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Decapod Crustacean Phylogenetics

edited by

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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 cannot 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

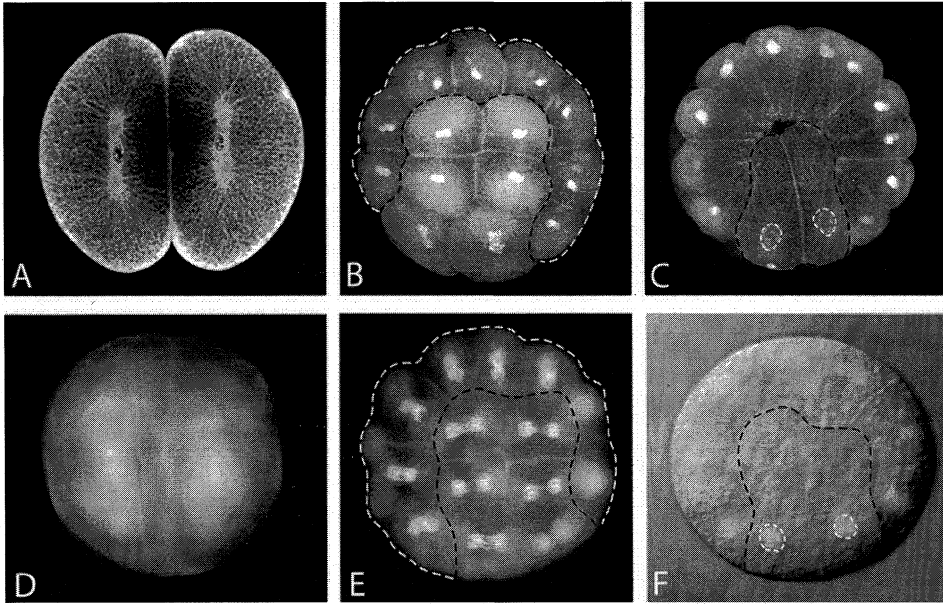


Figure 1. Different stages during early development of the dendrobranchiate shrimp *Penaeus monodon* (A-C) and of the euphausiacean *Meganyctiphanes norvegica* (D-F) stained with fluorescent dyes (Sytox A-C; Hoechst D-F). In F the fluorescence is combined with transmission light. The eggs show a low 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

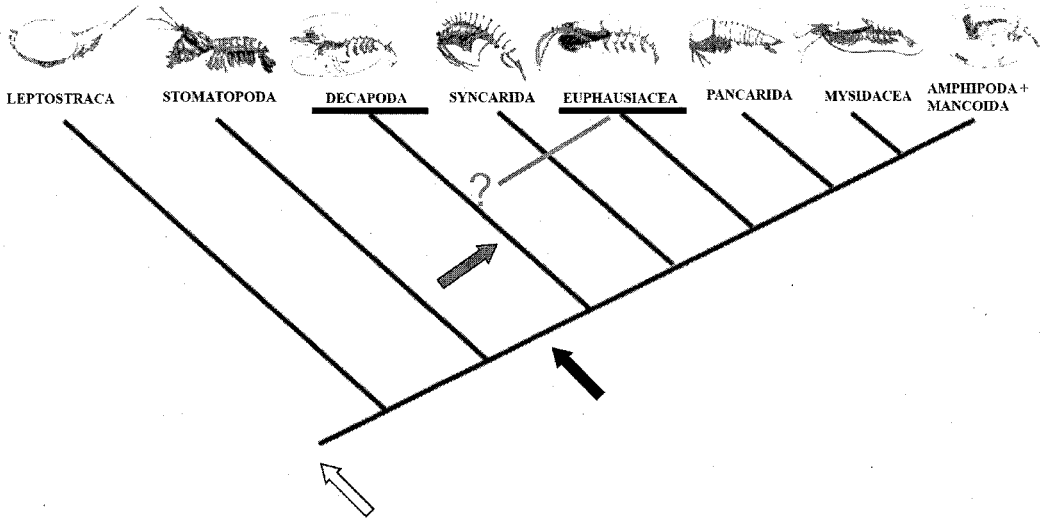


Figure 2. Malacostracan phylogeny according to Richter & Scholtz (2001). The arrows indicate the three possibilities for the evolution of the characteristic early development shared by Euphausiacea and Dendrobranchiata (Decapoda). The black arrow shows the possibility that the cleavage pattern evolved 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 representative 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

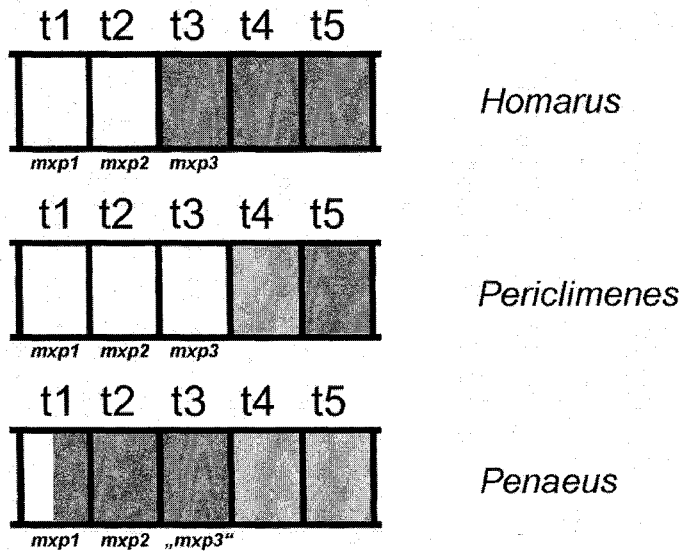


Figure 5. Scheme of the anterior expression of the UBX-AbdA protein in three decapod representatives with different degrees of pediform 3rd maxillipeds. *Homarus* and *Penaeus* with more pediform 3rd maxillipeds show a more anterior UBX expression boundary. *Penaeus* with the most pereopod-like 3rd maxilliped 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

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; Ah Yong & 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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