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Phylogenetic relationships between arietellid genera (Copepoda: Calanoida), with the establishment of three new genera

S. OHTSUKA

Fisheries Laboratory, Hiroshima University, 1294 Takehara, Hiroshima 725, Japan

G.A. BOXSHALL

Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, England

H.S.J. ROE

Institute of Oceanographic Sciences Deacon Laboratory, Brook Road, Wormley, Godalming, Surrey GU8 5UB, England

CONTENTS

Synopsis. Ten genera, including three new genera, *Crassarietellus*, *Campaneria* and *Paraugaptiloides*, of the family Arietellidae (Copepoda: Calanoida) are newly defined or redefined with special reference to the genital systems of the females and fusion patterns and armature elements of appendages. The present study revealed that the single specimen reported as the male of *Sarsarietellus abyssalis* (Sars, 1905) represents a new genus, *Crassarietellus*, and that *Paraugaptilus mohri* Björnberg, 1975 belongs to the genus *Arietellus*. Ancestral and derived states and character transformations of the genital systems and the appendages in the family are discussed. A cladistic analysis for all 10 genera except for *Rhapidophorus* revealed that the Arietellidae consists of two lineages, the *Crassarietellus*-*Paramisophria*-*Pilarella*-*Metacalanus*-group and the *Campaneria*-*Sarsarietellus*-*Paraugaptiloides*-*Scutogerulus*-*Paraugaptilus*-*Arietellus*-group. The deep-sea hyperbenthic genera *Crassarietellus* and *Campaneria* are the most plesiomorphic in each group, and the shallow-water hyperbenthic/epipelagic/cave-living *Metacalanus* and the bathypelagic *Arietellus* and *Paraugaptilus* are relatively apomorphic.

INTRODUCTION

The family Arietellidae Sars, 1902 has been regarded as one of the most primitive families in the Calanoida based on the segmentation of appendages and the genital systems (Andronov, 1974; Park, 1986; Huys & Boxshall, 1991). The Arietellidae had hitherto accommodated the following eight genera: *Rhapidophorus* Edwards, 1891, *Arietellus* Giesbrecht, 1892, *Paramisophria* T. Scott, 1897 (= *Parapseudocyclops* Campaner, 1977), *Metacalanus* Cleve, 1901 (= *Scottula* Sars, 1902), *Paraugaptilus* Wolfenden, 1904, *Scutogerulus* Bradford, 1969, *Sarsarietellus* Campaner, 1984, and *Pilarella* Alvarez, 1985. The genus *Phyllopus* Brady, 1883 was separated by Brodsky (1950) who proposed placing it in a new subfamily; it was later removed from the Arietellidae and placed in its own family, the Phyllopodidae

Table 1 Sampling date, locality, depth and gear used for arietellid collection.

Species	Sex	Number of specimens	Date	Locality	Depth (m)	Gear	Remarks
Crassarietellus huysi[1]	♀	1	18 IV 1977	20°18.5′N, 21°41.2′W 20°20.8′N, 21°53.0′W	3974–4036	RMT8	5–20 m off bottom
	♀	2	18 IV 1977	20°19.7′N, 21°51.3′W 20°18.4′N, 21°40.5′W	4008–4060	RMT8	5–20 m off bottom
Crassarietellus sp.[2]	♂	1	24 VI 1908	38°02′N, 10°44′W	0–4800	Richard net	
Campaneria latipes[3]	♂	1	4 X 1968	37°07′S, 177°14′E	1234–1260	Modified Menzies trawl	Some small stones
Paraugaptiloides magnus[4]	♂	1	11 X 1968	34°38′S, 174°36′E	1697	Modified Menzies trawl	
Arietellus aculeatus	♀	1	23 II 1979	15°00′–15°05′N 158°00′–158°01′W	400	IKMWT	
	♂	2	23 II 1979	15°10′–31°14′S 71°56′–71°58′W	400	IKMWT	
Arietellus mohri[5]	♀	1	24 VI 1962	31°10′–31°14′S 71°56′–71°58′W	1932–3142	Phlenger corer	
Arietellus pavoninus[6]	♀	1	28 XI 1965	28°05′N, 14°06′W	600–720	N113H	
Arietellus plumifer	♀	1	28 VI 1985	31°20′N, 25°17′W 31°18′N, 25°27′W	600–840	RMT1	
	♀[6]	1	26 XI 1965	28°07′N, 14°07′W	680–800	N113H	
	♂[6]	1	13 XI 1965	28°04′N, 14°12′W	360–410	N113H	
Arietellus setosus[6]	♂	1	29 XI 1965	28°05′N, 14°10′W	50–85	N113H	
Arietellus simplex[6]	♂	1	28 XI 1965	28°05′N, 14°06′W	750–900	N113H	
Arietellus sp.[6]	♀	1	11 XI 1965	28°04′N, 14°11′W	460–510	N113H	
Metacalanus sp. 1	♀	4	23 V 1989	26°17.9′N, 126°54.2′E	167	Sledge-net	
	♂	1	23 V 1989	26°17.9′N, 126°54.2′E	167	Sledge-net	
Metacalanus sp. 2	♀	4	23 V 1989	26°17.9′N, 126°54.2′E	167	Sledge-net	
Paramisophria giselae[7]	♀	2	3 IX 1970	23°19′S, 41°57′W	100	Plankton net adapted to dredge	
Paramisophria japonica[8]	♀	1	23 V 1989	26°17.9′N, 126°54.2′E	167	Sledge-net	
Paramisophria reducta[9]	♂	1	25 II 1984	Jameos del Agua	10–28	Plankton net	
Paraugaptilus buchani[6]	♀	1	16 XI 1969	17°41′N, 25°18′W	410–500	RMT1	
	♀	1	15 XI 1965	27°48′N, 13°55′W	450–510	N113H	
	♂	1	24 XI 1965	28°06′N, 14°08′W	775–830	N113H	
Paraugaptilus similis	♀	1	21 I 1978	04°02′S, 150°00′W	275	IKMWT	
	♂	1	21 I 1978	04°02′S, 150°00′W	275	IKMWT	
Pilarella longicornis[10]	♀	1	22 VI 1970	28°36′S, 47°55′W	135	Plankton net adapted to dredge	
Scutogerulus pelophilus[3]	♀	1	10 X 1968	34°56′S, 175°23′E	1383–1397	Modified Menzies trawl	*Globigerina* Ooze
Sarsarietellus abyssalis[2]	♀	1	4–5 VIII 1897	38°37′N, 28°14′W	1260	'Nasse'	

Sampling data after: [1] Boxshall & Roe (1980); [2] Sars (1925); [3] Bradford (1969); [4] Bradford (1974); [5] Björnberg (1975); [6] Currie et al. (1969); [7] Campaner (1977); [8] Ohtsuka et al. (1991); [9] Ohtsuka et al. (1993a); [10] Alvarez (1985).

(Campaner, 1977; Bowman & Abele, 1982).

Arietellids are widely distributed from neritic to oceanic waters and range vertically from the epipelagic zone to the bathypelagic hyperbenthic layer (Campaner, 1984). Recently, cave-living species of *Metacalanus* and *Paramisophria* have been discovered (Ohtsuka et al., 1993a). However, neither phylogenetic nor ecological studies on the family have been carried out in detail, partly because of the paucity of pelagic arietellids in the water column, and partly because of the lack of intense sampling effort in the hyperbenthic layers where many species are found.

Campaner (1984) first examined the relationships between arietellid genera. He divided them into two morphologically and ecologically different groups. The first group comprised *Arietellus*, *Paraugaptilus* and *Scutogerulus*, which are characterized by a reduced female leg 5 and complex male leg 5, and are distributed in the bathypelagic or deep-sea hyperbenthic zones. The second group consisted of *Metacalanus*, *Paramisophria*, *Rhapidophorus* and *Sarsarietellus* and was diagnosed by characters such as the relatively well developed leg 5 in the female (except for *Metacalanus*) and the simplified second exopod segments and reduction of endopod of leg 5 in the male. These are highly adapted hyperbenthic forms found in relatively shallow waters (<1000 m deep) or in epipelagic waters in neritic regions. However, Campaner's (1984) classification relied solely on the structure of the fifth legs although he recognized interspecific variation between congeners in leg characters.

The present paper describes a new arietellid genus collected from the deep-sea hyperbenthic community in the northeastern Atlantic, and establishes two new genera to accommodate previously known arietellids, the male of *Scutogerulus pelophilus* Bradford, 1969 and the male of *Paraugaptilus magnus* Bradford, 1974. Revised diagnoses of all known arietellid genera, except for *Rhapidophorus*, are given here together with supplementary descriptions. Character transformations of the genital systems and appendages of these arietellids are considered in detail. A cladistic analysis is employed to help clarify phylogenetic relationships between the arietellid genera.

Table 2 Characters used in the cladistic analysis for genera of the family Arietellidae. Codes 0 to 2 refer to transformation series of multi-state characters; 0: plesiomorphic state; 9: missing data.

1.	Gonopore and copulatory pore sharing common opening	yes/no	0/1
2.	Right and left copulatory pores	separate/fused	0/1
3.	Lengths of right and left antennules of female	equal/uneuqal	0/1
4.	Fusion of female antennulary segments I-III and IV	separate/fused	0/1
5.	Fusion between female antennulary segments XXIII and XXIV	separate/fused	0/1
6.	Aesthetasc present on female antennulary segment IV	present/absent	0/1
7.	Aesthetasc present on female antennulary segment VI	present/absent	0/1
8.	Aesthetasc present on female antennulary segment VIII	present/absent	0/1
9.	Aesthetasc present on female antennulary segment X	present/absent	0/1
10.	Aesthetasc present on female antennulary segment XII	present/absent	0/1
11.	Modification of seta into process on male antennulary segment XV	no/yes	0/1
12.	Fusion of male antennulary segments XXI & XXII	separate/fused	0/1
13.	Seta adjacent to aesthetasc on male antennulary segments II	present/absent	0/1
14.	Seta adjacent to aesthetasc on male antennulary segment III	present/absent	0/1
15.	Modification of seta into process on male antennulary segment XXII	no/yes	0/1
16.	Process on male antennulary compound segment XXIV-XXV	no/yes	0/1
17.	Seta on first endopod segment of antenna	present/absent	0/1
18.	Proximal inner seta on mid-margin of second endopod segment of antenna	present/absent	0/1
19.	Vestigial element on second endopod segment of antenna	present/absent	0/1
20.	1-segmented, rudimentary mandibular endopod with 1 or 2 setae	present/absent	0/1
21.	Outer terminal seta on fifth exopod segment of mandible	normal/reduced	0/1
22.	Process on maxillulary praecoxal arthrite	present/absent	0/1
23.	Inner basal enditic seta of maxillule	present/absent	0/1
24.	Third seta of maxillulary endopod	present/absent	0/1
25.	Inner angle seta of maxillulary endopod	present/absent	0/1
26.	Distal seta on first on first praecoxal endite of maxilla	present/absent	0/1
27.	Reduction of seta a on sixth endopod segment of maxilliped (length of seta at most as long as the segment)	no/yes	0/1
28.	Reduction of seta b on sixth endopod segment of maxilliped (length of seta at most as twice as long as segment)	no/yes	0/1
29.	Proximal spine on outer margin of third exopod segment of leg 1	present/absent	0/1
30.	Inner coxal seta of leg 4	present/absent	0/1
31.	Fusion between endopod and basis of female leg 5	separate/fused	0/1
32.	Inner margin of endopod of female leg 5 with proximal (seta A) and distal (seta B) setae	A+B present/ A or B absent	0/1
33.	One seta (A or B) on inner margin of endopod of female leg 5	present/absent	0/1
34.	Inner angle seta on distal margin of endopod of female leg 5	present/absent	0/1
35.	Exopod segment of female leg 5	partly defined/ unsegmented/absent	0/1/2
36.	Spine (element d) on outer distal angle of exopod of female leg 5	present/absent	0/1
37.	Left endopod of male leg 5 (including incomplete fusion)	2-segmented/ 1-segmented/absent	0/1/2
38.	Right endopod of male leg 5	1-segmented/absent	0/1
39.	Seta c on third exopod segment of left male leg 5	present/absent	0/1
40.	Setae e and f of left male leg 5 transformed into bifid process	no/yes	0/1
41.	Third exopod segment of left male leg 5 rotated so that vestigial outer margin elements now on inner surface	no/yes	0/1
42.	Seta f on third exopod segment of right male leg 5	well developed/minute	0/1
43.	Seta c on third exopod segment of right male leg 5	present/absent	0/1
44.	Fusion between coxa and basis of right male leg 5	separate/fused	0/1

Table 3 Character matrix for analysis using PAUP 3.0.

Crassarietellus	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	0	0	1	0	0	0	9	9	0
Paramisophria	1	1	1	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0
Metacalanus	1	0	1	1	0	1	1	1	1	0	0	1	1	1	1	0	0	1	1	0	0	1	1	1	1	1	0	0	1	1	1	1	1	1	1	1	2	1	1	0	0	0	1	0
Arietellus	1	1	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1	1	0	1	1	0	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	1	0	1	1	1
Paraugaptilus	1	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	0	1	1	1	1	2	2	1	0	1	1	1	1	1	1
Scutogerulus	0	0	0	0	0	1	0	0	0	0	9	9	9	9	9	9	1	0	0	0	0	1	0	1	1	1	1	1	1	1	0	1	1	1	0	1	9	9	9	9	9	9	9	9
Sarsarietellus	1	1	0	0	0	1	0	0	0	0	9	9	9	9	9	9	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	0	0	0	0	0	9	9	9	9	9	9	9	9
Pilarella	0	0	1	1	0	1	1	0	0	0	9	9	9	9	9	9	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	1	1	1	1	1	9	9	9	9	9	9	9	9
Campaneria	9	9	9	9	9	9	9	9	9	9	0	0	1	1	1	0	0	0	1	0	0	0	0	1	0	0	1	0	0	1	9	9	9	9	9	9	0	0	1	0	0	1	1	0
Paraugaptiloides	9	9	9	9	9	9	9	9	9	9	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	9	9	9	9	9	9	0	0	0	1	1	1	1	1

MATERIALS AND METHODS

The present study is based on collections deposited in The Natural History Museum, London, the New Zealand Oceanographic Institute, the United States National Museum, Smithsonian Institution, the Zoological Museum, University of Oslo, the University of Sao Paulo, and Hiroshima University. Sampling data and locality are summarized in Table 1. Specimens, except for those previously mounted, were dissected and mounted in Gum-chloral and observed with a differential interference contrast microscope (Olympus BH-2). The genital double-somites of females of several species were observed with a scanning electron microscope (Hitachi S-800). The morphological terminology is based on Huys & Boxshall (1991). Type specimens of the new genera are deposited in The Natural History Museum and the New Zealand Oceanographic Institute.

Phylogenetic relationships between genera were analyzed using PAUP version 3.0 prepared by D. Swofford, Illinois Natural History Survey. The character matrix (Tables 2,3) summarizes the character distributions among the 10 genera available for study. A multistate scoring system was employed and missing characters were scored 9. A hypothetical composite ancestor was included in the analysis which scored 0 for all characters. The options employed in the analysis were Branch and Bound, which guaranteed to find all the most parsimonious trees, and the MINF optimisation, which assigns character states so that the f-value is minimized. All characters were set as irreversible using the Camin-Sokal option.

The abbreviations used in the text and figures 1 to 37 are as follows: cd: copulatory duct; cp: copulatory pore; g: gonopore; o: oviduct; rd: receptacle duct; s: spermatophore remnant; sr: seminal receptacle.

SYSTEMATICS

Family Arietellidae Sars, 1902

Diagnosis (emend.) Female. Body of variable size (from ca. 0.8 to 7 mm), relatively robust, rarely compressed.Cephalosome and first pedigerous somite separate or weakly fused; fourth and fifth pedigerous somites completely fused. Cephalosome round or pointed at apex; rostrum produced ventrally, with pair of filaments. Posterior corner of prosome sharply or weakly produced, with or without dorsolateral and/or ventrolateral process. Urosome comparatively short, 4-segmented; genital double-somite with single or paired gonopores and copulatory pores; gonopore(s) located ventrolaterally or ventrally, with or without opercular plate; copulatory pore sharing common opening with gonopore or separate from gonopore, located ventro-medially or -posteriorly, rarely ventrally on right side; seminal receptacles usually paired, rarely left receptacle entirely lacking. Egg-sac present or absent. Caudal rami well defined, symmetrical or slightly asymmetrical, relatively short, with vestigial seta I, well developed or reduced setae II–III, well developed setae IV–VI and small seta VII.

Antennules symmetrical or asymmetrical, longer on left side than on right, sometimes differing in fusion pattern and armature; 16- to 22-segmented; segments I to III, rarely up to VI fused; segments X to XII more or less fused; segments XXIII and XXIV separate or fused; segments XXV and XXVI completely or incompletely fused; segments II, XXII–XXIV, XXVI and XXVII lacking aesthetasc; segment IV, VI, VIII–X, XII and XIII with or without aesthetasc; segment XIII with 1 or 2 setae; compound segment XXVI–XXVIII with 8 or 9 elements; posterior margin of proximal segments fringed with row of setules or not. Antenna: basal seta present; both rami separate from basis; endopod 2-segmented, first segment with 0–1 inner seta at midlength, second segment elongate, with 1–3 inner setae medially and 5 or 6 setae terminally; exopod indistinctly 6- to 10-segmented, ancestral segments I–III and IX unarmed. Mandible: gnathobase well chitinized, with 3 or 4 sharp teeth; endopod rudimentary, 1-segmented with 1 or 2 setae terminally or completely absent; first exopod segment with normal or reduced seta, fifth segment carrying 2 setae, one of which sometimes vestigial. Maxillule: praecoxal arthrite with 0–6 elements; coxal endite with 1 seta or unarmed; coxal epipodite carrying 5–9 setae; inner basal seta representing endite vestigial or absent; endopod bulbous, 1-segmented, with 0–3 setae or completely incorporated to basis; exopod lobate, bearing 3 long setae. Maxilla well developed; first praecoxal endite with 1 or 2 setae and 1 vestigial element, second praecoxal endite having 1 or 2 setae; first and second coxal endites each with 2 setae; basal spine stout, spinulose or bare; endopod 4-segmented, with chitinized long setae, setal formula 1,3,2,2. Maxilliped elongate; syncoxa with 1 medial and 2 terminal setae; basis with patches of setules or spinules and 2 setae medially; endopod 6-segmented, first segment almost fully incorporated into basis, setal formula 1,4,4,3 (rarely 2),3 (rarely 2),4, sixth segment with 2 outermost terminal setae (setae 'a' and 'b', see Fig. 5C) reduced or not.

Legs 1–4 with distinctly 3-segmented rami or, very rarely, with endopod segments of leg 1 incompletely fused. Seta and spine formula of legs 1–4 as shown in Table 4.

Leg 5 variable but not natatory, almost symmetrical; coxae and intercoxal sclerite separate or fused; basis and endopod separate or fused; endopod with 0–4 setae; exopod 1- to 3-segmented or completely fused with basis, carrying 0–5 elements.

Male. Body similar to that of female, but urosome 5-segmented. Left antennule geniculate, 16- to 20-segmented; segments I to IV fused; segments XI to XV more or less fused; segments XXI and XXII fused or rarely separate; segments XXIII and XXIV separate; segments XXV and XXVI completely or incompletely fused; segments II and III with 1 or 2 setae; segments X, XII–XIV and XX with anterior process; segments XIX and XXI with 2 processes; segment XIII with 0–1 seta; segments XV, XXII and XXIV with or without process; proximal segments often with row of setules along posterior margins. Mouthparts and legs 1–4 similar to

Table 4 Spine and seta formula of legs 1–4.

	Coxa	Basis	Exopod segment	Endopod segment
Leg 1	0–1	1–1	I–1;I–1;II/I,1/I,4	0–1;0–2;1,2,2
Leg 2	0–1	0–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4/3
Leg 3	0–1	0–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4/3
Leg 4	0–0/1	1–0	I–1;I–1;III,I,5	0–1;0–2;2,2,3/2

those of female or slightly different in armature elements of antennary second endopod segment and mandibular first exopod segment.

Leg 5 variable, but not natatory, almost symmetrical to strongly asymmetrical; coxae and intercoxal sclerite fused to form common base or separate; right basis sometimes fused with coxa; right endopod 1-segmented, bulbous or absent; right exopod distinctly or indistinctly 3-segmented, first and second segments each with seta on outer margin (rarely first segment unarmed), second segment with tuft of setules on inner distal angle of second segment, third segment with 0–3 elements terminally; left endopod 1- or 2-segmented, unarmed or completely absent; left exopod distinctly or indistinctly 3-segmented, first and second segments each with seta on outer margin, third segment with 1–3 elements terminally.

TYPE GENUS. *Arietellus* Giesbrecht, 1892.

REMARKS. The above diagnosis excludes *Rhapidophorus* Edwards, 1891, which was inadequately described and has never been redescribed. Although the family was briefly defined by Sars (1902), Rose (1933), Brodsky (1950) and Campaner (1977), the present amended definition includes new information on the genital systems of females and the armature elements on the appendages.

Genus Crassarietellus gen. nov.

DIAGNOSIS. Female. Body compact, prosome ovoid in dorsal view; cephalosome separate from first pedigerous somite; posterior corner of prosome produced posteriorly to form rounded lobe. Urosome short, at most one-third as long as prosome; genital double somite wider than long, with pair of gonopores ventrolaterally and paired copulatory pores each located beneath ventral projection; anal operculum not developed; caudal rami symmetrical, longer than wide, with vestigial seta I and normally developed seta II.

Antennule symmetrical reaching to posterior end of second pedigerous somite, 22-segmented; segments I–III fused, with 7 setae and 2 aesthetascs; segments IV, VI, XII and XIII each with 2 setae and 1 aesthetasc; segments XXIII and XXIV separate; compound segment XXVI–XXVIII with 8 setae and 1 aesthetasc; posterior margin of ancestral segments I to XIII fringed with long setules; segments IV–VIII with transverse row of long setules along distal end of segment. Antenna: first endopod segment with medial inner seta; second segment bearing 3 midlength and 5 terminal setae; exopod indistinctly 10-segmented exopod. Mandibular gnathobase with tuft of setules at midlength and 3 teeth on cutting edge. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long.

Maxillule: praecoxal arthrite with 5 stout, serrate spines and 1 process; coxal epipodite having 6 setae; coxal endite bearing long seta; second basal endite with vestigial seta; endopod rudimentary, 1-segmented with 2 setae. Maxilla: first syncoxal endite with 2 setae and vestigial element; second syncoxal endite with 2 setae; basal endite carrying stout spine with row of spinules medially. Maxilliped with second to sixth endopod segments bearing 4, 4, 3, 3 and 4 setae, respectively; innermost seta on fourth and fifth endopod segments not reduced; setae a and b on sixth endopod segment not reduced.

Leg 1 bearing 2 outer lateral spines on third exopod segment. Leg 5 having distinctly 1-segmented, rudimentary endopod with 2 setae and indistinctly 3-segmented exopod with 3 outer lateral and 2 terminal spines.

Male. Left antennule geniculate, 19-segmented; segments I–IV fused, with 9 setae and 4 aesthetascs; segments XXI and XXII fused; segments I to X fringed with setules along posterior margin; segments IV to VIII with transverse row of setules as in female. Mouthparts and legs similar to those of female.

Leg 5 with coxae and intercoxal sclerite incompletely fused to form common base; coxa separate from basis. Right leg lacking endopod; exopod, at least 2-segmented, first segment with outer spine on distal corner.Left leg: endopod incompletely 2-segmented, first segment expanded, second segment small, semispherical; exopod distinctly 3-segmented, first segment with spine on outer corner, second segment expanded, bearing outer spine at midlength, third segment small, having 2 small outer setules and chitinized, long terminal seta.

TYPE SPECIES. *Crassarietellus huysi*, gen. et sp. nov.

Other species. *Crassarietellus* sp. based on a male which was erroneously assigned to *Scottula abyssalis* Sars, 1905 by Sars (1924, 1925).

REMARKS. Sars (1924, 1925) assigned one male collected from off Lisbon to *Scottula abyssalis* Sars, 1905, the female of which was captured off the Azores. However, this male should be included in the new genus *Crassarietellus* based on the similarities of the mouthparts: the indistinctly 10-segmented antennary exopod (compare Fig. 1F with Fig. 7D); 5 serrate spines and a process on the praecoxal arthrite and 6 setae on the coxal epipodite of the maxillule (Figs 5A, 8A); 2 non-reduced setae on the sixth endopod segment of the maxilliped (Figs 5C, 8E). Additionally, a transverse row of setules is present, on each of the antennulary segments IV to VIII in the male (Fig. 7A), that is found only in the genus *Crassarietellus*. The ornamentation of the appendages of the male, such as the many tiny spinules along the outer margin of the mandibular palp and the stout, outer processes on the exopod segments of legs 1 to 4, also supports the proposal to place the male in *Crassarietellus*. The right leg 5 of the male lacks distal exopod segment(s), a condition which Sars (1924, 1925) misinterpreted as '1-segmented left' exopod.

ETYMOLOGY. The new generic name *Crassarietellus* (Latin crassus meaning thick) refers to the ovoid, compact body form of the new genus. The specific name is named in honour of Mr. Rony Huys.

ECOLOGICAL NOTE. The type species of the new genus was found in near-bottom samples taken at depths of 3974–4060 m. The plump body and the relatively short antennules indicates that the new genus is hyperbenthic.

Crassarietellus huysi gen. et sp. nov. (Figs 1–6)

MATERIAL EXAMINED. 3 ♀♀.

TYPES. Holotype: ♀, 18 IV 1977, North Atlantic (off western Africa), 20°8.5′N, 21°1.2′W–20°20.8′N, 21°53.0′W, 3974–4036 m in depth, dissected and mounted on slides, prosome and urosome preserved in 70% ethanol, BM(NH) 1993. 424. Paratype 1: ♀, 18 IV 1977, 20°19.7′N, 21°51.3′N–20°18.4′N, 21°40.5′W, 4008–4060 m in depth, dissected and mounted on slides, prosome preserved in 70%

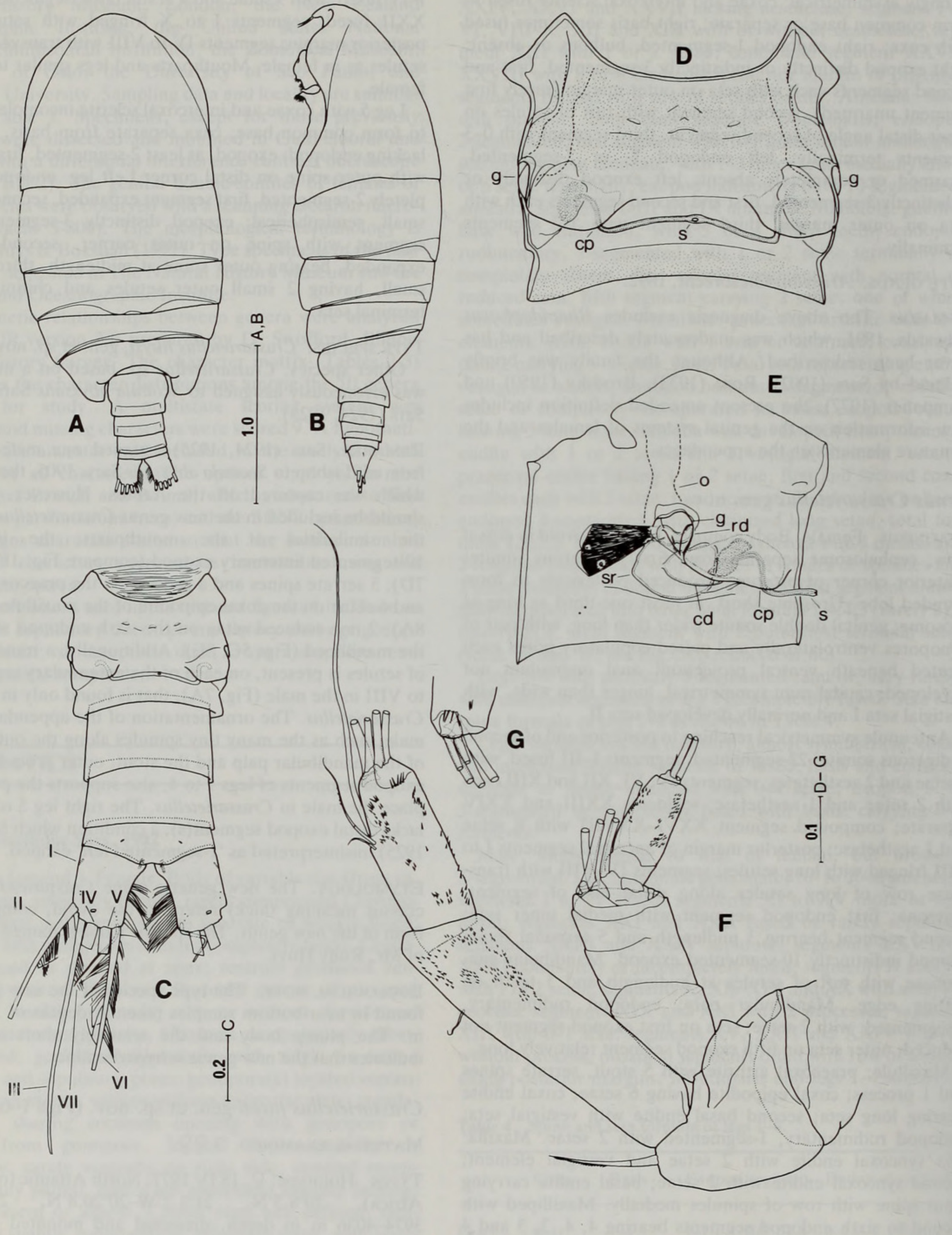

Fig. 1. *Crassarietellus huysi* gen. et sp. nov., female (holotype: F,G; paratype: A-E). A, Habitus, dorsal view; B, Habitus, lateral view; C, Urosome, ventral view; D, Genital double-somite, ventral view; E, Genital double-somite, lateral view, cd: copulatory duct; cp: copulatory pore; g: gonopore; rd: receptacle duct; o: oviduct; s: spermatophore remnant; sr: seminal receptacle; F, Antenna, one terminal seta on second endopod segment missing; G, Terminal part of second endopod of other antenna. Scales in mm.

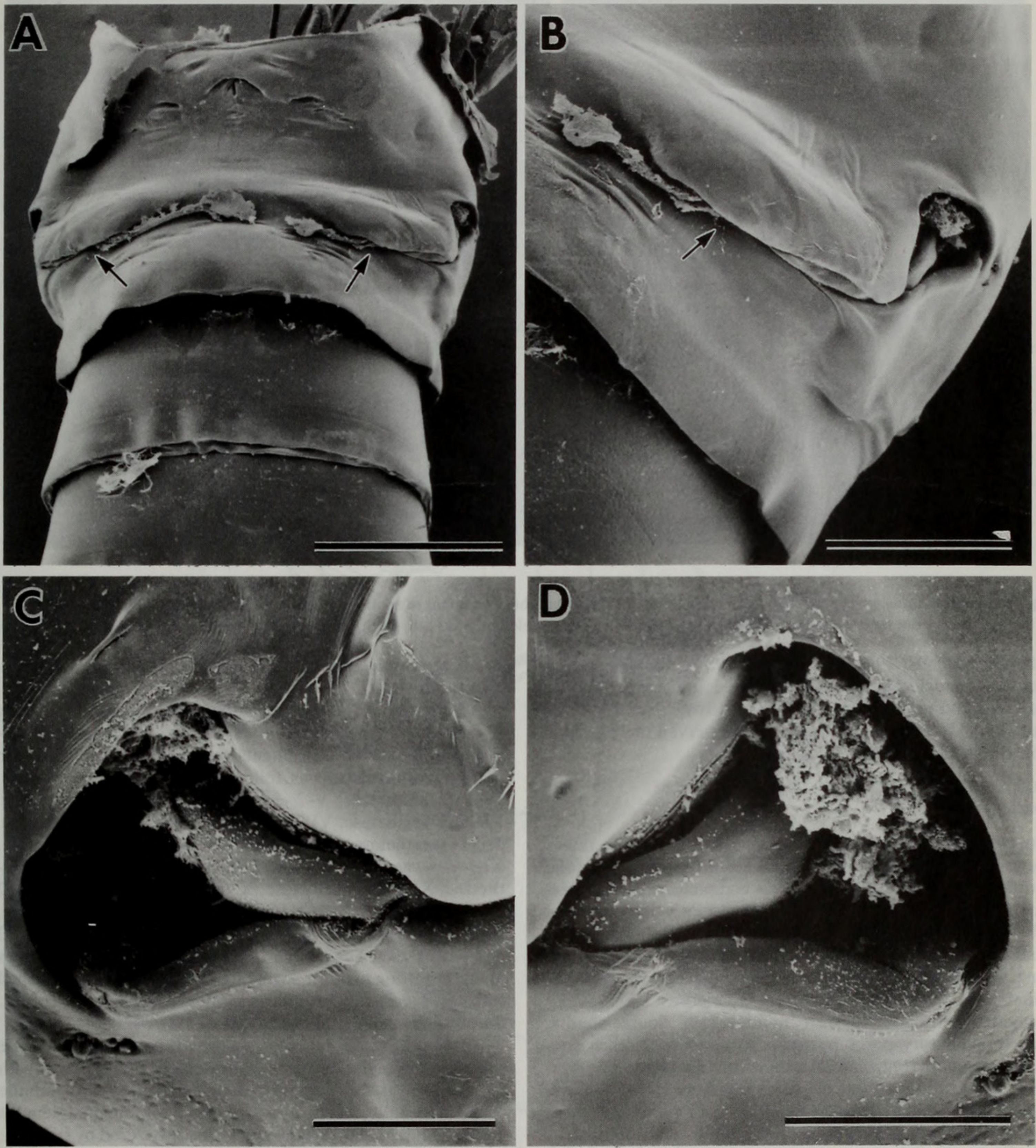

Fig. 2. *Crassarietellus huysi* gen. et sp. nov., female. SEM micrographs of genital double-somite of female. A, Genital double-somite, ventral view, scale bar = 200 μm (arrows indicating positions of copulatory pores); B, Gonopore and copulatory pore (indicated by arrow), scale bar = 100 μm; C, Right gonopore, scale bar = 30 μm; D, Left gonopore, scale bar = 30 μm.

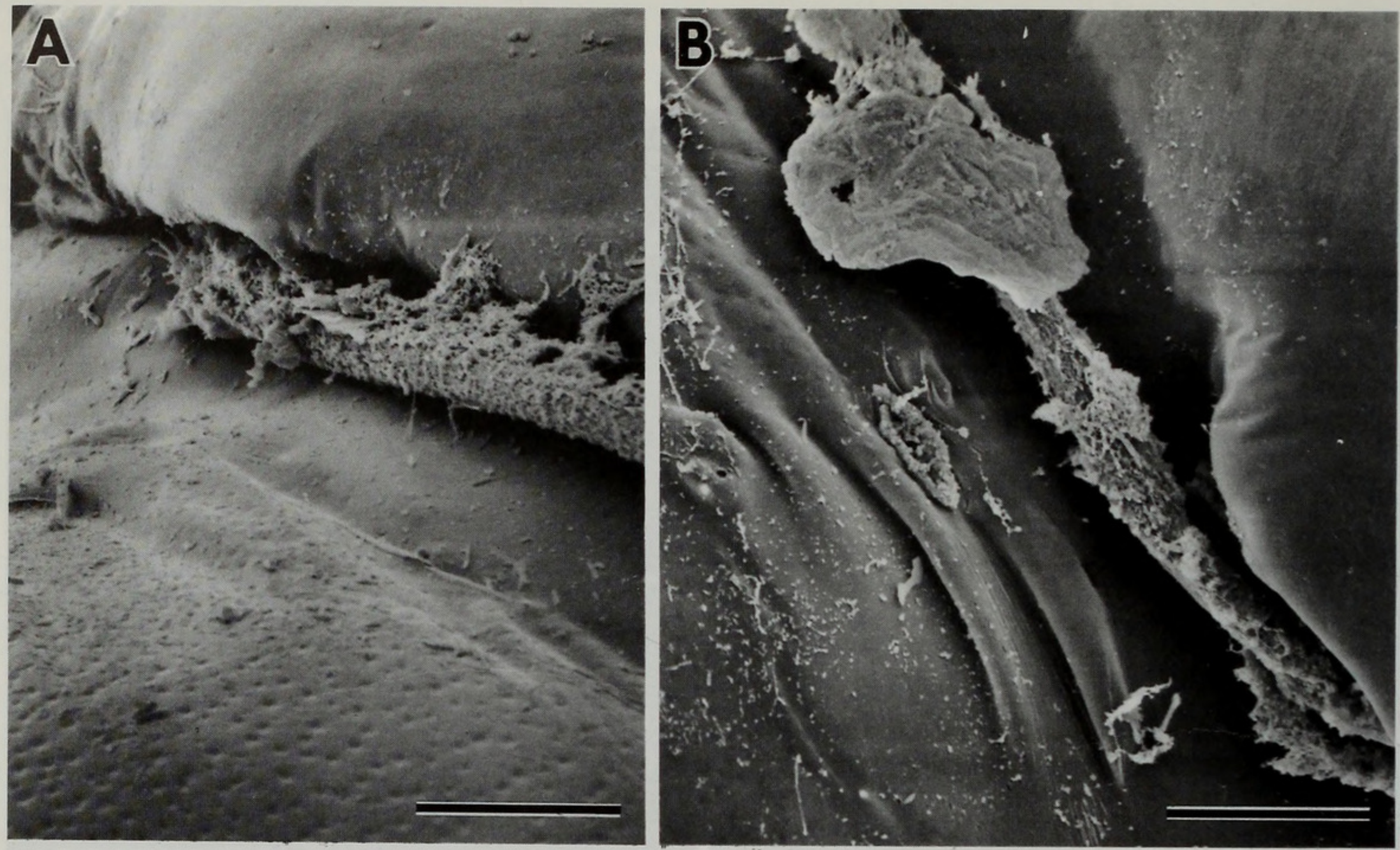

Fig. 3 *Crassarietellus huysi* gen. et sp. nov., female. SEM micro-graphs of remnant of spermatophore attached to genital double-somite of female. A, Spermatophore remnant penetrating copulatory pore, scale bar = 20 μm; B, Spermatophore remnant, scale bar = 20 μm.

ethanol, BM(NH) 1993. 425. Paratype 2: ♀, the same collection date and locality as in paratype 1, only legs 2 and 3 dissected and mounted on glass slides, urosome mounted on stub for SEM examination, prosome preserved in 70% ethanol, BM(NH) 1993. 426.

BODY LENGTH. 3.88 mm (holotype); 3.88, 3.85 mm (paratypes).

DESCRIPTION. Female. Body (Fig. 1A,B) oval in dorsal view. Cephalosome and first pedigerous somite separate; fourth and fifth pedigerous somites completely fused; posterior corner of prosome produced posteriorly into rounded lobe directed backwards, reaching half length of genital double-somite. Urosome (Fig. 1C) 4-segmented, one-third as long as prosome; genital double-somite (Figs 1D,E,2A,B) wider than long; pair of medial gonopores (Fig. 2C,D) located ventro-laterally near mid-level of double-somite; paired copulatory pores posterior to gonopores, each concealed beneath ventrolateral projection; remnants of divergent fertilization tubes of spermatophore (Fig. 3) still attached to genital double-somite of both paratypes, each connecting through posteroventral groove with copulatory pore beneath projection; copulatory duct swollen in ventrolateral projection, almost horizontal, extending to large seminal receptacle; 1 medial and 2 pairs of lateral shallow chitinized pits anteriorly; anal somite small, anal operculum not developed; caudal ramus (Fig. 1C) longer than wide, fringed with long setules along inner margin, with vestigial seta I and developed setae II to VI, seta VII originating dorsally near base of seta VI; inner margin near anus with patch of minute spinules. Integument of body and appendages pitted.

Antennules (Fig. 4A-C) equal in length, distinctly 22-segmented, reaching to posterior end of second pedigerous somite; distal 2 segments incompletely fused; fusion pattern and armature as follows: I–III–7 + 2 aesthetascs, IV–2 + aesthetasc, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs. Segments I to XIII fringed with long setules along posterior margin; segments IV to VIII each furnished with transverse row of minute setules near posterior corner. Sutures between segments I to III weakly visible.

Antenna (Fig. 1F,G): coxa unarmed; basis with spinulose seta at inner angle; endopod 2-segmented, first segment with minute seta at three quarters length, covered with minute spinules distally, second with 3 setae of unequal lengths medially and 5 setae distally and sparsely covered by spinules; exopod indistinctly 10-segmented, second to fourth segments almost fused; armature as follows: 0,0,0,1,1,1,1,1,0,3; ninth segment sparsely ornamented with minute spinules.

Mandible (Fig. 4D): gnathobase heavily chitinized, ventromedial margin with dense fringe of long setules; cutting edge with 3 acute teeth, dorsalmost of which bifid at tip; 2 patches of dagger-like spinules present dorsally; tuft of long setules present medially on knob; basis of palp with patches of

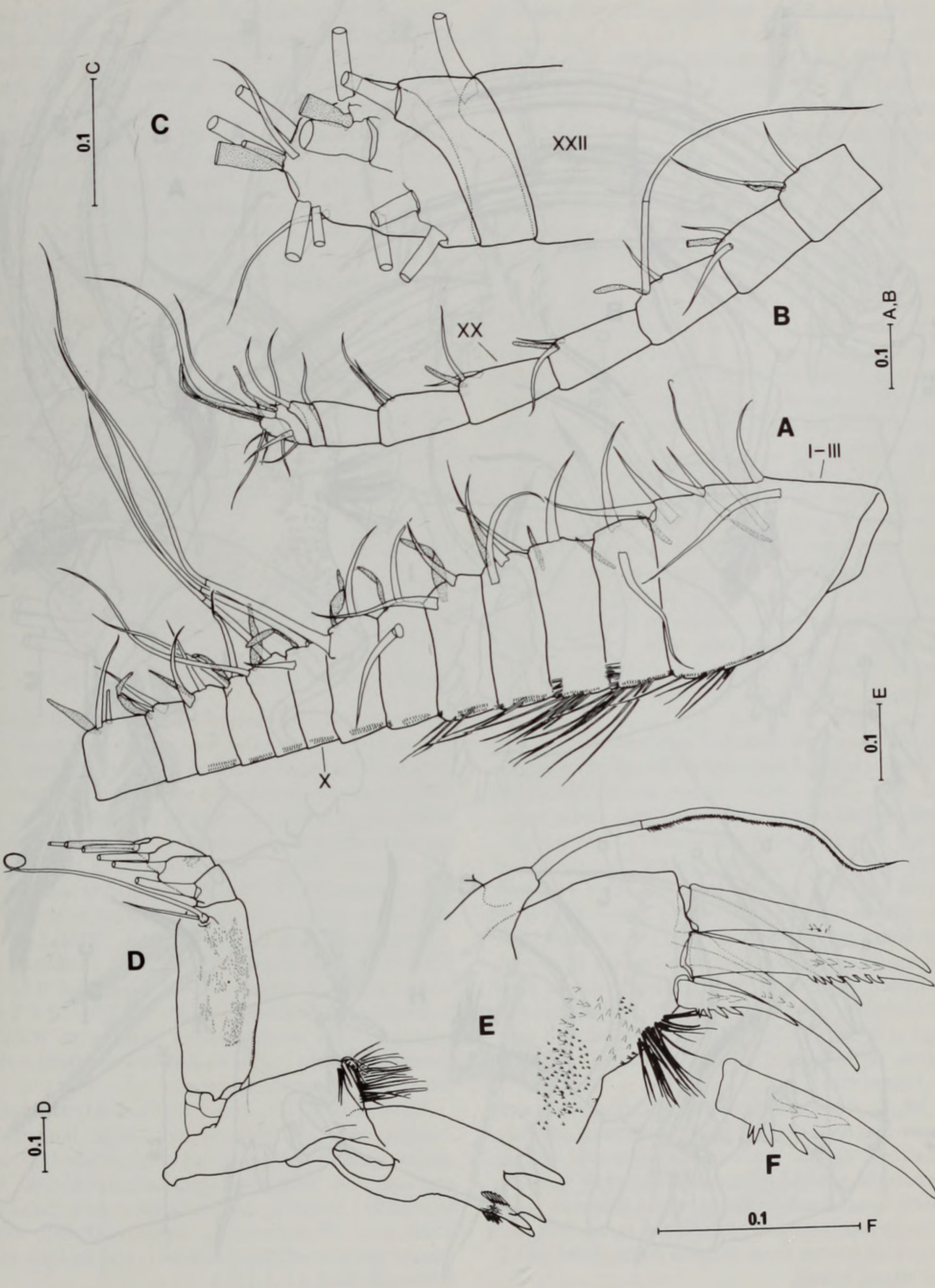

Fig. 4. *Crassarietellus huysi* gen. et sp. nov., female (holotype: E,F; paratype: A-D). A, Antennulary segments I to XV; B, Antennulary segments XVI to XXVIII; C, Antennulary segments XXII to XXVIII; D, Mandible; E, Maxillulary praecoxal arthrite and coxal endite; F, Proximal spine on praecoxal arthrite of maxillule. Scales in mm.

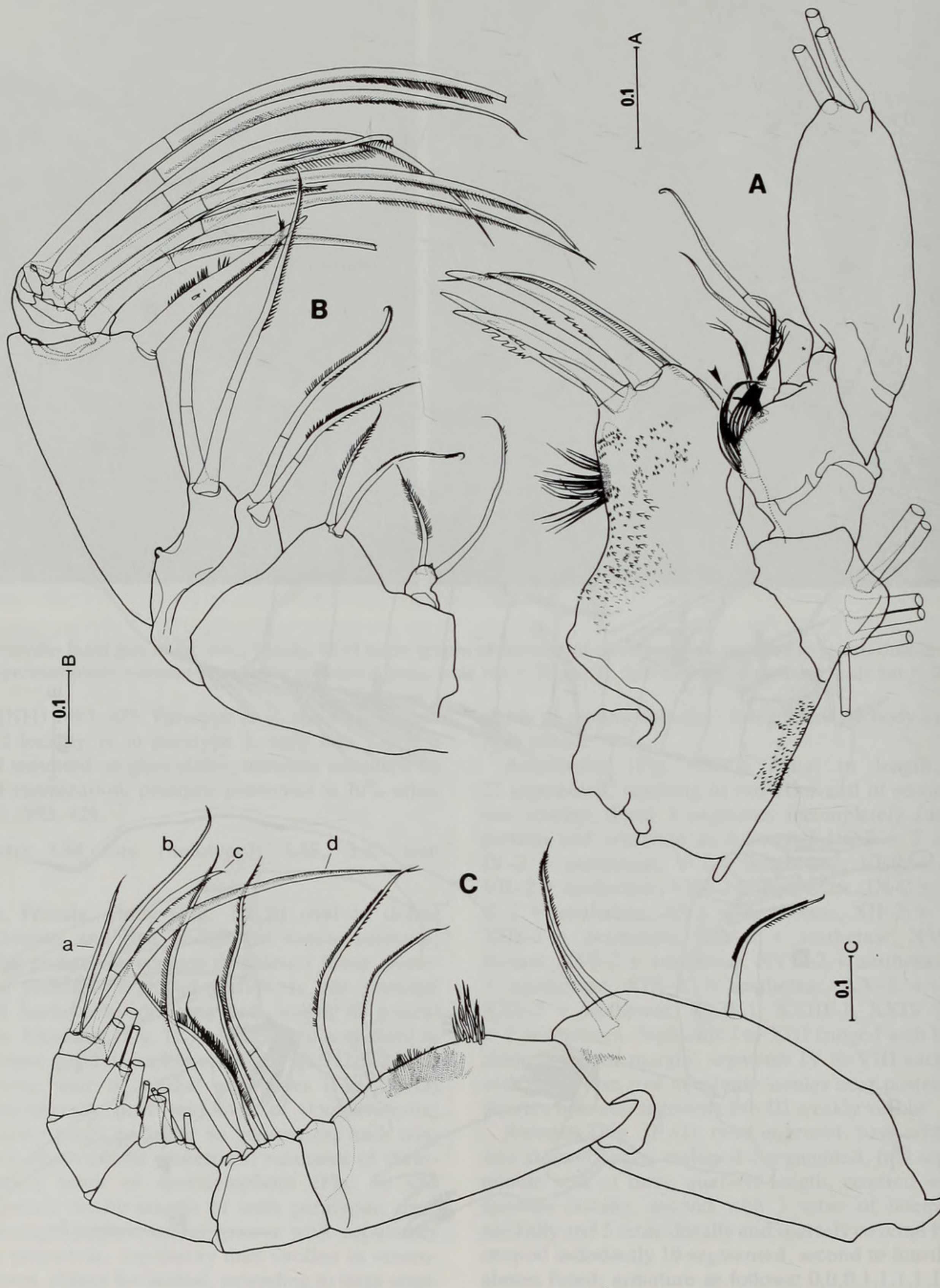

Fig. 5. *Crassarietellus huysi* gen. et sp. nov., female (holotype: C; paratype: A,B). A, Maxillule, with arrowhead indicating enditic seta of basis; B, Maxilla; C, Maxilliped. The armature elements on the sixth endopod segment of maxilliped are identified individually by the letters a to d. Scales in mm.

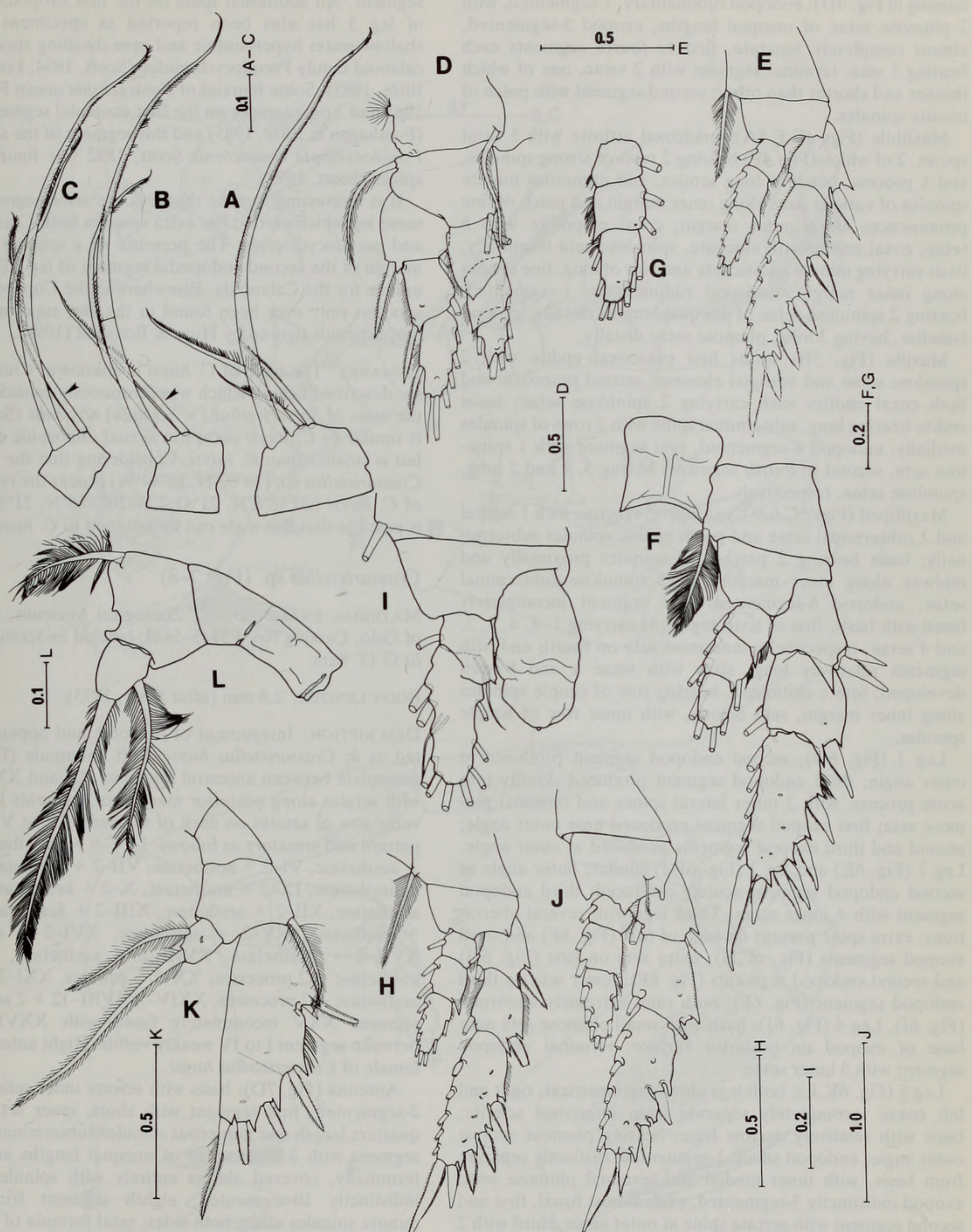

Fig. 6. *Crassarietellus huysi* gen. et sp. nov., female (holotype: A-C,J-L; paratypes: D-I). A, Second endopod segment of maxilliped; B, Third endopod segment of maxilliped, innermost seta indicated by arrowhead; C, Fourth endopod segment of maxilliped, innermost seta indicated by arrowhead; D, Leg 1, anterior surface; E, Leg 2, posterior surface; F, Aberrant leg 3, anterior surface; G, Right endopod of leg 3, anterior surface; H, Another aberrant leg 3, posterior surface; I, Extremely aberrant leg 3, anterior surface; J, Leg 4, posterior surface; K, Left leg 5, anterior surface; L, Right leg 5, anterior surface. Scales in mm.

minute spinules and row of long setules proximally (almost missing in Fig. 4D); endopod rudimentary, 1-segmented, with 2 plumose setae of unequal lengths; exopod 5-segmented, almost completely separate, first to fourth segments each bearing 1 seta, terminal segment with 2 setae, one of which thinner and shorter than other; second segment with patch of minute spinules.

Maxillule (Figs 4E,F,5A): praecoxal arthrite with 5 stout spines, 2 of which (Fig. 4F) bearing 2 rows of strong spinules, and 1 process, patch of long setules, and numerous minute spinules of various sizes along inner margin and patch of fine prominences along outer margin; coxal epipodite with 6 setae; coxal endite with elongate, spinulose seta terminally; basis carrying minute enditic seta and row of long, fine setules along inner margin; endopod rudimentary, 1-segmented, bearing 2 spinulose setae of unequal lengths distally; exopod lamellar, having 3 long, plumose setae distally.

Maxilla (Fig. 5B) stout; first praecoxal endite with 2 spinulose setae and vestigial element; second praecoxal and both coxal endites each carrying 2 spinulose setae; basal endite bearing long, subterminal spine with 2 rows of spinules medially; endopod 4-segmented, first segment with 1 spinulose seta, second to fourth segments having 3, 2 and 2 long, spinulose setae, respectively.

Maxilliped (Figs 5C,6A-C) elongate; syncoxa with 1 medial and 2 subterminal setae and patch of fine spinules subterminally; basis bearing 2 patches of spinules proximally and midway along inner margin and 2 spinulose subterminal setae; endopod 6-segmented, first segment incompletely fused with basis, first to sixth segments carrying 1, 4, 4, 3, 3, and 4 setae, respectively; innermost seta on fourth and fifth segments relatively long; sixth with setae a and b well developed, seta c chitinized, bearing row of simple spinules along inner margin, seta d long, with inner row of simple spinules.

Leg 1 (Fig. 6D); second endopod segment produced at outer angle; third endopod segment produced distally into acute process, with 2 outer lateral spines and terminal plumose seta; first exopod segment produced near outer angle; second and third exopod segments produced at outer angle. Leg 2 (Fig. 6E) and leg 3 (Fig. 6F-I) similar; outer angle of second endopod segment acutely produced; third endopod segment with 4 inner setae. Third legs with several aberrations: extra spine present on each of first (Fig. 6F) and third exopod segments (Fig. 6F,H); extra seta on first (Fig. 6H) and second endopod segments (Fig. 6F); fewer seta on third endopod segment (Fig. 6F); both rami extremely abnormal (Fig. 6I). Leg 4 (Fig. 6J): basis with small plumose seta near base of exopod on posterior surface; terminal endopod segment with 3 inner setae.

Leg 5 (Fig. 6K,L): both legs almost symmetrical; right and left coxae incompletely separate from intercoxal sclerite; basis with relatively narrow base, bearing plumose seta at outer angle; endopod small, 1-segmented, distinctly separate from basis, with inner medial and terminal plumose seta; exopod indistinctly 3-segmented, each almost fused, first and second segment with serrate spine at outer angle, third with 2 terminal and 1 lateral spines.

Male. Unknown.

Variability. The paratypic females have aberrant third legs (Fig. 6F,H,I). Both paratypes have 4 outer spines on the third exopodal segment of leg 3, but it is likely that the segment normally has 3 outer spines, because the males of *Crassarietellus* sp. and other arietellids carry only 3 spines on this segment. An additional spine on the first exopodal segment of leg 3 has also been reported in specimens of some shallow-water hyperbenthic and cave-dwelling species of the calanoid family Pseudocyclopiidae (Scott, 1894; Fosshagen & Iliffe, 1985). Some females of *Paracyclopia naessi* Fosshagen, 1985 had 2 outer spines on the first exopodal segment of leg 3 (Fosshagen & Iliffe, 1985) and this segment of the same leg in *Pseudocyclopia crassicornis* Scott, 1892 was figured with 2 spines (Scott, 1892).

It is interesting to note that it is the same segment of the same leg which carried the extra spine in both *Crassarietellus* and pseudocyclopiids. The presence of a seta on the outer margin of the second endopodal segment of leg 3 (Fig. 6F) is unique for the Calanoida. Elsewhere in the Copepoda such a seta has only ever been found in the two superornatiremid harpacticoids figured by Huys & Boxshall (1991).

Remarks. The male of *C. huysi* is unknown. *Crassarietellus* sp. described below, which was erroneously considered to be the male of *Sarsarietellus* (= *Scottula*) *abyssalis* (Sars, 1905), is similar to *C. huysi* except in sexual dimorphic characters, but is smaller than *C. huysi*. Considering that the locality of *Crassarietellus* sp. (38°02'N, 10°44'W) is near the type locality of *C. huysi* (20°18.5'N, 21°41.2'W-20°20.8'N, 21°53.0'W), it is possible that this male can be assigned to *C. huysi*.

Crassarietellus sp. (Figs 7–8)

Material examined. ♂, Zoological Museum, University of Oslo, Catalog No. F5445–5446, labeled as *Scottula abyssalis* G.O. Sars.

Body length. 2.8 mm (after Rose, 1933).

Description. Integument of urosome and appendages pitted as in *Crassarietellus huysi*. Left antennule (Fig. 7A-C) geniculate between ancestral segments XX and XXI, fringed with setules along posterior margins of segments I–X, transverse row of setules on each of segments IV to VIII; fusion pattern and armature as follows: I–IV–9 + 4 aesthetascs, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–1 + aesthetasc + 2 processes, XX–2 + process, XXI–XXIII–1 + aesthetasc + 2 processes, XXIV–XXVIII–12 + 2 aesthetascs; segment XXV incompletely fused with XXVI. Sutures between segment I to IV weakly visible. Right antennule as in female of *Crassarietellus huysi*.

Antenna (Fig. 7D): basis with serrate inner seta; endopod 2-segmented, first segment with short, inner seta at three quarters length and numerous spinules subterminally, second segment with 3 inner setae of unequal lengths and 5 setae terminally, covered almost entirely with spinules; exopod indistinctly 10-segmented, eighth segment fringed with minute spinules along both sides; setal formula of exopod as follows: 0,0,0,1,1,1,1,1,0,3.

Mandibular gnathobase (Fig. 7F) with 3 stout teeth, dorsalmost of which bifid at tip; tuft of long setules present near base of palp. Mandibular palp (Fig. 7E): basis elongate, furnished with numerous minute spinules and row of long setules along inner margin; endopod rudimentary, 1-segmented, bearing 2 unequal setae; seta on first exopod

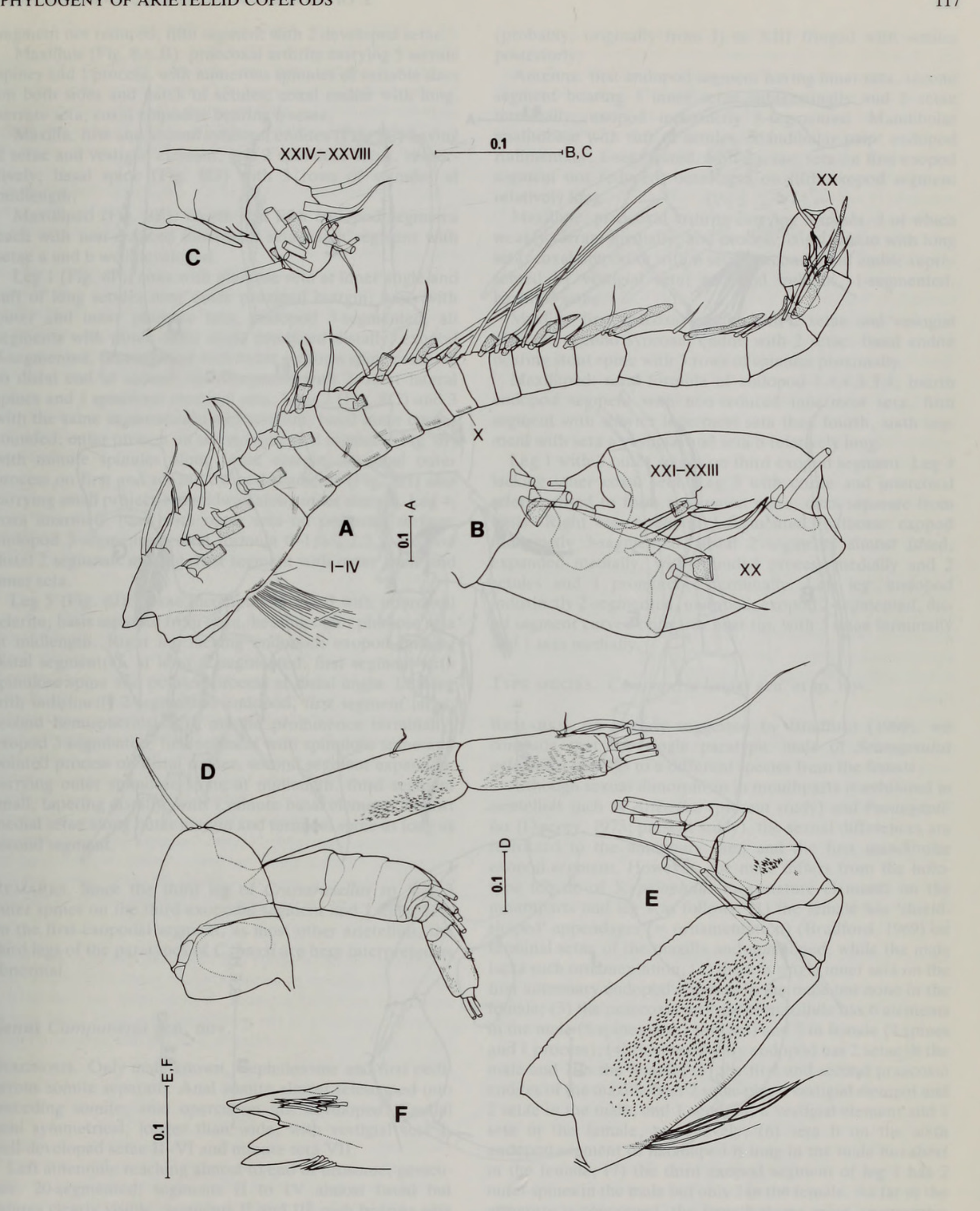

Fig. 7. *Crassarietellus* sp., male. A, Left antennule; B, Antennulary segments XIX to XXVIII, elements on segments XXIV–XXVIII omitted except for outer seta; C, Antennulary segments XXIV–XXVIII; D, Antenna; E, Mandibular palp; F, Mandibular gnathobasic cutting edge. Scales in mm.

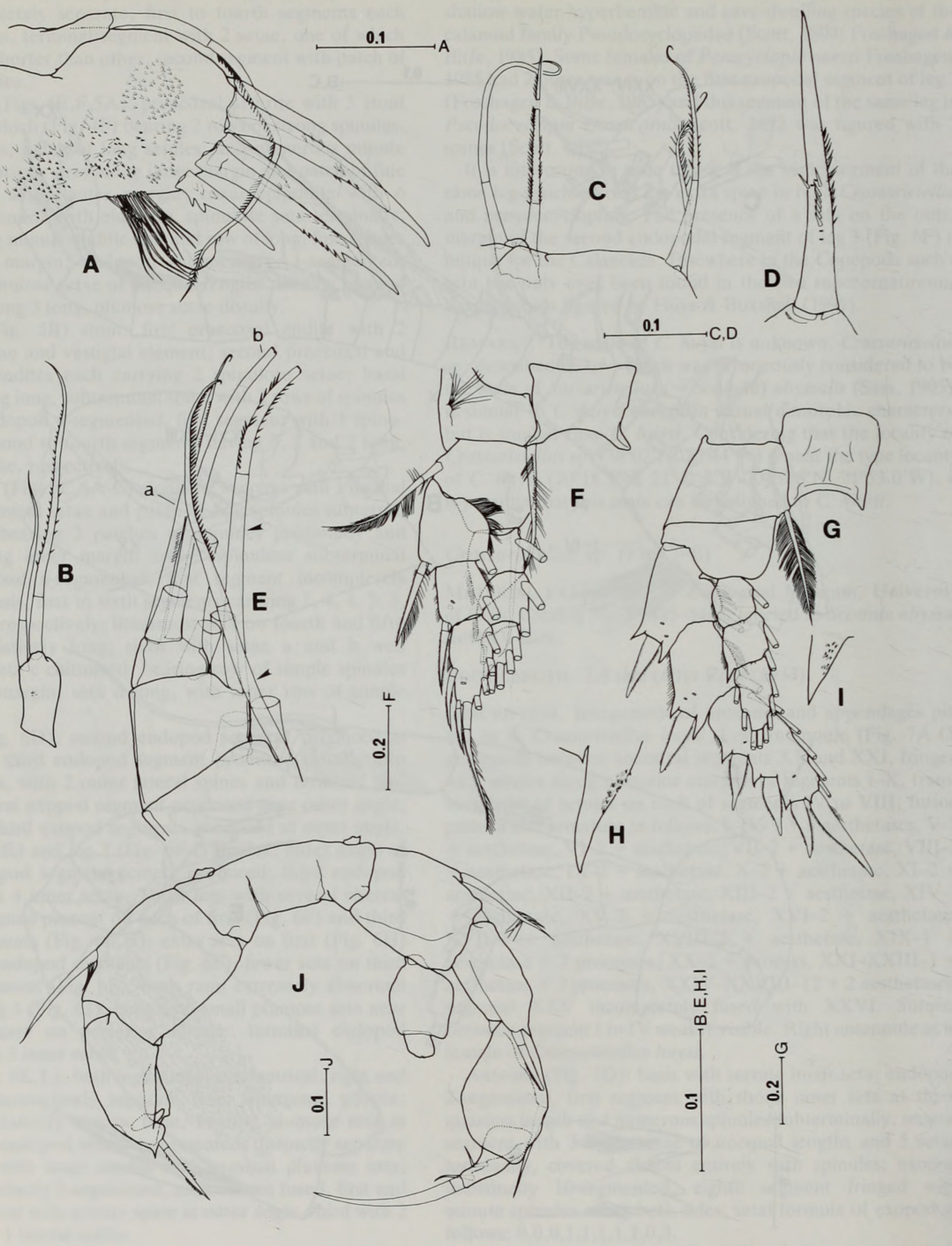

Fig. 8. *Crassarietellus* sp., male. A. Praecoxal arthrite and coxal endite of maxillule; B, Maxillulary endopod; C, First and second praecoxal endites of maxilla; D, Basal spine of maxilla; E, Fourth to sixth endopod segments of maxilliped, inner seta on fourth and fifth segments indicated by arrowhead; F, Leg 1, anterior surface; G, Leg 2, anterior surface; H, Outer distal process on second exopod segment of leg 3; I, Outer process on second endopod segment of leg 3; J, Leg 5, anterior surface, ancestral second and third segments of right exopod missing. Scales in mm.

segment not reduced, fifth segment with 2 developed setae.

Maxillule (Fig. 8A,B): praecoxal arthrite carrying 5 serrate spines and 1 process, with numerous spinules of variable sizes on both sides and patch of setules; coxal endite with long, serrate seta; coxal epipodite bearing 6 setae.

Maxilla: first and second syncoxal endites (Fig. 8C) having 2 setae and vestigial element, and 2 spinulose setae, respectively; basal spine (Fig. 8D) with 3 rows of spinules at midlength.

Maxilliped (Fig. 8E): fourth and fifth endopod segments each with non-reduced innermost seta, sixth segment with setae a and b well developed.

Leg 1 (Fig. 8F): coxa with plumose seta at inner angle and tuft of long setules near outer proximal margin; basis with outer and inner plumose seta; endopod 3-segmented, all segments with outer distal angle produced distally; exopod 3-segmented, first segment with outer setiform spine reaching to distal end of second, third segment with 2 outer lateral spines and 1 spiniform terminal seta. Legs 2 (Fig. 8G) and 3 with the same segmentation and setation; basal inner corner rounded; outer process on second endopod segment (Fig. 8I) with minute spinules along inner margin; terminal outer process on first and second exopod segments (Fig. 8H) also carrying small projections midway along inner margin. Leg 4: coxa unarmed; basis with outer seta on posterior surface; endopod 3-segmented, setal formula 0–1;0–2;2,2,3; exopod distal 2 segments missing, first segment with outer spine and inner seta.

Leg 5 (Fig. 8J): coxae incompletely fused with intercoxal sclerite; basis separate from coxa, bearing outer plumose seta at midlength. Right leg lacking endopod; exopod missing distal segment(s), at least, 2-segmented, first segment with spinulose spine and pointed process at distal angle. Left leg with indistinctly 2-segmented endopod, first segment large, second hemispherical with minute prominence terminally; exopod 3-segmented, first segment with spinulose spine and pointed process on distal corner, second segment expanded, carrying outer spinulose spine at midlength, third segment small, tapering distally, with 1 minute basal element, 2 short medial setae along outer margin and terminal spine as long as second segment.

REMARKS. Since the third leg of *Crassarietellus* sp. has 3 outer spines on the third exopodal segment and 1 inner seta on the first exopodal segment, as most other arietellids, the third legs of the paratypes of *C. huysi* are here interpreted as abnormal.

Genus Campaneria gen. nov.

DIAGNOSIS. Only male known. Cephalosome and first pedigerous somite separate. Anal somite almost telescoped into preceding somite; anal operculum not developed. Caudal rami symmetrical, longer than wide, with vestigial seta I, well-developed setae II–VI and minute seta VII.

Left antennule reaching almost to end of urosome, geniculate, 20-segmented; segments II to IV almost fused but sutures clearly visible, segments II and III each bearing seta and aesthetasc; segment XIII with seta, aesthetasc and process representing modified seta; segment XXI separate from XXII; segment XXV incompletely fused with XXVI; segment XIII with seta and process; compound segment XXVI–XXVIII with 8 setae and aesthetasc; segment II (probably, originally from I) to XIII fringed with setules posteriorly.

Antenna: first endopod segment having inner seta, second segment bearing 3 inner setae subterminally and 5 setae terminally; exopod indistinctly 8-segmented. Mandibular gnathobase with tuft of setules. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long.

Maxillule: praecoxal arthrite carrying 5 spines, 3 of which weakly serrate medially, and process; coxal endite with long seta; coxal epipodite with 6 setae; second basal endite represented by vestigial seta; endopod bulbous, 1-segmented, having 2 setae.

Maxilla: first syncoxal endite with 2 setae and vestigial element; second syncoxal endite with 2 setae; basal endite bearing stout spine with 3 rows of spinules proximally.

Maxilliped: setal formula of endopod 1,4,4,3,3,4; fourth endopod segment with non-reduced innermost seta, fifth segment with shorter innermost seta than fourth, sixth segment with seta a vestigial and seta b relatively long.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 lacking inner coxal seta. Leg 5 with coxae and intercoxal sclerite fused to form a common plate; coxa separate from basis. Right leg: endopod 1-segmented, bulbous; exopod indistinctly 3-segmented, distal 2 segments almost fused, expanded medially, with rounded process medially and 2 setules and 1 prominence terminally. Left leg: endopod indistinctly 2-segmented, unarmed; exopod 2-segmented, distal segment curved outwards near tip, with 3 setae terminally and 1 seta medially.

TYPE SPECIES. *Campaneria latipes* gen. et sp. nov.

REMARKS. As already suggested by Bradford (1969), we conclude that the single paratypic male of *Scutogerulus pelophilus* belongs to a different species from the female.

Although sexual dimorphism in mouthparts is exhibited in arietellids such as *Arietellus* (present study) and *Paraugaptilus* (Deevey, 1973; present study), the sexual differences are restricted to the antennary rami and the first mandibular exopod segment. However, the male differs from the holotype female of *S. pelophilus* in armature elements on the mouthparts and leg 1 as follows: (1) the female has 'shield-shaped' appendages (= ornamentation) (Bradford, 1969) on terminal setae of the maxilla and maxilliped, while the male lacks such ornamentation; (2) there is single inner seta on the first antennary endopod segment in the male but none in the female; (3) the praecoxal arthrite of maxillule has 6 elements in the male (5 spines and 1 process) and 5 in female (4 spines and 1 process); (4) the maxillulary endopod has 2 setae in the male and 1 in the female; (5) the first and second praecoxal endites of the maxilla bear 2 setae plus a vestigial element and 2 setae in the male, and 1 seta plus a vestigial element and 1 seta in the female, respectively; (6) seta b on the sixth endopod segment of maxilliped is long in the male but short in the female; (7) the third exopod segment of leg 1 has 2 outer spines in the male but only 1 in the female. As far as the armature is concerned, the female shows more apomorphic character states than the male. In particular, the magnitude of the differences in the antenna, maxilla, maxilliped and leg 1 is greater than not only variation within a species but also normal interspecific discrepancies between congeners. A new genus is, therefore, established to accommodate the male.

The male of the new genus is similar to that of *Crassarietellus*. However, the left antennule, the antennary exopod, the maxillulary praecoxal arthrite, and the fifth and sixth endopod segments of maxilliped are different: (1) left antennule reaching almost to end of urosome in *Campaneria*, but, possibly, at most to end of prosome in *Crassarietellus*; (2) antennulary segments II to IV partly fused in *Campaneria*, but almost completely so in *Crassarietellus*; (3) antennulary segments II and III each bearing single seta and aesthetasc in *Campaneria*, but 2 setae and aesthetasc in *Crassarietellus*; (4) antennulary segments XXI and XXII completely separate in *Campaneria*, but almost fully fused in *Crassarietellus*; (5) seta on antennulary segment XV modified into process in *Crassarietellus*, but not in *Campaneria*; (6) antennary exopod indistinctly 8-segmented in *Campaneria* but 10-segmented in *Crassarietellus*; (7) spines on maxillulary praecoxal arthrite finely serrate in *Campaneria*, but strongly serrate in *Crassarietellus*; (8) innermost seta on the fifth endopod segment of maxilliped relatively short in *Campaneria*, but long in *Crassarietellus*; (9) seta a on the sixth endopod segment of maxilliped relatively reduced in *Campaneria*, but not in *Crassarietellus*.

The leg 5 of *Campaneria* is also similar to that of *Crassarietellus* sp., particularly in having a 2-segmented left endopod, but can be distinguished by the presence of the right endopod and by the 2-segmented left exopod.

ETYMOLOGY. The new genus *Campaneria* is named in honour of the late Dr. A. Campaner who was the first to be interested in the phylogenetic relationships between arietellid genera (gender feminine). The specific name *latipes* (Latin *latus* meaning broad; Latin *pes* meaning leg) refers to the broad compound exopod segments of the right leg 5 of the male.

ECOLOGICAL NOTE. *Campaneria* was collected by a trawl from the near-bottom samples taken at depths of 1234–1260 m off northeastern New Zealand (Bradford, 1969). Since the genus has never been captured in plankton hauls, it is most likely hyperbenthic.

Campaneria latipes gen. et sp. nov. (Figs 9–10)

MATERIAL EXAMINED. ♂, New Zealand Oceanographic Institute Reg. No. 121, labelled as *Scutogerulus pelophilus* (♂).

BODY LENGTH. 3.9 mm (after Bradford, 1969).

DESCRIPTION. Anal somite (Fig. 9A) small, almost telescoped into preceding somite; caudal rami (Fig. 9A) symmetrical, seta I vestigial, setae II–VI developed, seta VII minute.

Left antennule (Fig. 9B-F): segment I damaged, but with 3 setae and aesthetasc (only this segment still remained on the body); segments II and III fused with suture visible anteriorly; segments III and IV, and XXIV–XXV and XXVI–XXVIII incompletely fused. Fusion pattern and armature elements as follows: II–IV–4 + 3 aesthetascs, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–1 + aesthetasc + process, XI–2 + aesthetasc, XII–1 + aesthetasc + process, XIII–1 + aesthetasc + process, XIV–1 + aesthetasc + process, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–1 + aesthetasc + 2 processes, XX–1 + aesthetasc + process, XXI-aesthetasc + 2 processes, XXII–XXIII–1 + process (XXII-process, XXIII–1), XXIV–XXVIII–12 + 2 aesthetascs.

Antenna: inner basal seta present; endopod (Fig. 9G) 2-segmented, first segment with short inner seta, second segment with 3 inner setae of unequal lengths subterminally and 5 setae terminally; exopod (Fig. 10A) indistinctly 8-segmented, second segment elongate, setal formula 0,1,1,1,1,1,0,3.

Mandibular palp (Fig. 10E): endopod rudimentary, 1-segmented, carrying 2 setae of unequal lengths; first exopod segment bearing non-reduced seta, fifth segment with 1 long and 1 shorter seta.

Maxillule: praecoxal arthrite (Fig. 10B) bearing 5 spines and 1 process, 3 of which serrate medially, with row of long setules and patch of minute spinules proximally; coxal endite (Fig. 10C) with long spinulose seta terminally; coxal epipodite with 6 setae; minute endite seta present on basis (Fig. 10D), endopod bulbous, 1-segmented, with 2 spinulose setae of unequal lengths.

Maxilla: first praecoxal endite with 2 spinulose setae and vestigial element, second endite with 2 bipinnate setae (Fig. 10F); basal spine (Fig. 10G) with 3 rows of spinules of different sizes proximally.

Maxilliped: fourth and fifth endopod segments (Fig. 10H) each having non-reduced, spinulose innermost seta, but seta on fourth segment much longer than on fifth; sixth endopod segment (Fig. 10I) with medium-length seta b and vestigial seta a.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 having outer basal seta, but lacking inner coxal seta.

Leg 5 (Fig. 10J): coxae and intercoxal sclerite almost fused, but suture visible on posterior surface; basis separate from coxa. Right leg: basal seta missing; endopod 1-segmented, with tuft of short setules terminally; exopod indistinctly 3-segmented, first triangular, carrying spine at outer angle, distal 2 segments almost fused, but suture visible on both surfaces, expanded medially, having outer seta proximally, round inner process with 3 minute prominences at tip medially, and 2 setae and 1 prominence along outer terminal margin. Left leg: basal seta missing; endopod indistinctly 2-segmented, unarmed; exopod 2-segmented, first segment triangular, bearing spine on outer corner, second segment expanded inwards, curved outwards at about three quarters length, with fine medial seta and 3 terminal setae of unequal lengths.

REMARKS. In her original description Bradford (1969) overlooked the antennary basal seta, the inner seta on the first antennary endopod segment, 3 short setae on the distal 2 endopod segments of the maxilliped, the outer basal seta of leg 4, and the fine midlength seta on the second exopod segment of left leg 5.

Genus *Paraugaptiloides* gen. nov.

DIAGNOSIS. Only male known. Body similar to that of *Paraugaptilus*; cephalosome separate from first pedigerous somite; prosome rounded anteriorly and produced posteriorly, with small dorsolateral prominence and bluntly produced lateral lobe on each side; lateral flap of cephalosome developed to cover bases of mouthparts. Caudal rami symmetrical with setae II and III normally developed.

Male left antennule 19-segmented, fringed with setules along posterior margin of first segment only; segments I and

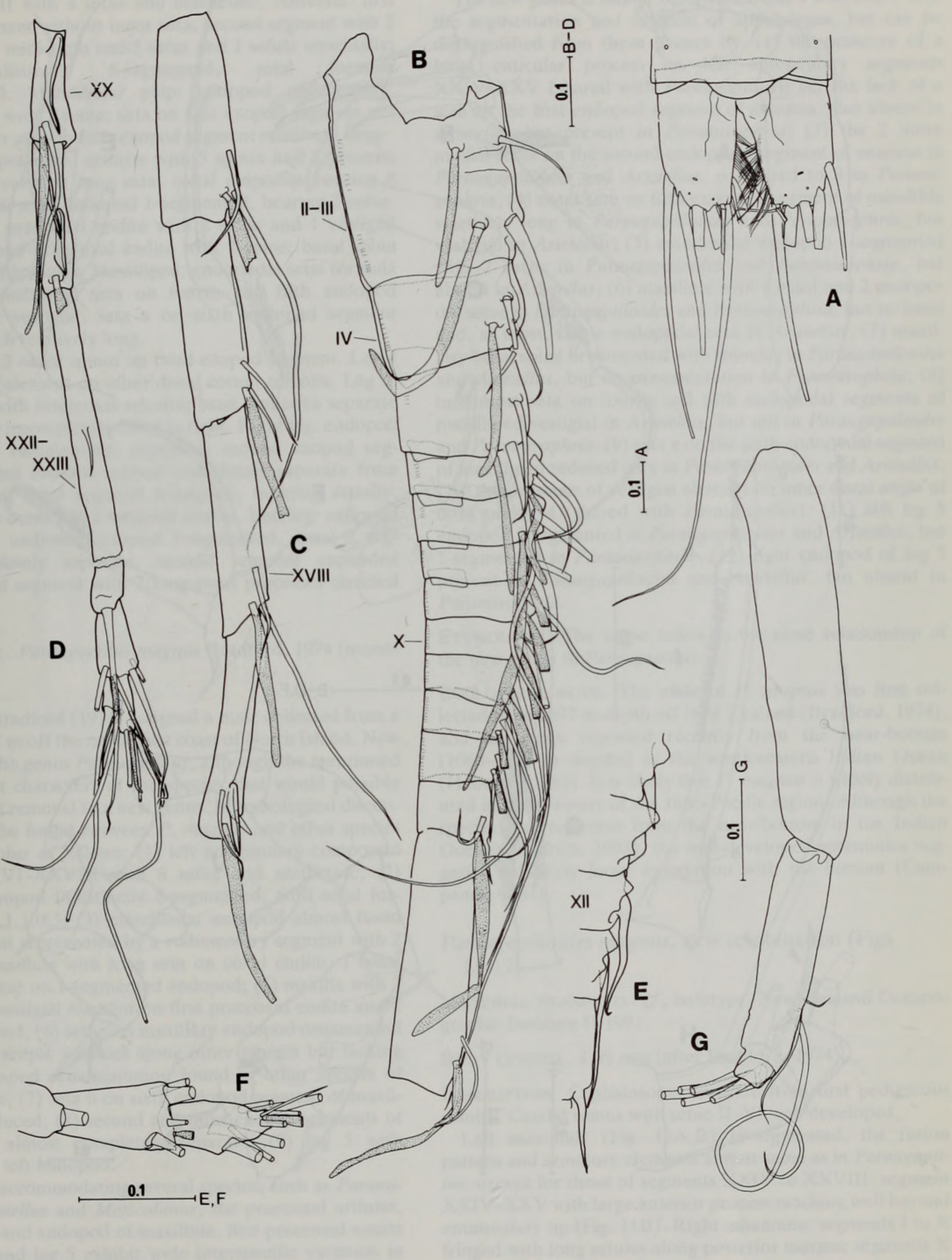

Fig. 9. *Campaneria latipes* gen. et sp. nov., male (holotype). A, Anal somite and caudal rami, dorsal view; B, Left antennulary segments II to XV; C, Left antennulary segments XVI to XIX; D, Left antennulary segments XX to XXVIII; E, Anterior processes on segments XX–XXIV of left antennule; F, Left antennulary segments XXIV to XXVIII; G, Antennary endopod. Scales in mm.

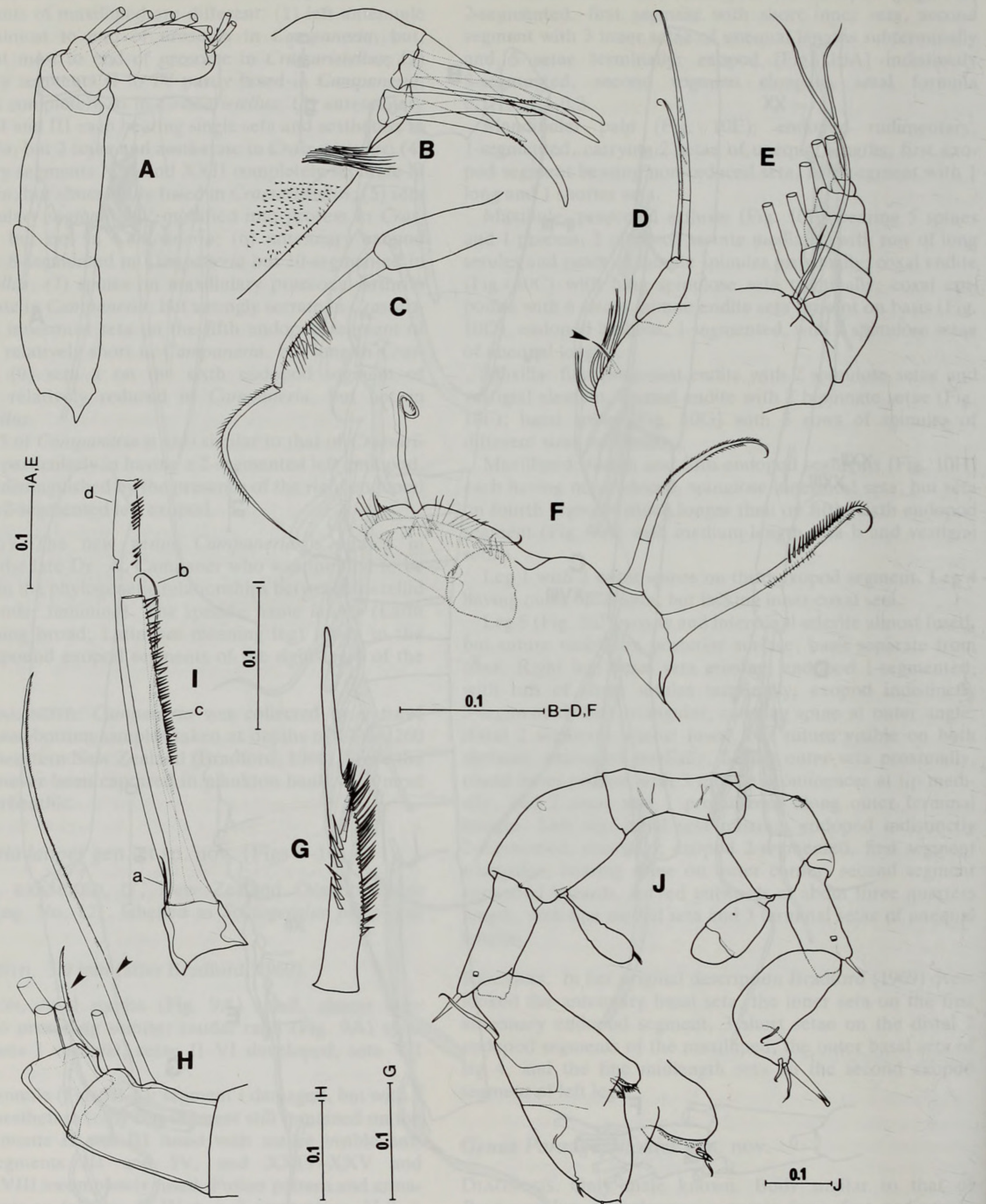

Fig. 10. *Campaneria latipes* gen. et sp. nov., male (holotype). A. Antennary exopod; B, Praecoxal arthrite of maxillule; C, Coxal endite of maxillule; D, Maxillulary endopod with basal seta indicated by arrowhead; E, Mandibular endopod and exopod; F, First and second praecoxal endite of maxilla; G, Basal spine of maxilla; H, Fourth and fifth endopod segments of maxilliped, innermost seta indicated by arrowhead; I, Sixth endopod segment of maxilliped; J. Leg 5, anterior surface. Scales in mm.

II each with 1 seta; segment XIII with seta and process; segment XXI fused with XXII; compound segment XXIV–XXV with large cuticular process; compound segment XXVI–XXVIII with 8 setae and aesthetasc. Antenna: first endopod segment without inner seta, second segment with 2 inner setae at midlength and 5 setae and 1 setule terminally; exopod indistinctly 8-segmented, setal formula 0,1,1,1,1,1,0,3. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long.

Maxillule: praecoxal arthrite with 5 spines and 1 process; coxal endite carrying long seta; coxal epipodite bearing 8 setae; no basal seta; endopod 1-segmented, bearing 2 setae. Maxilla: first praecoxal endite with 2 setae and 1 vestigial element; second praecoxal endite with 2 setae; basal spine with 2 rows of spinules. Maxilliped: endopodal setal formula 1,4,4,3,3,4; innermost seta on fourth and fifth endopod segments not vestigial; seta a on sixth endopod segment reduced, seta b relatively long.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 with vestigial element on inner distal corner of coxa. Leg 5: coxae fused with intercoxal sclerite; basis and coxa separate in left leg and incompletely fused in right. Right leg: endopod 1-segmented, rudimentary, unarmed; second exopod segment expanded inwards, almost completely separate from third segment, third segment triangular, tapering distally, with 1 minute outer and 1 terminal setules. Left leg: endopod 2-segmented, unarmed; exopod 3-segmented, distal 2 segments completely separate, second segment expanded inwards, third segment with 2 long stout processes directed laterally.

TYPE SPECIES. *Paraugaptilus magnus* Bradford, 1974 (monotypic).

REMARKS. Bradford (1974) assigned a male collected from a depth of 1697 m off the north-east coast of North Island, New Zealand, to the genus *Paraugaptilus*, although she mentioned seven distinct characters of the species that would possibly necessitate its removal to a new genus. Morphological discontinuities can be found between *P. magnus* and other species of *Paraugaptilus* as follows: (1) left antennulary compound segment XXVI–XXVIII with 8 setae and aesthetasc; (2) antennary exopod indistinctly 8-segmented, with setal formula 0,1,1,1,1,1,0,3; (3) mandibular endopod almost fused with basis, but represented by a rudimentary segment with 2 setae; (4) maxillule with long seta on coxal endite, 1 basal seta and 2 setae on 1-segmented endopod; (5) maxilla with 2 setae and 1 vestigial element on first praecoxal endite and 2 setae on second; (6) setae on maxillary endopod ornamented with row of simple spinules along inner margin but lacking triangular-shaped ornamentation found in other species of *Paraugaptilus*; (7) seta b on sixth endopod segment of maxilliped not reduced; (8) second and third exopod segments of right leg 5 almost completely separate; (9) leg 5 with 2-segmented left endopod.

In genera accommodating several species, such as *Paramisophria*, *Arietellus* and *Metacalanus*, the praecoxal arthrite, coxal endite and endopod of maxillule, first praecoxal endite of maxilla, and leg 5 exhibit wide interspecific variation in armature. However, the armature of the antennary exopod, mandibular palp, second praecoxal endite of maxilla, endopods of male leg 5 are relatively consistent within each genus. In particular, the significant differences found in the antennary exopod, the mandibular endopod and the second praecoxal endite of the maxilla support the proposal to assign *P. magnus* to a new genus, *Paraugaptiloides*.

The new genus is similar to *Arietellus* and *Paramisophria* in the segmentation and setation of appendages, but can be distinguished from these genera by: (1) the presence of a large cuticular process on left antennulary segments XXIV–XXV (shared with *Paraugaptilus*); (2) the lack of a seta on the first endopod segment of antenna, also absent in *Arietellus* but present in *Paramisophria*; (3) the 2 inner medial setae on the second endopodal segment of antenna in *Paraugaptiloides* and *Arietellus*, compared to 3 in *Paramisophria*; (4) outer seta on fifth exopodal segment of mandible relatively long in *Paraugaptiloides* and *Paramisophria*, but vestigial in *Arietellus*; (5) mandibular endopod 1-segmented with 2 setae in *Paraugaptiloides* and *Paramisophria*, but absent in *Arietellus*; (6) maxillule with 1 basal and 2 endopodal setae in *Paraugaptiloides* and *Paramisophria*, but no basal and, at most, single endopodal seta in *Arietellus*; (7) maxillary basal spine ornamented with spinules in *Paraugaptiloides* and *Arietellus*, but no ornamentation in *Paramisophria*; (8) innermost seta on fourth and fifth endopodal segments of maxilliped vestigial in *Arietellus*, but not in *Paraugaptiloides* and *Paramisophria*; (9) seta a on the sixth endopodal segment of maxilliped reduced only in *Paraugaptiloides* and *Arietellus*; (10) the presence of vestigial element on inner distal angle of coxa of leg 4 (shared with *Paraugaptilus*); (11) left leg 5 endopod 2-segmented in *Paraugaptiloides* and *Arietellus*, but 1-segmented in *Paramisophria*; (12) right endopod of leg 5 present in *Paraugaptiloides* and *Arietellus*, but absent in *Paramisophria*.

ETYMOLOGY. The name refers to the close relationship of the new genus to *Paraugaptilus*.

ECOLOGICAL NOTE. The male of *P. magnus* was first collected from 1697 m depth off New Zealand (Bradford, 1974), and has been reported recently from the near-bottom (1060–1070 m depths) in the southwestern Indian Ocean (Heinrich, 1993). It is likely that *P. magnus* is widely distributed in deep waters of the Indo-Pacific region. Although the species was collected from the near-bottom in the Indian Ocean (Heinrich, 1993), the well-developed antennules suggest a relatively loose association with the bottom (Campaner, 1984).

Paraugaptiloides magnus, new combination (Figs 11–12)

MATERIAL EXAMINED. ♂, holotype, New Zealand Oceanographic Institute H-199.

BODY LENGTH. 4.85 mm (after Bradford, 1974).

DESCRIPTION. Cephalosome separate from first pedigerous somite. Caudal ramus with setae II–VI well developed.

Left antennule (Fig. 11A,B) 19-segmented, the fusion pattern and armature elements almost same as in *Paraugaptilus*, except for those of segments XXIV to XXVIII: segment XXIV–XXV with large anterior process reaching well beyond antennulary tip (Fig. 11B). Right antennule: segments I to X fringed with long setules along posterior margin; segments X and XI, and XIV and XV only partly fused; segment XXIII and XXIV almost separate; segments XXV and XXVI almost fused with suture visible; fusion pattern and armature elements as follows: I–III–7 + 3 aesthetascs, IV–2 (element

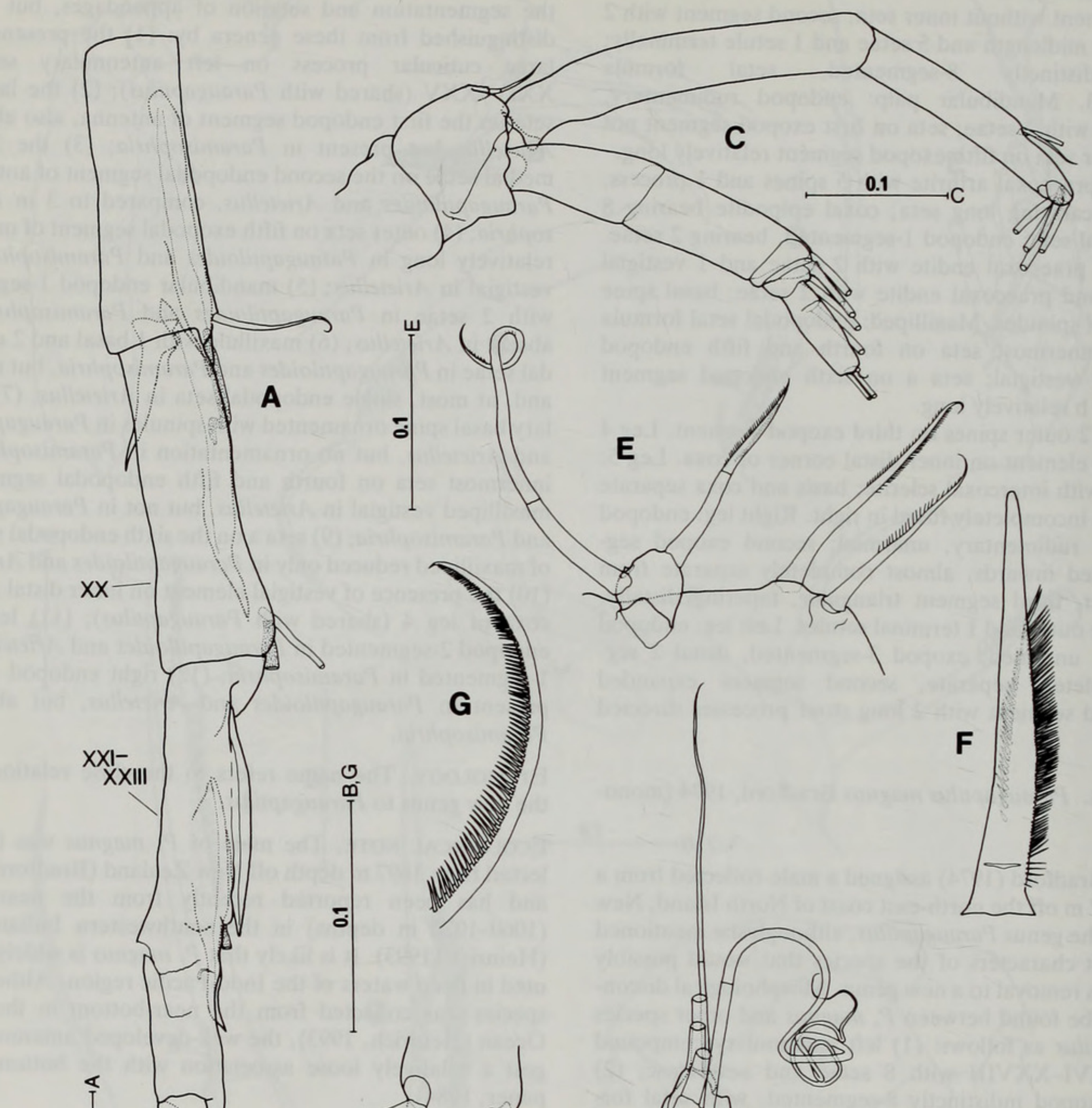

Fig. 11. *Paraugaptiloides magnus* gen. et sp. nov., male (holotype). A. Left antennulary segments XIX to XXVIII; B, Left antennulary segments XXVI to XXVIII; C, Antenna; D, Mandibular endopod and exopod; E, First and second praecoxal endites of maxilla; F, Basal spine of maxilla; G, Terminal seta on fourth endopod segment of maxilla. Scales in mm.

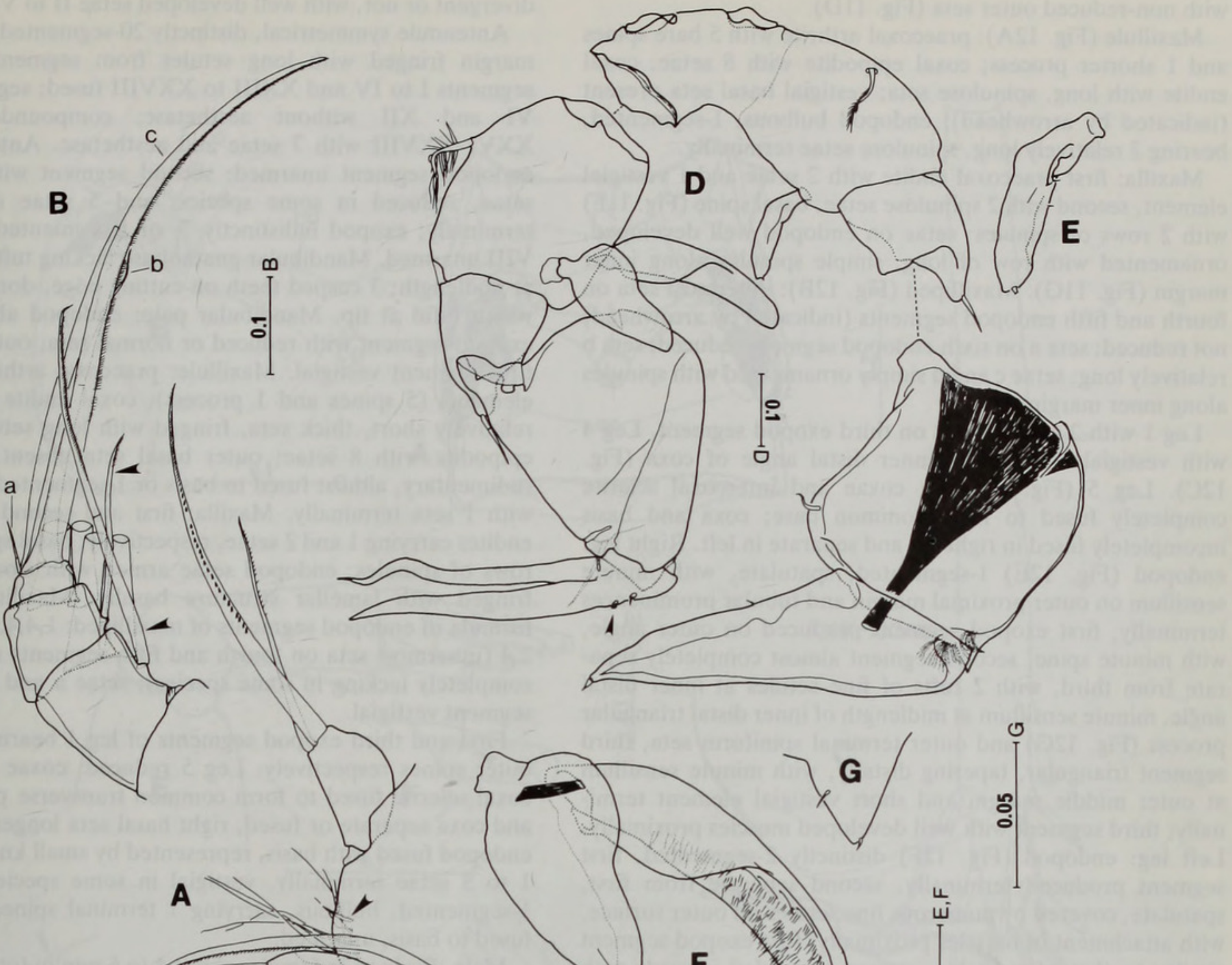

Fig. 12. *Paraugaptiloides magnus* gen. et sp. nov., male (holotype). A, Praecoxal arthrite, coxal endite, basal endite and endopod of maxillule, basal seta indicated by arrowhead; B, Fourth to sixth endopod segments of maxilliped, innermost seta on fourth and fifth segments indicated by arrowhead; C, Inner coxal seta of leg 4; D, Leg 5, posterior surface, scar of element on third exopod segment of left leg indicated by arrowhead; E, Right endopod of leg 5; F, Left endopod of leg 5; G, Inner distal process on second exopod segment of right leg 5. Scales in mm.

missing), V–1 + aesthetasc (element missing), VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–1 + aesthetasc + process, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–1 + aesthetasc + process, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–1 + aesthetasc (element missing), XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–2, XXV–2 + aesthetasc, XXVI–XXVIII–8 + aesthetasc).

Antenna (Fig. 11C): first endopod segment lacking inner seta, second segment with 2 inner setae of unequal lengths subterminally and 5 setae and 1 setule terminally; exopod indistinctly 8-segmented, setal formula 0,1,1,1,1,1,0,3.

Mandible: gnathobase with 3 cusped teeth, dorsalmost of which bifid at tip; the medial part of gnathobase is damaged and it is not known whether or not a tuft of setules is present. Mandibular endopod (Fig. 11D) rudimentary, 1-segmented, almost fused with basis, carrying 2 setae of unequal lengths; first exopod segment with well developed seta, fifth segment with non-reduced outer seta (Fig. 11D).

Maxillule (Fig. 12A): praecoxal arthrite with 5 bare spines and 1 shorter process; coxal epipodite with 8 setae; coxal endite with long, spinulose seta; vestigial basal seta present (indicated by arrowhead); endopod bulbous, 1-segmented, bearing 2 relatively long, spinulose setae terminally.

Maxilla: first praecoxal endite with 2 setae and 1 vestigial element, second with 2 spinulose setae; basal spine (Fig. 11F) with 2 rows of spinules; setae on endopod well developed, ornamented with row of long, simple spinules along inner margin (Fig. 11G). Maxilliped (Fig. 12B): innermost seta on fourth and fifth endopod segments (indicated by arrowhead) not reduced; seta a on sixth endopod segment reduced; seta b relatively long; setae c and d simply ornamented with spinules along inner margin.

Leg 1 with 2 outer spines on third exopod segment. Leg 4 with vestigial element on inner distal angle of coxa (Fig. 12C). Leg 5 (Fig. 12D-G): coxae and intercoxal sclerite completely fused to form common base; coxa and basis incompletely fused in right leg and separate in left. Right leg: endopod (Fig. 12E) 1-segmented, spatulate, with minute sensillum on outer proximal margin and tubular prominences terminally; first exopod segment produced on outer angle, with minute spine, second segment almost completely separate from third, with 2 tufts of fine setules at inner distal angle, minute sensillum at midlength of inner distal triangular process (Fig. 12G) and outer terminal spiniform seta, third segment triangular, tapering distally, with minute sensillum at outer middle margin and short vestigial element terminally; third segment with well developed muscles proximally. Left leg: endopod (Fig. 12F) distinctly 2-segmented, first segment produced terminally, second separate from first, spatulate, covered by numerous fine setules on outer surface, with attachment of muscles proximally; first exopod segment similar to that of right leg, second expanded inwards with outer seta subterminally, third segment small, separate from second, with 2 elongate, chitinized processes terminally and minute setule and scar of outer element proximally.

REMARKS. The fifth leg of the new genus exhibits a more primitive state than *Paraugaptilus* in: (1) 2-segmented left endopod; (2) both exopods 3-segmented. The right third exopodal segment of *Paraugaptiloides* is certainly movable with well-developed muscles originating in the preceding segment, while the counterpart of *Paraugaptilus* is almost fused with the preceding segment and has reduced musculature (see Figs 30F,32H). It is probably not movable. In addition, the second segment of the left endopod in *Paraugaptiloides* is likely to be movable as indicated by the presence of a muscle extending between first and second segments.

Genus Arietellus Giesbrecht, 1892

DIAGNOSIS (emended). Female. Body relatively large, measuring approximately 3 to 7 mm in total length. Prosome pointed or rounded frontally; cephalosome separate from first pedigerous somite; last prosomal somite with pair of blunt dorsolateral processes and paired ventrolateral processes, symmetrical or asymmetrical, strongly or weakly produced backwards. Genital double-somite longer than wide, with pair of gonopores ventrolaterally and copulatory pore ventromedially; seminal receptacle relatively large, bulbous, located laterally. Anal somite large; anal operculum not developed. Caudal rami symmetrical, longer than wide, divergent or not, with well developed setae II to VII.

Antennule symmetrical, distinctly 20-segmented; posterior margin fringed with long setules from segment I to X; segments I to IV and XXIII to XXVIII fused; segments IV, VI and XII without aesthetasc; compound segment XXVI–XXVIII with 7 setae and aesthetasc. Antenna: first endopod segment unarmed; second segment with 2 inner setae, reduced in some species, and 5 setae and setule terminally; exopod indistinctly 7- or 8-segmented, segment VIII unarmed. Mandibular gnathobase lacking tuft of setules at midlength; 3 cusped teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: endopod absent; first exopod segment with reduced or normal seta, outer seta on fifth segment vestigial. Maxillule: praecoxal arthrite with 6 elements (5 spines and 1 process); coxal endite bearing 1 relatively short, thick seta, fringed with long setules; coxal epipodite with 8 setae; outer basal seta absent; endopod rudimentary, almost fused to basis or 1-segmented, bulbous, with 1 seta terminally. Maxilla: first and second praecoxal endites carrying 1 and 2 setae, respectively; basal spine with 2 rows of spinules; endopod setae armed with stout spinules fringed with lamellar structure basally. Maxilliped: setal formula of endopod segments of maxilliped: 1,4,4,3 or 2,3 or 2,4 (innermost seta on fourth and fifth segments reduced or completely lacking in some species); setae a and b on sixth segment vestigial.

First and third exopod segments of leg 1 bearing 1 and 2 outer spines respectively. Leg 5 reduced; coxae and intercoxal sclerite fused to form common transverse plate; basis and coxa separate or fused; right basal seta longer than left; endopod fused with basis, represented by small knob bearing 1 to 3 setae terminally, vestigial in some species; exopod 1-segmented, bulbous, carrying 1 terminal spine or almost fused to basis, unarmed.

Male. Body as in female, about 4 to 6 mm in total length.

Left antennule 19-segmented, geniculate; segment XXI fused with XXII; segments II and III with 1 seta; segment XIII with seta; segments I to IX fringed with row of long setules along posterior margin.

Second endopod segment of antenna with 1 long and 1 short seta medially; first exopod segment of mandible with normally developed seta.

Leg 5: coxae and intercoxal sclerite fused to form common plate; right coxa and basis incompletely fused; right basal seta remarkably or normally elongate. Right leg: endopod 1-segmented, unarmed; exopod indistinctly 3-segmented, distal 2 segments incompletely fused, second segment with stout process on inner angle, third segment spatulate, with 0–2 vestigial elements. Left leg: endopod indistinctly 2-segmented or 1-segmented, unarmed; exopod 3-segmented, second segment expanded medially, third segment incompletely fused with preceding one, bearing 2 terminal spines, with or without outer minute spinule.

TYPE SPECIES. *Arietellus setosus* Giesbrecht, 1892 (monotypic).

OTHER SPECIES. *A. aculeatus* (T. Scott, 1894); *A. giesbrechti* Sars, 1905; *A. pavoninus* Sars, 1905; *A. plumifer* Sars, 1905; *A. simplex* Sars, 1905 (= *A. major* Esterly, 1906); *A. armatus* Wolfenden, 1911; *A. minor* Wolfenden, 1911; *A. pacificus* Esterly, 1913; *A. tripartitus* C.B. Wilson, 1950; *A.* sp. Bradford, 1974; *A. mohri* (Björnberg, 1975), new combination; *A.* sp. briefly described here.

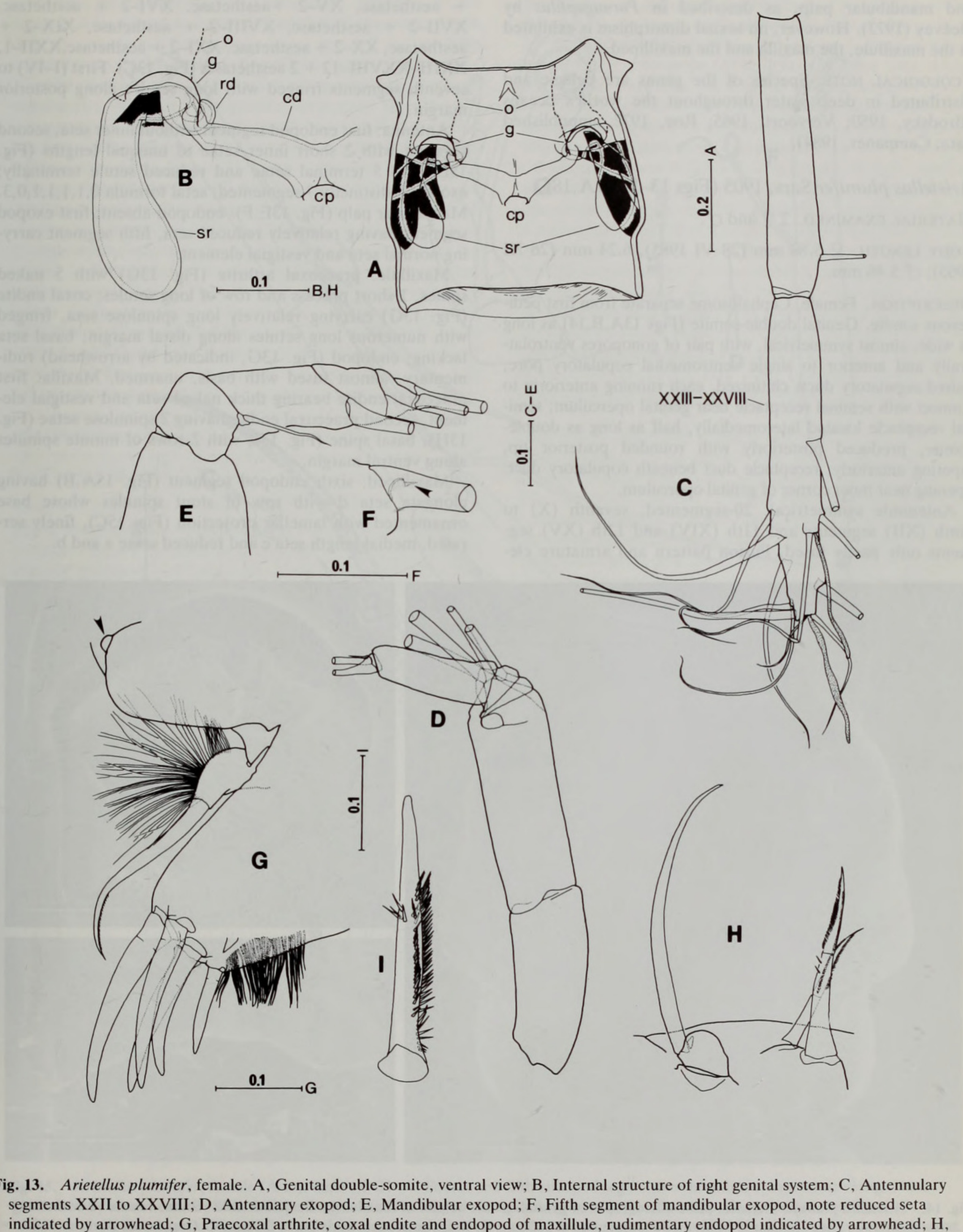

Fig. 13. *Arietellus plumifer*, female. A, Genital double-somite, ventral view; B, Internal structure of right genital system; C, Antennulary segments XXII to XXVIII; D, Antennary exopod; E, Mandibular exopod; F, Fifth segment of mandibular exopod, note reduced seta indicated by arrowhead; G, Praecoxal arthrite, coxal endite and endopod of maxillule, rudimentary endopod indicated by arrowhead; H, First and second praecoxal endites of maxilla; I, Basal spine of maxilla. Scales in mm.

REMARKS. The present study revealed that *Paraugaptilus mohri* Björnberg, 1975 belongs to the genus *Arietellus* (see below). *Arietellus* shows sexual dimorphism in the antenna and mandibular palp, as described in *Paraugaptilus* by Deevey (1973). However, no sexual dimorphism is exhibited in the maxillule, the maxilla and the maxilliped.

ECOLOGICAL NOTE. Species of the genus are pelagic and distributed in deep water throughout the world's oceans (Brodsky, 1950; Vervoort, 1965; Roe, 1972, unpublished data; Campaner, 1984).

Arietellus plumifer Sars, 1905 (Figs 13–15,17A,18L)

MATERIAL EXAMINED. 2 ♀ and ♂.

BODY LENGTH. ♀ 5.88 mm (28 VI 1985), 6.24 mm (26 XI 1965); ♂ 5.46 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Figs 13A,B,14) as long as wide, almost symmetrical, with pair of gonopores ventrolaterally and anterior to single ventromedial copulatory pore; paired copulatory ducts chitinized, each running anteriorly to connect with seminal receptacle near genital operculum; seminal receptacle located lateromedially, half as long as double-somite, produced posteriorly with rounded posterior tip, tapering anteriorly; receptacle duct beneath copulatory duct, opening near inner corner of genital operculum.

Antennule symmetrical, 20-segmented; seventh (X) to ninth (XII) segments and 11th (XIV) and 12th (XV) segments only partly fused. Fusion pattern and armature elements as follows: I–IV–9 + 2 aesthetascs, V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2, IX–2 + (small) aesthetasc, X–2, XI–2 + aesthetasc; XII–2, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 +aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc,XXII–1, XXIII–XXVIII–12 + 2 aesthetascs (Fig. 13C). First (I–IV) to seventh segments fringed with long setules along posterior margin.

Antenna: first endopod segment without inner seta, second segment with 2 short inner setae of unequal lengths (Fig. 15D) and 5 terminal setae and reduced setule terminally; exopod indistinctly 7-segmented; setal formula 0,1,1,1,1,0,3. Mandibular palp (Fig. 13E,F): endopod absent; first exopod segment having relatively reduced seta, fifth segment carrying normal seta and vestigial element.

Maxillule: praecoxal arthrite (Fig. 13G) with 5 naked spines, 1 short process and row of long setules; coxal endite (Fig. 13G) carrying relatively long spinulose seta, fringed with numerous long setules along distal margin; basal seta lacking; endopod (Fig. 13G, indicated by arrowhead) rudimentary, almost fused with basis, unarmed. Maxilla: first praecoxal endite bearing thick naked seta and vestigial element, second praecoxal endite having 2 spinulose setae (Fig. 13H); basal spine (Fig. 13I) with 2 rows of minute spinules along ventral margin.

Maxilliped: sixth endopod segment (Fig. 15A,B) having elongate seta d with row of stout spinules whose base ornamented with lamellar projection (Fig. 15C), finely serrated, medial-length seta c and reduced setae a and b.

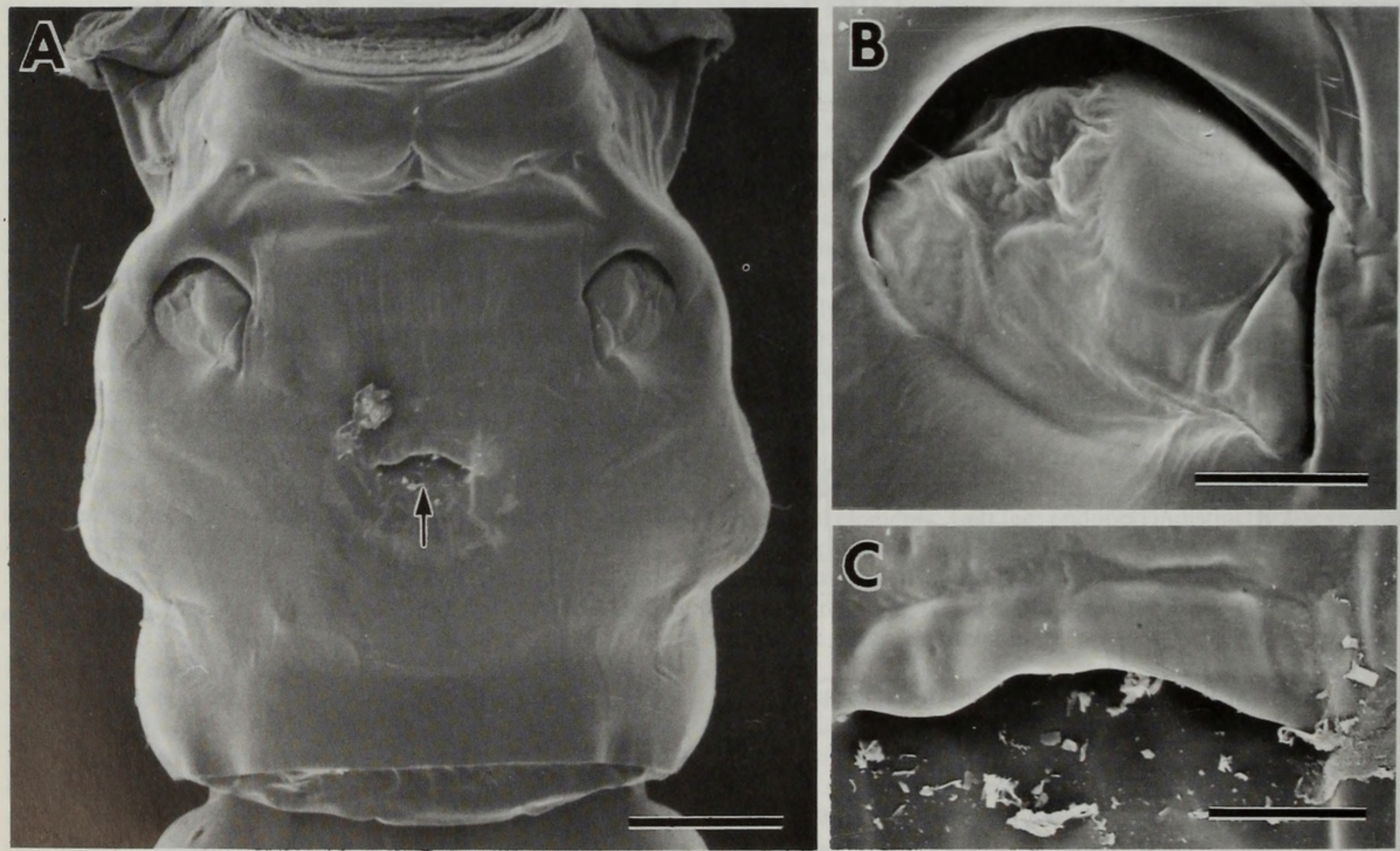

Fig. 14. *Arietellus plumifer*, female. SEM micrographs of genital double-somite of female. A, Genital double-somite, ventral view showing large copulatory pore (indicated by an arrow), scale bar = 100 μm; B, Right gonopore, scale bar = 30 μm; C, Copulatory pore, scale bar = 20 μm.

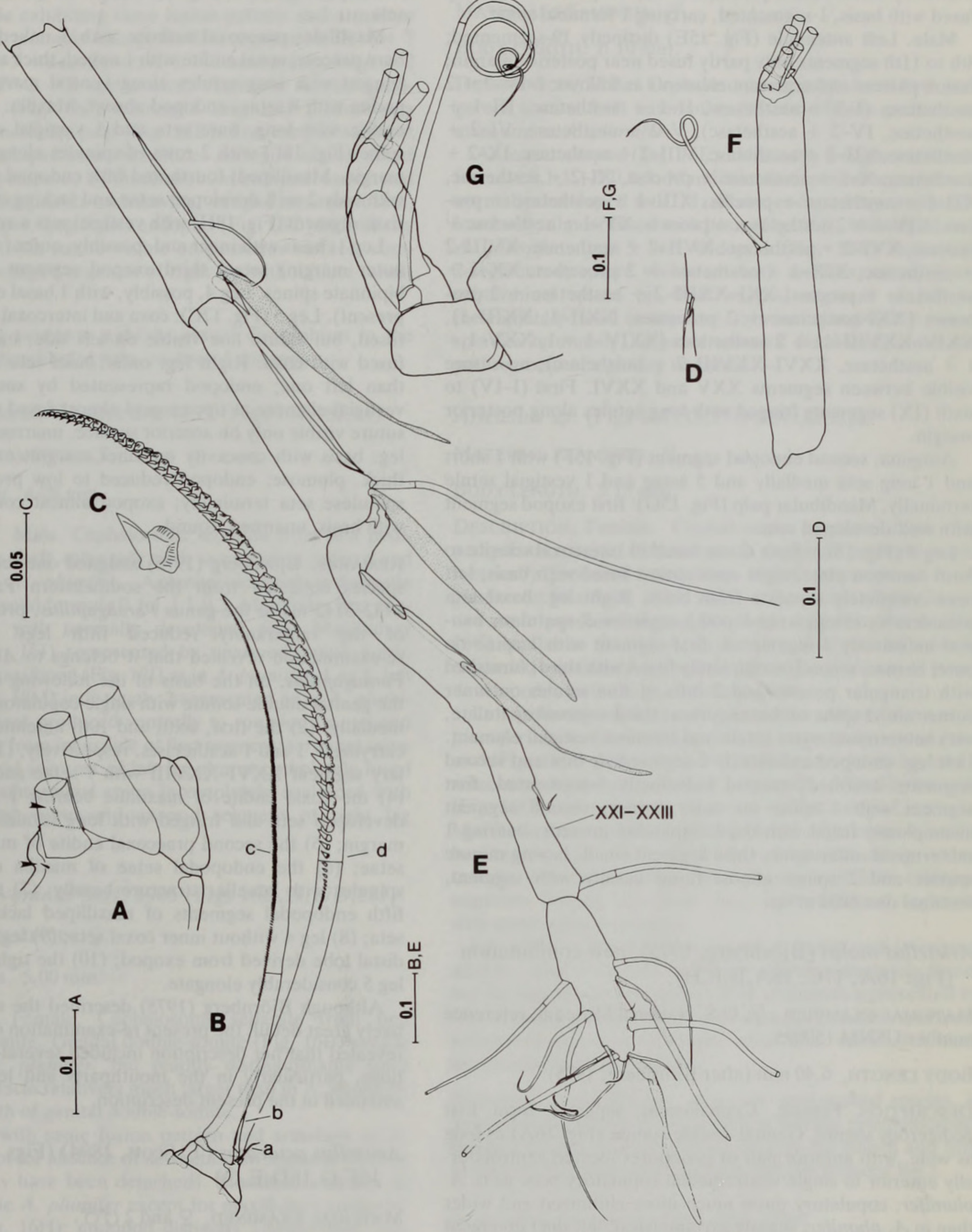

Fig. 15. *Arietellus plumifer*, female (A-D), male (E-G). A, Fourth and fifth endopod segments of maxilliped, innermost vestigial seta indicated by arrowhead; B, Sixth endopod segment of maxilliped; C, Spinule on seta d of sixth endopod segment of maxilliped; D, Mid-margin setae on second segment of antennary endopod; E, Left antennulary segments XIX to XXVIII; F, Second endopod segment of antenna; G, Mandibular exopod. Scales in mm.

Leg 1: third exopod segment with 2 subterminal serrate spines.

Leg 5 (Fig. 17A): coxae incompletely fused with intercoxal sclerite; right basal seta extremely elongate; endopod represented by knob with 2 plumose setae; exopod incompletely fused with basis, 1-segmented, carrying 1 terminal spine.

Male. Left antennule (Fig. 15E) distinctly 19-segmented; 8th to 11th segments only partly fused near posterior margin; fusion pattern and armature elements as follows: I–IV–7 + 2 aesthetascs (I–3 + aesthetasc, II–1 + aesthetasc, III–1 + aesthetasc, IV–2 + aesthetasc), V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–1 + aesthetasc + process, XI–2 + aesthetasc, XII–1 + aesthetasc + process, XIII–1 + aesthetasc + process, XIV–1 + 2 aesthetascs + process, XV–1 + aesthetasc + process, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–1 + aesthetasc + 2 processes, XX–1 + aesthetasc + process, XXI–XXIII–2 + aesthetasc + 2 processes (XXI-aesthetasc + 2 processes, XXII–1, XXIII–1), XXIV–XXVIII–11 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–7 + aesthetasc); no suture visible between segments XXV and XXVI. First (I–IV) to sixth (IX) segments fringed with long setules along posterior margin.

Antenna: second endopod segment (Fig. 15F) with 1 short and 1 long seta medially and 5 setae and 1 vestigial setule terminally. Mandibular palp (Fig. 15G): first exopod segment with well-developed seta.

Leg 5 (Fig. 18L): both coxae fused to intercoxal sclerite to form common plate, right coxa almost fused with basis, left coxa completely separate from basis. Right leg: basal seta considerably elongate; endopod 1-segmented, spatulate; exopod indistinctly 3-segmented, first segment with 1 spine on outer corner, second incompletely fused with third, furnished with triangular process and 2 tufts of fine setules on inner corner and 1 spine on outer corner, third segment spatulate, with subterminal outer setule and terminal vestigial element. Left leg: endopod indistinctly 2-segmented, first and second segments unarmed; exopod indistinctly 3-segmented, first segment with 1 spine on outer corner, second segment incompletely fused with third, expanded inwards, bearing 1 subterminal outer spine, third segment small, having minute spinule and 2 spines almost fused basally with segment, terminal one bifid at tip.

Arietellus mohri (Björnberg, 1975), new combination (Figs 16A, 17C, 18A,B,F,H)

MATERIAL EXAMINED. ♀, U.S. National Museum, reference number USNM 150095.

BODY LENGTH. 6.40 mm (after Björnberg, 1975)

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Fig. 16A) as long as wide, with anterior pair of gonopores located ventrolaterally anterior to single ventromedial copulatory pore as in *A. plumifer*; copulatory ducts much more chitinized and wider than in *A. plumifer*, slightly asymmetrical, left duct divergent into blind tubule near left genital operculum; seminal receptacle the same shape as in *A. plumifer*.

Right antennule (left antennule missing distal segments) with fusion pattern and armature as *A. plumifer* except for missing elements. Antenna: first endopod segment unarmed, second segment with 2 inner setae of unequal length medially and 5 setae and 1 vestigial setule terminally; exopod 7-segmented, setal formula: 0,1,1,1,1,0,3. Mandibular palp (Fig. 18A,B): endopod absent; exopod 5-segmented, first to fourth segments each with 1 seta, first segment with well-developed seta, fifth segment with 1 long seta and vestigial seta.

Maxillule: praecoxal arthrite with 5 naked spines and 1 bare process; coxal endite with 1 naked, thick seta terminally, fringed with long setules along ventral margin; coxal epipodite with 8 setae; endopod absent. Maxilla: first praecoxal endite with long, bare seta and 1 vestigial element; basal spine (Fig. 18F) with 2 rows of spinules along ventromedial margin. Maxilliped: fourth and fifth endopod segments each with only 2 well developed setae and lacking innermost seta, sixth segment (Fig. 18H) with vestigial seta a and short seta b.

Leg 1: basis with inner and, possibly, outer (scar present on outer margin) setae; third exopod segment with 2 lateral bipinnate spines. Leg 4, possibly, with 1 basal outer seta (scar present). Leg 5 (Fig. 17C): coxa and intercoxal sclerite almost fused, but suture line visible on left side; basis completely fused with coxa. Right leg: outer basal seta more elongate than left one; endopod represented by small knob with vestigial element at tip; exopod almost fused with basis, but suture visible only on anterior surface, unarmed, round. Left leg: basis with concavity on inner margin; outer basal seta thick, plumose; endopod reduced to low prominence with spinulose seta terminally; exopod almost completely fused with basis, unarmed, round.

REMARKS. Björnberg (1975) assigned one female of a new species collected from the southeastern Pacific (depths: 1932–3142 m) to the genus *Paraugaptilus*, probably because of the remarkably reduced fifth legs. The present re-examination revealed that it belongs to *Arietellus* not to *Paraugaptilus*, on the basis of the following characters: (1) the genital double-somite with single copulatory pore ventromedially; (2) the first, sixth and 10th antennulary segments carrying 2, 1 and 1 aesthetascs, respectively; (3) the antennulary segment XXVI–XXVIII with 7 setae and 1 aesthetasc; (4) the coxal endite of maxillule bearing 1 relatively well developed seta and fringed with long setules along ventral margin; (5) the second praecoxal endite of maxilla having 2 setae; (6) the endopodal setae of maxilla carrying sharp spinules with lamellar structure basally; (7) the fourth and fifth endopodal segments of maxilliped lacking innermost seta; (8) leg 4 without inner coxal seta; (9) leg 5 with distinct distal lobe derived from exopod; (10) the right basal seta of leg 5 considerably elongate.

Although Björnberg (1975) described the species in relatively great detail, the present re-examination of the holotype revealed that her description included several misinterpretations, particularly in the mouthparts and legs. These are amended in the present description.

Arietellus aculeatus (T. Scott, 1894) (Figs 16F,G,18D,E,O)

MATERIAL EXAMINED. ♀ and 2 ♂♂.

BODY LENGTH. ♀ 4.62 mm; ♂ 3.77, 3.79 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Left antennule similar to that of female *A. plumifer* except for following points: segments VIII and X each with minute aesthetasc; segment XIV carrying 2 setae and 2 aesthetascs. Antenna: second endopod segment (Fig. 16G) with 2 short inner setae medially and 5 setae and 1 vestigial seta terminally. Mandibular palp (Fig. 18D): first exopod segment with reduced, short seta.

Male. Cephalosome separate from first pedigerous somite. Left antennule exhibiting same fusion pattern and armature elements as *A. plumifer* except for first segment: I–IV–7 + 7 aesthetascs (I–3 + aesthetasc, II–1 + 2 aesthetascs, III–1 + 2 aesthetascs, IV–2 + 2 aesthetascs). Antenna: second endopod segment (Fig. 16F) bearing 1 long and 1 short seta medially. Mandibular palp (Fig. 18E): first exopod segment with well-developed seta. Maxillule: endopod almost fused with basis, represented by small knob. Maxilliped: fourth and fifth endopod segments each having vestigial innermost seta, as in *A. plumifer*. Leg 5: left endopod (Fig. 18O) indistinctly 2-segmented, with suture visible on posterior surface; compound distal exopod segment of right leg with minute terminal element.

REMARKS. *A. aculeatus* exhibits sexual dimorphism in the antenna and mandibular palp, as does *A. plumifer*.

Arietellus setosus Giesbrecht, 1892 (Figs 16J,18I,M)

MATERIAL EXAMINED. ♂.

BODY LENGTH. 4.28 mm.

DESCRIPTION. Male. Cephalosome separate from first pedigerous somite. Left antennule with same fusion pattern and armature as *A. plumifer*. Antenna: exopod indistinctly 7-segmented; setal formula 0,1,1,1,1,0,3. Mandible: first exopod segment with normally developed seta. Maxillulary endopod (Fig. 16J) represented by unarmed, small knob. Maxilla and maxilliped (Fig. 18I) as in *A. plumifer*. Leg 5: left endopod (Fig. 18M) indistinctly 2-segmented as in *A. plumifer*, first segment produced ventrally to rounded tip, second segment rising from inner side of first segment; terminal spine on third exopod segment of left leg almost completely fused to segment, subterminal spine incompletely coalesced with segment; distal compound exopod segment of right leg unarmed.

Arietellus pavoninus Sars, 1905 (Figs 16B,H,17B,18J)

MATERIAL EXAMINED. ♀.

BODY LENGTH. 5.00 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Fig. 16B) similar to that of *A. plumifer*, but readily distinguishable since seminal receptacle relatively much larger than in *A. plumifer*, over half length of genital double-somite.

Antennule with same fusion pattern and armature as *A. plumifer* except for absence of aesthetasc on segment IX (this aesthetasc may have been detached). Mouthparts similar to those of female *A. plumifer* except for maxillulary endopod. Maxillule (Fig. 16H): endopod distinctly 1-segmented, bulbous with 1 bipinnate seta. Maxilliped (Fig. 18J): fourth and fifth endopod segments each with reduced innermost seta, sixth segment with reduced setae a and b. Leg 5 (Fig. 17B): coxae incompletely fused with intercoxal sclerite, in particular, more fused in right leg; endopod represented by 2 plumose setae not so produced as in *A. plumifer*; exopods 1-segmented, separate from basis, carrying 1 unipinnate spine terminally.

Arietellus simplex Sars, 1905 (Figs 16E,I,18N)

MATERIAL EXAMINED. ♂.

BODY LENGTH. 6.10 mm.

DESCRIPTION. Male. Cephalosome separate from first pedigerous somite. Left antennule with same fusion pattern and armature as *A. plumifer*.

Antenna: exopod (Fig. 16E) indistinctly 8-segmented; setal formula 0,1,1,1,1,0,0,3. Mandible: first exopod segment with normally developed seta. Maxillule: endopod represented by low knob, almost fused with basis (Fig. 16I). Maxilliped as in *A. plumifer*. Leg 5: left endopod (Fig. 18N) indistinctly 2-segmented, suture visible on both surfaces; terminal and subterminal spines on third exopod segment of left leg incompletely fused to segment, terminal spine with 4 minute spinules terminally; terminal spine of distal compound exopod segment of right leg unarmed.

Arietellus sp. (Figs 16C,D,17D,18C,G,K)

MATERIAL EXAMINED. ♀.

BODY LENGTH. 5.15 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Posterolateral angles of prosome asymmetrically produced into sharp lateral processes as in *A. giesbrechti* (see Sars, 1924, 1925), left process slightly longer and more produced than right. Genital double-somite (Fig. 16C) similar to that of *A. mohri* in having pair of laterally expanded copulatory ducts, but differing in presence of better developed muscles to genital operculum.

Left antennule with same segmentation and armature as *A. plumifer*. Antennary endopod: first segment unarmed, second (Fig. 16D) with 1 long and 1 short seta medially, and 5 setae and 1 vestigial element terminally. Mandibular palp (Fig. 18C) with relatively long seta on first exopod segment. Maxillulary endopod completely fused with basis. Maxilla: basal spine (Fig. 18G) with 2 rows of spinules along ventral margin. Maxilliped (Fig. 18K): fourth and fifth endopod segments lacking innermost seta; sixth endopod segments with setae a and b reduced.

Leg 5 (Fig. 17D) similar to that of *A. mohri* with intercoxal sclerite, coxa, basis and both rami almost completely fused, but distinguishable by: seta on both endopods represented by low knob much better developed than in *A. mohri*; unarmed, lobate exopods more developed than in *A. mohri*; left basal seta longer than in *A. mohri*.

REMARKS. *Arietellus* sp., an as yet undescribed species, is most closely related to *A. mohri* in having synapomorphic characters such as no innermost seta on the fourth and fifth endopodal segments of maxilliped and the reduced leg 5.

Genus *Rhapidophorus* Edwards, 1891

TYPE SPECIES. *Rhapidophorus wilsoni* Edwards, 1891 (monotypic).

REMARKS. Fosshagen (1968) first pointed out the affinity of this genus with *Paramisophria*. Campaner (1977) later assigned the genus to the family Arietellidae. The genus,

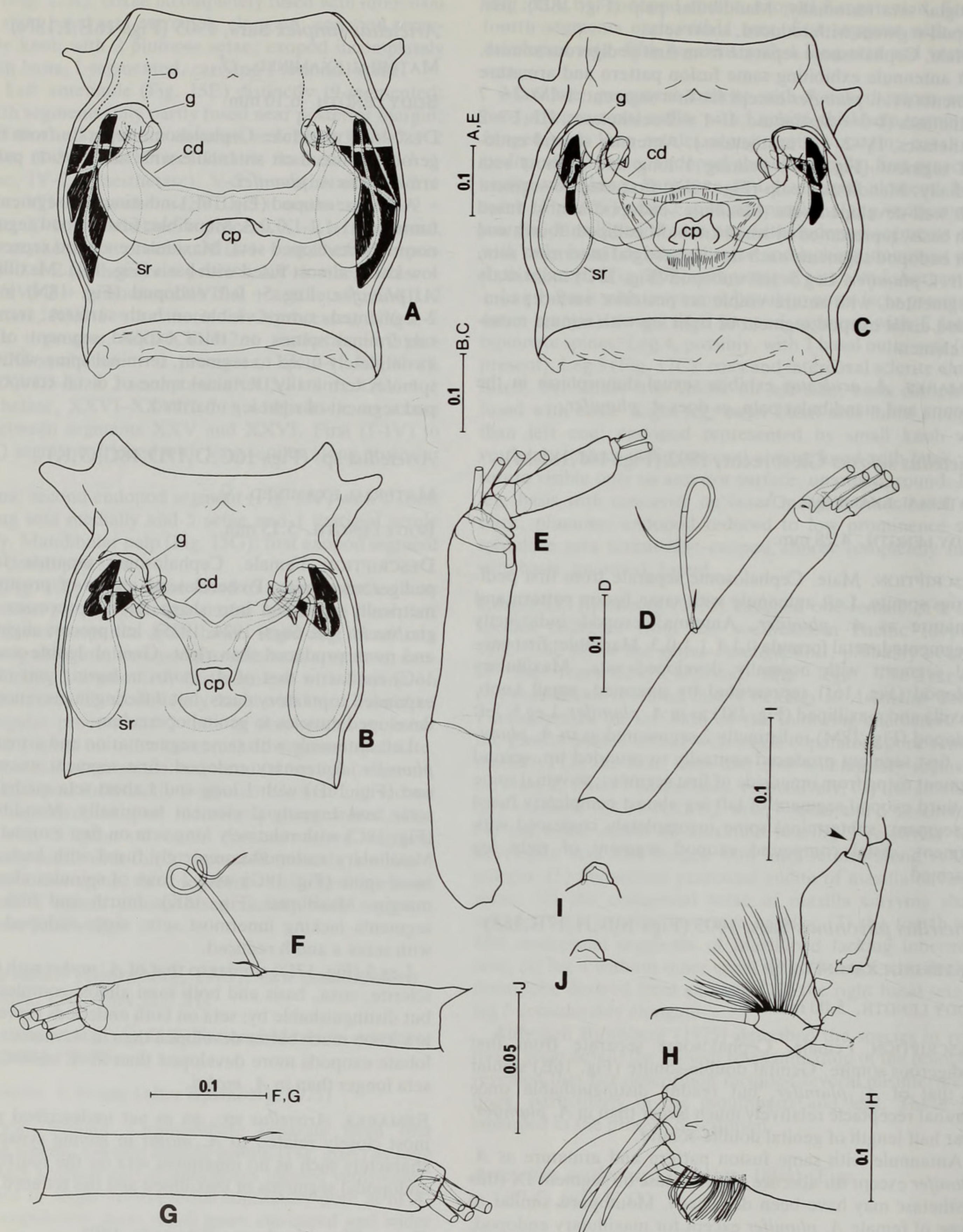

Fig. 16. *Arietellus mohri*, female (A); *A. pavoninus*, female (B,H); *A.* sp., female (C,D); *A. simplex*, male (E,I); *A. aculeatus*, female (G), male (F); *A. setosus*, male (J). A-C, Genital double-somite, ventral view; D,F,G, Second endopod segment of antenna; E, Antennary exopod; H, Praecoxal arthrite, coxal endite and endopod of maxillule, endopod indicated by arrowhead; I,J, Maxillulary endopod. Scales in mm.

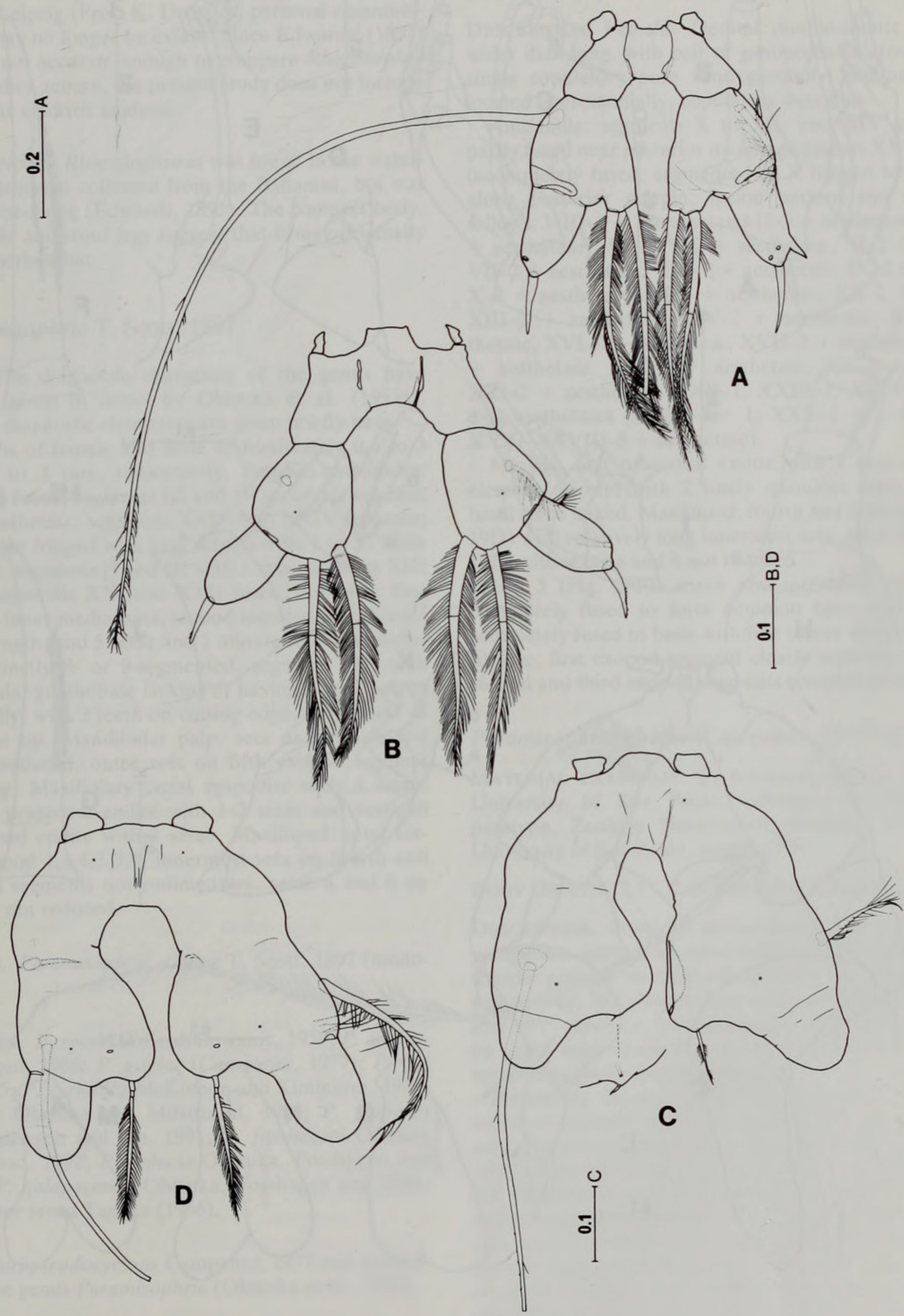

Fig. 17. Fifth legs of females of *Arietellus*. A, *A. plumifer*; B, *A. pavoninus*; C, *A. mohri*, vestigial element on right endopod represented by low knob incorporated in C; D, *A*. sp. Scales in mm.

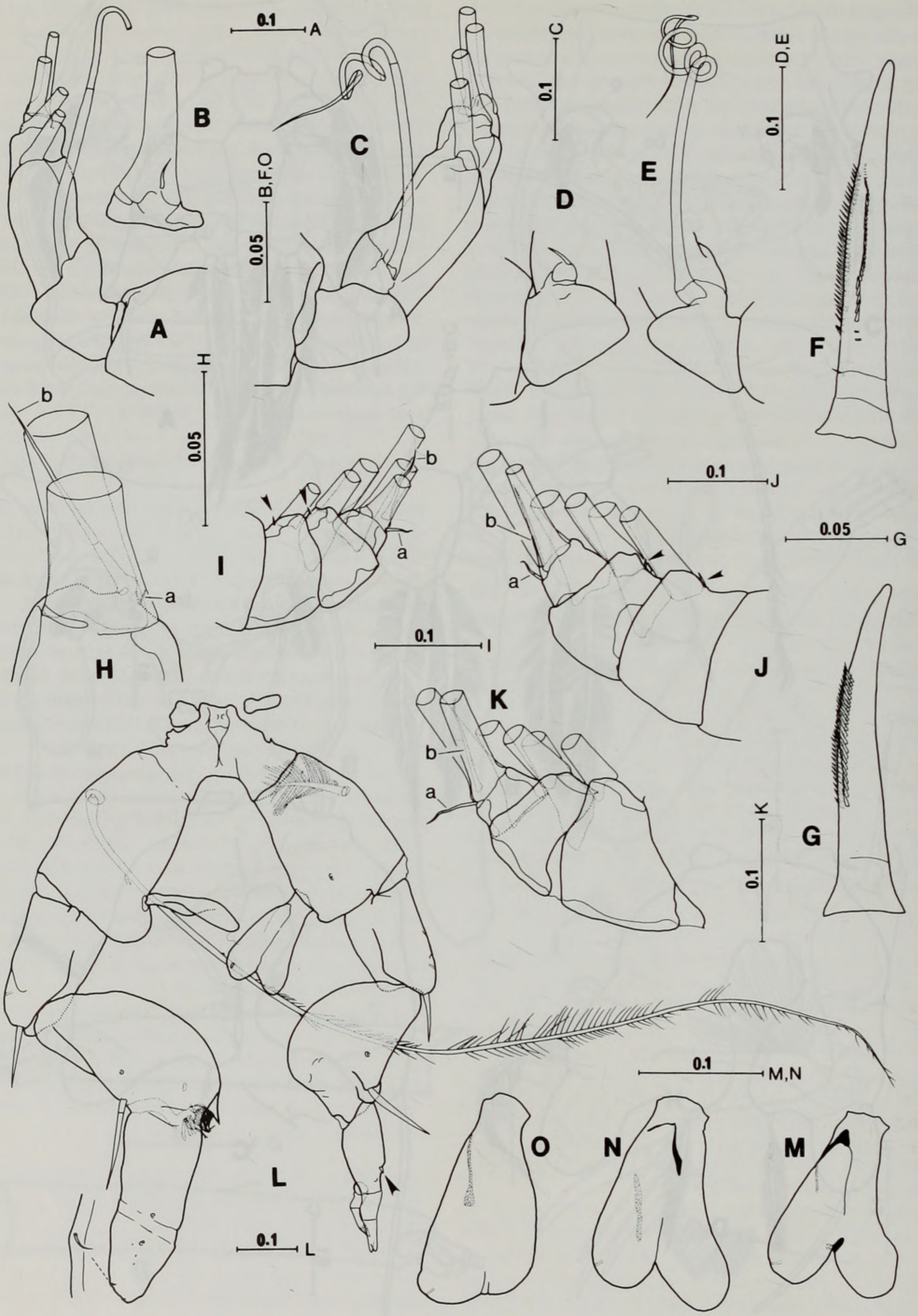

Fig. 18. *Arietellus mohri*, female (A,B,F,H); *A.* sp., female (C,G,K); *A. aculeatus*, female (D), male (E,O); *A. setosus*, male (I); *A. pavoninus*, female (J); *A. plumifer*, male (L); *A. setosus*, male (M); *A. simplex*, male (N). A,C, Mandibular exopod; B, Fifth exopod segment of mandible; D,E, First exopod segment of mandible; F,G, Maxillary basal spine; H, Sixth endopod segment of maxilliped; I-K, Fourth to sixth endopod segments of maxilliped; L, Leg 5, anterior surface; M-O, Left endopod of leg 5. Scales in mm.

however, has peculiar characters in the mandibular palp, maxillule, maxilliped and leg 1 as indicated by Fosshagen (1968). We were unable to re-examine the male type specimen; it is deposited neither in the Berlin Zoological Museum (Dr. H.-E. Gruner, personal communication) nor at the University of Leipzig (Prof. K. Drössler, personal communication), and may no longer be extant. Since Edwards' (1891) description is not accurate enough to compare *Rhapidophorus* with the other genera, the present study does not include the genus in the cladistic analysis.

ECOLOGICAL NOTE. *Rhapidophorus* was found in the water-lung of a holothurian collected from the Bahamas, but was stated to be free-living (Edwards, 1891). The compact body, short antennule and stout legs suggest that it may originally have been hyperbenthic.

Genus Paramisophria T. Scott, 1897

DIAGNOSIS. The diagnostic characters of the genus have already been given in detail by Ohtsuka et al. (1993a). Supplemental diagnostic characters are given briefly here.

Body lengths of female and male approximately 0.6 to 3 mm and 0.6 to 2 mm, respectively. Female antennules: segments I–III fused; segments III and IV separate; segment IV without aesthetasc; segments XXIII and XXIV separate; posterior margin fringed with long setules from I to X. Male left antennule: segments II and III with 1 seta; segment XIII with 1 seta; segments XXI and XXII fused. Antenna: first endopod with inner medial seta, second segment with 3 inner setae at midlength, and 5 setae and 1 minute seta terminally; exopod indistinctly 8- or 9-segmented, segment VIII with seta. Mandibular gnathobase lacking or having a small tuft of setules medially, with 3 teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillulary coxal epipodite with 8 setae. Maxilla: first praecoxal endite with 1–2 setae and vestigial element, second endite with 2 setae. Maxilliped: setal formula of endopod 1,4,4,3,3,4; innermost seta on fourth and fifth endopod segments not rudimentary, setae a and b on sixth segment not reduced.

TYPE SPECIES. *Paramisophria cluthae* T. Scott, 1897 (monotypic).

OTHER SPECIES. *P. spooneri* Krishnaswamy, 1959; *P. ammophila* Fosshagen, 1968; *P. giselae* (Campaner, 1977); *P. itoi* Ohtsuka, 1985; *P. variabilis* McKinnon and Kimmerer, 1985; *P. platysoma* Ohtsuka and Mitsuzumi, 1990; *P. japonica* Ohtsuka, Fosshagen and Go, 1991; *P. fosshageni* Othman and Greenwood, 1992; *P. reducta* Ohtsuka, Fosshagen and Iliffe, 1993; *P. galapagensis* Ohtsuka, Fosshagen and Iliffe, 1993; *P. cluthae* sensu Tanaka (1966).

REMARKS. *Parapseudocyclops* Campaner, 1977 was synonymized with the genus *Paramisophria* (Ohtsuka et al., 1991).

ECOLOGICAL NOTE. *Paramisophria* is mainly distributed in the near-bottom communities on the continental shelf (Ohtsuka et al., 1991), but also colonizes marine caves (Ohtsuka et al., 1993a).

Paramisophria japonica Ohtsuka, Fosshagen and Go, 1991 (Figs 19,20F)

MATERIAL EXAMINED. ♀.

BODY LENGTH. 1.85–2.08 mm (after Ohtsuka et al., 1991).

DESCRIPTION. Female. Genital double-somite (Fig. 19A) wider than long, with pair of gonopores anteroventrally and single copulatory pore ventromedially; seminal receptacle located lateromedially; copulatory duct thin.

Antennule: segments X to XII, and XIV and XV only partly fused near posterior margin; segments XXV and XXVI incompletely fused; segments I to X fringed by long setules along posterior margin; fusion pattern and armature as follows: I–III–7 + 2 aesthetascs (I–3 + aesthetasc, II–2, III–2 + aesthetasc), IV–2, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc).

Maxilla: first praecoxal endite with 1 seta and vestigial element, second with 2 finely spinulose setae (Fig. 19C); basal spine naked. Maxilliped: fourth and fifth segments (Fig. 19D) with relatively long innermost seta; sixth segment (Fig. 19E) with setae a and b not reduced.

Leg 5 (Fig. 20F): coxae and intercoxal sclerite almost completely fused to form common base; endopod almost completely fused to basis with fine suture visible on posterior surface; first exopod segment clearly separate from second; second and third exopod segments completely fused.

Paramisophria giselae (Campaner, 1977) (Fig. 20A-E)

MATERIAL EXAMINED. ♀, holotype, Museu de Zoologia, University of Sao Paulo, reference number 4004. ♀, paratype, Zoology Department, Instituto de Biociências, University of Sao Paulo, number 173.

BODY LENGTH. 2.55, 2.60 mm (after Campaner, 1977).

DESCRIPTION. Posterior lateral corners of second and third pedigerous somites asymmetrically produced: corners more sharply pointed on right side than on left. Genital double-somite (Fig. 20A) longer than wide; genital system similar to that of *P. japonica*, but differing in: copulatory pore located on right side; seminal receptacle located near gonopore; copulatory pore relatively thick.

Antennary exopod (Fig. 20B) indistinctly 9-segmented; terminal segment with 2 long plumose setae and vestigial seta. Mandibular gnathobase with small tuft of setules medially; 3 teeth on cutting edge, dorsalmost of which bifurcate at tip. Mandibular palp similar to that of *P. japonica*: endopod rudimentary, 1-segmented, with 2 setae of unequal lengths; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillule similar to that of *P. japonica* except for relatively long seta on coxal endite: praecoxal arthrite with 5 naked spines and 1 process; coxal epipodite with 8 setae; small basal seta present; endopod bulbous, 1-segmented with 3 setae of unequal lengths. Maxilla: first praecoxal endite (Fig. 20C) with 2 spinulose setae and rudimentary element, second (Fig. 20C) bearing 2 spinu-

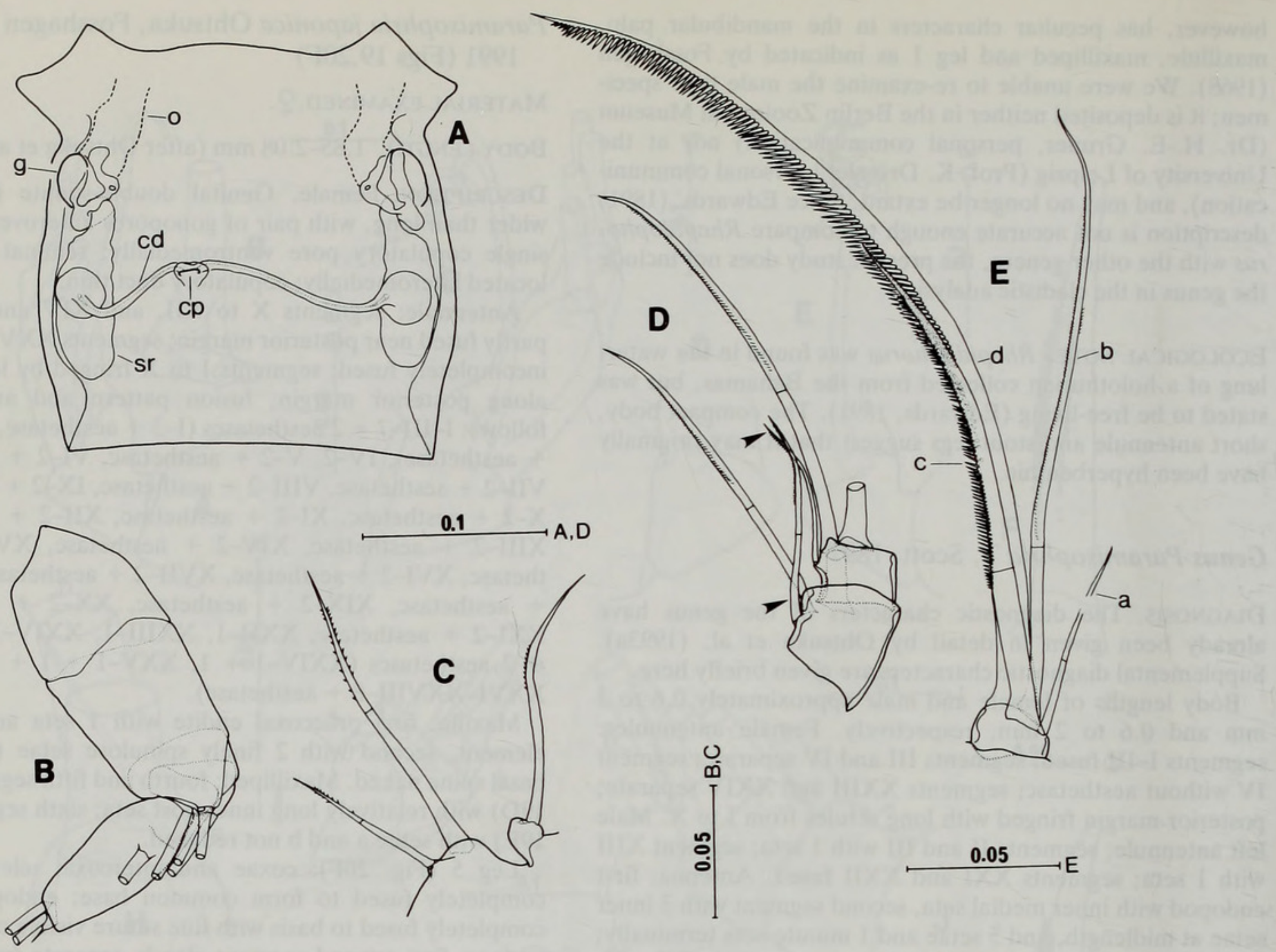

Fig. 19. *Paramisophria japonica*, female. A, Genital double-somite, ventral view; B, Antennary exopod; C, First and second praecoxal endites of maxilla; D, Fourth and fifth endopod segments of maxilliped; E, Sixth endopod segment of maxilliped. Scales in mm.

lose setae; basal spine (Fig. 20D) naked. Maxilliped with same setal formula as *P. japonica*.

Leg 5 (Fig. 20E): coxae and intercoxal sclerite clearly separate; setation and spinulation as in *P. japonica*; endopod completely fused to basis; exopod almost completely fused to basis with fine suture visible; first and second exopod segments fused with suture clearly visible on posterior surface; second and third exopod segments completely fused.

REMARKS. Re-examination of the holotype and paratype revealed the following: (1) since the antennules of both types are missing (the proximal half remains on one side only), we were unable to check the fusion and armature patterns; (2) the terminal segment of the antennary exopod has only 2 developed setae plus 1 minute seta although 3 developed setae were shown in the original description (Campaner, 1977); (3) the dorsalmost tooth on the mandibular gnathobase is bicuspid although it was originally drawn as monocuspid (Campaner, 1977); (4) the terminal segment of the mandibular exopod has 2 relatively well developed setae (one about 25% shorter than the other); (5) the setae on the mandibular endopod are missing but there are 2 scars visible, of different sizes, which suggests 2 unequal setae; (6) the coxal epipodite of the maxillule of the holotype is damaged: 5 long setae are present, then a gap due to damage, then a short seta; although the gap does not show clean scars where setae were broken off, the gap is only big enough for 2 setae – giving a total of 8 setae as in the paratype; (7) the first to sixth endopodal segments of the maxilliped bearing 1, 4, 4, 3, 3 and 4 setae, respectively; (8) no seta originating from the posterior surface of the first exopodal segment of leg 4.

Paramisophria reducta Ohtsuka, Fosshagen and Iliffe, 1993

MATERIAL EXAMINED. ♂, allotype, The Natural History Museum, BM (NH) Reg. No 1992. 1093.

BODY LENGTH. 1.60 mm (after Ohtsuka et al., 1993a).

DESCRIPTION. Male. Left antennule: segments XXI to XXIII, XXIV and XXV, and XXVI to XXVIII completely fused; segments XXIII and XXIV, and XXV and XXVI incompletely fused; fusion pattern and armature elements as follows: I–IV–7 + 4 aesthetascs (I–3 + aesthetasc, II–1 + aesthetasc, III–1 + aesthetasc, IV–2 + aesthetasc), V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–1 + aesthetasc + process, XI–2 + aesthetasc, XII–1 + aesthetasc + process, XIII–1 + aesthetasc + process, XIV–1 + aesthetasc + process, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–1 + aesthetasc + 2 processes, XX–1 + aesthetasc + process, XXI–XXIII–2 + aesthetasc + 2 processes (XXI-aesthetasc + 2 processes, XXII–1, XXIII–1), XXIV–XXV–4 + aesthetasc (XXIV–1 + 1, XXV–1 + 1 + aesthetasc), XXVI–XXVIII–8 + 2 aesthetascs.

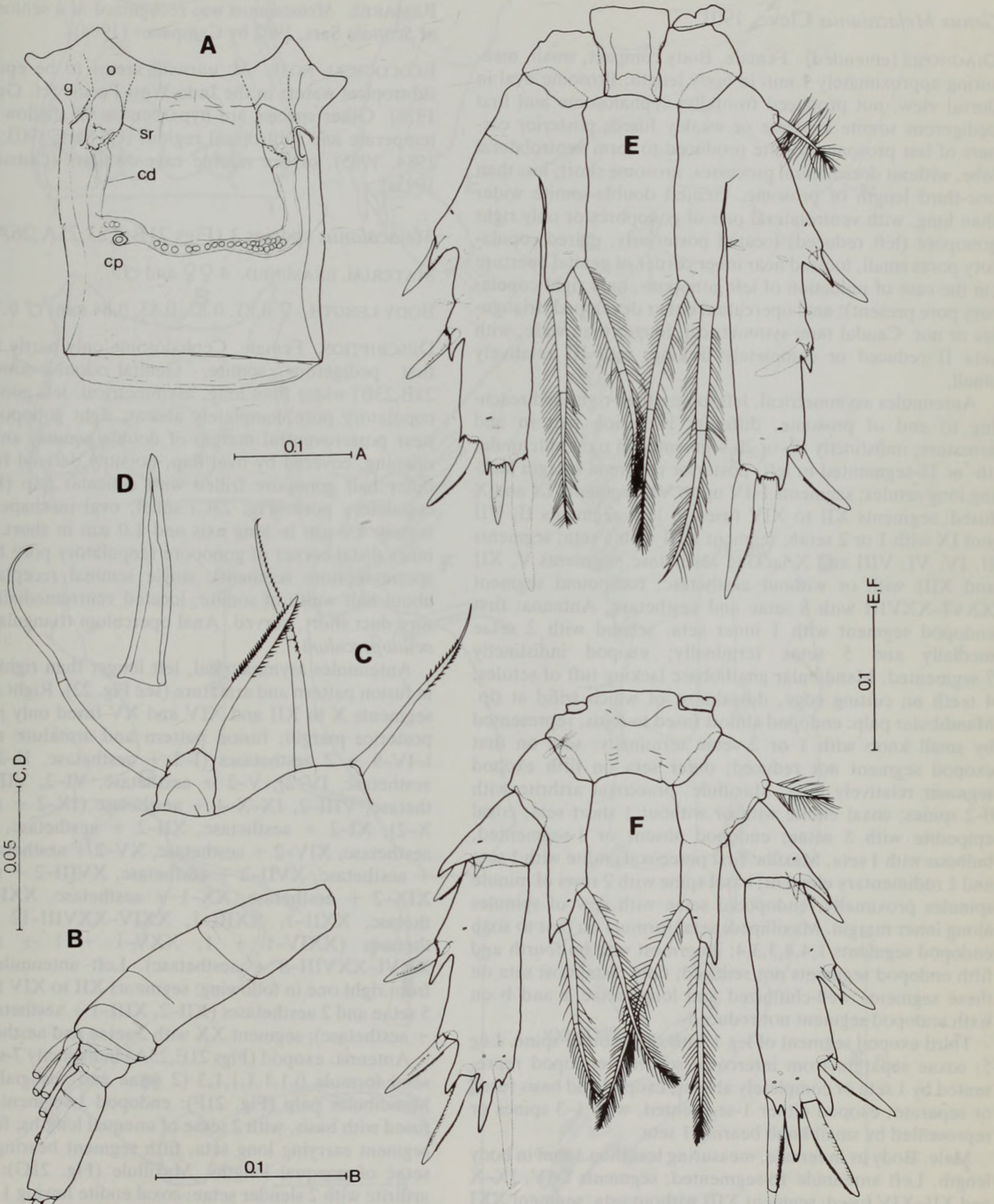

Fig. 20. *Paramisophria giselae*, female (A-E); *P. japonica*, female (F). A, Genital double-somite, ventral view; B, Antennary exopod; C, First and second praecoxal endites of maxilla; D, Basal spine of maxilla; E,F, Leg 5, anterior surface. Scales in mm.

REMARKS. The fusion pattern of the antennulary segments is slightly different from the male of *P. japonica* in which segments XXI and XXII are incompletely fused whereas segments XXIII and XXIV are separate.

Genus Metacalanus Cleve, 1901

DIAGNOSIS (emended). Female. Body compact, small, measuring approximately 1 mm in body length. Prosome oval in dorsal view, not produced frontally; cephalosome and first pedigerous somite separate or weakly fused; posterior corners of last prosomal somite produced to form ventrolateral lobe, without dorsolateral processes; urosome short, less than one-third length of prosome. Genital double-somite wider than long, with ventrolateral pair of gonopores or only right gonopore (left reduced) located posteriorly; paired copulatory pores small, located near inner corner of genital aperture (in the case of reduction of left gonopore, only right copulatory pore present); anal operculum either developed, triangular or not. Caudal rami symmetrical, longer than wide, with seta II reduced or completely lacking; seta III relatively small.

Antennules asymmetrical, left longer than right and reaching to end of prosome, different in fusion pattern and armature; indistinctly 18- or 20-segmented in right antennule, 16- or 18-segmented in left; posterior proximal margin lacking long setules; segments I–IV up to VI; segments IX and X fused; segments XII to XIV fused in left; segments II, VII and IX with 1 or 2 setae; segment XIII with 1 seta; segments II, IV, VI, VIII and X lacking aesthetasc; segments V, XII and XIII with or without aesthetasc; compound segment XXVI–XXVIII with 8 setae and aesthetasc. Antenna: first endopod segment with 1 inner seta, second with 2 setae medially and 5 setae terminally; exopod indistinctly 7-segmented. Mandibular gnathobase lacking tuft of setules; 4 teeth on cutting edge, dorsalmost of which trifid at tip. Mandibular palp: endopod almost fused to basis, represented by small knob with 1 or 2 setae terminally; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillule: praecoxal arthrite with 0–2 spines; coxal endite with or without 1 short seta; coxal epipodite with 5 setae; endopod absent or 1-segmented, bulbous with 1 seta. Maxilla: first praecoxal endite with 1 seta and 1 rudimentary element; basal spine with 2 rows of minute spinules proximally; endopodal setae with row of spinules along inner margin. Maxilliped: setal formula on first to sixth endopod segments 1,4,4,3,3,4; innermost seta on fourth and fifth endopod segments not reduced; only distalmost seta on these segments well-chitinized and long; setae a and b on sixth endopod segment not reduced.

Third exopod segment of leg 1 with single outer spine. Leg 5: coxae separate from intercoxal sclerite; endopod represented by 1 seta or completely absent; exopod and basis fused or separate; exopod either 1-segmented, with 1–3 spines or represented by small knob bearing 1 seta.

Male. Body as in female, measuring less than 1 mm in body length. Left antennule 16-segmented; segments I–IV, IX–X and XII–XIV fused; segment XIII without seta; segment XXI separate from XXII. Leg 5: coxae and intercoxal sclerite fused; basis separate from coxa; endopod absent; exopod 3-segmented, third segment with large seta almost fused with segment.

TYPE SPECIES. *Metacalanus aurivilli* Cleve, 1901 (= *Scottula ambariakae* Binet and Dessier, 1968) (monotypic).

OTHER SPECIES. *M. inaequicornis* (Sars, 1902); *M. acutioperculum* Ohtsuka, 1984; *M. curvirostris* Ohtsuka, 1985; *M.* species 1 and 2 from Okinawa.

REMARKS. *Metacalanus* was recognized as a senior synonym of *Scottula* Sars, 1902 by Campaner (1984).

ECOLOGICAL NOTE. *M. aurivilli* seems to be epipelagic in subtropical waters in the Indo-West Pacific (cf. Greenwood, 1978). Other species are hyperbenthic in shallow waters in temperate and subtropical regions (cf. Sars, 1903; Ohtsuka, 1984, 1985), or are marine cave-dwellers (Ohtsuka et al., 1993a).

Metacalanus species 1 (Figs 21B-I,23,25A,26A-G)

MATERIAL EXAMINED. 4 ♀♀ and ♂.

BODY LENGTH. ♀ 0.81, 0.83, 0.83, 0.84 mm; ♂ 0.77 mm.

DESCRIPTION. Female. Cephalosome only partly fused with first pedigerous somite. Genital double-somite (Figs 21B,23B) wider than long, asymmetrical, left gonopore and copulatory pore completely absent; right gonopore located near posteroventral margin of double somite, anterior half opening, covered by oval flap, possibly derived from leg 6; outer half gonopore frilled with cuticular flap (Fig. 23A); copulatory pore (Fig. 23C) small, oval in shape, approximately 4.0 μm in long axis and 1.0 μm in short axis, near inner distal corner of gonopore (copulatory pore blocked by spermatophore remnant); single seminal receptacle large, about half width of somite, located ventromedially; copulatory duct short, curved. Anal operculum triangular as in *M. acutioperculum*.

Antennules asymmetrical, left longer than right, different in fusion pattern and armature (see Fig. 22). Right antennule: segments X to XII and XIV and XV fused only partly near posterior margin; fusion pattern and armature as follows: I–IV–9 + 2 aesthetascs (I–3 + aesthetasc, II–2, III–2 + aesthetasc, IV–2), V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2, IX–X–4 + aesthetasc (IX–2 + aesthetasc, X–2), XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–1 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–1 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc). Left antennule different from right one in following: segments XII to XIV fused, with 5 setae and 2 aesthetascs (XII–2, XIII–1 + aesthetasc, XIV–2 + aesthetasc); segment XX with 2 setae and aesthetasc.

Antenna: exopod (Figs 21E,25A) indistinctly 7-segmented; setal formula 0,1,1,1,1,1,3 (2 setae and vestigial element). Mandibular palp (Fig. 21F): endopod 1-segmented, almost fused with basis, with 2 setae of unequal lengths; first exopod segment carrying long seta, fifth segment bearing 2 normal setae of unequal lengths. Maxillule (Fig. 21G): praecoxal arthrite with 2 slender setae; coxal endite having 1 short seta; coxal epipodite having 5 setae; basal seta absent; endopod (indicated by arrowhead) 1-segmented, bulbous, with short seta terminally. Maxilla: first and second praecoxal endites with 1 seta plus 1 vestigial element and 2 setae respectively (Fig. 21H); basal spine (Fig. 21I) with 2 rows of short spinules proximally. Maxilliped: fourth and fifth endopod segments

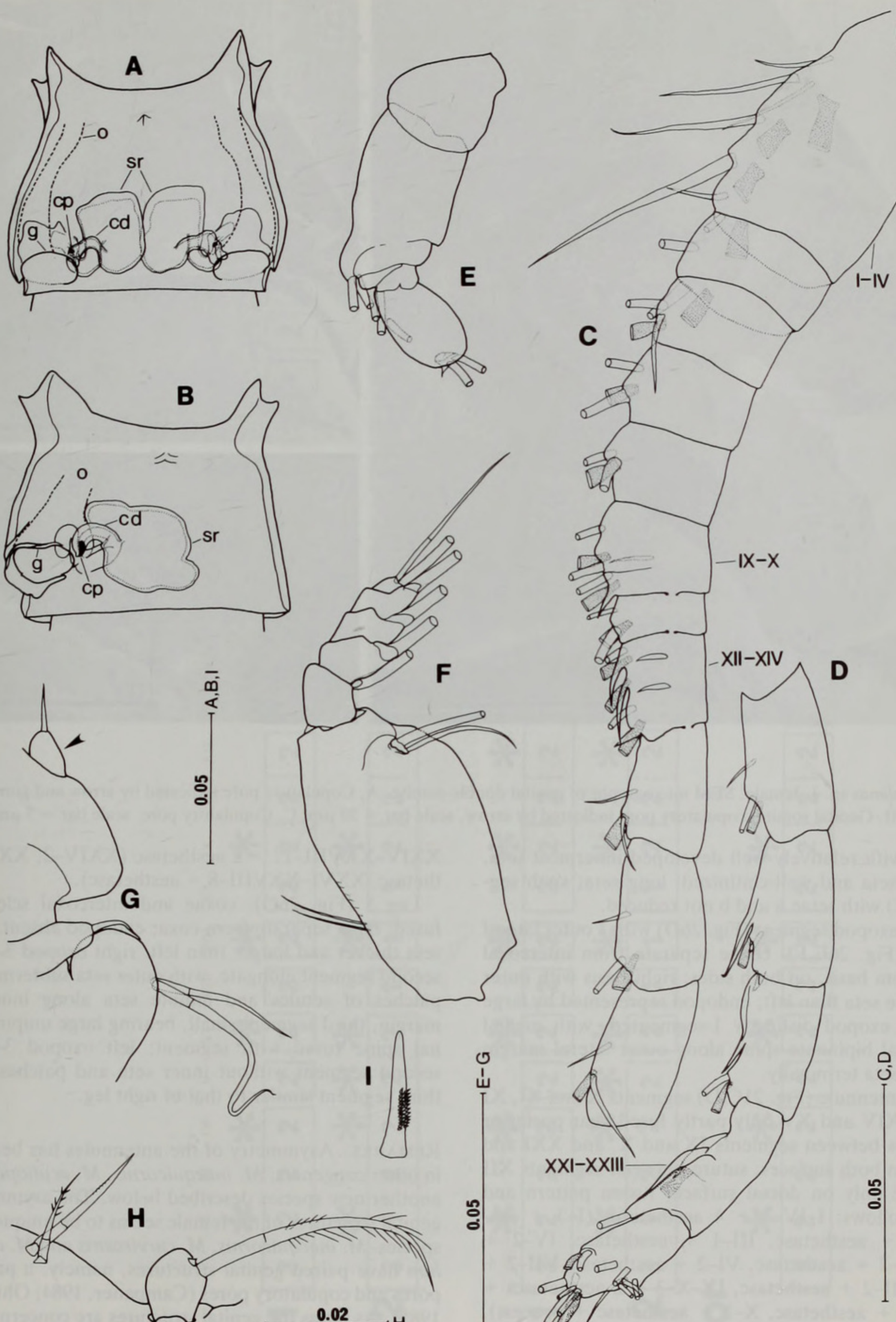

Fig. 21. *Metacalanus* sp. 1, female (B,E-I), male (C,D); *Metacalanus* sp. 2, female (A). A,B, Genital double-somite, ventral view; C, Left antennulary segments I to XVII; D, Left antennulary segments XVIII to XXVIII; E, Antennary exopod; F, Mandibular palp; G, Praecoxal arthrite, coxal endite and endopod of maxillule, endopod indicated by arrowhead; H, First and second praecoxal endites of maxilla; I, Basal spine of maxilla. Scales in mm.

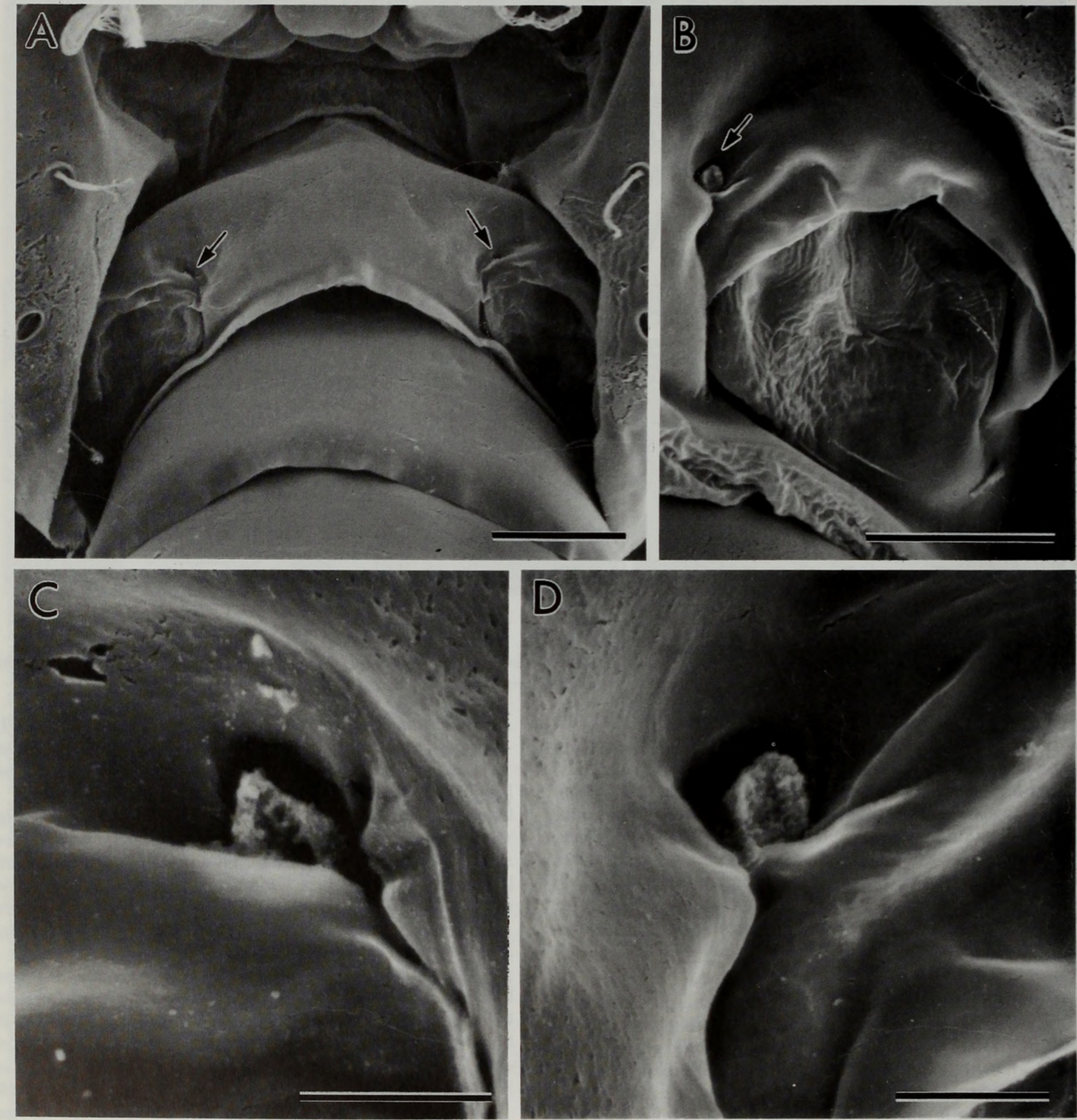

Fig. 24. *Metacalanus* sp. 2, female. SEM micrographs of genital double-somite. A, Genital somite, copulatory pores indicated by arrows, scale bar = 20 μm; B, Left gonopore and copulatory pore (indicated by an arrow), scale bar = 10 μm; C, Right copulatory pore, scale bar = 2 μm; D, Left copulatory pore, scale bar = 2 μm.

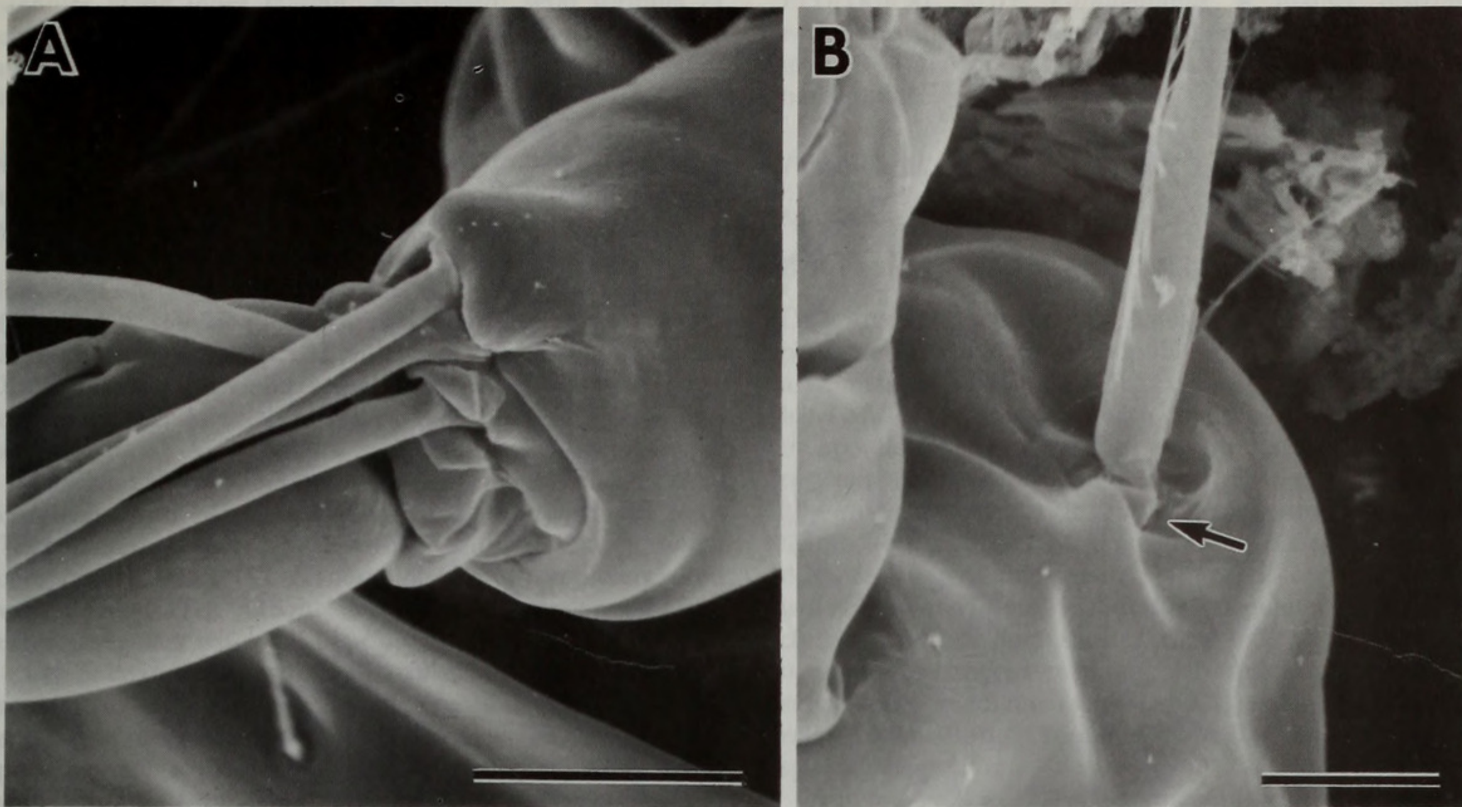

Fig. 25. *Metacalanus* sp. 1, female (A); *Metacalanus* sp. 2, female (B). SEM micrographs of mouthparts. A, Detail of segments IV to VIII of antennary exopod, scale bar = 10 μm; B, Mandibular endopod, indicated by arrow, scale bar = 5 μm.

Metacalanus species 2 (Figs 21A,24,25B,26H)

MATERIAL EXAMINED. 4♀♀.

BODY LENGTH. 0.84, 0.84, 0.86, 0.88 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Lateral lobe of last prosomal somite produced backwards reaching halfway along second urosomal somite (Fig. 24A). Genital double-somite (Figs 21A,24A) wider than long, symmetrical, with paired gonopores and copulatory pores located ventrolaterally near posterior end of somite; each gonopore lacking outer cuticular lateral flap found in *M.* species 1, anterior half opening, covered by oval flap; copulatory pore (Fig. 24C,D) small, round, ca. 1.4 μm in diameter, located near anterior inner corner of gonopore (spermatophore remnant attached to opening). Internal genital system similar to that of *M.* species 1. Anal operculum triangular as in *M.* species 1.

Antennule asymmetrical, left longer than right, different in fusion pattern and armature (see Fig. 22). Right antennule: segments X to XI, and XIV and XV only partly fused near posterior margin; fusion pattern and armature as follows: I–VI–12 + 2 aesthetascs (I–3 + aesthetasc, II–1, III–2 + aesthetasc, IV–2, V–2, VI–2), VII–1 + aesthetasc, VIII–1, IX–X–3 + aesthetasc (IX–1 + aesthetasc, X–2), XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–1 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–1 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc). Left antennule: segments X and XI partly fused near posterior margin; suture between segments XI and XII visible on both surfaces, XII and XIII only on one surface, XIII and XIV completely fused; fusion pattern and armature as follows: I–V–10 + 2 aesthetascs (I–3 + aesthetasc, II–1, III–2 + aesthetasc, IV–2, V–2), VI–2, VII–1 + aesthetasc, VIII–1, IX–X–3 + aesthetasc (IX–1 + aesthetasc, X–2), XI–XIV–7 + 2 aesthetascs (XI–2 + aesthetasc, XII–2, XIII–1, XIV–2 + aesthetasc), XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs (XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–8 + aesthetasc).

Antenna with same segmentation and setation as *M.* species 1. Mandibular palp: endopod (Fig. 25B) rudimentary, 1-segmented, with 1 plumose seta; exopod with setation as in *M.* species 1. Maxillule: praecoxal arthrite without elements; coxal endite with short seta; coxal epipodite with 5 setae; no basal seta; endopod represented by small, unarmed knob. Maxilla and maxilliped as in *M.* species 1.

Legs 1 to 4 with same segmentation and setation as *M.* sp. 1. Leg 5 (Fig. 26H): coxae separate from intercoxal sclerite; right basal seta thicker than left; endopod absent; right and left exopods each 1-segmented, bulbous, with spiniform seta terminally.

REMARKS. The fifth leg of this as yet undescribed species resembles that of *M. curvirostris* but it can be distinguished from the latter by the smaller body, the longer antennules, and by differences in the mouthparts.

Genus Paraugaptilus Wolfenden, 1904

DIAGNOSIS (emended). Female. Body relatively large, measuring about 3 mm in total length. Prosome: cephalosome narrowed anteriorly, separate from or weakly fused with first

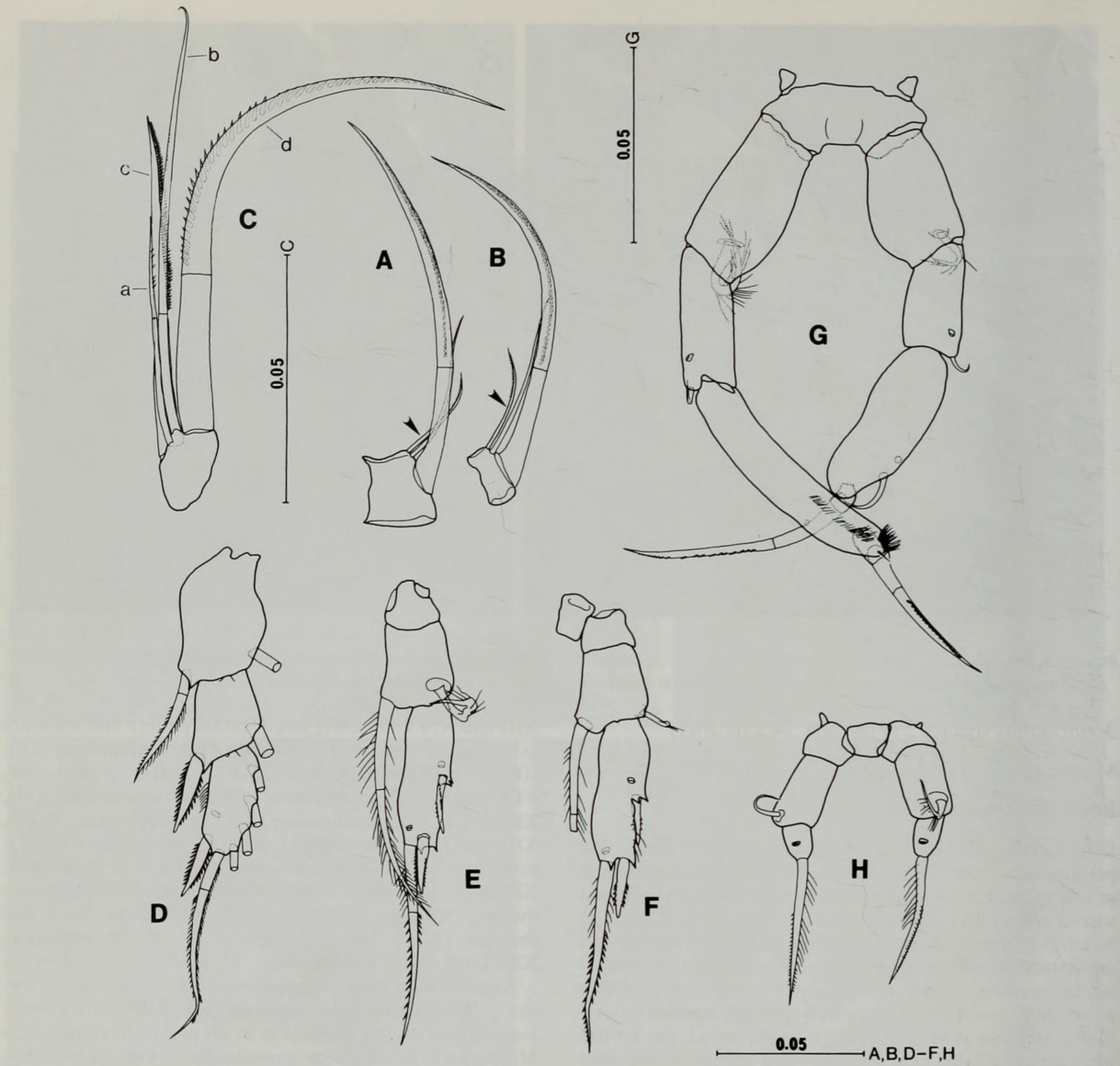

Fig. 26. *Metacalanus* sp. 1, female (A-F), male (G); *Metacalanus* sp. 2, female (H). A. Fourth endopod segment of maxilliped, innermost seta indicated by arrowhead; B, Fifth endopod segment of maxilliped, innermost seta indicated by arrowhead; C, Sixth endopod segment of maxilliped; D, Exopod of leg 1, anterior surface; E, Right leg 5, posterior surface; F, Left leg 5, anterior surface; G, Leg 5, anterior surface; H, Leg 5, posterior surface. Scales in mm.

pedigerous somite; last pedigerous somite with short prominence or curved process dorsally and weakly developed lobe laterally on each side. Genital double-somite with pair of gonopores located anteroventrally; copulatory pores asymmetrically distributed posteroventrally, each copulatory duct heavily chitinized; seminal receptacle relatively small. Caudal rami symmetrical, longer than wide, with setae II and III normally developed.

Antennule symmetrical or slightly asymmetrical in ornamentation of terminal segments (outer seta on segments XXV and XXVI with thicker setules in one antennule than in other) and in length, left slightly longer than right, 20-segmented; segments I to IV fused; segments XXIII–XXVIII fused; segments II, IV, VI, VIII–X, XII and XIII lacking aesthetasc; segment XIII with 2 setae; compound segment XXVI–XXVIII with 7 setae and 1 or 2 aesthetascs. Antenna: first endopod segment without inner seta, second segment bearing 1 seta medially, and 5 setae and vestigial seta terminally; exopod indistinctly 6-segmented, sixth segment rudimentary, unarmed. Mandibular gnathobase with tuft of setules; 3 teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: endopod absent; first exopod segment bearing vestigial seta, outer seta on fifth segment vestigial. Maxillule: praecoxal arthrite with 5 spines; coxal endite bearing no seta; coxal epipodite with 8 setae; endopod absent. Maxilla: first and second praecoxal endite bearing 1 seta and 1 rudimentary element, and 1 seta, respectively; basal spine bipinnate; endopodal setae with triangular spinules along inner margin. Maxilliped: setal formula of endopod 1,4,4,3,3,4; setae a and b on sixth endopod segment reduced; seta c heavily chitinized, terminal inner spinules fused to seta to form serrate margin.

Third exopod segment of leg 1 with 2 outer spines. Leg 4 with minute inner coxal seta, in addition to basal seta. Leg 5 rudimentary, represented by a plate with proximal (basal) seta and terminal or subterminal (endopod) seta.

Male. Body as in female, measuring around 3 mm in length. Left antennule 19-segmented; only first segment fringed with setules along posterior margin; segments II and III with seta; segment XIII with 2 setae; segment XXI and XXII fused; compound segment XXIV–XXV with large cuticular process; segment XXVI–XXVIII with 7 setae and aesthetasc.

Antenna: second endopod segment relatively shorter than in female, with 1–2 setae medially; exopod indistinctly 6- or 7-segmented, segment VIII with or without seta, terminal compound segment (IX–X) completely or incompletely fused with segment VIII, bulbous, unarmed. Mandibular palp: first exopod segment with well-developed seta.

Leg 5: coxae fused with intercoxal sclerite; basis and coxa separate in left leg and incompletely fused in right. Right leg: endopod 1-segmented, rudimentary, unarmed; second exopod segment expanded inwards, almost completely fused with third to form compound segment, tapering distally, carrying proximal seta and subterminal setule along outer margin. Left leg: endopod 1-segmented, unarmed; exopod 3-segmented, last 2 segments almost fused, second exopod segment swollen medially, third segment with 2 stout long, outwardly-directed process terminally.

Type species. *Paraugaptilus buchani* Wolfenden, 1904 (monotypic).

Other species. *P. similis* A. Scott, 1909; *P. meridionalis* Wolfenden, 1911; *P. mozambicus* Gaudy, 1965; *P. archimedi* Gaudy, 1973; *P. bermudensis* Deevey, 1973; *P. buchani* sensu Bradford, 1974.

Remarks. In *P. bermudensis* sexual dimorphism is exhibited in the mouthparts and leg 1 (Deevey, 1973): second endopodal segment of antenna carrying 1 short seta in female and 1 long plus 1 short seta in male, at midlength of the segment; relative lengths of endopod and exopod of antenna; antennary exopodal segment VIII unarmed in female, but bearing long seta in male; first exopodal segment of mandible unarmed (vestigial seta overlooked by Deevey (1973)) in female but with well-developed seta in male; endopod of leg 1 indistinctly 3-segmented in female but distinctly in male. Except for leg 1 the sexual dimorphism in *P. bermudensis* is also found in *P. similis* (present study).

Since the superfamily Arietelloidea Sars, 1902 generally exhibits distinctly 3-segmented rami in legs 1–4 (Andronov, 1974; Park, 1986) and no other congeners show such fusion in endopod of leg 1, the incomplete fusion of the endopodal segments in the female seems to be autapomorphic in *P. bermudensis*. *P. buchani* exhibits sexual dimorphism only in the relative lengths of the antennary rami and in the setation of the mandibular palp (Deevey, 1973; present study).

Brodsky (1950) mentioned, in his definition of *Paraugaptilus*, that the left antennules of females are possibly longer than the right, but *P. similis* has antennules of nearly equal length (Scott, 1909; present study).

Ecological note. *Paraugaptilus* is mainly distributed within the upper 1000 m, in particular, between 500 and 1000 m depths (Deevey, 1973). The genus appears to be meso- and bathypelagic.

Paraugaptilus similis A. Scott, 1909 (Figs 27–30)

Material examined. ♀ and ♂.

Body length. ♀ 3.32 mm; ♂ 3.03 mm.

Description. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Figs 27A-C,28A) asymmetrical, wider than long, swollen anteriorly, widest at level of paired gonopores; each gonopore (Fig. 28B) covered by operculum as in *Arietellus*, anterior half opening; copulatory pores remarkably asymmetrical, right pore located medially on right ventral side, slit-like, approximately 43 μm in length, left pore located ventromedially at about two-thirds distance along double-somite, with round opening, about 27 μm in diameter; both right and left copulatory ducts heavily chitinized; right duct shorter than left, widest near pore opening, constricted medially; left duct thick, with small subchamber medially (see Fig. 27B); seminal receptacles relatively small, right round in shape, left smaller than right, spindle-shaped.

Antennule (Fig. 27D) 20-segmented; seventh (X) to ninth (XII) segments and 11th (XIV) and 12th (XV) segments only partly fused near posterior margin; 20th (XXIII–XXV) and 21st (XXVI–XXVIII) incompletely fused with suture clearly visible. Fusion pattern and armature as follows: I–IV–9 + aesthetasc (I–3, II–2, III–2 + aesthetasc, IV–2), V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2, IX–2, X–2, XI–2 + aesthetasc, XII–2, XIII–2, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–XXVIII–12 + 2 aesthetascs (right), 12 + 3 aesthetascs (left) (XXIII–1, XXIV–1 + 1, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–7 + 1 (right) or 2 (left) aesthetascs). First (I–IV) to seventh segments fringed with long setules along posterior margin. Posterior setae on segments XXV and XXVI having thicker setules in right antennule than in left.

Antenna: first endopod segment without inner mid-length seta, second segment (Fig. 29B) about 1.8 times as long as first segment, with 1 inner short seta, and 5 setae and vestigial seta terminally; exopod (Fig. 29A) indistinctly 6-segmented, sixth segment bulbous, unarmed; setal formula 0,1,1,1,1,0. Mandibular palp (Fig. 29C): endopod absent; first exopod segment carrying vestigial seta, fifth segment having 1 normal and 1 reduced seta. Maxillule (Fig. 27E): praecoxal arthrite with 5 spines, 2 of which serrate subterminally, ornamented by minute spinules on both surfaces; coxal endite unarmed; coxal epipodite with 8 setae; basal seta and endopod absent. Maxilla: first praecoxal endite with 1 serrate seta and 1 vestigial element, second endite having single bipinnate seta (Fig. 30A); basal spine (Fig. 29D) with 3 rows of spinules. Maxilliped: fourth and fifth endopod segments (Fig. 27F) each bearing unipinnate innermost seta, sixth segment (Fig. 27G) carrying reduced setae a and b, medium-length serrate seta c whose tip chitinized, and elongate seta d with row of sharp triangular spinules along inner margin.

Leg 1: third exopod segment with 2 outer spines; endopod distinctly 3-segmented. Leg 4: vestigial coxal seta present at inner angle. Leg 5 (Fig. 30B): coxae, intercoxal sclerite, basis

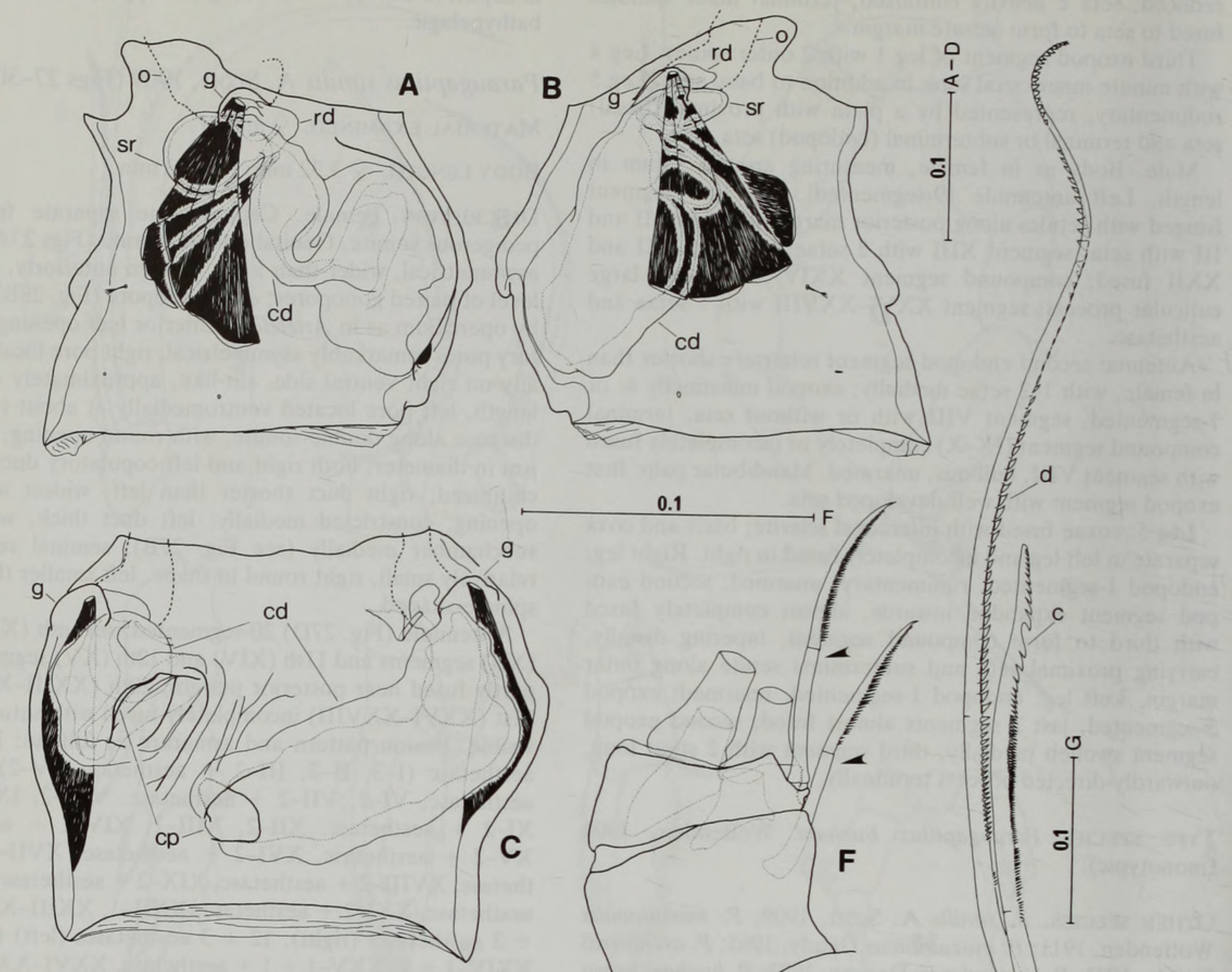

Fig. 27. *Paraugaptilus similis*, female. A, Genital double-somite, right lateral view; B, Genital double-somite, left lateral view; C, Genital double-somite, ventral view; D, Antennulary segments XXII–XXVIII; E, Praecoxal arthrite, coxal endite and inner margin of basis; F, Fourth and fifth endopod segments of maxilliped, innermost seta indicated by arrowhead, mid-margin seta on fourth segment missing; G, Sixth endopod segment of maxilliped. Scales in mm.

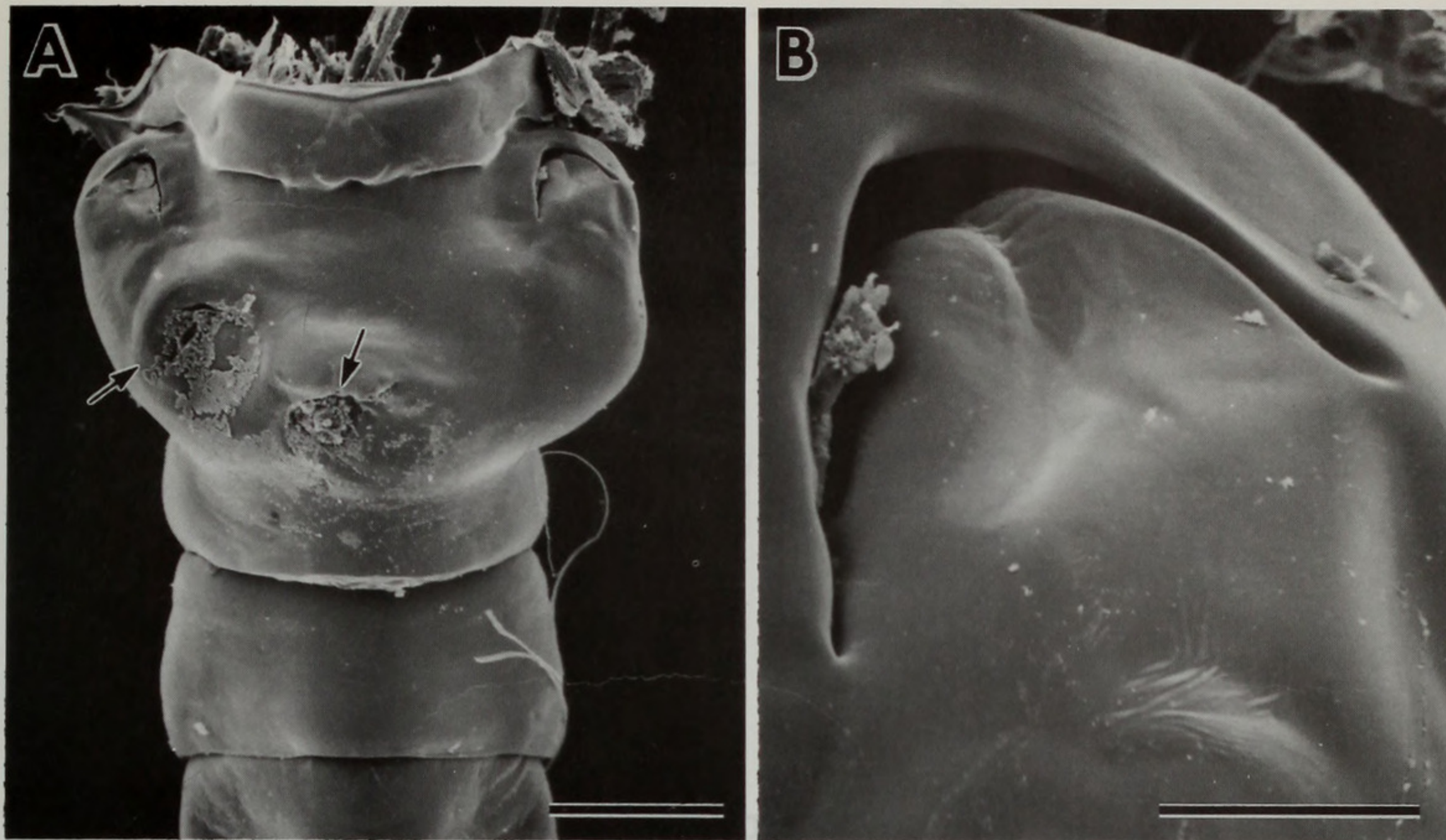

Fig. 28. *Paraugaptilus similis*, female. SEM micrographs of genital double-somite. A, Genital double-somite, ventral view, copulatory pores indicated by arrows, scale bar = 100 μm; B, Left gonopore, scale bar = 20 μm.

and endopod fused to form flattened plate; basal setae of almost equal length; endopod represented by plumose seta; exopod completely absent.

Male. Left antennule (Fig. 30C-E) 19-segmented; segments IX to XV only partly fused near posterior margin; segments XXI and XXII almost fused, but suture visible near anterior margin; segments XXIV–XXV and XXVI–XXVIII incompletely fused; fusion pattern and armature as follows: I–IV–7 + 4 aesthetascs (I–3 + aesthetasc, II–1 + aesthetasc, III–1 + aesthetasc, IV–2 + aesthetasc), V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–1 + aesthetasc + process, XI–2 + aesthetasc, XII–1 + aesthetasc + process, XIII–1 + aesthetasc + process, XIV–1 + aesthetasc + process, XV–1 + aesthetasc + process, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–1 + aesthetasc + 2 processes, XX–1 + aesthetasc + process, XXI–XXIII–1 + aesthetasc + 3 processes (XXI–aesthetasc + 2 processes, XXII-process, XXIII–1), XXIV–XXVIII–11 + 2 aesthetascs + process (1 seta missing in Fig. 30E) (XXIV–1 + 1 + process, XXV–1 + 1 + aesthetasc, XXVI–XXVIII–7 + aesthetasc). Only first segment fringed by short setules along posterior margin.

Antenna: second endopod segment (Fig. 29G) approximately 1.3 times as long as first segment, with 1 long and 1 short seta medially; exopod (Fig. 29E,F) indistinctly 7-segmented, terminal compound segment bulbous (IX–X), sixth (VIII) carrying long seta, seventh (IX–X) unarmed. Mandibular palp (Fig. 29H): first exopod segment with long seta.

Leg 5 (Fig. 30F): coxae and intercoxal sclerite almost completely fused; coxa and basis incompletely fused in right leg, but separate in left; right and left endopods consisting of 1 segment. Right exopod 2-segmented, ancestral second and third segments almost completely fused, proximal segment triangular, with short seta at outer angle, distal compound segment lamellar, expanded proximally, tapering distally, carrying short outer seta near base, triangular inner process and 2 patches of setules medially. Left exopod indistinctly 3-segmented, first segment with short seta at outer angle, second swollen inwards, bearing minute setule subterminally, third segment incompletely fused with second segment, having 2 processes, outer bifid at tip, and minute subterminal outer setule.

REMARKS. The large process on segment XXIV of the left antennule probably represents an extension of the cuticular surface rather than a modified setation element. The anterior subterminal process on the counterpart of the male left antennule of *Paraugaptiloides magnus* is possibly homologous to that of *Paraugaptilus*. The presence of 2 aesthetascs located immediately adjacent to each other on the extreme tip of the left antennule is interpreted here as an abnormality.

Paraugaptilus buchani Wolfenden, 1904 (Figs 31,32)

MATERIAL EXAMINED. ♀ and ♂.

BODY LENGTH. ♀ 3.14 mm; ♂ 3.25 mm.

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Genital double-somite (Fig. 31A) similar to that of *P. similis*, but relatively shorter, left copulatory pore located near posterior margin. Female left antennule (Fig. 32A) with same fusion pattern and armature as in female *P. similis* except for following: segment XXIII incom-

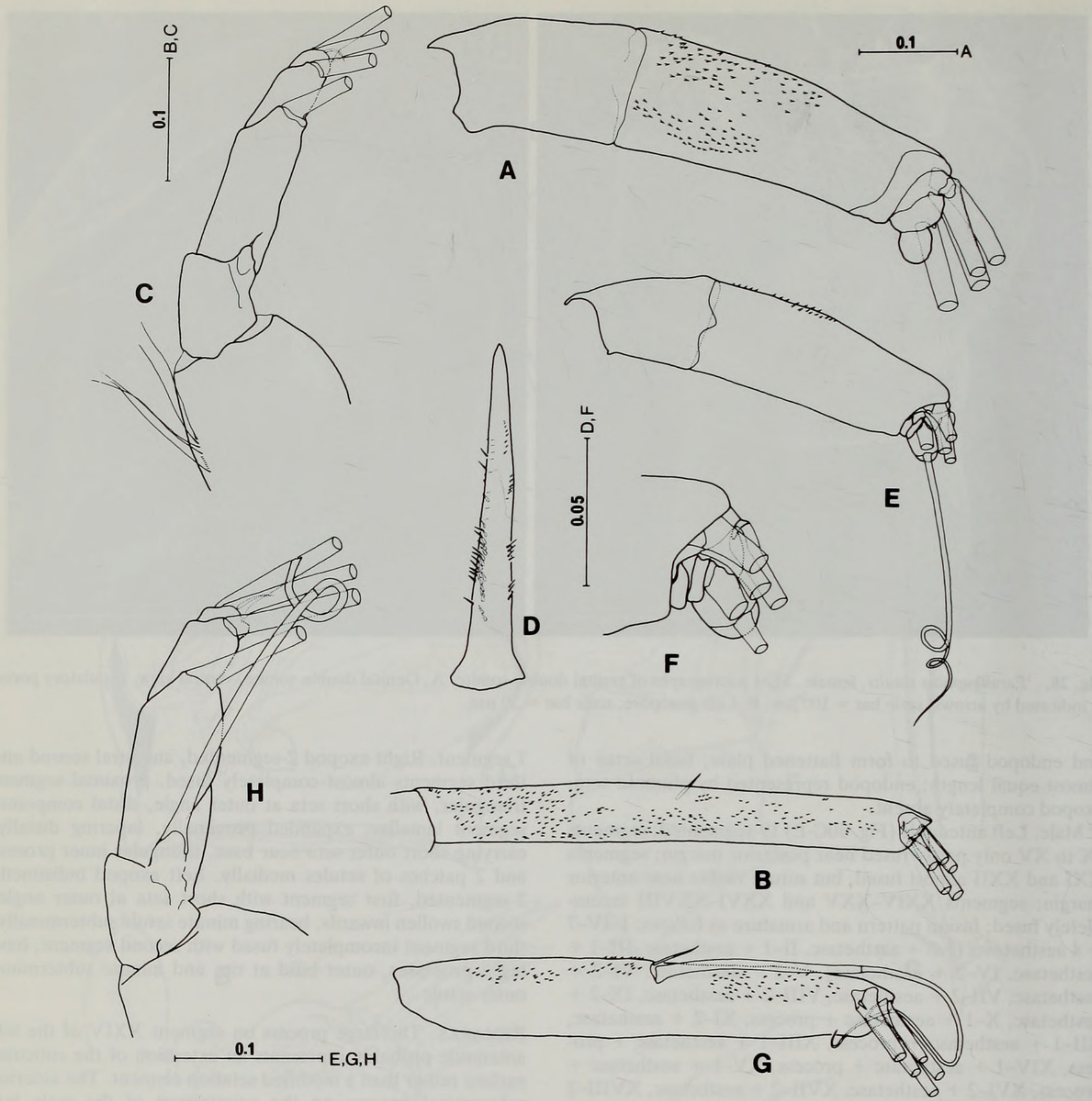

Fig. 29. *Paraugaptilus similis*, female (A-D), male (E-H). A, Antennary exopod; B, Second endopod segment of antenna; C, Mandibular exopod; D, Basal spine of maxilla; E, Antennary exopod; F, Detail of antennary exopod segments IV to X; G, Second endopod segment of antenna; H, Mandibular exopod. Scales in mm.

pletely fused with segments XXIV–XXV; segments XXV and XXVI incompletely fused; left compound segment XXVI–XXVIII with 7 setae and aesthetasc.

Antenna: second endopod segment about 1.9 times as long as first, with 1 minute inner seta at mid-length and 5 setae and 1 vestigial seta terminally, as in *P. similis*; exopod similar in segmentation and setation to that of female *P. similis*. Mandibular palp: first exopod segment with vestigial seta (Fig. 32B) as in female *P. similis*. Maxilliped: sixth endopod segment (Fig. 32E) similar to that of *P. similis*, but seta c with terminal spinules incompletely fused to seta.

Male. Left antennule (Fig. 32F) with same fusion pattern and armature as in *P. similis* except for following: seta on segment XXII not modified into process; process on segment XXIV–XXV not so developed as in male *P. similis*, not reaching beyond end of antennule, directed straight forwards. Antenna similar in segmentation and setation to that of female; second endopod segment ca. 1.4 times as long as first. Mandibular palp: first exopod segment with well-developed seta (Fig. 32G). Maxillule: praecoxal arthrite (Fig. 32C) with 5 spines; tubular gland opening on inner surface.

Leg 5: both coxae and intercoxal sclerite completely fused as in male *P. similis*; coxa and basis separate in left leg and incompletely fused in right (almost completely fused on

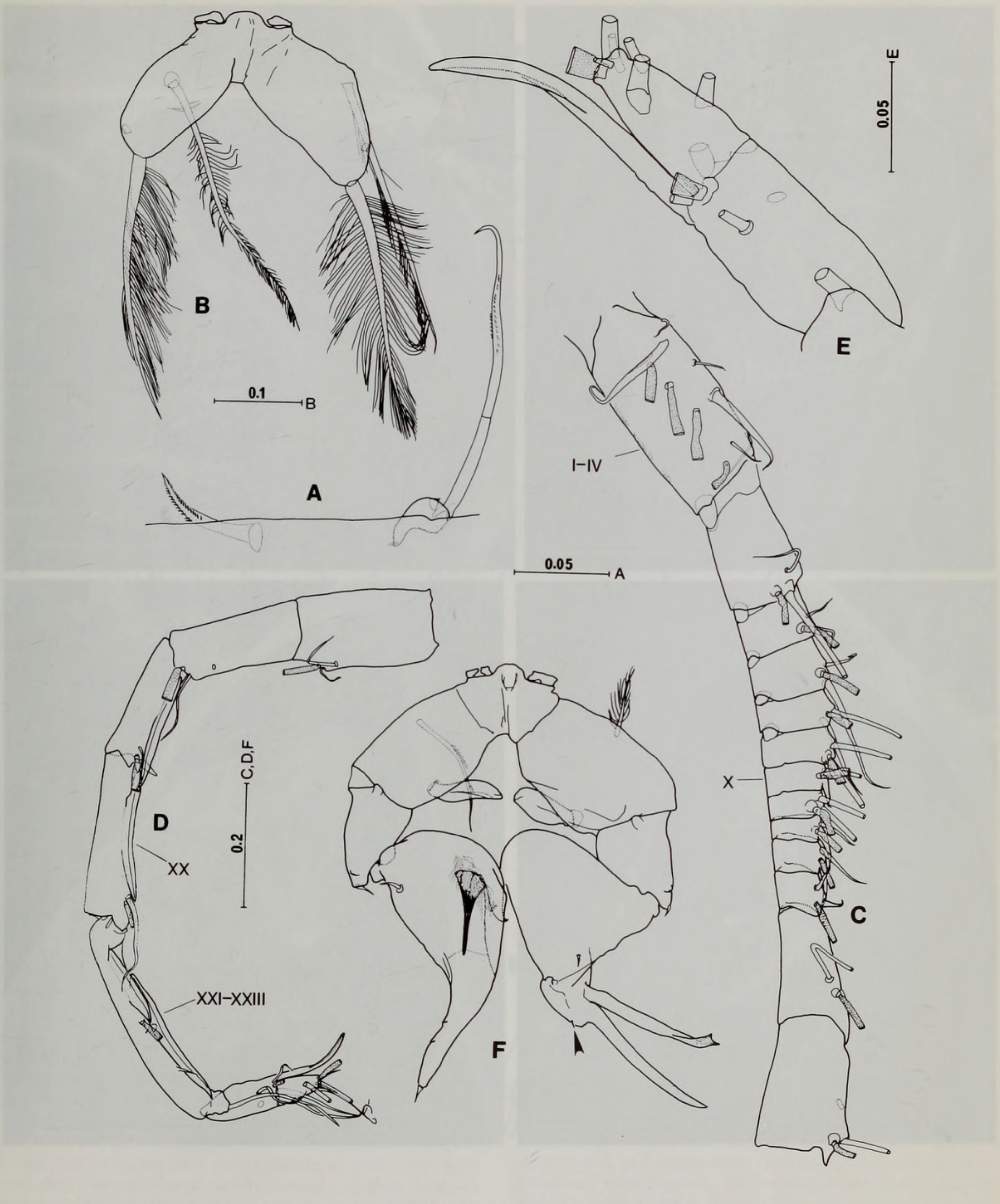

Fig. 30. *Paraugaptilus similis*, female (A,B), male (C-F). A, First and second praecoxal endites of maxilla; B, Leg 5, anterior surface; C, Left antennulary segments I to XVI; D, Left antennulary segments XVII to XXVIII; E, Left antennulary segments XXIV to XXVIII; F, Leg 5, anterior surface, minute seta indicated by arrowhead. Scales in mm.

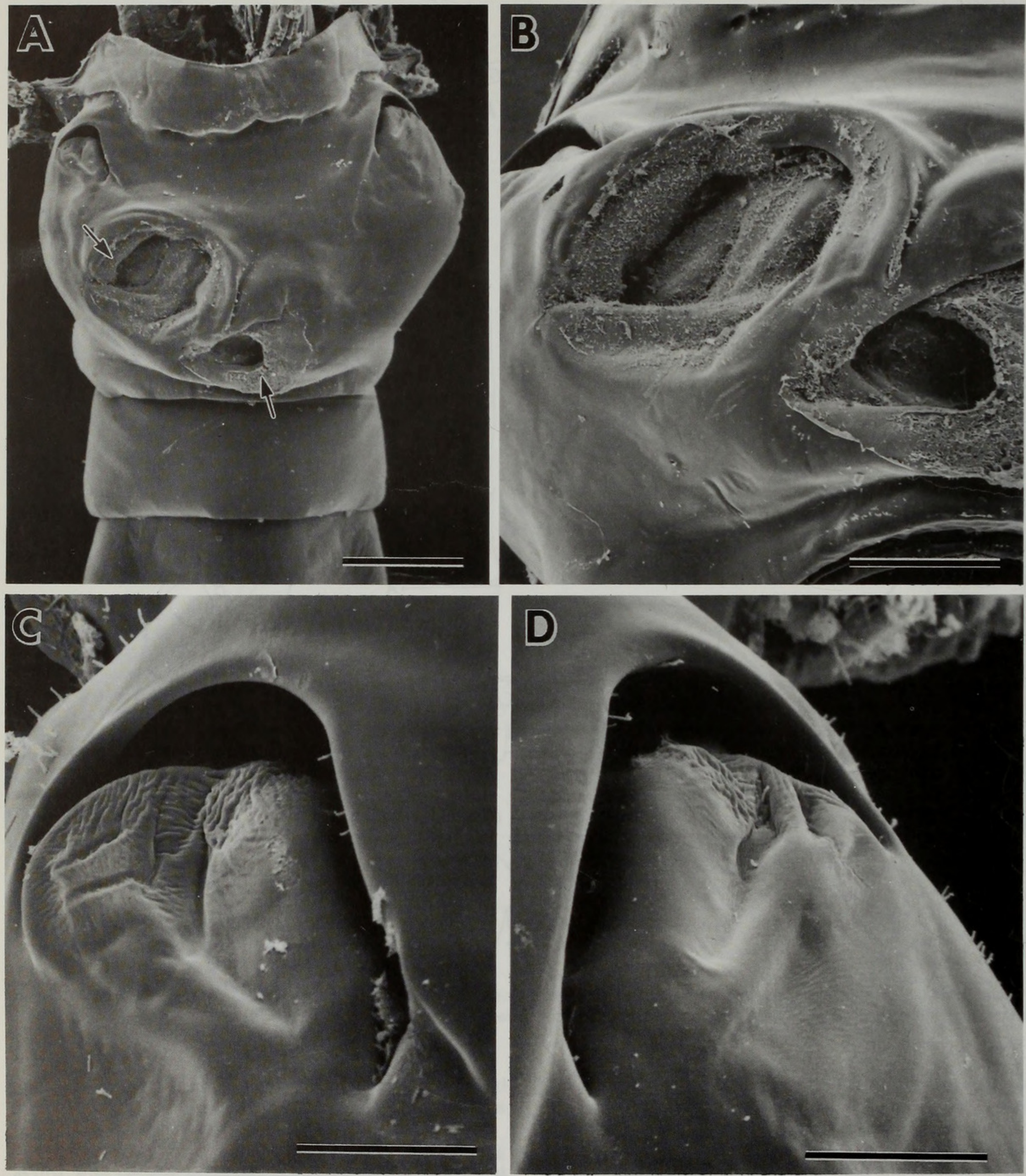

Fig. 31. *Paraugaptilus buchani*, female. SEM micrographs of genital double-somite. A, Genital double-somite, copulatory pores arrowed, scale bar = 100 µm; B, Copulatory pores, scale bar = 50 µm; C, Right gonopore, scale bar = 20 µm; D, Left gonopore, scale bar = 20 µm.

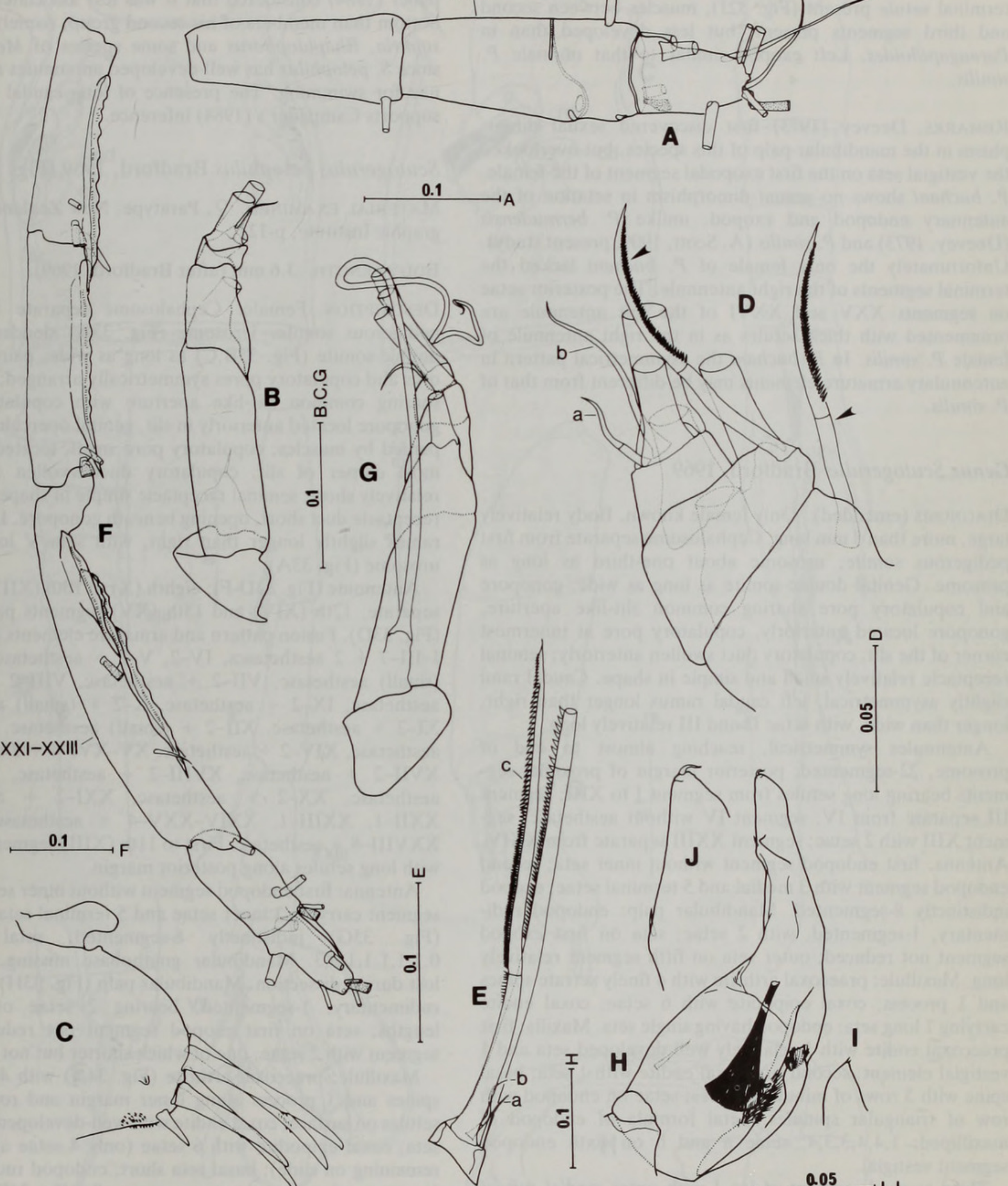

Fig. 32. *Paraugaptilus buchani*, female (A-E), male (F-J). A, Antennulary segments XXII to XXVIII; B, Mandibular exopod; C, Praecoxal arthrite and coxal endite of maxillule; D, Fourth to sixth endopod segments of maxilliped, innermost seta on fourth and fifth segments indicated by arrowheads; E, Sixth endopod segment of maxilliped; F, Antennulary segments XIX to XXVIII; G, Mandibular exopod; H, Second exopod segment of right leg 5; I, Inner medial process on second exopod segment of right leg 5; J, Outer margin of second exopod segment of right leg 5. Scales in mm.

posterior surface); both endopods 1-segmented, lobate. Right exopod (Fig. 32H-J): second and third segments almost completely fused to form lamelliform compound segment, tapering distally; inner medial triangular process with 2 minute spinules (Fig. 32I) at tip; 1 subterminal outer and 1 terminal setule present (Fig. 32J); muscles between second and third segments present, but less developed than in *Paraugaptiloides*. Left exopod similar to that of male *P. similis*.

REMARKS. Deevey (1973) first discovered sexual dimorphism in the mandibular palp of this species, but overlooked the vestigial seta on the first exopodal segment of the female. *P. buchani* shows no sexual dimorphism in setation of the antennary endopod and exopod, unlike *P. bermudensis* (Deevey, 1973) and *P. similis* (A. Scott, 1909; present study). Unfortunately the only female of *P. buchani* lacked the terminal segments of the right antennule. The posterior setae on segments XXV and XXVI of the left antennule are ornamented with thick setules as in the right antennule of female *P. similis*. In *P. buchani* the asymmetrical pattern in antennulary armature elements may be different from that of *P. similis*.

Genus Scutogerulus Bradford, 1969

DIAGNOSIS (emended). Only female known. Body relatively large, more than 3 mm long. Cephalosome separate from first pedigerous somite; urosome about one-third as long as prosome. Genital double-somite as long as wide; gonopore and copulatory pore sharing common slit-like aperture, gonopore located anteriorly, copulatory pore at innermost corner of the slit; copulatory duct swollen anteriorly; seminal receptacle relatively small and simple in shape. Caudal rami slightly asymmetrical, left caudal ramus longer than right, longer than wide, with setae II and III relatively long.

Antennules symmetrical, reaching almost to end of prosome, 22-segmented; posterior margin of proximal segments bearing long setules from segment I to XIII; segment III separate from IV; segment IV without aesthetasc; segment XIII with 2 setae; segment XXIII separate from XXIV. Antenna: first endopod segment without inner seta; second endopod segment with 3 medial and 5 terminal setae; exopod indistinctly 8-segmented. Mandibular palp: endopod rudimentary, 1-segmented, with 2 setae; seta on first exopod segment not reduced; outer seta on fifth segment relatively long. Maxillule: praecoxal arthrite with 4 finely serrate spines and 1 process; coxal epipodite with 6 setae; coxal endite carrying 1 long seta; endopod having single seta. Maxilla: first praecoxal endite with 1 relatively well developed seta and 1 vestigial element; second praecoxal endite with 1 seta; basal spine with 3 rows of minute spinules; setae on endopod with row of triangular spinules. Setal formula of endopod of maxilliped: 1,4,4,3,3,4; setae a and b on sixth endopod segment vestigial.

Third exopod segment of leg 1 with outer medial tuft of short setules and subterminal outer spine. Leg 5 biramous, carrying 1-segmented rudimentary endopod with 1 terminal seta and 2-segmented exopod with 1 outer spine on first segment and 2 terminal setae on second segment.

TYPE SPECIES. *Scutogerulus pelophilus* Bradford, 1969 (monotypic).

REMARKS. The new genus *Campaneria* is established for the paratypic male of *S. pelophilus*.

ECOLOGICAL NOTE. Bradford (1969) suggested that *S. pelophilus* is a deep-sea hyperbenthic species. However, Campaner (1984) considered that it was less associated with the bottom than members of his second group, namely, *Paramisophria*, *Rhapidophorus* and some species of *Metacalanus*, since *S. pelophilus* has well-developed antennules and antennae for swimming. The presence of long caudal setae also supports Campaner's (1984) inference.

Scutogerulus pelophilus Bradford, 1969 (Figs 33,34)

MATERIAL EXAMINED. ♀, Paratype, New Zealand Oceanographic Institute, p-121.

BODY LENGTH. 3.6 mm (after Bradford, 1969).

DESCRIPTION. Female. Cephalosome separate from first pedigerous somite. Urosome (Fig. 33A) slender. Genital double-somite (Fig. 33B,C) as long as wide; paired gonopores and copulatory pores symmetrically arranged; gonopore sharing common slit-like aperture with copulatory pore; gonopore located anteriorly in slit, genital operculum accompanied by muscles; copulatory pore small, located at innermost corner of slit; copulatory duct swollen anteriorly, relatively short; seminal receptacle simple in shape, pea-like; receptacle duct short, opening beneath gonopore. Left caudal ramus slightly longer than right, with seta V longer than urosome (Fig. 33A).

Antennule (Fig. 33D-F): eighth (X) to 10th (XII) segments separate; 12th (XIV) and 13th (XV) segments partly fused (Fig. 33D). Fusion pattern and armature elements as follows: I–III–7 + 2 aesthetascs, IV–2, V–2 + aesthetasc, VI–2 + (small) aesthetasc, VII–2 + aesthetasc, VIII–2 + (small) aesthetasc, IX–2 + aesthetasc, X–2 + (small) aesthetasc, XI–2 + aesthetasc, XII–2 + (small) aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–XVI–4 + 2 aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXV–4 + aesthetasc, XXVI–XXVIII–8 + aesthetasc. First to 11th (XIII) segments fringed with long setules along posterior margin.

Antenna: first endopod segment without inner seta, second segment carrying 3 inner setae and 5 terminal setae; exopod (Fig. 33G) indistinctly 8-segmented, setal formula 0,1,1,1,1,1,0,3. Mandibular gnathobase missing, probably lost during dissection. Mandibular palp (Fig. 33H): endopod rudimentary, 1-segmented, bearing 2 setae of unequal lengths; seta on first exopod segment not reduced, fifth segment with 2 setae, one of which shorter but not reduced.

Maxillule: praecoxal arthrite (Fig. 34A) with 4 spinulose spines and 1 process along inner margin and row of long setules on surface; coxal endite with well-developed spinulose seta; coxal epipodite with 6 setae (only 4 setae and 2 scars remaining on slide); basal seta short, endopod rudimentary, 1-segmented, with 1 short seta terminally (Fig. 34B). Maxilla (Fig. 34C): first praecoxal endite with spinulose seta and 1 vestigial element, second endite with bilaterally spinulose seta. Maxilliped: innermost seta on fourth and fifth endopod segments (Fig. 34E, indicated by arrowhead) not reduced; sixth endopod segment (Fig. 34F) bearing stout, elongate setae c and d with row of triangular spinules and reduced setae a and b.

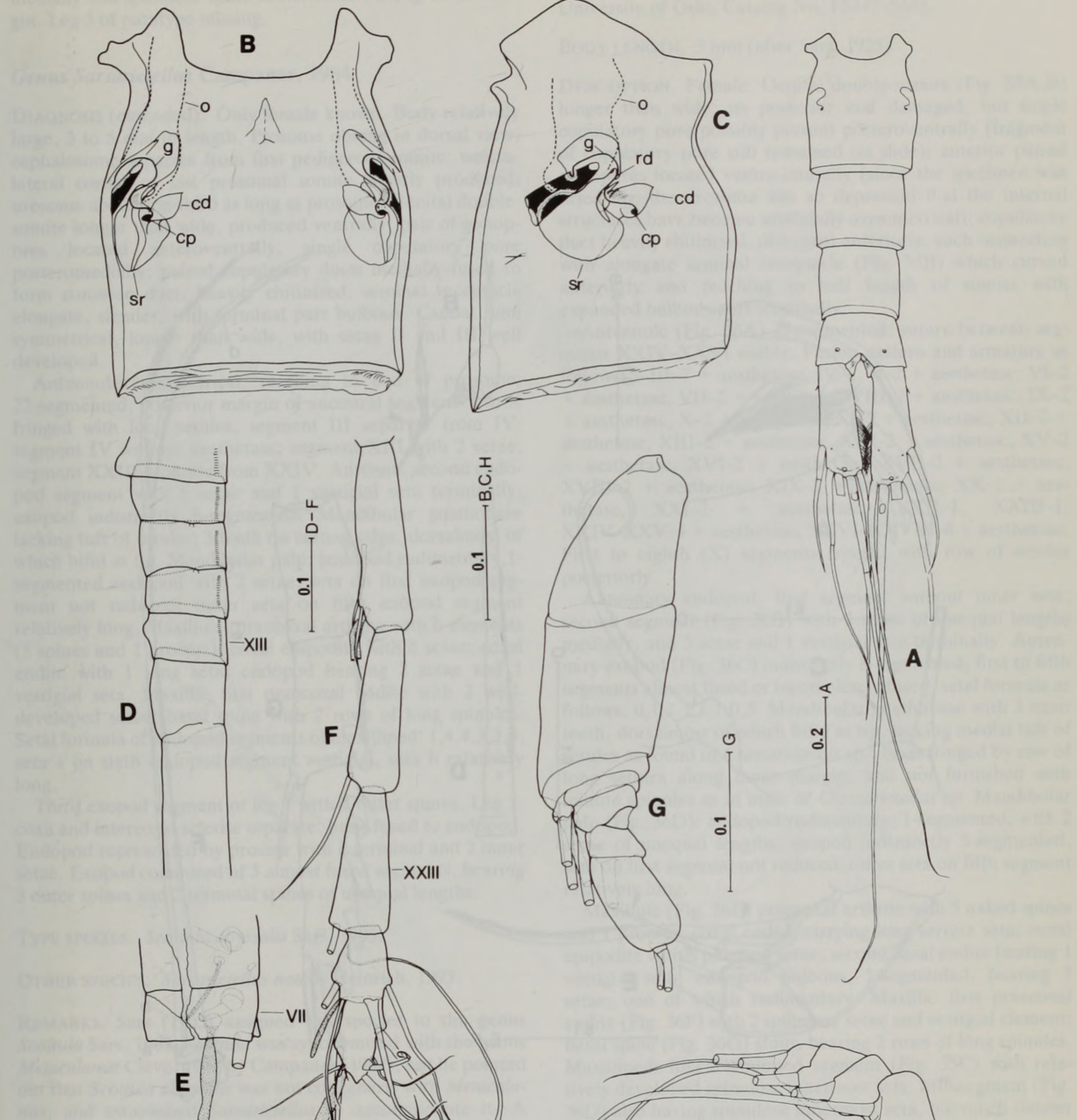

Fig. 33. *Scutogerulus pelophilus*, female (paratype). A, Urosome, ventral view; B, Genital double-somite, ventral view; C, Genital double-somite, lateral view; D, Antennulary segments IX to XIV, armature omitted; E, Antennulary segments VI and VII, note that aesthetasc on each segment differs in size; F, Antennulary segments XXI to XXVIII; G, Antennary exopod; H, Mandibular endopod and exopod. Scales in mm.

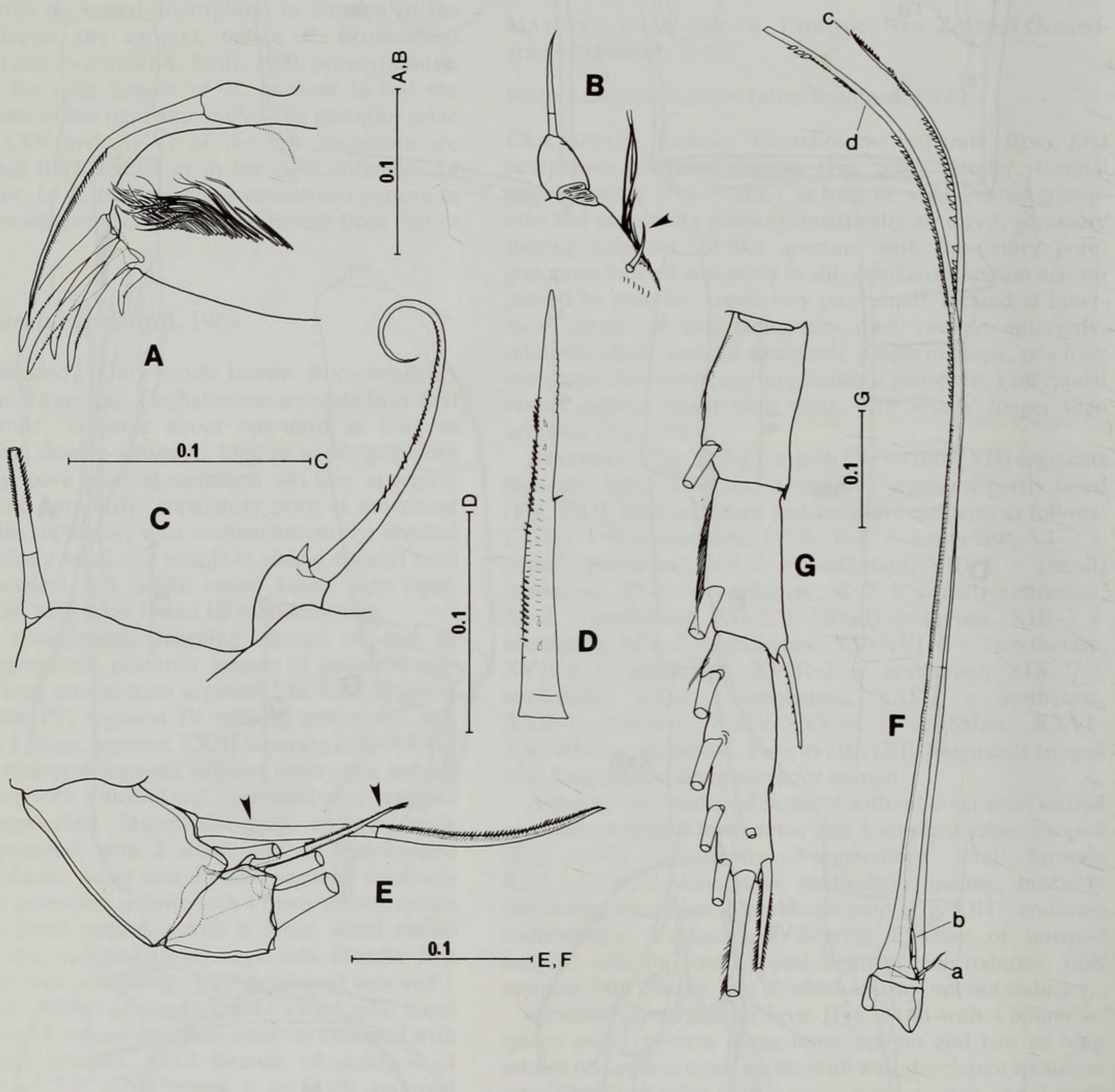

Fig. 34. *Scutogerulus pelophilus*, female (paratype). A, Praecoxal arthrite and coxal endite of maxillule; B, Maxillulary endopod, basal seta indicated by arrowhead; C, First and second praecoxal endites of maxilla; D, Basal spine of maxilla; E, Fourth and fifth endopod segments of maxilliped, innermost setae indicated by arrowheads; F, Sixth endopod segment of maxilliped; G, Exopod of leg 1, posterior surface. Scales in mm.

Leg 1 (Fig. 34G): first exopod segment missing element on outer corner, third segment with tuft of minute setules medially and spinulose spine subterminally along outer margin. Leg 5 of paratype missing.

Genus Sarsarietellus Campaner, 1984

DIAGNOSIS (emended). Only female known. Body relatively large, 3 to 5 mm in length. Prosome oblong in dorsal view; cephalosome separate from first pedigerous somite; ventrolateral corner of last prosomal somite slightly produced; urosome about one-third as long as prosome. Genital double-somite longer than wide, produced ventrally; pair of gonopores located anteroventrally, single copulatory pore posteromedially; paired copulatory ducts medially fused to form common duct, heavily chitinized; seminal receptacle elongate, slender, with terminal part bulbous. Caudal rami symmetrical, longer than wide, with setae II and III well developed.

Antennules symmetrical, reaching to end of prosome, 22-segmented; posterior margin of ancestral segments I to X fringed with long setules; segment III separate from IV; segment IV without aesthetasc; segment XIII with 2 setae; segment XXIII separate from XXIV. Antenna: second endopod segment with 5 setae and 1 vestigial seta terminally; exopod indistinctly 8-segmented. Mandibular gnathobase lacking tuft of setules; 3 teeth on cutting edge, dorsalmost of which bifid at tip. Mandibular palp: endopod rudimentary,1-segmented endopod with 2 setae; seta on first exopod segment not reduced; outer seta on fifth exopod segment relatively long. Maxillule: praecoxal arthrite with 6 elements (5 spines and 1 process); coxal epipodite with 8 setae; coxal endite with 1 long seta; endopod bearing 2 setae and 1 vestigial seta. Maxilla: first praecoxal endite with 2 well-developed setae; basal spine with 2 rows of long spinules. Setal formula of endopod segments of maxilliped: 1,4,4,3,3,4; seta a on sixth endopod segment vestigial, seta b relatively long.

Third exopod segment of leg 1 with 2 outer spines. Leg 5: coxa and intercoxal sclerite separate; basis fused to endopod. Endopod represented by process with 2 terminal and 2 inner setae. Exopod composed of 3 almost fused segments, bearing 3 outer spines and 2 terminal spines of unequal lengths.

TYPE SPECIES. *Scottula abyssalis* Sars, 1905.

OTHER SPECIES. *Sarsarietellus natalis* Heinrich, 1993.

REMARKS. Sars (1905) assigned this species to the genus *Scottula* Sars, 1902. *Scottula* was synonymized with the genus *Metacalanus* Cleve, 1901 by Campaner (1984), but he pointed out that *Scottula abyssalis* was not congeneric with *Metacalanus*, and established *Sarsarietellus* to accommodate it. A second species of *Sarsarietellus*, *S. natalis*, has been recently described from the near-bottom (1083–1090 m depth) in the southwestern Indian Ocean (Heinrich, 1993). *S. natalis* exhibits a few more apomorphic characters than *S. abyssalis*: (1) asymmetry in the genital double-somite; (2) reduction of the elements on the exopod of the fifth leg.

ECOLOGICAL NOTE. Campaner (1984) suggested that the genus is only loosely associated with the deep-sea near-bottom as is *Scutogerulus*. The recent discovery of a second congener from the near-bottom supports his opinion.

Sarsarietellus abyssalis (Sars, 1905) (Figs 35,36)

MATERIAL EXAMINED. ♀, Holotype, Zoological Museum, University of Oslo, Catalog No. F5447–5448.

BODY LENGTH. 3 mm (after Sars, 1925).

DESCRIPTION. Female. Genital double-somite (Fig. 35A,B) longer than wide; its posterior end damaged, but single copulatory pore possibly present posteroventrally (fragment of copulatory pore still remained on slide); anterior paired gonopores located ventro-laterally (since the specimen was dried up, the urosome was so depressed that the internal structures have become artificially asymmetrical); copulatory duct heavily chitinized, divergent anteriorly, each connecting with elongate seminal receptacle (Fig. 35B) which curved anteriorly and reaching to half length of somite with expanded bulbous part terminally.

Antennule (Fig. 36A) 22-segmented; suture between segments XXIV–XXVI visible. Fusion pattern and armature as follows: I–III–7 + aesthetasc, IV–2, V–2 + aesthetasc, VI–2 + aesthetasc, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXV–4 + aesthetasc, XXVI–XXVIII–8 + aesthetasc. First to eighth (X) segments fringed with row of setules posteriorly.

Antennary endopod: first segment without inner seta; second segment (Fig. 36B) with 3 setae of unequal lengths medially, and 5 setae and 1 vestigial seta terminally. Antennary exopod (Fig. 36C) indistinctly 8-segmented, first to fifth segments almost fused or incompletely fused, setal formula as follows: 0,1,1,1,1,1,0,3. Mandibular gnathobase with 3 stout teeth, dorsalmost of which bifid at tip, lacking medial tuft of setules as found in *Crassarietellus* sp.; basis fringed by row of long setules along inner margin, and not furnished with minute spinules as in male of *Crassarietellus* sp. Mandibular palp (Fig. 36D): endopod rudimentary, 1-segmented, with 2 setae of unequal lengths; exopod indistinctly 5-segmented, seta on first segment not reduced, outer seta on fifth segment relatively long.

Maxillule (Fig. 36E) praecoxal arthrite with 5 naked spines and 1 process; coxal endite carrying long serrate seta; coxal epipodite with 8 plumose setae; second basal endite bearing 1 vestigial seta; endopod bulbous, 1-segmented, bearing 3 setae, one of which rudimentary. Maxilla: first praecoxal endite (Fig. 36F) with 2 spinulose setae and vestigial element; basal spine (Fig. 36G) stout, bearing 2 rows of long spinules. Maxilliped: fourth endopod segment (Fig. 35C) with relatively developed spinulose innermost seta, fifth segment (Fig. 36D) also having spinulose innermost seta, but much shorter and thinner than on fourth segment; sixth endopod segment (Fig. 36E) with seta a reduced, seta b over half length of medial-length seta c, medium-length spinulose seta c, spinulose seta d elongate.

Leg 4 without inner coxal seta. Leg 5 (Fig. 36H): intercoxal sclerite more or less fused; endopod almost fused with basis, medial suture visible; exopod separate from basis, indistinctly 3-segmented, sutures between segments visible, terminal outer spine almost fused with segment.

REMARKS. Sars (1924, 1925) overlooked the vestigial seta on

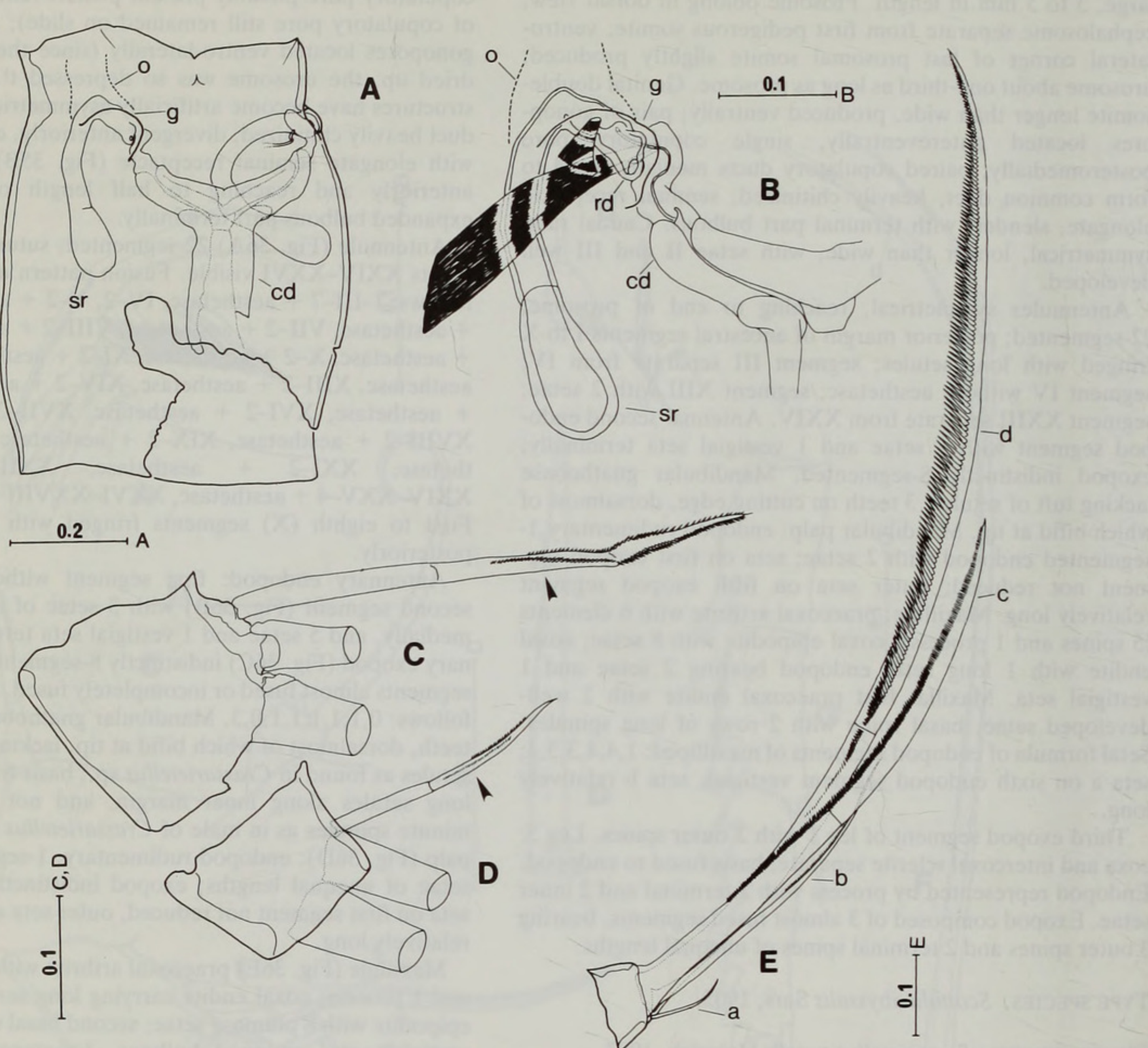

Fig. 35. *Sarsarietellus abyssalis*, female (holotype). A, Genital double-somite, ventral view, part around copulatory pore missing; B, Internal structure of right genital system; C, Fourth endopod segment of maxilliped, innermost seta indicated by arrowhead; D, Fifth endopod segment of maxilliped, innermost seta indicated by arrowhead; E, Sixth endopod segment of maxilliped. Scales in mm.

the second endopodal segment of the antenna, the rudimentary 1-segmented mandibular endopod with 2 setae, and the rudimentary seta on the second basal endite of the maxillule. The terminal segments of the female antennule were re-examined in detail, revealing that there were several misinterpretations of the segmental fusion pattern and of the setation pattern in Sars' (1924, 1925) descriptions.

Genus *Pilarella* Alvarez, 1985

DIAGNOSIS (emended). Only female known. Body relatively small, 1.5 to 1.7 mm in length. Prosome oblong in dorsal view; cephalosome separate from first pedigerous somite; ventrolateral corner of last prosome somite pointed; urosome nearly half as long as prosome. Genital double-somite slightly

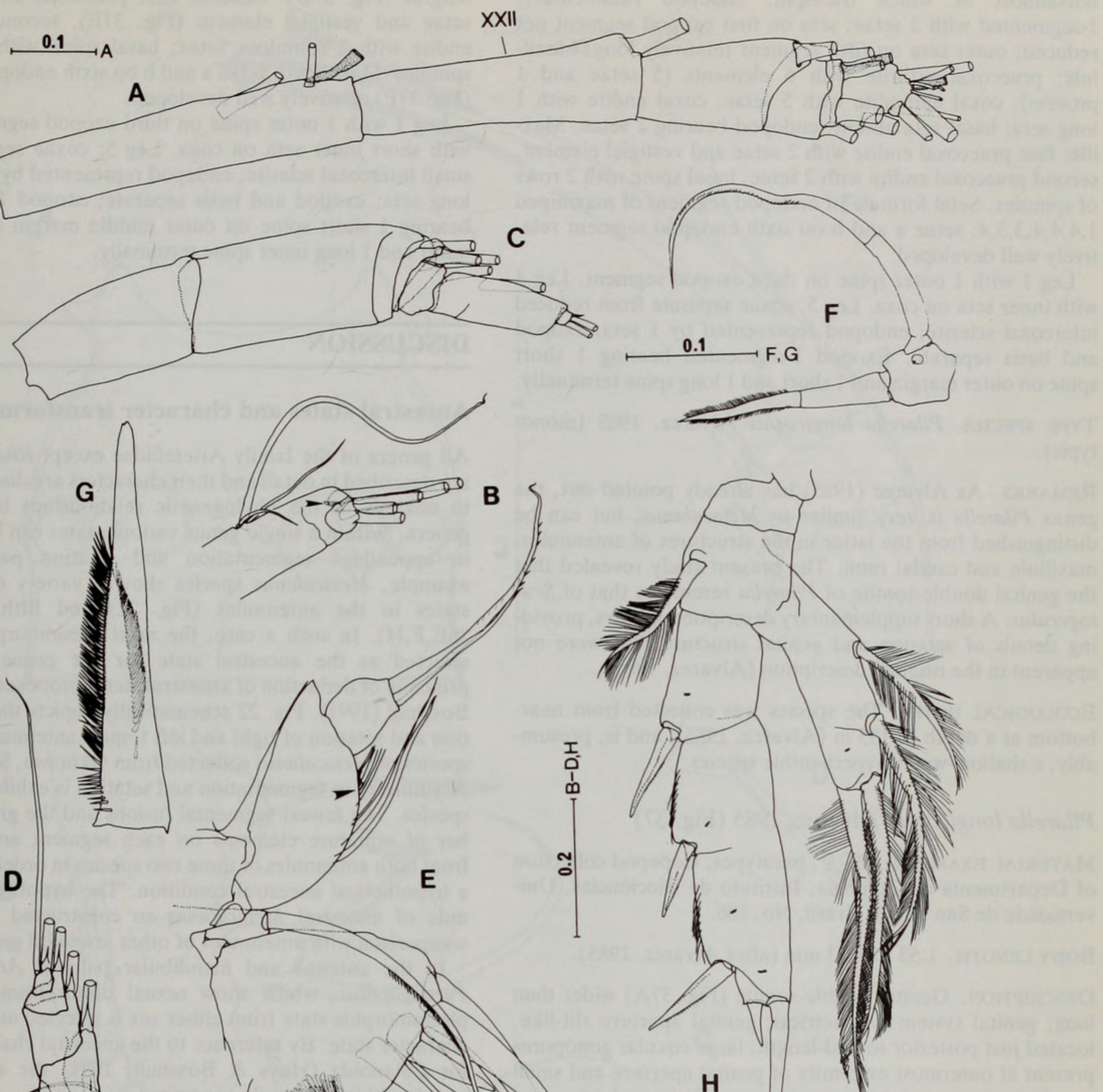

Fig. 36. *Sarsarietellus abyssalis*, female (holotype). A, Antennulary segments XXI to XXVIII; B, Terminal part of second endopod segment of antenna, vestigial innermost seta indicated by arrowhead; C, Antennary exopod; D, Mandibular endopod and exopod; E, Praecoxal arthrite, coxal endite, basis and endopod of maxillule, vestigial basal seta indicated by arrowhead; F, First praecoxal endite of maxilla; G, Basal spine of maxilla; H, Leg 5, posterior surface. Scales in mm.

wider than long; entire reproductive system paired, symmetrical; large circular gonopore and small copulatory pore located at outer and inner ends of slit-like aperture, respectively; copulatory duct short, simple; seminal receptacle relatively small, located medial to gonopore. Caudal rami slightly asymmetrical, with right ramus narrower and just shorter than left, with setae II and III relatively long.

Antennules asymmetrical, left longer than right and reaching to end of caudal rami; antennules 21-segmented on both sides; posterior proximal margin lacking long setules; segments I to IV fused, segments IX to XII partially fused; segments XXIV to XXVIII fused into compound apical segment. Antenna: first endopod segment with 1 mid-margin inner seta, second with 3 setae at midlength and 5 setae terminally; exopod indistinctly 7-segmented. Mandibular gnathobase lacking tuft of setules; 4 teeth on cutting edge, dorsalmost of which tricuspid; endopod rudimentary, 1-segmented with 2 setae; seta on first exopod segment not reduced; outer seta on fifth segment relatively long. Maxillule; praecoxal arthrite with 6 elements (5 setae and 1 process); coxal epipodite with 5 setae; coxal endite with 1 long seta; basal seta absent; endopod bearing 2 setae. Maxilla: first praecoxal endite with 2 setae and vestigial element, second praecoxal endite with 2 setae; basal spine with 2 rows of spinules. Setal formula of endopod segment of maxilliped 1,4,4,4,3,3,4; setae a and b on sixth endopod segment relatively well developed.

Leg 1 with 1 outer spine on third exopod segment. Leg 4 with inner seta on coxa. Leg 5: coxae separate from reduced intercoxal sclerite; endopod represented by 1 seta; exopod and basis separate. Exopod 1-segmented bearing 1 short spine on outer margin and 1 short and 1 long spine terminally.

Type species. *Pilarella longicornis* Alvarez, 1985 (monotypic).

Remarks. As Alvarez (1985) has already pointed out, the genus *Pilarella* is very similar to *Metacalanus*, but can be distinguished from the latter in the structures of antennules, maxillule and caudal rami. The present study revealed that the genital double-somite of *Pilarella* resembles that of *Scutogerulus*. A short supplementary description follows, providing details of setation and genital structure that were not apparent in the original description (Alvarez, 1985).

Ecological notes. The species was collected from near-bottom at a depth of 135 m (Alvarez, 1985), and is, presumably, a shallow-water hyperbenthic species.

Pilarella longicornis Alvarez, 1985 (Fig. 37)

Material examined. 3♀♀, paratypes, Copepod collection of Departmenta de Zoologia, Instituto de Biociências, Universidade de Sao Paulo, Brasil, No. 186.

Body length. 1.53 to 1.73 mm (after Alvarez, 1985).

Description. Genital double-somite (Fig. 37A) wider than long; genital system symmetrical; genital aperture slit-like, located just posterior to mid-length; large circular gonopores present at outermost extremity of genital aperture and small copulatory pore at innermost extremity; copulatory and receptacle ducts short; seminal receptacle relatively small, located medial to gonopore. Caudal rami slightly asymmetrical, with right ramus narrower and just shorter than left, with setae II and III relatively long.

Antennules (see Fig. 39) asymmetrical, left longer than right and reaching to end of caudal rami; both antennules 21-segmented; posterior proximal margin lacking long setules. Fusion pattern and armature as follows: I–IV–9 + 2 aesthetascs, V–2 + aesthetasc, VI–2, VII–2 + aesthetasc, VIII–2 + aesthetasc, IX–2 + aesthetasc, X–2 + aesthetasc, XI–2 + aesthetasc, XII–2 + aesthetasc, XIII–2 + aesthetasc, XIV–2 + aesthetasc, XV–2 + aesthetasc, XVI–2 + aesthetasc, XVII–2 + aesthetasc, XVIII–2 + aesthetasc, XIX–2 + aesthetasc, XX–2 + aesthetasc, XXI–2 + aesthetasc, XXII–1, XXIII–1, XXIV–XXVIII–12 + 2 aesthetascs.

Antenna: second endopod segment (Fig. 37B) with 3 setae of unequal lengths at midlength and 5 setae terminally; exopod indistinctly 7-segmented. Maxillule: praecoxal arthrite (Fig. 37C) with 6 elements (5 setae and 1 process); coxal epipodite with 5 setae; endopod bearing 2 setae of unequal lengths (Fig. 37D). Maxilla: first praecoxal endite with 2 setae and vestigial element (Fig. 37E), second praecoxal endite with 2 spinulose setae; basal spine with 2 rows of spinules. Maxilliped: setae a and b on sixth endopod segment (Fig. 37F) relatively well developed.

Leg 1 with 1 outer spine on third exopod segment. Leg 4 with short inner seta on coxa. Leg 5: coxae separate from small intercoxal sclerite; endopod represented by 1 relatively long seta; exopod and basis separate; exopod 1-segmented bearing 1 short spine on outer middle margin and 1 short outer and 1 long inner spine terminally.

DISCUSSION

Ancestral states and character transformation

All genera of the family Arietellidae except *Rhapidophorus* are described in detail and their characters are discussed prior to analysis of the phylogenetic relationships between the genera. Within a single genus various states can be observed in appendage segmentation and setation patterns. For example, *Metacalanus* species show a variety of character states in the antennules (Fig. 22) and fifth legs (Fig. 26E,F,H). In such a case, the most plesiomorphic state is selected as the ancestral state for the genus, using the principle of deduction of ancestral states proposed by Huys & Boxshall (1991). Fig. 22 schematically depicts the segmentation and setation of right and left female antennules of 2 new species of *Metacalanus* collected from Okinawa, South Japan. Asymmetry in segmentation and setation is exhibited in both species. The fewest segmental fusions and the greatest number of armature elements on each segment are combined from both antennules of these two species in order to arrive at a hypothetical ancestral condition. The hypothetical antennule of ancestral *Metacalanus* so constructed is used for comparison with antennules of other arietellid genera.

In the antenna and mandibular palp of *Arietellus* and *Paraugaptilus*, which show sexual dimorphism, the more plesiomorphic state from either sex is selected as the generic character state. By reference to the ancestral character states for Calanoida (Huys & Boxshall, 1991) the evolutionary trends within the family are traced.

1. Body plan. The most primitive condition in the family can be seen in *Crassarietellus* and *Sarsarietellus*. The body is symmetrical with complete separation between the cephalosome and the first pedigerous somite; there is no projection at the tip of the cephalosome, no strong dorso- and ventrolateral processes on the last prosomal somite, and no specialization of the caudal ramus.

Asymmetry in the body, except for female genital double-somites, can be seen in the ventrolateral processes on the last prosomal somite in *Arietellus giesbrechti* (Sars, 1924, 1925), *A. mohri* (Björnberg, 1975), and *A.* sp.; in the ventrolateral corners of the second and third pedigerous somites in *Paramisophria giselae* (Campaner, 1977); and in the prosome of *Paramisophria platysoma* (Ohtsuka & Mitsuzumi, 1990). These are more apomorphic states compared with congeners which have symmetrical counterparts. The asymmetrical prosome of *P. platysoma* appears to result from its specialized adaptation to the hyperbenthic zone (Ohtsuka & Mitsuzumi, 1990).

The cephalosome is separate from the first pedigerous

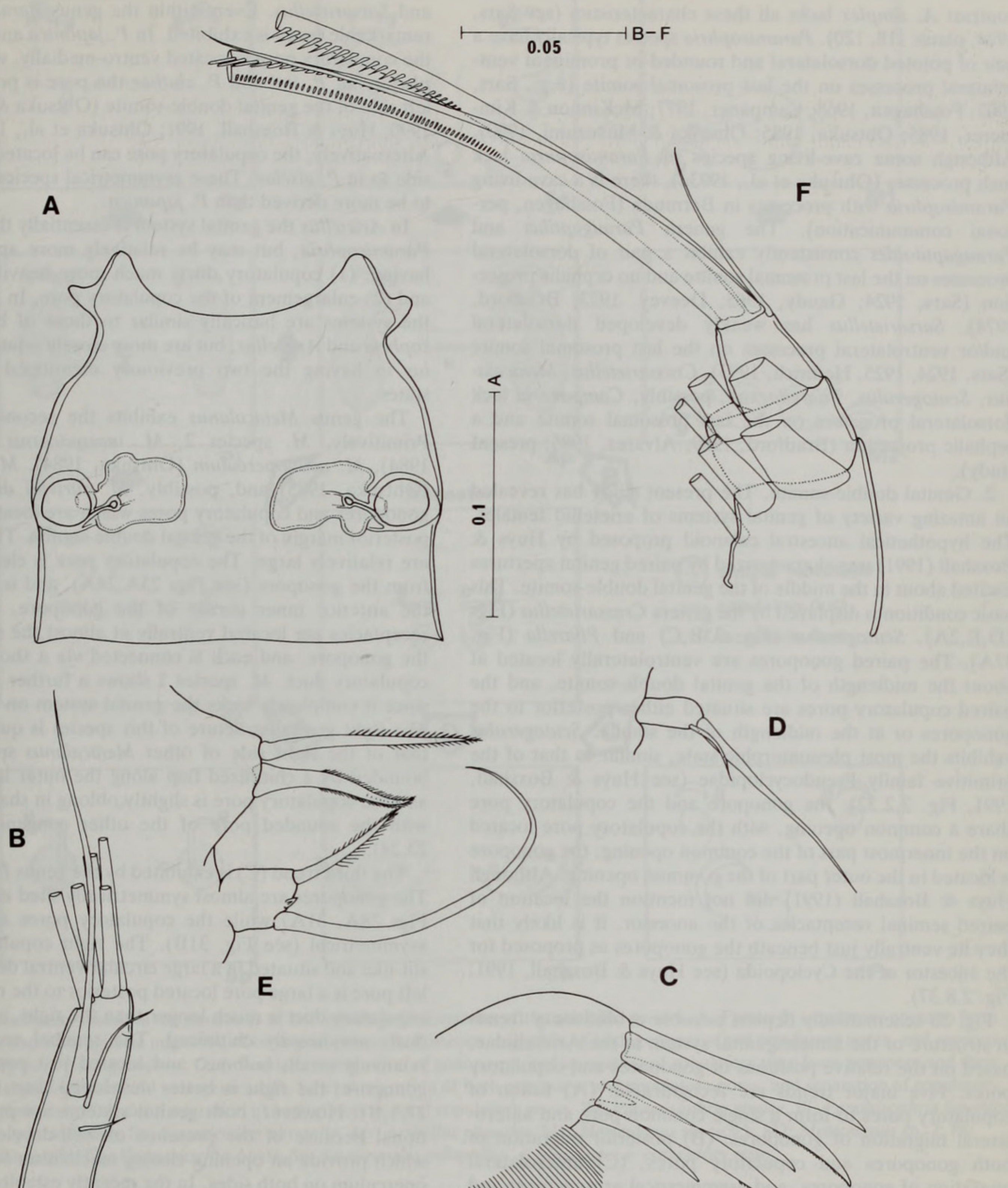

Fig. 37. *Pilarella longicornis*, female (paratype). A, Genital double-somite, ventral view; B, Apical endopod segment of antenna; C, Praecoxal arthrite of maxillule; D, Maxillulary endopod; E, Praecoxal endites of maxilla; F, Tip of endopod of maxilliped showing setae a and b. Scales in mm.

somite in almost all arietellids. Re-examination of those taxa in which the cephalosome and the first pedigerous somite were previously reported to be fused (for example, *Paraugaptilus magnus*), has revealed that these somites are clearly separate. In *Metacalanus* species 1 the cephalosome is weakly fused with the first pedigerous somite ventrolaterally. In all arietellids the fourth and fifth pedigerous somites are invariably fused, with or without a suture.

Within the genus *Arietellus*, *A. setosus* has a well-developed cephalic projection, a pair of strong ventrolateral processes on the last prosomal somite and a posteriorly swollen caudal ramus with remarkably elongate setae. In contrast *A. simplex* lacks all these characteristics (see Sars, 1924, plates 118, 120). *Paramisophria* species typically have a pair of pointed dorsolateral and rounded or prominent ventrolateral processes on the last prosomal somite (e.g., Sars, 1903; Fosshagen, 1968; Campaner, 1977; McKinnon & Kimmerer, 1985; Ohtsuka, 1985; Ohtuska & Mitsuzumi, 1990). Although some cave-living species of *Paramisophria* lack such processes (Ohtsuka et al., 1993a), there is a cave-living *Paramisophria* with processes in Bermuda (Fosshagen, personal communication). The genera *Paraugaptilus* and *Paraugaptiloides* consistently exhibit a pair of dorsolateral processes on the last prosomal somite and no cephalic projection (Sars, 1924; Gaudy, 1965; Deevey, 1973; Bradford, 1974). *Sarsarietellus* has weakly developed dorsolateral and/or ventrolateral processes on the last prosomal somite (Sars, 1924, 1925; Heinrich, 1993). *Crassarietellus*, *Metacalanus*, *Scutogerulus*, *Pilarella* and, possibly, *Campaneria* lack dorsolateral processes on the last prosomal somite and a cephalic projection (Bradford, 1969; Alvarez, 1985; present study).

2. Genital double-somite. The present study has revealed an amazing variety of genital systems of arietellid females. The hypothetical ancestral calanoid proposed by Huys & Boxshall (1991) was characterized by paired genital apertures located about in the middle of the genital double-somite. This basic condition is displayed by the genera *Crassarietellus* (Figs 1D,E,2A), *Scutogerulus* (Fig. 33B,C) and *Pilarella* (Fig. 37A). The paired gonopores are ventrolaterally located at about the midlength of the genital double-somite, and the paired copulatory pores are situated either posterior to the gonopores or at the midlength of the somite. *Scutogerulus* exhibits the most plesiomorphic state, similar to that of the primitive family Pseudocyclopidae (see Huys & Boxshall, 1991, Fig. 2.2.32): the gonopore and the copulatory pore share a common opening, with the copulatory pore located on the innermost part of the common opening; the gonopore is located in the outer part of the common opening. Although Huys & Boxshall (1991) did not mention the location of paired seminal receptacles of the ancestor, it is likely that they lie ventrally just beneath the gonopores as proposed for the ancestor of the Cyclopoida (see Huys & Boxshall, 1991, Fig. 2.8.37).

Fig. 38 schematically depicts possible evolutionary trends in structure of the female genital system in the Arietellidae, based on the relative positions of gonopores and copulatory pores. Five major trends are recognizable: (A) fusion of copulatory pores to form a single common pore and anterolateral migration of gonopores; (B) posterior migration of both gonopores and copulatory pores; (C) anterolateral migration of gonopores, and asymmetrical arrangement and enlargement of copulatory pores; (D) lateral migration of both gonopores and copulatory pores, and copulatory pore covered by ventral flap; (E) lateral migration of both gonopores and copulatory pores, copulatory pore uncovered. The first three trends (A-C) are accompanied by the formation of a pair of genital opercula, each of which closes off a gonopore and opens anteriorly with a posterior hinge. The gonopore is separate from the copulatory pore in all except the last trend (E). The first evolutionary trend (A) is exhibited in *Paramisophria*, *Arietellus* and *Sarsarietellus*. The copulatory ducts are heavily chitinized in *Arietellus* and *Sarsarietellus* (see Figs 13B,16A-C) but not so in *Paramisophria* (Figs 19A,20A). In addition, each copulatory duct is connected to a medial part of the seminal receptacle, but not so anteriorly as in *Arietellus* and *Sarsarietellus*. Even within the genus *Paramisophria*, a remarkable trend is exhibited. In *P. japonica* and *P. reducta*, the copulatory pore is located ventro-medially, whereas in *P. platysoma*, *P. itoi* and *P. cluthae* the pore is present on the left side of the genital double-somite (Ohtsuka & Mitsuzumi, 1990; Huys & Boxshall, 1991; Ohtsuka et al., 1991, 1993b). Alternatively, the copulatory pore can be located on the right side as in *P. giselae*. These asymmetrical species are thought to be more derived than *P. japonica*.

In *Arietellus* the genital system is essentially the same as in *Paramisophria*, but may be relatively more apomorphic in having: (1) copulatory ducts much more heavily chitinized; and (2) enlargement of the copulatory pore. In *Sarsarietellus* the systems are basically similar to those of both *Paramisophria* and *Arietellus*, but are more closely related to *Arietellus* in having the two previously mentioned apomorphic states.

The genus *Metacalanus* exhibits the second trend (B). Primitively, *M.* species 2, *M. inaequicornis* (Campaner, 1984), *M. acutioperculum* (Ohtsuka, 1984), *M. curvirostris* (Ohtsuka, 1985) and, possibly, *M. aurivilli* display paired gonopores and copulatory pores which are located along the posterior margin of the genital double-somite. The gonopores are relatively large. The copulatory pore is clearly separate from the gonopore (see Figs 23A,24A), and is located near the anterior inner corner of the gonopore. The seminal receptacles are located ventrally at almost the same level as the gonopore, and each is connected via a short, chitinized copulatory duct. *M.* species 1 shows a further derived state since it completely lacks the genital system on the left side. The right genital structure of this species is quite similar to that of the right side of other *Metacalanus* species, but is bounded by a chitinized flap along the outer lateral margin and the copulatory pore is slightly oblong in shape compared with the rounded pore of the other congeners (see Figs 23,24).

The third trend (C) is exhibited by the genus *Paraugaptilus*. The gonopores are almost symmetrically sited anteriorly (see Figs 28A, 31A) while the copulatory pores are extremely asymmetrical (see Fig. 31B). The right copulatory pore is slit-like and situated in a large circular ventral depression; the left pore is a large pore located posterior to the right. The left copulatory duct is much longer than the right, although both ducts are heavily chitinized. The seminal receptacles are relatively small, bulbous, and located just posterior to the gonopore; the right is better developed than the left (Fig. 27A,B). However, both genital systems are probably functional because of the presence of well-developed muscles which provide an opening-closing mechanism for the genital operculum on both sides. In the recently established calanoid family Hyperbionycidae (Ohtsuka et al., 1993b), only the left genital system is functional; the right side lacks musculature around the gonopore and is probably no longer functional. Only two species of *Paraugaptilus* were available for the present study but Gaudy's (1965) and Deevey's (1973) illustrations of the ventral surfaces of the female genital double-somites of *P. mozambicus* and *P. bermudensis* suggest that these species exhibit the same genital systems.

The fourth (D) and fifth trends (E) are displayed by *Crassarietellus*, and by *Scutogerulus* and *Pilarella*, respectively. Both trends show primitive states of the female genital system in the presence of paired and symmetrically arranged gonopores, copulatory pores and seminal receptacles. However, both trends exhibit different variations of the plesio-

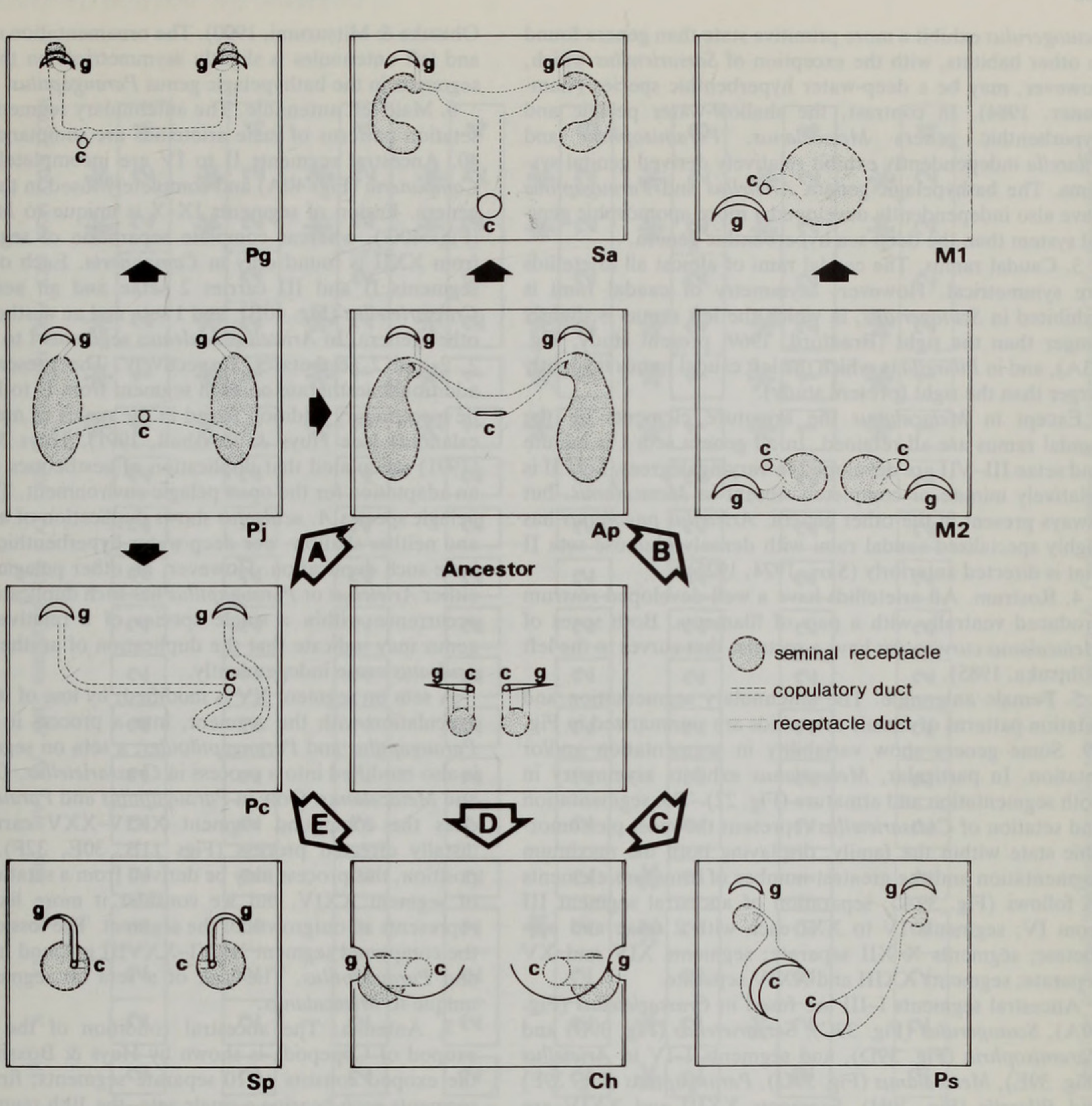

Fig. 38. Evolutionary trends in the structures of the female genital systems of the arietellid genera. A, Fusion of copulatory pores to form single pore, and anterolateral migration of both gonopores; B, Posterior migration of both gonopores and copulatory pores, and separation of copulatory pore from gonopore; C, Anterolateral migration of gonopores, and separation of copulatory pore from gonopore and their asymmetrical arrangement and enlargement; D, Lateral migration of both gonopores and copulatory pores, and separation of copulatory pore from gonopore; E, Lateral migration of both gonopores and copulatory pores. Pg: *Paramisophria giselae*; Pj: *Paramisophria japonica*; Pc: *Paramisophria cluthae*; Sa: *Sarsarietellus abyssalis*; Ap: *Arietellus plumifer*; M1: *Metacalanus* species 1; M2: *Metacalanus* sp. 2; Ps: *Paraugaptilus similis*; Ch: *Crassarietellus huysi*; Sp: *Scutogerulus pelophilus*. g: gonopore; c: copulatory pore.

morphic genital system. In *Scutogerulus* and *Pilarella* each copulatory pore shares a common opening with the gonopore, whereas in *Crassarietellus* each copulatory pore is separate from the gonopore and located beneath the ventral flap. The latter is probably more derived since the copulatory pores are separate from the gonopores. In both trends, the copulatory duct is relatively short and the seminal receptacle is a simple spherical shape.

In the specimens of *Crassarietellus* examined, a pair of fertilization tubes from the spermatophore remnant (Figs 2A,3) was still connected to the copulatory pores. In this genus each copulatory pore seems to be relatively large and opens onto the inner surface of the ventral flap. The end of the fertilization tube terminates in a mass of brownish opaque material (see Fig. 1E, dotted) positioned where the copulatory pore opens. The gonopore is not covered by a genital operculum, as in other arietellid genera (Fig. 2C,D). An exposed gonopore, as in *Crassarietellus*, is also found in the deep-sea hyperbenthic calanoid family Hyperbionycidae (Ohtsuka et al., 1993b). Owing to the complete absence of armature elements on leg 6 in the Calanoida, it is unknown whether the absence of a genital operculum in *Crassarietellus* represents a secondary loss or a more plesiomorphic state than other arietellids. Radiation of the genital systems of arietellids can be related to their different habitats. Generally, deep-sea hyperbenthic genera such as *Crassarietellus* and

Scutogerulus exhibit a more primitive state than genera found in other habitats, with the exception of *Sarsarietellus* which, however, may be a deep-water hyperbenthic species (Campaner, 1984). In contrast, the shallow-water pelagic and hyperbenthic genera *Metacalanus*, *Paramisophria* and *Pilarella* independently exhibit relatively derived genital systems. The bathypelagic genera *Arietellus* and *Paraugaptilus* have also independently developed a more apomorphic genital system than the deep-sea hyperbenthic genera.

3. Caudal ramus. The caudal rami of almost all arietellids are symmetrical. However, asymmetry of caudal rami is exhibited in *Scutogerulus*, in which the left ramus is slightly longer than the right (Bradford, 1969; present study, Fig. 33A), and in *Pilarella* in which the left caudal ramus is slightly larger than the right (present study).

Except in *Metacalanus* the armature elements on the caudal ramus are all retained. In all genera seta I is minute and setae III–VII are developed to varying degrees. Seta II is relatively minute or completely absent in *Metacalanus*, but always present in the other genera. *Arietellus pavoninus* has highly specialized caudal rami with densely plumose seta II that is directed anteriorly (Sars, 1924, 1925).

4. Rostrum. All arietellids have a well-developed rostrum produced ventrally with a pair of filaments. Both sexes of *Metacalanus curvirostris* have a rostrum that curves to the left (Ohtsuka, 1985).

5. Female antennule. The antennulary segmentation and setation patterns of female arietellids are summarized in Fig. 39. Some genera show variability in segmentation and/or setation. In particular, *Metacalanus* exhibits asymmetry in both segmentation and armature (Fig. 22). The segmentation and setation of *Crassarietellus* represent the most plesiomorphic state within the family, displaying both the maximum segmentation and the greatest number of armature elements as follows (Fig. 39A): separation of ancestral segment III from IV; segments IV to XXI each with 2 setae and aesthetasc; segments X–XII separate; segments XIV and XV separate; segments XXIII and XXIV separate.

Ancestral segments I–III are fused in *Crassarietellus* (Fig. 39A), *Scutogerulus* (Fig. 39C), *Sarsarietellus* (Fig. 39B) and *Paramisophria* (Fig. 39D), and segments I–IV in *Arietellus* (Fig. 39E), *Metacalanus* (Fig. 39G), *Paraugaptilus* (Fig. 39F) and *Pilarella* (Fig. 39H). Segments XXIII and XXIV are separate in *Crassarietellus*, *Paramisophria*, *Scutogerulus*, *Sarsarietellus*, *Metacalanus* and *Pilarella*, and fused in *Arietellus* and *Paraugaptilus*. The complete fusion of segments IX and X is unique to *Metacalanus*.

The loss of an aesthetasc on segment IV is found in seven genera; that on segment II in *Pilarella*; that on segment VI in *Arietellus*, *Paraugaptilus*, *Metacalanus* and *Pilarella*; those on segments VIII and X in *Paraugaptilus* and *Metacalanus*; that on segment XII in *Arietellus* and *Paraugaptilus*; those on segments XXII and XXIII in *Pilarella*. One element on segment XIII is reduced in *Paraugaptilus* and *Metacalanus*. One seta on compound segment XXVI–XXVIII is reduced in *Arietellus* and in *Paraugaptilus similis*.

The presence of a duplicated aesthetasc at the extreme tip of antennule of *Paraugaptilus similis* is interpreted here as an individual abnormality.

The right and left antennules are markedly asymmetrical in length in the genera *Paramisophria*, *Metacalanus* and *Pilarella*, which are mainly distributed near the sea bed. This asymmetry has been related to the peculiar swimming behaviour of these genera at the sediment-water interface (see Ohtsuka & Mitsuzumi, 1990). The ornamentation of the right and left antennules is slightly asymmetrical on the terminal segments in the bathypelagic genus *Paraugaptilus*.

6. Male left antennule. The antennulary segmentation and setation patterns of male arietellids are summarized in Fig. 40. Ancestral segments II to IV are incompletely fused in *Campaneria* (Fig. 40A) and completely fused in the other six genera. Fusion of segments IX–X is unique to *Metacalanus* (Fig. 40G), whereas complete separation of segment XXI from XXII is found only in *Campaneria*. Each of ancestral segments II and III carries 2 setae and an aesthetasc in *Crassarietellus* (Fig. 40B), and 1 seta and an aesthetasc in the other genera. In *Arietellus aculeatus* segments I to IV bear 1, 2, 2 and 2 aesthetascs, respectively. The presence of one additional aesthetasc on each segment from II to IV seem to be a secondary addition found in the males of many pelagic calanoids (see Huys & Boxshall, 1991). Huys & Boxshall (1991) speculated that duplication of aesthetascs in males is an adaptation for the open pelagic environment. The oceanic pelagic species *A. aculeatus* shows duplication of aesthetascs, and neither shallow- nor deep-water hyperbenthic arietellids have such duplication. However, no other pelagic species of either *Arietellus* or *Paraugaptilus* has such duplication, and its occurrence within a single species of a relatively derived genus may indicate that the duplication of aesthetascs in *A. aculeatus* arose independently.

A seta on segment XV is modified, by loss of its proximal articulation with the segment, into a process in *Arietellus*, *Paraugaptilus* and *Paraugaptiloides*; a seta on segment XXII is also modified into a process in *Crassarietellus*, *Campaneria* and *Metacalanus*. Only in *Paraugaptilus* and *Paraugaptiloides* does the compound segment XXIV–XXV carry a large distally directed process (Figs 11B, 30E, 32F). From its position, this process may be derived from a setation element of segment XXIV, but we consider it more likely that it represents an outgrowth of the segment. The loss of a seta on the compound segment XXVI–XXVIII is found in *Arietellus* and *Paraugaptilus*. The lack of a seta on segment XIII is unique to *Metacalanus*.

7. Antenna. The ancestral condition of the antennary exopod of Copepoda is shown by Huys & Boxshall (1991): the exopod consists of 10 separate segments; first to ninth segments each bearing a single seta, the 10th segment with 3 setae (Fig. 41A). The segmentation and setation patterns of the arietellid genera are schematically depicted in Fig. 41B-H. In all genera, ancestral exopodal segments I and II, V and VI, VI and VII, and VII and VIII are either completely separate or incompletely fused with a suture still visible. In all genera, ancestral segments IV, V, VI and VII each carry 1 seta while segments I, II, III and IX are unarmed. Segment X carries 3 setae except in *Paraugaptilus* (Fig. 41G,H). A seta is present on segment VIII in *Crassarietellus* (Fig. 41B), *Campaneria* (Fig. 41D), *Paraugaptiloides* (Fig. 41D), *Paramisophria* (Fig. 41D), *Metacalanus* (Fig. 41E), *Sarsarietellus* (Fig. 41D), *Scutogerulus* (Fig. 41D) and *Pilarella* (Fig. 41D), but absent in *Arietellus* (Fig. 41F) and female *Paraugaptilus* (Fig. 41H). Complete fusion of ancestral segments II–IV occurs in *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Metacalanus*, *Paraugaptilus*, *Sarsarietellus*, *Scutogerulus* and *Pilarella*. Complete fusion of segments VIII–IX occurs in *Arietellus*, *Metacalanus* and female *Paraugaptilus*. The most advanced state is found in female *Paraugaptilus* (Fig. 41H): ancestral segments VIII to X are completely fused to form an unarmed, bulbous compound segment in *P.*

Fig. 39. Schematic illustration of segmental fusion patterns and armature of female antennules of the arietellid genera. A, *Crassarietellus*; B, *Sarsarietellus*; C, *Scutogerulus*; D, *Paramisophria*; E, *Arietellus*; F, *Paraugaptilus*; G, *Metacalanus*; H, *Pilarella*. The number indicates the number of setae on each segment. Asterisk indicates segment without aesthetasc.

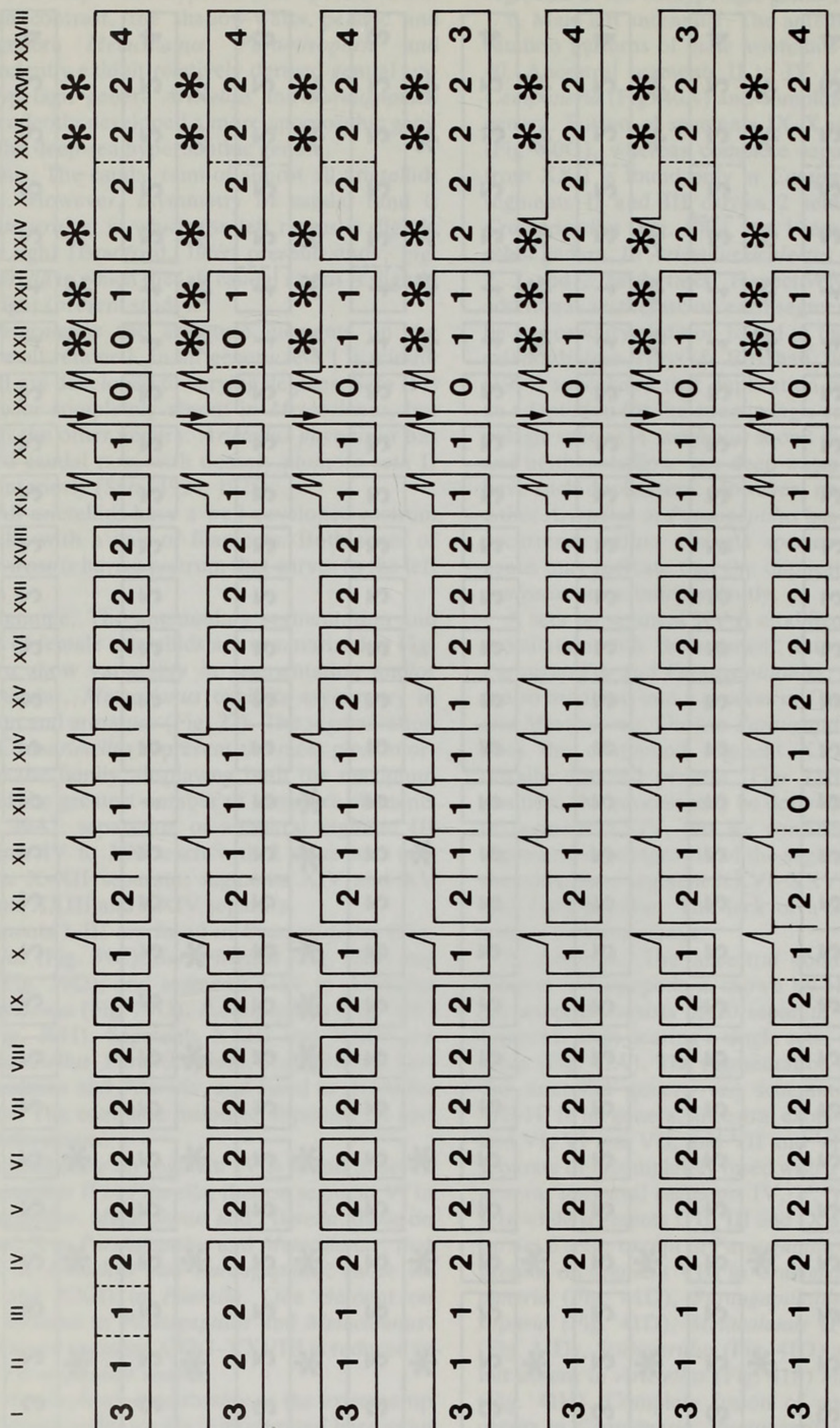

Fig. 40. Schematic illustration of segmental fusion patterns and armature of male antennules of the arietellid genera. A, *Campaneria*; B, *Crassarietellus*; C, *Paramisophria*; D, *Arietellus*; E, *Paraugaptiloides*; F, *Paraugaptilus*; G, *Metacalanus*. The number indicates the number of setae on each segment. Asterisk indicates a segment with no aesthetasc.

similis, *P. buchani*, *P. bermudensis* (Deevey, 1973) and *P. meridionalis* (= *P. buchani* sensu Sars, 1924, 1925). In contrast, males of *P. similis* and *P. bermudensis* are relatively plesiomorphic in that compound segment VIII–X retains a seta which is derived from ancestral segment VIII.

In contrast to the exopodal segmentation, the endopods of arietellids are constantly 2-segmented with the second to fourth ancestral segments almost completely fused. The first segment bears a single minute seta in *Crassarietellus*, *Campaneria*, *Paramisophria*, *Metacalanus* and *Pilarella*, and is unarmed in *Paraugaptiloides*, *Arietellus*, *Paraugaptilus*, *Sarsarietellus* and *Scutogerulus*. The number of inner setae on the second compound segment is variable: 3 in *Crassarietellus*, *Campaneria*, *Paramisophria*, *Sarsarietellus*, *Scutogerulus* and *Pilarella*; 2 in *Paraugaptiloides*, *Arietellus*, *Paraugaptilus* and *Metacalanus* (*Paraugaptilus* has 1 or 2 setae on it). The number of terminal setae on the compound segment is 6 in *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Paraugaptilus* and *Sarsarietellus*, and 5 in *Crassarietellus*, *Campaneria*, *Metacalanus*, *Scutogerulus* and *Pilarella*.

Sexual dimorphism is found in the antennary rami of *Arietellus* and *Paraugaptilus*. The reduction of one of the 2 medial setae on the second endopodal segment of *Arietellus* and some species of *Paraugaptilus* is retained only in the female. In *Paraugaptilus* the relative length of the first and second endopodal segments is different in the sexes. In addition, some species of *Paraugaptilus* (Deevey, 1973; present study) exhibit sexual differences in the exopod in that the ancestral segment VIII is completely fused with segment IX–X in the female and is unarmed, but incompletely fused with the compound segment and carrying 1 seta in the male. The male shows a more plesiomorphic state in antennary rami than the female.

8. Mandible. Arietellids are typically carnivorous, feeding on copepods and other small organisms (e.g., Ohtsuka & Mitsuzumi, 1990; Ohtsuka et al., 1991). Their mandibular gnathobases are well developed and heavily chitinized, with three or four sharp teeth.

The endopod is either reduced to 1 segment with 1 or 2 setae, or is unarmed and completely fused with the basis. The more plesiomorphic state is retained in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Paramisophria*, *Metacalanus*, *Sarsarietellus*, *Scutogerulus* and *Pilarella*, and the derived state found in *Arietellus* and *Paraugaptilus*.

The first exopodal segment has a normally developed seta in all genera, except for some species of *Arietellus* and *Paraugaptilus*. In these two genera this seta is sexually dimorphic. The males are furnished with a normally developed seta, whereas the females bear a vestigial seta (Sars, 1924; Deevey, 1973; present study). On the fifth exopodal segment, the remarkable reduction of the outer terminal seta is exhibited only by *Arietellus* (Figs 13D,18B) and *Paraugaptilus* (Fig. 32B).

9. Maxillule. Arietellids exhibit a wide variety of transformed states in the praecoxal arthrite, the coxal endite and epipodite, the basal endite and the endopod. These characters were used to define some arietellid genera by previous authors such as Sars (1903), Rose (1933), Brodsky (1950), Campaner (1977) and Ohtsuka et al. (1993a).

The maximum number of elements on the praecoxal arth-

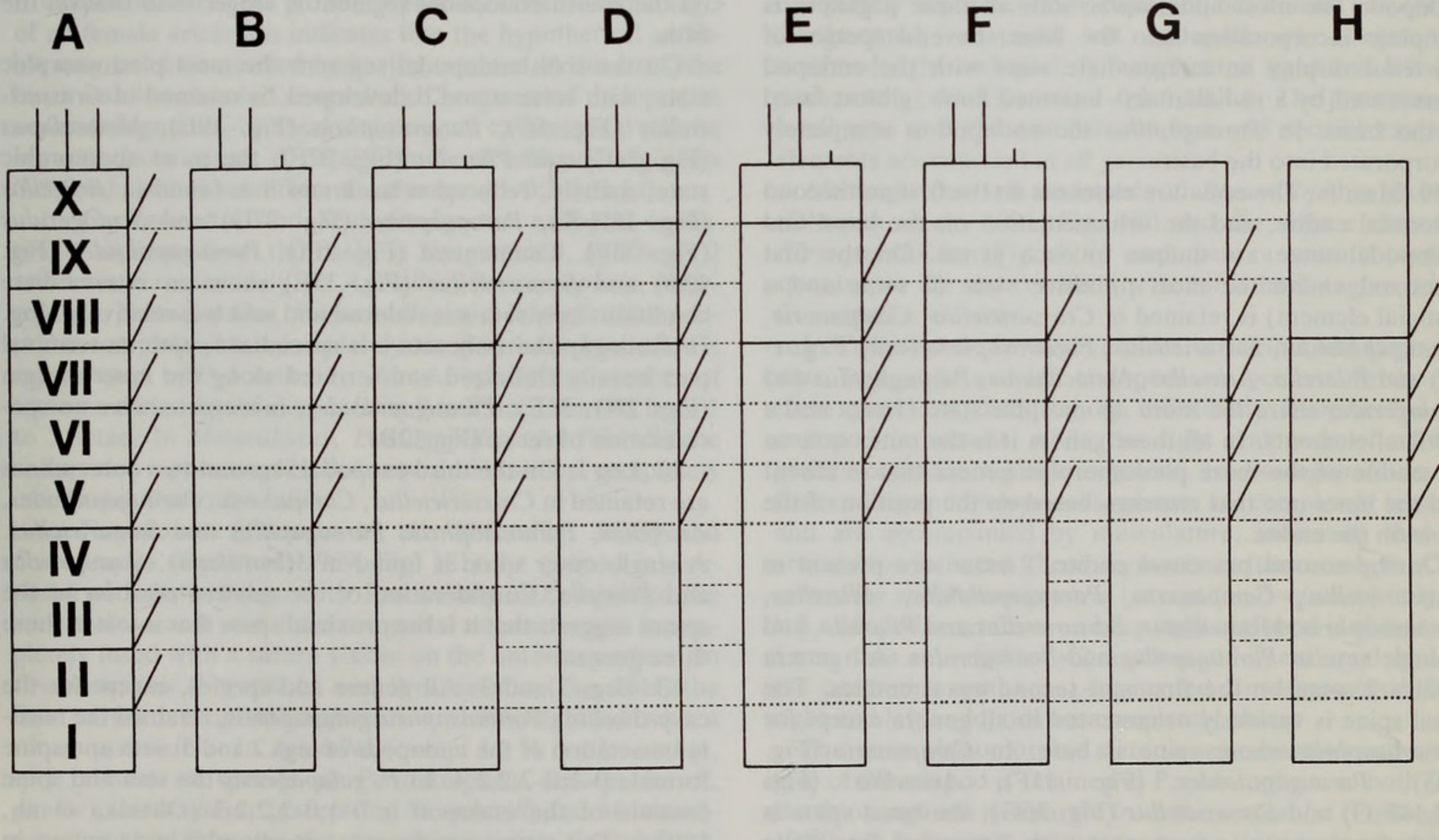

Fig. 41. Schematic illustration of fusion patterns and armature of antennary exopods of the arietellid genera. A, Hypothetical calanoid ancestor; B, *Crassarietellus*; C, *Paramisophria giselae*; D, *Campaneria*, *Paraugaptiloides*, *Paramisophria japonica*, *Sarsarietellus*, *Scutogerulus*; E, *Metacalanus*; F, *Arietellus*; G, *Paraugaptilus similis*, male; H, *P. similis*, female. Solid and dotted lines indicating complete separation between segments, and incomplete fusion or suture between segments, respectively.

rite (5 spines and process) occurs in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Sarsarietellus* and *Pilarella*. In *Sarsarietellus* the outer proximal spine is incompletely fused to the arthrite, while in the other six genera the fusion is complete enough to form a process. Both *Paraugaptilus* (5 spines) and *Scutogerulus* (4 spines and process) show more advanced states, and the reduced element may be the inner proximal spine in both genera. *Metacalanus* exhibits the most apomorphic state, in the number of elements (0–2 setiform spines), and the elements are not so strongly chitinized as in other genera.

On the coxal endite a single seta is present in all the genera except for *Paraugaptilus*. The relative length and the ornamentation of the seta are variable within polytypic genera. The number of setae on the coxal epipodite varies in arietellids. The maximum number (8 setae) is retained in *Paraugaptiloides*, *Arietellus*, *Paraugaptilus* and *Sarsarietellus*, whereas there are 6 in *Crassarietellus* and *Campaneria*, 5 in *Metacalanus*, *Scutogerulus* and *Pilarella*. A vestigial basal seta is present in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Paramisophria* and *Sarsarietellus*, but absent in *Arietellus*, *Metacalanus*, *Paraugaptilus* and *Pilarella*. The position of this seta indicates that it probably represents the second basal endite.

The endopod is variously modified. The most plesiomorphic state, 1-segmented with 3 setae, is found in several species of *Paramisophria*. A 1-segmented endopod with 2 setae is present in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Sarsarietellus* and *Pilarella*; a 1-segmented endopod with a single seta in *Arietellus*, *Metacalanus* and *Scutogerulus*. Species of *Arietellus* and *Metacalanus*, especially the former, exhibit a variety of transformed states in the endopod. The most apomorphic state in these 2 genera is complete incorporation into the basis. Several species of *Arietellus* display an intermediate state with the endopod represented by a rudimentary, unarmed knob, almost fused to the basis. In *Paraugaptilus* the endopod is completely incorporated into the basis.

10. Maxilla. The armature elements on the first and second praecoxal endite, and the ornamentation on the basal and endopodal setae are unique to each genus. On the first praecoxal endite the most primitive state (2 setae and a vestigial element) is retained in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Sarsarietellus*, *Paramisophria* (only *P. giselae*) and *Pilarella*. *Arietellus*, *Metacalanus*, *Paraugaptilus* and *Scutogerulus* share the more apomorphic state (1 seta and a vestigial element). In all these genera it is the outer seta on the endite of the more plesiomorphic genera that is absent and the inner one that remains, based on the position of the setae on the endite.

On the second praecoxal endite, 2 setae are present in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Metacalanus*, *Sarsarietellus* and *Pilarella*, and a single seta in *Paraugaptilus* and *Scutogerulus*. All genera exhibit 2 setae on the first and second coxal endites. The basal spine is variously ornamented in all genera except for *Paramisophria* whose spine is bare. In *Campaneria* (Fig. 10G), *Paraugaptiloides* (Fig. 11F), *Arietellus* (Figs 13I,18F,G) and *Sarsarietellus* (Fig. 36G), the basal spine is relatively elongate, ornamented with 2 rows of fine, long spinules densely distributed along the entire length except for the bare terminal part. *Crassarietellus* (Figs 5B,8D) also carries a long basal spine with 2 rows of relatively thick spinules distributed about at midlength. In *Paraugaptilus* (Fig. 29D) and *Scutogerulus* (Fig. 34D), the spinules are minute and sparsely distributed. *Metacalanus* (Fig. 21I) bears a basal spine unique within arietellids; the spine is relatively short, with 2 rows of minute, rigid spinules at midlength. In *Pilarella* the basal spine is elongate with a single row of spinules at midlength.

The ornamentation on the endopodal setae is also characteristic of each genus. In *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Paramisophria*, *Metacalanus*, *Sarsarietellus* and *Pilarella*, the inner margin of these setae is furnished with a row of slender, simple spinules (see Fig. 11G), whereas in *Arietellus*, *Paraugaptilus* and *Scutogerulus* the ornamentation is variable. *Arietellus* develops a lobate structure basally on each spinule (Fig. 15B,C), while both *Paraugaptilus* (Fig. 27G) and *Scutogerulus* (Fig. 34F) carry a row of triangular spinules along the inner margin of each seta. In arietellids such setal ornamentation on the maxilla is also found on the well-developed setae of the terminal endopod segments of the maxilliped. Bradford (1969) referred to the setal ornamentation on the maxilla and maxilliped of *Scutogerulus* as 'shield-shaped appendages' in her definition of the genus.

11. Maxilliped. Variation in arietellids can be found in the armature on the fourth to sixth endopodal segments. The innermost seta on the fourth and fifth segments is relatively well-developed in all the genera except for *Arietellus*, in which it is reduced to a vestigial element or is completely absent. In *Crassarietellus* (Figs 6B,C,8E), *Metacalanus* (Fig. 26A,B), *Paramisophria* (Fig. 19D), *Paraugaptilus* (Fig. 27F) and *Pilarella*, the innermost setae on the fourth and fifth endopodal segments are of almost equal length; in *Campaneria* (Fig. 10H), *Paraugaptiloides* (Fig. 12B), *Sarsarietellus* (Fig. 35C,D) and *Scutogerulus* (Fig. 34E) the innermost seta on the fourth endopodal segment is longer than that on the fifth.

On the sixth endopodal segment the most plesiomorphic state, with setae a and b developed, is retained in *Crassarietellus* (Fig. 5C), *Paramisophria* (Fig. 19E), *Metacalanus* (Fig. 26C) and *Pilarella* (Fig. 37F); the most apomorphic state, namely, reduced setae a and b is found in *Arietellus* (Fig. 18H-K), *Paraugaptilus* (Fig. 27G) and *Scutogerulus* (Fig. 34F). *Campaneria* (Fig. 10I), *Paraugaptiloides* (Fig. 12B) and *Sarsarietellus* (Fig. 35E) show an intermediate condition: only seta a is reduced and seta b is relatively long. In *Paraugaptilus* only seta c is specialized, with its terminal part heavily chitinized and serrated along the inner margin (Figs 27G, 32E). *Paraugaptiloides*, however, shows no specialization of seta c (Fig.12B).

12. Leg 1. On the third exopodal segment two outer spines are retained in *Crassarietellus*, *Campaneria*, *Paraugaptiloides*, *Arietellus*, *Paramisophria*, *Paraugaptilus* and *Sarsarietellus*. A single outer spine is found in *Metacalanus*, *Scutogerulus* and *Pilarella*. Consideration of the relative position of the spines suggests that it is the proximal spine that is lost in these three genera.

13. Legs 2 and 3. All genera and species, except for the cave-dwelling *Paramisophria galapagensis*, retained the maximum setation of the endopods of legs 2 and 3: seta and spine formula 0–1;0–2;2,2,4. In *P. galapagensis* the seta and spine formula of the endopod is 0–1;0–2;2,2,3 (Ohtsuka et al., 1993a). This represents the most apomorphic state known in arietellids.

14. Leg 4. An inner coxal seta or a vestigial element is present only in *Paraugaptiloides*, *Paraugaptilus* and *Pilarella*. It is absent in the other genera, although a fourth copepodid

stage of *Paramisophria* sp. collected from South Japan carries a minute inner coxal seta (Ohtsuka et al., 1991, Fig. 6J,K). The maximum setation on the third endopodal segment is retained in all the genera and species except for *P. galapagensis*: 2,2,2 in *P. galapagensis* and 2,2,3 in other taxa (Ohtsuka et al., 1993a).

15. Female leg 5. The female fifth legs of arietellids are variable, as in several other calanoid families and the misophrioid family Misophriidae by Huys & Boxshall (1991). Campaner (1984) compared the structure of leg 5 in both sexes but drew no strict homologies of segmentation and armature elements.

Fig. 42 schematically depicts apparent evolutionary trends in the structure of female leg 5 within the genera *Arietellus*, *Paraugaptilus*, *Paramisophria*, *Metacalanus* and *Pilarella*. Within the genus *Arietellus*, three obvious evolutionary trends in segmentation and setation can be recognized: incorporation of the endopod into the basis, reduction of endopodal setae, and fusion of coxa, basis and both rami.The genus *Paramisophria* also exhibits two distinct evolutionary trends: reduction in numbers of endopodal setae and of exopodal spines. In the genus *Metacalanus* reduction of the endopod, and fusion of both rami into the basis plus reduction in number of elements on the exopod occur. Based on these evolutionary trends, the derivation of the *Paraugaptilus* state from an *Arietellus*-like condition, the relationships between *Sarsarietellus* and *Paramisophria* spp., and the derivation of *Metacalanus* from a *Paramisophria*-like ancestor, as already proposed by Campaner (1984), are supported. The setation of *Crassarietellus* (Fig. 6K,L) suggests a close relationship with *Paramisophria*, especially in the endopod setation.

Consideration of the plesiomorphic states exhibited in leg 5 of all female arietellids indicates that the hypothetical ancestor may be characterized by having retained a) the coxa, the basis and 3-segmented exopod and 2-segmented endopod as separate segments; b) basal seta present; c) intercoxal sclerite separate from coxae; d) setal formula of endopod segments 0–2;0,1,1; and e) setal formula of exopod I–0;I–0;II,I,0.

In *Crassarietellus* and *Scutogerulus* the endopod is distinctly separate from the basis, is 1-segmented, and bears 2 and 1 setae respectively. In *Arietellus*, *Paramisophria*, *Metacalanus*, *Paraugaptilus*, *Sarsarietellus* and *Pilarella* the endopod is completely or incompletely fused with the basis, and is represented by 0–4 setae. In *Paramisophria* the number of setae on the endopod ranges from 0 to 2; in *Arietellus* from 1 to 3 setae. In *Metacalanus*, *Paraugaptilus* and *Pilarella* the endopod is represented by 0–1 seta, and is almost completely incorporated into the basis.

In *P. japonica* (Ohtsuka et al., 1991, Fig. 3F,G) and *Scutogerulus* (Bradford, 1969, Fig. 181) the exopod is composed of 2 distinct segments. Particularly in *P. japonica* the ancestral second and third exopodal segments are incompletely fused with a suture visible on the anterior surface. In *Crassarietellus* (Fig. 6K,L) and *Sarsarietellus* (Fig. 36H) the first to third exopodal segments are almost fused with a suture just visible. In *Arietellus* (except for *A. mohri* and *A.* sp.), almost all species of *Paramisophria* (except for *P. giselae*), *Metacalanus* (except for *M. aurivilli* and *M. acutioperculum*) and *Pilarella*, the exopod is distinctly 1-segmented, but variably armed. *Arietellus* carries only a single terminal spine; *Paramisophria* bearing 2 or 3 lateral and 2 terminal spines; *Metacalanus* has 1 terminal spine or 2 terminal and 1 lateral spine. The unarmed exopods of *A. mohri* and *A.* sp. are lobate and almost completely fused with the basis. In *M. aurivilli* and *M. acutioperculum* the exopod is represented by a small knob with a single terminal seta. In *Paraugaptilus* the exopod is completely incorporated into the basis.

The intercoxal sclerite and coxa are completely separate in *Sarsarietellus*, *Metacalanus*, *Pilarella* and *P. giselae*, and incompletely in *Crassarietellus* and *Arietellus* (except for *A. mohri* and *A.* sp.). In *Paramisophria* (except for *P. giselae*), *Paraugaptilus*, *A. mohri* and *A.* sp. fusion is almost or completely accomplished.

Little attention was paid to the variability within a genus by Campaner (1984). Within genera such as *Arietellus*, *Paramisophria* and *Metacalanus*, the reduction in segmentation and setation is more variable than expected. Reductions in segmentation and setation appear to occur independently within each genus. For instance, the fusion between coxa and intercoxal sclerite probably evolved independently in *Arietellus* (see Fig. 17) and *Paramisophria* (Fig. 20E,F). The number of elements on both rami vary widely in these genera, whereas the outer basal seta is consistently present in all genera and species. In *Arietellus* the right basal seta is slightly or considerably longer than the left.

16. Male leg 5. Campaner (1984) showed a possible relationship between the male fifth legs of arietellids, based mainly on the presence or absence of the endopod on either side. However, the homologies of segmentation and setation were not considered in detail. Compared with the female fifth legs, the male legs are less variable in segmentation and setation within a genus. A scheme indicating possible derivations of segmentation and setation is given in Fig. 43.

The hypothetical ancestral state is based on all taxa and consists of a) intercoxal sclerite and coxa separate; b) coxa completely separate from basis; c) basal seta present; d) 2-segmented, unarmed left endopod; e) 1-segmented, unarmed right endopod; f) 3-segmented right and left exopods; and g) setal formula I–0;I–1;III,I,0. The presence of a basal seta and the numbers of first and second exopodal elements are constant in all genera.

Although the left endopod of *Paramisophria japonica* (Ohtsuka et al., 1991, Fig. 4K) and the right endopod of *Paraugaptiloides* (Fig. 12E) each bear a minute terminal spinule, we are not certain whether it is homologous with a true setation element.

In *Campaneria*, *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*, both right and left endopods are present. In the first three genera a distinctly or indistinctly 2-segmented left endopod is present, while the right endopods of all four genera comprise a single segment. In *Paraugaptiloides* the first and second endopodal segments are completely separate and are accompanied by musculature, indicating that the articulation between these segments is functional. In *Crassarietellus* and *Paramisophria* (except for *P. cluthae*) only the left endopod is retained and the right endopod is absent; the former has an indistinctly 2-segmented left endopod while in the latter this ramus is 1-segmented. In *Metacalanus* both right and left endopods are completely absent.

The most plesiomorphic state in segmentation and armature of the exopod is retained in Paramisophria: in both legs, the third segment is separate from the second (cf. Fosshagen, 1968) and 4 elements are present on the third segment of both legs (see Ohtsuka & Mitsuzumi, 1990, Fig. 4E,F). In *Crassarietellus* and *Paraugaptiloides* a vestigial outer proximal element is present on the left third exopod segment, which carries 4 elements in total. The number of elements on the

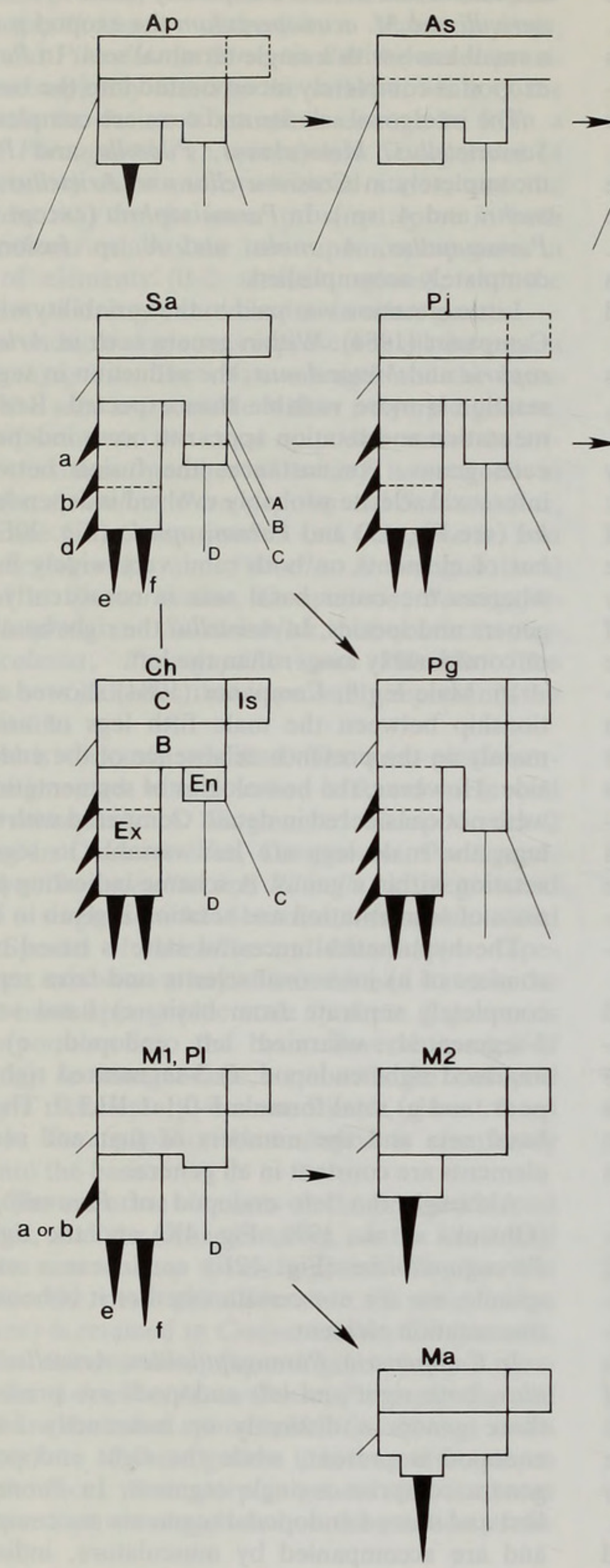

Fig. 42. Schematic comparison of patterns of segmentation and setation of female fifth legs in some arietellids. The arrows indicate possible derivations of setation and segmentation patterns and are not indicative of ancestor-descendant relationships between taxa. Ap: *Arietellus pavoninus*; As: *A.* sp.; Am: *A. mohri*; Ps: *Paraugaptilus similis*; Sa: *Sarsarietellus abyssalis*; Pj: *Paramisophria japonica*; Pi: *P. itoi*; Pp: *P. platysoma*; Pg: *P. giselae*; Pr: *P. reducta*; Ch: *Crassarietellus huysi*; M1: *Metacalanus* species 1; M2: *M.* species 2; Ma: *M. acutioperculum*; Pl: *Pilarella longicornis*. C: Coxa; B (in Ch): Basis; Is: Intercoxal sclerite; Ex: Exopod; En: Endopod. A-D (in Sa): setae on endopod; a-f: spines on exopod.

third exopod segment of the right leg is 3 in *Campaneria*, 2 in *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*, and 1 in *Metacalanus*; on the left leg it is 3 in *Campaneria* and *Arietellus* and 1 in *Metacalanus*. The distal two exopodal segments are separate in both legs in *Paraugaptiloides*, *Paramisophria* and *Metacalanus*, and fused in both legs of *Campaneria* and *Paraugaptilus* and in the right leg only in *Arietellus*. The distal two segments of the right leg are missing in the only known male of *Crassarietellus* sp. The terminal and subterminal elements on the third exopodal segment of the left leg are heavily chitinized and almost fused to the segment only in *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*.

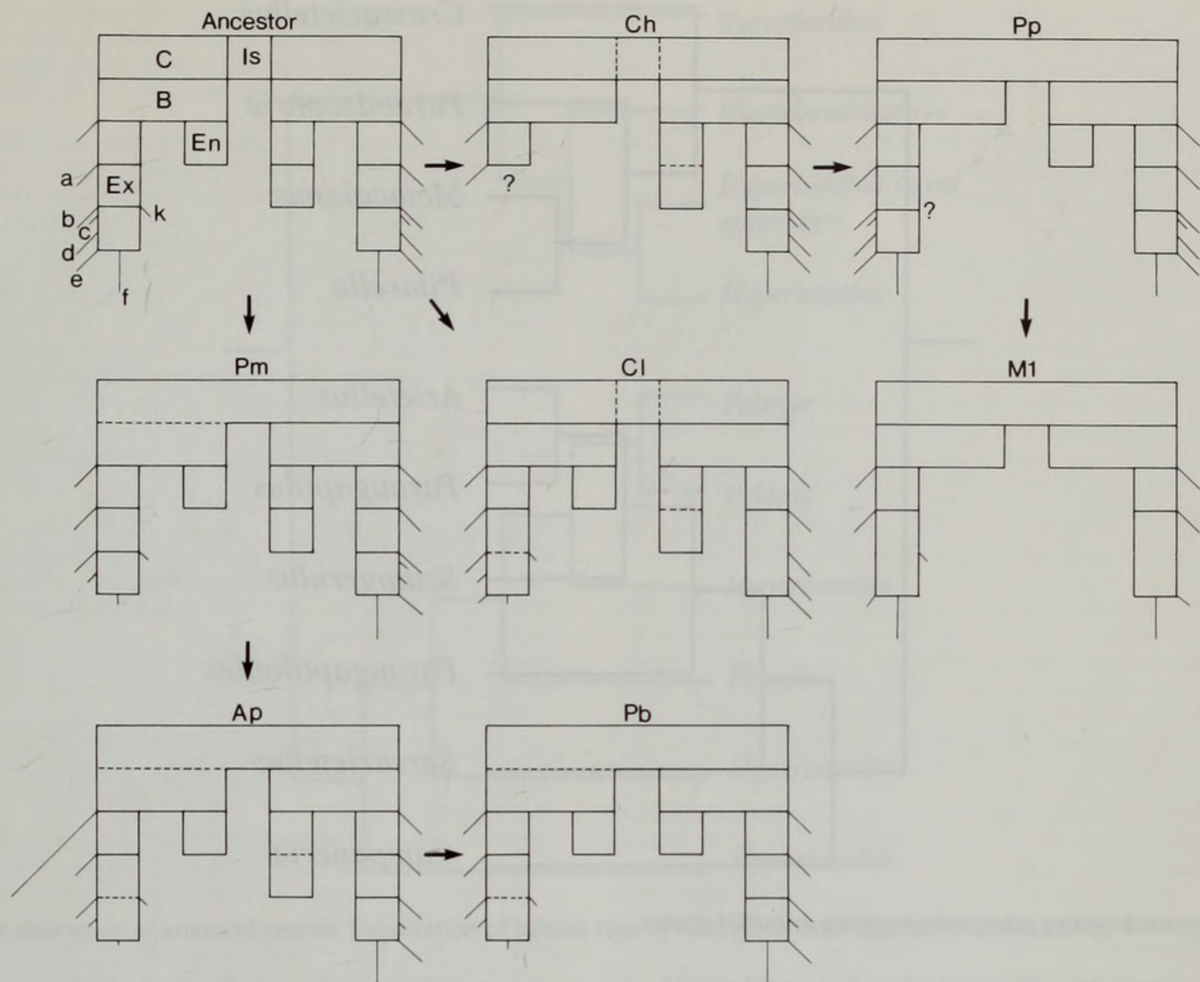

Fig. 43. Schematic comparison of segmentation and setation of male fifth legs in the Arietellidae. The arrows indicate possible derivations of setation and segmentation patterns and are not indicative of ancestor-descendant relationships between taxa. Ch: *Crassarietellus huysi*; Pp: *Paramisophria platysoma*; Pm: *Paraugaptiloides magnus*; Cl: *Campaneria latipes*; M1: *Metacalanus* species 1; Ap: *Arietellus plumifer*; Pb: *Paraugaptilus buchani*. C: Coxa; B: Basis; Is: Intercoxal sclerite; Ex: Exopod; En: Endopod. a-f,k: elements on exopod. Setae and spines are not distinguished here.

The intercoxal sclerite and both coxae are almost fused, with the suture clearly visible in *Crassarietellus* and *Campaneria*, while in the other genera fusion is complete. The basis and coxa are completely separate in both legs in *Crassarietellus*, *Campaneria*, *Paramisophria* and *Metacalanus*, almost completely fused in the right leg but completely separate in the left leg in *Paraugaptiloides*, *Arietellus* and *Paraugaptilus*.

Phylogenetic relationships between arietellid genera

Phylogenetic relationships between the 10 genera studied in this paper were analyzed using PAUP 3.0 on a matrix of 44 characters (Tables 2,3). The matrix contains a significant proportion of missing data, shown in the matrix by a '9' (Table 3). These missing data correspond to the unknown males of the genera *Scutogerulus*, *Sarsarietellus* and *Pilarella* and to the unknown females of *Campaneria* and *Paraugaptiloides*. Since most of the characters used in the analysis are sexually dimorphic (30 out of 44 characters), only a minority of characters (14 of 44) can be scored for all taxa. The phylogenetic scheme presented here is necessarily tentative, subject to re-examination as the gaps in the data matrix are filled by the discovery of unknown sexes.

Four trees were generated by the analysis, all with the same statistics: tree length = 179; consistency index = 0.263; homoplasy index = 0.737. These four trees differed only in the relative positions of *Campaneria*, *Paraugaptiloides* and *Sarsarietellus*. The relative positions of all other genera are the same. All three of these genera are known from only one sex. Tree 1 (Fig. 44) was selected as the best working hypothesis of relationships because *Campaneria* was the first offshoot of the *Arietellus*-group, as it was in three of the four trees, and because it placed *Sarsarietellus* as an earlier offshoot than *Paraugaptiloides* which we consider to be the more apomorphic genus of the two.

The genera of the Arietellidae form two lineages, the *Arietellus*-group comprising six genera, and the *Metacalanus*-group consisting of four genera. The *Arietellus*-group is diagnosed by the apomorphic reduction of seta a on the terminal segment of the maxillipedal endopod (character 27). The *Metacalanus*-group lacks a simple diagnostic character. The apomorphic state of character 38 (absence of endopod of male right fifth leg) is found only within the group, in *Crassarietellus*, *Paramisophria* and *Metacalanus* (the male of *Pilarella* is unknown), and the apomorphic state of character 3 (asymmetrical antennules in females) is found only in *Paramisophria*, *Metacalanus* and *Pilarella*. *Crassarietellus* retains the plesiomorphic state.

This analysis suggests that there may have been several

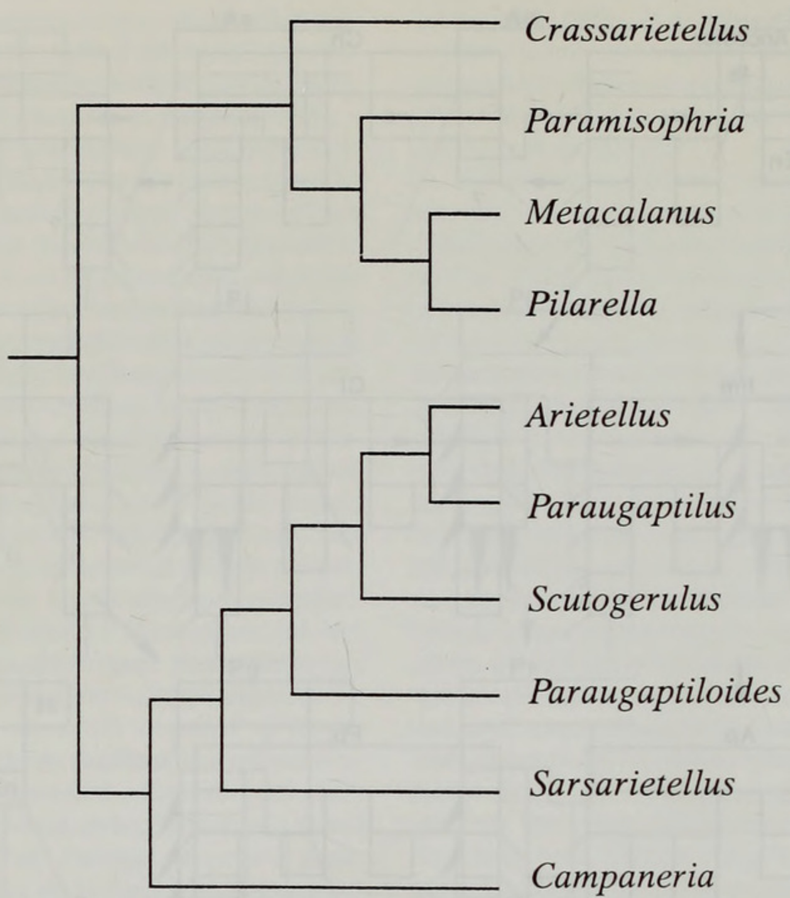

Fig. 44. Cladogram depicting relationships among arietellid genera.

shifts in habitat utilization during the evolutionary history of the family. Substitution of habitat type (Fig. 45) onto the cladogram shown in Fig. 44 indicates that the Arietellidae originated in the hyperbenthic zone. The most plesiomorphic representatives of both lineages still inhabit this zone. The *Metacalanus*-group has largely remained in the ancestral hyperbenthic habitat although it has successfully colonized anchialine caves (Ohtsuka et al., 1993a) and at least one species of *Metacalanus* is epipelagic. In contrast, the most apomorphic representatives of the *Arietellus*-group, the genera *Arietellus* and *Paraugaptilus*, have successfully colonized the open pelagic realm.

A similar analysis of habitat utilization was performed on the genera of the copepod family Misophrioidae by Boxshall (1989). The 10 genera of this family were placed in two lineages, both of which originated in the deep-water hyperbenthic zone. The first offshoot of the *Archimisophria*-lineage, represented by the genus *Archimisophria* Boxshall, 1983, has remained in the ancestral habitat but all the derived representatives of this lineage are found in anchialine caves and crevicular habitats. The most plesiomorphic representative of the *Misophria*-lineage, the genus *Misophriopsis* Boxshall, 1983, also inhabits the hyperbenthic zone but other members of the lineage have successfully colonized the pelagic zone, the shallow-water hyperbenthic zone and, independently, anchialine habitats.

There are interesting parallels between the Arietellidae and Misophriidae. The ancestry of both families appears to be closely associated with the deep-water hyperbenthic zone. Plesiomorphic genera in both families have remained in the ancestral habitat but more derived representatives now utilize a broader spectrum of habitat types, including the shallow-water hyperbenthic zone, the open pelagic realm and anchialine caves. Certain habitat shifts appear to have occurred at least twice, independently, within these two families. The colonization of anchialine habitats appears to have taken place twice in the Arietellidae, once within *Metacalanus* and once within *Paramisophria*, just as Boxshall (1989) found for the Misophriidae. Arietellids appear to have invaded the open pelagic zone three times (the *Arietellus-Paraugaptilus* group, *Paraugaptiloides*, and within the genus *Metacalanus*).

Key to genera of the family Arietellidae

1a Leg 1 with 1 outer spine on third exopod segment 2

1b Leg 1 with 2 outer spines on third exopod segment 3

2a Maxillule with 5 spines and 1 process on praecoxal arthrite; maxilla with 1 seta on distal praecoxal endite; caudal seta II developed; genital double-somite (♀) with paired genital system, each copulatory pore opening within slit-like genital slit, shared with gonopore .... *Scutogerulus* Bradford, 1969

2b Maxillule with 5 spines and 1 process on praecoxal arthrite; maxilla with 2 seta on distal praecoxal endite; caudal seta II developed; genital double-somite (♀) with paired genital system, each copulatory pore opening within common genital aperture, shared with gonopore .... *Pilarella* Alvarez, 1985

2c Maxillule with 0–2 elements on praecoxal arthrite; maxilla with 2 setae on distal praecoxal endite; caudal seta II reduced; genital double-somite (♀) with gonopore and copulatory pore separate and located posteriorly ..... *Metacalanus* Cleve, 1901

3a Maxillule with 6 setae on coxal epipodite 4

3b Maxillule with 8–9 setae on coxal epipodite 5

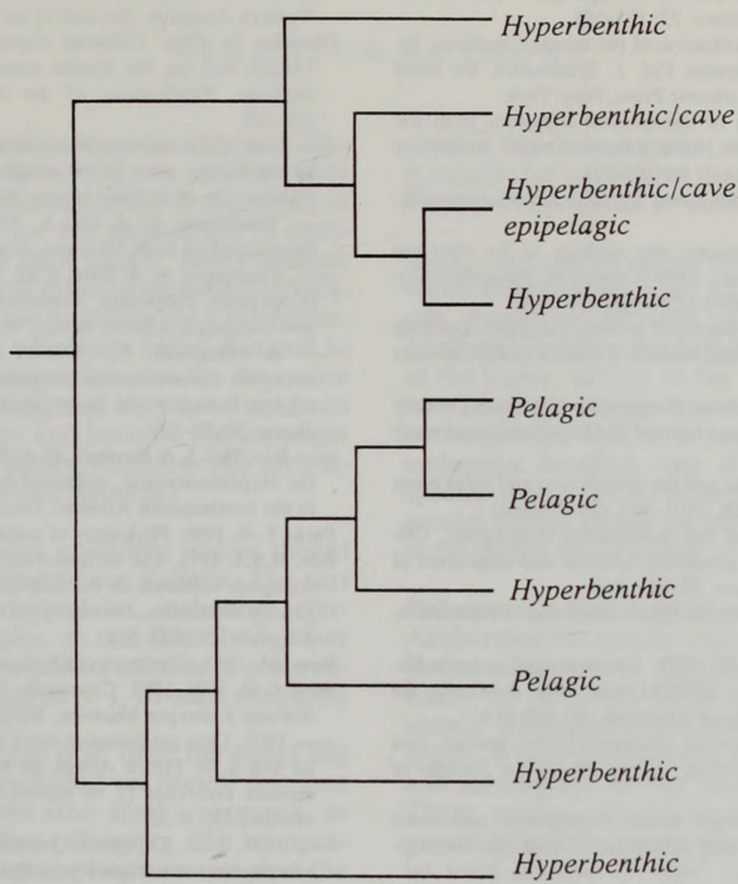

Fig. 45. Habitat cladogram of arietellid genera. Substitution of habitat type of each genus onto cladogram shown in Fig. 44.

4a Antennary exopod indistinctly 10-segmented; maxillulary praecoxal arthrite with strongly serrate spines; long innermost seta on fifth endopod segment of maxilliped; outermost seta on sixth endopod segment of maxilliped not reduced; left antennule (♂) with 2 setae on segments II and III, and segments XXI and XXII fused; right endopod of leg 5 (♂) lacking .... *Crassarietellus* gen. nov.

4b Antennary exopod indistinctly 8-segmented; maxillulary praecoxal arthrite with weakly serrate spines; short innermost seta on fifth endopod segment of maxilliped; outermost seta on sixth endopod segment of maxilliped reduced; left antennule with 1 seta on segments II and III, and segments XXI and XXII separate; right endopod of leg 5 (♂) present .... *Campaneria* gen. nov.

5a Innermost seta on fourth and fifth endopod segments of maxilliped vestigial .... *Arietellus* Giesbrecht, 1892

5b Innermost seta on fourth and fifth endopod of maxilliped not vestigial 6

6a Antennary exopod segment X unarmed .... *Paraugaptilus* Wolfenden, 1904

6b Antennary exopod segment X with 3 elements 7

7a Leg 4 with inner coxal seta; second antennary endopod segment with 2 inner setae at midlength .... *Paraugaptiloides* gen. nov.

7b Leg 4 without inner coxal seta; second antennary endopod segment with 3 inner setae at midlength 8

8a Antennulary segments XXV and XXVI separated; basal spine of maxilla ornamented with spinules; outermost seta on sixth endopod segment of maxilliped vestigial; genital double-somite (♀) with copulatory pore located midventrally on median line or on left side; copulatory duct heavily chitinized; seminal receptacle elongate, its distal end bulbous in shape; inner process (derived from endopod) of leg 5 (♀) with 4 setae .... *Sarsarietellus* Campaner, 1984

8b Antennulary segments XXV and XXVI fused; basal spine of maxilla bare; outermost seta on sixth endopod segment of maxilliped not vestigial; genital double-somite (♀) with copulatory pore located posteroventrally; seminal receptacle not elongate, its distal end not bulbous; inner process of leg 5 (♀) with 0–2 setae .... *Paramisophria* T. Scott, 1897

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