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First fossil stomatopod larva (Arthropoda: Crustacea) and a new way of documenting Solnhofen fossils (Upper Jurassic, Southern Germany)

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Abstract

We report the first undisputable fossil larval stomatopod, as previous records all refer to thylacocephalans. The single specimen has been found in the Upper Jurassic Solnhofen Lithographic Limestones (Bavaria). We documented the specimen using a UV-light microscope, taking over 700 single images. These were summed up to a large compound image adding images in z-axis and in x-y plane. The result is a very high resolution image of high depth of field showing delicate details. The specimen possesses a tri-flagellate antennula and sub-chelate raptorial appendages, identifying it as a stomatopod. Larval characters are a large immobile rostrum and a shield hiding all thoracomeres. The specimen is probably a *Sculda* sp. and possibly not a *S. pennata,* but based on the existing data it cannot be verified whether it represents a new species.

Keywords: Stomatopoda, fossil larvae, Solnhofen Lithographic Limestones, UV-microscopy.

Zusammenfassung

Wir beschreiben den ersten unstrittigen fossilen Nachweis einer Stomatopoden-Larve, da alle früher so gedeuteten Funde als Thylacocephala identifiziert wurden. Das Fossil stammt aus den oberjurassischen Solnhofener Plattenkalken (Bayern) und wurde ausführlich mit Hilfe eines UV-Mikroskops dokumentiert. Dabei wurden über 700 Einzelaufnahmen gemacht. Diese wurden zu einem einzigen großen Bild zusammengefügt, wobei sowohl Aufnahmen in Z-Richtung als auch in der X-Y-Ebene verrechnet wurden. Das Endprodukt ist ein hoch auflösendes Gesamtbild hoher Tiefenschärfe, das auch feinste Details zeigt. Das Fossil besitzt eine tri-flagellate Antennula und sub-chelate Raubbeine; beide Merkmale weisen das Fossil als Stomatopoden aus. Eindeutige Larvenmerkmale sind das lange unbewegliche Rostrum sowie die vom Schild überdeckten Thoracomeren. Das Fossil gehört wahrscheinlich zur Gattung *Sculda*, jedoch vermutlich nicht zur häufigen Art *S. pennata*. Ob es eine neue Spezies darstellt, ist momentan noch unklar.

1. Introduction

Compared to the general fossil record of Crustacea, the record of fossil crustacean larvae is rather scarce. The small-sized entomostracan crustaceans have a quite good fossil record of larval stages and even complete larval sequences are known, even from the Cambrian (Müller & Walossek 1988; Walossek 1993). Most of these fossils are preserved in the delicate 'Orsten'-type preservation (Maas et al. 2006) or a comparable delicate preservation through phosphatic impregnation in younger strata (Weitschat 1983; Smith 2000) These fossils are preserved uncompressed, three-dimensionally, not only with stronger sclerotised structures, but also with soft parts, such as eyes, arthrodial membranes, setae or setules. Within the 'Orsten'-type material not only entomostracans are preserved. There are also larvae and larval sequences of derivatives of basal crustacean offshoots below the level of Eucrustacea preserved (Müller & Walossek 1986; Maas et al. 2003).

For larvae of the large and diverse Malacostraca the fossil record is poorer. Despite the fact that larvae of the Malacostraca appear in large number in the oceans today (e.g. McConaugha 1992) and the good fossil record of adult Malacostraca, there are only a few examples of fossil malacostracan larvae. Of the few fossil deposits where these kinds of fossils have been found, the Upper Jurassic Solnhofen Lithographic Limestones have proven to be the richest fossil Lagerstätte. From there three types of palinurid phyllosomes (zoea stage equivalents) are known, two of them with thousands of specimens (Polz 1984). Based on these fossils ontogenetic sequences with several stages could be reconstructed (Polz 1972, 1973). In addition to these three zoea-type larvae, the so-called larva D, a specimen fossilised while moulting from a phyllosome into a puerulus, has also been reported from Solnhofen (Polz 1995). Polz (1995) also indicated the possibility that specimens described as *Palinurina pygmea* and *P. intermedia* may in fact represent puerulus-larvae.

The small eryonoidean *Knebelia schuberti* has been identified as a juvenile of *Cycleryon propinquus* (Garassino & Schweigert 2006), another eryonoidean, and could possibly represent the megalopa stage of this species, because of its morphological distinctiveness.

Non-Solnhofen fossil malacostracan larvae are a brachyuran zoea from the Cretaceous of Brazil showing exclusively a very poorly preserved head shield with eyes (MAISEY & DE CARVALHO 1995) and the fossil representatives of the supposed eryonoidean genus *Eryoneicus*, which has been interpreted as corresponding to the eryoneicus stage of Recent Eryonoidea (AGUIRRE-URRETA et al. 1990), a „post-larva", i. e. megalopa sensu WILLIAMSON (1969). The Stomatopoda are the only non-decapod malacostracan group where fossil larval specimens have been recorded (e.g. VAN STRAELEN 1938). Unfortunately, all these "stomatopod larvae" turned out to be Thylacocephala (cf. SCHRAM et al. 1999).

Here we report the first find of an undisputable fossil stomatopod larva from the Solnhofen Lithographic Limestones. The single specimen was provided by a private collector and was minutely documented with a new method using a UV-microscope together with special software programs.

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2. Material and Methods

Material: The here described specimen was discovered by one of the authors (M. E.) and will be deposited in the Jura-Museum Eichstätt with the registration number SOS 8073.

Locality: Eichstätt quarry area, Schernfelder-Leiten, from 'Fäule-Lagen' (finely laminated, soft clay-rich layers).

Horizon and age: Eichstätt Formation (Lower Tithonian, Hybonotum Zone, Riedense Subzone) (SCHWEIGERT 2007).

A mechanical preparation was not necessary. The specimen was carefully treated with a soft brush with water to get rid of a delicate calcareous layer. The fossil was not varnished.

The used documentation method is referred to as composite fluorescence micrograph in palaeobotany (BOMFLEUR et al. 2007). The specimen was documented using an Axio Scope 2 microscope with reflective UV-light (wavelength: 358 nm) and an AxioCam digital camera. Many, but not all crustacean fossils from the Solnhofen lithographic limestones show autofluorescence under UV light exposure (SCHWEIGERT & GARASSINO 2003). Also Recent crustaceans show large variations in their autofluorescent capabilities, even within different body parts of the same organism (MICHELS 2007). Other investigated specimens of *Sculda* sp. exhibit good autofluorescence (pers. obs.).

The larval specimen was documented by 734 single images, i. e. 128 image stacks of up to 9 images. The images of one stack were taken in distances of 15–18 µm. The stacks were then fused using the freely available software CombineZM, resulting in very sharp images with a high depth of field. These resulting images were arranged using Adobe Photoshop CS1 and the freely available software GIMP. The resulting image (Fig. 1A) is 29,102 pixels in maximum length; with a total length of the specimen of 18.5 mm one pixel equals a length of 0.64 µm. With this high resolution it is possible to zoom in and resolve also small details (Fig. 2). An interpretive drawing was produced by loading a smaller version of the complete image into Adobe Illustrator CS1 and redrawing prominent lines as vectors. Further processing was done in the freely available vector graphics software Inkscape (Fig. 1B). A preliminary 3D model (Fig. 1C) was also produced using the freely available software BLENDER.

The application of composite imaging on smaller Solnhofen fossils offers many advantages. Although the method is rather time consuming and depends on a special type of microscope, the results are worth the effort. The method reveals small details in a high resolution. Although we have to admit that especially the posterior part of specimen SOS 8073 is partly damaged and does not show many details, it demonstrates the power of intensive documentation of Solnhofen fossils. This new way of documenting Solnhofen fossils has the potential to facilitate the future detailed documentation of smaller and especially larval specimens.

3. Systematic Palaeontology

Arthropoda VON SIEBOLD & STANNIUS, 1845
Crustacea BRÜNNICH, 1772
Malacostraca LATREILLE, 1802
Hoplocarida CALMAN, 1904
Stomatopoda LATREILLE, 1817
Unipeltata LATREILLE, 1825
?Sculdidae DAMES, 1886
?*Sculda* MÜNSTER, 1840
?*Sculda* sp.

Description. – The specimen is preserved in almost perfect lateral aspect (Fig. 1A). Its total length is 18.5 mm from anterior to posterior. Anterior part covered by shield (concealing details of head and pereion), posterior portion pleon.

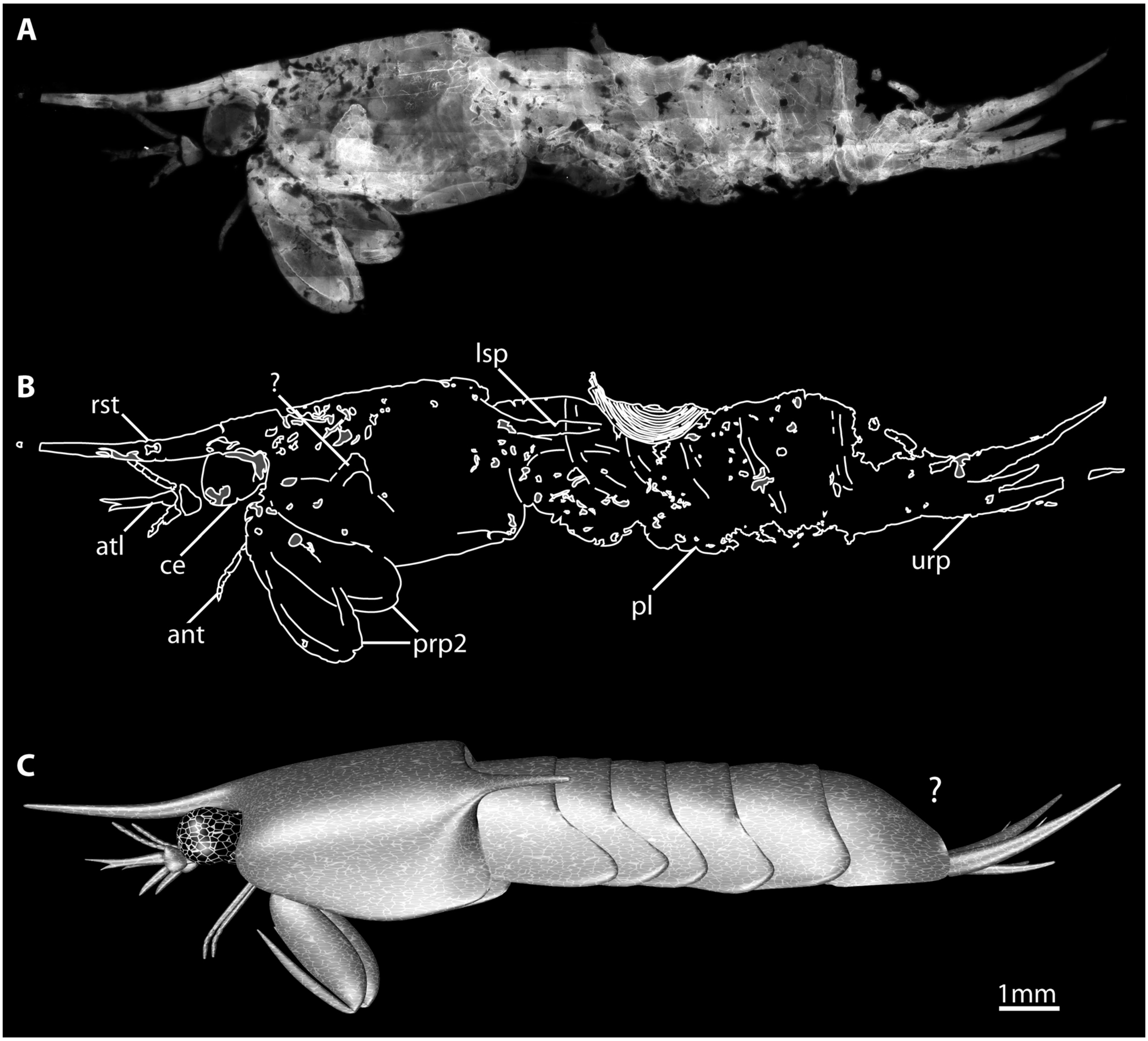

Fig. 1. Larva of ?*Sculda* sp.; overview images of specimen SOS 8073 from the Upper Jurassic Solnhofen Lithographic Limestones, Eichstätt Formation, Schernfeld near Eichstätt, Lower Tithonian, Hybonotum Zone, Riedense Subzone. – **A**. Compound image displaying the whole specimen with UV-fluorescence. **B**. Interpretive drawing. Marked details are rostrum (rst), antennula (atl), compound eye (ce), antenna (ant), second pereiopod (prp2), lateral spine (lsp), pleon (pl), uropod (urp), possible mandible imprints (?). **C**. Preliminary 3D model. ? indicates the poor preservation of the sixth pleomere and telson.

Maximum total shield length 4.3 mm (without rostrum and spines), maximum shield height 3.0 mm. Shield anteriorly drawn out into a 4.1 mm long immobile rostrum, posterior margin with one backward pointing latero-terminal spine of 2.1 mm length on each side.

Pleon with six pleomeres. Pleomeres curved backwards ventrally in lateral view. Maximum approximate length of the pleomeres 1: 1.4 mm, 2: 0.9 mm, 3: 0.9 mm, 4: 1.0 mm, 5: 1.3 mm; sixth pleomere damaged, no measurements were possible. Approximate height of pleon is 2.25 mm. The pleon appears smooth without any tubercle structures.

On the dorsal part of the third pleomere an alien structure covers the animal, possessing growth lines (Fig. 2B). This together with the general shape identifies it as a fish scale.

Ventral to the rostrum, a circular structure is interpreted as a compound eye, with an approximate diameter

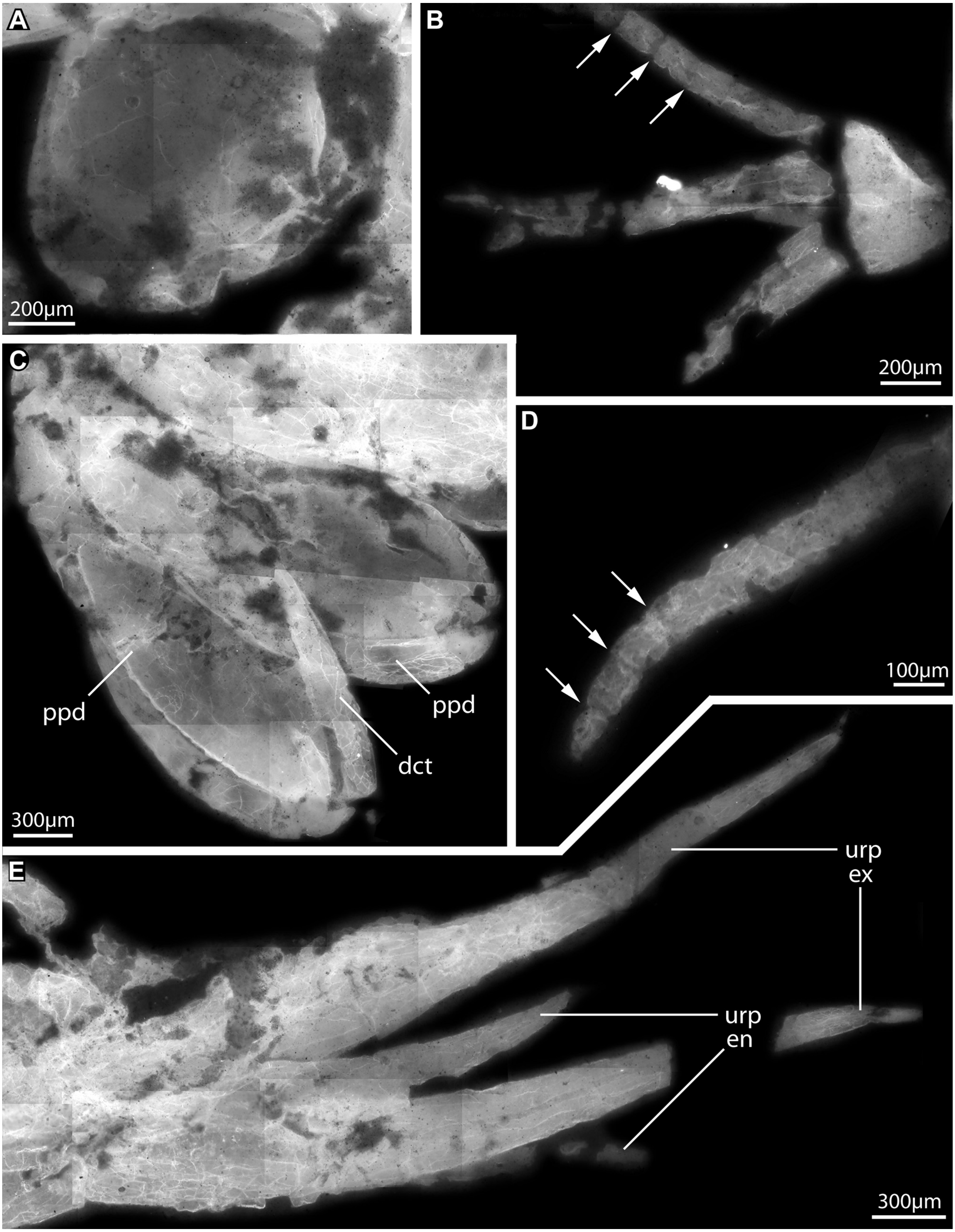

Fig. 2. Details of Fig. 1A with UV-fluorescence. – **A**. Compound eye. **B**. Antennula. Arrows indicating separations of portions. **C**. Second pereiopods with propodi (ppd) and dactylus (dct). **D**. Endopod of antenna. Arrows indicating separations of portions. **E**. Uropods (urp) with exopods (ex) and endopods (en).

of 0.9 mm (Fig. 2A). Ventro-anterior to the eye structure tri-flagellate antennula, with sub-triangular proximal portion with a base width of 0.5 mm and a height of 0.35 mm (Fig. 2B). Uppermost flagellum with at least 6, possibly 7 or more portions of equal size, approximately 0.15 mm long and 0.1 mm wide (separations marked by arrows in Fig. 2B); terminal tip hidden under rostrum. Second flagellum without visible subdivision 1.25 mm long, width 0.25 mm at the base, tapering towards the terminal tip, which is bifurcating at 0.85 mm. Third flagellum 0.65 mm long, width at the base 0.2 mm, tapering towards the terminal tip. Antenna only with terminal part of endopod (Fig. 2D) of 0.95 mm length, not concealed by shield. At least terminal part made up of three portions of equal length of 0.1 mm (separations marked by arrows in Fig. 2D), subdivision of more proximal parts not preserved. Width of the endopod 0.1 mm, tapering towards terminal tip, at the base of the terminal portion the width is 50 µm.

Raptorial appendages (Fig. 2C), pereiopod 2, with propodi of both appendages and one preserved dactylus, but twisted, thus, dactylus being on the posterior side of the propodus. Propodus of oval outline, 2.5 mm long, 1.0 mm wide. Dactylus gently curved, minimum length 1.3 mm, but broken off terminally; width 0.25 mm at the base, tapering terminally, being 50 µm at the broken end. No other pereiopods or pleopods identifiable besides the uropods.

Uropods with simple spine-like appearing exopod and endopod. Exact lengths difficult to distinguish, as exact border to sympodite unclear (Fig. 2E). Approximate length of uropodal exopod 2.6 mm, width at the presumed base 0.45 mm, tapering towards the terminal end. Endopod 1.15 mm long, 0.2 mm wide at the presumed base, tapering towards the terminal end. Telson not preserved (marked by "?" in Fig. 1C).

Other details are difficult to judge due to the preservation. Arched structures in the centre of the head shield may be imprints of the stronger sclerotised mandibular coxae from the inner side (marked by "?" in Fig. 1B).

Discussion. – For comparison the Recent *Neogonodactylus bredini* (Manning, 1969) is used. The larval stages of *N. bredini* have been precisely described by Morgan & Goy (1987). As Gonodactylidae appear to be a rather basal group within the Recent stomatopods (Hof 1998; Ahyong & Harling 2000) it is seen as an ideal species for comparison with our specimen. Two characters identify the specimen SOS 8073 as a stomatopod:

(1) The tri-flagellate antennula (Fig. 2B), which is an autapomorphy of Stomatopoda. The design of the antennula appears to be similar to that of the first post-larval stage of *N. bredini* (Morgan & Goy 1987, fig. 9A, B).

(2) The raptorial appendages (the second pereiopods) with a strong propodus and a blade-like dactylus (Fig. 2C).

Besides the fact that the antennula resembles that of the post-larval stage of *N. bredini*, a number of other characters demonstrate the true larval status of specimen SOS 8073. The rostrum is long and not set off from the shield (Fig. 1A), comparable to the last larval stage of *N. bredini* (Morgan & Goy 1987, fig. 8B). The thoracic segments are hidden under the shield (Fig. 1), unlike in adult stomatopods, but as in the larval stages of *N. bredini*. The shield also possesses laterally backward pointing spines on the shield, which is also only seen in larval stages in *N. bredini*.

All other records of stomatopod larvae have been identified as Thylacocephala (Schram et al. 1999), a group of arthropods of uncertain affinities. The specimen presented here is the first undisputable fossil record of a stomatopod larva.

The determination of this new specimen is partially problematical, as one of the most informative characters for exact phylogenetic placement within the Stomatopoda, the tail fan, is not well preserved (Fig. 2E). Probably, this specimen is a member of the mono-genetic extinct Sculdidae, thus belongs to the genus *Sculda* Münster, 1840, as the exopods of the uropods appear undivided (Fig. 2E) and the dactylus of the second pereiopods bears no teeth and is thin and blade-like (Fig. 2C) (Münster 1840; Hof 1998). Three species of *Sculda* are described from the Solnhofen Lithographic Limestones. The most abundant one is *S. pennata* Münster, 1840, the other two (*S. spinosa* Kunth, 1870 and *S. pusilla* Kunth, 1870) are known just from few specimens (Kunth 1870; Hof & Briggs 1997) and it might even be possible that these are in fact synonyms of *S. pennata*.

The studied specimen is most likely not a larval stage of *S. pennata*. One indication is the size. The minimum size of *S. pennata* is given as 22 mm by Schram & Müller (2004), but as *S. pusilla* may in fact be a synonym and its size is given as 9.5–10.8 mm, the actual minimum size of *S. pennata* with adult morphologies is probably much smaller. This is also supported by personal observation. As already very small specimens of *S. pennata* possess an adult morphology, their larvae should be even smaller, and specimen SOS 8073 is simply too large to be a larva of this species. Furthermore, the pleon of *S. pennata* shows a typical pattern of tubercles (e. g. Berry 1939), while the pleon of specimen SOS 8073 appears smooth, although this might be interpreted as a larval character.

Based on this, we see it as not justifiable to erect a new species at the moment. It will be necessary to re-investigate the *Sculda* material, also aiming to document developmental aspects. Nevertheless, the option that the larva described here represents a yet unknown unipeltatan stomatopod species, of which no adult forms have been found to date, should not be ruled out.

4. Importance of the new specimen

As already stated this is the first record of a true stomatopod larva and the first record of a non-decapod malacostracan larva at all. All so far described fossil malacostracan larvae are those of reptantian decapods: three phyllosomes (Polz 1972, 1973, 1984), a single phyllosome moulting into puerulus (Polz 1995), a single fragmentary crab zoea (Maisey & de Carvalho 1995) and the questionable eryoneicus larva (Aguirre-Urreta et al. 1990).

Fossil larvae are crucial for the understanding of the developmental patterns in the malacostracan ground pattern and with this of early crustacean evolution as a whole. As the Hoplocarida are the sister taxon to the remaining Eumalacostraca, but the Recent species all show many special autapomorphies, more data on early, in this case fossil representatives are essential. Although Sculdidae are in-group Unipeltata and the sister group to all Recent groups, they are one node lower on the phylogenetic tree than Recent Unipeltata and allow to add knowledge to a ground pattern of a more basal node. The specimen presented here does not add crucial information to this due to its imperfect preservation, but it demonstrates the potential for preservation of such specimens.

Moreover, the fossil demonstrates the importance of collecting smaller and, at first glance, not so impressive fossils. Probably, there are more specimens available that have been overlooked or misinterpreted as something else, as an important discriminating character, the rostrum, looks completely different in specimen SOS 8073 compared to adult *Sculda* sp. Thus, we hope that the specimen presented here also facilitates not only the review of the *Sculda* material, but also the discovery of more larval specimens in other collections.

The applied method of using a high resolution composite image of the specimen is seen to be promising for documenting smaller Solnhofen fossils in general. This new opportunity will also facilitate further detailed descriptions of smaller specimens, hopefully especially larvae.

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