A PHYLOGENETIC ANALYSIS OF THE ISOPODA WITH SOME CLASSIFICATORY RECOMMENDATIONS

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The phylogenetic relationships of the isopod crustacean suborders are assessed using cladistic methodology. The monophyly of the Flabellifera was tested by including all 15 component families separately in the analysis. Four other peracarid orders (Mysidacea, Amphipoda, Mictacea, and Tanaidacea) were used as multiple out-groups to root our phylogenetic estimates within the Isopoda. A broad range of possible characters for use in assessing isopod relationships is discussed and a final data (character) matrix was selected. This data matrix, comprising 29 taxa and 92 characters, was subjected to computer-assisted analysis using four different phylogenetic programs: HENNIG86, PAUP, PHYLIP, and MacClade. Phylogenetic hypotheses from the literature (particularly Wägele, 1989a) are discussed and compared with our own conclusions.

The following hypotheses are suggested by our analysis. The Isopoda constitutes a monophyletic group. The Phreatoicidea is the earliest derived group of living isopods, followed by an Asellota–Microcerberidea line, and next the Oniscidea. Above the Oniscidea is a large clade of 'long-tailed' isopod taxa (Valvifera, Anthuridea, Flabellifera, Epicaridea, Gnathiidea). The Microcerberidea is the sister group of the Asellota, but probably should not be included in the Asellota. The Oniscidea constitutes a monophyletic group. The monotypic taxon Calabozoidea is either a primitive oniscidean, or is a sister group of the Oniscidea (*Calabozoa* is not an asellotan). Our cladistic analysis suggests that the primitive isopod body plan was one in which well-developed lateral coxal plates were lacking, the pleopods were multiarticulate, the uropods arose on the posterior margin of the pleotelson, the telsonic region was not elongate, and the mandibular molar process was a broad flat grinding structure. Extant taxa with this body plan (Phreatoicidea, Asellota, Microcerberidea) occur primarily in relictual habitats. Oniscidea conform to this body plan except in possessing lateral coxal plates.

The long-tailed isopod morphology (broad flat uropods, an elongate telsonic region, and well-developed lateral coxal plates) appears to be a derived condition within the Isopoda. Suborders and families with this body plan appear to be most speciose, or to have had their origin, in the Southern Hemisphere. The 'caridoid'-like pleonal morphology of many long-tailed isopods (Flabellifera, Gnathiidea, Anthuridea) is thus secondarily derived and convergent to the condition seen in the mysidaceans and other true caridoid crustaceans. The broad, elongate tailfan of the long-tailed isopod taxa is not used for a caridoid-like tail locomotory behaviour (e.g. the 'caridoid escape reaction'), but rather as a steering/stabilising plane. The emergence of the long-tailed body plan seems to have coincided with a shift in isopod habits from infaunal to more active, swimming, epifaunal lifestyles. Accompanying this transition was enlargement of the lateral coxal plates (perhaps to increase hydrodynamic streamlining of the body) and a shift to active carnivory and predation, and eventually parasitism in several groups.

The Suborder Flabellifera (as it is currently recognised) is not a monophyletic taxon. Three taxa usually ranked at the subordinal level (Anthuridea, Gnathiidea and Epicaridea) have their phylogenetic origins within the lineage of families that currently constitutes the Flabellifera. The Protognathiidae is not closely related to the Gnathiidea. Protognathiidae is probably closely related to Anuropidae and is part of a clade culminating in the parasitic family Cymothoidae. Wägele's (1989a) recently proposed new classification of the Isopoda, including his new suborders Sphaeromatidea and Cymothoida (*sic*), is not corroborated by our phylogenetic analysis. Unambiguous sister group relationships cannot be hypothesised for the long-tailed isopod taxa with the current data base. A new formal classification of the order Isopoda must await better resolution of the phylogeny based upon an expanded data set. □ *Isopoda, phylogeny, classification, morphology, biogeography.*

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'Amidst this prudent love of obscurity, the one feature of moral character which they possess in common is strong evidence that all of them must have sprang from a common origin.'

The Reverend T.R.R. Stebbing (1893), Speaking of isopods.

Most of the isopod suborders were described and delineated in the early part of the nineteenth century, but for the past 150 years classification of these suborders and their families has been unsettled. Until fairly recently many workers included the Tanaidacea within the Isopoda and included either (or both) the Gnathiidea and Anthuridea within the Flabellifera (or 'Cymothoidea') (Bate and Westwood, 1863–68; Stebbing, 1893; Sars, 1897; Richardson, 1905; Smith and Weldon, 1923; Hale, 1929; Nierstrasz and Schuurmans-Stekhovan, 1930; Menzies, 1962; Naylor, 1972). Hansen (1916) and Monod (1922) recognised the necessity of separating the tanaidaceans from the isopods, and also removed the gnathiids and anthurideans from the Flabellifera. Some authorities sought to establish a fundamental split between the gnathiids and the remaining Isopoda. Monod (1922) called the gnathiids Decempedes ('10-footed'), and all other isopods the Quatuordecempedes ('14-footed'). Following Latreille (1804), Menzies (1962) used the name Tetracera for the non-gnathiid isopods. Menzies (1962) chose to retain the anthurideans within the Flabellifera, but later removed them (Menzies and Glynn, 1968).

Karaman (1933) allied *Microcerberus* with the Anthuridea, and many subsequent workers accepted this placement (Remane and Siewing, 1953; Chappuis and Delamare, 1954; Lang, 1960; Schultz, 1979; Kussakin, 1973). However, Lang (1961) created a new suborder for this genus, the Microcerberidea, and Wägele (1982b, 1983b) argued against any relationship between the microcerberids and anthurideans, instead suggesting that the former were highly specialized asellotans.

The name 'Cirolanoidea' has been used in different ways by different workers. Richardson (1905) considered it a synonym of her 'Flabellifera' (following Sars to include the Aegidae, Anthuridae, Cirolanidae, Corallanidae, Cymothoidae, Excorallanidae, Gnathiidae, Limnoriidae, Serolidae, and Sphaeromidae). Menzies (1962) considered the Cirolanoidea to be a subtribe of his tribe Flabellifera, synonymous to the Cymothoidea of some previous authors (including the Anuropidae, Cirolanidae, Limnoriidae, Sphaeromidae). Wägele (1989a) used Leach's (1814) spelling of 'Cymothoida', for his newly proposed suborder (for the Aegidae, Anuropidae, Bopyridae [=Epicaridea], Cirolanidae, Corallanidae, Cymothoidae, Gnathiidae, Phoratopodidae, Protognathiidae, and Tridentellidae).

In 1983 Van Lieshout erected a new monotypic suborder (Calabozoidea) for *Calabozoa pellucida*, a ground-water isopod from Venezuelan wells, and discussed its possible affinities to both the Oniscidea and the Asellota. Wägele (1989a) argued for placing the Calabozoidea near the Asellota, depicting these two suborders as sister groups on his phylogenetic tree.

Recent summaries by Bowman and Abele (1982), Brusca and Iverson (1985), Schram (1986), and Brusca and Brusca (1990) took the conservative approach in recognizing 9 suborders (Table 1, Figs 1–3), maintaining separate subordinal status for the Microcerberidea, Anthuridea, Gnathiidea, and Epicaridea.

An examination of previously published studies concerning isopod phylogeny reveals a fairly broad range of ideas (Fig. 4). Beginning with Hansen (1905), however, two taxa have dominated the literature as contenders for the title of 'most primitive living isopods', the Flabellifera and the Asellota. Schultz (1969, 1979) deviated markedly from this pattern, and his phylogeny depicted the Gnathiidea as the most primitive living isopod group. Schram (1974) appears to have been the only person to have previously specifically espoused the Phreatoicidea to be the earliest derived isopod suborder.

Supporters of the 'Asellota-are-primitive' hypotheses have included Hansen (1925), Monod (1922), Birstein (1951), Zenkevich and Birstein

FIG. 1. Examples of 'short-tailed' isopod suborders. A, Phreatoicidea (*Mesamphisopus depressus*, after Nicholls, 1943). B, Asellota (*Ianiropsis montereyensis*, after Menzies, 1952). C, Microcerberidea (*Microcerberus* sp., after Argano, 1988). D, Calabozoidea (*Calabozoa pellucida*, after Van Lieshout, 1983). E, Oniscidea (*Armadillidium vulgare*, after Sutton, 1972).

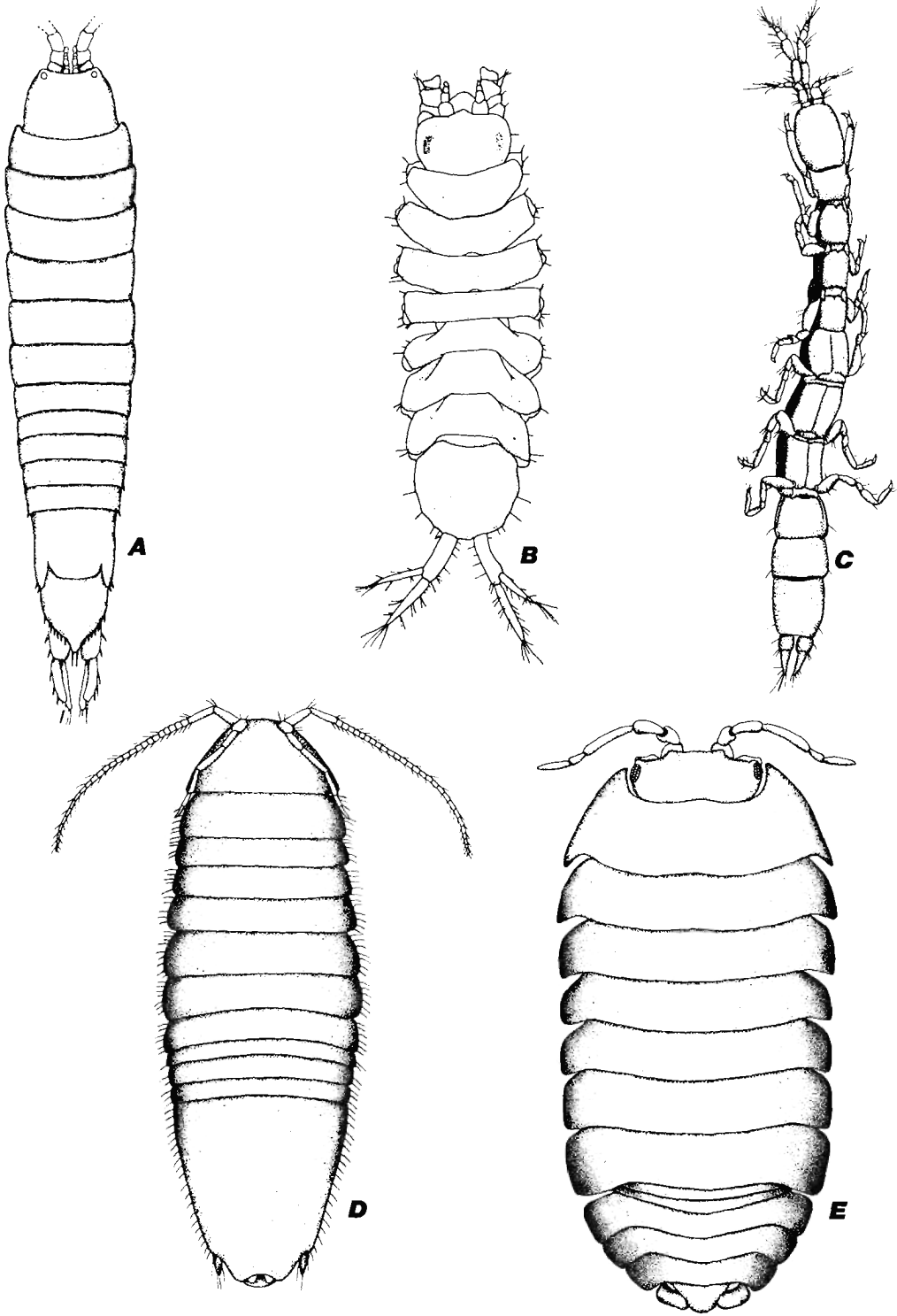

A
B
C
D
E

TABLE 1. Taxa analysed in the present study.

OUT-GROUPS
Order MYSIDACEA
Order MICTACEA
Order TANAIDACEA
Order AMPHIPODA
IN-GROUPS
Order ISOPODA
Suborder Phreatoicidea
Suborder Asellota
Suborder Microcerberidea
Suborder Oniscidea
Infraorder Tylomorpha
Infraorder Ligiamorpha
Suborder Calabozoidea
Suborder Valvifera
Suborder Epicaridea
Suborder Gnathiidea
Suborder Anthuridea
Suborder Flabellifera
Family Aegidae
Family Anuropidae
Family Bathynataliidae
Family Cirolanidae
Family Corallanidae
Family Cymothoidae
Family Keuphyliidae
Family Limnoriidae
Family Lynseiidae
Family Phoratopodidae
Family Plakarthriidae
Family Protognathiidae
Family Serolidae
Family Sphaeromatidae
Family Tridentellidae

(1961), Belyaev (1966), and most recently Schmalfuss (1989). Although Schmalfuss' tree has the appearance of a cladogram, it appears to be an intuitive tree based on *ad hoc* assumptions of ancestry. It used 4 specific synapomorphies to define 8 isopod suborders. Schmalfuss did not describe his method of tree construction, tree selection, character analysis, or character polarity assessment; did not calculate tree lengths or homoplasy values; did not describethe characters he utilised; and, rooted his tree based on ambiguous statements regarding *ad hoc* hypothetical morphotypes rather than on methods such as out-group or ontological analysis. It should be noted that for 8 taxa there exist 660,032 possible tree topologies (Felsenstein, 1978).

Supporters of 'Flabellifera-are-primitive' hypotheses have included Racovitza (1912), Strömberg (1972), Kussakin (1973, 1979), Bruce (1981), and Wägele (1989a). Among the Flabellifera, the Cirolanidae (especially *Bathynomus*) is usually chosen as the model for the archtypical ancestral isopod. Kussakin (1979) refined his earlier views to present a phylogeny in which a 'cirolanid-like ancestor' (but that was not yet a 'true' flabelliferan) gave rise to an Anthuridea/Microcerberidea line as the most primitive living isopod group, followed by the Oniscidea and Valvifera, with the extant Flabellifera, Phreatoicidea, and Asellota being the most highly derived taxa. Kussakin (1979) came to this conclusion despite his contention that the most primitive arrangement of pereopodal coxae occurs in the Asellota, a group in which he noted, 'the coxopodite still looks like a normal segment'. Within the flabelliferan line, Kussakin hypothesized three lineages. One lineage lead to predacious/parasitic lifestyles (Cirolanidae, Aegidae, Cymothoidae, and ultimately the Epicaridea); the other two lines were said to have given rise to benthic herbivores and detritivores, such as the Serolidae and Sphaeromatidae. He allied the Anuropidae with the Valvifera and Oniscidea, rather than with the Flabellifera. Kussakin described (but did not depict on his phylogenetic tree) the Asellota arising from a hypothetical ancestral cirolanid stem group, via the Phreatoicidea. Bruce (1981) supported Kussakin's (1979) views, and further hypothesised the Phoratopodidae to be the sister group of the Valvifera. Nicholls (1943, 1944), Dahl (1954), and Strömberg (1972) also argued that the Phreatoicidea originated from an ancient Flabelliferan stock close to the modern Cirolanidae.

Wägele (1981) claimed that 'general agreement exists among isopod workers that the ancestral isopod body shape and external features were certain to have been similar to those of living Cirolanidae (though perhaps lacking coxal plates),' but later stated that the Cirolanidae could not possibly be considered as primitive isopods and that they were the probable sister group of the Anthuridea. Still later Wägele (1989a) claimed that the (hypothetical) ancestor of the Isopoda was cirolanid-like, even though his 'Hennigian' phylogenetic analysis confirmed that the Cirolanidae was a highly derived group (Fig. 4D).

Strömberg (1972) counted the number of hypothesised plesiomorphic features occurring in each of the isopod suborders, concluding on this basis that the Flabellifera (notably the Cirolani-

dae) were the most primitive living group and the stem group from which all other isopod suborders were derived. He presented an argument for close alliance between the Flabellifera, the Epicaridea, and the Gnathiidea.

All of the above hypotheses, except Wägele (1989a), consisted of *ad hoc* tree construction and evolutionary narratives in the traditional, or orthodox, sense. Each was based on a small set of selected characters that held sway over all others. Most relied on a mix of both primitive and derived features to infer relationships. None was based on a large data set of empirically evaluated characters, and none used any strict analytical methodology. Most, if not all, relied upon the (stated or unstated) *ad hoc* selection of an extant group of isopods to represent a primitive ancestral morphotype. From these *a priori*-selected hypothetical ancestors, evolutionary scenarios were inferred, and trees were constructed based upon these scenarios. Because the phylogenetic scenarios cited above were not derived from empirical analyses of the data, nor utilized any repeatable methodology, it would be unfair (and difficult) to compare them directly to the present study. It is interesting to note that, despite the fact that the Phreatoicidea have the oldest known fossil record (Pennsylvanian; Schram, 1970, 1974), none of the above proposals hypothesised this group (or a phreatoicid-like morphology) to represent the ancestral isopod type.

The only previous attempt to undertake a phylogenetic analysis of the Isopoda based on a large data set and a specific methodology was Wägele's (1989a) recent study (Fig. 4D). Wägele proposed a sweeping reorganisation of isopod classification. Some of the many changes he proposed included the complete elimination of the Suborder Flabellifera, and the reduction to family status of the suborders Gnathiidea and Epicaridea (reducing the families of the latter to subfamilies and eliminating the name Epicaridea altogether). However, even though Wägele's study was based on a larger set of characters than any previous analysis, it was still based on an *ad hoc* hypothetical ancestral morphotype, the phylogenetic tree was computed by hand, and no attempt was made to achieve either global or in-group parsimony or utilise any strict criteria of tree construction or tree selection. Wägele's classification scheme was not strictly cladistic in that it did not recognise the sister group arrangements of his cladogram.

In data sets with more than a few taxa, the number of possible trees quickly becomes astronomical. An analysis of the 10 nominate isopod suborders alone requires assessment of 282 million possible trees, 34.5 million of which are bifurcating trees (Felsenstein, 1978). The present study analyses 29 taxa, for which there are 8.7×10^{36} possible bifurcating trees. Hence, to select a single shortest tree with the highest degree of parsimony and the lowest level of homoplasy by 'eyeballing the data' is difficult, if not impossible. Nevertheless, Wägele's (1989a) analysis was a very important step forward in isopod phylogenetics, and was the first published study at the subordinal level to use a relatively large data set and provide lists of general synapomorphies that define putative monophyletic lines. For these reasons, we compare our analysis closely to that of Wägele in the discussion section at the end of this paper.

METHODS

Out-Groups

The questions of peracarid monophyly and the phylogenetic sequence of appearance of the peracarid orders have long been favorite subjects of debate among carcinologists. Nearly every imaginable topology of phylogenetic relationships among the In 1981 peracarida has been proposed at one time or another. There is no need to review this debate here (Dahl, 1977; Watling, 1981, 1983; Schram, 1981, 1986; Dahl and Hessler, 1982; Hessler, 1983; Brusca, 1984). However, most published ideas over the years have suggested that the sister group of the Isopoda is either the Amphipoda or the Tanaidacea. The recently described Mictacea may also be closely related to the isopods (Schram, 1986). Because of this uncertainty, we use four out-groups in our analysis: Mysidacea, Amphipoda, Mictacea, and Tanaidacea. The increased accuracy of character polarity assessment and tree resolution that can be achieved by use of the multiple out-group method has been explained by Maddison *et al.* (1984) and others, the basic premise being that cladograms should be globally parsimonious.

In-Groups

Our in-group includes all 10 nominate isopod suborders (Table 1), plus the 15 nominate flabelliferan families. The relationships of the families included within the Flabellifera have been controversial, and it has been frequently suggested that the Flabellifera is a non-monophyletic taxon. Kussakin (1979), Bruce (1981), and

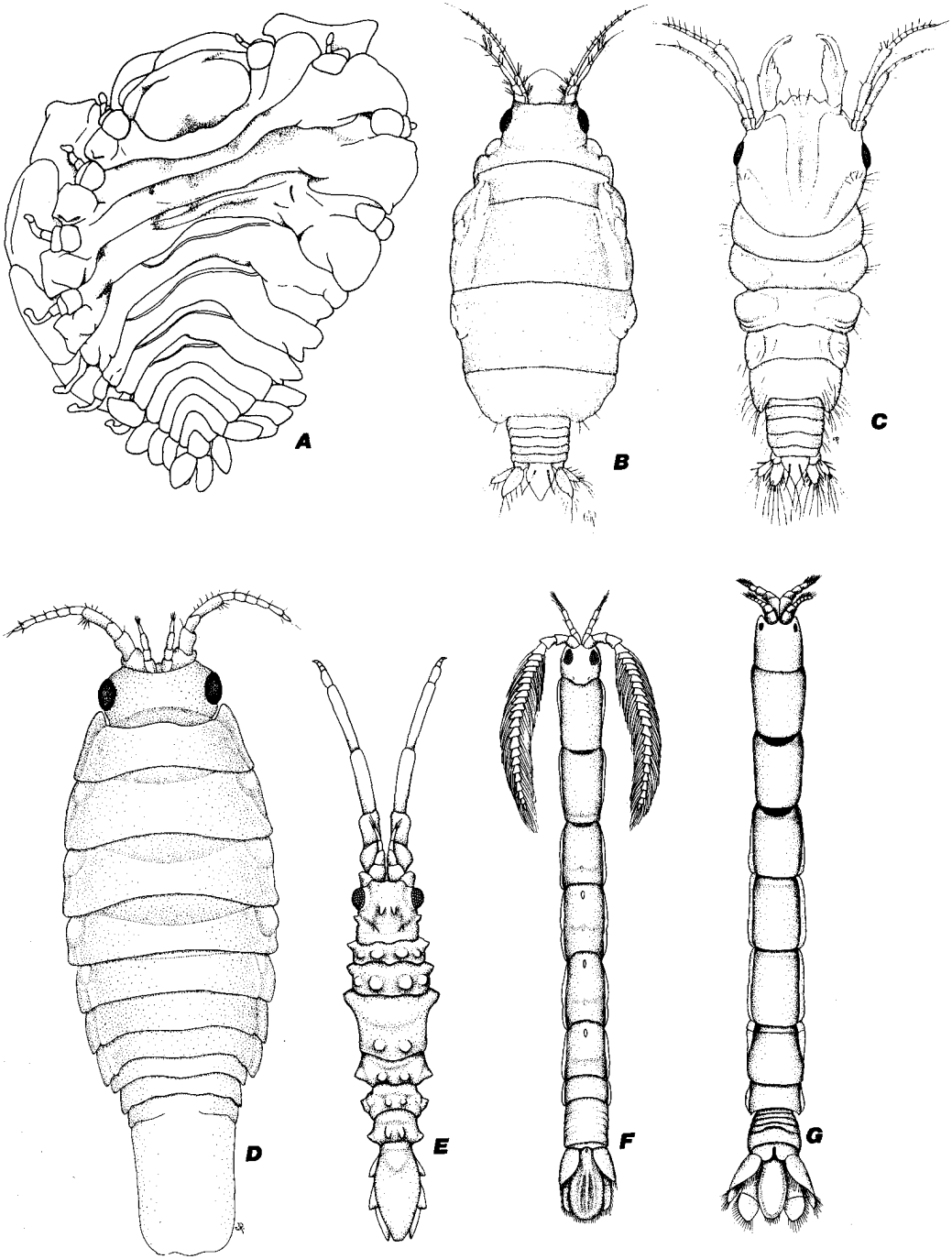


FIG. 2. Examples of various 'long-tailed' isopod suborders. A, Epicaridea (*Argeia pugettensis*). B–C, Gnathiidea (B, *Gnathia tridens* female; C, *Gnathia tridens* male). D, Valvifera, Idoteidae (*Idotea metallica*). E, Valvifera, Arcturidae (*Idarcturus hedgpethi*). F, Anthuridea, Anthuridae (*Haliophasma geminata* male). G, Anthuridea, Paranthuridae (*Paranthura elegans*).

Wägele (1989a) depicted this group paraphyletically on their trees of the Isopoda. Wägele (1989a) recommended a reorganisation of the Isopoda that would eliminate three currently recognized suborders, the Flabellifera, Epicaridea, and Gnathiidea. Although Wägele's tree and classification are not corroborated by the present study, the Flabellifera as it is currently recognized is almost certainly not a monophyletic taxon. Wägele reorganized the above suborders into two new groups, which he called the Cymothoida (*sic*) and the Sphaeromatoidea, subsuming the Gnathiidea, Epicaridea, and several flabelliferan families into the former. (Note that Wägele's Cymothoida is not the equivalent of Cymothoidea of Richardson, 1905, and others).

In the present study, we test the monophyly of the Flabellifera by including all of its component families in the analysis with the other suborders of the Isopoda. We recognize the following nominate families of Flabellifera: Aegidae Dana, 1853; Anuropidae Stebbing, 1893; Bathynataliidae Kensley, 1978; Cirolanidae Dana, 1853; Corallanidae Hansen, 1890; Cymothoidae Leach, 1818; Keuphyliidae Bruce, 1980; Limnoriidae White 1850; Lynseiidae Poore, 1987; Phoratopodidae Hale, 1925; Plakarthriidae Richardson, 1904; Protognathiidae Wägele and Brandt, 1988; Serolidae Dana, 1853; Sphaeromatidae Burmeister, 1834; and, Tridentellidae Bruce, 1984.

The two infraorders of Oniscidea Latreille, 1803 (Tylomorpha Vandel, 1943 and Ligiamorpha Vandel, 1943; see Holdich *et al.*, 1984) are also analysed separately because opinion has been divided on whether or not the Tylidae are true oniscideans (Kussakin, 1979; Holdich *et al.*, 1984; Wägele, 1989a; Schmalfuss, 1989).

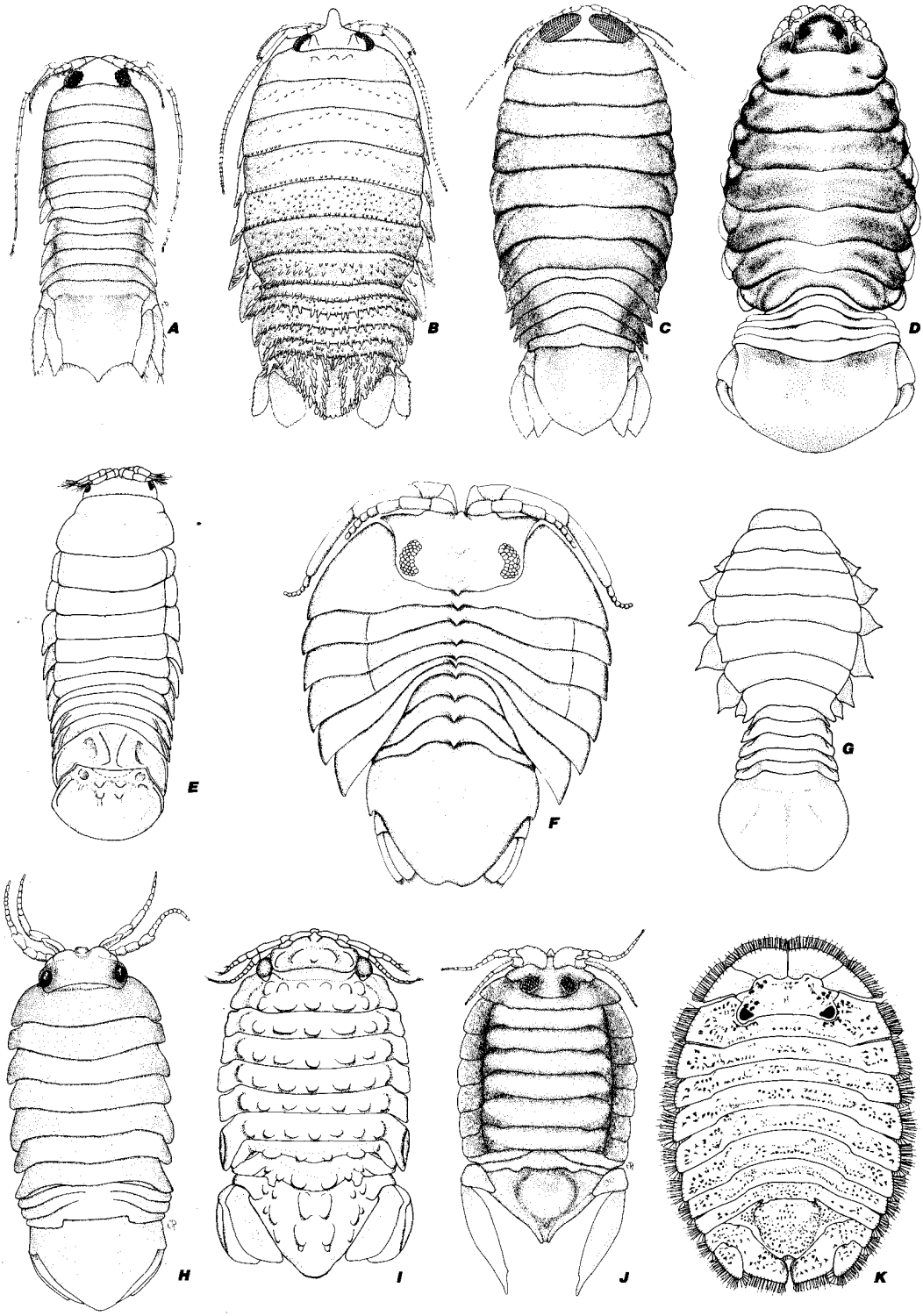
Three taxa that are included in our analysis require brief comment. The Calabozoidea is a monotypic ground-water (freshwater) taxon so far known only from Venezuela. In her original description, Van Lieshout (1983) suggested possible affinities of *Calabozoa* to both the Asellota and the Oniscidea. We have examined specimens of *Calabozoa* and found Van Lieshout's illustrations and description misleading; new illustrations of the male pleopods 1 and 2 are provided in Fig. 10. *Calabozoa* appears to possess no asellotan synapomorphies. Wägele and Brandt (1988) created the Protognathiidae based upon their examination of a single, apparently manca-stage, individual. Wägele (1989a) concluded that this new family was the sister group of the Gnathiidea. In the present study we argue that protognathiids share no unique synapomorphies with gnathiids, although some superficial similarities are present. Wägele (1983b, 1989a) has argued that the Microcerberidea are members of the asellote superfamily Aselloidea. Although the microcerberids have several features typically viewed as asellotan (6-articulate antennular peduncle; pleonites 3–5 fused with the pleotelson; females lacking first pair of pleopods; male second pleopod with endopod transformed into a complex gonopod), they lack other features generally also regarded as definitive synapomorphies of the Asellota (e.g. antennal peduncle with a scale; female pleopod 2 uniramous; exopods of male second pleopods modified to work with the elongate geniculate endopods in sperm transfer; and, possibly, the unique asellotan spermathecal duct). For these reasons we treat the Asellota and Microcerberidea as separate groups (OTU's) in our analysis.

Data Sources

Specimens were examined for all taxa treated except Protognathiidae. Material was examined on loan from a variety of institutions, and during visits to the U.S. National Museum of Natural History, Smithsonian Institution (USNM), Los Angeles County Museum of Natural History (LACM), Zoologisch Museum, Amsterdam (ZMA), Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM), Victoria Museum, Melbourne (VM), San Diego Natural History Museum (SDNHM), and Scripps Institution of Oceanography (SIO). In addition to examining specimens, the original literature was extensively perused.

Scoring of Characters

One of the advantages of the available computer-assisted numerical techniques (see below) is that they treat each character independently. Thus, if the state of a particular character is unknown, inapplicable, or we have simply been unable to resolve it to our satisfaction, we have scored it as 'missing data' (indicated by a '?' in the data matrix). In preliminary analyses, characters for which no clear polarity could be established were not coded in any primitive-derived sequence, but were left to change in any direction such that simple parsimony (fewest changes) was the arbiter. These unpolarised (nonadditive or unordered) characters are indicated in the character discussions below. These analyses proved useful in assessing character homoplasy.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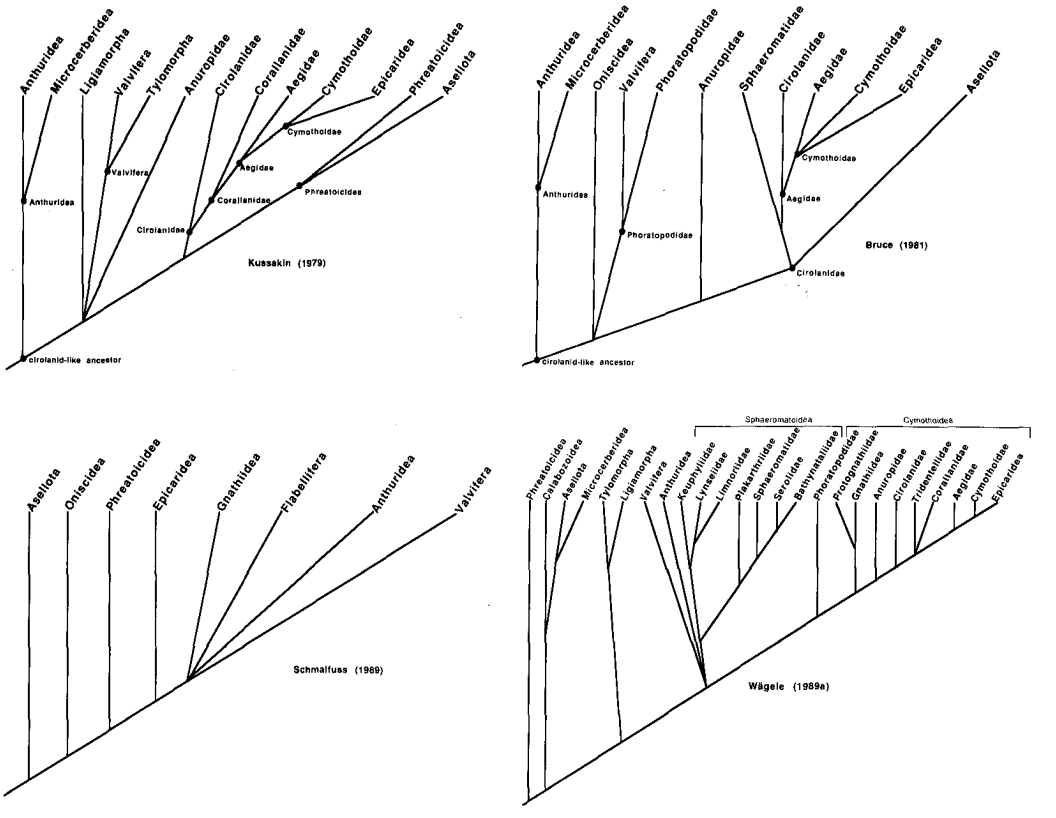


FIG. 4. Some evolutionary trees from previous studies, by Kussakin (1979), Bruce (1981), Schmalfuss (1989), and Wagele (1989a).

For the final analyses, however, we decided to analyse the data with all characters left unordered (nonadditive).

If a character state judged to be plesiomorphic is present for only some members of the taxon in question, e.g. 'accessory flagellum on antennule in most gammaridean amphipods', it is scored present in the data matrix for the entire taxon unless otherwise stated, i.e. the derived condition is presumed to define a subset within the taxon. Conversely, of course, if an apomorphic state is present in only some members of the taxon in question, the entire taxon is not scored apomorphic for that character, but is scored plesiomorphic. Initially polarized characters were scored as indicated in the ordering of the character state numbers: 0 = plesiomorphic, 1 = apomorphic, 2 = more apomorphic than 1, etc. Homology decisions were made on the basis of ontogenetic data and comparative morphology (positional data and anatomical similarity).

Phylogenetic Analysis

The character state data were analysed with four numerical cladistic analysis packages: HENNIG86 (version 1.5), PHYLIP (version

FIG. 3. Examples of various isopod families and genera of the suborder Flabellifera. A, Cirolanidae (*Metacirolana joanneae*, SDNHM). B, Tridentellidae (*Tridentella glutacantha*, from Delaney and Brusca, 1985). C, Aegidae (*Aega plebeia*, from Brusca, 1983). D, Cymothoidae (*Ceratothoa gilberti*, from Brusca, 1981). E, Limnoriidae (*Limnoria quadripunctata*). F, Serolidae (*Serolis carinata*, SDNHM A.0114). G, Anuropidae (*Anuropus bathypelagicus*). H, Sphaeromatidae (*Gnorimosphaeroma insulare*). I, Sphaeromatidae (*Exosphaeroma amplicauda*). J, Sphaeromatidae (*Bathycopea daltonae*). K, Sphaeromatidae (*Paraleptosphaeroma glynni*).

3.2), PAUP (version 3.0), and MacClade (version 2.1). HENNIG86 is advantageous because of its speed, successive weighting algorithm, ability to depict polytomous tree branches, and ability to store many equal-length trees in memory. The successive weighting program (Farris, 1969, 1989) is useful in reducing the impact of homoplasous characters on tree topology. Despite Platnick's (1989) recommendation of HENNIG86 as the program of choice, PAUP, MacClade, and the PHYLIP program package remain useful for comparative and analytical purposes (Sanderson, 1990). PAUP is by far the most user-friendly, is useful to check different character optimisations (a feature currently absent from HENNIG86) on the final trees, and to obtain detailed computations of C.I. (consistency index), character changes, and OTU apomorphy lists. The program MacClade 3.0 was used (on a Macintosh Computer) to branch swap on the final set of trees, in order to evaluate changes in tree length, homoplasy levels, and character placement on selected alternative trees, including those of Schmalfuss (1989), Wägele (1989a), and others. MacClade and PAUP are extremely useful in their user-friendly ability to generate graphic representations of character traces on trees, although MacClade is seriously hindered by its inability to depict multifurcations.

The principal statistics used in tree evaluation were overall tree length (step length) and consistency index (C.I.). Consistency and retention indices for each individual character were also computed and used to evaluate their overall homoplasy levels.

Carpenter (1988) recently argued that consensus trees should not be used to construct cladograms. However, we agree with Anderberg and Tehler (1990) that strict consensus trees are both useful and informative because they reduce the conclusions to only those components which all equal-length shortest trees have in common. In fact, they are probably a necessity when high levels of homoplasy invest a data set. Even if successive weighting (i.e. the successive approximations character weighting method of Farris, 1969) is used, multiple equally parsimonious trees may derive from a data set high in homoplasy. Thus, we believe that when numerous equally parsimonious trees exist, a strict consensus tree should be presented.

In order to distinguish between some closely related taxa, we included some characters that are currently known to be unique to a given suborder or family (Appendix III). However, because we were concerned in this study with identifying sister group relationships within the Isopoda, we did not make an effort to identify all of the unique synapomorphies that define only individual taxa (suborders or families). Some characters that proved to define only terminal taxa in our final trees were early-on suspected to be useful in distinguishing larger sister groups. These may be viewed as 'uninformative' characters in the final trees by some workers. However, they were important in comparative analyses and tree testing, and as additional taxa and data are described some of these characters may no longer remain unique to a single terminal taxon. For these reasons, we felt it was important to leave them in the data matrix, thus allowing others to use our data set as a starting point for further tree testing. The data set is available on diskette on request.

DISCUSSION OF CHARACTERS

Stalked Eyes

Mysidaceans and mictaceans have compound eyes set on short, movable eyestalks (although eyestalks are absent in the mictacean *Hirsutia*). In amphipods, a 'rudimentary eyestalk' has been reported from ingolfiellids. Dahl (1977) and Lowry and Poore (1989) have argued that this small process in ingolfiellids is not a true eyestalk, but rather is a cuticular process or scale. Lowry and Poore's argument hinged on the observation that unequivocal eye stalks in other peracarids have 'an attitude and position very different' than seen in the ingolfiellids. Dahl's argument was based on the absence of 'dioptric and nervous elements' in this structure. The first argument is not particularly strong because the position and attitude of peracarid eye stalks vary greatly. A positional change in the ingolfiellids could have been caused by a lateral rotation of the entire eye-antennular-antennal complex. Dahl's argument is stronger, although it relies on reductions rather than homologies. Among tanaidaceans, articulated eye-lobes occur in some Apseudomorpha and Tanaidomorpha, including those with eyes in a variety of positions ranging from that seen in the Mictacea to that seen in the ingolfiellids. In amphipods and isopods the eyes are entirely sessile, although they may be elevated on lobes of varying sizes in some species of Phreatoicidea, Gnathiidea, Valvifera, and Asellota. At the level of the Peracarida most workers might regard motile stalked eyes as the

ancestral condition, and sessile eyes (and loss of eyes) as derived conditions. However, as Bowman (1984) has noted, the primitive condition in Crustacea is still unknown. Thus we left this character unordered in all analyses. Character No.1 is: eyes stalked and basally articulated (0), *vs* eye stalks reduced, lobe-like, but sometimes with basal articulation (1), *vs* eyes sessile (2).

Carapace

Character 2 describes the development of the carapace. In mysidaceans the carapace generally covers all 8 thoracomeres and laterally covers the bases of the maxillae and maxillipeds (state 0). In all other peracarids, the carapace is either reduced or absent. In tanaidaceans and mictaceans, lateral carapace folds still cover the bases of the maxillae and maxillipeds (state 1). In amphipods and isopods a carapace is absent (or exists only as a head shield) and there are no lateral carapace folds (state 2). Because of controversy regarding the origin (and convergent reductions) of the crustacean carapace, character 2 was left unordered in initial analyses.

Moulting

Isopods are apparently unique among crustaceans in that the moulting is biphasic, the posterior exoskeleton being shed earlier than the anterior exoskeleton (George and Sheard, 1954; Price and Holdich, 1980a, b). The break between the two halves occurs at the junction of pereonites 4 and 5, and the two halves are out of synchrony throughout the moult cycle. Character 3 is: monophasic moulting (0) *vs* biphasic moulting (1).

Heart and Branchial Structures

Mysidaceans, tanaidaceans, and mictaceans utilise thin-walled vascularised regions on the carapace for respiratory exchange (pereopodal gills are absent). However, loss of free carapace folds in the Amphipoda and Isopoda necessitated the transfer of respiratory functions to other areas of the body (Grindley and Hessler, 1971). Amphipods have unique medial percopodal epipodites ('coxal gills') presumed to function in respiratory exchange. Whether the medial epipods of amphipods are homologous to the lateral epipods of other crustaceans is not known. In non-isopod peracarids, the heart is positioned in the thorax. The isopod heart is located in thoracomeres 7/8 and the pleon, and they utilize the pleopods for respiration. Character 4 is: heart entirely thoracic (0) *vs* heart thoraco-abdominal (1). Character 5 is: branchial structures cephalothoracic (0) *vs* branchial structures abdominal (1). Only isopods are scored apomorphic for these two characters.

Body Shape

Living mysidaceans are laterally compressed. Most isopods have dorsoventrally flattened bodies. Although the bodies of amphipods (gammarideans) and phreatoicideans superficially appear laterally compressed, their bodies are actually more cylindrical or tubular (semicircular in cross-section). The apparent lateral compression in these two groups is an illusion created by the large, ventrally expanded, pereonal coxal plates and pleonal epimeres in amphipods, and the large pleonal epimeres of most phreatoicideans. Some phreatoicideans also have lateral expansions of the pereonal tergites (i.e. true epimeres, or 'pleura') that hang down to give the body an amphipod-like appearance. The cylindrical nature of the phreatoicidean body was recognised long ago (Nicholls, 1943, 1944) although not all authors have acknowledged it (Wägele, 1989a). In mictaceans, and in anthuridean and microcerberid isopods (as well as many arcturid Valvifera and some Asellota) the body is also cylindrical, or semicircular in cross-section. Subcylindrical bodies also may occur in the Lynseiidae. Given the variety of body shapes that occur in the isopods and other peracarid orders, we can make no judgment on which shape is primitive and which is derived. Body form is probably strongly selective and based largely on a group's behaviour and preferred habitat, and therefore any real phylogenetic signal we may seek has a high probability of being obscured. For example, we could identify 'narrow and elongate' as a potentially homologous feature, but in fact this would introduce obvious homoplasy because the groups that would be so classified, the Anthuridea and the Microcerberidea, are probably narrow for entirely different reasons; the former are tubiculous and the latter are interstitial. Consequently, we have been cautious regarding use of body form in our analysis.

Some isopods carry the flattened (depressed) body form to an extreme. Several flabelliferan families (Bathynataliidae, Keuphyliidae, Plakarthriidae, and Serolidae) have extremely broad and flattened bodies, with broad coxal plates and the cephalon encompassed by the first pereonite or at least surrounded by the first pereonite coxal region (character 7) (*Serolis*, Fig. 3F). The Sphaero-

matidae also includes a number of genera with extremely flattened bodies (*Amphoroidella, Chitonopsis, Naesicopea, Paracasidina,Playtnympha, Platysphaera, Paraleptosphaeroma, Platycerceis*), as does the Idoteidae (*Moplisa*) and Cirolanidae (*Hansenolana*). However, these cases are uncommon and are assumed to represent derived conditions in these three families. They also differ from the above taxa in that the cephalon is not entirely encompassed by pereonite I and the lateral coxal plates are not free. Illustrations of the dorsal aspect of phoratopodids tend to depict these animals as markedly flat and broad. However, the body of phoratopodids is actually dorsally arched and straight-sided, reminiscent of the cirolanid genus *Politolana* and many sphaeromatids (Bruce, 1981, pers. obs.).

In the Anuropidae the body is greatly inflated and globular (character 89), reminiscent of certain hyperiid amphipods. Anuropids are apparently all parasites on gelatinous zooplankton, a feature also shared with most, if not all, hyperiid amphipods (character 90).

In two flabelliferan families, Limnoriidae and Lynseiidae, the orientation of the head on the pereon differs from that seen in all other isopods. In these two groups, the head is set off from the first pereonite (second thoracomere) and is capable of left-right rotation (character 40); in all other isopods the head fits snugly against the first pereonite and is usually somewhat immersed in it, restricting head movement to a flexion in the dorso-ventral plane.

In the family Serolidae, the tergite of the seventh pereomere (and sometimes also the sixth) is reduced and fused with the adjacent anterior tergite, rendering it indistinguishable dorsally (character 69).

Gut Tube

The gut tube of mysidaceans and amphipods has an endodermally derived midgut region (a 'true midgut'). It has long been known, however, that isopods lack an endodermally derived midgut (see recent reviews by Bettica *et al.*, 1984, Forgarty and Witkus, 1989, and Hames and Hopkin, 1989). The entire gut tube of an isopod is ectodermally derived; the only endodermally-derived structure is the 'hepatopancreas' (the digestive caeca). According to Scholl (1963) the gut of tanaidaceans may also be entirely ectodermal. The condition in mictaceans is not known. Character 8 is: gut tube with endodermally derived midgut (0) *vs* gut tube entirely ectodermally derived, without a true midgut region (1).

Striated Muscles

Nylund (1986), Nylund *et al.* (1987), and Tjønneland *et al.* (1987) have described a pattern of membrane systems in the heart myofibers of isopods that they claim is unique within the Malacostraca. We do not find the reasoning given by Nylund *et al.* (1987) for placement of the isopods as a sister group to all other eumalacostracans to be logical, because it relies on differences between groups rather than on similarities among them, to define relationships. Nevertheless, ultrastructure of the heart myofibres appears to be a unique synapomorphy for isopods. Character 9 is: striated muscles of typical malacostracan type (0) *vs* striated muscles with unique myofibril ultrastructure (1).

Second Thoracomere

Mysidaceans, mictaceans, amphipods, and most isopods have a free second thoracomere (thus one pair of maxillipeds), although the fossil pygocephalomorphans have two sets of maxillipeds. In gnathiid isopods, the second thoracomere is partly or wholly fused to the cephalon, and the second thoracopods form a second pair of maxillipeds (called pylopods). In the praniza stage these appendages are prehensile and used for attachment to the host; in adults they are more typically maxilliped-like. Gnathiids are the only isopods in which the second thoracomere and its appendages are entirely integrated into the head. Dorsal, medial-only fusion of the second thoracomere with the cephalon occurs in several genera in various other isopod suborders and families (Bathynataliidae, Serolidae, several sphaeromatid genera [*Ancinus, Bathycopea*], some Valvifera [*Lyidotea*, Arcturidae], some Asellota [*Stenasellus*], some Microcerberidea [*Microcerberus mexicanus*], and some Phreatoicidea), but these cases are not full fusion and do not incorporate the first pereopods into the mouth field, as in gnathiids. Complete fusion of the second thoracomere to the cephalon may occur in several deep-sea Asellota genera (*Haplomesus*) but, again, the first pereopods are not modified as maxillipeds or appendages of the buccal field. These represent derived conditions found within the Asellota and occur only in certain deep-sea forms. Character 10 is: second thoracomere free, not fused to cephalon (0) *vs* second thoracomere entirely fused to cephalon, with its appendages (the pylopods) functioning

with the cephalic appendages and serving as a second pair of maxillipeds. Gnathiidea is the only taxon scored apomorphic for character 10.

Thoracic Exopods

In mysidaceans and mictaceans, all the thoracopods (primitively) bear exopods. In tanaidaceans, only the anterior thoracopods have exopods. In amphipods and isopods, no thoracopods have exopods. Character 11 is: at least some thoracopods with exopods (0); exopods absent from all thoracopods (1).

Embryogeny and Hatching Stages

All Peracarida have direct development, and in all orders except Mysidacea and Amphipoda the young leave the marsupium as mancas, resembling small adults but with the last (seventh) pair of pereopods not yet developed. However, in some hyperiid amphipods the young do emerge as virtual mancas, with the seventh legs undeveloped or as little more than a limb bud (Bate, 1861; Laval, 1980). Brusca (1984) suggested that the mancoid stage in peracarids may be the product of variations in timing in embryogeny and hatching. Its absence in mysidaceans and amphipods may be tied to a more rapid embryological development (or to delayed postembryonic hatching) in these taxa (Steele and Steele, 1975). Manca-like hatching stages also occur in bathynellaceans (which may hatch with several posterior thoracopods undeveloped). Moreover, some thermosbaenaceans and bathynellaceans never develop posterior legs even as adults. In gnathiids, the young leave the marsupium as a morphologically very distinct mancoid stage called the praniza 'larva' (Wägele, 1988).

Mysidaceans and amphipods also differ from other peracarids by possession of ventral flexure of the embryo within the embryonic membrane, all other peracarids having a dorsal embryonic flexure. The embryos of mysidaceans and amphipods develop a ventral (=caudal) furrow that separates the caudal papilla from the ventral part of the rest of the embryo. This is presumably linked to the presence of ventrally curved embryos, completion of cleavage in the early stages, and early appearance of the egg-nauplius stage in these groups rapid early holoblastic cleavage. In all other peracarids that have been studied (except perhaps thermosbaenaceans), development is slower, the naupliar and metanaupliar somites appear nearly simultaneously, body somites begin proliferating before the the dorsal (=caudal) furrow forms, and the embryos curve dorsally, (Weygoldt, 1958; Strömberg, 1972). Eucarids in general tend to have ventral flexure of the embryos. Character 51 is: embryos curve ventrally (mysidaceans and amphipods) (0), *vs* embryos curve dorsally (all other peracarids) (1). Character 12 is: hatching stage not a manca (0) *vs* hatching stage a manca (1). Character 13 is: without a praniza stage (0) *vs* with a praniza stage (1). Characters 12 and 51 were left unordered in the initial analyses.

Body Symmetry

Only in the isopod Suborder Epicaridea does loss of body symmetry typically occur in adult females. Some species of Cymothoidae may become twisted to one side or the other, but this is not regarded as true asymmetry in the sense of loss of, or gross modification of, appendages on one side of the body, as in the epicarideans. Some epicarideans (most Cryptoniscidae and Entoniscidae) may be so modified as to resemble little more than large egg sacs. Character 14 is: adult females bilaterally symmetrical (0) *vs* adult females with loss of symmetry (1).

Parasitism

Adult female epicarideans are obligate parasites on other crustaceans; the miniature males live in close association with the female, usually buried among the female's pleopods. Character 15 is: adults not parasitic on other crustaceans (0) *vs* adults obligate parasites on other crustaceans (1); only Epicaridea is scored apomorphic for this character. Adult Cymothoidae are obligate and permanent hematophagic parasites on freshwater and marine fishes. Character 66 is: adults obligate and permanent parasites of fishes. Only the Cymothoidae are scored apomorphic for this character. Members of the Aegidae, Corallanidae, and Tridentellidae — which are often referred to as 'parasites' — do not attach permanently to their prey, nor do corallanids restrict their diet to fishes. Species in these families can be considered as micropredators or temporary parasites.

Cuticular Sensilla

Holdich (1984) has described two types of cuticular sensilla that he regards as unique to the Oniscidea. The first (character 16) is the cuticular tricorn sensillum, which he adequately documents for the Oniscidae (*Oniscus*) and Porcellionidae (*Porcellio*, *Porcellionides*), somewhat less convincingly for the Armadillidiidae (*Armadillidium*) and Armadillidae (*Venez-*

illo), and even less convincingly for the Ligiidae (*Ligia, Ligidium*), Philosciidae (*Philoscia*), Tylidae (*Tylos*), Platyarthridae (*Platyarthrus*), Trichoniscidae (*Androniscus, Trichoniscus*), and Scyphacidae (*Alloniscus, Deto*). Powell and Halcrow (1982) document tricorns on *Oniscus asellus*, but not on *Ligia baudiniana* or any non-oniscidean species they studied. Modified tricorns similar to those of the aquatic genus *Haloniscus* can been seen on SEM photographs of the uropods of *Calabozoa* (Van Lieshout, 1983, fig. 5d–e). We have scored both oniscidean infraorders (Tylomorpha and Ligiamorpha) and the Calabozoidea apomorphic (1) for this character. The second kind of sensillum is the 'antennal and uropodal spikes' (character 17), which are complex compound sensillar structures at the tips of the antennae and uropodal rami. We have scored both oniscidean infraorders apomorphic (1) for this character.

PEREON AND PEREOPODS

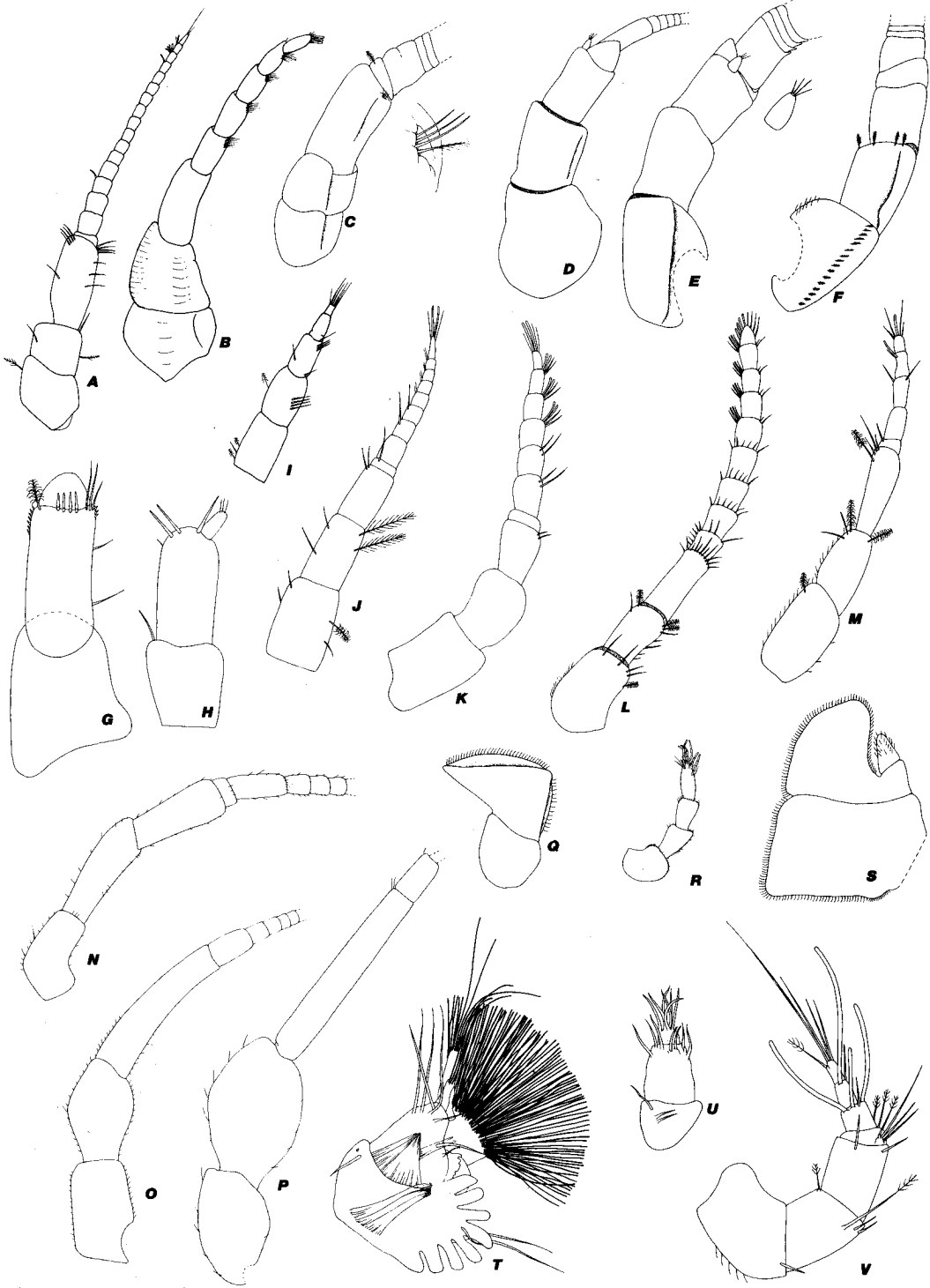
In Isopoda and other peracarid taxa, the pereopods tend to form two functional groups: an anterior set of legs that are directed forwards (antero-ventrally), and a posterior set of legs that are directed backwards (postero-ventrally). Often this grouping allows the anterior legs to have a somewhat (or extremely) different role in locomotion or feeding than the posterior legs.

In Phreatoicidea, Asellota, and Microcerberidea, the legs are grouped 4:3 (four pairs of anterior pereopods directed forwards and three pairs of posterior pereopods directed backwards). This seems to be the case with the terrestrial isopods and the Calabozoidea as well, although the strong isopody in these taxa tends to decrease the difference between the anterior and posterior groups. The 4:3 grouping may be a natural tagmosis for the isopods owing to the biphasic molt boundary between pereonites 4 and 5.

Nevertheless, most other isopods show a clear 3:4 tagmosis. The 3:4 condition prevails in all families of flabelliferans, as well as the Anthuridea, Gnathiidea, Epicaridea, and the genus *Hadromastax* (currently placed in the family Limnoriidae, but being elevated to separate family status by Bruce and Müller). The predatory and parasitic isopods (Anthuridea, Anuropidae, Cirolanidae, Corallanidae, Cymothoidae, Protognathiidae, Tridentellidae, Epicaridea) have 3 pairs of raptorial or grasping anterior limbs, while the 4 pairs of posterior limbs are dedicated more for locomotion. In the strictly parasitic Cymothoidae and Epicaridea, all 7 pairs of legs are strongly prehensile. However, the limbs of cymothoids and epicarideans appear fundamentally different. In epicarideans, the dactyl is a short acute hook that folds against a greatly enlarged or swollen propodus, which in turn usually articulates on a small triangular carpus. In cymothoids, the dactyl is greatly elongated and articulates on an elongate propodus; the carpus is not reduced or triangular shaped, and it usually has an indentation to receive the tip of the dactyl. We believe that Wägele's (1989a) homologisation of these two kinds of legs is probably in error.

The Plakarthriidae seems unique in its possession of a 1:6 arrangement of the legs; the basis of pereopod 1 is directed posteriorly, whereas in the rest of the legs the bases are directed anteriorly. However, this may be a secondary effect of the overall body form and orientation of the pereonites, so we have scored this character with a '?' for this family. Although the Gnathiidea have a more highly derived body tagmosis, their anterior 3 pereopods are still directed anteriorwards, and the remaining limbs are directed post-

FIG. 5. Examples of isopod antennules. A, Flabellifera, Aegidae (*Aega longicornis*, type). B, Flabellifera, Cymothoidae (*Nerocila acuminata*, from Brusca, 1978). C, Flabellifera, Cirolanidae (*Parabathynomus natalensis*, USNM 170251); note sensilla (insert figure to right). D, Flabellifera, Cirolanidae (*Bathynomus giganteus*, SDNHM). E–F, Flabellifera, Cirolanidae (*Bathynomus doderleini*, USNM 39321): E, ventral view, F, dorsal view; note 'scale' (insert figure to right of E). G, Oniscidea (*Ligia exotica*, USNM 43352). H, Oniscidea (*Ligidium ungicaudatum*, USNM 83070). I, Anthuridea (*Cyathura guaroensis*, from Brusca and Iverson, 1985). J, Anthuridea (*Calathura* sp., USNM 99253). K, Anthuridea (*Malacanthura caribbica*, USNM 173521). L, Phreatoicidea (*Phreatomerus latipes*, USNM 60659). M, Gnathiidea (*Bathygnathia curvirostris*, USNM 10580). N, Flabellifera, Bathynataliidae (*Bathynatalia gilchristi*, USNM 170549). O, Serolidae (*Serolis albida*, USNM 123900). P, Serolidae (*Serolis bromleyana*, USNM 123911). Q, Flabellifera, Anuropidae (*Anuropus antarcticus*, USNM 112260). R, Valvifera, Idoteidae (*Synidotea francesae*, from Brusca, 1983). S, Flabellifera, Plakarthriidae (*Plakarthrium punctatissium*, USNM 32500). T, Epicaridea (*Scalpelloniscus penicillatus*, after Grygier,1981). U, Epicaridea (*Pseudasmmetrione markhami*, after Adkinson and Heard, 1980). V, Flabellifera, Limnoriidae (*Limnoria kautensis*, after Cookson and Cragg, 1988).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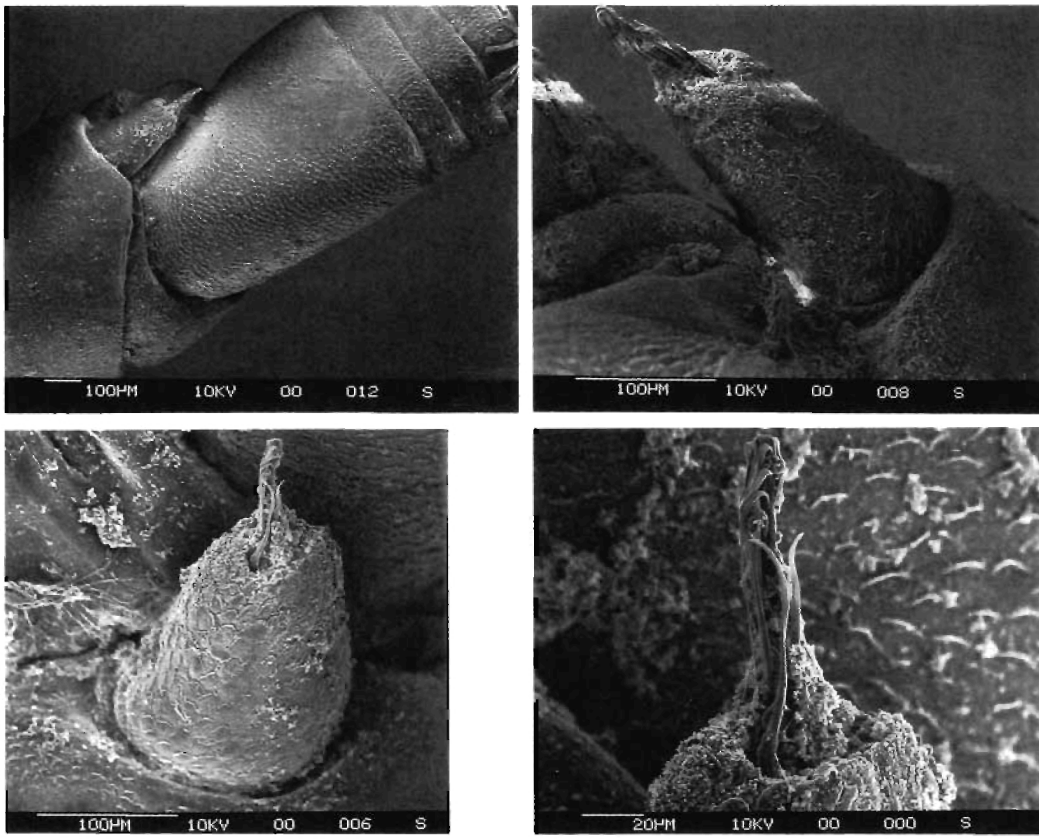


FIG. 6. Scanning electron micrographs of the antennular scale of *Bathynomus giganteus* (Flabellifera, Cirolanidae). Images show 4 different magnifications.

eriorwards; this is most easily seen in the active praniza stage.

In the Valvifera, both the 3:4 and 4:3 condition occurs; Arcturidae and Amesopodidae have the 4:3 condition, whereas Chaetiliidae, Holognathidae, Idoteidae and Xenarcturidae have the 3:4 condition. In the Pseudidotheidae the fourth leg is directed straight out to the side, and species in this family may appear to be 3:4 or 4:3, or even one condition on the left side and the other condition on the right. Because the 3:4 condition is considered primitive in this suborder (Brusca, 1984: 104) Valvifera are scored for that state.

The out-group taxa show a variety of functional groupings, which may or may not be homologous with the situation seen in the Isopoda. The tanaidaceans and gammaridean amphipods have a 4:3 grouping, similar to the Phreatoicidea. In mictaceans, the grouping appears to be 2:5. At least this is the case in *Mictocaris*; the condition in *Hirsutia* is less clear, but it appears to be the same. Mysidaceans have no distinct functional grouping of the pereopods, i.e. all legs arise more or less straight out, ventrolaterally from the body.

Hence, four pereopodal conditions, or 'states' exist for character 18: 2:5, 3:4, 4:3, and no functional grouping. The relative polarity or direction of evolutionary change(s) associated with this character is unknown, and this character was initially left unordered in the data set. The states of character 18 are assigned the following codes in the data matrix: 0 = no functional grouping (mysidaceans); 1 = 3:4; 2 = 4:3; 3 = 2:5.

In adult Gnathiidea, the seventh pereonite is reduced and without pereopods (character 19). Although the seventh pereonite may be lacking in some anthuridean genera (*Colanthura*, *Cruregens*, etc.; Poore, 1984) and in a few deep-sea Asellota (Wilson, 1976; 1989), this condition

is not regarded as primitive in these suborders. It is probable that genera of isopods in which sexually mature adults lack the seventh pereonites evolved by way of neotenic events.

In the Phoratopodidae, the posterior pereopods form sculling 'oars', and the dactyls are reduced or lost (character 88). Flattened posterior swimming pereopods also occur in some Munnopsidae (Asellota) and, to a limited extent, some Cirolanidae (*Natatolana*), but it is not the primitive condition for these two families.

True chelipeds do not occur in isopods, except for a few rare cases such as the unusual genera *Carpias* (Asellota) and *Chelanthura* (Anthuridea) although various subchelate and prehensile conditions do occur. In three groups, Aegidae, Cymothoidae, and Epicaridea, the pereopods are prehensile. In aegids, pereopods 1–3 only are prehensile; in cymothoids and epicarids all 7 pairs of pereopods are prehensile. We define a prehensile pereopod as one in which the dactyl is as long or longer than the propodus, acute, and recurved. Although the pereopods of most epicarideans are prehensile and used for clinging to their host (crustaceans), they differ fundamentally from the legs of aegids and cymothoids, as noted above, with which they may not be homologous. At least some of the anterior pereopods of serolids, phoratopodids, certain Sphaeromatidae (*Bathycopea*, *Tecticeps*), and astacillid valviferans are subchelate, but we do not regard these conditions as homologous to the prehensile pereopods of cymothoids, aegids or epicarideans. Character 65 is: pereopods not prehensile (except at most pereopod 1) (0); pereopods 1–3 prehensile (Aegidae, Cymothoidae, Epicaridea) (1).

Antennules

The antennules of mysidaceans, mictaceans, and amphipods are biramous. In these groups the flagella arise from the third peduncular article, as in other Peracarida and Eumalacostraca. The antennules of tanaidaceans may be either biramous, with the flagella arising from the fourth article (Apseudomorpha) or uniramous (Neotanaidomorpha, Tanaidomorpha). The antennules of nearly all isopods are uniramous (see Figs. 5 and 6 for examples of isopod antennules). However, the literature contains many allusions to taxa that allegedly possess antennular scales, or other structures said to represent vestigial flagella or remnants of the missing antennular ramus (presumably the exopod). These various taxa belong to three suborders: Flabellifera, Anthuridea, and Epicaridea. These matters are briefly reviewed below. In the following discussion, the 'peduncle' of the antennule is defined as the enlarged, basal region of the antennule that bears intrinsic musculature. The flagella of isopod antennules lack intrinsic musculature (i.e. no muscles have their origin in the flagellum); flagella arise from the distal-most peduncular article.

As in so many other instances, Calman (1909) appears to have been the first to comment on the possible generality and significance of scales on the antennules of isopods, noting their presence in two groups, the genus *Bathynomus* (Cirolanidae) and 'cryptoniscan larvae of certain epicarideans.' Calman did not indicate which epicarideans he was referring to, nor did he provide figures of these structures. However, he referred to them as 'minute vestiges of the inner flagellum', and was presumably referring to species of Bopyridae *sensu lato*. Hansen (1925) repeated Calman's remarks, as have many subsequent workers. Wägele (1983a) used Calman's comment as a basis for 'homologisation of this (scale-bearing) article with the last peduncular segment of other Malacostraca,' on the apparent assumption that the antennular peduncle of isopods is homologous to the protopod of the other segmental body appendages. Menzies (1957) added an overtone of generality with a passing comment in his widely cited limnoriid monograph, which reads: 'The conspicuous scale attached to the first antenna of *Paralimnoria* is also characteristic of the genus *Limnoria* and, as Calman remarks, of the genus *Bathynomus* (Cirolanidae) and cryptoniscids (suborder Bopyroidea). It has since been found on *Mesanthura* (Suborder Anthuridea, Miller and Menzies, 1952, p. 8) and the young of *Cirolana* (unpubl. data) and it is possibly characteristic of isopods in general' (*sic*). Menzies (1957) provided an illustration of this structure for *Paralimnoria andrewsi*.

In *Bathynomus* (*B. giganteus*, *B. doederleni*, *B. kapala*) the 'antennular scale' takes the form of a large, cuticularized, volcano-like process with a deep pit at the terminus from which arise numerous long setae (Fig. 6). Under light microscopy this scale resembles a large complex sensillum. However, SEM examination reveals the scale to be covered with a cuticle bearing the same type of cuticular surface structure seen on the rest of the body, and to be encircled basally by what may be an articular membrane. Thus, we tentatively interpret this structure as a true scale,

i.e. vestigial second ramus. However, in the similar appearing *Parabathynomus* a scale does not exist, although a sensory pit is present in the same position on the peduncle, and arising from it is the same kind of setal cluster seen in *Bathynomus*. The two kinds of sensory structures are precisely in the same place, and look very similar in all respects, except that in *Parabathynomus* the sensory pit sits on the cuticular surface, rather than at the end of a scale. In another very similar genus, *Booralana*, a cluster of sensory setae arises from a very shallow depression at this same location on the third peduncular article, but there is neither a 'scale' or a distinct pit.

As for the antennular 'scale' of the cryptoniscus stage, Calman appears to have been relying on Bonnier (1900) and Giard and Bonnier (1887), who stated that the antennules of epicarideans 'are often biramous, with numerous sensory filaments.' The cryptoniscus stage of the family Bopyridae *sensu lato* possesses complex antennules of uncertain homologisation. The first article, and often the second, typically bear toothed 'gnathobasic margins' that are of importance in species-level taxonomy. One to three lobes may arise from the third article, each highly invested with bundles of long setae. It is these sensory lobes that Bonnier and Calman presumably interpreted as scales, or vestigial rami or flagella. When several of these sensory lobes are present, only one (usually the largest) bears aesthetascs, the others are much smaller and bear only 'simple' sensory setae. Thus, the large lobe could reasonably be homologised to a reduced antennular flagellum, but the other one or two lobes appear to be large, complex sensilla, or possibly one of these represents a true antennular scale. Nielson and Strömberg (1973) described these lobes in an unidentified bopyrid as being 'heavily equipped with sensory hairs, densely crowded together...', and noted that the antennule is 'apparently an effective sensory organ as well as an accessory adhesive one.' The lobes have been clearly figured by Nielson and Strömberg (1965), Bourdon (1968), Grygier (1981), and others. Grygier (1981) described the antennular peduncles of *Scalpelloniscus penicillatus* and *S. binoculis* as 3-articulate, noting that the third article bears a 'pair of 1-merous rami and a large, ventrolateral bulb completely covered with brush-like bundle of capillary aesthetascs...'. Kensley (1979) has described the antennules of the cryptoniscus stage of *Zonophryxus trilobus* (Dajidae) also as bearing a trilobed second article.

In limnoriids, most species do possess an antennular scale on the distal margin of the third peduncular article. In some species, this 'scale' resembles little more than a large, simple seta (*Paralimnoria andrewsi* Calman). In most, however, it is a small, one-piece, articulating, setae-bearing structure not unlike that of young bopyrids. The antennular scales of limnoriids are very small and difficult to observe without the use of a scanning electron microscope (for good illustrations and SEM photographs see: Kussakin and Malytina, 1989, fig. 3; Cookson and Cragg, 1988, figs. 3d, 4d; Cookson, 1989, PhD Diss.). L.J. Cookson (pers. comm.) feels that the Keuphyliidae (*Keuphylia nodosa*) possesses a scale similar to that of limnoriids but we have not observed this scale ourselves nor was it illustrated by Bruce (1980).

In the case of the Anthuridea, 'scales' or vestigial flagellar processes almost certainly do not exist. We have examined dozens of anthuridean species and failed to find anything resembling a scale or vestigial ramus. We are aware of two reports of such structures in anthurideans. The first was by K.H. Barnard (1925) who claimed an antennular scale was present on *Xenanthura brevitelson*. Kensley (1980), using SEM techniques, showed this structure to merely be a large sensillum. The other claim was that of Miller and Menzies (1952), who noted an antennular scale in a single female specimen of *Mesanthura hieroglyphica* (from Hawaii). Miller and Menzies stated, 'An antennal scale here observed on the first antenna of a female specimen has not, to our knowledge, been reported previously in the Anthuridae. Because of its minute size and its position, it is not readily seen, hence may have been overlooked in other species in the family. It was not found, however, in the other Hawaiian anthurids described in this paper' (*sic*). Their 'scale' appears identical to the sensory seta shown by Kensley for *X. brevitelson*.

The final group said to possess antennular scales, 'the young of *Cirolana*', was cited by Menzies (1957) as, '...(unpubl. data)...'. To our knowledge, Menzies never published these 'data', nor has anyone else shown antennular scales in this genus. One of us (RCB) has examined hundreds of young Cirolanidae, in *Cirolana* and many other genera, and has never seen antennular scales in any genus of this family other than *Bathynomus*.

In summary, we conclude that only *Bathynomus*, limnoriids, the cryptoniscus stages of bopyrids, and perhaps keuphyliids may possess

structures on the antennules that might be reasonably interpreted as scales. Although we are not entirely convinced that these minute, uniarticulate structures are anything more than complex sensilla, we have entered this character into the data matrix anyway. For character 20, all four out-groups are scored as possessing a biramous antennule (or a scale), and among the isopods the epicarideans and limnoriids are scored the same (0); Cirolanidae is scored '?' because apparently only the genus *Bathynomus* (of a total of approx. 45 genera) has a scale; Keuphyliidae is also scored '?' because we are uncertain whether a scale is actually present in this group. All other isopods are scored 1 — lacking antennular scales.

Mysidaceans, mictaceans, amphipods, and other Eumalacostraca (except tanaidaceans) appear to primitively possess a 3-articulate antennular peduncle. It seems reasonable to homologise these articles to the 3-articulate protopod of other crustacean appendages. Nevertheless, this is not a certain homologisation because in all crustacean nauplii this appendage is uniramous. Moreover, the Apseudomorpha tanaidaceans have the accessory flagellum on the fourth article of the antennule, arguing for a four-articulate protopod in this group.

Most isopod workers have regarded the antennular peduncle of the Isopoda to be 3-articulate. However, Bruce (1981, 1986) felt that isopods 'primitively' have 4-articulate antennular peduncles because he interpreted the small fourth article that occurs in many groups (that most other workers view as the first flagellar article) as the last, or fourth, peduncular article. Due to this different interpretation of the fourth article of Cirolanidae (and other non-aselote/non-phreatoicidean groups), Bruce (1981, 1986) and Wägele (1983a) were at odds over whether the 'primitive' isopod antennular peduncle was 3-articulate (Wägele) or 4-articulate (Bruce). Wägele's opinion is based on the third article of *Bathynomus* bearing the scale, which he homologises with a vestigial second flagellum, and at this time we are inclined to accept this homology argument, especially given that the primitive eumalacostracan condition is almost certainly a 3-articulate antennular peduncle. We see no reason not to accept that the small fourth article of *Bathynomus* is homologous with the short fourth article of most other Cirolanidae, Anthuridea, Bathynataliidae, Gnathiidea, and other taxa (Fig. 5), but do not consider this article to be part of the peduncle. Our examination of the antennule of *Bathynomus giganteus* (cuticle cleared with xylene) indicates that the 4th article lacks intrinsic musculature, thus conforming to our definition of the flagellar article. Several other authors that have alluded to a 4-jointed antennular peduncle in *Bathynomus* may have been misinterpreting the first (proximal) article for two articles, due to the presence of a strong ridge on the medial surface of that joint, such that it could be easily mistaken for two pieces (Fig. 5 C–F). The fourth peduncular article of Bathynataliidae noted by Kensley (1978) and Bruce (1986) corresponds to the small first flagellar article of other flabelliferan families.

A 4-articulate antennular peduncle unquestionably does occur in two flabelliferan groups, Phoratopodidae and Serolidae. But, in both of these cases the 'extra' fourth article is neither basal nor does it appear to be homologous to the short fourth article noted above in other isopods, but rather appears to be the result of a subdivision of the third article into two large equi-width joints with continuous marginal contours. In the Serolidae we have examined, the fourth and fifth articles contain no intrinsic musculature. Van Lieshout's (1983) description of Calabozoidea states *Calabozoa pellucida* has a 3-articulate peduncle, but her figure 2C gives the appearance of a 4-articulate peduncle, possibly with a sensillum on the fourth article. Our observations of *Calabozoa* indicate that the antennule comprises only 4 articles, presumably a 3-articulate peduncle and uniarticulate flagellum (the terminal article bears one aesthetasc and one large seta). The antennules of oniscids are so reduced that we score them as undecided ('?') for this character. Character 21 is: antennular peduncle 3-articulate with an undivided third article (0) *vs* 4-articulate, presumably by way of subdivision of the third article (1). Only phoratopodids and serolids are scored apomorphic for this character.

Reduction of the antennules probably occurs in at least some species in every isopod suborder, and may occur in various conditions within a single suborder or family. When the antennules are reduced, a corresponding reduction of the deutocerebrum and its olfactory lobes also usually occurs (where it has been studied). The mode of reduction in the various suborders clearly differs. Reduction typically accompanies exploitation of parasitic or interstitial habitats. Valviferans have a 3-articulate peduncle, with the flagellum often reduced to one or a few

vestigial articles. Although antennular reduction is rare in gnathiids, some species also have a 2-articulate peduncle and the flagellum reduced to a few articles. In the interstitial Microcerberidea, reduction is such that the peduncle cannot be distinguished from the flagellum. A similar reduction takes place in the parasitic Cymothoidae and Epicaridea. Epicarideans have highly reduced antennules, usually of 2–3 articles; a 3-articulate peduncle is generally apparent during larval stages, but reduced in adults. In oniscideans reduction results in very small, 1-, 2-, or 3-articulate antennules, which in some cases are not even mobile (although Holdich, 1984: figs 24, 53, shows 4-articulate antennules in *Porcellio* and *Deto*). Setation on the second and/or third article suggests that loss of both peduncular and flagellar articles has probably occurred in the Oniscidea. Oniscidean antennules also differ in arising directly between the antennae, instead of antero-medially to them, as in most other isopods (character 22). Some anthuridean species also have small, 3-articulate antennules, with setation again suggesting loss of one of the peduncular articles as well as most of the flagellar articles.

Among the Flabellifera, all manner of antennule reduction occurs. In many cases, it appears that the two basal-most articles have fused, as in many Cirolanidae (*C. tuberculata*, Delaney, 1986; *C. triloba*, *C. furcata*, *C. similis*, and *C. victoriae*, Bruce, 1981; *Neocirolana bicrista*, Holdich *et al.*, 1981); many *Corallana* and *Excorallana* (Delaney, 1982, 1984), and perhaps *Plakarthrium*. In *Anuropus*, only two antennular articles remain, and their homology is uncertain. However, the second (distal) article in *Anuropus* is unique in being enormously expanded and scalloped (character 23). In most limnoriids, the peduncle appears to have lost one article, and the flagellum is also reduced to only a few articles, although mancas tend to have all 3 peduncular articles. In Lynseiidae and Keuphyliidae, all 3 peduncular articles are present and the flagellum is reduced to 3 very short articles. The antennules are very short in the Cymothoidae and the distinction between the peduncle and flagellum is indiscernible, the entire structure usually being reduced to 7 or 8 short articles (Fig. 5). Reduced antennular flagella are common in various species in many genera of Cirolanidae, wherein a 3-articulate peduncle bears a flagellum reduced either by loss or fusion (or both) of the flagellar articles (some *Eurydice*, *Metacirolana*, *Cirolana*, etc.).

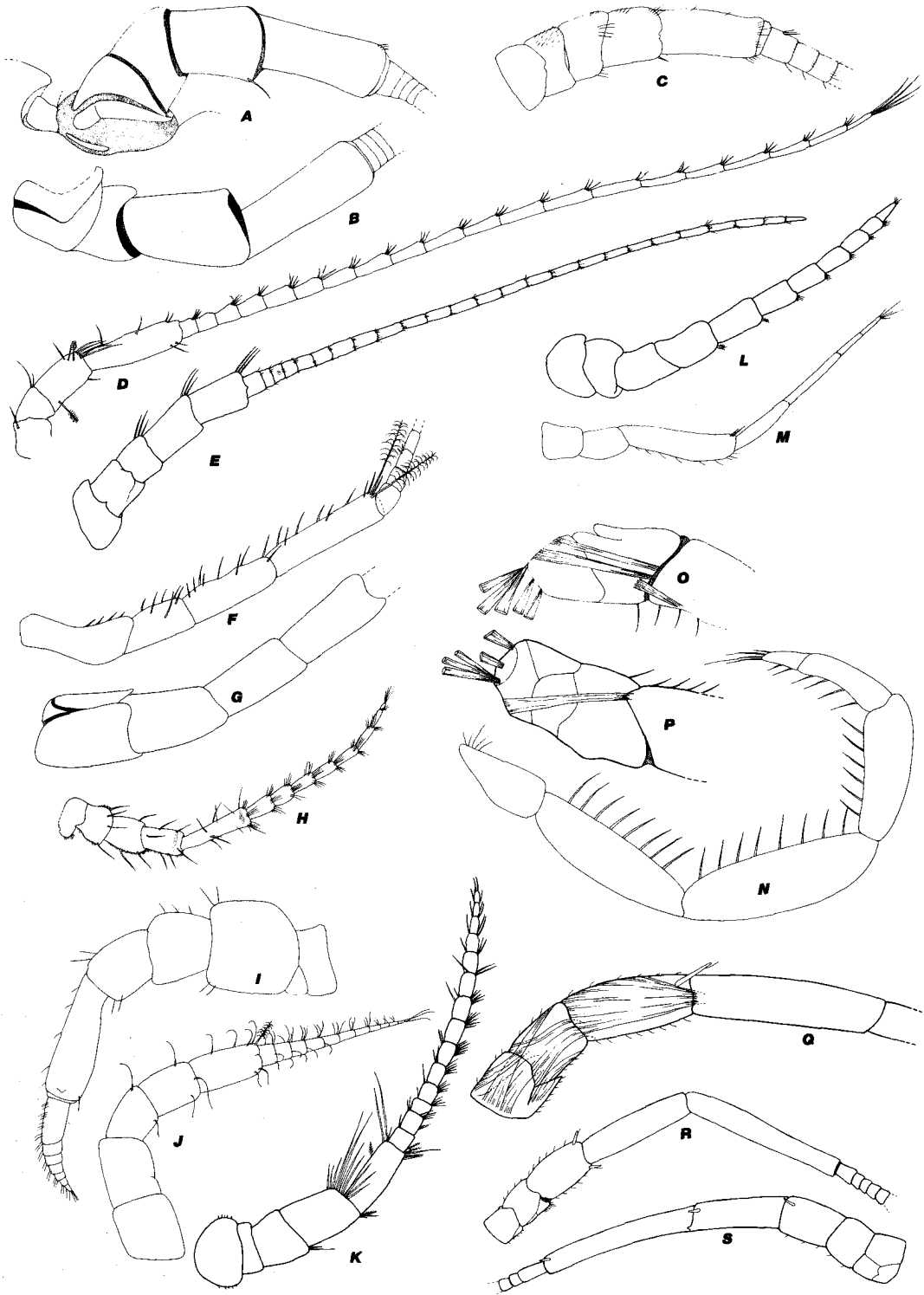
In examining these various antennular reductions, it is obvious that they are not all homologous. In fact, reduction in most, or even each, group could have been by entirely separate evolutionary events. Some may be homologous reductions, but until detailed ultrastructural and anatomical studies have been accomplished a judgment in this regard cannot be made. For this reason, we have not used antennular reduction as a character in the data set.

Antennae

A review of the literature suggests that confusion exists regarding the number of articles in the antennal peduncle of peracarids (Fig. 7). Much of this confusion seems to have derived from viewing the number of peduncular articles as a single feature, when in fact it should probably be examined as at least two separate features (the number of articles in the protopod; and, the number of proximal articles of the ramus that combines with the protopod to form a functional unit recognized as the peduncle). We define peduncle as the enlarged basal articles of the antenna that bear intrinsic musculature. The flagella of isopod antennae lack intrinsic musculature, i.e. no muscles have their origin in the flagellum.

The antenna of mysidaceans has a 3-articulate protopod (at least primitively, e.g. *Mysis*), which

FIG. 7. Examples of isopod antennae. A, Flabellifera, Cirolanidae (*Bathynomus giganteus*, SDNHM), dorsal aspect showing articulation with head, base of antennule, and floating cuticular piece on articulating membrane. B, Flabellifera, Cirolanidae (*Bathynomus doderleini*, USNM 39321, dorsal aspect). C, Phreatoicidea (*Phreatomerus latipes*, USNM 60659). D, Flabellifera, Cirolanidae (*Eurydice caudata*). E, Flabellifera, Aegidae (*Aega longicornis*, holotype). F, Gnathiidea (*Bathygnathia curvirostris*, USNM 10580), note fusion of distal articles (3 and 4, or 4 and 5). G, Valvifera, Idoteidae (*Synisoma* sp.). H, Valvifera, Idoteidae (*Synidotea francesae*, holotype). I, Anthuridea (*Malacathura caribbica*, USNM 173521). J, Anthuridea (*Calathura* sp., USNM 99253). K, Flabellifera, Cirolanidae (*Politolana wickstenae*, holotype). F, Flabellifera, Cymothoidae (*Nerocila acuminata*). M, Flabellifera, Anuropidae (*Anuropus antarcticus*, USNM 112260). N–P, Valvifera, Pseudidotheidae (*Pseudidothea miersii*, USNM 139139): N, entire antenna, with 4-articulate peduncle and 2-articulate flagellum; O–P, first two peduncular articles, seen from both sides. Q, Oniscidea, Ligiamorpha (*Ligia baudiniana*, SDNHM). R, Oniscidea, Ligiamorpha (*Ligia exotica*, USNM 43252). S, Oniscidea, Ligiamorpha (*Ligia occidentalis*, SDNHM).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combines with the first two or three flagellar articles to form a 5- or 6-articulate peduncle, although the protopod articles are fused into 1 or 2 pieces in most living species. A large lamellar scale (the scaphocerite) arises from the third protopodal article in mysidaceans. Mictaceans and amphipods have 2-articulate protopods, that combine with the first 3 flagellar articles to form 5-articulate peduncles (although this is reduced in some amphipods). Mictaceans, and perhaps some apseudomorph tanaidaceans, have a scale on the second article, suggesting that it could be homologous with the third protopodal article of mysidaceans. Amphipods lack an antennal scale. The antennal peduncle of most isopods also comprises 5 articles, although in some taxa it is reduced to 4 or fewer articles, and in the Asellota and Microcerberidea (and possibly some Cirolanidae) a 6-articulate peduncle occurs. A review of these conditions in isopods is given below.

Milne Edwards and Bouvier (1902) described the antennal peduncle of *Bathynomus* (Cirolanidae) as 6-articulate. However, they apparently mistook the large articulating membrane between articles 1 and 2 for an extra article (as noted by Bruce, 1986). Hansen (1903) also described the antennal peduncle of *Bathynomus* as 6-articulate, but Hansen was focusing on a minute strip of sclerotised cuticle at the base of the antennal peduncle, at the edge of the articulating membrane, that he considered to be the vestige of a proximal antennal article, or precoxa. Hansen's conclusion that this cuticular fragment is homologous to a precoxal article was based on the observation that it moved ('articulated') within the antennal socket when the antenna was moved. Hansen (1903) also claimed to have found 6-articulate antennal peduncles in several species of *Cirolana*, and in the asellote genera *Eurycope* and *Asellus*. Hansen (1905a, 1916) later added *Conilera* (Cirolanidae) and *Ligia* (Oniscidea) to the list of taxa with 6-articulate antennal peduncles, and in his 1925 review added *Janira maculosa* (another asellote), concluding that the 6-articulate condition was primitive in isopods, and loss of the precoxa was a derived condition.

In Hansen's view, then, the primitive isopod antenna was similar to that of mysidaceans, with a 6-articulate peduncle composed of a 3-articulate protopod (comprising the precoxa, coxa, and basis) plus the first three articles of the endopodite; the rest of the endopodite forming the flagellum. Hansen also noted that in most Asellota and in *Ligia* with a 6-articulate peduncle, the third article bears a movable scale, or 'squama', representing the vestigial exopod.

Calman (1909) agreed with Hansen's conclusions, noting that the antennal peduncle of isopods normally comprises 5 articles, but that in the Asellota, *Bathynomus*, and *Cirolana* it is 6-articulate, and in some Asellota with 6-articulate peduncles a scale occurs on the third article. Wägele (1983a; referring to the protopod as the 'basipodite') agreed with Hansen's conclusions that a 6-articulate peduncle is the primitive isopod condition. Wägele used figures taken from Hurley (1957) and Vandel (1960) to illustrate 6-articulate peduncles in an asellote (*Iathrippa longicauda*) and a ligiid (*Ligia italica*), following Hansen in his claim that in the Asellota and Ligiidae a small exopodite (scale) occurs on the third peduncular article. Wägele (1983b) also argued that a 6-articulate antennal peduncle is characteristic of the Microcerberidea. Other authors have agreed or disagreed with Hansen's opinion regarding the occurrence of a 6-articulate peduncle in isopods.

The literature thus contains references to 6-articulate antennal peduncles occurring in at least some genera in four groups: Asellota, Microcerberidea, Oniscidea (Ligiidae), and Cirolanidae. The contention of a 6-articulate peduncle in the Isopoda is tied to Hansen's and Calman's homologisation of isopod antennae with a 'primitive' crustacean somite appendage with a 3-articulate protopod comprising a precoxa, coxa and basis, with the paired rami arising from the latter. However, it is of considerable interest to note that, among the Malacostraca, an antennal precoxa (and hence a 3-articulate protopod) unquestionably occurs only in the groups described above — the mysidaceans and certain isopods. In all other malacostracans the protopod comprises only 2 articles, and the rami (or scale) arises from the second article. This suggests the possibility that the primitive state in Crustacea is a 2-articulate antennal protopod.

We have examined the cuticular piece noted by Hansen on the articulation membrane of the antenna of *B. giganteus* and also found it to move when the antenna is moved. However, this piece does not articulate with any other article, or with the head, but simply floats free upon the membrane. A similar free-floating cuticular piece occurs in many genera of Cirolanidae (as noted above), although it has rarely been noticed due to its small size and failure to be removed with the antenna upon dissection. Bruce (1986) commented on these structures, noting their presence

in at least 12 Australian genera of Cirolanidae and illustrating them for three species (*Bathynomus immanis*, *Cirolana cranchii*, and *Natatolana rossi*). Homologisation of this piece with a true basal, or 'precoxal' article seems a reasonable hypothesis, although in our opinion still very much open to testing. Moreover, we know of no flabelliferan isopod that has an antennal scale.

In Ligiidae, the antennal peduncle is usually 5-articulate, or occasionally 4-articulate. In this family, both the first and second article may be split by 'fracture lines' (often subcuticular) on one side, so that an observation from only one side of the appendage might give the illusion of there being more than one article present – a situation somewhat analogous to that noted above for the antennule of *Bathynomus*. We have examined *Ligidium ungicaudatum*, *Ligia occidentalis*, *L. baudiniana*, and *L. exotica* and can find no trace of a precoxal article. Richardson (1905), Van Name (1936), Sutton (1972), Kensley and Schotte (1989), and others have also noted that the antennal peduncle of Ligiidae is no more than 5-articulate. Fragmentation, splitting, ridges, etc. occur on the proximal articles of the antennal peduncles in many groups, including Ligiidae, Anthuridea, Phreatoicidea, and others. This splitting may have led some authors to mistakenly interpret one of the pieces as a small precoxal article (and thus describe a '6-articulate' peduncle). The first mention of an 'extra' article at the base of the antenna in ligiids was apparently Hansen (1916) who stated, '...in *Ligia oceanica* we found not only six joints in the peduncle, but even an exopod or squama on the third joint...'. Hansen's illustration shows what appears to us to be a 5-articulate peduncle, with the first and second articles fragmented; his 'precoxal remnant' appears to be a fragmented plate of the first article, and his 'scale' appears to be the protruding edge of a fragment on the second article. The inner margin of the second article is often slightly elevated, to form a low lobe-like ridge, that has perhaps been mistaken for a 'scale' in *Ligia*. Wägele's (1983a) illustration of *Ligia italica* (after Vandel, 1960), showing a 6-articulate peduncle and a scale, is probably such a misinterpretation.

In the Asellota, 6-articulate antennal peduncles do occur in numerous genera of many families (Fresi, 1972; Gruner, 1965; Hessler, 1970; Siebenaller and Hessler, 1977; Wilson, 1976; 1980a, 1986a; Wilson and Hessler, 1981): e.g. Haplomunnidae (*Haplomunna, Munella, Thylakogaster, Abyssaranea*); Desmosomatidae (*Balbidocolon, Eugerda, Chelator, Mirabilicoxa, Momedossa, Prochelator, Torwolia, Whoia, Thaumastosoma*); Nannoniscidae (*Hebefustis, Exiliniscus, Panetela, Rapaniscus, Regabellator*); Munnopsidae (*Eurycope*); Janiridae (Jaera, Ianiropsis); Pleurocopidae (*Pleurocope*); and Munnidae (*Munna*). Antennal scales occur on the third peduncular article in many of these same asellote taxa, and also on the third article of some species with fewer than 6 articles in the peduncle, such that one would interpret the antenna as retaining the 3-articulate sympod, but with only 1 or 2 articles of the endopod contributing to the peduncles.

Wägele (1982b, 1983b) illustrated a 5-articulate antennal peduncle for *Microcerberus mirabilis*, although he stated that a 6-articulate antennal peduncle is diagnostic for the Microcerberidea. Wägele (1983b) clearly shows a 'precoxal article' on the antenna of *Microcerberus tabai*. Baldari and Argano (1984) figured a 5-articulate peduncle in *Microcerberus redangensis*, but stated that it was 4-articulate. Pennak (1958) claimed *M. mexicanus* had a 5-articulate peduncle. Messana *et al.* (1978) clearly showed and stated that *Microcerberus anfindicus* has a 6-articled peduncle. Perhaps both the 5-articulate and 6-articulate conditions occur within the Microcerberidea but, since the 6-articulate condition definitely does occur we regard it as the primitive state.

Nicholls (1943, 1944) noted that the antennal peduncle of phreatoicids was 5-articulate, but that a ridge (or groove) lines the lower boundary of the antennal socket that might suggest the existence of a former proximal (precoxal) article that had been incorporated into the head. However, such a ridge occurs in many isopods, including *Bathynomus*, and Milne Edwards and Bouvier (1902) and Hansen (1903) regarded it as simply part of the head skeleton.

An antennal scale probably does not exist in the Anthuridea. In some species, such as *Malacanthura caribbica*, a minute, simple, unjointed, non-articulating structure exists on the 5th peduncular article; it appears to be a superficial cuticular structure, perhaps a sensillum of some kind. We have seen no such structure, or anything resembling a scale, in species of *Calathura* or *Mesanthura* that we have examined. Kensley (pers. comm.) has taken SEM photographs of many anthuridean species, including species that Menzies and K.H. Barnard claimed had antennal scales, and failed to find anything

other than various, small, superficial, cuticular structures (spines and setae).

In valviferans, the first two articles of the antennal peduncle are more-or-less fused and operate as a single unit, although the cuticle of these two articles often appears to be 'fragmented' into several pieces. Bruce (1980) described *Keuphylia nodosa* (Keuphyliidae) as having a 5-articulate antennal peduncle with a scale on the second article. We have examined this species and consider this structure is not a true 'scale'; it appears to be a cuticular fold or a one-piece sensory lobe, and it is on the second (not the third) peduncular article.

Character 24 is: antennal peduncle 6-articulate (0) *vs* antennal peduncle 5-articulate (1). Mysidaceans, tanaidaceans, microcerberids and asellotes are scored (0); all other taxa in the data matrix are scored (1). In Cirolanidae both conditions might exist (given the hypothesis that the small cuticular pieces on the articulating membrane in some species represents a vestigial basal article), and the condition in limnoriids and protognathiids is uncertain; hence these three taxa are scored (?). Character 24 was left unordered in initial analyses.

Character 25 is: antenna biramous, or with a vestigial second flagellum or scale (0) *vs* antenna uniramous, and without a vestigial second flagellum or scale (1). Mysidaceans, tanaidaceans, mictaceans, and asellotes are scored primitive for this character (0); all other taxa are scored (1). The 'scale' drawn by Bruce (1980) on *Keuphylia* appears to us to be a non-articulating sensory lobe on the second peduncular article.

Character 26 is: Antennae present (0) *vs* antennae vestigial in adults (1). Only Epicaridea is scored derived (1) for this character.

Mandibles

Of the many different 'characters' recognisable on isopod mandibles, many show so much homoplasy that they are of little use at the subordinal level of analysis. In some groups, such as many phreatoicids and asellotes, all of the typical peracaridan mandibular structures persist, at least on the left mandible. However, reduction, loss, or extreme specialisation of the mandibular palp, molar process, spine row, and lacinia mobilis appears to have occurred at least several times in most isopod suborders. Although clear trends can often be seen, especially within certain family clusters, the high level of overall homoplasy in modifications of most of these structures reduces their usefulness in phylogenetic analysis at the subordinal level.

The isopod mandibular palp, like that of other peracarids, is primitively 3-articulate. Kussakin (1979:26) illustrated a 4-articulate mandibular palp for *Caecocassidias patagonica* (Sphaeromatidae) and for *Cyathura polita* (Anthuridea), even though he described the Isopoda as having mandibular palps of 3 or fewer articles. Kussakin's figures of 4-articulate mandibular palps are almost certainly in error. Like Hansen (1890) and Bruce (1983, 1988) for several species of Aegidae, Kussakin probably mistook a fold at the base of the proximal palp article for an articulation.

Reduction of the mandibular palp (to one or two articles) has occurred in several taxa, and complete loss of the palp has occurred in many groups (Oniscidea, Calabozoidea, Keuphyliidae, Lynseiidae, Gnathiidea, Epicaridea, some Anthuridea, some Cirolanidae, many genera of Asellota, and all non-Hologhnathidae Valvifera). In gnathiids (praniza) and epicarideans, the mandibles are modified as small scythe-like pointed stylets with serrate cutting edges.

There are two fundamentally different kinds of mandibular molar processes in isopods. A broad, flat or truncated, grinding molar process is characteristic of Phreatoicidea, Asellota, Microcerberidea, Oniscidea, Valvifera, and most genera in the flabelliferan family Sphaeromatidae. A thin, elongate, blade-like, slicing molar process, with a row of teeth or denticles along the anterodistal margin, is characteristic of the primitive Anthuridea (Hyssuridae), and the flabelliferan families Anuropidae, Cirolanidae, Phoratopodidae, and Protognathiidae; a reduced blade-like molar process, or its apparent vestige, occurs in most species in the flabelliferan families Aegidae, Corallanidae, Cymothoidae, and Tridentellidae. Bruce (1981) suggested that the molar process of Phoratopodidae is 'vestigial'. However, our observations of *Phoratopus remex* Hale indicate that, while the molar is slightly reduced in size, it is nonetheless a well-developed, serrate, blade-like structure similar to that of Cirolanidae. The serrate condition also exists in the Anuropidae and Protognathiidae, in which it is (as in Cirolanidae) 'articulated' on the body of the mandible. In Corallanidae and Tridentellidae (and the cirolanid genus *Calyptolana* Bruce) the molar process is also 'articulated' and blade-like, but shows a loss of the serrate toothed margin and a reduction in size (and even complete disappearance in some genera and species).

In the primitive anthurideans (Hyssuridae) the blade-like molar process also occasionally 'articulates' on the body of the mandible and may bear a serrate or toothed margin (Poore and Lew Ton, 1988a; Wägele, 1981b).

In the sphaeromatid subfamilies Ancininae and Tecticeptinae (*Ancinus*, *Bathycopea*, and *Tecticeps*), the molar process is either absent or vestigial (Tecticeptinae) or modified as a thin blade-like structure (Ancininae). However, we do not regard the molar of Ancininae to be homologous to the blade-like molar described above for the Anthuridea and other flabelliferan families. In ancinines, the molar is apically acute (not rounded), lacks teeth or denticles at the antero-distal margin, and bears large knife-like serrations along the postero-distal margin. Ancininae and Tecticeptinae possess all the other features typical of Sphaeromatidae.

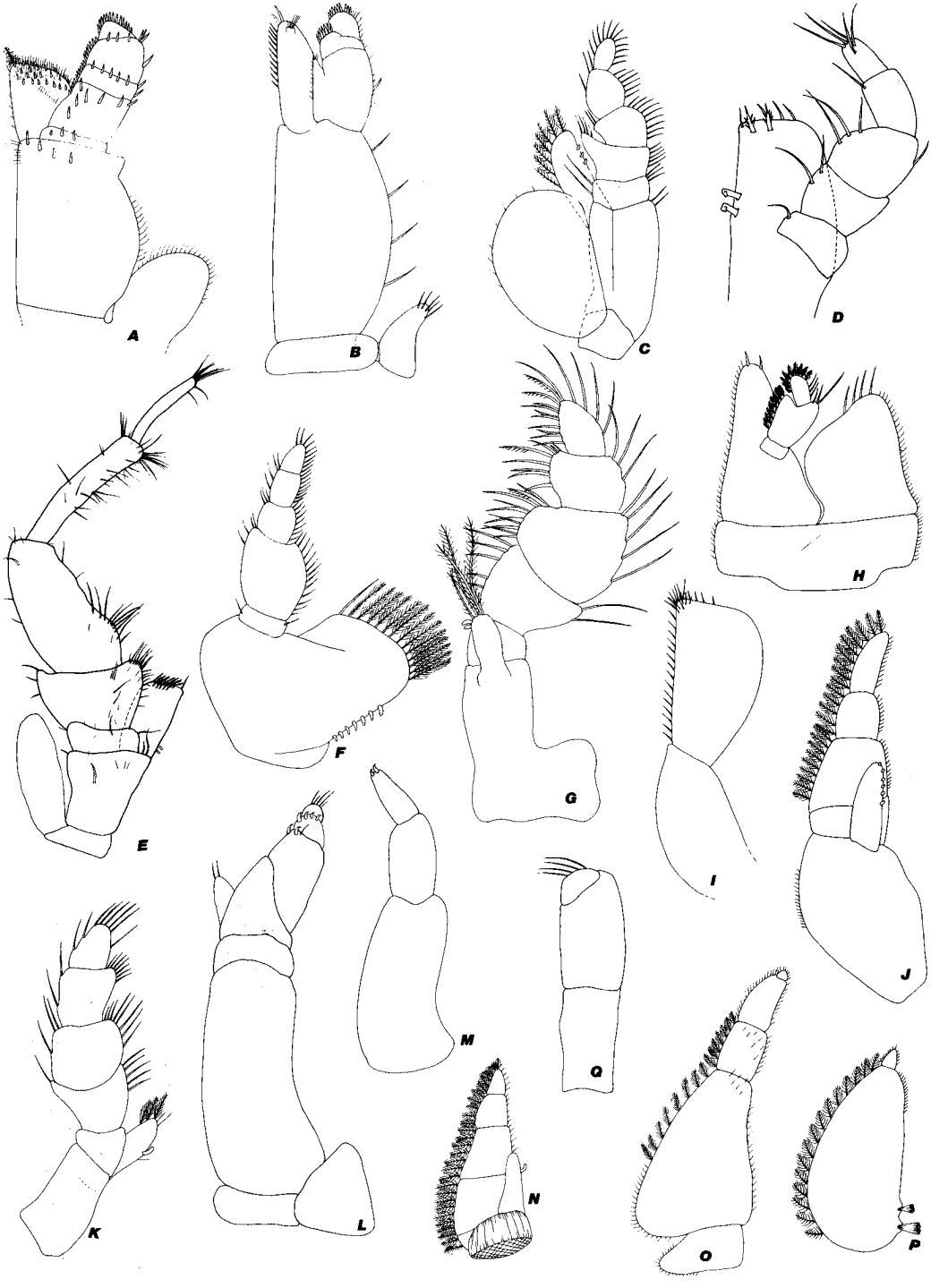
A molar process is absent in the Epicaridea and Gnathiidea, and in the flabelliferan families Limnoriidae, Lynseiidae, Bathynataliidae, Keuphyliidae, Plakarthriidae, and Serolidae. The molar process is also secondarily vestigial or absent in some genera of Sphaeromatidae and Idoteidae, and in a few anthuridean and oniscidean families.

In most isopods, the incisor is a multilobed grasping structure, but in groups specialised for predation or parasitism the incisor is typically blade-like and/or acute, for piercing tissues (Protognathiidae, Corallanidae, Tridentellidae, Aegidae, Cymothoidae, praniza stage of Gnathiidea). In most Limnoriidae the incisor process bears a unique 'rasp and file' structure, and a similar condition appears to be approximated in the Lynseiidae (Menzies, 1957; Poore, 1987; Cookson and Cragg, 1988).

The presence and size of the lacinia mobilis and spine row components vary greatly among the Peracarida. In the Isopoda, the nature of these structures appears to be closely tied to lifestyle (especially feeding behaviour) and hence strongly selected for and perhaps of limited phylogenetic value above the generic level. The presence of both a lacinia and spine row (on both the right and left mandible) is presumably the primitive peracaridan condition (Dahl and Hessler, 1982), and in many mysidaceans, mictaceans, and amphipods a gnathal lacinia and associated spine row persist. However, in many isopod groups these structures have been modified, reduced, or lost, especially on the right mandible. No doubt a wealth of phylogenetic information will become available once a more thorough understanding of pattern and homology among these structures has been achieved.

In most Phreatoicidea, Asellota, Oniscidea, Calabozoidea, and Valvifera, a lacinia and spine row, often closely associated with one another, are usually present (at least on the left mandible). The lacinia and spine row are often modified, reduced, or lost in the various flabelliferan families and genera. A distinct lacinia and spine row are usually absent in the Anthuridea, although remnants may persist in the primitive family Hyssuridae (Poore and Lew Ton, 1988a); the unique 'lamina dentata' of anthurideans is presumably the homologue of one or both of these mandibular structures. In the Microcerberidea, the lacinia is absent and only a row of small spines is present. In the Phreatoicidea, a spinose lobe may be present in lieu of a distinct lacinia and spine row, at least on the left mandible; the homology of this spinose lobe is uncertain, but it may represent either a fusion of the lacinia and spine row, or a loss of the lacinia and specialization of the spine row. A somewhat similar appearing modification occurs in certain Asellota (*Asellus*), Cirolanidae, and Keuphyliidae. The Limnoriidae have a somewhat similar structure (called the 'laciniod spine'), and in the unusual genus *Hadromastax* only a single simple spine remains. In the Serolidae, two spine-like structures of uncertain homology are usually present, both articulating; one may represent the lacinia and the other a single, enlarged spine of the spine row, or both may be enlarged spines. In the Phoratopodidae and Sphaeromatidae a large gnathal lacinia, with an associated spine row, is generally present. In the Bathynataliidae a large gnathal lacinia is also present, but with no trace of the spine row. In the Anuropidae, Protognathiidae, Corallanidae, Tridentellidae, Aegidae and Cymothoidae the lacinia and spine row is absent or reduced to a few, vestigial, spinelike structures. Mandibular characters used in the analysis follow.

Character 27 is: mandible with a lamina dentata — a synapomorphy unique to the Anthuridea. Character 28 is: mandibles of adult males grossly enlarged, projecting anteriorly, forceps-like — a synapomorphy unique to the Gnathiidea (although convergently approximated in the unique cirolanid species *Gnatholana mandibularis* Barnard). Character 29 is: mandibles lost in adult females — also a synapomorphy unique to the Gnathiidea. Character 30 is: molar process a broad flat grinding structure (0) *vs* molar process a thin blade-like slicing structure (1). Taxa in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which the molar process is absent are scored '2' for this character. Character 50 describes four states of the mandibular incisor: broad and multitoothed (0); teeth reduced to form a serrate or crenulate margin (1); teeth lost (or fused?) to from a conical projection with basal 'rasp and file' (2); and, incisor modified as a recurved, hooklike, acute or subacute piercing-slicing structure (3). Character 91 is: mandibles modified as elongate scythe-like structures with a serrate cutting edge (Epicaridea and Gnathiidea).

The following taxa are scored as lacking a mandibular palp (character 35): Ligiamorpha, Tylomorpha, Calabozoidea, Epicaridea, Gnathiidea, Keuphyliidae, and Lynseiidae. Loss of the mandibular palp in certain genera of Anthuridea and Asellota is assumed to have taken place independently after the evolution of these suborders, i.e. it is a secondarily derived feature in these taxa. The situation in Valviferans is debatable; Brusca (1984) suggested that presence of a mandibular palp was the primitive valviferan condition and loss of the palp occurred after the origin of the unique species *Holognathus stewarti*, whereas Poore (1990) suggested that the ancestral valviferan had already lost the mandibular palp and it reappeared later in *H. stewarti*. We choose the more parsimonious alternative and assume that the mandibular palp did not reappear within the Valvifera (*sensu* Brusca, 1984). Valviferans are thus scored '0' for character 35.

MAXILLULES

The typical isopod maxillule comprises 1 or 2 proximal articles, and two distal lobes — an inner (medial) and outer (lateral) lobe. Most workers regard these lobes as endites although the precise homologies of the maxillulary articles is uncertain, and the two distal lobes are referred to in the literature by a variety of terms, e.g. inner and outer lobes, plates, endites, or rami; or, exopod and endopod. Furthermore, the proximal articles and region of articulation between the articles and lobes are rarely figured in the literature. Calman (1909) and Hansen (1925) viewed this appendage as comprising only the articles of the protopod, the two proximal articles being the precoxa and coxa, the outer lobe the basis, and the inner lobe an endite of the precoxa.

In mysidacens, amphipods and tanaidaceans, at least primitively, there are also two lobes that are clearly endites arising from the second and third articles, as well as a short palp. In mictaceans two lobes also exist, but the nature of their articulation and the proximal lobes of this appendage are uncertain. Bowman and Iliffe (1984) refer to these lobes as both endites and as endopod (the distal 'endite') and exopod (the proximal 'endite'). Bowman *et al.* (1985) referred to these structures simply as the 'inner' and 'outer' lobes. Mictaceans, like isopods, lack a maxillulary palp.

In a number of isopod taxa the maxillules are highly modified. In the anthurideans, the outer lobe is a slender stylet and the inner lobe is minute (presumably vestigial) or absent. The maxillules of anthurideans have rarely been illustrated (Poore, 1978, fig. 17b; Poore and Lew Ton, 1988, fig. 7; and, Poore and Lew Tᵔn, 1990, fig. 3). In the primitive anthuridean family Hyssuridae the maxillule bears apical denticles or spines; in the more advanced families (Anthuridae, Antheluridae, Paranthuridae) the apical spines are largely reduced, or fused, often resulting in a simple serrate distal margin. Somewhat similar conditions (outer lobe a long slender stylet with apical teeth, inner lobe reduced or absent) exist in the Gnathiidea (praniza stage), Aegidae, Bathynataliidae, Cymothoidae, Lynseiidae, Plakarthriidae, and Tridentellidae. In the Corallanidae the maxillule is highly modified as a single elongate stylet with the apex forming an acute recurved piercing hook. It seems unlikely that these are all homologously

FIG. 8. Examples of isopod maxillipeds. A, Oniscidea, Ligiamorpha (*Ligia exotica*, male, USNM 43352). B, Oniscidea, Tylomorpha (*Tylos niveus*, male, USNM 67703). C, Phreatoicidea (*Phreatoicus australis*, male, USNM 59116). D, Asellota (*Paramunna quadratifrons*; coxa and epipod not shown; SDNHM specimen). E, Asellota (*Ianiropsis* sp., male; SDNHM specimen). F, Asellota (*Lirceus hoppinae*, male, USNM 230328). G, Flabellifera, Cirolanidae (*Anopsilana* sp., male; SDNHM specimen). H, Flabellifera, Serolidae (*Serolis albida*, gravid female, USNM 123900). I, Flabellifera, Anuropidae (*Anuropus antarcticus*, non-gravid female, USNM 173141). J, Gnathiidea (*Bathygnathia curvirostris*, male, USNM 10580). K, Flabellifera, Cirolanidae (*Excirolana chamensis*, paratype, LACM type No. 3014). L, Flabellifera, Aegidae (*Aega longicornis*; type). M, Flabellifera, Cymothoidae (*Lironeca convexa*, female, attached oostegite not shown, from Brusca 1981). N, Gnathiidea (*Gnathia stygia*, USNM 112376). O, pylopod of *Bathygnathia curvirostris*, male, USNM 10580). P, pylopod of *Gnathia stygia*, USNM 112376). Q, Anthuridea (*Cyathura guaroensis*, from Brusca and Iverson 1985).

derived morphologies. The maxillules are vestigial or lost in adult gnathiids and epicarids. Uncertainty regarding the homologies of the maxillulary articles limits the number of potential characters available on this appendage for phylogenetic analysis.

Character 31 is: maxillule present (0), *vs* reduced or vestigial in adults (1), *vs* lost in adults (2). Character 31 was left unordered in initial analyses. Character 32 is: maxillule with palp (0) *vs* without palp (1). Character 92, the single acute hook-like lobe, is unique to the Corallanidae.

Maxillae

The homologies of the maxillary articles of isopods are also unsettled. As with the maxillules, there are 1 or 2 proximal articles and 2 distal lobes — an inner (medial) lobe, and an outer (lateral) lobe; the outer lobe is generally divided into two. The proximal articles and articulation of the two distal lobes are rarely illustrated in the literature. Calman (1909) and Hansen (1925) viewed the maxilla as lacking rami and comprising only the protopodal articles with their endites; that is, precoxa, coxa, and basis, with the coxa being expanded as an endite forming the inner lobe, and the basis bearing an endite that forms the split (bilobed) outer lobe. As with the maxillules, the inner and outer lobes of the maxillae have usually been regarded as endites, but they have been referred to in the isopod literature as rami, lobes, plates, endites, and exopod/endopod.

The maxillae of mysidaceans retain both the endopod and exopod, as simple one- or two-articulate platelike structures, and both rami bear endites. Amphipod maxillae primitively resemble those of isopods but without the divided outer lobe, although in most modern groups they are reduced to one or two simple lobes (as in many oniscideans). The maxillae of mictaceans are very similar to those of most isopods, with a divided outer lobe. The maxillae of tanaidaceans also resemble those of isopods, at least in their primitive form (*Halmyrapseudes*, Sieg *et al.*, 1982), although in most tanaidaceans the maxillae are highly reduced. No isopods retain the primitive crustacean condition of a maxillary palp (the 'palp' of Cirolanidae referred to by Bruce, 1986 is actually the inner lobe).

Character 34 is: maxillary outer lobe undivided (0) *vs* divided into two lobes (1). Mictaceans, tanaidaceans, and isopods are apomorphic for this character, although in many groups (most scored '?' in the data matrix) the maxillae are highly modified or reduced to a single lobe or a stylet (see below). In some groups, the maxillae are extremely reduced, vestigial, or absent altogether (Gnathiidea, Epicaridea, Anthuridea). In the Anthuridea the maxillae are minute and more-or-less fused with the paragnath (hypopharynx), or absent altogether. In Protognathiidae the outer lobe is apparently absent (Wägele and Brandt, 1988). In the oniscids the maxillae are short and plate-like with 2 non-articulating lobes, but the homology of these 2 lobes is not clear. Because the variety of maxillary reductions in isopods are likely to be the result of different evolutionary processes (nonhomologous features), most of these characteristics have not been included in the data set. Character 36 is: maxilla modified into a stylet-like lobe with recurved apical (hooklike) setae, a condition seen in certain flabelliferan families (Corallanidae, Tridentellidae, Aegidae, Cymothoidae). Character 33 is: maxillae highly reduced and 'fused' to the paragnath, or absent altogether (Anthuridea only). Among the Isopoda, only the Phreatoicidea retain the primitive peracaridan filter setae row on the medial margin of the maxilla (character 74).

Maxillipeds

As in most other peracarids, the maxilliped of isopods consists of four distinct regions: a proximal article (the coxa); the basis, with an enlarged, distal, anteriorly directed, blade-like lobe (the endite); an epipod of varying size and shape, lateral to the coxa; and, a palp (primitively comprising the remaining 5 articles of the appendage — the ischium through dactylus) (Fig. 8). Amphipods differ from isopods in possessing (primitively) a 4-articulate maxillipedal palp, and two endites (an inner and an outer) arising from the basis and ischium respectively.

The maxillipedal palp is reduced in some taxa in almost all suborders (most Oniscidea [Trichoniscidae, Tylidae, Oniscidae, Armadillidiidae], Calabozoidea, many Anthuridea, Gnathiidea, Anuropidae, Aegidae, and Cymothoidae). Wägele's (1989a) claim that a 2-articulate maxillipedal palp with spines on only the terminal article is a synapomorphy uniting the genus *Rocinela* (Aegidae) as the sister group of the Cymothoidae is incorrect. Most (if not all) *Rocinela* have 3-articulate maxillipedal palps with spines on the two distalmost articles (the apical article is minute and easily overlooked). In most isopod taxa, the maxillipedal endites can

be hooked together by coupling setae (coupling hooks), e.g. Phreatoicidea, Asellota, some Valvifera, Epicaridea, Gnathiidea, most Flabellifera. Coupling setae also occur on the maxillipeds of some Mictacea and most Tanaidacea. Maxillipedal coupling setae are absent in Microcerberidea, Ligiamorpha, Tylomorpha, Calabozoidea, Anthuridea, and Amphipoda. They have presumably been lost in amphipods as a result of the maxillipeds being fused together; this is also the case in certain tanaid families in which the maxillipeds are fused, such as Leptognathiidae, Pseudotanaidae, and Nototanaidae. Coupling setae may be missing in the anthurideans owing to the immovable fusion of the maxillipedal coxae and epipods to the head. Coupling setae are also usually absent in isopod taxa that have reduced endites e.g. Corallanidae, Aegidae, Cymothoidae, Lynseiidae, some Cirolanidae; or highly modified maxillipeds (Anuropidae, Plakarthriidae, Protognathiidae, Serolidae).

In isopods (as in most peracarids) a lamellar epipod usually arises from the coxa of the maxilliped. In several groups, the epipod may have its proximal part marked off from its distal part by a transverse suture (many Valvifera, Phreatoicidea, and Flabellifera). In males and non-ovigerous females, the epipods often seem to function as 'cheeks', forming an operculum for the oral field. In gravid females of some taxa (Anthuridea, many Flabellifera), the epipods tend to be oriented in such a way to function as accessory marsupial plates to prevent loss of the embryos from the anterior region of the marsupium. The isopod epipod is never branchial, as it is in tanaidaceans. In mysidaceans, the epipod is posteriorly directed and carried under the carapace. Epipods are known from all isopod suborders except Epicaridea, Gnathiidea, Microcerberidea and Calabozoidea. Maxillipedal epipods are also apparently absent in the families Anuropidae, Corallanidae, and Plakarthriidae, and the unique genus *Hadromastax*. In Cirolanidae, Aegidae, and Cymothoidae the epipod is apparently reduced or absent in all life stages except brooding females. Wägele and Brandt's (1988) claim that *Protognathia* lacks maxillipedal epipods was based on their study of the single manca-stage individual. Because this genus (and family) was erected on the basis of manca specimens, the status of the adult maxilliped cannot be determined. Incomplete data on the precise distribution of occurrence of maxillipedal epipods prevent us from using this potentially important feature in the data analysis.

In at least some isopod groups (e.g. some Phreatoicidea, Asellota, Valvifera, Flabellifera, Epicaridea, and Gnathiidea), the maxillipeds of gravid females also bear posteriorly-directed, oostegite-like, often setose lappets. The function of these lappets is not known, but they may function as an oostegite (to close the anterior region of the marsupium), or they may drive a water current through the marsupium.

Several authors have suggested that the posterior cervical groove (*fossa occipitalis*) on the head of some isopods represents the incomplete line of fusion between the cephalon and first thoracomere. However, these lateral or complete grooves occur sporadically in many distantly related genera (*Mesamphisopus*, *Idotea*, *Ligia*, some Sphaeromatidae, etc.) in many suborders, thus rendering this character unsuitable for phylogenetic analysis at higher taxonomic levels.

Character 37 is: left and right maxillipeds fused together; this condition occurs only in amphipods and some tanaidaceans (not primitively, however). Character 38 is: coxae of maxillipeds fused to head; this derived condition occurs only in the Anthuridea. Character 39 is: maxillipedal endite without coupling setae (0) *vs.* with coupling setae (1). Mysidaceans lack coupling setae, but they occur in at least some mictaceans, tanaidaceans, and isopods. Because the character states of the mysidaceans and the amphipods may not be homologous, this character was left unordered in initial analyses. Character 41 is: maxilliped with 2–3 endites (0) *vs* 1 endite only (1). Amphipods have 2 maxillipedal endites (one on the basis and one on the ischium), mysidaceans have 0–3 endites, and all other taxa in the analysis have one endite (on the basis). Character 42 is: maxilliped biramous; in this analysis, only the mysidaceans have a biramous maxilliped (0), all other taxa have a uniramous maxilliped (1). Character 44 is: maxillipedal basis elongated and waisted (medially narrowed); this feature occurs only in the Lynseiidae and Limnoriidae.

Pereopodal Coxae

In many isopods and amphipods, the coxae of the pereopods are expanded laterally into flattened lamellar structures called coxal plates. We define lateral coxal plates as ventrolateral expansions of the pereopodal coxae that extend freely (as 'plates') to overhang the coxa-basis hinge of the leg. Within the Crustacea, such lateral coxal plates occur only among the isopods and amphipods.

In gammaridean amphipods, the presence of well-developed lateral coxal plates is generally viewed as the primitive condition, although this has not been demonstrated by any rigorous phylogenetic analysis of the Amphipoda as a whole. Coxal plates are lacking only in relatively specialized amphipod groups, such as the tube-building Corophioidea, the vermiform and interstitial Ingolfiellidae, the pelagic Hyperiidae, and the aberrant Caprellidae. In these groups, the coxae form simple rings around the bases of the pereopods. The lateral coxal plates of gammaridean amphipods are generally large and not fused to their respective pereonal tergites; they can usually be dissected free from the body with the leg.

The lateral coxal plates of isopods are generally fused dorsally and ventrally to their respective tergites, although on pereonites 2–7 (and occasionally pereonite 1) the line of dorsal fusion is usually demarcated. They are often quite large (flabelliferans, most valviferans, Tylomorpha), although in some they may be small (some Valvifera). In some isopod groups — Valvifera, Anthuridea, Calabozoidea, Serolidae, and some Epicaridea and Oniscidea (in *Porcellio*, but probably not in *Ligia*) — the coxae also expand inward over the sternum. These sternal coxal plates have rarely been figured or discussed (Sheppard, 1957), and they may be absent in females bearing oostegites. Sternal coxal plates are clearly absent in many taxa, in both males and females (Phreatoicidea, Asellota, Plakarthriidae, Phoratopodidae). Due to uncertainty regarding the accurate taxonomic distribution and nature of the sternal coxal expansions, we were unable to incorporate this feature into the data set. However, this anatomical feature clearly holds great potential as a source of important data on isopod relationships, and bears further investigation. It may eventually be shown that sternal coxal plates co-evolved with lateral coxal plates, but were subsequently lost in some families. The various conditions of isopod coxae are summarized below.

In the Anthuridea, the coxae are extremely elongated and fused almost indistinguishably with their respective somites; this is perhaps an adaptation to the elongate body form and tube-dwelling lifestyle of anthurideans. They may be well-defined ventrally, but at most are demarcated dorsally only by a faint line. Strictly speaking, because anthurideans do not have large coxal plates that hang free to cover their coxa-basis articulations, by the above definition they do not have true lateral coxal plates. However, the reduction and fusion of the coxae with the body wall is taken to be a derived state of 'coxal plates present' and thus this group is scored as possessing lateral coxal plates. In many anthuridean species, the coxae are expanded as sternal coxal plates and appear to be fused along the ventral midline such that there is no clear distinction between the sternite and the coxa.

In the Asellota, Microcerberidea, and Phreatoicidea the coxae may be small or expanded (see Figs. 1, 2, and 9), but they usually have well-defined, though largely immovable, articulations with their respective pereonites (at least on some somites). Although they may be expanded anteriorly or posteriorly along the edges of their respective somites, they never extend ventrolaterally as free lamellar plates overhanging the coxa-basis articulation (not even the enlarged first pair of coxae in the asellote *Stenetrium* hang ventrally to cover the coxa-basis articulation) (Schultz, 1978; Wilson, 1980a). Thus we do not regard these three groups as having lateral coxal plates. In species of Asellota and Phreatoicidea with small coxae, distinct tergal epimeres, lappets, or spines may be present.

In the Calabozoidea, the lateral coxal plates are large, though indistinguishably fused dorsally to their respective pereonites (Van Lieshout, 1983; pers. obs.). The lateral coxal plates of oniscideans are also large, and sometimes dorsal sutures are visible, as in the Tylidae.

In the Epicaridea, lateral coxal plates are present in females, but are highly variable in size, ranging from very small and often unrecognisable posteriorly (in Bopyrinae) to large and prominent (in Orbioninae and Ioninae). Sternal coxal plates appear to be present at least in the Bopyridae.

In the flabelliferan families, large lateral coxal plates are typically present on all pereonites (Fig. 3). Usually they are indistinguishably fused to the first pereonite (or largely so), but more clearly defined by so-called 'suture lines' on pereonites 2–7. In 4 families (Serolidae, Plakarthriidae, Keuphyliidae, and Bathynataliidae) all of the lateral coxal plates are enormously expanded, and coxae 2–6 or 2–7 freely articulate with their respective pereonites, including those of the first pereonite (Wilson *et al.*, 1976, Kensley, 1978; Bruce, 1980, pers. obs.). In Serolidae the degree of free articulation is minimal, but a clear articulatory suture is present and movement of the coxal plate results in movement of the ventral coxal region on the sternum. In the

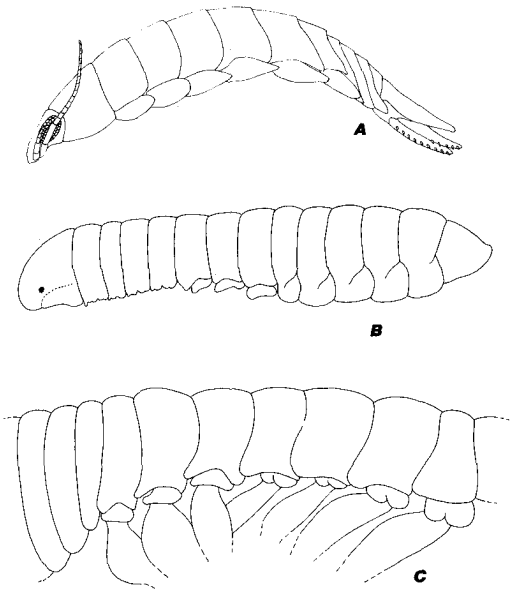

FIG. 9. Lateral views of a flabelliferan and two phreatoicideans, illustrating development of the pereopodal coxae. A, *Rocinela propodialis* (type, USNM 29248). B, *Phreatoicopsis terricola* (USNM 78431). C, *Phreatoicus australis* (USNM 59116; anterior is to the right).

Phoratopodidae (which is monospecific and known from only two female specimens) the coxal plates are enormously expanded ventrolaterally, clearly marked off from their respective pereonite, but yet they are not freely articulating (Hale, 1925; Bruce, 1981, pers. obs.).

Character 43 is: without lateral coxal plates (0), *vs* with lateral coxal plates (1). Character 85 is: lateral coxal plates, if present, not fused with their respective pereonites (Plakarthriidae, Keuphyliidae, and Bathynataliidae are score 1; Serolidae is scored '?').

Pereopodal Epipods

Character 45 is: with lateral epipods on pereopods (mysidaceans) (0) *vs* without lateral epipods on pereopods (mictaceans, tanaidaceans, amphipods, isopods) (1). Character 46 is: pereopods without medial epipods on pereopods (0) *vs.* with medial epipods on pereopods (1). Only the Amphipoda have medial epipodal gills arising from the coxae. In the gammarideans, these are usually paired, thin-walled, leaf-shaped, respiratory structures that are present on pereopods 2–7 (although they may be absent from 2 or 7). They may be stalked, foliate, or dendritic, and they are particularly large and convoluted in terrestrial species, presumably to compensate for loss of respiratory body surface area where the general body cuticle is hardened and waxy to prevent water loss. In some brackish and fresh-water amphipods, finger-like accessory gills and sternal gills may also occur (freshwater Gammaridae, Crangonycidae, Hyalellidae and Pontoporeiinae). Whether the medial epipodal gills of amphipods are homologous to the lateral epipodal gills of mysidaceans and other Malacostraca, or are uniquely derived in amphipods, is not known.

Oostegites

Although many isopods have oostegites on the first five pairs of pereopods, the number and placement actually varies considerably within any given suborder, and even within a family (and occasionally within a single genus, e.g. *Sphaeroma*). In some groups (Tylomorpha, Aegidae, Cymothoidae, many Epicaridea) oostegites may form on all 7 pairs of pereopods, whereas in some genera of Arcturidae (Valvifera) only a single pair of oostegites ever develops (on pereopods 4). The Asellota and the Phreatoicidea almost always have oostegites on pereopods 1–4, and sometimes on the maxillipeds as well. The anthurideans usually have 3 or 4 pairs of oostegites. Other isopods are much more variable. In gammaridean amphipods, marginally setose oostegites usually occur on the coxae of pereopods 2–5. In Mictacea, the marsupium is formed by oostegites that may be marginally setose and occur on the coxae of pereopods 2–6 (*Hirsutia*), or not setose and occur on pereopods 1–5 (*Mictocaris*). Among isopods, some groups have marginal setae on the oostegites and others lack setae.

Oostegites are reduced or lost in many unrelated isopod groups that have evolved alternative or accessory means of incubating the embryos. For example, the evolution of sternal pockets or folds for incubating embryos is often correlated with the habit of conglobation, or folding the body ventrally so that the cephalon and pleotelson are appressed. Harrison (1984a, b, c) provides an excellent overview of brood pouch morphology in the family Sphaeromatidae, illustrating the usefulness of these features at the generic level. Some sphaeromatids have the brood pouch composed only of oostegites. Other genera have a brood pouch composed of large, opposing, sternal pockets formed of cuticular folds; these may extend from the posterior mar-

gin of the sternum and open anteriorly (posterior pockets), or they may extend from the anterior sternal region to open posteriorly (anterior pockets). In still other sphaeromatid genera, paired invaginations of the sternal cuticle occur that extend into the body cavity but open via narrow slits (referred to as 'internal pouches'). Internal pockets and pouches occur in sphaeromatid genera that conglobate (or fold) and have reduced or lost the oostegites. In some cases, the oostegites are entirely lost (*Dynamenella*), and in other cases they are rudimentary (many species of *Sphaeroma*). All plant- and wood-boring species of *Sphaeroma* seem to show reduction of the oostegites; non-boring species have all the oostegites fully formed, presumably working in concert with the internal pockets to form the marsupium.

In the cirolanid genus *Excirolana*, there are 3 pairs of greatly reduced oostegites, but these do not form a marsupium. Instead, the eggs drop from the oviducts into a pair of sacs ('uteri') formed by a single layer of cells and located in the thorax lateral to the gut. These sacs have been viewed as enlarged oviducts (Klapow, 1970, 1972; Jones, 1983). The embryos are brooded here, and since the sacs do not open to the outside during development this may be viewed as a form of ovoviviparity. In the cirolanid genus *Eurydice* there are 5 pairs of oostegites, but in addition the sternum is displaced dorsally either side of the nerve cord, with the marsupium and developing embryos filling the entire pereon, surrounding the gut. Klapow (1970) suggested that the brooding modifications in *Excirolana* and *Eurydice* are related to the habitats in which most species occur — wave washed sand beaches. Harrison (1984a, b,c) suggested similar correlations in certain sand beach sphaeromatids that have large sternal brood pockets (*Tholozodium, Sphaeromopsis, Dynamenella, Ancinus, Leptosphaeroma, Paradella*).

Ligiamorphans belonging to the conglobating genera *Armadillo* and *Armadillidium* have a brood pouch composed of oostegites, but in addition the sternum bears 5 pairs of invaginations which surround the gut within the body cavity for brooding the embryos. The brood pouch in the conglobating genus *Helleria* is also composed of oostegites, but the posterior wall of the marsupium extends into the pleon as a large pouch (Mead, 1963; Mead and Gabouriaut, 1988). In the conglobating genus *Tylos*, portions of the sternites of ovigerous females are displaced dorsally and pressed against the dorsal cuticle, and the developing embryos fill the body.

Oostegites appear to be absent altogether in the Microcerberidea, and sternal invaginations or folds are also apparently absent, although the female has been described for only a single species (Wägele, 1982a, b). Wägele speculated that the embryos of microcerberids might be laid free among sand grains — a behaviour currently unknown in any isopod species. However, since all peracarids undergo direct development, and many isopods rely on internal brooding, it would seem more likely that the embryos of microcerberids would also be brooded internally, in uteri or the general body cavity.

In the parasitic epicaridean family Cryptoniscidae, the embryos are brooded in sternal invaginations formed by ventrolateral folds of the body wall, whereas in the family Dajidae the brood pouch is formed from ventral extensions of the sternites. Gnathiids lack oostegites altogether and brood the embryos within the body cavity. Klapow (1970) claimed that the fertilised ova develop within the ovaries themselves in *Paragnathia*. At least some amphipods are also known to utilise internal brood chambers (*Cystosoma*).

As seen from the above review, aspects of oostegite morphology may be useful within families and genera, but no clear pattern of oostegite morphology is discernible at the level of isopod suborders (except perhaps for the Phreatoicidea, the Asellota, and the Microcerberidea), and therefore oostegite characters were not included in the data analysis.

Spermathecal Duct

Wilson (1986b) summarised and elaborated upon our knowledge of a unique vagina-like anterodorsal copulatory structure, the 'spermathecal duct' (or less descriptively, the 'cuticular organ') that occurs in female Asellota. Although all other isopod suborders have not yet been systematically surveyed for this structure, preliminary studies have so-far failed to reveal its presence in any other groups. Character 47 is presence of the asellote 'cuticular organ' or spermathecal duct (Wilson, 1986b; Wilson, 1991). Only the Asellota is scored derived for this character.

Genital Pores

Information on isopod genitalia has been recently summarised (Wilson, 1991). Important patterns are apparent in the position of the genital pores. In the Malacostraca, genital pores typi-

cally occur on the coxae of thoracopod 6 in females, and thoracopod 8 in males. These are relatively conservative features, although the peracarids show some variation.

The Phreatoicidea are the only isopods with both female and male pores located on the coxae. In male phreatoicids, the genital papillae (penes) occur on the medial side of coxae 7 and can be quite large; they are likely to be the primary intromittent organs in this group. In all other isopod suborders, the penes are located on the sternum, usually near the posterior margin of the sternite of thoracomere 8, rather than on the coxae. A single, notable, and important exception to this occurs in the asellote genus *Vermectias* Sivertsen and Holthuis, 1980 in which the coxae of the seventh pereopods appear to be divided into 2 pieces, one of which is slightly expanded medially onto the sternum and bears the penes upon it (Just and Poore, pers. comm.). Within the Asellota, and the Isopoda in general, the penes show a trend toward migration medially, often with fusion at the midline. Fusion of the penes occurs throughout the Isopoda and this feature has probably evolved independently in several suborders (Wilson, in press) making it of little use for the present study. The coxae/penes condition noted above in *Vermectias* may represent an early evolutionary stage in the migration of the penes from the coxae to the sternum, and perhaps also an early stage in the evolution of sternal coxal plates upon which the penes may be borne. In two suborders (Valvifera and Oniscidea) the penes arise from the sternum of pleomere 1, or from the articulating membrane between pleomere 1 and pereonite 7. Among the non-isopod Peracarida, a variable pattern also exists. The Mysidacea and the Mictacea have coxal openings for the vas deferens, whereas the Amphipoda and Tanaidacea have penes on the eighth thoracosternite.

In most female isopods and tanaidaceans, the oopore is situated ventrally on the sternite of pereonite 5. In the phreatoicids, however, the pore is clearly present on the medial side of the coxa. Coxal oopores also are found in the Mysidacea, Amphipoda, and perhaps the Mictacea (although our inspection of non-ovigerous female *Mictocaris* failed to reveal any oopores, either sternal or coxal). The situation of the oopore is more complicated in those isopod groups where the coxae are expanded as sternal coxal plates covering the ventral surface. Available data do not allow us to assess whether the oopores simply moved medially with the coxae, or whether they first migrated onto the sternite and then subsequently penetrated the coxae when the pores were covered by the expanding coxal plates. Further, the precise position of the oopore is unknown for many groups. Character 48 is: male penes on coxae (0) *vs* penes on sternite (1). Character 49 is: penes on thoracomere 8 (0) *vs* penes on pleomere 1, or on the articulating membrane between pleomere 1 and thoracomere 8 (1). Only Valvifera, Ligiamorpha, Tylomorpha, and Calabozoidea are scored apomorphic for character 49.

Excretory Organs

The primary excretory organs among the Malacostraca are antennal glands and maxillary glands. All crustaceans have antennal glands during their ontogeny, but many lose them in adulthood and instead rely on maxillary glands as the primary excretory organs. Adult isopods, tanaidaceans, and cumaceans lack antennal glands, or possess only a rudimentary antennal gland, and the maxillary gland is well developed (Strömberg, 1972). Conversely, adult mysidaceans and amphipods (and the Eucarida) have well-developed antennal glands. Siewing (1952, 1953, 1956) noted that in at least some lophogastrid mysids (*Eucopia*) small functional maxillary glands may also be present, thus possibly reflecting an ancestral condition in which both pairs of segmental nephridia were functional in adults. The condition in Mictacea is not known. Schram and Lewis (1989) have suggested that a series of segmental glands may have primitively been present, one pair in each crustacean head somite. Character 52 is: primary adult excretory organ antennal gland (0) *vs* maxillary gland (1); no polarity is assumed.

Pleopods

The pleopods of isopods have multiple functions, including respiration, swimming, and copulation. Two key synapomorphies uniquely defining the Isopoda are: Character 4, thoracoabdominal heart, and Character 5, respiratory pleopods. These features are obviously functionally/anatomically linked. The only other malacostracans known to utilise the pleopods as the principal respiratory organs are the stomatopods (Burnett and Hessler, 1973; Kunze, 1981), in which the heart also extends into the pleon.

The primitive malacostracan pleopod is a narrow biramous limb with multiarticulate rami. This type of pleopod is found in the Mysidacea and the Amphipoda. Broad, flat pleopods with

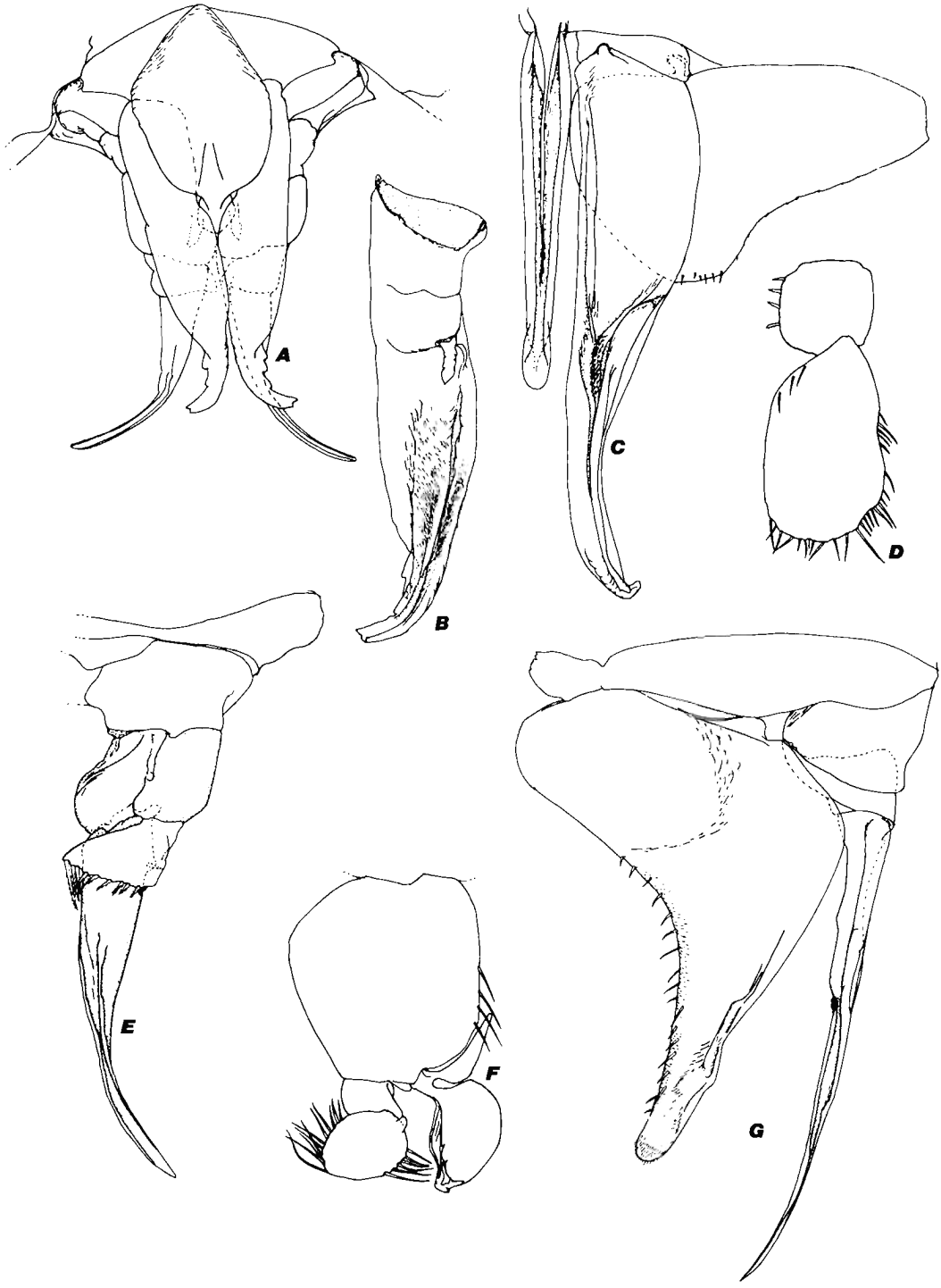
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TABLE 2. Comparison of basally derived Isopoda ('short-tailed' taxa). Legend: M = male; F = female.

	Reduction of pleomeres 1–2	Fusion of pleomeres 3–5	Condition of pleopod 1	Condition of pleopod 2	Condition of pleopod 3	Pereopodal coxae
Phreatoicidea	not reduced	free	M, biramous F, biramous	M, biramous F, biramous	biramous	free
Asellota	free, short & narrow (to variously fused)	fused	M, uniramous F, absent	M, biramous (endopod geniculate) F, uniramous	biramous	free
Microcerberidea	free, not short (ring-like)	fused	M, uniramous F, absent	M, biramous F, absent	uniramous	free
Atlantasellidae	free, broad	fused	M, uniramous F, absent	M, biramous F, absent	uniramous	free
Calabozoidea	strongly reduced	free	M, biramous (in juveniles) F, biramous	M, biramous F, biramous	biramous	fused dorsally; with sternal plates
Oniscidea	somewhat reduced	free	M, biramous F, biramous	M, biramous F, biramous	biramous	fused dorsally; with sternal plates

no more than two segments in the rami are found in the Mictacea, Tanaidacea, and the Isopoda. Character 53 is: narrow, multisegmented pleopodal rami (0) *vs* broad, flat, 1- or 2-articulate pleopodal rami (1). In phreatoicideans and many asellotes, especially primitive Asellota (Aselloidea, Stenetrioidea), the posterior pleopods bear 2-segmented exopods. In all other isopods the pleopodal exopods are always uniarticulate, although they may occasionally bear transverse 'suture lines'. Character 77 is: exopods of at least posterior pleopods biarticulate (0), *vs* no pleopods with biarticulate exopods (1).

In all non-isopod peracarids (except Mictacea), pleopods are primitively used for swimming. The pleopods of isopods are also well-developed for this function in most groups, with broad rami and swimming setae on at least some pairs. Several groups (Asellota, Microcerberidea, adult Epicaridea, Ligiamorpha, Tylomorpha, adult Cymothoidae) no longer swim with their pleopods, and use them only for respiration. Calabozoidea are said to swim (Van Lieshout, 1983:175), although behavioural observations may have not been made. In the groups that do swim, a trend occurs in most suborders wherein the posterior pleopods may be naked (with reduced or no marginal setae) and serve primarily for respiration. Loss of marginal setae typically occurs on pleopods 3–5, or 4–5, or just 5, and it may occur on both rami or only on the endopods. In the family Cymothoidae, the mancas and juveniles have swimming setae on the pleopods, but the obligate parasitic adults do not.

The Asellota and Microcerberidea share a number of pleopodal features. In both of these suborders females lack the first pair of pleopods (character 78), and in males the first pleopods (if present) are uniramous (character 81). The first pleopods of males are fused together to assist the second pleopods in sperm transfer in the higher Asellota. In addition, the male second pleopodal exopod is a small, non-lamellar structure, whereas the endopod is modified as a copulatory gonopod (character 79). Female microcerberids also lack pleopods on the second pleonite (character 82), and the third pleopods are uniramous and fused into a single piece to form an operculum over pleopods 4 and 5 (character 83). In male microcerberids, the second pleopodal exopod is reduced to a simple 1- or 2-articulate ramus, probably not involved in sperm transfer; the endopod is complex and highly variable in shape, but never geniculate (character 84). In the Asellota, females have uniramous second pleo-

FIG. 10. Comparison of male pleopods 1 and 2 in calabozoans, asellotans, and oniscideans. A, *Calabozoa* (Calabozoidea), penes and pleopods 1–2 in situ (ventral view). B, *Calabozoa* (Calabozoidea), left pleopod 1 (dorsal view). C, *Armadillidium* (Oniscidea), penes and right pleopod 1 in situ (dorsal view). D, *Asellus* (Asellota), right pleopod 1 (ventral view). E, *Calabozoa*, left pleopod 2 (ventral view). F, *Asellus*, right pleopod 2 (ventral view). G, *Armadillidium*, right pleopod 2 (ventral view).

pods (character 75), and males have the exopod of the second pleopod highly modified to function in concert with a large geniculate endopod in sperm transfer (character 76).

Terrestrial pleopodal respiration by use of pseudotracheae is found only in the Tylomorpha and Ligiamorpha, though not in all families (not Ligiidae or Trichoniscidae). In addition, the Oniscidea and the Calabozoidea share several unique pleopodal similarities (Table 2, Fig. 10). The endopods of male pleopods 1 and 2 are styliform and greatly elongated (only pleopod 2 in Ligiidae), presumably participating in copulation and/or sperm transfer (character 54). And, on pleopods 3–5 (in both sexes) the exopods are broad, heavily chitinised, and opercular, while the endopods are thick and tumescent (character 56). In most isopods, the endopods are thin walled and nearly the same size as the exopods.

In the recently described family Lynseiidae (Poore, 1987) the fifth pleopods are reduced to a single plate (character 70). Poore suggested that this attribute was the only unique apomorphy of this family, and we agree.

Other Pleonal Features

Most malacostracans have 5 free more-or-less equal pleonites, and primitively the 6th pleonite is free from the telson and pleomere 5. In the Microcerberidea and the Asellota, pleonites 1 and 2 are completely free and the remaining pleonites and telson are fused into a single unit with no lateral incisions indicating the fused somites. (The single exception to this appears to be the odd asellote *Vermectias*, which has 3 free pleomeres; Just and Poore, pers. comm.). A somewhat similar condition appears to be the primitive state for the Sphaeromatidae, but this is presumably a convergence. In sphaeromatids, the primitive condition exhibits lateral incisions demarcating the vestiges of the fused pleomeres, hence we do not regard this to be a condition homologous to that of asellotans. Some authors have suggested a close affinity between the Serolidae and certain Sphaeromatidae (*Ancinus, Tecticeps, Bathycopea*) on the basis of a similar pleonite reduction (Hansen, 1905a; Sheppard, 1933). However, in serolids pleonites 4–6 are fused to the telson and pleonite 1 is reduced, whereas in sphaeromatids pleonites 3–6 (at least) are fused with the telson, lateral incision lines primitively demarcate the positions of the fused pleomeres, and the first pleonite is never markedly reduced. Other isopods have variously modified pleonites, but no other suborders or families show a pleonite reduction like that seen in the Asellota and Microcerberidea as the primitive condition.

Character 80 is pleonites 1–5 either free or variously fused, but never (in the primitive condition) with pleonites 1–2 free and 3–5 fused to the pleotelson (0), *vs* pleonites 1–2 free and the remaining pleonites and telson fused into single integrated unit (1). The variety of pleonite reductions seen throughout the isopods make it difficult to find further useful homologies. In two taxa, Phreatoicidea and Limnoriidae, pleonite 5 is always manifestly longer than all other pleonites (character 73). In the Calabozoidea, pleomeres 1 and 2 are reduced to only the sternal plates (character 86).

Within the Malacostraca, broad fan-like uropods arising from the sixth pleomere and functionally associated with the telson is the plesiomorphic state. This 'tailfan' arrangement is an integral aspect of Calman's caridoid facies (Hessler, 1983). Unlike other Eumalacostraca, the Isopoda (and some other Peracarida) show a good deal of variation in uropod morphology and position (Figs 1–3) and the uropods function in a variety of ways. The caridoid-like tailfan of the Cirolanidae and related families has been taken by many workers as evidence that these taxa are primitive isopods, or at least that they represent an archtypical 'caridoid' isopod body plan. However, isopods (like amphipods, tanaids, and perhaps mictaceans) lack the 'caridoid escape behavior', and those groups with fan-like uropods do not use their flattened uropods for propulsion, as in true caridoids (e.g. mysidaceans, euphausiids, or natantians). Instead, they appear to use their uropods as lift planes and steering devices (unpubl. obs. of living *Bathynomus, Cirolana*, and other flabelliferans).

A review of the peracarid orders reveals a clear trend toward reduction of the caridoid tailfan morphology. Although it is well-developed among the Mysidacea, the telson and uropods of speleogriphaceans, mictaceans and thermosbaenaceans is less well developed as a true tailfan. This is presumably tied to loss of the 'caridoid escape behaviour' in these groups. However, in these three groups the flattened, paddle-like shape of the uropods is retained and these appendages probably assist in swimming in some way. In cumaceans, tanaids, amphipods, and many isopod taxa there is nothing resembling a caridoid tailfan.

In amphipods pleopods 4, 5 and 6 are modified as 3 pairs of uropods (Character 6). The amphi-

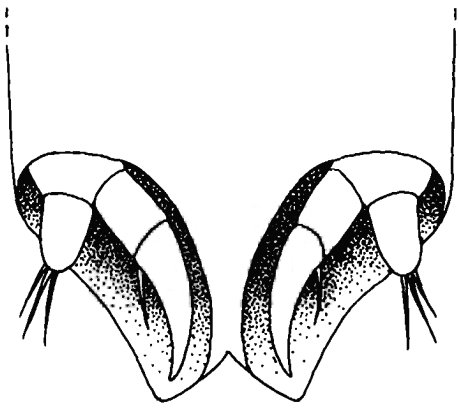

FIG. 11. *Keuphylia* (Keuphyliidae). Ventral view of pleotelson showing arrangement of uropods in ventral pocket.

pod urosome and uropods appear to be used primarily for strengthening the caudal portion of the body, and to permit jumping by rapid posterior flexion of the pleon (Barnard, 1969; Bousfield, 1973). In many Gammaridea, however, the third uropods still bear 'swimming' setae and may be used (along with the first two pairs) for paddling; males especially tend to have natatory third uropods (Barnard, 1969; Bousfield, 1973). However, the amphipod third uropod is usually substyliform and not fan-like. The majority of Gammaridea probably do not use the third uropods for active swimming and these structures are often reduced or occasionally absent in sedentary groups. The uropodal exopod in amphipods is biarticulate, and the endopod is typically uniarticulate.

In tanaidaceans, amphipods, cumaceans, and many isopods, the uropodal rami are styliform. The uropodal rami of tanaidaceans also are long, multiarticulate appendages, whereas in isopods, the rami are always short and uniarticulate. The mictacean uropodal rami can be either biarticulate (*Mictocaris*) or multiarticulate (*Hirsutia*).

In mictaceans, amphipods, and mysidaceans, the uropods arise from pleomere 6 and the telson is a distinct somite. In isopods and living tanaids, the sixth pleomere is fused with the telson, forming a 'pleotelson', although primitive fossil tanaids (see below) possessed free sixth pleomeres. Many isopods have a well developed, elongate telsonic region of the pleotelson upon which the anus and uropods are basally positioned. Other isopods have a reduced, shortened telsonic region of the pleotelson, and the anus and uropods are positioned in the posterior region of the pleotelson (terminal or subterminal). The uropods always arise on either side of the anus.

Dahl (1954) suggested that the primitive phreatoicidean condition was flabelliferan-like ('cirolanoid'-like), unlike the adult morphology of living Phreatoicidea. This argument was based on observations made on developmental stages taken from the brood pouch of the South African phreatoicid *Mesamphisopus capensis*. We do not find Dahl's argument (or his illustrations) convincing. The kinds of morphological changes he described can be easily explained by natural developmental allometry commonly seen in most crustaceans. Brenton Knott (pers. comm.) has seen no evidence of lamellar uropods or other 'cirolanoid' morphology in the developmental stages of any Australian phreatoicids.

Character 57 is: uropods broad and flattened (0); uropods flattened but only somewhat broadened (1); uropods styliform (2). This character was analysed unordered in initial analyses. Character 58 describes the shape of the pleotelson. State '0' is: telsonic region of the pleotelson well-developed and elongate, with the anus and uropods at the base of the pleotelson (at the position of pleomere 6) — this is the condition seen in mysidaceans, amphipods, mictaceans, and many isopods. State '1' is: telsonic region very short, with the anus and uropods positioned terminally on the pleotelson; this condition occurs in the Tanaidacea, Phreatoicidea, Asellota, Calabozoidea, Microcerberidea, Tylomorpha, and Ligiamorpha. Because the polarity and precise homology of these conditions is uncertain, character 58 was left unordered in initial analyses. A unique up-turned pleotelson apex occurs in the Phreatoicidea (character 72).

In mysidaceans, mictaceans, tanaidaceans, and amphipods, the uropodal rami are composed of 2 or more articles; in all isopods they are uniarticulate. Character 59 is: uropodal rami may be multiarticulate (0), *vs* uropodal rami always uniarticulate (1). In three families (Keuphyliidae, Bathynataliidae, Plakarthriidae) the uropods arise not on the anteorlateral margin of the pleotelson, but rather posterolaterally, where they lie in shallow ventral channels or furrows (character 55) (Fig. 11). In serolids there is also a tendency toward this feature, but it is not present in all species, hence they are scored '?' for this character.

Character 60 is: uropodal exopod folded dorsally over pleotelson (a unique synapomorphy of

FIG. 12. *Haliophasma geminata* (Anthuridea). SEM of pleon (lateral view). Note deep fluting between pleomeres 5 and 6, and between and between pleomere 6 and telson. Despite fluting, a continuious cuticular covering connects these somites and no articular membranes are present. Also note large opercular first pleopods (compliments of B. Kensley).

Anthuridea). Character 61 is: uropods modified as a pair of ventral opercula covering the entire pleopodal chamber (a unique synapomorphy for the Valvifera). Character 62 is: uropods form a ventral, operculate, anal chamber beneath pleotelson, covering the anus and distal-most pleotelson region but not covering the pleopods (a unique synapomorphy of the Tylomorpha). Character 63 is: uropods directed ventrally and identical to other pleopods (a unique synapomorphy of the Anuropidae, and presumably an adaptation to a swimming pelagic lifestyle). Character 67 is: uropodal endopod claw-like. We regard this as a unique synapomorphy of the Keuphyliidae. Although the uropodal endopod in *Paralimnoria* is acute, it is not recurved and claw-like as in Keuphyliidae (and, the endopod of *Limnoria* is neither acute nor claw-like). Character 68 is: uropodal exopod claw-like (a unique synapomorphy of the Limnoriidae). Character 71 is: uropods highly modified and represented by a single, elongate, clavate piece, or by an elongate, clavate peduncle with reduced rami — a unique apomorphy of the Bathynataliidae. Character 87 is: uropods of a single piece, rami fused to peduncle — a unique apomorphy of the Calabozoidea.

In all living tanaidaceans and isopods, the sixth pleomere is fused to the telson, forming a pleotelson. However, fossil tanaids of the infraorder Anthracocaridomorpha have 6 free pleomeres (and thus lack a pleotelson), and this is presumably the primitive condition for this group (Schram, 1974; Sieg, 1984; Schram *et al.*, 1986). Some cumaceans and thermosbaenaceans also have a pleotelson. A pleotelson is present in all isopods.

Many authors have alluded to a free telson in some genera of anthuridean isopods. The presence of a free (unfused) sixth pleomere in some Anthuridea has been debated at least since Calman (1909). Wägele (1981, 1989a) claimed that the sixth pleomere is always fused to the telson in anthurideans (thus a true pleotelson is always present). Bowman (1971) stated that the sixth pleomere was free in anthurideans. Kensley and Schotte (1989) stated, 'Pleonites 1–5 free or fused, pleonite 6 partly or completely fused with telson'. In his diagnosis of *Paranthura* Poore (1984) stated, 'Pleonites usually distinct from each other and from telson.' Poore and Lew Ton's (1985a) diagnosis of *Apanthura* stated, 'pleonite 6 free from others and from telson', and their diagnosis of *Cyathura* (1985b) stated, 'pleonite 6 free or fused to telson.' However, Poore (pers. comm.) has most recently stated that he no longer believes the sixth pleonite to ever be freely articulating with the telson in anthurideans.

The sixth pleomere is clearly fused to the telson (forming a pleotelson) in many anthurideans (*Pseudanthura*). However, in many genera pleomere 6 appears to be free (*Amakusanthura*, *Calathura*, *Exallanthura*, *Haliophasma*, *Heteranthura*, *Leptanthura*). In most species in these genera, under both light and scanning microscopy, pleomere 6 and the telson are clearly separated from one another dorsally by a deep groove (Poore and Lew Ton, 1988b, fig. 11a) and, using forceps, the telson can often be flexed against the sixth pleonite. This groove is often shown in drawings and electron micrographs of anthurideans (Fig. 12). Even in some species in which pleonites 1–5 are fused (medially or entirely), the sixth pleonite may appear free (*Haliophasma geminata*).

To resolve this issue, we sectioned specimens

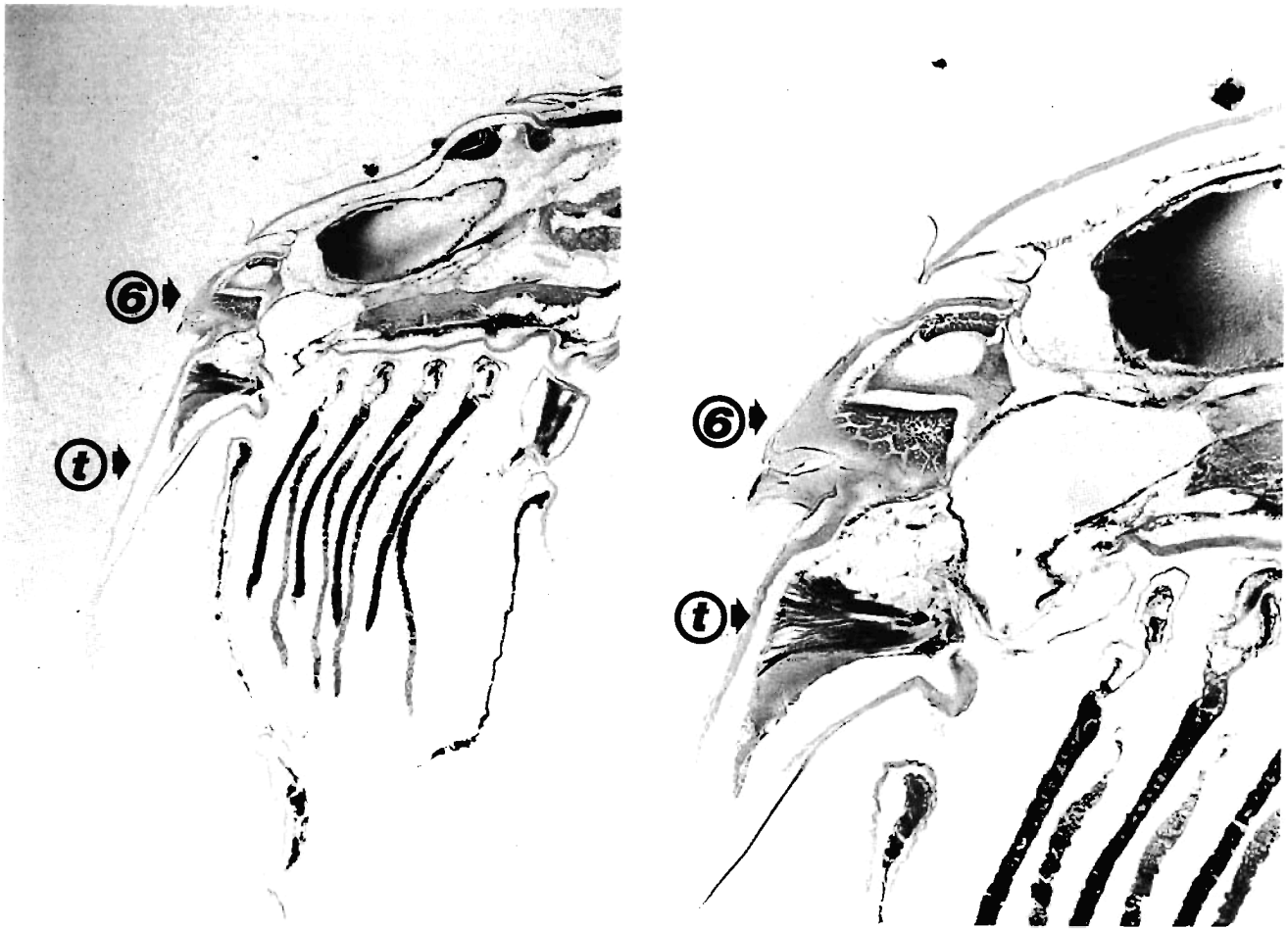

FIG. 13. *Paranthura elegans* (Anthuridea). Median saggital section through pleon showing fusion of pleomeres 5 and 6, and fusion of pleomere 6 with telson. Despite fluting, a continuous cuticular covering connects these somites and no articular membranes are present. Also note large opercular first pleopods. Arrows indicate pleomere and telson.

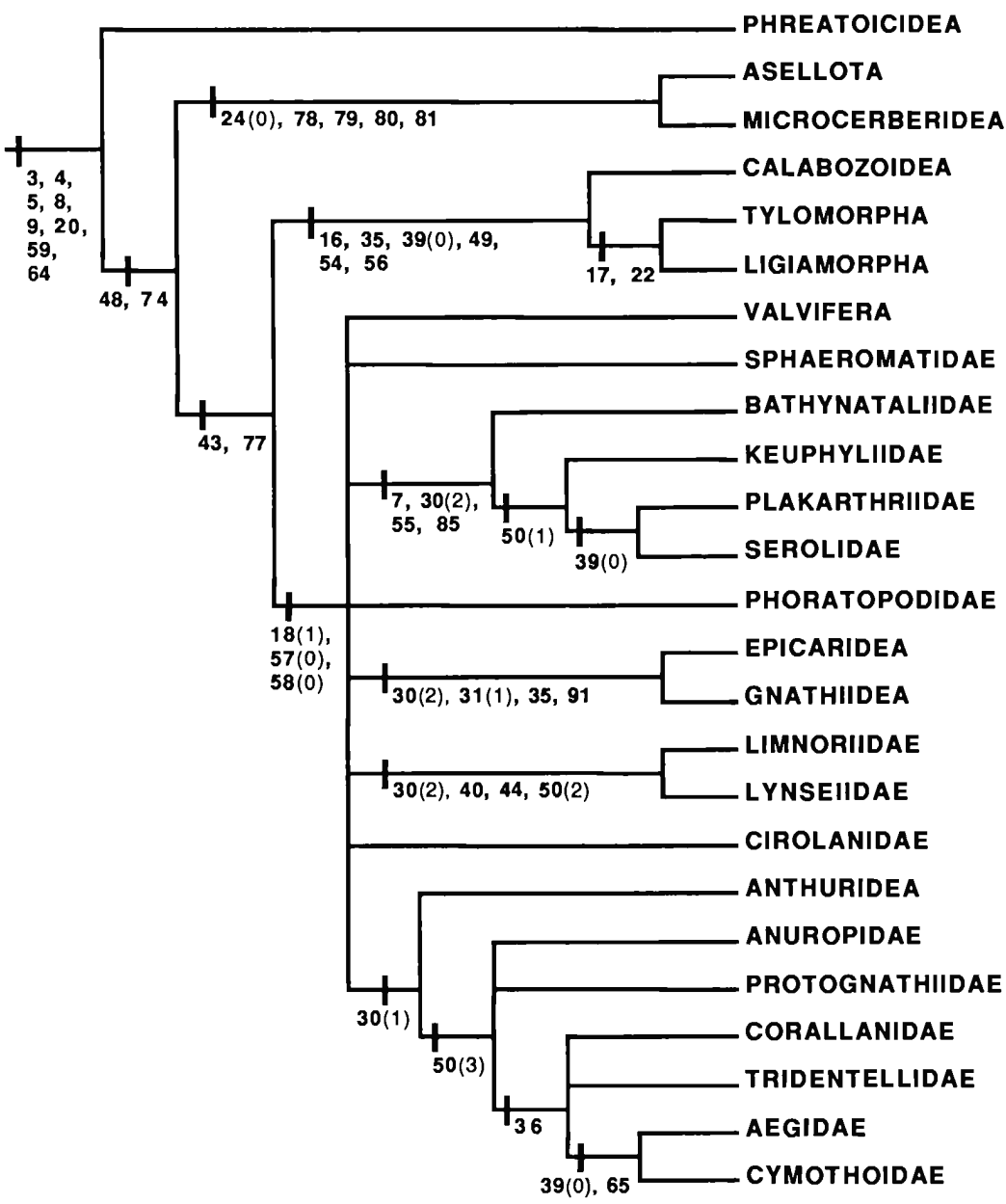

FIG. 14. Cladogram of the Isopoda (Nelson strict consensus tree, built from 16 equal-length trees). Length = 133; C.I.=0.75. Character numbers on tree correspond to character list in Appendix I. Synapomorphies of terminal taxa are not shown on tree (see Appendix III).

of *Paranthura elegans* a species common in San Diego Bay. Under SEM and light microscopy, this species appears to possess a free sixth pleomere. However, our longitudinal sections show unequivocally that no articular membrane is present between the telson and the sixth pleonite (Fig. 12). In fact, the cuticle is even thicker in the region of fusion than it is elsewhere

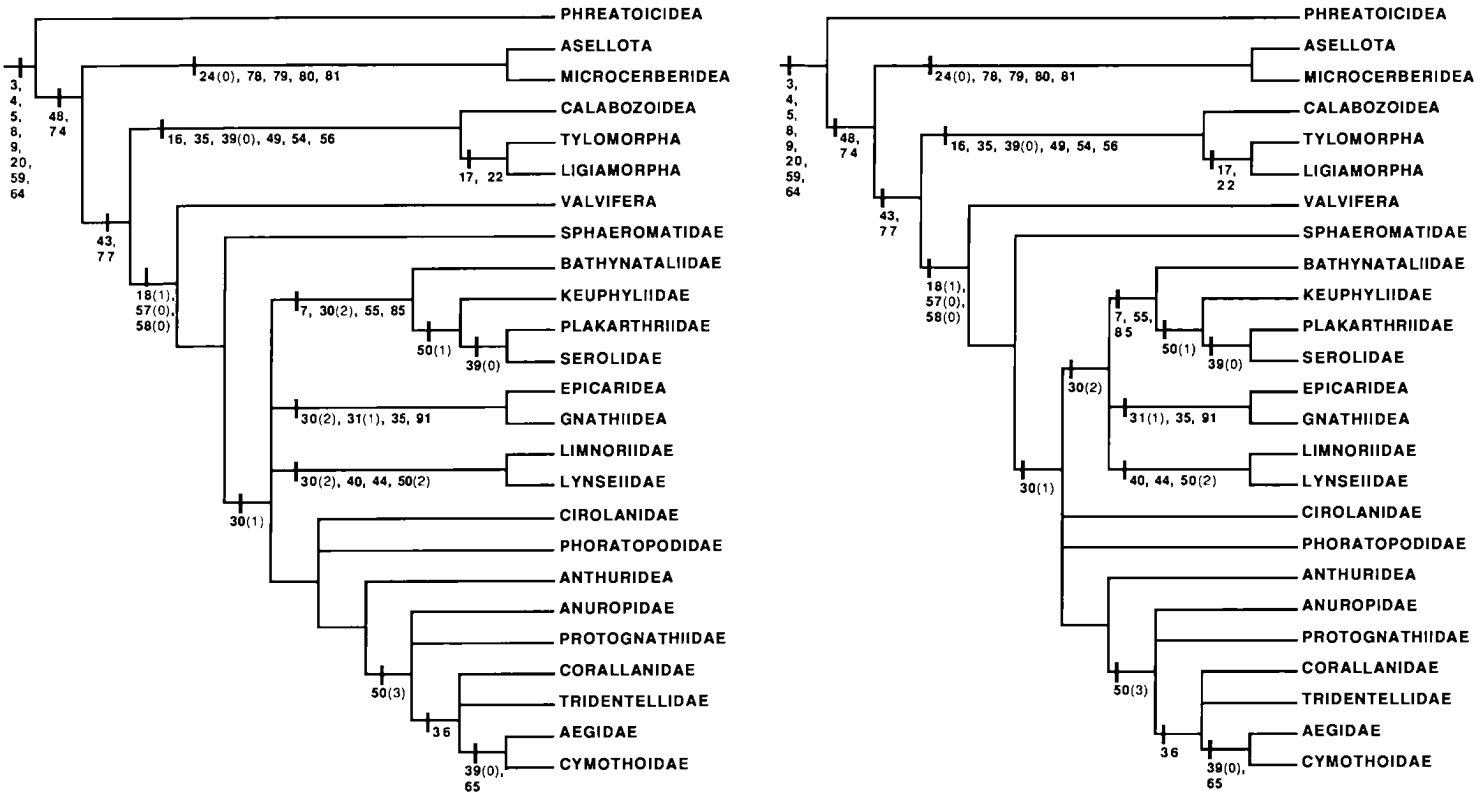

FIG. 15. Two of the 16 equal-length trees from which the consensus tree (Fig. 14) was constructed. These trees emphasize mandibular features (characters 27–30, 35, 50, 91) over character 39 (maxillipedal endite with *vs.* without coupling spines). Both trees are 129 steps long, with a C.I. of 0.78 (0.67 excluding uninformative characters).

on the pleon. Although specimens of *Paranthura* have some flexibility between these two segments, this is apparently due to the deep fluting of the cuticle at the area of fusion, and not due to a true articular membrane. This fluting is what creates the deep dorsal groove that is so visible in this, and presumably other, species. Hence, unless additional observations of other species indicate otherwise, we take the conservative approach and assume that anthurideans also possess a pleotelson.

Although fusion of pleomere 6 to the telson occurs in some species in at least four peracarid suborders (tanaids, cumaceans, thermosbaenaceans, isopods), it appears to have been derived independently in three, if not all four, of these groups. Only in the Isopoda do all species possess a pleotelson. Character 64 is: pleomere 6 freely articulating with telson (0); pleomere 6 always fused with telson, forming a pleotelson (1). Only isopods are scored (1).

RESULTS AND DISCUSSION

Analysis Procedure

Our analytical strategy was as follows. We assembled a data set based on the character analyses described above, and input data files were generated for HENNIG86, PAUP, and MacClade. The data were first analysed with PAUP and HENNIG86. A pool of multiple, equal-length trees was studied and all homoplasous characters were reassessed. Several characters were eliminated from the analysis at this stage because they were simply too high in homoplasy and/or their precise homologies seemed questionable, e.g. sternal coxal plates. The final character list (the numbered characters noted in the previous section) and OTU-character data matrix are provided in Appendices I and II.

Trees were first constructed with the characters polarised as indicated in the descriptive character analysis above. However, it quickly became evident that, due to high homoplasy levels (especially reversals) unambiguous judgments could not be made regarding character state transformations. Hence, the final analyses were done with all characters unpolarised, i.e. programs set to nonadditive, and allowed to change in any direction. This procedure makes no assumptions as to what the primitive or derived states are for any characters in the data set. In respect for the high levels of homoplasy inherent in such a large data set (especially for arthropods), comparisons of trees generated from ordered and unordered characters is an informative and cautious approach. In fact, binary characters are treated no differently in additive (ordered) *vs* nonadditive (unordered) analyses (unless such a program option is specifically selected); the only way in which the nonadditive analysis differs from the additive one is in its effect on multistate characters. The nonadditive analysis counts any character state change equally, as a single step, e.g. for a multistate character, a change from state 0 to state 2, or state 2 to state 0, is still counted as one step.

The non-additive analysis using the branch swapping algorithm of HENNIG86 (mhennig + bb) found 16 equally short trees (length = 129 steps; C.I. = 0.78). The Nelson strict consensus tree of these 16 trees is 133 steps long (C.I. = 0.75) and is shown in Fig. 14. This tree could not be improved by application of the successive character weighting method to the suite of 16 trees from which it was derived. These results were verified by analysing the data with PAUP 3.0. The PAUP analysis, using the MULPARS option, found the same 16 trees and produced an identical strict consensus tree. All statistics were identical for the PAUP and HENNIG86 trees.

Our final data set and consensus tree were coded into MacClade format, along with the trees of Wägele (1989a), Schmalfuss (1989), and others. MacClade was used to examine the effects on tree parsimony and character placement of different tree topologies generated by manual branch swapping, and to determine precisely how other trees differed from our own by graphically tracing character state changes for each character.

The Cladogram of Isopods

In the following discussion, character numbers (see appendix I) are indicated parenthetically in boldface. Synapomorphies defining terminal taxa are not shown on the tree (Fig. 14), but are listed in Appendix III and were noted in the previous section (character discussions). In our consensus tree (Fig. 14), the Phreatoicidea unambiguously arises as the basal most node, retaining two key symplesiomorphies that are lost in virtually all other isopod suborders: coxal penes (48) and the large row of filter setae on the medial margins of the maxillae (74). The notion that phreatoicids might represent an ancient isopod group was first advanced by Chilton (1883) and repeated by several other workers in the early part of this century. However, the specific hypothesis that Phreatoicidea are the most primitive living isopods has apparently

been previously suggested only by Schram (1974). Synapomorphies defining the Phreatoicidea include the upturned pleotelson (72) and elongate fifth pleomere (73). The most parsimonious tree depicts the loss of the antennal scale (25) at the origin of the isopod line, with its reappearance in the Asellota. An alternative, but less parsimonious scenario posits the loss of the antennal scale three times – in the Phreatoicidea, the Microcerberidea, and above the asellote-line in the cladogram.

The Asellota-Microcerberidea and Oniscidea-Calabozoidea lines arise next. The asellotans and microcerberids are sister groups. Among other things, they share the interesting attribute of a 6-articulate antennal peduncle (24), a feature that also occurs in mysidaceans, but is not seen in amphipods, mictaceans, tanaids, or any other isopod group. They also share the following additional synapomorphies: females lack first pair of pleopods (78); male second pleopods with a small non-lamellar exopod and a large endopod modified into a complex gonopod (79); pleomeres 1 and 2 free, 3–5 fused to pleotelson (80); and, male pleopod 1, if present, uniramous (fused and working with the second pleopods in sperm transfer in the higher Asellota) (81).

All isopod taxa beyond the Asellota-Microcerberidea line are distinguished by the presence of lateral coxal plates (43) and the absence of 2-articulate exopods on all pleopods (77). The Ligiamorpha and Tylomorpha are sister groups, supporting the contention that the Oniscidea is a monophyletic clade. The Calabozoidea is the sister group of the Oniscidea. (These three taxa are united by at least six synapomorphies: characters 16, 35, 49, 54, 56, and 39-reversal).

All isopod taxa above the oniscidean line are distinguished by three unique features: pereopods 1–3 are directed anteriorly, and pereopods 4–7 are directed posteriorly (18); the telsonic region of the pleon is greatly elongated, positioning the anus and uropod articulation anteriorly on the pleotelson (58); and, the uropods are broad and flat (not styliform) (57). We refer to these taxa as the 'long-tailed' isopods.

The relationships of the long-tailed isopod taxa cannot be unambiguously resolved with our data set. They comprise an unresolved 8-way polytomy on the consensus tree. Each of these 8 lines represents a distinct clade that appeared in all 16 primary trees. These 8 clades are: (1) Valvifera; (2) Sphaeromatidae; (3) Phoratopodidae; (4) Cirolanidae; (5) Epicaridea-Gnathiidea; (6) Limnoriidae-Lynseiidae; (7) a clade of 4 flat-bodied families (Bathnataliidae, Keuphyliidae, Plakarthriidae, and Serolidae); and, (8) a clade of 7 predacious-parasitic taxa, including the Anthuridea and 6 families currently recognised as flabelliferans. The latter clade culminates in the Cymothoidae, hence we refer to this group as the 'Cymothoid-line'.

Greater resolution of the long-tailed clade exists, of course, in each of the 16 primary trees. These 16 trees differed little from one another, and only in regard to subtle rearrangements of the 8 long-tailed lines noted above. If preference is given to mandibular characters (characters 27–30, 35, 50) over those of the maxillipedal coupling spines (character 39), much more resolution is achieved. Figure 15 shows two such trees. In these two trees the Valvifera and Sphaeromatidae are at the base of the long-tailed line. Of the long-tailed taxa, only these two groups retain the primitive grinding mandibular molar process (character 30); all taxa above Valvifera and Sphaeromatidae have a blade-like slicing molar process (or the molar process is lost).

According to our analysis, the ancestral isopod morphology included a very short telsonic region on the pleotelson, positioning the anus and styliform uropods terminally or subterminally on the pleotelson. We refer to the groups that possess this shortened pleotelsonic morphology as the 'short-tailed' isopods (Phreatoicidea, Asellota, Microcerberidea, Oniscidea, and Calabozoidea). This condition also occurs in extant tanaidaceans, although this could represent a parallelism because some fossil tanaidaceans are known to possess elongate telsons (Schram *et al.*, 1986). These short-tailed forms are largely infaunal and are not strong swimmers. Most are herbivores or scavengers.

The shift away from the short-tailed morphology to the long-tailed morphology (elongate telsonic region, positioning the anus and uropods basally on the pleotelson) occurred subsequent to the appearance of the oniscidean line. This reversion to a broad mysid-like tailfan within the Isopoda (characters 57 and 58 on the trees) appears to have corresponded to the emergence of isopods as active swimmers in the water column. However, as we noted earlier, isopods (and other non-mysidacean peracarids) lack the caridoid 'escape behaviour' and do not possess the massive pleonal musculature seen in the true caridoid taxa. Thus, the main effect of 're-invention' of a tailfan in swimming isopods was not

for direct propulsion, but more likely to provide a planar surface or rudder during swimming. We have observed this apparent function in swimming *Bathynomus*, *Cirolana*, juvenile Cymothoidae, and others. Within the long-tailed line, a trend can also be seen for enlargement of the lateral coxal plates. This may serve to increase the hydrodynamic streamlining of the body, perhaps in the same fashion as the enlarged pleura on many swimming caridoid malacostracans. Furthermore, as Hessler (1982) has noted, enlarged lateral coxal plates were impractical in the Asellota (and Phreatoicidea) because the coxae are still mobile in these groups. Also within the long-tailed line is a trend away from primary herbivory (Valvifera) and scavenging (Sphaeromatidae), to active predation and eventually parasitism. Within this lineage, only the Valvifera and Sphaeromatidae retain the primitive grinding mandibular molar process – all other taxa have a mandible modified more for carnivory, with the molar process (when present) modified as a slicing bladelike structure. Hence, emergence from the benthos appears to have been correlated with the evolution of a more active swimming lifestyle and carnivorous habits.

Corroborating evidence for this cladogram comes in the form of embryological and anatomical data from other studies. According to Wägele (1989a) the stomachs of phreatoicids and asellotans are the most primitive of the Isopoda, i.e. with straight, rather than curved, anterior filter channels. In addition, Strömberg (1972) has shown that the embryological median dorsal organs of isopods are of two types, one of which occurs in the Oniscidea, the other being restricted to the long-tailed taxa. Strömberg (1972) also demonstrated that the paired embryological lateral (= dorsolateral) organs of isopods are also of two types, one type in Valvifera, Flabellifera, and Anthuridea, the second type occurring only in Phreatoicidea and Asellota. Furthermore, Hessler (1982) observed that, of the isopods he studied, only the phreatoicids and the Asellota retain a coxa with the primitive capability of promotion/remotion, including an arthrodial membrane and some musculature.

Comparison With Wägele's Hypothesis

Wägele's (1989a) tree (Fig. 4D) is considerably longer than our tree (length = 153, CI = 0.65). However, the two trees share some important similarities. Both trees place the Phreatoicidea at the base of the isopod line. However, Wägele accepted Dahl's (1954) conclusion that phreatoicideans were derived from a cirolanoid ancestor, thus forcing Wägele to derive the short-tailed condition (terminal anus and uropods) in the Isopoda three separate times – in the phreatoicidean line, in the oniscid line, and in his asellote/calabozoidean line. Both our tree and Wägele's derive the Asellota after the Phreatoicidea. However, Wägele concluded that the Calabozoidea is the sister group of the Asellota, whereas we regard the calabozoids to be either primitive oniscideans, or the sister group of the Oniscidea. Both trees also derive the oniscideans above the phreatoicid/asellote lines, and then recognize several large groupings of the remaining taxa (the long-tailed isopods, as we have defined them). Both trees were unable to satisfactorily resolve the relationships of the long-tailed line. Beyond these generalities, our tree differs markedly from that of Wägele.

Wägele's tree (1989a, fig. 107) depicts 9 taxa: Phreatoicidea, Calabozoidea, Asellota, Microcerberidea, Oniscidea, Valvifera, Anthuridea, 'Sphaeromatidea' (*sic*), and 'Cymothoida' (*sic*). Wägele's Sphaeromatidea included 7 flabelliferan families: Keuphyliidae, Lynseiidae, Limnoriidae, Plakarthriidae, Sphaeromatidae, Serolidae, and Bathynataliidae. His Cymothoida included 8 flabelliferan families (Phoratopodidae, Protognathiidae, Anuropidae, Cirolanidae, Tridentellidae, Corallanidae, Aegidae, and Cymothoidae), plus the Gnathiidea and Epicaridea (Wägele reduces the latter suborder to family as the 'Bopyridae'). Wägele's suggested new Suborder Sphaeromatidea was not defined by any unique synapomorphies, but was based on a general suite of body shape criteria that we regard as (1) incorrect, (2) not applicable to all the groups included in this taxon, or (3) also present in other isopod taxa.

We have analysed most of the characters that Wägele used in his tree in our character discussions above, but we have coded/assigned many of them differently (and are thus not in agreement with Wägele's assignments of characters to taxa), or we have opted not to use some of them because we feel they are too poorly understood or are inappropriate due to their high levels of homoplasy at this level of analysis. Many character assignments in Wägele's analysis appear to be incorrect, e.g. the synapomorphic suite used to define his Sphaeromatidea; scoring the phreatoicideans as having laterally compressed bodies; assigning 2-articulate pleopodal exopods to Phreatoicidea but not Asellota; scoring the Asel-

lota as possessing an endopod on pleopod 1 of males; regarding *Rocinela* as having 2-articulate maxillipedal palps and protandric hermaphroditism, or they represent convergences/parallelisms hidden within other character complexes (styliform uropods, shortened pleotelson, vermiform body, etc.).

Wägele (1989a, b) has argued that a hypothetical, primitive, long-tailed morphology in isopods gave way to the short-tailed morphology on numerous occasions, independently, as a convergent adaptation to avoid predation by fishes. Our analysis suggests just the opposite, that the primitive condition in isopods was the short-tailed morphology, inherited from peracarid ancestors that already possessed a trend toward telson reduction and loss of the caridoid tailfan. Furthermore, it is the long-tailed isopods, not the short-tailed species, that are epibenthic and active swimmers and more often confront predatory fishes. The evolution of predator-avoidance strategies in isopods has not been extensively studied, but Brusca and Wallerstein (1979) and Wallerstein and Brusca (1982) provide comparative and experimental data suggesting that, at least for idoteids, they include features such as smaller reproductive size, cryptic colouration and body ornamentation, and certain behavioural traits.

Status of the Calabozoidea

It is evident from our observations of specimens of *Calabozoa pellucida* that it is not an asellotan isopod, but is either a primitive, aquatically-adapted oniscidean, or it is a unique creature closely related to the Oniscidea. Van Lieshout's (1983) and Wägele's (1989a) attempts to unite the Calabozoidea and Asellota were based largely on incorrect homology arguments regarding the pleopods. Although the copulatory part of the calabozoan first pleopod could be the exopod, no one has shown the uniramous pleopods of the Asellota to be either the exopod or the endopod. Furthermore, the detailed structures of the male first pleopod in both taxa are completely different (Fig. 10B *vs.* 10D). The synapomorphies proposed by Wägele for a Calabozoidea-Asellota sister group are incorrect or are symplesiomorphies. For example: a similar telsonic reduction and uropod arrangement occurs in the Phreatoicidea and the Oniscidea (hence these features should actually be symplesiomorphies on Wägele's tree); female asellotans (and microcerberideans) lack the first pair of pleopods (they are present and biramous in *Calabozoa*); and, in asellotan males the second pleopodal endopod is always geniculate (it is styliform in *Calabozoa*). The male first and second pleopods of *Calabozoa* most closely resemble those of oniscideans (Fig. 10). The presence of all 5 pairs of pleopods in female *Calabozoa*, and the absence of a 6-articulate antennal peduncle and the typical asellotan pleonite condition (pleonites 1 and 2 well-developed and usually modified as a narrow ring, pleonites 3–6 fused indistinguishably with telson) further argue against any relationship to the Asellota. In addition, calabozoans possess both dorsally-fused lateral coxal plates and sternal coxal plates, conditions typical of oniscideans but never seen in the Asellota (Table 2).

The pleopod morphology of *Calabozoa* shows many points of similarity to the highly modified copulatory structures found in the oniscideans (Fig. 10, Table 2). Male pleopods 1 and 2 possess elongate styliform gonopods, and the fused median penes arise from the articulation between pereonite 7 and pleonite 1. Furthermore, the pleopodal endopods of *Calabozoa* are somewhat thickened and tumescent as in terrestrial isopods. The adaptations of a primitive oniscidean to an aquatic lifestyle could predictably result in the differences seen between a typical oniscidean and *Calabozoa*. The maxillipeds of *Calabozoa* are very similar to those of the Ligiamorpha. The one feature of *Calabozoa* that distinguishes it from typical oniscideans is its possession of primitive, unmodified, trilobed maxillae. In oniscideans the maxillae are reduced to simple bilobed plates. The totality of these data and the positioning of the Calabozoidea on the cladogram suggest that this group represents either a very primitive, relict, aquatic oniscidean taxon, or a distinct taxon that has persisted from a line that led to the modern oniscideans.

Status of the Microcerberidea

Our analysis suggests a close relationship between the Asellota and the Microcerberidea. The synapomorphies shared between these two taxa include the following: (1) antennal peduncle 6-articulate; (2) female pleopod 1 absent; (3) male pleopod 2 with endopod modified into a complex gonopod; (4) pleomeres 1–2 free, 3–5 fused to pleotelson; and, (5) male pleopod 1 uniramous, if present (fused and working with second pleopods in sperm transfer in higher Asellota).

The Microcerberidea were regarded as anthurideans by Karaman (1933), Pennak (1958), Kussakin (1973), and others. Wägele (1983b,

1989a) reduced the Microcerberidea to a family of the asellote superfamily Aselloidea, along with Asellidae, Stenasellidae, and Atlantasellidae. Wägele's arguments for including the microcerberids in the Aselloidea relied strongly on similarities in the setae of the first pereopod, as well as the characters already mentioned. Similar setae, however, can be seen on the first pereopods of the Phreatoicidea, so setation may not be a synapomorphy at this taxonomic level. As Wägele (1983b) noted, the Atlantasellidae (originally included in the Aselloidea by Sket, 1979) have pleopods similar to the Microcerberidea, in which the second pair is absent in females and the third pair is uniramous and fused into a single piece that is operculate to pleopods 4 and 5 (in both sexes). Atlantasellids and microcerberids also share the unique 'tubular' molar process on the mandible.

We agree with Wägele (1983b) regarding the probable close relationship between *Atlantasellus* and the microcerberids. These two groups differ from each other primarily on the basis of features perhaps associated with body-size reduction and the interstitial habitus in the microcerberids (reduction of the mouth appendages, cylindrical body form), and *Atlantasellus* also bears several unique synapomorphies (inarticulate uropods, reduction of antennae). However, we consider these two groups to be distinct enough from the Asellota that we do not recommend placing them in that suborder, nor do we regard Wägele's (1989a) putative synapomorphies of the superfamily Aselloidea to be justified. All Asellota have a highly evolved male copulatory system, usually with a strongly geniculate endopod on the male second pleopod coupled with a short powerful exopod used for thrusting the endopod. Asellotans also have a distinct scale on the antenna, uniramous second pleopods in females, and a unique spermathecal duct; these features appear to be lacking in Microcerberidea and Atlantasellidae. In the latter taxa, the male second pleopodal endopod is an elongate, convoluted, straight or curved structure, and the exopod is degenerate. In addition, the third pleopod is fused into a single piece in microcerberids and atlantasellids, whereas in most Asellota both rami and the protopod are separate and unfused articles. Many of the attributes seen in microcerberids and atlantasellids constitute reductions, although the male copulatory pleopods of these groups are unlike anything seen in the Asellota.

In conclusion, the most conservative approach would be to simply transfer the Atlantasellidae to the Microcerberidea, allowing this suborder to stand as a sister group to the Asellota *sensu stricto*. We would recommend this working hypothesis until more data are available, particularly regarding the possible presence of the asellotan spermathecal duct in microcerberids and atlantasellids. In addition, we see no justification for the view espoused by Wägele (1983b) that the Microcerberidea evolved from aselloid ancestors in freshwater.

Status of the Protognathiidae

The only two described specimens of *Protognathia* (Schultz, 1977; Wägele and Brandt, 1988) appear to be mancas, although Wägele and Brandt's (1988) definition of the family assumes that the specimens are subadults or adults. The drawing of this animal by Wägele and Brandt (1988, fig. 1) even illustrates what appears to remnants of the embryonic yolk, typical of many isopod mancas. Wägele and Brandt claim that *Protognathia bathypelagica* Schultz, 1977, is a 'missing link', or 'intermediate between' the Cirolanidae and the Gnathiidea. Based on the published illustrations, we do not believe that Wägele and Brandt (1988) were actually dealing with the same species as Schultz (1977). In any case, in our opinion *Protognathia* only superficially resembles the Gnathiidea and more closely approximates the manca of a large, predatory, cirolanid-like or anuropid-like creature. The 'articulating', serrate, bladelike molar process on the mandible of *Protognathia* is characteristic of the Cirolanidae and the cymothoid-line, and this was no doubt the principal reason for Schultz's (1977) original assignment of *P. bathypelagica* to the genus *Cirolana*. The general body aspect is also similar to juveniles of the genus *Syscenus* (Aegidae), another flabelliferan family in the cymothoid-line.

The proposed Gnathiidea-*Protognathia* synapomorphies of Wägele and Brandt (1988) do not hold. First, the absence of the seventh pereopod and the expandable ventral cuticle is typical of isopod mancas. Second, the tailfan is identical to that of some cirolanids and aegids. Third, the mandible of *Protognathia* is not at all like that of the Gnathiidea, despite the possible similarity in function (predatory feeding). Homology arguments based on function alone should be viewed with caution. In fact, the mandible of *Protognathia* has features typical of Cirolanidae/Anuropidae (the articulated, serrate, bladelike molar process) and the cymothoid-line

in general (the acute bladelike incisor process of tridentellids, corallanids, aegids, and cymothoids). Fourth, the maxillae of *Protognathia* are quite different from those of gnathiids, in which they are highly reduced (males) or absent (females). The only derived feature that might be uniquely shared between *Protognathia* and the gnathiids is the plumose setation on the maxillipeds. *Protognathia*, however, has a similar setation on all of the other thoracopods as well, which is quite unlike the situation in gnathiids, suggesting that the maxillipedal setation of *Protognathia* is merely a reflection of segmental parallelism (or serial homology) in this animal and not a homologous synapomorphy shared with the gnathiids. Finally, gnathiids have but 5 pairs of walking legs, 6 free pereonites, 2 pairs of maxillipeds, and numerous other fundamental differences that suggest no close alliance whatsoever to *Protognathia*.

The above evidence forces us to conclude that *Protognathia* shares no synapomorphies with the Gnathiidea. Our phylogenetic analysis corroborates these arguments and further suggests that *Protognathia* is part of the cymothoid-line. The mandibles of *Protognathia* and *Anuropus* are enlarged and have similar 'articulations', being oriented more transversely and ventrally than in most isopods, suggesting a possible close affinity between these two groups. The large size of the pelagic *Protognathia* manca is also suggestive of *Anuropus*, which may attain an adult size in excess of 70mm (a 6.6–13.0mm manca could fit within an anuropid developmental sequence). Better resolution of protognathiid affinities must await the capture of adults of this group. Certainly Wägele and Brandt's (1988) claim that *Protognathia* is a 'surviving primitive isopod' is not correct; in both Wägele's (1989a) and our own tree, this taxon derives high up in the flabelliferan line.

Status of the Flabellifera

Our analysis corroborates the hypothesis of Wägele (1989a) and others that the Flabellifera, as it is currently recognised by most workers, is not a monophyletic taxon. The Anthuridea, Gnathiidea, and Epicaridea appear to derive from within the flabelliferan complex. However, the two suborders proposed by Wägele, Cymothoida and Sphaeromatidea, are not supported by our analysis.

Poore's (1987) proposed sister group relationship between the Lynseiidae and the Limnoriidae is corroborated by our analysis. The unusual South Pacific genus *Hadromastax* is currently placed in the family Limnoriidae. However, as Bruce (1988) noted, it appears to lack two key limnoriid attributes — a waisted maxillipedal basis and hook-like uropodal rami. Bruce and Müller (pers. comm.) plan to remove this genus to its own family. However, judging by the mandibular anatomy and other features, *Hadromastax* appears to be very closely related to the Limnoriidae/Lynseiidae clade.

The close relationship shown in our cladogram between Gnathiidea and Epicaridea is interesting and suggests that the possible common ancestor of these two groups might have been a hematophagous parasite. In addition to the synapomorphies noted on the cladogram, only in these two groups of isopods are the digestive caeca reduced to a single pair (Strömberg, 1972). Strömberg (1967, 1971, 1972) also recognised close ties between epicarideans, gnathiids, and flabelliferans, based on embryological data. Wägele's (1989a) alliance of the Epicaridea with the Cymothoidae appears unjustified. He united these taxa on the basis of five characters. Two of these characters are incorrect — epicarideans are not protandric hermaphrodites (they are facultative hermaphrodites) and cymothoids do not have quadrate uropodal peduncles. The third character, 'adults parasitic', is unlikely to be a homologous feature because cymothoids are parasites only on fishes and epicarideans only on crustaceans. The remaining two characters are apparent convergences (discussed in the previous section) resulting from the parasitic lifestyle of these taxa — hooklike pereopodal dactyls and reduced antennae. Retaining the Epicaridea as a separate suborder (or infraorder) has the further distinct advantage of not compressing the broad diversity of this group into a single highly heterogeneous family, as proposed by Wägele (1989a).

Recognition of the close relationships within a cymothoid-line (Fig. 14) is not a new idea. Brusca (1981) analysed this relationship for four of these families, and Bruce *et al.* (1982) and Delaney (1989) elaborated on this. The cymothoid-line (Fig. 14) is primarily carnivorous, emphasising predation and scavenging early on (Cirolanidae and Anthuridea), then largely predation (Anuropidae, Corallanidae, and probably Protognathiidae), then obligate predation or temporary parasitism (Aegidae and Tridentellidae), and finally obligate hematophagous parasitism (Cymothoidae).

We did not postulate any synapomorphies for

the family Sphaeromatidae, although four possible ones exist: pleonites 1–2 free (primitively), pleonites 3–6 fused to telson (with 0–3 pairs of lateral incisions demarcating fused somites); uropodal endopod more-or-less fused to peduncle and immovable; at least some maxillipedal palp articles expanded into lobes; and, pleotelson vaulted, with pleopods held in chamber. In addition, in most sphaeromatid genera at least some pleopods bear pleats and unique sqamiferous tubercles. However, because this family is so large and poorly understood, it is unclear whether these features represent true synapomorphies, i.e. are primitive for the family. A cladistic analysis and taxonomic revision of the Sphaeromatidae is greatly needed.

Some flabelliferan groupings are not fully resolved in our tree, suggesting that some families may be paraphyletic or, more likely, that we have simply been unable to find satisfactory character suites to eliminate all polytomies. This does not, however, affect the basic structure of the tree, or the sister group relationships of the clades that depict the phylogeny of the group as a whole.

If the relationships in our tree (Fig. 14) are correct, the Flabellifera should be expanded to once again include the Anthuridea, Gnathiidea, and Epicaridea, or it should be split into several separate new groupings. However, because of the unresolved nodes we do not recommend a classificatory change in the Flabellifera at this time. There seems little doubt, however, that the anthurideans, gnathiids, and epicarideans are derived from deep within the currently recognised Flabellifera. Classifying these three groups within the Flabellifera is not, of course, a new idea. Indeed, Sars (1882) created the group 'Flabellifera' specifically for those isopods with tail-fans composed of lateral uropods and an elongate pleotelson (hence the name). Stebbing (1893), Sars (1897), Richardson (1905), Smith and Weldon (1923), Menzies (1962), Naylor (1972), and many others generally followed Sars' concept of Flabellifera, and included the anthurideans (and usually the gnathiids) in this group. Sars (1897) was quite correct in his summary of the situation nearly 100 years ago, when he stated, 'It is not easy to give any exhaustive diagnosis of this tribe (Flabellifera), as it comprises isopods of extremely different structure. The only essential character common to all the forms, is the relation of the uropods, which are ... lateral and arranged in such a manner as to form, with the last segment of the metasome, a caudal fan, similar to that found in some of the higher Crustacea, the shrimps and lobsters.' The only synapomorphy we can add to Sars' statement is the fact that a 3:4 functional pereopod grouping seems to have evolved in concert with the long-tailed condition, and shortly thereafter the blade-like mandibular molar process.

Unresolved Phylogenetic Problems

Although we recommend some taxonomic changes (see conclusions), we do not propose a new classification of the entire order at this time. We feel that our phylogenetic hypotheses are still not robust enough to do so — the precise phylogenetic placement of several groups cannot yet be resolved to our satisfaction. Specifically, the relationships of the 8 long-tailed clades depicted in the consensus tree (Fig. 14) remain somewhat enigmatic. We believe Wägele (1989a) was premature in proposing his radical new classification of the Flabellifera. Because the long-tailed clade represents what appears to be a clearly monophyletic and easily-recognised group, with correlated anatomical and ecological attributes, we suggest that classificatory recognition of this clade is warranted and desirable.

Other Possible Tree Topologies

Because many workers have emphasised a hypothetical cirolanid-like (or flabellifera-like) ancestor for the Isopoda, we built several alternative trees to compare to ours. Each of these alternative trees was analysed with the program MacClade, with the same data set used to construct our tree (Appendices I and II). Trees identical to our cladogram (Fig. 14), but with the Cirolanidae placed at the base, are 135 steps long. Trees with the entire long-tailed grouping placed at the base, rooted in the Cirolanidae are 135 steps long. Trees with the long-tailed line at the bottom, but otherwise with the taxa in that group arranged exactly in our tree are 131 steps long. All of these trees are longer and less parsimonious than the 16 shortest trees (129 steps) summarised in our consensus tree (Fig. 14). It should be noted that if trees just one step longer are included for consideration, it can require that several hundred to several thousand new and different tree arrangements be considered. Thus selection of the shortest tree, even if it is shorter by only one step, allows one to reject entire suites of alternative hypotheses. The ability to rule out these large suites of alternative trees is, of course, the strength of the method of logical parsimony.

Biogeographic Considerations

Our analysis suggests that the Phreatoicidea and Asellota derived early in the evolution of the Isopoda, and are the most primitive living isopod taxa. According to Wägele (1981, 1983b), the occurrence of some members of these two groups in fresh water suggests that their common ancestor was a freshwater form, and that perhaps the Isopoda as a whole arose in fresh water, the marine environment having been invaded later. A more reasonable view, however, considers multiple invasions of fresh water from ancient marine stocks. There are several good reasons to accept this second alternative. First, the invasion of freshwater habitats has obviously occurred many times in the past, as evinced by the many unrelated isopod taxa that live in these habitats today, representing at least some genera in every suborder except perhaps the Gnathiidea (in addition to phreatoicideans, asellotans, and microcerberids, freshwater species occur in at least the following genera: Calabozoidea (*Calabozoa*), among the Oniscidea, *Brackenridgia*, *Cantabroniscus*, *Mexioniscus*, *Typhlotricholigioides*, *Xilitloniscus*; among Anthuridea, *Cruregens*, *Curassanthura*, *Cyathura*, *Paranthura*; among Cirolanidae, *Anopsilana*, *Antrolana*, *Bahalana*, *Bermudalana*, *Cirolanides*, *Faucheria*, *Haptolana*, *Mexilana*, *Speocirolana*, *Sphaeromides*, *Turcolana*, *Typhlocirolana*; among Cymothoidae, *Artystone*, *Asotana*, *Braga*, *Lironeca*, *Nerocila*, *Paracymothoa*, *Philostomella*, *Riggia*, *Telotha*; among Sphaeromatidae, *Sphaeroma*, *Thermosphaeroma*; among Valvifera, *Austridotea*, *Idotea*, *Mesidotea*, *Notidotea*; among Epicaridea, *Probopyrus*; and many others).

Second, fossil evidence (Schram, 1970, 1974) indicates that the Palaeozoic phreatoicideans, which are nearly indistinguishable from modern taxa, lived in marine environments, not freshwater habitats. Modern Phreatoicidea and Asellota that live in freshwater are likely to be relics of a past time when these groups were diversifying and invading many different environments. Outgroup data also suggest that the Isopoda probably evolved in a marine environment, because amphipods, mictaceans, and tanaidaceans are all primary marine groups. The fossil record is very sparse for isopods. There are no known asellotan fossils. The oldest isopod fossils are phreatoicideans: *Hesslerella shermani* Schram, 1970, from middle Pennsylvanian marine deposits of North America; Permian fossils from several marine or brackish-water localities of Laurasia; and Triassic material from Australia (fresh water). Thus, although phreatoicideans are restricted today to freshwater habitats in South Africa, Australia, New Zealand, and India, they must have had a broad global marine distribution during the Paleozoic. A few flabelliferans and presumed epicarideans are known from Mesozoic strata, while oniscideans and valviferans have been found only in Tertiary (Oligocene) deposits.

Very few specific biogeographic relationships reveal themselves in an analysis at this level. However, there are two striking patterns that are evident. First is the strong Gondwanan ties of the long-tailed clade. Many of the long-tailed lines are strictly or primarily Southern Hemisphere in distribution: Keuphyliidae is known only from the Australian region; Bathynataliidae from the southern Indian Ocean and Australia; Plakarthriidae from the Southern Hemisphere; Phoratopodidae from southern Australia; the Valvifera is probably Southern Hemisphere in origin (Brusca, 1984); and species of Serolidae occur primarily in the Southern Hemisphere. In addition, the majority of species of Cirolanidae and Sphaeromatidae also are probably known from the Southern Hemisphere. Interestingly, the earliest derived Asellota not restricted to fresh water are also largely Southern Hemisphere in distribution (Pseudojaniroidea, Stenetrioidea, and the shallow-water Janiroidean families Paramunnidae and Santiidae).

Secondly, all of short-tailed lines on the cladogram show strong relictual patterns of distribution. The Phreatoicidea, which were once widespread globally in marine environments, are now restricted to a few Gondwanan freshwater habitats. The higher Asellota (Janiroidea) are found primarily in the deep sea, where they have undergone a massive radiation to exploit an environment only recently invaded by other isopod groups. The Microcerberidea are interstitial forms. The Calabozoidea so-far are known only from freshwater wells (phreatic systems) in Venezuela. And the Ligiamorpha and Tylomorpha are, of course, the only crustaceans to have successfully radiated into all terrestrial environments.

Beyond these generalisations, the data are not yet available to discern clear historical patterns or test specific biogeographical hypotheses at the subordinal/family levels. Testable phylogenetic and biogeographic analyses are needed for each suborder, and each of the long-tailed clades, in order to determine putative ancestral geographic ranges for each of these groups (*viz.* Brusca, 1984) before more general statements can be

made regarding the biogeographic history of the Isopoda.

Future Research

Despite an extensive examination of available morphological characters, it is clear that the available data base needs to be expanded by the addition of new characters and by resolution of homology complexes in others. Useful new characters almost certainly exist in patterns of frontal lamina and clypeus design, details of mandibular anatomy (especially of the lacinia and spine row region), oostegite morphology, nature of the sternal coxal plates, and internal anatomy, but the existing literature is insufficient to assemble a data base on such features and additional direct observations are necessary. These data will be needed to further resolve the relationships within the long-tailed isopod clade. A phylogenetic analysis of the Sphaeromatidae is also needed and would provide valuable information for continued refinement of the flabelliferan taxa.

CONCLUSIONS

1. The Isopoda is a monophyletic group defined by the following synapomorphies: (a) sessile eyes; (b) complete loss of free carapace folds (carapace reduced to a cephalic shield); (c) thoracopods entirely uniramous; (d) antennae uniramous, without a scale (a 'scale' has either reappeared in the Asellota, or it was lost twice, once in the Phreatoicidea and again in all other non-Asellota); (e) pleomere 6 fused to telson, forming a pleotelson; (f) biphasic moulting; (g) heart thoraco-abdominal; (h) branchial structures abdominal; (i) gut tube entirely ectodermally derived, without a true midgut region; (j) striated muscles with unique myofibril ultrastructure; (k) loss of the maxillulary palp; (l) antennules uniramous, without a scale (scales reappear in the cirolanid genus *Bathynomus*, in the Limnoriidae, and perhaps in the Epicaridea); and, (m) uropodal rami always uniarticulate. Synapomorphies 'a–d' appear to be convergent in isopods and amphipods, although a strong corroboration of this must await further analyses of all peracarid suborders. Synapomorphy 'e' may (or may not) be convergent to the condition in many tanaidaceans. Synapomorphies 'f–m' are unique to the Isopoda.

2. The Phreatoicidea is the earliest derived taxon of living isopods.

3. The Microcerberidea is the sister group of the Asellota, but cannot be considered part of the Asellota unless the definition of the latter is expanded, which we do not recommend at this time.

4. The Oniscidea constitutes a monophyletic group.

5. The monotypic taxon Calabozoidea (*Calabozoa*) should be classified as primitive Oniscidea, or as the sister group of the Oniscidea (*Calabozoa* is neither an asellotan nor a sister group of the Asellota).

6. Isopods with broad, flat uropods and elongate telsonic regions (well-developed tailfans) arose subsequent to the appearance of the phreatoicid/asellote/microcerberid/oniscidean lines. The apparent 'caridoid'-like tailfan of these long-tailed isopods is thus not a primitive isopod feature, but is secondarily derived within the Isopoda and not homologous with the condition seen in the mysidaceans and other true caridoid crustaceans.

7. The evolution of the long-tailed morphology may have corresponded with the emergence of isopods from infaunal environments and a subsequent radiation as active epifaunal swimmers. Paralleling this trend was a shift from a primary scavenging/herbivorous lifestyle to active predatory habits, and eventually parasitism. Also paralleling this trend was an enlargement of the lateral coxal plates, perhaps functioning to increase hydrodynamic streamlining of the body.

8. Three taxa usually ranked at the subordinal level (Anthuridea, Gnathiidea and Epicaridea) had their phylogenetic origins within the lineage of families currently regarded as Flabellifera. Thus, the definition of Flabellifera must either be expanded to accommodate these taxa, and/or the suborder Flabellifera should be reorganised into several separate groups.

9. The Protognathiidae is part of the 'cymothoid-group' of families and may be closely related to the families Cirolanidae and Anuropidae. The Protognathiidae is not the sister group of the Gnathiidea.

10. The recently proposed new suborders of Wägele (1989a), Sphaeromatidea and Cymothoida (*sic*), are not corroborated by our phylogenetic analysis. Wägele's proposition that the ancestral isopod was a long-tailed form (flabelliferan, or cirolanid-like) is not supported by our analysis. Our analysis indicates that the ancestral isopod was a short-tailed form, with a shortened telson and styliform, terminal uropods. The Gnathiidea and Epicaridea should be retained at the subordinal ranking until further analyses bet-

ter resolve the relationships of the flabelliferan families.

11. All of the primitive, short-tailed isopod taxa (Phreatoicidea, Asellota, Microcerberidea, Oniscidea, Calabozoidea) exhibit what may be viewed as relictual distributions, in isolated freshwater habitats, in ground waters, in the deep sea, or in terrestrial habitats. The most primitive living isopods, the Phreatoicidea, also have the oldest known fossil record (middle Pennsylvanian) and a modern Gondwanan distribution (Australia, Tasmania, New Zealand, southern Africa, and India). However, fossil phreatoicids are known from North American and European marine deposits, suggesting that the present-day freshwater Gondwanan pattern is a relict distribution.

12. Unambiguous sister group relationships cannot be hypothesized for all isopod taxa with the current data base, and additional data are being sought in the form of new characters. A new formal classification of the Order Isopoda must await better resolution of the phylogeny based upon an expanded data set.

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APPENDIX 1. CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS

1. Eyes stalked and basally articulated (0) — Eye stalks reduced, lobe-like, but sometimes with basal articulation (1) — Eyes sessile (2).
2. Carapace covers all 8 thoracomeres and laterally covers the bases of the maxillae and maxillipeds (0) — Carapace reduced, lateral carapace folds still cover the bases of the maxillae and maxillipeds (1) — Carapace reduced to only a head shield, without lateral carapace folds (2).
3. Monophasic moulting (0) — Biphasic moulting (1).
4. Heart entirely thoracic (0) — Heart thoraco-abdominal (1).
5. Branchial structures cephalo-thoracic (0) — Branchial structures abdominal (1).
6. Pleomeres 4–6 not divided into two separate functional units (0) — Pleomeres 4–6 forming a functional unit (the urosome), and pleopods 4, 5, and 6 modified as uropods (1).
7. Body not unusually broadened and flat (0) — Body extremely broadened and flat, with large, expanded coxal plates, and with the cephalon deeply immersed in or surrounded by the first pereonite (1).
8. Gut tube with endodermally derived midgut (0) — Gut tube entirely ectodermally derived, without a true midgut region (1).
9. Striated muscles of typical malacostracan type (0) — Striated muscles with unique myofibril ultrastructure (1).
10. Second thoracomere (pereonite 1) free, not fused to cephalon (0) — Second thoracomere entirely fused to cephalon, with its appendages (the pylopods) functioning with the cephalic appendages and acting as a second pair of 'maxillipeds' (1).
11. At least some thoracopods with exopods (0) — Exopods absent from all thoracopods (1).
12. Hatching stage not a manca (0) — Hatching stage a manca (1).
13. Without a praniza stage (0) — With a praniza stage (1).
14. Adult females bilaterally symmetrical (0) — Adult females with loss of symmetry (1).
15. Adults not parasitic on other crustaceans (0) — Adults obligate parasites on other crustaceans (1).
16. Without cuticular tricorn sensilla (0) — With cuticular tricorn sensilla (1).

17. Without complex compound sensillar structures of the oniscidean type at the tips of the antennae and uropodal rami (0) — Complex compound sensillar structures at the tips of the antennae and uropodal rami (1).
18. No functional pereopodal grouping (0) — Functional pereopodal grouping 3:4 (1) — Functional pereopodal grouping 4:3 (2) — Functional pereopodal grouping 2:5 (3).
19. Seventh pereonite present and with pereopods (0) — Seventh pereonite reduced and without pereopods (1).
20. Antennule biramous, or with scale (0) — Antennule uniramous, without scale (1).
21. Antennular peduncle 3-articulate with an undivided third article (0) — Antennular peduncle 4-articulate, presumably by way of subdivision of third article (1).
22. Antennules arise above (anterodorsal to) antennae (0) — Antennules arise on same plane as antennae, directly between them (1).
23. Antennules not as described in the following (0) — Antennules greatly modified, 2-articulate, with second (distal) article greatly expanded and scalloped (1).
24. Antennal peduncle 6-articulate (0) — Antennal peduncle 5-articulate (1).
25. Antennae biramous, or with a vestigial second ramus or scale (0) — Antennae uniramous, without vestigial second ramus or 'scale' (1).
26. Antennae well developed (0) — Antennae vestigial (1).
27. Mandible without lamina dentata (0) — Mandible with lamina dentata (1).
28. Mandibles 'normal' (0) — Mandibles of adult males grossly enlarged, projecting anteriorly, forceps-like (1).
29. Mandibles present in adult females (0) — Mandibles lost in adult females (1).
30. Molar process of mandible a broad, flat, grinding structure (0) — Molar process of mandible an elongate, thin, blade-like, slicing structure (often attached to body of mandible by a flexible 'articulation', and often bearing marginal denticles or teeth) (1) — Molar process of mandible absent (2).
31. Maxillule present (0) — Maxillule reduced or vestigial in adults (1) — Maxillule lost in adults (2).
32. Maxillule with a palp (0) — Maxillule without a palp (1).
33. Maxillae not fused to paragnath (0) — Maxillae reduced, minute, fused to paragnath (or lost entirely) (1).
34. Maxillae outer lobe undivided (0) — Maxillae outer lobe divided into two lobes (1).
35. Mandible with a palp (0) — Mandible without a palp (1).
36. Maxillae not modified as follows (0) — Maxillae modified into stylet-like lobes with recurved apical (hooklike) setae (1).
37. Maxillipeds separate (0) — Left and right maxillipeds fused together (1).
38. Coxae of maxillipeds not fused to head (0) — Coxae of maxillipeds fused to head (1).
39. Maxillipedal endite without coupling spines (0) — Maxillipedal endite with coupling spines (1).
40. Head sunk into first pereonite, flexing dorsoventrally but not freely rotating (left to right) (0) — Head set off from pereon and freely rotating (1).
41. Maxillipeds with 2–3 endites (0) — Maxillipeds with only 1 endite (1).
42. Maxilliped biramous (0) — Maxilliped uniramous (1).
43. Without lateral coxal plates (0) — With lateral coxal plates (1).
44. Basis of maxilliped not elongate and waisted (0) — Basis of maxilliped elongate and waisted (1).
45. With lateral epipods on pereopods (0) — Without lateral epipods on pereopods (1).
46. Without medial epipods on pereopods (0) — With medial epipods on pereopods (1).
47. No special cuticular spermathecal ducts known to occur (0) — Unique spermathecal cuticular organs present (1).
48. Male penes on coxae (0) — Male penes on sternite (1).
49. Penes on thoracomere 8 (0) — Penes on pleomere 1, or on the articulation between thoracomere 8 and pleomere 1 (1).
50. Mandibular incisor process broad and multidentate (0) — Mandibular incisor process with teeth reduced to form serrate or crenulate margin (1) — Mandibular incisor process with teeth lost (or fused ?) to form conical projection with basal 'rasp and file' (2) — Mandibular incisor process modified into recurved or hooklike, acute or subacute, piercing-slicing structure (3).
51. Embryos curve ventrally (0) — Embryos curve dorsally (1).
52. Primary adult excretory organs are antennal glands (0) — Primary adult excretory organs are maxillary glands (1).
53. With narrow, multisegmented pleopodal rami (0) — With broad, flat, 1- or 2-articulate pleopodal rami (1).
54. Male pleopods 1 and 2 not as follows (0) — Male pleopod endopods 1 and 2 (only 2 in Ligiidae) elongate, styliform, and participating together in the copulatory process (1).
55. Uropods arise from anteroventral margin of

pleotelson (0) — Uropods arise on posteroventral surface of pleotelson, in shallow grooves or channels (1).

56. Both pleopodal rami thin and lamellar (0) — Pleopodal exopods broad and opercular; endopods thick and tumescent (1).
57. Uropods broad and flattened (0) — Uropods styliform (1).
58. Telsonic region of pleotelson well-developed, with anus and uropods at the position of pleomere 6 (at the base of pleotelson) (0) — Telsonic region greatly reduced and shortened, anus and uropods positioned terminally on pleotelson (1).
59. Uropodal rami multiarticulate (0) — Uropodal rami always uniarticulate (1).
60. Uropodal exopod not folded dorsally over pleotelson (0) — Uropodal exopod folded dorsally over pleotelson (1).
61. Uropods not modified as follows (0) — Uropods modified as a pair of opercula covering entire pleopodal chamber (1).
62. Uropods not modified as follows (0) — Uropods form ventral operculate chamber covering anal region (1).
63. Uropods unlike pleopods; associated with pleotelson (0) — Uropods directed ventrally; identical to, and functioning with, pleopods (1).
64. Pleomere 6 freely articulating with telson (0) — Pleomere 6 fused with telson, forming a pleotelson (1).
65. Pereopods 2–7 not prehensile (0) — Pereopods 1–3 (or 1–7) prehensile (1).
66. Adults not obligate and permanent parasites on fishes (0) — Adults obligate and permanent parasites on fishes (1).
67. Uropodal endopods not claw-like (0) — Uropodal endopods claw-like (1).
68. Uropodal exopods not claw-like (0) — Uropodal exopods claw-like (1).
69. Pereonite VII not as follows (0) — Pereonite VII tergite indistinct dorsally, shortened and largely or entirely fused to pereonite VI (1).
70. Pleopod 5 not reduced to a single plate (0) — Pleopod 5 reduced to a single plate (1).
71. Uropods not modified as follows (0) — Uropods modified as elongate, clavate structures with reduced rami (1).
72. Apex of pleotelson not curved dorsally (0) — Apex of pleotelson curved dorsally (1).
73. Pleomere 5 not markedly elongate and much longer than all others (0) — Pleomere 5 markedly elongate, manifestly longer than all other pleomeres (1).
74. Medial margin of maxilla with row of large filter setae (0) — Medial margin of maxilla without row of large filter setae (1).
75. Female pleopod 2 biramous (0) — Female pleopod 2 uniramous (1).
76. Male pleopod 2 not as follows (0) — Male pleopod 2 exopod modified to function in concert with large geniculate endopod in sperm transfer (1).
77. Exopods of at least posterior pleopods biarticulate (0) — No pleopods with biarticulate exopods (1).
78. Female pleopod 1 present (0) — Female pleopod 1 absent (1).
79. Male pleopod 2 with lamellar exopod (if present) and endopod either lamellar or modified (0) — Male pleopod 2 with small non-lamellar exopod and a large endopod modified into a complex gonopod (1).
80. Pleomeres not as follows (0) — Pleomeres 1 and 2 free, 3–5 always entirely fused to pleotelson (1).
81. Male pleopod 1 biramous, lamellar (0) — Male pleopod 1, if present, uniramous (fused and working with pleopod 2 in sperm transfer in higher Asellota) (1).
82. Female pleopod 2 present (0) — Female pleopod 2 absent (1).
83. Female pleopod 3 biramous, not fused into a single piece (0) — Female pleopod 3 uniramous and fused into a single piece forming an operculum over pleopods 4 & 5 (1).
84. Male pleopod 2 not as follows (0) — Male pleopod 2 exopod reduced to a simple, 1- or 2-articulate ramus, apparently not involved in copulation or sperm transfer; endopod complex and highly variable in shape, straight, curved, or slightly bent (but not fully geniculate) (1).
85. Lateral coxal plates 2–7 (if present) fused to their respective pereonites and not articulating (0) — Lateral coxal plates 2–7 (if present) not entirely fused to their respective pereonites (1).
86. Pleomeres 1 & 2 not reduced to sternal plates (0) — Pleomeres 1 & 2 reduced to sternal plates only (1).
87. Uropodal rami free (0) — Uropodal rami fused to peduncles (1).
88. Posterior pereopods 'normal' (0) — Posterior pereopods oar-like, with dactyls greatly reduced or absent (1).
89. Body not as follows (0) — Body deeply inflated (1).
90. Not parasites on gelatinous zooplankton (0) — Parasites on gelatinous zooplankton (1).
91. Mandibles not modified as follows (0) — Mandibles modified as elongate scythe-like structures with serrate cutting edge (l).
92. Maxillule not as follows (0) — Maxillule of a single elongate stylet-like lobe, with the apex forming an acute recurved piercing stylet (1).

APPENDIX II. THE DATA MATRIX

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Mysidacea      0000000000 0000000000 0000000000 0000000000 0000000000 0000000000
  0000000000 0000000000 0000?00000 00
Mictacea       11?0000??0 0100000300 0001000000 0101000010 1100100000 1?1000?000
  0000000000 000000?000 0000?00000 00
Tanaidacea     1100000100 0100000200 0000000000 0001000010 1100100100 1110001100
  0000000000 0000000000 0000?00000 00
Amphipoda      2200010000 1000000200 0001100000 0000001000 0110110100 0000001000
  0000000000 0000000000 0000100000 00
Phreatoic.     2211100110 1100000201 0001100000 0101000010 1100100000 1110001110
  0001000000 0110000000 0000?00000 00
Valvifera      2211100110 1100000101 0001100000 0101000010 1110100110 1110000010
  1001000000 0001001000 0000000000 00
Epicaridea     2211100110 1101100100 0001110002 210?100010 1110100102 1110000010
  0001100000 0001001000 0000000000 10
Gnathiidea     2211100111 1110000111 0001100112 110?100010 1110100102 1110000010
  0001000000 0001001000 0000000000 10
Anthuridea     2211100110 1100000101 0001101001 011?000100 1110100100 1110000011
  0001000000 0001001000 0000000000 00
Tylomorpha     2211100110 1100011?01 ?101100000 0101100000 1110100110 1111010110
  0101000000 0001001000 0000000000 00
Ligiamor.      2211100110 1100011?01 ?101100000 0101100000 1110100110 1111011110
  0001000000 0001001000 0000000000 00
Asellota       2211100110 1100000201 0000000000 0101000010 1100101100 1110001110
  0001000000 0001110111 1000?00000 00
Calabozo.      2211100110 1100010201 0?01100000 0101100000 1110100110 1111011110
  0001000000 0001001000 0000011000 00
Microcerb.     2211100110 1100000201 0000100000 010?000000 1100100100 1110001110
  0001000000 0001001111 1111?00000 00
Aegidae        2211100110 1100000101 0001100001 010?010000 1110100103 1110000010
  0001100000 0001001000 0000000000 00
Anuropidae     2211100110 1100000101 0011100001 010?0000?0 1110100103 1110000010
  0011000000 0001001000 0000000011 00
Bathynat.      2211101110 1100000101 ?001100002 0101000010 1110100100 111010?010
  0001000000 1001001000 0000100000 00
Cirolanid.     2211100110 1100000010? 000?100001 0101000010 1110100100 1110000010
  0001000000 0001001000 0000000000 00
Coralland.     2211100110 1100000101 0001100001 010?010000 1110100103 1110000010
  0001000000 0001001000 0000000000 01
Cymothoid.     2211100110 1100000101 ?001100001 010?010000 1110100103 1110000010
  0001110000 0001001000 0000000000 00
Keuphylid.     2211101110 1100000010? 0001100002 0101100010 1110100101 1110100010
  0001001000 0001001000 0000100000 00
Limnoriid.     2211100110 1100000100 000?100002 010?000011 1111100102 111000?010
  0001000100 0011001000 0000000000 00
Lynseiidae     2211100110 1100000101 0001100002 0101100001 1111100102 1110000010
  0001000001 0001001000 0000000000 00
Phoratopd.     2211100110 1100000101 1001100001 0101000010 1110100102 1110000010
  0001000000 0001001000 0000000100 00
Plakarth.      2211101110 1100000?01 0001100002 010?000000 1110100101 1110100010
  0001000000 0001001000 0000100000 00
Protognat.     2211100110 1100000101 000?100001 010?000000 1110100??3 1110000010
  0001000000 0001001000 0000000000 00
Serolidae      2211101110 1100000101 1001100002 0101000000 1110100101 1110?00010
  0001000010 0001001000 0000?00000 00
Sphaeromt.     2211100110 1100000101 0001100000 0101000010 1110100100 1110000010
  0001000000 0001001000 0000000000 00
Tridentll.     2211100110 1100000101 0001100001 010?010010 1110100103 1110000010
  0001000000 0001001000 0000000000 00
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APPENDIX III

Synapomorphies of terminal taxa. Note: this is not an exhaustive list of synapomorphies unique to each terminal taxon; it is a list of only those present in the data set used for the current analysis (see Methods section and Appendix I). Reversals and multi-state character changes are indicated by parentheses.

Anthuridea: 27, 33, 38, 39(0), 60.
Anuropidae: 23, 63, 89, 90.
Asellota: 24(0)[?], 47, 75, 76.
Bathynataliidae: 71.