PENSOFT
SENCKENBERG NATURE RESEARCH
Leibniz Association

Phylogeny of the fascinating and frustrating Peracarida: the past, the present and the future

Sarah Gerken[1], Magdalena Błażewicz[2], Kevin M. Kocot[3], Stefan Richter[4], Martin Schwentner[5], Regina Wetzer[6]

1 *Department of Biological Sciences, University of Alaska Anchorage, Anchorage, AK 99508, United States*
2 *Department of Invertebrate Zoology and Hydrobiology, Faculty of Biology and Environmental Protection, University of Lodz ul. Banacha 12/16, 90-237 Łódź, Poland*
3 *Department of Biological Sciences, University of Alabama, Tuscaloosa, AL 35487, United States*
4 *Allgemeine & Spezielle Zoologie, Institut für Biowissenschaften, Universität Rostock, Universitätsplatz 2, 18055 Rostock, Germany*
5 *3rd Zoological Department, Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria*
6 *Marine Biodiversity Center, Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA 90007, United States*

https://zoobank.org/1E89644A-789F-4B1E-B912-69A15691C622

Corresponding author: Regina Wetzer (rwetzer@nhm.org)

Received 30 November 2025
Accepted 14 April 2026
Published 9 July 2026

Academic Editor Andreas Zwick, Klaus-Dieter Klass

Citation: Gerken S, Błażewicz M, Kocot KM, Richter S, Schwentner M, Wetzer R (2026) Phylogeny of the fascinating and frustrating Peracarida: the past, the present and the future. Arthropod Systematics & Phylogeny 84: 549–563. https://doi.org/10.3897/asp.84.e180526

Abstract

Peracarida (Arthropoda: Crustacea) is one of Earth's most strikingly diverse animal groups. Often compared with their relatives, the decapods (crabs, shrimp, and lobsters), a better comparison would be with the hyperdiverse insects: small bodies, exceptional diversity of form, and pervasive habitat occupancy. Those traits, and that most live in the challenging ocean environment, have left the peracarids woefully underexplored. Each of the world's few peracarid taxonomists has an extensive backlog of new species waiting to be described, and every field trip that targets peracarids yields novel species – the scope for diversity discovery is nearly unlimited. The historically sparse diversity sampling has left our understanding of peracarid relationships in a murky state. Making sense of the group's diversity requires a solid phylogenetic framework to explain their evolutionary history. Here we summarize the 180 years of peracarid history with references to all key taxonomic discoveries and hypotheses. Beyond bringing a historical perspective to the group, we propose phylogenomic approaches to deciphering peracarid phylogeny enabled by current international projects. We welcome collaboration with all researchers working on Peracarida and are particularly interested in partnerships that broaden taxon sampling, expand geographic and habitat coverage, and support opportunities and training for the next generation of peracarid researchers.

Keywords

Amphipoda, Bochusacea, Cumacea, Ingolfiellida, Isopoda, Lophogastrida, Mictacea, Mysidacea, Spelaeogriphacea, Stygiomysida, Tanaidacea, Thermosbaenacea

1. Introduction

Peracarida is a clade of malacostracan crustaceans united by two morphological characters, brooding of the young by the female in a marsupium or brood pouch, and the presence of a lacinia mobilis on the mandible in the adults. Within the basic malacostracan body plan of five head segments, eight thoracic segments, and six pleonal segments, peracarids have at least the first thoracic segment fused to the head and the first pair of thoracic appendages modified as maxillipeds (also called unguiped; Grams et al. 2023), with up to three thoracic segments fused to the

Table 1. Taxon authors and dates. Superorder Peracarida Calman, 1904.

Year that the taxon was recognized as an order, sorted alphabetically:		**Taxa sorted in date order of appearance in the published literature.**	
1816	Order Amphipoda Latreille, 1816a	1816	Order Isopoda Latreille, 1816b
1998	Order Bochusacea Gutu & Iliffe, 1998	1883	Order Mysida Hayworth, 1825; originally published as Mysidacea, but unaccepted (Meland & Willassen 2007)
1846	Order Cumacea Krøyer, 1846	1846	Order Cumacea Krøyer, 1846
2017	Order Ingolfiellida Lowry & Myers, 2017	1849	Order Tanaidacea Dana, 1849
1816	Order Isopoda Latreille, 1816b	1883	Order Lophogastrida Boas, 1883; Meland & Willassen 2007
1883	Order Lophogastrida Boas, 1883; Meland & Willasseen 2007	1927	Order Thermosbaenacea Monod, 1927
1985	Order Mictacea Bowman, Garner, Hessler, Iliffe & Sanders, 1985	1930	†Order Pygocephalomorpha Beurlen & Glaessner, 1930; Taylor et al. 1998
1883	Order Mysida Hayworth, 1825; originally published as Mysidacea, but unaccepted (Meland & Willassen 2007)	1957	Order Spelaeogriphacea Gordon, 1957
1957	Order Spelaeogriphacea Gordon, 1957	1981	Order Stygiomysida Tchindonova, 1981; Meland & Willassen 2007
1981	Order Stygiomysida Tchindonova, 1981; Meland & Willassen 2007	1985	Order Mictacea Bowman, Garner, Hessler, Iliffe & Sanders, 1985
1849	Order Tanaidacea Dana, 1849	1998	Order Bochusacea Gutu & Iliffe, 1998
1927	Order Thermosbaenacea Monod, 1927	2017	Order Ingolfiellida Lowry & Myers, 2017
1930	†Order Pygocephalomorpha Beurlen & Glaessner, 1930; Taylor et al. 1998	1816	Order Amphipoda Latreille, 1816a

head and three pairs of maxillipeds. There are approximately 26,000 described peracarid species (WoRMS Editorial Board 2025) distributed across one fossil (Pygocephalomorpha) and 12 extant orders. The extant groups generally considered as comprising Peracarida are Amphipoda, Bochusacea, Cumacea, Ingolfiellida, Isopoda, Lophogastrida, Mictacea, Mysida, Spelaeogriphacea, Stygiomysida, Tanaidacea and Thermosbaenacea. Morphologically, peracarids are spectacularly diverse. Table 1 summarizes the currently accepted orders.

In the broader context, Pancrustacea (crustaceans and hexapods) account for 80% of described animal diversity on Earth (Roskov et al. 2022). Within Pancrustacea, peracarids represent about 39% of all non-hexapod pancrustacean diversity and about 65% of malacostracan diversity. The majority of peracarids are found in marine environments, but there are representatives in every environment on Earth, from terrestrial deserts to oceanic trenches. Peracarids occupy many ecological roles. They can be parasites of hosts from decapods to cnidarians, predators on smaller organisms, scavengers responsible for rapid recycling of benthic food falls, as well as filter feeders and deposit feeders cycling organic carbon back into the food web. Economic damage from peracarids can be extensive. Wood boring isopods known as gribbles (*Limnoria*) cause extensive damage to wooden docks, piers and boats. Parasitic bopyrid isopods afflict commercially harvested decapods, both wild caught and aquacultured, including *Macrobrachium* species (Gopalakrishnan et al. 2017). Peracarid bodies are remarkably morphologically plastic. This is especially true within Isopoda, which have body plans ranging from a standard roly-poly (Hornung 2011) to essentially formless parasites (Williams and Boyko 2012). Evolutionarily, peracarids are fascinating, with rapid molecular evolution and highly variable genome size (Rees et al. 2007; Hessen and Persson 2009; Jeffery 2015). There is evidence for multiple habitat transitions through time, from marine to terrestrial and freshwater environments (Wägele et al. 2003; Wilson 2009; Raupach et al. 2009; Riehl et al. 2014; Lins et al. 2017; Wetzer et al. 2018) and transitions from shallow marine waters to the deep sea (Raupach et al. 2009). The mode and tempo of these transitions remain incompletely understood. For example, some studies cast doubt on the monophyly of terrestrial isopods (Oniscidea; e.g., Dimitriou et al. 2019), yet two recent phylogenomic studies by Thomas Thorpe (2024) and Iwasa-Arai et al. (2025) recovered the group monophyletic and inferred a single transition to land in the Carboniferous–Permian.

Despite being generally accepted as a taxon for over 100 years, monophyly of Peracarida is not entirely clear, and neither are relationships within the group, as summarized in Fig. 1 and Table S1 (Boas 1883; Grobben 1892; Siewing 1963; Watling 1981, 1999; Hessler 1983; Schram 1984; Pires 1987; Wagner 1994; Mayrat and Saint Laurent 1996; Schram and Hof 1998; Wheeler 1998; Wills 1998; Jarman et al. 2000; Richter and Scholtz 2001; Poore 2005; Spears et al. 2005; Meland and Willassen 2007; Wilson 2009; Wirkner and Richter 2010; Schwentner et al. 2018; Lozano-Fernandez et al. 2019; Höpel et al. 2022; Bernot et al. 2023; Yu et al. 2024; Cannizzaro and Berg 2025; Iwasa-Arai et al. 2025). Recent studies that support peracarid monophyly had limited sampling of the extant orders (Höpel et al. 2022), mitochondrial genomes – 58%; (Bernot et al. 2023), nuclear protein-coding genes from transcriptomes and genomes – 50%; (Yu et al. 2024), genomes, transcriptomes, and raw RNA-seq reads – 41%, and ultraconserved elements (UCEs) – 45% (Cannizzaro and Berg 2025) and 63% (Iwasa-Arai et al. 2025).

Earlier molecular studies based on one or few PCR-amplified gene fragments that included more orders are not in agreement about peracarid monophyly (i.e., Mysida placed within Peracarida or not; summarized in Meland et al. 2015). There is no consensus on relationships within the group, regardless of the analysis methodology used (the various hypotheses are summarized in Fig. 1 and Table S1). The first-branching group within Peracarida has been suggested to be Amphipoda (Mayrat & de Saint Laurent 1996; Wirkner and Richter 2010; Bernot et al. 2023; Yu et al. 2024), or Mysida (Schram 1984; Schwentner et al. 2018), or Mysidacea + Amphipoda (Höpel et al. 2022), or Thermosbaenacea (Siewing 1963; Watling 1983; Pires 1987; Iwasa-Arai et al. 2025). Mancoida has been supported as monophyletic in both morphological studies (Richter and Scholtz 2001; Wilson 2009) and molecular studies (Schwentner et al. 2018; Höpel et al. 2022; Bernot et al. 2023), but taxon sampling has been very unbalanced, as these studies included multiple isopods but very few tanaids and cumaceans, prompting concerns about long-branch attraction. Depending on the molecular marker(s) used, peracarids exhibit moderate to severe branch length heterogeneity in molecular phylogenetic analyses (Spears et al. 2005; Bybee et al. 2011; Schwentner et al. 2018; Höpel et al. 2022; Bernot et al. 2023; Barta et al. 2025; Iwasa-Arai et al. 2025). The various hypotheses are summarized in Fig. 1 and Table S1.

All attempts to resolve peracarid phylogeny, whether based on morphological or molecular data, suffer from the same fundamental problems, limited character sampling on the one hand, limited taxon sampling on the other hand. Here, we review the current understanding of peracarid diversity and phylogeny based on both morphological and molecular approaches. We highlight open questions about peracarid evolution, describe work in progress, and opportunities for improving understanding of this fascinating group.

2. A historical summary

2.1. Morphology

Leach (1816) gave the first hint of peracarid affinities in coining the term Edriophthalma, a taxon containing Isopoda and Amphipoda. Ten years later, Latreille (1826) suggested the (similarly long lasting) taxon Schizopoda for including Mysidacea and Euphausiacea. Claus (1886) shows a diagram presenting the phylogenetic (genealogical) relationships of Malacostraca based on a detailed study. He derived all Malacostraca except for Leptostraca and Stomatopoda from a hypothetical "Urschizopod" ancestor without naming the clade and recognized Schizopoda closer to Decapoda. Claus was the first author to use Tanaiden (= Tanaidacea) as closely related to, but separate from, Isopoda. Grobben (1892) used the same tree as Claus, but also derived Stomatopoda from the hypothetical "Urschizopod" ancestor and named the clade Eumalacostraca (Fig. 3).

Boas' (1883) approach (although earlier) was more similar to what we recognize today than that of Claus (1886) and Grobben (1892). Boas (1883) was the first to recognize Peracarida as a distinct monophyletic group within Malacostraca, though without naming them (Fig. 2). He distinguished seven orders within Malacostraca: Euphausiacea, Mysidacea (with Lophogastrida and Mysida), Cumacea, Isopoda, Amphipoda, Decapoda and Squillacea (= Stomatopoda). Boas rejected Schizopoda but placed Amphipoda, Isopoda, Cumacea, Mysida, and Lophogastrida in a clade in his phylogenetic hypothesis, with Decapoda, Euphausiacea, and Stomatopoda inferred to branch earlier from the lineage that gave rise to Peracarida.

Thomson (1893) described a new "freshwater schizopod from Tasmania," *Anaspis tasmaniae* (today *Anaspides*), and characterized it as "in many of its characters […] to be allied, though somewhat remotely, to the Euphausiidae of Sars." At the same time, Hansen (1893), while unaware of the discovery of *A. tasmaniae*, recognized three divisions within Eumalacostraca. The first division contained Mysida, Cumacea, Isopoda, Tanaidae (now recognized as the order Tanaidacea), and Amphipoda, united by the possession of a lacinia mobilis on the mandibles; it is a strong tooth-like structure on the left mandible, which is oriented at a right angle to the remaining mandibular edge, but is a stalked, spine-like structure on the right mandible (Richter et al. 2002). The second division included Euphausiacea and Decapoda, and the third consisted of Stomatopoda. Hansen's first division was congruent with Boas (1883) in uniting Mysida, Cumacea, Isopoda, and Amphipoda.

Calman (1904, 1909) summarized previous approaches and presented a classification of Malacostraca, which is widely accepted today. He introduced the new names Peracarida and Eucarida for the first and second divisions of Hansen (1893) and associated Thomson's *Anaspides* together with the also newly discovered Bathynellacea (Vejdovský 1882) in the division Syncarida. The term Schizopoda continued to be used for some decades, but "as brief and rather practical" and not considered as a natural or monophyletic group (e.g., Hansen 1905, 1910).

In the middle of the 20th century Siewing (1951, 1953, 1956, 1963) conducted detailed studies of the internal anatomy of various peracarids and largely supported Calman's (1904, 1909) classification. For the first time, Siewing included Thermosbaenacea close to Peracarida. Siewing (1956) (Fig. 4) introduced the term Pancarida for Thermosbaenacea to emphasize that the "systematic rank" is the same as that of Peracarida, i.e., a "division" sensu Calman (1909). Within Peracarida, he suggested a clade comprising Cumacea, Tanaidacea, and Isopoda, and rejected closer affinities of Isopoda and Amphipoda, thus rejecting Edriophthalma of Leach (1816). It was Watling (1981) who suggested a superorder Mancoida, containing the orders Isopoda, Spelaeogriphacea, Tanaidacea, and Cumacea (see also Hessler 1983).

The position of Thermosbaenacea within Malacostraca has been argued for many decades. Fryer (1964) suggest-

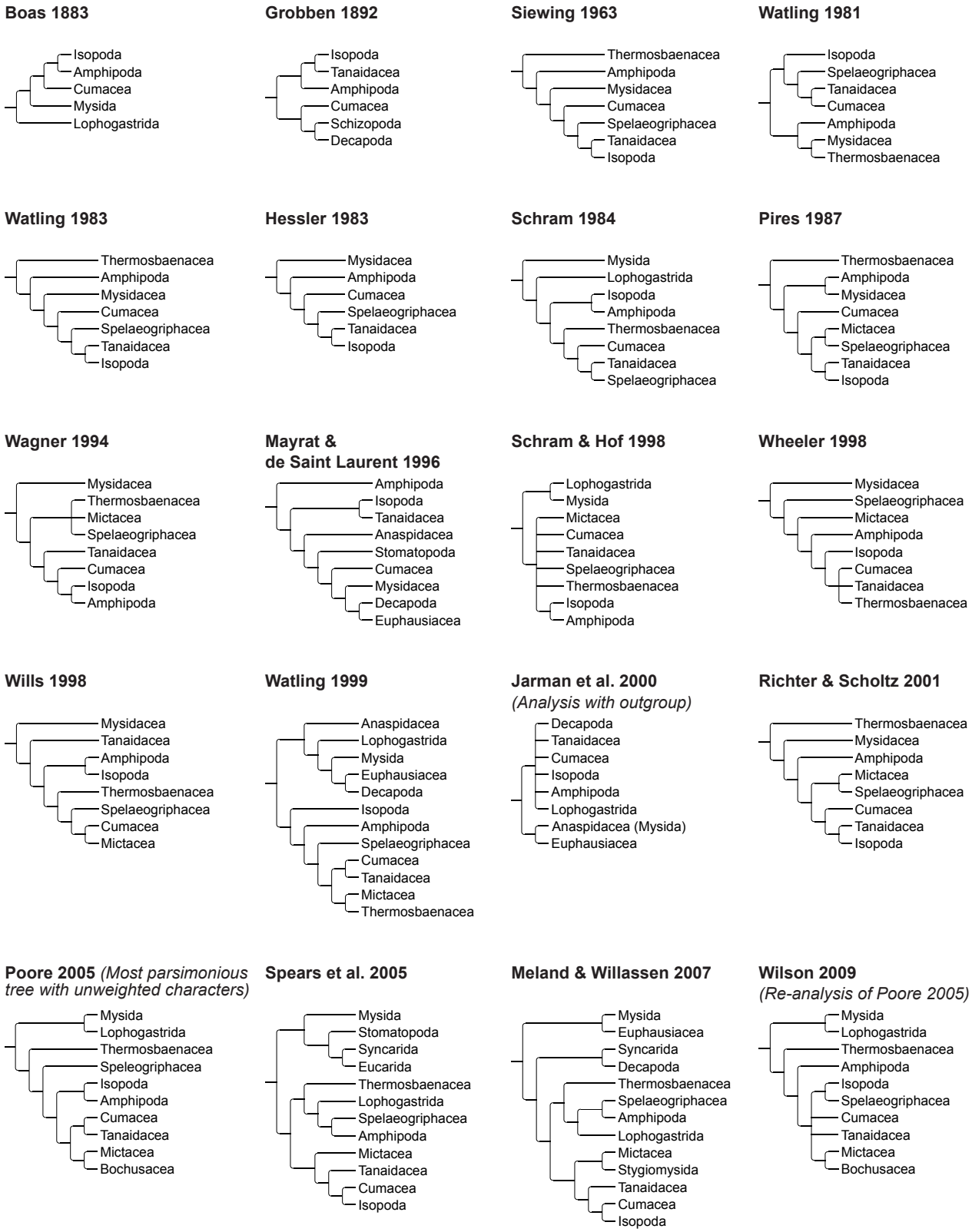

Figure 1 [Part A]. Phylogenetic hypotheses for Peracarida.

ed in his monograph on the thermosbaenacean *Monodella* (*Tethysbaena*) *argentarii* that thermosbaenaceans are ingroup peracarids with close affinities to Isopoda, Tanaidacea, and the newly discovered Spelaeogriphacea (*Spelaeogriphus lepidops* Gordon, 1957). Hessler (1983) found no reason to relate Thermosbaenacea to the mancoid lineage, or perhaps even to the peracarids and excluded Thermosbaenacea again from Peracarida. Sieg (1984) in his monograph on Tanaidacea provided a detailed discussion of the monophyly of Peracarida and the exclusion of Thermosbaenacea. He also argued that Tanaidacea and Isopoda are sister taxa with Spelaeogriphacea as sister group to the pair. After discovering a second species of spelaeogriphaceans, Pires (1987) included Mictacea (dis-

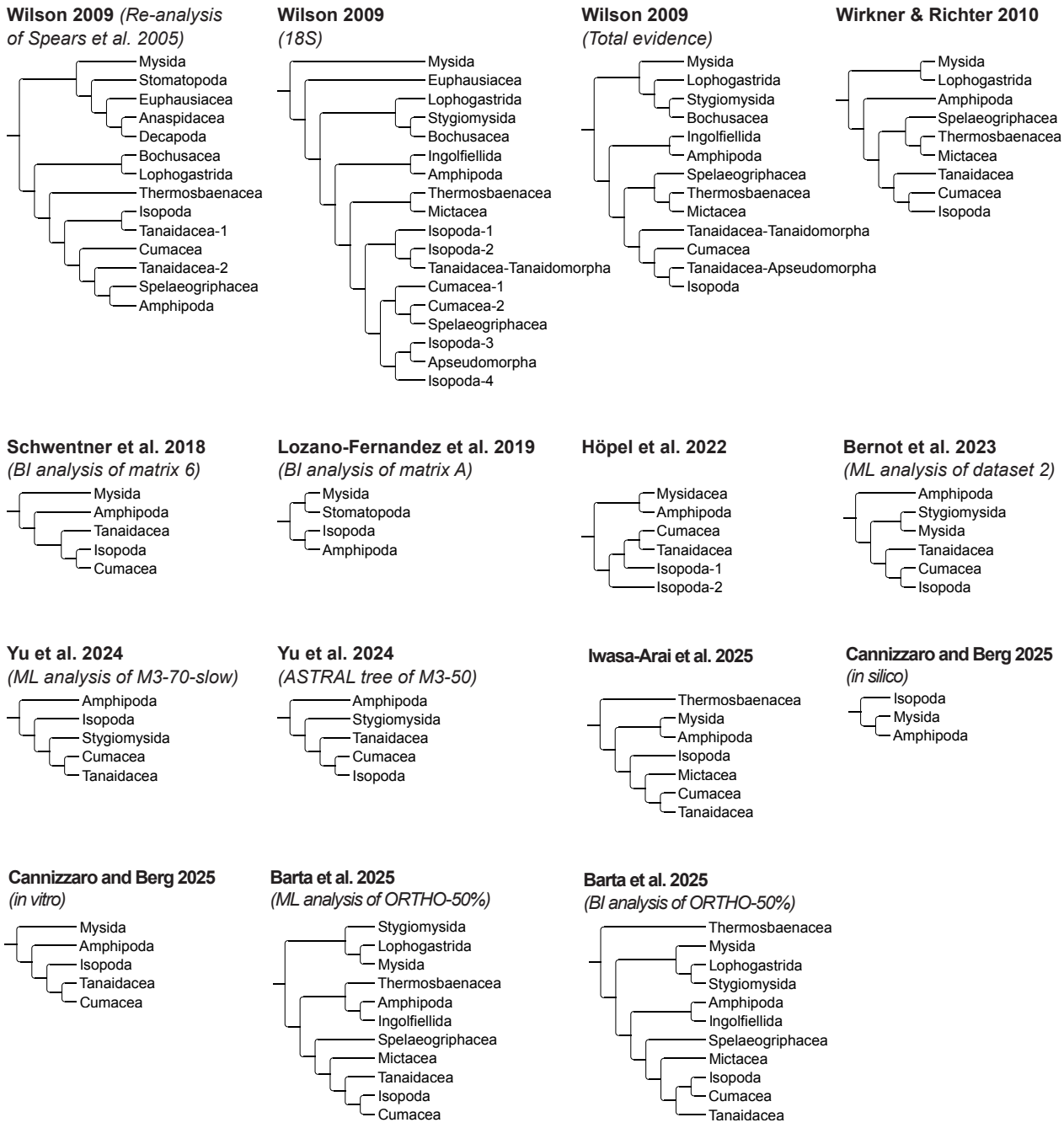

Figure 1 [Part B]. Phylogenetic hypotheses for Peracarida.

covered in 1985) in Peracarida for the first time, and suggested a sister group relationship for the Mictacea and Spelaeogriphacea. Schram (1981), Watling (1983, 1999), Nylund et al. (1987), and Watling et al. (2000) proposed various scenarios for the non-monophyly of Peracarida, yet successive morphological phylogenetic analyses mostly refuted these ideas (see Poore 2005 for further discussion).

Parsimony-based cladistic analyses started with Schram (1984, 1986), followed by Wagner (1994), Schram and Hof (1998), and Wills (1998), the lattermost attempting a phylogenetic analysis of Malacostraca within a broad sampling of extant and fossil crustaceans (without Leptostraca), supporting monophyly of Malacostraca with paraphyletic Syncarida at its base. Wills' (1998) analysis supported both monophyletic Eucarida and Peracarida, and placed Stomatopoda as the sister taxon to Eucarida. A later analysis (Wills et al. 2009) with a focus on Malacostraca produced similar results, but positioned Stomatopoda between Anaspidacea and Bathynellacea, while also showing differently resolved relationships within Peracarida.

A parsimony analysis by Richter and Scholtz (2001), including new anatomical details of the ommatidia, questioned monophyly of Eucarida by supporting a closer affinity of Euphausiacea to Syncarida and Peracarida, together forming Xenommacarida (originally proposed by Richter 1999). Additionally, the Richter and Scholtz (2001) analysis supported a monophyletic Mysidacea (= Lophogastrida + Mysida) as the sister group to the remain-

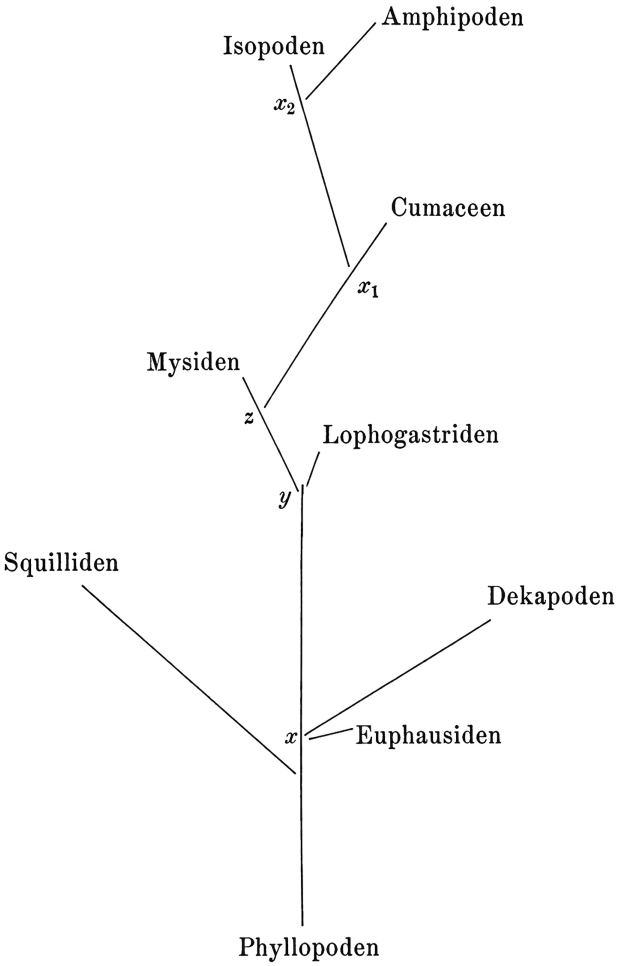

Figure 2. Phylogenetic tree (Stammbaum) of Malacostraca based on Boas (1883: 487) showing all representatives of today's Peracarida derived from a hypothetical ancestor with Lophogastrida closest to the ancestor ("dem Ausgangspunkte am nächsten stehen").

ing Peracarida. Poore (2005) used a mixture of ground plan (using hypothesized character states of higher taxa) and exemplar approaches (i.e., using actual species as terminals, sensu Prendini 2001) and included in his analyses for the first time single species representing Mictacea and Spelaeogriphacea. Poore's (2005) analysis supported monophyly of Peracarida, with Thermosbaenaecea as ingroup peracarids and with Isopoda and Amphipoda as sister taxa (i.e., Edriopthalma). He also concluded that Spelaeogriphacea and Mictacea are each monophyletic and possibly sister taxa. This was in contrast to Guțu and Iliffe (1998) and Guțu (1998), who pointed out significant differences between the two mictacean families, Mictocarididae and Hirsutiidae, and proposed new ordinal names for Hirsutiidae alone (Bochusacea) and Mictocarididae plus Spelaeogriphidae (Cosinzeneacea).

By further expanding the character matrix of Richter and Scholtz (2001) with extensive data on the circulatory system, Wirkner and Richter (2010) provided additional support for the phylogenetic hypothesis of Richter and Scholtz (2001). They also were among the first to apply an exemplar approach (sensu Prendini 2001) in morphology-based malacostracan phylogeny reconstruction, preceded only by Wilson (2009), who focused on isopods (including both morphological and molecular analyses). One of the results was the sister group relationship between Isopoda and Cumacea (Wirkner and Richter 2010). Thermosbaenacea was again suggested as an ingroup peracarid forming a clade with Mictocarididae and Spelaeogriphacea. The morphological analysis by Tabacaru and Danielopol (2011) went back to the more traditional ground plan approach. The newest morphological analysis by Grams et al. (2025) is partly already the result of the herein presented new project. Their multimethodological framework primarily aimed to compare various weighting schemes and, in particular, the novel option of character dependency consideration. Nonetheless, their diverse results gave highly consistent indications for the monophyly of Eucarida, Peracarida and Mysidacea (including Mysida, Lophogastrida and Stygiomysida). The relationships within Peracarida were less conclusive, including, e.g., the recurring, but debatable support for monophyletic Edriophthalma (Amphipoda + Isopoda). Further, the inclusion of Thermosbaenacea (surprisingly often associated with Bathynellacea) as either ingroup Peracarida or as a basal branch (i.e., sister group of remainder) therefore remained inconclusive.

The primary drawback of morphological approaches (notwithstanding their immense value for understanding transformational evolution) is the painstaking and time-consuming work and high level of expertise required to score highly detailed morphological characters, in conjunction with the difficulty in sampling and preserving specimens appropriately for such work. This has led to limited taxon sampling and overlap of the character sets used. With the development of technologies such as micro-CT and advanced microscopy techniques, highly detailed and higher throughput morphological analysis is becoming possible. However, morphological analysis alone is still likely insufficient to provide a stable peracarid phylogeny due to the morphological diversity across the group, which combines the evolution of novel characters with a strong tendency towards reduction, making the development of robust morphological datasets difficult, even with improved technology. Thus, the combination of molecular and morphological data might be the most appropriate way for analyzing phylogenetic relationships of Peracarida.

2.2. Molecular hypotheses

Molecular efforts to resolve the phylogeny of Peracarida began with Jarman et al. (2000) and were usually part of a malacostracan-wide studies. Based on a relatively small taxon set (seven peracarid species representing six orders) and a single gene, the 28S rRNA gene, Mysida was found to be more closely related to Euphausiacea than to other Peracarida including Lophogastrida (Jarman et al. 2000). The extensive work by Spears et al. (2005) based on the 18S rRNA gene included 21 species representing all nine peracarid orders recognized at the time (Amphipoda, Isopoda, Cumacea, Tanaidacea, Mysi-

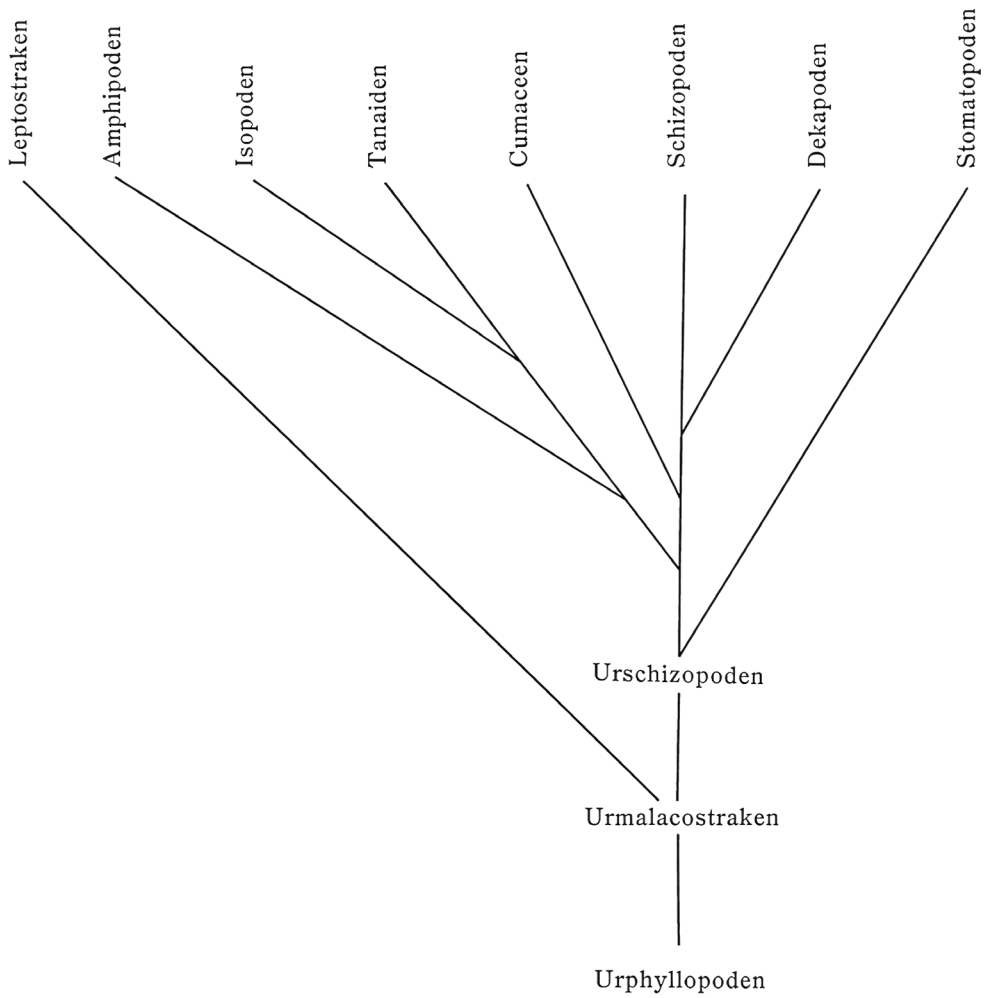

Fig. 2.

Figure 3. Phylogenetic tree (Stammbaum) of Malacostraca based on Grobben (1892: 272). He derived all extant Malacostraca from a hypothetical "Urmalakostraken" and all Eumalacostraca (a term introduced herein by Grobben) from a hypothetical "Urschizopoden", this is why the Schizopoda are in direct line with this hypothetical ancestor.

da, Lophogastrida, Spelaeogriphacea, Thermosbaenacea, and Mictacea). Spears et al.'s work was later extended by Meland and Willassen (2007) by adding more taxa with a strong focus on Mysidacea. These are still the most comprehensive molecular phylogenetic analyses with respect to sampling of taxa and the only peracarid molecular phylogenetic analyses that have included Mictacea, Thermosbaenacea and Spelaeogriphacea. These first molecular phylogenetic studies did not recover Peracarida monophyletic, as Mysida was recovered in a clade with either Eucarida + Syncarida + Stomatopoda (Spears et al. 2005) or Euphausiacea + Stomatopoda (Meland and Willassen 2007). Surprisingly, Lophogastrida and Stygiomysida were recovered within Peracarida, suggesting a non-monophyletic Mysidacea. Although these studies had good breadth across the orders, they depended on a single ribosomal RNA gene as a molecular marker, which, aside from containing a relatively small amount of information with respect to contemporary phylogenomic analyses (e.g., Bernot et al. 2023), has been shown to exhibit significant evolutionary rate heterogeneity and base compositional heterogeneity across metazoan lineages (Abouheif et al. 1998).

Höpel et al.'s (2022) analysis of mitochondrial genomes sampled 46 peracarid taxa representing seven (58%) of the orders, although 87% of the peracarid taxa belonged to Amphipoda or Isopoda. Their Bayesian Inference (BI) analysis of the 13 protein-coding genes and two rRNA genes recovered Peracarida, Mysidacea, Mysidacea + Amphipoda, and Mancoida as monophyletic with maximal support. However, within Mancoida, Isopoda was paraphyletic with respect to Cumacea and Tanaidacea with strong support. Results were similar in the maximum likelihood (ML) analysis of the same dataset with the striking exception that Tanaidacea was on an extremely long branch nested within Mysidacea as the sister taxon of Mysida. As in the BI analysis, the ML analysis recovered Cumacea in a strongly supported clade with Isopoda, but Isopoda was recovered monophyletic (albeit with low bootstrap support. This result underscores the need for denser, strategically targeted taxon sampling to fill phylogenetic gaps. Adding intermediate lineages of Tanaidacea, for example, would shorten long branches, which can lessen artifacts such as long-branch attraction and provide more data for estimating evolutionary parameters in model-based analyses.

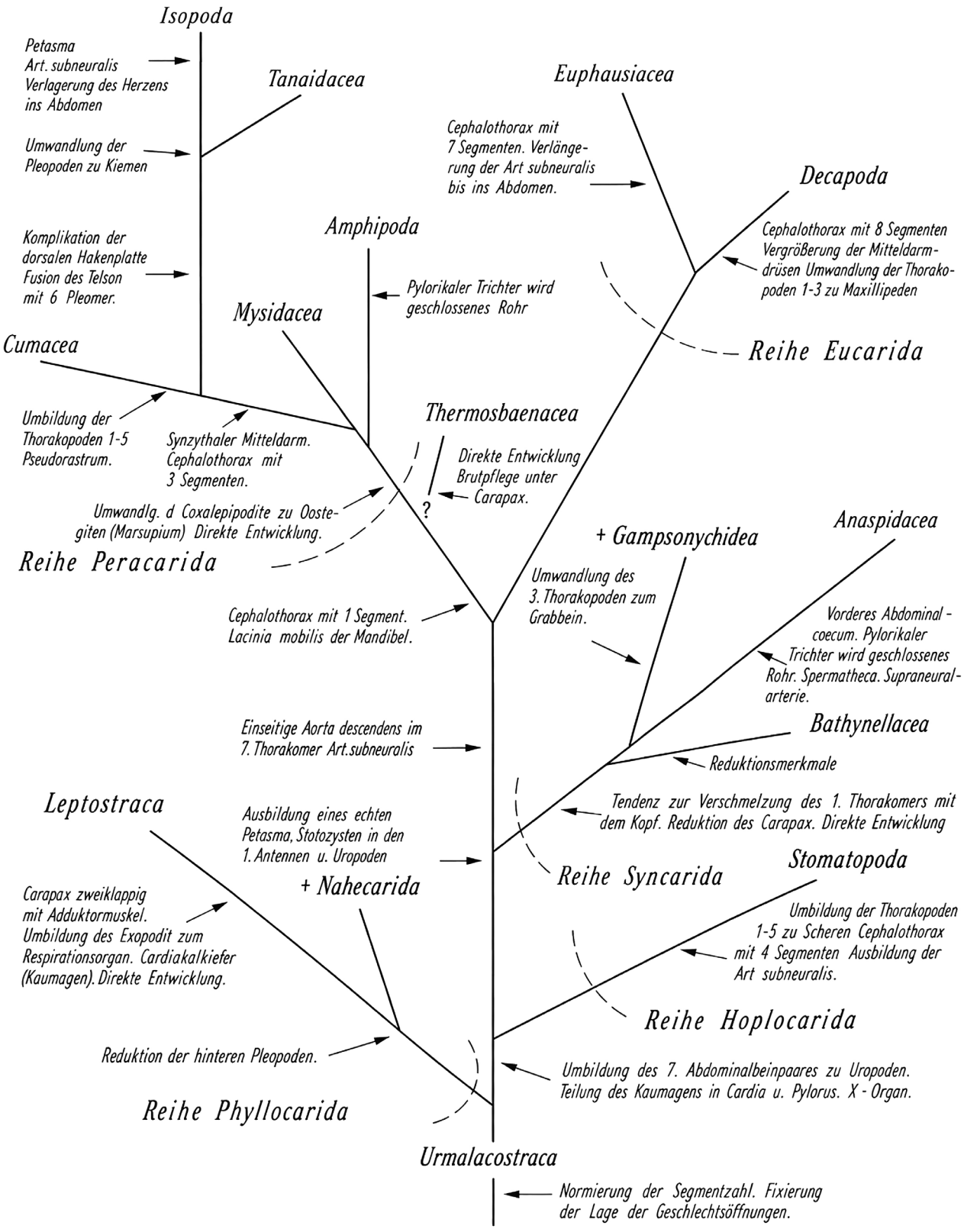

Diagramm 3

Figure 4. Phylogenetic tree (Stammbaum) of Malacostraca based on Siewing (1956: 168). The diagram also shows what we would consider as synapomorphies (although Siewing did not use the term).

Whereas Spears et al. (2005) and Meland and Willassen (2007) had a good representation of peracarid orders but sequenced just one molecular marker, the situation is reversed in more recent phylogenomic studies (Bybee et al. 2011; Schwentner et al. 2018; Bernot et al. 2023; Yu et al. 2024), which analyzed data from hundreds of nuclear protein-coding genes derived from transcriptomes and nuclear genomes, but had limited taxon sampling for

Peracarida. None of these phylogenomic studies targeted Peracarida specifically; all focused on broader pancrustacean relationships, and all included fewer than half of the peracarid orders, which were represented by only one to eleven taxa (reviewed by Bernot et al. 2023). For example, Bernot et al. (2023) sampled 28 peracarid species, 70% of which belonged to Amphipoda and Isopoda, and Yu et al. (2024) included only 11 taxa from five orders, 72% of them from Amphipoda and Isopoda.

Two recent phylogenomic studies show progress, but also some continuing instability in peracarid phylogeny. Iwasa-Arai et al. (2025) analyzed ultraconserved elements (UCEs) from 69 peracarid species representing 7 of 11 peracarid orders (64%). They recovered strong support for peracarid monophyly, Mancoida, and placement of Thermosbaenacea as the sister taxon of all other peracarids. This study provides a new UCE probe set that could be adopted for future phylogenomic investigations of Peracarida, although several smaller orders, including Lophogastrida, Stygiomysida, and Spelaeogriphacea, were not represented. A phylogenomic analysis by Barta et al. (2025; bioRxiv preprint, not yet peer-reviewed) incorporated extensive transcriptomic and genomic data for 128 peracarid species representing 10 of 11 peracarid orders (91%). For the first time in a phylogenomic framework, they included representatives of Mictacea, Spelaeogriphacea, and Ingolfiellida. Their analyses recovered strong support for peracarid monophyly and consistently supported a clade uniting Mancoida (Isopoda + Cumacea + Tanaidacea) with Mictacea and Spelaeogriphacea, as well as a monophyletic Mysidacea (Mysida + Lophogastrida + Stygiomysida). However, placement of Thermosbaenacea was inconsistent across analyses. Thermosbaenacea was recovered as either the sister taxon of Amphipoda + Ingolfiellida or the sister taxon of all non-mysidacean peracarids in ML analyses, whereas it was recovered as the sister taxon to all other peracarids in the BI analysis. Together, these recent studies underscore both the progress being made and the continued importance of broad taxon sampling for resolving relationships among peracarid orders.

Results from most phylogenomic studies to date tentatively suggest monophyletic Peracarida (Bybee et al. 2011; Schwentner et al. 2018; Bernot et al. 2023; Yu et al. 2024; Iwasa-Arai et al. 2025; Barta et al. 2025) and possibly monophyletic Mysidacea (Bernot et al. 2023; Barta et al. 2025). Mancoida (Isopoda, Cumacea, and Tanaidacea) was supported in several studies (Schwentner et al. 2018; Bernot et al. 2023; Yu et al. 2024; Cannizzaro and Berg 2025; Iwasa-Arai et al. 2025; Barta et al. 2025). However, these results were not always consistently recovered. For example, Peracarida was recovered monophyletic in only about half of the 28 different analyses performed in Schwentner et al. (2018); in the other analyses Mysida grouped with various combinations of Decapoda, Euphausiacea and Anaspidacea. Bernot et al. (2023) found that inference of pancrustacean relationships in their analyses was sensitive to taxon sampling, even when the same set of orthologs was analyzed. Surprisingly, relatively minor changes in taxon sampling and variation in gene coverage among taxa altered tree topology as much as the choice of loci. However, instability of peracarid relationships may stem less from the presence or absence of any single taxon than from uneven taxon sampling and variation in data completeness, which can lead to reduced resolving power, model parameter misestimations, and increased sensitivity to systematic errors (Roure et al. 2013; Al Jewari and Baldauf 2023; Yan et al. 2025).

As Bernot et al. (2023) demonstrated, limited and uneven taxon sampling remains the most serious obstacle to phylogenomic resolution of inter-ordinal relationships within Peracarida. Multiple studies have documented unusually long branches in peracarid lineages (Meland and Willassen 2007; Bybee et al. 2011; Schwentner et al. 2018; Yu et al. 2024). Such long branches, especially when combined with heterogeneous gene coverage, are known to heighten sensitivity to systematic error and can destabilize deeper pancrustacean relationships, as highlighted by Yu et al. (2024). Increasing both the number and the data completeness of strategically chosen peracarid taxa will therefore be essential for breaking up these long branches and improving model performance in future phylogenomic analyses.

3. Current understanding

After many studies utilizing a variety of approaches and data sources, we are essentially in the same place where we started. The natural grouping of the taxon Peracarida is generally accepted, but the exact composition of the group, monophyly of the group, and relationships within the group are not well resolved, with conflicting answers depending on the data and analytical approach. Persistent questions revolve around inclusion of Thermosbaenacea and Mysida, monophyly or paraphyly of Mysidacea, the identity of the earliest branching peracarid lineage, and the overall topology of the tree.

Thermosbaenacea is distinguished from other members of this superorder by being dorsal brooders, the pouch formed by the carapace. All other peracarids sensu lato are ventral brooders, with brood plates or oostegites derived from the coxa of the thoracopods. Their current inclusion in the Peracarida stems from morphological analyses, the most obvious shared synapomorphy is the presence of a lacinia mobilis in adults (Wagner 1994; Schram and Hof 1998; Wills 1998; Wirkner and Richter 2010) and single gene studies (Spears et al. 2005; Meland and Willassen 2007), as well as tradition.

The historical Mysidacea has been split into the extant orders Mysida, Lophogastrida, Stygiomysida and the extinct order Pygocephalomorpha. The relationships between the extant orders, and inclusion or exclusion of Mysida from Peracarida are all quite unclear. Various analyses suggest Mysidacea could be paraphyletic or monophyletic (see Höpel et al. 2022) for discussion), that the Lophogastrida are the sister group to the Mysida, or not. Stygiomysida has rarely been included in

analyses separately from the Mysida, as they were only recently recognized as a separate clade (Meland et al. 2015). Mysida has been variously suggested to be within Peracarida (as part of Mysidacea) or the sister taxon to Peracarida (Schwentner et al. 2018; Iwasa-Arai et al. 2025).

There is no robust or stable topology for relationships within Peracarida. Topologies are summarized in Fig. 1 and their tree files are offered in Table S1. Bernot et al. (2023) demonstrated comprehensively that small differences in taxon sampling had outsize impacts on phylogenetic reconstruction across Malacostraca, and especially within Peracarida. The recent analysis by Yu et al. (2024) points to long branch attraction as a major problem across Pancrustacea. There is one consistent grouping recovered within Peracarida in most analyses, Mancoida, consisting of Cumacea, Isopoda, and Tanaidacea, bearing in mind that not all peracarid taxa were included in these analyses. However, within Mancoida, all possible topologies have been recovered. Similarly, across Peracarida, a wide variety of topologies have been recovered. It is notable that of the 15 crucial taxa identified by Bernot et al. (2023) for resolving Pancrustacea phylogeny, 40% are peracarids, suggesting that instability in the peracarid phylogeny disproportionately destabilizes efforts to resolve the phylogeny of the entire Pancrustacea.

4. The future

Serendipitously, four projects across four countries have been funded to address peracarid phylogeny and evolution. At the same time, the ability to acquire data, both morphologically and molecularly, has increased exponentially with micro-CT and other advanced imaging techniques alongside the vast expansion and declining cost of next generation sequencing.

"A Backbone for the Peracarida" is funded by the United States National Science Foundation, concentrating on generating a phylogeny with family-level coverage across Peracarida using a combination of transcriptomes, genomes, and target capture. Simultaneously, "Transformations in the Evolution of Peracarida (Crustacea)" is funded by the Deutsche Forschungsgemeinschaft and Österreichischer Wissenschaftsfond, concentrating on studying higher-level phylogeny and evolutionary rates across the peracarids in comparison with reproductive strategy and habitat, using a combination of transcriptomes, genomic, and morphological analyses, with emphasis on Isopoda. Two projects funded by the National Science Centre in Poland aim to delineate the evolutionary arenas of shallow- and deep-sea Tanaidacea by reconstructing their phylogenetic history, assessing colonization pathways into the deep-sea and polar regions and identifying the morphological traits that are associated with diversification across marine habitats. All four of these projects are working hand-in-hand to generate a stable and well supported phylogenetic hypothesis for Peracarida.

Efforts to resolve the phylogeny of Peracarida have been impacted by both lack of taxon sampling (breadth) and lack of sufficient data in the taxa sampled (depth). New morphological and molecular tools can address the issues of limited data in phylogenetic studies, with advances in both morphological and molecular technology. Advanced imaging techniques like confocal laser microscopy (cLSM) and micro-computed tomography (micro-CT) have exponentially increased morphological data acquisition. Genomes and transcriptomes are becoming more cost effective, although these require material to be freshly collected, preserved in specific ways, and kept at very cold temperatures. Given the range of environments where peracarids are found (terrestrial deserts to deep-sea trenches), many taxa cannot easily be freshly collected, thus taxon sampling is still a problem even when using -omics tools that require frozen material. However, target capture techniques can be used to generate large amounts of data from ethanol-preserved specimens stored at room temperature, making museum specimens of rare taxa potentially available for expanding taxon sampling (e.g., Cannizzaro and Berg 2025; Iwasa-Arai et al. 2025).

Across the projects, we will be sequencing genomes from hitherto understudied orders (e.g., Cumacea, Mysida, Lophogastrida) and approximately 200 new peracarid transcriptomes from across the group. These reference datasets will be leveraged to design probes for conserved loci, and an additional 2,000 taxa will be sequenced using a target capture approach for a minimum of 250 loci. For samples that aren't suitable for target capture (e.g., due to their extremely small size), libraries will be sequenced at 30x without target capture. These genome skimming data will be de novo assembled, and target loci will be extracted bioinformatically. Overall, this approach is expected to address both of the current problems in resolving peracarid phylogeny, with a minimum of 250 genes per taxon sampled, and over 2,200 taxa sampled (more than 20x the taxa in the analyses with the greatest coverage to date). Coverage of taxa is expected to include the vast majority of recognized families. The anticipated stable, robust, and well-resolved phylogenetic hypothesis for Peracarida will allow research across the group to expand and grow.

The community of peracarid workers has been committed to trying to get a comprehensive phylogeny funded since 2010, and we are excited it is finally happening. These projects will only be successful with the participation of the global community, from providing specimens, to collaborating on workshops, to participating in symposia and discussions.

The first gathering in Rostock (hosted by Dr. Stefan Richter) in May 2024 brought together representatives from all the teams and established the cooperation and sharing of specimens and data. The July 2025 Crustacean Society Conference held in Paris brought together more than 30 global peracarid workers all participating in this effort and solidified our unified and supportive approach. A gathering will be held at the Natural History Museum of Los Angeles County in 2027 to synthesize the phylogenetic and genomic work and integrate vetted fossil

calibrations for divergence-time estimation. We are also planning future symposia on Peracarida, including the joint SICB/TCS meeting in 2027 and International Crustacean Congress XI.

Field-based taxonomy workshops provide rare, high-impact training for early-career researchers. By providing training in specimen collection, preservation, and identification with modern molecular and imaging approaches, these courses empower participants with a comprehensive skillset for twenty-first-century systematics research. The first "Confusing Crustaceans" peracarid workshop was a field-based workshop, held at the Smithsonian Tropical Research Institute in Bocas del Toro, Panama in August of 2024, where 26 established and early-career peracarid researchers learned and shared tropical sampling, sorting, identification, and preservation techniques with each other.

Taxonomy training workshops provide rare access to the collective expertise of multiple specialists from multiple parts of the world. During taxonomy workshops, trainees work side-by-side with expert taxonomists, gaining practical experience that is difficult to acquire through standard coursework, while also building professional networks and collaborative ties. Such immersive programs help sustain critical taxonomic expertise, foster a new generation of systematists, and strengthen the foundation for future biodiversity research and conservation efforts. "Confusing Crustaceans II," a taxonomy focused workshop held October 2025 in Wilhelmshaven, Germany trained 30 established and early career workers in species-level identification and description, and increased morphological capacity in the community. We are interested in expanding our program of workshops to other parts of the world, encouraging more peracarid research in collaboration with local hosts.

Outcomes of these projects will include a probe set targeting carefully-selected, conserved exons across all orders of Peracarida, several genomes, many transcriptomes, an expanded morphological character set, and new tools and techniques specific to Peracarida. Probes, laboratory workflows, sequence data, and bioinformatic scripts will be made publicly available in open repositories to enable immediate adoption by other peracarid researchers. Further, our field work will result in the collection of thousands of specimens that were carefully preserved with genetic and genomic work in mind. Vouchers and extra or unused specimens will be deposited in natural history museums (e.g., Natural History Museum of Los Angeles County, Senckenberg, and Alabama Museum of Natural History) where they will be available for loan requests by other researchers. We welcome collaboration with all researchers working on Peracarida and are especially interested in partnerships aimed at broadening taxon sampling, expanding geographic and habitat coverage, and providing opportunities and training for the next generation of peracarid researchers. We especially welcome help securing specimens of rare and hard-to-find taxa.

5. Acknowledgements

We are grateful to Jørgen Olesen, Kenneth Meland, and Gonzalo Giribet for their comments and suggestions for improving the manuscript. We thank the Encyclopedia of Life for funding the 2009 workshop held on Santa Catalina Island, California which was the impetus for seeking funding to build a molecular-based backbone phylogeny of Peracarida. This initial gathering of colleagues included: Jim Lowry, Magda Błażewicz, John Markham, Chris Boyko, Stefano Taiti, Kenneth Meland, Gary Anderson, Sarah Gerken, Daniel Roccatagliata, Dean Pentcheff, Gary Poore, Marilyn Schotte, Adam Wall, and Regina Wetzer (left-to-right, Fig. 5). Over the ensuing 15 years and five NSF funding attempts,

Figure 5. First grant brainstorming workshop on Santa Catalina Island.

this aspiration is now a reality. We thank Keith Crandall for his tireless support on four of these attempts, and Dean Pentcheff for his continual technical, editorial, and moral support. Ethan Kahn, thank you for help with the citations. This project is now funded by the following grants: United States National Science Foundation (DEB-2321306, DEB-2321307, DEB-2321308, OPP-2138993, OPP-2138934) awarded to Sarah Gerken, Regina Wetzer, and Kevin Kocot, by the Deutsche Forschungsgemeinschaft (DFG RI 837 29-1) awarded to Stefan Richter, and by the Österreichischer Wissenschaftsfond (FWF I6550) awarded to Martin Schwentner.

The projects are funded by the United States National Science Foundation (DEB-2321306, DEB-2321307, DEB-2321308), Deutsche Forschungsgemeinschaft (DFG RI 837 29-1), Österreichischer Wissenschaftsfond (FWF I6550), National Science Centre, Poland (2023/49/B/NZ8/03547; 2023/49/B/NZ8/04237).

6. References

Abouheif E, Zardoya R, Meyer A (1998) Limitations of metazoan 18S rRNA sequence data: Implications for reconstructing a phylogeny of the animal kingdom and inferring the reality of the Cambrian explosion. Journal of Molecular Evolution 47(4): 394–405. https://doi.org/10.1007/PL00006397

Al Jewari C, Baldauf SL (2023) Conflict over the eukaryote root resides in strong outliers, mosaics and missing data sensitivity of site-specific (CAT) mixture models. Systematic Biology 72(1): 1–16. https://doi.org/10.1093/sysbio/syac029

Barta AC, Grams M, Bracken-Grissom H, Brix S, Cordeiro LM, Cummings B, Collins S, Farris WJ, Gerken S, Höpel CG, Lörz AN, McKim S, Meland K, Kruckenhauser L, Olesen J, Peres PA, Richter S, Wetzer R, Williams J, Kocot KM, Schwenter M (2025 preprint) Phylogenomics supports monophyly of marsupial crustaceans: a journey to direct development. https://doi.org/10.1101/2025.11.06.686749

Bernot JP, Owen CL, Wolfe JM, Meland K, Olesen J, Crandall KA (2023) Major revisions in pancrustacean phylogeny and evidence of sensitivity to taxon sampling. Molecular Biology and Evolution 40(8): msad175. https://doi.org/10.1093/molbev/msad175

Beurlen K, Glaessner MF (1930) Systematik der Crustacea Decapoda auf stammesgeschichtlicher Grundlage. Zoologische Jahrbücher – Abteilung Systematik, Ökologie und Geographie der Tiere 60: 49–84.

Boas JEV (1883) Studien über die Verwandtschaftsbeziehungen der Malakostraken. Morphologisches Jahrbuch 8: 485–579.

Bowman TE, Garner SP, Hessler RR, Iliffe TM, Sanders HL (1985) Mictacea, a new order of Crustacea Peracarida. Journal of Crustacean Biology 5(1): 74–78. https://doi.org/10.2307/1548221

Bybee SM, Bracken-Grissom HD, Hermansen RA, Clement MJ, Crandall KA, Felder DL (2011) Directed next generation sequencing for phylogenetics: An example using Decapoda (Crustacea). Zoologischer Anzeiger 250(4): 497–506. https://doi.org/10.1016/j.jcz.2011.05.010

Calman WT (1904) On the classification of the Crustacea Malacostraca. The Annals and Magazine of Natural History, Series 7 13: 144–158.

Calman WT (1909) A Treatise on Zoology. Part VII Appendiculata. Third Fascicle Crustacea. Adam and Charles Black, London. https://www.biodiversitylibrary.org/page/859693

Cannizzaro AG, Berg DJ (2025) Brooding phylogenomics: target-capture probe sets for the analysis of ultraconserved elements in the Peracarida. Molecular Ecology Resources. https://doi.org/10.1111/1755-0998.70078

Claus C (1886) Neue Beiträge zur Morphologie der Crustaceen. Arbeiten aus dem Zoologischen Institute der Universität Wien und der Zoologischen Station in Triest 6: 1–108.

Dana JD (1849) Conspectus crustaceorum, quæ in orbis terrarum circumnavigatione, Carolo Wilkes, e Classe Republicæ Fœderatæ Duce, lexit et descripsit Jacobus D. Dana. Pars II. Proceedings of the American Academy of Arts and Sciences 2: 9–61.

Dimitriou AC, Taiti S, Sfenthourakis S (2019) Genetic evidence against monophyly of Oniscidea implies a need to revise scenarios for the origin of terrestrial isopods. Scientific Reports 9(1): 18508. https://doi.org/10.1038/s41598-019-55071-4

Fryer G (1964) IV. Studies on the functional morphology and feeding mechanism of *Monodella argentarii* Stella (Crustacea: Thermosbænacea). Earth and Environmental Science Transactions of The Royal Society of Edinburgh 66(4): 49–90. https://doi.org/10.1017/S008045680002336X

Gopalakrishnan A, Raja K, Trilles JP, Rajkumar M, Rahman MM, Saravanakumar A (2017) Bopyrid isopods parasitizing on the cultured fresh water prawn, *Macrobrachium malcolmsonii* in South India. Journal of Parasitic Diseases 41(1): 93–96. https://doi.org/10.1007/s12639-016-0756-7

Gordon I (1957) On *Spelaeogriphus*, a new cavernicolous crustacean from South Africa. Bulletin of the British Museum (Natural History) Zoology 5(2): 31–47. https://doi.org/10.5962/bhl.part.11717

Grams M, Klinger M, Richter S (2023) Neither leg nor jaw—nor always the same: a critical revision of the eumalacostracan maxilliped. Journal of the Linnean Society 197: 965–1004. https://doi.org/10.1093/zoolinnean/zlac083

Grams M, Torres A, Wirkner CS, Richter S (2025) A new morphological phylogeny of Malacostraca comparing the application of character dependencies and implied weighting. Cladistics 41(3): 283–303. https://doi.org/10.1111/cla.12611

Grobben K (1892) Zur Kenntnis des Stammbaums und des Systems der Crustaceen. Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Klasse der Kaiserlichen Akademie der Wissenschaften, Wien 101: 237–274.

Guțu M (1998) Spelaeogriphacea and Mictacea (partim) suborders of a new order, Cosinzeneacea (Crustacea, Peracarida). Travaux du Muséum national d'Histoire naturelle "Grigore Antipa" 40: 121–129.

Guțu M, Iliffe TM (1998) Description of a new hirsutiid (n.g., n.sp.) and reassignment of this family from order Mictacea to the new order, Bochusacea (Crustacea, Peracarida). Travaux du Muséum national d'Histoire naturelle "Grigore Antipa" 40: 93–120.

Hansen HJ (1893) Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insecten. Zoologischer Anzeiger 16: 193–198, 201–212.

Hansen HJ (1905) Preliminary report on the Schizopoda collected by H.S.H. Prince Albert of Monaco during the cruise of the "Princess Alice" in the year 1904. Bulletin du Musée océanographique de Monaco 30: 1–32.

Hansen HJ (1910) The Schizopoda of the Siboga Expedition. Siboga-Expéditie 37: 1–123. https://doi.org/10.5962/bhl.title.10421

Hessen DO, Persson J (2009) Genome size as a determinant of growth and life-history traits in crustaceans. Biological Journal of the Linnean Society 98(2): 393–399. https://doi.org/10.1111/j.1095-8312.2009.01285.x

Hessler RR (1983) A defense of the caridoid facies: wherein the early evolution of the Eumalacostraca is discussed. In: Schram FR (Ed.), Crustacean Phylogeny. Crustacean Issues. A. A. Balkema, Rotterdam, pp. 145–164. https://decapoda.nhm.org/pdfs/2497/2497.pdf

Höpel CG, Yeo D, Grams M, Meier R, Richter S (2022) Mitogenomics supports the monophyly of Mysidacea and Peracarida (Malacostraca). Zoologica Scripta 51(5): 603–613. https://doi.org/10.1111/zsc.12554

Hornung E (2011) Evolutionary adaptation of oniscidean isopods to terrestrial life: Structure, physiology and behavior. Terrestrial Arthropod Reviews 4(2): 95–130. https://doi.org/10.1163/187498311X576262

Iwasa-Arai T, Linse K, Andrade S.C.S., Giribet G (2025) Unpouching Peracarida relationships with ultraconserved elements. Molecular Phylogenetics and Evolution 216. https://doi.org/10.1016/j.ympev.2025.108523

Jarman SN, Nicol S, Elliott NG, McMinn A (2000) 28S rDNA evolution in the Eumalacostraca and the phylogenetic position of krill. Molecular Phylogenetics and Evolution 17(1): 26–36. https://doi.org/10.1006/mpev.2000.0823

Jeffery NW (2015) Genome size diversity and evolution in the Crustacea. PhD Thesis, University of Guelph, Guelph, Ontario, Canada, 262 pp. https://atrium.lib.uoguelph.ca/server/api/core/bitstreams/2-87b3e5b-f79f-4b57-b83c-9f5666515800/content

Krøyer H (1846) Karcinologiste Bidrag. Naturhistorisk Tidsskrift 2: 1–123.

Latreille PA (1816a) Nouveau Dictionnaire d'histoire naturelle, appliquée aux Arts, à l'Agriculture, à l'Economic rurale et domestique, à la Médecine, etc. (1). Deterville, Paris, pp. 467–469. https://www.biodiversitylibrary.org/page/21108457

Latreille PA (1816b) Les crustacés, les arachnides et les insectes. In: Cuvier GLCFD (Ed.), Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Déterville, Paris, xii, p. 653. https://www.biodiversitylibrary.org/page/28833400

Latreille PA (1829) Crustacés, arachnides et partie des insectes. In: Cuvier GLCFD (Ed.), Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Nouvelle édition, revue et augmentée. Chez Déterville, Libraire; et Chez Crochard, Libraire, Paris, pp. 1–584. https://www.biodiversitylibrary.org/page/33374495

Leach WE (1816) A tabular view of the external characters of four classes of animals, which Linné arranged under Insecta; with the distribution of the genera composing three of these classes into orders, &c. and descriptions of several new genera and species. Transactions of the Linnean Society of London 11 [for 1815](2): 306–400.

Lins LS, Ho SY, Lo N (2017) An evolutionary timescale for terrestrial isopods and a lack of molecular support for the monophyly of Oniscidea (Crustacea: Isopoda). Organisms Diversity & Evolution 17(4): 813–820. https://doi.org/10.1007/s13127-017-0346-2

Lowry JK, Myers AA (2017) A phylogeny and classification of the Amphipoda with the establishment of the new order Ingolfiellida (Crustacea: Peracarida). Zootaxa 4265(1): 1–89. https://doi.org/10.11646/zootaxa.4265.1.1

Lozano-Fernandez J, Giacomelli M, Fleming JF, Chen A, Vinther J, Thomsen PF, Glenner H, Palero F, Legg DA, Iliffe TM, Pisani D, Olesen J (2019) Pancrustacean evolution illuminated by taxon-rich genomic-scale data sets with an expanded remipede sampling. Genome Biology and Evolution 11(8): 2055–2070. https://doi.org/10.1093/gbe/evz097

Mayrat A, Saint Laurent M de (1996) Considérations sur la classe des Malacostracés (Malacostraca Latreille, 1802). In: Forest J (Ed.), Traité de Zoologie sous la direction de P.-P. Grassé 7 Fascicule 2 Généralités (suite) et systématique (Céphalocarides à Syncarides). Masson éditeur, Paris, pp. 841–863.

Meland K, Willassen E (2007) The disunity of "Mysidacea" (Crustacea). Molecular Phylogenetics and Evolution 44(3): 1083–1104. https://doi.org/10.1016/j.ympev.2007.02.009

Meland K, Mees J, Porter M, Wittmann KJ (2015) Taxonomic review of the orders Mysida and Stygiomysida (Crustacea, Peracarida). PloS ONE 10(4): e0124656. https://doi.org/10.1371/journal.pone.0124656

Monod Th (1927) *Thermosbæna mirabilis* Monod: Remarques sur sa position systématique. Faune Colonies Françaises 1: 29–49.

Nylund A, Okland S, Tjonneland A (1987) The crustacean heart ultrastructure and its bearing upon the position of the isopods in eumalacostracan phylogeny. Zoologica Scripta 16(3): 235–242. https://doi.org/10.1111/j.1463-6409.1987.tb00070.x

Pires AMS (1987) *Potiicoara brasiliensis*: a new genus and species of Spelaeogriphacea (Crustacea: Peracarida) from Brazil with a phylogenetic analysis of the Peracarida. Journal of Natural History 21(1): 225–238. https://doi.org/10.1080/00222938700770101

Poore GCB (2005) Peracarida: monophyly, relationships and evolutionary success. Nauplius 13(1): 1–27.

Prendini L (2001) Species or supraspecific taxa as terminals in cladistic analysis? Groundplans versus exemplars revisited. Systematic Biology 50(2): 290–300. https://doi.org/10.1080/10635150118650

Raupach MJ, Mayer C, Malyutina M, Wägele J-W (2009) Multiple origins of deep-sea Asellota (Crustacea: Isopoda) from shallow waters revealed by molecular data. Proceedings of the Royal Society B: Biological Sciences 276(1658): 799–808. https://doi.org/10.1098/rspb.2008.1063

Rees DJ, Dufresne F, Glemet H, Belzile C (2007) Amphipod genome sizes: first estimates for Arctic species reveal genomic giants. Genome 50(2): 151–158. https://doi.org/10.1139/G06-155

Richter S (1999) The structure of ommatidia of the Malacostraca (Crustacea) – a phylogenetic approach. Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF) 38: 161–204.

Richter S, Scholtz G (2001) Phylogenetic analysis of the Malacostraca (Crustacea). Journal of Zoological Systematics and Evolutionary Research 39(3): 113–136. https://doi.org/10.1046/j.1439-0469.2001.00164.x

Richter S, Edgecombe GD, Wilson GDF (2002) The lacinia mobilis and similar structures – a valuable character in arthropod phylogenetics? Zoologischer Anzeiger 241(4): 339–361. https://doi.org/10.1078/0044-5231-00083

Riehl T, Brenke N, Brix S, Driskell A, Kaiser S, Brandt A (2014) Field and laboratory methods for DNA studies on deep-sea isopod crustaceans. Polish Polar Research 35(2): 203–224. https://doi.org/10.2478/popore-2014-0018

Roure B, Baurain D, Philippe H (2013) Impact of missing data on phylogenies inferred from empirical phylogenomic data sets. Molecular Biology and Evolution 30(1): 197–214. https://doi.org/10.1093/molbev/mss208

Sars GO (1870) Monographi over de ved Norges Kyster forekommende Mysider. Første Hefte. (1). Brøgger & Christie's Bogtrykkert, Christiania, 64 pp., pls. I–V. https://www.biodiversitylibrary.org/page/10964150

Schram FR (1981) On the classification of Eumalacostraca. Journal of Crustacean Biology 1(1): 1–10. https://doi.org/10.2307/1548200

Schram FR (1984) Relationships within eumalacostracan Crustacea. Transactions of the San Diego Society of Natural History 20: 301–312.

Schram FR (1986) Crustacea. Oxford University Press, New York, 606 pp.

Schram FR, Hof CHJ (1998) Fossils and the interrelationships of major crustacean groups. In: Edgecombe GD (Ed.), Arthropod Fossils and Phylogeny. Columbia University Press, New York, pp. 232–302.

Schwentner M, Richter S, Rogers DC, Giribet G (2018) Tetraconatan phylogeny with special focus on Malacostraca and Branchiopoda: highlighting the strength of taxon-specific matrices in phylogenomics. Proceedings of the Royal Society B: Biological Sciences 285(1885): 20181524. https://doi.org/10.1098/rspb.2018.1524

Sieg J (1984) Neuere Erkenntnisse zum natürlichen System der Tanaidacea. Eine phylogenetische Studie. Zoologica (Stuttgart) 136: 1–132.

Siewing R (1951) Besteht eine engere Verwandtschaft zwischen Isopoden und Amphipoden? Zoologischer Anzeiger 147: 166–180.

Siewing R (1953) Morphologische Untersuchungen an Tanaidaceen und Lophogastriden. Zeitschrift für wissenschaftliche Zoologie: 333–426.

Siewing R (1956) Untersuchungen zur Morphologie der Malacostraca (Crustacea). Zoologische Jahrbücher – Abteilung für Anatomie und Ontogenie der Tiere 75: 39–176.

Siewing R (1963) Studies in malacostracan morphology: Results and problems. In: Whittington HB, Rolfe WDI (Eds), Phylogeny and Evolution of Crustacea. Museum of Comparative Zoology, Special Publications. Cambridge, Massachusetts pp. 85–103.

Spears T, DeBry RW, Abele LG, Chodyla K (2005) Peracarid monophyly and interordinal phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea: Malacostraca: Peracarida). In: Boyko CB (Ed.). Proceedings of the Biological Society of Washington 118(1): 117–157. https://doi.org/10.2988/0006-324X(2005)118%255B117:PMAIPI%255D2.0.CO;2

Tabacaru I, Danielopol DL (2011) Essai d'analyse critique des principales hypothèses concernant la phylogénie des malacostracés (Crustacea, Malacostraca). Travaux de l'Institut de Spéologi Émile Racovitza 50: 87–119.

Taylor RS, Yan-Bin S, Schram FR (1998) New pygocephalomorph crustaceans from the Permian of China and their phylogenetic relationships. Paleontology 41(5): 815–834, 2 pls.

Tchindonova JG (1981) Novyi otriad Stygiomysida (Crustacea, Mysidacea). Zoologicheskii Zhurnal 60(11): 1635–1638.

Thomas Thorpe JA (2024) Phylogenomics supports a single origin of terrestriality in isopods. Proceedings of the Royal Society B: Biological Sciences 291(2033): 20241042. https://doi.org/10.1098/rspb.2024.1042

Thomson GM (1893) Notes on Tasmanian Crustacea, with descriptions of new species. Papers and Proceedings of the Royal Society of Tasmania 1892: 45–76.

Vejdovský F (1882) Thierische Organismen in den Brunnengewässern von Prag. Selbstverlag, Prague, 66 pp. https://www.google.com/books/edition/_/okoFwt7RzksC?gbpv=1

Wägele J-W, Holland B, Dreyer H, Hackethal B (2003) Searching factors causing implausible non-monophyly: ssu rDNA phylogeny of Isopoda Asellota (Crustacea: Peracarida) and faster evolution in marine than in freshwater habitats. Molecular Phylogenetics and Evolution 28(3): 536–551. https://doi.org/10.1016/S1055-7903(03)00053-8

Wagner HP (1994) A monographic review of the Thermosbaenacea (Crustacea: Peracarida): A study on their morphology, taxonomy, phylogeny and biogeography. Zoologische Verhandelingen 291(3): 1–338.

Watling L (1981) An alternative phylogeny of peracarid crustaceans. Journal of Crustacean Biology 1(2): 201–210. https://doi.org/10.2307/1548159

Watling L (1983) Peracaridan disunity and its bearing on eumalacostracan phylogeny with a redefinition of eumalacostracan superorders. In: Schram FR (Ed.), Crustacean Phylogeny. Crustacean Issues. A. A. Balkema, Rotterdam, pp. 213–228.

Watling L (1999) Toward understanding the relationships of the peracaridan orders: The necessity of determining exact homologies. In: Schram FR, Vaupel Klein C von (Eds), Crustaceans and the Biodiversity Crisis. Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998. Brill, Leiden.

Watling L, Hof CHJ, Schram FR (2000) The place of the Hoplocarida in the malacostracan pantheon. Journal of Crustacean Biology 20(5): 1–11. https://doi.org/10.1163/1937240X-90000002

Wetzer R, Bruce NL, Pérez-Losada M (2018) Relationships of the Sphaeromatidae genera (Peracarida: Isopoda) inferred from 18S rDNA and 16S rDNA genes. Arthropod Systematics & Phylogeny 76(1): 1–30. https://doi.org/10.3897/asp.76.e31934

Wheeler WC (1998) Sampling, groundplans, total evidence and the systematics of arthropods. In: Fortey RA, Thomas RH (Eds), Arthropod Relationships. Systematics Association Special Volume Series. Chapman & Hall, London, pp. 87–96. https://doi.org/10.1007/978-94-011-4904-4_8

Williams JD, Boyko CB (2012) The global diversity of parasitic isopods associated with crustacean hosts (Isopoda: Bopyroidea and Cryptoniscoidea). PLoS ONE 7(4): e35350. https://doi.org/10.1371/journal.pone.0035350

Wills MA (1998) A phylogeny of recent and fossil Crustacea derived from morphological characters. In: Fortey RA, Thomas RH (Eds), Arthropod Relationships. Systematics Association Special Volume Series. Chapman & Hall, London, pp. 189–209. https://doi.org/10.1007/978-94-011-4904-4_15

Wills MA, Jenner RA, Dhubhghaill CN (2009) Eumalacostracan evolution: Conflict between three sources of data. Arthropod Systematics & Phylogeny 67(1): 71–90. https://doi.org/10.3897/asp.67.e31689

Wilson GD (2009) The phylogenetic position of the Isopoda in the Peracarida (Crustacea: Malacostraca). Arthropod Systematics & Phylogeny 67(2): 159–198. https://doi.org/10.3897/asp.67.e31696

Wirkner CS, Richter S (2010) Evolutionary morphology of the circulatory system in Peracarida (Malacostraca; Crustacea). Cladistics 26(2): 143–167. https://doi.org/10.1111/j.1096-0031.2009.00278.x

WoRMS Editorial Board (2025) World Register of Marine Species. Available from https://www.marinespecies.org at VLIZ. Accessed 2025-11-01. https://doi.org/10.14284/170

Yan B, Dietrich CH, Yu X-F, Jiang Y, Dai R-H, Du S-Y, Cai C-Y, Yang M-F, Zhang F (2025) Missing data and model selection in phylogenomics: A re-evaluation of Cicadomorpha (Hemiptera: Auchenorrhyncha) superfamily level relationships. Journal of Systematics and Evolution 63(5): 1203–1216. https://doi.org/10.1111/jse.13190

Yu HY, Chu KH, Tsang LM, Ma KY (2024) Incomplete lineage sorting and long-branch attraction confound phylogenomic inference of Pancrustacea. Frontiers in Ecology and Evolution 12: 1243221. https://doi.org/10.3389/fevo.2024.1243221

Supplementary Material 1

Table S1

Authors: Gerken S, Błażewicz M, Kocot KM, Richter S, Schwentner M, Wetzer R (2026)
Data type: .xlsx
Explanation notes: Phylogenetic hypotheses for Peracarida.

Link: https://doi.org/10.3897/asp.84.e180526.suppl1