

A PHYLOGENY AND A NEW CLASSIFICATION OF THE COROPHIIDEA LEACH, 1814 (AMPHIPODA)

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A B S T R A C T

Based on a phylogenetic analysis of 104 genera and 156 species of corophiidean amphipods, we present a new phylogeny and higher-level classification for the suborder Corophiidea Leach, 1814. The phylogeny divides the corophiideans into two infraorders, the Corophiida and the Caprellida, based on a hypothesis of the evolution of different feeding strategies. Members of the Corophiida are derived from bottom-feeding detritivores, whereas members of the Caprellida are derived from ancestors that fed on material suspended in the water column. Within the Corophiida there are unspecialized clades such as the aroids, whose members are mainly detrital feeders, as well as specialized forms feeding on living algae (family Ampithoidae) and on wood (superfamily Cheluroidea). In the Caprellida, members of the podocerid and caprellid clades often climb organisms such as hydroids in order to get their antennae as far up in the water column as possible to suspension-feed, whereas ischyrocerins build nests and then suspension-feed. Specialized forms include cyamids that attach to whales where they “feed on whale skin.” Barnard and Karaman (1984) divided the Corophiidea into two superfamilies (Corophiidea and Caprelloidea) within which were nine families. The classification presented here includes those two infraorders, with 11 superfamilies, 21 families, 13 subfamilies, and 5 tribes.

Barnard and Karaman (1984) proposed an untested scheme, which placed the infraorders Caprellida (as Caprelloidea) and Corophiida (as Corophioidea) in the suborder Corophiidea Leach (1814). It should be noted that Stebbing (1906) attributed the Corophiidae to Dana (1849), but this is in error. Leach (1814: 405) erected the Corophiidae (as the family Corophiini) where it has page placement priority over the family Caprellini. This error has since been perpetuated by all authors, including Barnard and Karaman (1984, 1991).

Within the corophiideans (*sensu lato*), the internal phylogenetic relationships have always been uncertain. Barnard and Karaman (1991) attempted no phylogenetic classification of their infraorder Corophiida, commenting that “the practical identification of family or subfamily groups in this conglomerate is very difficult.” Laubitz (1993) and Takeuchi (1993) both proposed untested schemes for the Caprelloidea (in the traditional sense).

The lack of clarity that surrounds the relationships of this group is not unique within the Amphipoda, but it has been particularly intractable in the corophiideans. We should not, however, be surprised. The punctuated nature of

evolution may always result in low-resolution trees, which are based on extant taxa. Whenever a new innovation occurs during the course of evolution, it is probably followed by explosive adaptive radiation as the innovator invades new niches, further developing and adapting its innovation. Most of the descendants of the early innovator will fail and become extinct; only a few will succeed to form new clades. Such bursts of evolutionary innovation make it difficult, if not impossible, to distinguish the dichotomous nature of character-state acquisition by examining only extant taxa. Interpretation of phylogeny through a cladistic study of living species will result in trees with unresolvable polychotomies. The precision of a cladistic analysis will vary with the hierarchical taxonomic level analyzed (and hence to temporal scale). Analyses of species groups should generally yield rather clear relationships, because there are fewer missing links, but the clarity will decrease, perhaps exponentially as earlier and earlier relationships are investigated. This means that we should, perhaps, be rather skeptical of a tree pertaining to family relationships that purports to be fully resolved. The best we can expect, and for the present with which

Table 1. Characters used in the analyses.

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1. Head (Fig. 3)
 1. free, not coalesced with pereonite 1
 2. partially or completely coalesced with pereonite 1
 2. Head (Fig. 3)
 1. rectangular, anterodistal margin recessed
 2. rectangular, anterodistal margin truncate
 3. triangular
 4. round with a distinct neck region
 5. columnar
 3. Head lateral cephalic lobe (Fig. 4)
 1. weakly or not extended, eye, if present, situated proximal to lobe
 2. extended, eye, if present, at least partly enclosed in extended lobe
 3. strongly extended, eye, if present, completely enclosed in extended lobe
 4. Head lateral cephalic lobe (Fig. 4)
 1. apically rounded
 2. apically acute
 5. Head anteroventral margin (Fig. 4)
 1. poorly to weakly recessed and moderately excavate (except where strongly excavate for reception of large antenna)
 2. moderately to strongly recessed and moderately excavate (except where strongly recessed and strongly excavate for reception for large antennae)
 3. obliquely truncate on spheroid head
 4. not recessed, on round head
 6. Body (Fig. 5)
 1. without sternal spines
 2. with sternal spines on some of pereonites 2 to 7
 7. Antenna 1 peduncular article 3 (Fig. 5)
 1. short (half or less the length of article 2)
 2. long (more than half, or usually much more than half, the length of article 2)
 8. Mandible molar
 1. present
 2. absent
 9. Mandible palp article 3 (Fig. 5)
 1. anterior and posterior margins asymmetrical, distally rounded, setae extending along most of posterodistal margin
 2. anterior and posterior margins subsymmetrical, distally flattened, setae mostly distal
 3. approximately parallel-sided
 10. Mandible palp article 3 (Fig. 5)
 1. posterior margin with setae of variable length
 2. posterior margin with comb of short setae and a few long slender setae
 11. Labium outer lobes (Fig. 5)
 1. inner margin evenly convex
 2. inner margin concave
 3. inner margin with strongly developed notch
 12. Labium outer lobe (Fig. 5)
 1. without distal slit
 2. with distal slit
 13. Pereonites 6–7 (Fig. 6)
 1. free and orientated ventrally
 2. fused and oriented posteriorly
 14. Pereonite 7 (Fig. 6)
 1. posterodistal margin weakly rotated or not rotated posteriorly
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Table 1. Continued.

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2. posterodistal margin rotated posteriorly (pereopod 7 directed posteriorly)
 15. Gnathopod 1
 1. not enlarged in either males or females
 2. enlarged in males and females or only in males
 16. Gnathopod 1 (Fig. 7)
 1. not forming a sieving structure in conjunction with gnathopod 2
 2. forming a sieving structure (dense sieving setae on posterior margin of carpus and merus or ischium) in combination with gnathopod 2
 17. Gnathopod 1 (female) (Fig. 8)
 1. coxa small (almost always smaller than coxa 2)
 2. coxa large (almost always larger than coxa 2)
 18. Gnathopod 1 (male) (Fig. 8)
 1. coxa greatly enlarged (occasionally anteroventrally produced)
 2. coxa or not weakly enlarged
 19. Gnathopod 2 (male) (Fig. 8)
 1. coxa subequal in size to coxa 3
 2. coxa greatly enlarged and shield-like, almost entirely covering coxa 1
 20. Gnathopod 2 merus (Fig. 8)
 1. not enlarged and fused along anterodistal margin of carpus, or broadened and fused along entire length with posterior margin of carpus
 2. enlarged and free along anterodistal margin of carpus
 21. Pereopods 3–4
 1. well developed
 2. reduced or absent
 22. Pereopods 3–4 bases (Fig. 9)
 1. nonglandular
 2. with glands in basis
 3. with glands in merus
 23. Pereopod 5 carpus (Fig. 9)
 1. long, subrectangular
 2. small, lunate or reniform
 24. Pereopods 5–7 (Fig. 9)
 1. not subchelate
 2. subchelate
 25. Pereopods 5–7 (Fig. 9)
 1. not prehensile
 2. prehensile, dactylus elongated and closing along most of posterior margin of propodus
 26. Pereopods 5–7 dactyli (Fig. 9)
 1. without accessory spines on anterior margin
 2. with accessory spines on anterior margin
 27. Pereopod 7 (Fig. 9)
 1. subequal to or not longer than $1.1 \times$ pereopod 6
 2. elongate, entire propodus extending beyond pereopod 6
 28. Pleonite 3 (Fig. 10)
 1. expanded ventrally to form an epimeron
 2. not expanded ventrally to form an epimeron
 29. Urosomites (Fig. 10)
 1. 1 not coalesced with urosomite 2
 2. 1 coalesced with urosomite 2
 30. Urosomites (Fig. 10)
 1. 2 not coalesced with urosomite 3
 2. 2 coalesced with urosomite 3
 31. Urosomites 1 or 1 and 2 (Fig. 10)
 1. short to long
 2. extremely long (length at least $3 \times$ breadth)
 32. Uropods 1–2 peduncle (Fig. 10)
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Table 1. Continued.

	1. without distoventral corona of cuticular spines
	2. with distoventral corona of cuticular spines
33.	Uropods 1–2 rami (Fig. 10)
	1. lacking a dense array of strong robust setae
	2. long, with a dense array of strong robust setae
	3. short, with a dense array of strong robust setae
34.	Uropod 3 peduncle (Fig. 11)
	1. short (length $2\times$ or less breadth), parallel sided
	2. short (length $2\times$ or less breadth), sides expanded or medially lobate
	3. long (length more than $2\times$ breadth), broad proximally and narrow distally
	4. long (length more than $2\times$ breadth), parallel sided
	5. vestigial or absent
35.	Uropod 3 (Fig. 11)
	1. with rami
	2. without rami
36.	Uropod 3 outer ramus (Fig. 11)
	1. with uniformly similar marginal and apical slender, flexible setae
	2. with a mixture of robust and slender setae
	3. with 1–2 recurved, robust apical setae
	4. with rudimentary setae or lacking setae
37.	Uropod 3 (Fig. 11)
	1. without recurved spines
	2. with recurved spines
38.	Telson
	1. laminar
	2. dorsoventrally thickened
39.	Telson (Fig. 11)
	1. without hooks or denticles
	2. with rows of recurved hooks
	3. with patches of small denticles
40.	Telson telsonic cusps (Fig. 11)
	1. absent
	2. present
41.	Telson shape
	1. not extremely reduced, lacking distolateral clumps of robust setae
	2. extremely reduced, with distolateral clumps of robust setae

we can be satisfied, is a weak signal of relationships that must be supported by other criteria.

To interpret the phylogeny of the corophiideans, we must attempt to understand the biology, ecology, and behavior of this group of amphipods. What innovations set apart the corophiideans from other amphipods and how was each new innovation within the suborder exploited to set the extant clades on their evolutionary trajectories?

The present work attempted to answer these questions. It was based on six workshops totaling over 1000 hours of analysis and discussion. The analysis was aimed at determining the phylogenetic relationships of the

major clades within the corophiidean amphipods.

The Hypothesis

The hypothesis proposed here is that the evolution of the Corophiidea proceeded along two pathways determined by feeding method: the exploitation of detritus settled out on the bottom; and specialization for the capture of water-borne particles. On this assumption, a number of morphological adaptations could be interpreted functionally. The hypothesis was used as the basis for testing (falsification in a Popperian sense) by phylogenetic analysis through cladistics.

MATERIALS AND METHODS

As a starting point, 135 characters were assembled in a DELTA (DEscription Language for TAxonomy; Dallwitz *et al.*, 1993, 1998) database for 156 species of corophiidean amphipods. The database was designed to contain all representative genera of these animals. Closely allied sibling genera were omitted to reduce the species list to a manageable size. A few poorly known genera were also omitted. Coding was carried out principally on females, because, in general, they lack secondary sexual characters and were assumed to be more conservative than males. Some male characters thought to have phylogenetic significance were included, as were males of taxa in which females were unknown. An analysis was run with PAUP version 4.0b8a using heuristic searches and the criterion of parsimony. The resultant tree was then transferred to MacClade version 3.08 and examined for parsimoniously uninformative characters, which were then removed. Branches were rearranged within MacClade to determine whether taxa sharing the same character state could be joined without increasing the length of the tree. Where taxa could be grouped with only minimal increase in tree length, the characters and character states were re-evaluated, and a further PAUP analysis was executed to see whether a shorter tree could be obtained using the re-evaluated characters. If the new tree was as short or shorter than the original tree, this new tree became the working tree for further refinement.

Homoplastic characters were re-examined in order to determine whether they were in fact homologous or might more reasonably be interpreted as convergent. If thought to be convergent, a character was very carefully re-evaluated and redefined. After many iterations, a database of 41 parsimoniously informative characters was established and run in PAUP to provide a shortest tree that most accurately represented the phylogenetic relationships of the taxa in the database.

The terminology for spines and setae follows Watling (1989).

RESULTS

Phylogenetic Analysis

Of the 41 characters used, 32 were binary and 9 were multistate (Table 1, Figs. 1–11). All states were unordered (Appendix I). One character, the telson shape (laminar or dorso-

ventrally thickened) was parsimoniously uninformative but was left in the analysis to root the tree with the outgroup. *Gammarus locusta* Linnaeus, 1758, was chosen as the outgroup, because of its generalized morphology and negligible podomere or article reduction.

Because the analysis used an iterative process between DELTA, PAUP, and MacClade, the choice of starting tree was not important, as long as it was a parsimoniously shortest tree. An arbitrary shortest PAUP tree was therefore selected as the starting tree.

The characters and character states used in the final analysis were the product of step-by-step improvements of the original characters and character states as a consequence of challenge by successive cladograms. The character and character state list (Table 1) is an important output of the study and is therefore presented in this section. Most previous cladistic analyses of Amphipoda have, by contrast, performed a cladistic analysis directly on a previously compiled "fixed" list of characters and character states.

The final tree length was 135 steps; the CI was 0.52, and the RI was 0.86.

Tree Description

The adjectival endings of formal taxon group names used in the present study are given in Table 2.

The corophiidean clade (Fig. 12) is a monophyletic group defined by glands in the basis of pereopods 3–4 (22.2), slender and robust setae on the rami of uropod 3 (36.2), and a dorsoventrally thickened telson (38.2).

The tree divides at the base into two large monophyletic clades, the corophiidan and caprellidan clades. Within the corophiidan clade, there are several clearly defined forms, but there does not appear to be any definable sequence of evolutionary progression. The base of the clade is weakly resolved, in effect, a polytomy of four primary clades. Although each clade forms a monophyletic group, any clade can be joined with any other clade without increasing the overall length of the tree. This indicates that taxa connecting the clades are either extinct or have not been discovered. The situation is no better in the caprellidan clade. The base of this clade is also an effective polytomy of six monophyletic clades.

The monophyletic corophiidan clade is defined by one homoplastic character, an enlarged coxa 1 in both sexes (17.2). Exceptions occur in

some *Leptocheirus* spp. and *Kuphocheira*. This character state occurs once in the caprellidan clade in the genus *Kamaka* (kamakid clade).

The basal cheluroid clade (monophyly, based on homoplasy) includes three genera of wood-eating amphipods. It is defined by five homoplastic character states. The outer lobe of the labium has the inner margin concave (11.2), a character state that has been independently derived in *Pareurystheus* in the protomeiine clade. The carpus of pereopod 5 is lunate (23.2), a character state that occurs nowhere else in the corophiidan clade, but is an independently derived character state within the siphonoecetin clade (caprellidan clade). Urosomites 1–2 (29.2) and 2–3 (30.2) are coalesced, which are character states that have been independently derived in some members of the corophiid clade (corophiidan clade) and also occur extensively in the podocerid clade and among the caprellids (caprellidan clade). The apical setae on the outer ramus of uropod 3 are vestigial (36.4), a state that occurs nowhere else in the corophiidan clade, but within the caprellidans, it occurs in *Paraphotis* in the priscomilitariid clade, and it defines the ischyrocerid clade.

The chevalioid clade (based on homoplasy) is defined by two character states. The first is the dactylus of pereopod 5, which has accessory spines (26.2), a state occurring nowhere else in the corophiidan clade, but it does occur within the caprellidan clade, in *Paraphotis* (priscomilitariid clade), some species of *Photis* (photid clade), and all members of the siphonoecetin clade. The second character state, urosomites 1 and 2 coalesced (29.2) has also been independently derived in some members of the corophiid clade (corophiidan clade) and in *Kamaka* in the kamakine clade (caprellidan clade).

The aoroid clade (monophyly based on homoplasy) is defined by one character state. Gnathopod 1 is enlarged in males and females or only in males (15.2). This character state has also been independently derived in *Melanesius* and *Paragrubia* in the amphithoid clade and in *Anonychocheirus* and *Leptocheirus* in the haplocheirin clade. In the caprellidan clade, it defines the neomegamphopid clade and occurs extensively in the kamakid clade. The aorid clade (monophyly, based on homoplasy) is defined by one character state, pereopod 7 is elongate, with the entire propodus extending beyond pereopod 6 (27.2). This character state (apparently independently derived) defines the

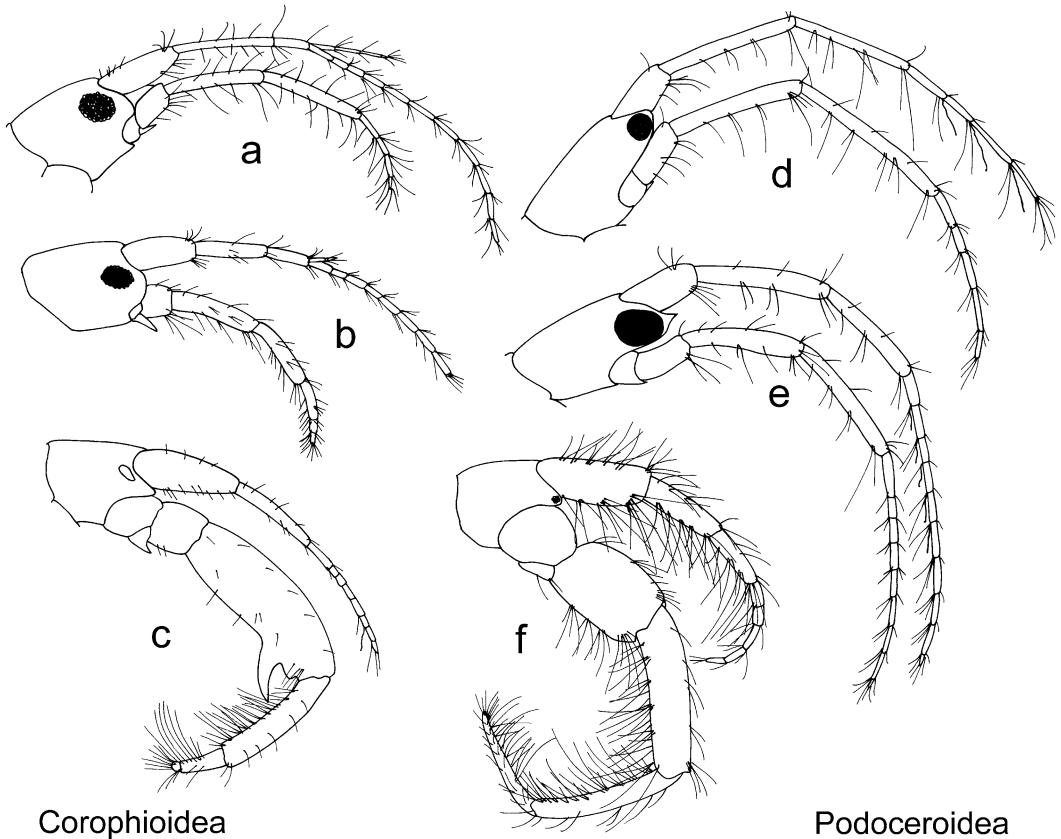


Fig. 1. Heads of Corophiida (a–c) and Caprellida (d–f): a) *Protolembos crouyensis* Myers; b) *Leptocheirus guttatus* (Grube); c) *Crassikorophium crassicorne* (Bruzelius) (after Bousfield and Hoover (1997)); d) *Scutischyrocerus scutatus* Myers; e) *Erichthonius pugnax* Dana; f) *Siphonoecetes sabatieri* de Rouville.

corophiine clade and in the caprellidans, again as an independently derived state, occurs in the kamakine and podocerid clades. The unciolid clade is paraphyletic. It is excluded from the aorid clade because pereopod 7 is not extremely elongate. Within the unciolid clade, the acuminodeutopine clade is defined by acute, triangular, lateral cephalic lobes (4.2). The uncioline clade is paraphyletic. Within this clade, two unusual genera occur. *Janice* has the merus of gnathopod 2 enlarged and free along its posterior margin (20.2), an independently derived character state that defines the paracorophiini clade within the corophiine clade. *Neohela* has a linear basis on each of pereopods 3–4 (22.2) and no epimera (28.2); both character states occur extensively in the caprelloid clade.

The corophioid clade is paraphyletic. It is excluded from the aorid clade because gnathopod 1 is not enlarged in either males or females.

Independently derived exceptions are *Paragrubia* and some species of *Exampithoe* in the amphithoid clade and *Anonychocheirus* and *Leptocheirus* in the haplocheirin clade. The amphithoid clade is a large, well-known group of alga-eating amphipods. All members have at least one large, recurved robust seta on the outer ramus of uropod 3 (36.3). Only members of the amphithoine clade have a strongly developed notch on the inner margin of the labium (11.3). Most amphithoines have apical cusps on the telson (40.2), a homoplastic character state that has also been independently derived in *Zoedeutopus* (uncioline clade) and in *Photis* and *Papuaphotis* (photid clade). The exampithoine clade is paraphyletic and excluded from the amphithoine clade because members lack a notch on the inner margin of the labium and they lack apical cusps on the telson.

The corophioid clade is paraphyletic. It is excluded from the amphithoid clade because it

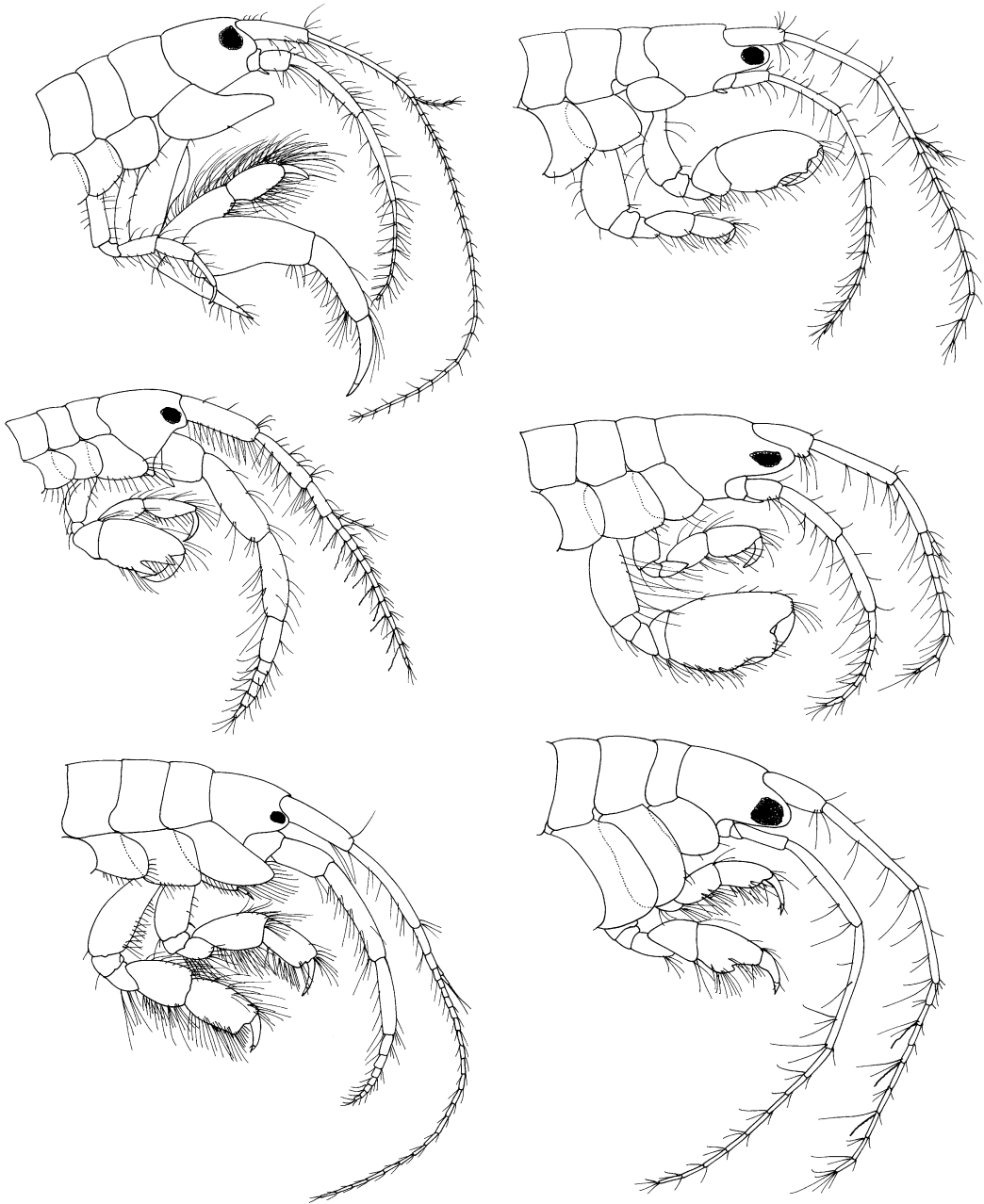


Fig. 2. Left: enlarged coxa 1 and short article 3 on antenna 1 in corophiids: top, *Aora*; center, *Cheiriphotis*; bottom, *Protomeideia* (after Conlan, 1983). Right: small coxa 1 and long article 3 on antenna 1 in caprelliids: top, *Paraloiloi*; center, *Gammaropsis*; bottom, *Photis*.

does not have recurved robust setae on the outer ramus of uropod 3. Within the corophiid clade, the basal protomeideiine clade is paraphyletic. It is excluded from the corophiine clade because it does not have a sieving structure on gnathopods 1 and 2. The coro-

phiine clade (monophyly based on synapomorphy) is a large, well-known group, defined by one character, a unique sieving structure composed of dense sieving setae on some podomeres of both gnathopods 1 and 2 (16.2). Within the corophiine clade, the paracorophi-

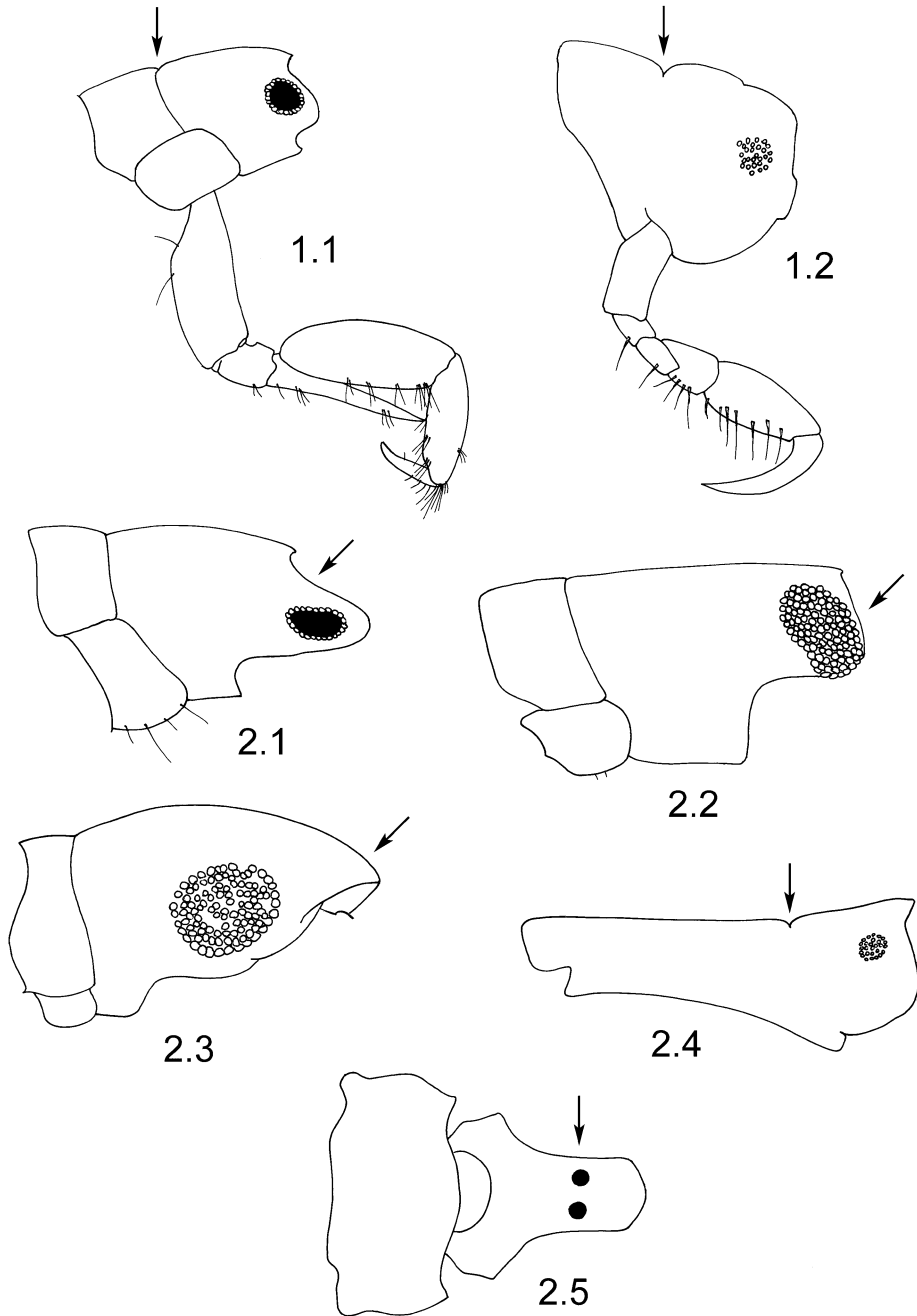


Fig. 3. Characters 1–2: 1.1 *Aora*, 1.2 *Caprella* (after Krapp-Schickel, 1993); 2.1 *Gammaropsis*, 2.2 *Parunciola* (after Ruffo, 1993), 2.3 *Dulichia* (after Laubitz, 1977), 2.4 *Caprella* (after Krapp-Schickel, 1993), 2.5 *Cyamus* (after Sars, 1895).

clade (monophyly, based on homoplasy) is defined by the merus of gnathopod 2, which is enlarged and free along its anterodistal margin (20.2), a homoplasy it shares with *Janice* (uncioid clade), and by coalesced urosomites 1 and 2 (29.2), a homoplasy considered to be

independently derived in *Chevalia* (chevalioid clade). A synapomorphy for the corophiian clade and the haplocheirin clades is the dense array of robust setae on short rami of uropod 3 (33.2–3). The haplocheirin clade is paraphyletic, but the corophiian clade is defined by

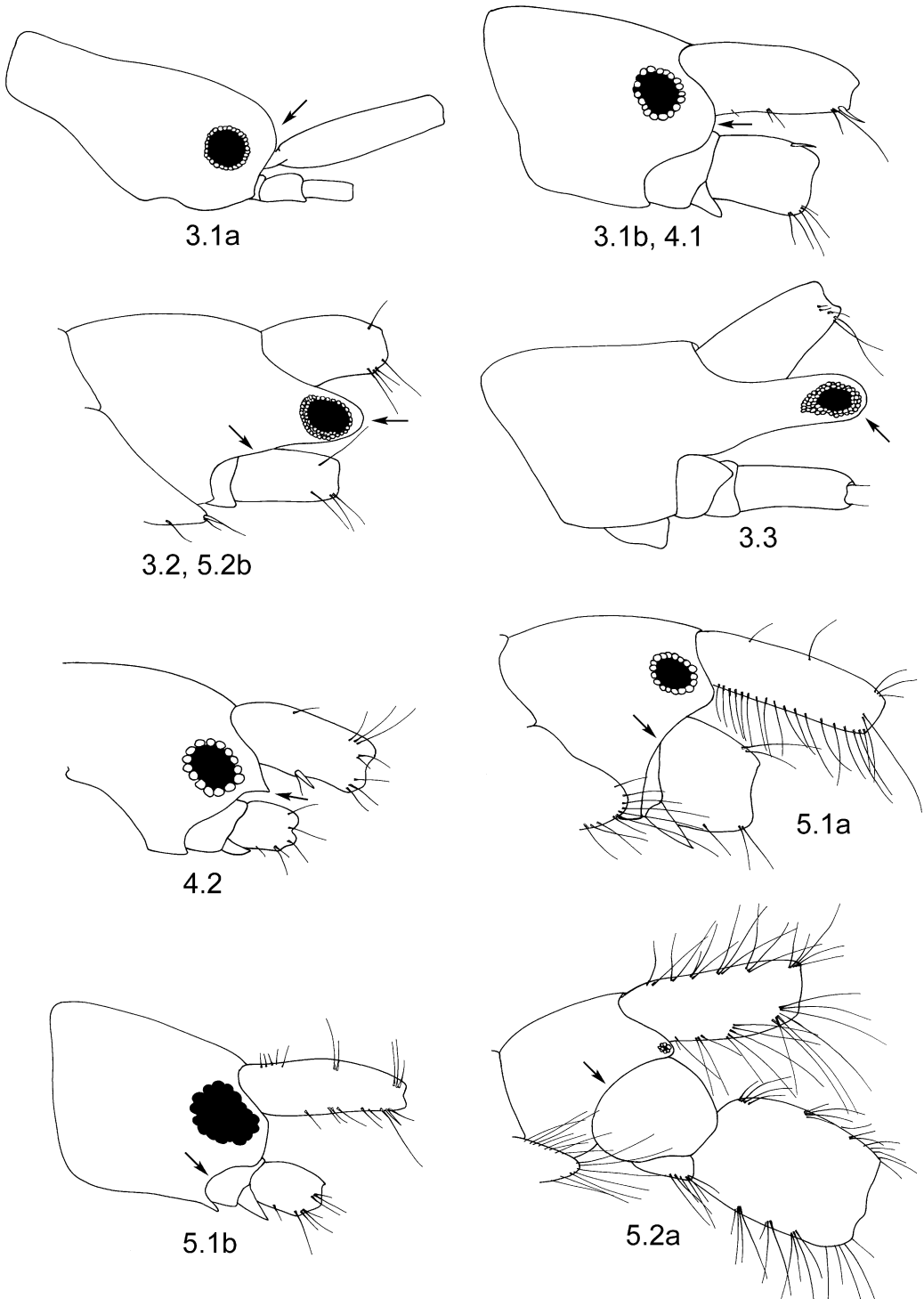


Fig. 4. Characters 3–5: 3.1a *Caprella* (after Sars, 1895), 3.1b *Microdeutopus*, 3.2 *Gammaropsella*, 3.3 *Ampelisciphotis* (after Pirlot, 1934); 4.1 *Microdeutopus*, 4.2 *Acuminodeutopus*; 5.1a *Cheiriphotis* (head anterior ventral margin strongly recessed and strongly excavate for reception of enlarged antenna), 5.1b *Bemlos* (weakly recessed and moderately excavate), 5.2a *Siphonoecetes* (strongly recessed and strongly excavate for reception of enlarged antenna), 5.2b *Gammaropsella* (strongly recessed and moderately excavate).

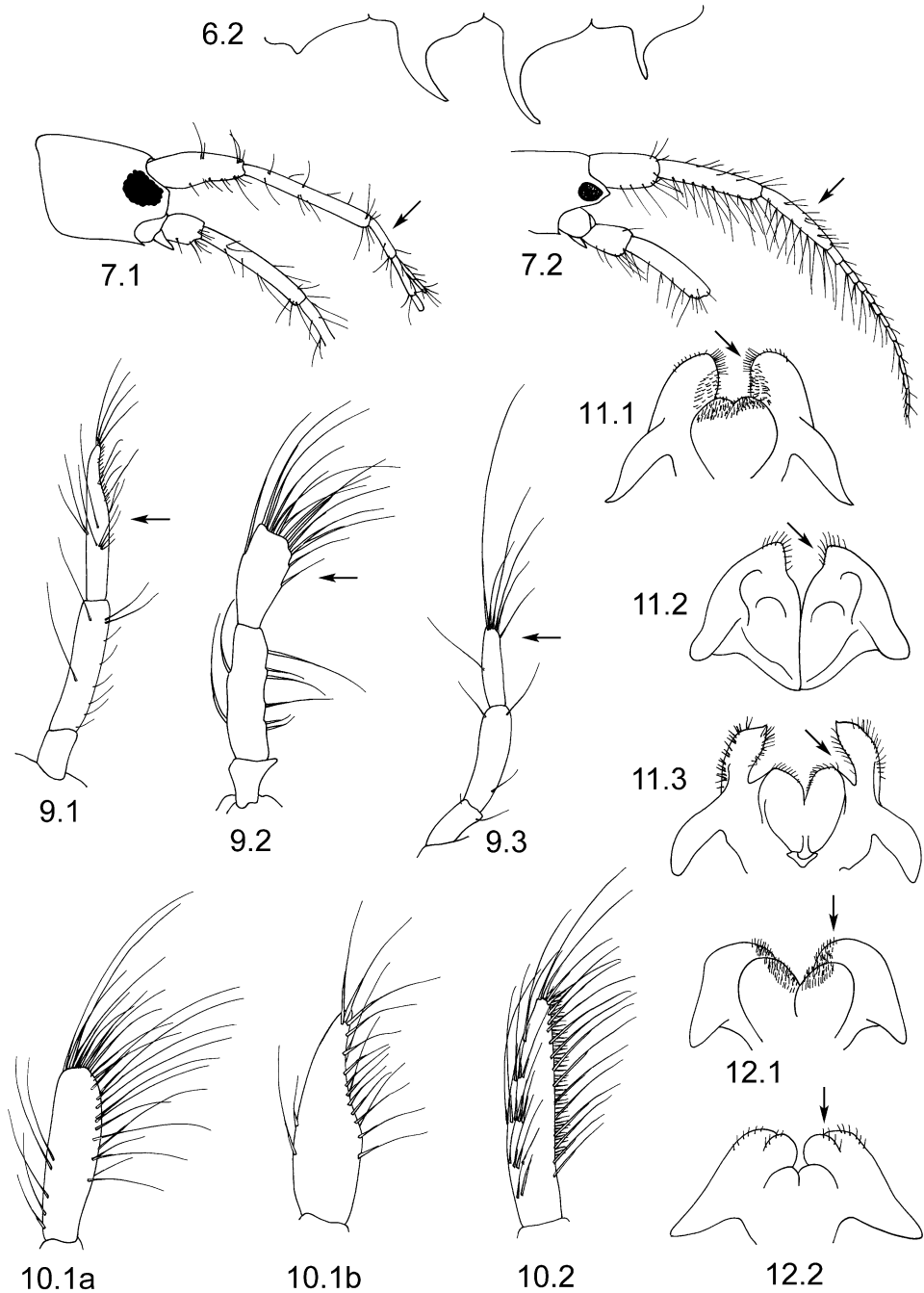


Fig. 5. Characters 6–12: 6.2 *Bemlos*; 7.1 *Bemlos*, 7.2 *Erichthonius*; 8.1 and 8.2 not shown; 9.1 *Autonoe*, 9.2 *Neomegamphopus*, 9.3 *Microprotopus*; 10.1a *Gammaropsis*, 10.1b *Lembos*, 10.2 *Tethylembos*; 11.1 *Meridiolembos*, 11.2 *Chelura* (after Sars, 1895), 11.3 *Ampithoe*; 12.1 *Gammaropsis*, 12.2 *Uncinotarsus* (after L'Hardy and Truchot, 1964).

pereopod 7, which has the entire propodus extending beyond pereopod 6 (27.2), an independently derived character state that defines the aorid clade (aoroid clade) and also

occurs in the kamakid and podocerid clades (caprellidan clade).

The second large monophyletic clade within the corophiidean clade is the caprellidan clade

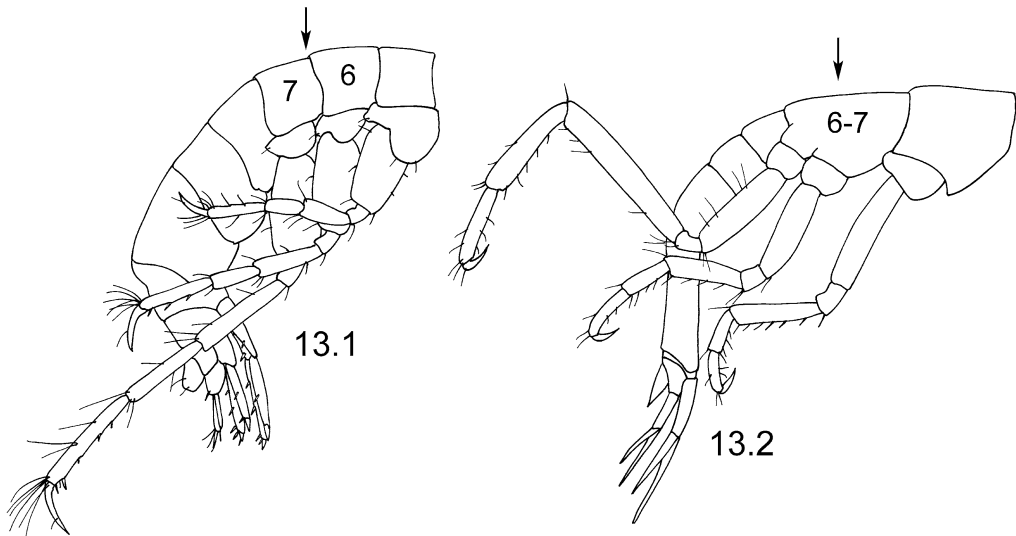


Fig. 6. Character 13: 13.1 *Aoroides*, 13.2 *Dulichia* (after Sars, 1895).

(monophyly based on synapomorphy), which is based on two character states: head with anteroventral margin moderately excavate (5.2) and antenna 1 with peduncular article 3 long, more than half (usually much more than half) length of article 2 (7.2).

At the base of the caprellidan clade is an enigmatic group known as the aetiopedesoid clade (monophyly based on synapomorphy). This clade is defined by pereopods 3–4 with silk glands in the merus and sometimes possibly in the carpus (22.3) and the extremely short and broad telson (41.2). Within the aetiopedesoid clade, the aetiopedesid clade is defined by several autapomorphies such as the toothed labrum and merochelate pereopods 3–4. The paragammarsopid clade is defined by a strongly extended lateral cephalic lobe with the eye completely enclosed in the lobe (3.3), which is a homoplastic character state that appears to be independently derived in the photoid clade, and by a lack of epimera (28.2), which is also a homoplastic character state that is widespread in the caprellid clade.

The rakiroid clade (monophyly, based on homoplasy) is based on an unusual monotypic genus with many plesiomorphic characters, but is defined by two character states: the coalescence of urosomites 2 and 3 (30.2), which is a character state that has been independently derived in *Laetmatophilus* (podocerid clade), the dulichiid clade, and all members of the caprellid clade; and the rami of uropods 1 and 2,

which are long and with a dense array of robust setae (33.2), a state that occurs no where else in the caprellidan clade but is independently derived in the corophiidans, in *Arctolembos* (aorid clade), and *Anonychocheirus* in the haplocheirin clade.

The neomegamphopoid clade is defined by article 3 of the mandibular palp, which is subsymmetrical and distally flattened with the setae mostly distal (9.2). This character state is confined to the caprellidan clade, where it is independently derived in the kamakid and photid clades. The priscomilitariid clade (monophyly, based on synapomorphy) has the coxa of gnathopod 2 enlarged and shield-like. The coxa covers most of coxa 1 and is much larger than coxa 3 (19.2), an autapomorphy for this group. The neomegamphopid clade (monophyly, based on homoplasy) is defined by an enlarged gnathopod 1 in males and females or only in males (15.2). In the caprellidan clade, this widespread homoplasy occurs in the kamakid clade. In the corophiidan clade, it defines the aorid clade and appears to be independently derived in *Exampithoe* and *Paragrubia* in the amphitoid clade and *Anonychocheirus* and *Leptocheirus* in the haplocheirin clade. All members of the clade, except *Maragopsis*, have a weakly extended lateral cephalic lobe (4.2).

The microprotopoid clade is paraphyletic. The isaeoid clade (monophyly, based on synapomorphy) is composed of two genera that are defined by a unique synapomorphy;

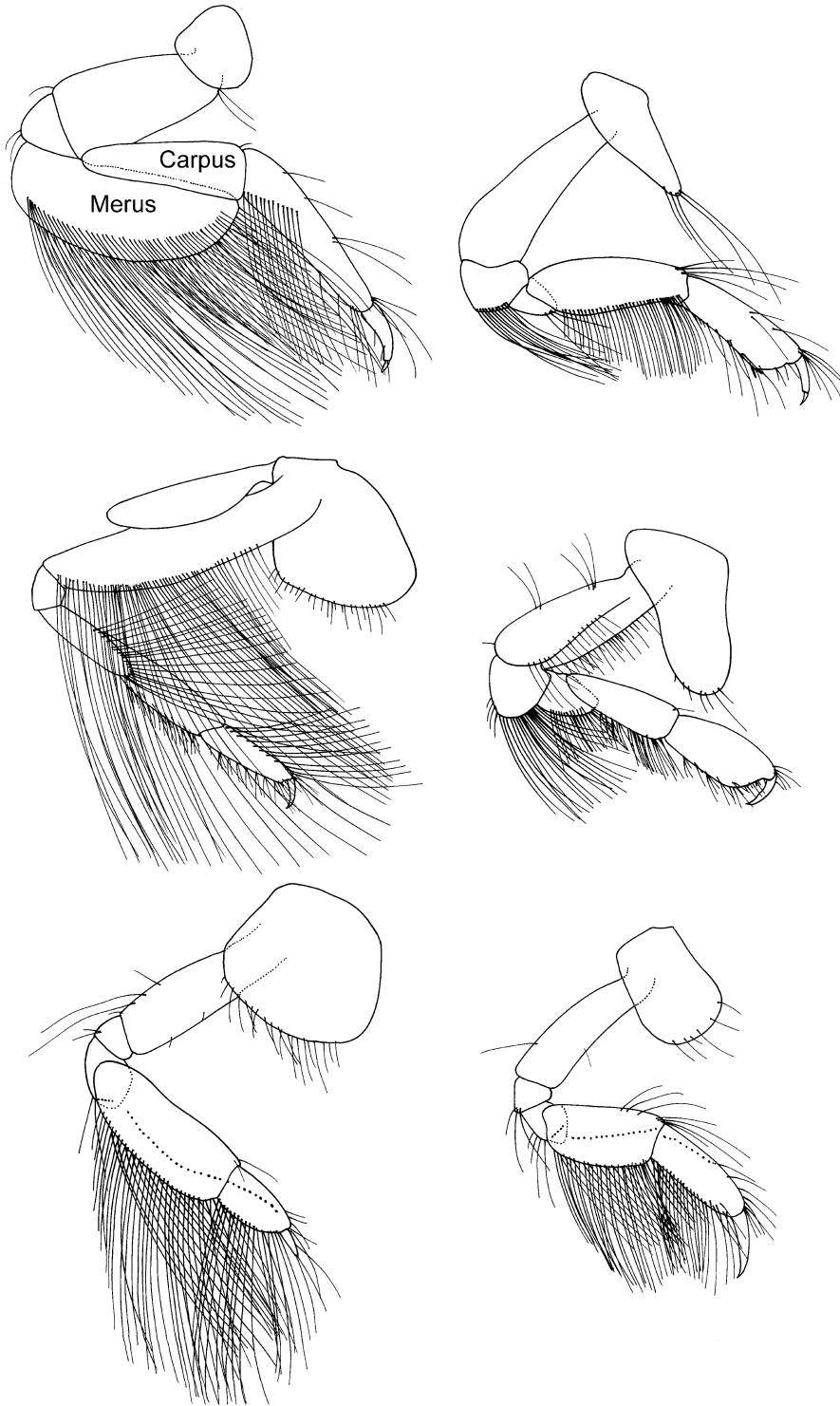


Fig. 7. Character 16.2: gnathopod 2 (left), gnathopod 1 (right) *Corophium* (top); *Leptocheirus* (center); *Kuphocheira* (bottom).

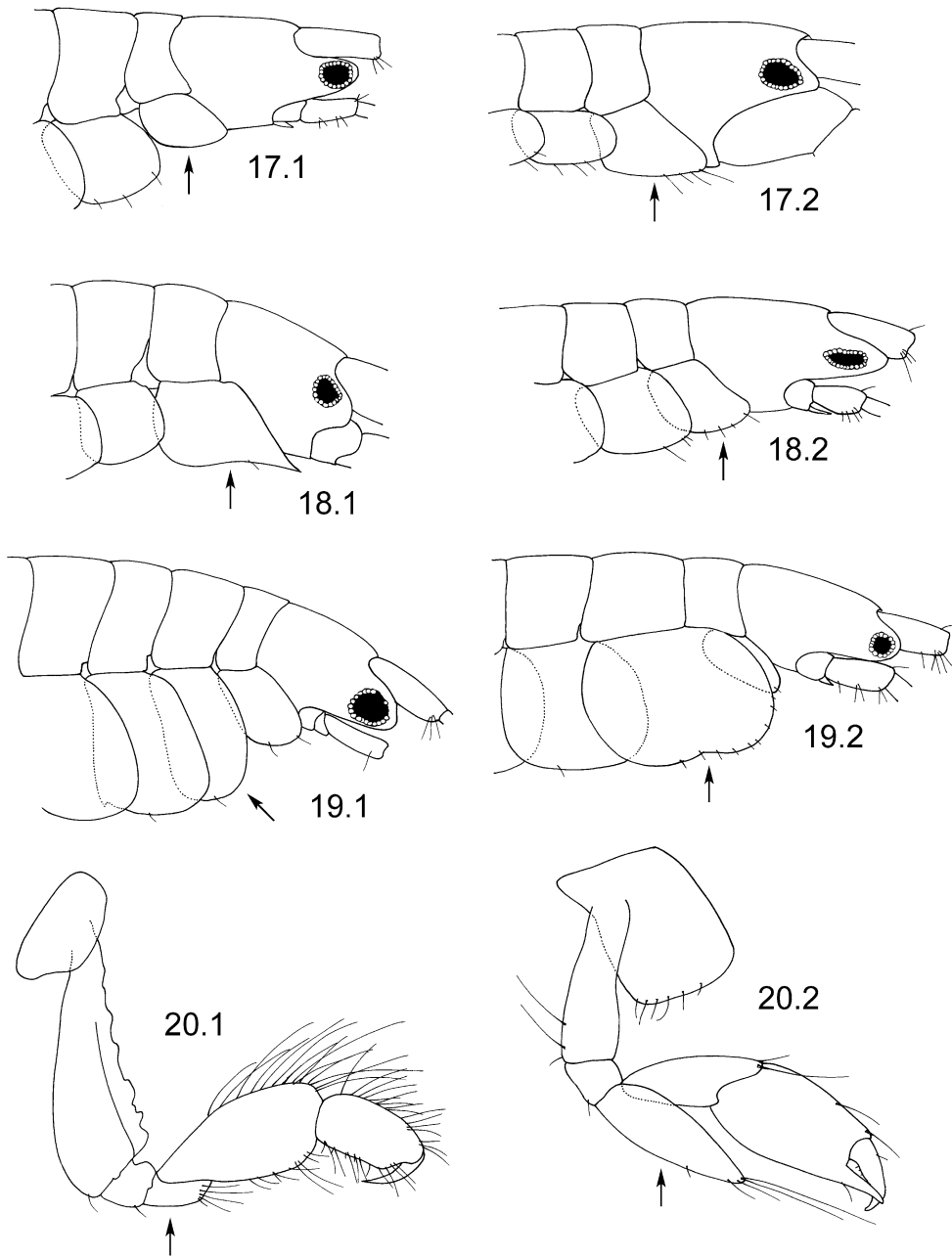


Fig. 8. Characters 17–20: 17.1 *Paraloiloi*, 17.2 *Cheiriphotis*; 18.1 *Aora*, 18.2 *Gammaropsis*; 19.1 *Photis*, 19.2 *Scutischyrocerus*; 20.1 *Grandidierella*, 20.2 *Paracorophium*.

pereopods 5 to 7 are subchelate, each with a well-developed palm and an opposable short dactylus (24.2).

The photoid and kamakid clades are both paraphyletic. The kamakids are excluded from the photoid clade because of the short peduncle of uropod 3. Within the kamakid clade, the

aorchine clade is defined by the lateral cephalic lobe, that is extended and has the eye partially enclosed (3.2), a homoplastic character state in most members of the neomegamphopid clade. The kamakine clade is defined by the lateral cephalic lobe, that is strongly extended and has the eye completely enclosed (3.3), a homoplastic

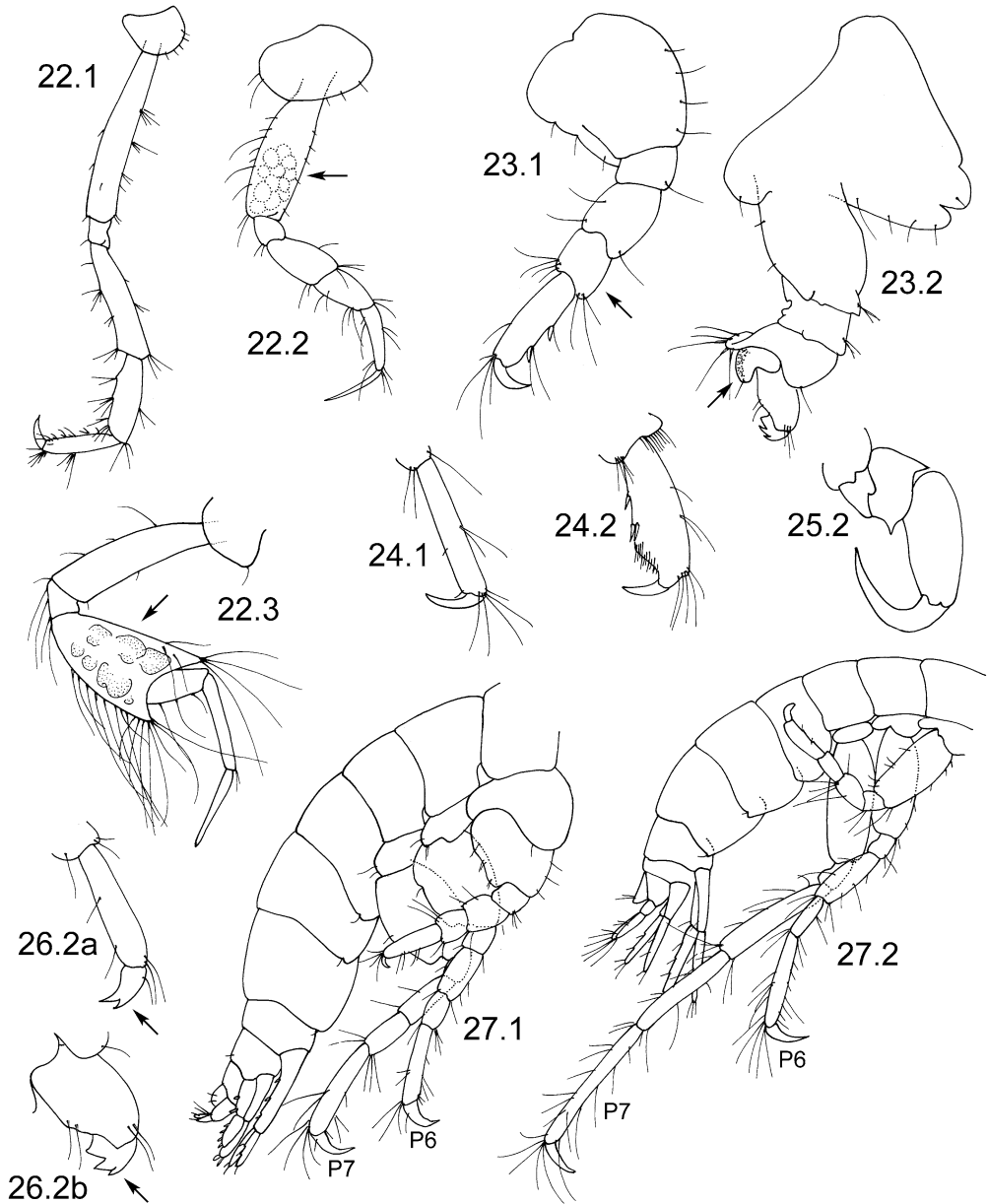


Fig. 9. Characters 22–27: 22.1 *Parunciola*, 22.2 *Meridiolembos*, 22.3 *Aetiopedes*; 23.1 *Gammaropsis*, 23.2 *Cerapus*; 24.1 *Photis*, 24.2 *Isaea*; 25.2 *Cyamus*; 26.2a *Chevalia*, 26.2b *Cerapus*; 27.1 *Gammaropsis*, 27.2 *Bemlos*.

character state that appears to be independently derived in *Ampelisciphotis* (photid clade) and in the paragammarosid clade.

The photid clade (monophyly based on homoplasy) is defined by the peduncle of uropod 3, which is long with parallel sides (34.4). This character state has also been independently derived in several genera in the amphitoid clade.

The ischyrocerid clade (monophyly based on synapomorphy) is defined by the peduncle of uropod 3 being long, broad proximally and narrow distally (34.3) and the rami of uropod 3 having tiny apical setae (36.4). This latter homoplastic character state has been independently derived in the cheluroid clade and in *Paraphotis* in the priscomilitariid clade. Within the ischyrocerid clade, there are several distinct

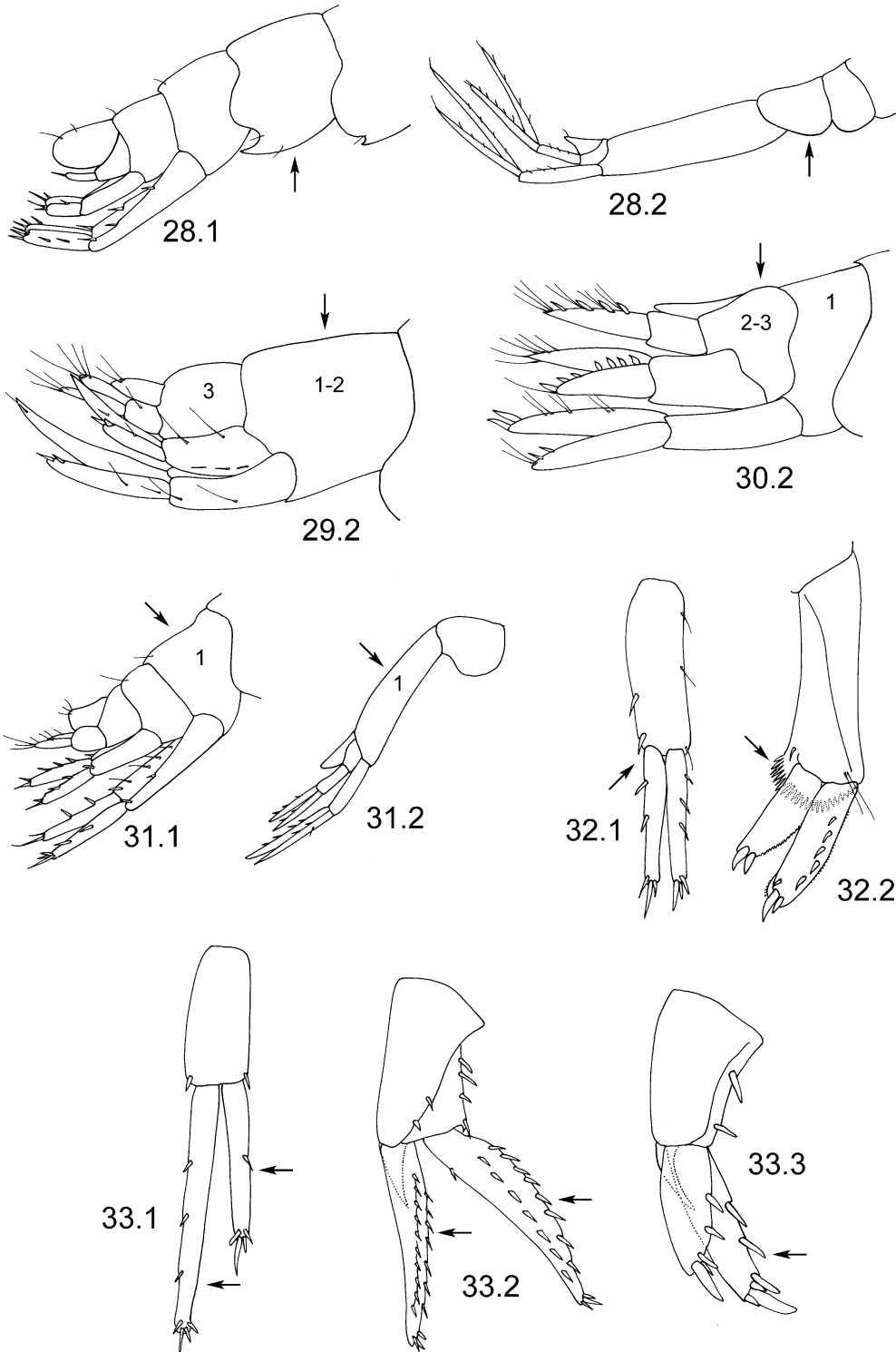


Fig. 10. Characters 28–33: 28.1 *Liocuna*, 28.2 *Dulichia* (after Laubitz, 1977); 29.2 *Chevalia*; 30.2 *Rakiroa* (after Lowry and Fenwick, 1982); 31.1 *Gammaropsella*, 31.2 *Dulichia* (after Laubitz, 1977); 32.1 *Microprotopus*, 32.2 *Siphonoecetes*; 33.1 *Ischyrocerus*, 33.2 *Arctolembos*, 33.3 *Leptocheirus*.

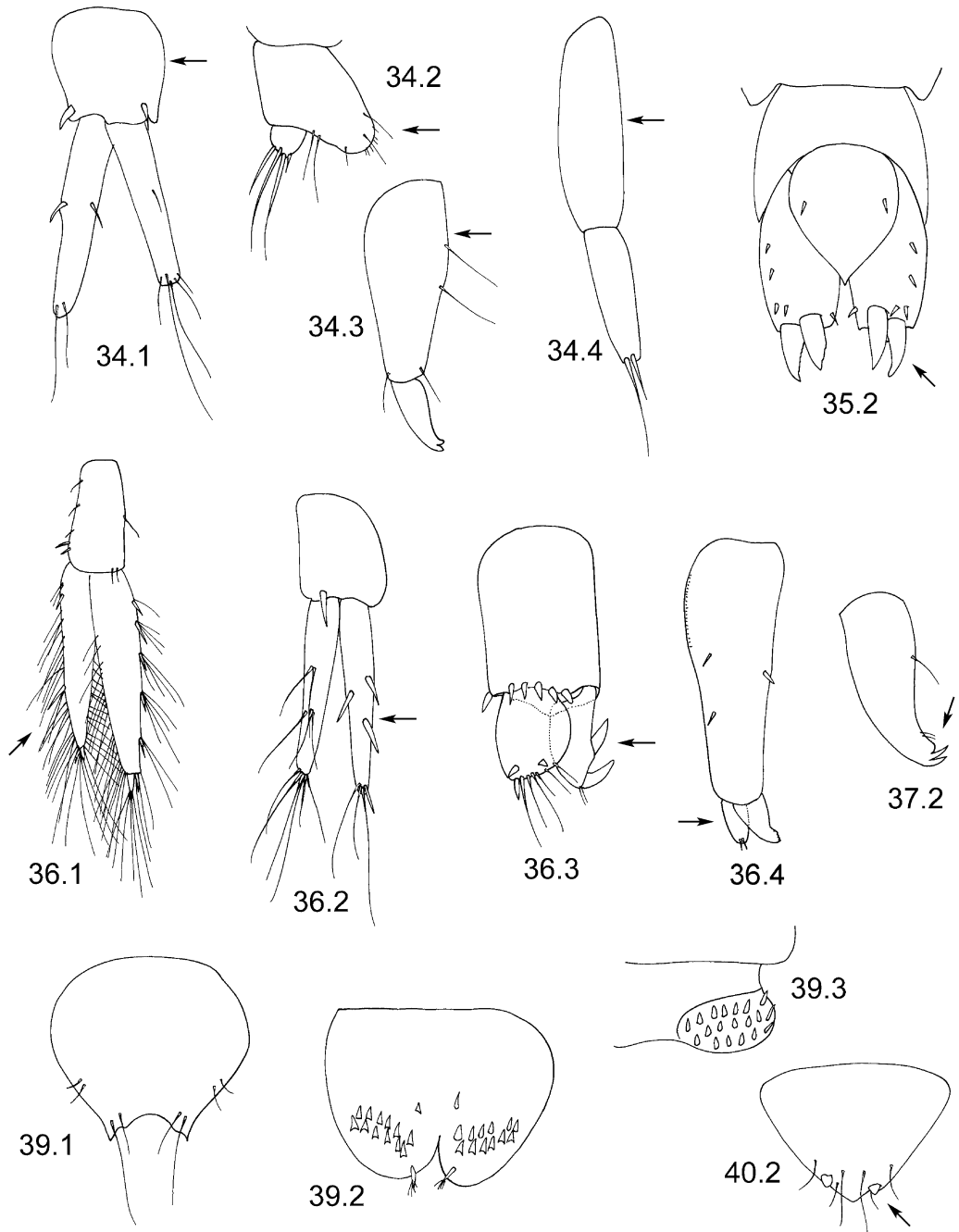


Fig. 11. Characters 34–40: 34.1 *Aorella*, 34.2 *Siphonocetes*, 34.3 *Erichthonius*, 34.4 *Papuaphotis*; 35.2 *Paradryope*; 36.1 *Gammarus*, 36.2 *Bemlos*, 36.3 *Ampithoe* (after Krapp-Schickel, 1982), 36.4 *Ischyrocerus*; 37.2 *Erichthonius*; 38.1 and 38.2 not shown; 39.1 *Bemlos*, 39.2 *Cerapus*, 39.3 *Erichthonius*; 40.2 *Papuaphotis*.

clades. The basal bonnierelline clade is paraphyletic. The ischyrocerine clade is defined by recurved apical spines on the outer ramus of uropod 3 (37.2). Within the ischyrocerine

clade, the ischyrocerin clade is paraphyletic. The siphonocetin clade (monophyly based on synapomorphy) is defined by two synapomorphies, a distal corona of spines on the

Table 2. Adjectival endings of formal taxon group names.

	Noun	Adjective
Suborder	Corophiidea	corophiidean
Infraorder	Corophiida	corophiidan
Superfamily	Corophioidea	corophioid
Family	Corophiidae	corophiid
Subfamily	Corophiinae	corophiine
Tribe	Corophiini	corophiin
Subtribe	Corophiina	corophiinan

peduncles of uropods 1 and 2 (32.2) and denticles (39.2) or recurved hooks (39.3) on the telson, and one homoplasy, accessory spines on the anterior margins of the dactyli of pereopods 5 to 7 (26.2), a character state that has been independently derived in *Photis* (photid clade) and *Paraphotis* (priscomilitariid clade) and in the chevalioid clade within the corophiidan clade.

The large caprellid clade (monophyly, based on synapomorphy) is defined by three synapomorphies: the modified head (2.1–4); an extremely elongate urosomite 1 (31.2)—in some derived members of the caprellids, it is highly modified; uropod 3 without rami (35.2), which occurs in all members of this clade except the basal genus *Parunciola*. This homoplastic character state has been independently derived in the corophiidan clade among some genera of the unciolid clade.

The podocerid clade is paraphyletic. It is excluded from the rest of the caprellid clade because pereonite 7 is never strongly rotated posteriorly (14.1). The dulichiid clade (monophyly, based on homoplasy) is defined by a triangular head (2.3) and pereonites 6 and 7 fused and orientated posterodistally (13.2). Members of the dulichiid clade have a glandular basis on pereopods 3 and 4 (22.2), an apparent reversal within the caprellid group. The caprellid clade (monophyly, based on synapomorphy) has the head partially or completely coalesced with pereonite 1 (1.2) and triangular or round with a distinct neck region (2.2–3). Most members have pereopods 3 and 4 reduced or absent (21.2), and all have pereopods 5–7 to some degree prehensile (25.2) and uropod 3 vestigial or absent (34.5).

The caprogammarid clade is paraphyletic. The cyamid clade is defined by having a columnar head (2.5). The caprellid clade (monophyly based on synapomorphy) is defined by having a round head with a distinct neck region (2.4). The paracercopine clade is defined by the

unique combination of round head with a distinct neck region, mandible molar absent, and urosomites 1 and 2 not coalesced. The phthisicine clade is defined by the unique combination of head round with a distinct neck region, mandible molar absent, and urosomites 1 and 2 coalesced. The caprelline clade is defined by a rounded head with a distinct neck region coupled with the possession of a mandible molar. The tree is presented as a formal classification in Table 3.

Tree Discussion

The corophiidean tree is well-resolved at the basal dichotomy and has a number of well-supported clades thereafter, but the “spine” supporting these clades is less well resolved. The basal resolution reflects early significant changes in corophiidean evolution, changes that are preserved by their own successful radiations. The weak relationships between clades within the tree indicates past extinctions of linking taxa. The well-resolved clades indicate successful recent radiations. The endpoints lack resolution because they are at a level that is not accommodated in the current analysis.

Only three unambiguous reversals occurs on our tree. In the dulichiid clade (glandular pereopods 3–4); in the haplocheirin clade (small coxa 1), and in *Falcigammaropsis* (photid clade) and *Luconacia* (caprellid clade) (antenna 1 short peduncular article 3). Homoplasy between families is extensive but not rampant, occurring in about half (21) of the 41 characters.

Many clades are paraphyletic or based on autapomorphies. Strongly supported clades within the corophiidan clade are the cheluroid, chevalioid, aroid and aroid, amphithoid and corophiine clades. Within the caprellidan clade, the rakiroid, neomegamphopoid, isaoid, photid, ischyrocerid, siphonoecetin, podocerid, dulichiid, and caprellid clades are all well supported. Weakly supported clades are the microprotopoid, priscomilitariid, and protomeideine clades. The tree terminates in some strong and some weak clades as a result of variations in character state support.

Weak (neutral) clades can align with several clades without any increase in tree length. Joining weakly supported clades with well-supported clades results in the taxa at the base of the strong clade no longer having synapomorphic characters to define them. For example, in the tree presented here, *Isaea* and *Pagurisea* are a clade (Isaеоidea) defined by a synapomorphy, while

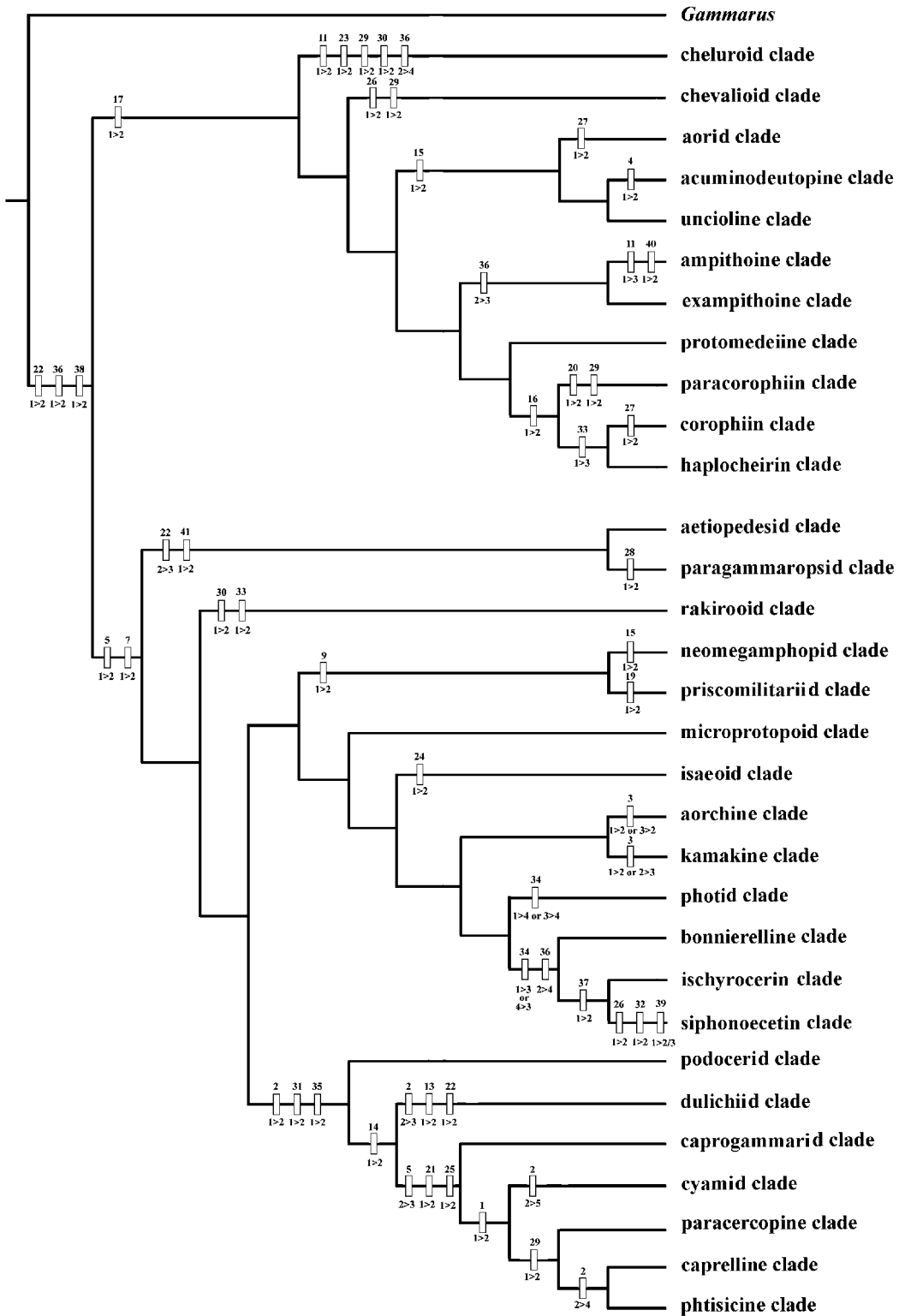


Fig. 12. Cladogram of the relationships of taxa within the Corophiidea. Boxes represent synapomorphies with character-state transformations.

Table 3. Classification of Suborder Corophiidea.

Infraorder Corophiida
Superfamily Aoroidea
Family Aoridae
Family Unciolidae
Subfamily Acuminodeutopinae
Subfamily Unciolinae
Superfamily Cheluroidea
Family Cheluridae
Superfamily Chevalioidea
Family Chevaliidae
Superfamily Corophioidea
Family Ampithoidae
Subfamily Ampithoinae
Subfamily Exampithoinae
Family Corophiidae
Subfamily Corophiinae
Tribe Corophiini
Tribe Haplocheirini
Tribe Paracorophiini
Subfamily Protomedeiinae
Infraorder Caprellida
Superfamily Aetiopedesoidea
Family Aetiopedesidae
Family Paragammaropsidae
Superfamily Caprelloidea
Family Caprellidae
Subfamily Caprellinae
Subfamily Paracercopinae
Subfamily Phtisicinae
Family Caprogammaridae
Family Cyamidae
Family Dulichiidae
Family Podoceridae
Superfamily Isaeoidea
Family Isaeidae
Superfamily Microprotopoidea
Family Microprotipidae
Superfamily Neomegamphoidea
Family Neomegamphopidae
Family Priscomilitariidae
Superfamily Photoidea
Family Ischyroceridae
Subfamily Bonnierellinae
Subfamily Ischyrocerinae
Tribe Ischyrocerini
Tribe Siphonoecetini
Family Kamakidae
Subfamily Aorchinae
Subfamily Kamakinae
Family Photidae
Superfamily Rakirooidea
Family Rakiroidae

Microtopus forms a clade of its own (Microprotopoidea) that has no synapomorphy with any other defined clade. These two clades will not join with any other clade, except each other, without increasing the tree length. Neither clade has the defining character of the isaeoid clade, but they are more aligned to the isaeoids than to any other group. Joining these two clades would

result in loss of the synapomorphy of the Isaeoidea. Consequently, we have left them as independent clades.

Two previous studies have attempted to elucidate the phylogenetic position of the corophiidean taxa within the Amphipoda. In a study by Kim and Kim (1989), the only corophiidean groups chosen were representatives of podocerids, caprogammarids, and caprellids, all members of the Caprelloidea. For Kim and Kim (1989), these taxa formed a monophyletic group with oedicerotid, dexaminid, and ampeliscid amphipods. In their strict consensus tree, this clade was defined by coalescing of the urosomites. Their conclusion is unacceptable to us for the following reasons. First, the sample size was too limited and too biased. It included only a small section of caprellidan amphipods and no representative corophiidan amphipods. Second, the coalesced urosomites do not define the Corophiidea or either of its infraorders. In our opinion, the coalescence of urosomites is a homoplastic character state that has been independently derived several times within the corophiidean amphipods and a number of times outside the group. Kim and Kim (1989) suggested that corophiidan and caprellidan amphipods form a monophyletic group. Their conclusion was based on the assumption that “podocerid” and “caprogammarid” amphipods were corophiids. We agree with their conclusion, but because podocerids and caprogammarids are both caprellidan amphipods, only the monophyly of the Caprellida is supported by their analysis.

In a recent paper by Berge *et al.* (2000), the Corophiidea of Barnard and Karaman (1984) was rejected as polyphyletic. They analyzed sixteen corophiidean taxa, which appear in their analysis in two clades. One group of corophiidean taxa associate with ten other families including the Gammaridae to form one clade, while another group of corophiideans associate with six other families, including the Oedicerotidae and Hyalidae, to form the other clade. It is not implicitly stated which corophiidean taxa are allocated to which clade (Corophiidae *sensu stricto* and Corophiidae (in part)). Clade 1 is said to be defined by two synapomorphies and clade 2 by 13 synapomorphies. Unfortunately, no information is provided concerning what character states are the basis for these synapomorphies (this information might have been presented in Appendix 3, but this appears to

have been omitted from the paper). It is, therefore, not possible to evaluate the highly unusual relationships that they propose, nor to compare the results of their study with that of ours or any other previously published study.

Evolutionary Biology of the Corophiidean Amphipods

The corophiideans are primarily domicolous amphipods characterized by a deep, dorsoventrally thickened telson, reduced in some highly derived taxa, which was almost certainly evolved at their origin as an adaptation to “nest” dwelling. A dorsoventrally thickened telson adorned with hooks, cusps, spines, or setae would be a valuable structure for maintaining an animal in its nest, and most living domicolous corophiideans possess such structures.

The corophiideans are also principally detritivores and evolved to exploit this resource in two different habitats—on or close to the bottom, or in the water column. One group of corophiideans (the corophiidan clade) evolved to exploit detritus settled out on the bottom and developed the second pair of antennae into structures for scraping detritus off the bottom and pulling it towards their mouthparts. This did not necessitate excessive lateral movement of the second antennae, and accordingly, extreme head recession was not required (Fig. 1a, b). In some taxa, an increase in the size of the second antennae required a significant excavation of the anterodistal part of the head to accommodate the huge bases of these podomeres (e.g., *Corophium*, Fig. 1c). This excavation has evolved independently in a few caprellidans (e.g., *Siphonoecetes*, Fig. 1f). The corophiidans also improved their tube-building abilities to facilitate a specialized type of filter feeding. This was the filtering of particles with modified appendages, usually gnathopods, from water drawn through the tube by the beating of the pleopods. The first pair of antennae, relieved of any food gathering deployment, were developed as receivers of sensory information, spread out in front of them to sense water-borne vibrations. Although the flagellum may have been lengthened to increase the distance for the gathering of sensory information, article 3 of the peduncle remained in its ancestral state, much shorter than peduncular article 2. Presumably even when flexed backwards over the tube, two articulations were sufficient. In some cases, the third peduncular article is no longer than

a flagellar article. Neither antenna 1 nor antenna 2 required the extensive setation of the filter-feeding caprellidans.

The other group, specializing in the capture of water-borne particles (the caprellidan clade), developed their first and second antennae as feeding structures. This was accomplished by lengthening the peduncular and flagellar articles and increasing the density of setae to form a filtering net. In order to spread this “net” as widely as possible, the lower margin of the head became deeply recessed. This facilitated lateral spread in the second antennae (Fig. 1d, e). The complex process of handling small particles collected by the antennae was carried out not only by the mouthparts but also by the first gnathopods, which, in some extant taxa (e.g., *Erichthonius*), have become effectively a second pair of maxillipeds. The passive filtering method evolved by caprellidans requires their use in moderate to strong water currents. In contrast to this, the active pump filter-feeding adopted by many corophiidans has allowed them to colonize areas of low, or almost no, water current, and their deposit-scraping strategy has actually required them to live in areas of high siltation and, consequently, low flow regimes.

During the evolution of both infraorders, considerable adaptive radiation occurred leading to parallel or convergent innovations (homoplasies). Nevertheless, the stamp of early evolutionary feeding strategies was retained. Once the anterodistal margin of the head had become recessed, there may have been little advantage in reversing the trend. However, further reduction of the entire head capsule in podocerids and eventually caprellids led to highly derived heads in these clades.

When antenna 1 required elongation for filter feeding in caprellidans, all three peduncular articles were lengthened. Because elongation carries with it penalties of increased fragility and decreased muscular efficiency, the end result was for the initially short article 3 and relatively short article 1 to be increased differentially compared with the primarily longer article 2 to provide three long articles. When the adoption of different evolutionary pathways by caprellidans necessitated secondary shortening of the antennae, all three articles tended to be shortened more or less equally, there being, apparently, no particular advantage in a return to the unequal peduncular articles, retained by the principally bottom feeding

corophiidans. Members of the corophiidan clade can, therefore, almost always be distinguished from the members of the caprellidan clade by the disparity in the length of article 3 compared with article 2 (Fig. 2).

Early in the evolution of the corophiidan line, pereonite 1 took on greater importance than had previously been the case. This led, in the aoroid clade, to the universal development of an enlarged gnathopod 1 (especially in males), which dominated in size over gnathopod 2. The importance of pereonite 1 in corophiidans is demonstrated, in most taxa, by the fact that coxa 1 is larger than, or at least equal in size to, coxa 2 even in those taxa (e.g., *Cheiriphotis*, Fig. 8, 17.2), where gnathopod 2 remains larger than gnathopod 1. Exceptions to this trend are seen in a few amphithoids and *Leptocheirus*. Gnathopod 1 dominance also expresses itself in nonaoroid corophiidans such as *Paragrubia* and *Exampithoe* (Amphithoidae) and in *Anonychocheirus* (Corophiidae). By contrast, in the few caprellidans where gnathopod 1 dominates gnathopod 2 (e.g., *Paraloiloi*, Fig. 8, 17.1), coxa 1 remains smaller than coxa 2. Only *Kamaka* (kamakine clade) and males of species of the neomegamphopoid clade exhibit an enlarged coxa 1.

Feeding Styles

From the basic lifestyle of the corophiidans and caprellidans emerged a number of more specialized clades. Within the corophiidan clade, one line moved from feeding on generalized organic detritus and algal debris to direct ingestion of living algal tissue (the amphithoids), or in one clade (cheluroids), of wood. Also within the corophiidans, arose the interstitial *Uncinotarsus*. It is clear that some, if not most, corophiideans can be opportunistic predators. *Microdeutopus gryllotalpa* Costa, 1853 (Corophiida, Aoridae) will seize and consume small crustaceans passing the opening of its tube (personal observation), and an undescribed species of *Grandidierella* (Corophiida, Aoridae) from northwestern Australia has been observed feeding on insect larvae (Roux, personal observation). Some species may be more dedicated, even obligate predators. *Falcigammaropsis excavata* Myers, 1995 (Caprellida, Photidae), for example, possesses a raptorial maxilliped with a strongly falcate and sharply pointed palp article 4, a vestigial mandibular molar (see Watling, 1993), and an acute epistome, all of which attest to a predatory

way of life. This and some other Ischyroceridae, such as *Bonnierella*, may be ambush “sit and wait” predators. In the Caprellidae, *Caprella aequilibra* Leach, 1814, has been recorded feeding on amphipods and polychaetes (McCain, 1968), although most *Caprella* species are probably suspension feeders.

Nothing is known about the feeding strategies of the aetiopedesoids.

Home-dwelling

A major evolutionary innovation of corophiideans was the development of glands in the bases of pereopods 3–4, which open through pores at the tips of the dactyls. These glands produce amphipod “silk” for the purposes of nest-building. Nest-building is common among corophiidans. Tubes may be quite flimsy, doing little more than lining a mud burrow, e.g., *Corophium volutator*, or holding together the edges of an algal blade (e.g., *Exampithoe kutti*, see Poore and Lowry, 1997), or they may be relatively substantial, able to maintain their integrity without additional material, although generally they do incorporate various types of debris (e.g., *Lembos websteri* Shillaker and Moore, 1978; *Corophium ellisi* Barnard *et al.*, 1988). Photoidea feeding from the water column (e.g., *Jassa*) also frequently inhabit nests. One innovation, found only in caprellidans, is the development of mobile homes. Within the Siphonoecetini, the *Cerapus*-group developed a strong tube that can be carried around and temporarily attached, allowing them to move to good feeding areas and then move away when conditions deteriorate. A somewhat different approach was adopted by the *Siphonoecetes*-group that use the empty shells of other organisms such as gastropods, scaphopods, or polychaetes. The basal group within the Siphonoecetini, the *Ericthonius*-group (see Lowry and Berents, 1996), have retained the fixed tube of the ancestral Ischyrocerinae. The *Siphonoecetes*-group and the *Cerapus*-group are the only corophiideans to exploit this lifestyle. For a more detailed classification of corophiidean tubes, see Barnard *et al.*, 1988.

Another group, the aetiopedesoids, have silk-glands in the merus of pereopods 3–4. It is not known whether this is an independently derived character state or whether all glandular pereopods in amphipods are homologous. If they are, then the Ampeliscidae become a sister taxon to the Corophiida as suggested by Moore and Myers (1988).

In the caprellidans, one evolutionary line led to the abandonment of a nest-dwelling life-style in favor of a free-living one. Members of the caprelloid clade, with the exception of dulichiids, lack silk glands in their pereopods. The caprelloids became efficient graspers on algae and sedentary animals, moving high up the substrate to filter feed in the water current sweeping past them (Barnard *et al.*, 1988). Today, this lineage is represented by the podocerids, dulichiids, caprogammarids, cyamids, and caprellids. Although unable to build tubes themselves, podocerids will nevertheless occupy tubes produced and vacated by tube-building corophiideans (Barnard *et al.*, 1988) thus indicating their domicolous ancestry. In podocerids and dulichiids, pereonites 5 to 7 together with their pereopods form a grasping structure that forms a rigid base for the movements of the more anterior region of the body. This has been taken even further in caprellids where the posterior and anterior regions are almost geniculate, with the anterior region becoming elongated and able to move freely for filter feeding, grazing, or predation, while still maintaining a rigid grasp on the substrate with pereopods 5–7. With this structure in place, the urosome probably became a liability and accordingly was reduced. The retention of at least a remnant of the urosome may have been necessary for the retention of a telson, although the function of a telson in caprellids is unclear. Another group of caprelloids took the major step of associating with cetaceans to form the cyamids.

Male Recognition Characteristics

Both infraorders of Corophiidea are primitively sedentary forms. This way of life evolved in combination with precopulatory “mate-guarding,” which, although not limited to sedentary forms within the Amphipoda, is probably a corollary of it. Mate-guarding leads to the development of male recognition characteristics (Conlan, 1991). Sexual dimorphism appears to be a fundamental feature of the Corophiidea and involves modification (usually enlargement) in the male of either, or both, pairs of gnathopods and occasionally of antenna 2. The ancestral state is an enlarged gnathopod 2, but in some corophiidans (all aoroids and some amphithoids and corophiids) and in some caprellidans (neomegamphopids and kamakids), gnathopod 1 becomes greatly enlarged. In a few neomegamphopids and kamakids, both

pairs of gnathopods are enlarged. Enlargement of antenna 2 in males has occurred in both caprellidans and corophiidans (although it is not always sexually dimorphic). Thus, a deep excavation of the anteroventral margin of the head has occurred independently in these two clades. It is a character state that has arisen from the weakly recessed and weakly excavate head of corophiidans as well as from the strongly recessed and weakly to moderately excavate head of caprellidans (Fig. 1c, f). The aetioepodesoids are unusual among corophiideans in exhibiting no sexual dimorphism.

Body Form

There is a much greater diversity of body form in the caprellidans than there is in the corophiidans. Caprellidans range from subcylindrical siphonoecetins, with strongly reduced lateral shields, through laterally flattened photids, with strongly developed lateral shield, to globular clinging podocerids, etiolated abdomen-reduced caprellids, and whale-clinging cyamids. Corophiidans, by contrast, show a greater uniformity of body form, the extremes being only the high degree of dorsoventral flattening in some corophiids, unciolids, and chelurids and the increased etiolation of some aorids.

KEY TO FAMILIES AND SUBFAMILIES OF COROPHIIDEA

1. Antenna 1 article 3 short, half or less length of article 2 2
 - Antenna 1 article 3 long, more than half length of article 2 10
2. Uropod 3 one ramus with recurved robust setae 3
 - Uropod 3 without recurved robust setae 4
3. Labium outer plate with distal notch
 - Ampithoinae (Ampithoidae)
 - Labium outer plate lacking distal notch
 - Exampithoinae (Ampithoidae)
4. Gnathopods 1–2 forming a sieving basket
 - Corophiinae (Corophiidae)
 - Gnathopods 1–2 not together forming a sieving basket 5
5. Some or all urosomites coalesced 6
 - All urosomites free 7
6. Uropod 3 uniramous, pereopods 5–7 lacking accessory spines Cheluridae
 - Uropod 3 biramous, pereopods 5–7 with accessory spines Chevallidae
7. Gnathopod 1 not enlarged
 - Protomedeiinae (Corophiidae)
 - Gnathopod 1 enlarged 8

8. Pereopod 7 disproportionately longer than pereopod 6 Aoridae
 – Pereopods 5, 6, and 7 in regular length progression 9
9. Head lateral cephalic lobes rounded Unciolinae (Unciolidae)
 – Head lateral lobes triangular, terminating acutely Acuminodeutopinae (Unciolidae)
10. Urosomites free 11
 – Urosomites coalesced Rakiroidae (Rakirooidea)
11. Pereopod 5–7 prehensile 12
 – Pereopod 5–7 not prehensile 17
12. Pereopods 5–7, palm well developed and opposable to a short dactylus Isaeidae (Isaeoidea)
 – Pereopods 5–7 dactylus elongated and closing along most of posterior margin of propodus 13
13. Head columnar Cyamidae (Caprelloidea)
 – Head rectangular or round 14
14. Head rectangular Caprogammaridae (Caprelloidea)
 – Head round with distinct neck region 15
15. Pereopods 3–4 absent Caprellinae (Caprellidae)
 – Pereopods 3–4 present (may be minute) 16
16. Urosomites 1 and 2 coalesced Phtisicinae (Caprellidae)
 – Urosomites 1 and 2 not coalesced Paracercopinae (Caprellidae)
17. Gnathopod 1 enlarged, much larger than gnathopod 2 Neomegamphopidae (Neomegamphopoidea)
 – Gnathopod 1 not enlarged, smaller than gnathopod 2 18
18. Uropod 3 peduncle long, more than 2 × as long as broad 19
 – Uropod 3 peduncle short, less than 2 × as long as broad, or vestigial 21
19. Uropod 3 peduncle narrower distally 20
 – Uropod 3 peduncle parallel-sided Photidae (Photoidea)
20. Uropod 3 with recurved spines Ischyrocerinae (Ischyroceridae) [in part]
 – Uropod 3 without recurved spines Bonnierellinae (Ischyroceridae)
21. Urosomite 1 or 1 and 2 extremely elongate, length at least three times breadth 22
 – Urosomite 1 or 1 and 2 not extremely elongate, less than three times breadth 23
22. Head triangular, bases of pereopods 3 and 4 expanded Dulichiidae (Caprelloidea)
 – Head rectangular, bases of pereopods 3 and 4 linear Podoceridae (Caprelloidea)
23. Coxa 2 in male greatly enlarged and shield-like Priscomilitariidae (Neomegamphopoidea)
 – Coxa 2 in male not greatly enlarged and shield-like 24
24. Uropod 3 peduncle with distoventral corona of fine spines Ischyrocerinae (Ischyroceridae) [in part]
 – Uropod 3 peduncle lacking a distoventral corona of fine spines 25
25. Head lateral cephalic lobes moderately to strongly produced 26
 – Head lateral cephalic lobes weakly produced Microprotopidae

26. Head lateral cephalic lobe moderately extended; eye, if present, situated proximal to the lobe Aorchinae (Kamakidae)
 – Head lateral cephalic lobe strongly extended; eye, if present, enclosed completely or partially in the extended lobe 27
27. Pereopods 3–4 with carpus enlarged and containing glands Kamakinae (Kamakidae)
 – Pereopods 3–4 with carpus not enlarged, without glands 28
28. Uropod 3 rami with dense covering of fine setae, epimera vestigial Paragammaropsidae (Aetiopedesoidea)
 – Uropod 3 rami with fine and robust setae on the lateral margins, epimera present Aetiopedesidae (Aetiopedesoidea)

DIAGNOSES

Corophiidea Leach, 1814

Diagnosis.—Pereopods 3+4 basis glandular. Uropod 3 with setae robust and slender. Telson dorsoventrally thickened.

Infraorder Composition.—Corophiida Leach, 1814; Caprellida Leach, 1814.

Corophiida Leach, 1814

Diagnosis.—Head lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe, anteroventral margin weakly recessed, rarely not recessed, and moderately excavate, or strongly excavate for reception of enlarged antenna 2. Antenna 1 peduncular article 3 almost always short, half or less length of article 2. Gnathopod 1 coxa enlarged in both sexes, generally larger than coxa 2. Uropod 3 with mixture of robust and slender setae, or with 1–2 recurved, robust apical setae. Telson with or without hooks or denticles.

Superfamily Composition.—Aoroidea Stebbing, 1899c; Cheluroidea Allman, 1847; **Chevalioidea** fam. nov.; Corophioidea Leach, 1814.

Aoroidea Stebbing, 1899c

Diagnosis.—Head rectangular, anterodistal margin recessed, lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe; anteroventral margin weakly recessed, moderately excavate. Mandible palp 3-articulate or absent, article 3, when present, asymmetrical, distally rounded, with setae extending along most of posterodistal margin, or approximately parallel-sided with distal setae only; posterior margin with setae of variable length, or with comb of short setae and few long, slender setae.

Gnathopod 1 enlarged in males and females, or only in males; coxa 1 enlarged, larger than coxa 2. Gnathopod 2 merus not enlarged. Pereopods 5–7 without accessory spines on anterior margin. Pereopod 7 longer or much longer than pereopod 6. Urosomites not coalesced. Uropods 1 and 2 without dense array of robust setae. Uropod 3 peduncle relatively short, length usually 2 times or less breadth; with 2, 1, or no rami. Telson without hooks or denticles.

Family Composition.—Aoridae Stebbing, 1899c; **Unciolidae** fam. nov.

Aoridae Stebbing, 1899c

Diagnosis.—Head anteroventral margin moderately excavate. Pereopod 7 very elongate, entire propodus extending beyond pereopod 6.

Generic Composition.—*Aora* Krøyer, 1845; *Aorella* Myers, 1981b; *Aoroides* Walker, 1898; *Archaeobemlos* Myers, 1988b; *Arctolembos* Myers, 1979a; *Australomicrodeutopus* Myers, 1988a; *Autonoe* Bruzelius, 1859; *Bemlos* Shoemaker, 1925; *Camacho* Stebbing, 1888; *Chevreuxius* Bonnier, 1896; *Columbaora* Conlan and Bousfield, 1982b; *Globosolembos* Myers, 1985; *Grandidierella* Coutière, 1904; *Lemboides* Stebbing, 1895; *Lembos* Bate, 1856; *Meridiolembos* Myers, 1988a; *Microdeutopus* Costa, 1853; *Paraoroides* Stebbing, 1910; *Paramicrodeutopus* Myers, 1988a; *Plesiolembos* Myers, 1988a; *Protolembos* Myers, 1988a; *Tethylembos* Myers, 1988a; *Xenocheira* Haswell, 1879.

Species Used in the Analysis.—*Aora adpressa* Myers and Moore, 1983; *A. hebes* Myers and Moore, 1983; *A. hircosa* Myers and Moore, 1983; *A. mortoni* (Haswell, 1879); *A. spinicornis* Afonso, 1976; *A. typica* Krøyer, 1845; *Aorella multiplex* Myers, 1981b; *Aoroides columbiae* Walker, 1898; *A. exilis* Conlan and Bousfield, 1982b; *A. vitiosus* Myers, 1995; *Archaeobemlos philacanthus* (Stebbing, 1888); *Arctolembos arcticus* (Hansen, 1887); *Autonoe rubromaculatus* (Ledoyer, 1973); *A. spiniventrus* Della Valle, 1893; *Bemlos podoceroides* (Walker, 1904); *B. pugiosus* Myers, 1995; *B. tigrinus* (Myers, 1979b); *B. waipio* (J. L. Barnard, 1970); *Camacho bathyplous* Stebbing, 1888 of J. L. Barnard, 1961; *Globosolembos ovatus* Myers, 1985; *G. tiafau* Myers, 1985; *Grandidierella bispinosa* Schellenberg, 1938 of Myers, 1985; *G. macronyx* K. H. Barnard, 1935; *G. spinicoxa* Myers, 1972; *Microdeuto-*

pus bifidus Myers, 1977; *M. stationis* Della Valle, 1893 of Myers, 1982a.

Unciolidae fam. nov.

Diagnosis.—Head anteroventral margin moderately excavate, or strongly excavate for reception of enlarged antenna 2. Pereopod 7 not very elongate, entire propodus not extending beyond pereopod 6.

Type Genus.—*Unciola* Say, 1818.

Subfamily Composition.—**Acuminodeutopinae** subfam. nov.; **Unciolinae** subfam. nov.

Acuminodeutopinae subfam. nov.

Diagnosis.—Head lateral cephalic lobes acute.

Type Genus.—*Acuminodeutopus* J. L. Barnard, 1959.

Generic Composition.—*Acuminodeutopus* J. L. Barnard, 1959; *Rudilemboides* J. L. Barnard, 1959; *Wombalana* Thomas and Barnard, 1991.

Species Used in the Analysis.—*Acuminodeutopus heteruropus* Barnard and Reish, 1959; *A. naglei* (Bousfield, 1973); *Rudilemboides stenopodus* J. L. Barnard, 1959; *Wombalana rachayai* Myers, 2002.

Unciolinae subfam. nov.

Diagnosis.—Head lateral cephalic lobes rounded.

Generic Composition.—*Dryopoides* Stebbing, 1888; *Janice* Griffiths, 1973; *Liocuna* Myers, 1981a; *Neohela* Smith, 1881; *Orstomia* Myers 1998; *Pediorophium* Karaman, 1981; *Pseudunciola* Bousfield, 1973; *Pterunciola* Just, 1977; *Ritaumius* Ledoyer, 1978; *Rildardanus* J. L. Barnard, 1969; *Uncinotarsus* L'Hardy and Truchot, 1964; *Unciola* Say, 1818; *Unciolella* Chevreux, 1911; *Zoedeutopus* J. L. Barnard, 1979.

Species Used in the Analysis.—*Dryopoides westwoodi* Stebbing, 1888; *Janice spinidactyla* Griffiths, 1973; *Liocuna caeca* Myers, 1981a; *Neohela monstrosa* Boeck, 1861 of Sars 1895; *Orstomia kanakia* Myers, 1998; *Pseudunciola obliqua* (Shoemaker, 1949); *Rildardanus tros* J. L. Barnard, 1969; *Uncinotarsus pellucidus* L'Hardy and Truchot, 1964; *Unciola crassipes* Hansen, 1888; *U. laticornis* Hansen, 1888; *U. serrata* Shoemaker, 1945; *Unciolella lunata* Chevreux, 1911; *Zoedeutopus cinaloanus* J. L. Barnard, 1979.

Remarks.—*Janice* can be placed within the “*Paracorophium* clade” with an increase of one step in the cladogram. *Janice* has a similar gnathopod 2 to *Paracorophium*, and we believe this to be a convergent character.

Neohela is placed here because it has the defining characters of a corophioid and the enlarged gnathopod 1 of an uncioline. In not having epimera, it resembles the caprellidans, but moving it to anywhere in that infraorder increases the tree length by seven steps.

Zoedeutopus can be placed in the Acumino-deutopinae without changing the tree length, but it does not have the distally acute lateral cephalic lobe that characterizes that group.

Cheluroidea Allman, 1847

Diagnosis.—Head lateral cephalic lobe weakly extended; eye situated proximal to lobe; anteroventral margin weakly recessed and weakly excavate. Mandible palp 3-articulate, article 3 asymmetrical, distally rounded, with setae extending along most of posterodistal margin. Labium outer plate weakly excavate. Gnathopod 1 not enlarged either in males or females; coxa 1 as large as coxa 2. Gnathopod 2 merus not enlarged. Pereopod 5 carpus small, lunate. Pereopods 5–7 without accessory spines on anterior margin. Urosomite 1–3 coalesced. Uropods 1 and 2 without dense array of robust setae. Uropod 3 outer ramus with vestigial apical setae. Telson without hooks or denticles.

Remarks.—The cheluroid clade can be combined with the chevalioid clade with no increase in tree length. We have kept them separate because cheluroids, although they are a basal taxon, have a unique life-style and are specialized herbivores that feed on wood.

Cheluridae Allman, 1847

Diagnosis.—As for superfamily.

Generic Composition.—*Chelura* Philippi, 1839; *Niplochelura* J. L. Barnard, 1959; *Tropichelura* J. L. Barnard, 1959.

Species Used in the Analysis.—*Chelura terebrans* Philippi, 1839 of Sars, 1895.

Chevalioidea superfam. nov.

Diagnosis.—Head lateral cephalic lobe weakly extended, eye situated proximal to lobe; anteroventral margin weakly recessed, moderately excavate. Mandible palp article 3 asymmetrical, distally rounded, setae extending along most of posterodistal margin, posterior margin with

setae of variable length. Gnathopod 1 not enlarged in either males or females; coxa 1 as large or larger than coxa 2. Gnathopod 2 in males larger than gnathopod 1. Pereopod 5 carpus small, lunate, dactylus with or without accessory spine on anterior margin. Urosomites 1 and 2 coalesced. Uropod 3 peduncle short, length 2 times or less breadth, with sides expanded; outer ramus without recurved spines. Telson without hooks or denticles.

Remarks.—See under Cheluroidea.

Chevaliidae fam. nov.

Diagnosis.—As for superfamily.

Type Genus.—*Chevalia* Walker, 1904.

Generic Composition.—*Chevalia* Walker, 1904.

Species Used in the Analysis.—*Chevalia aviculae* Walker, 1904.

Corophioidea Leach, 1814

Diagnosis.—Head lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe; anteroventral margin not recessed, weakly recessed and weakly to moderately excavate, or strongly recessed and strongly excavate. Mandible palp with 0, 2, or 3 articles, article 3, when present, asymmetrical and distally rounded with setae extending along most of posterodistal margin, or approximately parallel-sided with distal setae only. Gnathopod 1 enlarged or not; coxa 1 usually enlarged. Gnathopod 2 in male not larger, slightly larger, or much larger, than gnathopod 1. Gnathopod 2 merus not enlarged, or broadened and free, or broadened and fused along its entire length with posterior margin of carpus. Pereopods 5–7 without accessory spines on anterior margin. Pereopod 7 a little longer or much longer than pereopod 6. Urosomites free, or 1 and 2 coalesced or 1–3 coalesced. Uropods 1 and 2 with or without dense array of robust setae. Uropod 3 peduncle short or long, parallel sided; biramous or uniramous, with or without recurved spines. Telson without hooks or denticles.

Family Composition.—Ampithoidae Boeck, 1871; Corophiidae Leach 1814.

Ampithoidae Boeck, 1871

Diagnosis.—Labium outer plate with or without distal notch or excavation. Uropod 3 outer ramus with 2 recurved robust setae, or with 1 small, straight or weakly curved robust seta. Telson cusps present or absent.

Subfamily Composition.—Ampithoinae Boeck, 1871; Exampithoinae subfam. nov.

Ampithoinae Boeck, 1871

Diagnosis.—Mandible palp 3-articulate or absent. Labium outer plate with distal notch or excavation. Uropod 3 outer ramus with 2 recurved robust setae or with 1 small, straight or weakly curved robust seta.

Generic Composition.—*Ampithoe* Leach, 1814; *Amphithoides* Kossman, 1880; *Amphitholina* Ruffo, 1953; *Cymadusa* Savigny, 1816; *Macropisthopus* K. H. Barnard, 1916; *Paradusa* Ruffo, 1969; *Paragrubia* Chevreux, 1901; *Peramphithoe* Conlan and Bousfield, 1982a; *Plumithoe* Barnard and Karaman, 1991; *Pseudampithoides* Ortiz, 1976; *Pseudopleonexes* Conlan and Bousfield 1982a; *Sunamphitoe* Bate, 1857a.

Species Used in the Analysis.—*Ampithoe lacespota* Bate, 1858; *A. ramondi* Audouin, 1826; *A. kava* Myers, 1985; *Amphithoides mahafalensis* Ledoyer, 1967; *Amphitholina cuniculus* (Stebbing, 1874); *Cymadusa filosa* Savigny, 1816 of Krapp-Schickel, 1982; *C. brevidactyla* (Chevreux, 1907); *C. uncinata* (Stout, 1912) of Conlan and Bousfield, 1982a; *Paragrubia vorax* Chevreux, 1901; *Peramphithoe parmerong* Poore and Lowry, 1997; *Pseudampithoides incurvaria* (Just, 1977); *Sunamphitoe graxon* Freewater and Lowry, 1994.

Exampithoinae subfam. nov.

Diagnosis.—Mandible palp absent, 2- or 3-articulate. Labium outer plate without distal notch or excavation. Uropod 3 outer ramus with 2 recurved robust setae.

Type Genus.—*Exampithoe* K. H. Barnard, 1925.

Generic Composition.—*Exampithoe* K. H. Barnard, 1925; *Melanesius* Ledoyer, 1984.

Species Used in the Analysis.—*Exampithoe kutti* Poore and Lowry, 1997; *E. gracilipes* Ledoyer, 1984; *Melanesius cooki* Ledoyer, 1984.

Corophiidae Leach, 1814

Diagnosis.—Labium outer plate without distal notch or excavation. Uropod 3 outer ramus without recurved robust setae. Telson cusps absent.

Subfamily Composition.—Corophiinae Leach, 1814; **Protomedeiinae** subam. nov.

Corophiinae Leach, 1814

Diagnosis.—Gnathopods 1 and 2 together forming sieving structure with dense sieving setae on posterior margins of carpus and ischium. Pereopod 7 not much longer or markedly longer than pereopod 6. Uropods 1 and 2 rami with or without dense array of robust setae.

Tribe Composition.—Corophiini Leach, 1814; **Haplocheirini** tribe nov; **Paracorophiini** tribe nov.

Corophiini Leach, 1814

Additional Status

Diagnosis.—Pereopod 7 longer or much longer than pereopod 6. Uropods 1 and 2 lacking dense array of robust setae.

Generic Composition.—*Americorophium* Bousfield and Hoover, 1997; *Apocorophium* Bousfield and Hoover, 1997; *Chelicorophium* Bousfield and Hoover, 1997; *Corophium* Latreille, 1806; *Crassicorophium* Bousfield and Hoover, 1997; *Eocorophium* Bousfield and Hoover, 1997; *Hirayamaia* Bousfield and Hoover, 1997; *Laticorophium* Bousfield and Hoover, 1997; *Lobatocorophium* Bousfield and Hoover, 1997; *Medicorophium* Bousfield and Hoover, 1997; *Microcorophium* Bousfield and Hoover, 1997; *Monocorophium* Bousfield and Hoover, 1997; *Sinocorophium* Bousfield and Hoover, 1997.

Species Used in the Analysis.—*Crassicorophium crassicorne* (Bruzelius, 1859) after Bousfield, 1973; *Medicorophium rotundirostre* (Stephensen, 1915).

Haplocheirini tribe nov.

Diagnosis.—Pereopod 7 not markedly longer than pereopod 6. Uropods 1 and 2 rami with dense array of robust setae.

Type Genus.—*Haplocheira* Haswell, 1879.

Generic Composition.—*Anonychocheirus* Moore and Myers, 1983; *Haplocheira* Haswell, 1879; *Kuphocheira* K. H. Barnard, 1931; *Leptocheirus* Zaddach, 1844.

Species Used in the Analysis.—*Anonychocheirus richardsoni* Moore and Myers, 1983; *Haplocheira barbimana* Thomson, 1879 of Thurston, 1974; *Kuphocheira emancipata* Moore and Myers, 1983; *K. setimana* K. H. Barnard, 1931; *Leptocheirus bispinosus*

Norman, 1908 of Myers, 1982a; *L. guttatus* Grube, 1864; *L. pilosus* Zaddach, 1844.

Paracorophiini tribe nov.

Diagnosis.—Gnathopod 2 merus enlarged, free along anterodistal margin of carpus.

Type Genus.—*Paracorophium* Stebbing, 1899b.

Generic Composition.—*Chaetocorophium* Karaman, 1979a; *Paracorophium* Stebbing, 1899b; *Stenocorophium* Karaman, 1979b.

Species Used in the Analysis.—*Paracorophium chelatum* Karaman, 1979a; *Stenocorophium bowmani* Karaman, 1979b.

Protomedeiinae subfam. nov.

Diagnosis.—Gnathopod 1 and 2 not together forming sieving structure. Pereopod 7 not markedly longer than pereopod 6. Uropods 1 and 2 rami lacking dense array of robust setae.

Type Genus.—*Protomedeia* Krøyer, 1842.

Generic Composition.—*Cheirimedeia* J. L. Barnard, 1962a; *Cheiriphotis* Walker, 1904; *Goesia* Boeck, 1871; *Pareurystheus* Tzvetkova, 1977; *Protomedeia* Krøyer, 1842.

Species Used in the Analysis.—*Cheirimedeia macrocarpa* (Bulycheva, 1952); *C. similicarpa* Conlan, 1983; *C. zotea* J. L. Barnard, 1962a of Conlan, 1983; *Cheiriphotis pediformis* Myers, 1995; *C. rotui* Myers 1989c; *Pareurystheus dentatus* (Holmes, 1908); *P. tzetkovae* Conlan, 1983; *Protomedeia articulata* J. L. Barnard, 1962a; *P. fasciata* Krøyer, 1842; *P. grandimana* Bruggen, 1906; *P. prudens* J. L. Barnard, 1966 of Conlan, 1983.

Caprellida Leach, 1814

Diagnosis.—Head rectangular, anterodistal margin recessed; anteroventral margin moderately to strongly recessed, moderately excavate except where strongly recessed and strongly excavate for reception of enlarged antenna 2; antenna 1 article 3 long, more than half, usually much more than half, length of article 2. Coxa 1 small, almost always smaller than coxa 2. Uropod 3 with combination of slender and robust setae, with or without recurved spines. Telson with or without hooks, denticles, or recurved spines.

Superfamily Composition.—**Aetiopedesoidea** superfam. nov.; Caprelloidea Leach, 1814;

Isaeoidea Dana, 1852b; **Microprotopoidea** superfam. nov.; Neomegamphoidea Myers, 1981a; Photoidea Boeck, 1872; **Rakirooidea** superfam. nov.

Aetiopedesoidea superfam. nov.

Diagnosis.—Labrum notched (autapomorphy not used in analysis). Pereopods 3–4 with glands in enlarged merus. Epimera present or absent. Uropod 3 rami with marginal slender or robust setae. Telson extremely reduced, broad and short distolateral margins with clumps of robust setae.

Family Composition.—**Aetiopedesidae** fam. nov.; **Paragammaropsidae** fam. nov.

Remarks.—The aetiopedesoid clade presents a dilemma, because although it has glandular pereopods 3 and 4, the glands are situated in the merus and not in the basis. Nonetheless, we believe aetiopedesoids to be corophiideans because of their dorsoventrally thickened, if reduced, telson and corophiidean mouthparts and gnathopods. Within our tree (Fig. 12), they align themselves at the base of the caprellidan clade. Perhaps glandular masses were once distributed more extensively within the podomeres of pereopods 3 and 4 and, in caprellidans, became variously lost, limited to the basis or limited to the merus.

The aetiopedesoid clade can be placed on any stem clade in the caprellidan clade without changing the tree length.

Aetiopedesidae fam. nov.

Diagnosis.—Labrum notch with teeth. Pereopods 3–4 merus immensely enlarged. Epimera present. Uropod 3 rami with marginal slender and robust setae.

Type Genus.—*Aetiopedes* Moore and Myers, 1988.

Generic Composition.—*Aetiopedes* Moore and Myers, 1988.

Species Used in the Analysis.—*Aetiopedes gracilis* Moore and Myers, 1988.

Paragammaropsidae fam. nov.

Diagnosis.—Labrum notch without teeth. Pereopods 3–4 merus enlarged. Epimera absent. Uropod 3 rami with marginal slender setae.

Type Genus.—*Paragammaropsis* Ren “in” Ren and Huang, 1991.

Generic Composition.—*Paragammaropsis* Ren “in” Ren and Huang, 1991.

Species Used in the Analysis.—*Paragammaropsis prenes* Ren “in” Ren and Huang, 1991.

Caprelloidea Leach, 1814

Diagnosis.—Head partially or completely coalesced with pereonite 1, triangular, rectangular, or round, with distinct neck region, or free, not coalesced with pereonite 1; lateral cephalic lobe weakly or not extended; eye, if present, situated proximal to lobe; anterior ventral margin not recessed, weakly recessed and moderately excavate, or moderately to strongly recessed and moderately excavate. Antenna 1 peduncular article 3 more than half, usually much more than half, length of article 2 or (secondarily) short, half or less length of article 2. Mandible molar present or absent. Pereonites 6–7 free and orientated ventrally, or fused and orientated posteriorly. Pereonite 7 posterior distal margin not rotated posteriorly, or weakly to strongly rotated posteriorly (pereopod 7 directed posteriorly). Pereopods 3–4 well developed, reduced to 1 or 2 articles, or absent; bases glandular or nonglandular. Pereopods 5–7 prehensile or not prehensile, dactylus elongated and closing along most of posterior margin of propodus, without accessory spines on anterior margin. Pereopod 7 longer than, subequal to, or shorter than pereopod 6. Pleonite 3 not expanded, or expanded ventrally to form epimeron. Urosomites 1 or 1 and 2 extremely long, urosomite 1 coalesced with urosomite 2 or free; urosomite 2 coalesced with urosomite 3 or free. Uropod 3 peduncle short, length 2 times or less breadth, and parallel sided, or vestigial or absent; uniramous, or without rami. Telson without hooks or denticles.

Remarks.—The Caprelloidea exhibit a nested set of character states. Character state 29.2 (urosomites 1 and 2 coalesced) defines the Caprellidae; state 2.4 (head round with a distinct neck region) the Caprellidae; state 1.2 (head partially or completely coalesced with pereonite 1) the Caprellidae and Cyamidae; state 5.3 (head not recessed), the Caprellidae, Cyamidae, and Caprogammaridae; state 14.2 (pereonite 7 posterodistal margin rotated posteriorly) the Caprellidae, Cyamidae, Caprogammaridae, and Dulichiidae; state 31.2 (urosomites 1 or 1 and 2 extremely long) the Caprellidae, Cyamidae, Caprogammaridae, Dulichiidae, and Podoceri-

dae. Although these groups demonstrate an evolutionary progression and can be readily separated in a key, with the exception of the Cyamidae and Dulichiidae, they cannot be diagnosed by any synapomorphies present in our data set. These families do, however, accord well with groups previously recognized as distinct (Laubitz, 1993), and we therefore maintain them here at family level awaiting more detailed analysis from caprellid workers.

Caprellidae Leach, 1814

Diagnosis.—Head round with distinct neck region. Mandible molar present or absent. Pereopods 3–4 variable, fully segmented or reduced; pereopod 4 absent or pereopods 3 and 4 absent. Urosomites 1 and 2 coalesced or not coalesced.

Subfamily Composition.—Caprellinae Leach, 1814; Paracercopinae Vassilenko, 1972; Phtiscinae Vassilenko, 1968.

Caprellinae Leach, 1814 new status

Diagnosis.—Mandible molar present. Pereopods 3–4 absent.

Generic Composition.—*Abyssicaprella* McCain, 1966; *Aciconula* Mayer, 1903; *Aeginella* Boeck, 1861; *Aeginellopsis* Arimoto, 1970; *Aeginina* Norman, 1905; *Caprella* Lamarck, 1801; *Cyrtophium* Dana, 1853; *Deutella* Mayer, 1890; *Eugastraulax* Schurin, 1935; *Eupariambus* K. H. Barnard, 1957; *Fallotritella* McCain, 1968; *Hemiaegina* Mayer, 1890; *Heterocaprella* Arimoto, 1976; *Leipsuropus* Stebbing, 1899a; *Liropes* Arimoto, 1978; *Liropus* Mayer, 1890; *Luconacia* Mayer, 1903; *Mayerella* Huntsman, 1915; *Metacaprella* Mayer, 1903; *Metaprotella* Mayer, 1890; *Monoliropus* Mayer, 1903; *Noculacia* Mayer, 1903; *Orthoprotella* Mayer, 1903; *Paracaprella* Mayer, 1890; *Paradeutella* Mayer, 1890; *Paradicaprella* Hirayama, 1990; *Paraprotella* Mayer, 1903; *Pariambus* Stebbing, 1888; *Parvipalpus* Mayer, 1890; *Pedocolina* Carausu, 1941; *Pedrottrina* Arimoto, 1978; *Podobothrus* Barnard and Clark, 1985; *Postoparacaprella* Arimoto, 1981; *Premohemiaegina* Arimoto, 1978; *Pretritella* Arimoto, 1980; *Proaeginina* Stephensen, 1940; *Proliropus* Mayer, 1903; *Propodalirius* Mayer, 1903; *Protella* Dana, 1852b; *Protellina* Stephensen, 1944; *Protellopsis* Stebbing, 1883; *Protoaeginella* Laubitz and Mills, 1972; *Prototritella* Arimoto, 1977; *Pseudaeiginella* Mayer, 1890; *Pseudoliropus* Laubitz,

1970; *Pseudolirius* Mayer, 1890; *Pseudoprotella* Mayer, 1890; *Thorina* Stephensen, 1944; *Triantella* Mayer, 1903; *Triliropus* Mayer, 1903; *Triperopus* Mayer, 1903; *Tripotella* Arimoto, 1970; *Tritella* Mayer, 1890.

Species Used in the Analysis.—*Caprella acanthifera* Leach, 1814; *Fallotritella biscaynensis* McCain, 1968; *Luconacia incerta* Mayer, 1903; *Paradicaprella brucei* Hirayama, 1990; *Proaeginina norwegica* (Stephensen, 1931).

Paracercopinae Vassilenko, 1972

Diagnosis.—Head round with distinct neck region. Mandible molar absent. Pereopods 3+4 minute, 1-segmented. Urosomites 1+2 not coalesced.

Generic Composition.—*Cercops* Krøyer, 1843; *Paracercops* Vassilenko, 1972; *Pseudocercops* Vassilenko, 1972.

Species Used in the Analysis.—*Cercops* sp.

Phtisicinae Vassilenko, 1968

Diagnosis.—Mandible molar absent. Pereopods 3–4 variable, fully segmented or reduced, pereopod 4 present or absent. Urosomites 1+2 coalesced.

Generic Composition.—*Aeginoides* Schellenberg, 1926a; *Caprellina* Thomson, 1879; *Caprellinoides* Stebbing, 1888; *Chaka* Griffiths, 1974; *Dodecas* Stebbing, 1883; *Dodecasella* K. H. Barnard, 1931; *Hemiproto* McCain, 1968; *Hircella* Mayer, 1882; *Liriarchus* Mayer, 1912; *Metaproto* Mayer, 1903; *Paedaridium* Mayer, 1903; *Paraproto* Mayer, 1903; *Perotripus* Doughty and Steinberg, 1953; *Phtisica* Slabber, 1769; *Prellicana* Mayer, 1903; *Protogeton* Mayer, 1903; *Protomima* Mayer, 1903; *Protoplesius* Mayer, 1903; *Pseudocaprellina* Sundara Raj, 1927; *Pseudododecas* McCain and Gray, 1971; *Pseudoproto* Mayer, 1903; *Pseudoproto-mima* McCain, 1969; *Quadrisegmentum* Hirayama, 1988.

Species Used in the Analysis.—*Dodecas elongatus* Stebbing, 1888; *Phtisica marina* Slabber, 1769.

Caprogammaridae Kudrjaschov and Vassilenko, 1966

Diagnosis.—Head rectangular, not recessed, free, not coalesced with pereonite 1. Mandible molar present. Pereopods 3+4 greatly reduced. Urosomites 1+2 not coalesced.

Generic Composition.—*Caprogammarus* Kudrjaschov and Vassilenko, 1966;

Species Used in the Analysis.—*Caprogammarus gurjanovae* Kudrjaschov and Vassilenko, 1966.

Cyamidae Rafinesque, 1815

Diagnosis.—Head columnar, not coalesced with pereonite 1. Mandible molar absent. Pereopods 3–4 absent. Urosomites 1+2 not coalesced.

Generic Composition.—*Cyamus* Latreille, 1796; *Isocyamus* Gervais and van Beneden, 1859; *Neocyamus* Margolis, 1955; *Platycyamus* Lütken, 1870; *Scutocyamus* Lincoln and Hurley, 1974; *Syncyamus* Bowman, 1955.

Species Used in the Analysis.—*Cyamus boopis* Lütken, 1870.

Dulichiiidae Dana, 1849

Diagnosis.—Head triangular, anterior ventral margin moderately excavate. Pereopods 3+4 basis glandular. Pereonites 6 and 7 fused, oriented posteriorly.

Generic Composition.—*Dulichia* Krøyer, 1845; *Dulichiiopsis* Laubitz, 1977; *Dyopedos* Bate, 1857b; *Paradulichia* Boeck, 1871; *Paradyopedos* Andres and Rauschert, 1990; *Pseudoparadulichia* Rauschert, 1990.

Species Used in the Analysis.—*Dulichia spinosissima* Sars, 1895; *Dyopedos arcticus* (Murdoch, 1885) of Laubitz, 1977; *Paradyopedos antarcticus* Andres and Rauschert, 1990.

Podoceridae Leach, 1814

Diagnosis.—Head rectangular. Mandibular molar present. Pereopods 3+4 fully developed. Urosomites 1+2 not coalesced.

Generic Composition.—*Laetmatophilus* Bruzelius, 1859; *Leipsuropus* Stebbing, 1899a; *Neoxenodice* Schellenberg, 1926a; *Parunciola* Chevreux, 1911; *Podobothrus* Barnard and Clark, 1985; *Podocerus* Leach, 1814; *Styloxenodice* Laubitz, 1984; *Xenodice* Boeck, 1871.

Species Used in the Analysis.—*Laetmatophilus tuberculatus* Bruzelius, 1859; *Neoxenodice cryophile* Lowry, 1976; *Parunciola seurati* Chevreux, 1911 of Ruffo, 1993; *Podocerus manawatu* J. L. Barnard, 1972; *Xenodice frauenfeldti* Boeck, 1871 of Sars, 1895.

Remarks.—Ruffo (1993) placed *Parunciola* in the Podoceridae. We concur, and place it in the

Podoceridae (Caprelloidea). Although rami are present on uropod 3, whereas all caprelloids have lost the rami of uropod 3, it has a rectangular head, a synapomorphy for the Podoceridae + Caprogammaridae and an extremely long urosomite 1, a synapomorphy for the Caprelloidea.

Isaeoidea Dana, 1852b

Diagnosis.—Head rectangular, anterior distal margin recessed; lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe; anterior ventral margin moderately to strongly recessed and moderately excavate. Mandible palp article 3 asymmetrical, distally rounded, setae extending along most of posterior distal margin, posterior margin with setae of variable length. Gnathopod 1 not enlarged in either males or females. Gnathopod 2 in male larger than gnathopod 1, merus not enlarged. Pereopods 5–7 subchelate. Pereopod 7 subequal to or shorter than pereopod 6. Urosomites not coalesced. Uropod 3 peduncle short, length 2 times or less breadth, parallel sided; biramous; outer ramus without recurved spines. Telson without hooks or denticles.

Isaeidae Dana, 1852b

Diagnosis.—As for superfamily.

Generic Composition.—*Isaea* Milne Edwards, 1830; *Pagurisaea* Moore, 1983.

Species Used in the Analysis.—*Isaea montagui* Milne Edwards, 1830; *Pagurisaea schembrii* Moore, 1983.

Microprotopoidea superfam. nov.

Diagnosis.—Head rectangular, anterior distal margin recessed, lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe; anterior ventral margin moderately to strongly recessed and moderately excavate. Mandible palp article 3 nearly parallel-sided, posterior margin without, or with very few, setae. Gnathopod 1 not enlarged in either males or females. Gnathopod 2 in male larger than gnathopod 1, merus not enlarged. Pereopods 5–7 not subchelate, without accessory spines on anterior margin. Pereopod 7 longer than pereopod 6. Urosomites not coalesced. Uropod 3 peduncle short, length 2 times or less breadth, parallel sided, uniramous; ramus without recurved spines. Telson without hooks or denticles.

Microprotopidae fam. nov.

Diagnosis.—As for superfamily.

Type Genus.—*Microprotopus* Norman, 1867.

Generic Composition.—*Microprotopus* Norman, 1867.

Species Used in the Analysis.—*Microprotopus maculatus* Norman, 1867 of Myers, 1989a.

Neomegamphopoidea Myers, 1981a

Additional Status

Diagnosis.—Head rectangular, anterior distal margin recessed; lateral cephalic lobe extended, eye at least partly enclosed in extended lobe, anterior ventral margin moderately recessed and moderately excavate. Mandible palp article 3 subsymmetrical, distally flattened, with setae mostly distal. Gnathopod 1 enlarged. Gnathopod 2 in male enlarged or not. Pereopod 5 carpus long, subrectangular. Pereopods 5–7 not subchelate, without accessory spines on anterior margin; pereopod 7 longer than pereopod 6. Urosomites not coalesced. Uropod 3 peduncle short. Telson without hooks or denticles.

Family Composition.—Neomegamphopidae Myers, 1981a; Priscomilitariidae Hirayama, 1988.

Neomegamphopidae Myers, 1981a

Diagnosis.—Gnathopod 1 enlarged, strongly in males. Gnathopod 2 not enlarged.

Generic Composition.—*Konatopus* J. L. Barnard, 1970; *Maragopsis* Myers, 1973; *Neomegamphopus* Shoemaker, 1942; *Pseudomegamphopus* Myers, 1968; *Riwomegamphopus* Myers, 1995; *Varohios* J. L. Barnard, 1979.

Species Used in the Analysis.—*Konatopus pao* J. L. Barnard, 1970; *K. storyae* Myers, 2002; *Maragopsis bidentata* (Ledoyer, 1972); *Neomegamphopus heardi* Barnard and Thomas, 1987; *N. hiatus* Barnard and Thomas, 1987; *Pseudomegamphopus excavatus* Myers, 1968; *Riwomegamphopus bamus* Myers, 1995; *Varohios topianus* J. L. Barnard, 1979.

Priscomilitariidae Hirayama, 1988

Diagnosis.—Gnathopod 1 not enlarged in either males or females. Gnathopod 2 in male, larger than gnathopod 1, coxa enormously expanded partially obscuring coxa 1.

Generic Composition.—*Paraphotis* Ren, 1997; *Priscomilitarius* Hirayama, 1988.

Species Used in the Analysis.—*Paraphotis sinensis* Ren, 1997; *Priscomilitarius tenuis* Hirayama, 1988.

Photoidea Boeck, 1871

Additional Status

Diagnosis.—Head rectangular, anterior distal margin recessed, lateral cephalic lobe weakly to strongly extended; eye, if present, situated proximal to lobe at least partly enclosed in extended lobe, or completely enclosed in extended lobe, anterior ventral margin weakly to moderately recessed and moderately excavate, or strongly recessed and strongly excavate. Antenna 1 peduncular article 3 almost always more than half, usually much more than half the length of article 2, rarely short (*Falcigammaropsis*), half or less length of article 2. Mandible palp variable. Gnathopod 1 variable. Gnathopod 2 in male larger than gnathopod 1, merus not enlarged. Pereopod 5 carpus long, subrectangular, or small, lunate or reniform. Pereopods 5–7 with or without accessory spines on anterior margin. Pereopod 7 longer or much longer than pereopod 6. Urosomite 1 and 2 coalesced or free. Uropods 1 and 2 peduncle with or without distoventral corona of cuticular spines. Uropod 3 peduncle variable, biramous, or uniramous; outer ramus with or without recurved spines. Telson with horizontal rows of recurved hooks, with patches of small denticles, or without hooks or denticles.

Family Composition.—Ischyroceridae Stebbing, 1899c; **Kamakidae** fam. nov.; Photidae Boeck, 1871.

Ischyroceridae Stebbing, 1899c

Diagnosis.—Head lateral cephalic lobe not or weakly extended, eye, if present, situated proximal to lobe; anterior ventral margin moderately to strongly recessed and moderately excavate. Mandible palp, article 3 asymmetrical, distally rounded, setae extending along most of posterodistal margin, posterior margin with setae of variable length. Gnathopod 1 not enlarged in males or females. Gnathopod 2 enlarged in males and females. Pereopods 5–7 not subchelate. Urosomites not coalesced. Uropod 3 peduncle broad proximally and narrow distally; rami with tiny apical setae, outer ramus with recurved apical spines. Telson

with or without rows of recurved hooks, with or without patches of small denticles.

Subfamily Composition.—**Bonnierellinae** subfam. nov.; Ischyrocerinae Stebbing, 1899c.

Bonnierellinae subfam. nov.

Diagnosis.—Pereopods 5–7 dactyli without accessory spines on anterior margin. Uropods 1 and 2 peduncle without distoventral corona of cuticular spines. Uropod 3 rami without recurved spines. Telson without hooks or denticles.

Type Genus.—*Bonnierella* Chevreux, 1900.

Generic Composition.—*Bogenfelsia* J. L. Barnard, 1962b; *Bonnierella* Chevreux, 1900.

Species Used in the Analysis.—*Bogenfelsia incisa* J. L. Barnard, 1962b; *Bonnierella angolae* J. L. Barnard, 1962b.

Ischyrocerinae Stebbing, 1899c

Diagnosis.—Pereopods 5–7 dactyli with or without accessory spines on anterior margin. Uropods 1+2 peduncle with or without distoventral corona of cuticular spines. Uropod 3 rami with or without recurved spines. Telson without hooks or denticles or with rows of recurved hooks or with patches of small denticles.

Tribe Composition.—Ischyrocerini Stebbing, 1899c; Siphonocetini Just, 1983.

Remarks.—This subfamily is defined by having recurved spines on the outer ramus of uropod 3, a state that has been lost in the *Siphonocetes* group.

Ischyrocerini Stebbing, 1899c

Additional Status

Diagnosis.—Pereopod 5 carpus long, subrectangular. Pereopods 5–7 dactyli lacking accessory spines on anterior margin. Uropod 1 and 2 peduncle without distoventral corona of cuticular spines. Uropod 3 peduncle long, broad proximally, narrow distally. Telson without rows of hooks or patches of denticles.

Generic Composition.—*Bathypotis* Stephen, 1944; *Isaeopsis* K. H. Barnard, 1916; *Ischyrocerus* Krøyer, 1838; *Jassa* Leach, 1814; *Microjassa* Stebbing, 1899a; *Paradryope* Stebbing, 1888; *Parajassa* Stebbing, 1899a; *Pseudischyrocerus* Schellenberg, 1931; *Ruffojassa*

Vader and Myers, 1996; *Scutischyrocerus* Myers, 1995; *Ventojassa* J. L. Barnard, 1970; *Veronajassa* Vader and Myers, 1996.

Species used in the Analysis.—*Bathypnotis tridentata* Stephensen, 1944; *Ischyrocerus inexpectatus* Ruffo, 1959 of Myers, 1989b; *I. parma* Myers, 1995; *Jassa marmorata* Holmes, 1905; *Microjassa cumbraensis* Stebbing and Robertson, 1891; *Parajassa spinipalma* Ledoyer, 1979; *Scutischyrocerus scutatus* Myers, 1995.

Siphonoecetini Just, 1983
Changed Status

Diagnosis.—Pereopod 5 carpus small, lunate or reniform. Pereopods 5–7 dactyli with accessory spines on anterior margin. Uropod 1+2 peduncle with distoventral corona of cuticular spines. Uropod 3 peduncle short, with sides expanded, or long, broad proximally, narrow distally. Telson with rows of recurved hooks or with patches of small denticles.

Generic Composition.—*Africoecetes* Just, 1983; *Australoecetes* Just, 1983; *Bathypoma* Lowry and Berents, 1996; *Borneoecetes* Barnard and Thomas, 1984; *Bubocorophium* Karaman, 1981; *Caribboecetes* Just, 1983; *Cerapus* Say, 1817; *Concholestes* Giles, 1888; *Corocubanus* Ortiz and Nazábal, 1984; *Erichthonius* Milne Edwards, 1830; *Notopoma* Lowry and Berents, 1996; *Paracerapus* Budnikova, 1989; *Polyne-soecetes* Myers, 1989c; *Pseudericthonius* Schellenberg, 1926b; *Rhinoecetes* Just, 1983; *Runanga* J. L. Barnard, 1961; *Siphonoecetes* Krøyer, 1845.

Species Used in the Analysis.—*Bathypoma enigma* Lowry and Berents, 1996; *Cerapus alquira* (Barnard and Drummond, 1981); *C. pacificus* Lowry, 1985; *Erichthonius brasiliensis* (Dana, 1853) of Myers and McGrath, 1984; *E. pugnax* (Dana, 1852a) of Myers, 1995; *Siphonoecetes sabatieri* Rouville, 1894 of Myers, 1982b.

Kamakidae fam. nov.

Diagnosis.—Head lateral cephalic lobe weakly extended, or strongly extended, eye, if present, situated proximal to lobe or completely or partially enclosed in extended lobe; anteroventral margin moderately to strongly recessed and moderately excavate. Mandible palp article 3 asymmetrical, distally rounded, setae extending along most of posterodistal margin, or subsymmetrical with setae mostly distal. Gnathopod 2

in male larger than gnathopod 1, merus not enlarged. Pereopods 5–7 not subchelate. Pereopod 7 slightly longer than pereopod 6. Urosomites not coalesced. Uropod 3 peduncle short, parallel-sided; outer ramus without recurved spines. Telson without hooks or denticles.

Type Genus.—*Kamaka* Derzhavin, 1923.

Subfamily Composition.—**Aorchinae** subfam. nov.; **Kamakinae** subfam. nov.

Aorchinae subfam. nov.

Diagnosis.—Head lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe.

Type Genus.—*Aorcho* J. L. Barnard, 1961.

Generic Composition.—*Aloiloi* J. L. Barnard, 1970; *Amphideutopus* J. L. Barnard, 1959; *Aorcho* J. L. Barnard, 1961.

Species Used in the Analysis.—*Aloiloi nenu* J. L. Barnard, 1970; *Amphideutopus oculatus* J. L. Barnard, 1959; *A. dolicocephalus* Myers, 1968; *Aorcho delgadus* J. L. Barnard, 1961.

Kamakinae subfam. nov.

Diagnosis.—Head lateral lobe strongly extended, eye enclosed completely in extended lobe.

Generic Composition.—*Aorchoides* Ledoyer, 1972; *Cerapopsis* Della Valle, 1893; *Gammaropsella* Myers, 1995; *Kamaka* Derzhavin, 1923; *Ledoyerella* Myers, 1973; *Natarajphotis* Peethambaran “in” Lyla *et al.*, 1998; *Paraloiloi* Myers, 1995.

Species Used in the Analysis.—*Aorchoides crenatipalma* (K. H. Barnard, 1916); *A. dilatata* Ledoyer, 1972; *Cerapopsis longipes* Della Valle, 1893; *Gammaropsella pilosa* Myers, 1995; *G. simplex* Myers, 1995; *Kamaka derzhavini* Gurjanova, 1951; *K. kuthae* Derzhavin, 1923; *Ledoyerella caputphotis* (Ledoyer, 1982); *L. isochelatus* Ledoyer, 1972; *Paraloiloi vaga* Myers, 1995.

Remarks.—*Natarajphotis manieni* may be a species of *Kamaka*.

Photidae Boeck, 1871
Additional Status

Diagnosis.—Head lateral cephalic lobe weakly extended or strongly extended, eye, if present, situated proximal to lobe or completely or partially enclosed in extended lobe; anteroventral

margin moderately to strongly recessed and moderately excavate. Mandible palp article 3 asymmetrical, distally rounded, setae extending along most of posterodistal margin, or subsymmetrical with setae mostly distal. Gnathopod 2 in male larger than gnathopod 1, merus not enlarged. Pereopods 5–7 not subchelate. Pereopod 7 slightly longer than pereopod 6. Urosomites not coalesced. Uropod 3 peduncle short, with sides expanded, or long, parallel-sided or narrowing distally. Telson without hooks or denticles.

Generic Composition.—*Ampelisciphotis* Pirlot, 1938; *Audulla* Chevreux, 1901; *Dodophotis* Karaman, 1985; *Falcigammaropsis* Myers, 1995; *Gammaropsis* Lilljeborg, 1855; *Megamphopus* Norman, 1869; *Microphotis* Ruffo, 1952; *Papuaphotis* Myers, 1995; *Photis* Krøyer, 1842; *Posophotis* J. L. Barnard, 1979.

Species Used in the Analysis.—*Ampelisciphotis tridens* Pirlot, 1938; *Audulla chelifera* Chevreux 1901; *Falcigammaropsis excavata* Myers, 1995; *Gammaropsis christenseni* Myers, 1995; *G. gemina* Myers, 1995; *G. lacinia* Myers, 1995; *G. maculata* Johnston, 1828 of Krapp-Schickel and Myers, 1979; *G. planodentata* Myers, 1995; *G. siara* Myers, 1995; *Megamphopus cornutus* Norman, 1869; *Papuaphotis regis* Myers, 1995; *Photis aina* J. L. Barnard, 1970; *P. brevipes* Shoemaker, 1942; *P. kapapa* J. L. Barnard, 1970; *P. longicaudata* (Bate and Westwood, 1863); *P. paeowai* Myers, 1995; *P. pirloti* Myers, 1985.

Remarks.—*Ampelisciphotis* is attributable to the Photidae because of the long parallel-sided peduncle of uropod 3. It can also be placed in the Kamakinae, based on its deeply recessed lateral cephalic lobe.

Rakirooidea superfam. nov.

Diagnosis.—Head rectangular, anterior distal margin recessed, lateral cephalic lobe weakly extended, eye, if present, situated proximal to lobe; anterior ventral margin strongly recessed and strongly excavate. Antenna 1 peduncular article 3 long, usually much more than half length of article 2. Mandible palp article 3 asymmetrical, distally rounded, setae extending along most of posterior distal margin, posterior margin with setae of variable length. Gnathopod 1 not enlarged in either males or females; coxa 1 smaller than coxa 2. Gnathopod 2 in male, larger than gnathopod 1, merus not enlarged.

Pereopod 7 longer than pereopod 6. Urosomite 2 coalesced with urosomite 3. Uropods 1+2 rami with dense array of long robust setae. Uropod 3 peduncle short, length 2 times or less breadth, parallel sided; biramous; outer ramus without recurved spines. Telson without hooks or denticles.

Family composition.—**Rakiroidea** fam. nov.

Rakiroidea fam. nov.

Diagnosis.—As for the superfamily.

Type Genus.—*Rakiroa* Lowry and Fenwick, 1982.

Generic Composition.—*Rakiroa* Lowry and Fenwick, 1982.

Species Used in the Analysis.—*Rakiroa rima* Lowry and Fenwick, 1982.

Incertae Sedis

Paraneohela Oldevig, 1959

Remarks.—This genus is insufficiently described to be coded into our database. Accordingly, we are unable to allocate it anywhere within the above classification.

Excluded Taxon

Stebbing (1906) placed biancolinid amphipods in the Ampithoidae, Nicholls (1939) placed them in the Prophiantidae, and Gurjanova (1958) thought they were eophliantids. J. L. Barnard (1972) created the family Biancolinidae but was noncommittal about its affinities. Bousfield (1978) placed them in the Corophioidea without comment. Biancolinids are not corophiideans because they lack the three synapomorphies which define the group: silk glands on the basis of pereopods 3 and 4; slender and robust setae on the rami of uropod 3; and a dorsoventrally thickened telson (J. L. Barnard, 1972; Bousfield, 1978). In addition, they differ from corophiideans in having left and right asymmetry of the lacinia mobilis, no palp on maxilla 1, curl-tipped setae on the oostegite margins, and long pappose setae on the peduncles of the uropods. We consider them to be more closely related to the Hyalidae because of the curl-tipped setae on the oostegite margins.

DISCUSSION

Before a cladistic analysis can be attempted, it is necessary to develop a hypothesis of

relationships of the taxa under study by thoroughly understanding the characters being evaluated. This *a priori* approach may appear to preclude the possibility of discovering hitherto unperceived relationships. However, the hypothesis is used merely as a starting point to be successively tested and improved upon by an iterative process, in which characters and character states are assessed and reassessed following cladistic analysis. Awareness of new possible groupings, previously unsuspected, leads to the search for, and adoption of, additional characters and character states, as well as the reformulation of existing ones. The hypothesis as it becomes more and more modified is successively tested against the cladogram, and any stage is falsified if it is not compatible with a shortest, most parsimonious tree.

Ideally, an interpretation of the functional morphology of every character state is necessary if we are to understand the evolution of the taxa under study. Rarely has any attempt been made to incorporate functional morphology into cladistic analyses of amphipods, but a good example is the study of iphemedioids by incorporating mandible structure and function, which was carried out by Watling and Thurston (1989). Unfortunately, our understanding of amphipod behavior and functional morphology is rudimentary.

Pattern cladistics has problems because it requires dismantling of an animal into its constituent parts. Adaptation, however, affects the entire organism, and evolutionary hypotheses demand holistic solutions (Watling, personal communication).

We are of the opinion that because the morphological data available from extant taxa alone is limited, and because taxonomists are able to make use of only a minute proportion of the potential phylogenetic information in the genome, statistical analyses of consensus trees are inappropriate. Statistical techniques assume a level of precision in the data set, which is illusory. No tree is the correct representation of evolution. At a fundamental level, a tree is only as good as its character-state interpretation. Hopefully, most interpretations will be correct; some, however, inevitably will not be. The phylogeny presented here, therefore, is an approximation of the evolutionary pathways within the corophiideans as we envisage them. As a hypothesis, it was accepted, i.e., not falsified in the Popperian sense, because it was

supported by a shortest, most parsimonious tree. Future analyses based on different character suites will provide further testing for our hypothesis. We offer it as a step towards a better understanding of the relationships of this interesting but taxonomically intractable group. We anticipate that changes will be needed to clades such as the Kamakinae and Protomedeiinae that are not well supported in our cladogram.

Superimposing a strict Linnaean hierarchy onto a phylogenetic tree is not straightforward. In this case, it has been necessary to increase the number of hierarchical levels conventionally used in amphipod taxonomy (Table 2), resulting in categories not previously used in amphipod taxonomy. Infraorder, already in use for caprellidans and hyperiideans (Martin and Davis, 2001), has been placed between suborder and superfamily, and subfamily and tribe levels have been introduced where necessary. Through the use of infraorder, familiar family-level taxa, such as Aoridae, Ampithoidae, Caprellidae, and Ischyroceridae, remain. The introduction of tribes means that previously unrecognized taxa, such as Haplocheirini and the Paracorophiini, can be delineated. We anticipate the use of subtribes for taxa such as the cerapid clade of Lowry and Berents (1996). Because the highest level of the hierarchy is fixed by conventional taxonomy, terminal taxa in the tree receive low categories such as tribes and subtribes.

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NOTE ADDED IN PROOF

In the list of the Siphonocetini, we inadvertently omitted *Ambicholestes*. It should have been inserted at Ischyroceridae: Ischyrocerinae: *Ambicholestes* Just, 1988.

Reference:

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Appendix 1. Continued.

Characters	1	2	3	4	5	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	35	36	37	38	39	40	41									
<i>Photis</i>	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	4	1	2	1	2	1	2	1	2	1	2	1	2	1	1	1							
<i>Phthisica</i>	2	4	1	3	2	2	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	2	2	2	1	2	1	2	1	2	1	2	1	1	1	1						
<i>Podocerus</i>	1	2	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1					
<i>Priscosmittarius</i>	1	1	1	1	2	2	1	2	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	?	1	1	1	1	1	1	2	1	2	1	2	1	2	1	2	?	1	1				
<i>Proaegina</i>	2	4	1	3	2	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	2	1	1	2	1	1	2	2	2	1	1	1	5	2	1	2	1	2	1	2	1	1	1	1					
<i>Protomeleia</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1				
<i>Pseudamphithoides</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
<i>Rakiroa</i>	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1			
<i>Rildardanus</i> (male)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1		
<i>Riwomegamphopop</i>	1	1	1	1	2	2	1	2	1	1	1	1	1	2	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Rudlemboides</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Scutischyrocerus</i>	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Siphonocetes</i>	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Stenocorophium</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Sunamphitoe</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Ucinctotarsus</i>	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
<i>Ucinctella</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Varohios</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Wombalana</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Xenodice</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Zoedutopus</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1