A nisto larva of an Eocene slipper lobster (Neoscyllarida)

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Abstract

We re-describe a single specimen of a scyllarid lobster from the uppermost lower Eocene of Monte Bolca, Northern Italy. The specimen was described as *Parribacus cristatus* Förster, 1984, but has been recently ascribed to *Parsacus*. In this study, the specimen is re-documented using macro-fluorescence imaging. This re-investigation reveals that not only dorsal aspects, as originally described, but also numerous ventral details are preserved, including thoracopods 4–8 (pereiopods 1–5) as well as the thoracic sternum. Different aspects of the specimen, such as a lack of serrations of the shield and the antennae, the relatively small size, and the weak sclerotisation of the shield indicate that the specimen represents a last larval stage, a nisto. This is only the second case of a nisto in the fossil record.

Keywords: nisto larva, palaeo-evo-devo, Monte Bolca, Achelata.

1. Introduction

Larval stages are rarely preserved in the fossil record. Due to their small size and the usual lack of hard parts, they have a low preservation potential, and only under very special circumstances we get an insight into the ontogeny of a fossil organism (e.g., Haug J.T. et al. 2011b). In some organisms ontogeny leaves traces on older organisms, e.g. larval shells of molluscs (e.g., Nützel 2014 and references therein). In most moulting animals the case is different; here the fossilization of an instar will provide access only to this specific stage, as for example a larva. Among eucrustacean arthropods there are exceptional preserved examples, e.g. of Cambrian (500 million years old) branchiopod larvae (Walossek 1993) and thecostracan larvae (Müller & Walossek 1988; Zhang et al. 2010) with preserved details down to 0.2µm. Three-dimensional fossilized larval stages from the Palaeozoic are provided of a Silurian (about 450 million years old) cypris stage of a barnacle (Briggs et al. 2005) and Devonian (about 400 million years old) branchiopod and ascothoracid larval stages (Scourfield 1926, 1940; Haug C. et al. 2012, 2014). From the Mesozoic also exceptionally preserved larvae of ostracodes have been recorded (Smith 2000; similar larvae known from cuticle preservation: Gramann 1962).

Especially larvae of Malacostraca seem to have a higher potential to be preserved in the fossil record (Haug J.T. et al. 2014). The malacostracan ingroup Achelata has already provided numerous examples of preserved larval stages. Over a dozen types of fossil achelatan larvae are known, in some cases with thousands of specimens (Polz 1971, 1972, 1973, 1987, 1995, 1996; Tanaka et al. 2009; Haug J.T. et al. 2009, 2011a, 2013, 2014; Haug J.T. & Haug C. 2013). The larval phase of extant reptantians, including achelatans, is usually understood as comprising two distinct larval sub-phases, the zoea phase and the megalopa phase (sensu Williamson 1969, sometimes incorrectly referred as postlarva). The zoea larvae of achelatan species are highly specialized and called phyllosoma, referring to their leaf-like head and body. After up to ten phyllosoma stages the animal metamorphoses into the megalopa (Marinovic et al. 1994; Mikami & Greenwood 1997; Webber & Booth 2001; Inoue et al. 2004), a discrete stage, but morphologically often already resembling the juvenile to a larger degree. It mediates the change from the pelagic into the benthic realm (Felder et al. 1985). Within the two extant groups of achelatans, Neoscyllarida (modern slipper lobsters) and Palinurida (spiny lobsters), the megalopa received different names: in Palinurida, this stage is called puerulus, in Neoscyllarida this stage is called nisto.

Due to the comparably good record of achelatan larvae we also know some details of the developmental pattern of extinct achelatan species. While all extant achelatans develop in the way described above, many Mesozoic forms apparently developed in a more gradual pattern. In other words, the changes occurring in the metamorphic moult in modern forms are spread on more than one consecutive moults, instead of appearing in only one developmental step. This is demonstrated by fossil specimens that show a mixture of phyllosoma and post-phyllosoma characters (Haug J.T. et al. 2013). Thus, the transition from phyllosoma to the post-phyllosoma was less pronounced than in the modern forms. In addition, juvenile development was more gradual (e.g., Haug J.T. et al. 2009).

Therefore, unambiguous nisto or puerulus stages are significantly rarer than phyllosoma larvae or transitionary forms. Polz (1995) has suggested that certain small forms of the Jurassic palinurid *Palinurina* Münster, 1839, usually referred to *Palinurina pygmaea* Münster, 1839, could represent puerulus stage specimens of *Palinurina longipes*

Münster, 1839. This is a possible explanation, yet currently remains an open case, as it has not been investigated further, yet. A definite nisto stage was described by Audo & Charbonnier (2012) from the Cretaceous of Lebanon.

Parribacus cristatus Förster, 1984 a fossil scyllarid that possesses some aspects of a nisto stage was described from the Eocence of Italy (Monte Bolca). Förster (1984) pointed out that certain aspects of this fossil argue for a nisto stage, while others indicate a later developmental stage.

We provide a re-investigation of the specimen described by Förster (1984) with up-to-date imaging methods. Furthermore, we provide an interpretation of the specimen in the light of recent ideas about the evolution of development in Achelata.

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2. Material and methods

The single specimen is part of the Collection of the Museum für Naturkunde, Berlin ("Humboldt Museum"). It is stored under the repository number MB.A 88. According to original labels and Förster (1984) the specimen originates from the Monte Bolca Lagerstätte, Northern Italy. Hence it should be of uppermost lower Eocene (49 million years) in age.

The specimen was documented with a Canon Rebel T3i digital camera and a MPE-65mm macro lens. Three LED torches equipped with cyan filter provided illumination. A red-filter was placed in front of the lens. With this setup, we make use of the autofluorescence of the fossil (Haug J.T. et al. 2008, 2011b; Haug C. et al. 2009; Haug J.T. & Haug C. 2011; Kerp & Bomfleur 2011). Several image details of the specimens were recorded and stitched together using the photomerge function of Adobe Photoshop CS3 (Haug J.T. et al. 2012), resulting in a high resolution image that allowed to study details and general morphology. Further processing followed Haug J.T. & Haug C. (2011).

The documentation methods applied reveal not only dorsal features, but also ventral details, such as the thoracopods and the thoracic sternum. An elaborate description is provided as a descriptive matrix (Haug J.T. et al. 2012) (supplementary file).

3. Systematic palaeontology

Malacostraca Latreille, 1802
Decapoda Latreille, 1802
Reptantia Boas, 1880
Achelata Scholtz & Richter, 1995
Neoscyllarida Haug, J. T., Audo, Charbonnier, Palero, Petit, Abi Saad & Haug, C., in press

Parsacus Garassino, Bahrami, Yazdi & Vega, 2014

Type species: *Parsacus eocenicus*.

Parsacus? *cristatus* (Förster, 1984)
Figs. 1, 2

v*1984 *Parribacus cristatus* n. sp. – Förster, pp. 62–64, fig. 2.
. 2001 *Parribacus cristatus* – Garassino & Novati, pp. 251, 252, 258.
. 2007 *Parribacus cristatus* – Webber & Booth, pp. 36–38, 397, fig. 2.5.
. 2007 *Parribacus cristatus* – Vega et al., p. 408.
v 2014 *Parsacus cristatus* – Garassino et al., p. 49, fig. 5.

Diagnosis: Based on specific developmental stage, the nisto-larva (neoscyllaridan megalopa). Large overall size. Shield with no cervical incision, but apparent U-shaped furrow. Shield appears to be smooth. Pleomere tergopleura with few serrations on the lateral rim. Antenna large shovel-shaped, without apparent serrations. Distal element comparably small. Element three relatively large; anterior rim pronounced concave.

4. Discussion

4.1. New details revealed by modern imaging methods

Förster (1984) described almost exclusively dorsal aspects of specimen MB.A 88 (Fig. 1B). He only mentioned that the "mandibular sternum" and the excretory openings of the antennae can be seen through the shield as their outlines have been compressed through it. Although we acknowledge the work of Förster (1984), distinct differences between his description and our observations arose.

Our investigations show that almost the complete thoracopods four to eight (pereiopod 1–5) as well as the thoracic sternum are well-preserved, but can only be seen under fluorescence light (Fig. 1A, C). Furthermore, some aspects that Förster (1984) described cannot be confirmed. For example finely ordered tubercles on the shield (= carapace) as well as the serration of the antennal articles, which were reported by Förster (1984), have not been observed. The applied methods clearly have the potential to reveal such details (see references in method section), thus the fact that the details could not be observed leads us to conclude that Förster's (1984) reconstruction

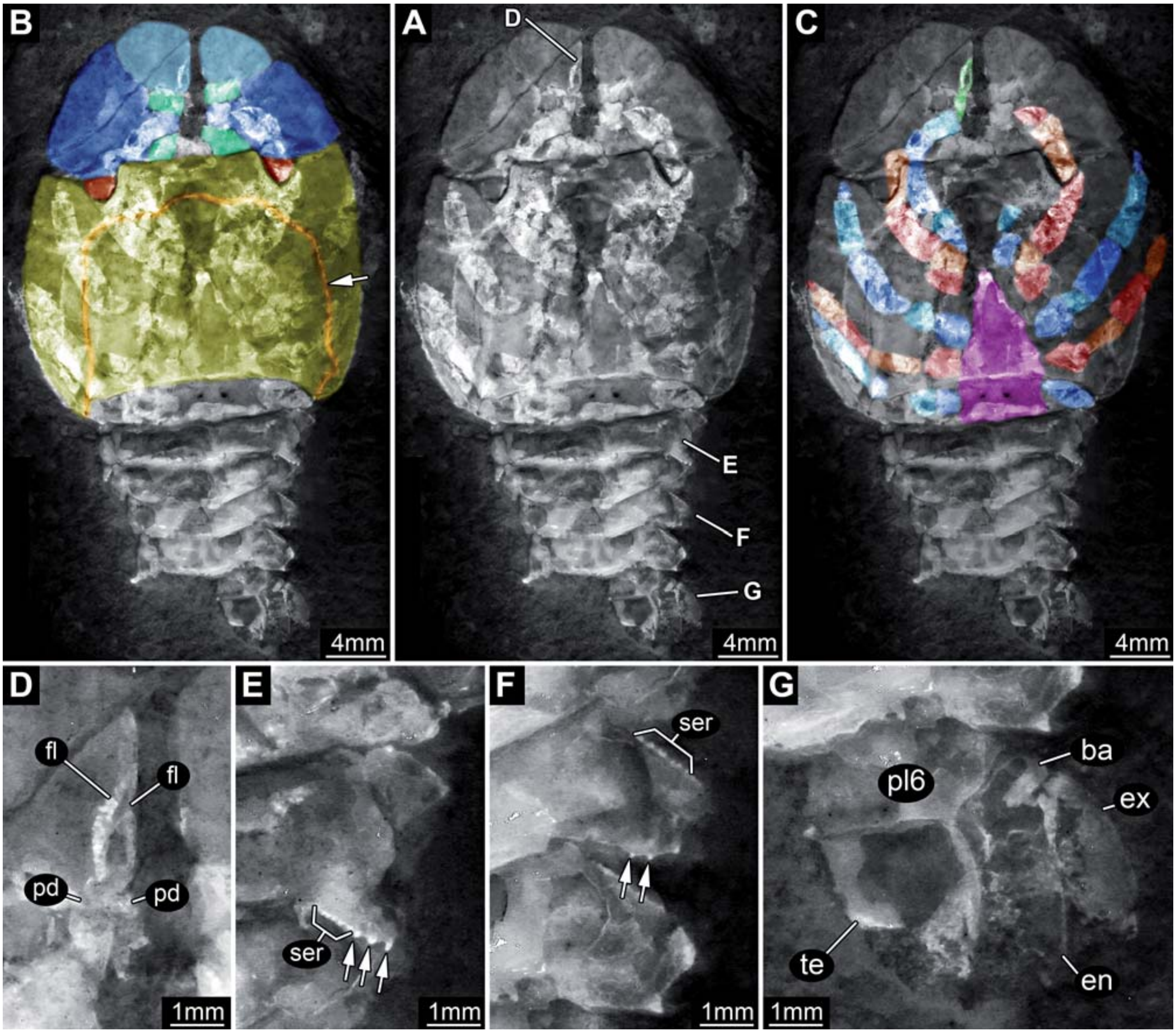

Fig 1. *Parsacus*? *cristatus*, specimen MB.A 88, under macrofluorescence settings. A. Overview image. B, C. Colour-marked versions of A. B. Dorsal structures: shield (yellow); cervical groove (orange; arrow); eyes (red); antenna element 2, 4 (light green); antenna element 3 (blue); antenna element 5 (cyan). C. Ventral structures: antennula (green); thoracopods (blue and red); thoracic sternum (violet). D. Close up on antennula. E, F. Close-ups on tergopleurae; arrows mark individual serrations. E. Pleomere 2. F. Pleomere 4 and 5. G. Terminal end. Abbreviations: ba = basipod; en = endopod; ex = exopod; fl = flagellum; pd = peduncle; pl6 = pleomere 6; ser = serrations; te = telson.

is idealized. Some erroneously supposed features of the shield may also have been caused by the compression of the legs and the sternum; other smaller details maybe caused by irregular shadows (discussion of irregular shadows in HAUG J.T. & HAUG C. 2014, HAUG et al. 2015). The supposed deep cervical incision appears to be a thin line on the shield, more like a fold but clearly not like an incision (Fig. 1B).

Overall, the shield surface seems deformed by the compression of ventral characters through the shield. FÖRSTER (1984) described characteristic grooves and furrows on the shield, which appear to be rather symmetric in the provided line drawing. However, these structures appear not to be that symmetric in his original photograph (FÖRSTER 1984). The more or less u-shaped cervical groove, which almost reaches the proximal rim of the shield, has been originally interpreted as a curved line between the lateral incisions of the shield. Again our applied method has the potential to resolve shield details, and has also resolved one prominent groove, but not the ones reconstructed by

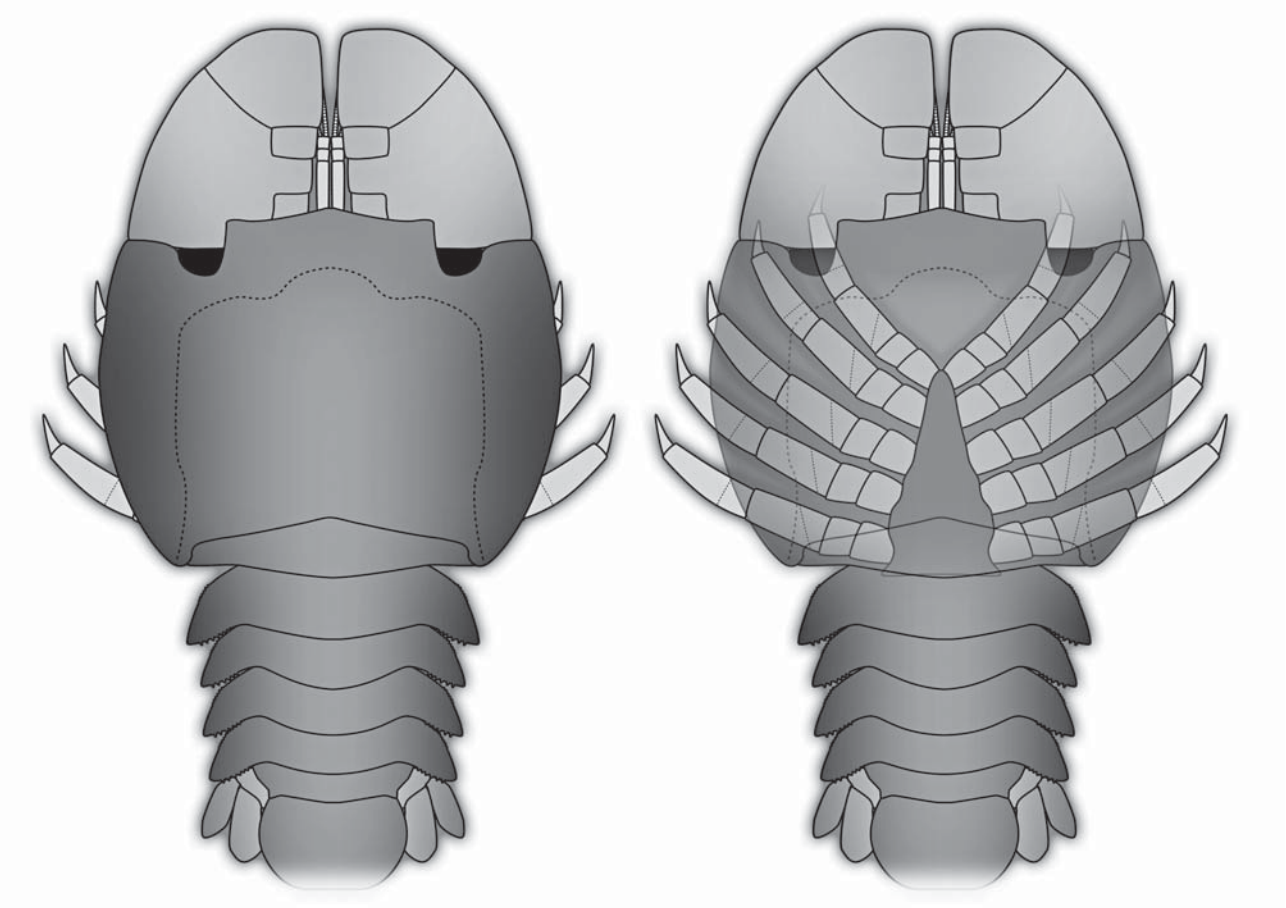

Fig. 2. *Parsacus*? *cristatus* restoration. Left: dorsal features. Right: shield shown as transparent to reveal ventral details. Posterior rim of telson partly unknown, therefore drawn as diminishing.

Förster (1984). We therefore interpret these as artifacts caused by folding of a thinner cuticle.

4.2. Ascription to *Parribacus*

Förster (1984) described the specimen as a new species *cristatus* and ascribed it to *Parribacus*. This ascription was based on the position of the eyes and a (supposed) strong cervical incision, the latter point being slightly doubtful following our observations, as the deep cervical incision of Förster (1984) appears to be a thin line and more like an artificial fold. The identification of the specimen as a representative of *Parribacus* based on characteristic grooves and furrows on the shield is difficult due to the preservation of the specimen.

Recently Garassino et al. (2014) erected the new genus *Parsacus* for a new species from the Eocene of Iran and also ascribed the species *cristatus* to this genus. The ascription of *Parribacus cristatus* to *Parsacus* by Garassino et al. (2014) relies also heavily on presumed dorsal characters from Förster's original work (1984). As discussed (see above) these most likely represent artifacts. Hence, also this interpretation should be seen cautious. For a reliable judgment of supposed close affinities of the species *cristatus* and the species of *Parsacus* described by Garassino et al. (2014) it would be ideal to investigate the specimens with the here applied methods. This would equalize any differences caused by a possible "documentary bias".

Still we can try comparing other observation on *P. cristatus* to the described morphology of *Parsacus eocenicus* (Garassino et al. (2014). The shield of the investigated specimen of Garassino et al. (2014) is characterized by a cervical and post-cervical incisions. Although these are rather weak and short, they are apparent. The shield of *P. eocenicus* also shows some serrations and tubercles. Yet the absence of such structures maybe due to different ontogenetic stages (see further below).

Other aspects should be carefully re-evaluated (at best after re-investigation of the material).

Garassino et al. (2014) described an antennular somite with a longitudinal groove. Compared to our fossil (and extant forms) this structure might correspond to the peduncles of the antennulae.

In addition, the antenna was described having six elements (Garassino et al. 2014) while modern forms possess only five. Otherwise the lateral edge of the antennae appears to have rudimentary serrations, which is different from our fossil, yet again this might be an ontogenetic effect (see next point)

4.3. Interpretation of the developmental stage

Förster (1984) discussed the possibility that MB. A 88 represents a nisto stage. The relatively small size of the specimen supports this interpretation. Nisto stages of extant species have shield lengths of up to 21 mm (Sekiguchi et al. 2007); MB. A 88 has a shield length of about 17 mm, which would fit well into this range. In fact in some extant species the nisto instar can possess a body length that is 1.5x that of MB. A 88 (see Yoneyama & Takeda 1998, fig. 6). Förster also pointed out the smoothness of the rims of antennae and shield which support the interpretation as a nisto. A new point supporting this interpretation is the finding that the ventral details, such as thoracopods and the thoracic sternum have been compressed through the shield. This is only possible if the shield was only weakly sclerotized, which is the case in nisto stages. Förster (1984) pointed out that the well-developed cervical incision that he described partly argues against such an interpretation. Yet, as pointed out we cannot support the presence of this well-developed incision, or serration on the antennae. Therefore, all observed details argue indeed for a nisto status of MB. A 88, and no observed character contradicts this interpretation.

If the MB.A 88 indeed represents a nisto the systematic ascription becomes more complicated. Differences to *P. eocenicus* may be because the known specimens of *E. eocenicus* represent not nisto stages but early juveniles. This would be compatible with rather weak incisions on the shield, tubercles restricted to certain areas and rudimentary serrations on the antennae. This furthermore complicates a comparison to modern form. We know the nisto stages only for few species, the early juvenile stages do traditionally not appear in the literature at all. Hence, when comparing *P. cristatus*, *P. eocenicus* and modern adults we in fact compare non-corresponding stages.

Given this complex situation, it may be for the moment the most effective way to treat the species as *Parsacus*? *cristatus*. Alternatively, the species could be even more carefully addressed to as *Neoscyllarida cristatus* (see discussion in Haug J.T. et al. accepted).

Another fossil that has been compared to *P. cristatus* was described by Vega et al (2007). This specimen might hence also represent a nisto larva or an early juvenile and should be re-investigated for this aspect.

4.4. Outlook

The here described and reconstructed fossil (Figs. 1, 2) is only the second case of a definite fossil nisto. It demonstrates that achelatans are indeed an interesting group of decapod crustaceans for palaeo-developmental studies (palaeo-evo-devo), as they provide various different developmental stages and modern forms develop through a pronounced metamorphosis (Haug & Haug 2013; Haug et al. 2013). Finding such examples is a first step for further-reaching comparative studies. It will also be necessary to incorporate more extant data. Numerous studies report the morphology of a single phyllosoma stage (e.g., Johnson 1951; Sekiguchi et al. 1996; Coutures 2001; Inoue et al. 2004; Lindley et al. 2004; Konishi et al. 2006; Palero et al. 2008), usually from plankton samples. Based on laboratory rearing parts of the phyllosma phase (e.g. Abrunhosa et al. 2008) or even complete phyllosoma development (e.g., Lesser 1978; Matsuda & Yamakawa 2000) have been described. Yet, these descriptions usually end with the last phyllosoma stage. The descriptions rarely extend further to include the puerulus or nisto (Marinovic et al. 1994; Mikami & Greenwood 1997; Webber & Booth 2001). We have found no example also describing the first "juvenile", i.e. the stage following the pelagic nisto or puerulus larva.

Studies on fossil species have shown that developmental patterns of achelatans have changed significantly during their evolution (e.g., Haug J.T. & Haug C. 2013; Haug J.T. et al. 2013; Haug J. T. et. al. in press) Therefore studies of entire ontogenetic sequences including juveniles should be the basis for a comparative approach, to reveal more evolutionary pattern in this group. Then it should be possible to also incorporate fossils like the here described and make full use of the information they provide.

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