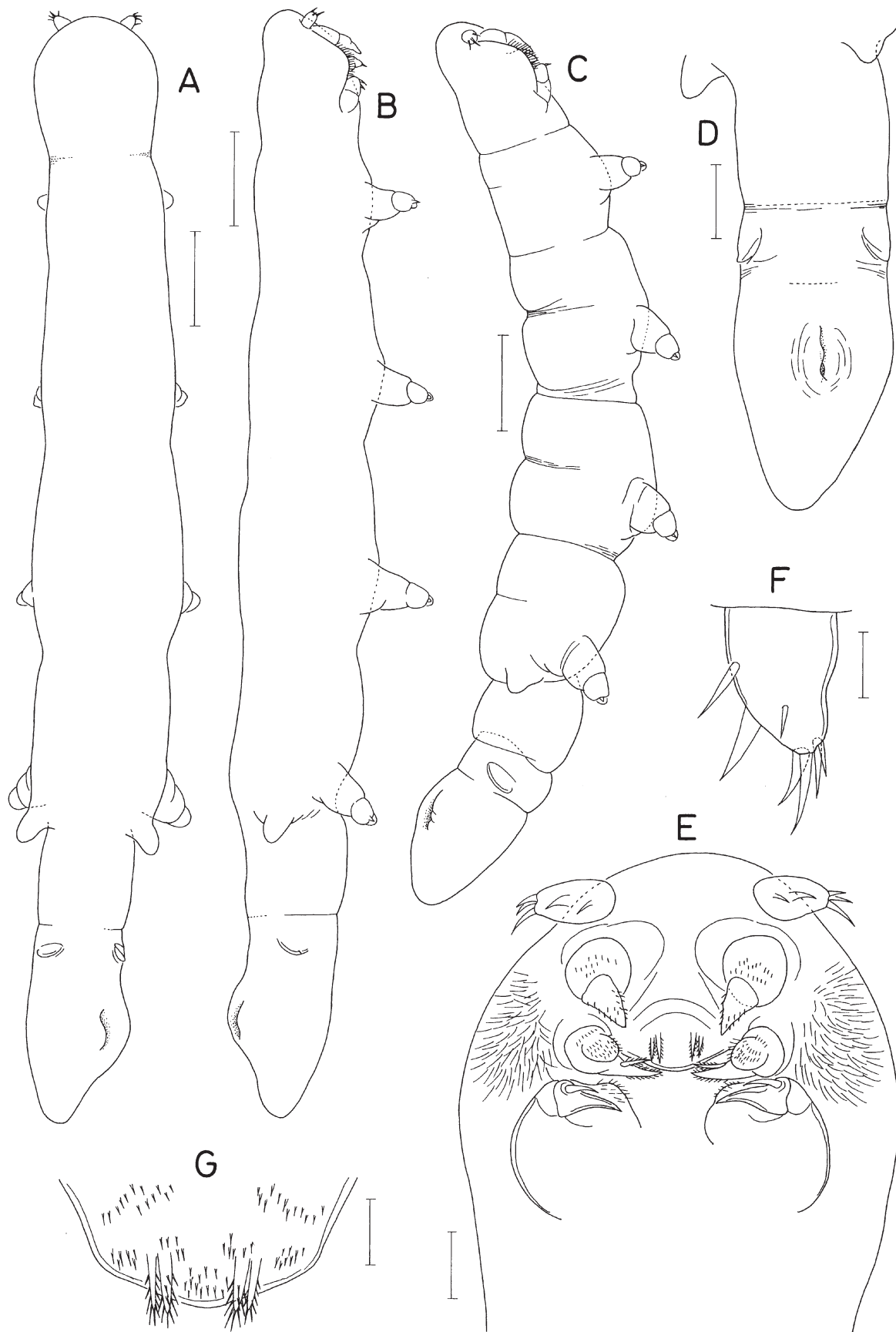
**Description of female.** Body (Fig. 179A-C) vermiform, cylindrical, elongate, unsegmented in expanded adult, but distinctly segmented in young adult (Fig. 179C). Mean body length 1.03 mm (0.86-1.16 mm, n=8); dissected young adult (Fig. 179C) 1.0 mm long. Cephalosome (Fig. 179E) slightly longer than wide, with patch of setules on ventrolateral surface lateral to oral region. Fourth pedigerous somite bearing pair of lateral, lobate processes just posterior to leg 4 (Fig. 179A-C). Genitoabdomen occupying about 18% of body length; genital apertures positioned dorsolaterally. Anal region elevated dorsally (Fig. 179A, B); part of genitoabdomen posterior to anus tapering towards blunt apical margin. Caudal rami and caudal seta absent.

Rostrum absent (Fig. 179E). Antennule (Fig. 179F) small, unsegmented, tapering, about 1.24 times longer than wide (21×17 µm), with convex ventral margin, and armed with 7 unequal, naked setae. Antenna (Fig. 180A) conical, 37×25 µm, incompletely 2-segmented; both segments unarmed but ornamented with numerous spinules; distal segment triangular, about half as long as proximal segment.

Labrum (Fig. 179G) with spinulose ventral surface, convex posterior margin, and armed with 2 pairs of slender, spinulose, setiform processes. Mandible absent. Maxillule (Fig. 180B) bilobed; narrower inner lobe tipped with 2 elements (1 plumose seta and 1 spinulose, setiform process); broader outer lobe tipped with 1 spiniform cusp and ornamented with spinules and setules on posterior and outer surfaces. Maxilla (Fig. 180C) massive, 2-segmented; proximal segment unarmed, with inflated, spinulose mediobasal protrusion; distal segment terminating in claw, bearing lateral spine proximally. Maxilliped absent.

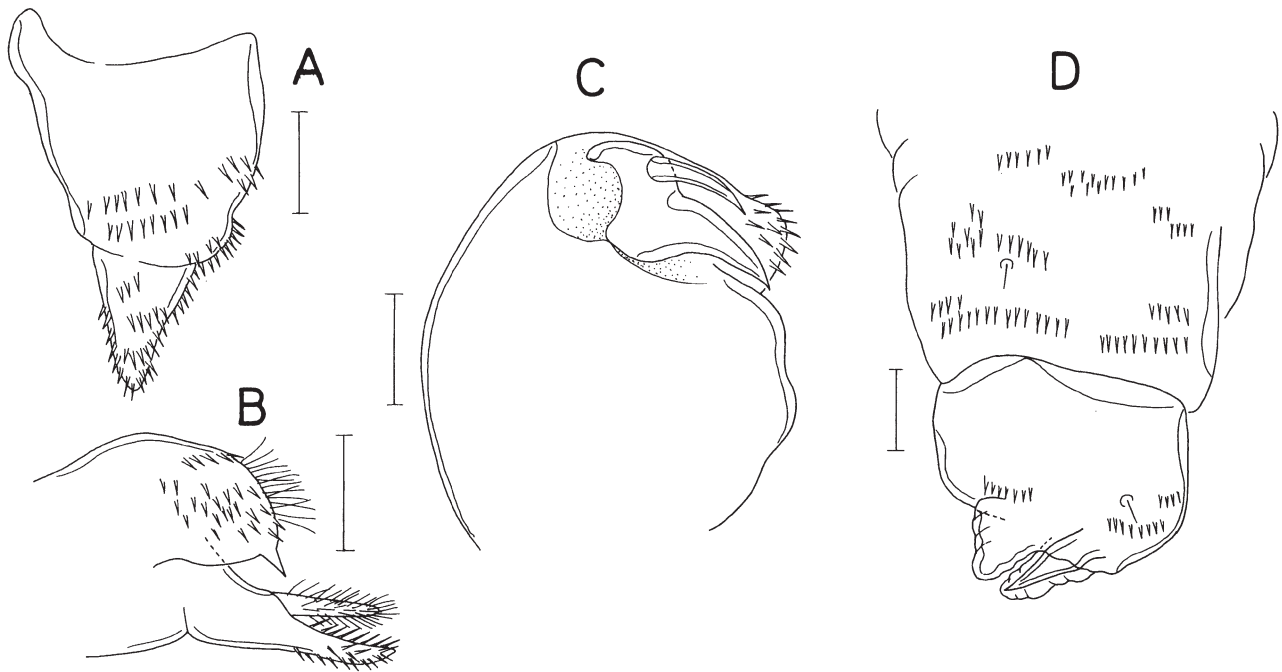
Leg 1 (Fig. 180D) biramous, with 2-segmented protopod; proximal and distal segments of protopod unarmed but ornamented with rows of spinules on anterior surface; rami small, vestigial; exopod claw-like with transparent covering; endopod fleshy, conical. Legs 2-4 same as leg 1. Leg 5 absent.

**Male.** Unknown.



**FIG. 179.** *Enteropsis elongata* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, habitus of young adult, right; D, genitoabdomen, dorsal; E, cephalosome, ventral; F, antennule, posterior; G, labrum. Scale bars: A-C, 0.1 mm; D, 0.05 mm; E, 0.02 mm; F, G, 0.01 mm.





**FIG. 180.** *Enteropsis elongata* sp. nov., female. A, antenna; B, maxillule; C, maxilla; D, leg 1. Scale bars: 0.01 mm.

**Remarks.** The most significant feature of *Enteropsis elongata* sp. nov. is the lack of caudal rami. This feature is shared with three congeners, *E. abbotti* Illg & Dudley, 1980, *E. fusiformis* Ooishi, 2009, and *E. minor* Illg & Dudley 1980. *Enteropsis elongata* sp. nov. is readily distinguishable from these species because in all three the distal segment of the antenna is transformed to a claw compared with the blunt, conical segment in *E. elongata* sp. nov. In addition, *E. elongata* sp. nov. has a labrum armed with 4 setiform processes and the outer lobe of the maxillule is tipped with a single cusp, both of which are unique features of the new species, differentiating it from all congeners.

***Enteropsis obtusa* sp. nov.**

(Fig. 181)

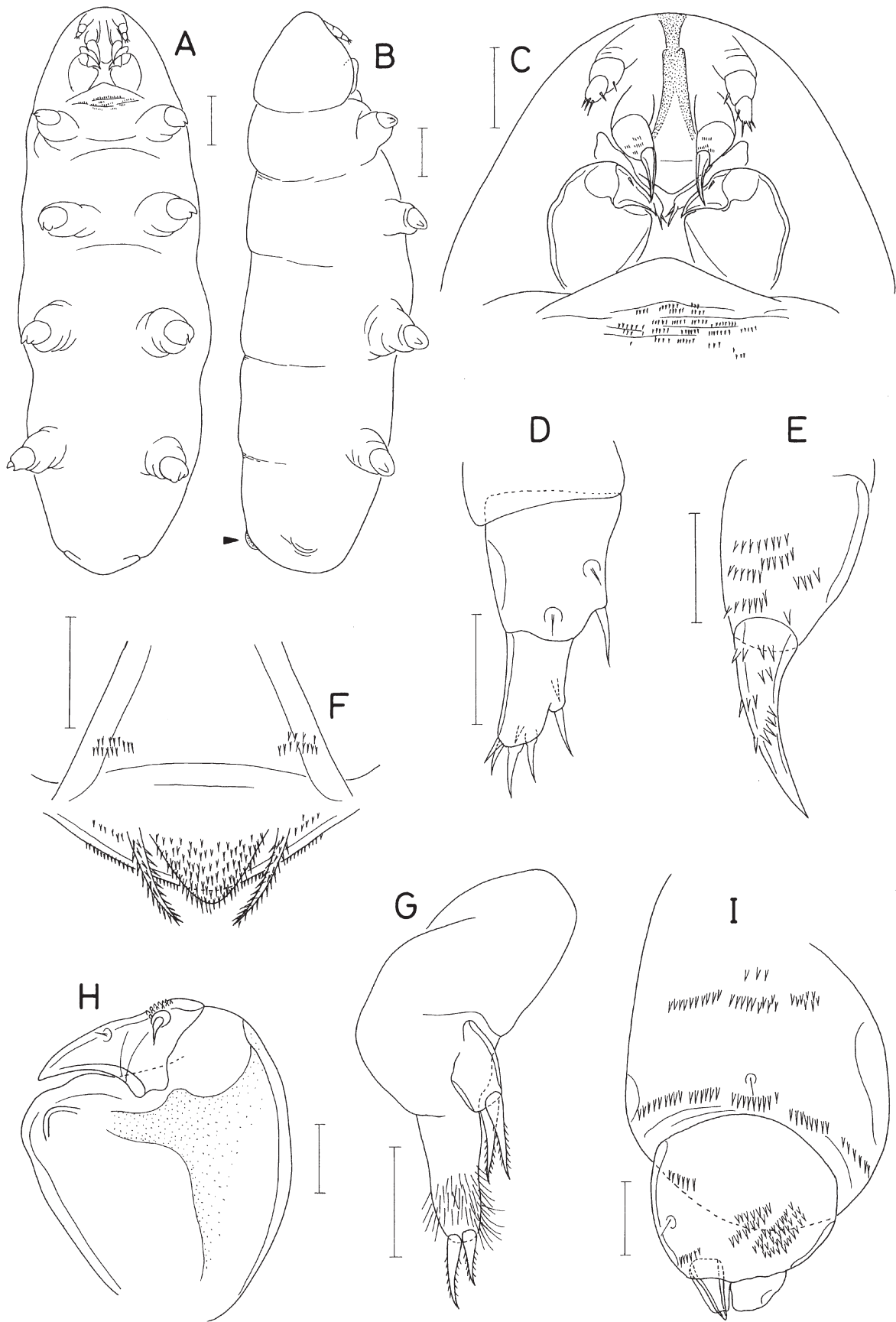
**Type material.** Holotype ♀ (MNHN-IU-2014-21584), 5 ♀♀ paratypes (MNHN-IU-2014-21585), and 1 ♀ paratype (dissected, MNHN-IU-2014-17399) from *Distaplia corolla* Monniot F., 1974 (MNHN-IT-2008-3694 = MNHN A3/DIS/35); Guadeloupe, Baille Argent face Nord, Stn 83-20, depth 1-3 m, Monniot coll., 04 April 1983.

**Etymology.** The name of the new species is derived from the Latin *obtus* (=blunt), referring to the blunt posterior end of body.

**Description of female.** Body (Fig. 181A, B) eruciform, stout, indistinctly 6-segmented, consisting of cephalosome, first to fourth pedigerous somites, and genitoabdomen. Mean body length 1.0 mm (0.78-1.17 mm, n=7); dissected specimen 1.17 mm; maximum width 393 µm (across third pedigerous somite). Cephalosome (Fig. 181C) narrowing anteriorly, with rounded anterior margin; first to fourth pedigerous somites lacking dorsal tergites. Genitoabdomen wider than long; anal prominence (indicated by arrowhead in Fig. 181B) small; genital apertures positioned subdistally on same plane as anal prominence. Caudal rami and caudal setae absent.

Rostrum absent, but sclerotized longitudinal sculpture present in rostral area (Fig. 181C). Antennule (Fig. 181D) 55 µm long, narrowing distally, 3-segmented; first segment unarmed; second segment with 1 seta on posterior margin; third segment slightly shorter than second, armed with 7 setae. Antenna (Fig. 181E) 67 µm long, unarmed, consisting of spinulose basal segment and spinulose distal claw; claw 34 µm long, curved, as long as basal segment, with acutely pointed tip.

Labrum (Fig. 181F) spinulose, with convex posterior margin, 1 broad, triangular, tongue-like medial process and 2 densely spinulose setiform processes, 1 either side of medial process. Mandible absent. Maxillule (Fig. 181G)



**FIG. 181.** *Enteropsis obtusa* sp. nov., female. A, habitus, dorsal; B, habitus, right; C, cephalosome, ventral; D, antennule; E, antenna; F, labrum; G, maxillule; H, maxilla; I, leg 1. Scale bars: A, B, 0.1 mm; C, 0.05 mm; D-I, 0.02 mm.

distally bilobed; longer inner lobe tipped with 2 spinulose setae and densely covered with setules in distal half of lobe; shorter outer lobe tipped with 2 equal, spinulose setae. Maxilla (Fig. 181H) massive, 2-segmented; proximal segment with strongly protruding medial margin and 1 blunt tubercle near apex of medial protrusion; distal segment terminating in strong claw, with 1 small seta proximally on posterolateral surface and patch of fine granular ornamentation near base of seta. Maxilliped absent.

Leg 1 (Fig. 181I) biramous with 2-segmented protopod; protopod spinulose on anterior surface. Rami rudimentary; exopod as conical claw, embedded in transparent covering; endopod wider than long, truncate. Legs 2-4 same as leg 1 in form and structure. Leg 5 absent. Leg 6 not visible in genital aperture.

**Male.** Unknown.

**Remarks.** *Enteropsis obtusa* **sp. nov.** can be clearly defined by its characteristic labrum which bears a broad, linguiform median process plus a pair of slender, setiform processes laterally. The caudal rami are absent in *E. obtusa* **sp. nov.**, as in four congeneric species (*E. abbotti*, *E. fusiformis*, *E. minor*, and *E. elongata* **sp. nov.**). However, in *E. obtusa* **sp. nov.** the antennule is 3-segmented, in contrast to the 1-segmented condition in these congeners, and the inner and outer lobes of the maxillule are each tipped with 2 distinct, basally articulating setae, compared to the armature of the inner and outer lobes each bearing 2 setae and 2 cusps in *E. abbotti*, 0 and 2 setae in *E. fusiformis*, 2 and 0 setae in *E. minor*, and 2 setae and 1 cusp in *E. elongata* **sp. nov.** The new species can be characterised by the combination of the armature of the labrum, the lack of caudal rami, the 3-segmented antennule, and the 2 setae-bearing lobes of the maxillule.

#### ***Enteropsis tromsoensis* sp. nov.**

(Figs. 182)

**Type material.** Holotype ♀ (MNHN-IU-2014-21586) and paratype ♀ (dissected, MNHN-IU-2014-21499) from *Polycarpa fibrosa* (Stimpson, 1852) (MNHN-IT-2008-6485 = MNHN S1/POL.B/54); off Tromsø, Norway, Norbi Cruise, RV “Jean Charcot”, Stn CP11 (69°52'N, 17°08'E), depth 250-300 m, Bouchet & Warén coll., 01 July 1975.

**Additional non-type material.** 2 ♀♀ (MNHN-IU-2014-21587, intact) in *Polycarpa porculus* Monniot C. & Monniot F., 1979; collected at type locality on same date.

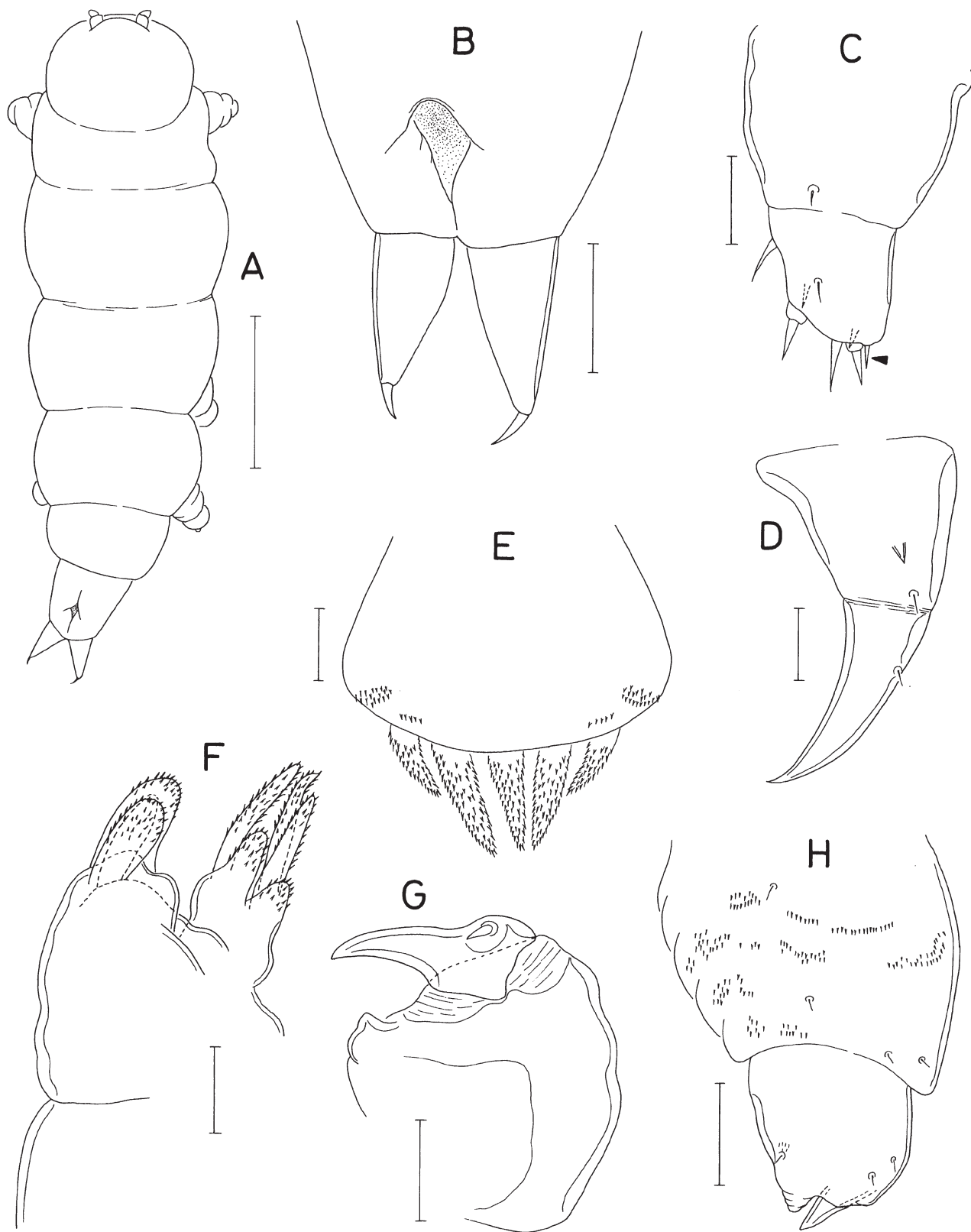
**Etymology.** The name of the new species is based on its type locality, Tromsø.

**Description of female.** Body (Fig. 182A) eruciform, incompletely 7-segmented, consisting of cephalosome, first to fourth pedigerous somites, genital complex, and 1-segmented abdomen. Body length 2.23 mm; maximum width 682 µm (across second pedigerous somite). Cephalosome 360×490 µm, distinctly defined from first pedigerous somite; posterior part of body from second pedigerous somite narrowing posteriorly. Genital apertures positioned laterally on genital complex. Abdomen 250×290 µm, gradually narrowing posteriorly; anus opening dorsally; anal prominence and anal operculum absent (Fig. 182B). Caudal rami (Fig. 182B) tapering, about 2.9 times longer than wide (208×71 µm), with straight, sclerotized lateral margin and oblique medial margin, and tipped with 1 small spine (55 µm long).

Rostrum absent. Antennule (Fig. 182C) broad, indistinctly 2-segmented, 70×50 µm; proximal segment unarmed; distal segment with 6 or 7 setae (3 setule-like and 2 with swollen articulated base); 1 small distal seta (indicated by arrowhead) present or absent. Antenna (Fig. 182D) consisting of proximal segment and large distal claw; proximal segment 45 µm long, with 1 small cusp subdistally; distal claw (or claw-like distal segment) 50 µm long, slightly curved, unarmed.

Labrum (Fig. 182E) armed with 5 broad, spinulose, setiform processes along posterior margin, middle 3 processes about 33 µm in length and about 1.5 times longer than lateral 2. Mandible absent. Maxillule (Fig. 182F) bilobed distally, with 5 elements on inner lobe and 3 elements on outer lobe, all elements ornamented with minute spinules; 5 elements of inner lobe consisting of 2 shorter processes and 3 slender setiform elements; elements on outer lobe all broad, blunt processes. Maxilla (Fig. 182G) massive, 2-segmented; broad proximal segment bearing 1 sclerotized tubercle on protruding medial margin; distal segment terminating in strong claw, with 1 small seta proximally. Maxilliped absent.

Leg 1 (Fig. 182H) 2-segmented; proximal segment unarmed, with scattered minute spinules on anterior surface; distal segment bearing 1 claw (representing exopod) and 1 shorter, tapering, corrugated process (endopod). Legs 2-4 same as leg 1. Leg 5 absent. Leg 6 not visible.



**FIG. 182.** *Enteropsis tromsoensis* sp. nov., female. A, habitus, dorsal; B, caudal rami, dorsal; C, antennule; D, antenna; E, labrum; F, maxillule; G, maxilla; H, leg 1. Scale bars: A, 0.5 mm; B, 0.1 mm; C-F, 0.02 mm; G, H, 0.05 mm.

**Male.** Unknown.

**Remarks.** *Enteropsis tromsoensis* **sp. nov.** can be clearly defined by the characteristic armature of the labrum and maxillule. Its labrum is armed with 5 setiform processes along the free posterior margin. Although Illg & Dudley (1980) recorded the presence of 5 or 6 “setae” on the labrum of *E. capitulata*, these elements were described as small, naked, and arranged along the anterior margin of the labrum. No other congeners are recorded as having 5 setae or processes on the labrum. The maxillule of *E. tromsoensis* **sp. nov.** is armed with 3 processes on the inner lobe and 5 processes on the outer lobe. The numbers of processes are extraordinary because they exceed the previously known maximum numbers, which are 2 on the inner lobe and 3 on the outer lobe (reported in five other species).

***Enteropsis tasmanica* sp. nov.**

(Figs. 183)

**Type material.** Holotype ♀ (MNHN-IU-2014-21588, dissected and mounted on a slide) from *Styela polypes* Monniot C., Monniot F. & Millar, 1976; Tasman Sea, RV “Galathea” Expedition, Stn 601 (45°51’S, 164°32’E), depth 4400 m, 14 January 1952.

**Etymology.** The name of the new species is derived from its type locality, the Tasman Sea,

**Description of female.** Body (Fig. 183A) fusiform, smooth, straight, unsegmented. Body length 3.15 mm; maximum width 0.89 mm (at anterior third). Cephalosome indistinctly defined from trunk by faint lateral wrinkles; posterior third of body tapering posteriorly; leg 4 positioned at 77% of body length. Abdomen (Fig. 183B, C) about 160×220 µm, discernible from trunk by weak constriction. Genital areas (Fig. 183B, C) located laterodistally on trunk, anterior to abdomen. Anal prominence weak, bilobed. Caudal rami narrow, widely separated from each other; each ramus (Fig. 183D) about 2.6 times longer than wide (94×36 µm), shorter than abdomen, tipped with 1 naked spine (42 µm long).

Rostrum (Fig. 183E) semicircular, bearing 8 sensilla (4 proximal, 2 middle, and 2 subdistal). Antennule (Fig. 183F) broad, tapering, unsegmented, about 110×73 µm, and ornamented with 3 setules; armed with 10 unequal setae (4 larger and 6 small, setule-like), 2 of larger setae articulating with swollen base. Antenna (Fig. 183G) unsegmented, about 2.3 times longer than wide (132×58 µm), with tapering proximal two-thirds and narrow distal third, spinulose in distal half; armed with 1 subdistal and 1 distal, sparsely spinulose spines; lengths of subdistal and distal spines 42 and 55 µm, respectively.

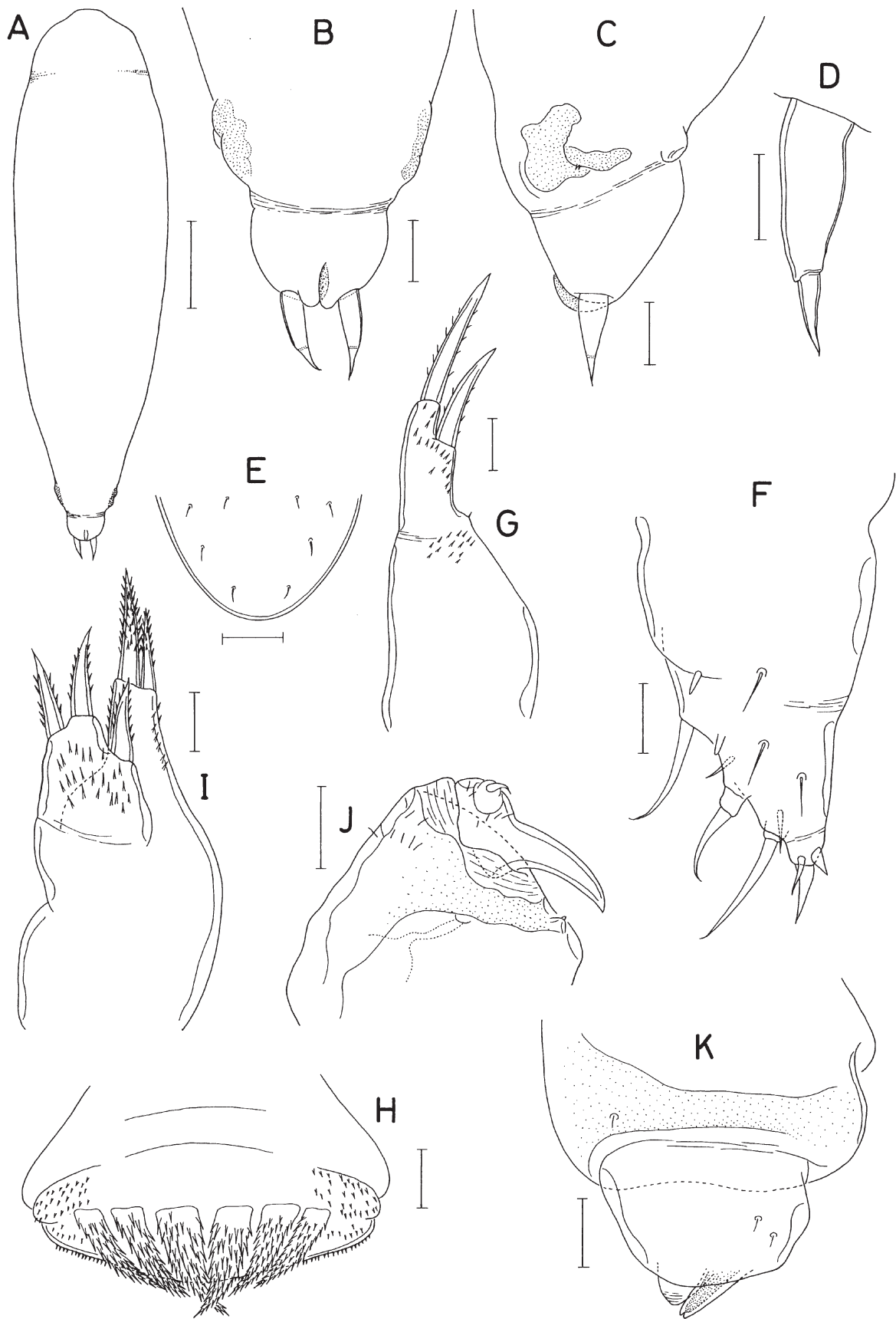
Labrum (Fig. 183H) broad, spinulose on ventral surface and along convex posterior margin; armed with 6 broad, medially curved, spinulose setiform processes, medial 2 longer and broader than lateral 4. Mandible absent. Maxillule (Fig. 183I) distally bilobed; inner lobe longer but narrower than outer lobe, tipped with 2 spinulose spines, 38 and 27 µm long; outer lobe spinulose, armed with 3 equal spines 28 µm long (2 on distal margin and 1 on medial margin). Maxilla (Fig. 183J) 2-segmented; proximal segment broad with 1 small tubercle on medial margin; distal segment terminating in strong claw, with 1 small seta proximally on lateral margin. Maxilliped absent.

Leg 1 (Fig. 183K) 2-segmented, both segments much wider than long; distal segment bearing rudimentary exopod and endopod; exopod sclerotized inside; endopod fleshy, shorter than exopod. Legs 2-4 same as leg 1. Leg 5 absent. Leg 6 probably represented by 2 minute spinules in genital area (Fig. 183C).

**Male.** Unknown.

**Remarks.** The labrum of *E. tasmanica* **sp. nov.** is armed with 6 setiform processes. Five other species of *Enteropsis* (*E. capitulata*, *E. fusiformis*, *E. georgiana*, *E. roscoffensis*, and *E. arctica*) also have 6 (or 5 or 6) processes on the labrum, like *E. tasmanica* **sp. nov.** The first four of these can be readily distinguished from the new species by the following characters: *E. capitulata* has rudimentary caudal rami and a distinctly 2-segmented antenna; *E. fusiformis* lacks caudal rami and has a claw-like distal segment of the antenna; *E. georgiana* has a longer, 4-segmented genitoabdomen and a 2-segmented antennule (Illg & Dudley, 1980); and *E. roscoffensis* has a claw-like distal part of the antenna and lacks a rostrum (Ooishi, 2008b).

The remaining species, *E. arctica*, is associated with several species of solitary ascidians in the White Sea (Marchenkov, 1994), and appears to be closely related to *E. tasmanica* **sp. nov.** However, in *E. arctica*, the body is



**FIG. 183.** *Enteropsis tasmanica* sp. nov., female. A, habitus, dorsal; B, posterior part of body, dorsal; C, posterior part of body, right; D, caudal ramus; E, rostrum; F, antennule; G, antenna; H, labrum; I, maxillule; J, maxilla; K, leg 1. Scale bars: A, 0.5 mm; B, C, 0.1 mm; D, E, J, K, 0.05 mm; F-I, 0.02 mm.

cylindrical (cf. fusiform in the new species), the caudal rami are vestigial with its terminal element not articulated from the ramus (cf. 2.6 times longer than wide), the antenna is 2-segmented (cf. unsegmented), the outer lobe of the maxillule is armed with 3 processes (cf. spines), and the 6 setiform processes on the labrum are small and subequal in length (cf. large, with median pair distinctly longer than lateral 4). These differences are sufficient to differentiate *E. tasmanica* **sp. nov.** from *E. arctica*.

### Genus *Mychophilus* Hesse, 1865

**Diagnosis.** Female: Body vermiform, unsegmented. Anus positioned dorsally, anterior to genital apertures. Caudal rami rudimentary, tipped with 1 small seta. Rostrum weakly developed or absent. Antennule small, 1- or 2-segmented, armed with few setae. Antenna 1- to 3-segmented; terminal segment usually claw-like. Labrum bearing 3 to 6 setiform processes (lacking processes in *M. capillatus* Kim I.H. & Moon, 2011; labrum unknown in *M. fallax* Stock, 1967). Mandible absent. Maxillule bilobed, with 0 or 2 setiform processes on inner lobe and 2 or 3 processes on outer lobe. Maxilla lobate, 1- or 2-segmented, tipped with 1 seta; if 2-segmented, distal segment very small (maxilla of *M. capillatus* unusual, *Enteropsis*-type). Legs 1-4 similar to those of *Enteropsis*. Legs 5 and 6 absent.

Male (of *M. roseus*): Body cycloform, with clear prosome-urosome division. Prosome consisting of cephalosome and first to fourth pedigerous somites. Urosome 6-segmented, including fifth pedigerous somite. Caudal rami armed with 6 setae. Rostrum well-developed. Antennule 6-segmented; armature formula 13, 2, 2, 2, 1, 6+2 aesthetascs. Antenna 3-segmented; first segment with 1 seta; terminal segment spiniform. Labrum rudimentary. Mandible absent. Maxillule small, 2-segmented, with unarmed proximal and 3 setae-bearing distal segment. Maxilla as in female. Maxilliped absent. Legs 1-4 biramous with 2-segmented protopod; coxae unarmed; basis with outer seta. Leg 1 exopod 2-segmented; other rami of legs 1-4 all 3-segmented. First endopodal segment of leg 1 unarmed. Second endopodal segment of leg 4 with 2 medial setae. Armature formula for legs 1-4 as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1:	0-0	1-0	I-0; I, I, 3	0-0; 0-1; 1, 1, 3
Leg 2:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-1; 1, 2, 3
Leg 3:	0-0	1-0	I-1; I-1; II, I, 5	0-1; 0-1; 1, 2, 3
Leg 4:	0-0	1-0	I-1; I-1; II, I, 4	0-1; 0-2; 1, 2, 2

Leg 5 represented by 2 separated setae on surface of fifth pedigerous somite. Leg 6 absent.

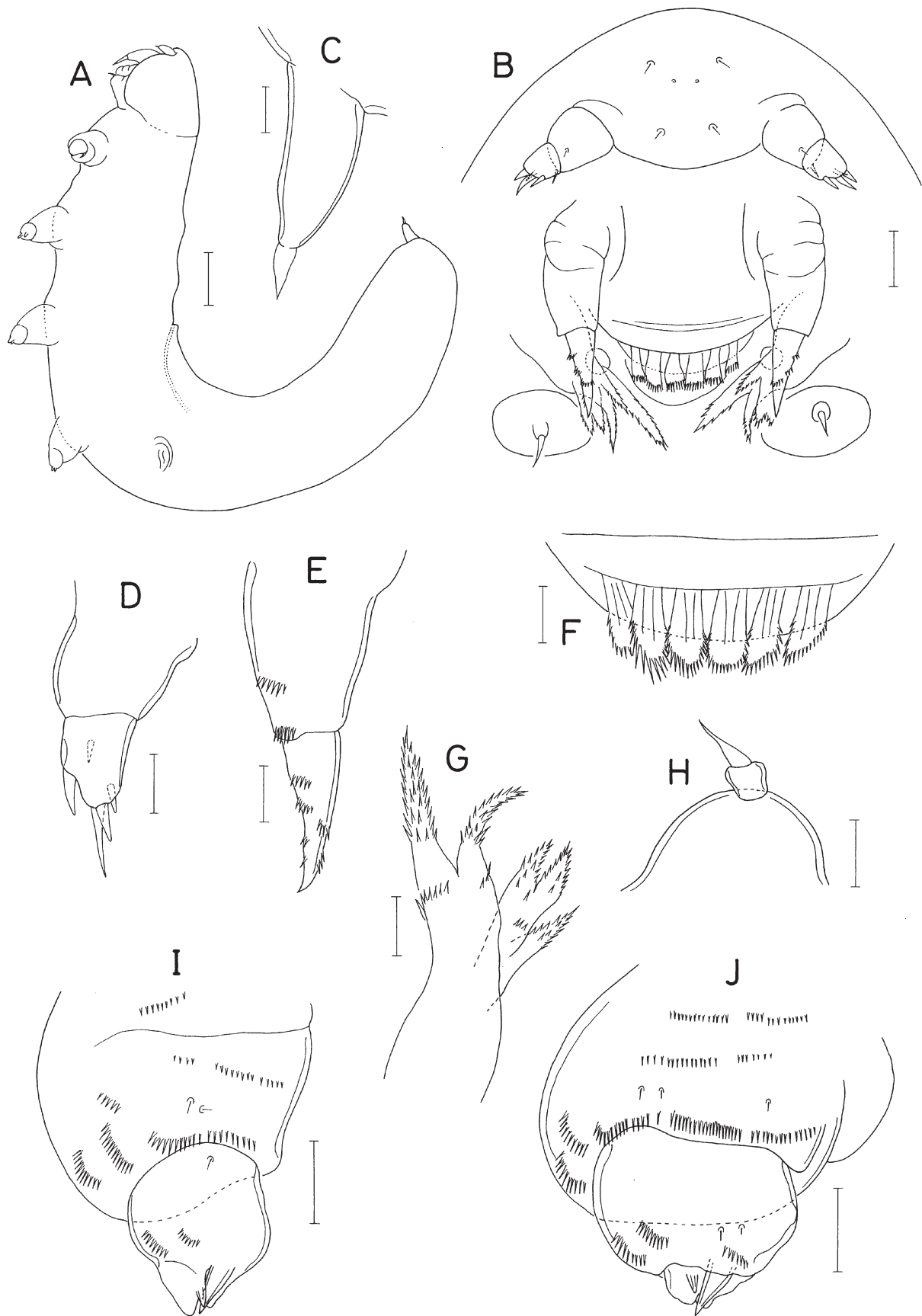
**Type species.** *Mychophilus roseus* Hesse, 1866 by original monotypy.

**Remarks.** Ooishi (2008c) redescribed both sexes of the type species of *Mychophilus*, *M. roseus* Hesse and *M. palmatus* López-González & Conradi, 1996. Subsequently Kim I.H. and Moon (2011) added a fourth species, *M. capillatus* Kim I.H. & Moon, 2011. *Mychophilus* has been characterized by the dorsally displaced anus positioned close to the level of genital apertures and by the lobate, unsegmented maxilla (Illg & Dudley, 1980; Boxshall & Halsey, 2004). *Mychophilus* is closely related to *Enteropsis*. Both genera share the same structure of the swimming legs and *M. capillatus* exhibits a *Mychophilus*-type position of the anus combined with an *Enteropsis*-type of maxilla, which is 2-segmented and bears a strong claw on the distal segment. *Mychophilus capillatus* was tentatively included in *Mychophilus* but its placement in this genus may need to be reviewed. Re-analysing of the relationships between these two genera will be facilitated by the discovery of the male of *Enteropsis*, which is currently unknown.

### *Mychophilus notialis* **sp. nov.**

(Fig. 184)

**Type material.** Holotype ♀ (MNHN-IU-2014-21589) and paratype ♀ (dissected, MNHN-IU-2014-21498) from *Botrylloides magnicoecum* (Hartmeyer, 1912); Kommetjie, Cape Town, South Africa, intertidal, Monniot coll., 05 February 1996.



**FIG. 184.** *Mychophilus notialis* sp. nov., female. A, habitus, left; B, cephalic appendages *in situ*, ventral; C, caudal ramus; D, antennule; E, antenna; F, labrum; G, maxillule; H, maxilla; I, leg 1; J, leg 4. Scale bars: A, 0.1 mm; B, I, J, 0.02 mm; C-H, 0.01 mm.



**Etymology.** The name *notialis* is from the Latin, meaning “southern”, alluding to the location of the type locality in the South Africa.

**Description of female.** Body (Fig. 184A) vermiform, cylindrical, unsegmented, recurved dorsally, consisting of cephalosome and trunk. Body length 1.63 mm; maximum width 273  $\mu\text{m}$ . Cephalosome defined from trunk by posterodorsal wrinkles. Genitoabdominal region longer than metasomal region; genital apertures positioned laterally at midlength of trunk. Anus located dorsally, positioned at level of insertion of leg 3. Caudal ramus (Fig. 184C) small, incompletely articulated from trunk, gradually narrowing distally, about 2.1 times longer than wide ( $40 \times 19 \mu\text{m}$ ), armed with 1 broad seta (12  $\mu\text{m}$  long) at apex.

Rostrum (Fig. 184B) as broad ridge connecting left and right antennules. Antennule (Fig. 184D) small, 35  $\mu\text{m}$  long, 2-segmented; proximal segment unarmed; distal segment shorter and narrower than proximal segment, armed with 5 setae. Antenna (Fig. 184E) 73  $\mu\text{m}$  long, 2-segmented, tapering, unarmed; proximal segment with 2 rows of spinules on lateral surface; distal segment claw-like, with pointed apex and several rows of spinules.

Labrum broad, with transverse row of 6 transparent, broad, tongue-like elements on ventral surface; elements subequal in length, marginally spinulose distally. Mandible absent. Maxillule (Fig. 184G) bilobed; larger inner lobe bearing 2 spinulose processes; smaller outer lobe bearing 3 spinulose processes (1 arising more proximally). Maxilla (Fig. 184H) 2-segmented; proximal segment unarmed; distal segment small, knob-like, tipped with 1 broad seta. Maxilliped absent.

Leg 1 (Fig. 184I) consisting of 2-segmented, unarmed protopod and rudimentary exopod and endopod. Proximal segment of protopod ornamented with several rows of spinules on anterior surface; distal segment with 2 or 3 rows of spinules on anterior surface. Exopod and endopod not articulated from protopod. Exopod sclerotized, claw-like, embedded in hyaline covering. Endopod fleshy, bearing 1 spiniform process on anterolateral surface. Legs 2, 3, and 4 (Fig. 184J) as leg 1 in form, but broader; exopod and endopod indistinctly articulated from distal segment of protopod. Legs 5 and 6 absent.

**Male.** Unknown.

**Remarks.** In *Mychophilus* the labrum and maxillule exhibit useful taxonomic characters. The labrum of *M. notialis* **sp. nov.** bears 6 setiform processes. Only *M. palmatus* is known to have this number of processes on the labrum (López-González & Conradi, 1996). Both species also have a maxillule bearing 2 processes on the inner lobe and 3 processes on the outer lobe. However *M. notialis* **sp. nov.** is easily distinguishable from *M. palmatus*, by having a 2-segmented antennule (cf. unsegmented in *M. palmatus*) and a 2-segmented antenna (cf. unsegmented in *M. palmatus*). The labrum is unknown in *M. fallax*, but this species is not confusable with *M. notialis* **sp. nov.** as it has a slender body, an antennule bearing 2 spinules distally, an antenna bearing a slender terminal claw, and a maxillule (referred to as the “mandible” by Stock, 1967) with a simple inner lobe.

The maxillule of *M. notialis* **sp. nov.** is armed with 2 processes on the inner lobe and 3 processes on the outer lobe as in *M. palmatus* and *M. roseus*. The type species, *M. roseus* has bipartite caudal rami, 3 processes on the labrum, and 3-segmented antenna (Ooishi, 2008c), and is therefore easy to distinguish from *M. notialis* **sp. nov.**

### *Mychophilus hesperius* **sp. nov.**

(Fig. 185)

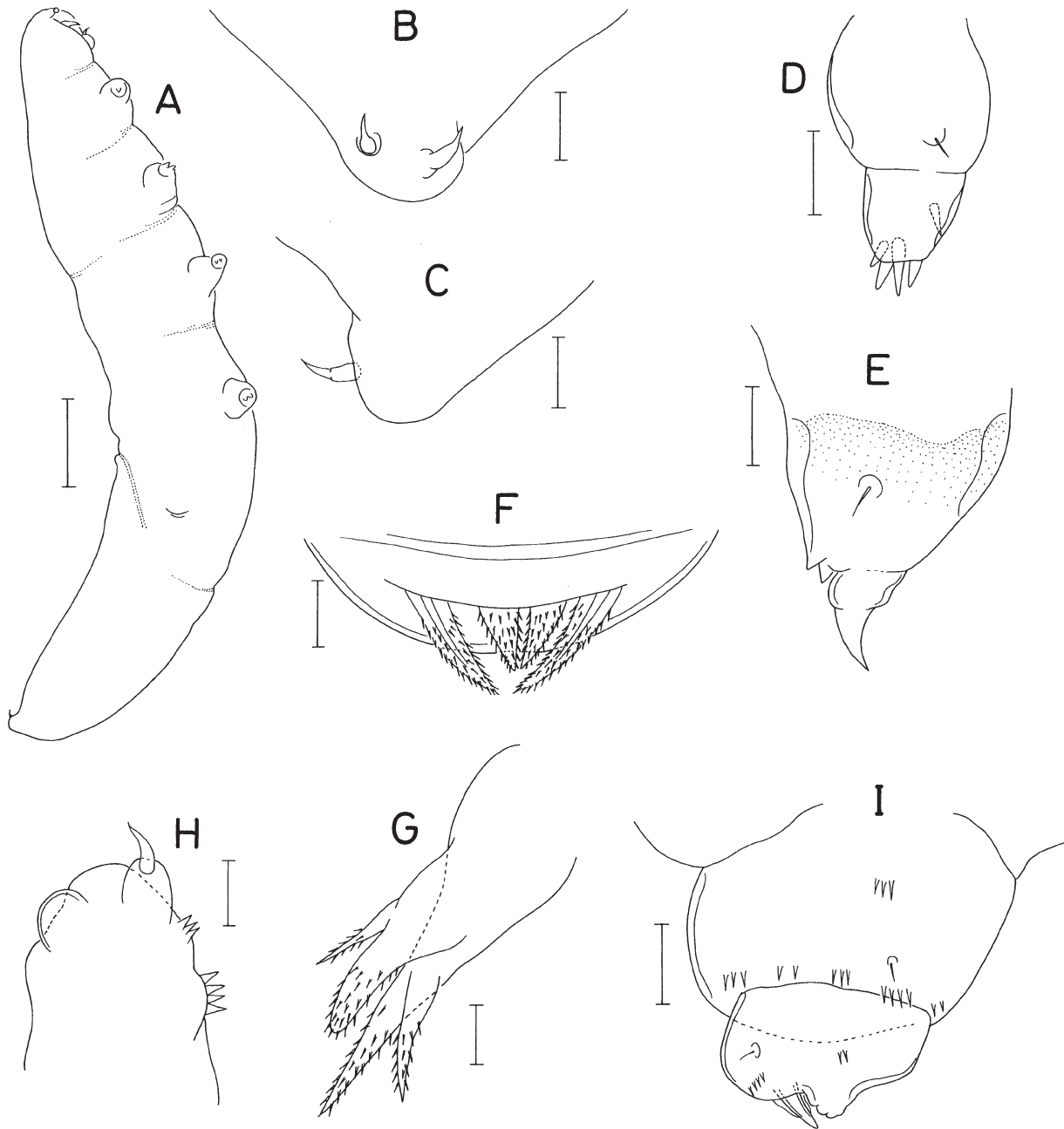
**Type material.** Holotype ♀ (MNHN-IU-2014-21590), 1 ♀ paratype (MNHN-IU-2014-21591), and 1 ♀ paratype (dissected, MNHN-IU-2014-21485) from *Symplegma brakenhielmi* (Michaelsen, 1904) (MNHN-IT-2008-8440 = MNHN S1/SYM/12); Saint François, côte sud de Grande Terre, Guadeloupe, Stn 18 (dive from quay of fishing port), Monniot coll., 25 December 1980.

**Etymology.** The name is derived from the Greek *hesper* (=western), referring to its collection from the West Indies.

**Description of female.** Body (Fig. 185A) vermiform, cylindrical, unsegmented, curved dorsally. Body length 1.80 mm; maximum width 327  $\mu\text{m}$  (at level of leg 4). First to fourth pedigerous somites obscurely defined by weak lateral constrictions. Genital apertures positioned laterally at 70% of body length. Anus positioned dorsally at 60% of body length (between level leg 4 and genital apertures). Region of genitoabdomen gradually narrowing poste-

riorly. Posterior part of body (Fig. 185B, C) lobate, bearing rudimentary caudal rami dorsally; each caudal ramus about 1.8 times longer than wide ( $9 \times 5 \mu\text{m}$ ), tipped with 1 small, broad seta,  $9 \mu\text{m}$  long.

Rostrum absent. Antennule (Fig. 185D) small, 2-segmented; proximal segment unarmed; distal segment slightly shorter and narrower than proximal segment; armed with 5 setae (1 proximal, 2 subdistal, and 2 distal). Antenna (Fig. 185E) 2-segmented; proximal segment unarmed, bearing 2 triangular processes at laterodistal corner; distal segment small, claw-like, obscurely articulated from proximal segment.



**FIG. 185.** *Mychophilus hesperius* sp. nov., female. A, habitus, right; B, distal part of body, dorsal; C, distal part of body, right; D, antennule; E, antenna; F, labrum; G, maxillule; H, maxilla; I, leg 1. Scale bars: A, 0.2 mm; B, C, I, 0.02 mm; D-H, 0.01 mm.

Labrum (Fig. 185F) broad, bearing 4 spinulose processes (medial pair shorter than lateral pair). Mandible absent. Maxillule (Fig. 185G) bilobed; longer inner lobe bearing 2 attenuated processes; shorter outer lobe bearing 1 broad, blunt process and 1 shorter, thin, setiform process. Maxilla (Fig. 185H) lobate, bearing 2 lobules subdistally, medial lobule tipped with 1 small seta, and ornamented with 2 groups (4 proximal and 3 distal) of spinules on medial margin. Maxilliped absent.

Leg 1 (Fig. 185I) consisting of 2-segmented, unarmed protopod and rudimentary rami. Protopod ornamented with scattered spinules on anterior surface. Exopod claw-like, articulated from distal segment of protopod; endopod not articulated at base, fleshy, with blunt tip. Legs 2-4 same as leg 1. Legs 5 and 6 absent.

**Male.** Unknown.

**Remarks.** *Mychophilus hesperius* **sp. nov.** can be differentiated from most of its congeners by the possession of 4 processes on the labrum. The exception is *M. fallax*, for which the labrum is unknown. However, *M. fallax* is not confusable with the new species because it carries a simple inner lobe and has 3 setiform elements on the outer lobe of the maxillule, and has an unsegmented maxilla (Stock, 1967). *Mychophilus hesperius* **sp. nov.** bears 2 processes on the inner and outer lobes of the maxillule. This is a unique feature of *M. hesperius* **sp. nov.**, which alone serves to characterize the species.

**Discussion.** Prior to this study, these four families collectively contained a total of 118 valid species classified in 15 recognized genera (Walter & Boxshall, 2020). Here we have added five new genera and 84 new species, taking the totals to 20 and 202, respectively. In common with previous studies of archinotodelphyid (Kim & Boxshall, 2020a) and notodelphyid copepods (Kim & Boxshall, 2020b) from the Monniot collection, this represents a dramatic increase in the documented species richness of the families. All three of these papers serve to emphasise the enormous gaps in our knowledge of the parasites and symbionts of marine invertebrate hosts. In order to better quantify the diversity of marine ecosystems and better understand energy flow through these systems, considerably more effort must be invested in collecting and describing symbiotic species.

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