Morphology and ontogeny of the Upper Jurassic mantis shrimp *Spinosculda ehrlichi* n. gen. n. sp. from southern Germany

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Abstract

We describe a new species and genus of Stomatopoda (mantis shrimps), *Spinosculda ehrlichi* n. gen. n. sp. from the Upper Jurassic Solnhofen Lithographic Limestones of southern Germany. The species is known from two fragmentary specimens that appear to represent different ontogenetic stages. Both specimens possess a pair of posteriorly projecting movable spines dorso-laterally on the tergite of the sixth pleomere, seen as a justification for regarding this material as a new species. The smaller specimen is preserved in dorsal aspect and shows less detail. The exopods of the uropods are of lanceolate shape but lack lateral spines. The pleotelson is unusual for stomatopods from the Solnhofen Lithographic Limestones in being elongate rather than rounded, and drawn out into two prominent spines. The shape of the pleotelson and the uropods indicates that the specimen represents a larval stage. The larger specimen, probably a juvenile, is preserved in lateral aspect. It exhibits features known also from other stomatopods from the Solnhofen Lithographic Limestones, such as the tri-flagellate antennula and the undivided uropod exopods with movable spines along the lateral margin. *Sp. ehrlichi* n. gen. n. sp. is assigned to the taxon Sculdidae. It adds to the diversity of stomatopods in the Mesozoic and demonstrates once more the potential for uncovering ontogenetic information from fossils from the Solnhofen Lithographic Limestones.

Keywords: Stomatopoda, Solnhofen Lithographic Limestones, Sculdidae, fossil larva.

Zusammenfassung

Wir beschreiben eine neue Art und Gattung von Stomatopoden (Fangschreckenkrebse), *Spinosculda ehrlichi* n. gen. n. sp. aus den oberjurassischen Solnhofener Plattenkalken von Süddeutschland. Von der Art liegen zwei Exemplare vor, beide sind unvollständig erhalten und stellen möglicherweise verschiedene ontogenetische Stadien dar. Beide Exemplare besitzen ein Paar nach hinten weisender, beweglicher Stacheln, welche dorso-lateral am Tergit des sechsten Pleomers ansitzen. Dieses charakteristische Merkmal rechtfertigt die Zuordnung der beiden Exemplare zu einer neuen Art. Das kleinere Exemplar ist in Dorsalansicht erhalten und zeigt weniger Details. Die Exopoditen der Uropoden sind lanzettlich geformt, besitzen jedoch keine Lateralstacheln. Das Pleotelson ist nicht abgerundet, sondern stark verlängert und in zwei markante Stacheln ausgezogen, eine für Stomatopoden aus den Solnhofener Plattenkalken ungewöhnliche Form. Die Gestalt des Pleotelsons und der Uropoden weisen dieses Stück als Larve aus. Das größere der beiden Tiere, vermutlich ein juveniles, ist in lateraler Lage eingebettet. Es weist Merkmale auf, welche auch von anderen Stomatopoden aus den Solnhofener Plattenkalken bekannt sind, wie z. B. die triflagellate Antennula oder die ungeteilten Exopoditen der Uropoden, die entlang des lateralen Randes bewegliche Stacheln besitzen. Wir deuten *Sp. ehrlichi* n. gen. n. sp. als Vertreter der Sculdidae. Durch diese neue Art wird nicht nur die Diversität der Stomatopoden des Mesozoikums erhöht, sondern auch ein weiteres Mal das Potential der Solnhofener Plattenkalke verdeutlicht, ontogenetische Informationen von fossilen Arten zu erhalten.

1. Introduction

The predatory mantis shrimps (Stomatopoda) are known for their extraordinary visual system (e. g. Kleinlogel & Marshall 2006; Chiou et al. 2008), their fast reactions (e. g. Patek et al. 2004) and their colourful appearance (e. g. Manning 1995; Erdmann & Boyer 2003). In addition to about 450 Recent species (Ahyong 2001) approximately 30 fossil species are known, ranging from the Carboniferous to Holocene strata (for complete lists see Schram & Müller 2004; Ahyong et al. 2007).

Three stomatopod species have been described from the Upper Jurassic Solnhofen Lithographic Limestones of southern Germany, namely *Sculda pennata* Münster, 1840, *S. spinosa* Kunth, 1870, and *S. pusilla* Kunth, 1870. In addition, a single larval specimen preliminarily assigned to the genus *Sculda*, and probably representing a new species, has been described recently (Haug et al. 2008).

Apparently, *Sculda pennata* and *S. spinosa* can best be differentiated in dorsal or ventral view. *S. spinosa* has been described as being broader in appearance than *S. pennata* and having a different number of tubercular dorsal structures and a difference in the shape of the rostrum (Kunth 1870). However, no rigorous morphometric and statistical analysis has yet been undertaken to test for a bimodal distribution of morphological characters to support the distinction of these two species rather than a case of continuous intraspecific variation. *S. pusilla* is known only from a single poorly preserved specimen and requires a reinvestigation. Similarly, the knowledge of the other described species of *Sculda* is only fragmentary, and the

Sculdidae as a whole needs re-study. This is necessary, not least because HOF (1998) has interpreted the Sculdidae as the sister-group to the remaining Unipeltata, which contain the crown-group stomatopods (and the Pseudosculdidae) and, accordingly, they have been used to root the trees in phylogenetic analyses of the Recent Stomatopoda (AHYONG 1997; HOF 1998; AHYONG & HARLING 2000).

We present the first results of our project on the restudy of the stomatopods from the Solnhofen Lithographic Limestones by describing a new genus and species of Sculdidae. Special emphasis will be placed on presenting ontogenetic information, knowledge of which is still limited to the single, most likely larval specimen described by HAUG et al. (2008). Adopting methods for the visualisation of two-dimensionally preserved fossil material, such as composite imaging combined with UV-fluorescence, reveals enough morphological information for detailed studies even on small specimens (HAUG et al. 2008). We aim at accumulating more information on this group, which likely will improve the understanding of the evolution of the Stomatopoda in general.

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2. Material and Methods

The material consists of two specimens. One was found in the Schernfelder-Leiten by MANFRED EHRLICH, Böhl-Iggelheim, and will be deposited in the Jura-Museum Eichstätt under repository number JME-SOS 8085. The second specimen is in the private collection of ROGER FRATTIGIANI, Laichingen, and was found at Wegscheid near Schernfeld.

Preparation of specimen JME-SOS 8085 was undertaken by MANFRED EHRLICH. The second specimen was prepared by ROGER FRATTIGIANI. A soft brush was used to get rid of the calcareous layer covering the fossils. Specimen JME-SOS 8085 was varnished with a glue-acetone mixture.

The method used for imaging the fossils is referred to in palaeobotany as 'composite fluorescence' imaging (BOMFLEUR et al. 2007) and was recently applied to specimens from the Solnhofen Lithographic Limestones (HAUG et al. 2008). Both specimens were documented using an Axio Scope 2 microscope and an AxioCam digital camera with reflective UV-light (358 nm).

About 400 single images were taken to document the whole of specimen JME-SOS 8085, consisting of 72 image stacks each of up to 10 images. For the other specimen about 1,000 single images in 149 stacks were taken with a maximum of 14 images per stack. Images of a stack were captured at 18 µm intervals. The image stacks were fused using the freely available software CombineZM, resulting in sharp images with a high depth of field, which were then arranged using Adobe Photoshop CS1 and the freely available software GIMP. The final images are about 14,300 pixels in maximum length for specimen JME-SOS 8085 and 23,430 pixels for specimen two; with a total length for the specimen of about 9 mm and 14.75 mm respectively, one pixel equals a length of 0.63 µm. With this high resolution it is also possible to zoom in and resolve fine details (Figs. 1C–D, 2 C–F). Interpretive drawings were produced by loading smaller versions of the complete images into Adobe Illustrator CS1 and redrawing prominent lines as vectors. Further processing was done in the freely available vector graphics software Inkscape (Figs. 1B, 2B). Preliminary 3D models (Fig. 3) also were produced using the freely available software BLENDER. For the reconstruction, information obtained from one specimen was amended for the other as necessary. This is seen as appropriate for producing a close-to-life reconstruction of the two ontogenetic stages of the species.

3. Systematic palaeontology

Arthropoda VON SIEBOLD & STANNIUS, 1845
Crustacea BRÜNNICH, 1772
Eucrustacea KINGSLEY, 1894
Malacostraca LATREILLE, 1802
Eumalacostraca GROBBEN, 1892
Hoplocarida CALMAN, 1904
Stomatopoda LATREILLE, 1817
Unipeltata LATREILLE, 1825
Sculdidae DAMES, 1886

Spinosculda n. gen.

Etymology: With reference to the prominent spines on the sixth pleomere and the otherwise similar genus *Sculda.*
Type species: *Spinosculda ehrlichi* n. sp.
Diagnosis: As for the species.

Spinosculda ehrlichi n. gen. n. sp.
Figs. 1–3

Etymology: In honour of MANFRED EHRLICH, Böhl-

Iggelheim, who discovered the specimen, designated as the holotype.

Holotype: Specimen housed in the Jura-Museum Eichstätt, repository number JME-SOS 8085; a fragmentary, presumed late larval stage.

Type locality: Eichstätt quarry area, Schernfelder-Leiten, southern Germany.

Type horizon: Eichstätt Formation (Lower Tithonian, Hybonotum Zone, Riedense Subzone) (SCHWEIGERT 2007). Finely laminated, soft clay-rich layers ('Fäule-Lagen').

Other material: A single unnumbered specimen from the Eichstätt Formation of Wegscheid near Eichstätt, collection of ROGER FRATTIGIANI, Laichingen.

Diagnosis. – Small stomatopod with two distinct, jointed, posteriorly projecting spines dorso-laterally on the tergite of the sixth pleomere.

Remarks. – The morphological differences between the two specimens are interpreted as ontogenetic effects. The holotype is probably a representative of a late larval stage, the other specimen is a representative of a later developmental stage, probably a juvenile. Therefore, two developmental stages are described for the species, each based on a single specimen.

Description. – Early developmental stage (based on the holotype): Small specimen; only dorsal features known due to preservational factors (Fig. 1). Total length 9.04 mm. Anterior body region covered by the cephalothoracic shield, posterior body region with pleon and pleotelson. Shield 3.15 mm long and 2.75 mm wide. Posterior part of shield rectangular, 1.55 mm long measured from posterior rim, anterior part triangular in shape, tip pointing anteriorly. Pleon 2.45 mm in maximum width, consisting of six pleomeres, respectively about 0.48 mm, 0.56 mm, 0.60 mm, 0.52 mm, 0.61 mm, and 0.65 mm long from anterior to posterior. A small laterally projecting structure from under the first pleomere, 0.26 mm long and 0.13 mm wide, possibly represents a part of one of the walking limbs. Sixth pleomere with a pair of backward pointing, jointed spines, inserting dorsolaterally on the posterior edge of the pleomere (Fig. 1C, D). Spines 1.15 mm long and 0.39 mm wide at the base, tapering distally. Pleotelson width 1.85 mm maximally measured at the anterior end, maximum length 3.00 mm. Pleotelson tapers terminally, merging into two 0.82 mm long spines. Three small spines occur along the lateral side of the pleotelson (Fig. 1C). Uropods with lanceolate- to spine-shaped sub-equal endopods and exopods, both 2.20 mm long and 0.30 mm wide proximally, tapering distally. Basipod hidden under telson. Smaller spine, 0.65 mm long and proximally 0.20 mm wide, arises between left uropod and pleotelson, possibly representing a basipodal spine of the uropod. Corresponding structure on opposite side apparently not preserved or hidden by the pleotelson.

Later developmental stage (based on the additional specimen): Small specimen; certain morphological aspects difficult to interpret because of its preservation in lateral aspect (Fig. 2). Total measurable length without appendages 11.65 mm. Specimen slightly curved, therefore, actual length most likely larger, approximately 13.25 mm. Body covered anteriorly by shield, posterior part of pereion with at least three free pereiomeres, pleon with six pleomeres and pleotelson. Measurable part of the shield approximately 3.10 mm long, but anterior part broken off in this specimen. Shield is 2.00 mm high at the anterior end, 3.10 mm high close to the posterior edge. Two structures projecting anteriorly from underneath the shield are interpreted as remains of the compound eyes. A pair of antennulae occurs antero-ventral to the compound eyes (Fig. 2F). Antennulae with three basal portions, each approximately 0.42 mm long and approximately 0.24 mm wide. From the third portion arise two structures, a flagellum (flagellum 1) and another portion being 0.36 mm long and 0.14 mm wide, which gives rise to two more flagella (flagella 2 and 3). Flagellum 1 with at least 11 portions, most proximal portion 0.27 mm long, more distal ones 0.12 mm long. Proximal width of flagellum 0.09 mm, tapering distally to 0.06 mm at most distal known portion. Flagellum 2 with at least 11 portions, flagellum 3 with at least four portions, all of comparable dimensions to the portions of flagellum 1, except for the enlarged proximal portion of flagellum 1, which is not present in the other flagella (Fig. 2F).

Pair of antennae ventral to the antennulae (Fig. 2C) shows endopod and exopod. Exopod paddle-shaped, 1.40 mm long and 0.59 mm wide; endopod preserved with at least 9, possibly up to 12 annuli of approximately 0.18 mm length and 0.15 mm width. A structure of oval outline projecting from underneath the shield is interpreted as the possible propodus of the second pereiopod, i. e. the second raptorial limb. Measurable length 0.76 mm (possible actual length up to twice as long), width 0.41 mm. Posterior to the shield at least three free pereiomeres visible, 0.36 mm in length, 2.40 mm high. Posterior to the pereion, pleon with six pleomeres present, about 2.90 mm high. Lengths of pleomeres respectively about 0.95 mm, 1 mm, 1.05 mm, 1.05 mm, 1.15 mm, and 0.70 mm from anterior to posterior. Sixth pleomere with a pair of posteriorly pointing, jointed spines, (latero-?) dorsally at the posterior margin (Fig. 2E). Only right spine visible because of preservation in lateral aspect: Spine is at least 1.00 mm long, 0.24 mm wide at its base, tapering and is broken off distally. Pleotelson behind the pleon 1.80 mm long and 1.70 mm high at pleon-pleotelson joint (Fig. 2D). Details of pleotelson unknown except that some posteriorly pointing spines stem from its posterior margin. Exact number and length of spines not obtainable. Uropods only partly known (Fig. 2D). Basipod unknown. Distal part of exopod elongate, paddle-shaped, with movable spines along the lateral margin and distal tip. In total at least eight marginal spines, one more medially, one terminally and six arising laterally

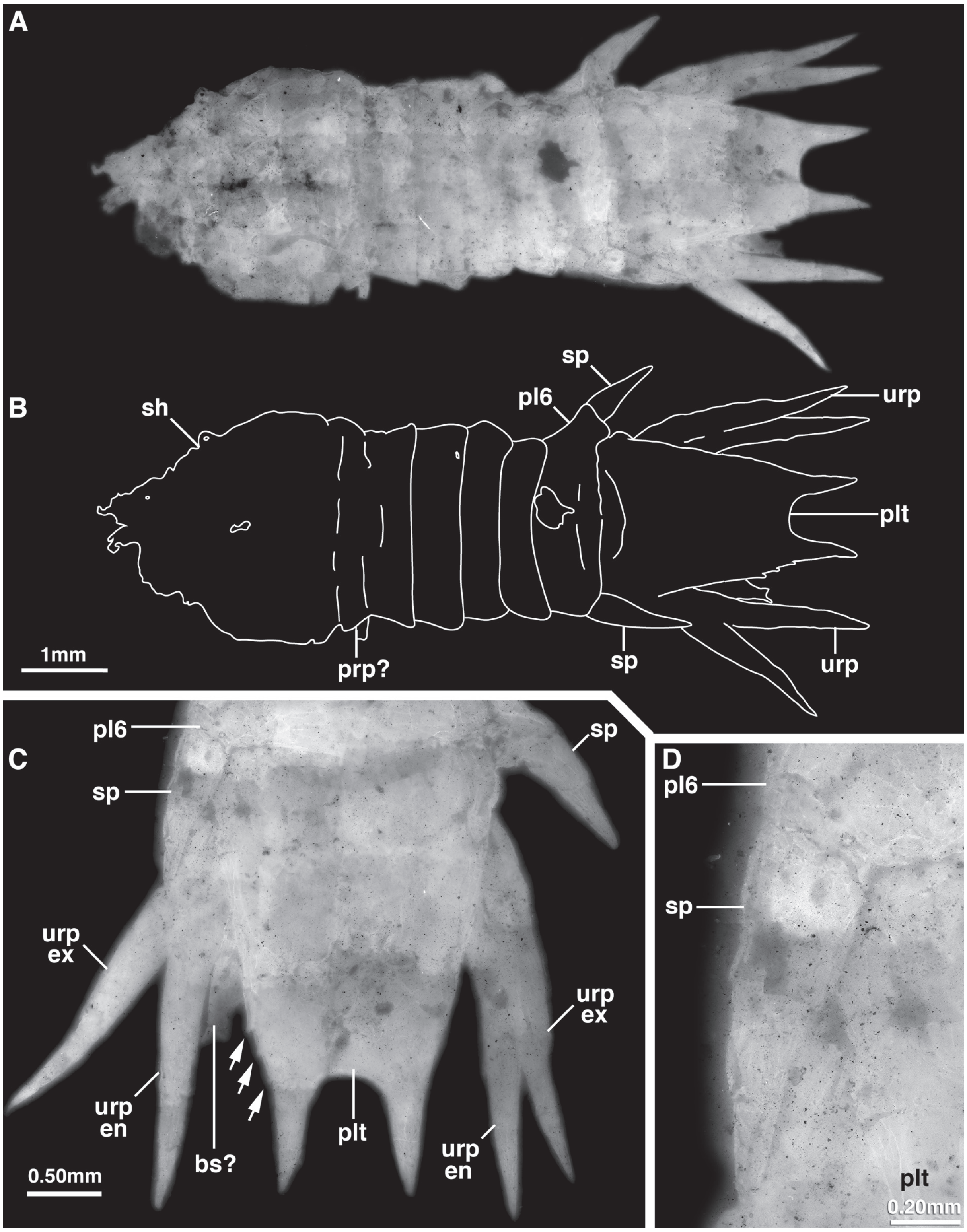

Fig. 1. Holotype of *Spinosculda ehrlichi* n. gen. n. sp.; late larval developmental stage (JME-SOS 8085). – **A**. Composite image of the entire specimen. **B**. Interpretive drawing of A. **C**. Detail of posterior region including sixth pleomere and pleotelson. Arrows indicate small (initial?) spines on the lateral side of the pleotelson. **D**. High magnification of the left movable spine of the sixth pleomere. – Abbreviations: bs?: possible basipodal spine; en: endopod; ex: exopod; pl6: sixth pleomere; plt: pleotelson; prp?: possible part of pereiopod; sh: shield; sp: spine; urp: uropod.

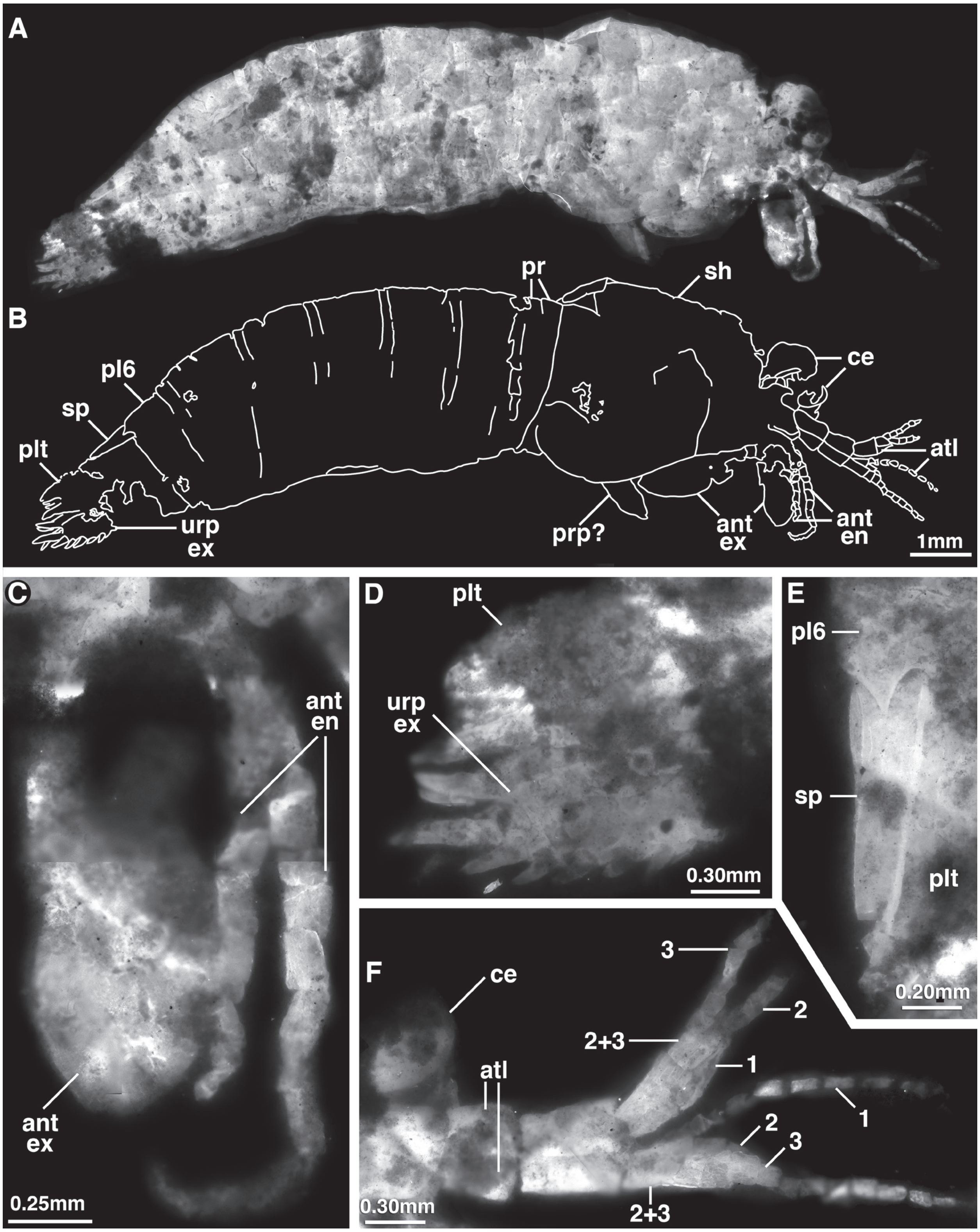

Fig. 2. Second known specimen of *Spinosculda ehrlichi* n. gen. n. sp.; juvenile (?) (Frattigiani collection). – **A**. UV-composite image of entire specimen. **B**. Interpretive drawing of A. **C**. High magnification of the antennae. **D**. Details of pleotelson and uropods. **E**. Enlarged image of the spine on the sixth pleomere. **F**. Branching pattern of the antennular flagella 1, 2 and 3 on both antennulae. – Abbreviations in addition to those of Fig. 1: ant: antenna; atl: antennula; ce: compound eyes; pr: pereiomere.

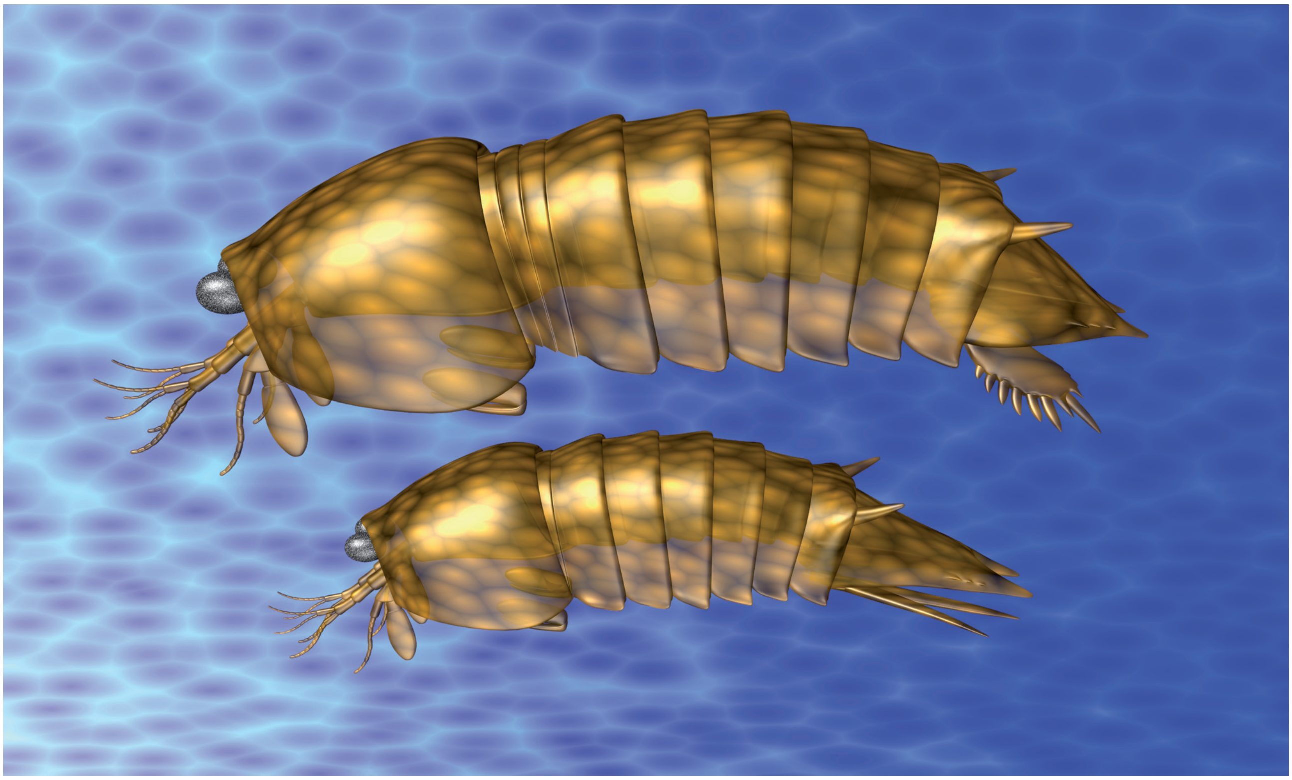

Fig. 3. Preliminary partial 3D reconstruction of *Spinosculda ehrlichi* n. gen. n. sp. The upper model represents a more advanced developmental stage. The lower model shows a larval stage. Colour pattern hypothetical.

from the outer margin. Terminal spine is the largest, 0.53 mm long and 0.12 mm wide at its base. More median spine slightly smaller. Lateral spines are progressively smaller, most proximal one 0.14 mm long and 0.07 mm wide at its base.

4. Discussion

4.1. Morphological stages

Our conclusion as to the larval status of the small specimen (JME-SOS 8085) is based on certain characters of the pereion, in being fully covered by the shield, and of the uropodal exopods, in having a more slender shape than the larger specimen and in lacking spines on the outer margin. However, the specimen appears to lack other typical larval features known from Recent forms, such as a long immovable rostrum and a pair of latero-terminal spines on the posterior border of the shield (see e. g., Morgan & Goy 1987; Rodrigues & Manning 1992). It is possible that these structures are absent because of preservational factors, as the entire anterior area of the shield is rather badly preserved. Alternatively, some typical larval features might be missing because the specimen is a very late larval stage – one already showing some post-larval characters. This assumption finds support in the small size difference between the smaller and the larger, apparently post-larval specimen. Such a mixture of larval and post-larval characters in a single developmental stage has not apparently been described from Recent stomatopods; however, that may reflect the fact that stomatopod ontogeny has not been intensely studied. Although decapods are a quite distantly related taxon, stages with intermediate morphologies have been reported for some species in this group, which have long larval sequences (e. g. Villamar & Brusca 1988). Therefore, the occurrence of such a stage in stomatopods is seen as, at least, a plausible explanation, especially bearing in mind that long larval sequences are also known from stomatopods in general (Morgan & Goy 1987).

4.2. Morphogenesis

P e r e i o n : The pereion of the holotype larval specimen is fully covered by the cephalothoracic shield, whereas at least three pereiomeres are not covered by the cephalothoracic shield in the presumed juvenile specimen. A comparable morphological change is known for the moult from the last larval to the post-larval stage in the Recent stomatopod *Neogonodactylus bredini* (Manning, 1969) (Morgan & Goy 1987). This morphological change thus supports the interpretation of the smaller specimen as being a larval stage.

Uropods: With regard to the morphogenesis of the uropods, only the exopods are known from both specimens and they differ significantly. In the supposed juvenile specimen they show at least eight movable spines along the outer margin, whereas those of the smaller specimen lack these structures. This observation corresponds again with the interpretation that the smaller specimen is a larval stage. In the Recent *Neogonodactylus bredini* the larvae also lack strong spines or show only a few small teeth as precursors, while the post-larval stage carries a number of strong spines along the outer margin of the exopods of the uropod (Morgan & Goy 1987). Also, the difference of the outline shape of the uropodal exopods, being either slender or more paddle-shaped respectively in the two fossil specimens, corresponds to the change in shape during the ontogeny of *N. bredini*.

Pleotelson: The pleotelson is difficult to compare between the two specimens of *Spinosculda ehrlichi* n. gen. n. sp., as it is only partly known in the presumed juvenile specimen. In the larva the pleotelson is significantly longer than in the older stage and has only two well-developed spines, whereas the supposed juvenile specimen appears to have more spines. Again this morphogenetic change (i. e., the increase in the number of spines) is present in the Recent *Neogonodactylus bredini* (Morgan & Goy 1987). A considerable change in the length of the pleotelson, as occurs in *Sp. ehrlichi* n. gen. n. sp., is not observed in *N. bredini* (although slight shape changes occur throughout the ontogeny); however, this might be a specific feature of *Sp. ehrlichi* n. gen. n. sp.

4.3. Differences between *Spinosculda ehrlichi* n. gen. n. sp. and species of *Sculda*

The diagnostic feature of *Spinosculda ehrlichi* n. gen. n. sp., the pair of spines on the sixth pleomere, is neither known from *Sculda*, nor from any other stomatopod species, regardless whether fossil or Recent. *S. pennata* and *S. spinosa* both exhibit a distinctive pattern of small tubercles or teeth (= Zähne; Kunth 1870). Such structures are not present in *S. pusilla* (Hof 1998) or in *Sp. ehrlichi* n. gen. n. sp. and the probably distinct species represented by a single larval specimen described by Haug et al. (2008). The larval stage of *Sp. ehrlichi* n. gen. n. sp. appears to lack tergopleurae; this absence may, however, simply be an ontogenetic effect, as larvae of the Recent *Neogonodactylus bredini* also lack tergopleurae whereas the post-larval stages have such structures (Morgan & Goy 1987). The corresponding area is not well enough preserved in the presumed juvenile stage of *Sp. ehrlichi* n. gen. n. sp. to judge whether it possesses tergopleurae. Similarly, other structures, such as the pleotelson and the rostrum, are also badly preserved in the supposed juvenile stage of *Sp. ehrlichi* n. gen. n. sp. and cannot be used for comparisons.

The morphologies of the antennulae and the antennae as seen in the presumed juvenile stage of *Spinosculda ehrlichi* n. gen. n. sp. have not previously been reported in this detail from any Jurassic stomatopod. In *Sp. ehrlichi* n. gen. n. sp. the antennular flagella 2 and 3 arise from a single portion, the third portion of the antennula, counted from the proximal end; flagellum 1 arises from the next proximal portion, the second portion of the antennula. The same morphology can be seen in Recent Stomatopoda (Schram 1969; Morgan & Goy 1987). In the "Archaeostomatopoda", the "Palaeostomatopoda" and the Aeschronectidae, which are the non-unipeltatan hoplocarids, the three flagella are described to arise from just one portion (e. g. Schram 1969; Schöllmann 2004), but this needs to be reviewed for more taxa.

The stomatopod larval specimen of uncertain affinities from the Solnhofen Lithographic Limestones, recently described by Haug et al. (2008), does not seem to be conspecific with *Spinosculda ehrlichi* n. gen. n. sp. Because of preservational factors some characters are difficult to compare; e. g. it is not certain whether or not the posteriorly pointing spine on the sixth pleomere is missing in the particular specimen described by Haug et al. (2008). Furthermore, the larval specimen of *Sp. ehrlichi* n. gen. n. sp lacks a long rostrum and a pair of latero-terminal spines on the posterior rim of the shield, both of which are well developed in the larval specimen described by Haug et al. (2008), but it remains unclear whether this is, again, a preservational artefact. Nevertheless, there are features that clearly indicate that the latter specimen represents a different species. Firstly, what is clearly a larval specimen (possession of long immovable rostrum, latero-terminal spines on the posterior border of the shield, lanceolate uropodal exopods and endopods lacking spines; Haug et al. 2008) is much longer (18.5 mm) than even the presumed juvenile specimen of *Sp. ehrlichi* n. gen. n. sp. (13.25 mm). It is considered unlikely that these two specimens belong to the same ontogenetic sequence, as although certain size variations can occur within a developmental stage, this is too large a difference to be explained just by variation. Secondly, the uropods of the two larvae show marked differences. The endopod and exopod of the uropods in the larva of *Sp. ehrlichi* n. gen. n. sp. are of about equal length, whereas the uropodal endopods in the larva described by Haug et al. (2008) are only about half the length of the exopods.

Further investigations of the Mesozoic stomatopods are necessary to deduce the phylogenetic relationships within Sculdidae. The two specimens investigated during this study were found during examination of only a dozen specimens from private collections putatively belonging to *Sculda*. Therefore, a lot of new information on stomatopod morphology, ontogeny and evolution can be expected from further re-investigations of fossil stomatopod material from the Solnhofen Lithographic Limestones.

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