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A new glimpse on Mesozoic zoo-plankton – 150 million years old lobster larvae

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Larvae of malacostracan crustaceans represent a large fraction of modern day zoo-plankton. 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 part of the fossil plankton, 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 a thalassinidean 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 zoo-plankton and demonstrate the preservation potential of lithographic limestones.

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2
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7
8   **Abstract**
9   Larvae of malacostracan crustaceans represent a large fraction of modern day zoo-plankton.
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11   important role in the ecosystems of the past as well. Unfortunately, our knowledge about plankton
12   composition of the past is still quite limited. As part of the fossil plankton, malacostracan larvae are
13   still a rarity in the fossil record; many types of malacostracan larvae dominating the modern
14   plankton have so far not been found as fossils. Here we report a new type of fossil malacostracan
15   larva, found in the 150 million years old lithographic limestones of southern Germany (Solnhofen
16   Lithographic Limestones). The three rather incomplete specimens mainly preserve the telson. A
17   pronounced middle spine on the posterior edge of these specimens indicates that they are either
18   larval forms of a clawed lobster or of a thalassinidean lobster, or of a closer relative to one of the
19   two groups. The tergo-pleura are drawn out into distinct spines in one specimen, further supporting
20   the interpretation as a larva of a clawed lobster or an early relative. The telson morphology also
21   shows adaptations to a prolonged planktic life style, the latero-posterior edges are drawn out into
22   distinct spines. Similar adaptations are known in larvae of the modern homarid lobster *Nephrops
23   norvegicus*, not necessarily indicating a closer relationship, but convergent life styles. The new
24   finds provide an important new insight into the composition of Mesozoic zoo-plankton and
25   demonstrate the preservation potential of lithographic limestones.
26
27   **Key words:** Homarida, Nephropida, Zoea, Solnhofen, Upper Jurassic
28
29
30   **Introduction**
31
32   Plankton describes the entirety of organisms floating in the water column without the ability to
33   actively swim against the current. Plankton has been recognised as an important basis for marine
34   ecosystems in modern seas. Our understanding of changes of composition of plankton are therefore
35   important in modern conservation biology and ecology, but are also of economic importance.
36   For long-time comparisons of changes in plankton composition, data of fossil plankton is of
37   major interest. Plankton must have been similarly important in the past times as it is today.
38   Unfortunately, our knowledge of plankton in the past is often limited to very specific groups of
39   organisms (examples in, e.g. Lipps 1969; Tappan & Loeblich 1973; Leckie 2009), while such
40   groups dominating the modern plankton often have a very scarce or absent fossil record (e.g. Signor
41   & Vermeij 1994; Rigby & Molsom 2000; Perrier et al. 2015). It is nevertheless already possible to
42   recognise that plankton was composed quite differently in the past (e.g. Nützel & Fryda 2003;
43   Servais et al. 2015)
44   In modern seas crustaceans are a major part of the zooplankton. Among these we need to
45   especially mention copepod crustaceans and larval stages of malacostracan crustaceans. Copepods
46   are mainly a part of the microplankton, while decapod larvae additionally include forms of meso-
47   and macroplankton.
48   So how about the fossil record of these groups? Fossil copepods are extremly rare. They are
49   limited to about only half a dozen instances, often only very incomplete or indirect findings
50   (Bennicke 1998; Cressey & Boxshall 1989; Cressey & Patterson 1973; Selden et al. 2010; Palmer
51   1960; Radwanska & Radwanski 2005; Radwanska & Poirot 2010). Also malacostracan larvae are
52   still rare in the fossil record, but new forms have have been identified repetetively in recent years

53   (e.g. Haug et al. 2008, 2011a, 2014, 2015a, b, c), currently limited to the Mesozoic. Despite the
54   rarity, each of these finds marks another important data point for our understanding of plankton in
55   the past.
56   Due to preservation biases especially large larval forms appear to be more commonly found
57   as fossils, not necessarily representing the original composition of the fauna, or the true diversity.
58   The most commonly found fossil malacostracan larvae are consequently the super-sized larvae of
59   spiny lobsters and slipper lobsters (with up to 150 mm in the extant fauna). These are represented
60   by at least a dozen different forms (Polz 1984, 1995, 1996; Haug et al. 2013a; Haug & Haug 2016),
61   some known from thousands of individuals (Polz 1971, 1972, 1973) and occurring in at least three
62   lagerstätten (Polz 1984; Pasini & Garassino 2009; Tanaka et al. 2009; Haug et al. 2011). Other more
63   uncommon fossils are also giant larval froms like those of the raptorial mantis shrimps (Haug et al.
64   2008, 2009, 2010, 2014, 2015b) or the polychelidan lobsters (today only represented by a relic
65   group, mostly deep sea; Haug et 2015c; Eiler et al. 2016). Groups of larvae dominating the modern
66   plankton, like larvae of true and false crabs (Brachyura and Anomala, the latter also called
67   Anomura) are very rare on the other hand (Luque 2015; Haug et al. 2015a; Hyžný et al. 2016), as
68   their larvae are significantly smaller and more unlikely to be preserved.
69   Also, brachyuran and anomalan crustaceans are "still on their way" in the Mesozoic, only
70   diversifying in the later Mesozoic (see discussion in Haug et al. 2015a). It is therefore not to be
71   expected that their larvae were as abundant as in modern oceans. Instead the lobster-like
72   crustaceans, especially polychelidan and clawed lobsters (and their relatives) were dominating parts
73   of the faunas as adults, especially in the mid-Mesozoic, hence the Jurassic. We should therefore
74   expect that larval forms of these groups have represented important parts of the Jurassic plankton.
75   Yet, so far no definite fossils of such planktic larvae have been identified. Possible late larvae of
76   Jurassic polychelidans are late transitory stages, not the truly planktic ones (Eiler & Haug 2016).
77   Some fragmentary specimens have been discussed as possible remains of small malacostracans
78   (Haug et al. 2011a, 2014) and might well be parts of larvae of clawed lobsters, but due to the
79   limitations of preservation this must remain speculative.
80   Here we can report the first definite finds of zoea-type larvae of clawed lobsters, hence
81   truly planktic larval forms of this group. We discuss the impact on this new finding and how it
82   should influence our strategies for finding further material of fossil malacostracan larvae.
83
84

Material and Methods

Material
Three specimens were available for this study (Fig. 1). All originate from the private collection of
Roger Frattigiani, Laichingen, and are now deposited in the Staatliches Museum für Naturkunde
Stuttgart (SMNS). NUMBERS WILL BE ADDED LATER Specimens were originally found in the
Birkhof quarry in the Blumenberg area near Eichstätt (Solnhofen Lithographic Limestones). For
comparison an extant albuneid zoea from the collections of the Muséum national d'Histoire
naturelle Paris was documented.

Documentation method
All specimens were documented on a Keyence BZ-9000 inverse epifluorescence microscope,
exploiting the autofluorescence of the fossils (Haug et al. 2011b). Blue-green fluorescence (GFP)
was used instead of the commonly used UV fluorescence (e.g., Tischlinger & Arratia 2013). UV
fluorescence is often unfortunate due to dust, which shows a very strong fluorescence and is in
many cases not removable from the fossils. This is especially true for the comparably high
magnifications as applied here (4x objective lens, resulting in 40x magnification). Due to the
magnification, depth of field and field of view were limited. To overcome these limitations several
stacks of images for several adjacent image details were recorded (see details Haug et al. 2008).
Additionally, in some areas where the fluorescence capabilites differed strongly, two stacks were

105 recorded, each with a different exposure time (Haug et al. 2013b).
106
107 *Image processing*
108 Stacks of images were fused to sharp images with CombineZP. Fused images were stitched to
109 panoramas using the photomerge function of Adobe Photoshop CS3 or Elements 11. Images of
110 different exposure times were combined into a single evenly illuminated image following the
111 procedure described in Haug et al. (2013b).
112
113
114 **Description and interpretation**
115
116 *Specimen 1*
117 Specimen 1 is most complete, but still largely represents fragmentary remains (Fig. 2). The overall
118 colour and texture of the surface already clearly indicate that these fragments are the remains of a
119 crustacean. This is also in concordance with the preserved structures.
120   Most anteriorly a shield structure is apparent. It appears to be embedded in a dorso-lateral
121 orientation. The anterior rim is drawn out into a distinct but stout rostrum. Along the edge at least
122 two spines are apparent (Fig. 2A). Close to the shield an elongate structure is preserved composed
123 of five elements. Further distal alements are narrower than proximal ones. The structure most likely
124 represents the flagellum of an antennula or antenna. Close to the posterior of the shield a piece of
125 rectangular outline is apparent, most likely representing an isolated element of one the trunk
126 appendages (posterior thoracopods, "pereiopods").
127   The posterior trunk (pleon) is incompletely preserved and an isolated piece is interpreted as
128 the tergite of pleon segment 3. It is domed, the latero-posterior edges are drawn out into distinct
129 spines. Medially along the posterior rim a posteriorly pointing spine is apparent.
130   The next posterior preserved piece resembles the tergite of pleon segment 3 in overall
131 morphology and is interpreted as the tergite of pleon segment 5. It is slightly larger than the tergite
132 of pleon segment 3, also the spines are more pronounced.
133   Articulated to pleon segment 5 is an elongated part posterioly extending into a more or less
134 triangular structure. This is interpreted as a compound part of pleon segment six and the telson,
135 hence a pleotelson. The posterior part of the pleon segment is partly twisted, and folded onto itself.
136 Still a principle triangular outline (in dorsal view) of the telson is apparent. The posterior rim bears
137 a prominent median spine (Fig. 2B). Left and right to it numerous hair-like structures are apparent.
138 It remains unclear whether these are jointed (true setae) or not (trichomes). The latero-posterior
139 corners are drawn out into elongate distally tapering spines. Close to the base of each large spine,
140 on its median side, slightly laterally from the hair-like structures is a smaller spine, about the same
141 length as the hair-like structures but more massive.
142
143 *Specimen 2*
144 In comparison to specimen 1, specimen 2 is clearly identified as an isolated telson (Fig. 3A-D). It
145 strongly resembles the posterior part of the pleotelson of specimen 1, but is not twisted and
146 therefore provides additional structural information. The overall size is similar to that of specimen
147 1. The outline is strongly triangular in dorsal view. The anterior edges, most likely marking the
148 transition to pleon segment 6 are marked by a pair of laterally extending small spines (Fig. 3A).
149   Postero-lateral edges are drawn out into massive spines, forming a shallow angle. The
150 number of hair-like structures along the posterior rim is 13 per side (Fig. 3D). They are all roughly
151 the same length and the distances between them appear evenly distributed.
152   Remains of the uropods appear to be preserved left and right to the telson (Fig. 3B, C). Most
153 likely these remains represent the outer, stronger sclerotised edges of the exopods. One small spine
154 appears to be preserved close to the distal end on the posterior surface of the exopod.
155
156 *Specimen 3*

157 This specimen strongly resembles specimen 2 and is therefore also interpreted as an isolated telson
158 (Fig. 3E-G). Size, principle morphology and number of structures are all similar to specimen 2. Yet,
159 it is not as complete; for example, the posterior edge right to the median spine is broken. It differs
160 from specimen 2 only in the angle of the posterior spines. These form a much narrower angle, as
161 they point less far laterally, but more posteriorly.

162
163
164 **Discussion**

165
166 *Systematic interpretation*
167 The specimens are considered conspecific, but differ in the angle between the postero-lateral spines.
168 As all specimens have a similar overall size of the telson region (Fig. 1), it seems unlikely that this
169 difference is a ontogenetic one indicating the presence of several instars. In comparison to modern
170 forms it seems most likely that the spines originally had a certain flexibility and that the difference
171 in angle reflects a preservational difference. We therefore see no possibility to diagnose different
172 forms and see conspecifity as the most parsimonious explanation.
173   The overall morphology of the specimens indicates that they represent larval
174 malacostracans. An important character in this aspect is the pronounced middle spine of the
175 posterior edge of the telson. In adult malacostracans the telson is often elongate triangular in dorsal
176 view, but with the tip pointing posteriorly, or rectangular to square-shaped in dorsal view. In many
177 larval forms, for example, in decapods, the telson appears forked with a pronounced median indent
178 or, similar to the adults, rectangular, with an evenly armed posterior edge (Martin et al. 2014).
179 Forward pointing triangular to tapezoid/trapezium telson shapes with a pronounced median spine
180 occur in modern forms only in larvae of nephropid or thalassinidean lobsters (Fig. 4).
181 Thalassinidean lobster larvae seem to lack tergo-pleura drawn out into posteriorly pointing spines
182 on the pleon (Dos Santos & González-Gordillo 2004; Pohle & Santana 2014). As such spines are
183 present in one of the fossils and in modern nephropid lobsters (Jorgensen 1925; Wear 1976; Smith
184 1987; Goy 2014), the fossil larvae most likely represent larvae of clawed lobsters, i.e., nephropids
185 or now extinct relatives of them.

186
187 *The difficulties with 'clawed lobsters'*
188 Modern clawed lobsters comprise the true lobsters and the reef lobsters, yet quite a number of fossil
189 forms also in principle resembles clawed lobsters, such as erymid or glypheid lobsters (Garassino &
190 Schweigert 2006). The exact relationship of these groups remains still partly unclear. As also
191 (some?) thalassinidean lobster larvae possess a pronounced median spine on the posterior edge of
192 the telson it is possible that this feature characterises a larger group including erymid and glypheid
193 lobsters. Therefore, we can currently not further narrow down the systematic interpretation of the
194 here described larvae. They may represent larval forms of nephropid, erymid or glypheid lobsters or
195 a form closely related to them.

196
197 *Functional comparison*
198 The telson of the here described larvae clearly shows adaptations to a prolonged life in the pelagic
199 realm. The overall size of the specimens is relatively large for a pelagic larvae (although not as
200 much as in polychelid or achelatan lobsters), and the telson bears pronounced latero-posterior
201 spines.
202   This distantly resembles the telson of larvae of *Nephrops norvegicus* (scampi). Here also the
203 latero-posterior corners of the telson are strongly drawn out into spines, even more so than in the
204 fossils (Fig. 4). As other nephropids, *N. norvegicus* larvae also possess a median spine on the
205 posterior edge. The telson of *N. norvegicus* larvae is also triangular in dorsal view, yet not as
206 pronounced as in other nephropids.
207   The overall morphology of the telson of the fossils additionally shows an overall similarity
208 to the larvae of certain false sand crabs (Albuneidae; e.g. Harvey et al. 2014), besides the fact that

209 these lack the median spine (Figs. 4, 5). Still the overall shape is triangular, the corners are drawn
210 out into spines and the posterior edge is armed. We can assume that the specialised telson of the
211 fossil larvae provided additional bouyancy for the rather large larvae, similar to albuneid larvae.
212
213 *Significance*
214 The fossil record of arthropod zoo-plankton appears to be very incomplete (Perrier et al. 2015). In
215 general, the overall reconstruction of fossil zoo-plankton seems based largely on estimations, larvae
216 are in such approaches rarely treated in detail (Rigby & Milsom 2000), and, although the fossil
217 record of malacostracan larvae is growing, it appears to be generally regarded as virtually absent
218 (see recent review of Perrier et al. 2015)
219   Yet, arthropods do play an important role in the modern plankton, especially the larval
220 stages of malacostracans. As pointed out above, clawed lobsters and their relatives, i.e. nephropid,
221 erymid and glypheid lobsters represent an important part of the marine benthic fauna in the
222 Mesozoic. We should therefore expect that their larvae are a major share of the plankton of that
223 time. Finding such larvae is thus important for corroborating this assumption.
224   As discussed above, the here described specimens show adaptations for prolonged life in the
225 plankton and therefore will represent the upper threshold of size for such larvae. Other larvae of
226 clawed lobsters will be significantly smaller. The larvae furthermore most likely represent only a
227 single specialised form of a wider range of different types of larvae. It has been demonstrated that
228 zoea-type larvae of achelatan lobsters were morphologically more diverse than the larvae of modern
229 forms (Haug et al. 2013a). We can expect that clawed lobster larvae also were morphologically
230 more diverse, possibly similarly diverse to larvae of modern meiuran forms.
231   The fossils demonstrate that it is possible to find such important components of the plankton
232 and also give an important hint what to look for. Haug et al. (2011a) suggested that some
233 imcomplete remains represent isolated shields of larvae, as these might have had a higher
234 preservation potential. The fossils described here show that quite the other end of such a larva, the
235 telson, might also have a high preservation potential. Focussed search for such remains should
236 provide additional insights into the plankton composition of the past.
237
238

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429   **Figure captions**
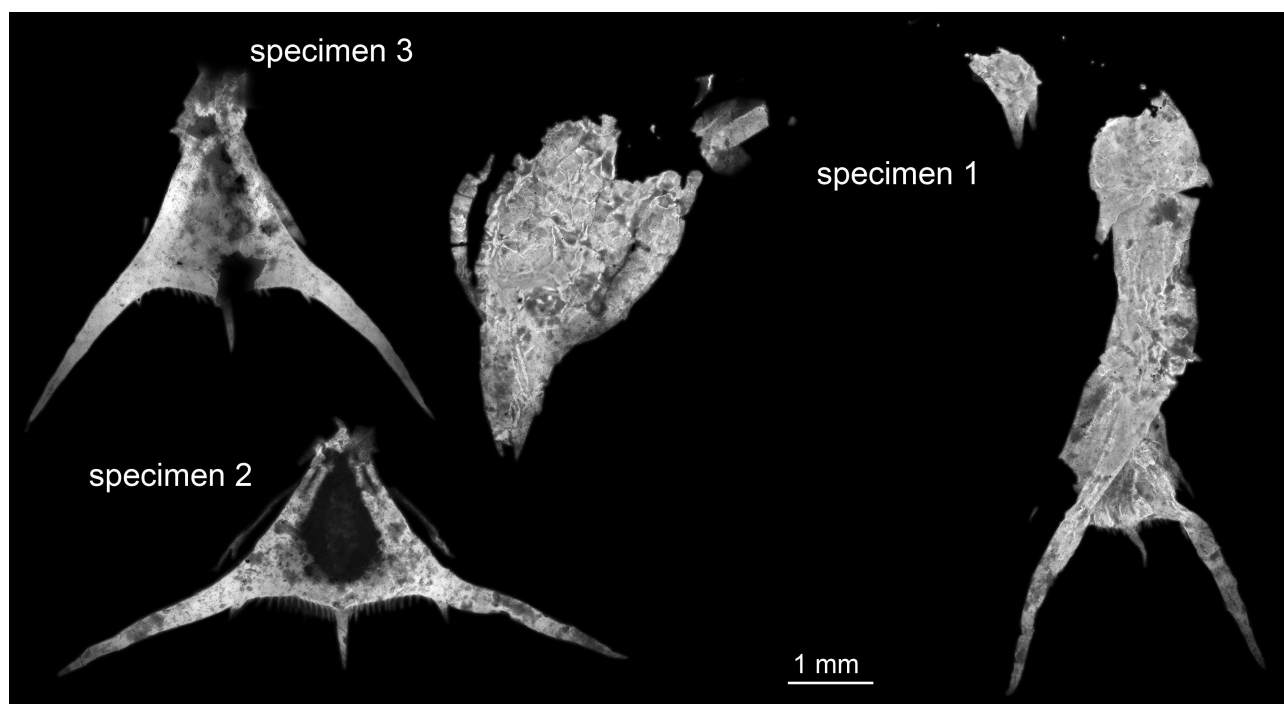
431 Fig. 1. <mark>Complete material</mark> of larval specimens, composite-fluorescence micrographs. All three
432 specimens shown in the same scale to allow relative size comparison. Matrix digitally removed for
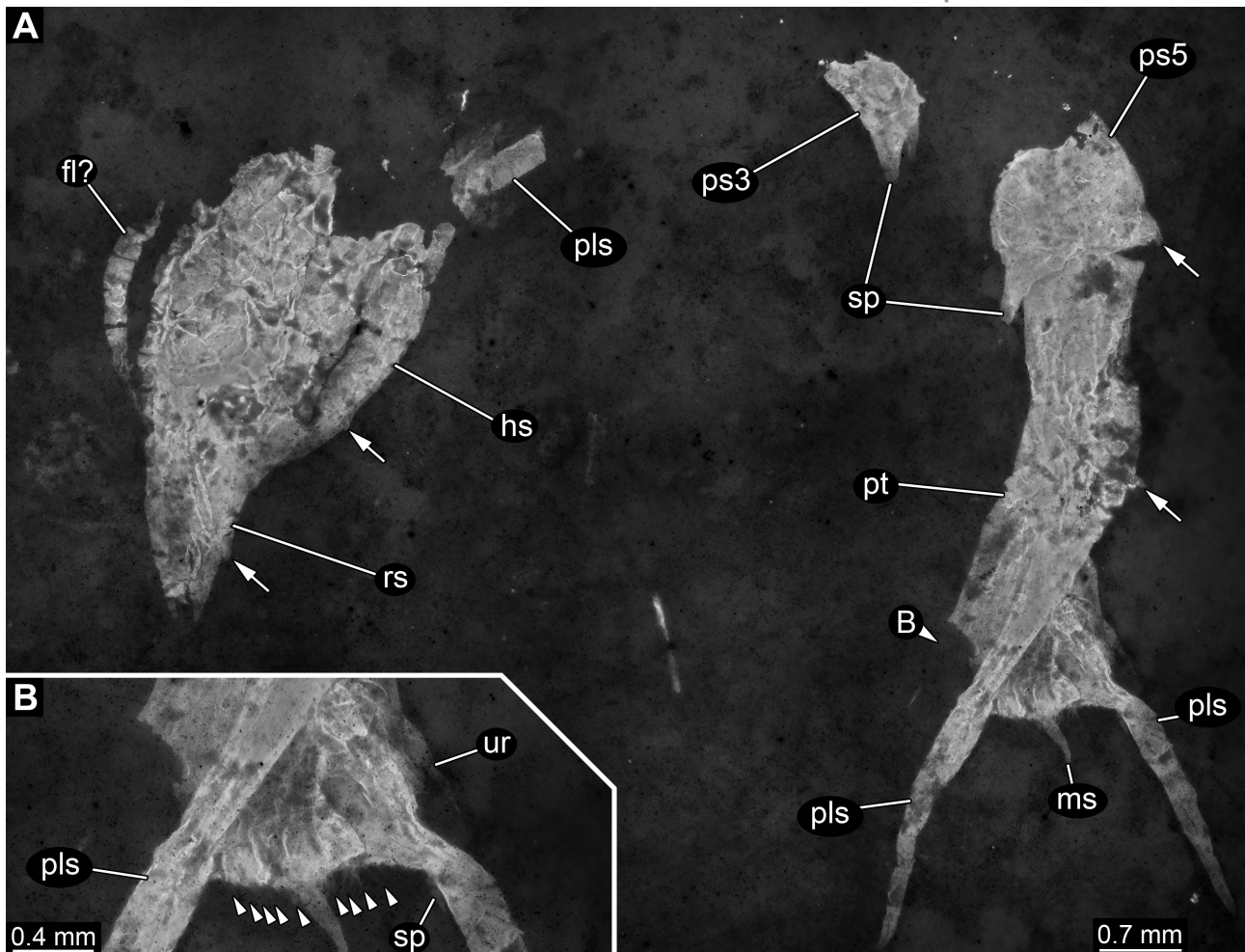433 clarity.
434

Fig. 2. Specimen 1, composite-fluorescence micrographs. A. Overview of entire specimen, although incomplete showing general organisation; arrows mark small spines. B. Close-up on posterior rim of telson; arrowheads point to small hair-like structures or setae. Abbreviations: fl? = possible flagellum of antennula or antenna; hs = head shield; ms = median spine; pls = postero-lateral spine; ps3, 5 = pleon segment 3, 5; pt = pleotelson; sp = spine; ur = uropod.
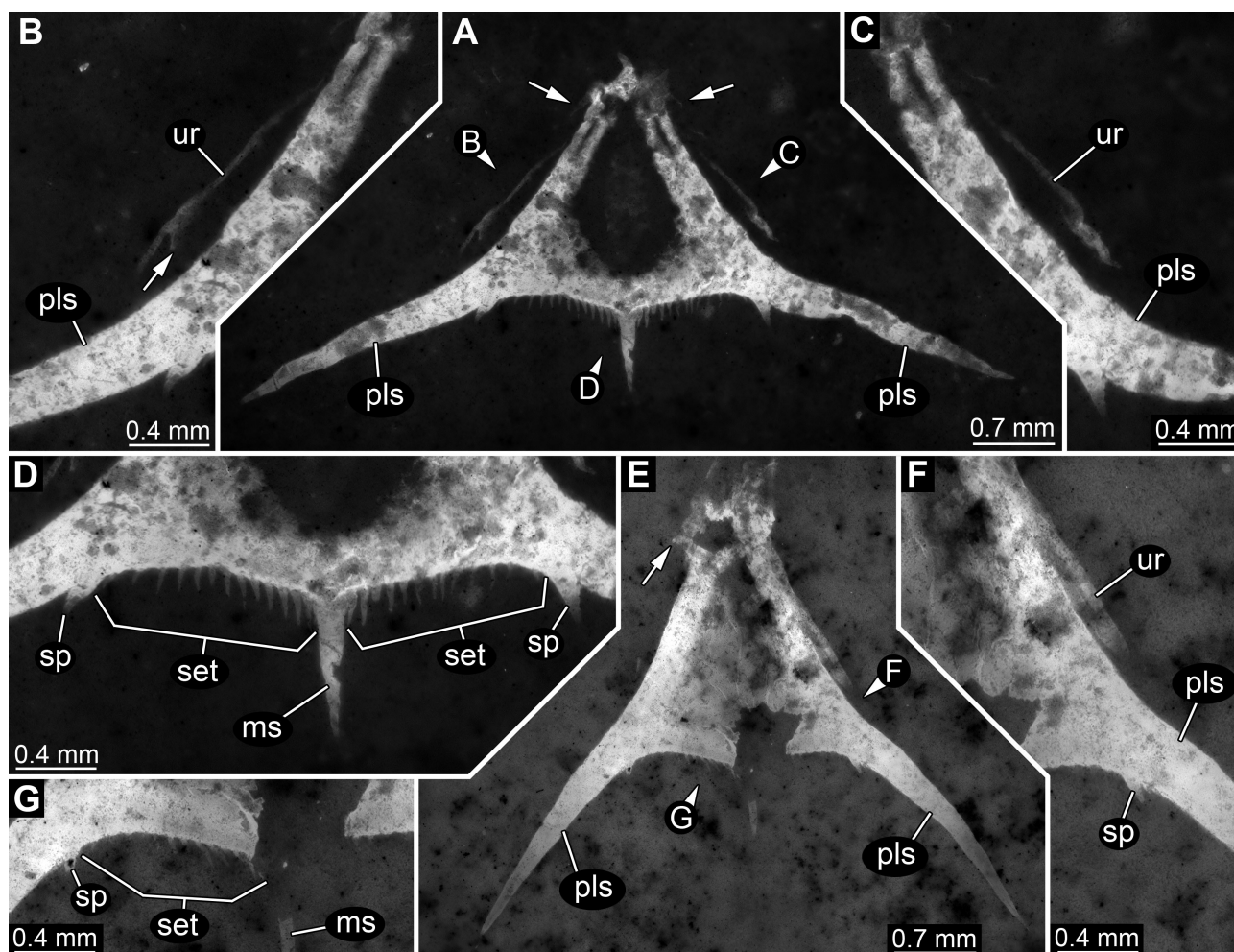
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447 Fig. 3. Specimens 2 and 3, each representing an isolated posterior part of a pleotelson (= telson)
448 composite-fluorescence micrographs. A–D. Specimen 2. A. Overview; arrows mark small spines. B.
449 Close-up on left lateral rim of telson; arrow points to small spine. C. Close-up on right lateral rim of
450 telson. D. Close-up on left posterior rim of telson. E–G. Specimen 3. E. Overview; arrow marks
451 small spines. F. Close-up on right lateral rim of telson. G. Close-up on left posterior rim of telson.
452 Abbreviations: ms = median spine; pls = postero-lateral spine; set = hair-like structures or setae; sp
453 = spine; ur = uropod.
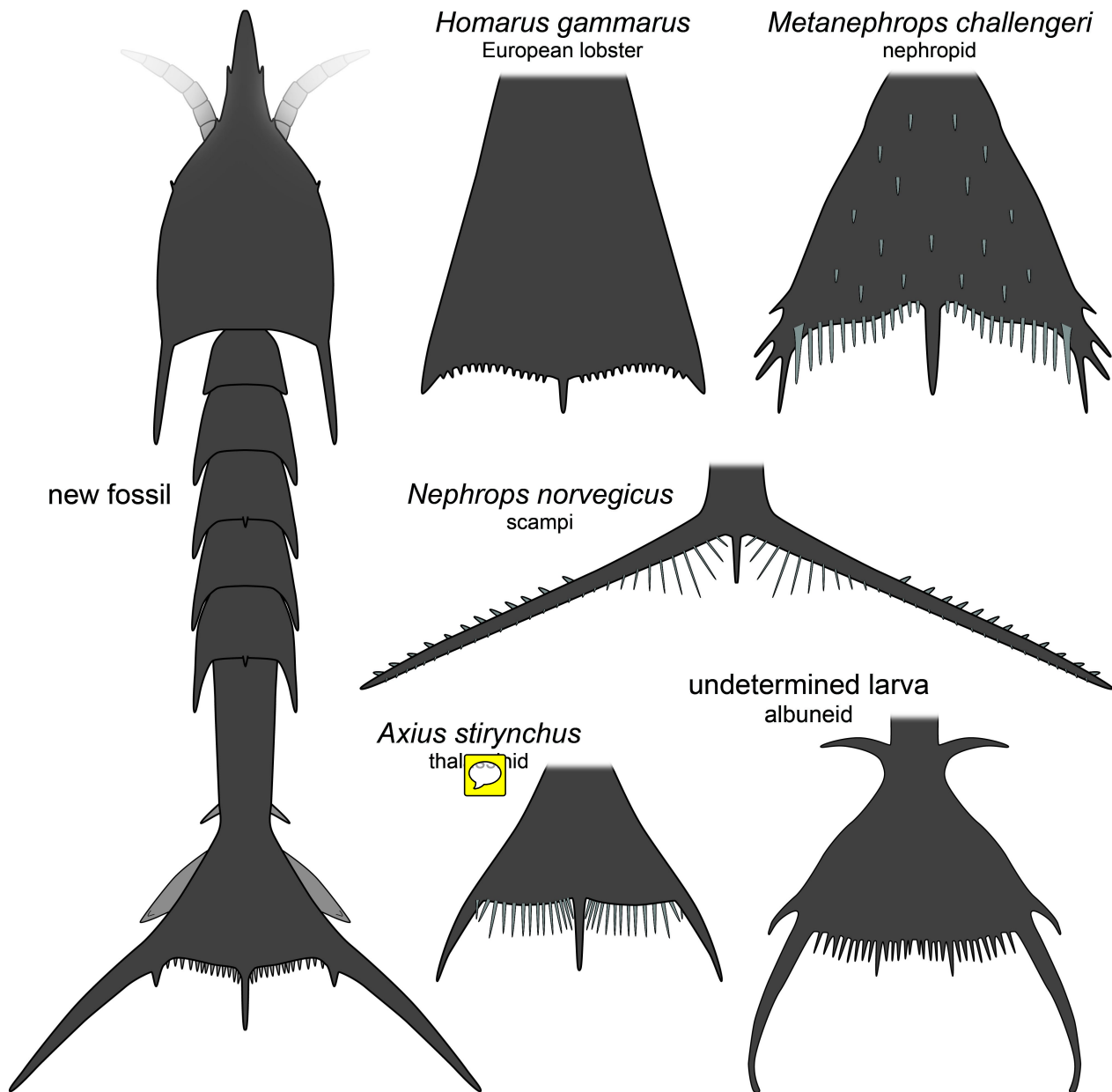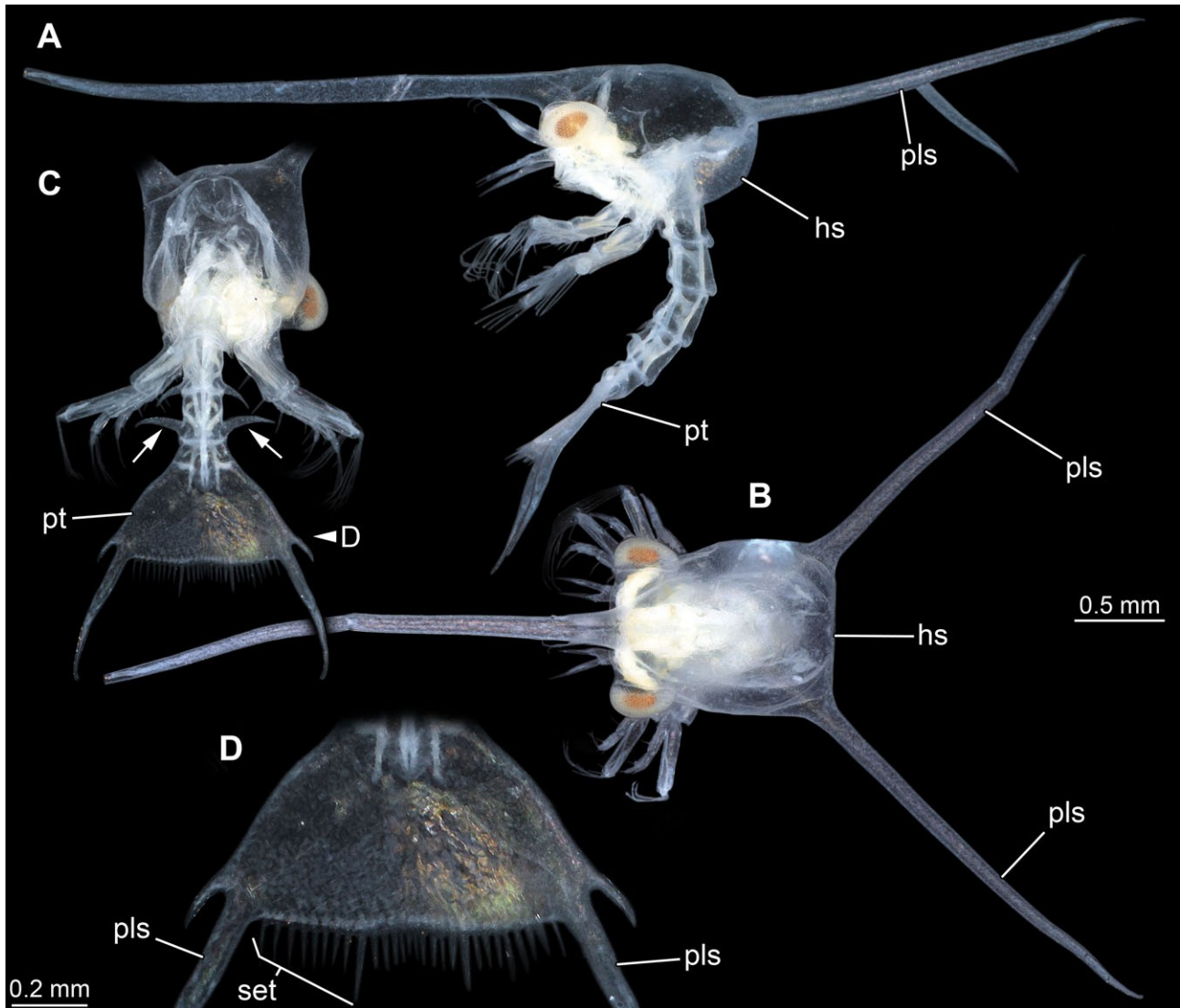454
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Fig. 4. Comparison of the new fossil larva with extant forms. New fossil larva as restoration in dorsal aspect; each of the others as an isolated telson in dorsal view. *Homarus gammarus* (European lobster); zoea III simplified from Rötzer & Haug (2015). *Nephrops norvegicus* (scampi, Kaisergranat); zoea III combined from Smith (1987) and Jorgensen (1925). *Metanephrops challengeri*; late zoea simplified from Wear (1976). *Axius stirhynchus*; late zoea simplified from Dos Santos & González-Gordillo (2005, fig. 2F). Undetermined albuneid larva; late zoea simplified from Fig. 5.

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.