

A SYSTEMATIC REVISION OF THE DEEP-SEA SUBFAMILY
LIPOMERINAE OF THE ISOPOD CRUSTACEAN FAMILY
MUNNOPSIDAE

A Systematic Revision of the
Deep-Sea Subfamily Lipomerinae
of the Isopod Crustacean Family
Munnopsidae

George D. F. Wilson

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DEDICATION

This monograph is dedicated to the late Abraham Fleminger whose contributions to my work and to crustacean systematics and ecology will long be remembered.

George D. F. Wilson
June 1988

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The deep-sea isopod collection of Robert Hessler's laboratory, amassed from Woods Hole Oceanographic Institution (WHOI) expeditions in the Atlantic, was the primary source of material for this research. These samples were collected by Howard Sanders, Robert Hessler, George Hampson, and J. Frederick Grassle. Other sources for the specimens are listed in Tables 3 and 4. The scientists directly involved with supplying some specimens are: J. Frederick Grassle and Susan Brown-Leger (WHOI), Michel Segonzac (Centre National de Tri d'Océanographie Biologique), Linda Pequegnat (LGL Ecological Associates), and Desmond E. Hurley (New Zealand Oceanographic Institute). Various sections were read and commented on by members of the Scripps Institution of Oceanography (SIO) and University of California, San Diego (UCSD): Robert R. Hessler, William Newman, Richard Rosenblatt, William Riedel, and Dan Lindsley (UCSD). This paper also benefited from discussions with or reviews by Abraham Fleminger (SIO), Richard Brusca (San Diego Museum of Natural History), Joseph Felsenstein (University of Washington), Jean Snider (National Oceanic and Atmospheric Administration), David Thistle (Florida State University), Mark Grygier, (National Museum of Natural History), and Thomas Bowman (National Museum of Natural History). Sue Stultz (SIO) helped convert microcomputer versions of the manuscript to the mainframe word-processing system, and officiated over the printing of drafts. Kittie Kuhns (SIO) was responsible for the editorial aspects of bringing this monograph to print. I sincerely thank these people for their help and interest. This research was supported by National Science Foundation Systematic Biology grants (DEB 80-07150, BSR 82-15942, and BSR 86-04573). Finally, I owe a great debt of gratitude to my wife Kathy Fries-Wilson, who put up with me during the research and writing, and helped with the editorial work.

ABSTRACT

The fully natatory families of the janiroidean Asellota, the munnopsids *sensu lato*, include a group of genera that blurs the distinction between the Ilyarachnidae and the Eurycopidae. This work determines the interrelationships of the ilyarachnid-like eurycopids, and shows that they are a monophyletic group. In so doing, the family-level systematics of the munnopsids is revised. The ilyarachnid-like eurycopids are assigned to a newly constituted subfamily, the Lipomerinae, and five genera are described, four of which are new. A diagnosis of the subfamily Lipomerinae with a key to the superspecific taxa is included in the taxonomic part. One species in each superspecific taxon is fully described. *Coperonus* n. gen. is a primarily Southern Hemisphere group with several species in the south Atlantic and around the Antarctic continent. The most ilyarachnid-like genus is *Hapsidohedra* n. gen., which may have a cosmopolitan distribution. *Lionectes* n. gen. is found in Antarctic waters. The pan-Atlantic genus *Lipomera* Tattersall is further divided into three new subgenera. One of these subgenera, *L. (Tetracope)* n. subgen., has a coiled gut, a rare occurrence among Crustacea. The cosmopolitan *Mimocopelates* n. gen. is represented by a North Atlantic species group based on the species *M. longipes* n. sp., and an equatorial species *M. anchibraziliensis* n. sp. Character analyses of most munnopsid genera present the characters that reveal relationships between taxa. The character states were assigned evolutionary polarities by comparison with characters in a presumed munnopsid sister group, the Acanthaspidiidae, and other janiroidean families. Computerized phylogenetic analyses produced cladograms that were not fully resolved, but had significantly lower homoplasy values than a tree based on previous classifications. The Lipomerinae were the most significantly monophyletic group of the munnopsid taxa, and a consensus tree of all possible cladograms confirmed the monophyly of the Lipomerinae. Because the previous classifications of the families were not consistent with the most parsimonious cladograms, the following proposals are made: all munnopsid families should be placed into one large family, the Munnopsidae; the Ilyarachnidae and the Munnopsidae *sensu stricto* should be demoted to subfamilial status; and the current subfamilies of the Eurycopidae should be retained. This new classification recognizes the monophyly of the Lipomerinae within the Munnopsidae. Alternatives to this classification are discussed. Supporting the text are appendices illustrating and defining morphological terms.

INTRODUCTION

DEEP-SEA ISOPODS

Isopod crustaceans living in accessible environments like meadows or tide pools are usually cryptic animals. To find them, one generally must look in hidden places - under rocks, in cracks and crevices, or in the gills of fishes. But in one environment, isopods live in the open. This is in the deep sea, the most extensive environment on our planet (Sverdrup et al. 1942).

Unlike isopods living anywhere else, those of the deep-sea benthos are a major feature of the biota. In most abyssal benthic samples, isopods of the suborder Asellota are among the most abundant crustacean taxa, and often account for a large fraction of all species present in an area (Sanders and Hessler 1969; Wilson and Hessler 1987). For example, isopods from the manganese nodule province of the equatorial Pacific represent the third most abundant macrobenthic taxon and their diversity possibly exceeds 125 species at one location (Wilson, unpublished data). In one program 153 isopods were counted from 15 quantitative samples from a 4500 m deep manganese nodule bottom (Wilson and Hessler 1987). The samples held 59 species, a high species richness considering that only 3.75 m² of the sea floor was sampled (*ibid.*).

Deep-sea isopods do not resemble their cryptic shallow marine, freshwater, and terrestrial counterparts. The archetypical isopod is dorsoventrally flattened and has 7 pairs of similar legs, hence the translation of their name "like-footed." A flattened body form is undoubtedly related to a cryptic lifestyle of creeping underneath objects and into cracks and crevices. Deep-sea asellote isopods, however, display a great variety of forms, including narrow walking-stick creatures, species resembling little rocket ships, and highly modified swimmers. Their varied body forms and high species diversity evince a great evolutionary radiation, one apparently in full flower.

Extreme morphological differences among the families of the deep-sea Asellota reflect evolutionary paths separate from other Isopoda: most of the families of deep-sea isopods probably evolved *in situ*, not in shallow water (Hessler and Thistle 1975; Hessler et al. 1979). The evolution of entire families in the deep sea also has biogeographic consequences. These families and most of their genera are cosmopolitan in the deep sea, but are found in shallow water only where special conditions permit their existence (e.g., high latitudes: Hessler and Wilson 1983). In spite of their ubiquity in the deep sea, evidence from some groups suggests that the new species are actively evolving (Wilson 1980a, 1983a), and species ranges are limited to small geographic areas and narrow depth ranges (Wilson 1982b, 1983b).

Although deep-sea isopods are ecologically important and biogeographically interesting, systematic knowledge on the most important families is sparse. The primary deep-sea families belong to the suborder Asellota, the systematics of which can best be described as superficial. The Asellota have been the subject of several major monographs and numerous smaller papers (best reviewed before 1960 by Wolff 1962). In the last three decades great interest in the taxon has been generated by the discovery of its high diversity of species and morphological types in the deep sea (Menzies 1962; Wolff 1962; Birstein 1963; Hessler and Sanders 1967; Hessler 1970; Hessler et al. 1979). This interest has engendered a rapid accumulation of new species and genera, described from deep-sea samples taken since the early 1960s. However, no major reorganization of the suprageneric taxa has been attempted since the landmark papers of Wolff (1962) and Menzies (1962). As a result, family-level groups tend to be poorly defined because of the wide variety of taxa they include.

This problem is most acute in a group of families called the "munnopsoids"¹ by Wilson and Thistle (1985): Munnopsidae, Eurycopidae, and Ilyarachnidae. The munnopsids include taxa phylogenetically intermediate between the Eurycopidae and the Ilyarachnidae (the genus *Betamorpha* Hessler and Thistle 1975). In addition, a group of munnopsids very similar to the Ilyarachnidae cannot be placed in that family because of the current unsatisfactory definitions of the munnopsid families (Wilson and Hessler 1981). These ilyarachnid-like Eurycopidae are the subject of this monograph. In it, I propose a solution to the systematic problem they present. In so doing, I consider the evolutionary paths taken by the deep-sea munnopsid isopods and their ancestors.

THE MUNNOPSIDS AND THE ILYARACHNID-LIKE EURYCOPIDS

The munnopsid families of the Asellota are often a dominant fraction of deep-sea sled and dredge samples, and are represented by many species and genera in single samples (Wilson and Hessler 1980, 1981). The success of the munnopsids may be related to their primary specialization, the swimming habit. Although primitive asellote isopods have lost the ancient crustacean ability to swim, the munnopsids have an integrated set of adaptations that allows them to swim rapidly and efficiently, but in a posterior direction. This ability resulted in an important adaptive radiation - the evolution of numerous offshoots from a basic swimming type - exemplified by the genus *Eurycope* (Fig. 1; see Appendix 1).

¹ The terms "munnopsoids" (Wilson and Thistle 1985) and "ilyarachnid eurycopids" (Wilson and Hessler 1981) will not be used here because of potential confusion with superfamily-level taxa. In their place, I substitute the terms "munnopsids" and "ilyarachnid-like eurycopids." "Munnopsids" could be construed to have two meanings in this paper, but is defined as having the broad meaning, i.e. including all three natatory families. The ilyarachnid-like eurycopids are assigned to the munnopsid subfamily Lipomerinae Tattersall, so these two terms are used synonymously.

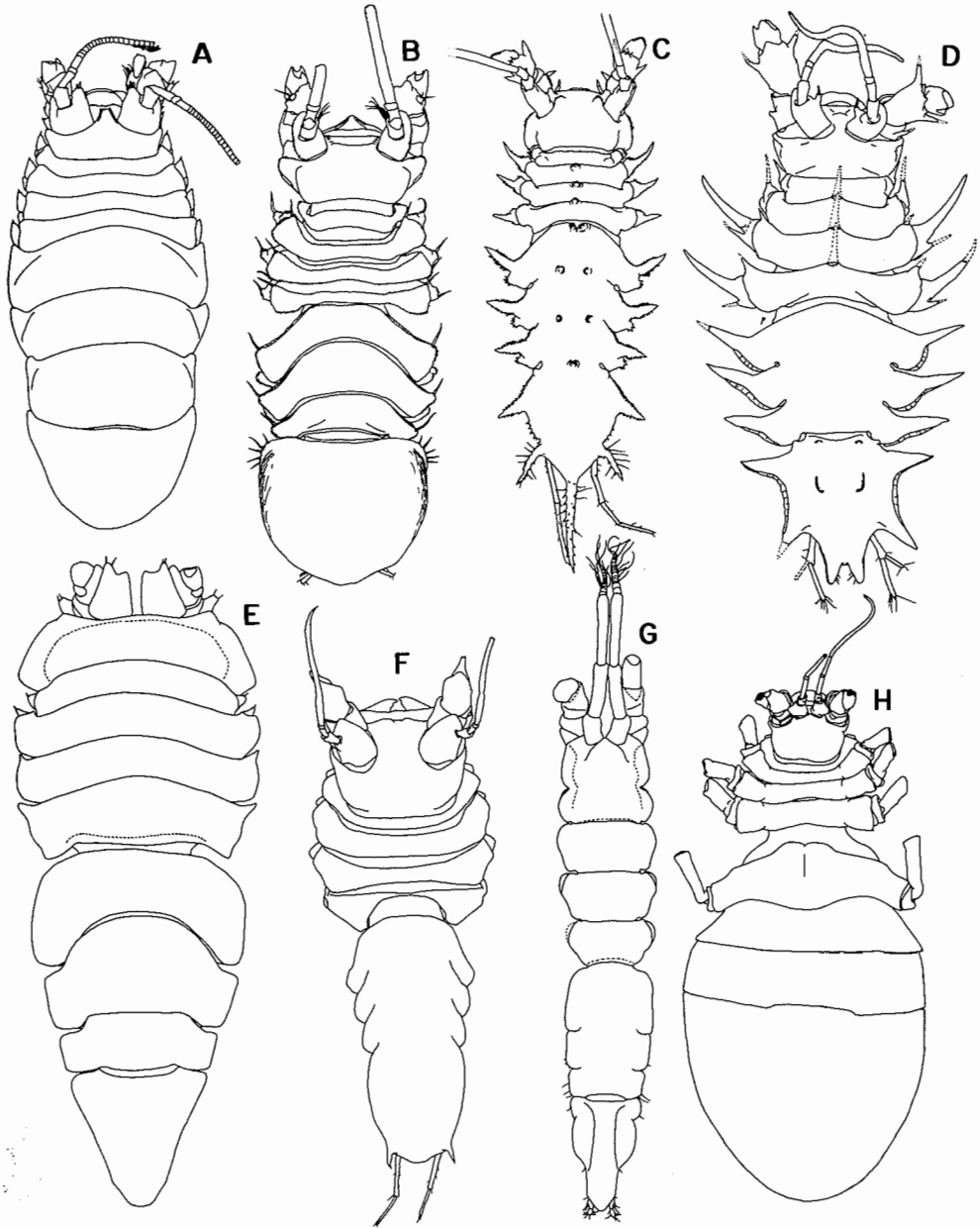


Figure 1. A sampling of the morphological diversity present in the munnopsids, those Isopoda Asellota with distinct natasomes. All are shown in dorsal view with anterior toward the top, not to same scale. A, *Eurycope*. B, *Munnopsurus*. C, *Acanthocope*. D, *Storthyngura*. E, *Ilyarachna*. F, *Munnopsis*. G, *Syneurycope*. H, *Paropsurus*.

TABLE 1.

Classification of the munnopsids (family Munnopsidae *sensu lato* of Sars, 1869) prior to the present study.

Crustacea Pennant, 1777

Class Malacostraca Latreille, 1806

Subclass Eumalacostraca Grobben, 1892

Superorder Peracarida Calman, 1904

Order Isopoda Latreille, 1817

Suborder Asellota Latreille, 1803

Superfamily Janiroidea Sars, 1899

Family Munnopsidae Sars, 1869 *sensu* Wolff, 1962

Genus *Paramunnopsis* Hansen, 1916

Family Eurycopidae Hansen, 1916

Subfamily Eurycopinae Hansen, 1916

Genus *Eurycope* Sars, 1864

Genus *Betamorpha* Hessler and Thistle, 1975

Subfamily Acanthocopinae Wolff, 1962

Subfamily Bathyopsurinae Wolff, 1962

Subfamily Syneurycopinae Wolff, 1962

Family Ilyarachnidae Hansen, 1916

Genus *Ilyarachna* Sars, 1864

Ilyarachnid-like Eurycopids, temporary group *incertae sedis*

Genus *Lipomera* Tattersall, 1905

(Taxa misplaced in the literature)

Ilyarachna aspidophora Wolff, 1962

Eurycope frigida Vanhöffen, 1914

Eurycope cf. frigida Nordenstam, 1933

This classification is extracted from: Bowman and Abele (1982); Hessler and Thistle (1975); and Wilson and Hessler (1981). The classification of Schram (1986) is not used. Only the genera discussed in the introduction are shown.

The munnopsids, a large family as originally conceived by G.O. Sars (1883, 1899), are now classified into three separate families (see Table 1): the Eurycopidae with several subfamilies, the Ilyarachnidae, and the Munnopsidae. Some munnopsids have taken the swimming life to its logical extreme by being holopelagic. Ilyarachnids, on the other hand, have specialized in burrowing into the sediment surface with paddle-shaped posterior legs (probably the source of Sars' appellation of "mud spider" for the type-genus of this group). Nevertheless, ilyarachnids retain the ability to swim.

As presently constituted, the Eurycopidae are more difficult to place in this functional scheme because many of the groups in the family have specializations that resemble those found in the other two families. Some similarities are true homologies, reflecting a common ancestry, such as the resemblance of the eurycopids *Betamorpha* and *Amuletta* to primitive members of the Ilyarachnidae (Thistle and Hessler 1977; Wilson and Thistle 1985). Other similarities undoubtedly are convergent on a common body form. Wilson and Thistle (1985) point out that the present classification of the munnopsids is inadequate to accurately classify taxa currently placed in the Eurycopidae.

Wilson and Hessler (1980, 1981) identified the group of genera within the Eurycopidae that are distinctly ilyarachnid-like (Figs. 2, 3). A comparison of the diagnostic characters of the Ilyarachnidae (Wolff 1962) with the features of these eurycopids (Table 2) reveals substantial similarities between the groups. The overall shape of the natasome and the cephalon are most compelling. In the current literature, these ilyarachnid-like eurycopids are only a collection of species and genera with no taxonomic status. On a purely typological basis (using similarities only), they should be classified with the Ilyarachnidae. The similarities, however, may result from convergence of unrelated taxa to a common body form, thus decreasing the naturalness and usefulness of such a phenetic classification. Therefore, these character complexes are examined in more detail.

The ilyarachnid-like eurycopids first appear in the literature with the description of *Lipomera lamellata* Tattersall, 1905 (1905a,b). Related species are *Eurycope frigida* Vanhöffen, 1914, *E. cf. frigida* Nordenstam, 1933, *Ilyarachna aspidophora* Wolff, 1962 (see Wilson and Hessler 1981). Species of this group appear in more than 60 samples of deep-sea isopods from the North and South Atlantic oceans (see next section). As in other deep-sea Asellota, the ilyarachnid-like eurycopids display high latitude emergence. The ilyarachnid-like eurycopids need revision because their numerical and biogeographic importance has received little attention in the literature.

Morphologically, eurycopids that look like ilyarachnids are fairly diverse. Although *Ilyarachna*-like features are found in all of them, the ilyarachnid-like Eurycopidae do not constitute a single genus-level taxon. The members of this group vary considerably in the development of the last thoracic segment and in

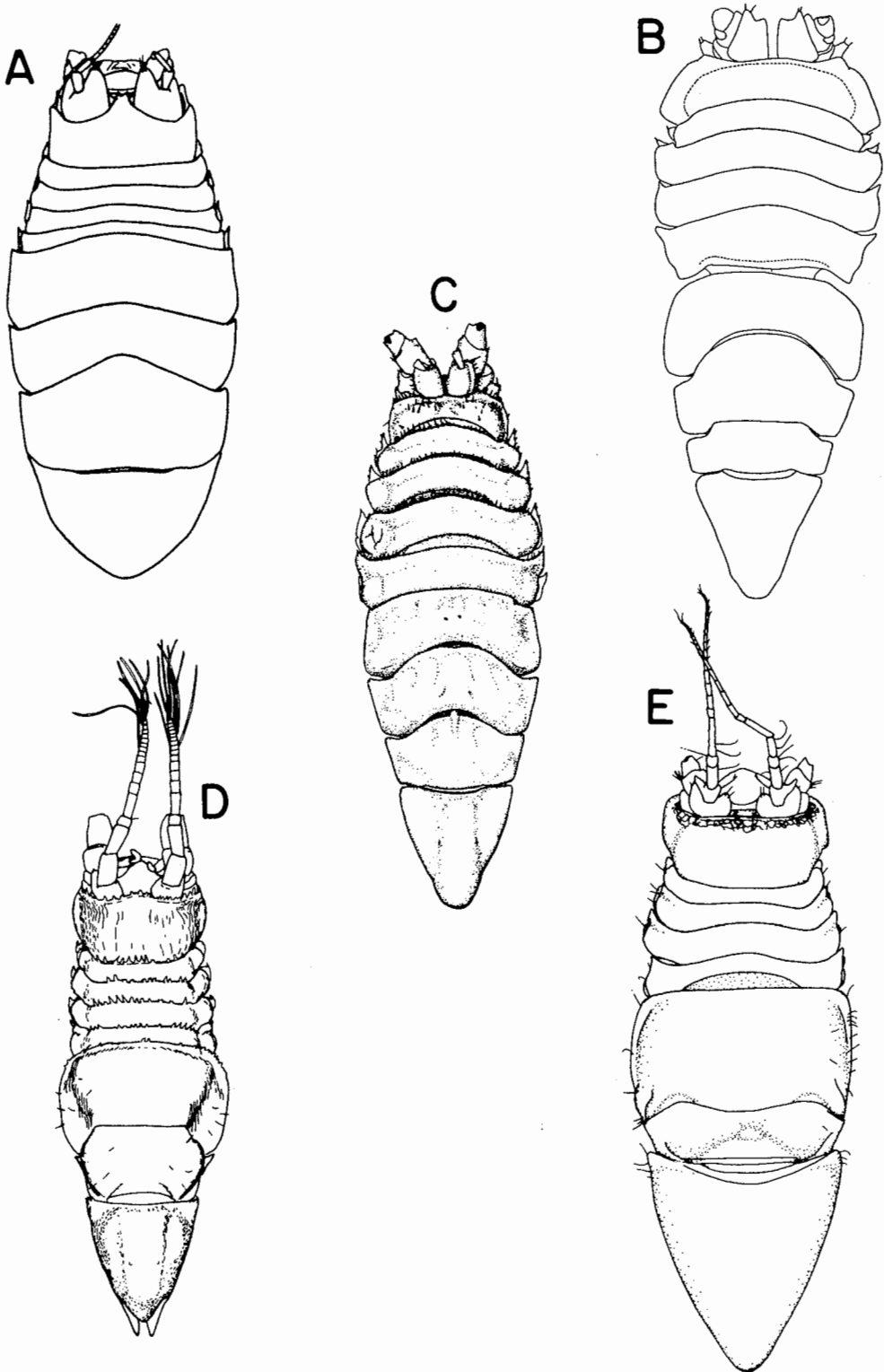


Figure 2. Dorsal views of several munnopsids to illustrate an ilyarachnid-like appearance. Not to same scale. A, *Eurycope*. B, *Ilyarachna*. C, *Amuleta*. D, *Lipomera*. E, *Mimocopelates* n. gen. Not to same scale.

the form of the cephalon; they also have definable differences in the uropods and pleotelson. In this paper, *Lipomera* Tattersall, 1905, is redescribed, and the species of this genus are divided into three subgenera. Four new genera are erected to contain the remaining species originally classified by Wilson and Hessler (1981) as the ilyarachnid-like Eurycopidae. These genera are grouped in the munnopsid subfamily Lipomerinae Tattersall, 1905 (originally proposed as a family). Finally, the phylogeny of the Lipomerinae (= ilyarachnid-like eurycopids) is studied to discover their relationship to the other natatory taxa. Because the Lipomerinae confound the distinction between the Ilyarachnidae and the Eurycopidae, this phylogenetic investigation must also include munnopsid evolution. The result is a new classification of the natatory deep-sea Asellota Janiroidea that uses Sars' original broad definition of the Munnopsidae.

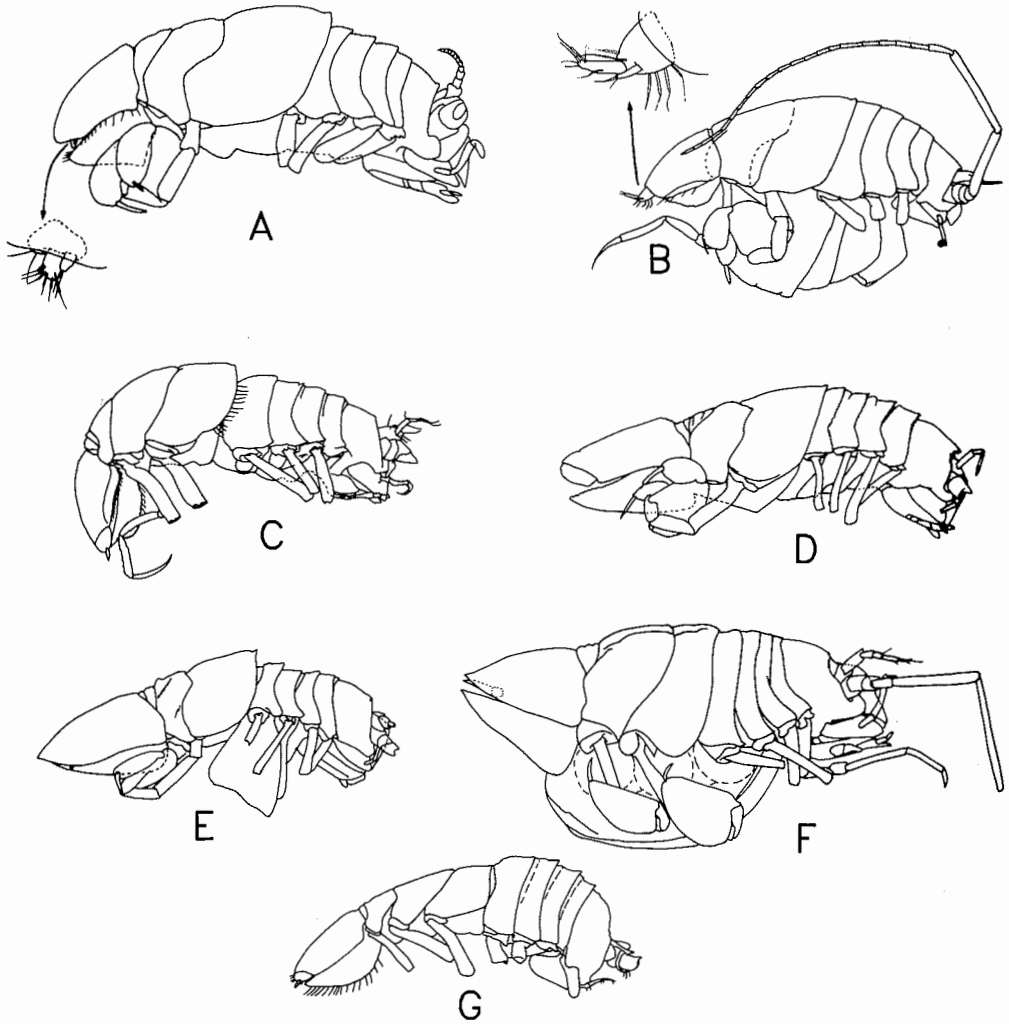


Figure 3. Examples of ilyarachnid-like eurycopids (Lipomerinae) in lateral view, with anterior to the right. A, *Coperonus* n. gen. B, *Lionectes* n. gen. C, *Hapsidohedra* n. gen. D, *Lipomera (Paralipomera)* n. subgen. E, *Mimocopelates* n. gen. F, *Lipomera (Tetracope)* n. subgen. G, *Ilyarachna* (for comparison). Not to same scale.

TABLE 2.

A comparison of the characters from the diagnosis of the Ilyarachnidae (Wolff 1962) with the Lipomerinae.

Ilyarachnidae	Lipomerinae
Pleotelson subtriangular	+
Head broad, without frontal area	+
Antennulae terminal or subterminal	+
Mandibles short and thick	+, -
Mandibles with obtuse incisive part	+, -
Mandibles with reduced setiferous molar process	-
Pereopods III and IV with short basis*	-
Uropods flattened, oval; setiferous protopod; reduced rami	+, -

"+" = Has similar character. "-" = No similar character. Characters found in all munnopsids omitted. * = Character is considered by Thistle and Hessler (1976) to be the principal diagnostic character separating the Ilyarachnidae from the Eurycopidae.

MATERIALS AND METHODS

Several techniques have been applied to the study of the ilyarachnid-like eurycypids, and the munnopsids in general. Often the taxonomic literature is unclear about a particular term, or procedures that are used to generate descriptions, hypotheses of relationship, or classifications. My procedures are explained below, and many of the taxonomic terms are defined in a glossary. The phylogenetic study uses techniques of numerical cladistics, a field in which controversy arises frequently.

SOURCES OF SPECIMENS

The specimens used in this study came from a variety of sources (Tables 4, 5, abbreviations in Table 3). The principal source was a series of deep benthic sampling transects in various basins of the Atlantic Ocean. These samples were collected by the Woods Hole Oceanographic Institution (WHOI) scientists under the direction of Howard Sanders, Robert Hessler, and J. Frederick Grassle. These samples include specimens from the Gay Head-Bermuda Transect, off New England (Sanders et al. 1965; Hessler and Sanders 1967). An important collection of Antarctic isopods was provided by John Rankin, University of Connecticut, from samples collected in the Weddell Sea during 1968 and 1969 (68Rankin and 69Rankin samples). Specimens from the South Shetland Islands were collected by Eric Mills, Institute of Oceanography, University of Dalhousie, and Robert Hessler, Scripps Institution of Oceanography, during the Hudson 70 Expedition to the Antarctic and subantarctic islands in the vicinity of the Palmer Peninsula (IODal samples). Some specimens from the Northeast Atlantic were collected by a joint European sampling program around the British Isles and in the Bay of Biscay (INCAL samples, see Sibuet 1979 for more information). Robert Hessler provided two samples from Hjeltefjord, Norway (HMB samples). Recent studies of slope fauna off the eastern United States, directed by James Blake and Nancy Maciolek-Blake of Battelle New England Marine Research Laboratory (U.S. Department of the Interior Minerals Management Service [MMS] contract 14-12-0001-30064), have provided samples that help establish the ranges of species found on the Gay Head-Bermuda Transect (BAT samples). An important collection of Gulf of Mexico Isopoda collected during 1983 and 1984 (LGL1, LGL2, LGL3 samples) was provided by Linda Pequegnat, LGL Ecological Research Associates (MMS contracts 14-12-0001-30046 and 14-12-0001-30212). Specimens collected from slope depths off New Zealand (NZOI samples) were kindly sent by Desmond Hurley, New Zealand Oceanographic Institute, and Roger Lincoln, British Museum, Natural History. These latter specimens are mentioned only briefly and will be the subject of a future paper describing New Zealand munnopsids.

TABLE 3.

Abbreviations used in the text.

Sources of Specimens

BAT	Battelle New England Marine Research Laboratory
HMB	Marine Biology Course at Herdla, Norway
INCAL	Joint European Expedition "Intercalibration"
IODal	Institute of Oceanography, Dalhousie
LGL	LGL Ecological Research Associates
NZOI	New Zealand Oceanographic Institute
RANKIN	John Rankin Samples, Weddell Sea
WHOI	Woods Hole Oceanographic Institution

Depositories of Specimens

BMNH	British Museum (Natural History)
MNHN	Museum National d'Histoire Naturelle, Paris
SIO	Robert Hessler collection, Scripps Institution of Oceanography
USNM	United States Museum of Natural History
ZMUC	Zoological Museum, University of Copenhagen

Other Abbreviations

bl	Body length, measured from frons to pleotelson tip
inds	Individuals, usually reporting number used in a measurement

TABLE 4. Samples containing Lipomerinae.

Genus*	Program and Station Number	Location	Midpoint Latitude	Midpoint Longitude	Midpoint Depth (m)
H*	R/V Galathea sta. 639 (Wolff 1962)	Off New Zealand	37° 31' S	177° 08' W	213
C*	Swedish Antarctic Expedition sta. 34 (Nordenstam 1933)	South Georgia			
		Off Cumberland Bay	54° 11' S	36° 18' W	281
LP1**	R/V Helga station (Tattersall 1905a,b)	Porcupine Bank	53° 58' N	12° 16' W	360
C*, LN*	Gauss Station (Vanhöffen 1914)	Eastern Antarctica	66° 02' S	89° 38' E	385
C	68Rankin 0001ES	S. Weddell Sea	74° 06' S	39° 38' W	650
C	68Rankin 0001AD	S. Weddell Sea	74° 06' S	39° 38' W	650
C	68Rankin 0018ES	S. Weddell Sea	72° 46' S	42° 45' W	1926
C	68Rankin 0055SBT	W. Weddell Sea	66° 48' S	49° 54' W	3338
C, LN	69Rankin 001AD	S. Weddell Sea	77° 49' S	42° 04' W	659
LP3	BAT M1-13-1-7	Off Delaware Bay, USA	37° 54' N	73° 45' W	1613
LP3	BAT S1-3-1-3	Off Cape Lookout, USA	34° 15' N	75° 40' W	1500
LP3	BAT S2-3-2-(1-9)	Off Cape Lookout, USA	34° 15' N	75° 40' W	1500
LP3	HMB Beyer 7-8/VII/78	Hjeltefjord, Norway	60° 34' N	04° 53' E	260
LP3	HMB RPsled 4/VII/78	Hjeltefjord, Norway	60° 34' N	04° 53' E	260
M1	INCAL DS13	NE Atlantic Ocean	46° 02' N	10° 12' W	4822
M1	INCAL OS04	NE Atlantic Ocean	46° 04' N	10° 17' W	4706
H	INCAL WS03	NE Atlantic Ocean	48° 19' N	15° 23' W	4829
C	IODal 6	S. Shetland Isl.	62° 40' S	60° 22' W	146
LN	IODal 7	S. Shetland Isl.	62° 29' S	58° 47' W	59
C, LN**	IODal 13	S. Shetland Isl.	61° 18' S	58° 00' W	282
L3	LGL1 C1/4	N. Gulf of Mexico	28° 03' N	90° 15' W	420
L3	LGL5 WC05/5	N. Gulf of Mexico	27° 47' N	91° 46' W	298
L3	LGL5 WC07/3	N. Gulf of Mexico	27° 46' N	91° 13' W	444

TABLE 4. (continued)

Genus*	Program and Station Number	Location	Midpoint Latitude	Midpoint Longitude	Midpoint Depth (m)
H	LGL1 C4	N. Gulf of Mexico	27° 30' N	89° 46' W	1378
H	LGL2 C2	N. Gulf of Mexico	27° 54' N	90° 06' W	595
H	LGL2 C4	N. Gulf of Mexico	27° 28' N	89° 47' W	1386
H	LGL3 C3	N. Gulf of Mexico	27° 49' N	90° 07' W	892
H	LGL3 C7	N. Gulf of Mexico	27° 44' N	89° 59' W	1020
H	LGL3 C9	N. Gulf of Mexico	27° 29' N	89° 48' W	1390
H	LGL4 E2	N. Gulf of Mexico	28° 16' N	86° 15' W	618
H	LGL5 WC06	N. Gulf of Mexico	27° 43' N	91° 33' W	554
H	LGL5 WC11	N. Gulf of Mexico	27° 24' N	92° 44' W	1225
LP2	LGL2 E4	N. Gulf of Mexico	28° 04' N	86° 35' W	1358
LP2	LGL2 W2	N. Gulf of Mexico	27° 25' N	93° 21' W	605
LP2	LGL2 W3	N. Gulf of Mexico	27° 11' N	93° 19' W	850
LP2	LGL3 C8	N. Gulf of Mexico	27° 31' N	89° 49' W	1147
LP2	LGL4 E3a	N. Gulf of Mexico	28° 29' N	87° 00' W	850
LP2	LGL4 E3b	N. Gulf of Mexico	28° 07' N	86° 19' W	860
LP2	LGL5 WC12	N. Gulf of Mexico	27° 20' N	91° 33' W	1236
M2	NZOI F719	Off New Zealand	40° 14' S	177° 13' E	604
M2	NZOI E753	Off New Zealand	44° 45' S	174° 30' E	810
M2	NZOI F911	Off New Zealand	34° 38' S	174° 36' E	1493
M2	NZOI P939	Off New Zealand	41° 20' S	166° 55' E	1780
M2	NZOI S147	Off New Zealand	44° 30' S	174° 19' E	760
M2	NZOI S153	Off New Zealand	45° 21' S	173° 36' E	1386

Descriptions and abbreviations of programs given in text. In trawl samples that have different start and finish positions, only the midpoints for the both latitudes, longitudes, and depths are given. All positions are rounded off to the nearest minute. The abbreviations for the genera are as follows: C, *Coperonus* n. gen.; H, *Hapsidohedra* n. gen.; LN, *Lionectes* n. gen.; LP1, *Lipomera* (*Lipomera*); LP2, *Lipomera* (*Paralipomera*) n. subgen.; LP3, *Lipomera* (*Tetracope*) n. subgen.; M1, *Mimocopelates longipes* n. gen., n.sp. species group; M2, *Mimocopelates anchibraziliensis* n. gen., n.sp. species group. Abbreviations with an asterisk (*) indicate a type locality. Abbreviations with a double asterisk (**) indicate a type locality for a generic type. All samples except those collected by the Woods Hole Oceanographic Institution programs (see Table 5).

TABLE 5.

Samples collected by the Woods Hole Oceanographic Institution.

Genus*	Program and Station Number	Location	Midpoint Latitude	Midpoint Longitude	Midpoint Depth (m)
M1	WHOI F1	Gay Head-Bermuda Transect	39° 47' N	70° 45' W	1500
M1	WHOI 64	Gay Head-Bermuda Transect	38° 46' N	70° 06' W	2886
M1	WHOI 66	Gay Head-Bermuda Transect	38° 47' N	70° 09' W	2802
M1, LP3	WHOI 73	Gay Head-Bermuda Transect	39° 47' N	70° 43' W	1400
M1	WHOI 85	Gay Head-Bermuda Transect	37° 59' N	69° 26' W	3834
M1	WHOI 103	Gay Head-Bermuda Transect	39° 44' N	70° 37' W	2022
LP3	WHOI 119	E. Gay Head-Bermuda Transect	32° 16' N	64° 32' W	2159
M1	WHOI 126	Gay Head-Bermuda Transect	39° 37' N	66° 46' W	3806
M1	WHOI 128	Gay Head-Bermuda Transect	39° 47' N	70° 45' W	1254
M1	WHOI 131	Gay Head-Bermuda Transect	36° 29' N	67° 58' W	2178
LP2	WHOI 142	Off Senegal, Africa	10° 30' N	17° 52' W	1710
M1	WHOI 156	Near St. Peter & St. Paul Rocks	00° 46' S	29° 26' W	3459
M2	WHOI 159	Off Brazil	07° 58' S	34° 22' W	887
C, M2	WHOI 162	Off Brazil	07° 59' S	34° 06' W	1493
LP2, M2	WHOI 167	Off Brazil	07° 54' S	34° 17' W	975
LP2, M2	WHOI 169	Off Brazil	08° 03' S	34° 24' W	587
LP1	WHOI 180	Off Walvis Bay	22° 54' S	13° 32' E	205
H	WHOI 189	Off Walvis Bay	23° 00' S	12° 45' E	1011
M1, LP3**	WHOI 209	Gay Head-Bermuda Transect	39° 47' N	70° 49' W	1597

TABLE 5. (continued)

Samples collected by the Woods Hole Oceanographic Institution.

Genus*	Program and Station Number	Location	Midpoint Latitude	Midpoint Longitude	Midpoint Depth (m)
M1, LP3	WHOI 210	Gay Head-Bermuda Transect	39° 43' N	70° 48' W	2044
C**	WHOI 236	Argentine Basin	36° 28' S	53° 32' W	508
C	WHOI 237	Argentine Basin	36° 33' S	53° 23' W	1002
C	WHOI 239	Argentine Basin	36° 49' S	53° 15' W	1670
H, M1	WHOI 243	Argentine Basin	37° 37' S	52° 24' W	3819
C, H	WHOI 245	Argentine Basin	36° 56' S	53° 01' W	2707
M1	WHOI 287	Eastern Caribbean Basin	13° 16' N	54° 53' W	4957
M1	WHOI 291	Eastern Caribbean Basin	10° 06' N	55° 14' W	3864
M1	WHOI 293	Eastern Caribbean Basin	08° 58' N	54° 04' W	1487
H**	WHOI 295	Eastern Caribbean Basin	08° 04' N	54° 21' W	1011
LP2	WHOI 297	Eastern Caribbean Basin	07° 45' N	54° 24' W	516
M1	WHOI 299	Eastern Caribbean Basin	07° 55' N	55° 42' W	2009
M1**	WHOI 321	NE Atlantic Ocean	50° 12' N	13° 39' W	2879
M1	WHOI 326	NE Atlantic Ocean	50° 05' N	14° 24' W	3859
H, M1	WHOI 328	NE Atlantic Ocean	50° 05' N	15° 45' W	4431
M1	WHOI 330	NE Atlantic Ocean	50° 43' N	17° 52' W	4632
H, M1	WHOI 334	Central North Atlantic Ocean	40° 43' N	46° 14' W	4400
H,LP2**,M1	WHOI 340	NW Atlantic Ocean	38° 16' N	70° 21' W	3310

See Table 4 for explanation.

REPORTING AND USE OF RATIOS

In this paper many ratios are used for descriptions. To avoid repeating the word "times," ratios are reported as a multiplier of an object of a telegraphic phrase to indicate the size of the subject of the phrase. For example, "endopod length 2.2 width" means "the length of the endopod is 2.2 times its width," or "palp second article 0.86 mandibular body length" means "the second article of the palp is 0.86 times the length of the mandibular body." Mathematically, these examples are equivalent to the equations " $L = 2.2W$ " and " $P = 0.86M$," respectively.

Ratios provide a precise, unambiguous description of shape as well as normalizing the size of an appendage or segment to the overall size of the specimen. Ratios are derived from measurements taken using a camera lucida on the microscope, or from camera lucida drawings. The precision of the ratios is reduced in most cases to 2 significant figures to accommodate individual variation and measurement error. Statistical accuracy, however, is not implied by the use of ratios because of small sample sizes. If the ratios are derived from more than one specimen, the number is reported parenthetically after the ratio.

Nouns are used as modifiers of other nouns, a practice that improves the readability of the necessarily dense telegraphic style used to describe the species. Used in this way, the modifier nouns identify larger sets of characters to the left so that the reader will be taken from general to specific, e.g. "male pleopod I distal tip inner lobe . . ." Each set indicated by a noun may include a modifier to specify position or appendage number.

DEFINITION OF TAXA AND MORPHOLOGICAL TERMS

Species are identified using the variation within and between samples of similar animals (Wilson and Hessler 1980; Wilson 1982a). For this paper, however, species-level taxa were not examined in detail, because my goal was to elucidate the higher level taxonomy of the ilyarachnid-like eurycopids. In fact, some species may include complexes of cryptic species; *Mimocopelates longipes* n. gen., n. sp., is suspected of being one such case because it has a broad distribution similar to the *Eurycope complanata* complex (Wilson 1982b). In such cases, individuals from other than the type locality are only provisionally referred to the species. These species problems are left for future study.

Genera are the main focus of this work and are defined using a system based on eurycopid morphology developed in Wilson and Hessler (1980, 1981). External morphology of munnopsids is illustrated in Appendix 1 and a glossary of morphological terms used in this work is provided in Appendix 2. Figure 4 illustrates terms referring to cephalic morphology. Generic characters are taken from the forms of the cephalon and the natasome. The cephalic characters, including the mandibles and their articulation to the cephalon, vary considerably among the janiroidean isopod families, and may express important differences in

feeding life styles between groups of species. The natasomal characters, such as the paddlelike swimming legs, are unique to (a synapomorphy of) the munnopsid taxa, and indicate the locomotory styles of their bearers. The natasome shows much variation among these taxa (for example, see Fig. 1), but is constant within species groups. As such, the natasome characters are ideal for generic definition within the munnopsids. Other characters, such as the form of uropods and the ambulatory limbs (when these legs have been seen; they typically break off during sampling and processing) are also important in defining genera. This system defines genera as distinctive groups of species, separated from other such groups by distinct morphological gaps (Mayr 1970). New genera are monophyletic clades of similar species, and existing genera are assumed to be monophyletic in the phylogenetic analyses.

PREPARATION AND ILLUSTRATION OF SPECIMENS

All specimens are stored in 80% ethanol. For study, they were placed on depression slides in ethylene glycol. The specimens were studied, dissected, and illustrated using a Wild M5 dissecting stereomicroscope or a Wild M20 compound microscope, both equipped with camera lucida attachments. Illustrations were originally done in pencil, and then inked by tracing onto translucent vellum. The illustrations cannot include all details of the animals, although effort was made to include all major surface structures, including setae. When rows of setae were encountered, such as those on the margins of the swimming pereopods, only a few representative setae were drawn and positions of the the rest were indicated by circular, u-shaped, or v-shaped marks (e.g., Fig. 6D), open in the direction of the setal shaft. This form of setal row illustration has been used because the plumose setae of the natapods are typically collected into a mass (see Wilson and Hessler 1980, their figure 13A). The typical representation of a setal row, a line connecting the tips of the setae not shown, is difficult to accurately represent; thus, representative setae are shown without tip indications for unillustrated setae. Some setae, such as plumose setae and broom setae, have many fine setules that do not reproduce well if all are illustrated; therefore, setules on setae are sparsely illustrated. Some cuticular structures, generally best studied with a scanning electron microscope, were often prominent on the specimens and were drawn partially to accentuate cuticular form. Most detail in the drawings represents surface structures. Frequent exceptions are the musculature and sperm tubes of male pleopods I and II, and sometimes structures on the mandibles. Subsurface detail is shaded, or represented by dashed lines. If not otherwise noted, the orientation of the illustrations is as follows: pereopods are illustrated in lateral view; maxillulae, maxillae, maxillipeds, and pleopods are illustrated in ventral view; antennulae are illustrated in dorsal view.

PHYLOGENETIC TECHNIQUES

The phylogenetic analysis was a two-step process: character analysis and computer-assisted estimation once a data set was chosen. The direct approach of leaving the derivations of the characters undetermined, and using the outgroup taxa in a single-step phylogenetic analysis proved to be inefficient because many characters were found to be unsuitable for the chosen systematic level. To reduce the number of possible misinterpretations, I evaluated each character separately with respect to the munnopsids and the outgroup taxa: the Janiridae, the Janirellidae, and the Acanthaspidiidae (see Phylogeny and Classification section for explanations of taxon choice). The numerical techniques are discussed first because of their use in the character studies.

Numerical Analysis

Numerical phylogenetic analysis (reviewed in Felsenstein 1979, 1982) was accomplished with two different systems: PHYLIP versions 2.7 - 2.8 (PHYLogeny Inference Package; Felsenstein 1985) and PHYSYS (computer assessment of phylogenetic relationships system, designed and written by J.S. Farris (described in Luckow and Pimentel 1985). PHYLIP was used on a IBM XT microcomputer. PHYSYS, which is installed on a CYBER 750 in the California State University central computer network, was accessed over telephone lines via modem. A third analysis package, PAUP (Phylogenetic Analysis Using Parsimony, by D. Swofford), became available during the final stages of editing this paper, and was not used for most analyses. PAUP was only used to verify the primary results of this paper: the monophyly of the Lipomerinae, the relationship of the Lipomerinae to the other munnopsids, and the improved parsimony values gained by including all munnopsids into a single family, rather than dividing them into three distinct monophyletic taxa of previous classifications.

PHYLIP has a variety of programs for determining phylogenies. MIX allows one of two parsimony algorithms for each character independent of the others: the Camin-Sokal method (Camin and Sokal 1965) and the Wagner method (Eck and Dayhoff 1966; Kluge and Farris 1969; Felsenstein 1978, 1979, 1981). MIX version 2.8 has a global branch-swapping routine that improves the probability of finding a tree with the fewest character changes. MIX is sensitive to taxon input order and must be run numerous times with different orderings. A modified version of the program, ITERMIX, randomly ordered the taxa into as many data sets as desired, and then evaluated all resulting data sets. Typically, "a" parsimonious tree was found within 5 iterations of MIX, but often different topologies with the lowest number of character changes appeared in runs of 30-50 iterations. For small data sets, the PHYLIP program PENNY, which employs a "branch and bound" algorithm (Hendy and Penny 1982), was used to find all parsimonious trees. During the creation of a cladistic hypothesis from the

literature, PENNY was effective for establishing the parsimonious arrangements of undefined clades of munnopsid taxa. PENNY could not be used for the complete set of munnopsid taxa because the total number of possible trees is astronomically high.

PHYSYS was accessed to use the WAGNER tree builder with global branch swapping (WAG.S) and the WISS tree builder (Weighted Invariant Step Strategy, described in Farris et al. 1970). The latter program calculates the most parsimonious trees on the basis of irreversible evolution, similar to the Camin-Sokal technique in PHYLIP. During the analyses, it was discovered that WAG.S is also sensitive to the input order of the taxa, even though publications imply otherwise (Luckow and Pimentel 1985). Therefore, PHYSYS runs were done on data sets that generated minimum-evolution trees in PHYLIP MIX. WAG.S or WISS each use only one parsimony method; because of this limitation, their results were considered advisory, and they were primarily used to derive weights for the characters.

Character Analysis

Polarities of character transformations were determined by outgroup analysis (Watrous and Wheeler 1981; Maddison et al. 1984). Detailed analyses of each character and the outgroup taxa are discussed in the section on phylogenetic analysis. Multistate characters were coded into binary characters using the method developed by Kluge and Farris (1969), implemented in PHYLIP by the program FACTOR. Some characters, however, had uncertain transformation series. Preliminary runs of ITERMIX were made to test all possible transformations to find those that generated the trees with the fewest character changes. These initial runs were done in the more restrictive Camin-Sokal method, with an ancestral rooting of all the characters and no weights for the different characters. Each of these data sets was run at least 10 times, although the more promising combinations were run 30-40 times. Once the most likely character transformations were found, character weights and parsimony methods were assigned to the data set for final evaluations.

Characters that introduced a large number of steps into the preliminary trees were re-evaluated to determine their interpretation. During this process many characters were rejected as useful at the systematic level of munnopsids. This process resembles compatibility analysis (Felsenstein 1982; Meacham and Estabrook 1985) because it uses those characters that agree on a particular form of the phylogeny. Nevertheless, some homoplastic characters were retained, because they helped resolve some branches, and because they were stable within most taxa. Convergences and parallelisms found in the preliminary trees were not divided into separate characters to improve parsimony levels unless some rationale external to the phylogenetic study for recoding them was found. For example, if an apomorphy appeared independently in two or more separate

clades, this character state would not be classified as two separate characters unless the states carried by the separate clades were morphologically nonhomologous. In this study, recoding was not done because many apparent homoplasies, such as the parallel loss of multiple plumose setae on the third pleopod, could not be discerned as morphologically different in the separate clades.

For the final analyses, each character was classified as to whether or not reversals were probable. Reversals were considered possible in characters based on simple changes in length or shape. These characters were analyzed with the Wagner method. Reversals were considered unlikely if the characters involved the following general aspects: fusion, extreme reduction, or loss of segments; and appearance of a new complex morphology. The nonreversible characters were analyzed with the Camin-Sokal method. This method, applied at a higher systematic level to the reduction characters (see below), would resemble the Dollo parsimony method (Felsenstein 1979) where a character is derived only once, and then lost many times. *Within* the munnopsids, however, such characters are plesiomorphies, making the Camin-Sokal method appropriate for their analysis. (See the section on phylogenetic analysis for a discussion of the derivation of each character.)

Character Weighting

Although character weighting is controversial (Patterson 1982), I have used it here for practical reasons: some homologies are more likely to have been misinterpreted than others, and should have a lesser effect on the analysis. For example, regressive (loss) characters should have an a priori low weight because of their potential for appearing many times independently but nevertheless being indistinguishable (Mayr 1970). Some characters are likely to evolve faster than others, and therefore may be less useful in evaluating phylogenies; if one can apply higher weights to those characters that change the fewest number of times, the resulting cladogram is more likely to resemble the true phylogeny.

The weighting schemes in PHYLIP permit either direct weighting or the threshold technique (Felsenstein 1981), which causes characters to be ignored in the construction of a phylogeny above a chosen number of character changes. This latter method allows a gradient between parsimony and compatibility techniques for generating trees. An a priori weighting was applied to the final series of analyses as follows. Characters hypothetically derived only once were given a weight of 2, and reduction apomorphies were given a weight of 1. A weighting based on successively derived, mean character consistencies (Farris 1969), which depend on their relationship to the overall phylogeny, was used to complement the a priori weights. The successive weighting algorithm is implemented in PHYSYS and can be applied to any data and tree form. A munnopsid data-set order found to produce a parsimonious tree in ITERMIX was

converted to PHYSYS format. The PHYSYS WAGS and WISS tree builders were both used in the successive weighting algorithm to derive two sets of character weights, which varied between 1 (the most consistent characters) and 0 (a completely informationless character within the phylogeny), with the most common weights being 1 and 0.5. These weights were then used in a final PHYLIP data set which applied the WISS weights to the Camin-Sokal characters and the WAGNER weights to the Wagner characters. The weights were converted to the PHYLIP integer format by multiplying them by 4 and then rounding upward to the nearest integer. Thus, PHYSYS weights of .76-1.0 had a PHYLIP weight of 4, weights of 0.26-0.5 became 2, etc.

Confidence Limits. The most parsimonious cladograms, those with the fewest character changes, may not be the best estimates of the "true" cladogram, simply because evolution is not constrained by parsimony. Bootstrap confidence estimates of monophyletic groups were derived by the PHYLIP program BOOT (Felsenstein, 1985). BOOT gives a rough estimate of statistical significance of monophyletic groups by providing a frequency of their appearance in iterated phylogenetic analyses with randomly differing combinations the character set with randomly varying weights. Groups based on only one character often fare poorly in such analyses, especially if the data are "non-Hennigian" (containing many incongruent characters)(*ibid.*).

TAXONOMY OF THE LIPOMERINAE

Isopoda, Asellota, Janiroidea
Family Munnopsidae Sars, 1869 *sensu lato*
Subfamily Lipomerinae Tattersall, 1905 *new definition*

DIAGNOSIS OF THE SUBFAMILY

Munnopsidae with following characteristics: Cephalon broader than long, robust, lacking rostrum, with high flattened frontal arch or with obsolete frons. Natasome (pereonites 5-7, pleotelson) triangular in dorsal view, broader than ambulosome. Pereonite 7 reduced or absent, fused medially on dorsal surface in all except *Coperonus*. Pereopod II not prehensile, similar to other walking legs. Pereopods II-IV approximately same length or slightly increasing in length posteriorly. Bases of pereopods I-IV subequal. Pereopod VII reduced to walking-leg state, rudimentary, or absent. Pleopods II of female covering anus. Pleopod III with 3 plumose setae on endopod, 2-3 plumose setae on exopod. Pleopod IV with 1 plumose seta on exopod. Uropods variously shaped: normal with broad protopod, enlarged and leaflike, or tiny.

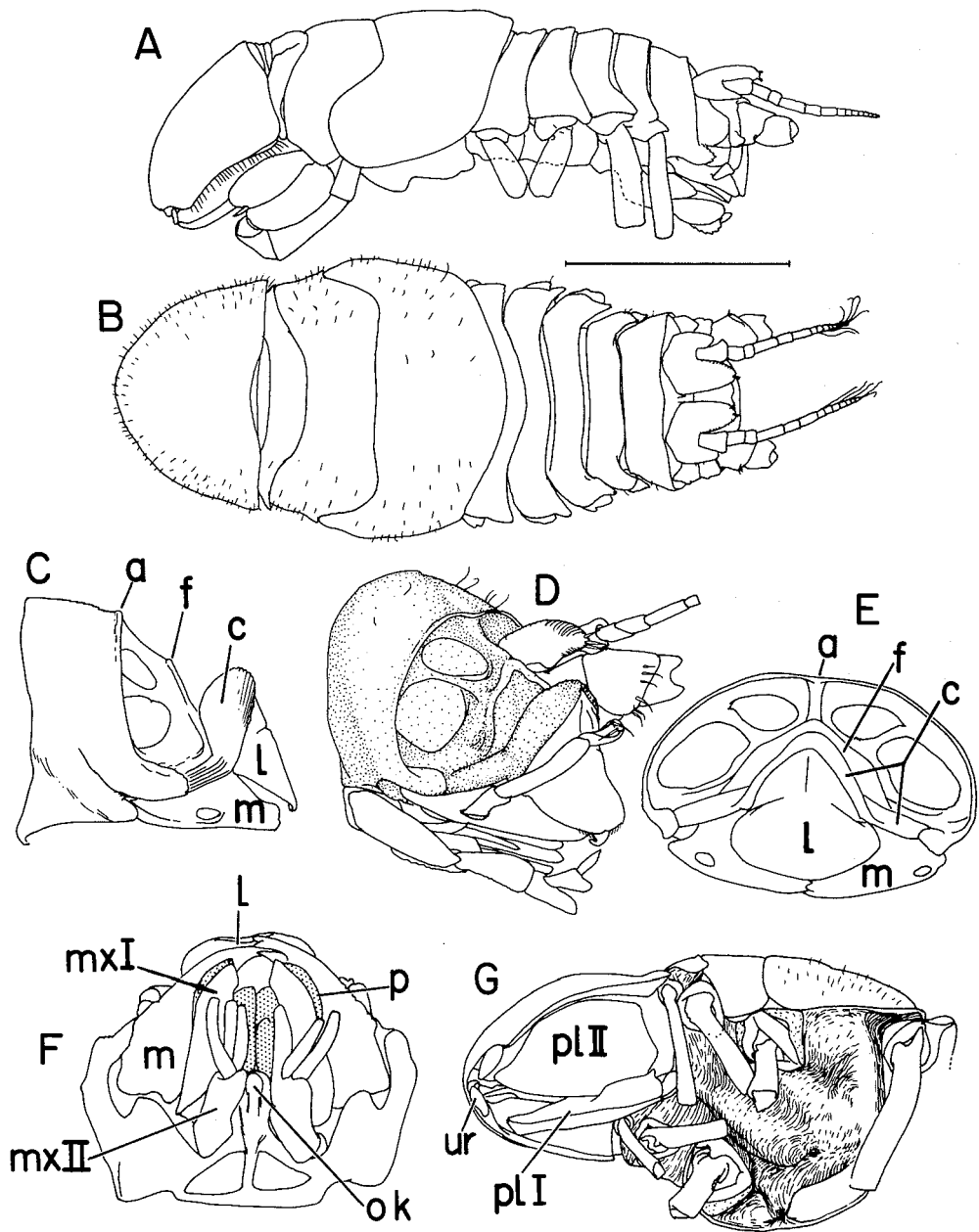


Figure 4. *Coperonus comptus* n. gen., n. sp. A-B, holotype male, lateral and dorsal views, scale bar 1.0 mm. C-F, cephalon, paratype brooding female, bl 2.8 mm, antennula and antenna removed from one or both sides to show frons. C, lateral view. D, frontal oblique view. E, anterior view. F, ventral view, maxilliped removed to show shape of mandibles and ventral cephalon. G, natasome, paratype male, bl 2.9 mm, ventral oblique view showing form of ventral surface and shapes of pereopodal bases. Labels on figure: a = apex of anterior dorsal margin; c = clypeus; f = frontal ridge; l = labrum; m = mandible; mxI = maxillula; mxII = maxilla; ok = oral knob (supports maxillipeds above mouthparts shown); p = paragnaths (shaded with dots); plI = male pleopod I; plII = male pleopod II; ur = uropod.

KEY TO THE GENERA AND DESCRIBED SPECIES OF THE LIPOMERINAE

- 1a. Pereopod VII large, similar to a walking leg but with plumose setae on carpus and propodus; antennula with pronounced medial lobe on article 1 2
- 1b. Pereopod VII rudimentary or absent; antennula with obsolete medial area or small medial lobe on article 1, medial lobe never near length of article 2 4
- 2a. Pereonite 7 of adult extends to lateral margin of pereon, not recessed into pleotelson 3
- 2b. Pereonite 7 recessed into pleotelson, not extending to lateral margin of pereon *Lionectes* n. gen.
- 3a. Uropod small, with thick protopod having pronounced medial projection, not leaflike; natasome posteriorly rounded, not strongly flexed ventrally; mandible normal, not enlarged *Coperonus* n. gen.
- 3b. Uropod large, with flattened leaflike protopod; natasome posteriorly angular, strongly flexed ventrally; mandible with massive molar process and blunt incisor process *Hapsidohedra* n. gen.
- 4a. Uropod large, flattened, never with exopod, extending to distal tip of pleotelson; pereopod V normal with short merus and distinct dactylus (*Lipomera* Tattersall, 1905) 5
- 4b. Uropod tiny, sometimes with rudimentary exopod, never reaching distal tip of pleotelson; pereopod V with elongate merus and rudimentary dactylus (*Mimocopelates* n.gen.) 7

- 5a. Uropod narrow, sometimes with distinct suture between ramus and protopod *Lipomera (Tetracope)* n. subgen.
- 5b. Uropod broad, leaflike, never with distinct suture between ramus and protopod 6
- 6a. Rudimentary pereopod VII present; cuticle of body surfaces not heavily calcified, having smooth anterior margins without denticles; cephalon not enlarged, same width as pereonite 1 *Lipomera (Lipomera)*
- 6b. Pereopod VII completely absent; cuticle of body surfaces indurate, often with denticles on anterior margins; cephalon enlarged, broader than pereonite 1 *Lipomera (Paralipomera)* n. subgen.
- 7a. Cephalon near width of or narrower than pereonite 1; mandibular molar process normal, not massive and blunt; cephalic frontal arch protruding anteriorly in lateral view; stylet of male pleopod II normal sized, approximately half length of protopod; musculature of pleopod II exopod extending to proximal margin of protopod *Mimocopelates longipes* n. sp. (species group)
- 7b. Cephalon enlarged, distinctly wider than pereonite 1; mandibular molar process massive and blunt; cephalic frontal arch flattened into frons, not protruding anteriorly; stylet of male pleopod II small, less than third length of protopod; musculature of pleopod II exopod not extending to proximal margin of protopod *Mimocopelates archibraziliensis* n. sp. (species group)

DESCRIPTIONS OF THE GENERA AND SPECIES OF THE LIPOMERINAE

COPERONUS New Genus

(Figures 4-7)

Type-Species. Coperonus comptus new species

Generic Diagnosis. Dorsal surface smooth, without spines. Cephalic anterior and lateral margin lightly calcified, not enlarged, semicircular in frontal view. Rostrum absent, vertex slightly convex in dorsal view. Frontal arch protruding anteriorly, with raised flattened area adjacent to clypeal attachment; frontal arch angular in anterior view. Clypeus medial section triangular in anterior view; dorsal apex higher than articulation with frons, slightly lower than apex of flattened area on frons. Labrum anteriorly flattened, height half that of cephalon. Body deepest and widest at pereonite 5. Natasome compact; pereonites 5-7 with distinct articulations dorsally but fused ventrally; pereonite 5 largest; pereonite 7 dorsally reduced to thin strip. Ventral surface of natasome enlarged at pereonite 5, compressed at pereonites 6-7, with large ventromedial bump medial to insertions of pereopods V. Antennular article 1 with distinct medial and lateral lobes; medial lobe rounded, longer than article 2; lateral lobe flattened. Antennal scale absent. Mandible not highly modified, without reduced functional areas: incisor process, lacinia mobilis, and molar process with pointed cusps or denticles; molar process distally concave; condyle roughly same length as molar process, with support ridge extending from posterior edge of condyle to posterolateral corner of mandibular body; palp slightly shorter than mandibular body. Pereopodal bases I-IV increasing slightly in length posteriorly, all longer than natapodal bases V-VII; basis V shortest and stoutest, bases VI-VII increasingly longer and less stout posteriorly. Pereopods V-VI natatory, with broad carpi and propodi. Pereopod VII near length of pereopod VI but carpus and propodus only slightly broadened, with fewer and shorter plumose setae on margins. Dactylus of pereopod V small, lenticular; dactyli VI-VII long, thin. Female pleopod II with small slit in distal tip. Uropod short and stout, recessed into posteroventral margin of pleotelson; protopod broader than long; both rami shorter than protopod.

Derivation of Name. *Coperonus* (Greek, masculine) may be construed to mean "isopod furnished with oars."

Composition. *Coperonus comptus* n. sp., *C. nordenstami* n. sp., *C. frigida* (Vanhöffen, 1914).

Remarks. *Coperonus* is the least modified genus of all the Lipomerinae. Although its members have the short, broad head and reduced frontal area of the Ilyarachnidae and the Lipomerinae, the pereon and pleotelson are much more characteristic of the Eurycopidae in the posteriorly rounded, bullet-shaped appearance. The uropods are also eurycopid-like, although somewhat reduced

and modified in their position. The only posterior feature that unequivocally identifies *Coperonus* as a member of the Lipomerinae is the reduction of pereonite 7 and its limb.

Coperonus may be distinguished from the other Lipomerinae by its rounded natasome and relatively unmodified uropod. A large, somewhat natatory pereopod VII is also useful for identification, clearly separating *Coperonus* from *Lipomera* Tattersall, 1905, and *Mimocopelates* n. gen., which lack functional seventh pereopods. *Coperonus* does not have the decidedly *Ilyarachna*-like appearance and flexed body of *Hapsidohedra* n. gen., or the low cephalon and terminal uropods of *Lionectes* n. gen.

In addition to the type-species, *Coperonus comptus* n. sp., the genus includes species originally placed in *Eurycope*. Most of the syntypes of *E. frigida* Vanhöffen, 1914 belong in *Coperonus*. Vanhöffen (1914) described 10 individuals under this species name, although one of the specimens belongs to *Lionectes* n. gen. (see discussion after diagnosis of *Lionectes*). In addition to the overall similarity of the body shape of the large specimen figured by Vanhöffen (1914, his figure 122), the maxilliped is practically identical to that of the type-species of *Coperonus*, and the male pleopods are similar, but not identical (Vanhöffen, 1914, his figure 123b-d). Because of these generic similarities, the 9 large specimens of the species *frigida* are assigned to the genus *Coperonus*. A lectotype of *C. frigida* is currently undesignated.

Nordenstam (1933) described *Eurycope* sp. cf. *frigida* but, for some undisclosed reason, did not feel confident enough to give it a new species name, even though he examined Vanhöffen's types and found his specimens different. *E. sp. cf. frigida* Nordenstam, 1933 is definitely a member of *Coperonus*; the illustrations (Nordenstam 1933, his figure 78) clearly show the distinctive body shape and the heterogeneous composition of natatory pereopods, with a reduced but still natatory pereopod VII, found only in *Coperonus*. Because Nordenstam's specimens are sufficiently well illustrated to establish their specific identity, they are assigned to a new species of *Coperonus*, *C. nordenstami*, in honor of their first describer (see diagnosis below).

Coperonus has a South Atlantic-Antarctic distribution. In addition to *C. frigidus* (Vanhöffen, 1914) and *C. nordenstami* n. sp. found off East Antarctica and South Georgia Island, respectively, three species, one of which is *C. comptus* n. sp., have been found in the Weddell Sea and Palmer Peninsula area, and three species were collected during Woods Hole Oceanographic Institution expeditions off Argentina and Brazil.

Coperonus comptus new species
(Figures 4-7)

Holotype. Copulatory male, bl 2.6 mm, ambulatory pereopods and antennae missing, USNM 227052.

Paratypes. Preparatory female, bl 2.8 mm, USNM 227053. Preparatory female, copulatory male, ZMUC. Preparatory female, copulatory male, MNHN Is.1813. Brooding female, copulatory male, BMNH 1985:417. 89 individuals, some dissected for description, SIO.

Type-Locality. WHOI 236, 36°27.0'-28.1'S, 53°31.0'-32.3'W, 497-518 m, collected 11 March 1971 during R/V *Atlantis* cruise number 60.

Other Material. WHOI 239, 37 individuals. WHOI 237, 36 individuals. WHOI 245, 2 fragments.

General Distribution. Argentine Basin in the southwestern Atlantic Ocean, 497-2707 m.

Derivation of Name. *Comptus* means "elegant" in Latin.

Diagnosis. Apex of cephalon only slightly convex, neither linear nor strongly convex. Pleotelson posterior margin in dorsal view smoothly curving, or heart-shaped. Male antennular article 3 shorter than article 2. Maxillipedal epipod distal tip pointed, not rounded. Pereopod VI only slightly shorter than pereopod V, pereopod VI length 0.94 pereopod V length. Male pleopod I distal tips concave in ventral view, with broadly angular inner and outer lobes.

Description. Adult body length 2.5-2.8 mm (5 inds), length 1.9-2.1 width (4 inds).

Body setation (Fig. 4A): Natasome with tiny setae on dorsal and lateral surfaces; other dorsal surfaces with only scattered fine setae.

Cephalon (Fig. 4C-F): Dorsal length 0.31 width, length 0.42 height. Ventral margin at posterior articulation of mandible with distinct indentation or notch.

Antennula (Fig. 5A-B): In males, length 0.35-0.36 (2 inds) body length; in females, 0.23-0.26 (2 inds). Male antennula with 14 articles and approximately 6 aesthetascs distally; female antennula with 10-11 articles and 2-5 aesthetascs distally. Article 1 medial length 1.1 width in male, 0.75-0.78 (2 inds) in female; medial lobe of both sexes with approximately 6 denticulate setae having long sensilla and 3-4 denticles on distal tips. Articles 2 and 4 with broom setae. Articles 2 and 3 only slightly geniculate at articulation. Article 2 slightly shorter than article 1 medial lobe in females, length 0.7 medial-lobe length in males. Article 3 length 0.61 article 2 length in male, 0.71 (2 inds) in females.

Mandible (Fig. 5C-I): Normally developed. Both mandibles with 3 distinct cusps on incisor processes. Lacinia mobilis reaching to tip of incisor process, with 4 cusps. Left spine row with 7 members. Molar process distal end with low circumgnathal denticles, lacking large pointed cusp on ventral margin; posterior

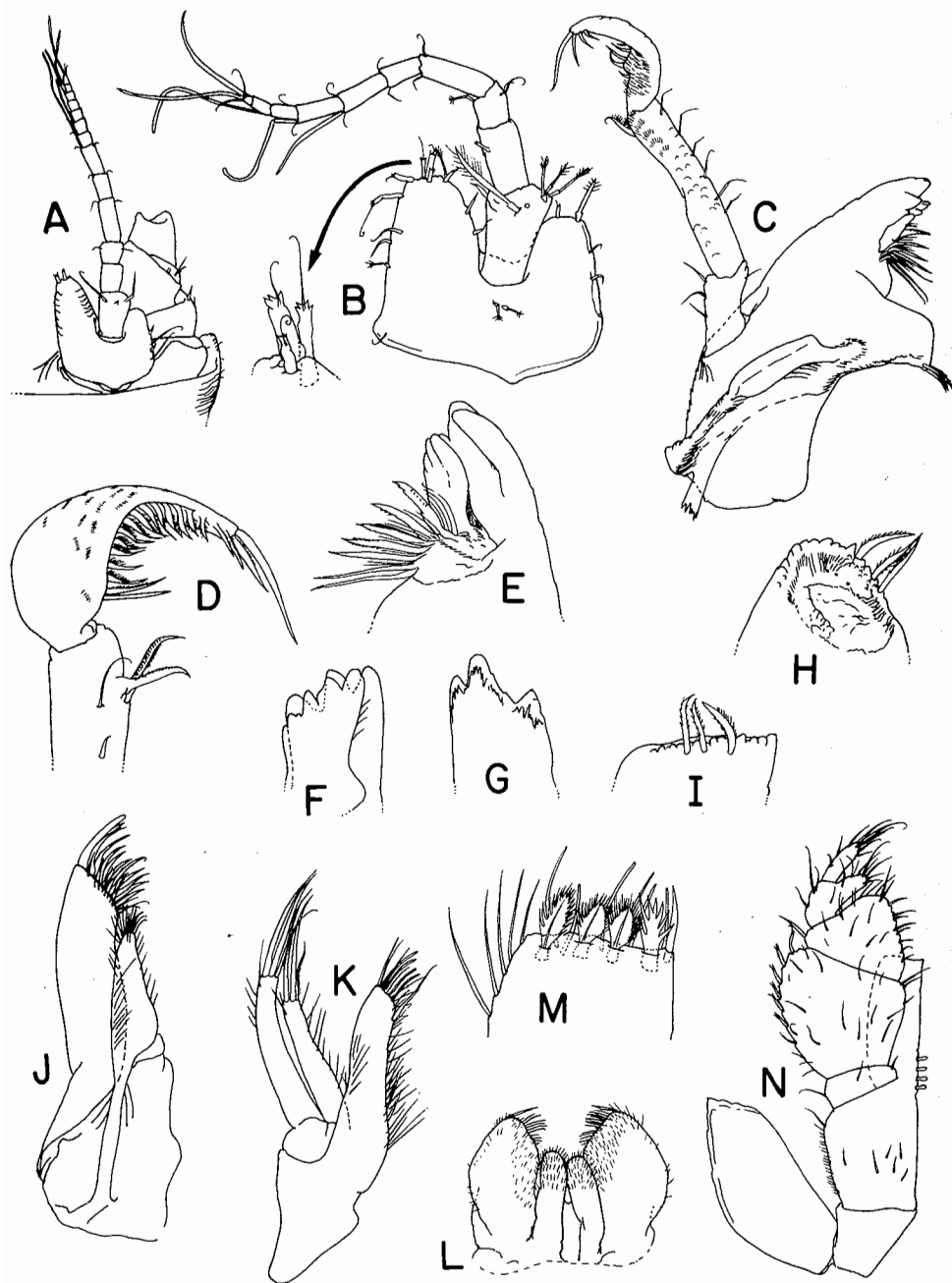


Figure 5. *Coperonus comptus* n. gen., n. sp. A, right anterior section of cephalon showing antennula and basal articles of antenna, holotype male. B-N, paratype brooding female, bl 2.8 mm. B, right antennula. C-F, H-I, left mandible. C, dorsal view. D, distal section of palp. E, incisor process, lacinia mobilis and spine row, ventral view. F, incisor process and lacinia mobilis, plan view. G, incisor process, right mandible, plan view. H-I, molar process, anterior and posterior views. J, right maxillula. K, right maxilla. L, paragnaths. M-N, right maxilliped, enlargement of endite and whole limb, respectively.

margin with 3 flattened setulate setae; triturating surface with approximately 4 sensory pores. Condyle length 0.27 mandibular body length. Palp second article length 0.49 mandibular body length.

Maxillula (Fig. 5J): Normally developed. Inner endite width 0.74 outer endite width.

Maxilla (Fig. 5K): Normally developed. Outer lobes shorter than inner lobe.

Maxilliped (Fig. 5M-N): Basis with 4 receptaculi and 4 fan setae distally, medial fan seta more robust, with fewer and broader branches than 3 lateral fan setae. Endite length 0.53 total basis length. Palp article 2 width greater than 2 times endite width, lateral length 1.6 medial length. Palp article 3 lateral length 0.19 medial length. Epipod short, narrow, and distally pointed; length 0.81 basis length; length 2.9 width.

Pereopodal Bases (Fig. 4G, 6C): Bases I-IV length-body length ratios in male holotype 0.22, 0.24, 0.23, 0.26; all similarly robust. Bases V-VII in brooding female shorter than bases I-IV; length-body length ratios 0.11, 0.18, 0.19.

Pereopod I (Fig. 5A-B): Sexually dimorphic. In males, pereopod I length 0.67 body length, with robust basis and ischium, and with tuft of setae on proximal venter of ischium; ischium length 0.48 basis length. In females, pereopod length 0.63 body length, with thin basis and ischium, and lacking tuft of setae on ischium; ischium length 0.43 basis length.

Natatory Pereopods (Fig. 6D-F): Natapods heterogeneous in form: pereopod V strongly natatory; pereopod VII resembling walking leg but with slightly broadened carpus and propodus, and with reduced plumose setae; pereopod VI intermediate in form. Bases, propodi, and dactyli increase in length posteriorly; ischia, meri, carpi, and natatory setae on carpus and propodus decrease in length posteriorly; widths of carpus and propodus decrease posteriorly. Pereopod V-VII length-body length ratios 0.70, 0.66, 0.60. Carpi V-VII length-width ratios 1.1, 1.3, 3.5. Propodi V-VII length-width ratios 1.6, 2.5, 5.6. Dactylus V tiny, with no distal claw (or unguis); dactyli VI-VII much longer, with claw.

Male Pleopod I (Fig. 7A-B). Pleopod widest proximally, abruptly narrowing midlength. Length 2.9 width; dorsal orifice 0.09 total length from distal tip. Distal tips bilobed, rounded in lateral view, slightly concave in ventral view. Fine setae on distal third of ventral surface, and 2 paired groups of setae on distal tip.

Male Pleopod II (Fig. 7C): Protopod broad proximally, narrowing to small rounded lobe distal to exopod; length 1.5 width. Small plumose setae on distolateral margin of protopod. Stylet short, half length of protopod; sperm duct opening at stylet midpoint. Exopod bare, without tuft of fine setae.

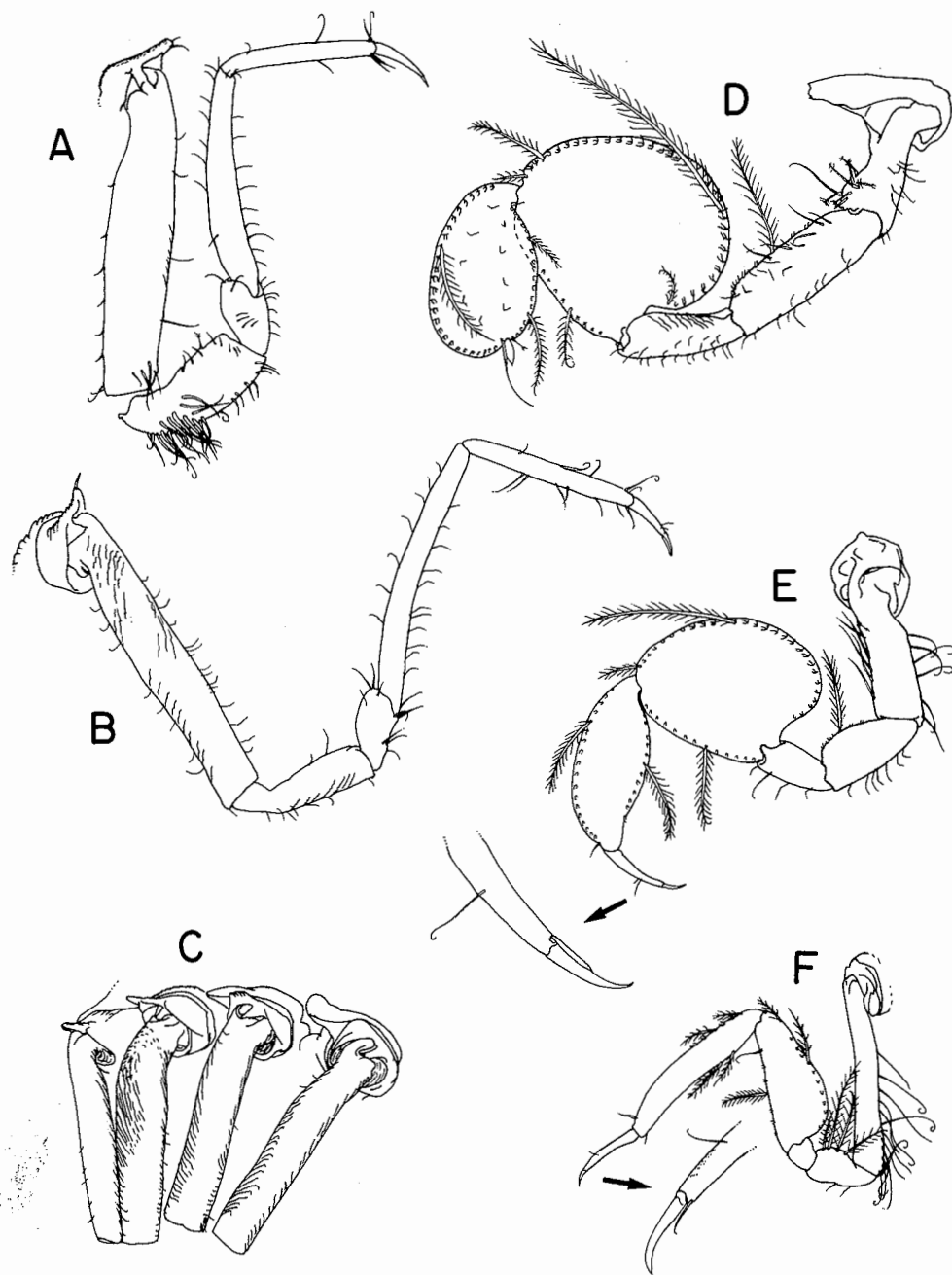


Figure 6. *Coperonus comptus* n. gen., n. sp. A, right pereopod I, male from WHOI 239, bl 2.7 mm. B, D-F, pereopods, brooding female from WHOI 239, bl 3.0 mm. B, right pereopod I. C, bases of pereopods I-IV, paratype male, bl 2.9 mm. D-F, natatory pereopods V-VII to same scale, with enlargements of claws of dactyli VI-VII.

Female Pleopod II (Fig. 7G-I): Keel deep, sharply defined from lateral fields. Dorsal surface with scattered setae; distolateral margins with small plumose setae. Length 0.81 width; depth 0.47 length. Apex anterior to length midpoint, lacking large seta.

Pleopod III (Fig. 7D): Exopod extending to distal tip of endopod, with 2 long plumose setae, and 1 simple seta on distal tip.

Uropod (Fig. 7J): Protopod medial length 0.61 distal width. Exopod 0.69 endopod length. Endopod 0.76 medial length of protopod. Distal margin of protopod with group of unequally bifid setae on medial lobe, and few setae laterally.

Remarks. *Coperonus* has 3 described species and 5 undescribed species known to me. *C. comptus* can be identified among these only by using a combination of characters: the cephalic and pleotelson form, the male antennulae and pleopods, the comparative sizes of pereopods V and VI, and the maxillipedal epipod. It is restricted to the Argentine Basin from just below the shelf break to below 2000 m.

Coperonus nordenstami new species

Synonym. *Eurycope* sp. cf. *frigida* Nordenstam, 1933.

Syntypes. Two small damaged females.

Type-Locality. Swedish Antarctic Expedition station 34. South Georgia Island, off the mouth of Cumberland Bay, 54°11'S, 36°18'W, 252-310 m, 5 June 1902. Sediment gray clay with a few stones.

General Distribution. South Georgia Island. Known only from type locality.

Derivation of Name. This species is named for Åke Nordenstam, the first to report it.

Diagnosis. Apex of cephalon linear. Pleotelson posterior margin in dorsal view appearing as rounded "V". Maxillipedal epipod distal tip rounded. Pereopod VI only slightly shorter than pereopod V.

Remarks. The above diagnosis is somewhat limited because males are unknown. The females differ from *C. comptus* in the form of the pleotelson, the cephalon, and the maxillipedal epipod (Nordenstam 1933, his figure 78).

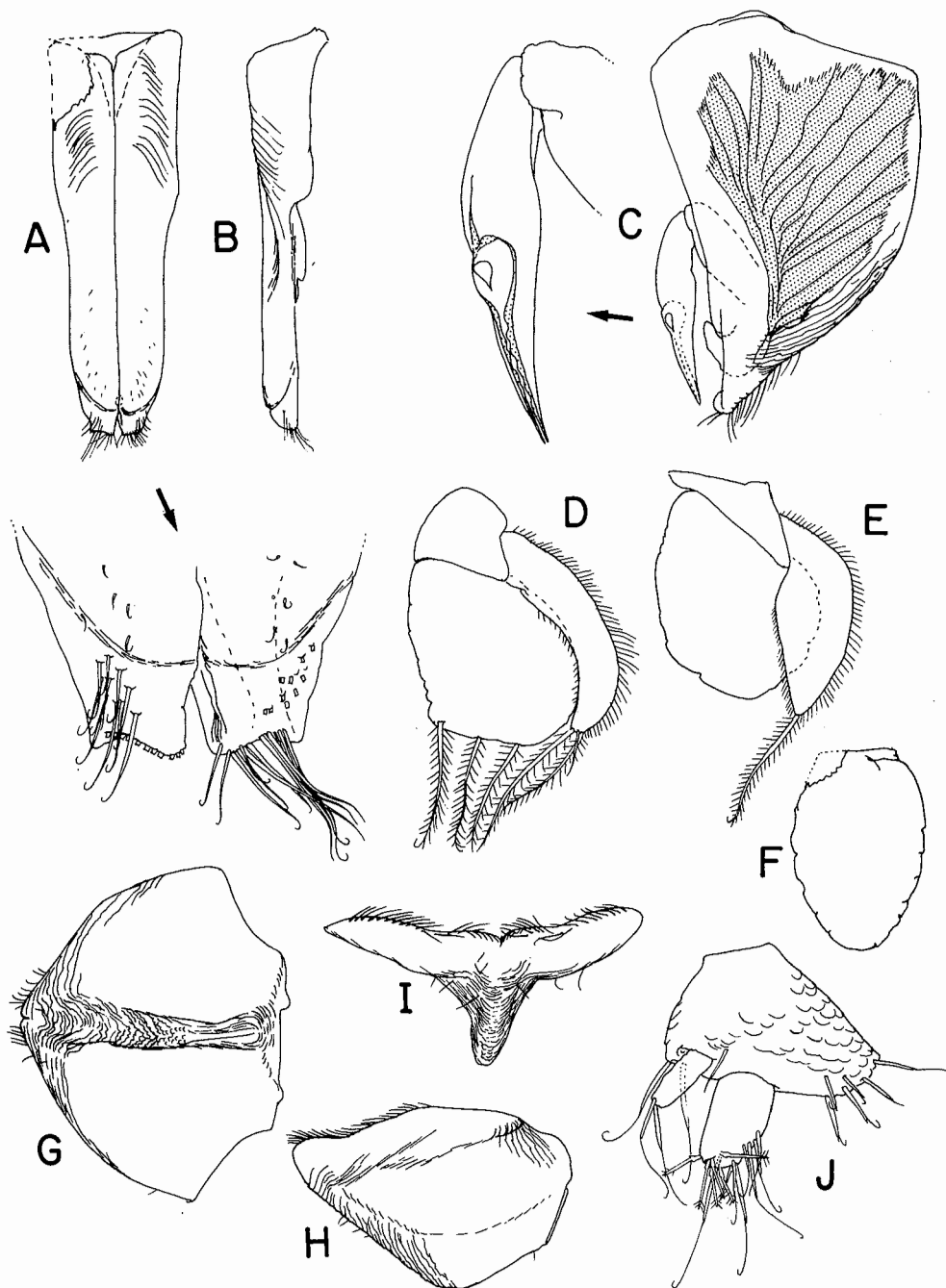


Figure 7. *Coperonus comptus* n. gen., n. sp. A-C, paratype male, bl 2.9 mm. D-J, paratype brooding female, bl 2.8 mm. A-B, male pleopod I, ventral and lateral views, with enlargement of distal tip, some setae shown only by basal attachments for clarity of reproduction. C, left male pleopod II, with enlargement of stylet; fringing setae on distolateral margin are plumose. D-F, left pleopods III-V. G-I, female pleopod II, ventral, lateral, and posterior views, respectively. J, right uropod.

HAPSIDOHEDRA New Genus
(Figures 8-13)

Type-Species. Hapsidohedra ochlera new species

Generic Diagnosis. Dorsal surface of body without spines. Cephalic lateral and frontal margins thickened and calcified; frontal area semicircular in frontal view, without rostrum or medial protrusions; vertex linear, without anterior or posterior curves. Clypeus thick and heavily sclerotized laterally; medially arched, anterior-most midpoint higher than attachment to frons. Labrum high and anteriorly flattened, height three-quarters that of cephalon. Body deepest at pereonite 5; broadest at posterior margin of pereonite 5. Natasome highly modified: dorsal surface greatly arched, so that pleotelson at right angle to axis of ambulosome; pereonite 7 reduced and dorsomedially fused to pereonite 6; sutures between pereonites 5-7 present ventrally. Pleotelson subtriangular, widest at anterior margin. Antennular first article broad, with distinct medial and lateral lobes; medial lobe rounded, lateral lobe dorsoventrally flattened; as few as 2 flagellar articles in adult female. Antenna article 3 without distinct scale. Mandible highly modified: incisor process with reduced rounded teeth; lacinia mobilis flattened, much smaller than incisor process, with reduced teeth; left spine row compressed next to base of lacinia, spines much shorter than lacinia; molar process massive, with broad, bilobate triturating surface lacking circumgnathal incisive ridges or denticles, setal row with few closely adjacent setulate setae; condyle enlarged, heavily sclerotized, extending from distal surface of molar process to proximity of posterolateral corner of mandibular body, length greater than half mandibular body length; palp thin, shorter than mandibular body. Pereopodal bases lengths heterogeneous: bases II and III subequal and shortest, bases IV and VI subequal and longest, bases I, V, and VII intermediate in length. Pereopod V and VI natatory, with broad carpi and propodi. Pereopod VII thin, reduced, with narrow carpus and propodus, and few natatory setae. Dactyli of pereopods V-VI thin, curved, lengths subequal; dactylus VII much longer, also thin. Pleopod II of female with slit dividing distal tip into halves. Uropod with broad, flattened, oval protopod and 1 short ramus. Uropods inserting subterminally and ventrally, covering anus with protopods.

Derivation of Name. *Hapsidohedra* (Greek, feminine) means "vaulted rump," referring to a high, arched natasome.

Composition. *Hapsidohedra ochlera* n. sp.; *H. aspidophora* (Wolff, 1962).

Remarks. *Hapsidohedra* is the most ilyarachnid-like of the Lipomerinae. The broad, dorsally tubular and robust cephalon, the triangular natasome tipped with a leaflike uniramous uropod, and a non-natatory pereopod VII are all seen in the Ilyarachnidae. Indeed, Wolff (1962) placed the species *aspidophora* in *Ilyarachna*, apparently overlooking characters that conflicted with his diagnosis of the Ilyarachnidae: a large, rounded, nonsetiferous mandibular molar; elongate

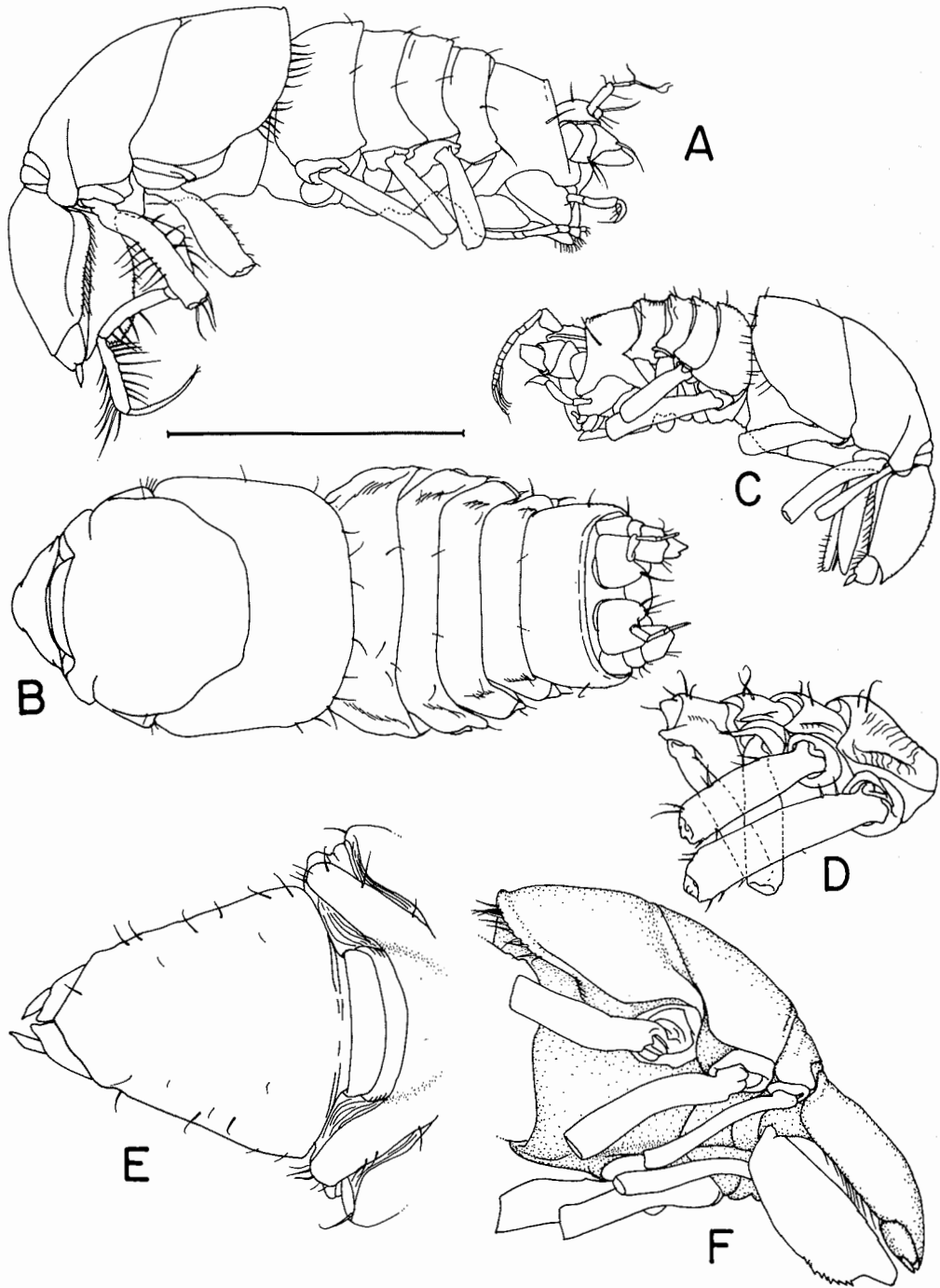


Figure 8. *Hapsidohedra ochlera* n. gen., n. sp. A-B, holotype preparatory female, lateral and dorsal views, scale bar 1.0 mm. C, paratype male, lateral view, same scale as female. D, paratype male, enlargement of left lateral margins of pereonites 1-4 and pereopodal bases, showing relative sizes of bases. E, pleotelson, holotype female. F, natasome, lateral oblique view, showing form of ventral surface and relative sizes of bases V-VII, paratype female, bl 1.7 mm.

bases of pereopods III-IV; and a bilobate, thick antennular article 1. This species resembles the reasonably well-defined and specialized Ilyarachnidae, but lacks this family's defining features. If this genus were the only known lipomerine, the current definition of the Ilyarachnidae would be in serious doubt. The other genera described in this paper, however, show that *Hapsidohedra* is part of an evolutionary line separate from the ilyarachnids, and that convergence to a similar body form is responsible for its resemblance.

Hapsidohedra shares several important characters with the other Lipomerinae. These characters also distinguish the genus from ilyarachnids. The molar process is not reduced, but is enlarged (taken to an extreme in this genus). The bases of pereopods III-IV are similar in length to basis II. Pereonites VI and VII are fused dorsally, but *Hapsidohedra* retains the primitive separation of the ventral surfaces of the natasomites. The clypeus is angular, and its anterior apex is higher than its insertion on the cephalic frons. All lipomerines have nearly identical pleopods III and IV, and *Hapsidohedra* is no exception.

The frons of *Hapsidohedra* is distinctive, but of the same general form found in all the Lipomerinae: the frontal area is reduced, with a disappearance of the cephalic arch and the frontal area above it. As in most lipomerines, the anterodorsal margin of the cephalon has become heavier, providing a support bridge for the mandibular attachments. In contrast, the frontal arch of the Ilyarachnidae, in which *Hapsidohedra* was previously placed, has become broadened under the antennae, providing the main part of the mandibular support bridge. This will be discussed in more detail in the phylogeny section.

Other characters help separate *Hapsidohedra* from the other Lipomerinae. The leaflike uropod is most useful for separating it from the other genera. This genus is closely related to *Coperonus* in the general form of the natasome, but its *Ilyarachna*-like appearance and massive mandible make it easy to separate from that genus. *Hapsidohedra* is superficially most similar to *Lipomera* in the uropod and the cephalon, but *Hapsidohedra* has a distinct ramus on the uropod, and a functional pereopod VII. *Hapsidohedra* lacks the terminal uropods and recessed pereonite 7 of *Lionectes*, and the highly modified natasome of *Mimocopelates*.

Hapsidohedra has only 2 described species at present: *H. ochlera* n. sp. from bathyal waters of the Caribbean Sea off northern South America, and *H. aspidophora* (Wolff, 1962) from shallow bathyal or deep shelf waters off East New Zealand. At least 3 other undescribed species have been collected in the North and South Atlantic, and the Gulf of Mexico. This genus may be regarded as cosmopolitan in view of its wide occurrences in the Atlantic and Pacific oceans.

Hapsidohedra ochlera new species
(Figures 8-12)

Holotype. Preparatory female, bl 2.5 mm, all pereopods except left seventh pereopod missing, USNM 227054.

Paratypes. Preparatory female, bl 2.3 mm; brooding female, bl 2.2 mm; male, bl 1.7 mm: USNM 227055. Brooding female, bl 2.3 mm; male, bl 1.6 mm: ZMUC. Brooding female, bl 2.3 mm; male, bl 1.6 mm: MNHN Is. 1814. Brooding female, copulatory male, BMNH 1985:418. 56 individuals, some dissected for description, SIO.

Type-Locality. WHOI 295, 8°04.2'N, 54°21.3'W, 1000-1022 m, collected off Surinam during R/V *Knorr* cruise 25, 28 February 1972.

Other Material. All at SIO: WHOI 293, 5 ind; LCL1C4, 5 ind; LGL2C2, 1 ind; LGL2C4, 1 ind; LGL3C3, 1 ind; LGL3C7, 2 ind; LGL3C9, 1 ind; LGL4E2, 1 ind; LGL5WC6, 3 ind; LGL5WC11, 1 ind.

General Distribution. Off Surinam, South America, 1000-1518 m, and in the Gulf of Mexico off Louisiana, 554-1390 m.

Derivation of Name. *Ochlera* (Greek) means "troublesome." The specific epithet refers to the troublesome, but superficial similarity of this species to the Ilyarachnidae.

Diagnosis. Antennular article 2 longer than medial lobe. Mandible with reduced spine row on incisor process; molar process with 3 serrate setae distally. Keel of female pleopod II terminating abruptly anterior to distal tip, with recurved or quadrate posterior margin in lateral view and with posteriorly directed denticles on ventral margin.

Description. Body Characters (Fig. 8A-C,E): Adult body length 1.7-2.5 mm, length (measured along curving body axis) 2.8 width in holotype female. Pleotelson ventral plan view length 1.0-1.1 width.

Body Setation (Fig. 8A,C,E-F): Cephalon with single large simple seta. Dorsal surface of ambulatory pereonites with sparse row of simple setae near anterior margins. Anterior margin of pereonite 5 with row of simple setae. Ventrolateral margin of pleotelson with thick row of plumose setae.

Cephalon (Fig. 9A-D): Dorsal length 0.42 width, length 0.49 height.

Antennula (Fig. 10A-C): Length 0.31-0.28 body length in males (2 measured), 0.15 in holotype female. Male antennula with 12-16 articles, approximately 6 aesthetascs distally. Female antennula with 6 articles and only 1 aesthetasc. Article 1 medial length 0.93 width in male, 0.79 in female; both sexes with lateral row of approximately 5 large setae; medial lobe with 4-5 large, unequally bifid or smaller broom setae. Articles 2 and 4 with broom setae. Articles 2 and 3 decidedly geniculate at articulation. Second article 0.62 medial length of article 1 in male, 0.76 in female.

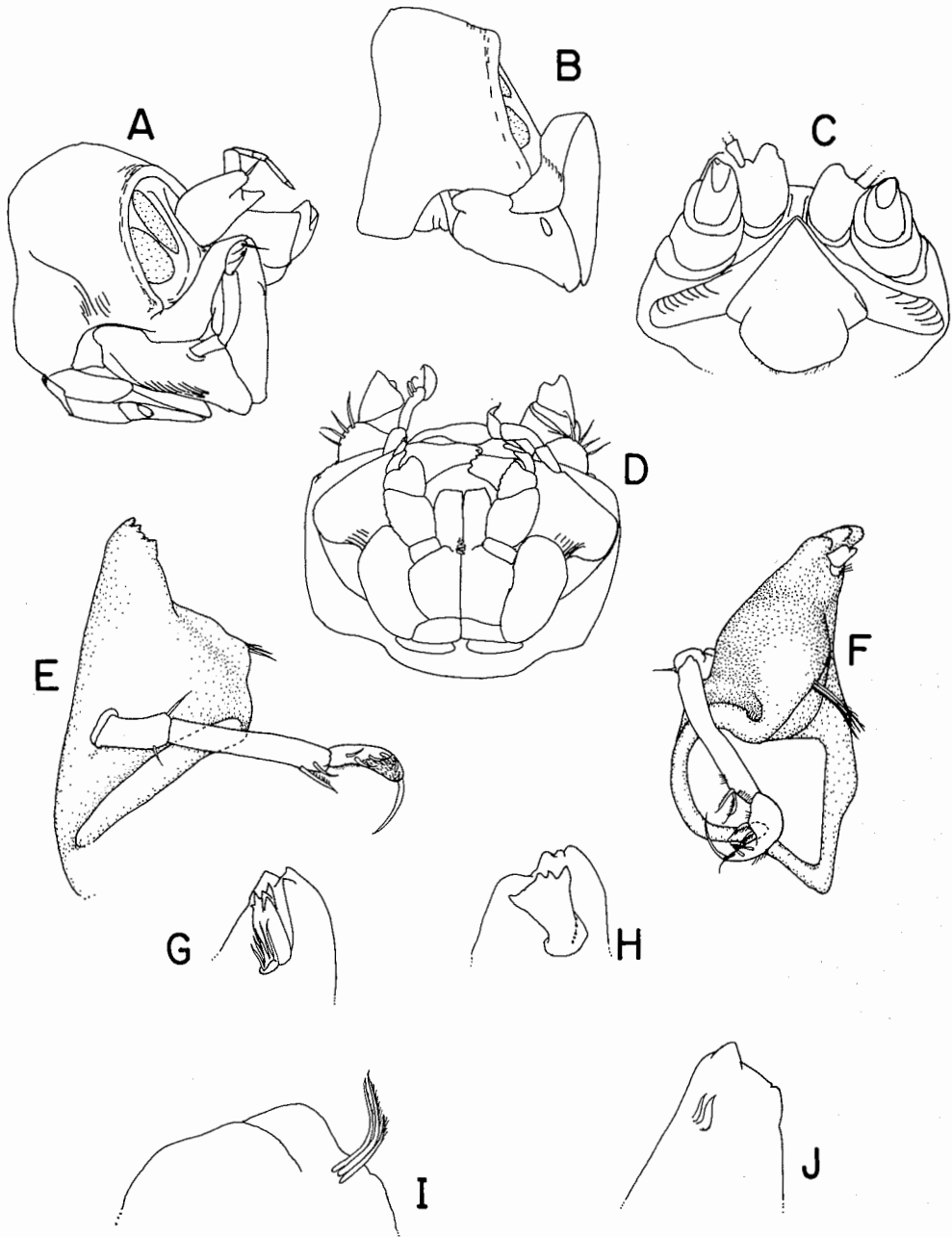


Figure 9. *Hapsidohedra ochlera* n. gen., n. sp. A-B, cephalon, frontal oblique and lateral views, antennula and antenna removed to show frons, paratype preparatory female, cephalon fragment only. C-D, paratype brooding female cephalon fragment. C-D, cephalon, anterior and ventral views, dorsal setation not shown. E-I, left mandible. E-F, dorsal and medial views. G, incisor process, lacinia mobilis, and spine row, ventral view. H, incisor process and lacinia mobilis, plan view. I, molar process, posteromedial view. J, incisor process, right mandible.

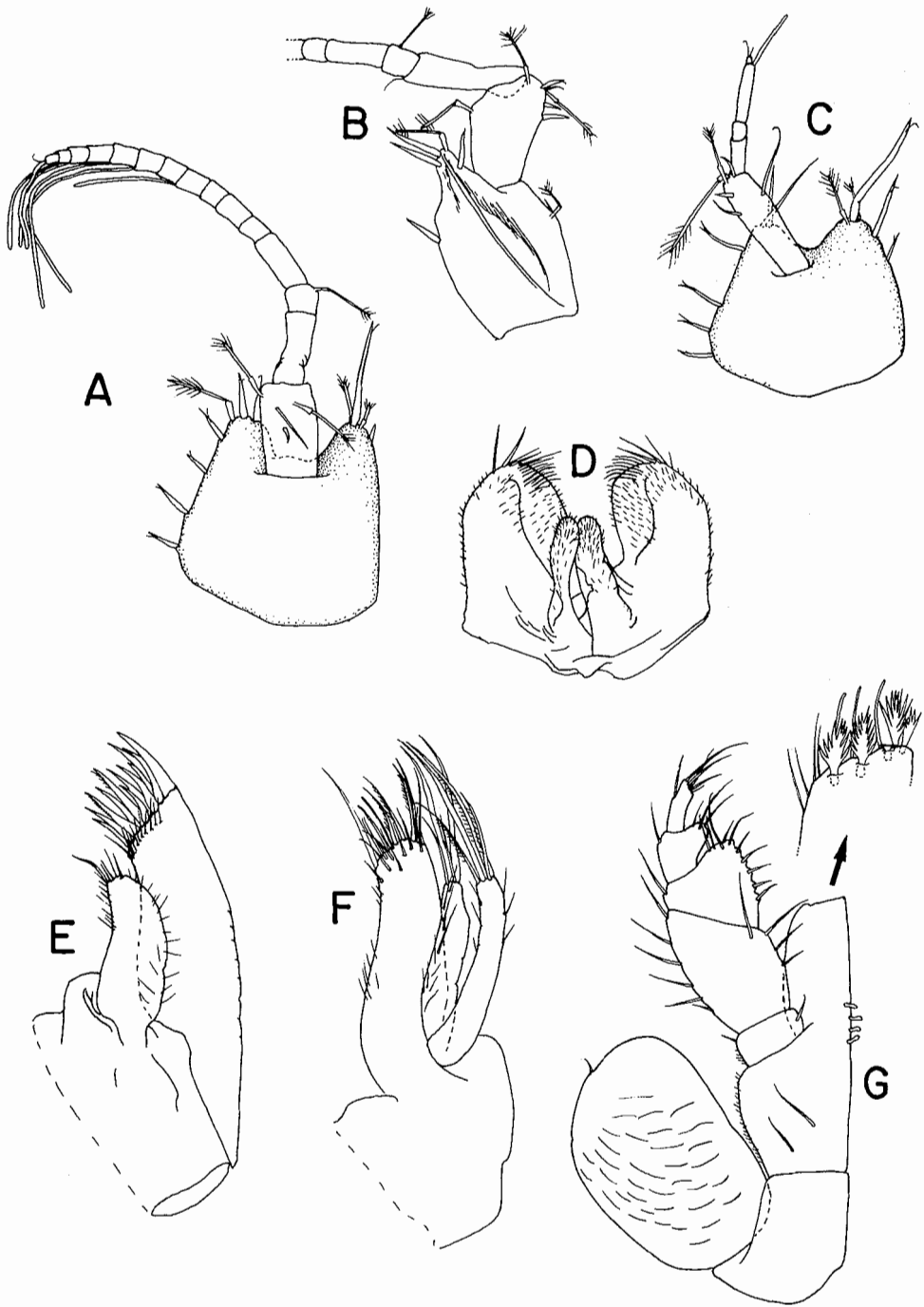


Figure 10. *Hapsidohedra ochlera* n. gen., n. sp. A-B, left antennula, dorsal and lateral views, paratype male, bl 2.0 mm. C, left antennula, paratype preparatory female, bl 2.0 mm. D-G, paratype brooding female cephalon fragment. D, paragnaths. E, left maxillula. F, left maxilla. G, right maxilliped with enlargement of endite distal tip.

Mandible (Fig. 9E-J): Left incisor process with 4 cusps, with gap between dorsal cusp and 3 ventral cusps. Right incisor with single large cusp, and low cusps dorsally and ventrally. Lacinia mobilis flattened, with 4 teeth. Left spine row with approximately 5 simple members, distinctly shorter than lacinia mobilis; right spine row with 2 members. Molar process with 3 closely-clumped setulate setae. Condyle length 0.54 mandibular body length. Palp second article length 0.43 mandibular body length.

Maxillula (Fig. 10E): Normally developed. Inner endite 0.64 width of outer endite.

Maxilla (Fig. 10F): Normally developed. Outer lobes distinctly shorter than inner lobe.

Maxilliped (Fig. 10G): Coxal plate large, nearly as long as width of epipod. Endite with 4 receptaculi medially and 5 fan setae distally. Palp article 2 lateral length 1.1 endite lateral length; lateral length 1.7 medial length. Palp article 3 lateral length 0.29 medial length. Epipod outline bean-shaped, with rounded lateral and distal margins; length 1.5 width; distal margin with single simple seta.

Pereopodal Bases (Fig. 8D,F; 11A-D): In female, bases I-VII length/body length ratios 0.19, 0.16, 0.17, 0.23, 0.19, 0.23, 0.20. In male, ratios for bases I-IV 0.18, 0.17, 0.17, 0.23. Male bases III-IV more robust than in female.

Pereopod I (Fig. 11A): Total length 0.77 body length. Carpus length subequal to basis length. Carpus and propodus thin, paucisetose.

Natatory Pereopods V-VI (Fig. 11B-C): Total lengths 0.69, 0.71 body length. Ischia lengths 0.75, 0.60 bases lengths. Carpi length/width ratios 1.4, 1.4. Propodi length/width ratios 2.0, 2.2. Dactyli short, curved, thin, lengths 0.47, 0.50 propodi lengths.

Pereopod VII (Fig. 11D): Total length 0.65 body length. Basis length 0.27 total length. Carpus and propodus narrow, with fewer setae on margins than on anterior natatory limbs; length/width ratios 5.7, 4.7. Dactylus long, thin, curved, length 1.2 propodus length.

Male Pleopod I (Fig. 12B): Fused pleopod pair long, thin, widest near proximal end, length 3.4 width; at dorsal orifice length 5.8 width. Distal tip bluntly rounded, almost quadrate. Inner and outer lobes continuous. Distal tip with setae dorsally, ventrally, and more proximally along midline. Setae thick and tubular proximally, narrowing abruptly at midlength, and thin, whiplike distally. Remainder of ventral surface without setae.

Male Pleopod II (Fig. 12C): Protopod long, narrow, distally rounded; length 3.6 width; lateral margin with 10 large plumose setae; distal and distolateral margin with short, fine, simple setae; 4 long simple setae on ventral surface. Endopod inserting 0.34 protopod length from distal tip. Stylet not extending to distal tip of protopod, with short sperm duct, length 0.46 protopod length.

Female Pleopod II (Fig. 12A): Pleopod narrow, widest midlength. Length 1.9 width. Keel thin, deep, with denticles along ventral margin. Fused pleopod pair depth 0.33 length. Lateral margins with 8 plumose setae. Long simple setae on distoventral edge, and on posterior half of keel. Distal tip slit length 0.11 total fused pleopod pair length.

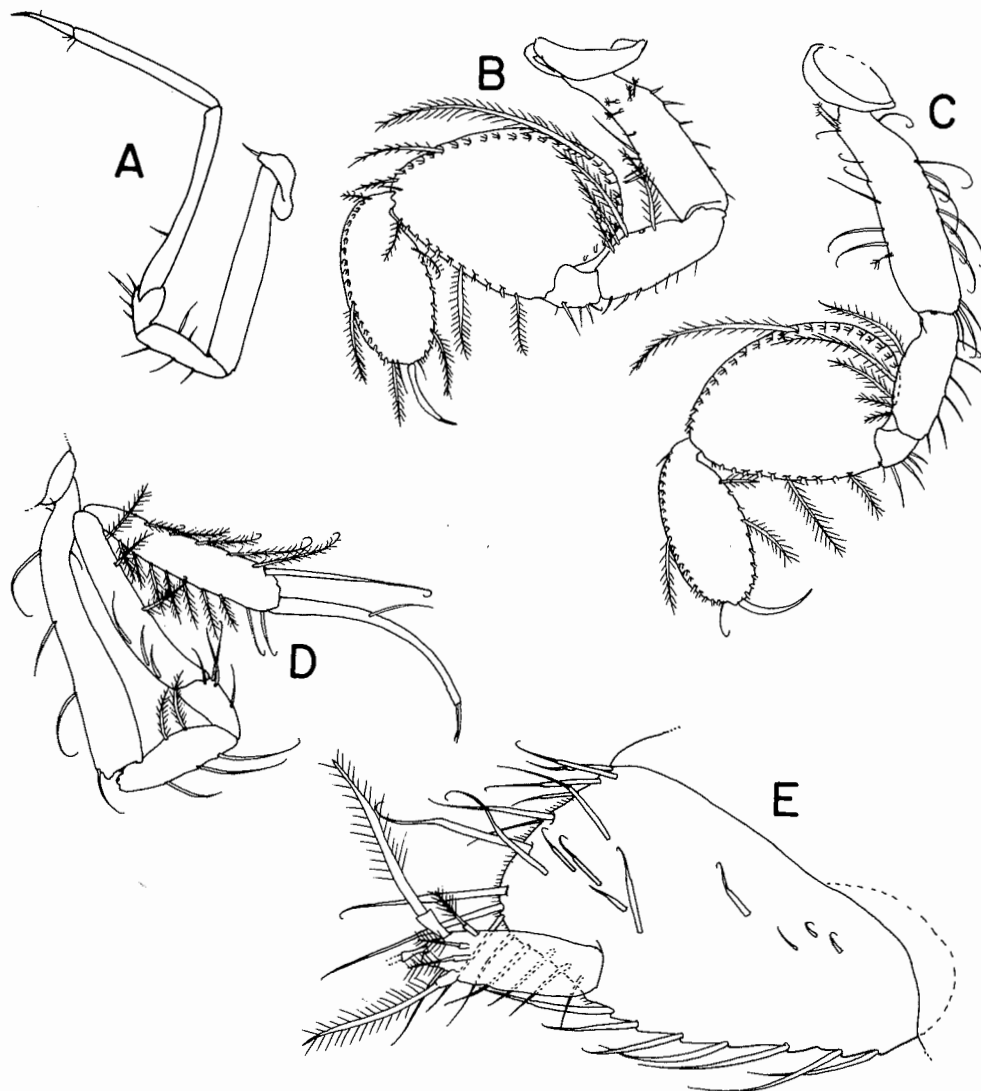


Figure 11. *Hapsidohedra ochlera* n. gen., n. sp. A, left pereopod I, paratype preparatory female, bl 1.8 mm. B-C, right natatory pereopods V-VI, paratype male, bl 2.0. D, left pereopod VII, paratype preparatory female, bl 2.0 mm. E, right uropod, *in situ*, holotype female.

Pleopod III (Fig. 12D): Exopod longer than endopod, distally rounded, with long, thin, simple setae on lateral margin, shorter, thin, simple setae on medial margin, and 2 long plumose setae having thick simple seta between them. Endopod with 3 long plumose setae. All plumose setae longer than exopod.

Pleopod IV (Fig. 12E): Exopod short, rounded, approximately half length of pleopod length; single long plumose seta on distal tip.

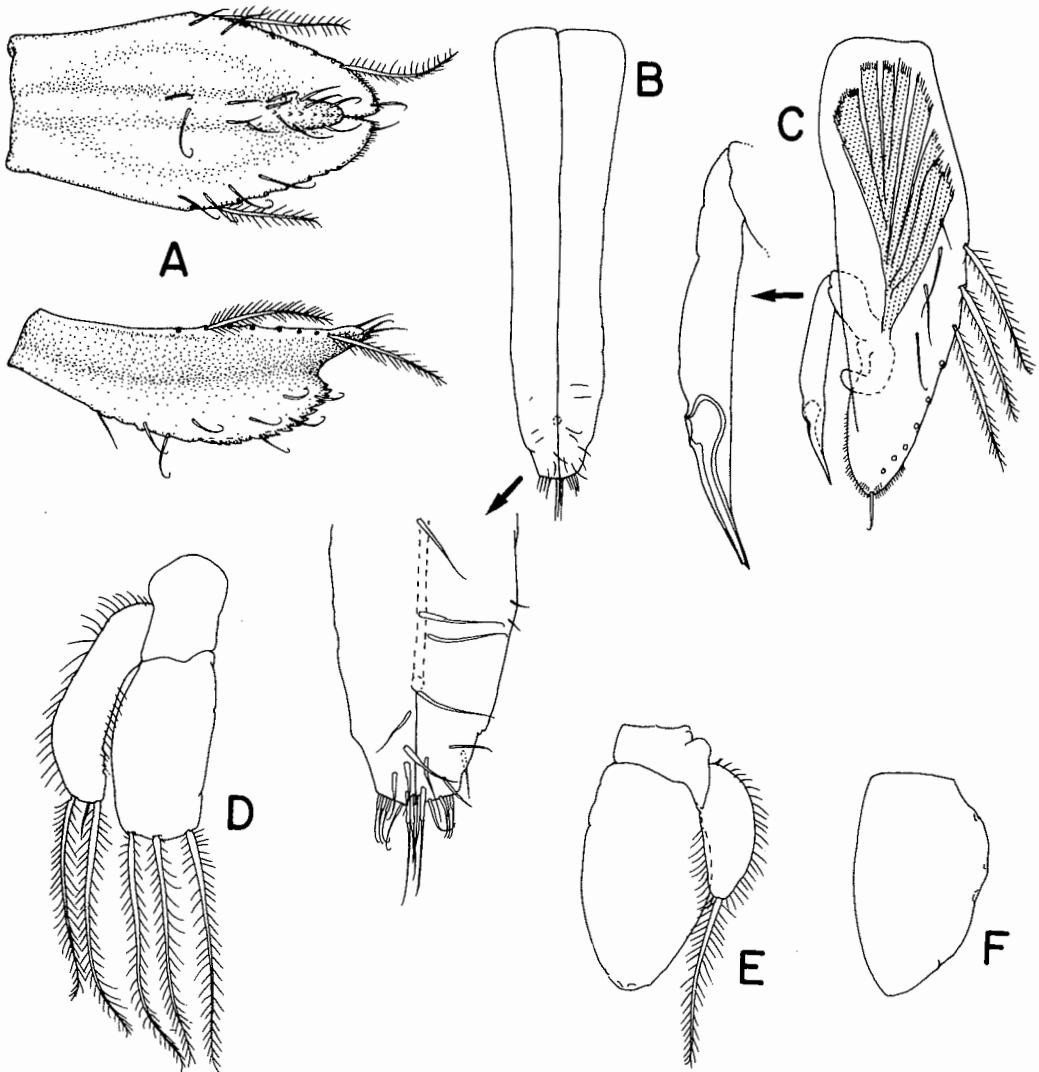


Figure 12. *Hapsidohedra ochlera* n. gen., n. sp. A, female pleopod II, ventral and lateral views, paratype preparatory female, bl 2.0 mm. B-F, pleopods, paratype male, bl 2.0 mm. B, pleopod I, with enlargement of distal tip. C, left pleopod II, with enlargement of stylet. D, right pleopod III. E-F, left pleopods IV-V.

Uropod (Fig. 11E): Length 0.28 (male) to 0.29 (female) pleotelson length. Single ramus length 0.43 (male) to 0.37 (female) protopod length. External margins of protopod with large setae. Distal tip of ramus with 2 large and several small broom setae.

Remarks. *Hapsidohedra ochlera* is most readily distinguished by a female pleopod II keel that has posteriorly directed denticles on ventral margin and an anteriorly recurved or truncate posterior margin. The shape of the proximal article of the antennula is also useful.

This species has been found in the shallow bathyal benthos of the Gulf of Mexico and the southern Caribbean Sea. It is not known, however, whether *H. ochlera* is continuously distributed, or whether it comprises disjunct populations interrupted by barriers such as the Yucatan Peninsula.

Hapsidohedra aspidophora (Wolff, 1962)

(Figure 13)

Synonym. *Ilyarachna aspidophora* Wolff, 1962, pp. 106-108.

Holotype. Brooding female with about 20 embryos in marsupium, bl 3.2 mm, body width 1.4 mm, ZMUC.

Type-Locality. R/V *Galathea* station 639, off East New Zealand, 37°31'S, 177°08'E, 213 m, bottom temperature about 14.7°C (Bruun 1959).

Distribution. Known only from type locality.

Diagnosis. Antennular article 2 shorter than medial lobe. Mandible lacking spine row on incisor process; molar process with only 1 serrate seta distally. Keel of female pleopod II dorsally and distally setose, lacking denticles on ventral margin, and sloping smoothly into distal tip.

Remarks. *Hapsidohedra aspidophora* is known from only a single, now partially dissected, brooding female (Wolff, 1962). It is much larger than all the specimens of *H. ochlera*, and differs in the form of the female pleopod II and the antennula. The mandibular characters, although less useful for sorting purposes, may be useful for distinguishing *H. aspidophora* from *H. ochlera*. The male of *H. aspidophora* is unknown.

Hapsidohedra aspidophora is known from surprisingly shallow (213 m) and warm (14°C) water off East New Zealand. The full range of this species and its preferred hydrographic regime will be of considerable biogeographic interest. *H. aspidophora* may be living under conditions similar to the deep-sea isopod fauna found in shallow (50 m) water in the Mediterranean Sea (Hessler and Wilson, 1983).

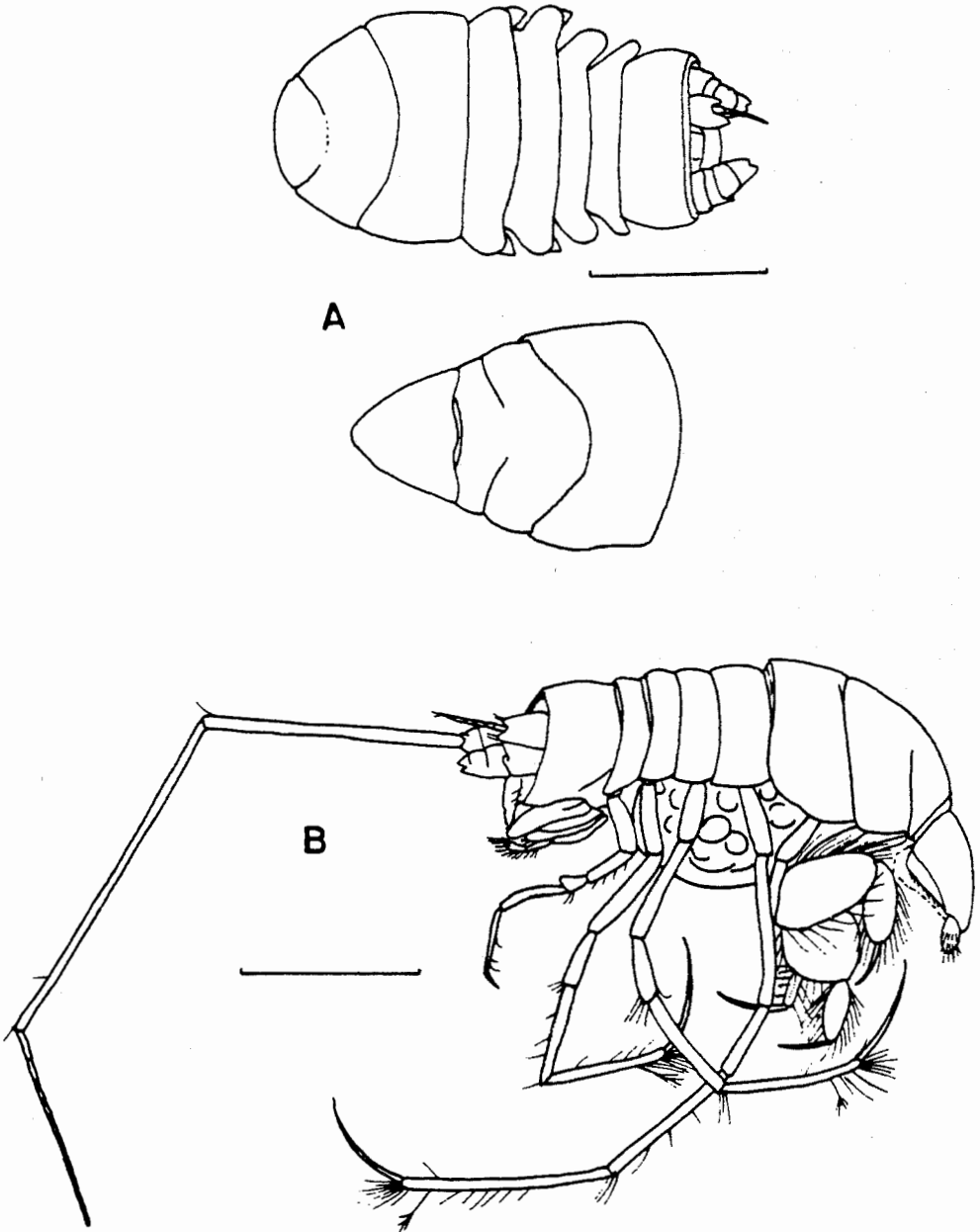


Figure 13. *Hapsidohedra aspidophora* (Wolff, 1962). A-B, dorsal and lateral views of holotype, after Wolff (1962), scale bar = 1.0 mm.

LIONECTES New Genus
(Figures 14-17)

Type-Species. *Lionectes humicephalotus* new species.

Generic Diagnosis. Dorsal surface smooth, without spines; in lateral view, dorsal surface forming smooth arc from cephalon to pleotelson. Cephalic anterior and anterolateral margins thin, dorsally flattened in frontal view. Rostrum absent, vertex slightly convex in dorsal view. Frontal arch between antennulae reduced, only slightly protruding, rounded dorsally, not heavily calcified. Clypeus medial section triangular in frontal view; broad, rounded dorsal apex of clypeus roughly horizontal, not sloping posteriorly to articulation with frons, lower than apex of frontal arch. Labrum high and anteriorly rounded, approximately three-quarters height of cephalon. Body deepest at pereonite 5. Natasome compact, conical in dorsal plan view; dorsal surface of pereonites 5-7 distinctly articulated laterally, indistinctly articulated medially between pereonites 5 and 6, and fused medially between pereonites 6 and 7; pleonite 1 articulating margins distinct; pereonite 7 reduced, not reaching lateral margin of natasome. Ventral surface of natasomal pereonites smoothly rounded, with indistinct or absent articulations between segments; insertions of pereopods VII medial to insertions of pereopods VI; posterior edge of pereon recessed into pleotelson. Antennular article 1 with distinct medial and lateral lobes; medial lobe rounded, longer than article 2; lateral lobe dorsoventrally flattened. Antennal scale absent. Mandible somewhat modified: spine row with few, posteriorly reduced members; molar process broad, distally rounded, with thin cuticle, lacking denticles, and with only 1 distal setulate seta; condyle enlarged, longer than molar process, with support ridge extending from posterior edge to protruding posterolateral corner of mandibular body; ventromedial region of mandibular body reduced, not protruding; palp not reduced, with robust segments. Lengths of pereopodal bases heterogeneous: bases I, II, III, and V lengths similar, shortest; basis VII longest; bases IV and VI lengths similar, intermediate lengths. Pereopods V-VI natatory, with broad carpi and propodi; pereopod V only slightly larger than pereopod VI; dactylus V tiny, rudimentary; dactylus VI-VII long and thin. Pereopod VII resembling walking leg, with few plumose setae on ventral margin of carpus only. Female pleopod II distal tip entire, lacking slit. Uropods terminal on pleotelson, visible in dorsal view, projecting from semicircular distal tip of pleotelson; protopod flattened, oval, dorsolaterally convex, with marginal whip setae; endopod large, fat; exopod small but distinct; both rami shorter than protopod.

Derivation of Name. *Lionectes* (Greek, masculine) means "smooth swimmer," referring to the very smooth dorsal surface of members of this genus.

Remarks. *Lionectes* is a member of the lipomerine group that has ambulatory seventh pereopods. In addition to *Lionectes*, the group includes *Coperonus* and

Hapsidohedra. Because this group has functional seventh pereopods, it is distinct from the genera *Lipomera* and *Mimocopelates*, which lack seventh pereopods (or at least functional ones). Although these three genera resemble each other in general form of the cephalon and the natasome, each has specializations, or lack thereof, that make them distinct. *Lionectes* is identified by a smooth, almost seedlike habitus in dorsal view, terminally placed uropods that protrude from a posterior opening in the pleotelson, a dorsoventrally flattened head, and a distal section of the pereon that is recessed into pockets in the pleotelson. Details of the mandible and the frons are also useful for identifying this genus.

The composition of *Lionectes* is currently complicated by *Eurycope frigida* Vanhöffen, 1914, described from 10 specimens collected at Gauss Station (8/II/1903) in fairly shallow water off eastern Antarctica. Vanhöffen's (1914:590) illustrations show two animals, one listed as an adult and another listed as a juvenile, although two species may actually be represented. The "adult" probably belongs to *Coperonus*, and the "juvenile" may be a member of *Lionectes*. The adult is much larger than the supposed juvenile - 2.5 mm versus 1 mm - and the juvenile is *not* a manca. In addition, the "juvenile" has a number of characters that conflict with the adult: the cephalon is anteriorly more compressed; the pleotelson is straight sided, not rounded; the antennulae are much shorter, with compressed flagellar articles; and the uropods project into dorsal view from the tip of the pleotelson. Unfortunately, Vanhöffen (1914) did not describe the uropods. The "juvenile" has one characteristic, in addition to the above differences with the "adult," that makes its identification as a species of *Lionectes* more certain: the seventh pereopods, which resemble walking legs, are placed medial to the sixth walking legs and appear in Vanhöffen's drawing (his figure 123A) to protrude from above the pleopod II, indicating that the posterior part of the pereon is recessed into the pleotelson - a diagnostic character of *Lionectes*. The larger individuals (Vanhöffen's figures 122A, 123C-D) are assigned to *Coperonus* because similarities in the overall body shape and size, in the length of the antennulae, in the male pleopods, and in the maxilliped (see discussion above, under *Coperonus*). The single small individual is assigned *Lionectes* species *incertae sedis* until it can be examined and described more fully.

The distribution of *Lionectes* is limited to Antarctic seas, with *L. humicephalotus* from the South Shetland Islands and the Weddell Sea, and *L. sp. incertae sedis* from eastern Antarctica. Known members of this genus are very small, so the restricted distribution may partially result from sampling artifacts. *Lionectes* has not been found in the relatively carefully sampled Atlantic Ocean, giving evidence that this genus is not cosmopolitan. Interestingly, species of *Lionectes* co-occur with those of *Coperonus* at all the localities where *Lionectes* has been found. *Coperonus*, however, is much more broadly distributed.

Lionectes humicephalotus new species
(Figures 14-17)

Holotype. Brooding female, bl 1.2 mm, all limbs on right side except pereopod I intact, USNM 227056.

Paratypes. Three brooding females, all bl 1.2 mm, partially or completely dissected for description, SIO.

Type-Locality. Institute of Oceanography, Dalhousie (IODal) benthic station 13, North of King George Island, South Shetland Islands, 61°18'S, 58°00'W, 282 m, collected with a small epibenthic sled on 7 February 1970 during Bedford Institute of Oceanography cruise Hudson 70.

Other Material. Female, IODal 7; damaged female, 69Rankin 001AD; damaged brooding female, 68Rankin 0055SBT. SIO.

General Distribution. South Shetland Islands to the Weddell Sea, 58.6-659 m.

Derivation of Name. *Humicephalotus* means "provided with flat head."

Diagnosis. See description. There is insufficient information on the species of this genus to allow a diagnosis at this time.

Description of Brooding Females Only. Body Characters (Fig. 14A-B): Adult body length 1.1-1.4 (4 inds) mm, length 1.9-2.0 (4 inds) width.

Body setation (Fig. 14B): Natasome with approximately 5 setae on each ventrolateral margin; other dorsal surfaces with scattered fine setae.

Cephalon (Fig. 14C-F): Dorsal length 0.35 width, length 0.68 height, width 0.67-0.70 (2 inds) width of body at pereonite 5. Ventral margin at posterior articulation of mandible lacking indentation or notch.

Antennula (Fig. 14C): Length 0.16 body length, with 7 articles and 2 aesthetascs distally. Article 1 medial length 0.94 width; medial lobe with approximately 3-4 broom setae. Article 2 with broom setae. Article 2 with 2 distal projections bearing broom setae: 1 dorsally and 1 laterally. Article 2 length (including dorsal projection) 0.58 article 1 medial-lobe length. Article 3 length 0.34 article 2 length.

Antenna (Fig. 14A): Total length greater than 1.6 (2 inds) body length (tip of flagellum broken). Article 5 shorter and more robust than article 6; article 5 length 0.58 article 6 length, 0.23 body length.

Mandible (Fig. 15A-G): Left mandible with 3 cusps on incisor process; right mandible with large central cusp, smaller cusp on either side, and 3 small denticles on dorsal margin. Lacinia mobilis only slightly narrower than left incisor process, with 3 cusps extending to tip of incisor process. Spine row reduced, with 3 members. Molar process with thin cuticle, not calcified, distal end with no circumgnathal denticles or large pointed cusp on ventral margin; posterior margin with 1 flattened setulate seta; triturating surface without evident sensory pores. Condyle length 0.35 (2 inds) mandibular body length. Palp

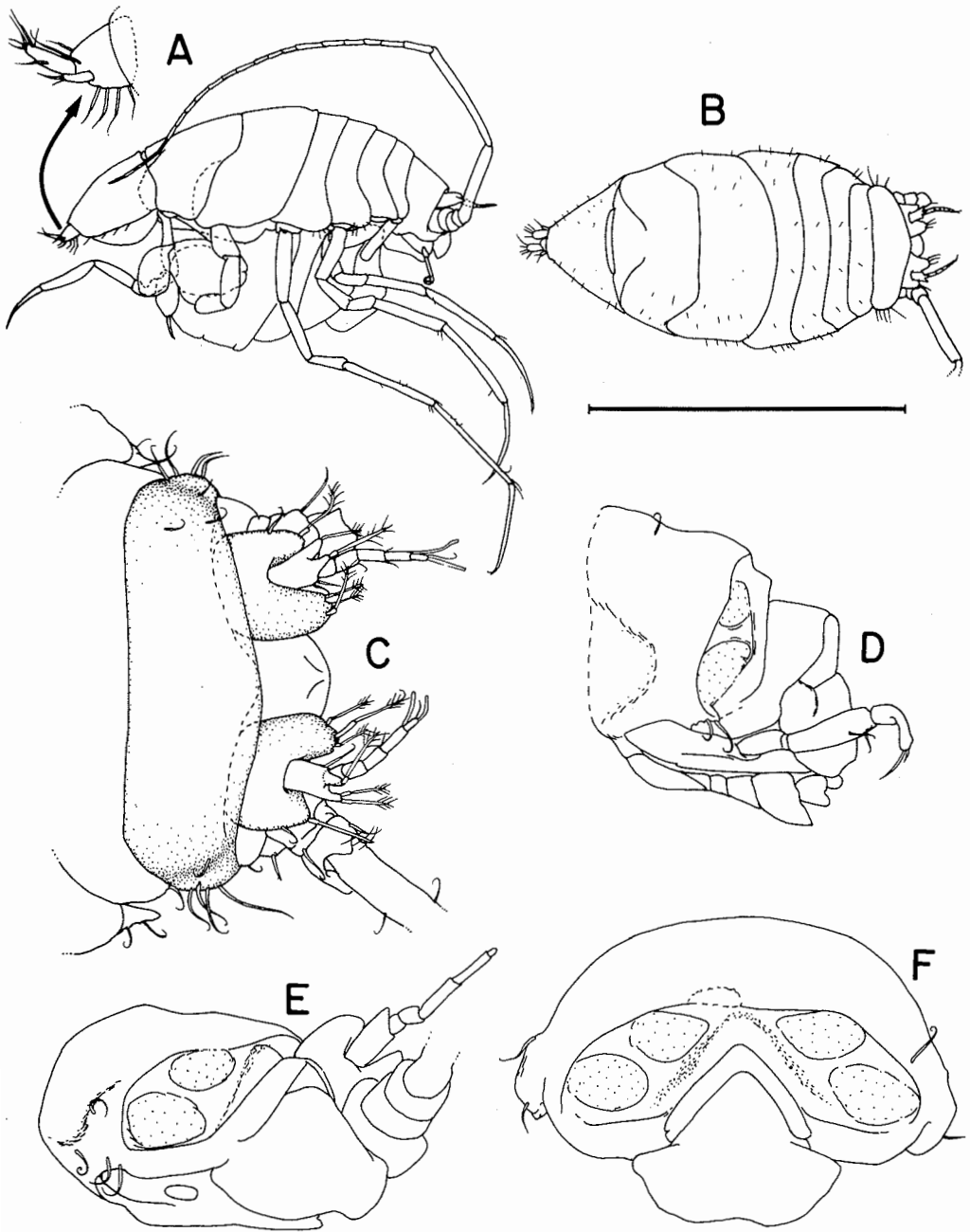


Figure 14. *Lionectes humicephalotus* n. gen., n. sp. A-C, holotype brooding female. A, lateral view, with enlargement of uropod. B, dorsal view, scale bar 1.0 mm. C, cephalon dorsal view. D-F, cephalon, paratype brooding female, bl 1.2 mm, lateral, frontal oblique and anterior views respectively.

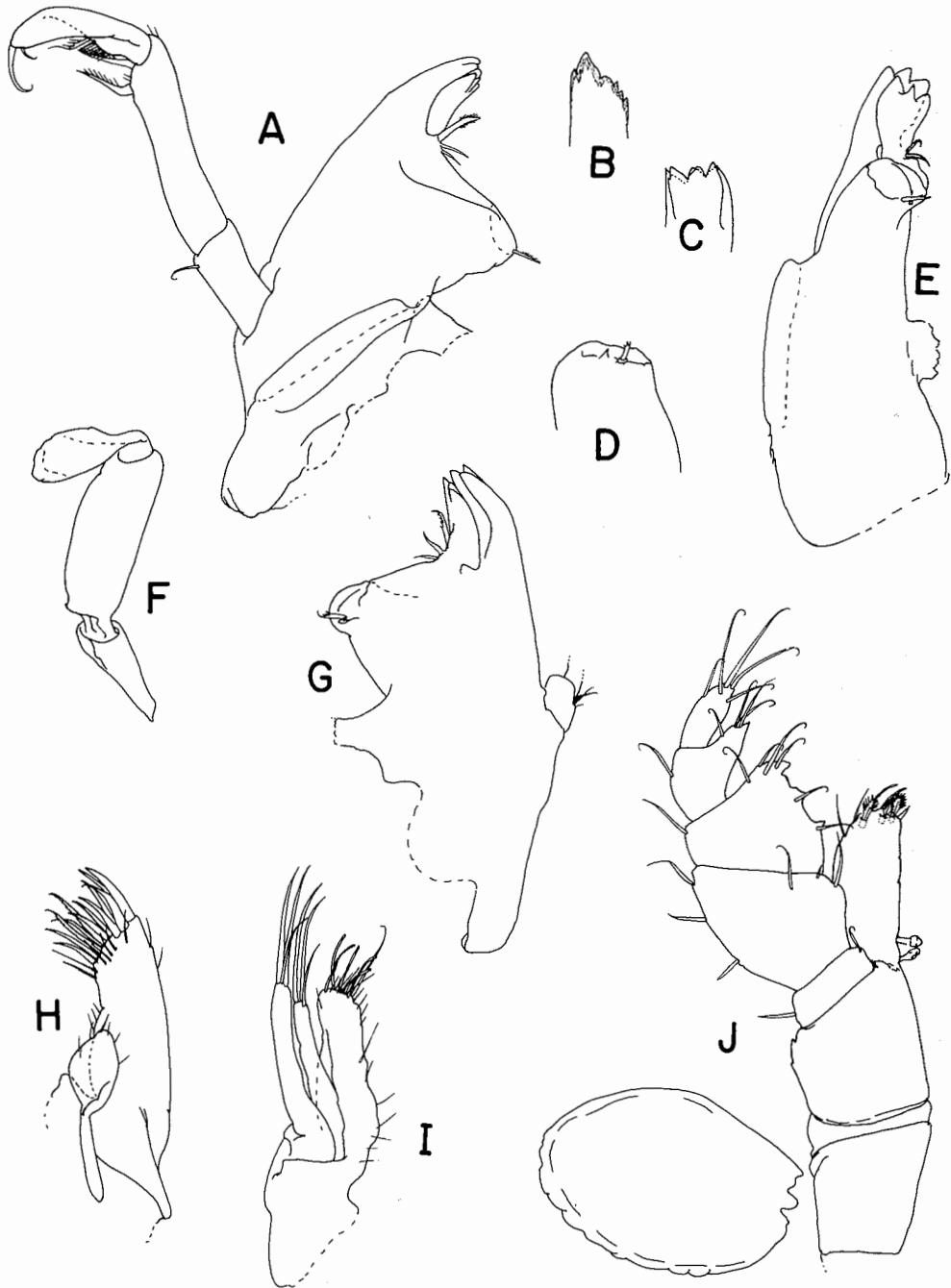


Figure 15. *Lionectes humicephalotus* n. gen., n. sp., paratype brooding female, 1.2 mm. A, C-G, left mandible. A, dorsal view. B, incisor process, right mandible. C, incisor process and lacinia mobilis, plan view. D, molar process, posterior view. E, posterior view of whole mandible. F, palp, lateral view, setae omitted. G, whole mandible, ventral view. H, left maxillula. I, right maxilla. J, right maxilliped.

second article length 0.36-0.38 (2 inds) mandibular body length; distal article robust, strongly curled.

Maxillula (Fig. 15H): Normally developed. Inner endite short and rounded, lacking large apical seta, but with several smaller setae, width 0.61 outer endite width.

Maxilla (Fig. 15I): Normally developed. Outer lobes approximately same length as inner lobe.

Maxilliped (Fig. 15J): Basis with 2 receptaculi and 3 fan setae distally. Endite length 0.52 total basis length. Palp article 2 width 1.9 endite width, lateral length 2.0 medial length. Palp article 3 lateral length 0.34 medial length. Epipod oval, lateral edge scalloped; length 0.88 basis length; length 1.5 width. Coxa elongate, subequal to basal section of basis.

Ambulatory Pereopods (Fig. 14A, 16A): Pereopods I-IV thin, lightly setose; length-body length ratios 0.61, 0.92, 1.0, 1.2. Bases I-IV length-body length ratios 0.17, 0.15, 0.17, 0.21.

Natatory Pereopods (Fig. 16C-E): Natapods heterogeneous in form: pereopod V with very broad carpus and propodus, many natatory setae, and rudimentary dactylus; pereopod VI with narrower carpus and propodus, many natatory setae, and long curved dactylus; pereopod VII resembling walking leg with narrow distal segments, approximately 4 natatory setae on ventral margin of carpus only, propodus longer than carpus. Pereopods V-VII increasing in length but becoming narrower posteriorly; length-body length ratios 0.74, 0.79, 0.83. Bases V-VII also increasing in length posteriorly; length-body length ratios 0.17, 0.21, 0.23. Carpi V-VII length-width ratios 1.0, 1.4, 3.7. Propodi V-VII length-width ratios 1.5, 2.5, 6.6; propodi V-VII length carpus length ratios 0.90, 0.84, 1.5. Dactyli VI-VII long, curved; length-propodus length ratios 0.90, 0.89. Dactylus V rudimentary.

Male Pleopods I and II: unknown.

Female Pleopod II (Fig. 17A-B): Keel narrow, rounded in lateral view, without distinct apex or large setae, deepest in proximal half of pleopod, distinctly set off from lateral fields. Ventral surface with only fine setae. Distolateral margins with approximately 10-12 long plumose setae on distal half of margins. Length 1.3 width; depth 0.36 length.

Pleopod III (Fig. 17D): Exopod distally truncate, longer than endopod, with 3 long plumose setae, and 1 simple seta on distal tip. Endopod with 3 distal plumose setae.

Uropod (Fig. 14A, 17G): Protopod length 1.4 width; length 0.08 body length. Exopod 0.54 endopod length. Endopod 0.68 protopod length. Distal margin of protopod with approximately 6 whip setae.

Remarks. *Lionectes humicephalotus* is currently known only from females; 4 brooding females were collected at the type locality off King George Island, and

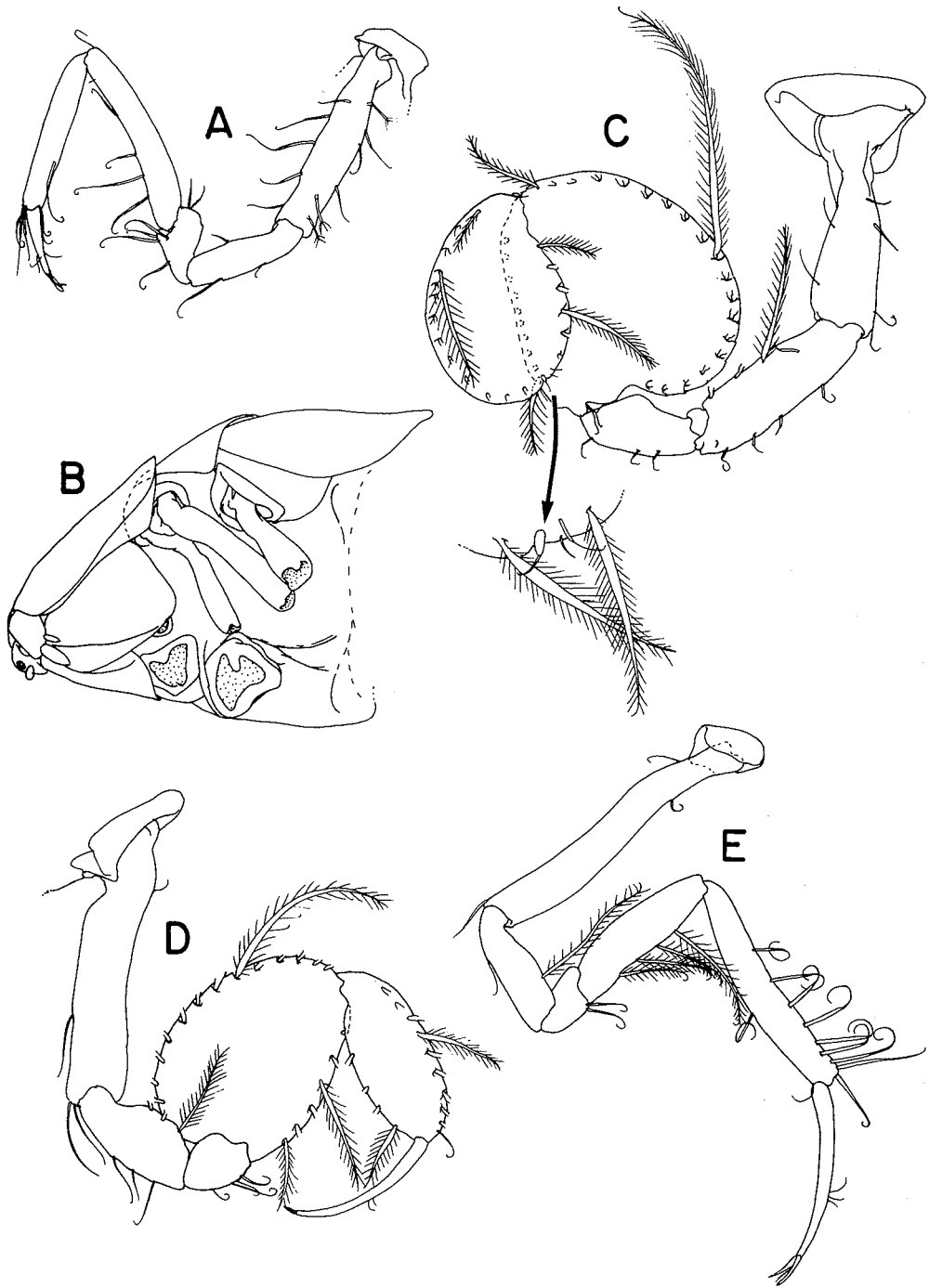


Figure 16. *Lionectes humicephalotus* n. gen., n. sp., paratype brooding female, bl 1.2 mm. A, left pereopod I. B, natasome, ventral oblique view, showing form of ventral surface and relative sizes of pereopodal bases. C, right pereopod V with enlargement of dactylus. D-E, left pereopods VI-VII.

the other two localities yielded only damaged females. *L. sp. incertae sedis* (Vanhöffen, 1914) is also known from a single female. There are differences between the illustrations of *L. sp. incertae sedis* and *L. humicephalotus* described here, but it is uncertain whether the illustrations of the former species are accurate in small details. These include the lateral margin of pereonite 7 extending to the body margin, the longer uropodal exopod, and the presence of an elongate dactyl on pereopod VII. Other differences might be developmental because Vanhöffen's specimen was not brooding. A more detailed characterization of *Lionectes* must await the capture of males.

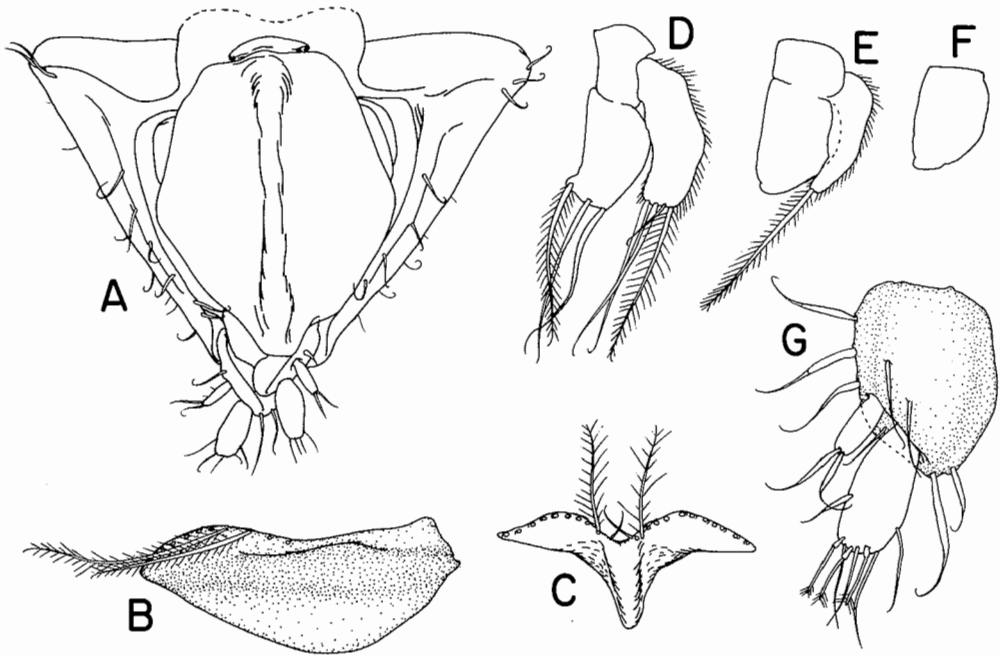


Figure 17. *Lionectes humicephalotus* n. gen., n. sp., paratype brooding female, bl 1.2. A, ventral view of pleotelson. B-C, pleopod II, lateral and posterior views. D-F, left pleopods III-V. G, left uropod, lateral view.

Genus *LIPOMERA* Tattersall, 1905
(Figures 18-27)

Type-Species. *Lipomera lamellata* Tattersall, 1905.

Generic Diagnosis. Body dorsal surface without large vertical spines or setae. Cephalic anterior and lateral margin lightly calcified, in frontal view semicircular; ventral margin folding into deep notch at posterior articulation of mandible, articular margin protruding laterally in dorsal view. Rostrum nearly absent, vertex smoothly convex in dorsal view. Frons broadly rounded, almost flat, lacking frontal arch, with distinct separation between antennulae. Clypeus arched, narrow strip, medial part triangular in frontal view, apex articulating directly to frons. Labrum high, height greater than half cephalon height. Body deepest at pereonite 5. Natasome triangular in dorsal view; pereonites 5 and 6 large; dorsal articulations distinct. Pereonite 7 reduced, fused to pereonite 6. Hindgut anterior to pleotelson with distinct bend or coil. Antennula first article with no medial lobe and distinct flattened lateral lobe; in females, antennula reduced to approximately 5 articles, male antennula not reduced. Antennular scale absent. Mandible with palp approximately same length as mandibular body; molar process variously enlarged; condyle with posterior support ridge extending to posterolateral corner of mandibular body. Pereopodal bases I-III and VI subequal, basis V longest, basis IV intermediate in length. Pereopods V-VI natatory; pereopod VII tiny and rudimentary, or completely absent. Dactyli of pereopods V-VI long, thin, lengths subequal. Female pleopod II tip with short fused slit. Uropod lacking rami; protopod flattened, leaflike.

Derivation of Name. In the name *Lipomera*, Tattersall (1905a, 1905b) seems to be referring to the lack of a well-developed seventh pereonite in this genus by combining *lipo-*, a prefix meaning "to be lacking," with *mera*, a latinized form of the feminine Greek word *meris* which means "a part."

Remarks. Tattersall (1905a) made this genus the type of his new family Lipomeridae, whereas the same author (1905b), in writing the full description of *Lipomera*, placed it in the Munnopsidae, which then included the current family Eurycopidae. Neave (1939) cites Tattersall (1905a), the report to the British Association for the Advancement of Science, as the original publication of the genus. Nierstrasz and Stekhoven (1930), Nordenstam (1933), and Hult (1941) list (possibly erroneously) Tattersall (1905b) as actually being published in 1906, although Hansen (1916) who was actively working at the time of publication, lists the date as 1905. Tattersall's second paper may possibly have come out late in 1905, making some authors believe it was published in 1906. If *Lipomera* is placed in the same family as *Eurycope*, but separate from the Munnopsidae, then the family must be called the Lipomeridae because a family-level name was not based on *Eurycope* until Hansen's (1916) Eurycopini. Under previous classifications, the Eurycopidae would be a junior synonym of the Lipomeridae, even though the former name has wide acceptance. The revised classification of

the munnopsid taxa (see phylogeny and classification section) places the Lipomerinae in a subfamily separate from the Eurycopinae, retaining this useful name.

Lipomera is easily distinguished from other Lipomerinae, none of which has a lamellar uropod that lacks rami and covers the anal region of the pleotelson. The cephalon of *Lipomera* is also unique: a frons lacking a frontal arch, and with the clypeus and labrum set low on the frons. The uropodal and cephalic characters are especially useful for separating *Lipomera* from the new genus *Mimocopelates*. Rudimentary or absent seventh pereopods distinguish *Lipomera* from the new genera *Coperonus*, *Hapsidohedra*, and *Lionectes*.

Lipomera must be divided into three subgenera - *L. (Lipomera)*, *L. (Tetracope)*, and *L. (Paralipomera)* - because important specializations identify groups of species within the genus but not the genus as a whole. Members of the subgenus *Lipomera* are short and broad, and have short heads, smooth dorsa without denticles on the anterior margins, and rudimentary seventh pereopods and pereonites. The subgenus *Tetracope* is similar to *L. (Lipomera)* in body shape and retention of a rudimentary pereopod VII, but it differs in the following ways: the gut is coiled or has an exaggerated bend (discussed below); pereonite 6 is larger than pereonite 5, pereopods V and VI are similar in size, and the uropods are narrow and pointed, not large and round. The subgenus *Paralipomera* is similar to *L. (Lipomera)* in having only a modest bend in the hindgut, pereonite 5 and pereopod V larger than pereonite 6 and pereopod VI, and large round uropods, but its members have longer and narrower bodies, longer, more robust heads, ornamented dorsal surfaces with denticles on the anterior margins, and no seventh pereopods or pereonites as adults.

As mentioned above, species of *Lipomera* have curved, strongly bent, or coiled hindguts (Fig. 24). This is highly unusual in the Crustacea. Few other groups are known to have coiled guts; Calman (1909) mentioned only two, a group of Cladocera and a single genus of Cumacea. Another Janiroidean genus, *Pleurocope*, also has a highly modified alimentary canal, although this latter form is different from a strictly coiled condition (Wilson, in prep.). A curved or coiled gut is a derived condition in this genus, because all other Lipomerinae, or munnopsids more generally, have straight guts. In another invertebrate taxon, the bivalve *Abra profundorum*, a coiled gut has been considered an adaptation to the food-poor environment of the deep sea (Allen and Sanders 1966). The midgut caeca are unusually large in *Lipomera*, supporting this hypothesis. Improved digestion does not necessarily explain the convoluted guts seen in *Lipomera*, although alternative hypotheses are not apparent at this time.

Lipomera is currently known only from the North and South Atlantic Ocean and the Gulf of Mexico.

Subgenus *LIPOMERA* Tattersall, 1905
(Figures 18, 24B)

Diagnosis. Dorsal surface of body with thin, smooth cuticle; anterior margins of pereonites without denticles. Cephalon not indurate. Pereonite V longer than pereonite VI. Mandible not heavily sclerotized and strengthened. Hindgut anterior to pleotelson curved, not coiled. Pereopod VI shorter than pereopod V. Pereopod VII present but rudimentary.

Composition. Monotypic: *Lipomera (Lipomera) lamellata* Tattersall, 1905.

Lipomera (Lipomera) lamellata Tattersall, 1905
(Figure 18)

Types. Eleven syntype individuals from 60 miles West of Achill Head, Ireland, August 1901, 199 fathoms (364 meters), 53°58N, 12°16'W. Length of adult female reported as 1.25 mm. Complete description by Tattersall (1905b, pp. 32-35, pl. viii, locality data on p. 75). No holotype or depository designated in original or later description. Types cannot be found (R. Lincoln, personal communication).

Distribution. Known only from the type-locality off the western coast of central Ireland at a depth of 364 m.

Diagnosis. Anterior margins of dorsal segments without denticles. Cephalon medial length approximately one-third cephalon width. Body dorsal surfaces smooth, with few setae; anterolateral corners of pereonites and pleotelson with long setae. Male antennula with 11-13 articles. Pleotelson wider than long, sides in dorsal view smoothly rounded; distal tip in dorsal view broadly pointed, almost rounded. Male pleopod I tip narrow, acutely pointed. Uropod posterior margin straight.

Remarks. *Lipomera (Lipomera) lamellata* has not been collected since its original capture in 1901. This may be because it inhabits a depth too shallow for many deep sea studies, and too deep for most shallow water benthic work. An undescribed species of *L. (Lipomera)* occurs off Walvis Bay, Africa, at a depth of approximately 200 m. *L. (L.) lamellata* differs from this other species in the collection by its larger size (the undescribed species has 0.8-mm-long adults!), and by its rounded pleotelson tip, pointed male pleopod I, and narrower cephalic vertex.

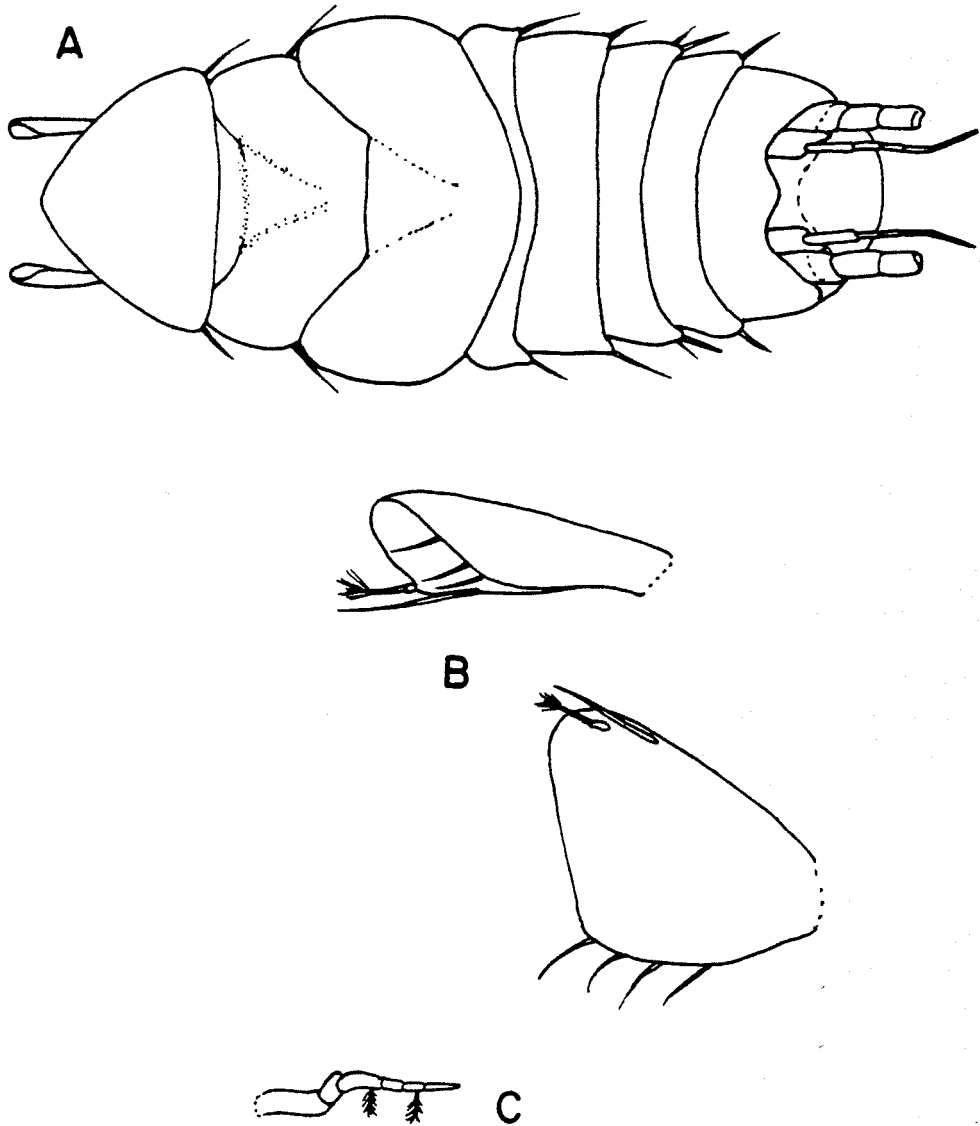


Figure 18. *Lipomera (Lipomera) lamellata* Tattersall, 1905. A, holotype female, dorsal view. B, uropod, ventral and lateral views. C, rudimentary pereopod VII. After Tattersall (1905b).

PARALIPOMERA New Subgenus
(Figures 19-22)

Diagnosis. Dorsal surface partially indurate, with denticles on anterior margins. Cephalon indurate. Pereonite V longer than pereonite VI. Mandible heavily sclerotized and strengthened. Hindgut anterior to pleotelson curved, not coiled. Pereopod VI shorter than pereopod V. Pereopod VII absent. Uropod large, leaflike, round, extending beyond distal tip of pleotelson.

Derivation of Name. *Paralipomera* (Greek, feminine) means "next to *Lipomera*."

Composition. *Lipomera (Paralipomera) knorrae* n. sp. Monotypic but with at least 3 undescribed species.

Lipomera (Paralipomera) knorrae new species
(Figures 19-22)

Holotype. Copulatory male, bl 1.2 mm, USNM 227057.

Paratypes. Brooding female, bl 1.5 mm, USNM 227058. Copulatory male, bl 1.2 mm, ZMUC. Brooding female, bl 1.4 mm, MNHN Is.1815. Ten individuals, some dissected for description, SIO.

Type-Locality. WHOI 340, 38°14.4-17.6'N, 70°20.3-22.8'W, 3264-3256 m, collected with an epibenthic sled, 3 December 1973, R/V *Knorr* cruise no. 35, leg 2.

General Distribution. Known only from type-locality, Western Atlantic on the Gay Head-Bermuda transect, 3256-3264 m.

Derivation of Name. This species of *Lipomera* is named *knorrae* after the R/V *Knorr* of the Woods Hole Oceanographic Institution.

Diagnosis. Anterior margins of cephalon and anterior 5 pereonites with numerous small spines. Cephalon medial length approximately half cephalon width. Body dorsal surfaces with fine cuticular ornamentation and scattered fine setae; anterolateral corners of pereonites and pleotelson with small fine setae only. Pleotelson longer than wide, sides in dorsal view with distinct angle at insertions of uropods; distal tip in dorsal view acutely rounded. Male antennula with 18-20 articles. Male pleopod I tip narrow, acutely pointed. Uropod posterior margin convexly curved.

Description. Body Characters (Fig. 19A-C): In adult males, body length 1.2-1.5 mm (4 inds); body length 2.6-2.7 width (4 inds). In adult females, body length 1.4-1.5 mm (4 inds); body length 2.6-2.8 width (4 inds).

Cephalon (Fig. 19D-G): Width 0.79 body width, ratio range 0.72-0.83 (8 inds). Medial dorsal length 0.54 width; length 0.72 height. Ventral margin at posterior articulation of mandible with distinct indentation or notch.

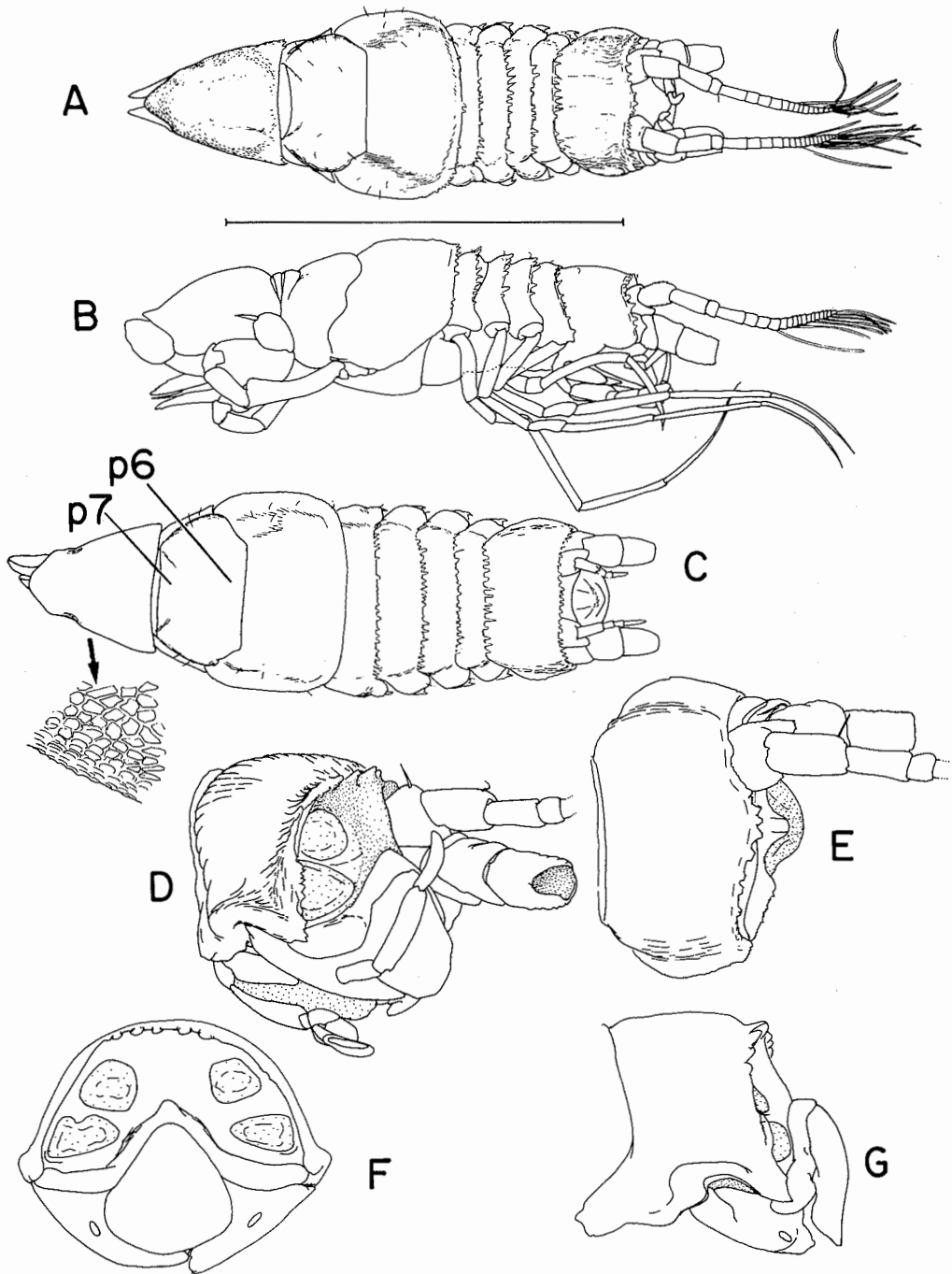


Figure 19. *Lipomera (Paralipomera) knorrae* n. subgen., n. sp. A-B, holotype male, dorsal and lateral views, scale bar 1.0 mm. C, paratype preparatory female, dorsal view, with detail of cuticular sculpturing on pleotelson; p6 = pereonite 6, p7 = pereonite 7. D-G, cephalon, antennula, and antenna removed to show frons, paratype male anterior body fragment: D, frontal oblique view; E, dorsal view; F, anterior view; G, lateral view.

Antennula (Fig. 19A-B, 20A-B): Highly sexually dimorphic: in males, length 0.45-0.46 body length; in females, 0.16. Male antennula with 15-17 articles and approximately 8 aesthetascs distally; female antennula with 5 articles and 1 aesthetasc distally. Article 1 not sexually dimorphic, medial length 0.77 width in female; medial side of both sexes with no setae; lateral lobe with single broom seta. Articles 2 and 4 with large broom setae. Article 2 subequal to or longer than article 1 lateral lobe in both sexes, article 2 broader in males than in females. Article 3 subequal to or slightly shorter than article 2 in males, article 3 length 0.43 article 2 length in females.

Mandible (Fig. 20C-G): Heavily sclerotized and modified. Left incisor process with 3 short, broad cusps; right incisor process with only 2 low, broad cusps. Lacinia mobilis reduced, narrower than incisor process, with 3 low cusps. Left spine row with 3 members; 4 on right side. Molar process distal surface convexly rounded, with no circumgnathal denticles and with single rounded cusp on posterior margin adjacent to 2 flattened setulate setae; triturating surface with approximately 2 sensory pores. Condyle elongate and curved, length of curved lateral margin 0.67 mandibular body length. Palp second article length 0.52 mandibular body length; palp distal article slightly curved and thin.

Maxillula (Fig. 20H): Normally developed. Inner endite width 0.41 outer endite width.

Maxilla (Fig. 20I): Normally developed. Outer lobes shorter than inner lobe.

Maxilliped (Fig. 20J): Basis with 2 receptaculi. Proximal part of basis very broad, with semicircular lateral margin, maximum width nearly 3 times endite width. Endite with 4 fan setae distally, medial fan seta more robust, with fewer and broader branches than 3 lateral fan setae; distomedial corner also with short bifurcate seta medial to robust fan seta. Endite length 0.41 total basis length. Palp article 2 width 1.8 endite width, lateral length 2.2 medial length. Palp article 3 lateral length 0.33 medial length. Epipod medial margin straight; distal tip rounded, with single seta; length 0.62 basis length; length 1.8 width.

Ambulatory Pereopods (Fig. 21A-E): Pereopods I-IV similar, thin, without large spinelike setae; length-body length ratios 0.64, 0.95, 0.93, 0.95. Pereopod I not sexually dimorphic. Bases I-IV length-body length ratios 0.18, 0.18, 0.18, 0.19. Bases II-IV with group of broom setae on anterior midpoint.

Natatory Pereopods (Fig. 21F-G): Natapods heterogeneous in form: pereopod V larger than pereopod VI, pereopod VII absent. Pereopod length-body length ratios 0.66 and 0.54. Bases V-VI length-body length ratios 0.21 and 0.17; both segments with long row of simple or whip setae. Basis V thickened distally, with distal group of broom setae. Carpi V-VI length-width ratios 1.3 and 1.6. Propodi V-VI length-width ratios 1.7 and 2.1. Dactyli V-VI long, thin, with marginal fringe of fine setae; length ratios with respective propodi both 0.71. Unguis V long and curved; unguis VI similar but very short.

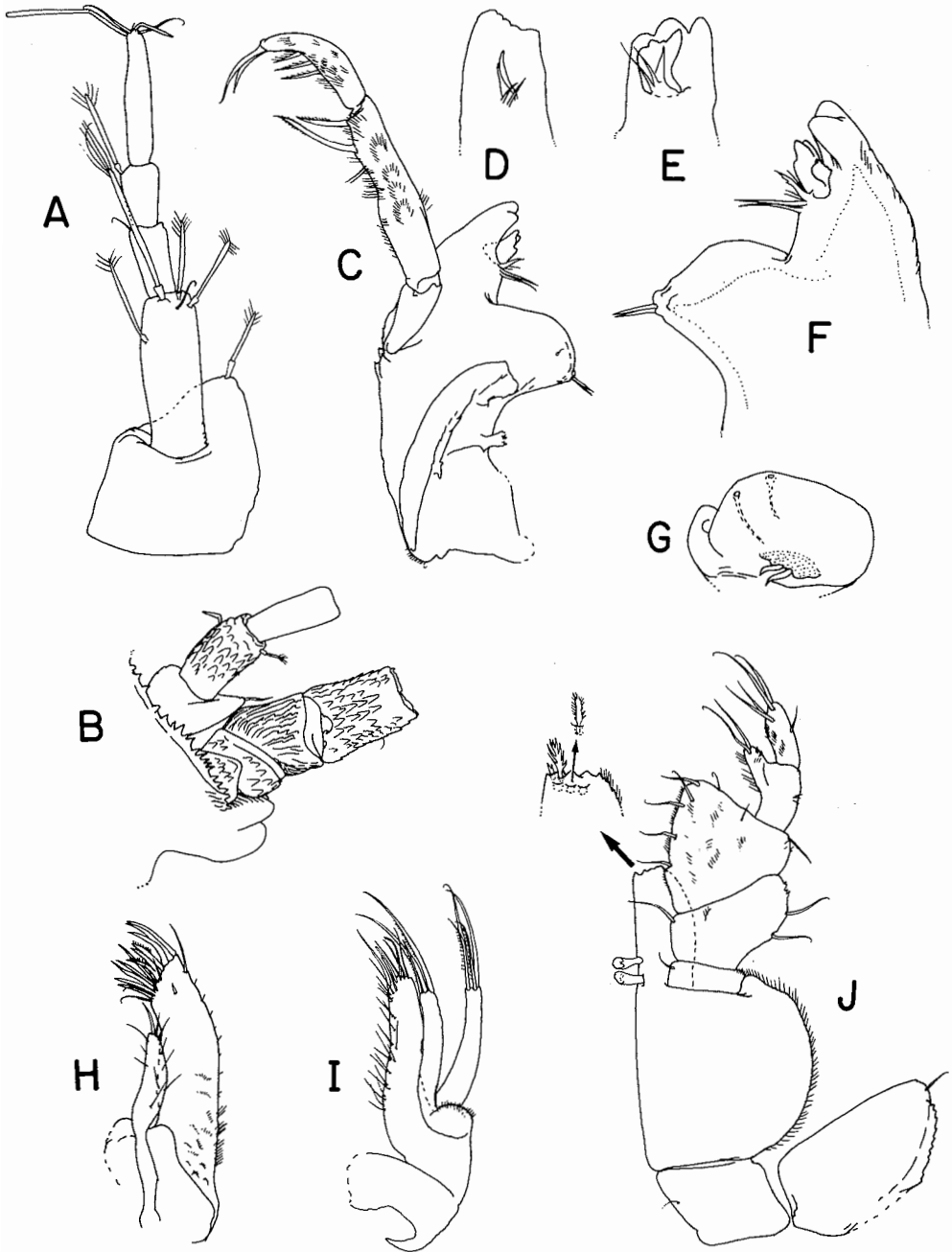


Figure 20. *Lipomera (Paralipomera) knorrae* n. subgen., n. sp. A, right antennula, paratype female, bl 1.4 mm. B-J, paratype male, bl 1.5 mm. B, right, antennula and antenna, basal segments, cuticular ridges shown, lateral view. C, E-G, left mandible. C, dorsal view. D, incisor process, right mandible, plan view. E, incisor process and lacinia mobilis, plan view. F, distal part of mandibular body, ventral view; dotted lines show thickness of sclerotization. G, molar process, medial view. H, left maxillula. I, left maxilla. J, maxilliped, with enlargement of distal tip, fan seta from subdistal row shown separately.

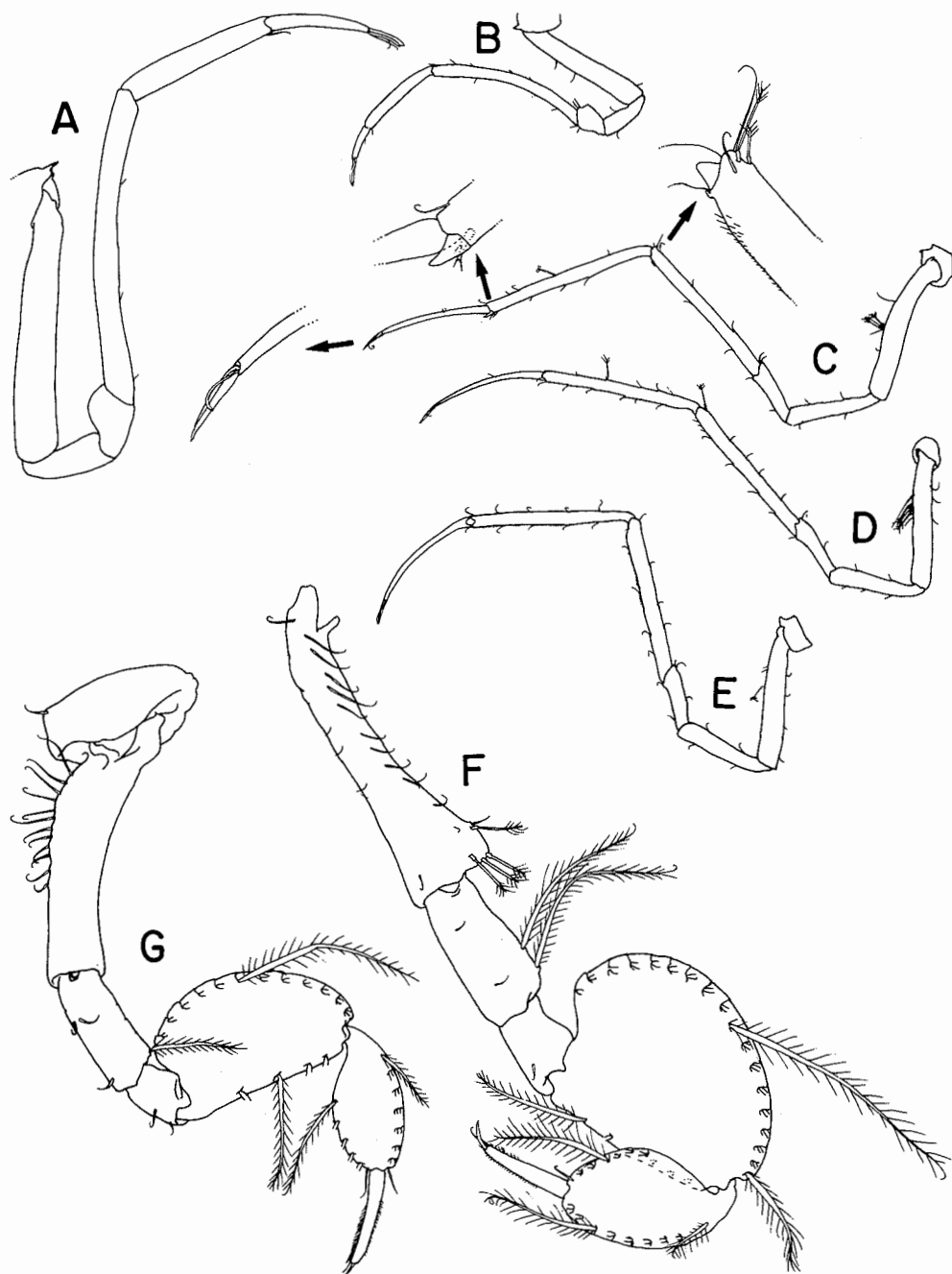


Figure 21. *Lipomera (Paralipomera) knorrae* n. subgen., n. sp. A, right pereopod I, male holotype, bl 1.2 mm. B-G, left pereopods I-VI, paratype male, bl 1.5 mm, pereopod II with enlargements of 2 joints and distal tip. B-E at half scale of A and G-F.

Male Pleopod I (Fig. 22A-B). Fused pleopod pair widest at insertion, tapering to distal tip. Length 2.7 width; width at dorsal orifice 0.43 total width. Dorsal orifice 0.24 total length from distal tip. Distal tips flattened in lateral view, tapering and bluntly pointed in ventral view, without distinct outer lobes. Setae only on distal tips: each with distodorsal groups of setae and setal row adjacent to midline.

Male Pleopod II (Fig. 22A,C-D): Protopod widest at insertion, tapering posteriorly to curved post-exopodal projection; length 2.8 width. Distal tip of protopod with medial groove enclosing exopod; groove lined with dense group of long, fine setae. Distal tip of protopod with lateral row of thick-bodied plumose setae. Stylet length 0.68 protopod length; sperm duct opening at midpoint of stylet; stylet inserting 0.39 length of protopod from distal tip. Exopod small, covered by ventral surface of protopod, with tuft of fine setae.

Female Pleopod II (Fig. 22H-J): Operculum triangular in ventral view, with tapering distal tip. Length 1.58 width; depth 0.39 length. Dorsal surface with few scattered fine setae; distal tip with approximately 10 plumose setae. Keel thick, deep, apex below posterior insertion; pleopod keel distinct from thick lateral fields.

Pleopod III (Fig. 22E): Exopod broad, width two thirds that of endopod; distal tip nearly extending as far as endopod; tip with with 2 long plumose setae, and 1 simple seta. Endopod with 3 long plumose setae.

Uropod (Fig. 22K): Protopod broad, rounded, and flattened, with dorsal fold having two plumose setae medially. Protopod dorsal length 1.49 width; medial length 0.12 body length. Distal margin of protopod with small group of simple setae and broom setae.

Remarks. *Lipomera (Paralipomera) knorrae* can be distinguished from 3 other undescribed species in this subgenus by the presence of spines on the anterior margins of the cephalon and pereonites, by the shape of the pleotelson, and its relative paucity of fine setae on the dorsal surface. This Northwestern Atlantic species is the deepest occurring member of the genus *Lipomera*. Undescribed species of *L. Paralipomera* are found at slope depths off Africa, Brazil, and the southern United States (in the Gulf of Mexico).

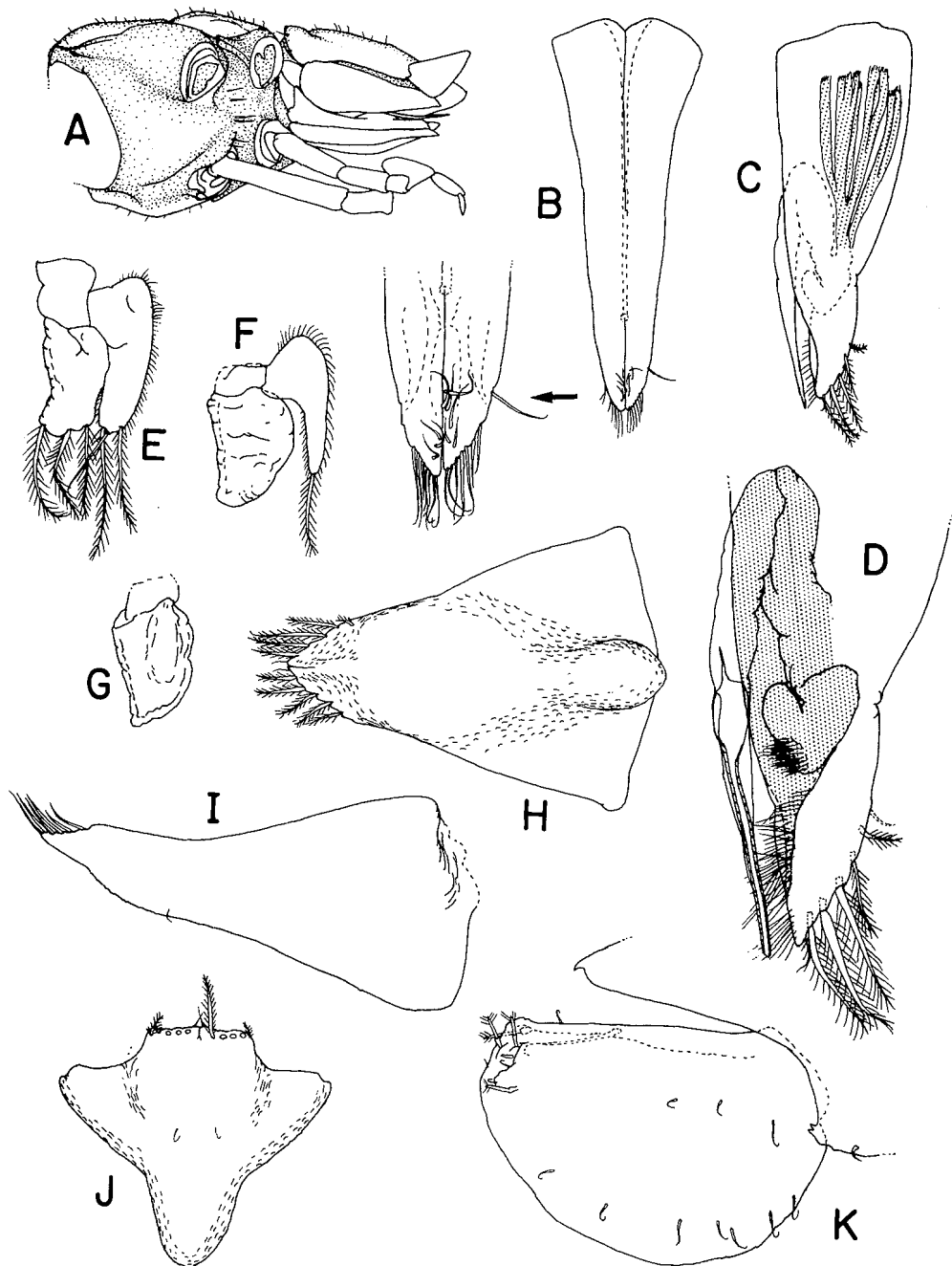


Figure 22. *Lipomera (Paralipomera) knorrae* n. subgen., n. sp. A-G, K, paratype male, bl 1.5 mm. A, ventral oblique view of natasome, showing form of ventral surface. B, pleopod I with enlargement of distal tip. C-D, left pleopod II, whole limb and enlargement of distal portion, showing endopod and exopod through ventral cuticle. E-G, left pleopods III-V. H-J, pleopods II, paratype female, bl 1.4 mm: ventral, lateral, and posterior views, respectively. K, right uropod, lateral view.

TETRACOPE New Subgenus
(Figures 23-27)

Diagnosis. Dorsal surface of body with thin, smooth cuticle; anterior margins without denticles. Cephalon not indurate. Pereonite V shorter pereonite VI. Mandible not heavily sclerotized and strengthened. Hindgut anterior to pleotelson coiled, or with exaggerated bend (Fig. 24). Pereopod VI approximately same length as pereopod V. Pereopod VII present but rudimentary (Fig. 24A). Uropod narrow, pointed, not extending beyond distal tip of pleotelson, with 2 segments in some species.

Composition. *Lipomera (Tetracope) intestinata* n. sp. Monotypic, but with at least 3 undescribed species.

Derivation of Name. *Tetracope* (Greek, feminine), which translates as "four oars," refers to the two pairs of similar natapods on pereonites 5 and 6.

Remarks. An undescribed species of the subgenus *Tetracope* demonstrates that the broad uropods of all members of the genus *Lipomera* are made up of the fused protopod and endopod. The setal homologies are distinctive (see Figs. 27M, O, and 22K). Both *L. (T.) curvintestinata* n. sp. and *L. (T.)* sp. have a long thin dorsal seta, a distal group of broom setae, and a pair of small curled setae on the lateral proximal margin. In *L. (T.)* sp., however, the uropod is clearly divided into two sections. Because the exopod is small or lost in most munnopsids, the large distal section is the uropodal endopod. Also the exopod never has broom setae on the distal tip, and the endopod does. The setal homologies may be extended to the other members of *Lipomera*, *L. (Paralipomera) knorrae*, for example. In this latter species the uropod is a single segment and leaflike. The distal tip has the same group of broom setae seen in species of the subgenus *Tetracope*, as well as the large thin seta on the dorsal margin of the uropod. In *L. (T.)* sp., the large seta is on the distal edge of the protopod and the broom setae are on the tip of the endopod. Therefore, the thin uropod *L. (T.) curvintestinata* and the broad uropod of *L. (P.) knorrae* must consist of the fused segments of the protopod and the endopod.

Lipomera (Tetracope) curvintestinata new species
(Figures 23-27)

Holotype. Copulatory male, bl 0.74 mm, only a few limbs broken off, USNM 227059.

Paratypes. Preparatory female, bl 0.87 mm, USNM 227060. Male, brooding female, BMNH 1985:419. Male, brooding female, MNHN Is.1816. Male, preparatory female, ZMUC. 44 specimens, some dissected for description, SIO.

Type-Locality. WHOI 209, 39.6-46.0', 70°49.9-49.5'W, 1501-1693 m, collected on the Gay Head-Bermuda Transect during R/V *Chain* cruise no. 88, 22 February 1969.

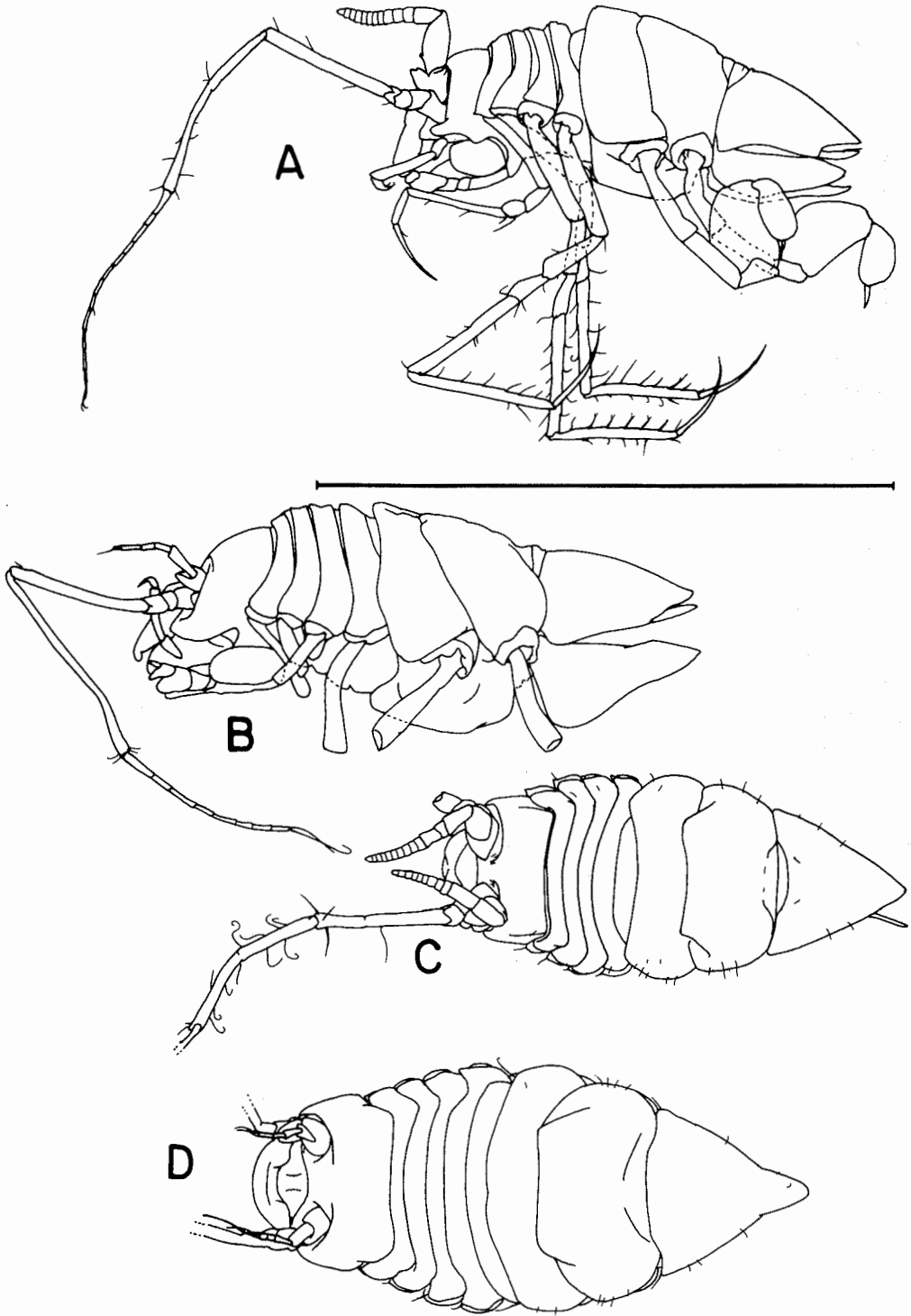


Figure 23. *Lipomera (Tetracope) curvintestina* n. subgen., n. sp. A, C, holotype male, lateral and dorsal views. B, D, paratype preparatory female, lateral and dorsal views. Scale bar 1.0 mm.

Other Material. WHOI 73, 4 brooding females. WHOI 210, 2 brooding females, 1 male. BAT M1-13-1-7, juvenile female. BAT S1-3-1-3, female. BAT S2-3-2-(1-9), juvenile male.

General Distribution. Slope depths off east coast of the United States, 1500-2064 m.

Derivation of Name. *Curvintestinata* means "provided with curved intestine," referring to the coiled gut of this species.

Diagnosis. Cephalon medial length approximately one half cephalon width; cephalon narrower than pereonite 1; frons rounded in dorsal view. Body dorsal surfaces with few fine setae and no pigmentation. Pleotelson length subequal to or shorter than combined length of pereonites 5-6. Hindgut anterior to pleotelson with 1 complete coil. Female antennular article 3 length approximately 2 times length of article 4. Adult male antennula with 14-15 articles. Pleotelson sides almost straight, terminating with rounded point in dorsal view; dorsal surface of pleotelson only weakly curving in lateral view. Male pleopod I tip narrow, rounded. Keel of female pleopod II flattened anteriorly, appearing as straight line in lateral view, with angular transition at anteroventral apex. Uropodal protopod and distal ramus fused, with no apparent suture (compare Fig. 27 M and O).

Description. Body Characters (Fig. 23A-D): Adult body length 0.74 mm (2 inds) in males, 0.89-0.90 mm (3 inds) in females; length 1.9-2.1 (4 inds) width, anterior segments subject to compression. Body form not sexually dimorphic, except females often widest at pereonite 4.

Cephalon (Fig. 25A-D): Dorsal length 0.38 width, length 0.54 height. Ventral margin at posterior articulation of mandible with deep fold projecting laterally.

Antennula (Fig. 26A-C): Strongly sexually dimorphic, being much more robust, longer, and with more articles and aesthetascs in male than in female; both sexes with geniculation between articles 2 and 3. In males length 0.43-0.45 (2 inds) body length; in females, 0.20-0.22 (3 inds). Male antennula with 14-15 articles and approximately 10 aesthetascs distally; female antennula with 6 (3 inds) articles and 1 aesthetasc distally. Article 1 medial and lateral lobes pointed distally, with broom setae only; medial length 0.84 width in male, 0.97 in female; medial lobe of both sexes with 2 broom setae. Articles 2 and 4 with broom setae. Article 2 length 3.6 article 1 medial lobe length in females, length 5.8 medial-lobe length in males. Article 3 length 0.58 article 2 length in female, 0.59 in male.

Mandible (Fig. 25E-N): Not greatly modified: some reduction in molar process setation and denticles, condyle large, but not heavily calcified. Both mandibles with 3 distinct cusps on incisor processes. Lacinia mobilis normal size, extending to tip of incisor process, width approximately three-quarters width of incisor process, with 3 large cusps and 3 small cusps dorsally. Left spine row with 4 members, right spine row with 5. Molar process posterodistal edge with

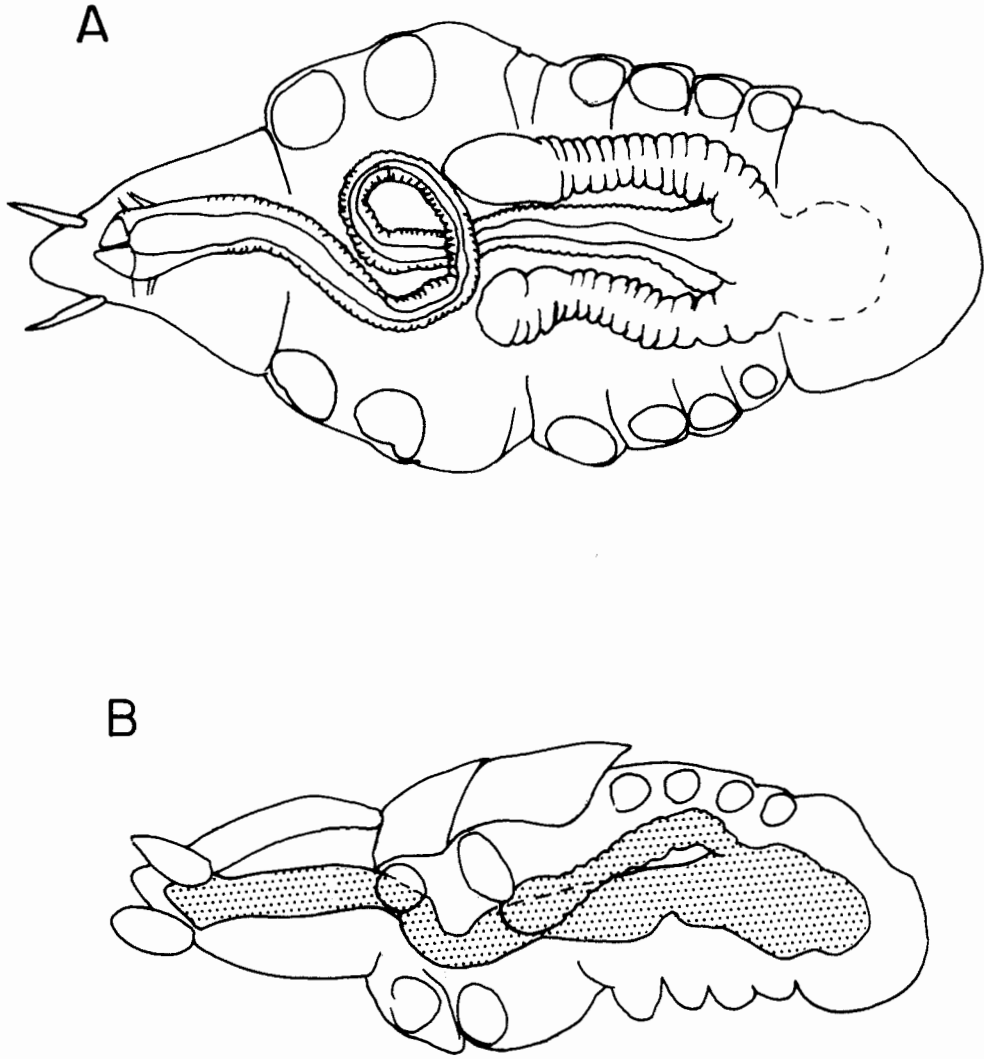


Figure 24. Hindgut form in two species of *Lipomera*. **A**, *Lipomera (Tetracope) curvintestinata* n. subgen., n. sp., paratype brooding female, bl 0.9 mm, view of alimentary canal and digestive caecae through ventral body surface. **B**, *Lipomera (Lipomera)* sp., male, bl 0.8 mm, WHOI 180, oblique view through ventral cuticle showing alimentary canal and digestive caeca.

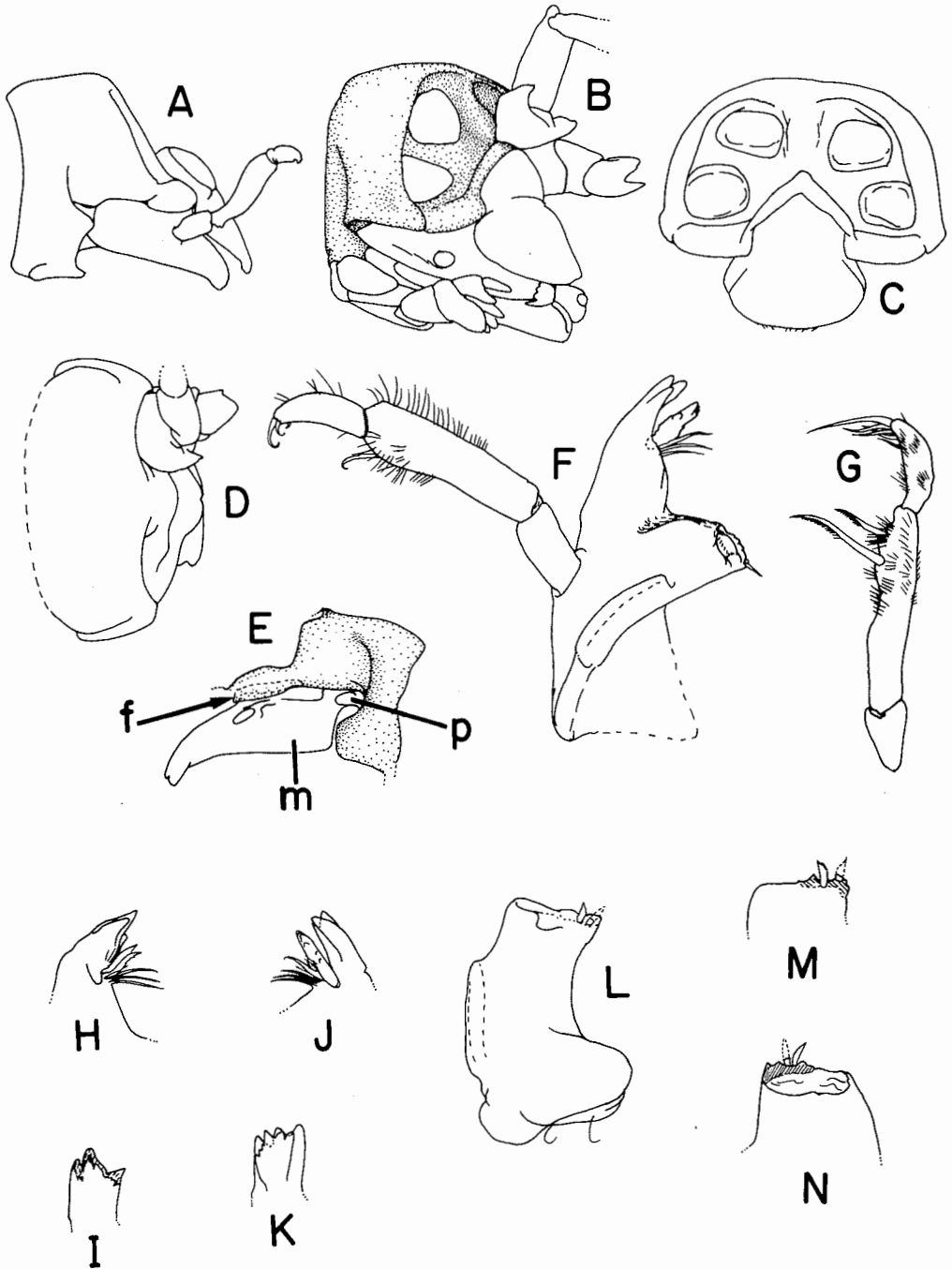


Figure 25. *Lipomera (Tetracope) curvintestina* n. subgen., n. sp., paratype male, bl 0.74 mm. A-D, cephalon, antennula and antenna removed to show frons: lateral, frontal oblique, anterior, dorsal views. E, ventral oblique view of cephalon and mandible, showing articulation; f = mandibular condyle articulating with cephalic fossa, m = left mandible without palp, p = posterior articulation between cephalon and mandible. F-G, J-N, left mandible. F, dorsal view. G, palp, lateral view. H-I, incisor process, right mandible, ventral and plan views. J-K, incisor process, lacinia mobilis, and spine row, ventral and plan views. L, molar process and condyle, posteromedial view. M-N, molar process, posterior and anterior views.

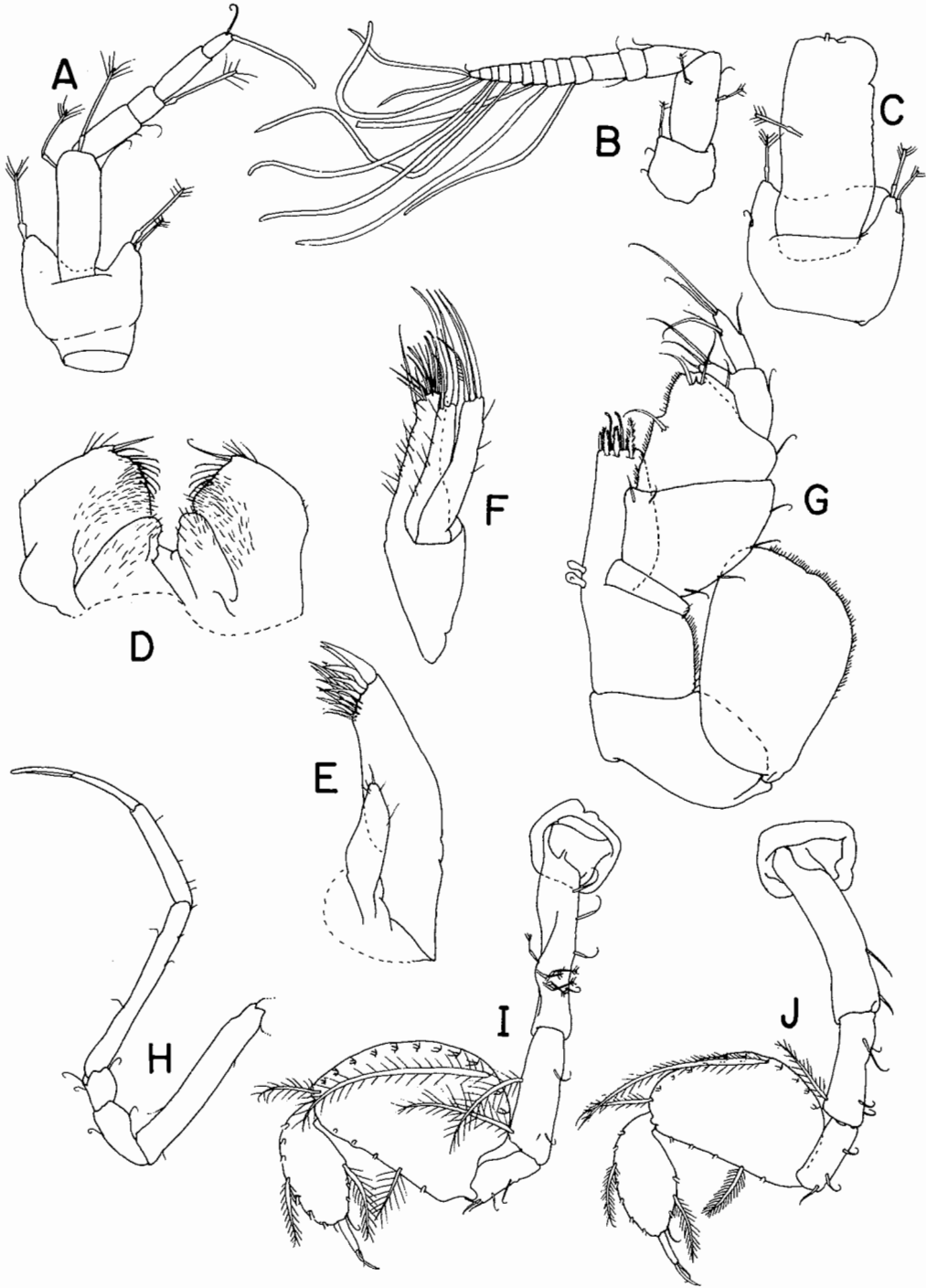


Figure 26. *Lipomera (Tetracope) curvintestina* n. subgen., n. sp. A, left antennula, paratype preparatory female, bl 0.84. B-J, paratype male, bl 0.74 mm. B-C, left antennula, lateral view of whole limb and dorsal view of proximal articles. D, paragnaths. E, left maxillula. F, left maxilla. G, left maxilliped. H, left pereopod I. I-J, right pereopods V-VI.

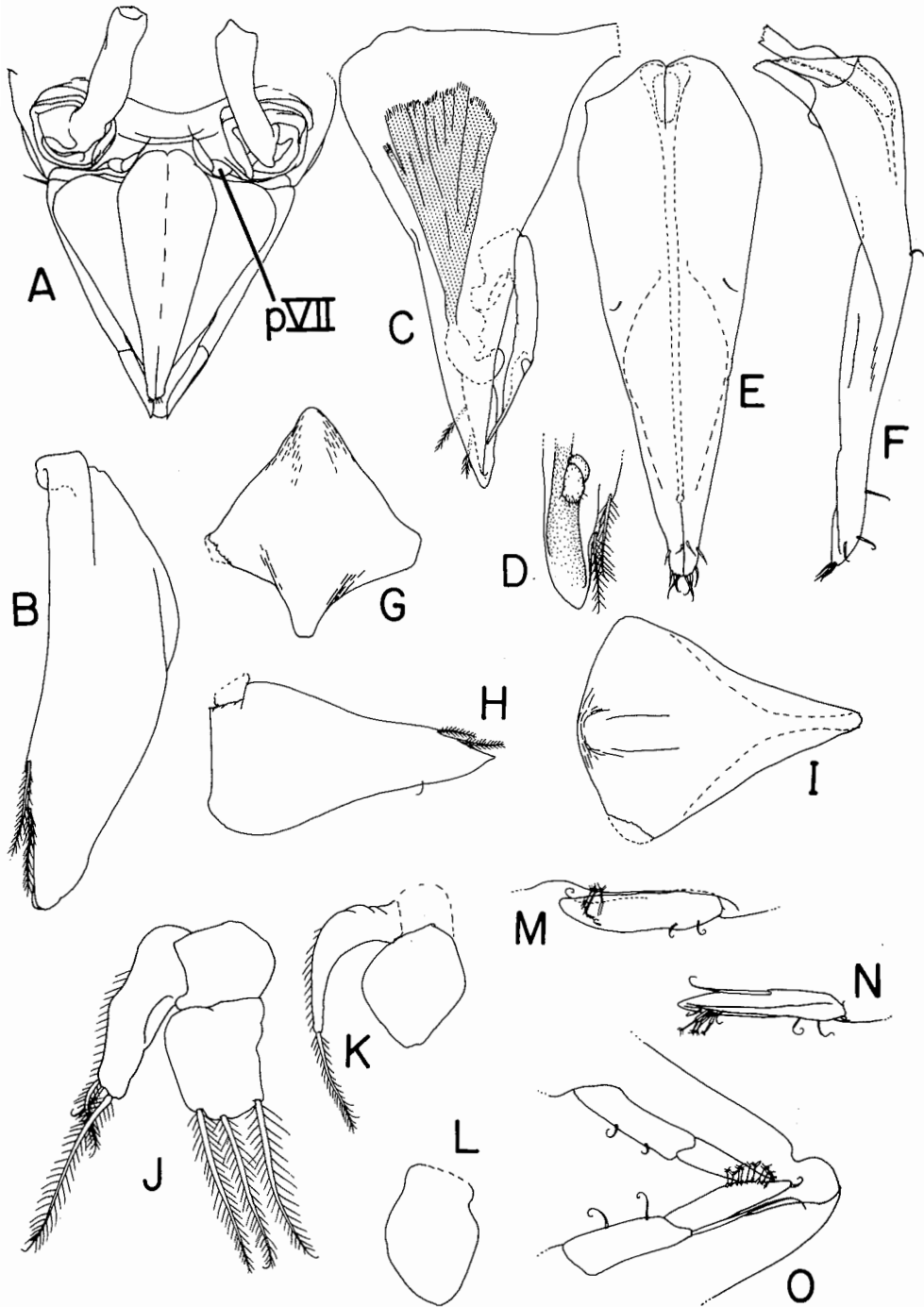


Figure 27. *Lipomera (Tetracope) curvintestina* n. subgen., n. sp. **A-F, J-N**, paratype male, bl 0.74 mm. **G-I**, paratype preparatory female, bl 0.84 mm. **A**, pleotelson and pereonites 6-7, ventral view, rudimentary pereopod VII indicated (pVII). **C**, pleopod II. **D**, pleopod II distal tip, medial view. **E-F**, pleopod I, ventral and lateral views. **G-I**, female pleopod II, posterior, lateral, and ventral views. **J-L**, right pleopods III-V. **M**, right uropod, lateral view. **N**, left uropod, ventral view. **O**, uropods, *Lipomera (Tetracope)* sp., brooding female, bl 1.1 mm, WHOI 119.

gnathal plate having 3 sharp denticles and 2 flattened setulate setae; triturating surface with no visible sensory pores. Condyle longer than molar process, distinct from posterior support ridge; length 0.31 mandibular body length. Palp second article length 0.51 mandibular body length. Distal article not strongly curved.

Maxillula (Fig. 26E): Normally developed. Inner endite width 0.45 outer endite width.

Maxilla (Fig. 26F): Normally developed. Outer lobes approximately same length as inner lobe.

Maxilliped (Fig. 26G): Basis with 2 receptaculi and 3 fan setae distally; proximal part of basis not expanded, lateral edge broadly rounded, almost straight. Endite length 0.57 total basis length. Palp article 2 width 0.5 endite width, lateral length 2.0 medial length. Palp article 3 lateral length 0.31 medial length. Epipod broadly curved on medial margin, strongly curved laterally, with fringe of fine setae distolaterally; length 0.84 basis length; length 1.4 width.

Ambulatory Pereopods (Fig. 23A, 26H): Pereopods II-IV with sparse row of thin setae on dorsal and ventral margins of carpus and propodus, pereopod I with few setae; length-body length pereopods I-IV ratios 0.90, 1.18, 1.23, 1.32. Pereopod I not sexually dimorphic. Bases I-IV length-body length ratios 0.25, 0.26, 0.28, 0.28. Bases II-IV with few setae.

Natatory Pereopods (Fig. 26I-J, 27A): Natapods V-VI similar in form, with broad carpi and propodi; pereopod VII present only as tiny, rudimentary 2- or 3-segmented appendage inserting medial to posterior edge of coxa VI. Pereopod V-VI length-body length ratios 0.93, 0.89. Bases V-VI length-body length ratios 0.26, 0.24; basis V with distal broadened area having group of broom setae. Carpi V-VI length-width ratios 1.3, 1.5. Propodi V-VI length 1.9 width. Dactyli V-VI short, but not rudimentary; length of both dactyli 0.29 propodi. Unguis shaped like seta, with accessory seta.

Male Pleopod I (Fig. 27A,E-F). Fused pleopod pair widest just distal to rounded proximal margin, afterwards triangular, with almost linear lateral margins and narrow distal tip. Proximal funnel with dorsal bend, enclosing elongate penes. Length 2.9 width; width at dorsal orifice 0.32 pleopod width. Dorsal orifice 0.14 total length from distal tip. Distal tips collectively semicircular in ventral view; outer lobes not expressed. Pleopod with few setae, each distal tip with 3 simple setae in adult male, 2 in juvenile male.

Male Pleopod II (Fig. 27A-D): Protopod triangular in ventral view, deep and rounded in lateral view; dorsolateral margin curled medially; distal tip pointed; length 1.8 width; 2 plumose setae on distolateral margin. Stylet thin, length 0.43 protopod length; sperm duct opening 0.42 total stylet length from distal tip; stylet inserting 0.43 length of protopod from distal tip. Exopod small, rounded, with few fine setae.

Female Pleopod II (Fig. 27G-I): Keel deep, acute in posterior view, apex near anterior margin, sloping posteriorly and laterally to dorsally recurved lateral fields. Dorsal surface with few fine setae; distolateral margins with 2 plumose setae on distolateral margin. Length 1.3 width; depth 0.48 length.

Pleopod III (Fig. 27J): Exopod distally rounded, longer and narrower than endopod, with 2 long plumose setae, and 1 simple seta on distal tip. Endopod quadrate, with 3 distal plumose setae.

Uropod (Fig. 27M-N): Protopod and endopod completely fused; exopod absent. Uropodal length 4.3 width; length 0.11 body length. Dorsomedial margin with 1 long seta; row of broom setae on distolateral surface.

Remarks. *Lipomera (Tetracope) curvintestinata* was the first isopod species I found with a complete coil in the hindgut. A survey of all the ilyarachnid-like eurycopids revealed that this condition was confined to the genus *Lipomera*, and reached the most complex development in this species and another undescribed species from Norway. Other species of *Lipomera* generally have distinct convolutions in their uncoiled guts (see Fig. 23B).

L. (T.) curvintestinata may be identified by a lack of pigment on the dorsal surfaces (which the species from Norway has), by a cephalon narrower than the first pereonite, and by a nonsegmented uropod. The form of the body segments and the antennulae may be useful indicators of species differences as well.

MIMOCOPELATES New Genus (Figures 28-35)

Type-Species. *Mimocopelates longipes* new species.

Generic Diagnosis. Dorsal surface smooth, without spines. Rostrum absent. Frons with triangular, flattened frontal arch adjacent to clypeal attachment; frontal arch angular in frontal view. Clypeus medial section rounded in frontal view; dorsal apex higher than articulation with frons, lower than apex of frontal arch. Labrum anteriorly rounded. Pereonites 5-7 fused ventrally but with distinct sutures dorsally; pereonite 5 largest; pereonite 7 dorsally reduced to thin strip. Ventral surface of natasome enlarged at pereonite 5, compressed posteriorly at pereonite 6; pereonite 7 absent ventrally; natasome deepest at large ventromedial hump between insertions of pereopods V. Antennular article 1 with short or undeveloped medial lobes, lateral lobes dorsoventrally flattened, shorter than article 2. Antennal scale absent. Mandible modified: molar process distally convex and heavily sclerotized, with reduced or absent circumgnathal armature; support ridge extending from posterior edge of condyle to posterolateral corner of mandibular body, appearing as separate articular process from body of mandible; palp slender, shorter than mandibular body. Pereopod VII absent in adults. Merus of natatory pereopod V greatly elongated, much longer than basis. Dactylus of pereopod V tiny, dactylus of pereopod VI long and

thin. Pereopodal bases I-IV subequal, all longer than natapodal bases V-VI; basis V shortest and stoutest, basis VI longer and less stout. Uropod short and somewhat flattened, recessed into posteroventral margin of pleotelson; exopod tiny, reduced to small button, or completely absent; endopod longer than protopod.

Derivation of Name. *Mimocopelates* (Greek, masculine) means an "imitator of a rower."

Composition. *Mimocopelates longipes* n. sp., *M. anchibraziliensis* n. sp.; at least 3 undescribed species.

Generic Remarks. *Mimocopelates* is remarkable because pereopod VII is completely absent, and pereopod VI is considerably reduced compared to pereopod V. If this trend were extrapolated, one could predict that somewhere in the deep sea a munnopsid exists or will exist (via continued evolution) that lacks both pereopods VI and VII. Increased reliance on pereopod V for swimming is indicated by the enlarged musculature in pereopod V, a more robust coxa and basis than is seen in most munnopsids, and increase in the length of the limb segments, ischium and merus, which extend the carpal and propodal paddles from the body. The elongation of the merus of pereopod V is unknown in any other munnopsid and is therefore a useful autapomorphy.

In addition to the form of the natatory pereopods and pereonites, the reduced uropods with tiny or absent exopods uniquely define this genus. *Mimocopelates* contains two distinctive groups: one represented by *M. longipes* n. sp., and the other by *M. anchibraziliensis* n. sp. Because these two species are so dissimilar in cephalic size and many other characters, I once believed they should be separate genera. The characters mentioned above, however, outweigh these considerations, and some of the specialized features that distinguish the two species, such as the size of the head, are known to vary within munnopsid genera. For example, compare the cephalic and mandibular development of *Eurycope iphthima* Wilson, 1981 and *E. juvenalis* Wilson, 1982b.

Species of the *Mimocopelates longipes* group are all similar, although several characters may be useful for distinguishing them. These are the shape of the vertex and the interantennular distance, the length of the endopod compared to the width of the protopod, and the shape of the male pleopod I tip and the number of setae on it.

Mimocopelates, like most deep-sea asellote genera, may be cosmopolitan: it has been found in the North, Equatorial, and South Atlantic. In addition, D.E. Hurley, New Zealand Oceanographic Institute, and R. Lincoln, British Museum (Natural History), have collected specimens of this genus from bathyal depths off New Zealand. The latter specimens represent an undescribed species.

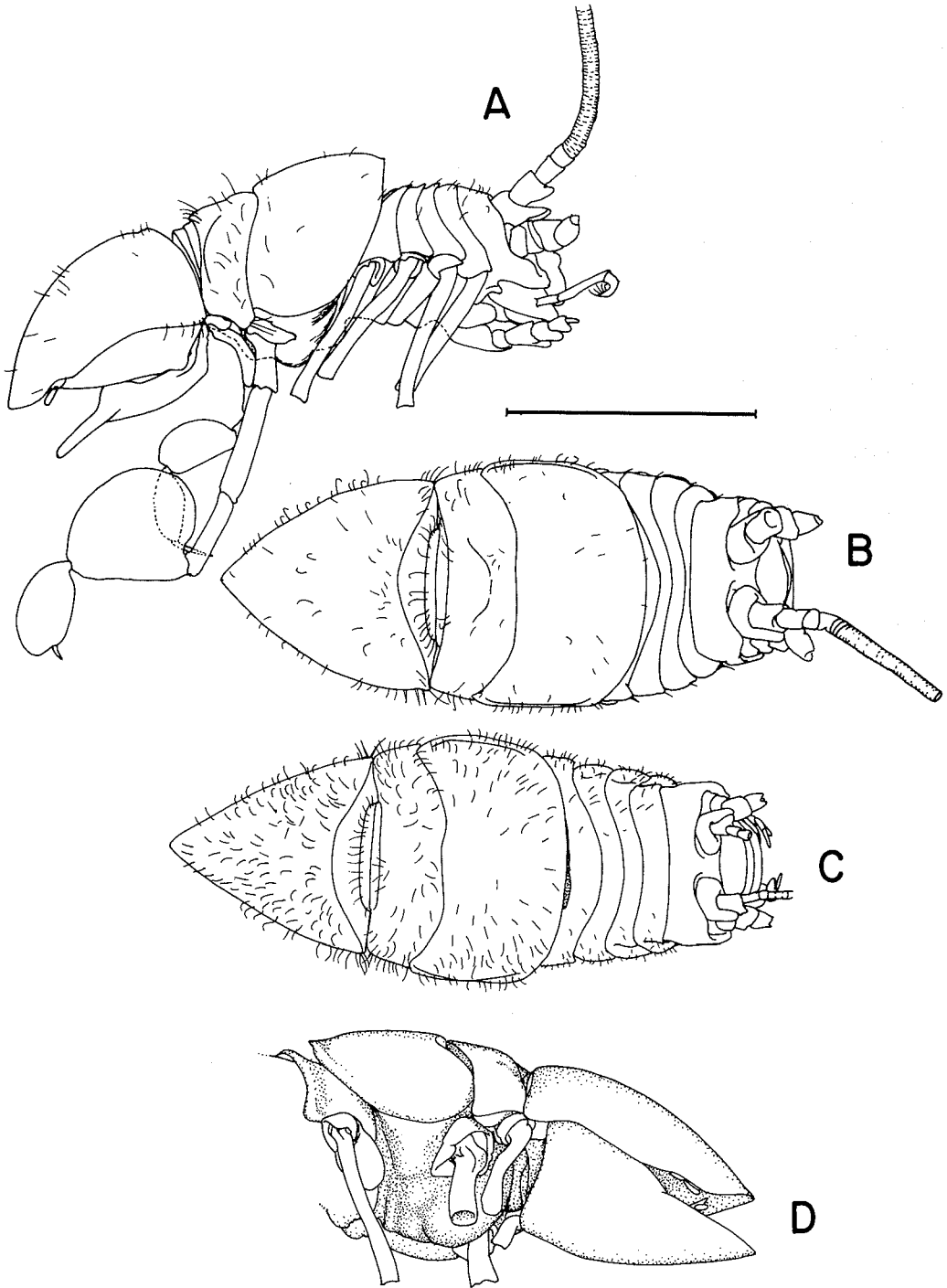


Figure 28. *Mimocopelates longipes* n. gen., n. sp. A-B, holotype male, lateral and dorsal views, scale bar 1.0 mm. C-D, paratype preparatory female, bl 1.9 mm. C, dorsal view. D, ventral oblique view of natasome, showing form of ventral surface and comparative sizes of pereopodal bases.

Mimocopelates longipes new species
(Figures 28-32)

Holotype. Copulatory male, bl 2.1 mm, distal parts of antennulae, antennae, and pereopods I-IV broken off, USNM 227061.

Paratypes. Preparatory female, bl 2.2 mm, USNM 227062. Brooding female and copulatory male, bl 2.2., 1.9 respectively, ZMUC. Brooding female, bl 2.2 mm, MNHN Is.1817. Preparatory female, BMNH 1985:420. 18 individuals, some fragmentary or dissected for description, SIO.

Type-Locality. WHOI 321, 50°12.3'N, 13°35.8'W, 2868-2890 m, collected on 20 August 1972 during R/V *Chain* cruise no. 106.

Other Material. All specimens at SIO: WHOI F1, 1 ind.; WHOI 64, 1 ind.; WHOI 66, 1 ind.; WHOI 73, 12 ind.; WHOI 85, 1 ind.; WHOI 103, 1 ind.; WHOI 128, 3 ind.; WHOI 131, 8 ind.; WHOI 156, 2 ind.; WHOI 209, 6 ind.; WHOI 210, 2 ind.; WHOI 326, 2 ind.; WHOI 328, 6 ind.; WHOI 330, 1 ind.; INCAL DS13, 1 ind.; INCAL OS04, 1 ind.

General Distribution. Eastern and western North Atlantic from 50° to equator, 1254-4822 m.

Derivation of Name. *Longipes* (Latin) means "long-footed," referring to the elongate natatory fifth pereopods.

Diagnosis. Cephalon not enlarged, narrower than pereonite 1, anteriorly sloping. Cephalic vertex without distinct line separating frons from cephalic dorsal surface. Cephalic frontal arch sloping in lateral view; distinctly anterior to vertex in dorsal view. Ventral margin of cephalon at posterolateral articulation of mandible with deep, heavily sclerotized indentation or notch. Interantennular distance broad: distance between medial corners of antennular insertions 0.17-0.20 (2 inds) cephalon width, not sexually dimorphic. Maxillipedal epipod distal tip rounded. Male pleopod I distal tip with 3 large and 1 small fat-based setae ventrally, 4 setae at distoventral midline, and 4 setae in dorsolateral group. Uropodal endopod length 2.8-3.0 width, length as long as or slightly shorter than protopod width; protopod distomedial corner projecting acutely; exopod present as tiny button.

Description. Body Characters (Fig. 28A-C): Adult body length 1.9-2.2 mm (6 inds), females as large as or larger than males; body length 2.1-2.3 width (6 inds). Pleotelson sexually dimorphic: in male, longer and more inflated compared to female; male pleotelson length 0.38 body length, in female, 0.34.

Body setation (Fig. 28A-C): Natasome with many fine setae on dorsal surfaces; ambulosome and cephalon with scattered fine setae.

Cephalon (Fig. 29A-C): Dorsal length 0.43 width, height 1.3 width.

Antennula (Fig. 30E-F): Flagellum and more proximal segments broken in all specimens examined. Male antennula more robust and possibly longer than

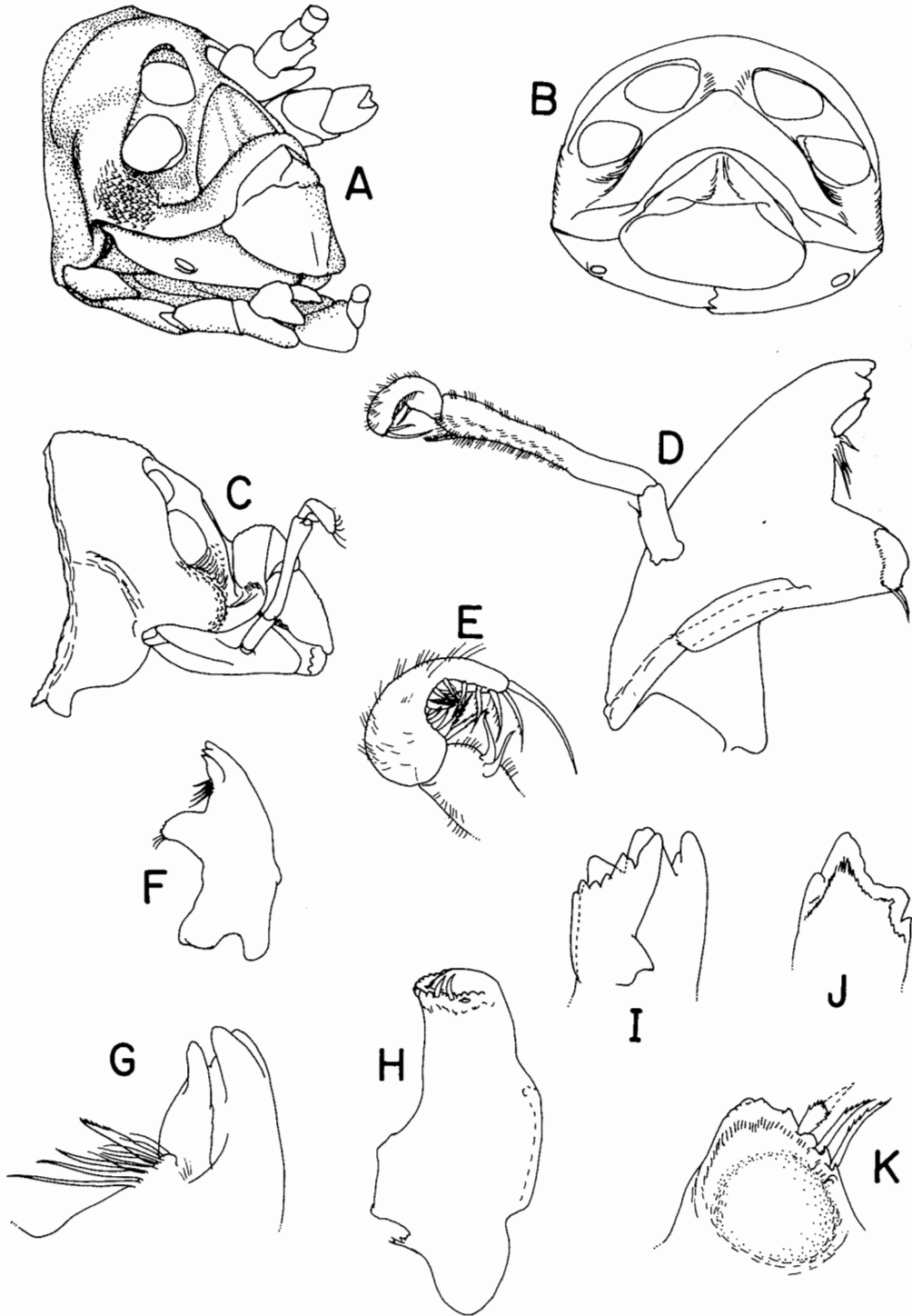


Figure 29. *Mimocapelates longipes* n. gen., n. sp., paratype female, bl 1.9 mm. A-C, cephalon, frontal oblique, anterior, and lateral views, antennula and antenna removed to show frons. D-I, K, left mandible. D, dorsal view. E, palp, distal segment. F-G, mandibular body and distal tip, ventral view. H, molar process and condyle, posterior view. I, incisor process and lacinia mobilis, plan view. J, incisor process, right mandible, plan view. K, molar process, anterior view.

female antennula; male flagellum with many thick and short articles. Aesthetascs unknown. Article 1 medial length 0.49 width in male, 0.51 in female; width 0.35-0.38 cephalon width in males (2 inds); 0.26-0.28 in females (3 inds); medial edge of both sexes with 2-3 broom setae. Articles 2 and 4 with broom setae. Articles 2 and 3 sexually dimorphic, being broader and more robust in males than in females. Article 2 with distolateral projection having broom setae on 2 points; article 2 length subequal to article 1 medial length in female, length 0.92 medial length in male; distal width 0.88 length in female, 1.14 in male. Article 3 length 0.75 article 2 length in male, 0.73 in female.

Mandible (Fig. 29D-K): Both mandibles with 1 small dorsal and 3 large teeth on incisor processes. Lacinia mobilis large, extending to tip incisor process, with 6 teeth, ventral tooth largest. Both spine rows with 5 members each. Molar process distal end with 5-6 low denticles on posterior margin, and low broad cusp on ventral margin; posterior margin with 3 flattened setulate setae; smooth, convexly rounded triturating surface projecting beyond level of circumgnathal armature; sensory pores not observed on triturating surface. Condyle roughly same length as molar process, thickened, heavily sclerotized; length 0.29 mandibular body length. Palp second article length 0.52 mandibular body length; distal article strongly curved, inner part of curve well armed with pointed setulate setae.

Maxillula (Fig. 30B): Normally developed. Inner endite width 0.64 outer endite width. Distal tip of inner lobe with several very fine, equally bifid setae.

Maxilla (Fig. 30C): Normally developed. Outer lobe length subequal to inner lobe. Central lobe shorter than inner lobe.

Maxilliped (Fig. 30D): Basis with 3 receptaculi medially and 6 fan setae distally; medial fan seta more robust, with fewer and broader branches than 5 lateral fan setae; lateral fan setae bifid, with deep separation between sides. Endite length 0.56 total basis length. Palp article 2 width 1.5 endite width, lateral length 1.5 medial length. Palp article 3 lateral length 0.27 medial length. Epipod short, oval, with fine cuticular combs around edge of ventral surface; length 0.62 basis length; length 1.5 width.

Ambulatory Pereopods (Fig. 31A-B): Bases I-IV subequal, lengths 0.31 body length. In male, pereopod I length 1.2 body length; ischium length 0.63 basis length.

Natatory Pereopods (Fig. 31C-E): Pereopod VII absent in adults. Natapods heterogeneous in form: pereopod V large, with elongate ischium and merus, broad carpus and propodus and tiny dactylus; pereopod VI much smaller, with narrowed carpus and propodus and long thin dactylus. Pereopods V-VI length-body length ratios 0.86 and 0.69. Coxa V large, robust, broader than length of basis; coxa VI small, much narrower than length of basis. Bases V-VI shorter than bases I-IV; length-body length ratios 0.11 and 0.17. Pereopod V merus length 0.73 ischium length. Carpi V-VI length-width ratios 1.1 and 1.7.

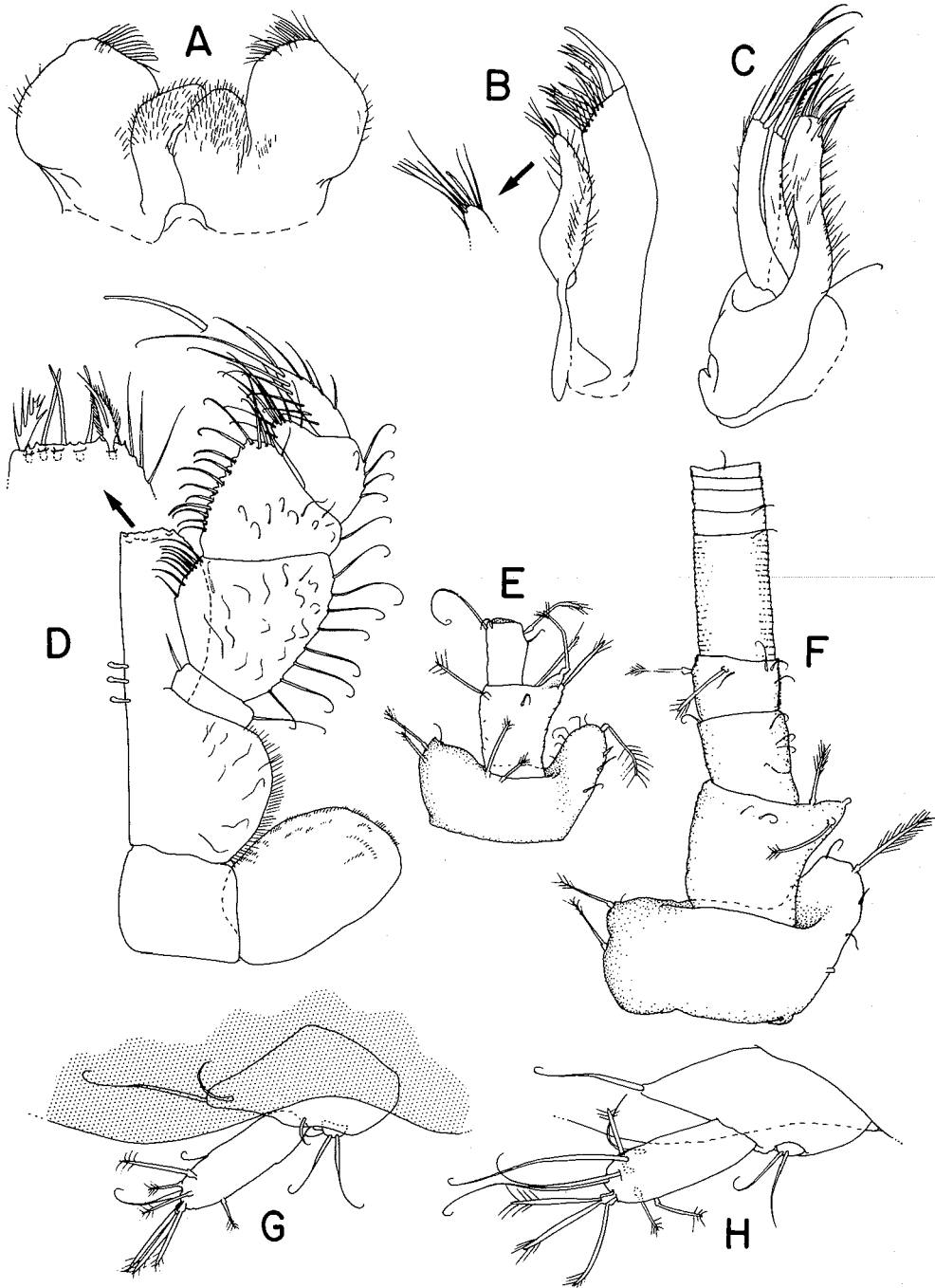


Figure 30. *Mimocopelates longipes* n. gen., n. sp. A-E, H, paratype preparatory female, bl 1.9 mm. A, paragnaths. B, left maxillula, with enlargement of distal tip of inner endite. C, right maxilla. D, left maxilliped with enlargement of endite distal tip. E, proximal articles of right antennula. F, proximal articles of right antennula, paratype male, bl 2.1 mm. G, right uropod, proximal parts seen through cuticle, holotype male, bl 2.1 mm. H, left uropod, medial view.

Propodi V-VI length-width ratios 1.9 and 2.9. Dactyli V-VI length-propodus length ratios 0.14 and 0.63.

Male Pleopod I (Fig. 32A-C). Fused pleopod pair highly convoluted: widest at rounded enlarged portion just distal to insertion, narrow waist at midlength in ventral view, dorsal locking folds enlarged, extending dorsally more than half depth of fused pleopod pair, dorsal stylet guides with dorsal edges extending medially and almost forming tubes, proximal funnel for elongate curved penes opening 0.22 length of fused pleopod pair. Length 3.1 width; width at dorsal orifice 0.56 pleopod width. Dorsal orifice 0.25 total length from distal tip. Distal tip flattened, distally rounded in lateral view, curved in ventral view; outer lobes appearing as small lateral corners. Each side of distal tip with 4 distinct groups of setae: 3 simple setae on lateral margins; 4 setae just medial and dorsal to outer tips; 4 setae on ventral side of distomedial margin; 4 unusual fat-based setae on ventral surface, inner seta distinctly smaller than others. Fused pleopod pair of juvenile male ventrally flattened, not convoluted, lacking distal setae.

Male Pleopod II (Fig. 32D-E): Protopod robust, muscular, laterally rounded, lacking lateral fields; length 1.8 width; approximately 9 plumose setae projecting dorsally on distolateral margin. Stylet short, distal tip not extending beyond protopod, length 0.47 protopod length; proximal sperm duct opening 0.34 stylet length from distal tip; stylet inserting 0.33 protopod length from distal tip. Exopod short, not extending medially beyond inner margin of protopod, with tuft of fine setae on dorsal side.

Female Pleopod II (Fig. 32I-L): Opercular pleopod pair triangular in ventral view, with tiny fused groove in distal tip. Keel broad, rounded, lateral fields not distinct from sides of keel; row of fine setae along keel. Lateral margins curling dorsally, distal part with simple setae grading into plumose setae. Length 1.3 width; depth 0.37 length. Apex ventral to insertion, but not extending anteriorly; apex lacking large seta.

Pleopod III (Fig. 32F): Exopod narrow distally, extending to tip of endopod, with 2 long plumose setae, and 1 simple seta on distal tip. Endopod with 3 distal plumose setae.

Uropod (Fig. 30G-H): Protopod broader than long, medial length 0.74 distal width; medial length 0.03 body length. Exopod tiny, with 2 simple setae. Endopod 1.3 medial length of protopod. Distal margin of protopod with 2 simple setae on posteromedial corner.

Remarks. *Mimocopelates longipes* may be distinguished from 3 other undescribed species of this genus by the following characters. The cephalic vertex is unmarked by a cuticular line, and the cephalic dorsal surface curves directly into the frons. The antennulae are set fairly far apart compared to one species where the interantennular distance is small. The uropodal endopods are longer and narrower than those seen in other similar species. Many characters distinguish *M. longipes* from the much larger *M. anchibraziliensis*. A less

massive head that is recessed into the first pereonite, and a large biramous uropod are probably the easiest characters by which to identify *M. longipes*.

The setal groups on the tip of male pleopod I (Fig. 32A) are unique, and are exactly the same for all males of *M. longipes* from the northeastern Atlantic. The males of this species from the Western Atlantic may have a large medial fat-based seta instead of a small one. Only fully mature males may be used for these male pleopod characters because the preceding juvenile male instar has a flat, almost featureless pleopod I. Maturity may be judged in this species (as in most Janiroidea) by a pleopod II stylet sperm tube which is open at both ends. Juvenile males generally have either closed or absent sperm tubes.

M. longipes has a broad distribution, both vertically and geographically, compared to distributions of other eurycopids from the north Atlantic (Wilson 1983a; 1982b). This species is found in some of the same localities as the *E. complanata* complex (Wilson 1982b), leading one to wonder whether a cryptic species complex is present. It is replaced, however, at a central North Atlantic station (WHOI 334) by another undescribed species, suggesting that it is limited to proximity of the continental margins.

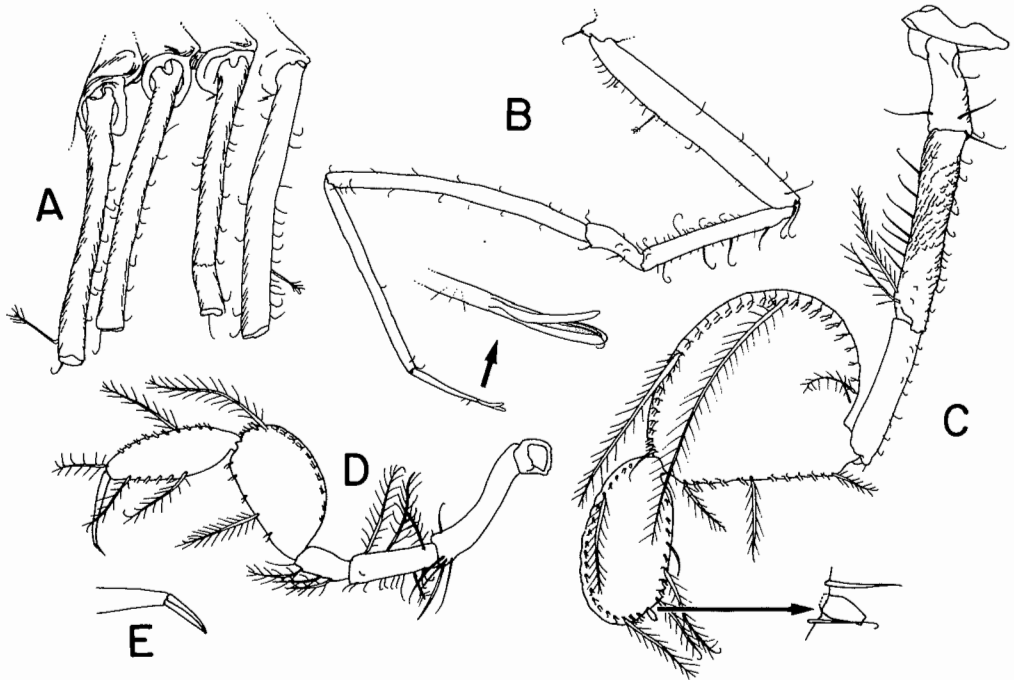


Figure 31. *Mimocopelates longipes* n. gen., n. sp. A, C-E, holotype male, bl 2.1 mm. A, bases of right pereopods I-IV, *in situ*. B, left pereopod I, paratype male, bl 2.1 mm, with enlargement of dactylar claw. C, right pereopod V, *in situ*, with enlargement of dactylus. D, right pereopod VI, *in situ*. E, pereopod VI enlargement of dactylar tip. Illustrations all to same scale.

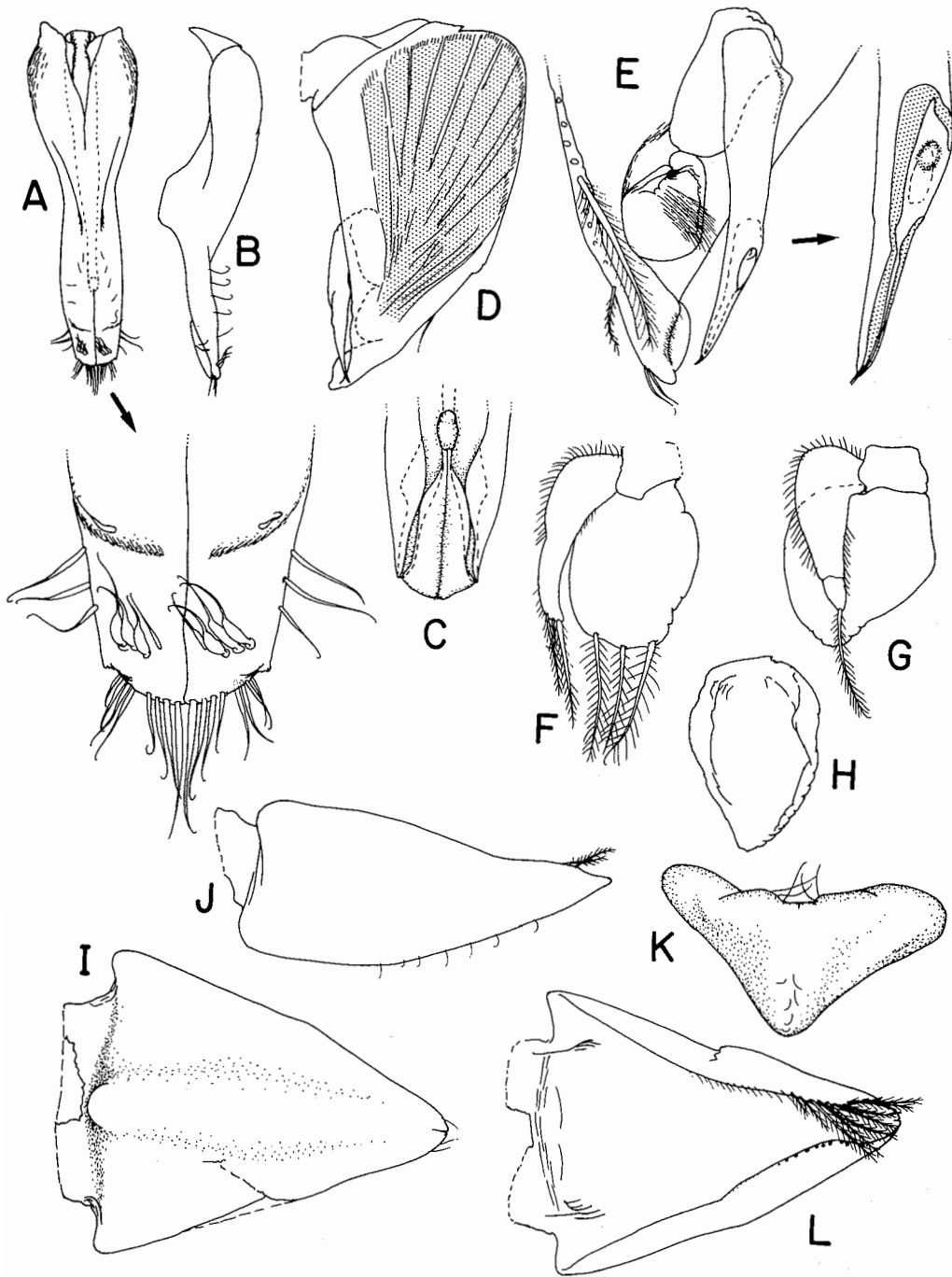


Figure 32. *Mimocopelates longipes* n. gen., n. sp. A-E, pleopods I-II, paratype male, bl 2.1 mm. F-L, pleopods II-V, paratype preparatory female, 1.9 mm. A-C, pleopod I, ventral view with enlargement of distal tip, lateral view, and dorsal view of distal tip. D-E, left pleopod II, ventral view and dorsal view of distal tip with enlargement of stylet tip. F-H, right pleopods III-V. I-L, pleopod II: ventral, lateral, posterior, and dorsal views, respectively.

Mimocopelates anchibraziliensis new species
(Figures 33-35)

Holotype. Preparatory female, bl 4.2 mm, distal parts of antennae, and pereopods I-IV broken off, USNM 227063.

Paratypes. Copulatory male, bl 3.2 mm, USNM 227064. 20 additional specimens, some dissected for description, SIO.

Type-Locality. WHOI 169, 08°02.0-03.0'S, 34°23.0-25.0'W, 587 m, collected on 21 February 1967 during R/V *Atlantis II* cruise no. 31.

Other Material. WHOI 167, 72 mostly fragmentary individuals; WHOI 159, 7 individuals; WHOI 162, 1 individual.

General Distribution. Equatorial Atlantic Ocean off Brazil, 587-1493 m.

Derivation of Name. *Anchibraziliensis* refers to the occurrence "near Brazil" in the bathyal waters offshore.

Diagnosis. Cephalon massive, heavily calcified, wider than pereonite 1, anteriorly flattened. Cephalic vertex linear medially, distinctly separating frons from cephalic dorsal surface. Cephalic frontal arch recessed into frons, not protruding beyond vertex in dorsal view, nearly vertical in lateral view. Cephalon lacking indentation at mandibular articulation. Widths of antennular articles 1 sexually dimorphic, wider in adult males than in adult females: in females, distance between medial corners of antennular insertions 0.19 (2 inds) cephalon width; in males, 0.10-0.11 (2 inds). Maxillipedal epipod distally scalloped. Male pleopod I distal tip with following paired setal groups: 5 fat-based setae ventral to dorsal orifice, 7 setae distally, and 4 setae laterally. Uropodal endopod length 1.9 width, length shorter than protopod width, ratio 0.9; protopod distomedial corner rounded, not projecting; exopod absent.

Description. Body Characters (Fig. 33A-C): Adult females larger than males, female body length 4.2-4.4 mm (2 inds), male body length 3.2-3.5 mm (2 inds). Length 2.7 width in both sexes. Pleotelson lengths sexually dimorphic: male pleotelson length 0.38 body length (2 inds); in female, 0.34-0.35 (2 inds).

Body setation (Fig. 33A-C): All dorsal surfaces with few scattered fine setae.

Cephalon (Fig. 33D-F): All surfaces heavily calcified, especially at anterior margins, with large platelike crystals in cuticle. In female, dorsal length 0.50 width, length 0.76 height. Ventral margin at posterior articulation of mandible heavily calcified, with no indentation or notch.

Antennula (Fig. 33A-B, 34A-D): Strongly dimorphic sexually: male antennula estimated length (not intact in any male specimens) greater than in female, with a higher number of more robust articles. Female antennula length 0.39 body length; female antennula with 18-19 articles (holotype only). Article 1 larger in males: width 0.36-0.37 (2 inds) cephalon width in males, 0.24-0.26 (2 inds) in females; article 1 medial lobe distinct but shorter than lateral lobe, length 0.49

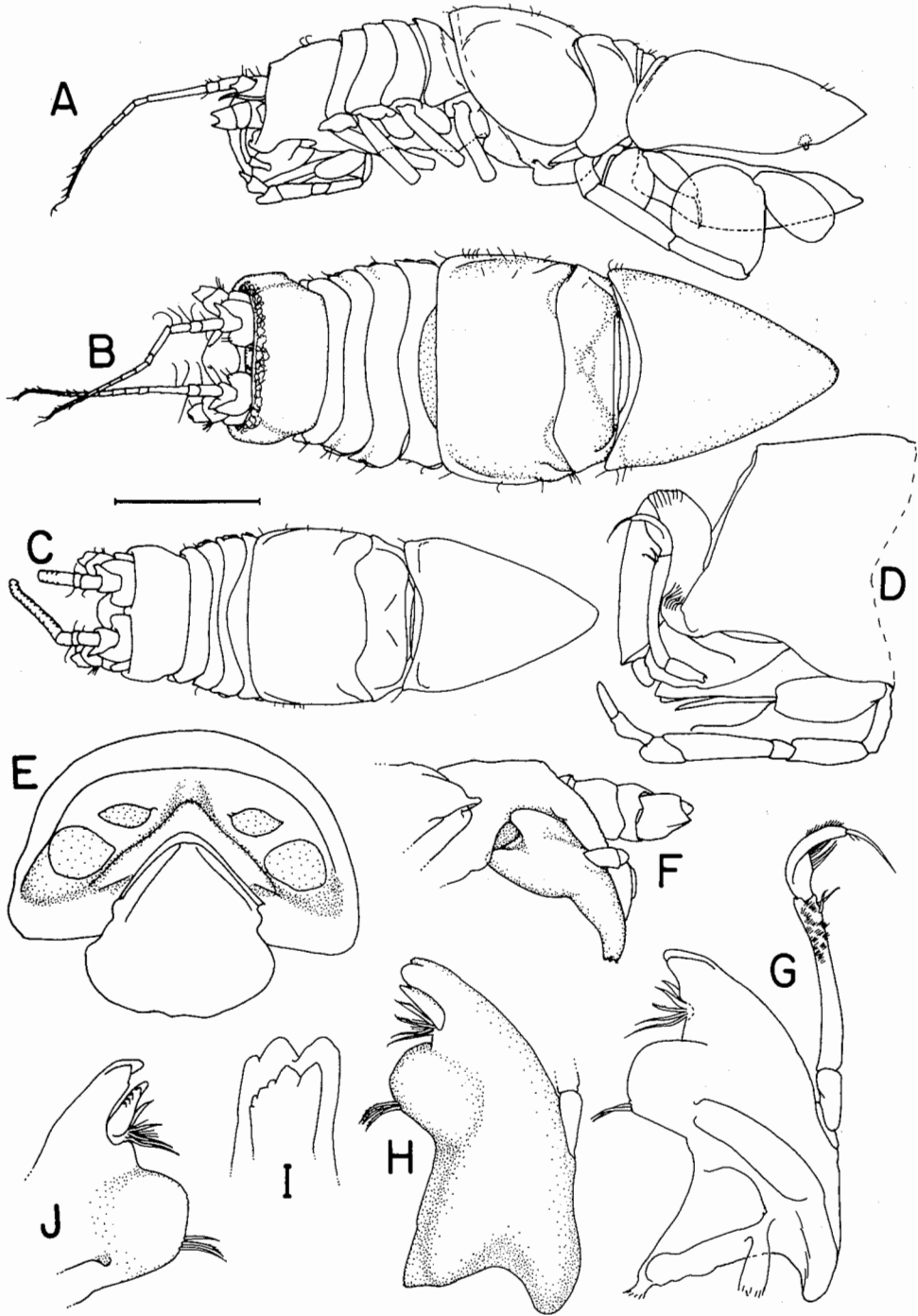


Figure 33. *Mimocopelates anchibraziliensis* n. sp. A-B, holotype preparatory female, lateral and dorsal views, scale bar 1.0 mm. C, paratype male, dorsal view. D-E, cephalon, lateral and anterior views, paratype preparatory female, bl 4.4 mm. F, cephalon and mandible, ventral oblique view, paratype male, bl 3.5 mm. G-J, mandibles, preparatory female, bl 4.4 mm. G, right mandible, dorsal view. H, left mandible, ventral view, palp omitted. I, left incisor process and lacinia mobilis, plan view. J, left mandible, incisor and molar processes, dorsal view.

width in male, 0.59 in female; medial lobe of both sexes with approximately 4 broom setae. Article 2 with blunt lateral spine bearing 2 broom setae; article 2 length 0.67 article 1 medial-lobe length in female, length 1.1 medial-lobe length in male. Article 3 length 0.75 article 2 length in female, 0.89 in male. Flagellar articles longer than wide in females, wider than long in males.

Mandible (Fig. 33F-J): Mandibles of both sexes heavily sclerotized and calcified. Both mandibles with 3 distinct cusps on incisor processes. Lacinia mobilis narrower than incisor process, with 6 low cusps. Left spine row with 4 members, right spine row with 5. Molar process distally dome shaped, with no circumgnathal denticles or cusps; posterior margin with 3 serrate setae; no sensory pores visible on triturating surface. Condyle strong, with anterior and posterior shelves; length 0.36 mandibular body length. Palp second article length 0.47 mandibular body length; distal article thin, forming flat curl.

Maxilliped (Fig. 34F): Ventral surfaces of basis, palp article 2, and epipodite with cuticular ridges and few setae. Basis with 4-5 receptaculi and 6 fan setae distally; 4 lateral fan setae bifid with distinct gap separating both sides; medial fan seta small, truncate; seta second from middle behind third seta more robust, with fewer and broader branches than 4 lateral fan setae. Endite distally quadrate, length 0.51 total basis length. Palp article 2 width 2.0 endite width, lateral length 2.0 medial length. Palp article 3 lateral length 0.22 medial length. Epipod short, round, broadly concave distally; length 0.66 basis length; length 1.5 width.

Pereopodal Bases: Bases I-IV short, not subequal to each other: length-body length ratios 0.19, 0.17, 0.18, 0.19.

Natatory Pereopods V-VI (Fig. 34G-H): Basically similar to those of *Mimocopelates longipes*. Pereopod V-VI length-body length ratios 0.65, 0.54. Pereopod V merus length 0.82 ischium length. Carpi V-VI length-width ratios 1.1, 1.3. Propodi V-VI length-width ratios 1.8, 2.6.

Male Pleopod I (Fig. 35A-D). Fused pleopod pair not highly convoluted: widest proximally, tapering gradually to narrow distal end, curving smoothly in lateral view, with small dorsal locking folds. Length 5.6 width; width at dorsal orifice 0.48 pleopod width. Dorsal orifice close to distal tip: 0.09 total pleopod length from distal tip. Distal tips similar in shape to *Mimocopelates longipes*. Penes elongate, curving posteriorly and down from ventral surface before entering proximal sperm tube funnel of fused pleopod pair.

Male Pleopod II (Fig. 35E-G): Protopod elongate, triangular, deeper in distal half where exopodal musculature attaches; length 2.3 width. Dorsally recurved distolateral margin with approximately 6 plumose setae. Stylet small with short sperm tube, length 0.30 protopod length; sperm duct proximal opening one-third total stylet length from distal tip; endopod inserting 0.19 length of protopod from distal tip. Exopod small, with fine setae on dorsomedial side.

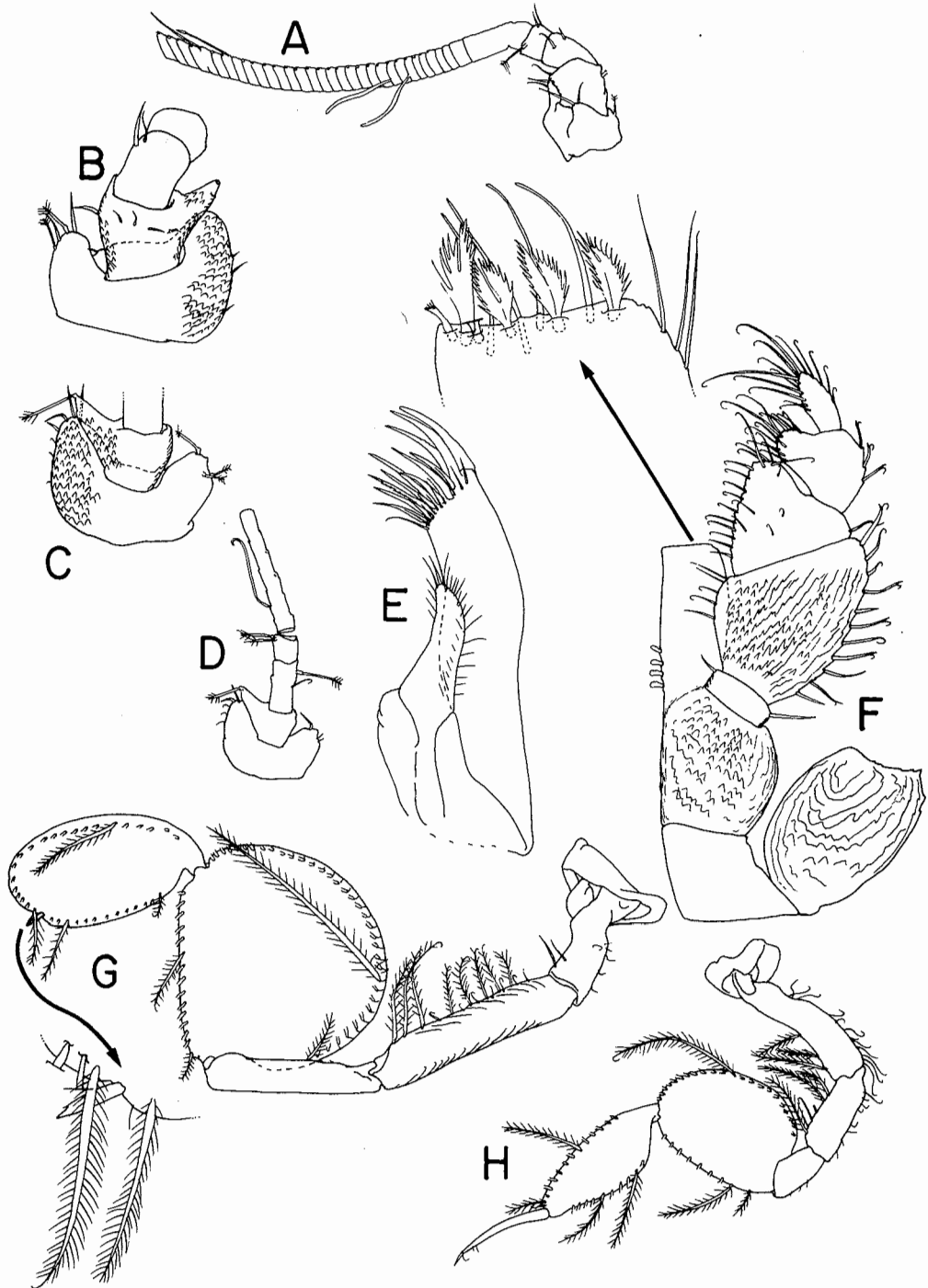


Figure 34. *Mimocopelates anchibraziliensis* n. sp. **A-B**, right antenna, lateral and dorsal views, paratype male, bl 3.5 mm. **C-H**, paratype preparatory female, bl 4.4 mm. **C-D**, dorsal views of left antenna: articles 1 and 2, and articles 1-5. **E**, left maxillula. **F**, left maxilliped with enlargement of distal tip of basis. **G**, right pereopod V, with enlargement of dactylus. **H**, right pereopod VI, same scale as **G**.

Female Pleopod II (Fig. 35K-L): Keel broad, with shallow rounded anterior prow and low hump 0.37 total length from proximal end; keel curving smoothly into rounded lateral fields. Ventral surface with few setae. Distolateral margins strongly recurved dorsally with approximately 11 plumose setae on each side. Length 1.3 width; depth 0.41 length.

Pleopod III (Fig. 35H): Exopod distally rounded, longer and wider than endopod, with 2 distal plumose setae and no apparent joint. Endopod with 3 distal plumose setae; setae longer than endopod.

Pleopods IV-V (Fig. 35I-J): Endopods of both limbs thick and triangular in ventral view. Exopod of pleopod IV long, flattened, lobelike, with single long plumose seta.

Uropod (Fig. 35M): Uropods small, uniramous, recessed into ventromedial margin of posterior pleotelson; only distal tip of endopod visible in lateral view. Protopod medial length 0.56 distal width. Endopod 1.6 medial length of protopod. Distal margin of protopod with few long setae, posterior margin lacking projection.

Remarks. *Mimocopelates anchibraziliensis* n. sp. is a very distinctive species: members are large, exceeding 4 mm as adults, the uniramous uropods are tiny, and the cephalon is enlarged and heavily calcified. In addition to these characters, the flat, triangular male pleopods are distinctly different from the robust, highly convoluted pleopods of *M. longipes*. In fact, the male pleopods II of *M. anchibraziliensis* are somewhat reminiscent of those seen in some Munnopsidae *sensu stricto* whose endopods, exopods, and intrinsic musculature are reduced. This species was collected only in a bathyal transect of stations off Recife, Brazil.

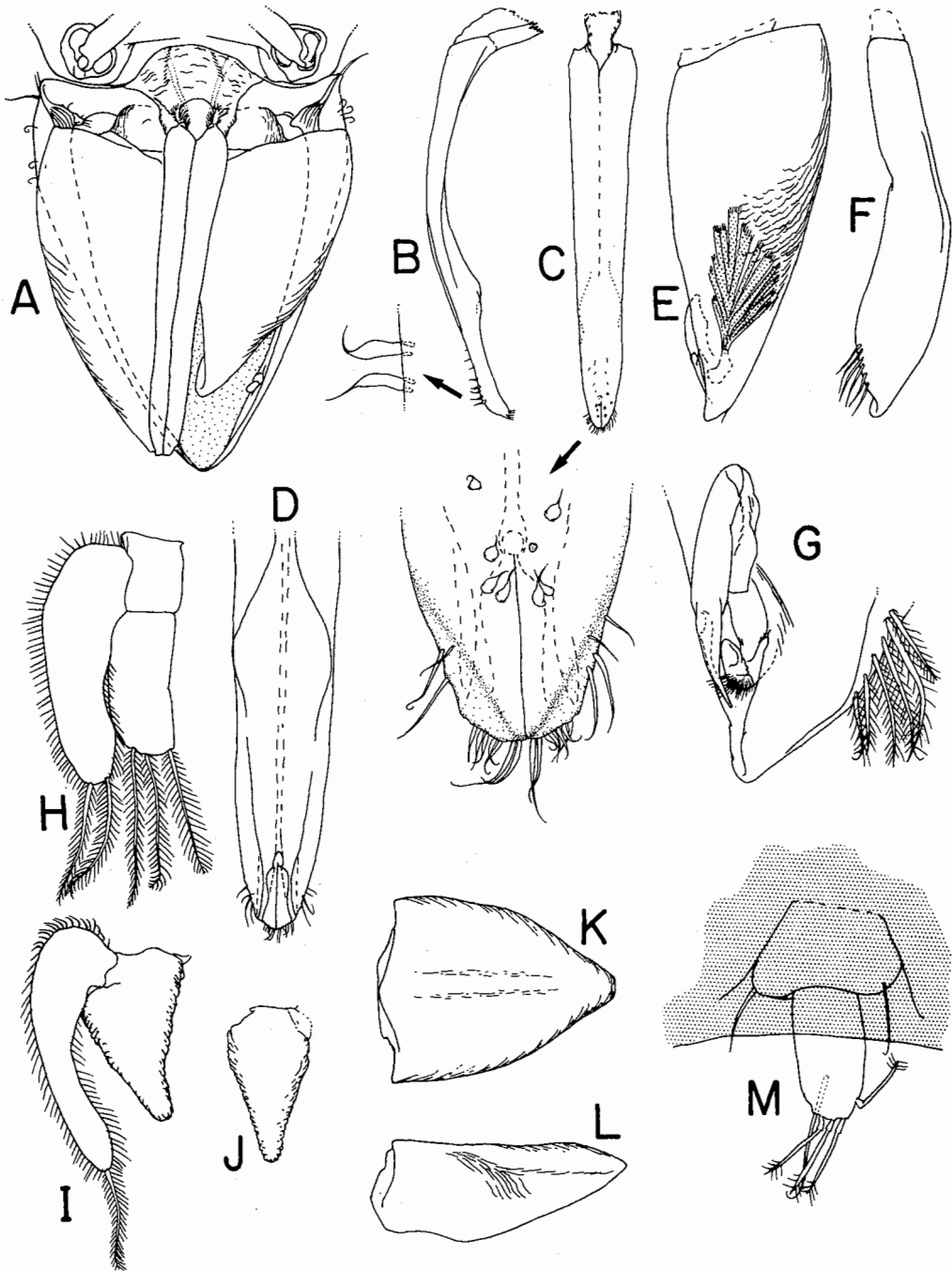


Figure 35. *Mimocopelates anchibraziliensis* n. sp. A-J, paratype male, bl 3.5 mm. A, pleotelson and pereonite 6, ventral view. B-D, pleopod I: B, lateral view with enlargement of ventral fat setae; C, ventral view with enlargement of distal tip; D, dorsal view of distal half. E-G, pleopod II: E, left side, ventral view; F, right side, lateral view; G, left side, enlarged dorsal view of distal tip. H-J, right pleopods III-V. K-L, pleopod II, ventral and lateral views, paratype preparatory female, bl 4.4 mm. M, uropod, holotype female, bl 4.2 mm, *in situ*, proximal portion seen through cuticle.

PHYLOGENY AND CLASSIFICATION

This section presents an evaluation of the systematic position of the subfamily Lipomerinae Tattersall, wherein the monophyly of these ilyarachnid-like animals is demonstrated. Computer-assisted numerical phylogenetic methods are used to compare the genera of the Lipomerinae with other major munnopsid taxa in an extended outgroup study. A side effect of confirming the monophyly of the Lipomerinae and their distinctiveness from the ilyarachnids is a realignment of the Ilyarachnidae, the Eurycopidae, and the Munnopsidae into one family. Characters that show relationships between the munnopsid taxa are used with a bias toward interpreting the systematic position of the ilyarachnid-like eurycopids. As a consequence, some taxa may not be identified by autapomorphies, because this analysis is designed to emphasize relationships between taxa. Many munnopsid taxa, of course, have a variety of unique specializations, but these characters were not the focus of the analysis. The estimated phylogeny and the conclusions reached here provide hypotheses to be tested in the future, although a preliminary conclusion concerning the classification of the munnopsids is reached.

TAXA USED

The Munnopsidae *sensu lato*

The diversity of munnopsids and the limited information on many of them requires a restriction in the number of taxa used in the phylogenetic analysis. Four independent criteria, based on the desire to properly place the ilyarachnid-like eurycopids, established the subset of taxa (Table 6) used in this analysis: (1) they are ilyarachnid-like eurycopids; (2) they are members of the subfamily Eurycopinae as previously recognized (Wolff 1962); (3) they are the least modified representatives of their group; (4) they are presumed to be closely related to the Ilyarachnidae. Some previously-defined taxa may overlap, such as the previous classification of *Hapsidohedra* n. gen. in the Ilyarachnidae (criteria 1, 2, and 4). All genera used in the analysis have been revised recently, or were evaluated directly from specimens. These criteria include most munnopsids, but the major taxa or genera not used are discussed below. The chosen taxa are presumed to represent major monophyletic groups within the munnopsids.

The eurycopid subfamily Bathyopsurinae, with the genera *Bathyopsurus* and *Paropsurus*, contains highly modified bathypelagic animals. This group may be derived from a *Munneurycope*-like ancestor (Wolff 1962). This subfamily is not included in the analysis because its genera have little in common with the ilyarachnid-like eurycopids.

The eurycopid subfamily Syneurycopinae contains two genera,

Syneurycope and *Bellibos*, that include a fairly wide range of morphologies. The subgenus *B.* (*Bellibos*) is the least modified with respect to the other munnopsids because its cephalon is not fused to the first pereonite, and the natasomal pereonites are not reduced in size. The species *B. (B.) buzwilsoni* Haugness and Hessler, 1979 is chosen as the syneurycopine representative in the analyses.

The Munnopsidae *sensu stricto* contains a variety of morphologies, but can be best represented by *Paramunnopsis*, which is the least derived member of the family. This genus is superficially similar to the eurycopid *Munneurycope* in overall appearance, which has been a source of taxonomic confusion (Wolff 1962). The type genus of the Munnopsidae, *Munnopsis*, can be scored almost identically to *Paramunnopsis* for the characters used here, and therefore was not included in the analysis.

The Ilyarachnidae has 5 genera with a basic body plan, and is well established as monophyletic (Wolff 1962; Thistle and Hessler 1976). The least modified genus, *Ilyarachna*, was chosen to represent this taxon.

Two eurycopid genera, *Microprotus* and *Munnicope*, were not included because they are poorly described and only 1 specimen of the latter genus was found in collections, eliminating the possibility of dissection. A preliminary inspection of *Munnicope* showed that this genus has characters in common with *Munnopsurus* so its omission from the analysis will not seriously hamper the results. *Microprotus* has been redescribed (Wilson et al., in press) too late to include in this analysis.

An Outgroup for the Munnopsidae

An effective phylogenetic analysis of the position of the Lipomerinae among the munnopsids must include at least one additional outgroup to establish the polarity of character changes, and to "root" the tree. Unfortunately, only one explicit phylogeny of the Asellota has been published that includes the families Ilyarachnidae, Eurycopidae, and Munnopsidae (Kussakin 1973). Wägele (in preparation) will propose a new phylogeny for the Janiroidea, but his results have become available too late to be included here. Kussakin's tree was presented without an explanation of its construction, although it is probably based on the taxonomic judgment of its author. In Kussakin's tree, the clade including the families Ischnomesidae, Macrostylidae, and Pseudomesidae is the sister group to the munnopsids. I find several problems with this hypothesis. First, the Pseudomesidae has been submerged into the Desmosomatidae and the Nannoniscidae (Svavarsson 1984). Second, both the Ischnomesidae and the Macrostylidae are highly modified taxa that share few apparent apomorphies with the munnopsids. Third, the entire phylogenetic structure of the Janiroidea must be reconsidered. A recent phylogenetic analysis of the superfamilies of the Asellota (Wilson 1987) shows that the Munnidae, the Santiidae (= Antiasidae), the Paramunnidae, and the Abyssianiridae were derived before the Janiridae.

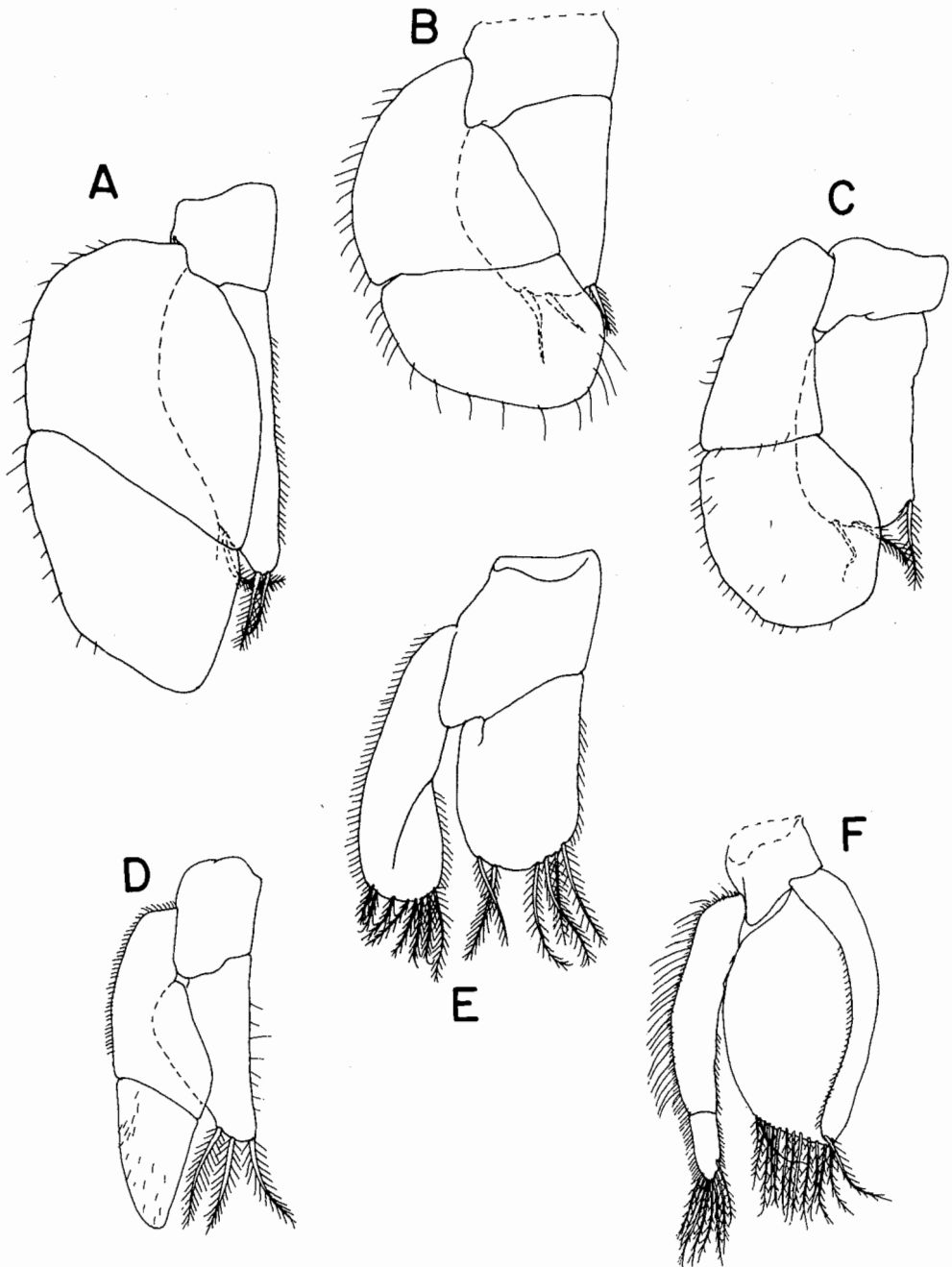


Figure 36. A comparison of third pleopods of various Asellota. A, *Stenetrium*, Stenetriidae, Stenetrioidea. B, *Pseudojanira*, Pseudojaniridae, superfamily Pseudojaniroidea. C, *Notasellus*, Janiridae, Janiroidea. D, *Munna*, Munnidae, Janiroidea. E, *Acanthaspidia*, Acanthaspidiidae, Janiroidea. F, *Amuletta*, Munnopsidae, Janiroidea.

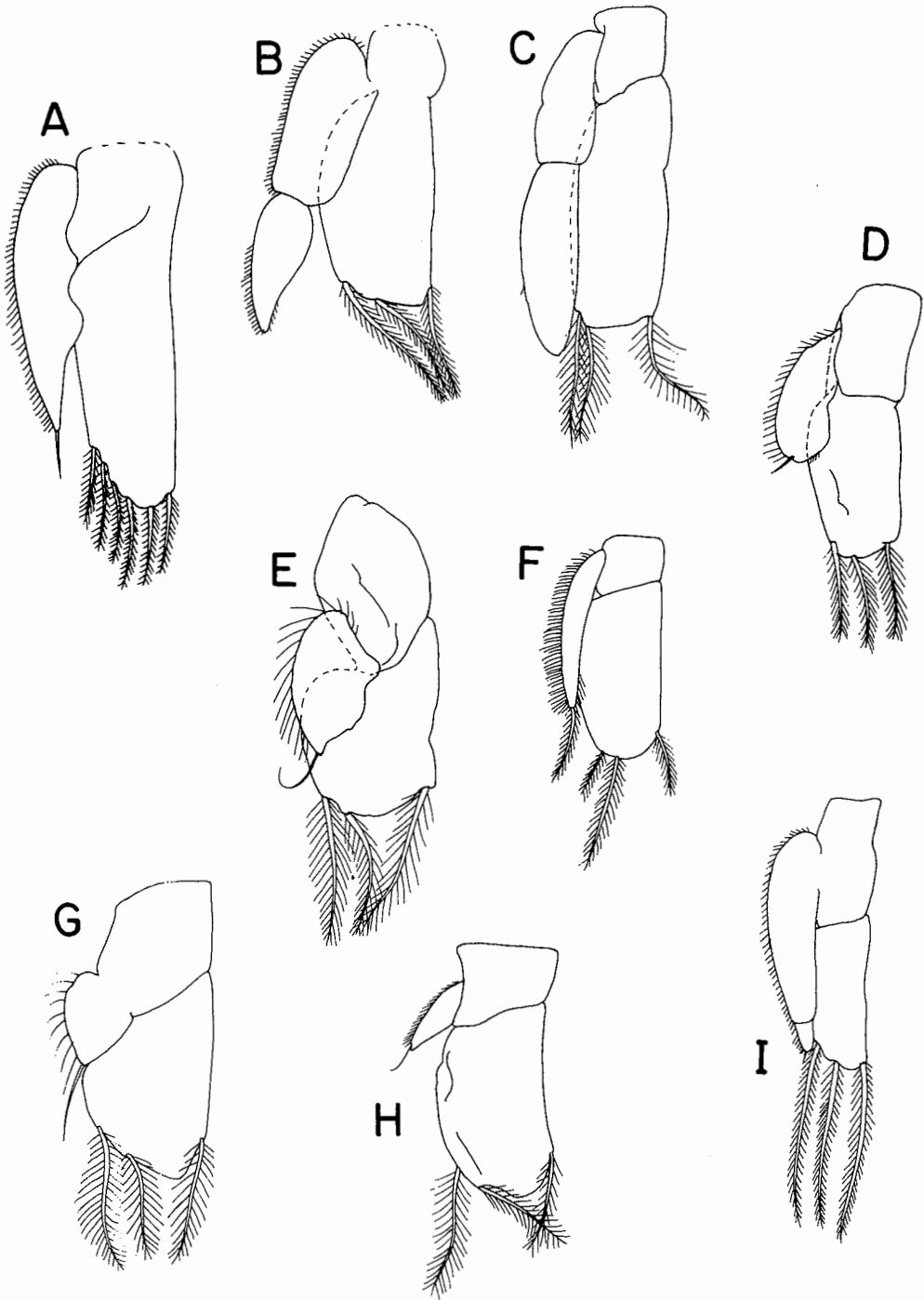


Figure 37. A comparison of third pleopods of various higher Janiroidea. **A**, *Janirella*, Janirellidae. **B**, *Dendrotion*, Dendrotiidae. **C**, *Thambema*, Thambematidae. **D**, *Mesosignum*, Mesosignidae. **E**, *Rapaniscus*, Nannoniscidae. **F**, *Ischnomesus*, Ischnomesidae. **G**, *Haploniscus*, Haploniscidae. **H**, *Momedossa*, Desmosomatidae. **I**, *Macrostylis*, Macrostylidae.

The Janiridae was previously considered the most primitive taxon of the Janiroidea, so the possible rooting of any evolutionary character analysis is changed considerably (Wilson *ibid.*).

Given these problems, a search for munnopsid apomorphies shared with other janiroideans was conducted. This included preliminary phylogenetic analyses of all the families of the Janiroidea (Wilson 1985). The most obvious specialization of the munnopsids is their ability to swim backward. This also appears in other families as well, specifically the Desmosomatidae, and has been used to relate the two groups (Hansen 1916; Kussakin 1965). This adaptation, however, is probably attained independently in the two taxa. Sars (1899) noted that both swim backward but do it quite differently, the munnopsids generally by rapid jumps through the water, and the desmosomatids by a sustained walking motion, which allows them to leave the bottom. The swimming setae are of quite different forms: the desmosomatid swimming seta has setules only distally (Hessler 1970), and the munnopsid seta has many setules from base to tip, giving it a featherlike appearance (Wilson and Hessler 1980). The base of the munnopsid swimming seta also has a specialized hinge and stop arrangement that is not seen in the Desmosomatidae. The desmosomatids are closely related to the Nannoniscidae (Siebenaller and Hessler 1977, 1981), and share apomorphies with the Macrostylidae, especially in the mandible and in the fossorial pereopods. A sister group relationship between the Desmosomatidae and the munnopsids is not likely (Hessler 1970).

If one ignores the swimming specializations of the least modified munnopsids, few apomorphies at the systematic level of the higher Janiroidea are shared with other families (Wilson 1985). The basic janiroidean mouthparts, antennulae, antennae, first pereopod, pleopods, and body form (not including the swimming modifications) are observed in the least modified munnopsids. The scanty evidence available to me indicates that the munnopsids arose early in the diversification of the deep-sea isopods, and therefore have much in common with more primitive shallow-water taxa, such as the Janiridae (*sensu lato*).

My survey of janiroidean synapomorphies revealed one munnopsid apomorphy shared with the poorly known family Acanthaspidiidae: many plumose setae on the distal tips of both rami of the third pleopod. Wolff (1962) placed the Acanthaspidiidae and the Janirellidae in the Janiridae, although later authors (Menzies and Schultz 1968; Kussakin 1973; Bowman and Abele 1982) continued to recognize these families. Throughout the Janiroidea, the third pleopod undergoes a series of reductions, both in size and in setation. In the sister group to the higher Janiroidea, the Pseudojaniridae Wilson (1986a; 1987), and in most of the within-group families, there are only 3 plumose setae on the third pleopod endopod. None of the families, except the munnopsids and the Acanthaspidiidae, has more than one plumose seta on the exopod (Figs. 36, 37). (The non-monophyletic family Janiridae (Wilson and Wägele, in preparation) currently contains genera, such as *Janiralata*, that have this apomorphy, although

these may also be closely related to the Acanthaspidiidae.) This setation of the third pleopod may be a synapomorphy of the two families, and is evidence for their common ancestry. The Janirellidae has more than 3 plumose setae on the endopod of the third pleopod, and is, therefore, also a candidate for sister group status with the munnopsids. The Janiridae may also function as an outgroup to the munnopsids. This last family, however, is highly heterogeneous, and no apomorphies apply to all janirid taxa (Wilson and Wägele, in preparation). For the character studies, the Janiridae was limited to genera that had enlarged accessory (third) claws on the pereopods. In the character studies, all three families (Acanthaspidiidae, Janirellidae, Janiridae) were used as outgroups. Munnopsid trees, however, were rooted using only the Acanthaspidiidae because most characters of the three outgroup families were similar.

CHARACTER ANALYSIS OF THE MUNNOPSID TAXA

The natatory morphology unites all the munnopsids, but the included taxa vary enormously in their overall body plan (Fig. 1), and in the form of less well understood features such as the cephalic frons and the pleopods. In this section, morphological data of the munnopsid taxa are evaluated for useful synapomorphies. The presumed sister group Acanthaspidiidae and other outgroups permit an assessment of the character polarities. Most characters discussed below are presumed synapomorphies of two or more munnopsid taxa. Their usefulness was determined by preliminary analyses of the munnopsid phylogeny.

Characters Found in All Munnopsids

The munnopsids have three synapomorphies that distinguish them from all other Janiroidea. Because the characters consist of complicated morphologies that are not easily lost without leaving evidence of their presence in ancestors, they were evaluated in the phylogenetic analysis using the Camin-Sokal parsimony method, and are given an a priori weight of 2. They are listed as characters A-C in the tables.

The first character is the most obvious: the swimming adaptations, which consist of paddlelike pereopods V-VII with fringing plumose setae on the carpi and the propodi, and enlargement of the musculature powering these limbs. Associated with the pereopodal features is an integrated natasome, a characteristic modification of the posterior pereonites and the pleotelson, making them more or less streamlined for posterior locomotion. So much variability in the natasome occurs throughout the munnopsids, however, that defining specific features common to all natasomes is difficult. Nevertheless, the natasome is recognized as a secondary division of the body, in which the pleotelson and posterior three thoracomeres function as a unit. A coalescence and anterior placement of neuronal ganglia of pereonites 5-7 may be diagnostic of the

natasome. This was first pointed out by Hult (1941), although his observations have been largely ignored by later workers. All other Janiroidea observed by Hult and myself have a more typical ladderlike arrangement. Some variation in the form and position of the fused ganglia appears, but they are fused or closely associated in all munnopsids examined so far. This coalescence is correlated with the presence of the natasome, which argues against the independence of this feature, but emphasizes the monophyletic derivation of the munnopsids. Hult (1941) even wished to create, on the basis of the fused ganglia, a munnopsid taxon separate from the remaining Janiroidea (which was recognized in his paper as a family, not a superfamily as it is now). This possibility is discussed in the classification section.

The second character is evidently independent of the first character: cupped or troughlike dactylar claws that enclose the paired distal sensillae. This condition is illustrated in Wilson and Thistle (1985, their Fig. 3D) for the first pereopod, but it occurs on all munnopsid pereopods where the claws are not reduced or greatly altered. Unmodified dactylar claws with free sensillae are found in the Acanthaspidiidae and Janirellidae.

A third character, shown by Wolff (1962) to occur in all the munnopsid families, is a "plate-like" first segment of the antennula. This character can be described as a flattened flange projecting laterally from the basal part, thereby broadening the first segment. The medial part of the segment is variously thickened in many of the munnopsids, with some having a medial lobe. In the Acanthaspidiidae and other janiroideans, the antennular first segment is more or less tubular. This munnopsid synapomorphy may not be completely independent from the swimming adaptation: the flattened lateral flange and medial thickening may improve the hydrodynamic characteristics of the antennula when the animal is swimming backward. This antennular character is retained in the analysis because it is not directly associated with natasome development, and may have evolved after backward swimming. Complex adaptations are not likely to have appeared fully developed in single ancestors, but may have appeared in steps. The swimming adaptations of the munnopsids may be analogous to the evolution of the janiroidean sexual structures (Wilson 1986b 1987) where major changes occurred independently but resulted in a highly successful (in terms of taxonomic diversity) reproductive morphology.

Fusion of the Natasomal Segments

The varied fusion of pereonites 5-7 is responsible for much of the morphological diversity in the munnopsids. The functional necessity of a strengthened cuticular framework for the powerful swimming muscles may be a driving force in the observed patterns of fusion seen in the munnopsids. In fact, the segmental arrangement of muscles is often lost by the migration of the internal muscular attachments into the segments anterior to their pereopodal

origins. Because fusion of the natasomal pereonites is a general trend in all munnopsids, with frequent apparent convergences, only certain patterns could be used. These characters were analyzed using Camin-Sokal parsimony, and were given an a priori weight of 2.

The plesiomorphic state is complete flexibility between pereonites 5-7 and the pleotelson. This state is seen in *Munnopsurus* and in *Munnicope*. The latter genus is most unusual in that pereonites 5-7 are the same size, and have relatively small pereopodal musculature. In this regard, *Munnicope* may be the least derived munnopsid.

Fusion of the natasomal pereonites may have begun on the ventral surface, resulting eventually in complete obliteration of the segmental boundaries. This is best seen in *Eurycope* (Wilson and Hessler 1980, 1981), but occurs in most of the other munnopsid genera. Notable exceptions are the Ilyarachnidae, *Amuletta*, and *Hapsidohedra*. The last genus is morphologically atypical in that the natasome is strongly flexed ventrally, possibly a factor in its retention of free ventral natasomites. The Ilyarachnidae are known to burrow backwards (Hessler and Strömberg, in preparation), suggesting that some flexibility in their wedgelike natasome is necessary. Little is known of *Amuletta*, so the function of natasomal flexibility in this genus cannot be evaluated. In *Storthyngura*, the natasomal pereonites vary from a condition where the ventral sutures are visible, but not flexible, to a totally fused condition. Fusion of the ventral natasomite boundaries was not used because of this variability, and because it introduces many steps into the cladograms.

In dorsal fusion of the natasomites, several patterns emerge. All Lipomerinae, except for *Coperonus*, have tergites of pereonites 6 and 7 that are fused medially (character 1 in list below). The eurycopids *Belonectes*, *Disconectes*, and *Tythhocope* have pereonites 5 and 6 fused dorsally (character 2). Lastly, complete fusion of all the natasomal pereonites occurs in *Baeonectes*, *Acanthocope*, some species of *Storthyngura*, and in the Syneurycopinae. This last character state may not indicate real shared ancestry between these taxa because it added as many steps as taxa to which it was attributed, indicating multiple convergences. The partially fused natasome characters are compatible with others used in the phylogeny, but they may be derived independently of the transition to the completely fused natasome. Therefore, the completely fused state of the natasome is not used in the analysis.

Comparative Sizes of the Natasomal Pereonites

A great variety in pereonites 5-7 sizes is seen in the munnopsids, with any one of these 3 segments dominating the natasome, depending on the taxon. The primitive state, subequal pereonites, is found in few taxa, i.e., *Munnopsurus* and *Munnicope*.

In *Eurycope* and many other genera, pereonite 7 becomes enlarged. An extreme is seen in the Munnopsidae *sensu stricto*, where the last pereonite is large, and pereonite 5 becomes compressed dorsally along the body axis to a narrow band. Unfortunately, the inclusion of this character state as a terminal apomorphy into the analysis considerably worsened the homoplasy level, indicating multiple derivations. An alternative hypothesis of character derivation is that many munnopsids are derived from an ancestor with an enlarged pereonite 7, and subsequently the size of the pereonite 7 was reduced independently in many of the taxa. Under such a derivation, the subequal natatory pereonites of *Munnopsurus* are difficult to score, being either secondary or primary. A choice between these two hypotheses cannot be made from the information at hand, so this character state is not used in the analyses.

One character that unites all Lipomerinae is a reduced seventh pereonite. In two genera, *Lipomera* and *Mimocopelates*, the last pereonite is rudimentary, and in the three other Lipomerinae, it is only a thin band that may be fused to the anterior segment. *Tythocope* also has a reduced pereonite 7, although it may have obtained this state independently. Because the states in these taxa are nevertheless similar, they are scored the same (character 3).

Hindgut Morphology

In all outgroups and most of the munnopsids, the hindgut anterior to the pleotelson is straight, or nearly so. A bent or coiled gut is a useful synapomorphy of the somewhat dissimilar subgenera of *Lipomera*. It is included here to permit defining these three subgenera as a monophyletic group in the analysis (character 4).

Spines on Body

The presence of body spines on munnopsids is unusual, although the genera *Acanthocope*, *Storothyngura*, and *Microprotus* are known to have them. At first, this might seem to be a derived character within the munnopsids, but the spination of these three genera is somewhat similar to the dorsal and lateral spines of the Acanthaspidiidae. On the other hand, the body plans of these spinose munnopsids are highly modified, indicating that they have diverged considerably from the munnopsid ancestor. Because the spines in the munnopsid taxa could be a reversion to the ancestral state, or the stem munnopsid may not have had spines, they are analyzed using the Wagner parsimony method (character 5).

Rostrum

The rostrum, an anterior projection of the cephalon, is an ancestral character of the Janiroidea (Wilson 1987), and is seen in somewhat modified

form in the Acanthaspidiidae (Fig. 38A). Most munnopsids have lost the rostrum, and the cephalon has a nonprotruding dorsal vertex (Fig. 38C-G). In some genera (*Munneurycope* and *Paramunnopsis*) even the vertex is indistinguishable, because the dorsal part of the cephalon slopes smoothly down to the frons. A rostrum is found in a few genera: *Eurycope* (Fig. 38B), *Tytthocope*, *Disconnectes*, *Belonectes*, and *Baeonectes* (Wilson and Hessler 1980, 1981; Wilson 1982a), although its form often deviates considerably from the primitive projection seen outside the munnopsids. In some of these taxa, the rostrum becomes very broad and rounded, and does not project from the frons. Because both a narrow, projecting rostrum and a broad, rounded rostrum are seen within some genera (*Eurycope*, *Disconnectes*), the rostrate genera are scored as having the plesiomorphic state of the rostrum (character 6).

Frontal Arch

The "frontal arch" is defined as an archlike thickening of the cephalic frons, providing a strengthened bridge between the fossal regions of the clypeus on either side of the frons. Much of the variety in the munnopsid frons is a result of changes in the form of the frontal arch. *Eurycope* and other rostrate genera show no evidence of having had a frontal arch. Some species of *Eurycope* have a pair of vertical ridges running from the clypeus to the rostrum forming an inverted "V" (Fig. 38B), but these same ridges are seen in the Janiridae. An incipient frontal arch is seen on the smoothly protruding frons of *Paramunnopsis*: the region just above the clypeus is flattened and arc-shaped (Fig. 38C). In *Munneurycope* (Fig. 38D) and *Storothyngura*, a fully developed frontal arch is seen, where the arch is a projection from the ventral part of the frons. These two genera also have the inverted "V"-shaped ridges of *Eurycope*, demonstrating that these ridges are not modified frontal arches. In other genera, the arch shows a variety of forms, appearing massive in some, such as *Munnopsurus* (Fig. 38E), *Acanthocope*, and *Ilyarachna* (Fig. 38F). The frontal arch of the Lipomerinae (Fig. 38G) is flattened, dorsally angular, and sometimes reduced completely. The flattened frons of these genera correlates with their possession of strengthened anterior margins of the cephalon, which may take over much of the mandibular support structure provided by the frontal arch of other taxa. These character states form a linear transformation series: no frontal arch, incipient frontal arch, well-developed frontal arch (in a variety of shapes), and a reduced and flattened frontal arch (character 7).

Mandible

At first, components of the mandible appeared to offer a variety of useful characters. Preliminary phylogenetic analyses showed, however, that their use often introduced a great deal of homoplasy. For example, an enlarged, rounded, and sclerotized molar process seemed useful because most Lipomerinae had this

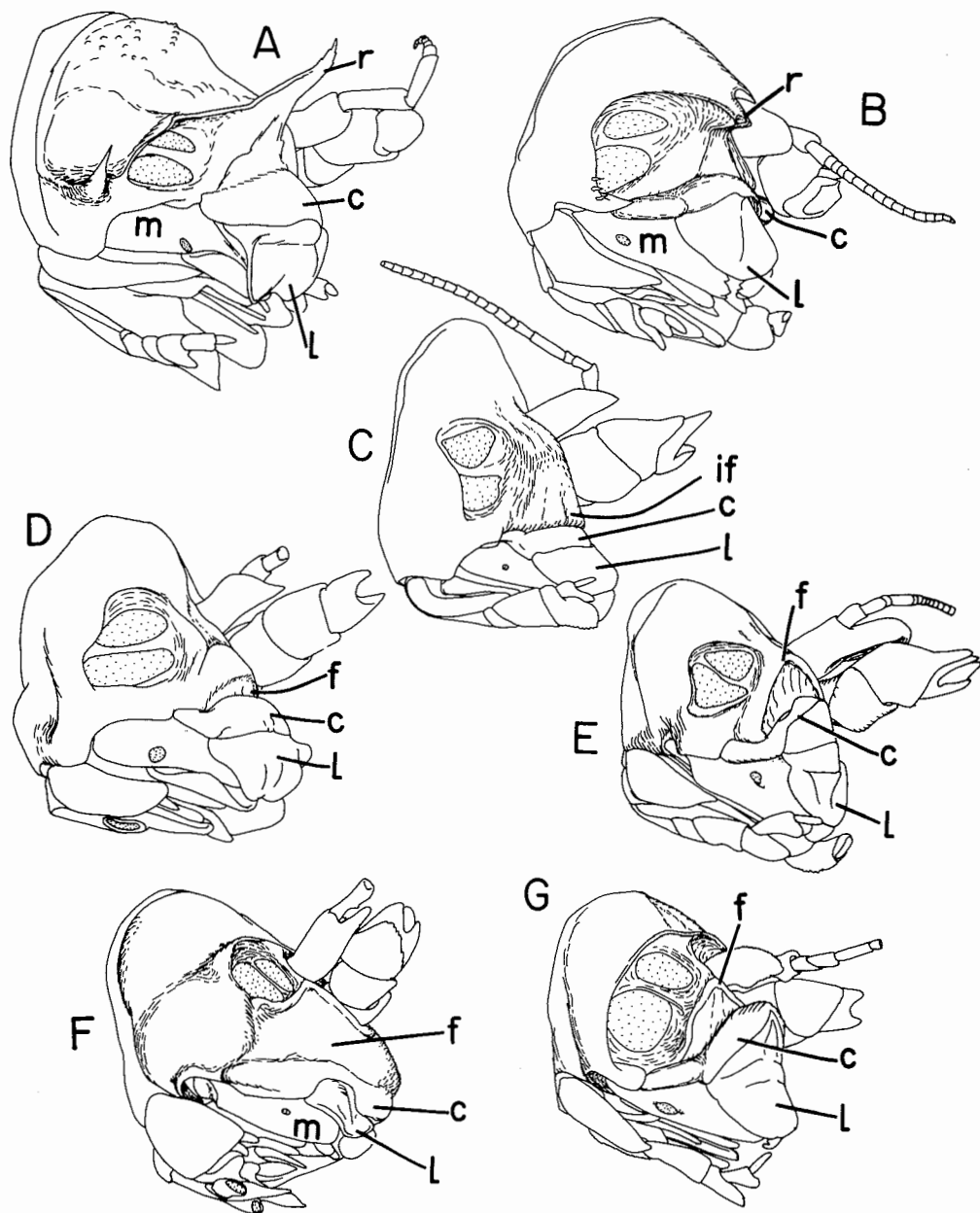


Figure 38. Cephalons of an acanthaspidiid and several munnopsids in frontal oblique view. A, *Acanthaspidia*. B, *Eurycope*. C, *Paramunnopsis*. D, *Munneurycope*. E, *Munnopsurus*. F, *Ilyarachna*. G, *Coperonus*. The left antennulae and left antennae have been removed to expose the frons of the cephalon. The mandibular palps on the left sides are also omitted. The maxillipedal palps of D and F are missing. Indications on figures: c = clypeus; f = frontal arch; if = incipient frontal arch; l = labrum; m = mandible; r = rostrum.

apomorphy. Nevertheless, this character state is found independently in other genera, such as *Eurycope* where the entire range is present from a primitive molar process to the enlarged rounded form. Another seemingly useful character state was a reduced molar process, although each taxon that might have been scored for such a reduction had a unique shape, again indicating independent derivation in each case.

An apomorphy of *Ilyarachna* used in the analysis was the presence of an enlarged, rounded, heavily sclerotized incisor process (character 8). A similar incisor is also found in *Munnopsis*. This genus was not included in the analysis because it is highly modified, and is closely related to *Paramunnopsis*, a possessor of a primitive, unmodified incisor process. The modified incisor of *Munnopsis* therefore is regarded as an independent derivation.

The second apomorphy used in the analysis was the absence of the mandibular palp, found only in *Amuletta* (character 9). The palp is also missing in the derived ilyarachnids *Aspidarachna* and *Echinozone*, which were not used in this analysis. Wilson and Thistle (1985) concluded that the ancestral ilyarachnid had a mandibular palp. Its absence both in some of the Ilyarachnidae and in *Amuletta* may indicate a propensity for this loss if a common ancestry of the two groups is accepted. The palp is also lost in some genera of the Munnopsidae *sensu stricto*, although it is present in the least modified *Paramunnopsis*. Here again, the loss of the palp is likely to be convergent at the level of the munnopsids, but it is included to define *Amuletta*.

Ambulatory Pereopods

Pereopods II-IV are the ambulatory pereopods, with pereopod I (sometimes II) performing a manipulative function, and pereopods V-VII being used for swimming (or burrowing). A primitive condition for the pereopods II-IV is all of them more or less the same length or perhaps becoming incrementally longer from front to rear. The bases of the pereopods in such a plesiomorphic state would also be approximately the same length. Although most munnopsids are collected with their fragile ambulatory pereopods broken off, enough information exists, in the form of published descriptions and occasional intact specimens in the collection, to use pereopod lengths in the analysis.

The ambulatory pereopods have several useful features. First, bases III-IV in some taxa are shorter than basis II (character 10). Of these taxa, bases III-IV are longer than wide in some, and in others they are stocky and robust, their length approximating their width. These two substates are placed in a linear transformation series. Second, the entire pereopods III-IV are greatly longer than pereopod II in many taxa (character 11). Although both apomorphies are undoubtedly functionally related, their distribution among the munnopsids indicates they were attained independently. A third apomorphy scored is a prehensile form of the second pereopod (character 12). This last character is

difficult to verify in some cases but was included because Wolff (1962) used it as a diagnostic family-level character. Because of the uncertainty in its derivation, the prehensile pereopod II character is analyzed using the Wagner parsimony method, which permits reversions. A fourth character state suggests a common ancestry for *Munnopsurus* and *Munneurycope*: elongate bases of the first pereopods (character 13).

Natatory Pereopods V-VII

The natapods display a variety of morphologies that are easily classified into a few discrete states. Because natatory pereopods are plesiomorphic *within* the munnopsids, but autapomorphic at the level of the Janiroidea, polarities are assigned by analogy, rather than by direct homology. Because pereopods V-VII are approximately the same size or perhaps increasing in length posteriorly in the outgroup taxa, the same is assumed for the munnopsids even though the outgroup pereopods have an ambulatory form, and the munnopsids have natapods instead.

The comparative lengths of the pereopod V-VII bases require the analogy assumption. In the outgroup Acanthaspidiidae, all the pereopodal bases are similar in length, as observed in many munnopsids. In others, bases V-VII are distinctly shorter than bases I-IV. Not all Lipomerinae are alike in this character: *Coperonus* and *Mimocopelates* have shortened bases as in *Disconectes* and *Belonectes*. Because character state reversals are possible in the lengths of the bases, this feature (character 14) was interpreted in the phylogenetic analysis using Wagner parsimony.

The species of *Mimocopelates* have a useful synapomorphy that justifies retaining *M. anchibraziliensis* in the genus and recognizing the genus as monophyletic: an elongated merus of pereopod V (character 15). In most munnopsids, this segment of the fifth pereopod is shorter than its basis, but in *Mimocopelates* it is distinctly longer. Although this character may have appeared only once without reversions, the Wagner parsimony method was used because reversals in length could be possible.

The pereopodal dactyli have several characters useful for the munnopsid phylogeny (character 16). In the outgroups and many of the genera of the munnopsids, the dactyli of pereopods V-VII are fairly large, although generally shorter than the propodi. A defining apomorphy of the Munnopsidae *sensu stricto* is the complete absence of the dactyli on the natatory pereopods. Three genera of the Lipomerinae show a different apomorphy: the dactylus of pereopod V is reduced to a tiny lobe, and the more posterior pereopods have large dactyli. These apomorphies are scored as states of the same character and are used in the analysis via nonadditive binary coding with Camin-Sokal parsimony.

Two taxa considered here lack pereopods VII as adults: *Mimocopelates* and *Lipomera*. Absence of the last pereopods may be a paedomorphic trend throughout all the Janiroidea that may happen many times (Wilson 1976).

Mimocopelates also has a reduced pereopod VI (character 17), indicating a trend toward greater reliance on the fifth pereopod for swimming. Two subgenera of *Lipomera* have subequal pereopods V and VI, although the more derived *L. (Paralipomera)* species also have a reduced pereopod VI. Because the subgenera of *Lipomera* are considered a single taxon in this analysis (see character 4), the genus is scored as having subequal anterior natapods, with the independent derivation of the apomorphy, reduced pereopod VI, in both *Mimocopelates* and *L. (Paralipomera)*.

In a majority of the munnopsids, the last pereopod is nearly the same size as the next to the last, both in length and breadth of the broadened carpi and propodi. *Tythocope* has a defining apomorphy in that the last pereopod is distinctly smaller than the more anterior natapods, but still functionally natatory. In some genera, such as *Belonectes* and *Baeonectes*, the last pereopod is 10%-15% shorter than pereopod VI, but it is just as robust and has long swimming setae, which is unlike the diminutive last pereopod of *Tythocope*. Therefore, only *Tythocope* is scored as having a reduced but natatory pereopod VII (character 18, state 1). An unrelated reduction of the last pereopod is seen in the Lipomerinae and in the Ilyarachnidae. They both have last pereopods in which the paddles have become narrow and most of the plumose setae are lost (character 18, state 2). This derived state resembles a walking leg, although the presence of a few plumose setae betrays its natatory ancestry. Because this apomorphy is incompatible with many others used in the phylogenetic analysis, it may have been derived independently in the Ilyarachnidae and in the Lipomerinae. As mentioned above, *Lipomera* and *Mimocopelates* take the reduction one step further: the last pereopod is degenerate or absent (character 18, state 3).

Cleft in the Tip of Female Pleopod II

A number of munnopsids, including the ilyarachnid-like eurycopids, have a notch or cleft in the tip of the female opercular pleopod. The polarity of this character is uncertain. In some munnopsid genera, the notch is large and seems to wrap the pleopod around the preanal ridge, thus leaving the anus exposed, as in the Janiridae. In the Acanthaspidiidae and the Janirellidae, the anus is covered by a distal extension of the female pleopod II, found also in a number of the munnopsids, notably *Eurycope* and *Munnopsurus*. In many munnopsids, the anus is covered, but a notch is present, indicating that the two sides of the cleft have grown together over the anus. These are scored as having the cleft. In some species of the Lipomerinae, the cleft is not seen, and the second pleopod covers the anus. The cleft does occur in congeners and closely related genera, which indicates that it is fused, not absent. The genus *Lionectes* is scored as having a fused cleft. *Acanthocope* has no cleft in the female second pleopod, but the anus is not covered. The Syneurycopinae also have a reduced female operculum and an exposed anus, although they have a cleft. Whether the absence

of the cleft is primary or secondary in *Acanthocope* is unknown, so this trait is left indeterminate for this genus. The transformation series for this character is "no notch" to "notch or cleft" to "cleft fused," with rooting at either "no notch" or "notch" (character 19). The transition between the first two states is interpreted with the Wagner method, and the second with the Camin-Sokal.

Proximal Fusion of Male Pleopods II

A synapomorphy of all the genera of the Munnopsidae *sensu stricto* is a fusion to greater or lesser degrees of the proximal margins of male pleopod II (character 20); this character was used by Wolff (1962) to help diagnose the family. This is a pedomorphic character because the male second pleopod passes through a state intermediate to the totally fused female form (janiroidean mancae are morphologically similar to females regardless of their ultimate sex) and the unfused, separated pleopods of the adult male. This character is analyzed using the Wagner method because reversions could be possible.

Pleopods III-IV

Supernumerary plumose setae on the exopod and endopod of pleopod III indicate a sister group relationship between the Acanthaspidiidae and the munnopsids (see Fig. 36). If the homology between acanthaspidiid and munnopsid pleopodal setation is accepted, then the plesiomorphic state within the munnopsids is a pleopod III with many plumose setae on both the endopod and the exopod. All pleopod setation characters discussed below are reduction characters and therefore should be weighted less than uniquely derived apomorphies. Because the setae are less likely to be regained after they are lost, the Camin-Sokal parsimony method was applied to them.

The loss of plumose setae on the exopod of pleopod III shows three states, each of which may appear independently. This interpretation was reached by trying several transformation series in the preliminary analyses, and picking the one that yielded the fewest steps in the overall tree. Two or three plumose setae on the exopod defines the Lipomerinae (character 21, state 1), but is also seen in *Tytthocope*. A single seta occurs on the exopod of *Baeonectes* (character 21, state 2), and a number of the genera, including *Eurycope*, have no plumose setae at all (character 21, state 3).

In many munnopsid taxa, the endopod of pleopod III has only three plumose setae, a reversion to the plesiomorphic state at the level of the Janiroidea (character 22). Within the munnopsids, however, it must be considered an apomorphy.

The exopod of pleopod IV also has plumose setae in many of the munnopsids. The Acanthaspidiidae have exopods with many plumose setae, indicating that this is the plesiomorphic state. The presence of only a single seta

on the exopod (character 23 - state 1) occurs in the Lipomerinae, but this state is seen in other taxa. A few taxa - *Acanthocope*, *Bellibos*, and *Paramunnopsis* - lack plumose setae on the exopod (character 23 - state 2). Parsimonious trees result from a linear transformation series: many setae to one seta to none.

Uropods

The munnopsids show a great variety in the form of the uropods, and it was originally hoped these could provide some characters for the analysis. However, the uropodal form is unique to each taxon, and attempts to score general characters were fraught with many assumptions. Moreover, when simply defined characters, such as whether the protopod is broad or tubular, are put into the analysis, they often added nearly as many steps as taxa scored with the apomorphic state. The uropod varies too much at the level of the munnopsids to be useful for this analysis.

Within the Lipomerinae, however, the uropod shows a few decipherable trends. The protopod is least modified in *Coperonus*, being large and robust (character 25, state 0) with a medial projection (character 24, state 0) bearing unequally bifid setae. This is similar to the form seen in *Eurycope* or *Amuletta*. In *Mimocopelates*, the uropod is greatly reduced in size (character 25, state 1), but still retains the protopodal medial projection in one species, *M. longipes*. In the three remaining genera, the medial projection on the protopod is lost (character 24, state 1) with this segment being longer and more flattened (character 25, state 2). The presence or absence of the medial lobe on the protopod has an uncertain rooting within the munnopsids. If one uses the outgroup state, then "no medial lobe" (state 0) would be ancestral because the Acanthaspidiidae and the Janiridae have more or less tubular protopods, as do many munnopsids. The scattered distribution of apparently similar broadened protopods in the munnopsids casts doubt on this interpretation. Because the plesiomorphic state is uncertain, the medial lobe character is analyzed with the Wagner method. The size of the protopod (character 25) is analyzed with the Camin-Sokal method, because the specialized flattened protopod is not likely to revert to the more primitive tubular state. The enlargement or reduction of the protopod from the primitive state found in *Coperonus* probably happened independently, so the two derived states are nonadditive in the analysis.

LIST OF CHARACTERS

This list contains the characters and their states used in the munnopsid-level phylogenetic analyses. Each character is assigned an ancestral state based on the form found in the outgroup taxa (0) and a number of derived states (1, 2, or 3). The previous section explains the ordering of multistate characters. Following the character states, the parsimony method (C = Camin-Sokal; W = Wagner) and the a priori character weight (Wt = 1 or 2) is indicated parenthetically. The methods section discusses weighting rationales. The distribution of the character states is shown in Table 6, and the analysis data with binary-coded, multistate characters is given in Table 7.

- A. Body without (0) or with (1) natasome and natapods. (C, Wt = 2).
- B. Dactylar claws of pereopods simple, not enclosing sensillae (0), or troughlike, enclosing sensillae (1). (C, Wt = 2)
- C. First segment of antennula tubular (0) or broadened with a flattened lateral flange, and thickened medially (1). (C, Wt = 2)
 1. Natasomites dorsally unfused (0) or only pereonite 5 and pereonite 6 fused medially (1). (C, Wt = 2)
 2. Natasomites unfused dorsally (0) or only pereonite 6 and pereonite 7 fused medially (1). (C, Wt = 2)
 3. Pereonite 7 present (0) or reduced/absent (1). (C, Wt = 1)
 4. Hindgut anterior to pleotelson straight (0) or hindgut with bend/loop (1). (C, Wt = 2)
 5. Spines on dorsal and lateral surface of pereon and pleotelson (0) or no spines (1). (W, Wt = 1)
 6. Rostrum present (0) or absent (1). (C, Wt = 2)
 7. No frontal arch (0), incipient frontal arch (1), frontal arch (2), frons flat, arch reduced (3). (C, Wt = 2)
 8. Mandible: incisor process normal (0) or enlarged and heavy (1). (C, Wt = 2)
 9. Mandibular palp present (0) or absent (1). (C, Wt = 1)
 10. Ambulatory pereopod bases approximately same length (0), bases III-IV shorter than basis II (1), or bases III-IV length near width and much shorter than basis II (2). (W & C, Wt = 2)

11. Pereopod III-IV similar in length to pereopod II (0) or much longer (1). (W, Wt = 1)
12. Pereopod II simple walking leg (0) or somewhat robust and prehensile (1). (W, Wt = 1)
13. Pereopod I basis length subequal to bases II-IV (0) or much longer (1). (W, Wt = 1).
14. Pereopods V-VII bases: near same length IV (0) or shorter than (1) basis IV. (W, Wt = 1)
15. Pereopod V merus shorter (0) or longer (1) than basis. (W, Wt = 2)
16. Pereopod V-VII dactyli long (0) or rudimentary/absent (1) or only pereopod V dactylus rudimentary/absent (2). (C, Wt = 2)
17. Pereopod VI near same size as pereopod V (0) or smaller (1). (C, Wt = 1)
18. Pereopod VII near size of pereopod VI (0), smaller than pereopod VI but functionally natatory (1), smaller than pereopod VI with narrow carpi and propodi (2), or rudimentary/absent (3). (C, Wt = 1)
19. Pleopod II of female without (0) or with notch or cleft in distal tip (1) or cleft fused (2). (W, Wt = 2; C, Wt = 1)
20. Pleopods II of male proximally not joined (0) or joined (1). (W, Wt = 2)
21. Pleopod III: exopod distal tip with many plumose setae (0), 2 or 3 plumose setae (1), 1 plumose seta (2), or none (3). (C, Wt = 1)
22. Pleopod III: endopod distal tip with more than 3 plumose setae (0) or 3 or less plumose setae (1). (C, Wt = 1)
23. Pleopod IV: exopod with many plumose setae (0), 1 plumose seta (1), or no plumose setae (2). (C, Wt = 1)

Characters analyzing the within-group relationships of the Lipomerinae.

24. Uropodal protopod without (0) or with (1) medial projection. (W, Wt = 2)
25. Uropodal protopod small (0), reduced (1), or enlarged and flattened (2). (C, Wt = 2)

TABLE 6.
Distribution of character states in selected munnopsid taxa.

CHARACTER	A	B	C	1	2	3	4	5	6	7	8	9	10	11
<i>Acanthaspidiidae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acanthocope</i>	1	1	1	0	0	0	0	0	1	2	0	0	0	0
<i>Amuletta</i>	1	1	1	0	0	0	0	1	1	2	0	1	1	?
<i>Baeonectes</i>	1	1	1	0	0	0	0	1	0	0	0	0	0	0
<i>Bellibos</i>	1	1	1	0	0	0	0	1	1	2	0	0	1	1
<i>Belonectes</i>	1	1	1	1	0	0	0	1	0	0	0	0	0	0
<i>Betamorpha</i>	1	1	1	0	0	0	0	1	1	2	0	0	B	1
<i>Coperonus</i>	1	1	1	0	0	1	0	1	1	2	0	0	0	0
<i>Disconectes</i>	1	1	1	1	0	0	0	1	0	0	0	0	0	0
<i>Eurycope</i>	1	1	1	0	0	0	0	1	0	0	0	0	0	0
<i>Hapsidohedra</i>	1	1	1	0	1	1	0	1	1	3	0	0	0	0
<i>Ilyarachna</i>	1	1	1	0	0	0	0	1	1	2	1	0	2	1
<i>Lionectes</i>	1	1	1	0	1	1	0	1	1	3	0	0	0	0
<i>Lipomera</i>	1	1	1	0	1	1	1	1	1	3	0	0	0	0
<i>Mimocopelates</i>	1	1	1	0	1	1	0	1	1	2	0	0	0	0
<i>Munneurycope</i>	1	1	1	0	0	0	0	1	1	2	0	0	0	0
<i>Munnopsurus</i>	1	1	1	0	0	0	0	1	1	2	0	0	0	0
<i>Paramunnopsis</i>	1	1	1	0	0	0	0	1	1	1	0	0	1	1
<i>Storthyngura</i>	1	1	1	0	0	0	0	0	1	2	0	0	1	1
<i>Tytthocope</i>	1	1	1	1	0	1	0	1	0	0	0	0	0	0

TABLE 6. (continued)
Distribution of character states in selected munnopsid taxa.

CHARACTER	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Acanthaspidiidae</i>	0	0	0	0	0	0	0	0	0	0	0	0	-	-
<i>Acanthocope</i>	0	0	1	0	0	0	0	?	0	0	1	2	0	0
<i>Amuletta</i>	?	0	0	0	0	0	0	1	0	0	0	0	-	-
<i>Baeonectes</i>	0	0	1	0	0	0	0	0	0	2	1	1	-	-
<i>Bellibos</i>	0	0	0	0	0	0	0	1	0	0	1	2	-	-
<i>Belonectes</i>	0	0	1	0	0	0	0	0	0	3	1	1	-	-
<i>Betamorpha</i>	0	0	0	0	0	0	0	1	0	0	0	0	-	-
<i>Coperonus</i>	0	0	1	0	2	0	2	1	0	1	1	1	1	0
<i>Disconectes</i>	0	0	1	0	0	0	0	0	0	3	1	1	-	-
<i>Eurycope</i>	0	0	1	0	0	0	0	0	0	3	1	1	-	-
<i>Hapsidohedra</i>	0	0	0	0	0	0	2	1	0	1	1	1	0	2
<i>Ilyarachna</i>	1	0	0	0	0	0	2	1	0	0	0	0	-	-
<i>Lionectes</i>	0	0	0	0	2	0	3	2	0	1	1	1	0	2
<i>Lipomera</i>	0	0	0	0	0	0	3	1	0	1	1	1	0	2
<i>Mimocopelates</i>	0	0	1	1	2	1	3	1	0	1	1	1	1	1
<i>Munneurycope</i>	0	1	1	0	0	0	0	0	0	3	1	1	0	0
<i>Munnopsurus</i>	?	1	0	0	0	0	0	0	0	0	0	1	-	-
<i>Paramunnopsis</i>	0	0	0	0	1	0	0	0	1	0	1	2	-	-
<i>Storhyngura</i>	0	0	0	0	0	0	0	1	0	0	0	0	-	-
<i>Tythocope</i>	0	0	1	0	0	0	1	0	0	1	1	1	-	-

See text for a description of the characters. Characters 24 and 25 were evaluated for only the Lipomerinae, *Acanthocope*, and *Munneurycope*. Character states that are not numbers: "B" = having both states, "?" = state unknown or indeterminate.

TABLE 7. (continued)

Character-Taxon data matrix of selected munnopsids used in phylogenetic analysis.

CHARACTER	13	14	15	16	16	17	18	18	18	19	19	20	21	21	21	22	23	23
PARSIMONY METHOD	W	W	W	C	C	W	C	C	C	W	C	W	C	C	C	C	C	C
A PRIORI WEIGHTS	1	1	2	2	2	1	1	1	1	2	1	2	1	1	1	1	1	1
SUCCESSIVE WEIGHTS	2	1	4	4	2	4	4	2	4	2	4	4	2	4	2	4	2	2
<i>Acanthaspidiidae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acanthocope</i>	0	1	0	0	0	0	0	0	0	?	0	0	0	0	0	1	1	1
<i>Amuletta</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Baeonectes</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0
<i>Bellibos</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
<i>Belonectes</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Betamorpha</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Coperonus</i>	0	1	0	0	1	0	0	1	0	1	0	0	1	0	0	1	1	0
<i>Disconectes</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Eurycope</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<i>Hapsidohedra</i>	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0
<i>Ilyarachna</i>	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
<i>Lionectes</i>	0	0	0	0	1	0	0	1	1	1	1	0	1	0	0	1	1	0
<i>Lipomera</i>	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0
<i>Mimocopelates</i>	0	1	1	0	1	1	0	1	1	1	0	0	1	0	0	1	1	0
<i>Munneurycope</i>	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	0
<i>Munnopsurus</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Paramunnopsis</i>	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1
<i>Storothyngura</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<i>Tythocope</i>	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0

Multistate characters have been factored to binary states. Character states that are not numbers: "B" = having both states, "?" = state unknown or indeterminate.

RESULTS OF PHYLOGENETIC ANALYSES

Munnopsid Cladograms

A variety of trees resulted from an extensive series of analyses using both PHYLIP and PHYSYS programs. None of them resulted in highly parsimonious trees: the homoplasy level varied from 42% to 67% more steps than one change per character: the a priori weighting scheme found trees that were 59 unweighted steps long, and the successive weighting trees had 60 unweighted steps. These parsimony values yield overall consistency indices of 0.61 and 0.60, respectively. Figures 39-40 show example trees from each of the weighting schemes used, illustrating the major differences in topology encountered in most analyses. Other trees found using the data were variations of these two trees. The shortest trees were derived from Wagner algorithms either using defined (55 steps) or undefined (51 steps) transformations for multistate characters. These strictly Wagner trees had topologies similar to the mixed parsimony method trees, but they were unacceptable because unlikely reversals occurred, such as the return of a lost dactylus on the pereopods. A greater variety of trees resulted from a compatibility method implemented by thresholds in ITERMIX, but too few characters were included in the trees for defining the important branches.

The two example trees in figures 39-40 show much homoplasy in the setation and reduction characters, but also in other characters. A notable convergence is the multiple derivation of the frontal arch from the incipient frontal arch. The incipient frontal arch of *Paramunnopsis* may be reinterpreted as a reduced form of the full frontal arch, thus shortening the trees by several steps. On the other hand, the distribution of frontal arch character states is not well known, especially in the other genera of the Munnopsidae *sensu stricto*. For this study, the interpretation of the frontal arch is not changed, but further research on variation in this character is desirable.

The trees permit predictions for the character states that have unknown or uncertain interpretations in specific taxa. *Amuletta* may have the advanced state of character 11 (pereopods III-IV much longer than pereopod II). *Munnopsurus* may have the primitive state of character 12 (unmodified pereopod II). *Betamorpha*, which shows both states of character 10 (0 or 1), should have the advanced state, pereopod III-IV bases short, assigned to its immediate ancestor; a reversion to unshortened bases then occurs within the genus. The female pleopod II of *Acanthocope* is probably derived from a pleopod that had a notch or cleft. Use of these predictions in the data does not change the form of the trees, although they may generate more parsimonious trees.

Interpretation of the Cladograms

The cladograms described above show a complexity that is somewhat difficult to interpret. Two questions arise at this point: Is the nesting hierarchy of these cladograms any more parsimonious than that of past classifications? How robust or meaningful are these results? The first question may be evaluated by generating a cladogram based on past classifications and comparing its parsimony and consistency to those in Figures 39 and 40. The second may be tested by using a bootstrap resampling algorithm on the data (Felsenstein 1985). Finally, a consensus tree shows the monophyletic groups that appear in all trees generated by the a priori and successive weights data.

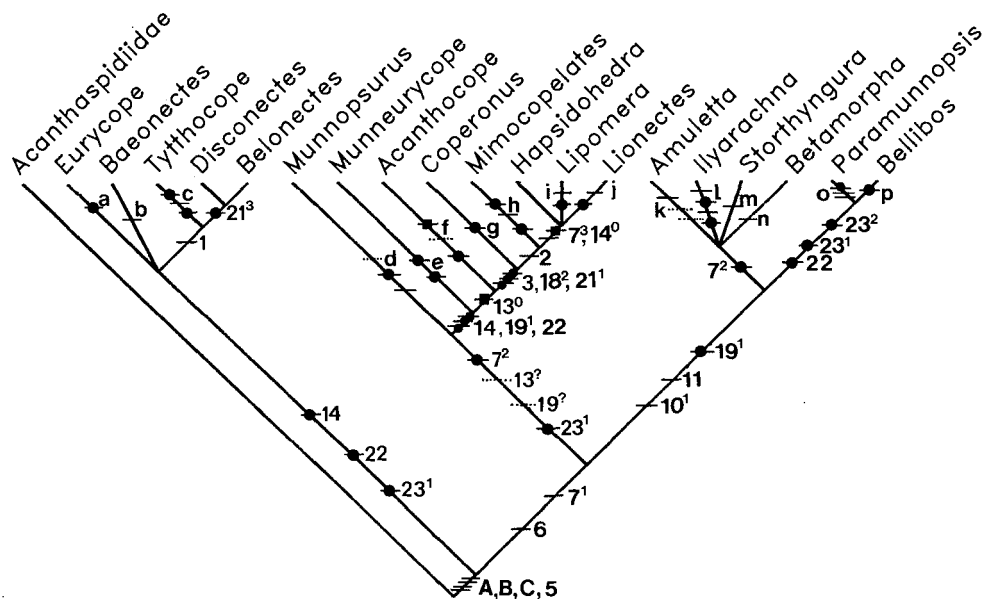


Figure 39. Cladogram of selected munnopsid genera. One of the trees generated using conservative a priori weights in the program ITERMIX. It has a parsimony value of 59 unweighted steps. Character meanings are described in text. The character changes - straight lines crossing branches - are marked to show where homoplasy has occurred: a closed circle is a convergence, and a closed square is a reversion. Character changes marked by dotted lines are uncertain changes. The character changes for the terminal taxa are indicated by lower-case letters. Their meanings are as follows: a = 21³; b = 21²; c = 3, 18¹, 21¹; d = 2², 13, 19⁰; e = 13, 21³; f = 5⁰, 19², 23²; g = 16²; h = 16², 17, 18³; i = 4, 18³; j = 16², 19²; k = 9, 11²; l = 8, 10², 12, 18²; m = 5⁰; n = 10⁰; o = 10², 16¹, 20; p = 7².

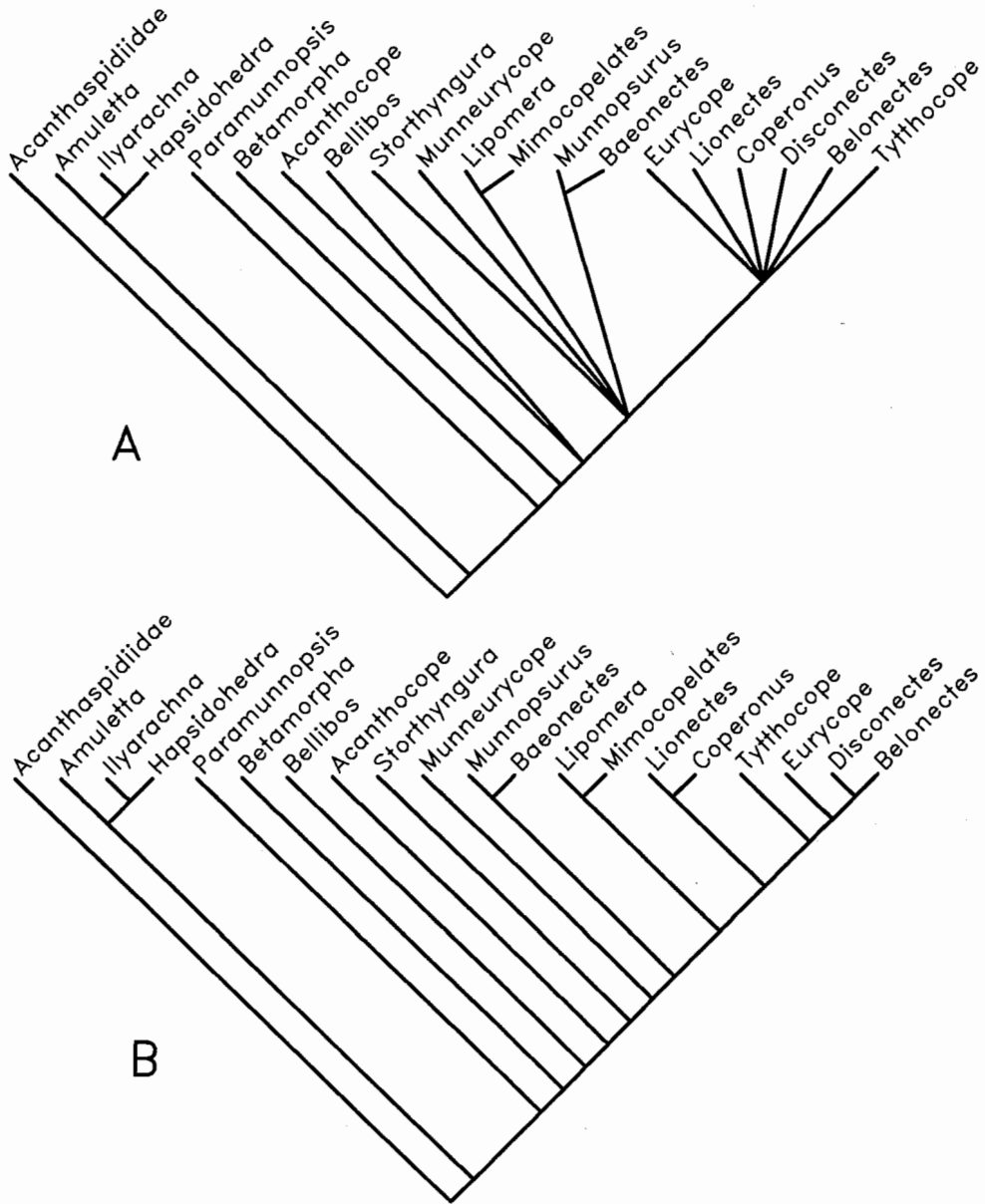


Figure 41. Cladograms based on hypothetical relationships derived from the literature. **A**, Cladogram with unresolved clades. **B**, Cladogram with clades resolved using PENNY to find the most parsimonious arrangements. Tree B requires 99 character changes using the data in Table 7.

4. Wilson and Hessler (1981) removed several new genera from *Eurycope* without establishing their relationships to other munnopsids. These are left as multiple sister groups of *Eurycope*.
5. Wilson and Hessler (1981) and Wilson (1982a) indicated that the genus *Baeonectes* was closely related to *Munnopsurus*, so these two genera were made sister groups.
6. Wilson and Thistle (1985) proposed that *Amuletta* was the sister group of the Ilyarachnidae.
7. *Hapsidohedra* is removed from *Ilyarachna* in this paper. The two genera are retained as sister groups.
8. *Coperonus* and *Lionectes* are removed from *Eurycope* in this paper; they are included in the polychotomy of *Eurycope* and its sister groups.

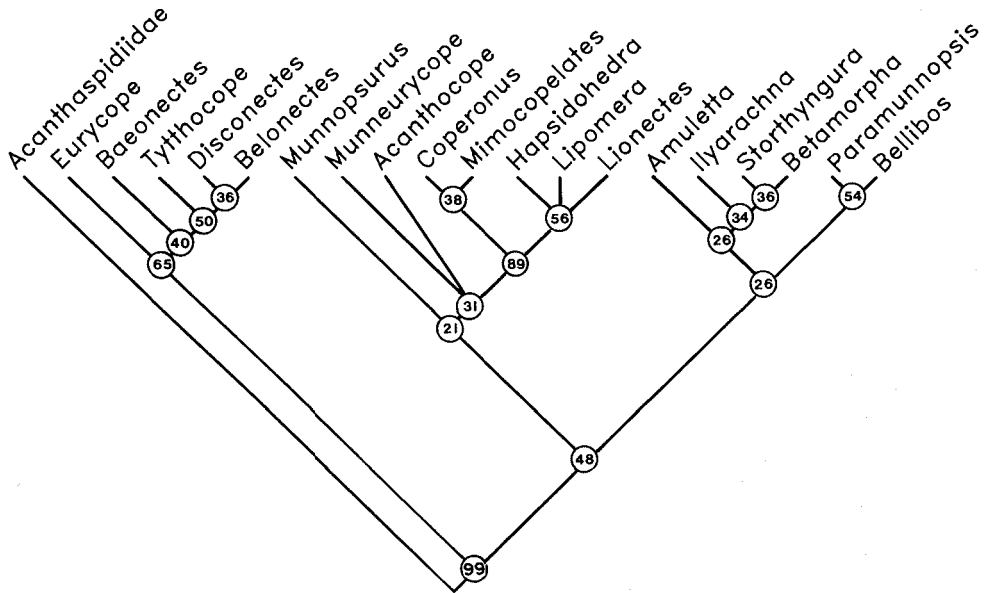


Figure 42. A tree based on 100 bootstrap estimates using the data in Table 7. The number in each circle indicates the frequency of the monophyletic group above each node. These frequencies are equivalent to the percentile confidence limits for the monophyletic groups.

These interpretations resulted in the unresolved cladogram shown in figure 41A. To find a more resolved and parsimonious topology of this tree, the polychotomous clades were analyzed with the PHYLIP program PENNY, resulting in the tree shown in figure 41B. The homoplasy level in this tree is high: 99 character changes are required, 2.75 times the number of steps in a one change per character tree. This is equivalent to an overall consistency index of 0.36. The new munnopsid trees have parsimony values (59-60 unweighted character changes) and consistency indices (0.60-0.61) that are two times better than those based on the previous classification. Nevertheless, the character set provided here is not sufficient to resolve all phyletic relationships between the munnopsids, as indicated by several multiply branching nodes.

Bootstrap Confidence Limits. The PHYLIP program BOOT (Felsenstein 1985) provides a measure of the robustness of the phylogenetic hypotheses described by the trees in Figures 39 and 40. One hundred bootstrap runs on the unweighted data set yielded the consensus tree shown in Figure 42, with the confidence levels for each monophyletic clade shown at its ancestral node. None of the clades exceed the 95% confidence level (for exact definition, see Felsenstein 1985), although the Lipomerinae appear most frequently (89%). This result indicates that none of clades has enough defining apomorphies to be insensitive to reevaluation of the characters, although the Lipomerinae are nearly in that category.

A Consensus Tree. Two runs of ITERMIX, using both weighting protocols, generated 140 trees similar to the those illustrated in figures 39 and 40. A strict consensus tree (Rohlf 1982) was derived using the program CONTREE. The resulting consensus tree had to be corrected for 0-length branches because PHYLIP programs generate only fully dichotomous trees (no polychotomes). The corrected consensus tree (Fig. 43) tree shows that the lipomerine taxa appear together in all trees resulting from both a priori and successive weighted data. The resolution of the remaining clades is decreased to a large polychotomy separated by two branching nodes from *Eurycope* and its allies. *Ilyarachna* clusters with two taxa previously thought to be closely related (*Betamorpha* and *Amuletta*), and with *Storhyngura*. Other relationships are poorly resolved, and will require more characters and more analysis.

Relationships Within the Lipomerinae

Because the subfamily Lipomerinae are reasonably well corroborated as a monophyletic group, phylogenetic relationships within the subfamily are evaluated. The munnopsid-level analysis indicates that *Munneurycope* or *Acanthocope* may be used as a sister group to the ilyarachnid-like eurycopids. Cladograms derived using either taxon were identical. The Lipomerinae were analyzed with the PHYLIP program PENNY, using the uropodal characters (Table 6). The tree shown in figure 44 is found regardless of the weighting

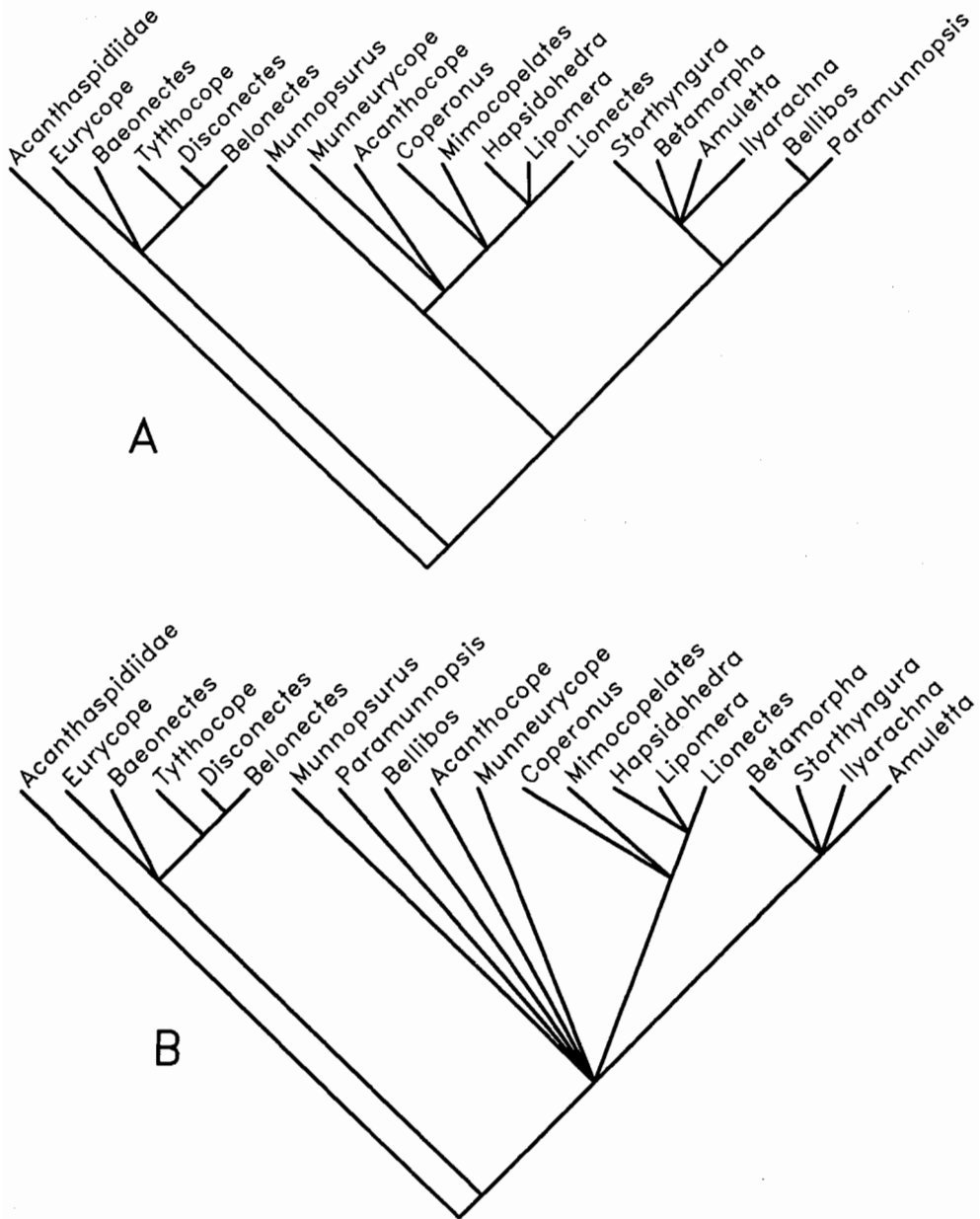


Figure 43. Strict consensus trees of the Munnopsidae *sensu lato* A. Consensus tree from 56 unique, fully bifurcating trees generated by the a priori weighting analyses. B. Consensus tree from 88 unique, fully bifurcating trees generated by the successive weighting analyses.

protocol used. This tree has a homoplasy level of 18% (3 extra steps in the 17 characters that change) and a consistency index of 0.85. The topology of this tree is identical to that of the lipomerine clade in the consensus tree (Fig. 43). Nevertheless, all these genera have many defining apomorphies; the reader is referred to the diagnoses in the taxonomy section. Two clades in the Lipomerinae are indicated by the cladogram (fig. 44): one contains *Coperonus* and *Mimocopelates*, and the other shows unresolved relationships between the genera *Hapsidohedra*, *Lipomera*, and *Lionectes*. The bootstrap confidence limits for these groups are so low that a formal classification for them is not warranted.

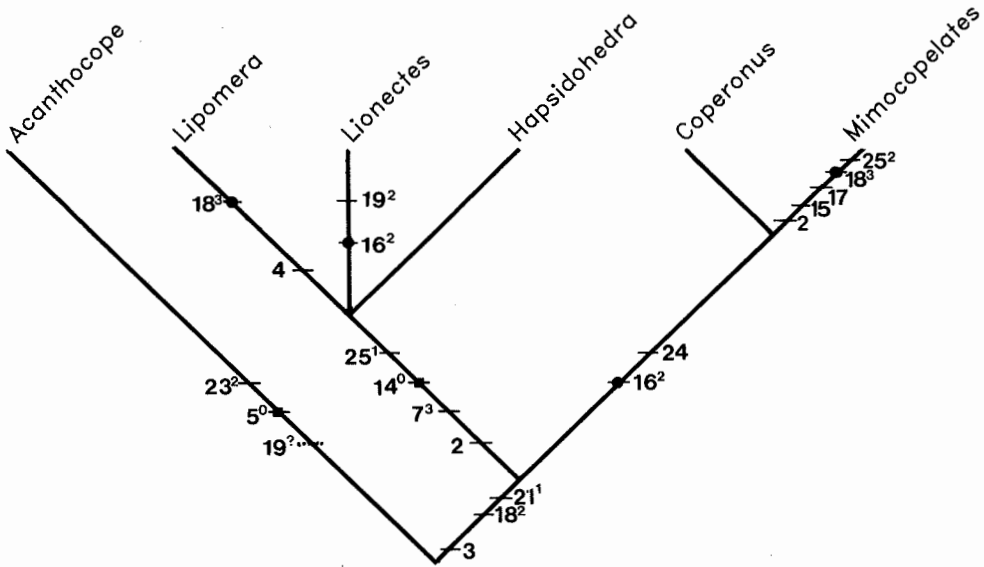


Figure 44. The cladogram of the Lipomerinae with *Acanthocope* as an outgroup. The tree is constructed using the data set in Table 7 and the added uropodal characters 24 and 25 (Table 6). Its parsimony value is 20 steps. The character changes - straight lines crossing branches - are marked to show where homoplasy has occurred: a closed circle is a convergence, and a closed square is a reversion that occurs in the general munnopsid cladogram. The character change marked by a dotted line is an uncertain change.

DISCUSSION AND PROPOSALS FOR A REVISED CLASSIFICATION

The Lipomerinae

The ilyarachnid-like eurycopids are the best corroborated monophyletic group within the Munnopsidae *sensu lato*. Their resemblance to the Ilyarachnidae results from convergent evolution in some characters, not to proximate common ancestry. The analysis confirms that they should be recognized as a munnopsid subfamily, for which I have proposed the name Lipomerinae, based on the available family name Lipomeridae Tattersall, 1905. The defining synapomorphies of the Lipomerinae are reduction of pereonite 7, loss or reduction of pereopod VII, and two or three setae on the exopod of pleopod IV. This subfamily also has characters that are characteristic of a larger subset of the munnopsids: a frontal arch, a cleft in the female pleopod, and no rostrum. The membership of this larger group is currently uncertain owing to the weakness of some dichotomies in the munnopsid cladogram.

The Munnopsidae and Its Subtaxa

Although definition of the Lipomerinae was the primary goal of this paper, other conclusions may be drawn that are relevant to munnopsid systematics. The sister group relationship between *Ilyarachna* and *Amuletta* proposed by Wilson and Thistle (1985) cannot be rejected on the basis of this analysis. The postulated close relationship between *Baeonectes* and *Munnopsurus* (Wilson and Hessler 1981; Wilson 1982a), however, is rejected.

Overall, the form of the munnopsid trees (Figs. 39 and 40) imply three large taxa, although some major branching nodes are based on homoplastic characters, such as those of the pleopods. The strict consensus trees (Fig. 43) show much less resolution than the cladograms in Figures 39 and 40. Nevertheless, the consensus trees demonstrate that the currently recognized family Eurycopidae is not monophyletic. In fact, eurycopid taxa such as *Storothyngura* and *Betamorpha* may have more synapomorphies with the Ilyarachnidae than they do with *Eurycope*. Previous classifications of the munnopsids that retained three separate families are not consistent with the phylogenetic consensus.

Because there are characters that define the Munnopsidae, I propose that the family Munnopsidae be re-expanded with the Eurycopidae and Ilyarachnidae placed within it as subfamilies. The other subfamilies of the Eurycopidae (Acanthocopinae, Bathyopsurinae, Syneurycopinae, and Lipomerinae) retain their current rank. This new classification for the Munnopsidae is presented in Table 8.

A great deal of justification can be found for this scheme. Members of this diverse family, as first recognized by Sars (1899), are united by basic swimming modifications. The defining synapomorphies of the Munnopsidae are: pereonites 5-7 enlarged, muscular, broadly joined, with the ventral nerve cord ganglia fused

TABLE 8.

A revised classification of the Munnopsidae and
the subfamily Lipomerinae.

Family Munnopsidae Sars, 1869

Subfamily Munnopsinae Sars, 1869

Munnopsis Sars, 1861
Acanthomunnopsis Schultz, 1978
Munnopsoides Tattersall, 1905
Paramunnopsis Hansen, 1916
Pseudomunnopsis Hansen, 1916

*Subfamily Acanthocopinae Wolff, 1962

Acanthocope Beddard, 1885

*Subfamily Bathyopsurinae Wolff, 1962

Bathyopsurus Nordenstam, 1955
Paropsurus Wolff, 1962

*Subfamily Eurycopinae Hansen, 1916

Eurycope Sars, 1864
Baeonectes Wilson, 1982
Belonectes Wilson and Hessler, 1981
Disconectes Wilson and Hessler, 1981
Tythycope Wilson and Hessler, 1981

Subfamily Ilyarachninae Hansen, 1916

Ilyarachna Sars, 1864
Aspidarachna Sars, 1899
Bathybadistes Hessler and Thistle, 1975
Echinozone Sars, 1899
Pseudarachna Sars, 1899

Subfamily Lipomerinae Tattersall, 1905

**Lipomera* Tattersall, 1905
Hapsidohedra n. gen.
**Lionectes* n. gen.
**Coperonus* n. gen.
Mimocopelates n. gen.

*Subfamily Syneurycopinae Wolff, 1962

Syneurycope Hansen, 1916
Bellibos Haugsness and Hessler, 1979

Incertae Sedis

Amuletta Wilson and Thistle, 1985
**Betamorpha* Hessler and Thistle, 1975
Microprotus Richardson, 1909
**Munneurycope* Stephensen, 1913
**Munnopsurus* Richardson, 1912
**Munnicope* Menzies and George, 1972
**Storthingura* Vanhöffen, 1914

The sequencing convention for displaying phylogenetic information in the classification (Wiley 1981) is not used for the genera; after the type-genus which is listed first, they are in alphabetical order. Subfamilies or unclassified genera marked with a "*" previously were placed in the family Eurycopidae. All subfamilies are *sedis mutabilis*.

into a single mass (Hult 1941); pereopods V-VII with many long, fully plumose setae and their carpi and propodi broadened and paddlelike; dactylar claws that enclose the distal sensillae in a hollow between the anterior and posterior claws; rami of pleopod III with many distal plumose setae; and broadened first articles of the antennulae. A formal diagnosis of the Munnopsidae is provided by Wilson et al. (in press). In addition, the subfamilies of the previous classifications are as different from one another as are the families, thereby making the hierarchical levels within the munnopsids incommensurate. The new classification in Table 8 is more natural than previous concepts: it places the previous families on the same level as the subfamilies, and it recognizes the basic monophyly of the munnopsids. Several classificatory problems remain, however, which require the incorporation of some of the previous munnopsid taxonomic structure. The systematic position of the genera assigned to the subfamily Eurycopinae presents the greatest problems.

The Eurycopinae and the Composition of the Subfamilies

The consensus tree of the Munnopsidae *sensu lato* forces a reconsideration of the composition of the subfamily Eurycopinae. Wolff (1962) placed the following genera in this subfamily: *Eurycope*, *Lipomera*, *Munneurycope*, *Munnopsurus*, and *Storthyngura*. Several new genera have been added since his paper, rendering the subfamily morphologically diverse. Wilson and Hessler (1981) added the genera *Disconectes*, *Belonectes*, and *Tyththocope*, and Wilson (1982a) added *Baeonectes*. Menzies and George (1972) ignored Wolff's classification when they erected *Munnicope*, so by default, perhaps, it should be placed in this subfamily. *Microprotus* Richardson, 1909 has been considered a member of the Janiridae (Wolff 1962), even though it clearly has been derived from an ancestor of *Storthyngura* (Wilson et al. in press). As proposed above, *Lipomera* is assigned to the Lipomerinae Tattersall, 1905, thereby simplifying the Eurycopinae somewhat.

Eurycope, and the genera with which it clusters (Fig. 43), lack the derived characters seen in the remainder of the munnopsid taxa: they retain a rostrum and lack a frontal arch (see Table 6). This presumptive monophyletic group is primarily defined by apomorphies that independently appear elsewhere on the tree, e.g., the pleopodal setation characters. The relationships within the group containing *Eurycope* may be subject to reinterpretation with further analysis, although *Disconectes*, *Belonectes*, and *Tyththocope* may form a natural taxon with the defining apomorphy of dorsally fused pereonites 5 and 6. Nevertheless, the strict consensus tree shows a relatively well resolved clade that includes *Eurycope*. Therefore I propose that the Eurycopinae be limited to *Eurycope* and the four genera with which it clusters: *Baeonectes*, *Tyththocope*, *Disconectes*, and *Belonectes*.

The remaining genera of the Eurycopinae *sensu lato* are each quite distinctive and therefore are difficult to place. Two genera included in the

analysis, *Munneurycope* and *Munnopsurus*, appear in the consensus tree at a low, unresolved level. *Munnicope* may be closely related to *Munnopsurus*, especially in the natasomal characters, but this has yet to be firmly established. As mentioned above, *Microprotus* is probably derived from a *Storthyngura*-like ancestor. *Storthyngura* may have some similarities to *Acanthocope* (Acanthocopinae; compare, for example, *S. brachycephala* Birstein, 1957 and *Acanthocope curticauda* Birstein, 1970). The consensus tree (Fig. 43), however, indicates that this resemblance may be superficial. On the other hand, the Ilyarachnids, represented by *Ilyarachna*, are a distinctive phylogenetic unit (Thistle and Hessler 1976) that should not be placed in the same subfamily with the remaining genera of its consensus clade (Wilson and Thistle 1985), which includes *Storthyngura*.

In view of the remaining difficulties in munnopsid systematics, this solution for the classification of the eurycopine genera must be temporary. The alternative, a classification based strictly on the consensus tree in figure 43, would be misleading and unstable. Consequently, only the best corroborated parts of the consensus tree, the Eurycopinae *sensu stricto* and the Lipomerinae, are used. The remaining eurycopine genera are *incertae sedis*. New subfamilies for *Munneurycope*, for *Munnopsurus* and *Munnicope*, and for *Storthyngura* and *Microprotus* are not warranted by the data used here. A final solution to this classificatory problem awaits the revision of most of the genera listed in subfamily *incertae sedis*. The need for revision is greatest in the genus *Storthyngura*, which contains at least two genus-level taxa (Wilson et al. in press).

In the new classification, the compositions of the non-eurycopine subfamilies are retained along with the new subfamilies demoted from family status the Munnopsinae and the Ilyarachninae. Some taxa suggested by the consensus tree are not used. The Munnopsinae and the Syneurycopinae are maintained as separate taxa because many autapomorphies distinguish them (Wolff 1962; Haugness and Hessler 1979). Generally speaking, the Munnopsinae are light-bodied, demersal benthic to holopelagic animals with enlarged swimming legs, and the Syneurycopinae include narrow, heavy-bodied, benthic animals that have reduced swimming legs and natasomes. For the classification of the Ilyarachnine clade (Fig. 43), I favor *Amuletta* as its sister group, but other genera in this clade of the consensus tree share the same hierarchical level. The Ilyarachninae are separate from the remaining genera, which are temporarily assigned to *incertae sedis*.

Other Hierarchies?

The existence of a family as large as the Munnopsidae with its 7+ subfamilies and 30+ genera creates a taxonomic difficulty for the classification of the superfamily Janiroidea: the family-level taxa no longer seem coordinate, due to the variety of morphologies they subsume. All other Janiroidean families have

characters by which genera can easily be allocated to the proper family. Moreover, most other families have a reasonable number of genera, although some taxa, such as *Haploniscus* and *Ischnomesus*, will be or already have been subdivided by revisions (e.g., Lincoln 1985a, 1985b).

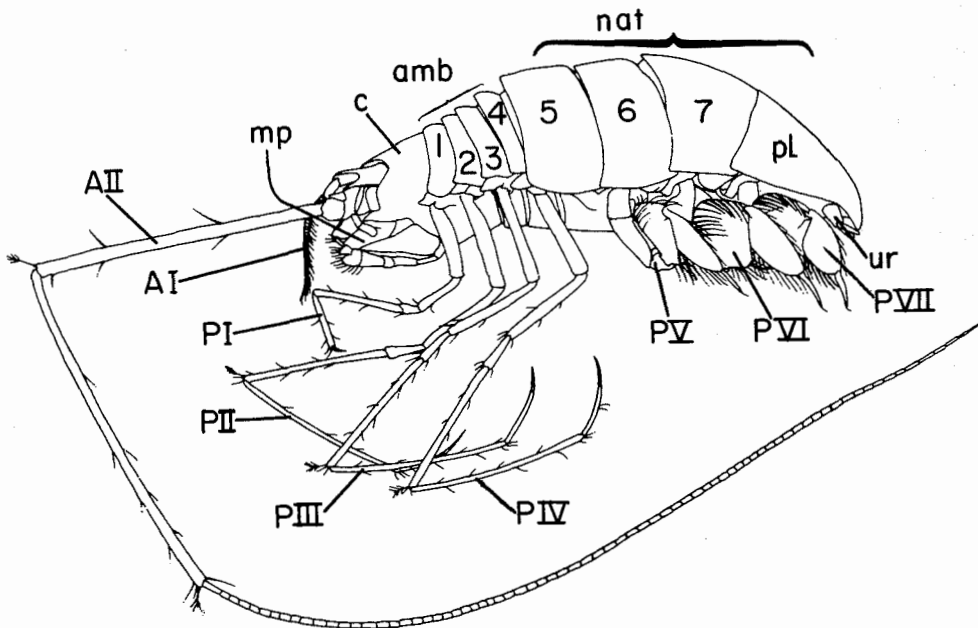
An alternative to my proposed classification would be to make each of the munnopsid subfamilies a family. To address the monophyly of the 7+ families thus created, a new taxonomic level in the janiroidean hierarchy between superfamily and family would have to be recognized. Such a proposal, which parallels that of Hult (1941), has its merits: known monophyletic groups of families in the Janiroidea (Wilson 1985, 1987) could be recognized by a "sub-superfamily" hierarchical level. For example, the families Nannoniscidae and Desmosomatidae have much in common (Siebenaller and Hessler 1977, 1981) and may represent such a "sub-superfamilial" taxon. Other candidates for being sister groups at the family level are: the Munnidae and the Santiidae (Wilson 1980b), the Paramunnidae and the Abyssianiridae (ibid.), and the Dendrotiidae and the Haplomunnidae (Wilson 1976). Unfortunately, the higher level relationships among the deep-sea isopod families are still poorly understood, so such a classification cannot be attempted at this time.

The failure to resolve the relationships of the subfamilies of the Munnopsidae *sensu lato* is not surprising in view of the morphological diversity of the included taxa. Such a variety of munnopsids probably did not arise in a short period of time. In a preliminary estimate of the phylogeny of the Janiroidea, the Munnopsidae branch off from the other deep-sea isopods within only a few branching nodes of their origin (Wilson 1985); other highly diverse taxa such as the Desmosomatidae and the Nannoniscidae are derived much later. The Munnopsidae may have had a long evolutionary history, during which they invaded most niches in the deep-sea benthos that are open to natatory Crustacea.

APPENDIX 1

GENERAL MUNNOPSISID EXTERNAL MORPHOLOGY

The morphology of a typical munnopsid, *Eurycope ipthima* Wilson (1981), in lateral view with anterior to the left. This figure is provided to illustrate some of the morphological terms defined in Appendix 2. The main body parts are the cephalon (**c**); ambulosome (**amb**), which is made of pereonites (segments of the thorax bearing legs) 1-4 (numbered in the figure), and the natasome, which is made of pereonites 5-7 (numbered in the figure) and the pleotelson (**pl**). The limbs from anterior to posterior are the antennula (**AI**), the antenna (**AII**), the mouth parts (**mp**) with only the mandible and maxilliped externally visible, the ambulatory pereopods (**PI-IV**); the natatory pereopods or natapods (**PV-VII**), and the uropod (**ur**). The limbs of the pleotelson - the pleopods, are obscured in this view by the natapods.



APPENDIX 2

A GLOSSARY OF MORPHOLOGICAL TERMS

This glossary contains definitions of crustacean morphological terms. Many definitions are specific to the study of isopod taxonomy, with an emphasis on the asellote superfamily Janiroidea, but some more general definitions are included for completeness.

Aesthetasc. A long, tubular, sensory seta having thin cuticle, found on the antennula or antenna. Aesthetascs may have a chemosensory function, because males generally have many more of these structures than females.

Ambulosome. The part of the thorax of munnopsid isopods that bears the walking legs. It consists of pereonites 1-4. (See Appendix 1.)

Ambulosomite. A body segment of the ambulosome. (See Appendix 1.)

Antenna (synonym, **second antenna**). The second, paired, cephalic appendage. It consists of four short, robust, proximal segments, two long, intermediate segments, and a long series of tapering annuli, called the flagellum. The third basal segment bears a smaller, lateral appendage called the antennular scale that is homologous to the exopod in other Crustacea. (See Appendix 1.)

Antennula (synonyms **first antenna**, **antennule**). The first paired cephalic appendage. In munnopsids, it consists of a wide, flattened basal segment, two segments of intermediate thickness, and distal annular segments of varying lengths. The most distal segments generally bear aesthetascs. (See Appendix 1.)

Appendix masculina. An alternative name for a styletlike copulatory structure on the male pleopod II. This structure is not homologous to similarly named structures found in non-isopod Eumalacostraca.

Article. A segment of any limb, but usually applied to the antennula or antenna.

Basis (plural **bases**). The second segment of a thoracic limb. See pereopod.

Biarticulate. Consisting of two articles or segments.

Bifid. A structure with two distal tips, as in *unequally bifid seta*.

Biramous. Having two branches, a typical condition for most primitive crustacean appendages.

Brooding Female. An adult female with fully extended oostegites on the coxae. In specimens from deep-sea samples, the developing embryos are often lost during sample processing, so it is generally not possible to tell whether the female was *in fact* brooding embryos, or whether she released the young before sampling.

Broom seta. A sensory seta that has a distinctly articulated pedestal, and two distal rows of long, extremely thin setules. It may be found on the antennulae or any of the pereopods.

Carpus (synonym **carpopodite**). The fifth segment of a thoracic limb. See pereopod.

Cephalic Dorsal Length. The length of the cephalon measured in a straight line along the dorsal midline from the posterior edge to the anterior vertex or rostrum, depending on which is present. (See Fig. 4.)

Cephalon. The head, or anteriormost body unit. In isopods, the cephalon bears the eyes, mouth, antennulae, antennae, and four pairs of mouthparts (mandibles, maxillulae, maxillae, and maxillipeds). (See Appendix 1.)

Chaetotaxy. The form, number, and shapes of the setae.

Circumgnathal. Around the biting or grinding surface, as in *circumgnathal denticles*.

Claw. A modified seta found on the distal segment of the walking legs that is heavily sclerotized and has a sharp tip.

Cleaning setae. Unusual setulate setae used to clean the antennae or antennulae. These setae are located on the distal segment of the mandibular palp.

Clypeus. An unpaired dorsal unit of the cephalon bearing the labrum medially and the mandibular fossae laterally. The fossae articulate with the dorsal condyle of the mandibles. (See Figs. 4, 38.)

Condyle. A heavily sclerotized projection of the mandible's dorsal surface that articulates with the cephalon in the clypeal fossa. (See Fig. 4.)

Copulatory Male. A fully adult male. In the janiroidea isopods, the male is identified by a sperm tube on the second pleopod's stylet, which is open at its sharp distal tip. In some specimens at this terminal stage, the vas deferens is visible through the cuticle connecting to the penile papilla.

Coxa. The first or basal segment of a thoracic appendage. See **pereopod**.

Cusplate. Having a sclerotized surface or margin with one or more rounded projections.

Cuticular. Of the cuticle.

Cuticular combs. Tiny, arc-shaped or linear groups of cuticular spines, most easily seen on the distal parts of the mandibular palp. They may occur elsewhere on the cephalic appendages.

Cuticular organ. The paired female copulatory organ of Asellota, found either ventrally or on the anterior dorsal margin of pereonite 5.

Dactylus (synonyms **dactyl**, **dactylopodite**). The seventh or distal segment of a thoracic appendage, bearing one or more distal claws. See **pereopod**.

Denticle. A short, pointed, toothlike projection of the cuticle.

Denticulate. Having denticles.

Denticulate seta. A generally robust seta with either a row of denticles or a group of distal denticles.

Dorsum (plural **dorsa**). The dorsal surface of a body segment.

Dorsal Orifice. The distal opening of the sperm tube in the janiroidean male's first pleopod.

Endopod (synonym **endopodite**). The medial or interior ramus of a crustacean appendage. In the Isopoda, another name for a thoracic appendage (exclusive of the coxa and basis), although more typically applied to the inner ramus of a pleopod or a uropod.

Epimere. A lateral fold of a somite's integument dorsal to the limbs. Sometimes called the pleurite or tergal fold.

Epipod (synonym **epipodite**). Laterally directed lobe (exite) of the basal segment (coxa) of the maxilliped.

Exopod (synonym **exopodite**). The lateral or exterior ramus of a crustacean basis. In the Isopoda, applied to the outer ramus of a pleopod or a uropod.

Fan seta. A specialized seta on the distal tip of the maxilliped's endite. It is made of thin, hyaline cuticle (difficult to see) and is usually broad with many laterally pointed lobes. In the munnopsids, it appears as two distinct types: a medial, more heavily sclerotized seta with fewer lobes, generally found on the distomedial corner of the maxillipedal endite; and a thin lamellar form placed in a row just proximal to the distal edge of the endite.

Flagellum (plural **flagella**). The long, tapering distal part of either the antennula or antenna, generally made of many annuli.

Foliaceous. Leaflike.

Fossa. A ventral trough in the clypeus into which the mandible's condyle articulates. (See Fig. 4.)

Frons. The anterior part of the cephalon bearing the clypeus. It is found between the antennulae and antennae, and below the rostrum or vertex. (See Figs. 4, 38.)

Frontal arch. A thickening of the cephalic frons that provides a strengthened arch between the fossal regions of the clypeus on either side of the frons. Generally associated with enlarged and heavily sclerotized mandibles. (See Figs. 4, 38.)

Geniculate. Kneelike, or displaying an acute angle between two segments. As in *geniculate* segments 2 and 3 of the antennula.

Gnathal. Of the biting or grinding surface on the mandible.

Habitus. Appearance of the whole animal.

Hemiplumose. A modified form of the plumose seta in which setules are found in a row on only one side.

Incisor Process. The distal biting part of the mandible that typically bears one or more pointed cusps. On its medial side, it bears the *spine row*.

Indurate. Heavily sclerotized or calcified, and often rough.

Instar. A discrete stage in a growth series, delimited by successive molting.

Interantennular. Between the antennae.

Ischium (plural *ischia*; synonym **ischiopodite**). The third segment of a thoracic appendage. See **pereopod**.

Labrum. An unpaired, flat segment of the cephalon that articulates with the clypeus, and anteriorly covers the mandibles.

Lacinia Mobilis (or **Lacinia**). An enlarged, nearly articulated spine of the mandible's spine row that is adjacent to the incisor process. It is found only on the left mandible. On the right mandible, it is replaced by a large spine similar in shape to the more posterior members of the spine row.

Lamella. A broad, flattened appendage.

Locking Folds, Dorsal. Paired projections of the male's first pleopod's dorsal cuticle. They form a seat for the medial edge of the second pleopods, allowing both pairs of pleopods to function together during mating or as an operculum.

Manca. In isopods and certain other Peracarida, one of the first three stages or instars of the postmarsupial life cycle, wherein the seventh pereopod is absent or rudimentary. In some janiroideans (e.g., *Lipomera*) this condition is retained in the adult; for these taxa, the manca stage cannot be identified by an absence of the last pereopod.

Mandible. The third cephalic appendage, and first mouthpart appendage of isopods. It generally has a lateral three-articled palp and is made up of the following functional regions: incisor process, spine row, molar process, dorsal condyle, and posterior articulation.

Marsupium. A ventral pereonal enclosure on females for developing embryos. It is composed of oostegites projecting medially from the coxae of the anterior pereopods (Pereopods I-VI in the munnopsids).

Maxilla (plural *maxillae*, synonym **second maxilla**). The third paired mouthpart and fifth cephalic appendage. In the Janiroidea, it consists of a basal segment bearing three setose lobes.

Maxilliped. Paired appendage on the posterior and ventral edge of the cephalon. Actually it is the first thoracic appendage, but its body somite is fused into the cephalon, and it is modified for feeding. It consists of the following functional parts: coxa, basis bearing a flattened and setose endite, palp with five segments (ischium, merus, carpus, propodus, dactylus), and epipod attached laterally to the coxa.

Maxillula (plural **maxillulae**, synonyms **maxillule**, **first maxilla**). The second mouth part and fifth cephalic appendage. In the Janiroidea, it consists of two setose lobes: a large outer lobe armed with robust, toothlike setae; and a smaller inner lobe with only small setae.

Merus (plural **meri**; synonym **meropodite**). The fourth segment of a thoracic appendage. See **pereopod**.

Molar Process. A medial process of the mandible. In the plesiomorphic condition, it has a broad, distal, triturating surface with circumgnathal denticles, a posterior row of broad, setulate setae, and sensory pores on the distal surface. (See Fig. 5H.)

Natapod. A natatory pereopod of a munnopsid janiroidean, the fifth through seventh pereopods. (See Appendix 1.)

Natasome. The often posteriorly streamlined body section of a munnopsid janiroidean consisting of the following body segments: heavily muscularized pereonites 5-7, and the pleotelson. (See Appendix 1.)

Natasomite. A pereonite of the natasome. (See Appendix 1.)

Oostegites. Lamellar lobes of cuticle extending medially from the coxa of an adult female isopod. They may be seen in two forms: developing oostegites are small fat lobes that do not cross the ventral midline; oostegites of the brooding female are broad, long lamellae that overlap on the ventral midline, forming a marsupium for the developing embryos.

Operculum (female pleopod[s] II). A plate over the branchial chamber of the abdomen of female janiroideans, consisting of the fused second pleopods. The first pleopods are absent in female Janiroidea. In males, pleopods I and II lock together to form an operculum somewhat similar to that seen in the females.

Ovigerous. Bearing developing embryos in the marsupium.

Palp. A lateral appendage of the mandible or the maxilliped.

Paragnaths (synonyms **paragnathae** or **lower lips**). A pair of ventral projections of the cephalic cuticle just posterior and medial to the mandibles. Each projection has two lobes, a broad lamellar outer lobe with hairlike setae on the inner margins and a thick inner lobe covered with many hairlike setae.

Paucisetose. Having few setae.

Pedestal seta. A spinelike seta that is raised above the dorsal surface of the body by a pedestal-like outpocketing of the cuticle.

Penile papillae (or **penes**). Male cuticular projections on the posterior and medial margin of the seventh pereonite of janiroidean isopods. They contain the openings of the vasa deferentia.

Pereon. Thoracic segments 2-8 bearing the locomotory appendages, or pereopods. (Thoracic segment 1 is part of the cephalon and bears the maxilliped.) (See Appendix 1.)

Pereonite. A segment of the pereon. (See Appendix 1.)

Pereopod. One of the seven pereonal appendages. Consists of the following segments: coxa, basis, ischium, merus, carpus, propodus, dactylus. The coxa of adult female bears oostegites. The distal five podomeres are homologous with the endopod of the more primitive biramous thoracic limb of other Crustacea. (See Appendix 1.)

Pleotelson. The abdominal part of the body, consisting of a short segment (pleonite 1) and a long and broad segment. The large segment is made of the fused more posterior pleonites and the telson, a terminal segment bearing the anus. Primitively, there are six pleonites; the anterior five bear ventral pleopods, and the sixth bears the uropods. In the Janiroidea, only the first pleonite is expressed as a free segment. (See Appendix 1.)

Pleonite. A segment of the pleotelson. (See Appendix 1.)

Pleopod. One of the five paired, biramous, ventral limbs of the pleotelson. In unmodified form, it consists of a basal segment - the protopod - and two distal rami called the endopod and the exopod. The rami may be biarticulate. Female Asellota lack the first pleopods. In male Asellota, the first pleopods are present only as uniramous structures (fused into a single elongate plate in the superfamily Janiroidea). The rami of the male second pleopod are modified as copulatory structures. Pleopods III-V have very thin cuticle and function as gills (branchiae).

Pleopodal cavity. The deeply concave ventral surface of the pleotelson that encloses the pleopods dorsally and laterally. Because the more posterior pleopods function as gills, the pleopodal cavity is sometimes called the branchial cavity.

Plumose seta. A featherlike seta that has two dense rows of thin, long setules beginning at the base of the seta and continuing to the tip.

Podomere. A segment of a crustacean appendage.

Preanal ridge. A raised, transverse ridge on the ventral surface of the pleotelson situated between the pleopodal (or branchial) cavity and the anus. In some munnopsids, this ridge becomes very large.

Preparatory female. An adult female that has developing oostegites and is in the instar just before the brooding condition.

Protopod (synonym **protopodite**). The basal segment of the pleopods and the uropods. It consists of the fused coxa and basis of the crustacean limb.

Propodus (plural **propodi**). The sixth segment of a thoracic appendage. See pereopod.

Quadrangular. Having a truncate distal margin at approximately right angles to the lateral sides.

Ramus (plural **rami**). A branch of an appendage.

Receptaculi (synonym **coupling hooks**). Modified setae that have bulbous recurved and denticulate tips. They are located on the medial margin of the maxilliped's basal endite and couple with their paired counterparts so that both maxillipeds can act as a single unit.

Recurved. Curved back on itself.

Rostrum (plural **rostra**). A projection of the cephalic frons that may also include the dorsal surface of the cephalon.

Sclerotized. With thick and sometimes calcified cuticle.

Sensilla (plural **sensillae**). A modified seta found on the dactylus of the pereopods. It is similar to an aesthetasc, but has a heavier cuticle that is covered with many tiny lobes (often only visible in a scanning electron micrograph).

Sensory Pore of the mandibular molar. A small pit in the distal surface of the mandible's molar process that can be seen to connect internally to a nerve process.

Serrate. Having a row of short, toothlike denticles.

Seta (plural **setae**). A cuticular process that is clearly articulated with the basal cuticle. This structure comes in many forms. Some authors call heavily sclerotized setae "spines," even though there are smaller counterparts of the same form named "setae" by the same authors. "Spinose seta" or "spinelike seta" is more accurate.

Setulate seta. A seta with one or more rows of setules. It is different from plumose or hemiplumose setae in that the row is limited to a section of the shaft, and does not extend from base to tip.

Setule. A spine on a seta.

Sperm Tube. A structure found only in male janiroidean Asellota taking one of two forms: 1. A cuticular tube in the stylet (distal segment of the endopod) of the male second pleopod, consisting of a ventral opening to a rounded chamber in the center of the stylet and a confluent tube to the tip of the stylet; 2. A cuticular tube formed by the medial fusion of the male first pleopods, consisting of a funnel-like proximal opening often covering the penile papillae and a confluent tube to a dorsal orifice roughly one quarter the length of the pleopods from their tips. During copulation, both tubes may form a single channel from the penile papillae to the female's cuticular organ.

Spermatheca. A sperm reservoir inside the female oviduct, with an opening to the cuticular organ.

Spine. A pointed outpocketing of the cuticle that is confluent with the cuticle at its base (not articulated).

Spine row, mandibular. A row of spines on the medial side of the mandible's incisor process. The lacinia mobilis on the left mandible is actually an enlarged member of the spine row.

Sternite. The ventral surface of a thoracic body segment.

Subchelate. Having the ability to grasp by folding together two adjacent podomeres of a limb.

Support ridge, posterior mandibular. A cuticular ridge on the body of the mandible that is a continuation of the dorsal condyle, but does not articulate with the fossa in the clypeus.

Supraclypeal. Above the clypeus.

Sympod (synonyms **protopod**, **protopodite**). An appendage segment made of the fused basis and coxa.

Telson. The terminal segment of a crustacean's body, bearing the anus. In most isopods, the telson is fused to the anterior pleonite.

Tergite. The dorsal surface of a body segment.

Thoracic. Of postcephalic segments 1 through 8.

Tridentate. With three denticles.

Triturating surface. The truncate distal surface of the mandible's molar process.

Unequally Bifid seta. A seta that is often spinelike and has a smaller thin seta or hair just proximal to its tip. The hair has a nerve extending into the cuticle and is probably the external expression of a sensory nerve.

Unguis (synonym **claw**). A modified seta on the tip of the dactylus.

Uniarticulate. With only a single segment.

Uniramous. With only a single branch.

Uropod. The terminal appendage of the body, belonging to the sixth pleonite. It consists of a basal segment - the protopod - and two uniarticulate rami - an endopod and an exopod.

Venter. The ventral side of the body.

Vertex. The anterior and medial margin of the cephalic dorsal surface.

Vas deferens. Male duct from the testis to the penile papilla for the passage of sperm.

Whip seta. Similar to the unequally bifid seta, except more slender. The sensory hair on the distal tip is long and curved.

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