

The planktonic copepods of the northeastern Atlantic Ocean: Harpacticoida, Siphonostomatoida and Mormonilloida

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Synopsis

Diagnoses of 17 species of planktonic harpacticoids are given, including two new mesopelagic genera, *Volkmannia* and *Neotisbella*, and 3 new species, *Volkmannia forficula*, *V. attenuata* and *Neotisbella gigas*, belonging to the family Tisbidae. The new genera are related to the genus *Bathyidia* Farran, and the male of the type species of this genus, *B. remota* Farran, is described for the first time. Ten species of planktonic siphonostomatoids are described, including 6 new bathypelagic species belonging to the genus *Hyalopontius* Sars (= *Megapontius* Hulsemann). The new species are *H. hulsemannae*, *H. alatus*, *H. spinatus*, *H. roei*, *H. cinctus* and *H. enormis*. The 2 species of *Mormonilla* Giesbrecht are described and the systematic position of this aberrant genus is considered. It is proposed to raise the family Mormonillidae to a new order, the Mormonilloida, derived from the podoplean line within the Copepoda.

Introduction

This revision of the minor planktonic copepod orders occurring in the northeastern Atlantic was prompted by the discovery of two new genera of planktonic harpacticoids and of six new

species of free-living bathypelagic siphonostomatoids. Good descriptions of the representatives of the minor orders, Harpacticoida, Siphonostomatoida and Mormonilloida, are often not available or are not readily accessible to plankton workers who tend to concentrate on the more dominant groups. Consequently, these groups are comparatively poorly studied and published data on occurrence, depth distribution and other aspects of their biology are scarce.

Materials and methods

This study is based on a day and night series of hauls taken at 'Discovery' station 7089 in the region of the Cape Verde Islands (18° N 25° W) using the RMT 1+8 net system. The details of hauls and the fractions examined are given in Boxshall (1977). The *Hyalopontius* material was caught using the same net system in the northeastern Atlantic at a number of stations fished between 1974 and 1977. Dr Howard Roe (I.O.S.) isolated the *Hyalopontius* material from these latter samples and kindly allowed me to work them up. The type material of several of the species redescribed below and other specimens from important collections were also examined. All the specimens examined are stored in the British Museum (Natural History); a maximum of ten registration numbers is assigned to any one species-collection. Body lengths were measured from the tip of the rostrum to the distal end of the caudal rami excluding the caudal setae, except in *Aegisthus* Giesbrecht. In this genus body length was measured from the base of the rostrum to the proximal end of the very elongate caudal rami.

Key to planktonic species belonging to the Harpacticoida, Siphonostomatoida and Mormonilloida found in the northeastern Atlantic Ocean

- | | | |
|----|---|-------------------------------------|
| 1 | Leg 5 present; second antenna exopod at most 4-segmented, sometimes absent | 2 |
| - | Leg 5 absent; second antenna exopod 8-segmented | (MORMONILLOIDA) 21 |
| 2 | Mandible stylet-like, located within an oral cone, without palp; inner seta present on coxa of legs 1-4 | (SIPHONOSTOMATOIDA) 18 |
| - | Mandible not stylet-like, usually with palp; coxal seta absent | (HARPACTICOIDA) 3 |
| 3 | First thoracic somite free (prosoma 5-segmented) | 4 |
| - | First thoracic somite fused to cephalothorax (prosoma 4-segmented). | 5 |
| 4 | Dorsal surface of prosoma without chitinous markings; rostrum absent in ♂, long in ♀; first antenna 6-segmented in ♀ | <i>Aegisthus mucronatus</i> |
| - | Dorsal surface of prosoma without chitinous markings; rostrum short in ♀; first antenna 7-segmented in ♀ | <i>Aegisthus spinulosus</i> |
| - | Dorsal surface of prosoma with chitinous markings; rostrum short in both sexes; first antenna 7-segmented in both sexes | <i>Aegisthus aculeatus</i> |
| 5 | Body small, fusiform (Figs 2A, B), without marked boundary between prosoma and urosome; caudal rami short; leg 1 with 3-segmented rami | 6 |
| - | These characters not combined | 7 |
| 6 | Body length 0.3-0.6 mm; inner caudal seta about 3 times longer than outer caudal seta and usually about as long as body | <i>Microsetella norvegica</i> |
| - | Body length 0.6-0.9 mm; inner caudal seta 7-10 times longer than outer seta and usually more than 1.5 times longer than body | <i>Microsetella rosea</i> |
| 7 | Both rami of leg 1 2-segmented | <i>Euterpina acutifrons</i> |
| - | At least one ramus 3-segmented | 8 |
| 8 | Leg 1 exopod 3-segmented; second antenna exopod 4-segmented; second maxilla reduced to basal segment with 1 seta and terminal claw (as Fig. 4F) | 9 |
| - | These characters not combined | 12 |
| 9 | Leg 1 endopod 2-segmented | <i>Neotisbella gigas</i> sp. nov. |
| - | Leg 1 endopod 3-segmented | 10 |
| 10 | Third endopod segment of leg 1 comprising about 14% of length of ramus; mandible endopod with 2 proximal and 5 apical setae | <i>Bathyidia remota</i> |
| - | Third endopod segment of leg 1 comprising about 3-5% of length of ramus; mandible endopod with 3 proximal and 6 apical setae | 11 |
| 11 | Endopod of leg 1 about 34% longer than exopod | <i>Volkmania forficula</i> sp. nov. |
| - | Endopod of leg 1 about 70% longer than exopod | <i>Volkmania attenuata</i> sp. nov. |

12	Maxilliped very squat and robust; leg 1 rami 3-segmented	<i>Parathalestris croni</i>
-	Maxilliped slender; one ramus of leg 1 with less than 3 segments	13
13	Leg 1 with 3-segmented endopod and 1-segmented exopod	14
-	Leg 1 with 2-segmented endopod and 3-segmented exopod	15
14	First antenna 8-segmented; leg 1 exopod with 4 setae	<i>Clytemnestra scutellata</i>
-	First antenna 7-segmented; leg 1 exopod with 3 setae	<i>Clytemnestra rostrata</i>
15	Cephalosome with a pair of large cuticular lenses	16
-	Cephalosome without cuticular lenses	<i>Macrosetella gracilis</i>
16	Exopod of second antenna 1-segmented with 2 distal setae	17
-	Exopod of second antenna absent	<i>Oculosetella gracilis</i>
17	Baseoendopod of leg 5 with 5 setae in ♂, 3 in ♂	<i>Miracia efferata</i>
-	Baseoendopod of leg 5 with 4 setae in ♀, 2 in ♂	<i>Miracia minor</i>
18	First antenna 11-segmented in both sexes	<i>Hyalopontius</i> (see p. 244)
-	First antenna 5- to 9-segmented	19
19	Second antenna exopod absent; leg 5 with free segment	20
-	Second antenna exopod 1-segmented; leg 5 without free segment	<i>Pontoeciella abyssicola</i>
20	First antenna 5-segmented in ♀, 7-segmented in ♂	<i>Ratania flava</i>
-	First antenna 7-segmented in ♀, 9-segmented in ♂	<i>Ratania atlantica</i>
21	First antenna 3-segmented; lateral seta of caudal ramus located about 33% of distance along ramus	<i>Mormonilla phasma</i>
-	First antenna 4-segmented; lateral seta of caudal ramus located about 16% of distance along ramus	<i>Mormonilla minor</i>

Description of species

HARPACTICOIDA

A total of 17 species belonging to 7 families are regarded here as being true planktonic forms. Many other harpacticoids have been recorded from the plankton, but they have usually been found in the neritic zone and can be regarded as temporarily displaced littoral forms (Wells, 1970). Occasionally littoral species are carried into oceanic waters by clinging to algae drifting in ocean currents (Yeatman, 1962), these can also be regarded as expatriated specimens as they are not permanent members of the plankton.

Family AEGISTHIDAE

Genus *AEGISTHUS* Giesbrecht, 1891

DIAGNOSIS. Prosome 5-segmented with first thoracic somite free and about equal in size to the following somite. Genital complex (♀) with dorsal and lateral transverse suture line. Caudal rami at least twice as long as whole body. Rostrum present or absent. First antenna (♀) 6- or 7-segmented, (♂) 7- or 8-segmented, weakly or not geniculate. Second antenna slender with 1-segmented exopod bearing 1 or 2 setae. Mandible (♀) with or without rudimentary palp; apparently absent in ♂. First maxilla (♀) well developed, (♂) bilobed, rudimentary. Second maxilla (♀) well developed, (♂) with well-developed basipod but rudimentary rami. Maxilliped 3-segmented; (♀) well developed, (♂) poorly developed. Legs 1-4 with 3-segmented rami, armature formula as follows:

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

Leg 5 elongate, bearing a short naked seta and 5 serrate setae (♀) and with 5 serrate setae and 2 additional plumose setae in ♂. Leg 6 with 1 or 2 small setae.

TYPE-SPECIES. *Aegisthus mucronatus* Giesbrecht, 1891.

REMARKS. Some differences of opinion exist over the homology of the caudal rami in this well-defined genus. Giesbrecht (1892), Scott (1894), Farran (1905), Rose (1933) and Wells (1970) have erroneously interpreted the structures on the anal somite as comprising very short caudal rami fused to the anal somite and each bearing an extremely long seta which is itself setate (see Scott, 1894; pl. 11, figs 31 & 44). In fact the caudal rami are extremely long (often as much as five times longer than the body), closely pressed together and armed with a lateral seta in the middle third of each ramus and at least 2 apical setae, one of which is plumose (Sars, 1916; Lang, 1948).

Aegisthus mucronatus Giesbrecht, 1891

Aegisthus mucronatus Giesbrecht, 1891: 476.

A. longirostris Scott, 1894: 104, pl. XI, figs 31–44.

A. dubius Sars, 1916: 8, 14, pl. VIII.

DIAGNOSIS. *Female*. Prosome without reticulate chitinous markings on dorsal surface; maximum body width at level of second free thoracic somite (Fig. 1A). Genital complex with dorsal and lateral transverse suture line, armed with spinules. Rostrum very long and anteriorly directed. First antenna 6-segmented with large hook-like process medially on proximal segment. Second antenna with 2 unequal distal setae on exopod. Maxilliped (Fig. 1B) 3-segmented with 3 enlarged spines and 1 seta on middle segment and 3 setae on distal segment. Leg 1 with 3-segmented rami, but suture lines between segments 2 and 3 sometimes indistinct; exopod segments 2 and 3 with short spines on outer margins. Leg 5 (Fig. 1C) free segment with 3 serrate setae on lateral margin, 1 serrate seta and a naked seta distally and 1 serrate seta subapically. Leg 6 (Fig. 1D) an elongate free segment with a short subapical and a long apical seta.

Body length of female from 1.90 to 2.55 mm.

Male. As ♀ except: cephalothorax (Fig. 1E) relatively narrow. Rostrum absent. First antenna 8-segmented. Second antenna (Fig. 1F) with 1 seta distally on exopod. First maxilla bilobed, rudimentary. Second maxilla with large claw-like process on basipod, rami rudimentary with 5 short setae. Maxilliped 3-segmented; weakly developed, carrying 2 short setae on apex of distal segment. Leg 5 (Fig. 1G) 2-segmented; first segment with small proximal seta and distal serrate seta on outer margin; second segment with 2 serrate seta on outer margin, 2 on distal margin (the inner just longer than the outer) and 2 plumose setae on inner margin.

Body length of male from 1.10 to 1.70 mm.

MATERIAL EXAMINED. 352 ♀♀, 48 ♂♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.155–164 (♀) and 1977.165–174 (♂). 3 ♀♀, 1 ♂ syntypes of *A. longirostris*: Gulf of Guinea, 1° 55' N 5° 55' E (Scott, 1894). BM(NH) registration numbers 1893.4.22.588–589.

REMARKS. Sars (1916) described *A. dubius* from male specimens and mentioned the similarities between it and female *A. mucronatus*. He regarded it as a separate species because of the absence of a rostrum, the structure of the first antenna and the marked reduction of the mouthparts. Farran (1926) suspected that *A. dubius* was the male of *A. mucronatus*, as *A. mucronatus* females were found in every haul from which *A. dubius* was recorded but he did not synonymize the two species because Scott (1894) had described both sexes of a new species, *A. longirostris*, the females of which had since been recognized as being synonymous with *A. mucronatus*. The syntype series of *A. longirostris* contains only 1 male specimen. This specimen lacks a rostrum and its appendages are as described by Sars (1916) for *A. dubius*. The arostrate males (*A. dubius* Sars, 1916) have been correctly regarded as the males of *A. mucronatus* by most authors since Lang (1948).

Aegisthus aculeatus Giesbrecht, 1891

DIAGNOSIS. *Female*. Cephalothorax and free thoracic somites with conspicuous reticulate markings (Fig. 1H); maximum width of body near mid-point of cephalothorax. Genital complex subdivided

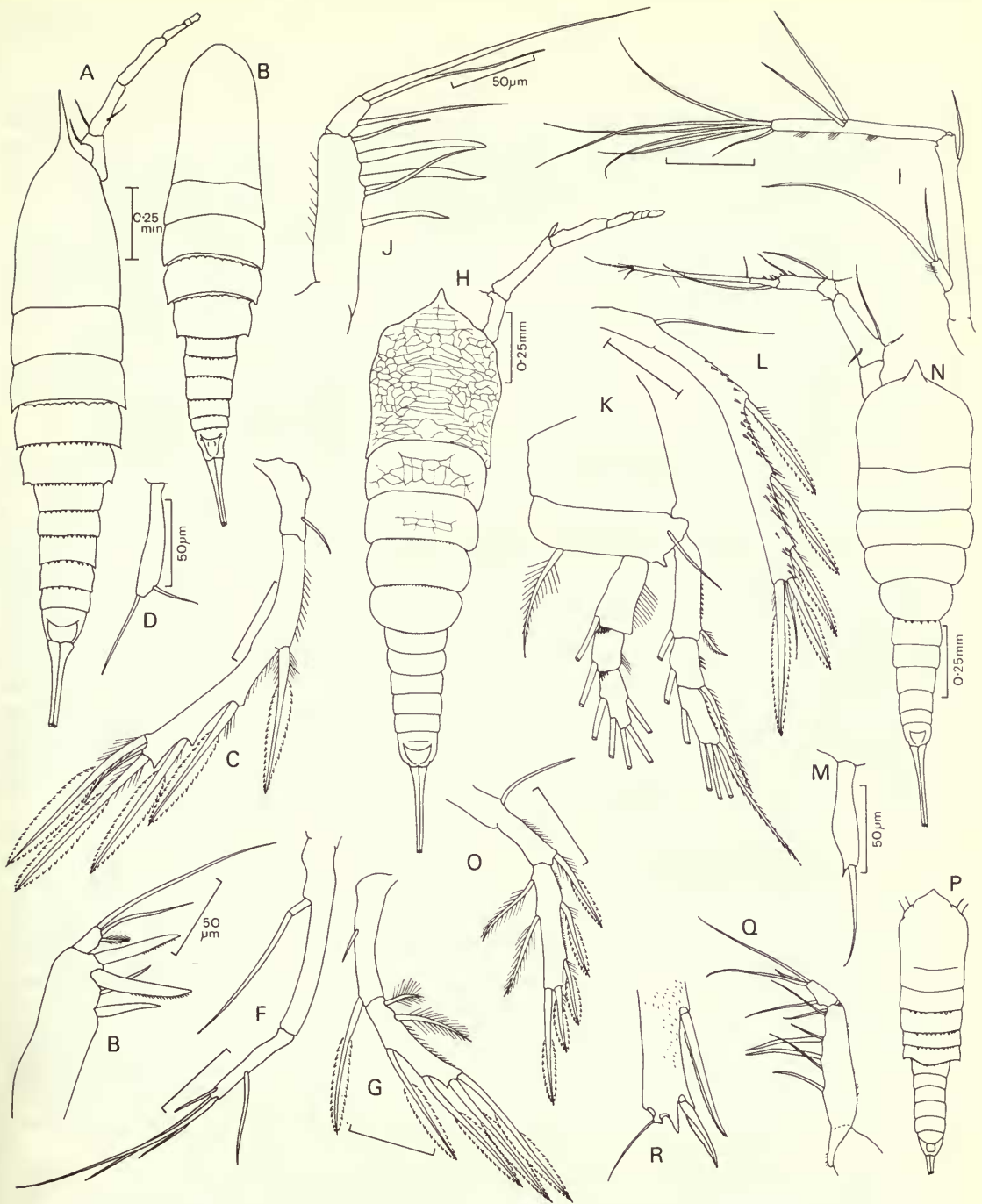


Fig. 1 *Aegisthus mucronatus*: A, female; B, maxilliped; C, fifth leg; D, sixth leg; E, male; F, second antenna; G, fifth leg. *A. aculeatus*: H, female; I, second antenna; J, maxilliped; K, first leg; L, fifth leg; M, sixth leg; N, male; O, fifth leg. *A. spinulosus*: P, female; Q, maxilliped; R, tip of fifth leg. (P-R redrawn from Farran, 1905). Scales 0.1 mm unless otherwise indicated.

dorsally and laterally by suture line. First antenna 7-segmented with small prominence medially on proximal segment. Second antenna (Fig. 1I) with 2 distal setae on exopod. Maxilliped (Fig. 1J) 3-segmented, bearing 3 enlarged spines and 2 slender setae on middle segment and 3 setae on distal segment. Leg 1 (Fig. 1K) with 3-segmented rami, exopod segments 2 and 3 with long spines on outer margin. Leg 5 (Fig. 1L) free segment with 3 serrate setae on outer margin and a short naked seta and 2 serrate setae on the distal margin; distal serrate seta on lateral margin 83% as long as middle serrate seta on lateral margin; inner apical seta 35–40% longer than outer. Leg 6 (Fig. 1M) an elongate free segment with a single long seta and a minute spinule apically.

Body length of female from 1.64 to 1.85 mm.

Male. As for ♀ except: prosome more squat in appearance (Fig. 1N); second free thoracic somite as wide as cephalothorax. First antenna 7-segmented. First maxilla bilobed, rudimentary. Second maxilla with well-developed basipod, claw-like process on basipod less curved than in ♂ *A. mucronatus*, rami rudimentary bearing 1 small and 5 long setae. Maxilliped 3-segmented, slender, with 2 setules on middle segment and 3 setae on distal segment. Leg 5 (Fig. 10) with armature elements as in ♂ *A. mucronatus* but inner distal margin seta about 35–40% longer than outer. Leg 6 with 2 long setae.

Body length of male from 1.28 to 1.35 mm.

MATERIAL EXAMINED. 154 ♀♀, 7 ♂♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.175–184 (♀) and 1977.185–191 (♂).

REMARKS. The male of *A. aculeatus* has only recently been discovered and partially described (Owre and Foyo, 1967). The mouthparts in male *Aegisthus* are reduced and are often difficult to observe. No structure was found in either *A. aculeatus* or *A. mucronatus* which could be positively identified as representing the mandible. The first maxilla was represented by a bilobed structure in males of both species; the larger lobe bearing 5 or 6 setae and the smaller 1 or 2. The second maxilla has a well-developed basipod and distal claw but the rami are reduced. The maxilliped is 3-segmented in both species. In *A. aculeatus* males the middle segment bears 2 setules and the distal segment 2 naked medial setae and a plumose apical seta. Reduction of this appendage has proceeded further in male *A. mucronatus* with the armature comprising only 2 small setae on the distal segment. The second maxillae and maxillipeds are better developed and closer to the female condition in *A. aculeatus* males than in *A. mucronatus* males.

Aegisthus spinulosus Farran, 1905

DIAGNOSIS. *Female.* Cephalothorax and free thoracic somites without chitinous reticulations (Fig. 1P); maximum width of body anterior to mid-point of cephalothorax. Rostrum short. Genital complex completely subdivided by suture line. First antenna 7-segmented. Second antenna and both maxillae as in *A. aculeatus*. Maxilliped (Fig. 1Q) 3-segmented, armed with 3 enlarged spines and 4 setae on middle segment and 4 setae on distal segment. Leg 1 with 3-segmented rami; exopod segments 2 and 3 with long spines on outer margins. Leg 5 (Fig. 1R) as in *A. aculeatus* except distal serrate seta on lateral margin only 57% as long as middle serrate seta on lateral margin. Leg 6 with 2 equal terminal setae.

Body length of holotype ♀ 1.74 mm.

MATERIAL EXAMINED. None.

REMARKS. In the original description of *A. spinulosus* Farran (1905) commented on its close affinity to *A. aculeatus*, but listed certain important characters which serve to distinguish between them. The significant differences are the absence of chitinous reticulations from the cephalothorax, the complete subdivision of the genital complex, the armature of the maxilliped (called the first maxillipede by Farran) and the sixth leg. If Farran's (1905) description is accurate *A. spinulosus* should be regarded as a valid species and not, as suggested by Lang (1948), as a possible last copepodid stage of *A. aculeatus*.

Family ECTINOSOMATIDAE

Genus *MICROSETELLA* Brady and Robertson, 1873

DIAGNOSIS. Body fusiform, without marked boundary between prosome and urosome; prosome 4-segmented with first thoracic somite fused to head, urosome 5-segmented. Rostrum very short, ventrally directed. Caudal rami short, each with a long apical seta. First antenna 6-segmented (Fig. 2C), with an aesthete on segment 3 or 4 and one on segment 6. Second antenna (Fig. 2D) with unarmed basis; exopod 3-segmented with single short seta on segment 1 and 2 long terminal setae. Mandible (Fig. 2E) blade with few weak teeth; palp well developed, exopod small with few setae, endopod large bearing several setae and a large unilaterally pinnate process (seta ?) with an apical seta. First and second maxillae (Figs 2F, G) small. Maxilliped (Fig. 2H) 3-segmented, robust. Legs 1-4 with 3-segmented rami, armature formula:

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

Leg 5 with baseoendopod and 1-segmented exopod; exopod bearing 1 ventral surface seta and either 3 (♀) or 2 (♂) marginal setae.

TYPE SPECIES. *Microsetella norvegica* (Boeck, 1864) (as *M. atlantica* Brady and Robertson, 1873).

Microsetella norvegica (Boeck, 1864)

Setella norvegica Boeck, 1864: 281.

Microsetella atlantica Brady and Robertson, 1873: 130, pl. IX, figs 11-16.

Ectinosoma atlanticum Brady, 1880: 13, pl. 38, figs 11-19.

DIAGNOSIS. Longest seta (inner seta on distal margin) of caudal ramus usually about as long as body, sometimes up to 1.5 times longer than body (Figs 2A, B); the second longest seta (outer seta on distal margin) about 33% as long as the longest caudal seta and between 0.3 and 0.5 times as long as body. Inner seta on baseoendopod of leg 5 (♀) less than half as long as outer seta (Fig. 2I). Lateral seta on distal margin of leg 5 exopod (♂) apparently naked (Fig. 2J).

Body length of female 0.35-0.57 mm; body length of male 0.33-0.42 mm.

MATERIAL EXAMINED. 2 ♀♀: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.192-193. 1 ♀: as *Ectinosoma atlanticum*, Faroe Channel. BM(NH) registration numbers 1901.9.27.101-2. 1 ♀, 1 ♂: Suez Canal Expedition (Gurney, 1927). BM(NH) registration number 1928.4.2.137. 5 ♀♀: as *E. atlanticum*, Loch Fyne. BM(NH) registration numbers 1956.9.25.45. 12 ♀♀: North Sea off Whitby. BM(NH) registration numbers 1976.653-662.

REMARKS. This small species is usually distinguished from the only other species of the genus, *M. rosea* (Dana, 1848), by the relative length of the body and the longest seta on the caudal ramus. This seta is often shorter than or about as long as the whole body (Lang, 1948; Owre & Foyo, 1967; Wells, 1970). However, in the material examined during the present study the length of the longest caudal seta was found to vary from 20% less than body length to 44% more than body length (Table 1). More reliable characters which could be used to separate the species are body size, the armature of the baseoendopod in the female leg 5 and the relative length of the second longest (outer seta on distal margin) caudal seta. This outer caudal seta is about one third (33%) as long as the inner caudal seta in *M. norvegica*.

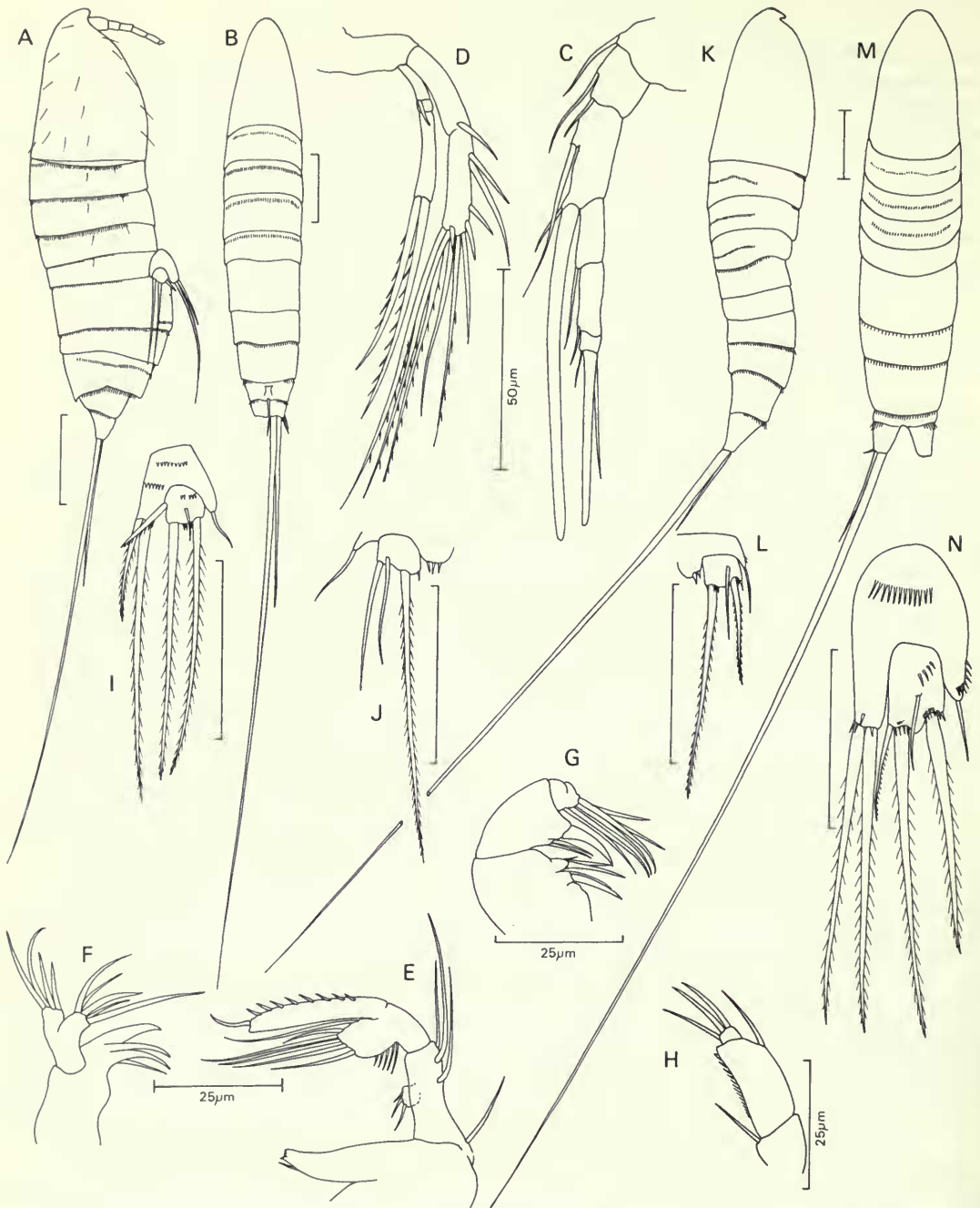


Fig. 2 *Microsetella norvegica*: A, female, lateral; B, female, dorsal; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; I, fifth leg; J, male fifth leg. *M. rosea*: K, male; L, fifth leg; M, female; N, fifth leg. Scales 0.1 mm unless otherwise indicated.

Table 1 Body and caudal seta lengths of examined specimens of *Microsetella*

Locality	Number examined	(A) Body length in mm	(B) Caudal seta length in mm	Ratio A : B
<i>Microsetella norvegica</i>				
'Discovery' Stn 7089	1 ♀	0.57	0.82	1 : 1.44
Faroe channel	1 ♀	0.57	0.59	1 : 1.04
Suez canal	1 ♂	0.33	0.28	1 : 0.85
Loch Fyne	5 ♀	0.52	0.43	1 : 0.83
		0.50	0.43	1 : 0.86
		0.50	0.43	1 : 0.86
		0.41	0.33	1 : 0.80
		0.50	0.44	1 : 0.88
Off Whitby	12 ♀	0.44	0.43	1 : 0.98
		0.43	0.41	1 : 0.95
		0.44	0.44	1 : 1
		0.41	0.39	1 : 0.95
		0.46	0.39	1 : 0.85
		0.43	0.43	1 : 1
		0.43	0.41	1 : 0.95
		0.46	0.44	1 : 0.96
		0.43	0.46	1 : 1.07
		0.43	0.41	1 : 0.95
		0.41	0.43	1 : 1.05
		0.41	0.41	1 : 1
<i>Microsetella rosea</i>				
Gulf of Guinea	2 ♀	0.67	1.17	1 : 1.75
		0.69	1.26	1 : 1.83
Hyeres	1 ♀	0.65	1.22	1 : 1.88
Off Co. Mayo	1 ♂	0.63	0.96	1 : 1.52

Microsetella rosea (Dana, 1848)*Harpacticus rosea* Dana, 1848: 153.*Microsetella rosea* Giesbrecht, 1891: 476.

DIAGNOSIS. Longest seta (inner seta on distal margin) of caudal ramus from 1.5 to 2 times as long as body (Figs 2K, M); second longest seta (outer seta on distal margin) about 10–15% as long as longest caudal seta and between 0.20 and 0.25 times as long as the body. Inner seta on baseoendopod of leg 5 (♀) about the same length as outer seta (Fig. 2N). Lateral seta on distal margin of leg 5 exopod (♂) bilaterally spinulate (Fig. 2L). Body length of female 0.64–0.85 mm; body length of male 0.6–0.7 mm.

MATERIAL EXAMINED. 2 ♀♀: as *M. atlanticum*. Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.219–223. 1 ♀: as *M. atlanticum*. Hyeres. BM(NH) registration number 1951.11.24.35. 1 ♂: off Co. Mayo (Farran, 1908). BM(NH) registration number 1911.11.8.42881.

REMARKS. Both sexes of *M. rosea* are much larger than in *M. norvegica*. Other characters which can be used to separate the species are the relative lengths of the two main caudal setae, the ratio of caudal seta length to body length (see Table 1) and the armature of the baseoendopod of the (♀) leg 5.

Family TISBIDAE

Genus *BATHYIDIA* Farran, 1926

DIAGNOSIS. Body not laterally compressed (Fig. 4A). Prosome 4-segmented, urosome 5-segmented in ♀, 6-segmented in ♂. Dorsal surface of prosome and whole surface of urosome more or less

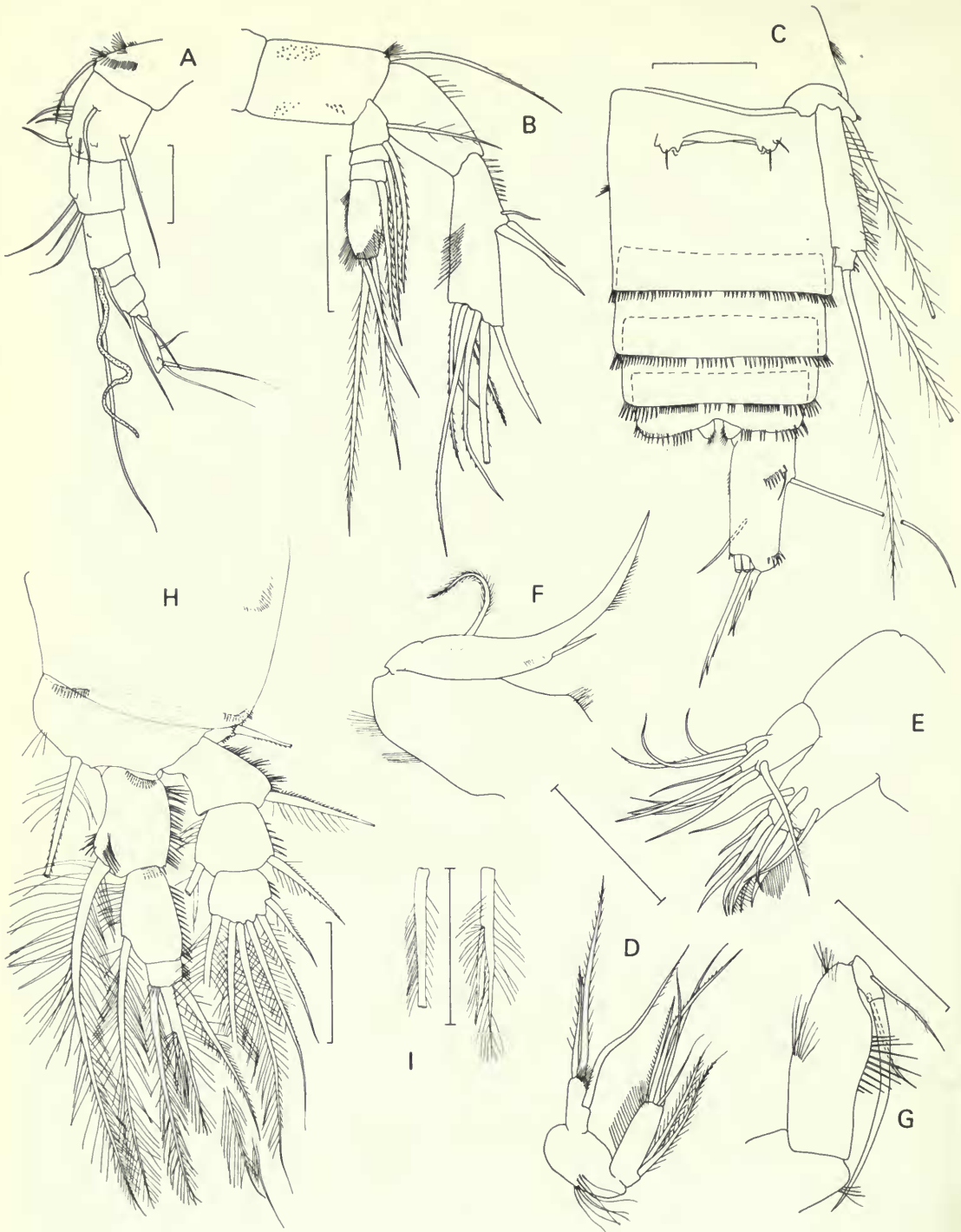


Fig. 3 *Bathyidia remota*, holotype female: A, first antenna; B, second antenna; C, urosome; D, mandible 'pulp'; E, first maxilla; F, second maxilla; G, maxilliped; H, first leg; I, middle setae of third endopod segments from both first legs. Scales 0.1 mm.

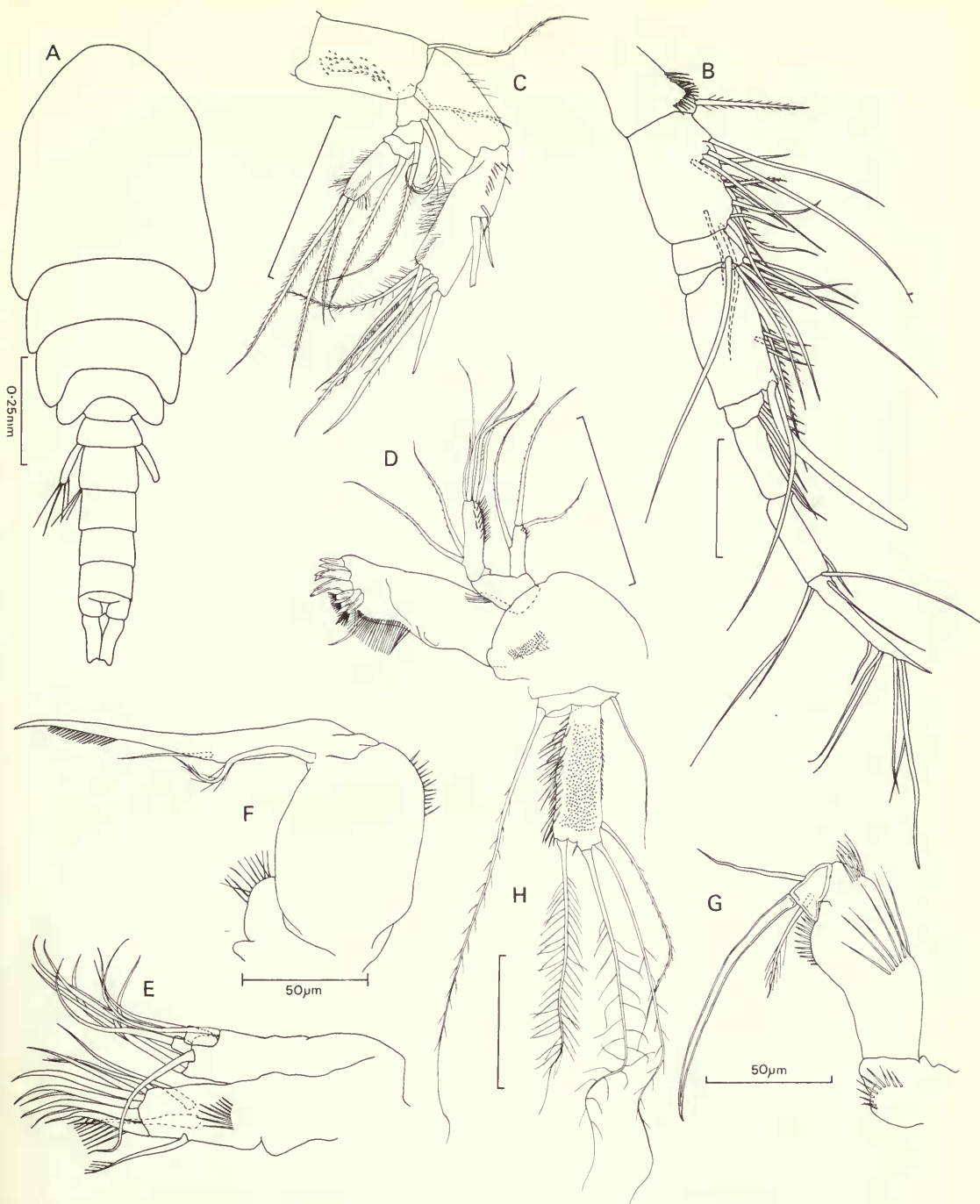


Fig. 4 *Bathyidia remota* male: A, dorsal; B, first antenna; C, second antenna; D, mandible; E, first maxilla; F, second maxilla; G, maxilliped; H, fifth leg. Scales 0.1 mm unless otherwise indicated.

covered with minute denticles. Genital complex (♀) subdivided by a dorsal and dorso-lateral suture line. Genital area probably with 3 short setae either side of oviduct openings (only 2 setae remaining in holotype ♀). Caudal rami more than twice as long as wide; with 2 lateral, 1 dorsal and 4 distal setae plus 2 additional elements on the distal margin.

First antenna 8-segmented (♀) with aesthete on segment 4; 9-segmented (♂) with aesthete on segment 5, geniculate between segments 7 and 8. Second antenna (Figs 3B, 4C) with 1 seta on basis; 2-segmented endopod, distal segment with 3 lateral and 7 terminal elements; 4-segmented exopod with segment 1 bearing 2 setae, segments 2 and 3 bearing 1 seta each and the distal segment with 3 setae. Mandible (Figs 3D, 4D) with unarmed basis and 1-segmented rami; endopod with 2 proximal setae on medial margin and 5 apical setae; exopod with 1 medial and 2 apical setae. First maxilla (Figs 3E, 4E) inner lobe (arthrite) armed with 11 elements, outer lobe including rudimentary rami bearing 10 elements. Second maxilla (Figs 3F, 4F) with 1 seta on basal segment, claw elongate bearing a spiniform seta and a distal row of pinnules. Maxilliped (Figs 3G, 4G) comprising 3-segments and a terminal claw; middle segment with 3 rows of setules, distal segment with 2 setae; displaying dimorphism with the distal segment bearing a strong chitinous process in ♂.

Legs 1-4 with 3-segmented rami; armature formula as follows:

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

Leg 1 endopod 20-25% longer than exopod; basis with spinulate lobe between bases of rami; inner spine on basis setiform; spines on outer margins of exopod segments 1 and 2 also setiform. Leg 2 displaying sexual dimorphism in structure of inner seta on (♂) endopod segment 1. Legs 1-4 with minute denticles on surface, especially on lateral surface of coxa and on both anterior and posterior surfaces of rami; also spinule rows present on posterior surfaces of endopod segments 2 and 3.

Leg 5 with small baseoendopod and elongate free segment; baseoendopod with outer plumose seta and single inner seta; armature of free segment consisting of 1 distal seta on inner and outer margins and 2 setae and a tiny setule around apex.

Leg 6 represented by 3 naked setae in ♂.

TYPE-SPECIES. *Bathyidia remota* Farran, 1926.

REMARKS. The genus *Bathyidia* was established by Farran (1926) to include a new bathypelagic species from the Bay of Biscay, *B. remota*. Farran's (1926) description of *B. remota* was incomplete. The generic diagnosis given here is based on re-examination of the holotype of *B. remota* and on the examination of two male specimens. *Bathyidia* is related to both *Tisbe* Lilljeborg, 1853 and *Paraidya* Sewell, 1940, as well as to the two new genera described below *Neotisbella* gen. nov. and *Volkmannia* gen. nov. The principal distinguishing characters of these five genera and the genera *Tisbella* Gurney 1927 and *Tisbintra* Sewell, 1940 are presented in Table 2. *Bathyidia* can readily be distinguished from *Paraidya* by the segmentation of the first antenna, and from *Neotisbella* and *Tisbella* by the segmentation of the endopod of leg 1. The differences between *Bathyidia*, *Tisbe* and *Volkmannia* are the armature of the mandibular palp, the relative size of the endopod segments of leg 1, the armature elements of both rami of leg 1, plus the structure and armature of the caudal rami.

Bathyidia remota Farran, 1926

Bathyidia remota Farran, 1926: 299-300, pl. 10, figs 13-17.

Tisbe remota Lang, 1948: 383, pl. 168, fig. 6.

DIAGNOSIS. Prosome of ♀ incompletely known, ♂ cephalothorax slightly indented laterally (Fig. 4A). Genital complex (♀) and urosome somites 3, 4, 5 and 6 (in ♂) provided with ventral and ventro-

lateral rows of spinules along posterior borders (Figs 3C and 5G). Genital area (♀) (Fig. 3C) with 2 short naked setae either side of oviduct openings, a third seta was probably present but is missing from the holotype ♀. Caudal ramus (Figs 3C and 5G) 2.2–2.6 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being 6.6–6.9 times longer than the ventro-lateral one), an oblique spinule row on the ventral surface extending distally from bases of the lateral setae, another spinule row proximal to the outer distal angle, a naked seta on the dorsal surface, a seta at the outer distal angle and one at the inner distal angle, 2 long setae on the inner portion of the distal margin and 2 elements towards the outer end of the distal margin. The latter 2 elements are flaccid and subdivided giving a forked appearance.

Relative lengths of ♀ first antenna (Fig. 3A) segments 15 : 19 : 15 : 14 : 7 : 9 : 5 : 16. Armature elements incomplete, first segment with 2 spinule rows. First antenna of ♂ (Fig. 4B) with segmental armature elements as follows: I–1, II–14, III–7, IV–2, V–6+1 aesthete, VI–3, VII–2, VIII–2, IX–9. First segment also bearing spinule row. Other cephalic appendages as in generic diagnosis.

Inner spine on basis of leg 1 (Figs 3H, 5A) with small distal pinnules and a few larger ones proximally; exopod segment 3 bearing 6 setiform elements, those on outer margin armed with shorter pinnules than those on distal margin; relative lengths of endopod segments about 46 : 40 : 14; outer element on endopod segment 3 setiform but armed with short pinnules, middle element a simple long plumose seta (holotype ♀ exhibits aberrant bifurcated condition on only one member of leg 1 pair (Figs 3H, I)), inner element a plumose seta similar in length to middle element.

Legs 2–4 (Figs 5B–F); exopod segment 3 with central patch of larger denticles on posterior surface (Fig. 5E); endopod segments 2 and 3 with some denticles and about 5 and 16 spinules respectively on their posterior surfaces (Fig. 5F). Leg 2 displaying sexual dimorphism with inner seta on endopod segment 1 armed with distal row of spinules (Fig. 5B).

Leg 5 of ♀ (Fig. 3C) with incomplete armature in holotype but traces of absent setae indicate armature similar to ♂. Leg 5 of ♂ (Fig. 4H) with single inner seta on baseoendopod about as long as free segment: free segment about 2.9 times longer than wide, its ventral surface covered with minute denticles and lateral surface with long spinules; bearing a plumose seta at distal end of expanded lateral margin; projecting distal margin with a tiny setule laterally and 2 long sparsely plumose setae apically; inner margin with single pinnate seta distally.

Leg 6 of ♂ (Fig. 5G) comprising 3 long naked setae situated laterally on genital lobes of urosome somite 2.

Body length of holotype ♀ 1.48 mm and ♂ 1.41 mm.

MATERIAL EXAMINED. Holotype ♀: Bay of Biscay (Farran, 1926). BM(NH) registration number 1926.12.6.41. 1 ♂: Sargasso Sea, Stn S (Deevey and Brooks, 1977). Florida State Museum collections. 1 ♂: N.E. Atlantic Ocean 18° N 25° W 'Discovery' Stn 7089. BM(NH) registration number 1977.225.

REMARKS. The males here assigned to *B. remota* agree closely with the holotype ♀ in the characteristic structure and armature of the leg 1. The bifurcate nature of the middle seta on endopod segment 3 in the holotype is regarded as aberrant because the middle seta on the other member of the leg 1 pair, although broken, displays no trace of a bifurcation at the same position on the seta (see Fig. 3I). The mouthparts are generally very similar in the males and the female. The male maxilliped differs from the female in the structure of the third segment, but the male maxillipeds of *Neotisbella gigas* gen. et sp. nov. and *Volkmannia forficula* gen. et sp. nov. also exhibit this character whereas their respective females do not.

The 2 male specimens are almost identical to the female in the detailed armature of their caudal rami; in the position of the spinule rows and especially in the relative lengths of the two lateral setae. These and other similarities strongly suggest that the two males are conspecific with the holotype ♀ of *B. remota*.

Genus *VOLKMANNIA* gen. nov.

DIAGNOSIS. Prosome 4-segmented, urosome 5-segmented in ♀ and 6-segmented in ♂. Dorsal

Table 2 A comparison between the seven genera of the *Tisbe* group

Character	<i>Paraidya</i>	<i>Tisbella</i> *	<i>Tisbintra</i> †
General facies	Laterally compressed, elongate	As for <i>Tisbe</i>	As for <i>Tisbe</i>
First antenna ♀: ♂	7: 8	7/8: 8	8: 9
Second antenna	1 seta on basis; Exp 3- or 4-segmented, with 1, 0, 3 or 1, 1, 2, 3 elements	1 seta on basis; Exp 4-segmented with 1, 1, 3 elements; segs 2 & 3 fused to seg. 4 in <i>T. pulchella</i>	1 seta on basis; Exp 2-segmented (segs 2, 3 & 4 fused) with 1, 2 proximal & 3 distal elements
Mandible	Basis unarmed, Enp with 3 medial & 6 distal setae, Exp with 2 setae	Basis unarmed, Enp with 3 medial & 7 distal setae, Exp with 2 setae	Basis with 1 small seta, Enp with 3 disto-medial & 5 or 6 distal setae, Exp with 2 setae
Maxilliped	Not exhibiting marked sexual dimorphism	Not exhibiting marked sexual dimorphism	Not exhibiting marked sexual dimorphism
Leg 1	3-segmented Enp less than 10% longer than Exp; Enp seg. 3 with 1 outer spine & 2 inner setae. Exp elements without combs of setules	2-segmented Enp; Enp seg. 2 with 1 outer spine, 2 distal setae & 1 inner seta. Exp elements without combs of setules	2-segmented Enp, about 60% longer than Exp; Enp seg. 2 with 1 inner seta & 1 or 2 distal elements. Exp elements without combs of setules
Leg 5	Free segment with 3 or 4 setae	Free segment with 5 plumose setae	Free segment with 4 or 5 setae
Caudal ramus	Less than 2.5 times longer than wide; with 6 elements including 1 lateral seta in distal half of ramus	As wide as long or just longer than wide; with 7 elements including 1 lateral seta in distal half of ramus	Shorter than wide; with 6 elements including 1 lateral seta in distal half of ramus

* Data from Yeatman (1963) and from re-examination of holotype ♀ of *Tisbella timsae* Gurney, 1927 from Imasilik Suez canal: BM(NH) registration number 1928.4.2.51.

† Data from Sewell (1940) and from examination of 2 ♀♀ & 2 ♂♂ specimens of *Tisbintra jonesi* Ummerkutty, 196 from Kuwait: BM(NH) registration numbers 1975.1201-1210.

surface of prosome and whole surface of urosome more or less covered with minute denticles. Rostrum small. Genital complex (♀) markedly subdivided by dorsal and dorso-lateral suture line, suture line absent ventrally; genital area with 1 short outer seta and 2 long naked setae either side of oviduct openings. Caudal rami about twice as long as wide, with 2 lateral, 1 dorsal and 4 distal setae plus 2 additional elements on the distal margin.

First antenna 8-segmented (♀) with aesthete on segment 4; 9-segmented (♂) with aesthete on segment 5, geniculate between segments 7 and 8. Second antenna with 1 seta on basis; 2-seg-

<i>Tisbe</i>	<i>Volkmania</i>	<i>Neotisbella</i>	<i>Bathytidia</i>
Not usually elongate, dorso-ventrally flattened	As for <i>Tisbe</i>	Prosome vaulted	As for <i>Tisbe</i>
8:9	8:9	8:9	8:9
1 seta on basis; Exp 4-segmented with 1 or 2, 1, 1, 3 elements respectively	1 seta on basis, Exp 4-segmented with 2, 1, 1, 3 elements	Basis unarmed; Exp 4-segmented with 1, 0, 1, 3 elements	1 seta on basis; Exp 4-segmented with 2, 1, 1, 3 elements
Basis with 1 or more setae; Enp with 3 medial & 5 or 6 distal setae, Exp with 3 setae	Basis unarmed; Enp with 3 medial & 6 distal setae, Exp with 3 setae	Basis unarmed; Enp with 1 medial & 4 distal setae, Exp with 3 setae	Basis unarmed; Enp with 2 medial & 5 distal setae, Exp with 3 setae
Not usually exhibiting marked sexual dimorphism	Marked sexual dimorphism in segment 3	Marked sexual dimorphism in segment 3	Marked sexual dimorphism in segment 3
3-segmented Enp, usually distinctly longer than Exp; Enp seg. 3 with 2 or 3 elements 1 of which armed with comb of setules; similar combs on outer elements of Exp segs 2 & 3	3-segmented Enp 25-30% longer than Exp; Enp seg. 3 with 1 outer spine & 2 inner setae; Exp elements without combs of setules	2-segmented Enp about 10% longer than Exp; Enp seg. 2 with 1 outer spine, 2 distal setae & 1 inner seta; Exp elements without combs of setules	3-segmented Enp 20-25% longer than Exp; Enp seg. 3 with 2 setiform elements; Exp elements without combs of setules
Free segment with 4 or 5 setae	Free segment with 4 plumose setae & 1 short naked seta	Free segment with 4 plumose setae & 1 short naked seta	Free segment with 4 plumose setae & a tiny spinule representing fifth seta
Usually wider than long, sometimes longer than wide, rarely more than twice as long; with 7 elements including 1 seta in distal half of ramus	2.0 or more times longer than wide; with 9 elements including 2 lateral setae in proximal half of ramus	Nearly twice as long as wide; with 9 elements including 2 lateral setae in proximal half of ramus	More than twice as long as wide; with 9 elements including 2 lateral setae in proximal half of ramus

mented endopod with distal segment bearing 3 lateral and 7 terminal elements; 4-segmented exopod with 2 setae on segment 1, 1 seta each on segments 2 and 3 and 3 setae on the distal segment. Mandible with unarmed basis and 1-segmented rami; endopod with 3 proximal setae on medial margin and 6 apical setae; exopod with 1 medial margin and 2 apical setae. First maxilla inner lobe armed with 9 elements, outer lobe with 11 elements. Second maxilla with 1 seta on basal segment, claw elongate with 1 plumose seta, a proximal curved row of tiny spinules and a distal row of pinnules. Maxilliped 3-segmented and with a terminal claw; middle segment with



Fig. 5 *Bathyidia remota* male: A, first leg, anterior; B, second leg; C, third leg; D, fourth leg; E, third exopod segment of fourth leg, posterior; F, second and third endopod segments of fourth leg, posterior; G, urosome. Scales 0.1 mm.

setule rows, distal segment with 2 setae; displaying sexual dimorphism with distal segment bearing strong chitinous process in ♂.

Legs 1-4 with 3-segmented rami; armature formula as follows:

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

Leg 1 endopod about 25–30% longer than exopod; inner spine on basis stout and spinulate; spine on outer margin of exopod segment 1 strongly developed, that on segment 2 setiform; endopod segment 3 very small bearing an outer spine, a distal seta and a small inner seta. Leg 2 displaying sexual dimorphism in armature of inner seta of endopod segment 1. Legs 1–4 with very minute denticles on surfaces of coxa, basis and rami; also spinule rows present on posterior surfaces of endopod segments 2 and 3 of legs 2–4.

Leg 5 with small baseopod and elongate free segment, ventral surface of latter covered with minute denticles; baseopod with outer plumose seta and 3 inner setae in ♀ or 1 in ♂; free segment expanded laterally with short spinules along outer margin; armature comprising 1 lateral seta positioned at apex of lateral expansion, 1 distal seta on inner margin and 2 plumose setae and a small naked seta around apex.

Leg 6 represented by 3 long plumose setae in ♂.

TYPE-SPECIES. *Volkmania forficula* sp. nov.

ETYMOLOGY. This genus is named after Dr Brigitte Volkmann in recognition of her work on the genus *Tisbe*.

REMARKS. The new genus can be distinguished from *Paraidya*, *Bathyidia*, *Tisbella*, *Neotisbella* gen. nov. and *Tisbintra* by the segmentation of the leg 1 and the armature of the mandibular palp. Although there is a close superficial resemblance between *Volkmania* and *Tisbe* there are significant differences in the mandible, leg 1 and caudal rami. The mandible of *Tisbe* possesses at least one seta on the basis whereas the mandible of *Volkmania* has an unarmed basis. The distal segment of the leg 1 endopod in *Tisbe* usually possesses only 2 (occasionally 3) armature elements at least one of which is armed with a distal comb of long setules; similar combs are also found on the outer margin elements of exopod segments 2 and 3 in *Tisbe* species. The distal segment of leg 1 endopod possesses 3 armed elements in *Volkmania* species, and none of the elements on either ramus is armed with a distal comb of setules. The caudal ramus of *Volkmania* closely resembles that found in *Bathyidia* and *Neotisbella*, but differs greatly in both structure and armature from that found in *Tisbe*.

Volkmania forficula sp. nov.

DIAGNOSIS. Prosome rounded, maximum body width about mid-point of prosome (Figs 6A, 8D). Genital complex (♀) and urosome somites 3, 4, 5 and 6 (in ♂) provided with ventral and lateral rows of spinules along posterior borders. Genital area (♀) (Fig. 6F) with a short outer plumose seta and 2 subequal long inner naked setae. Caudal ramus (Fig. 6D) about 2.6 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being about 1.9 times longer than the ventro-lateral one), an oblique spinule row extending from near base of lateral seta, another spinule row around outer distal angle, a naked seta on dorsal surface, a seta at the outer distal angle and 1 at the inner distal angle, 2 long plumose setae on the inner portion of the distal margin and 2 elements in the middle of the distal margin. The latter 2 elements are thin walled and flaccid.

Relative lengths of ♀ first antenna segments 14 : 18 : 20 : 16 : 5 : 8 : 3 : 16 (Fig. 7A); armature elements as follows; segment I–1, II–14, III–7, IV–4+1 aesthete, V–0, VI–4, VII–1, VIII–5; segment I also bearing 2 rows of spinules. First antenna (♂) armature as follows; segment I–1, II–11, III–4, IV–2, V–6+1, aesthete VI–2, VII–2, VIII–2, IX–11 (Fig. 8E); segment I also bearing 2 spinule rows.

Other cephalic appendages as in generic diagnosis (p. 213).

Maxilliped terminal claw with single spinule on concave margin in both sexes (Figs 6E, 8F).

Leg 1 provided with extremely minute denticles on its surface (as in *Bathyidia* and *Neotisbella* but too small to be accurately figured); inner spine on basis strongly developed, much shorter than endopod segment 1 and armed with long pinnules proximally and short pinnules distally (Fig. 7D). Outer margin of exopod segment 1 with well-developed spine, slightly swollen proximally; outer margins of exopod segments 2 and 3 bearing setiform elements armed with short

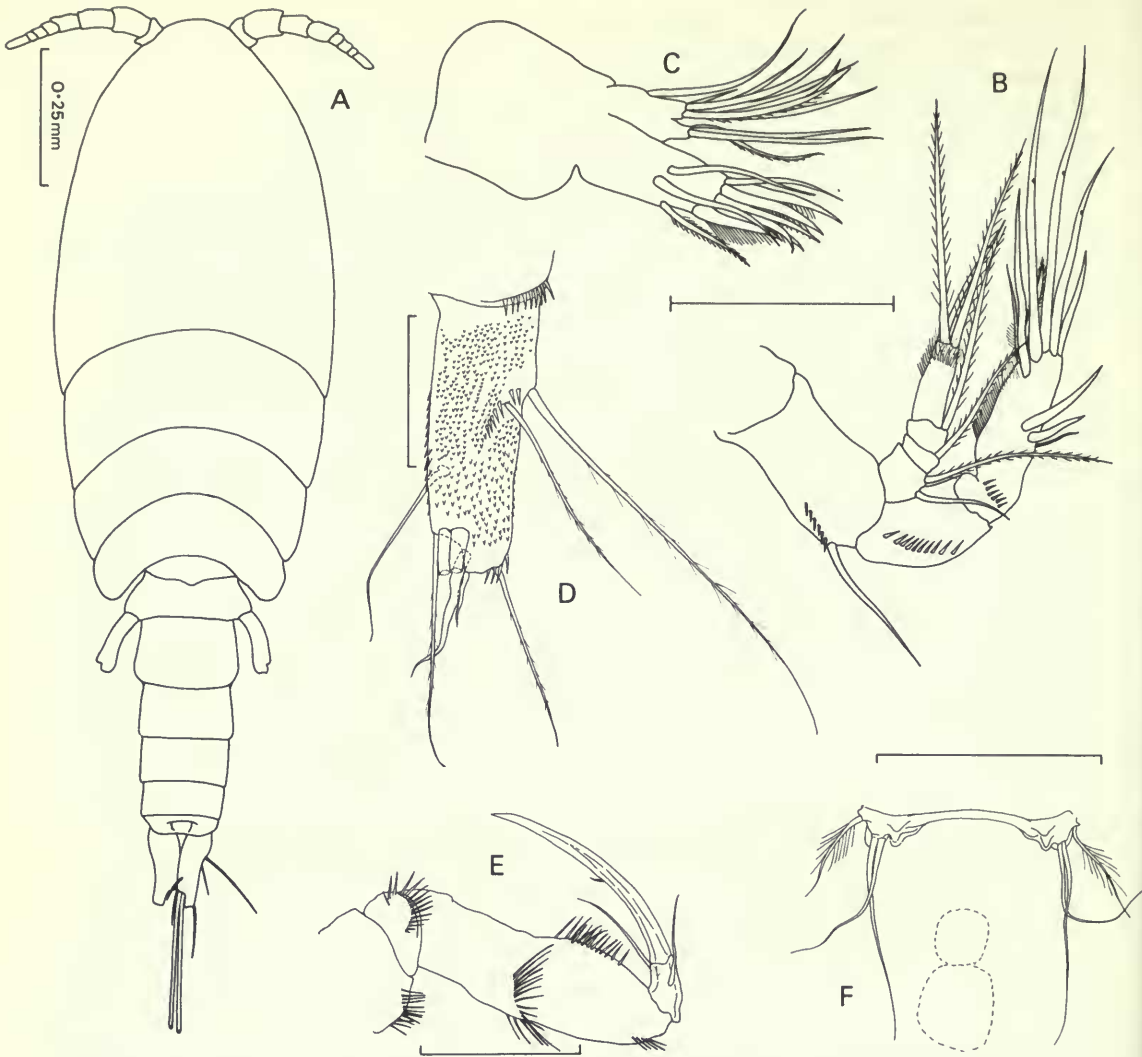


Fig. 6 *Volkmannia forficula* n. sp.: A, female; B, second antenna; C, first maxilla; D, caudal ramus; E, maxilliped; F, genital area. Scales 0.1 mm unless otherwise indicated.

pinnules. Endopod about 34% longer than exopod, relative lengths of endopod segments 56 : 39 : 5; outer element on endopod segment 3 setiform and sparsely provided with short spinules; middle element forked at tip in both sexes (Fig. 7E) and very sparsely pinnate, inner element a short and very slender naked seta.

Legs 2-4 (Figs 8A-C, G) provided with extremely minute denticles on their surfaces as in leg 1; exopod segment 3 with central patch of larger denticles on posterior surface; endopod segments 2 and 3 with some very minute denticles and about 5 and 12-16 spinules respectively on their posterior surfaces (Figs 8A, B). Leg 2 displaying sexual dimorphism, with inner seta on endopod segment 1 armed with an additional row of spinules distally in ♂ (Fig. 8G).

Leg 5 ♀ (Fig. 7F) with endopod represented by 3 setae on baseopod, a medium length inner seta with small pinnules, a long middle seta with small pinnules and a small outer naked seta; free segment expanded laterally, about 2.5 times longer than wide; ventral surface covered with irregularly arranged denticles of varying size and bearing a row of short spinules laterally; armature elements comprising 1 medium length plumose seta at the distal angle of the lateral



Fig. 7 *Volkmannia forcifcula* n. sp.: A, female first antenna; B, mandible; C, second maxilla; D, first leg; E, tip of apical seta of third endopod segment of first leg; F, fifth leg. Scales 0.1 mm unless otherwise indicated.

expansion, 1 minutely pinnate long seta at the inner distal angle, 2 long distal setae, the inner minutely pinnate and the outer plumose, and a short naked seta positioned between them and the lateral seta. Leg 5 (♂) as for female except only a single short and minutely pinnate seta present on baseopod (Fig. 8H); free segment about 2.3 times longer than greatest width, armature elements similar except the lateral plumose seta is relatively longer than in female.

Leg 6 (♂) comprising 1 medium length sparsely pinnate inner seta and 2 similar but longer outer setae positioned laterally on genital lobes of urosome somite 2 (Fig. 8I).

Body length of ♀♀ from 1.22 to 1.63 mm and ♂♂ from 1.04 to 1.18 mm.

MATERIAL EXAMINED. Holotype ♀, 2 ♂♂ and 6 ♀♀ paratypes: N.E. Atlantic Ocean 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.233 (holotype), 1977.234-5 (♂♂) and 1977.236-241 (♀♀).

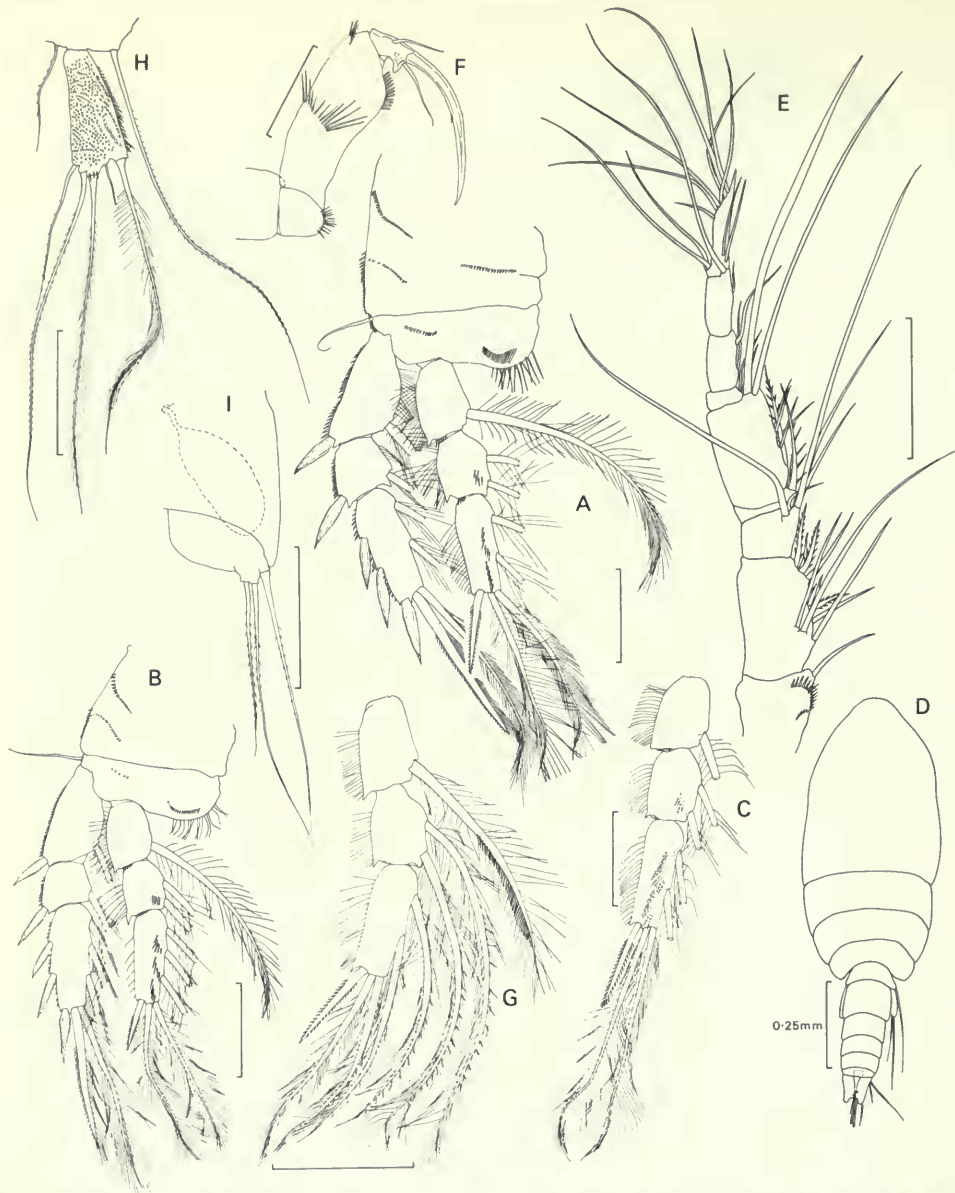


Fig. 8 *Volkmannia forficula* n. sp.: A, female second leg, posterior; B, third leg; C, endopod of fourth leg, anterior; D, male; E, first antenna; F, maxilliped; G, endopod of second leg, anterior; H, fifth leg; I, sixth leg. Scales 0.1 mm unless otherwise indicated.

REMARKS. The general similarity between the males and females described above and the presence of very distinctive characters in both sexes, such as the forked middle seta on the apex of leg 1 endopod, indicate that they are conspecific. Sexual dimorphism was noted in the third maxilliped segment, as in *Bathydia* and *Neotisbella*, and in the setation of the baseoendopod of leg 5, as in *Neotisbella*.

Volkmannia attenuata sp. nov.

DIAGNOSIS. Prosome very broad (possibly due to distortion), maximum body width about mid-point of prosome (Fig. 9A). Genital complex and urosome somites 3, 4 and 5 provided with spinule

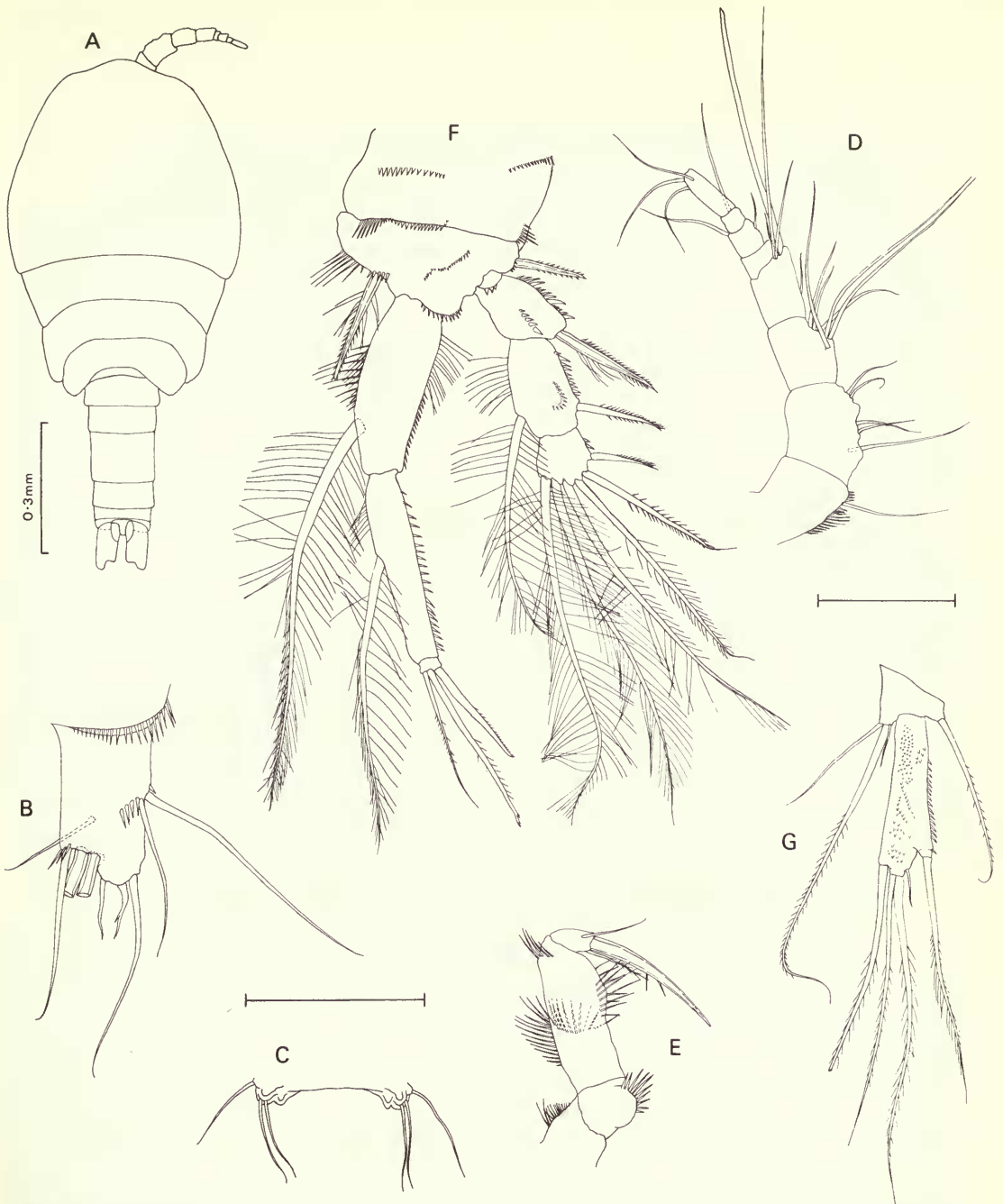


Fig. 9 *Volkmannia attenuata* n. sp., holotype female: A, dorsal; B, caudal ramus; C, genital area; D, first antenna; E, maxilliped; F, first leg; G, fifth leg. Scales 0.1 mm unless otherwise indicated.

rows all around posterior borders except ventrally on somite 3. Genital area (♀) with 3 approximately equal naked setae (Fig. 9C). Caudal ramus (Fig. 9B) about 2 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being about 1.7 times longer than the ventro-lateral one), an oblique spinule row on the ventral surface extending from

near base of ventro-lateral seta, some spinules at inner distal angle, a naked seta on dorsal surface, a seta at outer distal angle and 1 at inner distal angle, 2 long plumose setae on inner portion of distal margin and 2 elements on outer portion of distal margin. The latter 2 elements are thin walled and flaccid.

Relative lengths of ♀ first antenna segments 13 : 18 : 19 : 15 : 7 : 8 : 5 : 15 (Fig. 9D); armature incomplete, elements present as follows: segment I-1, II-5, III-6, IV-4+1 aesthete, V-0, VI-2, VII-1, VIII-3; segment 1 also bearing a row of spinules.

Other cephalic appendages as in generic diagnosis (p. 213).

Maxilliped (Fig. 9E) with 5 rows of setules on middle segment; terminal claw with 2 spinules on concave margin.

Leg 1 provided with extremely small surface denticles (too small to be accurately figured); inner spine on basis strongly developed, shorter than endopod segment 1, armed with long spinules proximally and short pinnules distally (Fig. 9F). Exopod segment 1 with well-developed outer margin spine and a row of 5 broad spinules on anterior surface; outer margins of exopod segments 2 and 3 bearing setiform elements armed with short pinnules. Endopod about 70% longer than exopod, relative lengths of endopod segments 47 : 50 : 3; outer element on endopod segment 3 spiniform and unilaterally provided with short pinnules, middle element subdivided at tip and sparsely pinnate, inner element a slender sparsely pinnate seta.

Legs 2-4 damaged and incomplete but the armature elements appear to be similar to those of *Volkmania forficula*.

Leg 5 (Fig. 9G) with endopod represented by 3 setae on baseoendopod, a small inner seta, a long middle seta with small pinnules, and a very small outer naked seta; free segment not markedly expanded laterally, about 3.2 times longer than greatest width; ventral surface with irregularly arranged denticles of varying sizes and a row of short spinules laterally; armature elements comprising 1 medium length plumose seta at outer distal angle, 1 pinnate seta (broken in holotype) at the inner distal angle, 2 medium length pinnate setae distally and a short naked seta positioned between them and the lateral seta.

Body length of holotype ♀ 1.18 mm. Male unknown.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9131 18. BM(NH) registration number 1977.324.

REMARKS. This species can be distinguished from *V. forficula* by the elongate endopod of leg 1 (from which the specific name is derived) and by the proportions of the leg 5 and caudal rami.

Genus *NEOTISBELLA* gen. nov.

DIAGNOSIS. Prosome 4-segmented, large and vaulted; urosome 5-segmented in ♀ and 6-segmented in ♂. Dorsal surface of prosome and whole surface of urosome more or less covered with minute denticles. Rostrum small. Genital complex (♀) subdivided by dorsal and dorso-lateral suture line; genital area with 1 long plumose outer seta and 2 short naked inner setae either side of oviduct openings. Caudal rami more than twice as long as wide, with 2 lateral, 1 dorsal and 4 distal setae, plus 2 additional elements on the distal margin.

First antenna 8-segmented (♀) with aesthete on segment 4; 9-segmented (♂) with aesthete on segment 5, geniculate between segments 7 and 8. Second antenna with unarmed basis; 2-segmented endopod, distal segment with 3 lateral and 7 terminal elements; 4-segmented exopod, segments 1 and 3 bearing 1 seta each, segment 2 unarmed and distal segment with 3 setae. Mandible with unarmed basis and 1-segmented rami; endopod with 1 proximal seta on medial margin and 4 apical setae; exopod with 1 medial and 2 apical setae. First maxilla inner lobe armed with 10 elements, outer lobe bearing 11 elements. Second maxilla with 1 seta on basal segment, claw elongate bearing 1 short plumose seta and a distal row of pinnules. Maxilliped comprising 3 segments and a terminal claw; middle segment with 3 rows of setules, distal segment bearing 2 setae; displaying sexual dimorphism with the distal segment bearing a strong chitinous process in ♂.

Leg 1 with 3-segmented exopod and 2-segmented endopod, legs 2-4 with both rami 3-segmented; armature formula as follows:

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

Leg 1 endopod about 10% longer than exopod; inner spine on basis long and pinnate; spines on outer margins exopod segments 1 and 2 setiform; endopod segment 2 with many slender spinules laterally and distally. Leg 2 displaying sexual dimorphism in structure of inner seta of endopod segment 1. Legs 1-4 with minute denticles on surfaces of coxa, basis and rami; also spinule rows present on posterior surfaces of endopod segments 2 and 3.

Leg 5 comprising small baseoendopod and elongate free segment, ventral surfaces of both covered irregularly with minute denticles; baseoendopod with outer plumose seta and inner plumose seta; free segment with slender spinules all along lateral and ventro-lateral surfaces, and on middle portion of medial surface; armature comprising 1 distal seta on both inner and outer margins and 2 plumose setae and a small naked seta around the apex. Leg 6 represented by 1 short and 2 long plumose setae in ♂.

TYPE-SPECIES. *Neotisbella gigas* sp. nov.

ETYMOLOGY. The generic name alludes to the superficial similarity between the new genus and *Tisbella*.

REMARKS. The only other genera in the subfamily Tisbinae which possess a 2-segmented endopod on the leg 1 are *Tisbella* and *Tisbintra*.

The reduction in the number of armature elements on leg 1 endopod serves to separate *Tisbintra* from both *Tisbella* and the new genus. Some of the significant differences between *Tisbella* and *Neotisbella* are tabulated in Table 2. Other differences are the relative size of the endopod segments of legs 2-4, and the presence of an outer spine on exopod segment 2 of the leg 1 in *Tisbella* compared with the setiform element present in *Neotisbella*.

Neotisbella gigas sp. nov.

DIAGNOSIS. Prosome angular and vaulted in appearance (Fig. 10A); maximum width in anterior third of cephalosome (Fig. 12A). Genital complex (♀) and urosome somites 3, 4, 5 and 6 (in ♂) provided with ventral and lateral rows of spinules along posterior borders. Genital area (♀) (Fig. 11G) with a short inner naked seta, a slightly longer naked middle seta and a long plumose lateral seta. Caudal ramus (Fig. 10F) about 1.9 times longer than greatest width; armed with 2 lateral setae in proximal half of ramus (the lateral being about 1.7 times longer than the ventro-lateral one), an oblique spinule row on ventral surface extending from near base of lateral seta, a spinule row just proximal to the distal margin, a naked seta on the dorsal surface, a seta at the outer distal angle and one at the inner distal angle, 2 medium length plumose setae on the inner portion of the distal margin and 2 elements in the middle of the distal margin. The latter 2 elements are thin-walled and bifurcated at different levels.

Relative lengths of ♀ first antenna segments 9 : 19 : 19 : 17 : 9 : 10 : 4 : 13 (Fig. 10B); armature elements as follows; segment I-1, II-13, III-9, IV-3+1 aesthete, V-2, VI-5, VII-1, VIII-5; all segments provided with minute denticles on surfaces and segment I bearing large area of spinules, segment III about 6 spinules and segment IV 3 irregular rows of spinules. First antenna (♂) armature elements as follows; segment I-1, II-15, III-8, IV-2, V-8+1 aesthete, VI-2, VII-2, VIII-0 (?), IX-11 (Fig. 12B); segment I with 2 spinule rows, segment 7 with several rows of short spinules on antero-ventral surface (see Fig. 12C).

Other cephalic appendages as in generic diagnosis (p. 222).

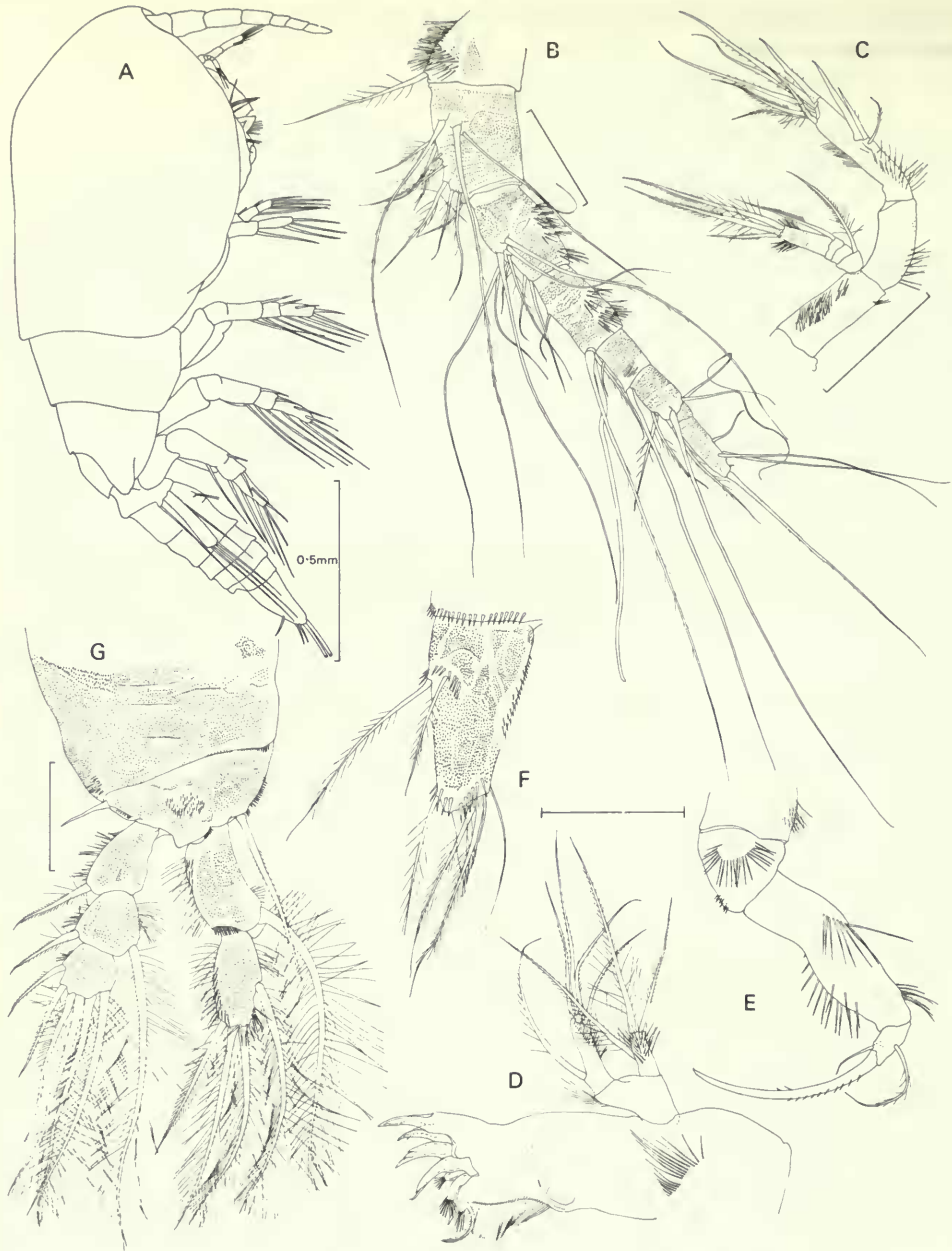


Fig. 10 *Neotibella gigas* n. sp.: A, female; B, first antenna; C, second antenna; D, mandible; E, maxilliped; F, caudal ramus; G, first leg, anterior. Scales 0.1 mm unless otherwise indicated.

Maxilliped terminal claw bearing a row of outer spinules on the convex margin in both sexes and two spinules on concave margin in ♀ (Fig. 10E); one spinule in ♂ (Fig. 12D).

Inner spine on basis of leg 1 much longer than endopod segment 1 and armed with small spinules in ♀ (Fig. 10G); shorter than segment 1 and apparently naked in ♂ (Fig. 12E). Armature elements on outer margins of exopod segments all setiform, those on segments 1 and 2 and the 3 proximal elements on segment 3 with shorter spinules than those on distal margin of segment 3; outer element on endopod segment 2 setiform but armed with shorter spinules than the outer



Fig. 11 *Neotisbella gigas* n. sp.: A, second leg, anterior; B, third leg; C, fourth leg; D, first maxilla; E, second maxilla; F, fifth leg; G, genital area; H, male endopod of second leg, posterior. Scales 0.1 mm.

two distal plumose setae; endopod segments 1 and 2 both with long spinules on lateral and disto-medial surfaces.

Legs 2-4 (Figs 11A-C); exopod segment 3 bearing central patch of larger denticles on posterior surface; endopod segments 2 and 3 armed with some denticles and about 7 and 16 spinules respectively on their posterior surfaces (Fig. 11H). Leg 2 displaying sexual dimorphism, the inner seta on endopod segment 1 stout and spiniform, and armed with distal row of stout spinules (Fig. 11H).

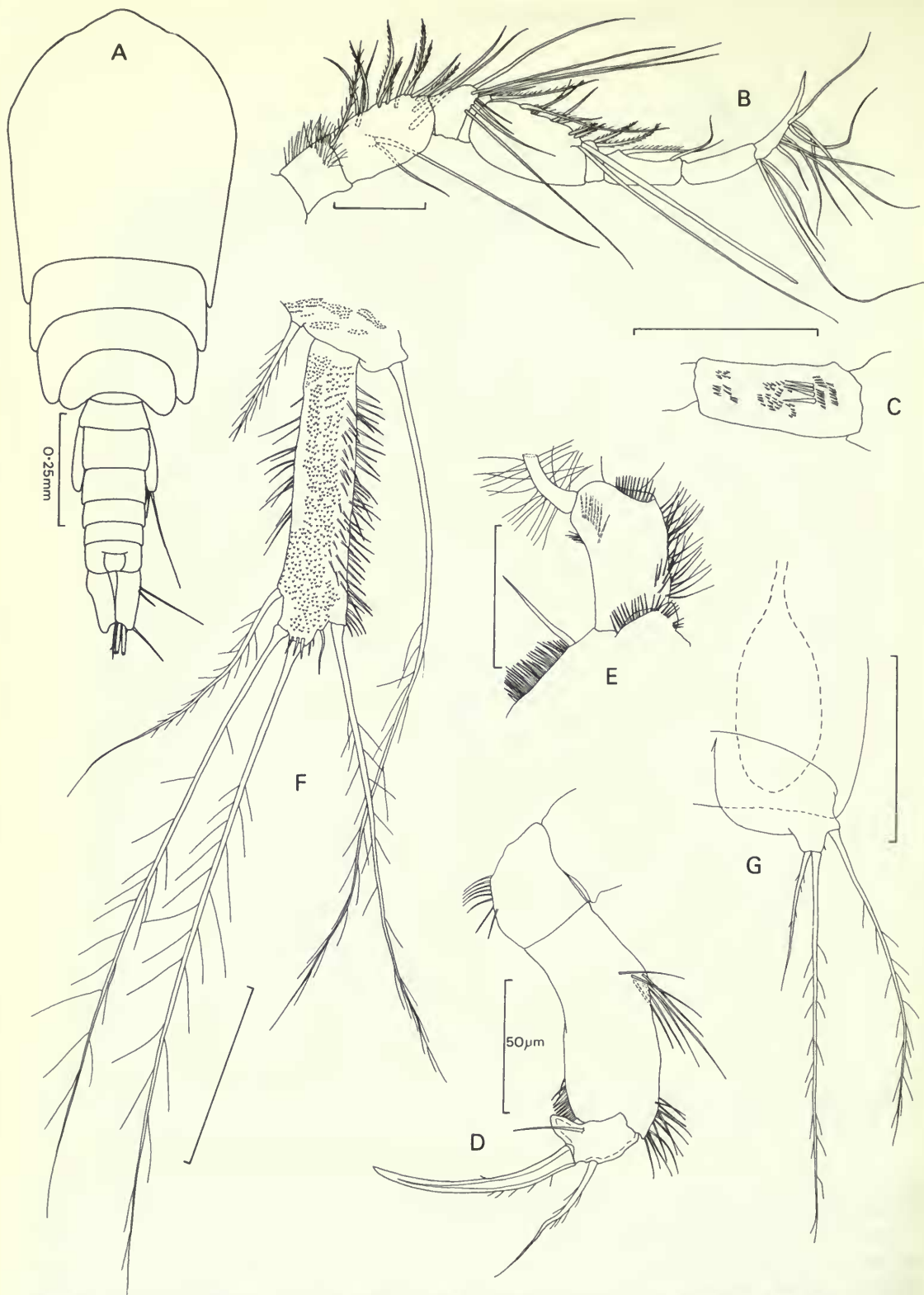


Fig. 12 *Neotisbella gigas* n. sp.: A, male; B, first antenna; C, detail of first antenna segment seven, postero-lateral; D, maxilliped; E, base of endopod of first leg; F, fifth leg; G, sixth leg. Scales 0.1 mm unless otherwise indicated.

Leg 5 ♀ (Fig. 11F) with single inner seta on baseoendopod about twice as long as free segment: free segment about 5.3 times longer than wide; its ventral surface covered with minute denticles; its lateral surface and the middle third of the medial surface bearing many spinules; armature elements comprising 1 long plumose seta each at the distal ends of the lateral and medial margins, 2 long plumose setae on the projecting distal margin and a short naked seta positioned between them and the lateral seta. Leg 5 in ♂ (Fig. 12F) as for female except inner seta on baseoendopod about half as long as free segment.

Leg 6 of ♂ (Fig. 12G) comprising 1 short sparsely pinnate inner seta and 2 long sparsely pinnate outer setae situated laterally on genital lobes of urosome somite 2.

Body length of ♀♀ from 1.85 to 2.00 and ♂ 1.26 mm.

MATERIAL EXAMINED. Holotype ♀, 1 ♂ and 5 ♀♀ paratypes: N.E. Atlantic Ocean, 18° N 25° W 'Discovery' Stn 7089. BM(NH) registration numbers 1977.226 (holotype), 1977.227 (♂) and 1977.228–232 (♀♀).

REMARKS. The similarities between the male and females described above strongly suggest that they are conspecific. Apart from the obvious characters of urosome segmentation, structure of the first antenna and the leg 6, differences between the sexes were noted in the maxilliped, leg 1 and leg 5. The presence of a spinous process on the third maxilliped segment has been recorded in males of *Bathydia remota* and *Volkmania forficula*. The minor differences between the sexes in the inner spine on the basis of the leg 1 and the inner seta on the baseoendopod of leg 5 can readily be attributed to sexual dimorphism.

Phylogenetic relationships of the new genera

It is interesting to examine the possible phylogenetic relationships of the two new genera, *Volkmania* and *Neotisbella*, to other genera in the family Tisbidae. The new genera belong to the subfamily Tisbinae which contains the following genera: *Tisbe*, *Tisbella*, *Tisbintra*, *Bathydia*, *Paraidya*, *Scutellidium* Claus, 1866 and *Sacodiscus* Wilson, 1924. The aberrant genus *Cholidya* Farran, 1914 is profoundly modified for its parasitic mode of life and is here regarded as representing a separate subfamily, the *Cholidiinae* subfam. nov. *Scutellidium* and *Sacodiscus* are closely related and will be called the *Scutellidium* group of genera, all other genera will be referred to as the *Tisbe* group. These two groups of genera are distinguished primarily by the structure of the mouthparts.

Within the *Tisbe* group the main characters used for separating the genera are the structure and armature of the second antenna, mandible, leg 1 and caudal ramus. Consideration of these characters within a phylogenetic framework suggested the following scheme of affinities (Fig. 13).

The main events occurring during the evolutionary radiation of this group of genera are designated, A, B and C (in Fig. 13). Event A resulted in the divergence of the ancestral stock into two lines, the VB lineage (*Volkmania*–*Bathydia*) and the TP lineage (*Tisbe*–*Paraidya*). Event A was the adoption of a planktonic habit by the VB lineage and the retention of the ancestral benthic habit by the TP lineage. The change to a planktonic existence appears to be associated with the acquisition of an elongate caudal ramus armed with 9 armature elements, as possessed by all 3 genera in the VB lineage. The benthic TP lineage typically possess a short caudal ramus bearing only 6 or 7 armature elements. The second major event (B) seems to have occurred twice, once in each main lineage. This was the divergence from an ancestral stock with a leg 1 endopod comprising three large segments of a stock with a reduced third endopod segment. The genera *Bathydia* and *Paraidya* both retained large third segments on their leg 1 endopods. The third major event (C) was the splitting off from an ancestral stock possessing a reduced third segment on the leg 1 endopod of a stock in which the separate third segment is lost altogether. This appears to have taken place at least twice, probably three times; once in the derivation of the *Neotisbella* line from the ancestral *Volkmania* stock and probably twice in the independent separation of the *Tisbella* and *Tisbintra* lines from the ancestral *Tisbe* stock.

This scheme of phylogenetic relationships allows for the obvious close relationship of *Volkmania*, *Neotisbella* and *Bathydia* (as indicated by their shared derived characters) despite their

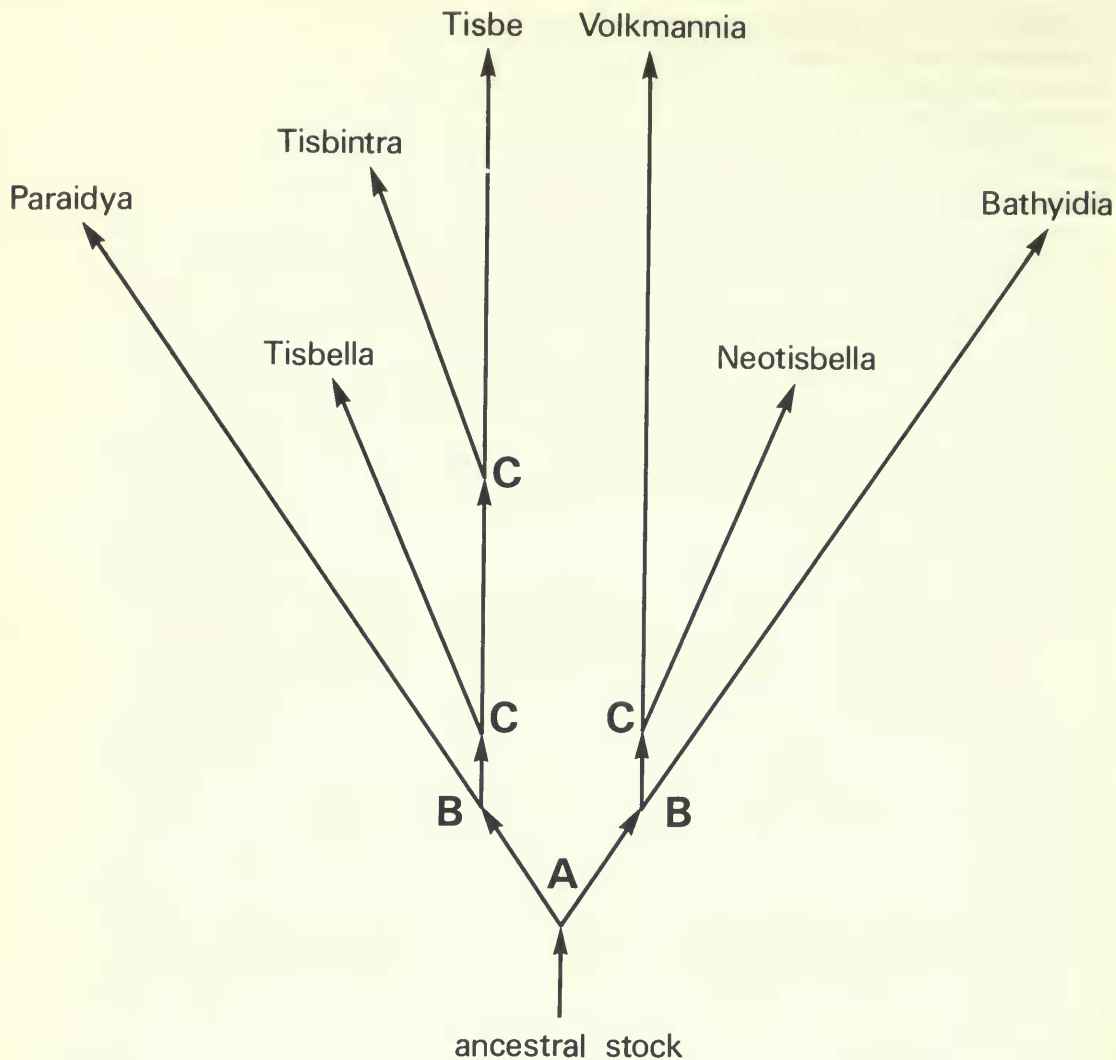


Fig. 13 The affinities of the seven genera of the *Tisbe* group within the subfamily Tisbinae.

close phenetic similarities to *Tisbe*, *Tisbella* and *Paraidya* respectively. The progressive reduction of the third segment of the leg 1 endopod has resulted in the formation of a 2-segmented endopod independently in *Neotisbella*, in *Tisbella* and in *Tisbintra*. In the first two genera the endopod is relatively short and the distal endopod segment retains the combined armature elements of both second (the single inner seta) and third segments (the 3 distal elements). This condition could have been derived from an endopod similar to that found in *Bathyidia* and *Paraidya*. In *Tisbintra* the endopod is much longer than the exopod and the distal endopod segment possesses 1 inner seta and only 1 or 2 distal elements. This condition was probably derived from a more *Tisbe*-like stock.

Family TACHIDIIDAE

Genus *EUTERPINA* Norman, 1903

DIAGNOSIS. As for type-species.

TYPE-SPECIES. *Euterpina acutifrons* (Dana, 1848).

Euterpina acutifrons (Dana, 1848)

Harpacticus acutifrons Dana, 1848 : 153.

Euterge gracilis Claus, 1863 : 110, pl. XIV, figs 1-13.

DIAGNOSIS. Prosome 4-segmented, first thoracic somite fused to head; urosome 5-segmented in ♀ (Fig. 14G) and 6-segmented in ♂. Genital complex (♀) without subdividing suture line. Rostrum well developed, anteriorly directed. Caudal rami just longer than wide. First antenna (♀) 7-segmented (Fig. 14H) with 2 terminal aesthetes; (♂) indistinctly 5-segmented, chirocerate and with 2 aesthetes on claw-like distal segment (Fig. 14K). Second antenna (Fig. 14I) with basis bearing 1-segmented exopod and 2-segmented endopod. Mandible with poorly developed biramous palp, without setae on basis. First maxilla arthrite well developed with about 12 mostly spiniform armature elements, rami rudimentary. Second maxilla with well-developed basis and small 2-segmented endopod. Maxilliped slender, 3-segmented; the long terminal claw armed with several strong setules. Rami of leg 1 short and 2-segmented, displaying weak sexual dimorphism with the rami being longer and more slender in ♂ (Fig. 14L) than in ♀. Legs 2-4 usually with 3-segmented rami, endopod of leg 2 in ♂ sometimes displaying incomplete separation of segments 2 and 3 giving 2-segmented appearance; armature formula as follows:

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

Leg 5 (♀) a flattened plate armed with 4 distal margin spines and 2 elements on the outer margin; a proximal seta, a short spine in the middle of the margin and a fine setule originating in the axil of this spine (Fig. 14J). Leg 5 (♂) with both legs fused into a single plate with a median notch in the distal margin, each leg bearing 2 distal margin spines and 3 elements on the outer margin, a proximal seta, a short spine in the middle of the margin and a fine setule originating in the axil of the spine (Fig. 14M).

Leg 6 (Fig. 14N) in ♂ a small prominence bearing 2 serrate spines apically.

Body lengths of ♀ 0.50-0.75 mm and ♂ 0.50-0.56 mm.

MATERIAL EXAMINED. 1 ♀: Antarctic, 'Terra Nova' Expedition (Farran, 1929). BM(NH) registration numbers 1930.1.1.1569-70. 4 ♀♀: Cheshire coast. BM(NH) registration numbers 1945.10.29. 21-23. 10 ♀♀, 1 ♂: Starcross, Devon. BM(NH) registration numbers 1911.11.8.43189-198.

REMARKS. Both sexes of this species are easily recognizable and are rarely confused with other species. The fine lateral setule present in the axil of the outer margin spine on leg 5 has been reported previously in both the male (e.g. Klie, 1913; Haq, 1965) and the female (e.g. Giesbrecht, 1892; Mori, 1964; Haq, 1965). This setule is not illustrated in either sex by Sars (1921) or in the male by Chappuis (1936) and Giesbrecht (1892). It is probable that the setule has been overlooked by the latter group of authors. It was even found to be present in both morphs of male *E. acutifrons* studied by Haq (1965).

Family THALESTRIDAE

Genus *PARATHALESTRIS* Brady and Robertson, 1873

DIAGNOSIS. Prosome 4-segmented, urosome 5-segmented in ♀ and 6-segmented in ♂. Body cylindrical or slightly laterally compressed; epimeral plates of free thoracic somites not markedly produced. Rostrum short, antero-ventrally directed.

First antenna (♀) 7- to 9-segmented, without plumose setae. Second antenna with allobasis and 2-segmented exopod. Mandible palp well developed; basis with 3 setae, both rami 1-segmented. First maxilla with 1-segmented exopod and endopod. Second maxilla with 3 endites on coxa, endopod rudimentary. Maxilliped with 2 robust basal segments and strong terminal claw.

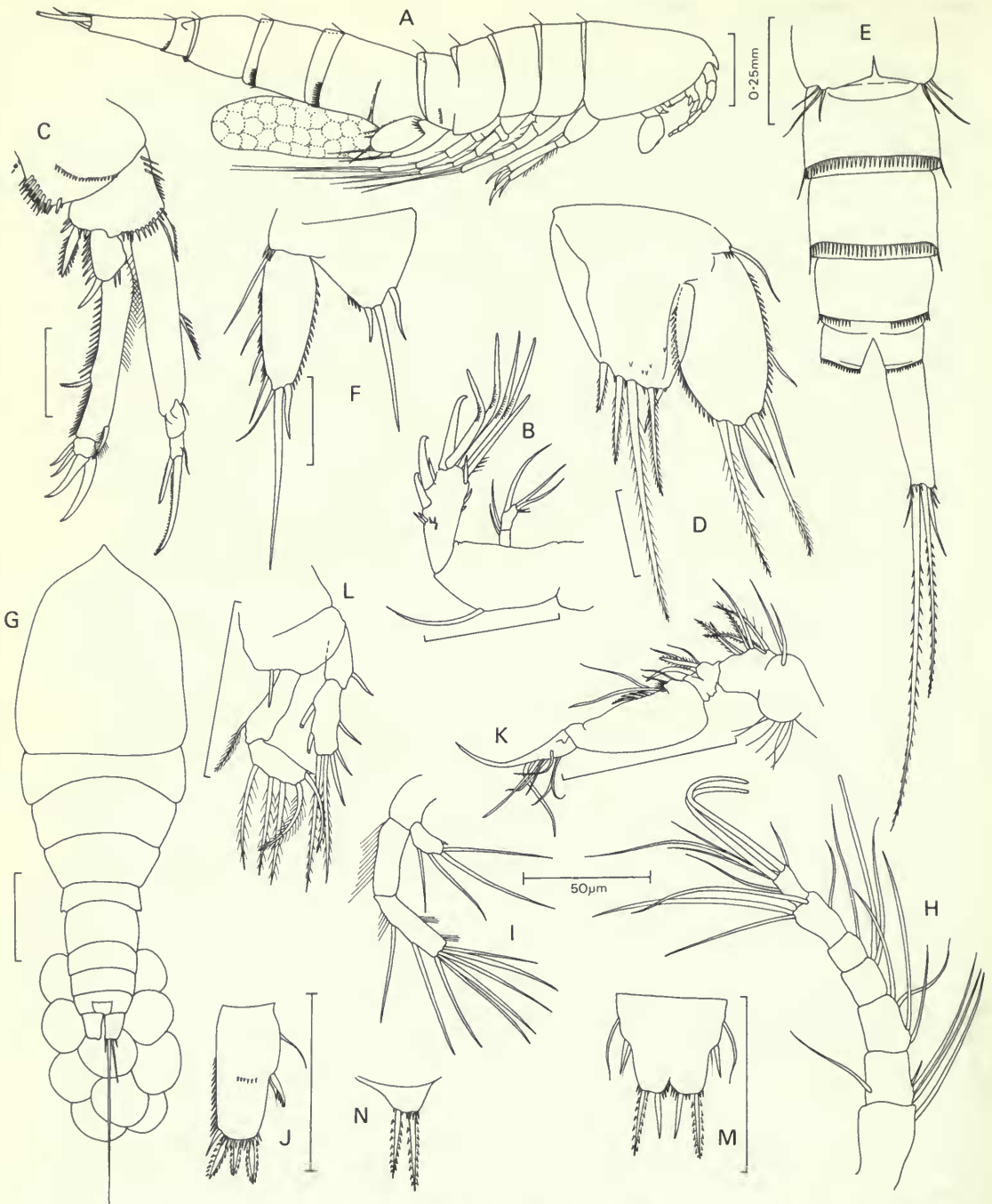


Fig. 14 *Parathalestris croni*: A, female; B, second antenna; C, first leg; D, fifth leg; E, male urosome; F, fifth leg. *Euterpina acutifrons*: G, female; H, first antenna; I, second antenna; J, fifth leg; K, male first antenna; L, first leg; M, fifth leg; N, sixth leg. Scales 0.1 mm unless otherwise indicated.

Leg 1 with both rami 3-segmented, about equal in length; exopod segment 2 and endopod segment 1 providing most of length of respective rami. Legs 2-4 with 3 segmented rami in ♀; leg 2 displaying sex dimorphism, with endopod usually 2-segmented in ♂. Armature formula as follows:

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

Leg 5 ♀ baseopod strongly projecting and usually bearing 5 setae, exopod usually with 6 or 7 setae. Leg 5 ♂ usually with 3 setae on baseopod and 6 or 7 on exopod.

Leg 6 in ♂ represented by 3 setae on genital lobes of urosome somite 2.

TYPE-SPECIES. *Parathalestris clausi* (Norman, 1868).

REMARKS. Sars (1905) erected a new genus, *Halithalestris*, to include the species *Harpacticus croni*, first recorded by Kroyer (1842). One of the major characters used by Sars to establish the new genus was the pelagic habits of *H. croni*. Lang (1948) recognized that *Halithalestris* was not a distinct genus and subsequently referred *H. croni* to *Parathalestris*.

Parathalestris croni (Kroyer, 1842)

Harpacticus croni Kroyer, 1842: pl. XLIII, figs 3a-n.

Thalestris serrulata Brady, 1880: 133, pl. LIX, figs 2-11.

Halithalestris croni Sars, 1905: 118, pl. LXXII.

DIAGNOSIS. Cephalosome small, comprising about 50% of length of prosome (Fig. 14A); genital complex in ♀ only subdivided laterally by a suture line. Anal somite markedly notched in middle of posterior border (Fig. 14E). Caudal rami divergent, about 3.5-4 times longer than maximum width.

First antenna of ♀ 9-segmented, bearing a large aesthete on segment 4; ♂ indistinctly 7-segmented with aesthetes on segments 3 and 4. Second antenna (Fig. 14B) with 1 seta on allobasis; exopod segments 1 and 2 with 1 and 4 setae respectively. First segment of maxilliped with 3 distal setae, terminal claw shorter than second segment.

Both rami of leg 1 (Fig. 14C) similar in length; inner claw on distal segment of endopod about 2 times longer than outer claw; exopod segment 3 with 4 armature elements. Leg 5 (♀) extending posteriorly as far as middle of genital complex; baseopod armed with 5 setae and extending just beyond mid-point of exopod; exopod oval in outline, about twice as long as wide and armed with 6 setae (Fig. 14D). Leg 5 (♂) smaller than in ♀, baseopod with 3 setae and exopod with 6 setae (Fig. 14F). Leg 6 in ♂ represented by 3 setae on lateral lobe of urosome 2 (Fig. 14E).

Body length of ♀ from 2.1 to 2.3 mm and ♂ about 1.7 mm.

MATERIAL EXAMINED. 1 ♀, 1 ♂; Firth of Forth. BM(NH) registration numbers 1911.11.8.46207-10.

REMARKS. This is one of the largest species of harpacticoid and is easily distinguished by its size, small cephalosome and long divergent caudal rami. Brady (1880) first described the male, as *Thalestris serrulata*, and figured the male leg 5. Wells (1970) misinterpreted Brady's figure when he redrew the leg 5, as he illustrated only 5 setae on the exopod (Wells, 1970: fig. 7e ♂) instead of the 6 in Brady's figure.

Family CLYTEMNESTRIDAE

Genus *CLYTEMNESTRA* Dana, 1848

DIAGNOSIS. Prosome 4-segmented, first thoracic somite fused to head, urosome 5-segmented in ♀, 6-segmented in ♂; body rather dorso-ventrally flattened, cephalosome and free thoracic somites

with large, conspicuous epimeral plates. Urosome slender; genital complex without subdividing suture line. Rostrum large, anteriorly directed. Caudal ramus at least as long as wide, with 6 armature elements, 2 of which are long in ♂.

First antenna 7- or 8-segmented, with several aesthetes. Second antenna comprising a basis, a 2-segmented endopod and either 1 or 2 plumose setae representing the exopod (Fig. 15F). Mandible reduced to slender blade and palp represented by single minute setule. First maxilla 2-segmented, proximal segment with 1 lateral seta, distal segment with 2 apical elements. Second maxilla reduced, 2-segmented, bearing 1 proximal seta and a distal endite armed with 2 setae on first segment and 3 setae on second segment. Maxilliped long, consisting of 2 segments and a terminal claw; showing weak sexual dimorphism with longer terminal claw in ♂ (Fig. 15G) than in ♀ (Fig. 15D).

Leg 1 with 3-segmented endopod and 1-segmented exopod. Legs 2-4 each with transversely elongate basis and 3-segmented rami: armature formula variable on legs 1 and 2 between species but within following limits:

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

Leg 5 without inner setae on baseoendopod; free segment elongate with 5 or 6 slender setae. Leg 6 in ♂ represented by an elongate lobe bearing 1 lateral and 2 apical setae.

TYPE-SPECIES. *Clytemnestra scutellata* Dana, 1848.

REMARKS. Lang (1948) in his monograph on the Harpacticoida retained Poppe's (1891) family-group name, Pseudopeltiidae, for the genus *Clytemnestra* which was its type and only genus. This action has been followed by several subsequent authors (e.g. Wells, 1970) but it contravenes the ICZN Article 11e as a family-group name must, when first published, be based on the name then valid for a contained genus. Thus the family-group name Clytemnestridae, first proposed by Scott (1909), is adopted here.

Clytemnestra scutellata Dana, 1848

Goniopelte gracilis Claus, 1891: 151, pl. I-II.

Clytemnestra hendorffi Poppe, 1891: 132, pl. I.

DIAGNOSIS. Caudal rami (Figs 15B, J) about 1.8 times longer than greatest width. First antenna 8-segmented; ♀ with 1 aesthete on segment 4 and 2 each on segments 5 and 8; relative lengths of segments 3: 10: 10: 10: 12: 10: 15: 30 (Fig. 15C); ♂ with 2 aesthetes each on segments 4, 5 and 8; relative lengths of segments 3: 7: 14: 3: 28: 5: 16: 24 (Fig. 15E). Exopod of second antenna (Fig. 15F) represented by 2 plumose setae. Basis of leg 1 (Fig. 15H) with outer margin seta; exopod with 4 distal setae. Leg 2 (Fig. 15I) exopod segment 1 without outer margin spine; endopod segment 1 of legs 2-4 as long as exopod segments 1 and 2 combined. Free segment of leg 5 typically with 6 setae in both sexes (Fig. 15K), occasionally with 5 (var. *quinqspinosus*).

Body length of ♀ from 1 to 1.24 mm, and of ♂ from 1.07 to 1.3 mm.

MATERIAL EXAMINED. 1 ♀, 1 ♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.194 (♀) and 1977.195 (♂). 1 ♀, 1 ♂: Suez Canal Expedition (Gurney, 1927). BM(NH) registration number 1928.4.2.136. 10 ♀♀, 2 ♂♂: as *C. rostrata*, Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.268-275.

REMARKS. This species can be distinguished from *C. rostrata*, the only other species in the genus, by the shape of the caudal rami and the segmentation of the first antenna when sorting undissected specimens. There are other significant differences between the two species, particularly in the armature of legs 1 and 2.

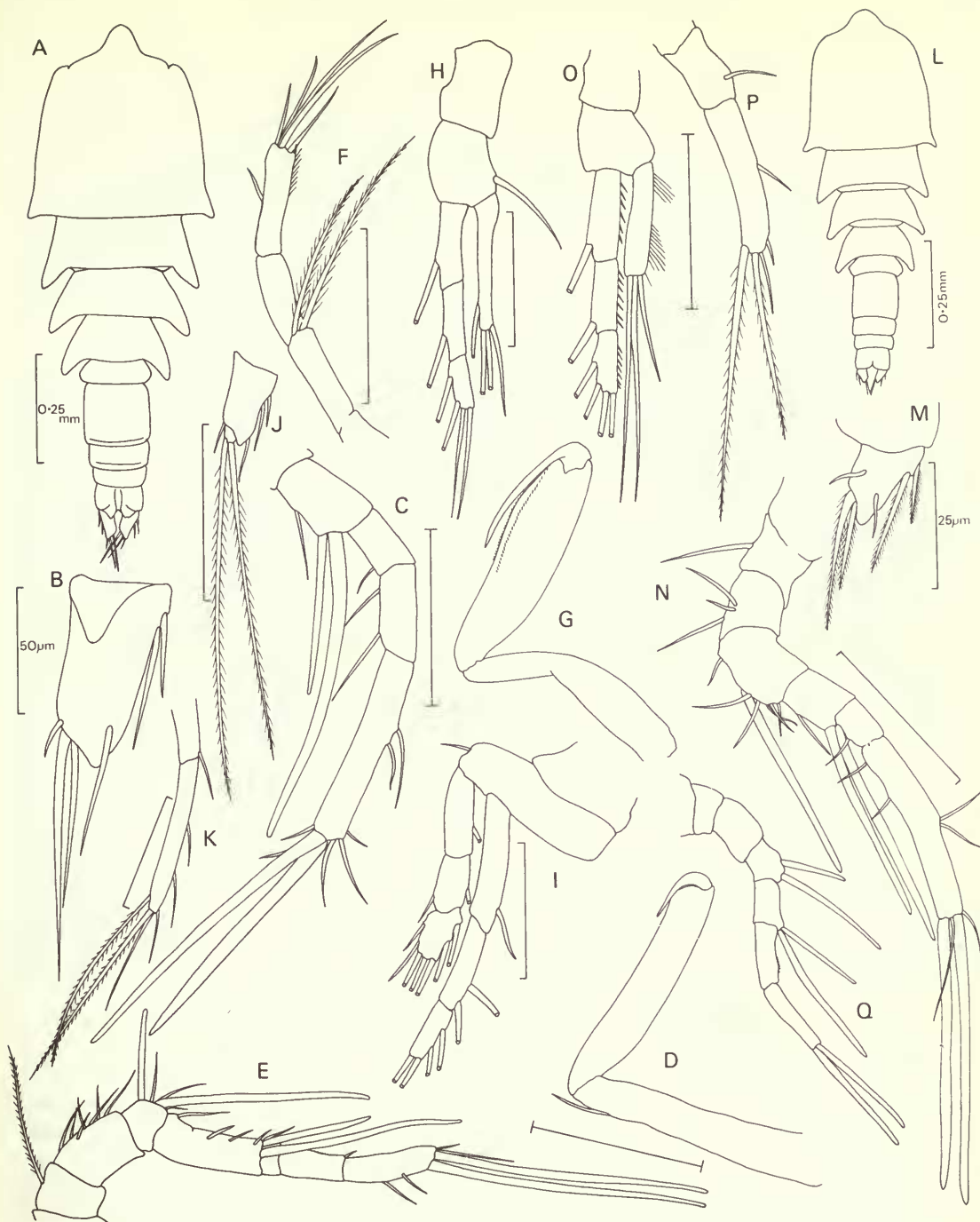


Fig. 15 *Clytemnestra scutellata*: A, female; B, caudal ramus; C, segments four to seven of first antenna; D, maxilliped; E, male first antenna; F, second antenna; G, maxilliped; H, first leg; I, second leg; J, caudal ramus; K, fifth leg. *C. rostrata*: L, female; M, caudal ramus; N, first antenna; O, first leg; P, fifth leg; Q, male first antenna. (Q redrawn from Giesbrecht, 1892.) Scales 0.1 mm unless otherwise indicated.

Clytemnestra rostrata (Brady, 1883)

Goniopsyllus rostratus Brady, 1883: 107, pl. XLII, figs 9–16.

DIAGNOSIS. Caudal rami (Fig. 15M) about 1–1.1 times longer than wide. First antenna 7-segmented; ♀ with 1 aesthete on segment 4 and 2 each on segments 5 and 7, relative lengths of segments about 3:12:6:10:12:11:46 (Fig. 15N); ♂ with 2 aesthetes on segments 4, 5 and 7, relative lengths of segments about 4:7:16:8:14:23:28 (Fig. 15Q). Exopod of second antenna represented by 1 plumose seta. Basis of leg 1 (Fig. 15O) without outer margin seta; exopod with 3 distal setae. Leg 2 exopod segment 1 with an outer margin spine, exopod segment 3 with only 6 armature elements compared with 7 in *C. scutellata*; endopod segment 1 of legs 2–4 almost as long as exopod segments 1 and 2 combined. Free segment of leg 5 typically carrying 5 setae in both sexes (Fig. 15P), occasionally reduced to 4 setae.

Body length of ♀ from 0.60 to 1.00 mm, and ♂ from 0.80 to 0.90 mm.

MATERIAL EXAMINED. Holotype ♀ as *Goniopsyllus rostratus*: Challenger Expedition (Brady, 1883). BM(NH) registration number CC. 46. 1 ♀: Great Barrier Reef Expedition (Farran, 1936). BM(NH) registration number 1948.4.28.120. 7 ♀♀: Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.268–275.

REMARKS. The holotype of *C. rostrata* was described by Brady (1883) as a male, but re-examination of this specimen has shown it to be a female. It possesses a 7-segmented first antenna, with 1 aesthete on segment 4, and 2 aesthetes on segments 5 and 7. The relative lengths of segments 5, 6 and 7 are 12:9:36 respectively (as percentages of the total appendage length). The armature and proportional lengths of the segments indicate that this appendage belongs to a female.

Family MIRACIIDAE

DIAGNOSIS. Prosome 4-segmented with first thoracic somite fused to head, urosome 5-segmented in ♀ and 6-segmented in ♂. Body slender, slightly laterally compressed. Rostrum variable. Caudal rami longer than wide. First antenna 7- to 8-segmented in ♀, 8- to 9-segmented and haplocerate in ♂. Exopod of second antenna 1-segmented or absent. Mandible with small toothed blades and rudimentary palp. First maxilla with several cutting elements on arthrite, rest of appendage rudimentary. Second maxilla with small number of endites. Maxilliped well developed, 2-segmented with third segment apparently fused to short terminal claw. Leg 1 with 3-segmented exopod and 2-segmented endopod; legs 2–4 with 3-segmented rami except for leg 2 displaying sexual dimorphism with 2-segmented endopod in ♂. Leg 5 (♀) comprising a short baseoendopod bearing 3–5 setae and elongate exopod armed with 6 setae. Leg 5 (♂) with short baseoendopod bearing 2 or 3 setae, exopod bearing 4 or 6 setae.

Genus *MIRACIA* Dana, 1846

DIAGNOSIS. Cephalosome quite large, rounded anteriorly and provided with a pair of large cuticular lenses (Fig. 16A). Rostrum inconspicuous. Urosome somites 3–5 (6 in ♂) each provided with a row of spinules ventrally along posterior border. Caudal rami about 3 times longer than wide. First antenna 8-segmented in ♀ carrying an aesthete on segment 4; in ♂ 9-segmented, with aesthete on segment 5 and geniculate between segments 6 and 7. Second antenna (Fig. 16B) with 1-segmented exopod bearing 2 apical plumose setae. Armature formula of legs 1–4 variable.

Leg 5 as in family diagnosis for both sexes. Leg 6 represented in ♂ by a small lateral lobe bearing 3 setae.

TYPE-SPECIES. *Miracia efferata* Dana, 1852.

REMARKS. The armature formula given by Lang (1948) for the genus *Miracia* applies only to *M. minor*, not *M. efferata*.

Miracia efferata Dana, 1852

DIAGNOSIS. Cuticular lenses on cephalosome touching. Second antenna (Fig. 16B) with allobasis, as basis and first endopod segment completely fused. Armature formula of legs 1-4 as follows:

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

Legs 5 (♀) with 5 setae on baseoendopod and 6 setae on exopod (Fig. 16C). Leg 5 (♂) with 3 setae on baseoendopod and 6 setae on exopod (Fig. 16D).

Body length of ♀ from 1.45 to 2 mm and ♂ from 1.4 to 1.6 mm.

MATERIAL EXAMINED. 31 ♀♀, 8 ♂♂: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.196-205 (♀♀) and 1977.206-213 (♂♂).

REMARKS. Both sexes of *M. efferata* were a bright bluish-purple colour even after a considerable time in preservative. The armature formula of legs 2-4 differs in several respects from that presented by Lang (1948) for the genus *Miracia*. The most significant differences are the presence of inner margin setae on endopod segment 1 of legs 2-4 and the presence of 3 outer margin spines on exopod segment 3 of legs 3 and 4. Lang's formula was presumably based only on data from *M. minor* Scott, 1894.

Miracia minor Scott, 1894

DIAGNOSIS. Body (Fig. 16E) more slender than in *M. efferata* (c.f. Fig. 16A). Cuticular lenses on cephalosome not touching. Second antenna apparently with basis and 2-segmented endopod. Armature formula of legs 1-4 as follows:

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

Leg 5 (♀) with 4 setae on baseoendopod, 1 very long and plumose, and with 6 setae on exopod (Fig. 16G). Leg 5 (♂) with 2 setae on baseoendopod and 4 setae on exopod, 2 distally and 2 on the lateral margin (Fig. 16F).

Body length of ♀ from 0.90 to 0.93 mm and ♂ 0.82 to 0.93 mm.

MATERIAL EXAMINED. Syntype series ♀♀ and ♂♂: Gulf of Guinea (Scott, 1894). BM(NH) registration numbers 1893.4.22.340 and 1894.1.20.76-87. 1 ♀, 1 ♂: as *Macrosetella oculata*, John Murray Expedition (Sewell, 1947), BM(NH) registration numbers 1949.12.31.584-5. 1 ♀: Gulf of Aden. BM(NH) registration number 1911.11.8.43199.

REMARKS. There is some confusion in the literature over the armature of the leg 5 in both sexes of *M. minor*. This arose because Scott (1894) in his original description illustrated 7 setae on the ♀ leg 5 exopod, and no outer margin seta on the baseoendopod. Examination shows that the armature of the ♀ leg 5 comprises 1 outer margin seta on the baseoendopod and 6 setae on the exopod in agreement with Giesbrecht (1895). Scott (1894) also figured the exopod of the ♂ leg 5 with 2 inner margin setae and 2 distal setae. The complete male specimen in the syntype series shows that in the slide (No. Z.D. 76) prepared by Scott the exopod had been accidentally rotated so the 2 outer margin setae (shown in Fig. 14F) appeared to be on the inner margin. Giesbrecht (1895) figured the ♂ leg 5 with 2 outer margin setae and 2 distal setae but most other authors (e.g. Owre and Foyo, 1967; Wells, 1970) redrew their illustrations from Scott (1894).

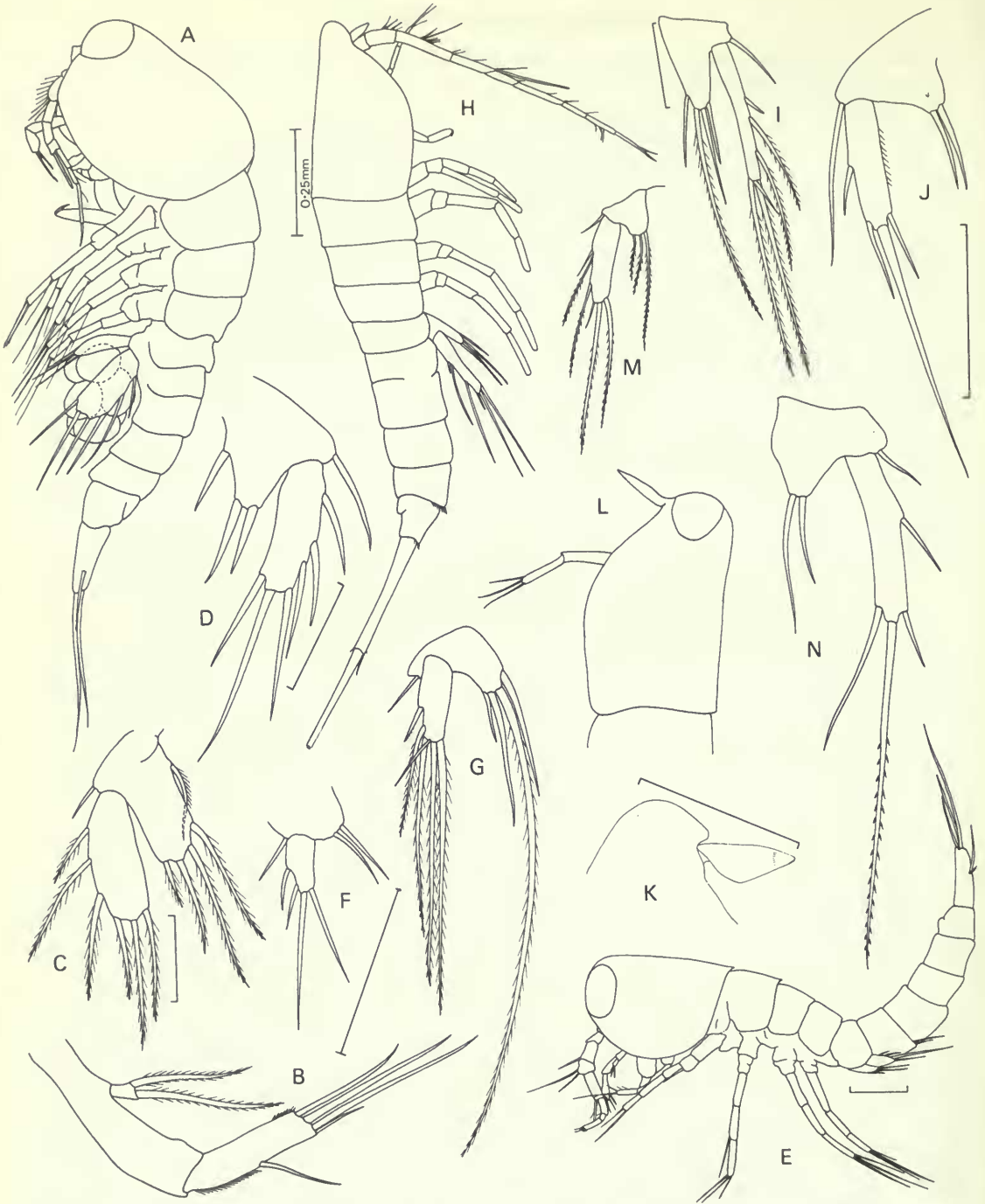


Fig. 16 *Miracia efferata*: A, female; B, second antenna; C, fifth leg; D, male fifth leg. *M. minor*: E, syntype male; F, fifth leg; G, female fifth leg. *Macrosetella gracilis*: H, female; I, fifth leg; J, male fifth leg; K, rostrum. *Oculosetella gracilis*: L, female cephalosome; M, fifth leg; N, male fifth leg. (L redrawn from Sars, 1916; M & N redrawn from Owre & Foyo, 1967.) Scales 0.1 mm unless otherwise indicated.

Genus *OCULOSETELLA* Dahl, 1895

DIAGNOSIS. As for type-species.

TYPE-SPECIES. *Oculosetella gracilis* (Dana, 1852).

Oculosetella gracilis (Dana, 1852)

Miracia gracilis Dana, 1852: 46.

Setella oculata Sars, 1916: 7, 13, Fig. VII.

Macrosetella oculata Rose, 1929: 54.

DIAGNOSIS. Cephalosome rounded anteriorly, provided with large cuticular lenses touching in the median line. Rostrum large, clearly delimited at base and ventrally directed (Fig. 16L). Urosome somites 3-5 (6 in ♂) each provided with a spinule row ventrally along posterior border. Caudal rami about 3 times longer than wide. First antenna 7-segmented in ♀; 8-segmented and geniculate in ♂. Second antenna (Fig. 16L) with allobasis; exopod absent.

Leg 5 (♀) with 3 setae on baseoendopod and 6 setae on exopod (Fig. 16M). Leg 5 (♂) with 2 setae on baseoendopod and 4 setae on exopod (Fig. 16N).

Body length of ♀ from 1.2 to 1.35 mm and ♂ from 1.15 to 1.3 mm.

MATERIAL EXAMINED. None.

REMARKS. This species is rather incompletely known as some of its appendages have not been described. The two specimens of *Macrosetella oculata* reported by Sewell (1947) were found on re-examination to be *Miracia minor*.

Genus *MACROSETELLA* Scott, 1909

DIAGNOSIS. As for type-species.

TYPE-SPECIES. *Macrosetella gracilis* (Dana, 1848).

Macrosetella gracilis (Dana, 1848)

Setella gracilis Dana, 1848: 155.

DIAGNOSIS. Cephalosome prolonged anteriorly (Fig. 16H), without cuticular lenses. Rostrum large, clearly delimited at base and ventrally directed (Fig. 16K). Caudal rami about 8 times longer than wide. First antenna 8-segmented in both sexes with aesthetes on segments 4 and 8. Second antenna with allobasis in ♀ and apparently with separate basis and 2-segmented endopod in ♂; exopod absent in both sexes. Mandible and first maxilla both comprising a toothed blade and a single seta representing the palp. Second maxilla with 1 (♂) and 2 (♀) endites. Maxilliped slender. Armature formula of legs 1-4 as follows:

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

Leg 5 (♀) with 4 setae on baseoendopod and 6 setae on exopod (Fig. 16I). Leg 5 (♂) with 2 setae on baseoendopod and 4 setae on exopod (Fig. 16J).

Body length of ♀ from 1.21 to 1.5 mm and ♂ from 1.13 to 1.16 mm.

MATERIAL EXAMINED. 21 ♀♀, 1 ♂: N.E. Atlantic Ocean, 18° N 25° W 'Discovery' Stn 7089. BM(NH) registration numbers 1977.214-223 (♀♀) and 1977.224 (♂).

REMARKS. This is the only member of the family Miraciidae without conspicuous cuticular lenses. It possesses only a simple eye spot.

SIPHONOSTOMATOIDA

This order as defined by Kabata (1979) comprises both the Caligoida, containing primarily parasites of fishes, and the Cyclopoida Siphonostoma, which are predominantly associated with or parasitic upon invertebrate hosts. Although adult and, more commonly, juvenile fish parasitic siphonostomatoids are occasionally recorded free in the plankton they are not true holoplanktonic forms and are not considered further. Siphonostomatoid copepods belonging to three genera, *Ratania* Giesbrecht, *Pontoeciella* Giesbrecht and *Hyalopontius* Sars (= *Megapontius* Hulsemann), have been found in the plankton of the N.E. Atlantic Ocean and can be regarded as members of the planktonic community. Species of these three genera are probably associated with planktonic invertebrates but no 'hosts' are known at present.

Family RATANIIDAE

Genus *RATANIA* Giesbrecht, 1891

DIAGNOSIS. Body unmodified; urosome 5-segmented in female, 6-segmented in male. Caudal ramus with 6-setae. Rostrum weakly developed. First antenna 5- to 7-segmented (♀) and 7- to 9-segmented (♂), with an aesthete on the terminal segment. Second antenna non-prehensile, 4-segmented and without trace of exopod. Oral cone short. Mandible an elongated blade, dentate apically and without palp. First maxilla bilobed; inner lobe with 3 equal setae, outer lobe with 3 setae and a short naked seta. Second maxilla 2-segmented, distal portion of second segment produced into a slightly curved claw. Maxilliped 3-segmented and with terminal claw armed with a spinulate seta.

Legs 1-4 with 3-segmented rami; armature formula for both sexes as follows:

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

Leg 5 with a free segment armed with 2 short medial and 3 long lateral setae.

Leg 6 represented by 2 small spines in the female and by a large postero-ventral flap bearing a single seta in the male.

TYPE-SPECIES. *Ratania flava* Giesbrecht, 1891.

REMARKS. *Ratania* shows a close affinity to the family Myzopontiidae, but differs from the genera of this family, primarily in the absence of an exopod on the second antenna, in the reduced number of segments in the first antenna, in the small oral cone and in the structure of the blade of the mandible (Heron & Damkaer, 1969).

Ratania flava Giesbrecht, 1891

DIAGNOSIS. *Female*. Prosome about 2.2 times longer than urosome. Ratio of lengths of urosome somites and caudal ramus (Fig. 17E) 14:30:12:11:16:17. Caudal ramus about 1.7 times longer than wide.

First antenna 5-segmented; relative lengths of segments (measured along posterior border) 23:7:5:35:30 (Fig. 17F); segmental armature elements I-6, II-2, III-2+1 aesthete, IV-5, V-5+2 aesthetes. Second antenna (Fig. 17G) with terminal seta about 3 times longer than distal segment. Tip of mandible (Fig. 17H) with two dentate areas well separated. Inner lobe of first maxilla (Fig. 17I) markedly longer than outer lobe. Free segment of leg 5 (Fig. 17E) somewhat expanded laterally, setae on leg 5 not conspicuously plumose.

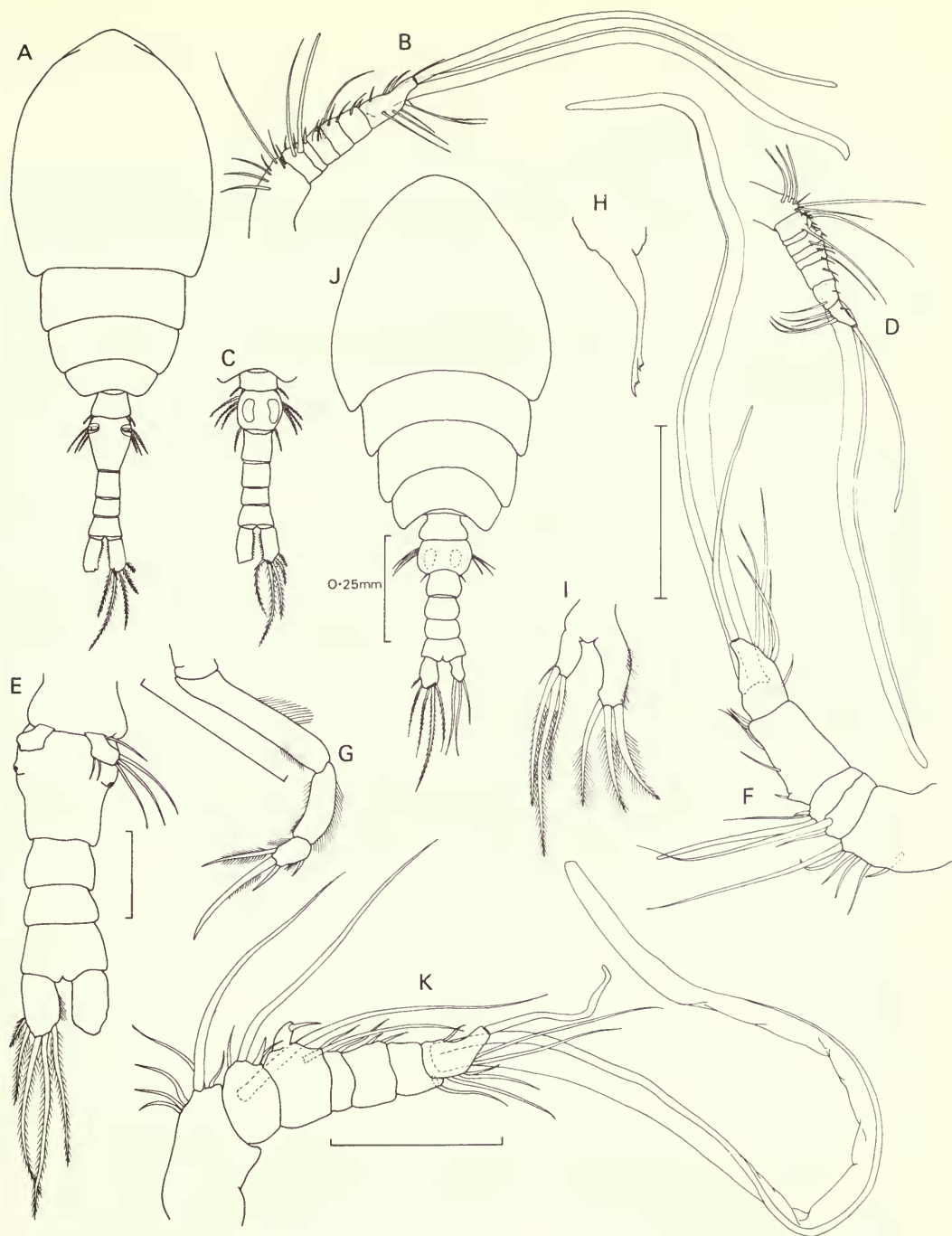


Fig. 17 *Ratania atlantica*: A, female; B, first antenna; C, male urosome; D, first antenna. *R. flava*: E, female urosome; F, first antenna; G, second antenna; H, mandible; I, first maxilla; J, male; K, first antenna. (A–D redrawn from Heron & Damkaer, 1969.) Scales 0.1 mm unless otherwise indicated.

Body length of female 1.1–1.2 mm.

Male. As for ♀ except: prosome about 1.9 times longer than urosome (Fig. 17J). Ratio of lengths of urosome somites and caudal ramus 14:16:14:13:11:14:18. First antenna (Fig. 17K) 7-segmented; relative lengths of segments 23:11:15:6:13:14:18. Segmental armature elements I–6, II–5, III–3, IV–1, V–2, VI–1, VII–6+2 aesthetes.

Body length of male 1–1.2 mm.

MATERIAL EXAMINED. 7 ♀♀ and 1 ♂; 'Discovery' Stn 7089. BM(NH) registration numbers 1977.242–248 (♀♀) and 1977.249 (♂).

REMARKS. Saraswathy (1961) reported that many of the segments of the 5-segmented first antenna in ♀ *R. flava* showed subdivisions. No significant subdivisions were observed in the present material, and the segmentation of the first antenna remains a useful character in distinguishing between the two species of *Ratania*.

Ratania atlantica Farran, 1926

DIAGNOSIS. *Female*. Prosome from 1.9 to 2.3 times longer than urosome (Fig. 17A); relative lengths of urosome somites and caudal ramus 14:29:15:10:13:19. Caudal ramus from 2.3 to 2.5 times longer than wide.

First antenna (Fig. 17B) 7-segmented, relative lengths of segments 25:8:4:8:9:13:33; segmental armature elements I–7, II–3+1 aesthete, III–2, IV–3, V–2, VI–2, VII–11+2 aesthetes. Tip of mandible with two dentate areas separated by small indentation. Inner lobe of first maxilla just longer than outer lobe. Free segment of leg 5 not markedly expanded laterally.

Body length 2.21–2.8 mm.

Male. Prosome about 1.9 times longer than urosome. Relative lengths of urosome somites and caudal ramus (Fig. 17C) 10:21:15:13:9:13:19. Caudal ramus about 2.2 times longer than wide.

First antenna (Fig. 17D) 9-segmented, relative lengths of segments 16:11:3:8:5:4:16:8:19; segmental armature elements I–4+3 aesthetes, II–4, III–2, IV–3; V–1, VI–1, VII–2, VIII–2+1 aesthete, IX–8+1 aesthete.

Body length 2.42–2.62 mm.

MATERIAL EXAMINED. Holotype ♀: Bay of Biscay (Farran, 1926). BM(NH) registration numbers 1926.12.6.40 (spirit) and 1926.12.6.52 (slide of appendages). 2 ♀♀: Antarctic (between 66° 30' and 76° S), Terra Nova Stns 276 and 285 (Farran, 1929). BM(NH) registration numbers 1930.1.1.1330–1333 (spirit) and 1930.7.24.91 (slide of appendages).

REMARKS. The holotype of *R. atlantica* is in poor condition. The slide of the appendages contains one of the first antennae, it is 7-segmented and the relative lengths of the segments are as follows 24:11:4:11:10:11:29. The armature elements remaining on the appendage are in agreement with the formula given by Heron & Damkaer (1969). The body length of the holotype, 2.34 mm, also serves to distinguish between *R. atlantica* and the smaller *R. flava*. The two Antarctic specimens are poorly preserved, but their large size and the 7-segmented nature of the first antennae of one of them confirm that these specimens are *R. atlantica*.

Family PONTOECIELLIDAE

Genus *PONTOECIELLA* Giesbrecht, 1895

DIAGNOSIS. *Female*. Body unmodified (Fig. 18A), urosome 5-segmented. Caudal ramus with 6 setae, ventral seta strongly spinulate. Rostrum weakly developed. First antenna (Fig. 18C) 8-segmented with an aesthete on segment VI. Second antenna (Fig. 18D) non-prehensile, with a 1-segmented exopod bearing 1 or 2 apical setae. Oral cone long, forming a true siphon (Fig. 18B). Mandible (Fig. 18E) a slender, elongate blade without a palp. First maxilla (Fig. 18F) a single

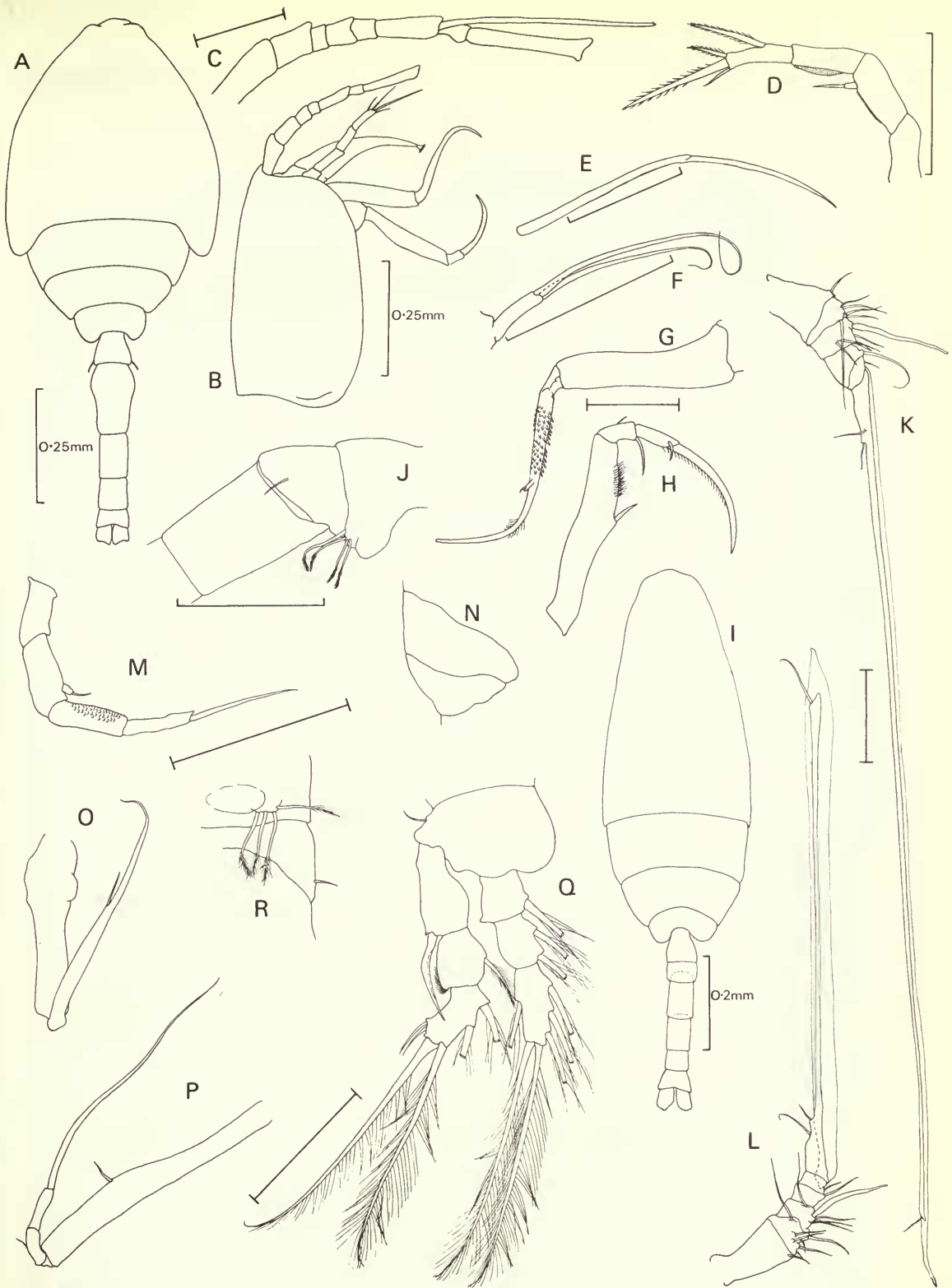


Fig. 18 *Pontoeeciella abyssicola*: A, holotype female; B, female cephalosome lateral; C, first antenna; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; I, male; J, anterior portion of urosome, lateral; K, first antenna; L, first antenna from another specimen; M, second antenna; N, oral cone, lateral; O, second antenna; P, maxilliped; Q, first leg; R, fifth and sixth legs. Scales 0.1 mm unless otherwise indicated.

lobe with 2 apical setae and (sometimes) a small spinule. Second maxilla (Fig. 18G) 2-segmented, distal segment curving through between 65 and 90°. Maxilliped (Fig. 18H) 4-segmented.

Legs 1-4 with 3-segmented rami; armature formula variable but usually as follows:

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

Leg 5 reduced to a single seta.

Male. Body unmodified (Fig. 18I); urosome 6-segmented, first somite with ventral swelling (Fig. 18J), second somite narrower ventrally, producing slightly flexed appearance in lateral view. Ventral seta on caudal ramus thin-walled, not spinulate.

First antenna (Figs 18K, L) 6-segmented, the distal segment providing between 75 and 90% of the overall length of the appendage; one aesthete present on segment III and one on segment V, the latter adhering along the entire length of the distal segment and projecting beyond its tip. Second antenna (Fig. 18M) with 1-segmented exopod and 2-segmented endopod bearing a single apical element. Mouth cone (Fig. 18N) short without true siphon. Second maxilla (Fig. 18O), distal segment armed with a single naked seta. Maxilliped (Fig. 18P) 4-segmented, terminal claw long but weakly developed. Legs 1-4 (Fig. 18Q) as in female. Leg 5 (Fig. 18R) a small lobe fused to somite and bearing 4 plumose setae. Leg 6 represented by a single seta.

TYPE-SPECIES. *Pontoeciella abyssicola* (Scott, 1894).

REMARKS. The new species described by Ummerkutty (1968), *Danodes panikkari*, obviously belongs to *Pontoeciella*.

Pontoeciella abyssicola (Scott, 1894)

? *Artotrogus abyssicolus* T. Scott, 1894: 128-129, pl. 12, figs 5-9, pl. 14, figs 11-18.

Pontoeciella abyssicola Giesbrecht, 1895: 186.

Carnegiella gracilis Wilson, 1942: 176, figs 20-25.

Danodes plumata Wilson, 1942: 182-183, figs 57-68.

Danodes panikkari Ummerkutty, 1968: 298-304, figs 1-13.

DIAGNOSIS. As for genus (p. 240).

MATERIAL EXAMINED. Holotype ♀ (as *Artotrogus abyssicolus*): Gulf of Guinea 1° 55' N 5° 55' E (T. Scott, 1894). BM(NH) registration number 1893.4.22.69a. 4 ♀♀, 1 ♂: Great Barrier Reef Expedition, Stns 20, 28, 45 and 48 (Farran, 1936). BM(NH) registration numbers 1948.4.28.132-135. 92 ♀♀, 4 ♂: 'Discovery' Stn 7089, 18° N 25° W. BM(NH) registration numbers 1977.250-259 (♀♀) and 1977.260-263 (♂).

REMARKS. This species is highly variable both in the shape and proportions of the body and in the structure and armature of some of the appendages. Female body length varies from 0.7 mm (Farran, 1936) to 1.65 mm (Heron & Damkaer, 1969) and body width relative to length ranges from 33 to 41% (Farran, 1936). Variation in appendage structure and armature has been recorded from the first antenna to leg 5.

According to Ummerkutty (1968), in *Danodes panikkari* the seta representing the female leg 5 is absent. This difference alone is not sufficient to warrant the establishment of a distinct species, because of the variability exhibited by *P. abyssicola*, especially as this seta is often difficult to observe (T. Scott in his original description did not observe this seta although it is still present on his holotype specimen). *Danodes panikkari* is therefore regarded as a junior synonym of *Pontoeciella abyssicola*. The structure illustrated by Ummerkutty (1968, Fig. 7) as the first maxilla is not the first maxilla of a *Pontoeciella*, which is unilobed, and requires re-examination.

Less variation has been recorded in the males of *P. abyssicola*. However, a comparison of Farran's (1936, text-fig. 24d) and Wilson's (1942, fig. 20) figures with Fig. 16I shows variation in

body form, especially in relative lengths of the urosome somites. The relative lengths of segments of the first antenna also vary markedly, with the distal segment providing between 75 and 90% of total appendage length. The male leg 5 is absent according to Scott (1894) and Wilson (1942), is represented by a single seta according to Farran (1936) or comprises four plumose setae (p. 242). Scott's male specimen is no longer extant but Farran's specimen from G.B.R. expedition Stn 20 was re-examined and the leg 5 was found to consist of 4 setae as in the 'Discovery' specimen illustrated in Fig. 18R. Only the most lateral seta is visible when the urosome is viewed from the dorsal aspect.

Family MEGAPONTIIDAE

Genus *HYALOPONTIUS* Sars, 1909

Syn. *Megapontius* Hulsemann, 1965.

DIAGNOSIS. Both sexes. Body unmodified. Urosome 5-segmented in female, 6-segmented in male. Caudal ramus with 2 lateral, 2 dorsal and 3 apical setae, the latter situated in a concave depression in the distal margin. Rostrum well developed, ventrally directed and sometimes truncate distally. First antenna 11-segmented; relative lengths of segments similar in all spp. 19 : 1 : 2 : 2 : 2 : 5 : 4 : 9 : 10 : 12 : 34; segmental armature usually as follows: I-6, II-1, III-2, IV-1; V-1, VI-6+1 spine, VII-1+1 spine, VIII-2, IX-2, X-2, XI-13+1 aesthete. Spine on segment VI usually pointed (Fig. 24E), that on segment VII often blunt (Figs 23D & 24E); aesthete on segment XI located near anterior margin about two thirds of distance along segment. Aesthete narrow and seta-like proximally, becoming thin-walled and flaccid distally. Second antenna 2- to 3-segmented; distal segment armed with a lateral spine, a small hirsute subapical seta and a very long terminal claw bearing a row of tiny spinules on its concave margin; exopod 1-segmented bearing lateral and medial naked setae and a sparsely pinnate apical seta.

Oral cone short and well developed, with elaborate buccal tube distally; buccal stylets present. Mandible an elongate blade, dentate at tip and without palp. First maxilla bilobed; larger inner lobe with 3 apical setae, outer lobe with small spine and a long spinulate seta apically. Second maxilla 2-segmented, distal segment curved and dentate towards apex. Maxilliped 3-segmented; first segment usually bearing a unilaterally pinnate seta; second segment with a naked seta and a row of hairs along inner margin; terminal segment bearing 2 subapical setae and a long apical claw armed with a row of tiny hairs.

Legs 1-4 with 3-segmented rami; armature formula within following range:

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

Leg 5 comprising basal segment armed with an outer seta and free segment bearing 1 apical and 2 lateral setae. Leg 6 represented by a single seta in female and by a genital lobe bearing 1 long seta and 2 spinules in male.

TYPE-SPECIES. *Hyalopontius typicus* Sars, 1909.

REMARKS. Sars (1909) described *H. typicus* in detail and comparison of his description with that of *Megapontius gigas* (Hulsemann, 1965) clearly demonstrates that the two genera, *Hyalopontius* and *Megapontius*, are synonymous. Sars (1909) placed *Hyalopontius* in the monotypic Pontocaelidae but there are significant differences between these two genera. Hulsemann (1965), with some reservations, referred *Megapontius* to the family Artotrogidae *sensu* Eiselt (1961). Heptner (1968) described a new species, *M. pleurospinus*, and erected a new family the Megapontiidae for the genus. Although *Megapontius* is now recognized as a synonym of *Hyalopontius* the family name is unchanged as it was based on a generic name which was valid at the time it was proposed.

Key to species of HYALOPONTIUS (females only)

- | | | |
|---|---|------------------------------|
| 1 | Outer margin spine present on exopod segment 1 of leg 1 | 3 |
| - | Outer margin spine absent from exopod segment 1 of leg 1 | 2 |
| 2 | Exopod segment 3 of leg 2 with 2 outer margin spines | <i>H. alatus</i> n. sp. |
| - | Exopod segment 3 of leg 2 with 3 outer margin spines | <i>H. hulsemannae</i> n. sp. |
| 3 | Distal segment of second antenna with lateral seta situated about 33% of distance along margin; outer margin spine present on exopod segment 2 of leg 1 | 4 |
| - | This seta situated within proximal 25% of margin; outer margin spine absent from exopod segment 2 of leg 1 | 5 |
| 4 | Exopod segment 3 of leg 1 with 2 outer margin spines | <i>H. typicus</i> |
| - | Exopod segment 3 of leg 1 with 3 outer margin spines | <i>H. pleurospinus</i> |
| 5 | Distal seta on lateral margin of leg 5 free segment shorter than segment | <i>H. cinctus</i> n. sp. |
| - | This seta longer than segment | 6 |
| 6 | Exopod segment 3 of leg 2 with 2 outer margin spines; lateral setae on caudal rami situated in proximal one-third of ramus | <i>H. spinatus</i> n. sp. |
| - | Exopod segment 3 of leg 2 with 3 outer margin spines; lateral setae on caudal rami in distal one-third of ramus | 7 |
| 7 | Body length greater than 7 mm, body squat, about 2.9 times longer than greatest width; exopod of second antenna about 4.6 times longer than wide | <i>H. enormis</i> n. sp. |
| - | Body length less than 6 mm, body about 4.3 times longer than greatest width; exopod of second antenna about 2 times longer than wide | <i>H. roei</i> n. sp. |

Hyalopontius typicus Sars, 1909

Megapontius gigas Hulsemann, 1965.

DIAGNOSIS. Female. Body relatively squat, about 3.4 times longer than greatest width (Fig. 19A); prosome about 1.8 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somites 2 and 3 pointed but not markedly produced posteriorly. Relative lengths of urosome somites and caudal rami 18 : 27 : 12 : 6 : 14 : 23; first urosome somite without additional spinose processes near posterior border; dentate hyaline membrane absent from posterior border. Posterior border of genital complex with dentate hyaline membrane. Caudal ramus about 3.2 times longer than wide; lateral setae in distal half of ramus.

Relative lengths of first antenna segments 19 : 2 : 2 : 2 : 3 : 5 : 4 : 7 : 8 : 11 : 37 (Fig. 19C). Second antenna (Fig. 19D) exopod 1.9 times longer than wide; endopod 2-segmented with lateral spine on distal segment strongly developed and located about 35–38% of distance along segment; terminal claw longer than rest of appendage. Maxilliped segments 1 and 2 incompletely separated, distal segment with long terminal claw, a small naked subapical seta and a lateral seta, relative lengths of these 3 elements 61 : 7 : 32 respectively.

Legs 1–4 armature formula as for generic diagnosis except:

	Exopod
Leg 1	I-1; I-1; II, 2, 3
Leg 2	I-1; I-1; III, I, 5
Leg 3	I-1; I-1; II, I, 5

Leg 5 basal segment with small inner spinose process (Fig. 19E); free segment with 1 long apical and 2 medium-length lateral setae.

Body length of female 4.87–5.3 mm.

Male. Body similar to that of female; relative lengths of urosome somites and caudal ramus 16 : 13 : 15 : 12 : 7 : 15 : 22 (Fig. 19F). Appendages as in female (Figs 19H, I). Leg 6 (Fig. 19J) a small projection bearing a long outer plumose seta, and two inner, subequal spinules.

Body length of males 4.6–5.05 mm.

MATERIAL EXAMINED. 18 ♀♀, 7 ♂♂: N.E. Atlantic Ocean 44° N 12° W, 'Discovery' Stns 8508 78 (7 ♀♀) and 8509 20 (11 ♀♀, 7 ♂♂). BM(NH) registration numbers 1977.302–311 (♀) and 1977.312–318 (♂).

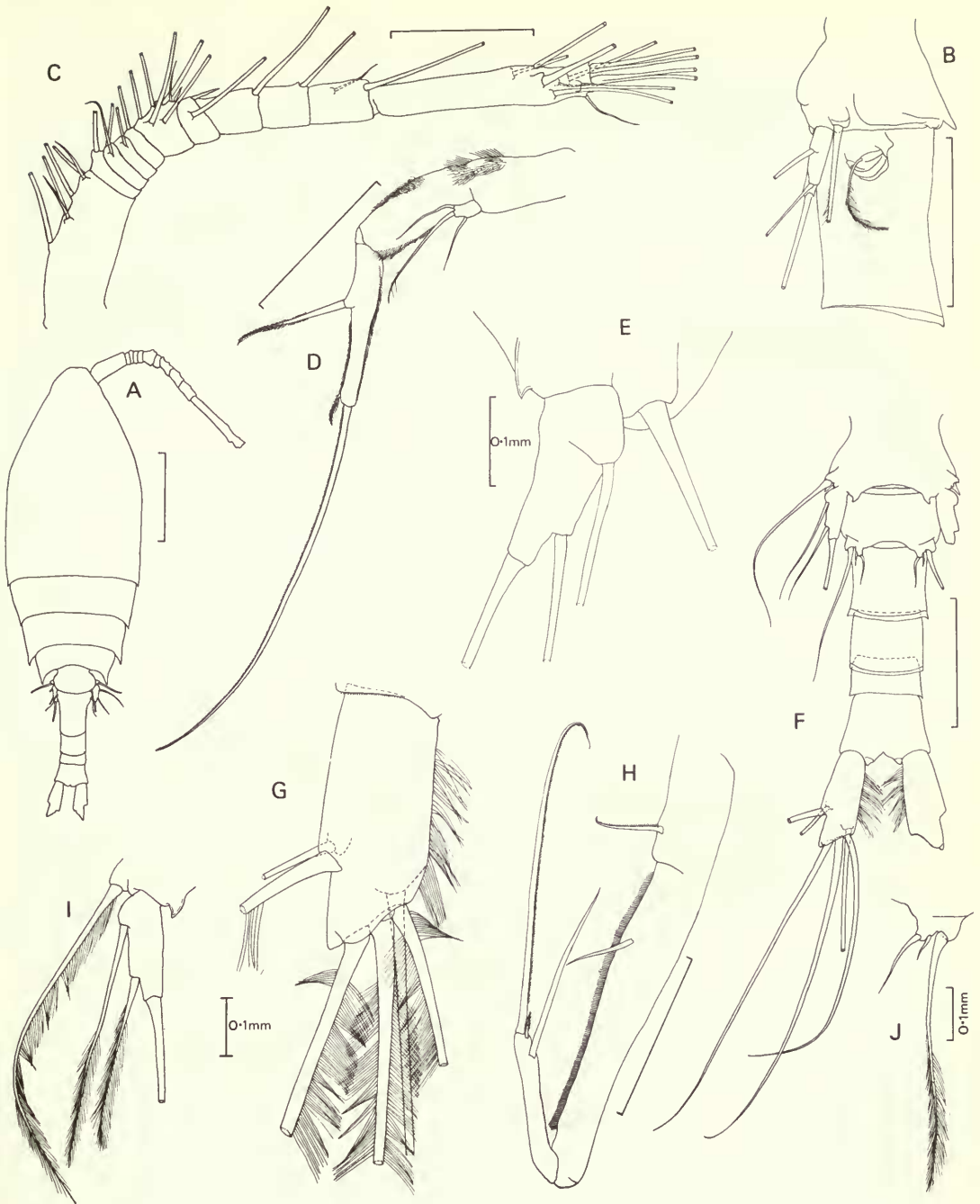


Fig. 19 *Hyalopontius typicus*: A, female; B, anterior portion of urosome; C, first antenna; D, second antenna; E, fifth leg; F, male urosome; G, caudal ramus; H, maxilliped; I, fifth leg; J, sixth leg. Scales 0.5 mm unless otherwise indicated.

REMARKS. The type material of *H. typicus* could not be located. It is not in the collections of the Musée Océanographique de Monaco where the other material described in the same paper (Sars, 1909) is stored (Testa, pers. comm.). The present 'Discovery' material is identified as *H. typicus* because of the agreement in size and body proportions with the specimen figured by Sars (1909), and because of the position of the lateral spine on the distal segment of the second antenna. This spine was described by Sars as being in the middle of the segment but his figure shows it to be rather more proximal in position. The position of the lateral spine in the 'Discovery' material, at 35–38% of the distance along the margin of this segment, is sufficiently similar for these specimens to be regarded as conspecific with Sars' material. In contrast, the six new species of *Hyalopontius* described below have the lateral seta on the second antenna situated within the proximal quarter (25%) of the distal segment.

There are no significant differences between the material described above as *H. typicus* and *Megapontius gigas* Hulsemann, 1965, which is thus regarded as a synonym.

Hyalopontius hulsemannae sp. nov.

DIAGNOSIS. *Female*. Body slender (Fig. 20A), about 4 times longer than greatest width; prosome about 1.3 times longer than urosome. Rostrum rounded at tip (Fig. 20B). Epimeral plates of free thoracic somite 2 pointed but not markedly produced; those of free thoracic somite 3 produced posteriorly into a slender projection extending almost as far as the posterior border of the first urosome somite (Fig. 20C). Relative lengths of urosome somites and caudal ramus 14 : 31 : 15 : 8 : 20 : 12. Dentate hyaline membrane present along posterior margins of urosome somites 1–4. First urosome somite with 2 small spinose processes dorso-laterally near posterior border. Caudal ramus about 2.1 times longer than wide; lateral setae in distal half of ramus (Fig. 20D).

Relative lengths of first antenna segments; 19 : 2 : 2 : 2 : 2 : 5 : 4 : 9 : 10 : 10 : 35 (Fig. 20E). Second antenna (Fig. 20F) exopod about 2 times longer than wide; lateral spine on distal endopod segment small, unilaterally plumose and situated about 7% of the distance along segment. Mandible (Fig. 20G) with reduced number of dentate projections at tip. Maxilliped (Fig. 20H) segments 1 and 2 distinctly divided; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 77 : 7 : 16: respectively.

Legs 1–4 armature formula as for generic diagnosis except:

	Exopod
Leg 1	0–1; 0–1; II, 2, 3
Leg 2	I–1; I–1; III, I, 5
Leg 3	I–1; I–1; II, I, 5

Leg 5 (Fig. 20I) bearing a small blunt inner process on basal segment; free segment with long apical and 2 medium-length lateral setae.

Body length of holotype ♀ 5.03 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9541 22. BM(NH) registration number 1977.322.

REMARKS. The species is named after Kuni Hulsemann who provided the first well-illustrated account of a species in this genus. This species can be distinguished from other species, except *H. alatus* n. sp., by the absence of an outer margin spine from exopod segment 1 of leg 1. It differs from *H. alatus* primarily in the position of the lateral spine on the distal segment of the second antenna, the degree of expansion of the epimeral plates of free thoracic somites 2 and 3 and the possession of 3 outer margin spines on exopod segment 3 of leg 2 (as compared to 2 in *H. alatus*).

Hyalopontius alatus sp. nov.

DIAGNOSIS. *Female*. Body slender (Fig. 21A), about 5.2 times longer than greatest width; prosome about 1.3 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somite 2 produced, those of somite 3 markedly produced posteriorly and expanded laterally

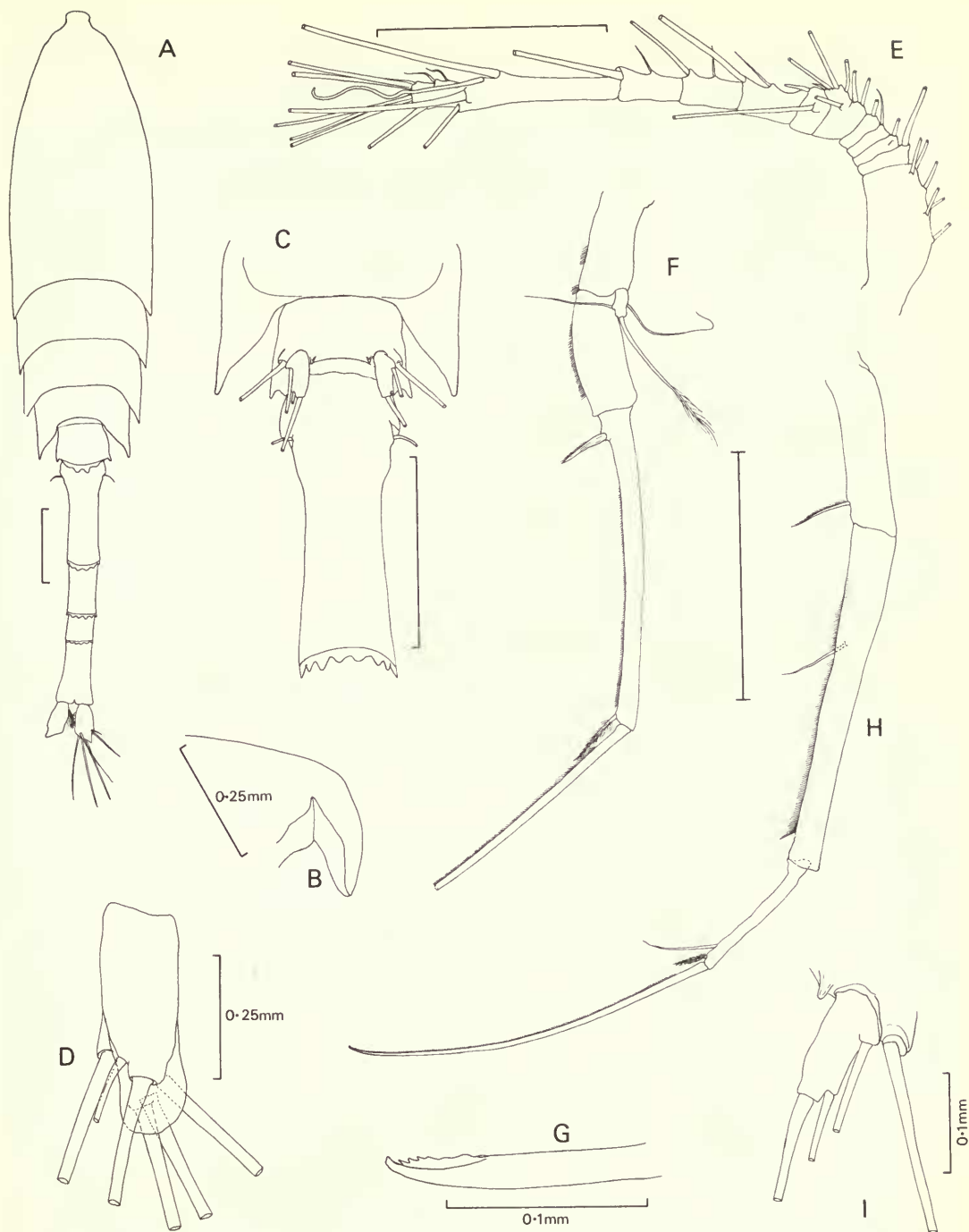


Fig. 20 *Hyalopontius hulsemannae* n. sp., holotype female: A, dorsal; B, rostrum; C, anterior portion of urosome; D, caudal ramus, lateral; E, first antenna; F, second antenna; G, tip of mandible; H, maxilliped; I, fifth leg. Scales 0.5 mm unless otherwise indicated.

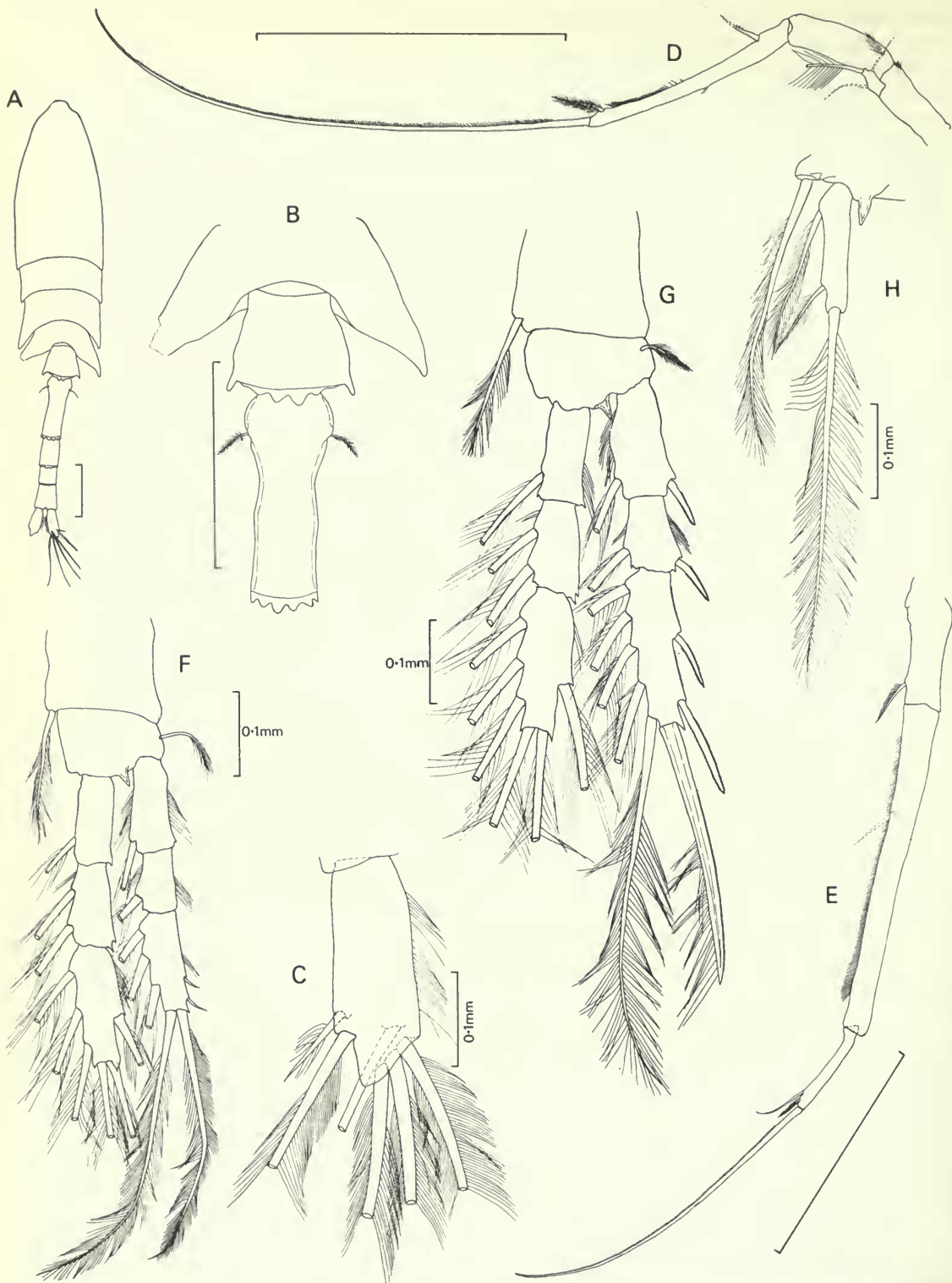


Fig. 21 *Hyalopontius alatus* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, caudal ramus; D, second antenna; E, maxilliped; F, first leg; G, second leg; H, fifth leg. Scales 0.5 mm unless otherwise indicated.

(Fig. 21B). Relative lengths of urosome somites and caudal ramus 16 : 32 : 15 : 10 : 12 : 15. Dentate hyaline membrane present on posterior margins of urosome somites 1-4. First urosome somite with 2 small spinose processes dorso-laterally near posterior border. Caudal ramus (Fig. 21C) about 2.8 times longer than wide; lateral setae in distal half of ramus.

First antennae incomplete on both sides. Second antenna (Fig. 21D) exopod about 2 times longer than wide; lateral spine on distal endopod segment situated about 15% of distance along segment; terminal claw much longer than rest of appendage. Maxilliped (Fig. 21E) segments 1 and 2 distinctly divided; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 81 : 6 : 13 respectively.

Legs 1-4 (Figs 21F, G) armature formula as for generic diagnosis except:

	Exopod
Leg 1	0-1; 0-1; II, 2, 3
Leg 2	I-1; I-1; II, I, 5
Leg 3	I-1; I-1; II, I, 5

Leg 5 (Fig. 21H) with medium-sized spinose process on basal segment; distal seta on lateral margin of free segment shorter than the segment.

Body length of holotype ♀ 4.16 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean. 'Discovery' Stn 9541 24. BM(NH) registration number 1977.323.

REMARKS. The specific name refers to the conspicuous wing-like expansion of the epimeral plates of free thoracic somite 3. This character, together with the armature formula of legs 1 and 2 and the position of the lateral spine on the distal segment of the second antenna, enables *H. alatus* to be distinguished from other species.

Hyalopontius spinatus sp. nov.

DIAGNOSIS. Female. Body slender (Fig. 22A), about 5.1 times longer than greatest width; prosome about 1.2 times longer than urosome. Rostrum truncate at apex (Fig. 22D). Epimeral plates of free thoracic somites 1 and 2 markedly produced posteriorly, those of somite 3 pointed but not markedly produced. Relative lengths of urosome somites and caudal ramus 14 : 32 : 14 : 9 : 11 : 20. First urosome somite with a pair of dorso-lateral spinose processes near the posterior border (Figs 22B, C); dentate hyaline membrane present along posterior margins of urosome somites 1-4. Caudal ramus about 4.4 times longer than wide; lateral setae situated in proximal half of ramus.

Relative lengths of first antenna segments 17 : 1 : 1 : 2 : 2 : 5 : 3 : 10 : 12 : 13 : 34 (Fig. 22F); segmental armature as in generic diagnosis but with additional seta on segment II. Second antenna (Fig. 22F) exopod about 2.2 times longer than wide, lateral spine on distal segment small and situated about 10% of distance along segment; terminal claw much longer than rest of appendage. Mandible (Fig. 22G) with two areas of dentate projections. First maxilla (Fig. 22H) and second maxilla (Fig. 22I) as in other species of genus. Basal segment of maxilliped (Fig. 22J) with 2 strong processes on medial surface; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 83 : 8 : 9 respectively.

Legs 1-4 (Figs 22K, L) armature formula as for generic diagnosis except:

	Exopod
Leg 1	I*-1; 0-1; II, 2, 3
Leg 2	I-1; I-1; II, I, 5
Leg 3	I-1; I-1; II, I, 5

* This spine very small.

Leg 5 (Fig. 22M) with large blunt inner process on basal segment; free segment with long apical and 2 medium-length lateral setae.

Body length of holotype ♀ 4 mm.

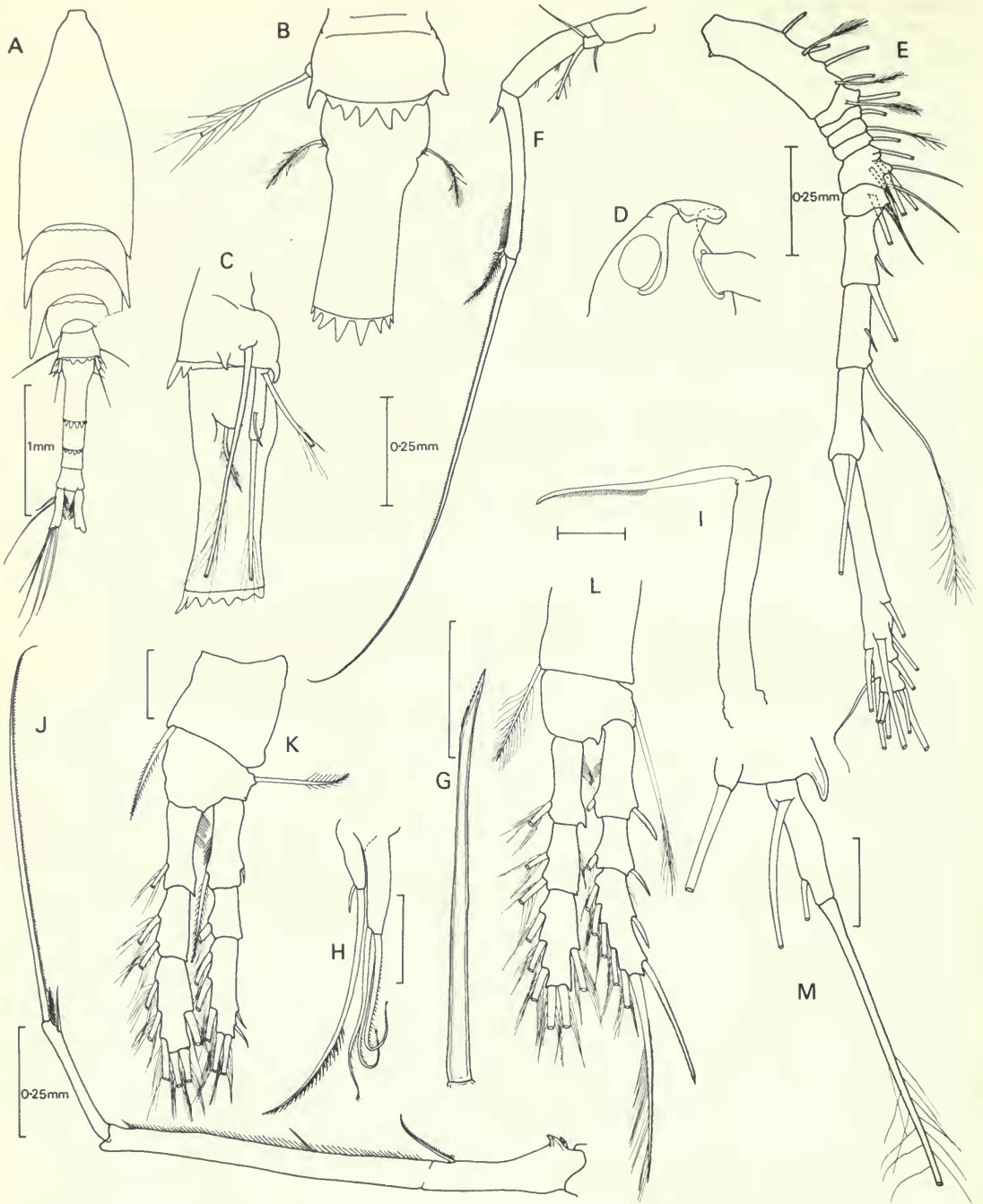


Fig. 22 *Hyalopontius spinatus* n. sp., holotype female: A, dorsal; B, anterior portion of urosome, dorsal; C, same, lateral; D, rostrum; E, first antenna; F, second antenna; G, mandible; H, first maxilla; I, second maxilla; J, maxilliped; K, first leg; L, second leg; M, fifth leg. Scales 0.1 mm unless otherwise indicated.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9541 18. BM(NH) registration number 1977.271.

REMARKS. The specific name refers to the spinose processes formed by the development of the epimeral plates of free thoracic somites 1 and 2. This character, together with the armature formula of legs 1-4 and the position of the lateral setae of the caudal ramus in the proximal half of the ramus, serves to separate *H. spinatus* from other species.

Hyalopontius roei sp. nov.

DIAGNOSIS. *Female*. Body moderately elongate (Fig. 23A), about 4.3 times longer than greatest width; prosome about 1.3 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somites pointed but not markedly produced. Relative lengths of urosome somites and caudal ramus 15 : 32 : 15 : 9 : 14 : 15. Dentate hyaline membrane present on posterior margins of urosome somites 1-4. First urosome somite with 2 small dorso-lateral processes near posterior margin (Fig. 23B). Caudal ramus about 2.6 times longer than wide; lateral setae in distal half of ramus.

Relative lengths of first antenna segments 19 : 1 : 2 : 2 : 2 : 5 : 4 : 11 : 10 : 12 : 32 (Fig. 23C). Second antenna (Fig. 23E) exopod about 2 times longer than wide; distal segment of endopod with lateral spine situated about 21% of distance along segment; terminal claw longer than rest of appendage. Mandible (Fig. 23F) with complex tip comprising a row of dentate projections, a blade-like process and an apical portion. First maxilla (Fig. 23G) as in other species of genus. Basal segment of maxilliped (Fig. 23H) with 3 small bumps proximally on inner surface and not distinctly separated from segment 2; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 83 : 6 : 11 respectively.

Legs 1-4 (Fig. 23I) armature formula as for generic diagnosis except:

	Exopod
Leg 1	I-1; 0-1; II, 2, 3
Leg 2	I-1; I-1; III, I, 5
Leg 3	I-1; I-1; II, I, 5

Leg 5 (Fig. 23J) with large inner spinose process on basal segment; free segment with long apical seta and long proximal seta on lateral margin, distal seta just longer than segment.

Body length of holotype ♀ 5 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean, 'Discovery' Stn 9131 23. BM(NH) registration number 1977.320.

REMARKS. This species is named after Dr Howard Roe who found most of the new *Hyalopontius* material described in this account. It can be distinguished by the combination of the following characters; the body proportions, the absence of marked epimeral plates, the position of the lateral spine at 21% of the distance along the distal segment of the second antenna endopod and the armature formula of legs 1-4.

Hyalopontius cinctus sp. nov.

DIAGNOSIS. *Female*. Body slender (Fig. 24A), about 4.7 times longer than greatest width; prosome about 1.3 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somite 2 slightly produced posteriorly; those of somite 3 also produced posteriorly but not reaching as far as posterior border of first urosome and not expanded laterally (Fig. 24B). Relative lengths of urosome somites and caudal ramus 14 : 37 : 14 : 9 : 14 : 12. Dentate hyaline membranes present around posterior borders of urosome somites 1-4. First urosome somite with a pair of large blunt processes situated dorso-laterally near posterior margin (Fig. 24B). Caudal ramus (Fig. 24C) about 2.4 times longer than wide; lateral setae in distal half of ramus.

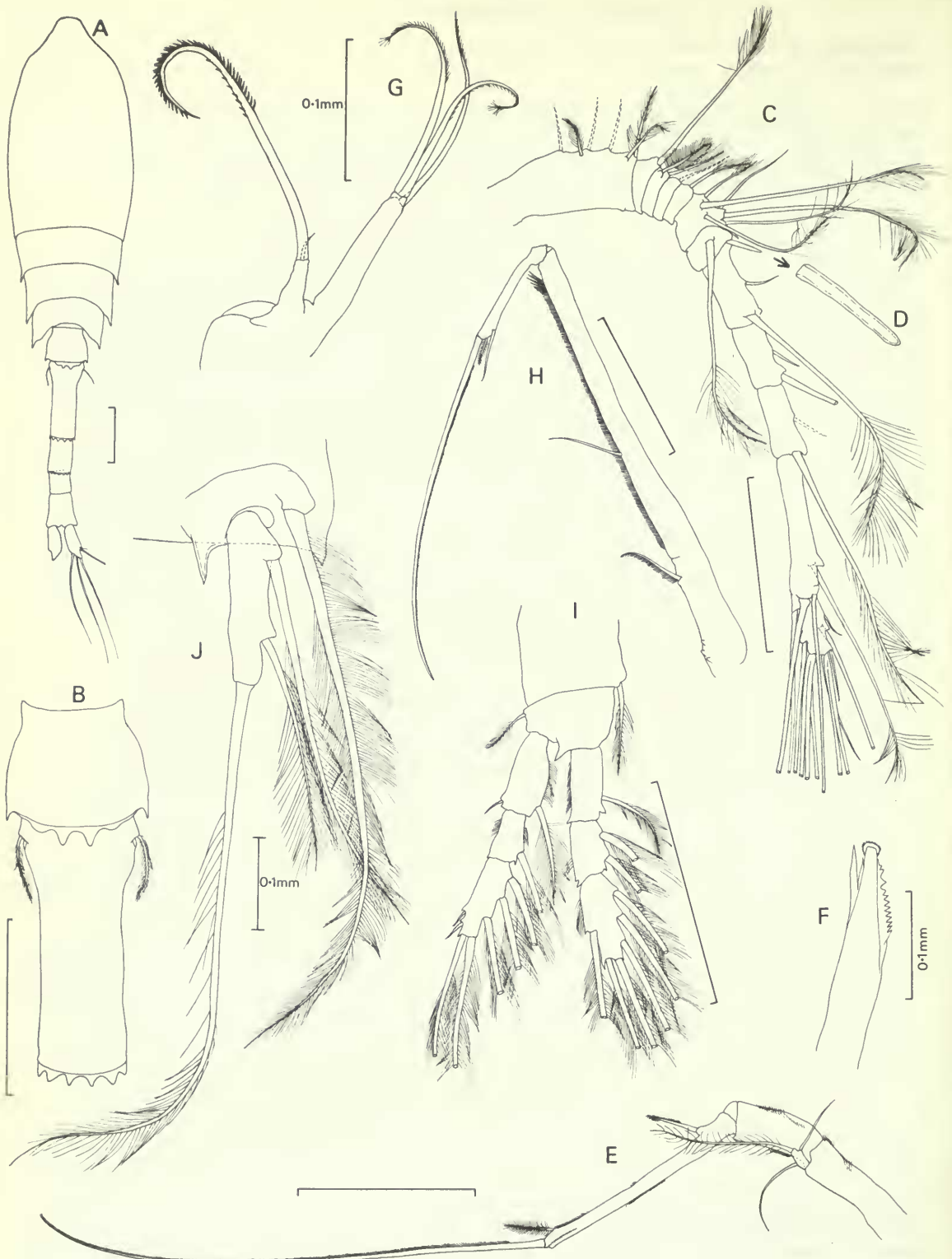


Fig. 23 *Hyalopontius roei* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, first antenna; D, spine from first antenna seg. 7; E, second antenna; F, tip of mandible; G, first maxilla; H, maxilliped; I, first leg; J, fifth leg. Scales 0.5 mm unless otherwise indicated.

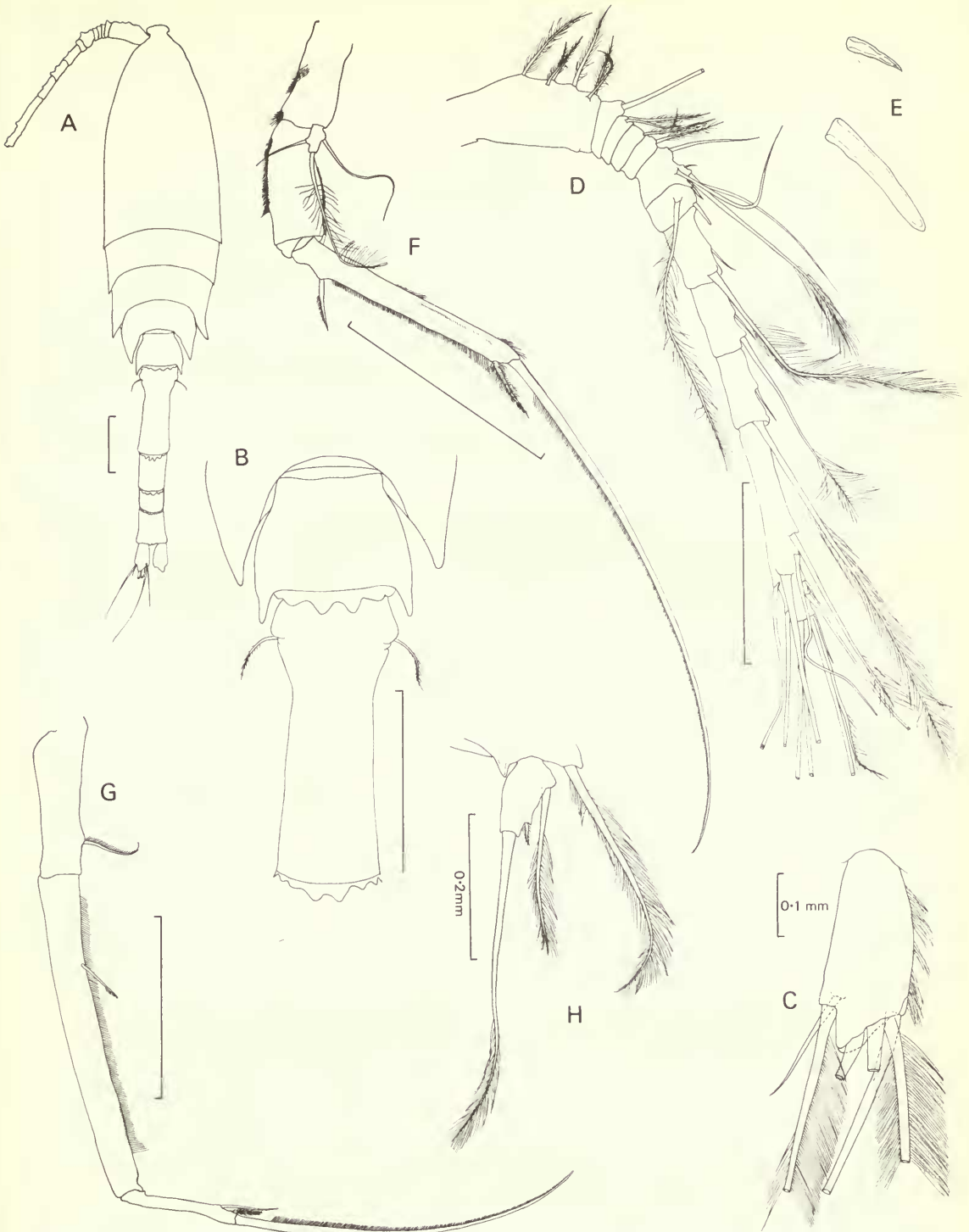


Fig. 24 *Hyalopontius cinctus* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, caudal ramus; D, first antenna; E, spines from first antenna segs 6 & 7; F, second antenna; G, maxilliped; H, fifth leg. Scales 0.5 mm unless otherwise indicated.

Relative lengths of first antenna segments 20 : 1 : 2 : 2 : 2 : 5 : 4 : 10 : 11 : 11 : 32 (Fig. 24D). Second antenna (Fig. 24F) robust; exopod about 1.9 times longer than wide; distal segment of endopod with lateral spine positioned about 22% of distance along segment; terminal claw longer than rest of appendage. Segments 1 and 2 of maxilliped (Fig. 24G) distinctly separated; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 81 : 6 : 13 respectively.

Legs 1-4 armature formula as for generic diagnosis except:

	Exopod
Leg 1	I-1; 0-1; II, 2, 3
Leg 2	I-1; I-1; II-III*, I, 5
Leg 3	I-1; I-1; II, I, 5

* Two spines are present on one member and three on the other.

Leg 5 (Fig. 24H) with small inner process on basal segment; free segment with long apical seta, medium length proximal seta and very short distal seta on lateral margin.

Body length of holotype ♀ 4.94 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9131 23. BM(NH) registration number 1977.321.

REMARKS. The specific name of this species alludes to the distinctive leg 5. The short distal seta on the lateral margin of the free segment of leg 5 serves to distinguish *H. cinctus* from the other described species of the genus.

Hyalopontius enormis sp. nov.

DIAGNOSIS. *Female*. Body large, squat in appearance (Fig. 25A); about 2.9 times longer than greatest width; prosome about 2 times longer than urosome. Rostrum rounded at apex. Epimeral plates of free thoracic somites hardly produced at all. Relative lengths of urosome somites and caudal ramus 17 : 27 : 14 : 8 : 14 : 20. Smooth hyaline membranes present on posterior margins of urosome somites 1-4. First urosome somite without spinose processes. Genital complex very broad (Fig. 25B), only 1.1 times longer than greatest width. Caudal ramus (Fig. 25C) about 2.5 times longer than wide; lateral setae in distal half of ramus.

Relative lengths of first antenna segments 19 : 1 : 1 : 2 : 2 : 6 : 3 : 8 : 10 : 13 : 35 (Fig. 25D). Second antenna (Fig. 25E) robust, first endopod segment fused to basipod; exopod about 4.6 times longer than wide; lateral seta on distal segment of endopod positioned 20% of distance along segment; terminal claw shorter than rest of appendage. Mandible (Fig. 25F) with complex tip comprising dentate margin, trilobed apical portion and hirsute lateral portion. First maxilla (Fig. 25G) and second maxilla (Fig. 25H, I) as in other members of genus. Maxilliped (Fig. 25J) with segments 1 and 2 fused; relative lengths of terminal claw, hirsute subapical seta and naked lateral seta 74 : 5 : 21 respectively. Legs 1-4 (Figs 25K, L) as for generic diagnosis except:

	Exopod
Leg 1	I-1; 0-1; II, 2, 3
Leg 2	I-1; I-1; III, I, 5
Leg 3	I-1; I-1; II, I, 5

Leg 5 (Fig. 25M) with small inner process on basal segment; free segment with long apical seta and 2 lateral setae of medium length.

Body length of holotype ♀ 7.6 mm.

MATERIAL EXAMINED. Holotype ♀: N.E. Atlantic Ocean 20° N 21° W, 'Discovery' Stn 9131 23. BM(NH) registration number 1977.319.

REMARKS. This is the largest known planktonic siphonostomatoid and can be distinguished from other species of the genus by its body proportions, the shape of the genital complex and the elongate exopod of the second antenna.

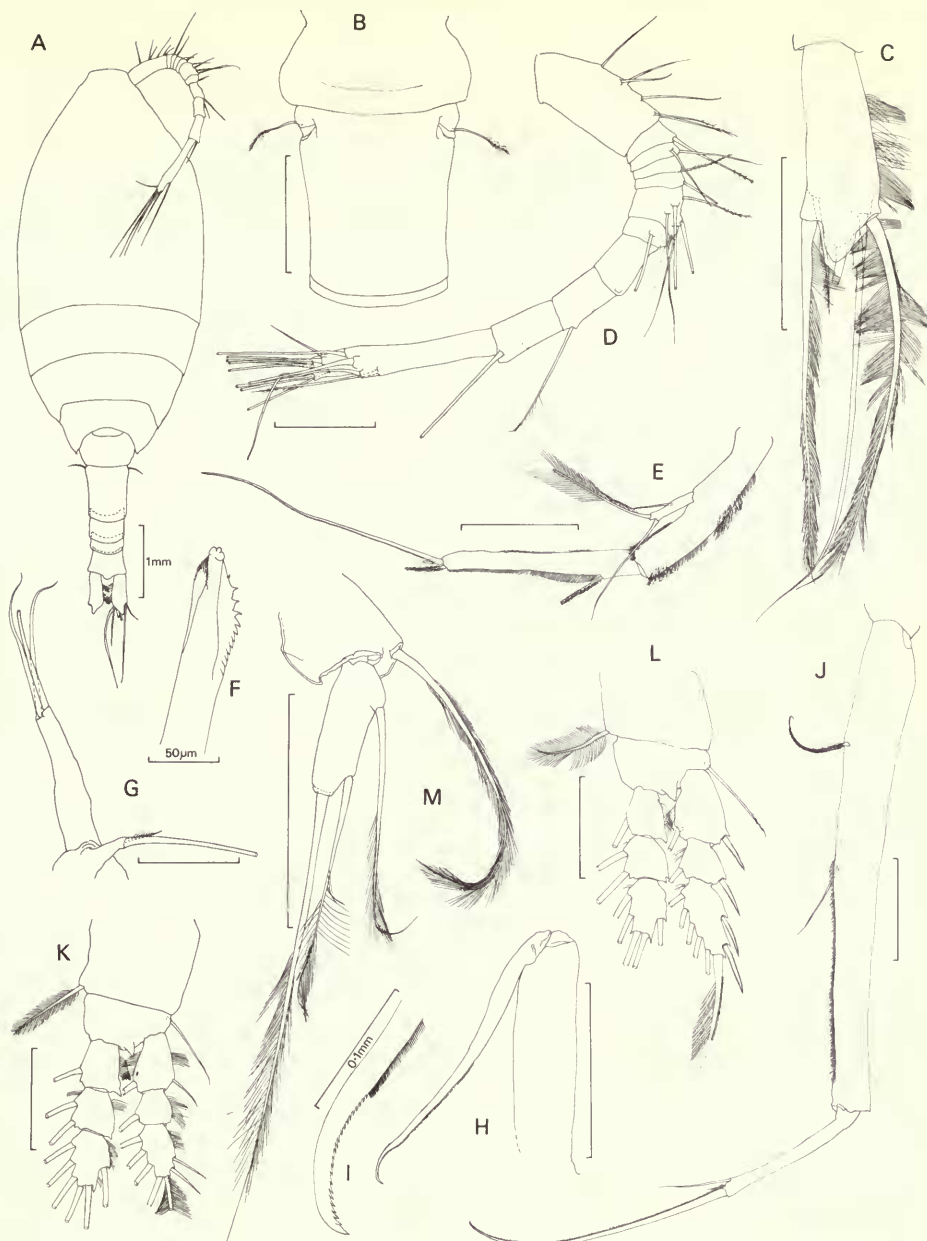


Fig. 25 *Hyalopontius enormis* n. sp., holotype female: A, dorsal; B, anterior portion of urosome; C, caudal ramus; D, first antenna; E, second antenna; F, tip of mandible; G, first maxilla; H, second maxilla; I, tip of second maxilla; J, maxilliped; K, first leg; L, second leg; M, fifth leg. Scales 0.5 mm unless otherwise indicated.

MORMONILLOIDA

The genus *Mormonilla* was first described by Giesbrecht in 1891, but because it exhibits a combination of podoplean and gymnoplean characters its position in the classification of the Copepoda is still uncertain. Giesbrecht (1891, 1892) placed it in a separate family, the Mormonillidae, within the Podoplea Ampharthandria, which also included the families Cyclopidae, Harpacticidae

and Monstrillidae. The latter three families were raised to subordinal level by Sars (1901). Sars (1902) placed *Mormonilla* in the family Tortanidae of the Calanoida, but later (1913) changed this opinion, and stated that the systematic position of the genus is very doubtful though it may perhaps be regarded as the type of a very anomalous family of the gnathostomous Cyclopoida. Few authors have considered the systematic position of the Mormonillidae since Sars. Rose (1933) adopted a cautious approach and placed the Mormonillidae in the Podoplea, but did not assign this family to any of the existing suborders.

In a recent work which deals with copepod systematics (Kabata, 1979), a more natural arrangement of the podoplean line is attained with the recognition of six orders: Harpacticoida, Monstrilloida, Misophrioida, Siphonostomatoida, Poecilostomatoida and Cyclopoida. The Mormonillidae appear to be more closely related to the Misophrioida than to any other order, in possessing a podoplean arrangement of the body somites and typically gymnoplean mouthparts. However, *Mormonilla* differs from the two genera that comprise the aberrant Misophrioida (*Misophria* Boeck and *Benthomisophria* Sars) in the absence of a 'heart', the small number of segments in the first antenna and the complete absence of the fifth leg. *Mormonilla* resembles the cyclopoid genus *Oithona* Baird 1843 in general body facies and the structure of the first antenna, but the presence of a well-developed exopod on the second antenna suggests that the shared characters owe more to convergence than to a true phylogenetic relationship. It is therefore proposed to raise the family Mormonillidae to ordinal level.

Family MORMONILLIDAE

Genus *MORMONILLA* Giesbrecht, 1891

DIAGNOSIS. Body slender, cycloform (Fig. 26A); with 5-segmented prosome and 4-segmented urosome. Genital complex with paired ventral genital openings and spinose areas laterally. Caudal ramus longer than urosome, bearing 6 armature elements. First antenna 3- or 4-segmented. Second antenna (Fig. 26D) with 8-segmented exopod and 2-segmented endopod. Mandible (Fig. 26E) blade with strongly incised teeth; palp comprising large basis fused to endopod and 1-segmented exopod; both rami armed with 6 plumose setae. First maxilla (Fig. 26F) with well-developed basis; gnathobase small but distinct and bearing 8 armature elements; both exopod and endopod 1-segmented, armed with 6 and 8 setae respectively. Second maxilla (Fig. 26G) elongate, 5-segmented; proximal segment with 3 endites, second segment with 1 endite and an isolated seta; remaining 3 segments with 1, 1 and 4 armature elements. Maxilliped 2- or 3-segmented.

Legs 1-4 biramous; leg 1 with 2- or 3-segmented rami; leg 2 exopod 2- or 3-segmented, endopod 1- or 2-segmented; leg 3 with 1 segmented endopod and 2- and 3-segmented exopod; leg 4 with 1-segmented endopod and 2-segmented exopod.

Legs 5 and 6 absent.

Male unknown.

TYPE-SPECIES. *Mormonilla phasma* Giesbrecht, 1891.

Mormonilla phasma Giesbrecht, 1891

DIAGNOSIS. Widest part of genital complex in anterior third (Figs 26B, C). Lateral seta on caudal ramus situated about 33% of distance along ramus (Fig. 26A). First antenna 3-segmented, relative lengths of segments about 56 : 28 : 16. Maxilliped (Fig. 26H) 2-segmented; proximal segment with 6 medial margin setae, distal segment with 7 setae.

Leg 1 (Fig. 26I) with spinose inner projections on coxa, basis and endopod segments; both rami 2-segmented; legs 2-4 with 2-segmented exopods and 1-segmented endopods; armature formula as follows.

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

Body length of female from 1.58 to 1.73 mm.

MATERIAL EXAMINED. 1507 ♀♀: N.E. Atlantic, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.272-281.



Fig. 26 *Mormonilla phasma*: A, female; B, genital complex, lateral; C, same, ventral; D, second antenna; E, mandible; F, first maxilla; G, second maxilla; H, maxilliped; I, first leg; J, second leg; K, third leg; L, fourth leg. Scales 0.1 mm unless otherwise indicated.

REMARKS. This species is most readily distinguished by the position of the lateral seta on the caudal ramus when sorting through large samples of *Mormonilla*. Other significant differences are found in the segmentation of the first antennae and legs 1–3.

Mormonilla minor Giesbrecht, 1891

Mormonilla minor Giesbrecht, 1891: 474.

Mormonilla polaris Sars, 1900: 120–126, pl. XXXIV.

Mormonilla atlantica Wolfenden, 1905: 16.

DIAGNOSIS. Widest part of genital complex about at mid-point (Fig. 27B). Lateral seta on caudal ramus located about 16% of distance along ramus (Fig. 27A). First antenna 4-segmented, relative lengths of segments about 25:28:25:22 (Fig. 27C). Maxilliped (Fig. 27D) indistinctly 3-segmented; proximal segment with 7 setae on medial margin, middle segment with 1 seta and distal segment with 5 setae. Leg 1 (Fig. 27E) with fringes of strong setules on inner margins of coxa, basis and endopod; both rami usually 3-segmented; leg 2 (Fig. 27F) with 3-segmented exopod and 2-segmented endopod; leg 3 with 3-segmented exopod and 1 segmented endopod; leg 4 with 2-segmented exopod and 1-segmented endopod. Armature formula as follows:

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

Body length of female from 1.2 to 1.38 mm.

MATERIAL EXAMINED. 274 ♀♀: N.E. Atlantic Ocean, 18° N 25° W, 'Discovery' Stn 7089. BM(NH) registration numbers 1977.282–291.

REMARKS. The segmentation of the first pair of swimming legs is rather variable with the leg 1 endopod being either 2- (Giesbrecht, 1891, 1892) or 3-segmented (Sars, 1900; Wolfenden, 1905). This variation appears to reflect merely the degree of separation of the two distal segments and is not regarded as significant (Farran, 1908).

Species depth distributions

The depth distribution data for all of the species recorded from the 'Discovery' Station 7089 Day and Night series are given in Table 3. The vertical migration patterns of the more abundant species are discussed below.

Aegisthus mucronatus: During the day female *A. mucronatus* were found between 210 and 790 m and over 80% of the population was concentrated at 210–290 m. At night the depth range was greater, 25–785 m, and there was some evidence of both upward and downward night scattering as 89% of the population was distributed between 110 and 400 m. The data for the males (Table 3) also provide some evidence of an upward vertical migration at night.

Aegisthus aculeatus: This species was distributed quite uniformly between 700 and 1220 m in the daytime. During the night the depth range was virtually the same although a small number of specimens was recorded at 505–700 m. The population appeared to be more concentrated at night as 86% of individuals were found between 800 and 1010 m. *A. aculeatus* was the dominant harpacticoid between 700 and 1250 m whilst its congener, *A. mucronatus*, was dominant in the 110–500 m depth range. There was little vertical overlap between the distribution of these two species.

Miracia efferata: *M. efferata* was found only within the upper 100 m of the water column both day and night and there is little evidence of any diurnal change in depth distribution.

Other harpacticoid species: The remaining species occurred in small numbers within the following depth ranges: *Macrosetella gracilis*, 55–300 m; *Clytemnestra scutellata*, 10–60 m; *Microsetella*

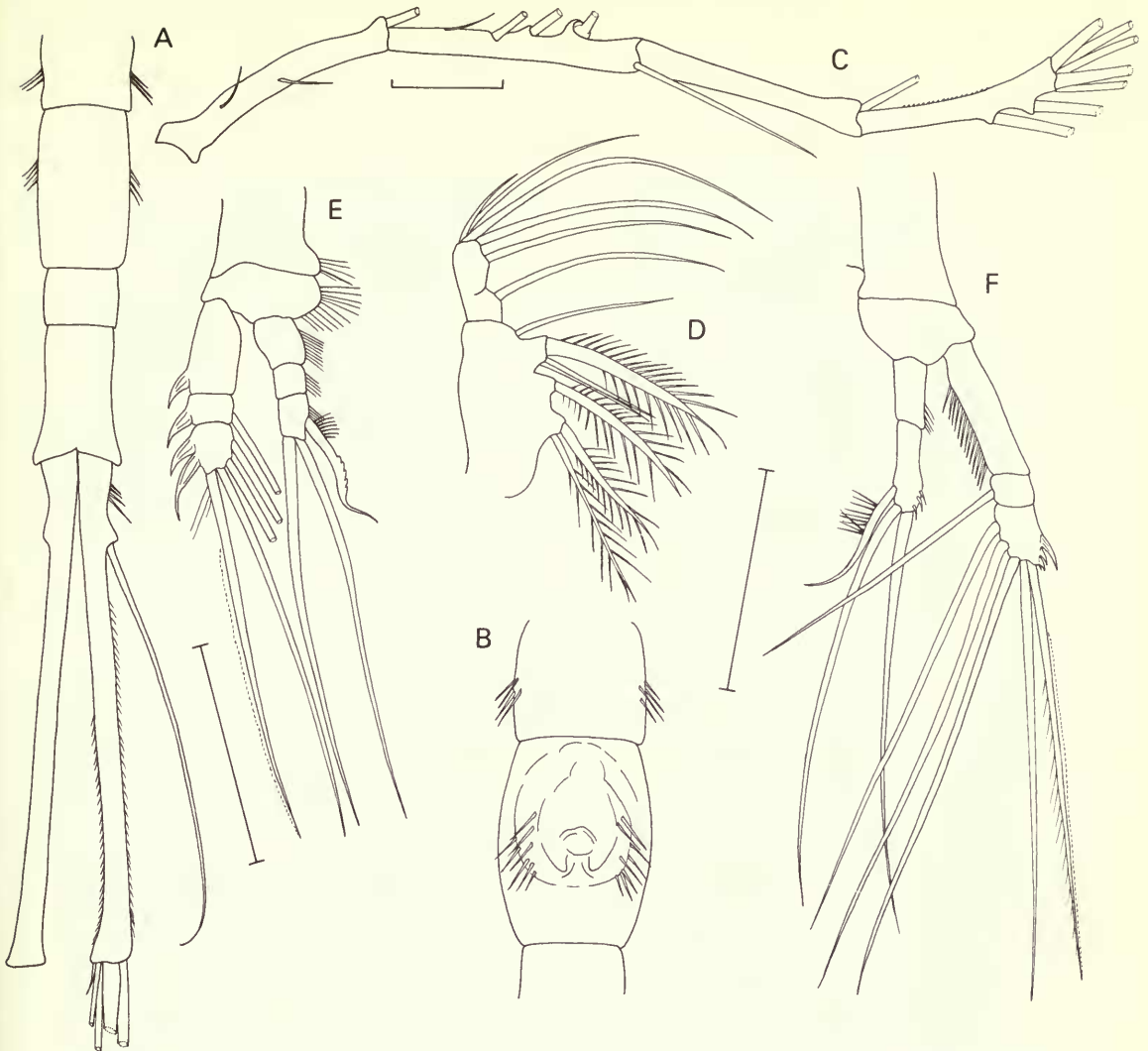


Fig. 27 *Mormonilla minor*: A, female urosome; B, genital complex, ventral; C, first antenna; D, maxilliped; E, first leg; F, second leg. Scales 0.1 mm.

norvegica, 0–290 m; *Neotisbella gigas*, 300–900 m; *Volkmania forficula*, 410–900 m; *Bathytia remota* 1000–1250 m and *Volkmania attenuata* 3760–3920 m.

Pontoeciella abyssicola: Females were recorded between 112 and 600 m during the day, with about 57% of the population distributed above 400 m. At night the depth range was 110–700 m and over 76% of the population was concentrated above 400 m. This indicates that an upward vertical migration of at least part of the population had occurred.

Other siphonostomatoid species: Small numbers of *Ratania flava* were found between 20 and 200 m. The species of *Hyalopontius* were recorded from the following depths: *H. typicus*, 2500–3100 m and 3000–3500 m; *H. hulsemannae*, 3740–3870 m; *H. alatus*, 3000–3500 m; *H. spinatus*, 3830–4060 m; *H. roei*, 3000–3500 m; *H. cinctus*, 3000–3500 m and *H. enormis* 3000–3500 m.

Mormonilla phasma: This species occurred primarily between 410 and 1250 m, with only occasional specimens taken in shallower hauls. The day and night depth distributions were similar with between 70 and 75% of the population concentrated at 410–700 m in the shallow mesopelagic zone.

Table 3. Species composition of the day and night series taken at 'Discovery' Station 7089 (18° N 25° W). (The numbers given are the estimated totals. contaminates are given in parentheses)

Day series Depth (m)	<i>Aegisthus micronatus aculeatus</i>		<i>Aegisthus setella</i>		<i>Micro- mannia forficula</i>		<i>Neotis- bella gigas</i>		<i>Clytem- nestra scutellata</i>		<i>Miracia efferata</i>		<i>Macro- setella gracilis</i>		<i>Pontoe- ciella abyssicola</i>		<i>Ratania flava</i>		<i>Mor- monilla phasma</i>		<i>Mor- monilla minor</i>	
	♀	♂	♀	♂	♀	♂	♀	♂	♂	♀	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
10-0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20-10	-	-	-	-	-	-	-	-	32	-	40	-	-	-	-	-	-	-	-	-	-	-
50-20	-	-	-	-	-	-	-	-	-	256	96	-	-	-	-	-	-	-	-	-	-	-
100-55	-	-	-	-	-	-	-	-	-	128	-	-	-	-	-	-	-	-	-	-	-	-
194-112	-	-	-	-	-	-	-	-	-	32	-	64	32	-	-	64	-	-	-	-	-	-
290-210	-	-	-	-	-	-	-	-	-	-	-	48	96	64	128	16	-	-	-	-	-	16
400-305	2240	160	-	-	-	-	-	-	-	(24)	(8)	-	-	-	64	24	-	-	-	-	-	24
500-410	272	32	-	-	-	-	-	-	-	(8)	-	-	-	144	-	-	-	-	-	-	-	1272
600-515	224	8	-	-	-	-	-	-	-	(8)	-	-	-	48	-	-	-	-	-	-	-	1456
700-610	8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	240
790-700	16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	88
890-800	8	-	-	-	-	-	-	-	-	-	-	-	(8)	-	-	-	-	-	-	-	-	88
1020-910	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	136
1220-1000	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	544
	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	220
Totals =	2768	200	512	16	24	40	8	8	32	456	96	208	32	448	40	80	3980	656				

Table 3 Continued

Night series Depth (m)	<i>Aegisthus mucronatus</i>		<i>Aegisthus aculeatus</i>		<i>Bathypedia remota</i>		<i>Volk- mannia forficula</i>		<i>Neotis- bella gigas</i>		<i>Clytem- nestra scutellata</i>		<i>Miracia efferata</i>		<i>Macro- setella gracilis</i>		<i>Pontoe- ciella abyssicola</i>		<i>Ratania flava</i>		<i>Mor- monilla phasma</i>		<i>Mor- monilla minor</i>		
	♀	♂	♀	♂	♂	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	
10-0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25-10	-	-	-	-	-	-	-	-	-	-	-	-	-	64	-	-	-	-	-	-	-	-	-	-	-
60-25	32	-	-	-	-	-	-	-	-	-	32	-	160	96	-	-	-	-	-	32	-	-	-	-	-
100-49	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
200-110	544	400	-	-	-	-	-	-	-	-	-	-	-	-	48	-	144	-	32	16	-	-	-	-	-
300-210	352	32	-	-	-	-	-	-	-	-	-	-	-	-	80	-	112	-	-	-	-	-	-	-	-
400-300	560	40	-	-	-	-	-	-	-	8	-	-	-	-	-	-	128	-	-	-	-	-	-	-	-
500-410	96	-	-	-	-	-	16	-	-	-	-	-	-	-	-	-	56	-	-	-	-	-	-	-	448
600-505	32	8	-	-	-	-	8	-	-	-	-	-	-	-	(8)	-	56	-	-	-	-	-	-	-	1840
700-610	8	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	56	-	-	-	-	-	-	-	2112
785-700	8	-	-	-	-	-	-	8	-	8	-	-	-	-	-	-	8	-	-	-	-	-	-	-	1688
900-800	-	-	-	-	-	-	-	-	16	16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	920
1010-900	(8)	-	-	-	-	-	-	-	16	16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	640
1250-1000	-	-	-	-	-	-	-	-	-	-	-	-	(12)	-	-	-	-	-	-	-	-	-	-	-	456
Totals=	1632	480	556	40	4	4	24	8	40	8	32	224	160	128	128	504	64	16	64	16	7756	1528	8	8	8

Mormonilla minor: *M. minor* has an almost identical depth distribution to that of *M. phasma*. The depth range is basically 410–1220 m with isolated records from shallower hauls. The distribution is slightly more concentrated in the 410–700 m depth zone with between 86 and 95% of the population occurring there.

The similarity between the depth distributions of the two species of *Mormonilla* is remarkable because the other two pairs of closely related forms found in the mesopelagic zone (i.e. the two species of *Aegisthus* and the two forms of *Oncaea ornata* Giesbrecht) both exhibit a marked degree of vertical segregation (see Boxshall, 1977a for *Oncaea ornata*).

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