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Eumalacostracan Evolution: Conflict between Three Sources of Data

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> Abstract

There is no consensus on the inter-ordinal relationships of eumalacostracans, despite the recent synthesis of several morphological matrices with data from four molecular markers. Signals from different molecules conflict with each other, and all are conspicuously at odds with morphology. Can fossils help to resolve the problem? Here, we utilize palaeontological data in two ways. Firstly we coded a selection of fossil taxa into our morphological matrix, and assessed their impact upon inferred phylogeny relative to that of their living counterparts (first order jackknifing). This revealed that our morphological tree is very sensitive to the precise taxon sample (a problem that must be addressed in future studies), but that our fossil groups were not disproportionately influential. Secondly, we asked whether the order in which groups appear in the fossil record provides a means to choose between competing trees. The congruence between morphological and stratigraphic signals was extremely weak and non-significant in most cases, precluding the use of fossil dates in this way. Many trees imply ghost ranges of duration near the theoretical maximum, and worse than for the majority of other animal groups so far investigated. An incomplete fossil record and fragile/weakly-supported trees combine with considerable molecular rate heterogeneity to make the Eumalacostraca extremely poorly suited to molecular clock studies. Future insights into their phylogeny are likely to come from the development of new molecular markers, as well as hard-won data on internal anatomy and ultrastructure.

> Key words

Eumalacostraca, total evidence, fossils, modified gap excess ratio, stratigraphic congruence.

1. Introduction

1.1. Background

The Eumalacostraca contains many of largest and most familiar species of crustaceans. They include decapods such as crabs, lobsters and shrimps – many of which are important sources of food – as well as the hugely diverse group of peracarids. The latter contains familiar forms such as woodlice (Isopoda), slaters (Isopoda), sandhoppers (Amphipoda) and mysids. However, despite their size, visibility and well over a century of study, the relationships of eumalacostracans remain problematic (SCHRAM 1984b; RICHTER & SCHOLTZ 2001; POORE 2005). Neither available morphological nor molecular sequence data analysed either separately or in combination currently provides sufficient signal to resolve their deep phylogeny (JENNER et al. 2009). Most strikingly, phylogenetic signals from morphology and molecules show significant conflict.

1.2. Morphological data

The most recent morphological cladistic analyses of eumalacostracan phylogeny are those of RICHTER & SCHOLTZ (2001), POORE (2005), and JENNER et al. (2009). The first and last of these encompassed all Eumalacostraca, while POORE concentrated on peracarids. JENNER et al. (2009) synthesized data from the

other two studies with portions of the older matrices of WILLS (1998b) and SCHRAM & HOF (1998), as well as information from WATLING (1999) and PIRES (1987). RICHTER & SCHOLTZ (2001), POORE (2005) and JENNER et al. (2009) agree on four things:

1. The Peracarida, including Thermosbaenacea (= Pancarida) is monophyletic. This contrasts with 18S rRNA and 28S rRNA studies that exclude the Mysida (JARMAN et al. 2000; SPEARS et al. 2005; MELAND & WILLASSEN 2007) and hypotheses that tentatively place Amphipoda as sister group to all other Eumalacostraca (WATLING 1983; MAYRAT & DE SAINT LAURENT 1996).

2. The Mysidacea (Mysida + Lophogastrida) is monophyletic. This contrasts with molecular studies that split them (SPEARS et al. 2005; MELAND & WILLASSEN 2007).

3. Either Thermosbaenacea or Mysidacea is the sister taxon to the remaining peracarids. This contrasts with trees that variously placed amphipods (SIEWING 1963; FRYER 1965), isopods (WATLING 1999) or some larger clade in this position.

4. The Mictacea and Spelaeogriphacea are sister taxa. This clade is also supported by PIRES (1987) and SCHRAM & HOF (1998). We note that several other workers resolved the group paraphyletically (WAGNER 1994; WILLS 1998b). SCHRAM (1986) and WATLING (1999) failed to find such a close relationship.

In addition, a clade of Amphipoda + Isopoda (= Edriopthalma) emerges from most parsimony based analyses of morphology (SCHRAM 1986; WAGNER 1994; SCHRAM & HOF 1998; WILLS 1998b; POORE 2005), although it was not found by RICHTER & SCHOLTZ (2001). Moreover, this grouping is rarely supported by molecular data (MELAND & WILLASSEN 2007). Where Amphipoda and Isopoda are separated, the isopods often resolve within a mancoid lineage, minimally comprising Cumacea + Tanaidacea + Isopoda (SIEWING 1956). Unfortunately, there remain many issues of disagreement, including the positions of Decapoda, Euphausiacea, Mysidacea, Thermosbaenacea, Cumacea, Tanaidacea, and Isopoda. Choosing between the existing morphological hypotheses will require the collection of new data. Recent exemplary work on internal anatomy and the structure of the circulatory (WIRKNER & RICHTER 2003, 2007a,b,c, 2008a,b) and neural (STEGNER et al. 2008) systems will greatly inform this process.

1.3. Molecular data

Molecular approaches to eumalacostracan phylogeny are not yet well developed. Until JENNER et al. (2009), there were just two published studies focusing on broad relationships (SPEARS et al. 2005; MELAND & WILLASSEN 2007), both using 18S rRNA sequences. JENNER et al. (2009) tested their results by combining sequences from 18S rRNA, 28S rRNA, 16S rRNA and cytochrome *c* oxidase subunit I for exemplars of all traditionally recognized eumalacostracan "orders". The results showed that the molecular data were not sufficient to establish eumalacostracan phylogeny reliably. The signals from the four loci produced significantly different hypotheses of relationships, evidenced by partitioned Bremer support (BAKER & DESALLE 1997) (Fig. 1A), incongruence length difference (ILD; MICKEVICH & FARRIS 1981) and topological incongruence length difference (TILD; WHEELER 1999) tests of partition homogeneity. Moreover, none of the trees were especially well supported according to either Bremer or bootstrap measures. Strikingly, there was very strong conflict between the molecular evidence on the one hand, and morphological evidence on the other (Fig. 1B). Hence JENNER et al. (2009) stressed the need to explore additional loci, and for much better taxon sampling of the four loci used in their study.

1.4. Fossil data

Considering the difficulty of reconstructing eumalacostracan phylogeny using only extant taxa (JENNER et al. 2009), it is reasonable to ask whether fossils can offer any unique insights. Fossils provide two, entirely distinct types of data that can inform our understanding of evolution (WILLS 2002, 2007). The first is morphology: fossils can be included readily in cladistic data matrices alongside living forms, thereby offering a more complete picture of the group. The second is stratigraphic data on the first (and last) occurrences of fossil species and higher groups. These two types of information are essentially independent: cladograms are usually inferred without reference to the absolute or relative ages of their constituent taxa (but see WAGNER 1998, 2002), and stratigraphic ranges are usually recorded with no consideration of phylogeny. Biologists frequently compare the two patterns by plotting cladograms onto stratigraphic range charts (NORELL & NOVACEK 1992; BENTON & HITCHIN 1997; CLYDE & FISHER 1997; WILLS et al. 2008). Where they are congruent, confidence in the accuracy and completeness of both is reinforced. Where the order of cladistic branching conflicts with the order in the rocks, it implies an inaccurate tree, a gappy fossil record, or both.

The principal advantage usually claimed for fossils in systematics is that they offer insights into morphologies not represented in the extant biota (DOYLE & DONOGHUE 1987; GAUTHIER et al. 1988; DONOGHUE et al. 1989; HUELSENBECK 1991).

Firstly, and most crudely, they provide a record of major clades or grades that would otherwise be entirely unknown, thereby increasing our knowledge

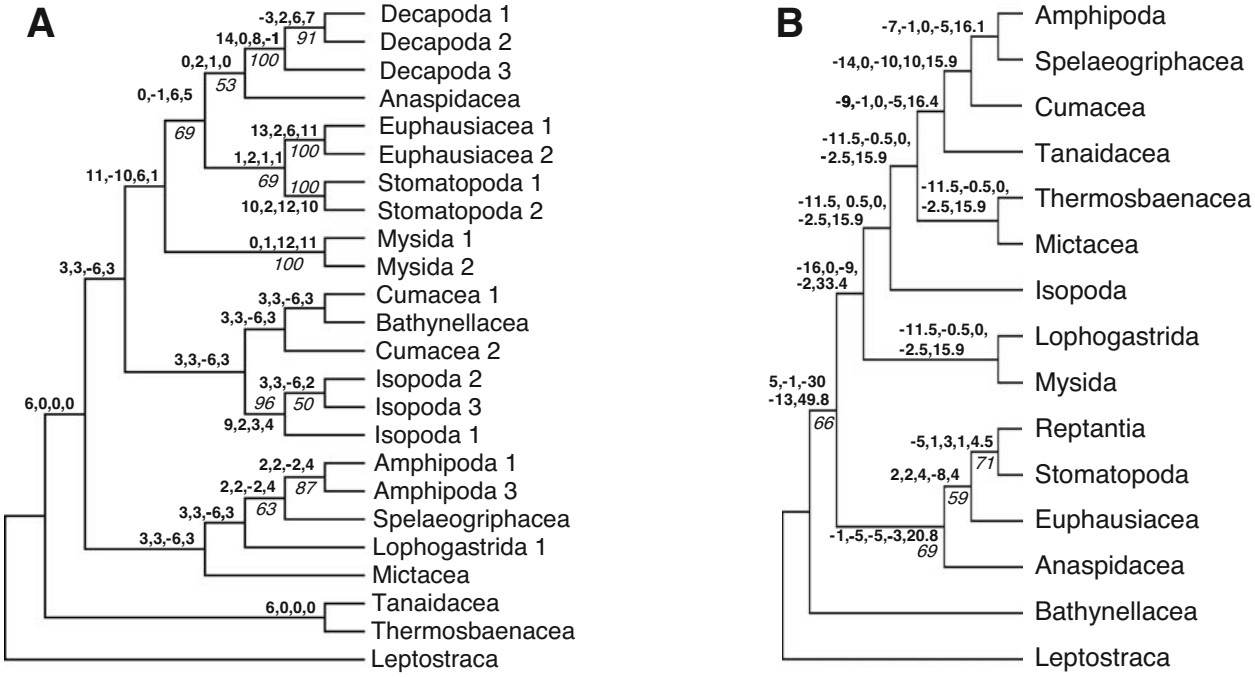


Fig. 1. Existing sources of phylogenetic data for the Eumalacostraca contain conflicting signals. Jenner et al. (2009) collated data on morphology, 18S rRNA, 28S rRNA, cytochrome *c* oxidase subunit I and 16S rRNA sequences. Fitch parsimony analysis of the combined molecular (A) and molecular plus morphological (B) data sets revealed single most parsimonious trees in both cases. However, bootstrap values (indicated in italics below branches where these were greater than 50%) were poor. Partitioned Bremer support values are listed in bold type above nodes for: 18S rRNA, 28S rRNA, cytochrome *c* oxidase subunit I, 16S rRNA and morphology (where applicable). Many nodes show strong conflict, especially between molecular and morphological data partitions. Figure adapted from Jenner et al. (2009).

of the tree. Studies of extant archosaurs (birds and crocodiles), however imaginative, could never have predicted the intervention of non-avian dinosaurs and pterosaurs between them in the phylogeny. Neither do living scorpions and horseshoe crabs offer many clues to the existence of giant marine eurypterids.

Secondly, and more subtly, they can significantly increase taxon sampling in regions of the tree that are otherwise inadequately represented, including extinct taxa that are temporally close to key cladogenetic events (Huelsenbeck 1991; Poe 1998; O'Leary 1999; Wagner 1999; Wills & Fortey 2000; Norell & Clarke 2001). In this way, fossils can alleviate problems caused by long branches that may otherwise stretch for hundreds of millions of years between adjoining extant lineages. This may not only cause local changes in inferred relationships, but may actually have marked repercussions throughout the tree (Cobbett et al. 2007). Even where sampling is already good, individual fossils can overturn a cladistic hypothesis, or significantly modify models of character evolution (Jenner & Wills 2007).

Thirdly, fossils preserve morphology directly from the evolutionary past (Huelsenbeck 1991; Wills & Fortey 2000). This can help alleviate the problem of the "over-writing" of phylogenetic signal caused by reversals and convergence during the intervening tens or hundreds of millions of years. In exceptional circumstances, sequences of character change can be fossilized and preserved intact (Dzik 2008). Where sampling is sufficiently intense, it arguably obviates the need for phylogenetic inference altogether: lineages can be mapped directly and stratophenetically (Roopnarine 2005; Georgescu et al. 2008).

In this paper we expand upon the study of Jenner et al. (2009) in two ways:

1. Investigating the phylogenetic effect of including or excluding individual taxa (first order jackknifing), including several fossil taxa that are thought to be close relatives of particular extant malacostracan subgroups.

2. Investigating the congruence between the stratigraphic record of Eumalacostraca and several published phylogenetic hypotheses.

2. Material and methods

2.1. The phylogenetic data set

All extant eumalacostracan orders were coded for 178 morphological characters, largely as detailed in Jenner

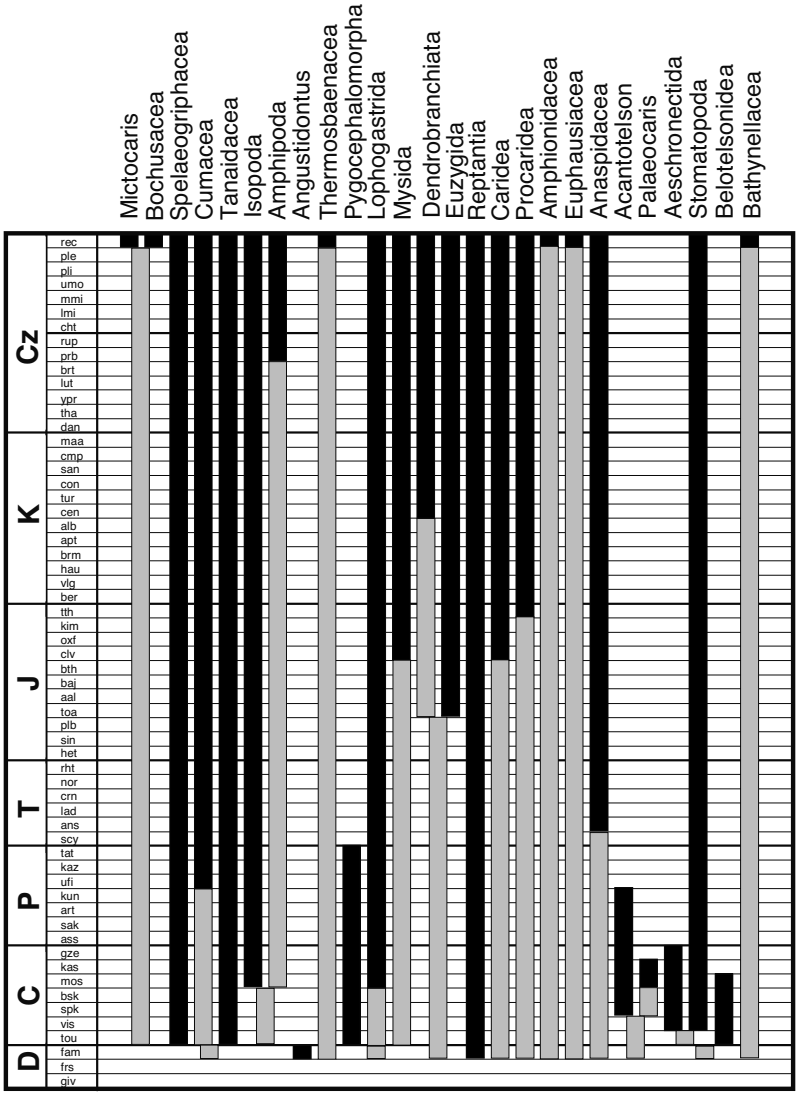


Fig. 2. Plotting stratigraphic ranges onto a cladogram. Known stratigraphic ranges (black vertical bars) are plotted onto our morphology-based cladogram of fossil and extant eumalacostracans (see Fig. 4). Where sister taxa originate in different horizons, a ghost range is inferred to connect them (grey vertical bars). These can be summed over the entire tree to calculate the minimum implied gap (MIG using absolute ages or MIGu using the number of intervals). The Famennian ghost range below Cumacea relates to the clade *Mictocaris* + Bochusacea + Spelaeogriphacea + Cumacea + Tanaidacea + Isopoda + Amphipoda. The Famennian ghost range below Lophogastrida relates to the clade Pygocephalomorpha + Lophogastrida + Mysida.

et al. (2009). We split the Mictacea, coding Bochusacea (*Thetispelecaris* + *Hirsutia*) apart from *Mictocaris*, allowing us to test the proposed grouping of this latter genus with the Spelaeogriphacea (GUTU & ILIFFE 1998; GUTU 2001). We did not consider *Stygiomysis* to be a separate taxon from the other mysids, as suggested by MELAND & WILLASSEN (2007).

JENNER et al. (2009) drew extensively on previously published matrices (PIRES 1987; SCHRAM & HOF 1998; WILLS 1998a,b; RICHTER & SCHOLTZ 2001; POORE 2005). In general, we coded higher taxa rather than specific exemplars, using polymorphic states. This minimized assumptions regarding the groundplans or plesiomorphic states for our terminals. Unless expressly stated otherwise, character descriptions refer to the morphology of adults. Characters relating to numbers of podomeres were divided into states that reflected fully the variation between orders. Several crustacean orders contain some species in which appendage branches are reduced (one or two podomeres) and other species in which they are absent altogether. For this reason, we have predominantly included "zero podomeres" as the end state in an ordered sequence of podomere numbers. Possible ordering and weighting schemes for multistate morphological characters have been explored comprehensively in detail elsewhere (WILLS 1998a). For present purposes, characters relating to numbers of limb elements (podomeres, endites, etc.) and numbers of somites have been ordered, while those relating to numbers of limb elements have also been ranged (weighted as 1/(states–1)). All data and assumptions are presented as Appendices I (character list below) and II (character matrix below and Nexus file in Electronic Supplement). We acknowledge that other interpretations are possible (WILLS 1998a). Analyses were performed using parsimony in PAUP* (SWOFFORD 2002). TBR branch swapping followed each of 500 random additions of taxa.

In addition, we coded six fossil taxa not included by JENNER et al. (2009). These fossils are a preliminary selection of extinct taxa that should eventually be integrated fully into eumalacostracan phylogeny,

Tab. 1. A variety of stratigraphic congruence indices for eleven phylogenetic trees of malacostracans. Stratigraphic range data principally from Benton (1993). All indices calculated assuming stratigraphic intervals of unit length. Topological GER (GERt) and Modified Gap Excess Ratio (GER*) values for fixed dates are based on 10,000 randomizations of stratigraphic data across each topology. GER and CI correlation based on 30,000 random trees.

Author(s)	Notes	Terminals	Measures of stratigraphic congruence					GER & CI correlation	
			GER	GERt	GER*	SCI	RCI	Spearman's rho	P
Jenner et al. (2009)	Morphological data only	20	0.2381	0.3016	0.5664	0.4444	18.10	-0.01118	0.05283
Jenner et al. (2009)	Morpological & molecular data	14	0.2345	0.3024	0.6084	0.3333	38.14	-0.06281	**< 0.00001**
Pires (1987)	Peracarida (her fig. 23)	8	0.1849	0.1966	0.4027	0.5000	28.86	n/a	n/a
Poore (2005)	Mostly Peracarida (his fig. 1b)	20	0.4455	0.5380	0.8876	0.5000	-25.23	0.06854	**< 0.00001**
Richter & Scholtz (2001)	Malacostraca (their fig. 7)	19	0.4415	0.4312	0.7770	0.4118	27.78	0.00045	0.93850
Schram (1986)	Eumalacostraca (his fig. 43.3)	22	0.0863	0.1277	0.1282	0.2500	15.20	n/a	n/a
Schram & Hof (1998)	Just Malacostraca (their fig. 6.8)	24	0.1163	0.1633	0.1878	0.3636	15.12	0.00095	0.86930
Watling (1981)	Peracarida	7	0.0441	0.0154	0.1667	0.4000	55.47	n/a	n/a
Watling et al. (2000)	Eumalacostraca	15	0.2870	0.2887	0.8031	0.3077	58.62	n/a	n/a
Wills (1998)	Just Malacostraca	23	0.0550	0.0414	0.0211	0.2857	4.64	0.00744	0.19680
Wills et al. (2009) (herein)	Morphology including fossils	26	0.0764	0.1414	0.4056	0.4800	7.06	0.01379	**0.01695**

combining all morphological and molecular evidence. Our selection here includes forms thought to be closely related to different extant groups, such as Stomatopoda (Aeschronectida), Syncarida (*Palaeocaris*, *Acanthotelson*) (Schram 1984a; Camacho & Valdecasas 2008), Peracarida (Pygocephalomorpha) (Schram 1974; Taylor et al. 1998) and Eucarida (Belotelsonidea) (Schram 1974, 1984b, 2006), or have less determined affinities, such as the Devonian *Angustidontus seriatus* (Rolfe & Dzik 2006).

2.2. Measuring the agreement or conflict between trees and stratigraphy

Several indices are used widely to quantify the agreement between cladograms and stratigraphic ranges (Siddall 1996; Hitchin & Benton 1997a,b; Siddall 1998; Benton et al. 1999; Wills 1999; Wagner & Sidor 2000; Wills et al. 2008). Many of these utilize ghost ranges between sister groups (or monophyla). Sister groups are those on either side of an internal cladogram node, and therefore inferred to be descended from a common ancestor. Because sister groups arise from the same cladogenetic event, they must have originated at the same time. However, their first occurrences may not be preserved or recognized simultaneously in the fossil record, and a ghost range is therefore inferred to bridge the first fossil appearance dates (Fig. 2). A direct or indirect tally of these ranges over the entire tree contributes to several indices, including the gap excess ratio (GER: Wills 1999), the Manhattan stratigraphic measure (MSM*: Siddall 1998; Pol & Norell 2001), the retention index of a stratigraphic character (Farris 1989; Finarelli & Clyde 2002) and the relative completeness index (RCI: Benton 1994). The sum of ghost ranges is denoted as the minimum implied gap (ΣMIG in Benton 1994, or simply the MIG in Wills 1999 and Wills et al. 2008). Ghost ranges can be measured in millions of years, or in variously defined stratigraphic units.

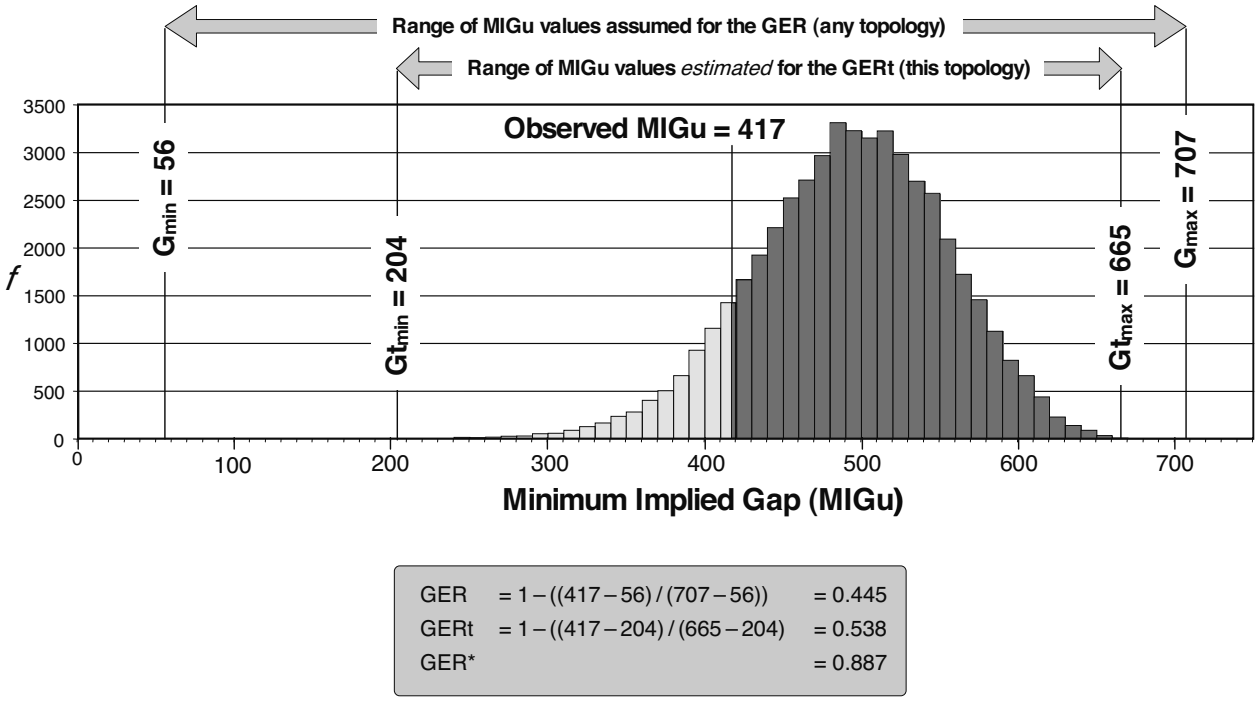


Fig. 3. Calculating the gap excess ratio (GER), topological gap excess ratio (GERt) and modified gap excess ratio (GER*) for the phylogeny of POORE (2005). The GER scales the observed sum of ghost ranges (MIG) between the minimum (G_{min}: GER = 1.0) and maximum (G_{max}: GER = 0.0) possible sum of ghost ranges for the given stratigraphic ranges on *any* topology. Values this low or this high may not be attainable on a given (non-pectinate) tree. The GERt therefore scales the minimum implied gap (in this case, for stratigraphic intervals of unit length: MIGu) between the mimimum (Gt_{min}: GERt = 1.0) and maximum (Gt_{max}: GERt = 1.0) achievable on the *given* topology. These bounds are estimated from a large number (herein 50,000) of randomly permuted data sets. The GER* takes the shape of this distribution into account, and is given simply by the fraction of randomized data sets with a MIGu greater than the observed MIGu (dark grey area under the histogram).

The GER (WILLS 1999) scales the MIG between the sum of ghost ranges obtained for the best (G_{min}) and worst (G_{max}) fits of a given set of stratigraphic data onto *any* tree topology. The resulting index varies from 0.0 (worst possible fit) to 1.0 (best possible fit).

$$GER = 1 - (MIG - G_{min}) / (G_{max} - G_{min})$$

Unfortunately, for most non-pectinate tree topologies, values of MIG can never reach G_{min} or G_{max}, and hence GER values can never reach 0.0 or 1.0. The topological GER or GERt (WILLS et al. 2008) overcomes this by scaling the MIG between its maximum and minimum possible values on a *given* tree topology:

$$GERt = 1 - (MIGu - Gt_{min}) / (Gt_{max} - Gt_{min})$$

where MIGu is the sum of ghost ranges for stratigraphic intervals *of unit length*, and Gt_{max} and Gt_{min} are the maximum and minimum possible values of MIGu. Here, we estimated Gt_{min}, Gt_{max} and hence GERt from 10,000 permutations of the stratigraphic data. A third index – the modified GER or GER* (WILLS et al. 2008) – was calculated from the underlying distribution of these randomized MIGu values. The GER* is estimated from the proportion of the area under a curve of permuted values corresponding to a MIGu value greater than the observed value. Figure 3 summarizes and illustrates the relationship between these three indices.

Values for the Stratigraphic Consistency Index (SCI) (HUELSENBECK 1994) and the Relative Completeness Index (RCI) (BENTON 1994; BENTON & STORRS 1994) are also presented.

All of the above indices measure aspects of the congruence between a single, rooted tree and a particular set of stratigraphic range data. A more general issue, however, is whether the phylogenetic (or non-random) signal within the morphological character matrix is consistent with that implied by the range data. To test this, we generated 30,000 random networks, and rooted them with the designated outgroup. We then optimized the character data onto these in PAUP* to calculate the ensemble consistency index (CI), and ran the same trees through Ghosts 2.4 (WILLS 1999) to calculate GER values. If the stratigraphic signal were consistent with the phylogenetic (or non-random) signal inherent in the covariance of morphological characters, we would expect the GER of trees to be negatively correlated with their length and positively correlated with CI (shorter trees should have a better GER, overall). Spearman's rho and corresponding P values are presented in Table 1. These cannot be inter-

preted straightforwardly, since points are not strictly independent and the sample will probably contain pseudoreplicates. However, failure to find a significant relationship means that there is probably no basis for using the GER as an ancillary criterion for choosing between otherwise equally optimal trees.

As well as testing the performance of our own data, we have also investigated that of some other published studies that explicitly included a character matrix: Poore (2005), Richter & Scholtz (2001), Schram & Hof (1998; considering just the eumalacostracan part of their tree), and Wills (1998b; just the eumalacostracans). Trees were also taken from Pires (1987), Schram (1986), Watling (1981), and Watling et al. (2000). Stratigraphic ranges for extant and fossil groups were taken from Benton (1993) and Watling et al. (2000), updated with more recent information where applicable.

3. Results and discussion

3.1. The effects of adding and deleting fossils

Analysis of the morphological data for extant and fossil taxa yielded a single most parsimonious tree with a CI' of 0.392 and RI of 0.611 (Fig. 4). Both the Eucarida (Euphausiacea + Decapoda) and Peracarida (including the Thermosbaenacea or "Pancarida") were monophyletic. The Syncarida, however, were polyphyletic: the Anaspidacea and Palaeocaridacea (*Acanthotelson* and *Palaeocaris*) resolved in paraphyletic succession to the clade of Eucarida + Peracarida, while the Bathynellacea resolved much closer to the root.

A first order taxon jackknife as described in Cobbett et al. (2007) was used to explore the effects of individual taxa upon these inferred relationships of all taxa. These are reported both in terms of symmetrical difference distances (*RF*) (Robinson & Foulds 1981) and maximum agreement subtree distances (*d1*) (Finden & Gordon 1985) (Fig. 4). Those taxa with the largest values are those whose removal has the greatest influence on tree topology. We illustrate these effects for six of the most influential taxa in Figure 5.

The largest effect on mean *RF* was exercised by the removal of the fossil group Aeschronectida (Fig. 5A). This caused the Euphausiacea to move to the base of the Peracarida, rendering the Eucarida paraphyletic, and also changed relationships *within* the remaining Eucarida. In addition, the Stomatopoda + Belotelsonidea resolved as the sister group to the Eucarida + Peracarida, while a paraphyletic series of all the Syncarida represented the first eumalacostracan divergences. The next five most influential taxa, however, were all extant. Deletion of *Mictocaris* (Fig. 5B) reduced resolution within the Peracarida, caused the fossil *Angustidontus* to move from the peracarids and to group with the Anaspidacea, and changed relationships of the other Syncarida. Deletion of the Lophogastrida (Fig. 5C) also reduced resolution in the Peracarida, and rendered the Eucarida paraphyletic by removal of the Euphausiacea. Removing the Bathynellacea (Fig. 5D) left the clade of Eucarida + Peracarida virtually unchanged, the only exception being *Angustidontus*, which was resolved with Anaspidacea as sister group to Eucarida + Peracarida. Relationships deeper in the phylogeny were also affected. Removing the Isopoda (Fig. 5E) changed peracaridan relationships: *Angustidontus* forming a clade with the Mysida among other differences. Finally, deleting the Leptostraca (Fig. 5F) caused the Hoplocarida (= Stomatopoda + Aeschronectida) + Belotelsonidea to resolve as sister clade to Eucarida + Peracarida, thereby also rendering the Syncarida paraphyletic rather than polyphyletic. Overall, the impact of fossils is similar to that of their extant counterparts (Mann-Whitney test: $U = 67$, $P = 0.818$). However, because the deletion of single taxa can have such marked effects, the precise composition of the taxon sample – be they fossil or Recent – may become critical.

To find large changes in apparent relationships upon small perturbations of the taxon sample is not unusual. Most morphological matrices across a range of higher taxa analysed using parsimony are subject to this problem (Cobbett et al. 2007). Our results support the inclusion of fossil data, not least because they provide a more complete taxon sample. However, we note that most eumalacostracan fossils are accommodated relatively easily within existing higher taxa. Genuine problematica – forms with anomalous or intermediate combinations of characters that defy taxonomic placement – are comparatively rare. Poore (2005) noted this in the context of peracarid evolution. Unfortunately, these are the types of fossils that are most likely to radically overhaul our understanding of the evolution of the group (Cobbett et al. 2007; Jenner & Littlewood 2008).

3.2. The stratigraphic congruence of cladograms

Values of stratigraphic congruence are given for eleven trees in Table 1. The GER for our morphological tree including fossils (Fig. 4) is poor (0.076) (theoretical values range from 0.0 to 1.0). Only two of the trees in Table 1 show a lower GER, namely the trees of Watling (1981) (GER = 0.044) and Wills (1998) (0.055), while the highest values were for those of Poore (2005) (0.445) and Richter & Scholtz (2001)

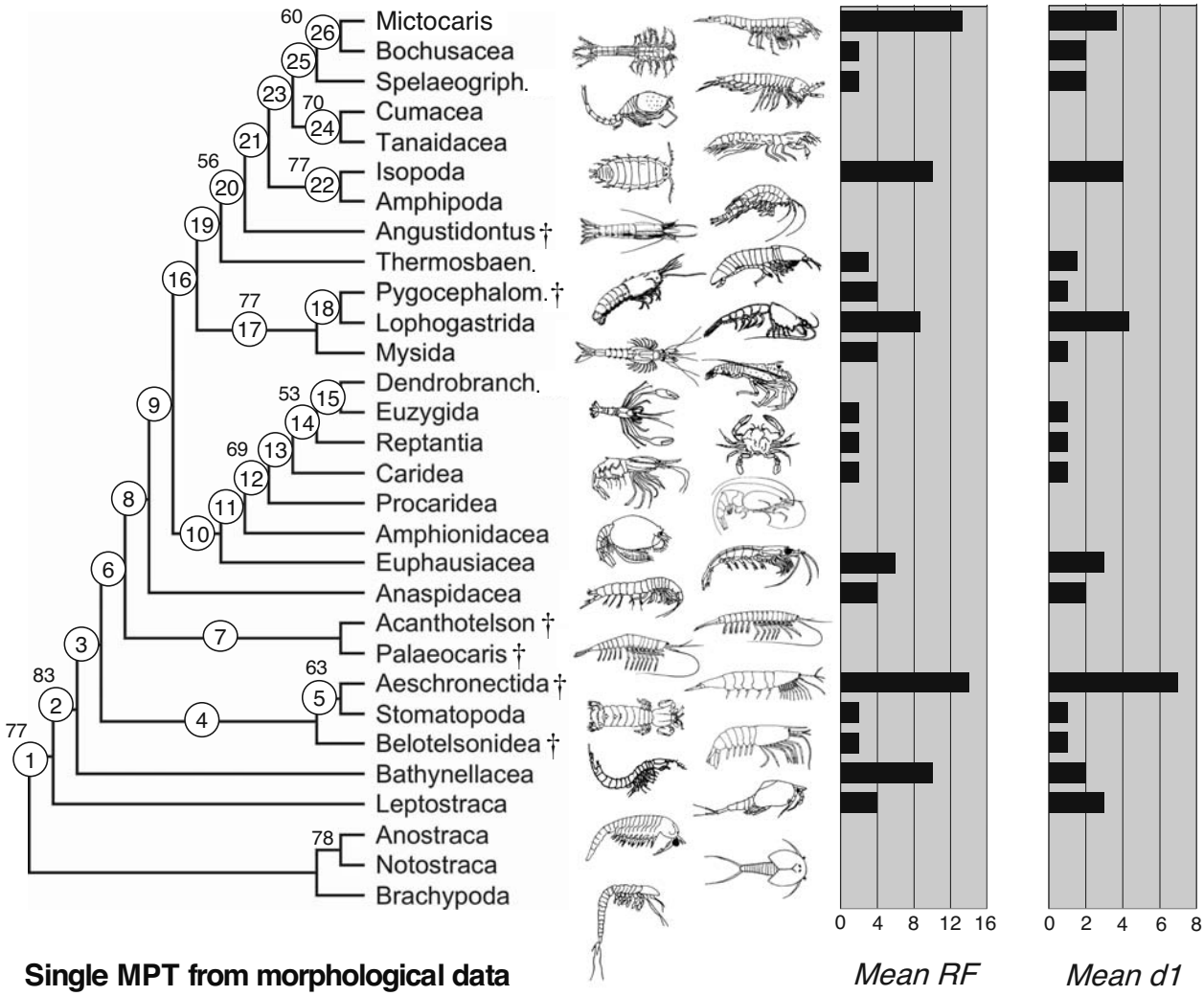


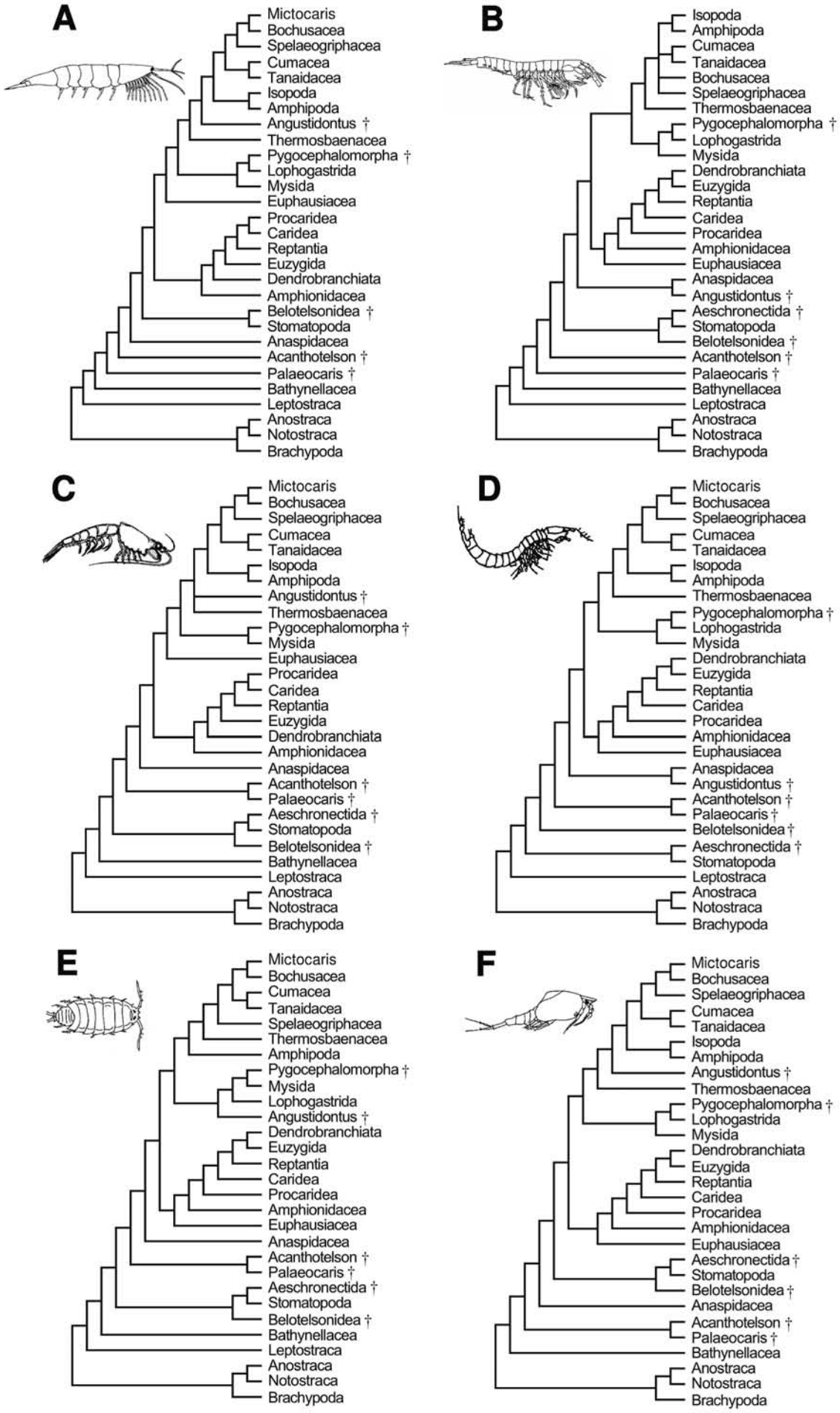
Fig. 4. Phylogeny of extant and selected fossil malacostracans derived from morphological data. Terminals known only from fossils are indicated with a dagger (†). Single MPT with CI' = 0.392 and RI = 0.611. Numbers in circles indicate internal branches for which apomorphies are listed below. Values above internal branches show support from 10,000 bootstraps, where these exceed 50%. Histograms indicate two measures of the impact of each terminal upon inferred relationships. RF is the symmetrical difference distance, and d1 is the maximum agreement subtree distance.

Apomorphies (delayed transformations): **1**. Antennule with an outer ramus. Antennal endopod with five podomeres. Antenna lacking a naupliar process. Mandibular endopod with three or four podomeres. Thoracopods two, three and four without protopodal endites. Twenty or more post-maxillary body segments. Trunk gut diverticula/caeca present. Ventral nerve cord with fused ganglia. Spermatophore present. **2**. Carapace adductor muscles absent. Antennnal exopod with one podomere. Paragnaths present. First thoracopod exopod linear in form. Thoracopod thorax-coxa articulation as a transverse hinge. Thoracopod coxa-basis articulation dicondylic along anteroposterior axis. One pair of uropods. Sixteen post-maxillary body segments. Pleon comprising six segments (excluding telson). Lateralia and inferolateralia anteriores present in the cardiac chamber. Metamorphic development. Free living larval stage absent. **3**. Rostrum fixed. Naupliar eye present. Bec oculair present. Antennular exopod with ten or more articles. Antennular exopod not scale-like. Antennular endopod with ten or more articles. Antennal exopod as scaphocerite. Antennal endopod with eight or more articles. Mandibular incisor stout and tooth-like. All pleonal limbs present. Last pleopods (uropods) broad and forming a tail fan with the telson. Telson dorsoventrally flattened. Inferomedianum anterius present. Anus ventral. Arteria subneuralis/supraneuralis present. Pleon musculature precaridoid. **4**. Carapace univalved. Cephalic pleural fold present. Cephalic doublure present. Scaphocerite as long or longer than peduncle articles three plus four. Well-developed epistome. **5**. Dorsal fold present in adult. Tergites with overlapping pleurae. Articulating rostrum. Cephalic kinesis present. Antennule triramous. Sixth pereopod exopod composed of one article. Gills present on pleon. Telson appendages (furca) absent. **6**. Second, third and fourth thoracic limb endopods with six podomeres. Third and fourth thoracic limb exopods with two podomeres. Sixth thoracopod exopods with two articles. Telson appendages (furca) absent. One pair of maxillipeds. **7**. Second maxilla without endites. **8**. One thoracomere incorporated into cephalothorax. Ommatidia with bipartite crystalline cones, each with just two cell processes. Eyes of superposition type. First thoracopod endopod with six podomeres. Second thoracopod exopod with two podomeres. Second, third and fourth thoracopod exopods flagelliform or elongate. Foregut dorsal caeca present. Superomedianum (unpaired) present. Heart with two pairs of ostia. Aorta descendens present. Pleon musculature caridoid. Tail fan escape reaction present. **9**. Carapace univalved. Dorsal fold present in adult. Cephalic pleural fold present. Antennal scale as long or longer than peduncle articles three plus four. Antennal gland present. Lacinia mobilis present on the larval mandible. Second maxilla exopod with one podomere. First thoracopod

epipodite expanded into branchial cavity. Inferomedianum posterius present. Atrium between the inferomediana connecting the primary filter grooves with the pyloric filter grooves present. Heart positioned in the thorax. **10**. Eight thoracomeres incorporated into cephalothorax. Ventral frontal organs present. Statocyst present in basal segment of antennule. Maxillary glands absent. Ventral frontal organ present. First thoracopod exopod with two to four podomeres. Heart short and bulbous. Appendices internae present. Sperm acrosome present. **11**. Crystalline cones of ommatidia tetrapartite, and with four cell processes. First thoracopod exopod with expanded basal section. Fourth thoracopod with pleurobranch gill. **12**. Tergites articulating with overlapping pleurae. Pleura of second pleon segment overlapping that of the first (and third). Cephalic doublure present. Dorsal frontal organ present. Second maxillary exopod modified as scaphognathite. First thoracic appendage endopod with three podomeres. Pleopods modified for brooding eggs. Two pairs of maxillipeds. Anterior section of foregut enlarged relative to posterior. Brood care attaching eggs to the pleopods. **13**. Paragnaths absent. Fourth thoracopod exopod absent. Thoracopods four and five chelate. Three or more maxillipeds. Heart with three pairs of ostia. Aorta descendens passes undivided through the CNS. Two globuli cell clusters in the deutocerebrum associated with the olfactory lobe. **14**. Cervical groove present. Lacinia mobilis absent from larval mandible. Epistome well developed. Second thoracopod with podobranch gills. Second, third and fourth thoracopods with arthrobranch gills. Sixth thoracopod chelate. **15**. Pleura of the second pleon segment not overlapping that of the first pleon segment. First thoracopod exopod with one podomere. First thoracopod endopod with four podomeres. Second and third thoracopods with pleurobranch gills. Appendices internae absent. **16**. Ommatidia with nuclei of the accessory cone cells distally displaced. Naupliar eye absent. Dorsal or nuchal organ absent. Lacinia mobilis present on adult mandible. First thoracopod epipodite producing a respiratory current. Third and fourth thoracopods without epipodites. At least one branch of epipodites carried under the thorax. Thoracopod coxa-basis articulation monocondylic. Posterior pleonal limbs reduced or absent. Entoderm as paired plates. Development epimorphic or direct. Marsupium formed from oöstegites. Yolk present in posterior part of embryo. Embryonic dorsal organ cup shaped. Sperm with cross-striated pseudoflagellum. **17**. Branchiostegal flaps present. Cervical groove present. Cephalic doublure present. Crystalline cones of ommatidia with two lateral extensions formed by one cone cell each. Ventral frontal organ present. Posterior tooth present on labrum. Second, third and fourth thoracopodal exopods with numerous (five or more) podomeres. Thoracopod thorax-coxa articulation anterioposterior. Thoracopod intrabasal articulation present. Trunk appendages laterally displaced relative to the body. Outer rami of uropods with two or more podomeres. Segmental arteries present. Number of ectoteloblasts variable. Ectoteloblasts forming a transverse row. **18**. Tergites with overlapping pleurae. **19**. Carapace with respiratory function. Antennular exopod with four to nine podomeres. Incisor and molar processes of mandible widely spaced. Second thoracopod with no epipodites. Thoracopod thorax-coxa articulation immobile. Foregut dorsolateral and midventral ridges with setae. One secondary filter groove in the inferomedianum posterius. Midgut formed at the border between the stomodaeum and proctodaeum. Arteria subneuralis/supraneuralis absent. Pleon musculature simple. Hatchling with seven pairs of thoracopods. **20**. Antennular endopod with one to nine podomeres. Pereopods with a row of long setae on all articles. **21**. Dorsal fold absent from adult. Ocular lobe present. Ommatidia of apposition type. Bec oculair absent. Antennal scale half the length of peduncle articles three plus four. Second maxilla exopod and endopod absent. First thoracopod exopod absent. Third and fourth thoracopods with oöstegites. Thoracopod eight with exopod. Segmental arteries present. Tail fan escape reaction absent. Manca stage present in development. Continuous anterioposterior decrease in the degree of appendage formation. Variable number of ectoteloblasts. Ectoteloblasts forming a transverse row. Spermatophore absent. **22**. Carapace absent or as a simple head shield. Cephalic pleural fold absent. Compound eyes sessile. Incisor and molar processes of mandible closely set. Second to seventh thoracopods with no exopods. Thoracic coxal plates present. Second pleopodal exopod with two podomeres. Inner rami of uropods composed of two or more podomeres. Outer rami of uropods absent. Superomedianum absent. Total cleavage. **23**. Carapace covering only the anteriormost thoracic segments. Antennal gland absent. First thoracopod epipodite modified as a cup or spoon-shaped respiratory structure. Oöstegites extending back as far as sixth or seventh thoracopod. Outer rami of uropods with two or more podomeres. Early embryo with dorsal fold. **24**. Two thoracomeres included in cephalothorax. Rostrum absent. Cephalic doublure present. Oöstegites reduced after each brood. Last pleopods oriented posteriorly and close to the telson, but not forming a tail fan with it. Foregut dorsal caeca absent. **25**. Compound eyes absent. Mandibular incisor blade-like or rudimentary. One globuli cell cluster in the deutocerebrum associated with the olfactory lobe. **26**. First maxillary endopod absent. Second maxillary endopod with one or two podomeres. First thoracopod with no epipodites. Thoracopods five to seven with pedunculate setae. Trunk appendages laterally displaced relative to the body. Inner rami of uropods with two or more podomeres.

(0.442). The SCI for the analysis shown in Figure 4 is also low in absolute terms (0.480), but closer to the maximum values (SCI = 0.500) for other published eumalacostracan trees (Richter & Scholtz 2001; Poore 2005) in Table 1. Topological GER values (GERt; those constrained by a given topology) are slightly higher than the corresponding GER values in all but three cases (Watling 1981; Wills 1998b; Richter & Scholtz 2001). GER* values are higher still, but range from 0.887 for the tree of Poore (2005) to 0.021 for that of Wills (1998). The morphological tree including fossils presented here (Fig. 4) lies in the middle of this range (GER* = 0.406).

Original character matrices were available for seven of the cladograms above. For these data sets, we assessed the correlation between the GER and CI for 30,000 random trees. Correlation was extremely weak in all cases. For both of the trees assessed from Jenner et al. (2009) it was slightly negative: significantly so in the case of their total evidence tree. This implies that the phylogenetic signal conflicts with the stratigraphic one, and that more parsimonious trees actually have a worse fit to the stratigraphic record, on average. Only two data sets yielded a significant and positive correlation: Poore (2005) and Wills (1998). Only in these cases is the use of stratigraphic congru-


A
Mictocaris
Bochusacea
Spelaeogriphacea
Cumacea
Tanaidacea
Isopoda
Amphipoda
Angustidontus †
Thermosbaenacea
Pygocephalomorpha †
Lophogastrida
Mysida
Euphausiacea
Procaridea
Caridea
Reptantia
Euzygida
Dendrobranchiata
Amphionidacea
Belotelsonidea †
Stomatopoda
Anaspidacea
Acanthotelson †
Palaeocaris †
Bathynellacea
Leptostraca
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Bochusacea
Spelaeogriphacea
Thermosbaenacea
Pygocephalomorpha †
Lophogastrida
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Dendrobranchiata
Euzygida
Reptantia
Caridea
Procaridea
Amphionidacea
Euphausiacea
Anaspidacea
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Aeschronectida †
Stomatopoda
Belotelsonidea †
Acanthotelson †
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Pygocephalomorpha †
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Mysida
Dendrobranchiata
Euzygida
Reptantia
Caridea
Procaridea
Amphionidacea
Euphausiacea
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Angustidontus †
Acanthotelson †
Palaeocaris †
Belotelsonidea †
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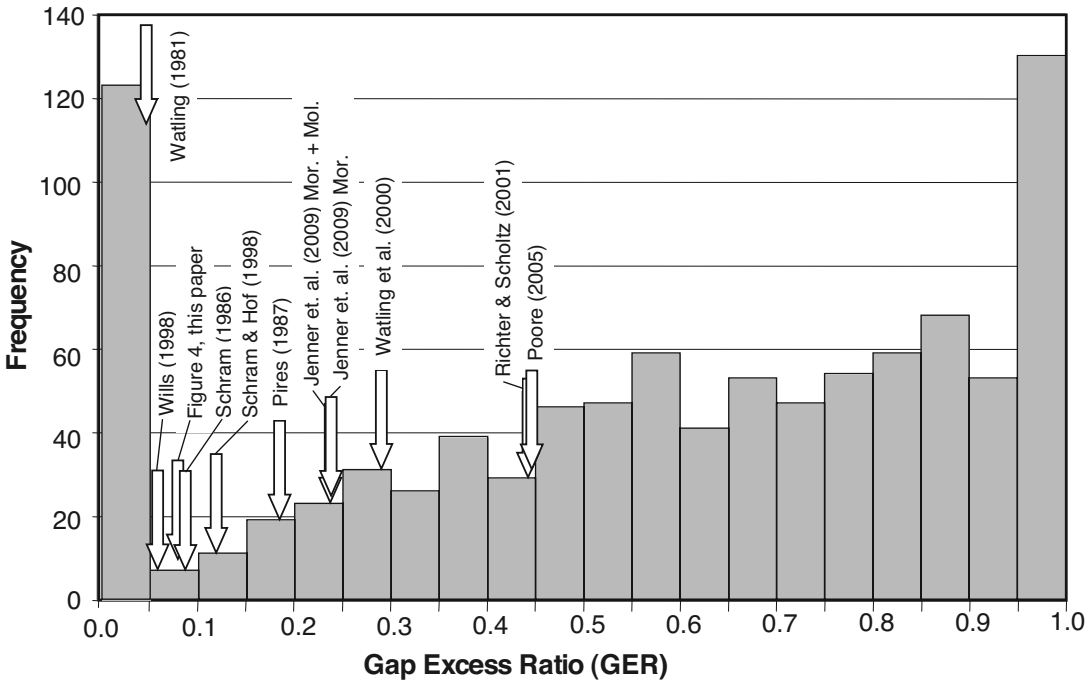

Fig. 6. How bad is stratigraphic congruence for cladograms of eumalacostracans? Gap excess ratio (GER) values from Tab. 1 are plotted onto the distribution of values from the data sets analysed by Benton et al. (2001) and Wills (2007), excluding cases where the GER is 0.00 by default (e.g., all origination dates are equal). This comprises 1,000 cladograms of animals and plants. Stratigraphic congruence for trees of eumalacostracans is poor, but not exceptionally so.

ence as an ancillary criterion for choosing between equally parsimonious trees defensible.

Overall, therefore, the stratigraphic congruence of eumalacostracan trees is extremely poor. Figure 6 indicates the GER values for the trees in Table 1, relative to the values for a large sample of 1,000 animal and plant trees (Benton et al. 2000; Wills 2007) (excluding the trivial cases where values are zero by definition). Wills (2001) also reported low GER and SCI values for a sample of 179 arthropod cladograms relative to trees of other animal groups, principally tetrapods, fish and echinoderms. However, our eumalacostracan trees have mediocre congruence, even relative to this sample. Our results contrast most starkly with those of Wills et al. (2008), who found GER* values of 0.990 or above for 17 out of 19 recently published cladograms of higher dinosaur taxa.

3.3. Why is stratigraphic congruence so poor?

One possibility is that all published cladograms of the group are hopelessly inaccurate. Given the lability of many trees upon even modest character and taxon resampling (Jenner et al. 2009), we are clearly far from a robust and stable consensus. However, all trees contain common relationships, which makes it unlikely that phylogenetic inaccuracy is the sole culprit.

Many eumalacostracan orders appear in the fossil record in a relatively rapid radiation from the Late Devonian to the Early Carboniferous (Schram 1984b; Wills 1998b). Those groups appearing in or just prior to the Recent almost certainly have a long history, and imply extensive ghost ranges. In the Thermosbaenacea, for example, the genus *Halosbaena* has representatives from Australia (Poore & Humphreys 1992), Japan (Shimomura & Fujita 2009), Venezuela and Spain (Bowman & Iliffe 1986), while a close relative in the same family, *Theosbaena cambodjiana*, has been described from Cambodia (Cals & Boutin 1985). These examples, along with other closely-related thermosbaenacean taxa isolated on either side of the Atlantic (Stock 1976; Stock & Longley 1981; Stock 1982; Bowman & Iliffe 1988) strongly suggest the breakup of an ancient group with a Tethyan or earlier biogeography (Maguire 1965; Wagner 1994). Similarly, the bochusacean genus *Hirsutia* is known from just two

Fig. 5. Single taxon deletion experiments and the impact on inferred phylogeny. Terminals known only from fossils are indicated with a dagger (†). The morphological tree produced in Fig. 4 has been re-estimated after removal of the following terminals. **A**: Aeschronectida, single most parsimonious tree (MPT). **B**: *Mictocaris*, strict consensus of two MPTs. **C**: Lophogastrida, strict consensus of two MPTs. **D**: Bathynellacea, single MPT. **E**: Isopoda, single MPT. **F**: Leptostraca, single MPT.

species almost at opposite ends of the Earth: one from deep waters off the northeastern coast of South America (SANDERS et al. 1985), the other north of Tasmania (JUST & POORE 1988). The reason for the absence of fossils is less clear. Small size is one possibility, invoked in another context to explain the paucity of plausible precursors of modern phyla in the Precambrian (FORTEY et al. 1996, 1997). This hypothesis requires an external trigger for size increase in numerous parallel lineages, which is difficult to envisage in the eumalacostracan case. We do note, however, that many of the orders with no or sparse fossil records are small: Bathynellacea, Thermosbaenacea, and Mictacea (*Mictocaris* and Bochusacea constituted a clade in all our analyses). A closely related issue is the nature of the cuticle. Several of the oldest fossils are from groups with a heavily mineralized exoskeleton (e.g., Reptantia, Stomatopoda, Belotelsonidea). Environmental factors controlling preservation potential are also not homogeneous across groups. The preservation potential of fully marine pelagic taxa (e.g., krill) and that of fresh water bottom dwellers (e.g., anaspidaceans) is certainly very different. Groups from ground water, marine caves and other marginal environments (e.g., bathynellaceans, mictaceans and thermosbaenaceans) may have the lowest potential of all.

Another possibility is that numbers of individuals (and possibly species) have been low throughout geological time. The Mictacea (*Mictocaris* + Bochusacea), for example, are known from just five species. *Mictocaris halope* is endemic to marine caves in Bermuda (BOWMAN et al. 1985; BOWMAN & ILIFFE 1985), while there are just two species of *Hirsutia* (SANDERS et al. 1985; GUTU & ILIFFE 1998) and two of *Thetispelecaris* (GUTU 2001; OHTSUKA et al. 2002). The Procarididea are represented by just a handful of highly similar species of *Procaris*, discovered relatively recently in the Ascension Islands (CHACE & MANNING 1972), Bermuda (HART & MANNING 1986), Yucatan (KENSLEY & WILLIAMS 1986) and Hawaii (HOLTHUIS 1973). Finally, the Amphionidacea contains just one living species (*Amphionides reynaudii*) (WILLIAMSON 1973), ubiquitous but seldom reported from depths in excess of 2000 m.

3.4. Implications for estimating divergence times

The fossil record shows that Malacostraca had originated at least by the Silurian (ROLFE 1962; BRIGGS et al. 2004; DZIK et al. 2004), and had started radiating by the Carboniferous at the latest (SCHRAM 1986; DAHL 1992; BENTON 1993; WILLS 1998b). Can we use the fossil record together with molecular sequence data to derive estimates of the major divergence events in eumalacostracan evolution? The extremely short lengths of internal branches in molecular trees (JENNER et al. 2009) might indicate a radiation that was particularly compressed in time. This severely reduces the chances that the first fossils of major lineages will occur in a sequence that reflects their actual branching order. If this is the case, it will be very difficult to derive molecular clock estimates from multiple calibration points, since only the basal node is likely to be reliable.

Any estimate of the time of origin of a clade can be subject to error in five broad categories, as defined by DONOGHUE & BENTON (2007). Two of these categories concern the absolute and relative dating of fossiliferous sediments. The other three categories refer to phylogenetic relationships, sampling of the fossil record, and taxonomic identification. Errors in the phylogeny will mislead estimates of clade origins, irrespective of the amount of molecular data available. Similarly, if the temporal order of fossils mostly reflects taphonomic artifacts, then they are unlikely to offer good calibration points. The very poor congruence between phylogenies and stratigraphy for eumalacostracans may indicate problems in both of these categories. A third problem is where poor preservation makes it difficult to assign fossils to the correct taxa. For example, the non-preservation of a diagnostic character might cause a fossil to be erroneously placed in the stem group rather than the crown (DONOGHUE & PURNELL 2009). Using such a misplaced fossil to calibrate a molecular clock may be misleading. The Upper Jurassic eumalacostracan fossil *Liaoningogriphus quadripartitus* (SHEN et al. 1998), is a case in point. Although originally described as a spelaeogriphacean, it lacks several features diagnostic of the crown group. POORE (2005) notes that it is extremely difficult to decide whether the absence of these characters is real, or merely the result of preservational bias.

Lastly, sequences for the most intensely sampled loci (JENNER et al. 2009) show marked rate heterogeneity across taxa, which also obfuscates clock estimates. In summary, our current understanding of the fossil record and phylogeny of Eumalacostraca make accurate molecular clock based divergence time estimates unlikely on the basis of available data.

4. Conclusions

1. There is still no stable and well-supported phylogeny for the Eumalacostraca. This is despite well over a century of morphological study, and the more recent synthesis of these data with that from multiple molecular markers. The phylogenetic signals from different loci are not especially strong across the species sampled thus far, neither are they particularly con-

cordant. Combining the data from different markers reveals relatively little "hidden support". More striking still is the conflict between morphological and molecular data. Total evidence analysis yields a tree more similar to that derived from morphology alone, despite the availability of six times as many informative nucleotide positions as morphological characters. The eumalacostracans arose in a relatively ancient (Devonian or earlier) but comparatively rapid radiation. Divergences of this type often present the biggest problems for molecular systematics (Wills & Fortey 2000). This is because of the conflict between selecting molecules evolving fast enough to acquire a signal during compressed cladogenesis, but simultaneously slow enough to maintain this signal over the intervening tens or hundreds of millions of years. Future studies will nonetheless benefit from the development of new molecular markers, and from significantly increased taxon sampling.

2. Fossils have the potential to preserve morphological data from close in time to the branching events that cladists seek to reconstruct. They can also significantly increase taxon sampling in largely or wholly extinct regions of the tree, can break up otherwise problematically long branches, and (as with extant taxa) can overturn phylogenetic hypotheses constructed in their absence. Our modest selection of fossils did not behave in this way, however. The removal of a living taxon was as likely to effect a change in inferred relationships as the removal of a fossil. Some of these changes revealed groups that have been proposed elsewhere in the literature, whereas others are more surprising (and, we venture, less likely to be true). Our preliminary analysis suggests that the paucity of fossils *per se* in published trees is *unlikely* to cripple them. Of course, it is perfectly possible that future discoveries will reveal many new, important and transitional forms. At present, however, it is not unreasonable to hope that a more complete understanding of extant taxa alone might eventually yield the correct phylogeny.

3. Our first order taxon jackknifing reveals unambiguously the considerable sensitivity of the morphological data set to the precise composition of the taxon sample. Equivalent assessments were not made for the available molecular data, but there is no reason to suppose that molecular trees are any less labile. Systematists rarely consider explicitly this issue: taxon deletion experiments are usually *ad hoc*, if conducted at all. This highlights the importance of adequate taxon sampling as something that future studies must address in more detail.

4. Published trees of the whole Eumalacostraca have a fit to the stratigraphic record that is mediocre at best, and significantly poorer than random at worst. There is probably no single reason for this. The enhanced preservation potential of more highly mineralized and derived forms is undoubtedly a significant factor. However, the small size of individuals in many lineages, coupled with their low abundance and species diversity must also contribute to the extensive ghost ranges within the group. The probable inaccuracy of most trees (all differ, and only one or none may be correct) is another factor. In most cases, therefore, it is unrealistic to employ stratigraphic congruence as an ancillary criterion for choosing between competing hypotheses (MPTs). The presence of extensive ghost ranges (coupled with considerable rate heterogeneity between lineages for the loci investigated thus far) also means that attempts to date events deep in eumalacostracan evolution using molecular clocks are likely to be misleading at present. We note that the fossil record *within* particular orders (e.g., stomatopods, tanaidaceans) may be much more congruent with their phylogeny.

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6. References

Baker, R.H. & R. DeSalle 1997. Multiple sources of character information and the phylogeny of Hawaiian drosophilids. – Systematic Biology **46**: 654–673.

Benton, M.J. 1993. The Fossil Record 2. – Chapman and Hall, London.

Benton, M.J. 1994. Paleontological data and identifying mass extinctions. – Trends in Ecology & Evolution **9**: 181–185.

Benton, M.J. & R. Hitchin 1997. Congruence between phylogenetic and stratigraphic data on the history of life. – Proceedings of the Royal Society of London Series B – Biological Sciences **264**: 885–890.

Benton, M.J., R. Hitchin & M.A. Wills 1999. Assessing congruence between cladistic and stratigraphic data. – Systematic Biology **48**: 581–596.

Benton, M.J. & G.W. Storrs 1994. Testing the quality of the fossil record - paleontological knowledge is improving. – Geology **22**: 111–114.

BENTON, M.J., M.A. WILLS & R. HITCHIN 2000. Quality of the fossil record through time. – Nature **403**: 534–537.

BOWMAN, T.E., S.P. GARNER, R.R. HESSLER, T.M. ILIFFE & H.L. SANDERS 1985. Mictacea, a new order of Crustacea Peracarida. – Journal of Crustacean Biology **5**: 74–78.

BOWMAN, T.E. & T.M. ILIFFE 1985. *Mictocaris halope*, a new unusual peracaridan crustacean from marine caves on Bermuda. – Journal of Crustacean Biology **5**: 58–73.

BOWMAN, T.E. & T.M. ILIFFE 1986. *Halosbaena fortunata*, a new thermosbaenacean crustacean from the Jameos del Agua marine lava cave, Lanzarote, Canary-Islands. – Stygologia **2**: 84–89.

BOWMAN, T.E. & T.M. ILIFFE 1988. *Tulumella unidens*, a new genus and species of thermosbaenacean crustacean from the Yucatan Peninsula, Mexico. – Proceedings of the Biological Society of Washington **101**: 221–226.

BRIGGS, D.E.G., M.D. SUTTON, D.J. SIVETER & D.J. SIVETER 2004. A new phyllocarid (Crustacea: Malacostraca) from the Silurian fossil-lagerstatte of Herefordshire, UK. – Proceedings of the Royal Society of London Series B – Biological Sciences **271**: 131–138.

CALS, P. & C. BOUTIN 1985. Discovery in Cambodia, former province in oriental Tethys, of a new living fossil *Theosbaena cambodjiana* n.g., n.sp. (Crustacea, Thermosbaenacea). – Comptes Rendus de l'Academie des Sciences Serie III – Sciences de la Vie **300**: 337–340.

CAMACHO, A.I. & A.G. VALDECASAS 2008. Global diversity of syncarids (Syncarida; Crustacea) in freshwater. – Hydrobiologia **595**: 257–266.

CHACE, F.A.J. & R.B. MANNING 1972. Two new caridean shrimps, one representing a new family from marine pools on Ascension Island, Crustacea Decapoda Natantia. – Smithsonian Contributions to Zoology **131**: 1–18.

CLYDE, W.C. & D.C. FISHER 1997. Comparing the fit of stratigraphic and morphologic data in phylogenetic analysis. – Paleobiology **23**: 1–19.

COBBETT, A., M. WILKINSON & M.A. WILLS 2007. Fossils impact as hard as living taxa in parsimony analyses of morphology. – Systematic Biology **56**: 753–766.

DAHL, E. 1992. Aspects of malacostracan evolution. – Acta Zoologica **73**: 339–346.

DONOGHUE, M.J., J.A. DOYLE, J. GAUTHIER, A.G. KLUGE & T. ROWE 1989. The importance of fossils in phylogeny reconstruction. – Annual Review of Ecology and Systematics **20**: 431–460.

DONOGHUE, P.C.J. & M.J. BENTON 2007. Rocks and clocks: calibrating the Tree of Life using fossils and molecules. – Trends in Ecology & Evolution **22**: 424–431.

DONOGHUE, P.C.J. & M.A. PURNELL 2009. Distinguishing heat from light in debate over controversial fossils. – Bioessays **31**: 178–189.

DOYLE, J.A. & M.J. DONOGHUE 1987. The importance of fossils in elucidating seed plant phylogeny and macroevolution. – Review of Palaeobotany and Palynology **50**: 63–95.

DZIK, J. 2008. Evolution of morphogenesis in 360-million-year-old conodont chordates calibrated in days. – Evolution & Development **10**: 769–777.

DZIK, J., A.Y. IVANTSOV & Y.V. DEULIN 2004. Oldest shrimp and associated phyllocarid from the Lower Devonian of northern Russia. – Zoological Journal of the Linnean Society **142**: 83–90.

FARRIS, J.S. 1989. The retention index and the rescaled consistency index. – Cladistics **5**: 417–419.

FINARELLI, J.A. & W.C. CLYDE 2002. Comparing the gap excess ratio and the retention index of the stratigraphic character. – Systematic Biology **51**: 166–176.

FINDEN, C.R. & A.D. GORDON 1985. Obtaining common pruned trees. – Journal of Classification **2**: 255–276.

FORTEY, R.A., D.E.G. BRIGGS & M.A. WILLS 1996. The Cambrian evolutionary 'explosion': Decoupling cladogenesis from morphological disparity. – Biological Journal of the Linnean Society **57**: 13–33.

FORTEY, R.A., D.E.G. BRIGGS & M.A. WILLS 1997. The Cambrian evolutionary 'explosion' recalibrated. – Bioessays **19**: 429–434.

FRYER, G. 1965. Studies on the functional morphology and feeding mechanism of *Monodella argenarii* Stella (Crustacea: Thermosbaenacea). – Transactions of the Royal Society of Edinburgh **66**: 49–90.

GAUTHIER, J., A.G. KLUGE & T. ROWE 1988. Amniote phylogeny and the importance of fossils. – Cladistics **4**: 105–209.

GEORGESCU, M.D., E.E. SAUPE & B.T. HUBER 2008. Morphometric and stratophenetic basis for phylogeny and taxonomy in Late Cretaceous gublerinid planktonic Foraminifera. – Micropaleontology **54**: 397–424.

GUTU, M. 2001. Emendations on the description of *Thetispelecaris remex* Gutu and Iliffe, 1998 and the diagnosis of the order Bochusacea (Crustacea: Peracarida). – Travaux du Museum National d'Histoire Naturelle "Grigore Antipa" **43**: 47–57.

GUTU, M. & T.M. ILIFFE 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 Museum National d'Histoire Naturelle "Grigore Antipa" **40**: 93–120.

HART, C.W. & R.B. MANNING 1986. Two new shrimps (Procarididae and Agostocarididae, new family) from marine caves of the western North-Atlantic. – Journal of Crustacean Biology **6**: 408–416.

HITCHIN, R. & M.J. BENTON 1997a. Congruence between parsimony and stratigraphy: Comparisons of three indices. – Paleobiology **23**: 20–32.

HITCHIN, R. & M.J. BENTON 1997b. Stratigraphic indices and tree balance. – Systematic Biology **46**: 563–569.

HOLTHUIS, L.B. 1973. Caridean shrimps found in landlocked salt water pools at four Indo West Pacific localities (Sinai Peninsula, Funafuti Atoll, Maui and Hawaii Islands) with the description of one new genus and four new species. – Zoologische Verhandelingen (Leiden) **128**: 1–48.

HUELSENBECK, J.P. 1991. When are fossils better than extant taxa in phylogenetic analysis. – Systematic Zoology **40**: 458–469.

HUELSENBECK, J.P. 1994. Comparing the stratigraphic record to estimates of phylogeny. – Paleobiology **20**: 470–483.

JARMAN, S.N., S. NICOL, N.G. ELLIOTT & A. MCMINN 2000. 28S rDNA evolution in the Eumalacostraca and the phylogenetic position of krill. – Molecular Phylogenetics and Evolution **17**: 26–36.

JENNER, R.A. & D.T.J. LITTLEWOOD 2008. Problematica old and new. – Philosophical Transactions of the Royal Society B – Biological Sciences **363**: 1503–1512.

Jenner, R.A., C. Ní Dhubhghaill, M.P. Ferla & M.A. Wills 2009. Eumalacostracan phylogeny and total evidence: limitations of the usual suspects. – BioMed Central Evolutionary Biology **9**: 21.

Jenner, R.A. & M.A. Wills 2007. The choice of model organisms in evo-devo. – Nature Reviews Genetics **8**: 311–319.

Just, J. & G.C.B. Poore 1988. Second record of Hirsutiidae (Peracarida: Mictacea) *Hirsutia sandersetalia*, new species, from southeastern Australia. – Journal of Crustacean Biology **8**: 483–488.

Kensley, B. & D. Williams 1986. New shrimps (families Procarididae and Atyidae) from a submerged lava tube on Hawaii. – Journal of Crustacean Biology **6**: 417–437.

Maguire, B. 1965. Extension of the known range of the crustacean order Thermosbaenacea to the western hemisphere. – Bulletin of the National Speleological Society **27**: 63.

Mayrat, A. & M. de Saint Laurent 1996. Considérations sur la classe des Malacostracés (Malacostraca Latreille, 1802). Pp. 841–863 *in*: J. Forest (ed.), Traité de Zoologie sous la direction de P.-P. Grassé. – Masson éditeur, Paris.

Meland, K. & E. Willassen 2007. The disunity of "Mysidacea" (Crustacea). – Molecular Phylogenetics and Evolution **44**: 1083–1104.

Mickevich, M.F. & J.S. Farris 1981. The implications of congruence in *Menidia*. – Systematic Zoology **30**: 351–370.

Norell, M.A. & J.A. Clarke 2001. Fossil that fills a critical gap in avian evolution. – Nature **409**: 181–184.

Norell, M.A. & M.J. Novacek 1992. Congruence between superpositional and phylogenetic patterns – comparing cladistic patterns with fossil records. – Cladistics **8**: 319–337.

O'Leary, M.A. 1999. Parsimony analysis of total evidence from extinct and extant taxa and the Cetacean-Artiodactyl question (Mammalia, Ungulata). – Cladistics **15**: 315–330.

Ohtsuka, S., Y. Hanamura & T. Kase 2002. A new species of *Thetispelecaris* (Crustacea: Peracarida) from submarine cave on Grand Cayman Island. – Zoological Science **19**: 611–624.

Pires, A.M.S. 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**: 225–238.

Poe, S. 1998. Sensitivity of phylogeny estimation to taxonomic sampling. – Systematic Biology **47**: 18–31.

Pol, D. & M.A. Norell 2001. Comments on the Manhattan stratigraphic measure. – Cladistics **17**: 285–289.

Poore, G.C.B. 2005. Peracarida: monophyly, relationships and evolutionary success. – Nauplius **13**: 1–27.

Poore, G.C.B. & W.F. Humphreys 1992. First record of Thermosbaenacea (Crustacea) from the southern hemisphere: a new species from a cave in tropical western Australia. – Invertebrate Taxonomy **6**: 719–725.

Richter, S. & G. Scholtz 2001. Phylogenetic analysis of the Malacostraca (Crustacea). – Journal of Zoological Systematics and Evolutionary Research **39**: 113–136.

Robinson, D.F. & L.R. Foulds 1981. Comparison of phylogenetic trees. – Mathematical Biosciences **53**: 131–147.

Rolfe, W.D.I. 1962. Grosser morphology of the Scottish Silurian phyllocarid crustacean, *Ceratiocaris papilio* Salter in Murchison. – Journal of Paleontology **36**: 912–932.

Rolfe, W.D.I. & J. Dzik 2006. *Angustidontus*, a Late Devonian pelagic predatory crustacean. – Transactions of the Royal Society of Edinburgh – Earth Sciences **97**: 75–96.

Roopnarine, P.D. 2005. The likelihood of stratophenetic-based hypotheses of genealogical succession. Pp 143–157 *in*: M.A. Purnell, P.C.J. Donoghue & D.J. Batten (eds.), Conodont Biology and Phylogeny: Interpreting the Fossil Record. – Palaeontological Association, Aberystwyth.

Sanders, H.L., R.R. Hessler & S.P. Garner 1985. *Hirsutia bathyalis*, a new unusual deep-sea benthic peracaridan crustacean from the tropical Atlantic. – Journal of Crustacean Biology **5**: 30–57.

Schram, F.R. 1974. The Mazon Creek caridoid Crustacea. – Fieldiana Geology **30**: 9–65.

Schram, F.R. 1984a. Fossil Syncarida. – Transactions of the San Diego Society of Natural History **20**: 189–246.

Schram, F.R. 1984b. Relationships within eumalacostracan Crustacea. – Transactions of the San Diego Society of Natural History **20**: 301–312.

Schram, F.R. 1986. Crustacea. – Oxford University Press, Oxford.

Schram, F.R. 2006. *Lobetelson mclaughlinae* n. gen., n. sp., a new genus and species of belotelsonid malacostracan from the Pennsylvanian of the Mazon Creek area. – Zoosystema **28**: 277–284.

Schram, F.R. & C.H.J. Hof 1998. Fossils and interrelationships of major crustacean groups. Pp. 233–302 *in*: G.D. Edgecombe (ed.), Arthropod Fossils and Phylogeny. – Columbia University Press, New York.

Shen, Y.-B., R.S. Taylor & F.R. Schram 1998. A new spelaeogriphacean (Crustacea: Peracarida) from the Upper Jurassic of China. – Contributions to Zoology **68**: 19–35.

Shimomura, M. & Y. Fujita 2009. First record of the thermosbaenacean genus *Halosbaena* from Asia: *H. daitoensis* sp. nov. (Peracarida: Thermosbaenacea: Halosbaenidae) from an anchialine cave of Minami Daito-jima Is., in Okinawa, southern Japan. – Zootaxa **1990**: 55–64.

Siddall, M.E. 1996. Stratigraphic consistency and the shape of things. – Systematic Biology **45**: 111–115.

Siddall, M.E. 1998. Stratigraphic fit to phylogenies: a proposed solution. – Cladistics **14**: 201–208.

Siewing, R. 1956. Untersuchnungen 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*: H.B. Whittington & W.D.I. Rolfe (eds.), Phylogeny and Evolution of Crustacea. – Museum of Comparative Zoology, Special Publication, Harvard.

Spears, T., R.W. DeBry, L.G. Abele & K. Chodyla 2005. Peracarid monophyly and interordinal phylogeny inferred from nuclear small-subunit ribosomal DNA sequences (Crustacea: Malacostraca: Peracarida). – Proceedings of the Biological Society of Washington **118**: 117–157.

STEGNER, M.E.J., S. RICHTER & C.S. WIRKNER 2008. Evolutionary morphology of the brain in Peracarida. – Journal of Morphology **269**: 1483.

STOCK, J.H. 1976. A new genus and two new species of the crustacean order Thermosbaenacea from the West Indies. – Bijdragen tot de Dierkunde **46**: 47–70.

STOCK, J.H. 1982. The influence of hadziid Amphipoda on the occurrence and distribution of Thermosbaenacea and cyclopoid Copepoda in the West Indies. – Polskie Archiwum Hydrobiologii **29**: 275–282.

STOCK, J.H. & G. LONGLEY 1981. Generic status and distribution of *Monodella texana*, the only known North American thermosbaenacean. – Proceedings of the Biological Society of Washington **94**: 569–578.

SWOFFORD, D.L. 2002. PAUP*4.0b10. Phylogenetic analysis using parsimony (*and other methods). – Sinauer Associates.

TAYLOR, R.S., Y.B. SHEN & F.R. SCHRAM 1998. New pygocephalomorph crustaceans from the Permian of China and their phylogenetic relationships. – Palaeontology **41**: 815–834.

WAGNER, H.P. 1994. A monographic review of the Thermosbaenacea (Crustacea: Peracarida): A study on their morphology, taxonomy, phylogeny and biogeography. – Zoologische Verhandelingen (Leiden) **291**: 1–338.

WAGNER, P.J. 1998. A likelihood approach for evaluating estimates of phylogenetic relationships among fossil taxa. – Paleobiology **24**: 430–449.

WAGNER, P.J. 1999. The utility of fossil data in phylogenetic analyses: a likelihood example using Ordovician-Silurian species of the Lophospiridae (Gastropoda: Murchisoniina). – American Malacological Bulletin **15**: 1–31.

WAGNER, P.J. 2002. Testing phylogenetic hypotheses with stratigraphy and morphology – a comment on Smith (2000). – Journal of Paleontology **76**: 590–593.

WAGNER, P.J. & C.A. SIDOR 2000. Age rank / clade rank metrics – Sampling, taxonomy, and the meaning of "stratigraphic consistency". – Systematic Biology **49**: 463–479.

WATLING, L. 1981. An alternative phylogeny of peracarid crustaceans. – Journal of Crustacean Biology **1**: 201–210.

WATLING, L. 1983. Peracaridan disunity and its bearing on eumalacostracan phylogeny with a redefinition of eumalacostracan superorders. Pp. 213–228 *in*: F.R. SCHRAM (ed.), Crustacean Phylogeny. – A.A. Balkema, Rotterdam.

WATLING, L., C.H.J. HOF & F.R. SCHRAM 2000. The place of the Hoplocarida in the malacostracan pantheon. – Journal of Crustacean Biology **20**: 1–11.

WATLING, L.L. 1999. Toward understanding the relationships of the peracaridan orders: the necessity of determining exact homologies. Pp. 73–89 *in*: F.R. SCHRAM & J.C. VON VAUPEL KLEIN (eds.), Crustaceans and the Biodiversity Crisis. – Brill, Leiden.

WHEELER, W. 1999. Measuring topological congruence by extending character techniques. – Cladistics **15**: 131–135.

WILLIAMSON, D.I. 1973. *Amphionides reynaudii*, representative of a proposed new order of eucaridan Malacostraca. – Crustaceana (Leiden) **25**: 35–50.

WILLS, M.A. 1998a. A phylogeny of recent and fossil Crustacea derived from morphological characters. Pp. 189–209 *in*: R.A. FORTEY & R.H. THOMAS (eds.), Arthropod Relationships. – Chapman and Hall, London.

WILLS, M.A. 1998b. Crustacean disparity through the Phanerozoic: comparing morphological and stratigraphic data. – Biological Journal of the Linnean Society **65**: 455–500.

WILLS, M.A. 1999. Congruence between phylogeny and stratigraphy: randomization tests and the gap excess ratio. – Systematic Biology **48**: 559–580.

WILLS, M.A. 2001. How good is the fossil record of arthropods? An assessment using the stratigraphic congruence of cladograms. – Geological Journal **36**: 187–210.

WILLS, M.A. 2002. The tree of life and the rock of ages: are we getting better at estimating phylogeny? – Bioessays **24**: 203–207.

WILLS, M.A. 2007. Fossil ghost ranges are most common in some of the oldest and some of the youngest strata. – Proceedings of the Royal Society B – Biological Sciences **274**: 2421–2427.

WILLS, M.A., P.M. BARRETT & J.F. HEATHCOTE 2008. The modified gap excess ratio (GER*) and the stratigraphic congruence of dinosaur phylogenies. – Systematic Biology **57**: 891–904.

WILLS, M.A. & R.A. FORTEY 2000. The shape of life: how much is written in stone? – Bioessays **22**: 1142–1152.

WIRKNER, C.S. & S. RICHTER 2003. The circulatory system in Phreatoicidea: implications for the isopod ground pattern and peracarid phylogeny. – Arthropod Structure & Development **32**: 337–347.

WIRKNER, C.S. & S. RICHTER 2007a. Comparative analysis of the circulatory system in Amphipoda (Malacostraca, Crustacea). – Acta Zoologica **88**: 159–171.

WIRKNER, C.S. & S. RICHTER 2007b. The circulatory system and its spatial relations to other major organ systems in Spelaeogriphacea and Mictacea (Malacostraca, Crustacea) – a three-dimensional analysis. – Zoological Journal of the Linnean Society **149**: 629–642.

WIRKNER, C.S. & S. RICHTER 2007c. The circulatory system in Mysidacea - implications for the phylogenetic position of Lophogastrida and Mysida (Malacostraca, Crustacea). – Journal of Morphology **268**: 311–328.

WIRKNER, C.S. & S. RICHTER 2008a. Evolutionary morphology of the circulatory system in Malacostraca. – Journal of Morphology **269**: 1472–1472.

WIRKNER, C.S. & S. RICHTER 2008b. Morphology of the haemolymph vascular system in Tanaidacea and Cumacea: Implications for the relationships of "core group" Peracarida (Malacostraca; Crustacea). – Arthropod Structure & Development **37**: 141–154.

Appendix I: List of morphological characters

Largely as Jenner et al. (2009). Original sources principally Pires (1987), Wills (1998), Schram & Hof (1998), Richter & Scholtz (2001) and Poore (2005).

Cephalic shield and tergites

1. Carapace: Absent or as a simple head-shield (0). Univalved or bivalved (1).
2. Posterior extent of carapace: Well-developed, covering the thorax (0). Short, covering only the anteriormost thoracic segments (1).
3. Dorsal fold on adult: Absent (0). Present (1). A fold arising from and attached to a thoracic segment. In Malacostraca, this always arises from the posterior margin of the cephalothoracic shield.
4. Branchiostegal flaps: Absent (0). Present (1).
5. Cephalic pleural fold: Absent (0). Present (1).
6. Carapace with respiratory function: Non-respiratory (0). Respiratory (1).
7. Ventral extent of carapace: Normal (0). All-enveloping (1).
8. Number of thoracomeres involved in forming the cephalothorax: None (0). One (1). Two (2). Three (3). Eight (4).
9. Articulation of tergites: With no overlap (0). With overlapping pleurae (1).
10. Pleura of the second pleon segment: Pleura not overlapping that of the anterior (first) pleomere (0). Pleura overlapping that of the anterior (first) pleomere (1).
11. Rostrum: Absent (0). Fixed (1). Articulating (2).
12. Cervical groove (just posterior of the maxillae): Absent (0). Present (1). (see also Poore 2005)
13. Cephalic kinesis / protocephalon: Absent (0). Present (1).
14. Males (at least) with transverse suture in cephalon, immediately behind the mandibles: Absent (0). Present (1).
15. Cephalic doublure: Absent (0). Present (1).
16. Carapace adductor muscles: Present (0). Absent (1).

Eyes and frontal organs

17. Compound eyes: Absent (0). Present (1).
18. Form of compound eyes: Sessile (0). Stalked (1). Lobed (2).
19. Ocular lobe: Absent (0). Present (1). An ocular lobe can be present in the absence of compound eyes, and vice versa.
20. Ultrastructure of ommatidia: Crystalline cone tetrapartite (0). Crystalline cone bipartite (1).
21. Ultrastructure of ommatidia: Crystalline cone completely round in transverse section, cone without any extensions (0). Cone with two lateral extensions (in transverse section button-like), formed by one cone cell each (1).
22. Ultrastructure of ommatidia: Crystalline cones with four cone cell processes (0). Only the two accessory cone cell processes are present; the processes of the main cone cells are missing (1). All cone cell processes missing (2).
23. Ultrastructure of ommatidia: All four cone cell nuclei lying in one plane on top of the cone (0). Nuclei of the accessory cone cells distally displaced (1).
24. Ultrastructure of ommatidia: No clear zone between crystalline cone and rhabdom (apposition eye) (0). Clear zone formed by retinular cells and/or distal pigment cells, cone and rhabdom not in direct contact (superposition eye) (1).
25. Naupliar eye sensu stricto: Absent (0). Present (1).
26. Dorsal frontal organ: Absent (0). Present (1).
27. Ventral frontal organ: Absent (0). Present (1).
28. Dorsal, nuchal or neck organ: Absent (0). Present (1).
29. Bec oculair: Absent (0). Present (1).

Antennule

30. Number of podomeres in outer ramus (exopod): 10 or more (0). 9 to 4 (1). 3 to 1 (2). Outer ramus absent (3).
31. Exopod scale-like: No (0). Yes (1).
32. Number of podomeres in inner ramus (endopod): 10 or more (0). 9 to 1 (1).
33. Statocyst in basal segment of first antenna: Absent (0). Present (1).
34. Antennule: Uniramous or biramous (0). Triramous (1).

Antenna

35. Number of podomeres in outer ramus (exopod): None (0). 1 (1). 2–4 (2). 18 or more (3).
36. Antennal exopod modified as scaphocerite: Not modified (0). Modified (1).
37. Antennal scale (scaphocerite): As long or longer than peduncle articles 3+4 (0). Half the length of peduncle articles 3+4 (1).
38. Number of podomeres in inner ramus (endopod): 1–2 (0). 3 (1). 5 (2). 8 or more (3).
39. Antennal gland: Absent (0). Present (1).
40. Antennal naupliar process: Absent (0). Present (1).

Mandible and mandibular region

41. Number of podomeres in endopod: None (endopod absent) (0). 1–2 (1). 3–4 (2).
42. Mandibular palp: With lateral setae on articles 2 and 3 (0). With distal setae on article 3 only (1).
43. Mandibular incisor: Stout and tooth-like (0). Thin and blade-like or rudimentary (1). Absent (2).
44. Mandible with marked molar process: Absent (0). Present (1).
45. Arrangement of molar and incisor elements: Short and compact, incisor and molar closely set (0). Long, incisor and molar widely-spaced (1). Scored as inapplicable for taxa lacking an incisor, molar or both.
46. Lacinia mobilis on the adult mandible: Absent (0). Present (1).
47. Lacinia mobilis on the larval mandible: Absent (0). Present (1).
48. Paragnaths: Absent (0). Present (1).
49. Labrum: Moderate (small to medium) (0). Enlarged to extend well posterior of the mouth field (massive) (1).
50. Posterior tooth on labrum: Absent (0). Present (1).
51. Labrum expression in larva: Moderate (0). Enlarged to extend well posterior of the mouth field (1).
52. Epistome: Absent or vestigial (0). Well-developed (1).

First maxilla

53. Number of podomeres in exopod: None (exopod absent) (0). 1–2 (1).

54. Number of podomeres in endopod: None (endopod absent) (0). 1–2 (1). 3 (2).

Second maxilla

55. Number of endites: 8–6 (0). 5–4 (1). 3–1 (2). None (3).

56. Basal endites: Longer than wide (0). About as wide as long (1).

57. Number of podomeres in exopod: None (exopod absent) (0). 1 (1). 2 (2).

58. Exopod modified as a scaphognathite: Not modified (0). Modified (1).

59. Number of podomeres in endopod: None (endopod absent) (0). 1–2 (1). 6 (2).

60. Maxillary glands: Absent (0). Present (1).

Sixth pair of appendages

61. Protopodal endites: Present (0). Absent (1).

62. Number of podomeres in exopod: None (exopod absent) (0). 1 (1). 2–4 (2). Very numerous (3).

63. Exopod: Linear (0). With expanded basal section (1).

64. "Caridean lobe" on exopod: Absent (0). Present (1).

65. Number of podomeres in endopod: 1–2 (0). 3 (1). 4 (2). 5 (3). 6 (4).

66. Number of epipodites: None (0). One (1). Two (2).

67. Role of epipodites of first thoracopod in respiration: Respiratory and similar to those of succeeding thoracopods (0). Epipodites producing a respiratory current (irrespective of whether or not the epipodite is respiratory itself) (1). Epipodites not producing a respiratory current (and epipodite not respiratory) (2).

68. Expansion of epipodite: Short, linear (or in Isopoda, not expanded into branchial cavity) (0). Expanded into branchial cavity (1).

69. Form of epipodite: Not modified (0). Modified as a cup or spoon-shaped (respiratory) structure (1).

Seventh, eighth and ninth pairs of appendages

70/79/88. Protopodal endites: Present (0). Absent (1).

71/80/89. Number of podomeres in exopod: None (exopod absent) (0). 1 (1). 2 (2). 3–4 (3). Very numerous (4).

72/81/90. Form of exopod: Flagelliform, or otherwise developed as an elongate process (0). Developed as a broad, lamelliform paddle or blade, or otherwise non-flagelliform (1).

73/82/91. Number of podomeres in endopod: 1 (0). 2–3 (1). 4 (2). 5 (3). 6 (4).

74/83/92. Number of epipodites: None (0). One (1). Two (2).

75/84/93. Oöstegites: Absent (0). Present (1).

76/85/94. Podobranch gills: Absent (0). Present (1).

77/86/95. Arthrobranch gills: Absent (0). Present (1).

78/87/96. Pleurobranch gills: Absent (0). Present (1).

General morphology of thoracic appendages

97. Position of epipodites on thoracopods 2–8: Lateral (0). At least one branch carried under the thorax (1). This character is scored as inapplicable for taxa without epipodites.

98. Posterior extent of oöstegites: As far back as thoracopod 8 (0). As far back as thoracopod 6 or 7 (1). This character is scored as inapplicable for taxa without oöstegites.

99. Reduction of the oöstegites after each brood: Oöstegites are not reduced (0). Oöstegites are reduced (1).

100. Thoracopod thorax-coxa articulation: Transverse hinge (0). Anterioposterior articulation (1). Immobile (2).

101. Thoracopods coxa-basis articulation: Dicondylic along anteroposterior axis (0). Monocondylic (1). Not articulated, or coxa and basis otherwise fused (2).

102. Thoracopods intrabasal articulation: Absent (0). Present (1).

103. Thoracopods 4 & 5: Achelate (0). Chelate (1).

104. Thoracopods 5–7, pedunculate setae: Absent (0). Present (1).

105. Thoracopods 5 & 6 (appendages 10 & 11), exopod: Present (0). Absent (1). Stomatopods bear exopods on the 6th thoracopods, but not on the 5th (fifth maxillipedes). They are therefore scored as (1,2).

106. Thoracopod 5 (pereopod 4) exopod of female: With two or more articles (0). With one article (1).

107. Thoracopod 6 (pereopod 5) exopod: With two or more articles (0). With one article (1).

108. Thoracopod 6: Achelate (0). Chelate (1).

109. Thoracopod 7 (pereopod 6) exopod: Of two or more articles (0). Of one article or absent entirely (1).

110. Thoracopod 8 (pereopod 7) exopod: Present (0). Absent (1).

111. Attitude of trunk appendages relative to body: Pendant (0). Laterally displaced (1).

112. Thoracic coxal plates: Absent (0). Present (1).

113. Oöstegites with marginal setae: Present (0). Absent (1).

114. Pereopods: With a few short setae on articles (0). With a row of long setae on all articles (1).

Abdominal/pleonal appendages

115. Pleonal limbs: All present (0). Just posterior limbs reduced or absent (1). Only anterior limbs present (2).

116. Number of podomeres in exopod of second abdominal appendage/pleopod: None (0). One or vestigial (1). Two (2). Annulate (3).

117. Number of podomeres in endopod of second abdominal appendage/pleopod: None (0). One or vestigial (1). Two (2). Annulate (3).

118. Abdominal appendages (pleopods) modified for brooding eggs: Unmodified (0). Modified (1).

119. Gills (as distinct filamentory or platelike structures) on pleon: Absent (0). Present (1).

Posteriormost appendages

120. Last pleopods: Small, far from the telson, and not forming a tail fan (0). Modified as broad uropods, forming a tail fan with the telson (1). Oriented posteriorly and close to the telson, but not forming a tail fan with it (2).

121. Number of podomeres in inner rami of uropods: One (0). Two or more (1).

122. Number of podomeres in outer rami of uropods: None (0). One (1). Two or more (2).

123. Uropod numbers: None (0). One set (1). Three sets (2).

Telson and furca

124. Gross form of telson: Approximately circular and segment-like in cross section (0). Dorsoventrally-flattened (1).

125. Telson appendages (furca): Absent (0). Present (1). Richter & Scholtz (2001) score telson appendages in the Leptostraca and Bathynellacea. Schram (1986) additionally records their presence in the Euphausiacea.

Tagmosis

126. Number of maxillipeds: None (0). One (1). Two (2). Three or more (3).

127. Number of post-maxillary body segments, *including* the telson or anal somite: 14–15 (0). 16 (1). 20 or more (2).

128. Number of segments in pleon (excluding the telson/terminal division): > 7 (0). 6 (1). 5 (2). 4 (3).

129. Pleomere size: First pleomere fully developed, of similar size and appearance to the more posterior pleomeres (0). First pleomere reduced, smaller than the second pleomere (1). More pleomeres reduced (2).

130. Fusion of telson to the pleonite: Not fused (0). Fused (1).

Internal organs

131. Foregut dorsal caeca: Absent (0). Present (1).

132. Foregut shape: Anterior section of similar size to posterior (0). Anterior section enlarged with respect to posterior (1).

133. Foregut dorsolateral and midventral ridges: With setae (0). With teeth or ossicles (1).

134. Lateralia and inferolateralia anteriores (lateral invaginations) in the cardiac chamber: Absent (0). Present (1).

135. Superomedianum (unpaired): Absent (0). Present (1).

136. Inferomedianum anterius (midventral cardiac ridge): Absent (0). Present (1).

137. Inferomedianum posterius (midventral pyloric ridge): Absent (0). Present (1).

138. Atrium between the inferomediana connecting the cardiac primary filter grooves with the pyloric filter grooves: Absent (0). Present (1).

139. Number of secondary filter grooves in the inferomedianum posterius: Numerous (0). Eight to six (1). Three (2). Two (3). One (4). Scored as inapplicable for taxa lacking an inferomedianum posterius.

140. Formation of the midgut: By ectoderm (0). At the border between the stomodaeum and proctodaeum (1).

141. Entoderm: Unpaired entoderm plates (0). Paired entoderm plates (1).

142. Trunk gut diverticula and/or caeca: Absent (0). Present (1).

143. Position of the anus: Terminal (0). Ventral (1).

144. Position of the heart: In whole thorax and pleon (0). In thorax (1). Only in posterior part of the thorax and pleon (2).

145. Gross morphology of the heart: Elongate (0). Short and bulbous (1).

146. Number of pairs of ostia in heart: More than five (0). Five (1). Three (2). Two (3). One (4). None (5).

147. Arteria subneuralis/supraneuralis: Absent (0). Present (1).

148. Aorta descendens (sternal artery) as the only connection between the heart and the arteria subneuralis/supraneuralis: Absent (0). Present (1). Coded as inapplicable in taxa lacking an arteria subneuralis/supraneuralis.

149. Aorta descendens: The undivided sternal artery passes through the ventral nervous system (0). Sternal artery branches off into three branches dorsal to the ventral nervous system, all branches passing separately through the nerve cord (1). Coded as inapplicable in taxa lacking an arteria subneuralis/supraneuralis.

150. Segmental arteries: Absent, arteries arising only from the anterior and posterior ends of the heart (0). Present (1).

151. Pleon musculature: Simple (0). Precaridoid (1). Caridoid (2).

152. Tail fan escape reaction: Absent (0). Present (1).

153. CNS: Ventral nerve cord with unfused, paired ganglia and double ventral commisures (0). Ventral nerve cord with fused ganglia (1).

154. Globuli cell clusters in the deutocerebrum asscociated with the olfactory lobe: One (0). Two (1).

Reproduction and development

155. Male gonopore location (post-maxillary trunk segment numbers): Segments 6–8 (0). Segment 11 (1).

156. First and/or second pleopods modified for sperm transfer in males: No modification or rudimentary modifications (0). Stomatopod petasma, including modifications of the exopod of the second pleopod (1). Endopod of the first pleopod completely modified for sperm transfer, modifications different in the second endopod (2).

157. Appendices internae: Absent (0). Present (1).

158. Development: Anamorphic (0). Metamorphic (1). Epimorphic or direct (2).

159. Free living larva: Present (0). Absent (1). Coded as inapplicable for taxa with epimorphic or direct development.

160. Orthonauplius: None (0). Egg nauplius only (1). Present without fronto-lateral horns (2).

161. Manca stage: Absent (0). Present (1).

162. Brood care: None (0). Brood care with thoracopods, but without feeding by the mother (1). Brood care attaching the eggs to the pleopods (2). Brood care using a dorsal brood pouch (3). Brood care using a marsupium formed by oöstegites (4). Brood care using elongated first pleopod (5).

163. Development of appendages: Advanced development of anterior head appendages (0). Continuous anterioposterior decrease in the degree of appendage formation (1).

164. Cleavage: Superficial (0). Mixed (1). Total (2).

165. Number of ectoteloblasts: Nineteen (0). Variable (1). None (2).

166. Arrangement of ectoteloblasts: Forming a ring around the caudal papilla giving rise to embryonic ventral and dorsal material (0). Forming a transverse row (only the ventral side of the embryo is formed by ectoteloblasts and the dorsal side is closed much later in development) (1).

167. Early embryo (nauplius larva): Ventrally folded (0). With a dorsal fold (1).

168. Yolk distribution in the embryo: Posterior part of the embryo contains no yolk (0). Posterior part of the embryo contains yolk (1).

169. Number of pairs of thoracic appendages in the hatchling: Eight (0). Seven (1). Six (2). Scored as inapplicable for taxa without direct development.

170. Embryonic dorsal organ: Present (0). Absent (1).
171. Embryonic dorsal organ: Simple layer (0). Cup shaped (1).
172. Transient paired lateral organs: Absent (0). Present (1).

Sperm
173. Sperm acrosome: Present (0). Absent (1).
174. Sperm filamentous arms: None (0). Present (1).
175. Sperm nuclear membrane: Present (0). Absent (chromatin diffuse) (1).
176. Spermatophore: None (0). Present (1).
177. Sperm centriole: Present (0). Doublet (1). Centriolar root homologue (cross-striated pseudoflagellum). (2). Absent (3).

Appendix II: Character matrix

Polymorphism is indicated as follows: A = states 0 and 1; B = states 1 and 2; C = states 2 and 3; D = states 3 and 4; E = states 0 and 2.

	10	20	30	40	50	60	70	80	90
Acanthotelson	0-000--000	1000011102	??????????0	00?0A11310	2?00-0?10?	?0023-0-??	????4????1	0-40000012	1410000121
Aeschronectida	10101?0011	2010?11102	??????????0	00?1110 3?0	??11??????	??02??0-2?	?10030---1	1130000011	1300000111
Amphionidacea	10101?1400	1000011100	-00????1?0	00?01101?0	0?21-0?100	?000201 01?	1210410101	1010000111	0200001110
Amphipoda	0-000--100	A0000110A1	0210000001	00000--310	A001011100	?00A200-00	00--30---1	0-40000010	?41A00010-
Anaspidacea	0-000--110	1001011101	0101110110	0010111300	2001000?100	?001200-11	0100420001	4042000014	0420000140
Angustidontus	10??1?0110	1000011102	??????????1	01?01103?0	B?0111?10?	?0?B0???B?	????2?????	40C??????4	0C??????40
Anostraca	0-000--000	-101011102	????101103	-1?00--001	A--1-00010	10003-0-11	0110120000	1112000001	1120000011
Bathynellacea	0-000--000	0000010-1-	----???0?2	11001A1200	2110-0?100	?000200-11	1100C10001	1021000011	0210000110
Belotelsonidea	10?11?0000	1000111102	??????????0	00?02103??	??0??????0	?1?2????2?	00--4????1	0-4??1??10	-4??1??10-
Bochusacea	11001?0100	A00A010-1-	----0????B	01?01113 0?	211111?100	?000200-11	00--40---1	204000001C	0401000130
Brachypoda	0-001--011	0000101-0-	----000003	-0?030-001	0--1-00010	1012002021	0210510000	2051000002	0510000020
Caridea	1000100411	1000111100	-001111110	0010110310	E001001000	0001201110	0111110101	0-41000011	0210000110-
Cumacea	1100110310	0000111B1?	????000001	01000--300	0?01111100	?101201001	0100411111	0-40000014	0401000140
Dendrobranchiata	1010010410	1110111100	-001111110	0010110310	1001000100	0101201110	00--320101	4031011114	0410011120
Euphausiacea	1010100400	1010011101	0111101110	0010110310	2001001100	0001201010	0200410101	2041000012	0410000120
Euzygida	1000100410	1100111102	????????10	00?0110310	2001000?000	0101201110	0100210101	1041011110	-41001110-
Isopoda	0-000--100	A000011011	0110000003	-100A113A0	2001011100	?000200-01	00--412001	0-40100010	-40100010-
Leptostraca	1010011010	2010001100	-000000102	11100--310	2011000000	?011201011	01A0310001	1131000011	1310000111
Lophogastrida	1011100110	1100111101	1111001010	0000110310	2001011101	?001201011	0100411-01	4041100014	0411000140
Mictocaris	1100110100	100001010-	----0????1	01?01113??	2011111100	?000200-11	00--40---1	2040100012	0401000120
Mysida	1011110300	1100111101	1111001010	0010110310	2001011101	?00A201010	0100411101	4040A00014	040A000140
Notostraca	10?0000000	0000101002	????100103	-1?00--001	0--1-00000	00003-0-11	0110110100	1111000001	1110000011
Palaeocaris	0-000--000	1001011102	??????????0	00?01113?0	B?0100?00?	?00B3-0-B?	????2????1	2141000012	1410000121
Procaridea	1000100411	1100111102	???1111110	00?0110310	2001002?100	0101201110	0311101?1	4041000014	0410000140
Pygocephalomorpha	10111?0?10	1100101102	??????????0	00?01103?0	???1????0?	?002??????	0???D????0	??D??????4	0300000140
Reptantia	1010100411	1100111100	-0011AA110	0010110310	2020-00000	0101201110	0210110101	3041011012	041011010-
Spelaeogriphacea	1110110100	AA00010-A-	----0??0?0	00?0A1A3?0	2011111100	?00A210-0?	00--411A11	2040100012	0401000120
Stomatopoda	1010100110	2010111100	-000111110	0001210300	2001000100	0101100-11	10--310001	0-31000010	-31000010-
Tanaidacea	1100110200	00001112A1	0?10000001	01001A1300	E001111100	?00A200-01	10--311111	2040000010	-40A00010-
Thermosbaenacea	1110110100	000A010-0-	----???0?1	0000A1-3?0	2011111100	?001211010	0100111101	0-40000012	0400000120

	100	110	120	130	140	150	160	170
Acanthotelson	4100000--?	??00000000	00-0011001	0111010100	00????????	?0????????	?????0????	??????????	???????
Aeschronectida	300000---?	??00011010	00-1012011	0111000100	??????????	??????????	?????0????	??????????	???????
Amphionidacea	300001---0	0000000011	00-0011001	0111010100	?0????????	?1111????0	??1?001110	050?????-?	???????
Amphipoda	4110001102	A0001--011	010A133002	1021010100	1001011130	1112020--1	00100002-1	A4122-0101	1000002
Anaspidacea	4200000--0	0100000000	00-0031001	01110A0100	10011100-0	0110041110	21100202-1	0002000001	000001?
Angustidontus	C?????????	??0?000000	00?10????1	0111010100	??????????	??1???????	?????0????	??????????	???????
Anostraca	1200000--2	2000011000	00-02---0-	--001020-0	00?00000-?	?000000--0	000?10000B	00021002-?	??11000
Bathynellacea	2100000--0	0000011000	?0-02---02	0110100201	?0?1??????	?101150--0	??1?000111	000????0?-?	???????
Belotelsonidea	4??1??????	??0?1--0-1	0000011001	0111100100	??????????	??????????	?????0????	??????????	???????
Bochusacea	D01000-1?2	1001000001	10011AA001	1211010100	1?????????	?11?0?????	??1?0002-?	14????????	???????
Brachypoda	5100000--2	2000000000	00-02---0-	--001020-0	?0?00000-?	?00?????0	00??000001	010?????-?	??000?3
Caridea	400001---0	0010000000	00-0011101	0111030100	1111111100	0111111100	2111001111	020A0000-1	0010010
Cumacea	401000-112	1000000001	0001112002	0211030B0A	0001111142	?1A1140--1	?01?0002-1	1410111111	1000002
Dendrobranchiata	4100110--0	0010011100	00-0011001	0111030100	1111111100	0111111100	2110020102	00022-00-0	-?00A13
Euphausiacea	4100001--0	0000011000	00-0011001	0211100100	1111111?0	0111131110	2110001102	00020000-0	-0101A?
Euzygida	4100110--0	0010000100	00-0011101	0111020110	1111111102	?11?1????1	2111000111	0201????-?	??100??
Isopoda	401000-012	10001--011	011112101A	1011010C21	0001011141	11A10310-1	00100002-1	1412111111	1100002
Leptostraca	3100000--2	??00001010	00-0112000	--00101001	00?00000-0	0100000--1	00100012-1	0100000001	0011010
Lophogastrida	4110001001	1100000000	1011133001	0211010100	1011111112	?111021111	21100002-1	040?110???	???????
Mictocaris	401000-1?2	1001000011	1011111001	1211010100	?0????????	?1A1040--?	??110002-?	14????1???	???????
Mysida	40A000-001	1100000000	10AAA11001	02110B0100	1111111120	1111031111	21100002-1	0400110101	1100012
Notostraca	1100000--2	2000011000	10-01---0-	--00102000	00?00000-?	?011000--0	000?1?000?	000?????-?	??11000
Palaeocaris	4100000--?	??00000000	00-0033001	0111010100	00????????	??1???????	?????0????	??????????	???????
Procaridea	4100010--0	0000000000	00-0031101	0111020100	11?1111100	01111?????	211?001111	020?000?-?	??10010
Pygocephalomorpha	300000---?	??00000000	10-0?????1	0211120100	??????????	??????????	??????????	??????????	???????
Reptantia	4101100--0	00100--100	10-0011101	0111030110	1111111100	0111121101	2111021111	020A0000-1	000A11E
Spelaeogriphacea	401000-1?2	100AA1A0AA	0011111001	0211010B00	00?1???14?	?111030--?	10110002-?	14????????	???????
Stomatopoda	3100000--0	0?00A--010	?0-0011011	0211030100	1111011100	01100010-1	1010011111	01000000-0	-000111
Tanaidacea	40A000-112	A000000000	000AA11002	0211010B20	0001111141	1101030--1	00100002-1	1411111110	-10000?
Thermosbaenacea	400000---2	1000000000	00-0210001	021101020A	1001101041	1101140--0	011?0002-?	A301000121	10?????