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Unique occurrence of polychelidan lobster larvae in the fossil record and its evolutionary implications

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23 Abstract

24 Larvae represent a specific life phase of an organism and often have very different life habits and
25 thus morphology than the adult. Like in adults, also larval traits most likely evolved gradually. We
26 describe a new larval form, recently discovered in the about 95 million years old (Cenomanian, Late
27 Cretaceous) Plattenkalks of Hadjoula (Lebanon). The two known specimens possess larval
28 characters and can be ascribed to polychelidan lobsters. They represent the youngest non-
29 ambiguous polychelidan in the fossil record and the single known occurrence of a fossil larval form
30 of a polychelidan lobster. Like their modern counterparts, eryoneicus larvae of Polychelidae, these
31 fossil larvae are relatively large and armed with numerous spines on their shield (carapace) and
32 pleon. They differ from extant eryoneicus larvae by their unusually long rostrum, their stalked eyes
33 with a developed cornea and a shield far less inflated than the balloon-like shield of modern
34 eryoneicus larvae. These fossil larvae demonstrate that the highly specialised morphology of
35 modern polychelid larvae evolved gradually and give important clues in which temporal order these
36 larval specialisations evolved. The specimens are another example of fossils providing crucial
37 insights into the evolution of specialised developmental patterns of modern groups, as previously
38 demonstrated for mantis shrimps, achelate lobsters, or early crustaceans, but also for other animal
39 groups.
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45 Keywords: Cretaceous; Hadjoula; eryoneicus larva; metamorphosis; larval specialisation.
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48 1. Introduction

49 Early developmental stages, including larvae, can apparently evolve independently from the adult
50 (Scholtz, 2005). Yet, the evolution of larval forms is still controversial in many aspects, and has also
51 triggered rather unusual evolutionary theories (e.g., Williamson, 2012 and references therein; but
52 see Hart and Grosberg, 2009; Willis and Cox-Foster, 2010). For understanding the evolution of
53 specific larval traits, some evolutionary lineages are especially interesting: those in which highly
54 specialised larvae derived from less specialised ones, or directly from a juvenile in the case of
55 ancestors with a direct development. For such cases, a gradual evolution of larval traits with further
56 and further specialised larval types appears to be a plausible evolutionary scenario.
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59 For the evolution of adult forms the fossil record has provided early representatives of
60 various lineages that allowed very detailed reconstructions of evolutionary scenarios, with very
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gradual, step-by-step transformations leading to the modern morphologies (e.g., Senter, 2010; Haug et al., 2010a). Such approaches have as well been applied successfully to developmental traits (Walossek, 1993; Haug et al., 2010b; Sánchez-Villagra, 2012).

Due to preservation issues, a comparable palaeontological approach on the evolution of larvae requires groups whose development includes large larvae with durable consistency. Arthropods are promising for such an approach: the earliest hatchlings already possess a chitinous cuticle, which can in principle persist on a geological time scale (e.g., Butterfield and Harvey, 2012); each subsequent larval stage also has chances to fossilize as exuvia are shed and may be preserved. Furthermore, numerous groups of arthropods possess larvae of astonishingly large sizes, growing up to several centimetres before developing the adult morphology, e.g., mantis shrimps, achelate lobsters, or polychelid lobsters.

Modern polychelid lobsters are blind, benthic, deep-sea inhabitants (Galil, 2000). Their up to several centimetres large larvae, called eryoneicus, are highly specialised for a planktic life style in the deep sea (500–4000 m: Bernard, 1953). The most prominent structure of modern eryoneicus larvae is their large cephalothoracic shield (carapace). It is reminiscent of a balloon and is quite transparent. Shield and pleon (“shrimp tail”) are armed with numerous strong spines. Additionally, fine setae cover parts of the shield and appendages. As adults, at least the first four pereopods bear chelae (females of a few species bear chelae on all pereopods: Bernard, 1953; Williamson, 1983; recent review in Martin, in press).

In the Jurassic (ca. 200–145 mya), polychelidan lobsters are well known, thanks to their preservation in the famous, extensive Solnhofen-type localities of southern Germany. These species seem to have lacked the specialised larvae of the modern forms; already quite small specimens strongly resemble the adults (Haug et al., 2011a, their fig. 2; Audo et al., 2014a).

Thus, larval stages of polychelidans are so far unknown from the fossil record. We present the first fossil specimens of eryoneicus larvae and try to reconstruct an evolutionary scenario for the adaptations of these larvae.

2. Material and methods

All studied specimens (fossil and extant) are part of the collection of the Muséum national d'Histoire naturelle Paris. The two fossil specimens were found in in the quarry of Hadjoula, Lebanon by one of the authors (Pierre Abi Saad). Fossils from this quarry are about 95 million years old (Cenomanian, Late Cretaceous). The age is based upon ammonite fauna (Hüchel, 1970; Hemleben, 1977) and was confirmed by Wippich and Lehmann (2004). Geological settings have been summarized in Audo and Charbonnier (2012, 2013).

Documentation followed the macro-fluorescence approach of Haug et al. (2011b) with a Canon Rebel T3i and a MP-E 65mm macro lens. Several images were recorded and stitched with Adobe Photoshop CS 3 (photomerge, reposition only or interactive layout).

Extant specimens were documented directly in alcohol under cross-polarised light with the same camera; smaller specimens with a MP-E 65mm macro lens, larger ones with an EF-S 18–55mm lens. Lighting was provided by a Canon Twin Flash MT-24. Several images were recorded at different focal planes to produce an image stack. Stacks were fused with the software programs CombineZM/ZP (for technical details see Haug et al., 2011b).

3. Description of the fossil specimens

3.1. Large specimen (MNHN.F.A48983)

Total length about 30 mm (Fig. 1A). Cephalothorax possesses a conjoined tergal area forming a cephalothoracic shield (carapace). Shield is anteriorly drawn out into a rostrum and armed with numerous spines grouped into about eleven rows from the rostrum to the posterior margin, with up to eleven spines per row (5 on each side, one along dorso-median axis); between the spines

1 numerous fine (probably sensorial) setae are present (Fig. 1B). The pleon segments bear large
2 spines along their median line. The tergopleura are drawn out into two spines each. The first
3 pleomere appears to bear five spines along its dorsal side (2 on each side, one median); the same
4 pattern is seen on pleomeres 4–6. Pleomeres 2–3 have two rows of five spines each. The tail fan
5 consists of an acute triangular telson and the uropodal rami, which appear also more or less
6 triangular, but shorter than the telson. The first pereopod is only incompletely preserved, but
7 appears larger than the succeeding one; the fixed finger appears to be preserved, but bent.
8 Pereiopods 2–4 are sub-similar; distally they all bear tiny chelae (also the fourth pereopod; Fig.
9 1C). The distal section of pereiopods, near the chela bears a row of elongate setae (Fig. 1C).

10 **3.2. *Small specimen (MNHN.F.A49029)***

11 The second specimen is considered to be an earlier stage (see discussion). Total length about 14 mm
12 (Fig. 1D). The smaller specimen is preserved with fewer details, yet preserves aspects not
13 observable on the larger specimen, e.g., the shield is more complete. The rostrum shows two
14 additional spines on the ventral side. Shield bears eleven rows of spines. Under the rostrum a
15 spherical structure most likely represents the compound eye, with a cornea, possibly with square-
16 shaped facets (Fig. 2A, B). Pleon and appendages are less well known. The pleomeres are also
17 spinose and equipped with paired spines on the tergopleurae. Thoracopods 5–8 also possess tiny
18 chelae and setal rows (Fig. 1E). Uropodal rami are also triangular and shorter than the, likewise
19 triangular, telson.
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25 **4. Discussion**

26 **4.1. *Systematic position***

27 Specimens MNHN.F.A48983 and A49029 are considered to be conspecific and to represent
28 different ontogenetic stages. The assumption of conspecificity is based on several similarities, namely
29 the spination of shield and pleomeres, the setae equipment, the stout chelae and the length ratios of
30 uropods and telson. All differences, mainly the stouter general appearance of the smaller specimen,
31 can well be understood as result of an ontogenetic effect.
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35 Both specimens possess five well-developed pereopods (= thoracopods 4–8), six pleomeres,
36 and a shield covering the entire cephalothorax, a typical decapod crustacean habitus. Within
37 decapods, the specimens can be confidently ascribed to Polychelida based on the following points:

38 (1) Their pereopods 2–4 bear a chela – especially the presence of a claw on pereopod 4 is a
39 very rare feature in decapods besides Polychelida. The chelae are quite small, the exact joint
40 appears to be below the resolution of the fossil. Yet, also in modern forms the fingers of the chelae
41 can be very small and appear to be not necessarily functional yet, even in large larvae. It is also
42 worth noting that the propodus is quite short in the specimens, while the carpus (as well as the
43 merus) is quite long. While a relatively long carpus might appear unusual for a decapod at first
44 sight, such a morphology is also found in modern eryoneicus larvae (Bernard, 1953, his figs. 4,
45 20.1).
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49 (2) The pleon morphology resembles that of many non-meiouran reptantians in appearing
50 more dorsoventrally flattened (as indicated by the orientation of the embedding). In caridean
51 shrimps the pleon usually possesses a distinct bent at the third pleomere, while here the pleon is
52 smoothly curved (as in lobsters). Furthermore, affinities to carideans (including the heavily
53 armoured glyphocrangonids, which distantly resemble the here described specimens) can also be
54 excluded as in carideans the tergopleura of pleomere two are significantly enlarged to overlap the
55 tergopleura of pleomeres one and three. This is obviously not the case in the here described
56 specimens.
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58 (3) While the pleon morphology indicates reptantian affinities, the telson morphology
59 resembles that of caridean and dendrobranchiate shrimps, as it is acute triangular. Such a triangular
60 telson rarely occurs in reptantians, the major exceptions being glypheideans (Charbonnier et al.
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2013) and polychelidans (most species, DA, personal observations). Most other reptantian lobsters, including the spiny achelate lobsters, possess a distinctly subrectangular telson. Hence, this specific combination, with apomorphic characters of reptantians (pleon) and the retention of plesiomorphic decapod characters (telson) is only found in Reptantia outside Eureptantia. Together with the morphology of the posterior thoracopods (chelae, long carpus in larvae) clearly indicate polychelidan affinities of the here described specimens.

(4) The very spinose shield and pleon (Figs. 2C, 3) indicate the larval status of the here described specimens. In addition, the comparably small size, the density of setae on shield and appendages, and the relatively short length of dactylus and fixed finger of the posterior chelae undoubtedly indicate that both specimens have not reached an adult morphology through metamorphosis. These specimens can be considered to represent a developmental stage equivalent to the eryoneicus larvae of modern Polychelidae.

(5) Both specimens clearly possess a marked cervical groove. Marked cephalothoracic grooves occurs in most decapod crustaceans, including most species of polychelidan lobsters except for *Eryon cuvieri*, all species of *Cycleryon* and *Knebelia bilobata* (Audo et al 2014a,b), in which it is almost effaced. For this reason, the presence of a marked cervical groove does not preclude an ascription to polychelidan lobsters.

4.2. Evolution of eryoneicus larvae in polychelidan lobsters

Polychelidan lobsters first occur in the fossil record about 230 mya (Late Triassic, Carnian). Surprisingly, no juvenile specimen is known before about 170 mya (Middle Jurassic, Bathonian-Bajocian of Monte Falano: Bravi et al. 2014). Other reported juvenile specimens are younger, about 165 mya (Callovian: Charbonnier, 2009; Charbonnier et al., 2010, in press) and about 150 mya (Kimmeridgian–Tithonian: Audo et al., 2014a). During the Cretaceous (145–65 mya) the polychelidan fossil record is very scarce, with only three species, each represented by a single specimen (Garassino et al., 2012 and references herein).

Dated from the Late Cretaceous, the here described specimens are only the second “eryoneicus-type” larvae reported, the other being *Eryoneicus sahelalmae* Roger, 1944 from the Santonian of Lebanon, a deep-sea palaeoenvironment (Audo and Charbonnier, 2013). However, the latter species has recently been reinterpreted as an achelate late larva or early juvenile (Haug et al. 2009, 2011a, 2013). Our specimens therefore represent the single known occurrence of an “eryoneicus-type” larva in the fossil record.

After the Cretaceous, only one fossil was ascribed with doubt to polychelidan lobsters: *Palaeopentacheles? starri* Schweitzer and Feldmann, 2001 (Schweitzer and Feldmann, 2001). However, a reinvestigation of the specimen shows that the structures in this fossil were misinterpreted: the specimen is a moult, a pectinate claw corresponds to a pair of third maxillipeds with their crista dentata, and the poorly preserved shield seems to be laterally flattened, as in nephropoid lobsters. This species is perhaps a nephropoid lobster, which implies that our larval specimens correspond to the last known occurrence of polychelidan lobster in the fossil record.

As MNHN.F.A48983 and A49029 can be recognised as “eryoneicus-like” larvae, but differ from modern forms, we can propose some conclusions about the evolution of larval traits within the polychelid lineage. With juveniles characterized by a small size and morphologies rather similar to that of the adult, it seems that most Jurassic groups such as Eryonidae, Palaeopentachelidae and perhaps Coleiidae did not possess an “eryoneicus-type” larva: the smallest specimens known of these polychelidan groups are significantly smaller than late stage eryoneicus larvae and than specimen MNHN.F.A48983 (Bernard, 1953). Yet, these small polychelidans show no specialised larval traits such as the spinose shield or pleon, but instead roughly resemble their corresponding adults. This also means that the larval phase of these earlier forms was comparably short and that the juvenile phase was longer, hence from small sizes onwards the adult morphology was established. In modern forms this is quite the opposite: the larval phase lasts longer, the adult morphology is established rather late. Thus, the late larval stages are quite large compared to the adult size (not necessarily in absolute dimensions).

Specimens MNHN.F.A48983 and A49029 therefore can be understood as an evolutionary 'step-in-between', developing through specialised stages, which already possess some of the larval features of a modern eryoneicus, but not all of them:

- (1) retention of eyes,
- (2) a well-developed rostrum (as developed in most decapod larvae) and
- (3) a non-balloon-shaped shield

which are all plesiomorphic characters, thus supporting the assumption of an evolutionary intermediate form. As a consequence, we can conclude that the relatively large size of the larvae of the specimens, which they share with modern forms, as well as the pronounced spination and setation, as also seen in their modern counterpart, evolved first and led to the larvae described herein (Fig. 3). Later in the evolutionary lineage towards modern polychelids additional specialisations must have evolved, such as the balloon-shaped shield and the reduction of the rostrum (Fig. 3).

Most fauna from Hadjoula probably used to live in the euphotic zone, some probably living in the reefs surrounding the depression where the Lagerstätte was deposited (Hückel, 1970; Hemleben, 1977; Audo and Charbonnier, 2012). With their functional cornea, both studied larvae probably did not live in a deep-sea environment. Thus, the additional characters of modern eryoneicus larvae could have been coupled to a habitat change into deeper waters. In this respect, it should be noted that no adult polychelidan lobster has ever been reported from Lebanon. As modern eryoneicus larvae probably grow in a different environment than where the adults live, it is possible that the lack of adult polychelidans in Lebanon, and perhaps also their extreme rarity in the Cretaceous, may result from adults living preferentially in deep water.

4.3. Gradual evolution of larval traits

The case of specimens MNHN.F.A48983 and A49029 is seen as an important example of a stepwise evolutionary acquisition of larval features. Other recently described examples of fossil arthropod larvae could also represent such examples of less specialised larvae (compared to their modern counterparts), e.g., mantis shrimps or achelate lobsters (Haug and Haug, 2013). Yet, it is more likely that the latter forms represent ontogenetically transitional forms from already highly specialised larvae to the juvenile. As the smaller specimen A49029 clearly lacks the same larval specialisations as the larger specimen, the two cannot be interpreted as such ontogenetically transitional forms. The here presented case therefore represents the first clear example of a stepwise evolution of larval traits in crustaceans.

Haug and Haug (2013) had hypothesised that the evolution of metamorphosis as a specific developmental pattern was coupled to two factors: 1) evolutionary increase of disparity of early (larval) stages, and 2) condensation of gradual developmental patterns with numerous moults to few drastic metamorphic moults. While other described fossil crustacean larvae can exemplify the second point (e.g., Walossek, 1993), this new case of polychelidan larvae is the first reliable example for point one.

Polychelids are often considered to have a "direct development" (Gurney, 1942, p. 229), most likely referring to a non-metamorphic type of ontogeny. Yet, the specialisations of their larval stages speak against such an assumption. Until now no ontogenetic transitional forms are known, which would bridge eryoneicus larvae and juvenile stage polychelidans, as the development of these deep-sea forms is impossible to study directly. This indicates that the last moult of the larva in modern polychelids is a metamorphic one. Given this consideration, polychelids are, together with the newly discovered fossils, another potential group for studying the evolution of development and metamorphosis with a palaeo-evo-devo approach.

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9

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Figure captions

1
2 **Fig. 1.** Fossil polychelid eryoneicus larvae (Hadjoula; Cretaceous, Lebanon). A–C, larger specimen
3 (MNHN.F.A48983). A, overview image, showing the spiny appearance of the specimen. B, close-
4 up on the setae on the shield. C, fourth pair of pereopods (= seventh pair of thoracopods), also
5 bearing chelae, a character for polychelidans. D–E, smaller specimen (MNHN.F.A49029). D,
6 overview, same scale as A. E, close-up on fourth pair of walking legs with chelae. ch, chela; cs,
7 cephalothoracic shield; es, eye structure; f?, possible finger; p, pereopod; pl, pleomere; rs, rostrum;
8 tf, tail fan.
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11
12 **Fig. 2.** Eye of fossil specimen and extant specimens for overall comparison. A–B, close-up on eye
13 of smaller fossil eryoneicus larva (MNHN.F.A49029). A, close-up. B, detail of A with colour-
14 marked ommatidia. C, two extant eryoneicus larvae for comparison with the fossil ones;
15 undetermined species, also unclear if the specimens are conspecific; left MNHN PA 1165, right
16 MNHN PA 1125.
17
18

19 **Fig. 3.** Reconstruction of the fossil eryoneicus larvae and evolutionary scenario. Top: 3D
20 reconstruction of the larger specimen; not preserved body parts amended from extant eryoneicus
21 larvae. Bottom: Evolutionary scenario describing the step-wise acquisition of larval characters in
22 the evolutionary lineage towards modern polychelids. Developmental pattern unclear for
23 Tetrachelidae and Coleiidae.
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Figure 1
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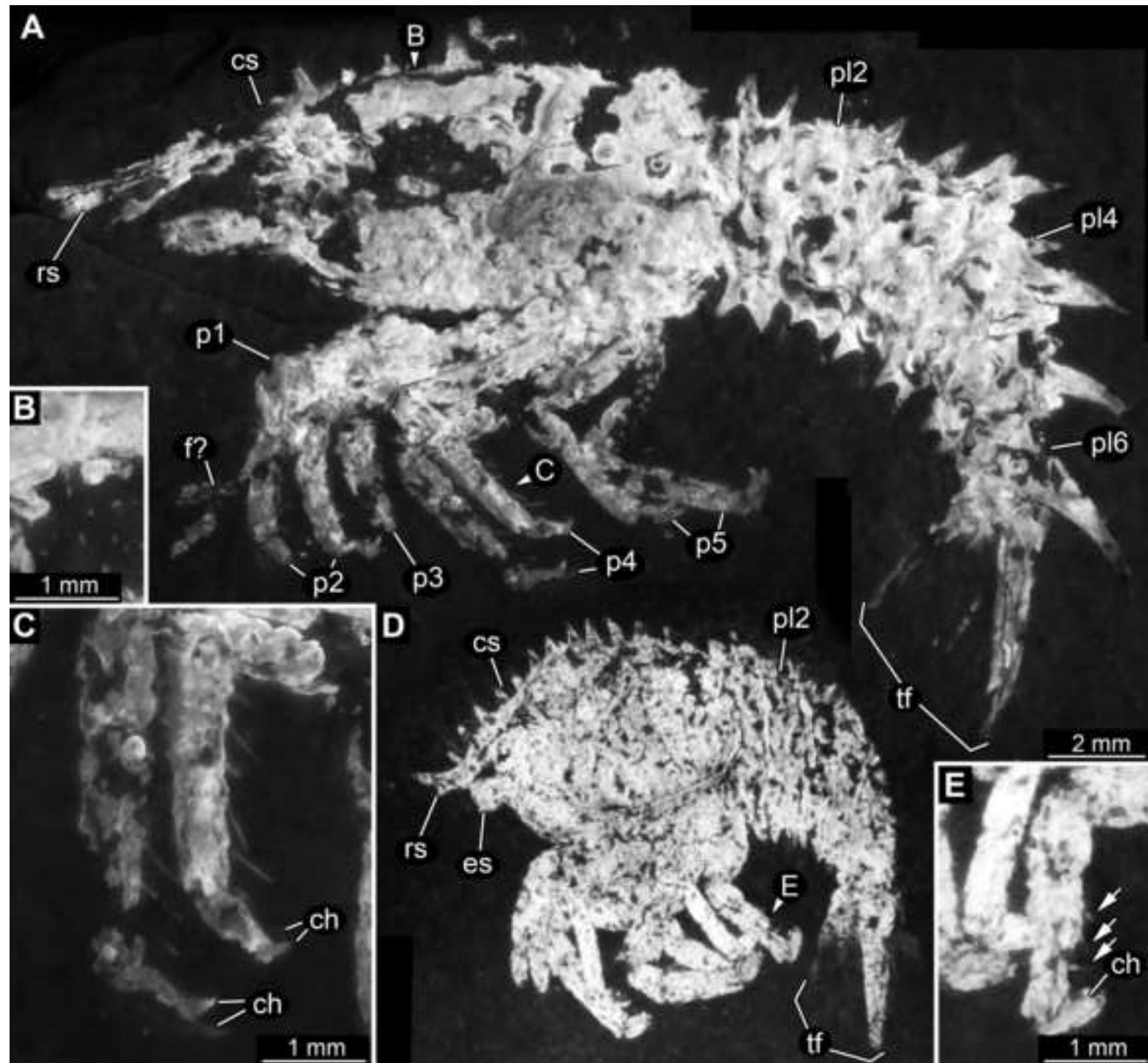


Figure 2
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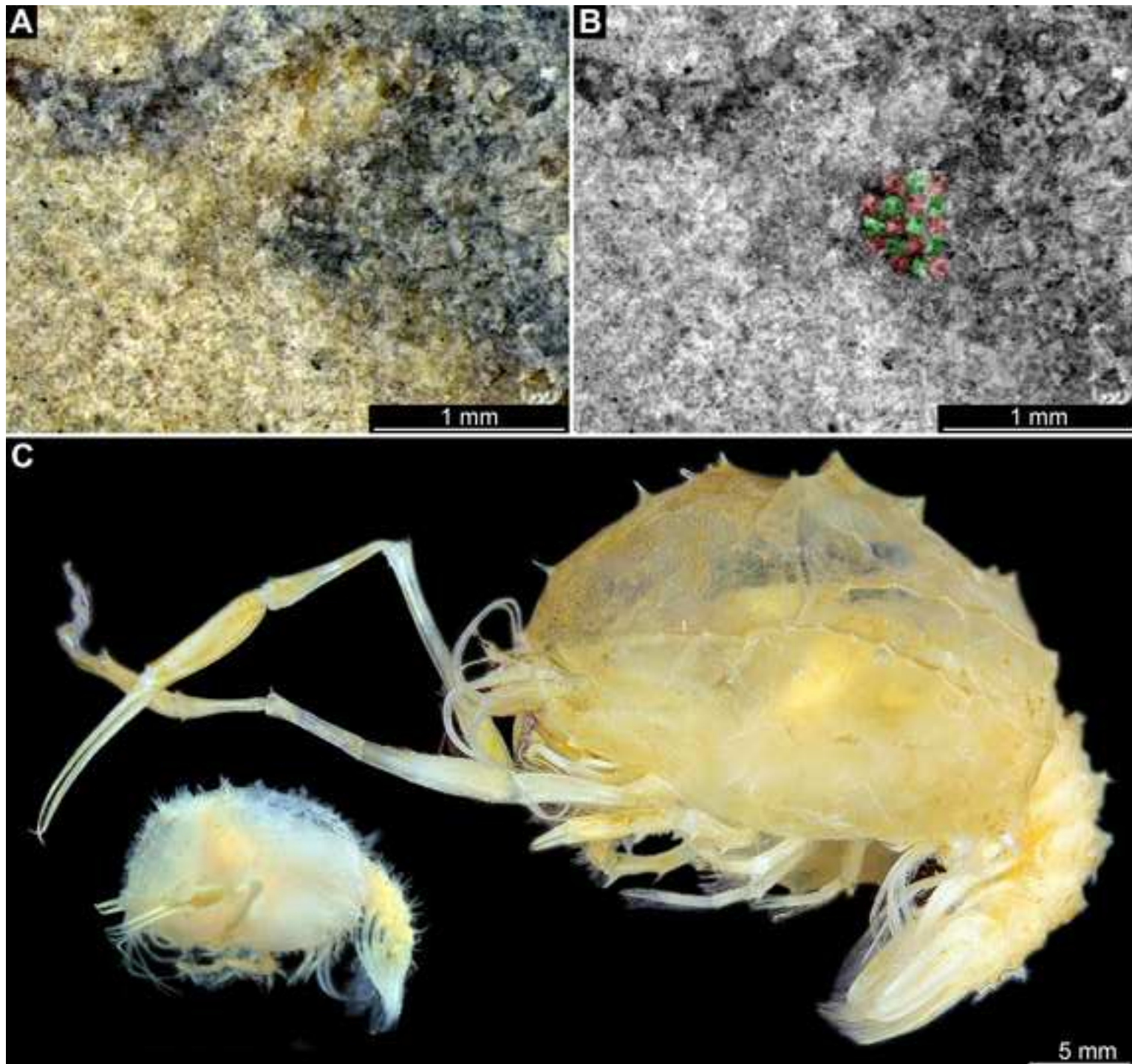
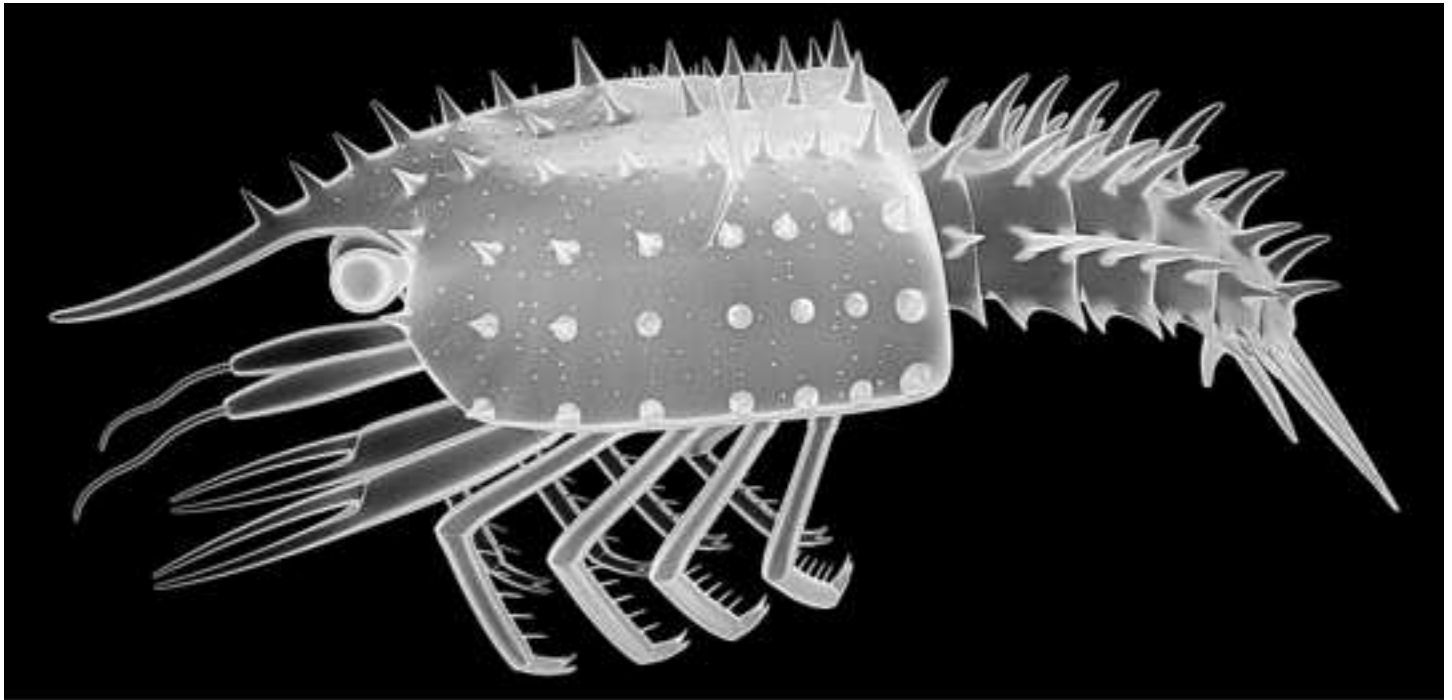


Figure 3
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Polychelida

Tetrachelidae?
Eryonidae
Palaeopentachelidae
Coleiidae?



reconstructed ancestral state:

- unmetamorphic ontogeny
- small larvae, short larval phase
- eyes with cornea
- larger larval rostrum
- shield not inflated
- rather smooth shield and pleon

new form



novelties:

- more metamorphic ontogeny
- giant larvae, longer larval phase
- larvae with spiny shield and pleon

ancestral characters:

- eyes with cornea
- larger larval rostrum
- shield not inflated

Polychelidae
the modern forms



novelties:

- loss of cornea
- tiny larval rostrum
- larval shield inflated