

Eoprosopon klugi (Brachyura) – the oldest unequivocal and most “primitive” crab reconsidered

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Abstract

We re-describe *Eoprosopon klugi*, the oldest and most “primitive” unequivocal brachyuran crab. Former studies appear to have been based exclusively on a cast of the specimen, more precisely of the part. We studied the original part and counterpart with advanced imaging techniques, including composite imaging under cross-polarised light, autofluorescence imaging, stereo imaging, and virtual surface reconstruction based on image stacks. Our observations demonstrate that certain morphological aspects described in former studies are apparently artefacts caused by the application of low-angle side light. *E. klugi* possesses already numerous features of other early brachyurans such as: 1) an anterior shift of the dactylus axis of the cheliped, 2) narrow anterior pleomeres, and possibly also 3) a further dorsal position of the last thoracopod. On the other hand, *E. klugi* also retains plesiomorphic traits not found in other brachyuran crabs, such as a strong prominent antenna. This character, as well as others, are shared with *Eocarcinus praecursor*. The last-named species has been relatively recently discarded from Brachyura. However, similarities of *Eoc. praecursor* and *E. klugi* support affinities of the first to Brachyura. We also briefly discuss the pattern of character evolution among early brachyurans.

Key words: Brachyura, carcinisation, *Eocarcinus praecursor*, Jurassic, morphotype evolution, optical artefacts.

1. Introduction

True crabs, Brachyura, are the most successful decapod crustaceans. They have conquered numerous different ecological niches, including freshwater and dry land. The early evolution of brachyuran crabs, and with this the reasons for their evolutionary success, is still very incompletely understood.

The first true crabs in the fossil record are known from the Lower Jurassic (about 185 mya); a putative Carboniferous specimen (*Imocaris tuberculata*, see SCHRAM & MAPES 1984; see also discussion in SCHRAM 2009) has been largely discarded, possibly representing a pygocephalomorph (e.g., FÖRSTER 1985a, b). BRÖSING (2008) reconstructed the diversification times of brachyuran groups based on phylogenetic attempts and concluded that a first diversification and adaptive radiation of brachyurans should have occurred in the Cretaceous, including first modern crabs and already representing a certain disparity; a true increase in species richness should not have occurred before the Eocene (50 mya; BRÖSING 2008). Yet, already in the Cretaceous diversity hotspots have been recognised (e.g., KLOMPMAKER et al. 2012).

The supposedly oldest fossil species with brachyuran affinities was for a long time *Eocarcinus praecursor* (e.g., FÖRSTER 1985a, 1986). Yet, FELDMANN & SCHWEITZER (2010) argued that *Eoc. praecursor* cannot represent a brachyuran and instead suggested that it represents an unusual anomalan (“anomuran”).

After discarding *Eocarcinus praecursor* as an early brachyuran, the next oldest true crab, which seems to be

widely accepted as such, is *Eoprosopon klugi* from the Jurassic found near Erlangen, southern Germany. Despite its crucial evolutionary and phylogenetic position, the single specimen of this species has been rarely directly studied. The original illustration of FÖRSTER (1986) is rather brief: only an overview photograph is provided, yet not of the specimen itself, but only of a cast of the part, alongside with a (rather sketchy) camera lucida drawing of it. The existence of the counterpart is mentioned, yet it is not figured.

Most subsequent studies (e.g., MÜLLER et al. 2000) simply reproduced the camera lucida drawing of FÖRSTER (1986). SCHWEITZER & FELDMANN (2010) provided a new photograph of the cast of the part. If *Eoprosopon klugi* is indeed the first representative of the brachyuran lineage, a detailed description of its morphology is of prime importance, as it should inform us about the early character evolution finally leading to the very distinct crab morphotype.

We provide here a detailed re-investigation of the single known specimen of *Eoprosopon klugi* with help of advanced imaging techniques. We discuss how this influences our understanding of the early evolution of Brachyura.

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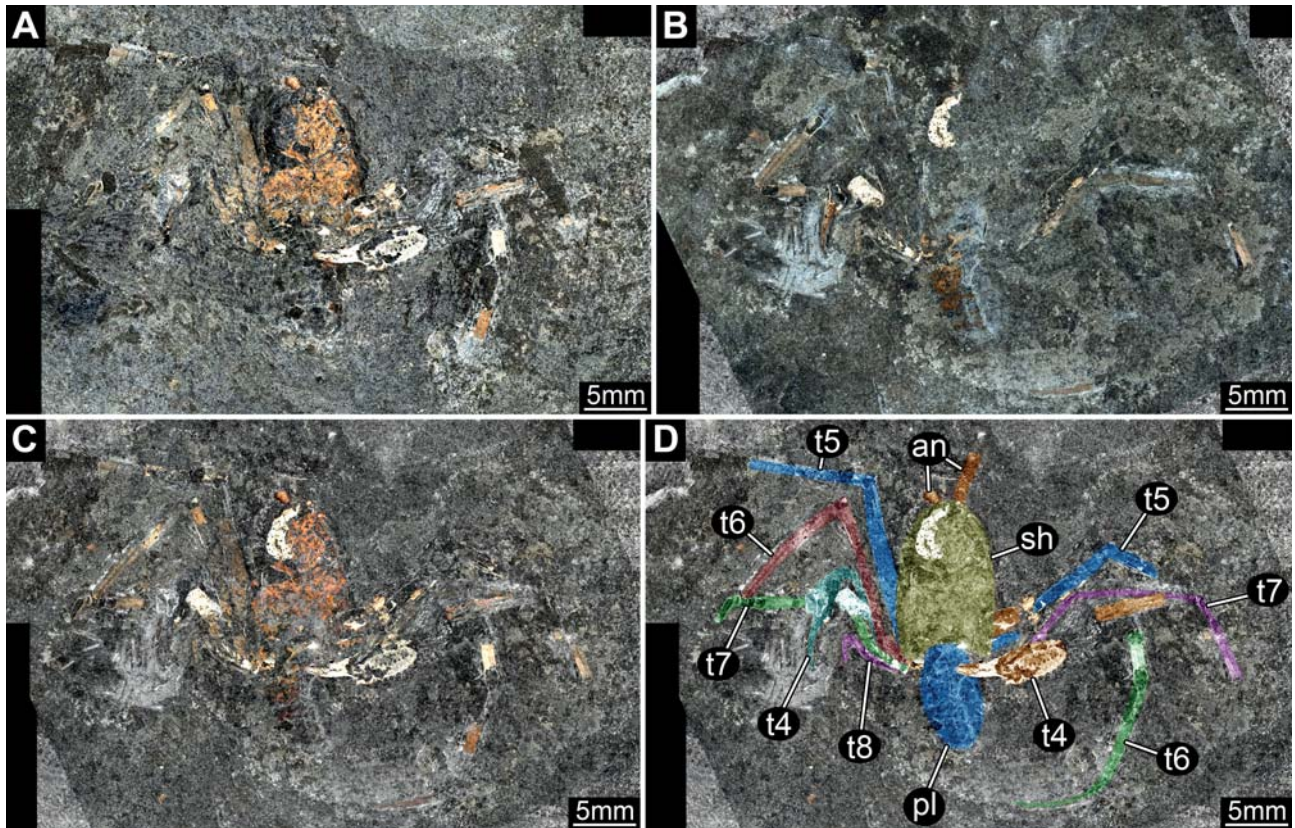


Fig. 1. Holotype and only known specimen of *Eoprosopon klugi*, BSPG 1986 I 19; composite images under cross-polarised light. **A.** Part. **B.** Counterpart. **C.** Maximum intensity projection of part and flipped counterpart. Note how the gaps become filled up, for example in the shield. **D.** Colour-marked version of C, highlighting two the two main tagmata and the distal parts of the appendages. Abbreviations: an = antenna; pl = pleon; sh = shield; t4–8 = thoracopod 4–8 (t4 = cheliped).

thanked for discussions about *Eoprosopon klugi* and *Eocarcinus praecursor*. The manuscript benefitted from comments of FRANCISCO VEGA, Mexico City and BARRY VAN BAKEL, Boxtel. All people involved in providing open source, open access or low-cost software programs, such as OpenOffice, CombineZM, Combine ZP, Microsoft Image Composite Editor, and Image Analyzer are heartily thanked for their continuing efforts.

2. Material and methods

2.1. Material

Only a single specimen of *Eoprosopon klugi* is known, the holotype. It is part of the collection of the Bayerische Staatssammlung für Paläontologie und Geologie München and is stored under repository number BSPG 1986 I 19. The specimen consists of part (Fig. 1A) and counterpart (Fig. 1B). No additional specimen has been found so far; the original locality, the Tongrube Marloffstein near Erlangen, southern Germany, appears to be no longer accessible.

2.2. Methods

Four different methods of documentation were applied in the present study:

1) **Composite imaging under cross-polarised light:** Part and counterpart were photographed with a Canon Rebel T3i equipped with a MP-E 65 mm macro lens (Fig. 1A, B). For an even illumination a Canon MT-24 Macro Twin Flash was used. Both parts of the flash were equipped with polarizer sheets. Another polarizer, oriented perpendicular to those of the flash, was placed in front of the camera lens. Cross-polarised light reduces reflections and enhances the colour contrast (HAUG C. et al 2011). It also facilitates to differentiate between colour and relief (HAUG C. et al. 2012; HAUG J. T. et al. 2012, 2013a). As the specimen is larger than the maximum size of the image detail it was documented with numerous, slightly overlapping images. For each image detail, a stack, i.e., several images in different focal planes (frames), was recorded and fused to an in-focus image with CombineZM or Combine ZP. These sharp images were stitched into a

large panorama showing the entire space of the specimen with the photomerge function of Adobe Photoshop CS3 or Microsoft Image Composite Editor. The resulting images for part and counterpart were manually aligned in Photoshop CS3, based on distinct landmarks. The two images were projected onto each other with FIJI, using Z-project maximum intensity (Fig. 1C).

2) **Composite autofluorescence imaging:** Part and counterpart were documented on a Keyence BZ-9000 fluorescence microscope (excitation wavelength 543 nm, green). Also here several stacks were recorded, fused and the resulting images were stitched to a large panorama image (Fig. 2A, B; HAUG J. T. et al. 2008, 2011; HAUG C. et al. 2009).

3) **Stereo imaging:** For documenting relief, stereo image pairs were recorded for the entire part and counterpart as well as for details of the part. For that purpose, also the Canon Rebel T3i was used; the MP-E 65 mm macro lens was used for details, an EF-S 18-55 mm lens for the overviews. Light was provided by a MeiKe LED ring light. Images from different angles were recorded and combined in Adobe Photoshop CS3. Of both half images, only the information of the desaturated red channel was used as

this channel yielded the highest contrast between fossil and matrix. Right half images were set to 46% transparency, and the red channel was deleted. The left half image was placed below; here the green and blue channel were deleted (Figs. 2C, D, 3A, 4A, D, F, G; HAUG C. et al. 2012; HAUG J. T. et al. 2012).

4) **Virtual surface reconstruction based on image stacks:** The same set-up as for detailed stereo images was used to record a stack of images with a very low depth of field (with an aperture of only 2.8). The stack was recorded with 20 micrometer steps of the propodus of the left cheliped of the counterpart. The resulting stack was processed in Image Analyzer (Fig. 4E; HAUG J. T. et al. 2012, 2013b; HAUG C. et al. 2013).

3. Results and discussion

3.1. Description of observed morphology and comparison to earlier observations

Our findings differ from earlier observations in important aspects. Instead of providing an entire description

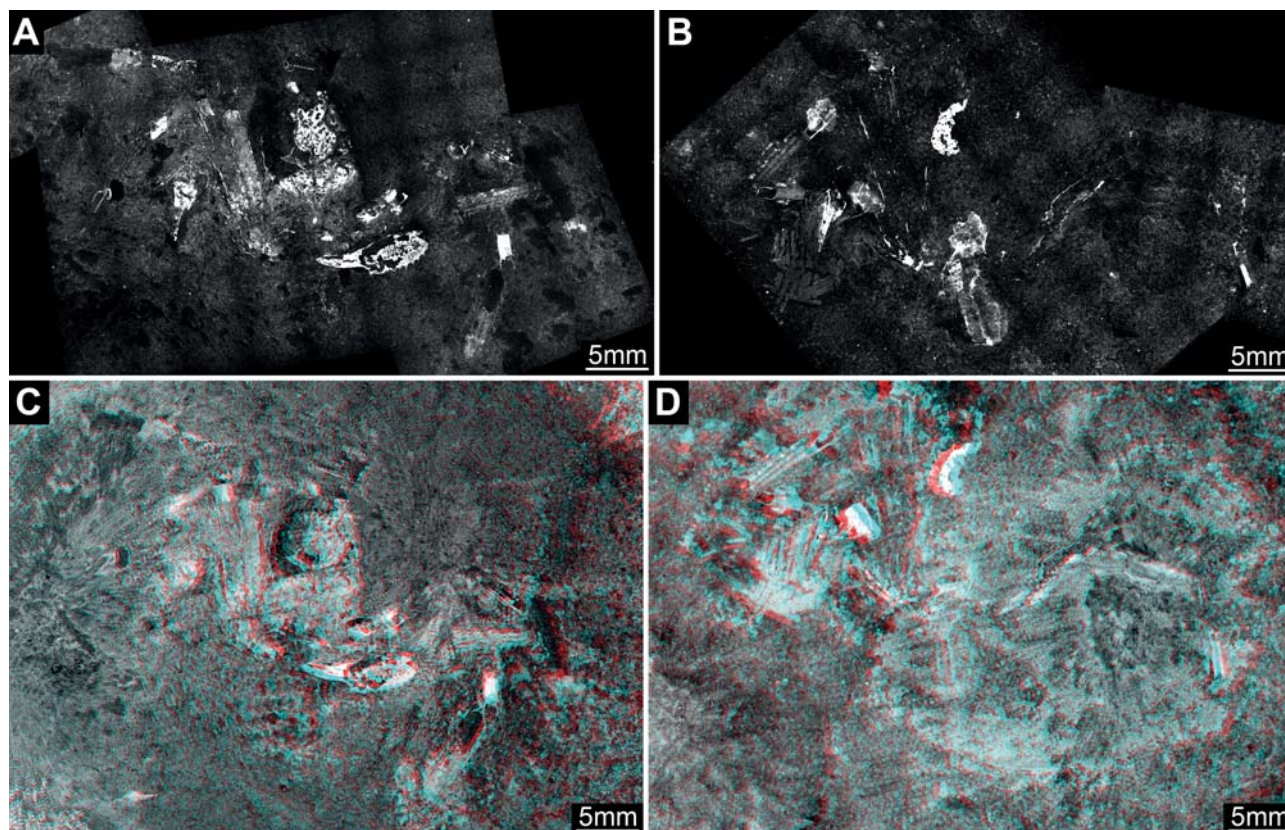


Fig. 2. Holotype and only known specimen of *Eoprosopon klugi*, BSPG 1986 I 19. **A, B.** Autofluorescence composite images. **A.** Part. **B.** Counterpart. **C, D.** Stereo-anaglyphs; please use red-cyan glasses to view. **C.** Part. **D.** Counterpart.

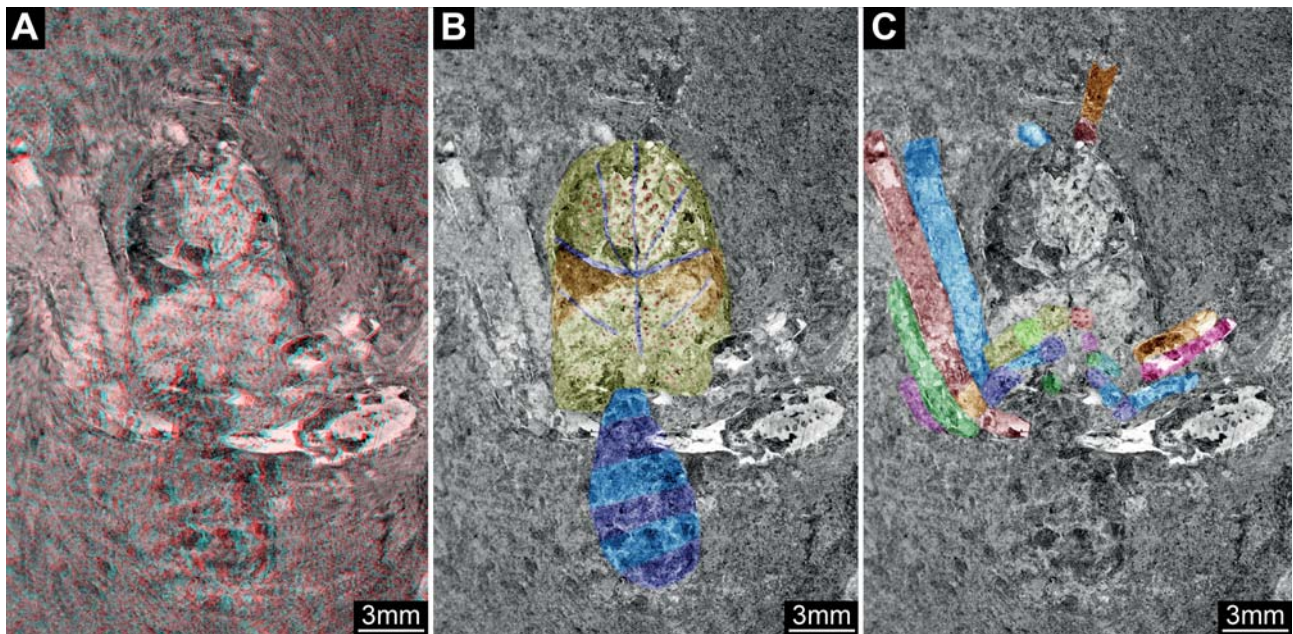


Fig. 3. Holotype and only known specimen of *Eoprosopon klugi*, BSPG 1986 I 19; close-up of the central body region. **A.** Stereo-anaglyph; please use red-cyan glasses to view. **B, C.** Colour-marked versions of A, highlighting details, which become apparent through their relief. **B.** Structures of the shield (yellow) and pleon (blue); note the elevated areas of the shield (darker yellow); grooves are marked in purple, tubercles in red; separate segments of the pleon coloured in different tones of blue. **C.** Structures of the appendages, especially the proximal ones (coxa and basipod); note how the coxae are arranged in a triangular way.

first and then providing a comparison to earlier observations, we will directly compare our observation of each structure with earlier observations and interpretations of it. As a general remark: the preservation is comparably coarse and less detailed than implied by FÖRSTER'S reconstruction (FÖRSTER 1986).

The "rostrum": FÖRSTER (1986) described a bilobed rostrum. Indeed, two bulbous structures can be identified anterior to the shield (carapace). Yet, as the stereo images indicate these are in fact set off from the shield (Figs. 2C, 3A). Furthermore the right one of these structures, clearly, is continuous with an elongate tube-shaped structure. Hence, this most likely represents an appendage, very probably the (second) antenna (Figs. 1D, 3C, 4A, 5A, B). The distal, tube-shaped part is very apparent, but appears to have been overlooked so far.

Shield: The grooves on the shield differ significantly from what FÖRSTER (1986) described (Figs. 2A, C, 3A, B, 5A). The preservation of the shield is not as good as FÖRSTER'S reconstruction indicates. A marked cervical groove matches the one reconstructed by FÖRSTER, as well as a pair of further posterior grooves parallel to it, the brachiocardiac grooves. Yet, it cannot be verified that their median endings curve backwards as shown by FÖRSTER. Additionally, a clear but thinner midline groove is apparent. Also a yet undescribed pair of similarly thin lines is

found which marks a narrower anterior, roughly triangular region. Two additional triangular regions, which are slightly elevated, are marked by the cervical groove anteriorly and by thinner lines posteriorly, the latter crossing the two grooves parallel to the cervical groove. Also not shown in FÖRSTER'S original reconstruction is a very rough tuberculation on the shield.

Differences of FÖRSTER'S observations most likely result from the different forms of illumination. Low-angle side light, which appears to have been applied in former studies, can produce severe artefacts (see also further below). The thinner grooves may well have been obscured by shadows of the tubercles. Additionally, as pointed out below, some ventral structures have become compressed through the shield, further complicating the recognition of dorsal features.

Distal parts of cheliped: The right chela has been interpreted to be preserved with dactylus and the fixed finger of the propodus. Yet, this appears to be an artefact of the low-angle illumination. Relief as well as colour contrast clearly show that the preserved structure is only the fixed finger of the propodus. Its surface is broken and partly collapsed and thus gives the impression of two parts (Fig. 4B–D).

Also the left chela is important in this aspect (Fig. 4E). Here the main part of the fixed finger of the propodus is

preserved on the counterpart. It shows the relatively blunt teeth on the inside of the finger (Fig. 5C), hence provides a clear orientation. It is curved; the same curvature can be observed on the right chela, supporting that this represents only the fixed finger.

Both cheliped appear to be oriented backwards (Figs. 1D, 2A, C); this is most likely an artificial position caused by the embedding; The chelipeds were originally oriented forward in life position, as seen in all other representatives of Reptantia. The entire cheliped appears to be in the same level as the body, otherwise it would be hidden deep in the matrix. In astacids or homarids the axis of movability of the movable finger of the chelae are in the same axis as the entire appendage (in both groups the finger is medi-

ally). In *E. klugi* the axis of movability of the movable finger appears to be perpendicular to the axis of the entire appendage. Reconstructing the entire cheliped as anteriorly directed, the movable finger appears to be positioned anteriorly (which might be also addressed to as “dorsally”; Fig. 5A, B). This interpretation fits well with interpreting *E. klugi* as an early brachyuran as we also see such an orientation of the joint axis of the dactylus of the cheliped in this group.

Distal parts of walking limbs: FÖRSTER (1986) interpreted the distal parts of the walking limbs as equipped with strong serrations. This is a clear artifact, demonstrating the shortcomings of low-angle illumination.

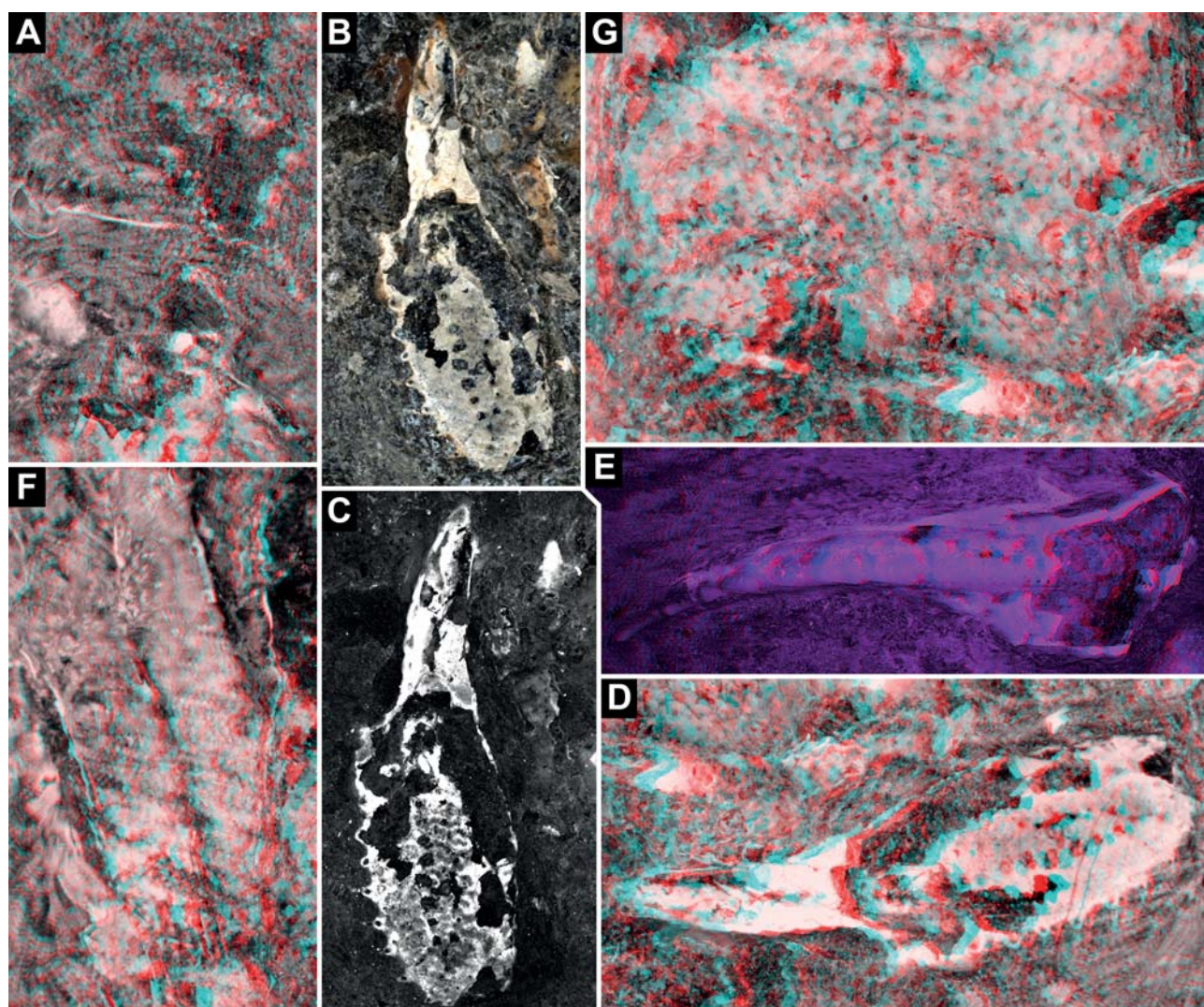


Fig. 4. Holotype and only known specimen of *Eoprosopon klugi*, BSPG 1986 I 19. Close-ups of different appendage parts, not to scale. **A.** Antennae. **B–E.** Propodi of chelae. **F.** Walking appendages; note how irregular the “side-walls” are broken. **G.** Proximal elements of walking appendages and sternal region, compressed through the shield. A and D–G are stereo-anaglyphs; please use red-cyan glasses to view; B cross-polarised light; C fluorescence light; E virtual surface reconstruction.

Shadows alone are no reliable cue of the exact three-dimensional shape of a structure (e.g., MAMASSIAN et al. 1998; HOWARD 2002). Here the margins of the appendages are broken in an irregular pattern, as can be seen in the stereo images (Figs. 3A, 4F). These structures can produce shadows which appear jagged and must have led FÖRSTER to interpret the appendages as serrated. The limbs

could have had an armature originally, yet the preservation is not good enough to resolve such details.

Proximal parts of thoracopods: These have not been observed before, but are compressed through the shield and can only be observed in the stereo images (Fig. 4G). The proximal parts consist of coxa, basipod, and the first endopod element (ischium). The

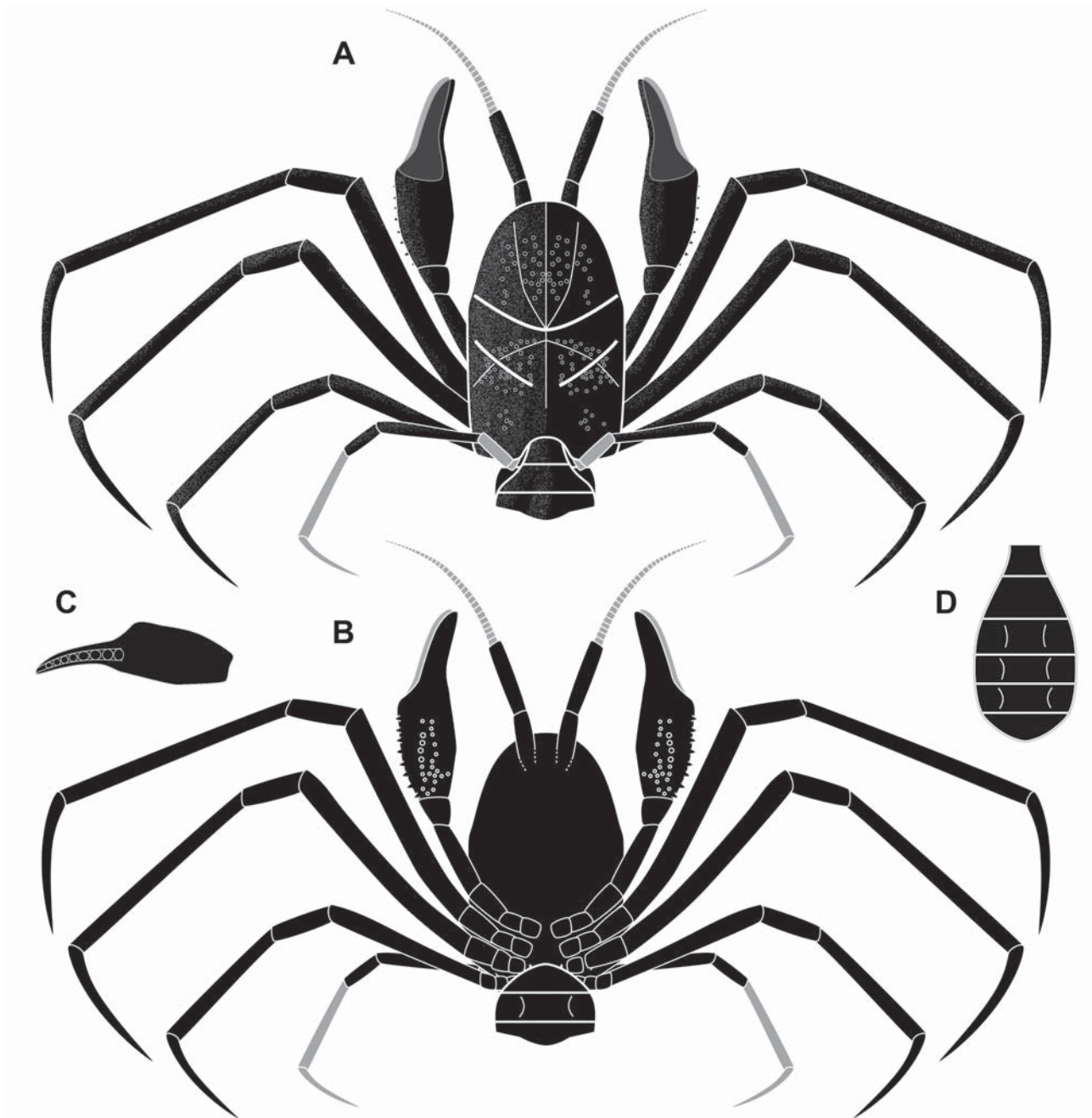


Fig. 5. Schematic restoration of *Eoprosopon klugi*. **A.** Dorsal view. **B.** Ventral view; parts of appendages which are unknown are either drawn stippled or in grey; dactyli drawn transparent to show the shape of the propodi. **C.** Occlusal view onto propodus, showing dentition. **D.** Dorsal view onto outstretched pleon.

coxae of the thoracopods four to seven (pereopods 1–4) are arranged in a triangle, indicating a likewise triangular sternum (Fig. 3C).

The corresponding three proximal elements of the last pair of thoracopod cannot be directly observed. Based on the available space and the tight arrangement of the more distal parts, it seems most likely that the insertion areas of the last pair of thoracopods were shifted dorsally as in early crabs such as homolodromiids (e.g., FÖRSTER 1985a).

Pleon: Especially the anterior part of the pleon is difficult to observe as this area is also crowded by parts of the appendages. Yet, also here the stereo images help to resolve the issue (Figs. 2C, 3A). The anterior pleomeres are significantly narrower than supposed before (Figs. 3B, 5D). This is well in concordance with an affinity with early brachyurans. It also strengthens the interpretation of the dorsally shifted position of the last pair of thoracopods (see above), as this would leave enough space for such an arrangement.

FÖRSTER described well-developed tergopleurae, which can be well seen in the photographs of the cast (FÖRSTER 1986, fig. 2; SCHWEITZER & FELDMANN 2010, fig. 1). Yet, again low-angle side light provides a misleading impression. Indeed, the pleomeres 3 to 5 show three rounded elevations, which clearly represent the axial region and the tergopleurae (Figs. 3A, 5D). However, the latter are not as distinctly set off as the shadows of the cast indicate.

FÖRSTER (1986) interpreted the outstretched position of the pleon as the original posture. This is unlikely to be the case. FÖRSTER appears to have assumed that Brachyura was evolutionary derived from a macruran ancestor (FÖRSTER 1985a, 1986). Yet, it has become quite clear in the last decades that Brachyura is the sister group to Anomala (“Anomura” of many authors), both being part of Meiura (e.g., SCHOLTZ & RICHTER 1995; DIXON et al. 2003; SCHRAM & DIXON 2004).

Within Anomala fully carcinised forms have generally been thought to evolve from lobster-like forms. Yet, new studies of character evolution indicate that some of these supposedly lobster-like forms are already partly “carcinised”, having certain adaptations for carrying the pleon partly curled (e.g., KEILER et al. 2013). It seems therefore plausible that the meiuran stem-species (more or less equivalent to ancestor) was already partly carcinised. This could also be supported by an outgroup comparison. A possible sister group of Meiura is Achelata (although this is currently only one of several available hypotheses). Within Achelata, scyllarids (slipper lobsters) as well as certain early palinurids (spiny lobsters, *Palinurina*) also held their pleon usually curled (see, e.g., discussion in SCHOLTZ 2014). Hence, to speculate, already the stem species of Achelata+Meiura might have possessed a curled pleon. Thus, based on phylogenetic consideration it seems unlikely that an early crab such as *E. klugi* had a straight pleon.

Also from a functional point of view an original straight posture of the pleon of *E. klugi* is not a plausible interpretation. The narrow anterior pleomeres make an effective tail-flip escape response very unlikely. This narrowing is most likely an adaptation to the dorsal shift of the last thoracopods, assuming that the pleon was held in a flexed position.

To conclude, a straight outstretched pleon in the single specimen of *E. klugi* is most likely a preservational artifact. In our reconstruction the pleon is therefore shown as curled, but not as fully flipped under as there are no indications for such a highly specialized posture (Fig. 5A, B).

3.2. *Eoprosopon klugi* – an early brachyuran?

FÖRSTER (1986) founded his assignment of *E. klugi* to Brachyura mainly on aspects of the shield, which we can only partly support. But, now we have additional characters of the ventral side and of the appendages. The broad triangular thoracic sternum is well compatible with a brachyuran affinity, yet also Anomala and Achelata possess such morphology. Two characters clearly argue for a brachyuran affinity: 1) the orientation of the movable finger of the cheliped, which is “dorsally” (anteriorly) shifted as in Brachyura; 2) the narrow anterior pleomeres, and the likely dorsally shifted insertions of the posterior thoracopods. These characters are considered to be crucial in “primitive” or “podotrematan” crabs (see discussions, e.g., in FELDMANN & SCHWEITZER 2010; SCHOLTZ 2014). In summary our findings support the interpretation of *E. klugi* as an early brachyuran. In fact, we can show (or at least make a plausible case) that *E. klugi* already possessed more brachyuran-type characters than previously anticipated.

So the question arises: are there more plesiomorphic characters in *E. klugi* than in modern “podotrematan” crabs? The very strong proximal part of the antenna is unknown among modern crabs and most likely represents a plesiomorphy. The quite cylindrical and elongate shield is also found among other early brachyurans, namely prosopids (e.g., FÖRSTER 1986; MÜLLER et al. 2000). Also other plesiomorphic characters further derived in eubrachyurans, such as the not fully flipped pleon, tergopleurae and others are also found among other early crabs (e.g., SCHOLTZ 2014). Other aspects can simply not be judged. Whether the hypostome (commonly called epistome) is fused to the shield or if orbits (which has been put forward as an important brachyuran character according to FELDMANN & SCHWEITZER 2010) are present or absent cannot be evaluated due to limitations of the preservation.

Significant may be the new details of the shield ornamentation. The presence of an anterior midline groove and a rough tuberculation has been observed, e.g., in erymid lobsters (BARRY VAN BAKEL pers. com. 2014) and hence may represent a plesiomorphy retained from lobster-like

forms. Yet, this character needs to be precisely compared to other meirurans and early achelatan in a future study before we can make a clear statement about this.

3.3. *Eoprosopon klugi* and *Eocarcinus praecursor*

After our re-investigation of the oldest known crab, we also need to comment on the slightly older, but now considered as a non-crab, *Eocarcinus praecursor*. A clear re-evaluation of *Eoc. praecursor* demands for a re-investigation of the original material, yet some new details of *E. klugi* also have bearings on our understanding of *Eoc. praecursor*.

First, it is important to note that the argumentation for the exclusion of *Eoc. praecursor* has certain shortcomings. The main argument for excluding it from Brachyura is that it does not possess all characters of Brachyura (FELDMANN & SCHWEITZER 2010), an observation which seems to be true. Yet, in a next step *Eoc. praecursor* is transferred to Anomala (originally Anomura; FELDMANN & SCHWEITZER 2010). This is a mere classificatory conclusion, but does not reflect phylogeny or evolution. If indeed *Eoc. praecursor* possesses some, but not all brachyuran characters, the best conclusion should be that it is the sister species of all (other) brachyurans. This possibility is even mentioned by FELDMANN & SCHWEITZER (2010), but is then apparently discarded. The authors also argue that the “definition of a brachyuran” would need to be changed to accommodate *Eoc. praecursor* within Brachyura. Again, this is a mere classificatory problem. Natural entities (independent whether these represent individuals or natural kinds) such as species and monophyletic groups do not care about definitions, they can only be characterised. If Brachyura is characterised by a certain set of characters, this set may be broken down into several steps by fossils. This has been done for numerous groups such as arthropods (MAAS et al. 2004), crustaceans (WALOSZEK 2003a, b; HAUG J. T. et al. 2010a, b), stomatopod crustaceans (HAUG J. T. et al. 2010c), or mantodean insects (GRIMALDI 2003). Hence, it would be a simple possibility to establish the name Brachyura sensu lato for a larger monophyletic group including *Eoc. praecursor* and all other brachyurans; the latter could then be termed Brachyura sensu stricto. As a short note: to avoid the problem of “splitting” character sets of distinct groups, a monophyletic group should be characterised by a single, well formulated autapomorphy, as proposed, e.g., by BÉTHOUX (2007) or BÉTHOUX et al. (2012).

The affinity of *E. klugi* to Brachyura has not been questioned so far. Yet, many aspects of the morphology remain unknown, e.g., fusion of hypostome and presence or absence of orbits. These two characters have been discussed for *Eoc. praecursor* by FELDMANN & SCHWEITZER (2010) and used as arguments for excluding the species. Hence, the unclear status in *E. klugi* at least should have

demand a comment. The overall habitus of *Eoc. praecursor* and *E. klugi* is very similar including the narrow anterior pleomeres and the strong antenna, although many aspects of the morphology of *E. klugi* remain unclear due to preservation. Hence, the exclusion of *Eocarcinus praecursor* from Brachyura is not easy to accept when comparing it to *E. klugi*.

Eocarcinus praecursor seems to retain more plesiomorphic traits than *E. klugi*. For example, the pleon has more pronounced tergopleurae (FÖRSTER 1986; FELDMANN & SCHWEITZER 2010). One interesting aspect of similarity between *Eoc. praecursor* and *E. klugi* is the quite strong antenna. With these character combinations, it is likely that FÖRSTER’S (1986) interpretation is correct that *E. klugi* is closer related to the remaining brachyurans than *Eoc. praecursor*.

A clearer statement about the exact relationships of early brachyurans and character evolution in the brachyuran lineage must await a re-investigation of certain key fossils. Among these are *Eoc. praecursor* and other crucial well-preserved forms, such as FÖRSTER’S prosopid species a and b (FÖRSTER 1985b). Our re-investigation of *E. klugi* is hence an important additional piece added to the complex jigsaw of brachyuran evolution.

4. Conclusions

Eoprosopon klugi represents an early brachyuran already possessing: a) an anterior rotation of the joint axis of the dactylus of the cheliped, b) narrow anterior pleomeres, and possibly c) dorsally shifted last thoracopods. On the other hand, *E. klugi* retains some plesiomorphic traits such as the quite strong antenna. *E. klugi* shows many similarities with *Eocarcinus praecursor*, supporting the affinities of *Eoc. praecursor* to Brachyura. Low-angle side light can produce severe optical artefacts; alternative methods for documenting relief should be applied.

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