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Advances in Crustacean Phylogenetics*

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* The title refers to a symposium held in Rostock from 7th–11th October 2008 organized by the authors. The symposium comprised 23 invited lectures and 46 posters on different aspects of crustacean phylogenetics. Papers published in this and the previous issue of 'Arthropod Systematics & Phylogeny' are based on lectures given at the meeting.

> Abstract

150 years after Darwin's 'Origin of Species' and 100 years after W.T. Calman's influential treatment on crustacean morphology and classification, crustacean phylogenetics remains an active, exciting and controversial field of research. An international symposium held from 7th–11th October 2008 at the University of Rostock attempted to summarize the latest developments. Molecular evidence suggests that crustaceans are paraphyletic with regard to the hexapods, though a few potential apomorphies of Crustacea can still be named. If Crustacea do turn out to be paraphyletic, the name should disappear from formal classifications, as simply including hexapods in the group would be tantamount to ignoring the different research histories. Nevertheless, 'crustaceans' will remain a colloquial term and crustaceanology (carcinology) an important field of research. Within crustaceans, Branchiopoda and Malacostraca are well supported monophyla. While the internal phylogeny of Branchiopoda seems almost to be settled, it is still highly controversial within Malacostraca, in particular with regard to the peracarid taxa. The same can be said of the Decapoda. It remains uncertain whether the Maxillopoda is monophyletic, and while the monophyly of the Thecostraca is well supported, the origin of Rhizocephala remains enigmatic. Advances have been made in applying molecular systematic techniques to almost all crustacean taxa, but morphological research has also moved on. New morphological techniques provide new insights in our understanding of evolutionary transformations.

> Key words

Evolutionary morphology, phylogenetics, classification, Tetraconata.

1. 150 years of crustacean evolutionary research

This year we celebrate 150 years of Darwinian evolutionary theory based on the publication of the first edition of the 'Origin of species' in November 1859. In 1864, Fritz Müller, in his famous book 'Für Darwin' (English version: 'Facts and Arguments for Darwin'), summarized arguments in favor of the Darwinian 'descent with modification', based entirely on examples from crustaceans. His study can be seen as the birth of crustacean evolutionary research. The first phylogenetic tree of crustaceans (Fig. 1) was drawn by Ernst Haeckel (1866) and the first detailed account written by Carl Claus (1876). J.E.V. Boas was another important figure in crustaceology, providing detailed phylogenetic accounts of Decapoda (1880) and Malacostraca (1883). Hansen (1893) contributed not only to crustacean classification, but also opened the way for discussions of correspondences between crustacean and hexapod limbs. It was W.T. Calman, however, in his major account from 1909, who provided the classification of Crustacea that is still widely accepted today. 150 years after Darwin and 100 years after Calman, then, it seems fitting to ask: quo vadis crustacean phylogenetics? An international symposium held from 7th–11th October 2008 at the University of Rostock at-

tempted to provide answers, almost 20 years after the last meeting dedicated to crustacean phylogenetics in 1990 in Kristineberg (Sweden). In this paper we summarize and discuss the latest developments based partly on the papers presented at the Rostock meeting.

2. Is Crustacea monophyletic?

The obvious central question when dealing with crustacean phylogenetics concerns crustacean monophyly. Crustaceans are easily distinguished from other arthropods by the simultaneous presences of diagnostic characters such as two pairs of antennae, mandibles and two pairs of maxillae (SCHRAM 1986; SCHRAM & KOENEMAN 2004). However, these features cannot serve as justification for crustacean monophyly because the mouthparts are shared by all mandibulates and the presence of a second pair of antennae represents a plesiomorphic state within mandibulates, which does not necessarily imply that its absence represents a synapomorphy of Myriapoda and Hexapoda. Toward the end of the 20th century, LAUTERBACH (1983) applied the methodology of phylogenetic systematics introduced by HENNIG (1950, 1966); he identified apomorphies for Crustacea and thus corroborated their monophyly. These apomorphies are the presence of two pairs of nephridia (antennal and maxillary) and of a nauplius eye. Later, WALOSSEK (1999) added several additional characters such as a 'fleshy labrum' to the list of crustacean apomorphies, and used these to distinguish between stem lineage and crown-group crustaceans (see WALOSSEK & MÜLLER 1990). Although those characters are not unambiguous in their interpretation, the monophyly of crustaceans was never challenged in the pre-molecular phylogenetic era. The earliest numerical cladistic analyses also supported this view (SCHRAM 1986; WILSON 1992). The few morphology-based cladistic analyses to have been conducted in recent years still support crustacean monophyly (EDGECOMBE 2004; GIRIBET et al. 2005). An important exception is the study by MOURA & CHRISTOFFERSEN (1996), who suggested that Remipedia is the sister group to tracheates on the basis of purely morphological evidence.

During the 1990s, however, phylogenetic analyses based on molecular data (colloquially termed 'molecular phylogenies') changed our view drastically. Most notably, crustaceans were recognized as the closest relatives of hexapods (FRIEDRICH & TAUTZ 1995), thus challenging the long held opinion that hexapods and myriapods form a monophylum. This closer relationship of crustaceans and hexapods found widespread support in the form of other molecular-based (e.g., BOORE et al. 1998; MALLATT & GIRIBET 2006; PODSIADLOWSKI et al. 2008; DUNN et al. 2008; REGIER et al. 2008) and combined analyses (GIRIBET et al. 2001, 2005), and was also backed up by morphological characters (DOHLE 2001; RICHTER 2002). The new finding attracted the attention of many scientists and led to the suggestion of two different names for a group comprising crustaceans and hexapods: Pancrustacea (ZRZAVÝ & ŠTYS 1997), and later Tetraconata (DOHLE 2001). We will return to the discussion on names later. At the same time, some of the apomorphies that had been considered supporting the monophyly of Tracheata were found to be highly ambiguous: homologues of the Tömösvary organs (temporal organs) might also occur among Malacostraca (KLASS & KRISTENSEN 2001), and head apodemes in the same position as the anterior (and posterior) tentorial arms are also present in various Malacostraca (see KLASS 2007, in press). Nowadays, all new 'molecular phylogenies' consistently result in a monophyletic Tetraconata, including those based on over 100 genes (DUNN et al. 2008). We regard this relationship to be generally accepted and highly probable.

On the other hand, these findings for the first time seriously questioned crustacean monophyly, as all molecular-based analyses resulted in paraphyletic crustaceans. Analyses of mitochondrial genome data even suggest that hexapods and crustaceans are mutually paraphyletic to each other (COOK et al. 2005; CARAPELLI et al. 2007). This finding *per se*, i.e., the paraphyly of crustaceans, however, is difficult to assess further at the moment as different taxa appear as sister groups to hexapods. Analyses with increased crustacean taxon sampling supported various relationships (GIRIBET et al. 2001, 2005; MALLATT & GIRIBET 2006; PODSIADLOWSKI et al. 2008). At one stage, the balance seemed to tip towards the branchiopods (a scenario also favored by the most extended phylogenomic approach carried out to date, by DUNN et al. 2008). This led to the proposal of a freshwater origin of hexapods (GLENNER et al. 2006a). On the other hand, neuroanatomical characters still favor malacostracans (together with remipeds) as the preferred sister group of hexapods (FANENBRUCK et al. 2004; HARZSCH 2006, 2007). Remipedia are interesting not only on the grounds of the neuroanatomical characters mentioned, but also because of the presence of a hemocyanin similar to that in hexapods (ERTAS et al. in press). In the most extensive study to date, with regard to both terminal taxa and molecular loci, REGIER et al. (2008) found remipeds and cephalocarids to be closest to hexapods.

Although the last word has certainly not been spoken, we will probably have to accept that Crustacea may be paraphyletic. If 'Crustacea' in the way the taxon has been recognized for at least the last 100 years is not monophyletic, the term should be eliminated from phylogenetic nomenclature. In our view,

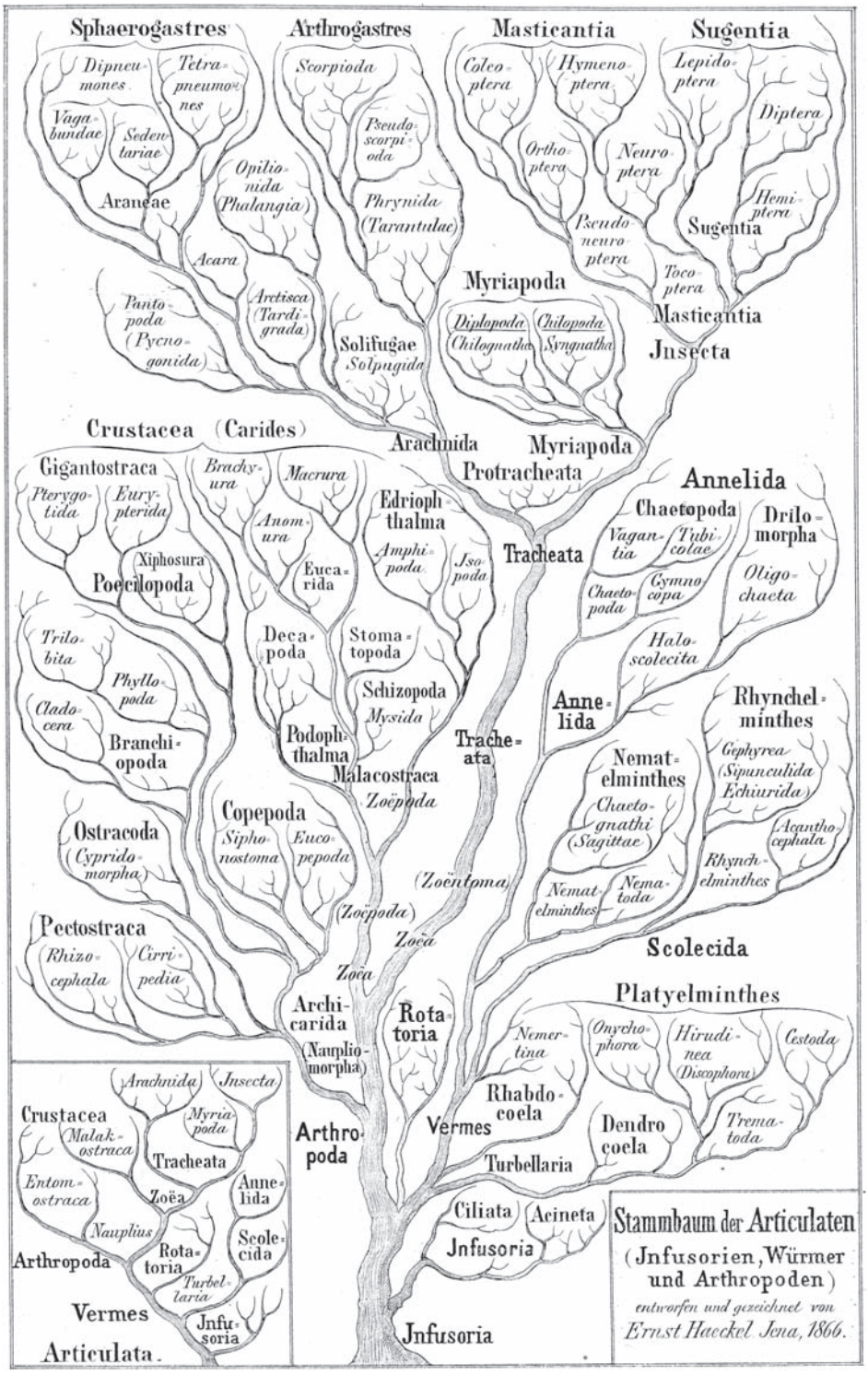

Fig. 1. 'Phylogenetic Tree' from HAECKEL (1866). With permission of the Ernst Haeckel Haus, Jena.

including Hexapoda in Crustacea is not plausible, as this would be to ignore over a century of independent research history (see also SCHRAM & KOENEMAN 2004). The colloquial use of the term 'crustaceans', which might still be of value to the community of crustaceologists (or carcinologists), should not be ruled out. The only exception that might be feasible concerns the Remipedia, which were discovered late in the history of crustaceology. If they turn out to be the sister group to hexapods with all remaining crustaceans forming a monophyletic clade, the latter could still be termed Crustacea in order to maintain taxonomic stability. As mentioned above, there is some disagreement about the proper name for a clade comprising all recent crustaceans and hexapods. Pancrustacea was the first name suggested (ZRZAVÝ & ŠTYS 1997; ZRZAVÝ et al.

1998), with the name Tetraconata introduced by DOHLE (2001) a few years later. Both terms have been used more or less equally often (REGIER et al. 2008; DUNN et al. 2008). We favor Tetraconata because Pancrustacea might easily be confused with Pan-Crustacea, a term that implies monophyletic crustaceans including their stem lineage representatives. The prefix 'pan' was suggested by LAUTERBACH (1989) to distinguish more comprehensive groups from their crown groups (crown groups are understood in this concept as taxa including both the last common ancestor of all extant species and all its descendants). This approach has not found many advocates (but see MEIER & RICHTER 1992), but has recently been adopted by the proponents of the PhyloCode (e.g., DE QUEIROZ 2007). Regardless of how widely the PhyloCode will be accepted, the parallel use of Pan-Crustacea and Pancrustacea will create confusion. A last word on the use of Tetraconata: the discovery that crystalline cones are made up of four cone cells (MÜLLER et al. 2003) in scutigeromorph chilopods, too, might appear to make the term unfortunate. In actual fact, in scutigeromorphs the splitting of the cone cells means the cones are made of more than four partitions, which leaves tetrapartite cones an exclusive character of crustaceans and hexapods, although derivations from this pattern are known (RICHTER 2002).

3. Are high rank crustacean taxa monophyletic?

If crustacean monophyly is uncertain, at best, where do we find firm ground? MARTIN & DAVIS (2001), in their seminal paper 'An updated classification of the Recent Crustacea', distinguished six higher taxa which they categorized as classes: Branchiopoda, Cephalocarida, Remipedia, Malacostraca, Maxillopoda and Ostracoda. Remipedia and Cephalocarida are two still enigmatic groups comprising relatively few species with unique morphologies, but as they were only described in the second half of the 20th century, phylogenetic research is just about to start. Within Remipedia, a first phylogenetic study on internal relationships (KOENEMANN et al. 2007a) coupled with mainly taxonomic research is greatly enhancing our knowledge (e.g., KOENENMANN et al. 2007c, 2008). Post-embryonic development in Remipedia has recently been unraveled too (KOENEMANN et al. 2007b, 2009). Also within Cephalocarida a first phylogenetic study has been undertaken (CARCUPINO et al. 2006) and our knowledge of the anatomy of *Hutchinsoniella macaracantha* is substantial at least, thanks to the impressive works by R.R. Hessler and R. Elofsson (e.g., ELOFSSON & HESSLER 1990; HESSLER & ELOFSSON 2001). Nonetheless, both Remipedia and Cephalocarida are generally thought to be monophyletic due to their uniform overall morphology. The taxa appear as sister groups in some molecular-based analyses (GIRIBET et al. 2001; REGIER et al. 2008), but whether this relationship represents some kind of 'long branch attraction' artifact in the analyses or actually reflects a real phylogenetic signal remains to be established.

Branchiopoda seems to be a well supported monophylum. All 'molecular phylogenies' based on various combinations of taxa support its monophyly (SPEARS & ABELE 1998, 1999, 2000; GIRIBET & RIBERA 2000; SHULTZ & REGIER 2000; REGIER et al. 2005), and the morphological support is also strong (OLESEN 2007). Although suggestions of branchiopod paraphyly have been rare, the idea has unfortunately found its way into some widely used textbooks (GRUNER 1993; AX 1999; RUPPERT et al. 2004). Data from the fossil record has contributed significantly to establishing the monophyly of the Branchiopoda, placing the earliest branchiopods in the Upper Cambrian (WALOSSEK 1993). A general consensus has been reached on the internal branchiopod relationships, with a monophyletic Cladocera and paraphyletic conchostracans being the main results but with the exact position of Notostraca and Laevicaudata still being unanswered (MØLLER et al. 2003; STENDERUP et al. 2006; RICHTER et al. 2007). OLESEN (2009) provides an excellent review of the relationships within the Branchiopoda, which may be the first higher crustacean taxon whose major evolutionary steps we will understand.

Malacostracan relationships are far more difficult to assess. Although their monophyly is well supported by morphological and molecular data (RICHTER & SCHOLTZ 2001; GIRIBET et al. 2005; MALLATT & GIRIBET 2006; REGIER et al. 2008), internal relationships are highly controversial. At least the position of Leptostraca as the sister group to the remaining Malacostraca (Eumalacostraca) is now widely accepted (despite SCHRAM & HOF 1998 appearing as the latest proponents of a closer relationship between leptostracans and branchiopods). Within Eumalacostraca, not only do studies based on morphological data contradict each other with regard to the monophyly of the high ranked taxa such as Eucarida (Decapoda plus Euphausiacea), Peracarida (Amphipoda, Isopoda and their allies) and Syncarida (Anaspidacea plus Bathynellacea), molecular phylogenies (SPEARS et al. 2005; MELAND & WILLASSEN 2007) and combined analyses (JENNER et al. 2009) also fail to give a clearer picture. WILLS et al. (2009), however, show that the inclusion of fossil taxa might help to clarify the situation, although broader taxon and gene samplings are also obvious requirements.

Basal splits within Eumalacostraca are especially unclear, greatly hampering evolutionary analyses. Dif-

ferent studies have suggested Stomatopoda (Siewing 1956; Richter & Scholtz 2001), Bathynellacea (Jenner et al. 2009), and a taxon composed of Stomatopoda, Mysida and Euphausiacea (Meland & Willassen 2007) as the sister group to the remaining eumalacostracans. Another minefield is the discourse on the monophyly of the Mysidacea (Lophogastrida plus Mysida). Classically considered the monophyletic sister group to the remaining peracarids (Siewing 1956; Richter & Scholtz 2001; Wirkner & Richter in press), they have also been suggested to be a paraphyletic grade on morphological evidence (Kobusch 1999; Watling et al. 2000) or even completely dissociated from each other on molecular grounds (Spears et al. 2005; Meland & Willassen 2007). A topic closely related to this is the question of the monophyly of Peracarida. While molecular data (Spears et al. 2005; Meland & Willassen 2007) do not corroborate monophyly, morphological data do (Richter & Scholtz 2001; Poore 2005; Wirkner & Richter in press). In the case of peracarid polyphyly, however, important characters such as the presence of oostegites and breeding the young in a marsupium, the presence of a lacinia mobilis in the adults and a row of a variable number of ectoteloblasts would have to be explained as convergencies. It also remains to be established whether Thermosbaenacea is the sister group of Peracarida (Richter & Scholtz 2001) or nested within them (Poore 2005; Wirkner & Richter in press). We suggest that the taxon name Peracarida should be protected in both cases for the entire clade, independently of the exact position of Thermosbaenacea.

Also notoriously difficult are relationships within Peracarida. The question of whether or not amphipods and isopods together form a monophyletic clade is particularly disputed (Siewing 1956; Schram 1986; Richter & Scholtz 2001). Any support for such a clade, named Edriophthalma by Leach (1814), and most recently provided by Poore (2005), has continuously been challenged. Wirkner (2009) provides new characters, including some from the circulatory system, which represent new arguments for a mancoid clade as proposed by Siewing (1956) but which place cumaceans (and not tanaidaceans) as the sister taxon to isopods (see also Wirkner & Richter in press). It is perhaps worth noting that this relation is also the one suggested by some molecular evidence (Spears et al. 2005). Using direct optimization and a combined approach Wilson (2009) also provides arguments for a mancoid clade, but regards tanaidaceans as the closest relatives of isopods, which reflects the original idea put forward by Siewing (1956). Tanaidaceans themselves need special treatment as the high number of homoplastic features they possess hampers their phylogenetic analysis. New approaches to resolving tanaidacean relationships as presented by Bird & Larsen (2009) are therefore of huge importance and very welcome. The monophyly of Stomatopoda and Decapoda has not been challenged so far. Whereas with regard to stomatopod phylogeny morphological and molecular data seem to be converging, as convincingly shown by Ahyong & Jarman (2009), decapod relationships remain more controversial. Nevertheless, the basal position of the 'natant' taxa and the monophyly of Reptantia now seem to be well supported by both morphological and molecular data (Scholtz & Richter 1995; Tsang et al. 2008; Ahyong & O'Meally 2004; Bracken et al. 2009). On the other hand, as shown by the impressive data set provided by Bracken et al. (2009), the anomalan/anomuran-brachyuran clade (Meiura Scholtz & Richter 1995), which is well supported by morphological data (Dixon et al. 2003), is not supported by the most recent molecular analyses. The holy grail of decapod phylogeny, the position of Lithodidae – the tale of the hermit who became a king (or vice versa) – is still discussed controversially, as Lemaitre & McLaughlin (2009) show.

Maxillopoda and Ostracoda remain the most controversial 'classes', starting with the question of whether ostracodes are actually part of Maxillopoda (Brusca & Brusca 1990). Maxillopodan monophyly has been suggested on the basis of morphological characters (Dahl 1956; Boxshall & Huys 1989; Walossek & Müller 1998). So far, no molecular-based analyses support maxillopodan monophyly with or without ostracodes, but it must be borne in mind that taxon sampling within the group has been limited so far, typically with only a few taxa for each of the maxillopodan lineages (Giribet et al. 2005; Mallatt & Giribet 2006; Regier et al. 2005, 2008).

Within Maxillopoda, Thecostraca is a now a well founded taxon, as argued by Høeg et al. 2009b (see also Pérez-Losada et al. 2009; Høeg et al. 2009a). It comprises not only barnacles (Cirripedia) but also Ascothoracida, Acrothoracica and Facetotecta, until recently only known as 'y-larvae'. An important step in advancing our knowledge of Facetotecta was made by Glenner et al. (2008), who, by inducing moulting in the y-cypris, identified the subsequent stage as slug-like and most probably specialized for endoparasitism, hinting at the convergent development of endoparasitism in the Thecostraca (Pérez-Losada et al. 2009). Several aspects of the phylogenetic relationships between Cirripedia are still unresolved. One of the contentious issues is the position of the parasitic Rhizocephala, most often considered as the sister group to a monophyletic Thoracica (Pérez-Losada et al. 2009; Høeg et al. 2009a,b). On the other hand, Scholtz et al. (2009) provide evidence that Thoracica might be paraphyletic with regard to Rhizocephala. The early cleavage patterns of two kentrogonids, *Sacculina* and *Peltogasterella,* are apparently very similar to those

described for the thoracican *Ibla quadrivalvis*. The position of *Ibla*, however, is by no means certain, as morphological and molecular data often disagree here (HØEG et al. 2009a,b). Within Rhizocephala, the monophyly of the traditionally accepted group Kentrogonida has also been questioned recently, whereas Akentrogonida seems to be well supported (GLENNER & HEBSGAARD 2006).

Other higher maxillopodan taxa, such as Copepoda, Mystacocarida and Ostracoda (if counted as Maxillopoda), remain somewhat separate. Even the monophyly of ostracodes has been disputed, with Myodocopa and Podocopa potentially representing separate lineages (REGIER et al. 2008). This could be explained by highly divergent evolutionary rates within the ostracodes, but still needs to be clarified (TINN & OAKLEY 2008). The monophyly of Copepoda is generally accepted (BOXSHALL & HALSEY 2004; DAHMS 2004; REGIER et al. 2008), and a sister group relationship between Copepoda and Mystacocarida has been discussed (BOXSHALL & HUYS 1989; WALOSSEK & MÜLLER 1998) but no further evidence has been provided since then. An interesting case is made for Branchiura, as elaborated by MØLLER (2009). The monophyletic status of the group was established on the basis of morphological evidence by MARTIN (1932). When WINGSTRAND (1972) discovered the high level of similarity between branchiuran and pentastomid sperm, most zoologists regarded the findings as an interesting case of convergence as pentastomids were seen as basal (prot-)arthropods (e.g., OSCHE 1963), a view that is still considered by some (MAAS & WALOSZEK 2001; WALOSZEK et al. 2006). A position completely outside the Arthropoda has also been suggested for pentastomids (ALMEIDA et al. 2008), but STORCH & JAMIESON (1992) presented further spermatological evidence for the inclusion of the Pentastomida in the Crustacea, and this has also been supported by molecular evidence (ABELE et al. 1989; PETERSON & EERNISSE 2001; ZRZAVÝ 2001; LAVROV et al. 2004). Now, with better in-group sampling of both Branchiura and Pentastomida, the inclusion of pentastomids within Crustacea is widely accepted, and MØLLER et al. (2008) placed them as the sister group to a monophyletic Branchiura, thus confirming the Ichthyostraca (see also ZRZAVÝ 2001).

In all crustacean taxa, effort has been made to shed light on phylogenetic relationships, yet many questions remain open. Interestingly enough, the contribution of molecular data varies between taxa, a phenomenon which is partly but not only due to highly disparate taxon sampling. The molecular data used so far seem to provide phylogenetic signals to a different extent in the various groups, often in ways not predictable on the basis of available knowledge regarding sequence and gene evolution. Enigmatically, the same molecular loci provide convincing evidence for the relationships within branchiopods and fail to do so for malacostracans, where relationships remain challenging and disconcerting.

4. Advances in crustacean research

Cladistic methodology and, in particular, 'molecular phylogenies', have revolutionized our understanding of crustacean phylogenetic relationships. Nevertheless, important advances have also been made in crustacean evolutionary morphological research. New techniques such as immunohistochemistry and confocal laser scanning microscopy (cLSM) as well as micro-computertomography (Micro-CT) in combination with computer based 3D reconstruction continue to provide completely new insights into the anatomy of various crustacean taxa. Advances in classical light microscopy, SEM and TEM have proven that these techniques are still useful (see articles by BOXSHALL & JAUME 2009; OLESEN 2009; HØEG et al. 2009b). The crustacean nervous system has been a particular focus in recent years, with exciting new results (HARZSCH 2006, 2007) following up the impressive works by N. Holmgren and B. Hanström (e.g., HOLMGREN 1916; HANSTRÖM 1947). The circulatory system has received renewed careful attention (WIRKNER 2009; WIRKNER & RICHTER in press) over 50 years after the seminal studies by R. Siewing (e.g., SIEWING 1956, 1963). As SCHOLTZ et al. (2009) show, early development such as cleavage pattern and gastrulation still contribute to our knowledge of the disparity of crustacean morphology. In recent studies, '4D microscopy' (i.e., adding the dimension of time to the spatial dimensions) has proven to be an important tool (WOLFF & SCHOLTZ 2006). However, the use of morphological research in an evolutionary context requires more than advances in morphological techniques. Investigating morphology requires careful description and equally careful interpretation. In an evolutionary framework, however, interpretation of morphological disparity includes a careful conceptualization of characters that is based on a detailed discussion and estimation of potential homology (RICHTER 2007; WIRKNER & RICHTER in press). Clear definitions formalized as ontologies are a necessary tool for establishing better comparability, transparency and objectivity in morphological research (RAMIREZ et al. 2007; VOGT 2009). To what extent these ontologies should depend on homology assumptions is disputed (EDGECOMBE 2008; VOGT 2008). After 150 years of studying crustacean evolution, however, it is not going to be possible to present descriptions of morphological features in a way completely devoid of evolutionary assumptions. We are also convinced that

morphological characters resulting from careful studies can contribute substantially to phylogenetic analyses, even if these are dominated by molecular data (see also SUDHAUS 2007). Maybe even more importantly, morphological studies are indispensable to our understanding of evolutionary transformations. Character distribution over terminals and a branching pattern resulting from a cladistic analysis are two sides of the same coin, and both are more or less meaningless without the other. This is not to deny the importance of phylogenetic hypotheses (which are often exclusively based on molecular data) in the interpretation of biogeographic patterns or ecological transformations.

One of the most exciting and controversial areas of interpretation of morphological disparity concerns crustacean (or more generally arthropod) limbs, as illustrated by BOXSHALL & JAUME (2009) and MAAS et al. (2009), both of whom emphasize the importance of including fossil taxa. Crustaceans possess various kinds of limbs, most notably characterized as stenopodous or phyllopodous. Both types are biramous and consist of two branches, an exopod and an endopod. A transformation series between phyllopodous and stenopodous limbs has been suggested within branchiopods (OLESEN et al. 2001). Throughout the crustaceans, however, the homology of these different leg types and the elements they contain is highly controversial. The same applies to the appendage and podomere homologies between crustaceans and other arthropods. Apparently independently of homology assumptions, the elements have either been named differently in different arthropods (basis, ischium, merus, carpus, propodus, dactylus vs. trochanter, femur, patella, tibia, tarsus), or been given the same name, as in the case of the 'coxa', whose homology status is uncertain (WALOSSEK 1993). Considering crustacean taxa only, 'epipodites' might be a comparably controversial issue (BOXSHALL & JAUME 2009; MAAS et al. 2009). Compiling an ontology of arthropod limbs would certainly help us to understand their disparity.

5. Conclusions

Crustacean phylogenetics is once again in the focus of evolutionary research. The idea that insects are nothing other than terrestrial crustaceans is a fascinating one that is receiving more and more support. Even if crustaceans turn out to be paraphyletic, we doubt that the affection which crustaceanologists feel for their group will change one bit! New techniques, new questions and new answers have arisen over the last 150 years and will arise in the next centenary. We know a lot, but there is still so much to find out. Crustacean phylogenetics will remain an exciting field for generations to come. The participation of so many young scientists in our symposium was a promising sign of that. Crustacean phylogenetics is cutting edge science and does not require general agreement. Indeed, disagreement encourages advances in science!

6. Acknowledgements

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8. Appendix

Invited lectures given at the symposium 'Advances in Crustacean Phylogenetics' held in Rostock from 7th–11th October 2008:

Boxshall, G.A. (London, United Kingdom): Comparative morphology of exopodites and epipodites.
Brandis, D. (Kiel, Germany): Pleopods as sperm transfer organs: gonopods and their implications for decapod phylogeny.
Crandall, K. (Provo, Utah, USA): The phylogenetic diversity of the decapod crustaceans.
Edgecombe, G.D. (London, United Kingdom): The place of arthropods in the Tree of Life: evidence from molecules, morphology and fossils.
Harzsch, S. (Jena, Germany): Can characters derived from nervous system architecture contribute to reconstructing arthropod phylogeny?
Høeg, J.T. (Copenhagen, Denmark), M. Perez-Losada & K. Crandall (Provo, Utah, USA): Phylogeny of thecostracan Crustacea: Evolution of larvae, sessility, parasitism and growth.
Huys, R. (London, United Kingdom): Maxillopodan conundrum: insights from SSU rDNA and Bayesian inference.
Jenner, R.A., C. Ní Dhubhghaill & M.A. Wills (Bath, United Kingdom): Molecular and morphological approaches to eumalacostracan phylogeny.
Larsen, L. (Recife, Brazil) & G. Bird (New Zealand): Tanaidacean phylogeny: where we stand and where we go from here.
Lemaitre, R. (Washington D.C., USA) & P.A. McLaughlin (Anacortes, Washington, USA): Recent conflicts in anomuran phylogenetic assessments and possible interpretations.
Martens, K. & I. Schoen (Brussels, Belgium): Are Ostracoda monophyletic?
Martinez-Arbizu, P. & H.-K. Schminke (Oldenburg, Germany): Phylogeny of Copepoda – A review.
Meland, K. & M. Porter (Bergen, Norway): The polyphyletic Mysidacea: Will the Peracarida ever be the same again?
Møller, O.S. (Rostock, Germany): Branchiuran phylogeny – ontogeny, morphology and molecules.
Olesen, J. (Copenhagen, Denmark): Branchiopod phylogeny – status and future challenges.
Poore, G. (Melbourne, Australia): Callianassidae and related families – a revised classification based on phylogeny (Thalassinidea).
Richter, S. (Rostock, Germany): Evolutionary morphology of compound and nauplius eyes in Crustacea.
Scholtz, G. (Berlin, Germany): Developmental characters and crustacean evolution.
Tudge, C.C. (Washington D.C., USA): Decapod phylogeny: a unique spermatological perspective.
Wägele, W., B. von Reumont & K. Meusemann (Bonn, Germany): Phylogenetic signal and noise in alignments.
Waloszek, D. (Ulm, Germany): Early crustacean evolution and the question of the appearance of epipodites/gills.
Wilson, G.D.F. (Sydney, Australia): Isopoda and the Peracarida – a total evidence study of their phylogeny.
Wirkner, C.S. (Rostock, Germany): Evolutionary morphology of the circulatory system in Malacostraca.

Fig. 2. Participants at the International Symposium 'Advances in Crustacean Phylogenetics' held in Rostock from 7th–11th October 2008. 1 Klaus-Dieter Klass; 2 Wolfgang Wägele; 3 Ole Larsen; 4 Martin Stegner; 5 ?; 6 Matz Berggren; 7 Dieter Waloszek; 8 Davide Maruzzo; 9 Charlotte Havermans; 10 Andreas Brösing; 11 Lars Podsiadlowski; 12 Carola Becker; 13 Johannes Dammbach; 14 Maria Belyaeva; 15 Thorid Zierold; 16 Terue Kihara; 17 Gregory Edgecombe; 18 Stefan Richter; 19 Jens Runge; 20 Björn von Reumont; 21 Christian Bauer; 22 Gerhard Scholtz; 23 Kenneth Meland; 24 Endre Wilassen; 25 Keith Crandall; 26 George Wilson; 27 Jens Hoeg; 28 Christoper Castellani; 29 Ronald Jenner; 30 Mathew Wills; 31 Christian Foth; 32 Heather Bracken; 33 Anne-Helene Tandberg; 34 Joana Matzen da Silva; 35 Anastasia Laggis; 36 Kalliopi Vasileiadou; 37 Kuldar Koiv; 38 Marlen Klann; 39 Ekaterina Ponomarenko; 40 Laura Pavesi; 41 Vera Hunnekuhl; 42 Shen Hong; 43 Gary Poore; 44 Christian Wirkner; 45 Kim Larsen; 46 Christian Schmidt; 47 Ole Møller; 48 Andrej Fuchs; 49 Günther Jirikowski; 50 Tino Pabst; 51 Carsten Wolff; 52 Francesco Paoli; 53 Leonardo Pileggi; 54 Thomas Harvey; 55 Luis Hernandez; 56 Fernando Mantelatto; 57 Chris Tudge; 58 Moritz Sonnewald; 59 Ekaterina Skolotneva; 60 Rafael Lemaitre; 61 Gregory Kolbasov; 62 Andreas Maas; 63 Jörgen Olesen; 64 Fabian Kilpert; 65 Martin Schwentner; 66 Martin Fritsch; 67 Susanne Böx; 68 Stephan Scholz; 69 Jonas Keiler; 70 Matthias Nuss; 71 Georg Brenneis; 72 Katarina Huckstorf; 73 Koen Martens; 74 Stefania Maniatsi; 75 Athanasios Baxevanis; 76 Theodore Abatzopoulos; 77 Steffen Harzsch; 78 Valerio Kettmeier; 79 Günther Pass; 80 Nikolaus Szucsich; 81 Cedric d'Udekem d'Acoz; 82 Geoffrey Boxshall; 83 Rony Huys.

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