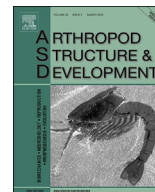




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“Intermetamorphic” developmental stages in 150 million-year-old achelatan lobsters – The case of the species *tenera* Oppel, 1862



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ABSTRACT

We re-investigated the fossil species *tenera* Oppel, 1862, an achelatan lobster (traditionally named *Palinurina tenera*) found in 150 million years old limestones of southern Germany. All known specimens attributed to this species show a mixture of characters, which in modern forms occur either in larvae or post-larval juveniles. Hence these specimens provide insight into a phase in ontogeny that is no longer present in the developmental sequence of any modern achelatan lobster, as the latter ones skip this phase and replace it by a drastic metamorphosis. Comparable cases have been described earlier, yet did only comprise single stages or two successive ones at most. In the here described case four developmental stages are preserved. The reconstructed ontogeny of *tenera* therefore represents the currently best known sequence of an early achelatan lobster that covers this specific intermediate phase. The largest known stage most likely still represents an immature of a yet undiscovered adult. These findings support the interpretation that early achelatan lobsters developed in a more gradual ontogenetic sequence than modern forms. It furthermore demonstrates that it was even more gradual than anticipated previously.

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1. Introduction

The Mesozoic appears to be an important time for the evolution of reptantian decapods, i.e. lobsters, crabs and alike (e.g., Klompmaker et al., 2013; Schweitzer and Feldmann, 2014). Many distinct evolutionary lineages appear and diversify in this time period. This is also true for the reptantian ingroup Achelata (Schweitzer and Feldmann, 2014) represented by spiny lobsters and slipper lobsters in the modern fauna. The adults of both groups possess a rather broad pleon and a tail fan with a fairly square-shaped telson and characteristic softer posterior areas (e.g., Holthuis, 1991; Scholtz and Richter, 1995; Chan, 2010). While spiny lobsters have very long and thin antennae, slipper lobsters possess broad, shovel-like ones (for an evolutionary scenario, see Haug et al., 2016). Achelatan lobsters are of special scientific interest, because of their highly specialised post-embryonic ontogeny, including the most profound metamorphosis among “higher” crustaceans (= malacostracans; Gurney, 1942). Thus, besides more obvious groups such as holometabolous insects, Achelata is a good candidate for

studying the evolution of metamorphosis (e.g., Haug and Haug 2013; Haug et al., 2013).

Early larval stages of achelatan lobsters are called phyllosoma larvae (Leach, 1817; Williamson, 1969). These can be considered to be the most aberrant crustacean larvae (maybe together with some stomatopod larvae; see Ah Yong et al., 2014). Their shield is leaf-like, thin, and transparent, with stalked eyes, antennulae and antennae at its front, with a large distance to the mouth parts. Also the thorax is thin, transparent and flat, the thoracopods 3 to 8 extend from it laterally. These thoracopods are very long and can span far more than 100 mm. This delicate overall habitus allows these sometimes giant larvae to float in the water column. Additionally, phyllosoma larvae also grab jellyfishes and “ride” on them while occasionally also preying upon them (e.g., Wakabayashi et al., 2012). The up to ten phyllosoma larva stages are followed by a drastic metamorphosis into the nisto or puerulus larva, which is lobster-like in morphology, resembling its corresponding juvenile (and with this also the adult) (e.g., Marinovic et al., 1994; Mikami and Greenwood, 1997; Webber and Booth, 2001).

Remarkably, such fragile appearing phyllosoma larvae have been found in the fossil record, in Mesozoic limestones (Polz, 1971, 1972, 1973, 1987, 1995, 1996; Pasini and Garassino, 2009; Haug et al., 2011a, 2013). In the lithographic limestones of the

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Solnhofen area thousands of specimens have been uncovered. More important, these fossils provide us insights into the evolution of the highly specialised ontogeny of modern achelatan lobsters. While most of the fossil larvae appear as “normal” phyllosoma larvae, some of the Mesozoic achelatan lobster larvae do not entirely resemble modern phyllosomes. Instead these fossils possess a mixture of phyllosoma and post-phyllosoma characters. More interestingly, different types of these larvae show different kinds of mixtures, i.e. in each case different characters are either expressed in a phyllosoma-type or in a post-phyllosoma-type manner (when compared to their modern counterparts) (Haug and Haug 2013; Haug et al., 2013).

Three different evolutionary interpretations of these observations on the larvae with mixed character states have been offered by Haug and Haug (2013) and Haug et al. (2013):

- 1) Some of these larvae could represent species that branched off before modern Achelata and did not yet possess as specialised larvae as do modern forms. In other words, these larvae would have acquired some, but not yet all of the specialisations that modern phyllosoma larvae possess.
- 2) Some of these larvae could represent species that possessed already fully specialised phyllosoma larvae, yet did not transform within a single moult into the lobster-like form, but performed this transition within several moults.
- 3) Some of these larvae could be paedomorphic adults, i.e. they retained certain larval features into the adult stage.

Haug et al. (2013) supposed that all three options are likely to be represented among the currently known material of Mesozoic achelatan larvae with “intermetamorphic” morphology, but could not yet identify for each of the specific larvae, which of these options occurred. Hence, they suggested to thoroughly re-investigate the material to facilitate such an identification.

Here we present new data on supposed adult specimens of the achelatan lobster *tenera* Oppel, 1862 (traditionally named *Palinurina tenera*) from the lithographic limestones of the Solnhofen area, Upper Jurassic of southern Germany. We demonstrate that all known specimens attributed to this species exhibit in fact a larval-type morphology, and discuss the impact of this finding.

2. Material and methods

2.1. Material

Specimens described here come from different collections (Fig. 1). The holotype of the species *tenera* (“*Palinurina tenera*”) is part of the Bayerische Staatssammlung für Paläontologie und Geologie München (BSPG AS I 995). Two specimens come originally from the private collection of Roger Frattigiani, Laichingen, Germany; one of these specimens is now part of the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS 65476). The second specimen will be referred to as “Larva D” specimen, as it was addressed in this way by Haug et al. (2014). Four additional specimens have been provided by private collectors from Germany, namely: Falk Starke, Bodenwerder; Manfred Ehrlich, Böhl-Iggelheim; Markus Gebert, Iphofen; Matthias and Marina Wulf, Rödelsee. Specimens had been prepared before this study, no further preparation was conducted. Many of the original specimens appear to be lost (Garassino and Schweigert, 2006). More not yet identified material is likely present in other collections. Images of all specimens described in

this paper have been deposited in the database MorphDBase (<https://www.morphdbase.de/>) (Supplementary Table 1).

2.2. Documentation methods

All specimens in this study have been documented with macro-fluorescence imaging (Haug et al., 2011b; Haug and Haug 2011). A Canon Rebel T3i camera was used with a MP-E 65 mm lens. Light was provided by three LED torches equipped with cyan filters. A red filter was placed in front of the lens of the camera. The specimens were documented with several images and stitched to a panorama with Adobe Photoshop CS3. Colour images were transformed to grey scale images either by taking only the red channel and desaturating it (Haug and Haug 2011) or by stepwise desaturating it by consecutively setting the lighting of different colours either to '0' or to '100'. Histogram, contrast and sharpness was optimised afterwards.

2.3. Description

An extensive description is provided as a descriptive matrix (Haug et al., 2012a). The descriptive matrix of Haug et al. (2013) was used as a basis and further amended. This procedure allows a description with many more observable details without having the technical description dominating this study. Furthermore, by using and amending an already existing descriptive matrix the two descriptions, and planned future ones, are directly comparable.

2.4. Taxonomic treatment

The here presented case represents a severe taxonomic problem when following classical Linnean taxonomy. Linnean taxonomy is, as most taxonomical and systematic concepts, adult-focused (e.g. Minelli et al., 2006); hence, already any attempt to apply such concepts in combination with evolutionary developmental studies will cause problems (one recent case in Haug et al., 2012b). In the present case we try to apply some of the practical aspects of the concept of cladotypic taxonomy as outlined and exemplified by Béthoux and co-workers (Béthoux, 2007a, b, c; 2010; Béthoux et al., 2012). We will discuss why the application of this concept is more efficient than classical Linnean taxonomy in the present case. One aspect of the cladotypic concept is the use of Lanham species names (named after Lanham, 1965), which does not use the genus name before the species name necessarily, but, similar to classical taxonomy, describer and year. Lanham species names have been claimed to be impractical (e.g., Wolsan, 2007), yet most of the critics appear simply to stem from a lack of knowledge. For example, one claimed difference is the addition of all describers and year to the species name (e.g., Wolsan, 2007). Yet, this is also of common use in classical Linnean taxonomy, and in both cases we simply skip this amendment after having it introduced at first occurrence of the species name in a publication. Furthermore, the use of Lanham species names counters the now common habit to address species of monotypic genera by only mentioning the genus name, which is a clear philosophic misunderstanding. Furthermore, it is not forbidden in the cladotypic concept to put additional information before the species name. It can even be the next named node (which would more or less equal the genus). Yet, especially in uncertain cases or if addressing a non-specialist audience it is also possible to use names of nodes further “down” the tree (check work of Béthoux, see refs. above).

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