

The importance of lithographic limestones for revealing ontogenies in fossil crustaceans

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Abstract Developmental biology has become a major issue for understanding the evolution of Arthropoda. While usually only the ontogenies of extant species are studied, developmental information of fossil arthropods may exhibit developmental patterns not present in living ones. Crustacea possess, basically, a more gradual development than, for example, pterygote insects and would, therefore, be appropriate candidates for the study of fossil ontogenies. Remarkably, famous fossil deposits like the Devonian Rhynie Chert or the Early Palaeozoic ‘Orsten’-type deposits do not comprise the generally macroscopic malacostracan Crustacea (although most probably adult malacostracan fossils have already been found in the Cambrian). By contrast, the Late Jurassic Solnhofen Lithographic Limestones of southern Germany provide thousands of specimens (although only few morphotypes) that can be identified as malacostracan larvae, together with juvenile specimens differing in certain morphological aspects from their conspecific adults. More recent investigations with up-to-date imaging methodology on additional malacostracan crustacean larvae yielded also reconstructible developmental sequences of species from the Solnhofen deposits. The very similar fossil deposits of the Cretaceous lithographic limestones of

Lebanon have also yielded malacostracan larvae and juvenile specimens. We present a summary of the occurrences of crustacean fossils providing developmental information and a demonstration of the potential of the lithographic limestones in this context. The importance of developmental data for understanding crustacean evolution is also highlighted.

Keywords Larvae · Phyllosoma · Solnhofen Lithographic Limestones · Ontogenetic development · Phylogeny · Evolution

Evolution and development

In recent years, evolutionary developmental biology has become a major contributor for the reconstruction of evolutionary scenarios, particularly in arthropods (e.g., Schram and Koenemann 2001, 2004; Damen 2007; Prpic 2008). Developmental information on fossil arthropods can contribute to arthropod evo-devo issues as well as data on extant species (e.g., Schram and Koenemann 2001; Olesen 2007), although it has, up to now, only rarely been taken into account. Here we do not aim to discuss how these data can be technically incorporated into such comparisons (for this issue the reader is directed to Walossek 1993; Schram and Koenemann 2001; 2004; Olesen 2007). We want to present a survey on which types of fossil preservation are detailed enough to contribute developmental data of fossils of the arthropod taxon Crustacea for reconstructing the phylogeny and evolution of this taxon. Our main focus is here on fossils from lithographic limestones, together with the presentation of hitherto unpublished specimens that demonstrate the potential of these fossil deposits.

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Contributions of 4-dimensional data

Ontogenetic data contribute in various ways to phylogenetic analyses and to the reconstruction of evolutionary scenarios. One aspect is that they allow the evaluation of the taxonomic validity of a species. In the past, larval stages of various taxa have been mistaken as separate species. Common examples are the larvae of decapod crustaceans, e.g. the so-called ‘zoëa’ and ‘megalopa’, both of which were originally described as separate genera (Bosc 1802; Leach 1814) and only later recognised as larvae of already known species (for a detailed discussion see Gurney 1942).

Solving such an issue for a fossil species is a more difficult task than for a living one, because it is not possible just to breed an unknown larval or juvenile specimen to an identifiable adult stage. Nevertheless, it is important to keep in mind when dealing with fossils that differences in morphology may not be simply due to the presence of two different species, but rather may indicate the presence of different ontogenetic stages of the same species. Considering this has led to a reduction of the number of species in several animal taxa—for example in such prominent groups such as the dinosaurs (e.g., Dodson 1996; Horner and Goodwin 2009). Including supposedly separate species into a phylogenetic analysis that may be juvenile (or larval) specimens of another species, which is also included in the same analysis, might cause artefacts. Before running a phylogenetic analysis it is, therefore, important to evaluate the taxonomic validity of the considered species.

Another aspect is that including ontogenetic stages into phylogenetic analyses facilitates the use of additional character sets. These can be ‘structural characters’ (sensu Hickman 1999), i.e., features that are only present in certain stages, or ‘process characters’ (sensu Hickman 1999), which add a significant set of data, as it becomes possible not only to include presence or absence of a special structure, but also timing of appearance, either relative to other structures or relative to the developmental stage.

A general difficulty of a phylogenetic analysis solely including adults is the assumption that these stages correspond to one another (discussion of this issue for arthropods in Minelli et al. 2006). But ‘heterochrony’, the change of developmental timing, may be one of the driving forces of evolution and can be found in many textbooks (examples from common textbooks: Futuyma 1998; Freeman and Herron 2004). In many cases the adult stage of one species does not correspond to the adult stage of another species, but to an earlier developmental stage (e.g., in case of neoteny, one example from arthropods in Mjöberg 1925). For identifying such heterochronic changes, especially with the correct polarisation, it is necessary to include developmental data into a phylogenetic analysis

and later carefully reconstruct the character evolution (e.g., Ramsköld 1988; Guilbert et al. 2008; Haug et al. 2010a).

Additionally, developmental data indirectly contribute to the evaluation of homology hypotheses. Similar morphogenetic pathways of possible homologous structures support a homology hypothesis (but compare Nielsen and Martinez 2003 for this issue). But it is important not to overemphasise this argument for homology, as dissimilar morphogeneses do not necessarily exclude homology. Early developmental patterns may change although the final appearance of the structure remains the same. Scholtz (2005) has argued for the evolutionary independence of all developmental stages, so that earlier stages might differ but lead to similar later stages, as it has already been emphasized by de Beer (1958) and renewed by modern evolutionary developmental biology (e.g., Damen 2007).

Developmental data from fossil arthropods

As for other character complexes, fossils can exhibit ontogenetic character conditions that are not expressed in extant animals. This is especially important for the reconstruction of ground patterns and for the understanding of the early evolution of a group. Developmental data of fossils have been successfully used in various non-arthropod taxa (e.g., Sevastopulo 2005; Nützel et al. 2006; Schoch and Fröbisch 2006; Bandel 2007; Sumrall and Wray 2007). For fossil arthropods, dorsal hard parts of trilobites or ostracod shields have mainly been used for ontogenetic studies (e.g., Gramm 1973; Schweitzer et al. 1986; Smith 2000; Hughes et al. 2006 and references therein). Ontogenetic stages of trilobites have been recognised since the work of Barrande (1887). Trilobites and ostracods possess an enormous advantage for reconstructing the ontogenetic sequence: their development is gradual with distinct developmental instars.

The reconstruction of the sequence, i.e., the unequivocal assignment of non-adult stages to certain species is more problematic in many other arthropod groups, e.g., in pterygote insects. There the reconstruction is additionally complicated by the lack of comparable data from extant species. The knowledge of the ontogeny of extant insect species is, in fact, mainly limited to adults or late nymphal stages, pupae and late larval stages. As some insects have several dozens of larval stages, and subsequent larval stages may differ significantly from each other, there exists only little knowledge of most of the developmental sequences of insects (e.g., Klausnitzer 1991). Nevertheless, there are rare examples demonstrating that fossil non-adult stages of insects contributed significantly to the understanding of the evolution of certain sub-groups in providing developmental patterns not expressed in extant representatives (e.g., Vršanský 2008). The situation is different for

the basically more gradually developing Crustacea, and literature on developmental sequences of extant species is available for many different groups ('Journal of Crustacean Biology' even has a separate column 'Larvae and Development', with articles published in each issue).

The Rhynie Chert

Historically, it took some time after the first finds of larval fossil arthropods, Barrande's trilobites (1887), until the first arthropod larvae were found with more than just dorsal "hard parts" preserved (meaning better-sclerotized cuticular areas like shields or tergites). Larvae of the entomostracan crustacean *Lepidocaris rhyniensis* SCOURFIELD 1926—probably a branchiopod (cf. Walossek 1993; Schram and Koenemann 2001; Olesen 2007)—from the Devonian Rhynie Chert were the first ones also exhibiting "soft-parts" like appendages (Scourfield 1926). As the fossils from the Rhynie deposits are enclosed in chert, they can be viewed in 3D with even finest details preserved (for details on palaeoenvironment and preservation of Rhynie fossils, see, e.g., Trewin 1994; Fayers and Trewin 2004).

While most of the larval specimens of *L. rhyniensis* were less well-preserved than the older juvenile and adult stages, later on Scourfield (1940) reported two more larval specimens of fine preservation, especially exhibiting the developing vestigial limbs of the trunk. This example of well-preserved fossil crustaceans providing developmental data indicates the potential of such data to enhance our view of the phylogeny and evolution of development of a taxon (Walossek 1993; Schram and Koenemann 2001; Olesen 2007, 2009).

Rather recently, a second crustacean from the Rhynie Chert has been described, *Castracollis wilsonae* FAYERS and TREWIN 2003. It is another, even better verified branchiopod, which is very likely closely related to tadpole shrimps (Notostraca; Fayers and Trewin 2003). The animal is not yet known from larval stages, but the material has brought up also immature specimens that possess significantly fewer segments and limbs than the putative adults. Therefore, developmental data at least of the posterior appendages should be obtainable, but have not been included in the original description. A revision focusing on them is desirable.

A third crustacean, represented by early larval specimens, was found in the Windyfield Chert, another site only 700 m away from the original Rhynie Chert site. The first assumption was that this could be a larval stage of an additional branchiopod (Fayers and Trewin 2004; Haug et al. 2009c), but our own re-investigations of the complete material (about 80 specimens) render this unlikely and rather point to maxillopodan affinities.

The 'Orsten'

A much older, and possibly phylogenetically even more important, example of the fossilisation of crustacean and euarthropod larvae is the 'Orsten'-type preservation. 'Orsten' fossils are not only completely uncompressed and fully three-dimensionally preserved, but they have also retained virtually all structural details of the entire body, e.g., appendages, eyes, membranous areas and even minute structures like pores or setules only 0.2 µm in diameter. This exceptional and rare type of preservation occurs on a worldwide scale, but is nonetheless very rare and is, as far as we know, limited to small-sized specimens from 0.1 to 2 mm (for details see Maas et al. 2006). It is, therefore, predestined for finding preserved crustacean larvae, which are the most numerous euarthropod larvae in the marine environment, and crustaceans apparently dominate the 'Orsten' fossil assemblages.

Indeed, for no less than ten species parts of the ontogenetic sequence, mostly with a number of successive instars, could already be reconstructed:

- *Agnostus pisiformis* (WAHLENBERG 1818) (Müller and Walossek 1987), not a crustacean, but a close relative or the putative sister taxon to crustaceans (Walossek and Müller 1990; Stein et al. 2005; Waloszek et al. 2007);
- Entomostracan Eucrustacea such as the thecostracan maxillopod *Bredocaris admirabilis* MÜLLER 1983 (Müller and Walossek 1988), the branchiopod *Rehbachchiella kinnekullensis* MÜLLER 1983 with 30(!) successive instars (Walossek 1993), and *Yicaris dianensis* ZHANG, SIVETER, MAAS & WALOSZEK 2007 (Zhang et al. 2007; still in uncertain position within the taxon);
- *Hesslandona unisulcata* MÜLLER 1982 as a representative of the Phosphatocopina, the possible sister taxon of the Eucrustacea (together forming the Labrophora) (Maas et al. 2003); and
- A number of "stem crustaceans", such as *Martinssonella elongata* MÜLLER and WALOSSEK 1986 (Müller and Walossek 1986a; Haug et al. 2010b), *Oelandocaris oelandica* MÜLLER 1983 (Stein et al. 2005, 2008), *Goticaris longispinosa* WALOSSEK and MÜLLER 1990 (Haug et al. 2009e), *Cambropachycope clarksoni* WALOSSEK and MÜLLER 1990 (Haug et al. 2009e) and *Henningsmoenicaris scutula* (WALOSSEK and MÜLLER 1990) (Haug et al. 2010a).

More species await detailed re-descriptions of their ontogenetic sequences (e.g., *Walossekia quinquespinosa* MÜLLER 1983). In addition, several early developmental stages have been uncovered, which could not be affiliated with any larger stages of the established species. Most abundant were the larvae of the so-called type A1 (Müller

and Walossek 1986b), which also have the longest record in time (see also Maas et al. 2006), few have been referred to the so-called types A2 (Walossek and Müller 1989) and C (Müller and Walossek 1986b). Another set of larvae with long spines on their hindbodies awaits detailed description.

The fossils from the ‘Orsten’ have contributed significantly to the understanding of particularly the early evolution of Crustacea and its in-groups, also especially through the knowledge of their developmental modes. Their ontogenetic data could be used for reliable systematic assignments. An example is *Bredocaris admirabilis*, which exhibits the same developmental mode as the extant Thecostraca within the Maxillopoda, such as barnacles and allied (particularly the delay of post-cephalic limb development and segment expression in the thorax region). Another example are the non-eucrustacean species (“stem crustaceans” or better derivatives of the stem lineage of Eucrustacea), which exhibit a so-called head larva that is not known from any living crustacean, but has to be stated for the euarthropod ground pattern (e.g., Müller and Walossek 1986a; Walossek and Müller 1990; Waloszek and Maas 2005).

Other fossil deposits

Besides the fossils of the ‘Orsten’ type and the Rhynie Chert, there are only few more reports of fossil larval crustaceans with preserved “soft parts”. An example is a putative single barnacle cypris larva has been described from the Herefordshire Lagerstätte (Silurian, England), co-occurring with a possible conspecific settled specimen (Briggs et al. 2005).

Ostracod eucrustaceans occur frequently in the fossil record (Ordovician to today; Ikeya et al. 2005), but they are mostly preserved with their shells only (examples of “soft part”- preservation reviewed in Becker 2005). Based on morphometrics and shell structures, ontogenetic sequences have been reconstructed for a number of such species (e.g., Gramm 1973; Schweitzer et al. 1986). Preservation of ventral morphology for such fossils is rather rare, and only three occurrences yield developmental information of such structures: Weitschat (1983) described *Triadocypris spitzbergensis* WEITSCHAT 1983 from the Triassic of Spitzbergen, not only based on adults, but also specimens of a sub-adult stage are briefly mentioned. For *Pattersoncypris micropapillosa* BATE 1972 from the Cretaceous of Brazil, the last four sub-adult stages have been reconstructed by Smith (2000). A single larval ostracod specimen with preserved appendages from the Jurassic of Germany is depicted by Gramann (1962).

Remarkably, all the occurrences of larval crustacean specimens mentioned above refer either to derivatives of the stem lineage toward Eucrustacea (only ‘Orsten’-type

preservation) or to entomostracan eucrustaceans (‘Orsten’ type and all others). Malacostracan larvae, although usually larger than those of entomostracan species but likewise abundant, appear to be much rarer, despite the relatively good fossil record of adults of at least some malacostracan subgroups, such as decapods. The long larval phase with a high number of instars and the abundance of malacostracan larvae in the extant marine fauna (e.g., McConaughy 1992) would make the presence of malacostracan larvae in the fossil record even more likely. Crabs are, counting the number of species, a major part of Malacostraca and have a relatively good fossil record for adults, but only a single fossil crab larva has become known so far: The small specimen of a so-called zoëa larva was found in the stomach of a fossil fish from the Cretaceous of Brazil (Maisey and De Carvalho 1995). This Lagerstätte additionally yielded isolated eyes, which have been interpreted as belonging to decapod larvae (Tanaka et al. 2009). Other examples of malacostracan larvae are exclusively known from lithographic limestones.

Crustacean ontogenies in lithographic limestones

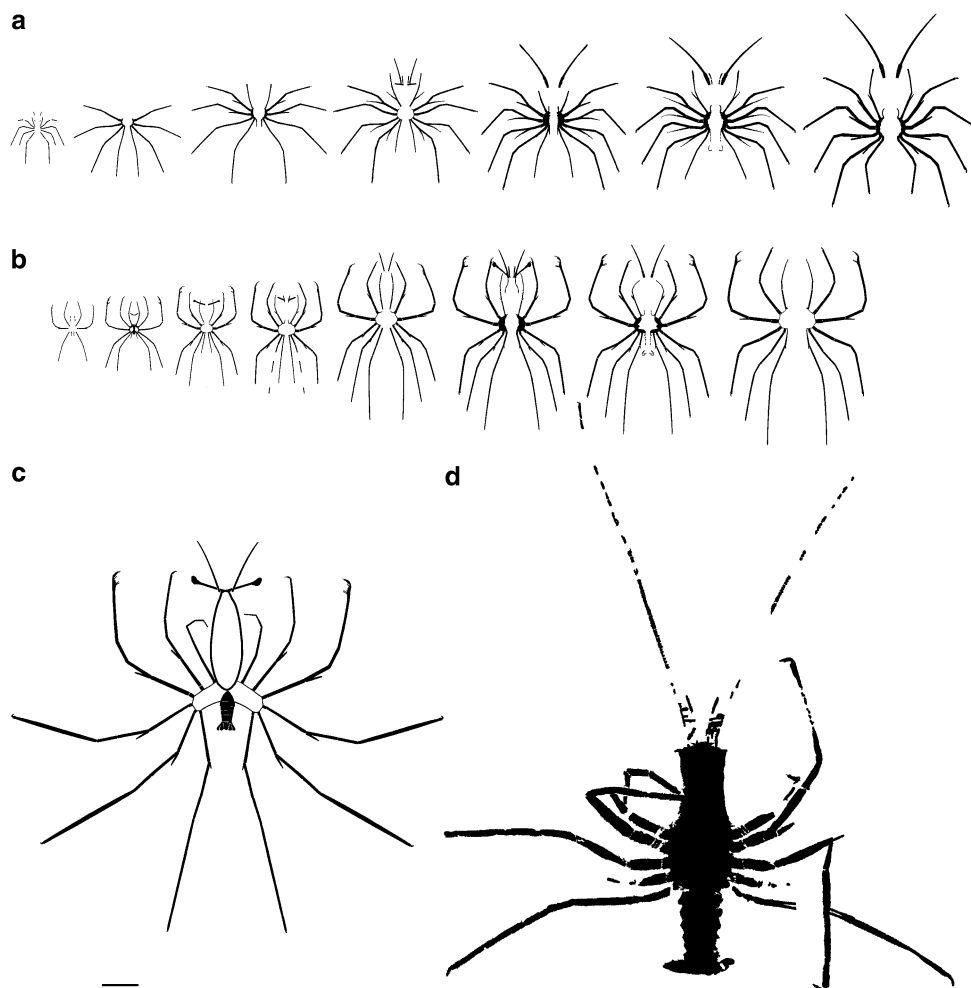
The Solnhofen Lithographic Limestones (Late Jurassic, Southern Germany) are richer in malacostracan crustacean larvae than other fossil Lagerstätten, at least if measured by quantity (see below). Additionally, while other Lagerstätten excel over the lithographic limestones in detail or three-dimensionality like the Rhynie Chert, and additionally by number of different larval morphotypes like the ‘Orsten’, those deposits lack larvae of Malacostraca.

Previous findings

Larvae

The Solnhofen Lithographic Limestones have yielded thousands of specimens of malacostracan larvae of the so-called ‘phyllosoma’ type, the zoëa-stage equivalent (sensu Williamson 1969) of the Achelata. This taxon comprises the spiny lobsters (Palinuridae), the slipper lobsters (Scyllaridae) and the rock lobsters (Synaxida) (Polz 1984). Phyllosoma larvae appear to be relatively large compared to other zoëa-equivalent larvae due to their enlarged cephalothorax and elongated pereopods, and very fragile (cf. Fig. 1), even being transparent in extant species, which makes their high abundance in the Solnhofen Lithographic Limestones rather astonishing. Achelata hatch as a phyllosoma and may undergo ten morphologically similar stages (also called phyllosoma) before moulting into the so-called ‘puerulus’ larva, the equivalent to the megalopa of other decapod malacostracans (sensu Williamson 1969).

Fig. 1 Four types of phyllosoma larvae known from the Solnhofen Lithographic Limestones. **a, b** Types A (= *Phalangites priscus*) and B (= *Palpipes cursor*) have been reconstructed with seven respectively eight successive stages (modified after Polz 1972, 1973). **c** Type C (= "*Dolichopus*" *tener*) is a composite of the body details from Polz (1971, 1987) and the head shield from Polz (1996). **d** Type D is redrawn after an UV image depicted in Polz (1995). Scale bar 10 mm



Three different types of phyllosoma larvae have been described from the Solnhofen deposits, at first as different species, *Palpipes cursor* ROTH 1851, *Phalangites priscus* MÜNSTER 1836 and "*Dolichopus*" *tener* WALTHER 1904. As these larvae probably correspond to certain achelate adults, their taxonomic names are most likely synonyms, either junior or senior synonyms (*Dolichopus* is pre-occupied, cf. Polz 1986). Polz has, therefore, argued for an abandoning of these names and referring to the three types as A (= *Phalangites priscus*), B (= *Palpipes cursor*) and C (= "*Dolichopus*" *tener*) until the larvae can be definitively assigned to "adult species" (Fig. 1a–c). Because of the enormous size of larva C (= "*Dolichopus*" *tener*), Polz (1971) also discussed the possibility of this type being a successive larval phase of type B (= *Palpipes cursor*), but later he excluded this assumption based on the detailed comparison of different morphological structures (Polz 1987).

The three larval types are not known from single developmental stages each, but in fact from series of stages. No less than seven stages have been reconstructed for type A (= *Phalangites priscus*) (Polz 1972), eight for

type B (= *Palpipes cursor*) (Polz 1973) and, based on the diagrams depicted in Polz (1987), at least three for type C (= "*Dolichopus*" *tener*) (Fig. 1a–c). These sets are not only based on morphometric measurements, but also on morphological changes of pereion, dactyli of the pereio-pods, and tail fan. With these ontogenetic details, the Solnhofen palinurids have a high potential to be taken into account for phylogenetic studies including fossil and extant species as soon as it is possible to assign the larvae to adult stages.

In addition to the three phyllosoma types, Polz (1995) described a single giant specimen, termed larva D, which he interpreted as a specimen killed and preserved while moulting from a phyllosoma stage into a puerulus stage. The specimen is much larger than the three other phyllosoma larvae types (Fig. 1d), and cannot be connected to one of them nor to any of the known adult species at present. Both phyllosoma type A (= *Phalangites priscus*) and type B (= *Palpipes cursor*) have a high potential of being a larval stage of *Palinurina longipes* MÜNSTER 1839; the other type might represent the larval stages of the only other species of *Palinurina* that is at the moment thought to

be valid, *Palinurina tenera* OPPEL 1862 (Garassino and Schweigert 2006). Polz (1995) furthermore pointed to the possibility of specimens of *P. pygmaea* (MÜNSTER 1837) and *P. intermedia* (MÜNSTER 1838) representing in fact puerulus stages of *P. longipes*. A re-investigation of the *Palinurina* material, best coupled to a morphometric approach, appears to be needed.

The phyllosoma type C (= “*Dolichopus*” *tener*) has been hypothesised to represent the larval stages of a species of the other achelate genus known from the Solnhofen Lithographic Limestones, the putative “stem-scyllarid” *Cancrinus claviger* MÜNSTER 1839 (Polz 1996). The morphological difference between the antenna of the adult *C. claviger* (the only valid species of this genus, see Garassino and Schweigert 2006) and the phyllosoma type C (= “*Dolichopus*” *tener*) appears to question the assignment, but newer findings may provide a solution to this problem (see below).

Other sub-adult stages

The phyllosoma larvae are the only true larvae described from the Solnhofen Lithographic Limestones until recently. Besides these larvae, later ontogenetic stages exhibiting

“post-larval” changes between juvenile stages and adults could be found (for difficulties with the term “post-larval” see Williamson 1969, also Haug et al. 2009d). These differing morphotypes of juvenile stages and adults were originally described as different species (see Garassino and Schweigert 2006). Recognising them as representatives of different developmental stages is extremely important for phylogenetic analyses at different levels, as already pointed out above.

Garassino and Schweigert (2006) recognised that the specimens of the eryonid species known as “*Knebelia schuberti*” (VON MEYER 1836) more likely represent early juvenile stages of another co-occurring eryonid, *Cycleryon propinquus* (SCHLOTHEIM 1822). The ontogenetic changes detected in this case can also be found in other *Cycleryon* species, like, e.g., in *Cycleryon elongatus* (MÜNSTER 1839) (Fig. 2). Schweigert (2001) recognised that the specimens referred to as *Cycleryon* “*spinimanus*” (GERMAR 1827) rather represent the females of *C. propinquus*. Thus, the three originally described species (“*K. schuberti*”, *C. “spinimanus”*, *C. propinquus*) indeed represent only a single species. Further re-investigation of the complete material (and new investigations of new material) of *C. propinquus*, *C. “spinimanus”* and “*K. schuberti*” should

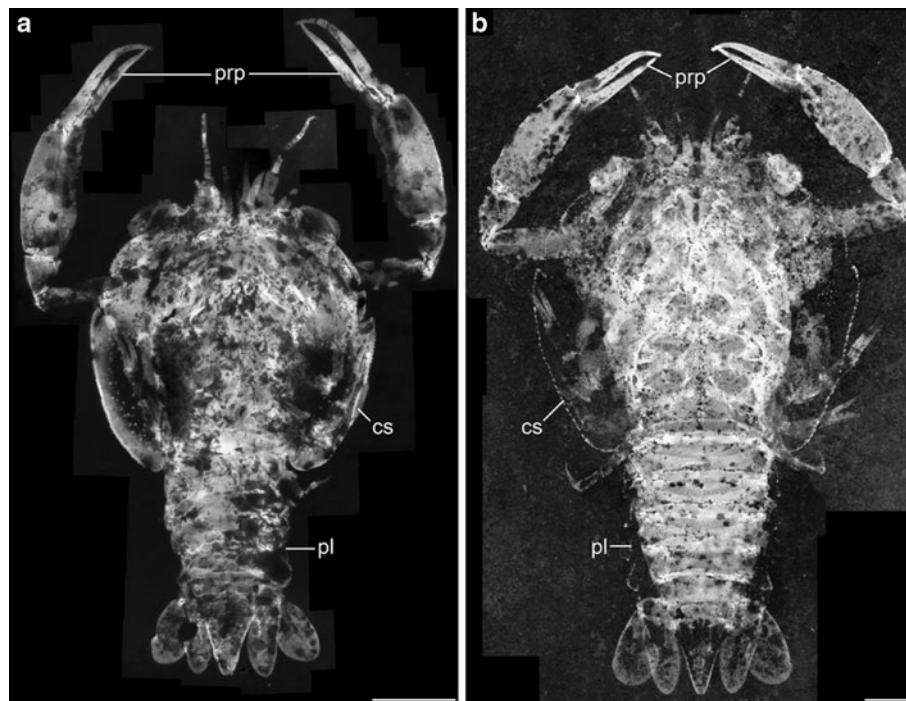


Fig. 2 Two specimens of *Cycleryon elongatus* (MÜNSTER 1839) from the Solnhofen Lithographic Limestones (Late Jurassic, Southern Germany), part of the private collection of Matthias Wulf, Rödelsee (Germany). Scale bars 2 mm. **a** Composite orange-green-fluorescence image of a specimen of a “*Knebelia schuberti*” stage, i.e., earlier developmental stage. It exhibits an almost circular cephalothoracic shield and, compared to the older instar depicted in **b**, relatively long

first pereiopods. Specimen found near Eichstätt. **b** Composite image under normal light, inverted for better comparability, of a later developmental stage. It has relatively shorter first pereiopods than the earlier ontogenetic stage shown in **a**. The cephalothoracic shield is more hexagonal and the pleon a bit larger than on the younger specimen. Specimen found near Zandt, collection number 9915. *cs* cephalothoracic shield, *pl* pleon, *prp* pereiopods

reveal more details on the ontogeny of *C. propinquus*. For example, it should be possible to find “*K. schuberti*” specimens that are juvenile representatives of *C. “spini-manus”*, i.e., juvenile females of *C. propinquus*. It might even be possible that the megalopa larva of *C. propinquus* is present in the “*K. schuberti*” material. The Meiura (the taxon that includes the true crabs and the anomalans, “short-tail” lobsters, hermit crabs etc.) have megalopa larvae differing significantly from juvenile and adult instars. However, the megalopa larvae of other reptantians differ only slightly from the juvenile stage and are by some authors also recognised as non-larvae (Felder et al. 1985). For the even more well-known eryonid *Eryon arctiformis* (SCHLOTHEIM 1820) Malz (1969) already recognised that juvenile specimens have longer appendages compared to later stages. This is also true for the “*Knebelia schuberti*” stages of *C. propinquus* compared to later instars, can also be recognised in many other species (e.g., erymids and aegerids) and might indeed be a general feature for Decapoda.

Newer developments

New methods

In order to detect morphogenetic changes in fossil crustacean species, the development and application of new methods for documenting also small specimens with even finer details was necessary. The usual way of taking one image of the whole specimen or few images of certain details is simply not sufficient for studies on larval and other sub-adult specimens with sizes of sometimes less than five millimetres. A method from palaeobotany called composite-fluorescence microscopy (Bomfleur et al. 2007) can be used for documenting small specimens from the Solnhofen Lithographic Limestones. This method is applicable, because many specimens found in lithographic limestones exhibit fluorescence when exposed to UV light (e.g., Polz 1993; Garassino and Schweigert 2006). The use of fluorescence enhances the contrast between fossil and matrix, and, together with the application of software programs for summing the information of several hundreds of images both in *z*-axis (image fusion) and *x*- and *y*-axis (image stitching), highlights the smallest preserved details (Haug et al. 2008a, b, 2009a, d).

Studying specimens that do not show UV fluorescence by using composite imaging under normal light conditions can still yield very good results (Haug et al. 2009d). Additionally, specimens from certain deposits like Zandt (Late Jurassic, Solnhofen Lithographic Limestones) or from Lebanese limestones (Late Cretaceous) that exhibit no UV fluorescence (for unknown reasons) emit orange light when exposed to green light (Haug et al. 2009b, cf. Fig. 4).

New larvae and developmental sequences

Recently, the first fossilized larva of an extinct mantis shrimp (Stomatopoda) has been discovered in the Solnhofen Lithographic Limestones (Haug et al. 2008a, b). The specimen could not be ascribed to any of the established stomatopod species from the lithographic limestones. Extant stomatopod larvae may be relatively large, at least the later larval stages, so they should in fact have at least some potential to be fossilized and recognised. And, in fact, further inspections of the fossil stomatopod material revealed more larval specimens: The newly described species *Spinosculda ehrlichi* HAUG, HAUG and WALOSZEK 2009 was originally based on two specimens (Haug et al. 2009a). The smaller one is interpreted as a larva. It is not very well preserved in the anterior part and cannot easily be identified as a stomatopod larva; but a unique structure, a pair of backward-pointing spines on the last segment of the pleon, links the larval specimen to a slightly larger juvenile specimen, which is an unequivocal stomatopod. The latter specimen exhibits the tri-flagellate antennula, with even its exact branching pattern recognisable, the tagmosis, and the tail fan as in other stomatopods.

In the meantime, more larval specimens of this species have been found, one being very similar to the holotype (Fig. 3a). With this, *Spinosculda ehrlichi* is the first case of a crustacean from the Solnhofen Lithographic Limestones, where we can confidently link larval stages to a (“post-larval”) juvenile instar. This may be facilitated by the fact that the preserved specimen is comparable to a so-called ‘early megalopa’, i.e., a last zoëa stage, which already exhibits some characters of a megalopa stage (Villamar and Brusca 1988). Such stages have only rarely been reported in extant animals, but as, for example, Anger (2006) emphasises, larval stages of Decapoda (and probably also Stomatopoda) exhibit certain variability, especially in long larval sequences. Therefore, early megalopae might be more widespread than their report indicates. Other fossil specimens from the Solnhofen Lithographic Limestones also might represent early megalopae like a recently reported ill-preserved, possible scyllarid phyllosoma (Haug et al. 2009d) or also phyllosoma type D (see above, Polz 1995).

The achelate *Cancrinus claviger* has been hypothesised to be a stem-lineage derivative of Scyllaridae, the slipper lobsters (Förster 1973, 1984, 1985). This was based on the large (second) antennae of *C. claviger* that have a flattened, paddle-shaped distal area, similar to the condition in slipper lobsters, but differing from the extant animals in being multi-annulated and not just comprised of a single element. New immature, but “post-larval” specimens assigned to *C. claviger* exhibit a more plesiomorphically-appearing morphology. In the smallest known specimen, the antennae

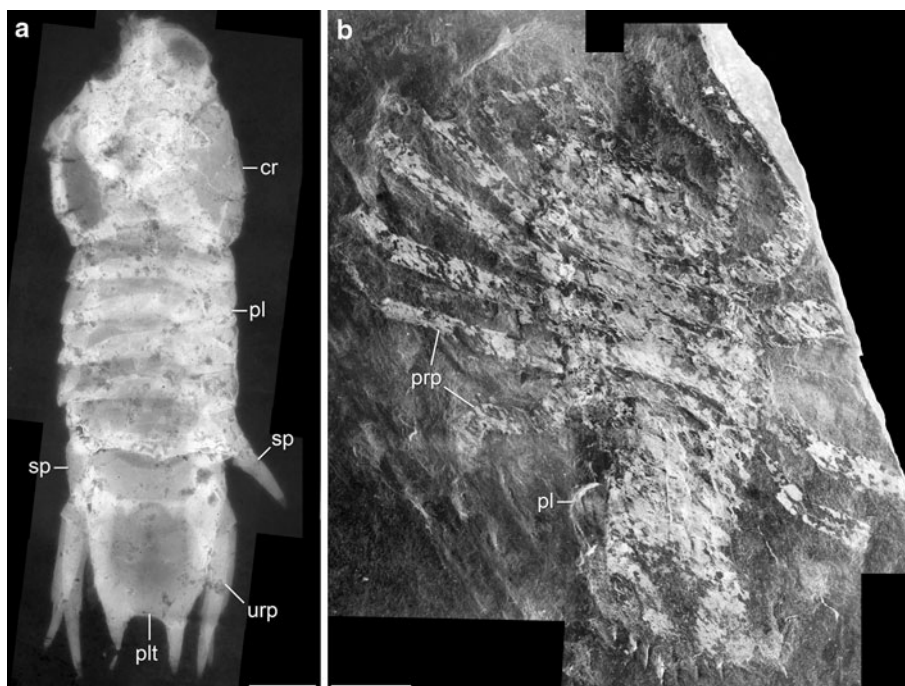


Fig. 3 New larval and juvenile specimens of malacostracan Crustacea from the lithographic limestones. **a** Composite orange-green-fluorescence image of a larval specimen of *Spinosculda ehrlichi* HAUG, HAUG & WALOSZEK 2009 (Wegscheid near Schernfeld, Eichstätt Formation, Early Tithonian). Specimen closely resembling the holotype. Part of the collection of Roger Frattigiani, Laichingen (Germany), no. D198100022/01. *Scale bar* 1 mm. **b** Composite inverted reflective-light image of a specimen of “*Eryoneicus*

sahelalmae” ROGER 1944 (Sahel Alma, Lebanon, Late Cretaceous, Santonian). This specimen might be a juvenile representative of *Cancrinus libanensis* GARASSINO and SCHWEIGERT 2006. Specimen from the collection of the Museum für Naturkunde der Humboldt-Universität zu Berlin MB.A.1665. *Scale bar* 5 mm. *cr* cephalothoracic region, *pl* pleon, *plt* pleotelson, *prp* pereiopods, *sp* spine, *urp* uropod

are simple long flagella, similar to those of spiny lobsters (Palinuridae). In the next larger known specimen the basal 18 annuli of the antennae are broadened. Therefore, the antenna of *C. claviger* is interpreted as developing from a palinurid-like flagellate antenna in earlier “post-larval” stages to a more scyllarid-like spatulate antenna in later “post-larval” stages. *Cancrinus* is, as a consequence, considered as the sister group to the slipper lobsters (now termed Scyllaridae *sensu stricto*, see Haug et al. 2009d), together forming Scyllaridae *sensu lato* (same reference). Furthermore, the ontogeny of *C. claviger* is seen as the basis for an evolutionary scenario, on how the Scyllaridae can be derived from a palinurid-like ancestor via the heterochronic process of peramorphosis (Haug et al. 2009d).

Additionally, these findings support an older assumption of possible affinities of one of the phyllosoma larvae from the Solnhofen Lithographic Limestones, namely form C (=“*Dolichopus*” *tener*). Phyllosoma type C (=“*Dolichopus*” *tener*) has been hypothesised by Polz (1996) to be a larval stage of *Cancrinus claviger*. But one morphological difference interfered with this assumption. The phyllosoma larva of type C (=“*Dolichopus*” *tener*) has, just like the other phyllosoma types, flagelliform antennae, while *C. claviger* has shortened spatulate antennae. As mentioned

above, the newly found juvenile specimens exhibit a partial transition from one status to the other. This new finding cannot directly support the affinities of phyllosoma type C (=“*Dolichopus*” *tener*) to *C. claviger*, but it solves the difficulties of the different types of antennae, as the new “post-larval” specimens bridge these differing morphologies.

Another possible immature specimen of *Cancrinus* has become known from Lebanon, therefore named *C. libanensis* by GARASSINO and SCHWEIGERT (2006). A comparable specimen has originally been described as *Eryoneicus sahel-almae* ROGER 1944 (Roger 1944), which might, therefore, be a juvenile stage of *C. libanensis* (Haug et al. 2009d). A specimen assigned to “*E. sahelalmae*” from the collection of the Museum für Naturkunde der Humboldt-Universität zu Berlin is relatively badly preserved (Fig. 3b), but does not contradict the above mentioned assumption by Haug et al. (2009d). “*Eryoneicus sahelalmae*” was previously interpreted as an equivalent to an eryoneicus larva of an eryonid (Roger 1944; Aguirre-Urreta et al. 1990), but there is no indication of possible eryonid affinities. Therefore, this report of larvae from lithographic limestones of Lebanon is considered to be erroneous.

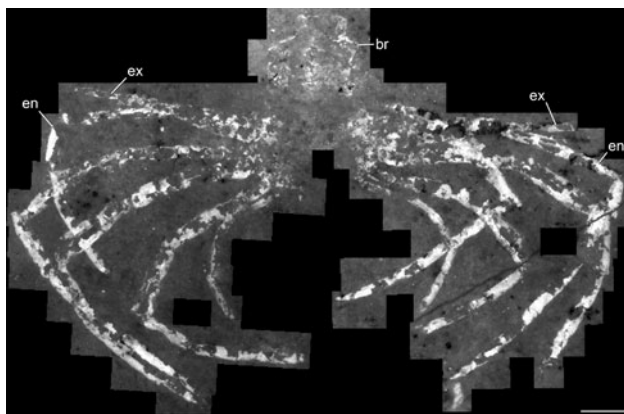


Fig. 4 Composite orange-green-fluorescence image of a phyllosoma from the lithographic limestones of Haqel (Late Cretaceous, Lebanon). Specimen no. 75102301 from the collection of Hermann Polz, Geisenheim (Germany), originally from the collection of Dr. U. Hückel. *Scale bar* 2 mm. *br* body remains, *en* endopod of pereopod, *ex* exopod of pereopod

A true phyllosoma larva has been found recently in the Cretaceous Lebanese lithographic limestones (Pasini and Garassino 2009). As the similarities of the Lebanese lithographic limestones to the Jurassic Solnhofen Lithographic Limestones are striking concerning faunal composition, and as phyllosoma larvae are very abundant in the Solnhofen deposits, the find of such a larva in the deposits from Lebanon was, hence, not too surprising. Pasini and Garassino (2009) mention further specimens in the private collection of Hermann Polz, Geisenheim (Germany) (Fig. 4), and at the Institut für Geowissenschaften of the University of Tübingen. Palinuridae that are candidates for being the possible adult species of these phyllosoma larvae in the lithographic limestones of Lebanon, are the species of the genus *Linuparus* WHITE 1847.

Where are the zoëa larvae?

In the light of the fact that phyllosoma larvae are very abundant in the Solnhofen Lithographic Limestones, the question arises, where are the larvae of all the other Crustacea? Phyllosoma larvae are soft and appear very fragile. So why are no other, and particularly those more firmly sclerotized, zoëa-stage larvae present? The stomatopod larvae, the only other larvae found in the Solnhofen Lithographic Limestones, may or may not be homologues to the zoëa stages of Decapoda (compare Gurney 1942 and Williamson 1969). But what is really different between phyllosoma and stomatopod larvae and zoëa stages of other taxa? One point may be that the former are larger than most other zoëa stages, but the same holds true for the size of eryoneicus larvae of extant eryonoids. The small size of most zoëa stages is probably the main

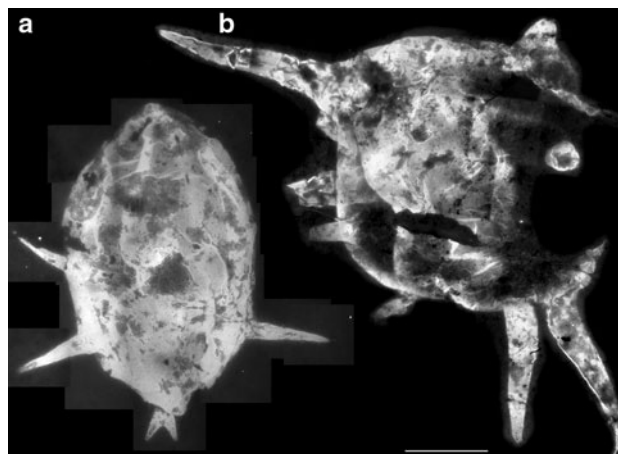


Fig. 5 Composite fluorescence images of two possible crustacean specimens from the Solnhofen Lithographic Limestones that might represent remains of zoëa larvae. **a** Specimen from the collection of Markus Gebert, Iphofen, found near Blumenberg, Eichstätt Formation, Early Tithonian. **b** Specimen from the collection of the Staatliches Museum für Naturkunde Stuttgart, SMNS 67534, from Wegscheid near Eichstätt, Eichstätt Formation, Early Tithonian. *Scale bar* 1 mm

reason, why there is only a single fossil report of a zoëa of a non-achelate, a crab zoëa from the Cretaceous of Brazil (Maisey and de Carvalho 1995). This incomplete specimen, consisting of a head shield with attached compound eyes, lacking trunk and appendages, has been found in the preserved stomach of a fossil fish (see above). Although the approach of finding small Crustacea in the stomach of fossil fishes appears to be promising, only one further attempt has been reported recently (Tanaka et al. 2009). Probably, fossil fishes are seen as too valuable for destruction in the attempt of extracting small-sized (and partly fragmentary) crustaceans, especially as one cannot be sure to find anything at all.

Nevertheless, it should be possible to find zoëa-stage specimens in the Solnhofen Lithographic Limestones. Indeed, possible remains of zoëa larvae from these deposits are available (Fig. 5a, b). These small remains probably are of crustacean origin, based on their substance and their fluorescence capacities. The specimens appear to be distorted, but a number of spines can be recognised (Fig. 5). Both specimens do not allow any confident interpretation. Still they might represent the head shields of larvae of either a stomatopod or maybe a sergestid penaeid shrimp, based on the number of spines. Both stomatopods and penaeids are present in the Solnhofen Lithographic Limestones (see also above). Extant penaeids have a relatively high number of larval stages and, thus, the find of a fossil penaeid larva in Solnhofen Lithographic Limestones appears to be plausible. Yet, the two specimens presented in Fig. 5 are far too badly preserved to allow a reliable phylogenetic placement.

Developmental data of another arthropod in the lithographic limestones

Another arthropod, but not a crustacean, from the Solnhofen Lithographic Limestones possibly also yielding developmental information has been described as *Mesolimulus walchi* (DESMAREST 1822), a horseshoe “crab” (Xiphosura, Chelicerata). Extant limulids hatch as a so-called ‘trilobite larva’. Until now, no such larva has been found, which could be assigned to *M. walchi* or any other species of fossil xiphosurans. The smallest specimen known to date measures approximately 2 cm (Fig. 6), therefore being much larger than the trilobite larva. As for Crustacea, the juvenile development of extant limulids is not described in detail in the literature, while detailed information is available of both embryonic and larval development (e.g., Korschelt and Heider 1936; Scholl 1977). Therefore, we lack ontogenetic data from extant xiphosurans for a comparison with this small specimen of *M. walchi*. Additionally, this specimen is relatively character-poor and does not allow a detailed comparison with older stages. Nevertheless, it demonstrates the possibilities to find also smaller specimens representing earlier developmental stages in the lithographic limestones. Since the xiphosuran trilobite larvae are not too small, they should have a certain potential to be present in the fossil record.

Future perspectives and conclusions

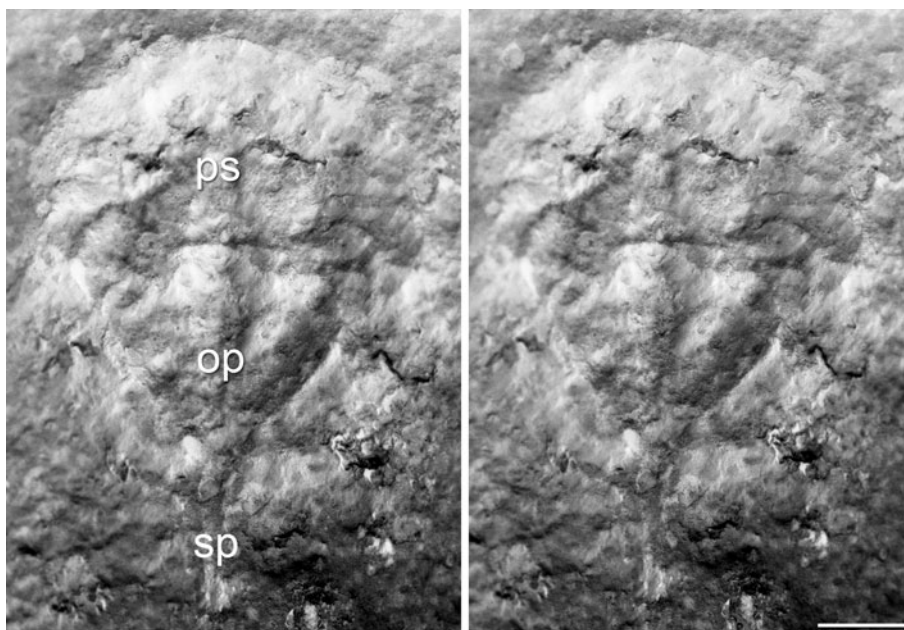
One topic for future research on crustaceans from lithographic limestones is the taxonomic validity of the described

species. Possibly, further described crustacean species from these deposits represent juvenile or larval stages of other species. One important character to distinguish malacostracan species from the Solnhofen Lithographic Limestones is the morphology of the rostrum. The rostrum, however, undergoes significant changes during ontogeny, for example in stomatopods and anomalans (e.g., Gore 1971; Morgan and Goy 1987; Wehrmann et al. 1996). Therefore, for species where the rostrum is an important diagnostic character, sub-adult specimens should be taken into account. Additionally, one should apply morphometrics to achieve further data. For the achelates this might finally facilitate the assignment of the phyllosoma larvae to particular adults of established species.

Also the combination with neontological investigations yields more potential, and the inclusion of fossil data into broader phylogenetic analyses is likewise important (Schram and Hof 1998; Schram and Dixon 2004). A palaeo-developmental approach has rarely been applied, or it was restricted to fossils in ‘Orsten’-type preservation (e.g., Walossek 1993; Stein et al. 2008; Haug et al. 2009e). As certain analyses of extant taxa heavily depend on larval information, for example in Achelata (e.g., McWilliam 1995), and as the fossils from the lithographic limestones can provide this information, the inclusion of fossil ontogenetic data appears to be easily possible. Furthermore, more data on the juvenile phase of extant taxa are necessary to better understand this ontogenetic phase also in fossil taxa.

The Solnhofen Lithographic Limestones yielded a number of fossil species in crucial phylogenetic positions for resolving still unstable phylogenies and confidently

Fig. 6 Stereo image of the smallest known specimen of *Mesolimulus walchi* (DESMAREST 1822) (Xiphosura, Chelicerata) from the Solnhofen Lithographic Limestones (Schernfeld, Eichstätt Formation, Early Tithonian). Part of the collection of Norbert Winkler, Stahnsdorf. *op* opisthosoma, *ps* prosoma, *sp* spine. Scale bar indicates 3 mm



reconstructing ground patterns of major taxa. For example, polychelid lobsters have been resolved as the sister group of the remaining reptantian lobsters in recent phylogenetic analyses (e.g., Scholtz and Richter 1995; Dixon et al. 2003). But Polychelida is the crown group of Eryonoidea. It is a highly specialised in-group taxon with a peculiar larva and adaptations to living in the deep sea, including reduction of eyes. Furthermore, there are only few extant eryonoid species (for a list of all fossil eryonoids see Schweitzer et al. 2010). For reconstructing the ground pattern of Reptantia, fossil eryonoids may, therefore, provide significant data (see Schram and Dixon 2004; Ah Yong 2009), especially for understanding the developmental mode, as extant eryonoids and Achelata, the most basal offshoot of the eurentantian lineage, have aberrant larvae.

A reconsideration of the evolution of the stomatopod malacostracans is currently under way. The earlier evolutionary history of this group is well known from various Carboniferous fossils (Schram 1969; Schram 2007). Also a plausible evolutionary scenario has been successfully established by Schram (2007). But the Mesozoic stomatopods have usually not been considered, as they are thought to be very similar to the crown group. As newer investigations have demonstrated (Haug et al. 2008a, b, 2009a), the disparity of the Mesozoic forms from the extant species is larger than estimated. These new finds will shed light on the stepwise evolution from Carboniferous to extant species and also provide additional developmental data.

Understanding the developmental pattern in early stomatopods also has a bearing on the eumalacostracan ground pattern. Gurney (1942) has homologised the larval stages and phases of Stomatopoda and Decapoda, while Williamson (1969, 1982) in his re-evaluation of Gurney's system restricted his theory to Decapoda. If indeed the larval stages of Stomatopoda are homologous to the decapod zoëa (or the zoëal stages), this larval stage must have already been part of the eumalacostracan ground pattern. The future aim is to include newly gathered developmental data from fossil species together with those of extant ones into phylogenetic analyses. First steps have been taken, new methods are available, now the consequent application to a large amount of material has to be pursued.

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