A new glimpse on Mesozoic zooplankton – 150 million years old lobster larvae

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Larvae of malacostracan crustaceans represent a large fraction of modern day zooplankton. Plankton is not only a major part of the modern marine ecosystem, but must have played an important role in the ecosystems of the past as well. Unfortunately, our knowledge about plankton composition of the past is still quite limited. As an important part of today's zooplankton, malacostracan larvae are still a rarity in the fossil record; many types of malacostracan larvae dominating the modern plankton have so far not been found as fossils. Here we report a new type of fossil malacostracan larva, found in the 150 million years old lithographic limestones of southern Germany (Solnhofen Lithographic Limestones). The three rather incomplete specimens mainly preserve the telson. A pronounced middle spine on the posterior edge of these specimens indicates that they are either larval forms of a clawed lobster or of an axiidean lobster, or of a closer relative to one of the two groups. The tergo-pleura are drawn out into distinct spines in one specimen, further supporting the interpretation as a larva of a clawed lobster or an early relative. The telson morphology also shows adaptations to a prolonged planktic life style, the latero-posterior edges are drawn out into distinct spines. Similar adaptations are known in larvae of the modern homarid lobster *Nephrops norvegicus*, not necessarily indicating a closer relationship, but convergent life styles. The new finds provide an important new insight into the composition of Mesozoic zooplankton and demonstrate the preservation potential of lithographic limestones.

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4
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7
8   **Abstract**

9   Larvae of malacostracan crustaceans represent a large fraction of modern day zooplankton.
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11   important role in the ecosystems of the past as well. Unfortunately, our knowledge about
12   plankton composition of the past is still quite limited. As an important part of today's
13   zooplankton, malacostracan larvae are still a rarity in the fossil record; many types of
14   malacostracan larvae dominating the modern plankton have so far not been found as fossils. Here
15   we report a new type of fossil malacostracan larva, found in the 150 million years old
16   lithographic limestones of southern Germany (Solnhofen Lithographic Limestones). The three
17   rather incomplete specimens mainly preserve the telson. A pronounced middle spine on the
18   posterior edge of these specimens indicates that they are either larval forms of a clawed lobster
19   or of an axiidean lobster, or of a close relative to one of the two groups. The tergo-pleura are
20   drawn out into distinct spines in one specimen, further supporting the interpretation as a larva of
21   a clawed lobster or an early relative. The telson morphology also shows adaptations to a
22   prolonged planktic life style, the latero-posterior edges are drawn out into distinct spines. Similar
23   adaptations are known in larvae of the modern homarid lobster *Nephrops norvegicus*, not
24   necessarily indicating a closer relationship, but convergent life styles. The new finds provide an
25   important new insight into the composition of Mesozoic zooplankton and demonstrate the
26   preservation potential of lithographic limestones.

27
28
29   **Introduction**
30
31   Plankton describes the entirety of organisms floating in the water column without the ability to
32   actively swim against the current. Plankton has been recognised as an important basis for marine
33   ecosystems in modern seas. Our understanding of changes in plankton composition are therefore
34   important in modern conservation biology and ecology, but are also of economic importance
35   (e.g., Duffy & Stachowicz 2006; Torres et al. 2013; Sardet 2015).
36   For long-time comparisons of changes in plankton composition, data of fossil plankton is
37   of major interest. Plankton must have been similarly important in the past as it is today.
38   Unfortunately, our knowledge of plankton in the past is often limited to very specific groups of
39   organisms, namely those with strongly sclerotised and/or mineralised morphological structures,
40   or those composed of certain decay-resisting substances such as resting cysts and the like
41   (examples in, e.g. Lipps 1970; Tappan & Loeblich 1973; Leckie 2009), while such groups
42   dominating the modern plankton (often lacking easily preservable structures) have a very scarce
43   or absent fossil record (e.g. Signor & Vermeij 1994; Rigby & Milsom 2000; Perrier et al. 2015).
44   It is nevertheless already possible to recognise that the plankton composition was quite different
45   in the past (e.g. Nützel & Frýda 2003; De Baets et al. 2012; Ritterbush et al. 2014; Servais et al.
46   2015).

47   In modern seas, crustaceans are a major part of the zooplankton. Among these we
48   especially need to mention copepod crustaceans and larval stages of malacostracan crustaceans.
49   Copepods
50   are mainly a part of the microplankton, while decapod larvae additionally include forms of meso-
51   and macroplankton.
52   So what about the fossil record of these groups? Fossil copepods are extremely rare. They
53   are limited to only few instances (Palmer 1960; Cressey & Patterson 1973; Cressey & Boxshall
54   1989; Bennike 1998; Huys et al. 2016), often only very incomplete (Selden et al. 2010) or
55   indirect findings (Radwańska & Radwański 2005; Radwańska & Poirot 2010). Malacostracan
56   larvae are also rare in the fossil record, but new forms have have been repetitively identified in
57   recent years (e.g. Haug et al. 2008, 2011a, 2014, 2015a, b, c; Hyžný et al. 2016) and are
58   currently limited to the Mesozoic. Despite their rarity, each of these finds marks another
59   important data point for our understanding of plankton in the past.
60   Due to preservation biases, large larval forms appear to be more commonly found as
61   fossils, not necessarily representing the original composition of the fauna, or the true diversity.
62   The most commonly found fossil malacostracan larvae are consequently the super-sized larvae of
63   spiny lobsters and slipper lobsters (with up to 150 mm in the extant fauna). These are represented
64   by at least a dozen different forms (Polz 1984, 1995, 1996; Haug et al. 2013a; Haug & Haug
65   2016), some known from thousands of individuals (Polz 1971, 1972, 1973) and occurring in at
66   least three Lagerstätten (Polz 1984; Pasini & Garassino 2009; Tanaka et al. 2009; Haug et al.
67   2011a). Other more uncommon fossils are also giant larval froms like those of the raptorial
68   mantis shrimps (Haug et al. 2008, 2009, 2010, 2014, 2015b) or the polychelidan lobsters (today
69   only represented by a relic group, mostly restricted to the deep sea; Haug et 2015c; Eiler et al.
70   2016). Groups of larvae dominating the modern plankton, like larvae of true crabs, false crabs
71   and their relatives (Meiura = Brachyura and Anomala, the latter also called Anomura), are very
72   rare on the other hand (Luque 2015; Haug et al. 2015a; Hyžný et al. 2016), as their larvae are
73   significantly smaller and more unlikely to be preserved.
74   Brachyuran and anomalan crustaceans are "still on their way" in the Mesozoic, only
75   diversifying in the later Mesozoic (see discussion in Haug et al. 2015a). It is therefore not to be
76   expected that their larvae were as abundant as in modern oceans. Instead the lobster-like
77   crustaceans, especially polychelidan and clawed lobsters (and their relatives) were dominating
78   parts of the faunas as adults, especially in the mid-Mesozoic, hence the Jurassic. We should
79   therefore expect that larval forms of these groups have represented important parts of the Jurassic
80   plankton. Yet, so far no definite fossils of such planktic larvae have been identified. Possible late
81   larvae of Jurassic polychelidans are late transitory stages, not the truly planktic ones (Eiler &
82   Haug 2016). Some fragmentary specimens have been discussed as possible remains of small
83   malacostracans (Haug et al. 2011a, 2014) and might well be parts of larvae of clawed lobsters,
84   but due to the limitations of preservation this must remain speculative.
85   Here we report the first definite finds of zoea-type larvae of clawed lobsters, hence truly
86   planktic larval forms of this group. We discuss the impact of this new finding on reconstructing
87   the plankton composition in the past and how this finding influences our strategies for detecting
88   further material of fossil malacostracan larvae.
89
90
91   **Material and Methods**
92

93   *Material*
94   Three specimens were available for this study (Fig. 1). All originate from the private collection
95   of Roger Frattigiani, Laichingen, and are now deposited in the Staatliches Museum für
96   Naturkunde Stuttgart (SMNS 70353/1, 70353/2, 70353/3). Specimens were originally found in
97   the Birkhof quarry in the Blumenberg area near Eichstätt (Solnhofen Lithographic Limestones,
98   Upper Jurassic, Tithonian, Hybonotum zone, Riedense subzone; Schweigert 2007). For
99   comparison an extant albuneid zoea from the collections of the Muséum national d'Histoire
100 naturelle Paris was documented (MNHN IU-2014-5527). High-resolution images of the
101 specimens are available at https://www.morphdbase.de/ (C_Haug_20161213-M-5.1,
102 C_Haug_20161213-M-6.1, C_Haug_20161213-M-7.1, C_Haug_20161213-M-9.1).
103
104 *Documentation method*
105 All specimens were documented on a Keyence BZ-9000 inverse epifluorescence microscope,
106 exploiting the autofluorescence of the fossils (Haug et al. 2011b). Blue-green fluorescence (GFP)
107 was used instead of the commonly used UV fluorescence (e.g., Tischlinger & Arratia 2013). UV
108 fluorescence is often unfortunate due to dust, which shows a very strong fluorescence and is in
109 many cases not removable from the fossils. This is especially true for the comparably high
110 magnifications as applied here (4x objective lens, resulting in 40x magnification). Due to the
111 magnification, depth of field and field of view were limited. To overcome these limitations,
112 several stacks of images for several adjacent image details were recorded (see details Haug et al.
113 2008). Additionally, in some areas where the fluorescence capabilites differed strongly, two
114 stacks were recorded, each with a different exposure time (Haug et al. 2013b).
115
116 *Image processing*
117 Stacks of images were fused to sharp images with CombineZP. Fused images were stitched to
118 panoramas using the photomerge function of Adobe Photoshop CS3 or Elements 11. Images of
119 different exposure times were combined into a single evenly illuminated image following the
120 procedure described in Haug et al. (2013b).
121
122
123 **Results**
124
125 *Specimen 1 (SMNS 70353/1)*
126 Specimen 1 is most complete, but still largely represents fragmentary remains (Fig. 2). The
127 overall colour and texture of the surface already clearly indicate that these fragments are the
128 remains of a crustacean (although these characters are hard to quantify, they are significantly
129 different to those in co-occurring groups such as insects, echinoderms or fishes, or also in
130 strongly calcified crustaceans such as isopods). This is also in concordance with the preserved
131 structures.
132   Most anteriorly a shield structure is apparent. It appears to be embedded in a dorso-lateral
133 orientation. The anterior rim is drawn out into a distinct but stout rostrum. Along the edge at
134 least two spines are apparent (Fig. 2A). Close to the shield an elongate structure is preserved
135 composed of five elements. Further distal elements are narrower than proximal ones. The
136 structure most likely represents the flagellum of an antennula or antenna. Close to the posterior
137 part of the shield, a piece of rectangular outline is apparent, most likely representing an isolated
138 element of one of the trunk appendages (posterior thoracopods, "pereiopods").

139   The posterior trunk (pleon) is incompletely preserved and an isolated piece is interpreted
140 as the tergite of pleon segment 3. It is domed and the latero-posterior edges are drawn out into
141 distinct spines. Medially along the posterior rim a posteriorly pointing spine is apparent.
142   The next posterior preserved piece resembles the tergite of pleon segment 3 in overall
143 morphology and is interpreted as the tergite of pleon segment 5. It is slightly larger than the
144 tergite of pleon segment 3, also the spines are more pronounced.
145   Articulated to pleon segment 5 is an elongated part posterioly extending into a more or
146 less triangular structure. This is interpreted as a compound part of pleon segment 6 and the
147 telson, hence a pleotelson. The posterior part of the pleon segment is partly twisted, and folded
148 onto itself. Still the triangular outline (in dorsal view) of the telson is apparent. The posterior rim
149 bears a prominent median spine (Fig. 2B). Left and right to it numerous hair-like structures are
150 apparent. It remains unclear whether these are jointed (true setae) or not (trichomes). The latero-
151 posterior corners are drawn out into elongate distally tapering spines. Close to the base of each
152 large spine, on its median side, slightly laterally from the hair-like structures is a smaller spine,
153 about the same length as the hair-like structures but more massive.
154
155 *Specimen 2 (SMNS 70353/2)*
156 In comparison to specimen 1, specimen 2 is clearly identified as an isolated telson (Fig. 3A-D). It
157 strongly resembles the posterior part of the pleotelson of specimen 1, but is not twisted and
158 therefore provides additional structural information. The overall size is similar to that of
159 specimen 1. The outline is strongly triangular in dorsal view. The anterior edges, most likely
160 marking the transition to pleon segment 6 are marked by a pair of laterally extending small
161 spines (Fig. 3A).
162   Postero-lateral edges are drawn out into massive spines, forming a shallow angle. The
163 number of hair-like structures along the posterior rim is 13 per side (Fig. 3D). They are all
164 roughly the same length and the distances between them appear evenly distributed.
165   Remains of the uropods appear to be preserved left and right to the telson (Fig. 3B, C).
166 Most likely these remains represent the outer, stronger sclerotised edges of the exopods. One
167 small spine appears to be preserved close to the distal end on the posterior surface of the exopod.
168
169 *Specimen 3 (SMNS 70353/3)*
170 This specimen strongly resembles specimen 2 and is therefore also interpreted as an isolated
171 telson (Fig. 3E-G). Size, general morphology and number of structures are all similar to
172 specimen 2. Yet, it is not as complete; for example, the posterior edge right to the median spine
173 is broken. It differs from specimen 2 only in the angle of the posterior spines. These form a much
174 narrower angle, as they point less far laterally, but more posteriorly.
175
176
177 **Discussion**
178
179 *Systematic interpretation*
180 The specimens are considered conspecific, but differ in the angle between the postero-lateral
181 spines. As all specimens have a similar overall size of the telson region (Fig. 1), it seems unlikely
182 that this difference is a ontogenetic one indicating the presence of several instars. By comparison
183 to modern forms it seems most likely that the spines originally had a certain flexibility and that
184 the difference in angle reflects a preservational difference. We therefore see no possibility to

185   diagnose different forms and see conspecifity as the most parsimonious explanation.
186   The overall morphology of the specimens indicates that they represent larval
187   malacostracans. An important character in this aspect is the pronounced middle spine of the
188   posterior edge of the telson. In adult malacostracans the telson is often elongate triangular in
189   dorsal view, but with the tip pointing posteriorly, or rectangular to square-shaped in dorsal view.
190   In many larval forms, for example, in decapods, the telson appears forked with a pronounced
191   median indent or, similar to the adults, rectangular, with an evenly armed posterior edge (Martin
192   et al. 2014). Forward pointing triangular to tapezoid/trapezium telson shapes with a pronounced
193   median spine occur in modern forms only in larvae of nephropid or axiidean lobsters (Fig. 4).
194   The latter seem to lack tergo-pleura drawn out into posteriorly pointing spines on the pleon (Dos
195   Santos & González-Gordillo 2004; Pohle & Santana 2014). As such spines are present in one of
196   the fossils and in modern nephropid lobsters (Jorgensen 1925; Wear 1976; Smith 1987; Goy
197   2014), the fossil larvae most likely represent larvae of clawed lobsters, i.e., nephropids or now
198   extinct relatives of them.
199
200   *The difficulties with 'clawed lobsters'*
201   Modern clawed lobsters comprise the true lobsters and the reef lobsters, yet quite a number of
202   fossil forms also resembles clawed lobsters, such as erymid or glypheid lobsters, in general
203   habitus (e.g., Garassino & Schweigert 2006; Charbonnier et al. 2013, 2015; Bracken-Grissom et
204   al. 2014; Hyžný et al. 2015; Schweitzer et al. 2016). The exact relationship of these groups
205   remains still partly unclear (see recent discussions in Charbonnier et al. 2015 and Hyžný et al.
206   2015). As also axiidean lobster larvae possess a pronounced median spine on the posterior edge
207   of the telson it is possible that this feature characterises a larger group including erymid and
208   glypheid lobsters. Therefore, we can currently not be more precise with the systematic
209   interpretation of the larvae described herein. They may represent larval forms of nephropid,
210   erymid or glypheid lobsters or a form closely related to them.
211
212   *Functional comparison*
213   The telson of the new fossil larvae clearly shows adaptations to a prolonged life in the pelagic
214   realm. Such a life style requires morphological specialisations for staying in the water column
215   without loosing much energy, which means that the buoyancy needs to be enhanced (e.g., Perrier
216   et al. 2015). This is especially important if the larvae reach relatively large body sizes such as the
217   specimens investigated here (although they are not as large as those of polychelidan or achelatan
218   lobsters).
219   The investigated specimens bear pronounced latero-posterior spines on the telson, with
220   this distantly resembling the telson of larvae of *Nephrops norvegicus* (scampi). Here also the
221   latero-posterior corners of the telson are strongly drawn out into spines, even more than in the
222   fossils (Fig. 4). As other nephropids, *N. norvegicus* larvae also possess a median spine on the
223   posterior edge. The telson of *N. norvegicus* larvae is also triangular in dorsal view, yet not as
224   pronounced as in other nephropids (Jorgensen 1925; Smith 1987).
225   The overall morphology of the telson of the fossils additionally shows an overall
226   similarity to the larvae of certain false sand crabs (Albuneidae; e.g. Knight 1970; Stuck &
227   Truesdale 1986; Harvey et al. 2014), besides the fact that these lack the median spine (Figs. 4, 5).
228   Still the overall shape is triangular, the corners are drawn out into spines and the posterior edge is
229   armed. We can assume that the specialised telson of the fossil larvae provided additional
230   buoyancy for the rather large larvae, similar to albuneid larvae.

231
232   *Significance*
233   The fossil record of arthropod zooplankton appears to be very incomplete (Perrier et al. 2015). In
234   general, the overall reconstruction of fossil zooplankton seems based largely on estimations, as
235   especially the microplankton is in focus of different studies, while the mesoplankton is usually
236   less studied. Larvae are in such approaches rarely treated in detail (Rigby & Milsom 2000), and,
237   although the fossil record of malacostracan larvae is growing, it appears to be generally regarded
238   as virtually absent (see recent review of Perrier et al. 2015)
239   Yet, arthropods do play an important role in the modern plankton, especially the larval
240   stages of malacostracans. As pointed out above, clawed lobsters and their relatives, i.e.
241   nephropid, erymid and glypheid lobsters represent an important part of the marine benthic fauna
242   in the Mesozoic. We should therefore expect that their larvae are a major share of the plankton of
243   that time. Finding such larvae is thus important for corroborating this assumption.
244   As discussed above, the newly described specimens show adaptations for prolonged life
245   in the plankton and therefore will represent the upper threshold of size for such larvae. Other
246   larvae of clawed lobsters will be significantly smaller. The larvae furthermore most likely
247   represent only a single specialised form of a wider range of different types of larvae. It has been
248   demonstrated that zoea-type larvae of achelatan lobsters were morphologically more diverse than
249   the larvae of modern forms (Haug et al. 2013a). We can expect that clawed lobster larvae also
250   were morphologically more diverse, possibly similarly diverse to larvae of modern meiuran
251   forms.
252   The fossils demonstrate that it is possible to find such important components of the
253   plankton and also give an important hint what to look for. Haug et al. (2011a) suggested that
254   some incomplete remains represent isolated shields of larvae, as these might have had a higher
255   preservation potential. The fossils described herein show that quite the other end of such a larva,
256   the telson, might also have high preservation potential. Focused search for such remains should
257   provide additional insights into the plankton composition of the past.
258
259

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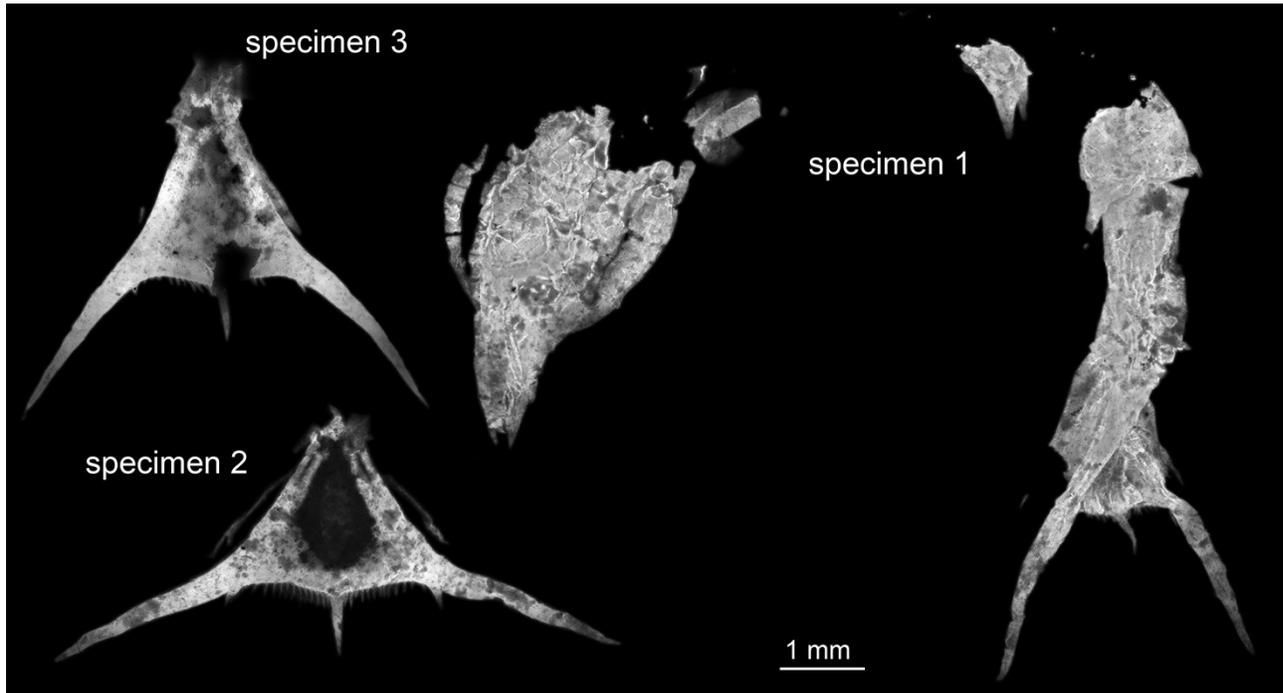
509   **Figure captions**

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511   Fig. 1. Entire material of larval specimens, composite-fluorescence micrographs. All three
512   specimens shown in the same scale to allow relative size comparison. Matrix digitally removed
513   for clarity.
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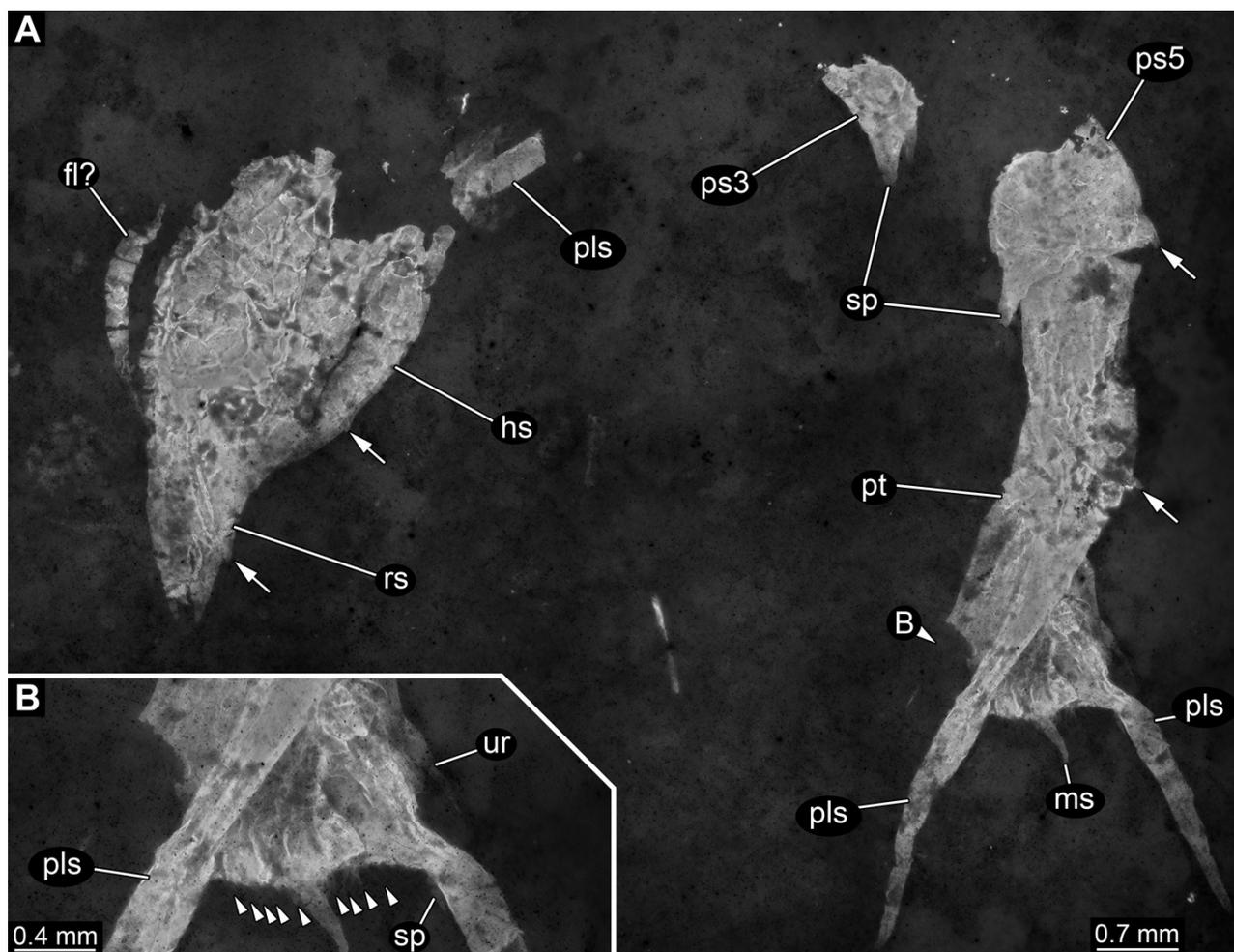
516
517 Fig. 2. Specimen 1 (SMNS 70353/1), composite-fluorescence micrographs. A. Overview of
518 entire specimen, although incomplete showing general organisation; arrows mark small spines.
519 B. Close-up on posterior rim of telson; arrowheads point to small hair-like structures or setae.
520 Abbreviations: fl? = possible flagellum of antennula or antenna; hs = head shield; ms = median
521 spine; pls = postero-lateral spine; ps3, 5 = pleon segment 3, 5; pt = pleotelson; rs = rostrum; sp =
522 spine; ur = uropod.
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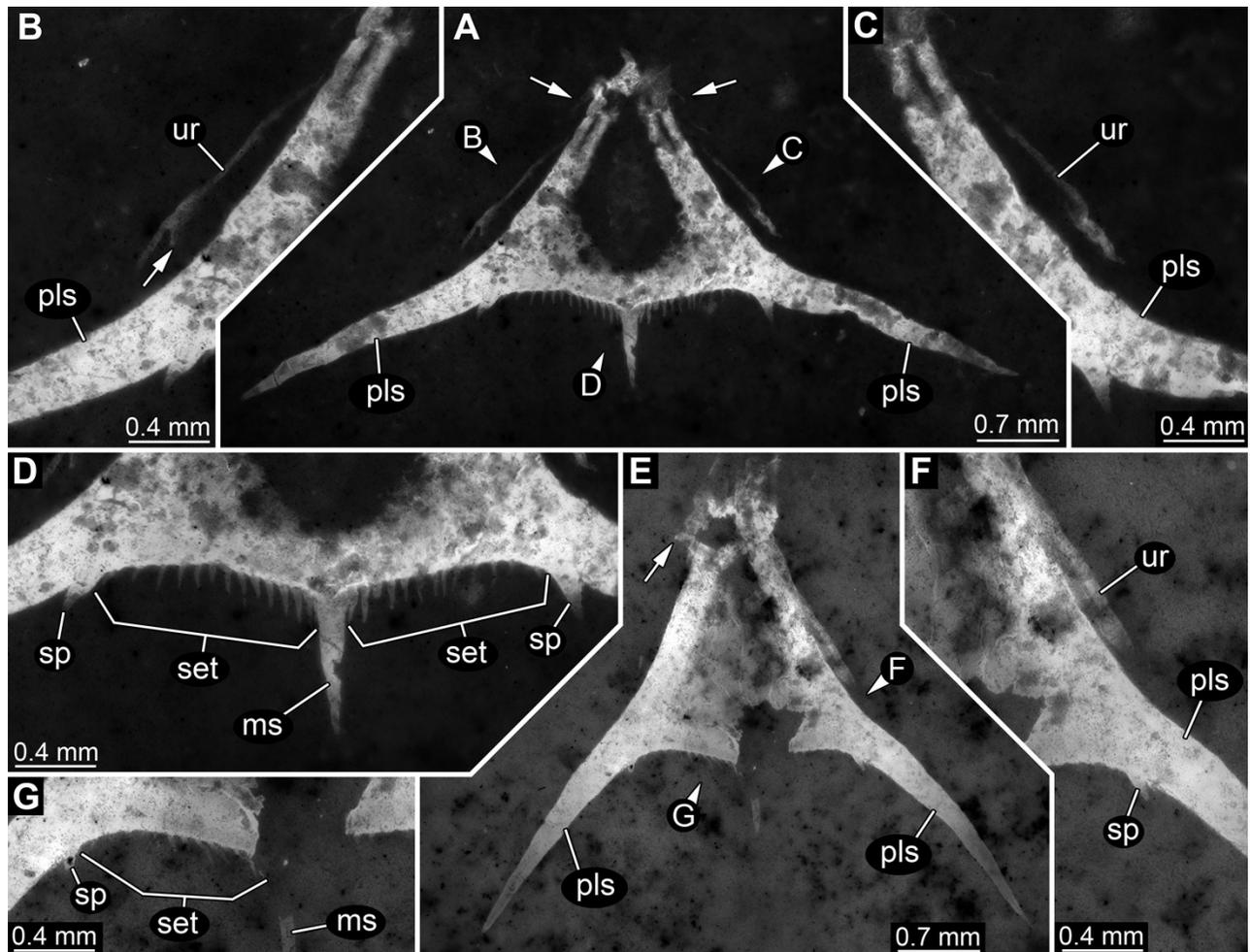
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528   Fig. 3. Specimens 2 (SMNS 70353/2) and 3 (SMNS 70353/3), each representing an isolated
529   posterior part of a pleotelson (= telson) composite-fluorescence micrographs. A–D. Specimen 2.
530   A. Overview; arrows mark small spines. B. Close-up on left lateral rim of telson; arrow points to
531   small spine. C. Close-up on right lateral rim of telson. D. Close-up on left posterior rim of telson.
532   E–G. Specimen 3. E. Overview; arrow marks small spines. F. Close-up on right lateral rim of
533   telson. G. Close-up on left posterior rim of telson. Abbreviations: ms = median spine; pls =
534   postero-lateral spine; set = hair-like structures or setae; sp = spine; ur = uropod.
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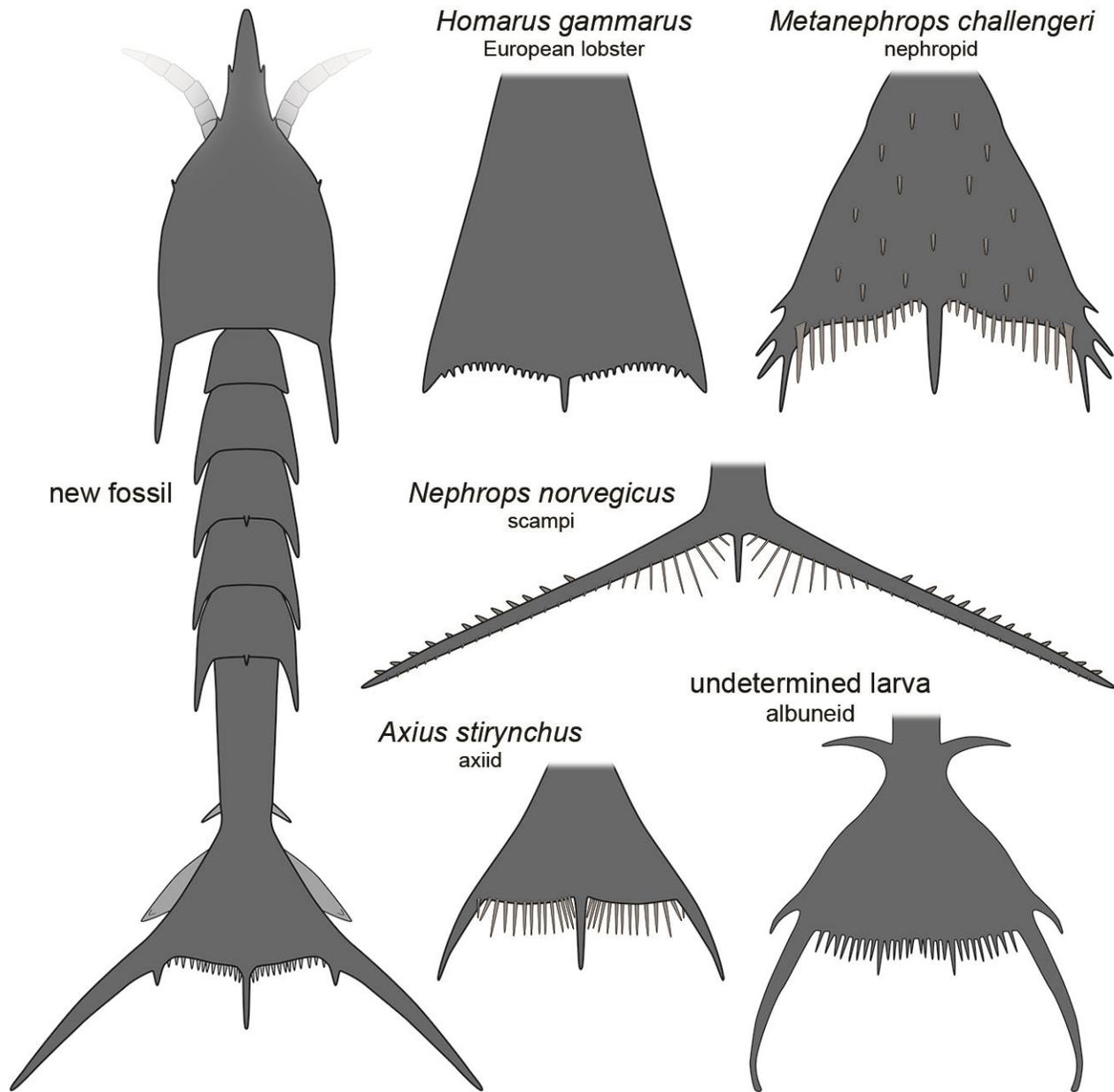
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539 Fig. 4. Comparison of the new fossil larva with extant forms. New fossil larva as restoration in
540 dorsal aspect; each of the others as an isolated telson in dorsal view. *Homarus gammarus*
541 (European lobster); zoea III simplified from Rötzer & Haug (2015). *Nephrops norvegicus*
542 (scampi, Kaisergranat); zoea III combined from Smith (1987) and Jorgensen (1925).
543 *Metanephrops challengeri*; late zoea simplified from Wear (1976). *Axius stirynchus*; late zoea
544 simplified from Dos Santos & González-Gordillo (2005, fig. 2F). Undetermined albuneid larva;
545 late zoea simplified from Fig. 5.
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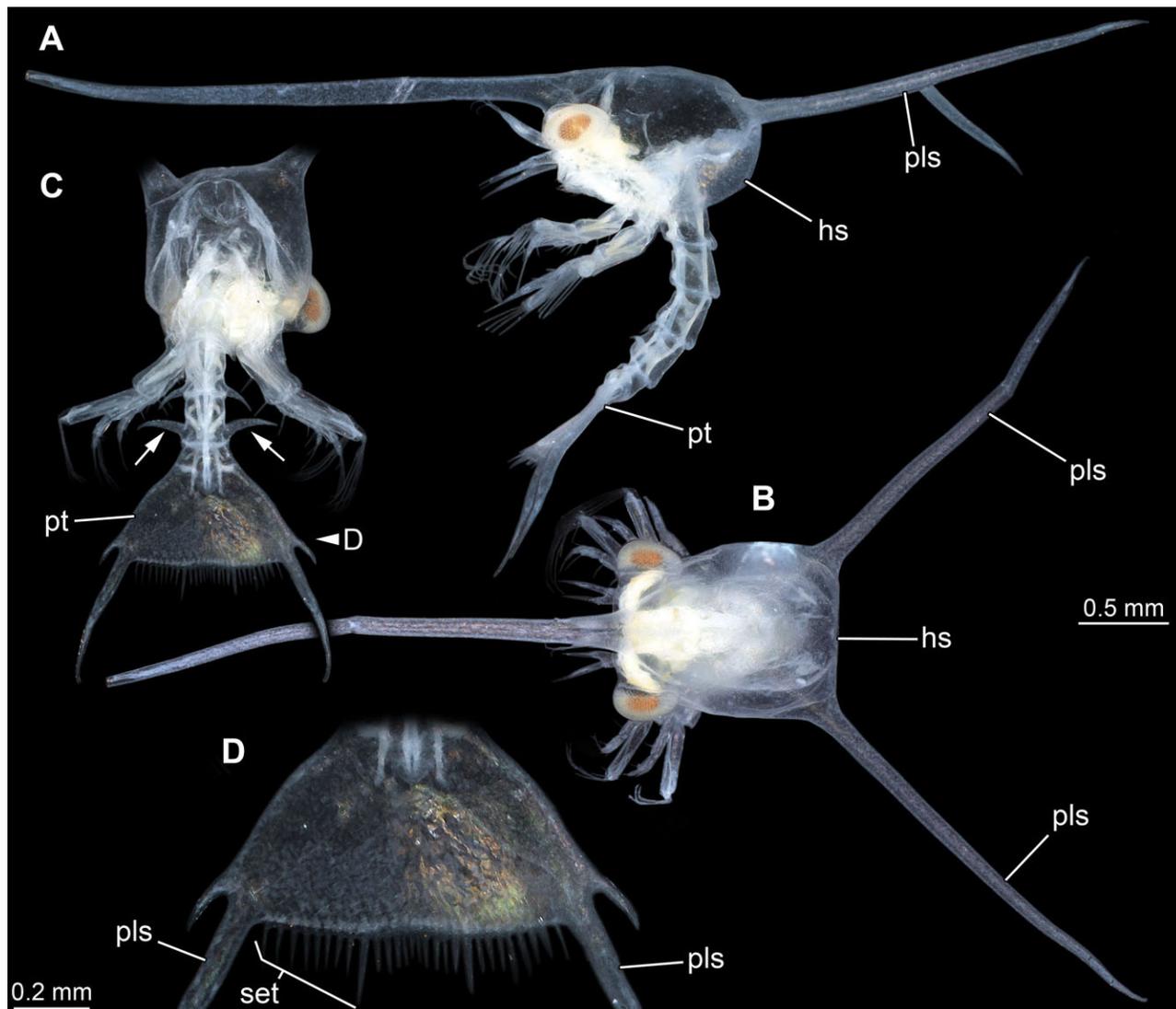
Fig. 5. Extant larva of an albuneid meiuran for functional comparison; cross-polarised macro images. Note the long postero-lateral spines on shield and telson and the triangular telson. A. Lateral view on left side. B. Dorsal view on head shield. C. Posterior view on anterior region; dorsal view on posterior pleon and pleotelson; arrows mark spines. D. Detail of the telson. Abbreviations: hs = head shield; pls = postero-lateral spine; pt = pleotelson; set = hair-like structures or setae.

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