Development in Mesozoic scyllarids and implications for the evolution of Achelata (Reptantia, Decapoda, Crustacea)

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A b s t r a c t

We describe four immature specimens belonging to the extinct genus *Cancrinos* (Achelata, Decapoda, Crustacea) of yet unclear systematic affinities, three from the Upper Jurassic Solnhofen Lithographic Limestones of southern Germany *(C. claviger)*, the fourth one from the Upper Cretaceous of Lebanon *(C. libanensis)*. Two of these specimens shed light on the "post-larval" development in *Cancrinos claviger*. In addition, we report a fragmentary specimen from the Solnhofen Lithographic Limestones that is interpreted as a very late larval stage at least of a scyllarid lobster, but a more detailed assignment is impossible. If correct, this would represent the first find of a scyllarid in the Solnhofen Lithographic Limestones. The immature fossils of *Cancrinos claviger* demonstrate that the spatulate antennae, a diagnostic character for the genus *Cancrinos*, develop after the larval phase. The earliest stage represented exhibits an antennal morphology comparable to palinurid lobsters (closely related to scyllarids) in possessing a long multi-annulated flagellum. In the next represented stage the 17 proximal annuli are thickened relative to the more distal ones. Adult specimens have about 20 flattened annuli that form together with the most distal peduncle element the large spatulate distal area of the antenna. The spatulate morphology of the distal area is interpreted as a synapomorphy uniting *Cancrinos* and Scyllaridae sensu stricto into Scyllaridae sensu lato. The development of *Cancrinos claviger* indicates the occurrence of two heterochronic events in early scyllarid evolution, i. e. hypermorphosis + pre-displacement (addition of a new developmental state late in ontogeny, as revealed in the spatulate antennal distal area) in the direct stem-lineage of Scyllaridae sensu lato and pre-displacement (shift of a structure developing late in ontogeny into earlier stages, visible by presence of the spatulate antennal flagellum already in the first "post-larval" stage) in the direct stem-lineage of Scyllaridae sensu stricto.

Keywords: *Cancrinos*, Solnhofen Lithographic Limestones, heterochrony, fossil ontogeny.

Z u s a m m e n f a s s u n g

Wir beschreiben vier Exemplare der bisher nicht eindeutig systematisch zugeordneten, ausgestorbenen Gattung *Cancrinos* (Achelata, Decapoda, Crustacea), welche verschiedene Entwicklungsstadien vor dem Adultzustand repräsentieren. Davon stammen drei aus den oberjurassischen Solnhofener Plattenkalken Süddeutschlands *(C. claviger)*, das vierte aus der Oberkreide des Libanon *(C. libanensis)*. Zwei dieser Exemplare dokumentieren zudem erstmals Aspekte der „postlarvalen" Entwicklung bei der Art *Cancrinos claviger*. Außerdem beschreiben wir ein fragmentarisch erhaltenes Fossil aus den Solnhofener Plattenkalken, welches vermutlich ein sehr spätes Larvalstadium eines Bärenkrebses (Scyllaridae) darstellt, doch eine exaktere Einordnung ist nicht möglich. Wenn dies zutrifft, wäre dies der erste definitive Fund eines Scyllariden aus den Solnhofener Plattenkalken. Die Exemplare von *Cancrinos claviger* zeigen, dass sich die Spatelform der distalen Antennenregion, ein diagnostisches Merkmal für die Gattung *Cancrinos*, erst während der nachlarvalen Morphogenese herausbildet. Beim frühesten vorliegenden Stadium weisen die Antennen ein langes multiannuliertes Flagellum auf, eine Morphologie vergleichbar derjenigen der zu den Decapoda zählenden Langusten (Palinuridae, nahe verwandt den Bärenkrebsen). Im nächsten bekannten Stadium sind die 17 proximalen Annuli deutlich verbreitert verglichen mit den distalen Annuli. Adulte Individuen besitzen ungefähr 20 verbreiterte, abgeflachte Annuli, welche mit dem fünften Pedunkelelement eine große spatelförmige distale Fläche bilden. Wir deuten die Spatelform der distalen Antennenregion als Synapomorphie für *Cancrinos* und Scyllaridae sensu stricto (= Autapomorphie des Taxons Scyllaridae sensu lato). Anhand der Individualentwicklung von *Cancrinos claviger* können wir zwei Heterochronie-Ereignisse, genauer Peramorphose-Ereignisse, in der frühen Evolution der Bärenkrebse ausmachen: Hypermorphose + Vorverlagerung (das Auftauchen eines neuen Entwicklungszustandes spät in der Ontogenese, hier der spatelförmigen distalen Antennenregion) in der direkten Stammlinie der Scyllaridae sensu lato und Vorverlagerung (Auftauchen einer Struktur eines späten Entwicklungsstadiums in einem früheren Entwicklungsstadium, hier das Vorhandensein eines spatelförmigen Antennenflagellums bereits im frühesten Stadium nach der Larvalentwicklung) in der direkten Stammlinie der Scyllaridae sensu stricto.

C o n t e n t s

1. Introduction

Scyllaridae, the slipper or bulldozer lobsters, are a distinct, morphologically readily recognisable group of reptantian decapod crustaceans. The characteristic features of these animals are the prominent antennae that have a shovel-like appearance and the likewise broad and flattened cephalothorax. The Scyllaridae are included with the Palinuridae, the spiny lobsters, and the Synaxidae (some authors recognise them as in-group Palinuridae, e. g. DAVIE 1990; PALERO et al. 2009) in the taxon Achelata (e. g. SCHOLTZ & RICHTER 1995; DIXON et al. 2003; PORTER et al. 2005).

The Achelata are characterised, as the name indicates, by the lack of chelae of the pereiopods, besides the fifth ones of the females (but certain astacids, the Glypheoidea, also lack true chelae; e. g. SCHRAM & DIXON 2004; GARASSINO & SCHWEIGERT 2006a). Furthermore, the Achelata share a special kind of zoëa-type larva, the so-called phyllosoma. Within the ontogeny there occur up to ten phyllosoma stages (e. g. GOLDSTEIN et al. 2008). This planktic larva is characterised by an enlarged thin shield, which acts as a floating device.

The taxon Achelata is in focus of different fields of research. Various achelatan species are of considerable economic importance (e. g. GOLDSTEIN et al. 2008), palinurids as well as scyllarids (example: the Moreton Bay Bugs or Bay Lobsters of northern Australia), and Achelata as a whole is a taxon of phylogenetic importance. The taxon Achelata has traditionally been united with the Eryonidae in the taxon Palinura (e. g. FÖRSTER 1973; but see also GARASSINO & SCHWEIGERT 2006a; TSANG et al. 2008). Recent morphology-based phylogenetic analyses of the reptantian decapods resolved the taxon, however, as a paraphylum or, even, polyphylum. Rather, Eryonidae (or their crown-group Polychelidae in most) seem to be the sister taxon of the Eureptantia (SCHOLTZ & RICHTER 1995; DIXON et al. 2003). Eureptantia comprises the sister groups Achelata and the remaining Eureptantia (Macrochelata) (SCHOLTZ & RICHTER 1995; AHYONG & O'MEALLY 2004), alternatively the Achelata represent the sister group to Meiura united by details of the antennular morphology (e. g. DIXON et al. 2003). The exact topology at the basal nodes within Reptantia has, however, a direct bearing on the reptantian ground pattern and thus for understanding the evolution of this group.

For any convincing resolution of this phylogenetic issue a reliable ground-pattern reconstruction of the Achelata is necessary. This is complicated by the fact that also the in-group phylogeny of Achelata is not well established. Mainly the synaxids have been discussed either to be the sister group to all other Achelata or an in-group of Palinuridae (e. g. DAVIE 1990; GEORGE 2006; PALERO et al. 2009).

Most phylogenetic analyses of Reptantia are based on Recent species exclusively (e. g. SCHOLTZ & RICHTER 1995; SCHRAM 2001; DIXON et al. 2003), but important information for such morphologically based analyses can be drawn out of fossils (SCHRAM & HOF 1998; SCHRAM & DIXON 2004). Although SCHRAM & DIXON (2004) included fossil species into their cladistic analysis, they argue that species based on imperfectly preserved fossil specimens may destabilise the tree topology and, therefore, not too many fossil species should be included into such an analysis. In contrast to that, SANTINI & TYLER (2004) demonstrated that also the inclusion of fossil species that are only known from imperfectly preserved specimens could be important for resolving phylogenies, as long as more than 25 % of all characters of a species are known. Furthermore, WALOSZEK and co-workers have demonstrated variously the value and importance of fossil data for reconstructing phylogenies (e. g. WALOSSEK & MÜLLER 1990, 1998; WALOSSEK 1993; MAAS et al. 2003; WALOSZEK et al. 2007).

Important representatives of fossil Achelata have been extracted from the Solnhofen Lithographic Limestones of southern Germany. There are at least two species of *Palinurina* MÜNSTER, 1839 (GARASSINO & SCHWEIGERT 2006a), three different types of phyllosoma larvae (e. g. POLZ 1972, 1973, 1984, 1996), some of which may be assigned to species of *Palinurina*, as well as specimens assignable to *Cancrinos claviger* MÜNSTER, 1839 (GARASSINO & SCHWEIGERT 2006a). Originally two species of *Cancrinos* MÜNSTER, 1839 were described (*C. claviger* and *C. latipes* MÜNSTER, 1839), but have been synonymised more recently (GARASSINO & SCHWEIGERT 2006a). Another species has been described from the Cretaceous of Lebanon as *Cancrinos libanensis* GARASSINO & SCHWEIGERT, 2006 (GARASSINO & SCHWEIGERT 2006b). Specimens of species of the genus *Cancrinos* are very rare and often only imperfectly preserved. *Cancrinos* has often been treated as being of uncertain phylogenetic affinities within the Achelata. FÖRSTER (1973, 1984, 1985) suggested that *Cancrinos* could be understood as an "intermediate" between palinurid and scyllarid morphologies. Similarly, BEURLEN (1930) even introduced an own monotypic family Cancrinidae and placed it besides Palinuridae and Scyllaridae. Thus, *Cancrinos* might add significantly to the understanding of the early evolution of scyllarids and may also contribute to the resolution of the basal achelatan phylogenetic splits and the reconstruction of the achelatan ground pattern.

With four newly discovered immature specimens from the Solnhofen Lithographic Limestones and the Upper Cretaceous of Lebanon we provide new data on the development of *Cancrinos claviger.* Additionally, we report a fragmentarily preserved specimen from the Solnhofen Lithographic Limestones, which is interpreted tentatively as a late scyllarid phyllosoma larva. Documentation with high-resolution composite imaging under normal light and

UV-fluorescence settings allows us to display very small morphological details. In this way, changes of tiny structures during ontogeny can by detected. Still the descriptions of our immature specimens are kept short here, as it is not the aim of the present paper to fully reconstruct the ontogenetic sequence of *C. claviger*, but to highlight certain aspects; a more complete reconstruction is postponed. Together with a discussion of the systematic placement of *Cancrinos*, evolutionary changes in ontogenies, i. e., heterochronic events, in Achelatan evolution can be identified.

2. Material and methods

In total we have directly investigated five specimens. In the following, numbers 1–5 will be assigned to these specimens and we will refer to this numeration in the course of this article. Four of these specimens belong to private collections. We are aware of the problem of further tracing of these specimens, but they are, in our view, too important to ignore them. We try to minimise the difficulties for further investigations on these specimens by our intensive documentation. High-resolution images of all specimens (up to 45,000 pixels long, one pixel ca. 0.64 µm long) will be deposited in the collection of the Staatliches Museum für Naturkunde Stuttgart.

Specimen 1 is an apparently immature specimen assignable to the species *Cancrinos claviger*. It is beautifully preserved in dorso-ventral orientation and with antennae, the smallest specimen presented here. The fossil was found in the Solnhofen Lithographic Limestones of Öchselberg (Zandt Formation, Upper Kimmeridgian, Beckeri Zone, Ulmense Subzone, *rebouletianum* horizon) (SCHWEIGERT 2007) and prepared by scraping with a small needle. It is part of the private collection of one of the authors (MW).

Specimen 2 is also an immature *Cancrinos claviger*, showing the same preservational aspect and details as specimen 1, but is significantly bigger. This specimen was found in the Solnhofen Lithographic Limestones of Lan-

genaltheim (Solnhofen Formation, Lower Tithonian, Hybonotum Zone, Rueppellianus Subzone, *rueppellianus* horizon) (SCHWEIGERT 2007) and prepared the same way as specimen 1. It also belongs to the private collection of one of the authors (MW).

Specimen 3, another immature *Cancrinos claviger*, is preserved slightly oblique and without antennae. It is the largest of all specimens considering the non-outstretched preservation. This fossil was found in the Solnhofen Lithographic Limestones of Schernfeld (Eichstätt Formation, Lower Tithonian, Hybonotum Zone, Riedense Subzone) (SCHWEIGERT 2007). Now it is part of the private collection of ROGER FRATTIGIANI, Laichingen.

Specimen 4 is also a possibly immature animal and is tentatively assigned to *Cancrinos libanensis*. This specimen was found in Hajoula, Lebanon (Cenomanian, Upper Cretaceous) and purchased via a fossil trader. The fossil had been amended with modelling putty and pencil drawings by one of the previous owners. At least the putty could be removed with acetone, but the pencil lines are still partially present. The specimen is stored in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS 66207).

Specimen 5 possibly is a phyllosoma larva of an unknown scyllarid lobster. It was found in the Solnhofen Lithographic Limestones of Painten (lower part of Painten Formation, uppermost Kimmeridgian, Beckeri Zone, *rebouletianum* horizon) (SCHWEIGERT 2007). It belongs again to the collection of ROGER FRATTIGIANI.

The smallest specimen of *Cancrinos claviger*, specimen 1, has been extensively documented (>5,000 images in >400 stacks, up to 33 images per stack) applying the composite UV-fluorescence-microscopy method (see BOMFLEUR et al. 2007; HAUG et al. 2008) on an Axio Scope 2 with an AxioCam. Software processing was done with Combine ZM, Adobe Photoshop CS3 and Gimp. The slabs of the other specimens were simply too large for this microscope, besides the possible scyllarid larva, but which showed no UV-fluorescence and could, therefore, not be documented this way.

All specimens were documented under a Leica Stereoscopic Microscope with an ocular camera DCM-500. Each specimen was documented with 17 to 33 image stacks with up to 24 images per stack. Stacks were fused with the software CombineZM; fused images were stitched together using the Photomerge automatic tool of Adobe Photoshop CS3 and partially by hand.

Prominent structures of the specimens were redrawn as vector graphics in Adobe Illustrator CS1. Based on the identifiable structures of the specimens combined with the knowledge of adult *Cancrinos claviger* as presented in GARASSINO & SCHWEIGERT (2006a) a 3D model was produced in Blender.

3. Results

3.1. Short descriptions of the specimens

S p e c i m e n 1 . – Immature specimen of *Cancrinos claviger*, published in FRICKHINGER (1999, fig. 76) as unknown decapod larva. Preserved in ventral aspect (Fig. 1A, B). Length of body 21.3 mm; maximum body width 6.6 mm. Cephalothorax and pleon present. Of the head structures antennulae and antennae preserved (Fig. 1C). Antennulae lacking any further details, only known from rough outline. Preservation of the antennae includes three (?) stronger basal annuli of about 1 mm width at the base of the most proximal one, distally tapering to the more slender distal annulated region of the antenna with at least 20 smaller annuli of ca. 0.26 mm width. Distal part possibly broken off, total length, therefore, unknown. Pereion with five pairs of appendages, all without chelae (Fig. 1D). Two basal parts of the pereiopods, coxa and basipod, and four distal parts of the endopod visible. Pereiopods strongly tuberculate (Fig. 1D). Pleon with six pleomeres, no pleopods preserved besides the outline of the tail fan, at least parts of the right side (Fig. 1E).

S p e c i m e n 2 . – Immature specimen of *Cancrinos claviger*, preserved in ventral aspect (Fig. 2). Length of body 28.3 mm; maximum body width 8.0 mm. Cephalothorax and pleon present (Fig. 2A, B). Preserved head structures include the antennulae and antennae (Fig. 2C). Antennulae with two flagella, each with at least eight flagellimeres. Antennae with three recognisable stronger basal annuli of 2.13 mm width. Distal annulated region of the antenna with differentiated annuli, proximal 17 annuli ca. 1.26 mm wide, from 15th annulus tapering to the 18th annulus of only ca. 0.43 mm width. Further distal annulated region of the antenna with at least nine annuli, but terminal part broken off; therefore total number and length unknown. Pereion with six pairs of appendages. Most anterior one presumably representing the third maxilliped, more anterior maxillipeds indicated by faint lines. Five pairs of walking legs posterior to the maxilliped. All legs without chelae, two basal parts, coxa and basipod, and four distal parts of the endopod visible. Pereiopods strongly tuberculate (Fig. 2E). Pleon with six pleomeres, no pleopods preserved besides the outline of the tail fan (Fig. 2D).

S p e c i m e n 3 . – Immature specimen of *Cancrinos claviger*, preserved in oblique aspect, almost dorsally, slightly laterally (Fig. 3A–C). Measurable length of body 29.4 mm, but pleon partially folded under the body (Fig 3A, B). Measurable maximum body width 9.4 mm. Cephalothorax and parts of pleon present. Whole surface strongly tuberculate. No anterior appendages preserved well enough for a detailed identification. Four legs of the left series of pereiopods and three of the right series preserved, all lacking chelae. Whole body surface and legs strongly tuberculate (Fig. 3C).

S p e c i m e n 4 . – Possibly immature specimen putatively belonging to *Cancrinos libanensis*, preserved in dorsal aspect (Fig. 3D–F). Maximally measurable body length 35.5 mm and width 15.5 mm. Body divided into cephalothorax (posterior outlines difficult to identify) and pleon (Fig. 3E, F), which is only imperfectly preserved. Anterior appendages not identifiable. Five legs of left series of pereiopods well preserved and three legs of right series present, but only more proximal parts. All pereiopods lacking chelae; strongly tuberculate surface (Fig. 3D).

S p e c i m e n 5 . – Possible late larval scyllarid, preserved in dorsal aspect (Fig. 4). Maximally measurable body length 25.6 mm. Division into cephalothorax and pleon. Shield rounded, heart-shaped, covering head and pereion, 12.3 mm long and 15.7 mm wide. Pleon not well preserved, consisting of six segments, followed by ill-preserved tail fan (telson plus uropods). A pair of short robust anteriorly orientated structures may represent the antennae. Other anterior structures not clearly identifiable. Parts of three legs of the left series of pereiopods and parts of two legs of the right series preserved. Legs thin, extremely long, number of segments not apparent. A small structure appears to arise from one of the right legs closer to the body and may represent the exopod (Fig. 4B), present in such larvae (e. g. MIKAMI & GREENWOOD 1997).

3.2. Morphogenesis

Based on specimens 1 and 2, together with the amended description of the adult stage of *Cancrinos claviger* given by GARASSINO & SCHWEIGERT (2006a), morphogenetic changes of certain structures can be recognised:

The three robust proximal elements of the antenna seen in specimen no. 2 can be homologised to the three robust elements seen in adult *Cancrinos claviger* as depicted by GARASSINO & SCHWEIGERT (2006a) and already by MÜNSTER (1839). For specimen no. 1 this is not exactly possible because of its preservation. Based on the homologisation of the proximal elements, the distal annuli can also be homologised.

The distal annulated region of the antenna undergoes significant changes (Fig. 5). In the first known stage it is simply flagelliform (the exact number of annuli cannot be observed, because of the preservation). In the second known stage the annuli of the distal annulated region of the antenna are differentiated. The proximal 17 annuli are thickened compared to the distal ones. The further distal annuli appear still as in the earlier stage. In the adult stage the ca. 20 proximal annuli are thickened and flattened to form a large spatulate distal region (e. g. GARASSINO &
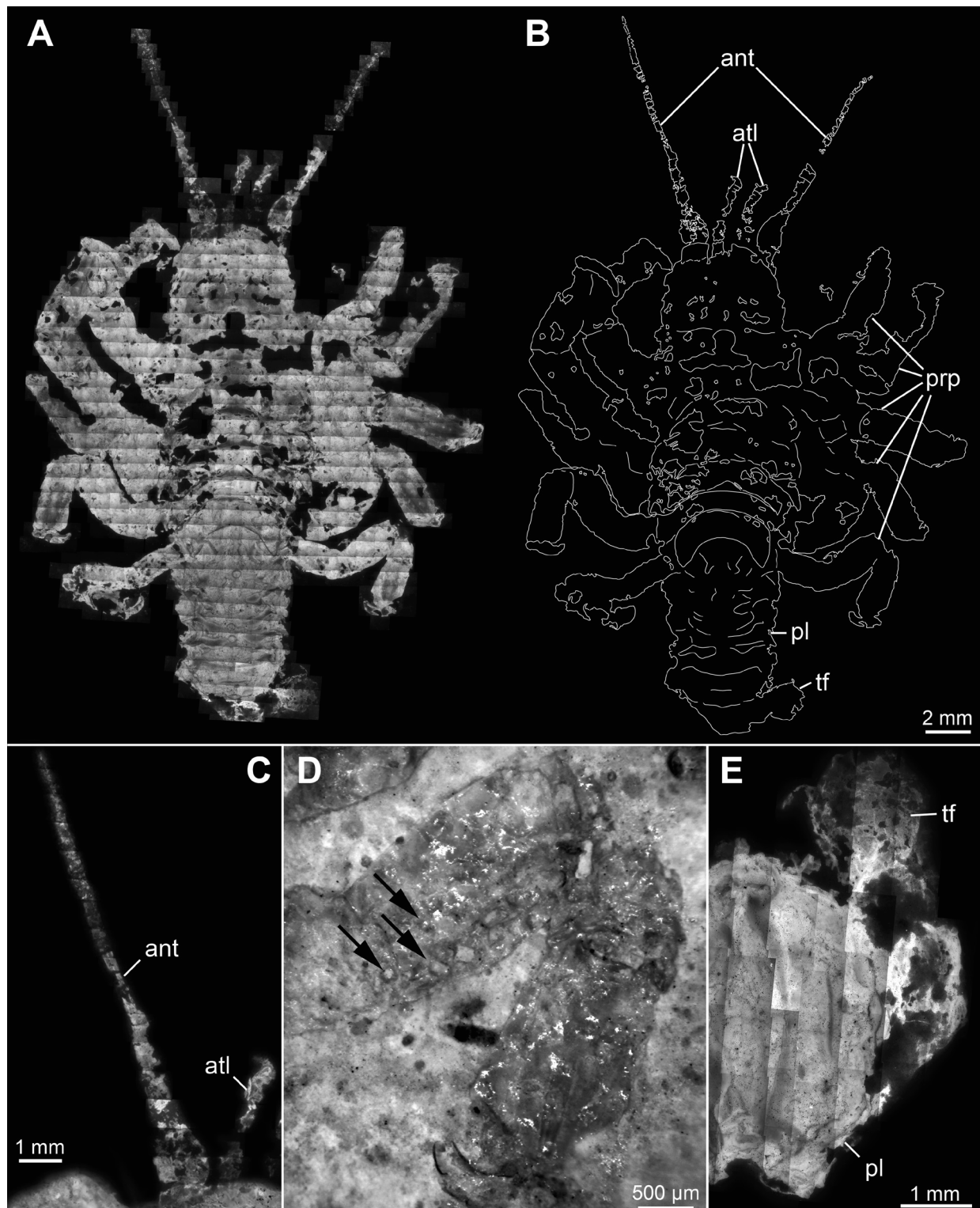
Fig. 1. Specimen 1. *Cancrinos claviger* MÜNSTER, 1839, smallest known specimen; Solnhofen Lithographic Limestones (Upper Jurassic, uppermost Kimmeridgian), Öchselberg (southern Germany); Coll. WULF. – **A**. UV-fluorescence composite image. **B**. Interpretive drawing of A. **C**. Detail of antennulae and antennae of left body side (UV-fluorescence). **D**. Details of the pereiopods showing the tuberculation (arrows; normal light). **E**. Detail of the tail fan (UV-fluorescence). – ant: antennae; atl: antennulae; pl: pleon; prp: pereiopods; tf: tail fan.
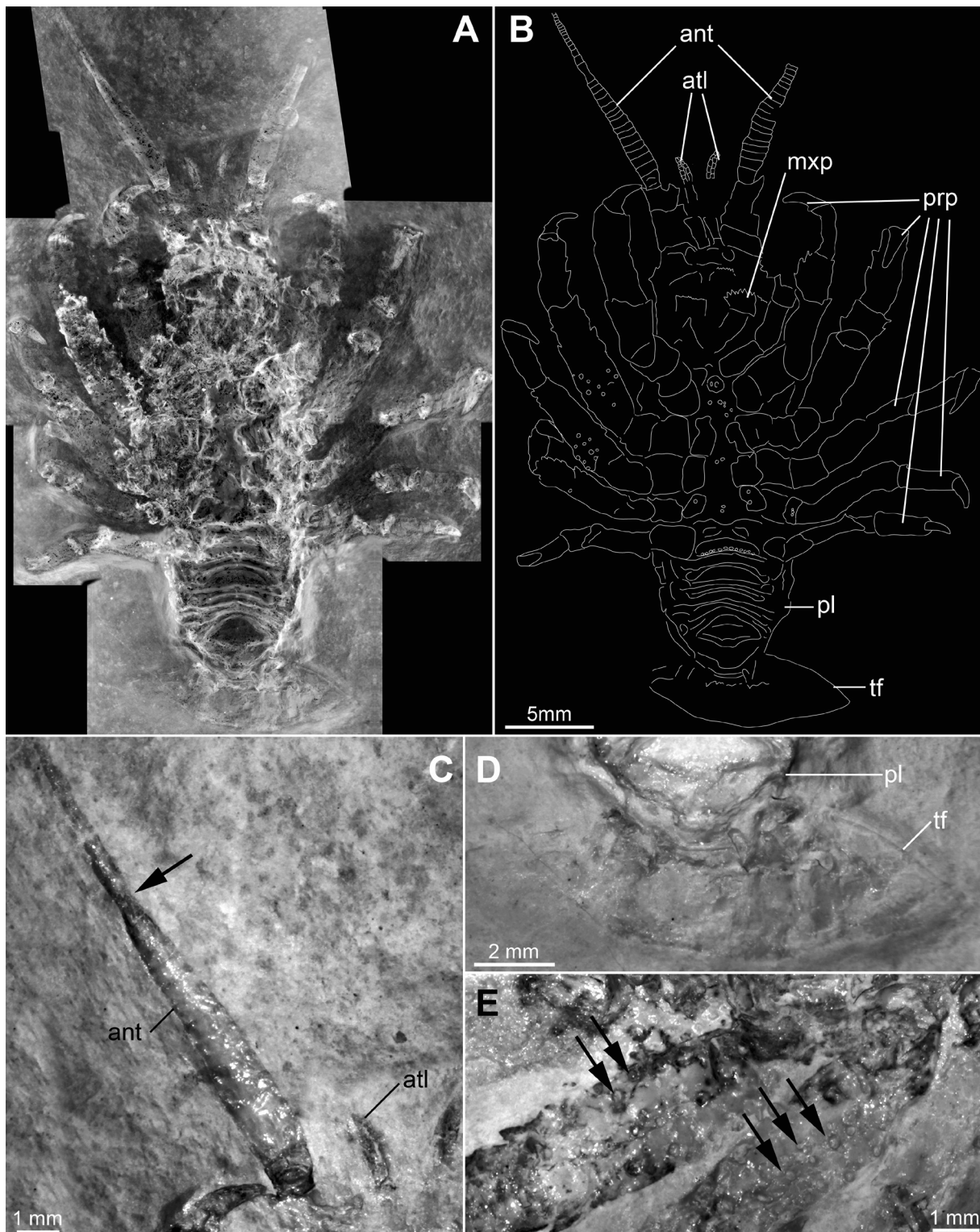
Fig. 2. Specimen 2. *Cancrinos claviger* MÜNSTER, 1839, immature specimen; Solnhofen Lithographic Limestones (Upper Jurassic, Lower Tithonian); Langenaltheim (southern Germany); Coll. WULF. – **A**. Composite image under normal light, inverted to enhance contrast. **B**. Interpretive drawing of A. **C**. Detail of anterior appendages of right body side (normal light). Arrow marks the change from the thickened annuli to normal ones. **D**. Higher magnification of the tail fan (normal light). **E**. Details of the pereiopods showing the tuberculation (arrows; normal light). – mxp: maxillipeds. For other abbreviations see Fig. 1.
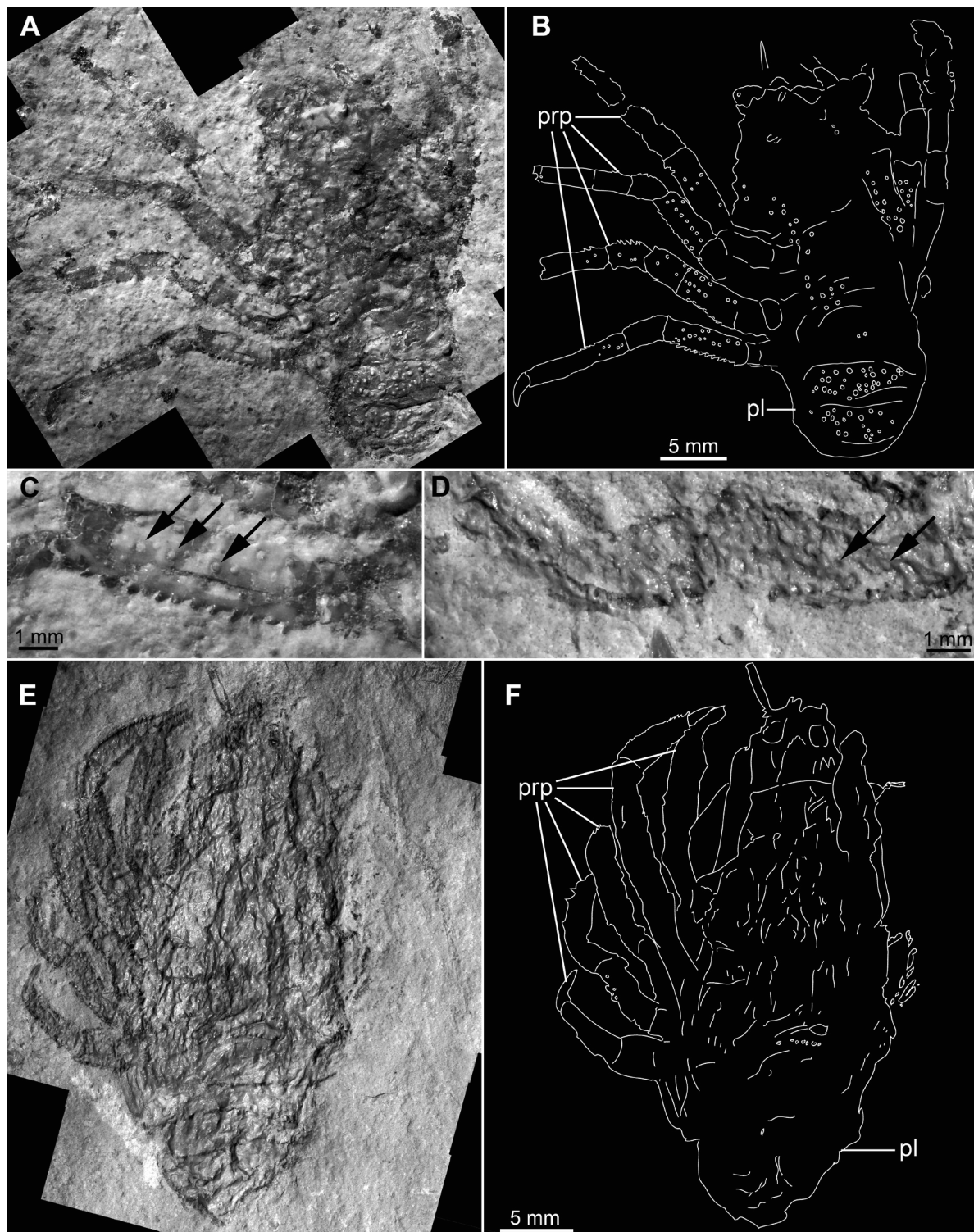
Fig. 3. Two immature *Cancrinos* specimens. **A–C**. Specimen 3. *Cancrinos claviger* Münster, 1839, immature specimen; Solnhofen Lithographic Limestones (Upper Jurassic, Lower Tithonian), Schernfeld (southern Germany); Coll. Frattigiani. – **A**. Composite image under normal light. **B**. Interpretive drawing of A. **C**. Detail of pereiopod (normal light), arrows showing the tuberculation. **D–F**. Specimen 4. *Cancrinos* (*libanensis*?) Garassino & Schweigert, 2006, possible immature specimen; Upper Cretaceous, Cenomanian, Hajoula (Lebanon); SMNS 66207. **D**. Detail of pereiopod (normal light), arrows showing the tuberculation. **E**. Composite image under normal light. **F**. Interpretive drawing of E. – For abbreviations see Fig. 1.
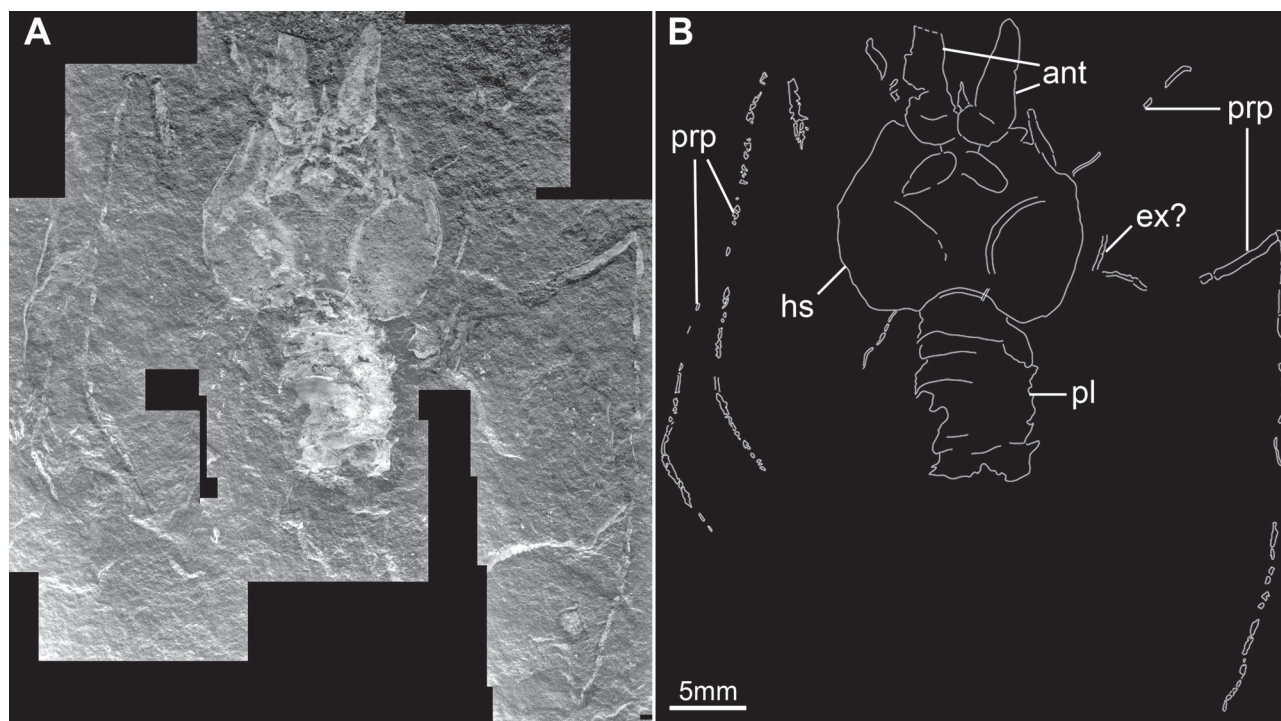
Fig. 4. Specimen 5. Possible scyllarid larva; Solnhofen Lithographic Limestones (Upper Jurassic, uppermost Kimmeridgian), Painten (southern Germany); Coll. FRATTIGIANI. – **A**. Composite image under normal light, inverted. **B**. Interpretive drawing of A. – ex?: possible exopod; hs: head shield; for other abbreviations see Fig. 1.

SCHWEIGERT 2006a). The distal annuli must be interpreted as lost during ontogeny.

Most other morphological features cannot be followed throughout the ontogeny of *Cancrinos claviger*, as they are not exactly known for all stages. What can be recognised, however, is the relative enlargement of the pleon, which is smallest in the first known stage, slightly larger in the second known stage and even larger in the supposed adults (GARASSINO & SCHWEIGERT 2006a). Unfortunately, the largest of the immature specimens of *C. claviger*, no. 3, possesses neither attached antennae nor an outstretched pleon; therefore, none of the two structures, known to undergo morphogenetic changes, is obtainable from this specimen. At least specimen 3 bridges the size gap between the immature specimens and the presumed adult specimens, being up to more than 10 cm in length (GARASSINO & SCHWEIGERT 2006a).

4. Discussion

The Solnhofen Lithographic Limestones are one of the few fossil Lagerstätten that contain also information on arthropod ontogeny with "soft-part preservation", besides the worldwide occurring 'Orsten'-type Lagerstätten (Cam-

brian to Ordovician), the Scottish Rhynie Chert (Devonian) and the Santana and Crato formations in Brazil (Cretaceous) (see HAUG et al. 2008). The present report amends the record of immature arthropod specimens facilitating the reconstruction of development of these fossil species from the Solnhofen Lithographic Limestones.

The four specimens interpreted here as immature specimens of *Cancrinos* sp. are obviously Achelata, based on the morphology of their appendages. The term immature is applied here as neutral description of post-phyllosoma stages, as it remains unclear whether the smallest specimen here might rather represent the so-called puerulus/nisto stage (megalopa equivalent sensu WILLIAMSON 1969), in which case the term larva may be applied, or if they are true juveniles. The general controversy about how to term stages following the larval phase is mainly caused by the fact that the term "post-larva", meaning nothing more than "after the larval phase" was used for a distinct stage by GURNEY (1942). This is seen as generally problematical (e. g. ANGER 2006). FELDER et al. (1985) have suggested calling all "post-larval" stages of Decapoda "post-larva", although they argue for a morphological distinctiveness of the first "post-larval" stage (their decapodid) compared to later ones. We also notice the difficulties with this terminology and use it in quotation marks to indicate that we

Fig. 5. Preliminary partial 3D reconstruction of the two different ontogenetic immature stages of *Cancrinos claviger* Münster, 1839 based on the specimens in Figs. 1 and 2 and literature data on the adult (Garassino & Schweigert 2006a). Note the change on the antennae (thickening of proximal annuli) and in the relative pleon size.

refer to stages after the larval phase and not to a "post-larva" sensu Gurney (1942).

There are at the moment three valid species of Achelata known in the Solnhofen Lithographic Limestones: *Palinurina longipes* Müller, 1839, *P. tenera* Oppel, 1862 and *Cancrinos claviger* (Garassino & Schweigert 2006a). The taxonomic status of other species of *Palinurina* (as well as the status of *P. tenera*) has already been questioned by Polz (1995) as representing either exuviae or different developmental stages of *P. longipes*. The here presented specimens no. 1–3 cannot be grouped with *Palinurina* for several reasons. *Palinurina* specimens have relatively slender pereiopods, while the pereiopods of our specimens appear stouter and more robust. *P. longipes* has a fine tuberculation on the pereiopods, arranged in parallel rows, while *P. tenera* also has fine tubercles, but irregularly and rarely. In contrast, our specimens show a very strong tuberculation (Figs. 1D, 2E, 3C, D), but also arranged in parallel rows. Such stouter and more robust pereiopods with a strong tuberculation in parallel rows are exclusively known from *C. claviger*. Additionally, the absence of any rostral structure – diagnostic character of *C. claviger* – further supports the assignment of specimens no. 1–3 to this species.

Furthermore, one specimen exhibits thickened proximal portions of the antennal flagella. These are not as broad as in large (adult?) specimens and have more annuli distally that are flagelliform, but are best interpreted as an ontogenetic intermediate stage between a "normal" antennal flagellum, as exhibited by the smallest specimen, and a spatulate appearance with just about 20 flagellimeres in later stages (Garassino & Schweigert 2006a).

Based on the assignment of the specimens no. 1–3, *Cancrinos claviger* appears to "change" from a palinurid-like morphology to a more scyllarid-like morphology throughout its "post-larval" phase, i.e. a thin antennal flagellum develops into a flattened/thickened spatulate flagellum. Although the largest of our immature specimens, no. 3, is only imperfectly preserved and lacks the antennae, its size closes the gap to the larger adult specimens (Garassino & Schweigert 2006a).

Although our descriptions of the immature specimens are kept short here, as it was not the aim of the present paper to fully reconstruct the ontogenetic sequence of *Cancrinos claviger*, the discovered ontogenetic pattern already allows us to evaluate an earlier assumption on the ontogeny of *C. claviger*. Polz (1996) pointed out that the phyllosoma of his type C larva might represent the larva of

C. claviger. This was originally a problematical assumption, as the type C larva does not possess prominent flattened antennae. Based on our new findings the assumption by PoLZ (1996) is seen as more likely now, because the newly described immature specimens serve to explain the gradual development of the prominent antenna to its spatulate condition in adult *C. claviger* (GARASSINO & SCHWEIGERT 2006a).

FÖRSTER (1984) assumed that *Cancrinos claviger* might be understood as an "intermediate" evolutionary step between Palinuridae and Scyllaridae. The flattened antennae in *Cancrinos* should, according to this author, be understood as a first step to the morphology seen in Scyllaridae, where the antenna is reduced to only five elements (FÖRSTER states four elements, it is unclear whether he missed the most proximal, fused elements).

In *Cancrinos claviger* the most proximal element of the antennae (the coxae) are fused to each other and immobilised, an autapomorphic character for Achelata. Like in Palinuridae the peduncle of the antenna of *C. claviger* is further composed of three robust elements. The fifth peduncle element is very small in Palinuridae and appears almost like a flagellimere. Based on positional homologisation (= homotopy) the same must be the case for *C. claviger*, thus the most basal element of the petaloid area of the antenna must be understood as the peduncle element five. In Recent Scyllaridae the main area forming the functional shovel is a laterally drawn out region of peduncle element three and the large, anteriorly rounded terminal element (element five). This element is very large and prominent and thus unlikely homologous to the very small peduncle element five of Palinuridae (and *C. claviger*), but might be understood as a fusion product of the peduncle element five and the distal flagellum, both of flattened shape. The terminal element of Scyllaridae is, furthermore, armed with many teeth that show in some cases deep incisions (e. g. HOLTHUIS 2006). This might be understood as a remnant of former subdivision.

A spatulate appearance of the distal region of the antenna, but exclusively formed of the antennal flagellum also appears in Recent palinurids. Here these morphologies are further restricted to larval (phyllosoma) stages and appear in a highly derived ingroup taxon of the Palinuridae (MCWILLIAM 1995). A spatulate distal antennal region comprising also peduncle element five is exclusively known from *Cancrinos* and Scyllaridae. Thus, a spatulate morphology of the distal antennal region is seen as a potential and plausible synapomorphy of *Cancrinos* and Scyllaridae.

Until now, the exact placement has been treated only vaguely as "intermediate" or "close to" the Scyllaridae (FÖRSTER 1984, 1985; GEORGE 2006). Based on FÖRSTER's (1984) scenario and the potential synapomorphic morphology of the antenna, *Cancrinos* can be understood as

the sister group to Scyllaridae. Other characteristics of Scyllaridae are missing in *Cancrinos*, such as the possible fusion of the flagellimeres to peduncle element five or the flattening of the cephalothoracic shield, so representing autapomorphies of Scyllaridae. The taxon including Scyllaridae and *Cancrinos* is, therefore, here named Scyllaridae sensu lato, and the old term Scyllaridae is restricted to Scyllaridae sensu stricto (Fig. 6). This phylogeny was already implicated indirectly in the publication by FÖRSTER (1984), but is now here formalised.

The new data on the development of *Cancrinos claviger* allow us to identify two possible peramorphic heterochronic events in the evolutionary lineage towards the Scyllaridae sensu stricto. The evolutionary change from a "normal" morphology of the distal antennal region throughout ontogeny to the appearance of a spatulate morphology late in "post-larval" ontogeny is best described as local hypermorphosis + pre-displacement. Hypermorphosis is easily identified as a global change, i. e. affecting the whole organism. In these cases it can also be described as 'terminal addition' (of a developmental stage). For a local hypermorphosis, i. e. affecting only certain structures of an organism, this interpretation is critical. But also the present example can be recognised as hypermorphosis, as it produces a recapitulation in the Haeckelian sense: the immature stages exhibit a plesiomorphic morphology (flagelliform), while later stages exhibit an apomorphic state (spatulate). Terminology of heterochrony is mainly based on growth curves; therefore, it is not designed for pseud-discontinuous development as it is present in arthropods, and mainly discussed for global events. But one must not forget that the terms of heterochrony are descriptive terms that simply try to classify and describe an evolutionary pattern. We, therefore, propose to add the descriptive term 'pre-displacement', another type of peramorphosis, to the descriptive term 'hypermorphosis' to more precisely describe the evolutionary change of ontogeny that must have occurred in this evolutionary lineage (see also see HAUG et al. submitted for a further discussion on heterochrony). The combination of these two terms is necessary as no new 'stage' appears in ontogeny, but new 'conditions' appear in a late, but already existing stage. The problem of the descriptive terms of heterochrony and their application to arthropods, and especially to local phenomena, is not satisfyingly solved yet; the terminology applied here remains preliminary.

The evolutionary shift to an earlier appearance of a spatulate antennal flagellum already in the first "post-larval" stage can be, more easily be described as pre-displacement (Fig. 6). In fact, already the phyllosoma larvae of Scyllaridae exhibit a non-flagelliform morphology of the antennal flagellum, but a true spatulate (shovel-like) appearance is present from the first "post-larval" (nisto) stage on (e. g. GOLDSTEIN et al. 2008). The occurrence of
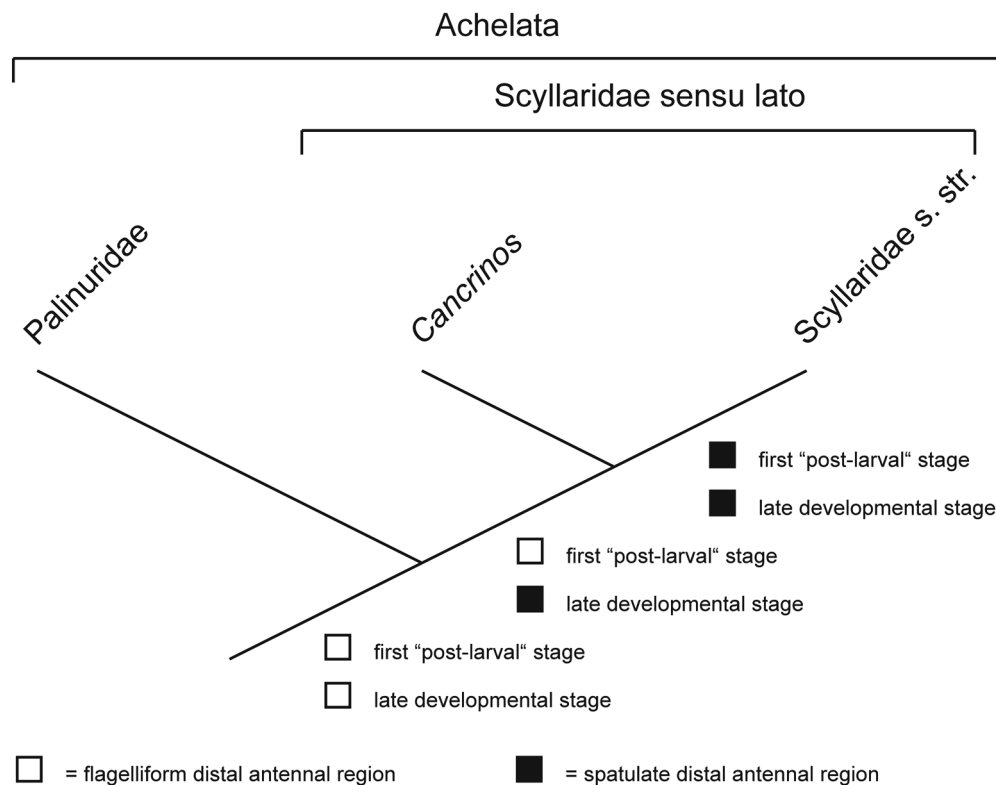
Fig. 6. Phylogeny of Achelata (problem of Synaxidae not included here) and position of *Cancrinos* with mapping of the condition of the distal antennal region in first "post-larval" and later developmental stages. The shift from the state in the achelatan ground pattern to the altered one in the stem-lineage of Scyllaridae sensu lato can be described as hypermorphosis + pre-displacement, occurrence of a new condition at the end of (or at least late in) ontogeny. The next change in the stem-lineage of Scyllaridae sensu stricto (forward shift of the former later condition to early stages) can be described as pre-displacement.

the fusion of the flagellimeres to the peduncle element five might also be the effect of a heterochronic event, but is not discussed here.

The single specimen from Lebanon, no. 4, appears to be a juvenile *Cancrinos libanensis* (GARASSINO & SCHWEIGERT 2006b), based on the overall similarities to the three immature specimens of *C. claviger* and its relatively close co-occurrence with *C. libanensis*. Interestingly, it furthermore shows superficial resemblance to a single specimen described by ROGER (1946) as *Eryoneicus sahel-almae* ROGER, 1946. Based on the images from the original description (ROGER 1946) the assignment of this specimen to the Eryonidae is doubted. At first, a large shield laterally extending as seen in other eryonids (e. g. GARASSINO & SCHWEIGERT 2006a) is not apparent in the images of the specimen described by ROGER (1946) (and also not in our specimen). Secondly, eryonid males possess chelae on the anterior four pairs of pereiopods, females on all five pairs (SCHOLTZ & RICHTER 1995). The specimen shown by ROGER (1946) lacks, similarly to our specimen, chelae on all pereiopods. Thirdly, eryonids have (plesiomorphically retained from the ground pattern of Decapoda) a triangular

telson (SCHOLTZ & RICHTER 1995); the specimen shown by ROGER (1946) possesses a rounded eureptantian telson (SCHOLTZ & RICHTER 1995), so revealing an in-group eureptantian feature. In summary, the specimen described by ROGER (1946) as the holotype of *E. sahelalmae* is interpreted here as a possible additional immature specimen of *C. libanensis*. Besides the recently described single phyllosome specimen from Hajoula (PASINI & GARASSINO 2009), this is the first report of preservation of developmental information in Lebanese decapod fossils. A formal revision of the species together with the problematical issue of these juveniles belonging to the Lebanese *C. libanensis* and a discussion of the question of priority have to be postponed until the original specimen from the Lebanon has been re-investigated.

Further understanding of early scyllarid evolution may be provided by other fossil scyllarids. Scyllaridae have been described from the Cretaceous of Lebanon and from Mexico (DAMES 1886; ROGER 1946; FÖRSTER 1984, 1985; VEGA et al. 2007). The presence of scyllarids in lithographic limestones from Lebanon also makes their presence in the Solnhofen Lithographic Limestones very likely, as the

two faunas are very similar in many components. This would further make the interpretation of the single specimen presented here as a possible scyllarid larva plausible.

The possible scyllarid phyllosoma larva specimen, no. 5, exhibits partially larval and "post-larval" features of Scyllaridae sensu stricto. The extremely thin and long pereiopods apparently resemble those of the characteristic phyllosoma larvae (MIKAMI & GREENWOOD 1997; GOLDSTEIN et al. 2008). The shield shape also resembles that of a phyllosoma, besides the already developed furrows that are present on "post-larval" stages of Scyllaridae sensu stricto (GOLDSTEIN et al. 2008). The short antennae of the specimen also more resemble that of "post-larval" stages, but they indicate the possible scyllarid affinity of the specimen. A missing free pereion may also be a "post-larval" feature, but in certain phyllosoma larvae the large shield superimposes the free pereion (e. g. SEKIGUCHI et al. 1996). The fully segmented pleon may again be a "post-larval" feature, but in some scyllarids the pleon is already well developed in the latest phyllosoma stage (MIKAMI & GREENWOOD 1997).

Another example of a fossil phyllosoma larva exhibiting a mixture of larval and "post-larval" features has been termed larva D by POLZ (1995). It has been interpreted as being fossilised in the act of moulting from a larva to a "post-larva" (POLZ 1995). Alternatively, both examples, our possible scyllarid larva and the larva D, could represent very late larval stages. In long ontogenetic sequences the individual stages can show significant variations (ANGER 2006) and the last larval stages may already expose certain "post-larval" characters. No examples for this phenomenon have been found in the literature for Achelata, but the long ontogenetic sequence in this taxon makes it likely, that an "early megalopa" (term from VILLAMAR & BRUSCA 1988 for a stage showing features of zoëa and megalopa) occurs in achelatan ontogeny.

In summary, the single phyllosoma-like specimen presented here is interpreted as a possible latest larval stage ("early megalopa") of an unknown scyllarid. Yet the specimen is too ill preserved to allow for a formal description of a new species.

5. Conclusions and outlook

The taxon *Cancrinos* is interpreted as the sister taxon of the Scyllaridae sensu stricto, both taxa representing the Scyllaridae sensu lato. The autapomorphy of this taxon is a spatulate distal antennal region. Details of the ontogeny of *Cancrinos claviger* demonstrate that the spatulate distal antennal region develops from a flagelliform distal antennal region, which represents the plesiomorphic state of this character present also in Palinuridae, the sister taxon to Scyllaridae sensu lato. Ontogenetic details led to the

identification of two heterochronic, better peramorphic events: hypermorphosis + pre-displacement in the direct stem lineage of Scyllaridae sensu lato and pre-displacement in the stem lineage of Scyllaridae sensu stricto (Fig. 6). This demonstrates again the importance of using fossil developmental data for reconstructing evolutionary scenarios.

A single specimen, possibly representing a late scyllarid phyllosoma larva, points to the presence also of scyllarids in the Solnhofen Lithographic Limestones. The potential of the Solnhofen Lithographic Limestones to preserve larval stages and ontogenetic information is seen as a promising starting point for future investigations on malacostracan evolution.

The knowledge of Achelata in the Solnhofen Lithographic Limestones is still imperfect. POLZ (1972, 1973, 1984, 1995, 1996) has made very important contributions and also has given farther-reaching implications, and he demanded for further investigations (POLZ 1995). These are, indeed, necessary to present a more detailed picture of the ontogenetic sequences. Moreover, further studies might reveal that specimens described as distinct species are in fact developmental stages of a different species, like POLZ (1995) has indicated for the species of *Palinurina.* The search for more specimens of *Cancrinos claviger*, especially immature ones, is also necessary to amend the here only partially reconstructed ontogeny and to allow a judgement whether the phyllosoma larvae of type C might represent the larval stages of this species (POLZ 1996).

The interpretation of *Eryoneicus sahelalmae* as a possible immature specimen of *Cancrinos libanensis* is of further importance, as it indicates the presence of ontogenetic information also in the Cretaceous fish beds of Lebanon. Just one larva have been reported from there so far (PASINI & GARASSINO 2009), the earlier reports of putative stomatopod larvae all refer to thylacocephalan arthropods (SCHRAM et al. 1999).

The potential of these Mesozoic Lagerstätten to add knowledge to the ontogeny of basal offshoots of certain evolutionary lineages (as shown here) is seen as high. These fossils can contribute enormously to a (future) larger-scale phylogenetic analysis (SANTINI & TYLER 2004; SCHRAM & DIXON 2004), as they are extinct and, thus, exhibit some morphological conditions not present in extant species (e. g. WALOSSEK & MÜLLER 1990; WALOSSEK 1993; WALOSZEK et. al 2007), but also in adding ontogenetic information to phylogenetic analyses (e. g. FELDER et al. 1985; HØEG 1992; WALOSSEK 1993; WALOSSEK & MÜLLER 1998; OLESEN 2007).

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