# Higher classification of the flabelliferan and related Isopoda based on a reappraisal of relationships

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*Abstract.* The history of the systematics of isopod suborders is summarised. Several authors have suggested that the traditional suborder Flabellifera is paraphyletic and includes one or more of the suborders Gnathiidea, Epicaridea and Anthuridea. Two suborders, Cymothoida and Sphaeromatidea, have been proposed as replacement taxa for the Flabellifera, but it has not been possible on the basis of phylogenetic analyses to elucidate significant relationships between the suborders and families. Morphological characters are used to explore relationships between 35 genus-, family- and suborder-level taxa of flabelliferan Isopoda in a cladistic analysis (using Phreatoicidea and Asellota as outgroups) and to derive a new classification. The analysis did not find a synapomorphy for 'Flabellifera' *sensu lato*, but recognises two diverging clades of 'long-tailed' isopods. Members of the Oniscidea are not part of either clade. Nor is the Tainisopidea, a new suborder erected for members of the family Tainisopidae. The Tainisopidea has many synapomorphic and plesiomorphic features, but does not share characters with either clade. The first clade comprises Phoratopidea (for *Phoratopus remex*) and sister-taxa Cymothoida and Limnoriidea. Representatives of these suborders have uropodal rami ventral to the pleotelson and articulating from side-to-side inside the branchial space. The new suborder, Phoratopidea, is for one species with unique, broad articles of pereopods 3 and 4 with reduced dactyls. It lacks the synapomorphies of the following two suborders. In members of the suborder Cymothoida, the mandibular molar is either a flat triangular blade, reduced to a conical process, or absent, and the maxillipedal endite is rarely longer than palp article 1 (or is absent), distally tapering and has few setae. The suborder Limnoriidea is diagnosed as lacking the mandibular molar, and the non-tapering, slender (except in *Keuphylia*) maxillipedal endite reaches to at least the distal margin of palp article 4. Members of the second clade share a vaulted pleotelson enclosing a branchial chamber defined by ventrolateral ridges and uropods lateral to the pleotelson margin that fold down alongside the branchial space. It comprises two suborders. Members of the Sphaeromatidea have pleonite 1 much narrower than pleonite 2 and a reduced (or absent) right lacinia mobilis fused to the spine row. They lack operculiform uropods, which characterise Valvifera. The suborder Anthuridea is reduced to superfamily rank and Epicaridea is reduced to two superfamilies within Cymothoida. Unambiguous relationships between most families are resolved, but Sphaeromatidae is suspected to be paraphyletic, *Paravireia* is placed as the most plesiomorphic of the Sphaeromatoidea and a new family, Basserolidae, is proposed. The Tainisopidea includes freshwater taxa in a relictual environment. The sole species of Phoratopidea is marine, rare, and its ecology is unknown. The Cymothoida is most diverse in tropical regions. Members of the most plesiomorphic family, the Cirolanidae, are mobile predators or scavengers and the more derived families are ectoparasites on fishes and other crustaceans. Members of the Limnoriidea are mainly tropical and at least one family is herbivorous. The Valvifera and Sphaeromatidea are benthic, with respiratory pleopods in a branchial chamber. They are most diverse in the temperate southern hemisphere, and most are detritivores.

## Introduction

In the traditional higher classification of the Crustacea Isopoda, ten suborders are recognised: Asellota Latreille, 1802, Oniscidea Latreille, 1802, Epicaridea Latreille, 1831, Flabellifera Sars, 1882, Valvifera Sars, 1882, Phreatoicidea Stebbing, 1893, Gnathiidea Hansen, 1916, Anthuridea Monod, 1922, Microcerberidea Lang, 1961 and Calabozoidea Van Lieshout, 1983. Few modern taxonomists believe that these reflect a natural grouping of component families, but Martin and Davis (2001), who briefly discussed unsuccessful attempts at attaining a more natural classification, were forced to resort to the traditional arrangement. The

disquiet of modern writers is reflected in views expressed in the nineteenth and early twentieth centuries. For example, authors generally placed the families Anthuridae Leach, 1814 and Gnathiidae Leach, 1814 within the Flabellifera (Sars 1882, 1897; Beddard 1886; Stebbing 1893; Richardson 1905).

Hansen (1916) proposed that Gnathiidae deserved a rank equivalent to that of Flabellifera and other suborders. Monod (1922) went further and classified the Isopoda into two subdivisions: Decempedes (for Gnathiidea alone) and Quatuordecempedes. The latter he divided into the two sections used by Bate and Westwood (1868), Aberrantia (which he renamed Anthuridea) and Normalia to include Asellota, Valvifera, Flabellifera, Epicaridea, Oniscidea and Phreatoicidea. Curiously, Monod's (1922) 'schémas', illustrated in a phylogenetic tree, show that he believed Anthuridea and Gnathiidea to be sister-taxa (to use modern parlance), Oniscidea and Asellota to be sister-taxa, and Flabellifera at the base of a third clade leading to Epicaridea and Valvifera. His classification was, therefore, not intended to reflect relationships.

Monod's views have not been universally accepted, although contrary opinions have not been argued on phylogenetic grounds. For example, Hurley (1961), Hurley and Jansen (1977) and Menzies (1962a) included Anthuridae (at superfamily level) within Flabellifera, but excluded Gnathiidea and Epicaridea.

Sars (1882) distinguished the Flabellifera from the other Isopoda by the possession of lateral or anterolateral uropods that form a tailfan with the pleotelson, similar to that found in other higher crustaceans, e.g. shrimps and lobsters (Sars, 1897: 43). All other Isopoda are characterised by styliform, terminal uropods. Anthuridae and Gnathiidae were considered by Sars (1897) to belong in the Flabellifera because these were also characterised by a tailfan. Strömberg (1972) discussed the isolation of Asellota, Phreatoicidea and Valvifera and the close alliance between flabelliferans and gnathiids, and their less close alliance with Anthuridea and Epicaridea, on the basis of morphological and palaeontological evidence. His embryological studies revealed very little about relationships. He remained uncertain about the position of Oniscidea.

Division of the more free-living flabelliferans into two groups was part of the classification of Menzies (1962a), who recognised the superfamilies Seroloidea and Cirolanoidea. Hurley and Jansen (1977) followed Menzies's classification, but accepted Monod's terminology. Their Seroloidea included only Serolidae, and Cirolanoidea included Plakarthriidae, Sphaeromatidae, Limnoriidae, Cirolanidae, Aegidae and Cymothoidae.

In the conclusion to his review of the Anthuridea, Wägele (1981) summarised 17 of the trees of relationships between isopod families and suborders presented in the literature up to that time. He argued that the tailfan is a plesiomorphic character for the Isopoda and, in his opinion, retained in those taxa for which fast escape reactions by ventral beats of the pleotelson are crucial, and that the tailfan is important for steering. He therefore supposed that the most ancient isopod possessed a tailfan and was probably more similar in this regard to the Flabellifera than to the Asellota (Wägele 1981: 96). As many Eumalacostraca are adapted to a benthic lifestyle, Wägele concluded in a later contribution (1989) that the tailfan could not be a synapomorphy of the Flabellifera and would be of little value to benthic taxa. Wägele used as evidence the diverse forms the uropod takes, for example, styliform in Asellota and Oniscidea, operculiform in Valvifera, and with a dorsal exopod in Anthuridea (Wägele 1981: 102). As the monophyly of the Flabellifera was not revealed in his later phylogenetic treatment, Wägele (1989) replaced it with two suborders, the Sphaeromatidea Wägele, 1989 and Cymothoida Wägele, 1989. These are similar to Menzies's (1962a) superfamilies Seroloidea and Cirolanoidea respectively. The relationships between Cymothoida, Sphaeromatidea, Anthuridea and Valvifera could not be decided by Wägele. Roman and Dalens (1999) did not discuss the composition of the Flabellifera, but followed the classification proposed by Wägele (1989).

Brusca and Wilson (1991) also reviewed the history of isopod systematics and summarised four competing cladograms in one figure. They showed convincingly that Flabellifera is paraphyletic on the basis of a cladistic analysis of all Isopoda using mostly family-level taxa and other peracarids as outgroups. Their cladogram was less resolved than that of Wägele (1989). Their paper was criticised by Wägele (1994b), who believed their data matrix to contain errors and misinterpretations, and problems that he thought were due to the application of computer cladistics. Wägele's paper was, in turn, rebutted by Wilson (1996), who attempted to justify cladistic methodology in the face of Wägele's (1989) 'Hennigian' groundpattern approach. In his summaries of isopod phylogeny, Wilson (1998, 2003) concluded that the Flabellifera *sensu lato* is a monophyletic clade including the families originally listed plus Valvifera, Anthuridea, Gnathiidea, and Epicaridea. Throughout this paper we use the term 'flabelliferan' is this broader sense.

The use of molecular genetics in an attempt to resolve isopod higher relationships has had limited success to date. Wetzer (2002) explored the use of *12S* and *16S* rRNA and *COI* mitochondrial genes separately, and in combination. Conflicting trees were found for 11 and 18 taxa; the most promising results were that valviferans had a sphaeromatid ancestor, and that oniscideans and sphaeromatids may be more closely related than previously thought. Michel-Salzat and Bouchon's (2002) analysis of mitochondrial LSU rRNA provided some support for Wetzer, but had anomalous results. They found Oniscidea (as represented by nine families) to be polyphyletic, with *Tylos* and *Ligia* related to *Idotea* and *Sphaeroma*, although most of the others, Crinocheta, were in

a monolithic clade. They discovered a relationship between *Idotea* (Valvifera) and *Sphaeroma* (Sphaeromatidae), but a second sphaeromatid genus was far removed. The only cirolanid in their analysis seemed related to the oniscidean, *Ligidium.* Dreyer and Wägele (2002) proposed a new taxon of unspecified rank, Scuticoxifera, on the basis of genetic analysis of nuclear *18S* SSU rRNA. This monophyletic group was supported by a reappraisal of morphological characters in an earlier paper (Dreyer and Wägele 2001). The Scuticoxifera comprises Oniscidea, Valvifera, Sphaeromatidea (*sensu* Wägele, 1989), Anthuridea, and Cymothoida (including Bopyridae or Epicaridea). The apomorphic state of coxae 1–7 (transformed into plates that are in contact with the entire length of the tergite) unites the taxon. Also, the anterior filter channels of the stomach of Scuticoxifera are derived, curving laterally, or in a transverse position (except in anthurideans; Wägele 1989). Dreyer and Wägele's supplementary morphological treatment added few new characters to those used by Wägele (1989), and the additional molecular data failed to further resolve relationships of the higher Isopoda. They, like Strömberg (1972), Wägele (1989) and Brusca and Wilson (1991), agree that Asellota, Phreatoicidea and Oniscidea are stem taxa of the Isopoda, but '….the unresolved relationships within the Scuticoxifera possibly indicate the occurrence of a rapid radiation, followed by a long period of divergent evolution of those groups that are now classified as suborders' (Dreyer and Wägele 2002).

In spite of the attention that has been paid to discovering relationships between what appear to be robust monophyletic families, the current practical classification does not reflect the emerging phylogeny. Tabacaru and Danielopol (1999) were not able to resolve the issue with their analyis of morphological characters because they treated the Flabellifera as monophyletic when all the evidence indicates otherwise.

Our experience with many families of flabelliferan Isopoda led us to question some of the characters used by Wägele (1989) and Brusca and Wilson (1991). We suspected some character states were misinterpreted. We also discovered new characters of apparent phylogenetic significance and believed it worthwhile to tackle the problem again. Our objective is to present a credible hierarchy of the flabelliferan and related Isopoda at the levels of suborder and superfamily. We do this by presenting the results of a cladistic analysis using external morphological characters.

## Methods

### Taxa chosen

Phylogenetic (cladistic) methods were used to generate cladograms as hypotheses of the relationships of flabelliferan and related isopod taxa. Typical species are illustrated in Figures 1 and 2. Implicit in most analyses carried out so far, and in many of the earliest classifications, is the paraphyly of the flabelliferans and the fact that some other suborders are derived from within it. The only exception is the analysis of Tabacaru and Danielopol (1999). We have, however, assumed the

monophyly of most families traditionally placed in Flabellifera, but for some this is doubtfully the case. For this reason we represented some families, such as the Sphaeromatidae and relatives, by more than one species. This strategy falls far short of resolving a family-level hierarchy, for the Sphaeromatidea in particular. This we leave for future study, including a more complete representation of genera. The monophyly of Sphaeromatidae genera is far from certain. Our interest was the relative phylogenetic position of the Sphaeromatidae and other families within the Sphaeromatidea. We have not reappraised the generally agreed stem positions of Asellota or Phreatoicidea, thought by Wilson (1998) to be sister-taxa. Instead, we treat them as outgroups.

The taxa, therefore, are a mixture of species, genera and higher-order groups. For most, a single species can be chosen to represent the taxon and these are listed in Appendix 1. Appendix 1 also lists some of the literature consulted and museum collections where specimens that we examined can be found. For the characters considered, any one of numerous species within a taxon might have been chosen without affecting the result; many species were referred to in the literature or collections. Of the suborders, there seems little doubt that the Gnathiidea (Gnathiidae) are monophyletic (Cohen and Poore 1994) and are represented in our new analysis by a single 'taxon', the praniza larva. Adults are too modified to provide comparable characters. Among the many gnathiid synapomorphies are: the praniza juvenile transforming to very different male and female forms; the mandibles are massive and project in males, and are absent in adult females; the pylopod (pereopod 1); and the narrow, tapering uropodal rami.

Similarly, the Valvifera (11 families) are undoubtedly monophyletic (Poore 2001*a*) and can be best exemplified by a species such as *Idotea metallica* Bosc, 1802. Other valviferans have a more plesiomorphic pleonal condition than this species. In all Valvifera, the uropod articulates laterally; its peduncle and short rami enclosing the pleopods in a branchial chamber.

The Anthuridea comprise the Hyssuridae and their sister-taxa, another five families (Poore 2001*b*). Although there is considerable morphological diversity among anthurideans, all share at least: an elongated, cylindrical body without expanded coxal plates; the mandibular spine row fused to a lamina dentata; molar a conical or blunt corneous process, or absent; maxilla 2 fused to the hypopharynx; pereopods 1–3 propodi subchelate; and uropodal exopod proximal and more or less folding over the pleotelson and endopod distal. No single species best represents the Anthuridea. *Belura pillara* and *Kupellonura biriwa* share many plesiomorphic characters (Poore and Lew Ton 1988) and alternative states were entered in the matrix.

The Bopyridae were chosen to represent the 11 families of the Epicaridea, but these isopods are so derived that their monophyly cannot be guaranteed on morphological grounds. Phylogenetic relationships between the families have never been investigated and their definition is based as much on host preference as on morphology. However, potential synapomorphies include the free-swimming cryptoniscid larva, and pleopods and uropod reduced or modified as arborescent branchiae. The epicaridean larval stage best represents the most plesiomorphic condition of Bopyridae (see Trilles 1999 for a modern description).

For small flabelliferan families of undisputed monophyly, single species were chosen for inclusion (see Appendix 1). Thus, the following families are known from only one genus and one or few species:

Anuropidae (*Anuropus* Beddard, 1886, 11 spp.) (Kensley and Chan 2001; Brandt and Retzlaff 2002), whose antenna 1 is greatly modified, antenna 2 is articulate, with the second article greatly expanded and scalloped, and whose uropod is pleopod-like.

Phoratopodidae (*Phoratopus remex* Hale, 1925) (Bruce 1981), whose uniquely broad pereopods 3 and 4 have a greatly reduced dactyls.
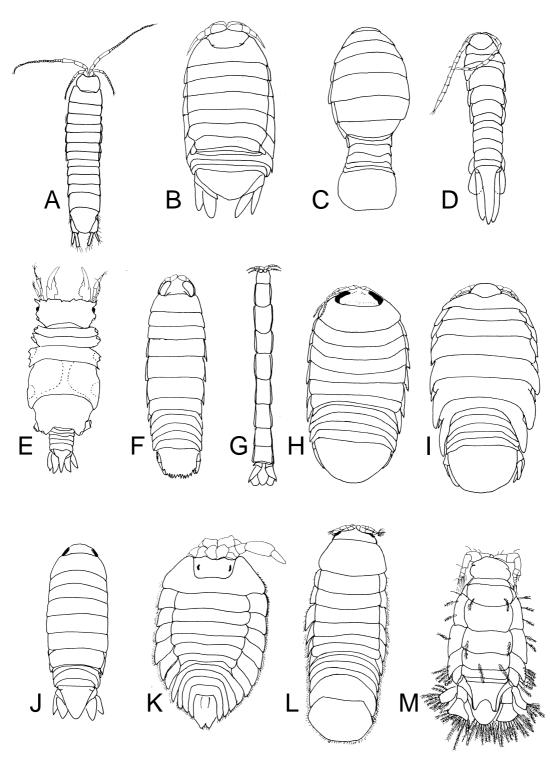
**Fig. 1.** Dorsal views of typical species of isopods of suborders Tainisopidea, Phoratopidea, Cymothoida and Limnoriidea, redrawn from original descriptions unless otherwise stated. *A*, Tainisopidea: *Tainisopus fontinalis* (from Wilson and Ponder 1992). *B*, Phoratopidea: *Phoratopus remex* Hale (from Bruce 1981). Cymothoida: *C*, Anuropidae: *Anuropus kussakini* Vasina, 1998; *D*, Protognathiidae: *Protognathia bathypelagica* Wägele & Brandt, 1988; E, Gnathiidae: *Euneognathia gigas* (Beddard, 1886) (after Brandt and Wägele 1991); *F*, Aegidae: *Aega komai* Bruce, 1996; *G*, Anthuridae: *Mesanthura looensis* Kensley & Schotte, 1987; *H*, Tridentellidae: *Tridentella namibia* Brandt & Poore, 2001; *I*, Cymothoidae: *Renocila ovata* Bruce, 1987; *J*, Cirolanidae: *Cirolana leptanga* Bruce, 1994. Limnoriidea: *K*, Keuphyliidae: *Keuphylia nodosa* Bruce, 1980h; *L*, Limnoriidae: *Limnoria quadripunctata* Holthuis, 1949 (from Kussakin 1979); *M*, Hadromastacidae: *Hadromastax polynesica* Bruce & Müller, 1991.
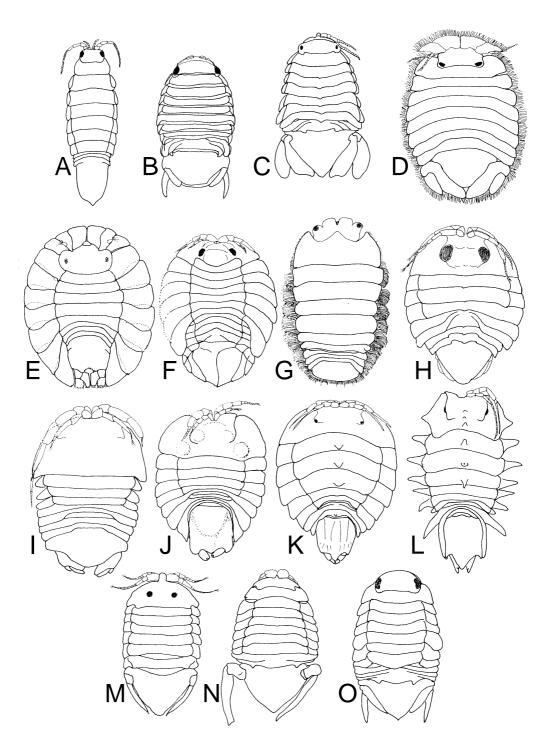
**Fig. 2.** Dorsal views of typical species of isopods of suborders Valvifera and Sphaeromatidea, redrawn from original descriptions unless otherwise stated. Valvifera: *A*, *Idotea neglecta* Sars, 1897. Sphaeromatidae: *B*, *Lekanesphaera teissieri* (Bocquet & Lejuez, 1967) (from Kussakin 1979); *C*, *Exosphaeroma amplicauda* (Stimpson, 1857) (from Kussakin 1979); *D*, *Paraleptosphaeroma indica* Müller, 1990. *E*, Plakarthriidae: *Plakarthrium australiense* Poore & Brandt, 2001. *F*, Schweglerellidae: *Schweglerella strobli* Polz (from Brandt *et al.* 1999). *G*, *Paravireia holdichi* Brökeland *et al.*, 2001. *H*, Serolidae: *Serolina holia* Poore, 1987. *I*, Basserolidae: *Basserolis kimblae* Poore, 1985. Bathynataliidae: *J*, *Naudea louwae* Kensley, 1979; *K*, *Biremia ambocerca* Bruce, 1985; *L*, *Bathynatalia gilchristi* Kensley, 1978. *M*, Ancinidae: *Ancinus belizensis* Kensley & Schotte, 1989; *N*, *Bathycopea typhlops* Tattersall, 1905 (from Bruce 1991); *O*, Tecticipitidae: *Tecticeps marginalis* Gurjanova, 1935 (from Kussakin 1979).

Protognathiidae (*Protognathia* Wägele & Brandt, 1988, 2 spp.) (Wägele and Brandt 1988; Kussakin and Rybakov 1995), with characteristic mouthparts, body shape and numerous plumose setae on pereopods 4–6.

Tridentellidae (*Tridentella* Richardson, 1905, 16 spp.) (Bruce 1984, 1988*b*; Brandt and Poore 2001), possessing a simplified maxilla 2 and unique maxilliped.

Keuphyliidae (*Keuphylia nodosa* Bruce, 1980), characterised by prolonged pleonal epimera 2–5 surrounding the pleotelson, and a claw-like uropodal endopod.

Hadromastacidae (*Hadromastax* Bruce, 1988, 2 spp.) (Bruce and Müller 1991), with unique pleonal armature.

Plakarthriidae (*Plakarthrium* Chilton, 1883, 3 spp.) (Poore and Brandt 2001), a distinctive family with antenna 2 articles 3 and 4 broad and extended anteriorly alongside the coxae, an elongated pereopod 1 carpus, and terminal uropods with marginal rami surrounding a branchial pore.

The fossil Schweglerellidae (*Schweglerella strobli* Polz, 1998) (Brandt *et al*. 1999), which display a unique form of pleonite fusion (pleonites 3–5 fused middorsally), and a suture between the tergite and the first dorsal coxal plate.

Limnoriidae (3 genera) (Cookson 1991), which possess a rasp-like surface on the left mandibular incisor and a blade on the right, and claw-like uropodal exopods.

Other families with few genera, whose monophyly is probable but debated (e.g. Bruce *et al*. 1982), were also represented by a single taxon: Corallanidae (7 genera) (Delaney 1989), in which maxilla 2 is significantly reduced; Cymothoidae (42 genera) (Bruce 1987, 1990); and Aegidae (6 genera) (Bruce 1983, 1993*a*; Brusca 1983; Brandt 1991). In fact, although these families have been diagnosed more than once and are relatively easily recognisable, undisputed synapomorphies are not revealed in the literature. In some cases, separate families have been suggested for anomalous genera. Analyses to determine whether these are sister-taxa to the remaining genera in the family, or simply highly derived examples, have not been done. Such a case is the aegid *Barybrotes* Schioedte & Meinert, 1879 (Monod 1934), whose place in isopod taxonomy will only be revealed by a thorough treatment of all aegid genera—a task beyond the limited scope of this paper.

For others families whose monophyly might be questioned, several or all genera were included in the analysis.

Members of 20 genera are typical of Serolidae and occupy a clade distinct from the anomalous serolid, *Basserolis* Poore, 1985 (results of a phylogenetic analysis by M. J. Storey, personal communication). This group was represented by a species of *Serolis* Leach, 1818 (Brandt 1988; Held 2000). These genera share many synapomorphies: pleonites 1–3 with a medial sternite plate; pereopod 1 propodus with a row of robust sensory setae plus a row of short setulated sensory setae; and pleopods 1–3 peduncles are triangular, laterally directed, with rami scarcely overlapping. *Basserolis* (Poore 1985) was treated separately. It is diagnosed as follows: pereonite 7 sternite fused to pleonite 1; antenna 2 peduncle with a groove on the posterior margin for antenna 1; and pereopod 1 propodus with a prominent distal robust scale-like seta.

All three genera of the Bathynataliidae, all monotypic, appear to share some similarities with *Basserolis* and representatives were entered separately in the analysis. The three species belonging to *Bathynatalia* Kensley, 1978, *Naudea* Kensley, 1979 and *Biremia* Bruce, 1985 can be differentiated easily.

Multiple genera were selected to represent the two largest families. Cirolanidae (56 genera) were represented by two genera. *Bathynomus* Milne Edwards, 1879 has sometimes been cited as the least advanced cirolanid because of the possession of an antennal scale, but its phylogenetic position within this family was considered uncertain by Wägele (1989: 206). The speciose *Natatolana* Bruce, 1986 (Keable and Bruce 1997) was the second cirolanid genus chosen, but at the level of detail

applicable to our analysis, most others would have suited equally. Phylogenetic relationships among the genera have not been explored and there is no evidence to suggest that the family is not monophyletic.

The Sphaeromatidae in the broadest sense are diverse, with ~100 accepted genera, and they are probably phylogenetically more complex than the current taxonomy suggests. The 13 species of *Tecticeps* Richardson, 1897 were recognised as a subfamily (Iverson 1982) and later a family, Tecticipitidae (Bruce 1993*b*). Their synapomorphies include an extremely enlarged and prolonged urpodod peduncle and a long exopod on the uropod.

Similarly, *Ancinus* Milne Edwards, 1840 was first placed in its own subfamily by Dana (1852); this was supported by Iverson (1982). The subfamily was elevated to family level (Ancinidae) by Bruce (1993*b*) and the genus *Bathycopea* Tattersall, 1905 was added.

The sphaeromatid subfamilies Sphaeromatinae, Dynameninae and Cassidininae are useful classificatory elements (e.g. Iverson 1982; Bruce 1993*b*), and were used as convenient groupings by all sphaeromatid taxonomists during the 1980s and 1990s. But even these have no phylogenetic support and may be polyphyletic (Bruce 1994). For our purposes, Sphaeromatinae and Dynameninae are represented by one species from *Sphaeroma* Bosc, 1802 (Harrison and Holdich 1984) and *Dynamene* Leach, 1814 (Holdich and Harrison 1980), respectively. Bruce (1993*b*) differentiated and described representatives of three genus-groups within Cassidininae and we have chosen species from three of these genera for our analysis: *Cassidina* Milne Edwards, 1840; *Cassidinidea* Hansen, 1905, and *Paraleptosphaeroma* Buss & Iverson, 1981. Trial scoring of some other genera added nothing to our analysis. The monophyly (or otherwise) of these groups can only be tested in a much more detailed analysis.

Another taxon, *Paravireia* Chilton, 1925, a genus with sphaeromatid affinities, was excluded from this family as presently defined by Brökeland *et al*. (2001). It lacks uropods.

The suborder Oniscidea is now not thought to be flabelliferan, but the uropodal structure of *Tylos* Latreille, 1826 (Tylomorpha) has been suggested as an apomorphy shared with Valvifera. This view is now largely discounted (Schmalfuss 1989), but was revived on the basis of a molecular analysis by Michel-Salzat and Bouchon (2002). Representatives of the genera *Tylos* and *Oniscus* Linnaeus, 1758 (Ligiamorpha) were included to represent the two infraorders currently in use. More contentious is the enigmatic family Tainisopidae. *Tainisopus* could not be placed in any isopod suborder by its authors (Wilson and Ponder 1992), but, following the erection of a second genus, was aligned with the limnoriids by Wilson (2003).

Outgroups were chosen from non-flabelliferan Isopoda. *Phreatoicus typicus* Chilton, 1883, a typical member of Phreatoicidea, is well described (Wilson and Fenwick 1999). An asellote with many plesiomorphic features is *Vermectias nelladanae* Just & Poore, 1992. *Mexistenasellus colei* Bowman, 1982 represents the asellote superfamily Aselloidea. The Calabozoidea were not used as an outgroup, but they have few flabelliferan features and were unlikely to improve our interpretation. The number of taxa was 38: 35 in the ingroup, and three in the outgroup.

### Characters

Examples of whole animal illustrations and dissected limbs can be found in Wägele (1989) and Brusca and Wilson (1991), as well as in many other sources. An atlas of typical character states was compiled from figures from the literature cited above and in Appendix 1 to enable direct comparison between antennae, mandibles, etc. for all taxa. This was supplemented and checked for accuracy and general applicability by reference to specimens of many species in the collections of Museum Victoria, Australia and the Zoological Museum, Hamburg and loans from other museums (see Appendix 1). Direct observations added enormously, and several published observations

were found to be incorrect. We relied only on published descriptions for: *Anuropus, Paravireia, Paraleptosphaeroma, Ancinus* and *Mexistenasellus*.

A database of 72 potentially synapomorphic characters was assembled using the software DELTA (Dallwitz *et al*. 1997). Many of the characters were those traditionally used in isopod family diagnoses, but many are newly discovered (Tables 1, 2). Two dilemmas present themselves: whether to score characters as multistate or comprised of binary states, and whether to score multispecies taxa as single state or polymorphic. We have much sympathy for the arguments of Pleijel (1995), who advocated binary over multistate characters, but in many cases it makes little practical difference how mutually exclusive states are scored. Where possible, several states of one character were combined, e.g. characters 24 and 26 (form of mandibular incisor and spine row) and 68 (manner of articulation of uropods). In other cases, it is not possible to combine states in this way, e.g. character 15 describes a series of fusion states of pleonites, whereas character 16 describes a peculiar sphaeromatid form of pleonal fusion. The consequence of this is that the plesiomorphic condition of character 16, seen in non-sphaeromatids, is variable and best expressed as 'not the apomorphic' state. In any large taxon comprising several families and hundreds of species, like Valvifera or Anthuridea, it is not difficult to find species displaying character states that are homoplasious with those in other taxa. For instance, in both the Valvifera and Anthuridea, some species have all or several of the pleonites fused to the telson. The question is, should this be scored as polymorphic (all states possible) or as the most plesiomorphic state, assuming this is indicated by the outgroups? Our view is that the latter is justifiable, although contrary views exist (Prendini 2001).

In the following explanation of characters, numbers in square brackets correspond to those in Tables 1 and 2.

### Life history

Isopods have various life history strategies; protandry is shared by two taxa [1].

### Body shape

Several taxa are characterised by a unique body shape, such as the elongated and cylindrical anthurideans. The outgroups differed from most ingroup taxa and provide little guidance. The chosen asellotes have parallel-sided bodies, but other asellotes are diverse. Phreatoicidea are uniquely laterally flattened. Oniscideans and most members of the ingroup are generally oval, widest at about pereonite 4 and more or less vaulted. The flat, broad, disc-like shape in several families is a potential synapomorphy [2], but there can be little doubt that not all 'flat' isopods are related, and the characters turned out to be very weakly supported. A few derived sphaeromatids, besides those scored here, are also flattened more than others, some like *Maricoccus* especially so (Poore 1994). In this case, and in 'flat' valviferans and cymothoidans, homoplasy is assumed.

In the primitive isopod, the head is attached anteriorly to pereonite 1, with slight or moderate forward extensions of the first coxae, and is more or less moveable. In some taxa, the head is flattened and immoveable, laterally overlapped by the first coxae, which reach to the anterior margin [3]. In some of these, and in other taxa the head and pereonite 1 are fused dorsally to the extent that a suture is invisible [4]. An unusual situation is seen in Limnoriidae and Hadromastacidae where the head is freely rotating within the anterior margin of the tergite and coxae rather than the more usual dorsoventral movement [5].

### Pereon and coxae

In Asellota and Phreatoicidea, the pereopodal coxae are short and ring-like, without ornamentation or medial or lateral expansion. The coxae are variously modified on one or more pereopods in different taxa. Dorsal coxal plates extend dorsally to replace the tergite and ventrolaterally over the pereopodal bases of most flabelliferans [6], but these extensions are variously reduced [7], extended, fused with the tergite or ornamented. It is these plates that Dreyer and Wägele (2002) used to define Scuticoxifera. The dorsal coxal plates 2–7 or 5–7 are entirely fused to their respective tergites (without a delineating suture) in Oniscidea, Sphaeromatidae and Serolidae [8]. Valviferans show a strong tendency to coxal fusion, but this is not the plesiomorphic condition in this suborder. Isopods are generally characterised by lacking a suture between coxa 1 and the tergite of pereonite 1; secondarily a suture is visible in *Plakarthrium* and *Hadromastax* [9]. A dorsal coxal plate 7 is absent in Serolidae and Bathynataliidae and dorsal coxal plate 6 and pleonite 1 or 2 are in contact [10].

Primitively, in the Isopoda, the pereopodal coxae are ring-like and on pereopod 7 the penes are close to the basis. In most flabelliferans the inner margins of the coxae are indistinct, but the medial position of the penes on pereonite 7 [14] suggests that the ventral exoskeleton is coxal rather than sternal. In Oniscidea, Bathynataliidae, Serolidae and Valvifera, the ventral coxal plates are well defined, extend mesially, meet in the midline, and replace the sternite on most pereonites [11]. Just and Poore (1992) recognised what they called a proximal sclerite on the posterior ventral margin of thoracic sternites in the primitive asellote, *Vermectias*. Although homologies are difficult to determine, we believe the proximal sclerite is fused with the ventral coxal plates in all higher isopods although grooves may indicate its ancestry. A medial plate separating coxae 7 in serolids and *Biremia* is presumed to be the proximal sclerite [12].

Pereonite 7 is much narrower than pereonite 6 and submerged between it and the pleon in Serolidae and some Bathynataliidae [13].

### Pleon

Pleonites 1–5 are primitively free and articulating, whereas in isopods, pleonite 6 is fused with the telson. A secondary ridge and groove between pleonite 6 and the telson in some anthurideans (which prompted some authors to describe the anthuridean telson as 'free') has been shown not to be a suture allowing articulation. The pleotelson progressively fuses with anterior pleonites, pleonite 5 (e.g. Valvifera), pleonite 4 (*Basserolis, Vermectias*), and pleonite 3 (*Mexistenasellus*) [15]. Within some larger groups, like Valvifera and Anthuridea, examples can be found with levels of fusion greater than that in the most plesiomorphic condition. Other groups are not part of this progression. Most sphaeromatids display a special case where pleonite 1 is free and pleonites 2–4 are fused to each other but free from the fused remaining pleotelson [16]; in some sphaeromatids, all pleonites are more or less fused. Pleonite 1 is much narrower than pleonite 2 and more or less immersed in it in many sphaeromatoid taxa [17]. The pleonal epimera are simple ventrolateral extensions over the bases of the pleopods. These are variously extended posteriorly to surround the pleotelson, but characteristically so in Bathynataliidae [18]. Some serolids are similar, but the epimera are not extended in most genera. A middorsal carina on the pleotelson may link Serolidae and *Schweglerella* [19].

In the plesiomorphic condition, the underside of the pleon and pleotelson is flat and the pleopods are confined laterally by the epimera (Fig. 3*a*). The uropods are terminal. With fusion of the posterior pleonites with the pleotelson, and the dominance of the fused over the articulating segments of the pleon, a vaulted branchial chamber forms to enclose the modified pleopods (Fig. 3*b*; see uropods below). The ventrolateral boundary of the branchial chamber is defined by the mesial ridge defining the inner margin of the lower edge of the pleotelsonic tergite [20]. High vaulting in the phreatoicideans does not involve inclusion of the pleopods in a branchial chamber. The lower edge may be narrow and rounded externally (e.g. Sphaeromatidae), or

broad and flat with both mesial and lateral ridges (e.g. *Biremia*) [21]. In taxa sharing this synapomorphy, the uropods articulate along an anteroposterior axis from a laterally to a ventrally directed orientation [see 70].

### Antennae and mouthparts

Two antennal characters were scored, but neither was informative [22, 23].

Mandibular structure provided several autapomorphies. Wägele (1994*b*) warned about interpreting similarities in mandibular structure in epicarideans and gnathiids as homologies; he thought mandibular structure to be highly homoplasious owing to a common ectoparasitic lifestyle. Obsolete incisor dentition is a feature of parasitic families. The mandibular incisor is primitively multidentate, usually with four or five cusps, but takes many forms, which are treated here in a multistate character [24]: tridentate with the most posterior tooth dominant in Cirolanidae; broadened in others; acute in some carnivorous and

parasitic taxa; and conical in Limnoriidae and Hadromastacidae (Fig. 4*A*–*G*). The lacinia mobilis is a modified distal spine of the spine row that defines the Peracarida (Figs 4*A*–*G*, 5*A*, *B*) (Richter *et al.* 2002). It is present on both sides, but is larger on the left in the outgroup and some ingroup taxa; present on the left side but reduced and fused with the spine row on the right in sphaeromatids and related taxa, and absent in cirolanids and all parasitic and carnivorous taxa [25]. In the outgroup and other taxa, the spines of the spine row [26] are multidentate and fused onto a common moveable base (Fig. 5*A*, *B*). In cirolanids and similar free-living taxa, the spine row comprises short simple spines, but is absent in some ectoparasitic and other unrelated taxa. Extreme reduction of the spines is evident in the lamina dentata, a flat, toothed blade that replaces the spine row in Anthuridea. Cirolanids are a special case where the spines are on a fleshy lobe not seen in other taxa (Figs 4*G*, 5*C*). The mandibular molar process is absent in some parasitic taxa (Fig. 4*C*) [27]. When present, the plesiomorphic condition is a prominent, complexly ridged and spinose triturative cylinder
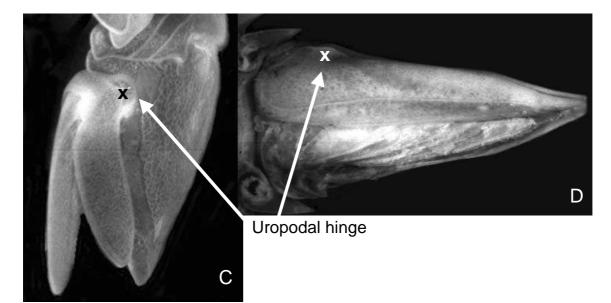


**Fig. 3.**  Pleotelsons of flabelliferan isopods. *A*, Cymothoida Cirolanidae: *Natatolana* sp., ventral view; *B*, *C*, Sphaeromatidea Sphaeromatidae: *Zuzara venosa* (Stebbing), ventral and lateral views; *D*, Valvifera Chaetiliidae: *Saduria entomon* (Linnaeus), ventral view, right uropod removed.

(Fig. 5*D*), modified as a blade-like or conical process in most cymothoidan taxa, a condition referred to as 'fundamentally different' by Brusca and Wilson (1991) [28]. A curved row of denticles along the distal margin of the blade is a feature of carnivorous Cirolanidae (Fig. 5*C*), but these are absent in other taxa with blade-like or reduced molars (Figs 4*A*–*F*) [29]. The molar takes the form of a distally denticulate spine in *Tecticeps*, Ancinidae and Serolidae [30] and is reduced to a stout spine in Bathynataliidae [31]. The mandibular palp is usually present and is primitively of three articles, but may be reduced

to one seta. It is absent in several taxa [32]. Unlike Brusca and Wilson (1991), we score it absent for Valvifera, following Poore and Lew Ton's (1990) argument that its occurrence in one species of Holognathidae is a reversal.

Characters describing maxilla 1 [33–35] were generally uninformative. The tendency for maxilla 1 of cymothoids to have an oblique setose margin and of sphaeromatideans to be truncate was difficult to code. According to Hansen (1925), the isopod maxilla 2 comprises three lobes, one coxal and two basal endites (Fig. 4*H*–*M*). Primitively,



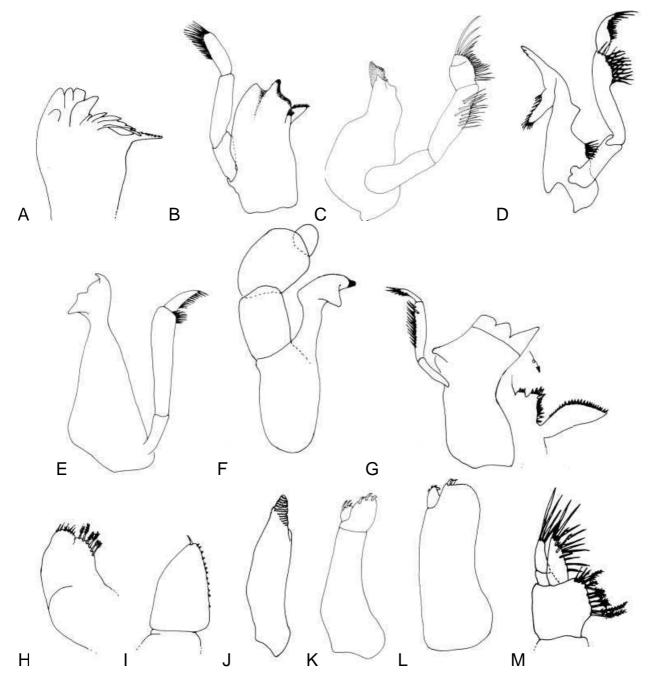**Fig. 4.** Mandibles of isopods. *A*, *Phoratopus remex*; *B*, *Anuropus pacificus*; *C*, *Argathona rostrata*; *D*, *Tridentella namibia*; *E*, *Aega plebeja*; *F*, *Rocinela quadrata*; *G*, *Natatolana woodjonesi*. Maxilla 2 of isopods. *H*, *Anuropus pacificus*; *I*, *Argathona rostrata*; *J*, *Tridentella namibia*; *K*, *Aega plebeja*; *L*, *Rocinela quadrata*; *M*, *Natatolana woodjonesi.*

these have rows of complex setae arranged along the oblique apices. There is no endopod. The coxal endite is present in all taxa and the basal endites are variously reduced from two to one to absent [36]. In the ectoparasitic taxa like Cymothoidae, the endites are simultaneously shortened and homologies are not immediately obvious—we interpret the two lobes lying alongside each other as a coxal and basal endite (Fig. 4*H*, *K*, *L*) and a solitary lobe as a coxal endite (Fig. 4*I*, *J*). Reduction of setation to just a few short setae or transformation to hooks is another character [37]. *Keuphylia* and *Hadromastax* have peculiarly shortened endites [38].

Characters describing the maxillipedal shape and segmentation [39–44] are mostly autapomorphies, but some valuable synapomorphies were found. The maxillipedal endite is normally much longer than the first article of the palp, but is considerably reduced in cirolanids and related carnivorous or parasitic groups [39]. In limnoriids and hadromastacids, the endite is elongate and non-tapering [40], and in ancinids, exceptionally truncate and with few setae [41]. Oblique segmentation and hooks are characteristic of cymothoids and aegids [42] and the pattern of article fusion defines seroloid taxa [43].

### Pereopods

Patterns of setation on the pereopods vary considerably between taxa, but were difficult to score for phylogenetic analysis. Setulated setae in distal transverse rows are evident on the superior and lateral

margins of the ischium–propodus of many taxa, but we were unable to define the character unambiguously. Dense brushes of hairs on the inferior margins of some distal articles of males was thought to be informative, but this too had a low consistency index [45]. Coxal keys (lobes on the anterior margin of coxae inserting into a groove on the posterior margin of the preceding coxa) are a feature of many sphaeromatid–serolid–valviferan taxa and also of *Keuphylia* [46]. The shape of the propodus of pereopod 1 [47, 48] and the presence of unusual setae [49–51] characterise small groups of genera. The prehensile nature of pereopods 1 and 2–7 are synapomorphies that differentiate Aegidae from Cymothoidae and Epicaridea [52, 53]. Although aegids are said to have prehensile pereopods 2 and 3, their structure is not the same as in pereopod 1. Cuticular processes are a feature of two limnoriidean families [54]. The highly sexually dimorphic pereopod 2 of serolids is also seen in *Tecticeps* and ancinids [55].

### Pleopods

Operculiform and thickened peduncles and rami of pleopod 1 are a feature of two species of Bathynataliidae [56]. Pleopods 1 are more or less operculiform in other taxa, but not in a homologous way, e.g. in Anthuridea (Hyssuridae excluded) and some sphaeromatids. Pleopod 4 is operculiform in serolids [57]. Pleopodal 1–2 rami are primitively parallel, oval–rectangular and more or less overlapping. In sphaeromatideans, the endopod is triangular and the exopod lies obliquely [58].
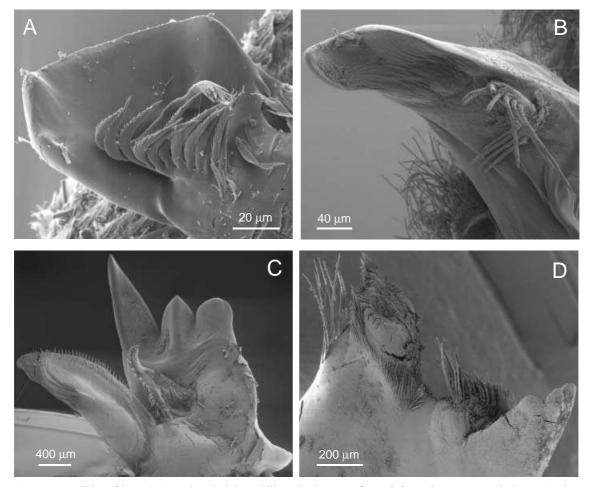
**Fig. 5.**    Mandibles of isopods. *A*, Incisor, lacinia mobilis and spine row of *Keuphylia nodosa* Bruce; *B*, incisor and spine row of *Limnoria stephenseni* Menzies; *C*, incisor, spine row and molar of *Natatolana albinota* (Vanhöffen); *D*, incisor, spine row and molar of *Exosphaeroma gigas* (Leach).

Within this group, pleopodal peduncles and rami may be further modified [59–61]. In the outgroup taxa, the endopods of pleopods 3 and 4 and both rami of pleopod 5 lack plumose marginal setae; the presence of such setae on one or both rami is a synapomorphy of most cymothoidan taxa [62–64]. Transverse fleshy ridges on rami of pleopods 4 and 5 [65, 66] and scale patches on the exopod of pleopod 5 [67] did not alone resolve sphaeromatoid subfamilies and families.

### Uropods

Characters were chosen avoid the debate between the apomorphy or otherwise of different forms of the isopod tailfan. Whereas Brusca and Wilson (1991) believed that what they called the 'long-tailed' morphology is a synapomorphy of the higher isopods, Wägele (1981, 1989, 1994*b*) believed it to be homologous to the caridoid form. He resolved the apparent contradiction of having the plesiomorphic pleotelson only among higher isopods by assuming styliform uropods were independently derived in asellotes and phreatoicideans (Wägele 1994*b*). The relationship between the uropods to the pleopods and the branchial space defined four mutually exclusive character states [68]. Terminal, usually styliform, uropods are thought to be plesiomorphic (asellotes, oniscideans). Phreatoicideans also have styliform uropods, but these appear attached laterally. However, it is only the extraordinary vaulting of the pleotelson that puts the uropods in this position and, when this is ignored, their position relative to the pleotelson is not much different from that of asellotes. In one of the two remaining states, uropods are ventral to the pleotelson and articulate from side-to-side along a vertical axis inside the branchial space (Fig. 3*A*), whereas in the alternative state, the uropods are lateral to the margin of pleotelson, articulate along a longitudinal axis, and fold down alongside branchial space (Fig. 3*B*, *C*). The valviferan condition is a special case of the latter (Fig. 3*D*). Although coding the characters in this way forced the analysis to discover two major flabelliferan clades, we were unable to argue how one condition could be derived from the other. Other uropodal characters defined small groups of genera [69–72]. Bathynataliids are reported to have a single ramus, but we found two rami on specimens examined closely.

### Cladistic analysis

A data matrix (available as Accessory Material on the journal website) was generated for input into the phylogenetic programme PAUP* 4.0b5 (β-test version for Windows, 2001) (Swofford 1998). All characters were unordered and treated as having equal weight in the first analysis (Table 1). Multistate characters were treated as polymorphisms.

An heuristic search (hsearch) was initiated, a treespace search using tree bisection and reconnection (TBR) with randomised addition of taxa (addseq = random); 1000 replications were completed setting branch swapping options to save no more than three trees with length greater than or equal to the shortest tree found in each replicate (nchuck = 3 chuckscore = 1 nreps = 1000 randomize = trees). Branches of these resultant trees were then swapped in a second search, retaining all minimum length trees (hsearch start = current nchuck = 0 chuckscore = 0). Strict and 50% majority-rule consensus trees were calculated.

Improved resolution was sought by the 'reweight' option in PAUP, whereby characters are reweighted to constant weight based on the initial rescaled consistency indices (*RI*). This was achieved in two 'reweight' runs, each using the heuristic search protocol described above.

Character transformations (found using PAUP's 'apolist' option) of two of the most distant (in treespace) of the shortest trees were compared. Only clades and character transformations common to both trees were retained and these were mapped on the reweighted consensus tree.

Stability of the reweighted trees was assessed using bootstrap (Felsenstein 1985). Bootstrap was implemented in PAUP based on 1000 pseudoreplicates. A treespace search used five random-addition sequence iterations with 10 trees saved per iteration. Trees were drawn using TreeView 1.6.5 (© Roderic D. M. Page, 2001).

## Results

The first analysis, using unweighted characters, produced 103 equally parsimonious trees of length 182 steps, consistency index (*CI*) 0.50, and retention index (*RI*) 0.77. As illustrated in the strict and majority-rule consensus trees (Fig. 6*A*, *B*), considerable structure exists: major cymothoidan, limnoriidean, sphaeromatidean, sphaeromatoid and seroloid clades can be recognised. The positions of the two oniscidean genera, Tainisopidae and *Plakarthrium* were clearer in the majority-rule tree.

Reweighting of characters decreased the weights of 45 of the 72 characters. Ten characters were given zero weight, and were therefore effectively excluded from the analysis, and a further nine were given a weight less than or equal to 0.2. Twenty-seven characters had a weight of 1, leaving 52 characters with weights between 0.2 and 1 (Table 2). This analysis produced 12 equally parsimonious trees (*CI* = 0.70, *RI* = 0.90); the majority-rule tree (not shown) was slightly better resolved than the strict consensus tree (Fig. 6*C*). In the majority-rule tree, the Oniscidea are clearly removed from the flabelliferan clade and the Tainisopidae are placed with the cymothoidans. Apart from Tainisopidae, whose position remained fluid, the only taxon whose affinities changed by reweighting was Epicaridea. In the 50% unweighted majority-rule tree Epicaridea aligned with Gnathiidae and Anthuridea; in the reweighted tree it aligned with Cymothoidae. Clade numbers of the reweighted strict consensus tree are shown in Fig. 6*C* and bootstrap support (bs) are shown in Fig. 6*D*.

The result of the reweighted analysis forms the basis of a new classification of the flabelliferan Isopoda into suborders and superfamilies (Table 3). Most of the relationships deduced by reweighting were found without weighting. Table 4 describes character transformations with reference to the clade numbers. In the explanation that follows, some characters with low weights are not mentioned. Character numbers are in square brackets. Synapomorphies of small taxon groups and autapomorphies of terminal taxa are not discussed, but can be investigated using Tables 2 and 4.

Clade 2 (bs = 86) in Fig. 6*C*, equivalent to Scuticoxifera, is defined by the presence of dorsal coxal plates [6] (as stated by Dreyer and Wägele 2002) and the medial position of the penes on pereonite 7 [14].

The two genera of Oniscidea appear as sister-taxa only in majority-rule trees, but we included no characters (minute antenna 1, pseudotracheal pleopods, etc.) usually cited as synapomorphies of this suborder. The family Tainisopidae has numerous autapomorphies (see Wilson and Ponder 1992) that differentiate it from other flabelliferans (clades 3 and 17).

Clade 3 comprises three taxa (*Phoratopus*, Cymothoida + Limnoriidea, bs = 66). The clade is defined by three

synapomorphies. The mandibular molar is a triangular blade-like, or conical process [28] and pleopods 4 and 5 have plumose setae on the margins of both rami [63, 64].

Clade 17 (suborders Valvifera and Sphaeromatidea, bs = 75), on the other hand, is defined by three interrelated characters. The pleotelson is vaulted with ridges defining the edge of a branchial chamber [20]. The uropods are lateral to the margin of the pleotelson, articulate along a longitudinal axis and fold down alongside the branchial space [68: state 4]. Pleopod 3 is roughly triangular (at least the inner angle is sharper than the outer) [60].

The monotypic *Phoratopus* lacks a seventh dorsal coxal plate [10] and has many unique synapomorphies (antennae and pereopods; see Hale 1925; Bruce 1981). More importantly, it does not share the characters of clades 4, 5 and 15.

Clade 4, sister-taxon to *Phoratopus*, is characterised by a broad mandibular molar [24, state 3], a state intermediate between what are assumed to be the most plesiomorphic and most apomorphic conditions.

Clade 5 (suborder Cymothoida, bs = 86) taxa lack a mandibular lacinia mobilis [25] (seen in other taxa), and share a mandibular spine row of independent short, simple spines [26], the maxillipedal endite is rarely longer than palp article 1 (or absent), distally tapering and with few setae [39], and pereopodal meri 1–3 have short, blunt, robust, setae [50]. Clade 5 comprises two branches: clades 6 and 14.

**Table 1. Character matrix of 38 taxa and 72 characters used in cladistic analysis of Isopoda**

| Taxa | Characters | | | | | | | |
|------|-----------|--|--|--|--|--|--|--|
| | 1234567891 | 1234567892 | 1234567893 | 1234567894 | 1234567895 | 1234567896 | 1234567897 | 12 |
| *Phreatoicus* | 111111---- | 1-11111111 | -1111111-1 | -111111111 | 111-111111 | 1111111111 | 1111111211 | 11 |
| *Vermectias* | 111111---- | 1-11311111 | -1111111-1 | -111111111 | 111-111111 | 1111111111 | 1111111111 | 11 |
| *Mexistenasellus* | 111111---- | 1-11311111 | -1111111-1 | -111111111 | 111-111111 | 1111111111 | 1111111111 | 11 |
| *Oniscus* | 1111121211 | 2112111111 | -1111111-1 | -211111111 | 11--111111 | 1111111111 | 1111111111 | 11 |
| *Tylos* | 1111121111 | 2112111111 | -1111111-1 | -211111111 | 11--111111 | 1111111111 | 1111111111 | 11 |
| Tainisopidae | 1111121111 | 1-12111111 | -1211111-1 | -111111111 | 111-111111 | 1111111111 | 1111111311 | 11 |
| *Phoratopus* | 1111121112 | 1-1?111111 | -111111211 | -111111111 | 111-?11111 | 1111111111 | 1222111311 | 11 |
| *Anuropus* | 1111121111 | 1-12111111 | -113321211 | -11112112- | -11-111112 | 1111111111 | 1222111311 | 11 |
| *Protognathia* | 1111121111 | 1-12111111 | -114351211 | -11112112- | -11-111112 | 1111111111 | 1222111311 | 11 |
| Gnathiidae | 1111122111 | 1-12111111 | -114352--- | -12--3--2- | -11-111111 | 1112111111 | 1222111311 | 11 |
| Anthuridea | 2111122111 | 1-12111111 | -1132412*1 | -11223--2- | -11-111112 | 1111111111 | 1222111311 | 11 |
| *Corallanidae* | 1111121111 | 1-12111111 | -11432*221 | -11222112- | -11-111112 | 1111111111 | 1223111311 | 11 |
| *Tridentella* | 1111121111 | 1-12111111 | -114351211 | -11222312- | -11-111112 | 1111111111 | 1223111311 | 11 |
| Aegidae | 1111121111 | 1-12111111 | -114351221 | -11222312- | -21-111112 | 1211111111 | 1223111311 | 11 |
| Cymothoidae | 2111121111 | 1-12111111 | -114351221 | -11232312- | -21-111111 | 1221111111 | 1111111311 | 11 |
| Epicaridea | 2111121111 | 1-12111111 | -1*4352--- | -22--3--2- | -11-111111 | 1221111111 | 1122111311 | 11 |
| *Bathynomus* | 1111121111 | 1-12111111 | -122331211 | -11111112- | -11-111112 | 1111111111 | 1222111311 | 11 |
| *Natatolana* | 1111121111 | 1-12111111 | -112331211 | -11111112- | -11-111112 | 1111111111 | 1223111311 | 11 |
| *Keuphylia* | 1221121111 | 1-12112111 | -113112--- | -211111211 | 111-121111 | 2111111111 | 1222111311 | 11 |
| Limnoriidae | 1111221111 | 1-12111111 | -125112--- | -111111102 | 111-111111 | 2112111111 | 1221111311 | 11 |
| *Hadromastax* | 1111221121 | 1-12312111 | -115352--- | -111111212 | 111-111111 | 1112111111 | 1222111311 | 11 |
| *Paravireia* | 1111121311 | 1-1?212112 | 11112111-1 | -111111111 | 111-1?1111 | 1111111112 | 1111111--- | -- |
| *Sphaeroma* | 1111121311 | 1-12222112 | 11112111-1 | -111111111 | 111-221111 | 1111111112 | 1211222412 | 11 |
| *Dynamene* | 1111121311 | 1-12222112 | 11112111-1 | -111111111 | 111-221111 | 1111111112 | 1211232412 | 11 |
| *Cassidina* | 1211121311 | 1-12222112 | 11112111-1 | -111111111 | 111-121111 | 1111111112 | 1211112412 | 11 |
| *Cassidinidea* | 1211121311 | 1-12222112 | 11112111-1 | -111111111 | 111-121111 | 1111111112 | 1211112412 | 11 |
| *Paraleptosphaeroma* | 1211121311 | 1-12222112 | 12112111-1 | -111111111 | 111-121111 | 1111111112 | 1211112412 | 11 |
| *Tecticeps* | 1111121311 | 1-12222112 | 11132111-2 | 1111111111 | 111-122111 | 1111211112 | 1231131412 | 11 |
| *Ancinus* | 1112121311 | 1-12222112 | 11112511-2 | 1111111111 | 211-222111 | 1111211112 | 1111112412 | 12 |
| *Bathycopea* | 1112121311 | 1-12222112 | 11112511-2 | 1111111111 | 211-122111 | 1111211112 | 1111112412 | 12 |
| *Plakarthrium* | 1211121121 | 1-12111112 | 1211212--- | -212311111 | 111-121111 | 1111111112 | 1133111411 | 11 |
| *Schweglerella* | 122?121111 | ??1?11?12? | ?11??????? | ?????????? | ?1?????11? | ??11?????? | ??????411 | 11 |
| *Biremia* | 1222121112 | 222?212212 | 21112111-2 | 1111212111 | 1122?21221 | 1111?11212 | 1131111421 | 21 |
| *Bathynatalia* | 1122121111 | 211?112212 | 21112511-2 | 2111?12111 | 1122122111 | 1111121222 | 2133111421 | 21 |
| *Naudea* | 1222121112 | 212?112212 | 21112511-2 | 2111?12111 | 1122?12121 | 1111?21222 | 2133111421 | 21 |
| *Basserolis* | 1222121212 | 2222312112 | 1113352--- | -111212111 | 112-111221 | 1111112212 | 1221111411 | 11 |
| Serolidae | 1222121212 | 2222312122 | 11131511-2 | 1111211111 | 1121222121 | 1111212112 | 1231111411 | 11 |
| Valvifera | 1111121111 | 2112311112 | 11111111-1 | -211111111 | 111-221111 | 1111111112 | 1211111411 | 21 |

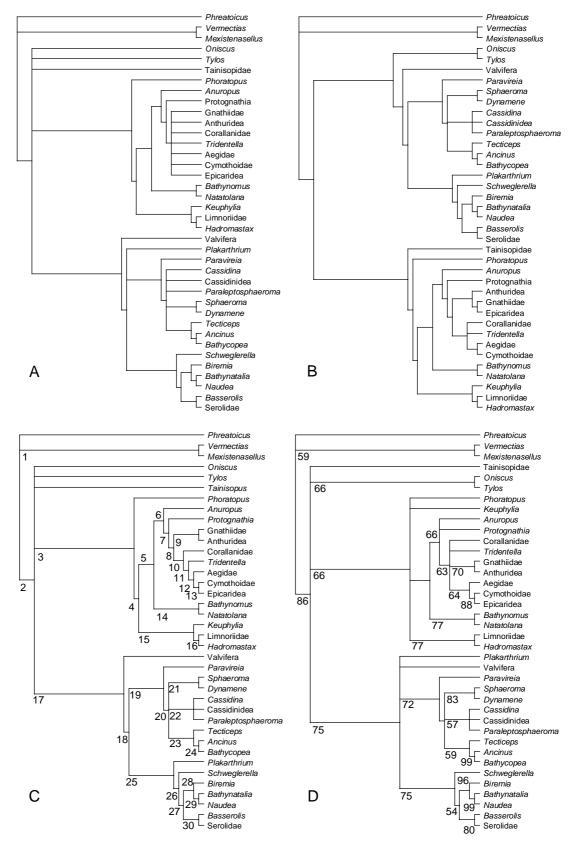-, Inapplicable; ?, unknown; *, alternative states 1 or 2.

**Fig. 6.** *A*, Strict consensus of 103 trees, unweighted data. *B*, Majority-rule consensus of 103 trees, unweighted data. *C*, Strict consensus of 12 trees, reweighted data. *D*, Bootstrap 50% majority-rule consensus of 12 trees, reweighted data.

**Table 2.    Characters and character states used in cladistic analysis of higher Isopoda**
Each character is terminated by a colon and the states, 1, 2, etc separated by semicolon. Character weights applied in the final heuristic search
follow in parentheses. All characters are treated as unordered. Autapomorphies are not included.

*Life history*
(*1*)    *Development:* (1) separate sexes; (2) protandric. (0.25)

*Body shape*
(*2*)    *Body shape:* (1) oval and vaulted; (2) flat, broad, disc-like. (0.17)
(*3*)    *Head:* (1) barely laterally overlapped by coxae of pereopods 1; (2) overlapped laterally by coxae of pereopods 1, flattened and extending to
         be continuous with anterior margin of head. (0.42)
(*4*)    *Head–pereonite 1:* (1) free; (2) fused. (0.42)
(*5*)    *Head:* (1) flexing dorsoventrally but not freely rotating (left to right); (2) set into pereonite 1, anterior margin of pereonite 1 tergite concave,
         rotating laterally and dorsoventrally. (1.00)

*Pereon and coxae*
(*6*)    *Dorsal coxal plates:* (1) absent; (2) present (secondarily reduced in some species). (1.00)
(*7*)    *Dorsal coxal plates:* (1) expanded ventrally or ventrolaterally over bases of pereopods; (2) reduced. (1.00)
(*8*)    *Dorsal coxal plates:* (1) 2–7 (or 2–6 if 7 absent) separated by suture from tergite; (2) 2–4 free, 5–7 (or 5–6 if 7 absent) separated by suture
         from tergite; (3) 2–7 fused to tergite. (0.60)
(*9*)    *Coxal plate of pereopod 1:* (1) fused to tergite; (2) free from tergite. (0.00)
(*10*)   *Dorsal coxal plate 7:* (1) present; (2) absent (dorsal coxal plate 6 and pleonal 1 or 2 epimeron in contact). (0.17)
(*11*)   *Ventral coxal plates 1–7 (medial extension of coxa replacing sternite):* (1) obsolete (not distinguished from sternite); (2) extending to
         midpoint (well defined and separated by suture). (0.24)
(*12*)   *Pereopod 7 ventral coxal plates (if present):* (1) meeting at middle; (2) not meeting in middle (separated by pair of plates, presumed proximal
         sclerite 7). (0.25)
(*13*)   *Pereonite 7:* (1) as wide as pereonite 6; (2) much narrower than pereonite 6 and buried under it. (0.33)
(*14*)   *Penial processes:* (1) at bases of pereopod 7; (2) medial, closer to midpoint than to pereopods. (1.00)

*Pleon*
(*15*)   *Pleonite fusion:* (1) pleotelson incorporating pleonite 6 only, pleonite 5 free from pleotelson; (2) only pleonite 5 fused to pleotelson,
         pleonites 1–4 free or variously fused; (3) only pleonites 4 and 5 fused to pleotelson, pleonites 1–3 free or variously fused. (0.24)
(*16*)   *Pleonite fusion:* (1) pleonites free or not fused as in state 2; (2) pleonite 1 free, 2–4 fused, 5 fused to pleotelson. (1.00)
(*17*)   *Pleonite 1:* (1) as wide as pleonite 2; (2) much narrower than pleonite 2 and more or less immersed in it. (0.20)
(*18*)   *Pleonal epimera 2–3:* (1) not prolonged; (2) prolonged, surrounding parallel–sided pleotelson. (1.00)
(*19*)   *Pleotelson, middorsal longitudinal carina:* (1) absent; (2) present, broadest anteriorly. (0.00)
(*20*)   *Pleotelson underside:* (1) flat, without ventrolateral ridges (pleopods not enclosed laterally as follows); (2) vaulted, branchial chamber
         defined by ridges along mesial margin of lateral edge. (1.00)
(*21*)   *Ventrolateral margins of pleon and pleotelson:* (1) narrow; (2) broad and flattened. (1.00)

*Antennae and mouthparts*
(*22*)   *Antenna 1:* (1) with cylindrical articles 1 and 2; (2) with articles 1 and 2 broad and extended anteriorly alongside coxae 1. (0.00)
(*23*)   *Antenna 1 scale:* (1) absent; (2) present. (0.00)
(*24*)   *Mandibular incisor:* (1) multidentate, usually 4 or 5 well defined teeth; (2) tridentate, most posterior tooth prominent; (3) broad, without or
         with obsolete teeth; (4) acute, projecting; (5) conical. (0.44)
(*25*)   *Mandibular lacinia mobilis:* (1) present on both sides; (2) present on left side, reduced and fused with spine row on right; (3) absent. (0.27)
(*26*)   *Mandibular spine row:* (1) solid base with rows of denticulate spines (sometimes reduced to single spine); (2) row of independent short
         simple spines; (3) on a fleshy lobe; (4) a denticulate blade; (5) absent (or a minute spike). (0.29)
(*27*)   *Mandibular molar:* (1) present; (2) absent. (0.05)
(*28*)   *Mandibular molar:* (1) a cylindrical process with triturative flat end (or not as follows); (2) flat triangular blade-like or conical process. (1.00)
(*29*)   *Mandibular molar blade:* (1) with curved row of denticles along distal margin; (2) smooth. (0.11)
(*30*)   *Mandibular molar:* (1) not spine-like; (2) spine-like. (0.42)
(*31*)   *Mandibular molar spine:* (1) distally denticulate, articulating; (2) a simple fixed cone. (1.00)
(*32*)   *Mandibular palp:* (1) present (at least 1 seta); (2) absent. (0.04)
(*33*)   *Maxilla 1:* (1) present; (2) reduced or vestigial in adults. (0.00)
(*34*)   *Maxilla 1 lateral endite:* (1) with 9–13 robust setae, some basally serrated; (2) with 1–7 setae, mostly robust and strongly curved. (0.40)
(*35*)   *Maxilla 1 inner endite:* (1) almost as long as outer lobe, with 3–4 setae; (2) small, with 0–1 seta; (3) absent. (0.27)
(*36*)   *Maxilla 2 basal endites:* (1) two; (2) one; (3) vestigial or fused to hypopharynx. (0.38)
(*37*)   *Maxilla 2 basal endites:* (1) with numerous setae; (2) each with 1 or 2 setae; (3) with hooked setae. (0.53)
(*38*)   *Maxilla 2 endites:* (1) much longer than wide; (2) as long as wide. (0.00)
(*39*)   *Maxillipedal endite:* (1) reaching at least distal margin of palp article 2, usually distally truncate and setose; (2) rarely longer than palp article
         1 (or absent), distally tapering and with few setae. (1.00)
(*40*)   *Maxillipedal endite:* (1) broad, rarely reaching beyond palp article 3 (or not as follows); (2) non-tapering, slender, reaching at least to palp
         article 4. (1.00)

**Table 2.** (continued)

*(41) Maxillipedal endite:* (1) variously broad or elongate, with or without plumose robust setae; (2) broad (wider than long), truncate, without robust setae. (1.00)

*(42) Maxillipedal palp, articles 4 and 5:* (1) set serially, without hooks; (2) set obliquely, with terminal hooks. (0.00)

*(43) Maxillipedal palp fusion:* (1) 5–articled (variously fused in some taxa but not as in state 2); (2) articles 2–3 fused and dominating, 4–5 fused and small (all fused in *Basserolis*). (1.00)

*(44) Maxillipedal palp (of 3 segments):* (1) fused articles 2–3 broadened distally, 4–5 quadrangular; (2) fused articles 2–3 oval, 4–5 min. (1.00)

*Pereopods*

*(45) Male pereopods, dense brushes of hairs on posterior margins of some distal articles:* (1) absent; (2) present. (0.06)

*(46) Coxal keys (lobes on anterior margin of coxa inserting into groove on posterior margin of preceeding coxa):* (1) absent; (2) present. (0.19)

*(47) Pereopod 1 propodus:* (1) not swollen, not proximally lobed over merus; (2) swollen, oval or proximally lobed over merus. (0.20)

*(48) Propodus 1 propodus:* (1) not as follows; (2) subchelate, barely tapering, palm straight. (0.00)

*(49) Pereopod 1 carpus:* (1) without 1–2 robust posterodistal setae opposing dactylus; (2) with 1–2 robust posterodistal setae opposing dactylus. (0.33)

*(50) Pereopodal 1–3 meri (sometimes ischia also):* (1) without short blunt robust setae (typical flagellate robust setae may be present); (2) with row of short blunt robust setae (in addition to slender setae). (0.24)

*(51) Pereopod 1 propodus:* (1) with single distal setulated seta on palm (or not with special seta); (2) with special strong mesial setulated seta adjacent to distal palmar seta. (0.00)

*(52) Pereopod 1:* (1) pereopod 1 subchelate or ambulatory; (2) prehensile, strongly curved. (1.00)

*(53) Pereopods 2–7:* (1) ambulatory; (2) all similarly prehensile. (1.00)

*(54) Pereopods, cuticular peg-like tubercles:* (1) absent; (2) present. (0.25)

*(55) Pereopod 2 of male:* (1) as in females; (2) subchelate, thinner that other pereopods. (0.33)

*Pleopods*

*(56) Pleopod 1:* (1) not thickened and operculiform; (2) peduncle and rami thickened and operculiform (tightly fitting with pleotelson). (1.00)

*(57) Pleopod 4:* (1) lamellate (not enclosing pleopods 4–5); (2) exopod operculiform (enclosing pleopod 4 endopod and pleopod 5 in chamber). (1.00)

*(58) Pleopods 1–3 peduncles:* (1) much shorter than rami; (2) longer than wide, almost as long as rami. (0.33)

*(59) Pleopod 3 peduncle:* (1) without broad mediodistal lobe; (2) with broad mediodistal lobe. (1.00)

*(60) Pleopod 3 endopod:* (1) more or less oval or rectangular, rounded distally; (2) roughly triangular (or at least with inner angle sharper than outer). (1.00)

*(61) Pleopod 3 exopod, article 1:* (1) not as following; (2) with 2 spaced setulated setae. (1.00)

*(62) Pleopod 3 with plumose setae:* (1) absent (or few apical) on endopod (at least in adults); (2) present on both rami. (0.11)

*(63) Pleopod 4 with plumose setae:* (1) absent on both rami; (2) present on both rami; (3) absent on endopod. (0.34)

*(64) Pleopod 5 with plumose setae:* (1) absent on both rami; (2) present on both rami; (3) absent on endopod. (0.14)

*(65) Pleopod 4 transverse fleshy ridges:* (1) absent; (2) on endopod or both rami. (1.00)

*(66) Pleopod 5, transverse fleshy ridges:* (1) absent; (2) present on endopod; (3) present on both rami. (0.00)

*(67) Pleopod 5 exopod:* (1) without scale patches; (2) with scale patches. (0.42)

*Uropods*

*(68) Uropodal rami:* (1) terminal; (2) ventral to margin of pleotelson, articulating in vertical axis; (3) ventral to pleotelson, articulating from side to side along vertical axis inside branchial space; (4) lateral to margin of pleotelson, articulating along longitudinal axis and folding down alongside branchial space. (1.00)

*(69) Uropod, position:* (1) not in posterior notch on pleotelson; (2) uropods lying obliquely in posterior notch on pleotelson and meeting at midpoint. (1.00)

*(70) Uropod, number of rami:* (1) biramous (or not as follows); (2) with exopod free, endopod fused to peduncle. (1.00)

*(71) Uropod peduncle, size:* (1) without enlarged peduncle, rami of normal size; (2) with extremely enlarged peduncle and embedded small rami. (0.33)

*(72) Uropod shape:* (1) with 2 rami or 1 ramus long and tapering; (2) with 1 long tapering ramus lying alongside telson. (1.00)

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Clade 15 (bs < 50) (suborder Limnoriidea) is defined by characters of low *CI*: pleonite 1 is narrower than pleonite 2 [17] and there is no mandibular molar [27]. The component clade 16, Limnoriidae + Hadromastacidae, has bs = 77.

Clade 6 (bs = 66) taxa have only one basal endite on maxilla 2 [36] and comprises a series of families. Clade 7 (bs < 50) taxa share an acute projecting mandibular incisor [24] and a spine row is absent [25]. Clade 8 (bs = 63) taxa share a smooth mandibular molar [29] and reduced setation on maxilla 1 endites. Gnathiidae and Anthuridea, clade 9

(bs = 70), taxa share reduced dorsal coxal plates [7] and maxilla 2 is fused to the hypopharynx [36]. Clades 10 and 11 are without bootstrap support, the latter taxa having a maxilla 2 with hooks on the basal lobes [37]. The taxa of clade 12 (Aegidae, Cymothoidae, Epicaridea, bs = 64) possess a maxillipedal palp with terminal articles set obliquely and with hooks [42], and a strongly curved pereopod 1 [52]. The sister-group relationship (clade 13, bs = 88) between Cymothoidae and Epicaridea is well supported. These taxa share: protandric development [1];

maxilla 1 inner lobe is absent [35]; retention of blunt setae on pereopods 1–3 meri [50]; pereopods 2–7 prehensile [53], and loss of marginal setae on pleopods 3 and 5 [62, 64].

Clade 14 (Cirolanidae, bs = 77) taxa have a tridentate mandibular incisor [24] and a spine row on a fleshy lobe [26].

**Table 3.    A new phylogenetically based classification of Isopoda Scuticoxifera into superfamilies and suborders**
The superfamily 'Cymothooidea' and the family 'Sphaeromatidae' are paraphyletic to accommodate existing higher monophyletic taxa and the names placed in quotes.

| Suborder | Superfamily | Family |
|---|---|---|
| Oniscidea Latreille, 1802 | See Martin and Davis 2002 | See Martin and Davis 2002 |
| Tainisopidea, new suborder | | Tainisopidae Wilson, 2003 |
| Phoratopidea, new suborder | | Phoratopodidae Hale, 1925 |
| Cymothoida Wägele, 1989 | 'Cymothooidea' Leach, 1814 | Aegidae White, 1850 |
| | | Anuropidae Stebbing, 1893 |
| | | Corallanidae Hansen, 1890 |
| | | Cymothoidae Leach, 1814 |
| | | Gnathiidae Leach, 1814 |
| | | Protognathiidae Wägele & Brandt, 1988 |
| | | Tridentellidae Bruce, 1984 |
| | Bopyroidea Rafinesque, 1815 | Bopyridae Rafinesque, 1815 |
| | | Dajidae Giard & Bonnier, 1887 |
| | | Entoniscidae Kossmann, 1881 |
| | Cryptoniscoidea Kosmann, 1880 | Asconiscidae Bonnier, 1900 |
| | | Cabiropidae Giard & Bonnier, 1887 |
| | | Cryptoniscidae Kossmann, 1880 |
| | | Cyproniscidae Bonnier, 1900 |
| | | Fabidae Danforth, 1963 |
| | | Hemioniscidae Bonnier, 1900 |
| | | Podasconidae Bonnier, 1900 |
| | Anthuroidea Leach, 1914 | Anthuridae Leach, 1814 |
| | | Antheluridae Poore & Lew Ton, 1988 |
| | | Expanathuridae Poore, 2001 |
| | | Hyssuridae Wägele, 1981 |
| | | Leptanthuridae Poore, 2001 |
| | | Paranthuridae Menzies & Glynn, 1968 |
| | Cirolanoidea Dana, 1852 | Cirolanidae Dana, 1852 |
| Limnoriidea Brandt & Poore, 2002 | Limnorioidea White, 1850 | Hadromastacidae Bruce & Müller, 1991 |
| | | Keuphyliidae Bruce, 1980 |
| | | Limnoriidae White, 1850 |
| Valvifera Sars, 1882 | | Antarcturidae Poore, 2001 |
| | | Arcturidae Dana, 1849 |
| | | Arcturididae Poore, 2001 |
| | | Austrarcturellidae Poore & Bardsley, 1992 |
| | | Chaetiliidae Dana, 1849 |
| | | Holidoteidae Wägele, 1989 |
| | | Holognathidae Thomson, 1904 |
| | | Idoteidae Samouelle, 1819 |
| | | Pseaudidotheidae Ohlin, 1901 |
| | | Rectarcturidae Poore, 2001 |
| | | Xenarcturellidae Sheppard, 1957 |
| Sphaeromatidea Wägele, 1989 | Sphaeromatoidea Latreille, 1825 | 'Sphaeromatidae' Latreille, 1825 |
| | | Tecticipitidae Iverson, 1982 |
| | | Ancinidae Dana, 1852 |
| | | *Paravireia* Chilton, 1925 incerta sedis |
| | Seroloidea Dana, 1852 | Basserolidae, new family |
| | | Plakarthriidae Hansen, 1905 |
| | | Schweglerellidae Brandt *et al*., 1999 |
| | | Serolidae Dana, 1852 |
| | | Bathynataliidae Kensley, 1978 |

Clade 17 (synapomorphies above) comprises sister-taxa, suborder Valvifera and clade 18 (suborder Sphaeromatidea). Several clearly defined synapomorphies, in particular operculiform uropods, define the Valvifera. The present analysis suggests that clade 18 (suborder Sphaeromatidea, bs < 50) taxa are characterised by: the ventral coxal plates of pereopod 7 not meeting in the middle [12]; pleonite 1 narrower than 2, and more or less immersed in it [17]; and a reduced lacinia mobilis fused with the spine row on the right [25]. Clade 18 includes two superfamilies, Sphaeromatoidea (clade 19) and Seroloidea (clade 25).

Clade 19 (superfamily Sphaeromatoidea, bs = 72) taxa share: dorsal coxal plates 2–7 fused to tergites [8]; pleonite 5 fused to the pleotelson [15], and the uropodal endopod fused to the peduncle [72]. One of its branches represents the unusual genus *Paravireia*, which has numerous autapomorphies. The other branch, clade 20 (bs = 73), comprises the small families Tecticipitidae and Ancinidae (clade 23, bs = 59) and the Sphaeromatidae, the latter which appears to be paraphyletic, at least as represented by the five genera analysed here. Clade 20 taxa are characterised by a free pleonite 1; pleonites 2–4 fused, and 5 fused to the pleotelson [16]; pleopod 3 with setae on both rami [62], and pleopod 5 exopod with scale patches [67]. Tecticipitidae and Ancinidae (clade 23) share a spine-like mandibular molar [30], swollen propodus on pereopod 1 [47], and subchelate male pereopod 2 [55]. Members of the Ancinidae (clade 24, bs = 99) have a fused head and pereonite 1 [4], loss of a spine row [26], a broad truncate maxillipedal endite without setae [41], and a tapering fused uropodal ramus [72].

Clade 25 (superfamily Seroloidea, bs < 50) comprises the highly derived *Plakarthrium* and clade 26. Synapomorphies of clade 25 taxa are: a flat disc-like body shape [2]; spine-like mandibular molar [30]; small inner lobe of maxilla 1 [35]; and loss of setae on the endopod of pleopod 4 [63]. Clade 26 (bs = 54), which comprises *Schweglerella* and clade 27 (bs = 94), taxa share: a head embedded and fused with pereonite 1 [3, 4]; ventral coxal plates 1–7 extending to midpoint [11]; no mandibular spine row [26]; maxilla 2 basal lobes with one or two setae [37]; 3-segmented maxillipedal palp [43]; and the peduncles of pleopods 1–3 longer than wide [58]. Members of clade 27 (families Bathynataliidae and Serolidae) lack a dorsal coxal plate 7 [10], such that pereonite 7 is narrower than pereonite 6 [13], and have characteristic setation of the pereopod 1 carpus [49]. Clade 28 (Bathynataliidae, bs = 96) is well defined by synapomorphies with *CI* = 1: pleonal epimera 2 and 3 prolonged and surrounding pleotelson [18]; ventrolateral margins of pleon and pleotelson broad and flattened [21]; maxillipedal palp with articles 2–3 fused and oval and articles 4–5 fused and minute [44]; and pleotelson with uropods in a posterior notch and with enlarged peduncle and small, embedded rami [69, 71]. Clade 30 (Serolidae + *Basserolis*, bs = 80) taxa can be recognised by: dorsal coxal

**Table 4. Synapomorphies of each clade and taxon in the weighted strict consensus cladogram generated by PAUP\* (Fig. 6)**

Only character transformations common to clades in the two most widely distant trees are listed. Superscripted numbers are the synapomorphic states, derived from state 1 unless otherwise indicated. Characters in bold have a weight of 1. 'Cymothooidea' + includes Anthuroidea, Bopyroidea and Cryptoniscoidea.

| Clade number or taxon | Characters changing and states |
|---|---|
| *Phreatoicus* | **68**$^2$ |
| Clade 1 | 15$^3$ |
| Clade 2 | **6**$^2$ **14**$^2$ |
| *Oniscus* | 8 $^2$ |
| Tainisopidae | 23$^2$ |
| Clade 3 | **28**$^2$63$^2$ 64$^2$ |
| *Phoratopus* | 10$^2$ |
| Clade 4 | 24$^3$ |
| Clade 5 – Cymothoida | 25$^3$ 26$^2$ **39**$^2$ 50$^2$ |
| Clade 6 – 'Cymothooidea'+ | 36$^2$ |
| Clade 7 | 24$^{3>4}$ 26$^{2>5}$ |
| Clade 8 | 29$^2$ 34$^2$ 35$^2$ |
| Clade 9 | 7$^2$ 36$^{2>3}$ |
| Gnathiidae | 27$^2$ 33$^2$ 50$^{2>1}$ 54$^2$ |
| Anthuridea | 1$^2$ 24$^{4>3}$ 25$^{3>2}$26$^{5>4}$ |
| Clade 10 | 64$^{2>3}$ |
| Corallanidae | 26$^{5>2}$ |
| Clade 11 | 37$^{1>3}$ |
| *Tridentella* | 29$^{2>1}$ |
| Clade 12 | 42$^2$ **52**$^2$ |
| Clade 13 | 1$^2$ 35$^{2>3}$ 50$^{2>1}$ **53**$^2$ 62$^{2>1}$ 64$^{3>1}$ |
| Cymothoidae | 63$^{2>1}$ |
| Epicaridea | 27$^2$ 32$^2$ 33$^2$ 36$^{2>3}$ 42$^{2>1}$ 64$^2$ |
| Clade 14 – Cirolanidae | 24$^{3>2}$ 26$^{2>3}$ |
| *Bathynomus* | 23$^2$ |
| *Natatolana* | 64$^{2>3}$ |
| Clade 15 – Limnoriidea | 17$^2$ 27$^2$ 38$^2$ 51$^2$ |
| *Keuphylia* | 2$^2$ 3$^2$ 32$^2$ 46$^2$ |
| Clade 16 | **5**$^2$ 24$^{3>5}$ **40**$^2$ 54$^2$ |
| Limnoriidae | 17$^{2>1}$ 23$^2$ 38$^{2>1}$ 64$^{2>1}$ |
| *Hadromastax* | 9$^2$ 15$^3$ 25$^3$ 26$^5$ 51$^{2>1}$ |
| Clade 17 | **20**$^2$ 60$^2$ 68$^4$ |
| Clade 18 – Sphaeromatidea | 12$^2$ 17$^2$ 25$^2$ |
| Clade 19 – Sphaeromatoidea | 8$^3$ 15$^2$ **70**$^2$ |
| *Paravireia* | 36$^2$ |
| Clade 20 | **16**$^2$ 62$^2$ 67$^2$ |
| Clade 21 | 45$^2$ **65**$^2$ 66$^2$ |
| *Dynamene* | 66$^{2>3}$ |
| Clade 22 | 2$^2$ |
| *Paraleptosphaeroma* | 22$^2$ |
| Clade 23 | 30$^2$ 47$^2$ 55$^2$ |
| *Tecticeps* | 24$^3$ 63$^3$ 66$^3$ 67$^{2>1}$ |
| Clade 24 – Ancinidae | 4$^2$ 26$^5$ **41**$^2$ 62$^{2>1}$ **72**$^2$ |
| *Ancinus* | 45$^2$ |
| *Bathycopea* | 35$^2$ |
| Clade 25 – Seroloidea | 2$^2$ 30$^2$ 35$^2$ 63$^3$ |
| *Plakarthrium* | 9$^2$ 17$^{2>1}$ 22$^2$ 27$^2$ 32$^2$ 34$^2$ 35$^{2>3}$ 64$^3$ |
| Clade 26 | 3$^2$ 4$^2$ 11$^2$ 26$^5$ 37$^2$ **43**$^2$ 58$^2$ |
| *Schweglerella* | 19$^2$ |
| Clade 27 | 10$^2$ 13$^2$ 49$^2$ |
| Clade 28 – Bathynataliidae | **18**$^2$ **21**$^2$ 44$^2$ 69$^2$ 71$^2$ |

(*continued next page*)

**Table 4.**    (continued)

| Clade number or taxon | Characters changing and states |
|---|---|
| *Biremia* | $15^2\ 26^{5>1}\ 48^2$ |
| Clade 29 | $12^{2>1}\ \mathbf{31^2}\ 47^2\ \mathbf{56^2}\ \mathbf{59^2}\ \mathbf{61^2}\ 64^3$ |
| *Bathynatalia* | $2^{2>1}\ 10^{2>1}\ 13^{2>1}\ 49^{2>1}$ |
| *Naudea* | $46^{2>1}$ |
| Clade 30 | $8^{\ 2}15^{\ 3}\ 24^3\ 25^{2>1}\ \mathbf{57^2}\ 62^2$ |
| *Basserolis* | $25^3\ 27^2\ 46^{2>1}\ 48^2\ 63^{3>2}$ |
| Serolidae | $19^2\ 37^{2>1}\ 45^2\ 47^2\ 55^2\ 58^{2>1}$ |
| Valvifera | $15^3\ 45^2\ 71^2$ |

plates 2–4 free and 5–7 fused to tergites [8]; pleonites 1–3 free and 4 and 5 fused to the pleotelson [15]; mandibular incisor broad [24]; mandibular lacinia mobilis present on both sides [25; reversal]; and pleopod 4 exopod operculiform and enclosing pleopod 4 endopod and pleopod 5 in a chamber [57]. The Serolidae and *Basserolis* each have many autapomorphies.

## Discussion

### New ideas and comparison with earlier phylogenies

Our new phylogeny restates and develops relationships realised much earlier and translates them into a revised classification. The phylogeny incorporates ideas introduced by Sars (1882) and schematised by Monod (1922). The concepts were elaborated by Wägele (1989), who derived relationships using 27 taxa of genus, family and suborder rank and 133 morphological characters. He followed Hennigian principles without using a computer-based programme or the criterion of parsimony. Figure 7*A* is a compilation of three of his dendrograms. In the first dendrogram (Wägele 1989: 231 ff., fig. 107), 42 characters defined the major clades and suborders of Isopoda. In the second, 52 characters defined families of his new suborder, Sphaeromatidea (Wägele 1989: 168 ff., fig. 79), and in the third, 39 characters provided synapomorphies of families of another new suborder, Cymothoida (Wägele 1989: 197 ff., fig. 93). In his scheme, the Flabellifera were effectively replaced by two new monophyletic suborders, but he did not explicitly countenance the possibility that either the Anthuridea or Valvifera, or both, might be clades within the others. His ideas were developed further later. Dreyer and Wägele (2001) used molecular characters plus 71 morphological characters in a revised phylogenetic analysis of the position of Bopyridae relative to other parasitic and semi-parasitic taxa. Their arguments were included in Wägele's textbook on phylogenetic systematics (Wägele 2000) as an example of his phylogenetic methodology. But, except for Roman and Dalens (1999), his classification has not been adopted.

Brusca and Wilson's (1991) cladistic analysis used 92 characters and 25 taxa, but they did not translate their weakly resolved cladogram (Fig. 7*B*) into a revised classification of Isopoda.

The new results are similar, especially to those of Wägele, but there are significant differences between the two phylogenies and classifications. Importantly, two of
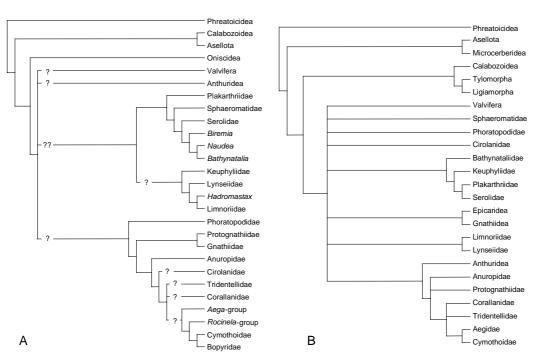


**Fig. 7.**    *A*, Relationships between suborders, families and genera postulated by Wägele (1989); a combination and redrafting of his figs 79, 93 and 107. *B*, Relationships between suborders and families postulated by Brusca and Wilson (1991: fig. 14).

Wägele's four subordinal clades are embedded in the others, and any similarities in phylogenetic structure are explained by very different synapomorphies. Our discussion will concentrate on explaining the major clades and investigating the differences between our results and those of Wägele, whose ideas are closest to ours.

The phylogenetic studies of Wägele (1989), Brusca and Wilson (1991) and our own recognise a taxon, the Oniscidea plus all the flabelliferan taxa in the widest sense, to which Dreyer and Wägele (2002) gave the name Scuticoxifera. All authors agree that members of this taxon have coxae extended as dorsal coxal plates. Dreyer and Wägele (2002) excluded *Tainisopus* from this clade, but the possession of dorsal coxal plates suggests it does belong in this group (Wilson 2003). Wägele (1989) included a character in which the anterior filter rows in the caudal part of the stomach are bent laterally, and our analysis discovered that all scuticoxiferans possess mesial penial processes. Tabacaru and Danielopol's (1999) results are quite different and include Calabozoidea in this clade as sister-taxon to Oniscidea.

A clade with Oniscidea excluded was defined by Wägele (1989) on the basis of stomach characters not considered by us: stomach sclerite 4 laterally connected to stomach sclerite 1, and stomach sclerite 3 present. Brusca and Wilson (1991), on the other hand, recognised a functional 3 + 4 pereopod grouping, broad and flattened uropods, and the well-developed telsonic region of the pleotelson with the anus on pleomere 6. We cannot disagree with Wägele, but we found no synapomorphies to support a flabelliferan clade. We have some doubts about the value of Brusca and Wilson's pereopodal grouping. The 'long-tailed' telson of Brusca and Wilson was treated by them as a single synapomorphy and by Wägele (1989, 1994*b*) as a symplesiomorphy. The difference between the two hypotheses lies more in the interpretation of homoplasy of styliform uropods in asellotes, phreatoicideans and oniscideans.

More important for us is the significant character-complex of the pleon, pleopods and uropods that groups most scuticoxiferans into two clades. In *Phoratopus* plus suborders Cymothoida and Limnoriidea, the uropodal rami are ventral to the pleotelson and articulate from side to side along a vertical axis posterior to, and in contact with, the pleopods. The pleopods all have marginal plumose setation, unlike those of the outgroup taxa and the sister-taxon. Valvifera and Sphaeromatidea, in contrast, have a vaulted pleotelson enclosing a branchial chamber defined by ventro-lateral ridges. Pleopods 3–5 lack some marginal setation. The uropods are not inside the well-defined branchial space, but are lateral to it and articulate along a longitudinal axis. In our view, the 'tailfans' of, for example, Cirolanidae and Sphaeromatidae are quite different. In the former, the uropods are under the pleotelson and able to be splayed horizontally, whereas in the latter, the uropods are lateral to the pleotelson and can rotate ventrally; horizontal splaying

is achieved only by the exopod. The Valvifera are a special case, simply derived from a sphaeromatid-like condition, where the uropods have rotated into a ventral position. We have no evidence to suggest the cymothoidan form is derived from the sphaeromatidean form or *vice versa*, but believe it likely they are independently evolved from a condition that could also be ancestral to the styliform condition of more primitive isopods. The only feature in common between them is that the uropodal rami are flattened—not expressed in our scoring of characters 20 and 68 in particular.

Tainisopidae do not fall clearly into either of these two major clades.

Within the non-oniscidean clades, we recognise six unambiguously related clades to which we give subordinal rank: Phoratopidea, Cymothoida and Limnoriidea in one clade, Valvifera and Sphaeromatidea in another, and Tainisopidea.

Wägele (1989) recognised only four of these clades and there are important differences between his results and ours (Fig. 7*A*).

(1) He was not aware of *Tainisopus* and did not recognise the unusual features of *Phoratopus*.

(2) He was undecided about relationships between the four taxa.

(3) The synapomorphies, said by Wägele to define the four clades, are different from those discovered in this study.

(4) Wägele was uncertain about the position of a fifth group, Anthuridea, which we place within Cymothoida.

(5) Limnoriidea, said by Wägele to be within Sphaeromatidea, was found to be sister-taxon to Cymothoida.

(6) Valvifera was found to be as sister-taxon to Sphaeromatidea (according to Wägele the position of Valvifera was uncertain).

In Brusca and Wilson's analysis (1991), the equivalent taxa were distributed in eight clades whose relationships were unresolved (Fig. 7*B*). The largest included most Cymothoida, incorporating Anthuridea but not Cirolanidae, Phoratopodidae, Epicaridea or Gnathiidae. The similarities among Sphaeromatidae, Serolidae and Bathynataliidae were not evident. The affinities of Limnoriidae and Keuphyliidae were not recognised (they included Lynseiidae, now a junior synonym of Limnoriidae, but not Hadromastacidae).

The unusual family Tainisopidae has numerous synapomorphies. More importantly, it does not share the characters of other taxa: it does not have the modified mandible, urpodal rami, or plumose pleopods 4 and 5 of taxa in the phoratopidean–cymothoidan–limnoriidean clade. Nor does it possess the vaulted fused pleonites and hinged uropod of the sphaeromatidean–valviferan clade. Wilson and Ponder (1992) did not place *Tainisopus* in a family or in any suborder. They argued, on the basis of numerous characters, that it could not be a phreatoicidean or asellote. Largely

because they were not confident in defining the 'Flabellifera', they could find no synapomorphies that might ally it with that group. On balance, they felt it had several plesiomorphic features (body shape, generalised mouthparts) suggesting divergence earlier than the flabelliferan taxa. Wilson (2003) placed the family with Limnoriidea, but admitted that the evidence was not strong. His only evidence came from maxillipedal shape, but this is highly variable and difficult to quantify unambiguously. We, in contrast, believe it deserves subordinal rank.

Likewise, *Phoratopus remex* has numerous autapomorphies, but its relationship to its sister-taxa (Cymothoida and Limnoriidea) could not be resolved. *Phoratopus* does not have the mandibular or maxillipedal structure of either the Cymothoida or Limnoriidea, or the pereopodal setation of Cymothoida or narrow pleonite 1 of Limnoriidea. In Wägele's (1989) cladogram, cymothoidan synapomorphies were used to exclude Phoratopodidae from the remainder, a decision also based on mouthpart features. Because we could not place *Phoratopus* in either suborder, we erect a new suborder for it.

Synapomorphies of the suborder Cymothoida, well supported by bootstrap, are seen in the mandibular spine row (independent short, simple spines), the absence of a lacinia mobilis, a short maxillipedal endite and pereopodal meri 1–3 with short blunt robust setae. Wägele (1989) characterised the Cymothoida by a mesially extended prolongation of the uropodal peduncle under the pleotelson, a broad incisor with three large teeth and a flat triangular molar. His uropodal character may be a different interpretation of the character we use to define the Cymothoida + Limnoriidea. The tridentate incisor is confined to Cirolanidae.

Within Cymothoida are two well-supported clades that we treat as superfamilies. The first, Cirolanoidea (single family, Cirolanidae), has a spine row on a fleshy lobe and a tridentate incisor. The Cirolanidae are an intermediate branch in Wägele's cladogram, and without synapomorphies (implying paraphyly), but our results provide good evidence for family placement outside the remaining cymothoidans. We could find no evidence among the many species assigned to this family to suggest that it is paraphyletic with respect to its sister-taxon. The family is the least modified of the cymothoidans, with scavenging or predatory rather than parasitic feeding (Jones and Pierpoint 1997). Relationships among the Cirolanidae were not identified by Brusca and Wilson (1991).

The second clade includes six families plus Anthuridea, Epicaridea and Gnathiidae—the latter three monophyletic taxa have each been assigned subordinal rank at some time. All are predatory or parasitic, at least at some stage in life history. All have only one basal endite on maxilla 2, or further reduction. None of Dreyer and Wägele's (2001) analyses of molecular data were able to unambiguously resolve relationships between all these taxa. In a later paper

(again using molecular data), Dreyer and Wägele (2002) proposed a similar clade on the basis of fewer families.

Although the exact relationships of the nine families differ, there are many similarities between Wägele's (1989) analyses (Fig. 7*A*) and the analyses presented here. For example, we too have a robust (bs = 88) Cymothoidae–Epicaridea clade, with aegids, tridentellids and corallanids possibly more basal. Wägele placed the Gnathiidae–Protognathiidae basally, but we found gnathiids and anthurideans to be sister-taxa. Few of the dichotomies in this part of the cladogram are corroborated by bootstrap. Although Wägele (1989) recognised the monophyly of the Anthuridea, with eight synapomorphies, he did not associate them with gnathiids. One of the most convincing characters uniting Anthuridea with Cymothoida is seen in the hyssurid *Belura pilara* (Poore and Lew Ton 1988). Its mandibular molar is a reduced version of the toothed blade seen in cirolanids. Wägele believed the synapomorphies of this clade (without anthurideans) to include: the dactyls of pereopods 1–3 transformed as hooks, at least as long as the propodus; maxillipedal palp with short, bent hooks; molar short and blunt, and incisor slender. In our analysis, this association is defined on the basis of a single basal endite on maxilla 2. There is strong molecular evidence for the Cymothoidae + Bopyridae clade (Dreyer and Wägele 2001, 2002). Dreyer and Wägele (2001) argued convincingly on the basis of life history and feeding strategy that these two are sister-taxa. Corallanidae are usually fish parasites, but the ability to be ectoparasitic on crustaceans is found in this family: *Tachaea caridophaga* on caridean shrimps (Riek 1967) and *Excorallana tricornis occidentalis* on mysidaceans (Guzman *et al*. 1988). The more derived epicarideans have specialised in crustacean parasitism.

Brusca and Wilson (1991) presented a very different tree with only partial resolution of these cymothoidan taxa (Fig. 7*B*). They placed Anthuridea as the most primitive taxon within the scavenging and parasitic clade comprising Anuropidae, Protognathiidae, Corallanidae, Tridentellidae and Aegidae + Cymothoidae. The synapomorphy of these families according to these authors is the reduced or vestigial maxilla 1. They considered Gnathiidae to be a sister-taxon to the epicarideans.

We propose a new suborder, Limnoriidea, for Limnoriidae, Hadromastacidae and Keuphyliidae. Although we have no bootstrap support for Keuphyliidae within this taxon, the only species in the family does share unique characters with Limnoriidae (special seta on pereopod 1) or Hadromastacidae (short maxilla 2 endites). Wilson (2003) found this unconvincing, but the alternative is even less so. The mandible is more like that of some cymothoidans, but the maxillipedal endite is not shortened and robust setae are absent on the pereopodal meri. The synapomorphies of the suborder are: pleonite 1 narrower than pleonite 2; broad (Keuphyliidae) or conical (other families) mandibular incisor

dentition; no mandibular molar; lobes of maxilla 2 as long as wide, and an extra strong serrate seta posterodistally on the propodus of pereopod 1. Wägele (1989) used similar characters, but added a non-subchelate pereopod 1. He and Brusca and Wilson included Lynseiidae, a family since synonymised with Limnoriidae (Cookson and Poore 1994). Bruce (1988*a*) and Bruce and Müller (1991) recognised the affinities of these families using characters of the head, antennae, all mouthparts, pereopods and pleopods. Hansen's (1916) and other early classifications recognised Limnoriidae as a subfamily of Sphaeromatidae and Wägele's (1989) analysis shows it is probably closest to this group (he indicated his doubt with a '?' in his fig. 79). The affinity of *Limnoria* to *Sphaeroma* was supported by molecular data (Dreyer and Wägele 2002). Wägele (1989) suggested that the Limnoriidae + Keuphyliidae clade shares with the Serolidae + Bathynataliidae + Plakarthriidae + Sphaeromatidae clade a discoid body shape, pereonite 1 laterally surrounding the head, and pleopods 4 and 5 larger than pleopods 1–3. In our opinion, this body shape is not a general feature of all groups and is rare in sphaeromatids in particular. The flattened form is a convergent character achieved in different ways. The head–pereonite 1 relationship differs markedly between these taxa: the head is freely attached in limnoriids, fused medially in serolids and bathynataliids, and separate (even if immobile) in sphaeromatoids.

We believe the Limnoriidea to be the sister-taxon of Cymothoida. No limnoriideans possess the well-defined branchial chamber, or vertically hinged uropods of the sphaeromatoids and valviferans. Instead, pleonites are free (except in *Hadromastax*) and do not form a branchial chamber. The uropods are reduced, but their ventral position is more likely cymothoidan than sphaeromatidean. Marginal pleopod setation, an important synapomorphy of the cymothoidan clade, is also a feature of limnoriideans.

The monophyly of the Valvifera is undisputed, but no previous author has been able to discover its affinities. The principal synapomorphy, the uropods forming a branchial chamber, is, in our view, derived from the sphaeromatidean condition. All 520 known species, with one exception, lack a mandibular palp (Poore and Lew Ton 1990). Wägele added another character, antenna 1 with only two flagellar articles, but this is not universal (Brusca 1984). The Sphaeromatidea–Valvifera relationship was corroborated in some analyses using molecular evidence (Wetzer 2002).

The Sphaeromatidea of Wägele (1989) included Bathynataliidae, Plakarthriidae, Serolidae and Sphaeromatidae, plus three taxa we assign to Limnoriidea. We disagree with his interpretation of all three characters that were used to define this clade (Wägele 1989: fig. 79). Wägele believed: a flattened disc-like body was a synapomorphic trait (most sphaeromatids are highly vaulted like other isopods); the head sunken into pereonite 1 was distinctive (we believe it is not more so than in other isopods); and pleopods 4 and 5 are

larger than 1–3 (if true, this trait is shared with Valvifera). He appears to have recognised no synapomorphies for the more restricted clade (those listed except Limnoriidea). We have recognised weak synapomorphies: pleonite 1 is narrower than 2 and immersed in it; the ventral coxal plates do not meed in the middle and the right lacinia mobilis is reduced and fused to the spine row—but the absence of valviferan characters is more convincing. Wägele (1989) did propose that the Sphaeromatidae and Bathynataliidae + Serolidae share a strong, subchelate pereopod 1, with broad propodus and short, triangular, ventrally produced carpus, but this is true only for Tecticipitidae, Ancinidae, Bathynataliidae and Serolidae, not for Sphaeromatidae *sensu stricto*. The same is true for his next character: pereopod 2 of male strong, subchelate, but smaller than pereopod 1. His third character for this clade—pleotelson relatively large, ventrally concave and forming a breathing chamber for the pleopods—parallels what we propose as a character linking all Sphaeromatidea and Valvifera. Sheppard (1933) also believed that Serolidae might be more closely related to Sphaeromatidae than to any other family.

Our analysis, with more sphaeromatidean taxa than included by Wägele, found two well-defined groups to which we give superfamily rank: Seroloidea and Sphaeromatoidea.

The relationships proposed here between Seroloidea genera and families differ from those of Wägele (1989) and Brusca and Wilson (1991). We consider *Plakarthrium*, whose position has always been enigmatic (Wilson *et al*. 1976; Poore and Brandt 2001), as the most primitive seroloid, although this relationship is without bootstrap support. Members of the superfamily are flat; the head is overlapped laterally by the coxae of pereopods 1; the distally denticulate flattened mandibular molar, and the small inner lobe of maxilla 1 have one seta. *Plakarthrium* has all these characters, but lacks a molar. More importantly, *Plakarthrium* does not have the fused uropodal endopod and fused dorsal coxal plates seen in Sphaeromatoidea.

Wägele (1989) recognised *Plakarthrium* as sister-taxon to Serolidae + Bathynataliidae + Sphaeromatidae, whereas Brusca and Wilson placed it as sister-taxon to Serolidae alone. The Bathynataliidae is the sister-taxon of Serolidae as Wägele (1989) and Brandt *et al*. (1999) proposed, not an outgroup to the Serolidae + Plakarthriidae + Keuphyliidae clade, as Brusca and Wilson (1991) thought. The relationship Wägele (1989) hypothesised between bathynataliid genera is identical to ours.

The fossil *Schweglerella* lacks limb characters, so its phylogenetic position has low bootstrap support. This is a common problem, particularly in fossils, when dealing with missing data (Kearney 2002). Nevertheless, *Schweglerella* shares with all seroloids, except *Plakarthrium*, a head embedded and probably fused with pereonite 1. It is not possible to derive the pleonal fusion of Serolidae from that

of *Schweglerella*, or *vice versa*, so we must conclude they share a common ancestor. The relationship to Bathynataliidae and Serolidae (+ Basserolidae) proposed by Brandt *et al.* (1999) is probable.

*Basserolis* would appear not to be a bathynataliid, despite its having a similar pereopod 1 and pleopods to those of *Biremia* (Bruce 1985). The genus has so many autapomorphies, as does its sister-taxon (the 20 genera of the Serolidae *sensu stricto*), that we erect a new family for it, Basserolidae, fam. nov. Serolidae and Basserolidae share an operculiform exopod of pleopod 4 that encloses the endopods of pleopods 4 and 5 in a chamber. Although serolids possess laterally directed peduncles of pleopods 1–3, basserolids have the plesiomorphic condition.

The Bathynataliidae bear prolonged pleonal epimera 2–3 that surround the pleotelson. The ventrolateral margins of the pleon and pleotelson are broad and flattened; a condition that we believe has developed from the simpler sphaeromatidean state. Wägele (1989) noted the character and the well-defined branchial chamber, but not its phylogenetic implications.

The superfamily Sphaeromatoidea is a new taxon with 72% bootstrap support; it includes genera that at some time have been included in Sphaeromatidae. The monophyly of Ancinidae and Tecticipitidae is confirmed, but we must conclude that the Sphaeromatidae are paraphyletic. Michel-Salzat and Bouchon (2002) placed two sphaeromatid genera on widely remote clades in their molecular treatment of Oniscidea, but this result must be anomalous. The family structure of this group can only be determined by analysis of the relationships of all genera. Wägele's (1989: fig. 79) characters defining Sphaeromatidae (he did not mention the other two families) included those found here to define the superfamily.

*Paravireia* has always been thought of as an aberrant sphaeromatid, without the pattern of pleonite fusion seen in most other genera. Its pleonal structure (pleonites 1–4 free) could have given rise to the typical sphaeromatid state: pleonite 1 free, 2–4 fused. Besides lacking the sphaeromatid pleon, the genus also lacks scale patches on the pleopod 5 exopod, but this state occurs in some typical sphaeromatid genera. However, given the uncertainty of the relationships between genera of Sphaeromatidae, and Tecticipitidae and Ancinidae, its familial status remains undecided.

As discussed earlier, we do not include *Plakarthrium* in Sphaeromatoidea.

### Limitations

We used more than one genus to represent large families in our treatment, with the result that some clades have weak support. In our cladogram, we treated the Aegidae as a monophyletic unit, although Wägele (1989) regarded the family as paraphyletic. He argued that the maxillipedal palp of the *Rocinela*-group has only two articles, like Cymoth-

oidae and Bopyridae (its sister-clade in his view). He believed the *Aega*-group, on the other hand, has a more developed maxillipedal palp and is basal to the others mentioned. Brusca and Wilson (1991) disagreed with these observations. Maxillipedal palp reduction is such a common event that we that we take the more conservative view until an analysis involving all aegid and cymothoid genera, and many more characters, is carried out.

Corallanidae (seven genera) and Tridentellidae (*Tridentella* only) are also two similar families and, whereas the former has been considered paraphyletic (Delaney and Brusca 1985), a rigorous cladistic analysis showed this not to be the case (Delaney 1989).

The monophyly of Epicaridea has not yet been unequivocally established. Dreyer and Wägele (2001) treated them as one family, Bopyridae, and, we assume, believed them to be monophyletic. The current classification of the 11 families into two superfamilies suggests a diverse taxon (Trilles 1999; Martin and Davis 2001).

Bruce (1993*b*, 1994) was unconvinced of the monophyly of the subfamilies of Sphaeromatidae. He concluded that the Tecticipitidae and Ancinidae are monophyletic and each defined by several synapomorphies, but that the remaining sphaeromatoids are unlikely to be monophyletic. He was unable to find any potential synapomorphies and analysis involving many genera is needed. For that reason, we attempted to account for sphaeromatid diversity by including representatives from all nominal subfamilies, but this falls far short of resolving relationships in this taxon of ~100 genera.

Our study convinces us of the value of looking at characters anew. The significant homologies in the branchial chambers of the Sphaeromatidea + Valvifera, their pleopods and the associated uropodal articulation are not evident in illustrations of dissected limbs. We have contrasted this arrangement with the arrangement of pleopods not in a branchial chamber and the uropods of Cymothoida + Limnoriidea. Although Wägele (1989) and Brusca and Wilson (1991) discussed the swimming ability of higher isopods, they did not recognise what we believe are major differences. We have no evidence to support the view that this is a single clade derived from an ancestral form. The pattern in phreatoicideans, oniscideans and asellotes might also be derived from this ancestral form. Although most cymothoidans have exposed pleopods, a branchial chamber has been created in some anthuroideans by operculiform first pleopods. An analogous situation is seen in some asellotes where pleopods 1 and 2 enclose the other respiratory pleopods.

The mouthparts of the scavenger–parasitic groups of Cymothooidea deserve reappraisal. Some homologies are explored for the first time, for example between the toothed blade-like mandibular molar of cirolanids and its reduced form in other cymothooidans, and between endites in

maxilla 2. Leptanthurid and paranthurid mandibular incisors are acute and lack molars, a situation converging on that in epicarideans. Homoplasy may exist among the latter groups and a more thorough morphological examination is warranted (Wägele 1994*b*). Apart from recognising Cymothoidae and Bopyridae as sister-taxa, major discrepancies still remain between our morphological and Dreyer and Wägele's (2002) molecular analysis. These authors admit to artefacts within the molecular phylogenies, in particular the failure to recognise aegid–cymothoid relationships.

It is not surprising in an analysis of a taxon as large and diverse as the flabelliferan Isopoda that homoplasy is high. As a consequence, we lack the formal confidence in some clades that we hoped the bootstrap test might give. Nevertheless, on the basis of the data used, we believe we have an acceptable evolutionary hypothesis upon which to base a classification.

*Radiation, ecology and biogeography*

Brusca and Wilson (1991) discussed the origin and phylogeny of the 'long-tailed' isopods as one clade that was most speciose and had its origin in the southern hemisphere. There, it developed its pleotelson morphology as it moved from an infaunal to epifaunal way of life. It is our view that all long-tailed morphologies are not homologous and we discuss Tainisopidea, Phorotopodidea, Cymothoida, Limnoriidea and Sphaeromatidea plus Valvifera separately. Our phylogeny and resulting classification reflect the possible relationship between morphology and lifestyle.

The Tainisopidea are freshwater taxa found only in north-western Australia and have a relictual ecology that reflects their isolated phylogenetic position (Wilson and Ponder 1992).

Phorotopidea are known from only two specimens of one species found in shelf waters of South Australia (Bruce 1981) and nothing more is known of its ecology.

Cymothoida comprise scavengers, ectoparasites and predators; essentially various carnivorous forms. Many are highly mobile, actively swimming out of the benthos into the water column in search of prey or carrion, at least at some stage of their life. Pleopods are exposed under the pleon and are broad and setose, enabling simultaneous swimming and respiration. The uropods are used for steering. Predation on small invertebrates is one feeding strategy adopted by some cirolanids (Bruce and Soares 1996). This strategy, and scavenging, as seen in Cirolanidae, would seem to be the plesiomorphic strategy within this clade. Some species of *Natatolana* are scavengers and will enter baited traps (Arntz and Gutt 1999; Marsden 1999; Storch *et al.* 2002). Cirolanid diversity is higher in tropical than cooler regions (Bruce 1986; Keable 1995) and correlates with a more diverse food supply, exemplified by the diversity of a typical food source: fishes. This is not to say that a few scavenging species do not reach high densities in cooler waters. Seven species of

*Natatolana* occur in the Southern Ocean (Storch *et al.* 2002). Only 18% of 429 species of Cirolanidae live at depths greater than 200 m (Kensley *et al.* 1996). Exceptions to this preference for warmer water are species of the upper slope genus *Bathynomus* (Soong and Mok 1994), which can reach depths below 2100 m. But this genus is also tropical and subtropical. Ectoparasitic and predatory taxa are also more diverse in tropical oceans: Cymothoidae (Segal 1987) (most species are tropical), Corallanidae and Tridentellidae (tropical to temperate), Gnathiidae (tropical to temperate), and epicarideans (mostly tropical, some temperate). Dreyer and Wägele (2001) hypothesised that parasitism of other crustaceans by Bopyridae (or epicarideans) evolved from their parasitism of fishes. In other words, bopyrids have evolved from a cymothoid-like ancestor. They pointed out that the mouthparts of the carnivorous cirolanids are more modified compared to omnivorous isopods, and that the step to the evolution of parasitic mouthparts is small. We agree with these authors and also with earlier similar opinions published by Menzies *et al.* (1955), Brusca (1981), Kussakin (1979) and Wägele (1989). We go further and suggest, based on the concordance of the phylogeny and the distributional and ecological evidence, that this transition took place in tropical waters.

The Limnoriidea are also principally a tropical taxon with relatively few cold-water representatives except in the cool temperate southern hemisphere. Hadromastacidae (Bruce and Müller 1991) and Keuphyliidae (Bruce 1980) are exclusively tropical and are associated with coral reefs. Limnoriids bore in and feed on wood, algae and seagrass (Cookson 1991; Brearley and Walker 1993, 1995). Cookson's (1989) phylogenetic analysis of Limnoriidae found that the most plesiomorphic genus, *Paralimnoria*, and species of *Limnoria* feed on wood in tropical environments and that seagrass and algae entered the diet only in the cool temperate environments of the southern hemisphere; the sea-grass-boring genus *Lynseia* (not part of Cookson's analysis) is found only in southern Australia.

Members of Valvifera and Sphaeromatidea are generally not as mobile as the representatives of other suborders. They are primarily benthic and, as a consequence, confinement of the pleopods in a breathing chamber through which water can be directed is advantageous. This is best developed in various ways: in Valvifera by enclosure of the pleopods by the uropods; in Serolidae by operculiform pleopods 4; some Sphaeromatidae with operculiform pleopods 1; and some sphaeromatids by a highly vaulted pleotelson, sometimes with a tube-tail (Bruce 1995). Serolidae are benthic predators and scavengers (Luxmoore 1985; Wägele 1989). Strong setose first pereopods suggest that perhaps Bathynataliidae, some chaetiliids, like *Saduria* and *Glyptonotus* (Green 1957; Leonardsson 1991), and some sphaeromatoids feed similarly. Members of some families, in particular Idoteidae and Holognathidae, are herbivorous (Bostrom and Mattila

1999), whereas most arcturoid valviferans are filter feeders (Wägele 1987). Most sphaeromatoids are detritivores, whereas others are herbivores (Menzies 1962*b*; Holdich 1981).

The present-day centre of diversity of Valvifera and Sphaeromatidea is the temperate southern hemisphere. Some families are, or are almost, exclusively southern: Plakarthriidae (Poore and Brandt 2001); Serolidae (Poore 1987; Brandt 1988; Wägele 1994*a*); Bathynataliidae (Bruce 1985); Holognathidae (Poore and Lew Ton 1990); Austrarcturellidae (Poore and Bardsley 1992); Arcturididae, Pseudidotheidae, Rectarcturidae, Xenarcturidae (Poore 2001*a*), and Holidoteidae (Poore 2003). Others are highly diverse in southern temperate or polar environments, but extend into the deep sea (Antarcturidae (Brandt 1990)), or to boreal environments: Arcturidae, Idoteidae (Brusca 1984; Poore and Lew Ton 1993) and Chaetiliidae. Although the present centre of diversity tells us nothing about a centre of origin, it is clear that the selective pressures that have driven the feeding specialisation and radiation of these taxa are very different from those of the Cymothoida and Limnoriidea.

Wilson (1998) concluded that the Asellota colonised the deep sea earlier, and with greater success, than the Flabellifera *sensu lato*. He supported this argument with reference to the early phylogenetic isolation of the Asellota, and their greater deep-sea family-level endemism. Although this is generally true, flabelliferan success in the deep sea is not universal and indicates multiple invasions of this habitat. Deep-sea representatives can be found in most families, but are relatively uncommon in the cirolanidan lineage—as Wilson (1998) argued, predators, scavengers and parasites may be disadvantaged in the abyss due to the rarity of prey. The cirolanid *Bathynomus* is an exception. On the other hand, some sphaeromatidean and valviferan families are concentrated and diverse in the deep sea, notably Antarcturidae, Austrarcturellidae, and, to a lesser extent, Arcturidae and Serolidae. All of these are now dominant in the southern hemisphere.

*A new classification*

Although discussions about isopod phylogeny have persisted for more than a century, no taxonomist, apart from Wägele (1989), has tried seriously to translate them into a phylogenetically based classification. Brusca and Wilson (1991) did not recommend a classificatory change. Wilson (2003) retained the subordinal name Flabellifera, which he described as well recognised but poorly defined. But in doing so, he broadened its definition to include other suborders listed by Martin and Davis (2001). Like Wägele (1989), we dispense with the suborder Flabellifera, which all agree can no longer be retained with its traditional meaning. There appears no disagreement regarding the monophyly of the Scuticoxifera.

Wägele's subordinal names, Cymothoida and Sphaeromatidea, are retained with a composition, as close as is practical, to his original concept. We erect the new suborders, Tainisopidea, Phoratopidea and Limnoriidea, because these taxa cannot be placed in other suborders and each has numerous supporting synapomorphies. No character ties the Tainisopidae to either of the two major clades discovered. *Phoratopus* lacks all the synapomorphies of its closest allies, Cymothoida and Limnoriidea. The three families of Limnoriidea were included by Wägele in Sphaeromatidea, but our analysis finds them closer to Cymothoida so the classification is adjusted accordingly.

The Cymothoida incorporate two monophyletic clades: the Cirolanidae, and other families plus the three former suborders. The classification we derive is a compromise between historical usage and phylogeny. One option would be to do away with higher taxa for Anthuridea and Epicaridea, and treat the whole Cymothoida as 24 families. Such a treatment would deny what is known about the monophyly and ecology of these groups. Our preference is to elevate Cirolanidae to superfamily rank, to treat Anthuridea as a superfamily, and Epicaridea as two superfamilies following Martin and Davis (2001). What remains is a paraphyletic group of eight families. For practical purposes we refer to these eight as 'Cymothooidea'.

We take this opportunity to diagnose the Basserolidae as new. Both it and its sister taxon, Serolidae, are characterised by numerous synapomorphies. Any similarity between *Basserolis* and some Bathynataliidae, *Biremia* in particular (Bruce 1985), must be seen as convergence or as expression of some plesiomorphic features.

The subordinal and superfamily taxa, plus the family Basserolidae, proposed as a result of this phylogenetic analysis (Table 3) are rediagnosed or diagnosed as new in the following section. Characters are from the table of synapomorphies, adjusted to encompass known variability and omit weak characters. Characters shown in bold are synapomorphies. Poore (2002) based his catalogues of Australian Isopoda on the work presented here, with the exception of Phoratopidea and Tainisopidea (treated as 'Enigmata'). His diagnoses of higher taxa differ in detail from those presented below. Dreyer and Wägele (2001: 176) proposed to treat the Epicaridea 'simply as family Bopyridae … to get a classification that is compatible with the assumed order of divergence events'. There are 11 epicaridean families recognised by most authors (Martin and Davis 2001) and elimination of these because they might be sister taxa of Cymothoidae or another family-level taxon is not necessary.

*Diagnoses*

The diagnoses are derived by combining and editing the characters from the DELTA data matrix to reflect the higher levels of the hierarchy derived from the cladistic analysis,

and selecting those that best diagnose the taxa. Presumed synapomorphies or highly diagnostic characters are shown in bold. A list of families is provided in Table 3.

## Suborder TAINISOPIDEA new suborder

*Diagnosis*

Pleonites 1–5 free, pleonite 1 similar to others. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Antenna 1 with scale. Mandibular lacinia mobilis present. Mandibular molar a cylindrical process with triturative flat end. Maxillipedal endite reaching beyond distal margin of palp article 2, distally truncate and setose. Dorsal coxal plate 7 similar to others. **Pleopodal endopods 2–5 of female and 3–5 of male expanding into two or three distinct lamellae.** Uropodal rami ventral to pleotelson, articulating from side to side along vertical axis.

The new suborder includes the family Tainisopidae comprising two described species of *Tainisopus* Wilson & Ponder, 1992, one species of *Pygolabis* Wilson, 2003 and unnamed species of both genera. Wilson and Ponder (1992) could not place *Tainisopus* into any suborder or family because of its combination of plesiomorphic and synapomorphic characters, but Wilson (2003: 6) believed his newly created family belonged in Limnoriidea, 'given a lack of strong evidence to the contrary'. These authors provided numerous autapomorphies.

## Suborder PHORATOPIDEA new suborder

*Diagnosis*

Pleonites 1–5 free, pleonite 1 similar to others. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Antenna 1 without scale. Mandibular lacinia mobilis present. Mandibular molar a flat triangular blade-like process. Maxillipedal endite reaching at least distal margin of palp article 2, distally truncate and setose. Dorsal coxal plate 7 reduced. Pleopods 3–5 endopods oval, rounded distally. Uropodal rami ventral to pleotelson, articulating from side to side along vertical axis inside branchial space.

The only species is recognised by the form of pereopods, notably its uniquely broad articles of pereopods 3 and 4 with greatly reduced dactyls.

## Suborder CYMOTHOIDA Wägele

*Diagnosis*

Pleonites 1–5 free, pleonite 1 similar to others (some pleonites fused in some species). **Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally).** Antenna 1 without scale (except in *Bathynomus*).

Mandibular lacinia mobilis absent (in some Anthuroidea present as part of lacinia mobilis). **Mandibular molar flat blade-like or conical process** (sometimes absent). Maxillipedal endite rarely longer than palp article 1 (or absent), distally tapering and with few setae. Dorsal coxal plate 7 similar to others. Pleopods 3–5 endopods more or less oval or rectangular, rounded distally. **Uropodal rami ventral to pleotelson, articulating from side to side along vertical axis inside branchial space.**

## Superfamily CIROLANOIDEA Dana

*Diagnosis*

**Mandibular incisor tridentate, most posterior tooth prominent. Mandibular spine row comprised of independent short simple spines on fleshy lobe.** Maxilla 2 with two basal endites, with numerous setae.

Only the family Cirolanidae is included. Some examples of mouthpart reduction may be found, especially among freshwater species, but these are considered convergences with some cymothoids.

## Superfamily CYMOTHOOIDEA Leach

*Diagnosis*

Mandibular incisor obscurely toothed or acute. Mandibular spine row comprised of independent short simple spines, or absent, or extremely reduced; not on fleshy lobe. **Maxilla 2 with two or one basal endite(s), with numerous setae (Corallanidae, Anuropidae), or with hooked setae (Aegidae, Cymothoidae), or vestigial (Gnathiidae).**

Cymothooidea are a paraphyletic taxon, families of one clade except those included in Anthuroidea, Bopyroidea and Cryptoniscidae. Refer to Poore (2001*b*) for a diagnosis of Anthuroidea and to Trilles (1999) for the two epicaridean taxa.

## Suborder LIMNORIIDEA Brandt & Poore

*Diagnosis*

Pleonites 1–5 or 1–4 free, pleonite 1 similar to others or narrower. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Antenna 1 with or without scale. Mandibular lacinia mobilis present or absent. **Mandibular molar absent. Maxillipedal endite reaching at least distal margin of palp article 4, non-tapering, slender** (except *Keuphylia*). Dorsal coxal plate 7 similar to others. Pleopods 3–5 endopods more or less oval or rectangular, rounded distally. Uropodal rami ventral to pleotelson, articulating from side to side along vertical axis or distal.

The taxon was first diagnosed in Poore (2002: 196).

## Suborder **SPHAEROMATIDEA** Wägele

*Diagnosis*

Pleonites variously fused (rarely 1–5 free), pleonite 1 narrower than others (similar in *Plakarthrium*). **Pleotelson underside vaulted, branchial chamber defined by ridges along mesial margin of lateral edge**. Antenna 1 without scale. Mandibular lacinia mobilis present on left side, reduced and fused with spine row on right or absent. Mandibular molar a cylindrical process with triturative flat end. Maxillipedal endite reaching at least distal margin of palp article 2, usually distally truncate and setose. **Pleopod 3 endopod roughly triangular (or at least with inner angle sharper than outer)**. Dorsal coxal plate 7 similar to others (rarely shorter). **Uropodal rami lateral to margin of pleotelson, articulating along longitudinal axis and folding down alongside branchial space**.

## Superfamily **SPHAEROMATOIDEA** Latreille

*Diagnosis*

**Dorsal coxal plates 2–7 not separated by suture from tergite**. Pereopod 7 ventral coxal plates not meeting at middle. **Pleonite 1 free, 2–4 fused, 5 fused to pleotelson, or more pleonites fused**. Maxilla 1 inner endite almost as long as outer, with 3–4 setae.

Pleopod 5 endopod **with scale patches** (except Tecticipitidae, *Paravireia*). **Uropod with exopod free** (if present), **endopod fused to peduncle**.

## Superfamily **SEROLOIDEA** Dana

*Diagnosis*

**Dorsal coxal plates 2–7 (or 2–6 if 7 absent) separated by suture from tergite, or 2–4 free, 5–7 (or 5–6 if 7 absent) separated by suture from tergite. Pereopod 7 ventral coxal plates (if present) meeting at middle, or not meeting in middle (separated by pair of plates, presumed proximal sclerite 7)**. Pleotelson incorporating pleonite 6 only (*Plakarthrium*), or pleotelson variously fused with up to three more anterior pleonites. **Maxilla 1 inner endite short, with 1–2 setae**. Pleopod 5 endopod without scale patches. **Uropod biramous** (except *Spinoserolis*).

## Family **BASSEROLIDAE**, fam. nov

*Type genus*: *Basserolis* Poore, 1985.

*Diagnosis*

Head and pereonite 1 **fused, broader than pereonite 2**. Pereopods 5 and 6 ventral coxal plates meeting at middle. Pereonites 6 and 7 tergites visible, free. Pleonites 1–3 without medial sternite plate. Pleotelson, middorsal longitu-dinal carina absent. Antenna 2 peduncle **with groove on posterior margin for antenna 1**. Mandibular incisor **with obsolete dentition**. Mandibular lacinia mobilis **absent**. Mandibular spine row **absent**. Maxilla 1 lateral lobe **with 2–7 setae**. Maxillipedal palp **1-articled**. Male pereopods without dense brushes of hairs on inferior margins of some distal articles. Propodus 1 propodus **subchelate, barely tapering, palm straight**. Pereopod 1 carpus **not reaching proximal margin of palm, not opposing dactylus**. Pereo-pod 1 propodus **with prominent distal robust scale-like seta**. Pereopod 1 propodus with 1 posterior row of sensory setae or irregular setae. Pereopod 2 of male ambulatory, as in females. Pleopods 1–3 peduncles not triangular.

## Family **SEROLIDAE** Dana

*Diagnosis*

Head and pereonite 1 fused, not broader than pereonite 2. Pereopods 5 and 6 ventral coxal plates **not meeting at middle (separated by pair of plates comprising fused presumed proximal sclerites 5–7)**. Pereonite **6 visible laterally only, 7 not visible, submerged between pereonite 6 and pleonite 2**. Pleonites 1–3 **with medial sternite plate**. Pleotelson, middorsal longitudinal carina usually **present, broadest anteriorly**. Antenna 2 peduncle without groove on posterior margin for antenna 1. Mandibular incisor multi-dentate. Mandibular lacinia mobilis present. Mandibular spine row present. Maxilla 1 lateral lobe with 9–13 stout setae. Maxillipedal palp of three articles, **fused articles 2–3 broadened distally, 4–5 quadrangular**. Male pereopods with dense brushes of hairs on inferior margins of some distal articles. Propodus 1 propodus subchelate, oval, palm convex. Pereopod 1 carpus reaching proximal margin of palm, opposing dactylus. Pereopod 1 propodus with distal robust seta not scale-like. Pereopod 1 propodus **with one row of robust sensory setae plus one row of short setulated sensory setae**. Pereopod 2 of male **subchelate, shortened**. Pleopods 1–3 peduncles **triangular, laterally directed, rami scarcely overlap**.

## Suborder **VALVIFERA** Sars

*Diagnosis*

**Pleonite 6, usually more pleonites, fused to pleotelson**, pleonite 1 similar to others (rarely reduced). **Pleotelson underside vaulted, branchial chamber defined by ridges along mesial margin of lateral edge**. Antenna 1 without scale. Mandibular lacinia mobilis present. Mandibular molar a cylindrical process with triturative flat end, occasionally obsolete. Dorsal coxal plate 7 similar to others (rarely narrower). **Pleopod 3 endopod roughly triangular (or at least with inner angle sharper than outer). Uropods**

**lateral to margin of pleotelson, peduncle and short rami enclosing pleopods in branchial chamber**.

The Valvifera are further defined by having no mandibular palp (except in *Holognathus karamea*).

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**Appendix 1. Exemplar species used in the coding of higher taxa, with literature sources and locations of museum material examined**

| Taxon | Exemplar species | Literature references | Material |
|---|---|---|---|
| *Phreatoicus* | *P. typicus* Chilton, 1883 | Wilson and Fenwick 1999 | MV, other species |
| *Vermetias* | *V. nelladanae* Just & Poore, 1992 | Just and Poore 1992 | MV |
| *Mexistenasellus* | *M. colei* Bowman, 1982 | Bowman 1982 | – |
| *Oniscus* | *O. asellus* Linnaeus, 1761 | Sars 1898 | ZMH; MV, many other species |
| *Tylos* | *T. australis* Lewis & Bishop, 1990 | Lewis and Bishop 1990 | MV |
| Tainisopidae | *Tainisopus fontinalis* Wilson & Ponder, 1992 | Wilson and Ponder, 1992 | MV, 2 species |
| *Phoratopus* | *P. remex* Hale, 1925 | Hale 1925; Bruce 1981 | AM, SAMA |
| *Anuropus* | *A. pacificus* Lincoln & Jones, 1973 | Lincoln and Jones 1973, Kensley and Chan 2001, Brandt and Retzlaff 2002 | ZMH, other species |
| *Protognathia* | *P. waegeli* Kussakin & Rybakov, 1995; *P. bathypelagica* (Schultz, 1977) | Kussakin and Rybakov 1995 | RUB |
| Gnathiidae | *Paragnathia formica* (Hesse, 1864): praniza stage | Monod 1926 | MV, many species |
| *Tridentella* | *T. benguela* Brandt & Poore, 2001; *T. namibia* Brandt & Poore, 2001 | Bruce 1984, 1988*b*; Brandt and Poore 2001 | MV |
| Corallanidae | *Tachaea caridophaga* (Riek, 1953) | Delaney 1989 | MV |
| Aegidae | *Aega plebeia* Hansen, 1897; *A. antartica* Hodgson, 1910 | Brusca 1983; Brandt 1991 | MV, plus other species; ZMH |
| Anthuridea | *Belura pillara* Poore & Lew Ton, 1988; *Kupellonura biriwa* Poore & Lew Ton, 1988 | Poore and Lew Ton 1988 | MV, plus other species |
| Cymothoidae | *Nerocila orbignyi* (Guérin-Méneville, 1832) | Bruce 1987 | MV, plus other species |
| Epicaridea | epicaridean larval stage | Trilles 1999 | MV |
| *Bathynomus* | *B. immanis* Bruce, 1986 | Bruce 1986 | MV, ZMH |
| *Natatolana* | *N. woodjonesi* (Hale, 1924) | Bruce 1986 | MV, plus other species |
| Keuphyliidae | *K. nodosa* Bruce, 1980 | Bruce 1980 | MV |
| Limnoriidae | *Paralimnoria andrewsi* (Calman, 1910) | Cookson 1991 | MV, plus other species |
| *Hadromastax* | *H. polynesica* Bruce & Müller 1991 | Bruce and Müller 1991 | MV |
| Valvifera | *Idotea metallica* Bosc, 1802 | Poore and Lew Ton 1993 | MV, ZMH, plus other species |
| *Paravireia* | *P. holdichi* Brökeland, Wägele, & Bruce, 2001 | Brökeland *et al.* 2001 | – |
| *Sphaeroma* | *S. quoianum* Milne Edwards, 1840; *S. serratum* Fabricius, 1787 | – | MV, ZMH, plus other species |
| *Dynamene* | *D. curalii* Holdich & Harrison, 1980 | Holdich and Harrison 1980 | MV |
| *Cassidina* | *C. typa* Milne Edwards, 1840 | – | MV |
| *Cassidinidea* | *C. korpie* Bruce, 1993 | Bruce 1993*b* | MV, unidentified species |
| *Paraleptosphaeroma* | *P. brucei* Kussakin & Malyutina, 1993 | Kussakin and Malyutina 1993 | – |
| *Tecticeps* | *T. marginalis* Gurjanova, 1935 | Kussakin 1979 | SPM, 5 species |
| *Ancinus* | *Ancinus belizensis* Kensley & Schotte, 1987 | Kensley and Schotte 1987 | – |
| *Bathycopea* | *B. typhlops* Tattersall, 1905 | Bruce 1991 | MV |
| *Plakarthrium* | *P. australiensis* Brandt & Poore, 2001 | Brandt and Poore 2001 | MV, all 3 species; ZMH |
| *Schweglerella* | *S. strobli* Polz, 1998 | Brandt *et al.* 1999 | BMMS |
| *Biremia* | *B. ambocerca* Bruce, 1985 | Bruce 1985 | AM |
| *Bathynatalia* | *B. gilchristi* Barnard, 1957 | Kensley 1978 | SAM |
| *Naudea* | *N. louwae* Kensley, 1979 | Kensley 1979 | SAM |
| *Basserolis* | *B. kimblae* Poore, 1985 | Poore 1985 | MV |
| Serolidae | *Serolis bouvieri* Richardson, 1909 | Brandt 1988; Held 2000 | MV, ZMH, plus other species |

Museums are abbreviated: BMMS, Bürgermeister-Müller-Museum Solnhofen; AM, Australian Museum; MV, Museum Victoria; RUB, Ruhr-Universität Bochum; SAM, South African Museum; SAMA, South Australian Museum; SPM, St Petersburg Museum; ZMH, Zoological Museum of Hamburg.