Revision of the thylacocephalan biota from the Upper Triassic Polzberg Konservat-Lagerstätte, Austria

THOMAS LAVILLE, PETRA LUKENEDER, and ALEXANDER LUKENEDER

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Known for over 140 years, the Upper Triassic Polzberg Konservat-Lagerstätte is an exceptional early Carnian marine assemblage discovered in the Northern Calcareous Alps of Lower Austria. The Polzberg biota is composed of a diverse marine fauna, including two species of thylacocephalans, an enigmatic group of fossil euarthropods that was highly diversified during the Triassic and thus representing a major component of many marine faunas throughout the Triassic. Recent excavations at the Polzberg lead to the discovery of new thylacocephalan specimens. In this study, we examine in detail this new thylacocephalan material as well as the type material. Four thylacocephalan taxa are now reported from the Polzberg Biota, making it one of the most diverse faunas from the Late Triassic. *Paraostenia striata* nov. comb., which was previously assigned to *Austriocaris* and later to *Atropicaris*, and *Paraostenia* cf. *ambatolokobensis* correspond to the first mention of *Paraostenia* in the Late Triassic. A new taxon, *Atropicaris*? sp, is reported for the first time from Polzberg. In addition, the presence of gills and muscles of the posterior trunk in *Austriocaris carinata* and *Paraostenia* cf. *ambatolokobensis* is the first trace of soft tissue preservation in Polzberg thylacocephalans. Additionally, we discuss the similarities of the Polzberg thylacocephalan fauna with other Triassic and Jurassic faunas. It shows great similarity with the Late Triassic Kozja dnina fauna, but also more surprisingly with the Middle Jurassic La Voulte fauna. This can be explained by the connection between the Neotethys and the Alpine Tethys during the Early Jurassic.

Key words: Arthropoda, Thylacocephala, Austria, Carnian Pluvial Episode, Palaeobiota, Polzberg Konservat-Lagerstätte, Triassic.

Thomas Laville [thomas.laville1@univ-tlse3.fr; ORCID: https://orcid.org/0000-0001-9081-7150], GET—Geosciences Environment Toulouse, Université Toulouse III—Paul Sabatier, 14 avenue Edouard Belin, 31400 Toulouse, France.
Petra Lukeneder [a0501032@unet.univie.ac.at; ORCID: https://orcid.org/0000-0003-4399-1214], Doctoral School of Ecology and Evolution, University of Vienna, Djerassiplatz 1, 1030 Vienna, Austria.
Alexander Lukeneder [alexander.lukeneder@nhm-wien.ac.at; ORCID: https://orcid.org/0000-0002-8384-3366], Department of Geology and Palaeontology, Natural History Museum Vienna, Burgring 7, 1010 Vienna, Austria.

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Introduction

Known for over 140 years (Stur 1874), the Upper Triassic Polzberg Konservat-Lagerstätte preserves an exceptional early Carnian marine assemblage discovered in the Northern Calcareous Alps of Lower Austria. Dated from the Carnian Julian 2 Ib, the Polzberg biota offers a unique insight into the evolution of marine ecosystems during one of the major geological Triassic events: the Carnian Pluvial Episode (CPE; Lukeneder et al. 2012, 2024; Ruffel et al. 2015; Dal Corso et al. 2020; Simms and Ruffel 2018). The CPE is characterised by a global warming and enhanced humidification during the early Carnian. This climate change led to an increase in siliciclastic influx towards the north-western branch of the Tethys, resulting in the deposition of the fossiliferous Reingraben formation at Polzberg.

The Polzberg biota is composed of a diverse marine fauna, with intermittent freshwater influences, as indicated by the presence of some freshwater inhabitants (Lukeneder and Lukeneder 2021). It yielded plant remains, bivalves, cephalopods, gastropods, polychaetes, arthropods, echinoids, vertebrate remains and coprolites, providing important new insights into Carnian food webs (Lukeneder and Lukeneder 2023).

Among arthropods, thylacocephalans are quite diverse and abundant in the Polzberg biota. Thylacocephalans are enigmatic fossil euarthropods characterised by a shield enveloping most of the body, hypertrophied compound eyes, three pairs of large raptorial appendages and a posterior

trunk formed of eight to 22 elongated segments. Known at least from the Silurian (Haug et al. 2014) to the Cretaceous (e.g., Charbonnier et al. 2017), thylacocephalans were highly diversified during the Triassic, representing a major component of many marine faunas throughout the Triassic (e.g., Arduini and Brasca 1984; Dalla Vecchia 2012; Charbonnier et al. 2019; Ehiro et al. 2019; Ji et al. 2021; Laville et al. 2024). However, for the Carnian, the fossil record of thylacocephalans is very scarce, being restricted to the Kozja dnina Member, Slovenia, that yielded three taxa (Laville et al. 2024), and to the Polzberg Konservat-Lagerstätte (Glaessner 1931; Forchielli and Pervesler 2013). The Polzberg thylacocephalan fauna includes two species: *Austriocaris carinata* Glaessner, 1931, and *Austriocaris striata* Glaessner, 1931. The latter species has been the subject of many speculations. Since the 1980s, it has been successively reassigned to *Ostenocaris* (Arduini et al., 1984) by Briggs and Rolfe (1983), to *Atropicaris* Arduini & Brasca, 1984, by Schram (2014) and to *Microcaris* Pinna, 1974, by Ji et al. (2021). To date no definitive decision has been made regarding its systematic affinities and it is therefore necessary to revise this species.

The present study provides new insights into the Polzberg thylacocephalan fauna. We revised all known Polzberg thylacocephalans, including the type material and new findings made during recent excavations. Additionally, we discuss the similarities of the Polzberg thylacocephalan fauna with other Triassic and Jurassic faunas.

Institutional abbreviations.—GBA, Geological Survey Austria (GeoSphere Austria since 2023); MSNM, Museo di Storia Naturale di Milano, Italy; NHMW, Naturhistorisches Museum Wien, Austria.

Other abbreviations.—Aad, anterodorsal angle; Aav, anteroventral angle; Apd, posterodorsal angle; Apv, posteroventral angle; Ha, anterior height; Hmax, maximal height; Hp, posterior height; Lr, rostrum length; Ls, total shield length; Lw, shield length without the rostrum.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:0F3508F1-AB47-45F3-A62E-313F406814CE.

Geological setting

The Upper Triassic outcrops at Polzberg are located on the western slope of Mount Schindelberg (1066 m), north of the Ois River, 4 km northeast of Lunz am See in Lower Austria. The locality Schindelberg is synonymous with the locality Polzberg (= Pölzberg; Stur 1874, 1886; 1:50 000, geological map, sheet 71 Ybbsitz; Ruttner and Schnabel 1988, and sheet 72 Mariazell; Bauer and Schnabel 1997; Lukeneder and Lukeneder 2021; Fig. 1). The northernmost tectonic elements of the Northern Calcareous Alps (NCA, Bajuvaric Units) in Lower Austria are the Frankenfels Nappe, followed to the south by the Lunz Nappe. Within the Lunz Nappe, the Reifling Basin (Krystyn 1991; Lukeneder and Lukeneder 2021, 2024; Lukeneder et al. 2024)—a Late Triassic intraplatform basin—is located between Polzberg and Großreifling. The exact position of the fossiliferous localities in the southern area of the Lunz Nappe within the lower, fossiliferous part of the Reingraben formation was determined by GPS (global positioning system): N 47°53’4.98” and E 15°4’28.15”, town Gaming, federal district Scheibbs.

The deposits at Polzberg can be assigned to three units (Lukeneder et al. 2024), in stratigraphic order the Reifling Formation (formalized), the Göstling Formation (= Göstling limestones, Göstlinger Kalke; not formalized; frequently noted as Göstling Formation of the uppermost part of the Reifling Formation) and the Reingraben formation (= Reingraben Shales, Reingrabener Schiefer; not formalized). The thylacocephalans described herein derive from the basal three meters, calcareous to argillaceous of the Reingraben formation.

Material and methods

The present study is based on 72 thylacocephalan specimens housed in the Palaeontological collections of the Naturhistorisches Museum Wien, Austria. The material was collected over the last 140 years (field campaign GBA 1886 and NHMW 1909). Birgitt and Karl Aschauer (both Waidhofen an der Ybbs, Lower Austria) contributed with private collections from the last 20 years. Two of us (PL and AL) also contributed to these extensive collections with their own findings over the last 4 years. Rock matrix was removed and specimens were mechanically prepared using hammer, chisel and awls, subsequently using various types of pneumatic tools (e.g., air scribes).

Most specimens are compressed laterally. Ten specimens are preserved in butterfly configuration, suggesting they are possibly exuviae (see Laville et al. 2021). Five specimens show soft tissue preservation (GBA 2021/002/0010; NHMW 1901/0015/0005, 1901/0015/0009, 1901/0015/00010, 1901/0015/0045).

Specimens were photographed with a Nikon Digital Camera, D 5200 SLR, lens Micro SX SWM MICRO 1:1 Ø52 Nikon AF-S, processed by the free graphic software tool digiCamControl version V.2.1.2.0 at the NHMW. Digital high-quality photomicrographs were taken using a Discovery.V20 Stereo Zeiss microscope. The magnifications were ×10, ×20 and ×40 in incident light mode. Data from the AxioCam MRc5 Zeiss were processed and documented using the AxioVision SE64 Rel. 4.9 imaging system at the NHMW. In some photographs, specimens were whitened with ammonium chloride sublimate before photography to enhance details of ornamentation. Processing of pictures (histogram optimization, contrast, brightness)

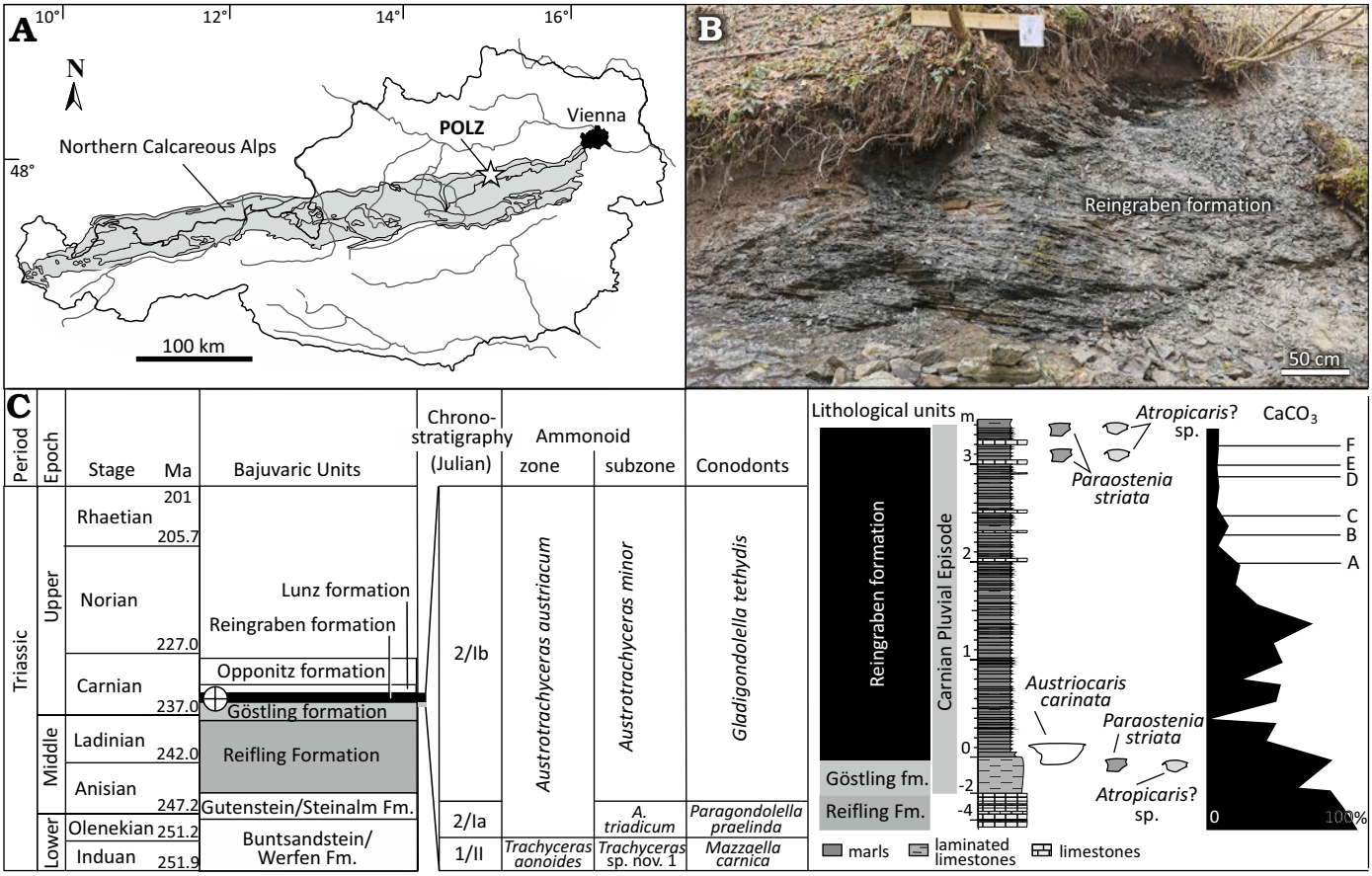

Fig. 1. Locality map of the Upper Triassic (lower Carnian) Polzberg area. **A**. Polzberg area (white star – POLZ) within the Northern Calcareous Alps (NCA), Lower Austria. **B**. Outcrop situation of the basal laminated Reingraben formation at Polzberg. **C**. Stratigraphic position of the lower Carnian Reingraben formation (cross-circle) at Polzberg with the layers comprising the Polzberg paleobiota within the Austrotrachyceras austriacum Zone. Log with indicated lithological units, thickness of the Polzberg section, $CaCO_3$ content and calcareous dolostone-layers A–F; NCA area in gray. Adapted after Lukeneder and Lukeneder 2021 and Lukeneder et al. 2024. Abbreviations: *A*., *Austrotrachyceras*; Fm./fm., Formation/formation.

was made with GIMP 2.10 (GNU). Plates and line drawings were made with Inkscape 1.2 (GNU).

Measurements on the shield follow the scheme defined by Laville et al. (2021). They were taken directly from digital photographs using Fiji (GNU; Schindelin et al. 2012).

Systematic paleontology

Euarthropoda Lankester, 1904

Thylacocephala Pinna et al., 1982

Genus *Atropicaris* Arduini & Brasca, 1984

Type species: *Atropicaris rostrata* Arduini & Brasca, 1984, by original designation—Argilliti di Riva di Solto Formation, Sevatian, Norian, Upper Triassic; Ponte Giurino, Valle Imagna, Italy.

Included species: *Atropicaris lintveri* Laville et al., 2024, Anisian, Middle Triassic, Slovenia; *Atropicaris* aff. *lintveri*, Anisian, Middle Triassic, Slovenia (Laville et al. 2024); *Atropicaris rostrata* Arduini & Brasca, 1984, Upper Triassic, Italy; *Atropicaris*? sp., Anisian, Middle Triassic, China (Feldmann et al. 2015); *Atropicaris*? sp., Carnian, Upper Triassic, Austria (this study); *Atropicaris* sp., Ladinian, Middle Triassic, Switzerland (Bürgin et al. 1991); *Atropicaris* sp., Carnian, Upper Triassic, Slovenia (Laville et al. 2024).

Diagnosis (after Laville et al. 2024).—Thylacocephala with a triangular rostrum ending in a spatulate tip, a serrate dorsal midline, a concave posterior margin, a spiny posteroventral corner, and dorsal and ventral intercalary ridges.

Stratigraphic and geographic range.—Anisian to Carnian, Middle to Late Triassic; Asia (China) and Europe (Austria, Italy, Slovenia, Switzerland).

Atropicaris? sp.

Fig. 2.

Material.—24 specimens: NHMW 1910/0015/0033, 0035; NHMW 2021/0123/0059, 0767, 0769, 0776, 0777, 0779, 0780, 0782–0784, 0787, 0788, 0790, 0793, 0795; NHMW 2021/0123/0078, 0101–0106. All from Reingraben formation, *Austrotrachyceras austriacum* Zone, *Austrotrachyceras minor* Biohorizon, Julian 2 Ib, Carnian, Late Triassic; Polzberg near Lunz am See, Austria.

Dimensions.—Due to the deformation and distortion of the specimens, we only provide rough estimates for the length and maximal height of the shield: Ls >15.5 mm; Hmax ≈ 8.5 mm.

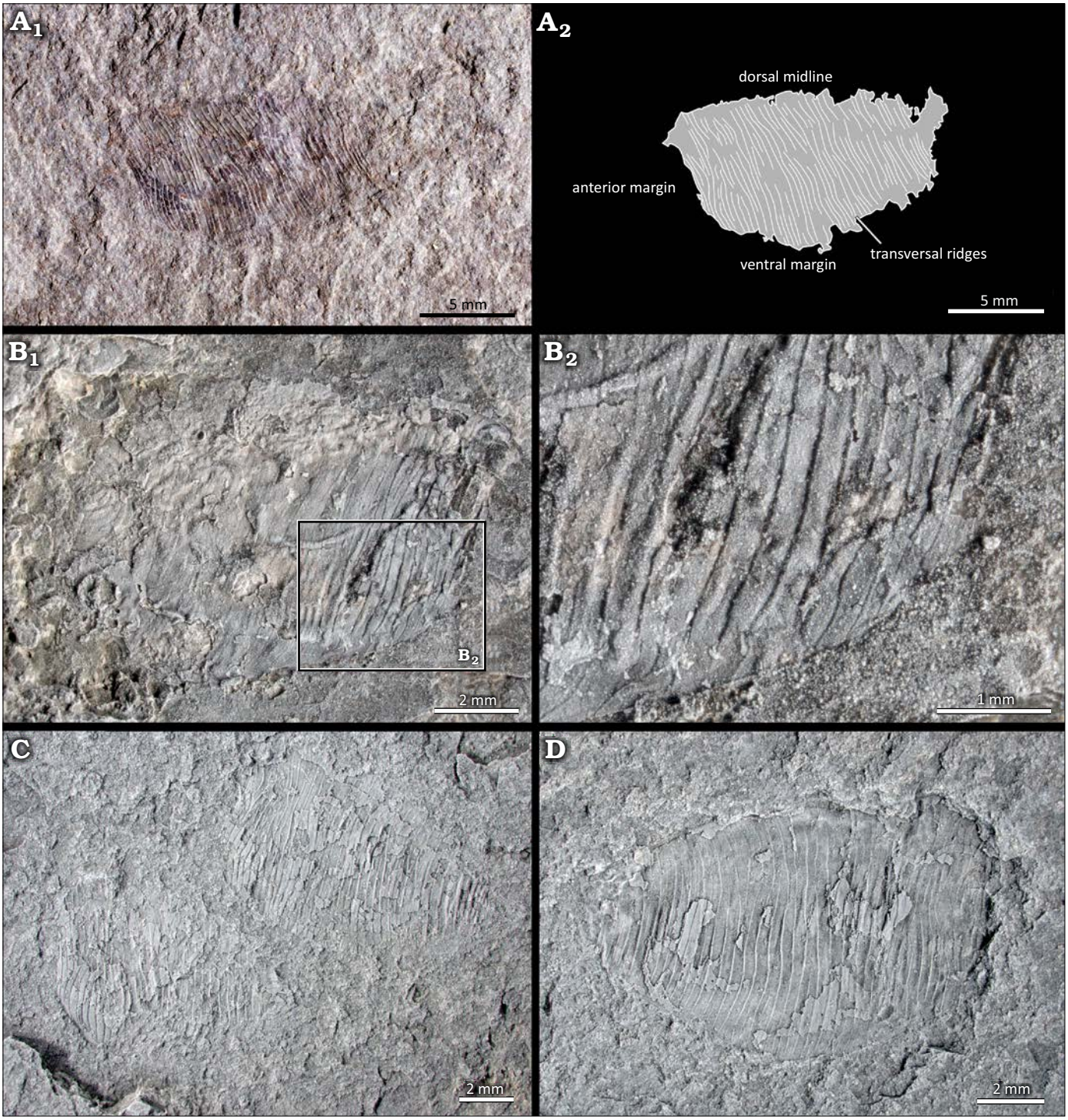

Fig. 2. Thylacocephalan arthropod *Atropicaris*? sp. from the Upper Triassic Polzberg Konservat-Lagerstätte, Austria. **A**. NHMW 1910/0015/0035; A_1, lateral view; A_2, explanatory drawing. **B**. NHMW 2021/0124/0102; B_1, left lateral view (ammonium chloride coating); B_2, close-up of anteroventral corner (ammonium chloride coating). **C**. Left lateral view of NHMW 2021/0124/0101 (ammonium chloride coating). **D**. Right lateral NHMW 2021/0124/0103 (ammonium chloride coating).

Description.—Shield morphology: Trapezoidal shield in lateral view, longer than high (Fig. 2). Maximal height reached around mid-length. Straight anterior margin slightly inclined posteroventrally (Fig. 2A, B). Anterodorsal corner not preserved. Convex dorsal midline, poorly preserved. Posterodorsal corner, posterior margin and posteroventral corner not preserved. V-shaped ventral margin consisting in an anterior part and a posterior one of equal length. Rounded anteroventral corner (Fig. 2B). Marginal fold delimited by a shallow groove at least near the ventral margin (Fig. $2B_1$).

Shield macro-ornamentation: Shield covered of at least 57 transverse sigmoid ridges, posteroventrally oriented with

at least 49 primary ridges, three dorsal intercalary ridges and five ventral intercalary ridges (Fig. 2).

Other structures: Appendages, posterior trunk and soft parts not preserved.

Remarks.—Some of the specimens described here were previously assigned to *Austriocaris striata* (now *Paraostenia striata* comb. nov.; see below). However, their morphology differs from the one of the type material (and thus from *Paraostenia*). Even though all specimens possess transversal ridges, the specimens described above have a straight and anterior margin slightly inclined posteroventrally, without any optic notch, an anterior part of the ventral margin anterodorsally tilted and a straight posterior part of the ventral margin while the type material of *P. striata* has an anterior margin formed of a large optic notch, occupying the entire margin, a ventral margin with a horizontal anterior part and a slightly concave posterior part. Therefore, those specimens do not belong to *P. striata*.

One of the main features of our specimens is the presence of transverse ridges. This kind of ornamentation is well known in multiple thylacocephalans taxa such as species of *Ankitokazocaris* Arduini, 1990, *Atropicaris*, *Concavicaris* Rolfe, 1961, *Ferrecaris* Calzada and Mañé, 1993, *Harrycaris* Briggs and Rolfe, 1983, *Kamnikaris* Laville et al., 2024, *Keelicaris* Teruzzi & Charbonnier in Charbonnier et al., 2017, *Microcaris* Pinna, 1974, *Paraconcavicaris* Rak et al., 2018, and *Thylacocephalus* Lange et al., 2001.

The species described here differ from those of *Ankitokazocaris*, *Concavicaris*, *Harrycaris*, and *Paraconcavicaris* by the absence of an optic notch. Additionally, species of *Paraconcavicaris* has a ventral margin with a horizontal anterior part, longer than the posterior one. Our specimens have similarities with species of *Kamnikaris*, including a convex dorsal midline and a straight anterior margin, slightly tilted posteroventrally. However, they differ from this taxon by their pattern of macro-ornamentation: species of *Kamnikaris* have vertical arcuate ridges on its anterior part, and sigmoid ridges on its median and posterior parts while the studied specimens only has sigmoid ridges on the entire surface of its shield. Moreover, species of *Kamnikaris* have a ventral margin, which has an anterior part much shorter than the posterior one, while it is of equal length in our specimens. This is also the case for species of *Thylacocephalus* and *Microcaris*. Moreover, these of *Microcaris* are characterised by a straight dorsal midline and a horizontal anterior part of the ventral margin. The specimens described herein also differ from species of *Thylacocephalus* by the absence of spines on the anterior margin, of a dorsal carina and of numerous pores on the lateral surface of the shield. The morphology of species of *Keelicaris* is also quite different from the one of our specimen. In *Keelicaris*, the shield is keel-shaped with straight transverse ridges anteroventrally tilted, the anterior margin is made of an optic notch and the ventral margin is formed of a concave posterior part and a horizontal ventral part.

Species of *Atropicaris* and *Ferrecaris* display several similarities with our specimens: a straight anterior margin, slightly tilted posteroventrally, convex dorsal midline, v-shaped ventral margin with straight posterior and anterior parts of equal lengths. It is therefore most likely that our specimens belong to one of these taxa. *Atropicaris* and *Ferrecaris* differ by their rostrum morphology (spatulate tip for *Atropicaris;* sharp, triangular tip for *Ferrecaris*), the ornamentation of their dorsal midline (serrate vs. smooth), the morphology of their posterior margin (concave surrounded by a posterodorsal and a posteroventral spine vs. straight with rounded posterodorsal and posterodorsal corners). Unfortunately, the rostrum and the posterior part are not preserved in our specimens and the dorsal midline is only poorly preserved, not allowing the observation of the ornamentation. It is therefore almost impossible to assign to one or the other taxon. As it seems that only species of *Atropicaris* show ventral intercalary ridges, this feature could be useful to accurately identify our specimens. Thus, our specimens most probably belong to a species of *Atropicaris*. Nevertheless, in view of the poor preservation of the type material of *Ferrecaris*, the latter character should be taken with caution as it would be possible for such ridges to be observed if better preserved material was discovered. Based on those comparisons, we leave our specimens in open nomenclature, although probably belonging to a species of *Atropicaris*.

Genus *Austriocaris* Glaessner, 1931

Type species: *Austriocaris carinata* Glaessner, 1931, by original designation, Reingraben formation, *Austrotrachyceras austriacum* Zone, *Austrotrachyceras minor* Biohorizon, Julian 2 Ib, Carnian, Upper Triassic, Polzberg, Austria.

Included species: Austriocaris sp., Carnian, Upper Triassic, Slovenia (Laville et al. 2024); *Austriocaris secretanae* Laville et al., 2023, Callovian, Middle Jurassic, France.

Emended diagnosis.—Thylacocephala with an optic notch occupying only the ventral part of the anterior margin, presence of a straight dorsal midline and a sharp posterodorsal corner.

Remarks.—In their diagnosis of *Austriocaris*, Laville et al. (2023) erroneously mentioned the presence of a sharp posteroventral corner. In reality, it is the posterodorsal angle that is sharp and diagnostic for *Austriocaris*.

Stratigraphic and geographic range.—Carnian, Late Triassic of Austria.

Austriocaris carinata Glaessner, 1931

Figs. 3–5.

1931 *Austriocaris carinata* sp. nov.; Glaessner 1931: 483, text-figs. 5, 6.
1969 *Austriocaris carinata* Glaessner, 1931; Rolfe 1969: R317, fig. 140.2.
1983 *Austriocaris carinata* Glaessner, 1931; Briggs and Rolfe 1983: 270, text-fig. 6C.
1990 *Austriocaris carinata* Glaessner, 1931; Dalla Vecchia and Muscio 1990: 41.
2014 *Austriocaris carinata* Glaessner, 1931; Schram 2014: 349.
2017 *Austriocaris carinata* Glaessner, 1931; Ji et al. 2017: 175.
2018 *Austriocaris carinata* Glaessner, 1931; Rak et al. 2018: 278, table 1.

Table 1. Descriptive statistics of morphometric measurements. Abbreviations: N, number of specimens measured; Na, number of specimens for which a specific measurement has not been made; NA, non-applicable; SD, standard deviation.

Mesures		*Austriocaris carinata* (N = 3)	*Paraostenia* cf. *ambatolokobensis* (N = 1)	*Paraostenia striata* (N = 2)
Total shield length (mm)	mean (SD)	86.45 (12.46)	31.35 (NA)	27.16 (1.31)
	minimum-maximum	76.06–100.26	31.35–31.35	26.23–28.09
	Na	0	0	0
Shield length without the rostrum (mm)	mean (SD)	76.68 (11.04)	NA (NA)	NA (NA)
	minimum-maximum	67.97–89.10	NA	NA
	Na	0	1	2
Rostrum length (mm)	mean (SD)	9.83 (1.53)	NA (NA)	NA (NA)
	minimum-maximum	8.17–11.18	NA	NA
	Na	0	1	2
Anterior height (mm)	mean (SD)	29.17 (4.09)	14.98 (NA)	12.96 (0.59)
	minimum-maximum	26.27–32.06	14.98–14.98	12.54–13.38
	Na	1	0	0
Maximal height (mm)	mean (SD)	NA (NA)	19.36 (NA)	15.96 (1.19)
	minimum-maximum	NA	19.36–19.36	15.12–16.80
	Na	3	0	0
Posterior height (mm)	mean (SD)	7.71 (2.37)	4.56 (NA)	6.23 (0.02)
	minimum-maximum	6.04–9.39	4.56–4.56	6.22–6.25
	Na	1	0	0
Anterodorsal angle (°)	mean (SD)	61.15 (0.87)	68.52 (NA)	67.13 (1.94)
	minimum-maximum	60.53–61.77	68.52–68.52	65.76–68.50
	Na	1	0	0
Anteroventral angle (°)	mean (SD)	82.28 (1.14)	71.31 (NA)	74.16 (4.02)
	minimum-maximum	81.37–83.56	71.31–71.31	71.32–77.00
	Na	0	0	0
Posteroventral angle (°)	mean (SD)	145.76 (0.77)	107.32 (NA)	90.52 (0.67)
	minimum-maximum	145.22–146.30	107.32–107.32	90.05–91.00
	Na	1	0	0
Posterodorsal angle (°)	mean (SD)	82.27 (1.61)	97.70 (NA)	76.20 (16.65)
	minimum-maximum	80.56–83.76	97.70–97.70	64.43–87.98
	Na	0	0	0
Maximal height/total shield length ratio	mean (SD)	NA (NA)	0.62 (NA)	0.59 (0.02)
	minimum-maximum	NA	0.62–0.62	0.58–0.60
	Na	3	0	0

2019 *Austriocaris carinata* Glaessner, 1931; Charbonnier et al. 2019: table 1.

2021 *Austriocaris carinata* Glaessner, 1931; Ji et al. 2021: table 1.

2021 *Austriocaris carinata* Glaessner, 1931; Laville et al. 2021: table 1.

2021 *Austriocaris carinata* Glaessner, 1931; Lukeneder and Lukeneder 2021: fig. 3L, table 1.

2023 *Austriocaris carinata* Glaessner, 1931; Lukeneder and Lukeneder. 2023: fig. 3Q, table 1.

Holotype: NHMW 1910/0015/0041; sub-complete shield with well-preserved ornamentation.

Type locality: Polzberg near Lunz am See, Austria.

Type horizon: Reingraben formation, *Austrotrachyceras austriacum* Zone, *Austrotrachyceras minor* Biohorizon, Julian 2 Ib, Carnian, Upper Triassic.

Material.—Type material and 37 specimens: GBA 2021/002/0010, NHMW 1910/0015/0001–0017, 0037–0039, 0040, 0044–0050; NHMW 2021/0123/0002, 0203, 0764–0766; NHMW 2021/0124/0108–0110. All from type locality and horizon.

Dimensions.—See Table 1.

Description.—*Shield morphology*: Sub-trapezoidal shield in lateral view, much longer than high (Fig. 3A$_1$, A$_3$). Maximal height reached around mid-length. Anterior margin made of an optic notch in its ventral part, sinuous and posteroventrally oriented in its dorsal part (Fig. 3A–C). Anterodorsal corner expressed as a sharp, short triangular rostrum (Fig. 3B). Straight and horizontal dorsal midline, divided into two branches near the posterodorsal angle and thus delimiting this later (Fig. 4A$_1$–A$_3$). Posterodorsal corner expressed as a spine (Fig. 3D, E). Short, straight and vertical posterior margin. Ventral margin divided into a straight posterior part, anteroventrally oriented, and a straight horizontal anterior part (Fig. 3C). Anterior part longer than the posterior one. Both parts merging approximately at the posterior third of the length. Rounded anteroventral corner. Marginal fold delimited by a shallow groove near all free margins (Fig. 4D$_1$, D$_2$).

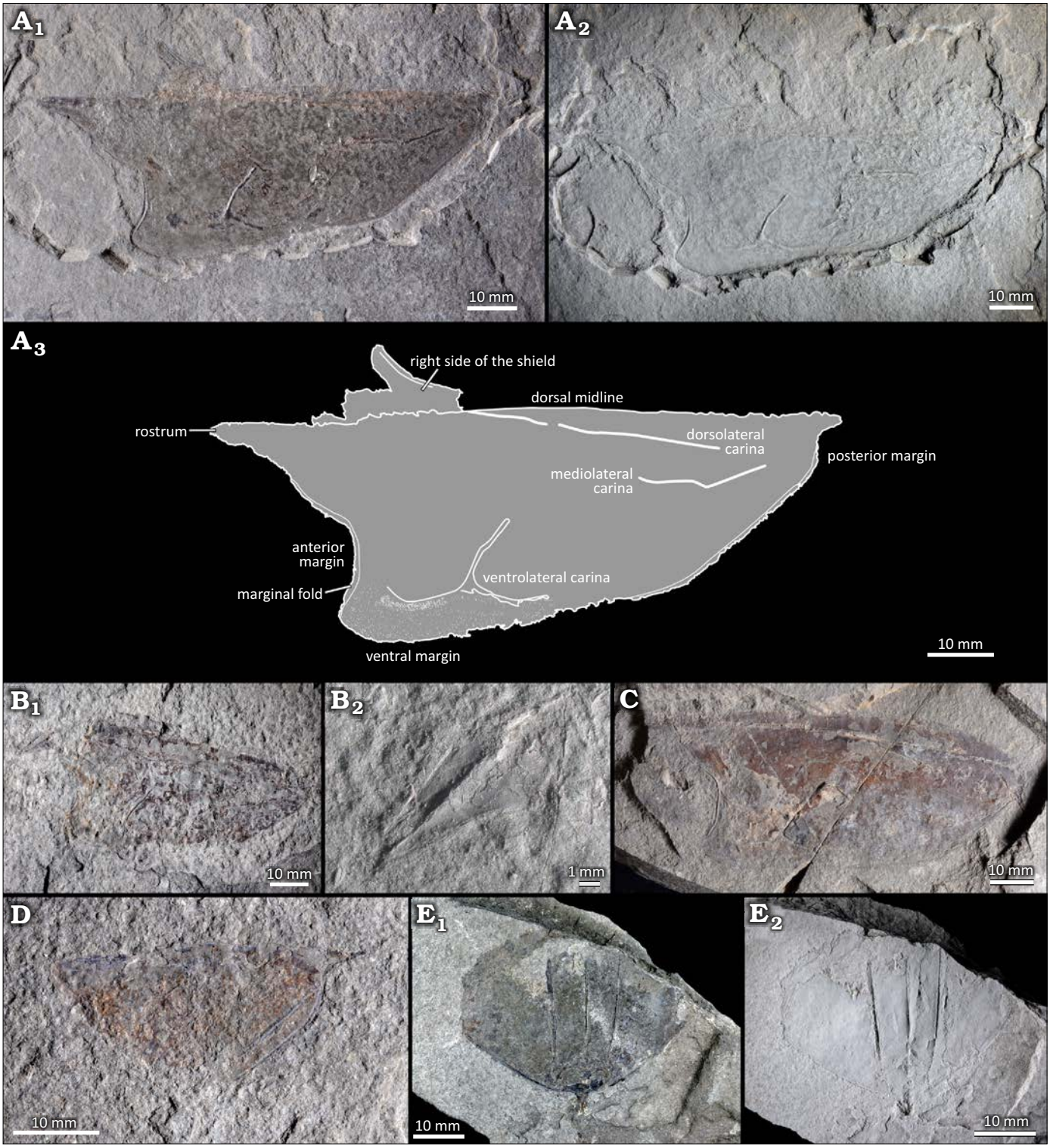

Fig. 3. Thylacocephalan arthropod *Austriocaris carinata* Glaessner, 1931, from the Upper Triassic Polzberg Lagerstätte, Austria. **A**. NHMW 1910/0015/0041 (holotype); A_1, left lateral view; A_2, left lateral view (ammonium chloride coating); A_3, explanatory drawing. **B**. NHMW 1910/0015/0002; B_1, left lateral view; B_2, close-up of rostrum (ammonium chloride coating). **C**. NHMW 1910/0015/0014, left lateral view. **D**. NHMW 1910/0015/0001, left lateral view. **E**. NHMW 1910/0015/0039; E_1, dorsal view; E_2, dorsal view (ammonium chloride coating).

Shield macro-ornamentation: Shield with a straight dorsolateral carina, slightly tilted posteroventrally (Fig. 4D_1, D_2). Dorsolateral carina converging with the dorsal midline at about one fifth of the length. Dorsolateral carina adorned with at least 30 tubercles, which might be remains of spines. Mediolateral carina located in the posterior half of the shield (Fig. 3A). Mediolateral carina divided into a posterior half, anteroventrally tilted, and straight horizontal anterior half.

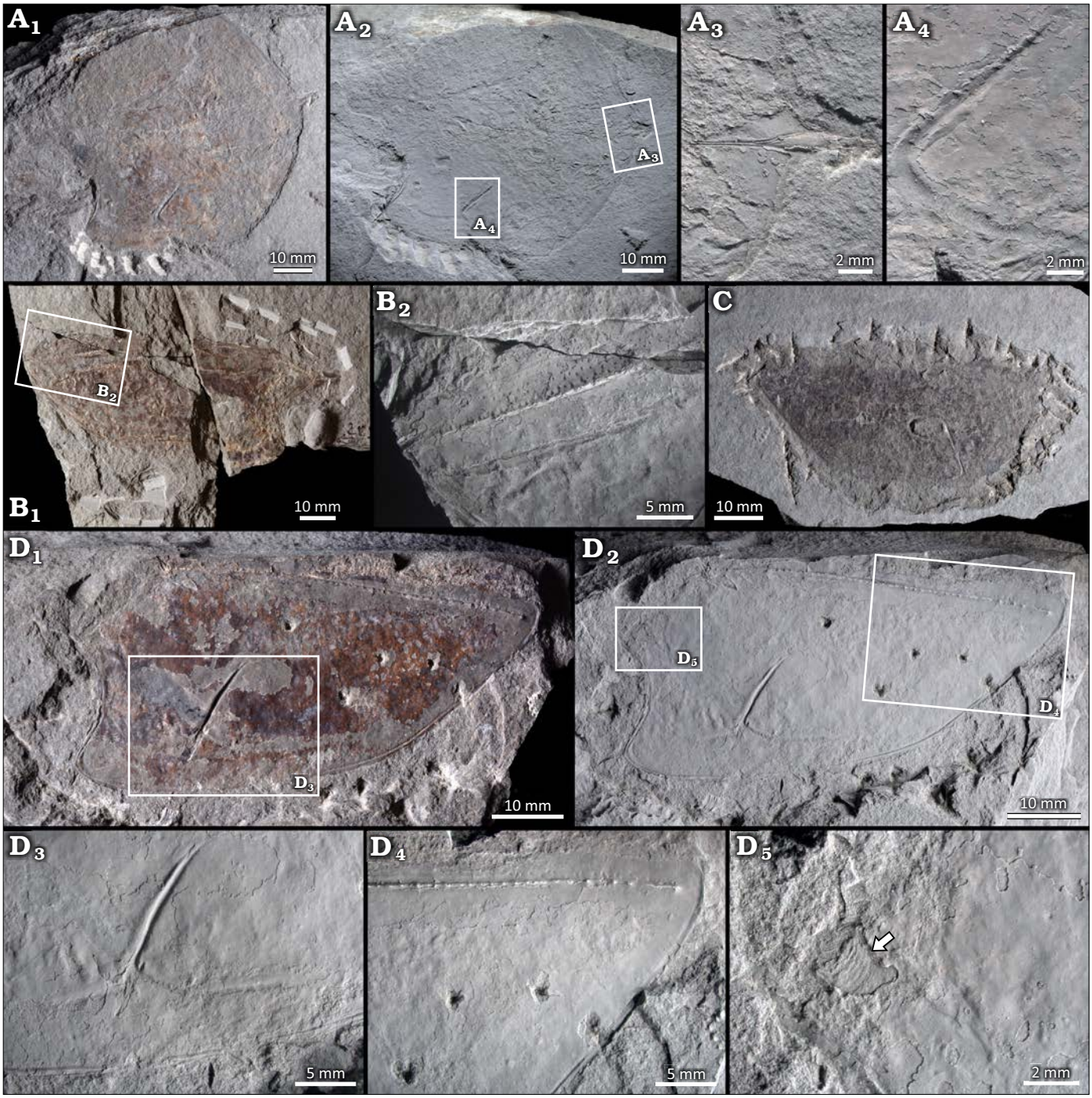

Fig. 4. Thylacocephalan arthropod *Austriocaris carinata* Glaessner, 1931, from the Upper Triassic Polzberg Lagerstätte, Austria. **A**. NHMW 1910/0015/0050; A_1, dorsal view; A_2, dorsal view (ammonium chloride coating); A_3, close-up of posterodorsal corner; A_4, close-up of ventrolateral carina. **B**. NHMW 2021/0123/0764a; B_1, right lateral view; B_2, close-up of dorsolateral part of the shield (ammonium chloride coating). **C**. NHMW 1910/0015/0044, right lateral view. **D**. NHMW 1910/0015/0045; D_1, left lateral view; D_2, left lateral view (ammonium chloride coating); D_3, close-up of ventrolateral carina (ammonium chloride coating); D_4, close-up of dorsolateral carina (ammonium chloride coating); D_5, close-up of gills (ammonium chloride coating).

C-shaped ventrolateral carina, located in the anterior half of the shield (Figs 3A, $4A_1$, A_2, A_4). Concavity of the carina directed posteriorly. In some specimens, ventrolateral carina associated with a large oval bulge near its dorsal tip (Fig. 4C). Short straight lateral carina dividing the rostrum into two parts (Fig. 4B). Fields of small punctuations visible between the anteroventral corner and the ventrolateral carina (Fig. $4D_1$, D_3), and in the dorsal part of the shield, above the dorsolateral carina (Fig. 4B). High density of punctuations on the ventral branch of the ventrolateral carina, and on the part symmetrical to the ventral branch, in relation to the dorsal branch, giving the impression of having a third branch to the carina (Fig. 3A).

Posterior trunk: Posterior trunk made of at least five

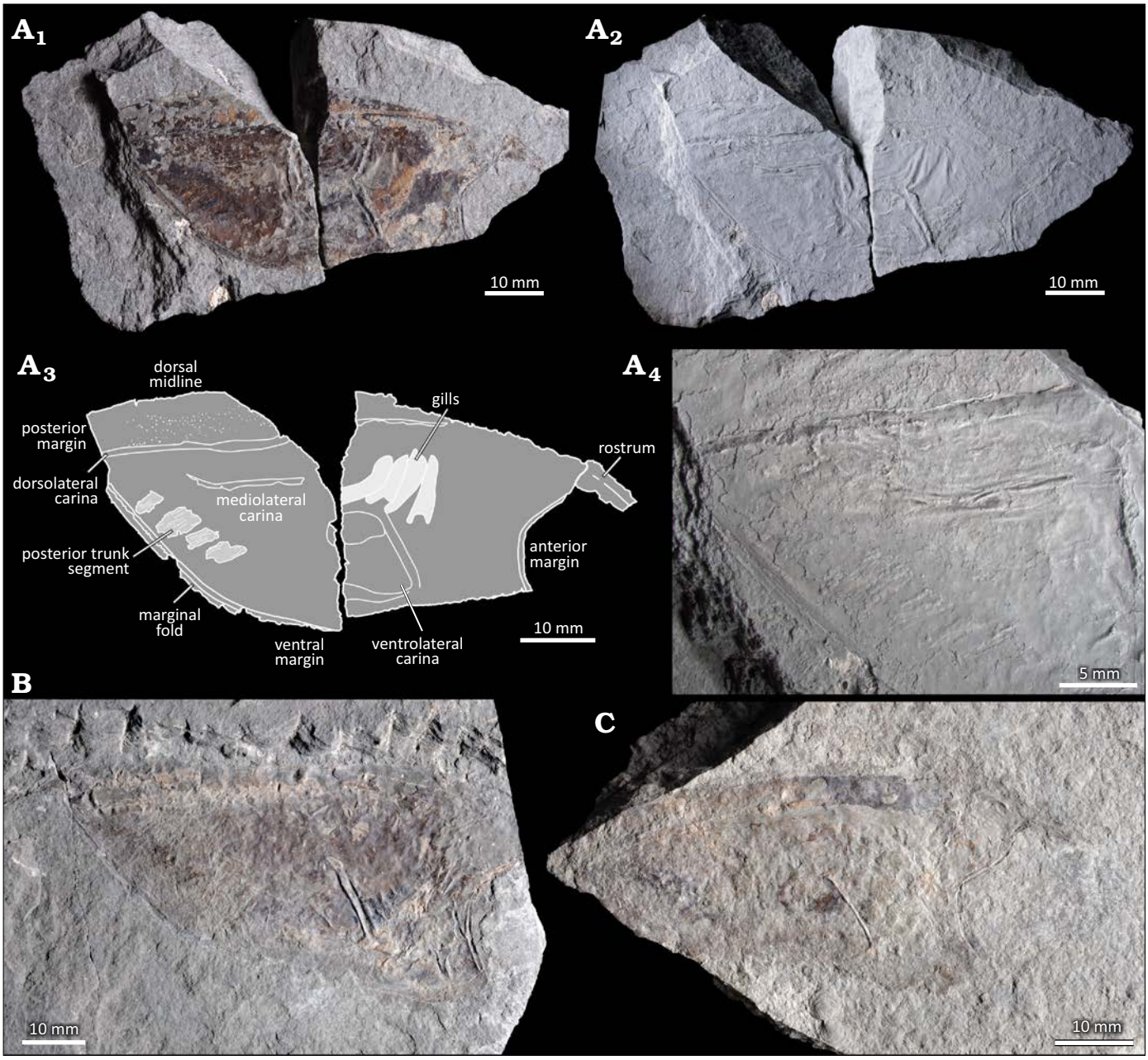

Fig. 5. Thylacocephalan arthropod *Austriocaris carinata* Glaessner, 1931 from the Upper Triassic Polzberg Lagerstätte, Austria. **A**. NHMW 1910/0015/0009; A_1, right lateral view; A_2, right lateral view (ammonium chloride coating); A_3, explanatory drawing; A_4, close-up of posterior trunk (ammonium chloride coating). **B**. Right lateral view of NHMW 1910/0015/0005. **C**. Right lateral view of NHMW 1910/0015/0010.

segments, visible by their lateral musculature in the posterior part of the shield (Fig. 5).

Gills: Set of four gills located in the central part of the shield. Gills with an elliptic shape, becoming arcuate near the dorsal midline (Figs. $4D_5$, $5A_1$–A_3).

Other structures: Compound eyes and raptorial appendages not preserved.

Remarks.—In its original description of *Austriocaris carinata*, Glaessner (1931) had reversed the orientation of the specimens, the posterior part being at the front. This influenced his description, leading for example to describe the optical notch as a posterior notch, from which the abdomen came out. Rolfe (1969) and Forchielli and Pervesler (2013) later followed this orientation.

Since the original description, *A. carinata* has been recognised as a thylacocephalan, and new species of *Austriocaris* have been described (Laville et al. 2023, 2024). This allowed to clarify the orientation of *Austriocaris*.

Two other morphological characters have also been misidentified in the past. The first is the anterior part of the ventral margin. Indeed, this structure is actually not anteroventrally tilted, as depicted by Glaessner (1931) and Rolfe (1969), but it is horizontal, as shown in Fig. 3C. The second character is the presence of a rostral plate. The posterodorsal

spine delimited by the dichotomy of the dorsal midline has been interpreted as a rostral plate based on the comparison with phyllocarids. However, this spine neither is a rostrum and nor is articulated (absence of hinge) and thus is not movable as in phyllocarids.

With this redescription, we also provide new details that were previously unknown such as the presence of tubercles on the dorsolateral carina. A tuberculate dorsolateral carina was already known in one species of *Austriocaris*, *Austriocaris secretanae* Laville et al., 2023. The most important character newly described is the soft-part-preservation. Indeed, several gills as well as the lateral musculature of some posterior trunk segments are reported here. This is the first record of soft part preservation in Polzberg thylacocephalans.

Stratigraphic and geographic range.—Carnian, Upper Triassic of Austria.

Genus *Paraostenia* Secrétan, 1985

Type species: *Paraostenia voultensis* Secrétan, 1985, by monotypy—*gracilis* Biozone, lower Callovian, Middle Jurassic; La Voulte-sur-Rhône, Ardèche, France.

Species included: *Paraostenia ambatolokobensis* (Arduini, 1990), Dienerian/Smithian, Lower Triassic, Madagascar; *Paraostenia striata* (Glaessner, 1931) comb. nov., Carnian, Upper Triassic, Austria; *Paraostenia voultensis* Secrétan, 1985, Callovian, Middle Jurassic, France; *Paraostenia* sp. Ehiro & Kato in Ehiro et al., 2015, Spathian, Lower Triassic, Japan.

Emended diagnosis (after Laville et al. 2023).—Thylacocephala with a symmetric optic notch, a sharp anterodorsal corner, a dorsal carina, a concave posterior margin, rounded posterodorsal and posteroventral corners, long and gracile appendages.

Stratigraphic and geographic range.—Dienerian to Callovian, Early Triassic to Middle Jurassic; Asia (Japan), Africa (Madagascar) and Europe (Austria, France).

Paraostenia striata (Glaessner, 1931) comb. nov.

Fig. 6.

1931 *Austriocaris striata* sp. nov.; Glaessner, 1931: 483, 484, text-figs. 7, 8.
1984 *Ostenia striata* (Glaessner, 1931); Briggs and Rolfe 1983: 270, text-fig. 6b.
1984 *Austriocaris striata* Glaessner, 1931; Arduini and Brasca 1984: 92.
1986 *Austriocaris striata* Glaessner, 1931; Tintori et al. 1986: 241.
1990 *Austriocaris striata* Glaessner, 1931; Dalla Vecchia and Muscio 1990: 41.
2014 *Atropicaris striata* (Glaessner, 1931); Schram 2014: 352.
2015 *Ostenocaris striata* (Glaessner, 1931); Ehiro et al. 2015: 279, table 1.
2019 *Austriocaris striata* Glaessner, 1931; Teruzzi and Muscio 2019: 54.
2019 *Atropicaris striata* (Glaessner, 1931); Charbonnier et al. 2019: table 1.
2021 *Microcaris* (*Atropicaris*) *striata* (Glaessner, 1931); Ji et al. 2021: 311, table 1.
2021 *Atropicaris striata* (Glaessner, 1931); Laville et al. 2021: table 1.
2021 *Atropicaris striata* (Glaessner, 1931); Lukeneder and Lukeneder 2021: fig. 3M, table 1.
2023 *Atropicaris striata* (Glaessner, 1931); Lukeneder and Lukeneder 2023: fig. 3P, table 1.
2024 *Atropicaris striata* (Glaessner, 1931); Lukeneder et al. 2024: 21.

Holotype: NHMW 1910/0015/0042, complete shield.

Type locality: Polzberg near Lunz am See, Austria.

Type horizon: Reingraben formation, *Austrotrachyceras austriacum* Zone, *Austrotrachyceras minor* Biohorizon, Julian 2 Ib, Carnian, Upper Triassic.

Diagnosis (this study).—*Paraostenia* with thin transversal and slightly sigmoid ridges on the shield.

Material.—Type material and eight specimens: NHMW 1910/0015/0034, 0036, 0043; NHMW 2021/0123/0770, 0772, 0791, 0796, 0797. All from the type locality and horizon.

Dimensions.—See Table 1.

Description.—*Shield morphology*: Curved pentagonal-shaped shield in lateral view, longer than large (Fig. 6A_1–A_3, B_1–C_2). Maximal height reached around mid-length. Anterior margin made of a well-developed, symmetric optic notch, occupying the entire margin (Fig. 6B). Sharp anterodorsal corner. Convex dorsal midline. Rounded posterodorsal and posteroventral corners. Short, concave posterior margin, posteroventrally tilted (Fig. 6A_1–A_3). Ventral margin made of a horizontal anterior part and a slightly concave posterior one, anteroventrally tilted; both parts having approximately the same length (Fig. 6A). Rounded anteroventral corner (Fig. 6C_3). Marginal fold delimited by a shallow groove near all free margins (Fig. 6A_4).

Shield macro-ornamentation: Shield with a comma-shaped ventrolateral furrow (Fig. 6A_1–A_3). Anterior part of the ventral margin adorned with at least 17 small tubercles near the anteroventral corner (Fig. 6C_3). Shield covered of at least 140 thin slightly sigmoid transverse ridges, posteroventrally oriented in the first quarter of the shield, vertical in the second quarter; in the second half of the shield, ridges being vertical in the dorsal part and becoming anteroventrally tilted near the posterior part of the ventral margin (Fig. 6A_1–A_4).

Other structures: Appendages, posterior trunk and soft parts not preserved.

Remarks.—The species *A. striata* was first assigned by Glaesnner (1931) to *Austriocaris*. Many years later, Briggs and Rolfe (1983) noticed the differences between the specimens of *A. striata* and *Austriocaris*. *Austriocaris* has a rostrum, an optic notch restricted to the ventral part of the anterior margin, a straight dorsal midline, a spiny posterodorsal corner, a straight dorsal margin and a shield covered by three lateral carinae while *A. striata* does not have a rostrum and lateral carinae but have a convex dorsal midline, a rounded posterodorsal corner and a concave dorsal margin. Briggs and Rolfe (1983) thus decided to assign this species to *Ostenocaris* Arduini et al., 1984 (known as *Ostenia* at that time). However, *A. striata* differs from *Ostenocaris* species by the morphologies of the anterior margin (optic notch in *A. striata*, sinuous and proverse in *Ostenocaris*)

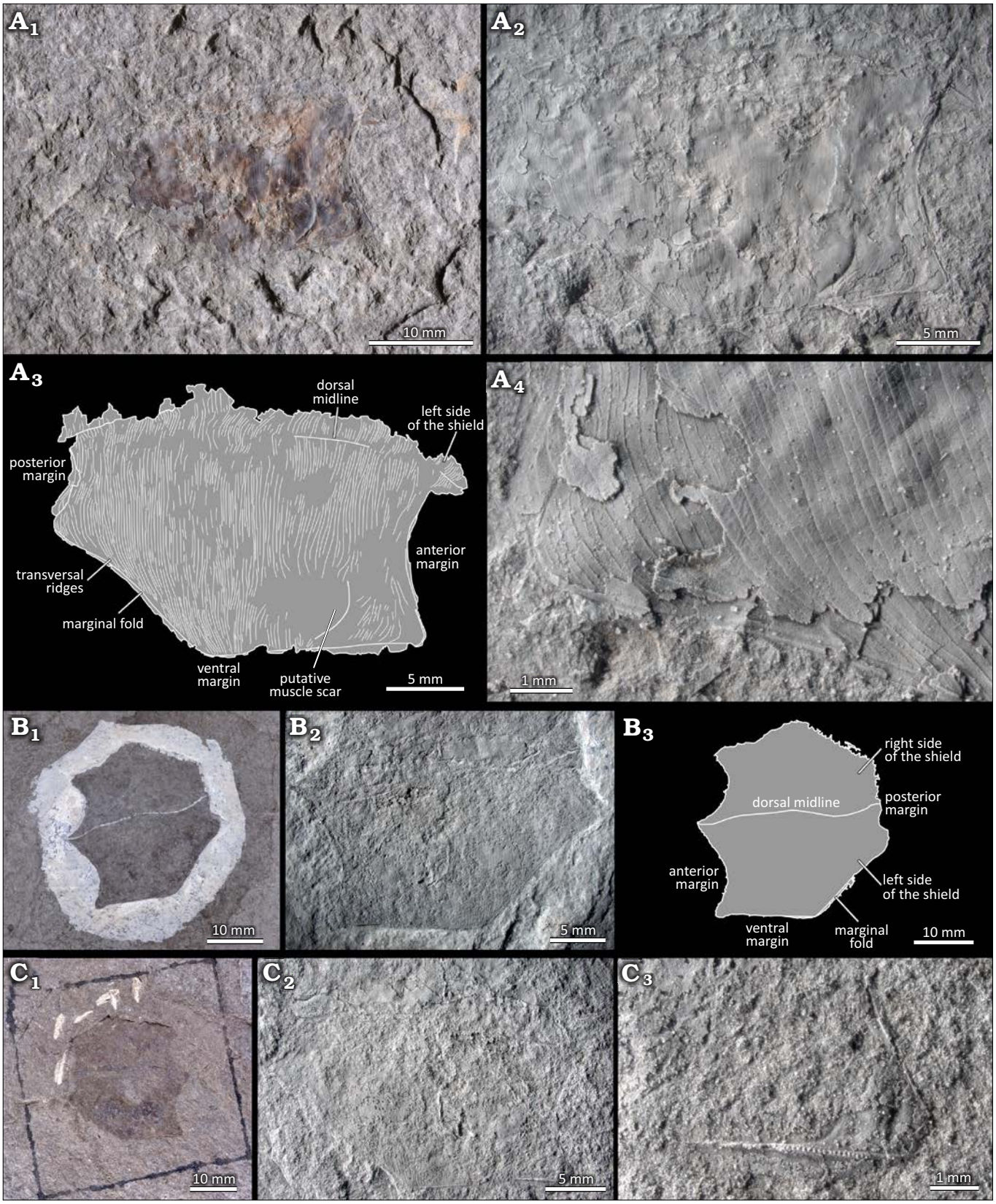

Fig. 6. Thylacocephalan arthropod *Paraostenia striata* (Glaessner, 1931) from the Upper Triassic Polzberg Lagerstätte, Austria. **A**. NHMW 1910/0015/0034; A_1, left lateral view; A_2, left lateral view, ammonium chloride coating; A_3, explanatory drawing; A_4, close-up of posteroventral corner, ammonium chloride coating. **B**. NHMW 1910/0015/0042 (holotype, counter-part); B_1, dorsal view; B_2, close-up of left side of the shield, ammonium chloride coating; B_3, explanatory drawing. **C**. NHMW 1910/0015/0042 (holotype, part); C_1, dorsal view; C_2, close-up of right side of the shield, ammonium chloride coating; C_3, close-up of anteroventral corner, ammonium chloride coating.

and of the posterior margin (concave vs. straight). The confusion of Briggs and Rolfe (1983) might come from the fact that in the original description of *Ostenocaris cypriformis* Arduini et al., 1984, the type species of *Ostenocaris*, some specimens of *Paraostenia* have been assigned, provoking many misidentifications as explained by Laville et al. (2021).

A year after Briggs and Rolfe (1983), Arduini and Brasca (1984) reassigned *A. striata* to *Atropicaris* based mostly on the presence of ridges and of a rostrum. This choice was later followed by most authors (e.g., Dalla Vecchia and Muscio 1990; Schram 2014; Ehiro et al. 2015; Ji et al. 2021 as *Microcaris* (*Atropicaris*) *striata*; Laville et al. 2021). As explained above for *Atropicaris*? sp., several specimens assigned to *A. striata* actually have a morphology quite different from the holotype, and are most likely belonging to *Atropicaris*. However, the holotype and additional specimens mentioned here differ from *Atropicaris* species especially by the absence of a rostrum, by the presence of an optic notch and by the horizontal morphology of the anterior part of the ventral margin.

Actually, *A. striata* possesses the typical characters of *Paraostenia* Secrétan, 1985: a large optic notch, a sharp anterodorsal corner, a rounded anteroventral corner, a concave posterior margin, a rounded posterodorsal corner and a horizontal anterior part of the ventral margin. *A. striata* should be assigned to *Paraostenia*. We therefore propose a new combination *Paraostenia striata* comb. nov. for this species.

Paraostenia striata display a unique character among *Paraostenia*: the thin transversal ridges. Even though shield macro-ornamentation is well-known in other *Paraostenia* species (horseshoe-like ornamentation in *Paraostenia voultensis* Secrétan, 1985; longitudinal ridges in *Paraostenia ambatolokobensis* [Arduini, 1990]), thin transversal ridges are only known in *P. striata*.

In addition, *P. striata* does not carry any lateral or dorsal carina, unlike other species. Nevertheless, due to the poor preservation of the dorsal midline or to the butterfly configuration of the specimens, it is difficult to accurately determine the presence or absence of a dorsal carina.

Stratigraphic and geographic range.—Carnian, Upper Triassic of Austria.

Paraostenia cf. *ambatolokobensis* (Arduini, 1990)

Fig. 7.

Material.—NHMW 2024/0201/00012 from the Reingraben formation, *Austrotrachyceras austriacum* Zone, *Austrotrachyceras minor* Biohorizon, Julian 2 Ib, Carnian, Upper Triassic; Polzberg near Lunz am See, Austria.

Dimensions.—See Table 1.

Description.—*Shield morphology*: Curved hexagonal-shaped shield in lateral view, longer than large (Fig. 7A$_1$, A$_2$). Maximal height reached around mid-length. Anterior margin made of a well-developed, symmetric optic notch, occupying the entire margin. Anterodorsal corner not pre-

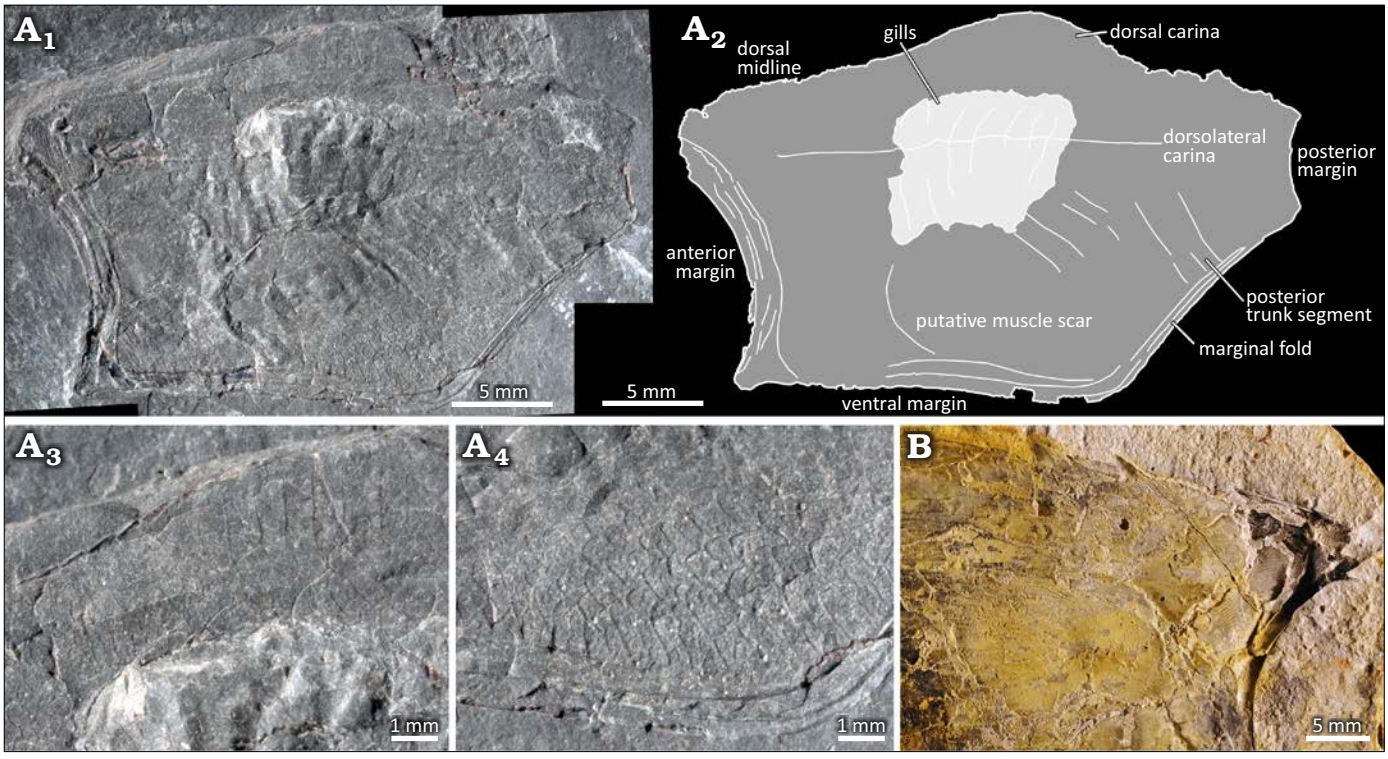

Fig. 7. Comparison of thylacocephalan arthropods *Paraostenia* cf. *ambatolokobensis* (Arduini, 1990), from the Upper Triassic Polzberg Lagerstätte, Austria (A) and *Paraostenia ambatolokobensis* (Arduini, 1990) from the Upper Triassic, Madagascar (B). **A**. NHMW 2024/0201/0001; A$_1$, left lateral view; A$_2$, explanatory drawing; A$_3$, close-up of dorsal carina; A$_4$, close-up of ventral margin. **B**. MSNM i27655 a/b, right lateral view.

served. Convex dorsal midline with a large fin-like carina (Fig. 7A$_3$). Rounded posterodorsal corner. Short, concave posterior margin. Rounded posteroventral corner. Ventral margin made of a horizontal anterior part and a slightly concave posterior one, anteroventrally tilted; both parts having approximately the same length (Fig. 7A$_1$, A$_2$). Rounded anteroventral corner. Marginal fold delimited by a shallow groove near anterior and ventral margin (Fig. 7A$_4$).

Shield macro-ornamentation: Shield with a comma-shaped ventrolateral furrow, being most probably a muscle scar (Fig. 7A$_1$, A$_2$). Long dorsolateral carina running along almost the entire length of the shield. Shield covered of short, transversal ridges. Ridges having a comma-like shape below the dorsal carina and near the anterodorsal and anteroventral corners (Fig. 7A$_3$), and a scale-like shape on the rest of the shield (Fig. 7A$_4$).

Posterior trunk: Posterior trunk made of at least four segments (Fig. 7A$_1$, A$_2$).

Gills: Set of eight gills located in the central part of the shield. Gills with an elliptic shape, becoming arcuate near the dorsal midline (Fig. 7A$_1$, A$_2$).

Remarks.—The specimen described above have key features of *Paraostenia* Secrétan, 1985: a large optic notch, a dorsal carina, a concave posterior margin, rounded posterodorsal and posteroventral corners and a horizontal anterior part of the ventral margin. It differs from the other *Paraostenia* specimens from Polzberg by the presence of a dorsal carina and by its pattern of macro-ornamentation (scale-like ridges vs long, transverse ridges). In terms of size, the specimen is a bit longer and taller than *Paraostenia striata* and the Hmax/Ls ratios are quite similar (see Table 1). The specimen resembles the specimens of *Paraostenia ambatolokobensis* from the Lower Triassic of Madagascar (Arduini 1990). Indeed, they both have a dorsal carina and a dorsolateral carina but most importantly they share a unique pattern of macro-ornamentation among species of *Paraostenia*: the presence of short transverse comma-like ridges on the dorsal area of the shield, and the presence of scale-like ridges on the rest of the shield (see Fig. 7B for *P. ambatolokobensis*). This pattern has not been described in any other *Paraostenia* species. It is therefore most probable that this specimen belongs to *P. ambatolokobensis*. However, due to the poor preservation of some morphological features (e.g., anterodorsal corner) in our specimens and to the fact that only one specimen of this taxon has been recovered from the Polzberg Lagerstätte, we refrain to assign this specimen to a particular species and let it in open nomenclature.

Discussion

Oval bulge in *Austriocaris carinata*: a trace of parasitism?—Glaessner (1931) mentioned the fact that the oval bulge associated with the mediolateral carina is not preserved in several specimens of *A. carinata*, as it disappeared under pressure. We do not concur with this explanation. Indeed, among the specimens that we studied, some are well-preserved and do not show any deformation or wrinkling. Moreover, in those specimens (e.g., NHMW 1910/0015/0041, Fig. 3A; NHWM 1910/0015/0045, Fig. 4D$_1$–D$_4$), some structures are preserved in 3D such as the carinae. Therefore, if present, this bulge should have been preserved in those specimens.

Another hypothesis could explain the presence/absence of the oval bulge: parasitism. Indeed, the presence of parasites in pancrustaceans is far from new, whether in extant (e.g., O'Brien and Van Wyk 1985; Williams and Boyko 2012) or fossil specimens (see Klompmarker and Boxshall 2015 for a review). In pancrustaceans, some parasites may cause swelling or cysts in the shield of some hosts (McDermott 1991; Klompmaker et al. 2014). These bulges are generally located near the branchial region, as is the case for some of our specimens. In fossil pancrustaceans (mainly decapods), the origin of these swellings has generally been attributed to bopyrid isopods, although no fossils from this group have been found so far. It is therefore possible that a similar phenomenon affected some of the individuals of *A. carinata*. In order to confirm or not the possible parasitism, it would be necessary to find the parasite itself. Pending such confirmation, this hypothesis cannot be ruled out for the time being.

Diversity and palaeogeographic distribution.—We report four thylacocephalan taxa from the Polzberg Konservat-Lagerstätte. Two were already known (*Austriocaris carinata* and *Paraostenia striata* comb. nov.; Glaessner 1931; Forchielli and Pervesler 2013) and two are here reported for the first time as part of the Polzberg biota (*Atropicaris*? sp.; *Paraostenia* cf. *ambatolokobensis*). The diversity of the Polzberg thylacocephalan biota is, with four taxa, relatively high in comparison to most other Late Triassic thylaccocephalan faunas. Indeed, other Late Triassic thylacocephalan-bearing formations have low diversities, with only one known taxon (Pinna 1974, 1976; Arduini and Brasca 1984; Dalla Vecchia 1993), with the exception of the Forni Dolomites Formation (Norian, Upper Triassic; Italy; Dalla Vecchia 2012) and the Martuljek Limestone Formation (Carnian, Upper Triassic; Slovenia; Laville et al. 2024), which have a taxonomic diversity close to the Polzberg biota, with three taxa.

Until now, *Austriocaris* was the only known taxon described from the Polzberg biota. Since then, it has been reported from two other deposits: Kozja dnina, Slovenia (Laville et al. 2024) and La Voulte-sur-Rhône Lagerstätte (Laville et al. 2023). *Atropicaris* is a well-known taxon from the Middle (China: Feldmann et al. 2015; Slovenia: Laville et al. 2024; Switzerland: Bürgin et al. 1991) and Upper Triassic (Italy: Arduini and Brasca 1984; Dalla Vecchia and Muscio 1990; Dalla Vecchia 2012; Slovenia: Laville et al. 2024) and it is therefore not surprising to find this taxon in Polzberg. *Paraostenia* is known from the Lower Triassic (Japan: Ehiro

et al. 2015; Madagascar: Laville et al. 2021) and from the Lower and Middle Jurassic (France: Secrétan 1985; Italy: Arduini et al. 1980) but not from the Middle and Upper Triassic. Therefore, *Paraostenia striata* and *Paraostenia* cf. *ambatolokobensis* from the Polzberg Konservat-Lagerstätte corresponds to the first mention of this taxon from the Upper Triassic.

Interestingly, the Polzberg thylacocephalan fauna displays particular affinities with two other faunas: one from the Late Triassic, the Kozja dnina biota, another one from the Middle Jurassic, the La Voulte-sur-Rhône Lagerstätte. The Kozja dnina biota has a similar diversity as the Polzberg biota, with three thylacocephalan taxa reported, two of which are also known in the Polzberg: *Austriocaris* and *Atropicaris* (Laville et al. 2024). The La Voulte Lagerstätte has a much greater diversity than the Polzberg Konservat-Lagerstätte, with seven taxa described (Laville et al. 2023). Nevertheless, two of these taxa are also known in the Polzberg: *Austriocaris* and *Paraostenia*. The similarity of the Polzberg thylacocephalan fauna with the Kozja dnina biota is not surprising. Both deposits are of Carnian age (Polzberg: Julian; Kozja dnina: Tuvalian). They are both located in the Meliata-Maliac Ocean (Stampfli et al. 2002), even though they belong to two different branches of the ocean (Meliata for the Polzberg, Maliac for Kozja dnina). Finally, they were both formed in a similar environment (deep-water setting within an intraplatform basin; see Lukeneder and Lukeneder [2021] for the Polzberg and Celarc and Kolar-Jurkovšek [2008] for Kozja dnina). On the other hand, the similarity with the La Voulte Lagerstätte is much more surprising. The age difference is about 60 Ma and they were belonging to two different oceans (Meliata-Maliac Ocean for Polzberg, Alpine Tethys for the La Voulte Lagerstätte). However, these two oceans were probably connected during the Early Jurassic, through the Neotethys (Frizon de Lamotte et al. 2015). It probably allowed the dispersal of the fauna of the Neotethys and thus of the Meliata-Maliac ocean, towards the Alpine Tethys. Moreover, both faunas were located in deep environments, close to the slope-basin transition (Charbonnier et al. 2014). All these factors can explain the similarity between both faunas.

Conclusions

The revision of thylacocephalans from the Polzberg Konservat-Lagerstätte made it possible to study its diversity in detail. Four thylacocephalans taxa are now reported from Polzberg, making it one the most diverse Late Triassic faunas. *Paraostenia striata* nov. comb., which was previously assigned to *Austriocaris* or *Atropicaris*, and *Paraostenia* cf. *ambatolokobensis* correspond to the first mention of *Paraostenia* in the Late Triassic. A new taxon, *Atropicaris*? sp. is reported for the first time from Polzberg. In addition, the presence of gills and muscles of the posterior trunk in *Austriocaris carinata* and in *Paraostenia* cf. *ambatolokobensis are* the first traces of soft part preservation in Polzberg thylacocephalans. Finally, comparisons with other Jurassic but also Triassic thylacocephalan faunas show the similarity of the Polzberg thylacocephalan fauna with the Late Triassic Kozja dnina fauna, and more surprisingly with the Middle Jurassic La Voulte fauna.

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References

Arduini, P. 1990. Studies on Permo-Trias of Madagascar. 1. Thylacocephala from the Lower Trias of Madagascar. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano* 131: 197–204.

Arduini, P. and Brasca, A. 1984. *Atropicaris*: nuovo genere della classe Thylacocephala. *Atti della Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano* 125: 87–93.

Arduini, P., Pinna, G., and Teruzzi, G. 1980. A new and unusual Lower Jurassic cirriped from Osteno in Lombardy: *Ostenia cypriformis* n. g. n. sp. *Atti della Società italiana di scienze naturali e del museo civico di storia naturale di Milano* 121: 360–370.

Arduini, P., Pinna, G., and Teruzzi, G. 1984. *Ostenocaris* nom. nov. pro *Ostenia* Arduini, Pinna e Teruzzi, 1980. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano* 125 (1–2): 48.

Bauer, F.K. and Schnabel, W. 1997. *Geologische Karte der Republik Österreich. Sheet Mariazell 72, 1:50.000*. Geologische Bundesanstalt.

Briggs, D.E.G. and Rolfe, W.D.I. 1983. New Concavicarida (new order:? Crustacea) from the Upper Devonian of Gogo, Western Australia, and the palaeoecology and affinities of the group. *Special Papers in Palaeontology* 30: 249–276.

Bürgin, T., Furrer, H., and Eichenberger, U. 1991. Die Prosanto-Formation: eine fischreiche Fossil-Lagerstätte in der Mitteltrias der Silvretta-Decke (Kanton Graubünden, Schweiz). *Eclogae Geologicae Helvetiae* 84: 921–990.

Calzada, S. and Mañé, R. 1993. Primera cita de un Tilacocéfalo (Crustacea) (*Ferrecaris* n. gen. *magransi* n. sp.) en el Ladiniense español. *Trabajos Del Museo Geológico Del Seminario* 246: 12–16.

Celarc, B. and Kolar-Jurkovšek, T. 2008. The Carnian–Norian basin-platform system of the Martuljek Mountain Group (Julian Alps, Slovenia): progradation of the Dachstein carbonate platform. *Geologia Carpathica* 59: 211–224.

Charbonnier, S., Audo, D., Caze, B., and Biot, V. 2014. The La Voulte-sur-Rhône Lagerstätte (Middle Jurassic, France). *Comptes Rendus Palevol* 13: 369–381.

Charbonnier, S., Brayard, A., and The Paris Biota Team. 2019. New thylacocephalans from the Early Triassic Paris Biota (Bear Lake County, Idaho, USA). *Geobios* 54: 37–43.

Charbonnier, S., Teruzzi, G., Audo, D., Lasseron, M., Haug, C., and Haug,

J.T. 2017. New thylacocephalans from the Cretaceous Lagerstätten of Lebanon. *Bulletin de la Société géologique de France* 188: 19.

Dal Corso, J., Bernardi, M., Sun, Y., Song, H., Seyfullah, L.J., Preto, N., Gianolla, P., Ruffell, A., Kustatscher, E., Roghi, G., Merico, A., Hohn, S., Schmidt, A.R., Marzoli, A., Newton, R.J., Wignall, P.B., and Benton, M.J. 2020. Extinction and dawn of the modern world in the Carnian (Late Triassic). *Science Advances* 6: article eaba0099.

Dalla Vecchia, F.M. 1993. Segnalazione di crostacei nell'Unità Fonte Santa (Triassico Sup.) presso Filettino (Lazio, Italia). *Gortania* 14: 59–69.

Dalla Vecchia, F.M. 2012. *Il Friuli 215 milioni di anni fa. Gli straordinari fossili di Preone: finestra su di un mondo scomparso*. 224 pp. Comune di Preone, Preone.

Dalla Vecchia, F.M. and Muscio, G. 1990. Occurrence of Thylacocephala (Arthropoda, Crustacea) from the Upper Triassic of Carnic Prealps (NE Italy). *Bollettino della Società-Paleontologica Italiana* 29: 39–42.

Ehiro, M., Sasaki, O., Kano, H., and Nagase, T. 2019. Additional thylacocephalans (Arthropoda) from the Lower Triassic (upper Olenekian) Osawa Formation of the South Kitakami Belt, Northeast Japan. *Palaeoworld* 28: 320–333.

Ehiro, M., Sasaki, O., Kano, H., Nemoto, J., and Kato, H. 2015. Thylacocephala (Arthropoda) from the Lower Triassic of the South Kitakami Belt, Northeast Japan. *Paleontological Research* 19: 269–282.

Feldmann, R.M., Schweitzer, C.E., Hu, S., Huang, J., Zhou, C., Zhang, Q., Wen, W., Xie, T., and Maguire, E. 2015. Spatial distribution of Crustacea and associated organisms in the Luoping Biota (Anisian, Middle Triassic), Yunnan Province, China: evidence of periodic mass kills. *Journal of Paleontology* 89: 1022–1037.

Forchielli, A. and Pervesler, P. 2013. Phosphatic cuticle in thylacocephalans: a taphonomic case study of *Austriocaris* (Arthropoda, Thylacocephala) from the Fossil-Lagerstätte Polzberg (Reingraben shales, Carnian, Upper Triassic, Lower Austria). *Austrian Journal of Earth Sciences* 106: 46–61.

Frizon de Lamotte, D., Fourdan, B., Leleu, S., Leparmentier, F., and de Clarens, P. 2015. Style of rifting and the stages of Pangea breakup. *Tectonics* 34: 1009–1029.

Glaessner, M.F. 1931. Eine Crustaceenfauna aus den Lunzer Schichten Niederösterreichs. *Jahrbuch der Geologischen Bundesanstalt* 81: 467–486.

Haug, C., Briggs, D.E.G., Mikulic, D.G., Kluessendorf, J., and 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: article 159.

Ji, C., Tintori, A., Jiang, D., and Motani, R. 2017. New species of Thylacocephala (Arthropoda) from the Spathian (Lower Triassic) of Chaohu, Anhui Province of China. *PalZ* 91 (2): 171–184.

Ji, C., Tintori, A., Jiang, D., Motani, R., and Confortini, F. 2021. New Thylacocephala (Crustacea) assemblage from the Spathian (Lower Triassic) of Majiashan (Chaohu, Anhui Province, South China). *Journal of Paleontology* 95: 305–319.

Klompmaker, A.A. and Boxshall, G.A. 2015. Fossil crustaceans as parasites and hosts. *In*: K. De Baets and D.T.J. Littlewood (eds.), *Advances in Parasitology, Vol. 90*, 233–289. Academic Press, Amsterdam.

Klompmaker, A.A., Artal, P., Bakel, B.W.M. van, Fraaije, R.H.B., and Jagt, J.W.M. 2014. Parasites in the fossil record: A Cretaceous fauna with isopod-infested decapod crustaceans, infestation patterns through time, and a new ichnotaxon. *PLOS ONE* 9: article e92551.

Krystyn, L. 1991. Die Fossillagerstätten der alpinen Trias. *In*: D. Nagel and G. Rabeder (eds.), *Exkursionen im Jungpaläozoikum und Mesozoikum Österreichs*, 24–78. Österreichische Paläontologische Gesellschaft Wien, Wien.

Lange, S., Hof, C.H.J., Schram, F.R., and Steeman, F.A. 2001. New genus and species from the Cretaceous of Lebanon links the Thylacocephala to the Crustacea. *Palaeontology* 44: 905–912.

Lankester, E. 1904. The structure and classification of the Arthropoda. *Journal of Cell Science* 2: 523–582.

Laville, T., Forel, M.-B., and Charbonnier, S. 2023. Re-appraisal of thylacocephalans (Euarthropoda, Thylacocephala) from the Jurassic La Voulte-sur-Rhône Lagerstätte. *European Journal of Taxonomy* 898: 1–61.

Laville, T., Hitij, T., Forel, M.-B., Gašparič, R., Žalohar, J., and Charbonnier, S. 2024. Middle and Late Triassic thylacocephalans from Slovenia: implications for their diversification. *Bulletin of Geosciences* 99: 219–253.

Laville, T., Smith, C.P.A., Forel, M.-B., Brayard, A., and Charbonnier, S. 2021. Review of Early Triassic Thylacocephala. *Rivista Italiana di Paleontologia e Stratigrafia* 127: 73–101.

Lukeneder, A. and Lukeneder, P. 2021. The Upper Triassic Polzberg palaeobiota from a marine Konservat-Lagerstätte deposited during the Carnian Pluvial Episode in Austria. *Scientific Reports* 11: article 16644.

Lukeneder, A. and Lukeneder, P. 2023. New data on the marine Upper Triassic palaeobiota from the Polzberg Konservat-Lagerstätte in Austria. *Swiss Journal of Palaeontology* 142: article 9.

Lukeneder, A. and Lukeneder, P. 2024. Ammonoid taxonomy of the Carnian Polzberg Konservat-Lagerstätte in Austria. *Jahrbuch der Geologischen Bundesanstalt* 162: 27–55.

Lukeneder, S., Lukeneder, A., Harzhauser, M., İslamoğlu, Y., Krystyn, L.,, and Lein, R. 2012. A delayed carbonate factory breakdown during the Tethyan-wide Carnian Pluvial Episode along the Cimmerian terranes (Taurus, Turkey). *Facies* 58: 279–296.

Lukeneder, A, Lukeneder P., Sachsenhofer, R., Roghi, G., and Rigo. M. 2024. Multi-proxy record of the Austrian Upper Triassic Polzberg Konservat-Lagerstätte in light of the Carnian Pluvial Episode. *Scientific Reports* 14: article 11194.

McDermott, J.J. 1991. Incidence and host-parasite relationship of *Leidya bimini* (Crustacea, Isopoda, Bopyridae) in the brachyuran crab *Pachygrapsus transversus* from Bermuda. *Ophelia* 33: 71–95.

O'Brien, J. and Van Wyk, P. 1985. Effects of crustacean parasitic castrators (epicaridean isopods and rhizocephalan barnacles) on growth of crustacean hosts. *In*: A.M. Wenner (ed.), *Crustacean Issues 3: Factors in Adult Growth*, 191–218. Balkema, Rotterdam.

Pinna, G. 1974. l crostacei della fauna triassica di Cene in Val Seriana (Bergamo). *Memorie della Società italiana di scienze naturali in Milano* 21: 5–34.

Pinna, G. 1976. I crostacei Triassici dell'alta Valvestino (Brescia). *Natura Bresciana* 13: 33–42.

Pinna, G., Arduini, P., Pesarini, C., and 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.

Rak, Š., Broda, K., and Kumpan, T. 2018. First Carboniferous thylacocephalan from Europe and its significance for the understanding of functional morphology of Concavicarididae Schram, 2014. *Crustaceana* 91: 265–285.

Rolfe, W.D.I. 1961. *Concavicaris* and *Quasicaris*, substitute names for *Colpocaris* Meek, 1872, and *Pterocaris* Barrande, 1872. *Journal of Paleontology* 35: 1243–1243.

Rolfe, W.D.I. 1969. Phyllocarida. *In*: R.C. Moore (ed.), *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Vol. 1,* R296–R331, Geological Society of America and University of Kansas Press, Lawrence.

Ruffell, A., Simms, M.J., and Wignall, P.B. 2015. The Carnian Humid Episode of the late Triassic: A review. *Geological Magazine* 153: 271–284.

Ruttner, A. and Schnabel, W. 1988. *Geologische Karte der Republik Österreich. Sheet Ybbsitz 71, 1:50.000*. Geologische Bundesanstalt.

Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D.J., Hartenstein, V., Eliceiri, K., Tomancak, P., and Cardona, A. 2012. Fiji: an open-source platform for biological-image analysis. *Nature Methods* 9: 676–682.

Schram, F.R. 2014. Family level classification within Thylacocephala, with comments on their evolution and possible relationships. *Crustaceana* 87: 340–363.

Secrétan, S. 1985. Conchyliocarida, a class of fossil crustaceans: relationships to Malacostraca and postulated behaviour. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 76: 381–389.

Simms, M.J. and Ruffell, A.H. 2018. The Carnian Pluvial Episode: from

discovery, through obscurity, to acceptance. *Journal of the Geological Society* 175: 989–992.

Stampfli, G.M., Borel, G.D., Marchant, R., and Mosar, J. 2002. Western Alps geological constraints on western Tethyan reconstructions. *Journal of the Virtual Explorer* 8: 77–106.

Stur, D. 1874. Neue Aufschlüsse im Lunzer Sandsteine bei Lunz und ein neuer Fundort von Wengerschiefer im Pölzberg zwischen Lunzersee und Gaming. *Verhandlungen der kaiserlich königlichen Geologischen Reichsanstalt* 1: 271–273.

Stur, D. 1886. Vorlage des ersten fossilen Schädels von *Ceratodus* aus den ober triadischen Reingrabner Schiefern von Pölzberg nördlich bei Lunz. *Verhandlungen der kaiserlich königlichen Geologischen Reichsanstalt* 15: 381–383.

Teruzzi, G. and Muscio, G. 2019. Thylacocephalans from the Anisian (Middle Triassic) of the Carnic Alps. *Gortania* 40: 49–55.

Tintori, A., Bigi, E., Crugnola, G., and Danini, G. 1986. A new Jurassic Thylacocephala *Rugocaris indunensis* gen. n. sp. n. and its paleoecological significance. *Rivista Italiana di Paleontologia e Stratigrafia* 92: 239–250.

Williams, J.D. and Boyko, C.B. 2012. The global diversity of parasitic isopods associated with crustacean hosts (Isopoda: Bopyroidea and Cryptoniscoidea). *PLoS One* 7: e35350.

Appendix 1

List of studied specimens.

Repository number	Specimen number	Identification	Layer	Observations
GBA 2021/002/0010		*Austriocaris carinata*		
NHMW 1910/0015/0001		*Austriocaris carinata*		
NHMW 1910/0015/0002		*Austriocaris carinata*		
NHMW 1910/0015/0003		*Austriocaris carinata*		
NHMW 1910/0015/0004		*Austriocaris carinata*		
NHMW 1910/0015/0005		*Austriocaris carinata*		
NHMW 1910/0015/0006		*Austriocaris carinata*		
NHMW 1910/0015/0007		*Austriocaris carinata*		
NHMW 1910/0015/0008		*Austriocaris carinata*		
NHMW 1910/0015/0009		*Austriocaris carinata*		
NHMW 1910/0015/0010		*Austriocaris carinata*		
NHMW 1910/0015/0011		*Austriocaris carinata*		
NHMW 1910/0015/0012		*Austriocaris carinata*		
NHMW 1910/0015/0013		*Austriocaris carinata*		
NHMW 1910/0015/0014		*Austriocaris carinata*		
NHMW 1910/0015/0015		*Austriocaris carinata*		
NHMW 1910/0015/0016		*Austriocaris carinata*		
NHMW 1910/0015/0017		*Austriocaris carinata*		
NHMW 1910/0015/0033		*Atropicaris*? sp.		
NHMW 1910/0015/0034		*Paraostenia striata*		
NHMW 1910/0015/0035		*Atropicaris*? sp.		
NHMW 1910/0015/0036		*Paraostenia striata*		
NHMW 1910/0015/0037		*Austriocaris carinata*		
NHMW 1910/0015/0038		*Austriocaris carinata*		
NHMW 1910/0015/0039		*Austriocaris carinata*		
NHMW 1910/0015/0040		*Austriocaris carinata*		
NHMW 1910/0015/0041		*Austriocaris carinata*		holotype
NHMW 1910/0015/0042		*Paraostenia striata*		holotype
NHMW 1910/0015/0043		*Paraostenia striata*		
NHMW 1910/0015/0044		*Austriocaris carinata*		
NHMW 1910/0015/0045		*Austriocaris carinata*		
NHMW 1910/0015/0046		*Austriocaris carinata*		
NHMW 1910/0015/0047		*Austriocaris carinata*		
NHMW 1910/0015/0048		*Austriocaris carinata*		
NHMW 1910/0015/0049		*Austriocaris carinata*		
NHMW 1910/0015/0050		*Austriocaris carinata*		
NHMW 2021/0123/0002	1501	*Austriocaris carinata*	-50 cm to 0 cm	
NHMW 2021/0123/0059		*Atropicaris*? sp.		
NHMW 2021/0123/0203	2077	*Austriocaris carinata*	-50 cm to 0 cm	
NHMW 2021/0123/0764		*Austriocaris carinata*		
NHMW 2021/0123/0765	39	*Austriocaris carinata*	-50 cm to 0 cm	
NHMW 2021/0123/0766	52	*Austriocaris carinata*	-50 cm to 0 cm	
NHMW 2021/0123/0767	194	*Atropicaris*? sp.	-50 cm to 0 cm	
NHMW 2021/0123/0769	273	*Atropicaris*? sp.	-50 cm to 0 cm	
NHMW 2021/0123/0770		*Paraostenia striata*		
NHMW 2021/0123/0772	1193	*Paraostenia striata*	-50 cm to 0 cm	
NHMW 2021/0123/0776	4320	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0777	4323	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0779	4331	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0780	4334	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0782	4335	*Atropicaris*? sp.	300 cm to 320 cm	

NHMW 2021/0123/0783	4412	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0784	4456	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0787	4464	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0788	4466	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0790	4540	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0791	4445	*Paraostenia striata*	300 cm to 320 cm	
NHMW 2021/0123/0793	4739	*Atropicaris*? sp.	300 cm to 320 cm	
NHMW 2021/0123/0795	4864	*Atropicaris*? sp.	320 cm to 340 cm	
NHMW 2021/0123/0796	4894	*Paraostenia striata*	320 cm to 340 cm	
NHMW 2021/0123/0797		*Paraostenia striata*		
NHMW 2021/0124/0078		*Atropicaris*? sp.		
NHMW 2021/0124/0101		*Atropicaris*? sp.		
NHMW 2021/0124/0102		*Atropicaris*? sp.		
NHMW 2021/0124/0103		*Atropicaris*? sp.		
NHMW 2021/0124/0104		*Atropicaris*? sp.		
NHMW 2021/0124/0105		*Atropicaris*? sp.		
NHMW 2021/0124/0106		*Atropicaris*? sp.		
NHMW 2021/0124/0108		*Austriocaris carinata*		
NHMW 2021/0124/0109		*Austriocaris carinata*		
NHMW 2021/0124/0110		*Austriocaris carinata*		
NHMW 2024/0201/0001		*Paraostenia* cf. *ambatolokobensis*	300 cm to 340 cm	

Appendix 2

Measurements (in mm) made on the specimens. Abbreviations: Aad, anterodorsal angle; Aav, anteroventral angle; Apd, posterodorsal angle; Apv, posteroventral angle; Ha, anterior height; Hmax, maximal height; Hp, posterior height; Lr, rostrum length; Ls, total shield length; Lw, shield length without the rostrum; NA, non-applicable.

Specimen	Species	Ls	Lw	Lr	Ha	Hmax	Hp	Aad	Aav	Apv	Apd
NHMW 1910/0015/0002	*Austriocaris carinata*	83.023	72.972	10.126	NA	NA	6.036	NA	81.919	145.215	83.763
NHMW 1910/0015/0041	*Austriocaris carinata*	100.259	89.099	11.179	32.062	NA	9.388	60.532	83.555	146.304	82.497
NHMW 1910/0015/0050	*Austriocaris carinata*	76.059	67.965	8.17	26.271	NA	NA	61.767	81.369	NA	80.562
NHMW 1910/0015/0034	*Paraostenia striata*	28.086	NA	NA	12.539	16.796	6.215	68.502	77.001	90.051	87.975
NHMW 1910/0015/0042_part	*Paraostenia striata*	26.061	NA	NA	13.678	15.127	6.206	68.189	73.36	92.131	64.568
NHMW 1910/0015/0042_counter-part	*Paraostenia striata*	26.394	NA	NA	13.078	15.104	6.291	63.339	69.272	89.86	64.301
NHMW 2024/0201/0001	*Paraostenia* cf. *ambatolokobensis*	31.354	NA	NA	14.979	19.362	4.560	68.516	71.310	107.324	97.696