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# A new thylacocephalan crustacean from the Upper Jurassic lithographic limestones of southern Germany and the diversity of Thylacocephala

FLORIAN BRAIG, JOACHIM T. HAUG, MARIO SCHÄDEL & CAROLIN HAUG

## Abstract

Thylacocephala is a group of extinct eucrustaceans of presumably predatory nature. We describe here a new genus and species of thylacocephalan crustaceans from the Upper Jurassic Solnhofen limestones of Eichstätt (Altmühltal Formation), *Falcatacarid bastelbergi* n. g. n. sp. (about 150 million years old). *Falcatacarid bastelbergi* n. g. n. sp. is the fourth species of Thylacocephala found in these deposits. The species differs significantly from other thylacocephalans, especially by characters of the shield. The shield of the specimen is rather low (short in dorsoventral extent) and it bears a long rostrum but no elongated posterior spine. For comparative purposes, we provide an overview of the shield morphology of known thylacocephalan species from literature as well as a morphological analysis of the group. An elliptic Fourier analysis is used to compare the different shield shapes of thylacocephalans to each other; results are presented in PCA plots. Shield length and anterior or posterior shield extensions are the characters with the most variation in thylacocephalan shield morphology.

**Key words:** Eucrustacea, *Falcatacarid bastelbergi* n. g. n. sp., Jurassic, palaeobiology, elliptic Fourier analysis, morphospace.

## 1. Introduction

### 1.1. What is a thylacocephalan?

Thylacocephala is an extinct monophyletic group of arthropodans, representatives of which occurred from at least the Silurian to the Cretaceous (SCOURFIELD 1937; HAUG et al. 2014; CHARBONNIER et al. 2017). From early on, fossils now understood as thylacocephalans have been interpreted as crustaceans (summarised e.g. by LANGE et al. 2001) closer related to the one or other ingroup of Eucrustacea, but their phylogenetic affinity remained enigmatic for a long time. Only rather recently, exceptionally preserved fossils revealed details of the feeding apparatus that finally provided clear characters for supporting an ingroup position of Thylacocephala within Eucrustacea (HAUG et al. 2014).

Thylacocephalans can be recognised as such by few, but distinct features of their body. Not surprisingly for a eucrustacean, the body is organized in a series of segments (PINNA et al. 1985). The head dorsally forms a prominent large bivalved shield enveloping the body with a long ventral gap, leaving space for a number of protruding appendages. Most species are known exclusively by their shield, which is apparently the structure with the highest preservation potential.

The shield usually has an anterior indentation or notch, often termed ‘optical notch’ as in better preserved specimens a pair of prominent compound eyes is apparent in this region. The assumed plesiomorphic condition for

these compound eyes is stalked and moderately large, as demonstrated by the early representatives from the Silurian (HAUG et al. 2014). Later in the evolution, the eyes have become extremely prominent, dominating the anterior body region in many species. Whether these super-sized eyes are still stalked remains unknown so far.

Many species, known from better preserved fossils, have three pairs of often very long, presumably raptorial appendages. These three pairs of appendages possibly represent maxillulae, maxillae and the first pair of maxillipeds (appendages of the two posterior head segments and first trunk segment) as indicated by some well-preserved fossils from the Jurassic and the Silurian (ROLFE 1985; HAUG et al. 2014). Further posterior, along the segmented trunk on the ventral side, thylacocephalans possess a series of paddle-like smaller appendages that were probably used for swimming (e.g., SCHRAM et al. 1999). While many species are known to bear eight pairs of such appendages, there are several species with higher numbers of appendages as well (HAUG et al. 2014).

Overall, the trunk segments are rather short in anterior-posterior axis, but large in dorsal-ventral axis, which makes the body look rather short and stout, while the overall number of segments can be quite large. The exact organisation of the body, however, is not yet known for many species. Especially the inner morphology of the thylacocephalan crustaceans is far from being well understood, though recently VANNIER et al. (2016) provided details on this. For example, the presence of a set of gills, presumably eight pairs, is well known for several species

(SÉCRÉTAN & RIOU 1983; SÉCRÉTAN 1985). Their exact segmental correlation, however, is still not well understood.

### 1.2. A phylogenetic framework for Thylacocephala

Despite the more or less distinct set of features (depending on the quality of preservation) characterising Thylacocephala, the group has only been recognised as such at the end of the last century. Interestingly, the group was recognised three times independently at around the same time, by three different teams of researchers, but on different sets of representatives (ARDUINI et al. 1980; PINNA et al. 1982; BRIGGS & ROLFE 1983; SÉCRÉTAN & RIOU 1983). This was only to realize shortly afterwards, that all these arthropod fossils belong to a single monophyletic group.

An ingroup position within Eucruseacea has always been supposed; yet, a thorough reasoning was often missing. For example, it has been suggested that supposed antennulae and antennae, found in some Cretaceous specimens, indicate such a position (LANGE et al. 2001). Yet, these characters are neither characterising Eucruseacea (e.g., HAUG et al. 2013a) nor are the structures that were described as such in the fossils indeed antennulae and antennae (CHARBONNIER et al. 2017).

When first encountered, thylacocephalans had been interpreted as larvae of mantis shrimps (Stomatopoda; FRAAS 1878; HILGENDORF 1885; DAMES 1886). Later, they were interpreted as representatives of Decapoda (SÉCRÉTAN 1985) and Cirripedia (ARDUINI et al. 1980). SCHRAM (1990) also pointed out similarities to remipedians. Details of their feeding apparatuses indeed support a closer relationship between Remipedia and Thylacocephala and represent a potential synapomorphy of the two groups (HAUG et al. 2014). The overall morphological difference between Remipedia and Thylacocephala, a point raised by VANNIER et al. (2016) against this interpretation, does not exclude a closer relationship between the two groups in a phylogenetic framework; phylogenetic relationships are not evaluated based on differences but on shared derived characters (synapomorphies).

### 1.3. Fossil record of Thylacocephala

Thylacocephalan fossils have been found all around the world, with the exception of Antarctica and South America (HEGNA et al. 2014). The oldest definite fossils occur in the Llandovery (Silurian, about 435 million years ago; SCOURFIELD 1937; MIKULIC et al. 1985a, b). A supposedly older representative was reported by VANNIER et al. (2006), but remains questionable. The youngest fossils are known from the Late Cretaceous (84 million years ago; SCHRAM et al. 1999). The Silurian specimens are espe-

cially informative as they retain numerous plesiomorphic traits. Other well-preserved forms are known from the Devonian (STIGALL & HENDRICKS 2007), Carboniferous (SCHRAM 1990), Triassic (EHIRO et al. 2015; BRAYARD et al. 2017), Jurassic (POLZ 2001; HAUG et al. 2014), and Cretaceous (CHARBONNIER et al. 2017). Additionally, especially fossils from the Jurassic show a comparatively high degree of morphological details. In general, fossils from the lithographic limestones of southern Germany have the potential to provide even finest morphological details down to the setation of the feeding apparatus (e.g., HAUG et al. 2014).

So far, three species of Thylacocephala have been described from the Altmühltal Formation (“Solnhofen lithographic limestones”), partly with well-preserved appendages, offering new details on the structure of appendages in Thylacocephala. The first known species was *Clausocaris lithographica* OPPENHEIM, 1888 (originally assumed to be a representative of *Clausia*). This thylacocephalan has long appendages and extremely large eyes. The second one, *Mayrocaris bucculata* POLZ, 1994 has smaller appendages and its shield has a straighter outline, while that of *C. lithographica* is very round. As a third form, *Dollocaris michelorum* POLZ, 2001 is closer to *M. bucculata*, yet has a shield shape that resembles a species from the Middle Jurassic of France (*Dollocaris ingens*; see CHARBONNIER et al. 2009). Moreover, it is significantly smaller.

Here, we report a fourth species of Thylacocephala from the Solnhofen lithographic limestones. We furthermore provide an overview of the diversity of shield shapes within Thylacocephala and elaborate why the new species is special in this aspect.

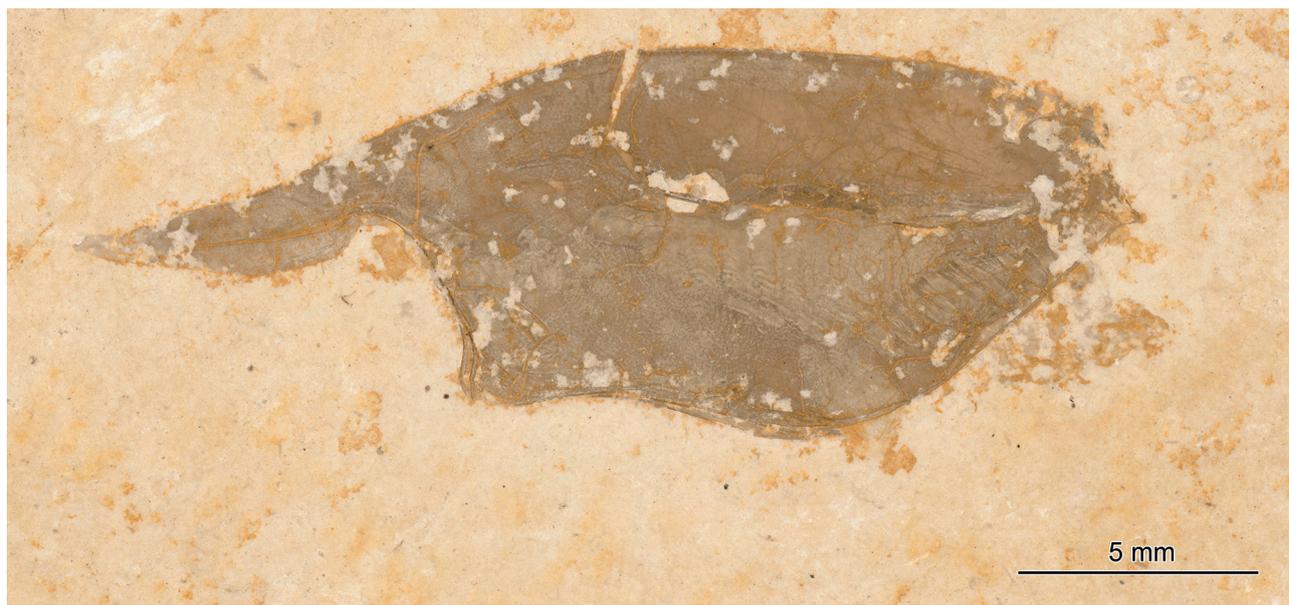
## 2. Material and methods

### 2.1. Material

A single specimen is in the focus of this study. The specimen is preserved in a limestone slab, a counterpart is not available. The specimen originates from the private collection of Dr. THOMAS BASTELBERGER. It will be deposited in the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS) under repository number 70487.

### 2.2. Geological setting

The specimen described in this study comes from a field site in the vicinity of Eichstätt (Bavaria, Germany). The sediment that contains the fossil is a micritic limestone with fine lamination. This type of sediment is often referred to as lithographic limestone or Plattenkalk. In this case, the sediment is part of the Eichstätt Member of



**Fig. 1:** Overview of *Falcatacaris bastelbergeri* n. g. n. sp., preserved on a limestone slab in lateral view, under white ring light and without HDR.

the Altmühltal Formation, which, as a lithostratigraphic unit, covers a complex of well-known fossil sites including the famous Solnhofen site. The Altmühltal Formation is Early Tithonian (Late Jurassic) in age and corresponds to a numeric age of ca. 150 million years (SCHWEIGERT 2007).

Among the species found in the Altmühltal-Formation are the famous *Archaeopteryx lithographica* v. MEYER, 1861 and *Compsognathus longipes* WAGNER, 1859, but also pterosaurs, fishes, molluscs, echinoderms, shrimps, other arthropods and insects, and rare terrestrial plants occur (WELLNHOFER 2008; ARRATIA et al. 2015).

The palaeoenvironment for the Solnhofen-type Lagerstätte was interpreted as a restricted lagoon with elevations and basins (VIOHL 2015). Due to the lack of water transfer between the lagoon and the sea, salinity levels at ground levels could increase, leading to hostile conditions on the seafloor (BARTHEL et al. 1990). The high salinity in the benthic environment is thought to have caused a lack of epi- and infaunal organisms, which resulted in a reduction, or even a complete absence of bioturbation. Bioturbation is a major force that prevents the fossilisation of delicate organisms such as articulated remains of arthropods.

### 2.3. Documentation methods

In order to extract all possible information from the fossil, different documentation methods were used. The fossil was first documented with a Keyence BZ-9000 inverse epifluorescence microscope using UV and blue light (with

DAPI and GFP filters) with lens magnification levels of 2x, 4x, and 10x (resulting in 20x, 40x and 100x magnification; following HAUG et al. 2008, 2011). This imaging technique is extremely useful because the auto-fluorescence properties of the fossil enables the detection of structures hidden under fine layers of sediment, which would otherwise not be accessible. To overcome limitations in depth of field, stacks of images with changing focus levels were recorded. For overcoming limitations in field of view, several adjacent image details were recorded, each with a stack of images. Areas that were too weak in signal, resulting in too dark images, were recorded again under longer exposure time (HAUG et al. 2013b).

White light images were recorded on a Keyence VHX-6000 digital microscope with a 20–2000x lens. Two illumination methods were used: Cross-polarized coaxial light and ring light, both with a magnification of 100x, 200x and 500x. The built-in high-dynamic-range (HDR) function was used in some cases to cope with differences in the brightness of the object. Furthermore, red-cyan stereo anaglyphs were created based on rendered images of a 3D-model that was generated by a depth-from-defocus algorithm (virtual surface reconstruction; e.g. HAUG et al. 2013c, d) implemented in the digital microscope.

### 2.4. Image processing

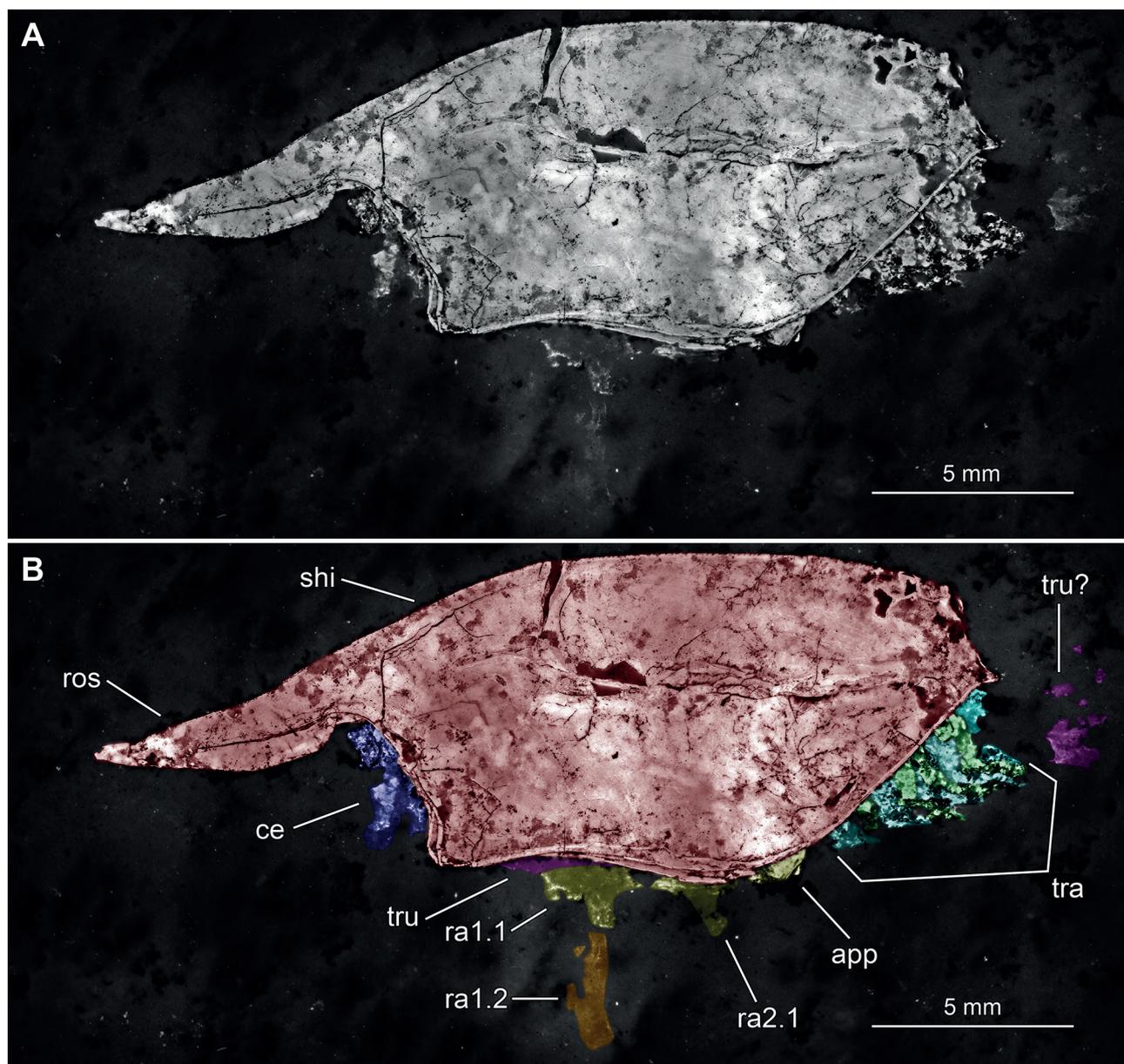
The resulting data from the fluorescence documentation process (z-stacks of images) was further processed

with CombineZP (ALAN HADLEY, GNU). Here, in-focus regions of each image stack were combined to a single (in-focus) image (focus-stacking). These resulting sharp images were then stitched to a large panorama image using Photoshop CS3, in order to get a sharp image of the entire specimen (see, e.g., HAUG et al. 2008).

Data acquired with the Keyence VHX-6000 digital microscope were processed automatically with the implemented software of the digital microscope.

All of the resulting images were adjusted for brightness, contrast, and colour using Adobe Photoshop CS6. Additionally, important areas were colour-marked, using Photoshop CS6, to make the images easier to understand for the reader.

In order to generate 3D images of the specimen, stereo-images were created, using Photoshop CS6 to create the impression of three-dimensionality. For this, two white light images, taken with slightly different angles



**Fig. 2:** Fluorescence image of *Falcatacarid bastelbergi* n. g. n. sp. **A** – Overview. **B** – Colour-coded version of **A**, with the features of the outer body morphology marked in different colours. Abbreviations: **app**: appendage element without exact identification, **ce**: compound eye, **ra**: element of anterior prominent appendage, **ros**: rostrum, **tra**: trunk appendages, **tru**: remains of the trunk, **tru?**: possible remains of the trunk without exact interpretation, **shi**: shield.

were used. From one the red colour channel was deleted, from the other the blue and green colour channels were deleted. The opacity of the top layer was set to 50% and the images were combined.

### 2.5. Morphometrical analysis

Additionally to the morphological analysis, a statistical comparative analysis of the morphology of the specimen was conducted in comparison to other thylacocephalans. The shields of 40 thylacocephalans were drawn in lateral projection using Adobe Illustrator CS2. The shields were redrawn based on figures from published literature on thylacocephalans. Using the software SHAPE (© National Agricultural Research Organization of Japan), an elliptic Fourier analysis was performed. The outlines of the (reconstructed) shield drawings were transformed into a vectorised object (chain code). This requires a vector-based stepwise approximation of an ellipse to the outline of the shield. The vectorised shapes (chain codes) are represented by numeric values, which are then transformed into normalised elliptic Fourier descriptors (EFDs). This technique represents a variation of the well-known Fourier transformation, practically applied on shapes of natural objects rather than (other) mathematical functions. The 40 EFDs were finally analysed with a principal component analysis (PCA). The entire procedure including the PCA was applied following IWATA and UKAI (2002). The results of the PCA were visualized using the R-statistics environment 3.4.3, utilizing the interface R-studio. Packages used were readxl and ggplot2.

## 3. Results

### 3.1. Overall description of the slab

The specimen is located on a small flat slab with cuticle remains and some traces interpreted as former soft tissue (Fig. 1). Preserved is the more or less intact body of a thylacocephalan in left lateral view (Figs. 2, 3). Accessible is mostly the shield that envelops most of the rest of the body, as well as remains of the prominent anterior appendages and the trunk appendages. Remains of large compound eyes are evident as well. Structures of inner organs are visible by difference in colour and additionally by the 3D relief of the slab (Fig. 4). The tip of the rostrum appears to be broken off; its visible parts measure a total of 5.85 mm in length. In total, the specimen measures 22.22 mm in length (anterior-posterior axis) and 7.9 mm in height (dorsal-ventral axis).

### 3.2. Description of the specimen

Body segmented and organized into functional units, exact organization, however, difficult to distinguish. Anterior body region apparently forms dorsally a shield.

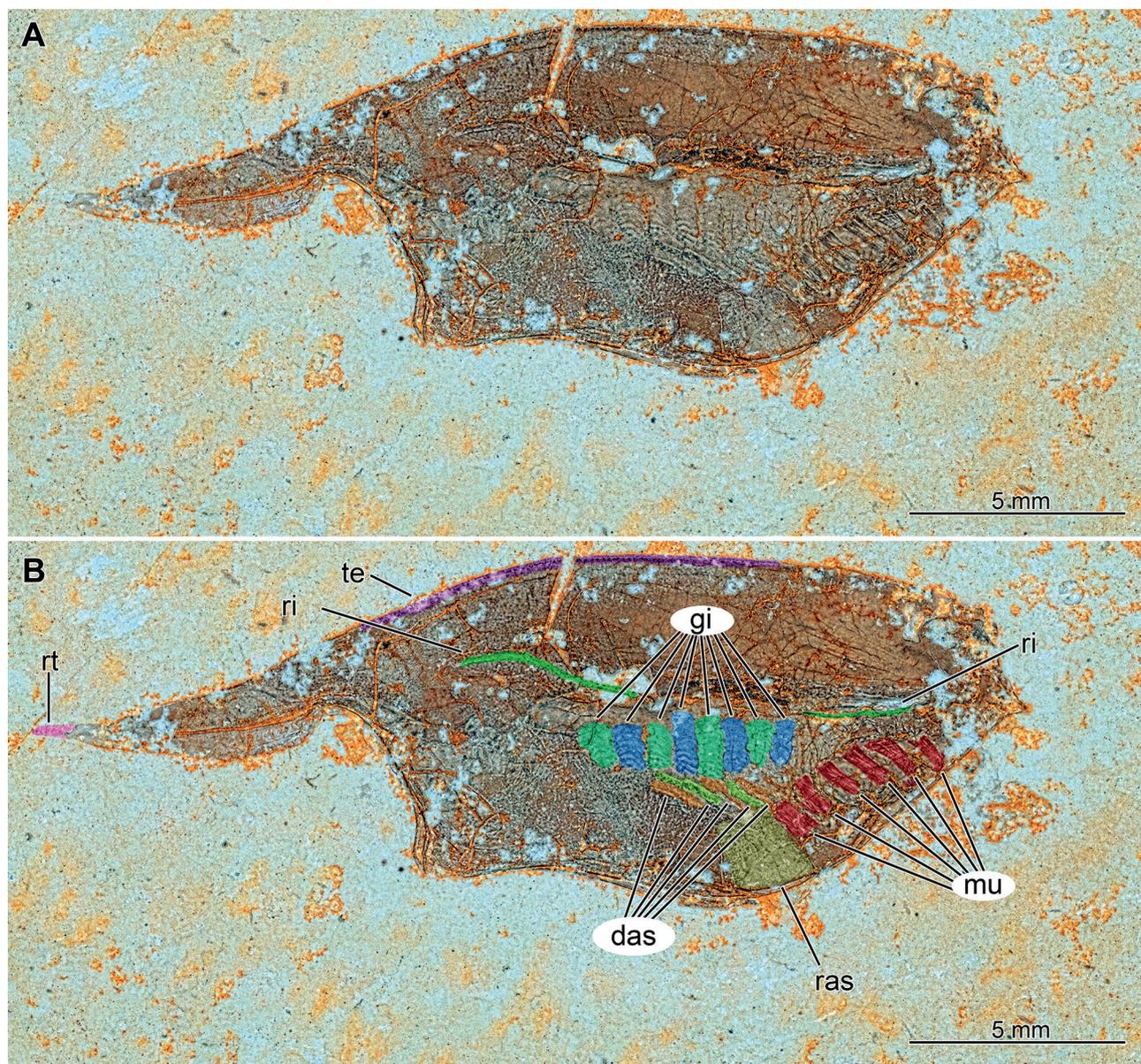
The shield is large, bivalved and envelops almost the entire body. Anteriorly drawn out into a distinct rostrum, posteriorly into a dorsal spine; shield leaving a long ventral gap, reaching from underneath the rostrum anteriorly to the posterior dorsal spine posteriorly (Fig. 2). The dorsal midline of the shield appears slightly convex. Along this dorsal edge, there are small teeth-like structures recognizable. From the rostrum, the shield outline runs ventrally with a slight posterior inclination. Shortly before the anterior outline of the shield merges with the ventral outline it reverses this inclination to form a small bulging corner that faces anteriorly. Further posteriorly the ventral outline forms a shallow concavity that stretches as far as the middle of the body length, representing a ventral notch. From the end of the concavity, the ventral outline runs further posteriorly and dorsally (here with a stronger inclination than anteriorly).

At its posteriormost end and on the same level as the rostrum, the shield forms a small spine that reaches out posteriorly. From there, the outline runs almost straight upwards to meet the dorsal outline, only with a small concavity, forming the posterior notch. Additionally, in the anterior part of the shield and at the same height as the rostrum, a ridge is present in the middle of the shield (Fig. 3). For a short distance, it runs parallel to the dorsal shield outline, than it turns posterior-ventrally for roughly the same distance before turning straight posteriorly again and running directly into the posterior spine. The pointed rostrum roughly resembles the shape of a kitchen knife in that its dorsal outline is rather straight while its ventral outline is convex and starts with a short, straight ventrally orientated section. It is roughly 2.5 times as long as high (Fig. 2).

Remains, interpreted as those of the compound eyes, reach anteriorly from the shield from underneath the rostrum (Fig. 2). The remains of the eyes appear rectangular in outline, about three times as long as wide, with the more distal side of the rectangle being slightly concave.

Ventrally of the shield, there are remains of at least two (or possibly three) prominent anterior appendages, which are not fully accessible (Fig. 2). The two more anterior ones protrude ventrally between the valves at the ventral notch of the shield. The third one protrudes a little further posterior to the ventral notch at the ventral bump of the shield. This third remaining appendage could also represent a further posterior trunk appendage. Its correlation is rather unclear due to the poor preservation of the appendage.

There are proximal elements of at least two of the prominent anterior appendages visible (Fig. 2); from the



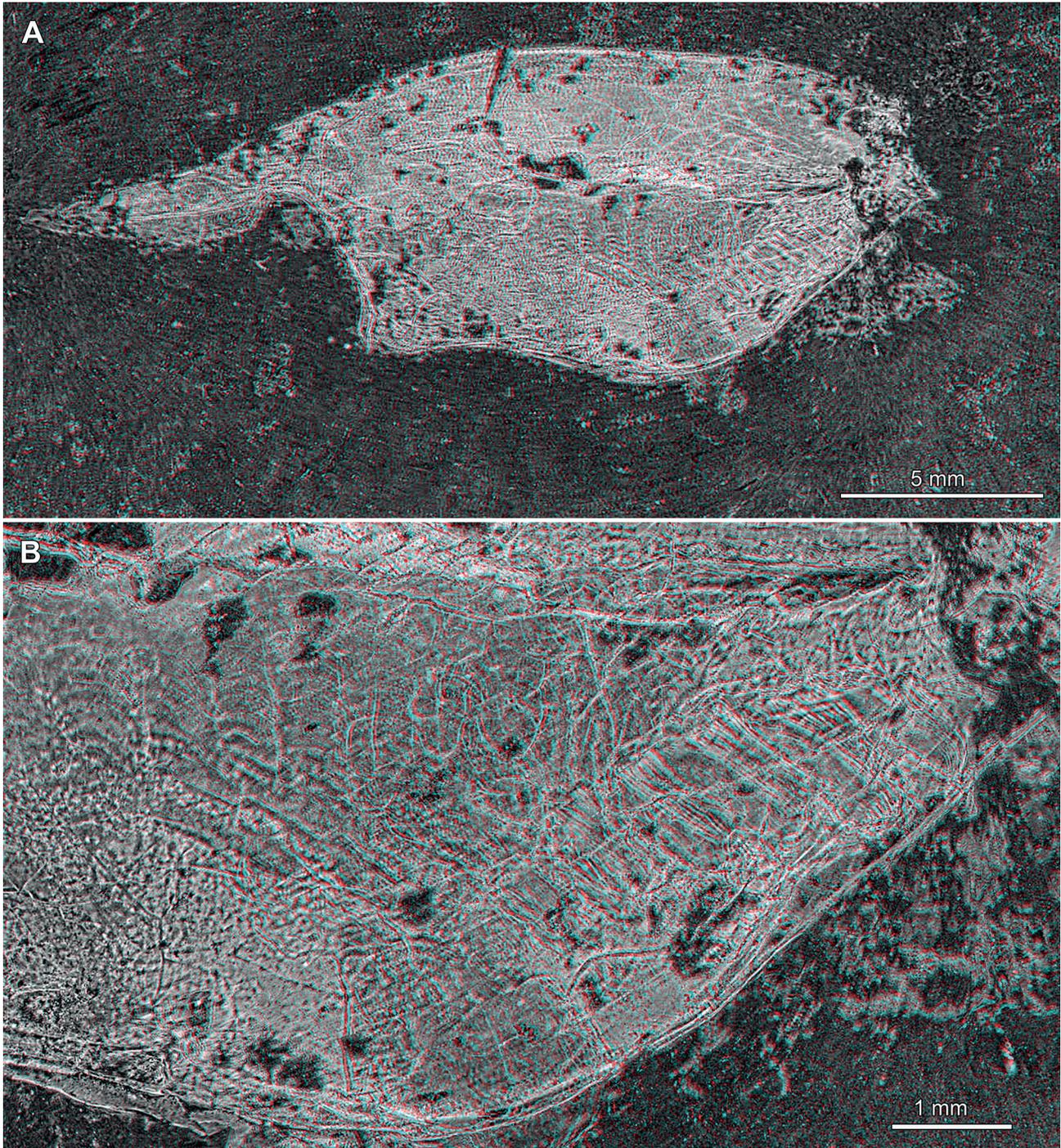
**Fig. 3:** Cross-polarized white light image with HDR of *Falcatacaris bastelbergi* n. g. n. sp. **A** – Overview. **B** – Colour-coded version of A, with the features of mostly the inner body morphology and some special external features marked in different colours. Abbreviations: **das**: diagonally oriented rectangular structures, **gi**: gill, **mu**: muscle strand, **ras**: raptorial appendage element, **ri**: shield ridge, **rt**: rostrum tip, **te**: shield teeth.

proximal element of the first prominent anterior appendage, there is a second element pointing ventrally (Fig. 2). The proximal element of prominent anterior appendage 1 (and to a certain degree also of prominent anterior appendage 2; Fig. 2) is shaped like a squatted letter T, with the dorsal-ventral line being relatively short, and on average are 1.5 times as wide as long. The second element of the first prominent appendage is roughly rectangular, almost four times as long as wide and has a slight curva-

ture. Additionally, dorsal to the presumed third anterior prominent appendage there is a larger element covered by the shield (Fig. 3). This is presumably part of the proximal element of this third anterior prominent appendage and has roughly the shape of a bulging rectangle only with an upper rounded end. The structure is about 1.5 times as long as wide at its dorsal end and about as long as wide at its ventral end.

Presumably nine trunk appendages (exact number difficult to assess) insert posterior to the last prominent anterior appendage, with the beginning inclination of the shield, and reach until the beginning of the posterior notch of the shield (Fig. 2). Their shape is composed of two geo-

metrical forms: an elongate dorso-ventrally orientated rectangle and a triangle facing posteriorly to postero-ventrally. The width of the rectangles as well as the base of the triangles are on average a quarter of their length. The triangle tips are rounded and only moderately pointed.



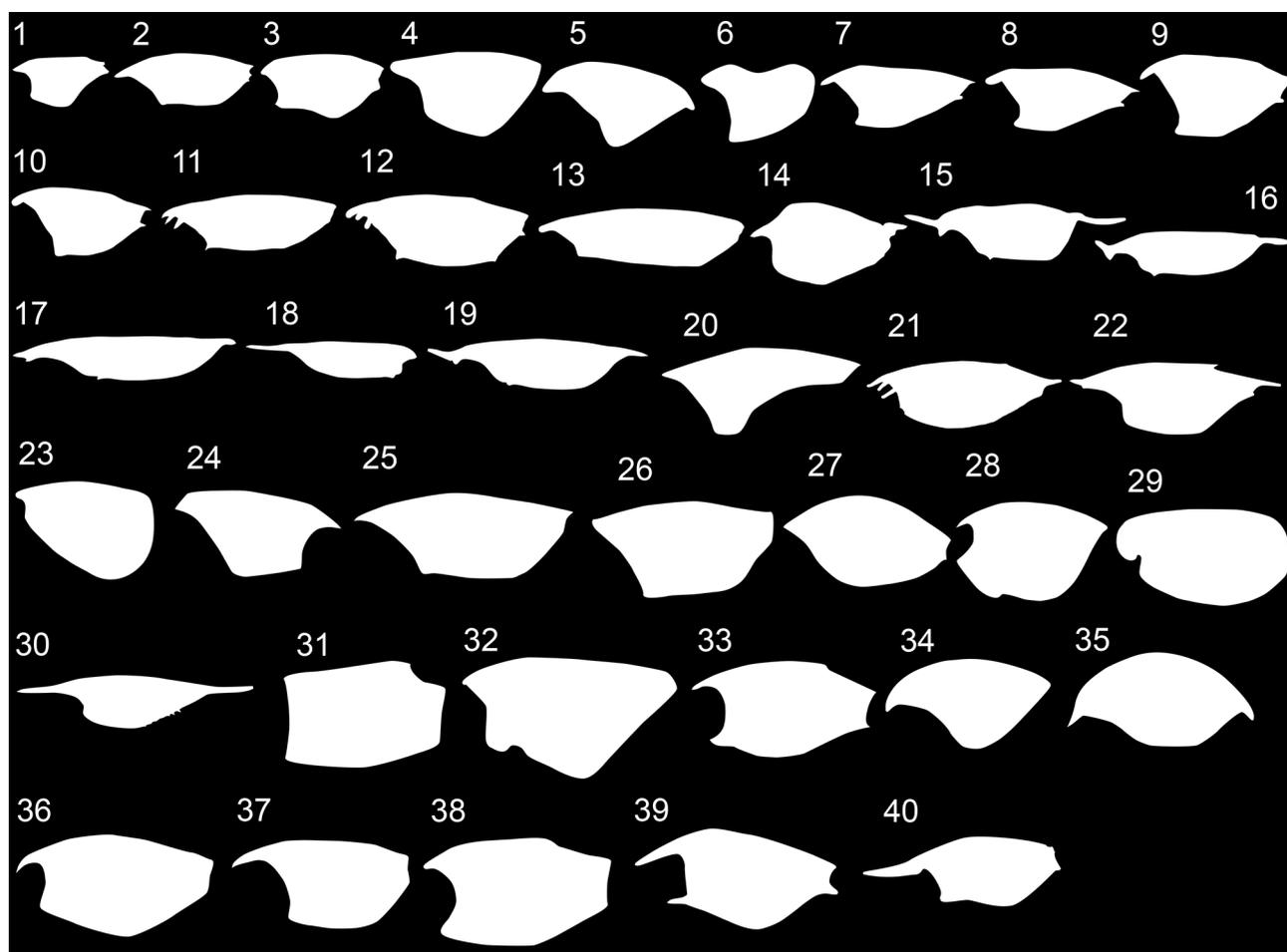
**Fig. 4:** Red-cyan stereo anaglyph of *Falcatacarid bastelbergi* n. g. n. sp. **A** – View of the complete specimen. **B** – Detailed view of the inner body morphology.

The angles in which the triangles are bent from the dorsal-ventral axis of the rectangles are larger for the more anterior appendages and become smaller in the more posterior appendages. They seem to increase progressively in size towards the posterior-most appendage. Alternatively, the part of the appendage that is covered by the shield is smaller in the posterior appendages.

Eight pairs of presumable gills are located in the middle of the shield, right underneath the anterior-posterior shield ridge (Fig. 3). They lie next to each other on an anterior-posterior axis. The shape of the gills resembles more or less rectangles with additionally small semicircles on the dorsal and ventral sides of the rectangle. The anteriormost three gills are roughly 1.5 times as long as

wide, the fourth, the fifth and the sixth gills are roughly two times as long as wide, and the last two gills are only 1.2–1.3 times as long as wide. The gills are lamellate with stacked half-rings, the concave sides of the lamellar elements being ventrally.

Posterior to the gills, there are six distinct strand-like structures interpreted as the remains of muscles. These are orientated from antero-dorsally to postero-ventrally (Fig. 3). The rectangular muscle strands seem to be formed by visible muscle fibres and are roughly two times as long as wide. The most posterior muscle strand is almost meeting the shield outline with its lower end, while the other muscle strands increase the distance between their lower ends and the shield from posterior to anterior.



**Fig. 5:** Overview of the shield outlines used for the elliptic Fourier analysis. Sources of the originals are given in Appendix 2. Abbreviations: 1: *Victoriacaris muhiensis*, 2: *Polzia eldoctorensis*, 3: *Dollocaris ingens*, 4: *Kilianicaris lerichei*, 5: *Clausocaris ribeti*, 6: *Paraostenia voutensis*, 7–10: *Paradollocaris vannieri*, 11–13: *Thylacocaris schrami*, 14: *Globulocaris garassinoi*, 15–19: *Hamaticaris damesi*, 20: *Keelicaris deborae*, 21: *Thylacocephalus cymolopos*, 22: *Pseuderichthus cretaceus*, 23: *Thylacares brandonensis*, 24: *Victoriacaris muhiensis*, 25: *Polzia eldocotrensis*, 26: *Ostenocaris cypriformis*, 27: *Concavicaris mazonensis*, 28: *Concavicaris georgeorum*, 29: *Concavicaris rempes*, 30: *Protozoeta hilgendorfi*, 31: *Paraostenia voutensis*, 32: *Mayrocaris bucculata*, 33: *Dollocaris ingens*, 34: *Clausocaris lithographica*, 35: *Zhenghecaris shankouensis*, 36: *Kitakamicaris utatuensis*, 37: *Ankitokazocaris bandoi*, 38: *Ostenocaris* sp., 39: *Dollocaris michelorum*, 40: *Falcatocaris bastelbergeri* n. g. n. sp.

Ventrally to the gills and anteriorly to the muscle strands, there are five slim rectangular structures, about five to six times as long as wide. They are orientated from antero-dorsally to postero-ventrally and lie close to each other. The second and third structures are slightly longer than the first, fourth and fifth. These may be interpreted as elements of further appendages or simply as indication of a body segmentation in this region.

### 3.3. Elliptic Fourier analysis

A total of 40 specimens (Fig. 5) were compared using an elliptic Fourier analysis. The results were visualized in a two-dimensional plot depicting the two most important dimensions (Fig. 6). A visual representation of the factor loadings for each dimension is given in Appendix 1.

The PCA plot of the elliptic Fourier analysis shows the position of the entire 40 specimens in the multidimensional space. Hereby, the first dimension (Y-axis, PC1) is mainly influenced by the height of the shield while the second dimension (X-axis, PC2) seems to be heavily influenced by the shape and length of the anterior and posterior shield extensions (rostrum, spines) (Appendix 1).

In the plot, representatives of each of the different groups cluster more or less closely together. Remarkable exceptions are representatives of *Hamaticaris* and *Paradollocaris*, which are aligned above each other on a line parallel to the Y-axis with quite some space between the specimens. The specimen that is subject to this study has the number 40 and plots at the top left border of the scatter plot.

## 4. Discussion

### 4.1. Preservation of the fossil

The fossil is overall quite well-preserved and enables the detection of important external body features, such as the shield, remains of appendages and the compound eyes. Due to the 3D relief of the specimen and different colouring of fossil and matrix, details of the inner body morphology, such as the gills and a couple of muscle fibres are accessible as well. Astonishingly enough, these soft tissue microstructures are mostly visible in white light microscopy, more precisely as relief, but not under fluorescent light (quite differently from usual experience, see e.g. HAUG et al. 2014; CHARBONNIER et al. 2017).

However, there is some information covered under a fine layer of matrix that is only visible under fluorescent light. Ventrally of the visible eye structure, there are structures hidden, as well as the additional leg element of the prominent anterior appendage and finally the majority of

trunk appendages. Of these trunk appendages, supposedly nine separate appendages can be distinguished. Posterior to them there seems to be an “empty” region, which could possibly have carried more appendages that are just not preserved.

Orientation-wise the specimen is not preserved in perfect lateral view, but slightly shifted. This becomes obvious at the antero-ventral outline of the shield. Here the two edges of the right and left side of the shield are visible next to each other. Also the rostrum shows a distinct edge reaching from its posterior insertion medially in anterior direction to the middle of the rostrum. This is likely an artefact of preservation as well and can be simply explained by the left ventral edge of the rostrum overlaying the right side of the rostrum. This mode of preservation points again to the bivalved character of the shield.

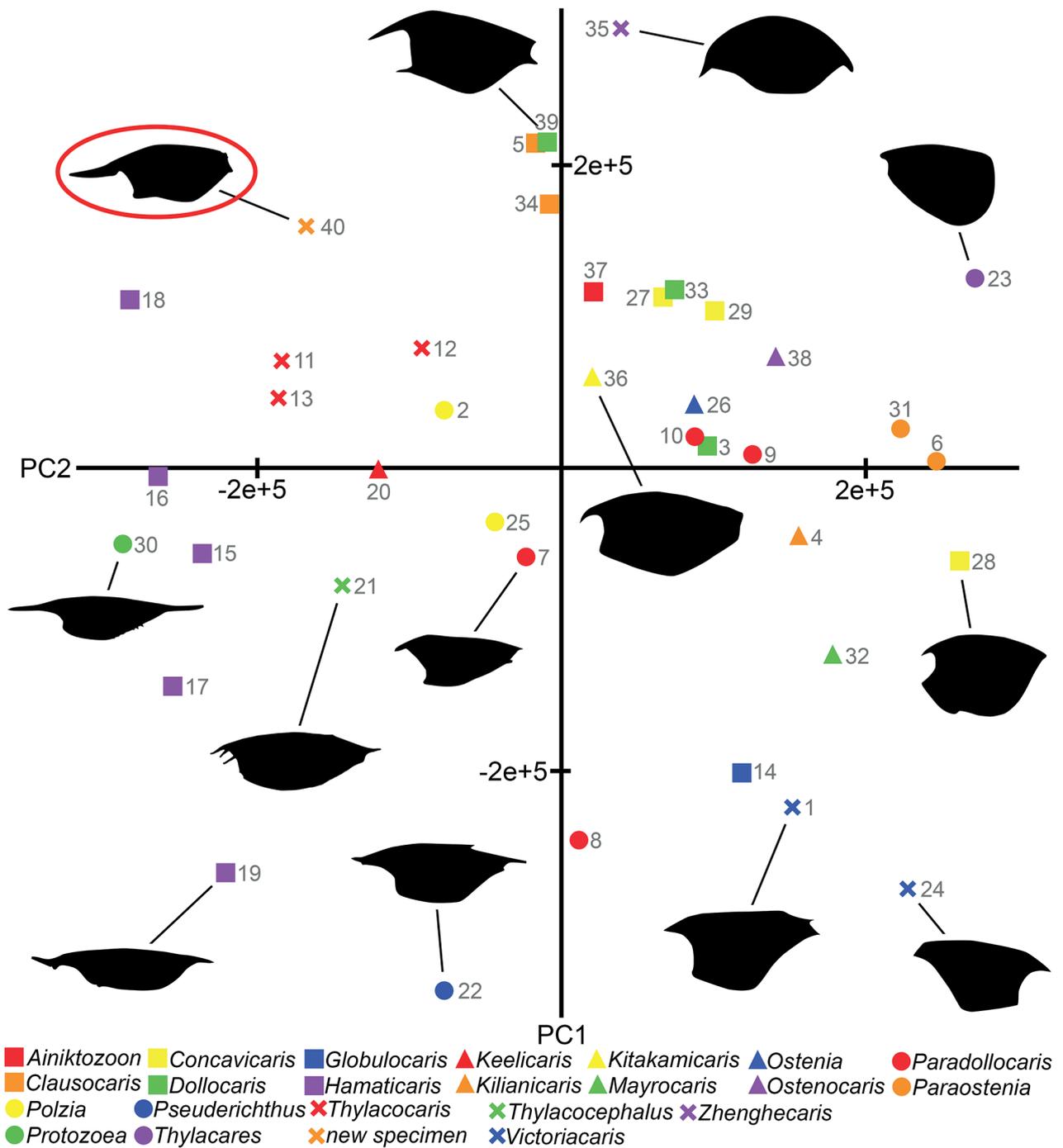
The appendages are unfortunately not well preserved. They do show more details under fluorescent light and allow a rough distinction between different appendages, but they do not show any more details on the exact appendage structure of the prominent anterior appendages and trunk appendages. For the latter, it is even hard to distinguish the appendages themselves; therefore, our interpretation of nine trunk appendages remains arbitrary.

Furthermore, the shield is slightly damaged in its centre, which makes the detection of the lateral shield ridge more challenging. Also, the tip of the rostrum seems to be broken off. The rough outline of the complete rostrum is accessible in white light though (see reconstruction in Fig. 3B). Posteriorly, the shield is damaged as well, and potential further spines that inserted here might be missing.

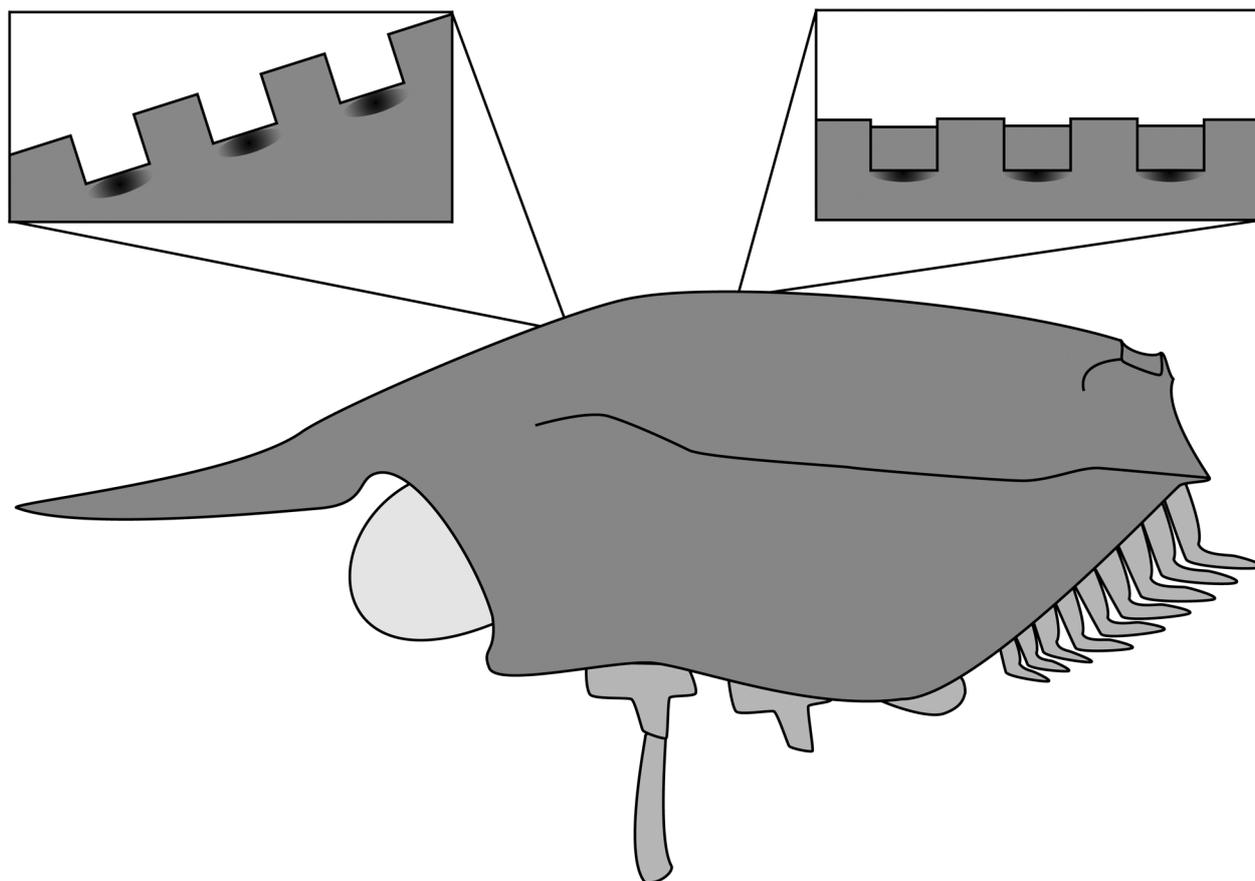
Posterior of the shield are potential further structures (Fig. 2) but an exact identification of them is not possible. These structures appear spread out, most likely broken, and do not show any distinct features. They could be either remains of another fossil, artefacts or parts of the trunk of the specimen that lost association to the rest of the body during diagenesis. Another possibility is that these structures are representing certain posterior appendages, which have been reported for other thylacocephalans (e.g., SECRETAN 1985). However, neither of these interpretations can be further supported with the available material.

### 4.2. Interpretation of body morphology

The specimen has three distinct notches in its shield. The anterior shield notch, as it occupies the eyes of the specimen, corresponds to the ‘optical notch’ of other thylacocephalans (HEGNA et al. 2014; CHARBONNIER et al. 2017). The ventral notch seems most likely to be an appendage-related notch that probably creates space for the prominent anterior appendages. The posterior notch was interpreted as further appendage-related notch in some thylacoceph-



**Fig. 6:** Morphospace depiction of the results of the principal component analysis resulting from the elliptic Fourier analysis, additionally supplemented with some of the corresponding shield drawings. Numbers of the data points correspond with the numbers of the shield reconstruction drawing overview (Fig. 5). Factor loadings and sources of the images are given in the Appendices 1 and 2.



**Fig. 7:** Restoration drawing of external morphology of *Falcatocaris bastelbergeri* n. g. n. sp. in lateral view, appendages simplified. Detail drawings show presumed structure along the dorsal shield rim. Left detail: shield outline of a single valve; right detail: shield outline of both valves interconnecting.

alans (SECRÉTAN 1985) that enveloped further posterior paddle-like trunk appendages.

Another feature of this shield is the series of somewhat square-shaped tooth-like structures along the dorsal margin of the shield (Fig. 7). They can be seen from the base of the rostrum up to the middle of the body and resemble structures that can be observed in some specimens described by CHARBONNIER et al. (2017, figs. 3, 4, 6). These “teeth” might indicate the presence of a true joint between the two valves of the shield. Structurally, they would gear into each other like a zipper. This interpretation, however, remains object of discussion.

The eyes of the specimen might have been damaged due to bad preservation and now seem to be of rectangular shape (Fig. 2). When they were intact, they probably had a more round, hemispheric shape pointing anteriorly or antero-ventrally away from the body as it is the case for other thylacocephalans from the Jurassic (CHARBONNIER et

al. 2009, fig. 6) and is indicated by a somewhat distinct edge that indicates a breaking edge (Fig. 2).

The prominent anterior appendages are most likely, as known in many more completely preserved thylacocephalans, the remains of prominent raptorial appendages (e.g., POLZ 2001; HAUG et al. 2014). Since for most other species of Thylacocephala three pairs of these raptorial appendages are described, it is tempting to make the assumption that the proximal appendage element in between the two anterior raptorial appendages and the trunk appendages is an element of a third raptorial appendage. Its bulkier appearance might, for example, be explained by an overlap of a left and a right appendage. Yet, due to the poor preservation in this area, the posterior position and the morphological difference, we can only guess whether this element belongs to a raptorial appendage or a trunk appendage.

When trying to trace the structure of the trunk appendages, a correlation between visible trunk appendages and muscle strands becomes apparent. When tracing them further, the muscle strands are somehow connected via the diagonally oriented rectangular structures ('das' in Fig. 3; appendage remains?). This resembles morphological details apparent in specimens from La Voulte (e.g., CHARBONNIER et al. 2009).

The trunk appendages and the gills therefore are arising from distinctly posteriorly bent L-shaped segments. Such a deformation of the trunk segments is well-known in Silurian thylacocephalans (HAUG et al. 2014) and is therefore not surprising. Yet, a major weakness of this interpretation is that the numbers of the structures do not really match (discussed later in this section).

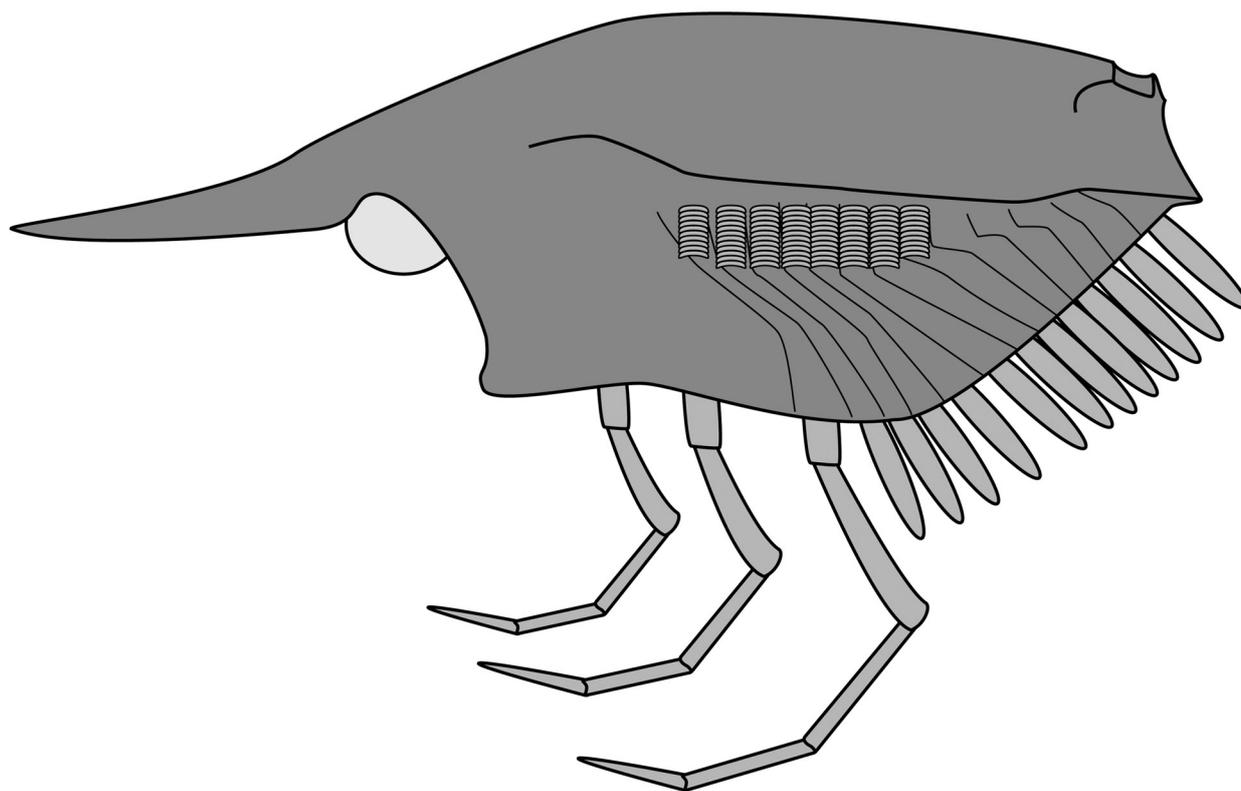
We can therefore only propose the following interpretation with more certainty: The specimen at hand has an ocular segment with prominent compound eyes. Following are five post-ocular segments related to the head region, i.e. segments of the antennulae, antennae, mandibles, maxillulae representing the first pair of raptorial appendages, maxillae representing the second pair of raptorial appendages (as in other thylacocephalan species).

The following segment, the first trunk segment, carries the maxillipeds, i.e. the third pair of raptorial appendages. Posterior to that are segments bearing trunk appendages (exact number of segments unclear, most likely nine).

What still remains unclear is the identity of segments from which the gills arise. Due to the spatial organization it seems likely that the supposed gills are arising from the more anterior trunk segments and that there are at least eight of them. The gills seem to be connected to the muscle strands via the diagonally oriented rectangular structures ('das' in Fig. 3). The dorsal ends of the diagonally oriented rectangular structures are positioned underneath the ventral ends of some of the gills; the ventral ends of the diagonally oriented rectangular structures are positioned right dorsal to the proximal ends of some of the muscle strands. The muscle strands on the other hand seem to be directly correlated to the trunk appendages.

There are only six muscle strands, while nine trunk appendages can be distinguished. These numbers neither match with the eight pairs of gills nor with the five diagonally oriented rectangular structures.

Speculating further, we could assume that the first five of the eight pairs of gills are correlated with the five diag-



**Fig. 8:** Alternative interpretation of *Falcatacaris bastelbergi* n. g. n. sp. in lateral view, inner organs and appendages are simplified, a potential segmental correlation is indicated.

onally oriented rectangular structures (three more could have been present, but are not preserved) and further are connected to the first five of the six muscle strands (two more could have been present, but are not preserved) and finally are correlated to five of the eight trunk appendages that lay directly ventrally to their correlating muscle strands. This proposed organization would leave one trunk appendage without a corresponding gill. Due to the non-optimal preservation of the trunk appendages, however, it could very well be the case that there even are just eight trunk appendages (depending on interpretation). Furthermore, maxilliped one, which is in our interpretation the third raptorial appendage, arises from the first trunk segment, and in this interpretation it would then be without a corresponding gill as well. While partly speculative, this interpretation would well explain the observed morphology in correlation to other known thylacocephalan crustaceans.

#### 4.3. Alternative interpretation

Clearly, the inner morphology and body organisation of the specimen is difficult to interpret and also allows for different interpretations. Intriguingly, there are a few details in this fossil visible in stereo images (Fig. 4) that trigger interpretations differing from the “simple” one outlined above, but should be still discussed here.

When looking onto the relief of the fossil, the assumption that underneath the rostrum a huge compound eye was positioned is challenged. In this way of documentation it appears that the eye structure is limited to the dorsal part, observable by colouring in the matrix and height difference in the stereo image (Figs. 3, 4). If this is true, the eyes would not be huge compound eyes but rather small and possibly stalked. This would be a more plesiomorphic trait, as we know this character only from stratigraphically older specimens, e.g. from the Silurian (HAUG et al. 2014). It would therefore raise new questions about the phylogeny and evolution of Thylacocephala.

Furthermore, anterior to and slightly ventrally from the gills, there is a ridge running anteriorly across the shield, ending underneath the “stalked eye”, observable only in the stereo image (Fig. 4). This structure could be interpreted as appendage element, and if this is not an artefact of preservation, it could be the “missing” first raptorial appendage, i.e. the maxillula, due to its more anterior position compared to the two raptorial appendages. This in return would make the “third” anterior proximal appendage element indeed a trunk appendage element. This interpretation would also fit better with the overall position of the raptorial appendages. The “third” anterior proximal appendage element seemed to be located too far posteriorly to be of raptorial nature in comparison to other thy-

lacocephalans, in which the raptorial appendages attach closely to each other. This would allow a more “relaxed” correlation of the posterior trunk segments (Fig. 8).

#### 4.4. Comparison to other Jurassic thylacocephalans

The Solnhofen lithographic limestones in the wider sense have so far yielded three distinguishable species of thylacocephalans: *Clausocaris lithographica*, *Mayrocaris bucculata* and *Dollocaris michelorum* (POLZ 1989, 1994, 2001; HAUG et al. 2014). These are three of the so far eight known species of thylacocephalans from the Jurassic (PINNA et al. 1985; CHARBONNIER et al. 2009; HAUG et al. 2014).

When comparing the new fossil to its relatives from the Solnhofen lithographic limestones (*C. lithographica*, *M. bucculata* and *D. michelorum*), one feature clearly separates it from the three known species: its prominent anterior rostrum. This feature is shared with no other Solnhofen representative of Thylacocephala described so far.

In fact, also no other species from the Jurassic shows this feature. All eight species possess more or less distinct rostra, but none of them is comparable to the new specimen with respect to the relative length. There are thylacocephalans with comparatively long rostra – namely *Hamaticaris* CHARBONNIER et al., 2017 and *Protozoëa* DAMES, 1886 from the Cretaceous (Santonian) of Lebanon, more precisely from Sahel Alma (CHARBONNIER et al. 2017). Both additionally stand out from other thylacocephalans by having large posterior spines of a similar length to their rostra. We cannot fully exclude that the specimen at hand once had such a large posterior spine as well, but the structure is not preserved in this specimen. However, posterior spines in thylacocephalans in most cases come with a postero-dorsally running shield outline ventrally of the rostrum base, so that there is a smooth transition from shield to spine. In the new specimen, however, one can observe a distinct shield outline starting from the existing small posterior spine running antero-dorsally (away from a potential large posterior spine). This makes the base of the “potential posterior spine” much narrower and creates a contrast to *Hamaticaris* and *Protozoëa*. In general, the shield outline in the new specimen is very different from that of *Hamaticaris* and *Protozoëa*.

Furthermore, the new specimen has a distinct appendage-related notch ventrally of the shield, which is known for other Jurassic thylacocephalans, for example in *D. ingens*. Yet, they are never developed in a comparable size and extent.

Another feature that distinguishes the new specimen from other Jurassic thylacocephalans is the number of trunk appendages. Most of the better-preserved thylacocephalans appear to have a higher number of trunk appendages, while the new specimen has nine pairs at most. From

the Jurassic, only *Ostenocaris cypriformis* ARDUINI, 1980 shows eight pairs of trunk appendages (PINNA et al. 1985).

When comparing the overall shield morphology, the new specimen again differs from other forms from the Solnhofen lithographic limestones. These show rather high shields (longer in dorsal-ventral extent) and a bulged extension centrally of their ventral shield outline. These characters are absent in the new specimen, which shows a comparatively flat shield, almost streamlined in comparison. Species that seem to be more similar in terms of shield morphology are *D. ingens* (from the Middle Jurassic of France) and *Polzia eldoctorensis* HEGNA et al., 2014 (from the Cretaceous of Mexico). An important distinction, again, is the elongated rostrum, which is known neither in *D. ingens*, nor in *P. eldoctorensis*.

A potential explanation for morphological difference in arthropods is often the developmental state of the examined specimen. Therefore, we want to acknowledge this aspect as well. Knowledge on the ontogeny of thylacocephalans is, however, strongly limited. Size differences within the group, and even more importantly, within some species are indeed known to occur. *D. ingens* for example has been reported with a body size of a few centimetres up to a few decimetres (CHARBONNIER et al. 2009). True larval stages, however, tend to differ strongly from their adult stages in many eucrustacean ingroups (e.g., HAUG accepted) and such ontogenetic differences have not been reported for Thylacocephala so far. In addition, no larval stages have been described for Thylacocephala to this point. Furthermore, the specimen at hand does not show any differences in traits with relevance for the functional morphology compared to the record of Thylacocephala. It therefore seems rather unlikely that it is a larval or juvenile stage, but we cannot fully dismiss this theory given that we only have one specimen so far. Of course, if it would turn out that every so far described thylacocephalan representative is in fact a larval form, than we would have to revise this statement.

Sexual dimorphism could also explain the morphological differences of the specimen at hand to its thylacocephalan relatives. But since the sex of thylacocephalans cannot be determined so far (CHARBONNIER et al. 2017) and there is also no knowledge on their reproductive systems, this criterion cannot be used for interpretation so far. It would first demand for fossil data that enables sex determination and evidence for sexual dimorphism in order to use it as a criterion for interpretation.

The combination of a distinct and long rostrum, the absence of a large posterior spine, a moderately dorso-ventrally compressed body and a distinct appendage-related notch is a unique set of characters among all described thylacocephalan specimens. We therefore interpret the specimen at hand as a representative of a new species of Thylacocephala.

#### 4.5. Systematic palaeontology

Arthropoda *sensu stricto sensu* MAAS et al., 2004

Euarthropoda *sensu* WALOSZEK, 1999

Crustacea *sensu lato sensu* STEIN et al., 2008  
amend. HAUG et al., 2010

Eucrustacea *sensu* WALOSZEK, 1999

Thylacocephala PINNA et al., 1982

*Falcatacaris* gen. nov.

**E t y m o l o g y:** Referring to the shape of the rostrum, which resembles a blade weapon of the falcata type.

**T y p e s p e c i e s:** *Falcatacaris bastelbergeri* sp. nov., monotypic.

*Falcatacaris bastelbergeri* sp. nov.

**E t y m o l o g y:** Referring to Dr. THOMAS BASTELBERGER, the collector who found the fossil.

**T y p e m a t e r i a l:** Only holotype, SMNS 70487.

**T y p e l o c a l i t y a n d h o r i z o n:** Vicinity of Eichstätt (Bavaria, Germany), Altmühl Formation (Upper Jurassic, Lower Tithonian).

**D i a g n o s i s:** Shield with anterior large optic notch confined by an elongate prominent rostrum and antero-ventral process; small posterior concave notch limited by dorso-posterior end of the shield and short median-posterior spine; ventral concave notch limited by antero-ventral process.

**R e m a r k s:** The phylogenetic relationships within Thylacocephala are largely unresolved. It is therefore not possible to identify species to an already existing sub-group of Thylacocephala. The species is distinctly different from other species and cannot be identified as a representative of an existing species group (genus).

#### 4.6. Increase of morphological diversity in thylacocephalans

While the phylogeny of Thylacocephala is still largely unresolved, the new species can be easily recognised as “something different”. The results of the elliptic Fourier analysis reflect this statement more or less explicitly.

The general approach of the Fourier analysis, however, demands for some comments. The initial drawings are either based on photographic images or on reconstruction drawings; the latter are a subject of interpretation and thus do not depict completely neutral representations. When images were used, the preservation often was not optimal; therefore, artefacts hindered a perfect representation of the shield outlines in some cases.

The size of the shields could not be taken into account for each specimen, as often scales were not available in the literature. Also for most species only one representative was drawn, the sample size is therefore rather small.

That being said, the different known groups of Thylacocephala cluster more or less nicely together in the plot (Fig. 6). Interestingly, *F. bastelbergi* plots closest to the group of *Thylacocaris* in this morphospace. Nevertheless, its position is somewhat separated from all others, supporting our interpretation as a new species.

The plot further demonstrates that the most diverse dimensions in Thylacocephala shield morphology are the heights of the shield outlines as well as the dorsal lengths of the shield outlines, i.e. if they have rostra or long posterior spines. With having only a rostrum and a rather low shield, *F. bastelbergi* shows a new combination of characters and extends the morphospace of Thylacocephala remarkably.

The results, however, also show that a phylogenetic interpretation of the group based on morphological characters and statistical methods is rather difficult. Some representatives of *Dollocaris*, for example, plot closer to representatives of *Concavicaris* than to other *Dollocaris* specimens. Similar patterns can be observed in *Polzia* and *Paradollocaris*. On the other hand, representatives of *Hamaticaris* have more or less the same values for PC2 but vary drastically in PC1.

Nonetheless, the method allows for a gross but comprehensible comparison of thylacocephalan shield forms. Yet, an improved quality of documentation in the source material would allow for more precise results.

## 5. Conclusions

The newly described thylacocephalan, *Falcatocaris bastelbergi* n. g. n. sp., further extends our knowledge of thylacocephalan species:

- *Falcatocaris bastelbergi* n. g. n. sp. shows a new combination of morphological characters for the group of Thylacocephala.
- The specimen at hand is open to interpretation and demonstrates the difficulty of interpreting 3D body organization from 2D fossil preservations.

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## 6. References

- ARDUINI, P., PINNA, G. & TERUZZI, G. (1980): A new and unusual lower Jurassic cirripede from Osteno in Lombardy: *Ostenia cypriformis* n. g. n. sp. (Preliminary note). – Atti della Società italiana di Scienze naturali e del Museo Civico di Storia Naturale di Milano, **121**: 360–370.
- ARRATIA, G., SCHULTZE, H.-P., TISCHLINGER, H. & VIOHL, G. (2015): Solnhofen – Ein Fenster in die Jurazeit. 620 pp.; München (Pfeil).
- BARTHEL, K. W., SWINBURNE, N. H. M. & CONWAY MORRIS, S. (1990): Solnhofen – A Study in Mesozoic Paleontology. 236 pp.; Cambridge, New York & Melbourne (Cambridge University Press).
- BRAYARD, A., KRUMENACKER, L. J., BOTTING, J. P., JENKS, J. F., BYLUND, K. G., FARA, E., VENNIN, E., OLIVIER, N., GOUEMAND, N., SAUCÈDE, T., CHARBONNIER, S., ROMANO, C., DOGUZHAeva, L., THUY, B., HAUTMANN, M., STEPHEN, D. A., THOMAZO, C. & ESCARGUEL, G. (2017): Unexpected Early Triassic marine ecosystem and the rise of the modern evolutionary fauna. – Science Advances, **3**: e1602159.
- BRIGGS, D. E. G. & ROLFE, W. D. I. (1983): New *Concavicarida* (new order: ?Crustacea) from the Upper Devonian of Gogo, Western Australia, and the paleoecology and affinities of the group. – Special Papers in Paleontology, **30**: 249–276.
- BRODA, K., HEGNA, T. A. & ZATOŃ, M. (2015): Thylacocephalans. – Geology Today, **31**(3): 116–120.
- CHARBONNIER, S., VANNIER, J., HANTZPERGUE, P. & GAILLARD, C. (2009): Ecological significance of the arthropod fauna from the Jurassic (Callovian) La Voulte Lagerstätte. – Acta Palaeontologica Polonica, **55** (1): 111–132.
- CHARBONNIER, S., TERUZZI, G., AUDE, D., LASSERON, M., HAUG, C. & HAUG, J. T. (2017): New thylacocephalans from the Cretaceous Lagerstätten of Lebanon. – Bulletin de la Société géologique de France, **188** (3): 19.
- DAMES, W. (1886): Ueber einige Crustaceen aus den Kreideablagerungen des Libanon. – Zeitschrift der Deutschen Geologischen Gesellschaft, **38**(3): 551–576.
- EHIRO, M., SASAKI, O., KANO, H., NEMOTO, J. & KATO, H. (2015): Thylacocephala (Arthropoda) from the Lower Triassic of the South Kitakami Belt, Northeast Japan. – Paleontological Research, **19**(4): 269–282.
- FRAAS, O. (1878): Geologisches aus dem Libanon. – Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg, **34**: 257–391.
- HAUG, C., BRIGGS, D. E. G., MIKULIC, D. G., KLUESSENDORF, J. & HAUG, J. T. (2014): The implications of a Silurian and other thylacocephalan crustaceans for the functional morphology and systematic affinities of the group. – BMC Evolutionary Biology, **14**: 159.
- HAUG, C., NYBORG, T. & VEGA, F. J. (2013c): An exceptionally preserved upogebiid (Decapoda: Reptantia) from the Eocene of California. – Bolétin de la Sociedad Geológica Mexicana, **65**: 235–248.
- HAUG, J. T. (accepted): Metamorphosis in crustaceans. – In: ANGER, K., HARZSCH, S. & THIEL, M. (eds.): The Natural History of the Crustacea, VII, Developmental Biology and Larval Exology. Oxford (Oxford University Press).
- HAUG, C., SHANNON, K. R., NYBORG, T. & VEGA, F. J. (2013b): Isolated mantis shrimp dactyli from the Pliocene of North

- Carolina and their bearing on the history of Stomatopoda. – *Bolétin de la Sociedad Geológica Mexicana*, **65**: 273–284.
- HAUG, J. T. & HAUG, C. (2016): “Intermetamorphic” developmental stages in 150 million-year-old achelatan lobsters – The case of the species *tenera* Oppel, 1862. – *Arthropod Structure & Development*, **45**: 108–121.
- HAUG, J. T., HAUG, C. & EHRLICH, M. (2008): First fossil stomatopod larva (Arthropoda: Crustacea) and a new way of documenting Solnhofen fossils (Upper Jurassic, Southern Germany). – *Palaeodiversity*, **1**: 103–109.
- HAUG, J. T., HAUG, C., KUTSCHERA, V., MAYER, G., MAAS, A., LIEBAU, S., CASTELLANI, C., WOLFRAM, U., CLARKSON, E. N. K. & WALOSZEK, D. (2011): Autofluorescence imaging, an excellent tool for comparative morphology. – *Journal of Microscopy*, **244**: 259–272.
- HAUG, J. T., MAAS, A., HAUG, C. & WALOSZEK, D. (2013a): Evolution of crustacean appendages. – In: WATLING, L. & THIEL, M. (eds.): *Functional Morphology and Diversity. The Natural History of the Crustacea*: 34–73; Oxford (Oxford University Press).
- HAUG, J. T., MAAS, A. & WALOSZEK, D. (2010): †*Henningsmoenicaris scutula*, †*Sandtorpia vestrogothiensis* gen. et sp. nov. and heterochronic events in early crustacean evolution. – *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **100**: 311–350.
- HAUG, J. T., MÜLLER, C. H. G. & SOMBKE, A. (2013d): A centipede nymph in Baltic amber and a new approach to document amber fossils. – *Organisms Diversity & Evolution*, **13**: 425–432.
- HAUG, J. T. & RUDOLF, N. R. (2015): A nisto larva of an Eocene slipper lobster (Neoscyllarida). – *Palaeodiversity*, **8**: 113–119.
- HEGNA, T. A., VEGA, F. J. & GONZÁLEZ-RODRÍGUEZ, K. A. (2014): First Mesozoic thylacocephalans (Arthropoda, ?Crustacea; Cretaceous) in the Western Hemisphere, new discoveries from the Muhi Quarry Lagerstätte. – *Journal of Paleontology*, **88** (3): 606–616.
- HILGENDORF, F. (1885): Ueber cretacische Squilliden-Larven vom Libanon. – *Sitzungs-Berichte der Gesellschaft naturforschender Freunde zu Berlin*, **10**: 184–185.
- IWATA, H. & UKAI, Y. (2002): SHAPE: A computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. – *Journal of Heredity*, **93**: 384–385.
- LANGE, S., HOF, C. H. J., SCHRAM, F. R. & STEEMAN, F. A. (2001): New genus and species from the Cretaceous of Lebanon links the Thylacocephala to the Crustacea. – *Palaeontology*, **44** (5): 905–912.
- LANGE, S. & SCHRAM, F. R. (2002): Possible lattice organs in Cretaceous Thylacocephala. – *Contributions to Zoology*, **71** (4): 10.
- MAAS, A., WALOSZEK, D., CHEN, J., BRAUN, A., WANG, X. & HUANG, D. (2004): Phylogeny and life habits of Early Arthropods—Predation in the Early Cambrian Sea. – *Progress in Natural Science*, **14** (2): 158–166.
- MEEK, F. B. & WORTHEN, A. H. (1868): Preliminary notice of a scorpion, a *Eurypterus?*, and other fossils from the Coal Measures of Illinois. – *American Journal of Science, Series 2*, **46**: 19–28.
- MIKULIC, D. G., BRIGGS, D. E. G. & KLUESSENDORF, J. (1985a): A Silurian soft-bodied biota. – *Science*, **228**: 715–717.
- MIKULIC, D. G., BRIGGS, D. E. G., & KLUESSENDORF, J. (1985b): A new exceptionally preserved biota from the lower Silurian of Wisconsin, U.S.A. – *Philosophical Transactions of the Royal Society of London, (B)*, **311**: 75–85.
- PINNA, G., ARDUINI, P., PESARINI, C. & TERUZZI, G. (1982): Thylacocephala: una nuova Classe di Crostacei fossili. – *Atti della Società italiana di Scienze naturali e del Museo Civico di Storia Naturale di Milano*, **123**: 469–482.
- PINNA, G., ARDUINI, P., PESARINI, C. & TERUZZI, G. (1985): Some controversial aspects of the morphology and anatomy of *Ostenocaris cypriformis* (Crustacea, Thylacocephala). – *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**: 373–379.
- POLZ, H. (1989): *Clausocaris* nom. nov. pro *Clausia* OPPENHEIM 1888. – *Archaeopteryx*, **7**: 73.
- POLZ, H. (1992): Zur Lebensweise der Thylacocephala. – *Archaeopteryx*, **10**: 1–12.
- POLZ, H. (1994): *Mayrocaris bucculata* gen. nov. sp. nov. (Thylacocephala, Conchyliocarida) aus den Solnhofener Plattenkalken. – *Archaeopteryx*, **12**: 35–44.
- POLZ, H. (2001): *Dollocaris michelorum* sp. nov. (Thylacocephala, Concavicularida) aus den Solnhofener Plattenkalken. – *Archaeopteryx*, **19**: 45–55.
- ROLFE, W. D. I. (1985): Form and function in Thylacocephala, Conchyliocarida and Concavicularida (?Crustacea): a problem of interpretation. – *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **76**: 391–399.
- SCHRAM, F. R. (1990): On Mazon Creek Thylacocephala. – *Proceedings of the San Diego Society of Natural History*, **3**: 1–16.
- SCHRAM, F. R., HOF, C. H. J. & STEEMAN, F. A. (1999): Thylacocephala (Arthropoda: Crustacea?) from the Cretaceous of Lebanon and implications for thylacocephalan systematics. – *Palaeontology*, **42** (5): 769–797.
- SCHWEIGERT, G. (2007): Ammonite biostratigraphy as a tool for dating Upper Jurassic lithographic limestones from South Germany – first results and open questions. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **245** (1): 117–125.
- SCOURFIELD, D. J. (1937): An anomalous fossil organism, possibly a new type of chordate from the Upper Silurian of Lesmahagow, Lanarkshire – *Ainiktozoon loganense* gen. et sp. nov. – *Proceedings of the Royal Society of London, (B)*, **121**: 533–547.
- SECRÉTAN, S. (1985): *Conchyliocarida*, a class of fossil crustaceans: relationship to Malacostraca and postulated behaviour. – *Transactions of the Royal Society of Edinburgh*, **76**: 381–389.
- SECRÉTAN, S. & RIOU, B. (1983): Un groupe énigmatique de crustacés. Ses représentants du Callovien de La Voulte-sur-Rhône. – *Annales de Paléontologie*, **69**: 59–97.
- STEEMAN, F. A. (1999): Udforskningen af Thylacocephala – en mærkelig gruppe af Leddyr. – *Geologisk Tidsskrift*, **2**: 24–28.
- STEIN, M., WALOSZEK, D., MAAS, A., HAUG, J. T. & MÜLLER, K. J. (2008): The stem crustacean *Oelandocaris oelandica* re-visited. – *Acta Palaeontologica Polonica*, **53** (3): 461–484.
- STIGALL, A. L. & HENDRICKS, J. R. (2007): First report of a concavicularid interior (Crustacea: Thylacocephala) from the Devonian of North America. – *Northeastern Geology & Environmental Sciences*, **29** (2): 102–106.
- VANNIER, J., CHEN, J.-Y., HUANG, D.-Y., CHARBONNIER, S. & WANG, X.-Q. (2006): The Early Cambrian origin of thylacocephalan arthropods. – *Acta Palaeontologica Polonica*, **51** (2): 201–214.
- VANNIER, J., SCHOENEMANN, B., GILLOT, T., CHARBONNIER, S. & CLARKSON, E. (2016): Exceptional preservation of eye structure in arthropod visual predators from the Middle Jurassic. – *Nature Communications*, **7**: 10320.

- VAN STRAELEN, V. (1923): Les Mysidacés du Callovien de La Voulte-sur-Rhône (Ardèche). – *Bulletin de la Société Géologique de France*, **23**: 431–439.
- VIOHL, G. (2015): Der geologische Rahmen: die Südliche Frankenalb und ihre Entwicklung. – In: ARRATIA, G., SCHULTZE, H.-P., TISCHLINGER, H. & VIOHL, G. (eds.): *Solnhofen – Ein Fenster in die Jurazeit*: 56–62; München (Pfeil).
- WALOSZEK, D. (1999): On the Cambrian diversity of Crustacea. – In: SCHRAM, F. R. & VON VAUPEL KLEIN, J. C. (eds.): *Crustaceans and the Biodiversity Crisis*: 3–27; Leiden (Brill).
- WELLNHOFER, P. (2008): *Archaeopteryx – Der Urvogel von Solnhofen*. 256 pp.; München (Pfeil).

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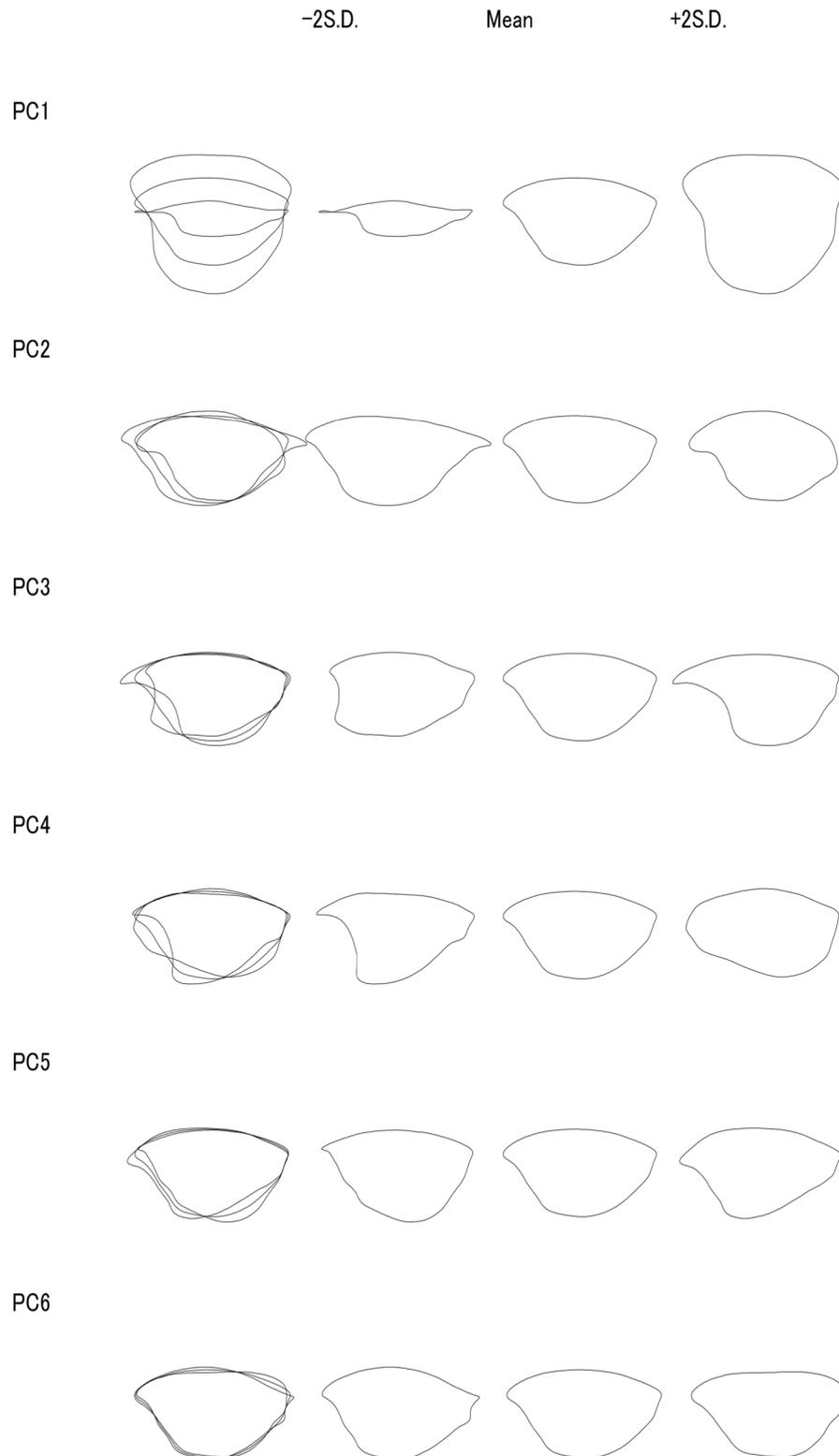
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## Appendices

**Appendix 1:** Visualization of the first six Principal Components of the PCA that resulted from the elliptic Fourier analysis that had the most influence on variation in the plot.



**Appendix 2:** Source table of reconstruction drawings and images used for the elliptic Fourier analysis.

Number	Taxon	Reference
1	<i>Victoriacaris muhiensis</i>	BRODA et al. 2015, fig. 1C
2	<i>Polzia eldoctorensis</i>	BRODA et al. 2015, fig. 1D
3	<i>Dollocaris ingens</i>	CHARBONNIER et al. 2009, fig. 5B
4	<i>Kilianicaris lerichei</i>	CHARBONNIER et al. 2009, fig. 5C
5	<i>Clausocaris ribeti</i>	CHARBONNIER et al. 2009, fig. 5D
6	<i>Paraostenia voutlensis</i>	CHARBONNIER et al. 2009, fig. 5E
7	<i>Paradollocaris vannieri</i>	CHARBONNIER et al. 2017, fig. 2A
8	<i>Paradollocaris vannieri</i>	CHARBONNIER et al. 2017, fig. 2G
9	<i>Paradollocaris vannieri</i>	CHARBONNIER et al. 2017, fig. 3A
10	<i>Paradollocaris vannieri</i>	CHARBONNIER et al. 2017, fig. 4A
11	<i>Thylacocaris schrami</i>	CHARBONNIER et al. 2017, fig. 6A
12	<i>Thylacocaris schrami</i>	CHARBONNIER et al. 2017, fig. 7A
13	<i>Thylacocaris schrami</i>	CHARBONNIER et al. 2017, fig. 8A
14	<i>Globulocaris garassinoi</i>	CHARBONNIER et al. 2017, fig. 9B
15	<i>Hamaticaris damesi</i>	CHARBONNIER et al. 2017, fig. 10A
16	<i>Hamaticaris damesi</i>	CHARBONNIER et al. 2017, fig. 10C
17	<i>Hamaticaris damesi</i>	CHARBONNIER et al. 2017, fig. 10E
18	<i>Hamaticaris damesi</i>	CHARBONNIER et al. 2017, fig. 10H
19	<i>Hamaticaris damesi</i>	CHARBONNIER et al. 2017, fig. 10K
20	<i>Keelicaris deborae</i>	CHARBONNIER et al. 2017, fig. 11A
21	<i>Thylacocephalus cymolops</i>	CHARBONNIER et al. 2017, fig. 12F
22	<i>Pseuderichthus cretaceus</i>	CHARBONNIER et al. 2017, fig. 12H
23	<i>Thylacares brandonensis</i>	HAUG et al. 2014, fig. 10
24	<i>Victoriacaris muhiensis</i>	HEGNA et al. 2014, fig. 2 1
25	<i>Polzia eldocotrensis</i>	HEGNA et al. 2014, fig. 2 2
26	<i>Ostenocaris cypriformis</i>	PINNA et al. 1982, fig. 1
27	<i>Concavicularis mazonensis</i>	SCHRAM 1990, fig. 13
28	<i>Concavicularis georgeorum</i>	SCHRAM 1990, fig. 7
29	<i>Concavircaris rempes</i>	SCHRAM 1990, fig. 10
30	<i>Protozoa hilgendorfi</i>	SCHRAM et al. 1999, fig. 2A
31	<i>Paraostenia voutlensis</i>	STEEMAN 1999, fig. 2
32	<i>Mayrocaris bucculata</i>	VANNIER et al. 2006, fig. 1D
33	<i>Dollocaris ingens</i>	VANNIER et al. 2006, fig. 4A1
34	<i>Clausocaris lithographica</i>	VANNIER et al. 2006, fig. 4B1
35	<i>Zhenghecaris shankouensis</i>	VANNIER et al. 2006, fig. 4C1
36	<i>Kitakamicaris utatuensis</i>	EHIRO et al. 2015, fig. 4
37	<i>Ankitokazocaris bandoi</i>	EHIRO et al. 2015, fig. 6
38	<i>Ostenocaris</i> sp.	EHIRO et al. 2015, fig. 10
39	<i>Dollocaris michelorum</i>	POLZ 2001, fig. 1
40	<i>Falcatacaris bastelbergeri</i> n. g. n. sp.	This paper, Fig. 1