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The Phylogenetic Position of the Isopoda in the Peracarida (Crustacea: Malacostraca)

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> Abstract

The sister group to the isopod crustaceans remains a controversial proposition. Previous studies have used idealised composite taxa or few exemplars, resulting in conflicting assertions about the placement of the Isopoda among the Malacostraca. A recent morphological study argued for an Amphipoda-Isopoda clade, whereas a molecular study using SSU rDNA (18S) data found other relationships. Within isopods, the morphologically-specialised Phreatoicidea are generally regarded as the earliest-derived taxon, based on their fossil record and several published cladograms. These hypotheses were tested using 18S sequences and 202 morphological characters from 75 exemplars (52 isopods and 23 other malacostracans). The partitions were analysed separately and combined, and the sequence data were analysed using dynamic homology. To find the best sequence substitution, insertion-deletion and gap insertion costs, scores based on finding accepted monophyletic taxa were used to select the optimal parameters. Separately and combined, both partitions rejected the Amphipoda-Isopoda clade hypothesis. The 18S analysis placed the phreatoicideans high in the tree, rather in a basal position. The morphological analysis found a basally branching Phreatoicidea-Asellota group. The combined analysis found an Apseudomorpha (Tanaidacea) + Isopoda clade, with Phreatoicidea still well separated from the isopod ancestral root. The parasitic subgroups of the Cymothoida (families Cymothoidae and Gnathiidae, and superfamily Bopyroidea) comprised the basal branch of the isopods, which is a novel hypothesis that argues against the monophyly of the suborder Cymothoida. The 18S data alone are inadequate at this phylogenetic level and the combined data provided novel hypotheses that require additional evidence from detailed morphological studies and DNA markers for confirmation.

> Key words

Malacostraca, Peracarida, Isopoda, phylogeny, combined analysis, small subunit rDNA, morphology, terminology, dynamic homology, direct optimisation.

1. Introduction

1.1. Phylogenetic relationships of the Isopoda in the Peracarida

After several centuries of crustaceology[1], the relationships of the order Isopoda remain uncertain. Many studies have found relatives either among the mancoid peracarids (those where the first postmarsupial stage lacks the last legs; e.g., CALMAN 1909; SIEWING 1963; PIRES 1987; RICHTER & SCHOLTZ 2001), or as a sister group with the amphipods (WATLING 1981, 1983, 1999; WAGNER 1994; SCHRAM & HOF 1998; POORE 2005). But isopods stand alone with numerous unique morphological traits that define the order, such as biphasic moulting (VERNET & CHARMANTIER-DAURES 1994) and a specialised heart musculature (NYLUND et al. 1987) and that make them unlike any of the other extant peracarid orders. They also have a long fossil history starting in the Carboniferous period, when malacostracan diversity was bursting on the evolutionary scene (SCHRAM 1974). Paradoxically, putative sister groups for the isopods do not appear in the record until much later. The oldest Amphipoda are known from the Eocene, and another possible sister group, Tanai-

[1] I prefer LEACH's (1814) term over the more often used but less general "carcinology".

dacea, does not have Palaeozoic fossils belonging to the crown group (VONK & SCHRAM 2007).

The general relationships within the isopods may appear to be settled (cf. WÄGELE 1989; BRUSCA & WILSON 1991), but one cannot be certain. CALMAN (1909: 218) commented "The structure of the Isopoda is so diversified, and the number of forms included in the Order is so large, that their classification is a matter of some difficulty". The relationships of the higher isopods (e.g., "Flabellifera sensu lato" of WILSON 1998, 1999) have remained especially unclear. Recent analyses of the group (BRANDT & POORE 2003) have proposed a revised classification, but doubts remain on the usefulness of that classification (WILSON 2003, 2008a). Most recent studies of isopod relationships have placed the suborder Phreatoicidea as the sister group of the remaining isopods, in accord with their fossil record. Phreatoicideans have many specialisations that are not seen in other isopods (WILSON & KEABLE 2001). Hints of a sister group relationship between Asellota and the Phreatoicidea have emerged (WILSON 1999), but these were not objectified by explicit analyses. The fossil record does not completely answer the questions. Based on a recent find of new fossils (P. Schirolli, Italy, pers. comm.), Asellota may be found in the Triassic. After this period, sphaeromatoid-like isopods appear in the fossil record (GUINOT et al. 2005). By the Triassic, however, crown group Phreatoicidea were well established in fresh water (WILSON & EDGECOMBE 2003). Although Oniscidea do not appear until the Eocene as modern taxa (records in SCHMALFUSS 2003), they also appear basal to the remainder of the higher isopods in phylogenetic studies (WÄGELE 1989; BRUSCA & WILSON 1991; SCHMIDT 2008). SCHMALFUSS (1989) even places the Asellota as the sister group to the rest of the isopods, with the next group being the Oniscidea (SCHMIDT 2008). TABACARU & DANIELOPOL (1999), however, found a sister group relationship between the Oniscidea and Valvifera. The remainder of the isopods are a diverse group of taxa, with largely uncertain relationships. Given the uncertainties and complexities involved, this contribution cannot presume to settle all issues, so it is limited to the test of two ideas, with some discussion of other implications.

The first question, the sister taxon to the isopods, seems to be a recurring issue in peracarid systematics. An idea recently arisen from disfavour is that the amphipods are the sister group (POORE 2005). Most treatments of the Isopoda from SARS (1899) and CALMAN (1909) onwards have treated the Tanaidacea as most closely related (cf. SIEWING 1963; PIRES 1987; HESSLER 1983; MAYRAT & DE SAINT LAURENT 1996), with earlier classifications (e.g., SARS 1899) failing to find the two taxa as separate. Nevertheless, scattered contributions over the past few decades (SCHRAM 1986; WAGNER 1994; SCHRAM & HOF 1998; WILLS 1998; POORE 2005; JENNER et al. 2009; WILLS et al. 2009) have found a close placement of the Amphipoda and the Isopoda. Most of the morphological studies make fundamental assumptions about the terminal taxa (often as higher level taxa rather than species exemplars) that are either invalid or at least not universally true. Molecular studies (WHEELER 1998; SPEARS et al. 2005; JENNER et al. 2009), which have the advantage of explicit terminals, have not produced well-defined results on this issue and suffer from limited numbers of peracarid taxa or relevant sequences.

Two differing views on the sister group of the isopods are current. For the amphipod-isopod clade, POORE (2005: tab. III) argues that this relationship is supported by 8 apomorphic character states, in agreement with several other publications (mentioned above). Because JENNER et al. 2009 (also WILLS et al. 2009) used data from POORE (2005), their morphology results are similar. A close inspection of the evidence for this clade, however, finds that it is only poorly supported. The absence of exopods on the pereopods of the two taxa is amplified by its appearance in 4 separate characters, a technical issue that is discussed below in Methods. Several character states supporting the relationship (POORE 2005: 6–7) are overgeneralisations (e.g., 23-1: "mandibular spine row and lacinia mobilis: short and compact, incisor and molar closely-set" or 46-1: "maxilliped epipod short, linear or in Isopoda not expanded into branchial cavity"). Some of these scorings are not accurate when specific taxa are considered, which is a fundamental problem with using "ground pattern" states to represent higher level taxa (YEATES 1995; WILSON 1996). Some states in POORE's (2005) character matrix also are misscored. For example, character 86, the foregut superomedianum is present in isopods (KOBUSCH 1999; personal observations), not "absent" as scored in POORE (2005). Additionally, the dataset has other problems, such as attributing uropodal endopod traits to the exopod. Several important characters that refute the isopod-amphipod clade are not used (such as embryonic cleavage pattern, thoracopod III form or the midgut dorsal caeca). A re-analysis of POORE's (2005) corrected data finds a different placement for the isopods, and a basal position for the amphipods between the Thermosbaenacea and the mancoid peracarids (Fig. 1; see Electronic Supplement file 3: a NEXUS file for Mesquite, see MADDISON & MADDISON 2009). Analyses of these data are, however, not stable because small changes or additions result in substantially differing topologies.

SPEARS et al. (2005), using SSU (small subunit) rDNA (18S) data, find a less well-defined placement of the isopods in the peracarids, but none of their analyses associate the amphipods with the isopods,

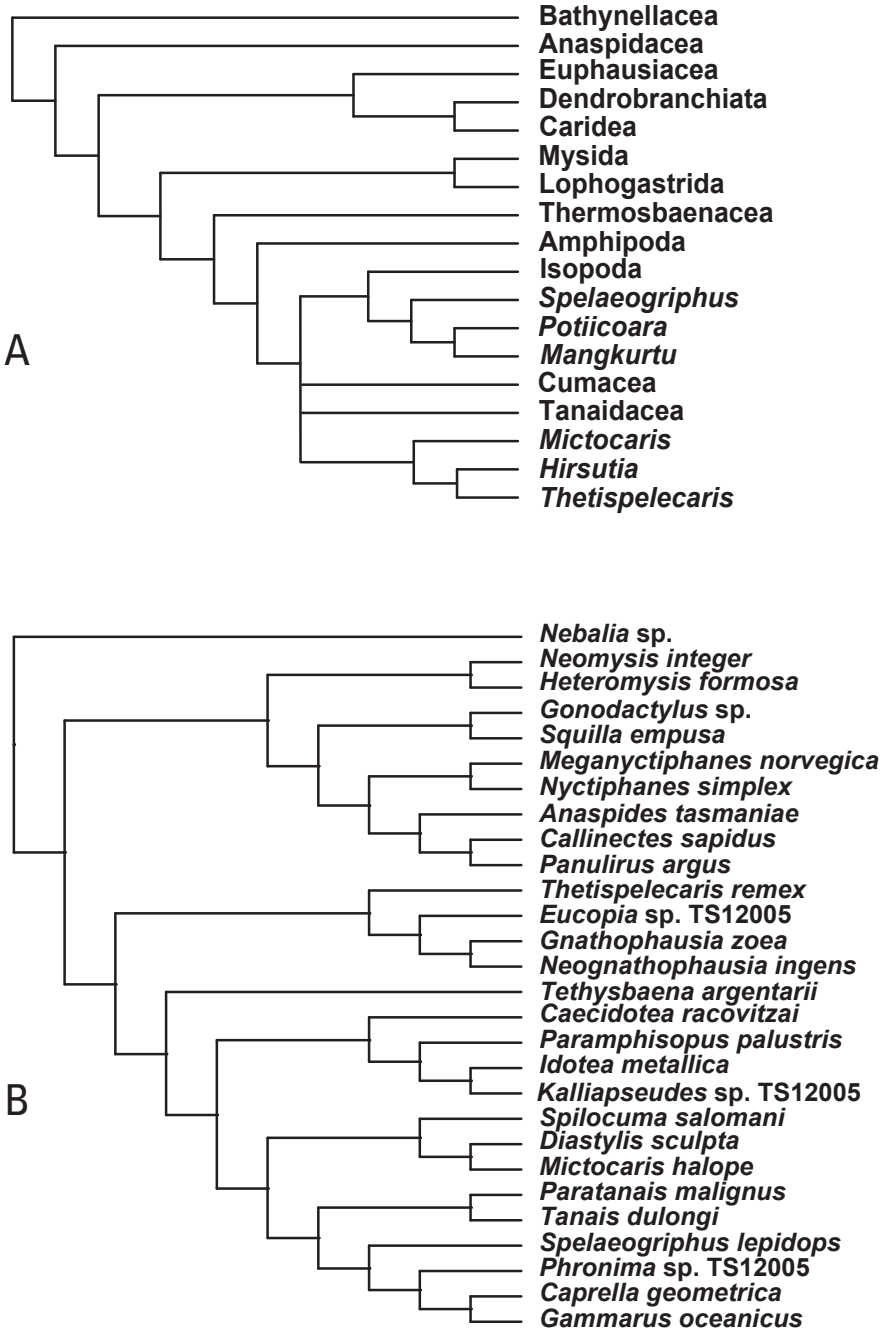

Fig. 1. Trees resulting from reanalysis of two published datasets. **A**: Strict consensus of 5 trees resulting from parsimony analysis of recoded data from Poore (2005), fossil taxa deleted. **B**: Single tree resulting from parsimony analysis using direct optimisation of the data from Spears et al. (2005). *Mictocaris halope* (accession number GQ175864) was included for comparability. The unaligned data were segmented into 9 fragments (see section 2.2.3. for method) and analysed using POY 4 with the same parameters as found by the taxonomic congruence analysis (tcm 211).

either paraphyletically or monophyletically. Uniquely, they find Spelaeogriphacea as the sister clade to Amphipoda. Their analysis had only 15 taxa, which may not sufficiently define the ancestral nodes for each ordinal level taxon. The 18S gene of peracarid species has highly variable regions for which standard alignment procedures fail to find unambiguous arrangements. Spears et al. (2005) deleted these regions from the analysis, even though an inspection of these regions shows blocks of sequences that appear to define groups of species. A reanalysis (methods described below) of their data with *Mictocaris* included yields a result different to that found in their paper (Fig. 1; see Electronic Supplement file 4), but with the same sister group relationship between the Amphipoda and Spelaeogriphacea.

For the second query, the basal relationships of the isopods are evaluated. Despite that they are highly

specialised (e.g., pleonal musculature: ERHARD 1998, 1999), should the earliest derivation of the phreatoicideans be accepted? Certainly fossil evidence supports this position, but other possibilities exist (WILSON 1999). Consequently, the second query asks whether the basal placement of the suborder Phreatoicidea can be supported by the weight of evidence, and if not that group, which one?

1.2. Approach

To address these problems, data from GenBank (www.ncbi.nlm.nih.gov/Genbank/index.html) and from several new sequences were assembled with the aim of providing a broad sampling of 75 taxa, with a concentration on the Isopoda and a good sampling of the putative sister taxa Amphipoda and Tanaidacea. Rather than using a two step analytical paradigm (fixed alignment followed by phylogenetic estimation) employed by SPEARS et al. (2005), the analysis was limited to direct optimisation (DO) parsimony (WHEELER 1996; WHEELER et al. 2006). This method has the advantage of allowing combined analysis of sequence data with the morphological evidence without introducing assumptions about models, other than the possible identity of parsimony with "no common mechanism" models of maximum likelihood (GOLDMAN 1990; TUFFLEY & STEEL 1997; HUELSENBECK et al. 2008). Parsimony is the appropriate choice because the extreme length variation in peracarid 18S (SPEARS et al. 2005) may result in the bases evolving heterogeneously where they are not identically distributed, conditions under which maximum likelihood and Bayesian methods may be strongly biased and statistically inconsistent (KOLACZKOWSKI & THORNTON 2004). DO will be discussed further below.

This study, which uses a combined dataset of morphology and 18S rDNA, avoids the omission of data, as far as possible. Taxa with problematic data are not omitted, except in extreme cases where a sequence was suspect. Unlike many 18S analyses that delete ambiguously aligned regions from the sequences (e.g., SPEARS et al. 2005), the entire published sequence was used. Higher numbers of taxa were used to break long branches in the phylogeny and provide a better optimisation of bases within each clade. LI et al. (2008) found limits to the use of more taxa (as opposed to using only one per high-rank taxon) in the reconstruction of ancestral states. This argues for choosing taxa appropriate to reconstruction, rather than employing all available taxa. By "appropriate", I mean using those taxa that provide a broad sampling of the diversity present in the group, which should provide the best opportunity to reconstruct ancestral states. Therefore the taxa were chosen to provide a broad range of available forms from each major taxon (nominally suborders or superfamilies).

Although molecular data often are used as independent tests of morphological concepts, this analysis asks how well the molecular data perform at finding accepted monophyletic taxa. This method is essentially a topological congruence test such as employed by WHEELER (1995), but based on accepted higher level classifications rather than a separate dataset. Phylogenetists evaluate, either implicitly or explicitly, a particular analytical result against what is known about the included taxa. In this contribution, the background knowledge of accepted monophyly is used explicitly. Among the peracarids, many taxa are so well understood that a contradicting analysis would be treated as biased or flawed. For example, no one would reject the monophyly of the Isopoda (see below). Given this approach, and needing a way of picking the best set of parameters for the analysis, a methodological query is proposed that asks which parameter set produces the best result.

The outcomes of this analysis are not definitive, and should be considered a guide for future research. The evidence for peracarid relationships is becoming more extensive, as witnessed by the many sequences now available on GenBank and papers evaluating particular morphological character systems across the group. Research on peracarid relationships should converge on the best arrangement although, in some areas, the data need more study. Isopod relationships cannot be fully addressed by this combined analysis because certain key taxa are missing from the data on GenBank; in particular these include species from the families Microcerberidae and the Calabozoidae, as well as numerous families in the Asellota.

1.3. Monophyly – the Peracarida and the Isopoda

At the outset, fundamental assumptions of monophyly are given here to support the underlying philosophy used in the analysis. Rather than ignoring or rejecting background knowledge of monophyly, this analysis uses it explicitly. Assuming monophyly has heuristic value for benchmarking the performance of analytical results (explained in Methods).

Despite many analyses not supporting a monophyletic Peracarida (reviewed in SPEARS et al. 2005; POORE 2005), apomorphic features define the group. The list below contains evidence for their monophyly in the form of complex features (particularly points 1–3). The basal group Mysidacea has attracted differing compositions and phylogenetic positions (MELAND & WILLASSEN 2007). Although other basal relation-

ships have been proposed for the peracarids, the complex evidence below must be explained. The following complex traits are considered to be homologous among peracaridans and autapomorphies of the Peracarida. The monophyly of the peracarids, however, is not explicitly tested in this analysis, owing to the use of a limited number of potential outgroup taxa.

1. Brood pouch and direct-developing young (reviewed in JOHNSON et al. 2001) is fundamental to the Peracarida, with the exception that the Thermosbaenacea brood embryos in their enlarged carapace fold. The coxal articulation of peracarid thoracic limbs is related to the presence of brood plates because they put a mechanical limitation on the movement of the coxae. The thorax-coxa hinge line is oriented on an anterior-posterior axis (HAUPT & RICHTER 2008) and the thoracopods may have a monocondylic coxa-basis articulation (HESSLER 1982). The coxa-basis joint is heterogeneous in basal taxa, such as the mysidaceans.

2. Heteromorphic lacinia mobilis present on both mandibles is a detailed synapomorphy of the Peracarida (RICHTER et al. 2002) not found in any other arthropod group.

3. Elongate non-flagellate sperm bodies (the "pennant sperm" of WIRTH 1984; see also COTELLI et al. 1976; POCHON-MASSON 1994) with an elongate striated acrosomal process. This complex feature alone is the best evidence for a monophyletic Peracarida, although more taxa should be surveyed.

4. Hypervariable regions in the 18S rDNA was shown by SPEARS et al. (2005) to characterise most Peracarida, although the location of the variation is not consistent across the group. Whether this is a useful apomorphic feature for the peracarids, relative to other malacostracans, needs further research and is outside the scope of this contribution.

The monophyly of the Isopoda is used as one of the topological benchmarks in the survey of analytical parameters (described below in section 2.2.4.), and therefore is assumed as background knowledge. The characters that support isopod monophyly are unusual among the Peracarida. A few are not exclusive because they are found in other peracarids.

1. Biphasic moulting seems to be a universal trait in the isopods, which may have advantages for calcium sequestration (VERNET & CHARMANTIER-DAURES 1994). This form of moulting is unknown in any other peracarid.

2. A posterior location of the heart in isopods (WIRKNER & RICHTER 2003; WIRKNER 2005) is related to their primary source of respiration occurring in the pleopods. The anterior extent of the heart varies considerably between and within the suborders of Isopoda, but the posterior border is practically always in the pleotelson, except in those Asellota where the pleotelson is substantially reduced.

3. All isopods have internal fertilisation and an associated copulatory organ (appendix masculina) on the male second pleopod (WILSON 1991). Morphological detail may be lost in parasitic taxa, especially where a microscopic male lives on the female. Some other peracarids have internal fertilisation as well (e.g., Thermosbaenacea; WAGNER 1994), but most appear to be externally fertilised (JOHNSON et al. 2001).

4. The walking legs of isopods (pereopods II–VII) have a small plate on the distal part of the propodus that may not be present in any other peracarid. Because this structure provides one of the two articulation points for the dactylus, it has been called the "articular plate" (WILSON & KEABLE 2001; WILSON 2003). In some taxa, particularly Asellota, this plate may allow a small amount of dactylar movement perpendicular to the plane of the limb.

5. Thoracopodal ischium (pereopods II–VII) is elongate, with a major basis-ischium flexure in the limb plane. This feature is shared with the Spelaeogriphacea. Most other peracarids have a short ischium, with only minor flexure in the limb plane.

6. The thoracopodal exopods are absent in all isopods as a suppression of expression (C. Wolff, pers. comm.) during the embryonic development. Notably, the apseudomorphan tanaidaceans in the genus *Kalliapseudes* display similar developmental patterns in the thoracopods (LANG 1956), although the suppression does not occur until after the manca stage. This supression is distinct from a developmental fusion of both rami into a telopod as in the amphipods (WOLFF & SCHOLTZ 2008).

7. Where present, the eyes lack expression of the eye stalks or lobes. In the Phreatoicidea, the eye lobe remnants are expressed as an indentation in the anterior margin of the head. Within the Isopoda, the position of the eyes varies considerably, and is a phylogenetically useful character. The eyes are not expressed at all in many clades of Isopoda.

8. As an outlier in the peracarid trend for reductions of the carapace, the Isopoda lack a carapace entirely. This absence may be related to transferring respiration to the pleopods. This is one of the few features shared with the amphipods. Additionally, the articulation between the cephalon and the first thoracosomite is also not expressed and the boundary between them may be expressed as a cervical indentation or groove.

9. The antennular lateral flagellum of the isopods is never fully expressed, and may be either completely absent or expressed as a tiny basally-articulated, seta-bearing segment. The broad distribution of the rudimentary lateral flagellum (BRUSCA &WILSON 1991; WILSON & KEABLE 2001; WILSON 2003) suggests that it is plesiomorphic within the Isopoda.

2. Material and methods

2.1. Molecular data: sources and assembly

The ribosomal nuclear small subunit gene (18S) was chosen for the analysis. Owing to research by Spears and co-workers (e.g., SPEARS et al 1994, 1999, 2005) and Wägele and co-workers (DREYER & WÄGELE 2002; RAUPACH et al. 2004, 2008), the 18S gene has a broad coverage over many crustacean taxa. In this study, taxon sampling, however, was limited to one or two species from each major taxonomic group, typically at the suborder or superfamily rank. Within the Isopoda, representative families received more detailed sampling. Seventy-five taxa were chosen (52 isopods and 23 other malacostracans; see Tab. 1) using the following criteria for choosing particular sequences:

1. Complete 18S sequence was present from GenBank (Tab. 1). Several sequences not in GenBank were kindly provided by other colleagues: *Pygolabis humphreysi* (GQ161216), Isopoda, Tainisopidae (C. Francis, University of Western Australia); *Apseudes bermudeus* (GQ175865), Tanaidacea, Apseudomorpha; and *Mictocaris halope* (GQ175864), Mictacea, Mictocaridae (S. Richter, University of Rostock, Germany). The *M. halope* sequence is not complete and shows low similarity to other malacostracans. This sequence (GQ175864) was used nevertheless because it is the only available sequence for the Mictacea.

2. Five species each of Amphipoda and Tanaidacea were chosen. Because the monophyly of both taxa is uncontested, they provide additional sensitivity for the parameter exploration described below in section 2.2.4. Within the tanaidaceans, no sequences of Neotanaidae were available.

3. Each sequence was submitted to a BLAST (ALTSCHUL et al. 1990) search and neighbour joining analysis (the "treeview widget", as provided by online "blastn" tool (www.ncbi.nlm.nih.gov/blast/Blast.cgi), that provides a distance tree of the results using the default fast minimum evolution method, with a maximum between sequence distance of 0.75. If these tests indicated that a sequence was at least related to some eumalacostracans, then it was used. In some cases, divergent sequences were used (e.g., *Paragnathia formica* AF255687.1), for which the most similar sequences were found among Collembola (hexapods), stomatopods and decapods, because the sequence was the only representative available.

4. The taxonomic diversity of each clade was sampled broadly wherever possible. Multiple species from the major taxonomic groups were chosen: for example, family-level exemplars from two of three suborders in the Tanaidacea (neotanaidomorphan 18S sequences were not available) were used.

5. If several sequences of closely related taxa (i.e., within the same genus or same family) were available and only one could be included, the longest sequence was chosen. Because peracarid 18S is highly length variable, those taxa that had longer sequences may provide greater differences between taxa, and therefore allowing the tree search to be more decisive, based on uninferred sequence data. Deletions could also add more decisive length, but these are inferred rather than actual data.

The data are used as provided in GenBank, with the problem that the taxonomic identity cannot be verified for many species. Many sequences have associated vouchers, as is the case for many newly contributed sequences, but many do not. PLEIJEL et al. (2008) have argued rightly that the scientific content of molecular data is diminished without an organised vouchering system. Nevertheless, the identification data in the current study are presented as extracted from GenBank. Similarly, sequencing errors and contamination cannot be completely discounted, so the results should be considered provisional until more taxa in each clade are sequenced, with better vouchering systems. Some divergent sequences, e.g., *Paragnathia formica*, should be revisited, and more taxa in each group should be sequenced.

2.2. Direct optimisation

2.2.1. Why fixed alignments were not used

Phylogenetic analyses of molecular data typically proceed in two steps: an alignment step followed by a phylogenetic estimation step. Dynamic homology as implemented by the algorithm 'direct optimisation' in the program POY (WHEELER et al. 2006; VARÓN et al. 2008) eliminates the alignment step and avoids the inconsistency of using different parameters for an alignment step from those used in the analysis (WHEELER 1996; WHEELER & GIRIBET 2009). Although some authors (e.g., OGDEN & ROSENBERG 2006) have argued that POY provides results with less topological accuracy than the two step method, affine indel costs (explained below) improve POY's topological accuracy so that it may exceed the accuracy of the two step method (LUI et al. 2009). Why fixed multiple alignments were not used in this dataset is further explained here.

Stem regions of 18S ribosomal rDNA show a high degree of conservation across taxa. These highly conserved regions have less information, or phylogenetic evidence, owing to their relative constancy. Hypervariable or "loop" regions, however, have much more phylogenetic information owing to the presence of many indels (GIRIBET & WHEELER 1999), despite the possibility of saturation in parts of the sequence. As

described by Spears et al. (2005), these regions are characteristically more variable in most peracarid sequences than in other crustaceans, with length increases of the 18S gene up to 2800 bp. These hypervariable regions, however, are difficult to use in the fixed alignment paradigm. Assigning homologous positions in a fixed alignment can be subjective, especially when the method "alignment by eye" is used (Giribet 2005). Fixed alignments of such regions are considered "ambiguous" and often deleted (as in Spears et al. 2005), which results in discarding phylogenetically useful evidence. Some authors using direct optimisation approaches also have deleted hypervariable regions in cases of extreme length variation between closely related species (e.g., Giribet et al. 2000), but these deletions were limited to only small sections. In the current set of analyses (described below), none of the sequence fragments was deleted because this is not desirable in a total evidence approach.

Using different optimality criteria during an analysis is another important problem. Multiple alignments use a "guide tree" that is created using one set of optimality criteria. This tree then becomes a background assumption that is employed as evidence to estimate phylogenies under a different set of criteria. The optimality criteria for a multiple alignment often differ from those used in a tree search. This means that tree topologies found in the analysis are influenced by a prior alignment parameter set. Rarely do investigators employ different fixed alignments to investigate their influence on the final result; when this is done (e.g., Wheeler 1995; Wägele 1995; Morrison & Ellis 1997), the results depend on the alignments used. Because direct optimisation can use only one set of cost parameters in each analysis and no starting alignment, inconsistency between the alignment step and analysis step is avoided.

"Gap" states are applied to all taxa in fixed alignments but gaps are not observations (Wheeler 1996; Wheeler & Giribet 2009), but are treated as such in a fixed alignment. Insertion/deletion (indel) events, however, only occur on inferred branches of a phylogeny and not among all taxa. Consequently, adding sequence "gaps" in a prior alignment step introduces a logical inconsistency into the analysis (Wheeler 1996; Wheeler & Giribet 2009). Indels are an important source of phylogenetic information (Giribet & Wheeler 1999), but may occur only in a subset of the taxa. As a result, an implied alignment derived from a direct optimisation analysis will not resemble a fixed alignment (Giribet 2005) because the latter may place nonhomologous indels in the same column. Multiple alignments also may position indels according to a total alignment score but may ignore other equally parsimonious solutions in a tree alignment (de Laet 2005). The Editor (while improving my sometimes obscure text) also proposed that dynamic homology should allow for more parsimonious solutions than fixed alignment analyses because base homologies are adjusted simultaneously with inferring the placement of indels.

2.2.2. Dynamic homology

Although the reasoning behind and operation of dynamic homology are described elsewhere (Wheeler 1996; Giribet 2001; Wheeler et al. 2006), a short explanation of the direct optimisation (DO) method may assist understanding of the analyses reported here. Nucleotide bases do not contain complex information, so assessing homology of base positions across taxa requires a consistent and logical approach. By including hypothetical ancestral states to find an optimal alignment of the sequences, hypotheses of homology are proposed about base correspondences between terminals in the analysis. In DO, indels or "gaps" represent change events rather than character states (cf. the "fifth state" of fixed alignment approaches). In this analytical framework, sequences transform by indel events and by substitution of bases. The optimality criterion to be minimised, however, is the cost of transformations, which includes substitutions and insertion/deletion (indels) events, as summed for each fragment at each node in an inferred tree. The best trees are those for which total cost (substitutions + inferred indel events) is minimised. In this method, indels are local events, rather than global.

Direct optimisation (DO) has several advantages. Because events are estimated directly during the tree search (hence "direct optimisation"), no pre-alignment step is required. Therefore all data can be used, despite that they may contain substantial length variation. DO uses the parsimony optimality criterion. Although model-based methods are currently popular, parsimony requires few assumptions other than the standard models (i.e., ordered, Farris 1970, or unordered, Fitch 1971); therefore parsimony has greater explanatory power than likelihood-based inference (reviewed in Farris 2008). As mentioned above, parsimony is a better choice for highly length variable peracarid 18S because it avoids biased and statistically inconsistent behaviour of model-based methods (Kolaczkowski & Thornton 2004). Parsimony is also heuristically useful in a dynamic homology context because it is computationally quicker than likelihood, which is an important consideration. Although parsimony methods may be equivalent to a "no common mechanism" maximum likelihood model (Tuffley & Steel 1997), parsimony is much faster than current maximum likelihood implementations of it.

Tab. 1. Taxa, classification and GenBank accession numbers for the 18S data. Taxa marked with an asterisk were assumed to be monophyletic for the 18S parameter performance survey (Tab. 2).

Species name	GenBank	Higher Taxon	Family Classification	Notes
Gonodactylus viridis	AY743947.1	Stomatopoda	Gonodactylidae	erroneously spelled 'viridus'
Penaeus semisulcatus	DQ079766.1	Decapoda; Penaeoidea	Penaeidae	voucher KC1269
Euphausia superba	DQ201509.1	Euphausiacea	Euphausiidae	
Anaspides tasmaniae	L81948.1	Anaspidacea	Anaspididae	
Neognathophausia ingens	AY781416.1	Mysidacea	Lophogastrida; Gnathophausiidae	
Stygiomysis holthuisi	AM422479.1	Mysidacea	*Mysida; Stygiomysidae	
Heteromysis formosa	AY781419.1	Mysidacea	*Mysida; Mysidae	
Tethysbaena argentarii	AY781415.1	Thermosbaenacea	Monodellidae	
Thetispelecaris remex	AY781421.1	Hirsutiacea	Hirsutiidae	new ordinal name
Mictocaris halope	GQ175864	Mictacea	Mictocaridae	Stefan Richter, 12/12/2005
Gammarus troglophilus	AF202983.1	*Amphipoda	Gammaridea; Gammaridae	
Arrhis phyllonyx	AF419235.1	*Amphipoda	Gammaridea; Oedicerotidae	
Protella gracilis	AB295396.1	*Amphipoda	Caprelloidea; Caprellidae	
Ingolfiella tabularis	DQ378054.1	*Amphipoda	Ingolfiellidea; Ingolfiellidae	
Hyperietta stephenseni	DQ378051.1	*Amphipoda	Hyperiidea; Hyperiidae	
Apseudes bermudeus	GQ175865	*Tanaidacea	*Apseudomorpha; Apseudidae	Stefan Richter, 12/12/2005
Kalliapseudes sp.	AY781430.1	*Tanaidacea	*Apseudomorpha; Kalliapseudidae	isolate TS-2005
Leptochelia sp.	AF496660.1	*Tanaidacea	*Tanaidomorpha; Leptocheliidae	isolate sp. WW-2002
Paratanais malignus	AY781429.1	*Tanaidacea	*Tanaidomorpha; Paratanaidae	
Tanais dulongii	AY781428.1	*Tanaidacea	*Tanaidomorpha; Tanaidae	
Diastylis sculpta	AY781431.1	*Cumacea	Diastylidae	
Spilocuma salomani	AY781432.1	*Cumacea	Bodotriidae	
Spelaeogriphus lepidops	AY781414.1	Spelaeogriphacea	Spelaeogriphidae	
Colubotelson thomsoni	AF255703.1	*Phreatoicidea	Phreatoicidae	
Paramphisopus palustris	AY781425.1	*Phreatoicidea	Amphisopidae	
Asellus aquaticus	AF255701.1	*Asellota	*Asellidae	
Caecidotea racovitzai	AY781426.1	*Asellota	*Asellidae	'Asellus racovitzai' is a junior synonym
Stenasellus racovitzai	AF496663.1	*Asellota	Stenasellidae	
Stenetriid sp.	AY461453.1	*Asellota	Stenetriidae	isolate JW-2004
Iathrippa trilobatus	AF279606.1	*Asellota	*Janiroidea; Janiridae	
Janira maculosa	AF255700.1	*Asellota	*Janiroidea; Janiridae	
Neojaera antarctica	AY461454.1	*Asellota	*Janiroidea; Janiridae	
Joeropsis coralicola	AF279608.1	*Asellota	*Janiroidea; Joeropsididae	isolate JW-2004
Dendromunna sp.	AY461464.1	*Asellota	*Janiroidea; Dendrotionidae	isolate JW-2004
Thylakogaster sp.	AY461470.1	*Asellota	*Janiroidea; Haplomunnidae	
Acanthaspidia drygalskii	AY461458.1	*Asellota	*Janiroidea; Acanthaspidiidae	isolate JW-2004
Janirella sp.	AY461475.1	*Asellota	*Janiroidea; Janirellidae	isolate BF191
Betamorpha fusiformis	EF116543.1	*Asellota	*Janiroidea; *Munnopsidae; Betamorphinae	
Eurycope sarsi	AY461479.1	*Asellota	*Janiroidea; *Munnopsidae; Eurycopinae	
Ilyarachna antarctica	AY461481.1	*Asellota	*Janiroidea; *Munnopsidae; Ilyarachninae	
Munnopsis typica	AF496661.1	*Asellota	*Janiroidea; *Munnopsidae; Munnopsinae	
Haploniscus nudifrons	DQ435680.1	*Asellota	*Janiroidea; Haploniscidae	
Ischnomesus sp.	AY461472.1	*Asellota	*Janiroidea; Ischnomesidae	isolate JW-2004
Mesosignum cf. *usheri*	AY461478.1	*Asellota	*Janiroidea; Mesosignidae	
Eugerda sp.	AY461463.1	*Asellota	*Janiroidea; *Desmosomatidae; Desmosomatinae	isolate JW-2004
Eugerdella natator	AY461462.1	*Asellota	*Janiroidea; *Desmosomatidae; Eugerdellatinae	
Macrostylis sp.1	AY461476.1	*Asellota	*Janiroidea; Macrostylidae	isolate JW-2004
Ligia oceanica	AF255698.1	*Oniscidea	*Diplocheta; Ligiidae	
Ligia italica	AY048177.1	*Oniscidea	*Diplocheta; Ligiidae	
Ligidium germanicum	AY048179.1	*Oniscidea	*Diplocheta; Ligiidae	
Haplophthalmus danicus	AJ287066.1	*Oniscidea	Synocheta; Trichoniscidae	

Tab. 1. Continuation.

Species name	GenBank	Higher Taxon	Family Classification	Notes
Porcellio scaber	AJ287062.1	*Oniscidea	*Crinocheta; Porcellionidae	
Oniscus asellus	AF255699.1	*Oniscidea	*Crinochaeta; Oniscidae	
Limnoria quadripunctata	AF279599.1	Limnoriidea	Limnoriidae	
Idotea baltica	AJ011390.1	*Valvifera	Idoteidae	
Cleantis prismatica	AF255697.1	*Valvifera	Holognathidae	
Glyptonotus antarcticus	AF255696.1	*Valvifera	Chaetiliidae	
Antarcturus spinacoronatus	AF279604.1	*Valvifera	Arcturidae	
Sphaeroma serratum	AF255694.1	Sphaeromatidea	*Sphaeromatidae	
Cassidinidea sp.	AF255693.1	Sphaeromatidea	*Sphaeromatidae	
Campecopea hirsuta	AF279601.1	Sphaeromatidea	*Sphaeromatidae	
Cymodoce tattersalli	AF255695.1	Sphaeromatidea	*Sphaeromatidae	
Cyathura carinata	AF332146.1	*Anthuroidea	Cyathuridae	
Paranthura nigropunctata	AF279598.1	*Anthuroidea	Paranthuridae	
Pygolabis humphreysi	GQ161216	Tainisopidea	Tainisopidae	Cara Francis, pers. comm. 2005
Hemiarthrus abdominalis	AF255684.1	Bopyroidea	*Bopyridae	
Probopyrus pacificiensis	AF255683.1	Bopyroidea	*Bopyridae	
Zonophryxus quinquedens	DQ008451.1	Bopyroidea	Dajidae	
Riggia paranensis	AF255685.1	*Cymothooidea	Cymothoidae	
Anilocra physodes	AF255686.1	*Cymothooidea	Cymothoidae	
Aega antarctica	AF255689.1	*Cymothooidea	Aegidae	
Excorallana quadricornis	AF255688.1	*Cymothooidea	Corallanidae	
Eurydice pulchra	AF255690.1	*Cymothooidea	Cirolanidae	
Natatolana meridionalis	AF255691.1	*Cymothooidea	Cirolanidae	'Natatolana albinota' is a junior synonym
Paragnathia formica	AF255687.1	*Cymothooidea	Gnathiidae	

Direct optimisation, however, has constraints. DO is computationally intensive because it combines two hard problems (mathematical described problems referred to as *NP-complete*; Wheeler et al. 2006): (1) estimating homology of substitutions and indels, given a tree, on a fragment by fragment basis; (2) finding shortest tree, given analytical data (taxa + characters + optimisation). A DO analysis may be several orders of magnitude slower that a fixed alignment parsimony analysis. Moreover, once a parsimonious solution is found for a data set, the resulting trees cannot be compared directly other than by the cost of each tree because the optimisation of the data onto internal nodes is topology specific. As a post-analysis step, one can generate an implied alignment that then can be used for several purposes (Wheeler 2003; Giribet 2005; Wheeler & Giribet 2009).

POY version 4.0, build 2881, or version 4.1.1 (Varón et al. 2008) was used to perform DO on a microcomputer equipped with a quad-core central processing unit, under a LINUX operating system. POY 4 was compiled for parallel processing so that each core ran independently.

2.2.3. Data partitions

The division of the sequences into homologous fragments improves the effectiveness of DO (Giribet 2001). Some workers have divided the 18S gene into fragment partitions using secondary structure (e.g., Spears et al. 2005; Meland & Willassen 2007). POY 4, using "transform(auto_sequence_partition)", divides 18S sequences into 3 fragments along the primer boundaries, but other workers have used more partitions in the 18S gene (e.g., 29 in Giribet et al. 2005). A conservative partitioning was employed herein that was intermediate between finding many fragments using secondary structure and simply using the primer boundaries. A CLUSTALW (Thompson et al. 1994; in the program BioEdit: Hall 1999) multiple alignment using default parameters was performed on all sequences. A partition division marker ("#") was inserted in sections of the sequences that included 6 or more invariant bases. Gaps were then removed, and a FASTA file was generated for analysis. By this procedure, the data were divided into 10 partitions, each of which included both stem and loop parts of the sequences.

2.2.4. 18S analysis parameters and taxonomic congruence

SPEARS et al. (2005) found that the 18S rDNA gene was not saturated in the Peracarida, so they did not weight transitions differently from transversions. This parameter (equal weights for transitions & transversions) was used in the current analyses, although the relative impact of transition/transversion weights should be further tested using DO. The cost of indels, however, can have a substantial effect on the results, because this cost controls how all transformations are optimised. Consequently, testing of indel parameters was required. Because 18S sequence lengths in the Peracarida vary considerably, even among closely related taxa, indels are important for assessing phylogeny. As a guideline, SPAGNA & ALVEREZ-PADILLA (2008) found that the maximum indel cost should be no more than 4, the weighting used in WILSON et al. (2009) on mtDNA data. The extreme length variation in peracarid 18S, however, means that substitution costs and indel costs must be balanced. If the cost of indels is too high (DO finds fewer indels), the obviously frequent changes in sequence length in the Peracarida may not be optimised correctly, and substitutions might be forced where an indel would explain the data more efficiently. The cost of indels, however, has a lower limit, owing to the path length inequality. This was described by WHEELER (1993) as the "triangle inequality", but it can also be understood as a transformation path. If each substitution costs more than two indel events, then DO will find all transformations to be indels and no substitutions, where each base can transform into any other base by way of one deletion plus one insertion. Thus the substitution/indel ratio has a well-defined minimum at 2:1.

The "gap opening" cost is an additional indel parameter that sets the cost of opening a block of one or more gaps to a specified value. This cost is in addition to the cost of the indel as specified by a given transformation cost matrix (VARÓN et al. 2008: 111). The gap extension cost and the gap opening cost together are the "affine" costs (AAGESEN et al. 2005; LIU et al. 2009). Although the gap opening cost is set to zero by default in POY 4, the substantial variation in the peracarid 18S sequence lengths indicates that indels might occur in blocks of multiple bases, so the gap opening cost must be included in the analysis. Topological accuracy of DO or congruence among data partitions is improved when affine indel costs are used in an analysis (AAGESEN et al. 2005; LIU et al. 2009), compared to using simple indel costs (without the "gap opening" parameter).

Ordinarily, sensitivity analysis (GIRIBET & WHEELER 1999, 2007; WHEELER et al. 2005) can assess the effectiveness of the parameters in a character congruence context. To find the best balance between substitution, indel and gap opening costs, I employed well-established knowledge in peracarid systematics. This method is similar to that used by WHEELER (1995) to evaluate differences in alignment parameters for topological congruence between morphology and molecular data. Rather than starting with a clean slate, figuratively speaking, in assessing phylogenetic patterns, well-accepted monophyletic groups were assumed at the outset as topological benchmarks for evaluating substitution and affine indel costs. For example, the monophyly of the major species-rich orders of the Peracarida, i.e., Amphipoda, Cumacea, Tanaidacea and Isopoda, is well accepted. Within the Isopoda, the monophyly of many groups also can be employed as background assumptions (as in the choice of terminals in WÄGELE 1989 and BRUSCA & WILSON 1991). One can then use this background knowledge as a benchmark on the performance of a DO parameter set (substitutions plus indel costs), and also evaluate the overall performance of the data itself. If a well-accepted monophyletic group is not found under any parameter set, then the data may be insufficient, within the methodological framework, to estimate the overall phylogeny. An analytical protocol assessed the parameters in their performance at finding monophyletic groups. Rather than simply running a predetermined range of parameters (as is typically done in sensitivity analysis of molecular data: WHEELER 1995; GIRIBET & WHEELER 1999; GIRIBET et al. 2005), this protocol seeks the parameter set that yields topologies with the highest congruence with the presumed monophyletic groups. The parameters thus chosen were then applied to the combined analysis of 18S and morphological data (see section 2.4.). The taxa that were used in the analysis and their current classification are shown in Tab. 1. The monophyletic groups that were assumed for the analysis are as follows (number of terminal taxa): Amphipoda (5); Tanaidacea (5), Apseudomorpha (2), Tanaidomorpha (3); Cumacea, (2); Isopoda (52), Phreatoicidea (2), Asellota (22), Asellidae (2), Janiroidea (18), Munnopsidae (4), Desmosomatidae (2), Oniscidea (6), Diplochaeta (Ligiidae) (3), Crinochaeta (2), Valvifera (4), Sphaeromatidae (4), Anthurida (2), Cymothoida excluding Anthurida (6), Cymothoidae (2), Cirolanidae (2), Bopyridae (2). Several groups may not be strictly monophyletic – in particular, the Cymothoida (cf. BRUSCA & WILSON 1991) – although a partial analysis of the isopods (BRANDT & POORE 2003) supported this clade. The boundaries of the Janiroidea are not completely understood (WILSON 1987), but for the taxa used in this analysis, this name represents a monophyletic clade.

The parameter sets (Tab. 2) used a range from 1 to 3 for substitutions and indels and 0–2 for gap extension costs, but not all possible combinations were

Tab. 2. Results of monophyly survey on small subunit data from taxa listed in Tab. 1. Parameters tested were: substitution cost, indel cost, gap opening cost, respectively in the 'tcm' (transformation cost matrix) header row. Transitions were equal to transversions in all runs. Each run was performed for a minimum of 12 hours, but most were run for several days to ensure that the shortest tree was found. In the cells, a score of 1 means that the group was found in a particular run, whereas 0.5 means that the group was found to be monophyletic if one branch was pruned. The monophyly score is the sum of the individual scores divided by the number of groups used for the test (21), converted to a percentage. The monophyly frequency (frequency of topological congruence with the chosen monophyletic groups) is the percentage of runs where a chosen group was found monophyletic.

Presumed monophyletic group	# taxa	tcm 110	tcm 120	tcm 130	tcm 131	tcm 111	tcm 121	tcm 210	tcm 211	tcm 212	tcm 220	tcm 310	tcm 311	tcm 320	tcm 321	tcm 331	mono phyly freq.
Amphipoda	5								1								07%
Tanaidacea	5																00%
Apseudomorpha	2																00%
Tanaidomorpha	3							1	1	1		0.5	0.5	1	0.5	1	46%
Cumacea	2							1	0.5	0.5		1	1	1		0.5	37%
Phreatoicidea	2	1				1		1	1	1		1	1	1	1	1	71%
Asellota	22																00%
Asellidae	2	1				0.5	0.5	1	1	0.5	1	1	0.5	0.5	0.5		71%
Janiroidea	18	1				1		1	1	1	1	1	1	1	1	1	50%
Munnopsidae	4	1						1	1	1	1	1	1	1			50%
Desmosomatidae	2							1	1	1		1		1	1		43%
Oniscidea	6																00%
Diplochaeta (Ligiidae)	3																00%
Crinochaeta	2	1				1		1	1	1	1	1	1		1	1	64%
Valvifera	4							1	1	1		1	0.5	1	1		46%
Sphaeromatida	4																00%
Anthurida	2								1	1			1				21%
Cymothoida	6																00%
Cymothoidae	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	93%
Cirolanidae	2	0.5	0.5	0.5	0.5	0.5	0.5			1					1	0.5	43%
Bopyridae	2	1		1	1	1	1	1	1	1	1	1	1	1	1	1	93%
Monophyly Score		36%	07%	12%	12%	29%	14%	52%	60%	57%	29%	50%	43%	45%	43%	33%	

employed owing to the "triangle equality" (Wheeler 1993). An indel cost of 4 (the maximum recommended by Spagna & Alverez-Padilla 2008) was tested initially, but produced even poorer results, so this limit was not tested fully. Other preliminary runs with costs higher than 3, for either substitutions or affine gap costs, performed extremely poorly. Each parameter set was scored for number of monophyletic nodes found. For each group, a parameter set was given a score 1 if the group was found to be monophyletic, a score of 0 if group was not found and a score of 0.5 if pruning a single internal branch resulted in monophyly of the group (i.e., the group is present but is paraphyletic owing to the inclusion of a single non-group clade or terminal). The results are summarised in Tab. 2 in the monophyly score (percent monophyletic taxa for one parameter set) and the taxon monophyly frequency (percent occurrence of monophyly for each group across all parameters).

2.2.5. POY 4 analyses

The heuristic algorithms in POY 4 (version 4.1.1) are explained in Varón et al. (2008), but only a subset of the available methods were employed. Initial runs employed a mixture of tree building, branch swapping, parsimony ratchet (Nixon 1999), tree fusing (Goloboff 1999) and tree drifting (Goloboff 1999), but consistency between runs of differing lengths was not assured. POY 4 has an automated search method that standardises these heuristic methods into one iterated routine ("search()"). The default strategy for the automated search includes many iterations of tree building, swapping using TBR, perturbation using ratchet, and tree fusing. Tab. 3 has the command file for a typical search using POY version 4.1.1. Owing to memory and time limitations, analyses were kept relatively short but still found to be effective within the time frame (single runs of 0.5–1 day). Initial runs over much longer periods evaluated the effectiveness at finding the shortest tree length for a given parameter set. Analyses were run for 12–24 hours, and the best parameters (= highest monophyly score) were run sequentially for up to 5 days. Searches using the best trees from prior runs were repeated for each parameter setting until subsequent searches found trees identical to previous runs. The final analyses under the chosen parameter set were run for 1 day using the script in Tab. 3. To show branch lengths on the best tree (Fig. 2), an implied alignment was generated using POY 4 and used in Mesquite (Maddison & Maddison 2009) with that tree.

Tab. 3. Typical command file for a search using POY version 4.1.1. Comments, which are not executed, are surrounded by brackets & asterisks. The commands are explained in VARÓN et al. (2008).

```
(* automated search 18S data, Isopoda and Peracarida *)
(* manual segmented, 4.1.1, subst=2, indel=1, gap_opening 1*)
read("Isopoda_18s_KL8.fas")
read("KL8_211_input2.tre") (* tree from previous 3 day run *)
set(log:"iso18s_KL8_211.log",root:"Gonodactylus_viridis")
set(timer:0)
transform(tcm:(2,1),gap_opening:1)
report("KL8_211.dat",data)
search (max_time:0:6:0, memory:mb:512) (* Search for 6 hours, memory 512mb *)
report("KL8_211a.tre",trees:(total)) (* provides intermediate results *)
search (max_time:0:6:0, memory:mb:512) (* Search for 6 hours, memory 512mb *)
report("KL8_211aa.tre",trees:(total))
search (max_time:0:6:0, memory:mb:512) (* Search for 6 hours, memory 512mb *)
report("KL8_211b.tre",trees:(total))
search (max_time:0:6:0, memory:mb:512) (* Search for 6 hours, memory 512mb *)
report("KL8_211bb.tre",trees:(total))
search (max_time:0:6:0, memory:mb:512) (* Search for 6 hours, memory 512mb *)
report("KL8_211c.tre",trees:(total))
search (max_time:0:6:0, memory:mb:512) (* Search for 6 hours, memory 512mb *)
report("KL8_211cc.tre",trees:(total))
search (max_time:0:6:0, memory:mb:512) (* Search for 6 hours, memory 512mb *)
select()
set (iterative:approximate:4)
swap(around)
select()
report("iso18s_KL8_211.tre",trees:(total))
report("iso18s_tre_KL8_211.ps",graphtrees:collapse)
report("iso18s_con_KL8_211.ps",graphconsensus)
report("iso18s_diag_KL8_211.txt",diagnosis)
set(nolog)
exit()
```

2.3. Morphological data

2.3.1. Terminology

Standardising the terminology for Crustacea and Malacostraca may minimise confusion regarding homologies. Additionally, considerable analytical power can be gained by creating a consistent ontology of crustacean anatomy, based on homology and standardised terminology (RAMIREZ et al. 2007; EDGECOMBE 2008). Variation in terms employed for the head limbs is substantial, even though the homologies of these parts are reasonably well known (CALMAN 1909; MCLAUGHLIN 1980). A generalised numbering system and limb spellings are used in this paper. Limbs are given Roman numerals (Th I–VIII; Per I–VII for thoracopods and pereopods, respectively) and body and limb segments are Arabic numerals. The numbering scheme (e.g., as employed by CALMAN 1909: fig. 121; WOLFF 1962) is similar to that used in other arthropods (spiders, myriapods, insects) and has the advantage that abbreviations can be used without ambiguity; e.g., "per 6" refers to the sixth pereonite, and "per VI" refers to the sixth walking leg. The spellings "pereopod" and "pereonite" are preferred over the longer spellings using "pereio-" or "peraeo-".

Crustacean taxonomists have often used the terms antenna 1 and antenna 2, maxilla 1 and maxilla 2 to describe head limbs. Used this way, the terms convey an assumption that they are part of a similar homologous series. Because each head limb represents a distinct structure, the unique terms antennula, antenna, maxillula and maxilla are preferred. Authors sometimes use the terms "antennule" and "maxillule" (e.g., CALMAN 1909), which are French in derivation, but do not use the parallel terms "antenne" and "maxille". If anatomical descriptions in English are meant to be consistent, then the terms antennula and maxillula should be used.

In the composition of the antennula and antenna, authors have used the vague term "peduncle" for the basal part of the limbs or podomeres that contain intrinsic musculature. In using this terminology, the "peduncle" is often described by counting the segments present. Because "peduncle" is not clear about the segmental homologies in the antennula and antenna, its usage should be avoided. To clarify the homologies of the individual basal podomeres (with intrinsic musculature) in the antennula and antenna, generalised terms should be employed. These details will be further discussed in the character analysis (section 2.3.3.). "Peduncle" is, however, a potentially useful term for the anatomy of the eyes as it identifies a single, distinct structure.

2.3.2. Coding morphological characters

Wherever relevant, serially homologous characters are separated. Malacostracans show a strong tendency for independent evolution of limbs on adjacent somites. As a consequence, using characters that assume serial homonomy at the outset does not recognise the fundamental evolutionary trajectories that each limb has undergone, and therefore misses useful transitions, or worse confuses evolutionary patterns among limbs. If a structure is present on multiple limbs but in various forms, then the structure is treated as separate characters on the limbs where it occurs. If, however, the structure is absent on all limbs, then this absence of the structure is treated as a single transition. Previous peracarid phylogeny studies have used a mixed coding (e.g., state 1 "form A", state 2 "form B", state 3 "absent"), which conflates the logical presence/absence characters, and the forms of the structure. Maintaining logical consistency of multistate characters (FITZHUGH 2006) was an important consideration, so that presence/absence characters were separated from structural characters (e.g., shape of exopods on thoracopods). For example, character 124 describes whether exopods are present on any of the thoracic limbs, and also considers evidence of types of absence: state 0, present; state 1, absent, not separated from endopod

embryonically (amphipod state, Wolff & Scholtz 2008); state 2, not expressed in adult, but present as embryonic rudiment (C. Wolff, pers. comm.). The following characters then describe the structure of the exopod on each limb, if the exopod is present in the adult, e.g., character 125 Thoracopod II exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary (= 1–3 articles, shorter than thoracosomite). This separation of the limbs amplifies some potentially homonomous transitions but, as *Spelaeogriphus* shows, exopods can have a different structure on different limbs (Grindley & Hessler 1971).

Detailed anatomical characters were extrapolated within monophyletic taxa where no evidence of variation was known. For example, characters from the haemovascular system are unknown for most species used in the analysis, but variation is at least known for a few family-level taxa (Wirkner & Richter 2003; Wirkner 2005; Wirkner & Richter 2007a–c, 2008, 2009). Similarly, sperm structure, which has been studied in only a few species (Cotelli et al. 1976; Johnson et al. 2001) was also extrapolated to entire clades. These fairly extensive assumptions represent hypotheses that can be tested by further anatomical investigation. The taxa chosen for this analysis are discussed in the molecular data section.

2.3.3. Character analysis

The morphological dataset (character matrix Tab. 4) was assembled using Mesquite (version 2.6, Maddison & Maddison 2009) from many sources. Brusca & Wilson (1991) provided the starting point for the character matrix, but with changes to the terminology and updates on some of the scorings. Wägele (1989) contributed additional Isopoda characters, especially for the foregut. A small dataset from Wilson (1987) was used for the Asellota. Wilson (1985) contains an unpublished analysis of the asellotan superfamily Janiroidea, from which several characters were extracted. Richter & Scholtz (2001; malacostracan characters) was used extensively. Some character scorings were taken from a presentation of G.D.F. Wilson & S. Ahyong (Crustacean conference 2001; "peracarid characters"). Additional sources are cited below in the following character list. This character list is by no means comprehensive, as detailed features within groups have not been fully surveyed. All datasets are available online (see Electronic Supplement files of this contribution).

1. Sperm body form (Pochon-Masson 1994; Wirth 1984): state 0, compact, rounded; state 1, elongate; state 2, horse-shoe shaped (e.g., Syncarida, Pochon-Masson 1994).

2. Sperm subacrosomal process, also called "pseudoflagellum" by some authors, consists of a long crystalline proteinaceous striated rod extending from acrosome, which is a general form for peracarids (Wirth 1984; Reger et al. 1979; Pochon-Masson 1994). The sperm head lacks a true flagellum. State 0, no process; state 1, elongate striated filament, weakly coiled.

3. Spermatophore. A decapod character referring to sperm bundling – a proteinaceous sheath secreted prior to exiting vas deferens; in peracarids, the spermatophore is reduced to a small proteinaceaous cap on holding the sperm bundles (Fain-Maurel et al. 1975; Cotelli et al. 1976; Pochon-Masson 1994). This is a modification of Richter & Scholtz's (2001) chr 80 in recognition that the peracarids also have a spermatophore of a different type. State 0, protein cap on acrosomes of sperm bundle; state 1, secretion surrounding sperm.

4. Sex ratio. Hermaphroditism or nonfeeding male: state 0, balanced sex ratio; state 1, skewed sex ratio, adult males non-feeding & rare. The derived feature is a rarity of males in population samples that contain mostly females and juveniles. Mature males typically have degenerate mouthparts and may have abbreviated life spans compared to females. This abundance pattern, found in tanaidaceans and hirsutiids, is sufficiently consistent in both groups to be treated as a phylogenetic character. The first reports of hirsutiids (including Ohtsuka et al. 2002) described only females. Only when a large population had been collected (Jaume et al. 2006) did the modified nonfeeding adult males come to light. This feature is already well known in the tanaidaceans (Johnson et al. 2001), across all of the groups (Gutu & Sieg 1999). Non-feeding adult males occur in some isopod groups (e.g., Hyssuridae, Wägele 1981) although not among the taxa scored here.

5. Penile papillae (penes) position (Brusca & Wilson 1991: chr 48): state 0, on coxa; state 1, on narrow medial projection of coxa; state 2, medially placed, on broad projection of coxa; state 3, medially placed on sternite (coxal projection not differentiated); state 4, medially placed, emerging from anterior pleonite.

6. Penile papillae shape, if on coxa: state 0, short, shorter than coxal width; state 1, elongate, longer than coxal width.

7. Penile papillae shape, if on sternite: state 0, distinctly separated; state 1, adjacent tapering tips; state 2, short cone, individual penes merged into single structure; state 3, elongate, extending beyond protopod of pleopod I.

8. Oostegites used for brooding embryos, whether present on any limb: state 0, absent; state 1, present.

9. Manner in which embryos are brooded: state 0, multiple oostegites; state 1, carapace; state 2, oostegal sac.

10. Oostegite on particular limbs. The number and position of oostegites varies greatly among the peracarids, which indicates that, like many other malacostracan features, the oostegite on each limb evolved independently rather than as a serially homologous unit across the limbs. Consequently, this and the following two characters identify specific oostegites on particular segments. Basal taxa of the Asellota and the Phreatoicidea have an oostegite on the maxilliped, but it is not present in many other taxa. Information on this structure is limited in many taxa. Oostegite thoracopod I: state 0, present; state 1, absent.

11. Oostegite thoracopod VI: state 0, present; state 1, absent. This oostegite is present on most isopods, but absent in Phreatoicidea and Asellota.

12. Oostegites thoracopod VIII: state 0, absent; state 1, present.

13. Oostegal brooding type (if oostegites present), where taxa use pouches or pockets in the ventral surface; HARRISON (1984): state 0, oostegites only; state 1, ventral pouches or pockets.

14. Insemination type (JOHNSON et al. 2001): state 0, external; state 1, internal

15. Spermathecal duct position: state 0, in posterior oopore; state 1, lateral on pereonite 5 in articular membrane; state 2, dorsal on pereonite 5; state 3, adjacent to oopore; state 4, in oopore anterior. Applicable only to taxa having a spermathecal duct (primarily Asellota; WILSON 1986).

16. Female insemination receptacle: state 0, deep cuticle lined oopore; state 1, shallow pocket in oopore; state 2, funnel in oopore; state 3, closed tube-funnel adjacent to oopore; state 4, spermathecal duct separate from oopore (positioned either laterally or dorsally; see WILSON 1986).

17. Spermathecal duct opening (asellotan character; WILSON 1986): state 0, shallow funnel; state 1, deep round pocket.

18. Spermathecal duct – appendix masculina tip insertion site (WILSON 1985, 1987: chr 02): state 0, female cuticular pocket or blind-ending tube adjacent to cuticular organ; state 1, no pocket or blind tube, appendix masculina inserted directly into female cuticular organ.

19. Oopore position: state 0, on coxa; state 1, adjacent to coxae; state 2, midway along sternite; state 3, anteriorly on sternite.

20. Embryonic cleavage (RICHTER & SCHOLTZ 2001: chr 85; WEYGOLDT 1994): state 0, holoblastic (total); state 1, meroblastic (superficial); state 2, mixed type.

21. Ectoteloblasts: state 0, present; state 1, absent. RICHTER & SCHOLTZ's (2001) chr 86 is separated into two characters, with the next shape character.

22. Ectoteloblast arrangement (WEYGOLDT 1994; RICHTER & SCHOLTZ 2001: chr 86): state 0, circle (19 around blastopore); state 1, in row of 12 to 25, generally but not always curved.

23. Dorsal organ (RICHTER & SCHOLTZ 2001: chr 91): state 0, present; state 1, absent.

24. Dorsal organ form (if present; RICHTER & SCHOLTZ 2001: chr 92): state 0, a non-projecting cell layer; state 1, projecting (cup-like).

25. Larval type (advanced embryos = those with thoracic limbs prior to release); revised wording of (RICHTER & SCHOLTZ 2001: chr 82): state 0, nauplius; state 1, advanced.

26. Embryo flexure (applicable only to taxa with advanced embryos: those with thoracic limbs in the egg; JOHNSON et al. 2001; WEYGOLDT 1994): state 0, dorsal; state 1, ventral.

27. Manca (first free-living juvenile stage lacks last thoracopods): state 0, absent; state 1, present.

The following circulatory system characters (28–40) have been reviewed recently (WIRKNER & RICHTER 2003: tab.1; WIRKNER 2005; WIRKNER & RICHTER 2007a–c, 2008, 2009).

28. Heart shape (a revision of RICHTER & SCHOLTZ 2001: chr 63): state 0, tubular; state 1, bulbous.

29. Heart position (BRUSCA & WILSON 1991: chr 4; heart extends to some degree into the pleotelson): state 0, thoracic; state 1, thoraco-pleonal.

30. Heart anterior border: state 0, thoracosomite 2–3; state 1, thoracosomite 4–6; state 2, posterior to thoracosomite 6.

31. Heart posterior border, if thoraco-pleonal: state 0, extending to pleonites IV–V; state 1, extending to pleonite I only.

32. Heart myocardial ultrastructure, level of T tubules (NYLUND et al. 1987; WIRKNER & RICHTER in press): state 0, branching at H level; state 1, branching at AI level.

33. Heart ostia number (varies to smaller numbers within groups): state 0, more than 2 pair; state 1, two pair; state 2, one pair.

34. Heart posterior ostia position: state 0, at same level as anterior ostia; state 1, displaced vertically relative to anterior ostia. State 1 is peculiar to Mysidacea (WIRKNER & RICHTER 2007).

35. Heart with descending cardiac arteries: state 0, present (e.g., Mysidacea); state 1, absent.

36. Descending artery connecting to ventral arteries: state 0, one; state 1, five–six; state 2, four; state 3, three.

37. Cardiac artery 5 form: state 0, descending and extending into pleotelson (e.g., Isopoda); state 1, extending into pleotelson from terminus of heart (apomorphy for Cumacea and Tanaidacea). This scoring is different than that used in WIRKNER & RICHTER (2003, 2008), which finds a similarity between the isopod and cumacean states owing to their sharing the fifth arterial branches in the pleotelson, and lack of branches in the tanaidaceans.

38. Ventral artery (either ventral or dorsal to the ventral nerves – RICHTER & SCHOLTZ 2001: chr 64): state 0,

multiple separate vessels only; state 1, neural (extending below or just above the ventral nerve cord); state 2, thoracic (found in some isopods, extending anteriorly above the ventral nerve cord).

39. Lateral stomach artery (Huber 1992): state 0, absent; state 1, present. This is assumed to be absent in all except oniscideans, tanaidaceans, thermosbaenaceans and spelaeogriphaceans.

40. Posterior dorsal aorta: state 0, present; state 1, absent.

41. Moulting (Brusca & Wilson 1991: chr 3): state 0, monophasic; state 1, biphasic.

42. Antennal gland (adult): state 0, present; state 1, reduced; state 2, absent.

43. Maxillary gland (adult): state 0, present; state 1, reduced; state 2, absent.

44. Foregut inferomedianum posteriorus (Richter & Scholtz 2001: chr 70): state 0, absent; state 1, present.

45. Foregut inferomedianum posteriorus filter grove number: De Jong-Moreau & Casanova (2001) show basal Mysida have 2–3 posterior filter grooves, and six or more may more generally describe larger malacostracans. "Many" of Richter & Scholtz (2001) is not greatly different from 8–6. State 0, six or more; state 1, two–three; state 2, one.

46. Midgut dorsal caeca (Richter & Scholtz 2001: chr 75): state 0, present; state 1, absent.

47. Foregut inferomedianum anteriorus (filterplate) shape (Isopoda – shape of the "clatri setarum anteriores"; the scoring is derived from Wägele (1989: 50, fig. 26): state 0, linear along body axis, posterior branch only; state 1, arc-shaped, posterior and lateral branches; state 2, lateral branch straight; state 3, lateral branch elongate and curved; state 4, posterior branch curved; state 5, filter setae reduced (epicaridean condition).

48. Foregut sclerite 3 (Wägele 1989: 232, chr 27): state 0, absent; state 1, present. This and the next character were not scored in non-isopodan taxa. Kobusch (1999) did not classify the peracarid taxa into the sclerite homology scheme developed by Wägele (1989), and only referred to them as "stiffenings" or "apodemes". Classifying the taxa from Kobusch's illustrations seemed subjective, so all non-isopod taxa were scored unknown ("?"). Similarly, the Janiroidea in the Asellota were mostly unknown because the foregut within the superfamily is subject to much variation, most of which is not well understood.

49. Foregut sclerites 1 and 4 (Wägele 1989: 232, chr 26): state 0, separate; state 1, merged.

50. Eyes or eye lobes present: state 0, present; state 1, absent.

51. Eye lobe shape (although some taxa may be blind, they still retain eye lobes): state 0, pedunculate; state 1, flattened; state 2, sessile; state 3, merged on midline.

52. Eye position (if present and separated; cumaceans scored inapplicable): state 0, anterior, on margin near antenna; state 1, anterolateral, separated from antenna; state 2, posterolateral, near posterior margin of head; state 3, dorsoposterior, often embedded in pereonite 1 (sphaeromatid synapomorphy).

53. Ommatidia clear zone (Fincham 1980; Richter 1999): state 0, present (superposition); state 1, absent (apposition).

54. Ommatidia crystalline cone parts (Richter 1999): state 0, tetrapartite; state 1, bipartite.

55. Ommatidia accessory cone cells nuclei (Richter 1999): state 0, proximal to cone cell; state 1, displaced distally.

56. Ommatidia retinular cells (data from Richter 1999, although not used in Richter & Scholtz 2001): state 0, eight; state 1, seven; state 2, five; state 3, three.

57. Nauplius eye (Elofsson 1965, 1992; scoring from Richter & Scholtz 2001: chr 53): state 0, present; state 1, absent.

58. Cephalisation of thoracopods. This character describes a pattern of tagmosis rather than the shape of the limb. "Cephalised" means that the limb is rotated medially and anteriorly along the body axis and rests under the head. This is a developmental trajectory that describes homologous states of evolution of the anterior three thoracopods, so each limb was not scored separately. State 0, all thoracopods similar, none cephalised; state 1, thoracopod I cephalised; state 2, thoracopods I–II cephalised; state 3, thoracopods I–III cephalised.

59. Rostral region on anterior margin of head (absent or indented vs. present or projecting): state 0, indented or sublinear; state 1, projecting.

60. Rostral type (Wilson 1987: chr 16); state 1, slightly protruding; state 2, elongate, basally narrow; state 4, basally broad, antennulae well separated.

61. Carapace type: state 0, thoracosomal; state 1, branchiostegal; state 2, limited to cephalon only. Thoracosomal means that the carapace is attached to all thoracic somites dorsally; branchiostegal means attached to only anterior thoracic somites, usually only thoracosomites 1–3.

62. Carapace size: state 0, full; state 1, extends over thoracosomite 2; state 2, extends over thoracosomite 3; state 3, extends only over thoracosomite 1 (e.g., *Mictocaris*). "Partial" means some of the thoracosomites are covered, while "full" means all thoracosomites are covered.

63. Antennula size: state 0, large, much longer than basal article of antenna, longer than head; state 1, minute, length less than basal article of antenna (oniscid synapomorphy); state 2, abbreviated, near length of head (typical of many deep-sea isopods). Although this character may appear to be *ad hoc* gap coded, the

oniscid antennula is distinct and fundamentally different from other antennulae. The second state, abbreviated, is less distinct, and less likely to be a homologous state across this dataset. Many deep-sea isopods have a short antennula, so it might be locally homologous.

64. Antennula flagellum: state 0, multiarticulate, well-developed aesthetascs; state 1, few (less than 5) articles and aesthetascs.

65. Antennula accessory flagellum: state 0, present; state 1, absent or rudimentary.

66. Antennula basal articles orientation: state 0, projecting anteriorly; state 1, projecting laterally. This is characteristic of the more derived, actively swimming isopods.

67. Antenna exopodal region: state 0, small basally-articulated scale (small projection, often with setae, articulation present; not plate-like); state 1, unarticulated spine or projection (small projection or spine with unclear articulation); state 2, without projection; state 3, scaphocerite (a large plate). Large scales, the scaphocerite (plesiomorphic), are plate-like. Rudimentary exopods are small angular projections that are often fused – never plate-like.

68. Antennal podomere articles distal to protopod (podomeres distal to protopod that may be of 1–3 articles): state 0, three articles; state 1, two articles; state 2, one article.

69. Antennal basal article (BRUSCA & WILSON 1991: chr 24): state 0, present; state 1, absent. The basal podomere is present in Asellota and Tainisopidae. In some phreatoicideans, this is defined only by several plates laterally and dorsally, and is not ring-like.

70. Mandibular molar process region (BRUSCA & WILSON 1991: chr 30): state 0, distally broad trituritative structure: state 1, elongate, thin, blade-like, slicing structure (cymothoid form); state 2, penicils (several setulate setae); state 3, thin, triangular, setose; state 4, narrow and spine-like; state 5, low, rounded, not projecting.

71. Mandibular incisor process region (BRUSCA & WILSON 1991: chr 50): state 0, robust multidentate; state 1, robust monodentate (crushing mandible as in *Ilyarachna*); state 2, robust monodentate with rasp surface (limnoriid condition); state 3, curved and spine-like (modified into recurved or hook-like, acute or subacute, piercing-slicing structure; suctorial taxa); state 4, thin multidentate.

72. Mandibular region proximal to incisor process: state 0, ridge; state 1, spine row; state 2, lamina dentata (Anthurida).

73. Mandibular lacinia mobilis on both sides but with differing morphology (peracarid synapomorphy; RICHTER et al. 2002): state 0, absent; state 1, present.

74. Mandibular right lacinia mobilis (different shape from left side): state 0, indistinguishable from spine row; state 1, separate from spine row; state 2, member of spine row but differentiated.

75. Mandibular palp (BRUSCA & WILSON 1991: chr 35): state 0, present; state 1, absent.

76. Paragnaths: state 0, single lobe; state 1, bilobed.

77. Paragnath distal process: state 0, absent; state 1, present, as in Tanaidacea and Hirsutiidae.

78. Maxillula (BRUSCA & WILSON 1991: chr 31): state 0, two endites; state 1, one endite.

79. Maxillula palp (BRUSCA & WILSON 1991: chr 32): state 0, present; state 1, absent.

80. Maxilla hooks (BRUSCA & WILSON 1991: chr 36): state 0, absent; state 1, present.

81. Maxilla palp (endopod): state 0, absent; state 1, present.

82. Maxilla endite lobes: state 0, three; state 1, two, medial lobe rudimentary; state 2, one; state 3, two, outer lobe rudimentary; state 4, vestigial or merged with ventral surface.

83. Maxilla exopod: state 0, absent; state 1, present.

84. Dorsal midline spines (WILSON 1985: chr 18): state 0, absent; state 1, present.

85. Ventral midline spines (WILSON 1985: chr 19): state 0, absent; state 1, present.

86. Tergal projections (asellotan character): state 0, absent; state 1, present.

87. Tergal projections, if any (WILSON 1985: chr 16) (Not to be confused with coxae): state 0, plate extending over coxae; state 1, spines or lappets (flattened spine), coxa may be visible in dorsal view.

88. Thoracopodal (pereopodal) tagmosis, functional groupings (BRUSCA & WILSON 1991: chr 18): state 0, none; state 1, 3:4 typically, the first 3 are prehensile or at least more robust; state 2, 4:3 a general tagmosis of the last 3 limbs projecting posteriorly, and the first 4 projecting anteriorly.

89. Thoracic coxa-basis joint, anterior pereonites (thoracopods II–V; HESSLER 1982): state 0, dicondylic; state 1, monocondylic; state 2, modified dicondylic.

90. Thoracic coxa-basis joint, posterior pereopods (thoracopods VI–VIII; HESSLER 1982): state 0, dicondylic; state 1, monocondylic; state 2, modified dicondylic (Amphipoda: dicondylic except for last limb that shows a monocondylic form that differs in muscle attachment).

91. Distal limb plane bending (merus-carpus only or that plus propodus-dactylus as in isopods via articular plate; essentially this is presence absence of articular plate on propodus): state 0, merus-carpus only (articular plate absent); state 1, merus-carpus and propodus-dactylus (articular plate present).

92. Branchial structures (position) (BRUSCA & WILSON 1991: chr 5): state 0, cephalothoracic; state 1, pleonal.

93. Coxal plate articulation (BRUSCA & WILSON 1991: chr 43 & 85): state 0, coxa ring-like, not broadened into a plate; state 1, plate with inflexible articulation; state 2, plate with flexible functional articulation.

94. Coxa intrabasal articulation, "mysidacean" form (Hessler 1982; Richter & Scholtz 2001) state 0, absent; state 1, present. The interbasal joint of the mysidaceans and euphausiaceans appears to be different from the interbasal joint of the anaspidaceans (Haupt & Richter 2008). Stygiocarids are less well known on this account, but have been similarly scored.

95. Thoracopodal coxa form (Haupt & Richter 2008): state 0, robust & solid; state 1, open ring-like structure (peracarid synapomorphy).

96. Thorax-coxa articulation relative to body axis (Hessler 1982; Haupt & Richter 2008): state 0, transverse; state 1, parallel.

97. Thoracopodal coxae, lateral margin: state 0, ring-like, occupying only part of lateral margin; state 1, broad, occupying most of lateral margin; state 2, broad, occupying all of lateral margin, projecting ventrally.

98. Thoracopodal coxae, ventromedial margin form: state 0, elongate arc covering most of ventrolateral margin (e.g., Cirolanidae or Aegidae; these also have an elongate channel, not shown in Wägele 1989: fig. 26); state 1, extending onto sternite as narrow or triangular plates; state 2, platelike, replacing sternite; state 3, simple arc only part of ventrolateral margin.

99. Thoracopod I coxa articulation with body: state 0, present; state 1, absent.

100. Thoracopod I endites: state 0, none; state 1, basis; state 2, basis + ischium; state 3, coxa.

101. Thoracopod I epipod: state 0, present; state 1, absent.

102. Thoracopod I epipod form (scored inapplicable if apparently absent): state 0, bailer; state 1, gill; state 2, plate.

103. Thoracopod I exopod (scored inapplicable if apparently absent): state 0, styliform, flagellate; state 1, elongate lamellar; state 2, lamellar-gill; state 3, rudimentary.

104. Thoracopod I maxillipedal endite coupling hooks (receptaculi) (Brusca & Wilson 1991: chr 39): state 0, present; state 1, absent.

105. Thoracopod I maxillipedal basis medial margins (maxillipeds with structures for attachment to host): state 0, separated; state 1, joined, at least partially.

106. Thoracopod III (Per II in isopods) cephalisation form. The limb can function as a mouthpart, with the coxa ventral, rather than lateral; a prehensile limb may be held anteriorly, still has coxa positioned laterally, or it may be a robust limb that is larger than more posterior limbs (cf. tanaidaceans and hirsutiids). "Mouthpart" is a general form of cephalisation, as seen in Cumacea. State 0, walking leg; state 1, mouthpart; state 2, prehensile (either subchelate or chelate); state 3, robust stronger than posterior limbs with robust setae.

107. Thoracopods III–VIII (Per II–VII in isopods) prehensile (if any) (Brusca & Wilson 1991: chr 65): state 0, ambulatory; state 1, some prehensile or hook-like (II–III, or II–VII).

108. Thoracopods III–VII (Per II–VII in isopods) prehensile (which ones, if prehensile): state 0, thoracopods III–IV; state 1, all; state 2, thoracopods III only (amphipod state).

109. Thoracopodal (Per II–VII) ischium length and articulation: state 0, short (not much longer than wide to shorter than wide), often robust, minimal basis-ischium flexure in limb plane (see Hessler 1982: fig. 17 for Cumacea); state 1, elongate (much longer than wide), major basis-ischium flexure in limb plane (see Hessler 1982: fig. 20); state 2, elongate, minor basis-ischium flexure in limb plane (as for *Palaemon* in Hessler 1982). This new character recognises three different articulations and sizes of the ischium among the peracarids. Most peracarids have a short ischium with minimal flexure at the basis-ischium joint, whereas isopods have an elongate ischium that shows substantial flexure at the basis-ischium joint. Decapods have a third kind of ischium where ischium is long, but the flexure is minimal. Tanaidaceans and cumaceans have an exceptionally short ischium, although this was not scored separately. Thermosbaenacea have an elongate ischium with some ability to flex, but the basis-ischium together are quite different from other peracarids, owing to the robust basis (e.g., *Thermosbaena juriaani* in Wagner 1994: figs. 104–109); consequently, *Thermosbaena* was scored 0/1. Of all the peracarids, only the Spelaeogriphacea have an isopod-like leg, so this state is not unique to the Isopoda. Stomatopods have a peculiar composition to the walking legs, including the presence of a precoxa, so this was scored inapplicable.

110. Thoracopodal (Per II–VII) articular plate on distal margin of propodus (isopod synapomorphy): state 0, present; state 1, absent.

111. Thoracopodal (Per II–VII) dactyli accessory seta (Wilson 1985: chr 20). State 0, absent; state 1, present.

112. Thoracopodal (Per II–VII) 1 dactyli accessory seta, if present (Wilson 1985: chr 21): state 0, claw-like; state 1, simple.

113. Thoracopodal (Per II–VII) dactylus third claw (discussed in Wilson 1987 as an apomorphy of the Janiridae): state 0, absent; state 1, present as seta or claw.

114. Thoracopodal (Per II–VII) dactyli posterior (ventral) claw, if present (size) (Wilson 1985: chr 22): state 0, smaller than dorsal claw; state 1, as large as dorsal claw.

115. Thoracopodal (pereopodal) dactylus distal sensillae (Wilson 1989: chr B): state 0, not enclosed by claws; state 1, enclosed by claws.

116. Thoracopodal (Per II–VII) dactylus posterior claw (if present) cross-section shape (Wilson 1985: chr 24): state 0, rounded; state 1, flattened.

117. Thoracopod II (Per I) cephalisation (with two states: the limb can function as a mouthpart, with the coxa ventral, rather than lateral; a prehensile limb may be held anteriorly and still has the coxa positioned laterally): state 0, walking leg; state 1, mouthpart; state 2, prehensile either subchelate or modified chelate; state 3, chelate.

118. Thoracopod II (Per I) opposing segments – major rotation (WILSON 1987: chr 14): state 0, dactyl vs. propodus; state 1, dactyl vs. propodus and propodus vs. carpus; state 2, propodus vs. carpus.

119. Thoracopod II (Per I) carpus shape (JUST & WILSON 2004). The thoracopod II (Per I of isopods) carpus can be short and triangular, carpus and propodus with restricted articulation that cannot oppose one another to participate in grasping, or carpus trapezoidal, with an articulation between carpus and propodus that is only partially restricted and can oppose one another by means of strong spine-like setae or spines on carpus, or elongate (not triangular) where the carpus and the propodus have a free articulation and can oppose one another to participate in grasping. State 0, elongate, oval; state 1, trapezoidal; state 2, triangular.

120. Thoracopod II (Per I) dactylar claws. State 0, one; state 1, two.

121. Thoracopod II (Per I dactylus) (WILSON 1985: chr 13): state 0, long – dactylus and propodus with free articulation and can oppose one another to participate in grasping; state 1, pereopod I dactylus short – dactylus and propodus with restricted articulation, participate in grasping as a unit.

122. Pereopod IV in male (whether modified for coupling): state 0, similar to female pereopod (i.e., not shortened and prehensile); state 1, shortened and prehensile. Basal Asellota (Asellidae, Janiridae and scattered other taxa) and practically all Phreatoicidea have precopula (mate guarding) wherein the adult male will grasp and carry a subadult female until its maturation and the posterior section of its body is moulted. The pereopod IV is primary limb for carrying the female, and is substantially modified for grasping, is shorter and often more robust. Where mate guarding is not practised, the limb resembles that of the female.

123. Pereopods V–VII (thoracopods VI–VIII) differentiated (discussed in WILSON 1989): state 0, similar to other pereopods; state 1, carpus propodus broad, fringing plumose setae (Munnopsidae); state 2, carpus & propodus fringing distally setulate setae (Desmosomatidae).

Thoracic exopods. The scoring of exopods on the limbs of peracarids has received many different types of scoring, but G.D.F. Wilson & S. Ahyong (Crustacean Conference presentation, 2001) found that many peracarids have unique compositions of exopods on the thoracic limbs. Amphipods and isopods lack them entirely, presumably as single but independent evolutionary events. In the scheme below, the presence/absence characters are separated from the exopod form characters, and each thoracopodal form is scored separately. If the exopod is absent on a particular limb, its state is scored as inapplicable ("-").

124. Thoracic limb exopods (if any on thoracopods II–VIII): state 0, present; state 1, absent, not separated from endopod embryonically (see WOLFF & SCHOLTZ 2008); state 2, not expressed in adult, but embryonic rudiment present (Carsten Wolff, pers. comm., poster at Crustacean Phylogeny Conference 2008). Our knowledge of embryonic development is incomplete for most peracarids, although presence of exopods in most taxa combined with the late exopodal suppression in *Kalliapseudes* (as illustrated by LANG 1956) shows that suppression seems to be a common developmental trajectory, whereas the amphipod condition appears to be unique.

125. Thoracopod II exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary. Elongate lamellar (2) defined as having large basal segment and flattened, conjoint distal article(s) – see Spelaeogriphacea (GORDON 1957). Lamellar and gill states (1) are thought to be synonymous. Rudimentary (3) means 1–3 articles that are distinctly shorter than basis, as in the tanaidacean group Apseudomorpha.

126. Thoracopod III exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary.

127. Thoracopod IV exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary.

128. Thoracopod V exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary.

129. Thoracopod VI exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary.

130. Thoracopod VII exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary.

131. Thoracopod VIII exopod: state 0, styliform, flagellate; state 1, lamellar-gill; state 2, elongate lamellar; state 3, rudimentary.

132. Thoracic limb epipods (if any on thoracopods II–VIII): state 0, present; state 1, absent.

133. Epipod form, if present: state 0, lateral; state 1, posteromedial.

134. Pleonite pleurae, projecting ventrally: state 0, margin not projecting; state 1, pleonites 1–5; state 2, pleonites 1–3; state 3, pleonites 3–5; state 4, pleonites 2–3, merged.

135. Pleonal musculature: state 0, non-spiral; state 1, caridoid, spiral.

136. Pleon form: state 0, broad, flat (broader than deep); state 1, narrow, vaulted (synapomorphy of the Phreatoicidea); state 2, broad, vaulted.
137. Dorsal pleonite number (derived from Brusca & Wilson 1991: chr 80). Although many isopods have lost the medial articulation of the pleonites, they are still visible at least laterally: state 0, five; state 1, three (pls. 1–3); state 2, two (pls. 1–2); state 3, one (pl. 1); state 4, none laterally distinct.
138. Pleonites width compared to pleotelson: state 0, subequal; state 1, narrower (apomorphy of some Asellota); state 2, broader.
139. Pleonite 5 length (Brusca & Wilson 1991: chr 73): state 0, subequal to more anterior pleonites; state 1, longer than other pleonites; state 2, shorter and narrower than other pleonites.
140. Pleotelson posterolateral marginal spines: state 0, absent; state 1, present. This character is commonly found among the Asellota, particularly the deep-sea taxa such as Desmosomatidae.
141. Pleotelson posterolateral marginal spines shape: state 0, single denticle near uropods; state 1, denticle row anterior to uropods; state 2, several elongate spines; state 3, elongate dorsally placed spines.
142. Pleotelson articulation: state 0, only moderate flexion possible; state 1, strongly hinged, with powerful internal muscles (phreatoicidean apomorphy; Erhard 1998).
143. Telson articulation: state 0, present; state 1, absent.
144. Telson region shape (Brusca & Wilson 1991: chr 58, additional information from Knopf et al. 2006) state 0, longer than wide; state 1, reduced or effectively absent; state 2, broad (pl 6 & telson triangular); state 3, anal segment, telson not expressed.
145. Anus position on telson: state 0, proximal, ventral; state 1, distal, posterior.
146. Anus position with respect to pleopodal chamber (Wilson 1987: chr 18): state 0, external; state 1, internal.
147. Pleopodal swimming: state 0, present; state 1, absent (the pleopods can be present but are not used for swimming). An asellotan synapomorphy, although swimming is absent elsewhere for other reasons, e.g., Thermosbaenacea, where the first two pleopods are present, but only as rudiments. Swimming is limited in the Phreatoicidae, although the Amphisopidae can still swim poorly. Taxa with highly reduced pleopods in all stages were scored inapplicable.
148. Opercular pleopods (defined as the pleopod that is largest and covering more posterior pleopods): state 0, none, all similar size; state 1, pl III; state 2, male pl I, female pl II; state 3, male pl I–II, female pl II; state 4, pl I.
149. Pleopods epipodal gills (epipodite-like accessory lamellae or other processes on pleopods): state 0, absent; state 1, present.
150. Pleopod protopods shape: state 0, elongate; state 1, broad, flattened; state 2, rudimentary, without articulation; state 3, quadrangular, approximately length subequal width.
151. Pleopods I–V homonomy (although homonomous, males may have an appendix masculina): state 0, all similar in form (e.g., Phreatoicidea); state 1, pleopods individually specialised (e.g., Asellota).
152. Pleopod exopods (if all are similar): state 0, present; state 1, absent.
153. Pleopod exopod shape (if present, and all similar): state 0, styliform; state 1, broad, flattened; state 2, flagellate, multiarticulate; state 3, reduced; state 4, flattened multiarticulate.
154. Pleopod endopods (if all are similar): state 0, present; state 1, absent.
155. Pleopods endopod shape (if present, and all similar): state 0, styliform; state 1, broad, flattened; state 2, flagellate, multiarticulate; state 3, reduced; state 4, flattened multiarticulate.
156. Pleopods I–III rami shape: state 0, styliform, flagellate; state 1, broad, flattened; state 2, reduced; state 3, flattened flagellate.
157. Pleopod IV rami shape: state 0, styliform; state 1, flattened, few articles; state 2, flagellate, multiarticulate; state 3, reduced; state 4, flattened flagellate; state 5, uropod 1 (e.g., Amphipoda).
158. Pleopod V rami: state 0, two; state 1, one. When only one ramus is present on the last pleopod, deciding between exopod and endopod may be equivocal.
159. Pleopod V rami shape: state 0, styliform; state 1, flattened, few articles; state 2, flagellate, multiarticulate; state 3, reduced; state 4, flattened flagellate; state 5, uropod 2 (e.g., Amphipoda).
160. Pleopod I appendix masculina: state 0 (e.g., Oniscidea Crinochaeta; Schmidt 2008), present; state 1, absent.
161. Female pleopod I: state 0, present; state 1, absent (apomorphy of the Asellota).
162. Male pleopods I size (within the Asellota): state 0, less than half pleon length (e.g., Asellidae, Stenasellidae, Stenetriidae); state 1, greater than half pleon length (janiroidean families).
163. Male pleopods I rami basal articulation with protopod (in the Asellota: J. Just, pers. comm., indicates that expression is absent on the dorsal side, but it not illustrated in many species): state 0, present; state 1, absent.
164. Male pleopod I distal tips dorsolateral stylet guides (character limited to the Asellota): state 0, absent; state 1, present.

165. Male pleopods I basal segments (WILSON 1985: chr 03): state 0, separate medially; state 1, joined medially.
166. Male pleopods I distal segments (character limited to the Janiroidea, WILSON 1985: chr 04): state 0, separate medially without medial sperm tube; state 1, joined medially with medial sperm tube.
167. Female pleopod II form (character limited to the Asellota): state 0, biramous; state 1, uniramous; state 2, merged into one piece.
168. Male pleopod II length (character limited to the Asellota): state 0, less than half pleon length; state 1, greater than half pleon length.
169. Male pleopod II protopod size (character limited to the Asellota): state 0, distinctly shorter than rami; state 1, elongate and robust, longer than exopod.
170. Male pleopod II endopod position on protopod: state 0, apical; state 1, subapical; state 2, medial. This can also be interpreted using angle of insertion: 0 = parallel to body axis; 1 = at angle to body axis; 2 = normal to body axis.
171. Male pleopod II appendix masculina: state 0, present; state 1, absent.
172. Male pleopod II endopod form (character limited to the Asellota): state 0, linear; state 1, geniculate.
173. Male pleopod II geniculate endopod: state 0, articles free; state 1, articles fused.
174. Male pleopod II appendix masculina type: state 0, grooved rod; state 1, complex grooved rod; state 2, distal pocket; state 3, longitudinal fold; state 4, distal groove; state 5, closed tube.
175. Male pleopod II endopod appendix masculina shape (WILSON 1985: chr 09): state 0, thick distally, not stylet-like; state 1, stylet-shaped.
176. Male pleopod II endopod appendix masculina grooves or tubes (WILSON 1985: chr 11): state 0, with open groove or pocket; state 1, with tube opening only on distal tip.
177. Male pleopod II appendix masculina groove start: state 0, proximal; state 1, medial; state 2, subdistal.
178. Male pleopod II endopod proximal article shape (character limited to the Asellota): state 0, not modified; state 1, ridge; state 2, horn.
179. Male pleopod II exopod position on protopod (character limited to the Asellota): state 0, apical; state 1, subapical-medial.
180. Male pleopod II exopod form (character limited to the Asellota): state 0, both articles flat; state 1, distally flat only; state 2, narrow, thick (not flat), longer than wide; state 3, stout, length near width; state 4, rudimentary.
181. Male pleopod II exopod articulation between articles (WILSON 1985: chr 07): state 0, present (2 articles); state 1, absent (1 article).
182. Male pleopod II exopod hook on distal article: state 0, absent; state 1, present.
183. Pleopod III exopod segments: state 0, two, suture present; state 1, one, suture absent.
184. Pleopod III endopod segments (WILSON 1985: fig. 4.17, chr 31): state 0, one, suture absent; state 1, two, suture present.
185. Pleopod III endopod plumose setae (WILSON 1985: chr 31): state 0, none; state 1, more than three distal; state 2, three distal setae. Many janiroidean isopods have specifically 3 elongate plumose setae on the pleopod III endopod, often in a well-defined pattern (two medial and one lateral). Those taxa that have more than 3 plumose setae will often have many more, and will lack the particular patterning of the setae. Other isopods lack elongate plumose setae on the margin of endopod III.
186. Pleopod III exopod width (WILSON 1985: chr 29): state 0, broader than endopod; state 1, same width as endopod; state 2, narrower than endopod.
187. Pleopod III exopod length (WILSON 1985: chr 30): state 0, longer than endopod; state 1, near same length as endopod; state 2, distinctly shorter than endopod.
188. Pleopod IV exopod articles: state 0, two; state 1, one.
189. Pleopod IV exopod width: state 0, broad, length near width; state 1, narrow, length much greater than width.
190. Pleopod IV exopod plumose setae (basal taxa have many setae around exopodal margin, but reducing to few or none on the tip): state 0, many, distal and lateral; state 1, many, distal article only; state 2, one–three distally; state 3, no setae.
191. Uropod position on pleotelson (BRUSCA & WILSON 1991: chr 55; modified; if telson free, state is 0 typically): state 0, anteroventral margin; state 1, posteroventral surface, in groove or channel; state 2, posterior margin; state 3, above posterior margin on dorsal surface (e.g., *Dendromunna*).
192. Uropod protopod axis of rotation (relative to body axis; corrected & simplified from BRANDT & POORE 2003): state 0, perpendicular to plane of body axis (plesiomorphic state, allows movement in horizontal plane along medial-lateral axis); state 1, in plane of body axis (derived state, allows movement along a dorsal ventral axis); state 2, articulation suppressed (protopod fixed).
193. Uropods forming operculum for pleopodal chamber: state 0, not modified; state 1, opercular (valviferan synapomorphy).
194. Uropod rami orientation: state 0, exopod lateral to endopod; state 1, exopod dorsal to endopod.
195. Uropod rami relative position (if both are present): state 0, adjacent; state 1, exopod proximal, endopod distal, distinctly separated (anthuridean state); state 2, exopod distal, endopod proximal, distinctly separated (oniscid state).

196. Uropod exopod: state 0, present; state 1, absent. In isopods, the smaller exopod is considered absent if only one ramus is present.
197. Uropod exopod segments: state 0, one article; state 1, two articles. No peracarid is known to have more than 2 articles in the uropodal exopod.
198. Uropod exopod ramus (shape): state 0, rod-like, rounded tip; state 1, robust, spine-like; state 2, flattened.
199. Uropod endopod (present/absent): state 0, present; state 1, absent.
200. Uropod endopod proximal articulation: state 0, present; state 1, absent.
201. Uropod endopod segments (Brusca & Wilson 1991: chr 59): state 0, two articles; state 1, one article; state 2, three or more articles. State 2 is seen in Cumacea, Tanaidacea and Hirsutiidae.
202. Uropod endopod ramus (shape) (Brusca & Wilson 1991: chr 57): state 0, rod-like, rounded tip; state 1, robust, spine-like; state 2, flattened.

2.3.4. Morphological data analysis

The morphological data were analysed using PAUP* version 4.0b10 (Swofford 1998), with all character transitions set to unordered, Fitch (1971) parsimony. Starting trees were obtained via random stepwise addition. A treespace sampling protocol (Just & Wilson 2004) was used, including 10,000 samples of 3 trees (PAUP* commands: hsearch addseq=random nchuck=3 chuckscore=1 nreps=10000 randomize=trees; hsearch start=current nchuck=0 chuckscore=0). A strict consensus was obtained using PAUP* to assess congruence of the phylogenetic hypotheses. To assess variation in their topologies, the most distant tree from an arbitrary tree (tree 1) was found using PAUP* symmetric distance tree metric in the treedist and filter trees commands. One of the most distant trees found was then used as the root to find other most distant trees. These trees were chosen for comparison. Jackknife (Farris et al. 1996) branch support values were obtained for the combined dataset based on 1000 randomised samples of the data (PAUP* settings for each iteration: hsearch addseq=random nchuck=10 chuckscore=1 nreps=10 randomize=trees). The jackknife method used 33% characters deleted from each of the 1000 replicates. Bremer support was calculated using a script generated by MacClade 4.0 (Maddison & Maddision 2000) and analysed in PAUP*.

2.4. Combined analysis

2.4.1. Weighting strategy

The costs (= tree lengths) of the two datasets (18S; morphology) are substantially different. Morphology (202 static characters) contributed approximately 1.5% to the cost of a combined unweighted dataset. Several higher weightings of the morphology relative to the molecular data were tried, but the equally weighted data are reported here. In the current case, the sequence data matrix used a transformation cost matrix that gives substitutions a cost of 2, indels a cost of 1 and gap opening events a cost of 1, as determined by the monophyly survey (Tab. 2). Equal weightings for all transformations were achieved by assigning a weight of 0.5 to the molecular matrix, and a weight of 1 to all morphological characters. Down weighting the molecular matrix was preferred because the weighting is applied to all dynamic transitions equally. Two other possible approaches to equal weights were not employed in this analysis. Under the paradigm that each dynamic homology character is a fragment that transforms during evolution, the dynamic characters could be down weighted so that their contribution would equal to that of each of the static morphological characters. A second approach to equal weighting would down weight the dynamic characters so that their contribution to the cost of the tree exactly equals that of the static characters. Although these alternative weightings were not tried for this analysis, both might result in the dynamic molecular characters being swamped by the static morphological characters, so that such analyses might resemble the morphological tree only.

2.4.2. Analyses

The 18S data were analysed as 10 fragments as explained in section 2.2. The morphological data were converted to a Hennig86/Nona format (see Goloboff et al. 2008 and references cited therein) for input into POY 4. The best dynamic parameter set (substitutions = 2, indels = 1, gap opening = 1; see Tab. 2) and weights as explained above was used to analyse 18S and morphological data simultaneously. The relevant script for the iterated combined analysis runs is shown in Tab. 5. Bremer support was calculated in POY 4.1.1 using a script described in Varón et al. (2008).

Tab. 4. Morphological data matrix of 75 taxa listed in Tab. 1 and 202 morphological characters. Polymorphism is indicated as follows: A = states 0 and 1; B = states 0 and 2; C = states 1 and 2. See section 2.3.3. for character analysis.

Character #	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
	0	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**3**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**4**	**5**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**
Gonodactylus viridis	0	0	0	0	0	0	-	0	-	-	-	-	-	1	-	-	-	-	0	1	1	0	1	-	1	1	0	0	1	0	0	0	0	0	0	1	-	1	0	?	0	0	0	1	0	0	0	?	?	0
Penaeus semisulcatus	0	0	1	0	0	0	-	0	-	-	-	-	-	0	-	-	-	-	0	0	1	0	1	-	0	1	0	1	0	0	-	0	0	0	0	0	-	1	0	0	0	0	2	1	0	0	0	?	?	0
Euphausia superba	0	0	1	0	3	-	-	0	-	-	-	-	-	0	-	-	-	-	0	0	0	0	1	-	0	1	0	1	0	0	-	0	0	0	0	0	-	1	0	0	0	0	0	0	-	0	0	?	?	0
Anaspides tasmaniae	2	?	?	0	3	-	-	0	-	-	-	-	-	0	-	-	-	-	0	0	0	0	0	0	1	1	0	0	1	0	0	0	2	-	0	0	-	1	0	0	0	2	0	0	-	0	0	?	?	0
Neognathophausia ingens	1	1	0	0	0	0	-	1	0	1	0	1	0	0	-	-	-	-	0	1	0	1	0	1	1	1	0	0	0	0	-	0	0	1	0	0	-	1	0	0	0	0	0	1	0	0	0	?	?	0
Heteromysis formosa	1	1	0	0	0	0	-	1	0	1	0	1	0	0	-	-	-	-	0	1	0	1	0	1	1	1	0	0	0	0	-	0	1	1	0	0	-	1	0	0	0	0	2	1	1	0	0	?	?	0
Stygiomysis holthuisi	1	1	0	0	0	0	-	1	0	1	0	1	0	0	-	-	-	-	0	1	0	1	0	1	1	1	0	0	0	0	-	0	0	1	0	0	-	1	0	0	0	0	2	1	1	0	0	?	?	0
Thetispelecaris remex	?	?	?	1	3	-	0	1	B	1	0	0	0	?	-	-	-	-	1	?	?	?	?	?	1	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	?	?	?	?	?	?	1
Ingolfiella tabularis	1	1	0	0	3	0	2	1	0	1	0	0	0	0	-	-	-	-	0	0	1	-	0	0	1	1	0	0	0	0	-	0	0	0	0	3	-	-	0	0	0	0	2	1	1	0	0	?	?	0
Arrhis phyllonyx	1	1	0	0	3	0	2	1	0	1	0	0	0	0	-	-	-	-	0	0	1	-	0	0	1	1	0	0	0	0	-	0	0	0	0	3	-	-	0	0	0	0	2	1	1	0	0	?	?	0
Protella gracilis	1	1	0	0	3	0	2	1	0	1	0	0	0	0	-	-	-	-	0	0	1	-	0	0	1	1	0	0	0	0	-	0	0	0	0	3	-	-	0	0	0	0	2	1	1	0	0	?	?	0
Hyperietta stephenseni	1	1	0	0	3	0	2	1	0	1	0	0	0	0	-	-	-	-	0	0	1	-	0	0	1	1	0	0	0	0	-	0	0	0	0	3	-	-	0	0	0	0	2	1	1	0	0	?	?	0
Gammarus troglophilus	1	1	0	0	3	-	2	1	0	1	0	0	0	0	-	-	-	-	0	0	1	-	0	0	1	1	0	0	0	0	-	0	0	0	0	3	-	-	0	0	0	0	2	1	1	0	0	?	?	0
Tethysbaena argentarii	1	1	0	0	0	0	-	0	1	-	-	-	-	?	-	-	-	-	0	2	0	0	0	0	1	1	1	?	0	0	-	0	2	-	1	-	-	-	1	1	0	0	1	1	1	1	0	?	?	0
Mictocaris halope	1	1	0	0	0	-	0	1	0	1	0	0	0	0	-	-	-	-	0	?	?	?	?	?	1	0	1	0	0	0	-	0	2	-	1	-	-	-	0	1	?	?	?	1	2	1	1	?	?	0
Spilocuma salomani	1	1	0	0	0	0	-	1	0	1	0	0	0	0	-	-	-	-	0	1	0	1	0	1	1	0	1	0	0	0	-	0	2	-	0	1	1	-	0	1	0	2	0	1	2	1	0	?	?	0
Diastylis sculpta	1	1	0	0	0	0	-	1	0	1	1	0	0	0	-	-	-	-	0	1	0	1	0	1	1	0	1	0	0	0	-	0	2	-	0	1	1	-	0	1	0	2	0	1	2	1	0	?	?	0
Spelaeogriphus lepidops	1	1	0	0	0	1	-	1	0	0	0	0	0	0	-	-	-	-	0	1	?	1	?	?	?	?	0	0	0	0	-	0	1	0	1	-	-	-	1	1	0	2	1	1	2	1	0	?	?	0
Apseudes bermudeus	1	1	0	1	3	-	2	1	2	1	0	0	0	0	-	-	-	-	1	2	0	1	1	-	1	0	1	0	0	0	-	0	1	-	0	1	1	-	1	1	0	2	0	1	2	1	0	?	?	0
Kalliapseudes sp.	1	1	0	1	3	-	2	1	2	1	0	0	0	0	-	-	-	-	1	2	0	1	1	-	1	0	1	0	0	0	-	0	1	-	0	1	1	-	1	1	0	2	0	1	2	1	0	?	?	0
Leptochelia sp.	1	1	0	1	3	-	2	1	2	1	0	0	0	0	-	-	-	-	1	2	0	1	1	-	1	0	1	0	0	0	-	0	1	-	0	1	1	-	1	1	0	1	0	1	2	1	0	?	?	0
Paratanais malignus	1	1	0	1	3	-	2	1	2	1	0	0	0	0	-	-	-	-	1	2	0	1	1	-	1	0	1	0	0	0	-	0	1	-	0	1	1	-	1	1	0	1	0	1	2	1	0	?	?	0
Tanais dulongii	1	1	0	1	3	-	2	1	2	1	0	0	0	0	-	-	-	-	1	2	0	1	1	-	1	0	1	0	0	0	-	0	1	-	0	1	1	-	1	1	0	1	0	1	2	1	0	?	?	0
Paramphisopus palustris	1	1	0	0	0	1	-	1	0	0	1	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	0	-	0	1	1	1	0	1	2	1	0	0	0	0
Colubotelson thomsoni	1	1	0	0	0	1	-	1	0	0	1	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	0	-	0	1	1	1	0	1	2	1	0	0	0	0
Stenasellus racovitzai	1	1	0	0	0	1	-	1	0	0	1	0	0	1	0	2	1	0	1	1	0	1	0	1	1	0	1	0	1	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1	2	1	0	0	0	1
Caecidotea racovitzai	1	1	0	0	3	-	0	1	0	0	1	0	0	1	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1	2	1	0	0	0	0
Asellus aquaticus	1	1	0	0	3	-	0	1	0	0	1	0	0	1	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1	2	1	0	0	0	0
Stenetriid sp.	1	1	0	0	3	-	0	1	0	1	1	0	0	1	0	1	1	0	3	1	0	1	0	1	1	0	1	0	1	1	1	1	1	0	0	1	0	?	0	1	1	1	0	1	2	1	0	0	0	0
Janira maculosa	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	1	1	0	1	0	1	1	0	1	0	1	2	1	1	1	0	0	1	0	0	0	1	1	1	0	1	2	1	0	?	?	0
Joeropsis coralicola	1	1	0	0	3	-	2	1	0	1	1	0	0	1	2	4	0	1	2	1	0	1	0	1	1	0	1	0	1	2	1	1	1	0	0	1	0	?	0	1	1	1	0	1	2	1	0	?	?	0
Iathrippa trilobatus	1	1	0	0	3	-	2	1	0	0	1	0	0	1	1	4	1	1	1	1	0	1	0	1	1	0	1	0	1	2	1	1	1	0	0	1	0	0	0	1	1	1	0	1	2	1	0	?	?	0
Haploniscus nudifrons	1	1	0	0	3	-	2	1	0	1	1	0	0	1	2	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Acanthaspidia drygalskii	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Neojaera antarctica	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	0
Thylakogaster sp.	1	1	0	0	3	-	2	1	0	1	1	0	0	1	2	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Dendromunna sp.	1	1	0	0	3	-	2	1	0	1	1	0	0	1	2	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Eurycope sarsi	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Ilyarachna antarctica	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Munnopsis typica	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Betamorpha fusiformis	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Mesosignum cf. *usheri*	1	1	0	0	3	-	2	1	0	1	1	0	0	1	2	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Macrostylis sp.1	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Janirella sp.	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Ischnomesus sp.	1	1	0	0	3	-	2	1	0	1	1	0	0	1	2	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Eugerdella natator	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Eugerda sp.	1	1	0	0	3	-	2	1	0	1	1	0	0	1	1	4	0	1	2	1	0	1	0	1	1	1	1	0	1	2	1	1	1	0	0	?	0	?	0	1	1	1	0	1	2	1	0	?	?	1
Zonophryxus quinquedens	1	1	0	0	3	-	2	1	0	0	0	0	0	1	-	0	-	-	0	0	0	1	0	1	1	0	1	0	1	2	1	1	1	0	1	-	-	-	-	1	1	1	0	1	?	?	5	?	?	1
Probopyrus pacificiensis	1	1	0	0	3	-	2	1	0	0	0	1	0	1	-	0	-	-	0	0	0	1	0	1	1	0	1	0	1	2	1	1	1	0	1	-	-	-	0	1	1	1	0	1	2	1	5	?	?	0
Hemiarthrus abdominalis	1	1	0	0	3	-	2	1	0	0	0	1	0	1	-	0	-	-	0	0	0	1	0	1	1	0	1	0	1	2	1	1	1	0	1	-	-	-	0	1	1	1	0	1	2	1	5	?	?	0
Paragnathia formica	1	1	0	0	3	-	2	1	0	1	-	0	0	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	2	0	1	C	-	0	?	?	?	0	1	1	1	0	1	2	1	?	?	?	0
Riggia paranensis	1	1	0	0	3	-	2	1	0	1	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	2	0	1	2	0	0	2	-	0	0	1	1	1	0	1	2	1	3	1	1	0
Anilocra physodes	1	1	0	0	3	-	2	1	0	1	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	2	0	1	2	-	0	2	-	0	0	1	1	1	0	1	2	1	3	1	1	0
Cymodoce tattersalli	1	1	0	0	3	-	2	1	0	1	1	0	1	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	2	-	0	?	1	1	1	0	1	2	1	3	1	1	0
Campecopea hirsuta	1	1	1	0	3	-	2	1	0	1	1	0	1	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	2	-	0	?	1	1	1	0	1	2	1	1	1	1	0
Sphaeroma serratum	1	1	0	0	3	-	2	1	0	1	1	0	1	1	-	0	-	-	0	1	0	1	0	1	0	0	0	0	1	1	0	1	1	0	0	2	0	0	?	1	1	1	0	1	2	0	3	1	1	0
Cassidinidea sp.	1	1	0	0	3	-	2	0	0	1	1	0	1	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	2	-	0	?	1	1	1	0	1	2	1	1	1	1	0
Limnoria quadripunctata	1	1	0	0	3	-	0	1	0	?	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	1	0	1	C	-	0	1	0	?	0	1	1	1	0	1	2	1	1	1	1	0
Eurydice pulchra	1	1	0	0	3	-	2	1	0	?	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	2	0	1	1	0	0	2	-	0	0	1	1	1	0	1	2	1	3	1	1	0
Excorallana quadricornis	1	1	0	0	3	-	2	1	0	?	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	2	0	1	1	0	0	2	-	0	0	1	1	1	0	1	2	1	3	1	1	0
Natatolana albinota	1	1	0	0	3	-	2	1	0	?	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	2	0	1	1	0	0	2	-	0	0	1	1	1	0	1	2	1	3	1	1	0
Aega antarctica	1	1	0	0	3	-	2	1	0	?	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	2	0	1	2	-	0	2	-	0	0	1	1	1	0	1	2	1	3	1	1	0
Ligia oceanica	1	1	0	0	3	-	3	1	0	1	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	1	0	1	2	-	0	1	0	-	1	1	1	1	0	1	2	1	1	0	0	0
Ligia italica	1	1	0	0	3	-	3	1	0	1	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	1	0	1	2	-	0	1	0	-	1	1	1	1	0	1	2	1	1	0	0	0
Ligidium germanicum	1	1	0	0	3	-	3	1	0	1	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	1	0	1	2	-	0	1	0	-	1	1	1	1	0	1	2	1	1	0	0	0
Haplophthalmus danicus	1	1	0	0	3	-	3	1	0	1	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	1	1	0	1	1	0	1	2	-	0	1	0	-	1	1	1	1	0	1	2	1	1	0	0	0
Porcellio scaber	1	1	0	0	3	-	3	1	0	1	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	1	1	0	1	1	0	1	2	-	0	1	0	-	1	1	1	1	0	1	2	1	1	0	0	0
Oniscus asellus	1	1	0	0	3	-	3	1	0	1	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	1	1	0	1	1	0	1	2	-	0	1	0	-	1	1	1	1	0	1	2	1	1	0	0	0
Paranthura nigropunctata	1	1	0	0	3	-	2	1	0	1	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	2	0	1	1	0	0	3	-	-	0	1	1	1	0	1	2	1	4	1	1	0
Cyathura carinata	1	1	0	0	3	-	2	1	0	1	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	0	0	1	2	0	1	1	0	0	3	-	-	0	1	1	1	0	1	2	1	4	1	1	0
Pygolabis humphreysi	1	1	0	0	2	-	0	1	0	0	0	0	0	1	-	0	-	-	0	1	0	1	0	1	1	0	1	0	1	2	0	1	C	-	0	?	?	?	0	1	1	1	0	1	2	1	1	?	?	1
Idotea baltica	1	1	0	0	4	-	3	1	0	0	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	1	0	0	1	1	1	1	0	1	2	1	1	1	1	0
Glyptonotus antarcticus	1	1	0	0	4	-	3	1	0	?	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	1	1	0	1	1	0	1	1	0	0	1	0	0	1	1	1	1	0	1	2	1	1	1	1	0
Cleantis prismatica	1	1	0	0	4	-	3	1	0	?	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	1	1	0	1	1	0	1	1	0	0	1	0	0	1	1	1	1	0	1	2	1	1	1	1	0
Antarcturus spinacoronatus	1	1	0	0	4	-	3	1	0	?	0	0	0	1	-	0	-	-	1	1	0	1	0	1	1	0	1	0	1	1	0	1	1	0	0	1	0	?	1	1	1	1	0	1	2	?	1	1	1	0

Tab. 4. Continuation.

Character #	051	052	053	054	055	056	057	058	059	060	061	062	063	064	065	066	067	068	069	070	071	072	073	074	075	076	077	078	079	080	081	082	083	084	085	086	087	088	089	090	091	092	093	094	095	096	097	098	099	100
Gonodactylus viridis	0	0	1	0	1	1	0	3	1	4	0	0	0	0	0	0	3	1	0	1	0	0	0	-	0	?	0	0	0	0	1	0	0	0	0	0	-	-	0	0	0	A	0	0	0	0	0	3	0	0
Penaeus semisulcatus	0	0	0	0	0	1	0	3	1	2	0	0	0	0	0	0	3	1	0	0	0	0	0	-	0	1	0	0	0	0	1	1	1	0	0	0	-	-	0	0	0	0	0	0	0	0	0	3	1	1
Euphausia superba	0	0	0	1	1	1	0	3	1	2	0	0	0	0	0	0	3	0	0	0	0	0	0	-	0	1	0	0	0	0	1	1	1	0	0	0	-	0	0	0	0	0	0	0	1	0	0	3	0	3
Anaspides tasmaniae	0	0	0	1	0	0	0	0	0	-	2	-	0	0	0	0	3	1	0	0	0	A	1	-	0	1	0	0	1	0	0	1	0	0	0	0	-	0	0	0	0	0	0	0	1	0	0	3	0	3
Neognathophausia ingens	0	0	0	1	1	1	1	2	1	2	1	0	0	0	0	0	3	0	0	0	0	1	1	1	0	1	0	0	1	0	1	1	1	0	0	0	-	0	0	0	0	0	0	1	1	1	0	3	1	2
Heteromysis formosa	0	0	0	1	1	1	1	2	0	-	1	0	0	0	0	0	3	0	0	0	0	1	1	1	0	1	0	0	1	0	1	1	1	0	0	0	-	0	0	0	0	0	0	1	1	1	0	3	0	2
Stygiomysis holthuisi	1	0	-	-	-	-	1	2	1	2	1	0	0	0	0	0	0	2	1	5	0	1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	-	1	0	0	0	0	0	1	1	1	0	3	1	3
Thetispelecaris remex	-	-	-	-	-	-	-	2	1	1	1	1	0	0	0	0	0	0	1	0	4	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	0	1
Ingolfiella tabularis	1	0	-	-	-	-	-	1	1	1	2	-	0	0	0	0	2	1	1	4	0	1	1	2	1	1	0	0	0	0	0	1	0	0	0	0	-	2	0	2	0	0	2	0	1	1	0	3	1	1
Arrhis phyllonyx	2	0	1	1	1	2	1	1	1	1	2	-	0	0	0	0	2	1	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	-	2	0	2	0	0	2	0	1	1	2	3	1	2
Protella gracilis	2	0	1	1	1	2	1	1	0	-	2	-	0	0	0	0	2	1	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	-	2	0	2	0	0	2	0	1	1	2	3	1	2
Hyperietta stephenseni	2	0	1	1	1	2	1	1	1	1	2	-	0	0	0	0	2	1	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	-	2	0	2	0	0	2	0	1	1	2	3	1	2
Gammarus troglophilus	2	0	1	1	1	2	1	1	1	1	2	-	0	0	0	0	2	1	1	0	0	1	1	1	0	1	0	0	0	0	0	1	0	0	0	0	-	2	0	2	0	0	2	0	1	1	2	3	1	2
Tethysbaena argentarii	1	0	-	-	-	-	-	2	0	-	1	2	0	0	0	0	2	1	1	4	4	1	1	1	0	0	0	0	0	0	1	0	1	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	0	1
Mictocaris halope	1	0	-	-	-	-	-	1	0	-	1	3	0	0	0	0	0	0	1	0	4	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	0	1
Spilocuma salomani	3	-	1	1	1	3	1	3	0	-	1	2	0	0	0	0	2	1	1	0	4	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1	1	0	0	0	0	1	1	0	3	0	0
Diastylis sculpta	3	-	1	1	1	3	1	3	0	-	1	2	0	0	0	0	2	1	1	0	4	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1	1	0	0	0	0	1	1	0	3	0	0
Spelaeogriphus lepidops	1	0	-	-	-	-	-	2	1	1	1	1	0	0	0	0	0	1	1	0	4	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	0	1
Apseudes bermudeus	1	0	1	1	1	0	1	2	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	0	1
Kalliapseudes sp.	1	0	1	1	1	0	1	2	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	0	1
Leptochelia sp.	1	0	1	1	1	0	1	2	1	1	1	1	2	1	1	0	2	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	1	1
Paratanais malignus	1	0	1	1	1	0	1	2	1	1	1	1	2	1	1	0	2	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	1	1
Tanais dulongii	1	0	1	1	1	0	1	2	1	1	1	1	2	1	1	0	2	0	1	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	-	0	1	1	0	0	0	0	1	1	0	3	1	1
Paramphisopus palustris	2	0	1	1	1	0	1	1	0	-	2	-	0	0	1	0	2	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	-	2	1	1	1	1	0	0	1	1	0	3	0	1
Colubotelson thomsoni	2	0	1	1	1	0	1	1	0	-	2	-	0	0	1	0	2	0	1	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	-	2	1	1	1	1	0	0	1	1	0	3	0	1
Stenasellus racovitzai	-	-	-	-	-	-	1	1	0	-	2	-	0	0	1	0	0	0	0	3	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Caecidotea racovitzai	2	1	1	1	1	0	1	1	0	-	2	-	0	0	1	0	2	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Asellus aquaticus	2	1	1	1	1	0	1	1	0	-	2	-	0	0	1	0	2	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Stenetriid sp.	2	1	1	1	1	0	1	1	1	4	2	-	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Janira maculosa	2	1	1	1	1	0	1	1	0	-	2	-	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Joeropsis coralicola	2	1	1	1	1	0	1	1	1	4	2	-	2	1	1	0	2	0	0	4	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Iathrippa trilobatus	2	1	1	1	1	0	1	1	1	2	2	-	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Haploniscus nudifrons	-	-	-	-	-	-	-	1	1	4	2	-	2	1	1	0	1	0	0	0	0	1	1	2	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Acanthaspidia drygalskii	-	-	-	-	-	-	-	1	1	2	2	-	0	0	1	0	1	0	0	4	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Neojaera antarctica	2	1	1	1	1	0	1	2	0	-	2	-	2	1	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Thylakogaster sp.	-	-	-	-	-	-	-	1	0	-	2	-	0	0	1	0	2	0	0	4	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	-	2	1	1	1	1	0	0	1	1	0	3	0	1
Dendromunna sp.	-	-	-	-	-	-	-	1	0	-	2	-	0	0	1	0	2	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	-	2	1	1	1	1	0	0	1	1	0	3	0	1
Eurycope sarsi	-	-	-	-	-	-	-	1	0	-	2	-	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Ilyarachna antarctica	-	-	-	-	-	-	-	1	0	-	2	-	0	0	1	0	0	0	0	5	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Munnopsis typica	-	-	-	-	-	-	-	1	0	-	2	-	0	0	1	0	0	0	0	5	1	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	-	2	1	1	1	1	0	0	1	1	0	3	0	1
Betamorpha fusiformis	-	-	-	-	-	-	-	1	0	-	2	-	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Mesosignum cf. *usheri*	-	-	-	-	-	-	-	1	1	4	2	-	0	0	1	0	2	0	0	4	0	1	1	2	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Macrostylis sp.1	-	-	-	-	-	-	-	1	1	4	2	-	2	1	1	0	2	0	0	3	0	1	1	2	1	1	0	0	1	0	0	0	0	0	1	1	0	2	1	1	1	1	0	0	1	1	0	3	0	1
Janirella sp.	-	-	-	-	-	-	-	1	1	2	2	-	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Ischnomesus sp.	-	-	-	-	-	-	-	1	1	4	2	-	0	0	1	0	2	0	0	0	0	1	1	0	A	1	0	0	1	0	0	0	0	1	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Eugerdella natator	-	-	-	-	-	-	-	1	1	4	2	-	2	1	1	0	0	0	0	3	0	1	1	0	0	1	0	0	1	0	0	0	0	0	1	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Eugerda sp.	-	-	-	-	-	-	-	1	1	4	2	-	2	1	1	0	0	0	0	3	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	1	1	2	1	1	1	1	0	0	1	1	0	3	0	1
Zonophryxus quinquedens	-	-	-	-	1	-	-	1	0	-	2	-	0	1	1	1	2	2	1	4	3	0	0	-	1	0	0	1	1	0	0	4	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	1	1
Probopyrus pacificiensis	2	2	1	1	1	0	1	1	0	-	2	-	0	1	1	1	2	2	1	4	3	0	0	-	1	0	0	1	1	0	0	4	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	0	1
Hemiarthrus abdominalis	2	2	1	1	1	0	1	1	0	-	2	-	0	1	1	1	2	2	1	4	3	0	0	-	1	0	0	1	1	0	0	4	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	0	1
Paragnathia formica	2	1	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	4	3	0	0	-	1	0	0	1	1	0	0	2	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	0	1
Riggia paranensis	2	2	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	1	3	0	0	-	0	0	0	0	1	1	0	2	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	0	1	1
Anilocra physodes	2	2	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	1	3	0	0	-	0	0	0	0	1	1	0	2	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	0	1	1
Cymodoce tattersalli	2	3	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	0	0	1
Campecopea hirsuta	2	3	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	0	0	1	1	1	1	?	0	0	0	0	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	0	0	1
Sphaeroma serratum	2	3	0	1	1	0	1	1	0	-	0	-	0	0	1	1	2	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	0	0	1
Cassidinidea sp.	2	3	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	0	0	1	1	1	0	1	0	0	1	1	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	0	0	1
Limnoria quadripunctata	2	1	1	1	1	0	1	1	0	-	2	-	2	1	1	1	2	0	1	5	2	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	1	0	1
Eurydice pulchra	2	2	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	1	0	1	1	1	0	1	0	0	1	0	0	1	0	0	0	0	-	1	1	1	1	1	2	0	1	1	1	0	1	1
Excorallana quadricornis	2	2	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	1	3	0	0	-	0	1	0	0	1	1	0	1	0	0	0	0	-	1	1	1	1	1	2	0	1	1	1	0	1	1
Natatolana albinota	2	2	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	1	0	1	1	1	0	1	0	0	1	0	0	1	0	0	0	0	-	1	1	1	1	1	2	0	1	1	1	0	1	1
Aega antarctica	2	2	1	1	1	0	1	1	0	-	2	-	0	0	1	1	2	0	1	1	3	0	0	-	0	1	0	0	1	1	0	1	0	0	0	0	-	1	1	1	1	1	2	0	1	1	1	0	1	0
Ligia oceanica	2	1	1	1	1	0	1	1	0	-	2	-	1	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	3	0	0	0	0	-	0	1	1	1	1	1	0	1	-	1	2	0	1
Ligia italica	2	1	1	1	1	0	1	1	0	-	2	-	1	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	3	0	0	0	0	-	0	1	1	1	1	1	0	1	-	1	2	0	1
Ligidium germanicum	2	1	1	1	1	0	1	1	0	-	2	-	1	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	3	0	0	0	0	-	0	1	1	1	1	1	0	1	-	1	2	0	1
Haplophthalmus danicus	2	1	1	1	1	0	1	1	0	-	2	-	1	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	3	0	0	0	0	-	0	1	1	1	1	1	0	1	-	1	2	0	1
Porcellio scaber	2	1	1	1	1	0	1	1	0	-	2	-	1	1	1	0	2	0	1	2	0	1	1	1	1	1	0	0	1	0	0	3	0	0	0	0	-	0	1	1	1	1	1	0	1	-	1	2	0	1
Oniscus asellus	2	1	1	1	1	0	1	1	0	-	2	-	1	1	1	0	2	0	1	2	0	1	1	1	1	1	0	0	1	0	0	3	0	0	0	0	-	0	1	1	1	1	1	0	1	-	1	2	0	1
Paranthura nigropunctata	2	1	1	1	1	0	1	1	0	-	2	-	0	1	1	0	2	0	1	1	3	2	1	1	0	1	0	0	1	0	0	4	0	0	0	0	-	1	1	1	1	1	2	0	1	1	1	1	1	1
Cyathura carinata	2	1	1	1	1	0	1	1	0	-	2	-	0	1	1	0	2	0	1	1	0	2	1	1	0	1	0	0	1	0	0	4	0	0	0	0	-	1	1	1	1	1	2	0	1	1	1	1	1	1
Pygolabis humphreysi	-	-	-	-	1	-	-	1	0	-	2	-	0	0	1	0	2	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0	0	0	-	1	1	1	1	1	2	0	1	1	1	1	0	1
Idotea baltica	2	1	1	1	1	0	1	1	0	-	2	-	2	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	0	1
Glyptonotus antarcticus	2	1	1	1	1	0	1	1	0	-	2	-	2	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	0	1
Cleantis prismatica	2	1	1	1	1	0	1	1	0	-	2	-	2	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	0	1
Antarcturus spinacoronatus	2	1	1	1	1	0	1	1	0	-	2	-	2	1	1	0	2	0	1	0	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	-	1	1	1	1	1	1	0	1	-	1	2	0	1

Tab. 4. Continuation.

Character #	1 0 1	1 0 2	1 0 3	1 0 4	1 0 5	1 0 6	1 0 7	1 0 8	1 0 9	1 1 0	1 1 1	1 1 2	1 1 3	1 1 4	1 1 5	1 1 6	1 1 7	1 1 8	1 1 9	1 2 0	1 2 1	1 2 2	1 2 3	1 2 4	1 2 5	1 2 6	1 2 7	1 2 8	1 2 9	1 3 0	1 3 1	1 3 2	1 3 3	1 3 4	1 3 5	1 3 6	1 3 7	1 3 8	1 3 9	1 4 0	1 4 1	1 4 2	1 4 3	1 4 4	1 4 5	1 4 6	1 4 7	1 4 8	1 4 9	1 5 0
Gonodactylus viridis	0	2	-	1	0	1	0	-	2	1	0	-	-	-	-	-	-	1	0	2	0	0	0	0	0	-	-	-	-	0	0	0	1	-	0	0	0	0	0	1	0	-	0	0	0	0	0	0	0	0	3
Penaeus semisulcatus	0	0	0	1	0	1	0	-	2	1	0	-	-	-	-	-	-	1	-	-	0	-	0	0	0	0	0	2	2	2	1	-	0	0	1	1	1	0	2	0	0	-	0	0	0	0	0	0	0	0	0
Euphausia superba	0	1	3	1	0	0	0	-	2	1	0	-	-	-	-	-	-	0	1	0	0	0	0	0	0	1	1	1	1	1	3	-	0	0	1	1	0	0	2	0	0	-	0	0	0	0	0	0	0	0	0
Anaspides tasmaniae	0	2	0	1	0	0	0	-	0	1	0	-	-	-	-	-	-	0	1	0	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	1	0	0	2	0	0	-	0	0	0	0	0	0	0	0	0
Neognathophausia ingens	0	0	2	-	0	0	0	-	0	1	0	-	-	-	-	-	-	0	1	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0	1	1	0	0	2	0	0	-	0	0	0	0	0	0	0	0	0
Heteromysis formosa	0	0	2	1	0	0	0	-	0	1	0	-	-	-	-	-	-	0	2	0	0	0	0	0	0	1	1	1	1	1	1	1	1	-	0	1	0	0	2	0	0	-	0	0	0	0	0	0	0	0	0
Stygiomysis holthuisi	0	0	3	1	0	0	0	-	0	1	0	-	-	-	-	-	-	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	-	0	1	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0
Thetispelecaris remex	1	-	-	1	0	3	0	-	0	1	0	-	-	-	-	-	-	2	2	0	0	0	0	0	0	3	3	0	0	0	0	-	0	1	0	0	0	0	2	0	0	-	0	0	1	1	0	0	0	0	0
Ingolfiella tabularis	1	-	-	1	0	2	1	2	0	1	0	-	-	-	-	-	-	2	2	0	0	0	0	0	1	-	-	-	-	-	-	-	1	-	0	0	1	0	2	2	0	-	0	0	2	0	0	-	0	0	2
Arrhis phyllonyx	1	-	-	1	0	2	1	2	0	1	0	-	-	-	-	-	-	2	0	0	0	0	0	0	1	-	-	-	-	-	-	-	0	1	2	0	1	0	2	2	0	-	0	0	2	0	0	0	0	0	0
Protella gracilis	1	-	-	1	0	2	1	2	0	1	0	-	-	-	-	-	-	2	0	0	0	0	0	0	1	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	0	2	0	0	-	-	-	-
Hyperietta stephenseni	1	-	-	1	0	2	1	2	0	1	0	-	-	-	-	-	-	2	0	0	0	0	0	0	1	-	-	-	-	-	-	-	0	1	2	0	1	0	2	2	0	-	0	0	2	0	0	0	0	0	0
Gammarus troglophilus	1	-	-	1	0	2	1	2	0	1	0	-	-	-	-	-	-	2	0	0	0	0	0	0	1	-	-	-	-	-	-	-	0	1	2	0	1	0	2	2	0	-	0	0	2	0	0	0	0	0	0
Tethysbaena argentarii	0	0	2	1	0	0	0	-	A	1	0	-	-	-	-	-	-	2	2	0	0	0	0	0	0	0	2	2	2	2	2	2	2	0	1	0	0	0	0	2	0	0	-	0	1	0	1	0	-	0	0	2
Mictocaris halope	1	-	-	1	0	0	0	-	0	1	0	-	-	-	-	-	-	0	2	0	0	0	0	0	0	0	2	2	2	2	2	-	-	0	1	1	0	0	0	2	0	0	-	0	0	0	0	0	-	0	0	2
Spilocuma salomani	0	1	-	-	0	1	0	-	0	1	0	-	-	-	-	-	-	1	-	0	0	0	0	0	0	-	0	0	0	0	2	-	-	0	-	0	0	0	0	2	0	0	-	0	0	0	1	0	0	0	0	0
Diastylis sculpta	0	1	-	-	0	1	0	-	0	1	0	-	-	-	-	-	-	1	-	0	0	0	0	0	0	-	0	0	0	0	2	-	-	1	-	0	0	0	0	2	0	0	-	0	0	0	1	0	0	0	0	0
Spelaeogriphus lepidops	0	1	-	0	0	0	0	-	1	1	0	-	-	-	-	-	-	0	2	0	0	0	0	0	0	2	2	2	1	1	1	1	1	-	1	0	0	0	2	0	0	-	0	0	1	1	0	0	0	0	0
Apseudes bermudeus	0	1	-	0	0	3	0	-	0	1	0	-	-	-	-	-	-	3	0	0	0	0	0	0	0	3	3	-	-	-	-	-	1	-	0	0	0	0	2	0	0	-	0	1	1	1	0	0	0	0	0
Kalliapseudes sp.	0	1	-	0	0	3	0	-	0	1	0	-	-	-	-	-	-	3	0	0	0	0	0	0	0	3	3	0	0	0	0	-	1	-	0	0	0	0	2	0	0	-	0	1	1	1	0	0	0	0	0
Leptochelia sp.	0	1	-	1	1	0	0	-	0	1	0	-	-	-	-	-	-	3	0	0	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	3
Paratanais malignus	0	1	-	1	1	0	0	-	0	1	0	-	-	-	-	-	-	3	0	0	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	3
Tanais dulongii	0	1	-	1	1	0	0	-	0	1	0	-	-	-	-	-	-	3	0	0	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	3
Paramphisopus palustris	0	2	-	0	0	0	0	-	0	0	1	0	0	0	0	0	2	0	2	0	0	1	0	2	-	-	-	-	-	-	-	1	-	1	0	1	0	0	1	0	-	1	1	1	1	0	0	0	1	3
Colubotelson thomsoni	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	2	0	2	0	0	1	0	2	-	-	-	-	-	-	-	1	-	1	0	1	0	0	1	0	-	1	1	1	1	0	1	0	1	3
Stenasellus racovitzai	0	2	-	0	0	0	0	-	1	0	1	0	1	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	2	0	-	0	-	0	1	1	1	0	1	1	0	3
Caecidotea racovitzai	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	2	0	2	0	0	1	0	2	-	-	-	-	-	-	-	1	-	0	0	0	2	1	-	0	-	0	1	1	1	0	1	1	0	3
Asellus aquaticus	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	2	0	2	0	0	1	0	2	-	-	-	-	-	-	-	1	-	0	0	0	2	1	-	0	-	0	1	1	1	0	1	1	0	3
Stenetriid sp.	0	2	-	0	0	0	0	-	1	0	1	0	1	1	0	0	2	0	1	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	2	1	-	1	0	0	1	1	1	0	1	1	0	3
Janira maculosa	0	2	-	0	0	0	0	-	1	0	1	0	1	1	0	0	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	3	1	-	1	1	0	1	1	1	0	1	3	0	3
Joeropsis coralicola	0	2	-	0	0	0	0	-	1	0	1	0	1	1	0	0	0	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	3	1	-	1	1	0	1	1	1	0	1	3	0	3
Iathrippa trilobatus	0	2	-	0	0	0	0	-	1	0	1	0	1	1	0	0	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	3	1	-	1	1	0	1	1	1	0	1	3	0	3
Haploniscus nudifrons	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	1	0	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	4	1	-	0	-	0	1	1	1	0	1	3	0	3
Acanthaspidia drygalskii	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	3	1	-	1	1	0	1	1	1	1	1	3	0	3
Neojaera antarctica	0	2	-	0	0	0	0	-	1	0	1	0	0	1	0	0	0	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	3	1	-	1	0	0	1	1	1	0	1	3	0	3
Thylakogaster sp.	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	2	3	1	-	0	-	0	1	1	1	1	1	3	0	3
Dendromunna sp.	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	1	4	1	-	0	-	0	1	1	1	1	1	3	0	3
Eurycope sarsi	0	2	-	0	0	0	0	-	1	0	1	0	0	0	1	0	2	2	0	0	1	0	1	2	-	-	-	-	-	-	-	1	-	0	0	1	3	1	-	0	-	0	1	1	1	1	1	3	0	3
Ilyarachna antarctica	0	2	-	0	0	0	0	-	1	0	1	0	0	0	1	0	2	2	0	0	1	0	1	2	-	-	-	-	-	-	-	1	-	0	0	1	3	1	-	0	-	0	1	1	1	1	1	3	0	3
Munnopsis typica	0	2	-	0	0	0	0	-	1	0	1	0	0	0	1	0	2	2	0	0	1	0	1	2	-	-	-	-	-	-	-	1	-	0	0	1	3	-	-	0	-	0	1	1	1	1	1	3	0	3
Betamorpha fusiformis	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	1	0	2	2	0	0	1	0	1	2	-	-	-	-	-	-	-	1	-	0	0	1	3	1	-	0	-	0	1	1	1	1	1	3	0	3
Mesosignum cf. *usheri*	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	0	2	0	?	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	1	4	-	-	1	1	0	1	1	1	0	1	3	0	3
Macrostylis sp.1	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	1	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	1	4	-	-	1	0	0	1	1	1	0	1	3	0	3
Janirella sp.	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	1	4	1	-	1	1	0	1	1	1	1	1	3	0	3
Ischnomesus sp.	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	1	2	2	0	1	1	0	0	2	-	-	-	-	-	-	-	1	-	0	0	1	3	1	-	0	-	0	1	1	1	0	1	3	0	3
Eugerdella natator	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	1	2	2	0	1	1	0	2	2	-	-	-	-	-	-	-	1	-	0	0	1	3	1	-	1	0	0	1	1	1	0	1	3	0	3
Eugerda sp.	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	1	2	2	0	1	1	0	2	2	-	-	-	-	-	-	-	1	-	0	0	1	3	1	-	1	0	0	1	1	1	0	1	3	0	3
Zonophryxus quinquedens	1	-	-	1	0	0	1	1	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	4	-	-	0	-	0	1	-	0	0	0	-	-	-
Probopyrus pacificiensis	1	-	-	1	0	0	1	1	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	2	0	0	-	0	1	0	0	0	0	0	0	1
Hemiarthrus abdominalis	1	-	-	1	0	0	1	1	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	2	0	0	-	0	1	0	0	0	0	0	0	1
Paragnathia formica	1	-	-	1	1	0	0	-	1	0	1	0	0	0	0	0	1	-	-	0	0	0	-	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Riggia paranensis	1	-	-	1	1	0	1	1	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Anilocra physodes	1	-	-	1	1	0	1	1	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Cymodoce tattersalli	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	4	0	2	1	0	-	0	-	0	1	0	0	1	0	0	0	1
Campecopea hirsuta	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	4	0	2	3	1	-	0	-	0	1	0	0	1	0	0	0	1
Sphaeroma serratum	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	1	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	4	0	2	1	0	-	0	-	0	1	0	0	1	0	0	0	1
Cassidinidea sp.	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	4	0	2	3	0	-	0	-	0	1	0	0	1	0	0	0	1
Limnoria quadripunctata	0	2	-	0	0	0	0	-	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	1	0	-	0	1	0	0	0	0	0	0	1
Eurydice pulchra	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Excorallana quadricornis	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Natatolana albinota	1	-	-	0	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Aega antarctica	1	-	-	1	1	0	1	0	1	0	1	0	0	0	0	0	2	0	2	0	2	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	0	0	-	0	1	0	0	0	0	0	0	1
Ligia oceanica	0	2	-	1	0	0	0	-	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	3	0	0	0	2	0	0	-	0	1	1	1	0	1	0	0	1
Ligia italica	0	2	-	1	0	0	0	-	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	3	0	0	0	2	0	0	-	0	1	1	1	0	1	0	0	1
Ligidium germanicum	0	2	-	1	0	0	0	-	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	3	0	0	0	2	0	0	-	0	1	1	1	0	1	0	0	1
Haplophthalmus danicus	0	2	-	1	0	0	0	-	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	3	0	0	0	2	0	0	-	0	1	1	1	0	1	0	0	1
Porcellio scaber	0	2	-	1	0	0	0	-	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	3	0	0	0	2	0	0	-	0	1	1	1	0	1	0	0	1
Oniscus asellus	0	2	-	1	0	0	0	-	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	3	0	0	0	2	0	0	-	0	1	1	1	0	1	0	0	1
Paranthura nigropunctata	0	2	-	1	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	0	0	1	0	-	0	1	0	0	1	0	4	0	1
Cyathura carinata	0	2	-	1	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	0	0	0	0	2	-	-	-	-	-	-	-	1	-	0	0	0	0	0	1	0	-	0	1	0	0	1	0	4	0	1
Pygolabis humphreysi	0	2	-	0	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	1	0	0	0	0	1	0	-	0	1	0	0	0	0	0	0	1
Idotea baltica	0	2	-	0	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	2	0	1	2	2	-	0	-	0	1	0	0	1	0	0	0	1
Glyptonotus antarcticus	0	2	-	0	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	2	0	1	2	2	-	0	-	0	1	0	0	1	0	0	0	1
Cleantis prismatica	0	2	-	0	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	2	0	1	1	0	-	0	-	0	1	0	0	1	0	0	0	1
Antarcturus spinacoronatus	0	2	-	1	0	0	1	0	1	0	1	0	0	0	0	0	0	2	0	2	1	0	0	0	2	-	-	-	-	-	-	-	1	-	2	0	1	2	0	-	0	3	0	1	0	0	1	0	0	0	1

Tab. 4. Continuation.

Character #	1 5 1	1 5 2	1 5 3	1 5 4	1 5 5	1 5 6	1 5 7	1 5 8	1 5 9	1 6 0	1 6 1	1 6 2	1 6 3	1 6 4	1 6 5	1 6 6	1 6 7	1 6 8	1 6 9	1 7 0	1 7 1	1 7 2	1 7 3	1 7 4	1 7 5	1 7 6	1 7 7	1 7 8	1 7 9	1 8 0	1 8 1	1 8 2	1 8 3	1 8 4	1 8 5	1 8 6	1 8 7	1 8 8	1 8 9	1 9 0	1 9 1	1 9 2	1 9 3	1 9 4	1 9 5	1 9 6	1 9 7	1 9 8	1 9 9	2 0 0	2 0 1	2 0 2
Gonodactylus viridis	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	2	0	0	1	2
Penaeus semisulcatus	0	0	4	0	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	2	0	0	1	2
Euphausia superba	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	2	0	0	1	2
Anaspides tasmaniae	0	0	2	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	2	0	0	1	2
Neognathophausia ingens	0	0	2	0	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	2	0	0	1	2
Heteromysis formosa	0	0	2	0	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Stygiomysis holthuisi	0	0	3	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	2	0	0	1	2
Thetispelecaris remex	0	0	4	0	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	0	0	0	2	0
Ingolfiella tabularis	1	-	-	-	-	2	5	0	5	-	0	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	2	0	0	0	0	0	1	0	0	1	1
Arrhis phyllonyx	1	-	-	-	-	0	5	0	5	-	0	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	2	0	0	0	0	0	1	0	0	1	1
Protella gracilis	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hyperietta stephenseni	1	-	-	-	-	0	5	0	5	-	0	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	2	0	0	0	0	0	1	0	0	1	1
Gammarus troglophilus	1	-	-	-	-	0	5	0	5	-	0	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	2	0	0	0	0	0	1	0	0	1	1
Tethysbaena argentarii	1	-	-	-	-	2	-	1	-	-	0	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	0	0	0	1	0
Mictocaris halope	0	-	3	0	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	0	0	0	0	0
Spilocuma salomani	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	0	0	0	1	0
Diastylis sculpta	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	0	0	0	1	0
Spelaeogriphus lepidops	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	1	2	0	0	1	2
Apseudes bermudeus	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	0	0	0	0	1	0	0	0	2	0
Kalliapseudes sp.	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	0	0	0	0	1	0	0	0	2	0
Leptochelia sp.	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	0	0	0	0	1	0	0	0	0	0
Paratanais malignus	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	0	0	0	0	1	0	0	0	0	0
Tanais dulongii	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	0	0	0	0	0	1	0	0	0	0	0
Paramphisopus palustris	1	-	-	-	-	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	-	0	1	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	1	1
Colubotelson thomsoni	1	-	-	-	-	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	1	0	0	1	1
Stenasellus racovitzai	1	-	-	-	-	1	1	0	1	1	1	0	0	0	0	0	1	0	1	1	0	1	0	3	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	2	0	0	0	0	0	1	0	0	1	1
Caecidotea racovitzai	1	-	-	-	-	1	1	0	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	2	0	0	2	2	0	1	0	1	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	1	1
Asellus aquaticus	1	-	-	-	-	1	1	0	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	2	0	0	2	2	0	1	0	1	0	0	0	0	0	0	0	3	2	0	0	0	0	0	0	0	0	1	0
Stenetriid sp.	1	-	-	-	-	1	1	1	1	1	1	0	0	0	1	0	2	0	1	1	0	1	0	4	0	0	1	1	1	2	1	1	0	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	0
Janira maculosa	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	2	2	0	0	1	2	2	0	0	0	0	0	0	0	0	1	0
Joeropsis coralicola	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	2	2	0	1	1	2	2	2	0	0	0	0	0	0	0	1	0
Iathrippa trilobatus	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	2	2	0	0	1	2	2	0	0	0	0	0	0	0	0	1	0
Haploniscus nudifrons	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	2	2	2	1	1	2	2	2	0	-	0	1	-	-	0	0	1	0
Acanthaspidia drygalskii	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	1	1	1	1	1	3	2	2	0	-	-	1	-	-	0	0	1	0
Neojaera antarctica	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	2	1	0	1	1	2	2	2	0	0	0	0	0	0	0	1	0
Thylakogaster sp.	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	2	1	0	1	1	2	2	2	0	-	-	1	-	-	0	0	1	0
Dendromunna sp.	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	2	2	0	1	1	2	3	2	0	-	-	1	-	-	0	0	1	0
Eurycope sarsi	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	1	2	0	1	1	2	2	2	0	0	0	0	0	0	0	1	0
Ilyarachna antarctica	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	1	1	1	1	1	2	2	2	0	0	0	0	0	0	0	1	0
Munnopsis typica	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	0	2	0	1	1	2	2	2	0	-	-	1	-	-	0	0	1	0
Betamorpha fusiformis	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	0	0	1	2	0	1	1	2	2	2	0	0	0	0	0	0	0	1	0
Mesosignum cf. *usheri*	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	2	2	2	1	1	2	2	2	0	-	-	1	-	-	0	0	1	0
Macrostylis sp.1	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	2	2	2	1	1	2	2	2	0	-	-	1	-	-	0	0	1	0
Janirella sp.	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	1	2	1	0	1	2	2	2	0	-	-	1	-	-	0	0	1	0
Ischnomesus sp.	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	2	2	1	1	1	2	2	2	0	0	0	A	0	0	0	0	1	0
Eugerdella natator	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	2	2	2	1	1	2	2	2	0	0	0	0	0	0	0	0	1	0
Eugerda sp.	1	-	-	-	-	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	0	1	0	5	1	1	1	1	1	3	1	1	1	0	2	2	2	1	1	2	2	2	0	0	0	0	0	0	0	0	1	0
Zonophryxus quinquedens	0	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Probopyrus pacificiensis	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	0	0	0	0	2	0	0	1	-
Hemiarthrus abdominalis	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	0	0	0	0	2	0	0	1	-
Paragnathia formica	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Riggia paranensis	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Anilocra physodes	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	?	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Cymodoce tattersalli	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	1	0	0	0	0	0	2	0	1	1	2
Campecopea hirsuta	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	1	0	0	0	0	0	2	0	1	1	2
Sphaeroma serratum	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	1	0	0	0	0	0	2	0	1	1	2
Cassidinidea sp.	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	1	0	0	0	0	0	2	0	1	1	2
Limnoria quadripunctata	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	0	0	-	-	-	-	-	-	-	0	0	0	0	0	0	0	1	0	0	1	2
Eurydice pulchra	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Excorallana quadricornis	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Natatolana albinota	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Aega antarctica	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	0	0	0	2	0	0	1	2
Ligia oceanica	1	-	-	-	-	1	1	0	1	1	0	0	0	-	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	-	-	-	1	0	0	0	0	1	0	3	2	0	0	1	0	0	0	1	0	0	1	1
Ligia italica	1	-	-	-	-	1	1	0	1	1	0	0	0	-	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	-	-	-	1	0	0	0	0	1	0	3	2	0	0	1	0	0	0	1	0	0	1	1
Ligidium germanicum	1	-	-	-	-	1	1	0	1	1	0	0	0	-	0	-	0	0	0	0	0	0	-	0	0	0	0	0	0	0	-	-	-	1	0	0	0	0	1	0	3	2	0	0	0	1	0	0	1	0	0	1	1
Haplophthalmus danicus	1	-	-	-	-	1	1	0	1	0	0	0	0	-	0	-	0	0	0	0	0	0	-	0	1	0	0	0	0	0	-	-	-	1	0	0	0	0	1	0	3	2	0	0	0	2	0	0	1	0	0	1	1
Porcellio scaber	1	-	-	-	-	1	1	0	1	0	0	0	0	-	0	-	0	0	0	0	0	0	-	0	1	0	0	0	0	0	-	-	-	1	0	0	0	0	1	0	3	2	0	0	0	2	0	0	1	0	0	1	0
Oniscus asellus	1	-	-	-	-	1	1	0	1	0	0	0	0	-	0	-	0	0	0	0	0	0	-	0	1	0	0	0	0	0	-	-	-	1	0	0	0	0	1	0	3	2	0	0	0	2	0	0	1	0	0	1	0
Paranthura nigropunctata	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	1	0	0	2	0	0	1	2
Cyathura carinata	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	0	0	0	0	1	0	0	2	0	0	1	2
Pygolabis humphreysi	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	1	0	0	-	0	0	-	-	-	-	-	-	-	-	-	-	-	2	0	-	0	0	0	0	0	0	1	1
Idotea baltica	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	0	0	-	-	-	-	-	-	-	0	1	1	0	-	1	-	-	0	0	1	2
Glyptonotus antarcticus	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	0	0	-	-	-	-	-	-	-	0	1	1	0	-	1	-	-	0	0	1	2
Cleantis prismatica	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	0	0	-	-	-	-	-	-	-	0	1	1	0	0	0	0	2	0	0	1	2
Antarcturus spinacoronatus	0	0	1	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	0	0	-	0	0	0	-	0	0	0	0	0	0	-	-	-	-	-	-	-	0	1	1	0	0	0	0	2	0	0	1	2

Tab. 5. Command file for a combined analysis search using POY version 4.1.1. Comments, which are not executed, are surrounded by brackets & asterisks. The commands are explained in VARÓN et al. (2008).

```
(* automated search 18S data + morphology; Isopoda and Peracarida *)
(* manual segmented, POY build 4.1.1, DNA subst=2, indel=1, gap_opening 1 *)
(* DNA data weighted 0.5x morph transitions *)
set(log:"KL8-morph9_dwts05.log")
read("Isopoda_18s_KL8.fas","Morph_Isopod-percarid_9.ss","run4.tre")
set(root:"Gonodactylus_viridis")
set(timer:0)
transform(tcm:(2,1),gap_opening:1)
transform(dynamic, weightfactor:0.5) (* DNA data dynamic weighted by half *)
report("KL8-morph9_dwts05.dat",data)
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
report("KL8-morph9_dwts05_a.tre",trees:(total))
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
report("KL8-morph9_dwts05_b.tre",trees:(total))
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
select()
report("KL8-morph9_dwts05_c.tre",trees:(total))
set (iterative:approximate:4)
swap(around)
set(normal_do)
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
report("KL8-morph9_dwts05_d.tre",trees:(total))
search (max_time:0:3:0, memory:mb:768) (* Search for 3 hours, memory 768mb *)
report("KL8-morph9_dwts05_e.tre",trees:(total))
select()
set (iterative:approximate:4)
swap(around)
set(normal_do)
select()
report("KL8-morph9_dwts05.tre",trees:(total))
report("KL8-morph9_dwts05_tre.pdf",graphtrees:collapse)
report("KL8-morph9_dwts05_con.pdf",graphconsensus)
report("KL8-morph9_dwts05_diag.txt",diagnosis)
set(nolog)
exit()
```

3. Results

3.1. 18S parameter exploration

A series of analyses explored the parameter space defined by substitution, indel and gap opening costs. The results of the parameter exploration and monophyly tests are shown in Tab. 2. The parameter set "substitutions = 2, indels = 1, gap opening = 1" produced the highest monophyly score (60%). This set uses substitutions equal to 2 indels but with an added cost for gap extension. Taxa that were never monophyletic under any parameter combination include: Tanaidacea, Isopoda, Asellota, Oniscidea, Diplochaeta (Ligiidae), Sphaeromatidae, Cymothoida. Because major taxa were not found in this analysis, the prospects for assessing relationships in the Peracarida using 18S alone are limited. Nevertheless, the 18S marker appears to be useful for the lower systematic levels in the Isopoda, at least. Several family-level taxa were present in the topologies, regardless of the parameters: the families Bopyridae and Cymothoidae both had the highest monophyly frequency (frequency of topological congruence) of 93% and 100%, respectively. Other taxa, such as the Phreatoicidea and the Asellidae had a monophyly frequency of 71%. The large superfamily Janiroidea (18 taxa) and the large deep-sea family Munnopsidae showed a relatively high frequency of 50% of the parameter sets. This is not a general result because some family-level taxa (e.g., the Ligiidae) were found in none of the analyses. The absence of a Sphaeromatidae clade in all analyses was caused by the sequence from one species (*Cymodoce tattersalli*), a result that should be reconfirmed with new sequence data. The relationships of the families Cirolanidae and Aegidae may need to be re-assessed because a species of Aegidae (*Aega antarctica*) was frequently nested within a clade of two cirolanid species (*Eurydice pulchra* and *Natatolana meridionalis*).

3.2. Direct optimisation analysis of 18S data

The direct optimisation analysis using POY 4.1.1 of the 18S sequence data (Tab. 1) used the selected parameter set "substitutions = 2, indels = 1, gap opening = 1", with transitions equal to transversion costs. This analysis found a single least-cost tree (Fig. 2; length 44,594).

Although the monophyly of the Amphipoda was retained in this cladogram, many of the other peracarid taxa were not found to be monophyletic, including the Isopoda. As other 18S analyses of the peracarids, Mysidae were placed external to the peracarid clade, and *Thetispelecaris* was included among the remainder of the Mysidacea, sister to *Stygiomysis*. This last result confirmed the relative BLAST similarity of the two sequences (87%). The cumacean clade was diluted by an internal placement of *Spelaeogriphus*. The apseudomorph tanaidaceans were placed separately and internally to the isopod clade. The tanaidomorph tanaidaceans were monophyletic but sister to the gnathiid *Paragnathia* and the cymothoids *Riggia* and *Anilocra*. Within the isopods, the Asellota were split into several clades: a basal stenetriid clade, a stenasellid/asellid clade, and a janiroidean clade. Overall, this is not a coherent result relative to the classification.

Regarding the primary aim of the analysis, however, the amphipods are clearly not the sister group of the isopods, in agreement with the analysis of SPEARS et al. (2005). None of the differing parameter sets found this sister group relationship. Given that several isopod taxa cluster with several tanaidacean taxa, the 18S results appear to support Tanaidacea as the sister group of the Isopoda.

The analysis suggests a basal position for the Asellota (as proposed by SCHMALFUSS 1998), although its non-monophyly and the position of several parasitic isopod clades external to the main isopod clade makes this less clear. Surprisingly, the two species of the Phreatoicidea are not near the main root of the isopods but are positioned internally, sister group to the tainisopid, *Pygolabis*.

3.3. Morphology: unweighted parsimony

Parsimony analysis of the 75 taxon, 202 character data-set (Tab. 4) yielded 38,079 trees of length 711. The strict consensus (Fig. 3) of these trees is unresolved basally within the isopods and within the mancoid peracarids. Isopods are strongly monophyletic based on the Bremer and Jackknife support values. Amphipods were placed external to the mancoid peracarids (which include Thermosbaenacea) in all trees, with moderately strong support values at the branch separating them from mancoid peracarids. The same data, but analysed with the constraint amphipods and isopods as sister groups, found a length of 751, fully 40 steps longer than the shortest unconstrained analysis. A clade of the Phreatoicidea and Asellota occurs in nearly all of the trees, but with differing basal positions. All trees find a sister group relationship between Hirsutiidae and Tanaidacea.

An exploration of the most distant trees in the analytical treespace found a surprising diversity of hypotheses regarding the basally derived clade of the isopods (Fig. 4). The tree distance analysis did not settle on two or three most different trees, but found two nearby trees at one edge (Fig. 4A,B) and 108 trees at 45 symmetric distance units away that produced different tree hypotheses. The first two trees are similar but had two distinctly different outcomes for the isopod clade of large coxal plates (BRUSCA & WILSON 1991; DREYER & WÄGELE 2002) based on the position of the Oniscidea. In both trees, the terrestrial isopods, whose lateral margins are defined by large coxae rather than tergites, are placed relatively basal, supporting the hypothesis of SCHMALFUSS (1998). Fig. 4A shows a clade of the Phreatoicidea, Asellota, and Oniscidea, whereas Fig. 4B defines a large-coxa clade. A sister group relationship between the Spelaeogriphacea and the Isopoda was a novel result.

The set of 108 distant trees was subjected to a distance survey and two trees were selected that show most different hypotheses (Fig. 4C,D). Both hypothesise a basal position for the Isopoda among the mancoid peracarids, with the remainder of the groups being in a sister clade. They differ in the location of *Spelaeogriphus*, either as sister to the hirsutiid-tanaidacean clade or to *Mictocaris*.

3.4. Combined analysis

Direct optimisation of the 18S sequence data (Tab. 1) used the selected parameter set "substitutions = 2, indels = 1, gap extension = 1", with transition costs equal to transversion costs. In combination with the static homology morphological data (Tab. 4), where the dynamic homology characters were down weighted by a multiplicative factor of 0.5, found a single shortest (least costly) tree of length 23,567. Again, as described for the sequence data analysis, a single tree results owing to the high cost distribution. The Bremer branch supports were uniformly low, ranging from 320 steps (1.4% of total cost) to 443 steps (1.9% of total cost). The low values for the Bremer supports suggests that small changes to the data will result in topologies different from this, thus limiting the strength of inference made from this analysis.

The single tree shows the strong influence of the molecular data, but also finds many more of the accepted monophyletic groups used for the monophyly survey. The position of the Amphipoda in this tree unsurprisingly reflects the independent molecular and morphology analyses, with a basal position external to the mancoid peracarids. The monophyly of the Mysidacea is diluted by the anomalous hirsutiid sequence from *Thetispelicaris*.

The blind subterranean grouping of the Thermosbaenacea, Spelaeogriphacea and Mictacea appears basal to the mancoid peracarids. Within the mancoid clade, the cumaceans are inserted in a paraphyletic sequence between the tanaidacean clades Tanaidomorpha and the Apseudomorpha. The Apseudomorpha are sister to a monophyletic Isopoda. Reflecting the strong position near the tanaidomorphan tanaidaceans in the 18S analysis, the parasitic isopods consisting of the Bopyroidea, Gnathiidae and Cymothoidae are the basal group of the Isopoda in the combined analysis, but are sister to one sphaeromatid species (*Cymodoce tattersalli*). This result must be tested with additional genes and more detailed morphological data. The *Cymodoce* sequence is clearly anomalous, and will need further confirmation. Within the morphological data, the clade membership of the parasitic taxa with the remainder of the Cymothoida is based on fairly general features and tenuous homologies on reduced mouthparts. A paraphyletic Asellota is the next internal isopod group, reflecting a pattern of derivation that fits several published hypotheses (WILSON 1985, 1987; WÄGELE 1989). Notably the deep-sea janiroidean isopods show a single origin beginning with the monophyletic clade of *Acanthaspidia*, *Thylakogaster* and *Dendromunna*. The pectinate pattern of the janiroidean clade places the morphologically specialised family Munnopsidae (WILSON 1989) in the most derived position. The Phreatoicidea are the next clade emerging

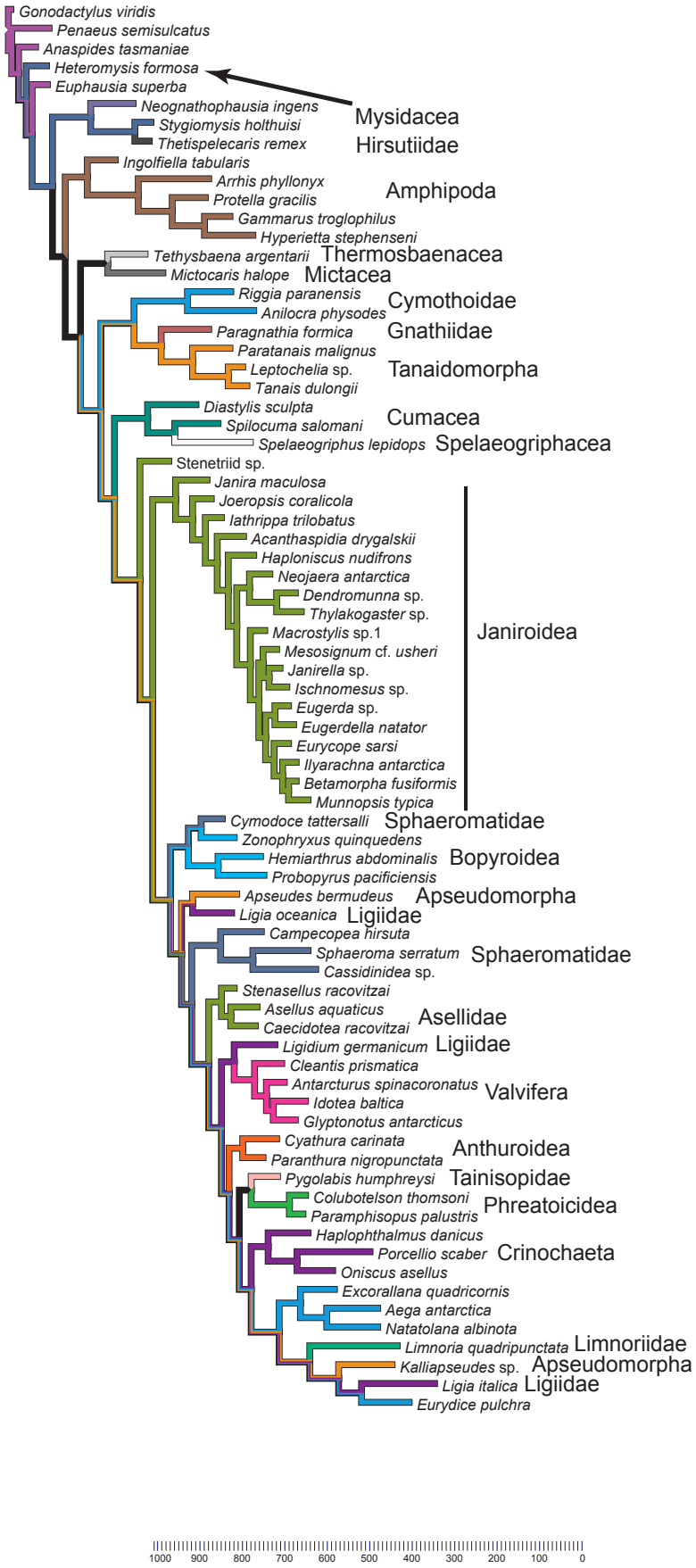

Fig. 2. Single tree resulting from POY 4 direct optimisation parsimony analysis of 18S data from taxa in Tab. 1, using the selected parameter set (tcm 211). Total cost of tree 44,594. Branches colour coded according to groupings, either family-level or order-level (see Tab. 1); basal branches with multiple colours indicate clades that have been separated. Branch lengths were based on an implied alignment generated after the analysis, scale indicated at the bottom.

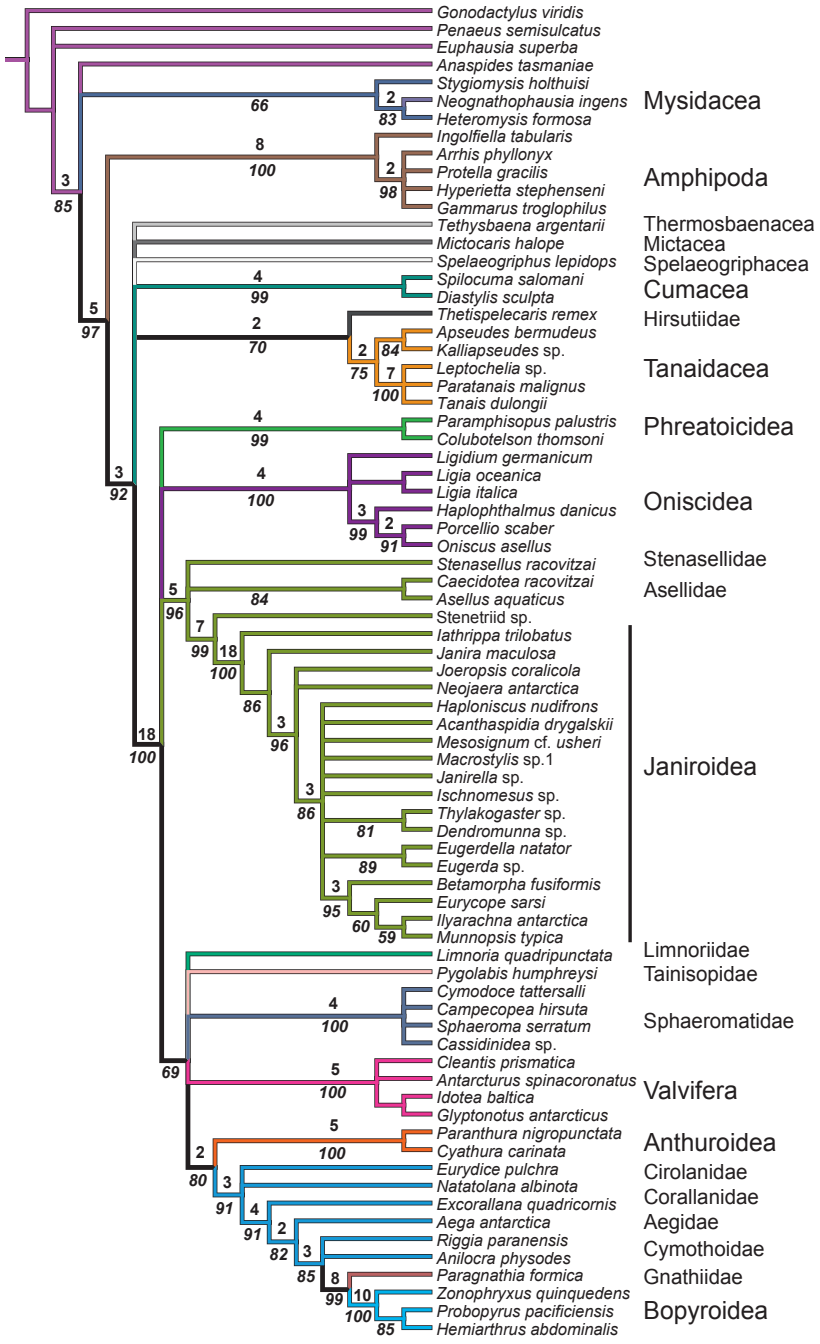

Fig. 3. Strict consensus of 38,079 trees (length 711) resulting from parsimony analysis of taxa in Tab. 1 and the morphological data in Tab. 4. Branches colour coded according to groupings, either family-level or order-level (see Tab. 1). Bremer support values shown above branches, values less than 2 not shown. Jackknife support values (33% deleted, 1000 repetitions) shown in italics below branches.

after the paraphyletic Asellota, with a splitting of the monophyletic "scutocoxiferan" clade between oniscideans and the Tainisopidae, and the remainder. Again the strong influence of the 18S data can be seen in the derived position of the Phreatoicidea and the Oniscidea. This tree also does considerable violence to the current classification of the Isopoda, in particular concerning the absence of a clade of Cymothoida Wägele, 1989, with the free-living cymothoidans strongly separated from the parasitic ones.

4. Discussion

4.1. Effectiveness of the analyses

Many previous peracarid and isopod phylogeny analyses (Siewing 1963; Pires 1987; Watling 1981, 1983, 1999; Wagner 1994; Schram & Hof 1998; Richter & Scholtz 2001; Spears et al. 2005; Poore 2005) have

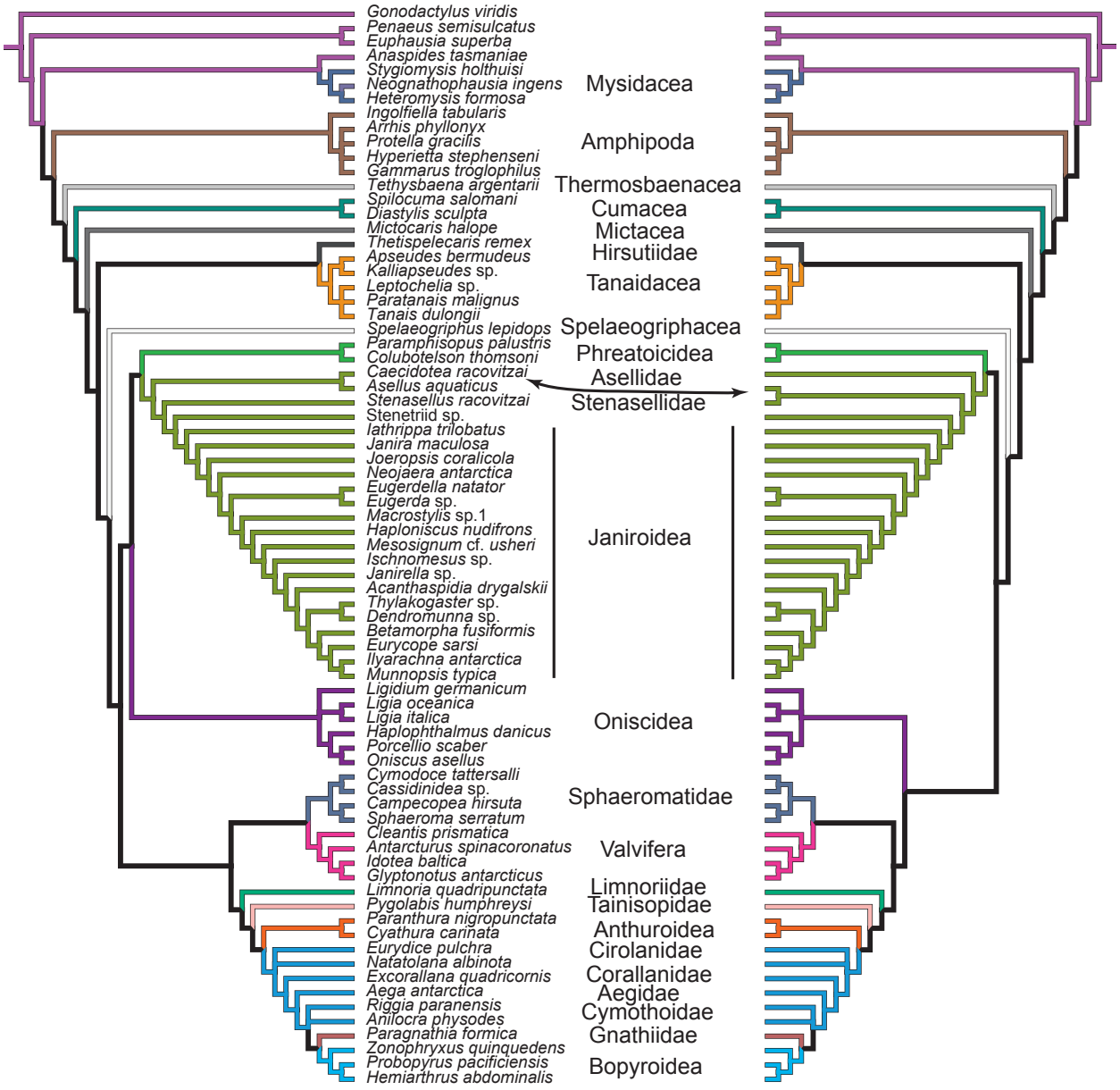

Fig. 4. Four most different trees selected from 38,079 trees (length 711) resulting from parsimony analysis of the morphological data in section 2.3.3. and taxa in Tab. 1 (see data matrix in Tab. 4). Branches colour coded according to groupings, either family-level or order-level. Double-headed arrows indicate differing placements of terminal taxa concerned.

used limited numbers of terminal taxa and did not test the ability of the data to find monophyletic groups. The analyses presented herein ask how well the data work in the context of generally accepted monophyletic groups, a form of sensitivity analysis that can provide a definitive result (WHEELER 1995). The introduction of this background knowledge limits the power of the analysis to test broad hypotheses, but in the current context (the test of two limited hypotheses), the criterion of monophyly for component taxa does not impact the test of the sister group of the Isopoda, and the exploratory aim of the basally derived isopod group. The component clades used as background information only constrained the selection of the 18S parameter set and were free to optimise on the tree.

Although many sequences are available for peracarids on GenBank, this analysis could not use them all for strictly operational reasons: the analysis needed to finish this century! Other sequences that would fill out the major isopod groups are missing or were only present as partial sequences, so molecular zoologists may focus on these missing taxa if isopod phylogeny is their aim. The analysis is somewhat weakened by the presence of anomalous sequences, such as those for *Thetispelicaris* and *Cymodoce*). They were included nevertheless because they fit the criteria for selection and their removal would be *ad hoc*.

Incorporating much detail from secondary structure is another approach with the 18S sequences that could provide better resolution with the direct optimisation

Fig. 4. Continuation.

analysis. Other projects (e.g., Giribet et al. 2000) have used information from secondary structure and divided the 18S sequences into as many as 47 fragments based on secondary structure. Giribet (2001), however, cautions that picking fragments introduces background assumptions into the analysis. If one uses the automatic partitioning method in POY 4.1, it invariably draws the boundaries of the fragments on the primer positions, producing 3 fragments for the 18S sequences. Spears et al. (2005) separated 9 variable regions of the 18S sequences from the stem regions, which results in fewer fragments than if detailed secondary structure is used. Based on experience with POY 3, I chose to use even fewer fragments (10) that bracketed the variable regions with highly conserved regions (explained in Methods section). Although the parameter set for the transformation cost matrix (2,1,1) was applied universally to the sequence data, another approach might apply differing parameter sets to different sections of the data. In the instance that secondary structure was used to generate many homologous fragments, then the parameter optimisation could investigate differing transformation cost matrices for different types of fragments (stem vs. variable regions).

4.2. Aims reached in the analysis

The 18S analysis (Fig. 2) strongly rejects a sister group relationship between the Isopoda and Amphipoda, and

casts doubt on the basal position of the Phreatoicidea. The overall results, however, were not satisfying because several sequences, or groups of sequences, optimised in anomalous locations in the tree topology. Although this result was based on months of computer analysis with parameter exploration, the lack of resolution indicates that 18S is not sufficient on its own to resolve peracarid relationships. Nevertheless, quite a few clades were found using many of the parameter sets (Tab. 2). Given that resolution was better at lower systematic levels, such as families or superfamilies, 18S may be more informative at these levels, but with some constraints. Some easily recognised groups, like the Ligiidae, were scattered through the isopod tree, so such groups probably require the use of other sequence markers to resolve their relationships on a molecular basis. Recent analyses have successfully included the 18S marker (e.g., LINDGREN et al. 2004) with several other genes in combination with morphological data, so this now standard approach is the way forward for combined analyses of the peracarids.

The morphological dataset should be considered preliminary. It was built from multiple datasets, and much effort was spent standardising the terminology and homologies implied by the categorical data. During the survey, several new characters were introduced, but in general, much of the rich information that is available for isopods was not represented in the current morphological data. For example, the author's data on the Phreatoicidea (WILSON 2008b) alone currently includes 177 phylogenetic characters, and is derived from a taxonomic database comprising 730 characters. Additionally some characters, which have been used in past analyses (e.g., general body shape), were not used owing to unclear and poorly defined homologies. To some extent, the preliminary nature of the dataset explains why so many trees were found in the morphology analysis, with a weakly resolved consensus tree (Fig. 4). Much of the available detail has not been included, in particular for major groups like the deep-sea Asellota, the Oniscidea, the Sphaeromatidae, the Valvifera and the Cymothoida. Were these data included, the findings may have been better defined. Although not shown here because the primary aim was to provide a combined analysis, several different weighting regimes (implied weights, successive weighting) substantially minimised the number of trees. Both of these weighted analyses found a topology that resembles previous analyses (BRUSCA & WILSON 1991; WÄGELE 1989) with the progression of the Phreatoicidea, Asellota, Oniscidea and the remainder of the Isopoda in differing positions.

In combination, each dataset resolves some of the weaknesses of the other dataset, and this displays each dataset's strengths and weaknesses. On the improvement side, the apseudomorph tanaidaceans are removed from an internal position within the Isopoda and many isopod groups are found to be monophyletic, as expected. Both datasets agree on the position of the amphipods, and both find a non-basal position for the Phreatoicidea (albeit differently). Both agree on the general pattern of derivation of the internal asellotan taxa. The morphological dataset allowed for multiple hypotheses for the sister group of the isopods and relationships to the remainder of the peracarids, but in combination the result becomes better defined, even though the tanaidaceans are rendered nonmonophyletic. The 18S data also influence the results negatively. The anomalous position for the *Thetispelicaris* remains as such, and the basal position of the parasitic groups in the Isopoda is difficult to accept because the morphological analysis strongly supports their inclusion in a Cymothoida clade. Overall, the combined analysis provides new hypotheses of relationship that require further tests.

Because the aims were kept to simple achievable tests of isopod and peracarid phylogeny, the analysis finds a well supported result with regard to the sister group of the isopods, and several new hypotheses for the basal sister group relationship within the isopods.

We can now put to rest the idea that Isopoda and Amphipoda are sister groups, thus vindicating the ideas of the early crustacean zoologists concerning the classification of the peracarids (CALMAN 1906; SIEWING 1963). Also supporting their ideas, the tanaidaceans remain in the best position for being the sister group. Indeed, the 18S analysis supported the idea, at least partially, that tanaidaceans were part of the isopods. The spelaeogriphacean-isopod sister group relationship from the morphological results requires more investigation. A few derived features support this relationship, such as the elongate ischium of the walking legs. Although not included in the current morphological data, I have noted a similarity between mandibular bodies of *Spelaeogriphus* and the Asellidae and some other asellotans. While most isopod mandibles have an abbreviated mandibular body posterior to the insertion of the palp, the body is elongate and marked by bands of muscular insertions in the Asellota and in *Spelaeogriphus*. To understand this form, however, the internal head musculature must be examined, which is currently poorly detailed for many peracarid taxa.

For the second aim of this analysis, we are at sea amongst competing hypotheses. We are left contemplating a downfall of the once comfortable idea that the Phreatoicidea are the sister group of the remaining Isopoda. Our comfort with this idea stemmed partially from morphological analyses (WÄGELE 1989; BRUSCA & WILSON 1991), but also from their ancient position in the fossil record (SCHRAM 1970). The major events of phreatoicidean morphological evolution are probably ancient because Triassic fossils are crown clade phrea-

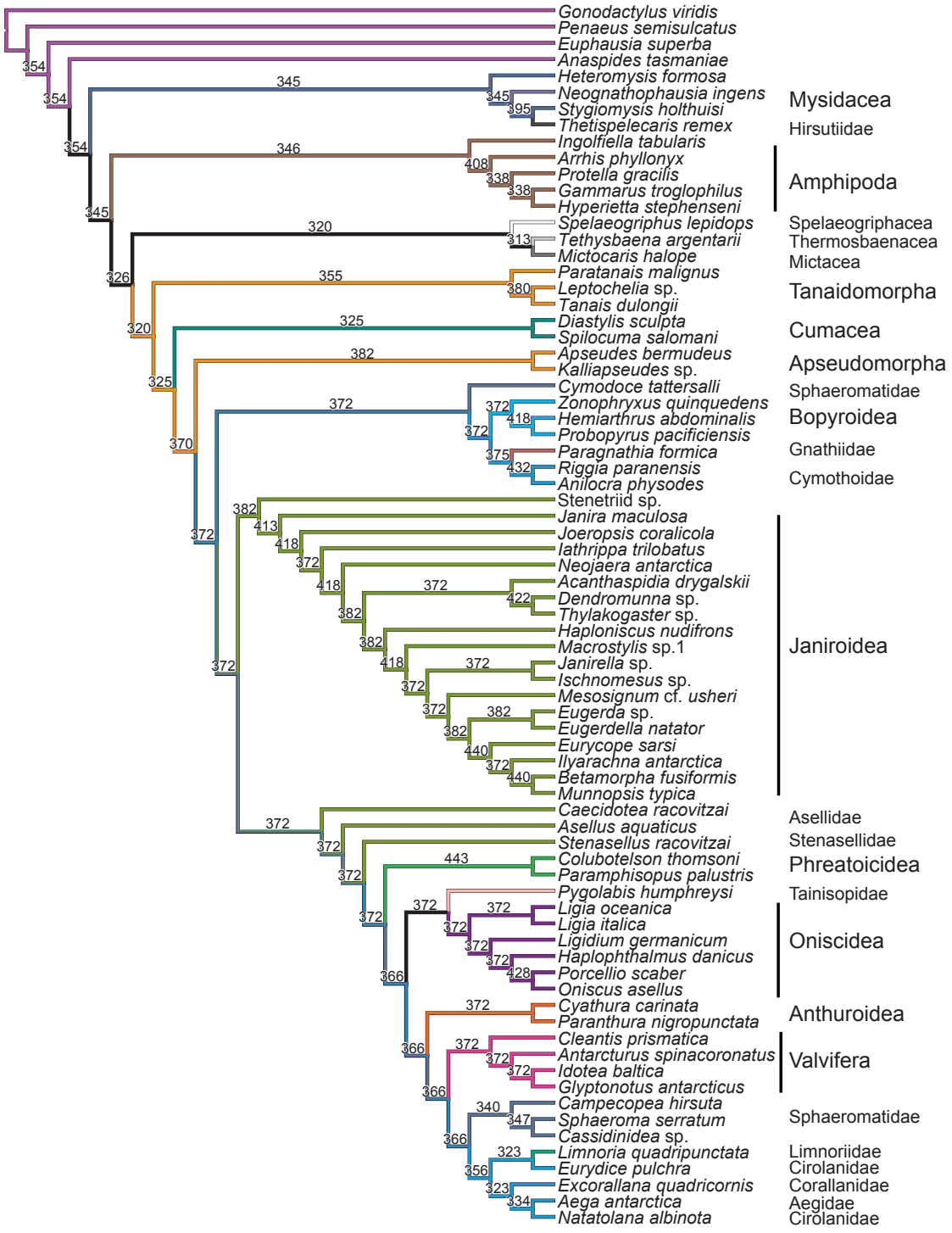

Fig. 5. Single tree resulting from POY 4 direct optimisation parsimony analysis of 18S data and morphological data from taxa in Tab. 1, using the selected parameter set (tcm 211) and sequence data down weighted by 50%. Total cost of tree 23,567. Branches colour coded according to groupings, either family-level or order-level. Bremer support values are given on each branch, representing 1.4–1.9% total cost of the tree.

toicideans, and not basal at all (Wilson & Edgecombe 2003). The Carboniferous fossil *Hesslerella* Schram, 1970 may also be a member of the crown phreatoicideans, although this is yet to be tested.

Based on preliminary study (Wilson 1999), one hypothesis presented a division of the Isopoda into a Phreatoicidea + Asellota clade and another clade of higher isopods, with Oniscidea branching off basally in the latter clade. Peculiarities seen in the former clade include a near universal presence of a modified male pereopod IV in the Phreatoicidea, which is also present in the Asellidae and several other basal asellotans, and oostegites limited to the first 5 thoracopods. The oniscideans and other higher isopods typically show ooste-

gites VI, and none have a similarly modified male pereopod IV.

But the combined analysis goes further, with the phreatoicideans and onscideans placed into clearly non-basal positions. Certainly the Oniscidea are a highly specialised terrestrial group (SCHMIDT 2008), with a recent fossil record only, so this hypothesis, although upsetting previous ideas, can be accommodated. Perhaps we have been overly impressed with the fossil record. As we cannot expect the fossil record to be complete, especially with respect to originations, ancestral isopods potentially arose even earlier in the Paleozoic than the Carboniferous. The phreatoicideans are not generalised isopods, being highly modified for their infaunal lifestyle.

In all analyses, the Asellota are placed near but not at the origin of the Isopoda, although the details differ between the analyses. Setting the peculiarities of the Asellota aside, however, asellotans are fairly generalised isopods, at least in the basal subgroups, e.g., Asellidae and Stenasellidae, and have coxal configurations that are found elsewhere in the Peracarida (HESSLER 1984; HAUPT & RICHTER 2008). The freshwater biogeographic record of these two basal asellotan families also indicates that they are ancient (WILSON 2008a), with distributions that are either complementary to (e.g., Asellidae) or congruent with (e.g., Protojaniridae) the Gondwanan distribution of the Phreatoicidea.

A basal position of the parasitic Cymothoida remains a contradictory hypothesis that requires additional analyses. The analysis suggests that the unity of the Cymothoida remains uncertain, with some but not all of its subgroups being basally derived. Parasitic members of the Cymothoida, the Bopyridae, were established in a broad range of decapod hosts during the Jurassic and Cretaceous (MARKHAM 1986), and sphaeromatoid fossils are known from the Triassic (e.g., BASSO & TINTORI 1994). Given that we know that isopods were present in the Paleozoic (Phreatoicidea), placing the date of origin of most of the major groups in this era may be a reasonable hypothesis. But given that a basal position of the Phreatoicidea and the Asellota is under question, the phylogenetic arrangements and classification of the Isopoda must be revisited with new analyses and more data.

4.3. Other implications

4.3.1. Classification

Making changes to the higher level classification and nomenclature is currently unwarranted, owing to the many open questions and deficiencies in data sources. At the same time, some of the established classifications can be called into question. At the peracarid level, the subterranean groups (Mictocaridae, Hirsutiidae (also deep-sea), Spelaeogriphidae, and Thermosbaenacea) are not especially stable regarding their positions relative to the other, larger groups. The nomenclature introduced for their classification should be set aside for the moment and reconsidered as more evidence comes to light.

The evidence does allow for a few observations, however. The Thermosbaenacea consistently appear among the mancoid peracarids and can be considered part of the group, a departure from SIEWING's (1963) original concept. The lack of oostegites is no longer a sufficient reason to maintain a separate Pancarida. The Hirsutiidae have affinities with the Tanaidacea; if the second thoracopod exhibited a chela, no one would have had any difficulty placing this family among the tanaidaceans. Therefore, its relationship to the Tanaidacea should be tested in more detail. With the revised position for the Hirsutiidae, the order Mictacea can be confined to the Mictocaridae.

Within the Isopoda, the suborder Cymothoida is rejected by the molecular data but supported by the morphological data. The molecular data prevail over the morphological data in combination, but the existing classification should be retained until further research can address this question. The cymothoidan families Cirolanidae, Corallanidae and Aegidae are not clearly separated by this analysis, and are not even monophyletic owing to the insertion of *Limnoria*. Admittedly, the position of *Limnoria* was unstable in the analyses, but at least this result suggests that the entire family-level classification of the superfamily Cymothoidea requires revisiting. BRANDT & POORE (2003) proposed a subordinal rank for the Tainisopidae, although their cladogram was unresolved, and included only one exemplar of this family. The current analysis finds multiple positions for *Pygolabis humphreysi*, with the combined analysis aligning it rather contradictorily with the oniscideans.

4.3.2. Deep-sea origins?

A molecular approach (RAUPACH et al. 2004, 2009) to evaluate patterns of colonisation of the deep sea supported patterns proposed by earlier studies (WILSON 1980; HESSLER & WILSON 1983). Multiple clades that are found in the deep sea appear to have independent phylogenetic origins according to RAUPACH et al. (2004, 2009), which was argued to be evidence for multiple colonisations of the deep-sea. The current analyses, either for separate data partitions or combined, find a single phylogenetic origin for a diverse set of deep-sea taxa, in contradiction to these molecular results. Caution is required, however, in interpreting branch-

ing patterns in phylogenetic trees as relevant to biogeographic origins. Although we may observe that a generalised habitat type may optimise on a tree in a particular pattern, we cannot be certain that the marine ancestors were present in that habitat, especially because the oceanographic conditions of earlier eras were quite different than those that are found today (Hessler & Wilson 1983). Moreover, recent information (Wilson 2006) suggests that "deep-sea" isopods may not be necessarily confined to the deep-sea, but may be found on the outer shelf in the tropics. This habitat was identified by Hessler & Wilson (1983) as a possible source of deep-sea fauna during the Mesozoic Era. Nevertheless, this opens the question as to how exactly one defines a "deep-sea isopod" if such taxa can be found on the environmentally variable tropical outer shelf at temperatures above 18–20°C.

4.4. Further research

Looking forward, the results show that detailed morphological studies are needed. These include horizontal studies (across many taxa) of skeletomusculature, reproductive organs, nervous systems and embryology. A lack of information was one of the weaknesses of scoring large numbers of taxa for such systems. As a result, many scorings in this dataset rely on presuming a "ground pattern" for certain clades because only a few species have been investigated. Testing the morphological ground pattern is therefore an essential research program. Vertical studies, where many major systems are evaluated in single key taxa like the Hirsutiidae (e.g., *Thetispelicaris*) are also urgently needed. The scorings for this latter taxon necessarily contained many unknowns because the internal anatomy is poorly known. Finally, as mentioned above, more sequence data are needed. Representatives from more families, especially within the Isopoda (e.g., Munnidae, Santiidae, Protojaniridae, Calabozoidae, Microcerberidae), should be sequenced. In so doing, other markers, both coding and non-coding, nuclear and mitochondrial, should be surveyed across a wide range of taxa with the fundamental aim to understand peracarid crustacean phylogeny. In combination, these efforts should resolve the many questions left unanswered.

5. Acknowledgements

This paper is derived from the accumulation of information from many sources, and efforts of numerous investigators, all of whom are thanked but cannot all be mentioned here. Several investigators are notable: Tom Iliffe, for discovering rare cave species that enrich our understanding of crustaceans; Trish Spears & Larry Abele, who pioneered the use of SSU rDNA data in crustacean phylogenetics; J.-W. Wägele & co-workers, for adding many new 18S sequences to GenBank; Christian Wirkner & Stefan Richter for describing new anatomical homologies, and Robert Hessler, for his fundamental research on crustacean anatomy. I am grateful for the assistance of others who helped in various ways: Shane Ahyong, who collaborated on our 2001 presentation at the Crustacea conference; Kim Larsen, who advised on tanaidacean matters; Gonzalo Giribet, Andres Varón & the POY mail list, who assisted with POY technical issues; and Claudia Arango, who checked the analysis. Stefan Richter and Cara Francis provided new 18S sequences that were used in the analysis. Claudia Arango, Klaus-Dieter Klass, Stefan Richter, Christian Wirkner and two referees made helpful suggestions that substantially improved this manuscript. None of these colleagues, however, is responsible for any faults remaining in this paper.

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Electronic Supplement Files

at http://www.arthropod-systematics.de/ ("Contents")

File 1: Isopoda_18S_KL8.fas. Unaligned small subunit sequence data (18S) with partition markers ("#") inserted. See Tab. 1 for taxon specific data and accession numbers.

File 2: Morph_Isopod_percarid_9.ss. The morphological data in Hennig86 format (see GOLOBOFF et al. 2008 and references cited therein). Tab. 4 contains the data in tabular form.

File 3: Poore_2005_chng_Mesquite.nex. Data from POORE (2005), fossil taxa deleted, recoded as described in section 1.1.

File 4: Spears_etal_2005_18S.fas. Unaligned small subunit sequence (18S) data from SPEARS et al. (2005) with partition markers ("#") inserted. *Mictocaris halope* (accession number GQ175864) included for comparability.