

The position of crustaceans within Arthropoda - Evidence from nine molecular loci and morphology

GONZALO GIRIBET¹, STEFAN RICHTER², GREGORY D. EDGECOMBE³ & WARD C. WHEELER⁴

¹ *Department of Organismic and Evolutionary Biology, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.*

² *Friedrich-Schiller-Universität Jena, Institut für Spezielle Zoologie und Evolutionsbiologie, Jena, Germany*

³ *Australian Museum, Sydney, NSW, Australia*

⁴ *Division of Invertebrate Zoology, American Museum of Natural History, New York, U.S.A.*

ABSTRACT

The monophyly of Crustacea, relationships of crustaceans to other arthropods, and internal phylogeny of Crustacea are appraised via parsimony analysis in a total evidence framework. Data include sequences from three nuclear ribosomal genes, four nuclear coding genes, and two mitochondrial genes, together with 352 characters from external morphology, internal anatomy, development, and mitochondrial gene order. Subjecting the combined data set to 20 different parameter sets for variable gap and transversion costs, crustaceans group with hexapods in Tetraconata across nearly all explored parameter space, and are members of a monophyletic Mandibulata across much of the parameter space. Crustacea is non-monophyletic at low indel costs, but monophyly is favored at higher indel costs, at which morphology exerts a greater influence. The most stable higher-level crustacean groupings are Malacostraca, Branchiopoda, Branchiura + Pentastomida, and an ostracod-cirripede group. For combined data, the Thoracopoda and Maxillopoda concepts are unsupported, and Entomostraca is only retrieved under parameter sets of low congruence. Most of the current disagreement over deep divisions in Arthropoda (e.g., Mandibulata versus Paradoxopoda or Cormogonida versus Chelicerata) can be viewed as uncertainty regarding the position of the root in the arthropod cladogram rather than as fundamental topological disagreement as supported in earlier studies (e.g., Schizoramia versus Mandibulata or Atelocerata versus Tetraconata).

1 INTRODUCTION

Crustaceans show a remarkable amount of morphological disparity with respect to tagmosis, limb morphology, and internal anatomy (Schram 1986). Improving our knowledge of the phylogenetic relationships of crustaceans is, therefore, always a challenge. For more than a century, phylogenetic scenarios have shown as much diversity as the taxon itself.

The position of Crustacea within the arthropods is a matter of incessant debate. Paleontologists often favored a closer relationship between Crustacea and Chelicerata (Cisne 1974; Bergström 1979), whereas most neontologists (with the exception of the Manton school) argued for a monophyletic Mandibulata with Crustacea as a sister group to Tracheata or Atelocerata (myriapods + hexapods). During the last decade, however, increasing evidence supports a closer relationship between crustaceans and hexapods, leaving the myriapods outside (Fig. 1). Early molecular analyses (e.g., Turbeville et al. 1991) favored a crustacean-hexapod clade, named Pancrustacea (Zrzavý & Štys 1997) or Tetraconata (Dohle 2001), which has subsequently been substantiated in almost all molecular analyses of arthropods (e.g., Wheeler et al. 1993: fig. 8; Friedrich & Tautz 1995; Giribet et al. 1996, 2001; Hwang et al. 2001; Regier & Shultz 2001; Kusche et al. 2003; Mallatt et al. 2004). In addition, mitochondrial genome rearrangements (Boore et al. 1998) and certain morphological characters were proposed as support for a crustacean-hexapod clade (Averof & Akam 1995; Whittington 1995; Dohle 2001). However, the traditional concept of a monophyletic Atelocerata still has advocates (Klass & Kristensen 2001; Kraus 2001).

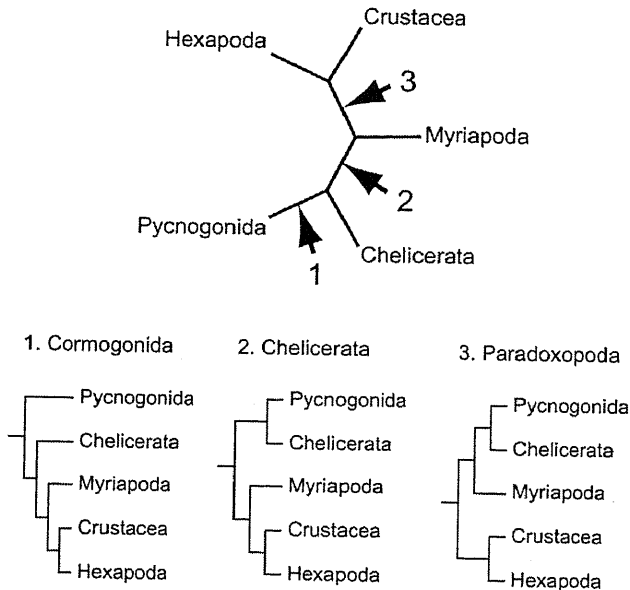


Figure 1. Alternative hypotheses of arthropod relationships and putative positions of the root. Rooting point 1 supports monophyly of Cormogonida; rooting point 2 implies a single origin of chelicerates or chelifores; rooting point 3 shows monophyly of Paradoxopoda as the sister group to Tetraconata.

Other aspects of arthropod relationships have also been debated intensively. Myriapods have been suggested to be paraphyletic, with Progoneata as a sister group to the Hexapoda, and Chilopoda as a sister group to Progoneata + Hexapoda (Kraus 1998, 2001). Others have considered myriapods as being the monophyletic sister taxon of Tetraconata (Edgecombe & Giribet 2002) (Fig. 1). However, some molecular studies favor a clade including Myriapoda and Chelicerata (e.g., Friedrich & Tautz 1995; Hwang et al. 2001; Mallatt et al. 2004),

recently named Paradoxopoda (Mallat et al. 2004) or Myriochelata (Pisani et al. 2004). Some correspondences in the development of the nervous system might even support this relationship from a morphological point of view (Dove & Stollewerk 2003; Kadner & Stollewerk 2004), whereas recent studies on compound eye structure (Müller et al. 2003) and mandible morphology (Edgecombe et al. 2003) have added support for the Mandibulata hypothesis, contradicting Paradoxopoda (see a review in Richter & Wirkner 2004).

Independent of those questions, crustacean monophyly itself remains unresolved (see Schram & Koenemann 2004a, 2004b). Crustacean monophyly was suggested by Lauterbach (1983) after a careful analysis of the morphological evidence available at that time, and has been defended by Waloszek (Walossek 1999; Waloszek 2003) based on extant morphology and evidence from fossil taxa. Cladistic morphological analyses also support a monophyletic Crustacea (Wheeler et al. 1993; Wheeler 1998; Schram & Hof 1998; Wills 1998; Zrzavý et al. 1998; Edgecombe et al. 2000; Giribet et al. 2001; Edgecombe 2004; Wheeler et al. 2004). On the contrary, with few exceptions (e.g., Negrisolo et al. 2004), analyses based solely on molecular data and including at least two major crustacean taxa suggest non-monophyly (Friedrich & Tautz 1995 2001; Giribet & Ribera 2000; Hwang et al. 2001). Paraphyly with respect to hexapods is a recurring pattern in these analyses. Additionally, in light of the Tetraconata concept, an increasing number of morphological characters support crustacean paraphyly. In particular, Malacostraca is a good candidate as a potential sister group of Hexapoda because of the shared presence of certain neuroanatomical features such as specific pioneer neurons (Whittington 1996) and neuroblasts (Harzsch 2001). However, these characters might also be present in branchiopods (Duman-Scheel & Patel 1999) and they are not well studied in the maxillopodan taxa (see Richter 2002, for a review of these characters). Recently, a close relationship between hexapods, malacostracans and remipedes has been suggested based on brain characters (Fanenbruck et al. 2004). A hexapod-malacostracan clade is also supported by the presence of two optic chiasmata between the optic ganglia (Harzsch 2002; Sinakevitch et al. 2003). Some of the mentioned molecular analyses indeed favor a closer relationship between malacostracans and hexapods (Wilson et al. 2000; Hwang et al. 2001), sometimes including remipedes (Regier & Shultz 2001: fig. 1A), but others support a closer relationship of branchiopods to hexapods (Friedrich & Tautz 2001).

Concerning the higher crustacean groups, there seems to be no doubt that the two smaller taxa, Cephalocarida and Remipedia, with their unique morphology, are each monophyletic. There is also increasing evidence from both morphology and molecular data that Branchiopoda and Malacostraca are each monophyletic (Walossek 1999; Giribet & Ribera 2000; Spears & Abele 2000; Giribet et al. 2001; Richter & Scholtz 2001). Concerning Maxillopoda, molecular analyses failed to show its monophyly (Giribet et al. 2001; Mallat et al. 2004) and morphological support for the group seems to be weak (but see Walossek 1999 for a different opinion).

The relationships among these main clades, Remipedia, Cephalocarida, Branchiopoda, Malacostraca, and the putative Maxillopoda have been discussed for a long time, although mostly in the context of crustacean monophyly. In particular, Thoracopoda - including Cephalocarida, Branchiopoda and Malacostraca (see Hessler 1992; Ax 1999; Edgecombe et al. 2000; Richter 2002) and Entomostraca - including Cephalocarida, Branchiopoda and Maxillopoda - as sister taxon to Malacostraca (Walossek 1999; Waloszek 2003) represent reasonable alternatives (Fig. 2).

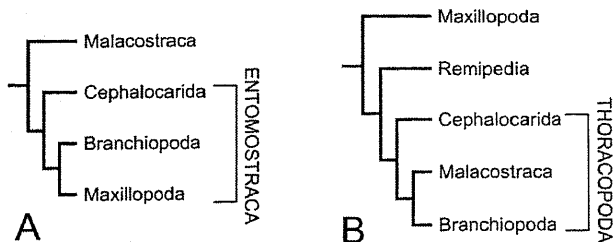


Figure 2. Two alternative hypotheses showing suggested relationships of Crustacea. (A) According to Walossek (1999), Entomostraca is monophyletic. (B) Relationships based on Edgecombe et al. (2000) supporting the Thoracopoda concept of Hessler (1992).

One obvious issue that has become evident is that crustacean phylogeny can be only sensibly discussed in the framework of global arthropod relationships (see also Schram & Jenner 2001; Richter 2002). However, only a few phylogenetic analyses that deal with arthropods using a broad sample of crustacean taxa are available based on molecular data (Giribet & Ribera 2000; Hwang et al. 2001; Mallatt et al. 2004), or using a combined approach of molecules and morphology (Edgecombe et al. 2000; Giribet et al. 2001; Wheeler et al. 2004). Here we present a re-analysis of arthropod relationships based upon the most comprehensive data set yet assembled to study such problem, the 52-taxon, 303-morphological character, eight-gene data set of Giribet et al. (2001). To that analysis we have added 15 taxa, mostly crustaceans (24 crustaceans are represented in the new analyses versus the previous 13), refined the terminal taxa by decreasing the number of composite taxa, refined morphological codings and added another 50 morphological characters, and added ca. 25% new sequences for the eight previous loci. Moreover, we have added a new gene (elongation factor-2), and increased the previous sampling of the D3 region of 28S rRNA to the complete gene sequence. We also doubled the length of the COI gene fragment used in our previous analyses. With the new data, we attempt to shed new light on the long-standing controversies in arthropod phylogenetics, especially for those aspects that concern the position of crustaceans, their monophyly, and the relationships among its constituent lineages.

2 METHODOLOGY

We analyze data for 67 taxa (Appendix 1, Tables 1 and 2), 352 morphological characters (Appendices 2 and 3), and 9 molecular loci for over 10 Kb per complete taxon. The data are analyzed as in several of our previous studies by using the direct optimization method (Wheeler 1996) and in the computer software POY version 3.0 (Wheeler et al. 2002).

2.1 *Taxa*

The analyses here presented include data from 67 terminal taxa, 2 Onychophora, 2 Tardigrada, and 63 Arthropoda (3 Pycnogonida, 10 Chelicerata, 13 Myriapoda, 13 Hexapoda, 1

Remipedia, 1 Cephalocarida, 8 Malacostraca, 6 Maxillopoda [including 1 Pentastomida], and 8 Branchiopoda).

We agree with Prendini (2001) that one should use species as terminals for phylogenetic studies. In that respect, we have attempted to select our terminals based on well-studied species both at morpho-anatomical and molecular levels, and a large proportion of our taxa are based on an exemplar approach. Whenever this was not possible, and always with the aims of representing the maximum amount of available data per terminal, we combined representatives of several species within the same genus; sometimes this combination includes unidentified species within the genus. In a few cases, suprageneric terminals were created by pooling data from different species only if the evidence for the monophyly of such taxa is undisputed. That way, we represent the following suprageneric terminals in our analyses: Peripatidae, Buthidae, Scorpionidae, Scolopendridae, Geophilidae, Pauropodinae, Polyxenidae, Sphaerotheriidae, Acerentomidae, Campodeidae, Japygidae, Meinertellidae, Machilidae, Lepismatidae, Remipedia, Oniscidea, Calanoida, Stomatopoda, and Pentastomida. The exact species pooled to constitute these terminals are available in Appendix 1 (Table 1).

2.2 *Morphological characters*

The data we present, 352 characters, are based on the data set presented by Giribet et al. (2001), later more explicitly described and updated (Edgecombe 2004). Characters have been refined since then, especially for crustaceans, and new data available since the publication of the previous articles were incorporated into the new matrix (Appendix 2). The matrix in NDE (Page 2000) format is available upon request from the authors.

All morphological characters were considered unordered, with the exception of characters 3, 28, 92, 153, 173, 185 and 232. Character 300, referring to the male gonopods, includes 13 character states to reflect its broad variability across arthropods. This character required independent coding because it needed special analysis (most programs cannot handle more than 10 character states). As such, character 300 was coded as all '?' in the file used for analyses (file **artmor1.ss**), and a second file containing a single Sankoff character with the 13 states was generated (file **artmor2.ss**). This improves upon our previous analyses (Giribet et al. 2001; Edgecombe 2004), in which the gonopod character presented 11 states, but the 11th state was coded as '?' for Remipedia. Treatment of more than 10 character states in the program POY required novel implementation by one of us (WCW).

2.3 *Molecular sampling*

The data presented here include information on nine molecular loci. Compared to our previous analysis (Giribet et al. 2001), we were able to add DNA sequence information for several extra taxa, but we also made an effort to fill in many sequence data that did not amplify in our previous analysis. For 28S rRNA, we are now using the complete gene for a large proportion of the samples, although some remain partial (but longer than 2 Kb), and a few more remain at ca. 350 bp for the D3 expansion fragment. We also added the novel data on elongation factor-2 published by Regier & Shultz (2001), which were not available

when we published our previous studies. Therefore, we use molecular data for the following markers (approximate number of bp used indicated in parentheses): 18S rRNA (ca. 1,800 bp), 28S rRNA (ca. 3,600 bp), U2 sn rRNA (130 to 133 bp), histone H3 (327 bp), elongation factor-1 α (1,092 bp), elongation factor-2 (2,178 to 2,184 bp), RNA polymerase II (1,161 bp), cytochrome *c* oxidase subunit I (1,230 bp), and 16S rRNA (437 to 540 bp). This amounts to over 12 Kb of genetic information per complete taxon and includes genes evolving in very different manners, including nuclear coding and non-coding markers, and mitochondrial coding and non-coding. No comparable molecular data set has ever been compiled to study the evolution of any group of invertebrate animals.

2.4 Analytical methods

All data were analyzed simultaneously under direct optimization using the program POY version 3.0. Our choice for analyzing data in such a fashion is straightforward; we do not think that DNA-based homology can be assigned independently of topology.

Homology is the relationship between features that is derived from their shared, unique origin on a cladogram. Two features are homologous if their origin can be traced back to a specific transformation on a specific branch of a specific cladogram. The same features may or may not be homologous on alternate cladograms. Therefore, homology is entirely cladogram dependent and the relative optimality of alternate cladograms determines whether or not features have this relationship. The dynamic homology framework (Wheeler 2001) extends through optimization of transformations to the correspondences among features (often referred to as 'putative' or primary homology) themselves. The joint scenario of correspondence and transformation is chosen such that the overall cladogram cost is minimal. In this framework, there is no distinction between 'putative' or 'primary' and 'secondary' homology - all variation is optimized *de novo* for each cladogram (contra Simmons 2004).

In our study morphological data are analyzed using a static homology framework, and several fragments of DNA sequences of protein-coding genes were analyzed this way. Not all coding fragments could be analyzed that way, and they pose identical (or even harder) challenges to homology recognition as in non-coding regions. Therefore, 'alignment-issues' should not be a reason for preferring coding versus non-coding genes, despite the claim of some authors.

All data were analyzed using a combination of branch swapping and refining techniques that included 20 random addition replicates followed by tree fusing (Goloboff 1999), ratcheting (Nixon 1999), TBR branch swapping, and another round of tree fusing. The data were run under 20 parameter sets, and the resulting trees for each parameter set were pooled into a file and submitted to tree fusing once more, for each of the parameter sets analyzed. Variables studied were different indel costs and transversion/transition ratios (Wheeler 1995). The relative weight of the morphological matrix was increased as the molecular costs increased, so its signal would not be obliterated by the much larger costs assigned to indel events or transversions (i.e., morphological transformation weight = indel weight). Nodal support was evaluated by jackknifing (Farris et al. 1996), as implemented in POY.

Splitting of large DNA sequences into smaller fragments speeds up analyses (Giribet 2001), and it helps to incorporate information on secondary structure or for refining original

homology statements (Giribet & Wheeler 2001). In that respect, we have partitioned several of the markers employed in our analyses as follows:

- 18S rRNA was divided into 29 sequence fragments, four of which (fragments 4, 9, 21 and 28) were deactivated due to extreme length variation (even within species) that would cause random matching of bases at no cost.
- 28S rRNA was divided into 31 sequence fragments from which 10 were deactivated (fragments 1, 7, 9, 10, 16, 18, 22, 25, 30, and 31) due to extreme length variation or to the presence of missing data for most taxa.
- 16S rRNA was divided into 9 sequence fragments from which fragment 1 was deactivated.
- Cytochrome *c* oxidase subunit I (COI hereafter) was divided into 12 sequence fragments using the translation to amino acids, and fragment 9 was deactivated due to the lack of sequence data for most taxa (this fragment connects our previously used fragment between primers LCO and HCO and a new COI fragment used in this analysis). The COI fragments showed length variation and therefore were analyzed under a dynamic homology framework.
- Elongation factor-2 was divided into six sequence fragments, analyzed under dynamic homology due to presence of sequence length variation.
- Elongation factor-1 α was analyzed in five prealigned sequence fragments.
- RNA polymerase II was divided into six sequence fragments, from which fragments 2 and 5 were deactivated (due to lack of sequence data for most taxa) and was analyzed under static homology.
- The other two loci were analyzed as single fragments, U2 sn rRNA under dynamic homology, and histone H3 under static homology.

3 RESULTS

3.1 *Morphological analysis*

The analysis of the morphological data set resulted in three trees at 740 steps. The strict consensus of these trees, with jackknife proportions over 50%, is presented in Figure 3.

This tree places pentastomids outside of Arthropoda, and shows monophyly of the main arthropod lineages; Pycnogonida, Chelicerata¹, Myriapoda, Hexapoda, and Crustacea, as well as the higher groups Pycnogonida + Chelicerata, Mandibulata and Tetraconata. While the major arthropod taxa receive jackknife support values above 50%, none of the relationships among these taxa receives jackknife support above 50%. The monophyly of Arthropoda also has low jackknife support, and only when pentastomids are considered arthropods does one get jackknife support above 50% (Fig. 3).

¹ For many authors, the taxon Chelicerata is formed by Pycnogonida and by a clade formed of Xiphosura + Arachnida, which is often referred to as Euchelicerata. Due to the possible paraphyly of Chelicerata *s. lat.*, we prefer to adopt the terms Pycnogonida and Chelicerata, the latter referring to what other authors term Euchelicerata. We follow this nomenclature throughout this chapter.

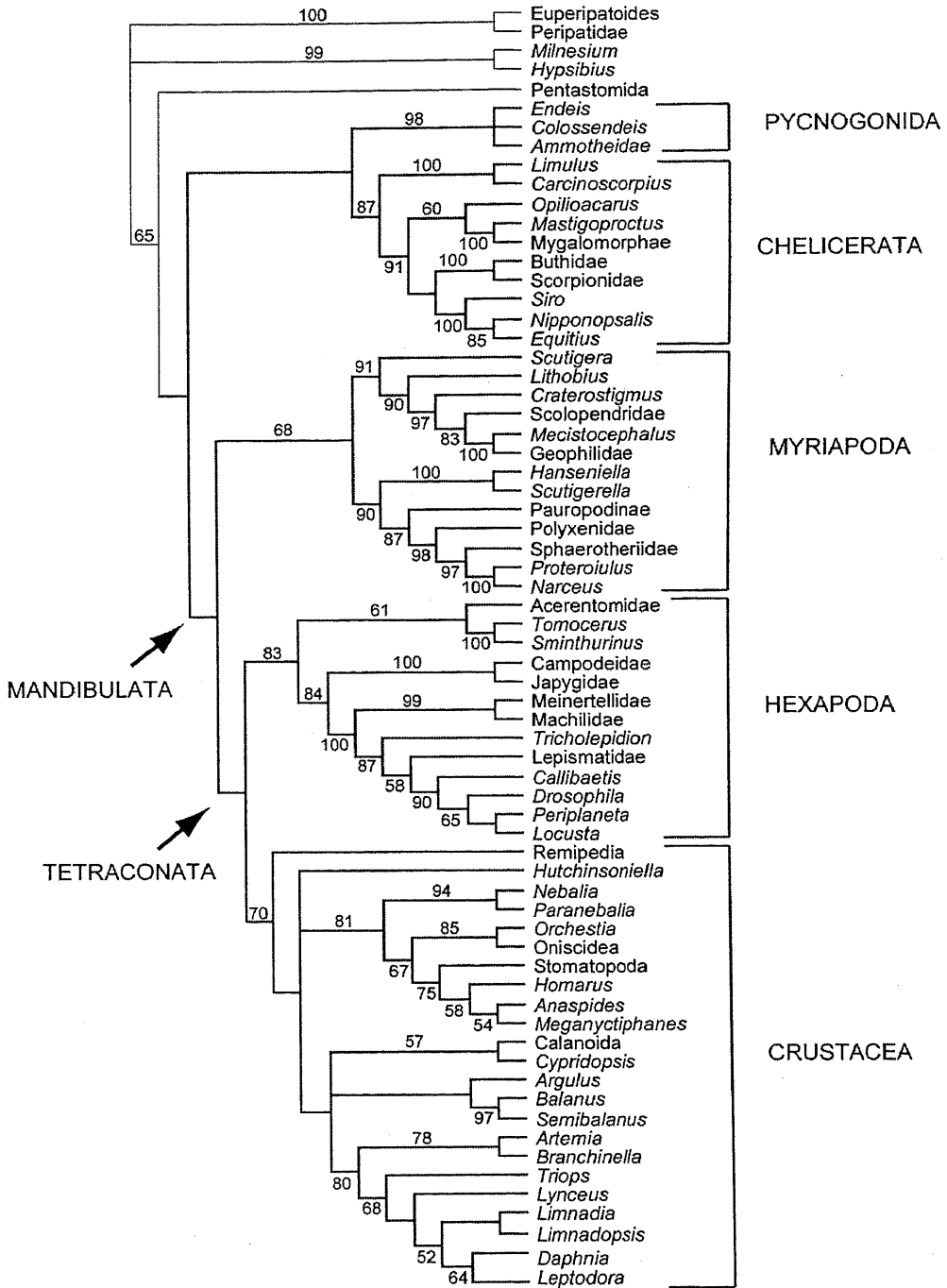


Figure 3. Strict consensus of 3 trees at 740 steps for the parsimony analysis of the morphological data set from Appendix 3 (see Appendix 2 for character descriptions). Numbers on branches indicate jack-knife support values above 50%.

Relationships within Crustacea show Remipedia as the sister group to the remaining taxa, which form a polytomy of three clades, Cephalocarida, Malacostraca, and a clade of Maxillopoda + Branchiopoda, although maxillopodans do not form a resolved clade in the strict consensus tree (they are monophyletic in one of the three optimal trees). The branching pattern among these clades conflicts, and the two possible relationships have been summarized in Figure 4. Basically, the morphological data are unable to generate a stable hypothesis of the main crustacean groups, other than suggesting a sister group relationship of remipedes to other crustaceans, and the Maxillopoda + Branchiopoda clade, although jackknife support is below the 50% threshold in both cases.

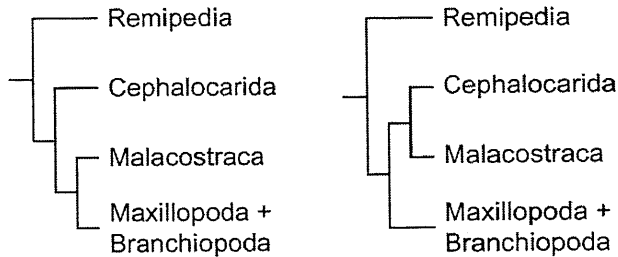


Figure 4. Alternative minimal length resolutions of the crustacean relationships summarized in Figure 3. See Appendix 1 (Table 1) for detailed overview of taxa.

3.2 Combined analysis

The combined analysis of all nine genes plus morphology (see Fig. 5 for the results under the optimal parameter set) is best summarized in Figures 6 and 7, which represent the sensitivity plots ('Navajo rugs') for several major arthropod clades. When pentastomids are considered as arthropods (as favored by most molecular systematists), arthropod monophyly is found under most parameter sets, but not under equal weights because tardigrades appear within the progoneate myriapods. Tardigrades also nest within this group in one other case (indel cost = 2; transversions/transitions = 1).

Within arthropods, Chelicerata + Pycnogonida is supported by most parameter sets, whereas the alternative Cormogonida occurs only under two (see complementary Navajo rugs in Fig. 6). A monophyletic Mandibulata is found under most analyses, and the alternative Paradoxopoda hypothesis appears only under two parameter sets. Myriapoda, Tetraconata, and Hexapoda appear to be monophyletic under most analytical conditions, whereas Crustacea is found under 13 parameter sets, especially for those with higher indel costs (and higher weight for the morphological partition). In almost all cases in which Crustacea is monophyletic, pentastomids are included within Crustacea except for two of the analyses (shaded squares in the Crustacea plot in Fig. 6). In three of the analyses without support for Crustacea, a clade comprising Cephalocarida + Ostracoda + Cirripedia is sister to Hexapoda (+ Remipedia in the analysis which minimizes the ILD [Incongruence Length Difference]; appendix 1, Table 3). There is no support for a Malacostraca-Hexapoda clade. In three of the analyses in which Crustacea is not monophyletic, hexapods are also not monophyletic.

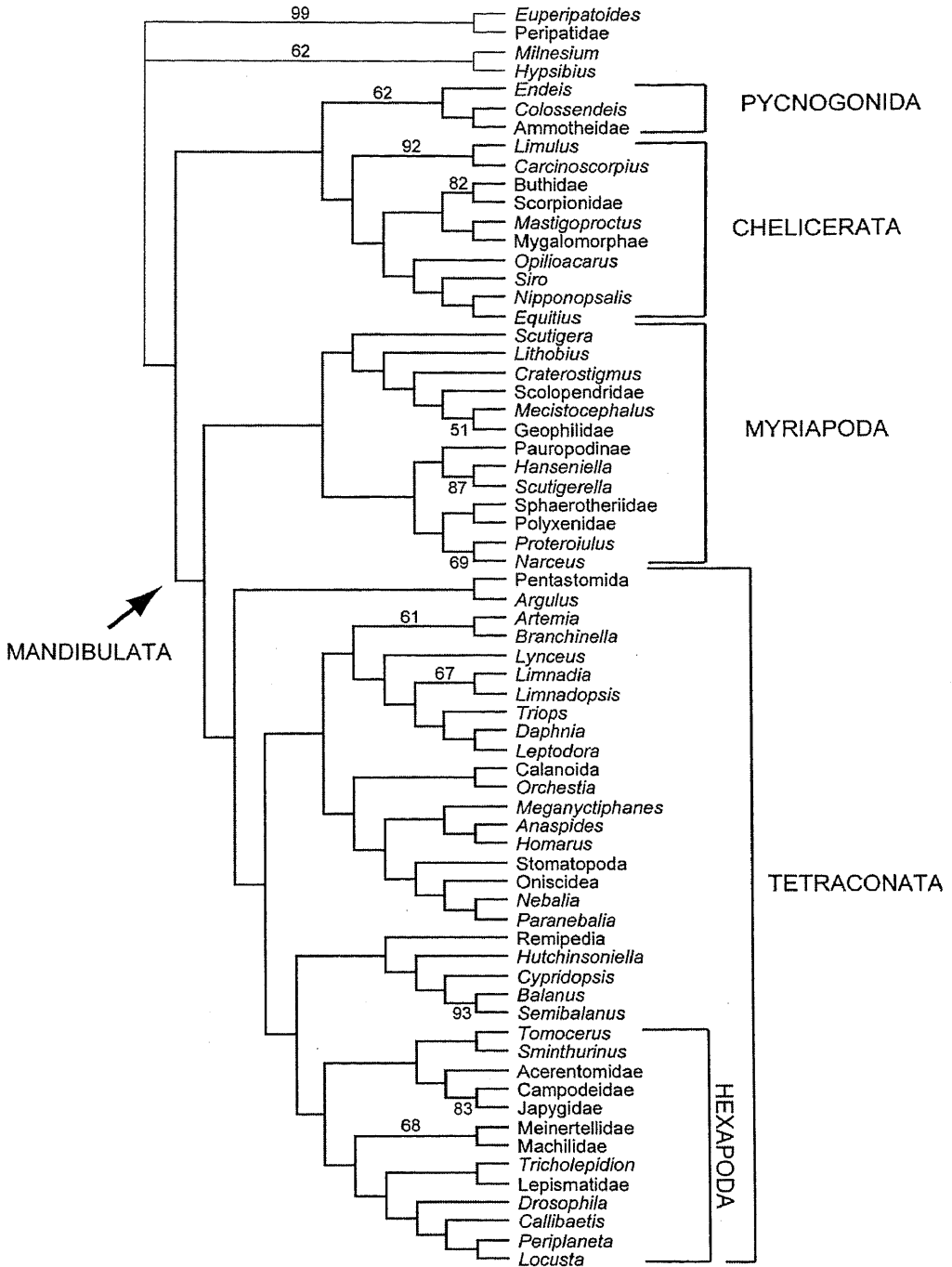


Figure 5. Most parsimonious cladogram at cost 109,957 for the optimal parameter set (indel/transversion cost of 1 and transversion/transition cost of 4) for nine genes and morphology. Numbers on branches represent jackknife support values above 50%.

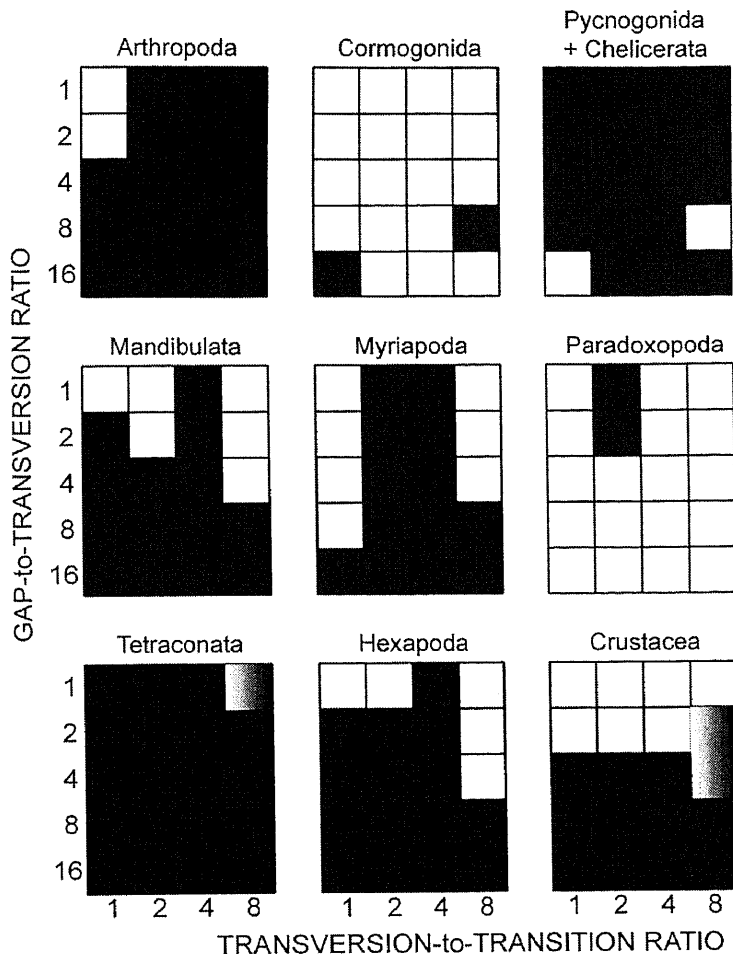


Figure 6. Navajo rugs (sensitivity plots) for higher arthropod relationships based on combined analysis of nine genes and morphology. Black squares indicate monophyly; white squares indicate non-monophyly. For Tetraconata and Crustacea shaded square indicates that Pentastomida is not included.

Internal relationships of the crustacean clades are summarized in Figure 7. Within Crustacea (or Tetraconata if Crustacea is not supported), Malacostraca and Branchiopoda are monophyletic under most parameter sets. In the single case in which Branchiopoda is not supported, a malacostracan species is included within Branchiopoda. In the analyses where Malacostraca is not monophyletic, four show the copepod terminal included in the otherwise monophyletic clade. The internal relationships within Branchiopoda and Malacostraca vary throughout the parameter space of the combined analysis.

Maxillopoda does not find any support in our analyses. In the morphological analyses maxillopodans are unresolved, and only one of the three optimal trees shows maxillopodan monophyly. However, one clade within Maxillopoda, an ostracod-cirripede clade is supported under almost all parameter sets in the combined analyses (Fig. 7). As well, a pentastomid-branchiuran clade is supported in 17 of 20 analyses.

None of the major hypotheses of internal crustacean relationship is well supported by our data. The Thoracopoda concept is not supported by a single parameter set, and even the core group Malacostraca + Branchiopoda finds only support in one analysis. The alternative Entomostraca concept is supported in seven analyses (but also including Pentastomida), and one additional analysis excluding the pentastomid-branchiuran clade. Concerning the position of Remipedia, three alternatives are represented in 16 of the 20 analyses: Remipedia + Cephalocarida, Remipedia + Calanoida, and Remipedia + Malacostraca.

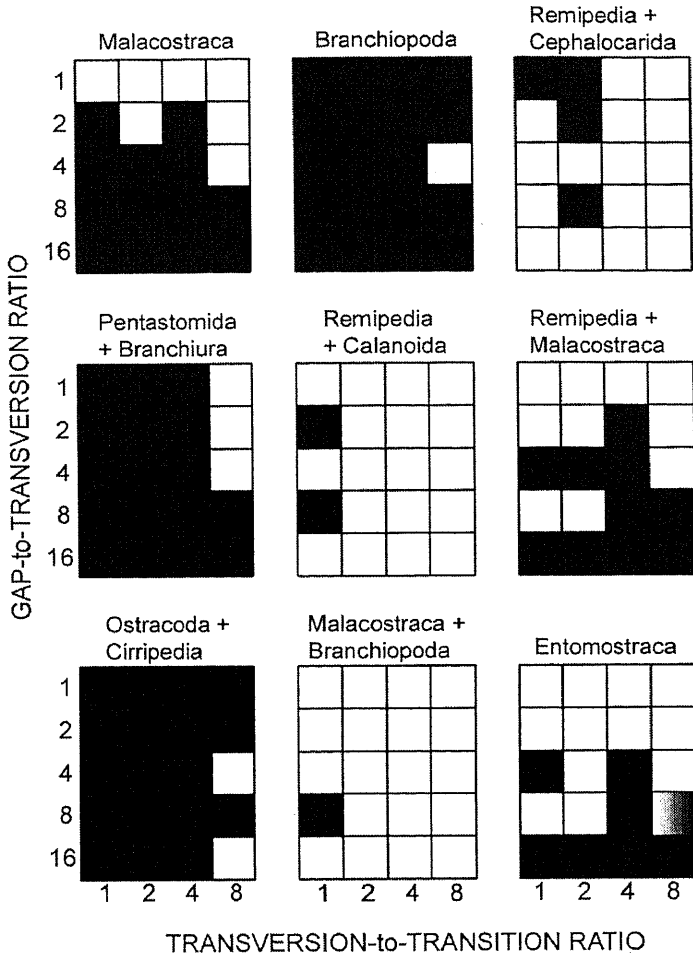


Figure 7. Navajo rugs (sensitivity plots) for crustacean relationships based on combined analysis of nine genes and morphology. Black squares indicate monophyly; white squares indicate non-monophyly. For Entomostraca black squares include Pentastomida; shaded square excludes Pentastomida and Branchiura.

For the parameter set that minimizes incongruence between the nine genes and morphology (indel/transversion = 1, transversion/transition = 4), the groupings Pycnogonida + Chelicerata, Mandibulata and Tetraconata are supported by the data, but with jackknife

support values below 50% (Fig. 5). The fundamental divisions within Chelicerata (= Xiphosura and Arachnida) and Myriapoda (= Chilopoda and Progoneata) are congruent with the morphological cladogram (Fig. 3). Crustaceans are resolved as paraphyletic with respect to a monophyletic Hexapoda, the latter dividing into Entognatha and Ectognatha. A branchiuran-pentastomid group resolves basal to other Tetraconata. The ostracod-cirripede clade is represented in this tree forming a clade with cephalocarids and remipedes. Malacostraca and Branchiopoda are resolved as sister groups but malacostracans include copepods. Jackknife support values for this tree are in general below the 50% threshold, and only a few clades receive meaningful values, such as Onychophora (99%), Tardigrada (62%), Pycnogonida (62%), Xiphosura (92%), Scorpiones (82%), Geophilomorpha (51%), Symphyla (87%), Juliformia (69%), Anostraca (61%), Spinicaudata (67%), Cirripedia (93%), Diplura (83%), and Archaeognatha (68%). This low proportion of nodes with high jackknife values contrasts with the large number of clades supported under most parameter sets (see Giribet 2003).

4 DISCUSSION

Our analysis represents the most comprehensive account in terms of taxa studied and amount of data (morphological and molecular) used to understand arthropod relationships to date. Nevertheless, many clades are still not clearly resolved and disagreements with several hypotheses based on morphological data alone are obvious; some of the resulting clades in our analyses even might appear as 'nonsense clades'. Nevertheless, we are convinced that a combined approach using as much data as possible is a more sensible way to deal with the information explored from nature than ignoring some particular data because of the seemingly nonsensical results they might create. To distinguish between 'nonsense clades' and evolutionary patterns that we just do not understand might be hazardous. However, what is most important is to test the stability of certain assumptions. Particular clades that show stability throughout an entire parameter space have a much higher degree of corroboration than those favored by only a few parameter sets (or even by a single evolutionary model) (Giribet 2003). Therefore, we refer to the 'Navajo rugs' as a summary of our results. Based on those, we can accept clades with a high degree of confidence.

4.1 *Arthropod relationships*

Arthropod relationships in general, and the position of crustaceans in particular, have remained contentious for several decades. While current analyses including molecular data tend to support Tetraconata - including crustaceans and hexapods - other issues remain controversial. Although fossils may have a fundamental role in elucidating arthropod relationships (e.g., see Edgecombe 1998) as shown in the few combined analyses of morphology and molecules including several fossil arthropod taxa (Giribet et al. 2002; Wheeler et al. 2004), no fossil species has been included in this study. Therefore, we caution the reader to interpret our results and conclusions in the absence of fossils. Disregarding the possibility of monophyly of Atelocerata for the sake of simplicity, most molecular and combined analyses tend to view arthropod relationships as a conflicting set of hypotheses as summa-

rized in Figure 1. Different authors have argued more or less strongly for the hypotheses based on their data, such as Mandibulata versus Paradoxopoda; both supported by the same data in at least one case (Giribet et al. 1996). Another current debate shows conflict in the monophyly of arthropods with the first appendage in the form of chelicerae or chelifores (pycnogonids, xiphosurans and arachnids) versus the Cormogonida concept (Zrzavý et al. 1998), which considers pycnogonids as the sister group to all other arthropods, thus rendering chelicerae as the plesiomorphic condition for the first pair of arthropod appendages. In reality all these hypotheses can be reduced easily to a rooting issue, as illustrated in Figure 1. Rooting problems are common in phylogenetic analyses when distant outgroups are selected, massive extinction may have occurred in the stem lineage of a taxon, or molecular and morphological change is fast (e.g., Wheeler 1990; Giribet et al. 2000). In the case of arthropods, which were subjected to massive extinction since they diverged from a common ancestor shared with Cambrian lobopodians (e.g., Budd 2002), rooting with onychophorans and tardigrades has been problematic in some cases due to the autapomorphic degree of molecular data in the two outgroups. It is in this respect that we prefer to view arthropod relationships as one possibly well-solved topology (Fig. 1) with alternative rooting places.

As for our data, rooting position 2 (arthropods with chelicerae as the sister group to Mandibulata) is supported in most analyses. However, a few parameter sets also support the Cormogonida hypothesis (Zrzavý et al. 1998; Giribet et al. 2001) or the Paradoxopoda hypothesis (Turbeville et al. 1991; Friedrich & Tautz 1995; Giribet et al. 1996; Hwang et al. 2001; Mallatt et al. 2004). Besides the rooting issue at the base of the arthropod tree, our data support myriapod monophyly in 13 of 20 parameter sets, with a division into Chilopoda and Progoneata (Edgecombe 2004). Noteworthy as well is the monophyly of Hexapoda across most of the explored parameter space (15 out of 20 parameter sets). Hexapod monophyly has moderate morphological support (Fig. 3) but has not been retrieved in most previous molecular analyses (see a review in Giribet et al. 2004).

4.2 *Crustacean relationships*

Crustacean relationships will remain controversial. Nevertheless, a few landmarks become manifest. This concerns in particular the monophyly of both Malacostraca and Branchiopoda. Our analysis supports the monophyly of Malacostraca, which is found under most parameter sets. This is also found in previous molecular (Spears & Abele 1998; Giribet & Ribera 2000; Shultz & Regier 2000) and combined (Giribet et al. 2001) analyses, although now with a more extensive taxon sampling (8 terminals). Malacostraca is also well supported by our morphological data as shown in previous morphological analyses (Richter & Scholtz 2001). Previous assumptions of a closer relationship of Leptostraca and Branchiopoda (e.g., Schram 1986; Schram & Hof 1998) cannot be substantiated. The relationships within Malacostraca are not stable and are outside the focus of the present study; though at least our morphological analysis and some of the combined analyses support the sister group relationship between Leptostraca and Eumalacostraca.

Branchiopod monophyly is still controversially discussed by morphologists. Whereas monophyly is advocated, e.g., by Walossek (1993), Schram & Hof (1998), and Richter (2004) using different characters, paraphyly has been suggested by Ax (1999). In our pre-

sent analysis, the monophyly of Branchiopoda is found under almost all parameter sets for our extended taxon sampling (8 terminals), which is also in agreement with previous molecular (Spears & Abele 1998, 1999, 2000; Giribet & Ribera 2000; Shultz & Regier 2000) and combined (Giribet et al. 2001) analyses. Within Branchiopoda the two cladocerans form a clade (18 of 20 analyses) which is in agreement with previous morphological and molecular analyses (Olesen et al. 1996; Spears & Abele 2000; Braband et al. 2002). A close relationship between Spinicaudata and Cladocera is found in some of the analyses (8 of 20), a relationship which has been previously suggested by Braband et al. (2002). However, *Cyclestheria hislopi* (Cyclestherida) as potential closest cladoceran relative was not considered in our analysis.

Martin & Davis (2001: 20) stated that "the Maxillopoda continues to be a terribly controversial assemblage". Maxillopodan monophyly has been suggested by Boxshall & Huys (1989) and by Walossek (1993, 1999) and Ax (1999). It is also found in one of our most parsimonious trees based on morphology alone. However, as in previous molecular analyses (see for example Spears & Abele 1998; Giribet & Ribera 2000), there is no support for Maxillopoda in our combined analyses.

What appears to be very interesting is the strong support for an ostracod-cirripede clade, found for the first time for molecular or combined analyses. Within Maxillopoda, Boxshall & Huys (1989) suggested a separation between a thecostracan-branchiuran-ostracod clade and a mystacocarid-coepod clade. Within the first clade they proposed a sister group relationship between Thecostraca + Branchiura with Ostracoda as the sister group to both taxa, but this particular relationship has not been found in any of our analyses. However, a sister group relationship of ostracods and thecostracans has been proposed by Ax (1999) under the name Thecostracomorpha, although the single apomorphy mentioned by him, a bivalved carapace with adductor muscle, is certainly problematic because it also occurs in Malacostraca and Branchiopoda.

Remipede relationships also remain mysterious. Previously suggested close relationships to copepods (Ito 1989), to cephalocarids (Spears & Abele 1998; Giribet et al. 2001) and to malacostracans (Fanenbruck et al. 2004) have been also found in some of our analyses. However, none of these hypotheses can be considered as much more favored than any other although the remiped-malacostracan clade occurs especially in those analyses with higher indel costs (and higher weight for the morphological partition).

4.3 *Pentastomid relationships*

The unusual morphology of pentastomids (tongue worms), a group composed entirely of parasitic species, has long intrigued zoologists. Two main hypotheses are currently favored. A crustacean affinity with a possible relationship to maxillopodan branchiurans has been suggested based on sperm ultrastructure (Wingstrand 1972; Riley et al. 1978; Jamieson & Storch 1992), 18S rRNA sequence data (Abele et al. 1989; Zrzavý 2001), and amino acid analysis of 12 mitochondrial genes (Lavrov et al. 2004) (but see a relationship to nematodes suggested by the same data in their figures 1a and 1b). A second hypothesis suggests that pentastomids branched off the arthropod stem lineage between tardigrades and the (eu)arthropod stem group (Walossek & Müller 1994), rather than being especially closely related to crustaceans. Interestingly, our data also support both of these hypotheses. The

morphological data set suggests a sister group relationship between pentastomids and the other arthropods when rooted with onychophorans and tardigrades (Fig. 3), although further testing should include more distantly related outgroups. In fact, Jenner (2004) suggested that the extreme morphological modification of parasitic groups such as pentastomids may mislead morphological cladistic analyses. Our molecular and combined analyses, which include novel 18S and 28S rRNA data for one pentastomid species, mostly support a relationship between pentastomids and branchiurans as in previous molecular analyses (Abele et al. 1989; Zrzavý 2001) (Figs. 5, 7). A three parameter sets do not find a sister group relationship between Pentastomida and *Argulus* (Fig. 7).

5 CONCLUDING REMARKS

Arthropod relationships and especially the relationships within the clade Tetraconata remain contentious in many respects, but application of the most strict taxonomic sampling and inclusion of evidence from external morphology, internal anatomy, mitochondrial gene order data and DNA sequence data under a wide range of parameter sets allows us to scientifically evaluate previous hypotheses formulated in more restricted studies. Our studies differ from those of other studies of arthropod relationships in that we are not interested in presenting a single hypothesis derived from a more or less inclusive set of data. On the contrary, we are interested in exploring the variation of phylogenetic hypotheses in a sensitivity analysis framework (variation to parameter choice) because this is the only way that we will be able to trace where and how transitions between topological representations occur, regardless of data set or data partition. We cannot justify either eliminating information by applying arbitrary decisions to exclude sequence data (e.g., Nardi et al. 2003) or taxa (e.g., Regier and Schultz 2001; Nardi et al. 2003). We will continue to attempt to overcome problems of taxon and data deficiencies in expanded versions of the data sets presented in this study.

ACKNOWLEDGEMENTS

We are indebted to Stefan Koenemann for inviting this contribution and for his careful editorial work, and to Buz Wilson and Ron Jenner for their reviews of an early version of this chapter. Wolfgang Boeckeler kindly supplied tissue samples of the pentastomid species used in this study, Mikael Agolin advised on pentastomid morphology, and Jon Mallatt kindly provided the 18S and 28S rRNA sequence data for the pentastomid as well as important criticism on a previous version of this chapter. Kelly DeMeo assisted in generating novel sequence data presented in this article. This material is based upon work supported by the NASA Fundamental Biology Program (Award NCC2-1169) to WCW and GG, and through a Lerner Gray Research Fellowship from the AMNH to SR.

APPENDIX 1

Table 1. Taxonomy of the non-crustacean terminals employed in the analyses. When single species are used per line, that species is coded; if more than one species is listed per genus, a generic ground-plan is implied. When more than one genus is listed, the higher taxon name underlined is used in the analyses.

Phylum		Family	Species		
Onychophora		Peripatopsidae	<i>Euperipatoides leuckartii</i> , <i>E. rowelli</i>		
		<u>Peripatidae</u>	<i>Peripatus</i> sp., <i>Oroperipatus corradei</i>		
Tardigrada	Eutardigrada	Milnesiidae	<i>Milnesium tardigradum</i>		
		Hypsibiidae	<i>Hypsibius dujardini</i>		
Phylum?	<u>Pentastomida</u>	Raillietiellidae	<i>Raillietiella</i> sp.		
Arthropoda	Pycnogonida	Endeidae	<i>Endeis laevis</i> , <i>E. spinosa</i> , <i>E. flaccida</i>		
		Colossendeidae	<i>Colossendeis</i> sp.		
		<u>Ammotheidae</u>	<i>Achelia echinata</i> , <i>Ammothella</i> sp., <i>Tanystylum</i> sp.		
		Chelicerata	Xiphosura	Limulidae	<i>Limulus polyphemus</i>
				Limulidae	<i>Carcinoscorpius rotundicauda</i>
			Scorpiones	<u>Buthidae</u>	<i>Androctonus australis</i> , <i>Lychas marmoreus</i> , <i>L. mucronatus</i> , <i>Centruroides exilicauda</i>
				<u>Scorpionidae</u>	<i>Heterometrus spinifer</i> , <i>Pandinus imperator</i>
			Uropygi	Thelyphonidae	<i>Mastigoproctus giganteus</i>
			Araneae	<u>Mygalomorphae</u>	<i>Atrax</i> sp., <i>Aphonopelma</i> sp.
			Opiliones	Sironidae	<i>Siro acaroides</i> , <i>S. valleurum</i>
				Nipponopsalididae	<i>Nipponopsalis abei</i>
				Trienonychidae	<i>Equitius doriae</i>
			Acari	Opilioacaridae	<i>Opilioacarus texanus</i>
		Myriapoda	Chilopoda	Scutigerae	<i>Scutigera coleoptrata</i>
				Lithobiidae	<i>Lithobius obscurus</i> , <i>L. variegatus</i> , <i>L. forficatus</i>
Craterostigmidae	<i>Craterostigma tasmanianus</i>				
<u>Scolopendridae</u>	<i>Cormocephalus monteithi</i> , <i>Scolopendra polymorpha</i> , <i>Ethmostigmus rubripes</i>				
Mecistocephalidae	<i>Mecistocephalus</i> sp., <i>M. tahitiensis</i>				
<u>Geophilidae</u>	<i>Ribautia</i> sp., <i>Pachymerium ferrugineum</i>				

Table 1 continued.

Phylum		Family	Species
	Symphyla	ScutigereUidae	<i>Hanseniella</i> sp.
		ScutigereUidae	<i>ScutigereUa</i> sp.
	Pauropoda	Pauropodidae	pauropodine spec.
	Diplopoda	<u>Polyxenidae</u>	<i>Polyxenus fasciculatus</i> , <i>Unixenus</i> sp.
		<u>Sphaerotheriidae</u>	<i>Epicyliosoma</i> sp., sphaerotheriid spec.
		Blaniulidae	<i>Proteroiulus fuscus</i>
		Spirobolidae	<i>Narceus americanus</i>
Hexapoda	Protura	<u>Acerentomidae</u>	<i>Acerentulus traegardhi</i> , <i>Nipponentomon</i> sp., <i>Acerentomon</i> sp.
	Diplura	<u>Campodeidae</u>	<i>Campodea tillyardi</i> , <i>Eumescampa frigidis</i>
		Japygidae	<i>Heterojapyx</i> sp., <i>Metajapyx</i> sp.
	Collembola	Tomoceridae	<i>Tomocerus</i> sp., <i>T. minor</i>
		Katiannidae	<i>Sminthurinus bimaculatus</i>
	Archaeognatha	<u>Meinertellidae</u>	<i>Allomachilis froggatti</i> , <i>Machiloides</i> sp.
		<u>Machilidae</u>	<i>Dilta littoralis</i> , <i>Pedetontus saltator</i> , petrobiine spec.
	Zygentoma	Lepidotrichidae	<i>Tricholepidion gertschi</i>
		<u>Lepismatidae</u>	<i>Thermobia domestica</i> , <i>Ctenolepisma lineata</i>
	Ephemeroptera	Baetidae	<i>Callibaetis ferrugineus ferrugineus</i>
	Blattodea	Blattidae	<i>Periplaneta americana</i>
	Orthoptera	Acrididae	<i>Locusta migratoria</i>
	Diptera	Drosophilidae	<i>Drosophila melanogaster</i>
Crustacea			
	Branchiopoda	Anostraca	Artemiidae
			<i>Artemia salina</i> , <i>A. franciscana</i>
			Thamnocephalidae
			<i>Branchinella</i> sp., <i>B. occidentalis</i>
		Notostraca	Triopsidae
			<i>Triops cancriformis</i> , <i>T. longicaudus</i> , <i>T. australiensis</i>
		Laevicaudata	Lynceidae
			<i>Lynceus gracilicornis</i> , <i>L. tatei</i> , <i>L. brachyurus</i>
		Spinicaudata	Limnadiidae
			<i>Limnadia lenticularis</i>
			Limnadiidae
			<i>Limnadopsis birchii</i>
		Cladocera	Leptodoridae
			<i>Leptodora kindtii</i>
			Daphniidae
			<i>Daphnia</i> sp., <i>D. pulex</i> , <i>D. galeata</i>

Table 1 continued.

Phylum		Family	Species	
Malacostraca	Leptostraca	Paranebaliidae	<i>Paranebalia longipes</i>	
		Nebaliidae	<i>Nebalia</i> sp., <i>N. longicornis</i> , <i>N. hessleri</i>	
		<u>Stomatopoda</u>	<i>Kempina mikado</i> , <i>Squilla empusa</i> , <i>Gonodactylus smithii</i>	
	Anaspidacea	Anaspididae	<i>Anaspides tasmaniae</i>	
	Reptantia	Nephropidae	<i>Homarus americanus</i>	
	Euphausiacea	Euphausiidae	<i>Meganyctiphanes norvegica</i>	
	Amphipoda	Talitridae	<i>Orchestia cavimana</i>	
	Isopoda, <u>Oniscidea</u>		<i>Armadillidium vulgare</i> , <i>Porcellio scaber</i>	
	Maxillopoda	Copepoda, <u>Calanoida</u>		<i>Calanus finmarchicus</i> , <i>C. pacificus</i> , <i>C. marshallae</i> , <i>Eurytemora affinis</i>
			Branchiura	Argulidae
Cirripedia		Balanidae	<i>Balanus balanus</i>	
		Balanidae	<i>Semibalanus balanoides</i>	
Ostracoda		Cypridopsidae	<i>Cypridopsis</i> sp., <i>C. vidua</i>	
Cephalocarida		Hutchinsoniellidae	<i>Hutchinsoniella macracantha</i>	
<u>Remipedia</u>		Speleonectidae	<i>Speleonectes gironensis</i> , <i>S. tulamensis</i> , <i>Lasionectes exleyi</i>	

Table 2. GenBank accession numbers for the non-crustacean terminals utilized in the analyses. Loci abbreviations are: 18S (18S rRNA), 28S (28S rRNA), H3 (histone H3), U2 (sn U2 rRNA), EF1 (elongation factor-1alpha), POL (RNA polymerase II), EF2 (elongation factor 2), COI (cytochrome *c* oxidase subunit I), 16S (16S rRNA).

	18S	28S	H3	U2	EF1	POL	EF2	COI	16S
<i>Euperipatoides</i>	U49910	-	AF110849	AF110880	AF137394	AF139015	-	U62426	-
Peripatidae	AY210837	AY210836	AF110848	AF110879	AF137395	AF139017	AF240835	U62429	-
<i>Milnesium</i>	U49909	AY210826	-	-	AF063419	AH010426	AF240833	-	-
<i>Hypsibius</i>	Z93337	-	CD449232	-	CK325900	CK325867	-	CK326084	-
<i>Raillietiella</i>	AY744887	AY744894	-	-	-	-	-	-	-
<i>Endeis</i>	AF005441	AF005462	-	-	AF063409	AH010424	AF240819	AF259656	AF448567
<i>Colossendeis</i>	AF005440	AF005461	-	-	AF063406	AF138974	-	AF259659	-
Ammonotheidae	AF005438	AF005459	AF110874	AF110903	AF063417	AF139013-4	AF240831	AF259657	AF370854
<i>Limulus</i>	U91490	U91492	AF370813	AF110902	U90051	U90037	AF240821	AF370827	U09397
<i>Carcinoscorpius</i>	U91491	U91493	AF370814	AF370820	AF063407	AF138975	-	AF370828	U09396
Buthidae	X77908	AF124955	AF110876	AF110905	AF240840	AF240988	-	AF370829	AF370855
Scorpionidae	AY210831	AY156529	-	-	AF240847	AH010441	-	AY156574	AY156559
<i>Mastigoproctus</i>	AF005446	AF062989	-	-	U90052	U90038	AF240823	AF370830	AF370856
Mygalomorphae	AF370784	X90464	AF110877	AF110906	U90045	U90035	-	AF370831	AF370857
<i>Siro</i>	AY639490	AY639490	AY639458	-	AF240855	AH010449	-	AY639678	AY639551
<i>Nipponopsalis</i>	AF124948	AF124975	-	-	AF137391	AF138993-5	AF240824	-	-
<i>Equitius</i>	U37003	U91503	AF110875	AF110904	AF240867	AH010461	-	AY744908	-
<i>Opilioacarus</i>	AF124935	AF124963	-	-	AF240849	AH010443	-	-	-
<i>Scutigera</i>	AF173238	AF173269	AY744902	-	AH009886	AF240951	-	AF370834	AF370859

Table 2 continued.

	18S	28S	H3	U2	EF1	POL	EF2	COI	16S
<i>Lithobius</i>	AF334271	AF334292	AF110853	-	AF240799	AH010406	-	AF334311	AF334333
<i>Craterostigmus</i>	AF000774	AF000781	AF110850	AF110882	AF240793	AH010400	-	AF370835	AF370860
Scolopendridae	AF173249	AF173280	AF110855	AF110885	AF137393	AF139006	AF240828	AF370836	AF370861
<i>Mecistocephalus</i>	AF173254	AF173285	AF110852	-	-	-	-	AF370837	AF370862
Geophilidae	AF173263	AF370803	AF110851	AF110883	AF240807	AF240949	-	AF370838	AF370863
<i>Hanseniella</i>	AY210823	AF173268	AF110856	AF110886	U90049	AF138982	-	AF370839	AF370864
<i>Scutigera</i>	AF007106	AF005464	-	-	AF137392	AF139003	AF240827	-	-
Paupodinae	AF005451	AF005466	AF110857	AF110887	-	-	-	-	-
Polyxenidae	AF173235	AF173267	AF110859	AF110889	U90055	AF139001-2	AF240826	AF370840	-
Sphaerotheriidae	AF370785	-	AF110858	AF110888	AF24808	AH010416	-	AF370841	AF370865
<i>Proterotulus</i>	AF173236	AF370804	-	-	AF063415	AF139000-240942	AF370842	AF370866	-
<i>Narceus</i>	AF370786-7	AF370805	-	-	U90053	U90039-AF240927	AF370843	AF370867	-
Acerentomidae	AF173233	AF005469	AF110861	-	AH009876	-	-	-	-
Campodeidae	AF173234	AF005471	AF110860	-	AF137388	AF138978	AF240818	AF370844	AF370868
Japygidae	AY555524	AY555537	AY555567	-	AF137389	AF138987-8	-	AF370845	AF370869
<i>Tomoceris</i>	AY555516	AY555530	AY555562	-	U90059	AF139011-2	AF240830	-	-
<i>Smnithurinus</i>	AY555522	AY555536	AY555566	-	-	-	-	AY555545	AY555555
Meinertellidae	AF370788	AF370806	AF110864	AF110893	AF137390	AF138990-2	AF240822	AF370846	AF370870
Machilidae	AF005457	AF005473	AF110865	-	U90056	U90041	-	AF370847	AF370871
<i>Tricholepidion</i>	AF370789	AF370807	AF110863	AF110892	-	-	-	AY191994	AY191994
Lepismatidae	AF370790	AF370808	AY555568	-	AF063405	AF138973	-	AF370848	AF370872
<i>Callibaetis</i>	AF370791	-	AF370815	AF370821	-	-	-	AF370849	AF370873
<i>Periplaneta</i>	AF370792	AF321248	AF370816	AF370822	U90054	U90040	-	AF370850	AF262620

Table 2 continued.

	18S	28S	H3	U2	EFI	POL	EF2	COI	I6S
<i>Locusta</i>	AF370793	AF370809	AF370817	AF370823	AY077627	-	-	X80245	X80245
<i>Drosophila</i>	M21017	M21017	X81207	X04256	X06869	M27431	X15805	M57910	X53506
<i>Artemia</i>	X01723	X01723	-	-	X03349	U10331	AF240815	X69067	X69067
<i>Branchinella</i>	AY744888	AY744895	AF110871	AF110900	-	-	-	AF308964	AF527558
<i>Triops</i>	AF144219	AY744896	AF110870	AF110898	U90058	U90043	-	-	AF200964
<i>Lynceus</i>	AF144215	AY137136	-	-	AF526294	-	-	-	-
<i>Linnadia</i>	L81934	AY137135	-	-	AF063412	AF138989	-	-	-
<i>Limnadorpsis</i>	AY744889	AY744897	AY744903	-	AF526290	-	-	-	-
<i>Leptodora</i>	AF144214	AY137130	-	-	AF526278	-	-	-	-
<i>Daphnia</i>	AF014011	AF532888	-	AF370824	-	-	-	AF117817	AF064189
<i>Paranebaltia</i>	AY744891	AY744899	AY744905	-	-	-	-	-	AY744909
<i>Nebalia</i>	L81945	AF169699	AF110869	AF110897	AF063413	AF138996	-	-	-
<i>Stomatopoda</i>	AF370802	AY210842	AF110873	AF110901	-	-	-	AF205233	AF107615
<i>Anaspides</i>	L81948	AF169703	-	-	-	-	-	AF048821	AF133679
<i>Homarus</i>	AF235971	AF370812	AF370819	AF370826	-	-	-	AF370853	AF370876
<i>Meganyctiphanes</i>	AY744892	AY744900	AY744906	-	-	-	-	AF177191	AY744910
<i>Orchestia</i>	AY744893	-	AY744907	-	-	-	-	-	AY744911
<i>Oniscidea</i>	AJ267293	AY744901	-	-	U90046	AF138970	AF240816	AF255779	AJ419996
<i>Calanoida</i>	L81939	AF385466	-	-	AF063408	AF138977	-	AF259651	AF295335
<i>Argulus</i>	M27187	AY210804	-	-	-	-	-	-	-
<i>Balanus</i>	AY520628	AY520594	AY520696	AF370825	-	-	-	-	AY520730
<i>Semibalanus</i>	AY520626	AY520694	AY520592	-	AF063404	AF138971-2	AF240817	AF242660	AY520728

Table 2 continued.

	18S	28S	H3	U2	EF1	POL	EF2	COI	16S
<i>Cypridopsis</i>	AY457057	AY455765	-	-	AF063414	AF138997-9	AF240825	-	-
<i>Hutchinsoniella</i>	AF370801	AF370811	AF110867	-	AF063411	AF138984	AF240820	AF370852	AF370875
<i>Rempedia</i>	AF370794	AF370810	AF110868	AF110895	AF063416	AF139008	AF240829	AF370851	AF370874

Table 3. Tree lengths and ILD values at 20 different parameter set combinations ranging from a gap to transversion ratio (g:v) of 1 to 16 and transition to transition ratio (v:s) of 1 to 8. The parameter set that minimizes ILD is shown in bold font type. Abbreviations for the different partitions are as follows: 18S (18S rRNA), 28S (28S rRNA), H3 (histone H3), EF1 (elongation factor-1alpha), EF2 (elongation factor 2), POL (RNA polymerase II), U2 (sn U2 rRNA), COI (cytochrome c oxidase subunit I), 16S (16S rRNA), MOR (morphology), MOL (molecular: all loci analyzed simultaneously), TOT (total evidence: molecular + morphology).

g:v	v:s	18S	28S	H3	EF1	EF2	POL	U2	COI	16S	MOR	MOL	TOT	ILD
1	1	4111	4520	1484	7034	6495	6840	255	6627	4399	740	43338	44309	0.04071
1	2	5987	6649	2188	10288	9770	10283	373	10170	7063	1480	65008	66849	0.03886
1	4	9530	10794	3502	16572	16060	16880	590	16963	12017	2960	106445	109957	0.03719
1	8	16208	18373	6057	28988	28453	29892	1014	30220	14303	5920	184924	192594	0.06836
2	1	4468	5036	1484	7034	6588	6840	272	6707	5019	1480	45114	46898	0.04201
2	2	6625	7672	2188	10288	9873	10283	397	10300	8017	2960	67977	71521	0.04080
2	4	10798	12762	3502	16572	16267	16880	628	17172	13625	5920	112493	119146	0.04213
2	8	18339	21032	6057	28988	29012	29892	1084	30843	13541	11840	192503	207570	0.08162
4	1	4889	5637	1484	7034	6593	6840	289	6712	5432	2960	46681	50144	0.04535
4	2	7426	8819	2188	10288	9908	10283	432	10273	8810	5920	71035	77600	0.04192
4	4	12256	14920	3502	16572	16313	16880	691	17157	14240	11840	117545	130502	0.04698
4	8	20798	22791	6057	28988	29089	29892	1199	30791	13860	23680	198721	228266	0.09253
8	1	5376	6317	1484	7034	6593	6840	317	6716	5576	5920	48184	54832	0.04849
8	2	8200	9943	2188	10288	9904	10283	474	10281	9018	11840	73537	86276	0.04471
8	4	13647	16765	3502	16572	16306	16880	771	17173	14256	23680	121461	147018	0.05078
8	8	22746	24221	6057	28988	29050	29892	1359	30817	13770	47360	202788	257594	0.09058
16	1	5743	6770	1484	7034	6593	6840	352	6720	5625	11840	49253	61873	0.04642
16	2	8656	10670	2188	10288	9904	10283	533	10284	9080	23680	74926	99636	0.04085
16	4	14247	17952	3502	16572	16306	16880	872	17164	14160	47360	123756	173014	0.04623
16	8	23911	24932	6057	28988	29050	29892	1540	30817	13707	94720	204894	311186	0.08860

APPENDIX 2

Description of characters used in morphological analysis. See Edgecombe (2004) for key literature citations. New characters or those with revised character state descriptions are indicated by an asterisk after the character number.

1. Non-migratory gastrulation: (0) absent; (1) present.
2. Early cleavage: (0) total cleavage with radially oriented position of cleavage products; (1) intralecithal cleavage.
3. Blastokinesis: (0) absent; (1) open amnionic cavity; (2) closed amnionic cavity, amnioserosal fold fuses beneath the embryo.
4. Blastodermal cuticle: (0) absent; (1) present.
5. Dorsal closure of embryo: (0) definitive dorsal closure; (1) provisional dorsal closure.
6. Ectoteloblasts: (0) absent; (1) present at anterior border of blastopore.
7. Caudal papilla: (0) absent; (1) present.
8. Origin of fat body: (0) vitellophagal; (1) mesodermal.
9. Midgut developed within the yolk: (0) midgut cells enclose the yolk; (1) lumen of embryonic midgut lacking yolk globules.
10. Fate map ordering of embryonic tissues: (0) presumptive mesoderm posterior to presumptive midgut; (1) presumptive mesoderm anterior to midgut; (2) mesoderm midventral, cells sink and proliferate, midgut internalizes during cleavage; (3) mesoderm diffuse through ectoderm; (4) midgut develops from anterior / posterior rudiments at each end of midventral mesoderm band.
11. Embryological development: (0) with a growth zone giving rise to both the prosoma and opisthosoma; (1) with a growth zone giving rise to the opisthosoma.
12. *engrailed* expressed in mesoderm patterning: (0) present; (1) absent.
13. Epimorphic development: (0) absent; (1) present.
14. Nauplius larva (orthonauplius) or egg nauplius: (0) absent; (1) present.
15. Pupoid stage: (0) absent; (1) present.
16. Imaginal molt: (0) present; (1) absent.
- 17.* Cyclic parthenogenesis as part of the life cycle: (0) absent; (1) present.
18. Sclerotization of cuticle into hard, articulated exoskeleton: (0) absent; (1) present.
19. Cuticle calcification: (0) absent; (1) present.
20. Cilia: (0) present in several organ systems, including photoreceptor, nephridia, and genital tracts; (1) present in (at most) sperm.
21. Tendon cells with tonofilaments penetrating epidermis: (0) absent; (1) present.
22. Dorsal longitudinal ecdysial suture with forking on head: (0) absent; (1) present.
23. Transverse and antennocellar sutures on head shield: (0) absent; (1) present.
24. Resilin protein: (0) absent; (1) present.
25. Molting gland: (0) absent; (1) present.
26. Bismuth staining of Golgi complex beads: (0) not staining; (1) staining.
27. Metanephridia with sacculus with podocytes: (0) absent; (1) present.
28. Distribution of segmental glands: (0) on many segments; (1) on at most last four cephalic segments and first two post-cephalic segments; (2) on second antennal and maxillary segments only.
29. Maxillary nephridia: (0) absent in postembryonic stadia; (1) paired; (2) fused nephridia of both maxillary segments.

30. Coxal gland orifice, leg I: (0) absent; (1) present.
31. Tömösváry organ ('temporal organs' at side of head behind insertion of first antenna): (0) absent; (1) present.
32. Salivary gland reservoir: (0) absent; (1) present.
33. Malpighian tubules formed as endodermal extensions of the midgut: (0) absent; (1) present.
34. Malpighian tubules formed as ectodermal extensions of the hindgut: (0) absent; (1) single pair; (2) multiple pairs.
35. Form of ectodermal Malpighian tubules: (0) elongate; (1) papillate.
36. Neck organ: (0) absent; (1) present.
37. Hemoglobin: (0) absent; (1) present.
38. Subcutaneous hemal channels in body wall: (0) absent; (1) present.
39. Dorsal heart with segmental ostia and pericardial sinus: (0) absent; (1) present.
40. Internal valves formed by lips of ostiae: (0) absent; (1) present.
41. Circumesophageal circulatory loop with trumpet-shaped opening: (0) absent; (1) present.
- 42.* Aorta descendens connects heart and ventral vessel: (0) absent; (1) present.
43. Slit sensilla: (0) absent; (1) present.
44. Ganglion formation: (0) ganglia formed by invagination of the ventral organ; (1) neuroblasts.
45. Early differentiating neurons aCC, pCC, RP2, U-CQ, EL and AUN: (0) absent (1) present.
46. EC neurons: (0) Eca and Ecp only; (1) Eca, Ecp and Ecl.
- 47.* Anterior pair of serotonergic neurons with neurites that cross to contralateral side: (0) absent; (1) present.
- 48.* Posterior pair of serotonergic neurons with neurites that cross to contralateral side: (0) absent; (1) present.
- 49.* Serotonergic somata clustered: (0) unclustered; (1) clusters of about 10 cells.
- 50.* Serotonergic cell group 'b' of Harzsch (2004): (0) absent; (1) present.
- 51.* Single median serotonergic neurons 'c' and 'd' of Harzsch (2004): (0) absent; (1) present.
52. Globuli cells: (0) confined mainly to brain, in massive clusters; (1) making up majority of neuropil and ventral layer of ventral nerve cord.
53. Corpora allata: (0) absent; (1) present.
54. Intrinsic secretory cells in protocerebral neurohemal organ: (0) absent; (1) present.
55. Enlarged epipharyngeal ganglia: (0) absent; (1) present.
56. Innervation of mouth area by anterior stomogastric nervous system: (0) absent; (1) present.
57. Ganglia of pre-esophageal brain: (0) protocerebrum; (1) protocerebrum and deutocerebrum; (2) proto-, deuto- and tritocerebra.
58. Ganglia of post-oral appendages fused into single nerve mass: (0) absent; (1) present.
59. Fan-shaped body in brain with neurons extending laterally into protocerebral lobes: (0) absent; (1) present.
60. Midline neuropil (ml1): (0) absent; (1) present.
61. Midline neuropil 2: (0) absent; (1) present.
62. Arcuate body in brain: (0) absent; (1) present.
63. Ellipsoid body in brain: (0) absent; (1) present.
64. Noduli in brain: (0) absent; (1) present.
65. Protocerebral bridge: (0) absent; (1) present.
66. Mushroom body calyces: (0) absent; (1) present.
- 67.* Deutocerebral olfactory lobe with glomeruli: (0) absent; (1) present.
- 68.* Deutocerebral olfactory-globular tract: (0) absent; (1) uncrossed; (2) with chiasma.

- 69.* Deutocerebrum with bipartite antennular neuropils: (0) absent; (1) present.
70. Cephalon composed of one pair of pre-oral appendages and three or more pairs of post-oral appendages: (0) absent (1) present.
- 71.* Cephalic tagma with four post-pedipalpal locomotory limbs: (0) fewer locomotory limbs; (1) present.
72. Prosomal shield: (0) absent; (1) present.
73. Transverse furrows on prosomal carapace corresponding to margins of segmental tergites: (0) absent; (1) present.
74. Cephalic kinesis: (0) absent; (1) present.
- 75.* Carapace adductor: (0) absent; (1) present.
76. Flattened head capsule, with head bent posterior to the clypeus, accommodating antennae at anterior margin of head: (0) absent; (1) present.
77. Clypeofrontal suture: (0) absent; (1) present.
78. Lateral eyes: (0) absent; (1) simple lens with cup-shaped retina; (2) stemmata; (3) compound (mostly facetted); (4) onychophoran eye.
79. Compound eyes medial margins: (0) separate; (1) medially contiguous; (2) fused.
80. Compound eye stalked, basally articulated: (0) absent (eye sessile); (1) present.
81. Compound eyes internalized early in ontogeny, shifted dorsally into a cuticular pocket: (0) absent; (1) present.
82. Ophthalmic ridges: (0) absent; (1) present.
- 83.* Number of corneagenous cells: (0) many; (1) two.
- 84.* Corneagenous cells containing pigment grains: (0) corneagenous cells lacking pigment grains; (1) corneagenous cells are primary pigment cells.
- 85.* Bipartite distal pigment cells with an inner pigment free portion, and an outer pigment bearing portion separated by an extracellular space: (0) distal pigment cells not bipartite; (1) distal pigment cell bipartite.
- 86.* Interommatidial pigment cells attached to cornea and basement membrane: (0) absent; (1) present.
87. Ommatidium with crystalline cone: (0) cone absent; (1) cone present.
88. Crystalline cone cells: (0) tetrapartite crystalline cone, lacking accessory cells; (1) cone bipartite, with two accessory cells; (2) pentapartite cone; (3) tripartite cone.
89. Reduction of processes of crystalline cone-producing cells: (0) all cells have processes that pass through clear zone and rhabdom; (1) only accessory cells have processes.
90. Distally displaced nuclei of accessory crystalline cone cells: (0) absent; (1) present.
91. Clear zone between dioptric apparatus and retina: (0) absent (apposition eye); (1) present (superposition eye).
- 92.* Optic chiasma between lamina and medulla: (0) absent (uncrossed axons); (1) present.
- 93.* Medulla divided into two layers by Cuccati bundle: (0) undivided; (1) divided.
- 94.* Lobula or protolobula receiving crossed axons from medulla: (0) absent; (1) present.
- 95.* Third optic neuropil (lobula) separated from protocerebrum: (0) protolobula contiguous with protocerebrum or absent; (1) lobula separated from protocerebrum.
- 96.* Fourth optic neuropil (lobula plate), receiving uncrossed axons from medulla: (0) absent; (1) present.
97. Lateral eye rhabdoms with quadratic network: (0) absent; (1) present.
98. Number of median eyes: (0) none; (1) four; (2) three; (3) two; (4) one, embryonic.
99. Inverted median eye: (0) absent; (1) present.

100. Median eyes fused to naupliar eyes: (0) absent; (1) present.
101. Type of naupliar eye: (0) inverse; (1) everse.
102. Tapetal cells in cups of naupliar eye: (0) absent; (1) present.
103. Dorsal frontal organ (malacostracan type): (0) absent; (1) present.
104. Ocular tubercle: (0) absent; (1) present.
105. Trichobothria innervated by several sensory cells: (0) absent; (1) present.
106. Basal bulb in trichobothria: (0) absent; (1) present.
107. Head/mouth orientation: (0) prognathous, mouth directed anteroventrally; (1) hypognathous, mouth directed ventrally; (2) mouth directed posteriorly.
108. Labrum: (0) absent; (1) present.
109. Fleshy labrum: (0) absent; (1) present.
110. Entognathy (overgrowth of mandibles and maxillae by cranial folds): (0) absent; (1) present.
111. Admentum differentiated lateroventrally on each side of head capsule: (0) absent; (1) present.
112. Sclerotic sternum formed by antennal to maxillary sternites: (0) absent; (1) present.
113. Tritosternum: (0) absent; (1) present.
114. Hypopharynx: (0) absent or only median lingua; (1) complete hypopharynx of lingua and paired superlinguae.
115. Fulturae: (0) absent or limited to a hypopharyngeal suspensor; (1) present, in a groove between arthrodial membrane of maxilla and labium.
116. Posterior process of tentorium fused anteriorly with hypopharyngeal bar and transverse bar: (0) absent; (1) present.
117. Triradiate pharyngeal lumen: (0) absent; (1) present.
- 118.* Flexible buccal tube and stylet apparatus: (0) absent; (1) present.
119. Three-branched epistomal skeleton supporting pharyngeal dilator muscles: (0) absent; (1) present.
120. Stomothecae: (0) absent; (1) present.
121. Post-cephalic filter feeding apparatus with sternitic food groove: (0) absent; (1) present.
122. Appendage of second (deutocerebral) head segment: (0) locomotory leg 1; (1) antenna (antennula in crustaceans); (2) chelicera / chelifore; (3) jaw.
- 123.* Antennal rami: (0) uniramous; (1) polyramous; (2) one ramus + scale. Remipedia scored after Boxshall (2004).
124. Antennal apical cone sensilla: (0) absent; (1) present.
125. Two lateral areas bearing club-like sensilla on terminal antennal article: (0) absent; (1) present.
126. Intrinsic muscles of antennae: (0) present; (1) absent. Remipedia scored after Boxshall (2004).
127. Scape and pedicel differentiated, with Johnson's organ: (0) absent; (1) present.
128. Antennal circulatory vessels: (0) joined; (1) separate; (2) absent.
129. Ampullo-ampullary dilator and ampullo-aortic dilator: (0) absent; (1) present.
130. Statocyst in basal segment of first antenna: (0) absent; (1) present.
131. Cheliceral segmentation: (0) three segments, the last two forming a chela; (1) two segments, subchelate.
132. Plagula ventralis: (0) absent; (1) present.
133. Cheliceral tergo-deutomerite muscle: (0) absent; (1) present.
134. Appendage on third (tritocerebral) head segment: (0) unspecialized locomotory limb; (1) second antenna; (2) absent (intercalary segment); (3) pedipalp; (4) oral papilla with slime glands and adhesive glands.
135. Antennal scale: (0) absent; (1) present.

136. Antennal naupliar protopod: (0) short; (1) long.
- 137.* Scorpionid-type chelate pedipalps: (0) absent; (1) present.
138. *Distal-less* expressed in mandible (or positionally equivalent limb): (0) present; (1) absent.
139. Mandible: (0) absent; (1) present.
140. Mandibular base plate: (0) absent; (1) present.
141. Telognathic mandible with muscled gnathal lobe, flexor arising dorsally on cranium: (0) absent; (1) present.
142. Pectinate lamellae: (0) absent; (1) present.
- 143.* Mandibular gnathal edge: (0) consisting of molar and incisor process; (1) only ellipsoid molar present; (2) number of teeth arranged in a row; (3) shovel with terminal teeth; (4) group of paired teeth and hair pad.
144. Mandibular cranial articulation: (0) absent; (1) present.
145. Ball-and-socket mandibular articulation: (0) absent; (1) present, formed between clypeal condyle and mandibular ridges.
146. Mandibular scutes: (0) absent; (1) present.
- 147.* Mandibular palp: (0) present; (1) absent in adults
148. 'Movable appendage' between pars incisivus and pars molaris of mandible: (0) absent; (1) present in the adults.
149. Posterior tentorial apodeme: (0) absent; (1) present as metatentorium.
150. Pre- and metatentorium fused: (0) absent; (1) present.
151. Anterior tentorial arms: (0) absent; (1) cuticular tentorium developed as ectodermal invaginations; (2) cuticular fulcro-tentorium.
152. Posterior suspension of anterior apodemes to cranial wall: (0) absent; (1) present.
153. Anterior tentorium: (0) separate, rod-like anterior tentorial apodemes; (1) anterior part of tentorial apodeme forms arched, hollow plates that approach each other mesially but remain separate; (2) anterior tentorium an unpaired roof.
154. Swinging tentorium: (0) absent; (1) present.
155. Mandibular articulation with tentorium: (0) gnathal lobe articulates with epipharyngeal bar; (1) mandible articulates with hypopharyngeal bar.
156. Suspensory bar: (0) absent; (1) present.
157. Interognathal connective lamina: (0) present; (1) absent.
158. Mandibulo-hypopharyngeal muscle: (0) absent; (1) present.
159. Cephalic post-occipital ridge: (0) absent; (1) present.
160. Ovigera: (0) absent; (1) present.
- 161.* Enlarged apodemes on coxae of legs 1 and 2: (0) absent; (1) present.
- 162.* Walking leg II longer than adjacent legs and modified as a feeler: (0) absent; (1) present.
163. Salivary gland position: (0) ectodermal, on second maxilla; (1) mesodermal segmental organs on first maxilla.
164. Maxillary salivary gland opening: (0) pair of openings at base of second maxilla; (1) median opening in midventral groove on labium; (2) median opening on salivarium, between labium and hypopharynx.
165. First maxilla: (0) absent; (1) present.
166. First maxillary precoxa: (0) absent; (1) present.
167. Number of medially directed lobate endites on first maxilla: (0) two endites; (1) one endite.
168. First maxillary palps: (0) present (including telopodite of positionally equivalent limb in chelicerates); (1) absent.

169. First maxillary palp hypertrophied: (0) absent; (1) present.
- 170.* First maxillary palp an elongate cleaning organ: (0) absent; (1) present.
171. First maxilla divided into cardo, stipes, lacinia, and galea, with similar musculature and function: (0) absent; (1) present.
172. Interlocking of galea and superligua: (0) absent; (1) present.
173. First maxilla coalesced with sternal intermaxillary plate: (0) absent; (1) present, with unfused stipital and intermaxillary components; (2) mental elements of gnathochilarium consolidated.
174. Second maxillae on fifth metamere: (0) appendage developed as trunk limb; (1) well developed maxilla differentiated as mouthpart; (2) vestigial appendage; (3) appendage lacking; (4) well developed, not a mouth part.
175. Egg tooth on second maxilla: (0) absent (no embryonic egg tooth on cuticle of fifth limb-bearing metamere); (1) present.
176. Maxillary plate: (0) absent; (1) present.
177. Coxae of second maxillae medially fused: (0) absent (coxae of fifth metamere not fused); (1) present.
178. Symphylian-type labium: (0) absent; (1) present.
179. Linea ventralis: (0) absent; (1) present.
180. Divided glossae and paraglossae: (0) undivided pair of glossae and paraglossae; (1) glossae and paraglossae bilobed.
181. Rotation of labial *Anlagen*: (0) absent; (1) present.
182. Widened apical segment of labial palp: (0) absent; (1) present.
183. Collum covering posterior part of head capsule and part of segment II: (0) absent; (1) present.
184. Direct articulation between first and fourth articles of telopodite of maxilliped: (0) absent (first and fourth articles of telopodite of sixth metamere lack a common hinge); (1) present.
185. Coxosternite of maxilliped sclerotized in midline: (0) coxae separated medially, with sternite present in adult; (1) coxosternal plates meeting medially, with flexible hinge; (2) coxosternal plates meeting medially, hinge sclerotized and non-functional.
186. Coxosternite of maxilliped deeply embedded into cuticle above second trunk segment: (0) not embedded; (1) embedded.
187. Maxilliped segment with pleurite forming a girdle around coxosternite: (0) small lateral pleurite; (1) large girdling pleurite.
188. Sternal muscles truncated in maxilliped segment, not extending into head: (0) sternal muscles extended into head; (1) sternal muscles truncated.
189. Maxilliped tooth plate (anteriorly-projecting, serrate coxal endite): (0) absent; (1) present.
190. Maxilliped poison gland: (0) absent; (1) present.
191. Maxilliped distal segments fused as a tarsungulum: (0) separate tarsus and pretarsus; (1) tarsus and pretarsus fused as tarsungulum.
192. Oblique muscle layer in body wall: (0) absent; (1) present.
193. Longitudinal muscles: (0) united sternal and lateral longitudinal muscles; (1) separate sternal and lateral longitudinal muscles, with separate segmental tendons.
194. Superficial pleural muscles: (0) absent; (1) present.
195. Crossed, oblique dorsoventral muscles: (0) absent; (1) present.
196. Deep dorsoventral muscles in trunk: (0) absent; (1) present.
197. Circular body muscle: (0) present; (1) suppressed.
198. Discrete segmental cross-striated muscles attached to cuticular apodemes: (0) absent; (1) present.

199. Trunk muscles: (0) straight; (1) twisted.
200. Proventriculus: (0) absent; (1) present.
201. Lateralia and inferolateralia anteriores in the cardiac chamber: (0) absent; (1) present.
202. Unpaired superomedianum: (0) absent; (1) present.
203. Inferomedianum anterius (midventral cardiac ridge): (0) absent; (1) present.
204. Inferomedianum posterius (midventral pyloric ridge): (0) absent; (1) present.
205. Atrium between inferomediana connecting cardiac primary filter grooves with pyloric filter grooves: (0) absent; (1) present.
206. Gut caecae: (0) absent; (1) present along midgut; (2) restricted to the anterior part of midgut.
207. Proctodeal dilation: (0) posterior section of hindgut simple, lacking a dilation; (1) proctodeum having a rectal ampulla with differentiated papillae.
- 208.* Pyloric region with ring of flattened cells with thick intima: (0) absent; (1) present.
209. Peritrophic membrane: (0) absent; (1) present.
210. Tubular diverticula: (0) absent; (1) present.
211. Fusion of all (opisthosomal) tergites behind opercular tergite into a thoracetrone: (0) absent; (1) present.
212. Opisthosoma greatly reduced, forming a slender tube emerging from between posterior-most legs, with a terminal anus: (0) absent; (1) present.
213. Lamellate respiratory organs derived from posterior wall of opisthosomal limb buds: (0) absent; (1) present.
214. Position of lamellate respiratory organs: (0) on opisthosomal segments 3-7; (1) on opisthosomal segments 4-7; (2) on opisthosomal segments 2-3.
215. Type of lamellate respiratory organs: (0) book gills; (1) book lungs.
216. Appendage on first opisthosomal segment: (0) appendage present on eighth limb-bearing metamere in post-embryonic stages; (1) appendage absent on eighth metamere.
217. Limb VII as chilaria: (0) absent; (1) present.
- 218.* Pectines: (0) absent; (1) present.
219. First opisthosomal segment: (0) broad; (1) narrow.
- 220.* Claspers as modified anterior thoracopods (applicable for taxa with phyllopodous limbs only): (0) absent; (1) one pair of claspers (at least movable finger); (2) two pairs of claspers.
221. Abdomen (limb-free somites between the terminal segment and limb-bearing trunk segments; if known posterior to expression domain of *Ubx*, *abdA* and *abdB*): (0) absent; (1) present.
222. Limb bearing trunk: (0) not divided; (1) divided into thorax and pleon (with different locomotory functions)
223. Thorax with three limb-bearing segments: (0) absent; (1) present.
224. Meso- and metathorax in mature stages bearing wings: (0) absent; (1) present.
225. Wing flexion: (0) absent; (1) present.
226. Segmentation of pleon: (0) seven segments (1) six segments.
227. Diplosegments: (0) absent; (1) present.
228. Endosternum (ventral tendons fused into prosomal endosternum): (0) absent; (1) present.
229. Dorsal endosternal suspensor of fourth post-oral segment with anterolateral carapacial insertion: (0) absent; (1) present.
230. Tergal scutes extend laterally into paratergal folds: (0) absent; (1) present.
231. Paramedian sutures: (0) absent; (1) present.
232. Intercalary sclerites: (0) absent; (1) developed as small rings; (2) developed as pre-tergite and pre-sternite.

233. Trunk heterotery: (0) absent; (1) present.
234. Trunk sternites: (0) large sternum; (1) sternal area divided into two hemisternites by linea ventralis; (2) sternum mostly membranous, with pair of small sternites; (3) sternal plate bears Y-shaped ridge/apodeme; (4) sternites extended rearwards to form substernal laminae; (5) thoracic sternal areas reduced and partly invaginated along median line; (6) sternal plate absent.
235. Endoskeleton of trunk in each segment: (0) pair of lateral connective plates; (1) pair of sternocoxal rods (ventral apodemes); (2) complex connective endosternite; (3) mainly cuticular, composed of two intrasegmental furcal arms and intersegmental spinal process.
236. Pleural part of trunk segments: (0) pleurites absent; (1) supracoxal arches on each segment; (2) pleural part of thoracic segments II and III consisting of a single sclerite with a large pleural process; (3) pleuron in each thoracic segment composed of a single sclerite divided into anterior and posterior parts by pleural suture.
237. Procoxal and metacoxal pleurites surround coxa: (0) pleurites absent or incompletely surrounding coxa; (1) procoxa and metacoxa surround coxa.
238. Elongate coxopleurites on anal legs: (0) absent; (1) present.
239. Pleuron filled with small pleurites: (0) absent; (1) present.
240. Complete body rings: (0) absent (sternites and/or pleurites free); (1) present (sternites, pleurites and tergites fused).
241. Longitudinal muscles attach to intersegmental tendons: (0) absent; (1) present.
242. Lobopods with pads and claws: (0) absent; (1) present.
243. Limbs (mostly articulated) with intrinsic muscles: (0) absent; (1) present.
- 244.* Telescopic legs: (0) absent; (1) present.
245. Biramy: (0) absent; (1) present.
246. Paddle-like epipods: (0) absent; (1) present.
247. Trunk limbs with lobate endites formed by folds in limb bud: (0) absent; (1) present.
248. Coxal swing: (0) coxa mobile, promotor-remotor swing between coxa and body; (1) coxa with limited mobility or immobile, promotor-remotor swing between coxa and trochanter.
249. Coxopodite articulation: (0) arthrodial membrane; (1) pleural condyle; (2) sternal condyle; (3) sternal and pleural condyles; (4) internal plate.
250. Coxal vesicles: (0) absent; (1) present at limb base on numerous trunk segments; (2) on distal part of first abdominal segment (modified as *Ventraltubus*).
251. Styli: (0) absent; (1) present.
- 252.* Furcula: (0) absent; (1) present.
253. Musculi lateralis: (0) absent; (1) present.
254. Coxotrochanteral joint: (0) simple; (1) complex.
255. Trochanteronotal muscle: (0) absent; (1) present.
256. Trochanter distal joint: (0) mobile; (1) short, ring-like trochanter lacking mobility at joint with prefemur.
257. Trochanterofemoral joint of walking legs: (0) transverse bicondylar; (1) vertical bicondylar.
258. Unique trochanteral femur-twisting muscle: (0) absent; (1) present.
259. Unique femur-tibia pivot joint: (0) absent; (1) present.
260. Patella/tibia joint: (0) free; (1) fused.
261. Patellotibial joint of walking legs: (0) dorsal monocondylar; (1) simple bicondylar; (2) vertical bicondylar; (3) dorsal hinge.
262. Femoropatellar joint: (0) transverse dorsal hinge; (1) bicondylar articulation.

263. Origin of posterior transpatellar muscle: (0) arises on distodorsal surface of femur, traverses femoropatellar joint ventral to axis of rotation, receives fibers from wall of patella; (1) arises on distal process of femur, traverses femoropatellar joint dorsal to axis of rotation, does not receive fibers from patella
264. Tibiotarsus: (0) separate tibia and tarsus; (1) unjointed tibiotarsus.
265. Elastic arthrodial sclerites spanning the tibia-tarsus joints: (0) absent; (1) present.
266. Tarsus segmentation: (0) not subsegmented; (1) subsegmented.
267. Tarsal organ: (0) absent; (1) present.
268. Pretarsal depressor muscle origin: (0) on tarsus; (1) on tibia or patella.
269. Pretarsal levator muscle: (0) present; (1) absent (depressor is sole pretarsal muscle).
270. Pretarsal claws: (0) paired; (1) unpaired.
271. Pretarsal claw articulation: (0) on pretarsal base; (1) on distal tarsomere.
272. Plantulae: (0) absent; (1) present.
273. Tracheae/spiracles: (0) absent; (1) pleural spiracles; (2) spiracles at bases of walking legs, opening into tracheal pouches; (3) single pair of spiracles on head; (4) dorsal spiracle opening to tracheal lungs; (5) open-ended tracheae with spiracle on second opisthosomal segment; (6) many spiracles scattered on body; (7) pair of spiracles in the collar region; (8) four pairs of opisthosomal stigmata with irregular unprotected opening.
274. Longitudinal and transverse connections between segmental tracheal branches: (0) tracheae not connected; (1) tracheae connected.
275. Pericardial tracheal system with chiasmata: (0) dendritic tracheae; (1) long, regular pipe-like tracheae with specialized molting rings.
276. Abdominal spiracles: (0) present (pleural spiracles on posterior part of trunk); (1) absent on first abdominal segment; (2) absent on all abdominal segments.
277. Abdominal segmentation (in hexapods): (0) six segments; (1) ten segments; (2) eleven segments; (3) twelve segments.
278. Annulated caudal filament: (0) absent; (1) present.
279. Abdominal segment XI modified as cerci: (0) absent; (1) present.
280. Articulate furcal rami: (0) absent; (1) present.
281. Uropods: (0) absent; (1) present.
282. Tail fan escape reaction: (0) absent; (1) present.
283. Telson shape: (0) round; (1) laterally depressed; (2) dorsoventrally depressed.
284. One pair of dorsal telsonal setae: (0) absent; (1) present.
285. Styliform post-anal telson: (0) absent; (1) present.
286. Paired terminal spinnerets: (0) absent; (1) present.
287. Anal segment with pair of large sense calicles, each with a long sensory seta: (0) absent; (1) present.
288. Egg cluster guarded until hatching, female coiling around egg cluster: (0) absent; (1) female coils ventrally around cluster; (2) female coils dorsally around egg cluster.
289. Peripatoid and foetoid stages protected by mother: (0) absent; (1) present.
290. Female gonopod used to manipulate single eggs: (0) absent; (1) present.
291. Female abdomen with ovipositor formed by gonapophyses of segments VIII and IX: (0) absent; (1) present.
292. Gonangulum sclerite fully developed as ovipositor base, articulating with tergum IX and attached to 1st valvula/valvifer: (0) not developed; (1) fully developed.
293. Ovipositor: (0) absent; (1) present.

294. Legs of seventh trunk segment transformed into gonopods: (0) absent; (1) present.
295. Penes: (0) absent; (1) present.
296. Penis (spermatopositor): (0) absent; (1) present.
297. Penis form: (0) short, membranous, undivided; (1) long, chitinous, divided into shaft and glans.
298. Male parameres: (0) undifferentiated; (1) pair of lateral plates on segment XI; (2) pair of parameres on segment IX; (3) incorporated into phallic apparatus as sclerites.
299. Penis on abdominal segment IX: (0) absent; (1) present.
300. Male gonopore location: (0) posterior end (opisthogoneate); (1) somite 11 (sixth trunk segment); (2) somite 12 (seventh trunk segment); (3) somite 8 (first opisthosomal segment); (4) behind legs of somite 8 (second pair of trunk legs); (5) somite 13 (eighth trunk segment); (6) somite 17 (twelfth trunk segment); (7) somite 16; (8) on multiple leg bases; (9) between segments VIII and IX, more or less hidden by hind border of sternum VIII; (10) somite 19; (11) somite 9 (fourth trunk segment); (12) dorsally.
301. Female gonopore position: (0) on same somite as male; (1) two segments anterior to male; (2) six segments anterior to male; (3) seven segments anterior to male.
- 302.*Female gonopore parity: (0) paired; (1) median, unpaired.
303. Genital operculum divided, incorporated into pedicel: (0) absent; (1) present.
304. Genital operculum overlapping third opisthosomal sternite: (0) absent; (1) present.
305. Postgenital appendages: (0) opercular and/or lamellar; (1) poorly sclerotized or eversible; (2) absent.
306. Embryonic gonoduct origin: (0) gonoduct arising as a mesodermal coelomoduct; (1) gonoduct arising as a secondary ectodermal ingrowth; (2) gonoduct arising in association with splanchnic mesoderm.
307. Lateral testicular vesicles linked by a central, posteriorly-extended deferens duct: (0) absent; (1) present.
308. Testicular follicles with pectinate arrangement: (0) absent (elongated testicular sac or sacs); (1) several pectinate follicles present.
309. Spermatophore web produced by 'Spingriffel' structure: (0) absent; (1) present.
310. 'By-passing' foreplay, spermatophore transfer on web, 'waiting' ritual by female: (0) absent; (1) present.
311. Sperm dimorphism: (0) absent; (1) present (microsperm and macrosperm).
312. Acrosomal complex in sperm: (0) bilayered (filamentous actin perforatorium present); (1) monolayered (perforatorium absent); (2) acrosome absent.
- 313.*Pseudoacrosome with dorsal ribbon, granulosome, apical membrane and pseudoacrosomal granular material: (0) absent; (1) present.
314. Perforatorium bypasses nucleus: (0) absent (perforatorium penetrates nucleus); (1) present.
315. Periacrosomal material: (0) absent; (1) present.
316. Striated core in subacrosomal space: (0) absent; (1) present.
317. Centrioles in sperm: (0) proximal and distal centrioles present, not coaxial; (1) coaxial centrioles; (2) single centriole; (3) centrioles absent; (4) doublet centrioles with radial 'foot'.
318. Centriole adjunct: (0) absent; (1) present.
319. Sperm 'accessory bodies' developed from centriole: (0) absent; (1) present.
320. Cristate, non-crystalline mitochondrial derivatives in sperm: (0) absent; (1) present.
321. Three filamentous mitochondria symmetrically disposed between nucleus and axoneme: (0) absent; (1) present.
322. Connecting bands between axoneme and mitochondria: (0) absent; (1) present.

323. Axoneme parallels entire length of nucleus: (0) absent; (1) present.
324. Supernumerary axonemal tubules (peripheral singlets): (0) absent; (1) present, formed from the manchette; (2) present, formed from axonemal doublets.
325. Number of protofilaments in wall of accessory tubules: (0) 13; (1) 16.
- 326.*Mediodorsal peripheral doublet (doublet 1) connected to dorsal ribbon by an obliquely oriented membrane: (0) absent; (1) present.
327. Axonemal endpiece 'plume': (0) endpiece not extended; (1) endpiece extended, plume-like.
328. Sperm flagellum: (0) present; (1) absent.
329. Nucleus of sperm forms spiral ridge: (0) absent; (1) present.
330. Sperm nucleus with manchette of microtubules: (0) absent; (1) present.
331. Coiling of spermatozoa flagellum: (0) absent (filiform); (1) present.
332. Medial microtubules in spermatozoan axoneme: (0) 9 + 2; (1) 9 + 3; (2) 9 + 0; (3) 12 + 0.
333. Sperm conjugation: (0) absent; (1) present.
334. Female spermathecae formed by paired lateral pockets in mouth cavity: (0) absent; (1) present.
335. Ovary shape: (0) sac- or tube-shaped, entire; (1) divided into ovarioles; (2) ovarian network.
- 336.*Location of ovary germarium: (0) germarium forms elongate zone in the ventral or lateral ovarian wall; (1) germarium in the terminal part of each egg tube; (2) single, median mound-shaped germarium on the ovarian floor; (3) paired germ zones on ovarian wall; (4) median germ zone on ovarian roof.
337. Site for oocyte growth: (0) in ovarian lumen; (1) on outer surface of ovary, in hemocoel, connected by egg stalk.
- 338.*Ventral marsupium formed by oostegites: (0) absent; (1) present.
339. Coxal organs on last pair of legs: (0) absent; (1) present.
340. Crural glands: (0) absent; (1) present.
341. Pair of repugnatorial glands in the carapace: (0) absent; (1) present.
342. Pleural defense glands with benzoquinones: (0) absent; (1) present.
- 343.*Aculeus with sting / opisthosomal venom glands: (0) absent; (1) present.
344. Labial expression domain: (0) expressed over multiple segments; (1) expression confined to second antennal/intercalary segment.
345. *proboscipedia* expression domain: (0) collinear with *labial* and *Deformed* domains; (1) anterior boundary of main expression domain of *proboscipedia* behind anterior boundary of *Deformed*.
346. *Deformed* expression domain: (0) expressed over three or more segments; (1) expression confined to mandibular and first maxillary segments.
347. *Antennapedia* expression domain: (0) strong throughout trunk; (1) restricted from the posterior of embryo.
348. Relative position of COI and COII: (0) COI/COII; (1) COI/L2/COII.
- 349.*Relative position of tRNA-L: (0) lsu rRNA/L1/L2/NADH 1; (1) lsu rRNA/L1/NADH 1; (2) NADH 1/H'/lsu rRNA/L1; (3) lsu rRNA/NADH 1; (4) lsu rRNA/L1/L2/Cytb.
- 350.*Relative position of tRNA-R and tRNA-N: (0) R/N; (1) R/K/N; (2) N/E/R; (3) N/A/S1/R; (4) R/S1.
- 351.*Relative position of tRNA-C and tRNA-Y: (0) Y/C; (1) Y/Q/C; (2) C/Q; (3) Q/Y/C; (4) Q/Y/F; (5) Q/I/C.
- 352.*Relative position of tRNA-P and tRNA-T: (0) T/-P; (1) -P/T; (2) T between W and Cytb; (3) P between NADH 4L and NADH 1; (4) T between S2 and NADH 1.

APPENDIX 3

Morphological data matrix for the terminals studied. Special characters used: A = character state 10; B = character state 11; C = character state 12; D = [0,1]

	1	11	21	31	41	51	61
Peripatidae	?????-???	-?100?0000	00-00010-?	0100-0011?	?-0???????	?10-0?00??	???????????
Milnesium	0?00?0-???	-?100?000?	00-0010--?	0000-0?00-	?-0???????	??0-0100??	???????????
Hypsibius	0?00?0-???	-?100?000?	00-0010--?	0000-0?00-	?-0???????	??0-0100??	???????????
Endeis	000???-???	-?000?0101	100?010--?	0000-0001?	?-00???????	??0?0?10??	???????????
Colossendeis	??????-???	-?000?0101	100?010--?	0000-0001?	?-00???????	??0?0?10??	???????????
Ammotheidae	0?0???-???	-?000?0101	100?010--?	0000-0001?	?-00???????	?00?0?100?	?10000????
Limulus	0101?0-???	0?10000101	100?0111-0	0000-0001?	?000?0010	00000?1101	0100000001
Carcinoscorpis	0101?0-???	0?10000101	100?0?11-0	0000-0?01?	?000?0010	?0000?11??	???????????
Buthidae	0100?0-???	0?10010101	10010?11-0	0010-0001?	??10?0?010	?001011101	?10000????
Scorpionidae	0100?0-???	0?10010101	10010?11-0	0010-0001?	??10?0?010	?001011101	?10000????
Mastigoproctus	??????-???	1?10010101	100?0?11-1	0010-0001?	??1?0?0?010	?0010?1101	01000?0?01
Mygalomorphae	0100?0-???	1?100D0101	100?0?11-1	0010-0001?	??10?0?010	??010111?1	???????????
Siro	??????-???	??100?0101	100?0?11-0	0000-0?01?	??1?0?0?010	?0000?11??	???????????
Nipponopsalis	??????-???	??100?0101	100?0?11-0	0000-0?01?	??1?0?0?010	?0000?11??	???????????
Equitius	??????-???	??100?0101	100?0?11-0	0000-0?01?	??1?0?0?010	?0000?11??	???????????
Opilioacarus	??????-???	??100?0101	100?0?11-0	0010-0?01?	??1?0?0?010	?0000?11??	???????????
Scutigera	??01?0-???	-?00000101	100?1?1120	1001000010	0000?0?0?010	??010120??	???????????
Lithobius	??????-???	-?00000101	101?1?1120	1001000010	100?0?0101	1001012001	?00001?0?01
Craterostigma	??????-???	-?000?0101	101?0?1100	100100?011	000?0?0?010	??0?0?20??	???????????
Scolopendridae	010000-100	-010000101	1001?11100	0001000011	00000?0?0?010	??01012001	100001?0?01
Mecistocephalus	??????-???	-?10000101	100?0?1100	000100?01?	000?0?0?010	??010?20??	???????????
Geophilidae	??????-???	-?10000101	100?0?1100	000100?011	000?0?0?010	??010?20??	???????????
Hanseniella	000100-013	-?00000101	100?0?1110	100100?01?	?000?0?0?010	??000?20??	???????????
Scutigera	??????-???	-?000?0101	100?0?1110	100100?01?	?00?0?0?010	??000?20??	???????????
Paupropodinae	000100-013	-?001?0101	100?0?1110	100100?00-	?-00?0?0?010	??0?0?20??	???????????
Polyxenidae	??????-???	-?00100101	100?1?1110	100100?01?	?-0?0?0?010	??000?20??	???????????
Sphaerotheriida	0001?0-013	-?00100111	100?0?1110	100100?01?	?-00?0?0?010	??000?20??	???????????
Proteroiulus	??????-???	-?00100111	100?0?1110	000100001?	?-0?0?0001	100?0?2000	000000?0?01
Narceus	??01??-???	-?00100111	100?1?1110	000100001?	?-0?0?0?010	?00?0120??	???????????
Acerentomidae	??????-???	-?00?010101	100?0?1100	100210?01?	0-0?0?0?010	??101?20??	???????????
Tomocerus	000110-103	-?10000101	100?0?1110	1000-0001?	1-0?11?????	?0101?1011	100000?0?01
Sminthurinus	00011? -103	-?10000101	100?0?0?010	1000-0?01?	?-0?0?0?010	?0101?10??	???????????
Campodeidae	010110-103	-?10000101	110?0?1110	000210?01?	1-0?0?0?010	??000?10??	???????????
Japygidae	??????-???	-?10?00101	110?0?1110	0000-0?01?	1-0?0?0?010	??100?10??	???????????
Meinertellidae	??????-???	-?10000101	110?0?1110	000200?01?	?-0?0?0?010	??1?0?20??	???????????
Machilidae	001110-104	-?10000101	110?1?11?0	000200001?	1-0?0?0?010	??1?0?20??	???????????
Tricholepidion	??????-???	-?0?0?0101	110?0?11?0	000200?01?	?-0?0?0?010	??0?0?0?010	???????????
Lepismatidae	012110-104	-110000101	110?1?1110	000200001?	1-01111100	00110?2011	1000001111
Callibaetis	012?0? -1??	-?10000101	110?1?1100	000200001?	0-0?0?0?010	??1?0?20??	???????????
Periplaneta	??2?0? -1??	-?10010101	11011?1100	000200001?	0-0?0?1100	0011012011	1011111111
Locusta	012?10-104	-?10010101	1101111100	000200001?	0-01111100	0011012011	1011111111
Drosophila	0120?0-10?	-110010101	11011?1100	000200001?	0-0111????	?011012011	1011111111
Remipedia	???????????	-??0?0?010?	100?0?1210	0000-0?01?	?00?0?0?010	?00?01211	?000?01211
Hutchinsoniella	???????????	-?000?0101	100?0?1210	0000-0?01?	0-0?0?1100	000?0110??	?0000?0?01
Artemia	0000?00?0?1	-1010?0101	10-?0?1210	0000-1101?	0-0?0?1100	0?000110??	????????0001
Branchinella	???????????	-?010?0101	10-???1210	0000-1101?	0-0?0?0?010	??0?0110??	???????????
Triops	0?0?0?0?0?0?	-1010?0101	100?0?1210	0000-1101?	0-011?1100	0?0?0110??	???????????
Lynceus	????????0?0?	-?01010101	100?0?1210	0000-1?01?	0-0?0?0?010	??0?0?0?010	???????????
Limnadia	????????0?0?	-?01010101	100?0?1210	0000-1101?	0-0?0?0?010	??0?0?0?010	???????????
Limnadopsis	????????0?0?	-?01010101	100?0?1210	0000-?01?	0-0?0?0?010	??0?0?0?010	???????????
Daphnia	0000?00?0?1	-?00001101	100?0?1210	0000-1101?	0-0?0?0?010	??0?0?0?010	???????????
Leptodora	0100?00?0?0?	-?00001101	100?0?1210	0000-1?01?	0-01???????	??0?0?0?010	???????????
Calanoida	0000?0?0?0?1	-?01010101	1001?12?0	0000-1101?	?-0?0?0?010	??0?0120??	?????00001
Balanus	0000?00?0?0?	-?01000111	10-???1210	0000-0100-	--0?0?1100	0?0?0120??	???????????
Semibalanus	0000?00?0?0?	-?01000111	10-???1210	0000-0100-	--0?0?1100	??0?0120??	???????????
Cypridopsis	?0?0?0?0?0?0?	-?01010101	100?0?1210	0000-?000-	0-0?0?0?010	??0?0?0?010	???????????
Argulus	????????0?0?	-?00000101	100?0?1210	0000-?001?	0-0?0?0?010	??0?0?0?010	???????????
Pentastomida	?001????0?0?	-?000?0001	10-????-0	0000-0?00-	--0?0?0?010	??0?0?0?010	???????????
Nebalia	0100?11?0?1	-?0?0?0101	100?1?1210	0000-1?01?	0-0?0?1000	0?0?0?20??	????0?0?01
Paranebalia	????????0?0?	-?0?0?0101	100?0?1210	0000-?001?	?0?0?0?010	??0?0?0?010	???????????

	I	II	2I	3I	4I	5I	6I
Stomatopoda	0100?11?P1	-?01000101	100?1?1210	0000-1001?	000?P?????	?P000120??	?????????P1
Anaspidae	0000?11?P01	-?0100?0101	100?1?1210	0000-1?01?	010?P??1000	000?0?201?	?0000-?????
Orchestia	0000?01?P?	-100000101	100?1?1200	0000-1?01?	0-01???????	?P?0?0?20??	?????????P1
Oniscidea	0100?10?P?	-100000111	100?111210	0000-0001?	0-01101000	0000012011	10001-1211
Meganycitiphanes	0000?11?P?	-?010?P0101	100?1?1200	0000-1?01?	010?P?????	?P?0?0?20??	?????????P1
Homarus	0100?11?P01	-101000111	100?111200	0000-1001?	0101101000	000?012011	10000-1211

	7I	8I	9I	10I	11I	12I	13I
Peripatidae	-----?4--	00--?-?----	-----0--	---00-?0-0	--??-?10--	03--?-?----	---4-----0-
Milnesium	-----?0--	-0-?-?----	-----0--	---00-?0-0	--??-?11--	00--?-?----	---0-----0-
Hypsibius	-----?0--	-0-?-?----	-----0--	---00-?0-0	--??-?11--	00--?-?----	---0-----0-
Endeis	101---?0--	-0-?-?----	-----100	---10-?0-0	-???-010--	02-----	000---0-0-
Colossendeis	101---?0--	-0-?-?----	-----100	---10-?0-0	-???-010--	0-----	003---0-0-
Ammonotheidae	10?---?0--	-0-?-?----	-----100	---10-?0-0	-???-010--	02-----	0003---0-0-
Limulus	110---?300	010?P?00--	?100-?0300	--?00-2100	-00?-00000	02-----	0000---000-
Carcinoscorpius	110---?300	01??P??P--	?100-?0300	--?00-2100	-00?-00000	02-----	00?0---0?0-
Buthidae	111---?1--	000??-0--	?-----0310	--?0100100	-00?-00011	02-----	0013---1?0-
Scorpionidae	111---?1--	000??-0--	?-----0310	--?0100100	-00?-00011	02-----	0013---1?0-
Mastigoproctus	110---?1--	000??-?--	?-----1310	--?0100100	-01?-00000	02-----	1103---0?0-
Mygalomorphae	110---?1--	000??-0--	?-----1310	--?0100100	-01?-00000	02-----	1103---000-
Siro	11?---?0--	-0-?-?----	-----0--	---?00-0100	-00?-00011	02-----	0013---0?0-
Nipponopsalis	111---?0--	-0-?-?----	-----310	---?10-0100	-00?-000?1	02-----	0013---0?0-
Equitius	110---?0--	-0-?-?----	-----310	---?10-0100	-00?-000?1	02-----	0013---0?0-
Opilioacarus	11?---?1--	00??P?-?--	?-----10--	---?00-0100	-00?-000?0	02-----	00?3---0?0-
Scutigera	0-0-0?P300	0001?110??	?000-000--	-000-0100	00?00100--	01000100-0	--2---?10
Lithobius	0-0-0-102--	000?-0-??	?-----00--	-000-0100	00?00100--	01000000-0	--2---?10
Craterostigma	0-0-0-102--	00?-?-?--	??????P?0--	-000-0100	00?00100--	01000000?0	--2---?10
Scolopendridae	0-0-0-102--	000??-0--	?-----00--	-000-0100	00?00100--	01000000-0	--2---?10
Mecistocephalus	0-0-0-100--	-0-?-?----	-----0--	-000-0100	00?00000--	01001000-0	--2---?10
Geophilidae	0-0-0-100--	-0-?-?----	-----0--	-000-0100	00?00000--	01001000-0	--2---?10
Hanseniella	0-0-0-000--	-0-?-?----	-----0--	-00110100	00?10100--	01000000-0	--2---?11
Scutigereila	0-0-0-000--	-0-?-?----	-----0--	-00110100	00?10100--	01000000-0	--2---?11
Paupropodinae	0-0-0-0?0--	-0-?-?----	-----0--	-00110100	00?10100--	01000002-0	--2---?10
Polyxenidae	0-0-0-002--	000?P?10??	?-----00--	-00110100	00?P0100--	0101000?P?	--2---?11
Sphaerotheriida	0-0-0-002--	000?P-0-??	?-----?0--	-000-1100	00?P0100--	01010000-0	--2---011
Proteroiulus	0-0-0-002--	000?P-0-??	?-----?0--	-000-0100	00?P0100--	0101000?P?	--2---?11
Narceus	0-0-0-002--	000?P-0-??	?-----?0--	-000-0100	00?P0100--	0101000?P?	--2---?11
Acerentomidae	0-0-0-000--	-0-?-?----	-----0--	-000-0101	00?11000--	0-----	--2---?10
Tomocerus	0-0-0-00300	0011??10??	?0?P??P0100	--?00-?101	00?11000--	01000002-0	--2---110
Smithurinus	0-0-0-00300	0011??10??	????P?0100	--?00-1101	00?11000--	01000002-0	--2---?10
Campodeidae	0-0-0-000--	-0-?-?----	-----?0--	-000-0101	10?11000--	01000000-0	--2---?10
Japygidae	0-0-0-000--	-0-?-?----	-----?0--	-000-0101	10?11000--	01000000-0	--2---?10
Meinertellidae	0-0-0-00310	0011??1???P	?11100?200	--?00-1100	00?11000--	0100011100	--2---?10
Machilidae	0-0-0-00310	0011??1000	0111000200	-000-1100	00?11000--	0100011100	--2---?10
Tricholepidion	0-0-0-01300	0011??10??	?1?P??P0200	-000-1100	00?00000--	0100011?P?	--2---?10
Lepismatidae	0-0-0-01300	0011??10??	011??P?0200	-000-1100	00?00000--	0100011100	--2---110
Callibaetis	0-0-0-01300	0011??10??	?1?P??P0200	-000-1100	00?10000--	01000111-0	--2---?10
Periplaneta	0-0-0-00300	0011??10??	?1111?0300	-000-1100	00?00000--	0100011110	--2---?10
Locusta	0-0-0-01300	0011??10??	0111??P0200	-000-1100	00?00000--	0100011110	--2---110
Drosophila	0-0-0-01300	0011??110??	0111110200	-000-1100	00?00000--	0100011110	--2---10-
Remipedia	0-0-0-0?0--	-0-?-?----	-----0--	--?00-2110	01??-000--	0100000?P?	--10?-?10
Hutchinsoniella	0-0-0-0?0--	-0-?-?----	-----0--	--?00-2110	01??-000--	0100000?P?	--100-?10
Artemia	0-0-0-0?301	00100?1000	00000?0201	01000-2110	01??-000--	1100000?P?	--101-010
Branchinella	0-0-0-0?301	00?P????P??	?P????P0201	01000-2110	01??-000--	1100000?P?	--101-?10
Triops	0-0-000?300	10100?1000	0000000101	01000-2110	01??-000--	1100000?P?	--101-?10
Lynceus	0-0-010?300	10?P?1000	0000??P101	01000-2110	????-00?-	1100?00?P?	--101-?10
Limnadia	0-0-010?320	10100?1200	00000??P101	01000-2110	?1??-000--	1100000?P?	--101-?10
Limnadopsis	0-0-010?320	10?P?P1200	00000??P101	01000-2110	????-00?-	1100?00?P?	--101-?10
Daphnia	0-0-010?320	10100?1200	00000?0101	0?000-2110	?1??-000--	1100000?P?	--10--?10
Leptodora	0-0-000?320	10?P?P1200	00000?0?01	?P000-2110	????-00?-	0100?00?P?	--101-?10
Calanoida	0-0-0-0?0--	-0-?-?----	-----201	01000-2110	01??-000--	0100000?P?	--100-?10
Balanus	0-0-0?0?300	00?P?101300	0?-----201	01000-?110	????-000--	01-----	-----0-?10
Semibalanus	0-0-0?0?300	00?P?P1???P	?P-----201	01000-?110	????-000--	01-----	-----0-?10
Cypridopsis	0-0-010?0--	-0-?-?----	-----201	0?000-?110	????-000--	0100000?P?	--10?-?10
Argulus	0-0-0-0?300	00?P?101000	00?P?0?0201	0?000-?110	????-000--	0100000?P?	--10?-?10

	71	81	91	101	111	121	131
Pentastomida	0--0-0?0--	----?----	-----0--	--000-?0-0	????-000--	0?------	---?-----0-
Nebalia	0--110?301	00100?1000	01010100--	--000-2110	?1??-000--	01200000-0	---10--?10
Paranebalia	0--110?301	00? ????????	???????	--?00-2110	????-000--	0120000?0-	---10--?10
Stomatopoda	0--100?301	0010011000	01011?0201	10100-2110	?1??-000--	0110000?0-1	---11--?10
Anaspides	0--0-0?301	0010011111	11011?0401	10100-2110	01??-000--	01100000-1	---11--?10
Orchestia	0--0-0?300	0010001111	01?1?00--	--000-2110	0???-000--	0100000?0-	---10--010
Oniscidea	0--0-0?300	00100111-1	01011100--	--000-2110	01??-000--	01000000-0	---10--010
Meganyctiphanes	0--000?301	0010011111	11?1?0201	10000-2110	????-000--	0110000?0-	---11?-?10
Homarus	0--000?301	0010011000	1101110201	10100-2110	?1??-000--	01100000-1	---11--010

	141	151	161	171	181	191	201
Peripatidae	-----0-	0-----?--0	-0?-0-----	-----	-----	-1?---000-	-----00?10
Milnesium	-----0-	0-----?-0	-0?-0-----	-----	-----	-0-?0?110-	-----00?00
Hypsibius	-----0-	0-----?-0	-0?-0-----	-----	-----	-0-?0?110-	-----00?00
Endeis	-----0-	0-----?-1	00?-0-?000	--00000--	--0--?00	-0??-?1100	-----10?01
Colossendeis	-----0-	0-----?-1	00?-0-?000	--00000--	--0--?00	-0??-?1100	-----10?01
Ammotheidae	-----0-	0-----?-1	00?-0-?000	--00000--	--0--?00	-0??-?1100	-----10?01
Limulus	-----0-	0-----?-0	00?-0-?000	--00000--	--0--?00	-0??1?1100	-----10?01
Carcinoscorpius	-----0-	0-----?-0	00?-0-?000	--00000--	--0--?00	-0??1?1100	-----10?01
Buthidae	-----0-	0-----?-0	10?-0-?000	--00000--	--0--?00	-0??0?1100	-----10?01
Scorpionidae	-----0-	0-----?-0	10?-0-?000	--00000--	--0--?00	-0??0?1100	-----10?01
Mastigoproctus	-----0-	0-----?-0	00?-0-?000	--00000--	--0--?00	-0??0?1100	-----10?01
Megalomorphae	-----0-	0-----?-0	00?-0-?000	--00000--	--0--?00	-0??0?1100	-----10?01
Siro	-----0-	0-----?-0	00?-0-?000	--00000--	--0--?00	-0??0?1100	-----10?01
Nipponopsalis	-----0-	0-----?-0	01?-0-?000	--00?00--	--0--?00	-0??0?1100	-----10?01
Equitius	-----0-	0-----?-0	01?-0-?000	--00?00--	--0--?00	-0??0?1100	-----10?01
Opilioacarus	-----0-	0-----?-0	00?-0-?000	--00000--	--0--?00	-0??0?1100	-----1???1
Scutigera	110--1100-	10000100-0	00001-?000	0-011000--	-?-0000001	0000101100	-----00?10
Lithobius	114--1100-	10010100-0	00001-?000	0-011010--	-?-0100001	1000101100	-----00010
Craterostigmus	114--1100-	10010100-0	00001-?000	0-01?010--	-?-0211111	1011111100	-----00??0
Scolopendridae	114--1100-	10010100-0	00001-?000	0-011010--	-?-1211111	1011111100	-----00010
Mecistocephalus	01?-0100-	10000000-0	00001-?000	0-01?010--	-?-1211101	1011111100	-----00?10
Geophilidae	01?-0100-	10000000-0	00001-?000	0-011010--	-?-1211101	1011111100	-----00?10
Hanseniella	100--0110-	1001?000-0	001-1-?1--	0-0101010-	--00-0000	00??1?1100	-----00?10
Scutigera	100--0110-	10010000-0	001-1-?1--	0-0101010-	--00-0000	0000101100	-----00?10
Pauropodinae	00?-0100-	100110?0-0	001-1-?1--	0-13-0----	--00--0000	00001?1100	-----00??0
Polyxenidae	110--0100-	10011000-0	001-1-?1--	0-13-0----	--00--0?00	00001?1100	-----00?10
Sphaerotheriida	110--0100-	1001?000-0	001-1-?1--	0-23-0----	--00--0?00	000??11100	-----00?10
Proteroiulus	110--0100-	10011000-0	001-1-?1--	0-23-0----	--10--0?00	000??11100	-----00??0
Narceus	110--0100-	10011000-0	001-1-?1--	0-23-0----	--10--0?00	000??11100	-----00??0
Acerentomidae	00?0-0100-	2000?10000	00011-?000	1001?10010	?0-0--0000	00????1100	-----00000
Tomocerus	0000-0100-	1000?10000	00011-?000	100101001?	0--0--0000	001?1?1100	-----00110
Sminthurinus	00?0-0100-	1000?10000	00011-?000	100101001?	?--0--0000	001?1?1100	-----0?1?0
Campodeidae	0030-0100-	0---?00000	00011-?000	110101000?	10-0--0?00	00-?1?1100	-----01010
Japygidae	0030-0100-	0---?00000	00011-?000	1101?1000?	10-0--0?00	00??1?1100	-----0?010
Meinertellidae	0000-01010	1110?00000	00021-?010	1001?10001	?0-0--0?00	000?1?1110	-----21?10
Machilidae	0000-01010	1110?00000	00021-?010	1001010001	00-0--0?00	000?1?1110	-----21010
Tricholepidion	0001001010	1120?00010	00021-?000	1001?10000	?1-0--0?00	000??1?1100	-----???10
Lepismatidae	0001001010	1120?01110	00021-?000	1001010000	01-0--0?00	000?1?1101	?????21010
Callibaetis	00?1001011	1120?01110	00021-?000	1001010000	?0-0--0?00	000??11101	?????21010
Periplaneta	00?1101011	1120?01110	00021-?000	1001010000	?0-0--0?00	000??11101	?????21010
Locusta	00?1101011	1120?01110	00021-?000	1001010000	00-0--0?00	000??11101	?????21010
Drosophila	-----11	1120?-1-10	00021-?000	1001010000	00-0--0?00	000??11100	-----01010
Remipedia	000--0100-	0---0??-0	00?-110000	0-01?000--	-?-0--?00	-0??1?1100	-----10??0
Hutchinsoniella	000--0100-	0---0??-0	00?-100000	0-000000--	-?-0--?00	-0??1?1100	-----20??0
Artemia	001--0100-	0---00?-0	00?-10-1--	0-020000--	-?-0--?00	-0??1?1100	-----20?10
Branchinella	001--0100-	0---00?-0	00?-10-1--	0-020000--	-?-0--?00	-0??1?1100	-----20?10
Triops	002--0100-	0---00?-0	00?-10-1--	0-020000--	-?-0--?00	-0??1?1100	-----20?10
Lynceus	002--0100-	0---0??-0	00?-??-1--	0-020000--	-?-0--?00	-0??1?1100	-----20??0
Limnadia	001--0100-	0---00?-0	00?-1?-1--	0-020000--	-?-0--?00	-0??1?1100	-----20?10
Limnadopsis	001--0100-	0---0??-0	00?-??-1--	0-020000--	-?-0--?00	-0??1?1100	-----?0??0
Daphnia	001--0100-	0---00?-0	00?-10-1--	0-020000--	-?-0--?00	-0??1?1100	-----20?10
Leptodora	00?-0100-	0---0??-0	00?-10-1--	0-020000--	-?-0--?00	-0??1?1100	-----?0??0
Calanoida	00?-0000-	0---0??-0	00?-110000	0-010000--	-?-0--?00	-0??1?1100	-----00??0
Balanus	00?-0100-	0---0??-0	00?-1?-1--	0-010000--	-?-0--?00	-0??1?1100	-----20?10

	141	151	161	171	181	191	201
Semibalanus	00?-0100-	0---0??-0	00?-1?-1-	0-010000--	?-0---?00	0-????1100	-----20?10
Cypridopsis	00?-00?0-	0---0??-0	00?-1??000	0-010000--	?-0---?00	0-????1100	-----20???
Argulus	00?-0100-	0---0??-0	00?-1--000	0-?40000--	?-0---?00	0-????1100	-----20???
Pentastomida	-----0-	0---??-0	0-?-0----	-----	-----?	0-????0?00	-----00?00
Nebalia	000--0000-	0---00?-0	00?-101001	0-010000--	?-0---?00	0-??1?1101	0100000???
Paranebalia	000--0000-	0---0??-0	00?-101001	0-010000--	?-0---?00	0-??1?1101	?????0?0??
Stomatopoda	000--0000-	0---00?-0	00?-101000	0-010000--	?-0---?00	0-??1?1101	1011120?10
Anaspides	000--0000-	0---00?-0	00?-101000	0-010000--	?-0---?00	0-??1?1101	1110020???
Orchestia	000--0110-	0---0??-0	00?-1011--	0-010000--	?-0---?00	0-??1?1101	1011120???
Oniscidea	000--0110-	0---0??-0	00?-1011--	0-020000--	?-0---?00	0-??1?1101	1011120?00
Meganocythanes	000--0000-	0---0??-0	00?-101000	0-010000--	?-0---?00	0-??1?11?1	11?0?0?0?0
Homarus	000--0000-	0---0??-0	00?-101000	0-010000--	?-0---?00	0-??1?1101	1111120?10

	211	221	231	241	251	261	271
Peripatidae	--0----0--	0-00--00--	---??-?---	0100000--0	00??-??-?	?-??-?-?-?	--6----000
Milnesium	--0----0--	0-00--00-0	---??-?---	0011000--0	00??-??-?	?-??-?-?-?	--0----000
Hypsibius	--0----0--	0-00--00-0	---??-?---	0011000--0	00??-??-?	?-??-?-?-?	--0----000
Endeis	-10--0000-	0-00--00-0	000??-?---	0010000000	00?0?00???	0?0?01?00?	?-0----000
Colossendeis	-10--0000-	0-00--00-0	000??-?---	0010000000	00?0?00???	0?0?01?00?	?-0----000
Ammonotheidae	-10--0000-	0-00--00-0	000??-?---	0010000000	00?0?00???	0?0?01?00?	?-0----000
Limulus	101000100-	0-00--0101	000??-?---	1010100000	0000?00???	0000?00?01	?-0----000
Carcinoscorpis	101000100-	0-00--0101	000??-?---	1010100000	0000?00???	0000?00?01	?-0----000
Buthidae	001111010-	0-00--0101	000??-?---	10100001-0	0000?00???	111?110100	?-0----000
Scorpionidae	001111010-	0-00--0101	000??-?---	10100001-0	0000?00???	111?110100	?-0----000
Mastigoproctus	001211001-	0-00--0110	000??-?---	10100001-0	0011?00???	0000?01100	?-0----000
Mygalomorphae	001211001-	0-00--0110	000??-?---	10100001-0	0011?00???	000?011100	?-0----000
Siro	000--1000-	0-00--0100	000??-?---	10100001-0	0000?01???	211?110101	?-5-----000
Nipponopsalis	000--1000-	0-00--0100	000??-?---	10100001-0	0000?01???	211?110101	?-5-----000
Equitius	000--1000-	0-00--0100	000??-?---	10100001-0	0000?01???	211?110101	?-5-----000
Opilioacarus	000--1000-	0-00--0100	000??-?---	10100001-0	0000?00???	300?0?0100	?-8-----000
Scutigera	0-0----00-	0-00--00-0	0010?10000	1010000020	00?0?1???	?-0?1??11	0-400--000
Lithobius	0-0----00-	0-00--00-0	0010010000	1010000020	00?0?1???	?-0?1??11	0-1000-000
Craterostigma	0-0----00-	0-00--00-0	0110?010100	1010000020	00?0?1???	?-0?0??11	0-1000-000
Scolopendriidae	0-0----00-	0-00--00-0	1110011100	1010000020	00?0?1???	?-0?1??11	0-1100-000
Mecistocephalus	0-0----00-	0-00--00-0	1200011110	1010000020	00?0?1???	?-0?0??11	0-1110-000
Geophilidae	0-0----00-	0-00--00-0	1200011110	1010000020	00?0?1???	?-0?0??11	0-1110-000
Hanseniella	0-0----00-	0-00--00-0	0002100000	1010000021	10?0?0???	?-0?0??11	0-3-----000
Scutigera	0-0----00-	0-00--00-0	000210-0-0	1010000021	10?0?0???	?-0?0??11	0-3-----000
Paupropodinae	0-0----00-	0-00--00-0	000610-0-0	1010000000	00?000???	?-0?1??11	0-0-----000
Polyxenidae	0-0----00-	0-00--10-0	000?1?0000	1010000100	00?000???	?-0?1??11	0-2-----000
Sphaerotheriida	0-0----00-	0-00--10-0	00001?0000	1010000020	00?0?0???	?-0?0??11	0-2-----000
Proteroiulus	0-0----00-	0-00--10-0	00001?0001	1010000020	00?0?0???	?-0?0??11	0-2-----000
Narceus	0-0----00-	0-00--10-0	00001?0001	1010000020	00?0?0???	?-0?0??11	0-2-----000
Acerentomidae	0-0----00-	0-10--00-0	0003210000	1010000032	00?0?0?001	?-0?0??11	0-0---3000
Tomocerus	0-0----00-	0-10--00-0	0001210000	1010000042	01?0?0?001	?-1?0??11	0-0---0000
Sminthurinus	0-0----00-	0-10--00-0	0001210000	1010000042	01?0?0?001	?-1?0??11	0-70020000
Campodeidae	0-0----00-	0-10--00-0	0003210000	1010000021	10?0?0?111	?-0?0??11	0010021010
Japygidae	0-0----00-	0-10--00-0	0003210000	1010000021	10?0?0?111	?-0?0??11	0010001010
Meinertellidae	0-0----00-	0-10--00-1	0000220000	1010000011	10?0?10?001	?-0?1??11	1010012110
Machilidae	0-0----00-	0-10--00-1	0000220000	1010000011	10?0?10?001	?-0?1??11	1010012110
Tricholepidion	0-0----00-	0-10--00-1	0000210000	1010000011	10?0?10?001	?-0?1??11	1011002110
Lepismatidae	0-0----00-	0-10--00-1	0004210000	1010000010	10?0?10?001	?-0?1??11	1011002110
Callibaetis	0-0----00-	0-110-00-1	0000330000	1010000010	10?0?10?001	?-0?1??11	1011002110
Periplaneta	0-0----00-	0-111-00-1	0000330000	1010000010	10?0?10?001	?-0?1??11	1111002010
Locusta	0-0----00-	0-111-00-1	0000330000	1010000010	00?0?10?001	?-0?1??11	1111002010
Drosophila	0-0----00-	0-111-00-1	0005330000	1010000010	00?0?10?001	?-0?1??11	1011002000
Remipedia	0-0----00-	0000--00-1	0000??-?--	1010100000	00?????????	?-?????????	?-0----001
Hutchinsoniella	0-0----00-0	1000--00-1	000??-?--	1010110000	00?????????	?-?????????	?-0----001
Artemia	0-0----00-0	1000--00-1	000??-?--	1010110000	00?????????	?-?????????	?-0----001
Branchinella	0-0----00-0	1000--00-1	000??-?--	1010110000	00?????????	?-?????????	?-0----001
Triops	0-0----00-0	1000--00-1	000??-?--	1010110000	00?????????	?-?????????	?-0----001
Lynceus	0-0----00-1	0000--00-?	000??-?--	0?01011000	00?????????	?-?????????	?-0----000
Limnadia	0-0----00-2	0000--00-?	000??-?--	1010110000	00?????????	?-?????????	?-0----001
Limnadopsis	0-0----00-2	0000--00-?	000??-?--	1010110000	00?????????	?-?????????	?-0----001
Daphnia	0-0----00-1	?000--00-?	000??-?--	1010110000	00?????????	?-?????????	?-0----001

	211	221	231	241	251	261	271
Leptodora	0-0---00--	?000--00-?	000????--0	?010001000	00?????????	??-????????	?-0---000
Calanoida	0-0---00--	1000--00-1	000????--0	1010100000	00?????????	??-????????	?-0---001
Balanus	0-0---00--	1000--00--	000????--0	1010100000	00?????????	??-????????	?-0---000
Semibalanus	0-0---00--	1000--00--	000????--0	1010100000	00?????????	??-????????	?-0---000
Cypridopsis	0-0---00--	1000--00-?	000????--0	1010100000	00?????????	??-????????	?-0---001
Argulus	0-0---00--	1000--00-?	000????--0	?010100000	00?????????	??-????????	?-0---000
Pentatomida	0-0---00--	?000--00--	000????--0	?010000--0	00?????????	??-????????	?-0---000
Nebalia	0-0---00-0	1100--00-1	000????--0	1010110000	00?????????	??-????????	?-0---001
Paranebalia	0-0---00-0	1100--00-1	000????--0	?010110000	00?????????	??-????????	?-0---001
Stomatopoda	0-0---00--	0100--100-1	0000????--0	1010110000	00?????????	??-????????	?-0---000
Anaspides	0-0---00--	0100--100-1	0000????--0	1010110000	00?????????	??-????????	?-0---000
Orchestia	0-0---00--	0100--100-1	0000????--0	?010110000	00?????????	??-????????	?-0---000
Oniscidea	0-0---00--	0100--100-1	0000????--0	1010100000	00?????????	??-????????	?-0---000
Meganyctiphanes	0-0---00--	0100--100-?	0000????--0	?010110000	00?????????	??-????????	?-0---000
Homarus	0-0---00--	0100--100-?	0000????--0	1010110000	00?????????	??-????????	?-0---000

	281	291	301	311	321	331	341
Peripatidae	--??00000-	0-0000-0-0	00---0000?	0?0????2000	0001?00000	0?00001001	000???????? ??
Milnesium	--??00000-	0-0000-0-0	01---?000?	000?00????	0000-0001?	000001?000	000???????? ??
Hypsibius	--??00000-	0-0000-0-0	01---?000?	000?00????	0000-001??	000001?000	000???????? ??
Endeis	0-??00000-	0-0000-008	00---0000?	0?????????	????????0??	0?00001000	000???????? ??
Colossendeis	0-??00000-	0-0000-008	00---0000?	???????????	???????????	????00?2000	000???????? ??
Ammonotheidae	0-??00000-	0-0000-008	00---0000?	???????????	???????????	0?000?2000	000???????? ??
Limulus	0-??10000-	0-0000-003	0000?000?	0000001000	0000-00000	0000201000	000?????000 00
Carcinoscorpius	0-??10000-	0-0000-003	00000?000?	0000001000	0000-00000	0200201000	000???????? ??
Buthidae	0-??10000-	0-0000-003	0100000000	000?001000	0000-00000	0200201000	001???????? ??
Scorpionidae	0-??10000-	0-0000-003	0100000000	000?001000	0000-00000	0200201000	001?????00? ??
Mastigoproctus	0-??00000-	0-0000-003	011120000?	000?001000	0000-0-011	1100001000	000???????? ??
Mygalomorphae	0-??00000-	0-0000-003	0111100000	000?001000	0000-0-011	1100001000	0000000013 04
Siro	0-??00000-	0-10010003	01002?000?	000000?000	0000-00000	02000?2000	100???????? ??
Nipponopsalis	0-??00000-	0-10011003	01002?000?	???????????	???????????	????00?2000	100???????? ??
Equitius	0-??00000-	0-10011003	01002?000?	???????????	???????????	????00?2000	100???????? ??
Opilioacarus	0-??00000-	0-1000-003	01001?????	000000????	-----?100	--00????000	000???????? ??
Scutigera	0-??000001	0-0000-000	01---00000	1000002100	0000-01010	00000?2000	000?????044 00
Lithobius	0-??000001	0-0000-000	01---?0010	110-002100	0000-01010	0000000010	0000001000 50
Craterostigma	0-??000010	0-0000-000	01---?101?	?10-00?100	0?????1010	0?????0?10	000???????? ??
Scelopendridae	0-??000011	0-0000-000	01---01010	110-002100	0000-01010	0000000010	000???????? ??
Mecistocephalus	0-??000010	0-0000-000	01---?101?	???????????	???????????	????00?2010	000???????? ??
Geophilidae	0-??0000210	0-0000-000	01---?1010	010-002100	0000-01010	00000?0?10	000???????? ??
Hanseniella	0-??011100-	0-0000-004	01---1000?	???????????	???????????	????1020000	000???????? ??
Scutigera	0-??011100-	0-0000-004	01---?0000	110-012000	0000-00000	0001020000	000???????? ??
Paupodinae	0-??00000-	0-0010-004	01---1000?	020---2000	0000-01000	0000020000	000???????? ??
Polyxenidae	0-??00000-	0-0010-004	00---10000	010-003--0	-----100	--00020000	000???????? ??
Sphaerotheriida	0-??00000-	0-0000-004	00---10000	010-00????	-----100	--00030000	000???????? ??
Proteroiulus	0-??00000-	0-0110-004	00---?000?	010-013--0	-----100	--0003?000	010???????? ??
Narceus	0-??00000-	0-0110-004	00---?0000	010-01????	-----100	--1003?000	010?????000 43
Acerentomidae	0-??00000-	0-0000-100	01---?000?	010-00?100	0000-00000	0300010000	000???????? ??
Tomocerus	0-??00000-	0-0000-000	01---20000	0000002001	-000-0-100	-000000000	000???????? ??
Sminthurinus	0-??00000-	0-0000-000	01---20000	0000002001	-000-0-100	-000000000	000???????? ??
Campodeidae	0-??00000-	0-0000-009	01---?0000	000?00?0?1	0002000000	0?00010000	000???????? ??
Japygidae	0-??00000-	0-0000-009	01---?000?	000?00?0?1	0002000000	0000110000	000???????? ??
Meinertellidae	0-??00000-	100000-010	11---?0100	???????????	???????????	????0110000	000???????? ??
Machilidae	0-??00000-	100000-210	11---?0100	000?102111	0002100000	0000110000	000???????? ??
Tricholepidion	0-??00000-	1?0000-210	11---?0101	000?02111	0002100000	0010110000	000?????110 00
Lepismatidae	0-??00000-	110000-210	11---20101	000?102111	0002100000	0010110000	0001111?? ??
Callibaetis	0-??00000-	0-0000-?10	11---?010-	0?0?002001	0?20000000	0200110000	000???????? ??
Periplaneta	0-??00000-	110000-310	11---?010-	0?0?10?101	0102100000	0000110000	000???????? ??
Locusta	0-??00000-	110000-310	11---2010-	000010?101	0102100000	0000110000	000?????100 00
Drosophila	0-??00000-	0-0000-310	11---2010-	010-0?0?101	0002?00000	0000110000	0001111110 00
Remipedia	0-?0000??-	0-0000-00A	30---0000?	0000003--0	0000-0000?	00000?2000	000?????122 20
Hutchinsoniella	0-?000000-	0-0000-001	00---0000?	0000003--0	-----10?	--00010000	000?????011 31
Artemia	0-0000000-	0-0000-006	01---0000?	020---2000	-----100	--00000000	000?????1110 00
Branchinella	0-0000000-	0-0000-006	01---0000?	020---2000	-----100	--000?2000	000???????? ??
Triops	0-0100000-	0-0000-007	00---0000?	020---2000	-----100	--00010000	000?????110 00
Lynceus	0-1100000-	0-0000-007	00---0000?	020---2000	-----100	--000?2000	000???????? ??
Limnadia	0-1100000-	0-0000-007	00---0000?	???????????	???????????	?????0?2000	000???????? ??

	281	291	301	311	321	331	341
Limnadopsis	0-1100000	0-0000-007	00---0000?	???????????	???????????	??00??000	000???????
Daphnia	0-1100000	0-0000-00C	00---0000?	020---2000	-----100	--000?0000	000?????110 00
Leptodora	0-0100000	0-0000-00C	0?---0000?	020---2000	-----100	--000??000	000???????
Calanoida	0-0000000	0-0000-002	00---0000?	070??3--0	-----100	--00010000	000???????
Balanus	0-?000000	0-0000-002	20---0000?	070?00?000	0010-00000	00000?0000	000?????110 01
Semibalanus	0-?000000	0-0000-002	20---0000?	070?00?000	0010-00000	00000?0000	000?????110 01
Cypridopsis	0-?000000	0-0000-00?	?0---0000?	070???????	-----110	--000?0000	000???????
Argulus	0-?000000	0-0000-00B	00---0000?	021---?000	1000-10100	-0000?1000	000?????131 12
Pentastomida	0-?000000	0-0000-00?	?1---?000?	021---2000	1000-10100	-000041000	000?????131 10
Nebalia	000000000	0-0000-005	10---0000?	020---2000	-----100	--000?0000	000???????
Paranebalia	000000000	0-0000-005	10---0000?	???????????	???????????	??00??000	000???????
Stomatopoda	102000000	0-0000-005	10---0000?	0000004700	-----100	--000?0000	000???????
Anaspides	112000000	0-0000-005	10---0000?	000100??-0	-----100	--000??000	000???????
Orchestia	102000000	0-0000-005	10---0000?	07?????????	???????????	??00??100	000???????
Oniscidea	102000000	0-0000-005	10---0000?	0001004000	-----100	--00010100	0001011???
Meganectiphanes	112000000	0-0000-005	10---0000?	07?????????	???????????	??00??000	000???????
Homarus	112000000	0-0000-005	10---0000?	0000004000	-----100	--000?0000	000?????1110 00

REFERENCES

- Abele, L.G., Kim, W. & Felgenhauer, B.E. 1989. Molecular evidence for inclusion of the phylum Pentastomida in the Crustacea. *Mol. Biol. Evol.* 6: 685-691.
- Averof, M. & Akam, M. 1995. Insect-crustacean relationships: Insights from comparative developmental and molecular studies. *Phil. Trans. R. Soc. London, B*, 347: 293-303.
- Ax, P. 1999. *Das System der Metazoa II. Ein Lehrbuch der phylogenetischen Systematik*. Stuttgart: Gustav Fischer Verlag.
- Bergström, J. 1979. Morphology of fossil arthropods as a guide to phylogenetic relationships. In: Gupta, A.P. (ed.), *Arthropod Phylogeny*: pp. 3-56. New York: Van Nostrand Reinhold.
- Boore, J.L., Lavrov, D.V. & Brown, W.M. 1998. Gene translocation links insects and crustaceans. *Nature* 392: 667-668.
- Boxshall, G.A. 2004. The evolution of arthropod limbs. *Biol. Rev.* 79: 253-300.
- Boxshall, G.A. & Huys, R. 1989. New tantulocarid, *Stygiotantulus stocki*, parasitic on harpacticoid copepods, with an analysis of the phylogenetic relationships within the Maxillopoda. *J. Crustacean Biol.* 9: 126-140.
- Braband, A., Richter, S., Hiesel, R. & Scholtz, G. 2002. Phylogenetic relationships within the Phyllopoda (Crustacea, Branchiopoda) based on mitochondrial and nuclear markers. *Mol. Phylogenet. Evol.* 25: 229-244.
- Budd, G.E. 2002. A palaeontological solution to the arthropod head problem. *Nature* 417: 271-275.
- Cisne, J.L. 1974. Trilobites and the origin of arthropods. *Science* 186: 13-18.
- Dohle, W. 2001. Are the insects terrestrial crustaceans? A discussion of some new facts and arguments and the proposal of the proper name Tetraconata for the monophyletic unit Crustacea + Hexapoda. *Ann. Soc. Entomol. Fr., N.S.*, 37: 85-103.
- Dove, H. & Stollewerk, A. 2003. Comparative analysis of neurogenesis in the myriapod *Glomeris marginata* (Diplopoda) suggests more similarities to chelicerates than to insects. *Development* 130: 2161-2171.
- Duman-Scheel, M. & Patel, N.H. 1999. Analysis of molecular marker expression reveals neuronal homology in distantly related arthropods. *Development* 126: 2327-2334.
- Edgecombe, G.D. 1998. *Arthropod Fossils and Phylogeny*. New York: Columbia Univ. Press.

- Edgecombe, G.D. 2004. Morphological data, extant Myriapoda, and the myriapod stem-group. *Contrib. Zool.* 73: 207-252.
- Edgecombe, G.D. & Giribet, G. 2002. Myriapod phylogeny and the relationships of Chilopoda. In: Llorente Bousquets, J.E. & Morrone, J.J. (eds.), *Biodiversidad, taxonomía y biogeografía de artrópodos de México; Hacia una síntesis de su conocimiento*: pp. 143-168. Mexico D.F.: Prensas de Ciencias, Univ. Nac. Autónoma México.
- Edgecombe, G.D., Richter, S. & Wilson, G.D.F. 2003. The mandibular gnathal edges: Homologous structures throughout Mandibulata? *African Invertebrates* 44: 115-135.
- Edgecombe, G.D., Wilson, G.D.F., Colgan, D.J., Gray, M.R. & Cassis, G. 2000. Arthropod cladistics: Combined analysis of Histone H3 and U2 snRNA sequences and morphology. *Cladistics* 16: 155-203.
- Fanenbruck, M., Harzsch, S. & Wägele, J.W. 2004. The brain of the Remipedia (Crustacea) and an alternative hypothesis on their phylogenetic relationships. *Proc. Nat. Acad. Sci. USA* 101: 3868-3873.
- Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99-124.
- Friedrich, M. & Tautz, D. 1995. Ribosomal DNA phylogeny of the major extant arthropod classes and the evolution of myriapods. *Nature* 376: 165-167.
- Friedrich, M. & Tautz, D. 2001. Arthropod rDNA phylogeny revisited: a consistency analysis using Monte Carlo simulation. *Ann. Soc. Entomol. Fr., N.S.*, 37: 21-40.
- Giribet, G. 2001. Exploring the behavior of POY, a program for direct optimization of molecular data. *Cladistics* 17: S60-S70.
- Giribet, G. 2003. Stability in phylogenetic formulations and its relationship to nodal support. *Syst. Biol.* 52: 554-564.
- Giribet, G., Carranza, S., Bagnà, J., Riutort, M. & Ribera, C. 1996. First molecular evidence for the existence of a Tardigrada + Arthropoda clade. *Mol. Biol. Evol.* 13: 76-84.
- Giribet, G., Distel, D.L., Polz, M., Sterrer, W. & Wheeler, W.C. 2000. Triploblastic relationships with emphasis on the acoelomates and the position of Gnathostomulida, Cycliophora, Plathelminthes, and Chaetognatha: A combined approach of 18S rDNA sequences and morphology. *Syst. Biol.* 49: 539-562.
- Giribet, G., Edgecombe, G.D., Carpenter, J.M., D'Haese, C.A. & Wheeler, W.C. 2004. Is Ellipura monophyletic? A combined analysis of basal hexapod relationships with emphasis on the origin of insects. *Org. Divers. Evol.* 4: 319-340.
- Giribet, G., Edgecombe, G.D. & Wheeler, W.C. 2001. Arthropod phylogeny based on eight molecular loci and morphology. *Nature* 413: 157-161.
- Giribet, G., Edgecombe, G.D., Wheeler, W.C. & Babbitt, C. 2002. Phylogeny and systematic position of Opiliones: a combined analysis of chelicerate relationships using morphological and molecular data. *Cladistics* 18: 5-70.
- Giribet, G. & Ribera, C. 2000. A review of arthropod phylogeny: new data based on ribosomal DNA sequences and direct character optimization. *Cladistics* 16: 204-231.
- Giribet, G. & Wheeler, W.C. 2001. Some unusual small-subunit ribosomal RNA sequences of metazoans. *Am. Mus. Novitates* 3337: 1-14.
- Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics* 15: 415-428.
- Harzsch, S. 2001. Neurogenesis in the crustacean ventral nerve cord: homology of neuronal stem cells in Malacostraca and Branchiopoda? *Evol. Dev.* 3: 154-169.

- Harzsch, S. 2002. The phylogenetic significance of crustacean optic neuropils and chiasmata: a re-examination. *J. Comp. Neurol.* 453: 10-21.
- Hessler, R.R. 1992. Reflections on the phylogenetic position of the Cephalocarida. *Acta Zool.* 73: 315-316.
- Hwang, U.W., Friedrich, M., Tautz, D., Park, C.J. & Kim, W. 2001. Mitochondrial protein phylogeny joins myriapods with chelicerates. *Nature* 413: 154-157.
- Ito, T. 1989. Origin of the basis in copepod limbs, with reference to remipedian and cephalocarid limbs. *J. Crust. Biol.* 9: 85-103.
- Jamieson, B.G.M. & Storch, V. 1992. Further spermatological evidence for including the Pentastomida in the Crustacea. *Int. J. Parasitol.* 22: 95-108.
- Jenner, R.A. 2004. Quo Vadis? *The Systematist* 23: 12-16.
- Kadner, D. & Stollewerk, A. 2004. Neurogenesis in the chilopod *Lithobius forficatus* suggests more similarities to chelicerates than to insects. *Dev. Genes Evol.* 214: 367-379.
- Klass, K.D. & Kristensen, N.P. 2001. The ground plan and affinities of hexapods: Recent progress and open problems. *Ann. Soc. Entomol. Fr., N.S.*, 37: 265-298.
- Kraus, O. 1998. Phylogenetic relationships between higher taxa of tracheate arthropods. In: Fortey, R.A. & Thomas, R.H. (eds.), *Arthropod Relationships*: pp. 295-303. London: Chapman & Hall.
- Kraus, O. 2001. "Myriapoda" and the ancestry of the Hexapoda. *Ann. Soc. Entomol. Fr., N.S.*, 37: 105-127.
- Kusche, K., Hembach, A., Hagner-Holler, S., Gebauer, W. & Burmester, T. 2003. Complete subunit sequences, structure and evolution of the 6 x 6-mer hemocyanin from the common house centipede, *Scutigera coleoptrata*. *Europ. J. Biochem.* 270: 2860-2868.
- Lauterbach, K.-E. 1983. Zum Problem der Monophylie der Crustacea. *Verh. Naturwiss. Ver. Hamburg* 26: 293-320.
- Lavrov, D.V., Brown, W.M. & Boore, J.L. 2004. Phylogenetic position of the Pentastomida and (pan)crustacean relationships. *Proc. R. Soc. London, B*, 271: 1471-2954.
- Mallatt, J.M., Garey, J.R. & Shultz, J.W. 2004. Ecdysozoan phylogeny and Bayesian inference: first use of nearly complete 28S and 18S rRNA gene sequences to classify the arthropods and their kin. *Mol. Phylogenet. Evol.* 31: 178-191.
- Martin, J.W. & Davis, G.E. 2001. An updated classification of the recent Crustacea. *Nat. Hist. Mus. Los Angeles Co., Contrib. Sci.* 39: 1-124.
- Müller, C.H.G., Rosenberg, J., Richter, S. & Meyer-Rochow, V.B. 2003. The compound eye of *Scutigera coleoptrata* (Linnaeus, 1758) (Chilopoda: Notostigmophora): an ultrastructural reinvestigation that adds support to the Mandibulata concept. *Zoomorphology* 122: 191-209.
- Nardi, F., Spinsanti, G., Boore, J.L., Carapelli, A., Dallai, R. & Frati, F. 2003. Hexapod origins: Monophyletic or paraphyletic? *Science* 299: 1887-1889.
- Negrisoló, E., Minelli, A. & Valle, G. 2004. The mitochondrial genome of the house centipede *Scutigera* and the monophyly versus paraphyly of myriapods. *Mol. Biol. Evol.* 21: 770-780.
- Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407-414.
- Olesen, J., Martin, J.W. & Roessler, E.W. 1996. External morphology of the male of *Cyclestheria hislopi* (Baird, 1859) (Crustacea, Branchiopoda, Spinicaudata), with a comparison of male clasplers among the Conchostraca and Cladocera and its bearing on phylogeny of the "bivalved" Branchiopoda. *Zool. Scripta* 25: 291-316.
- Page, R.D.M. 2000. NDE, Version 0.4.8. Program online available at: <http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html>

- Pisani, D., Poling, L.L., Lyons-Weiler, M. & Hedges, S.B. 2004. The colonization of land by animals: molecular phylogeny and divergence times among arthropods. *BMC Biology* 2: 1-10.
- Prendini, L. 2001. Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. *Syst. Biol.* 50: 290-300.
- Regier, J.C. & Shultz, J.W. 2001. Elongation factor-2: a useful gene for arthropod phylogenetics. *Mol. Phylogenet. Evol.* 20: 136-148.
- Richter, S. 2002. The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea. *Org. Divers. Evol.* 2: 217-237.
- Richter, S. 2004. A comparison of the mandibular gnathal edges in branchiopod crustaceans: implications for the phylogenetic position of the Laevicaudata. *Zoomorphol.* 123: 31-44.
- Richter, S. & Scholtz, G. 2001. Phylogenetic analysis of the Malacostraca (Crustacea). *J. Zool. Syst. Evol. Res.* 39: 113-136.
- Richter, S. & Wirkner, C. 2004. Kontroversen in der phylogenetischen Systematik der Euarthropoda. In: Richter, S. Sudhaus, W. (eds.), *Kontroversen in der Phylogenetischen Systematik der Metazoa*: pp. 73-102. Sber. Ges. Naturf. Freunde Berlin 43.
- Riley, J., Banaja, A.A. & James, J.L. 1978. The phylogenetic relationships of the Pentastomida: The case for their inclusion within the Crustacea. *Intern. J. Parasitol.* 8: 245-254.
- Schram, F.R. 1986. *Crustacea*. New York: Oxford Univ. Press.
- Schram, F.R. & Hof, C.H.J. 1998. Fossils and the interrelationships of major crustacean groups. In: Edgecombe, G.D. (ed.), *Arthropod Fossils and Phylogeny*: pp. 233-302. New York: Columbia Univ. Press.
- Schram, F.R. & Jenner, R.A. 2001. The origin of Hexapoda: a crustacean perspective. *Ann. Soc. Entomol. Fr., N.S.*, 37: 243-264.
- Schram, F.R. & Koenemann, S. 2004a. Are the crustaceans monophyletic? In: Cracraft, J. & Donoghue, M.J. (eds.), *Assembling the Tree of Life*: pp. 319-329. New York: Oxford Univ. Press.
- Schram, F.R. & Koenemann, S. 2004b. Developmental genetics and arthropod evolution: On body regions of Crustacea. In: Scholtz, G. (ed.), *Evolutionary Developmental Biology of Crustacea*: pp. 75-92. Lisse: Balkema.
- Shultz, J.W. & Regier, J.C. 2000. Phylogenetic analysis of arthropods using two nuclear protein-encoding genes supports a crustacean + hexapod clade. *Proc. R. Soc. London, B*, 267: 1011-1019.
- Simmons, M.P. 2004. Independence of alignment and tree search. *Mol. Phylogenet. Evol.* 31: 874-879.
- Sinakevitch, I., Douglass, J.K., Scholtz, G., Loesel, R. & Strausfeld, N.J. 2003. Conserved and convergent organization in the optic lobes of insects and isopods, with reference to other crustacean taxa. *J. Comp. Neurobiol.* 467: 150-172.
- Spears, T. & Abele, L.G. 1998. Crustacean phylogeny inferred from 18S rDNA. In: Fortey, R.A. & Thomas, R.H. (eds.), *Arthropod Relationships*: pp. 169-187. London: Chapman & Hall.
- Spears, T. & Abele, L.G. 1999. Phylogenetic relationships of crustaceans with foliaceous limbs: an 18S rDNA study of Branchiopoda, Cephalocarida, and Phyllocarida. *J. Crust. Biol.* 19: 825-843.
- Spears, T. & Abele, L.G. 2000. Branchiopod monophyly and interordinal phylogeny inferred from 18S ribosomal DNA. *J. Crust. Biol.* 20: 1-24.
- Turbeville, J.M., Pfeifer, D.M., Field, K.G. & Raff, R.A. 1991. The phylogenetic status of arthropods, as inferred from 18S rRNA sequences. *Mol. Biol. Evol.* 8: 669-686.
- Walossek, D. 1993. The Upper Cambrian *Rehbachella* and the phylogeny of Branchiopoda and Crustacea. *Fossils & Strata* 32: 1-202.

- Walossek, D. 1999. On the Cambrian diversity of Crustacea. In: Schram, F.R. & Vaupel-Klein, J.C. (eds.), *Crustaceans and the Biodiversity Crisis. Proc. 4th Int. Crust. Congr., Amsterdam 1998, Vol. I*: pp. 3-27. Leiden: Brill.
- Waloszek, D. 2003. Cambrian 'Orsten'-type preserved arthropods and the phylogeny of Crustacea. In: Legakis, A., Sfenthourakis, S., Polymeni, R. & Thessalou-Legaki, M. (eds.), *The New Panorama of Animal Evolution*: pp. 69-87. Sofia: Pensoft.
- Walossek, D. & Müller, K.J. 1994. Pentastomid parasites from the Lower Palaeozoic of Sweden. *Trans. R. Soc. Edinburgh, Earth Sci.*, 85: 1-37.
- Wheeler, W.C. 1990. When is an outgroup not an outgroup and how to root DNA sequence based topologies without an outgroup. *Cladistics* 6: 363-367.
- Wheeler, W.C. 1995. Sequence alignment, parameter sensitivity, and the phylogenetic analysis of molecular data. *Syst. Biol.* 44: 321-331.
- Wheeler, W.C. 1996. Optimization alignment: the end of multiple sequence alignment in phylogenetics? *Cladistics* 12: 1-9.
- Wheeler, W.C. 1998. Sampling, groundplans, total evidence and the systematics of arthropods. In: Fortey, R.A. & Thomas, R.H. (eds.), *Arthropod Relationships*: pp. 87-96. London: Chapman & Hall.
- Wheeler, W.C. 2001. Homology and the optimization of DNA sequence data. *Cladistics* 17: S3-S11.
- Wheeler, W.C., Cartwright, P. & Hayashi, C.Y. 1993. Arthropod phylogeny: a combined approach. *Cladistics* 9: 1-39.
- Wheeler, W.C., Gladstein, D. & DeLaet, J. 2002. POY version 3.0. Program and documentation online available at American Museum of Natural History: <ftp.amnh.org/pub/molecular>
- Wheeler, W.C., Giribet, G. & Edgecombe, G.D. 2004. Arthropod systematics. The comparative study of genomic, anatomical, and paleontological information. In: Cracraft, J. & Donoghue, M.J. (eds.), *Assembling the Tree of Life*: pp. 281-295. New York: Oxford Univ. Press.
- Whittington, P.M. 1995. Conservation versus change in early axonogenesis in arthropod embryos: A comparison between myriapods, crustaceans and insects. In: Breidbach, O. & Kutsch, W., (eds.), *The Nervous System of Invertebrates; An Evolutionary and Comparative Approach*: pp. 181-219. Basel: Birkhäuser.
- Whittington, P.M. 1996. Evolution of neural development in the arthropods. *Seminars Cell Dev. Biol.* 7: 605-614.
- Wills, M.A. 1998. A phylogeny of recent and fossil Crustacea derived from morphological characters. In: Fortey, R.A. & Thomas, R.H. (eds.), *Arthropod Relationships*: pp. 189-209. London: Chapman & Hall.
- Wilson, K., Cahill, V., Ballment, E. & Benzie, J. 2000. The complete sequence of the mitochondrial genome of the crustacean *Penaeus monodon*: are malacostracan crustaceans more closely related to insects than to branchiopods? *Mol. Biol. Evol.* 17: 863-874.
- Wingstrand, K.G. 1972. Comparative spermatology of a pentastomid, *Raillietiella hemidactyli*, and a branchiuran crustacean, *Argulus foliaceus*, with a discussion of pentastomid relationships. *K. Dan. Vidensk. Selsk. Biol. Skr.* 19: 1-72.
- Zrzavý, J. 2001. The interrelationships of metazoan parasites: a review of phylum- and higher-level hypotheses from recent morphological and molecular phylogenetic analyses. *Folia Parasitologica* 48: 81-103.
- Zrzavý, J. & Štýs, P. 1997. The basic body plan of arthropods: insights from evolutionary morphology and developmental biology. *J. Evol. Biol.* 10: 353-367.

Zrzavý, J., Hypša, V. & Vlaskova, M. 1998. Arthropod phylogeny: taxonomic congruence, total evidence and conditional combination approaches to morphological and molecular data sets. In: Fortey, R.A. & Thomas, R.H. (eds.), *Arthropod Relationships*: pp. 97-107. London: Chapman & Hall.