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Decapod Crustacean Phylogenetics

edited by

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Contents

Development, Genes, and Decapod Evolution

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ABSTRACT

Apart from larval characters such as zoeal spines and stages, developmental characters are rarely used for inferences on decapod phylogeny and evolution. In this review we present examples of comparative developmental data of decapods and discuss these in a phylogenetic and evolutionary context. Several different levels of developmental characters are evaluated. We consider the influence of ontogenetic characters such as cleavage patterns, cell lineage, and gene expression on our views on the decapod ground pattern, on morphogenesis of certain structures, and on phylogenetic relationships. We feel that developmental data represent a hidden treasure that is worth being more intensely studied and considered in studies on decapod phylogeny and evolution.

1 INTRODUCTION

The morphology of decapod crustaceans shows an enormous diversity concerning overall body shape and limb differentiation. On the two extreme ends, we find representatives such as shrimps with an elongated, laterally compressed body, muscular pleon, and limbs mainly adapted to swimming, and groups like the Brachyura exhibiting a dorsoventrally flattened, strongly calcified, broad body with a reduced pleon and uniramous walking limbs. In addition, hermit crabs show a peculiar asymmetric soft and curved pleon, and among all larger decapod taxa there are species with limbs specialized for digging, mollusc shell cracking, and all other sorts and numbers of pincers and scissors. These few examples indicate that the decapod body organization is varied to a high degree. It is obvious that this disparity has been used to establish phylogenetic relationships of decapods and that it is a challenge for considerations of decapod evolution (e.g., Boas 1880; Borradaile 1907; Beurlen & Glaessner 1930; Burkenroad 1981; Scholtz & Richter 1995; Schram 2001; Dixon et al. 2003). One major example for the latter is the controversial discussion about carcinization—the evolution of a crab-like form, which, as the most derived body shape and function, desires an explanation at the evolutionary level (e.g., Borradaile 1916; Martin & Abele 1986; Richter & Scholtz 1994; McLaughlin & Lemaitre 1997; Morrison et al. 2002; McLaughlin et al. 2004).

A closer look at decapod development shows a similarly wide range of different patterns as is found in adult morphology (e.g., Korschelt 1944; Fioroni 1970; Anderson 1973; Schram 1986; Weygoldt 1994; Scholtz 1993, 2000). One can observe decapod eggs with high and low yolk content, with total cleavage and superficial cleavage types, with a distinct cell division and cell lineage pattern, and without these determinations. There are different kinds of gastrulation, ranging from invagination to immigration and delamination, and multiple gastrulation modes and phases within a species. In addition, the growth zone of the embryonic germ band is composed of different numbers of stem cells in the ectoderm, the so called ectoteloblasts (Dohle et al. 2004). Even at the level of

gene expression patterns, the few existing publications on decapods reveal some differences between species (e.g., Averof & Patel 1997; Abzhanov & Kaufman 2004). Some groups hatch as a nauplius larva, whereas others hatch at later stages (such as zoea larvae) or exhibit direct development with hatchlings looking like small adults (Scholtz 2000).

With the notable exception of zoeal larval characters (e.g., Gurney 1942; Rice 1980; Clark 2005, this volume), surprisingly little attention has been paid to this developmental diversity and to decapod development in general when the phylogenetic relationships or evolutionary pathways have been discussed.

Here we present some examples of how ontogenetic data, such as cleavage, cell division, and gene expression patterns, can be used to infer phylogenetic relationships and evolutionary pathways among decapod crustaceans. It must be stressed, however, that this is just the beginning. Most relevant data on decapod ontogeny have yet to be described.

2 CLEAVAGE PATTERN, GASTRULATION, AND THE DECAPOD STEM SPECIES

It is now almost universally accepted that the sister groups Dendrobranchiata and Pleocyemata form the clade Decapoda (Burkenroad 1963, 1981; Felgenhauer & Abele 1983; Abele & Felgenhauer 1986; Christoffersen 1988; Abele 1991; Scholtz & Richter 1995; Richter & Scholtz 2001; Schram 2001; Dixon et al. 2003; Porter et al. 2005; Tsang et al. 2008). The monophyly of dendrobranchiates is largely based on the putatively apomorphic shape of the gills, which are highly branched, and perhaps on the specialized female thelycum and male petasma (Felgenhauer & Abele 1983). Nevertheless, the monophyly of Dendrobranchiata has been doubted based on characters of eye morphology (Richter 2002). Dendrobranchiata contains sergestoid and penaeoid shrimps, which have a largely similar life style (Pérez Farfante & Kensley 1997). In contrast to this, the pleocyematans include shrimp-like forms, such as carideans and stenopodids, but also the highly diverse reptants, which include lobsters, crayfishes, hermit crabs, and brachyuran crabs among others. When Burkenroad (1963, 1981) established the Pleocyemata, he stressed the characteristic brood-care feature of this group, namely, the attachment of the eggs and embryos to the maternal pleopods. With few exceptions, such as *Lucifer*, which attaches the eggs to the 3rd pleopods (Pérez Farfante & Kensley 1997), dendrobranchiates simply release their eggs into the water column. The monophyly of Pleocyemata is furthermore supported by brain characters (Sandeman et al. 1993).

The early development is quite different between Dendrobranchiata and Pleocyemata. Dendrobranchiates show relatively small, yolk-poor eggs with a total cleavage, a stereotypic cleavage pattern resulting in two interlocking cell bands, a determined blastomere fate, and a gastrulation initiated by two large cells largely following the mode of a modified "invagination" gastrula (e.g., Brooks 1882; Zilch 1978, 1979; Hertzler & Clark 1992; Hertzler 2005; Biffis et al. in prep) (Fig. 1). They hatch as nauplius larvae (Scholtz 2000). Pleocyematans mostly possess relatively large, yolky eggs with a superficial or mixed cleavage, no recognizable cell division pattern, and an immobile embryonized egg-nauplius (see Scholtz 2000; Alwes & Scholtz 2006). There are a few exceptions found in some carideans, hermit crabs, and brachyurans among reptants, which display an initial total cleavage (e.g., Weldon 1887; Gorham 1895; Scheidegger 1976), but these cleavages never show a consistent pattern comparable to that of Dendrobranchiata. The gastrulation is highly variable, and very often it implies immigration and no formation of a proper blastopore (Fioroni 1970; Scholtz 1995). The question is, which of these two types of developmental pathways—the one exhibited by the Dendrobranchiata or the less specified type exhibited by the Pleocyemata—is plesiomorphic within the Decapoda? This can only be answered with an outgroup, since two sister groups with two alternative sets of character states cannnot tell us which states are plesiomorphic. The answer to this question allows inferences on the origin and ground pattern of decapods; in particular, it might inform us as to whether the ancestral decapod was a swimming shrimp-like animal of the dendrobranchiate type or a benthic reptant. A pelagic lifestyle in malacostracan Crustacea is not necessarily

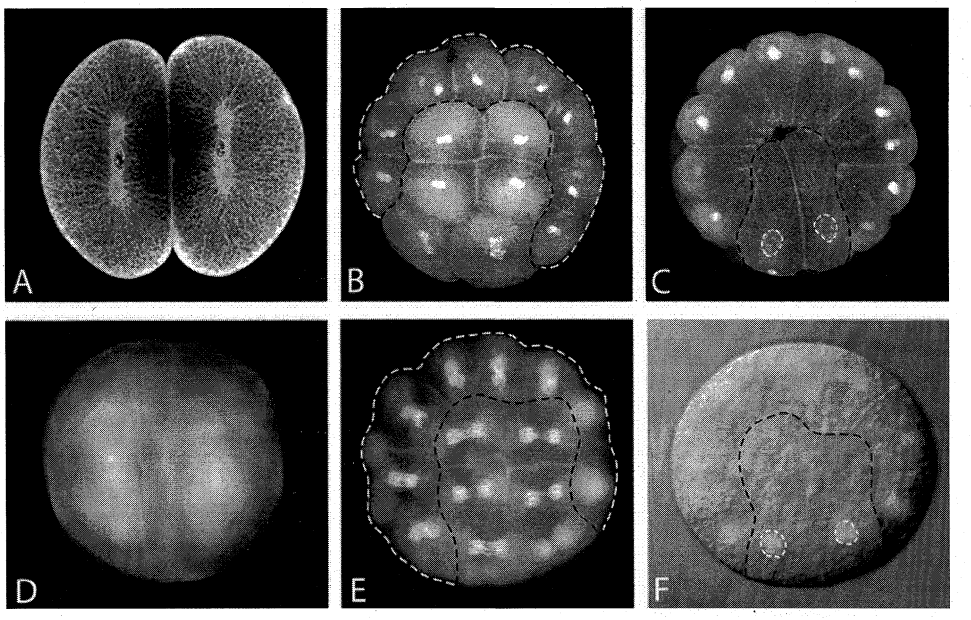

Figure 1. Different stages during early development of the dendrobranchiate shrimp *Penaeus monodon* (A-C) and of the euphausiacean *Meganyctiphanes norvegica* (D-F) stained with fluorescent dyes (Sytox A-C; Hoechst D-F). In F the fluorescence is combined with transmission light. The eggs show a low yolk content and total cleavage with a characteristic size and arrangement of the blastomeres. A and D: 2-cell stage. B and E: 32-cell stage. A stereotypic cleavage pattern leads to two interlocking cell bands, a "tennis ball pattern" (surrounded by white and black broken lines each). In B, the mitoses of the previous division are just completed, while in E the cells show the anaphase of the next division. C and F: 62-cell stage. Notice the center of the egg with two differently sized large mesendoderm cells (black broken lines), which arrest their division and initiate gastrulation.

combined with, but facilitates, the absence of brood care, whereas benthic malacostracans always show some degree of investment into the embryos and early larvae.

A comparison with the early development of Euphausiacea helps to polarize the developmental characters of Dendrobranchiata and Pleocyemata. Euphausiacea are either the sister group (Siewing 1956; Christoffersen 1988; Wills 1997; Schram & Hof 1998; Watling 1981, 1999) or are more remotely related to Decapoda (Richter 1999; Scholtz 2000; Jarman et al. 2000; Richter & Scholtz 2001). The Euphausiacea studied show remarkable similarities to dendrobranchiate decapods concerning their early embryonic and larval development (Taube 1909, 1915; Alwes & Scholtz 2004). They also release their eggs into the water column and show no brood care, with some apparently derived exceptions (Zimmer & Gruner 1956). Furthermore, they exhibit a corresponding cleavage pattern, arrangement and fate of blastomeres, and mode of gastrulation (Fig. 1). Like Dendrobranchiata, Euphausiacea hatch as a free nauplius. In particular, the formation of two interlocking germ bands, the origin and fate of the two large mesendoderm cells that initiate the gastrulation, and the formation of distinct cell rings (crown cells) at the margin of the blastopore find a detailed correspondence between dendrobranchiates and euphausiids (Hertzler & Clark 1992; Alwes & Scholtz 2004; Hertzler 2005) (Fig. 1). It must be stressed, however, that the nauplius larvae of dendrobranchiate decapods and Euphausiacea might be the result of convergent evolution (Scholtz 2000). It is furthermore not clear when this type of cleavage and early development evolved within malacostracans. The similarities in early development might indicate that euphausiaceans are the sister group to decapods (see Alwes & Scholtz 2004) (Fig. 2), in agreement with previous suggestions (e.g., Siewing 1956; Christoffersen 1988; Wills, 1997; Schram & Hof 1998; Watling

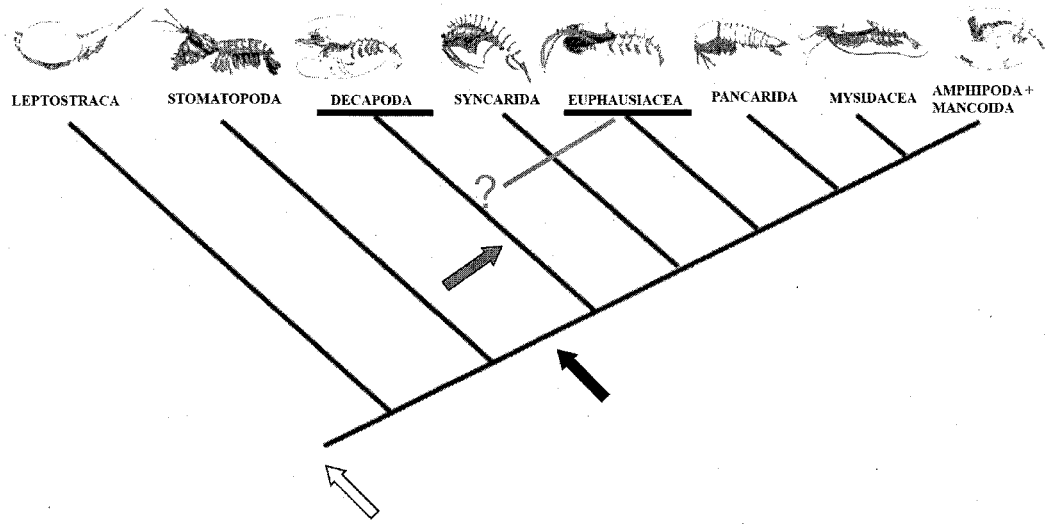

Figure 2. Malacostracan phylogeny according to Richter & Scholtz (2001). The arrows indicate the three possibilities for the evolution of the characteristic early development shared by Euphausiacea and Dendrobranchiata (Decapoda). The black arrow shows the possibility that the cleavage pattern evolved in the lineage of Caridoida. The grey arrow indicates a shared evolution of the cleavage pattern for Decapoda and Euphausiacea in combination with the view of a sister group relationship between these two groups (Eucarida), as is indicated with a question mark and light grey line. The white arrow symbolizes an older origin of the developmental pattern, perhaps even in non-malacostracans.

1981, 1999). On the other hand, if we accept the analysis of Richter and Scholtz (2001), the pattern must have evolved in the stem lineage of Caridoida (Fig. 2). However, it might be even older since similar patterns occur in some non-malacostracan crustaceans (Kühn 1913; Fuchs 1914, see Alwes & Scholtz 2004) (Fig. 2).

In either case, this corresponding early development of euphausiids and dendrobranchiate decapods to the exclusion of Pleocyemata strongly suggests that originally decapods did not care for the brood but released their yolk-poor eggs freely into the water. Furthermore, these eggs developed via a stereotypic cleavage pattern with largely determined cell fates and a specific mode of gastrulation. All of this indicates that the early development of Dendrobranchiata is plesiomorphic within Decapoda. In addition, this allows for the conclusion that the ancestral decapod was a more pelagic shrimp-like crustacean.

The oldest known fossil decapod is the late Devonian species *Palaeopalaemon newberryi* (see Schram et al. 1978). According to these authors, this fossil is a represenative of the reptant decapods (see also Schram & Dixon 2003). This was disputed by Felgenhauer and Abele (1983), who claimed that the shrimp-like scaphocerite instead indicates an affinity to dendrobranchiates or carideans. Our conclusions, based on ontogenetic data, might lead to reconsidering the affinities of *Palaeopalaemon* as a dendrobranchiate-like decapod. At least there is no morphological structure that contradicts this assumption. This interpretation would furthermore fit with the ideas of Schram (2001) and Richter (2002) who independently concluded, based on eye structure and other arguments, that it is likely that decapods originated in deeper areas of the sea.

3 WAS THE ANCESTRAL DECAPOD A DECAPOD?

One of the apomorphies for Malacostraca is the possession of eight thoracic segments and their corresponding eight thoracopods (Richter & Scholtz 2001). In the various malacostracan groups, the thoracopods are diversified to different degrees, with the most conspicuous transformation being

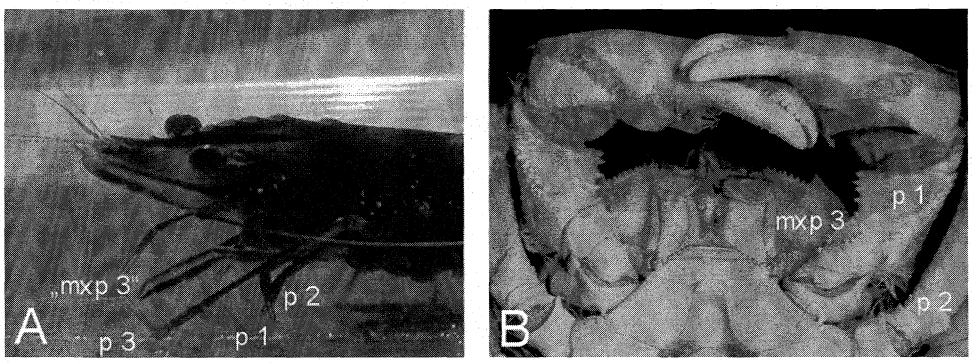

Figure 3. Evolution of 3rd maxillipeds in decapods. (A) The dendrobranchiate shrimp *Penaeus monodon* with pediform 3rd maxillipeds (mxp 3), which are not very different from the 1st anterior pereopods (p1 to p3). (B) The 3rd maxilliped (mxp3) of the brachyuran *Eriocheir sinensis* is highly transformed compared to the first two pereopods (p1, p2).

the modification of anterior thoracic limbs to secondary mouthparts, the maxillipeds. Depending on the number of thoracopods transformed to maxillipeds, the number of walking limbs (pereopods) varies. In most malacostracans we find either none (Leptostraca, Euphausiacea), one (e.g., Isopoda, Amphipoda, Anaspidacea) to two (Mysidacea), and sometimes three (Cumacea, most Decapoda) or even five (Stomatopoda) pairs of maxillipeds, which correspondingly means eight, seven, six, five, or three pairs of pereopods (Richter & Scholtz 2001). It is quite safe to assume that the plesiomorphic condition in malacostracans was the absence of any maxillipeds and that the number increased convergently in the course of malacostracan evolution. Only the anteriormost maxilliped might be homologous between those malacostracan taxa that possess it (Richter & Scholtz 2001). Decapods, as the name indicates, are characterized by five pairs of pereopods, which lie posterior to three pairs of maxillipeds. However, the concept of what has to be considered a maxilliped is not very sharp, because it relates to a combination of morphological deviation and different function from a locomotory limb, which is assumed to represent the ancestral throracopod state. Indeed, the locomotory pereopods of malacostracans are often also involved in food gathering and processing of some sort, and the large chelipeds of a lobster, for instance, are seldom used for locomotion. On the other hand, the morphology of some, in particular the posteriormost, maxillipeds is not very different from that of the pereopods. For instance, the 3rd maxillipeds of lobsters are more leg-like than those of most brachyuran crabs in which these form the operculum covering the mouth field (Scholtz & McLay this volume) (Fig. 3).

In particular, in some dendrobranchiates the 3rd maxillipeds are morphologically not really discernible from the pereopods (Fig. 3). They have the same length and segment number as the pereopods and are not kept closely attached to the mouth field. Accordingly, the question arises as to whether the stem species of decapods was equipped with only two pairs of maxillipeds and hence six pairs of pereopods (see Scholtz & Richter 1995; Richter & Scholtz 2001)—in other words, whether it was a dodecapod (dodeka: Greek for twelve) rather than a true decapod.

In their seminal work, Averof and Patel (1997) developed a new molecular criterion for maxillipeds. They found that the Hox gene ultrabithorax (UBX) is expressed in thoracic regions with pereopods, whereas in segments bearing maxillipeds, this gene is not expressed. UBX is needed to differentiate trunk segments, and the absence of UBX expression allows the transformation towards mouthparts (Averof & Patel 1997). This is true for all crustaceans investigated in this respect. Interestingly enough, the two decapod species studied by Averof and Patel (1997) differed slightly in the anterior margin of UBX expression depending on the degree of deviation from a pereopod-like appearance of the 3rd maxillipeds (see Fig. 5). In the lobster, with a more pediform 3rd maxilliped

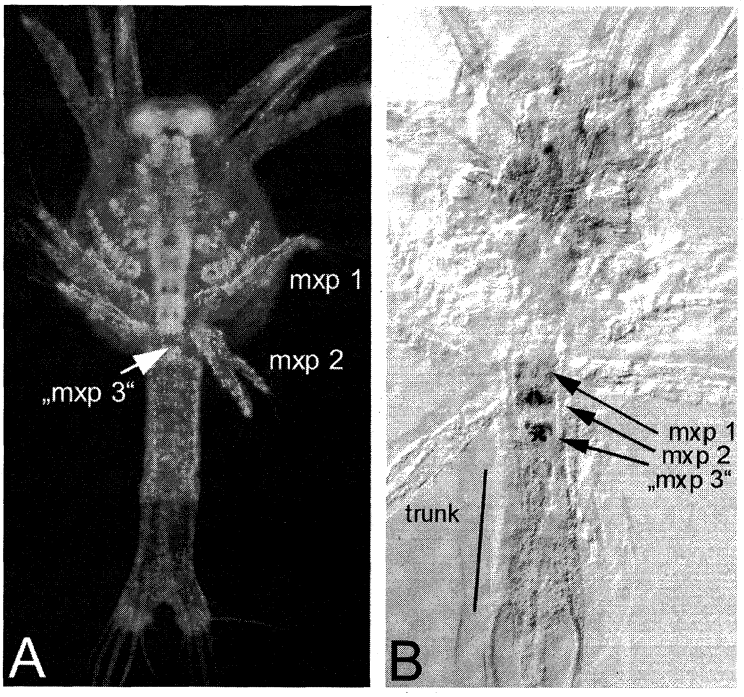

Figure 4. Expression of the UBX-AbdA protein in the protozoea of *Penaeus monodon* as seen with the antibody FP6.87. (A) 1st protozoea stained with the nuclear dye Hoechst, showing the overall shape, the limbs, and the central nervous system. The two anterior pairs of maxillipeds (mxp1, 2) are present and the corresponding ganglion anlagen are recognizable. The 3rd maxilliped pair is not yet differentiated but the ganglion is forming (mxp3). (B) 1st protozoea showing UBX expression in the ganglia of the 2nd and 3rd maxillipeds (mxp2, 3) and in the posterior part of the ganglion of the 1st maxilliped segment (mxp1). The anterior expression boundary of UBX is parasegmental. In addition, there is a weak expression in the forming trunk segments. No limbs are stained, which might be due to penetration problems through the well-developed cuticle.

(concerning length, overall shape, and the occurrence of five endopodal articles), the expression, at least in early stages, was also seen in this body segment. However, in the caridean shrimp, with a derived 3rd maxilliped (stout and only three endopodal articles; see, e.g., Bruce 2006), the anterior boundary of UBX expression was always behind the segment bearing the 3rd maxilliped. To test this phenomenon in dendrobranchiate decapods, we used the same antibody against the UBX-AbdA product (FP6.87) as Averof and Patel (1997) to study the expression of UBX in *Penaeus monodon* (Fig. 4). This species is characterized by a pediform 3rd maxilliped that still shows five endopodal segments and that is, compared to most pleocyemate species, still long and slender (Motoh 1981) (Fig. 3). In *Penaeus monodon* protozoea larvae, we find an anterior expression boundary of UBX in the forming nervous system slightly anterior to the 2nd maxilliped segment, which is the anterior-most expression found in a decapod to date (Figs. 4, 5). This result indicates that the specification of the 3rd maxilliped in dendrobranchiates has not reached the degree found in the other decapods and that most likely a 3rd maxilliped in the true sense was absent in the decapod stem species. It furthermore suggests that a true 3rd maxilliped evolved convergently several times within Decapoda. Interestingly enough, a closer look at the situation in the Amphionida, a possible candidate as the sister group to decapods (Richter and Scholtz 2001), supports this conclusion. This group possesses a well-defined maxilliped on the 1st thoracic segment and a reduced 2nd thoracic limb that nevertheless resembles the maxilliped in its overall shape. The 3rd to 8th thoracic appendages are all pereopods with a different morphology (Schram 1986).

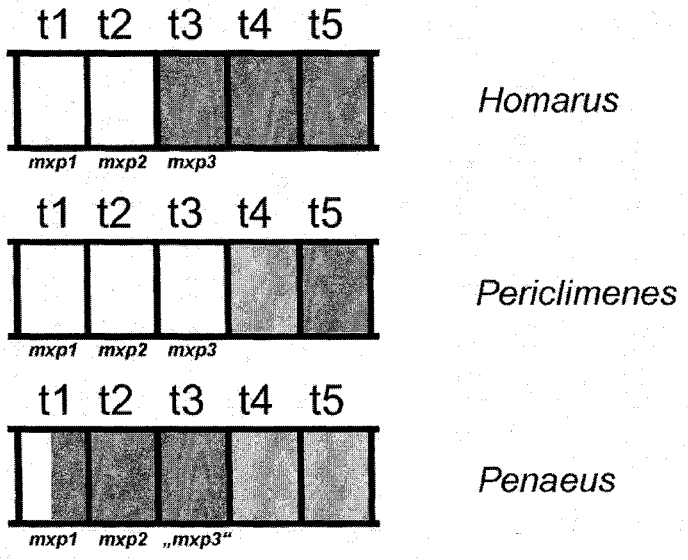

Figure 5. Scheme of the anterior expression of the UBX-AbdA protein in three decapod representatives with different degrees of pediform 3rd maxillipeds. *Homarus* and *Penaeus* with more pediform 3rd maxillipeds show a more anterior UBX expression boundary. *Penaeus* with the most pereopod-like 3rd maxilliped reveals the most anterior boundary in the 1st thoracic segment. *Homarus* and *Periclimenes* after Averof & Patel (1997), *Penaeus* this study. Light grey = weak expression, dark grey = strong expression. (mxp1,2,3 =1st to 3rd maxillipeds, t1 to t5 = 1st to 5th thoracic segments).

4 THE ORIGIN OF THE SCAPHOGNATHITE

The scaphognathite is a large flattened lobe at the lateral margin of the 2nd maxillae of decapods and amphionids (Fig. 6). The scaphognathite is equipped with numerous plumose setae at its margin and is closely fitted to the walls of the anterior part of the branchial chamber. This allows it to create a water current through the branchial chamber depending on the movement of the 2nd maxilla. This current supplies the gills with fresh oxygen-rich water for breathing. Hence, the scaphognathite is a crucial element of the gill/branchial chamber complex that is apomorphic for Decapoda (including Amphionida). The morphological nature and origin of this important structure, however, have been a matter of debate for more than a century. This relates to the general difficulty in assigning the elements of the highly modified decapod mouthparts to the parts of biramous crustacean limbs, such as the endopod, exopod, or epipods. Accordingly, several authors claim that the scaphognathite is a composite structure formed by the fusion of the exopod and epipod of the 2nd maxilla (Huxley 1880; Berkeley 1928; Gruner 1993). Huxley (1880) even discusses the alternative that it is exclusively formed by the epipod. In contrast to this, carcinologists such as Calman (1909), Giesbrecht (1913), Hansen (1925), Borradaile (1922), and Balss (1940) interpret the scaphognathite as of solely exopod origin. These different traditions are still expressed in recent textbooks (see Gruner 1993; Gruner & Scholtz 2004; Schminke 1996; Ax 1999). But Kaestner (1967: 1073) and Schram (1986: 245), discussing the morphology of decapod 2nd maxillae, state that "Homologie noch unklar!" (homology not clear) and "This appendage is so extensively modified that to suggest homologies with the various components of other limbs is a questionable exercise."

We studied the development of the 2nd maxillae in the embryos of a freshwater crayfish, the parthenogenetic Marmorkrebs (Scholtz et al. 2003; Alwes & Scholtz 2006), applying the means

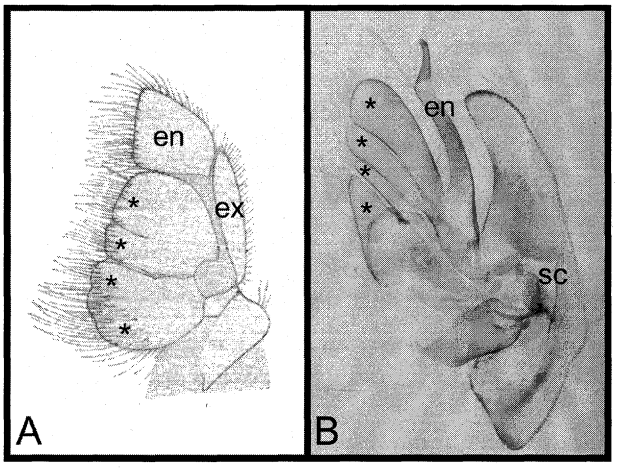

Figure 6. The shape and elements of the 2nd maxillae. (A) The 2nd maxilla of the euphausicaean *Meganyctiphanes norvegica* (after Zimmer & Gruner 1956). (B) The 2nd maxilla of the decapod *Axius glyptocereus*. The maxillae of both species show an endopod (en) and four enditic lobes (asterisks). The scaphognathite (sc) characteristic for decapods has such a special shape and function that the homology to the exopod (ex) in euphausiaceans and other malacostracans is controversial.

of histology, scanning electron microscopy, and immunochemistry (Distal-less) to clarify the issue of scaphognathite origins (Fig. 7). The Distal-less gene is involved in the adoption of a distal fate of limb cells in arthropods and is thus a marker for the distal region of arthropod limbs (e.g., Panganiban et al. 1995: Popadic et al. 1998; Scholtz et al. 1998; Williams 1998; Olesen et al. 2001; Angelini & Kaufman 2005). The early limb bud of the 2nd maxilla is undivided. After a short period, the tip of the bud shows a slight cleft that deepens with further development. This process is typical for the early development of crustacean biramous limbs (Hejnol & Scholtz 2004; Wolff & Scholtz 2008). The tips of the undivided limb buds, as well as the later-forming two separate tips, express Distal-less. Again, this is characteristic for biramous crustacean limbs and indicates that the two tips represent the exopod and endopod, since epipods do not express Dll (with the notable exception of the transient expression in epipods of *Artemia* and *Nebalia*, Averof & Cohen 1997; Williams 1998). With further development, the outer branch widens and grows in anterior and posterior directions, eventually adopting the characteristic lobed shape of the adult decapod scaphognathite (Fig. 7). In these later stages endopod and exopod still express Dll (Fig. 7D). A forming epipod is not recognizable at any stage of development, as is also revealed by the comparison to other limb anlagen which are equipped with an epipod.

Our results clearly support the idea that the scaphognathite of decapods is a transformed exopod and that an epipod is not involved in its formation. A comparison with other malacostracans reveals that in no case is the 2nd maxilla equipped with an epipod, but just endopods and exopods with different degrees of deviation from a "normal" limb branch. In addition, the overall shape of the scaphognathite is not so unusual for an exopod if we consider the shape of the exopods of phyllobranchious thoracic limbs in Branchiopoda and Leptostraca (Pabst & Scholtz 2009).

5 EMBRYONIC CHARACTERS HELP TO CLARIFY FRESHWATER CRAYFISH MONOPHYLY

Freshwater crayfish, Astacida, show a very disparate geographical distribution. In the Northern Hemisphere, the Cambaridae are found in East Asia and in the eastern part of North America, whereas the Astacidae occur in western Asia, Europe, and in the western parts of North America.

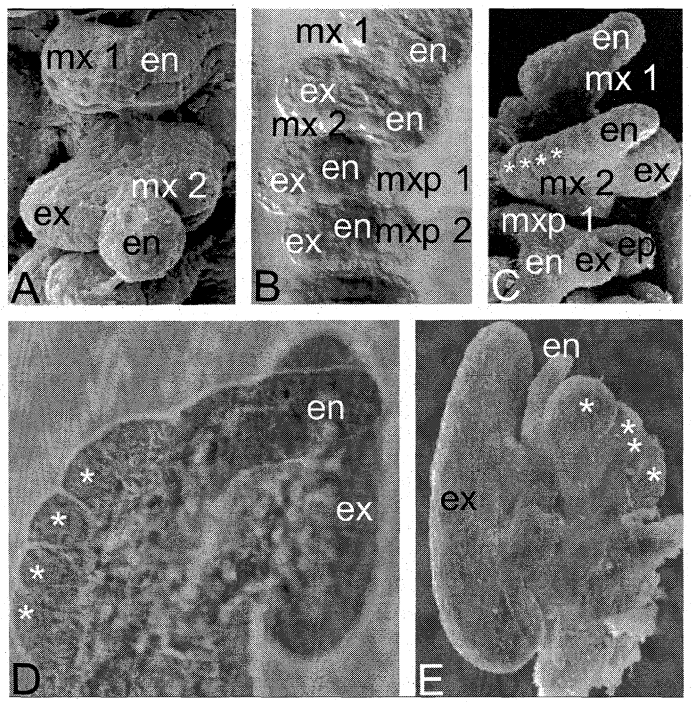

Figure 7. Development of the 2nd maxilla and the scaphognathite in the parthenogenetic Marmorkrebs (Astacida). (A) SEM image of the early 1st and 2nd maxillae (mx1, mx2) showing the forming two branches of the endopod (en) and exopod (ex) in the 2nd maxilla. (B) Expression of Distal-less (Dll) in early limb anlagen. Dll is expressed (darker areas) in the tips of the endopods (en) and exopods (ex) of the 2nd maxilla and the maxillipeds (mxp1, 2). The uniramous bud of the 1st maxilla (en) also expresses Dll. (C) SEM image showing the further differentiation of the parts of the 2nd maxilla (mx2). The four enditic lobes are forming (asterisks), and the exopod (ex) begins to form a lobe structure. The 1st maxilliped (mxp1) differentiates an epipod (ep), which finds no correspondence in the two maxillae. (D) Dll expression in an advanced stage. The expression (darker areas) is found in the tip of the endopod and around the margin of the exopod. The asterisks indicate the forming four enditic lobes. (E) SEM image of a 2nd maxilla shortly before hatching. The general shape of the adult maxilla is present (compare with Fig. 6).

Even if both groups, Astacidae and Cambaridae, are not monophyletic as has recently been suggested (Scholtz 1995, 2002; Crandall et al. 2000; Rode & Babcock 2003; Braband et al. 2006; Ahn et al. 2006), this distribution pattern is difficult to explain. The Parastacidae of the Southern Hemisphere live in Australia, New Zealand, some parts of South America, and Madagascar. Crayfish are absent from continental Africa. This is also true for the Indian subcontinent, and in more general terms, there is a crayfish-free circum-tropical zone. To explain this disparate distribution of freshwater crayfish, several hypotheses on the origin and evolution of crayfish have been discussed during the last 130 years. Most authors favored the idea that freshwater crayfish had multiple origins from different marine ancestors, i.e., are polyphyletic, and that they independently invaded freshwater many times (e.g., Huxley 1880; Starobogatov 1995; for review see Scholtz 1995, 2002). This view is based on the fact that freshwater crayfish do not tolerate higher salinities and that an explanation is needed for the occurrence of Astacida on most continents without the possibility of crossing large marine distances. Only Ortmann (1897, 1902) suggested a common origin for freshwater crayfish and a single invasion into freshwater habitats. He hypothesized East Asia as the center of origin from which Astacida spread all over the world, using assumed low sea levels to migrate to other continents (since the concept of continental drift was unknown at that time).

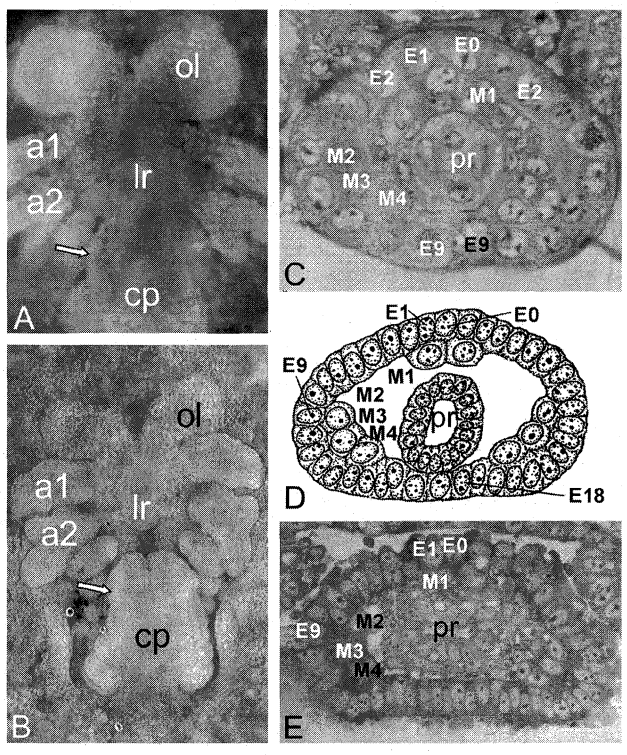

Figure 8. Teloblasts in decapod embryos. (A) Ventral view of the germ band of an embryo of the thalassinid *Callianassa australiensis*. The arrow indicates the area where the teloblasts form a ring (ectoderm and mesoderm) around the ventrally folded caudal papilla (cp). (a1, a2 = 1st and 2nd antennae, lr = labrum, ol = optic lobe). (B) Ventral view of the germ band of an embryo of the crayfish *Cambaroides japonicus* (labels as in A). Note the higher number of cells compared to A. (C) Transverse section through the caudal papilla of the American lobster *Homarus americanus* at the level of the teloblast rings; 19 ectoteloblasts (one unpaired E0 and nine paired E1 to E9 teloblast cells) and 8 mesoteloblast (four pairs in a specific arrangement) surround the forming proctodaeum (pr). (D) Transverse section through the caudal papilla of the Australian crayfish *Cherax destructor* at the level of the teloblast rings. In contrast to *Homarus*, there are about 40 teloblasts in the ectoderm. The mesoteloblasts show the same pattern as in the lobster. (E) Transverse section through the caudal papilla of the Japanese crayfish *Cambaroides japonicus* at the level of the teloblast rings. The pattern in this Northern Hemisphere crayfish is the same as in the Southern Hemisphere representative *Cherax* (after Scholtz 1993; Scholtz & Kawai 2002).

The investigation on cell division patterns in the germ band of embryos of the Australian freshwater crayfish *Cherax destructor* produced the surprising result that the growth zone of this species differs from that of all other malacostracan crustaceans studied so far in this respect (Scholtz 1992). The growth zone of malacostracans is situated in the posterior region of the embryo, immediately anterior to the telson anlage. It is formed by large specialized cells, the teloblasts, which bud off smaller cells only toward the anterior (see Dohle et al. 2004) (Fig. 8). This stem-cell-like cell type occurs in the ectoderm (ectoteloblasts) and the mesoderm (mesoteloblasts), and both sets of teloblasts produce most of the ectodermal and mesodermal material of the post-naupliar germ band. In the ground pattern of Malacostraca, we find 19 ectoteloblasts and 8 mesoteloblasts in circular arrangements (Dohle et al. 2004) (Fig. 8C). These figures are also present in most decapods studied in this respect, such as caridean shrimps, Achelata, Homarida, Thalassinida, Anomala, and Brachyura (Oishi 1959, 1960; Scholtz 1993). In contrast to this, in the freshwater crayfish *Cherax destructor* an individually variable number of more than 40 ectoteloblasts occurs, whereas the 8 mesoteloblasts

are conserved (Fig. 8D). Subsequent studies in other crayfish species from the Northern and Southern Hemispheres covering Astacidae, Cambaridae, and Parastacidae revealed that the pattern found in *Cherax* is a general freshwater crayfish character (Scholtz 1993) (Fig. 8E). This different growth zone pattern is hence a clear apomorphy of the Astacida, strongly indicating their monophyly.

This result is corroborated by a number of other developmental, in particular postembryonic, characters (see Scholtz 2002). In addition, phylogenetic analyses based on molecular datasets strongly support the monophyly of Astacida (e.g., Crandall et al. 2000; Ahyong & O'Meally 2004; Tsang et al. 2008). The question of freshwater colonization can now be addressed anew based on the strong support for Astacida monophyly. Monophyly alone is, of course, no proof for a single invasion into freshwater habitats, but parsimony and, in particular, several apomorphic freshwater adaptations strongly argue for a crayfish stem species already living in freshwater (see Scholtz 1995, 2002; Crandall et al. 2000). The modern and almost worldwide distribution of Astacida is thus best explained by the assumption of a freshwater colonization during the Triassic or even earlier before the break-up of Pangaea, which started in the Jurassic (Scholtz 1995, 2002).

6 CONCLUSIONS

With these examples, we demonstrate the different levels of impact on our views on decapod evolution resulting from comparative developmental studies (see Scholtz 2004). Including developmental characters in phylogenetic analyses expands our suite of characters for phylogenetic inference. In some cases, ontogenetic characters can be decisive in resolving phylogenetic relationships that cannot be inferred from adult characters alone. An example of this is the resolution of the common origin of astacoidean and parastacoidean crayfish. However, based on ontogenetic data, far-reaching conclusions can be drawn. For instance, the morphological "nature" of adult structures can be clarified with developmental analyses. This touches the core of morphology as a science. Morphological structures are transformed in the course of evolution; they change form and function to various degrees. In addition, new structures (novelties) emerge. These are, however, formed by pre-existing morphological precursors. Developmental analyses offer the possibility to trace these transformations and novelties. The analyses presented here of the 3rd maxillipeds and the scaphognathite of the 2nd maxillae in decapods provide examples for this approach. In the latter case, a century-old controversy was resolved and the evolutionary flexibility of limb structures was shown. In the former case, the correlation between an evolutionary shift of gene expression and altered morphology and function is revealed. Furthermore, evolutionary scenarios can be inferred based on ontogenetic data. This is shown by the timing of the gene expression shift. The transformation of a thoracic limb to a mouthpart takes place at the morphological and functional levels before gene expression has changed to the same degree (see Budd 1999). As is the case in adult structures, several ontogenetic characters are correlated with a certain lifestyle. If these characters are shared between an outgroup and part of the ingroup, it is possible to deduce the ancestral lifestyle of a given taxon. This approach is exemplified by the analysis of the early development of Dendrobranchiata. Yolk-poor eggs with a distinct cleavage pattern are found in shrimp-like crustaceans with a more pelagic lifestyle and a lack of brood care, such as euphausiaceans and, to a certain degree, anaspidaceans. This allows the conclusion that the decapod stem species was a pelagic shrimp-like animal rather than a benthic reptantian and thus strongly corroborates inferences based on the morphology of adults.

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