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A new interpretation of the enigmatic fossil arthropod *Anhelkocephalon handlirschi* Bill, 1914 – important insights in the morphology of Cyclida

Mario Schädel & Joachim T. Haug

Abstract

Anhelkocephalon handlirschi Bill, 1914 has been described as a representative of Isopoda (woodlice and relatives). Fossils of *A. handlirschi* come from the Grès à Voltzia Formation in western France, close to the German border. The Grès à Voltzia Formation (Voltziensandstein) is Triassic in age; lithostratigraphically, it belongs to the Buntsandstein Group. Based on the morphology of the type material and one additional specimen, we interpret *A. handlirschi* not as a representative of Isopoda, but as a representative of Cyclida. Cyclida is an extinct group of Euarthropoda, the representatives of which have a circular to oval outline of the body (in dorsal view). One of the herein studied specimens has aspects of appendage morphology preserved, which, in general, is a rare case for cyclidans. The herein studied specimens also add new features to the knowledge about the morphology of Cyclida, such as a net-like pattern on the dorsal body side.

Keywords: Cycloid, Grès à Voltzia Formation, Voltziensandstein, Vosges, taphonomy.

1. Introduction

Cyclida is a group of fossil organisms, generally interpreted as an ingroup of Euarthropoda and furthermore of Eucrustacea. Representatives of Cyclida – herein termed ‘cyclidans’ to avoid confusion with representatives of Cyclidae (often termed ‘cyclids’) – are characterised by an overall circular outline of the entire body in dorsal view. The overall body shape of species with three-dimensionally preserved specimens varies from almost hemispheric (Woodward 1870) to flat-cylindrical (Fraaije et al. 2003). In most fossils of Cyclida only a single large dorsal sclerite (shield, ‘carapace’) is preserved

Cyclida is an extinct group with a fossil record stretching from the Early Carboniferous (Clark et al. 2020; Feldmann & Schweitzer 2019) to the Late Cretaceous (Fraaije et al. 2003). With 52 reviewed species (Schweitzer et al. 2020), the fossil record of the group is quite rich. Yet, due to taphonomic constraints, only for a few species the morphology of the appendages is known (Woodward 1905; Hopwood 1925; Gall 1971, 1997; Schram et al. 2006; Dzik 2008; Feldmann & Schweitzer 2019; Clark et al. 2020; Schweitzer et al. 2020).

Early studies hypothesised a close relationship of Cyclida with Xiphosura (e.g., Packard 1885). Hopwood (1925) proposed a position within Branchiura for Cyclida. Later, Cyclida has been proposed to be the sistergroup of Copepoda (Schram et al. 1997). Recently, Dzik (2008) returned to the hypothesis on the position of Cyclida within Branchiura, based on his reconstruction of the respiratory system.

Due to the lack of soft part preservation for most fossil localities and the rather simple shape of the large shield of cyclidans, there have been incidents where fossil remains of animals of different groups of Euarthropoda have been interpreted as a large shield of cyclidans. *Stagmacaris quenstedti* Schweigert, 2006 was described as a representative of Cyclidae (Schweigert 2006), but was later reinterpreted as the tergite of the sixth segment of the pleon of a symmetrical hermit crab (Pylochelidae) (Van Bakel et al. 2011; Fraaije et al. 2012). Also, shields from other origins have been interpreted as cyclidans. *Mesoprosopon triasinum* Stolley, 1915 was described as a representative of Cyclida (Glaessner 1928) and was recently reinterpreted as a possible zoea-stage larva of a representative of Eumalacostraca (Hyžný et al. 2016).

The ‘Grès à Voltzia’ Formation (Voltziensandstein) is early Middle Triassic in age (ca. 243 million years old) and crops out in the northern part of the Vosges in France (Selden & Nudds 2012; Fig. 1). The ‘Grès à Voltzia’ Formation is itself part of the Upper Buntsandstein Group (Gall 1985). We herein present fossils that come from the lowermost unit (Grès à meules, Werkstein) of the ‘Grès à Voltzia’ Formation (Schwebel et al. 1983). The Grès à meules unit is composed of fine grained sandstones mixed with laminated clay and silt lenses and layers of calcareous sandstone and sandy dolomites (Gall & Grauvogel-Stamm 2005; Selden & Nudds 2012). Fossils of Euarthropoda, such as the herein described fossils, are preserved in the clay lenses. The palaeoenvironment of the Grès à Voltzia deposits has been reconstructed as a deltaic area close to the sea (Germanic Basin) and the clay lenses have most likely formed in ponds between the river channels that eventually dried out (Gall 1985; Gall & Grauvogel-Stamm 2005; Selden & Nudds 2012). Some parts of the arthropod fauna (e.g., the presence of horseshoe crabs) in the Grès à Voltzia Formation indicate a marine influence (see discussion in Selden & Nudds 2012).

With *Halicyne ornata* Trümpy, 1957, there is already a record of Cyclida from the 'Grès à Voltzia' Formation (Bill 1914; Gall 1971; Gall & Grauvogel-Stamm 2005; Selden & Nudds 2012). Here, we take a closer look at another fossil, *Anhelkocephalon handlirschi* Bill, 1914. *Anhelkocephalon handlirschi* was briefly described in the amendment section of a publication (Bill 1914) that summarised the fossil crustaceans from the 'Grès à Voltzia' Formation. The original type material was interpreted by Anton P. J. Handlirsch as remains of a flat and oval fossil of Isopoda, similar to representatives of the extant group *Serolis* (Bill 1914). Consequently, Bill (1914: 338) stated that: "The reduced number of abdominal segments, the large telson and especially the head, which is deeply pushed into the first thoracic segment, argues for that [the interpretation as an isopod]." Philipp C. Bill died in the same year of the description of *A. handlirschi*, during a battle of World War I.

Van Straelen (1928) tried to locate the type material in the collection of the Institute of Geology in Strasbourg but did not succeed. In 1967, the collection, where the type material was supposed to be, was destroyed by fire (Schwebel et al. 1983). Based on Bill's description, Schwebel (1983) designated a neotype and a paraneotype from the same formation, less than 30 km away from the original site (Fig. 1).

Schwebel (1983) stated that *A. handlirschi* would most closely resemble representatives of the extant groups Serolidae and Idoteidae (another ingroup of Isopoda). This interpretation was also shared by Basso & Tintori (1994). Quite on the contrary, Brandt et al. (1999) rejected the interpretation of *A. handlirschi* as a representative of Serolidae and raised doubts about the interpretation as an isopod in general. Schädel et al. (2020 in press), in their review of Triassic fossils of Isopoda, supported this view, but pointed out the need of a re-investigation. They briefly mentioned a certain similarity of the fossils to Cyclida. We herein provide a reinterpretation of *A. handlirschi* as a cyclidan. This is based on the morphology of the neotype and accompanying material from the same region and formation.

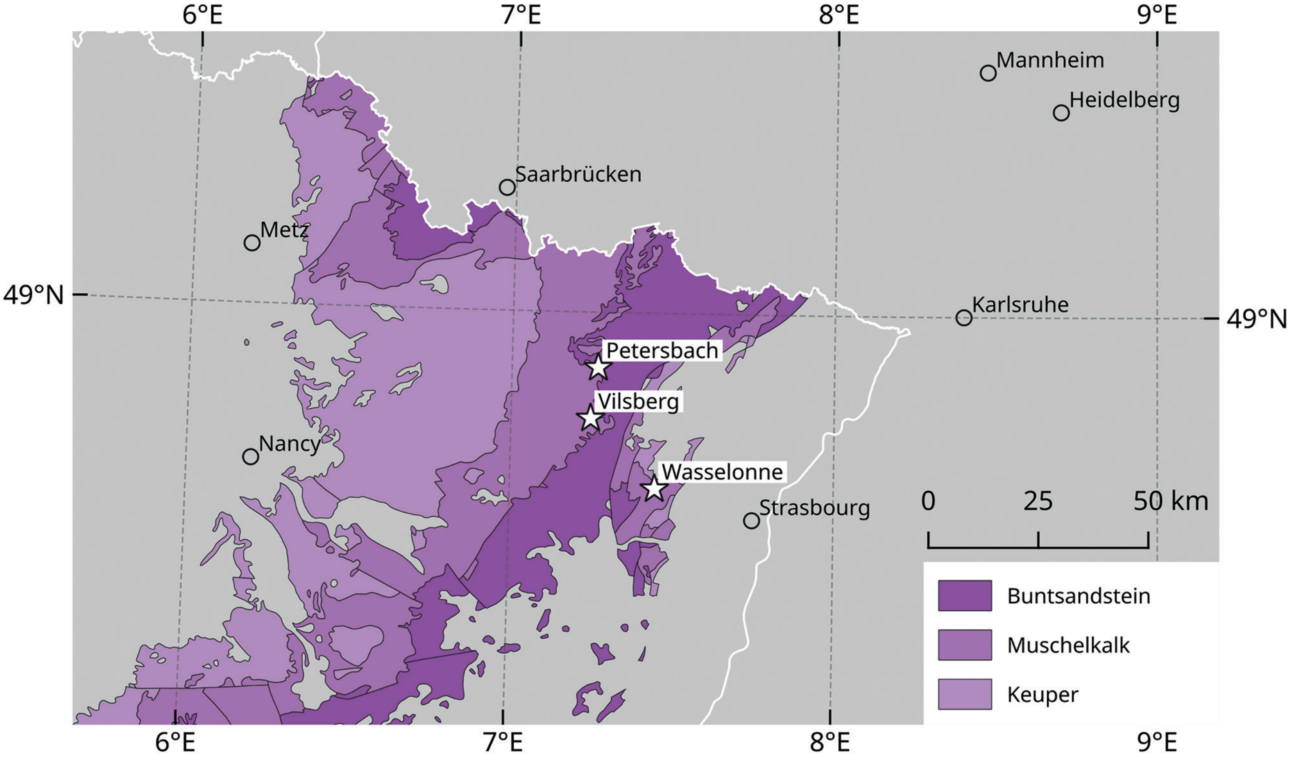

Fig. 1. Geological map of the northern Vosges. The field sites of *Anhelkocephalon handlirschi* are marked by white asterisks. SMNS 75641-1 (neotype) and SMNS 75641-3, Vilsberg; SMNS 75641-2, Petersbach; original type material of Bill (1914), Wasselonne.

2. Materials and methods

Photographic images were obtained using a Canon EOS 700D DSLR camera and a Canon MP-E 65 mm objective on a photo-stand with two flashes. To overcome the limitations of the depth of field and the field of view, multiple stacks of images were recorded, using a modified microscopy table to adjust the level of the fossil relative to the camera. For all images, cross-polarised light was used to avoid reflections (Bengtson 2000). The image stacks were combined to in-focus images using the software CZBatch (batch mode of CombineZP, GPL) (Haug et al. 2011). The in-focus images were then aligned and blended to panoramic images using GIMP 2.10.14 (GPL). Colour markings and image adjustments (histogram optimisation, etc.) were also done in GIMP. The figure plates were arranged using Inkscape 0.92 (GPL). Measurements were done using ImageJ (public domain).

A map was created in QGIS 3.4 (GPL) using map data from the BRGM (Geological service of France, intellectual property of the BRGM, geological map of France, scale of 1/1000000, created June 2006, http://www.geocatalogue.fr/Detail.do?id=4162), Openstreetmaps (OpenStreetMap.org, ODbL 1.0) and Natural Earth (naturalearthdata.com, public domain).

The exact arrangement of the mouthparts in Cyclida is not known; thus, the correspondence between the further posterior appendages in representatives of Cyclida and other arthropod groups is unclear as well. Therefore, we do not adopt the nomenclature suggested by Schram (1997) – referring to the anterior-most walking or grasping appendages as maxillula, maxilla and maxilliped. Instead, we herein use more general terms to address these appendages. For the lobed structures on the dorsal shield also a more general terminology (cf. Feldmann & Schweitzer 2019) was used, as the lobes in the herein presented specimens could not unambiguously be brought into correspondence with lobes of specimens in the literature (see Discussion).

3. Results

Description of the neotype SMNS 75641-1: Bilateral, symmetrical body. Six pairs of articulated appendages visible in the fossil: two pairs of anterior appendages (possible antennula and antenna) and four pairs of further posterior appendages (walking or grasping appendages). Body increasing in width towards the posterior-most appendages; body decreasing in width posterior to the posterior-most appendages. Large continuous sclerite posterior to the posterior-most appendages (interpreted as an out of place dorsal sclerite, shield in the following, ‘carapace’ in the literature) (Fig. 2A–C), about 22 mm long and 17 mm wide (estimated due to poor preservation).

Possible antennula differentiated into a proximal peduncle region and a distal flagellum region; peduncle region consisting of at least two elements (proximal region not well preserved). Proximal peduncle element longer than wide, dense fringe of setae on the median and the mediodistal margin, mediodistal corner rounded, laterodistal corner more angular. Second peduncle element shorter and narrower than the preceding element, median margin rounded, lateral margin straight. Distal flagellum much narrower and about as long as or slightly longer than the elements of the peduncle combined; a subdivision into multiple elements is not visible in the fossil (area is badly preserved; Fig. 3A, B).

Possible antenna differentiated into a proximal peduncle region and a distal flagellum region. Peduncle consisting of at least three elements (proximal region not well preserved). Proximal-most discernible peduncle element short and about as long as wide, dense fringe of setae on the lateral margin. Second peduncle element longer than the preceding element, about 2.5 times, distal part wider than the proximal part, distal part wider than the distal part of the preceding element, dense fringe of setae on the lateral margin. Third peduncle element slightly longer and more slender than the preceding element, distal part wider than the proximal part, dense fringe of setae on the proximal part of the lateral margin. Flagellum longer than the peduncle, nearly 2 times, with at least 21 individual elements (distal part not well preserved), individual elements gradually decreasing in size towards the distal end of the flagellum, proximal elements wider than long. Round lateral bulge posterior to the antenna (might represent a proximal element of the antenna) with dense fringe of setae on the lateral margin (Fig. 3A, B). Anterior margin of the body pointed at the midline, with an angle of about 130° (Fig. 3A). Possible mouthparts not visible.

First (anterior-most) walking or grasping appendage presumably consisting of 5 elements (distal-most element not preserved). Proximal element large, wider in its distal portion, with a fringe of setae on the posterior margin. Second element roughly triangular in dorsoventral projection, much shorter than the preceding element, with a fringe of setae on the posterior margin. Third element longer than the preceding element, with a straight posterior margin and a somewhat rounded convex anterior margin. Fourth element shorter than the preceding element, with a strongly convex anterior margin and a less convex posterior margin (Figs. 2A, B, 3C, D).

Second walking or grasping appendage presumably consisting of 5 elements (distal-most element not preserved), slightly longer than the preceding appendage. Proximal element large, anterior margin convex, posterior margin straight, longer on the anterior side, with a fringe of long setae on the posterior margin. Second element much smaller and roughly triangular in shape, with a straight posterior margin, with a fringe of long setae on the posterior margin. Third element much longer than the preceding element, about as long as the proximal-most element, anterior margin concave, posterior margin straight, fringe of long setae on the posterior margin, postero-distal corner rounded. Fourth element only preserved in its proximal portion, anterior margin strongly convex, posterior margin slightly concave with a fringe of long setae. Fifth element not preserved (Fig. 3C, D).

Third walking or grasping appendage presumably consisting of 5 elements (distal-most element not preserved), slightly longer than the preceding appendage. Proximal element large, wider in its distal portion, anterior margin convex, posterior margin slightly convex, with a fringe of long setae on the posterior margin, longer on the anterior side. Second element much smaller and roughly triangular in shape, with a straight posterior margin, with a fringe of long setae on the posterior margin. Third element roughly rectangular in dorsoventral projection, much longer than the preceding element, about as long as the proximal-most element, anterior margin straight, posterior margin straight with a fringe of long setae, postero-distal corner rounded. Fourth element slightly shorter and wider than the preceding element, strongly convex anterior margin with a fringe of setae in the distal portion, posterior margin straight with a fringe of setae, postero-distal corner rounded. Fifth element much shorter and narrower than the preceding element, narrowing towards the distal end, no setae visible (Fig. 3C, D).

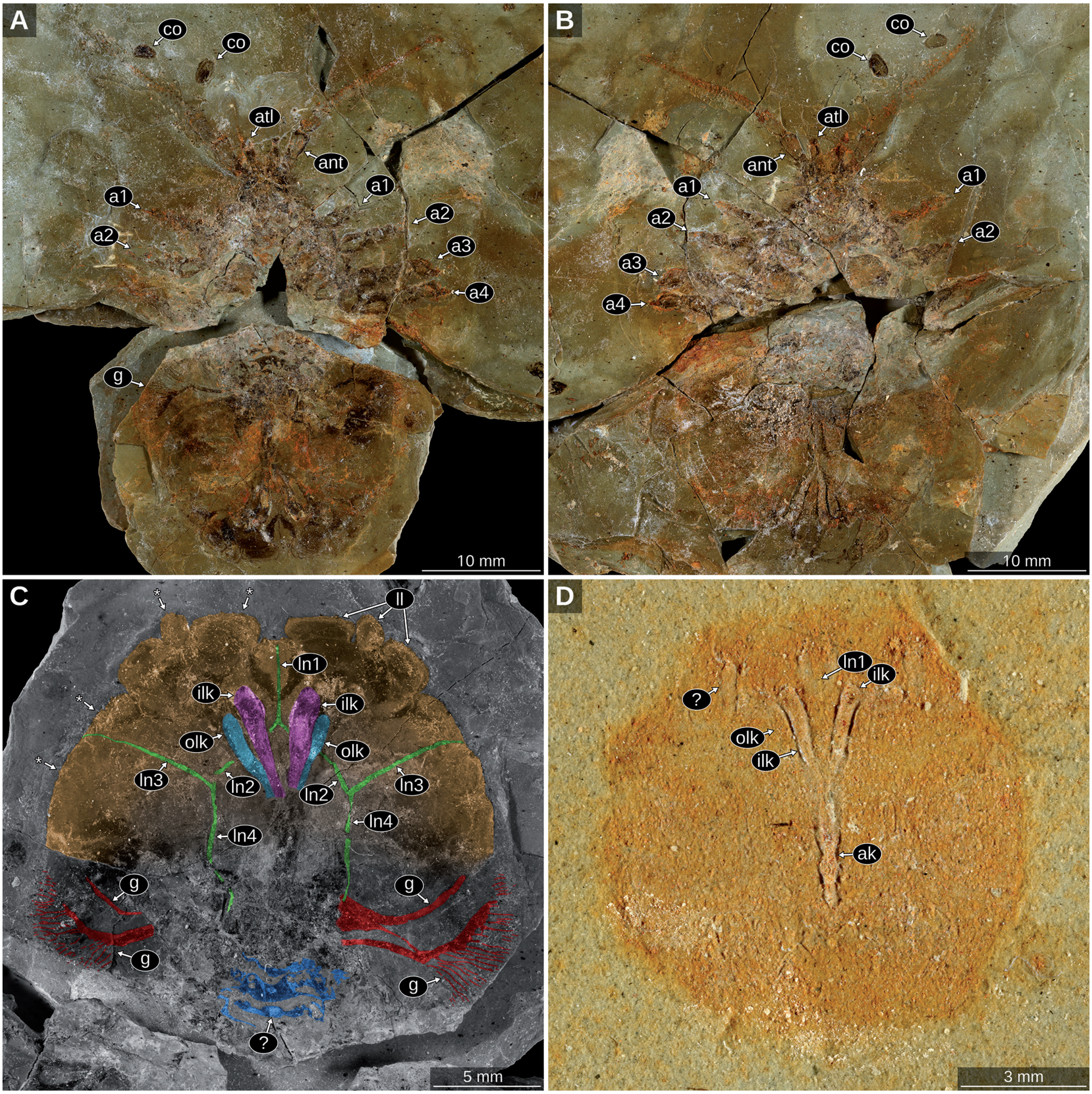

Fig. 2. A–C – *Anhelkocephalon handlirschi*, neotype, SMNS 75641-1, cross-polarised light photography. **A:** Overview, side 1; **B:** overview, side 2; **C:** detail of the shield with colour markings, side 1, rotated by 180° relative to Fig. 2A, asterisks mark short spines on the margin of the shield. **D** – *Anhelkocephalon handlirschi*, paraneotype, SMNS 75641-2, cross-polarised light photography. Abbreviations: **ant**, antenna; **ak**, axial keel; **a1–4**, appendages 1–4; **atl**, antennula; **cho**, chonchostracan shell; **g**, gill; **ilk**, inner lyrate keel; **ll**, lateral lobes; **ln1–4**, lines 1–4; **olk**, outer lyrate keel; **?**, unknown structures.

Fourth walking or grasping appendage presumably consisting of 5 elements (distal-most element not preserved), about as long as the preceding appendage; morphology similar to the preceding appendage; proximal element with a narrow proximal side and a much wider distal side, antero-distal corner rounded; fifth element with a convex anterior side and a straight posterior side, with a pointed tip (Fig. 3C, D).

Shield, roughly circular in dorsoventral projection (posterior margin not preserved; see discussion about the presumed orientation of this body part); total length 18.0 mm, total width 22.7 mm (Fig. 2A–C). Anterior margin with distinct lobes: Median unpaired lobe with two, paired notches on the anterior margin (Figs. 2C). Three pairs of lateral lobes (≠ lateral lobes sensu Feldmann et al. 2019; see discussion; ‘ll’ in Fig. 2C).

Anterior-most lateral lobe large, distal margin slightly convex, with at least 6 spines on the distal margin. Second lateral lobe much narrower and protruding further distal than the preceding lobe, distal margin strongly convex with at least 4 spines. Third lobe similar to the anterior-most lobe, with at least 7 spines on the distal margin, postero-distal corner more rounded than the antero-distal corner.

Shield with a net-like pattern of thin, paired and unpaired lines (Fig. 2C). Unpaired line (line 1) from the anterior part of the (unpaired) median lobe along the mid-line, posterior end forming a bifurcation posterior to the level of the lateral lobes (junction to lines 2). Line 2 paired, branching off from line 1 line with an angle of ca. 45°, of about the same length as line 1, terminating in a junction with two other lines (line 3 and 4).

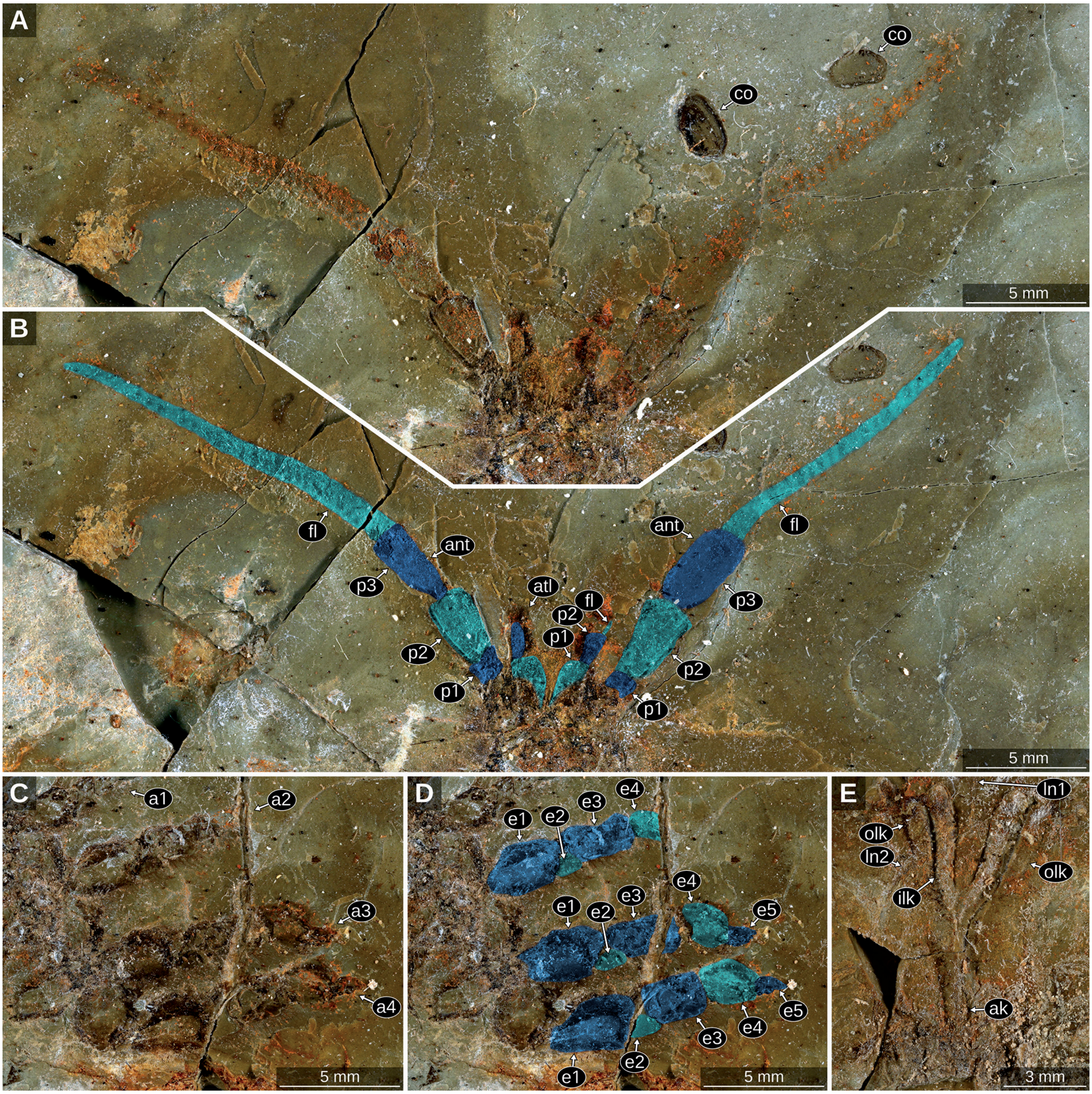

Fig. 3. A–E – *Anhelkocephalon handlirschi*, neotype, SMNS 75641-1, cross-polarised light photography. **A, B:** Detail of the anterior body region, side 2; **B:** with colour markings. **C–D:** Detail of the appendages, side 1; **D:** with colour markings on appendages 2–4. **E:** Detail of the lyrate keels and the axial keel, side 2. Abbreviations: **ak**, axial keel; **ant**, antenna; **atl**, antennula; **cho**, conchostracan shell; **e1–5**, element 1–5 of the appendages; **fl**, flagellum; **ilk**, inner lyrate keel; **ln1–2**, lines 1–2; **olk**, outer lyrate keel; **p1–3**, peduncle elements 1–3.

Line 3 paired, from junction with line 2 in anterolateral direction towards the distal margin of the shield, with an angle of ca. 70° to the mid-line, slightly longer than line 2. Line 4 paired, from junction with line 2 and 3 parallel to the mid-line in posterior direction, of about the same length as line 3.

Y-shaped structure in the centre of the shield, consisting of 5 regions; two paired oblique bulges (inner lyrate keel and outer lyrate keel sensu Feldmann & Schweitzer 2019), converging towards the posterior ends; unpaired bulge on the mid-line, posterior to the paired bulges (axial keel sensu Feldmann & Schweitzer 2019) (Figs. 2A–C, 3E). Two pairs of branched structures preserved, possibly representing gills, consisting of a proximal/median ramus and distal/lateral lamellae, distal part of the ramus bent towards the anterior side of the shield. Anterior pair of possible gills with only about 9 lamellae preserved (taphonomic feature). Posterior pair of possible gills oriented parallel to the preceding pair, with at least 29 lamellae. At least 3 consecutive, unpaired sclerites of uncertain affinity posterior to the rami of the gills (or posterior to the walking or grasping appendages; see discussion about the presumed orientation of this body part) (Fig. 2A, C).

Description of the paraneotype SMNS 75641-2: Circular outline; total length 10.4 mm, total width 10.1 mm; prominent Y-shaped structure in the centre of the

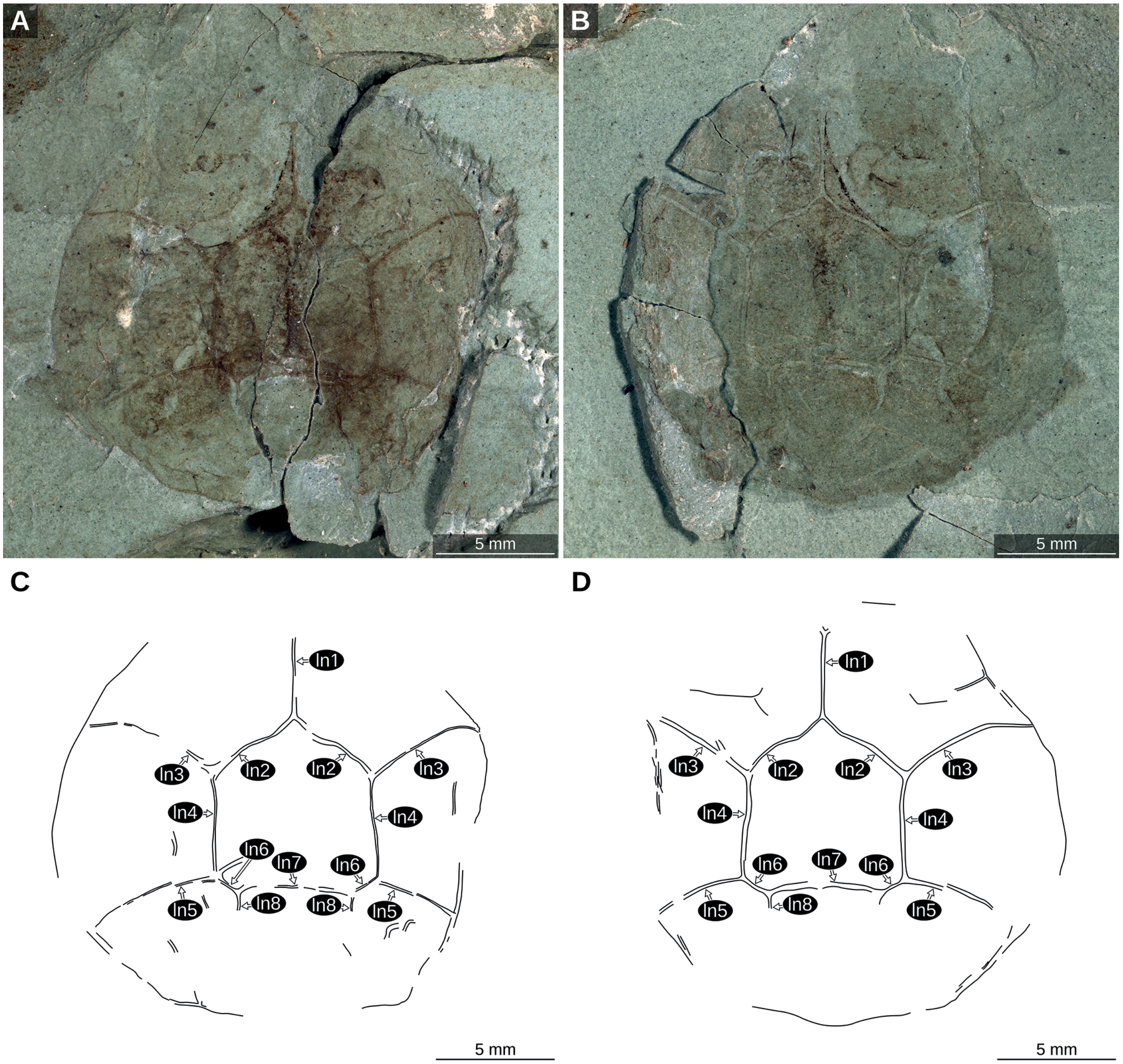

Fig. 4. A–D – cf. *Anhelkocephalon handlirschi*, SMNS 75641-3. **A:** Overview, side 1, cross-polarised light photography; **B:** overview, side 2, cross-polarised light photography; **C:** line drawing of side 1; **D:** line drawing of side 2. Abbreviations: **ln1–7**, lines 1–7.

outline (inner lyrate keels and axial keel); short paired bulges antero-lateral to the inner lyrate keels, parallel to the mid-line; unpaired oval lobe antero-median to the inner lyrate keels.

Unpaired line (line 1) from the anterior part of the (unpaired) median lobe along the mid-line, posterior end forming a bifurcation (junction to the paired line 2) between the inner lyrate keels (Fig. 2D).

Description of the further specimen SMNS 75641-3: Circular outline; total length 16.2 mm, total width 18.4 mm; with a net-like pattern of thin, paired and unpaired lines (Fig. 4). Unpaired line (line 1, interpreted as along the mid-line due to the bilateral symmetry of the system of lines and as anterior due to the correspondence with the lines on the neotype), posterior end forming a bifurcation (junction to lines 2). Line 2 paired, branching off from line 1 with an angle of ca. 50°, of about the same length as line 1, terminating in a junction with two other lines (junction to line 3 and 4). Line 3 paired, from junction with line 2 in antero-lateral direction towards the distal margin of the shield, with an angle of ca. 60° to the mid-line, slightly longer than the preceding line, distal portion curved in lateral direction (anterior side convex). Line 4 paired, from junction with line 2 and 3 parallel to the mid-line in posterior direction, of about the same length as line 2, terminating in a junction with two other lines (line 5 and 6). Line 5 paired, from junction with line 4 in postero-lateral direction towards the margin, slightly curved in posterior direction (anterior side convex). Line 6 paired, short, from junction with line 4 in postero-median direction, with an angle of ca. 60° to the mid-line, terminating in a junction with two other lines (line 7 and 8). Line 7 unpaired, orthogonal to the midline, connecting the two posterior ends of line 6. Line 8 paired, from junction with line 6 and 7 in posterior direction, parallel to the midline, only anterior part preserved or very short.

4. Discussion

4.1. Correspondence to the original type material

Due to the brief nature of the original description of *Anhelkocephalon handlirschi* (Bill 1914), it cannot be excluded that the original material, on which Bill based his description, were remains of a different – not necessarily closely related – species than that of the herein studied neotype from Schwebel (1983) (see discussion in Basso & Tintori 1994). The description of Bill certainly matches the morphology of many species of Isopoda. Schwebel's designation of a neotype for *A. handlirschi* is therefore stained with some uncertainty. Yet, since the original type material has either been destroyed or is still lost (see introduction), this does not disagree with the existing taxonomy. Yet, it seems advisable to references the species as '*sensu* Schwebel, 1983'.

4.2. Correspondence between the studied specimens

Three individual specimens of *Anhelkocephalon handlirschi* are available from the Grès à Voltzia Formation. Although the lithology of the surrounding sediment and the preservation of the specimens is different in all three specimens, a correspondence between the specimens is well supported. A correspondence between the neotype (SMNS 75641-1) and the paraneotype (SMNS 75641-2) has, obviously, already been suggested by Schwebel (1983) – yet, based on the assumption that SMNS 75641-2 represented the pleon of an isopod. The prominent Y-shaped structure in the neotype (Figs. 2A–C, 3E) can also be found in SMNS 75641-2. The position and shape of the structure corresponds between the two specimens and the preservation of the structure in SMNS 75641-2 is similar to the preservation in side 2 of the neotype (Fig. 3E). Also, in SMNS 75641-2 the anterior part of the line pattern can be seen as faint lines (Fig. 2D). The remarkably similar line pattern on the large circular sclerite (cf. Fig. 2C and Fig. 4) argues for a correspondence between the neotype (SMNS 75641-1) and the, slightly smaller, specimen SMNS 75641-3. A Y-shaped structure is not clearly evident from SMNS 75641-3 (Fig. 4A, B). Both fossils come from the same field site and the same sediment complex. Thus, we propose a species-level correspondence between all three specimens.

4.3. Morphological features and systematic interpretation

The morphology in each of the three fossils is not compatible with an interpretation of *Anhelkocephalon handlirschi* as a representative of Isopoda (as in Schwebel et al. 1983; Basso & Tintori 1994). Circular body shapes in principal exist within Isopoda (e.g., Brandt & Poore 2003); however, the circular body shape in these circular forms is achieved by broadened individual tergites (shields of the trunk). According to the interpretation of Schwebel (1983, fig. 3), the oval body shape is mainly achieved by the large sclerite, which he interpreted as the pleotelson (posterior-most trunk segment conjoined with the telson). His interpretation is heavily based on the alleged presence of uropods (appendages of the pleotelson). Schwebel (1983) identified the three, paired, lateral lobes at the posterior-most part of SMNS 75641-1 (anterior margin of the shield in our interpretation) as uropods. However, these lobes are neither separated from the rest of the sclerite, nor are there joints proximal to the lobes or between the individual lobes. Overall, there are no features in the fossils at hand that are unique to Isopoda or strongly indicative for Isopoda. Thus, it is highly unlikely that *A. handlirschi* is a representative of Isopoda.

Anhelkocephalon handlirschi resembles representatives of Cyclida in many aspects. The circular shape of the shield ('carapace' in the literature) is typical for most cyclidans (e.g., Dzik 2008). The most conspicuous

Table 1: Species of Cyclida with a prominent Y-shaped complex formed by the inner and outer lyrate keels and the axial keel.

Taxon	**Reference**
Americlus americanus (PACKARD, 1885)	PACKARD (1885); SCHRAM et al. (1997); FELDMANN et al. (2017)
Americlus johnsoni (WOODWARD, 1894)	WOODWARD (1894, 1905); HOPWOOD (1925); FELDMANN & SCHWEITZER (2019)
Americlus scotti (WOODWARD, 1894)	WOODWARD (1894); HOPWOOD (1925)
Cyclida sp.	ŻYŁA et al. (2013)
Cyclus radialis (PHILLIPS, 1836)	PHILLIPS (1836); WOODWARD (1894); FELDMANN & SCHWEITZER (2019)
Halicyne agnota (MEYER, 1838)	MEYER (1847); WOODWARD (1894); SCHWEIGERT (2007)
Halicyne oosterinkorum SCHWEITZER, FELDMANN, & SCHINKER, 2019	KLOMPMAKER (2019); SCHWEITZER et al. (2019).
Halicyne ornata TRÜMPY, 1957	TRÜMPY (1957); GALL (1971); FELDMANN & SCHWEITZER (2019)
Halicyne plana SEEBACH, 1857	SEEBACH (1857); MÜLLER (1955)
Litocyclus torosus (WOODWARD, 1870)	WOODWARD (1870)
Opolanka decorosa DZIK, 2008	DZIK (2008)
Prolatcyclus martinensis (GOLDRING, 1967)	GOLDRING (1967); MYCHKO et al. (2019)
Schramine montanaensis (SCHRAM, BOERE & THOMAS, 2006)	DZIK reference after SCHRAM et al. (2006)
Uralocyclus miloradovitchi (KRAMARENKO, 1961)	MYCHKO & ALEKSEEV (2018)
Yunnanocyclus nodosus FELDMANN, SCHWEITZER & HU *in* FELDMANN, SCHWEITZER, HU, HUANG, ZHANG, ZHOU, WEN, XIE & MAGUIRE, 2017	FELDMANN et al. (2017)

similarity between the herein studied fossils and many representatives of Cyclida is the Y-shaped structure on the shield (Table 1). It consists of three elongated bulges: two pairs of oblique bulges in the anterior part (inner lyrate keel and outer lyrate keel sensu FELDMANN & SCHWEITZER 2019) and an unpaired bulge (axial keel sensu FELDMANN & SCHWEITZER 2019) (Figs. 2C, D, 3E). HOPWOOD (1925) theorised that the Y-shaped complex is a result of the consolidation of one median shield with a pair of lateral sclerites. The Y-shaped complex could, however, as well be the result of internal aspects of the morphology, such as muscle attachment sites.

The orientation of the lyrate keels suggests that the shield is in reverse position in relation to the rest of the body (Figs. 2A, B), indicating that the shield has detached from the rest of the body at the anterior part first. This is unusual for the moulting behaviour of most eucrustaceans with a similar body shape (e.g. Brachyura). On the other hand, this arrangement does not have to be related to moulting; it can also be a result of decay on a carcass or physical damage to a living individual or a carcass.

After taking into account the reconstructed orientation of the shield, the lobes on the anterior part of the sclerite are quite similar to those on some cyclidans (e.g., *Halicyne oosterinkorum* SCHWEITZER, FELDMANN & SCHINKER, 2019; KLOMPMAKER 2019). However, it proved to be difficult to bring those lobes into exact correspondence to lobes in different cyclidan species, as the remains of *A. handlirschi* are severely compressed, obscuring the original three-dimensional morphology.

A distinct rostral lobe (anterior protrusion of the shield) and corresponding postero-lateral recesses (optic notches; see FELDMANN & SCHWEITZER 2019 for the terminology) are not apparent in *Anhelkocephalon handlirschi*. The condition in *A. handlirschi* is very similar to the one in *Halicyne oosterinkum* (Fig. 5).

Antennulae and antennae of *A. handlirschi* are overall quite similar to those of representatives of Cyclida; however, it should be mentioned that there is much variation in the length and the proportion of those anterior appendages among cyclidan species (*Opolanka decorosa* vs. *Americlus americanus*; DZIK 2008; SCHRAM et al. 1997). In *A. handlirschi* the antenna is much longer than the antennula. This is in contrast to some representatives of the group *Americlus*; there, the antennula is much longer than the antenna. This might either be a result of strong variation within the group Cyclida, or due to a possible misinterpretation of the two appendages in specimens of *Americlus*. In those specimens, where the antennula is preserved (Schram et al. 1997, fig. 2; Feldmann & Schweitzer 2019, fig. 3C; Clark et al. 2020), the most proximal elements are not visible and it could be that the dorsally visible part of the antennula is projected further posterior than the antenna.

The leg morphology of *A. handlirschi* is different to many of the cyclidans with preserved appendages. Often, the distal-most element of the leg is proportionally much longer than in *A. handlirschi*. There, especially in the anterior appendages, the distal-most element can be subchelate to the next proximal element (e.g., Schram et al. 1997; Clark et al. 2020). The rough proportions of the legs are very similar to those in *Opolanka decorosa* (Dzik 2008). However, *Opolanka decorosa* has robust spines on the penultimate element of the leg – in contrast to *A. handlirschi* (Dzik 2008; Fig. 3C, D). The low number of walking or grasping appendages in *A. handlirschi* is intriguing; however, considering that SMNS 75641-1 might represent a decaying carcass, it is likely that some appendages are missing due to taphonomical reasons. Sternal elements are apparent in many representatives of Cyclida in which the legs are preserved (e.g., Clark et al. 2020, fig. 4C). In the herein presented material no sternal elements are apparent. This is likely due to the mode of preservation in SMNS 75641-2 and SMNS 75641-3 and the bad preservation in SMNS 75641-1 (i.e. large crack in the sediment matrix where sternal elements could be expected).

The net-like pattern on the shield, which is present on all three herein studied fossils, has never been described for cyclidans. Yet, in at least two other species there are indications of a quite similar pattern. In *Opolanka decorosa* (Dzik 2008, fig. 2K) and *Halicyne oosterinkorum* (Schweitzer et al. 2019, fig. 1; Fig. 5) faint, similar appearing, lines are visible on the shield. In *Halicyne oosterinkorum* also the position of the lines is very similar to the lines in *A. handlirschi* (cf. Figs. 2C, 4C, D vs. Fig. 5). These lines could potentially be present in more species but are obscured by the ornamentation on the dorsal surface. It is unclear of which biological origin these lines are, they might be comparable to grooves on the thoracic shield of lobsters that are probably linked to muscle attachment sites (Tshudy & Babcock 1997). A marginal rim is not apparent in the herein presented material. This is likely due to the low relief of the presented fossils, which preserve very little or no original three-dimensional features.

In the posterior part of the shield, there are two pairs of branched structures (Fig. 2A, C), the fine branches in the lateral part of the structures suggest a function that needs surface area enlargement. It is similar in scale to internal gills of eucrustaceans such as crabs (Brachiyura; e.g., Martin & Davis 2003). However, in crabs for example, the orientation of the lamellae is about perpendicular to the orientation in *A. handlirschi* and other cyclidans (Schram et al. 1997; Dzik & Sulej 2007; Dzik 2008; Feld-

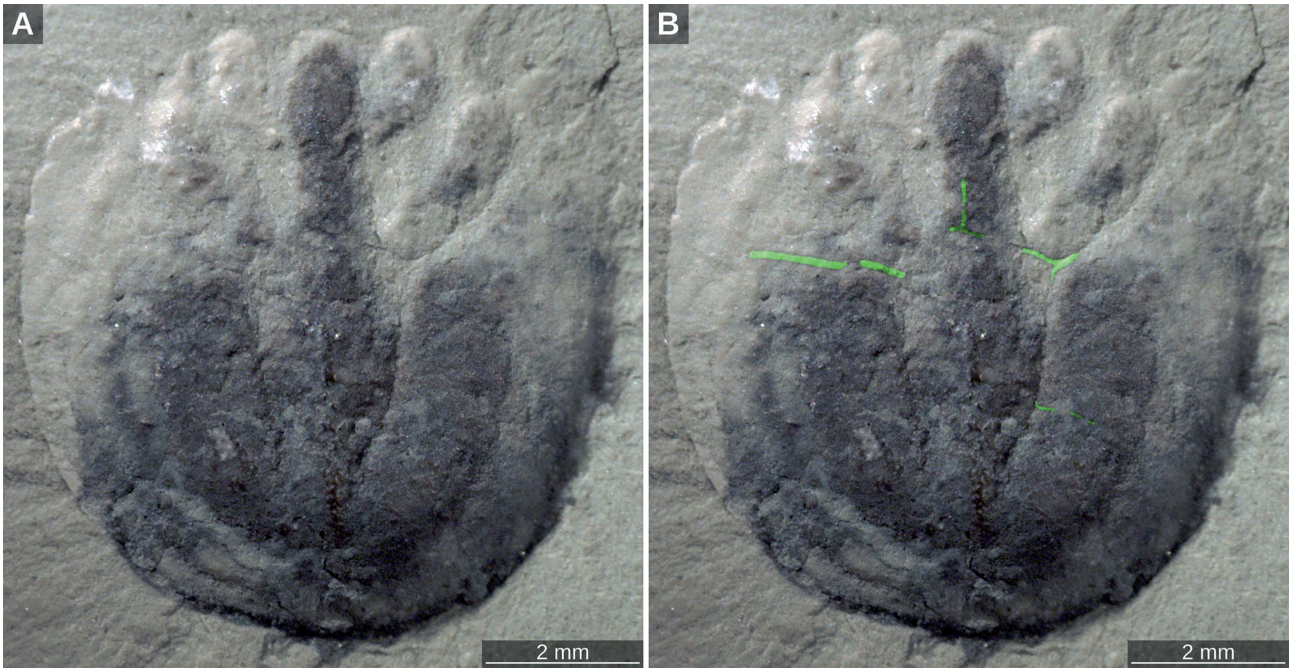

Fig. 5. A, B: *Halicyne oosterinkum*, holotype, MAB k. 003756, dorsal view; image from C. Schweitzer. with permission. **B:** lines on the shield marked in green colour.

MANN et al. 2017; FELDMANN & SCHWEITZER 2019). The branched structures in *A. handlirschi* differ considerably from known gills in Cyclida. It is possible that the structures in *A. handlirschi* represent only one or two lamellae of the gill apparatus (see reconstruction in DZIK 2008), whereas in other fossils of Cyclida the entire gill apparatus is preserved.

In SMNS 75641-1 there are at least 3 consecutive unpaired structures, roughly orthogonal to the midline, preserved as dark (organic?) matter (Fig. 2A, C blue color and indicated by a question mark). SCHWEBEL (1983) interpreted these structures as sternites (ventral sclerites of the trunk). There is, however, no correspondence of those structures to appendages of the trunk. It is unclear whether those structures are indeed sclerites or remains of internal organs. The colour of the structures is similar to the rami of the supposed gills, to which they are in close proximity. This makes it possible that these structures belong to the respiratory apparatus. We could not find comparable structures in other cyclidans.

Paired posterior processes ('caudal rami' in the literature) are present in some well-preserved fossils of Cyclida (e.g., SCHRAM et al. 1997, fig. 5.1). In the herein presented fossils they are not apparent. This means that the paired processes are either not present in *A. handlirschi* or they are present, but not preserved in the specimens. In SMNS 75641-1 the dorsal shield might overlay the paired processes due to the mode of preservation (see discussion above).

4.4. Diagnostic features

Due to the different modes of preservation, it is difficult to differentiate *A. handlirschi* from many cyclidan species based on morphological characters, because many species are represented by uncompressed or little compressed three-dimensional fossils without preserved appendages. *Americlus johnsoni* differs from *A. handlirschi* in having walking or grasping appendages with a distal-most peduncle element that is relatively smaller compared to *A. handlirschi* (WOODWARD 1905; HOPWOOD 1925; FELDMANN & SCHWEITZER 2019). *Americlus americanus* differs from *A. handlirschi* in having walking or grasping appendages with a distal-most peduncle element that is relatively smaller compared to *A. handlirschi* and in having subchelate appendages (SCHRAM et al. 1997; FELDMANN & SCHWEITZER 2019). *Americlus obesus* (SCHRAM, VONK & HOF, 1997) and *Americlus rankini* (WOODWARD, 1870) differ from *A. handlirschi* in having subchelate appendages (SCHRAM et al. 1997; CLARK et al. 2020). *Schramine max* (SCHRAM, VONK & HOF, 1997) differs from *A. handlirschi* in having much longer distal-most elements of the legs; also the margin of the shield in *Schramine max* is serrated, while in *A. handlirschi* the margin is smooth with sparse short spines (see asterisks in Fig. 2C; SCHRAM et al. 1997; FELDMANN & SCHWEITZER 2019). *Schramine montanaensis* (SCHRAM, BOERE & THOMAS, 2006) differs from *A. handlirschi* in having proportionally slenderer penultimate elements of the legs and longer distal-most elements of the legs. Also, the antennae in *S. montanaensis* are of the same width as the corresponding antennulae, while in *A. handlirschi* the antennae are much broader than the corresponding antennulae (SCHRAM et al. 2006). *Opolanka decorosa* DZIK, 2008 differs from *A. handlirschi* in having much shorter antennae; the characteristic lobate posterior margin of the shield in *O. decorosa* is either not present or not preserved in *A. handlirschi* (DZIK 2008). *Schramine gondwanae* (BRAMBILLA et al., 2002) differs from *A. handlirschi* in having more slender walking or grasping appendages and proportionally longer distal-most elements of the legs (DZIK 2008). *Schramine mamoroi* (PASINI & GARASSSINO, 2007) differs from *A. handlirschi* in having more slender walking or grasping appendages and proportionally longer distal-most elements of the legs (DZIK 2008). A probable representative of *Cyclus* from the Early Triassic of Madagascar (DZIK 2008; MSNM i2623) differs from *A. handlirschi* in having more slender walking or grasping appendages and proportionally longer distal-most elements of the legs. *Halicyne ornata* TRÜMPY, 1957 differs from *A. handlirschi* in having proportionally longer distal-most elements of the legs and robust setae on the penultimate elements of the legs (GALL 1971; SELDEN & NUDDS 2012). The type material of *Halicyne oosterinkum* does not comprise remains of the appendages. The shield is similar to *A. handlirschi*; however, the anterior margin of the inner and outer lyrate keels (Y-shaped structure) are further posterior than in *A. handlirschi* (SCHWEITZER et al. 2019).

4.5. Palaeoecology

The sedimentary environment, in which the remains of *Anhelkocephalon handlirschi* are preserved, is linked with mostly benthic organisms (GALL 1985). The clam shrimps (Spinicaudata, cf. *Palaeolimnadia alsatica* REIBLE, 1962) that are within the same sediment layer ('microtaphocoenosis') as the neotype (SMNS 75641-1; Figs. 2A, B, 3A) are indicative for temporary water bodies (GALL 1985). The geological and palaeontological context indicates a deltaic environment with a possible marine influence – making it likely that *A. handlirschi* lived in brackish or fresh water. The preserved appendages of *A. handlirschi* are not specialised as in other cyclidans (e.g., subchelate appendages in *Halicyne ornata*; GALL 1971), that would allow to make speculations about the autecology.

5. Systematic palaeontology

Arthropoda *s. str. sensu* Maas et al., 2004

Euarthropoda *sensu* Waloszek, 1999

Cyclida Dzik, 2008 (= Cycloidea Glaessner, 1928 *sensu* Schram, Vonk & Hof 1997)

Anhelkocephalon Bill, 1914 (*sensu* Schwebel, 1983)

Etymology: From Greek: an (ἄν, untranslatable), helkō (ἕλκω, to draw) and cephalon (head), describing the morphology of the anterior body region of the (lost) original type material.

Type species: *Anhelkocephalon handlirschi* Bill, 1914, monotypic.

Anhelkocephalon handlirschi Bill,
1914 (*sensu* Schwebel, 1983)
Figs. 2–4

1914 *Anhelkocephalon Handlirschi* Bill, p. 338.
1928 *Anhelkocephalon Handlirschi*. – Van Straelen, p. 27.
non 1957 *Anhelcocephalon handlirschi*. – Brooks, p. 923.
1969 *Anhelkocephalon handlirschi*. – Hessler, p. R379.
1983 *Anhelkocephalon handlirschi*. – Schwebel et al., p. 307, figs. 1–4.
1989 *Anhelkocephalon handlirschi*. – Wägele, p. 19.
1999 *Anhelkocephalon handlirschi*. – Brandt et al., p. 666, tab. 1
1993 *Anhelkocephalon handlirschi*. – Briggs et al. in Benton, p. 332.
1995 *Anhelkocephalon handlirschi*. – Basso & Tintori, p. 806.
2020 *Anhelkocephalon handlirschi*. – Schweitzer et al., p. 50.

Material: SMNS 75641-1 (neotype), SMNS 75641-2 (paraneotype), SMNS 75641-3.

Type locality and horizon: The locality for the lost original type material is Wasselonne (Wasselnheim, Dépt. Bas-Rhin, France, 48°38'28.5"N 7°26'52.8"E) (Bill 1914). The locality of the neotype (SMNS 75641-1) is Vilsberg (Wilsberg, Dépt. Moselle, France, 48°46'58.1"N 7°14'48.0"E) (Schwebel et al. 1983). Vilsberg is also the locality of SMNS 75641-3. The paraneotype (SMNS 75641-2) is from Petersbach (Dépt. Bas-Rhin, France, 48°53'12.6"N 7°16'02.0"E) (Schwebel et al. 1983). All are from the lower part of the Grès à Voltzia Formation (Grès à meules), Upper Buntsandstein (Anisian).

Diagnosis: See discussion above.

6. Conclusions

Anhelkocephalon handlirschi clearly is not a representative of Isopoda; it shows remarkable resemblance to some species within Cyclida. The systematic position of Cyclida and the relationship of the species and ingroups of Cyclida are still not well understood. *Anhelkocephalon handlirschi* adds interesting morphological features to the knowledge about cyclidans, which could prove useful for future analyses. The palaeontological content of the sediment in which it is preserved, suggests a brackish or a freshwater habitat for *Anhelkocephalon handlirschi* (e.g., Selden & Nudds 2012). From another perspective – with *A. handlirschi* not being an isopod, we have to assume that the morphological diversity of Isopoda in the Triassic was lower than previously assumed.

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