

New records of Mesozoic mantis shrimp larvae and their implications on modern larval traits in stomatopods

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Abstract

We present new data on two species of stomatopods from the Upper Jurassic Solnhofen Lithographic Limestones of southern Germany. One is a new species, *Gigantosculda ehrlichfeckeii* n. gen. n. sp. It is known from two specimens, probably representing two larval stages. The species is characterised by a larval morphology with a long rostrum, long postero-lateral spines on the head shield, uropods with basipodal spines about twice as long as the telson, and a comparably large size. The second species is the already known species *Spinosculda ehrlichi*. Here newly observed features of the late larval stages include the mandibles and the maxillipeds 2–5. The comparison of the two species described in this study reveals possible plesiomorphic larval characters in Stomatopoda: 1) a head shield protruding over the thorax, and 2) lanceolate uropodal exopods without moveable spines. It also reveals possible synapomorphies of *Gigantosculda* n. gen. and Verunipeltata (the group including all modern representatives): 1) comparably large size of later larval stages, and 2) presence of an elongate rostrum and postero-lateral spines on the head shield in the larvae. The descriptions add information to the diversity and ecology of Mesozoic mantis shrimps, as well as to the evolution of stomatopods.

Key words: Stomatopoda, Verunipeltata, larval specialisation, character evolution.

1. Introduction

Stomatopods, or mantis shrimps, are predatory malacostracans with an obligate carnivorous lifestyle (e.g., SCHRAM 1986). Modern representatives of Stomatopoda, Verunipeltata (HAUG J. T. et al. 2010a), possess numerous exceptional specializations, such as their highly complex visual system (KLEINLOGEL & MARSHALL 2006; CHIOU et al. 2008) and their extraordinarily fast strike (PATEK et al. 2004; MURPHY & PATEK 2012).

A reconstruction of the evolutionary pathways leading to such highly specialized structures can benefit enormously from the investigation of early fossil forms (e.g., DONOGHUE et al. 1989; RUST 2006). There are about 500 extant species of stomatopods known (AHYONG et al. 2014), and about 60 fossil ones (SCHRAM & MÜLLER 2004; AHYONG et al. 2007; HAUG C. et al. 2013). The fossil record is mostly restricted to adult specimens, and only recently the first records of fossil stomatopod larvae emerged (e.g., HAUG J. T. et al. 2008, 2010a, 2011a, 2014; HAUG C. et al. 2009a), all from the famous lithographic limestones of southern Germany.

Extant stomatopod larvae already possess raptorial appendages and a predatory lifestyle in their pelagic stages. Compared to the adult forms, the larval stages are morphologically very diverse (e.g., GIESBRECHT 1910; SHANBHOUE 1975; AHYONG et al. 2014; HAUG C. & HAUG J. T. 2014). In addition, the development differs significantly between the different morphotypes of larvae (e.g., GIESBRECHT 1910; MORGAN & PROVENZANO 1979; HAMANO & MATSUURA 1987).

Currently, there are four formally described stomatopod species from the Upper Jurassic Solnhofen Lithographic Limestones of southern Germany (ca. 150 ma). These include three species of *Sculda*, namely *S. pennata*, *S. pusilla*, *S. spinosa*, and one species of *Spinosculda*, namely *Sp. ehrlichi*. KUNTH (1870) distinguished *S. spinosa* and *S. pennata* by the shape of the rostrum and number of tubercles on the pleon dorsally. After examination of a larger number of specimens by HAUG J. T. et al. (2010a) this differentiation has been doubted and discussed to be variation caused by different preservation. The validity of the third species of *Sculda*, *S. pusilla*, has also been doubted due to the problematic characters that were used by KUNTH (1870) to describe the species (HAUG J. T. et al. 2010a). We use here the reference to groups of specimens as ?*S. pennata/spinosa* and ?*S. pusilla*, as suggested by HAUG J. T. et al. (2010a).

A single specimen ascribed to *Sculda* (but without species affiliation) has been discussed to represent an earlier developmental stage, possibly representing a larva (HAUG J. T. et al. 2010a, 2014). The specimen was interpreted as possibly representing *S. pennata* (HAUG J. T. et al. 2014), hence ?*S. pennata/spinosa*.

A fourth formally undescribed species has also been assigned to *Sculda* (but without species affiliation), clearly representing a larva (HAUG J. T. et al. 2008, 2014). A clear differential diagnosis was not possible so far.

Here we describe new material of fossil stomatopod larvae from the lithographic limestones of southern Germany. The new material reveals additional insights into the larval morphology of these 150 million years old

creatures, which represent an important reference point for understanding the evolution of highly specialised larval traits in modern forms.

Acknowledgements

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2. Material and methods

The material investigated here consists of eight specimens ascribed to *Spinosculda ehrlich* and two specimens ascribed to *Gigantosculda ehrlichfecke* n. gen. n. sp. in

this study. Most specimens originate from the same area (Blumenberg/Wegscheid/Schernfeld, near Eichstätt); just one comes from a different area (Zandt). Therefore, we assume that the locality where the specimens were found has no significant impact on our interpretations. For further details see Table 1. The larval stages of *Sp. ehrlich* represent two size clusters (Table 2; Fig. 1), possibly representing two successive stages. Additionally, a single specimen was interpreted to represent a juvenile stage (HAUG C. et al. 2009a), and was not included in the size cluster graph.

The ‘composite fluorescence’ method (KERP & BOMFLEUR 2011) was used for the documentation of the fossils. This method has proven to be successful for specimens from the Solnhofen Lithographic Limestones in previous studies (e.g., HAUG J. T. et al. 2008, 2012; HAUG C. et al. 2009b). Specimens were documented using a Keyence BZ-9000 fluorescence microscope and a Zeiss Axio-Scope 2 microscope (with an AxioCam digital camera). The objectives used were 4x, 5x or 10x (resulting in about 40x, 50x or 100x magnification). Light of different excitation wavelengths (358nm or 365nm = UV, 473nm = Blue, 546nm = Green) was used for illumination, using the auto-fluorescence capacities of the specimens (e.g., HAUG C. et

Table 1. Known specimens of *Spinosculda ehrlich* and *Gigantosculda ehrlichfecke* n. gen. n. sp.. Excitation wavelengths: 358nm = UV; 473nm = Blue; 546nm = Green. Collectors: H.P. = HERMANN POLZ, Geisenheim; M.E. = MANFRED EHRLICH, Böhl-Iggelheim; M.F. = MICHAEL FECKE, Langenberg; M.W. = MATTHIAS & MARINA WULF, Rödelsee; R.F. = ROGER FRATTIGIANI, Laichingen. Repositories: JME = Jura-Museum Eichstätt; SMNS = Staatliches Museum für Naturkunde Stuttgart; other specimens are in the corresponding private collections.

Figure	Species	Excitation Wavelength	Locality	Collector	Repository Number	referred to in
2A,B	<i>Gigantosculda ehrlichfecke</i> n.gen.n.sp.	546nm	Blumenberg near Eichstätt	M.F.	SMNS 70305	this study
2C,D	<i>Gigantosculda ehrlichfecke</i> n.gen.n.sp.	358nm	Eichstätt quarry area, Schernfelder-Leiten, from „Fäule-Lagen“	M.E.	JME-SOS 8073	Haug J. T. et al. 2008, 2014
3A	<i>Spinosculda ehrlich</i>	546nm	Wegscheid near Eichstätt	H.P.	SMNS 67634	Haug J. T. et al. 2014
3B	<i>Spinosculda ehrlich</i>	546nm	Zandt	M.W.	9203	Haug J. T. et al. 2014
3C, 5A, B	<i>Spinosculda ehrlich</i>	546nm	Blumenberg near Eichstätt	M.E.	01-2011 M.E.	this study
3D, 4A-D	<i>Spinosculda ehrlich</i>	546nm	Wegscheid near Eichstätt	H.P.	SMNS 67591	Haug J. T. et al. 2014
3E	<i>Spinosculda ehrlich</i>	358nm or 365nm	Eichstätt quarry area, Schernfelder-Leiten	M.E.	JME-SOS 8085	Haug C. et al. 2009a, Haug J. T. et al. 2014
3F	<i>Spinosculda ehrlich</i>	546nm	Wegscheid near Schernfeld	R.F.	D198100022/01	Haug J. T. et al. 2011
3G, 5C	<i>Spinosculda ehrlich</i>	473nm	Schernfeld	R.F.	JW-2015-A1	this study
3H	<i>Spinosculda ehrlich</i>	358nm	Wegscheid near Schernfeld	R.F.	JW-2015-A2	Haug C. et al. 2009a

Table 2. Measurements of the larval specimens of *Spinosculda ehrlich* in mm. Specimen JW-2015-A2 represents the juvenile and is therefore not considered.

Specimen	length total	length telson	length longest uropodal spine	length pleomere 3–5
SMNS 67634	6.0	missing	1.7	1.4
9203	6.5	1.6	1.6	1.3
01-2011 M.E.	7.8	2.6	2.0	1.9
SMNS 67591	9.2	3.1	2.0	1.8
JME-SOS 8085	9.0	3.0	2.1	2.0
D198100022/01	9.5	3.0	2.4	2.0
JW-2015-A1	8.3	2.1	2.2	1.9

al. 2009b; HAUG J. T. et al. 2011b). Specimens documented under polarized light were photographed with a Canon EOS Rebel T3i equipped with a EF-S 18–55mm lens. For illumination the Canon macro twin flash MT 24-EX was used and the light was cross-polarized (e.g., HAUG J. T. et al. 2013). Measurements were made using the freely available software ImageJ.

Stacks of single images were recorded and fused for a high depth of field, using the freely available software CombineZP. If the specimens could not be captured in one stack, multiple stacks were stitched together using Adobe Photoshop CS3. For further processing, more precisely optimizing brightness, contrast, sharpness and color-coding structures, Adobe Photoshop CS3 and CS2 was used. For the colour-coding, structures were selected and copied as a new layer, and then given colour via image-mode: variations. Reconstructions were done using Adobe Illustrator CS2 and Adobe Photoshop CS2 and further processing was performed with Adobe Photoshop CS2 and CS3.

3. Systematic palaeontology

Arthropoda s. str. sensu MAAS et al. 2004

Crustacea s. l. sensu STEIN et al. 2008, amend. HAUG J. T. et al. 2010b

Eucrustacea sensu WALOSSEK 1999

Malacostraca LATREILLE, 1802

Eumalacostraca GROBBEN, 1892

Hoplocarida CALMAN, 1904

Stomatopoda LATREILLE, 1825

Unipeltata s. l. sensu HAUG J. T. et al. 2010a

Gigantosculda n. gen.

Ety m o l o g y: With reference to the large overall body size and with reference to the earlier idea of a closer relationship to *Sculda*.

Type species: *Gigantosculda ehrlichfecke* n. sp.

D i a g n o s i s: As for the species.

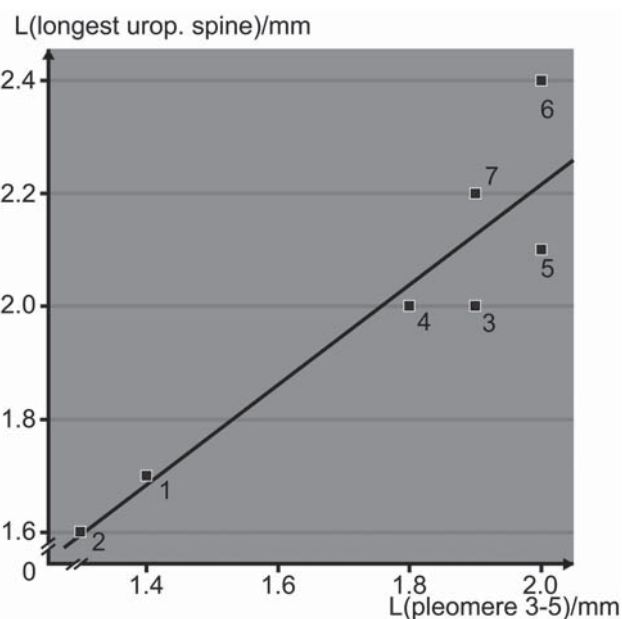


Fig. 1. Diagram on length of pleomeres 3–5 vs length of the longest uropodal spine of seven specimens of *Spinosculda ehrlich* with regression line. 1: SMNS 67634, 2: 9203, 3: 01-2011 M.E., 4: SMNS 67591, 5: JME-SOS 8085, 6: D198100022/01, 7: JW-2015-A1.

Gigantosculda ehrlichfecke n. gen. n. sp.

v 2008 “Larva of ?*Sculda* sp.”. – HAUG J. T. et al. p.105, fig. 1, p.106, fig. 2.

2009a “stomatopod larval specimen of uncertain affinities”. – HAUG C. et al. p. 117.

2010 “tentatively assigned to *Sculda* (...) probably a juvenile”. – SCHRAM, p. 31.

2010a “single known specimen of a larval stomatopod from the Solnhofen Lithographic Limestones, which also probably represents a new species”. – HAUG J. T. et al., p. 15.

2013 “one still to be named form”. – HAUG J. T. & HAUG C., p. 202.

2013 “new species (...) yet to be named”. – HAUG C. et al., p. 281.

v 2014 “giant yet-unnamed larva” – HAUG J. T. et al. p. 179, fig. 32.2.

2014 “which probably represents a new species”. – HAUG J. T. et al. p. 177.

2014 “extinct Sculdidae (...) identified from the Jurassic Solnhofen deposits”. – AHYONG et al., p.187

Etymology: In honour of MANFRED EHRLICH, Böhl-Iggelheim, who discovered the specimen designated as holotype, and MICHAEL FECKE, Langenberg, who discovered the second specimen.

Holotype: Specimen deposited in the Jura-Museum Eichstätt (JME), repository number JME-SOS 8073; larva preserved in lateral aspect.

Type locality: Eichstätt quarry area, Schernfelder-Leiten, from ‘Fäule-Lagen’ (finely laminated, soft, clayey layers).

Type horizon: Altmühltal Group, Eichstätt Subformation (Lower Tithonian, Hybonotum Zone, Riedense Subzone) (SCHWEIGERT 2007; NIEBUHR & PÜRNER 2013).

Other material: A single specimen collected by MICHAEL FECKE (deposited in the Staatliches Museum für Naturkunde Stuttgart, SMNS 70305).

Diagnosis: Known only from larval semaphoronts, with long, distinct rostrum and two long, postero-lateral spines on the head shield. Presumed basipodal spine of uropod about twice as long as the telson.

Remarks: The description is based on two larval specimens in different condition and different overall body length; representing two developmental stages.

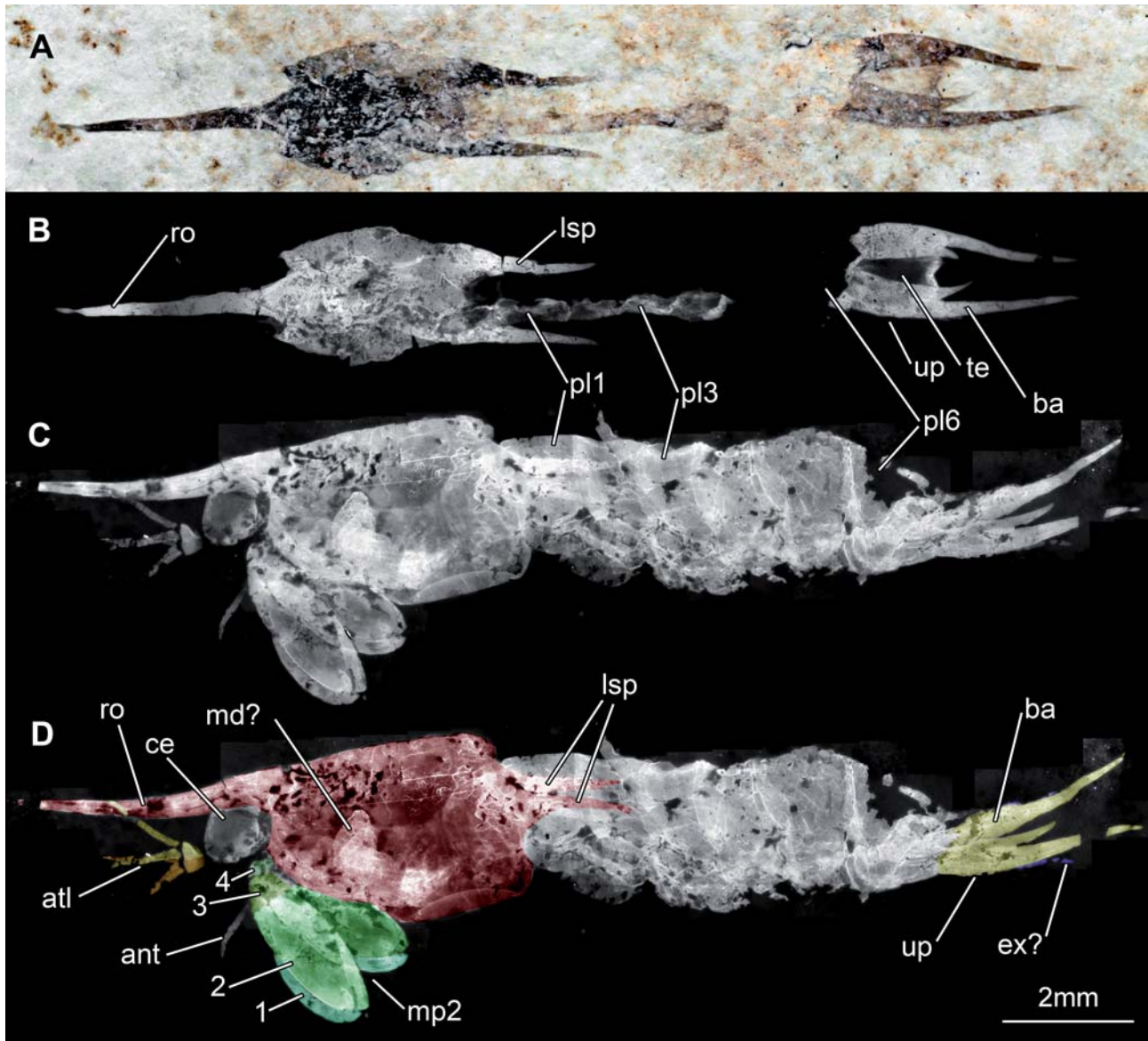


Fig. 2. *Gigantosculda ehrlichfeckeii* n. gen. n. sp., larvae. A, B: Earlier developmental stage, dorsal view (SMNS 70305). C, D: Later developmental stage (JME-SOS 8073), lateral view (D: Highlighted structures). A: Polarized light. B-D: Composite autofluorescence images. Abbreviations: 1–4: main elements 1–4, ant: antenna, atl: antennula, ba: basipod, ce: compound eye, ex?: possible uropodal exopod, lsp: lateral spines, md?: possible mandible, mp 2: maxilliped 2, pl: pleomere, ro: rostrum, te: telson, up: uropod.

Descriptions:

Earlier larval stage (Fig. 2A, B): Body anteriorly organised in head with pronounced head shield and thorax concealed by the head shield; posterior region with pleon and telson.

Head shield sub-elliptic in dorsal view (without spines). Anteriorly drawn out into long rostrum and two small, acute drawn-out parts laterally; posteriorly drawn out into two long postero-lateral spines. With notches at the anterior margin lateral to base of the rostrum. Rostrum about 5.1x as long (anterior-posteriorly) as maximum width of the rostrum (medio-laterally). About 1.3x as long (anterior-posteriorly) as the head shield (without spines). Postero-lateral spines about 0.8x as long (anterior-posteriorly) as the head shield (without spines).

Head region and thorax with appendages unknown due to the preservation.

Pleon about 2x as long as the head shield (without rostrum and spines). Pleomeres 1–4 about 0.25x as long (anterior-posteriorly) as the length of the head shield. Pleomeres 5–6 unknown due to preservation.

Uropod with basipod presumably carrying endopod and exopod. Basal part of basipod sub-rectangular in dorsal view. Drawn out part distally tapering into one spine with two tips of different length; with lateral tip about 2.6x as long (proximo-distally) as medial tip. Lateral tip about 0.4x as long (anterior-posteriorly) as the pleon.

Telson probably sub-rectangular in dorsal view. With medial notch at the distal margin. Probably only half of the width of the telson visible.

Later larval stage (Fig. 2C, D): Body anteriorly organised in head with pronounced head shield and thorax concealed by the head shield; posterior region with pleon and telson

Head shield sub-rectangular in lateral view (without spines). Bulbous (towards the ventral margin), with almost straight dorsal margin (in lateral view). Anteriorly drawn out into long rostrum and two small, acute drawn-out parts laterally; posteriorly drawn-out into two long postero-lateral spines. With notches at the anterior margin lateral to base of the rostrum. Rostrum about 5.6x as long (anterior-posteriorly) as maximum width of the rostrum (medio-laterally). About as long (anterior-posteriorly) as the head shield (without spines). Postero-lateral spines about 0.6x as long (anterior-posteriorly) as the head shield (without spines). With slightly longer rostrum and spines than in earlier developmental stage.

Head region with compound eyes, antennula and antenna, possibly also parts of the mandible. Compound eye circular in lateral view. About 0.3x as long (approximate diameter) as rostrum (anterior-posteriorly). Antennula organised in peduncle and three distal flagella of about equal width. Flagella arising from proximal, sub-rectangular element. Uppermost flagellum (flagellum I) subdivided in at least six elements of equal size. Antenna with flagellum, presumably arising from endopod.

Thorax with all appendages except maxilliped 2 unknown due to preservation. With raptorial claw (maxilliped 2) protruding under the head shield at the height of the antenna. Maxilliped 2 with 1st (most distal) main element (dactylus) claw-like, strongly developed; not bearing any spines. Slightly curved inwards. About 0.8x as long as 2nd main element. 2nd main element (propodus) of maxilliped 2 elliptic in lateral view with tapered proximal margin; without long, distinct spines. About 2.4x as long (proximo-distally) as maximum width of the element (latero-medially). 3rd main element sub-triangular in lateral view, tapering proximally. With distal margin about 1.4x as wide (latero-medially) as proximo-distal axis of the element.

Pleon about 1.8x as long as the head shield (without rostrum and spines). Smooth, without tubercle structures. With six in lateral view ventrally backwards curved pleomeres. With each pleomere about 0.4x as long (anterior-posteriorly) as the length of the head shield (without rostrum and spines).

Uropod with basipod presumably carrying endopod and exopod. Basal part of basipod sub-rectangular in ventral view. Drawn out part distally tapering into one spine with two tips of different length; lateral tip about 2.2x as long (proximo-distally) as medial tip. Lateral tip about 0.3x as long (anterior-posteriorly) as the pleon. Uropodal exopod lanceolate.

Telson unknown due to preservation.

Remarks: The description of the later developmental stage (based on specimen JME-SOS 8073) in this study deviates to some extent from the earlier description by HAUG J. T. et al. (2008). These deviations include:

1) The maxilliped 2, and more precisely the determination of dactylus and propodus. HAUG J. T. et al. (2008) interpreted the dactylus of the lower maxilliped 2 as “twisted, thus, (...) being on the posterior side of the propodus”. After closer inspection the case seems to be different: the actual dactylus is situated at the anterior-facing margin of the propodus (the natural condition). This is indicated by the slightly inwards curved shape, which is characteristic for fossil and extant specimens of stomatopod larvae, as well as by the fine but distinct transition line between this element and the propodus (Fig. 2D). A structure of corresponding position, shape and size can be identified on the propodus of the other maxilliped 2, indicating that this structure is not only an artefact caused by fraction in the propodus, but indeed the dactylus (Fig. 2D). On the contrary, the structure previously described as the dactylus in the lower maxilliped 2 is missing on the upper and represents most likely an artefact caused by fraction.

2) The uropod. HAUG J. T. et al. (2008) interpreted the long, distal spine-like structures of the uropod as exo- and endopod. We now interpret them as the drawn-out parts of the uropodal basipod, the basipodal spine. For more details, see discussion.

3) The antennula. HAUG J. T. et al. (2008) described the antennula as tri-flagellate, with the flagella arising from a sub-triangular proximal element. Furthermore, the second flagellum was interpreted as tapering distally and being bifurcated, and the uppermost flagellum as being only about half as wide as the other two (HAUG J. T. et al. 2008).

We now interpret the arrangement slightly differently, with the three flagella of the antennula as being of approximately equal width and the second flagellum not as tapering and bifurcated. The element proximal to the flagella is now interpreted as sub-rectangular. This interpretation results from the new assumption that both antennulae are visible in specimen JME-SOS 8073 instead of one, with one superimposing the other (see also colour coding in Fig. 2D). This interpretation is based on the visible proximo-distal transition lines in the lowest and second lowest distal structure, formerly interpreted as second and third flagellum (HAUG J. T. et al. 2008), as well as in the proximal structure. In the uppermost distal structure, no proximo-distal transition lines are visible. We conclude that the uppermost distal structure represents a single flagellum, the middle distal structure two crossed-over flagella of two antennulae, the lower two parallel orientated flagella of one antennula, and the element proximal to the flagella two parallel orientated peduncles of two antennula (Fig. 2D).

Due to the preservation, some characters were missing or only partly preserved. Of the pleon in the earlier developmental

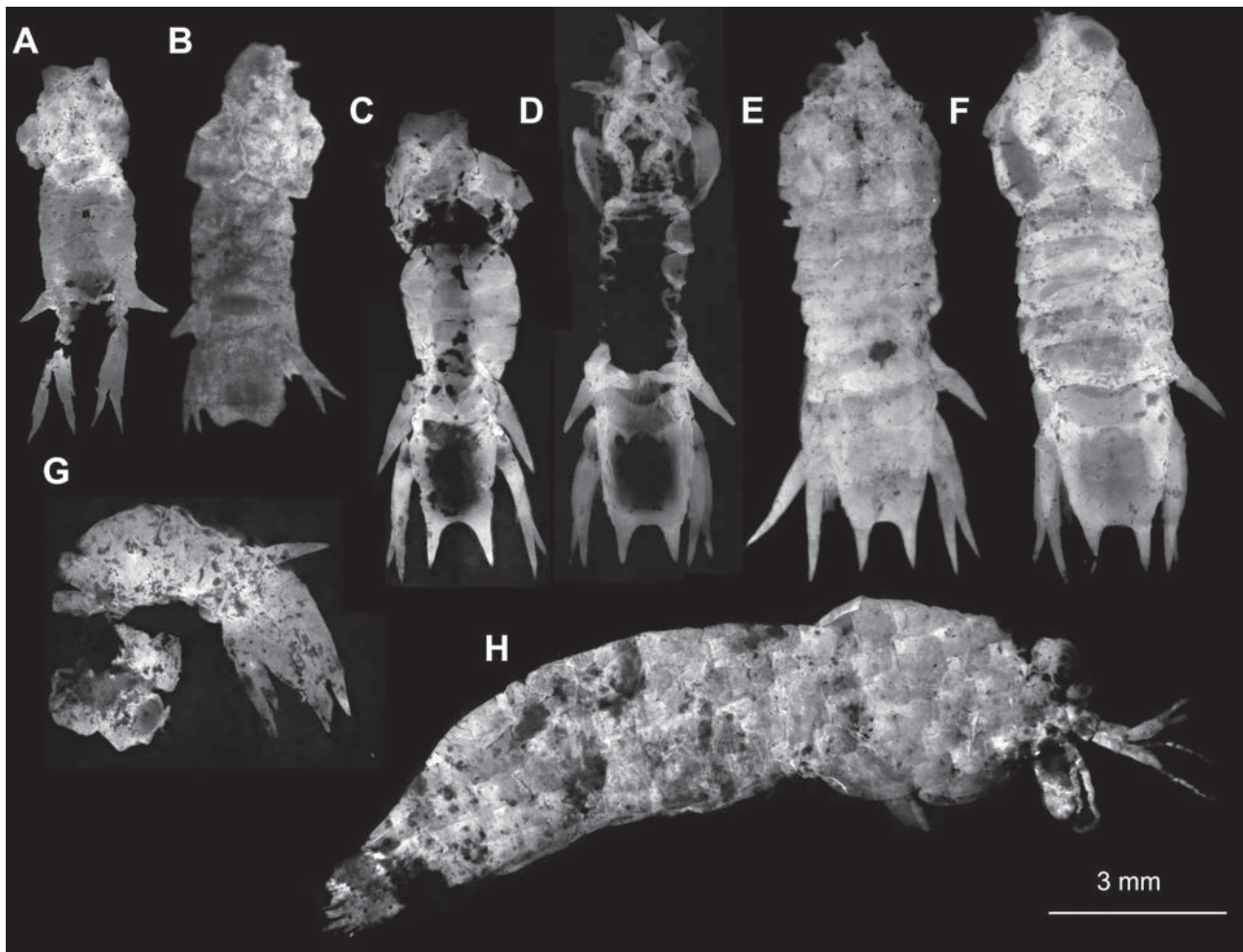


Fig. 3. Overview of the known specimens of *Spinosculda ehrlichii*. A, B: Earlier larval stage. C–G: Later larval stage. H: Juvenile. All composite autofluorescence images. A: SMNS 67634, B: 9203, C: 01-2011 M.E., D: SMNS 67591, E: JME-SOS 8085, F: D198100022/01, G: JW-2015-A1, H: JW-2015-A2.

stage, for example, only the pleomeres 1–4 are visible (Fig. 2A, B). As a result, the missing structures (pleomeres 5, 6) leave a gap between the pleon and telson. Whether, and to what extent, the telson was shifted away from the pleon during the conservation process cannot be said with certainty. However, the orientation and location of the telson in comparison to the rest of the specimen makes it plausible that this preservation represents the in situ condition.

Spinosculda ehrlichii HAUG C., HAUG, J. T. & WALOSZEK, 2009

Known material: The specimens 9203, SMNS 67634, SMNS 67591, JME-SOS 8085, D198100022/01 and JW-2015-A2 have been at least partly described in previous studies (see Table 1). The specimens JME-SOS 8085 and JW-2015-A2 have been described in greater detail in the original species description of *Spinosculda ehrlichii* (HAUG et al. 2009a); JME-SOS 8085 is the

holotype. SMNS 67591 has not been described yet with regard to the raptorial appendages. 01-2011 M.E. and JW-2015-A1 have not been presented yet.

Description (additional to the description by HAUG C. et al. 2009a): The description is based on different specimens with different preservation, which are assigned to the same stage based on spine and pleomere measurements (Table 1).

Later larval stage (Fig. 3C–G, Figs. 4–6): Head shield sub-elliptic in dorsal view, with short rostrum anteriorly (Fig. 4A, B); with notches at the anterior margin lateral to base of the rostrum (Fig. 3F). Rostrum about 0.2x as long (anterior-posteriorly) as the head shield (without rostrum); about 1.7x as long (anterior-posteriorly) as maximum width of the rostrum (medio-laterally) (Fig. 4A, B).

With antennula and antenna at head region. Antennula arising from elliptic basal sclerite (sclerite at similar position as, and possibly representing, the “supposed anterior part of hypostome” in HAUG C. et al. 2012: fig. 3A). Antennula with presumably 3 peduncles followed by one element bearing the flagella

(Fig. 4A–C). 1st main element (most distal one) sub-rectangular in ventral view, curved outwards. About 2.2x as long (proximo-distally) as wide (latero-medially). 2nd main element sub-rectangular in ventral view; about 0.3x as long (proximo-distally) as 1st main element. Distal margin as wide (latero-medially) as that of 1st element. 3rd main element sub-rectangular in ventral view. About 0.4x as long (proximo-distally) as 1st main element. Distal margin as wide (latero-medially) as that of 1st element. 4th main element sub-rectangular in ventral view; tapering distally (Fig. 4A–C).

Antenna with exo- and endopod arising from basipod. Endopod with flagellate, subdivided distal part. Exopod with distal, paddle-shaped part (Fig. 4C). Mandible with at least 4 teeth of different size at gnathal edge (Fig. 5A, B).

Thorax with four appendages preserved (maxilliped 2–5). Maxilliped 2 consisting of 6 main elements (numbered from distal to proximal) (Fig. 4D). 1st main element claw-like, probably curved inwards. 2nd main element sub-elliptic in dorsal view, about 1.5x as long (proximo-distally) as 4th main element of maxilliped 2. About 2.3x as long (proximo-distally) as maximum width of the element (latero-medially). 4th main element sub-elliptic in dorsal view. With saddle-like structure on distal half of the element. 5th main element about as long as 4th main element. Maxilliped 3 and 4 with 6th main element rectangular in dorsal view (Fig. 4D). Main elements 1–4 not preserved; 5th main element only partly visible due to the preservation. Maxilliped 5 with only 5th main element visible; 5th main element only partly visible due to the preservation.

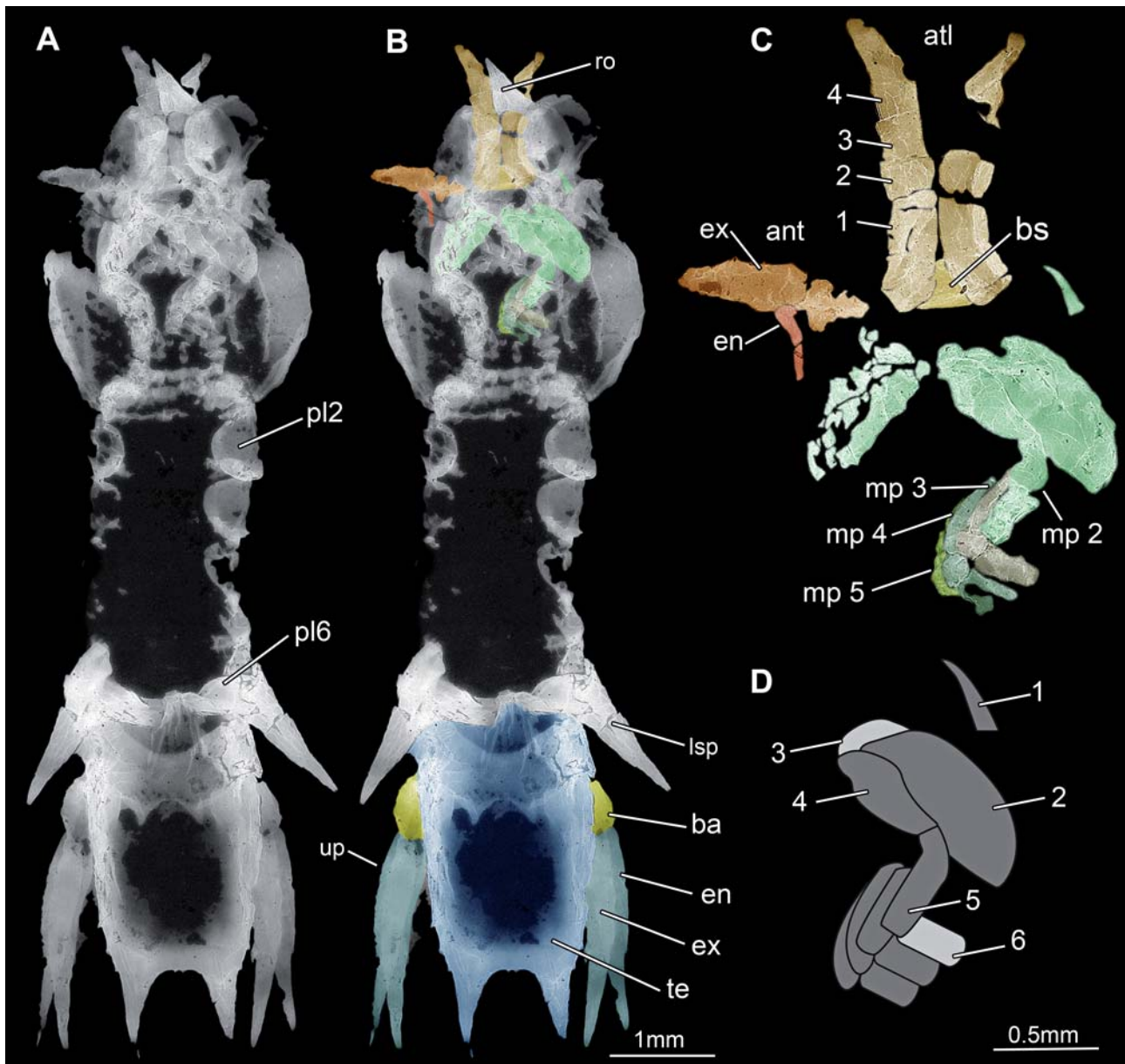


Fig. 4. *Spinosculda ehrlichi*, later larval stage, SMNS 67591. A, B: Total view. C: Appendages of the head region. D: Interpretation of the maxillipeds 2–5. A–C: Composite autofluorescence images. Abbreviations: 1–6: main elements 1–6, ant: antenna, atl: antennula, ba: basipod, bs: basal sclerite, en: endopod, ex: exopod, lsp: lateral spine, mp: maxilliped, pl: pleomere, ro: rostrum, te: telson, up: uropod.

Pleon with six pleomeres. Anterior pleomeres (pleomere 1–5) not described in detail (see HAUG et al. 2009). Pleomere 6 with two stout, posterior facing spines on the sternite medially. Posterior median spines on the sternite about 0.3x as long (anterior-posteriorly) as the posterior spines on the telson; about 0.7x as long (anterior-posteriorly) as maximum width (medio-laterally).

Remarks: The label “later larval stage” in the description above refers to the specimens 01-2011 M.E., SMNS 67591, JME-SOS 8085, D198100022/01 and JW-2015-A1. The amended description is based on those later larvae, as:

- Specimens of the earlier larval stage (Fig. 3A, B) do not show morphological differences to those of the later larval stage except body size
- The juvenile specimen (Fig. 3H) has already been described in detail in HAUG C. et al. (2009a).

Some characters of the later larvae were difficult to identify due to the preservation of the specimens. This applies, for example, to the maxillipeds 2–5 in specimen SMNS 67591.

While the maxillipeds 2–5 can be rather easily distinguished from each other in specimen SMNS 67591 (Figs. 3D, 4), the borders between the single main elements of the maxillipeds are not always distinguishable from artefacts, such as cracks. This difficulty becomes apparent in the most proximal elements of the maxillipeds 3 and 4 in Fig. 4C. It appears that the 6th main element of maxilliped 3 and 4 in specimen SMNS 67591 is followed by a sub-circular element distally (Fig. 4). This structure is found at the same position in two maxillipeds, but the possibility that this represents an artefact caused by friction must be considered. This could be a subdivision absent in modern stomatopods, as these only possess 6 elements along the main axis, while ancestrally eumalacostracans have 7. More material will be necessary to further enlighten this phenomenon. Besides the shape of the 6th main element in maxilliped 3 and 4, no characters of the maxillipeds 3–5 could be identified due to preservation. A 5th main element is visible in the maxillipeds 2–5, but in the maxillipeds 3–5 this element is mostly superimposed.

Determining the location of the posterior median spines of the sternite of the pleomere 6 in specimen SMNS 67591 was also difficult. One interpretation would be a dorsal location, as it can be seen in many extant stomatopod larvae (e.g., MANNING & PROVENZANO 1963; MICHEL & MANNING 1972; PROVENZANO & MANNING 1978; HAMANO & MATSUURA 1987; MORGAN & GOY 1987). However, specimen D198100022/01, preserved in dorsal view, revealed a probable ventral location of these median spines. Both spines are visible at the same position as in specimen SMNS 67591 (also preserved in dorsal view). In specimen D198100022/01 the telson is completely preserved and the spines only slightly visible (Fig. 3F). In specimen SMNS 67591 the telson is not preserved at the height of the spines, and the spines are clearly visible (Fig. 3D). We therefore conclude that the two postero-median spines are situated ventrally, and in situ dorsally concealed by the telson.

4. Discussion

4.1. Morphological stages

Gigantosculda ehrlichfeckeii: We propose both larvae as being conspecific to the species *G. ehrlichfeckeii*, and interpret them as two different developmental stages of the same species, based on their morphological similarities. These include:

1. The distinct rostrum and postero-lateral spines of the head shield in both specimens (Fig. 2). The rostrum and spines in the smaller specimen are longer (in relation to the head shield without spines and rostrum) than in the larger specimen (Fig. 2A, B vs C, D). This proposes that the larger specimen represents a later developmental stage of the smaller one, gradually decreasing the larval condition of a long rostrum and postero-lateral spines. Adults and juveniles typically lack these structures (GIESBRECHT 1910; LEWINSOHN & MANNING 1980; HAMANO & MATSUURA 1987; MANNING & CHACE 1990).

2. The morphology of the uropodal spines. In both cases, the uropods show two distinct, spine-like structures of different length distally, probably representing the distal part of the uropodal basipod (Fig. 2). In the larger specimen the lateral spine is smaller in relation to the pleon, as opposed to the one in the smaller specimen (Fig. 2C, D vs A, B). The similar shape, but slightly different length of the two structures implies that they represent the condition of two developmental stages in the same ontogenetic sequence, closely following each other.

The larger specimen, JME-SOS 8073, was interpreted as a juvenile instead of a larva by SCHRAM (2010). This assumption is problematic, as this specimen shows a long and prominent rostrum and spines (Fig. 2C, D). In extant stomatopods, this represents a larval trait, which is being abandoned from the juvenile stage on (e.g., MANNING & PROVENZANO 1963; MICHEL & MANNING 1972; PROVENZANO & MANNING 1978; HAMANO & MATSUURA 1987).

Spinoscultura ehrlichii: The specimens of *Sp. ehrlichii* presumably represent three different developmental stages (supporting HAUG C. et al. 2009a). Measurements of the length of the pleomeres 3–5 and the longest uropodal spine resulted in two larval size clusters (plus the juvenile form, specimen JW-2015-A2) (Tab. 2, Fig. 1). Each size cluster was interpreted as representing a developmental stage. Yet, it is not clear if these three developmental stages are directly following each other.

Extant stomatopods typically develop through multiple developmental stages (e.g., MANNING & PROVENZANO 1963; PYNE 1972; PROVENZANO & MANNING 1978; HAMANO & MATSUURA 1987), and a larval phase with only a few stages (e.g. three stages in *Heterosquilla tricarinata*; GREENWOOD & WILLIAMS 1984) can be seen as extremely abbreviated (GREENWOOD & WILLIAMS 1984). It can therefore be assumed that *Sp. ehrlichii* develops through more than 2 larval stages before reaching the juvenile.

4.2. Differences between *Gigantosculda ehrlichfeckeii* and *Spinoscultura ehrlichii*

A comparison of the two species described in this study reveals several differences between the both. Those differences lie in the following structures:

Head shield: Larval specimens of *Sp. ehrlich* lack the long, prominent rostrum and postero-lateral spines on the head shield (Figs. 3–6). These structures are very distinct in larval specimens of *G. ehrlichfecke* (Fig. 2).

Pleon: In comparison of the here described species of *G. ehrlichfecke* with *Sp. ehrlich*, the absence of prominent spines on the sixth pleomere in *G. ehrlichfecke* larvae becomes apparent (Fig. 2 vs 3–6). These spines in

the larval forms characterise *Sp. ehrlich* (HAUG C. et al. 2009a) and differentiate it from *G. ehrlichfecke*.

Uropods: The identification of the substructures found in the uropods in *G. ehrlichfecke* larvae is difficult, as only two incompletely preserved specimens are available (larval specimens) (Fig. 2). However, it already becomes noticeable that the spine-like distal elements of the uropod do not show the clear subdivision into two

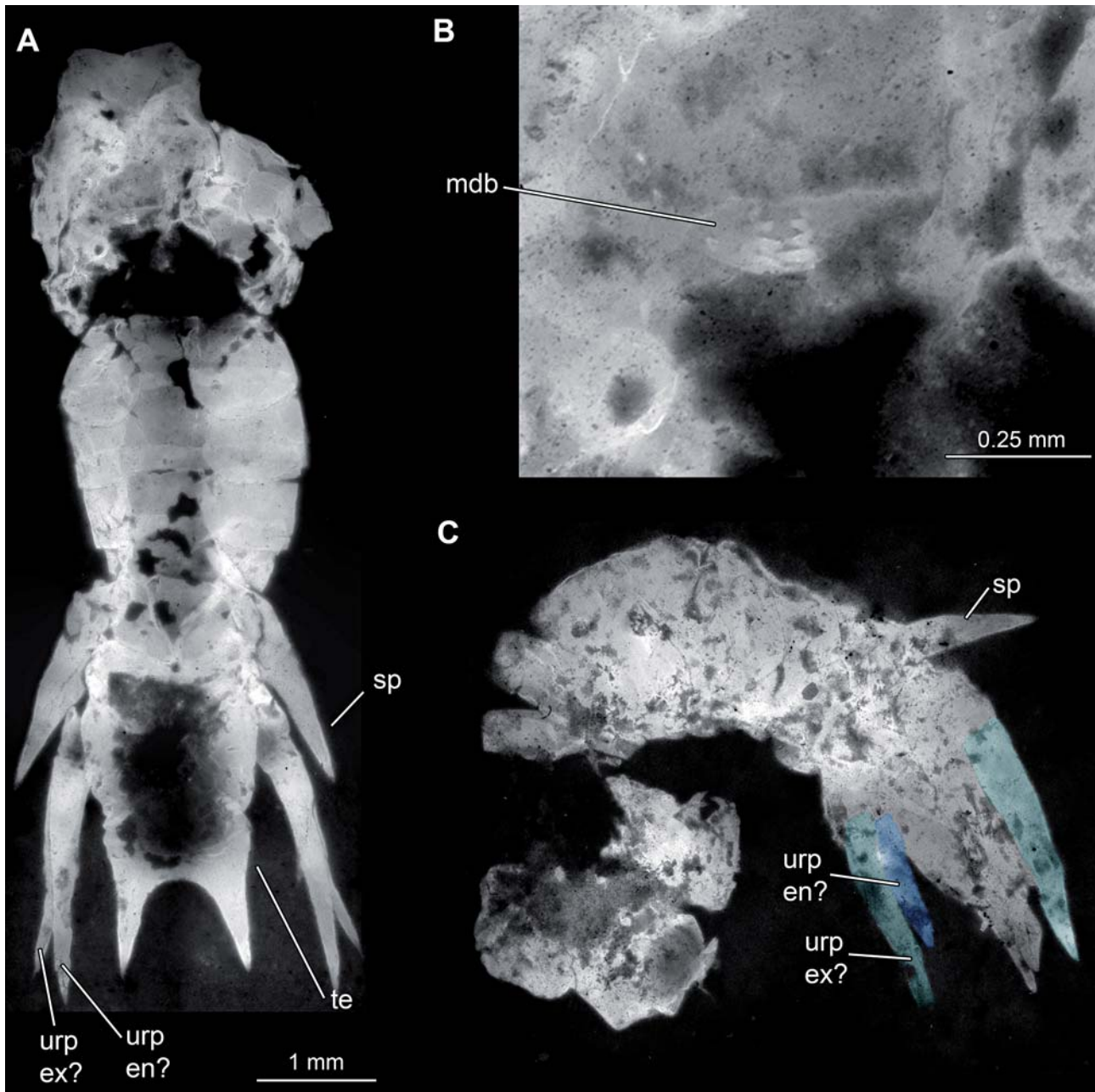


Fig. 5. *Spinosculda ehrlich*, larva. A: total view (01-2011 M.E.). B: Close-up on mandibles. C: Larva in lateral view. All composite autofluorescence images. Abbreviations: lsp: lateral spine, mdb: mandibles, pl: pleomere, te: telson, urp en?: assumed uropodal endopod, urp ex?: assumed uropodal exopod.

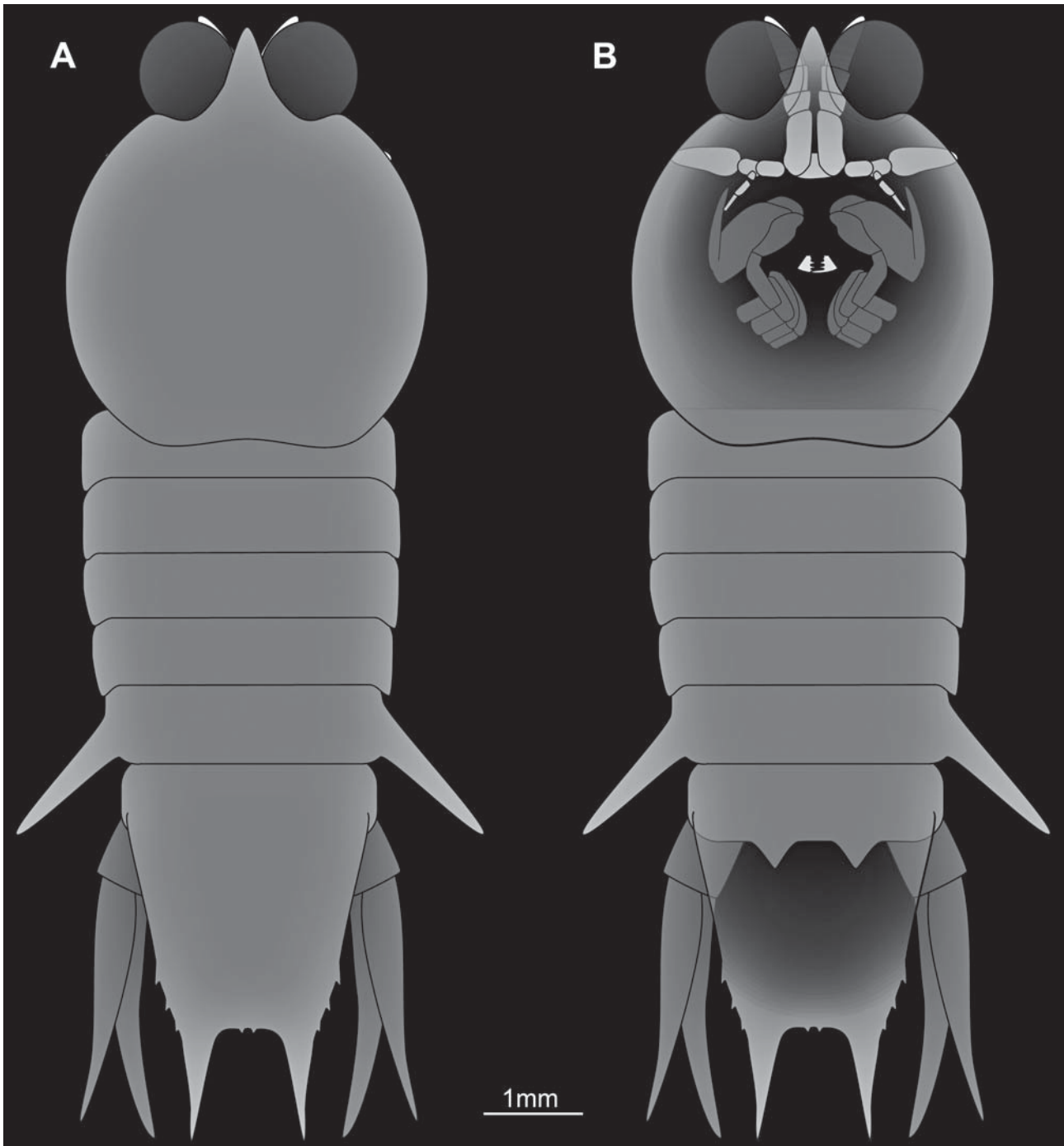


Fig. 6. Preliminary reconstruction of a later larval stage of *Spinosculda ehrlichi*. A: Dorsal view. B: Dorsal view with transparent head shield and telson. Reconstruction based on specimens in Fig. 3.

moveable elements as in larval specimens of *Sp. ehrlichi* (Fig. 2A, B vs 3–6). In the latter, these structures have been discussed as the uropodal endopod and exopod, based on the fact that they are seemingly set off from a proximal structure, most likely representing the basipod, by a distinct joint (HAUG C. et al. 2009a). Hence, there are

prominent endopods and exopods developed, and only a very indistinct basipodal spine (HAUG J. T. et al. 2010a) in *Spinosculda ehrlichi*. In *G. ehrlichfECKEi* the basipodal spine is very prominent, only one possible branch is present (Fig. 2A, B).

4.3. Differences between *Gigantosculta ehrlichfecke* and *Sculda* (?*S. pennata/spinosa*, ?*S. pusilla*, *Sculda* sp.)

A comparison of the larvae of *G. ehrlichfecke* (based on the description in the present study) with previous descriptions of species of *Sculda* (e.g. SCHRAM & MÜLLER 2004; HAUG J. T. et al. 2010a) reveals important differences between the two. Those differences comprise the following structures:

Body: One difference to ?*S. pennata/spinosa* is the overall body size. The minimum size of *S. pennata* is less than 5 mm (HAUG J. T. et al. 2010a), whereas larval specimens of the here described species already reach a body size of at least 18.5 mm (Fig. 2C, D). It can be assumed that the adult of *G. ehrlichfecke* is a fair amount bigger in body length. As those already small specimens of *S. pennata* (as well as *S. spinosa*) possess features characterising them as juveniles (see HAUG J. T. et al. 2010a), the larval specimens should be even smaller. *G. ehrlichfecke* is therefore too large to be conspecific to ?*S. pennata/spinosa*.

The remaining species in the species group *Sculda*, ?*S. pusilla*, has a body size given as 9.5–10.8 mm (SCHRAM & MÜLLER 2004); it is therefore also too small to belong to *G. ehrlichfecke*. The larval form of *G. ehrlichfecke* exceeds the adult form of ?*S. pusilla* almost twofold in body size.

Uropods: A small specimen of ?*S. pennata/spinosa*, interpreted as an earlier developmental form (possibly the larva), has been described as possessing uropods with elongate lanceolate endopods and exopods without teeth or setae (HAUG J. T. et al. 2010a). The endo- and exopods protrude slightly over the telson, but no basipodal structure is visible (see HAUG J. T. et al. 2010a: fig. 6G). In *G. ehrlichfecke*, the structures protruding over the telson probably represent the spines of the basipod, and exceed the elongate structures in the possible larva of ?*S. pennata/spinosa* more than two-fold (Fig. 2A, B vs HAUG J. T. et al. 2010a: fig. 6G). The lack of these vastly elongated basipodal spines in the possible larva of ?*S. pennata/spinosa* differentiate it from larvae of *G. ehrlichfecke*.

The differences to the formally described species in the lithographic limestones of Southern Germany justify recognising *G. ehrlichfecke* as a new, separate species. This species is characterised by the comparatively large overall body size in the late larval stages, also featuring a prominent rostrum and postero-lateral spines, the spineless pleon, and the long uropodal basipods, being twice as long as the telson.

4.4. Evolutionary implications

The present study revises some previous interpretations of the specimen now representing the holotype of *Gigantosculta ehrlichfecke*, which was tentatively ascribed to a species of *Sculda* (Sculdidae) (see HAUG J. T. et al. 2008).

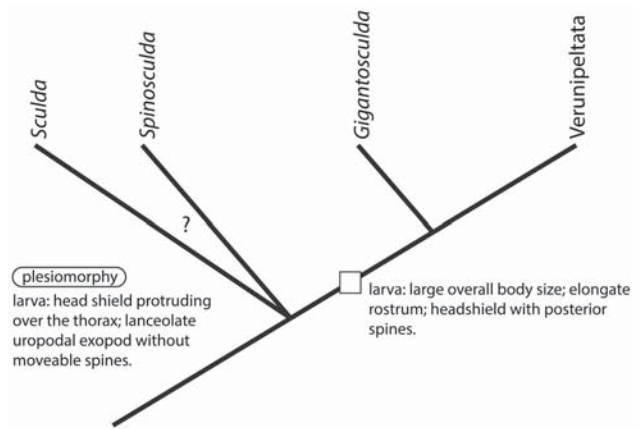


Fig. 7. Phylogram summarising the assumed phylogenetic position of the studied species within Stomatopoda (after HAUG J. T. et al. 2010a). Question marks refer to uncertain relationships. *Pseudosculta* was not considered since no larval stages are available.

Larval specimens of *G. ehrlichfecke* share larval traits (relatively large size compared to other crustacean larvae, long rostral spine and postero-lateral spines) with modern stomatopods, Verunipeltata (e.g. GIESBRECHT 1910; SHANB-HOGUE 1975; TANG 2009). Larval specimens of *Sculda* and *Spinosculta ehrlichi* lack these characters. These larval traits are therefore interpreted as synapomorphies of *Gigantosculta* and Verunipeltata (Fig. 7). Larval stages of pseudosculdids, the presumed sistergroup of Verunipeltata (HAUG J. T. et al. 2010a) are unknown; hence, the relative relationship of Verunipeltata, Pseudosculdidae and *Gigantosculta* can currently not be resolved. The position of the new species *ehrichfecke* in the tree also makes the erection of a new genus for it necessary under the current rules of the ICZN (but see e.g. BÉTHOUX 2007).

The larvae of *Sculda*, *Spinosculta*, *Gigantosculta* and modern forms all possess a head shield protruding over the thorax (in contrast to an exposed thorax in juveniles and adults), and uropodal exopods without moveable spines (in modern forms at least in earlier stages). These characters therefore represent a plesiomorphy; it remains unclear where in the tree these characters might represent an apomorphic state. So far, we lack larval stages of Carboniferous stomatopods, which branch off “further down the tree”.

4.5. Palaeoecology

HAUG J. T. et al. (2015) recently reported a first possible micro-predator in the original fauna of the lithographic limestones, a brachyuran crab larva. The new details of the late larva of *Sp. ehrlichi* reveal a possible predatory lifestyle of this larva. This assumption is based

on the well developed raptorial apparatus and presence of toothed mandibles in larval stages (Figs. 4, 5A, B). While already being too large to represent a micro-predator, the larvae described here (hence also *G. ehrlichfeckei*) represent planktic meso-predators of this 150 million years old fauna. Step by step we will be able to further resolve the ecological roles of the single species/stages from this fauna and ultimately will be able to reconstruct at least parts of the food web.

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