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The evolution of a key character, or how to evolve a slipper lobster

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ABSTRACT

A new fossil lobster from the Cretaceous of Lebanon, *Charbelicaris maronites* gen. et sp. nov., is presented here, while the former species '*Cancrinos*' *libanensis* is re-described as *Paracancrinos libanensis* comb. nov. *P. libanensis* is shown to be closer related to the contemporary slipper lobsters than to *Cancrinos claviger* (lithographic limestones, Jurassic, southern Germany). A finely-graded evolutionary scenario for the slipper-lobster morphotype is reconstructed based on these fossil species and extant forms. The evolutionary changes that gave rise to the current plate-like antennae of Scyllaridae, a key apomorphy of this group, are traced back through time. The antenna of what is considered the oldest slipper lobster became petaloid and consisted of about 20 fully articulated elements. For this group the name Scyllarida *sensu lato* tax. nov. is introduced. In a next evolutionary step, the proximal articles became conjoined and a lateral extension appeared on peduncle element 3. The entire distal petaloid region is conjoined already at the node of Verscyllarida tax. nov. In modern slipper lobsters, Neoscyllarida tax nov., the distal region is no longer petaloid in shape but asymmetrical. The study also emphasizes that exceptionally preserved fossils need to be documented with optimal documentation techniques to obtain all available information.

1. Introduction

Distinct morphotypes have been discussed repeatedly within Decapoda in recent years, with a focus on evolutionary scenarios leading to these morphotypes. A particularly 'hot' topic has been the process of 'carcinisation', or the evolution of the 'crab' morphotype, respectively, the evolution of a crab-like habitus (e.g. McLaughlin and Lemaitre, 1997; McLaughlin et al., 2004; Hiller et al., 2010; Tsang et al., 2011; Scholtz, 2014). In evolutionary terms, any form of crab has evolved from an ancestral macruran or "lobster" morphotype. An interesting and much less studied case of departure from the simple "lobster" morphotype are the slipper lobsters, or scyllarids, easily differentiable from other decapod lobsters due to their unique morphology (e.g. Jones, 1990). The group Scyllaridae forms a sharply characterised natural group, distinguished by wide and flat segments of the peduncle of the antennae (a2, second antennae) and by having the antennal flagellum transformed to a single broad and flat element without a trace of articulation. Scyllarid lobsters can be considered to represent a distinct 'morphotype' (note that the term used here is more or less equivalent what other authors term 'bauplan'; yet this has a quite difficult meaning in German), and this is especially apparent when comparing them to their closest relatives, the palinurid lobsters (e.g. Palero et al., 2009; Bracken-Grissom et al., 2014). Scyllaridae and Palinuridae form together Achelata (Scholtz and Richter, 1995), characterized by the lack of true claws (i.e. no index or fixed finger is opposed to the dactylus, or it is very short) and the presence of a phyllosoma larva. Contrary to the most familiar lobster types, slipper lobsters are dorsoventrally flattened, so that their cephalo-thoracic dorsal shield (also called carapace) is sometimes very wide, often square-shaped (in dorsal view) or even anteriorly widened. The dorsoventrally flattened body and, more

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importantly, the distinctive antennae of scyllarid lobsters must have evolved in their own evolutionary lineage.

The structure of the highly specialized, shovel-like antennae of scyllarid lobsters is remarkable. According to Holthuis (1991) the basal element of the antennal peduncle is conjoined with the carapace; so it is only visible ventrally (treated as peduncle element 1 in the following). The second and third element are conjoined to a single element which is short and broad and may bear teeth on the anterior margin (treated as peduncle element 2). In most scyllarids this element is free. In *Scyllarus*, however, it is immovably connected with the antennular somite and the carapace, thereby forming an integral part of the orbit (Holthuis, 1985). The fourth element is large, broad and flat; it usually bears teeth on its margins (treated as peduncle element 3). The fifth segment is narrow and small; it may bear teeth on the inner margin (treated as peduncle element 4). The last element of the antenna, which represents the flagellum, is very broad and flat, sometimes with teeth on the margin. This element, together with the fourth one, is what makes the antenna into a broad, shovel-like organ for which the vernacular names 'shovel nose shrimp' and 'bulldozer lobster' are given to species of scyllarids. By providing "intermediate forms", fossils have the potential to provide further insights in the origin of key synapomorphies, such as the scyllarid antenna. Phylogenetically expressed, early fossil representatives of a group often have only part of the apomorphies of the modern group, while still lacking others. In this way the sequence in which the specializations of a morphotype evolved can be broken down into several, more gradual evolutionary transformations (examples in Senter, 2010; Haug et al., 2010).

The Upper Jurassic Solnhofen lithographic limestones (ca. 150 million years old, southern Germany) yielded the fossils of *Archaeopteryx lithographica*, an important early representative of birds still lacking some autapomorphies of the modern representatives, thus representing an example of a fossil providing an "evolutionary step in between". But the Solnhofen lithographic limestones also yielded an important early representative of slipper lobsters, which provides insight into the evolution of their specific morphotype. *Cancrinos claviger* resembles spiny lobsters in general habitus. Yet, its antennae have a rather stout petaloid shape and comprise only about 20 elements. Förster (1973, 1984, 1985) therefore suggested that *C. claviger* represents an evolutionary step towards slipper lobsters. Haug et al. (2009a) could add additional insights into the evolutionary transition from the morphotype of spiny lobsters to *C. claviger*. Early juveniles of *C. claviger* still possess an elongate multi-annulated antenna and develop the petaloid shape gradually, by widening of the proximal elements and finally loss of the distal feeler-like part. Yet, the further evolutionary transition from the morphology of *C. claviger*, which mainly appears like a highly specialized spiny lobster, to the very distinct morphotype of slipper lobsters is still unclear.

We present new fossils from the Cretaceous of Lebanon that further close the gap of knowledge about the evolution of the morphotype of slipper lobsters. Based on these we reconstruct a possible scenario for the evolution of the slipper lobster morphotype.

2. Material and methods

2.1. Material

Most material is part of the palaeontological collections of the Muséum national d'Histoire naturelle, Paris, France (acronym: MNHN.F). The material was collected during a field campaign in 2011 (SC, DA, GP) in the Late Cretaceous Lagerstätten of Lebanon: Hadjoula and Hakel (Cenomanian, ~95 Ma) and Sahel Alma (Santonian, ~85 Ma). Comparative specimens are housed in the palaeontological collections of the Museo civico di Storia naturale di Milano (acronym: MSNM).

Lebanese Lagerstätten are well-known for their exquisitely preserved crustacean faunas. For details see: Brocchi 1875; Fraas 1878; Dames 1886; Glaessner 1945; Roger 1946; Garassino 1994, 2001; Larghi 2004; Garassino and Schweigert 2006; Ahyong et al., 2007; Feldmann 2009; Garassino et al., 2009; Feldmann and Charbonnier 2011; Pasini and Garassino 2011; Petit and Charbonnier 2012; Charbonnier et al., 2013; Haug et al., 2013. For geological setting, see Ferry et al. (2007) and Audo and Charbonnier (2012, 2013).

2.2. Methods

Specimens from Paris have been documented using the macro-fluorescence settings described by Haug et al. (2011a) and Haug and Haug (2011). In most cases grey scale images of fluorescence images were produced by deleting blue and green channel, desaturating the red channel and optimizing the histogram. In some cases a better contrast was achieved by the following procedure: saturation dialog was opened, brightness of 'blue' and 'cyan' was set to '0', the brightness of 'red' was set to '100'. The resulting image was desaturated, and the histogram was optimized. Some specimens were additionally documented as stereo images (see e.g. Haug et al., 2011b, 2012a). Stereo images had their brightness values inverted to enhance the contrast.

Specimens from Milano were imaged by a Nikon D700 digital camera equipped with a Sigma 105 mm macro-lens with or without extension tube. Fossils display autofluorescence under UV light (yellow) and green light (orange) (see Haug et al., 2009b). Macro-fluorescence was therefore used to document their anatomy. Under cross-polarized light, spotlights and lens were equipped with linear polarizing filters arranged so that reflexions would be minimal. Under UV light, a portable UV light set to short wave UV (emission peak around 254 nm) was used. Under green–orange fluorescence, spotlights were equipped with medium blue–green gelatine filter and camera macro-lens equipped with a red filter to cancel all light but orange fluorescence. All raw image files were processed in Adobe Camera Raw and Gimp to adjust white balance and levels.

2.3. Description

The description of the here presented specimens is provided as a descriptive matrix (Haug et al., 2012b). This is thought to allow the taxonomically interested reader to access all necessary information, without centering this paper on this aspect.

2.4. Phylogenetic reconstruction

The present study focuses on the evolution of a series of characters of the antenna which resolve without character conflict. For this reason, there was no need to use computer-based phylogenetic analyses. This situation also has the advantage to avoid "hiding" apomorphies in a large matrix where they would be mixed with various characters, and the contribution of each character might end up difficult to assess. We will therefore concentrate on discussing the primary homology assumptions and the resulting evolutionary scenario.

3. Taxonomy

Eucrustacea *sensu* Walossek, 1993
Malacostraca Latreille, 1802
Decapoda Latreille, 1802