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A Phylogeny and Classification of the Amphipoda with the establishment of the new order Ingolfiellida (Crustacea: Peracarida)

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Abstract

A classification is proposed for the order Amphipoda. The Amphipoda includes six suborders, the Pseudingolfiellidea, Hyperiidea, Colomastigidea, Hyperiopsidea, Senticaudata (described in a previous contribution (Lowry & Myers 2013)) and Amphilochidea. The suborder Ingolfiellidea is raised to order status. A cladistic tree, based on morphology, is presented illustrating the relationships of the Amphipoda at parvorder level. A tree for the families of the Physomatidira and Physocephalatidira, a tree for the Maxillipiidira, Oedicerotidira, Eusiridira and Amphilochidira and a tree for the Synopiidira, Haustoriidira and Lysianassidira, are provided. Families are listed together with their included genera. New families are diagnosed.

Key words: Phylogeny, Classification, Crustacea, Amphipoda, Ingolfiellida, New Suborders, New Infraorders, New Parvorders, New Superfamilies, New Families

Introduction

The Amphipoda is one of the largest orders of the Crustacea, Malacostraca with 223 families, 1618 genera and a little less than 10,000 species. Species diversity is greatest in the newly created parvorder Lysianassidira, followed closely by the newly created parvorders Amphilochidira, Caprellidira and Hadziidira (Fig. 1). The majority of amphipods (about 81%) are marine or estuarine. Freshwater amphipods make up about 19%, of which the vast majority (about 17%) are found in the parvorders Crangonyctidira or Gammaridira. About 3% of amphipods, all in the Talitridira, are supralittoral or terrestrial. Most marine amphipods are benthic detrital-feeders, deposit-feeders, suspension-feeders or predators, although information is often not precise enough to put them into specific groups. Among the lysianassidirans, a little more than half are scavengers, making up about 6% of all amphipod species. Parasitism is rare in amphipods. Laval (1980) reviewed hyperiidean amphipods as crustacean parasitoids associated with gelatinous zooplankton. In his opinion all hyperiideans are parasitoids, but he found evidence for parasitism mainly in the Physocephalatidira (about 2% of amphipods). If all hyperiideans are considered as parasitoids then the figure is nearly 3%.

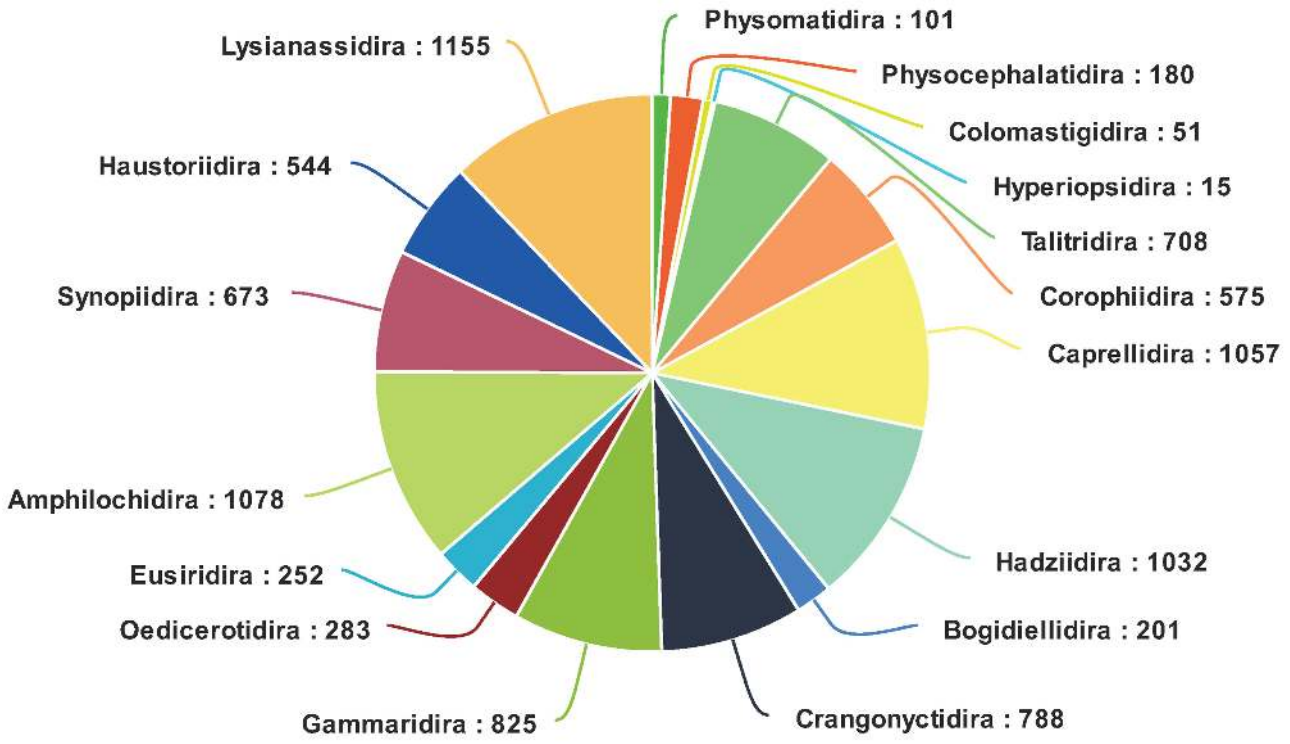

FIGURE 1. The relative species contribution of each parvorder to the Amphipoda. Excluded from pie chart: Carangoliopsidira (2 species); Maxillipiidira (3 species); Pagetinidira (4 species); Podosiridira (1species); Pseudingolfiellidira (4 species).

The current higher classification of the Amphipoda is not phylogenetic and consequently is in need of revision. Families have traditionally been placed in alphabetical order (Barnard & Karaman 1991, Martin & Davis 2001). This paper completes the work reported earlier by Myers & Lowry (2003) and Lowry & Myers (2013) on the higher classification of the Amphipoda. A full classification of the Ingolfiellida and the Amphipoda is provided.

Previous morphological phylogenetic analyses of amphipod higher taxa have been either 'phenetic' (Bousfield & Kendall 1994, Bousfield & Hendrycks 1995a, 1995b, 1997, 2002, Wang & Holsinger 2001), a now almost universally discarded method; 'phyletic', a somewhat unclear method espoused by E.L. Bousfield (2001) that creates trees based on ill-defined "first principles"; or 'cladistic' (Berge *et al*. 2000; Serejo 2004; Krapp-Schickel 2009, 2011). The methodology of these cladistic analyses has been to establish a list of characters with character states, process them through a phylogenetic inference package and then publish the resulting tree. In our studies, by contrast, the first tree is merely a starting point for our work. We use successively modified trees to determine possible synapomorphies, delete uninformative characters and re-examine homoplastic characters. We identify and examine character conflict and weigh evidence for homology. Only after many iterations do we come up with a phylogenetic hypothesis expressed as a tree.

Statistical methods have played an increasingly important role in phylogenetic studies. Bootstrap, % jackknife resampling, and other statistical measures are used at nodes to support cladistics trees. These internal tests of robustness are, however, fundamentally phenetic and more importantly they do not test the quality of synapomorphies. As Buhay (2009) has demonstrated, pumpkin pie can be shown to be the sister taxon to a crayfish with 100% bootstrap support.

There have also been several molecular genetic studies on amphipod higher taxa e.g. Englisch *et al.* (2003), MacDonald *et al.* (2005), Ito *et al*. (2007), Havermans *et al*. (2010), Hurt *et al*. (2013) and Verheye *et al.* (2015). Each new molecular phylogeny produced for any given set of taxa is not built on any previous hypotheses but is separate and unrelated (Mooi *et al.* 2011). There is no progress in understanding—only a different and ever-changing picture of relationships that is tied to the ingenuity of the mathematics (Mooi *et al.* 2011). Molecular studies rely on similarity between aligned sequences. Similarity is nothing more than two objects compared in some way. Homology, by contrast, is a three-item relationship in which two homologs are more closely related to each other than they are to a third. When homology is not addressed in molecular systematics there is a risk of making unsupportable claims of relationship (Ebach *et al.* 2011). Many published molecular trees, unlike morphology based trees, are not falsifiable, because their synapomorphies are not retrievable by the reader. Molecular studies such as those of Verheye *et al*. (2015) use retrospective evidence, selecting only those morphological synapomorphies that support their molecular tree while dismissing as homoplasies, any morphological synapomorphies that do not support their tree. We determine synapomorphies on the basis of carefully assessed morphological evidence, we do not pick and choose only those synapomorphies that fit some preconceived notion of a correct tree. Molecular phylogeneticists also tend to ignore the fact that genes are not free from homoplasy which can be viewed as noise that hides phylogenetic information (Hassanin *et al*. 1998).

Verheye *et al*. (2015) dismiss the senticaudate character of apical robust setae on uropods 1 and 2 (established by Lowry & Myers, 2013) as convergent on the basis of a small number of taxa outside the Senticaudata that exhibit this character. Our work is based on the entire known world families of Amphipoda. Our studies revealed a very strong synapomorphy for the senticaudates (apical robust setae on uropods 1–2) and Lowry & Myers (2013) clearly stated that a few species outside the senticaudate clade have secondarily developed robust setae on the apices of uropods 1 and 2 rami.

Molecular studies rarely justify unexpected relationships revealed by their hypothesised phylogenies. For example, Verheye *et al.* (2015) show *Salentinella* Ruffo, 1948 (Salentinellidae) to be a sister taxon to *Haustorius* Müller, 1775 (Haustoriidae) and *Syrrhoe* Goës, 1866 (Synopiidae) to be a sister taxon to *Bactrurus* Hay, 1902 and *Crangonyx* Spence Bate, 1859 (Crangonyctidae). These relationships do not fit any previous understanding of amphipod family relationships. They are extraordinary to say the least and require discussion, but none is provided.

Molecular studies question morphologically based classifications, but their studies are based on extremely few taxa and as a consequence they are not able to propose any new classification to replace the existing classifications.

We do not decry molecular methods, indeed we believe that morphological and molecular data should be viewed as complementary. Myers & Lowry (2003) reduced the suborder Caprellidea to the status of a superfamily within the suborder Corophiidea based on a morphological cladistic study. Later, Ito *et al*. (2011) came to the same conclusion based on molecular studies. When morphological and molecular results coincide, it increases the

confidence in the hypothesis. We reject the concept that molecular phylogenies are implicitly 'correct' and morphological phylogenies by inference are incorrect and should consequently be abandoned. As pointed out by Dilman & Hilton (2011), "there is no "truth" in systematics—morphological or molecular—which, in part, is what makes it a science".

In our analysis of parvorders we chose *Metaingolfiella* as our outgroup. The Ingolfiellida are the sister group to the Amphipoda. Wilson (2009) in his paper on the phylogenetic position of the Isopoda places Ingolfiella as an outgroup to the four diverse Amphipoda included in his analysis. According to Ruffo (1969) and Vonk & Schram (2003), *Metaingolfiella* lies at the base of the ingolfiellidan clade. For the analyses of the Amphilochidira, Physomatidira and Physocephalatidira we chose *Pseudingolfiella* as our outgroup because it was shown in our parvorder analysis to be at the base of the amphipod clade. In our analysis of one infraorder (Lysianassida) we used Lundberg rooting. In Lundberg rooting the shortest ingroup network is rooted at the internode to which the hypothetical ancestor attaches most parsimoniously (Lundberg, 1972). This gave us much better resolution on the tree than did *Pseudingolfiella*.

The problem with large analyses of many taxa is that characters and character states have to be chosen to represent adequately all taxa in the analysis. This leads to redundant characters for some clades in the tree. Also characters/states that have high phylogenetic value to some clades may have low phylogenetic inference to others. We decided that we would achieve higher resolution of family relationships by analysing infraorders separately. Accordingly, our all-family tree was used simply as a basis for determining parvorders and infraorders for the next analyses. Infraorders were then analysed individually using a subset of relevant characters/states. Accordingly separate analyses were carried out for the Hyperiidea, Amphilochida and Lysianassida in order to introduce greater resolution to the classification of those infraorders. Within the Lysianassida, a separate analysis was carried out for the Haustoriidira and the results are shown here as a composite infraorder cladogram.

In this contribution, one new order Ingolfiellida Hansen, 1903 **stat. nov.**, and four new suborders: Pseudingolfiellidea Lowry & Myers, 2012a **stat. nov.**; Colomastigidea Stebbing, 1899 **stat. nov.**; Hyperiopsidea Bovallius, 1886 **stat. nov.** and Amphilochidea Boeck, 1871 **stat. nov.** are erected. These join the existing suborders Hyperiidea H. Milne Edwards, 1830 and Senticaudata Lowry & Myers 2013. Within these six amphipod suborders there are 13 infraorders: Pseudingolfiellida Lowry & Myers, 2012a **stat. nov.**, Physosomata Pirlot, 1929; Physocephalata Bowman & Gruner, 1973; Colomastigida Stebbing, 1899 **stat. nov.**; Hyperiopsida Bovallius, 1886 **stat. nov.**; Carangoliopsida Lowry & Myers, 2013; Talitrida Rafinesque, 1815 (Serejo, 2004); Corophiida Leach, 1814 (Lowry & Myers 2013); Hadziida S. Karaman, 1943 (Lowry & Myers 2013); Bogidiellida Hertzog, 1936 (Lowry & Myers 2013); Gammarida Latreille, 1802 (Lowry & Myers 2013); Amphilochida Boeck, 1871 **stat. nov.** and Lysianassida Dana, 1849 **stat. nov.** There are 23 amphipod parvorders, 15 of which are new: Metaingolfiellidira Ruffo, 1969 **stat. nov.**, Pseudingolfiellidira Lowry & Myers, 2012a **stat. nov.**, Physomatidira Pirlot, 1929 **stat. nov.**; Physocephalatidira Bowman & Gruner, 1973 **stat. nov.;** Colomastigidira Stebbing, 1899 **stat. nov.**; Pagetinidira K.H. Barnard, 1931 **stat. nov.**; Hyperiopsidira Bovallius, 1886 **stat. nov.**; Podosiridira Lowry & Myers, 2012b **stat. nov.**; Carangoliopsidira Lowry & Myers, 2013; Talitridira Rafinesque, 1815 (Lowry & Myers, 2013); Corophiidira Leach, 1814 (Lowry & Myers 2013); Caprellidira Leach, 1814 (Lowry & Myers, 2013); Hadziidira S. Karaman, 1943 (Lowry & Myers 2013); Bogidiellidira Herztog, 1936 (Lowry & Myers 2013); Crangonyctidira Bousfield, 1973 (Lowry & Myers 2013); Gammaridira Latreille, 1802 (Lowry & Myers 2013); Maxillipiidira Ledoyer, 1973 **stat. nov.**; Oedicerotidira Lilljeborg, 1865b (Bousfield, 1979) **stat. nov.**; Eusiridira Stebbing 1888 **stat. nov.**; Amphilochidira Boeck, 1871 **stat. nov.**; Synopiidira Dana, 1852 **stat. nov.**; Haustoriidira Stebbing, 1906 **stat. nov.** and Lysianassidira Dana, 1849 **stat. nov.** In addition two recently described senticaudate families and three recently described hyperiidean families are included for completeness: Australomicroprotopidae Myers, Lowry & Billingham, 2016, Zaramillidae Lowry & Myers, 2016, Amphithyridae Zeidler, 2016, Eupronoidae Zeidler, 2016 and Thamneidae Zeidler, 2016.

The relative contribution of each parvorder to the Amphipoda is shown in Fig. 1.

Materials and methods

The basis of our analyses was an unpublished database to the families of world Amphipoda, based on a wide representative selection of genera, built up over many years by one of us (JKL). A DELTA (Dallwitz 2005)

database of 300 characters each with two or more character states was analysed in PAUP version 4.0b8a (Swofford 2003) using heuristic searches and the criterion of parsimony, to give a first tree. This tree was then analysed in MacClade (version 3.08) to determine which characters were potentially useful synapomorphies, which were uninformative and which appeared to be homoplastic. Characters that appeared to be homoplastic were re-examined to see if a supposed character state was actually two or more characters that could be redefined with separate states. If so, the newly defined characters and states were then put back into the analysis and another run was performed. Synapomorphies were challenged by each successive tree. This process of reanalysis and reiteration was then continued until the shortest tree with the most resolved synapomorphies resulted. In this analysis almost 100 iterations were performed. In the analyses, only synapomorphies were used. For the taxon diagnoses, each character state was checked using the intkey option in the Delta database of world families. Diagnostic descriptions sometimes used characters that were autapomorphies, and therefore could not be used in the phylogenetic analyses.

A synapomorphy is defined as a shared uniquely derived character state. In the process of evolution a character state can be transformed. One possible transformation is 'lost'. For example, in insects a synapomorphy is 'wings', but fleas have no wings because in the process of evolution, the wings have been lost. It follows that not all members of a clade may necessarily share a given synapomorphy. In determining synapomorphies we record a character state as synapomorphic if it is present in the majority, not necessarily all, of the members of a family or higher taxon. If a character state is present in a number of members of a clade, the most parsimonious solution is that it has been derived through an evolutionary lineage from an ancestor and is thus a synapomorphy. The alternative is that is has been evolved independently in each taxon that exhibits the character state and is therefore an autapomorphy for each taxon. This alternative is much less parsimonious.

An important synapomorphy for the Iphimedioidea is the acuminate pereopod 4 coxa, even though this state does not occur in a few small specialised families, the Laphystiopsidae, Sicafodiidae, Vicmusiidae and some (but not all) of the Acanthonotozomellidae. Here we are left with two hypotheses. Firstly, that the acuminate coxa 4 has evolved independently in nine families (Amathillopsidae, Epimeriidae, Lafystiidae, Dikwidae, Iphimediidae, Stilipedidae, Acanthonotozomatidae, Ochlesidae and the Odiidae, i.e. nine autapomorphies, or secondly that the Iphimedioidea are monophyletic (i.e. the character state is derived from a common ancestor), and that the character state has been modified (loss of acuminate tips) during descent in a few small aberrant families. We believe that the second hypothesis (monophyly) is the most parsimonious.

An important synapomorphy for the parvorder Amphilochidira is the pereopod 4 carpus shorter than the propodus. It has been modified in the Amphilochidae, Cyproideidae, Amathillopsidae and some Ochlesidae. However, it remains a synapomorphy for 18 out of the 22 families in the Amphilochidira. The discovery of some taxa that do not possess the character state, does not falsify our hypothesis.

A fundamental attribute of science is that each new scientific discovery builds on, and is informed by, past scientific endeavours. Science advances by building on the bricks of past workers. When studying amphipod phylogeny we can refer to the works of scientists such as G.O. Sars and T.R.R. Stebbing in the nineteenth century and J.L Barnard and E.L Bousfield in the twentieth century along with hundreds of other amphipodologists who have together established a broad framework for our understanding of amphipod relationships. We use this accumulated knowledge to assist us in recognising homoplasies. If a character state is shared (synapomorphy) by members of a clade, but is also present in a taxon outside that clade, in a 'distant' part of our cladistic tree, we use the historical knowledge of amphipod relationships together with our cladistics analysis (showing the pattern of synapomorphies), to determine whether the character state in the 'distant' taxon is a homoplasy. For example, the presence of apical robust setae on uropods 1 and 2 is a synapomorphy for the Senticaudata (Lowry & Myers, 2013), but we find this character state also in some Phoxocephalidae. The acquired knowledge from all past studies is that the Phoxocephalidae are not closely related to any senticaudates, strengthening our assumption that this is a homoplasy. The assumption is complemented by our finding of several other synapomorphies that place the Phoxocephalidae in the Haustorioidea of the Lysianassida. The combination of synapomorphies from our analysis and the perceived wisdom of past amphipodologists direct our assumptions. When we examine the phoxocephalids in question we find that their appendages are covered in robust setae. This is due to their burrowing habits. If numerous robust setae are developed over their appendages to assist burrowing, it is not unexpected that they have also developed robust setae on the apices of their uropods.

It is worth noting that molecular studies depart from normal scientific progress by not building on, nor taking

cognisance of, any previous work. Each molecular analysis stands in isolation and the results are taken as 'correct' without any reference to past understanding, including other molecular studies with which they may be conflicting.

The analysis of very large databases provides a useful overview of relationships but can give weak phylogenetic relationship information below the infraorder level because some of the characters/states chosen for the large analysis are not applicable to individual parvorders. Better results may be obtained at the family level by analysing infraorder clades separately and choosing only the appropriate characters/states for each analysis. Accordingly separate analyses were carried out for the Hyperiidea, Amphilochida and Lysianassida in order to introduce greater resolution to the classification of those infraorders.

In the all-family analysis we used 118 characters (Figs 2–10) for 126 taxa. In the parvorder analysis we analysed 21 taxa using 27 characters. In the infraorder Amphilochida analysis there were 34 families in two parvorders and 72 characters were used. In the infraorder Lysianassida analysis there were 54 families in three parvorders and 77 characters were used and in the suborder Hyperiidea analysis there were 32 families in two infraorders and two parvorders using 80 characters. Matrices of the original character sets used in these analyses are available as Supplementary files on the body page of this paper in the website of Zootaxa.

Two measures of tree performance are given. The consistency index (CI)—the minimum number of changes divided by the number required on the tree (CI = 1 if there is no homoplasy) and the retention index (RI) calculated by taking the maximum number of changes on a tree minus the number of changes on the tree and dividing by the maximum number of changes on the tree minus the minimum number of changes in the dataset.

The terminology for spines and setae follows Watling (1989). The classification of calceolus types follows Lincoln & Hurley (1981). Also we are using terminology more in line with that used for other peracaridan groups. For mouthparts, the inner and outer plates of the maxilla 1 and maxilla 2 are termed the basal endite and ischial endite respectively. Jaume *et al*. (2009) interpret the maxillae plates as coxal and basal endites. This confusion can only be rectified by embryological studies and for the moment we prefer to use a terminology that is consistent between maxillae and maxilliped. We also prefer to retain the terms antenna 1 and antenna 2 instead of antennules and antennae and likewise maxilla 1 and maxilla 2 instead of maxillule and maxilla, simply because we feel these terms are less subject to confusion.

Characters used in the analysis
(Figs 2–10)

Subequal = within 1.1% difference.

1. Body
    1. laterally compressed
    2. subcylindrical
    3. laterally compressed with small coxae
    4. small, coxae often fused to body
    5. vermiform
    6. dorsoventrally flattened
    7. subglobular in males and females
    8. subglobular in males, globular in females
2. Head
    1. as long as deep
    2. longer than deep
    3. deeper than long
    4. much deeper than long (at least 1.5 ×)
3. Head anteroventral margin
    1. recessed
    2. concave
    3. rounded
    4. vertical
    5. oblique
    6. acute/subacute
    7. produced
4. Head rostrum
    1. vestigial or absent
    2. present

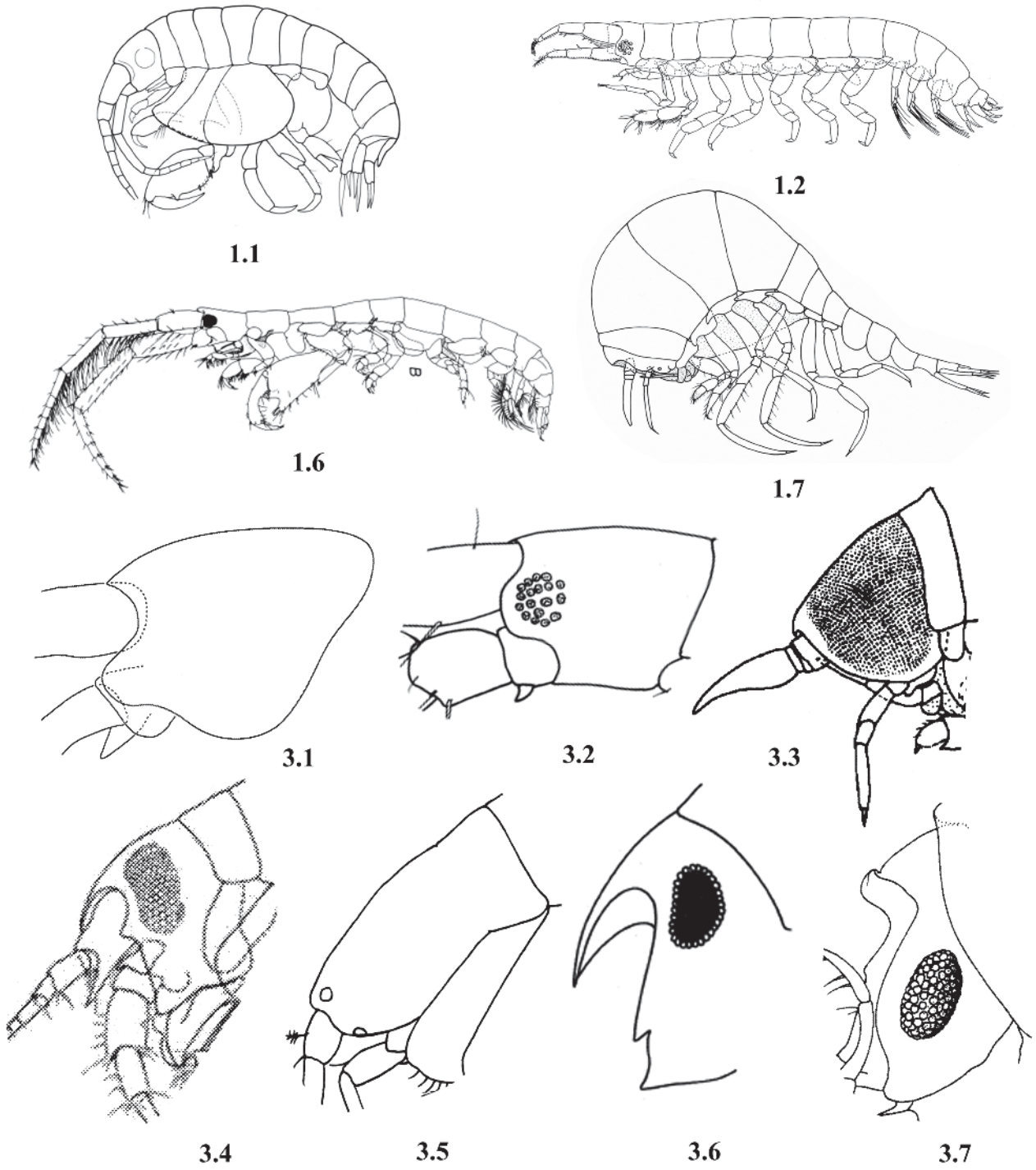

FIGURE 2. Body shape and head anteroventral margin. 1.1 laterally compressed (after Krapp-Schickel, 2006a); 1.2 subcylindrical (after LeCroy 1995); 1.6 dorsoventrally flattened (after Barnard & Drummond 1981); 1.7 subglobular (after Zeidler 2012); 3.1 recessed (after d'Udekem d'Acoz 2010); 3.2 concave (after Myers *et al*. 1987); 3.3 rounded (after Zeidler 2003b); 3.4 vertical (after Coleman 2010); 3.5 oblique (after King 2009); 3.6 acute (after Coleman 1994); 3.7 produced (after Just 1990).

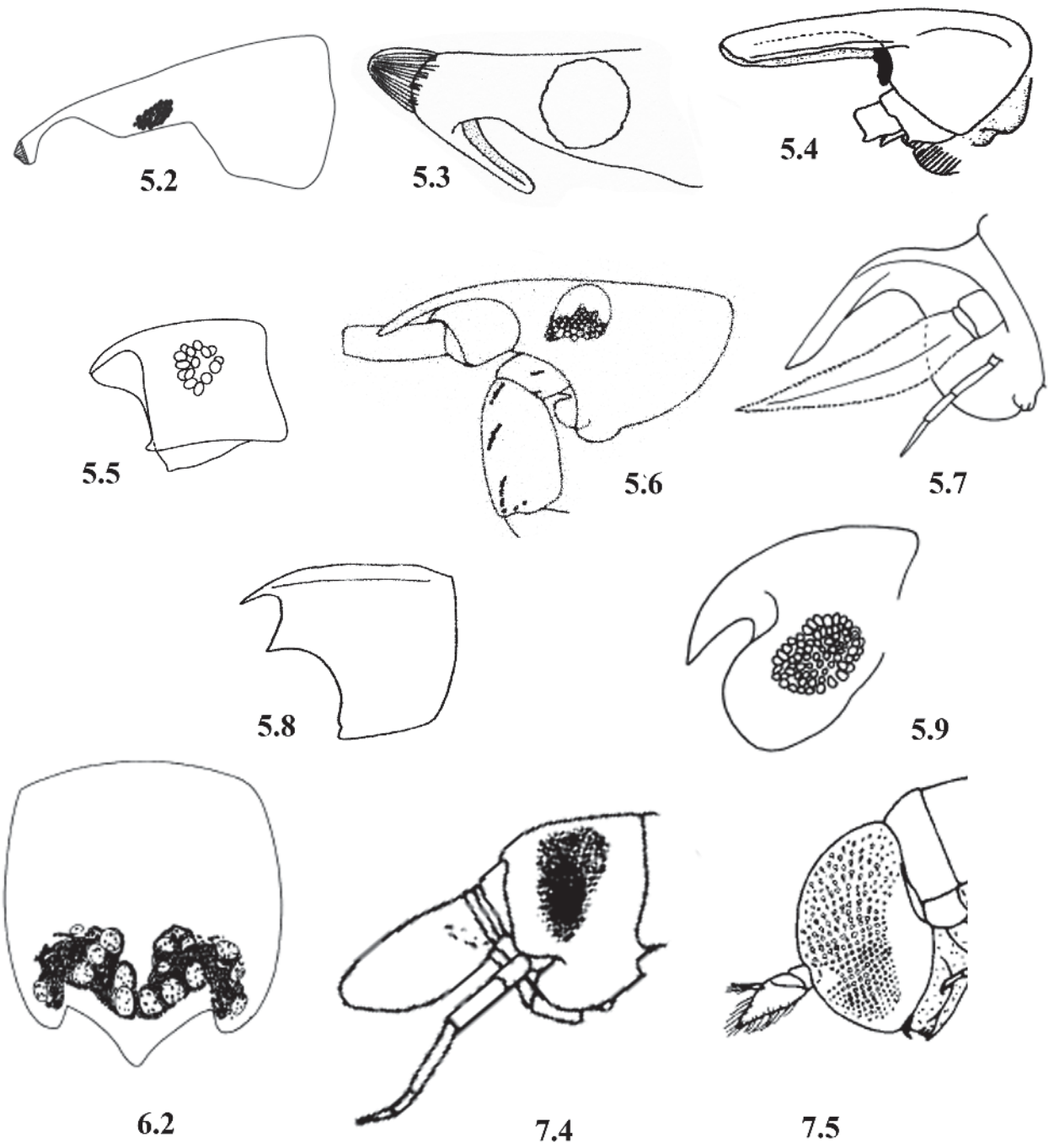

FIGURE 3. Rostrum. 5.2 cylindrical (after Souza-Filhol 2011) 5.3 cylindrical with anteroventral keel (after J.L. Barnard & Drummond 1979); 5.4 dorsoventrally flattened (after J.L. Barnard 1999); 5.5 laterally flattened (after White & Thomas 2009); 5.6 visor-like (after J.L. Barnard & Drummond 1978); 5.7 lanceolate (after Zeidler 2012); 5.8 spine-like (after Lowry & Myers 2003); 5.9 recurved (after J.L. Barnard 1970). Eye. 6.2 coalesced (after Thomas & Barnard 1985); 7.4 ventrally tapered (after Zeidler 2003b); 7.5 occupying most of lateral surface of head (after Zeidler 2004).

5. Head rostrum
    1. absent
    2. cylindrical
    3. cylindrical with anteroventral keel
    4. dorsoventrally flattened
    5. laterally flattened
    6. visor like
    7. lanceolate
    8. spine-like
    9. recurved
6. Eyes
    1. not coalesced
    2. coalesced
    3. absent
7. Eye shape
    1. round
    2. ovoid
    3. reniform
    4. ventrally tapered
    5. occupying most of lateral surface of head
    6. vestigial or absent
8. Antenna 1–2
    1. type 3 calceolus absent (lysianassoid-type)
    2. type 3 calceolus present (lysianassoid-type)
9. Antenna 1–2
    1. type 7 calceolus absent (oedicerotoid-type)
    2. type 7 calceolus present (oedicerotoid-type)
10. Antenna 1–2
    1. type 8 calceolus absent (haustorioid-type)
    2. type 8 calceolus present (haustorioid-type)
11. Antenna 1
    1. subequal in length to antenna 2
    2. longer than (more than 1.1 ×) antenna 2
    3. shorter than (less than 0.9 ×) antenna 2
    4. shorter than peduncle of antenna 2

11A. Antenna 1
    1. inserted on anterior surface of head
    2. inserted on anteriolateral surface of head
    3. inserted on ventral surface of head

12. Antenna 1
    1. not spear-like
    2. spear-like
13. Antenna 1 peduncle
    1. 3-articulate
    2. 1- or 2-articulate
14. Antenna 1 peduncular article 1
    1. subequal to article 2
    2. longer than (more than 1.1 ×) article 2
    3. shorter than (less than 0.9 ×) article 2
15. Antenna 1 peduncle
    1. with sparse robust and slender setae
    2. with many robust and slender setae
    3. with many slender setae only
    4. with sparse slender setae only
16. Antenna 1 primary flagellum
    1. 5- or more articulate
    2. less than 5-articulate
17. Antenna 1 callynophore
    1. well-developed (2-field)
    2. weakly developed (1-field)
    3. absent
18. Antenna 1 accessory flagellum
    1. present
    2. vestigial or absent (1-articulate or scale-like)
19. Antenna 1 accessory flagellum
    1. not forming cap
    2. forming cap
20. Antenna 2
    1. medium length (0.33 to 0.66 × body length)
    2. short (less than 0.33 × body length)
    3. long (0.66 × to subequal body length)
    4. greater than body length
    5. absent

20A. Antenna 2
    1. inserted on anterior surface of head
    2. inserted on ventral surface of head
    3. absent in female
21. Antenna 2
    1. articles not folded in zigzag fashion
    2. male peduncular and flagellar articles folded in zigzag fashion
22. Antenna 2 peduncle
    1. with sparse robust and slender setae
    2. with sparse or no slender setae
    3. with many slender setae
    4. with many robust and slender setae
    5. absent
23. Antenna 2 peduncle
    1. article 1 not enlarged
    2. article 1 bulbous
24. Antenna 2 brush setae—adult male
    1. absent
    2. present
25. Antenna 2 flagellum
    1. subequal with peduncle
    2. shorter than peduncle
    3. longer than peduncle
    4. absent

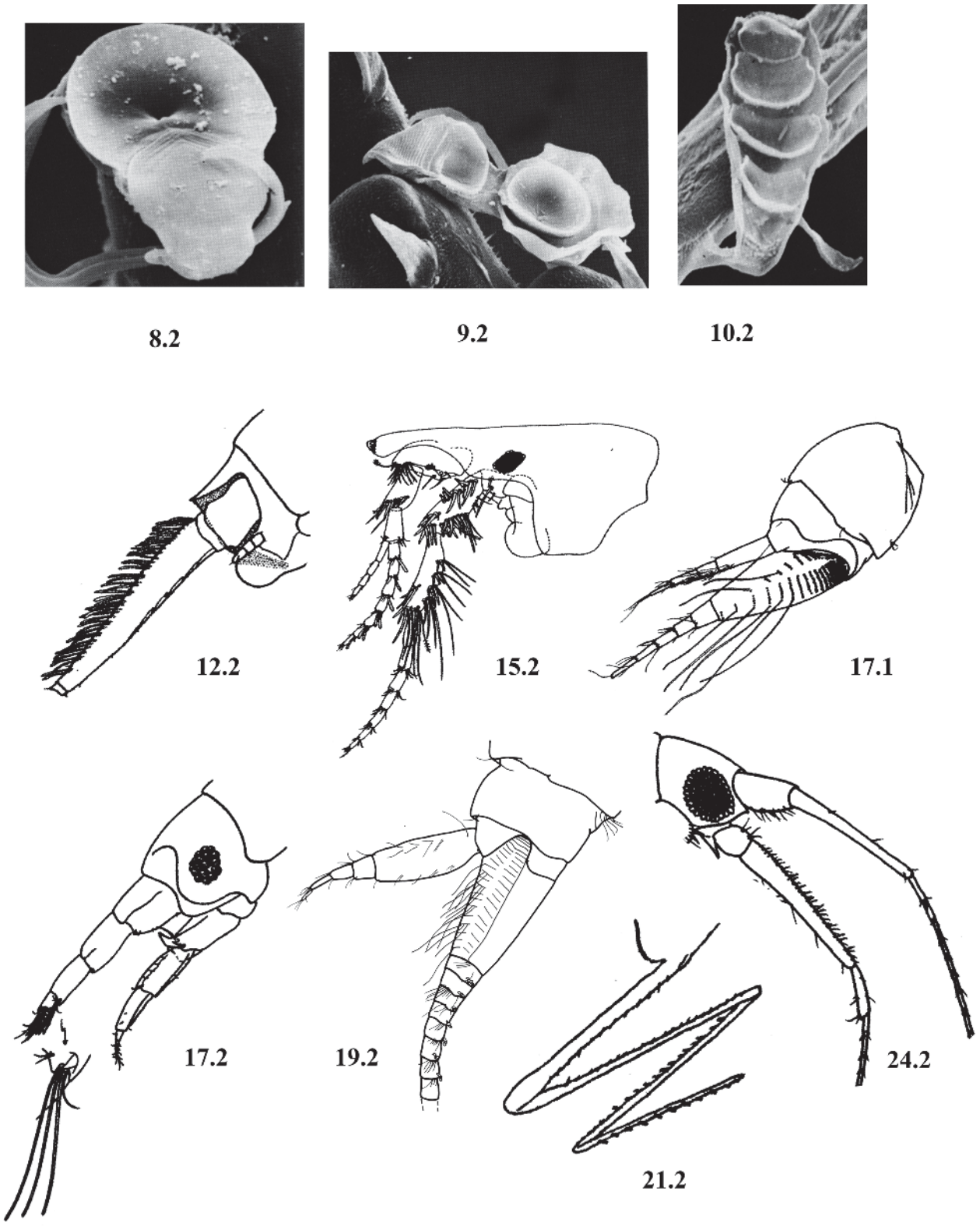

FIGURE 4. Antennae. 8.2 calceolus type 3 (after Lincoln & Hurley 1981); 9.2 calceolus type 7 (after Lincoln & Hurley 1981); 10.2 calceolus type 8 (after Lincoln & Hurley 1981); 12.2 antenna 1 spear-like (after Chang-tai Shih & Hendrycks 1996); 15.2 antenna 1 peduncle with many robust or slender setae (after Thurston 1982); 17.1 antenna 1 callynophore well developed (after Lowry & Stoddart 1995b); 17.2 antenna 1 callynophore weakly developed (1-field) (after LeCroy 1995); 19.2 antenna 1 accessory flagellum forming a cap (unpublished); 21.2 antenna 2 male peduncular and flagellar articles folded in zigzag fashion (after Vinogradov, Volkov & Semenova 1982); 24.2 antenna 2 with brush setae (after Myers & LeCroy 2009).

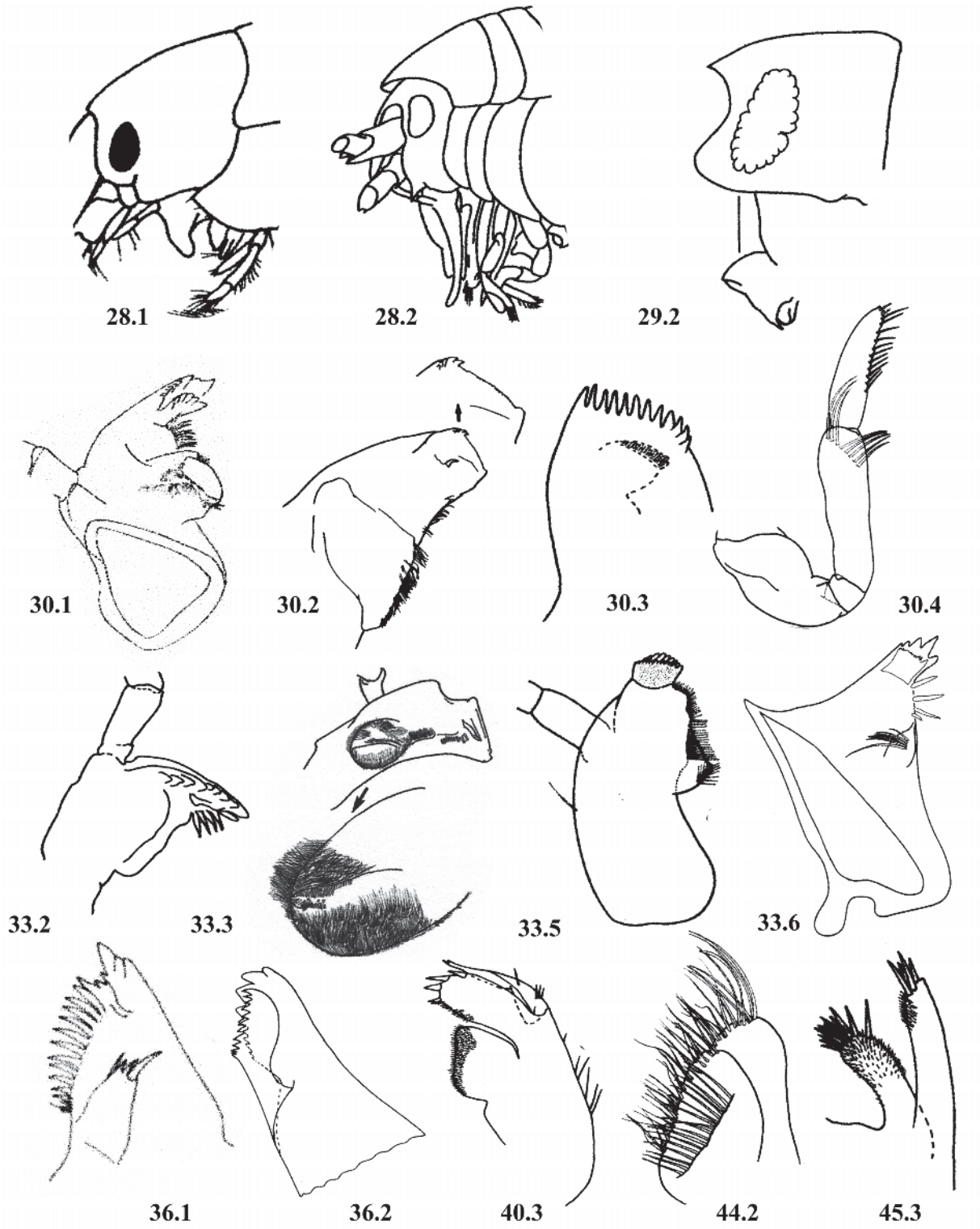

FIGURE 5. Mouthparts. 28.1 mouthpart bundle subquadrate (after Lowry & Springthorpe 2005); 28.2 mouthpart bundle subconical (after Coleman & Lowry 2006); 29.2 labrum, epistome complex separate (after Lowry & Stoddart 1997); 30.1 mandible incisor dentate (after Coleman 1998); 30.2 mandible incisor smooth (after Lowry & Stoddart 1994); 30.3 mandible incisor minutely serrate (after Zeidler 2004); 30.4 mandible incisor absent (after Lowry & Stoddart 1994); 33.2 mandible molar non-setose, smooth (after Azman 2009); 33.3 mandible molar a fully setose tongue (after Stoddart & Lowry 2004); 33.5 mandible molar a broad setose flap (after Ruffo 1978); 33.6 mandible molar a smooth protuberance with large robust setae (after d'Udekem d'Acoz 2010b); 36.1 mandible accessory setal row present (after J.L. Barnard & Drummond 1978); 36.2 mandible accessory setal row absent (after Berge *et al.* 2000): 40.3 maxilla 1 basal endite covered in setae (after Zeidler 2009); 44.2 maxilla 2 basal endite with oblique setal row (after Hughes 2009); 45.3 maxilla 2 basal endite covered in setae (after Zeidler 2009).

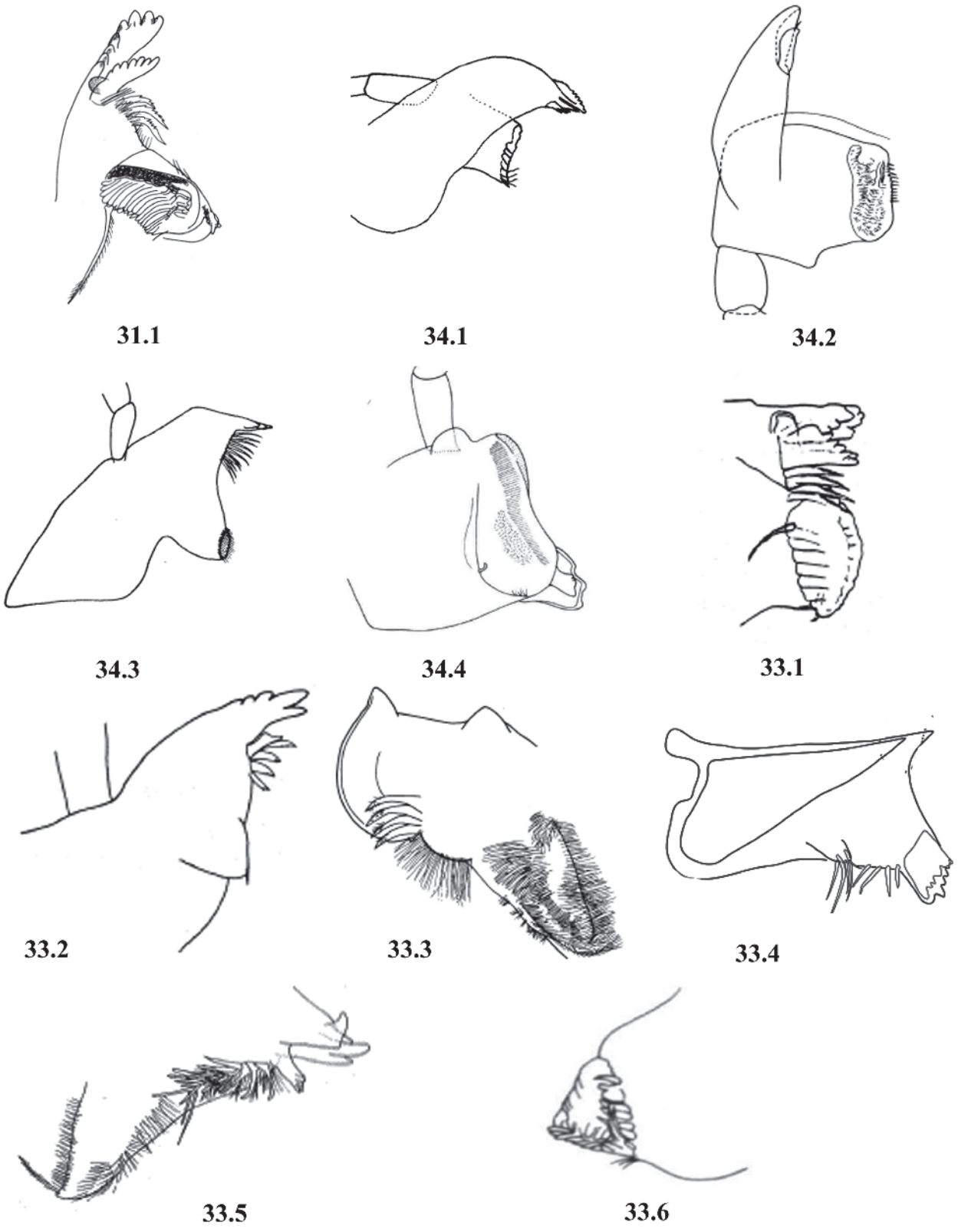

FIGURE 6. Mouthparts. 31.1 molar triturative (after Barnard 1970); 33.1 molar not setose (after Bousfield & Hendrycks 1994): 33.2 molar non-setose, smooth (after Holsinger 1980); 33.3 molar with fully setose tongue (after Lowry & Stoddart 1995); 33.4 molar with smooth setose protuberance (after d'Udekum d'Acoz 2010b); 33.5 molar with broad setose flap (after Lowry & Stoddart 1996); 33.6 molar protuberance with large robust setae (after Barnard & Drummond 1978); 34.1 mandibular molar medium (after Moore 1992b); 34.2 mandibular molar large (after Barnard & Thomas 1998); 34.3 mandibular molar small (after Myers 1974); 34.4 mandibular molar completely dominating mandible (after Barnard 1972).

26. Antenna 2 flagellum
    1. 5 or more articulate
    2. less than 5-articulate
    3. absent
27. Antenna 2 flagellum—adult male
    1. not elongated compared with female
    2. greatly elongated compared with female
    3. absent
28. Mouthpart bundle
    1. subquadrate
    2. subconical
29. Labrum, epistome complex
    1. entire
    2. separate
30. Mandible incisor
    1. dentate
    2. smooth
    3. minutely serrate
    4. vestigial or absent
31. Mandible molar
    1. triturative
    2. non-triturative
    3. vestigial or absent
32. Mandible molar
    1. strongly triturating
    2. weakly triturating
    3. not triturating
33. Mandible molar
    1. not setose
    2. non-setose smooth molar
    3. fully setose tongue
    4. a smooth setose protuberance
    5. a broad setose flap
    6. a smooth protuberance with large robust setae
34. Mandible molar
    1. medium
    2. large
    3. small
    4. completely dominating mandible
    5. vestigial or absent
35. Mandible lacinia mobilis
    1. present on both sides
    2. present on left side only
    3. absent
36. Mandible, accessory setal row
    1. well-developed
    2. vestigial or absent
37. Mandible molar
    1. setal patch absent
    2. patch of fine setae
38. Mandible palp
    1. present in both sexes
    2. present in male, absent in female
    3. vestigial or absent in both sexes
39. Maxilla 1 basal endite (inner plate)
    1. present
    2. absent
40. Maxilla 1 basal endite (inner plate)
    1. setose apically
    2. strongly setose along medial margin
    3. covered in setae
    4. without setae
    5. absent
41. Maxilla 1 ischial endite (outer plate) (used only for Aristioidea and Lysianassoidea)
    1. with 7/4 setal-tooth arrangement
    2. with 6/5 setal-tooth arrangement
    3. with 7/4 crown setal-tooth arrangement
    4. with 8/3 setal-tooth arrangement
    5. with 3–6 in one row
    6. with complex arrangement
    7. with 2 + 3–5 vestigial setal-teeth
    8. setal-teeth absent
42. Maxilla 1 palp
    1. well-developed
    2. vestigial or absent
43. Maxilla 2 basal endite (inner plate)
    1. present, endites free
    2. present, fused with ischial endite
    3. absent
44. Maxilla 2 basal endite (inner plate)
    1. without oblique setal row
    2. with oblique setal row
    3. absent
45. Maxilla 2 basal endite (inner plate)
    1. without setae on medial margin
    2. with strongly setose medial margin
    3. covered in setae
    4. absent
46. Maxilliped basal endite (inner plate) fusion
    1. separate
    2. fused medially
    3. vestigial or absent

47. Maxilliped ischial endite (outer plate)
    1. small (longer than palp article 1, not longer than palp article 2)
    2. large (longer than palp article 2, not longer than palp article 3)
    3. very large (longer than palp article 3)
    4. vestigial or absent (not longer than palp article 1)

47A. Maxilliped
    1. palps present
    2. palps absent

48. Pereonites
    1. separate
    2. 1–2, 1–3, 1–4 or 1–5 fused

49. Coxal gills
    1. unstalked
    2. stalked

50. Coxae 1–3
    1. none vestigial or reduced
    2. coxa 1 reduced or absent
    3. coxa 2 reduced
    4. coxae 1–2 vestigial
    5. coxae 1–3 reduced or vestigial
    6. fused to pereonites

51. Coxae 1–4 overlapping or not
    1. overlapping
    2. discontiguous
    3. fused to pereonites

52. Coxae 1–4
    1. longer than broad
    2. subequal in length and breadth
    3. broader than long
    4. fused to pereonites

53. Coxae 1–4
    1. not acuminate
    2. acuminate
    3. fused to pereonites

54. Gnathopod 1
    1. similar in size to gnathopod 2
    2. smaller (or weaker) than gnathopod 2
    3. larger (or stouter) than gnathopod 2
    4. absent

55. Gnathopod 1
    1. subchelate
    2. simple
    3. carpochelate
    4. parachelate
    5. chelate
    6. absent

56. Gnathopod 1 coxa
    1. subequal to coxa 2
    2. smaller than coxa 2
    3. larger than coxa 2
    4. vestigial, hidden or partially hidden by coxa 2
    5. vestigial, not hidden by coxa 2
    6. fused to pereonite

57. Gnathopod 1 dactylus
    1. large
    2. reduced
    3. small to minute, strongly or weakly covered in setae
    4. absent

58. Gnathopod 2
    1. subchelate
    2. simple
    3. carpochelate
    4. parachelate
    5. chelate
    6. eucarpochelate

59. Gnathopod 2
    1. not mitten-shaped
    2. mitten-shaped

60. Gnathopod 2 coxa
    1. subequal to coxa 3
    2. smaller than but not hidden by coxa 3
    3. smaller than, mostly hidden by coxa 3
    4. larger than coxa 3
    5. fused to pereonite

61. Gnathopod 2 ischium
    1. short (length less than 2 × breadth)
    2. long (length at least 2 × breadth)

62. Gnathopod 2 carpus
    1. short (length less than 2 × breadth)
    2. long (length at least 2 × breadth)

63. Gnathopod 2 carpus
    1. subequal to propodus
    2. shorter than (less than 0.9 ×) propodus
    3. longer than (more than 1.1 ×) propodus

64. Gnathopod 2 carpus
    1. not produced along posterior margin of propodus
    2. strongly produced along posterior margin of propodus
    3. produced along posterior margin of propodus

65. Gnathopod 2 dactylus
    1. well-developed
    2. reduced
    3. absent

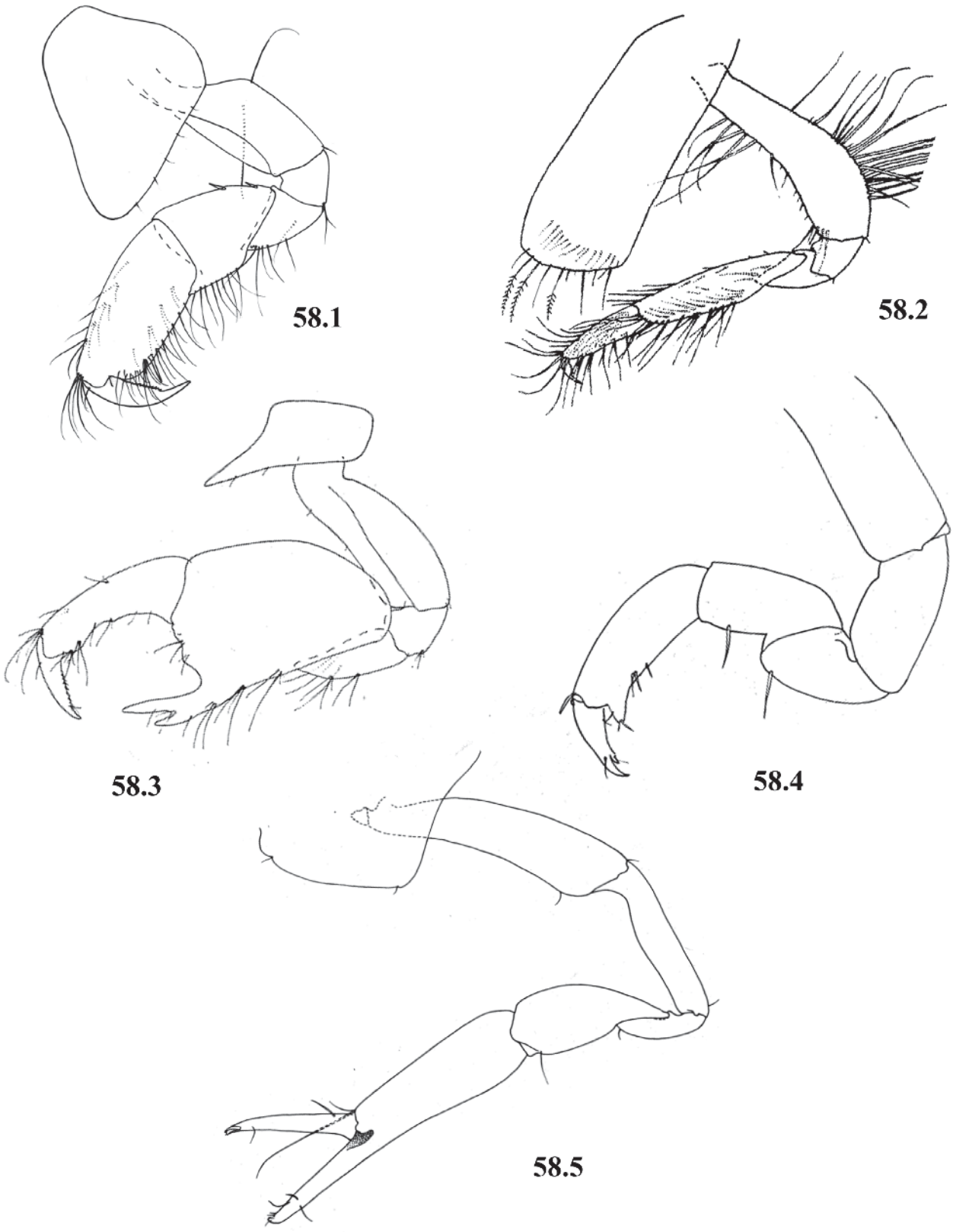

FIGURE 7. Pereon. 58.1 gnathopod 2 subchelate (after Myers 2012); 58.2 gnathopod 2 simple (after Bellan-Santini & Diviacco 1990); 58.3 gnathopod 2 carpochelate (after Myers 1977); 58.4 gnathopod 2 parachelate (after Barnard 1972b); gnathopod 2 chelate (after Barnard 1970).

66. Pereopods
    1. 3–7 without hooded dactyli
    2. some or all of 3–7 with hooded dactyli
67. Pereopods 3–4
    1. without glands
    2. glandular
68. Pereopod 3 coxa
    1. subequal in length and breadth
    2. longer than broad
    3. broader than long
    4. fused to pereonite
69. Pereopod 3 merus
    1. subequal to propodus
    2. shorter than (less than 0.9 ×) propodus
    3. longer than (more than 1.1 ×) propodus
    4. more than 2 × longer than propodus
70. Pereopod 3 carpus
    1. subequal to propodus
    2. shorter than (less than 0.9 ×) propodus
    3. longer than (more than 1.1 ×) propodus
71. Pereopod 3 carpus
    1. not produced
    2. strongly produced posteriorly
    3. produced anteriorly
72. Pereopod 3 dactylus
    1. well-developed
    2. small or poorly developed
    3. minute or absent
73. Pereopod 4 coxa
    1. subequal to coxa 3
    2. smaller than coxa 3
    3. larger than coxa 3
    4. vestigial
    5. fused to pereon
74. Pereopod 4 coxa
    1. without posteroventral lobe
    2. with well-developed posteroventral lobe
    3. with small posteroventral lobe

74A. Pereopod 4 coxa
    1. not acuminate
    2. acuminate ventrally
75. Pereopods 5–6 basis
    1. not or moderately enlarged
    2. greatly enlarged
76. Pereopods 5–7
    1. similar in length
    2. pereopod 5 shorter, pereopods 6 and 7 similar length
    3. pereopods 5 to 7 progressively longer
    4. pereopods 5 to 7 progressively shorter
    5. pereopods 5 and 6 similar in length, pereopod 7 shorter
    6. pereopods 5 and 6 same length, pereopod 7 much longer
    7. pereopods 5 and 7 same length, pereopod 6 much longer
    8. pereopods 5 and pereopod 7 same length, pereopod 6 extremely long—whip-like
    9. pereopod 5 longer than pereopods 6 to 7
77. Pereopods 5–7
    1. with few or no robust or slender setae
    2. with many rows of facial and/or marginal robust and/or slender setae
78. Pereopods 5–7 merus
    1. linear
    2. strongly expanded
    3. slightly expanded
    4. with anterodistal and posterodistal lobes
79. Pereopods 5–7 merus
    1. posterior margin weakly setose
    2. posterior margin strongly setose
    3. posterior margin without slender setae
80. Pereopod 5
    1. simple
    2. carpochelate
    3. subchelate
81. Pereopod 5
    1. subequal to pereopod 6
    2. shorter than pereopod 6
    3. longer than pereopod 6
82. Pereopod 5 coxa
    1. subequal to coxa 4
    2. smaller than coxa 4
    3. larger than coxa 4
    4. vestigial
    5. fused to pereonite
83. Pereopod 5 coxa
    1. without lobes
    2. equilobate
    3. with posteroventral lobe
    4. with anteroventral lobe
    5. with posterodorsal lobe

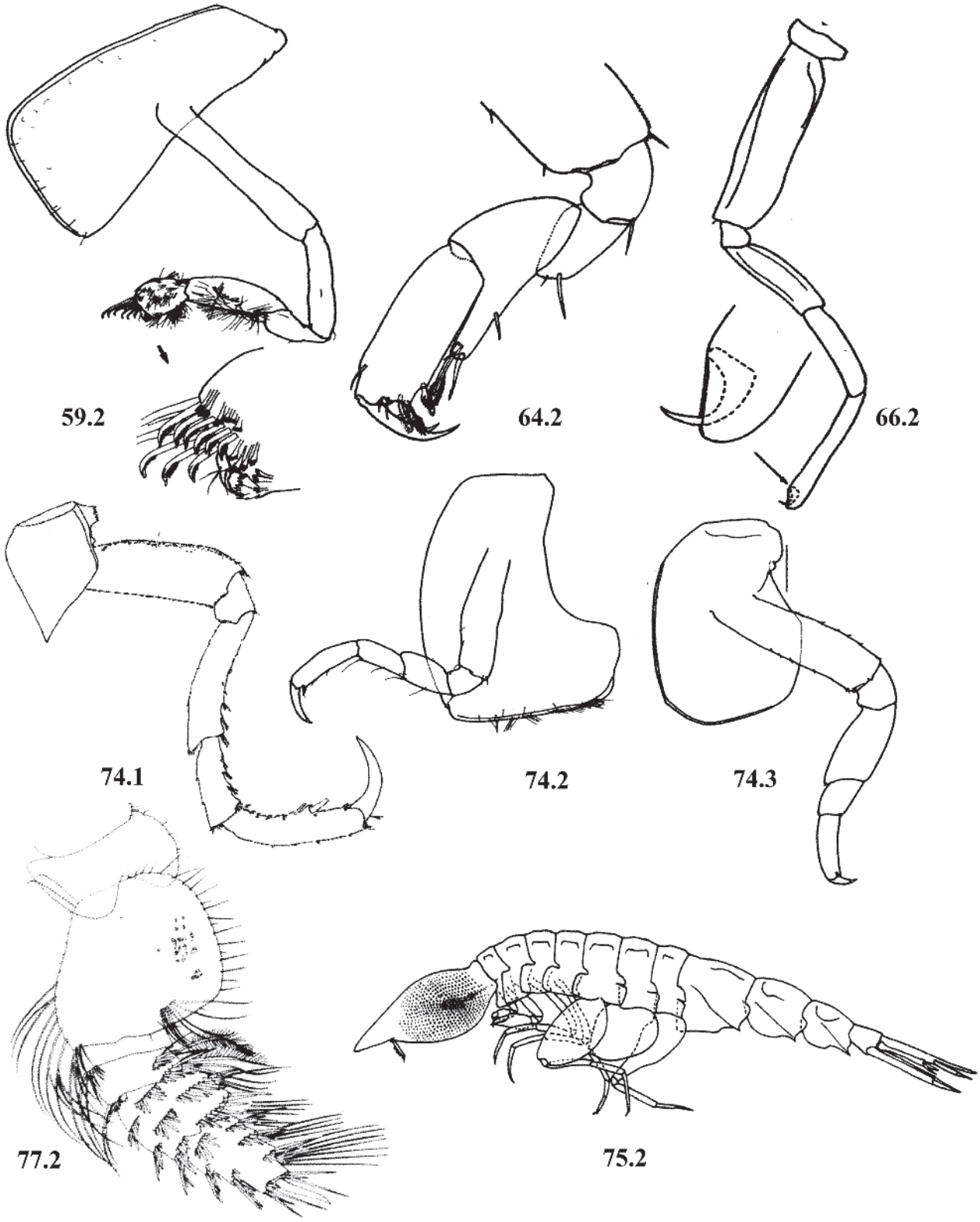

FIGURE 8. Pereon. 59.2 gnathopod 2 mitten-shaped (after Lowry & Stoddart 1995b); 64.2 gnathopod 2 carpus strongly produced along posterior margin of propodus (after J.L. Barnard & Drummond 1982); 66.2 pereopods 3–7 with hooded dactyli (after Zeidler 2009); 74.1 pereopod 4 coxa without posteroventral lobe (after Coleman 1998); 74.2 pereopod 4 coxa with well-developed posteroventral lobe (after Lowry & Stoddart 1994); 74.3 pereopod 4 coxa with small posteroventral lobe (after Lowry & Stoddart 1994); 75.2 pereopods 5–6 basis greatly enlarged (after Zeidler 1999). 77.2 pereopods 5–7 with many rows of facial and marginal robust and slender setae (after J.L. Barnard & Drummond 1982b).

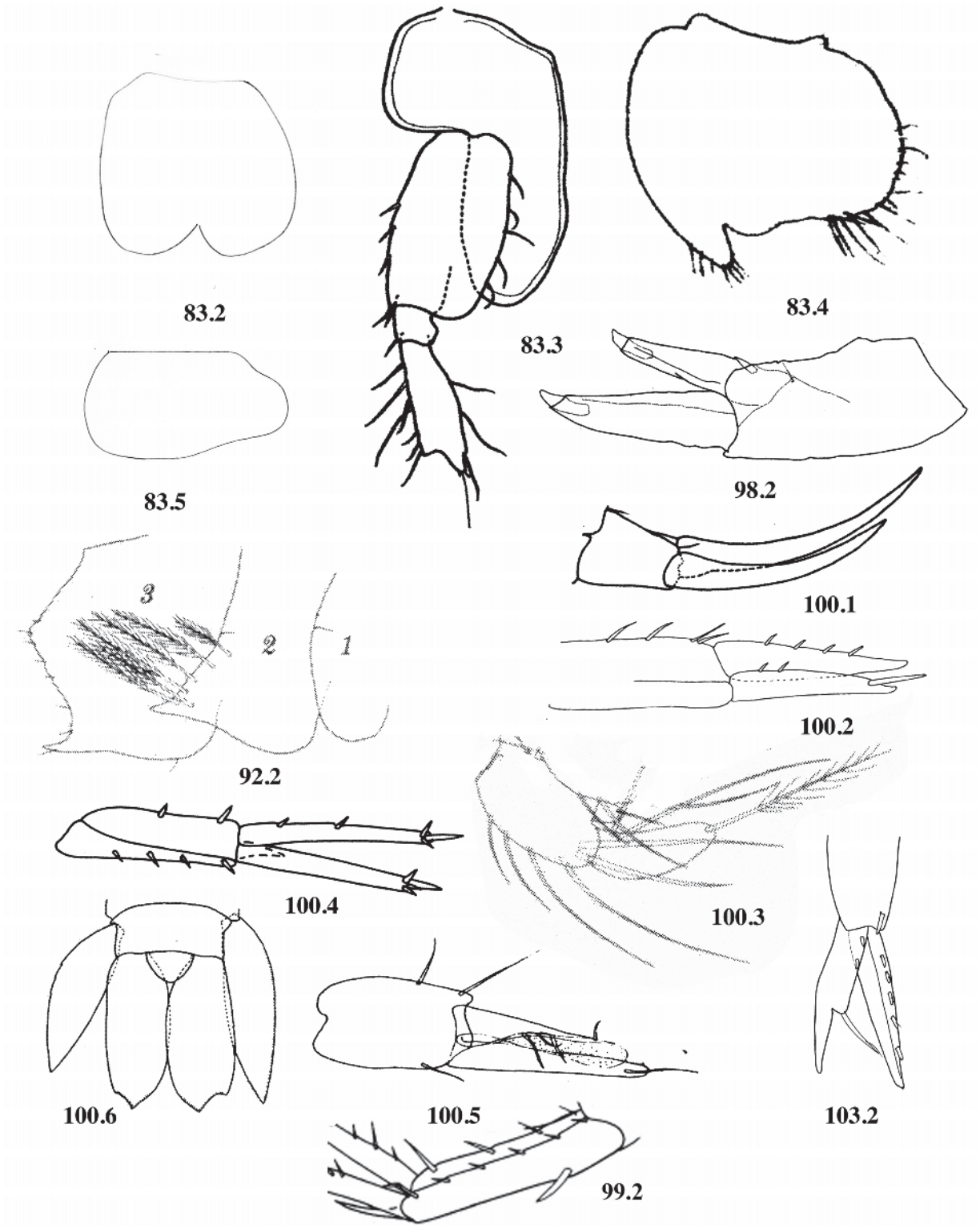

FIGURE 9. Pereon & Pleon. 83.2 pereopod 5 coxa equilobate (after Barnard & Drummond 1982a); 83.3 pereopod 5 coxa with posteroventral lobe (after Azman 2009); 83.4 pereopod 5 coxa with anteroventral lobe (after Bousfield & Kendall 1994); 83.5 pereopod 5 coxa with posterodorsal lobe (after Bowman 1973); 92.2 epimeron 2 with plumose setae (after J.L. Barnard & Drummond 1982b); 98.2 uropod 1–2 rami apices with embedded setae (after Lowry & Stoddart 1995b); 99.2 uropod 1 basofacial robust seta (after Myers 1985); 100.1 uropod 1 rami styliform (after Barnard 1970); 100.2 uropod 1 rami lanceolate (after King 2009); 100.3 uropod 1 rami linguiform (after Barnard & Drummond 1982b); 100.4 uropod 1 rami ferrulate (after Myers 1995); 100.5 uropod 1 rami stylospatulate (after Noodt 1959); 100.6 uropod 1 rami paddle-shaped (after Bowman 1978); 103.2 uropod 2 endopod with constriction (after Lowry & Stoddart 2009).

84. Pereopod 5 basis
    1. subrectangular
    2. subquadrate
    3. subovate
    4. subtriangular
    5. round
85. Pereopod 5 basis
    1. strongly expanded
    2. slightly expanded
    3. linear
86. Pereopod 5 carpus
    1. linear
    2. strongly expanded
    3. slightly expanded
87. Pereopod 5 dactylus
    1. well-developed
    2. small or poorly developed
    3. minute
    4. absent
88. Pereopod 6 basis
    1. strongly expanded
    2. slightly expanded
    3. linear
89. Pereopod 7
    1. subequal to pereopod 5
    2. shorter than pereopod 5
    3. longer than pereopod 5
90. Pereopod 7
    1. similar in structure to pereopod 6
    2. different in structure from pereopod 6
91. Pleonites 1 to 3
    1. without dorsal spines
    2. with dorsal spines
92. Epimeron 2
    1. without plumose setae
    2. with plumose setae
    3. epimeron 2 absent
93. Urosome
    1. not carinate
    2. carinate
94. Urosomites
    1. 1 to 3 free
    2. 1 to 2 free, urosomite 3 absent
    3. 1 to 3 coalesced
    4. 1–2 coalesced, 3 free
    5. 1 free, 2–3 coalesced
95. Urosomite 1
    1. longer than urosomite 2 or 2–3 (up to 2 ×)
    2. shorter than (less than 0.9 ×) urosomite 2 or 2–3
    3. subequal to urosomite 2 or 2–3
    4. much longer than urosomite 2 or 2–3 (at least 3 ×)
96. Urosomite 1
    1. without distoventral robust seta
    2. with distoventral robust seta
97. Uropods 1–2 rami
    1. without apical robust setae
    2. with apical robust setae
98. Uropods 1–2 rami
    1. apices without embedded setae
    2. apices with embedded setae
99. Uropod 1 peduncle
    1. without basofacial robust seta
    2. with basofacial robust seta
100. Uropod 1 rami
    1. styliform
    2. lanceolate
    3. linguiform
    4. ferrulate
    5. stylospatulate
    6. paddle-shaped
101. Uropod 2 rami
    1. styliform
    2. lanceolate
    3. linguiform
    4. ferrulate
    5. stylospatulate
    6. paddle-shaped
    7. vestigial
    8. absent
102. Uropod 2 endopod
    1. subequal to exopod
    2. shorter than (less than 0.9 ×) exopod
    3. longer than (more than 1.1 ×) exopod
    4. absent
103. Uropod 2 endopod
    1. without constriction
    2. with constriction
104. Uropod 3 peduncle
    1. short (length less than 2 × breadth)
    2. long (length at least 2 × breadth)
    3. vestigial
    4. fused to rami

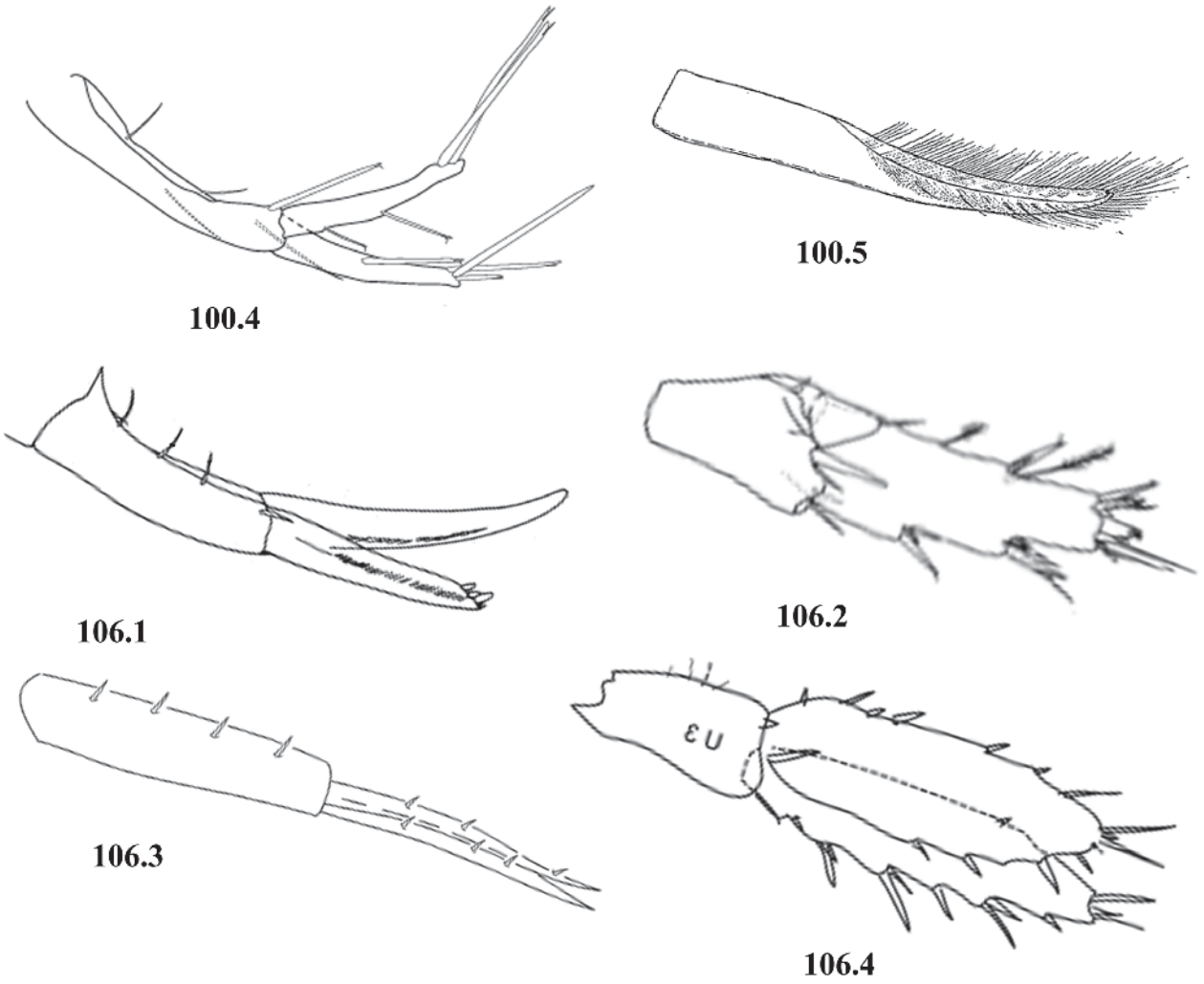

FIGURE 10. Uropods. 100.4 uropod 1 rami ferrulate (after Souza-Filhol 2011); 100.5 uropod 1 ramus stylospatulate (after Ruffo 1969); 106.1 uropod 3 rami styliform (after Barnard 1970); 106.2, uropod 3 ramus linguiform (after Williams & Barnard 1988);106.3 uropod 3 rami lanceolate (after White & Reimer 2012); 106.4 uropod 3 rami paddle-shaped (after Krapp-Schickel 2009).

105. Uropod 3 rami
    1. biramous
    2. uniramous
    3. rami absent
106. Uropod 3 rami
    1. styliform
    2. linguiform
    3. lanceolate
    4. paddle-shaped
    5. vestigial
    6. absent
107. Uropod 3 rami
    1. without fringing plumose setae
    2. with fringing plumose setae
    3. absent
108. Uropod 3 endopod
    1. not apically setose
    2. apically setose
    3. absent
109. Uropod 3 endopod
    1. subequal to exopod
    2. longer than (more than 1.1 ×) exopod
    3. shorter than (less than 0.9 ×) exopod
    4. minute
    5. absent

110. Uropod 3 exopod
    1. subequal to peduncle
    2. longer than (more than 1.1 ×) peduncle
    3. shorter than (less than 0.9 ×) peduncle
    4. absent
111. Uropod 3 exopod
    1. 2-articulate
    2. 1-articulate
    3. absent
112. Telson
    1. entire (including notched or emarginate)
    2. cleft
    3. absent
113. Telson
    1. laminar
    2. dorsoventrally thickened
114. Telson
    1. as long as broad
    2. longer than broad
    3. broader than long
    4. absent
115. Telson
    1. without apical robust setae
    2. with apical robust setae

Phylogenetic analysis

All characters were unweighted with the exception of the calceoli types and the mitten-shaped gnathopod 2, each of which was given a weight of 4. These are complex structures which should have a good index of monophyly and we thus felt justified in giving a weighting factor to these unique characters.

Because the analysis employed an iterative process between DELTA, PAUP and MacClade, the choice of starting tree was unimportant as long as it was a parsimoniously shortest tree. When a number of shortest trees were available they were not significantly different from each other.

The all-family tree had a CI of 0.60 and a RI of 0.60. The parvorder tree had a CI of 0.76 and a RI of 0.70. The Amphilochida tree had a CI of 0.66 and a RI of 0.44. The Lysianassida tree had a CI of 0.70 and a RI of 0.53, while the Hyperiidea tree had a CI of 0.59 and a RI of 0.57.

Tree description

The Pseudingolfiellida is a small infraorder of free-living freshwater amphipods (Fig. 11) characterised by reduced discontiguous coxae and vestigial epimeral plates. The Hyperiidea (Figs 11, 12) is a monophyletic suborder characterized by having a minutely serrate mandibular incisor, no palps on the maxilliped and urosomite segments 2 and 3 coalesced. In addition most taxa (except Vibilioidea and some Platysceloidea) have subglobular to globular bodies, a head deeper to much deeper than long, a mandible generally without molar, though it is present in some Physocephalata; no mandibular accessory setal (raker) row, pereopod 4 coxa without posteroventral lobe and an entire telson. The Colomastigida is a monophyletic infraorder (Fig. 11) characterized by having urosomites 2 and 3 coalesced, loss of the mandible lacinia mobilis on both sides and fused basal endites on the maxilliped. They also have a subcylindrical body, antenna 1 and antenna 2 with less than 5-articulate flagellum and pereopod 4 coxa lacking a posteroventral lobe. The Hyperiopsida (Fig. 11) is a monophyletic though poorly supported infraorder, characterized by sub-cylindrical body, pereopod 3 merus longer than propodus and pereopod 5–7 bases linear. The Senticaudata (Fig. 11) is a monophyletic suborder characterized by uropod 1 and 2 having apical robust setae and uropod 3 with ferulate rami. The Amphilochidea is a monophyletic suborder containing the infraorders Amphilochida and the Lysianassida and based on the weak synapomorphy, presence of brush setae in adult males. The monophyletic infraorder Amphilochida (Fig. 13) is defined by coxae 1–4 overlapping and uropod 3 exopod longer than peduncle. The Lysianassida (Fig. 14) is a large well-defined monophyletic infraorder characterised by a short carpus on the second gnathopod, lanceolate rami on uropods 1 to 3.

Within the infraorder Colomastigida, members of the Colomastigidira sometimes possess a callynophore which is always lacking in pagetinidirans. The colomastigidirans have a simple gnathopod 1 whereas it is subchelate in pagetinidirans. In pagetinidirans, coxa 5 is smaller than coxa 4 but in colomastigidirans they are subequal.

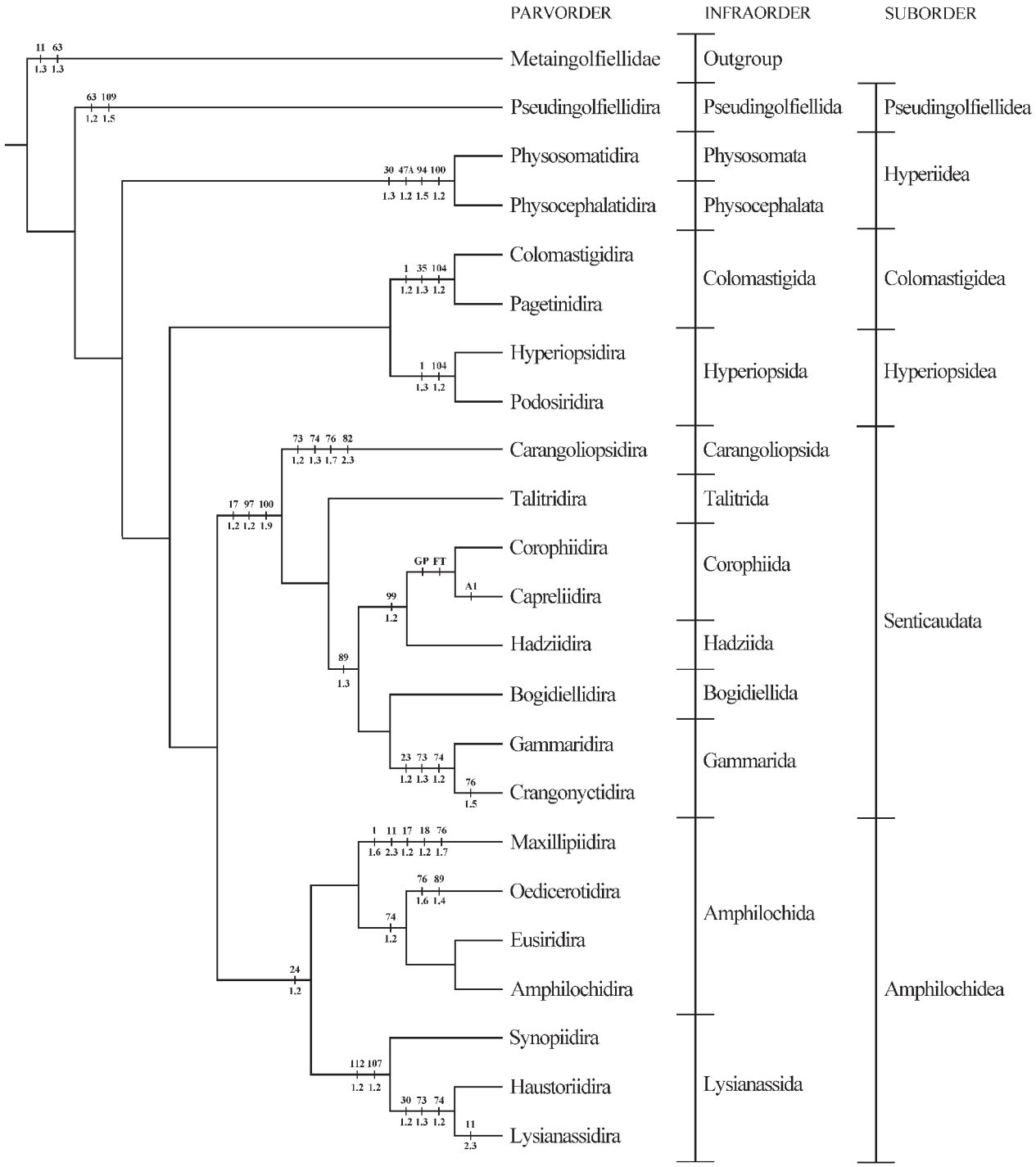

FIGURE 11. Cladogram of relationships of parvorders within the Amphipoda with Metaingolfiellidae as the outgroup. Cross-lines represent significant synapomorphies with character state transformation. A1 = peduncular article 3 long. FT = fleshy telson. GP = glandular pereopods 3–4.

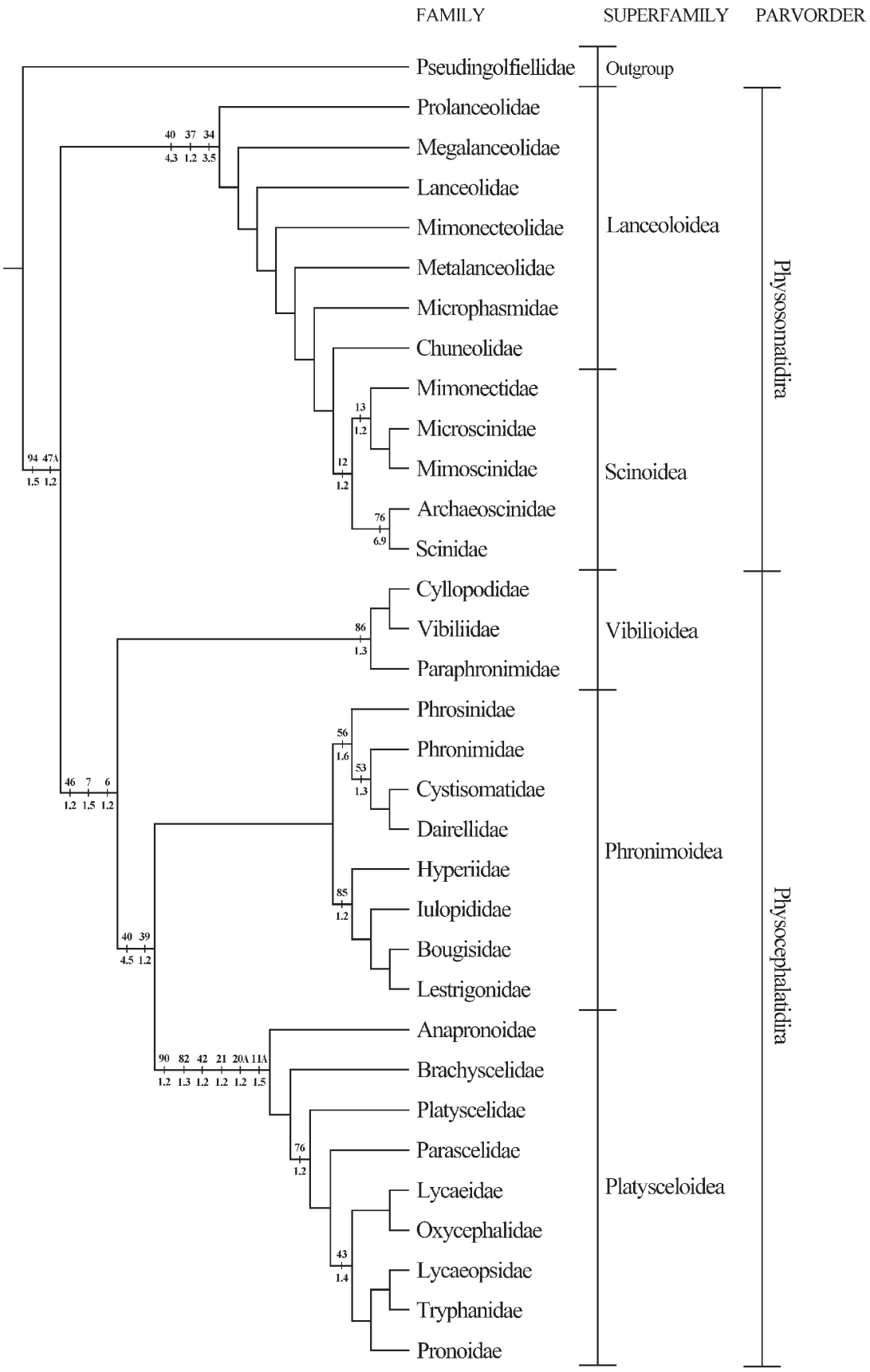

FIGURE 12. Cladogram of relationships of Hyperiidea with Pseudingolfiellidae as the outgroup. Cross-lines represent significant synapomorphies with character state transformation.

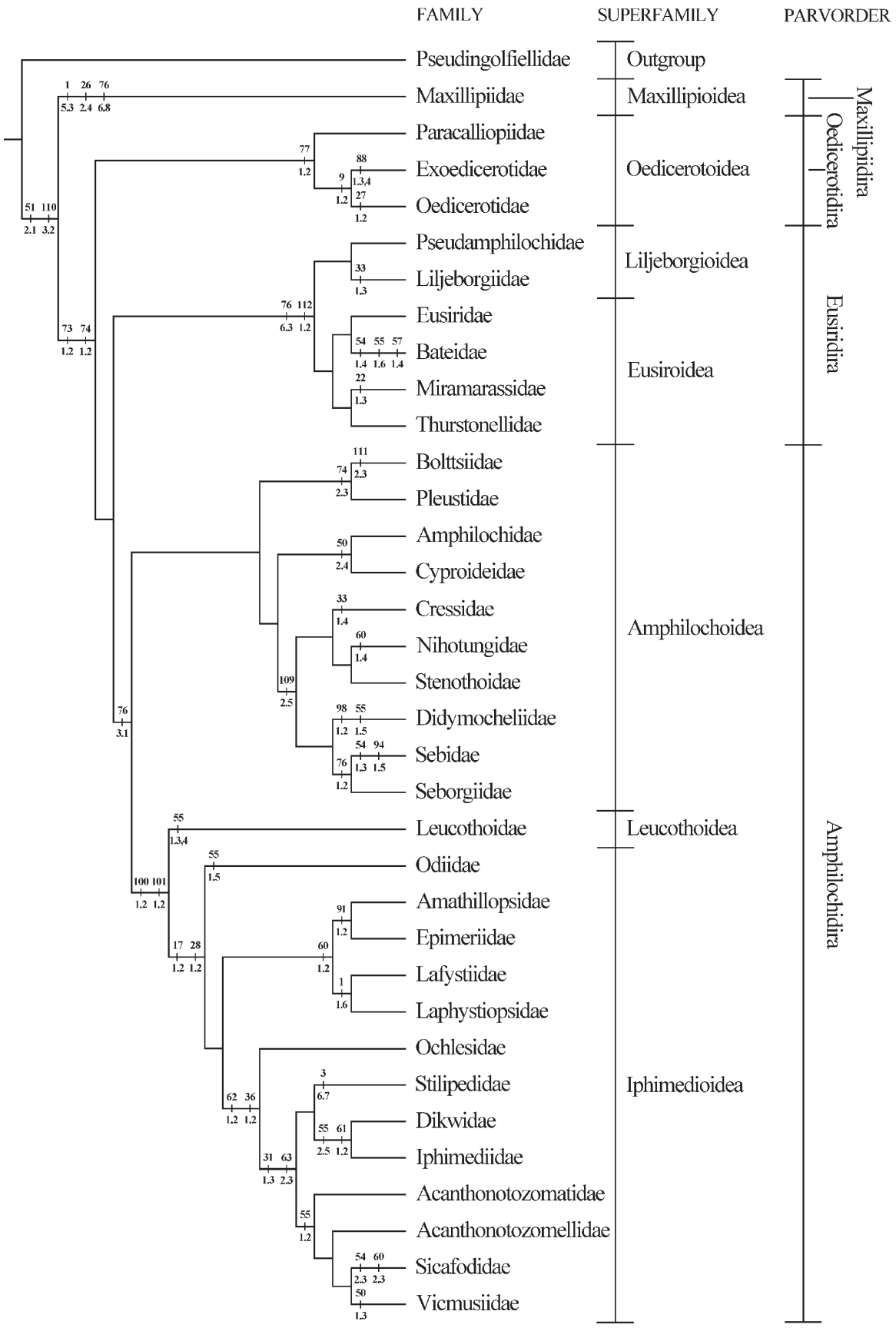

FIGURE 13. Cladogram of relationships of Amphilochida with Pseudingolfiellidae as the outgroup. Cross-lines represent significant synapomorphies with character state transformation.

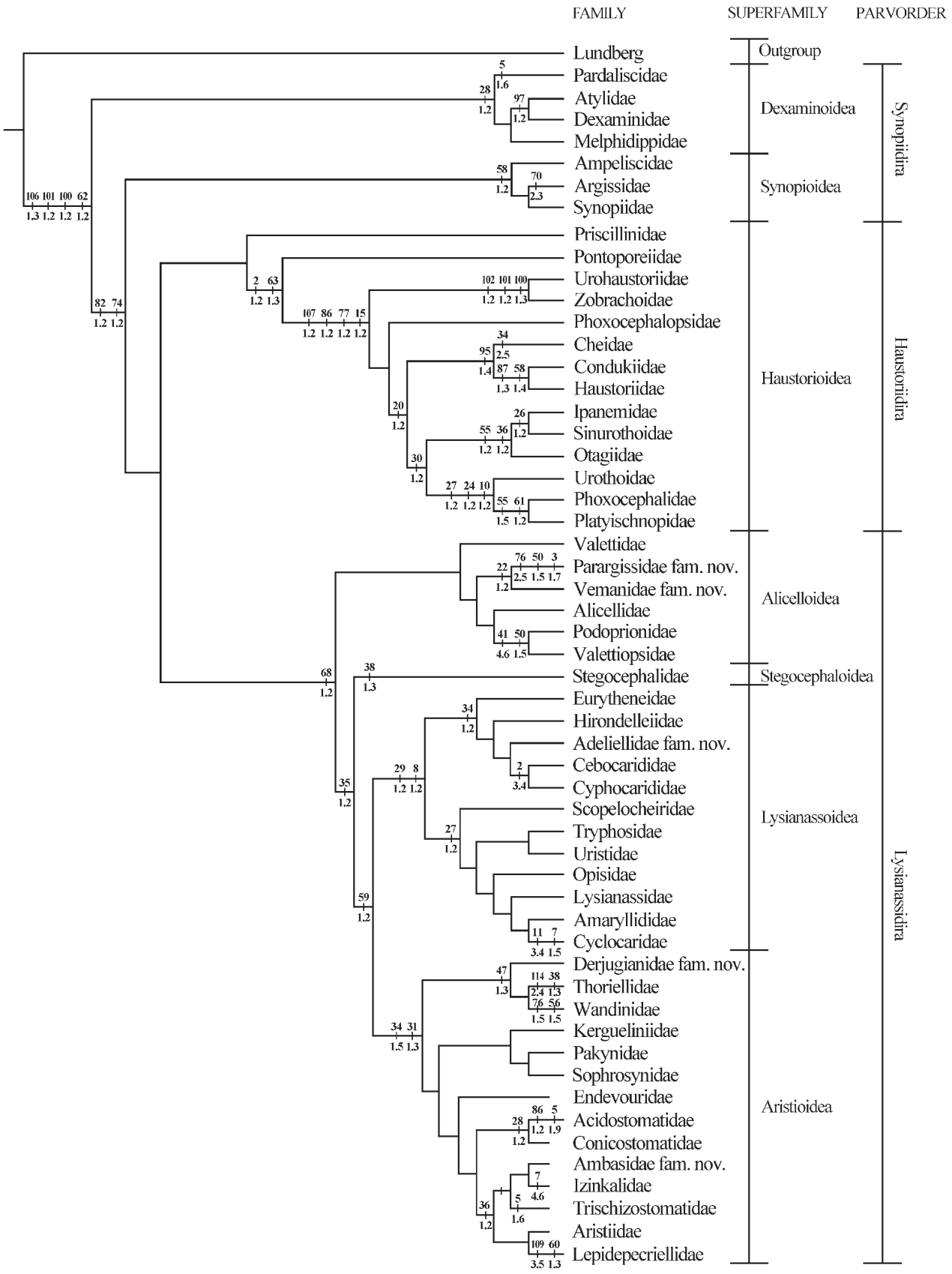

FIGURE 14. Cladogram of relationships of Lysianassida with Lundberg rooting. Cross-lines represent significant synapomorphies with character state transformation.

The Hyperiopsidira have a callynophore, a long pereopod 3 merus, coxa 4 subequal with coxa 3 and without a posteroventral lobe, coxa 5 smaller than coxa 4, linear bases on pereopods 5 and 6 and urosomite 1 much longer than urosomite 2. The Podosiridira have a subcylindrical body, a head that is longer than deep, antenna 1 with peduncular articles 1 and 2 subequal, antenna 2 flagellum longer than the peduncle, mandible molar small, coxae 1–4 broader than long, gnathopod 1 smaller than gnathopod 2 and subchelate, pereopod 3 merus longer than the propodus, coxa 4 smaller than coxa 3, pereopod 7 basis linear, uropod 3 endopod and exopod subequal and telson entire.

The Infraorders and Parvorders of the Senticaudata have already been discussed by Lowry & Myers (2013).

Within the Amphilochida (Fig. 13) there are four parvorders. The Maxillipiidira is a well-defined monophyletic parvorder based on a laterally compressed body with short coxae, second antennae much longer than the body and sixth pereopods extremely elongate. The Oedicerotidira is a small group of three families defined by having many rows of robust or slender setae on pereopods 5 to 7. Within the parvorder two of the three families (Paracalliopiidae and Exoedicerotidae) have an oblique setal row on the basal endite of maxilla 2 and coalesced urosomites 2 and 3. The six families of the Eusiridira have pereopods 5 to7 progressively longer, uropods 1 and 2 with lanceolate rami and the telson is cleft. The Amphilochidira is a large weakly supported monophyletic parvorder with three superfamilies and 24 families. It is defined by having the carpus of pereopod 4 shorter than the propodus and pereopods 5 to 7 of similar length. In addition the molar is generally small, non-triturative or absent, gnathopod 1 is usually simple or chelate and the uropod 2 endopod is generally longer than exopod. Within the Lysianassida (Fig. 14) the Synopiidira have a greatly elongated second antenna in the adult males, often urosomite 1 is free and 2–3 are coalesced and the telson is always cleft. The Haustoriidira have dorsoventrally flattened bodies and pereopods 5–7 with many rows of facial or marginal robust and slender setae. The Lysianassidira have the head deeper than long, generally a well-developed callynophore, gnathopod 2 mitten-shaped (may be poorly developed in basal taxa) and with a long ischium, uropods 1 and 2 often with embedded setae and uropod 3 endopod generally shorter than exopod and two-articulate.

Tree discussion

The amphipod tree has three major clades: one of which includes the basal pseudingolfiellideans, one of which includes the hyperiideans and the third that contains the remainder of the Amphipoda (Fig. 11). The pseudingolfiellidean clade contains only the Pseudingolfiellidae, a small freshwater family known only from South America and some subantarctic islands. It is apparently the closest living relative of the Ingolfiellida. The hyperiidean clade, contains the Physosomata and Physocephalata of the well-supported Hyperiidea. It is a sister to all other amphipods except the Pseudingolfiellida. The pagetinidiran and colomastigidiran parvorders that form the relatively well-supported Colomastigidea and are both sister taxa to the hyperiopsideans. The hyperiopsidiran and podosiridiran parvorders form the not as well-supported Hyperiopsidea which are planktonic/pelagic. In the third clade there are two suborders, the Senticaudata (see Lowry & Myers 2013) and the Amphilochidea. There are two infraorders in the Amphilochidea, the Amphilochida and the Lysianassida both of which are monophyletic.

Current ingolfiellidans are highly derived interstitial crustaceans with a worm-like body, vestigial coxae, etc. It is possible that extinct ingolfiellidans with a more generalised form, epigean habit, large coxae, pedunculate eyes, etc., gave rise to true amphipods like the amphilochids.

There are six suborders, 13 infraorders and 23 parvorders among the Amphipoda. We consider the Ingolfiellida to be a sister taxon to the Amphipoda. Amphipods are broadly differentiated from other peracaridans by the sessile eyes, no carapace, coxal gills and a urosome of three segments with epimera and with three uropods. Ingolfiellida are similar to Amphipoda in that they have no carapace and coxal gills, but they have vestigial pedunculate eyes, a pleosome of six segments without epimera and with reduced pleopod/uropod appendages. These significant characters justify the exclusion of the Ingolfiellida from the Amphipoda. Accordingly, we establish the new order Ingolfiellida. Verheye *et al*. (2015), carried out an 18S rDNA analysis, using a very small selection of amphipod species. *Ingolfiella tabularis* represented the Ingolfiellida and was basal in their maximum likelihood tree.

The six suborders represent the broadest evolutionary groups among the amphipods. Basal pseudingolfiellideans are benthic free-living freshwater amphipods with reduced discontiguous coxae and vestigial epimeral plates. Basal colomastigideans are benthic, with short coxae and subcylindrical bodies, free-living or

commensals. Basal hyperiopsideans are pelagic or benthic. One group, the hyperiopsoids are at least superficially similar to hyperiidean amphipods. At some stage, apparently relatively early in the history of the amphipods, a basal benthic amphipod moved up into the pelagic realm and diversified into a large, morphologically diverse group of predators (large-eyed Physocephalata) and larval parasites (small-eyed Physosomata) on jellyfish (Laval 1980, Madin & Harbison 1977 and Harbison, Biggs & Madin 1977). They retain entire telsons. Laval (1980) suggested that they basically traded one benthic surface for another.

Another group, the senticaudates, successfully invaded the shallow-water marine environment and world-wide freshwater and terrestrial environments. These taxa have completely lost the callynophore and developed apical robust setae on the rami of uropods 1 and 2. The males developed large gnathopods for mate-guarding (Conlan 1991).

The Amphilochidea form a large diverse group of 88 families in seven parvorders. At the base of the Amphilochidira are the Amphilochoidea which are near in form to the hypothesized original amphipod type. While the Amphilochoidea are not basal in our cladogram, they have retained many plesiomorphic attributes while other branches have diversified and evolved into the manifold forms extant today. We believe that the ancestral amphipod was a clinger in anastomoses that used the reflexed urosome as a means of propulsion. The stiffened uropods provided grip on the substrate for the propulsive force. Clinging to anastomoses is best attained if the opposing limbs are close together. This explains the characteristic features of an amphipod—presence of uropods, reflexed abdomen and laterally flattened form. In a laterally flattened animal, the coxae can increase in size without it having a detrimental effect on locomotion. The enlarged coxae can then act as shields protecting body parts and in females, eggs. We therefore consider enlarged coxae to be a plesiomorphic character state. Amphilochids have no special reproductive modifications such as brush setae, elongate second antennae or plumose setae on the rami of the third uropods, often found in more advanced amphilochideans. Strategic reproductive character states such as brush setae and elongate second antennae first appear among the Eusiroidea and the Oedicerotoidea.

But within the Amphilochidea there is evidence of evolution into major habitats. Within the Synopiidira dexaminoids have developed the swimming male reproductive strategy as have the soft bottom suspension feeding ampeliscids in the Synopioidea; iphimediids live among corals and in anastomoses etc. and also swim actively in both sexes; haustoriidirans live in shallow water soft bottom habitats or high energy sand habitats and also take advantage of the swimming male reproductive strategy to enhance their gene mixing.

The majority of highly derived lysianassidiran amphipods moved into a new habitat for the Amphipoda as scavengers on dead animals. They retain the swimming male reproductive strategy, but usually have a callynophore in the male and female for detecting odours in the water column, they developed a smooth slicing incisor and a tongue-like molar and the setal-teeth on maxilla 1 modified into a fork-like arrangement in highly derived scavengers such as the uristids. The alicelloid amphipods are deep water scavengers which retain the lacinia mobilis on both mandibles, a 7/4 setal-tooth arrangement and an entire telson. The gigantic alicellids have a gammaroid-like calceolus uncharacteristic of lysianassidirans. At least two species of Valettidae occur in the alimentary canal of deep sea holothurians (Thurston 1989b). Parargissids are uncharacteristic lysianassidirans which share asymmetrical palps on maxilla 1 with hyperiopsids, but the legs are atypical of lysianassidirans, while podoprionids have highly serrated incisor uncharacteristic of lysianassidirans. Stegocephaloids are the sister taxa to the remaining lysianassidirans. According to Berge & Vader (2001) stegocephalids appear to be micro-predators often in association with hydroids and bryozoans (Sars 1891) and with sponges and tunicates (Vader 1984), but they are also reported as scavengers (Lowry & Stoddart 1995b, Berge & Vader 2003).

The remaining members of the Lysianassidira are characterised by a mitten-shaped second gnathopod and a left lacinia mobilis only. One group, the Lysianassoidea, is made up almost entirely of scavengers often with a type 3 lysianassoid calceolus and a cleft telson. Several families, the Adeliellidae, Amaryllididae, Cyphocarididae (pelagic predators) Cebocaridae and Opisidae are not scavengers. No Aristioidea are scavengers. Families such as the thoriellids, wandinids, acidostomatids, trischizostomatids and aristiids appear to be associated with other invertebrates, or in the case of the trischizostomatids, epiparasites on sharks.

Discussion

This is first ever attempt at a phylogenetic classification of the entire order Amphipoda. The order is well known for its morphological convergence in unrelated lineages occupying similar environments (Barnard & Karaman

1975; Bousfield 1977; Barnard & Barnard 1983). This may explain why no attempt has previously been made at a complete phylogenetic classification of the Amphipoda.

In this study, many of the clades are supported by several strong synapomorphies, but some inevitably are more weakly supported. Our aim in this work was to provide a complete classification, so we did not have the option of ignoring weakly supported clades.

We do not stand over the exact relationship of each and every family one to another. Further work is necessary to clarify some of these relationships. Our main aim was to provide a framework classification to superfamily level. Most of the higher taxa (above family level) can be clearly diagnosed. Our classification of the Amphipoda is a hypothesis for future testing by both morphological and molecular analyses.

While many morphological and molecular studies have produced conflicting results, some show good agreement. Good conformity is shown between the present work and the molecular study of Hurt *et al*. (2013). The physomatidiran part of our hyperiidean tree shows the lanceoloids and the scinoids as two distinct lines of evolution and this is in agreement with Hurt *et al*. (2013). Like their study, the present work also shows a primarily phronimid—phrosinid clade and a vibiliid—cyllopodid clade. Another example, the good conformity between the results of a morphological study (Myers & Lowry 2003) and a molecular study (Ito *et al*. 2011) in the case of the caprellid amphipods, was described earlier in this paper.

Classification

A full classification of the Ingolfiellida and the Amphipoda is provided for completeness and to indicate at a glance changes in higher taxa (Table 1). Families are listed in alphabetical order for ease of use.

TABLE 1. Classification of the Ingolfiellida and the Amphipoda including the Senticaudata (Lowry & Myers 2013).

Order Ingolfiellida
Suborder Ingolfiellidea
Infraorder Ingolfiellidamorpha
Parvorder Ingolfiellidira
Superfamily Ingolfielloidea
Family Ingolfiellidae
Parvorder Metaingolfiellidira
Superfamily Metaingolfielloidea
Family Metaingolfiellidae
Order Amphipoda
Suborder Pseudingolfiellidea
Infraorder Pseudingolfiellida
Parvorder Pseudingolfiellidira
Superfamily Pseudingolfielloidea
Family Pseudingolfiellidae
Suborder Hyperiidea
Infraorder Physosomata
Parvorder Physosomatidira
Superfamily Lanceoloidea
Family Chuneolidae
Family Lanceolidae
Family Megalanceolidae
Family Metalanceolidae
Family Microphasmidae
Family Mimonecteolidae
Family Prolanceolidae
Superfamily Scinoidea
Family Archaeoscinidae
Family Microscinidae
Family Mimonectidae
Family Mimoscinidae
Family Scinidae
Infraorder Physocephalata
Parvorder Physocephalatidira
Superfamily Vibilioidea
Family Cyllopodidae
Family Paraphronimidae
Family Vibiliidae
Superfamily Cystisomatoidea
Family Cystisomatidae
Superfamily Phronimoidea
Family Bougisidae
Family Dairellidae
Family Hyperiidae
Family Iulopididae
Family Lestrigonidae
Family Phronimidae
Family Phrosinidae
Superfamily Platysceloidea
Family Amphithyridae
Family Anapronoidae
Family Brachyscelidae
Family Eupronoidae
Family Lycaeidae
Family Lycaeopsidae
Family Oxycephalidae
Family Parascelidae
Family Platyscelidae
Family Pronoidae
Family Thamneidae

Family Tryphanidae
Suborder Colomastigidea
Infraorder Colomastigida
Parvorder Colomastigidira
Superfamily Colomastigoidea
Family Colomastigidae
Parvorder Pagetinidira
Superfamily Pagetinoidea
Family Pagetinidae
Suborder Hyperiopsidea
Infraorder Hyperiopsida
Parvorder Hyperiopsidira
Superfamily Hyperiopsoidea
Family Hyperiopsidae
Family Vitjazianidae
Parvorder Podosiridira
Superfamily Podosiroidea
Family Podosiridae
Suborder Senticaudata
Infraorder Carangoliopsida
Parvorder Carangoliopsidira
Superfamily Carangoliopsoidea
Family Carangoliopsidae
Family Kairosidae
Infraorder Talitrida
Parvorder Talitridira
Superfamily Biancolinoidea
Family Biancolinidae
Superfamily Caspicoloidea
Family Caspicolidae
Superfamily Kurioidea
Family Kuriidae
Family Tulearidae
Superfamily Talitroidea
Family Ceinidae
Family Chiltoniidae
Family Dogielinotidae
Family Eophliantidae
Family Hyalellidae
Family Hyalidae
Subfamily Hyacheliinae
Subfamily Hyalinae
Family Najnidae
Family Phliantidae
Family Plioplateidae
Family Talitridae
Family Temnophliantidae
Infraorder Corophiida
Parvorder Corophiidira
Superfamily Aoroidea
Family Aoridae
Family Unciolidae
Subfamily Acuminodeutopinae
Subfamily Unciolinae
Superfamily Cheluroidea
Family Cheluridae
Superfamily Chevalioidea
Family Chevaliidae
Superfamily Corophioidea
Family Ampithoidae
Subfamily Ampithoinae
Subfamily Exampithoinae
Family Corophiidae
Subfamily Corophiinae
Tribe Corophiini
Tribe Haplocheirini
Tribe Paracorophiini
Subfamily Protomedeiinae
Parvorder Caprellidira
Superfamily Aetiopedesoidea
Family Aetiopedesidae
Family Paragammaropsidae
Superfamily Caprelloidea
Family Caprellidae
Subfamily Caprellinae
Subfamily Paracercopinae
Subfamily Phtisicinae
Family Caprogammaridae
Family Cyamidae
Family Dulichiidae
Family Podoceridae
Superfamily Isaeoidea
Family Isaeidae
Superfamily Microprotopoidea
Family Australomicroprotopidae
Family Microprotopidae
Superfamily Neomegamphopoidea
Family Neomegamphopidae
Family Priscomilitariidae
Superfamily Photoidea
Family Ischyroceridae
Subfamily Bonnierellinae
Subfamily Ischyrocerinae
Tribe Ischyrocerini
Tribe Siphonoecetini
Family Kamakidae
Subfamily Aorchinae
Subfamily Kamakinae
Family Photidae
Superfamily Rakirooidea
Family Rakiroidae
Infraorder Hadziida
Parvorder Hadziidira
Superfamily Hadzioidea
Family Crangoweckeliidae
Family Eriopisidae
Family Gammaroporeiidae
Family Hadziidae
Family Maeridae
Family Melitidae
Family Metacrangonyctidae
Family Nuuanuidae

Superfamily Calliopioidea
Family Calliopiidae
Family Cheirocratidae
Family Hornelliidae
Family Megaluropidae
Family Pontogeneiidae
Infraorder Bogidiellida
Parvorder Bogidiellidira
Superfamily Bogidielloidea
Family Artesiidae
Family Bogidiellidae
Family Salentinellidae
Infraorder Gammarida
Parvorder Crangonyctidira
Superfamily Allocrangonyctoidea
Family Allocrangonyctidae
Family Crymostygiidae
Family Dussartiellidae
Family Pseudoniphargidae
Family Kergueleniolidae
Superfamily Crangonyctoidea
Family Austroniphargidae
Family Chillagoeidae
Family Crangonyctidae
Family Giniphargidae
Family Kotumsaridae
Family Neoniphargidae
Family Niphargidae
Family Paracrangonyctidae
Family Paramelitidae
Family Perthiidae
Family Pseudocrangonyctidae
Family Sandroidae
Family Sternophysingidae
Family Uronyctidae
Parvorder Gammaridira
Superfamily Gammaroidea
Family Acanthogammaridae
Family Anisogammaridae
Family Baikalogammaridae
Family Bathyporeiidae
Family Behningiellidae
Family Falklandellidae
Family Gammaracanthidae
Family Gammarellidae
Family Gammaridae
Family Iphigenellidae
Family Lucioblividae
Family Macrohectopidae
Family Mesogammaridae
Family Micruropodidae
Family Pachyschesidae
Family Pallaseidae
Family Paraleptamphopidae
Family Phreatogammaridae
Family Pontogammaridae
Family Sensonatoridae
Family Typhlogammaridae
Family Zaramillidae
Incertae Sedis
Family Iciliidae [Senticaudata]
Family Sanchoidae [Senticaudata]
Suborder Amphilochidea
Infraorder Amphilochida
Parvorder Maxillipiidira
Superfamily Maxillipioidea
Family Maxillipiidae
Parvorder Oedicerotidira
Superfamily Oedicerotoidea
Family Exoedicerotidae
Family Oedicerotidae
Family Paracalliopiidae
Parvorder Eusiridira
Superfamily Eusiroidea
Family Bateidae
Family Eusiridae
Family Miramarassidae
Family Thurstonellidae
Superfamily Liljeborgioidea
Family Liljeborgiidae
Subfamily Idunellinae
Subfamily Liljeborgiinae
Family Pseudamphilochidae
Parvorder Amphilochidira
Superfamily Amphilochoidea
Family Amphilochidae
Family Bolttsiidae
Family Cressidae
Family Cyproideidae
Family Didymocheliidae
Family Nihotungidae
Family Pleustidae
Subfamily Atylopsinae
Subfamily Austropleustinae
Subfamily Dactylopleustinae
Subfamily Eosymtinae
Subfamily Mesopleustinae
Subfamily Neopleustinae
Subfamily Parapleustinae
Subfamily Pleusirinae
Subfamily Pleustinae
Subfamily Pleustoidinae
Subfamily Pleusymtinae
Subfamily Stenopleustinae
Family Sebidae
Family Seborgiidae
Family Stenothoidae
Superfamily Leucothoidea
Family Leucothoidae
Superfamily Iphimedioidea
Family Acanthonotozomatidae
Family Acanthonotozomellidae

Family Amathillopsidae
Subfamily Amathillopsinae
Subfamily Cleonardopsinae
Subfamily Parepimeriinae
Family Dikwidae
Family Epimeriidae
Family Iphimediidae
Family Lafystiidae
Family Laphystiopsidae
Family Ochlesidae
Family Odiidae
Family Sicafodiidae
Family Stilipedidae
Subfamily Astryinae
Subfamily Alexandrellinae
Subfamily Stilipedinae
Family Vicmusiidae
Infraorder Lysianassida
Parvorder Synopiidira
Superfamily Dexaminoidea
Family Atylidae
Subfamily Anatylinae
Subfamily Atylinae
Subfamily Lepechinellinae
Subfamily Nototropiinae
Family Dexaminidae
Subfamily Dexamininae
Subfamily Dexaminoculinae
Subfamily Polycheriinae
Subfamily Prophliantinae
Family Melphidippidae
Family Pardaliscidae
Superfamily Synopioidea
Family Ampeliscidae
Family Argissidae
Family Synopiidae
Parvorder Haustoriidira
Superfamily Haustorioidea
Family Cheidae
Family Condukiidae
Family Haustoriidae
Family Ipanemidae
Family Otagiidae
Family Phoxocephalidae
Subfamily Harpiniinae
Subfamily Phoxocephalinae
Family Phoxocephalopsidae
Family Platyischnopidae
Family Pontoporeiidae
Family Priscillinidae
Family Sinurothoidae
Family Urohaustoriidae
Family Urothoidae
Family Zobrachoidae
Parvorder Lysianassidira
Superfamily Alicelloidea
Family Alicellidae
Family Parargissidae
Family Podoprionidae
Family Valettidae
Family Valettiopsidae
Family Vemanidae
Superfamily Stegocephaloidea
Family Stegocephalidae
Subfamily Andaniexinae
Subfamily Andaniopsinae
Subfamily Bathystegocephalinae
Subfamily Parandaniinae
Subfamily Stegocephalinae
Superfamily Lysianassoidea
Family Adeliellidae
Family Amaryllididae
Subfamily Amaryllidinae
Subfamily Vijayiinae
Family Cebocaridae
Family Cyclocaridae
Family Cyphocarididae
Family Eurytheneidae
Family Hirondelleidae
Family Lysianassidae
Subfamily Lysianassinae
Subfamily Waldeckiinae
Family Opisidae
Family Scopelocheiridae
Subfamily Paracallisominae
Subfamily Scopleocheirinae
Family Tryphosidae
Family Uristidae
Superfamily Aristioidea
Family Acidostomatidae
Family Ambasiidae
Family Aristiidae
Family Conicostomatidae
Family Derjugianidae
Family Endevouridae
Family Izinkalidae
Family Kergueleniidae
Family Lepidepecreellidae
Family Pakynidae
Family Sophrosynidae
Family Thoriellidae
Family Trischizostomatidae
Family Wandinidae

Superorder Peracarida

Order Ingolfiellida Hansen, 1903 stat. nov.

Diagnosis. Head with vestigial pedunculate eyes. Gnathopods 1–2 eucarpochelate. Pleosome with 6 relatively undifferentiated segments, without epimera, with reduced pleopods and uropods.

Remarks. The important apomorphies that define the order are the eucarpochelate gnathopods and the six-segmented pleosome. The eucarpochelate gnathopods occur when the propodus is reduced and combined with the dactylus to form a dactylar complex, both close onto an expanded carpus. This situation is approached in amphipods in some species of the ischyrocerid genus *Ericthonius* and the aorid genus *Grandidierella*, but this is considered as convergent.

Suborder Ingolfiellidea Hansen, 1903 (Ruffo, 1970)

Diagnosis. As for order.

Infraorder Ingolfiellidamorpha Hansen, 1903 stat. nov.

Diagnosis. As for suborder.

Parvorder Ingolfiellidira Hansen, 1903 stat. nov.

Diagnosis. Body vermiform. Pleopods modified. Uropod 3 uniramous.

Included superfamilies. Ingolfielloidea Hansen, 1903 **stat. nov.**

Superfamily Ingolfielloidea Hansen, 1903 stat. nov.

Diagnosis. As for parvorder.

Included families. Ingolfiellidae Hansen, 1903.

Family Ingolfiellidae Hansen, 1903

Included genera. *Ingolfiella* Hansen, 1903; *Proleleupia* Vonk & Schram, 2003; *Rapaleleupia* Vonk & Schram, 2007; *Stygobarnardia* Ruffo, 1985; *Troglolelеupia* Ruffo, 1975.

Parvorder Metaingolfiellidira Ruffo, 1969 stat. nov.

Diagnosis. Mandible palp present. Body subcylindrical. Pleopods well-developed. Uropod 3 biramous.

Included superfamilies. Metangolfielloidea Ruffo, 1969 **stat. nov.**

Superfamily Metaingolfielloidea Ruffo, 1969 stat. nov.

Diagnosis. As for parvorder.

Included families. Metaingolfiellidae Ruffo, 1969.

Family Metaingolfiellidae Ruffo, 1969

Included genera. *Metaingolfiella* Ruffo, 1969.

Order Amphipoda Latreille, 1816

Diagnosis. Head with sessile eyes. Carapace absent. Coxal gills present. Abdomen with 6 segments, differentiated into a pleosome with 3 segments, with epimera (vestigial in *Pseudingolfiella*) and urosome with 3 segments. Last three pairs of pleopods converted into uropods, pleopods and uropods usually well-developed.

Suborder Pseudingolfiellidea Lowry & Myers, 2012a stat. nov.

Diagnosis. Body vermiform. Maxilliped palps well developed; ischial endites small, not longer than palp article 2. Coxae greatly reduced, discontiguous. Gnathopods subchelate. Pleopods reduced. Epimera vestigial. Urosome poorly defined. Uropods 1–2 rami without apical robust setae.

Included infraorders. Pseudingolfiellida Lowry & Myers, 2012a **stat. nov.**

Remarks. The urosome is weakly differentiated but the vestigial uropods are notched into the urosome. Lowry & Myers (2013) excluded Pseudingolfiellidae from the Senticaudata based on the lack of apical robust setae on uropods 1 and 2.

Infraorder Pseudingolfiellida Lowry & Myers, 2012a stat. nov.

Diagnosis. As for Suborder.

Included parvorders. Pseudingolfiellidira Lowry & Myers, 2012a **stat. nov.**

Parvorder Pseudingolfiellidira Lowry & Myers, 2012a stat. nov.

Diagnosis. As for Suborder.

Included superfamilies. Pseudingolfielloidea Lowry & Myers, 2012a **stat. nov.**

Superfamily Pseudingolfielloidea Lowry & Myers, 2012a stat. nov.

Diagnosis. As for Suborder.

Included families. Pseudingolfiellidae Lowry & Myers, 2012a **stat. nov.**

Family Pseudingolfiellidae Lowry & Myers, 2012a

Included genera. *Pseudingolfiella* Noodt, 1965.

Suborder Hyperiidea H. Milne Edwards, 1830

Diagnosis. Maxilliped without palps. Urosomite 1 free, 2–3 coalesced. Uropods 1–2 rami without apical robust setae.

Included infraorders. Physosomata Pirlot, 1929; Physocephalata Bowman & Gruner, 1973.

Infraorder Physosomata Pirlot, 1929 (Bowman & Gruner, 1973)

Diagnosis. Eyes small or absent (except Vibiliidae). Urosomites 2–3 partially fused. Male genital papillae present.

Included parvorders. Physosomatidira Pirlot, 1929 **stat. nov.**

Remarks. Zeidler (2006) indicates two new characters for the Physosomata: 'a partial ventral suture between urosomites 2 & 3 in all specimens and the presence of male genital papillae'.

Parvorder Physosomatidira Pirlot, 1929 stat. nov.

Diagnosis. Molar with patch of fine setae. Maxilla 1 basal endite present. Maxilliped basal endite separate.

Included superfamilies. Lanceoloidea Bovallius, 1887 (Bowman & Gruner, 1973); Scinoidea Stebbing, 1888 (Bowman & Gruner, 1973).

Superfamily Lanceoloidea Bovallius, 1887 (Bowman & Gruner, 1973)

Diagnosis. Head deeper than long. Antenna 2 adult male flagellum not greatly elongate. Maxilla 1 basal endite covered in setae. Pereonites separate. Pereopod 4 coxa subequal or smaller than coxa 3.

Included families. Chuneolidae Woltereck, 1909; Lanceolidae Bovallius, 1887; Megalanceolidae Zeidler, 2009; Metalanceolidae Zeidler, 2009; Microphasmidae Stephensen & Pirlot, 1931; Mimonecteolidae Zeidler, 2009; Prolanceolidae Zeidler, 2009.

Family Chuneolidae Woltereck, 1909

Included genera. *Chuneola* Woltereck, 1909.

Family Lanceolidae Bovallius, 1887

Included genera. *Lanceola* Say, 1818b; *Scypholanceola* Woltereck, 1905.

Family Megalanceolidae Zeidler, 2009

Included genera. *Megalanceola* Pirlot, 1935; *Megalanceoloides* Zeidler, 2009.

Family Metalanceolidae Zeidler, 2009

Included genera. *Metalanceola* Pirlot, 1931.

Family Microphasmidae Stephensen & Pirlot, 1931

Included genera. *Microphasma* Woltereck, 1909; *Microphasmoides* Vinogradov, 1960.

Family Mimonecteolidae Zeidler, 2009

Included genera. *Mimonecteola* Woltereck, 1909.

Family Prolanceolidae Zeidler, 2009

Included genera. *Prolanceola* Woltereck, 1907.

Superfamily Scinoidea Stebbing, 1888 (Bowman & Gruner, 1973)

Diagnosis. Mandible lacinia mobilis present only on left side; palp absent. Gnathopods 1–2 simple (except in some Scinidae).

Included families. Archaeoscinidae Stebbing, 1904; Microscinidae Zeidler, 2012; Mimonectidae Bovallius, 1885; Mimoscinidae Zeidler, 2012; Scinidae Stebbing, 1888.

Remarks. Zeidler (2012) rejects the family status of Proscinidae Pirlot, 1933a and transfers species of the genus *Proscina* to *Mimonectes* and *Mimoscina* (see Zeidler 2012).

Family Archaeoscinidae Stebbing, 1904

Included genera. *Archaeoscina* Stebbing, 1904; *Paralanceola* K.H. Barnard, 1930.

Remarks. The placement of this family in the Scinoidea is contentious. It differs from all other Scinoidea in having mandibular palps. Vinogradov, Volkov & Semenova, 1982 placed it in the superfamily Archaeoscinoidea. Zeidler (pres. com.) believes that this family should be placed in the Lanceoloidea.

Family Microscinidae Zeidler, 2012

Included genera. *Microscina* Zeidler, 2012.

Family Mimonectidae Bovallius, 1885

Included genera. *Cheloscina* Shih & Hendrycks, 1996; *Mimonectes* Bovallius, 1885; *Pseudomimonectes* Vinogradov, 1960.

Family Mimoscinidae Zeidler, 2012

Included genera. *Mimoscina* Pirlot, 1933a.

Family Scinidae Stebbing, 1888

Included genera. *Scina* Prestandrea, 1833; *Acanthoscina* Vosseler, 1901; *Ctenoscina* Wagler, 1926; *Spinoscina* Bowman & Gruner, 1973.

Infraorder Physocephalata Bowman & Gruner, 1973

Diagnosis (after Bowman & Gruner 1973)**.** Head large, longer than pereonite 1. Eyes large occupying most of head (small to moderately large in Vibiliidae and Bougisidae). Maxilla 1 without basal endite (inner lobe) (except Cyllopodidae, Paraphronimidae). Maxilliped basal endites (inner lobes) completely fused (except Lycaeopsidae). Male genital papillae absent or very small (Zeidler 2006).

Included parvorders. Physocephalatidira Bowman & Gruner, 1973 **stat. nov.**

Parvorder Physocephalatidira Bowman & Gruner, 1973 stat. nov.

Diagnosis. As for Infraorder.

Included superfamilies. Phronimoidea Dana, 1852 (Bowman & Gruner, 1973); Platysceloidea Spence Bate, 1862 (Bowman & Gruner, 1973); Vibilioidea Dana, 1852 (Bowman & Gruner, 1973).

Remarks. Bowman & Gruner (1973) erected a monotypic superfamily (Lycaeopsoidea) for the family Lycaeopsidae Chevreux, 1913. In our analysis the Lycaeopsidae is a sister taxon to the Tryphanidae and both together form a sister group to the Pronoidae within the superfamily Platysceloidea. Zeidler (pers. com.) has questioned this relationship.

Superfamily Vibilioidea Dana, 1852 (Bowman & Gruner, 1973)

Diagnosis. Antenna 1 inserted on anterior surface of head. Antenna 2 flagellum not elongated. Maxilliped basal endite fused medially. Body subcylindrical or laterally compressed, coxae small. Pereopods 5, 6 similar in length, pereopod 7 shorter.

Included families. Cyllopodidae Bovallius, 1887; Paraphronimidae Bovallius, 1887; Vibiliidae Dana, 1852.

Family Cyllopodidae Bovallius, 1887

Included genera. *Cyllopus* Dana, 1853.

Family Paraphronimidae Bovallius, 1887

Included genera. *Paraphronima* Claus, 1879.

Family Vibiliidae Dana, 1852

Included genera. *Vibilia* H. Milne Edwards, 1830; *Vibilioides* Chevreux, 1905b.

Superfamily Phronimoidea Dana, 1852 (Bowman & Gruner, 1973)

Diagnosis. Antenna 1 peduncular article 1 longer than article 2. Antenna 1 inserted on anterior surface of head. Mandible lacinia mobilis present on both sides. Maxilla 1 basal endite absent. Pereopod 4 coxa fused to pereonite or subequal to that of pereopod 3. Urosomite 1 subequal or longer than urosomite 2 or 2–3. Uropod 2 endopod subequal to or shorter than exopod or absent.

Included families. Bougisidae Zeidler, 2004; Cystisomatidae Willemöes-Suhm, 1875; Dairellidae Bovallius, 1887; Hyperiidae Dana, 1852; Iulopididae Zeidler, 2004; Lestrigonidae Zeidler, 2004; Phronimidae Dana, 1852; Phrosinidae Dana, 1852.

Remarks. A new superfamily, Cystisomatoidea, was proposed by Zeidler (2003) to accommodate the family Cystisomatidae, primarily based on the unique method of brooding the young. We did not use this character in our analysis. In our analysis the Cystisomatidae is a sister taxon to the Dairellidae and deeply embedded in the Phronimoidea. It should be noted that Browne *et al*. (2007) and Hurt *et al*. (2013) found support for placing the Cystisomatidae with the Physosomata.

Family Bougisidae Zeidler, 2004

Included genera. *Bougisia* Laval, 1966.

Family Cystisomatidae Willemöes-Suhm, 1875

Included genera. *Cystisoma* Guérin-Méneville, 1842.

Family Dairellidae Bovallius, 1887

Included genera. *Dairella* Bovallius, 1887.

Family Hyperiidae Dana, 1852

Included genera. *Hyperia* Latreille, 1823; *Hyperiella* Bovallius, 1887; *Hyperoche* Bovallius, 1887; *Laxohyperia* Vinogradov & Volkov, 1982; *Pegohyperia* K.H. Barnard, 1931; *Prohyperia* Zeidler, 2015; *Themisto* Guérin, 1825.

Remarks. According to Bowman *et al*. (1982) "The amphipod genus *Themisto* Guérin-Méneville, 1825, was replaced with *Euthemisto* by Bovallius (1887) because it was a junior homonym of the nudibranch *Themisto* Oken (1815). *Parathemisto* Boeck (1870) and *Themisto* Guérin-Méneville were combined under *Themisto* by Stephensen (1924), corrected by K.H. Barnard (1930) to *Parathemisto,* the name currently used by most zoologists. Volume 3 of *Okens Lehrbuch der Naturgeschichte* (1815) was placed, however, on the Official List of Rejected Works by Opinion 417 of the International Commission of Zoological Nomenclature (1956), which ruled that no name published in Oken's volume 3 acquired the status of availability by reason of having been so published. Consequently the name *Themisto,* first made available by Guérin and a senior synonym of *Parathemisto,* is the valid name of the amphipod genus".

Family Iulopididae Zeidler, 2004

Included genera. *Iulopis* Bovallius, 1887.

Family Lestrigonidae Zeidler, 2004

Included genera. *Hyperietta* Bowman, 1973; *Hyperioides* Chevreux, 1900; *Hyperionyx* Bowman, 1973; *Lestrigonus* H. Milne Edwards, 1830; *Phronimopsis* Claus, 1879; *Themistella* Bovallius, 1887.

Family Phronimidae Dana, 1852

Included genera. *Phronima* Latreille, 1802; *Phronimella* Claus, 1871.

Family Phrosinidae Dana, 1852 (Stebbing, 1888)

Included genera. *Anchylomera* Milne Edwards, 1830; *Phrosina* Risso, 1822; *Primno* Guérin-Méneville, 1836.

Superfamily Platysceloidea Spence Bate, 1862 (Bowman & Gruner, 1973)

Diagnosis. Eyes occupying most of lateral surface of the head. Mandible molar vestigial or absent. Maxilla 1 basal endite absent. Maxilliped palps absent. Urosomite 1 shorter than urosomites 2 or 3.

Included families. Amphithyridae Zeidler, 2016; Anapronoidae Bowman & Gruner, 1973; Brachyscelidae Stephensen, 1923; Eupronoidae Zeidler, 2016; Lycaeidae Claus, 1879; Lycaeopsidae Chevreux 1913; Oxycephalidae Spence Bate, 1862; Parascelidae Bovallius, 1887; Platyscelidae Spence Bate, 1862; Pronoidae Claus, 1879; Thamneidae Zeidler, 2016; Tryphanidae Boeck, 1871.

Remarks. The following character states occur in all family level taxa except the Lycaeopsidae: antenna 1 inserted on ventral surface of the head; antenna 2 articles folded on one another in zigzag fashion; pereopods 5–6 basis greatly enlarged.

Family Amphithyridae Zeidler, 2016

Included genera. *Amphithyropsis* Zeidler, 2016; *Amphithyrus* Claus, 1879; *Paralycaea* Claus, 1879.

Family Anapronoidae Bowman & Gruner, 1973

Included genera. *Anapronoe* Stephensen, 1925c.

Family Brachyscelidae Stephensen, 1923

Included genera. *Brachyscelus* Spence Bate, 1861.

Remarks. Zeidler (2016) reserved the Brachyscelidae for *Brachyscelus* and removed *Thamneus* to a new monotypic family Thamneidae Zeidler, 2016.

Family Eupronoidae Zeidler, 2016

Included genera. *Eupronoe* Claus, 1879; *Parapronoe* Claus, 1879.

Family Lycaeidae Claus, 1879

Included genera. *Lycaea* Dana, 1852; *Simorhynchotus* Stebbing, 1888 (*Fide* Vinogradov *et al*. 1982).

Family Lycaeopsidae Chevreux, 1913

Included genera. *Lycaeopsis* Claus, 1879.

Family Oxycephalidae Spence Bate, 1862

Included genera. *Calamorhynchus* Streets, 1878; *Cranocephalus* Bovallius, 1890; *Glossocephalus* Bovallius, 1887; *Leptocotis* Streets, 1877; *Oxycephalus* H. Milne Edwards, 1830; *Rhabdosoma* White, 1847; *Streetsia* Stebbing, 1888; *Tullbergella* Bovallius, 1887.

Family Parascelidae Bovallius, 1887

Included genera. *Euscelus* Claus, 1879; *Parascelus* Claus, 1879; *Schizoscelus* Claus, 1879; *Thyropus* Dana, 1852.

Family Platyscelidae Spence Bate, 1862

Included genera. *Hemityphis* Claus, 1879; *Paratyphis* Claus, 1879; *Platyscelus* Spence Bate, 1862; *Tetrathyrus* Claus, 1879.

Remarks. Zeidler (2016) removed *Amphithyrus* Claus, 1879 to Amphithyridae Zeidler, 2016**.**

Family Pronoidae Claus, 1879

Included genera. *Pronoe* Guérin-Méneville, 1836.

Remarks. Zeidler (2016) moved *Eupronoe* Claus, 1879 and *Parapronoe* Claus, 1879 to the Eupronoidae Zeidler, 2016 and *Paralycaea* Claus, 1879 to Amphithyridae Zeidler, 2016.

Family Thamneidae Zeidler, 2016

Included genera. *Thamneus* Bovallius, 1887.

Family Tryphanidae Boeck, 1871

Included genera. *Tryphana* Boeck, 1871.

Suborder Colomastigidea Stebbing, 1899 stat. nov.

Diagnosis. Body subcylindrical. Maxilliped palps present. Urosomite 1 free, 2–3 coalesced. Uropods 1–2 rami without apical robust setae.

Included infraorders. Colomastigida **stat. nov.**

Infraorder Colomastigida Stebbing, 1899 stat. nov.

Diagnosis. As for suborder.

Included parvorders. Colomastigidira Stebbing, 1899 **stat. nov.**; Pagetinidira K.H. Barnard, 1931 **stat. nov.**

Parvorder Colomastigidira Stebbing, 1899 stat. nov.

Diagnosis. Antenna 1 callynophore present. Mandible palp absent. Maxilla 1 palp absent. Gnathopod 1 simple. Uropod 3 biramous.

Included superfamilies. Colomastigoidea Stebbing, 1899 **stat. nov.**

Superfamily Colomastigoidea Stebbing, 1899 stat. nov.

Diagnosis. As for parvorder.

Included families. Colomastigidae Stebbing, 1899

Family Colomastigidae Stebbing, 1899

Included genera. *Colomastix* Grube, 1861; *Yulumara* J.L. Barnard, 1972a.

Parvorder Pagetinidira K.H. Barnard, 1931 stat. nov.

Diagnosis. Antenna 1 callynophore absent. Mandible palp present. Maxilla 1 palp present. Gnathopod 1 subchelate. Uropod 3 uniramous.

Included superfamilies. Pagetinoidea K.H. Barnard, 1931 **stat. nov.**

Superfamily Pagetinoidea K.H. Barnard, 1931 stat. nov.

Diagnosis. As for parvorder.

Included families. Pagetinidae K.H. Barnard, 1931.

Family Pagetinidae K.H. Barnard, 1931

Included genera. *Pagetina* K.H. Barnard, 1931.

Suborder Hyperiopsidea Bovallius, 1886, stat. nov.

Diagnosis. Body laterally compressed with small coxae. Mandible molar triturative. Maxilliped palps well developed. Pereopod 4 coxa without posteroventral lobe. Uropods 1–2 rami without apical robust setae.

Included infraorders. Hyperiopsida Bovallius, 1866 **stat. nov.**

Remarks. Basal hyperiopsideans are similar to physocephalatan hyperiideans, particularly vibilioids and phronimoids.

Infraorder Hyperiopsida Bovallius, 1886, stat. nov.

Diagnosis. As for suborder.

Included parvorders. Hyperiopsidira Bovallius, 1866 **stat. nov.**; Podosiridira Lowry & Myers, 2012b **stat. nov.**

Parvorder Hyperiopsidira Bovallius, 1886, stat. nov.

Diagnosis. Antenna 1 accessory flagellum present; with callynophore, weakly to well developed. Gnathopod 1 simple. Pereopod 3 coxa subequal to that of 4. Pereopod 5 coxa smaller than that of 4.

Included superfamilies. Hyperiopsoidea Bovallius, 1866 **stat. nov.**

Superfamily Hyperiopsoidea Bovallius, 1886, stat. nov.

Diagnosis. As for parvorder.

Included families. Hyperiopsidae Bovallius, 1886; Vitjazianidae Birstein & Vinogradov, 1955.

Family Hyperiopsidae Bovallius, 1886

Included genera. *Hyperiopsis* Sars, 1885; *Protohyperiopsis* Birstein & Vinogradov, 1955.

Family Vitjazianidae Birstein & Vinogradov, 1955

Included genera. *Vitjaziana* Birstein & Vinogradov, 1955.

Parvorder Podosiridira Lowry & Myers, 2012b stat. nov.

Diagnosis. Antenna 1 accessory flagellum absent; without callynophore. Gnathopod 1 subchelate. Pereopod 3 coxa larger than that of 4. Pereopod 5 coxa subequal to that of 4.

Included superfamilies. Podosiroidea Lowry & Myers, 2012b **stat. nov.**

Superfamily Podosiroidea Lowry & Myers, 2012b stat. nov.

Diagnosis. As for parvorder.

Included families. Podosiridae Lowry & Myers, 2012b

Family Podosiridae Lowry & Myers, 2012b

Included genera. *Podosirus* Bellan-Santini, 2007.

Suborder Senticaudata Lowry & Myers, 2013
(see Lowry & Myers, 2013)

Suborder Amphilochidea Boeck, 1871 stat. nov.

Diagnosis. Body laterally compressed or dorsoventrally flattened with large or occasionally small coxae. Antenna 2 peduncle with brush setae (weakly developed). Maxilliped palps well-developed. Pereopod 4 coxa smaller or larger than that of 3. Uropods 1–2 rami without apical robust setae.

Included infraorders. Amphilochida Boeck, 1871 **stat. nov.**; Lysianassida Dana, 1849 **stat. nov.**

Remarks. The Amphilochidea is a monophyletic clade, although the defining character state (brush setae present) is weak. All Amphilochidea have laterally compressed or dorsoventrally flattened bodies with large coxae except the Pardaliscidae and Synopiidae which have laterally compressed bodies with relatively shortened coxae, apparently a homoplasious character.

Infraorder Amphilochida Boeck, 1871 stat. nov.

Diagnosis. Body laterally compressed or dorsoventrally flattened. Mandible incisors dentate [except, Sicafodiidae]. Coxae 1–4 overlapping [except Miramarassidae]. Pereopod 4 coxa subequal or larger than that of 3. Pereopod 6 subequal or shorter than pereopod 7 or immensely elongate [except Dikwidae]; urosomites 1–3 free [except Paracalliopiidae, Sebidae]. Uropod 3 exopod 1 articulate [except Didymocheliidae, Nihotungidae, Sebidae, Stenothoidae].

Included parvorders. Amphilochidira Boeck, 1871 **stat. nov.**; Eusiridira Stebbing 1888 **stat. nov.**; Maxillipiidira Ledoyer, 1973 **stat. nov.**; Oedicerotidira Lilljeborg, 1865b (Bousfield, 1979) **stat. nov.**

Remarks. The Amphilochida are monophyletic, but they are defined by rather weak apomorphic character states: coxae 1–4 overlapping and uropod 3 exopod longer than peduncle. They can be diagnosed by the above diagnostic characters with several exceptions. A number of small highly derived taxa (Nihotungidae, Didymocheliidae, Dikwidae, Miramarassidae, Paracalliopiidae, Sebidae and Sicafodiidae) are anomalous. The large family Stenothoidae has coxa 4 enlarged without a posteroventral lobe and uropod 3 with a 2-articulate exopod. As a consequence it does not conform to the diagnosis.

We place the family Eusiridae in the Amphilochida, but taxa such as *Rhachotropis* confound the diagnosis. We believe that the family Eusiridae is too broadly defined.

Parvorder Maxillipiidira Ledoyer, 1973 stat. nov.

Diagnosis. Body dorsoventrally flattened. Pereopod 6 immensely elongate, flagellate.

Included superfamilies. Maxillipioidea Ledoyer, 1973 **stat. nov.**

Superfamily Maxillipioidea Ledoyer, 1973 stat. nov.

Diagnosis. As for parvorder.

Included families. Maxillipiidae Ledoyer, 1973.

Family Maxillipiidae Ledoyer, 1973

Included genera. *Maxillipides* Ledoyer, 1984; *Maxillipius* Ledoyer, 1973.

Parvorder Oedicerotidira Ledoyer, 1973, stat. nov.

Diagnosis. Pereopod 4 coxa with well-developed posteroventral lobe. Pereopod 5 coxa equilobate. Pereopod 7 immensely elongate. Pereopod 7 different in structure to pereopod 6. Telson entire.

Included superfamilies. Oedicerotoidea Ledoyer, 1973 **stat. nov.**

Superfamily Oedicerotoidea Lilljeborg, 1865b (Bousfield, 1979)

Diagnosis. As for parvorder.

Included families. Exoedicerotidae Barnard & Drummond, 1982a; Oedicerotidae Lilljeborg, 1865b; Paracalliopiidae Barnard & Karaman, 1982.

Family Exoedicerotidae Barnard & Drummond, 1982a

Included genera. *Bathyporeiapus* Schellenberg, 1931; *Exoediceroides* Bousfield, 1983; *Exoediceropsis* Schellenberg, 1931; *Exoediceros* Stebbing, 1899; *Kanaloa* J.L. Barnard, 1970; *Methalimedon* Schellenberg, 1931; *Metoediceropsis* Dang, 1968; *Metoediceros* Schellenberg, 1931; *Notoediceros* Bousfield, 1983; *Parhalimedon* Chevreux, 1906b; *Patuki* Cooper & Fincham, 1974; *Vadosiapus* Barnard & Thomas, 1988a.

Family Oedicerotidae Lilljeborg, 1865b

Included genera. *Aborolobatea* Ledoyer, 1984; *Acanthostepheia* Boeck, 1871; *Aceroides* G.O. Sars, 1892; *Americhelidium* Bousfield & Chevrier, 1996; *Ameroculodes* Bousfield & Chevrier, 1996; *Anoediceros* Pirlot, 1932; *Arrhinopsis* Stappers, 1911; *Arrhis* Stebbing, 1906; *Bathymedon* G.O. Sars, 1892; *Carolobatea* Stebbing, 1899; *Caviphaxus* Ren, 1992; *Chitonomandibulum* Jo, 1990; *Cornudilla* Barnard & Karaman, 1991; *Deflexilodes* Bousfield & Chevrier, 1996; *Eochelidium* Bousfield & Chevrier, 1996; *Finoculodes* J.L. Barnard, 1971; *Gulbarentsia* Stebbing, 1894; *Halicreion* Boeck, 1871; *Hartmanodes* Bousfield & Chevrier, 1996; *Hongkongvena* Hirayama, 1992; *Imbachoculodes* Kim, Hendrycks & Lee, 2012; *Kroyera* Spence Bate, 1857; *Limnoculodes* Bousfield & Chevrier, 1996; *Lopiceros* J.L. Barnard, 1961; *Machaironyx* Coyle, 1980; *Monoculodes* Stimpson,

1853; *Monoculodopsis* Ledoyer, 1973; *Monoculopsis* G.O. Sars, 1892; *Oedicerina* Stephensen, 1931; *Oediceroides* Stebbing, 1888; *Oediceropsis* Lilljeborg, 1865a; *Oediceros* Krøyer, 1842; *Orthomanus* Kim, Hendrycks & Lee, 2012; *Pacifoculodes* Bousfield & Chevrier, 1996; *Paramonoculopsis* Alonso de Pina, 1997; *Paraperioculodes* K.H. Barnard, 1931; *Parexoediceros* Bousfield, 1983; *Paroediceroides* Schellenberg, 1931; *Paroediceros* G.O. Sars, 1892; *Perioculodes* G.O. Sars, 1892; *Perioculopsis* Schellenberg, 1925; *Pontocrates* Boeck, 1871; *Rostroculodes* Bousfield & Chevrier, 1996; *Sinoediceros* Shen, 1955; *Synchelidium* G.O. Sars, 1892; *Westwoodilla* Spence Bate, 1857.

Family Paracalliopiidae Barnard & Karaman, 1982

Included genera. *Doowia* Barnard & Drummond, 1987; *Indocalliope* Barnard & Karaman, 1982; *Katocalliope* Barnard & Drummond, 1984; *Paracalliope* Stebbing, 1899; *Yhi* Barnard & Thomas, 1991.

Parvorder Eusiridira Stebbing, 1888 stat. nov.

Diagnosis. Body laterally compressed with large coxae. Antenna 1 callynophore weakly developed (1-field) or absent. Mandible incisor dentate. Pereopods 5–7 progressively longer.

Included superfamilies. Eusiroidea Stebbing, 1888 (Bousfield, 1979); Liljeborgioidea Stebbing, 1899 (Bousfield, 1979).

Superfamily Eusiroidea Stebbing, 1888 (Bousfield, 1979)

Diagnosis. As for parvorder plus antenna 2 flagellum shorter than peduncle; mandible molar triturative.

Included families. Bateidae Stebbing, 1906; Eusiridae Stebbing, 1888; Miramarassidae Lowry, 2006; Thurstonellidae Lowry & Zeidler, 2008.

Family Bateidae Stebbing, 1906

Included genera. *Batea* Müller, 1865.

Family Eusiridae Stebbing, 1888

Included genera. *Cleonardo* Stebbing, 1888; *Eusirella* Chevreux, 1908b; *Eusirogenes* Stebbing, 1904; *Eusiropsis* Stebbing, 1897; *Eusirus* Krøyer, 1845; *Harcledo* J.L. Barnard, 1964c; *Meteusiroides* Pirlot, 1934; *Pareusirogenes* Birstein & Vinogradov, 1955; *Rhachotropis* S.I. Smith, 1883; *Sennaia* Bellan-Santini, 1997; *Triquetramana* Hendrycks & Conlan, 2003.

Remarks. *Sennaia* is listed in the World Amphipoda Database (Horton *et al*. 2017) in the Pontogeneiidae, but the lack of apical robust setae on uropods 1 and 2 exclude it from the Senticaudata and it is here placed in the Eusiridae as originally specified by Bellan-Santini 1997.

Family Miramarassidae Lowry, 2006

Included genera. *Miramarassa* Ortiz, Lalana & Lio, 1999.

Family Thurstonellidae Lowry & Zeidler, 2008

Included genera. *Thurstonella* Lowry & Zeidler, 2008.

Superfamily Liljeborgioidea Stebbing, 1899

Diagnosis. As for parvorder plus gnathopod 1 present and uropod 3 endopod shorter than exopod.

Included families. Liljeborgiidae Stebbing, 1899; Pseudamphilochidae **fam. nov.**

Family Liljeborgiidae Stebbing, 1899

Included subfamilies. Idunellinae d'Udekem d'Acoz, 2010; Liljeborgiinae Stebbing, 1899.

Remarks. d'Udekem d'Acoz, 2010 established the subfamilies Idunellinae and Liljeborgiinae. Species of Idunellinae have apical robust setae on the rami of uropods 1 and 2, species of Liljeborgiinae do not. This suggests that the apical robust setae of Idunellinae are homoplasious.

Subfamily Idunellinae d'Udekem d'Acoz, 2010

Included genera. *Idunella* G.O. Sars, 1894; *Listriella* J.L. Barnard, 1959a; *Sextonia* Chevreux, 1920.

Subfamily Liljeborgiinae Stebbing, 1899 (d'Udekem d'Acoz, 2010)

Included genera. *Isipingus* Barnard & Karaman, 1987; *Liljeborgia* Spence Bate, 1862.

Remarks. d'Udekem d'Acoz (2010) provisionally considered *Isipingus* to be a subgenus of *Liljeborgia*.

Family Pseudamphilochidae fam. nov.

Pseudamphilochidae Barnard & Karman, 1982: 184 (invalid attribution to Schellenberg, 1931: not considered as new).—Barnard & Karaman, 1991: 667.—De Broyer & Jażdżewski, 1993: 88.—Gutt, Sirenko, Arntz, Smirnov & De Broyer, 2000: 67.—De Broyer *et al*. 2007: 199.

Type genus. *Pseudamphilochus* Schellenberg, 1931.

Diagnosis (based on world family database)**.** Body laterally compressed with large coxae. Head, eyes round. Antenna 1 shorter than antenna 2; antenna 1 accessory flagellum absent, callynophore absent. Antennae 1–2 calceoli absent. Mandible molar vestigial or absent. Maxilla 1 basal endite with apical setae. Maxilliped outer plate longer than palp article 1, not longer than palp article 2. Gnathopods 1–2 subchelate, carpus not produced along posterior margin of propodus; propodus palms with row of robust setae along margin. Gnathopod 1 coxa large, not hidden by 2. Uropods 1–2 rami without apical robust or embedded setae. Uropod 3 biramous; endopod shorter than exopod. Telson laminar, moderately cleft.

Included genera. *Pseudamphilochus* Schellenberg, 1931.

Habitat. Marine, epigean.

Distribution. South Georgia (Schellenberg 1931), Weddell Sea (Gutt *et al*. 2000), Southern Ocean.

Remarks. According to Barnard & Karaman (1982: 184) 'This family has not been properly heralded in the literature before and is brought to light from a provisional proposal (Schellenberg, 1931: 92)'. Schellenberg (1931) placed his new genus *Pseudamphilochus* in the family Amphilochidae, with the suggestion that there could be a family Pseudamphilochidae. Barnard & Karaman (1982) diagnosed the family but attributed authorship to Schellenberg (1931). In accordance with Article 13 of the International Code of Zoological Nomenclature (ICZN 1999, fourth edition) they needed to state that they were making a new family for the name to be considered valid. The original and only illustrations of *Pseudamphilochus* are of a female and do not include some of the important morphology. For instance pereopods 3, 5 and 6 are not illustrated. New collections are available but the taxon has

not yet been redescribed (Gutt *et al*. 2000).

Parvorder Amphilochidira Boeck, 1871 stat. nov.

Diagnosis. Body laterally compressed or dorsoventrally flattened. Antenna 1 callynophore weakly developed (1-field) or absent [except Stilipedidae]. Antenna 2 without many robust setae. Gnathopod 1 well developed. Gnathopod 2 simple, subchelate [except Didymocheliidae], not mitten-shaped. Pereopod 6 and 7 similar in structure, not immensely elongate. Urosomites 1–3 free, not coalesced [except Sebidae]. Telson entire.

Included superfamilies. Amphilochoidea Boeck, 1871 **stat. nov.**; Iphimedioidea Boeck, 1871 **stat. nov.**

Remarks. Amphilochidirans are a well-defined group based on the current set of characters. Three families are slightly aberrant. The Didymocheliidae have gnathopod 2 chelate, the Stilipedidae maintain a well-developed callynophore and the Sebidae have coalesced urosomites.

Superfamily Amphilochoidea Boeck, 1871 stat. nov.

Diagnosis. Body laterally compressed. Antenna 1 callynophore weakly-developed or absent. Mouthpart bundle subquadrate (except Didymocheliidae). Gnathopod 1 simple or subchelate. Gnathopod 2 carpus subequal or shorter than propodus.

Included families. Amphilochidae Boeck, 1871; Bolttsiidae Barnard & Karaman, 1987; Cressidae Stebbing, 1899; Cyproideidae J.L. Barnard, 1974; Didymocheliidae Bellan-Santini & Ledoyer, 1986; Nihotungidae J.L. Barnard, 1972a; Pleustidae Buchholz, 1874; Sebidae Walker, 1907; Seborgiidae Holsinger, 1980; Stenothoidae Boeck, 1871.

Remarks. Didymocheliids are difficult to allocate because they align with the Amphilochoidea in the chelate second gnathopods and the non-distally acuminate coxae 1–4, but they share the conical mouthpart bundle with the Iphimedioidea.

Pleustids are also difficult to allocate because they share many iphimedioid character states but they do not have the conical mouthpart bundle nor the distally acuminate coxae 1–4 of the Iphimedioidea.

Family Amphilochidae Boeck, 1871

Included genera. *Afrogitanopsis* G. Karaman, 1980b; *Amphilochella* Schellenberg, 1926a; *Amphilochoides* G.O. Sars, 1892; *Amphilochopsis* Stephensen, 1925b; *Amphilochus* Spence Bate, 1862; *Apolochus* Hoover & Bousfield, 2001; *Cyclotelson* Potts, 1915; *Frigora* Ren, 1991; *Gitana* Boeck, 1871; *Gitanogeiton* Stebbing, 1910; *Gitanopsilis* Rauschert, 1994; *Gitanopsis* G.O. Sars, 1892; *Hourstonius* Hoover & Bousfield, 2001; *Paramphilochoides* Lincoln, 1979; *Paramphilochus* Ishimaru & Ikehara, 1986; *Rostrogitanopsis* G. Karaman, 1980b.

Remarks. *Frigora* Ren, 1991 is here transferred from the Eusiridae to the Amphilochidae.

Family Bolttsiidae Barnard & Karaman, 1987

Included Genera. *Bolttsia* Griffiths, 1976.

Remarks. *Bolttsia* has an extraordinarily disjunct distribution from Lake Sebaya, a coastal lake previously connected to the sea in western South Africa (Griffiths 1976) and estuarine mangroves on the Great Barrier Reef, Australia (Azman 2009). From the middle Jurassic (170 Ma) to late Jurassic (152 Ma) a continuous coastline ran from south-western Africa along the 'northern' coast of India and the northern coast of Australia. By the early Cretaceous (~125 Ma) this link was no longer in place. The last time these regions were in contact was in the late Jurassic, a presumed marker for the minimum age of this genus. A similar situation occurs in the deep water aristioid genus *Izinkala* Griffiths, 1977 which is only known from off the south-western African coast and the east coast of Australia.

Family Cressidae Stebbing, 1899

Included Genera. *Cressa* Boeck, 1871; *Cressina* Stephensen, 1931.

Family Cyproideidae J.L. Barnard, 1974

Included genera. *Austropheonoides* J.L. Barnard, 1972a; *Cyproidea* Haswell, 1879b; *Gbroidea* Lowry & Azman, 2008; *Hoplopheonoides* Shoemaker, 1956; *Hoplopleon* K.H. Barnard, 1932; *Metacyproidea* Ariyama, 2016; *Mokuoloe* J.L. Barnard, 1970; *Moolapheonoides* J.L. Barnard, 1974; *Narapheonoides* J.L. Barnard, 1972a; *Neocyproidea* Hurley, 1955; *Paracyproidea* Stebbing, 1899; *Peltocoxa* Catta, 1875; *Peltopes* K.H. Barnard, 1930; *Pseudopeltocoxa* Schiecke, 1977; *Sisalia* Ortiz & Winfield, 2014; *Stegoplax* G.O. Sars, 1883; *Terepeltopes* Hirayama, 1983; *Unguja* Griffiths, 1976; *Unyapheonoides* J.L. Barnard, 1972a; *Victorhensenoides* Rauschert, 1996.

Family Didymocheliidae Bellan-Santini & Ledoyer, 1986

Included genera. *Aidamochelia* Thomas & Watling, 2012; *Apodidymochelia* Thurston, 1997; *Didymochelia* K.H. Barnard, 1931.

Remarks. The family exhibits some character states (antenna 1 callynophore weak (1-field) and gnathopod 2 chelate with a short ischium) of the Iphimedioidea.

Family Nihotungidae J.L. Barnard, 1972a

Included genera. *Nihotunga* J.L. Barnard, 1972a.

Family Pleustidae Buchholz, 1874

Included subfamilies. Atylopsinae Bousfield & Hendrycks, 1994a; Austropleustinae Bousfield & Hendrycks, 1994a; Dactylopleustinae Bousfield & Hendrycks, 1994a; Eosymtinae Bousfield & Hendrycks, 1994a; Mesopleustinae Bousfield & Hendrycks, 1994a; Neopleustinae Bousfield & Hendrycks, 1994a; Parapleustinae Bousfield & Hendrycks, 1994a; Pleusirinae Bousfield & Hendrycks, 1994a; Pleustinae Buchholz, 1874; Pleustoidinae Bousfield & Hendrycks, 1994a; Pleusymtinae Bousfield & Hendrycks, 1994a; Stenopleustinae Bousfield & Hendrycks, 1994a.

Subfamily Atylopsinae Bousfield & Hendrycks, 1994a

Included genera. *Atylopsis* Stebbing, 1888; *Myzotarsa* Cadien & Martin, 1999.

Subfamily Austropleustinae Bousfield & Hendrycks, 1994a

Included genera. *Austropleustes* K.H. Barnard, 1931; *Tepidopleustes* Karaman & Barnard, 1979.

Subfamily Dactylopleustinae Bousfield & Hendrycks, 1994a

Included genera. *Dactylopleustes* Barnard & Karaman, 1979.

Subfamily Eosymtinae Bousfield & Hendrycks, 1994a

Included genera. *Eosymtes* Bousfield & Hendrycks, 1994a.

Subfamily Mesopleustinae Bousfield & Hendrycks, 1994a

Included genera. *Mesopleustes* Stebbing, 1899.

Subfamily Neopleustinae Bousfield & Hendrycks, 1994a

Included genera. *Neopleustes* Stebbing, 1906; *Pleustostenus* Gurjanova, 1972; *Shoemakeroides* Hendrycks & Bousfield, 2004.

Subfamily Parapleustinae Bousfield & Hendrycks, 1994a

Included genera. *Chromopleustes* Bousfield & Hendrycks, 1995a; *Commensipleustes* Bousfield & Hendrycks, 1995a; *Gnathopleustes* Bousfield & Hendrycks, 1995a; *Incisocalliope* J.L. Barnard, 1959b; *Micropleustes* Bousfield & Hendrycks, 1995a; *Parapleustes* Buchholz, 1874; *Trachypleustes* Bousfield & Hendrycks, 1995a.

Subfamily Pleusirinae Bousfield & Hendrycks, 1994a

Included genera. *Pleusirus* J.L. Barnard, 1969a.

Subfamily Pleustinae Buchholz, 1874

Included genera. *Pleustes* (*Catapleustes*) Bousfield & Hendrycks, 1994b; *Pleustes* (*Pleustes*) Spence Bate, 1858 (Bousfield & Hendrycks, 1994b); *Thorlaksonius* Bousfield & Hendrycks, 1994b.

Subfamily Pleustoidinae Bousfield & Hendrycks, 1994a

Included genera. *Pleustoides* Gurjanova, 1972.

Subfamily Pleusymtinae Bousfield & Hendrycks, 1994a

Included genera. *Anomalosymtes* Hendrycks & Bousfield, 2004; *Budnikopleustes* Hendrycks & Bousfield, 2004; *Heteropleustes* Hendrycks & Bousfield, 2004; *Holopleustes* Hendrycks & Bousfield, 2004; *Kamptopleustes* Hendrycks & Bousfield, 2004; *Pleustomesus* Gurjanova, 1972; *Pleusymtes* J.L. Barnard, 1969b; *Rhinopleustes* Hendrycks & Bousfield, 2004.

Subfamily Stenopleustinae Bousfield & Hendrycks, 1994a

Included genera. *Arctopleustes* Gurjanova, 1972; *Domicola* Pretus & Abello 1993; *Gracilipleustes* Hendrycks &

Bousfield, 2004; *Stenopleustes* G.O. Sars, 1893.

Remarks. *Domicola* Pretus & Abello, 1993 is apparently not considered in the monographs of Bousfield & Hendrycks (1994a, b; 1995a) or Hendrycks & Bousfield (2004). Based on the key to subfamilies in Bousfield & Hendrycks (1994a) it appears to fit best in the subfamily Stenopleustinae.

Family Sebidae Walker, 1907

Included genera. *Seba* Spence Bate, 1862.

Family Seborgiidae Holsinger, 1980 stat. nov.

Included genera. *Relictoseborgia* G. Karaman, 1982; *Seborgia* Bousfield, 1970.

Family Stenothoidae Boeck, 1871

Included genera. *Antatelson* J.L. Barnard, 1972a; *Aurometopa* Barnard & Karaman, 1987; *Ausatelson* J.L. Barnard, 1972a; *Chuculba* J.L. Barnard, 1974; *Goratelson* J.L. Barnard, 1972a; *Hardametopa* Barnard & Karaman, 1991; *Knysmetopa* Barnard & Karaman, 1987; *Kyphometopa* Krapp-Schickel, 2013; *Ligulodactylus* Krapp-Schickel, 2013; *Malvinometopa* Krapp-Schickel, 2011; *Mesometopa* Gurjanova, 1938; *Mesoproboloides* Gurjanova, 1938; *Metopa* Boeck, 1871; *Metopella* G.O. Sars, 1892; *Metopelloides* Gurjanova, 1938; *Metopoides* Della Valle, 1893; *Parametopa* Chevreux, 1901; *Parametopella* Gurjanova, 1938; *Paraprobolisca* Ren, 1991; *Parathaumatelson* Gurjanova, 1938; *Probolisca* Gurjanova, 1938; *Proboloides* Della Valle, 1893; *Prometopa* Schellenberg, 1926a; *Prostenothoe* Gurjanova, 1938; *Prothaumatelson* Schellenberg, 1931; *Pseudothaumatelson* Schellenberg, 1931; *Ptychotelson* Krapp-Schickel, 2000; *Pycnopyge* Krapp-Schickel, 2000; *Raukamara* Krapp-Schickel, 2000; *Raumahara* J.L. Barnard, 1972a; *Sandrothoe* Krapp-Schickel, 2006a; *Scaphodactylus* Rauschert & Andres, 1993; *Stenothoe* Dana, 1852; *Stenothoides* Chevreux, 1900; *Stenula* J.L. Barnard, 1962b; *Sudanea* Krapp-Schickel, 2015; *Synkope* Krapp-Schickel, 1999; *Thaumatelson* Walker, 1906b; *Thaumatelsonella* Rauschert & Andres, 1991; *Torometopa* Barnard & Karaman, 1987; *Verticotelson* Krapp-Schickel, 2006b;*Victometopa* Krapp-Schickel, 2011; *Vonimetopa* Barnard & Karaman, 1987; *Wallametopa* J.L. Barnard, 1974; *Yarra* Krapp-Schickel, 2000; *Zaikometopa* Barnard & Karaman, 1987.

Remarks. Historically there have been two subfamilies, Stenothoinae Boeck, 1871 (J.L. Barnard, 1972b) and Thaumatelsoninae Gurjanova, 1938 (J.L. Barnard, 1972a). However we were not able to confidently place some genera in either subfamily. Krapp-Schickel (pers comm) thinks that the subfamily concept no longer works for this group and that several key characters have been independently derived several times.

Superfamily Leucothoidea Dana, 1852 (Bousfield, 1979)

Diagnosis. Maxilliped palps well developed. Gnathopods 1–2 carpochelate. Pereopod 4 coxa larger than that of pereopod 3.

Included families. Leucothoidae Dana, 1852.

Remarks. The Leucothoidea is the only taxon in the Amphilochida with both gnathopods carpochelate.

Family Leucothoidae Dana, 1852

Included genera. *Anamixis* Stebbing, 1897; *Leucothoe* Leach, 1814; *Nepanamixis* Thomas, 1997; *Paraleucothoe* Stebbing, 1899; *Paranamixis* Schellenberg, 1938.

Superfamily Iphimedioidea Boeck, 1871 stat. nov.

Diagnosis. Antenna 1 accessory flagellum vestigial or absent. Gnathopod 1 coxa not vestigial. Gnathopod 2 coxa subequal or smaller than that of coxa 3. Pereopod 4 coxal lobe well-developed or absent.

Included families. Acanthonotozomatidae Stebbing, 1906; Acanthonotozomellidae Coleman & Barnard, 1991a; Amathillopsidae Pirlot, 1934; Dikwidae Coleman & Barnard, 1991a; Epimeriidae Boeck, 1871; Iphimediidae Boeck, 1871; Lafystiidae Sars, 1893; Laphystiopsidae Stebbing, 1899; Ochlesidae Stebbing, 1910; Odiidae Coleman & Barnard, 1991a; Sicafodiidae Just, 2004; Stilipedidae Holmes, 1908; Vicmusiidae Just, 1990.

Family Acanthonotozomatidae Stebbing, 1906

Included genera. *Acanthonotozoma* Boeck, 1876.

Family Acanthonotozomellidae Coleman & Barnard, 1991a

Included genera. *Acanthonotozomella* Schellenberg, 1926a; *Acantonotozomoides* Schellenberg, 1931; *Amatiquakius* Coleman & Barnard, 1991b.

Family Amathillopsidae Pirlot, 1934

Included subfamilies. Amathillopsinae Pirlot, 1934; Cleonardopsinae Lowry, 2006; Parepimeriinae Lowry, 2006.

Subfamily Amathillopsinae Pirlot, 1934

Included genera. *Amathillopsis* Heller, 1875.

Subfamily Cleonardopsinae Lowry, 2006

Included genera. *Cleonardopsis* K.H. Barnard, 1916.

Subfamily Parepimeriinae Lowry, 2006

Included genera. *Parepimeria* Chevreux, 1911b.

Family Dikwidae Coleman & Barnard, 1991a

Included genera. *Dikwa* Griffiths, 1974.

Family Epimeriidae Boeck, 1871

Included genera. *Actinacanthus* Stebbing, 1888; *Epimeria* Costa, 1851; *Metepimeria* Schellenberg, 1931; *Paramphithoe* Bruzelius, 1859; *Uschakoviella* Gurjanova, 1955.

Family Iphimediidae Boeck, 1871

Included genera. *Anchiphimedia* K.H. Barnard, 1930; *Anisoiphimedia* G. Karaman, 1980c; *Coboldus* Krapp-Schickel, 1974; *Echiniphimedia* K.H. Barnard, 1930; *Gnathiphimedia* K.H. Barnard, 1930; *Iphimedia* Rathke, 1843; *Iphimediella* Chevreux, 1911b; *Labriphimedia* K.H. Barnard, 1931; *Maxilliphimedia* K.H. Barnard, 1930; *Nodotergum* Bellan-Santini, 1972; *Paranchiphimedia* Ruffo, 1949; *Parapanoploea* Nicholls, 1938; *Pariphimedia* Chevreux 1906a; *Pseudiphimediella* Schellenberg, 1931; *Stegopanoploea* G. Karaman, 1980c.

Family Lafystiidae Sars, 1893

Included genera. *Lafystius* Krøyer, 1842; *Paralafystius* Bousfield, 1987; *Protolafystius* Bousfield, 1987.

Family Laphystiopsidae Stebbing, 1899

Included genera. *Laphystiopsis* G.O. Sars, 1893; *Prolaphystiopsis* Schellenberg, 1931; *Prolaphystius* K.H. Barnard, 1930.

Family Ochlesidae Stebbing, 1910

Included genera. *Ochlesis* Stebbing, 1910; *Curidia* Thomas, 1983; *Meraldia* Barnard & Karaman, 1987; *Ochlesodius* Ledoyer, 1982.

Family Odiidae Coleman & Barnard, 1991a

Included genera. *Antarctodius* Berge, Vader & Coleman, 1999; *Cryptodius* Moore, 1992a; *Gordonodius* Ariyama, 2011; *Imbrexodius* Moore, 1992a; *Odius* Lilljeborg, 1865a; *Postodius* Hirayama, 1983.

Family Sicafodiidae Just, 2004

Included genera. *Sicafodia* Just, 2004.

Family Stilipedidae Holmes, 1908

Included subfamilies. Astryinae Pirlot, 1934; Alexandrellinae Holman & Watling, 1983; Stilipedinae Holmes, 1908.

Subfamily Astryinae Pirlot, 1934

Included genera. *Astyra* Boeck, 1871; *Eclysis* K.H. Barnard, 1932.

Subfamily Alexandrellinae Holman & Watling, 1983

Included genera. *Alexandrella* Chevreux, 1911b; *Astyroides* Birstein & Vinogradov, 1960; *Bathypanoplea* Schellenberg, 1939.

Subfamily Stilipedinae Holmes, 1908

Included genera. *Stilipes* Holmes, 1908.

Family Vicmusiidae Just, 1990

Included genera. *Acanthonotozomopsis* Watling & Holman, 1980.

Infraorder Lysianassida Dana, 1849 stat. nov.

Diagnosis. Antenna 1 primary flagellum 5 or more articulate (except Izinkalidae and Vemanidae). Antenna 1 and 2 without eusiroid calceolus. Gnathopod 2 carpus long (except Melphidippidae, Haustoriidae), longer than propodus (except Priscillinidae and Vemanidae). Coxae 1–4 not acuminate [except Haustoriidae, Ipanemidae, Priscillinidae, Stegocephalidae]. Pereopod 7 not immensely elongate. Pleonites without dorsal spines (except Priscillinidae).

Included parvorders. Synopiidira Dana, 1852 **stat. nov.**; Haustoriidira Stebbing, 1906 **stat. nov.**; Lysianassidira Dana, 1849 **stat. nov.**.

Remarks. The Lysianassida are defined by the above diagnostic characters, but a number of small highly derived taxa (Haustoriidae, Izinkalidae, Melphidippidae, Priscillinidae and Vemanidae) are anomalous. The large family Haustoriidae has a short carpus on gnathopod 2. In this respect it does not conform to the diagnosis.

Parvorder Synopiidira Dana, 1852 stat. nov.

Diagnosis. Antennae 1–2 calceoli absent. Antenna 2 peduncle with brush setae; flagellum in adult male greatly elongate. Pereopods 5–7 with few or no robust setae. Telson cleft (except in some *Synopia*).

Included superfamilies. Dexaminoidea Leach, 1814; Synopioidea Dana, 1852 (Bousfield, 1979).

Remarks. Bousfield & Kendall (1994) indicate that male atylids have elongate second antennae, but they illustrate some species with a short second antenna.

Superfamily Dexaminoidea Leach, 1814 (Bousfield, 1979)

Diagnosis. Antenna 2 brush setae present in adult males, Mandible lacinia mobilis present on both sides. Pereopods 5–7 similar in length or 5 shorter and 6–7 similar length, with few or no robust or slender setae. Pereopod 5 basis linear.

Included families. Atylidae Lilljeborg, 1865a; Dexaminidae Leach, 1814; Melphidippidae Stebbing, 1899; Pardaliscidae Boeck, 1871.

Family Atylidae Lilljeborg, 1865a

Included subfamilies. Anatylinae Bulycheva, 1955; Atylinae Lilljeborg, 1865a; Lepechinellinae Schellenberg, 1926a; Nototropiinae Bousfield & Kendall, 1994.

Subfamily Anatylinae Bulycheva, 1955

Included genera. *Anatylus* Bulycheva, 1955; *Kamehatylus* J.L. Barnard, 1970.

Subfamily Atylinae Lilljeborg, 1865a

Included genera. *Atylus* Leach, 1815.

Subfamily Lepechinellinae Schellenberg, 1926a (Bousfield & Kendall, 1994)

Included genera. *Lepechinella* Stebbing, 1908; *Lepechinelloides* Thurston, 1980; *Lepechinellopsis* Ledoyer, 1982; *Lepesubchela* Johansen & Vader, 2015; *Paralepechinella* Pirlot, 1933b.

Subfamily Nototropiinae Costa 1853 (Bousfield & Kendall, 1994)

Included genera. *Aberratylus* Bousfield & Kendall, 1994; *Nototropis* Costa, 1853.

Family Dexaminidae Leach, 1814

Included subfamilies. Dexamininae Leach, 1814; Dexaminoculinae Bousfield & Kendall, 1994; Polycheriinae Bousfield & Kendall, 1994; Prophliantinae Nicholls, 1939.

Subfamily Dexamininae Leach, 1814

Included genera. *Delkarlye* J.L. Barnard, 1972a; *Dexamine* Leach, 1814; *Dexaminella* Schellenberg, 1928b; *Paradexamine* Stebbing, 1899; *Sebadexius* Ledoyer, 1984; *Syndexamine* Chilton, 1914.

Subfamily Dexaminoculinae Bousfield & Kendall, 1994

Included genera. *Dexaminoculus* Lowry, 1981.

Subfamily Polycheriinae Bousfield & Kendall, 1994

Included genera. *Polycheria* Haswell, 1879b; *Tritaeta* Boeck, 1876.

Subfamily Prophliantinae Nicholls, 1939

Included genera. *Guernea* Chevreux, 1887; *Haustoriopsis* Schellenberg, 1938; *Prophlias* Nicholls, 1939.

Family Melphidippidae Stebbing, 1899

Included genera. *Melphidippa* Boeck, 1871; *Melphidipella* G.O. Sars, 1894; *Melphisana* J.L. Barnard, 1962a; *Melphisubchela* Andres, 1981b.

Family Pardaliscidae Boeck, 1871

Included genera. *Andeepia* Biswas, Coleman & Hendrycks, 2009; *Antronicippe* Stock & Iliffe, 1990; *Arculfia* J.L. Barnard, 1961; *Caleidoscopsis* G. Karaman, 1974; *Epereopus* Mills, 1967; *Halice* Boeck, 1871; *Halicella*

Schellenberg, 1926a; *Halicoides* Walker, 1896; *Macroarthrus* Hendrycks & Conlan, 2003; *Necochea* Barnard, 1962c; *Nicippe* Bruzelius, 1859; *Octomana* Hendrycks & Conlan, 2003; *Parahalice* Birstein & Vinogradov, 1962; *Pardalisca* Krøyer, 1842; *Pardaliscella* G.O. Sars, 1893; *Pardaliscoides* Stebbing, 1888; *Pardaliscopsis* Chevreux, 1911a; *Parpano* J.L. Barnard, 1964a; *Princaxelia* Dahl, 1959; *Rhynohalicella* G. Karaman, 1974; *Spelaeonicippe* Stock & Vermeulen, 1982; *Tosilus* J.L. Barnard, 1966.

Superfamily Synopioidea Dana, 1852 (Bousfield, 1979)

Diagnosis. Gnathopod 2 simple (also some pardaliscids). Pereopod 4 coxa with well-developed posteroventral lobe. Pereopods 5–7 with few or no robust or slender setae.

Included families. Ampeliscidae Krøyer, 1842; Argissidae Walker, 1904; Synopiidae Dana, 1852.

Family Ampeliscidae Krøyer, 1842

Included genera. *Ampelisca* Krøyer, 1842; *Byblis* Boeck, 1871; *Byblisoides* K.H. Barnard, 1931; *Haploops* Liljeborg, 1856.

Family Argissidae Walker, 1904

Included genera. *Argissa* Boeck, 1871.

Remarks. *Argissa* is in need of revision. The distribution, depth range and morphological variation attributed to *A. hamatipes* are implausible when attributed to a single species.

Argissa hamatipes (Norman, 1869) was originally described from shallow water in St Magnus Bay, Shetland Islands, Scotland. *Argissa stebbingi* Bonnier, 1896 was described from 940 m depth in the Bay of Biscay, France. These two species are currently in synonymy and many more records have been added so that based on current taxonomy the climatic distribution of *Argissa hamatipes* extends from Iceland (Sub-Arctic) to Sri Lanka (high tropics), the depth distribution extends from the shallow subtidal (14 m depth) to the lower bathyal (nearly 1000 m depth) and the geographic distribution is one of the widest of any non-hyperiidean amphipod species, from California to the Sea of Japan in the Pacific Ocean, from southern India and Sri Lanka to Madagascar and southern Africa in the Indian Ocean, and in the Atlantic Ocean from West Africa and the Azores, to the Mediterranean Sea and along the European coast to Norway, and across the northern North Atlantic to Iceland and Greenland and from the Gulf of St Lawrence to New England in North America.

A number of records have been published without illustrations (Walker, 1904 (Sri Lanka); Stephensen, 1940 (Iceland); Schellenberg, 1942; Reid, 1951 (West Africa)). More were published with illustrations: Chevreux & Fage, 1925 (Bay of Biscay, the Azores and West Africa); Shoemaker, 1930 (Gulf of St Lawrence); Gurjanova, 1951; Nagata, 1965 (Sea of Japan); J.L. Barnard, 1967 (southern California); Bousfield, 1973 (New England); Griffiths, 1976 (Cape Province, South Africa); Lincoln, 1979 (British Isles) and Ledoyer, 1982 (Madagascar)). These illustrations often indicate species level morphological differences. For instance, based on morphology, the well-illustrated material of Rabindranath (1972) from Trivandrum, Kerala, India should be considered as a new species.

Most authors have accepted the synonymy without question. Ruffo (1982) maintained two species, but the problem is that the taxon is so confused that trying to maintain the two names does not help. There has to be a revision based on all available material.

Family Synopiidae Dana, 1852

Included genera. *Austrosyrroe* K.H. Barnard, 1925; *Bruzelia* Boeck, 1871; *Bruzeliopsis* Chevreux, 1911a; *Cardenio* Stebbing, 1888; *Garosyrrhoe* J.L. Barnard, 1964a; *Ileraustroe* J.L. Barnard, 1969b; *Jeddo* J.L. Barnard, 1962c; *Latacunga* J.L. Barnard, 1972c; *Metatiron* Rabindranath, 1972; *Priscosyrrhoe* J.L. Barnard, 1972c;

Pseudotiron Chevreux, 1895; *Stephobruzelia* J.L. Barnard, 1969b; *Synopia* Dana, 1852; *Syrrhoe* Goës, 1866; *Syrrhoites* G.O. Sars, 1893; *Telsosynopia* G. Karaman, 1986; *Tiron* Lilljeborg, 1865b.

Remarks. J.L. Barnard (1969b: 460) described the new genus *Ileraustroe* and then later described the genus as new for a second time (J.L. Barnard 1972c: 34).

Parvorder Haustoriidira Stebbing, 1906 stat. nov.

Diagnosis. Head rostrum present. Antenna 1 and 2 peduncles and pereopods 5–7 with many robust and slender setae (except Pontoporeiidae and Priscillinidae). Pereopod 3 merus longer than propodus. Epimeron 2 with plumose setae (except Pontoporeiidae, Priscillinidae and Platyischnopidae).

Included superfamilies. Haustorioidea Stebbing, 1906.

Remarks. The basal families Pontoporeiidae and Priscillinidae do not have the many robust and slender setae on the peduncles of antenna 1 and 2 and on pereopods 5–7, nor the plumose setae on epimeron 2 that are typical of most Haustorioidea. However, both families share with phoxocephalids, the characteristically dissimilar pereopods 6 and 7. Pontoporeiids share embedded setae on the rami of uropods 1 and 2 with the Phoxocephalidae. Also the Phoxocephalidae, Pontoporeiidae and Priscillinidae are the only families in the parvorder with reniform eyes.

Superfamily Haustorioidea Stebbing, 1906 (Barnard & Drummond, 1982b)

Diagnosis. As for parvorder.

Included families. Cheidae Thurston, 1982; Condukiidae Barnard & Drummond, 1982b; Haustoriidae Stebbing, 1906; Ipanemidae Barnard & Thomas, 1988b; Otagiidae Hughes & Lörz, 2013; Phoxocephalidae G.O. Sars, 1891; Phoxocephalopsidae Barnard & Drummond, 1982b; Platyischnopidae Barnard & Drummond, 1979; Pontoporeiidae Dana, 1853; Priscillinidae d'Udekem d'Acoz, 2007; Sinurothoidae Ren, 1999; Urohaustoriidae Barnard & Drummond, 1982b; Urothoidae Bousfield, 1979; Zobrachoidae Barnard & Drummond, 1982b.

Family Cheidae Thurston, 1982

Included genera. *Cheus* Thurston, 1982; *Microcheus* Souza-Fihlo, 2011; *Ruffosius* Souza-Fihlo, 2011.

Family Condukiidae Barnard & Drummond, 1982b

Included genera. *Condukius* Barnard & Drummond, 1982b.

Family Haustoriidae Stebbing, 1906

Included genera. *Acanthohaustorius* Bousfield, 1965; *Eohaustorius* J.L. Barnard, 1957b; *Haustorius* Müller, 1775; *Lepidactylus* Say, 1818a; *Neohaustorius* Bousfield, 1965; *Parahaustorius* Bousfield, 1965; *Protohaustorius* Bousfield, 1965; *Pseudohaustorius* Bousfield, 1965.

Family Ipanemidae Barnard & Thomas, 1988b

Included genera. *Ipanema* Barnard & Thomas, 1988b.

Family Otagiidae Hughes & Lörz, 2013

Included genera. *Otagia* Barnard & Karaman, 1991.

Family Phoxocephalidae G.O. Sars, 1891

Included subfamilies (based on De Broyer *et al*. 2007)**.**

Remarks. Barnard & Drummond (1998) established nine subfamilies for the world phoxocephalid species (Birubiinae Barnard & Drummond, 1978; Brolginae Barnard & Drummond, 1978; Harpiniinae Barnard & Drummond, 1978; Joubinellinae Barnard & Drummond, 1978; Leongathinae Barnard & Drummond, 1978; Palabriaphoxinae Gurjanova, 1977; Phoxocephalinae G.O. Sars, 1891; Pontharpiniinae Barnard & Drummond, 1978; Tipimeginae Barnard & Drummond, 1978). Barnard & Karaman (1991) partially revised this system but were unable to unequivocally place a number of genera into specific subfamilies.

Jarrett & Bousfield (1994a) established the Metharpiniinae for several new genera and incorporated some difficult genera. De Broyer *et al*. (2007) recognised only two subfamilies Harpiniinae and Phoxocephalinae in the catalogue of Antarctic Amphipoda. Alonso de Pina *et al*. (2008) was critical of the scheme and excluded subfamilies when cataloguing the Antarctic taxa.

Because of the confusion in the classification of this family, we follow the classification of De Broyer *et al*. 2007.

Subfamily Harpiniinae Barnard & Drummond, 1978

Included genera. *Basuto* Barnard & Drummond, 1978; *Cocoharpinia* G. Karaman, 1980a; *Coxophoxus* J.L. Barnard, 1966; *Feriharpinia* Barnard & Karaman, 1982; *Harpinia* Boeck, 1876; *Harpiniopsis* Stephensen, 1925b; *Heterophoxus* Shoemaker, 1925; *Proharpinia* Schellenberg, 1931; *Pseudharpinia* Schellenberg, 1931; *Torridoharpinia* Barnard & Karaman, 1982.

Subfamily Phoxocephalinae G.O. Sars, 1891 (Barnard & Drummond, 1978)

Included genera. *Baliphoxus* Ortiz & Lalana, 1999; *Bathybirubius* Senna, 2010; *Beringiaphoxus* Jarrett & Bousfield, 1994a; *Birubius* Barnard & Drummond, 1978; *Booranus* Barnard & Drummond, 1978; *Brolgus* Barnard & Drummond, 1978; *ephalophoxoides* Gurjanova, 1977; *Cephalophoxus* Gurjanova, 1977; *Cunmurra* Barnard & Drummond, 1978; *Diogodias* Barnard & Drummond, 1978; *Elpeddo* Barnard & Drummond, 1978; *Eobrolgus* J.L. Barnard, 1979; *Eusyrophoxus* Gurjanova, 1977; *Eyakia* J.L. Barnard, 1979; *Foxiphalus* J.L. Barnard, 1979; *Fuegiphoxus* Barnard & Barnard, 1980; *Ganba* Barnard & Drummond, 1978; *Grandiphoxus* J.L. Barnard, 1979; *Griffithsius* Jarrett & Bousfield, 1994b; *Hopiphoxus* Barnard & Drummond, 1978; *Indophoxus* Dang & Le, 2005; *Japara* Barnard & Drummond, 1978; *Jerildaria* Barnard & Drummond, 1978; *Joubinella* Chevreux, 1908a; *Kondoleus* Barnard & Drummond, 1978; *Kotla* Barnard & Drummond, 1978; *Kulgaphoxus* Barnard & Drummond, 1978; *Kuritus* Barnard & Drummond, 1978; *Leongathus* Barnard & Drummond, 1978; *Leptophoxoides* J.L. Barnard, 1962c; *Leptophoxus* G.O. Sars, 1891; *Limnoporeia* Fearn-Wannan, 1968; *Linca* Alonso de Pina, 1993; *Majoxiphalus* Jarrett & Bousfield, 1994a; *Mandibulophoxus* J.L. Barnard, 1957a; *Matong* Barnard & Drummond, 1978; *Mesophoxus* Gurjanova, 1977; *Metaphoxoides* Ledoyer, 1968; *Metaphoxus* Bonnier, 1896; *Metharpinia* Schellenberg, 1931; *Microphoxus* J.L. Barnard, 1960; *Palabriaphoxus* Gurjanova, 1977; *Parafoxiphalus* Alonso de Pina, 2001; *Parajoubinella* Gurjanova, 1977; *Paramesophoxus* Gurjanova, 1977; *Parametaphoxus* Gurjanova, 1977; *Paraphoxus* G.O. Sars 1891; *Parharpinia* Stebbing, 1899; *Phoxocephalus* Stebbing, 1888; *Phoxorgia* Barnard & Barnard, 1980; *Pontharpinia* Stebbing, 1897; *Protophoxus* K.H. Barnard, 1930; *Pseudfoxiphalus* Andres, 1991; *Rhepoxynius* J.L. Barnard, 1979; *Rikkarus* Barnard & Drummond, 1978; *Ringaringa* Barnard & Karaman, 1991; *Synphoxus* Gurjanova, 1980a; *Tickalerus* Barnard & Drummond, 1978; *Tipimegus* Barnard & Drummond, 1978; *Trichophoxus* K.H. Barnard, 1930; *Uldanamia* Barnard & Drummond, 1978; *Urophoxus* Gurjanova, 1977 (=*Pontharpinia* according to Barnard & Karman, 1991); *Vasco* Barnard & Drummond, 1978;

Vietophoxus Dang & Le, 2005; *Waipirophoxus* Gurjanova, 1980b; *Waitangi* Fincham, 1977; *Wildus* Barnard & Drummond, 1978; *Yammacoona* Barnard & Drummond, 1978; *Yan* Barnard & Drummond, 1978.

Family Phoxocephalopsidae Barnard & Drummond, 1982b

Included genera. *Eophoxocephalopsis* Thurston, 1989a; *Phoxocephalopsis* Schellenberg, 1931; *Pseudurothoe* Ledoyer, 1986; *Puelche* Barnard & Clark, 1982a; *Urothopsis* Ledoyer, 1968.

Remarks. Sittrop *et al*. (2014) removed *Pseudurothoe* and *Urothopsis* from the Urothoidae and placed them in the Phoxocephalopsidae.

Family Platyischnopidae Barnard & Drummond, 1979

Included genera. *Eudevenopus* Thomas & Barnard, 1983; *Indischnopus* Barnard & Drummond, 1979; *Platyisao* Chiesa & Alonso, 2014; *Platyischnopus* Stebbing, 1888; *Skaptopus* Thomas & Barnard, 1983; *Tiburonella* Thomas & Barnard, 1983; *Tittakunara* Barnard & Drummond, 1979; *Tomituka* Barnard & Drummond, 1979; *Yurrokus* Barnard & Drummond, 1979.

Family Pontoporeiidae Dana, 1853

Included genera. *Diporeia* Bousfield, 1979; *Monoporeia* Bousfield, 1979; *Pontoporeia* Krøyer, 1842.

Remarks. The genus *Zaramilla* Stebbing, 1888, historically placed in the Pontoporeiidae, has recently been moved to the new monotypic family Zaramillidae Lowry & Myers, 2016 in the Senticaudata.

Family Priscillinidae d'Udekem d'Acoz, 2007

Included genera. *Priscillina* Stebbing, l888.

Remarks. In this study the Priscillinidae sits isolated at the base of the haustoriidiran clade next to the Pontoporeiidae. There is no support to maintain the superfamily Pontoporeiidoidea for the Priscillinidae and Pontoporeiidae. d'Udekem d'Acoz (2007) maintained that the Pontoporeiidae and the Priscillinidae were most similar to the Gammaroidea, but there is little support for this view. Priscillinids, like pontoporeiids have important haustoriidiran features, such as setose antennae and pereopods and pereopods 6 and 7 different in structure and uropods 1 and 2 without apical robust setae.

Family Sinurothoidae Ren, 1999

Included genera. *Sinurothoe* Ren, 1999.

Family Urohaustoriidae Barnard & Drummond, 1982b

Included genera. *Dirimus* Barnard & Drummond, 1982b; *Gheegerus* Barnard & Drummond, 1982b; *Huarpe* Barnard & Clark, 1982b; *Narunius* Barnard & Drummond, 1982b; *Nepelle* Barnard & Drummond, 1991; *Tottungus* Barnard & Drummond, 1982b; *Tuldarus* Barnard & Drummond, 1982b; *Urohaustorius* Sheard, 1936; *Warragaia* Berents, 1985.

Family Urothoidae Bousfield, 1979

Included genera. *Carangolia* J.L. Barnard, 1961; *Carangolioides* Sittrop, Serejo, Souza-Filho & Senna, 2014; *Coronaurothoe* Sittrop, Serejo, Souza-Filho & Senna, 2014; *Cunicus* Griffiths, 1974; *Urothoe* Dana, 1852; *Urothoides* Stebbing, 1891.

Family Zobrachoidae Barnard & Drummond, 1982b

Included genera. *Bumeralius* Barnard & Drummond, 1982b; *Chono* Clark & Barnard, 1987; *Prantinus* Barnard & Drummond, 1982b; *Tonocote* Clark & Barnard, 1986; *Zobracho* J.L. Barnard, 1961.

Parvorder Lysianassidira Dana, 1849 stat. nov.

Diagnosis. Body laterally compressed with large coxae. Antenna 1 callynophore well-developed. Mandible incisor smooth (except Alicelloidea); lacinia mobilis on left side only or vestigial on right [except Valettiopsidae]. Gnathopod 1 ischium long (except Parargissidae, Vemanidae and Valettidae).

Included superfamilies. Alicelloidea Lowry & De Broyer, 2008; Stegocephaloidea Dana, 1852 (Bousfield, 1979); Lysianassoidea Dana, 1849 (Bousfield, 1979); Aristioidea Lowry & Stoddart, 1997.

Remarks. Members of the distinctive Alicelloidea do not fit well into the diagnostic framework of the Lysianassidira, for example lysianassoids and aristioids have the lacinia mobilis present on the left side only. In the Alicelloidea by contrast the Alicellidae and the Valettiopsidae have the lacinia mobilis on both sides. Other alicelloids such as Vemanidae and Parargissidae are too poorly described to determine.

Superfamily Alicelloidea Lowry & De Broyer, 2008 stat. nov.

Diagnosis. Mandible molar and palp present. Maxilla 1 basal endite strongly setose along medial margin. Gnathopod 2 not mitten-shaped.

Included families. Alicellidae Lowry & De Broyer, 2008; Parargissidae **fam. nov.**; Podoprionidae Lowry & Stoddart, 1996; Valettidae Stebbing, 1888; Valettiopsidae Lowry & De Broyer, 2008; Vemanidae **fam. nov.**

Family Alicellidae Lowry & De Broyer, 2008

Included genera. *Alicella* Chevreux, 1899; *Apotectonia* Barnard & Ingram, 1990; *Diatectonia* Barnard & Ingram, 1990; *Paralicella* Chevreux, 1908a; *Tectovalopsis* Barnard & Ingram, 1990; *Transtectonia* Barnard & Ingram, 1990.

Family Parargissidae fam. nov.

Type genus. *Parargissa* Chevreux, 1908c.

Diagnosis (based on world family database)**.** Antenna 1 article 2 much longer than article 3, forming a dorsal flange. Maxilla 1 palps asymmetrical. Gnathopod 1 coxa smaller than 2. Gnathopods 1–2 merus linear, much loner that propodus. Pereopod 3 prehensile, merus much longer than propodus. Uropods 1–2 without apical robust setae. Telson moderately cleft.

Habitat. Marine, epigean, deep sea.

Included genera. *Parargissa* Chevreux, 1908c.

Distribution. Off Durban, south-western Indian Ocean, 4360 m; off Acapulco-Panama, eastern Central Pacific Ocean, 3570 m; off the Azores, North Atlantic Ocean.

Remarks. *Parargissa* was formally assigned to the Hyperiopsidae. It forms a new monotypic family here

which appears to be the sister group of vemanids. Both have sparse or no slender setae on the peduncle of antenna, flagellum longer than peduncle; maxilla 1 strongly setose on medial margin; gnathopod 1 smaller than gnathopod 2; pereopod 5 basis subrectangular; pereopod 7 different in structure from pereopod 6 and telson, long, laminar and cleft.

Family Podoprionidae Lowry & Stoddart, 1996

Included genera. *Podoprion* Chevreux, 1891.

Remarks. The Podoprionidae, formerly assigned to the Lysianassoidea is reassigned to the Alicelloidea.

Family Valettidae Stebbing, 1888

Included genera. *Valettia* Stebbing, 1888.

Family Valettiopsidae Lowry & De Broyer, 2008

Included genera. *Valettietta* Lincoln & Thurston, 1983; *Valettiopsis* Holmes, 1908.

Vemanidae fam. nov.

Type genus. *Vemana* J.L. Barnard, 1964a.

Diagnosis (based on world family database)**.** Antenna 1 shorter than antenna 2; callynophore well-developed; accessory flagellum short or minute. Antennae 1–2 calceoli absent. Mandible incisor dentate; molar large, triturative. Maxilla 1 basal endite setose along medial margin. Maxilla 2 basal endite with oblique setal row. Maxilliped palps well-developed. Gnathopods 1–2 subchelate. Pereopods 1–4 coxae not ventrally acute. Pereopod 4 coxa subequal or smaller than pereopod 3 coxa. Uropods 1–2 without apical robust setae. Telson laminar, moderately cleft.

Included genera. *Vemana* J.L. Barnard, 1964a.

Habitat. Marine, deep sea.

Distribution. Madagascar, Western Indian Ocean, western North America, north-eastern Pacific Ocean, Caribbean basin, tropical western Atlantic.

Remarks. *Vemana* was thought to be most similar to a hyperiopsid or a vitjazianid by J.L. Barnard (1964a). He placed it in the Vitjazianidae based on the morphology of maxilla 1. Ledoyer (1986) contrasted *Vemana* and *Vitjaziana* and questioned whether they should be in the same family. He showed similarities between *Vemana* and the lysianassids. In our analyses the Vemanidae aligns with the Parargissidae in the Lysianassidira.

Superfamily Stegocephaloidea Dana, 1852 (Bousfield, 1979)

Diagnosis. Body laterally compressed with large coxae. Mandible molar and palp absent. Gnathopod 2 not mitten-shaped; ischium long.

Included families. Stegocephalidae Dana, 1852.

Family Stegocephalidae Dana, 1852

Included subfamilies. Andaniexinae Berge & Vader, 2001; Andaniopsinae Berge & Vader, 2001; Bathystegocephalinae Berge & Vader, 2001; Parandaniinae Berge & Vader, 2001; Stegocephalinae Dana, 1852.

Subfamily Andaniexinae Berge & Vader, 2001

Included genera. *Andaniexis* Stebbing, 1906; *Andaniotes* Stebbing, 1897; *Glorandaniotes* Ledoyer, 1986; *Mediterexis* Berge & Vader, 2001; *Metandania* Stephensen, 1925b; *Parandaniexis* Schellenberg, 1929; *Stegosoladidus* Barnard & Karaman, 1987.

Subfamily Andaniopsinae Berge & Vader, 2001

Included genera. *Andaniopsis* G.O. Sars, 1891; *Sinoandaniopsis* Ren, 2012; *Steleuthera* J.L. Barnard, 1964a.

Subfamily Bathystegocephalinae Berge & Vader, 2001

Included genera. *Bathystegocephalus* Schellenberg, 1926b.

Subfamily Parandaniinae Berge & Vader, 2001

Included genera. *Parandania* Stebbing, 1899.

Subfamily Stegocephalinae Dana, 1852 (Berge & Vader, 2001)

Included genera. *Alania* Berge & Vader, 2001; *Austrocephaloides* Berge & Vader, 2001; *Austrophippsia* Berge & Vader, 2001; *Bouscephalus* Berge & Vader, 2001; *Gordania* Berge & Vader, 2001; *Phippsia* Stebbing, 1906 ; *Pseudo* Berge & Vader, 2001 (=*Schellenbergia* Berge & Vader, 2001); *Stegocephalexia* Moore, 1992a; *Stegocephalina* Stephensen, 1925b (=*Stegophippsiella* Bellan-Santini & Ledoyer, 1974); *Stegocephaloides* G.O. Sars, 1891; *Stegocephalus* Krøyer, 1842 (=*Phippsiella* Schellenberg, 1925) (=*Stegocephalopsis* Schellenberg, 1925); *Stegomorphia* Berge & Vader, 2001; *Stegonomadia* Berge & Vader, 2001; *Tetradeion* Stebbing, 1899.

Superfamily Lysianassoidea Dana, 1849 (Bousfield, 1979)

Diagnosis. Antennae 1–2 type 3 lysianassoid calceolus present (except Acidostomatidae and Conicostomatidae). Gnathopod 2 mitten-shaped (except Amaryllididae). Pereopod 5 propodus posterodistal spur absent.

Included families. Adeliellidae **fam. nov.**; Amaryllididae Lowry & Stoddart, 2002; Cebocaridae Lowry & Stoddart, 2011a; Cyclocaridae Lowry & Stoddart, 2011a; Cyphocaridiidae Lowry & Stoddart, 1997; Eurytheneidae Stoddart & Lowry, 2004; Hirondelleidae Lowry & Stoddart, 2010a; Lysianassidae Dana, 1849; Opisidae Lowry & Stoddart, 1995b; Scopelocheiridae Lowry & Stoddart, 1997; Tryphosidae Lowry & Stoddart, 1997 **stat. nov.**; Uristidae Hurley, 1963.

Family Adeliellidae fam. nov.

Type genus. *Adeliella* Nicholls, 1938.

Diagnosis (based on world family database)**.** Antenna 1 subequal in length to antenna 2. Maxilla 1 ischial endite with 6 setal-teeth. Gnathopod 1 subchelate. Gnathopod 2 minutely parachelate (mitten-shaped). Pereopod 4 coxa with small posteroventral lobe or without posteroventral lobe. Telson moderately or weakly cleft.

Habitat. Marine, epigean.

Included genera. *Adeliella* Nicholls, 1938.

Remarks. It is difficult to see similarities between Adeliellidae and other lysianassoid families. In our tree it

sits in the eurytheneid clade between the scavenging hirondelleids and the predatory cyphocaridids.

Distribution. Southern Ocean. Western Indian Ocean. Eastern tropical Atlantic Ocean.

Family Amaryllididae Lowry & Stoddart, 2002

Included subfamilies. Amaryllidinae Lowry & Stoddart, 2002; Vijayiinae Lowry & Stoddart, 2002.

Subfamily Amaryllidinae Lowry & Stoddart, 2002

Included genera. *Amaryllis* Haswell, 1879a; *Bamarooka* Lowry & Stoddart, 2002; *Erikus* Lowry & Stoddart, 1987; *Wonga* Lowry & Stoddart, 2002.

Subfamily Vijayiinae Lowry & Stoddart, 2002

Included genera. *Bathyamaryllis* Pirlot, 1933b; *Devo* Lowry & Stoddart, 2002; *Pseudamaryllis* Andres, 1981a; *Vijaya* Walker, 1904.

Family Cebocaridae Lowry & Stoddart, 2011a

Included genera. *Cebocaris* J.L. Barnard, 1964a; *Crybelocephalus* Tattersall, 1906; *Crybelocyphocaris* Shoemaker, 1945; *Cyphocarioides* Birstein & Vinogradov, 1970; *Mesocyclocaris* Birstein & Vinogradov, 1964; *Mesocyphocaris* Birstein & Vinogradov, 1960; *Metacyclocaris* Birstein & Vinogradov, 1955; *Metacyphocaris* Tattersall, 1906; *Paracyphocaris* Chevreux, 1905a.

Family Cyclocaridae Lowry & Stoddart, 2011a

Included genera. *Cyclocaris* Stebbing, 1888

Family Cyphocarididae Lowry & Stoddart, 1997

Included genera. *Cyphocaris* Boeck, 1871; *Procyphocaris* J.L. Barnard, 1961.

Family Eurytheneidae Stoddart & Lowry, 2004

Included genera. *Eurythenes* S.I. Smith, 1882.

Family Hirondelleidae Lowry & Stoddart, 2010a

Included genera. *Hirondellea* Chevreux, 1889.

Family Lysianassidae Dana, 1849

Included subfamilies. Lysianassinae Dana, 1849**;** Waldeckiinae Lowry & Kilgallen, 2014a.

Subfamily Lysianassinae Dana, 1849

Included genera. *Acosta* Özdikmen, 2012; *Aruga* Holmes, 1908; *Arugella* Pirlot, 1936; *Azotostoma* J.L. Barnard, 1965; *Bonassa* Barnard & Karaman, 1991; *Concarnes* Barnard & Karaman, 1991; *Dartenassa* Barnard & Karaman, 1991; *Dissiminassa* Barnard & Karaman, 1991; *Kakanui* Lowry & Stoddart, 1983; *Lysianassa* H. Milne Edwards, 1830; *Lysianassina* Costa, 1867; *Lysianopsis* Holmes, 1905; *Macronassa* Barnard & Karaman, 1991; *Nannonyx* G.O. Sars, 1891; *Parawaldeckia* Stebbing, 1910; *Phoxostoma* K.H. Barnard, 1925; *Pronannonyx* Schellenberg, 1953; *Pseudambasia* Stephensen, 1927; *Riwo* Lowry & Stoddart, 1995b; *Shoemakerella* Pirlot, 1936; *Socarnella* Walker, 1904; *Socarnes* Boeck, 1871; *Socarnoides* Stebbing, 1888; *Socarnopsis* Chevreux, 1911c; *Tantena* Ortiz, Lalana & Varela, 2007; *Thaumodon* Lowry & Stoddart, 1995a.

Subfamily Waldeckiinae Lowry & Kilgallen, 2014a

Included genera. *Waldeckia* Chevreux, 1906a.

Family Opisidae Lowry & Stoddart, 1995b

Included genera. *Normanion* Bonnier, 1893; *Opisa* Boeck, 1876; *Podoprionella* G.O. Sars, 1895; *Podoprionides* Walker, 1906a.

Family Scopelocheiridae Lowry & Stoddart, 1997

Included subfamilies. Scopelocheirinae Lowry & Stoddart, 1997 (Kilgallen & Lowry, 2015a); Paracallisominae Kilgallen & Lowry, 2015a.

Subfamily Paracallisominae Kilgallen & Lowry, 2015a

Included genera. *Anisocallisoma* Hendrycks & Conlan, 2003; *Austrocallisoma* Kilgallen & Lowry, 2015a; *Bathycallisoma* Dahl, 1959; *Eucallisoma* J.L. Barnard, 1961; *Haptocallisoma* Horton & Thurston, 2015; *Paracallisoma* Chevreux, 1903; *Pseudocallisoma* Horton & Thurston, 2015; *Scopelocheiropsis* Schellenberg, 1926a; *Tayabasa* Kilgallen & Lowry, 2015a.

Subfamily Scopelocheirinae Lowry & Stoddart, 1997 (Kilgallen & Lowry, 2015a)

Included genera. *Aroui* Chevreux, 1911c; *Paracallisomopsis* Gurjanova, 1962; *Scopelocheirus* Spence Bate, 1857.

Family Tryphosidae Lowry & Stoddart, 1997 stat. nov.

Included genera. *Allogaussia* Schellenberg, 1926a; *Bruunosa* Barnard & Karaman, 1987; *Cedrosella* Barnard & Karaman, 1987; *Cheirimedon* Stebbing, 1888; *Coximedon* Barnard & Karaman, 1991; *Elimedon* J.L. Barnard, 1962c; *Falklandia* De Broyer, 1985; *Glorieusella* Kilgallen & Lowry, 2014; *Gronella* Barnard & Karaman, 1991; *Hippomedon* Boeck, 1871; *Lepidepecreoides* K.H. Barnard, 1931; *Lepidepecreum* Spence Bate & Westwood, 1868; *Lepiduristes* Barnard & Karaman, 1987; *Lysianella* G.O. Sars, 1883; *Metambasia* Stephensen, 1923; *Microlysias* Stebbing, 1918; *Onesimoides* Stebbing, 1888; *Orchomene* Boeck, 1871; *Orchomenella* G.O. Sars, 1890; *Orchomenopsis* G.O. Sars, 1890; *Orchomenyx* De Broyer, 1984; *Orenoquia* Bellan-Santini, 1997;

Ottenwalderia Jaume & Wagner, 1998; *Paracentromedon* Chevreux & Fage, 1925; *Paralysianopsis* Schellenberg, 1931; *Paratryphosites* Stebbing, 1899; *Paronesimoides* Pirlot, 1933b; *Patonga* Lowry & Kilgallen, 2014b; *Photosella* Lowry & Stoddart, 2011b; *Psammonyx* Bousfield, 1973; *Pseudokoroga* Schellenberg, 1931; *Pseudonesimoides* Bellan-Santini & Ledoyer, 1974; *Pseudonesimus* Chevreux, 1926a; *Pseudorchomene* Schellenberg, 1926a; *Rifcus* Kudrjaschov, 1965; *Rimakoroga* Barnard & Karaman, 1987; *Schisturella* Norman, 1900; *Stephensenia* Schellenberg, 1928a; *Tasmanosa* Lowry & Kilgallen, 2014b; *Thrombasia* J.L. Barnard, 1966; *Tryphosa* Boeck, 1871; *Tryphosella* Bonnier, 1893; *Tryphosites* G.O. Sars, 1891; *Ulladulla* Lowry & Kilgallen, 2015; *Wecomedon* Jarrett & Bousfield, 1982.

Remarks. *Tryphosoides* Schellenberg, 1931 is considered to be a junior synonym of *Cheirimedon* Stebbing, 1888 by Kilgallen & Lowry (2015b).

The families Lysianassidae, Tryphosidae and Uristidae are based on morphological characters. Corrigan *et al*. (2014), using molecular techniques, considered these family groups to be polyphyletic. Together these families contain nearly 100 genera. For their analysis Corrigan *et al*. (2014) analysed selected species from only five genera in the complex and four genera from other lysianassoid family groups, based on an unusual choice of outgroups. This is not a basis for a reclassification of this large set of families.

By raising the Tryphosinae to family level we have considerably reduced the amount of morphological diversity in the Lysianassidae. There may be further taxonomic groupings within the family based around genera such as *Hippomedon*.

Family Uristidae Hurley, 1963

Included genera. *Abyssorchomene* De Broyer, 1984; *Anonyx* Krøyer, 1838; *Caeconyx* Barnard & Karaman, 1991; *Centromedon* G.O. Sars, 1891; *Cicadosa* Barnard & Karaman, 1991; *Debroyerella* Lowry & Kilgallen, 2015; *Des* Lowry & Kilgallen, 2014c; *Eclecticus* Lowry & Stoddart, 1997; *Euonyx* Norman, 1867; *Galathella* Barnard & Karaman, 1987; *Gippsia* Lowry & Stoddart, 1995a; *Ichnopus* Costa, 1853; *Koroga* Holmes, 1908; *Kyska* Shoemaker, 1964; *Menigrates* Boeck, 1871; *Menigratopsis* Dahl, 1945; *Nagada* Lowry & Stoddart, 1995b; *Onisimus* Boeck, 1871; *Paralibrotus* Stephensen, 1923; *Parschisturella* Andres, 1983; *Stephonyx* Lowry & Stoddart, 1989; *Tmetonyx* Stebbing, 1906; *Uristes* Dana, 1849.

Remarks. Based on the current concept of *Abyssorchomene*, it would form three different genera according to the molecular study of Havermans *et al*. 2010.

Superfamily Aristioidea Lowry & Stoddart, 1997 stat. nov.

Diagnosis. Antenna 1–2 without calceoli (except Thoriellidae). Mouthpart bundle subquadrate. Gnathopod 2 mitten-shaped.

Included families. Acidostomatidae Stoddart & Lowry, 2012; Ambasiidae **fam. nov.**; Aristiidae Lowry & Stoddart, 1997; Conicostomatidae Lowry & Stoddart, 2012b **stat. nov.**; Derjugianidae **fam. nov.**; Endevouridae Lowry & Stoddart, 1997; Izinkalidae Lowry & Stoddart, 2010c; Kergueleniidae Lowry & Stoddart, 2010d; Lepidepecreellidae Stoddart & Lowry, 2010b; Pakynidae **nom. nov.**; Sophrosynidae Lowry & Stoddart, 2010b; Thoriellidae Lowry & Stoddart, 2011a; Trischizostomatidae Lilljeborg, 1865b; Wandinidae Lowry & Stoddart, 1990.

Remarks. The Aristioidea have ovoid or rounded eyes and non-triturating molars, they have entire telsons (except ambasiids) and lack calceoli (except thoriellids).

Family Acidostomatidae Stoddart & Lowry, 2012

Included genera. *Acidostoma* Liljeborg, l865a; *Shackletonia* K.H. Barnard, 1931.

Family Ambasiidae fam. nov.

Type genus. *Ambasia* Boeck, 1871.

Diagnosis (based on world family database)**.** Antennae 1–2 calceoli absent. Mandible lacinia mobilis absent; accessory setal row absent; molar absent. Maxilla 1 basal endite with apical setae. Maxilla 2 basal endite without oblique setal row. Maxilliped ischial endite longer than palp article 2, not longer than palp article 3. Gnathopod 1 simple; coxa reduced, tapering. Gnathopod 2 minutely subchelate (mitten-shaped). Urosomite 1 dorsally carinate. Uropods 1–2 rami without apical robust setae. Telson deeply cleft.

Habitat. Marine, epigean.

Included genera. *Ambasia* Boeck, 1871; *Ambasiella* Schellenberg, 1935.

Distribution. Arctic Ocean; North Atlantic, Greenland, Iceland, Norway, off south-west Ireland.

Remarks. The sister taxon of ambasiids appears to be the Izinkalidae. They share the absence of a lacinia mobilis, a reduced coxa 1, expanded merus on pereopods 5 and 6, a carinate urosome and apical robust setae on the telson.

Family Aristiidae Lowry & Stoddart, 1997

Included genera. *Aristias* Boeck, 1871; *Boca* Lowry & Stoddart, 1997; *Memana* Stoddart & Lowry, 2010a; *Perrierella* Chevreux & Bouvier, 1892; *Pratinas* Stoddart & Lowry, 2010a.

Family Conicostomatidae Lowry & Stoddart, 2012b stat. nov.

Included genera. *Acontiostoma* Stebbing, 1888; *Amphorites* Lowry & Stoddart, 2012b; *Conicostoma* Lowry & Stoddart, 1983; *Ocosingo* J.L. Barnard, 1964b; *Scolopostoma* Lowry & Stoddart, 1983; *Stomacontion* Stebbing, 1899.

Family Derjugianidae fam. nov.

Type genus. *Derjugiana* Gurjanova, 1962.

Diagnosis (based on world family database)**.** Antenna 1 with well-developed callynophore. Antennae 1–2 calceoli apparently absent. Mandible incisors minutely dentate; accessory setal row absent; molar absent. Maxilla 2 basal endite without oblique setal row. Maxilliped ischial endites longer than palp article 3. **Gnathopod 1 chelate**. Gnathopod 2 minutely chelate (mitten-shaped). Pleonite 3 and urosomite 1 each with dorsal carina. **Uropod 3 present, rami absent**. Telson entire.

Habitat. Marine, epigean.

Included genera. *Derjugiana* Gurjanova, 1962.

Distribution. *Russia*. Okhotsk Sea: Sakhalin Island (Gurjanova, 1962).

Remarks. Derjugianidae are in a clade with Thoriellidae and Wandinidae. They share a vertical anterior margin on the head, 6/5 setal-tooth arrangement on the ischial endite of maxilla 1 (Wandinidae), maxilliped ischial endite very large and uropod 3 endopod absent (Thoriellidae).

Family Endevouridae Lowry & Stoddart, 1997

Included genera. *Endevoura* Chilton, 1921; *Ensayara* J.L. Barnard, 1964d.

Family Izinkalidae Lowry & Stoddart, 2010c

Included genera. *Izinkala* Griffiths, 1977.

Remarks. See remarks for Bolttsiidae.

Family Kergueleniidae Lowry & Stoddart, 2010d

Included genera. *Clepidecrella* J.L. Barnard, 1962c; *Kerguelenia* Stebbing, 1888.

Family Lepidepecreellidae Stoddart & Lowry, 2010b

Included genera. *Lepidepecreella* Schellenberg, 1926a.

Pakynidae nom. nov.

Pachynidae Lowry & Stoddart, 2012a: 5 (homonym).—De Broyer *et al.*, 2007: 157 (*nomen nudum*).

Included genera. *Acheronia* Lowry, 1984; *Coriolisa* Lowry & Stoddart, 1994; *Drummondia* Lowry, 1984; *Ekelofia* Lowry, 1984; *Figorella* J.L. Barnard, 1962c; *Pachychelium* Stephensen, 1925b; *Pakynus* **nom. nov.**; *Prachynella* Barnard, 1964b; *Renella* Lowry & Stoddart, 2012; *Sheardella* Lowry, 1984; *Smaraldia* Lowry & Stoddart, 2012; *Ultimachelium* Lowry & Stoddart, 2012.

Habitat. Marine, epigean.

Distribution. Cosmopolitan.

Remarks. It was recently brought to our attention by Tony Rees (CSIRO Marine and Atmospheric Research) that the generic name *Pachynus* was a *nomen nudum*, originally proposed by Rafinesque (1815) for a genus of cephalopod (preoccupied by *Hippurites* Lamarck, 1801), by Reichenow (1881) and for a psittaciforme bird (preoccupied by *Graydidascalus* Bonaparte, 1854). Even though *Pachynus* Rafinesque, 1815 and *Pachynus* Reichenow, 1881 are unjustified emendations, they are still available names (ICZN art. 33). Thus *Pachynus* Rafinesque 1815 is the senior available name and *Pachynus* Bulycheva, 1955 must be considered as preoccupied. We propose the new name *Pakynus* to replace *Pachynus* Bulycheva, 1955 in accordance with Article 39 of the International Code of Zoological Nomenclature (1999, fourth edition).

Family Sophrosynidae Lowry & Stoddart, 2010b

Included genera. *Sophrosyne* Stebbing, 1888.

Family Thoriellidae Lowry & Stoddart, 2011a

Included genera. *Chevreuxiella* Stephensen, 1915*; Danaella* Stephensen, 1925a; *Parachevreuxiella* Andres, 1987; *Thoriella* Stephensen, 1915.

Family Trischizostomatidae Lilljeborg, 1865b

Included genera. *Trischizostoma* Boeck, 1861.

Family Wandinidae Lowry & Stoddart, 1990

Included genera. *Pseudocyphocaris* Ledoyer, 1986; *Wandin* Lowry & Stoddart, 1990.

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