

UNIVERSITY OF CALIFORNIA

SAN DIEGO

The Systematic Position of the Ilyarachnoid Eurycopidae

(Crustacea, Isopoda, Asellota)

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Marine Biology

by

George D.F. Wilson

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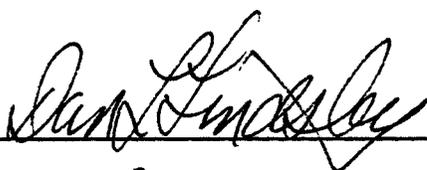
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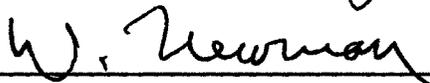
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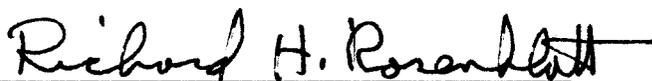
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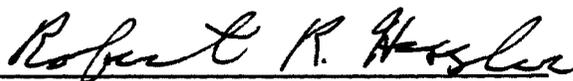
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Chairman

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To Kath,
Mom and Dad,
Judie and Jackie
and the Fur Babies.

TABLE OF CONTENTS

	Page
List of Figures	ix
List of Tables	xii
Acknowledgments	xiii
Vita	xvii
Abstract	xxi
1. An Introduction to deep-sea isopods and the systematic problems in the classification of the ilyarachnoid Eurycopidae (Crustacea, Isopoda, Asellota)	1
1.1. Introduction.....	1
1.2. The munnopsoid families and the ilyarachnoid Eurycopidae ..	11
1.3. Synopsis of the thesis	23
2. The taxonomy of the ilyarachnoid Eurycopidae	27
2.1. Introduction	27
2.2. Materials and methods	27
2.2.1. Sources of specimens	27
2.2.2. Reporting and use of ratios	32
2.2.3. Definition of taxa and morphological terms	33
2.2.4. Preparation and illustration of specimens	35
2.3. Taxonomy	37
2.3.1. <u>Coperonus</u> new genus	37
2.3.2. <u>Coperonus comptus</u> new species	42
2.3.3. <u>Coperonus nordenstami</u> new species	54
2.3.4. <u>Hapsidohedra</u> new genus	55
2.3.5. <u>Hapsidohedra ochlera</u> new species	61
2.3.6. <u>Hapsidohedra aspidophora</u> (Wolff, 1962)	74
2.3.7. <u>Lionectes</u> new genus	78
2.3.8. <u>Lionectes humicephalotus</u> new species	84
2.3.9. <u>Lipomera</u> Tattersall, 1905a	95
2.3.10. <u>L.</u> (<u>Lipomera</u>) new subgenus	101
2.3.11. <u>L.</u> (<u>Lipomera</u>) <u>lamellata</u> Tattersall, 1905a	101
2.3.12. <u>L.</u> (<u>Paralipomera</u>) new subgenus	103
2.3.13. <u>L.</u> (<u>Paralipomera</u>) <u>knorrae</u> new species	103
2.3.14. <u>L.</u> (<u>Tetracope</u>) new subgenus	117
2.3.15. <u>L.</u> (<u>Tetracope</u>) <u>curvintestina</u> new species	117
2.3.16. <u>Mimocopelates</u> new genus	134
2.3.17. <u>Mimocopelates longipes</u> new species	139
2.3.18. <u>Mimocopelates anchibraziliensis</u> new species	154

TABLE OF CONTENTS, continued

	Page
3. <u>Amuletta</u> , a new genus for <u>Ilyarachna abyssorum</u> Richardson (Isopoda, Asellota, Eurycopidae)	166
3.1. Abstract	166
3.2. Introduction	167
3.3. Materials and Methods	168
3.4. The systematic position of <u>Ilyarachna abyssorum</u>	169
3.5. <u>Amuletta</u> new genus	178
3.6. <u>Amuletta abyssorum</u> (Richardson)	180
3.7. Acknowledgments	190
4. An outgroup for the munnopsoid families: phylogenetic analyses of the suborder Asellota and the superfamily Janiroidea	191
4.1. Introduction	191
4.2. Materials and Methods	192
4.2.1. Specimens	192
4.2.2. Data on janiroidean character states	194
4.2.3. Phylogenetic techniques	195
4.3. A redescription of <u>Pseudojanira stenetrioides</u> Barnard	200
4.3.1. Introduction	200
4.3.2. Pseudojaniridae new family	203
4.3.3. <u>Pseudojanira stenetrioides</u> Barnard, 1925	204
4.3.4. Discussion	209
4.4. The female reproductive apparatus of the Asellota	212
4.4.1. Introduction	212
4.4.2. A survey of the female reproductive apparatus	217
4.4.3. Character states of the cuticular organ	232
4.5. Character analysis of the asellotan superfamilies	237
4.5.1. Introduction	237
4.5.2. Superfamily classification and taxa used	238
4.5.3. The characters and their states	238
4.5.4. Results of the character analysis	254

TABLE OF CONTENTS, continued

	Page
4.6. A preliminary phylogenetic analysis of the Asellota	258
4.6.1. Previous phylogenies	258
4.6.2. Results of the phylogenetic analysis	258
4.6.3. Discussion	263
4.6.4. Implications for the classification of the Asellota ...	268
4.6.5. Evolution of Reproductive Structures	269
4.7. Phylogenetic analysis of the Janiroidea	271
4.7.1. Introduction	271
4.7.2. Taxa used	271
4.7.3. Choice and scoring of characters	275
4.7.4. Character analysis	279
4.7.5. The results of the character analysis	293
4.7.6. The phylogenetic analysis	298
4.7.7. Discussion	304
5. A proposed phylogeny and classification of the munnopsoid taxa with special reference to the ilyarachnoid Eurycopidae .	306
5.1. Introduction	306
5.2. Taxa Used	307
5.3. Methods	308
5.4. Character analysis of the munnopsoid taxa	310
5.4.1. Fusion of the natasomal segments	311
5.4.2. Comparative sizes of the natasomal pereonites	312
5.4.3. Midgut	313
5.4.4. Clypeus	316
5.4.5. Rostrum	316
5.4.6. Frontal arch	317
5.4.7. Mandible	318
5.4.8. Ambulatory pereopods	319
5.4.9. Natatory pereopods V-VII	320
5.4.10. Cleft in the tip of female pleopod II	323
5.4.11. Pleopods III-IV	324
5.4.12. Uropods	325
5.4.13. Results of the character analysis	327
5.5. Results of the phylogenetic analysis	332
5.5.1. The estimated phylogeny	332
5.5.2. Discussion and proposals for a revised classification .	335
5.6. Conclusions	341

TABLE OF CONTENTS, continued

	Page
Literature Cited	343
Appendix 1: A glossary of morphological terms	353
Appendix 2: Output of the Program ITERMIX for the analyses of the Asellota and the Janiroidea	370
Appendix 3: Output of the program CLIQUE for the analyses of the Asellota and the Janiroidea	385
Appendix 4: Output of the program ITERMIX for the analysis of selected genera of munnopsoids showing various tree topologies	393

LIST OF FIGURES

	Page
Figure 1.1. An ilyarachnoid eurycopid	2
Figure 1.2. Numerical species richness of Isopods	4
Figure 1.3. Morphological variety of deep-sea Janiroidea	7
Figure 1.4. The morphology of a typical munnopsoid	12
Figure 1.5. Morphological diversity in the munnopsoids	14
Figure 1.6. The appearance of the Ilyarachnidae	17
Figure 1.7. Examples of ilyarachnoid Eurycopidae	21
Figure 2.1. <u>Coperonus comptus</u> new genus, new species	40
Figure 2.2. <u>Coperonus comptus</u> new genus, new species	45
Figure 2.3. <u>Coperonus comptus</u> new genus, new species	49
Figure 2.4. <u>Coperonus comptus</u> new genus, new species	52
Figure 2.5. <u>Hapsidohedra ochlera</u> new genus, new species	60
Figure 2.6. <u>Hapsidohedra ochlera</u> new genus, new species	63
Figure 2.7. <u>Hapsidohedra ochlera</u> new genus, new species	66
Figure 2.8. <u>Hapsidohedra ochlera</u> new genus, new species	69
Figure 2.9. <u>Hapsidohedra ochlera</u> new genus, new species	72
Figure 2.10. <u>Hapsidohedra aspidophora</u> (Wolff, 1962)	75
Figure 2.11. <u>Lionectes humicephalotus</u> new genus, new species	83
Figure 2.12. <u>Lionectes humicephalotus</u> new genus, new species	86
Figure 2.13. <u>Lionectes humicephalotus</u> new genus, new species	90
Figure 2.14. <u>Lionectes humicephalotus</u> new genus, new species	93
Figure 2.15. <u>Lipomera</u> (<u>Lipomera</u>) <u>lamellata</u> Tattersall, 1905a	100
Figure 2.16. <u>Lipomera</u> (<u>Paralipomera</u>) <u>knorrae</u> new species	105

LIST OF FIGURES, continued

	Page
Figure 2.17. <u>Lipomera</u> (<u>Paralipomera</u>) <u>knorrae</u> new species	108
Figure 2.18. <u>Lipomera</u> (<u>Paralipomera</u>) <u>knorrae</u> new species	111
Figure 2.19. <u>Lipomera</u> (<u>Paralipomera</u>) <u>knorrae</u> new species	115
Figure 2.20. <u>Lipomera</u> (<u>Tetracope</u>) <u>curvintestinata</u> new species	119
Figure 2.21. <u>Lipomera</u> (<u>Tetracope</u>) <u>curvintestinata</u> new species	121
Figure 2.22. <u>Lipomera</u> (<u>Tetracope</u>) <u>curvintestinata</u> new species	125
Figure 2.23. <u>Lipomera</u> (<u>Tetracope</u>) <u>curvintestinata</u> new species	128
Figure 2.24. <u>Lipomera</u> (<u>Tetracope</u>) <u>curvintestinata</u> new species	131
Figure 2.25. <u>Mimocopelates</u> <u>longipes</u> new genus, new species	138
Figure 2.26. <u>Mimocopelates</u> <u>longipes</u> new genus, new species	142
Figure 2.27. <u>Mimocopelates</u> <u>longipes</u> new genus, new species	145
Figure 2.28. <u>Mimocopelates</u> <u>longipes</u> new genus, new species	148
Figure 2.29. <u>Mimocopelates</u> <u>longipes</u> new genus, new species	151
Figure 2.30. <u>Mimocopelates</u> <u>anchibraziliensis</u> new species	156
Figure 2.31. <u>Mimocopelates</u> <u>anchibraziliensis</u> new species	159
Figure 2.32. <u>Mimocopelates</u> <u>anchibraziliensis</u> new species	163
Figure 3.1. <u>Amuletta</u> <u>abyssorum</u> (Richardson, 1911)	173
Figure 3.2. <u>Amuletta</u> <u>abyssorum</u> (Richardson, 1911)	175
Figure 3.3. <u>Amuletta</u> <u>abyssorum</u> (Richardson, 1911)	184
Figure 3.4. <u>Amuletta</u> <u>abyssorum</u> (Richardson, 1911)	187
Figure 4.1. <u>Pseudojanira</u> <u>stenetrioides</u> Barnard, 1925	202
Figure 4.2. <u>Pseudojanira</u> <u>stenetrioides</u> Barnard, 1925	208
Figure 4.3. Previous concepts of female reproductive organs	214

LIST OF FIGURES, continued

	Page
Figure 4.4. Female reproductive system of <u>Asellus</u>	219
Figure 4.5. Female reproductive system of <u>Stenetrium</u>	222
Figure 4.6. Female reproductive system of <u>Pseudojanira</u>	225
Figure 4.7. Female reproductive system of <u>Munna</u>	228
Figure 4.8. Female reproductive system of <u>Notasellus</u>	231
Figure 4.9. Mating in the Asellota	236
Figure 4.10. Male copulatory organs in <u>Asellus</u> and <u>Stenetrium</u>	241
Figure 4.11. Male copulatory organs in several Janiroidea	244
Figure 4.12. Comparison of asellotan first pereopods	252
Figure 4.13. Previous phylogenies for the Asellota	260
Figure 4.14. Phylogeny of the Asellota proposed by Wägele	262
Figure 4.15. A new phylogeny for the Asellota	265
Figure 4.16. A comparison of the dactylar claws	284
Figure 4.17. A comparison of asellotan third pleopods	287
Figure 4.18. A comparison of higher janiroidean third pleopods	291
Figure 4.19. Preliminary phylogenetic tree for the Janiroidea	300
Figure 5.1. Cephalons of an acanthaspidiid and munnopsoids	315
Figure 5.2. Estimated phylogeny of selected munnopsoid genera	334
Figure 5.3. Estimated phylogeny of the Lipomerinae	337

LIST OF TABLES

		Page
Table 1.1.	The current classification of the munnopsoids	10
Table 1.2.	Diagnostic characters of the Ilyarachnidae	18
Table 2.1.	Abbreviations used in text	28
Table 2.2.	Locality Data	30
Table 2.3.	Locality Data, Woods Hole Oceanogr. Inst. samples	31
Table 4.1.	Asellota: presence and position of cuticular organ	216
Table 4.2.	Taxon-character matrix for the Asellota	257
Table 4.3.	Families used for janiroidean phylogenetic analysis	273
Table 4.4.	Taxon-character matrix for janiroidean analysis	296
Table 4.5.	Actual data for janiroidean phylogenetic analysis	297
Table 5.1.	Taxon-character matrix for munnopsoid analysis	330
Table 5.2.	Actual data for munnopsoid phylogenetic analysis	331
Table 5.3.	A revised classification of the munnopsoids	338

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A systematist is severely handicapped with limited collections of specimens to study. Much of the information in this thesis would be impossible without the thousands of deep-sea isopods amassed in Dr. Hessler's laboratory from Woods Hole Oceanographic Institution expeditions in the Atlantic. These these samples were collected by Dr. Howard Sanders, Dr. Hessler, and more recently Dr. J. Frederick Grassle. Other sources for the specimens are listed in chapter 2.

The study of deep-sea isopods is what it is today because of an important monograph on the Asellota by Dr. Torben Wolff, Zoological Museum of the University of Copenhagen. In bringing together all the literature on these isopods, organizing it into a workable scheme, and setting an example for the necessary quality of work, he has made a lasting impact on all later work. Robert Hessler extended this tradition by writing a valuable monograph on the Desmosomatidae of the Gay Head-Bermuda Transect.

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ABSTRACT OF THE DISSERTATION

The Systematic Position of the Ilyarachnoid Eurycopidae

(Crustacea, Isopoda, Asellota)

by

George D.F. Wilson

Doctor of Philosophy in Marine Biology

University of California, San Diego, 1985

Professor Robert R. Hessler, Chairman

Although isopod crustaceans of the suborder Asellota are a dominant part of the deep-sea benthic macrofauna, the systematic relationships between the major families are poorly understood. The fully natatory families, Munnopsidae, Eurycopidae, and Ilyarachnidae, are in the greatest need of study. Within this munnopsoid group, the ilyarachnoid Eurycopidae, a poorly described assemblage of genera, confound the definitions between the Ilyarachnidae and the Eurycopidae. This thesis determines how the ilyarachnoid eurycopids are related to the other taxa, and shows whether they are a monophyletic group or only a polyphyletic assemblage.

In the descriptive section, the ilyarachnoid Eurycopidae are found to include 5 genera, 4 of which are new. The definition of the Ilyarachnidae is improved by the removal of the species Ilyarachna abyssorum to the eurycopid genus Amuletta, and weaknesses in the classification of the munnopsoid families are discussed.

The superfamilies of the Asellota are phylogenetically analysed to find appropriate outgroups for the superfamily Janiroidea, which includes the munnopsoids. Pseudojanira stenetrioides is redescribed because it is related to the janiroideans, but distinct from this and other superfamilies. The relationships of the superfamilies of the Asellota are illuminated by a morphological study of a female copulatory structure called the cuticular organ. These morphological data are combined with other characters to derive a well resolved phylogeny of the asellotan superfamilies. The outgroup for the munnopsoids is found by analyzing the Janiroidea for characters in the morphology of the dactylar claws, the third pleopods, and other little used aspects of the janiroidean form. The phylogenetic estimates derived from all these characters nominate the Acanthaspidiidae as the best candidate for an outgroup to the munnopsoids.

Character analyses of selected munnopsoid genera is made possible by comparison with character states in the Acanthaspidiidae. The resulting character-taxon matrix produces phylogenetic estimates that are not fully resolved, but have a generally consistent form. Because the current classification of the families is not reflected in the phylogeny, a proposal is made to place all the munnopsoids into one family, the Munnopsidae. The ilyarachnoid Eurycopidae are a monophyletic group and are assigned to the subfamily Lipomerinae.

CHAPTER 1

AN INTRODUCTION TO DEEP-SEA ISOPODS AND THE SYSTEMATIC PROBLEMS IN THE CLASSIFICATION OF THE ILYARACHNOID EURYCOPIDAE (CRUSTACEA, ISOPODA, ASELOTA)

INTRODUCTION

Isopod crustaceans that live in such accessible environments as a backyard or any shallow marine habitat are cryptic animals. To find isopods, often one must look in hidden habitats, such as under a rock, in cracks and crevices, or buried in the gills of a fish. But in one environment, isopods live in the open. This is in the deep sea, on the sea floor and water column below the photic zone, the most extensive environment on our planet (Sverdrup et al, 1942).

Unlike anywhere else, isopods of the deep-sea benthos are a major feature of the biota. In most deep-sea benthic samples isopods are among the most abundant crustacean taxa, and often account for a large fraction of the species present in an area (Sanders and Hessler, 1967; Wilson and Hessler, unpublished manuscript; Wilson, in progress). For example, in the equatorial Pacific manganese nodule province, isopods represent the third most abundant macrobenthic taxon and their diversity possibly exceeds 85 species (fig. 1.2). In one program

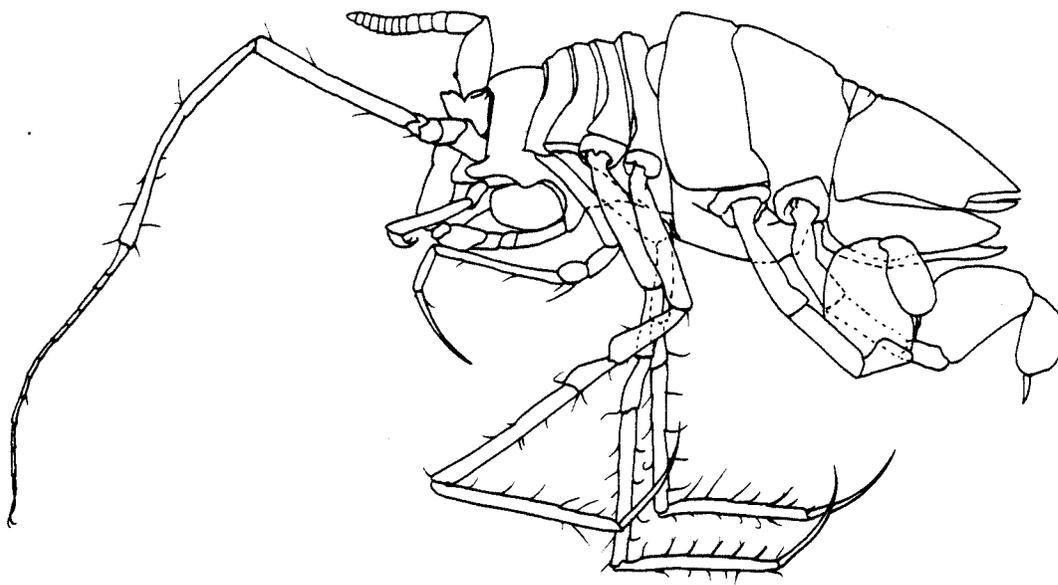
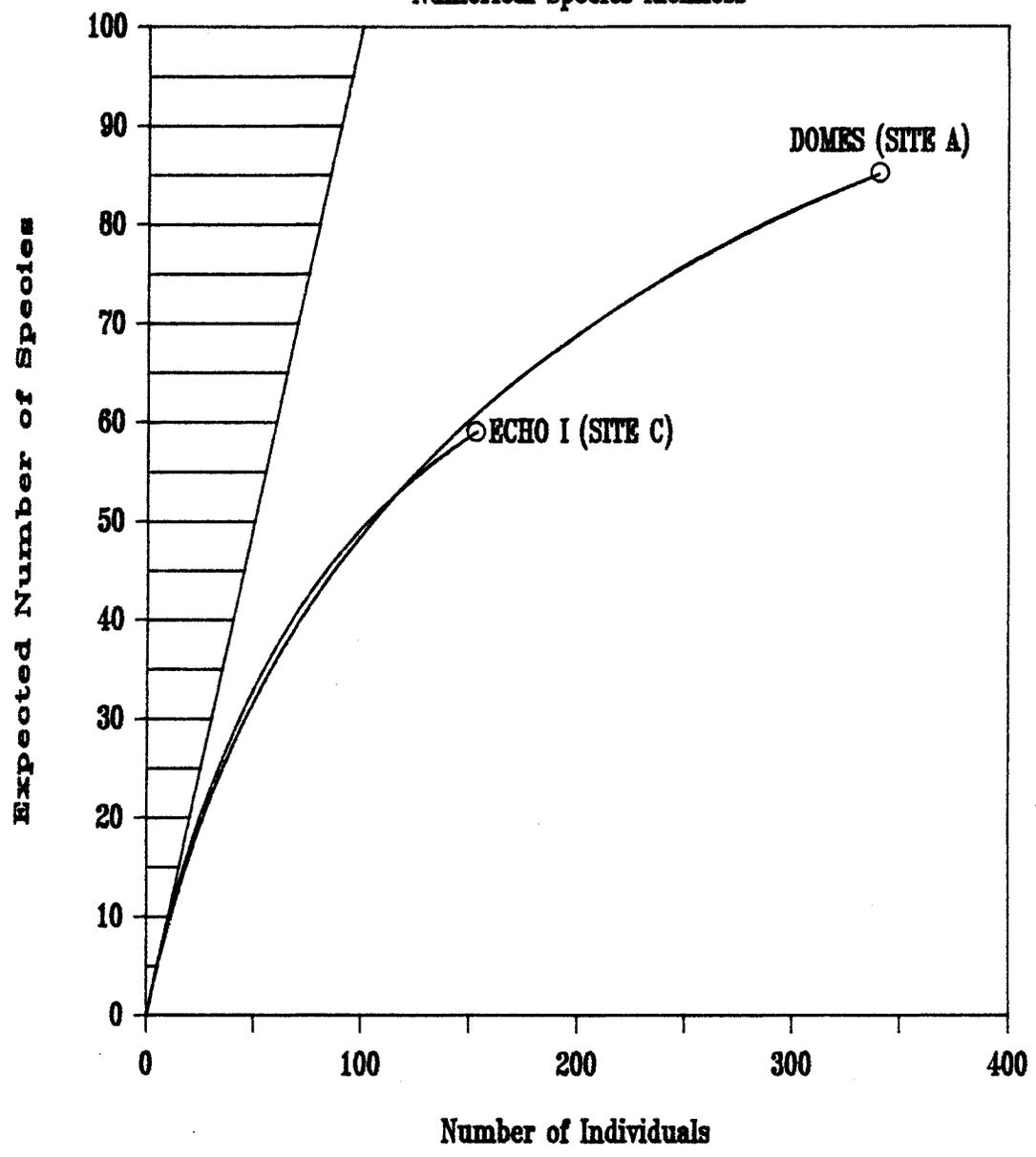


Figure 1.1. An example of an ilyarachnoid eurycopid (Crustacea, Isopoda, Asellota), in lateral view.

Figure 1.2. The numerical species richness of two localities in the Equatorial Pacific Ocean. The expected number of species curves for the lumped data of each locality were calculated using the Hurlbert (1971) rarefaction technique. The straight line intersecting the origin traces the maximum of one species per individual. The samples were collected with 0.25^2 box corers. The DOMES (Deep Ocean Mining Environmental Survey) site A samples ($N = 50$) are from approximately $9^{\circ} 30' N$, $151^{\circ} 30' W$, 5100-5200 m. The samples ($N = 15$) from the Scripps Institution of Oceanography cruise ECHO leg I (DOMES site C) are from approximately $14^{\circ} 40' N$, $125^{\circ} 25' W$, 4500 m. The two sites are predominantly manganese nodules bottoms.

ISOPODA

Numerical Species Richness

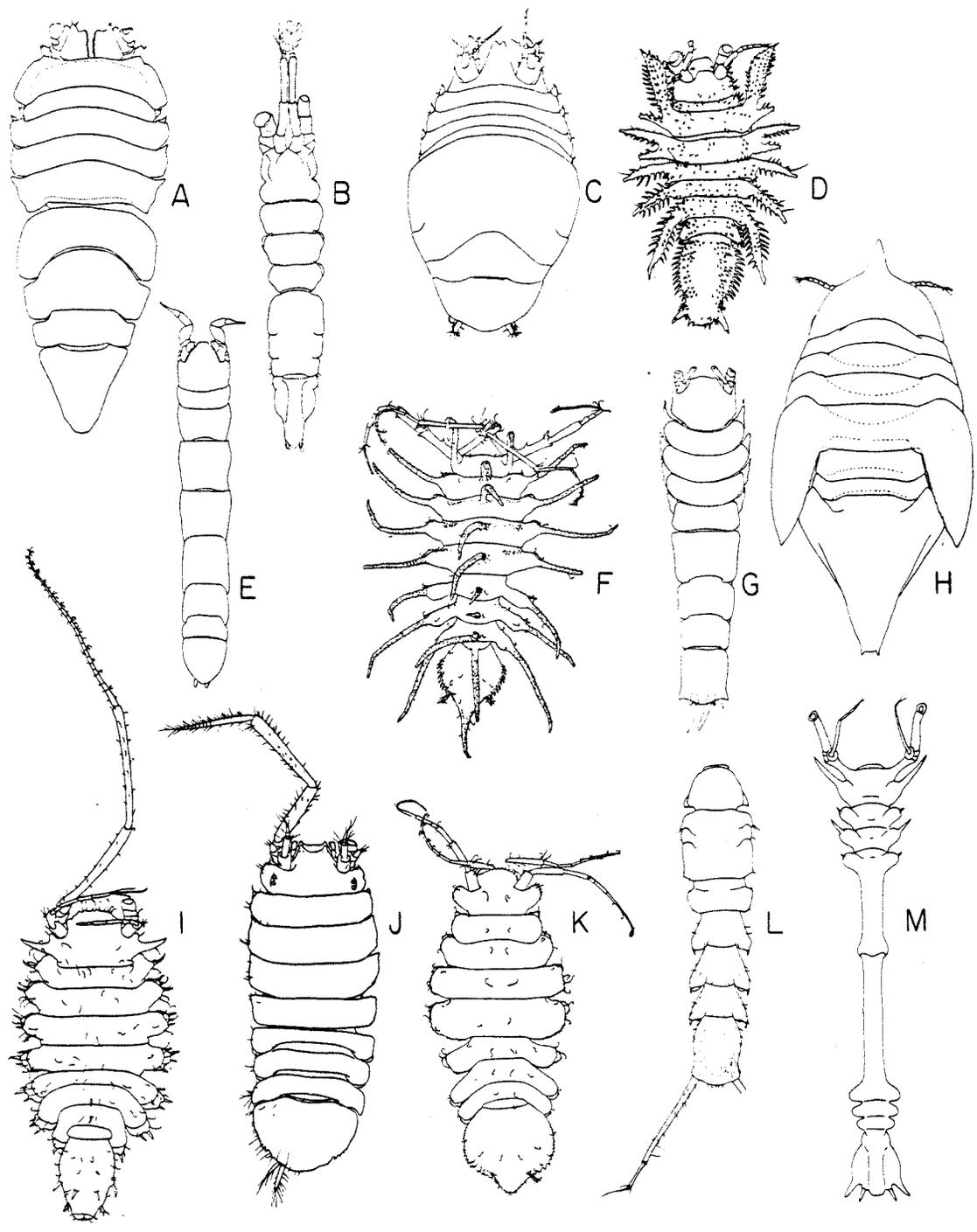


where 15 quantitative samples were collected from a 4500 m deep manganese nodule bottom, 154 specimens of isopods were counted (Wilson and Hessler, unpublished manuscript). These specimens comprised 59 separate species, a high species richness considering that only 3.75 m² of the sea floor was sampled (Wilson, in progress).

Deep-sea isopods do not resemble their cryptic shallow marine, fresh water, and terrestrial counterparts. The archetypical isopod is dorsoventrally flattened and has 7 pairs of similar legs, hence the translation of their name "like footed." This body form is undoubtedly related to their cryptic life style of creeping underneath objects and in cracks and crevices. Deep-sea isopods, however, display a great variety of forms, from narrow walking-stick creatures to things that look like little space ships and highly modified swimmers. Their body forms are evidence for a great evolutionary radiation, one apparently in full flower. A few examples of these unusual animals are shown in figure 1.3.

These morphological differences reflect evolutionary paths separate from those of other Isopoda: the best evidence collected to date indicates most of the families of deep-sea isopods evolved there, and not in shallow water (Hessler and Thistle, 1975; Hessler, Wilson, and Thistle, 1979). The evolution of entire families in the deep-sea also has biogeographic consequences. These families and most of their

Figure 1.3. A few examples of the morphological variety of Isopoda Asellota, superfamily Janiroidea, from the deep sea. Notice that most of the genera represented here lack eyes, practically a diagnostic characteristic of deep-sea isopods. Dorsal views, not to same scale, although most specimens shown are approximately 1-3 mm long. A, Ilyarachna, Ilyarachnidae. B, Syneurycope, Eurycopidae, subfamily Eurycopinae. C, Disconectes, Eurycopidae, subfamily Eurycopinae. D, Mesosignum, Mesosignidae. E, Exiliniscus, Nannoniscidae. F, Notoxenoides, Paramunnidae. G, Momedossa, Desmosomatidae. H, Aspidoniscus, Haploniscidae. I, Munna, Munnidae. J, Austrofilius, family incertae sedis. K, Abyssianira, Abyssianiridae. L, Macrostylis, Macrostylidae. M, Haplomesus, Ischnomesidae.



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 evolution of new species is actively occurring (Wilson, 1980a, 1983a), and species ranges are small geographic areas and narrow depth ranges (Wilson, 1983b, 1983c).

Although deep-sea isopods are ecologically important and biogeographically interesting, systematic knowledge on the most important families is limited. The primary deep-sea families belong to the suborder Asellota, the systematics of which can best be described as unstable. The Asellota has 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 both species and morphological types in the deep-sea (Menzies, 1962; Wolff, 1962; Birstein, 1963; Hessler and Sanders, 1967; Hessler, 1970; Hessler, Wilson, and Thistle, 1979). This interest has resulted in the rapid accumulation of new species and genera, described from deep-sea samples taken since the early 60's. In spite of this new information, no major reorganization of the suprageneric taxa has been attempted since the landmark papers of Wolff (1962) and Menzies (1962). As a result, the family-level groups have become poorly defined as they have been forced to include a broad variety of taxa.

This problem is most acute in a group of families called the munnopsoids: Munnopsidae, Eurycopidae, and Ilyarachnidae. Taxa have been described that appear to be intermediate between the Eurycopidae and the Ilyarachnidae (the genus Betamorpha Hessler and Thistle, 1975), and a group of eurycopids has been discovered that are very similar to the Ilyarachnidae but cannot be placed there owing to the current definitions of the families (Wilson and Hessler, 1981). These ilyarachnoid Eurycopidae are the subject of this thesis. In it, I present a solution to the systematic problem they present. In so doing, some light will be shed on the evolutionary paths taken by the deep-sea asellote isopods and their ancestors.

Table 1.1. The current classification of the munnopsoids (family Munnopsidae sensu lato of Sars, 1883, temporary group Incertae sedis). (extracted from: Bowman and Abele, 1982; Hessler and Thistle, 1975; and Wilson and Hessler, 1981). Only the genus-level taxa discussed in the text are shown.

Crustacea

Class Malacostraca

Subclass Eumalacostraca

Superorder Peracarida

Order Isopoda

Suborder Asellota

Superfamily Janiroidea

Family Munnopsidae sensu stricto

Genus Paramunnopsis Hansen, 1916

Family Eurycopidae

Subfamily Eurycopinae

Genus Eurycope Sars, 1864

Genus Betamorpha Hessler and Thistle, 1975

Subfamily Acanthocopinae

Subfamily Bathyopsurinae

Subfamily Syneurycopinae

Family Ilyarachnidae

Genus Ilyarachna Sars, 1864

Ilyarachna abyssorum Richardson, 1911

(temporary genus incertae sedis)

Ilyarachnoid Eurycopids, temporary group incertae sedis

Genus Lipomera Tattersall, 1905a

(Taxa misplaced in the literature)

Ilyarachna aspidophora Wolff, 1962

Eurycope frigida Vanhoeffen, 1914

Eurycope cf. frigida Nordenstam, 1933

THE MUNNOPSOID FAMILIES AND THE ILYARACHNOID EURYCOPIDAE

The munnopsoid families of the isopod suborder 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). Figure 1.4 illustrates the morphology of a common munnopsoid isopod. The success of the munnopsoids may be related to their primary specialization, the swimming habit. Although primitive asellote isopods have lost the ancient crustacean ability to swim, the Munnopsoids have an integrated set of adaptations that allow them to swim rapidly and efficiently, but in a posterior direction. This ability has resulted in an important adaptive radiation, with the evolution of numerous offshoots from the basic swimming type exemplified by the genus Eurycope (fig. 1.5).

The munnopsoids, a large family as originally conceived by G.O. Sars (1883, 1899), are now classified into three separate families (see table 1.1): the Eurycopidae with several subfamilies, the Ilyarachnidae, and the Munnopsidae. The munnopsids have taken the swimming life to its logical extreme: some of its members are holopelagic. Ilyarachnids, on the other hand, have gone to the opposite extreme by specializing 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.

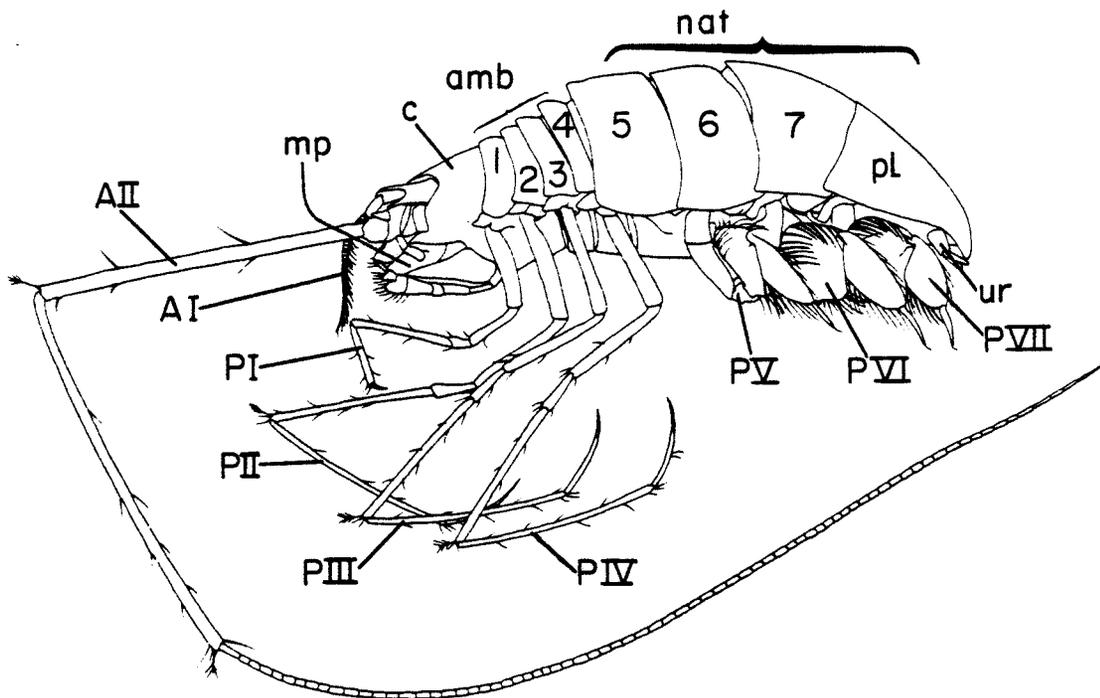
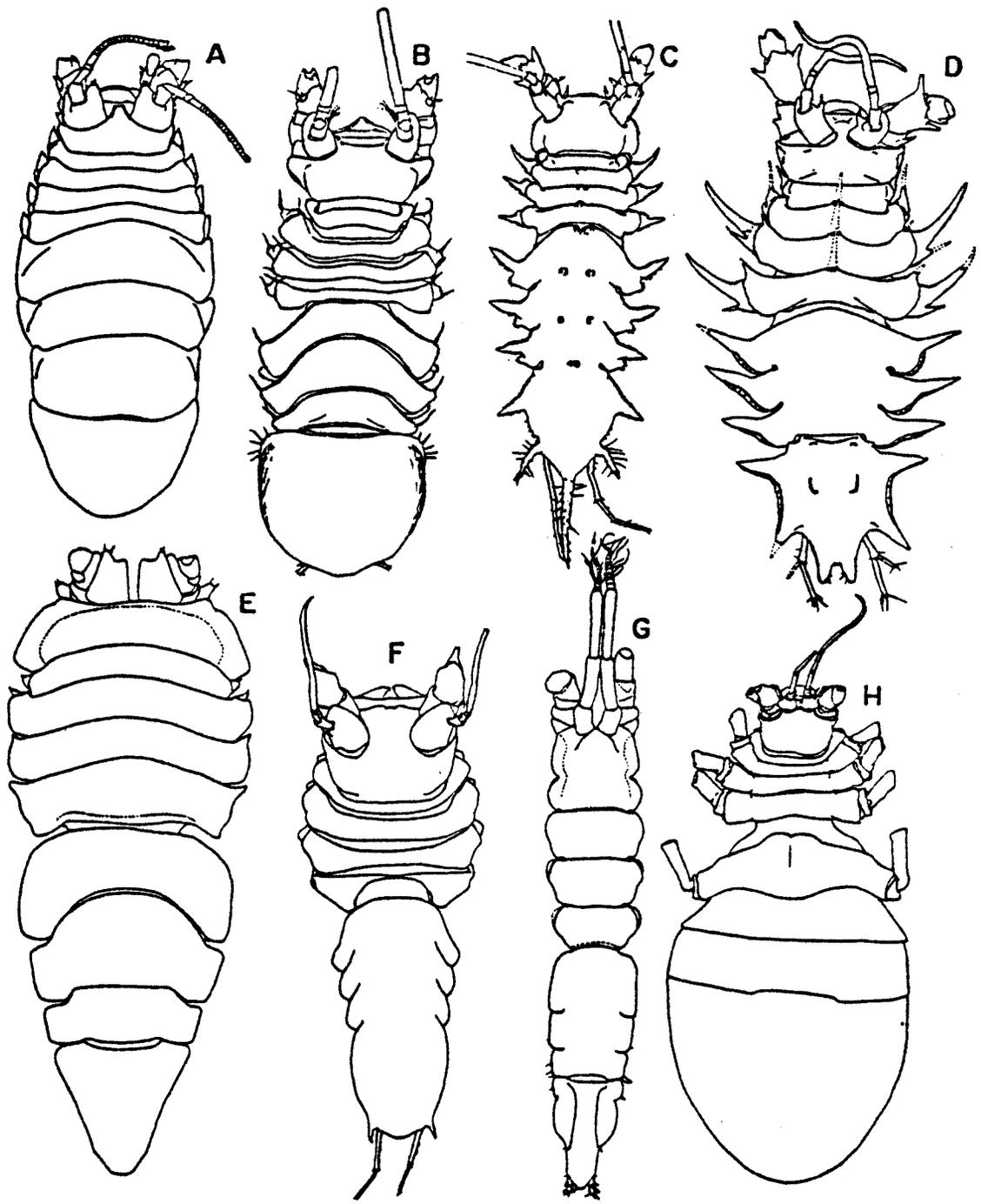


Figure 1.4. The morphology of a typical munnopsoid, *Eurycope iphthima* Wilson (1981), in lateral view with anterior to the left. The main body parts are the cephalon (c), the ambulosome (amb) which is made of pereonites (segments of the thorax bearing legs) 1-4 (numbered in the figure), and the natasome 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.

Figure 1.5. A sampling of the morphological diversity present in the munnopsoids, those Isopoda Asellota with distinct natasomes. All are shown in dorsal view with anterior toward the top. A, Eurycope. B, Munnopsurus. C, Acanthocope. D, Storthyngura. E, Ilyarachna. F, Munnopsis. G, Syneurycope. H, Paropsurus.



As presently constituted, eurycopids are more difficult to classify under this functional scheme because many of the groups in the family have specializations that resemble those found in the other two families. Some of these similarities are true homologies, reflecting a common ancestry, such as the resemblance of the eurycopid Betamorpha to primitive members of the Ilyarachnidae (Thistle and Hessler, 1977). Other similarities are undoubtedly convergences to a common body form.

Recent revisionary work (Wilson and Hessler 1980, 1981) has identified a group of genera within the Eurycopidae that have an "ilyarachnoid facies" (Fig. 1.6, 1.7). A comparison of the diagnostic characters of the Ilyarachnidae (Wolff, 1962) with the features of these eurycopids (Table 1.2) reveals substantial similarities between the two groups. The overall shape of the natasome and the cephalon are most compelling. In the current literature, these ilyarachnoid eurycopids are only an informal collection of species and genera with little formal systematic status. On a purely typological basis (using similarities only), they should be classified with the Ilyarachnidae. The similarities, however, may be due to convergence of unrelated taxa to a common body form, thus decreasing the naturalness and usefulness of such a phenetic classification. Therefore, these character complexes should be examined in some detail.

Figure 1.6. Dorsal views of several munnopsoids to illustrate the appearance of the Ilyarachnidae. A, Eurycope. B, Ilyarachna. C, Ilyarachna abyssorum. D, Lipomera. E, a new genus of the ilyarachnoid eurycopids.

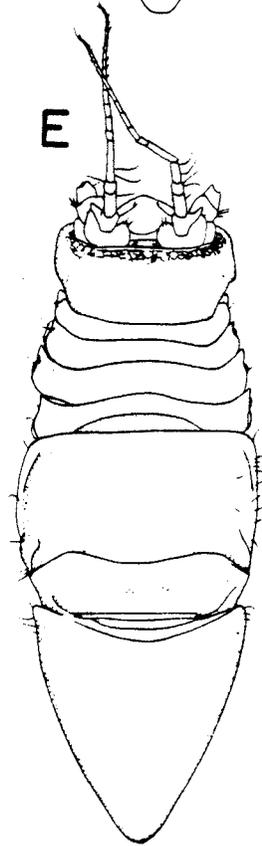
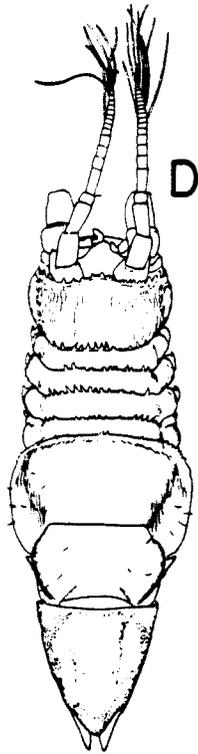
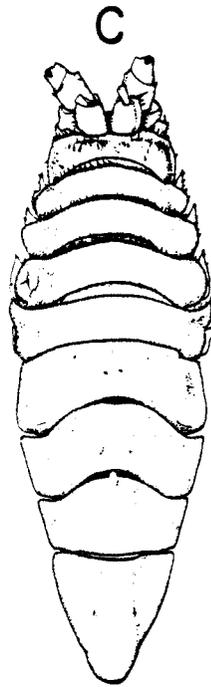
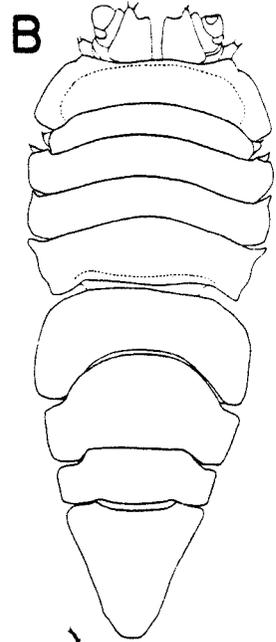
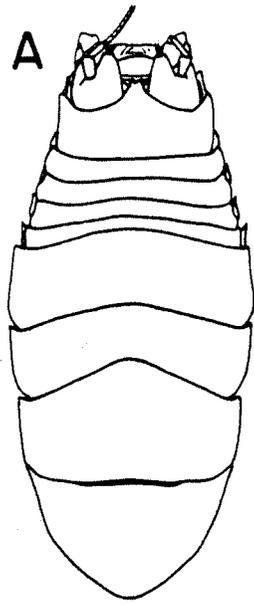


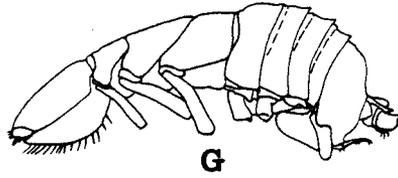
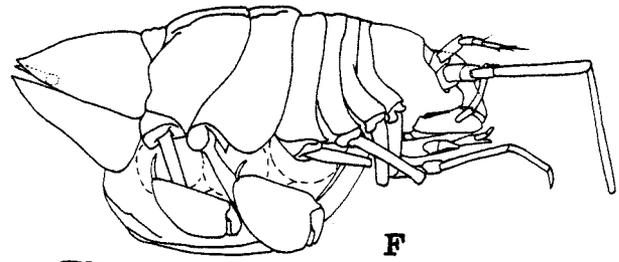
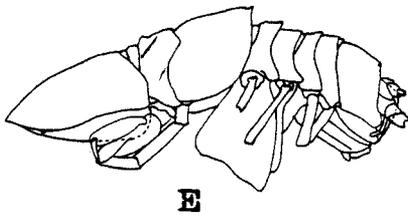
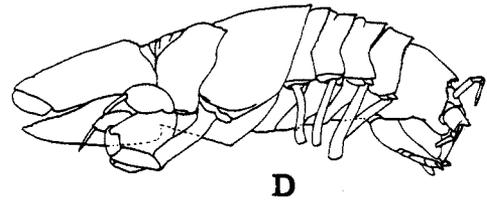
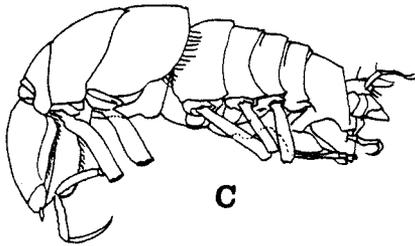
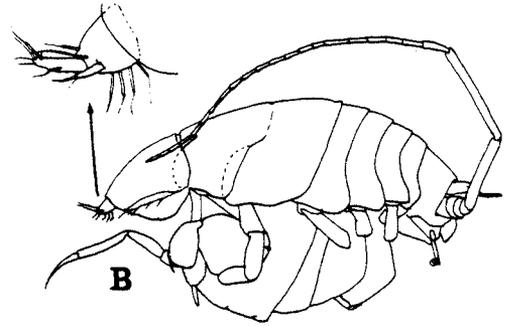
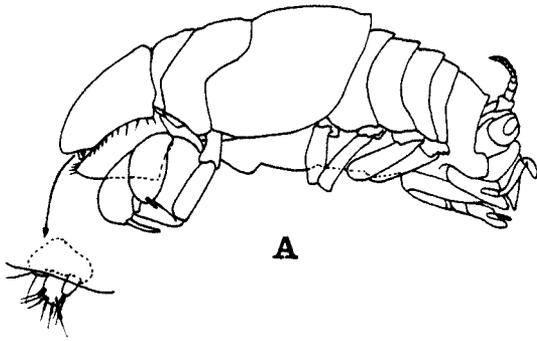
TABLE 1.2: A comparison of the characters from the diagnosis of the Ilyarachnidae (Wolff, 1962) with the ilyarachnoid eurycopids. "+" = Has similar character. "-" = No similar character. Characters found in all the munnopsoids omitted.

Character from the diagnosis of the Ilyarachnidae	Ilyarachnoid Eurycopids
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 with flattened, oval, setiferous basal segment and reduced rami	+, -

* This character is considered by Thistle and Hessler (1976) to be the principal diagnostic character separating the Ilyarachnidae from the Eurycopidae.

Members of the ilyarachnoid eurycopids first appear in the literature with a description of Lipomera lamellata Tattersall 1905a (1905b). Related species are Eurycope frigida Vanhoffen 1914, E. cf. frigida Nordenstam 1933, Ilyarachna aspidophora Wolff 1962. Recently, these species were recognized as an informal taxon having an "ilyarachnoid facies" within the Eurycopidae similar to, but possibly independent of the Ilyarachnidae (Wilson and Hessler, 1981). In spite of the limited treatment, species of this group appear in more than 60 samples of deep-sea isopods from the North and South Atlantic Oceans, some samples having more than 90 specimens and two or more species. Similar to other advanced deep-sea taxa, the ilyarachnoid eurycopids display high latitude emergence. A previously unknown species was discovered in a sample collected by Robert Hessler from Norwegian coastal waters, a region of intensive investigation over the last century. Thus, the ilyarachnoid eurycopids are particularly worthy of systematic attention because they are a numerically and biogeographically important group of genera that has received little attention in the literature.

Figure 1.7. Examples of ilyarachnoid eurycopids in lateral view, anterior is to the right. A-C and E-F are examples of new genera described in chapter 2. D is a new species of the previously described genus Lipomera Tattersall. G is a member of Ilyarachna Sars for comparison.



Because the ilyarachnoid eurycopids confound the overall distinction between the Ilyarachnidae and the Eurycopidae, a systematic investigation of these isopods reveals much about the evolution within the munnopsoids. Kussakin (1973) proposed a phylogeny for the established families of the Asellota that showed the close relationship of the munnopsoid families, but he omitted details of the phylogenetic construction, preventing any analysis on the nature of this relationship. Little of this basic systematic work has been attempted since.

In the following chapters, the ilyarachnoid eurycopids are described, and then analysed using phylogenetic techniques in order to discover their relationships to the other natatory taxa. By analyzing the potential links between the munnopsoid families, our knowledge of their systematic relationships can be placed on a more solid foundation.

SYNOPSIS OF THE THESIS

The primary aim of the research reported here will be to determine whether the similarities between the ilyarachnoid Eurycopidae and the Ilyarachnidae are synapomorphies, uniquely derived and shared specializations, or whether they are homoplasies, convergences that reveal little about the phylogenetic relationships between groups. Because the Eurycopidae, as a family, is morphologically and potentially phylogenetically heterogeneous, an important question is how the ilyarachnoid eurycopids should be classified vis-á-vis the other munnopsoid taxa. As the final chapter will show, this inquiry results in a new systematic organization for the munnopsoids. A related question is whether the ilyarachnoid eurycopids are a monophyletic group rather than a "facies", a polyphyletic assemblage of species with the same overall appearance.

Before these questions can be answered, other information must be added to the inquiry because the ilyarachnoid Eurycopidae are largely ignored or unknown in the current literature. Chapter 2 remedies this situation with detailed descriptions of the genera of this little known group. Special attention will be paid to the morphology of the natasome and cephalon in order to lay a firm foundation for the phylogenetic analysis. As the reader will see, four new genera are described, and Lipomera Tattersall is divided into three subgenera.

To understand the composition of the Ilyarachnidae, the species Ilyarachna abyssorum Richardson must be defined carefully and its systematic position considered. This is the content of chapter 3, in which this species is removed from the Ilyarachnidae, and is assigned to a new genus, Amuletta. Moreover, some of the difficulties with the current classification of the munnopsoids are discussed.

A serious problem with the study of phylogenetic relationships of the munnopsoid families is that their sister group or groups are unknown. In fact, as touched on above, little is known of the relationships of all the families in the Janiroidea. Chapter 4 delves into these questions by taking the analysis to a higher systematic level, the superfamilies of the isopod suborder Asellota, and then working back to the family-level groups.

A poorly known South African isopod called Pseudojanira stenetrioides Barnard has an important role in this study. Although it has previously been classified in the janiroidean family Janiridae, a detailed study of its male and female reproductive morphology shows that it does not belong in the superfamily Janiroidea. In the first section of chapter 4, Pseudojanira is redescribed as the type of a new family of Asellota, with uncertain superfamily relationships.

As Pseudojanira shows, an understanding of reproductive morphology is a key to understanding the relationships of the asellotan superfamilies. Female copulatory organs found in most Janiroideans, called "cuticular organs" by a number of authors (Veuille, 1978b), are shown in chapter 4 to occur in all asellotans

examined. The presence of these organs does not define the Janiroidea, but their position with respect to the female oopores does help to delimit a major group of families within the Janiroidea.

The information on the cuticular organs is combined with a number of other characters that help define major groups of the Asellota to provide a new phylogeny for the entire suborder. This analysis reaffirms the evolutionary hypotheses presented by earlier authors and argues against the recent concept of asellotan phylogeny presented by Wägele (1983). New structure is added to the evolution of the Asellota by the recognition of Pseudojanira as the sister group to the Janiroidea, and by the startling conclusion that the families Munnidae and Pleurocopidae must be derived from the ancestral stock of the Janiroidea before the Janiridae.

All this sets the stage for the goal of chapter 4, the identification of the outgroup to the munnopsoids. A series of little understood characters seen in the Janiroidea are analysed in the last section; examples of such characters are the setation and size of the rami of the third pleopod. These characters generate a poorly resolved estimate of the phylogeny of the Janiroidea, although the single result sought, the outgroup for the munnopsoids, is attained. That group is shown to be a spiny, but otherwise little modified, deep-sea isopod family called the Acanthaspidiidae.

To answer questions concerning systematic position of the ilyarachnoid eurycopids, chapter 5 provides the results of an analysis of a great many characters, narrowed down to a few attributes that help to define groups within the munnopsoids. These characters are used in a new phylogenetic treatment of a selected subset of the genera of all the munnopsoid families, including the taxa of the ilyarachnoid eurycopids. The estimated evolutionary structure of the munnopsoids bears little resemblance to the concept of three separate families, so they are submerged into the broader family concept of Sars, the single family Munnopsidae for all the genera. Chapter 5 concludes that the ilyarachnoid eurycopids are a monophyletic group, and assigns them to the subfamily Lipomerinae.

CHAPTER 2

THE TAXONOMY OF THE ILYRACHNOID EURYCOPIDAE

INTRODUCTION

The isopods of the family Eurycopidae that have the "ilyarachnoid facies" (Wilson and Hessler, 1981) are a fairly diverse group. Although they have Ilyarachna-like features tying them all together, they 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 the form of the cephalon, as well as having definable differences in the uropods and pleotelson. As a result, this chapter redescribes Lipomera Tattersall, 1905a, and divides the species of this genus into three subgenera. Four new genera are erected to contain the remaining bulk of the specimens originally classified as ilyarachnoid Eurycopidae.

MATERIALS AND METHODS

SOURCES OF SPECIMENS

The specimens used in this study came from a variety of sources, indicated by abbreviations (meanings in table 2.1) in table 2.2 and table 2.3. The largest contributor to the collection of ilyarachnoid eurycopids came from a series of deep benthic sampling transects in various basins of the Atlantic Ocean conducted by the Woods Hole Oceanographic Institution (WHOI) under the direction of

Table 2.1. Abbreviations used in text.

Sources of Specimens

<u>Abbreviation</u>	<u>Meaning</u>
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

<u>Abbreviation</u>	<u>Meaning</u>
MNHNP	Museum National d'Histoire Naturelle, Paris
SIO	Robert Hessler collection, Scripps Institution of Oceanography
USNM	United States National Museum of Natural History
ZMUC	Zoological Museum, University of Copenhagen

Other Abbreviations

<u>Abbreviation</u>	<u>Meaning</u>
bl	Body Length, measured from frons to pleotelson tip
inds	Individuals, usually reporting number used in a measurement.

Howard Sanders, and, at different times, Robert Hessler or J. Fredrick Grassle. These samples include the Gay Head-Bermuda Transect, off New England (Sanders et al, 1965; Hessler and Sanders, 1967). An important collection of Antarctic Isopoda was provided by John Rankin, University of Connecticut, from samples collected in the Weddell Sea during the years 1968 and 1969 (68Rankin and 69Rankin samples). Specimens from the South Shetland Island 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 Penninsula (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 2 samples that were collected in the Hjeltefjord during a marine biology course at Herdla, Norway (HMB samples). Recent studies of the slope fauna off the Eastern United States, directed by James Blake and Nancy Maciolek-Blake of Battelle New England Marine Research Laboratory has provided several 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 (LGL83 and LGL84 samples) was provided by Linda Pequegnat, LGL Ecological Research Associates. Specimens collected from slope depths off New Zealand (NZOI samples) were kindly sent by Desmond Hurley,

Table 2.2. Samples That Contained Ilyarachnoid Eurycypids. Descriptions and abbreviations of programs given in text. In samples, taken with trawls, that have 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) n. subgen.; LP2, Lipomera (Paralipomera) n. subgen.; LP3, Lipomera (Tetracope) n. subgen.; M1, Mimocopelates n. gen. longipes n.sp. species group; M2, Mimocopelates anchibraziliensis n. gen., n.sp. species group. Generic abbreviations with an asterisk (*) indicate a type locality for a described or new species. Generic abbreviations with a double asterisk (**) indicate a type locality for the type species of the genus. All samples except those collected by the Woods Hole Oceanographic Institution programs.

Genus	Program and Station Number	Location	Midpoint Latitude	Midpoint Longitude	Midpoint Depth (m)
C*	(Nordenstam, 1933)				
	Swedish Antarctic Expedition sta. 34	South Georgia off Cumberland Bay	54° 11' S	36° 18' W	281
LP1**	(Tattersall, 1905)				
	R/V Helga station	Porcupine Bank	53° 58' N	12° 16' W	360
C*, LN*	(Vanhöffen, 1914)				
	Gauss Station	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 OSO4	NE Atlantic Ocean	46° 04' N	10° 17' W	4706
H	INCAL WSO3	NE Atlantic Ocean	48° 19' N	15° 23' W	4829
C	IODa1 6	S. Shetland Isl.	62° 40' S	60° 22' W	146
LN	IODa1 7	S. Shetland Isl.	62° 29' S	58° 47' W	59
C, LN**	IODa1 13	S. Shetland Isl.	61° 18' S	58° 00' W	282
L3	LGL83 C1/4/5-10	N. Gulf of Mexico	28° 03' N	90° 15' W	420
H	LGL83 C4/3/0-5	N. Gulf of Mexico	27° 29' N	89° 46' W	1378
H	LGL84 C2/2/1	N. Gulf of Mexico	27° 54' N	90° 06' W	595
H	LGL84 C4/6/2	N. Gulf of Mexico	27° 28' N	89° 47' W	1386
LP2	LGL84 E4/2/1	N. Gulf of Mexico	28° 04' N	86° 35' W	1358
LP2	LGL84 W2/1/1	N. Gulf of Mexico	27° 25' N	93° 21' W	605
LP2	LGL84 W3/1/1	N. Gulf of Mexico	27° 11' N	93° 19' W	860
LP2	LGL84 W3/3/1	N. Gulf of Mexico	27° 10' N	93° 19' W	841
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

Table 2.3. Samples collected by the Woods Hole Oceanographic Institution.

See previous page for explanation.

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	68° 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	Nr. 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° 08' 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
M1, LP3	WHOI 210	Gay Head-Bermuda Transect	39° 43' N	70° 46' 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

New Zealand Oceanographic Institute, and Roger Lincoln, British Museum, Natural History. These latter specimens are mentioned only briefly here and will be the subject of a future paper describing New Zealand munnopsoid isopods.

REPORTING AND USE OF RATIOS

Many ratios are used in describing the species herein. In order to avoid the repetitive use of the word "times", ratios are reported as a multiplier of the object of a telegraphic phrase in order 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 "article 2 of palp 0.86 mandibular body length" means "the second article of the palp is 0.86 times the length of the mandibular body." Note that often nouns are used as modifiers of nouns without adjectival endings; this practice improves the readability of the necessarily dense telegraphese used to describe the species. When used in this way, the modifier nouns will include larger sets to the left so that reading left to right will take the reader 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.

Ratios are used because they accomplish two things. First, they provide a specific, unambiguous description of shape in a form that is readily understood. Second, they normalize the size of an appendage or segment to the overall size of the specimen being used, thereby imparting some generality to the measurement. The ratios are derived

from measurements taken directly from the animals using a camera lucida attachment on the microscope, or from drawings made of the specimens. The precision of the ratios is reduced in most cases to 2 significant figures in order to accommodate individual variation and measurement error. The ratios are meaningful in that they report the shape of a particular body part, a shape that has been verified by examining several specimens, or more for externally visible characters. Large departures from the reported ratio can be seen easily, whereas small differences, say plus or minus 10 per cent, require careful measurement. Statistical significance, however, is not implied by the use of ratios. If the ratios are derived from more than one specimen, their count is reported parenthetically immediately after the ratio.

DEFINITION OF TAXA AND MORPHOLOGICAL TERMS

Species are identified using techniques developed and discussed in previous papers (Wilson and Hessler, 1980; Wilson, 1983). In general, this involves the study of variation within and between populations (samples) of similar animals. Species level taxa were not studied intensively for this work, because the main purpose was to elucidate the higher level taxonomy of the ilyarachnoid eurycopids. In fact, some of the species may include complexes of very similar species; Mimocopelates longipes n.gen., n. sp., is suspected of being one such case because it has a broad distribution similar to that of the Eurycope complanata complex (Wilson, 1983b). These species level problems are left to 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). A glossary to the morphological terms used in this work is provided in appendix 1. Figure 1.4 shows the overall morphology of a typical munnopsoid, and figure 2.1 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, show a great deal of variation among the janiroidean isopod families, and seem to indicate important differences in feeding life styles between groups of species. The natasome characters, such as the size and shape of the swimming leg segments, are unique to (a synapomorphy of) the munnopsoid families Ilyarachnidae, Eurycopidae, and Munnopsidae, and indicate the locomotory life styles of their bearers. The natasome shows a great deal of variation among these taxa (for example see figure 1.5), but is constant among groups of species. As such, the natasome characters are ideal for generic definition within the munnopsoids. 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.

The goal of this morphological system is to define genera as distinctive groups of species, separated (as Mayr (1970) wrote) from other such groups by distinct gaps. Genera are, therefore, defined as clades of similar species. We may be able to distinguish genera only

because intermediate species have become extinct, or because they simply have not been collected yet, a common occurrence for deep-sea taxa. Although genera may be only a taxonomic convenience to help categorize the evolutionary hierarchy, they may also include those animals that go about their business in similar ways, and thus be of potential interest to ecologists.

PREPARATION AND ILLUSTRATION OF SPECIMENS

All specimens for this study are stored in 80% or 95% ethanol. For study, they were placed on depression slides in ethylene glycol, which is miscible with ethanol. 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 of the specimens were originally done in pencil, and then inked by tracing onto translucent velum. The illustrations, of course, cannot include all the detail of the animals, although effort was made to include all major surface structures, including all 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 a circular, u-shaped, or v-shaped marks. An open mark shows the direction that the seta lies on the animal. Some types of setae, such as plumose setae and broom setae, have many fine setules that would not reproduce well if all were illustrated. Therefore, setules on setae are generally illustrated much more sparsely than they really are. Some

cuticular structures, generally best studied with a scanning electron microscope, were sometimes prominent on the specimens and were partially drawn in order 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. All the pereopods are illustrated in lateral view. The maxillulae, maxillae, maxillipeds, and pleopods are illustrated in ventral view. The antennulae are illustrated in ventral view.

TAXONOMY

COPERONUS New Genus

(Figures 2.1 - 2.5)

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 frontal view. Clypeus medial section triangular in frontal 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

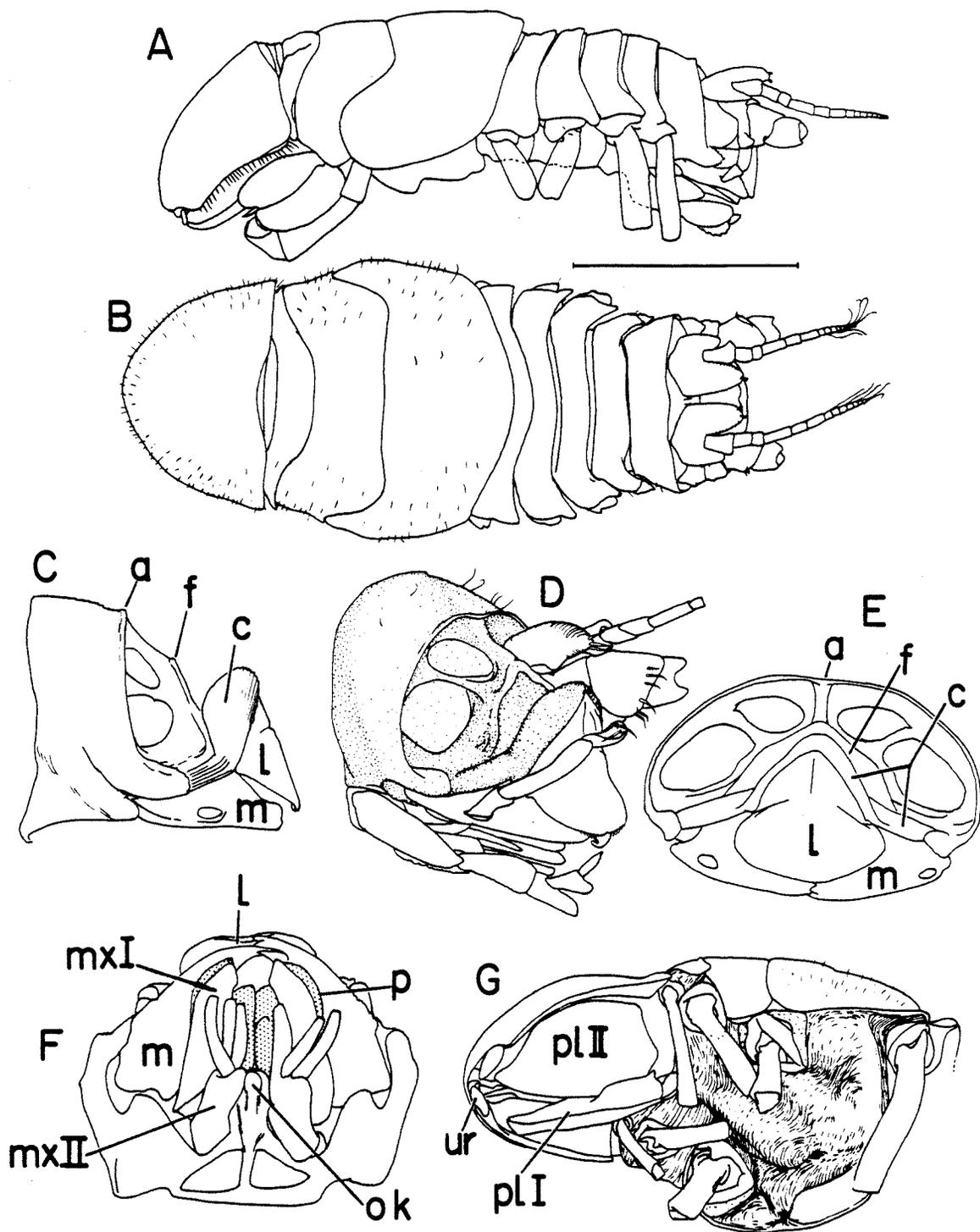
than mandibular body. Pereopodal bases I-IV increasing slightly in length posteriorly, all longer than natapodal bases V-VII; basis V shortest and stoutest, bases VI-VII increasingly longer and less stout posteriorly. Pereopods V-VI natatory, with broad carpi and propodi. Pereopod VII near length of 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 ilyarachnoid eurycopids. Although its members have the short, broad head and reduced frontal area characteristic of the Ilyarachnidae and the ilyarachnoid eurycopids, the pereon and pleotelson are much more characteristic of the Eurycopidae in the posteriorly rounded, bullet-shaped appearance. The uropods are also very eurycopid-like, although somewhat reduced and modified in their position. The only feature of the posterior half of the body that unequivocally identifies Coperonus as a member of the ilyarachnoid eurycopids is the reduction of pereonite 7 and its limb.

Figure 2.1. Coperonus comptus new genus, new species. 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; plI - male pleopod I; plII - male pleopod II; ur - uropod.



Coperonus may be distinguished from the other ilyarachnoid eurycopids by its rounded natasome and relatively unmodified uropod. A large pereopod VII that retains some of its natatory function is also useful for identification, clearly separating Coperonus from Lipomera Tattersall, 1905a, 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 Vanhøffen, 1914 belong in Coperonus. Vanhøffen (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 Vanhøffen (1914, his figure number 122), the maxilliped is practically identical to that of the type-species of Coperonus, and the male pleopods are similar, but not identical (Vanhøffen, 1914, his figure number 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 Vanhøffen's types and found his specimens different. E. sp. cf. frigida Nordenstam, 1933 is

definitely a member of Coperonus; the illustrations (Nordenstam, 1933, his fig. 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 is a South Atlantic and Antarctic genus. 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 by Woods Hole Oceanographic Institution expeditions off Argentina and Brazil.

Coperonus comptus new species

(Figures 2.1 - 2.5)

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

Paratypes.--Preparatory female, USNM. Preparatory female, copulatory male, ZMUC. Preparatory female, copulatory male, MNHNP. 90 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
arced, not "V" 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.

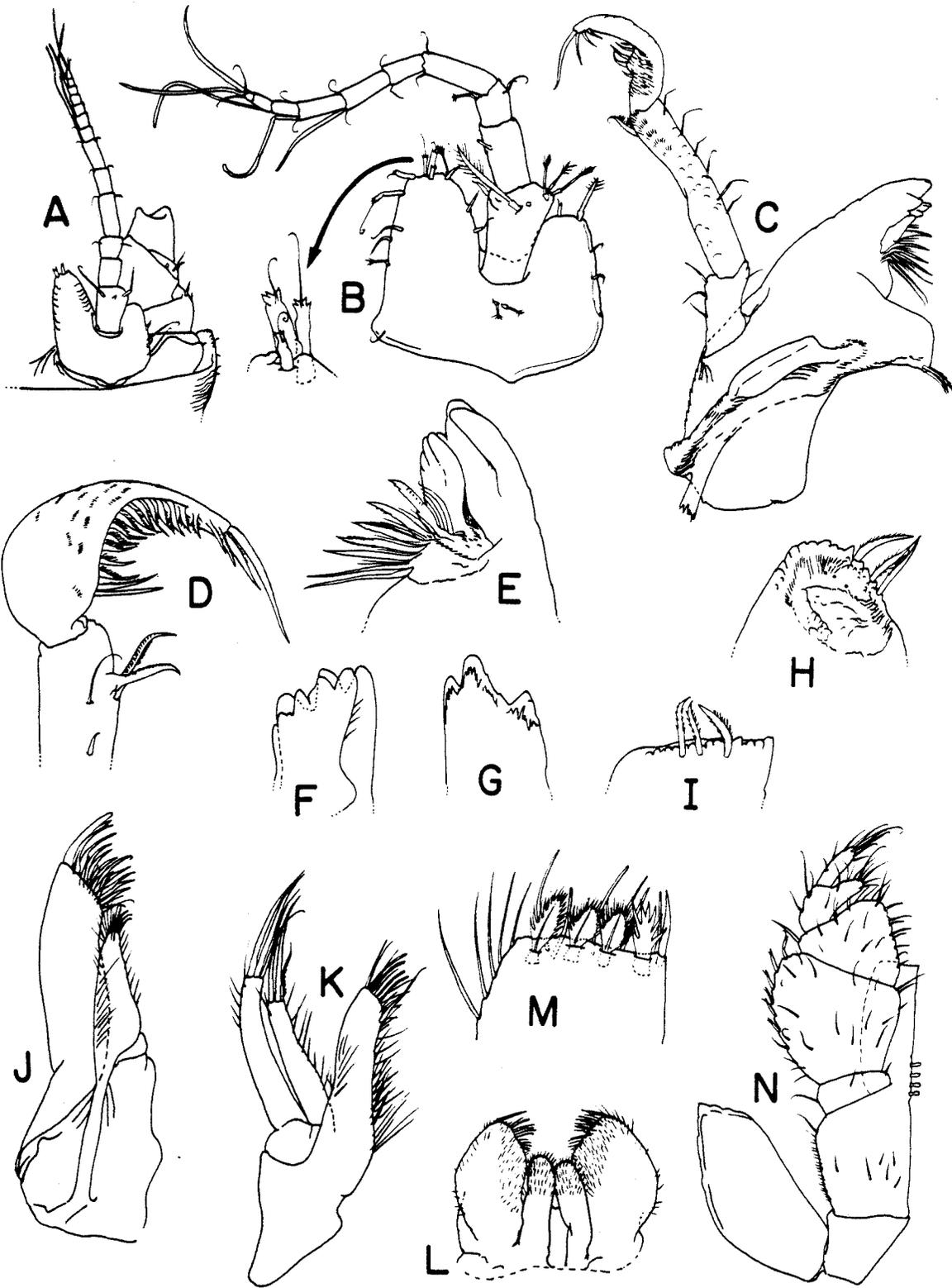
Description.--Adult body length 2.5-2.8 mm (5 inds), length 1.9-2.1
width (4 inds).

Body setation (fig. 2.1A): Natasome with tiny setae on dorsal and
lateral surfaces; other dorsal surfaces with only scattered fine
setae.

Cephalon (fig. 2.1C-F): Dorsal length 0.31 width, length 0.42 height.
Ventral margin at posterior articulation of mandible with distinct
indentation or notch.

Antennula (fig. 2.2A-B): In males length 0.35-0.36 (2 inds) body
length; in females, 0.23-0.26 (2 inds). Male antennula with 14

Figure 2.2. Coperonus comptus new genus, new species. 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.



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. 2.2C-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 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. 2.2J): Normally developed. Inner endite width 0.74 outer endite width.

Maxilla (fig. 2.2K): Normally developed. Outer lobes shorter than inner lobe.

Maxilliped (fig. 2.2M-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

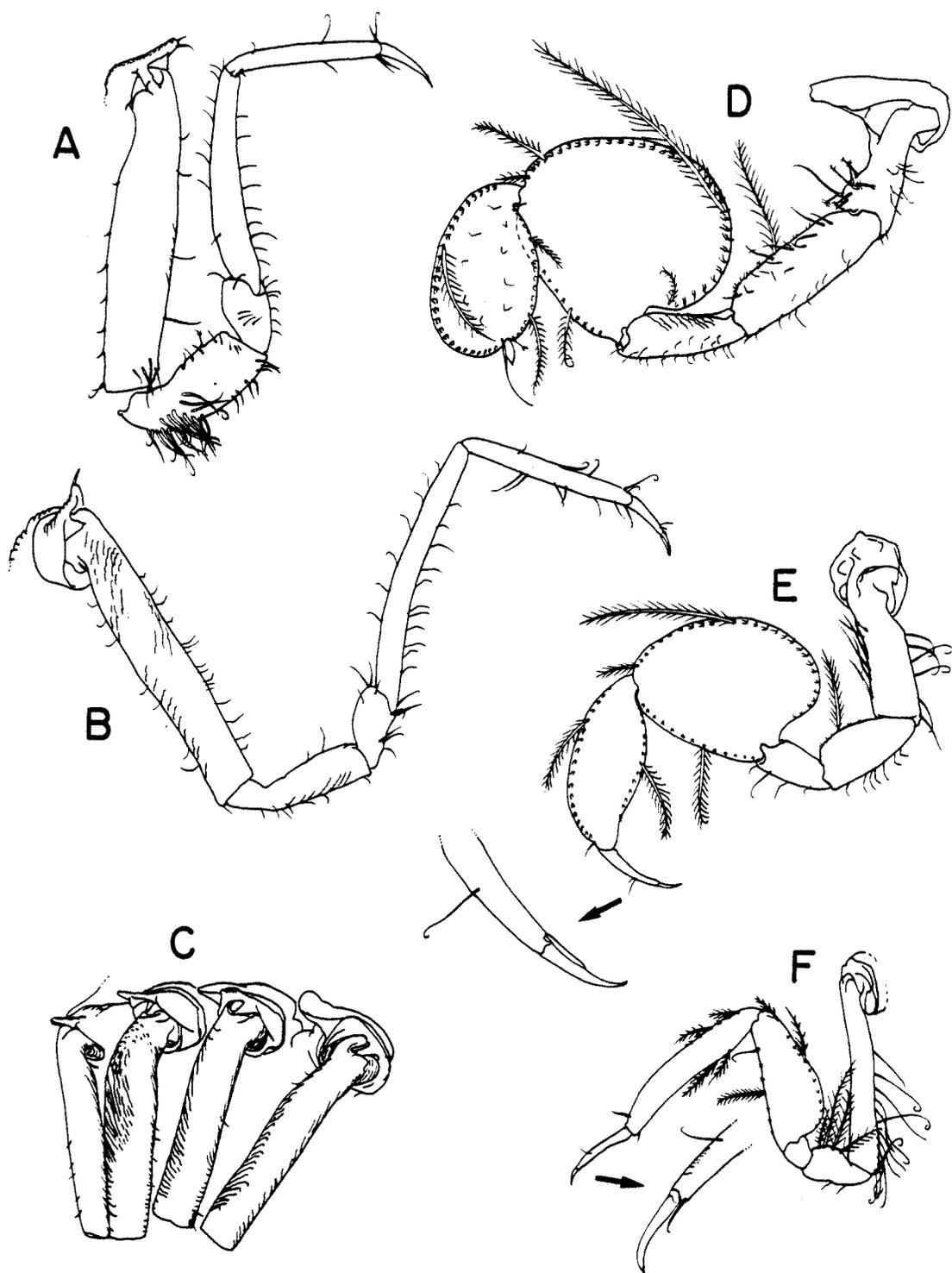
article 2 width greater than 2 times endite width, lateral length 1.6 medial length. Palp article 3 lateral length 0.19 medial length. Epipod short, narrow, and distally pointed; length 0.81 basis length; length 2.9 width.

Pereopodal Bases (fig. 2.1G, 2.3C): Bases I-IV length-body length ratios in male holotype 0.22, 0.24, 0.23, 0.26, respectively; all similarly robust. Bases V-VII in brooding female shorter than bases I-IV; length-body length ratios 0.11, 0.18, 0.19, respectively.

Pereopod I (fig. 2.3A-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. 2.3D-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; width of carpus and propodus decrease posteriorly. Pereopod V-VII length-body length ratios 0.70, 0.66, 0.60, respectively. Carpi V-VII length-width ratios 1.1, 1.3, 3.5, respectively. Propodi V-VII length-width ratios 1.6, 2.5, 5.6, respectively. Dactylus V tiny, with no distal claw (or unguis); dactyli VI-VII much longer, with claw.

Figure 2.3. Coperonus comptus new genus, new species. 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.



Male Pleopod I (fig. 2.4A-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.

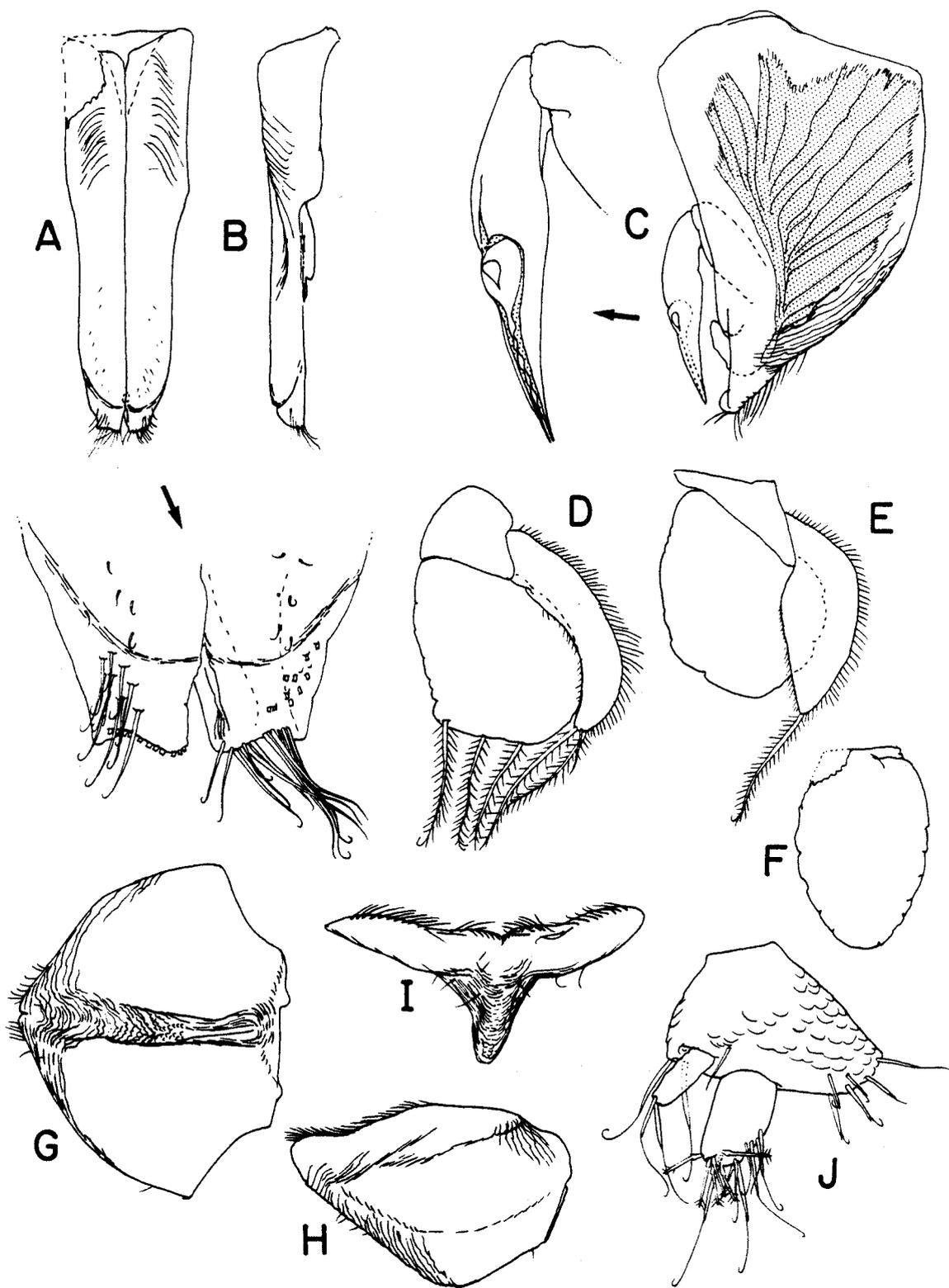
Male Pleopod II (fig. 2.4C): Protopod broad proximally, narrowing to small rounded lobe distal to exopod; length 1.5 width. Small plumose setae on distolateral margin of protopod. Stylet short, half length of protopod; sperm duct opening at stylet midpoint. Exopod bare, without tuft of fine setae.

Female Pleopod II (fig. 2.4G-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. 2.4D): Exopod extending to distal tip of endopod, with 2 long plumose setae, and 1 simple setae on distal tip.

Uropod (fig. 2.4J): 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.

Figure 2.4. Coperonus comptus new genus, new species. 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.



Remarks.--Coperonus has three 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-Localities.--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 after its describer, Åke Nordenstam.

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 of Coperonus nordenstami n. sp. are unknown. The females of this species are different from C. comptus in the form of the pleotelson, the cephalon, and the maxillipedal epipod (Nordenstam, 1933, his figure 78).

HAPSIDOHEDRA new genus

(Figures 2.5 - 2.9)

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; flagellar articles as few as 2 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, thin also. Pleopod II of female with slit dividing distal tip into two halves. Uropod with broad, flattened, oval protopod and 1 short ramus; uropod inserts subterminally and ventrally, covering anus with protopod.

Derivation of Name.--Hapsidohedra (Greek, feminine) means "vaulted rump," referring to the high, arched natasome of species of this genus.

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

Remarks.--Hapsidohedra is the most ilyarachnid-like of the ilyarachnoid eurycopids. The broad, dorsally tubular and robust cephalon, the triangular natasome tipped with a leaf-like uniramous uropod, and a non-natatory pereopod VII are all seen in the Ilyarachnidae. Indeed, Wolff (1962) chose to place the species aspidophora in Ilyarachna, apparently overlooking characters that conflicted with his diagnosis of the Ilyarachnidae: a large, rounded,

non-setiferous mandibular molar; elongate bases of pereopods III-IV; and a bilobate, thick antennular article 1. This species provided the impetus for this work; it is shocking that an animal can resemble the members of a reasonably well-defined and specialized taxon, and yet can lack the features that define the taxon. If this genus was the only one known of the ilyarachnoid eurycopids, the current definition of the Ilyarachnidae would be seriously deficient. 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 the resemblance.

Hapsidohedra shares the several important characters with the other ilyarachnoid eurycopids. These characters also make the genus different 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 ilyarachnoid eurycopids have almost identical pleopods III and IV, and Hapsidohedra is no exception.

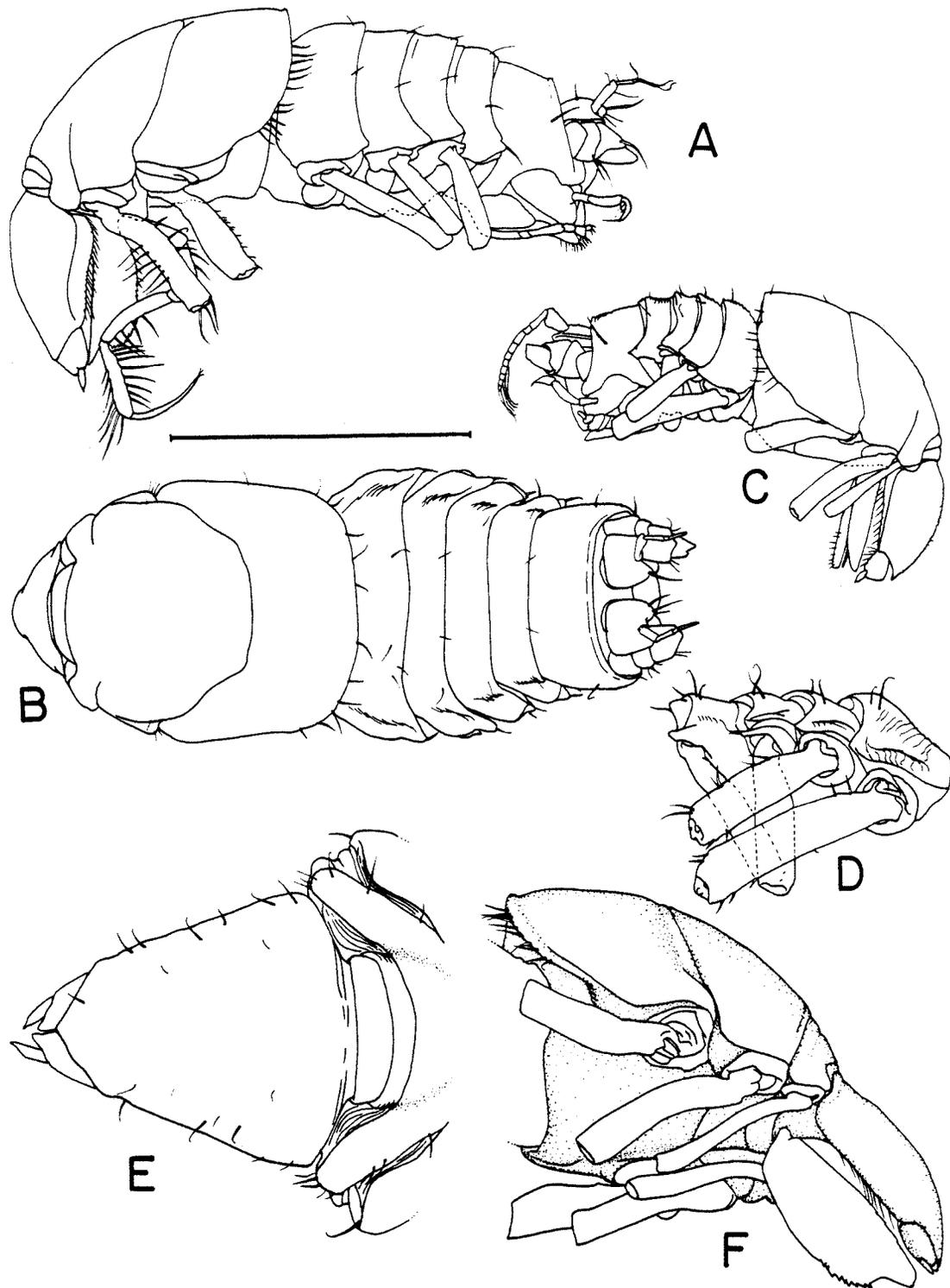
The frons of Hapsidohedra is distinctive, but the same general cephalic form is found in all the ilyarachnoid eurycopids: the frontal area is reduced, with a disappearance of the cephalic arch and the frontal area above it. As in most ilyarachnoid eurycopids, the anterodorsal dorsal margin of the cephalon 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 chapter 6.

Other characters help separate Hapsidohedra from the other ilyarachnoid eurycopids. The leaf-like 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 form of 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 two 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 the wide occurrences in the Atlantic and Pacific Oceans.

Figure 2.5. Hapsidohedra ochlera new genus, new species. 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.



Hapsidohedra ochlera new species

(Figures 2.5 - 2.9)

Holotype.--Preparatory female, bl 2.5 mm, all pereopods except left Per VII missing, USNM.

Paratypes.--Preparatory female, bl 2.3 mm; brooding female, bl 2.2 mm; male, bl 1.7 mm: USNM. Brooding female, bl 2.3 mm; male, bl 1.6 mm: ZMUC. Brooding female, bl 2.3 mm; male, bl 1.6 mm: MNHNP. 58 individuals, some dissected for description, SIO.

Type-Locality.--WHOI 295, 8° 04.2' N, 54° 21.3' W, 1000-1022 m, 8 February 1972, collected with an epibenthic sled.

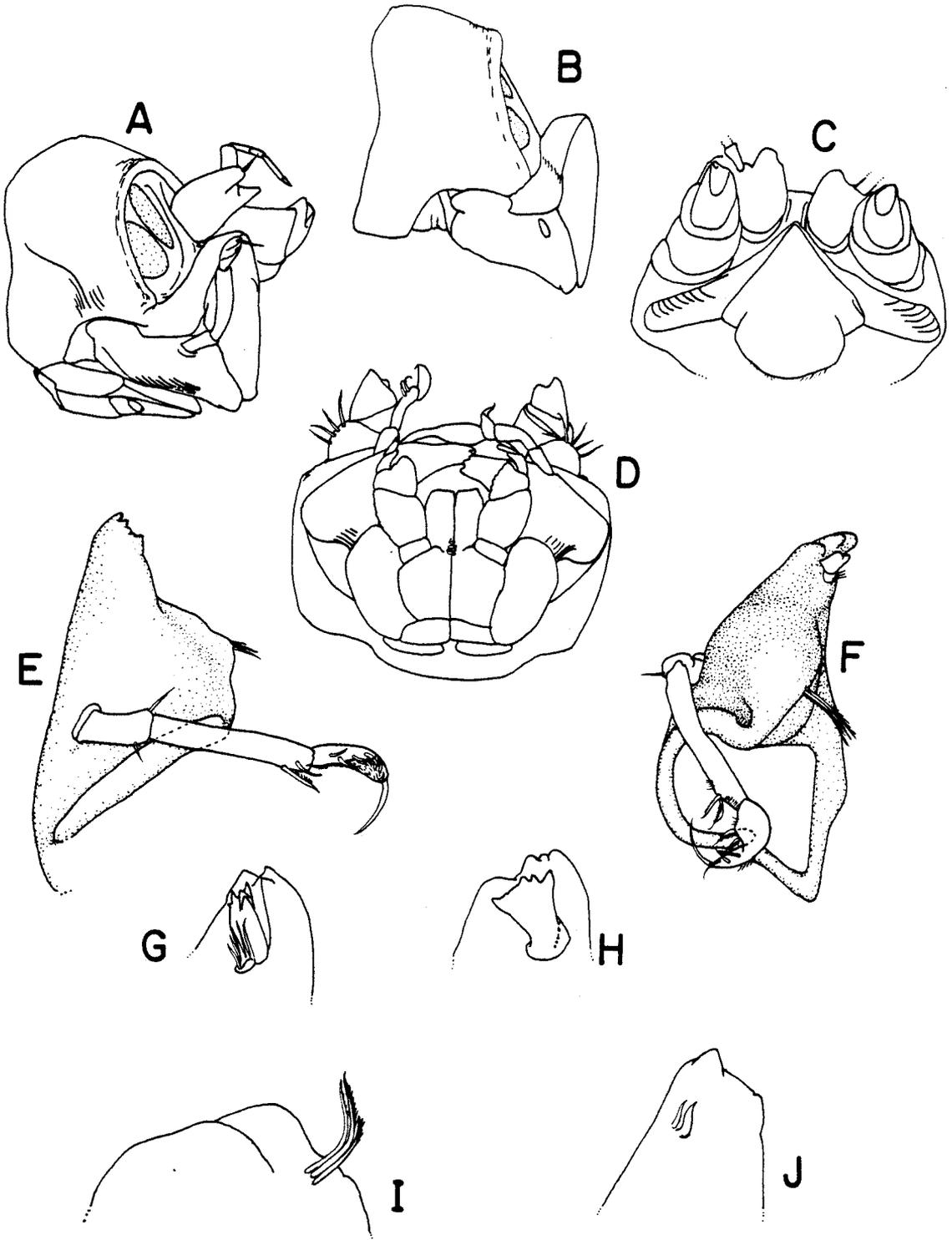
Other Material.--Five specimens, WHOI 293. Preparatory female, LGL84 C4/6; fragmentary copulatory male, LGL84 C2/2.

General Distribution.--Off Surinam, South America, 1000-1518 m, and in the Gulf of Mexico off Louisiana, 595-1386 m.

Derivation of Name.--Ochlera (Greek, feminine) 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.

Figure 2.6. Hapsidohedra ochlera new genus, new species. A-B, cephalon, frontal oblique and lateral views, antennula and antenna removed to show frons, paratype preparatory female, cephalon fragment only. C-J, paratype brooding female cephalon fragment. C-D, cephalon, anterior and ventral views, dorsal setation not shown. E-I, left mandible, 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.



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

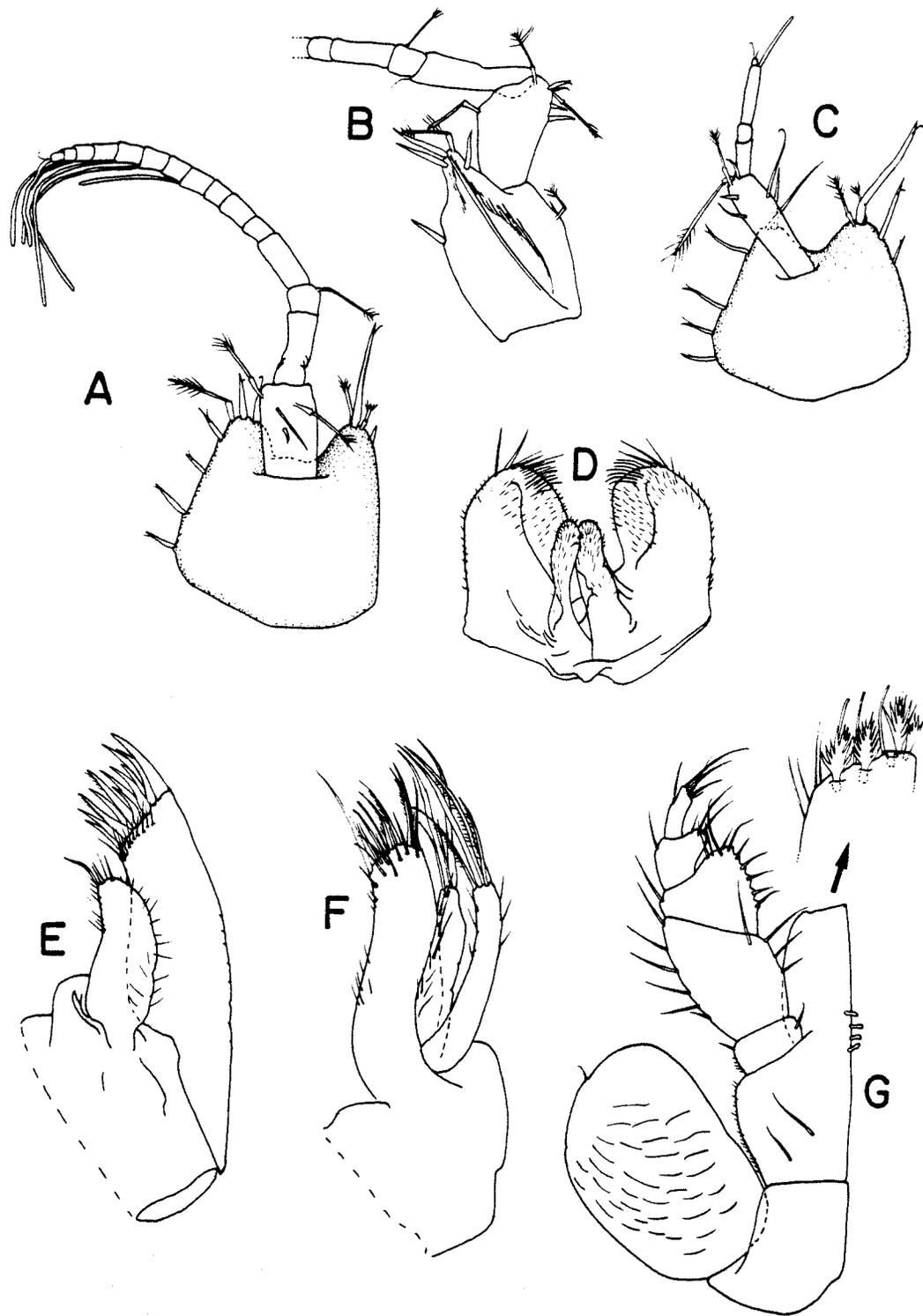
Body Setation (fig. 2.5A,C,E-F): Cephalon with single large simple seta. Dorsal surface of ambulatory pereonites with sparse row of simple setae near anterior margins. Anterior margin of pereonite 5 with row of simple setae. Ventrolateral margin of pleotelson with thick row of plumose setae.

Cephalon (fig. 2.6A-D): Dorsal length 0.42 width, length 0.49 height.

Antennula (fig. 2.7A-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 one 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. Article two 0.62 medial length of article one in male, 0.76 in female.

Mandible (fig. 2.6E-J): Left incisor process with 4 cusps, with gap between dorsal cusp and three 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 two members. Molar process with three closely-clumped

Figure 2.7. Hapsidohedra ochlera new genus, new species. 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.



setulate setae. Condyle length 0.54 mandibular body length. Palp second article length 0.43 mandibular body length.

Maxillula (fig. 2.7E): Normally developed. Inner endite 0.64 width of outer endite.

Maxilla (fig. 2.7F): Normally developed. Outer lobes distinctly shorter than inner lobe.

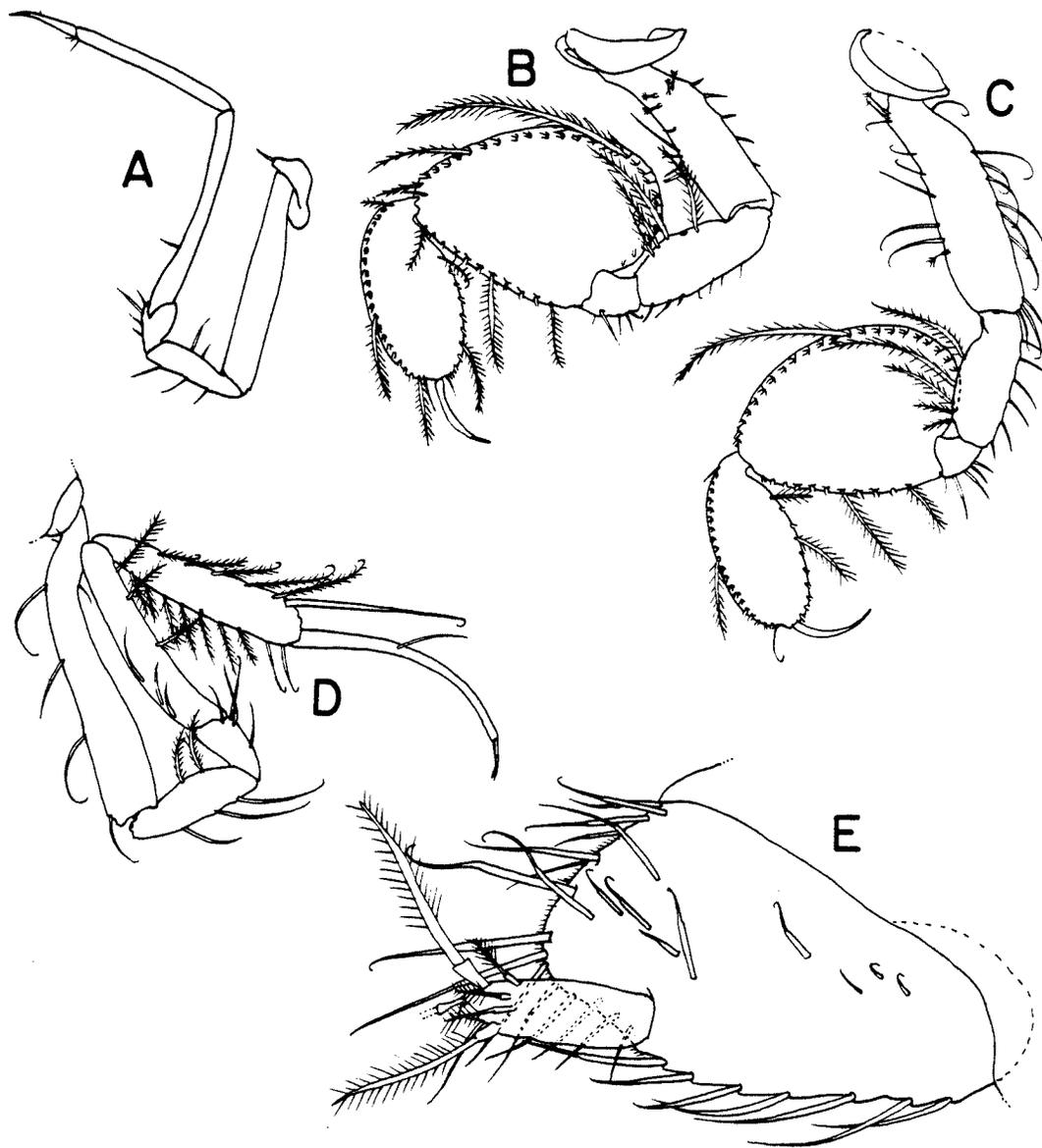
Maxilliped (fig. 2.7G): Coxal plate large, nearly as long as width of epipod. Endite with 4 receptaculi medially and 5 fan setae distally. Palp article 2 lateral length 1.1 endite lateral length; lateral length 1.7 medial length. Palp article 3 lateral length 0.29 medial length. Epipod outline bean-shaped, with rounded lateral and distal margins; length 1.5 width; distal margin with single simple seta.

Pereopodal Bases (fig. 2.5D,F; 2.8A-D): In female, bases I-VII length/body length ratios 0.19, 0.16, 0.17, 0.23, 0.19, 0.23, 0.20, respectively. 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. 2.8A): Total length 0.77 body length. Carpus length subequal to basis length. Carpus and propodus thin, paucisetose.

Natatory Pereopods V-VI (fig. 2.8B-C): Total lengths 0.69, 0.71 body length, respectively. 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.

Figure 2.8. Hapsidohedra ochlera new genus, new species. 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.



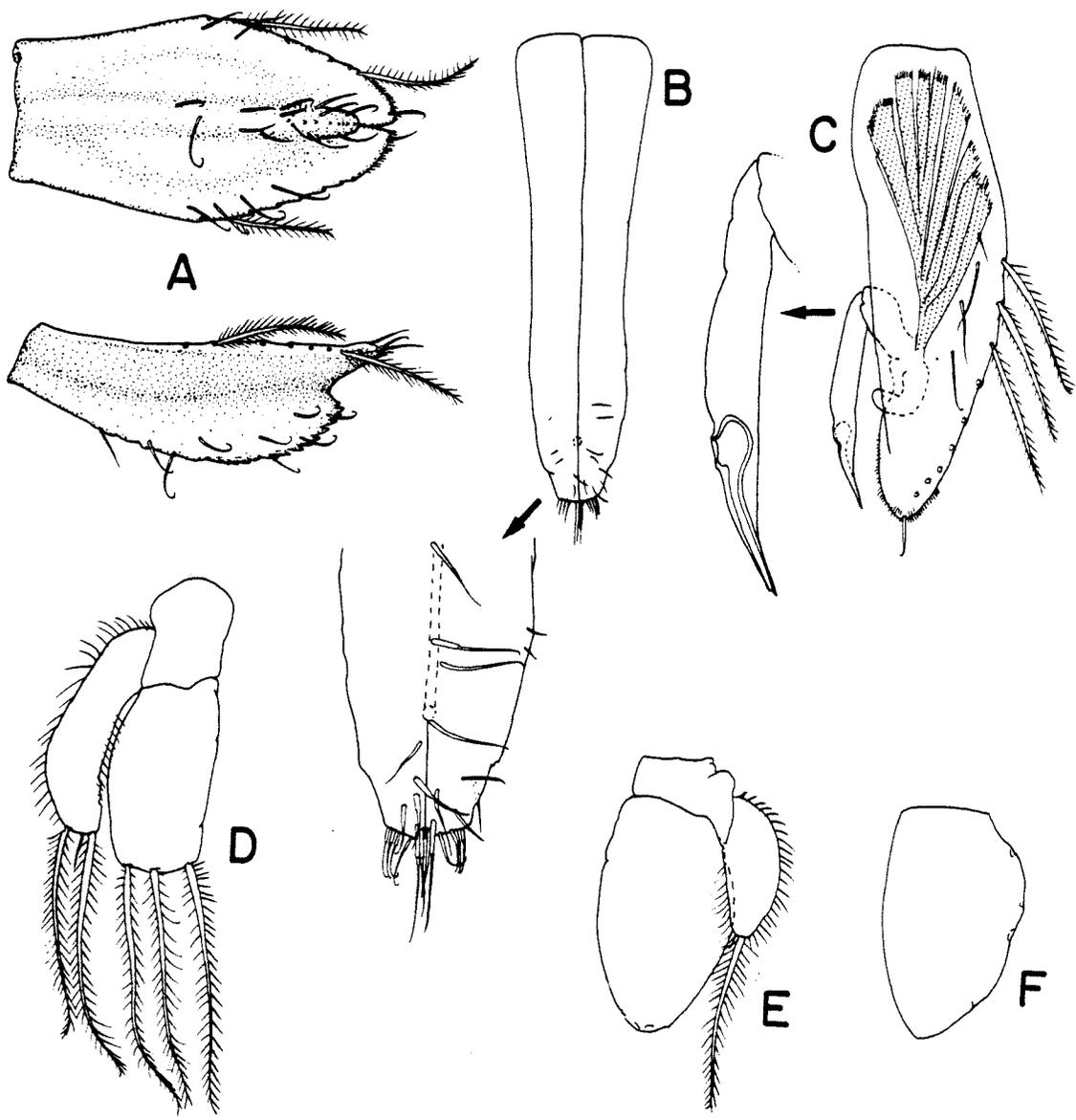
Pereopod VII (fig. 2.8D): Total length 0.65 body length. Basis length 0.27 total length. Carpus and propodus narrow, with fewer setae on margins than on anterior natatory limbs; length/width ratios 5.7, 4.7 respectively. Dactylus long, thin, curved, length 1.2 propodus length.

Male Pleopod I (fig. 2.9B): 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, marked only by rounded angles. Distal tip with setae dorsally, ventrally, and more proximally along midline. Setae thick and tubular proximally, narrowing abruptly at midlength, and thin, whip-like distally. Remainder of ventral surface without setae.

Male Pleopod II (fig. 2.9C): 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. 2.9A): Opercular fused pleopod pair narrow, horseshoe shaped in dorsal view, 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 2.9. Hapsidohedra ochlera new genus, new species. 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.



Pleopod III (fig. 2.9D): Exopod longer than endopod, distally rounded, with long thin simple setae on lateral margin, shorter thin, simple setae on medial margin, and two long plumose setae distally having thick simple seta between them. Endopod with three long plumose setae. All plumose setae longer than exopod.

Pleopod IV (fig. 2.9E): Exopod short, rounded, approximately half length of pleopod length; single long plumose seta on distal tip.

Uropod (fig. 2.8E): 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 identified by the form of the keel of the female pleopod II 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 useful as well.

This species has been found on shallow bathyal bottoms in the Gulf of Mexico and in the Southern Caribbean Sea. It will be interesting to discover whether it is continuously distributed, or whether the species is made of disjunct populations interrupted by barriers such as the Yucatan Penninsula.

Hapsidohedra aspidophora (Wolff, 1962)

(Figure 2.10)

Synonym.--Ilyarachna aspidophora: Wolff (1962), p. 106-108.

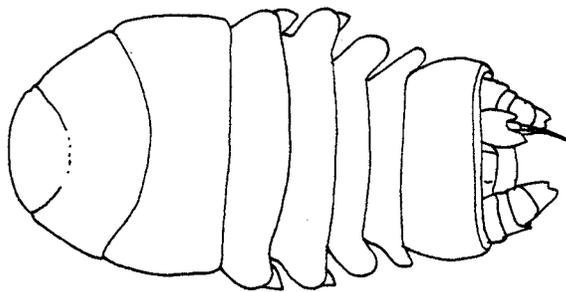
Holotype.--Brooding female with about 20 embryos in marsupium, bl 3.2 mm, body width 1.4 mm (not seen by me). No other types.

Type-Locality.--R/V Galathea station 639, off East New Zealand, 37° 31' S, 177° 08' E, 213 m, bottom temperature circa 14.7° C (see Brunn (1959) for more information).

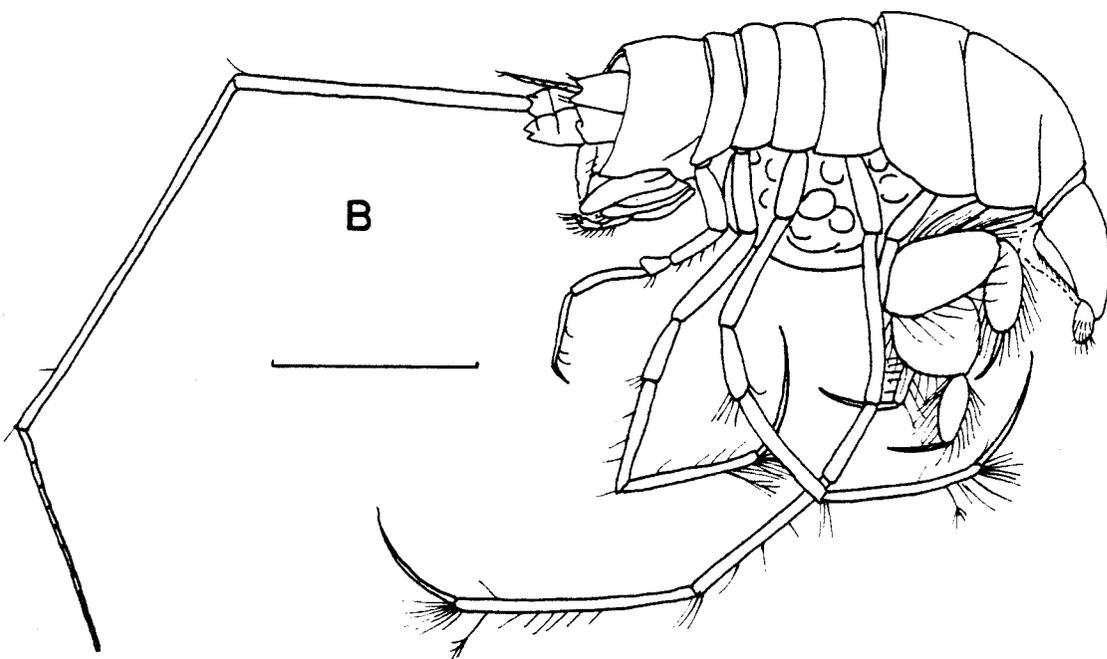
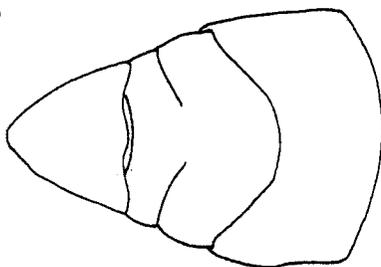
Diagnosis.--Antennular article 2 shorter than medial lobe. Mandible lacking spine row on incisor process; molar process with only 1 serrate seta distally. Keel of female pleopod II dorsally and distally setose, lacking denticles on ventral margin, and sloping smoothly into distal tip.

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 is different in the form of the female pleopod II and the antennula. The mandibular characters, although less useful for sorting purposes, may also be useful for distinguishing H. aspidophora from H. ochlera. The male of H. aspidophora is unknown.

Figure 2.10. Hapsidohedra aspidophora (Wolff, 1962). A-B, dorsal and lateral views of holotype, after Wolff (1962).



A



B

Hapsidohedra aspidophora is known from surprisingly shallow (213 m) and warm (14° C) waters off East New Zealand. It will be of considerable biogeographic interest to know the full range of this species and its preferred hydrographic regime. 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).

LIONECTES New Genus

(Figures 2.11 - 2.14)

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. Pereopodal bases lengths 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 group of ilyarachnoid eurycopid genera that have seventh pereopods resembling walking legs; in addition to this genus, the group includes Coperonus and Hapsidohedra. Because this group has functional seventh pereopods, it is distinct

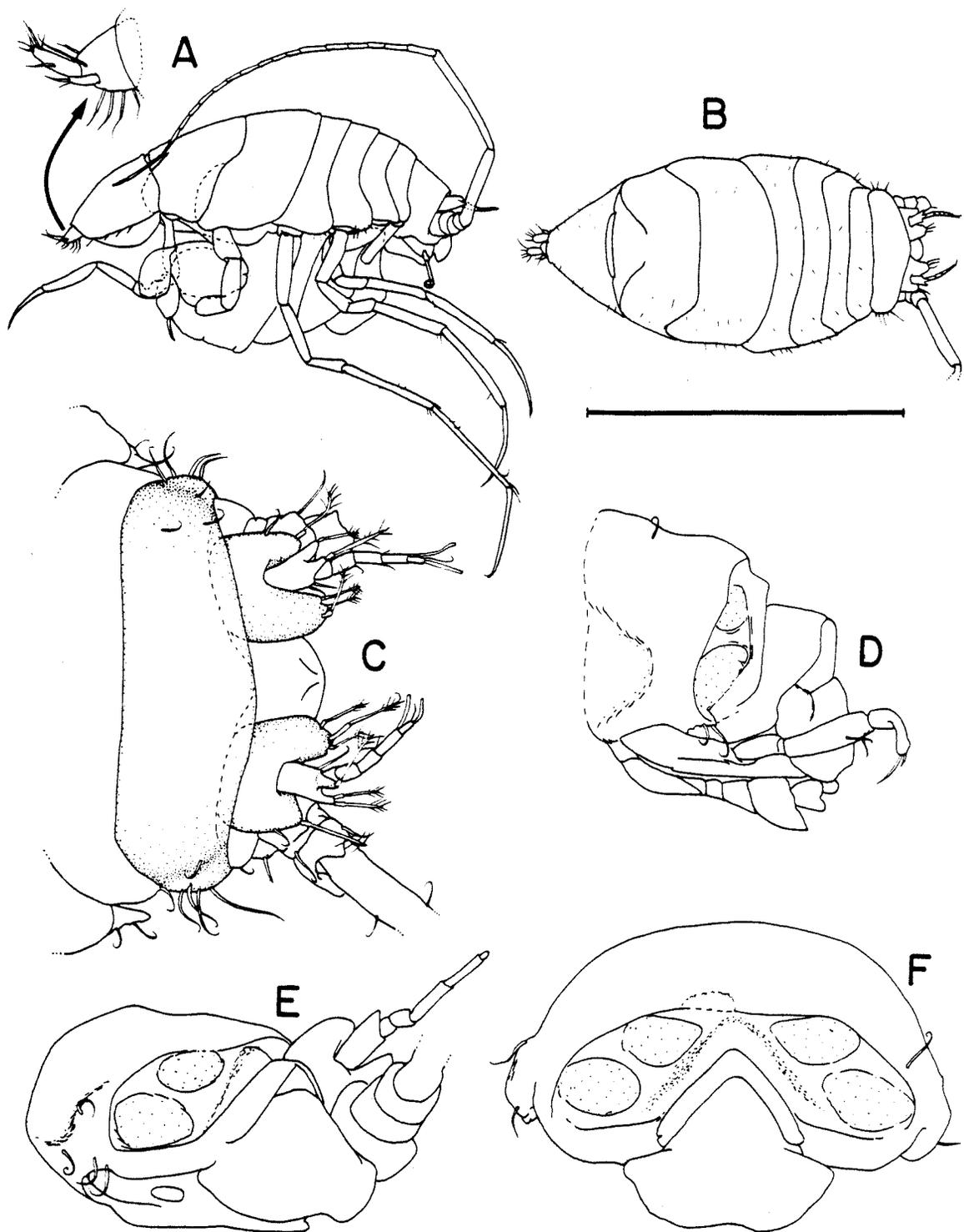
from the genera Lipomera and Mimocopelates which lack seventh pereopods (or at least functional ones). Although these three genera resemble each other in general form of the cephalon and the natasome, each one has specializations, or lack thereof, that make them distinct. Lionectes is identified by a smooth almost seed-like 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 East Antarctica. Vanhöffen's (1914) illustrations (p. 590) 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 make 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 owing to 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 their restricted distribution may be partially due to 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.

Figure 2.11. Lionectes humicephalotus new genus, new species. 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.



Lionectes humicephalotus new species

(Figures 2.11 - 2.14)

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

Paratypes.--3 brooding females, 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.

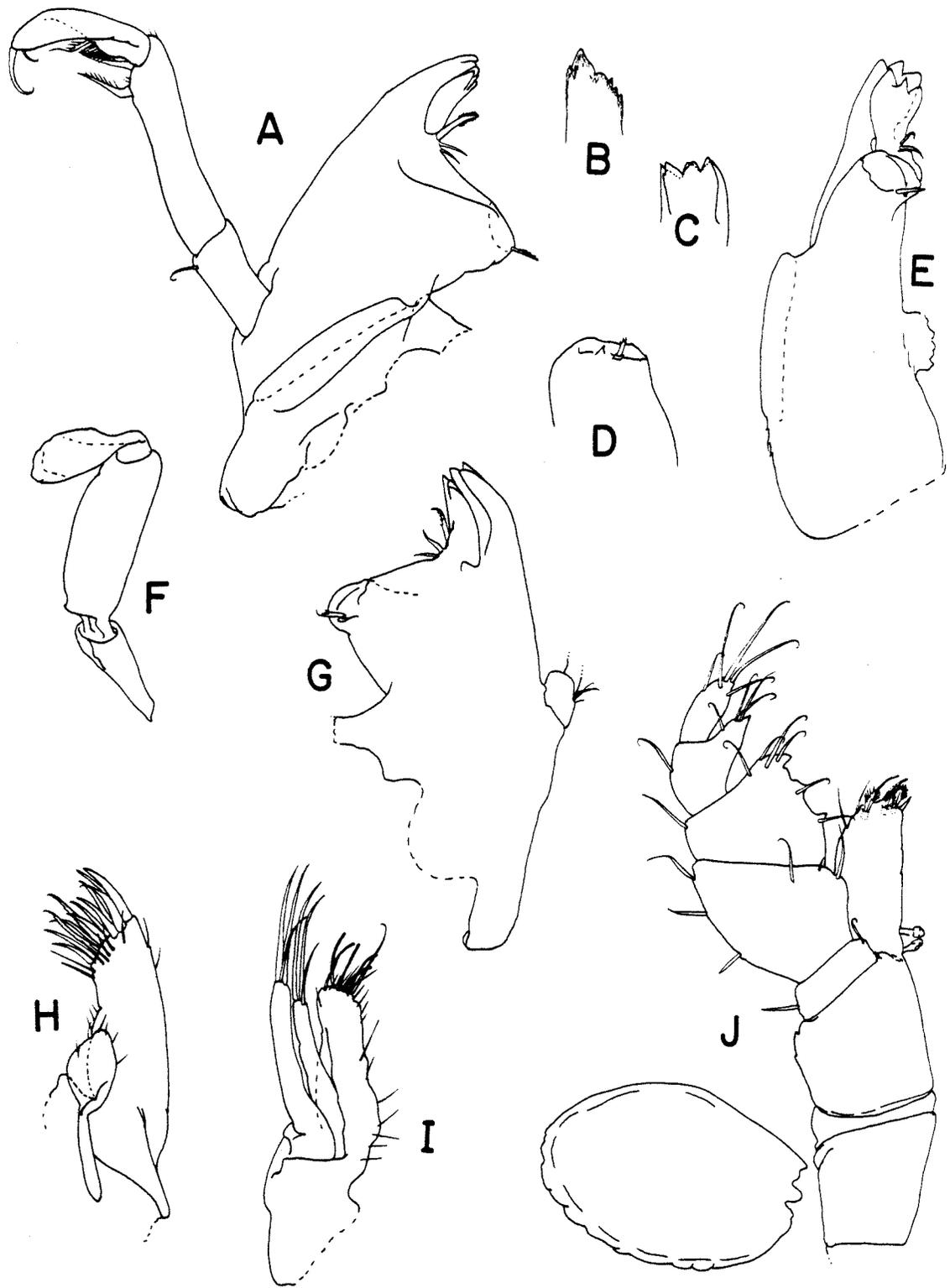
General Distribution.--South Shetland Islands to the Weddell Sea, 58.6-659 m.

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. 2.11A-B): Adult body length 1.1-1.4 (4 inds) mm, length 1.9-2.0 (4 inds) width.

Figure 2.12. Lionectes humicephalotus new genus, new species, 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.



Body setation (fig. 2.11B): Natasome with approximately 5 setae on each ventrolateral margin; other dorsal surfaces with scattered fine setae.

Cephalon (fig. 2.11C-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. 2.11C): 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. Articles 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. 2.11A): 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. 2.12A-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 second article length 0.36-0.38 (2 inds) mandibular body length; distal article robust, strongly curled.

Maxillula (fig. 2.12H): Normally developed. Inner endite short and rounded, lacking large apical seta, but with several smaller setae, width 0.61 outer endite width.

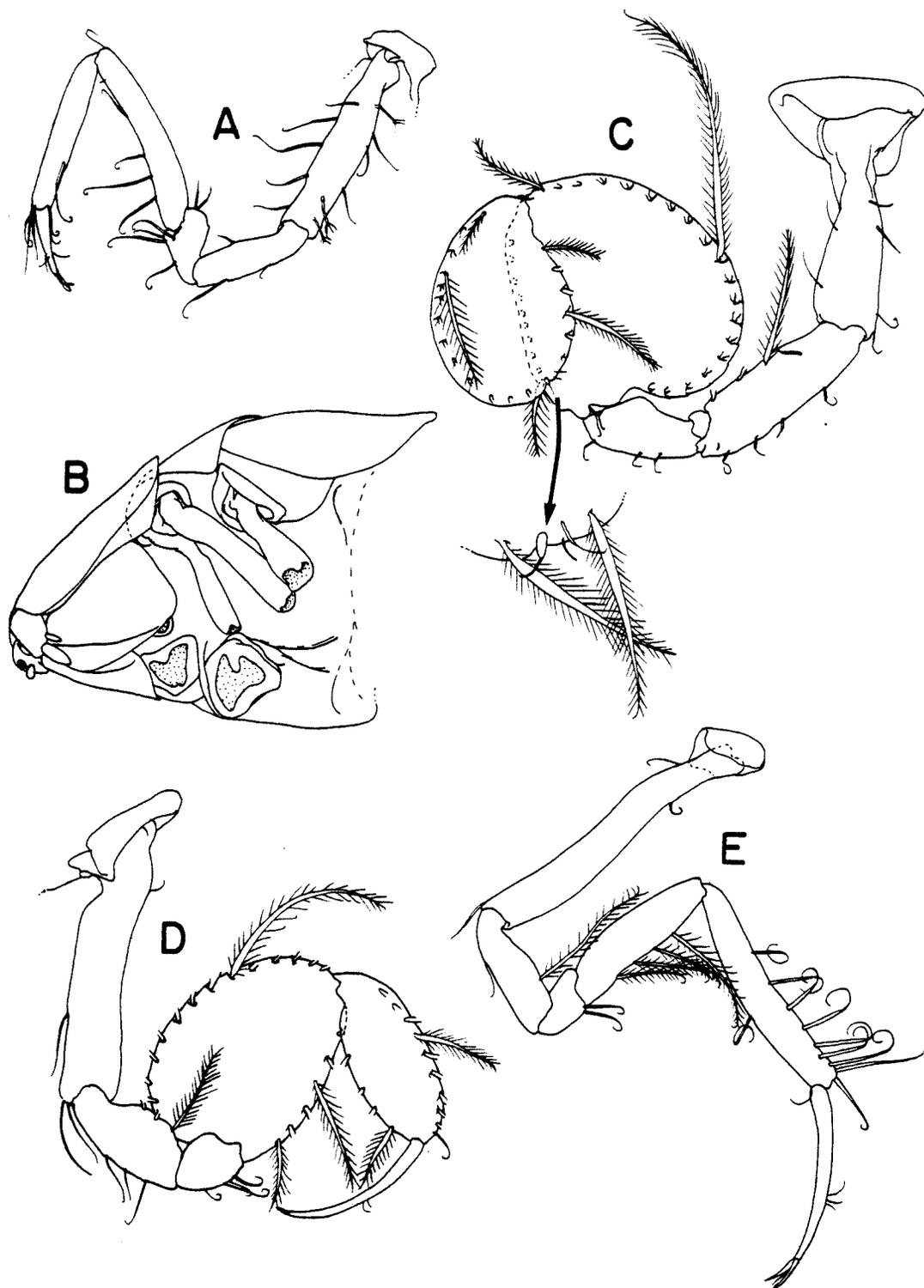
Maxilla (fig. 2.12I): Normally developed. Outer lobes approximately same length as inner lobe.

Maxilliped (fig. 2.12J): 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. 2.11A, 2.13A): Pereopods I-IV thin, lightly setose; length-body length ratios 0.61, 0.92, 1.0, 1.2, respectively. Bases I-IV length-body length ratios 0.17, 0.15, 0.17, 0.21, respectively.

Natatory Pereopods (fig. 2.13C-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

Figure 2.13. Lionectes humicephalotus new genus, new species, 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.



carpus. Pereopods V-VII increasing in length but becoming narrower posteriorly; length-body length ratios 0.74, 0.79, 0.83, respectively. Bases V-VII also increasing in length posteriorly; length-body length ratios 0.17, 0.21, 0.23, respectively. Carpi V-VII length-width ratios 1.0, 1.4, 3.7, respectively. Propodi V-VII length-width ratios 1.5, 2.5, 6.6, respectively; propodi V-VII length carpus length ratios 0.90, 0.84, 1.5, respectively. Dactyli VI-VII long, curved; length-propodus length ratios 0.90, 0.89, respectively. Dactylus V rudimentary.

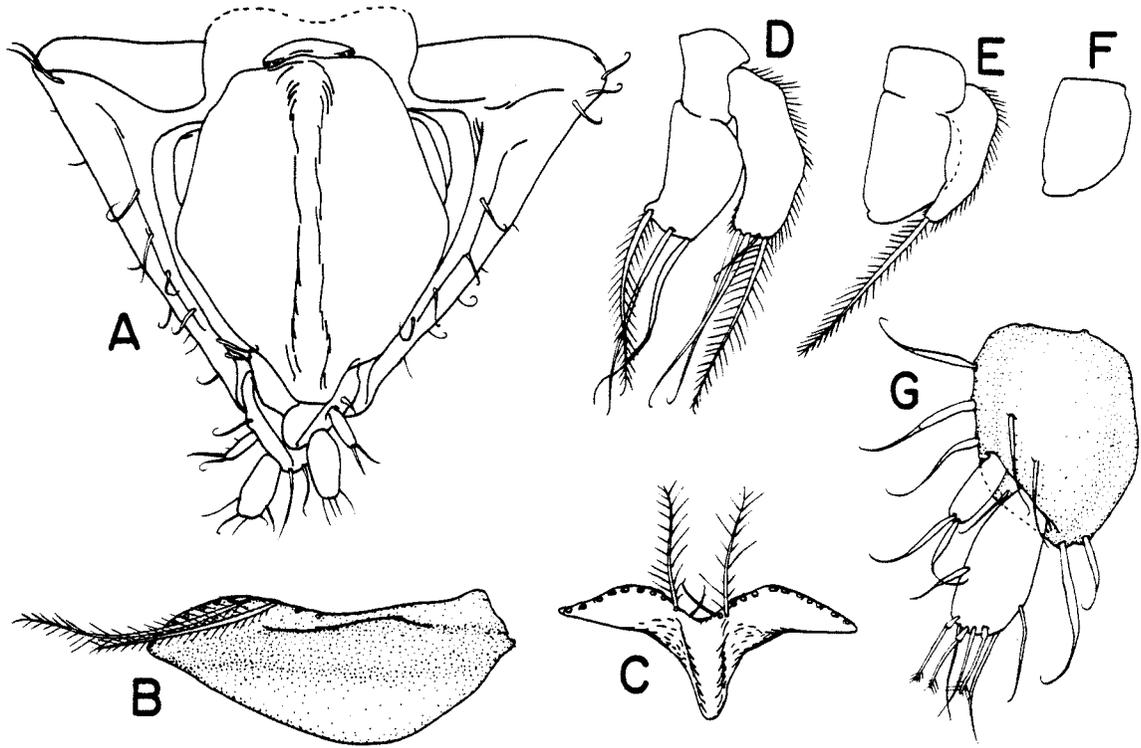
Male Pleopods I and II: unknown.

Female Pleopod II (fig. 2.14A-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. 2.14D): 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. 2.11A, 2.14G): 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.

Figure 2.14. Lionectes humicephalotus new genus, new species,
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.



Remarks.--Lionectes humicephalotus is currently known only from females; 4 brooding females were collected at the type locality off King George Island, and 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 since Vanhöffen's specimen was not brooding. A more detailed characterization of Lionectes must await the capture of males.

Genus LIPOMERA Tattersall, 1905a

(Figures 2.15 - 2.24)

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

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. Midgut 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, leaf-like.

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."

Generic Remarks.--Tattersall (1905a) made this genus the type of a new family, Lipomeridae, whereas the same author (1905b), in writing the full description of Lipomera, placed it into the Munnopsidae, which then included the current family-group 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 first paper may possibly have come out late in 1905, making some authors believe it was published in 1906. Note that if Lipomera is placed in the same family with Eurycope but separate from the Munnopsidae, then the family must be called Lipomeridae because a family-level name was not based on Eurycope until Hansen's (1916) Eurycopini. Eurycopidae would be a junior synonym of Lipomerinae. A better resolution of this problem is the revised classification of the munnopsoid taxa (see chapter 5).

Lipomera is easily separated from other ilyarachnoid eurycopids. None of the other ilyarachnoid genera 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 somewhat similar new genus Mimocopelates. Rudimentary or absent seventh pereopods distinguish Lipomera from the new genera Coperonus, Hapsidohedra, and Lionectes.

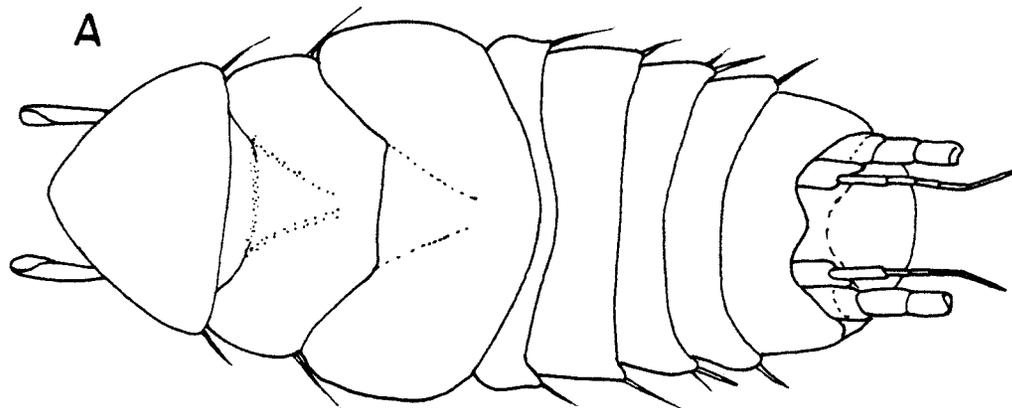
Lipomera must be divided into three new subgenera, L. (Lipomera), L. (Tetracope), and L. (Paralipomera), because important specializations identify groups of species within the genus but not the genus a whole. Subgenus Lipomera contains the generic type-species, L. (L.) lamellata, and consists of short and broad species that have short heads, smooth dorsa without denticles on the anterior margins, and rudimentary pereopods VII and pereonites 7. Subgenus Tetracope is similar to L. (Lipomera) in body shape and retention of a rudimentary pereopod VII but 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. Subgenus Paralipomera is similar to L. (Lipomera) in having only a modest bend in the midgut, pereonite 5 and pereopod V larger than pereonite 6 and pereopod VI, and having 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.

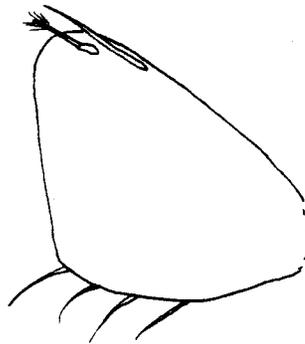
Species of Lipomera have curved, strongly bent, or coiled midguts (figure 2.21). This is highly unusual in the Crustacea. Few other groups are known to have coiled guts; Calman (1909) mentioned only two, a group of Cladocera and a single genus of Cumacea. A curved or coiled gut is a derived condition in this genus, because all of the other ilyarachnoid eurycopids, or munnopsoids more generally, have straight guts (personal observations). In another invertebrate taxon, the bivalve Abra profundorum, a coiled gut has been associated with an adaptation to the food poor conditions of the deep sea (Allen and Sanders, 1966). The caeca off the anterior portion of the midgut are unusually large in Lipomera, supporting this hypothesis. There is no certainty that improved digestion is the reason convoluted guts are seen in Lipomera, although alternative hypotheses are not apparent at this time.

Lipomera is currently known only from the Atlantic Ocean: north, south, and the Gulf of Mexico.

Figure 2.15. Lipomera (Lipomera) lamellata Tattersall, 1905a, new subgenus. A, holotype female, dorsal view. B, uropod, ventral and lateral views. C, rudimentary pereopod VII. After Tattersall (1905b).



B



C

LIPOMERA New Subgenus

(Figures 2.15, 2.21B)

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. Midgut curved, not coiled. Pereopod VI shorter than pereopod V. Pereopod VII present but rudimentary.

Composition.--Monotypic: Lipomera (Lipomera) lamellata Tattersall, 1905a.

Lipomera (Lipomera) lamellata Tattersall, 1905a

(Figure 2.15)

Types.--Eleven syntype individuals from 60 miles West of Achill Head, Ireland, August 1901, 199 fathoms (364 meters), 53° 58' N, 12° 16' W. Length of (figured?) 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 not examined.

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

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 due to its inhabiting a depth that is too shallow for many deep sea studies, and too deep for most shallow water benthic work. Another undescribed species of L. (Lipomera) occurs off Walvis Bay, Africa, at a depth of approximately 200 m. L. (L.) lamellata is different 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.

PARALIPOMERA New Subgenus

(Figures 2.16 -2.19)

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

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

Lipomera (Paralipomera) knorrae new species

(Figures 2.16 - 2.19)

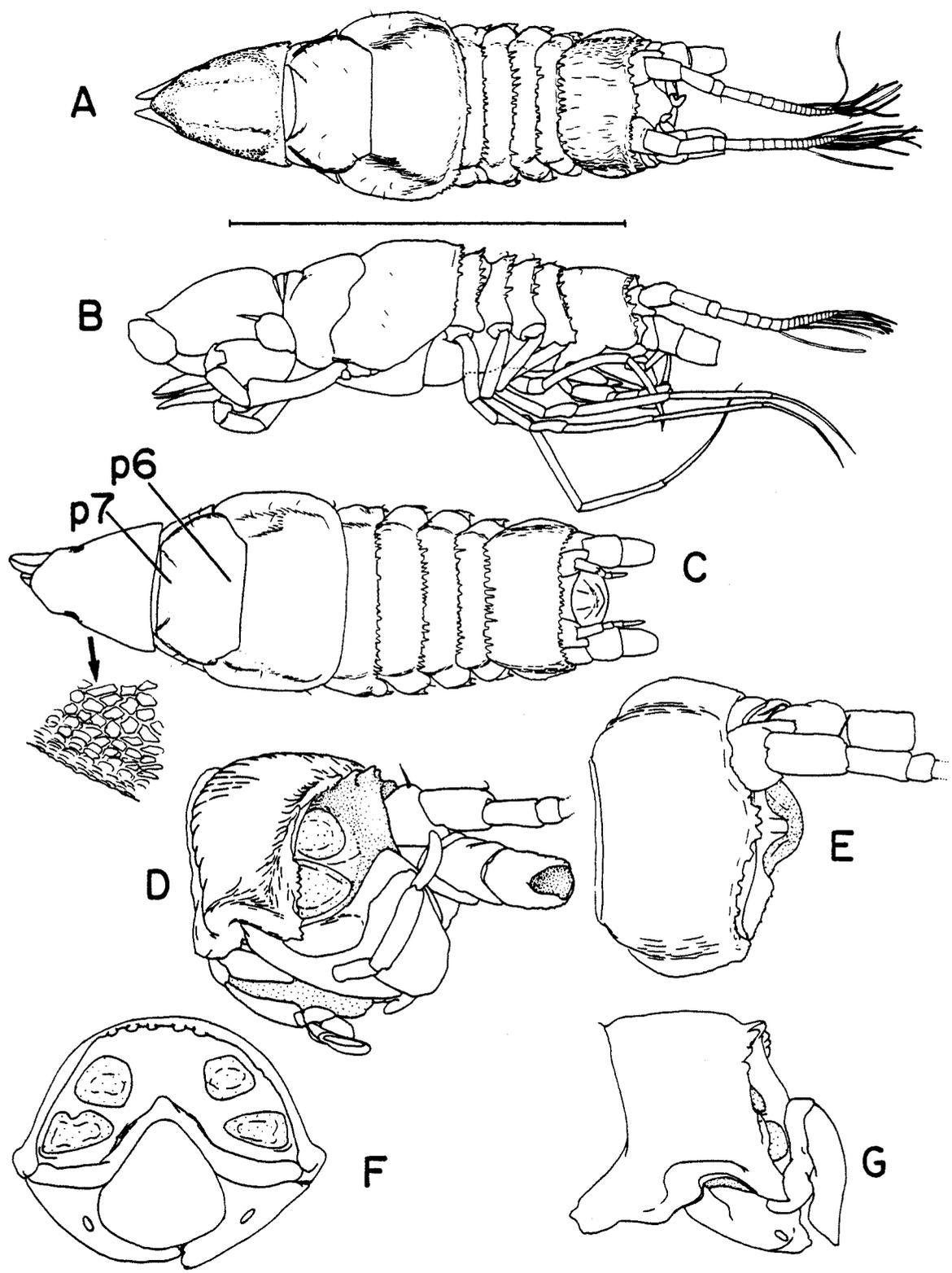
Holotype.--Copulatory male, bl 1.2 mm, USNM.

Paratypes.--Brooding female, bl 1.5 mm, USNM. Copulatory male, bl 1.2 mm, ZMUC. Brooding female, bl 1.4 mm, MNHNP. 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.

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

Figure 2.16. Lipomera (Paralipomera) knorrae new subgenus, new species. 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.



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

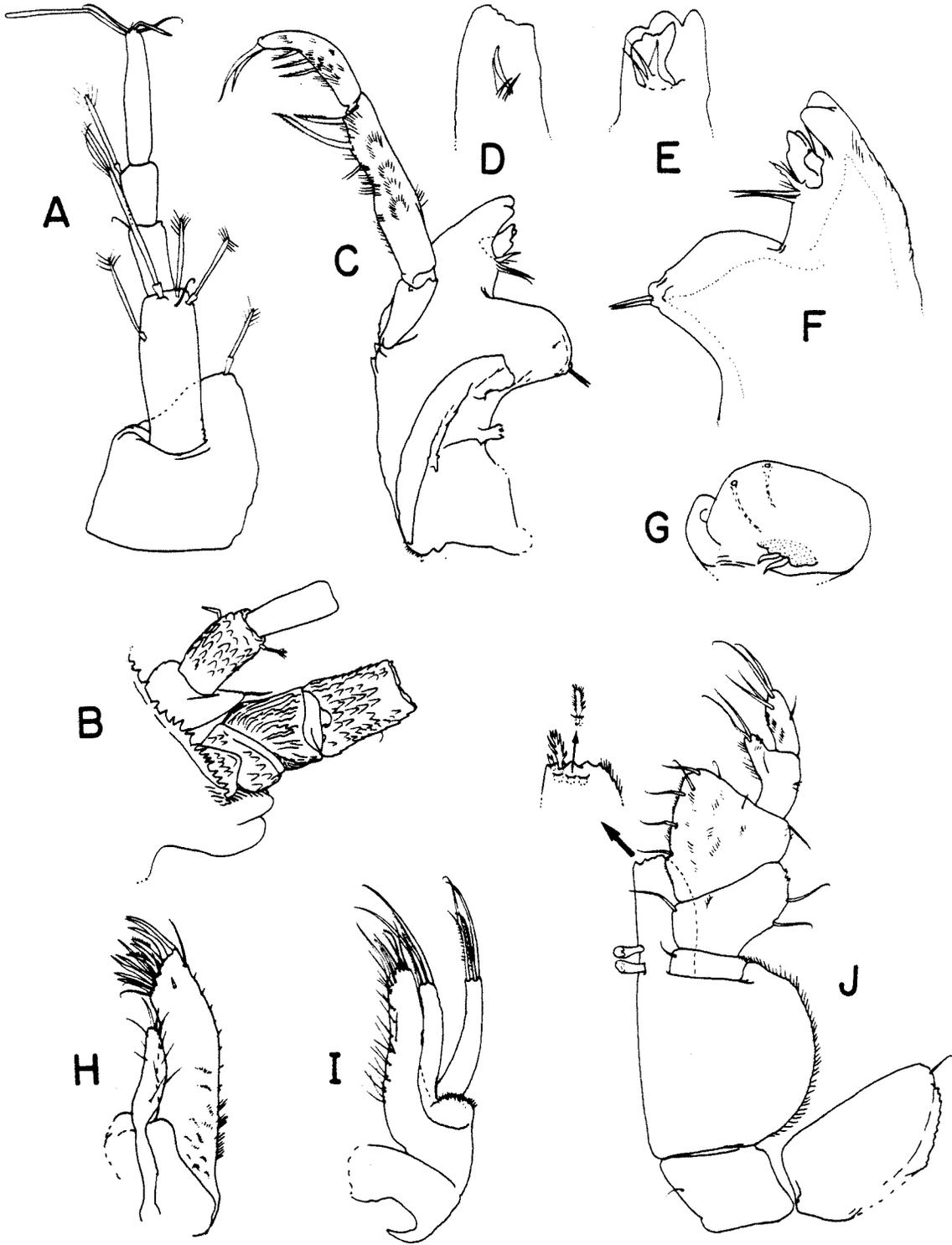
Diagnosis.--Anterior margins of cephalon and anterior 5 pereonites with numerous small spines. Cephalon medial length approximately half cephalon width. Body dorsal surfaces with fine cuticular ornamentation and scattered fine setae; anterolateral corners of pereonites and pleotelson with small fine 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. 2.16A-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. 2.16D-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.

Antennula (fig. 2.16A-B, 2.17A-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;

Figure 2.17. Lipomera (Paralipomera) knorrae new subgenus, new species. 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, lateral fan seta shown separately.



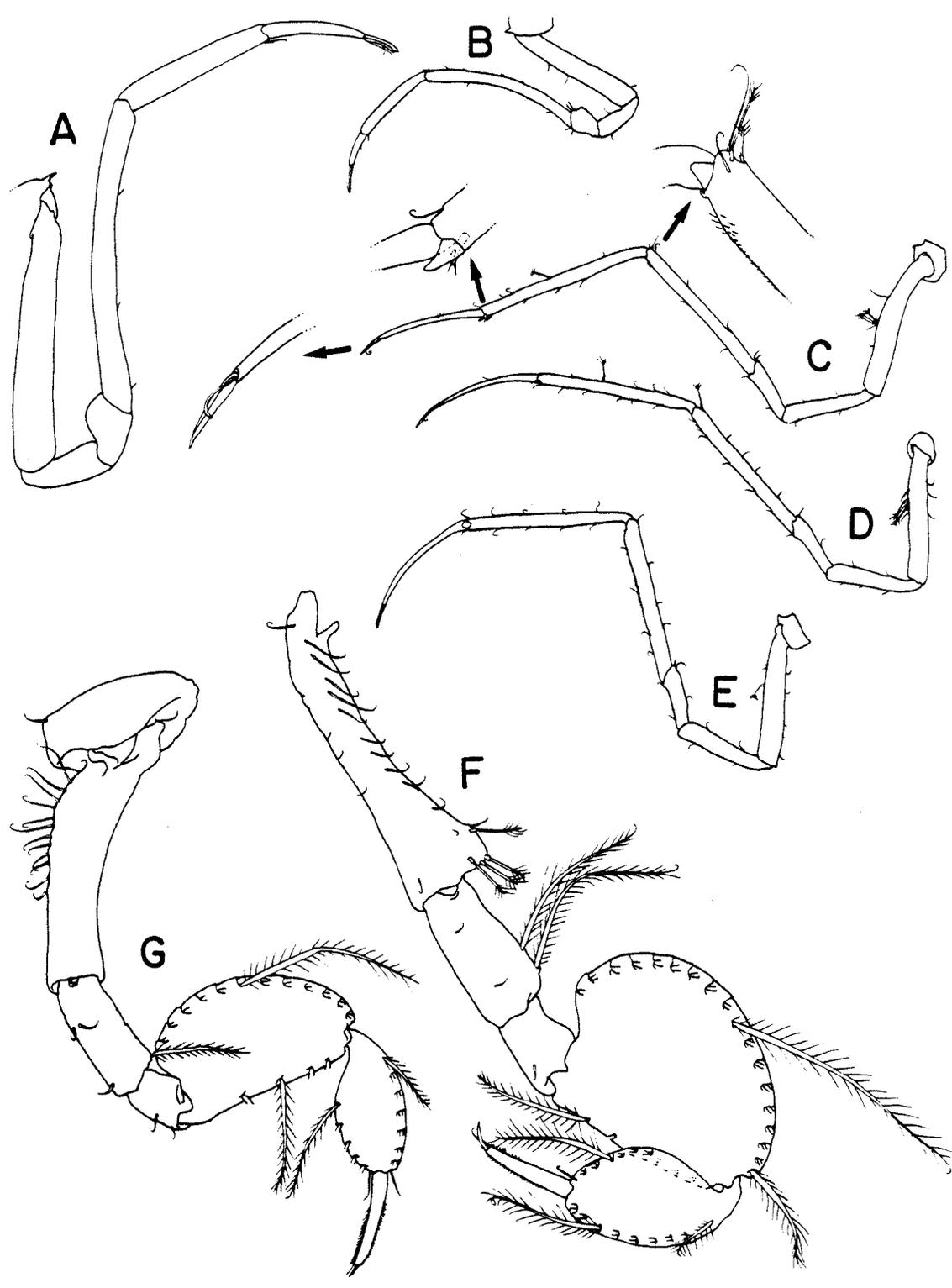
medial side of both sexes with no setae; lateral lobe with single broom seta. Articles 2 and 4 with large broom setae. Article 2 subequal to or longer than article 1 lateral lobe in both sexes, article 2 broader in males than in females. Article 3 subequal to or slightly shorter than article 2 in males, article 3 length 0.43 article 2 length in females.

Mandible (fig. 2.17C-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. 2.17H): Normally developed. Inner endite width 0.41 outer endite width.

Maxilla (fig. 2.17I): Normally developed. Outer lobes shorter than inner lobe.

Figure 2.18. Lipomera (Paralipomera) knorrae new subgenus, new species. 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.



Maxilliped (fig. 2.17J): 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. 2.18A-E): Pereopods I-IV similar, thin, without large spine-like setae; length-body length ratios 0.64, 0.95, 0.93, 0.95, respectively. Pereopod I not sexually dimorphic. Bases I-IV length-body length ratios 0.18, 0.18, 0.18, 0.19, respectively. Bases II-IV with group of broom setae on anterior midpoint.

Natatory Pereopods (fig. 2.18F-G): Natapods heterogeneous in form: pereopod V larger than pereopod VI, pereopod VII absent. Pereopod length-body length ratios 0.66 and 0.54, respectively. Bases V-VI length-body length ratios 0.21 and 0.17, respectively; 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, respectively. Propodi V-VI length-width ratios 1.7 and 2.1, respectively. Dactyli V-VI long, thin, with marginal fringe of fine setae; length ratios with respective propodi both 0.71. Unguis V claw-like, long, and curved; unguis VI similar but very short.

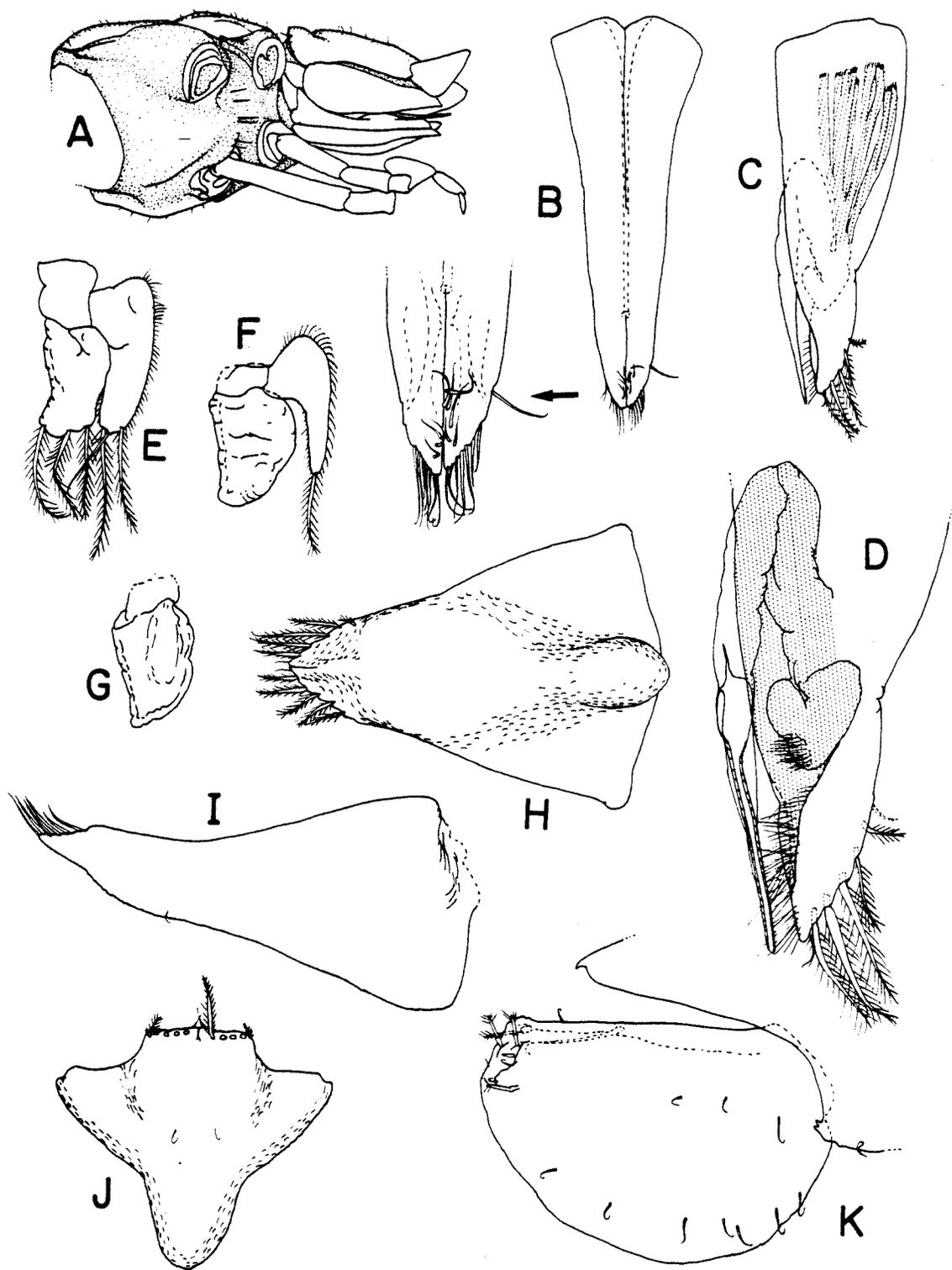
Male Pleopod I (fig. 2.19A-B). Fused pleopod pair widest at insertion, tapering to distal tip. Length 2.7 width; width at dorsal orifice 0.43 total width. Dorsal orifice 0.24 total length from distal tip. Distal tips flattened in lateral view, tapering and bluntly pointed in ventral view, without distinct outer lobes. Setae only on distal tips: each with distodorsal groups of setae and setal row adjacent to midline.

Male Pleopod II (fig. 2.19A,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. 2.19H-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. 2.19E): 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.

Figure 2.19. Lipomera (Paralipomera) knorrae new subgenus, new species. 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, ventral, lateral, and posterior views, respectively. K, right uropod, lateral view.



Uropod (fig. 2.19K): 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 other 3 undescribed species of its 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 species is the deepest occurring member of the genus Lipomera. The 3 undescribed species of the subgenus Paralipomera are found at slope depths off Africa, Brazil, and the southern United States in the Gulf of Mexico.

TETRACOPE New Subgenus

(Figures 2.20 - 2.24)

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. Midgut coiled, or with exaggerated bend (fig. 2.21A). Pereopod VI approximately same length as pereopod V. Pereopod VII present but rudimentary (2.24A). Uropod narrow, pointed, not extending beyond distal tip of pleotelson, with 2 segments in some 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.

Lipomera (Tetracope) curvintestinata new species

(Figures 2.20 - 2.24)

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

Paratypes.--Preparatory female, bl 0.87 mm, USNM; 50 specimens, some dissected for description, SIO.

Type-Locality.--WHOI 209, 39° 47.6-46.0' N, 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 2.20. Lipomera (Tetracope) curvintestinata new subgenus, new species. A, C, holotype male, lateral and dorsal views. B, D, paratype preparatory female, lateral and dorsal views. Scale bar 1.0 mm.

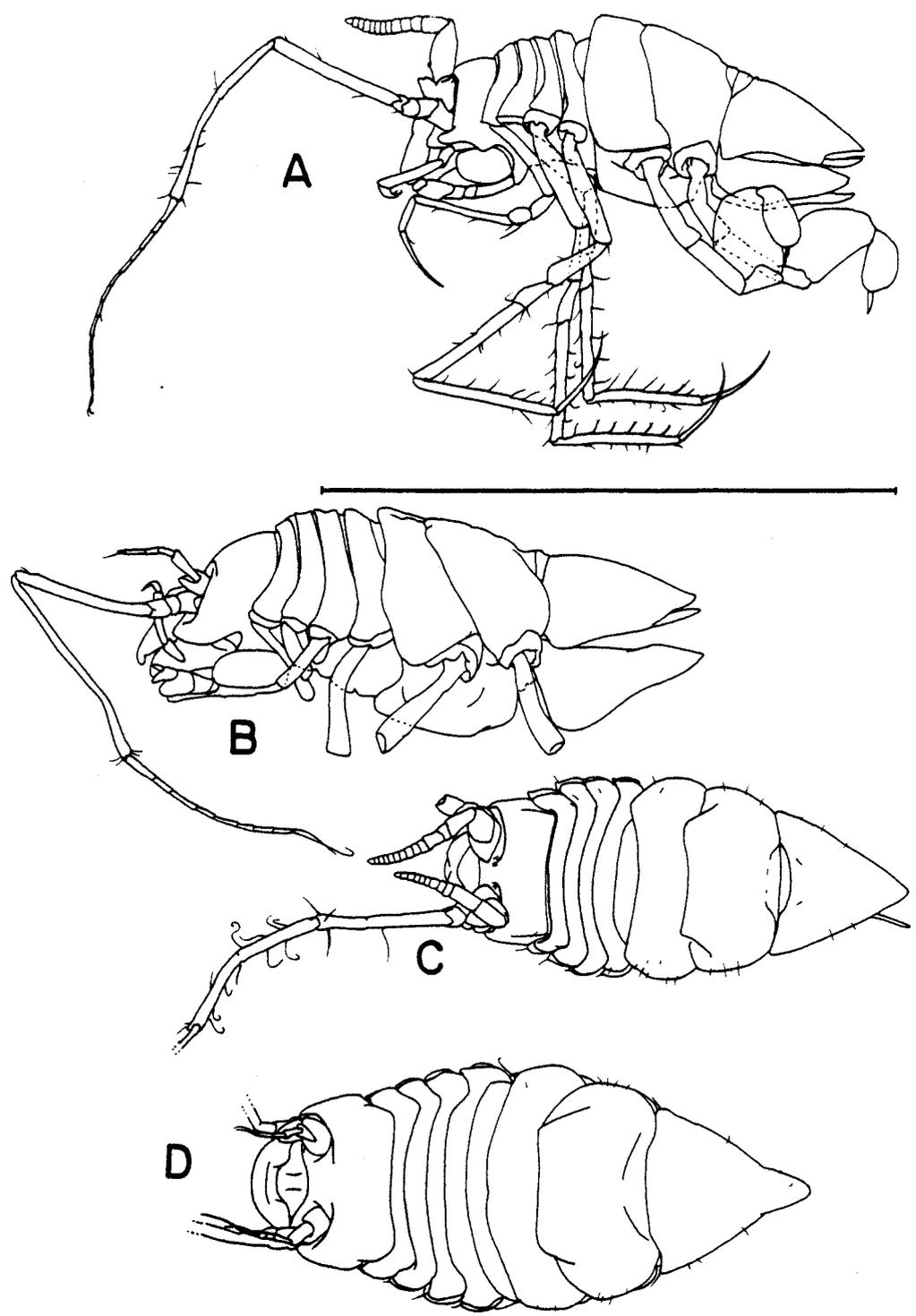
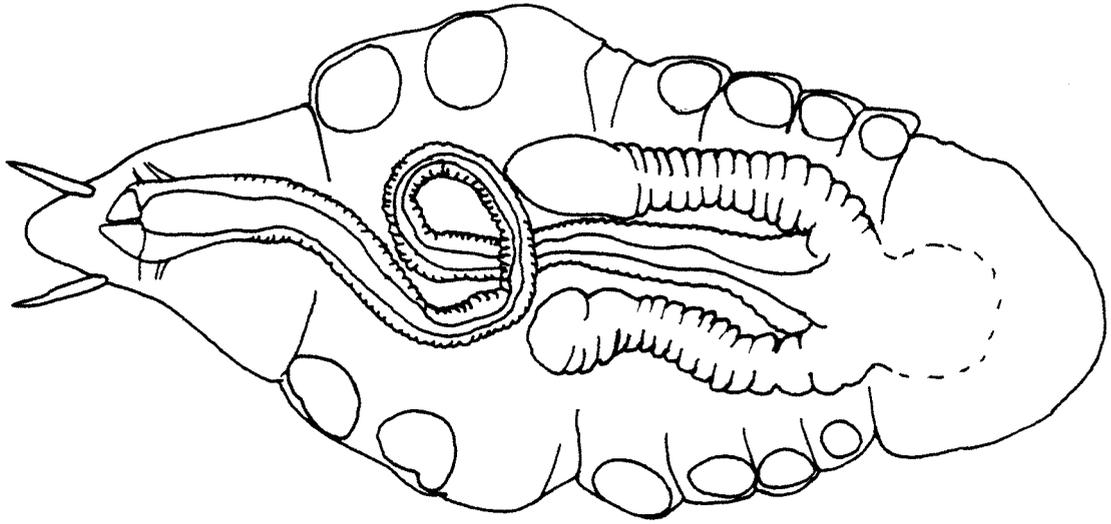
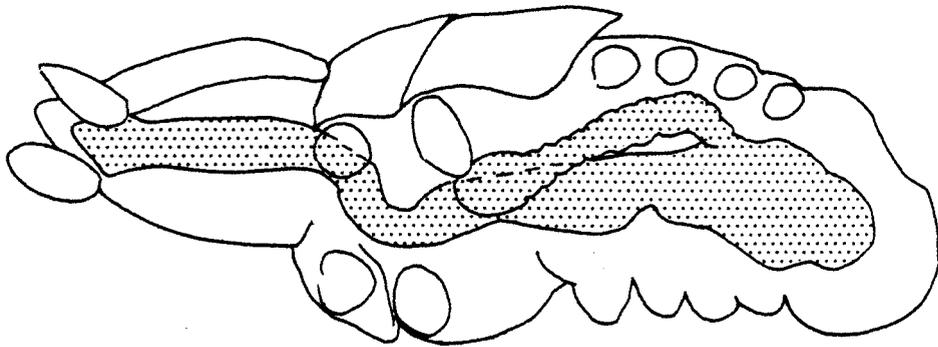


Figure 2.21. A, Lipomera (Tetracope) curvintestinata new subgenus, new species, paratype brooding female, bl 0.9 mm, view of alimentary canal and digestive caeci through ventral body surface. B, Lipomera (Lipomera) sp., male, bl 0.8 mm, WHOI 180, oblique view through ventral cuticle showing alimentary canal and digestive caeca through ventral body surface.

A



B



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 U.S.A., 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. Midgut 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; in lateral view dorsal surface of pleotelson only weakly curving. 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. 2.24 M and O).

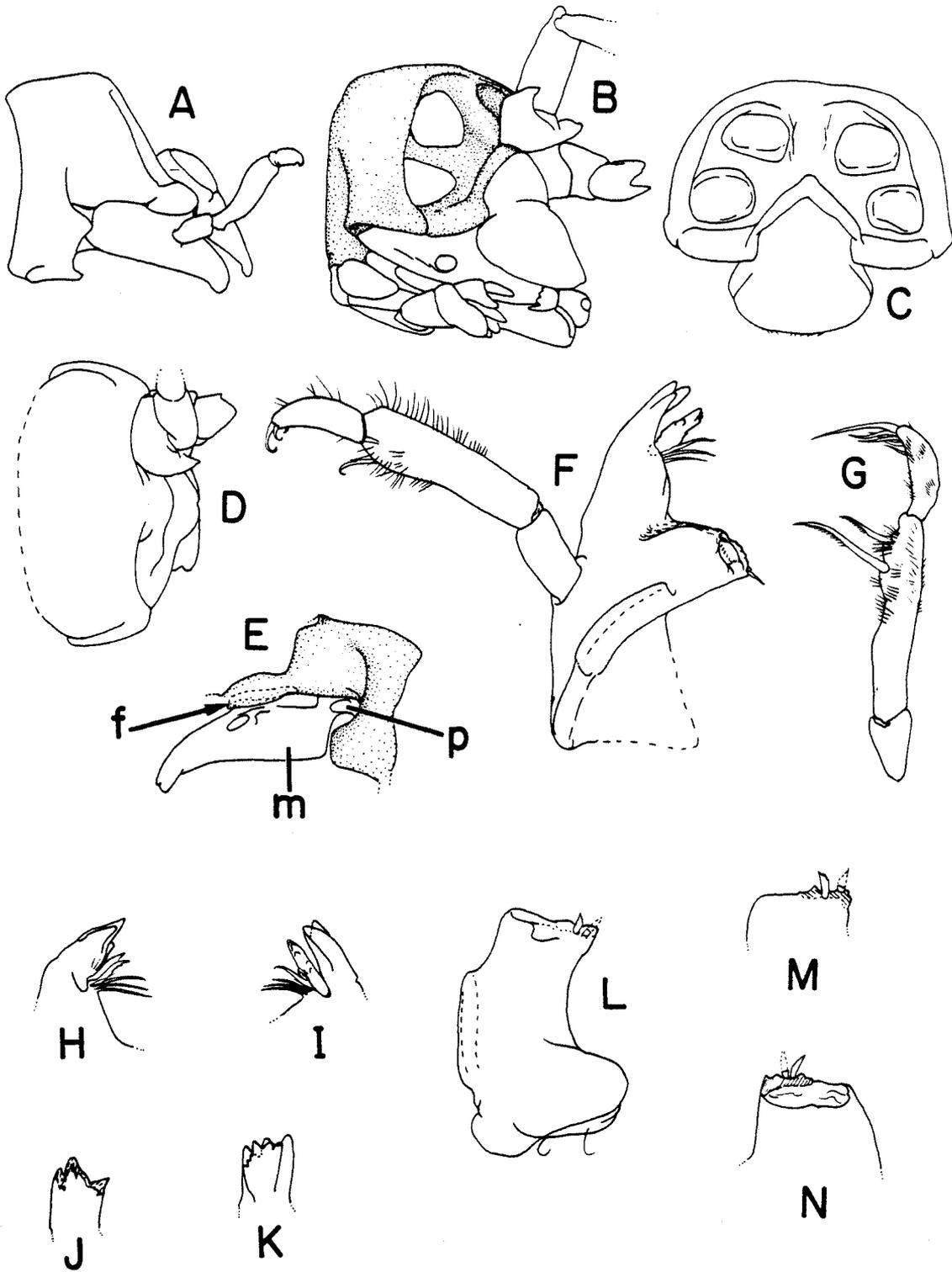
Description.--Body Characters (fig. 2.20A-D): Adult body length 0.74 mm (2 inds) in males, 0.89-0.90 mm (3 inds) in females; length 1.9-2.1 (4 inds) width, anterior segments subject to compression. Body form not sexually dimorphic, except females often widest at pereonite 4.

Cephalon (fig. 2.22A-D): Dorsal length 0.38 width, length 0.54 height. Ventral margin at posterior articulation of mandible with deep fold projecting laterally.

Antennula (fig. 2.23A-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. 2.22E-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 gnathal plate having 3 sharp denticles and 2 flattened setulate

Figure 2.22. Lipomera (Tetracope) curvintestinata new subgenus, new species, paratype male, bl 0.74 mm. A-D, cephalon, antennula and antenna removed to show frons: lateral, frontal oblique, anterior, dorsal views, respectively. 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, lateral and plan views. L, molar process and condyle, posteromedial view. M-N, molar process, posterior and anterior views.



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.

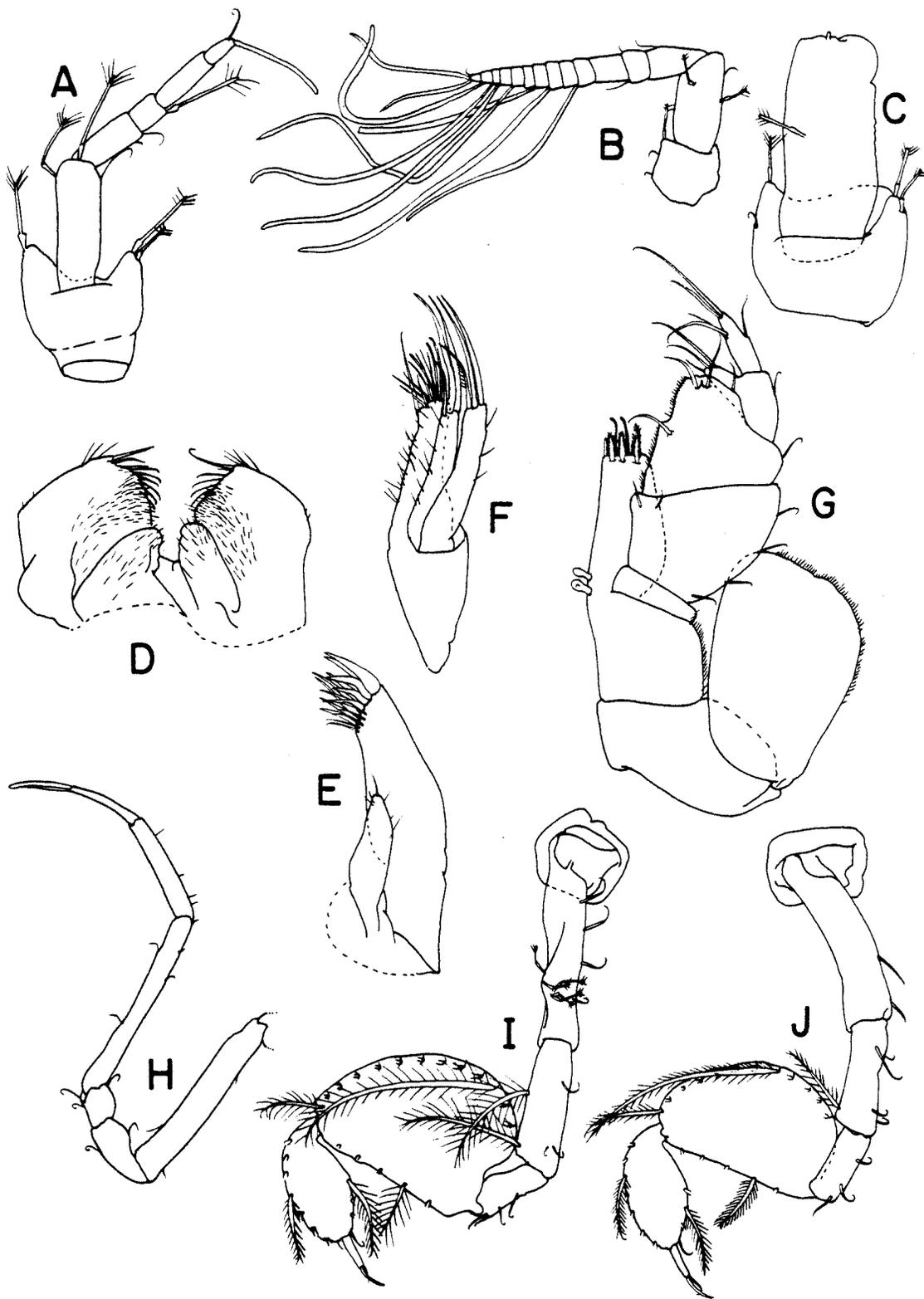
Maxillula (fig. 2.23E): Normally developed. Inner endite width 0.45 outer endite width.

Maxilla (fig. 2.23F): Normally developed. Outer lobes approximately same length as inner lobe.

Maxilliped (fig. 2.23G): 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. 2.20A, 2.23H): 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 ratios 0.90, 1.18, 1.23, 1.32, respectively. Pereopod I not sexually dimorphic. Bases I-IV length-body length ratios 0.25, 0.26, 0.28, 0.28, respectively. Bases II-IV with few setae.

Figure 2.23. Lipomera (Tetracope) curvintestinata new subgenus, new species. A, left antennula, paratype preparatory female, bl 0.84. B-J, paratype male, bl 0.74 mm. B-C, left antennula, lateral 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.

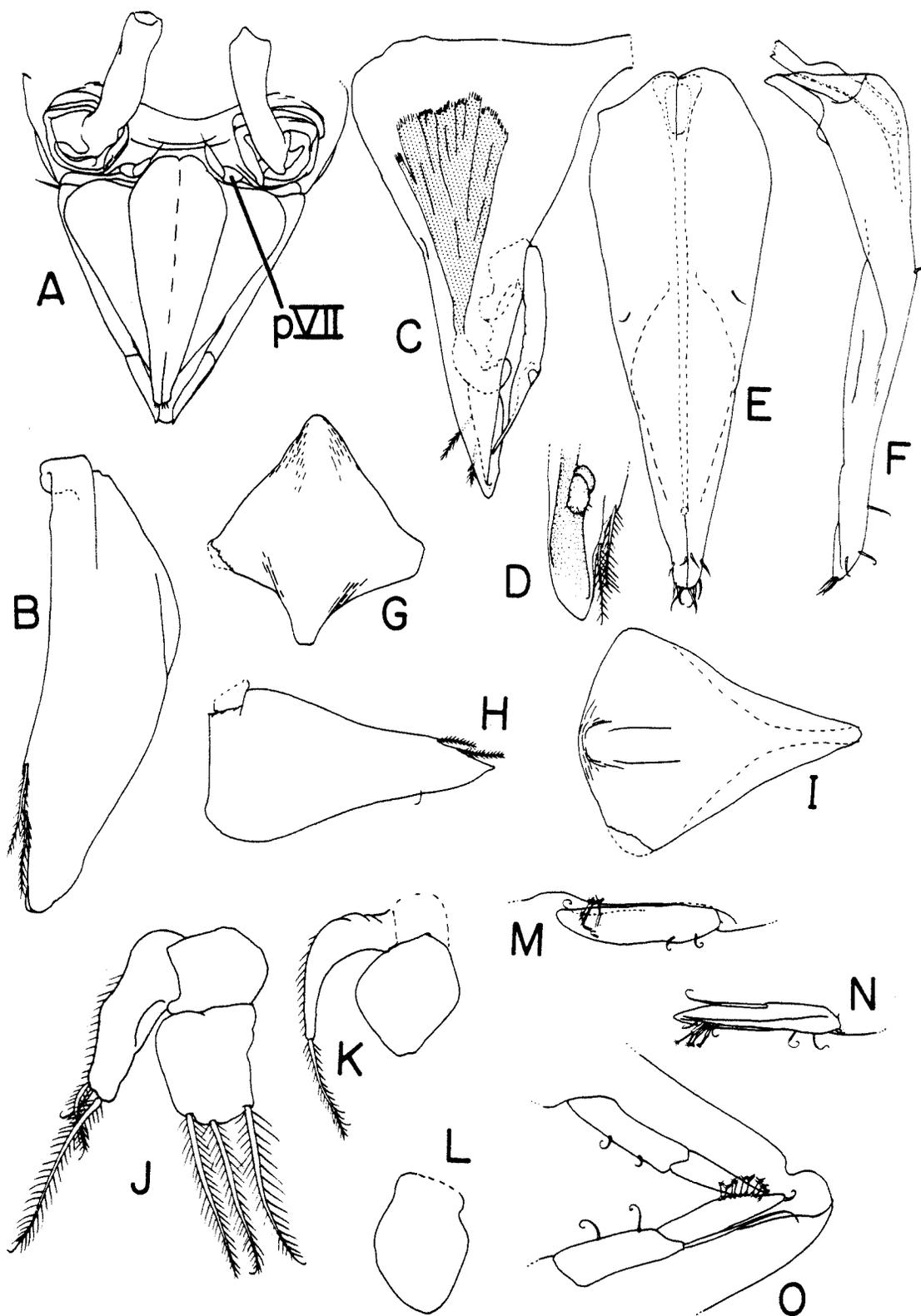


Natatory Pereopods (fig. 2.23I-J, 2.24A): Natapods V-VI similar in form, with broad carpi and propodi; pereopod VII present only as tiny, rudimentary 2 or 3 segmented appendage inserting medial to posterior edge of coxae VI. Pereopod V-VI length-body length ratios 0.93, 0.89, respectively. Bases V-VI length-body length ratios 0.26, 0.24, respectively; basis V with distal broadened area having group of broom setae. Carpi V-VI length-width ratios 1.3, 1.5, respectively. 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. 2.24A,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. 2.24A-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.

Figure 2.24. Lipomera (Tetracope) curvintestinata new subgenus, new species. 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). B-C, pleopod II, lateral and ventral view. D, pleopod II distal tip, medial view. E-F, pleopod I, ventral and lateral view. G-I, female pleopod II, posterior, lateral, and ventral views. J-L, right pleopods III-V. M-N, right uropod, lateral and ventral views. O, uropods, Lipomera (Tetracope) sp., brooding female, bl 1.1 mm, WHOI 119.



Female Pleopod II (fig. 2.24G-I): Keel deep, acute in posterior view, apex near anterior margin, sloping posteriorly and laterally to curled under 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. 2.24J): 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. 2.24M-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 midgut. A survey of all the ilyarachnoid 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 a distinct bend in the gut, but not coiled, similar to L. (Lipomera) sp. (undescribed, see fig. 2.20B).

Another 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 fig. 2.24 M, 2.24O, and 2.19K). Both L. (T.) curvintestinata 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 munnopsoids, 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 leaf-like. 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.

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 non-segmented uropod. The form of the body segments and the antennulae may be useful indicators of species differences as well.

MIMOCOPELATES New Genus

(Figures 2.25 - 2.32)

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," a combination derived from the nouns mimus, "an imitator," and copelates, "a rower."

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 would predict that somewhere in the deep-sea an eurycopid 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 eurycopids, 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 munnopsoid and, is, therefore, a useful autapomorphy.

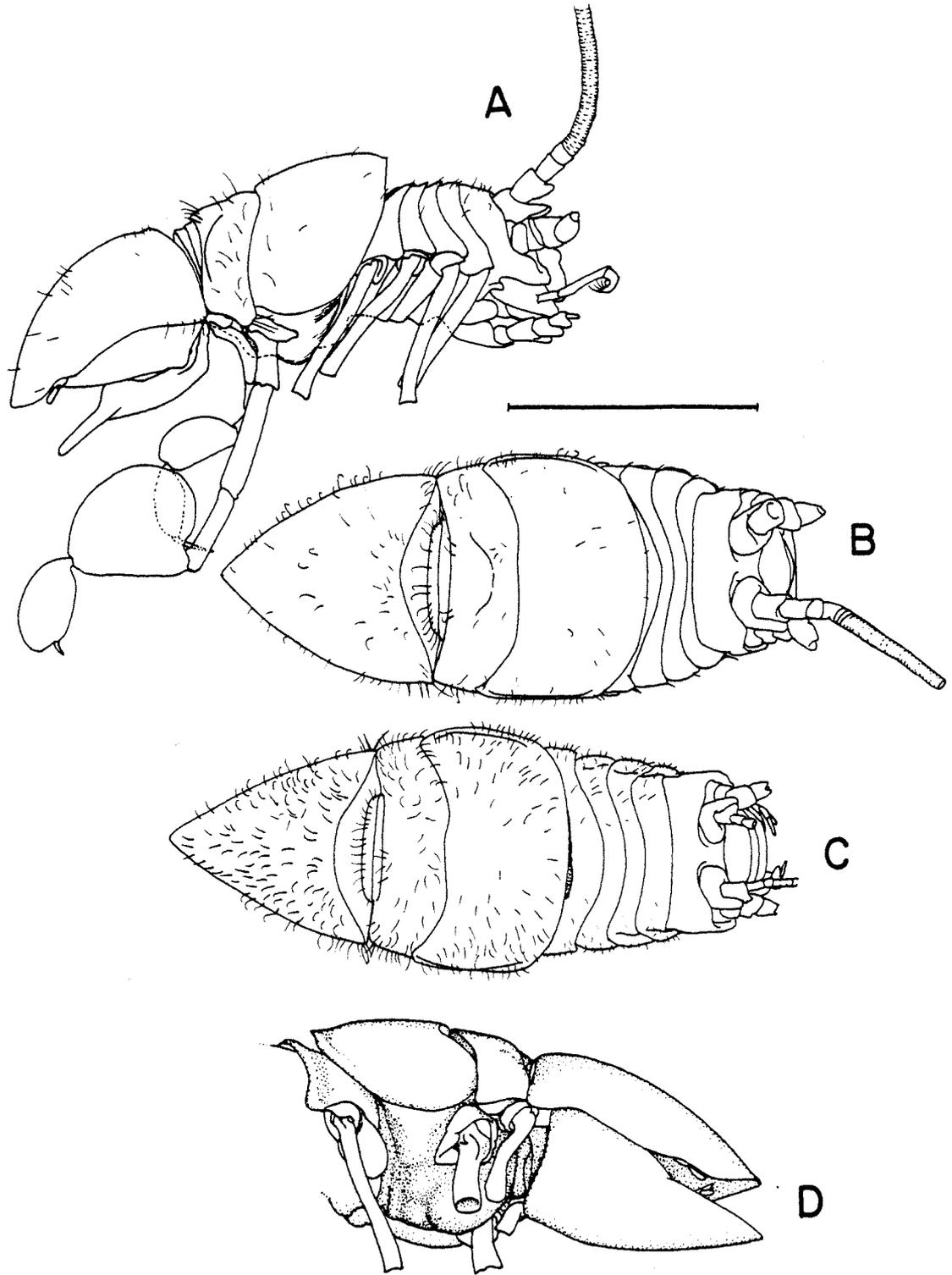
In addition to the form of the natatory pereopods and pereonites, the reduced uropods with tiny or absent exopods uniquely define this genus. Mimocopelates contains two distinctive groups: one represented by M. longipes n.sp., and the other by M. anchibraziliensis n.sp. Because these two species are so dissimilar in cephalic size and many other characters, I once believed they should be separate genera. However, the characters mentioned above 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 the same genus of munnopsoid. For example, compare the cephalic and mandibular development of Eurycope iphthima Wilson, 1981 and E. juvenalis Wilson, 1983.

Species of the Mimocopelates longipes group are all similar to each other, although several characters may be useful for discriminating 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 belong to an undescribed species that will be the subject of a future paper in which the munnopsoids from New Zealand will be described.

Figure 2.25. Mimocopelates longipes new genus, new species. A-B, holotype male, lateral and dorsal views, scale bar 1.0 mm. C, dorsal view, paratype preparatory female. D, ventral oblique view of natasome, showing form of ventral surface and comparative sizes of pereopodal bases, paratype preparatory female, bl 1.9 mm.



Mimocopelates longipes new species

(Figures 2.25 - 2.29)

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

Paratypes.--Preparatory female, bl 2.2 mm, USNM; brooding female and copulatory male, bl 2.2., 1.9 respectively, ZMUC; brooding female, bl 2.2 mm, MNHN; 20 individuals, some fragmentary or dissected for description, SIO.

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

Other Material.--All specimens in 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 distally 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.

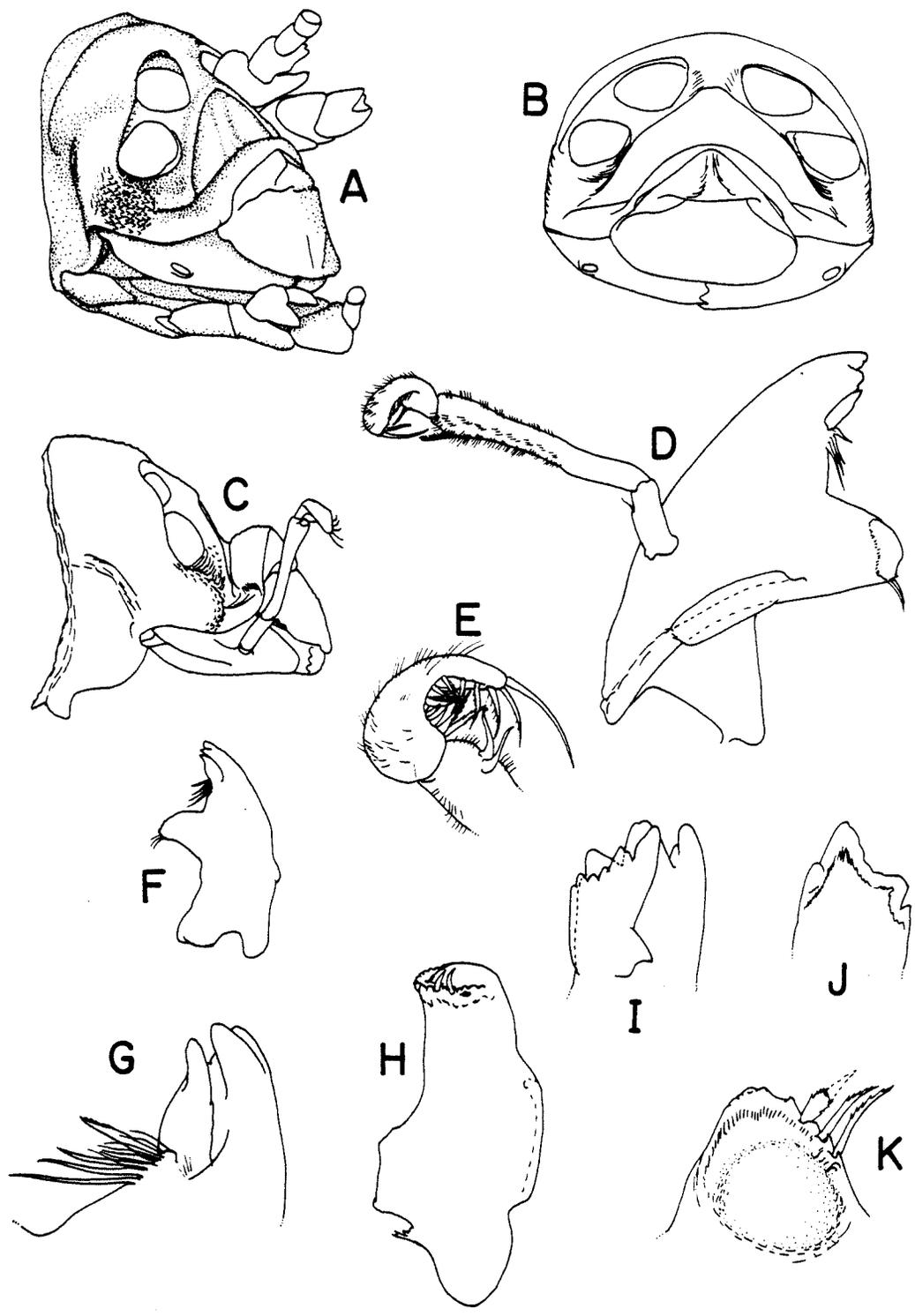
Description.--Body Characters (fig. 2.25A-C): Adult body length 1.9-2.2 mm (6 inds), females as large as or larger than males; body length 2.1-2.3 width (6 inds). Pleotelson sexually dimorphic: in male, longer and more inflated compared to female; male pleotelson length 0.38 body length, in female, 0.34.

Body setation (fig. 2.25A-C): Natasome with many fine setae on dorsal surfaces; ambulosome and cephalon with scattered fine setae.

Cephalon (fig. 2.26A-C): Dorsal length 0.43 width, height 1.3 width.

Antennula (fig. 2.27E-F): Flagellum and more proximal segments broken in all specimens examined. Male antennula more robust and possibly longer than 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

Figure 2.26. Mimocopelates longipes new genus, new species, paratype female, bl 1.9 mm. A-C, cephalon, antennula and antenna removed to show frons, views: frontal oblique, anterior, lateral, respectively. D-I, K, left mandible. D, dorsal view. E, palp, distal segment. F, ventral view. H, molar process and condyle, anteromedial view. I, incisor process and lacinia mobilis, plan view. J, incisor process, right mandible, plan view. K, molar process, anterior view.



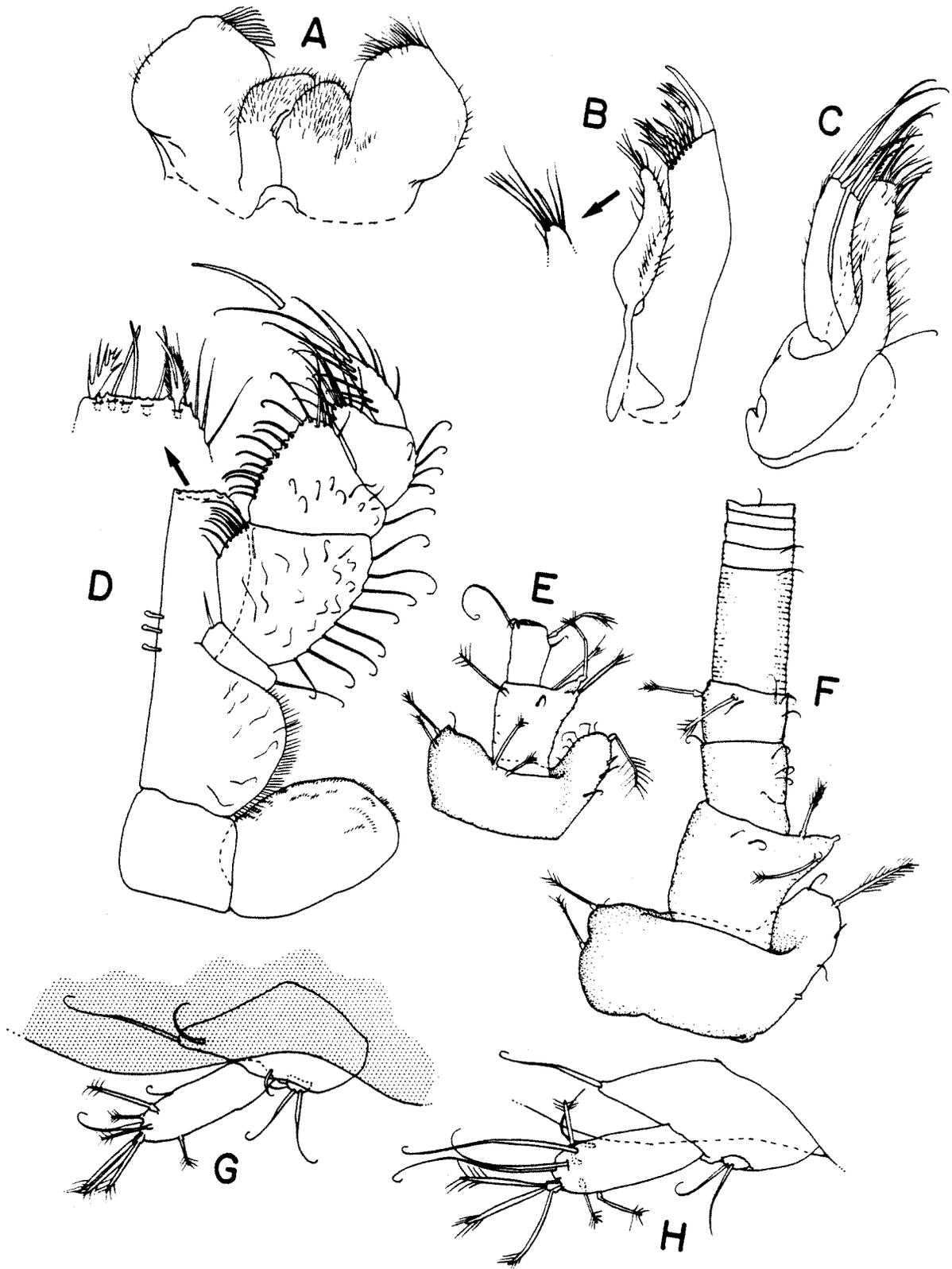
2-3 broom setae. Articles 2 and 4 with broom setae. Articles 2 and 3 sexually dimorphic, being broader and more robust in males than in females. Article 2 with distolateral projection having broom setae on 2 points; article 2 length subequal to article 1 medial length in female, length 0.92 medial length 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. 2.26D-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. 2.27B): Normally developed. Inner endite width 0.64 outer endite width. Distal tip of inner lobe with several very fine, equally bifid setae.

Maxilla (fig. 2.27C): Normally developed. Outer lobe length subequal to inner lobe. Central lobe shorter than inner lobe.

Figure 2.27. Mimocopelates longipes new genus, new species. 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 antennula. F, proximal articles of the antennula, paratype male, bl 2.1 mm. G, right uropod, proximal parts seen through cuticle, in situ, holotype male, bl. 2.1 mm. H, left uropod, medial view.

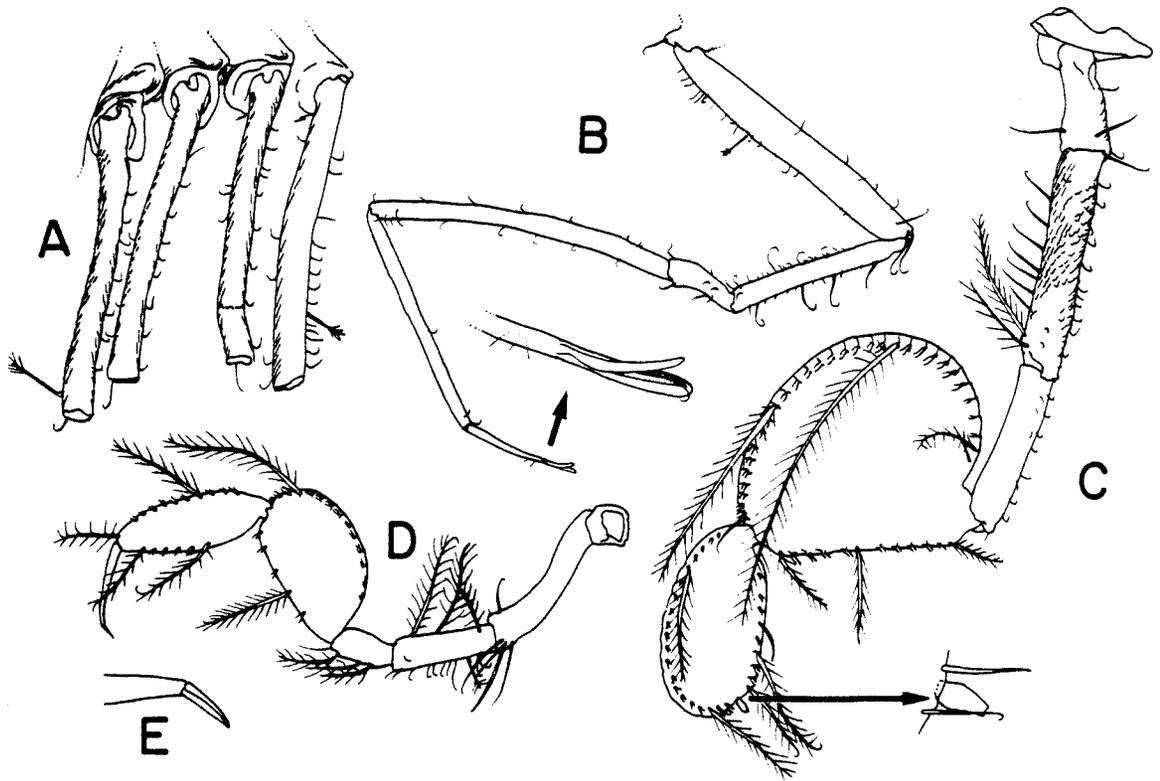


Maxilliped (fig. 2.27D): Basis with 3 receptaculi medially and 6 fan setae distally; medial fan seta more robust, with fewer and broader branches than 5 lateral fan setae; lateral fan setae bifid, with deep separation between sides. Endite length 0.56 total basis length. Palp article 2 width 1.5 endite 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. 2.28A-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. 2.28C-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 respectively. 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, respectively. Pereopod V merus length 0.73 ischium length. Carpi V-VI length-width ratios 1.1 and 1.7, respectively. Propodi V-VI length-width ratios 1.9 and 2.9, respectively. Dactyli V-VI length-propodus length ratios 0.14 and 0.63, respectively.

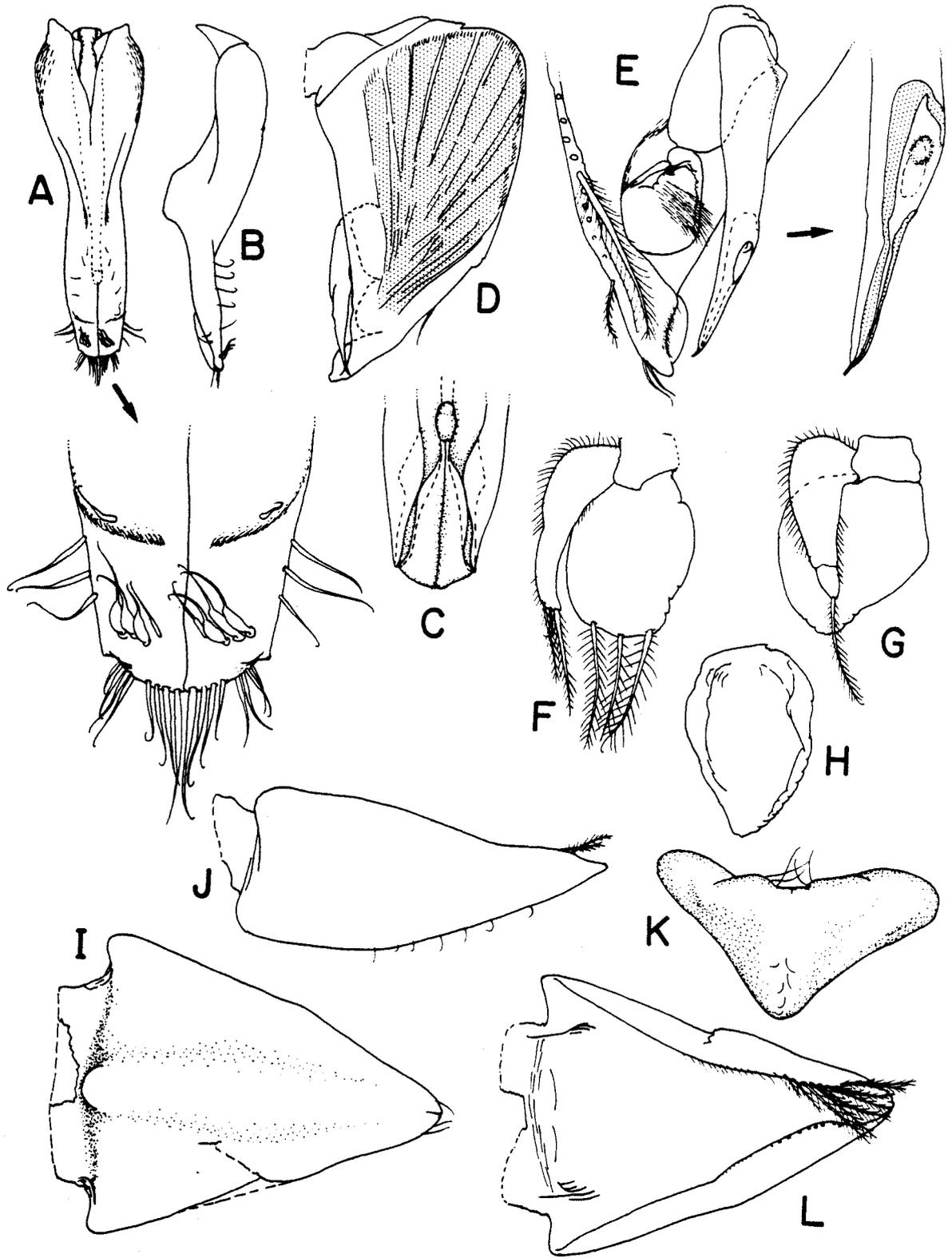
Figure 2.28. Mimocopelates longipes new genus, new species. A, C-E, holotype male, bl 2.1 mm. A, bases of right pereopods I-IV, in situ. B, left pereopod I, paratype male, bl 2.1 mm, with enlargement of dactylar claw. C, right pereopod V, in situ, with enlargement of dactylus. D, right pereopod VI, in situ. E, pereopod VI enlargement of dactylar tip. Illustrations all to same scale.



Male Pleopod I (fig. 2.29A-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. 2.29D-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.

Figure 2.29. Mimocopelates longipes new genus, new species. 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, respectively. D-E, left pleopod II, ventral view and dorsal view of distal tip with enlargement of stylet tip, respectively. F-H, right pleopods III-V. I-L, pleopod II: ventral, lateral, posterior, and dorsal views, respectively.



Female Pleopod II (fig. 2.29I-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. 2.29F): 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. 2.27G-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 the 3 other similar species (currently undescribed) of this genus by the following characters. The cephalic vertex is unmarked by a cuticular line so that 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. 2.29A) 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, 1983b). This species is found in some of the same localities as the E. complanata complex (Wilson, 1983b), 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.

Mimocopelates anchibraziliensis new species

(Figures 2.30 - 2.32)

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

Paratypes.--Copulatory male, bl 3.2 mm, USNM; 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.

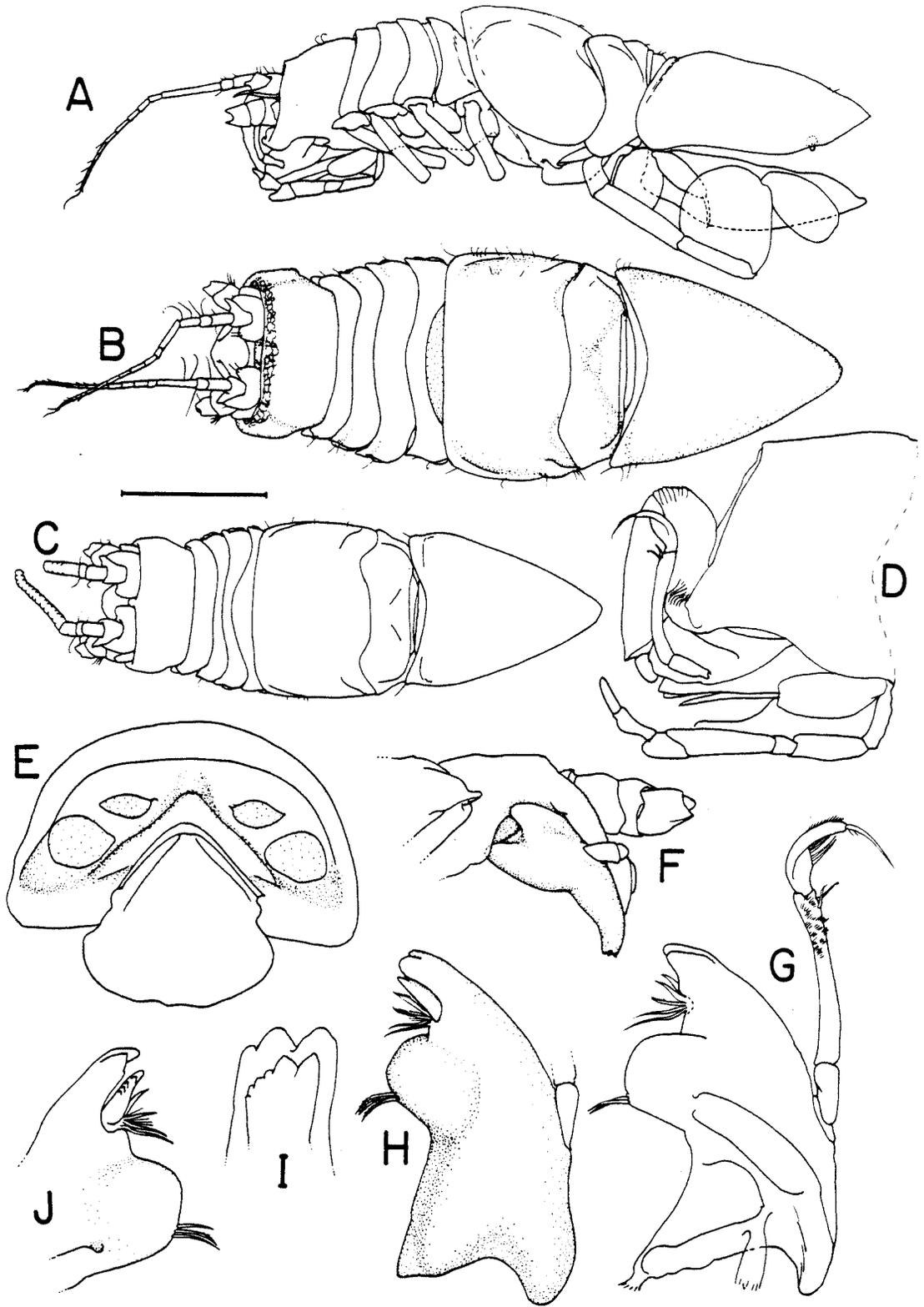
Other Material.-- WHOI 167, 72 mostly fragmentary individuals; WHOI 159, 7 individuals; WHOI 162, 1 individual.

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

Derivation of Name.--This species of Mimocopelates was given the name anchibraziliensis because it is found 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,

Figure 2.30. Mimocopelates anchibraziliensis new species. 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.



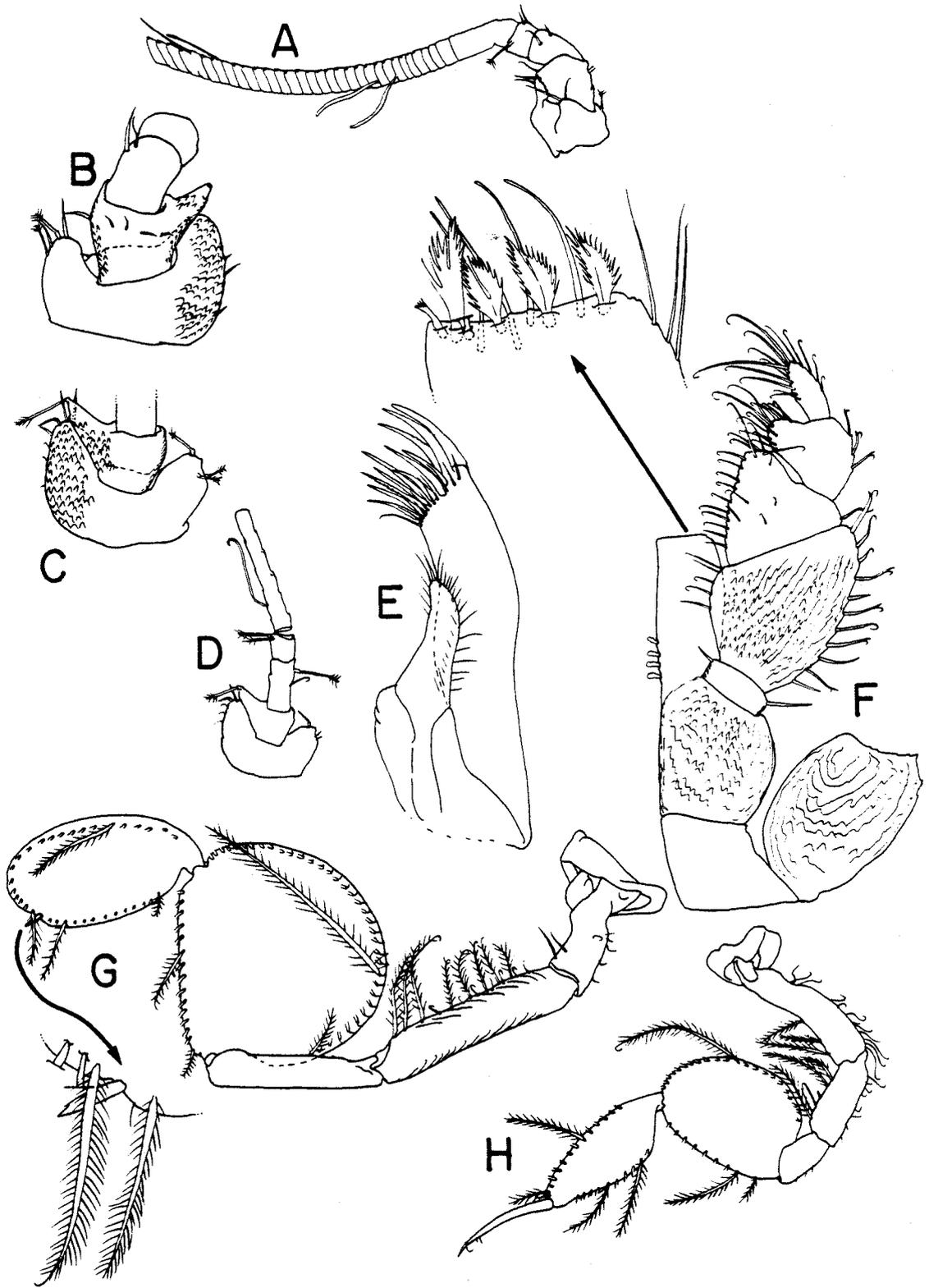
distance between medial corners of antennular insertions 0.19 (2 inds) cephalon width; in males, 0.10-0.11 (2 inds). Maxillipedal epipod distally scalloped. Male pleopod I distal tip with following paired setal groups: 5 fat-based setae ventral to dorsal orifice, 7 setae distally, and 4 setae laterally. 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. 2.30A-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. 2.30A-C): All dorsal surfaces with few scattered fine setae.

Cephalon (fig. 2.30D-F): All surfaces heavily calcified, especially at anterior margins, with large plate-like 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.

Figure 2.31. Mimocopelates anchibraziliensis new species. A-B, right antennula, 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 antennula: articles 1 and 2, and proximal 5 articles respectively. 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.



Antennula (fig. 2.30A-B, 2.31A-D): Strongly dimorphic sexually: male antennula longer, with higher number of more robust articles, than in female. Female antennula length 0.39 body length (not intact in any males seen); 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 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. 2.30F-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 moderate flat curl.

Maxilliped (fig. 2.31F): Ventral surfaces of basis, palp article 2, and epipodite with cuticular ridges and few setae. Basis with 4-5

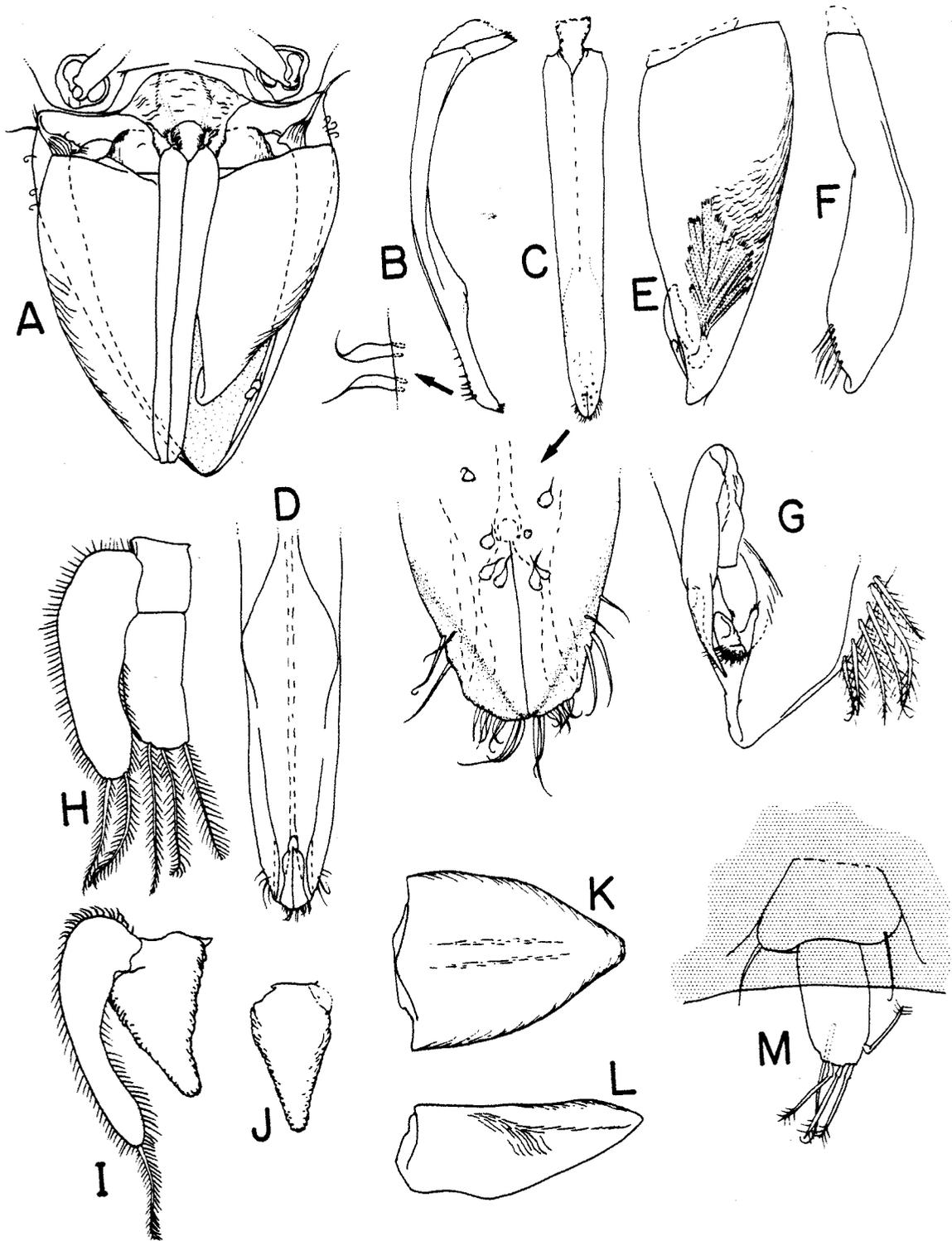
receptaculi and 6 fan setae distally; 4 lateral fan setae bifid with distinct gap separating both sides; medial fan seta small, truncate; seta second from middle behind third seta more robust, with fewer and broader branches than 4 lateral fan setae. Endite distally quadrate, length 0.51 total basis 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, respectively.

Natatory Pereopods V-VI (fig. 2.31G-H): Basically similar to those of Mimocopelates longipes. Pereopod V-VI length-body length ratios 0.65, 0.54, respectively. Pereopod V merus length 0.82 ischium length. Carpi V-VI length-width ratios 1.1, 1.3, respectively. Propodi V-VI length-width ratios 1.8, 2.6, respectively.

Male Pleopod I (fig. 2.32A-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.

Figure 2.32. Mimocopelates anchibraziliensis new species. 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, paratype preparatory female, bl 4.4 mm. M, uropod, holotype female, bl 4.2 mm, in situ, proximal portion seen through cuticle.



Male Pleopod II (fig. 2.32E-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.

Female Pleopod II (fig. 2.32K-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. 2.32H): 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. 2.32I-J): Endopods of both limbs thick and triangular in ventral view. Exopod of pleopod IV long, flattened, lobe-like, with single long plumose seta.

Uropod (fig. 2.32M): 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 very 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 whose endopods, exopods, and intrinsic musculature are reduced. This species was collected only in a bathyal transect of stations off Recife, Brazil.

CHAPTER 3

AMULETTA, A NEW GENUS FOR ILYARACHNA ABYSSORUM RICHARDSON 1911

(ISOPODA, ASELOTOTA, EURYCOPIDAE)¹

by George D.F. Wilson and David Thistle²

ABSTRACT

Amuletta, new genus, is proposed for Ilyarachna abyssorum Richardson 1911. A detailed description, new illustrations, and new records are presented with a discussion of the systematic position of this species. It must be placed in the Eurycopidae, in spite of its resemblance to the presumed ancestor of the Ilyarachnidae. This difficulty arises because the present classification of these janiroidean families has become obsolete. This species is apparently limited to the northeast Atlantic, where it has a broad depth distribution. However, sampling device avoidance may account for the infrequent records of this species, implying it may have a broader geographic range. The gut contents of one specimen contained a high proportion of calcareous Foraminifera, suggesting that it was actively feeding on forams.

¹ This chapter was published as an article of the same title and authorship in the Journal of Crustacean Biology, volume 5, pages 350-360, 1985.

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INTRODUCTION

Ilyarachna abyssorum Richardson 1911 has been an enigma since it was described. Richardson's original description was brief, and she provided no figures. Further, she was unsure of the appropriateness of placing the new species in Ilyarachna. Ilyarachna abyssorum was pivotal in discussions of the origin of the Ilyarachnidae by Thistle and Hessler (1976), who treated it as Ilyarachna. Schultz (1976), on the other hand, transferred the species to Echinozone. Difficulties with the placement of I. abyssorum arise, at least in part, from the intermediate nature of this species. Witness, for example, Thistle and Hessler's (1976) arguments that the species can be used to understand the evolutionary transition from the Eurycopidae to the Ilyarachnidae. In this paper, we hope to dispell confusion about I. abyssorum by presenting a discussion of its systematic position and a diagnosis of a new genus, Amuletta, based on a complete redescription of the original type-specimens and new material from the Northeast Atlantic.

MATERIALS AND METHODS

The types of Ilyarachna abyssorum were kindly lent to us by Dr. J. Forest, Museum National d'Histoire Naturelle, Paris, and Dr. T.E. Bowman, National Museum of Natural History, Washington, D.C. Additional specimens came from the research collection of Dr. R.R. Hessler, Scripps Institution of Oceanography, the sources of which are described in Wilson and Hessler (1980).

The descriptive terms and methods used here are those of Thistle and Hessler (1977) and Wilson and Hessler (1980). In the following discussions, the term "munnopsoids" is taken to refer to an informal (but useful) taxon made up of the truly natatory families of the Janiroidea: Munnopsidae, Eurycopidae, and Ilyarachnidae.

THE SYSTEMATIC POSITION OF ILYARACHNA ABYSSORUM

Richardson (1911) placed the species abyssorum into Ilyarachna because of apparent similarities to known species of that genus. She felt abyssorum most resembled I. plunketti Tattersall 1905a (= I. longicornis Sars; see Thistle, 1980) but noted that the two species differed in the form and the position of epimeres of the anterior four pereonites, the size and the shape of natasomal segments, and the shape of the carpus of pereopod VII. These observations have gone unnoticed in the literature until their significance became apparent during our redescription of abyssorum.

Our work on the families Eurycopidae and Ilyarachnidae has convinced us that Richardson's familial placement of abyssorum must be revised. Below we present arguments for the removal of the species from the Ilyarachnidae, and its placement in a new genus of the Eurycopidae.

Richardson (1911) mentioned that the carpus of pereopod VII was broadened in abyssorum. Among munnopsoids, this is a primitive character state with respect to all Ilyarachnidae, in which the last pereopod is reduced to an almost ambulatory-appearing condition. Although none of our adult specimens retained this limb segment, Richardson's statement is corroborated by two bits of evidence. First, inspection of a sagittally bisected individual showed that pereonite 7 is as well muscled as the anterior natasomal segments and is not reduced as in Ilyarachna. Also, the basis of pereopod VII is nearly as robust as that of pereopod VI (fig. 3.1G), rather than

clearly thinner as in Ilyarachna. Second, in the manca 3 of abyssorum, the carpus of the developing pereopod VII (fig. 3.1E) is somewhat broadened, a condition intermediate between that seen in the Eurycopidae (e.g. Eurycope iphthima, see Wilson, 1981) and that of the Ilyarachnidae, such as I. antarctica. Taxa in which the adult limb is not broadened show no broadening in the manca 3 pereopod VII. Therefore, the seventh pereopod carpus of abyssorum is likely to be wider than that of the ilyarachnids, but narrower than in the eurycopids.

In abyssorum, the mandibular molar process (fig. 3.2H,L) is little modified from the primitive janiroidean condition; it is distally broad, concave, with many setae and teeth on its distal margins. This morphology is different from the reduced, setiferous molar process used as a primary diagnostic character of the Ilyarachnidae by Wolff (1962). The rest of the abyssorum mandible (fig. 3.2F-N) is different from that typical of ilyarachnids. The incisor process is not reduced and rounded, the mandibular body is not shortened, and the dorsal condyle is small, rather than elongate and curved. Because the mandible is not highly specialized as in the ilyarachnid condition, the cephalon is not greatly broadened to accommodate enlarged mandibular articular supports. All these mandibular characters in abyssorum are primitive compared to those of the Ilyarachnidae.

The mandibular palp is absent in abyssorum but the generalized form of the mandible indicates that this reduction was derived independently of the Ilyarachnidae. The absence of a palp in some genera of the Ilyarachnidae, such as Echinozone, is convergent because the highly modified ilyarachnid mandible has a palp in other genera.

The significance of the abyssorum uropod requires the comparison of the primitive state of this character within the munnopsoids, determined through inspection of the uropods of other janiroidean families, such as the Desmosomatidae and the Janiridae. The primitive uropod has a tubular protopod that may be oval in cross-section, and two elongate, unequal rami; the distal margins of the protopod and the rami have rows or groups of setae. This is the type of uropod seen in Eurycope and Storothyngura. The uropod of abyssorum (fig. 3.1I-K) is modified from the primitive condition: the distal margin of the protopod is elongated medially and tilted to face laterally, and the rami are very short and stout. The protopod, however, is not flattened but is more or less oval in cross-section. All members of the Ilyarachnidae have a flattened, foliaceous uropodal protopod, and the rami are reduced or absent, a morphology even further removed from the primitive munnopsoid uropod than that of abyssorum. If the abyssorum uropod form is related to that of the Ilyarachnidae, it is as a precursor. The triangular natasome and the enlarged cephalon with no rostral projection in abyssorum (figs. 3.1A, 3.2A-E) is characteristic of the Ilyarachnidae. This general facies, however, is

Figure 3.1. A-B, paralectotype female (USNM 42172), body length (BL) 10.3 mm. A, dorsal view, scale bar at left is 2 mm long. B, ventral oblique view. C,F, lectotype preparatory female. C, dorsal view. F, lateral view. D-E, K, manca 3, WHOI 328. D, dorsal view, scale bar at lower right is 1 mm long. E, ventral view of pleotelson. G-H, female paralectotype natasome fragment, "Talisman" station 135. G, lateral view. H, dorsal view of pleotelson. I-J, female paralectotype pleotelson fragment, "Talisman" station 134. I, oblique ventral view of pleotelson, pleopod II in plan view. J, uropod, in situ, lateral view. K, uropod, ventral view.

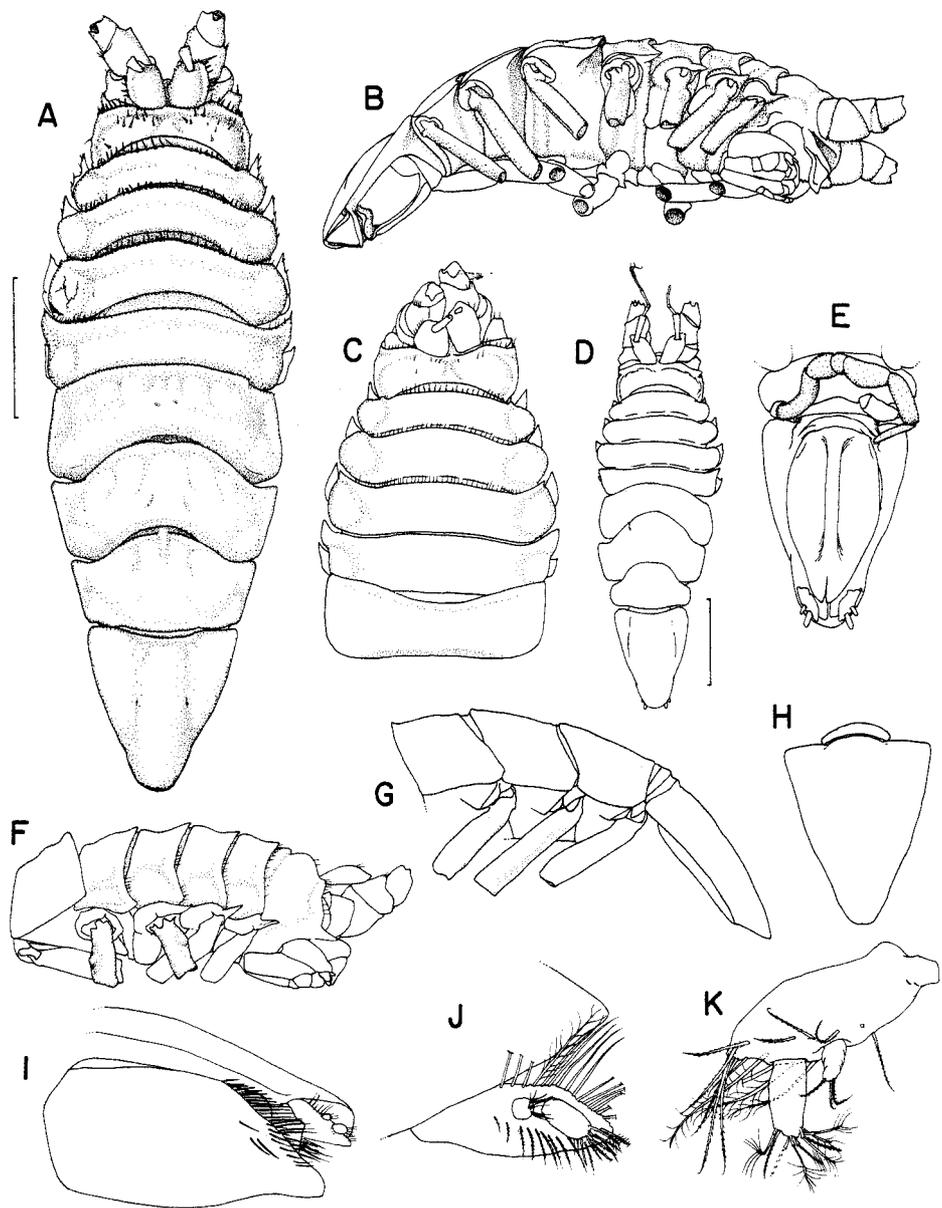
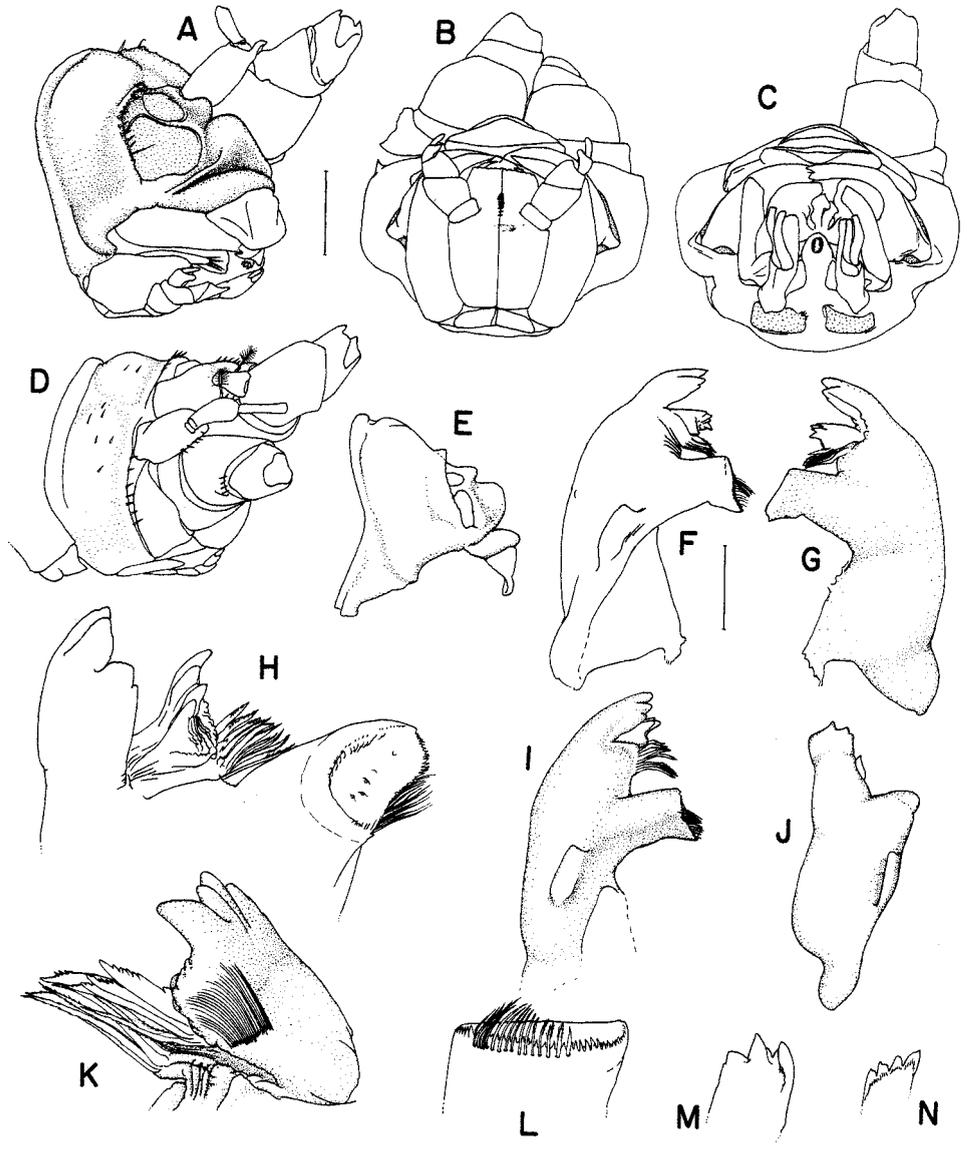


Figure 3.2. A, C, E-F, H-N, preparatory female, estimated BL 14.9 mm, INCAL WSO2. B, lectotype female. G, paralectotype male, "Talisman" station 135. A-E, cephalon, scale bar to right of A is 1 mm long: A, frontal oblique view, right antennula and antenna removed; B, ventral view, all mouthparts in place; C, ventral view, maxilliped removed; D, dorsal oblique view; E, lateral view, antennula and antenna removed. F-N, left mandible, scale bar to right of F is 0.5 mm long: F,I, dorsal view; G, dorsal view; H, dorsal oblique view of distal parts; J, lateral view; K, lacinia mobilis and spine row, ventral view; L, molar process, posterior view; M, incisor process, posterior view; N, lacinia mobilis, posterior view.



also found in the Syneurycopinae, Storthyngura, and in Betamorpha. If these characters are useful for determining phylogenetic affinities, they define a group larger than the family Ilyarachnidae.

Hessler and Thistle (1975) believed the primary character identifying the members of the Ilyarachnidae to be the shortened bases of the third and fourth pereopods. Although the bases of pereopods III and IV are shortened in abyssorum (fig. 3.1B,F), they are not as short as in the Ilyarachnidae. The use of this character as a unique descriptor of the Ilyarachnidae is in doubt because shortened bases III-IV are found in Bellibos Haugsness and Hessler 1979, Munneurycope nodifrons (Hansen, 1916) and similar species, and to a lesser extent in some species of Storthyngura. Extremely short, robust bases of pereopods III and IV are also characteristic of the Munnopsidae. Although the short bases of the Munnopsidae may have been derived independently, the other taxa mentioned above may delineate a transformation series from the elongate bases III-IV considered to be primitive in the munnopsoids, to the short and robust ones typical of the Ilyarachnidae. The form of the bases in abyssorum would therefore be intermediate. Although this view may disagree with Thistle and Hessler's (1976) contention that the length of the bases III-IV provides the diagnostic difference between the Ilyarachnidae and the Eurycopidae, we believe that the ilyarachnids are still diagnosable by the unique shape of their cephalon and mandibles, their uropods, their reduction of the seventh pereopods, and their general body form.

In sum, no character shared between the Ilyarachnidae and abyssorum is unique to these taxa. Therefore, we conclude that abyssorum must be placed in the Eurycopidae, in spite of the possibility that this species may be similar to the ancestral ilyarachnid. This ancestor would not be included in the same genus with abyssorum because it would have had a mandibular palp.

Much of the difficulty with determining the position of abyssorum lies not in indecision about the meaning of its characters, but in the general weakness of the present system of classification of the munnopsoid families. The Eurycopidae, as the central taxon of the munnopsoids, should be recognized as paraphyletic, containing members of related phyletic lines leading to the various subfamilies of the Eurycopidae, and to the Ilyarachnidae and the Munnopsidae. The confusion in the present classification occurs because the advanced members of the eurycopid subfamilies are no more similar to each other than they are to the other families of the munnopsoids. Despite these dissimilarities, intermediate taxa such as abyssorum and Betamorpha eliminate distinct gaps which would simplify the classification, increasing the difficulty but not the interest of munnopsoid systematics. Research in progress by one of us (GDFW) on eurycopids having the ilyarachnoid facies (Wilson and Hessler, 1981) and other taxa in the Eurycopidae will attempt to reclassify the munnopsoid taxa in a more phylogenetically natural fashion. We will not, therefore, suggest a subfamilial placement for the new genus Amuletta, proposed here for the species abyssorum.

Amuletta new genus

Type-Species.-- Ilyarachna abyssorum Richardson 1911, by monotypy.

Diagnosis.-- Dorsal surface of body without spines. Cephalic lateral margins not greatly broadened; frontal area without rostrum, but with 2 medial protrusions: small dorsal lobe between closely adjacent antennulae; supraclypeal ridge enlarged, thick and rounded medially, flattened laterally under antennal insertions. Segments of natasome flexibly articulated and distinct ventrally, decreasing in width posteriorly. Pleotelson distinctly longer than wide, with rounded posterior tip in dorsal view. Antennular first article longer than wide, thick and rounded distomedially, flattened and projecting anteriorly on distolateral margin. Antenna without scale. Mandible without palp; incisor process and lacinia mobilis cusped; molar process large, with many setae and teeth on circumgnathal margin. Coxal plates on pereopods I-III with pointed anterior projections; pereonite 4 anterolateral corner protruding in similar manner. Bases of pereopods III-IV two-thirds length of basis II, with distinct lateral bumps. Bases of natatory pereopods as long as or longer than bases of ambulatory pereopods. Pereopod VII with broad natatory carpus, not reduced. Uropodal protopod not foliaceous, subcylindrical, pointed distomedially, with 2 distinct rami.

Derivation of Name.--Amuletta (feminine) is derived from the French word for amulet or talisman, referring to the "Talisman", the ship from which the genus was first collected.

Generic Remarks.--Within the Eurycopidae, Amuletta is most similar to Betamorpha, Bellibos, and some species of Storthyngura. These similarities are in the general shape of the body, cephalon, antennulae, antennae, pereopods, and pleopods. Each of these genera, however, is unique in some way. Amuletta's small distomedial lobe on the uropodal protopod and lack of a mandibular palp make it immediately distinct from Betamorpha. The natatory pereonites of Bellibos are fused into one inflexible unit, unlike the free pereonites of Amuletta. Species of Storthyngura that lack lateral and dorsal spines do not have the compact uropod with short rami or the triangular pleotelson of Amuletta. As discussed above, this genus cannot be confused with the genera of the Ilyarachnidae because it does not have the specialized cephalon, mandibles, seventh pereopods, and uropods of that family.

Amuletta abyssorum (Richardson)

Synonymy.--Ilyarachna abyssorum, Richardson 1911, p. 533; Ilyarachna abyssorum, Hessler and Thistle 1975, p. 157; Thistle and Hessler 1976, pp. 112-113; Echinozone abyssorum, Schultz 1976, p. 10.

Lectotype.--Fragmentary preparatory female (designated from syntype series) from Northeast of the Azores, "Talisman" dredge station no. 134, 4060 m., 42° 19' N, 23° 36' W, 24 August 1883 (station no. 147 in Smith, 1889; see appendix in Crosnier and Forest, 1977), deposited in Museum national d'Histoire naturelle, Paris. Features of type: only head and anterior 5 pereonites remaining; right pereopods represented by at most coxa and basis.

Paralectotypes.--Four fragmentary specimens, "Talisman" dredge station no. 134; 3 fragmentary specimens, "Talisman" dredge station no. 135 (149 in Smith, 1889), 4165 m., 43° 15' N, 21° 40' W, from Northeast of the Azores, 25 August 1885; deposited in Muséum d'Histoire naturelle de Paris. Preparatory female, body length 10.3 mm, "Talisman" dredge no. 135, deposited in the United States National Museum of Natural History (possibly by Richardson), catalog number USNM 42172.

Additional Material.--Four juvenile specimens (one is a cephalon fragment only), Woods Hole Oceanographic Institution deep benthic station (WHOI) 328, 4426-4435 m., 50° 4.7' N, 15° 44.8' W, 23 August 1972, Southeast of Ireland. One manca, "Sarsia" station 50 (collected by John Allen, University Marine Biological Laboratories, Millport, Isle of Cumbrae, Scotland), 2379 m., 43° 46.7' N, 3° 38' W, 18 July

1967, in the Bay of Biscay. Preparatory female, pleotelson missing, estimated body length 14.9 mm, completely dissected for illustration, Expedition "Intercalibration" (INCAL; for description of program, see Sibuet, 1979) station WSO2, 2498-2505 m., $50^{\circ} 19.3'-20'$ N, $12^{\circ} 55.8'-56.0'$ W, 30 July 1976. Copulatory male, body length 13 mm, partially dissected for illustration, INCAL station WSO4, 4829 m., $48^{\circ} 18.9'-18.3'$ N, $15^{\circ} 14.4'-13.3'$ W, 2 August 1976.

General Distribution.—Abyssal Northeast Atlantic, 2379-4829 m.

Description.—Body Characters (fig. 3.1A-H): Total body length 2.8 times body width, in manca length 2.9 times width; body widest at pereonite 4. Adult body lengths range from 10.2 mm (preparatory female, USNM 42172) and 13 mm (copulatory male, INCAL WSO4) to 14.9 mm (preparatory female, INCAL WSO2, estimated length); manca 3 (WHOI 328) body length 4.1 mm. Dorsal surface of pereonites with scattered simple setae; pereonites 1-5 with row of setae on anterior margins; marginal setae decrease in size posteriorly. Dorsal surface of pereonites complex: anterior margins flaring slightly upward, posterior margins distinctly depressed under flange of next posterior pereonite, patches of cuticle over muscle attachments slightly raised or depressed. Pleotelson length 1.1 - 1.4 times width in adult, length 1.4 times width in manca 3.

Cephalon (fig. 3.2A-E): Cephalon length in dorsal view from dorsal antennal socket margin to posterior articulation 0.39 times width (2 females measured); in manca 3 length 0.43 times width. Dorsal surface domed, slightly bilobed by medial sagittal depression;

surface with many setae, sometimes on low cuticular bumps on dorsum, very fine setae on sides. Anterior margins of antennal sockets with rows of setae. Posterior margin with rounded transverse ridge having row of setae. Clypeus short, broad, dorsally rounded, shorter than length of labrum.

Antennula (fig. 3.3A-B): Basal article longer than broad, length 1.4 times width; medial and central part thick; lateral margin thin, flattened, anteriorly projecting, with unequally bifid and simple marginal setae. More distal articles elongate and thin. Second article slightly longer than third article, length 0.54 times basal article length (about 0.6 in male). Article 4 less than one-fifth length of article 3. Broom setae on proximal 2 articles only. In male, flagellar articles shorter, wider and more numerous than in female; each article of about distal two-thirds of flagellum with single aesthetasc inserting ventrally.

Antenna (fig. 3.1B, 3.2A-D): Basal 4 segments large, robust, indicating long appendage. Basal segments decrease in width distally. Scale on third article absent, former position possibly marked by clump of setae.

Left Mandible (fig. 3.2F-N): Incisor process with 3 teeth. Lacinia mobilis with 4 teeth, broad grinding surface posterior to teeth, and many hair-like spines on ventral surface. Spine row with 11 members on strongly curved and compressed basal ridge. Molar process large, with 13-17 setae on distal posterior edge; distal

tritulating surface concave, oval, heavily cuticularized, with distinct sensory pores. Dorsal condyle shorter than molar process, somewhat recessed into mandibular body. Posterior part of mandibular body with large articular lobe.

Maxillula (fig. 3.3F): Inner lobe very setose, nearly as long as outer lobe, with one large distal seta. Outer lobe with 12 claw-like setae, one spine-like seta at base of sixth claw seta from lateral end, and row of thin flattened setae at ventral base of larger distal setae; second large seta from outside resting in concavity on medial surface of first seta.

Maxilla (fig. 3.3G): Inner lobe wider than both outer lobes together. All lobes very setose. Basal region covered with many cuticular combs.

Maxilliped (fig. 3.3H-I): Endite with 7-9 coupling hooks in adult (3 in manca 3); distal tip sharp-toothed laterally with 9 short (4 in manca 3) and 1 long fan setae; endite length (measured from medial insertion of palp to distal tip) 0.32 times total basis length. Palp article 2 width 1.2 times endite width; medial length 0.38 times lateral length. Palp article 3 medial length 3.0 times lateral length. Epipod distally rounded with no lateral projection; length 2.2 times width.

Pereopod I (fig. 3.3C-D): Limb robust. Basis longest segment. Ischium with row of setae on dorsal distomedial margin. Merus with

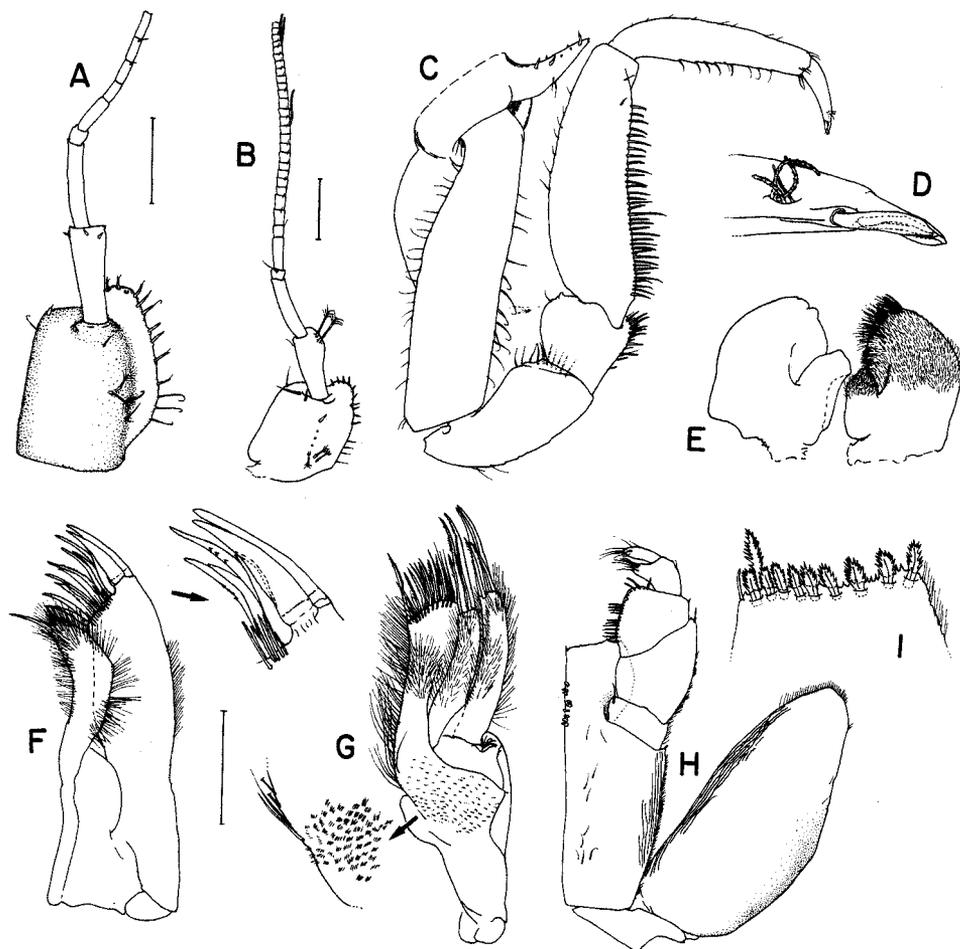


Figure 3.3. A, C, E-I, preparatory female, INCAL WS02. Scale bars are all 0.5 mm long; A, C, E, H have the same scale. B, copulatory male, INCAL WS04. D, paralectotype female, USNM 42172. A-B, antennula, distal articles missing. C, pereopod I. D, pereopod I dactylus, medial view. E, paragnaths. F, maxillula, with enlargement of distolateral setae. G, maxilla, with enlargement of setal combs on mediobasal region. H, maxilliped. I, enlargement of maxilliped endite distal tip.

patch of setae on ventral distomedial margins. Carpus length 0.88-0.92 times basis length, with 23-36 setae on opposing margin of carpus. Propodus length 0.69-0.72 times carpus length.

Bases of Pereopods I-VII (fig. 3.1B, F-G): Basis VI longest, bases III-IV shortest; basis length-body length ratios 0.13, 0.17, 0.11, 0.11, 0.15, 0.20, 0.17, respectively. Bases III-IV with distinct lateral bump about midway along length. Basis VII as robust as bases V-VI.

Male Pleopod I (fig. 3.4A-C): Pair complex long and narrow, widest proximally, narrowest distally, length 3.4-3.5 times proximal width, length 8.5 times width at dorsal orifice. Dorsal orifice close to distal tip, 0.09 times total pleopod length from distal tip. Ventral surface with broad paired rows of many plumose setae extending nearly full length of pleopod. Distal tip with 3 paired, dense groups of simple setae: on dorsal surface of distal margin, on ventral surface behind outer lobe, on ventral surface in broad row extending proximally from region below dorsal orifice to around two-thirds length of pleopod. Inner lobe rounded; outer lobe bluntly recurved.

Male Pleopod II (fig. 3.4D-F). Protopod length 2.3 times width; many plumose setae on lateral margin and posterior half of ventral surface; simple setae on ventral surface below exopod. Endopod and exopod small, inserting close to distal tip; endopod inserting 0.26 times total protopod length from distal tip. Stylet not extending beyond distal tip; length 0.39 times total protopod length; distal tip of stylet with tiny lateral denticles. Exopod with very dense

group of fine simple setae on posterior curve.

Female Pleopod II (fig. 3.1E,I): Operculum narrow with deep keel. Length 1.9 times width in manca 3. Keel narrow, ventrally rounded, with no distinct apex nor setae. Lateral margins and posterior part of lateral fields with many plumose setae. Distal tip bifurcate with distinct incision, incision length subequal to medial length of uropodal protopod.

Pleopod III (fig. 3.4G): Endopod with around 14 distal brush setae in adult. Exopod narrow, length 5.6 times width, rounded with around distal 8 brush setae in adult, lateral margin with small plumose setae on proximal article.

Pleopod IV (fig. 3.4H): Exopod narrow, decreasing in width distally, with 3 brush setae on tip.

Uropod (fig. 3.1E, I-K): Protopod large compared to rami; about round in cross-section; distal margin (where rami attach) forming acute angle with medial margin, with circa 15 short setuled plumose setae on ventral margin (10 in manca 3) and circa 15 long setuled plumose setae on dorsal margin (5 in manca 3). Endopod short and stubby, length 0.33 times medial length of protopod in manca 3; distal tip with tuft of broom and short setule plumose setae. Exopod about half length of endopod, with distal tuft of short setuled plumose setae.

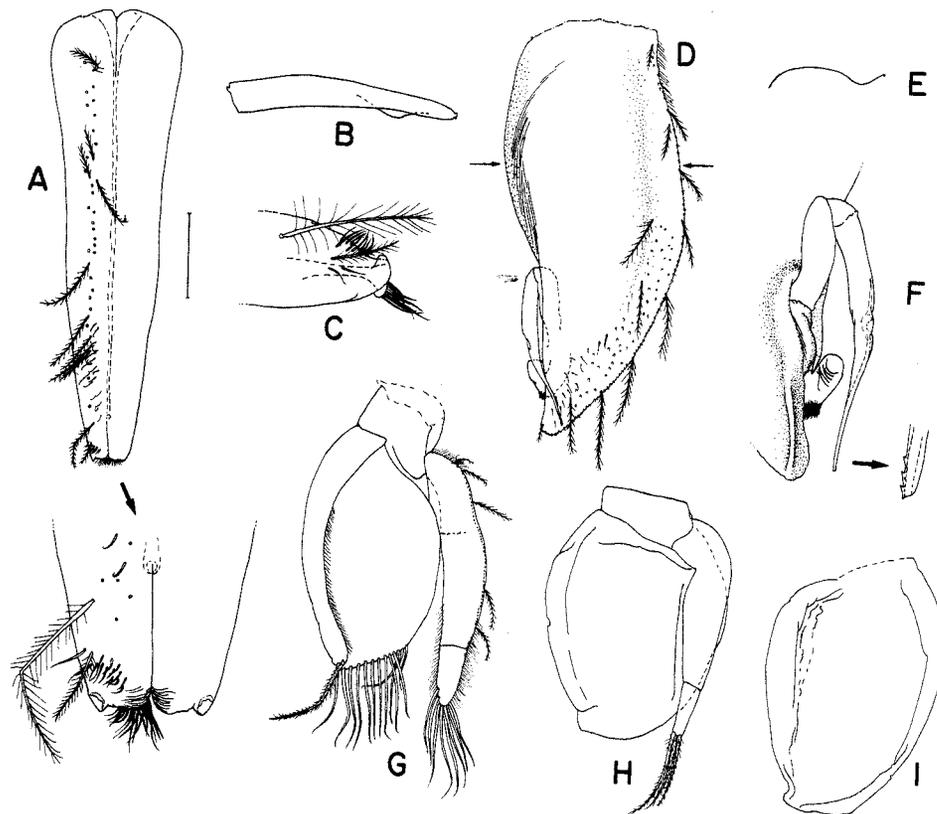


Figure 3.4. Pleopods from copulatory male, INCAL WSO4. A-C, pleopod I, scale bar to right of A is 0.5 mm long: A, ventral view, setae shown on right side, some plumose setae indicated by insertion points only; B, lateral view, setae omitted; C, lateral view of distal tip. D-F, pleopod II: D, ventral view, some plumose setae indicated by insertion points only; E, contour of ventral surface at position of small arrows in D; F, endopod with stylet and exopod, dorsal view, with enlargement of stylet distal tip. G-I, pleopods III-V.

Remarks.--Schultz (1976) considered abyssorum to be a member of Echinozone Sars 1899 because it has biramous uropods and lacks mandibular palps. Amuletta abyssorum, however, is different from the species of Echinozone in the following major characters: lacinia mobilis and molar process not reduced as in most ilyarachnids, coxal plates large on pereonites 1-3, antennal scale absent, and no spines on dorsal surfaces. [Concerning this last character, Schultz (1976) described Echinozone as possibly having dorsal spines tipped with stout setae, i.e., pedestal setae: a diagnostic character of Bathybadistes Hessler and Thistle 1975. None of the species of Echinozone (ibid, list on p. 157) has such setae.] The inclusion of A. abyssorum in Echinozone would unnecessarily and unnaturally broaden the definition of the latter genus.

Amuletta abyssorum is a large species, with adult body sizes between 1.0 and 1.5 cm. It is larger than any species in the Ilyarachnidae and most species of the Eurycopidae. Species of Betamorpha, and the Syneurycopinae sometimes approach 1 cm in length, and Storthyngura pulchrum is known to exceed 3 cm (specimens in the collection of R.R. Hessler from off southern California). A. abyssorum falls in the middle of the size range of the large members of the Eurycopidae.

A. abyssorum has been found only in the northeast Atlantic Ocean despite the intensive deep-sea sampling that has been conducted in most parts of the Atlantic. The species has a broad depth range, 2379-4829 m., suggesting it is somewhat eurytopic by deep-sea isopod

standards. The geographic distribution of A. abyssorum may be much greater than reported here. A. abyssorum is about the same size as Storothyngura pulchrum, a species which also appears rarely in epibenthic-sled samples but is taken abundantly in large trawls (Markham, 1978; and personal observations). Therefore, the paucity of specimens of A. abyssorum may be due to avoidance of the epibenthic sled used to collect most of the Atlantic deep-sea samples we have examined.

The gut contents of a large female specimen (INCAL WSO2) were removed during dissection. This material consists of amorphous sediment and detritus, and many whole or partially broken calcareous Foraminifera (roughly 20% by volume). Their abundance in this specimen's gut indicates that A. abyssorum may be actively selecting Foraminifera as food items. Some of the amorphous material could have been agglutinating Foraminifera, which would quickly become unrecognizable under the attention of the mouthparts and gastric mill. Consumption of Foraminifera by deep-sea isopods may be more common than has been reported until now. We have often seen calcareous forams in the guts of other Janiroidean genera, although not as many as in the A. abyssorum specimen. Furthermore, the abundance of Foraminifera in the deep-sea (Thiel, 1975; Bernstein et al., 1978; Snider, et al., 1985) suggests that these protozoans should be an important food source for isopods and other macrofauna.

ACKNOWLEDGMENTS

Thomas Bowman, United States National Museum, and Jacques Forest, Museum national d'Histoire naturelle Paris, loaned the type-specimens of Ilyarachna abyssorum needed for this study. The manuscript was reviewed by Robert Hessler, William Newman, Richard Rosenblatt and Hans Thierstein, all of Scripps Institution of Oceanography, and two outside reviewers provided by the Journal of Crustacean Biology. The INCAL material analysed in this study was sorted by the Centre National de Tri d'Océanographie Biologique, and the Laboratory at Oban of the Scottish Marine Biological Association. This work was supported by National Science Foundation grant BSR 8215942. We sincerely thank these people and institutions for their part in this research.

CHAPTER 4

AN OUTGROUP FOR THE MUNNOPSOID FAMILIES: PHYLOGENETIC ANALYSES OF THE SUBORDER ASELLOTA AND THE SUPERFAMILY JANIROIDEA

INTRODUCTION

The ilyarachnoid Eurycopidae clearly belong among the munnopsoid families, but how they should be classified in this group is uncertain without knowing the ancestral state of the munnopsoids. Knowledge of the evolutionary sequence from primitive to derived in a taxonomic group's characters is a primary requirement of successful phylogenetic analysis (Hennig, 1966). The most successful technique for determining this evolutionary sequence is outgroup analysis (Watrous and Wheeler, 1981; Maddison et al., 1984). In the following pages, the results of several outgroup analyses of the Asellota will be reported with the goal of finding the most likely sister group of the munnopsoid families, Eurycopidae, Ilyarachnidae, and Munnopsidae. With this knowledge, the systematic position of the ilyarachnoid Eurycopidae may be determined. In well-developed classifications, broad ranging systematic work of the type reported here would be unnecessary. One simply would consult existing authoritative works for the best estimate of the outgroups. For the Asellota, however, no such works exist. Evolutionary relationships at the superfamily-level

are poorly resolved, and published studies of the asellotan taxa generally do not use consistent phylogenetic techniques. This chapter is a partial remedy to this situation, and is the springboard to the work reported in the final chapter.

To accomplish the objectives of this chapter, a new taxon, the family Pseudojaniridae, is introduced into the classification of the Asellota, using morphologies overlooked by my contemporaries. The Pseudojaniridae is important because this monotypic family has characters that are clearly intermediate between the superfamily Stenetriodea and the superfamily Janiroidea. The latter superfamily contains the munnopsoids. At the superfamilial level, the morphology of the cuticular organ, a female copulatory organ, was found to be very useful for ascertaining the evolution of the Janiroidea. Within the Janiroidea, the third pleopod and the seemingly insignificant claws on the pereopodal dactyli are used extensively. All these characters are described below and their evolutionary polarities are determined. These data are then used in two phylogenetic analyses, one at the superfamilial level of the suborder Asellota and one at the familial level of the superfamily Janiroidea.

MATERIALS AND METHODS

SPECIMENS

The holotype female and male specimen of Pseudojanira stenetrioides were kindly loaned by M.G. van der Merwe, Marine Biology Technical Officer of the South African Museum (SAM). The accession

numbers for these two specimens are SAM A6295 and SAM A15345, respectively. The holotype female was collected off the Zululand coast, among coral found in the eulittoral zone. The male specimen comes from off South Africa ($24^{\circ} 53' S$, $34^{\circ} 56' E$) in fine gray sand at a depth of 55 m. The remaining examples of the genera discussed in this chapter were taken from the research collection of Robert Hessler. The specimens of Munna, Paramunna, Notasellus and Santia were collected at Palmer Station, Palmer Peninsula of Antarctica (Richardson, 1976). Asellus was collected by Robert Hessler near Lund, Sweden. The remaining specimens were collected in various localities in the deep Atlantic Ocean by vessels of the Woods Hole Oceanographic Institution.

For studies of the cuticular organ, the holotype of Pseudojanira stenetrioides was studied in lactic acid after staining with methylene blue. Other specimens were bisected sagittally, and one half of each was macerated in potassium hydroxide solution kept at a temperature of $60^{\circ} C$. After all tissues except the cuticle were dissolved away, the specimens were either studied in lactic acid - methylene blue or were stained in Ehrlich's triple stain (Guyer, 1953, p. 246), rapidly dehydrated into 100 percent ethanol, and transferred to turpineol for examination. All macerated specimens are stained and stored in turpineol. The illustrations in this chapter were inked from pencil drawings made using a Wild M20 microscope fitted with a camera lucida drawing tube. Previous discussion of the evolution of the Asellota have typically relied on simple outline drawings of limbs for comparison. The fine details of asellotan construction, however, are

often phylogenetically important (Wägele, 1983). For example, an outline of the endopod of male pleopod II would not show the difference between the stylet of Pseudojanira and that of the Janiroidea. Therefore this chapter will provide more pictorial information than has been typically offered in the past. In the illustrations of body parts, and especially the cuticular organs, anterior is toward the top of the page.

DATA ON JANIROIDEAN CHARACTER STATES

Information on the character states of the families of the Janiroidea was taken from many literatures sources. A pictorial card file and these literature sources were used to survey the character states used. This card file, compiled by various workers in Hessler's laboratory, including me, contains photocopied illustrations from the literature of a large proportion of the Janiroidean genera.

Data on the dactylar claws of the pereopods was derives from a survey of these characters conducted by Robert Hessler, Bryan Burnett, and me. The information consists of numerous polaroid photographs of scanning electron microscope images, arranged by taxon. The images are views from different directions of the pereopod II dactylus of specimens from most of the Janiroidean families, as well as from the Stenetrioidea and other isopodan suborders. If no images of a taxon were available, the literature generally provided the needed data.

PHYLOGENETIC TECHNIQUES

Phylogenies were estimated primarily using techniques codified by Hennig (1966), and explained in modified form by Wiley (1980). Hennig's method relies on knowledge of ancestral and derived character states, from which the taxa are arranged in a hierarchical branching sequence. Parsimony is the criterion for arranging the taxa; this criterion chooses an estimated phylogeny that hypothesizes the fewest total changes in character states from the observed distribution of character states among the taxa. Using such a criterion allows one to derive phylogenies in those cases where several sets of characters provide conflicting estimates of the true phylogeny.

This form of phylogenetic estimation relies on knowledge of the polarity of the characters, that is, which character states are ancestral or plesiomorphies and which are derived or apomorphies. A series of character states from ancestral to derived is called a transformation series. The most reliable way of determining the polarity in a transformation series is to use outgroup analysis (Watrous and Wheeler, 1981; Maddison et al., 1984). Watrous and Wheeler (1981) give a simple rule for determining polarity: for a character with 2 or more states within a taxon, the state found in that taxon's most closely related group, the sister group, is the plesiomorphy within the taxon. Maddison, Donoghue, and Maddison (1984) point out that this rule fails when the characters vary in potential sister groups. They advocate the use of an algorithm that uses an estimate of the phylogeny of the all the taxa, both outgroups and the ingroup, to assign the most parsimonious estimate of a

character state to the outgroup node (the ancestral species of the sister group and the ingroup). Once the ancestral states are known from this procedure, the phylogeny of the ingroup can be estimated. Maddison et al. (1984) show that this two step procedure can achieve the most parsimonious estimate of the phylogeny for both the outgroups and the ingroups, a quality they call "global parsimony."

A phylogenetic tree, here considered the same as a cladogram, may be constructed using the logical rule of parsimony, although one cannot be certain that all the most parsimonious trees have been investigated for cases that have more than a few characters and taxa. Numerical techniques for evaluating phylogenies are useful when the complexity of the data set exceed one's ability to find all possible trees. For the work reported here, both logical and numerical techniques were used to estimate phylogenies. Both methods yielded essentially the same results. The numerical methods also give parsimony values and trees automatically, allow the testing the effect of various topologies of transformation series, and give results in a few minutes rather than hours of careful work.

The numerical methods used here were developed by Joseph Felsenstein, University of Washington, and colleagues, and are supplied by him as PASCAL programs that may be easily compiled into machine language for many different kinds of computers. The programs, called PHYLIP (PHYlogeny Inference Package), use a variety of algorithms for determining phylogenies, discussed in Felsenstein (1979; 1982). The programs were modified by me to run on an

International Business Machines XT microcomputer, and turned into machine language by a compiler, Turbo Pascal, distributed by Borland International.

The PHYLIP program used most heavily for my analyses was MIX, which allows the use of weights and two different parsimony algorithms for each character separately. The two algorithms are the Camin-Sokal method (Camin and Sokal, 1965) and the Wagner method (Eck and Dayhoff, 1966; Kluge and Farris, 1969). The assumptions of these methods are stated in Felsenstein (1978, 1979, 1981). Both methods assume that characters and lineages evolve independently, that the evolutionary rates are sufficiently low that any change in character state is unique, and is unlikely to be duplicated in another lineage for the taxa under consideration, and that retention of polymorphism is less probable than a change from an ancestral (state 0) to a derived state (state 1). The most important difference between the two methods is that the Camin-Sokal method does not allow reversions, and the Wagner method does. The Wagner method also does not assume an ancestral state, whereas the Camin-Sokal method requires knowledge of the ancestral state. In the analyses, however, the ancestral state was generally given for either method to "root" the trees.

The program MIX operates by taking the first three taxa from the taxon-character matrix given, and finding a most parsimonious tree for the distribution of characters and the assigned parsimony methods. It then sequentially adds taxa to the tree by placing each one on the branch between nodes that adds the fewest changes in character states.

This process is continued until all the taxa are assigned branches on the tree. (See appendix 2 for example of program output for Asellota data.) This algorithm does not investigate all possible tree topologies because the number of trees quickly becomes astronomical even with a few taxa (Felsenstein, 1982). As a consequence, MIX is sensitive to the input order of the taxa and must be run numerous times with different orderings. This process was automated by writing a PASCAL module for MIX that randomly orders the taxa into as many data sets as desired, and then runs the program iteratively until all the data sets are evaluated. This method proved to be most effective because after the new program, ITERMIX, was started, it could run automatically for long periods of time without user intervention. Typically, "a" most parsimonious tree was found within 10 iterations, but often different topologies with the same low value appeared in runs of 30 or more iterations (see appendix 2).

Some of the characters had uncertain transformation series. This made it necessary to do multiple runs of the ITERMIX in order to test all possible combinations of the uncertain transformation series. 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. Fortunately, only three 3-state characters had uncertain transformation topologies, and only 12 different data sets were tested. Each of these data sets was run at least 10 times, although the more promising combinations were run 30-40 times. This resulted in a ordering of the data with transformation

topologies that produced the single most parsimonious tree. Character weightings and mixed parsimony methods were added to the data set, and the final version of the tree was generated. This procedure was necessary only for the data set of the janiroidean family-level groups, which contained many conflicting characters. The Asellota data set contained highly compatible characters, so that every run produced precisely the same result.

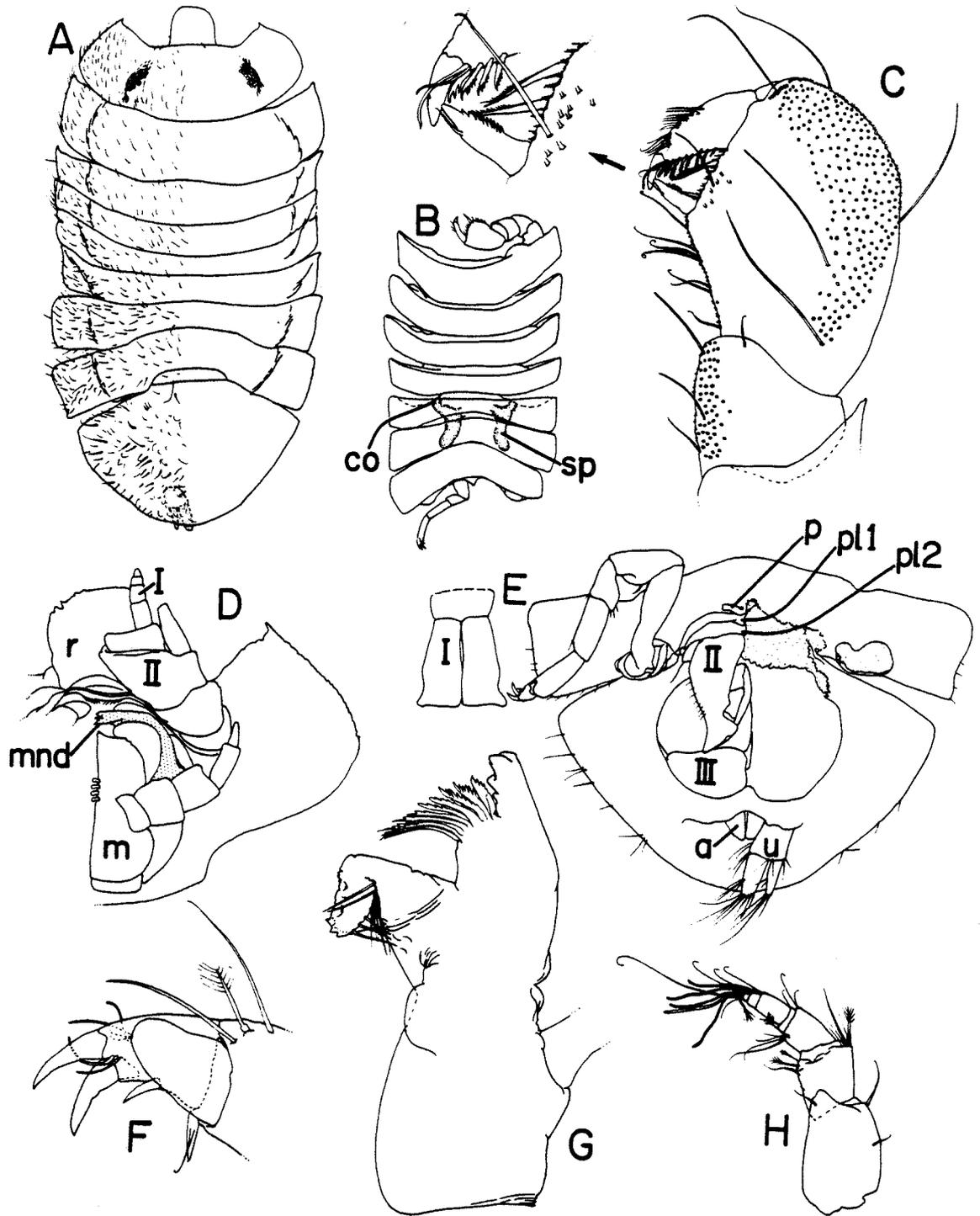
PHYLIP also contains programs that use radically different methods for evaluating trees. The one used here was CLIQUE, which uses the character compatibility method (Estabrook, Johnson, and McMorris, 1976a, 1976b; Bron and Kerbosch, 1973). This method uses two state discrete characters for which the ancestral state is unknown, assumes that changes in character states occur only once, and finds the tree that has the largest "clique" of compatible characters. Compatible characters are those that do not produce conflicting estimates of the branching sequence of the phylogenetic tree. This method has been criticized because it does not use all the data to estimate a tree (Hill, 1975). Here it proved to be ineffective in generating well resolved trees for the data sets with a high degree of homoplasy (or incompatibility), and therefore was used only as a check on the results of the Camin-Sokal and Wagner algorithms. (See Appendix 3 for results of CLIQUE runs on the two final data sets assembled in this chapter.)

A REDESCRIPTION OF PSEUDOJANIRA STENETRIOIDES BARNARD

INTRODUCTION

The discovery of unusual female and male copulatory organs in Pseudojanira stenetrioides Barnard, 1925, made it necessary to include a redescription of this unique animal. P. stenetrioides is a small isopod from South Africa, recently redescribed by Kensley (1977) and classified by that author as a member of the family Janiridae, superfamily Janiroidea. This species (fig. 4.1, 4.2) has a stenetrioid habitus and a male first pleopod intermediate between the conditions seen in the Stenetrioidea and in the Janiroidea. An examination of 2 specimens of this species from the South African Museum confirmed Kensley's figures (1977), and revealed the presence of a new type of female genital organ which will be described in the survey of asellotan cuticular organs. Because the combination of characters found in P. stenetrioides, a new family is erected for the genus Pseudojanira. The superfamilial classification, however, is left undecided; proper determination of the superfamilies must be based on a complete morphological survey of all the families of the "lower" Asellota (see discussion after the phylogenetic analysis below).

Figure 4.1. Pseudojanira stenetrioides Barnard, 1925. A, C-H, male, 2.8 mm. B, holotype female, reported intact length 3 mm. A, dorsal view, setae on right side omitted. B, dorsal view of female pereonal fragment, co - position of cuticular organ seen through dorsal cuticle, sp - spermatheca seen through dorsal cuticle; specimen was cleared with lactic acid and stained with methylene blue to make this possible. C, pereopod I of male, distal segments only, with enlargement of opposing setation on propodus and dactylus. Carpus and propodus had many long tubular setae; their insertions are indicated by 'u' or circular marks, and a few are drawn in to give an approximate length of the ones omitted. Some of the setae in the enlargement are illustrated in the same manner. D, ventral view of left side of cephalon (right side had been dissected); I - antennula, II - antenna, r - rostrum, m - maxilliped, mnd - mandible. Note how the rostrum is nearly as long as the antennula, the tip of which is protruding past the basal articles of the antenna. E, Ventral view of male pereonite 7 and pleotelson, with pleopod I shown at the same scale; I - pleopod I, II - pleopod II, III - pleopod III, p - penile papillae, pl.1 - presumed pleonite 1, pl.2 - presumed pleonite 2, a - anus, u - uropod. F, dactylus of pereopod mounted on slide, possible pereopod VII as in Kensley (1977). Note presence of 2 subequal claws and a more proximal accessory seta on dactylus. G, right mandible, dorsal view, palp omitted. H, right antennula, ventral view.



ORDER ISOPODA, SUBORDER ASELLOTA, SUPERFAMILY INCERTAE SEDIS

PSEUDOJANIRIDAE NEW FAMILY

(Figures 4.1, 4.2)

Type-Genus.--Pseudojanira Barnard, 1925, by original designation.

Previous Assignments of Type.--Jaeridae: Barnard (1925, p. 406).

Janiridae: Wolff (1962, p. 252); Kensley (1977, p. 251). Ianiridae:
Kensley (1977, p. 253).

Diagnosis.--Asellota with broad pereonal tergites extending laterally and ventrally, hiding coxae from dorsal view. Cephalon with dorsal eyes, broad lateral lappets, and large frontal rostrum. Pleotelson with only 1 free pleonite visible dorsally, 2 ventrally. Pereopod I robust, with enlarged setose propodus; grasping occurring by opposition between dactylus and propodus; carpus short, quadrangular, setose, not participating in grasping. Male first pleopods fused at basal segments, distal rami separate; distolateral corners with dorsal grooves; distal margins quadrate, with simple setae. Male pleopod II basal segment enlarged, with endopod and exopod projecting medially; distal tip of basal segment enlarged, thickened, with transverse distomedial groove supplied with fine setae; endopod distal segment stylet-shaped, with open ventral groove and distolateral barbs; endopod proximal segment with thickened cuticular ridge; exopod comprising only single short, robust segment, with thickened dorsal hook on setose anterodistal corner. Male pleopods I and II together not opercular. Female second pleopods (not seen by me) fused into single opercular segment lacking setae on margins. Pleopod III

exopod broad, rounded, with fringe of simple setae; endopod with 3 large plumose setae; in male, exopod opercular. Uropods short, biramous, setose, barely extending beyond posterior margin of pleotelson.

Pseudojanira stenetrioides Barnard, 1925

(Figures 4.1, 4.2)

Previous Descriptions.--Pseudojanira stenetrioides: Barnard (1925: p. 406-407); Kensley (1977, p. 251-253).

Holotype.--Adult female, 2 poorly preserved fragments (cephalon and pereon), pleotelson missing, reported original length 3 mm, width 1.3 mm, SAM 6295. Type locality: "Zululand coast, in a coral (H.W. Bell-Marley, 1920). . ." (verbatim from original description, Barnard, 1925).

Additional Material.--Partially dissected adult male, with removed limbs on a slide, length (including rostrum) 2.8 mm, width at sixth pereonite 1.4 mm, SAM A15345. Locality: ". . . 24° 53' S, 34° 56' E, 55 metres, from fine gray sand" (verbatim from Kensley, 1977).

Description (in addition to familial diagnosis Kensley, 1977).--Body characters (fig. 4.1A,B): Lateral margins of pereonites oval in dorsal view. Body surfaces covered with fine setae. Body dorsoventrally thin but highly vaulted: tergites extending beyond main part of body and angling sharply downward. Pereonite 1 sexually dimorphic, longer and more robust in males than in females.

Female Cuticular Organ (fig. 4.1B): Described below in section on male and female copulatory organs in *Asellota*.

Cephalon (fig. 4.1A,D): Rostrum anteriorly rounded; thin, broad, and nearly as long as short antennulae; projecting anteriorly from frons, below linear anterior margin of cephalic dorsum. Lateral margins broad, flattened, with small anterior spine. Eyes projecting dorsolaterally from domed central portion of cephalon, positioned roughly halfway between midline and lateral margins.

Pleotelson (fig. 4.1A,E): Broader than long. Pleopodal cavity small, width half width of pleotelson, cavity separate from anus. Lateral margins not denticulate, smoothly curving.

Antennula (fig. 4.1H): Very short, length approximately length of antennal segments 1-4, basal segment largest. Broom setae on segments 2 and 4; aesthetascs on distal three segments.

Antenna (fig. 4.1D): Basal segment 3 with large, unfused scale.

Right Mandible (fig. 4.1G): Spine row with 10 members. Articular condyle on dorsal surface distinctly shorter than length of robust molar process. Molar process with approximately 9 setae on denticulate posterior circumgnathal surface.

First pereopod (fig. 4.1C): Claw of dactylus opposing large spine-like serrate seta on propodus. Row of small tapering setulate setae leaning toward more posterior large spine-like seta. Oppositional

margin of dactylus armed with row of short multiply-toothed setae. Carpus and propodus with several dense groups of long, thin setae.

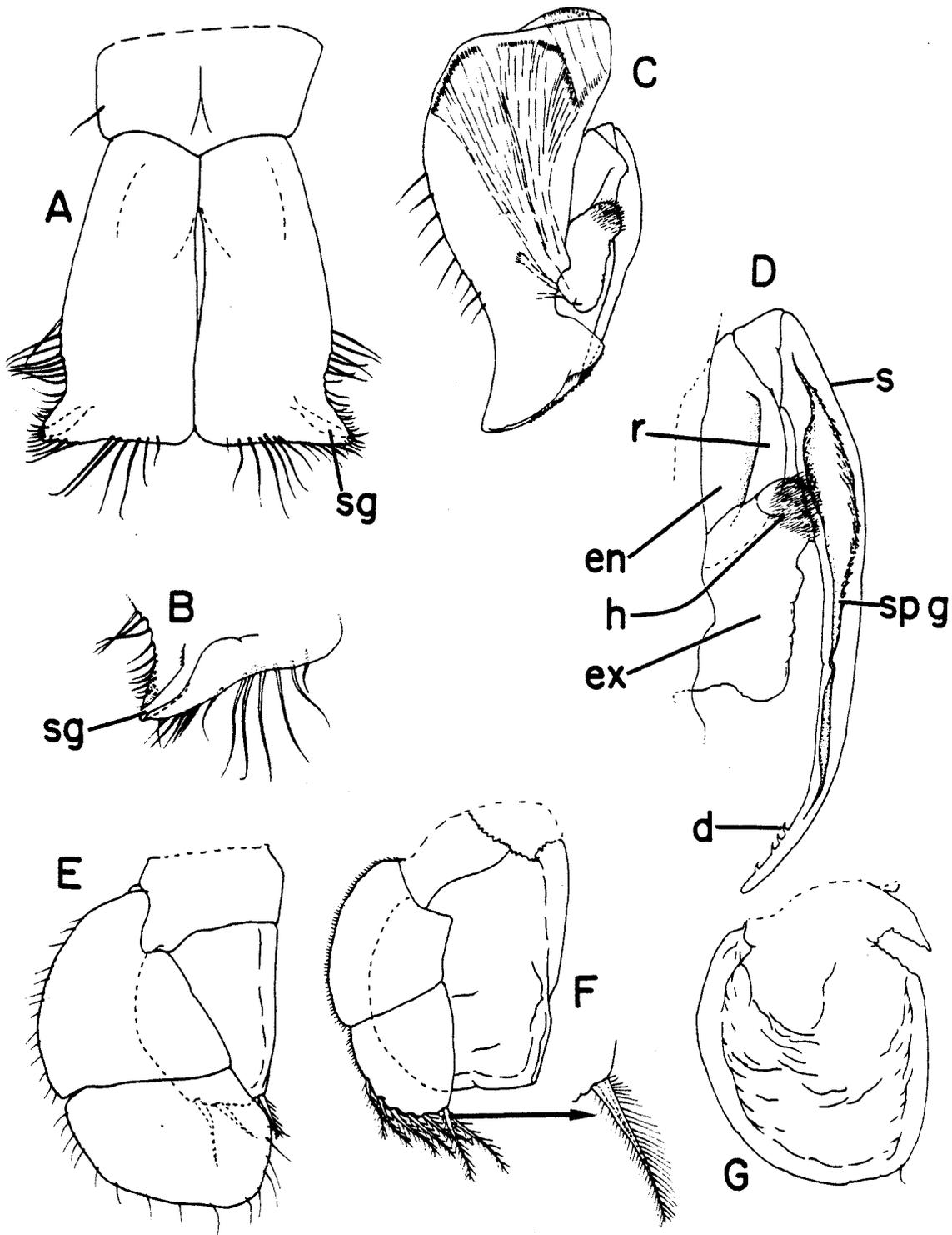
Dactylar claws of the walking legs (fig. 4.1F). Distal tips of walking legs with 2 robust claws of similar size, and more proximal small claw-like accessory seta.

Male Pleopod I (fig. 4.2A,B): Length 0.42 pleotelson length, distal segments covering rami of pleopod II. Basal segments fused medially. Distal rami separate, distally quadrate with fringe of simple setae posteriorly and laterally. Dorsal side of distolateral corners with stylet grooves (sg in fig. 4.2B).

Male Pleopod II (fig. 4.2C,D): Length subequal to pleopod I, with endopod and exopod inserting in center of medial margin. Distal tip broad, curving laterally to acute angle, with setose groove in posteromedial margin. Lateral margin of basal segment with row of simple setae. Endopod proximal segment robust, with pronounced ridge on ventromedial edge. Endopod stylet present, with convoluted groove on ventral surface and 4 small denticles on lateral margin of distal tip. Exopod robust, powerfully muscled, with rounded hook and fine setae on anterodistal edge.

Pleopod III (fig. 4.2E). Exopod broad, fringed with simple setae, covering pleopods IV and V; endopod somewhat less broad, dorsal to exopod.

Figure 4.2. Pseudojanira stenetrioides Barnard, 1925. Dissected parts on slide from male paralectotype. A-B, pleopod I. A, ventral view; B, dorsal (interior) view of distolateral corner; sg - stylet groove. C-D, pleopod II; C, ventral view, exopodal musculature shown through cuticle; D, enlargement of stylet: d - denticles, en - endopod, ex - exopod, h - position of dorsally directed hook on exopod, r - ridge on proximal segment of endopod, s - stylet (distal segment of endopod), spg - sperm groove. Note the ridge on proximal segment of the endopod; this ridge allows the well-muscled exopod to hook onto the endopod during copulation. E-G, pleopods III-V, respectively; plumose seta on pleopod IV enlarged.



Pleopod IV (fig. 4.2F): Endopod broader than exopod. Exopod with 2 free, laterally rounded segments, and 7 plumose setae on distal tip.

Pleopod V (fig. 4.2G): Endopod longer and broader than endopod of pleopod IV. Basal segment and endopod fused, exopod absent.

DISCUSSION

The primary reason Pseudojanira stenetrioides must be placed in a distinct family is that the male pleopods (fig. 4.2A-D) have a unique combination of characters. Because the current scheme of the superfamilies of the Asellota is based on the pleopods, the forms of these limbs in Pseudojanira make it difficult to place in the current superfamilies. The first male pleopod of Pseudojanira has a mix of janiroidean and stenetrioid characters. As in Stenetrium, the basal segment is large, quadrate, and medially fused. The two sides of the distal segment are free from each other. The distal tip, however, is setose and the distolateral corners have deep, laterally-curving grooves on the dorsal surface, clearly homologous the same structure in the Janiroidea that functions as a guide for the stylet of the second pleopod. This determination of homology is made on the basis of having the same position and functional relationship with the stylet. The form of the male second pleopod is interesting not only in its similarity to the janiroidean condition, but also for specializations that are seen only in this species. Characters shared with the Janiroidea are the pointed stylet, the ridge on the proximal segment of the endopod, and the club-like hooked form of the exopod with its enlarged musculature and distal group of fine setae.

However, the stylet has only a ventral groove and terminates with tiny barbs, unlike any janiroidean. The distal tip of the basal segment is also highly unusual: it narrows distal to the exopod, and then broadens both laterally and medially. Its distal tip is curved, grooved, and covered with tiny fine setae. The distal portion of the stylet rests in the groove of the basal segment's tip. It must somehow function as an additional stylet guide, or perhaps as the top part of an enclosed sperm channel.

The description of Pseudojanira states that one free pleonite is visible dorsally (fig. 4.1A), and two ventrally (fig. 4.1E). This observation is made with some misgivings since the only specimen where this could be studied had been damaged in the region of the ventral 2 pleonites. If more specimens come to light, the pleonites should be re-examined. If true, it would be another character which places Pseudojanira at an position intermediate to the Janiroidea (1 free pleonite) and the Stenetrioidea (2 free pleonites, 1 reduced).

The chaetotaxy and form of the first pereopod requires special mention: in many respects, they are similar to that seen in Stenetrium (see fig. 4.12B for comparison), and in Gnathostenetroides. Although Wägele (1983) makes a strong case for the similarity of the chaetotaxy of the Stenasellidae, Atlantasellidae, and Microcerberidae (see his figure 1, p. 253), some of the similarities may be plesiomorphies for those taxa: many of the same types of setae are also seen in Pseudojanira, Stenetrium, and Gnathostenetroides.

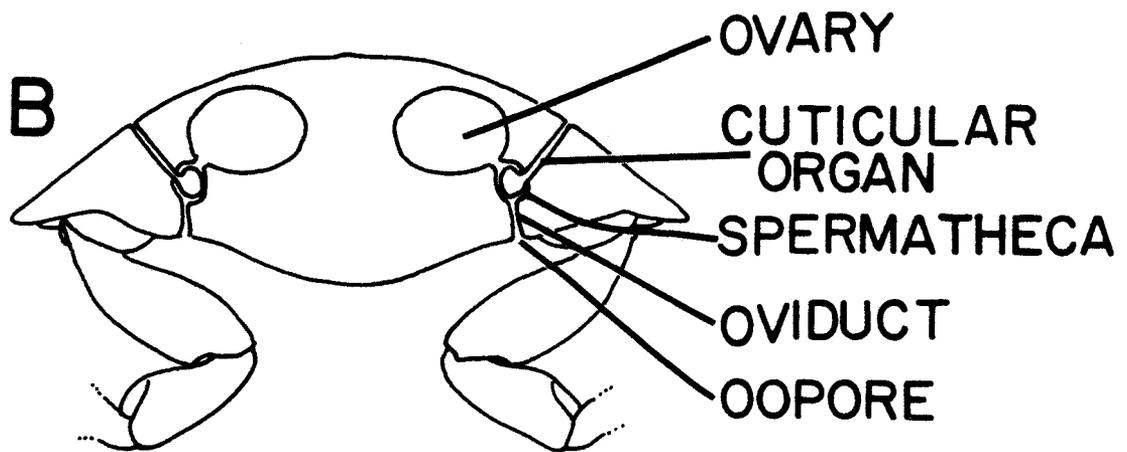
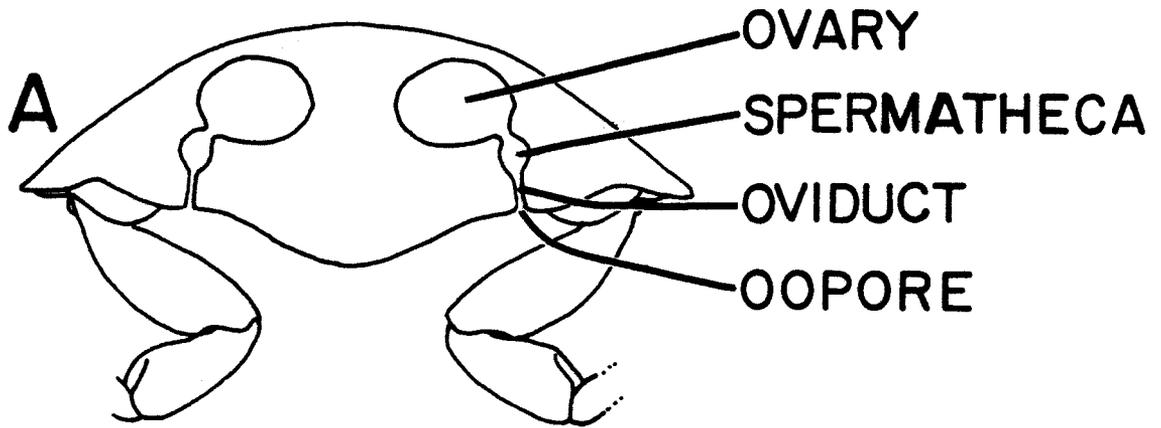
The accessory seta on the dactyli of pereopods II-VII is close in position to the third accessory claw found in the janiroidean family Janiridae and also in the Protojaniridae, and is nearly identical in position to an accessory seta on the dactyl of the Stenasellidae (see Magniez, 1974, p. 33). This seta is presumed to be homologous to the third claw of these other groups, and could well be a plesiomorphy of the Asellota.

THE FEMALE REPRODUCTIVE APPARATUS OF THE ASELLOTA

INTRODUCTION

There is some variety in the female reproductive morphology over the various suborders of the Isopoda (Menzies, 1954; Ridley, 1983). Current knowledge displays two seemingly different female reproductive organs within the Asellota (fig. 4.3): fertilization through either a ventral oopore on the fifth pereonite or a vagina-like anterodorsal organ called a "cuticular organ." Asellus, as an example for most of the asellote superfamilies, has the typical fertilization site at the ventral oopore (Maercks, 1931; Unwin, 1920). Within the oviduct, which opens at the oopore, there is a spermatheca that receives the sperm and hold it until release of the eggs. A dorsal cuticular organ is found only within the asellote superfamily Janiroidea. This bilaterally paired organ consists of an opening and an often complex cuticular tube that leads to a spermatheca in the oviductal tissues. It opens on the anterodorsal surface of the fifth pereonite (sixth thoracic segment), although the exact position of the organ varies somewhat among the various taxa in the superfamily. The existence of this structure has been known for some time (Forsman, 1944; Wolff, 1962; Veuille, 1978b; Lincoln and Boxshall, 1983), although only recently has the cuticular organ and its behavioral function been carefully described (Veuille, 1978b).

Figure 4.3. Previous concepts of female reproductive organs in the Asellota. Diagrammatic cross sections of two Asellota showing literature concepts of the morphology of the female reproductive system in Asellus and the Asellidae (A) and in Jaera and the superfamily Janiroidea (B). Illustrations derived from Ridley (1983). As will be shown, Asellus and other non-Janiroidea also have a cuticular organ, but it is positioned adjacent to the oopore. The cuticular organ of lower Asellota is more difficult to see because it is buried in the tissues of the oviduct.



How did a single orifice female reproductive system evolve into a two orifice system, separating the two functions? Veuille (1978b) suggested that an intermediate situation might be a "traumatic insemination" in which the male uses its needle-like stylet (sperm transferral organ) on the second pleopod to break the surface of the female's cuticle and inject the sperm into the spermatheca of the oviduct; he noted this type of insemination occurs in some insects. Fortunately, the solution to this problem is much simpler than the hypothesis suggested by Veuille: all female Asellota have a cuticular organ that connect to a separate spermatheca. As seen below, the cuticular organ of the lower Asellota is adjacent to the oopore and buried inside the tissues of the oviduct. Thus it cannot be seen until the oviductal tissues are removed by potassium hydroxide maceration. Another question concerns whether the cuticular organ evolved in unison with the specialized male genital organs characteristic of the Janiroidea. This section provides data for these problems, the answers to which will be evaluated after adding information from other characters in the next section.

TABLE 4.1. Taxa of Asellota examined for presence and position of the cuticular organ. An "*" marks a literature report of a cuticular organ. Abbreviations: "V", cuticular organ is placed ventral and opening adjacent to oopore; "D", cuticular organ is placed dorsally, opening distinctly separated from the ventral oopore.

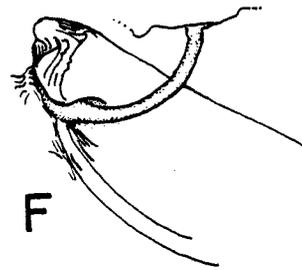
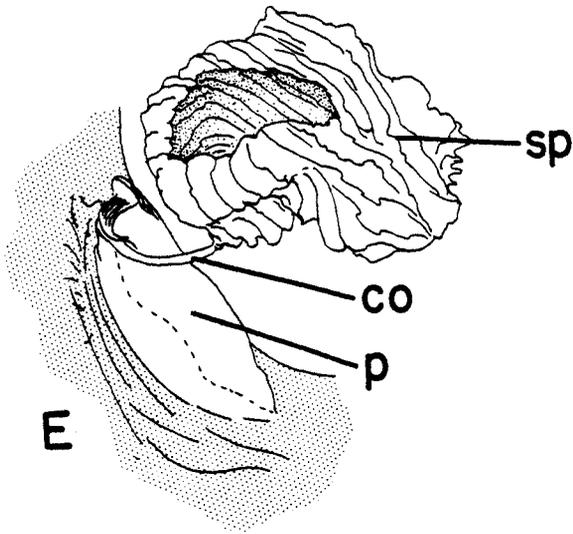
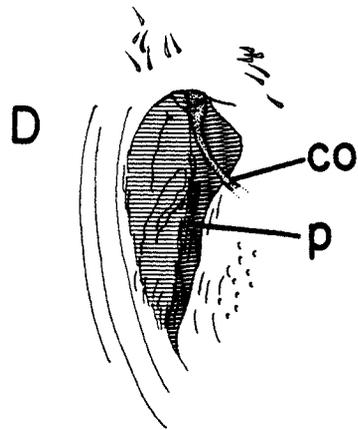
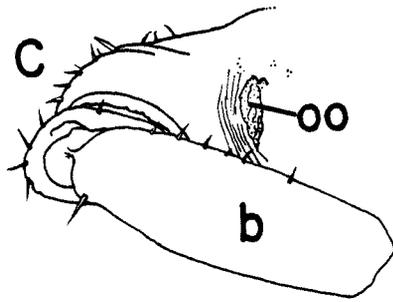
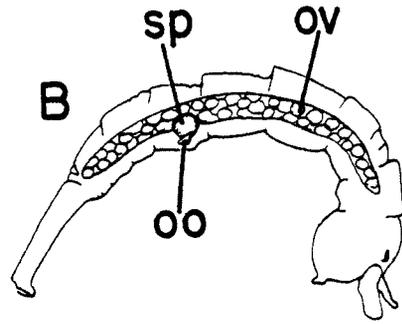
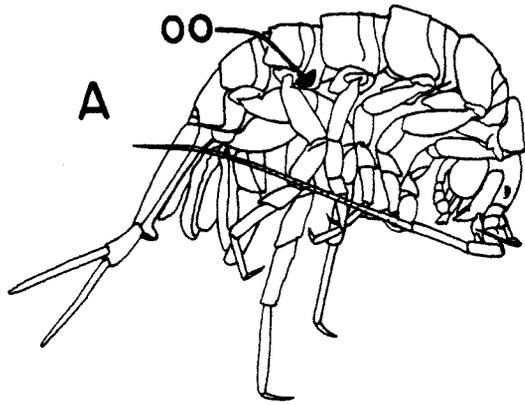
GENUS	SUPERFAMILY AND FAMILY	POSITION OF CUTICULAR ORGAN
<u>Asellus</u>	Aselloidea, Asellidae	V
<u>Stenetrium</u>	Stenetrioidea, Stenetriidae	V
<u>Pseudojanira</u>	Superfamily <u>Incertae Sedis</u> Pseudojaniridae n. fam.	V
<u>Jaera</u> *	Superfamily Janiroidea Janiridae	D
<u>Notasellus</u>	Janiridae	D
<u>Munna</u>	Munnidae	V
<u>Santia</u>	Pleurocopidae	V
<u>Paramunna</u>	Paramunnidae	D
<u>Abyssianira</u>	Abyssianiridae	D
<u>Acanthaspida</u>	Acanthaspidiidae	D
<u>Eugerda</u>	Desmosomatidae	D
<u>Amuletta</u>	Eurycopidae	D
<u>Eurycope</u>	Eurycopidae	D
<u>Tytthocope</u>	Eurycopidae	D
<u>Dendrotion</u>	Dendrotiidae	D
<u>Dendromunna</u> *	Dendrotiidae	D
<u>Haploniscus</u> *	Haploniscidae	D
<u>Ischnomesus</u>	Ischnomesidae	D
<u>Macrostylis</u>	Macrostylidae	D
<u>Mesosignum</u>	Mesosignidae	D

A SURVEY OF THE FEMALE REPRODUCTIVE APPARATUS

Veuille (1978) described the cuticular organ in janiroidean genus Jaera. It had been previously noted in the Haploniscus (Wolff, 1962), and recently the organ has been described in Dendromunna (Lincoln and Boxshall, 1983). An inspection of specimens of deep-sea Janiroidea shows the anterodorsally positioned cuticular organ to occur in most of the major families (see table 4.1). Exceptions are the genera Munna and Santia, in which the cuticular organ is ventral and associated with the opening to the oviduct. Various types of ventral cuticular organs also occur in the non-janiroidean asellotes, such as Asellus, Stenetrium, and Pseudojanira. The major morphologies of the cuticular organ from these taxa are described below.

Asellus (fig. 4.4).--The external appearance and configuration of the female copulatory and egg-laying organ has been described by Maercks (1931). Because of its size, Asellus aquaticus proved to be an excellent subject for study. In an unmacerated specimen (as in fig. 4.4B), the cuticular structures are enclosed inside the tissues of the much larger oviduct, and are not visible. In the preparatory female of Asellus, the cuticular organ opens on the anterior edge of the oviduct's ventral attachment. Internally the cuticular organ begins as a tube surrounded by a fold of a cuticular pocket. The tube narrows and curves dorsally to connect with a large filmy sac, the spermatheca, covered with parallel folds. The spermatheca is so thin that it cannot be seen unless the specimen is heavily stained with a cuticular stain. This sac has a large opening on its anterodorsal surface.

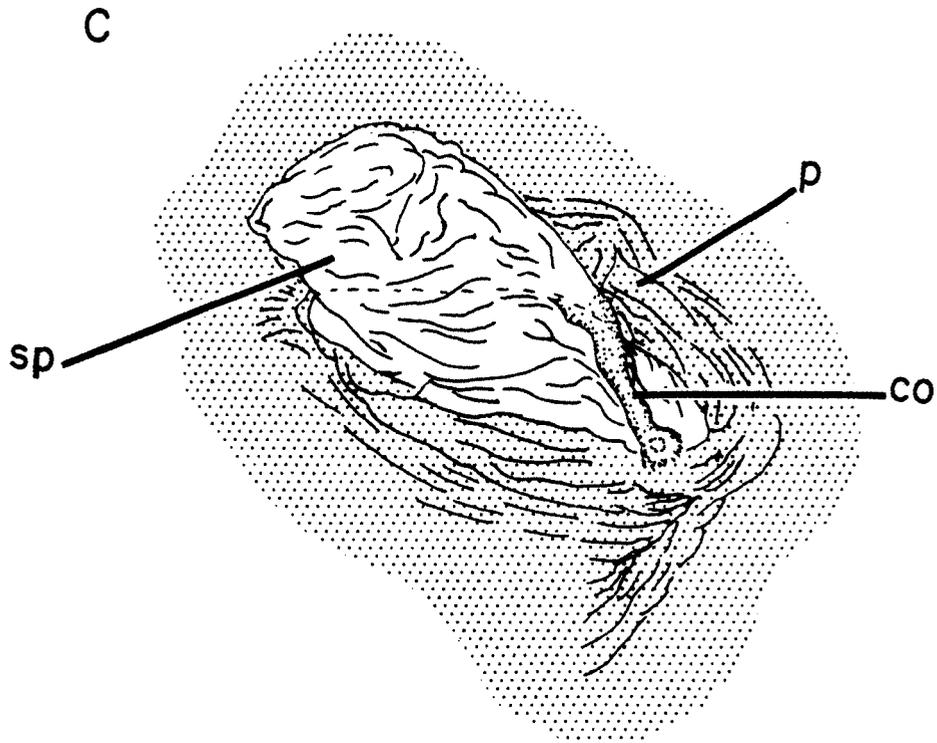
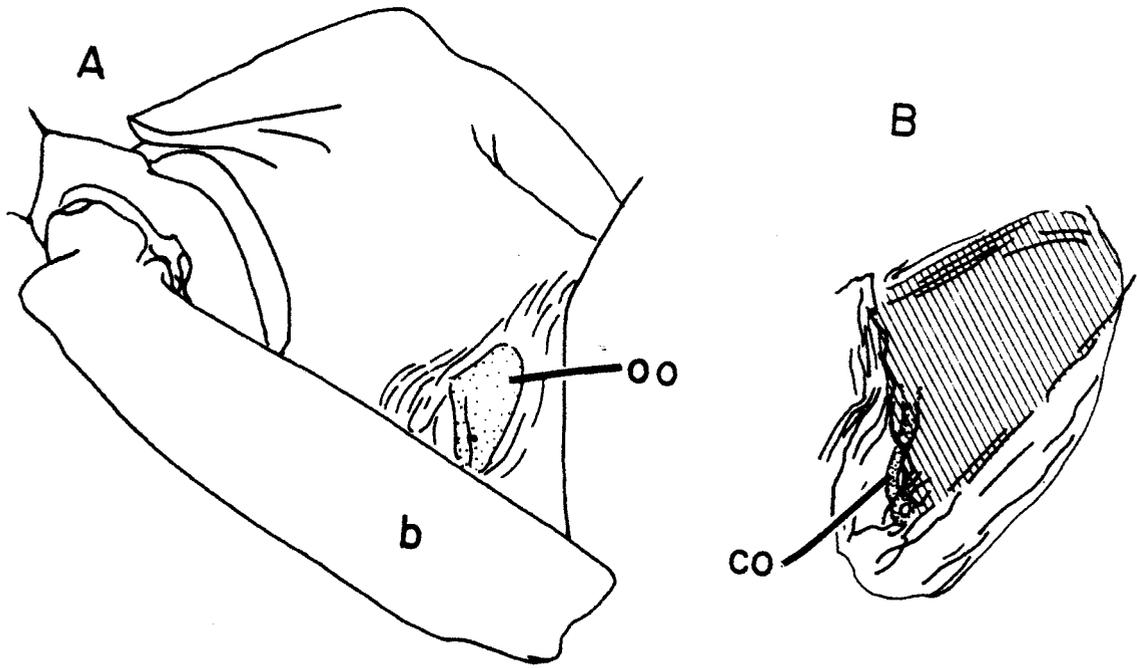
Figure 4.4. The female reproductive system of Asellus. A, lateral view of preparatory female of A. aquaticus. A female in this stage would mate during the next molt cycle after which the fertilized ova would be released into the marsupium (made of plates extending medially from the coxae of pereopods I-IV). B, semidiagrammatic internal view of reproductive system. C, ventral view of pereonite 5 on a preparatory female, right side, showing location of oopore (opening of the oviduct). D, cuticular structure of oopore in macerated, cleared, and stained preparatory female, showing structures through ventral cuticle. In the preparatory stage, the pocket is closed by the cuticular surface. During the molt to the brooding stage when copulation takes place (after the posterior molt is cast off, and before the anterior part of the body molts), the pocket receives the blunt copulatory organ of the male. Note the anterior position of the opening to the cuticular organ (shown as a thin tube). E, internal view of same structures as in D, showing pocket, cuticular organ, and spermatheca. The oviduct, which surrounds the spermatheca and the pocket at its origin, is removed during the maceration process that leaves only cuticular material. The darkened area is the ventral cuticle. F, enlargement of the anterior junction between the pocket and the cuticular organ, same view as E. b - basis of pereopod V; c - cuticular organ; ov - ovary; oo - oopore; sp - spermatheca; p - cuticular pocket.



During mating, the pocket that covers the internal part of the female oopore receives the male copulatory organ, the enlarged distal portion of the male's pleopod II endopod (Maercks, 1931; see fig. 4.9A-B). The motions made by the endopod during copulation (Maercks, 1931) would bring the opening of the cuticular organ in direct contact with the sperm holding part of the endopod. At this point, presumably, the sperm would be released into the cuticular organ.

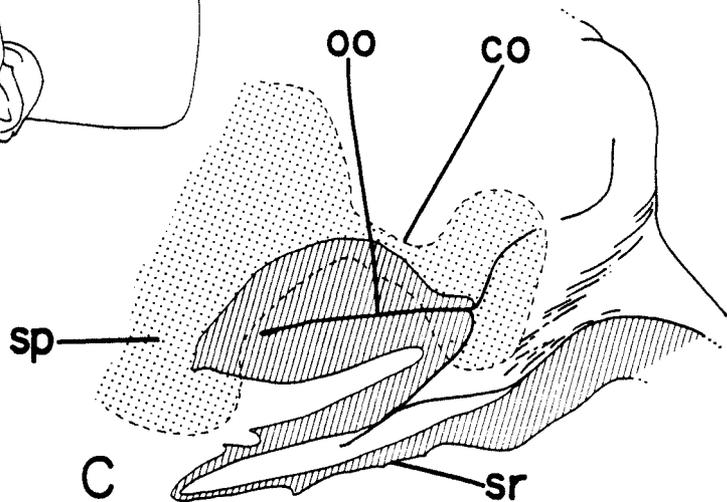
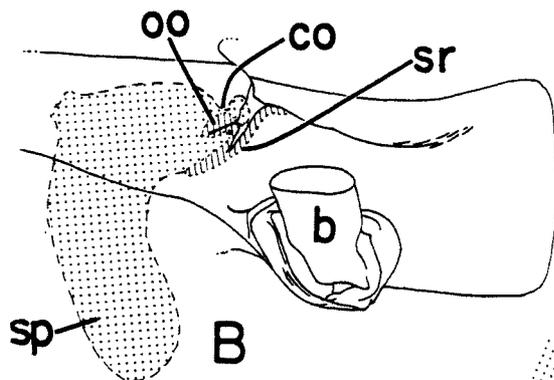
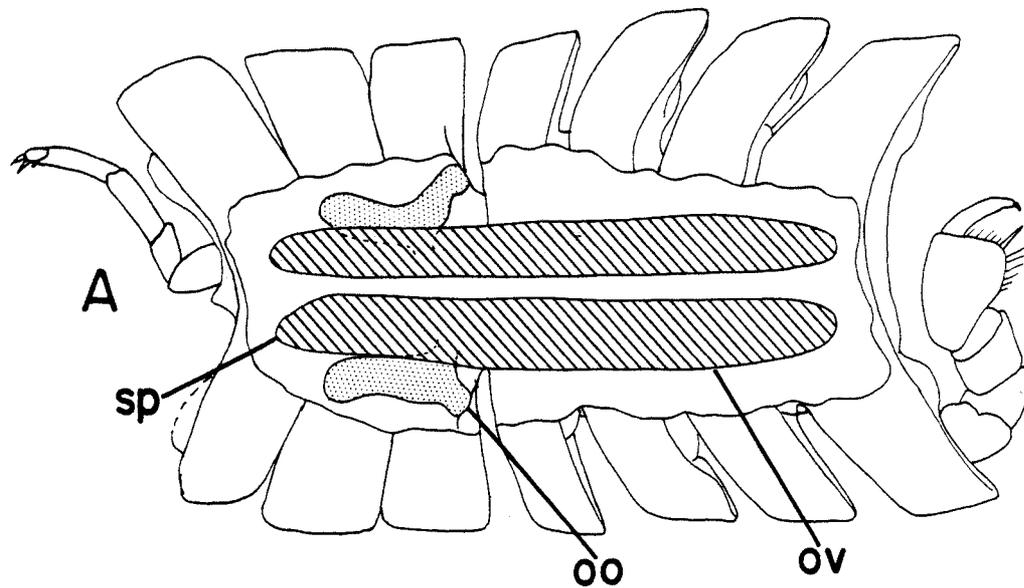
Stenetrium (fig. 4.5).--The cuticular organ is not developed in preparatory females, and was seen only in brooding females of Stenetrium dagama. This probably means that fertilization takes place only immediately after the molt of the posterior half of the preparatory female, and before the molt of the anterior part when the oostegites would be deployed. Asellus has similar mating habits (Maercks, 1931). In the brooding female, the cuticular organ opens at the posteromedial edge of the oviduct's ventral attachment. Internally, the organ is directly connected to an pocket at the opening of the oviduct. A short tube connects the cuticular organ's orifice to a thin sac, which is confluent with the oopore pocket. Although the pocket and spermatheca are attached, they may be homologous with that of Asellus, because they are similar in location.

Figure 4.5. Female reproductive system of Stenetrium, brooding female. A, ventral view of pereonite 5, right side, showing position of oopore. b, enlargement of oopore area. Note tube of cuticular organ visible through cuticle. Also note that cuticular organ opening has a more medial position than in Asellus. C, internal view of oopore region showing cuticular organ, pocket, and spermatheca attached as single unit. b - basis of pereopod V; co - cuticular organ; oo - oopore; p - cuticular pocket; sp - spermatheca.



Pseudojanira (fig. 4.6).--Because only the preparatory female holotype of Pseudojanira stenetrioides was available, a macerated specimen of this species was not examined. However, the female did clear well in lactic acid, which allowed the inspection of the cuticular organ close to the ventral surface. The cuticular organ opens on the anterior edge of the attachment of the oviduct to the ventral cuticle, and is adjacent to a cuticular fold that is, in effect, a blind tube just below the ventral surface. This closed tube opens anteriorly to a groove in the anteroventral edge of the fifth pereonite that curves dorsally. The opening of the cuticular organ is surrounded by a bulbous, thickened funnel that appears to open almost directly into a large spermathecal sac. The cuticular organ is also positioned anterior to the oopore and is almost separate from it. This could be an intermediate state to cuticular organ-oopore relationships seen in the lower Asellota and the Janiroidea, although the dissimilarity of the Pseudojanira female organ makes the homologies uncertain. The spermatheca protrudes posteriorly into the sixth pereonite and was observed to contain translucent, heavily staining material similar to sperm masses seen in other species of Asellota. There is a pocket-like structure beneath the external position of the oopore but it is much smaller than that seen in Asellus or Stenetrium.

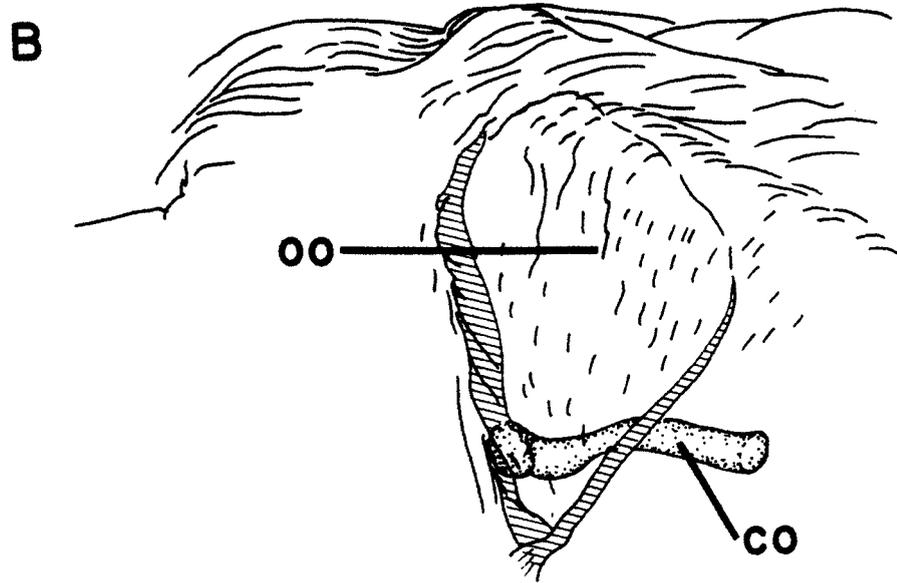
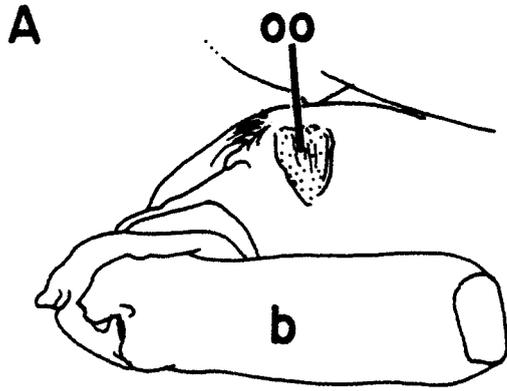
Figure 4.6. Female reproductive system of Pseudojanira, preparatory female. A, semidiagrammatic dorsal view of the reproductive organs, showing what they would look like if the dorsal surface of the pereon were removed. Anterior is to the right, cephalon and pleotelson broken off. B, ventral view of pereonite 5, left side, showing oopore region and spermatheca through the ventral surface. C, enlargement of oopore region showing structures beneath the cuticle. ov - ovary; oo - oopore; co - cuticular organ; sp - spermatheca; sr - stylet receptacle; b - basis of pereopod V truncated (shown only partially).



Mating has not been observed in Pseudojanira as it has been in Asellus (Maercks, 1931) or Jaera (Veuille, 1978a), although the configuration of the male and female sexual organs suggests their function (see fig. 4.9E). The closed tube adjacent to the opening of the cuticular organ is approximately the same diameter on the inside as the outside diameter of the tip of the male stylet on pleopod II. If the stylet were inserted into the tube, the groove in the stylet would be adjacent to the opening of the female's cuticular organ. Therefore, I assume that this closed tube is a stylet receptacle, and will refer to it as such in this paper. The barbs on the stylet tip would help hold the limb in place while sperm transfer takes place. An alternative hypothesis, the insertion of the stylet directly into the tube of the cuticular organ, seems less likely since the barbs of the stylet potentially could damage the tissues of the spermatheca and oviduct. The stylet receptacle may not be homologous with the oopore pockets seen in Asellus and Stenetrium, because a reduced pocket is inside of the oopore.

Munna (fig. 4.7).--A large preparatory female of Munna antarctica showed a well-developed cuticular organ. The opening of the organ is in about the same position as was found in Stenetrium, the posteromedial corner of the oviduct's attachment point. The cuticular organ is not associated with any surficial cuticular folds or pockets, other than two cuticular thickenings extending anteriorly and medially from the organ's opening. The tube of the organ is long and

Figure 4.7. The female reproductive system of Munna, preparatory female. A, ventral view of pereonite 5, right side, showing oopore region. B, enlargement of oopore region showing cuticular organ beneath ventral surface. Note that the cuticular organ is adjacent to the oopore opening and is positioned somewhat posteriorly. No pocket was apparent beneath the cuticle covering the oopore. oo - oopore, co - cuticular organ, b - basis of pereopod V.

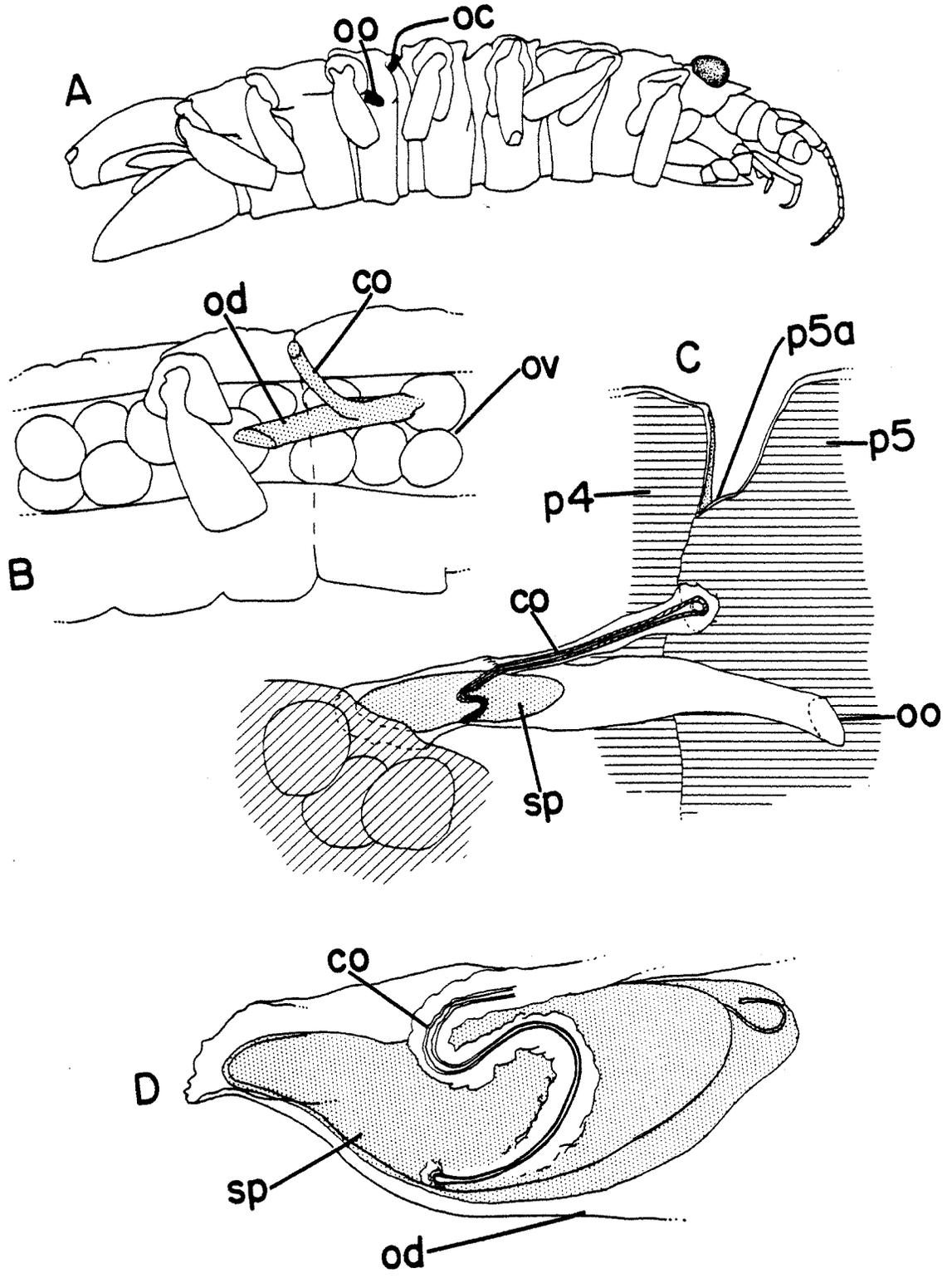


terminates without any cuticular sac for the spermatheca, similar to all Janiroidea examined by me (see table 4.1). Therefore, the spermatheca must be a fleshy sac enclosed in the tissues of the oviduct, as in Notasellus (see below). Female specimens of Santia mawsoni showed a similar configuration of the cuticular organ.

Because the male stylets of the Pleurocopidae and Munnidae have hollow tubes extending to their tips, members of these taxa probably mate by inserting the stylet directly into the long tube of the cuticular organ. This would be in accord with what is observed in Jaera, although the openings to the cuticular organ are in completely different locations in the two taxa.

Notasellus (fig. 4.8).--A large preparatory female of Notasellus sarsi provided an excellent lactic acid cleared preparation of the cuticular organ; therefore this organ can be described in somewhat better detail than in the above taxa. In potassium hydroxide macerated and stained specimens of Notasellus, the cuticular organ is easily seen to open on the anterodorsal part of the fifth pereonite. The opening is actually in the articular cuticle between the fifth and fourth pereonites. The cuticular organ starts as a small funnel and continues anteriorly as a long, thin tube. At its internal end, the tube has a "S" shaped bend. In the lactic acid cleared specimen, the cuticular organ is imbedded in the tissues of the oviduct. These tissues form a "Y" shape

Figure 4.8. Female reproductive system of Notasellus. A, ventrolateral view of preparatory female with oopore and cuticular organ opening areas on pereonite 5 darkened. B, diagrammatic view through cuticle of the reproductive system, enlarged compared to A. C, internal medial view of reproductive system. Note that the oviductal tissues form a "Y" shape, with one end attaching to the oopore, one end surrounding the cuticular organ, and one end containing the spermatheca and attaching to the ovary. D, enlarged ventral view of spermatheca seen through the tissues of the oviduct, showing the "S" shaped distal end of the cuticular organ and its attachment to the spermatheca. The spermatheca seemed to be made of several layers and between two of the layers at the posterior end was a small bit of cuticular tube, possibly a remainder of the cuticular organ from a previous molt (many large Asellota are iteroparous). oo - oopore, oc - opening of the cuticular organ, od - oviduct or tissues of the oviduct, co - cuticular organ, sp - spermatheca, p4 - internal surface of pereonite 4, p5 - internal surface of pereonite 5, p5a - articular region of pereonite 5 (see how the cuticular organ opens at the extreme anterior edge of pereonite 5).



with two of the ends attached to the external cuticle at the opening to the cuticular organ and to the ventral opening of the oviduct. The third end opens into the ovary in the fourth pereonite. The sheath of oviductal tissues surround the tube of the cuticular organ for its entire length, including the parts of the tube inside the walls of the oviduct. After entering the oviduct, the tube and its sheath of tissues bend sharply to the posterior and then curve under the body of the spermatheca, which is also inside the oviduct. The cuticular tube opens into the spermatheca on its ventral side. The tissue sheath of the cuticular organ appears to become part of the spermatheca at this point.

Veuille (1978b) described a two-layered spermatheca from thin histological sections of the female reproductive organs. He showed a primary spermatheca surrounding a smaller sac of the secondary spermatheca. Jaera and Notasellus are likely to have the same types of structures. Therefore his primary spermatheca may be the same as the wall of the oviduct, and his secondary spermatheca is the true spermathecal sac which is inside the lumen of the oviduct.

CHARACTER STATES OF THE CUTICULAR ORGAN

The above survey of the cuticular organ within the Asellota shows that this complex structure is not a defining synapomorphy of the Janiroidea, because it occurs in other superfamilies of the Asellota, i.e., the Aselloidea and the Stenetrioidea. Therefore, the question of how the cuticular organ developed is set to a higher systematic level. The distribution of this structure in the Isopoda and other

Peracarida is of considerable interest but is outside the scope of this paper. Here, the relationship of the Janiroidea with the other superfamilies of the Asellota is the primary concern.

Because the distribution of the cuticular organ outside the Asellota is unknown and because the sister group for the Asellota is yet to be determined, it will not be possible to assign polarities to the transformation series derived here for the cuticular organ. I prefer the condition seen in Asellus as the plesiomorphic state of the cuticular organ. This preference is based on the overall plesiomorphic state in the Aselloidea of many of the characters used in the next section, and on the fact that something as odd as the dorsal cuticular organ would surely have been noted if it existed outside of the Asellota.

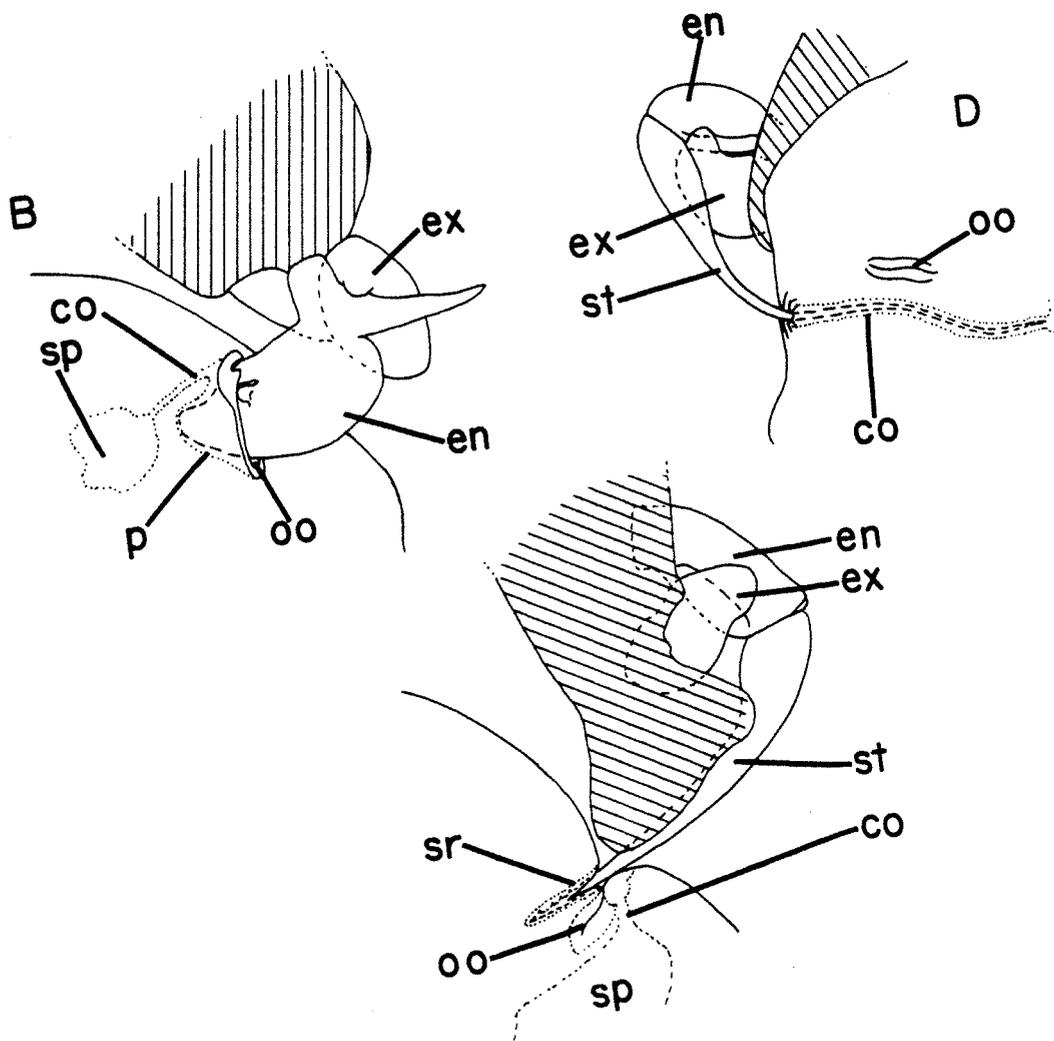
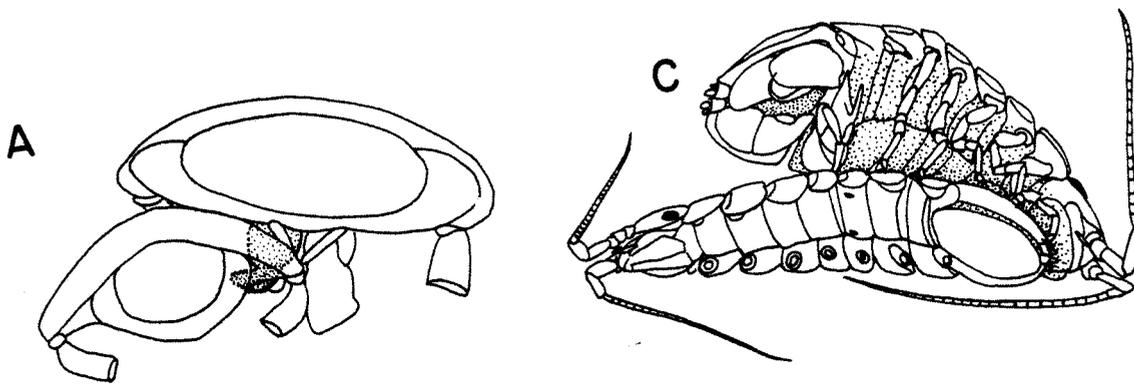
The cuticular organ has two characters that may be used here for phylogenetic analysis: the position of the opening of the cuticular tube, and the manner in which the cuticular organ receives the male copulatory organ. Figure 4.9 diagrammatically shows the character states found in three of the taxa studied.

The position of the cuticular organ's opening will be considered here to have two states: the opening directly associated with the opening of the oviduct and the opening on the anterodorsal surface of the fifth pereonite. The two character states could be further subdivided into substates describing the exact position of the cuticular organs with respect to landmarks on the fifth pereonite. For example, in those taxa which have the cuticular organ associated

with the ventral oviductal opening, there are two substates: an anterior position as in Asellus, and Pseudojanira (fig. 4.4, 4.6), or a posteromedial position as in Stenetrium and Munna (fig. 4.5, 4.7). Among the janiroidean families, the details of the cuticular organ opening show considerable variation, from distinctly dorsal and set well back from the pereonite articulation in the Dendrotiidae to a position associated with the articular cuticle between pereonites 4 and 5 in Notasellus. The distribution of this sub-character set is poorly known and requires further research before it can be used in phylogenetic analysis.

The interaction between the cuticular organ and the male copulatory organ has potentially three character states. In the first, exemplified by Asellus (see Maercks, 1931) and Stenetrium, the essentially club-shaped male organ is inserted into the cuticular pocket adjacent to the opening of the cuticular organ (fig. 4.9A,B). Pseudojanira has the second state in which the male copulatory organ is stylet-shaped and inserts into a closed tube adjacent to the opening (fig. 4.9E). The insertion of the stylet directly into the opening of the cuticular organ is the third state of this character series (fig. 4.9C,D). It is uncertain whether the character state found in Pseudojanira is an intermediate between the aselloid state and the janiroid state, is derived from one of the other two states, or is the ancestral state (although this is unlikely). For simplicity, these character states are reduced to a binary character pair: the male copulatory organ inserted into an organ adjacent to the cuticular organ or inserted directly into the cuticular organ.

Figure 4.9. Mating in the Asellota. A-B, Copulation in Asellus, after Maercks (1931). A, semidiagrammatic cross-section views of male (above) and female (below) pereonites 5 during copulation, posterior view. Darkened left pleopod II of male, shown behind right tergite of female, is inserting into right oopore region of female. B, enlarged view of right oopore region, showing how the endopod of the male fits into the pocket and presses close to the opening of the cuticular organ. C-D, Copulation in Jaera, after Veuille (1978a). C, male astride female, inserting stylet of pleopod II into the opening of the cuticular organ. The pereopods of the female are omitted for clarity. (Veuille (1978a) was able to observe this by pouring liquid nitrogen on a copulating pair, and then thawing the specimens in fixative.) D, diagrammatic view of copulation, showing how the stylet inserts into the cuticular organ. E, Copulation in Pseudojanira (hypothetical). If the stylet were placed into the stylet receptacle, it would be held in place while the sperm flowed from the penile papillae (not shown) along the groove in the stylet to the opening of the cuticular organ adjacent to the oopore. en - endopod; ex - exopod, st - stylet, co - cuticular organ, oo - oopore, p - pocket, sp - spermatheca, sr - stylet receptacle.



CHARACTER ANALYSIS OF THE ASELOTAN SUPERFAMILIES

INTRODUCTION

To determine successfully the polarity and transformation of characters within the Asellota, the immediate sister group of the Asellota should be determined. This presents a problem, however, because no detailed phylogeny of the Isopoda has been attempted. Numerous opinions as to general relationships have been published. For example, Kussakin (1973, p. 21) wrote "Asellota probably originated from the ancient Phreatoicoidea." The newest suborder, Calabozoidea, has been considered most closely related to the Asellota (van Lieshout, 1983), although this taxon is specialized and has a number of reduced features. In addition, the Calabozoidea were not compared with the Phreatoicoidea, leaving van Lieshout's analysis somewhat weak. A phylogenetic analysis of the Isopoda is well beyond the scope of this work, since the aim here is to understand the evolutionary structure within the Janiroidea by analyzing the superfamilies of the Asellota. Therefore many of the arguments below will rely on the common or prevalent form of a particular character over all the suborders of the Isopoda in comparison with the Asellota. This may not be as weak as it seems because many of the general characters, such as the form of the first pereopod or the male pleopods, recur in all the suborders.

SUPERFAMILY CLASSIFICATION AND TAXA USED

The classification used here is that of Bowman and Abele (1983) with the following corrections and emendations. The superfamily Protallocoxoidea is not valid and should not be included in further classifications of the Asellota (Sket, 1979; Wilson, 1980). Wägele (1983) presented the families Gnathostenetroididae and Protojaniridae as belonging to separate superfamilies; his usage is followed here. The superfamilial taxa used, then, are the Aselloidea, Stenetrioidea, Gnathostenetroidoidea, Protojaniroidea, Pseudojanira (superfamily incertae sedis), and Janiroidea. Within the Janiroidea, I recognize three groups of families. These are: (1) Munnidae and Pleurocopidae, (2) Paramunnidae and Abyssianiridae, and (3) the remaining families. In the previous section, the Munnidae and Pleurocopidae were shown to have a cuticular organ positioned differently than in the remainder of the janiroideans (see table 4.1). As is shown below, the form of the first pereopod also allows one to separate the Paramunnidae and the Abyssianiridae from the remainder of the Janiroidea.

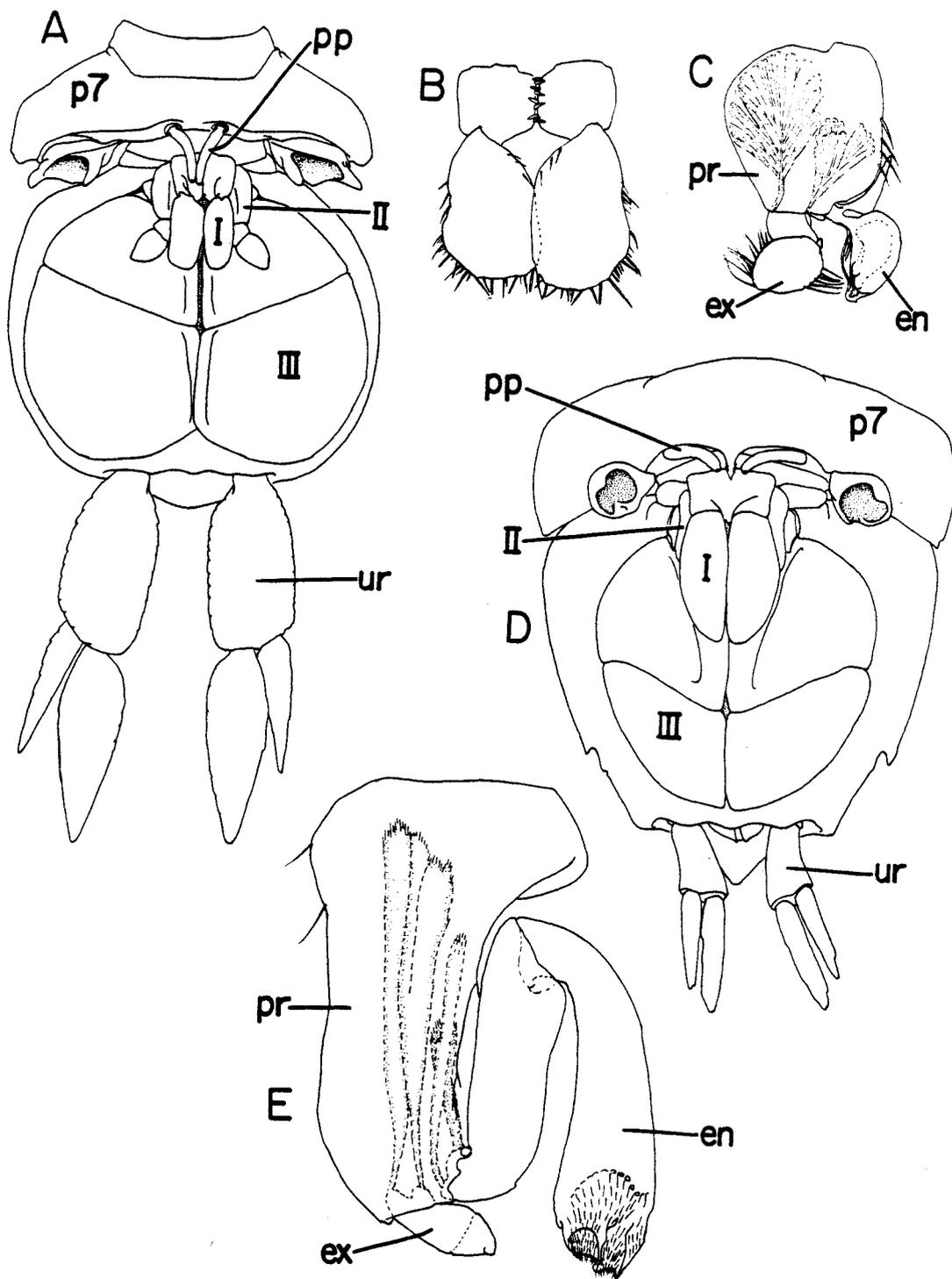
THE CHARACTERS AND THEIR STATES

Although the evolution of the cuticular organ is useful for determining large phylogenetic patterns within the Asellota, more characters must be introduced in order to fully evaluate these patterns. The characters used here are those introduced as useful by previous workers with some new additions. Hansen (1905) demonstrated that the pleopods help form a natural arrangement of the asellotan families. His results were amplified by later workers (Amar, 1957; Fresi et al., 1980; Wägele, 1983). Because the male and female

anterior pleopods of the Asellota are strongly dimorphic, they will be considered separately. The complexity of the male pleopods provides several characters, which are surprisingly independent of each other. The variation in the third pleopod is discussed but will not be used in the phylogenetic estimate. A comparison of the first pereopod in a large number of isopodan taxa, both of the Asellota and non-Asellota, has revealed that the overall formation of this limb is similar across all the suborders of the Isopoda, but varies within the Janiroidea. A decisive character state pattern in the form of the first pereopod discovered during an analysis of the families of the Janiroidea is also used. Overall, a small number of character are introduced into this analysis, so any conclusions drawn below must be considered preliminary. More characters could not be used because many key taxa, such as Protojanira, are very poorly described, and specimens were not available.

Male pleopods I (fig. 4.2, 4.10, 4.11).--The male pleopod I through all Asellota is similar: paired uniramous, and typically small limbs. At the level of the Isopoda, this is a apomorphy since most of the suborders have biramous first pleopods. In the Calabozoidea, the pleopods I are essentially uniramous, although there is a rudimentary endopod (Van Lieshout, 1983). The least modified state of the pleopod I in the Asellota, as exemplified by Asellus, are uniramous, two-segmented limbs (fig. 4.10A). Although both sides of the paired

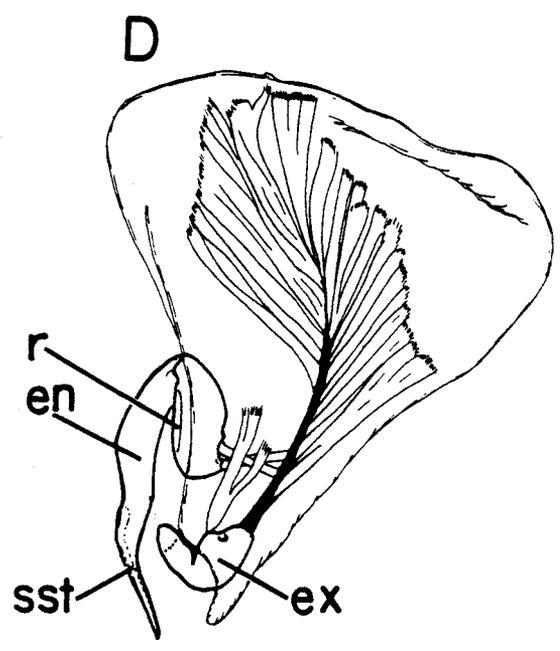
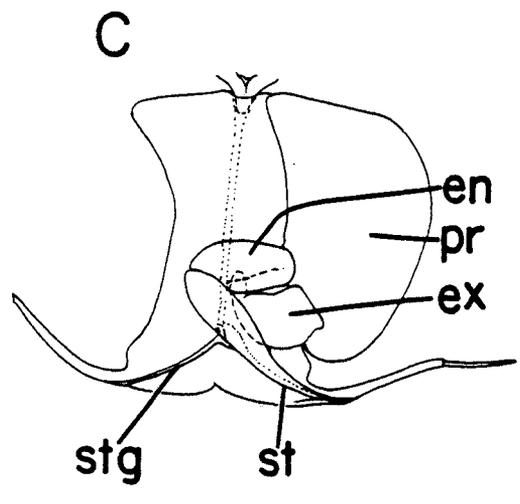
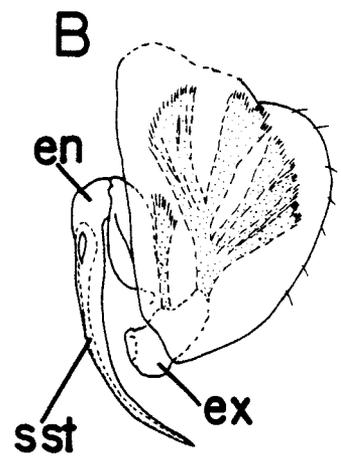
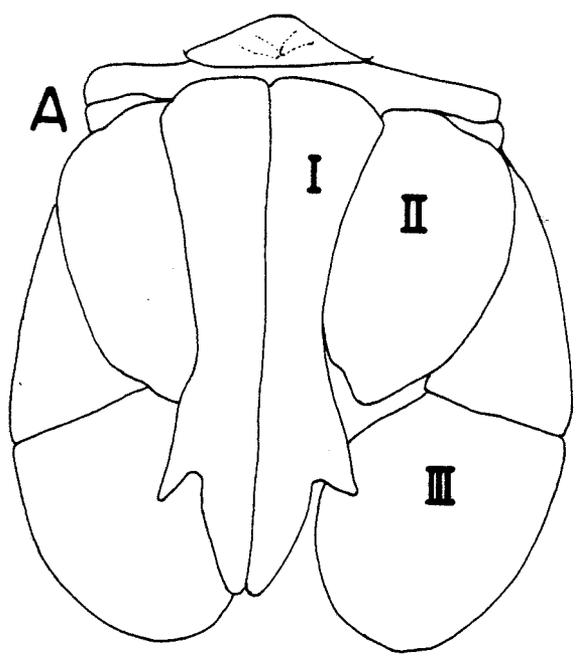
Figure 4.10. Male copulatory organs in two Asellota. A-C, Asellus, A, drawn from specimen in collection, B-C, after Maercks (1931). A, ventral view of pereonite 7 and pleotelson of male. B, enlargement of pleopods I. Note that the basal podomeres are separate. C, enlargement of right pleopod II. Note that the endopod of pleopod II (en) has a large internal pocket (indicated by dotted line) for transmitting the sperm placed there by the elongate penile papillae (pp). D-E, Stenetrium. D, ventral view of pereonite 7 and pleotelson of male. E, enlargement of pleopod II. The stenetriid male endopod lacks the internal pocket seen in the asellids, but has fine cuticular combs and spines on the distal tip, apparently for holding the setae for transfer. (No one has reported mating in a stenetriid.) Compare the musculature to the exopod of both groups. I - pleopod I, II - pleopod II, III - pleopod III, pp - penile papilla, en - endopod of pleopod II, ex - exopod of pleopod II, ur - uropod, p7 - pereonite 7.



pleopods are not connected, they may be connected by coupling hooks on the basal segment. The first pleopods are small compared to pleopods III-V, but they may cover the second pleopods. The first pleopods of Asellus take no part in sperm transmission, as the penes are brought into contact with the endopod of the second pleopod for this purpose (Maercks, 1931). The tips of the first pleopods in Asellus also have several tufts of setae. A modification of this form is the fusion of the basal segments, so that both members of the pair are forced to act together, thus eliminating the need for coupling hooks. Fused basal segments are found in Stenetrium (fig. 4.10D), Pseudojanira (fig. 4.2A), and the Janiroidea (fig. 4.11A,C).

Another set of character states is whether or not the left and right sides of the first pleopods are completely fused, the basal segments are greatly reduced, and a cuticular tube for sperm conduction exists at the line of their fusion (see Veuille, 1978a; see fig. 4.11A,C). In asellotes that have this character complex, the proximal end of the tube is a funnel into which the penes fit, and the distal end opens on the dorsal side of the fused pleopods above the distal segment of the second pleopodal endopod. The presence of such modified pleopods helps define the Janiroidea from all other Asellota, those which have unfused distal rami of the pleopods I. The latter state is plesiomorphic since all the other suborders of isopods have separate first pleopods.

Figure 4.11. Male copulatory structures in several Janiroidea. A, pleopods of Notasellus, ventral view. B, pleopod II of Notasellus, ventral view. C, pleopods I and II of Jaera, dorsal view, showing how they operate together during copulation (after Veuille, 1978a). In this genus, the stylet grooves on the distal corners of pleopod I (stg) extend laterally as closed "copulatory horns"; most Janiroidea lack the copulatory horns but have the stylet grooves. D, pleopod II of Eurycope, a highly modified deep-sea janiroidean. Note that this pleopod is very similar in general detail to the two less modified janiroideans. Compare the size of the two opposing exopodal muscles seen through the cuticle of D. I - pleopod I, II - pleopod II, III - pleopod III, en - endopod, st - stylet, sst - stylet sperm tube, ex - exopod, pr - protopod (basal segment), r - ridge on proximal segment of endopod where the exopod couples during copulatory movements.



A second character is found in the presence or absence of stylet guides. These guides are grooves on the dorsal surface of the tips of first pleopods, which are somewhat broad and quadrate. The stylets on the endopods of the second pleopod fit neatly into these grooves, which direct the motion of the stylets during copulation (Veuille, 1978a). These features are seen only in Pseudojanira (fig. 4.2A,B) and in the Janiroidea (fig. 4.11C). The guides and function of the stylet are intimately related to one another, implying that those taxa that have stylet-like endopods on pleopods II but lack the guides must mate in ways different from the Janiroidea and Pseudojanira. The dorsal side of the first pleopod also has a pair of cuticular tabs which help lock the first pleopod in position between the two second pleopods, effectively making both limbs operculiform. This character is apparently linked to the presence of the stylet guides, and therefore is not independent. Lack of the stylet guides is plesiomorphic because nothing similar occurs in any non-asellotan.

The Gnathostenetroidoidea and the Protojaniroidea have male first pleopods that are different from other Asellota: they are large, broad, and lamellar. Other Asellotes have male first pleopods that are either small or narrow, and all are generally thicker. The large lamellar first pleopods are assigned the apomorphic state although the true ancestral state is unknown.

Male Pleopods II (fig. 4.2C,D; 4.10C,E; 4.11B-D).--The primitive condition for the male asellote pleopod II is well established (Wägele, 1983), although the phylogenetic significance of some of its details has gone unnoticed. Within the Asellota, the basal segment is somewhat enlarged and muscular, and both rami have two segments each. The endopod is geniculate, and is distally elaborated either with a groove or pocket for transferring the sperm. The exopod and the endopod have structures that allow them to couple and act in concert during the copulatory act (e.g. Asellus, Maercks, 1931; Jaera, Veuille, 1978a); the exact form of the coupling mechanism varies among the asellotan taxa. This interlocking of the endopod and exopod may be homologous in all asellotan taxa because they all have elongated and enlarged exopodal musculature, apparently for the copulatory function. The entire limb is as small as or smaller than the first pleopod.

None of the taxa examined had all these features unmodified, although this configuration is exhibited by the Stenasellidae (e.g. Magniez, 1975) of the Aselloidea. Non-asellotan taxa also have copulatory male pleopods II but the derived form of this limb described here found does not occur in any of them, especially the linking of the exopod to the endopod for copulation. The typical non-asellotan male pleopod II is a biramous structure with a smaller basal segment and more or less lamellar rami. The endopod generally bears a narrow, cylindrical, and blunt appendix masculina. Whether the true outgroup of the Asellota has two or one segmented exopods remains uncertain because in some suborders (including the Calabozoidea) the

exopod is an unsegmented lamella, and in others, like the Phreatoicidea or the Anthurida (which has a primitive pleonite and telson configuration), the exopod has two segments.

The first character of the male second pleopod to be considered is the exopod: whether it is made of one or two segments. As just said, it is not certain which is the plesiomorphic state, although a two-segmented exopod (fig. 4.10C) is favored because it is found in the least modified asellotes and in the somewhat similar Phreatoicidea. This ramus is short and uniarticulate in Stenetrium, Pseudojanira, and in the Janiroidea (fig. 4.2C,D; fig. 4.10E; fig. 4.11B-D).

In Pseudojanira, and in the Janiroidea, the exopod forms a blunt hook that links with a groove in the proximal article of the endopod, making the second character for the exopod the presence or absence of the hook. Because none of the non-asellotan taxa has a short, hook-shaped exopod, the lack of this form is plesiomorphic.

The endopod displays divergent trends among the Asellota. In Asellus, both articles of the endopod are fused, although this ramus retains its geniculate form (fig. 4.10C); in the Stenasellidae and the other superfamilies, the endopod remains biarticulate thus limiting its usefulness here for phylogenetic analysis. A more useful character is the presence or absence of a stylet-like endopod. Non-asellotan taxa lack any of the endopodal specializations seen in the Asellota, so it is difficult to establish the plesiomorphic state on these grounds alone. Some ontogenetic evidence, however, is provided

by the development of the stylet in juvenile male Janiroideans (Hessler, 1970; Wilson, 1981). At the first molt where the endopod of male pleopod II is expressed, this ramus is an undeveloped, club-shaped process, sometimes with a groove on its distal ventral end. After the maturation molt, the stylet becomes sharp distally, the sperm tube develops, and the tube is open at its tip. The ontogeny of the male stylet in the Janiroideans thus suggests that the plesiomorphic state is the club-shaped process, and the hypodermic needle-like stylet of the Janiroidea is an apomorphy. The distal article of the endopod is elongate and pointed both in the Janiroidea (fig. 4.11B-D) and in Pseudojanira (fig. 4.2D), different from the club-shaped limbs in Asellus and Stenetrium (fig. 4.10C,E). A stylet-like endopod is also seen in the Protojaniridae (Wägele, 1983).

Another pair of character states can be derived from the form of the sperm transmitting surface of the distal segment of the endopod. All asellotes have either a pocket or a groove on this part of pleopod II. For example, in Pseudojanira, the stylet has an elongate groove on the ventral surface (fig. 4.2D), and the Aselloidea have variously formed pockets (fig. 4.10C). In the Janiroidea, the groove has become closed into a tube that opens on the bulbous proximal part of the segment and on the distal tip only (fig. 4.11B-D). The presence or absence of this stylet sperm tube is useful in dividing the Janiroidea from all the other Asellota. The sperm tube is the apomorphic state because sperm tubes have not been reported from the endopod of the male pleopods II of any non-asellotan taxon.

Pseudojanira has unique barbs on the tip of the stylet (fig. 4. 2D), could be either a synapomorphy of this taxon, or an intermediate state in the evolution of the Janiroidea. Here it is assumed to be a synapomorphy.

Female Pleopod II. In the Aselloidea, the second pleopods are separate, round, uniramous, and lamellar. In other Asellota, the left and right sides of the female second pleopods are fused into a single shield-like structure, which may or may not be opercular. Although the aselloid pleopods II are not biramous, they are most similar to the condition seen in most non-asellotans in that the two sides are not fused together. Therefore the separate pleopods are the plesiomorphic state and the fused pleopods are the apomorphic state.

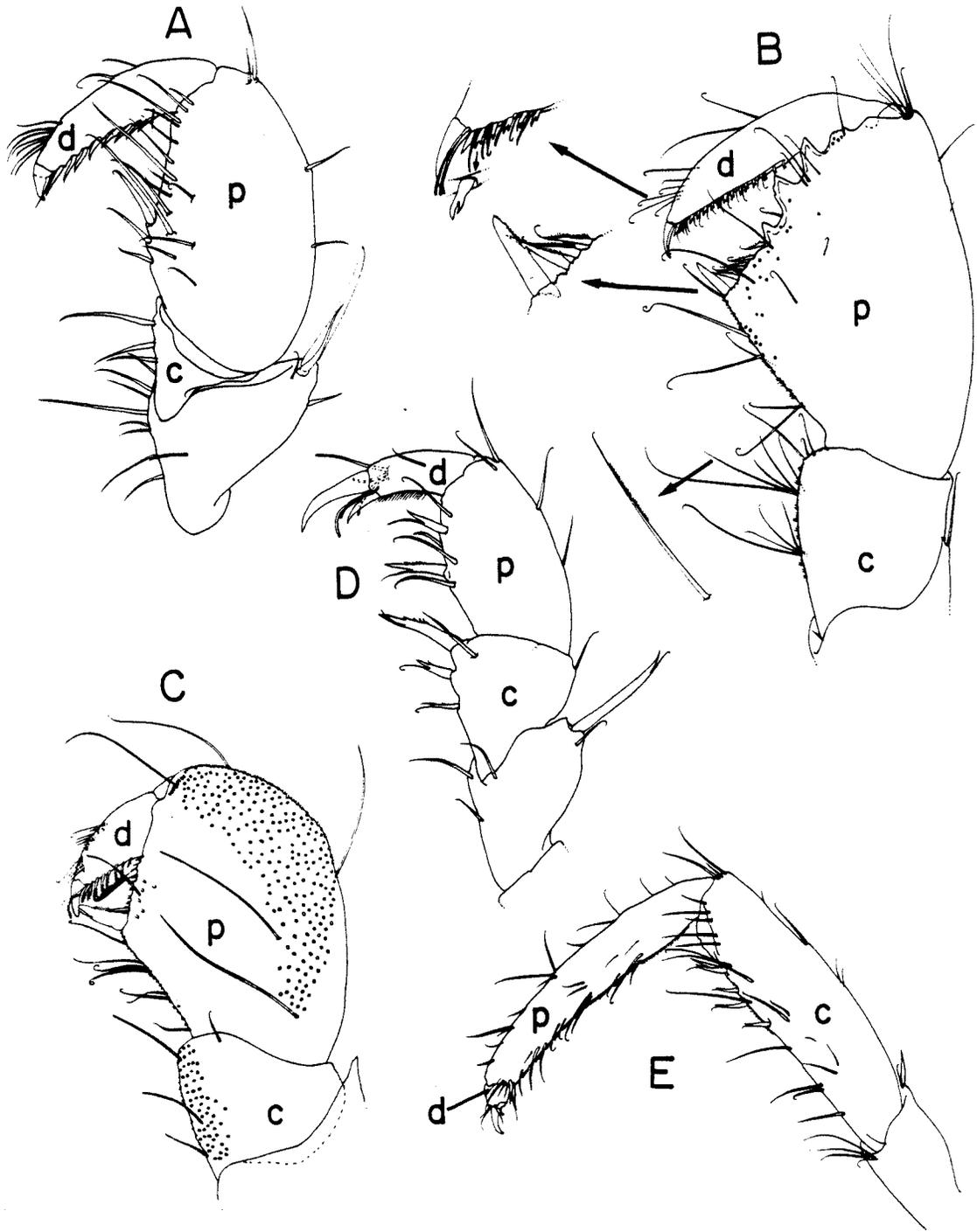
Pleopod III and Opercular Pleopods.--Even though these characters are not used in the analysis, it is necessary to discuss them because others have considered them important factors in the phylogeny of the Asellota. Wägele (1983) presents arguments that the primitive third pleopods of the Asellota are biramous structures each with two rami (endopod and exopod) of similar size, but not covering the more posterior pleopods IV and V. On this basis, he divides the Asellota into a "janiroid line" in which pleopods I and II are opercular, and a "aselloid line" in which pleopods III are opercular. The janiroid line included the superfamilies Janiroidea, Protojaniroidea and Gnathostenetroidoidea, and the aselloid line with the Aselloidea had the Stenetrioidea as an offshoot unrelated to the ancestral janiroideans. The ancestor of the Asellota did not have opercular

third pleopods at the outgroup node, because pleopods I-V of all the potential outgroups are large, biramous, lamellar, and nearly similar. The immediate ancestor of the Asellota, however, may have had opercular pleopods III owing to their appearance in most of the major taxa of the suborder. This character state is a plesiomorphy of the Janiroidea, because males of Notasellus and Jaera have it in a form nearly identical to that seen in Stenetrium and Pseudojanira (fig. 4.2E; fig. 4.10D). The opercular nature of the third pleopod is lost in females of Notasellus and Jaera, and in all other Janiroidea.

Using the opercular function as a character could potentially lead to confusion in developing a stable phylogenetic estimate of the Asellota. Because the character is one of function rather than of morphology, convergence may be likely among the various groups. For example, Wägele (1983) considers that pleopods I in the males of Janiroidea and Gnathostenetroidoidea are similar because they are opercular, even though the physical structure of these pleopods are quite different. Here opercular pleopods characters are not used to avoid these problems, and the physical makeup of the pleopods is considered separately.

First Pereopod (fig. 4.12).--The pereopod I (the second thoracic appendage) proves to be valuable for differentiating major taxa in the Asellota. In most Isopoda and other Peracarida, this limb is a grasping appendage with the opposing surfaces between the propodus and

Figure 4.12. A comparison of the first pereopods of various Asellota. A, Asellus. B, Stenetrium, with enlargements of the setae on the oppositional margins of the dactylus and propodus. C, Pseudojanira. D, Munna. E, Notasellus, the basic form of the first pereopod for most of the Janiroidea. This figure demonstrates the evolutionary transition in the first pereopod from the form seen in most Isopoda where the dactylus and propodus can oppose one another (A-D), to the form where the carpus and the propodus can oppose one another (E). Munna is intermediate because the carpus is enlarged and can oppose the movable dactylus along with the propodus. Compare the size and the shape of the carpus (c) in these taxa. d - dactylus, p - propodus, c - carpus.



dactylus. The carpus is short, broad, and nearly triangular, and does not take part in the grasping function. The propodus and dactylus typically have stout setae of various types, apparently to aid in the grasping function. Because this type of first pereopod occurs in all non-asellotan taxa, it is the plesiomorphic state for the Asellota. The plesiomorphic state is found in Asellus, Stenetrium, and Pseudojanira. Of the Janiroidea, only the Munnidae, Pleurocopidae, Paramunnidae, and Abyssianiridae have a pereopod similar to the plesiomorphic state, although modified in that the carpus is more robust and has elongate stout setae which participate in grasping. The propodus is somewhat reduced in these latter taxa. The higher Janiroidea have a pereopod I which closely resembles the more posterior pereopods: the dactylus is short and stout, the flexure between the dactylus and the propodus is restricted so that they do not oppose one another, the propodus and the carpus are elongate, and the carpus and propodus fully oppose one another. The transformation series derived here seems counterintuitive, because one would expect the first pereopod of an isopod to resemble the more posterior walking limbs in its most plesiomorphic state. But because of similarities of all non-asellotans, a grasping first pereopod is the plesiomorphic state, and the walking leg form of the higher Janiroidea is the apomorphic state at the level of the suborder Asellota.

Cephalic Rostrum (fig. 4.1A, D).--Many janiroidean taxa have a cuticular projection on the cephalic frons between the antennulae which is sometimes prominent and sometimes not. This projection is separate and distinct from the tergal cuticle of the cephalon. A

homologous, prominent structure occurs in Stenetrium and in Pseudojanira. A similar rostrum does not appear in the Aselloidea or in the primitive members of other isopodan suborders, although taxa in these latter groups may have a rostrum-like projection of the cephalic tergum. Therefore the frontal rostrum of the Janiroidea is presumed to be apomorphy shared with this superfamily and the Stenetrioidea and Pseudojanira.

RESULTS OF THE CHARACTER ANALYSIS

The following is a list of the character states, their transformations, and polarities derived above. It also includes the information from the section on the cuticular organ. The distribution of the character states among the taxa are shown in table 4.2.

1. Cuticular organ opening ventral, adjacent to opening of oviduct (0), or cuticular organ opening dorsal, separate from opening of oviduct (1). Ancestral state not known.
2. Male pleopod II endopod tip inserted into female cuticular pocket or closed tube adjacent to cuticular organ (0), or male pleopod II endopod tip inserted directly into female cuticular organ (1). Ancestral state not known.
3. Male pleopods I basal segments separate medially (not fused) (0), or male pleopods I basal segments joined (fused) medially (1).

4. Male pleopods I distal segments separate medially (not fused) without medial sperm tube (0), or male pleopods I distal segments joined medially (fused) with medial sperm tube (1).
5. Male pleopods I distal tips without dorsolateral stylet guides (0), or male pleopods I distal tips with dorsolateral stylet guides (1).
6. Male pleopods I small or narrow, thick (0), or male pleopods I large and lamellar (1).
7. Male pleopod II exopod of 2 articles (0), or male pleopod II exopod of 1 article (1). Ancestral state not known.
8. Male pleopod II exopod lobe-like, unelaborated (0), or male pleopod II shaped like blunt hook, shape corresponding to groove on proximal article of endopod (1).
9. Male pleopod II endopod thick distally, not stylet-like (0), or male pleopod II stylet shaped (1).
10. Male pleopod II endopod distal tip without barbs (0), or male pleopod II endopod distal tip with barbs (1). The latter character is seen only in those taxa with stylets.
11. Male pleopod II endopod distal segment with open groove or pocket (0), or male pleopod II endopod distal segment with tube opening only on distal tip and more proximally (1).

12. Female pleopods II separate and unfused medially (0), or female pleopods II fused medially so that they form single shield-like limb (1).
13. Pereopod I dactylus long; dactylus and propodus with free articulation and can oppose one another to participate in grasping (0), or pereopod I dactylus short; dactylus and propodus with restricted articulation and cannot oppose one another to participate in grasping (1).
14. Pereopod I carpus short and triangular; carpus and propodus with restricted articulation and cannot oppose one another to participate in grasping (0), or pereopod I carpus trapezoidal, articulation between carpus and propodus only partially restricted, can oppose one another by means of strong spine-like setae or spines on carpus (1) or long and not triangular; carpus and propodus with free articulation and can oppose one another to participate in grasping (2).
15. No rostral projection on cephalic frons (0), or cephalic frons with rostrum (1).

TABLE 4.2. TAXON-CHARACTER MATRIX FOR THE ASELLOTA. The character numbers correspond to those listed in text.

TAXON	CHARACTERS														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Ancestor	?	?	0	0	0	?	?	0	0	0	0	0	0	0	0
Aselloidea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protojaniroidea	?	?	1	0	0	1	0	0	1	0	0	1	0	0	0
Gnathostenetroideoidea	?	?	1	0	0	1	0	0	0	0	0	1	0	0	0
Stenetrioidea	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1
<u>Pseudojanira</u>	0	0	1	0	1	0	1	1	1	1	0	1	0	0	1
Munnidae-Pleurocopidae	0	1	1	1	1	0	1	1	1	0	1	1	0	1	1
Paramunnidae-Abyssianiridae	1	1	1	1	1	0	1	1	1	0	1	1	0	1	1
Higher Janiroidea	1	1	1	1	1	0	1	1	1	0	1	1	1	2	1

A PRELIMINARY PHYLOGENETIC ANALYSIS OF THE ASELLOTA

PREVIOUS PHYLOGENIES

Many implied phylogenies of the Asellota have been presented as classifications, but only three works (Kussakin, 1973; Fresi et al., 1980; Wägele, 1983) display the relationships of the asellotan subtaxa in explicit branching diagrams. Kussakin (1973) and Fresi et al. (1980) present the majority opinion on the evolution of the Janiroidea based on previous classifications and their own work (fig. 4.13). Their conception places the Stenetrioidea near the Aselloidea but on the line leading to the Janiroidea. These authors place the Gnathostenetroidoidea (and the Protojaniridae) between the Stenetrioidea and the Janiroidea. Wägele (1983), on the other hand, proposes that the Stenetrioidea belong on the aselloid line, which includes the Aselloidea, and have a descent separate from the ancestral janiroidean (fig. 4.14).

RESULTS OF THE PHYLOGENETIC ANALYSIS

A phylogeny for the Asellota different from the above two concepts may be constructed using the characters discussed above (table 4.2, fig. 4.15). The taxa used are the superfamilies recognized by Wägele (1983), with the exceptions that Pseudojanira is added, and the Janiroidea are divided into 3 groups, the members of which have the same distributions of characters used here: the Munnidae and the Pleurocopidae, the Paramunnidae and the Abyssianiridae, and all the remaining families of the Janiroidea.

Figure 4.13. Previous phylogenetic relationships proposed for the Asellota. A, Tree of Kussakin (1973). B, Tree of Fresi et al (1980).

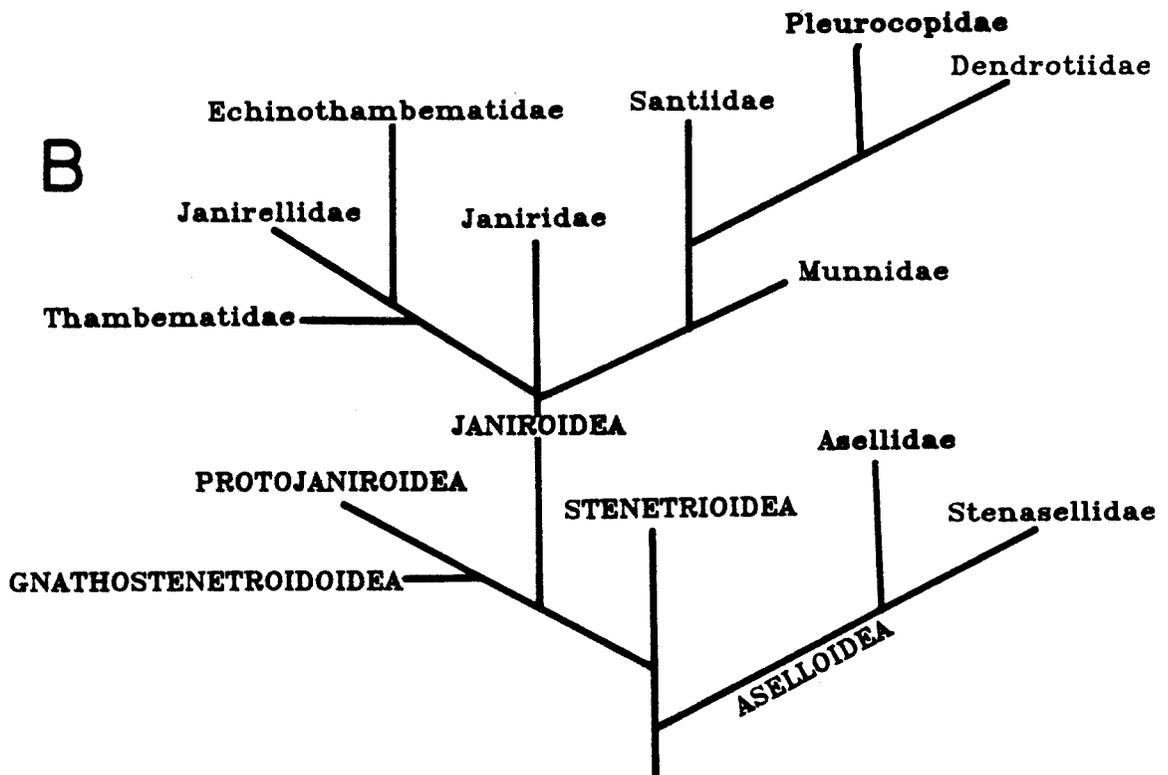
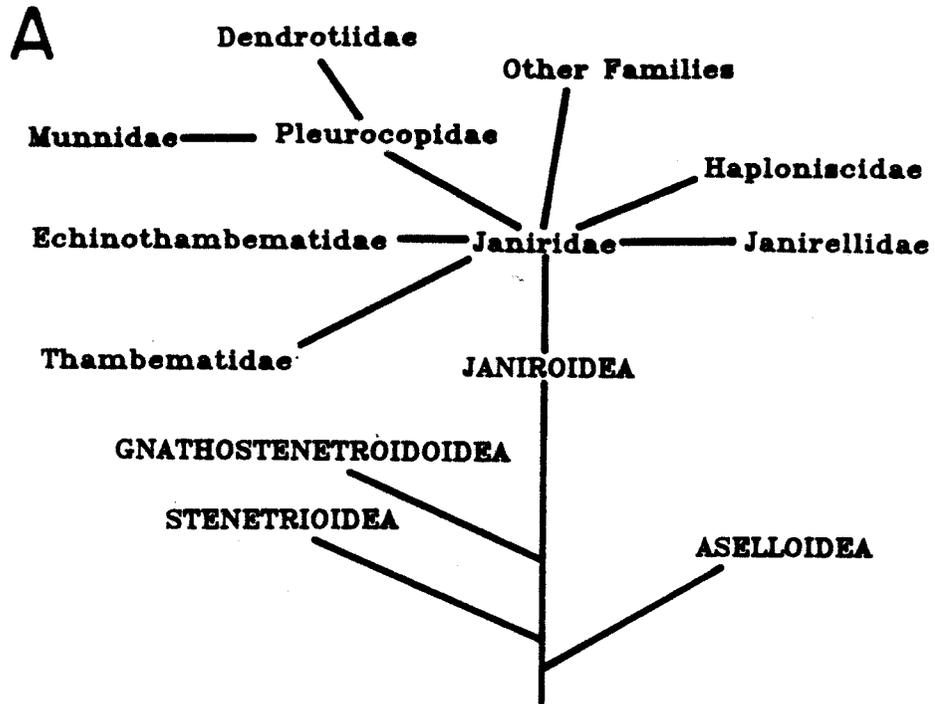
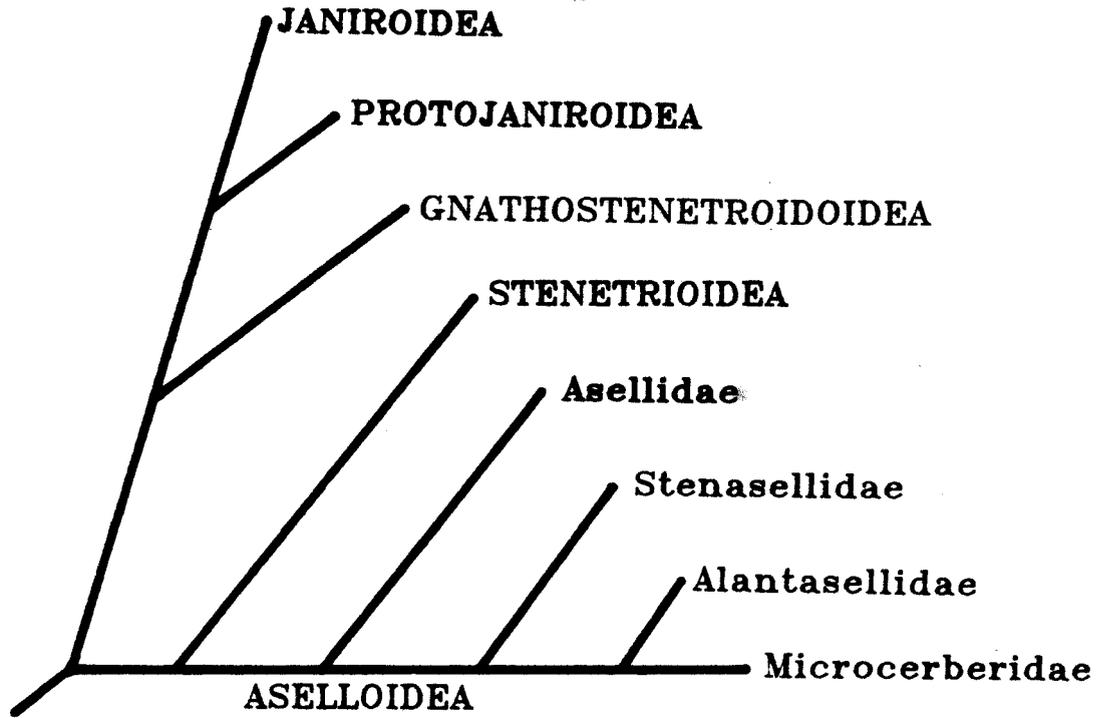


Figure 4.14. The proposed phylogeny for the Asellota of Wägele (1983). His tree opposes previous concepts because the Stenetrioidea are not in the clade containing the Janiroidea, but rather more closely allied to the Aselloidea.



The similarities of the members of the first two groups are discussed in Wilson (1980). The third group, here called "the Higher Janiroidea" merely for convenience, includes highly diverse families and morphologies, and yet, at the systematic level discussed here with the characters presented above, are all astonishingly constant. The relationships within the Higher Janiroidea will be discussed in the next section.

The tree (fig. 4.15) is very stable in its configuration, regardless of whether Camin-Sokal or Wagner parsimony methods, or the compatibility method are being used (see appendices 2, 3). This is primarily due to the almost complete lack of homoplasy, or conflicting characters. Only one character, the stylet-shaped endopod of the male pleopod II must be derived twice.

DISCUSSION

At the superfamilial level, the proposed phylogeny resembles those presented by Kussakin (1973) and Fresi et al. (1980), but the Protojaniridae and the Gnathostenetroididae are placed before the Stenetrioidea, because they lack the following apomorphies: frontal rostrum, and single segmented male pleopod II exopod. This phylogeny conflicts with the superfamily concept of Whiggele (1983), who commented that "connections" between the aselloid line, which contained the Stenetrioidea, and the janiroid line "are impossible." Nevertheless, placing the Stenetrioidea in the "janiroid line" and away from a close

Figure 4.15. A new proposal for the phylogeny of the Asellota. This tree is similar to those proposed in the past except: 1. The Protojaniroidea and Gnathostenetroidoidea are derived before the Stenetrioidea. 2. The Stenetrioidea are not in the aselloidean clade as proposed by Wägele (1983). 3. The new group represented by Pseudojanira is added between the Stenetrioidea and the Janiroidea. 4. The Janiroidea are divided into three subclades. 5. The Janiridae is not in the earliest derived group of the Janiroidea. The numbers marked on the tree are the apomorphies listed in table 4.2; note that character 14 is a three state character and that the two derived states are represented by 14 and 14', respectively.

relationship with the Aselloidea removes some of the potential homoplasies created by his proposed phylogeny. The female second pleopods of Stenetrium are fused into a single sympod, as in Pseudojanira and the Janiroidea, an apomorphy not found in the Aselloidea. Also the reduction of the male pleopod II exopod to a single segment is derived only once instead of twice as in Wägele's scheme.

The unique genus Pseudojanira is placed at the outgroup node of the Janiroidea because of the apomorphies shared with this superfamily in the form of the male pleopods. Two branching nodes separate Pseudojanira from the higher Janiroidea and the Janiridae in which it has been previously classified (Barnard, 1925; Kensley, 1977), forcing a reconsideration of the correct placement of this taxon.

A large reorganization of the presumed evolutionary relationships within the Janiroidea is necessary. The clade including the Pleurocopidae and the Munnidae is a sister group to all other Janiroidean families; additionally, these families are further subdivided by an early derivation of the ancestor of the Paramunnidae and the Abyssianiridae. The Dendrotiidae (and the closely related Hapломunnidae) is a full-fledged member of the higher Janiroidea and is not derived from a Pleurocope-like or a Santia-like ancestor as suggested by Fresi et al. (1980) and Kussakin (1973), respectively.

In the phylogenetic schemes of Kussakin (1973) and Fresi et al. (1980) the Janiridae is the central taxon in the evolutionary development of all the remaining janiroid families. This family has

been considered the archtypical janiroidean because many of its features are those found in other superfamilies, giving it the appearance of the presumed ancestor of the group. Such characters are a flattened body with broad tergites; presence of an antennal scale; large biramous uropods; unmodified walking legs; and other typically isopodan characters. These characters are plesiomorphies at the level of the Asellota, and can be found in the genus Santia, in the Paramunnidae, and other non-janiroid taxa, such as Asellus. Therefore, they cannot be used to establish relationship. In addition, the Janiridae have apomorphies at the level of the superfamily Janiroidea, such as tergal lappets (lateral projections of the dorsal cuticle anterior or posterior to the dorsally visible pereopodal coxae; see next section), that set them off from many of the higher Janiroidea. Several distinct phyletic lines, such as that leading to the munnids and paramunnids, had diverged from the basal stock of the Janiroidea before a recognizable janirid had evolved. These results effectively remove the Janiridae as the model for an ancestral morphology of the entire Janiroidea.

IMPLICATIONS FOR THE CLASSIFICATION OF THE ASELLOTA

The classification of the Asellota should match the best estimate of the phylogeny of its taxa. Asellotan phylogeny, however, will undoubtedly need refinement as more information is collected on the Gnathostenetroididae and the Protojaniridae, and on the details of the female reproductive system in these and other families. Therefore, this paper will not attempt a systematic revision on the basis of the cladogram in figure 4.15, although a formal classification for Pseudojanira and some of the implications of this study must be discussed.

Pseudojanira stenetrioides previously has been placed in the family Janiridae (Barnard, 1925; Kensley, 1977), although it must be removed from the superfamily Janiroidea based on the evidence presented here. To include Pseudojanira would dilute any potential definition of the Janiroidea that might be proposed. Alternately, it cannot be placed in any of the other superfamilies of the Asellota because of its clear affinities to the Janiroidea. At this point, a new superfamily could be proposed for Pseudojanira because of its non-correspondence to any of the existing taxa. This trend is already well established in the literature with the creation of new superfamilies for presumedly new morphological combinations discovered (vis. Gnathostenetroidoidea (Amar, 1957); Protojaniridae Friesi et al., 1980, elevated to superfamily by Whiggele, 1983; Protallocaloxoidea Schultz, 1978). A continuation of this trend could result in "superfamily inflation," severely diminishing utility of the superfamily concept in the Asellota. A series of similar taxa sharing

possible apomorphies, such as Stenetrium, Gnathostenetroides, and Pseudojanira could be placed in separate superfamilies because their male pleopod morphology differed. The Asellota, save for the Janiroidea, vary in their pleopod morphology, leading to the conclusion that there was considerable evolutionary experimentation in the methods of sperm transfer and fertilization in the ancestors of this isopod suborder. Only in the Janiroidea are the pleopods stable morphologically throughout many species, genera and families. Although the pleopods are useful for the classification of the Asellota, future phylogenetic arrangements of these taxa must be based on additional characters. This agrees with the position taken by Wägele (1983, p. 257). Therefore, Pseudojanira is classified here as suborder Asellota, superfamily incertae sedis (non-Janiroidea), family Pseudojaniridae, until a careful re-evaluation the "lower asellotes" is made.

EVOLUTION OF REPRODUCTIVE STRUCTURES

The phylogenetic analysis of the Asellota answers a question posed earlier about the potential coevolution of the cuticular organ with male copulatory organ. Because it is found in all Asellota, the cuticular organ must predate the stylet form of the male pleopod II endopod. On the other hand, the stylet evolved to a hypodermic needle-like organ diagnostic of Janiroidea, as seen in the Pleurocopidae and the Munnidae, before the opening of the cuticular organ became separate from the oviduct. Because the male and female systems undergo major changes at different hierarchical levels, they must have evolved independently of one another.

The male copulatory system is highly evolved within the Janiroidea, and is its chief defining apomorphy. This pleopodal system, however, does not appear suddenly with all its components in place. Parts of the system are found in non-janiroidean taxa, indicating that it evolved gradually with some of the specializations appearing independent of others. This is an important point, because the use of these characters in the phylogenetic analysis depends on their being independent. In face of the enormous diversity of the Janiroidea, one is left wondering whether their highly directed and stereotyped system for delivering sperm to the females has been a major factor in their evolutionary radiation.

PHYLOGENETIC ANALYSIS OF THE JANIROIDEA

INTRODUCTION

The previous section found the outgroups for the Janiroidea. It showed that the Pseudojaniridae n. fam. is the sister group to all the Janiroidea. In addition, the "higher Janiroidea" have a sister group in the families Munnidae and Pleurocopidae. For this analysis, both outgroups will be used in order to lend certainty to the polarities used in the character analysis. The analyses establish the evolutionary continuity of all the families, and show that the "janiroid" condition common to most of the families did not occur in a single step, but arose gradually. The primary goal of the phylogenetic analysis, however, is to discover the sister group of the families Eurycopidae, Ilyarachnidae, and Munnopsidae. Therefore, this analysis is only preliminary in nature and should not be expected to be completely stable under further scrutiny. I do believe the results obtained will remain the same in their broad outlines, regardless of the exact placement of certain families, such as the Haploniscidae or the Dendrotiidae.

TAXA USED

The composition of the Janiroidea and of its families has been somewhat unstable, largely due to poor and incomplete descriptions common in the literature. Although no attempt is made to remedy the myriad problems currently facing the student of this superfamily, some preliminary re-assignments will be made in order to restrict the characters included for the families.

Table 4.3 shows the taxa used here for analysis. The classification used here is that of Bowman and Abele (1983) with the following corrections and emendations. Following Sivertsen and Holthuis (1980), "Jaeropsididae" is more correctly spelled Joeropsididae. "Acanthomunnopsidae" Schultz, 1978, is not a valid family, being based on a member of the family Munnopsidae (Wilson, 1982). Because recent publications have perpetuated the error of Wilson (1980), it is necessary to reiterate that the correct name for the taxon defined as the "Pleurogoniidae" in Wilson (1980) is Paramunnidae Vanhöffen, 1914, by priority. Svavarsson (1984) presented cogent arguments for the elimination of the family Pseudomesidae, with the division of its two genera between the Desmosomatidae and the Nannoniscidae. His changes are accepted here.

Because the large scale evolutionary features of the Janiroidea are being investigated here, pairs of some families were used as single taxa. The close relationships within the pair Munnidae and Pleurocopidae (name for old Antiasidae), and the pair Paramunnidae and Abyssianiridae are discussed in Wilson (1980). The similarities between the families Haplomunnidae and Dendrotiidae are detailed in Wilson (1976).

TABLE 4.3. Taxa (Families or Groups of Families) used for Phylogenetic Analysis of the Superfamily Janiroidea. The references cited contain the reasons why the taxa are grouped in this manner. See text for further discussion.

TAXON	REFERENCE
Acanthaspidiidae	Menzies (1962)
Dendrotiidae and Haplomunnidae	Wilson (1976)
Desmosomatidae	Hessler (1970)
Haplomiscidae	Wolff (1962)
Ischnomesidae	Wolff (1962)
Janirellidae	Menzies (1962)
Janiridae (limited composition)	This paper
Joeropsididae	Sivertsen and Holthuis (1980)
Macrostylidae	Wolff (1962)
Mictosomatidae and Mesosignidae	This paper and Schultz (1969)
Munnidae and Pleurocopidae	Wilson (1980)
Munnopsoids	Wilson and Thistle (1985)
Nannoniscidae	Siebenaller and Hessler (1981)
Paramunnidae and Abyssianiridae	Wilson (1980)
Pseudojaniridae New Family	This paper
Thambematidae	Wolff (1962)

As discussed in Wilson and Thistle (1985), important specialized characters are shared throughout the families Eurycopidae, Ilyarachnidae, and Munnopsidae. These families are of the greatest interest in this analysis, which was undertaken with the hope of establishing an appropriate outgroup for them. In this paper, the three families are united under an informal name, the munnopsoids, because if they are formally merged their family name will be Munnopsidae Sars, 1869.

The Microparasellidae includes highly modified, interstitial forms. They are not included in this analysis, because information is lacking on a number of key features, and because many of the reductional characters found in this family are likely to be derived independently from those seen in the taxa used. The Echinothambematidae is not included in the analysis because specimens are few, and the described species are not well known.

A number of key apomorphies are shared between Mesosignum and Mictosoma. Because of this only the better known family Mesosignidae was used in the analysis. The Mesosignidae, however, may be submerged into the Mictosomatidae in the future.

The Janiridae presented the greatest difficulties in this study. Although I do not regard what is presented here as a revision for the family, some patterns are fairly clear. The diagnosis of the family given by Wolff (1962) is made entirely of plesiomorphies at the level of the Janiroidea. The single apomorphy that might define this family is an enlarged accessory seta on the dactyli of the pereopods, giving

the three-clawed condition the the walking legs. The current composition of this family (Wolff, 1962) includes both 2 and 3 clawed forms. For the purposes of this analysis, the Janiridae are limited to the 3 clawed forms. An additional apomorphy shared with other families is the presence of "lappets" or paired lateral projections on the anterior pereonites. This character is more difficult to use because the lappets are reduced or absent in many species. The genera included under this definition of the Janiridae are: Carpias Richardson, 1902 (= Bagatus Nobili, 1906, and Janatus Carvacho, 1983), Ectias Richardson, 1906, (= Ianiroides Kensley, 1976), Ianiropsis Sars, 1899, Ias Bovallius, 1886, Iollella Richardson, 1905, Jaera Leach, 1814, Janira Leach, 1814, Janiralata Menzies, 1951 (= Rachura Richardson, 1908?), Notasellus Pfeffer, 1887 (= Iathrippa Bovallius, 1886? or visa versa?), and Vermetias Sivertsen and Holthuis, 1980. This limited composition of the Janiridae leaves out some genera: Janthura Wolff, 1962; Fritzianira De Castro and Lima, 1977; Austrofilius Hodgson, 1910; and Neojaera Nordenstam, 1933 (= Ianisera Kensley, 1976). These genera have distinct apomorphies useful at the family level, and need to re-examined for proper classification. This list also excludes the genera of the Microparasellidae, which were included into the Janiridae by Wolff (1962).

CHOICE AND SCORING OF CHARACTERS

The families of the Janiroidea are morphologically diverse, often with no continuity of resemblance from family to family. As a result many of the characters that define the families are not particularly

useful for determining the relationships among families, because the characters define only single families. Such autapomorphies add nothing to the matrix of among family relationships. To simplify the data, and accentuate the effect of characters that may show among family relationships, the autapomorphies were not included in the analysis. For example, the specializations for burrowing that help define the Macrostylidae, such as fusion of the anterior pereonites, are found in no other family and therefore tell nothing about relationships of the Macrostylidae to other groups. Other important autapomorphies omitted from the analysis are the natatory specializations of the munnopsoid families. Swimming is also found in the Desmosomatidae and the Nannoniscidae, but is clearly derived independently from the munnopsoids: both families lack a well defined natasome, the swimming setae are constructed differently, and the swimming modifications are often polymorphic within species.

In order to evaluate interfamilial relationships, an effort was made to find characters that do not change a great deal within families or groups of families, but show some change over all the Janiroidea. The characters introduced in the next section are not those used in current taxonomy of the janiroidean families. In fact, they may seem insignificant to some who are well versed in the systematics of the field. This lack of significance may stem from the low amount of change in the characters, which is a necessary requirement for the analysis.

Two main character complexes were found useful: the third pleopod and the dactylar claws. The third pleopod is useful because it lost its stereotyped opercular function in evolving from the ancestral state, thereby releasing the form of the exopod to vary. In the janiroideans, there is a trend of reductions in the previously opercular exopod, with a few important novelties such as extra plumose setae. The dactylar claws show a variety of reductions and novelties as well often uniquely marking groups of families. Other characters, such as the body form and spines on the midline, are included as well, because they also help identify groups of families. The characters from the previous analysis of the asellotan superfamilies are included to aid in the definition of the outgroup states.

The use of characters of reduction must be approached with caution, as will be seen in the results. They quite clearly appear a number of times independently, thus introducing apparent incongruencies into the phylogenetic estimate. Because reductional characters are being used, I do not expect most of the characters to be compatible, that is, to give low homoplasy values. The analysis will seek the most parsimonious arrangement of the observed character states, and if a state is arranged so that it must appear independently more than once, then the arrangement will be assumed to be correct if it is the most parsimonious arrangement of all the characters defining the tree. Although it is not attempted for this analysis, multiple derivations of the same character state should be re-examined to determine whether they are homologous or not.

In the final analysis, a conservative weighting scheme is applied to the characters. Those that demonstrate the relationships between the Janiroidea and the outgroup taxa, characters 1-15, are given a high weight to prevent conflicting reduction characters from affecting the resulting tree. The remaining characters are either given a weight of 1 or 2 depending on whether they are reduction characters, such as loss of setae, or are unique derivations, such as modifications of the dactylar claws. Although there is no theoretically justifiable use of character weighting (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 affect on the analysis.

The scoring of the characters for each taxon used was sometimes difficult, especially since certain families taken as a whole were polymorphic for the reduction characters. For polymorphic characters in the families, the more plesiomorphic state of a reduction character was chosen. If the character being surveyed was unique, however, and also polymorphic over a taxon taken as a whole, then the state that occurred in the least modified members of the taxon was chosen for the taxon as a whole. The rationale for this procedure is to estimate the character state in the ancestor of each taxon without having to perform a phylogenetic analysis of all the genera of the taxon (which in many cases is currently impossible due to inadequate information in the literature). The choice of the plesiomorphic reduction character state should accomplish this goal, and the choice of a unique character state over the lack of it should account for any cases where

the character state was gained and then lost in the more specialized members of a group.

CHARACTER ANALYSIS

The following characters are those chosen after examining a broad range of janiroidean taxa for which there were adequate descriptions, or with which I had direct experience. They should be regarded as a restricted subset of the possible characters to be used to define the families of the Janiroidea. The resulting character matrix with the distribution of the characters discussed below among the taxa, is shown in table 4.4.

Lateral Projections of the Tergites.--The use in janiroid taxonomy of the appearance or non-appearance of pereopodal coxae in dorsal view is based on variation in the shape and size of tergal projections of the pereonites. Whether one can see the coxae in dorsal view is sometimes subjective, often depending on the condition of the specimens and the experience of the observer. Determining the presence and shape of the tergal projections is much more useful and concise, and will be used here.

The outgroup taxa, Stenetrium and Pseudojanira, have tergal projections, that is, tergite margins that project laterally beyond the coxae. In many of the Janiroidean taxa these are lost, but those that have them display two distinctive configurations. The first is a single projection on each lateral margin. In many taxa, this projection is broad and covers the coxae, and in others it can become

spine like. If a spinose projection is present it is always single in these forms, and is seen in genera that have related genera with broad lateral projections. In another group of taxa that have lateral projections, the lateral margins of the anterior pereonites 2-4 are concave, and there are two "lappets" on each side of a tergite. The paired lappets may be tongue-like or spinose. In the more advanced deep-sea families, the lappets are present only as spines but retain their paired configuration.

The evolutionary polarity of the two types of lateral projections is not completely certain, although a preliminary assessment may be made. Stenetrium is known to have both types, although the paired lappets are primarily restricted to concave lateral margins. Pseudojanira and the munnid-pleurocopid group of families have only single lateral projections. If the doublet rule (Maddison, et al., 1984) can be applied here, then one can conclude that paired lappets within the Janiroidea that are in the sister group of the munnid-pleurocopid group are apomorphies, and single tergal projections are plesiomorphies. Lack of any tergal projections could be derived from either condition independently, and therefore is not used.

Body Form.--All the outgroup taxa have moderately broad bodies. This broadness is independent of tergal projections, as can be shown by some species of Stenetrium or Munna that have no projections but have broad, or at least ovoid bodies. Many janiroideans have narrow, worm-like bodies, clearly a derived condition. Although the use of this character may introduce some homoplasy into the phylogenetic analysis,

this apomorphy defines whole groups of families.

Spines on the Body Midline.--Deep-sea Isopoda are characteristically spiny, with sharp projections located on practically any part of the body. There are, however, two classes of spines that occur repeatedly and may be present in the absence of other spines: spines on the dorsal midline, and spines on the ventral midline. Interestingly these two types of spines do not co-occur. Because such spines are not seen in the outgroups, both characters are separately derived apomorphies.

Dactylar Claws (fig. 4.16).--"Claws" on the dactyli of the walking legs are nothing more than modified setae, mechanically strengthened to aid the animal in walking. For this character it is easy to establish the janiroidean ancestral state. All the "lower" Asellota, including the Aselloidea, Stenetrioidea, and the outgroup Pseudojanira, have two large, similarly sized, distal claws and one more proximal accessory seta (fig. 4.16A). The position of the accessory seta varies, but outside of the Janiroidea, it never resembles the distal claws. Within the Janiroidea, the pereopodal claws undergo important modifications that help distinguish major groupings of the families.

The Janiridae, as defined here, includes those genera in which the accessory seta is not lost, but enlarged and often moved distally so that it functions as a third claw (fig. 4.16C). This is a synapomorphy of the Janiridae and the Joeropsididae.

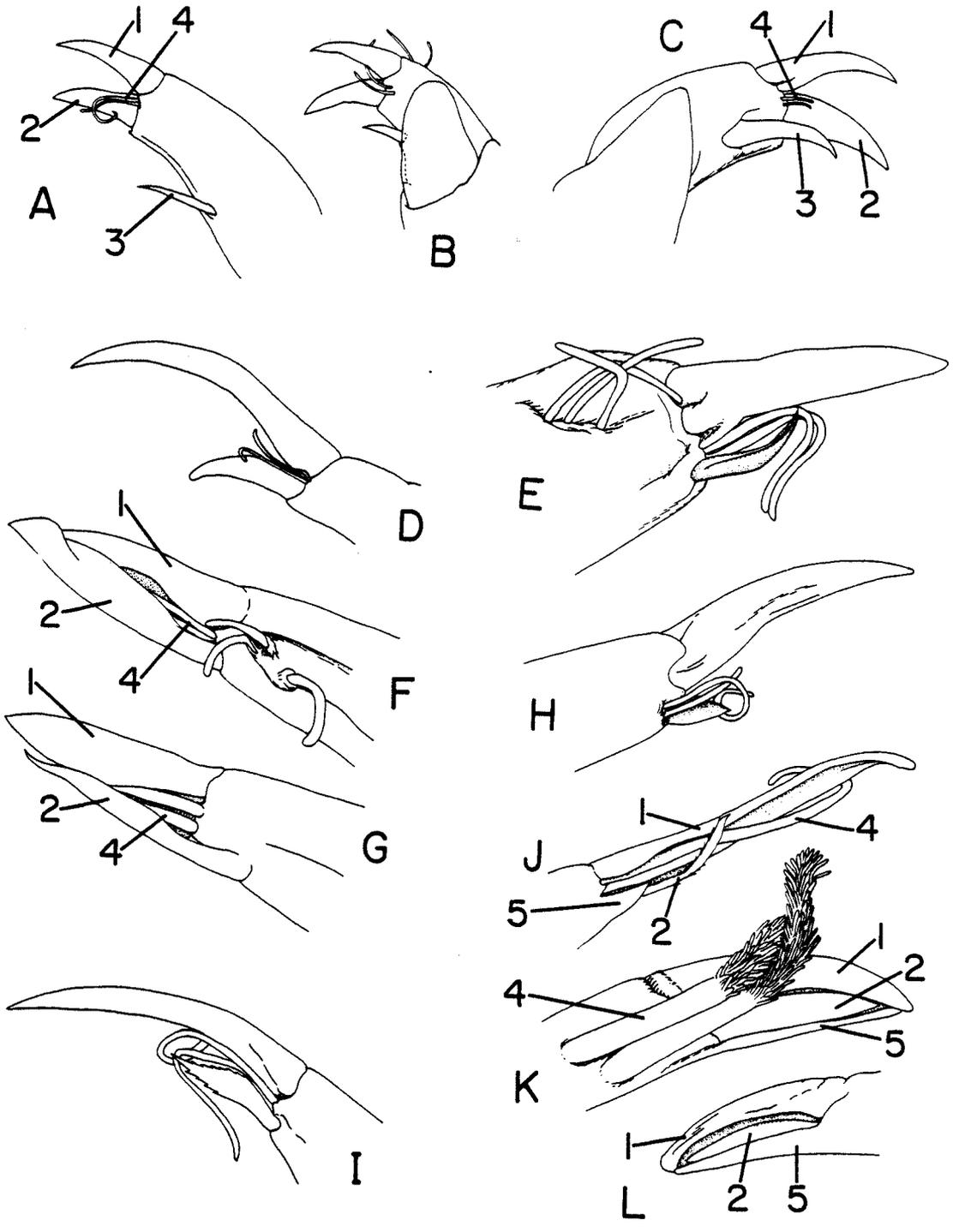
The remaining janiroidean families have lost the accessory seta, and many have the posterior claw reduced and modified to varying degrees (fig. 4.16D-L). Simple reduction or losses are difficult to use because they could have occurred many times. More useful are unique specializations of the claws that involve more than simple reductions. Therefore, the apomorphic character states "loss of the accessory seta" and "reduction in length alone of the posterior claw" will be given low weights in the phylogenetic analyses.

The families Munnopsidae, Ilyarachnidae, and Eurycopidae have an unusual synapomorphy: the anterior and posterior claws curl around each other, enclosing the sensillae between them (fig. 4.16F-G). The claws are subequal in length, indicating they may not have undergone the length reduction of the posterior claw seen in most janiroidean families. More parsimonious trees result, however, if this highly modified claw is interpreted as derived from a reduced claw.

A short posterior claw is flattened (fig. 4.16 H) in many of the families, and is an apomorphy. The plesiomorphic state is a posterior claw that is more or less rounded in cross-section.

A group of families, within the set of families that have flattened posterior claws, also have fine serrations on the margins of the posterior claw (fig. 4.16 I,J). Because similar serrations do not occur in Pseudojanira, the presence of serrations is an apomorphy.

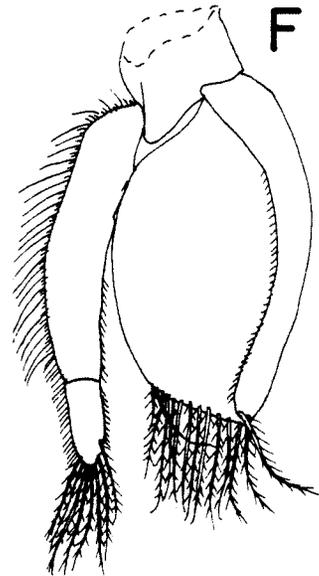
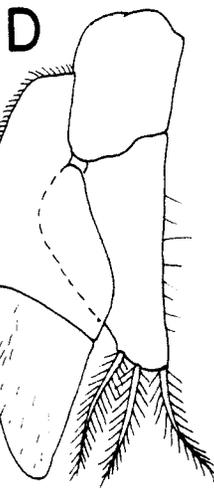
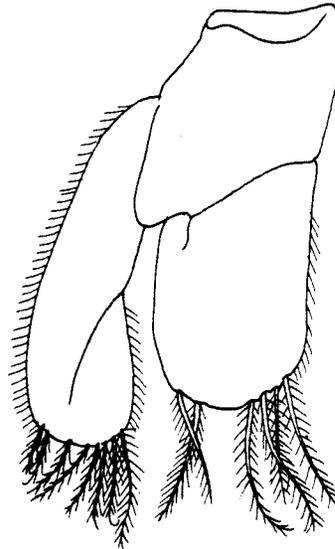
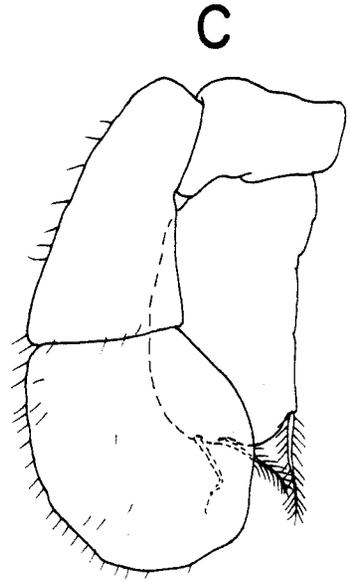
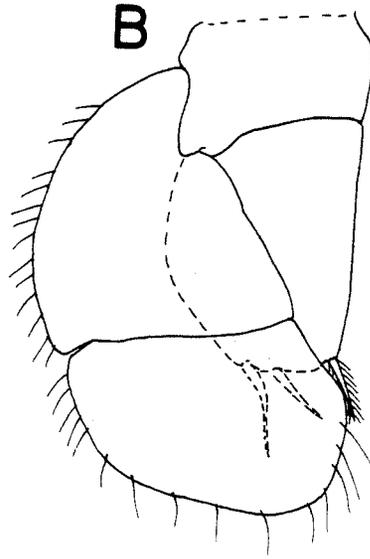
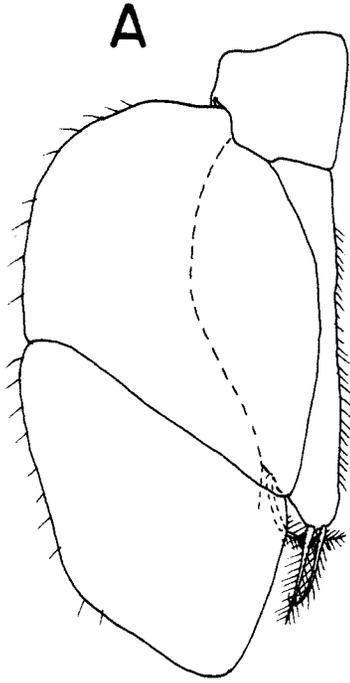
Figure 4.16. A comparison of the dactylar claws on the second pereopod of Stenetrium, Pseudojanira, and various Janiroidea. All dactyli seen in medial view, except for G and L. A, Stenetrium, Stenetriidae. B, Pseudojanira, Pseudojaniridae n. fam. C, Janiralata, Janiridae. D, Munna, Munnidae. E, Ischnomesus, Ischnomesidae. F, Munnopsis, Munnopsidae. G, Ilyarachna, Ilyarachnidae, lateral view. H, Haploniscus, Haploniscidae. I, Nannoniscus, Nannoniscidae. J, Eugerdia, Desmosomatidae. K-L, Macrostylis, Macrostylidae, medial and lateral views. 1 - anterior claw, 2 - posterior claw, 3 - accessory seta, 4 - sensillae between anterior and posterior claws, 5 - cuticular shelf posterior to posterior claw.



The Desmosomatidae have the last two apomorphies, and have two additional dactylar claw apomorphies (fig. 4.16 J). The first is a thin and curled posterior claw. Therefore, it is an extension of the transformation series involving reductions and modifications of the posterior claw. The second is a posterior groove in the anterior claw in which the sensillae lie. All potential outgroups have a round cross section for the anterior claw. The Ischnomesidae also have a thin and curled posterior claw on the dactyli, but initial phylogenetic analyses showed the most parsimonious tree results if it was derived independently in the two families. The character state "thin and curled posterior claw" is therefore assigned to two separate characters, one for the Desmosomatidae and one for the Ischnomesidae.

The Macrostylidae, which are highly specialized for burrowing in many of their features, also have a autapomorphy in the form of the dactylar claws of the anterior pereopods (fig. 4.16 K,L). The sensillae sit outside of the gap between the anterior and posterior claws, and are large and robust, with many fat tendrils. The anterior claw has the posterior groove seen also in the Desmosomatidae, but the groove contains the flattened posterior claw, instead of the sensillae. The most unusual feature of the macrostylid dactylus is a flattened extension of cuticle posterior to the posterior claw that extends to the tip of the anterior claw. The dactylus has a strengthened, tripartite construction not seen in any other janiroidean family or in Pseudojanira, and is a autapomorphy of the Macrostylidae.

Figure 4.17. A comparison of third pleopods of various Asellota. A, Stenetrium, Stenetriidae. B, Pseudojanira, Pseudojaniridae n. fam. C, Notasellus, Janiridae. D, Munna, Munnidae. E, Ianthopsis, Janiridae. F, Amuletta, Eurycopidae.



Pleopod III (figs. 4.17, 4.18).--The third pleopod has been little used in the familial taxonomy of the Janiroidea, although its states figure heavily in the phylogenies of the superfamilies of the Asellota (Wägele, 1983). In the character analysis of the superfamilies, the presence of an opercular third pleopod in males of Notasellus (fig. 4.17 C) and Jaera was shown to establish the continuity of opercular third pleopods throughout the Asellota. Because most janiroideans have opercula made of the first and second pleopods, the previously opercular third pleopods are released evolutionarily from that function, and vary throughout the families.

Although most of the characters are reduction characters, and undoubtedly introduce apparent homoplasy into the phylogenetic analysis, the third pleopod characters are useful because they vary at the level of families, and tend to change much less at the level of genera and species. The reduction characters receive low weightings in the final phylogenetic analysis to reduce the effects of possible independent duplication of the same character state in several taxa. The primary reduction series are in the size of the exopod. The plesiomorphic state is a very large exopod that is both longer and broader than the endopod.

The first transformation series is a decrease in width of the exopod: the plesiomorphic state "broader than endopod," the intermediate state "approximately same width as endopod," and the terminal apomorphy "narrower than endopod." Once reduced from a larger state, the exopod is much less likely to become large, thus

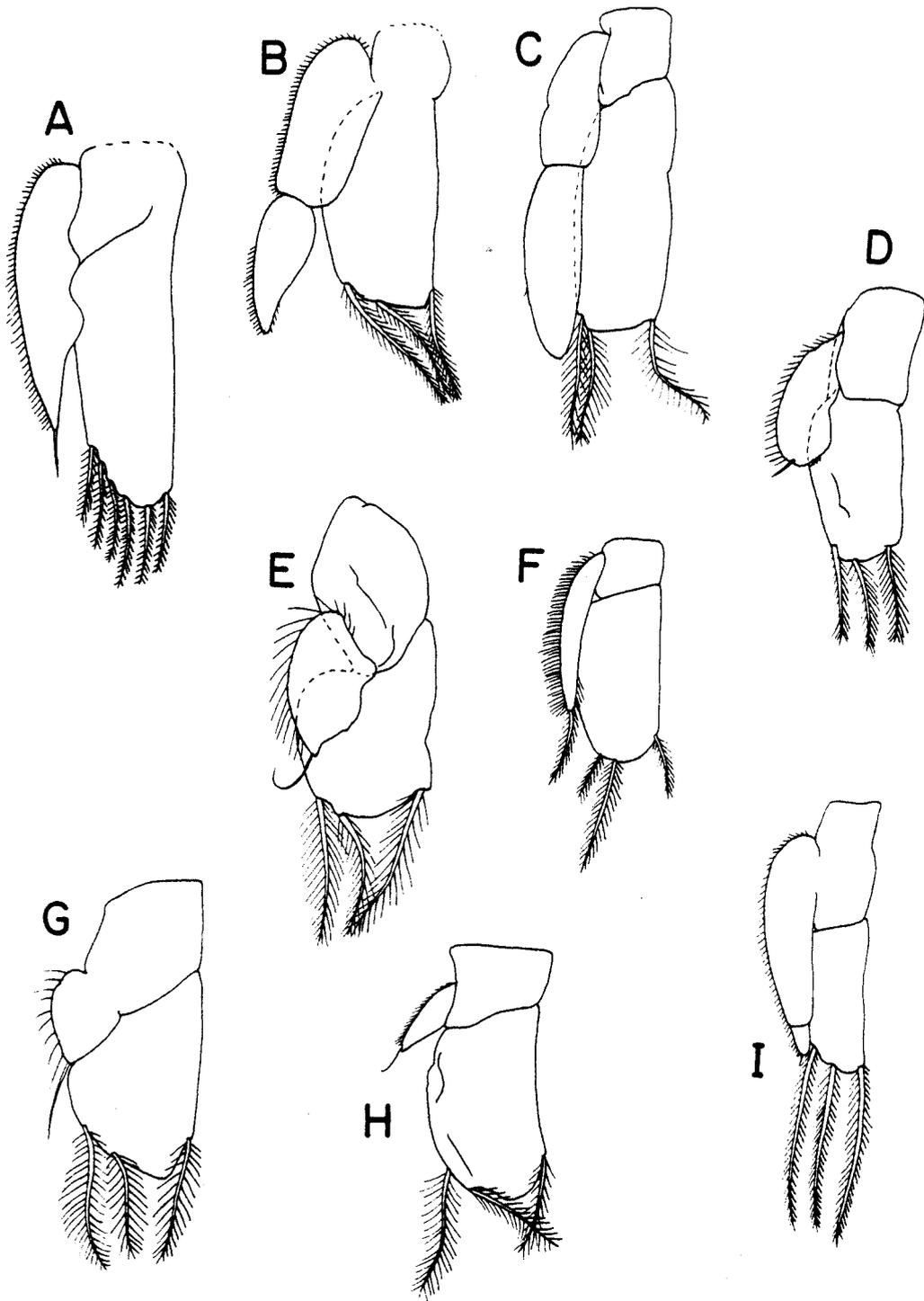
limiting the possible combinations for this transformation series. Possible combinations are a "fork" where the exopod goes directly from the ancestral state to either of the reduced states, or a "straight line" where the intermediate width exopod is truly intermediate evolutionarily. Both combinations were tested in the phylogenetic analyses and the "straight line topology" produced the trees with the fewest changes of all the character states.

The second transformation series is in the length of the exopod compared to that size of the endopod. The character states are "longer than endopod," "near same length as endopod," or "distinctly shorter than endopod." This series can also be represented by a "fork" or a "straight line," requiring the testing of both possibilities in the phylogenetic analysis. Again the "straight line" produced the most parsimonious trees.

The fusion of the exopod in many taxa yields a two state character: "exopod with two segments" or "exopod with only one segment." The exopods of Pseudojanira, Munna, and Paramunna have two segments, so the first state must be a plesiomorphy, and the second state an apomorphy.

Some of the family level taxa of the Janiroidea vary in the setation of the third pleopod. This setation is very conservative in the "lower" Asellota, making it easy to assess the ancestral state. The two immediate outgroups of the Janiroidea, Stenetrium and Pseudojanira, have nearly identical setation on the third pleopods

Figure 4.18. 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.



(fig. 4.17 A-B), although some Stenetrium have extra plumose setae on the endopod. The ancestral state of the Janiroidea should be the same using the doublet rule of Maddison et al. (1984). In these two taxa and in Notasellus, the endopod has three large plumose setae and the exopod has simple setae only. Ignoring the shape of the exopod, this is the configuration of setae seen in many of the Janiroidea. In some families, however, are found additional plumose setae, providing several useful character states.

The first character is whether or not the endopod has more than 3 plumose setae (fig. 4.17 E-F; 4.18 A). As said above the plesiomorphic state is "only 3 plumose setae" and the apomorphic state is "more than 3 plumose setae." In taxa which have more than 3 plumose setae on the endopod, the exact number can vary considerably so that, given current information, the apomorphic state cannot be subdivided accurately. Such subdivision may be useful for species-level or genus-level taxa.

The second transformation series contains three possible states: "no plumose setae on exopod," "one plumose seta on exopod (fig. 4.18 F)," and "more than one plumose seta on exopod (fig. 4.17 E-F)." The plesiomorphic state is an absence of plumose setae, and the simplest description of this transformation is that plumose setae appeared on the exopods only once, indicating a straight line topology for the transformation series would be best. The phylogenetic analyses, however, showed that the best tree for the Janiroidea resulted from an independent derivation of the two states, a forked topology.

THE RESULTS OF THE CHARACTER ANALYSIS

The following list gives a brief description of each character state and its polarity based on the above outgroup analysis, the weights (Wt = n) used in the final phylogenetic analysis, and whether Wagner (W) or Camin-Sokal (C) parsimony methods were used. The first 15 characters are those from the section analyzing the relationships among the superfamilies (see table 4.2). These first 15 characters were given a weight of 5 because they were already shown to be highly compatible. They were analysed using the Camin-Sokal parsimony method. The distribution of the character states among the taxa is shown in table 4.4, and the taxon-character matrix factored to completely binary states, with the parsimony methods and weights, is shown in table 4.5.

1.-15. See previous section.

16. Tergal projections, if any, single broad plate (0), or tergal projections as paired lappets on anterior pereonites (1). (Wt = 1, W)

17. Body at least moderately broad (0), or body narrow or worm-like (1). (Wt = 1, C)

18. No spines on dorsal midline (0), or spines on dorsal midline (1). (Wt = 2, W)

19. No spines on venter (0), or spines on ventral midline (1). (W = 2, W)

20. Pereopodal dactyli with (0), or without (1) accessory seta.
(W = 2, C)
21. Pereopodal dactyli with simple (0), or claw-like (1) accessory seta. (W = 2, W)
22. Pereopodal dactyli with large (0), or small (1) posterior claw.
(W = 1, C)
23. Pereopodal dactylar claws do not (0), or do enclose (1) the sensillae. (W = 2, C)
24. Pereopodal dactylar posterior claw rounded (0), or flattened (1) in cross-section. (W = 2, C)
25. Pereopodal dactylar posterior claw without (0) or with (1) marginal serrations or teeth. (W = 2, C).
26. and 34. Pereopodal dactylar posterior claw not thin and curled (0) or thin and curled (1). (This character independently derived in two taxa. W = 2, C)
27. Pereopodal anterior dactylar claw without (0) or with (1) posterior groove. (W = 2, C)
28. Pereopodal dactylus without (0) or with (1) flattened extension of cuticle posterior to the posterior claw giving claws a strengthened tripartite form. (W = 2, C)

29. Exopod of pleopod III broader than endopod (0), same width as endopod (1), or narrower than endopod (2). This sequence has a linear derivation with state (1) as the intermediate. (W = 1, C)
30. Exopod of pleopod III longer than endopod (0), near same length as (1), or distinctly shorter than endopod (2). This sequence has a linear derivation with state (1) as the intermediate. (W = 1, C)
31. Exopod of pleopod III 2 segmented (0) or fused into a single segment (1). (W = 1, C)
32. Endopod of pleopod III with three plumose setae (0) or more than three plumose setae (1). (W = 2, W)
33. Exopod of pleopod III with no (0), one (1), or many (2) plumose setae. Character states 1 and 2 are independently derived from 0. (W = 2, W)

TABLE 4.4. Character States for the Taxa used in the Phylogenetic Analyses. Description of the characters in text.

TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34			
Pseudojaniridae	0	0	1	0	0	1	1	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Munnidae & Pleurocopidae	0	1	1	1	0	1	1	1	1	0	1	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
Paramunnidae & Abyssianiridae	1	1	1	1	0	1	1	1	1	0	1	1	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
Acanthaspidiidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0		
Dendrotiidae & Haplomunnidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	0	0	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	
Desmosomatidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	0	1	0	1	1	0	1	0	1	1	1	1	0	2	2	1	0	0	0	0	0	
Haploniscidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	0	0	0	0	1	0	1	0	1	0	0	0	0	2	2	1	0	0	0	0	0	
Ischnomesidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	1	1	1	0	1	0	1	0	1	0	0	0	0	2	1	0	0	2	1	0	0	
Janirellidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	1	0	1	0	1	0	1	0	0	0	0	0	0	2	1	0	1	0	0	0	0	
Janiridae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Joeropsididae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Macrostylidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	0	1	0	1	1	0	1	0	1	0	0	1	1	2	1	0	0	0	0	0	0	0
Mictosomatidae & Mesosignidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	1	0	0	0	1	0	1	0	0	0	0	0	0	2	2	1	0	0	0	0	0	0
Munnopsoid Families	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	1	0	1	0	1	0	1	1	0	0	0	0	0	2	0	0	1	1	0	0	0	0
Nannoniscidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	0	1	0	1	1	0	1	0	1	1	0	0	0	2	2	1	0	0	0	0	0	0
Thambematidae	1	1	1	1	0	1	1	1	1	0	1	1	1	2	1	0	1	0	0	1	0	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0

TABLE 4.5. Actual Taxon-Character Matrix used in Phylogenetic Analysis. Multistate characters are factored to binary data.

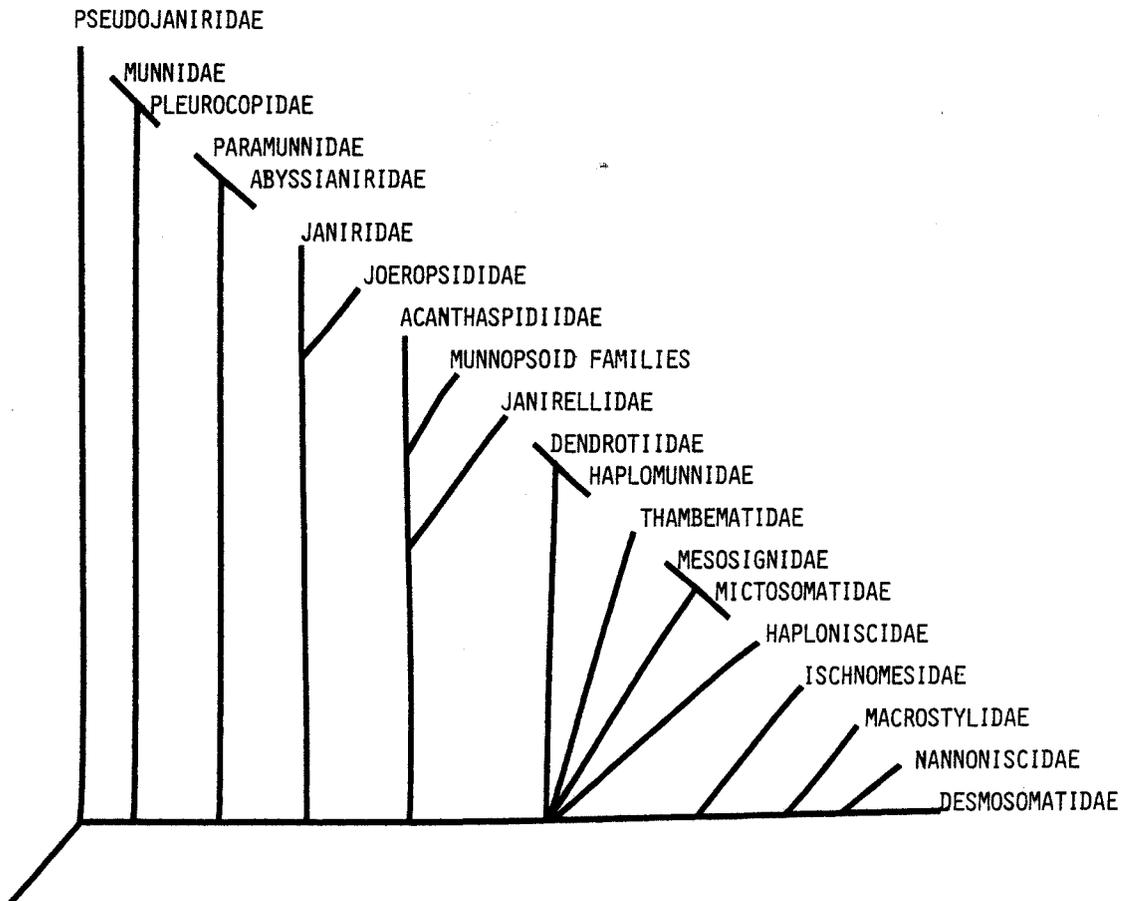
Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	29	30	30	31	32	33	33	34		
Parsimony Method	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	W	C	W	W	C	W	C	C	C	C	C	C	C	C	C	C	C	C	C	C	W	W	W	C
Weights Used	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	1	1	2	2	1	2	1	2	2	2	2	2	2	1	1	1	1	1	1	2	2	2	2	
Ancestral States	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudojaniridae	0	0	1	0	0	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Munnidae & Pleurocopidae	0	1	1	1	0	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Paramunnidae & Abyssianiridae	1	1	1	1	0	1	1	1	1	1	0	1	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Acanthaspidiidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	
Dendrotlidae & Haplomunnidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Desmosomatidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	1	1	0	1	0	1	1	1	1	0	1	1	1	1	1	1	1	0	0	0	0
Haploniscidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	1	0	1	0	1	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
Ischnomesidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	0	1	0	1	0	1	0	0	0	0	1	1	1	0	1	0	0	1	1
Janirellidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	1	0	0	0	0	0
Janiridae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Joeropsididae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Macrostylidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0
Mictosomatidae & Mesosignidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0
Munnopsoid Families	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0
Nannoniscidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	1	1	0	1	0	1	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0
Thambematidae	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0

THE PHYLOGENETIC ANALYSIS

Figure 4.19 shows the general form of the most parsimonious trees after the generation of more than 300 separate trees. The multifurcation in the tree represents a location of several different topologies at the lowest parsimony level, as well as relationships that cannot be determined with the data available (branch lengths of 0 changes in characters). The general topology of all trees derived was very near that shown, and the parsimony values varied only in the range of 7 steps. The outgroup taxa, Pseudojaniridae, Munnidae/Pleurocopidae, and Paramunnidae/Abyssianiridae, were very stable in their position even without weighting of the characters that determined their outgroup position.

If all the characters were completely compatible, there would be only a single change in each character for all the taxa, giving a minimum parsimony value of 37 steps for the cladogram. The tree form shown here has 61 character changes, or 24 more than the minimum. This yields a fairly high homoplasy value of 65% (24/37). As discussed earlier, a highly resolved tree was not expected because many of the characters were reduction characters that could be derived many times. This is especially true in the loss of the dactylar accessory seta, the reduction in the length of the posterior dactylar claw, and the reduction in length and width of the pleopods. Because of the poor resolution of the tree, it is difficult to assign unique positions to each character change. Therefore this was not done in figure 4.19.

Figure 4.19. Preliminary phylogenetic tree for the Janiroidea. The tree is not highly resolved; note the large multifurcation. This tree suggests that most deep-sea isopods are derived from the same ancestral group. The closest ancestral group for the munnopsoids is the Acanthaspidiidae. The distal horizontal bars indicate groups of families analysed as a single taxon.



The derivation of a character was reinterpreted in one place because the true ancestral state was uncertain. The specialized dactylar claws of the munnopsoids have long but modified posterior claws. It was initially assumed that this long modified claw was derived from a long unmodified claw, a choice that forces the independent derivation of short claws in the two sister groups, the Acanthaspidiidae and the Janirellidae. If the precursor state was the shortened but otherwise unmodified claws of the munnopsoid sister groups, then the derivation of the shortened posterior claws can be moved lower in the cladogram, with an exchange of 3 character changes for 1 change. This procedure was not carried out with the many other homoplasies in the tree because it would result in unreasonable character changes. For example, any reductions in the size of the exopod of the third pleopod are unlikely to be followed by an expansion to a more primitive larger size because the exopod does not function as an operculum.

In every single version of the tree, the sister group to the munnopsoids was the Acanthaspidiidae. The most important apomorphies shared by these taxa are the extra plumose setae on the endopod and exopod of the third pleopod. Spines on the dorsal midline and the presence of tergal lappets also help define these two taxa, but the derivation of these characters is less certain, due to their multiple derivations on the tree. These two groups also lack many of the specializations characteristic of many of the other deep-sea Janiroidea, such as greatly reduced third pleopodal exopods. I do not believe that the munnopsoids and the Acanthaspidiidae are as closely

related as, say, the Nannoniscidae and the Desmosomatidae because the munnopsoids have many autapomorphies not used in this tree, evidence for great deal of evolutionary time after the separation of the former two groups.

The Janirellidae are another possible sister group of the munnopsoids. This family, however, is highly modified in characters that could easily be reductions from the acanthaspidiid condition, such as the loss of plumose setae from the third pleopodal exopod and its subsequent reduction. These characters were not coded using this interpretation, although it is suggested by the association of the Janirellidae to the clade bearing the Acanthaspidiidae. These two families also share a tendency toward spininess, corroborating this impression. (General spininess, however, is found in so many of the deep-sea taxa that it was not useful for the phylogenetic analysis.) Therefore, the best choice for a sister group of the munnopsoids is the more generalized Acanthaspidiidae.

In Kussakin's (1973) phylogeny, sister groups to the munnopsoids are the Janiridae, or more distantly the Joeropsididae, the Macrostylidae, or the Pseudomesidae. At the time of his paper, the Acanthaspidiidae was submerged in the Janiridae, following the classification of Wolff (1962). Therefore, some of Kussakin's (1973) presumed phylogeny of the Janiroidea may be justified, although it was never made clear how his tree was derived.

The tree derived here contains a single multifurcation at the node leading to the Dendrotiidae/Haplomunnidae, the Mictosomatidae/Mesosignidae, the Haplomunnidae, the Thambematidae, and the remaining narrow-bodied deep-sea Janiroidea. Of this latter group, the Desmosomatidae is associated with the families Macrostylidae and Nannoniscidae, and these three families are well removed from the ancestral janiroidean, as befit their highly derived body and pereopodal forms. The Dendrotiidae/Haplomunnidae are associated with other deep-sea taxa, and do not appear near the basal branches of the Janiroidea. These latter two families are probably not derived from a pleurocopid or munnid ancestor as had been previously proposed (see phylogenies of Kussakin, 1973; Fresi et al., 1980).

DISCUSSION

The estimated phylogeny of the Janiroidea makes the Acanthaspidiidae the sister group for the munnopsoid families Eurycopidae, Ilyarachnidae and Munnopsidae. Because these groups are placed in the phylogeny near the position of more plesiomorphic families such as the Janiridae and the Joeropsididae, the munnopsoids may have been in existence for a relatively long time compared to the other janiroidean deep-sea families. (Only relative time can be determined because the branch lengths of the phylogeny are unknown from the inference techniques used here.) This suggestion is corroborated by the enormous variety of munnopsoid forms that have radiated into all the major deep-sea environments, as well as back into shallow water.

The inferred phylogeny also has immediate biogeographic implications. One of the theses of Wilson (1980) is that the Munnidae/Pleurocopidae and the Paramunnidae/Abyssianiridae groups are independently derived and have entered the deep sea independently from each other. A similar assertion may be made for the Janiridae, which has a few deep-sea members but is primarily a shallow-water group. This is a pattern of the primitive janiroideans having shallow-water distributions but with some representatives in the deep sea.

The remainder of the Janiroidea may show a different pattern. Although Kussakin (1983) advocated a deep-sea colonization by most of the families independently, Hessler and Thistle (1975) and Hessler, Wilson and Thistle (1979) were able to show that many of the families

had a substantial portion of their evolution in the deep sea. The known distributions of the Janiroidea (Hessler and Thistle, 1975) and the preliminary phylogeny (fig. 4.19) indicates that a single ancestral group may have given rise to all the deep-sea families. This possible ancestor still had eyes because eyes occur in both the outgroups (Janiridae or Joeropsidiidae) and in a few genera of the deep-sea taxa: Ianthopsis, Acanthaspidiidae; Acanthomunna, Dendroitiidae. These two genera have what might be called a "Gondwanaland" shallow bathyal distribution, with records from Antarctica, New Zealand, Kerguelen, southern South America and southern Africa. This suggests that the ancestor to all the deep-sea isopods may have arisen before or during the breakup of Gondwanaland, giving a very approximate time of origin of the deep-sea isopods of in the Jurassic, around 175 million years ago (van Andel, 1979). It is not my intent to develop this hypothesis any further, but this is a possible answer to a question that has been asked many times: how old are the deep-sea isopods?

CHAPTER 5

A PROPOSED PHYLOGENY AND CLASSIFICATION OF THE MUNNOPSOID TAXA, WITH SPECIAL REFERENCE TO THE ILYARACHNOID EURYCOPIDAE

INTRODUCTION

At this point, an evaluation of the systematic position of the ilyarachnoid Eurycopidae is possible. The basis for the unity of the munnopsoid form has been established, and the taxonomic variety of the ilyarachnoid eurycopids has been described. The Ilyarachnidae are better defined by the removal of a potential sister group, Amuletta, from that family. The systematic position of the munnopsoid janiroideans within the isopod suborder Asellota is now better known, yielding a possible outgroup for the munnopsoids, the Acanthaspidiidae.

This chapter finds characters that help establish the relationships between the munnopsoid taxa. The characters are then used to derive an estimate of their phylogeny, with the limitation that the phylogeny is biased toward interpreting the systematic position of the ilyarachnoid eurycopids. Therefore, the conclusions reached here are not general for the munnopsoids, although their estimated phylogeny provides hypotheses to be tested in the future.

TAXA USED

The diversity of the munnopsoid taxa and the limited information on many of them makes it necessary to restrict the number of taxa used in the phylogenetic analysis. Another limitation is that the computerized algorithms are excessively slowed by data sets with more than 19-20 taxa. Four criteria establish the subset of taxa (see table 5.1) analysed here. They are ilyarachnoid Eurycopids; they are members of the subfamily Eurycopinae; they are the least modified representatives of their group; or they are presumed to be closely related to the Ilyarachnidae. All genera have been revised recently, or were evaluated directly from specimens in the collections.

The eurycopid subfamily Bathyopsurinae, which includes the genera Bathyopsurus and Paropsurus, are highly modified bathypelagic genera. This group is possibly derived from a Munneurycope-like ancestor. They are not included in the analysis because information on these genera are limited, and because they seem to have little in common with the ilyarachnoid eurycopids.

The eurycopid subfamily Syneurycopinae contains two genera, Syneurycope and Bellibos, that subsume a fairly wide range of morphologies. The subgenus Bellibos (Bellibos) seems to be the least modified with respect to the other munnopsoids. The species B. (B.) buzwilsoni Haugness and Hessler, 1979, is chosen as the synerucyopine model for the analyses.

The Munnopsidae sensu stricto contains a variety of morphologies, but can be best represented by Paramunnopsis. This genus is similar to the eurycopid genus Munneurycope in overall appearance.

The Ilyarachnidae has 5 genera with more or less a common body plan. The least modified type-genus Ilyarachna was chosen to represent this family-level 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 the collections, eliminating the possibility of dissection for some of the characters. A preliminary inspection of Munnicope showed that this genus has much in common with Munnopsurus so its omission from the analysis will not seriously hamper the results.

METHODS

The techniques for the character and phylogenetic analyses are primarily those used in chapter 4. An initial character analysis was performed, using those characters that appeared to vary little over all the munnopsoids. The primitive state of each character was based on homologies in the outgroups. The data sets were subjected to preliminary phylogenetic analyses, and the effect of different topologies for the transformation series were tested for the lowest parsimony values (fewest number of character state changes to derive a particular tree). Camin-Sokal or Wagner parsimony methods were chosen for each character transition, based on whether or not character state

reversals seemed possible. The characters that introduced a large number of steps into the trees were re-evaluated in order to determine whether they were interpreted properly.

For example, Eurycope was originally thought to have a frontal arch but scoring this genus as having this character state generated trees with high amounts of homoplasy. On reinspecting all the taxa for this character, it was discovered that Notasellus in the family Janiridae had ridges on the frons homologous to those seen in some species of Eurycope, and that none of the potential outgroup taxa had anything resembling the frontal arches seen in Amuletta, Munneurycope, or Betamorpha. The decisive observation was that Munneurycope had ridges on the frons between the antennulae (in the same position as in Eurycope) above the frontal arch. Therefore, the frontal arch was interpreted as a unique apomorphy of some of the munnopsoid taxa, and Eurycope was scored as lacking this apomorphy.

During this process many characters were rejected as useful at the systematic level of munnopsoids. Among these were the forms of the uropods and the mandibles, the shape of the antennular first article and the length of the antennula, the presence of an enlarged pereonite 7, fusion of the ventral natasomites, and the absence of dorsal or lateral spines. Most of these are known to vary within genera, corroborating their lack of usefulness at the familial level. This process resembles compatibility analysis (Felsenstein, 1982) because it uses those characters that agree on a particular form of the phylogeny. Some homoplasous characters were retained, because

they helped resolve some branches, and because they were stable in most taxa. The plumose setation of pleopods III and IV was the primary example of this type of character.

Once reasonable values for a set of characters were obtained, a conservative weighting was applied to them for the final series of analyses. Uniquely derived characters, such as the frontal arch and the fusion of the natasomal segments, were given a weight of 2, and reduction apomorphies, such as the loss of plumose setae, were given a weight of 1. The rationale for this is that unique characters are much less likely to be derived more than once than are reduction characters. The problem of weighting is discussed in more detail in chapter 4.

CHARACTER ANALYSIS OF THE MUNNOPSOID TAXA

The natatory morphology unites all the munnopsoids, but the included taxa vary enormously in their overall body plan (fig. 1.5), and in the form of such less well recognized features as the cephalic frons and the pleopods. Here an attempt will be made to draw these morphological data together into an analysis of the relationships between the munnopsoid taxa. The outgroup found in the previous chapter, the Acanthaspidiidae, permits assessing the polarities of the characters. In most cases, knowledge of the character states in this family is sufficient to determine the polarities within the munnopsoids. In a few cases, however, a suite of outgroups, including the Janiridae and the Janirellidae, are used.

FUSION OF THE NATASOMAL SEGMENTS

The varied degrees of fusion of pereonites 5-7 the segments is one of the sources of the morphological diversity in the munnopsoids. The functional necessity to form a strengthened cuticular framework for the powerful swimming muscles may be a driving force in the observed patterns of fusion seen in the munnopsoids. 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 the munnopsoids, only certain special patterns could be singled out for the analysis.

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 through 7 are also the same size, and have relatively small pereopodal musculature. Fusion of the natasomal pereonites seems to first appear ventrally with nearly complete obliteration of the segmental boundaries. This is best seen in Eurycope, but occurs in most of the other munnopsoid genera. Notable exceptions are the Ilyarachnidae, Amuletta, and Hapsidohedra. The last genus is morphologically atypical in that the natasome is strongly flexed ventrally, a potential factor in its retention of free ventral natasomites. The Ilyarachnidae are known to be posterior burrowers, suggesting that some flexibility in the wedge-like natasome of these taxa is necessary. Little is known of Amuletta (see chapter 3), so

the function of natasomal flexibility in this genus cannot be guessed. In Storthyngura, the natasomal pereonites vary from a condition where the sutures are visible, but not flexible, to a totally fused condition.

For dorsal fusion of the natasomites, several patterns emerge. All the ilyarachnoid eurycopids have the tergite of pereonites 6 and 7 fused medially, an important factor in estimating their relationships. The eurycopids Belonectes, Disconectes, and Tytthocope have pereonites 5 and 6 fused dorsally. Lastly, complete fusion of all the natasomal pereonites occurs in Baeonectes, Acanthocope, and the Syneurycopinae. This last character state does not indicate real shared ancestry between the last three taxa. Its inclusion in the phylogenetic analyses 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 do not provide information on the transition from the partially fused to the completely fused natasome. Therefore the completely fused state is not used in the analysis.

COMPARATIVE SIZES OF THE NATASOMAL PEREONITES

A great variety in the sizes of pereonites 5 - 7 is seen in the munnopsoids, with any one of these 3 segments dominating the natasome, depending on the taxon. The primitive state, all equal sized pereonites, is found in few taxa, such as 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

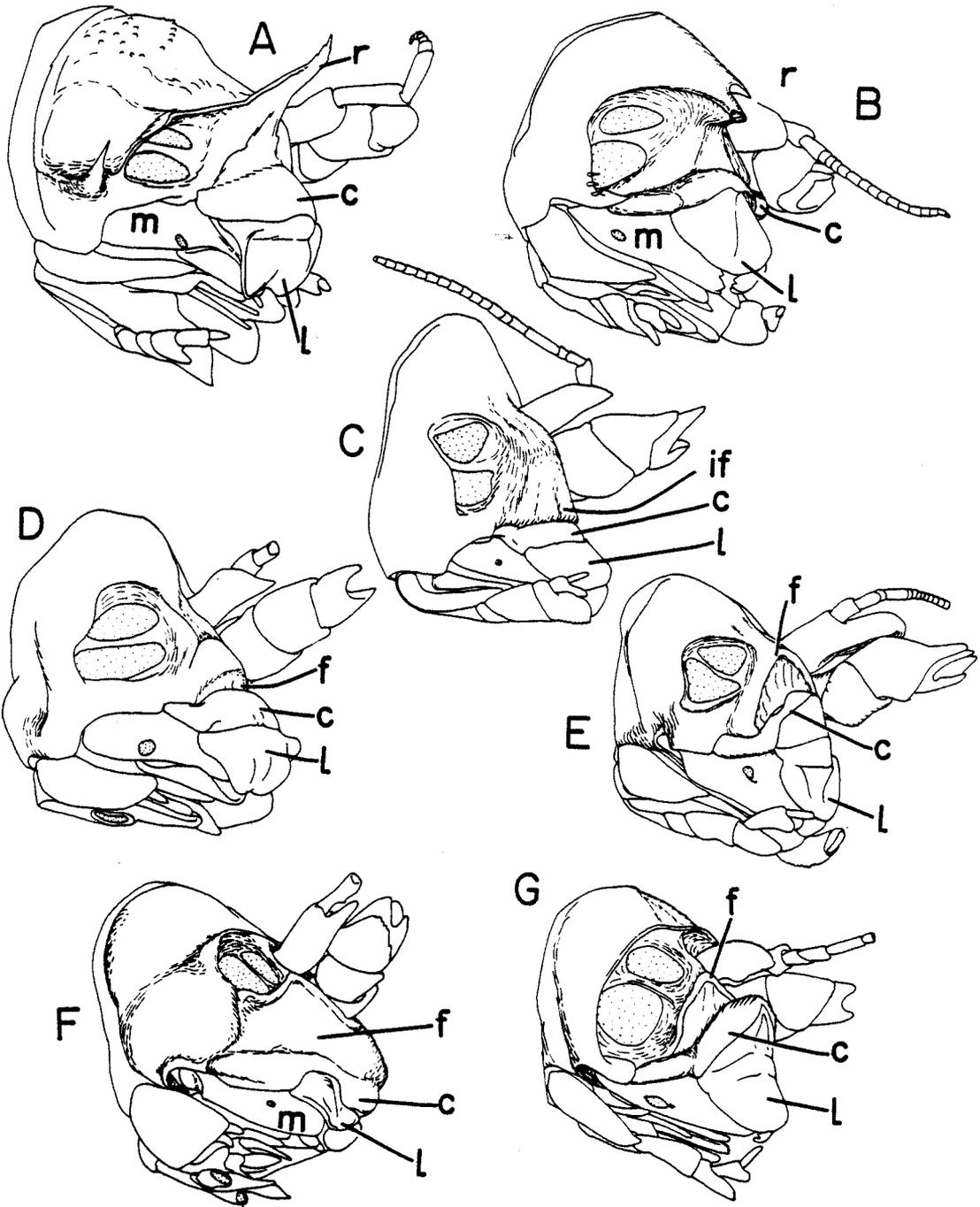
pereonite is large and pereonite 5 becomes compressed dorsally along the body axis to a narrow band. Unfortunately, the inclusion of this character state into the analyses only worsens the homoplasy level, possibly indicating multiple derivations. An alternative hypothesis is that many of the munnopsoids are derived from an ancestor with an enlarged pereonite 7, and subsequently the size of the pereonite 7 was reduced in many of the taxa independently. This latter hypothesis would exclude Munnopsurus and Munnicope from the taxon containing most of the munnopsoids. 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 state of the seventh pereonite that unites the ilyarachnoid eurycopids is extreme reduction in size. In two genera, Lipomera and Mimocopelates, the last pereonite is rudimentary, and in the other three ilyarachnoid eurycopids, it is only a thin band fused to the anterior segment. Tytthocope also has a highly 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.

MIDGUT

In all outgroups and most of the munnopsoids, the midgut is straight, or nearly so. A bent or coiled gut is a useful synapomorphy of the subgenera of Lipomera, and is included here as a justification for using these three subgenera as a single group in the analysis.

Figure 5.1. Cephalons of an acanthaspidiid and several munnopsoids 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, and 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.



CLYPEUS

The clypeus on the cephalic frons displays a variety of modifications, although all forms may be classified in two states. The first is a dorsomedially rounded clypeus that slopes upward posteriorly to its attachment point on the frons of the cephalon. This type of clypeus is found in the Acanthaspidiidae, and in most of the munnopsoid taxa (fig. 5.1A-D,F). It is the plesiomorphic state. The second type is a "pushed-in" clypeus where it is dorsomedially angular, and the medial margin in lateral view slopes downward, often abruptly, to its insertion into the frons. This apomorphy is seen in the ilyarachnoid eurycopids (fig. 5.1G), and in Munnopsurus (fig. 5.1E) and Acanthocope. Within the first taxon, there are two substates: a steep slope in lateral view from the anterior vertex of the clypeus to its frons insertion (Coperonus, Hapsidohedra, and Mimocopelates), and a gradual, sometimes almost level slope (Lipomera and Lionectes). It is not certain which of these two substates is ancestral.

ROSTRUM

An anterior projection of the cephalon, the rostrum, is ancestral in the Janiroidea and is seen in somewhat modified form in the Acanthaspidiidae (fig. 5.1A). Most munnopsoids have lost the rostrum, and have a nearly nonprotruding dorsal vertex of the cephalon. In some genera, Munneurycope (fig. 5.1C-G) 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. 5.1B), Tyththocope, Disconectes, Belonectes, and

Baeonectes (Wilson and Hessler, 1980, 1981; Wilson, 1982), although its form often deviates considerably from the primitive projection seen outside the munnopsoids. In some of these taxa the rostrum becomes very broad and rounded, and does not project from the frons. Because a narrow, projecting rostrum and a broad, rounded rostrum are seen within single genera (Eurycope, Disconectes), the rostrate genera are scored as having the plesiomorphic state of the rostrum.

FRONTAL ARCH

One of the surprises of this work was the realization that some of the munnopsoids have developed a new structure on the cephalic frons, the frontal arch. This structure forms the basis for much of the variety in the frons seen in the munnopsoids. Eurycope, and the other rostrate genera show no evidence of having had a frontal arch. Eurycope often does have a pair of ridges running vertically from the clypeus to the rostrum (fig. 5.1B), but these same ridges are seen in the Janiridae. An incipient frontal arch is seen on the smoothly convoluted frons of Paramunnopsis: the region just above the clypeus is flattened and arc-shaped (fig. 5.1C). In Munneurycope (fig. 5.1D) and Storothyngura, a fully developed frontal arch is seen, where the arch is a distinct projection from the ventral part of the frons. In addition, these two genera also retain the inverted "V" ridges seen in Eurycope, demonstrating that the ridges in the latter genus are not a modified form of the frontal arch. In other genera, the arch shows a variety of forms, often being massive in some, such as Munnopsurus (fig. 5.1E), Acanthocope, and Ilyarachna (fig. 5.1F). Within the

ilyarachnoid eurycopids (fig. 5.1G), the frontal arch 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. The character states described here form a linear transformation series: no frontal arch, incipient frontal arch, well-developed frontal arch (in a variety of shapes), to a reduced and flattened frontal arch.

MANDIBLE

At first, the mandible appeared to offer a variety of useful character states in its various subsections. Preliminary phylogenetic analyses showed, however, that more often than not their use introduced a great deal of homoplasy. For example, an enlarged, rounded, and sclerotized molar process seemed useful because most of the ilyarachnoid eurycopids had this apomorphy. On the other hand, this apomorphy 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 possibly useful character state was a reduced molar process, although each taxon that might have been scored for such a reduction had a unique shape to the reduced molar process, indicating again it happened independently in each case.

One apomorphy used in the analysis was the presence of an enlarged, rounded, heavily sclerotized incisor process. In the taxa used in the analysis, this is found only in Ilyarachna. 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 second apomorphy used in the analysis was the absence of the mandibular palp, scored for Amuletta. The palp is also missing in the derived ilyarachnids Aspidarachna and Echinozone, which were not used in this analysis. In chapter 3, it was concluded that the ancestral ilyarachnid had a mandibular palp. Its absence in both some of the Ilyarachnidae and Amuletta may indicate a propensity for this loss if a common ancestry for both is accepted.

AMBULATORY PEREPODS

Pereopods II through IV can be considered the ambulatory pereopods, with pereopod I performing a manipulative function, and pereopods V-VII being used for swimming (or burrowing). A primitive condition for the pereopods would be all of them more or less the same length or perhaps getting 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 munnopsoids are collected with their fragile ambulatory pereopods broken off, enough literature records of these pereopods exist to use their lengths in the analysis.

The ambulatory pereopods have two useful apomorphies. First, bases III-IV in some taxa are shorter than basis II. 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. Although these apomorphies are undoubtedly functionally related, their distribution among the munnopsoids indicates they were attained independently.

NATATORY PEREPODS V-VII

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

The lengths of the bases of pereopods V-VII in comparison to the more anterior bases requires less of the analogy assumption. In the outgroup, Acanthaspidiidae, all the bases of the pereopods are near the same length. This is also seen in many of the munnopsoids. In the others the bases V-VII are distinctly shorter than the anterior bases. Not all the ilyarachnoid eurycopids agree on this character:

Coperonus and Mimocopelates have the same shortened bases seen in Disconectes and Belonectes. Because character state reversals are possible in the lengths of the bases, this feature was interpreted in the phylogenetic analysis using the Wagner parsimony method.

Mimocopelates has an useful autapomorphy that justifies retaining M. anchibraziliensis in the genus: an elongated merus of pereopod V. For the same reasons as the previous characters, the Wagner parsimony method was used.

The pereopodal dactyli show several character states useful for the munnopsoid phylogeny. In the outgroups and many of the genera of the munnopsoids, the dactyli of pereopods V-VII are fairly large, although generally shorter than the propodi. A defining apomorphy of the Munnopsidae is the complete absence of the dactyli on the natatory pereopods. Three genera of the ilyarachnoid eurycopids show a different apomorphy: the dactylus of pereopod V is reduced to a tiny lobe, and the more posterior pereopods have large dactyli.

Two taxa considered here lack pereopods VII: Mimocopelates and Lipomera. Mimocopelates is also characterized by a reduced pereopod VI, indicating a trend toward greater reliance on the fifth pereopod for swimming. The less modified species of Lipomera have subequal pereopods V and VI, although the more derived Paralipomera species also have a reduced pereopod VI. Because the subgenera of Lipomera are considered a single taxon in this analysis, they are 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 munnopsoids, the last pereopod is near the same size, both in length and in breadth of the broadened carpi and propodi, to pereopod VI. Tytthocope 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 the swimming setae are long, unlike the diminutive last pereopod of Tytthocope. Therefore, only Tytthocope is scored as having a reduced but natatory pereopod VII.

An unrelated reduction of the last pereopod is seen in the ilyarachnoid eurycopids and in the Ilyarachnidae. They both have reduced last pereopods in which the paddles have become narrow and most of the plumose setae are lost. This derived state resembles a walking leg, although the presence of plumose setae betrays its natatory ancestry. Because this character is incompatible with many others used in the phylogenetic analysis, it is presumed to have been derived independently in the Ilyarachnidae and in the ilyarachnoid eurycopids. As mentioned above, this latter taxon takes the reduction one step further in two of the genera: the last pereopod is degenerate or absent.

CLEFT IN THE TIP OF FEMALE PLEOPOD II

A number of munnopsoids, including the ilyarachnoid eurycopids, have a distinct notch or cleft in the tip of the female opercular pleopod. The polarity of this character is uncertain. In some genera the notch is large and seems to wrap the pleopod around the preanal ridge, thus leaving the anus exposed, just as seen in the Janiridae. In the Acanthaspidiidae and the Janirellidae, the more immediate outgroups, the anus is covered by an extension of the female pleopod II, much like the form seen in a number of the munnopsoids, notably Eurycope and Munnopsurus. In many munnopsoids, the anus is covered, but a distinct notch is present indicating the two sides of the cleft have grown together over the anus. These are scored as having the cleft. In some of the ilyarachnoid eurycopids, however, the cleft is fused totally giving the condition seen in, say, Munnopsurus, but the cleft is present in congeners or a closely related genus. Acanthocope has a small round female operculum with no evidence of the cleft, although the anus is completely exposed. The absence of the cleft in this genus is regarded as having had a different derivation from that of other munnopsoids which lack clefts.

These character states are all related to whether the anus is covered or not. A preliminary examination of these two states of the female pleopod form reveals two possible routes that a lineage could develop a covered anus. The first was described above: the fusion of the cleft in pleopod II of the female. A second route is the elongation of the distal tip of the pleopod, so that the cleft becomes convex rather than concave, thereby covering the anus. In some

groups, it is impossible to decide whether the first or second route was followed to develop the covered anus. In the ilyarachnoid eurycopids, however, a choice was possible, as discussed in the previous paragraph. This problem parallels the use of opercular or non-opercular pleopods to help define the taxa of the Asellota which was discussed in the previous chapter.

PLEOPODS III-IV

The setation of pleopod III, particularly the presence of supernumary plumose setae on the exopod and endopod, is important in establishing the sister group relationship between the Acanthaspidiidae and the munnopsoids. Within the munnopsoids, the variety in this setation can be applied toward discriminating relationships. All of the pleopod setation characters are reduction characters, and therefore must be weighted less than uniquely derived apomorphies.

The primitive form of the pleopod III within the munnopsoids is one which has many plumose setae on both the endopod and the exopod. In many of the munnopsoid taxa, the endopod has only three plumose setae, which must be considered an apomorphy within the group but is a plesiomorphy at the level of the Janiroidea. An explanation of this might be that the endopod setation has unexpressed polymorphisms that may or may not appear, depending on their genetic and developmental environment within a species. If this is the case, the extra plumose setae are still useful for defining the munnopsoid ancestry, but their

loss within the taxon may occur several times in the overall phylogeny.

The loss of plumose setae on the exopod of pleopod III shows three states, each of which apparently appears independently. This interpretation was arrived at by trying a number of different transformation series in the phylogenetic analysis, and picking the one that yielded the fewest steps in the overall tree. Two or three plumose setae on the exopod defines the ilyarachnoid eurycopids, but is also seen in Tytthocope. A single seta occurs on the exopod of Baeonectes, and a number of the genera, including Eurycope, have no plumose setae at all.

The exopod of pleopod IV also has plumose setae in many of the munnopsoids. The outgroups have exopods with many plumose setae, indicating this is the plesiomorphic state. The presence of only a single seta on the exopod helps define the ilyarachnoid eurycopids, but this state is seen in a number of the other taxa. A few taxa, Acanthocope, Bellibos, and Paramunnopsis, lack plumose setae on the exopod. The most parsimonious trees result from a linear transformation series: many setae to one seta to none.

THE UROPODS

The munnopsoids show a great variety in the form of the uropods, and it was originally hoped these could provide some characters for the analysis. Unfortunately, the uropodal form is unique in many of the taxa, and attempts to score general characters were fraught with many assumptions. Additionally, when some fairly simply defined

characters, such as whether the protopod is broad or tubular, are added to the analysis, they often add nearly as many steps as taxa scored with the apomorphic state. The uropod varies too much at the level of the munnopsoids to be useful for this analysis.

At the systematic level of the Ilyarachnoid eurycopids, the uropod shows a few trends. The protopod is least modified in Coperonus, being large and robust, with a medial projection bearing unequally bifid setae. This is similar to the form seen in Eurycope or Amuletta. In Mimocopelates, the uropod becomes reduced, but still retains the protopodal medial projection in one of the species, M. longipes. In the three remaining genera, the protopod takes a different direction, that of lengthening and becoming flattened. In Lionectes, the protopod is still fairly small but round and flat. Its endopod is flattened somewhat as well. Hapsidohedra continues this trend with a large, leaf-like protopod, surprisingly similar to the uropod of the Ilyarachnidae. Lipomera has the most unusual uropod. Although it is superficially similar to that of Hapsidohedra in its broadest form in subgenera Lipomera and Paralipomera, setal homologies show that the broad leaf-like structure is made of a fusion of the flattened endopod and the protopod (see chapter 2 in the remarks after the description of L. (Tetracope) curvintestina).

RESULTS OF THE CHARACTER ANALYSES

The following is a list of characters and their states derived from the above character analyses that is used for the munnopsoid-level phylogenetic analysis. 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). Following the character states, the parsimony method (C = Camin-Sokal; W = Wagner) and the character weight (Wt = 1 or 2) used in the final phylogenetic analysis is indicated parenthetically. See the methods section of this chapter for the weighting rationale. The distribution of the character states is shown in table 5.1, and the actual data used in the analysis with factored multistate characters is given in table 5.2.

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 or absent (1). (C, Wt = 1)
4. Midgut straight (0) or midgut with distinct bend or loop (1).
(C, Wt = 2)
5. Clypeus dorsally rounded (0) or dorsally high and angular (1).
(C, Wt = 2)
6. Rostrum present (0) or absent (1). (C, Wt = 2)

7. No frontal arch (0), incipient frontal arch (1), distinct 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). (C, Wt = 2)
12. Pereopods V-VII bases: near same length of anterior bases (0), or shorter than anterior bases (1). (W, Wt = 1)
13. Pereopod V merus short (0) or long (1). (W, Wt = 2)
14. Pereopod V-VII dactyli long (0), or rudimentary/absent (1), or only pereopod V dactylus rudimentary absent (2). (C, Wt = 2)
15. Pereopod VI near same size as pereopod V (0) or smaller (1). (C, Wt = 1)
16. 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)

17. 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)
18. 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)
19. Pleopod III: endopod distal tip with more than 3 plumose setae (0), or 3 or less plumose setae (1). (C, Wt = 1)
20. Pleopod IV: exopod with many plumose setae (0), 1 plumose seta (1), or no plumose setae (2). (C, Wt = 1)

Characters added for analysis of the ilyarachnoid eurycopid within-group relationships.

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

Table 5.1. Distribution of character states in selected munnopsoid taxa. See text for a description of the characters. Characters 21 and 22 were evaluated for only the Ilyarachnoid eurycopid genera and Munnopsurus. In Parsimony Method, "C" means Camin-Sokal method and "W" means Wagner method.

CHARACTERS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
PARSIMONY METHOD	C	C	C	C	C	C	WC	C	C	WC	C	W	W	C	C	C	W	C	C	C	C	W	
<u>Acanthaspidiidae</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-
<u>Acanthocope</u>	0	0	0	0	1	1	2	0	0	0	0	1	0	0	0	0	0	0	1	2	-	-	
<u>Amuletta</u>	0	0	0	0	0	1	2	0	1	1	?	0	0	0	0	0	1	0	0	0	-	-	
<u>Baeonectes</u>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2	1	1	-	-	
<u>Bellibos</u>	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	1	0	1	2	-	-	
<u>Belonectes</u>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	1	1	-	-	
<u>Betamorpha</u>	0	0	0	0	0	1	2	0	0	0	1	0	0	0	0	0	1	0	0	0	-	-	
<u>Coperonus</u>	0	0	1	0	1	1	2	0	0	0	0	1	0	2	0	2	1	1	1	1	1	0	
<u>Disconectes</u>	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	1	1	-	-	
<u>Eurycope</u>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	3	1	1	-	-	
<u>Hapsidohedra</u>	0	1	1	0	1	1	3	0	0	0	?	0	0	0	0	2	1	1	1	1	0	2	
<u>Ilyarachna</u>	0	0	0	0	0	1	2	1	0	2	1	0	0	0	0	2	1	0	0	0	-	-	
<u>Lionectes</u>	0	1	1	0	1	1	3	0	0	0	0	0	0	2	0	2	2	1	1	1	0	2	
<u>Lipomera</u>	0	1	1	1	1	1	3	0	0	0	0	0	0	0	0	3	1	1	1	1	0	2	
<u>Minocopelates</u>	0	1	1	0	1	1	2	0	0	0	1	1	1	2	1	3	1	1	1	1	1	1	
<u>Munneurycope</u>	0	0	0	0	0	1	2	0	0	0	0	1	0	0	0	0	0	3	1	1	-	-	
<u>Munnopsurus</u>	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
<u>Paramunnopsis</u>	0	0	0	0	0	1	1	0	0	1	1	1	0	1	0	0	0	0	1	2	-	-	
<u>Storothyngura</u>	0	0	0	0	0	1	2	0	0	1	1	0	0	0	0	0	1	0	0	0	-	-	
<u>Tyththocope</u>	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	-	-	

Table 5.2. Character-Taxon data matrix used in phylogenetic analysis. Multistate characters have been factored to binary states.

CHARACTER	1	2	3	4	5	6	7	7	7	8	9	10	10	11	12	13	14	14	15	16	16	16	17	17	18	18	18	19	20	20		
PARSIMONY METHOD	C	C	C	C	C	C	W	C	C	C	C	W	C	C	W	W	C	C	C	C	C	C	W	C	C	C	C	C	C	C		
WEIGHTS	2	2	1	2	2	2	2	2	2	2	2	2	2	2	1	2	2	2	1	1	1	1	1	2	1	1	1	1	1	1		
ANCESTOR	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0		
<u>Acanthocope</u>	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1		
<u>Amuletta</u>	0	0	0	0	0	1	1	1	0	0	1	1	0	?	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0		
<u>Baeonectes</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	
<u>Bellibos</u>	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	
<u>Belonectes</u>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<u>Betamorpha</u>	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
<u>Coperonus</u>	0	0	1	0	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	1	1	0
<u>Disconectes</u>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<u>Eurycope</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
<u>Hapsidohedra</u>	0	1	1	0	1	1	1	1	1	0	0	0	0	?	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	1	0	
<u>Ilyarachna</u>	0	0	0	0	0	1	1	1	0	1	0	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
<u>Lionectes</u>	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	1	1	0	0	1	1	0	
<u>Lipometra</u>	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	
<u>Mimocopelates</u>	0	1	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	1	1	0	1	1	1	0	1	0	0	1	1	0		
<u>Munneurycope</u>	0	0	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	0	
<u>Munnopsurus</u>	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<u>Paramunnopsis</u>	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	
<u>Storothyngura</u>	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
<u>Tytthocope</u>	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	

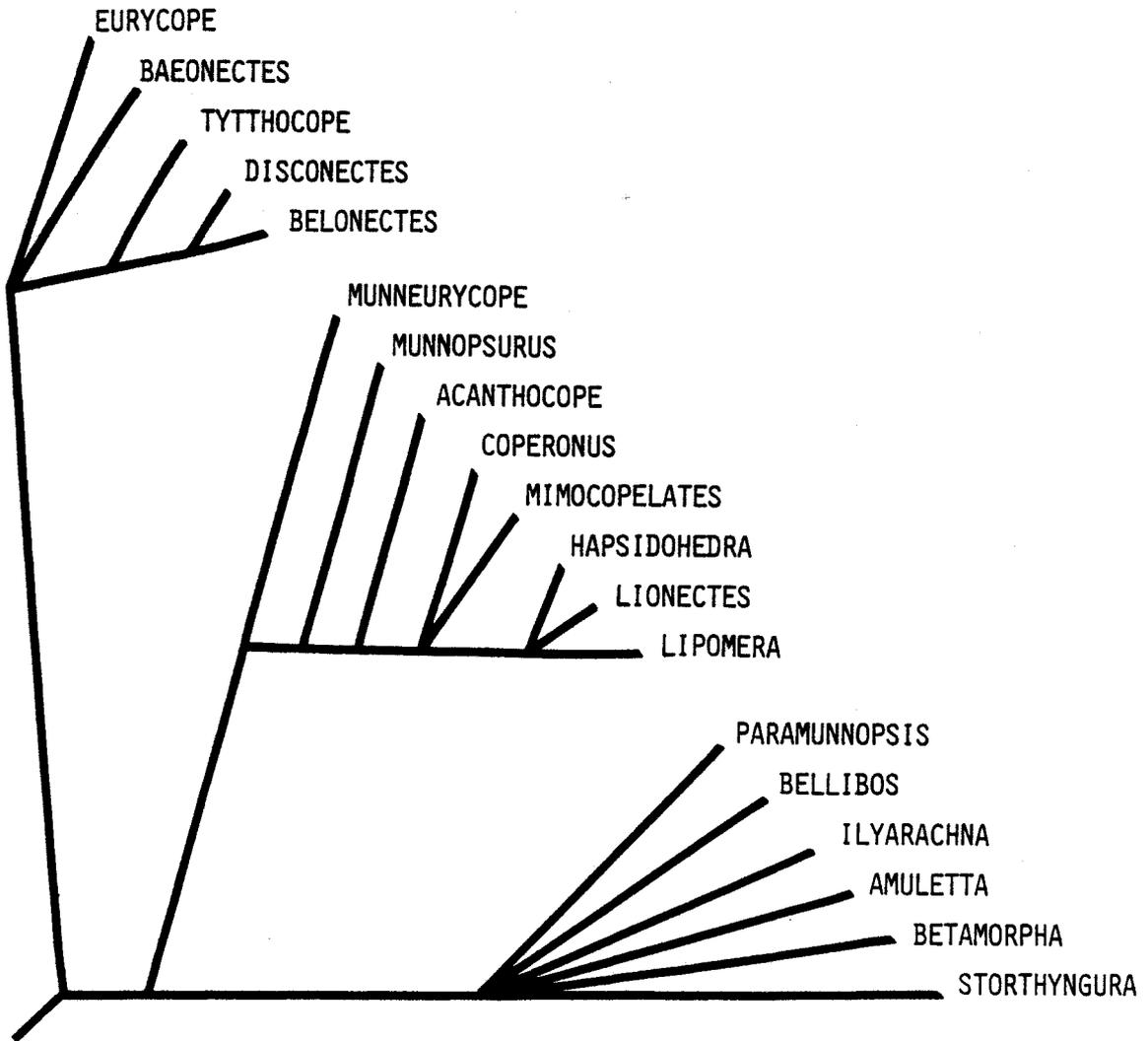
RESULTS OF THE PHYLOGENETIC ANALYSIS

THE ESTIMATED PHYLOGENY

Figure 5.2 shows the general form of the most parsimonious trees that can be inferred from the character states developed above. It contains several multifurcations at points where a number of equally parsimonious topologies resulted. The homoplasy level is quite high, approximately 73% for the characters used or approximately 22 unweighted steps more than the minimum. As in the phylogenetic estimate of the Janiroidea, the apomorphies are not shown on the tree because there is often no unique position for their derivation. Appendix 4 gives the output for a number of different trees generated by the program ITERMIX.

The form of the general tree implies three large taxa, although the some of the major branching nodes are based on multiply derived characters. Eurycope and the genera with which it clusters lack the derived characters seen in the remainder of the munnopsoid taxa: they all have character states such as retaining a rostrum and not having a definable frontal arch (see table 5.1). These genera are primarily defined by character states that appear elsewhere on the tree, such as the pleopodal setation characters. The relationships within the group containing Eurycope may be subject to reinterpretation with further analysis even though Disconectes, Belonectes, and Tytthocope may form a natural taxon with a defining apomorphy (dorsally fused pereonites 5 and 6).

Figure 5.2. Estimated phylogeny of selected munnopsoid genera.



In a single case, a taxon may be incorrectly placed. The sister group of the Ilyarachnoid eurycopids is shown to be Acanthocope. Nevertheless, evidence from the variety of morphologies within the poorly defined genus Storthyngura indicates these two genera share a common ancestry. A comparison of Storthyngura brachycephala Birstein, 1957, and Acanthocope curticauda Birstein, 1970, shows that taxa classified as Storthyngura have the enlarged muscular cephalon that is characteristic of Acanthocope. Because Storthyngura shares apomorphies with the Amuletta-Betamorpha complex of genera (characters 10 & 11: short bases III-IV and elongate pereopods III-IV), the absence of these critical apomorphies in Acanthocope may be due to a secondary loss. A weakness in this analysis is that the full range of character states in many of the genera are not known owing to poor or incomplete descriptions.

DISCUSSION AND PROPOSALS FOR A REVISED CLASSIFICATION

The estimated phylogeny shows that the taxa in the family Eurycopidae are not closely associated with one another. In fact, taxa such as Storthyngura and Betamorpha have more in common with the Ilyarachnidae than they do with Eurycope at this phylogenetic level. Thus the previous classification of the munnopsoids as three separate families is not reflected in the estimated phylogeny. Because all munnopsoids have characters that unite them, I propose that the family Munnopsidae sensu lato of Sars, 1899, be reestablished, with the existing family groups demoted to subfamilies, except for the subfamilies of the Eurycopidae which will retain their current rank. A new classification for the Munnopsidae is shown in table 5.3. The

defining apomorphies of the Munnopsidae are: pereonites 5-7 enlarged, muscular, broadly joined, with their ventral nerve cord ganglia fused into a single mass (Hult, 1941); pereopods V-VII with many long, fully plumose setae and their carpi and propodi broadened and paddle-like; dactylar claws that enclose the distal sensillae in a hollow between the anterior and posterior claws; and the rami of pleopod III with many distal plumose setae.

The ilyarachnoid eurycopids remain associated in all versions of the phylogenetic estimate (see appendix 4). Therefore, they may be recognized as a distinct subfamily of the Munnopsidae. Their defining apomorphies are: dorsal fusion of pereonites 6 and 7, reduction of pereonite 7, and loss or reduction of pereopod VII. I propose the subfamily name Lipomerinae for this new taxon, derived from the available family-level name Lipomeridae Tattersall, 1905a. With the placement of the Acanthocopinae near Storthyngura (discussed above), the closest sister group for the Lipomerinae is Munnopsurus. If the taxa of the Lipomerinae are analysed using the added uropodal characters (table 5.1) with Munnopsurus as the outgroup to root the tree, the subfamily resolves into two sub-subfamilial groups (fig. 5.3). One group contains Coperonus and Mimocopelates, and the other shows unresolved relationships between the genera Hapsidohedra, Lipomera, and Lionectes.

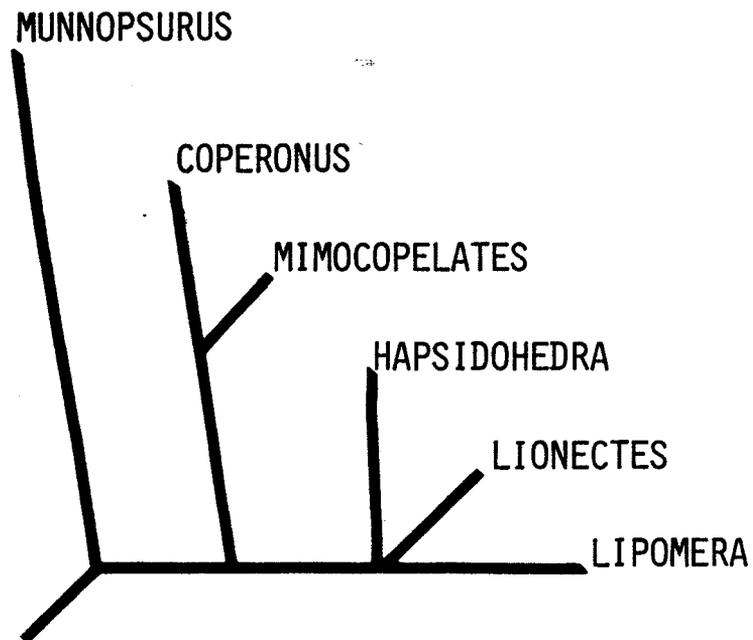


Figure 5.3. An estimated phylogeny of the Lipomerinae (ilyarachnoid eurycopids). The genus Munnopsurus is included as an outgroup.

Table 5.3. A revised classification of the Munnopsoid Asellota and the Ilyarachnoid Eurycopidae. The sequencing convention for displaying phylogenetic information in the classification (Wiley, 1981) is not used for the genera; after the type-genus, they are in alphabetical order.

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 Kussakin, 1967

Family Munnopsidae Sars, 1869

Subfamily Munnopsinae Hansen, 1916 sedis mutabilis

Genera included:

Munnopsis Sars, 1861

Acanthomunnopsis Schultz, 1978

Munnopsoides Tattersall, 1905b

Paramunnopsis Hansen, 1916

Pseudomunnopsis Hansen, 1916

Subfamily Acanthocopinae Wolff, 1962 sedis mutabilis

Genera included:

Acanthocope Beddard, 1885

(? Storthyngura Vanhöffen, 1914)

Subfamily Bathyopsurinae Wolff, 1962 sedis mutabilis

Genera included:

Bathyopsurus Nordenstam, 1955

Paropsurus Wolff, 1962

Subfamily Eurycopinae Hansen, 1916 sedis mutabilis

Genera included:

Eurycope Sars, 1864

Baeonectes Wilson, 1983

Belonectes Wilson and Hessler, 1981

Disconectes Wilson and Hessler, 1981

Tytthocope Wilson and Hessler, 1981

Subfamily Ilyarachninae Hansen, 1916 sedis mutabilis

Genera included:

Ilyarachna Sars, 1864

Aspidarachna Sars, 1899

Bathybadistes Hessler and Thistle, 1975

Echinozone Sars, 1899

Pseudarachna Sars, 1899

Table 5.3, continued. A revised classification of the Munnopsoid Asellota and the Ilyarachnoid Eurycopidae.

Subfamily Lipomerinae Tattersall, 1905a sedis mutabilis

Genera included:

Lipomera Tattersall, 1905a

Coperonus n. gen.

Hapsidohedra n. gen.

Lionectes n. gen.

Mimocopelates n. gen.

Subfamily Syneurycopinae Wolff, 1962 sedis mutabilis

Genera included:

Syneurycope Hansen, 1916

Bellibos Haugness and Hessler, 1979

Subfamily incertae sedis

Genera included:

Amuletta Wilson and Thistle, 1985

Betamorpha Hessler and Thistle, 1975

Microprotus Richardson, 1909

Munneurycope Stephensen, 1913

Munnopsurus Richardson, 1912

Munnicope Menzies and George, 1972

(? Storthyngura Vanhøffen, 1914)

The estimated phylogeny of the Munnopsidae sensu lato forces a reconsideration of the composition of the subfamily Eurycopinae. Wolff (1962) places the following genera in this subfamily: Eurycope, Lipomera, Munneurycope, Munnopsurus, and Storthyngura. Lipomera is here assigned to the Lipomerinae Tattersall, 1905a. Storthyngura may possibly be assigned to the Acanthocopinae. The remaining genera are each quite distinctive and therefore difficult to place. A temporary solution is to place the four genera which cluster with Eurycope in the Eurycopinae, and assign all the remaining genera to subfamily incertae sedis.

CONCLUSIONS

The failure to resolve the relationships of the subfamilies of the Munnopsidae sensu lato is not surprising in view of the diversity of the included taxa. Such a variety of munnopsids could not arise in a short period of time. It was shown in chapter 4 that the Munnopsidae branch off from the other deep-sea isopods within only a few branching nodes of their origin. If there is any truth to the hypothesis proposed in chapter 4, that the deep-sea isopods arose from a single ancestor in the mid Jurassic, then the Munnopsidae may have had a long evolutionary history with plenty of time to invade most of the niches available to epibenthic Crustacea that swim.

Proposing a family as large as the Munnopsidae with its 7+ subfamilies and 30+ genera creates a difficulty for the remainder of the Janiroidea: the family-level taxa no longer seem coordinate in the variety of morphologies they subsume. All the other families have distinctive characters by which genera can easily be allocated to the proper family. Moreover, most of the other families have a manageable number of genera (although many of the genera, such as Haploniscus and Ischnomesus would benefit from a revision).

The 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 has merits: known monophyletic groups of families in the Janiroidea (see chapter 4) could be recognized by a

sub-superfamily hierarchical level. Unfortunately, the relationships between many of the deep-sea isopod families are still poorly known, so such a classification cannot be attempted at this time.

The goal of this thesis, to establish the systematic relationships of the Ilyarachnoid eurycopids, has been achieved. These isopods belong in a monophyletic subfamily called the Lipomerinae, within the family Munnopsidae. The sister group of the Lipomerinae is probably the genus Munnopsurus, although the unresolved relationships of the munnopsid subfamilies make this less certain. The resemblance of the Lipomerinae to the Ilyarachninae is due to convergent evolution in some of their characters, not to proximate common ancestry.

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APPENDIX 1

A GLOSSARY OF MORPHOLOGICAL TERMS

This glossary contains definitions of morphological terms used throughout the text. The definitions given are specific to the study of isopod taxonomy, with an emphasis on the asellote superfamily Janiroidea.

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

Ambulosome. The part of the thorax of munnopsoid isopods that bears the walking legs. It consists of pereonites 1-4. (See fig. 1.4)

Ambulosomite. A body segment of the ambulosome. (See fig. 1.4)

Annulus (plural annuli). A distal segment of either the antenna or antennula, generally tubular in form.

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 fig. 1.4)

Antennula (synonyms first antenna, antennule). The first paired cephalic appendage. In munnopsoids, 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 fig. 1.4)

Appendix Masculina. An alternative name for a stylet-like copulatory structure on the male pleopod II. This structure is not homologous to similarly named structures found in non-Isopod Malacostraca.

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 most deep-sea samples, the developing embryos are 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 and had not molted to a preparatory stage.

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

Carpus. 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. 2.1)

Cephalon. The head, or anteriormost body unit. In isopods, the cephalon bears the eyes, mouth, antennulae, antennae, and 4 pairs of mouthparts (mandibles, maxillulae, maxillae, and maxillipeds). (See fig. 1.4, 2.1)

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

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

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

Cleaning Setae. The unusual multisetulate setae found on the distal segment of the mandibular palp that are used to clean the antennae or antennulae.

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 fig. 2.1)

Condyle. A heavily sclerotized projection of the mandible's dorsal surface that articulates with the cephalon in the clypeal fossa. (See fig. 2.1)

Copulatory Male. A fully adult male in the asellote isopod superfamily Janiroidea identified by having a sperm tube of the second pleopod's stylet that is open at its sharp distal tip. In some specimens at this terminal stage, the vas deferens connecting to the penile papilla is visible through the cuticle.

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

Cusperate. 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, but 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. (See fig. 4.4, 4.8)

Dactylus. The seventh or distal segment of a thoracic appendage, bearing one or more distal claws. See pereopod.

Denticle. A short, pointed, tooth-like 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 first pleopod.

Endopod. 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 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. Laterally directed lobe (exite) of the basal segment (coxa) of the maxilliped.

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

Facies. An appearance or similarity, as in Ilyarachnoid Facies.

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 munnopsoids, 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. Leaf-like.

Foregut (synonym Stomodeum). The crop-like anterior portion of the gut that is lined with cuticle and has openings to the lateral digestive caeca and the posterior midgut.

Fossa. A ventral trough in the clypeus into which the mandible's condyle articulates. (See fig. 2.1)

Frons. The anterior part of the cephalon bearing the clypeus and lying between the antennulae and antennae and below the rostrum or vertex. (See fig. 2.1)

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 fig. 2.1)

Geniculate. Knee-like, 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.

Gravid. Bearing fully formed ova or embryos in the ovary. This is the condition of fully mature preparatory females.

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.

Hindgut (synonym Proctodeum). The posterior portion of the gut connected to the anus and lined with cuticle.

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). 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 first pleopods' dorsal cuticle. They form a seat for the medial edge of the second pleopods, allowing both pairs of pleopods to function together as an operculum, or during mating.

Manca. One of the first three stages or instars of an isopod's postmarsupial life cycle, wherein the seventh pereopod is absent or rudimentary. In certain neotenic Asellota this condition is retained in the adult, in which the manca stage cannot be identified by these criteria.

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 (Pers. I-VI in the munnopsoids).

Maxilla (plural Maxillae, synonym Second Maxilla). The third paired mouth part 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 5 segments (ischium, merus, carpus, propodus, dactylus), and epipod attached laterally to the coxa.

Maxillula (plural Maxillulae, synonyms Maxillule, Second 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, tooth-like setae; and a smaller inner lobe with only small setae.

Merus (plural Meri). The fourth segment of a thoracic appendage. See pereopod.

Midgut. The central region of the crustacean gut. Unlike the fore and hind gut, this region lacks cuticle.

Molar Process. A medial process of the mandible. Primitively it has a broad, distal, triturating surface with circumgnathal denticles, a posterior row of broad, setulate setae, and sensory pores on the distal surface.

Natapod. A natatory pereopod of a munnopsoid janiroidean, the fifth through seventh pereopods. (See fig. 1.4)

Natasome. The often posteriorly streamlined body section of a munnopsoid janiroidean consisting of the following body segments: heavily muscularized pereonites 5-7, and the pleotelson. (See fig. 1.4)

Natasomite. A pereonite of the natasome. (See fig. 1.4)

Oopore. A paired female opening in the ventral cuticle of pereonite 5, through which the fertilized ova are released via the oviduct into the marsupium.

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 Janiroidean Isopods.

Oviduct. An often complex female organ connecting the ovaries to the oopores. In the Asellota, it consists of the following functional subsections: outer tissues surrounding internal parts; spermatheca, which may or may not be covered with cuticle; and cuticular organ, an often complex cuticular tube.

Ovigerous. Bearing developing embryos in the marsupium. (See also gravid).

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. It consists of two pairs of lobes, a broad lamellar outer pair with hair-like setae on their inner margins and a thick inner pair covered with many hair-like setae.

Paucisetose. Having few setae.

Pedestal Seta. A spine-like 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. 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 fig. 1.4)

Pereonite. A segment of the pereon. (See fig. 1.4)

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 fig. 1.4)

Pleotelson (synonym Pleon). 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 a terminal segment bearing the anus, the telson. Primitively, there are six pleonites, the anterior five of which bear ventral pleopods, and the sixth bearing the uropods. In the Janiroidea, only the first pleonite is expressed as a free segment. (See fig. 1.4)

Pleonite. A segment of the pleotelson. (See fig. 1.4)

Pleopod. One of the first five paired, biramous, ventral limbs of the pleotelson. In unmodified form, it consists of a basal segment, the protopod, and two distal rami, 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 a 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 it is sometimes called the branchial cavity.

Plumose seta. A feather-like 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 munnopsoids, this ridge becomes very large.

Preparatory Female. An adult female that has developing oostegites.

Protopod. The basal segment of the pleopods and the uropods. It consists of the fused coxa and basis of the crustacean limb.

Propodus. 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 on the medial margin of the maxilliped's basal endite that have bulbous recurved and denticulate tips. They couple with their paired counterparts so that both maxillipeds can act as a single unit.

Recurved. Curved back on itself.

Rostrum. A projection of the cephalic frons that may also include the dorsal surface of the cephalon.

Sclerotized. With thick and sometimes calcified cuticle.

Sensilla. 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, 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 tooth-like denticles.

Seta (plural Setae). A cuticular process that is clearly articulated with the basal cuticle. This structure comes in many forms. There is a unfortunate tendency in the literature for some authors to call heavily sclerotized setae "spines", even though they have smaller counterparts of the same form named "setae" by the same authors. "Spinose seta" or "spine-like 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. 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 functional 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. (See fig. 2.1)

Sympod (synonym Protopod). A 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 post-cephalic segments 1 through 8.

Tridentate. With three denticles.

Triturating Surface. The truncate distal surface of the mandible's molar process that opposes the same surface on its counterpart.

Unequally Bifid Seta. A seta that is often spine-like and has a smaller thin seta or hair just proximal to its tip. The hair can be seen to have 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 primitively two uniarticulate rami, a larger endopod and a smaller exopod. (See fig. 1.4)

Venter. The ventral side of the body.

Vertex. The anterior and medial margin of the cephalic dorsal surface. (See fig. 2.1)

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 that it is generally more slender, and the sensory hair is on the distal tip and is long and curved.

APPENDIX 2

APPENDIX 2A: Phylogenetic analyses of the Asellota

Output of several runs of the program ITERMIX, which is derived from the program MIX written by J. Felsenstein, University of Washington

Mixed parsimony algorithm, version 2.51

8 species, 16 characters
Wagner parsimony method

Ancestral states:

??00? 0?0?0 00000 0

Character-state data:

Munn-Pleur	01110	11110	11010	1
Gnathosten	??101	00000	01000	0
Higher Jan	11110	11110	11111	1
Stenetrioi	00100	01000	01000	1
Aselloidea	00000	00000	00000	0
Para-Abyss	11110	11110	11010	1
Protojanir	??101	00010	01000	0
Pseudojani	00100	11111	01000	1

Aselloidea

```

! Higher Jan
! !
! *--Para-Abyss
! !
! *-----Munn-Pleur
! !
! *-----Pseudojani
! !
! *-----Stenetrioi
! !
! !           Protojanir
! !           !
! *-----*--Gnathosten

```

/ requires a total of 17.000

steps in each character:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!		1	1	1	1	1	1	1	1	2
10!	1	1	1	1	1	1	1			

Mixed parsimony algorithm, version 2.51

8 species, 16 characters

Wagner parsimony method

Ancestral states:

??00? 0?0?0 00000 0

Character-state data:

```

Protojanir   ??101 00010 01000 0
Stenetrioi  00100 01000 01000 1
Aselloidea  00000 00000 00000 0
Pseudojani  00100 11111 01000 1
Gnathosten  ??101 00000 01000 0
Munn-Pleur  01110 11110 11010 1
Higher Jan  11110 11110 11111 1
Para-Abyss  11110 11110 11010 1
  
```

Aselloidea

```

!
! Gnathosten
! !
! *--Protojanir
! !
! ! Stenetrioi
! ! !
! ! ! Pseudojani
! ! ! !
! ! ! ! Higher Jan
! ! ! ! !
! ! ! ! *--Para-Abyss
! ! ! ! !
*-*-----*-*-----Munn-Pleur
/
  
```

requires a total of 17.000

steps in each character:

```

      0  1  2  3  4  5  6  7  8  9
*-----
0!      1  1  1  1  1  1  1  1  1  2
10!    1  1  1  1  1  1  1  1
  
```

best guesses of ancestral states:

```

      0  1  2  3  4  5  6  7  8  9
*-----
0!      0  0  0  0  0  0  0  0  0  0
10!    0  0  0  0  0  0  0  0
  
```


Mixed parsimony algorithm, version 2.51

8 species, 16 characters

Wagner parsimony method

Ancestral states:

??00? 0?0?0 00000 0

Character-state data:

```

Munn-Pleur  01110 11110 11010 1
Protojanir  ??101 00010 01000 0
Aselloidea  00000 00000 00000 0
Stenetrioi  00100 01000 01000 1
Higher Jan  11110 11110 11111 1
Para-Abyss  11110 11110 11010 1
Pseudojani  00100 11111 01000 1
Gnathosten  ??101 00000 01000 0
  
```

Aselloidea

```

!
! Pseudojani
! !
! ! Higher Jan
! ! !
! ! *--Para-Abyss
! ! !
! *--*-----Munn-Pleur
! !
! *-----Stenetrioi
! !
! ! Protojanir
! ! !
! *--*-----*--Gnathosten
/
  
```

requires a total of 17.000

steps in each character:

	0	1	2	3	4	5	6	7	8	9
0!		1	1	1	1	1	1	1	1	2
10!	1	1	1	1	1	1	1			

best guesses of ancestral states:

	0	1	2	3	4	5	6	7	8	9
0!	0	0	0	0	0	0	0	0	0	0
10!	0	0	0	0	0	0	0			

APPENDIX 2B. Phylogenetic Analysis of the Janiroidea

Output of several most parsimonious trees from ITERMIX. Because the characters are weighted, the parsimony values are multiplied by the weights for each characters. Note that mixed parsimony methods are being used: W - Wagner method, S - Camin/Sokal method.

Mixed parsimony algorithm, version 2.51

16 species, 30 characters

Parsimony methods:

SSSSS SSSWS WWSWS SSSSS SSSSS SWWWS

Characters are weighted as follows:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!		5	5	5	5	5	5	5	5	1
10!	1	2	2	1	2	1	2	2	2	2
20!	2	2	1	1	1	1	1	2	2	2
30!	2									

Ancestral states:

00000 00000 00000 00000 00000 00000

Character-state data:

Nannonisc	11110	11101	01101	01100	01111	10000
Pseudojan	00011	00000	00000	00000	00000	00000
Janirellid	11110	11110	10101	00000	01110	11000
Ischnomes	11110	11111	10101	01000	01110	10011
Dend/Haplo	11110	11100	00101	00000	01100	00000
Para/Abyss	11110	01000	10101	00000	01000	00000
Desmosomat	11110	11101	01101	01111	01111	10000
Thambemat	11110	11101	00101	00000	01100	00000
Janiridae	11110	11110	00010	00000	00000	00000
Haplonisc	11110	11100	00101	01000	01111	10000
Joeropsid	11110	11100	00010	00000	01100	00000
Munn/Pleur	01110	01000	00101	00000	01000	00000
Macrostyl	11110	11101	01101	01001	11110	00000
Acanthasp	11110	11110	10101	00000	01000	01100
Mesosignid	11110	11110	00101	00000	01111	10000
Munnopsoid	11110	11110	10101	10000	01100	01100

Mixed parsimony algorithm, version 2.51

16 species, 30 characters

Parsimony methods:

SSSSS SSSWS WWSWS SSSSS SSSSS SSWWS

Characters are weighted as follows:

	0	1	2	3	4	5	6	7	8	9
*	-----									
0!		5	5	5	5	5	5	5	5	1
10!	1	2	2	1	2	1	2	2	2	2
20!	2	2	1	1	1	1	1	2	2	2
30!	2									

Ancestral states:

00000 00000 00000 00000 00000 00000

Character-state data:

Haplonisc	11110	11100	00101	01000	01111	10000
Macrostyl	11110	11101	01101	01001	11110	00000
Thambemat	11110	11101	00101	00000	01100	00000
Janiridae	11110	11110	00010	00000	00000	00000
Para/Abyss	11110	01000	10101	00000	01000	00000
Munn/Pleur	01110	01000	00101	00000	01000	00000
Mesosignid	11110	11110	00101	00000	01111	10000
Desmosomat	11110	11101	01101	01111	01111	10000
Dend/Haplo	11110	11100	00101	00000	01100	00000
Joeropsid	11110	11100	00010	00000	01100	00000
Nannonisc	11110	11101	01101	01100	01111	10000
Acanthasp	11110	11110	10101	00000	01000	01100
Pseudojan	00011	00000	00000	00000	00000	00000
Janirellid	11110	11110	10101	00000	01110	11000
Munnopsoid	11110	11110	10101	10000	01100	01100
Ischnomes	11110	11111	10101	01000	01110	10011

Mixed parsimony algorithm, version 2.51

16 species, 30 characters

Parsimony methods:

SSSSS SSSWS WWSWS SSSSS SSSSS SWWWS

Characters are weighted as follows:

	0	1	2	3	4	5	6	7	8	9
*	-----									
0!		5	5	5	5	5	5	5	5	1
10!	1	2	2	1	2	1	2	2	2	2
20!	2	2	1	1	1	1	1	2	2	2
30!	2									

Ancestral states:

00000 00000 00000 00000 00000 00000

Character-state data:

Mesosignid	11110	11110	00101	00000	01111	10000
Nannonisc	11110	11101	01101	01100	01111	10000
Haplonisc	11110	11100	00101	01000	01111	10000
Macrostyl	11110	11101	01101	01001	11110	00000
Ischnomes	11110	11111	10101	01000	01110	10011
Pseudojan	00011	00000	00000	00000	00000	00000
Para/Abyss	11110	01000	10101	00000	01000	00000
Acanthasp	11110	11110	10101	00000	01000	01100
Thambemat	11110	11101	00101	00000	01100	00000
Janirellid	11110	11110	10101	00000	01110	11000
Desmosomat	11110	11101	01101	01111	01111	10000
Munnopsoid	11110	11110	10101	10000	01100	01100
Munn/Pleur	01110	01000	00101	00000	01000	00000
Dend/Haplo	11110	11100	00101	00000	01100	00000
Janiridae	11110	11110	00010	00000	00000	00000
Joeropsid	11110	11100	00010	00000	01100	00000


```

Higher Jan
!
*--Munn-Pleur
!
*-----Stenetrioi
!
*-----Gnathosten
/

```

requires a total of 15.000

steps in each character:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!		1	1	1	1	1	1	1	1	1
10!	0	1	1	1	1	1	1			

best guesses of ancestral states:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!	0	?	0	0	0	0	?	0	0	
10!	0	0	0	0	0	0	0			

```

Aselloidea
!
! Gnathosten
! !
! ! Stenetrioi
! ! !
! ! ! Munn-Pleur
! ! ! !
*--*--*--*--Higher Jan
/

```

requires a total of 15.000

steps in each character:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!		1	1	1	1	1	1	1	1	1
10!	0	1	1	1	1	1	1			

best guesses of ancestral states:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!	0	0	0	0	0	0	0	0	0	0
10!	0	0	0	0	0	0	0			

```

Aselloidea
|
| Higher Jan
| |
| *--Para-Abyss
| |
| *-----Munn-Pleur
| |
| *-----Stenetrioi
| |
| *-----Gnathosten

```

requires a total of 15.000

steps in each character:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!		1	1	1	1	1	1	1	1	1
10!	0	1	1	1	1	1	1			

best guesses of ancestral states:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!	0	0	0	0	0	0	0	0	0	0
10!	0	0	0	0	0	0	0	0	0	0

```

Aselloidea
|
| Gnathosten
| |
| *--Protojanir
| |
| | Stenetrioi
| | |
| | | Munn-Pleur
| | | |
| | | | Para-Abyss
| | | | |
| *-----*-----*-----*-----Higher Jan

```

requires a total of 16.000

steps in each character:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!		1	1	1	1	1	1	1	1	2
10!	0	1	1	1	1	1	1			

APPENDIX 3

Output from program CLIQUE, provided by J. Felsenstein,
University of Washington. Results of two runs are given: 3A, Asellota
analysis; and 3B, Janiroidea analysis.

APPENDIX 3A: Compatibility Analysis of Asellota Data

Largest Clique program, version 2.4

9 species, 16 character states

Species	Character states
Ancestor	00000 00000 00000 0
Aselloidea	00000 00000 00000 0
Protojanir	00101 00010 01000 0
Gnathosten	00101 00000 01000 0
Stenetr	00100 01000 01000 1
Pseudojan	00100 11111 01000 1
Munn-Pleur	01110 11110 11010 1
Para-Abyss	11110 11110 11010 1
Higher Jan	11110 11110 11111 1

Character Compatibility Matrix

```

1111111111111111
1111111111111111
1111111111111111
1111111111111111
1111111011111111
1111111111111111
1111111011111111
1111111111111111
1111111111111111
1111010111111110
1111111111111111
1111111111111111
1111111111111111
1111111111111111
1111111111111111
1111111111111111
1111111111111111
1111111011111111

```

Largest Cliques

Characters: (1 2 3 4 5 6 7 8 10 11 12 13 14 15 16)

6 7 8 16 2 4 11 14 1 3 5 12 10 13 15

!-1-----1-----1--1--1--1--1-----1--1	Higher Jan
! 1 1 1 1 1 1 1-----	Para-Abyss
! 1 1 1 1 1 1-----	Munn-Pleur
! 1 1-----1-----	Pseudojan
!-----0-----0-----0-----0-----	Ancestor
! 0 0 0 0-----	Aselloidea
! 0 0-----1-----	Protojanir
! 0 0 1-----	Gnathosten
!-----	Stenetr

APPENDIX 3B: Compatibility analysis of the Janiroidea data.

Largest Clique program, version 2.4

16 species, 30 character states

<u>Species</u>	<u>Character states</u>
Pseudojan	00011 00000 00000 00000 00000 00000
Munn/Pleur	01110 01000 00101 00000 01000 00000
Para/Abyss	11110 01000 10101 00000 01000 00000
Acanthasp	11110 11110 10101 00000 01000 01100
Dend/Haplo	11110 11100 00101 00000 01100 00000
Desmosomat	11110 11101 01101 01111 01111 10000
Haplonisc	11110 11100 00101 01000 01111 10000
Ischnomes	11110 11111 10101 01000 01110 10011
Janirellid	11110 11110 10101 00000 01110 11000
Janiridae	11110 11110 00010 00000 00000 00000
Joeropsid	11110 11100 00010 00000 01100 00000
Macrostyl	11110 11101 01101 01001 11110 00000
Mesosignid	11110 11110 00101 00000 01111 10000
Munnopsoid	11110 11110 10101 10000 01100 01100
Nannonisc	11110 11101 01101 01100 01111 10000
Thambemat	11110 11101 00101 00000 01100 00000

Characters: (1 2 3 4 5 6 7 8 12 14 16 17 18 19 21 24 28 29 30)

24 17 6 8 12 1 14 18 28 2 3 5 7 16 19 21 29 30 4

!-1-1-----1-----1-----1-----	Desmosomat
! 1 1 1-----1-----1-----	Nannonisc
! 1 1 1-----1-----1-----	Macrostyl
! 1 1-----1-----1--1---	Ischnomes
! 1 1-----1-----1-----	Haplonisc
! 1-----1-----1-----	Janirellid
! 1-----1-----1-----	Mesosignid
!-----0-0-----0-----0-0-1-0-----	Pseudojan
! 0 0 0-----0-----0-----	Munn/Pleur
! 0 0-----0-----0-----	Para/Abyss
!-----1-----1-----1-----	Janiridae
!-----1-----1-----1-----	Joeropsid
!-----1-----1-----1-----	Munnopsoid
!-----1-----1-----1-----	Acanthasp
!-----1-----1-----1-----	Dend/Haplo
!-----1-----1-----1-----	Thambemat

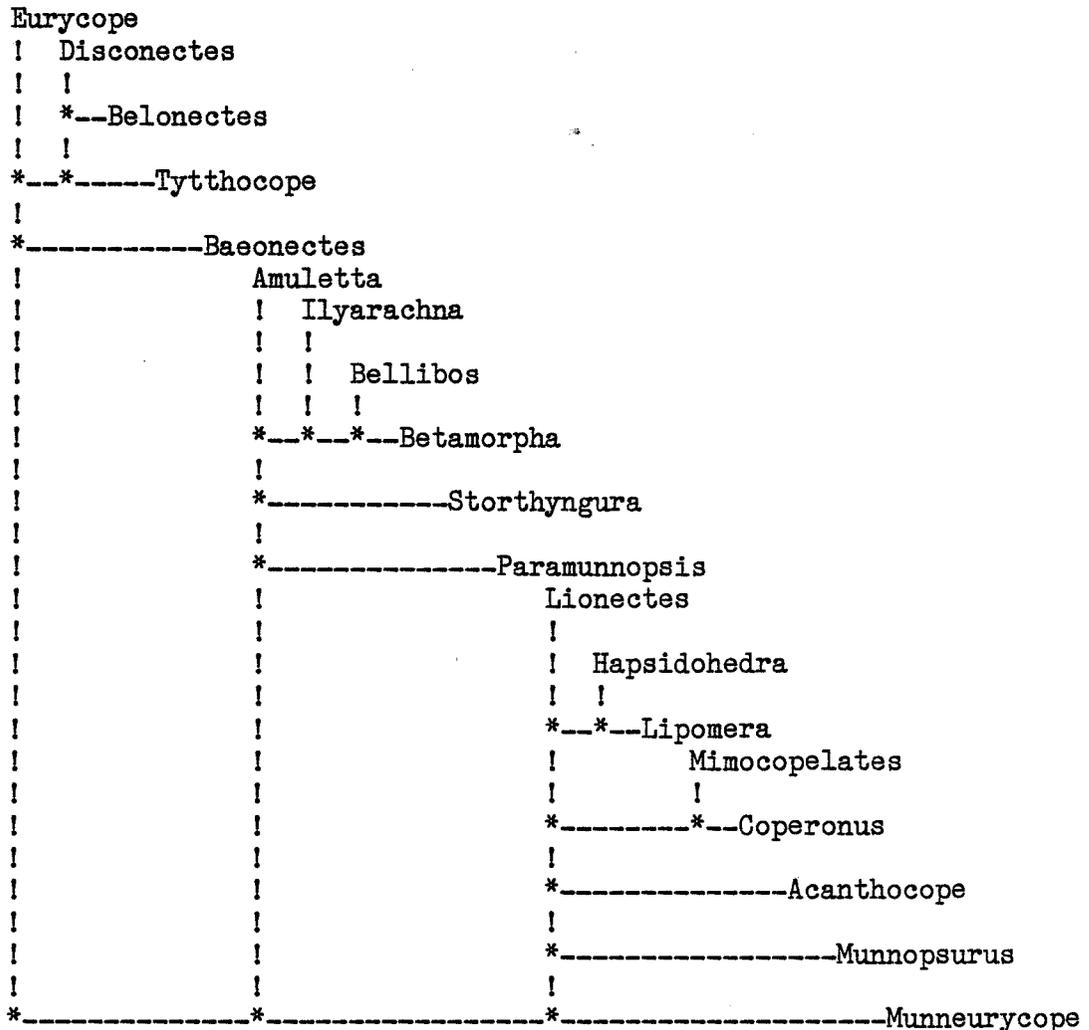
Characters: (1 2 3 4 5 6 7 8 12 14 16 17 18 19 21 27 28 29 30)

17 6 8 12 27 1 14 18 28 2 3 5 7 16 19 21 29 30 4

!-1-----1-----1-----1-----	Desmosomat
! 1 1-----1-----1-----	Nannonisc
! 1 1-----1-----1-----	Macrostyl
! 1-----1-----1--1---	Ischnomes
! 1-----1-----1-----	Haplonisc
!-----0-0-----0-----0-0-1-0-----	Pseudojan
! 0 0 0-----0-----0-----	Munn/Pleur
! 0 0-----0-----0-----	Para/Abyss
!-----1-----1-----1-----	Munnopsoid
!-----1-----1-----1-----	Acanthasp
!-----1-----1-----1-----	Janirellid
!-----1-----1-----1-----	Janiridae
!-----1-----1-----1-----	Joeropsid
!-----1-----1-----1-----	Dend/Haplo
!-----1-----1-----1-----	Mesosignid
!-----1-----1-----1-----	Thambemat

APPENDIX 4

Munnopsoid Analyses: Examples of various tree topologies in the output of the program ITERMIX.



/ requires a total of 73.000

weighted steps in each character:

	0	1	2	3	4	5	6	7	8	9
*-----										
0!		2	4	2	2	2	2	2	4	2
10!	2	2	2	4	2	4	2	2	2	1
20!	1	2	2	4	1	2	1	3	5	4
30!	3									

