

The Tetraconata concept: hexapod-crustacean relationships and the phylogeny of Crustacea**

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Abstract

A growing body of evidence indicates that Crustacea and Hexapoda are sister groups, rather than Hexapoda and Myriapoda. Some recent molecular data even suggest that Mandibulata is not monophyletic, with Myriapoda and Chelicerata instead being sister groups. Here, arguments for homology of the mandible throughout mandibulate arthropods and for a monophyletic Mandibulata will be presented, as well as arguments supporting the taxon Tetraconata (i.e. Crustacea + Hexapoda). The latter include molecular data (nuclear and mitochondrial ribosomal RNAs and protein coding genes), and morphological characters such as ommatidial structure, the presence of neuroblasts and a very similar axonogenesis of pioneer neurons. However, crustaceans are insufficiently sampled for the molecular data, and studies of neurogenesis are lacking for many crustacean taxa. Remipedia, Cephalocarida and Maxillopoda are particularly problematic. This is important for the entire problem, because monophyly of the Crustacea has not yet been proven beyond doubt and several molecular analyses suggest a paraphyletic Crustacea. Here, arguments for the monophyly of the Crustacea are reviewed and two alternatives for the relationships between the five higher taxa Remipedia, Cephalocarida, Maxillopoda, Branchiopoda and Malacostraca are discussed: the Entomostraca concept sensu Walossek with Malacostraca as sister group to Cephalocarida, Maxillopoda and Branchiopoda, and the Thoracopoda concept sensu Hessler with Cephalocarida, Branchiopoda and Malacostraca forming a monophylum.

Key words: Pancrustacea, *Distal-less*, epipod, compound eye, optic neuropils, proventriculus

Introduction

For many decades it was generally accepted that Hexapoda and Myriapoda are sister groups forming the monophylum Antennata or Atelocerata (e.g., Kraus & Kraus 1994, Kraus 1998, 2001, Kristensen 1998). Characters such as the absence of appendages at the intercalary segment, the tentorial cephalic endoskeleton, the ectodermal malpighian tubules and postantennular organs support this relationship (see, for example, Klass & Kristensen 2001 for a detailed review). Whether Myriapoda is a monophyletic taxon (e.g., Ax 1999, Edgecombe & Giribet 2002), or whether it is paraphyletic with the Progoneata as sister group to the Hexapoda (e.g., Dohle 1980, Kraus & Kraus 1994, Kraus 1998, 2001), is an open point in the context of the Antennata concept.

Beginning in the early 1990s, an increasing number of studies using molecular data (Turbeville et al. 1991, Ballard et al. 1992, Adoutte & Philippe 1993, Friedrich & Tautz 1995; for later references see below) have suggested a sister group relationship between Crustacea and Hexapoda. This relationship also found support from different morphological character complexes (Averof & Akam 1995, Osorio et al. 1995, Whittington 1995). Quite a few reviews have already been published, dealing with different character complexes (Dohle 1997, 1998, 2001, Klass & Kristensen 2001, Kraus 2001, Deutsch 2001, Simpson 2001). A monophylum combining Crustacea and Hexapoda was introduced as Pancrustacea (Zrzavý & Štys 1997) and has been renamed Tetraconata by Dohle (2001) based on the shared unique structure of ommatidia in the compound eyes. Although some of these analyses explicitly suggest different crustacean

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taxa as sister group of the Hexapoda, implying a paraphyletic Crustacea, the phylogenetic relationships of the Crustacea and within them were not the focus of most of the studies and recent reviews dealing with the Pancrustacea/Tetraconata concept (but see Schram & Jenner 2001).

The main issue of this review is to present the arguments for a sister group relationship between Hexapoda and Crustacea with the phylogeny of the Crustacea as background. It will be shown that most characters supporting the Tetraconata are only known for some of the crustacean taxa. In the present paper I adopt as a working hypothesis that Myriapoda is monophyletic, based on the evidence presented by Edgecombe & Giribet (2002), although this monophyly has been questioned repeatedly in the context of the Atelocerata concept (e.g., Dohle 1980, Kraus & Kraus 1994, Kraus 1998, 2001). The Hexapoda is a well established monophylum (e.g., Kristensen 1998).

Not only are relationships within the Mandibulata under debate, but Mandibulata itself has been challenged several times. Old concepts such as the Schizoramia include Crustacea and Chelicerata but exclude Myriapoda and Hexapoda (e.g., Cisne 1974, Bergström 1980), and the Uniramia concept includes Onychophora, Myriapoda and Hexapoda, but excludes Crustacea (e.g., Manton 1973, 1977). Some recent molecular studies also favour the non-monophyly of the Mandibulata, and a sister group relationship between Myriapoda and Chelicerata is postulated (Friedrich & Tautz 1995, Cook et al. 2001, Hwang et al. 2001, Kusche & Burmester 2001, but see Kusche et al. 2002 supporting a monophyletic Mandibulata). Therefore, it seems justified to deal with a few aspects of mandibulate monophyly.

Discussion

Monophyly of the Mandibulata

At least four characters support the monophyly of the Mandibulata (comprising Myriapoda, Crustacea, and Hexapoda): the mandible, the 1st maxilla, ommatidia with crystalline cones (or precursors), and a moulting gland (e.g., Wägele 1993, Ax 1999). Here, I will focus only on the character 'mandible'. There is increasing evidence that not only crustacean mandibles are gnathobasic, but also those of hexapods and myriapods (e.g., Lauterbach 1972, Wägele 1993, Bitsch 2001b), rather than the latter being whole-limb mandibles (e.g., Manton 1964, Fryer 1996, Kraus & Kraus 1994). This means that the gnathal edge is always formed by a process of the proximal part, and not by more distal parts of the mandible. As is the case in several crustaceans, the mandibular palp would have been reduced in myriapods and hexapods. Recent gene expression data of the gene *Distal-less* (*Dll*) – which

plays an important role in arthropod limb development and is expressed in distal parts of arthropod appendages – support homology of the mandibles (e.g., Panganiban et al. 1995, Popadic et al. 1996, 1998, Scholtz et al. 1998, reviewed by Scholtz 2001).

Scholtz et al. (1998) studied the *Dll* expression of several arthropods including malacostracan crustaceans, myriapods and hexapods. In the amphipod *Gammarus pulex*, which develops a mandibular palp, *Dll* expression appears in the early limb bud but in more advanced stages it is restricted to the region of the outgrowth of the mandibular palp. In those malacostracan crustaceans which do not possess a palp, such as the terrestrial isopod *Porcellio scaber* or the amphipod *Orchestia cavi-mana*, *Dll* expression starts early, but during development of the limb bud the expression is restricted to an area that can be interpreted as a vestigial anlage of the palp. The same expression pattern can be found in the diplopod *Glomeris marginata* where also only a temporary expression of *Dll* in a lateral position is present. This expression can also be interpreted as the vestigial anlage of a palp. This implies that also in adult Myriapoda (at least Diplopoda) no distal parts of the mandible are present, and therefore a whole-limb mandible does not exist. In the studied hexapods, *Dll* expression is totally absent, indicating the lack of even a vestige of a palp (e.g., Panganiban et al. 1995, Popadic et al. 1996, 1998, Scholtz et al. 1998). Therefore, the expression pattern of *Dll* strongly supports the hypothesis that myriapod and hexapod mandibles are gnathobasic. This receives some additional support from the expression of *dachshund* in the beetle *Tribolium castaneum* (see Prpic et al. 2001). Based on the similarity in size and expression of *dachshund* in all three gnathal appendages in embryos mutant for *Tc' Dll*, the authors argued for a serial homology of the entire mandible with the coxal parts of maxilla and labium, and the coxae of the legs.

Although we have convincing evidence for gnathobasic mandibles in all mandibulate groups, we still have to ask whether the gnathal part of the mandibles in Myriapoda, Hexapoda and Crustacea is formed by a homologous part of the proximal portion. In Crustacea the mandibular gnathal edge is formed by the coxa which is obvious in examples where both parts of the protopod (coxa and basis) as well as endopod and exopod are present, such as in copepods (e.g., Gruner 1993). In cases where no palp is present (even in early developmental stages), such as in myriapods and hexapods, no definitive decision can be made. According to Walossek (1993, 1999), the coxa of certain crustacean legs has its origin in a so-called 'proximal endite', a lobate endite at the inner proximal edge of the basipodite which is not present in chelicerates. The proximal portion of the chelicerate legs is therefore suggested as being homologous to the crustacean basipodite (Walossek & Müller 1998a).

The exact conditions for the myriapod and hexapod mandibles, however, are an open point in the argumentation of Walossek & Müller (1998b: 203) who admit: "Regrettably, it is not yet possible to recognise either the original basipod-endopod system or a coxa-basipod-endopod system in the uniramous legs of tracheates."

Recent data on expression of the gene *dachshund* in several arthropods (Abzhanov & Kaufman 2000) can be interpreted in a way that one additional proximal limb segment is present in hexapods and crustaceans (two limb segments without *dachshund* expression proximal from two or more segments showing expression) in comparison to chelicerates (one limb segment without *dachshund* expression proximal from two showing expression). This could be an indication that the 'coxae' in hexapods and crustaceans are indeed homologous (for homologies between uniramous and biramous limbs see the review by Bitsch 2001a).

Another phenomenon supporting the homology of the gnathal edges of the mandibles in Crustacea, Myriapoda and Hexapoda is the total absence of *Dll* expression in the corpus mandibularis in advanced stages of embryonic mandibles of certain malacostracans, hexapods and diplopods (Scholtz et al. 1998, Scholtz 2001). This means that in the gnathal part of these mandibles *Dll* is not expressed. The transitory expression of *Dll* in the mandibles in *Glomeris marginata* and in malacostracan crustaceans that lack a mandibular palp is restricted to an area which can be interpreted as the anlage of the palp, whereas in hexapods mandibular *Dll* expression is completely missing. This is in contrast to the conditions in the maxillula and maxilla (labium) where *Dll* might be expressed in the inner lobes as well (Scholtz et al. 1998). A similar *Dll* expression pattern can be seen in the phyllopod branchiopod *Cyclestheria hislopi*. No expression occurs in the gnathal edge of the mandible, but a distinct expression is seen in an area that can be interpreted as the early anlage of the mandibular palp (Fig. 1), al-

though in *Cyclestheria* there is no outgrowing palp in any stages (Olesen 1999). On the other hand, *Dll* expression is present in the endite on the maxillula and maxilla (Fig. 1).

The hypothesis of homology of the mandibular gnathal edges is also supported by morphological substructures such as the separation into a pars incisivus and a pars molaris, which is known from several crustaceans, myriapods and hexapods. In contrast, a lacinia mobilis as a movable element between the two parts does not belong to the ground pattern of either Hexapoda, Myriapoda, Crustacea, or even Mandibulata. A lacinia mobilis or similar structures (with different names) probably evolved several times independently (see Richter et al. in press).

In summary, several lines of evidence in addition to the position of the mandible (as the limb of the second post-antennular segment) support the homology of the mandibles in Myriapoda, Crustacea and Hexapoda. The mandible is, therefore, still a convincing argument for the monophyly of the Mandibulata (see also Bitsch 2001b).

Crustacean phylogeny

Before we can start to discuss potential arguments for a sister group relationship between Hexapoda and Crustacea (or a part of the Crustacea) we should have a closer look at the Crustacea itself. How many higher taxa are involved? What are the arguments for crustacean monophyly? What are the internal relationships? In the most recent classification of the Crustacea, Martin & Davis (2001) recognise six higher taxa (called 'classes') within Recent Crustacea: Branchiopoda, Remipedia, Cephalocarida, Maxillopoda, Ostracoda, and Malacostraca. The most problematic taxon is the Maxillopoda which in other classifications includes the Ostracoda (e.g., Brusca & Brusca 1990).

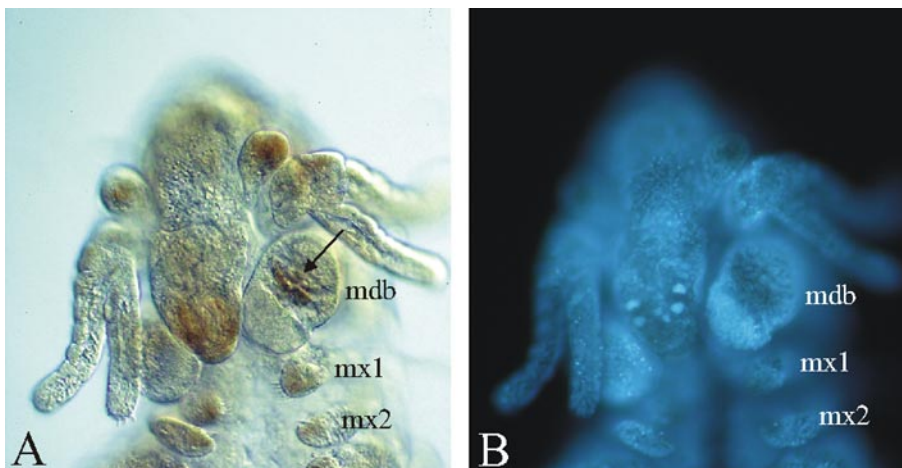


Fig. 1. Head of *Cyclestheria hislopi* (Branchiopoda). **A.** *Dll* is expressed in a lateral part of the mandible (arrow) but not at the inner edge. The inner edges of both maxillae show *Dll* expression. **B.** Hoechst staining: cells without *Dll* expression white, cells which are *Dll* positive dark. Abbreviations: mdb = mandible, mx1 = maxillula, mx2 = maxilla.

Here, the term Crustacea will be used for the crown-group Crustacea which comprises the last common ancestor (stem species) of Remipedia, Cephalocarida, Branchiopoda, Maxillopoda (including Ostracoda), and Malacostraca, as well as all its descendants. In the instance that Hexapoda (and/or Myriapoda) could be shown to belong to this taxon, the Crustacea would be paraphyletic. Any extension of the taxon name Crustacea to Hexapoda and/or Myriapoda would create serious confusion and should therefore be avoided. In the case of crustacean paraphyly the taxon names Pancrustacea/Tetraconata (see below) and Mandibulata would be available for the more inclusive taxa.

Because most characters playing an important role in the recent discussion of crustacean-hexapod relationships are internal characters which are not available for fossil taxa (this is also true for molecular markers), the discussion will be restricted to extant taxa. Potential representatives of the stem lineage of Crustacea and their phylogenetic relationships are discussed in detail by Walossek & Müller (1990, 1998a, b) and Walossek (1993, 1999).

Cephalocarida and Remipedia are taxa comprising only a few species each. After their discovery in the 1950s and 1980s, respectively, both groups were suggested as 'primitive' and 'most basal' for the Crustacea or as representing the 'ur-crustacean' (e.g., Sanders 1957 and Hessler 1992 for Cephalocarida, Schram 1986 and Schram & Hof 1998 for Remipedia). However, the two groups are very different in general appearance of their members. Cephalocarida possess a head, a nine-segmented thorax, and a ten-segmented abdomen without limbs. The thoracopods are of particular interest because they are more or less homonomous; this also applies to the maxilla. It is therefore improbable that a maxilla as a specialised mouthpart belongs to the ground pattern of Crustacea or even Mandibulata (Lauterbach 1986, Walossek 1993). Remipedia possess a cephalothorax including one thoracic segment, and a trunk with up to 36 segments. The postmaxillipedal limbs are swimming appendages. Maxillulae, maxillae and the maxilliped are well developed, uniramous, raptorial limbs. Cephalocarida and Remipedia each are certainly monophyletic groups because of some very unique autapomorphic characters. Interestingly enough, these two very different taxa appear as sister groups in some molecular or combined phylogenetic analyses (Spears & Abele 1998, Giribet et al. 2001).

The Malacostraca include the highest number of species within Crustacea. Several autapomorphies support malacostracan monophyly, e.g. a constant number of trunk segments, eight limb-bearing thoracomeres, and a pleon with six limb-bearing segments. Only in the Leptostraca is there a 7th, limb-less pleomere present in the adults, which according to Lauterbach (1975) corresponds to the limb-less abdomen of the non-malacostracan crustaceans. Other characters which support the

monophyly of the Malacostraca include the constant position of the genital openings (in the 6th thoracomere in females, in the 8th in males) and the formation of the postnaupliar germ band by a ring of exactly 19 ectoteloblasts. All these characters are also present in the Leptostraca, a taxon which sometimes has been suggested as not belonging to the Malacostraca but being more closely related to the Branchiopoda (Schram 1986, Schram & Hof 1998). However, the characters shared by Leptostraca and the remaining Malacostraca make this hypothesis quite improbable. Within the Malacostraca, the Leptostraca and Eumalacostraca (including Stomatopoda) are sister groups. The internal phylogeny of the Malacostraca has recently been analysed and reviewed by Richter & Scholtz (2001). The monophyly of the Malacostraca and the sister group relationship between Leptostraca and Eumalacostraca are well supported by molecular (Spears & Abele 1998, Giribet & Ribera 2000, Shultz & Regier 2000) and combined (Giribet et al. 2001) phylogenetic analyses.

The Branchiopoda comprises Anostraca, Notostraca and Diplostraca, the latter comprising Laevicaudata, Spinicaudata, *Cyclestheria hislopi* (formerly combined as Conchostraca) and Cladocera. Although several arguments support the monophyly of the Branchiopoda, including sperm ultrastructure (Wingstrand 1978) and the particular post-mandibular filter apparatus with a thoracic sternal food groove (Walossek 1993), some authors still question its monophyly (e.g., Gruner 1993, Ax 1999). In addition to the morphological characters, molecular (Spears & Abele 1998, 1999, 2000, Giribet & Ribera 2000, Shultz & Regier 2000) and combined (Giribet et al. 2001) phylogenetic analyses strongly support the monophyly of the Branchiopoda. Within the Branchiopoda, Anostraca and Phyllopoda are sister groups, the latter comprising Notostraca and Diplostraca (e.g., Walossek 1993, Negrea et al. 1999). Monophyly of Anostraca as well as of Phyllopoda is also supported by molecular phylogenetic analyses (Remigio & Hebert 2000, Braband et al. in press).

The most controversial taxon is the Maxillopoda (see Martin & Davis 2001 for a review of controversies). It comprises such different taxa as Cirripedia, Ascothoracida, Copepoda, Branchiura, Mystacocarida, and in some approaches the Ostracoda. Several authors support the monophyly of this taxon based on morphological characters (e.g., Dahl 1956, Grygier 1983, Boxshall & Huys 1989, Walossek & Müller 1998b). Arguments which have been used include the presence of seven thoracic segments and four abdominal segments (further reductions within the Maxillopoda are known), and the original use of thoracopods exclusively for locomotion (implying that the feeding mode of adult cirripedes is derived) (Walossek & Müller 1998b). There is no support for the Maxillopoda in molecular phylogenetic analyses

(see for example Spears & Abele 1998, Giribet & Ribera 2000), therefore evidence for its monophyly is not as strong as for the other four taxa. Nevertheless, I consider the Maxillopoda concept including the Ostracoda as a working hypothesis for the present review. One additional character which unites at least some of the maxillopodan taxa will be presented below.

Monophyly and internal relationships of the Crustacea

Several of the studies supporting a closer relationship between Crustacea and Hexapoda imply paraphyletic crustaceans with only a part of the Crustacea being the sister taxon to the Hexapoda. Others only deal with one or few of the crustacean taxa, leaving it as an open point whether a particular feature characterises the entire Crustacea or only a part of it (see below). Therefore, some of the arguments for the monophyly of the Crustacea will be presented for a better estimation of the relevance of contradictory characters that support paraphyly of the Crustacea.

Following an extensive review of diagnostic characters of the Crustacea, Lauterbach (1983) concluded that only two apomorphic characters support the monophyly of the Crustacea: 1) the nauplius eye as a single organ formed by four ocelli (the ocelli are separated from each other in other arthropods) – this single organ, however, is completely missing in some crucial taxa such as Remipedia (Schram 1986) and Cephalocarida (Elofsson & Hessler 1990) – and 2) the restriction of the segmental excretory organs to a maximum of two (antennal and maxillary nephridial organ, see also Wägele 1993). The only other detailed discussion is by Walossek (1999), also based on fossil material from the Upper Cambrian 'Orsten' fauna of Sweden. Walossek (1999) suggested several autapomorphic characters for the entire Crustacea, including the stem lineage (Pan-Crustacea sensu Lauterbach 1989) as well as the crown-group Crustacea (Eucrustacea sensu Walossek 1999). Supporting characters of different levels (evolved within the ancestral lineage of crown-group Crustacea) include a non-sclerotised labrum with posterior glandular openings and a pair of furcal rami of the telson. Unfortunately, for many of the characters introduced by Walossek it is difficult to exclude that they have been lost in the ancestral lineages of the Hexapoda and/or Myriapoda. One of these characters should be discussed briefly: the presence of a nauplius larva (orthonauplius) with an antennula and two additional pairs of limbs (see also Ax 1999). Walossek (1999) convincingly argued that the original larva in Euarthropoda possessed four pairs of limbs (called a 'head-larva' by Walossek & Müller 1990, 1998a). The nauplius larva with three pairs of appendages and the specific shape of the naupliar appendages should therefore be interpreted

as autapomorphic for the Crustacea. However, Lauterbach (1983) and Wägele (1993) stressed that it cannot be excluded that this kind of larva was reduced in the ancestral lineage of the Hexapoda and/or Myriapoda. Though this is certainly true, one weak or even speculative argument could support the hypothesis by Walossek (1999). In Crustacea without a free-living orthonauplius, e.g. Stomatopoda, Anaspidacea, most Decapoda, a particular embryonic stage called an egg-nauplius occurs (Scholtz 2000). Nothing comparable is known in hexapods or myriapods. This is not trivial because since Palaeozoic times the period without a free-living larva should be more or less the same. However, the argument that the nauplius larva was indeed restricted to the Crustacea would be more convincing if something like an 'egg-head-larva' were present in hexapods or myriapods, which seems not to be the case (see Scholtz 1998).

Comprehensive morphological cladistic analyses of the Arthropoda always result in monophyletic Crustacea (Wills 1998, Wills et al. 1998, Wheeler 1998, Zrzavý et al. 1998, Schram & Hof 1998, Edgecombe et al. 2000, morphological data in the combined analysis by Giribet et al. 2001). Edgecombe et al. (2000) listed 16 autapomorphic characters for the Crustacea, many of them based on Walossek (1999). Although the phylogenetic interpretation/optimisation of some of the characters from the different analyses can be questioned, the evidence in favour of the monophyly of the Crustacea is stronger than often supposed.

In recent years several phylogenetic or cladistic analyses dealt with the relationships of major crustacean taxa (e.g., Wilson 1992, Moura & Christoffersen 1996, Wills 1998, Wills et al. 1998, Walossek & Müller 1998b, Schram & Hof 1998, Walossek 1999, Ax 1999, Edgecombe et al. 2000), with quite different results and conclusions. Here, I would like to present two general alternatives both accepting crustacean monophyly (Fig. 2). Walossek (1999) proposed a monophylum Entomostraca comprising Cephalocarida, Branchiopoda and Maxillopoda, and the Malacostraca as sister group to the Entomostraca (Fig. 2A). According to Walossek (1999), the autapomorphies for the Entomostraca include an abdomen made up of at least four limb-less somites and a maxillula with a basis having four median enditic lobes. Within the Entomostraca, Maxillopoda and Branchiopoda are suggested as sister groups based on the presence of an osmoregulatory dorsal organ. In consequence, the Cephalocarida would be the sister taxon to Branchiopoda + Maxillopoda. The Remipedia is not considered by Walossek (1999).

One of the potential alternatives is based on the Thoracopoda concept by Hessler (1992), a taxon which includes Cephalocarida, Branchiopoda and Malacostraca, and is based on similarities in limb structure (Fig. 2 B). This concept has been revived recently by Ax (1999) and

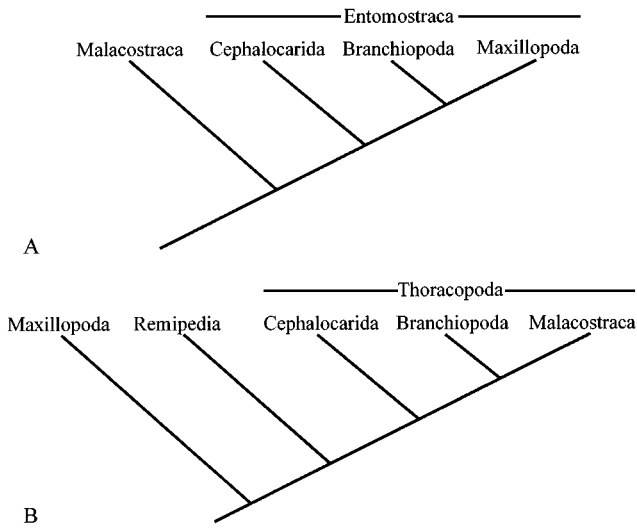


Fig. 2. Two alternative cladograms showing suggested relationships of Crustacea. **A.** According to Walossek (1999), the Entomostraca represents a monophylum. The Remipedia is not considered by Walossek. **B.** Relationships based on Edgecombe et al. (2000) supporting the Thoracopoda concept (Hessler 1992). For characters see the original references.

is also the result of the cladistic analysis by Edgecombe et al. (2000). The Maxillopoda would be the sister group of the Thoracopoda, the Remipedia the sister group to all other Crustacea (Ax 1999) or vice versa (Edgecombe et al. 2000). Within the Thoracopoda, the Branchiopoda and Malacostraca are sister groups (Edgecombe 2000, according to Ax 1999 the Branchiopoda is not monophyletic). According to the cladistic analysis by Zrzavy et al. (1998) Cephalocarida and Branchiopoda are sister groups, with the Malacostraca as sister taxon to both.

Similarities and differences between the limbs of branchiopods and malacostracans (in particular leptostracans) have been controversially discussed. Schram (1986) and Schram & Hof (1998) suggested a taxon comprising Branchiopoda, Leptostraca and Cephalocarida, based on the shared character 'phyllopodous limbs'. On the other hand, Walossek (1993) and Martin & Christiansen (1995) emphasised the differences in limb structure between Leptostraca and Branchiopoda and suggested that phyllopodous limbs evolved independently, a hypothesis which has been supported recently by a molecular phylogenetic analysis (Spears & Abele 1999) and by developmental data (Williams 1999, Schram & Koenemann 2001).

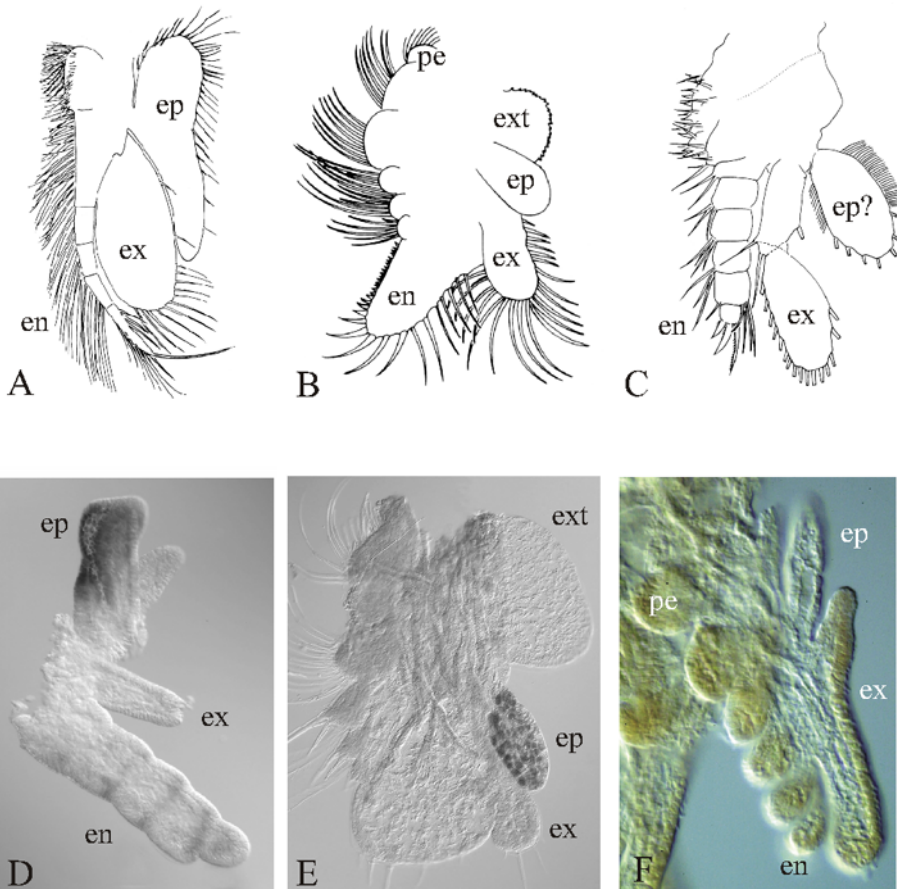


Fig. 3. Limbs of representatives of different Crustacea. **A–C.** Schematic drawings after Walossek (1993). **A.** *Branchipus stagnalis* (Anostraca). **B.** *Speonebalia cannoni* (Leptostraca). **C.** *Sandersiella acuminata* (Cephalocarida). **D–E.** Expression of *pdm* restricted to a single epipod (after Averof & Cohen 1997). **D.** *Pacifastacus leniusculus* (Malacostraca). **E.** *Artemia franciscana* (Anostraca). **F.** *Dll* expression in a limb of *Cyclestheria hislopi* (original). *Dll* is expressed at the entire margins of the exopod, the endites, and the endopod; the epipod shows no *Dll* expression. Abbreviations: en = endopod, ep = epipod, ex = exopod, ext = exite, pe = proximal endite. D–E courtesy of M. Averof.

Nevertheless, the limb structure provides at least one potential synapomorphy of Malacostraca and Branchiopoda, the presence of an epipod (the Cephalocarida will be discussed separately), because there is no a priori evidence that Remipedia or Maxillopoda might have lost an epipod (Walossek 1993, but see Lauterbach 1979 for a different opinion). Wägele (1993), however, noted that there is no convincing evidence for the homology of the different exites called epipods, and it seems unclear whether their function is the same: in malacostracans the gill function of the epipods seems well established (e.g., Grindley & Hessler 1971), in certain branchiopods the distal epipod has an osmoregulatory function (reviewed by Martin 1992, Walossek 1993) but a respiratory function has been suggested as general for the branchiopods (Dumont & Negrea 2002).

Apart from their presumably different function, there are some arguments in favour of homology of a single epipod per thoracopod in Malacostraca and Branchiopoda. In the Leptostraca one epipod per thoracopod is present (Fig. 3A), in the Stomatopoda there is also only one epipod per thoracopod but epipods are restricted to the three posterior thoracopods which are not transformed into maxillipeds. Within the Caridoida (the Eumalacostraca of other authors) the number of epipods per thoracopod increased to two or more (Lauterbach 1979, Richter & Scholtz 2001). Therefore, probably only one epipod per thoracopod belongs to the malacostracan ground pattern (Richter & Scholtz 2001). Within the Branchiopoda, the Phyllopoda also possess only one epipod per thoracopod (except for haplopod and onychopod cladocerans where epipods are absent). The representatives of the Anostraca in addition to one distal epipod possess one or even two more proximal exites (Fig. 3B) sometimes also called epipods (e.g., Walossek & Müller 1998a).

A study of the expression pattern of *pdm* (*nubbin*), *apterous* and *Dll* in the developing limbs of the anostracan *Artemia franciscana* and the malacostracan *Pacifastacus leniusculus* offers new insight into the question of homology of the epipods (Averof & Cohen 1997). Of particular interest is the expression pattern of *pdm* and *apterous*. In *Artemia* the *pdm* and *apterous* genes are expressed over most of the developing limb bud in early stages, but as soon as the appendage shows some differentiation this expression becomes restricted to the distal epipod (Fig. 3E). In *Pacifastacus* two distinct patterns of *pdm* expression can be observed: throughout a single distal epipod, and in a set of rings along the leg (Fig. 3D). In my opinion, this quite specific expression pattern is a strong argument for homology of the distal epipod in Anostraca with a single distal epipod in Decapoda.

On the other hand, in *Artemia* the *Dll* gene seems to be expressed non-specifically in more or less all limb outgrowths (Averof & Cohen 1997). However, if one

compares the *Dll* expression pattern in more detail, in *Artemia* it is found in the endites, endopod, exopod and in the proximal exite, while the expression in the (distal) epipod seems to be very weak (see also Panganiban et al. 1995). In the anostracan, *Thamnocephalus platyurus*, *Dll* is expressed in both exites, but in later stages *Dll* expression in the proximal exite is maintained while *Dll* is lost in the more distal epipod (Williams et al. 2002). This agrees in some respects with the findings by Williams (1998) in *Triops* sp., and by Olesen et al. (2001) in the phyllopod *Cyclestheria hislopi* where *Dll* is not expressed in the single epipod (see also Fig. 3F). The absence of *Dll* expression in the branchiopod epipods therefore could provide additional support for their homology, but it is important to note that this might simply reflect the absence of setae (Williams et al. 2002, see also Mittmann & Scholtz 2001). Nevertheless, the different expression patterns of *Dll* in the distal and proximal exite in Anostraca and in particular the restriction of *pdm* and *apterous* expression to the distal epipod in *Artemia* make it probable that in the Anostraca exites of different origin are present (see also Linder 1941). In summary, we have good arguments to homologise the single epipod present in the Phyllopoda with the distal epipod in Anostraca as well as with one epipod in the Malacostraca. This is also supported by the general similarity in development of the epipod in *Nebalia* species (see Olesen & Walossek 2000) and the phyllopod *Cyclestheria hislopi* (see Olesen 1999). The assumed difference in function of these epipods provides no strong evidence against their homology.

In the Cephalocarida the protopod carries a five-segmented endopod and a partly foliaceous three-segmented exopod. The proximal portion of the latter, and not the protopod, is the origin of another foliaceous structure with marginal setae (Fig. 3C), originally interpreted as a pseudopod (e.g., Sanders 1957, Hessler 1964), later as an epipod (e.g., Lauterbach 1979, Ito 1989, Hessler & Wakabara 2000) or as part of the exopod (e.g., Walossek 1993). In my opinion, the different origin of this limb part and the presence of setae are not strong enough evidence to reject the possibility of homology with the branchiopod and malacostracan epipod (but see Walossek 1993), but positive evidence is also weak (see discussion in Hessler & Newman 1975, Lauterbach 1979, Ito 1989).

There is a long history of speculation about homology between crustacean epipods and certain limb structures in other arthropods. Snodgrass (1952), for example, suggested the flabellum on the last prosomal leg of the xiphosurans as being an epipod, but Walossek & Müller (1998a) argued that the flabellum represents the homologue of the exopod. The strong *Dll* expression in the developing flabellum supports this view (Mittmann & Scholtz 2001). There is also no evidence for homology

between epipods and any limb parts of trilobites or other fossil arthropods of uncertain relationships (Walossek 1993, Edgecombe & Ramsköld 1999). The coxal vesicles of certain Hexapoda (e.g., Machilidae) and Myriapoda (e.g., Symphyla) have also been suggested as being homologous to epipods (Hennig 1969), but there is no detailed similarity to the respiratory/osmoregulatory epipods of crustaceans. Even the homology between the coxal vesicles in the different hexapod and myriapod taxa has been questioned (Dohle 1980).

The most challenging potential homology for the epipods has been suggested based on the already mentioned expression pattern of *pdm* and *apterous*: the homology with insect wings (Averof & Cohen 1997). In insects, homologues to the two genes are expressed throughout the prospective wings or specifically on the dorsal surface of developing wings. These correspondences provoked Averof & Cohen (1997) to suggest a homology between ‘gills’ and ‘wings’, although the authors also discuss the possibility that wings independently co-opted a number of gene functions that were already used in epipods. Although the correspondences in the developing mechanisms between insect wings and epipods cannot be ignored, this does not necessarily imply that common structural progenitors represented gills/osmoregulatory organs comparable to the epipods in malacostracans and branchiopods. Therefore, there is no convincing evidence that epipods should have belonged to the ground pattern of Crustacea or Mandibulata or even Euarthropoda (as suggested by, e.g., Hennig 1969, Hessler & Newman 1975, Lauterbach 1979, Budd 1996), an approach which was already questioned by Walossek (1993).

Crustacea and Hexapoda as sister groups

In the following, morphological and molecular evidence will be discussed which could support a sister group relationship between Crustacea and Hexapoda. Zrzavý & Štys (1997) suggested the name Pancrustacea for a such a monophylum comprising Crustacea and Hexapoda. Dohle (2001) introduced the name Tetraconata based on the presence of four cone cells in the ommatidia (see below). I prefer the latter name because Pancrustacea might be easily confused with the ‘Pan-Monophylum’ sensu Lauterbach (1989), a term introduced for an inclusive group which comprises the crown group and all representatives of the stem lineage (stem group) of this crown group (see also Meier & Richter 1992).

Molecular support for the Tetraconata

Different kinds of molecular data strongly support the Tetraconata concept: mitochondrial gene order, the complete mitochondrial genome, several nuclear genes, both

protein-coding and ribosomal RNA genes, and combined (total evidence) approaches.

An important character is the order of 13 protein-coding genes, 22 tRNA and two rRNA genes located on the mitochondrial genome (Boore et al. 1995, 1998). In all studied hexapods (representing 10 ‘orders’) and in the studied crustaceans (representatives of Malacostraca, Branchiopoda, Remipedia) the tRNA-Leu (UUR) gene is located between the cytochrome c oxidase subunit I and subunit II genes. In myriapods, chelicerates and onychophorans its relative position is between tRNA-Leu (CUN) and NADH dehydrogenase subunit 1. Unambiguously, the ‘translocation’ of the tRNA-Leu (UUR) gene can be interpreted as an autapomorphy of the monophylum embracing Hexapoda and Crustacea (Boore et al. 1998). Although other cases of gene ‘translocations’ within the mitochondrial genome are known (e.g., Hwang et al. 2001), this particular ‘translocation’ seems to be unique.

Several studies are based on the protein-coding genes of the mitochondrial genome (Garcia-Machado et al. 1999, Wilson et al. 2000, Hwang et al. 2001). The most inclusive study is by Hwang et al. (2001) who included a representative of the Chilopoda (*Lithobius forficatus*) in addition to two branchiopods (*Artemia franciscana*, *Daphnia pulex*) and two malacostracans (*Penaeus monodon*, *Pagurus longicarpus*), as well as several hexapods and chelicerates. Different analyses based on 12 mitochondrial protein sequences resulted in a closest relationship between hexapods and crustaceans. The Crustacea are paraphyletic in relation to the Hexapoda, with the two malacostracans more closely related to the hexapods than the two branchiopods (also supported by the analyses by Garcia-Machado et al. 1999 and Wilson et al. 2000). At least the clade including malacostracans and hexapods is well supported by tree support values used by the authors.

Friedrich & Tautz (2001; an extended version of their 1995 study) studied two nuclear ribosomal RNA genes, 18S RNA and 28S RNA, using a maximum likelihood approach. The Tetraconata concept is also supported by their analyses. Interestingly, the Crustacea are again paraphyletic, though in this analysis the representative of the branchiopods is the closest relative to the hexapods and not that of the malacostracans. The Tetraconata concept as well as the paraphyly of the Crustacea seem to be well supported (by branch probability values), but the taxonomic sampling of only 14 species is quite limited. Giribet & Ribera (2000) included 139 taxa in their analysis of the 18S rRNA and 28S rRNA genes using direct optimisation (Wheeler 1996). The results derived from different analytical parameters to test for stability are not always concurrent. Consequently, Giribet & Ribera (2000) described only “trends shown by the data”, which include a basal position of Chelicerata and Myriapoda

(with symphylans and pauropods being labile on the trees) and support for the monophyly of the Tetraconata. Some earlier analyses of the 18S RNA alone (Turbeville et al. 1991, Adoutte & Philippe 1993) or of a combination of 18S and 28S RNA (Wheeler 1998, Wheeler & Hayashi 1998), although very different in details, also resulted in support for a crustacean-hexapod clade.

In different analyses (parsimony, maximum likelihood) based on three nuclear protein-coding genes – the elongation factor 1 α (EF-1 α), the elongation factor 2, and the largest subunit of RNA polymerase II (Pol II) – the Tetraconata is supported and the Crustacea turn out as paraphyletic (Shultz & Regier 2000, Regier & Shultz 2001, see also Regier & Shultz 1997). However, the exact relationships between the various crustaceans and the hexapods differ between the different analyses. In a combined analysis of 17 euarthropod species and one representative each of the Tardigrada and Onychophora, Regier & Shultz (2001) found strong support for the Tetraconata. In this analysis, the remipede *Speleonectes tulumensis* occurs as the sister group to the Hexapoda.

Kusche et al. (2002) studied 25 arthropod hemo-cyanin and phenoloxidase sequences. The more inclusive data set of 707 amino acid positions comprises the complete sequences without the regions overlapping with signal peptides. This data set (using different analysis methods and branch support values) strongly supports a monophyletic Tetraconata and also gives some support for the monophyly of the Mandibulata.

The most inclusive approach has been used by Giribet et al. (2001) in their 'combined analysis' of eight molecular markers and 303 morphological characters (extended version of the character matrix by Edgecombe et al. 2000). A total of 51 taxa were included in several direct optimisation analyses using different parameter sets. The analysis with the lowest incongruence between morphological and molecular data (the preferred analysis) strongly supports the monophyly of the Mandibulata, with a monophyletic Tetraconata and Myriapoda as sister groups. Within the Tetraconata, the Crustacea and Hexapoda are each monophyletic, except for a nonsensical clade including *Drosophila*, Japygidae and Balanidae. There is no evidence that either Malacostraca or Branchiopoda could be more closely related to the Hexapoda (see also Wheeler et al. 1993, Wheeler 1998, Zrzavý et al. 1998 for earlier combined analyses).

Only one molecular analysis supports the Antennata concept. Wägele & Stanjek (1995) re-analysed 12S rRNA data of Ballard et al. (1992). This analysis, based on an 'improved alignment', resulted in a monophyletic Antennata and a monophyletic Mandibulata.

Apart from all the differences between the results of the mentioned analyses it cannot be ignored that completely independent data sets – nuclear ribosomal RNA,

nuclear protein-coding, mitochondrial protein-coding and mitochondrial ribosomal RNA genes – analysed by different alignment and phylogenetic procedures support the Tetraconata concept. I consider this equivalent to a morphology-based analysis where various characters from different morphological character complexes support a particular monophylum.

Morphological characters supporting the Tetraconata

One of the most convincing homologous character complexes shared by Crustacea and Hexapoda but not by any other arthropods is the particular ommatidia structure in the compound eyes (e.g., Grenacher 1879, Parker 1891, Hesse 1901). Representatives of crustaceans and hexapods possess ommatidia which are composed of two corneagenous cells (two primary pigment cells in hexapods), four crystalline cone cells (Semper cells), and eight retinula cells. In addition, a variable number of accessory pigment cells surround the ommatidium (e.g., Paulus 1979, 2000). However, the similarities are even more detailed. A particular pattern in the arrangement of the cone cell processes (proximal extensions in the area of the rhabdom) in relation to the retinula cells is shared by several crustaceans and hexapods (Melzer et al. 1997, Dohle 2001, Fig. 4B). Homology of the ommatidia is also supported by the affinity of a monoclonal antibody – raised against a specific glycoprotein (3G6) – to crystalline cones (Edwards & Meyer 1990), and by the detailed similarities in ommatidial development (cell recruitment) between hexapods and crustaceans (Hafner & Tokarski 1998, Melzer et al. 2000). In summary, there can be no doubt about homology concerning this particular kind of ommatidium. Here, I will focus on the problem of whether or not this ommatidium can be hypothesised for the ground pattern of each of the five higher crustacean taxa, Remipedia, Cephalocarida, Malacostraca, Branchiopoda and Maxillopoda. This would be particularly important if the Crustacea are not monophyletic.

Considering the ground pattern of the five crustacean taxa, a major problem is that Remipedia (Schram 1986) and Cephalocarida (Elofsson & Hessler 1990) do not possess any compound eyes. The findings by Burnett (1981) in the cephalocarid *Hutchinsoniella macracantha* have been shown to be a misinterpretation of paired nervous structures in the clypeus (Elofsson & Hessler 1990). Therefore, even if it seems likely that the remote ancestors of these two groups possessed compound eyes, nothing can be said about ommatidial structure in these eyes.

Within the Malacostraca, the two basal taxa Lepidostreacra and Stomatopoda and also the Decapoda possess the typical ommatidia as described above (e.g., Claus 1888, Meyer-Rochow 1975, Schönenberger

1977). Therefore, it is reasonable to hypothesise these conditions for the ground pattern of the Malacostraca as well. On the contrary, representatives of the other malacostracan taxa with compound eyes, Anaspidacea, Euphausiacea, and Peracarida, possess ommatidia in which only two crystalline cone cells build the cones. The two other cells are not reduced but present as accessory cone cells. There are also only two cone cell processes which belong to the accessory cone cells (e.g., Hallberg 1977, Richter 1999). These differences among ommatidia have been interpreted as autapomorphies for a taxon Xenomacarida comprising Syncarida, Euphausiacea and Peracarida (Richter 1999, Ax 1999, Richter & Scholtz 2001).

Within the Branchiopoda, representatives of the Notostraca possess ommatidia which show exactly the pattern described above (Diersch et al. 1999). The ommatidia of the Anostraca are also characterised by crystalline cones built by four cone cells and by the presence of four cone cell processes, although it seems that there are not more than six retinula cells (e.g., Elofsson & Odselius 1975). Several representatives of the diplostracan taxa, 'Conchostraca' and Cladocera, possess pentapartite crystalline cones and also five cone cell processes (e.g., Nilsson et al. 1983, Richter unpublished), which represents the derived condition within Branchiopoda. Notostracan ommatidia most probably represent branchiopod ground pattern conditions.

The Maxillopoda are problematic concerning this character. Some of the maxillopodan taxa such as Copepoda and Mystacocarida do not possess any compound eyes (Gruner 1993). Within Thecostraca, the larvae of the Cirripedia (Hallberg & Elofsson 1983) and of the As-

cothoracida (Hallberg et al. 1985) possess compound eyes with ommatidia with tripartite crystalline cones, each of the cone cells possessing one process (Fig. 4C–E). This unique kind of ommatidia can be interpreted as an autapomorphy of the Thecostraca (Hallberg et al. 1985). Within the Ostracoda, only representatives of the Myodocopa possess compound eyes (Gruner 1993). According to Andersson (1979), the ommatidia of two species studied, *Cypridina norvegica* and *Philomedes globosa*, consist of two corneagenous cells, crystalline cones built by two cone cells including two processes (no accessory cone cells are present), and a rhabdom constituted by six retinula cells (Fig. 4F). This arrangement, which is different from but still similar to the proposed ground pattern of the Tetraconata, makes it very improbable that the ostracod eyes evolved de novo as proposed by Parker (1995) and Oakley & Cunningham (2002). There is one maxillopodan taxon whose representatives possess ommatidia that correspond to the proposed ground pattern – the Branchiura. In the fishlouse *Argulus foliaceus* the ommatidia consist of tetrapartite cones with cone cell processes that exactly show the proposed original pattern (Hallberg 1982; Fig. 4B), and eight retinula cells as proven by recent findings (Meyer-Rochow et al. 2001).

An additional interesting point pertains to maxillopodan compound eyes. In the ommatidia of the cypris larva of the cirriped *Balanus crenatus* there is a pair of pigmented cells, in a position resembling that of corneagenous cells, which in addition continue as distal pigment cells (Hallberg & Elofsson 1983; Fig. 4D). Similar bipartite pigment-bearing cells surrounding the cone are present in *Argulus foliaceus* (Hallberg 1982; Fig. 4A)

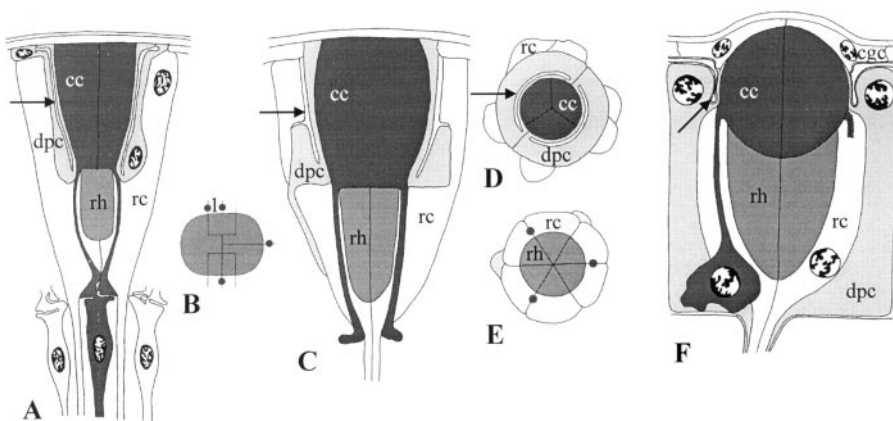


Fig. 4. Schematic drawings of ommatidia of Maxillopoda. **A–B.** Branchiura: *Argulus foliaceus* (after Hallberg 1982). **A.** Overview. **B.** Transverse section through the rhabdom; retinula cell 1 between two cone cell processes, eighth retinula cell not shown. **C–E.** Cirripedia: *Balanus crenatus* (after Hallberg & Elofsson 1983). **C.** Overview. **D.** Transverse section through the cone and the distal pigment cells. **E.** Transverse section through the rhabdom; three cone cell processes are present. **F.** Ostracoda: *Cypridina norvegica* (after Andersson 1979). Note the extracellular space (arrow) between the distal pigment cells in all three species (A, C, D, F). Abbreviations: cc = crystalline cone, cgc = corneagenous cells, dpc = distal pigment cells, rc = retinula cell, rh = rhabdom.

and in the ostracods studied, but in the latter there are additionally two corneagenous cells (Andersson 1979; Fig. 4F). In particular the conditions in the Cirripedia and the Branchiura could indicate that primary pigment cells might not have been evolved in the hexapods but already belonged to a common crustacean-hexapod ground pattern. Within Crustacea, the pigment producing ability of the corneagenous cells would then have been lost. However, the composition of the ostracod ommatidia where both cell types, bipartite distal pigment cells and corneagenous cells, are present might contradict this hypothesis. Nevertheless, such bipartite pigment cells with an inner pigment-free portion and an outer pigment-bearing portion separated by an extracellular space seem to be unique for the ommatidia of Cirripedia, Branchiura, and Ostracoda. They might represent an autapomorphy of the Maxillopoda or at least of the 'Thecostracan line' sensu Walossek & Müller (1998b) within the Maxillopoda.

Except for the Cephalocarida and Remipedia where no compound eyes are present, we can hypothesise ommatidia with the same cell composition as in the proposed common crustacean-hexapod ancestor (Paulus 1979, 2000, Dohle 2001) for the ground pattern of the other major crustacean taxa.

Amongst the other Recent Euarthropoda, only representatives of the Scutigermorpha (Chilopoda) and Xiphosura (Chelicerata) possess compound eyes. Crystalline cones are present only in the Scutigermorpha (e.g., Paulus 1979) whereas in xiphosurans the extended cornea is responsible for the light refraction (Fahrenbach 1999). In the lateral eyes of the diplopod *Polyxenus lagurus* four so-called 'vitreous bodies' are present (Paulus 2000, Spies 1981 described only two of them). These 'vitreous bodies' can be interpreted as reduced cone cells (Paulus 2000), and the number four is indeed suggestive. However, an interpretation as crystalline cone precursors would not be less probable. Therefore, also in the context of the Tetraconata concept it might be justified to suggest 'ommatidia with crystalline cones' for the mandibulate ground pattern. The presence of the crystalline cones or of precursors can be interpreted as an apomorphic state in comparison to the Xiphosura (Ax 1999). Nevertheless, there is no a priori evidence that the particular cell composition found in hexapods and crustaceans was ever present in the ancestors of the myriapods, which implies that the specific ommatidial cell composition is still valid support for the monophyly of the Tetraconata.

The number and structure of the optic neuropils is another important compound eye structure. Generally, many malacostracan crustaceans and hexapods possess three optic neuropils: from the periphery to the centre these neuropils are: lamina ganglionaris, medulla (also called medulla externa), and lobula (also called medulla

interna). Lamina ganglionaris and medulla as well as medulla and lobula are connected by neural chiasmata. Non-malacostracan crustaceans possess only two optic ganglia, lamina and medulla, and the neural connections are not arranged in a chiasma (see, e.g., Hanström 1928, Nilsson & Osorio 1998). In the representatives of the Myriapoda also only two neuropils seem to be present (Hanström 1928, Melzer et al. 1996/97). As early as 1926, Hanström suggested a closer relationship between Malacostraca and Hexapoda based on the presence of a third optic neuropile. However, the details are more complicated. Within Hexapoda, Collembola (Neanurinae), Archaeognatha (*Machilis* sp.) and Zygentoma (*Lepisma saccharina*, *Thermobia domestica*) seem to have only the two outer optic neuropils (Strausfeld 1998), although Elofsson (1970) recorded a small lobula in Zygentoma. Within the Malacostraca, Leptostraca also probably have only two neuropils (Elofsson & Dahl 1970, Scholtz 1992b). Although the lobula might have been reduced in certain cases within pterygote insects (Strausfeld 1998, Klass & Kristensen 2001), its absence in all basal taxa within Hexapoda and in the sister group to the Eumalacostraca, even in species with a reasonable size and well developed eyes, makes it more plausible that this is the plesiomorphic character state for Crustacea and Hexapoda. In summary, it seems to be much more reasonable to suggest that the third optic neuropil evolved independently within Malacostraca (see Richter & Scholtz 2001) and within Hexapoda (as an autapomorphy of the Dicondylia or Pterygota).

It is interesting to note that the presence or absence of an outer chiasma is a character independent from the number of neuropils involved (the presence of the inner chiasma depends, of course, on the presence of the lobula). Such an outer chiasma between lamina and medulla is present in Eumalacostraca and Pterygota but is also known from *Nebalia bipes* (Leptostraca) (Scholtz 1992b) and from representatives of the Zygentoma, *Lepisma saccharina* and *Thermobia domestica* (Strausfeld 1998). Despite the more inclusive distribution of this character there still remain serious problems in the interpretation of this outer chiasma as a potential synapomorphy of Malacostraca and Hexapoda. On the one hand, the chiasma between lamina and medulla is absent in representatives of the Archaeognatha (Strausfeld 1998), animals with well developed compound eyes where we have no a priori reason to suppose that the chiasma has been lost. This argumentation is independent from the general question whether it might be impossible to reduce such a chiasma as supposed by Nilsson & Osorio (1998), a statement which is certainly debatable (Strausfeld 1998, Klass & Kristensen 2001). Therefore, convergent evolution of a chiasma between lamina and medulla in Dicondylia and Malacostraca would be at least equally plausible, in particular if the Malacostraca are part of

a monophyletic Crustacea (see above). On the other hand, such a chiasma is also present in the Xiphosura (Hanström 1926), and Nilsson & Osorio (1998) also discuss that the cellular anatomy of the xiphosuran optic ganglia might be very similar to that described for certain crustaceans and hexapods (see Osorio 1991), which could indicate that such a chiasma is a plesiomorphic character for Hexapoda and Crustacea. The presence of a chiasma in the Scutigermorpha seems to be questionable (pers. comm. of Strausfeld in Klass & Kristensen 2001). Therefore, there are at present no correspondences between the optic neuropils of Malacostraca and Hexapoda which can be interpreted with reasonable confidence as synapomorphies of the two taxa. Nevertheless, there can be only little doubt that the last common ancestor of Hexapoda and Crustacea possessed compound eyes consisting of a number of ommatidia with a particular cell composition and at least two optic neuropils developing in a very similar and particular manner from three proliferation zones (Harzsch & Walossek 2001). The assumption that compound eyes in crustaceans (at least non-malacostracans) and hexapods evolved independently from single ocelli (Nilsson & Osorio 1998) does not seem well supported. The important question, whether the compound eyes as a general character in Xiphosura, apart from the different ommatidial cell composition, are homologous to those of Hexapoda and Crustacea, is not decided yet. The same is true for the compound eyes in the Scutigermorpha.

A common character of all Euarthropoda – as well as of other taxa (see Scholtz 2002, this volume) – is the ladder-like organisation of the ventral nerve cord. There-

fore, one would expect that the development of the nervous system would also be similar throughout the euarthropods. However, detailed similarities in nerve cell proliferation and neuron patterning can only be found in hexapods and crustaceans but not in myriapods (see reviews by Whitington 1995, 1996, Whitington & Bacon 1998, Dohle 2001, Simpson 2001).

In all studied hexapods a common mode of neurogenesis is found. Ganglion mother cells are produced by repeated, asymmetrical divisions of large stem cells called neuroblasts (Wheeler 1891, 1893). Each of the ganglion mother cells produced by the neuroblasts divides once symmetrically to generate neurons and/or glia cells. The number and arrangement of neuroblasts in each of the thoracic hemisegments is very stable throughout hexapods, including a representative of the Zygentoma. There are mostly 29–31 lateral neuroblasts arranged in 6–7 transverse rows and four longitudinal columns, and in addition one unpaired posterior median neuroblast is present (see Whitington & Bacon 1998; Fig. 5A). Not only the similar arrangement but also a temporally accurate sequence of gene expression (*engrailed*, *fushi tarazu*, *prospero*, *seven-up*) supports the homology of particular neuroblasts between different hexapods (e.g., Broadus & Doe 1995).

What can we say about the ground pattern of the major crustacean groups? Within Malacostraca, representatives of the Decapoda and of the Peracarida possess lateral neuroblasts showing similarities with those of hexapods, in particular in producing vertical columns of neuron precursors by repeated asymmetrical divisions with spindles perpendicular to the surface of the germ

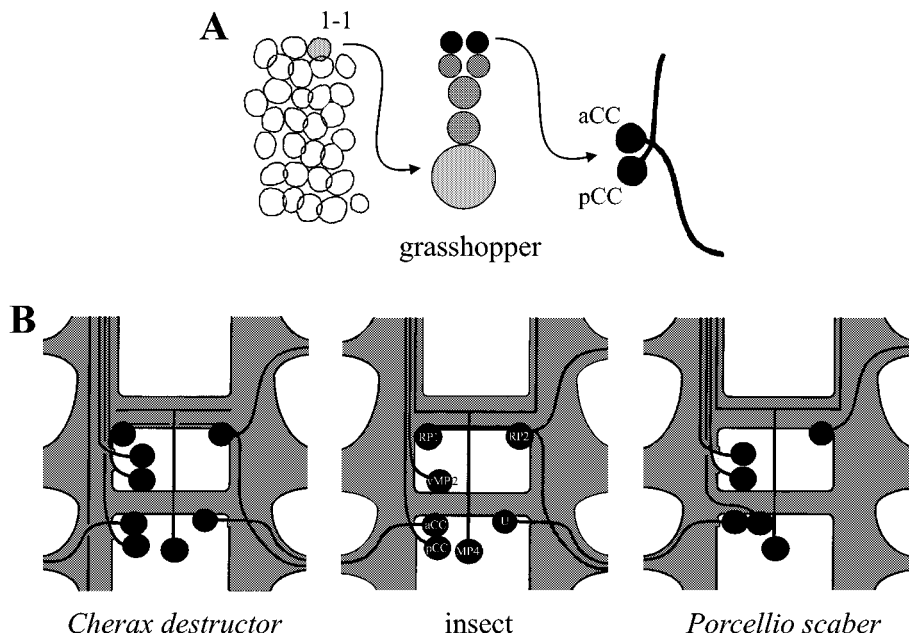


Fig. 5. Neurogenesis and pioneer neuron axon growth in Hexapoda and Malacostraca. **A.** Neuroblasts in a grasshopper (Insecta), and origin of the pioneer neurons aCC and pCC which are both products of the division of the first ganglion mother cell of neuroblast 1-1 (based on Whitington & Bacon 1998). **B.** Pioneer neurons in *Cherax destructor* and *Porcellio scaber* (Malacostraca) showing detailed similarities in possessing homologues to the insect neurons aCC, pCC, MP4, RP1, RP2, vMP2 and U (after Whitington & Bacon 1998).

band (e.g., Dohle 1976, Dohle & Scholtz 1988, Scholtz 1992a, Harzsch et al. 1998). In the crayfish *Cherax destructor*, 25–30 neuroblasts arranged in 6–7 rows and 4–5 columns have been described (Scholtz 1992a), the number and arrangement being very suggestive in comparison to hexapods. In addition, in the crayfish *Procambarus clarkii* an *engrailed* expression in the neurogenic regions similar to that in hexapods has been found which might support the homology of these neuroblasts (Duman-Scheel & Patel 1999), although admittedly it is not yet possible to identify the crayfish neuroblasts for certain by *engrailed* expression alone (Scholtz pers. comm.). In addition, it is likely that the ganglion mother cells in malacostracans, as in hexapods, undergo exactly one more division before their daughter cells differentiate into neurons, although this also seems not to be beyond doubt (Scholtz & Gerberding 2002). Whether the lateral neuroblasts of malacostracans contribute to the formation of glia in the segmental ganglia is also an open question (Scholtz & Gerberding 2002). In addition to the lateral neuroblasts there is, as in hexapods, one median neuroblast in malacostracans which is part of a column of cells forming a midline in the post-naupliar germ band (Scholtz 1992a, Gerberding & Scholtz 1999, 2001, Harzsch 2001).

It cannot be ignored that some important differences exist between hexapod and malacostracan neuroblasts. Hexapod neuroblasts differentiate during delamination from the surface layer of neuroectodermal cells, whereas those of the malacostracans remain at the surface. Furthermore, the neuroblasts of malacostracans differentiate continuously, whereas the neuroblasts of hexapods are formed in waves. The neuroblasts of hexapods are embedded in a number of specialised cells such as cap cells and sheath cells; these are not present in malacostracans. Some malacostracan neuroblasts give rise to epidermal cells after they have begun to produce ganglion mother cells (Scholtz & Gerberding 2002). Indications that this also happens in hexapods (Tamarelle et al. 1985) are not well documented.

Based on these differences (but also in light of the previously favoured Antennata concept), the convergence of malacostracan and hexapod neuroblasts has been favoured (Dohle & Scholtz 1988, Scholtz 1992a). However, some of the differences might not be insurmountable. The irreversible determination of hexapod neuroblasts has been changed experimentally in *Drosophila* by altering levels of *Notch* signalling (Simpson 2001). Other differences can be explained as being derived from a common ground pattern (e.g., the presence of cap cells and sheath cells in hexapods) or as plesiomorphic remnants of an earlier mode of neurogenesis (e.g., the delamination of neuroblasts in hexapods, see below). In my opinion, all this implies that homology of hexapod and malacostracan neuroblasts is quite well

corroborated (but see Dohle 2001 for a more cautious assessment).

There are a few indications that neuroblasts are also present in the Branchiopoda. In the cladoceran *Leptodora kindtii* divisions of the lateral neuroectoderm cells are unequal, with spindles perpendicular to the surface. These neuroblasts remain on the surface and function as stem cells like in malacostracans. An unpaired median neuroblast is missing (Gerberding 1997). Based on the *engrailed* expression pattern, Duman-Scheel & Patel (1999) concluded that neuroblasts, also including a median neuroblast, are present in *Artemia franciscana* and *Triops longicaudatus*, although they presented only indirect evidence. Harzsch (2001) demonstrated the presence of actively dividing cells in *Triops cancriformis* and *Artemia salina*, using the proliferation marker BrDU. He interpreted them as neuroblasts, although they are much smaller in comparison to those of malacostracans. According to Harzsch (2001) there is no median neuroblast in the two studied species. Nothing is known about the presence or absence of neuroblasts in other crustacean taxa besides Malacostraca and Branchiopoda.

Some of the early differentiating neurons, the so-called pioneer neurons, produced by the symmetrical divisions of ganglion mother cells are also strongly conserved throughout Hexapoda. *Drosophila melanogaster* and the grasshoppers *Locusta migratoria* and *Schistocerca americana* share a set of at least 12 identified neurons some of which are involved in the initial establishment of connectives, commissures and peripheral nerves. In some cases, confidence in homology of particular neurons in the different species can be extremely high. For example, the neurons aCC and pCC share not only the same position and the same kind of axon growth, but are also both products of the division of the first ganglion mother cell of neuroblast 1-1 (Whittington & Bacon 1998, Fig. 5A). The zygentoman *Ctenolepisma longicaudata* possesses at least nine of these early-differentiating neurons with a very similar axon growth. However, differences from the Pterygota also exist. For example, in *Ctenolepisma* the median neuron MP4 is missing (Whittington et al. 1996). These differences are not really surprising but show that we indeed have a complex pattern of developing neurons in which each single neuron is independent in its evolutionary fate. This may increase our confidence in homology of the entire pattern. Based on the expression pattern of the *even-skipped* gene, which is specific for a few pioneer neurons including the motor neurons aCC and RP2 and the interneuron pCC, these cells could also be detected in the collembolan *Folsomia candida* (Duman-Scheel & Patel 1999). Although not all crucial taxa have been studied (e.g., Protura, Diplura, Archaeognatha), it seems reasonable to hypothesise for the ground pattern of the

Hexapoda the presence of some very specific pioneer neurons (e.g., aCC, pCC, RP2), as well as early neurogenesis via a specific number of neuroblasts.

There are also some detailed similarities in position and axon growth of the pioneer neurons between hexapods and malacostracans (e.g., Thomas et al. 1984). Whittington et al. (1993) studied the axonogenesis in embryos of the two malacostracans *Cherax destructor* (Decapoda) and *Porcellio scaber* (Isopoda). Despite some differences between the two species as well as differences from the hexapods, there are detailed similarities between malacostracan and hexapod axonogenesis, e.g. in the presence of homologues to the neurons aCC, pCC, RP1, RP2 and MP4 (Fig. 5B); Here, the position of the cell somata, direction and relative timing of the axon

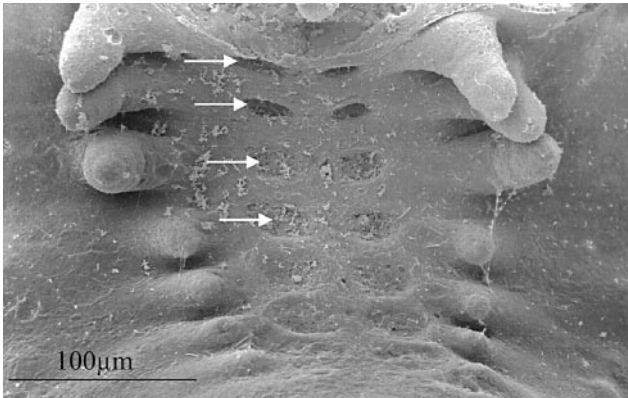


Fig. 6. Formation of 'ventral organs' in the diplopod *Glomeris marginata* (original).

outgrowth, axon morphology and branching were regarded as indicators of homology. Therefore, it is quite reasonable to suggest that both patterns are derived from a common ground pattern including these similarities (e.g., Whittington 1996, Whittington & Bacon 1998). The axonogenesis of pioneer neurons of non-malacostracan crustaceans has not been studied in detail. Based on the *even-skipped* expression pattern, homologues of some neurons (e.g., aCC, pCC, RP2) are present in *Artemia franciscana* and *Triops longicaudatus* (Duman-Scheel & Patel 1999). Nothing is known about the other major crustacean taxa.

Both developmental processes, early neurogenesis via neuroblasts as well as establishment and axon growth of pioneer neurons, show enough detailed similarities between hexapods and (at least) malacostracans to argue for their homology. Nevertheless, it should be emphasised that both processes are independent from each other. Also, if hexapod and crustacean (malacostracan and/or branchiopod) neuroblasts were not homologous, our confidence in homology of their pioneer neurons would not be influenced or reduced. Homologous organs do not need to share identical development (e.g., Whittington 1996, Dohle 2001, Scholtz & Gerberding 2002).

A crucial point for this problem is the condition in the Myriapoda. Studies of neurogenesis in different myriapods have generally failed to detect cells with the morphological characteristics of neuroblasts (Heymons 1901, Tiesgs 1940, 1947, Dohle 1964). The formation of ventral ganglia is associated with the formation of 'ventral organs' (Tiesgs 1940, 1947), shallow holes which de-

	gene order (Boore et al. 1998)	18S + 28S rDNA (Friedrich & Tautz 2001)	mitochondrial genome (Hwang et al. 2001)	combined approach (Giribet et al. 2001)	ommatidial structure	lateral neuroblasts	median neuroblast	specific pioneer neurons (Whittington 1996)	proventriculus (Klass 1998)
Hexapoda	+	+	+	+	+	+	+	+	+
Malacostraca	+	+	+	+	+	+	+	+	+
Branchiopoda	+	+	+	+	+	+	-/?	+	-
Maxillopoda	?	?	?	+	+	?	?	?	-
Cephalocarida	?	?	?	+	-	?	?	?	-
Remipedia	+	?	?	+	-	?	?	?	-

Fig. 7. Overview of molecular data supporting the Tetraconata, as well as morphological character complexes shared by Hexapoda and various Crustacea. The information on presence of a median neuroblast in Branchiopoda is contradictory.

velop within the ectoderm external to the ganglia (Fig. 6) and which in some cases are subsequently incorporated as cavities into the ganglion (Whittington & Bacon 1998). This process shows some affinities to the ganglion formation in chelicerates (Weygoldt 1985; but see Stollewerk et al. 2001). The delamination of hexapod neuroblasts might be a reminiscence of this mode of ganglion formation. The absence of neuroblasts in the centipede *Ethmostigmus rubripes* has been confirmed by the use of BrdU labelling (Whittington et al. 1991). This is also the only study dealing with axon growth of the pioneer neurons in myriapods. Whittington et al. (1991) were not able to detect any putative homologues of the defined pioneer neurons found in hexapods and crustaceans.

Klass (1998) found similarities between the armarium of the proventriculus of *Ctenolepisma lineata* (Zygentoma) and the cardia of *Carcinus maenas* (Decapoda), including a similar shape and arrangement of the sclerites and denticles, a similar pattern of apodemes, and similar symmetry relations. Klass (1998) concluded that the armarium of Dicondylia and the foregut of the Malacostraca may be homologous and such a foregut may belong to the ground pattern of the Mandibulata (accepting the Antennata concept). The similarities were later also discussed as potential support for a closer crustacean-hexapod relationship (Klass & Kristensen 2001). A major problem with this approach is that such proventriculi are only present in Lepismatidae, some odonatan nymphs and some Blattaria within the Hexapoda (Klass 1998), and in the Malacostraca (e.g., Siewing 1956). Comparable foregut structures are missing in non-malacostracan crustaceans and non-dicondylarian hexapods. Scutigermorph chilopods, however, possess a foregut which seems to show some similarities to those of Malacostraca and Dicondylia (Seifert 1967). Nevertheless, the presence of a proventriculus showing the above-mentioned detailed similarities could be used as support for a Malacostraca-Hexapoda clade. It has been shown that foregut characters are indeed valuable characters in phylogenetic analyses, at least on a lower level of relationships (e.g., Wägele 1989, Kobusch 1998, Brösing et al. 2002), and they certainly reflect phylogenetic relationships. A major problem, however, is that most of the mentioned similarities are not represented in the foregut of the Leptostraca (Siewing 1956). Other Malacostraca also possess foreguts quite different from those of decapods (e.g., Siewing 1956, Kunze 1981, Wägele 1989, Kobusch 1998), although it should not be excluded that some similarities can be determined (see Klass 1998). Therefore, parallel evolution of the similarities between the zygentoman and decapod proventriculi seems more probable to me, although homology and reduction in the other taxa is also a possibility (Klass 1998, Klass & Kristensen 2001).

Conclusions

More and more studies support a closer relationship between crustaceans and hexapods, implicitly contradicting the old Antennata concept. In the beginning, support for the new concept came mainly from molecular phylogenetic studies, but now several morphological characters can also be cited in support of a taxon Tetraconata sensu Dohle (2001). Nevertheless, there still are serious arguments for the Antennata concept (e.g., Kraus & Kraus 1994, Kraus 1998). In my opinion, no decision can be made with the necessary certainty at the moment. Why this caution? I think the strongest evidence in favour of the Tetraconata concepts comes from molecular data. The order of the genes on the mitochondrial genome and different kinds of genes (nuclear and mitochondrial ribosomal RNAs and protein-coding genes) support the Tetraconata, independent of the method of alignment and phylogenetic strategies or philosophies. However, the number of investigated genes and in particular the taxon sampling still have to be improved. The morphological characters are more ambiguous. In some cases, homology of particular structures shared by certain hexapods and certain crustaceans is questionable (e.g., proventriculus, some brain structures). Other characters such as the ommatidia and the pioneer neurons show so many detailed and complex similarities that we should have a very high degree of confidence in homology of these structures. Here, the crucial point is not homology but synapomorphy. At the moment we cannot exclude with enough certainty that the ancestors of myriapods never possessed these structures. The other important problem concerns the Crustacea. Many of the characters used as support for the Tetraconata are not known from all major crustacean taxa (Fig. 7). This is an important point because crustacean monophyly and the major relationships within Crustacea are still under debate. Therefore, a decision on the Tetraconata versus Antennata concept will have to be preceded by much more extensive study of crustacean morphology and phylogeny.

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