

## Article

# New Material of Thylacocephala from the Early Ladinian (Middle Triassic) of Northern Grigna (Lecco, Lombardy, Northern Italy)

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**Abstract:** Here we report and describe a new assemblage of Thylacocephala (Crustacea) from the Early Ladinian Buchenstein Fm. (Middle Triassic) of Grigna, Northern Italy. The assemblage consists of at least four species from three different genera: *Ankitokazocaris lariensis* sp. n., *Ankitokazocaris* sp., *Austriocaris* sp., *Stoppanicaris grignaensis* gen. et sp. n. This thylacocephalan assemblage is rather diverse compared to the others of the Triassic. The largest size and ornamentation type of thylacocephalan species is compared among different periods of the Triassic and indicates that taxa with ridges on the carapace are generally smaller than those with smooth carapaces. This may be related to their different modes of life, such as inside or above the sediment with low oxygen levels. Large and smooth taxa were possibly more adapted to a life above sandy bottoms in shallow waters, under a somewhat high wave energy, while small, ornamented taxa are better suited for deeper environments with muddy bottoms, inside which they could move freely. The EDS analysis of *Austriocaris* sp. reveals that the cuticle mainly consists of apatite, which is in accordance with previous interpretations.

**Keywords:** Thylacocephala; new taxa; diversity; ornamentation; gigantism; Middle Triassic; Italy



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## 1. Introduction

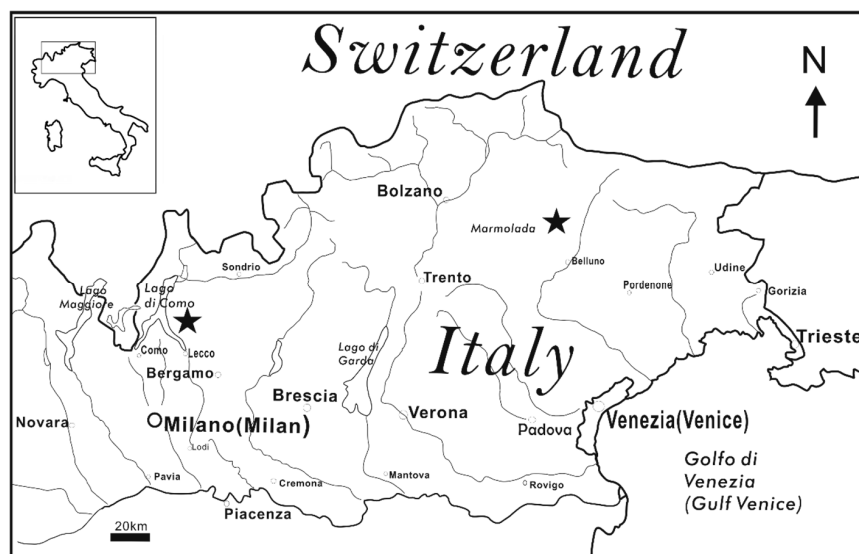
Thylacocephala is a group of Arthropoda and has a long fossil record, possibly from the Cambrian to the Cretaceous (see, e.g., Refs. [1–8] for a review). They generally have carapace made of a pair of valves of various shapes, compound eyes, 3 pairs of raptorial appendages, and 8–16 sets of posterior appendages [8,9]. The Triassic has been proposed to be the period with highest level of biodiversity of Thylacocephala, with more than 25 species against the total 70 described ones [8,10]. Especially during the Early Triassic, they were reported to have the widest paleogeographic distribution globally, including South China and Japan (East Tethys), Italy and Madagascar (West Tethys), and USA (Panthalassa). Multiple localities were reported to have yielded more than three different species/genera within a short time interval, such as Japan, China and USA [10–14], although rarely it was recorded that their presence as assemblage from a single bed or similar very short interval. Compared to the Early Triassic, fewer species have been described from Middle and Late Triassic and each locality was mostly dominated by one or two species, such as Spain and Italy [10,15–17]. Recently, new material was reported in Slovenia from the Anisian and Carnian [8,18]. Additionally, material has not been found from most of the major fauna-yielding Triassic marine vertebrates, such as Panxian Fauna (Anisian, Southern China) and Xingyi Fauna (Ladinian, Southern China), while in Luoping (latest Anisian, Southern China) and Monte San Giorgio (Anisian-Ladinian,

Northern Italy/Switzerland), they seem to be very rare and mostly represented by a single taxon.

The majority of the Triassic thylacocephalans are relatively small in size, with carapace lengths below 60 mm [13]. Very rarely, the carapace is over 100 mm, such as in *Austriocaris carinata* from the Carnian (Late Triassic) of Austria [19]. Here, we describe new materials collected in a lower Ladinian fossiliferous level in the Buchenstein Fm. that yields mainly fishes [20–22] although rare invertebrates are also present such as a single species of star fish [23]. Furthermore, we also describe a single specimen recently found in the same unit (Buchenstein Fm.) in the Dolomites near Selva di Cadore (Belluno).

## 2. Geological Settings

It was during a field excursion with students in 1981 that one of us (AT) found some scattered fish remains in the lower part of the Buchenstein Formation (Early Ladinian) in the area of Scudi Tremare on the southern slope of the Northern Grigna Mountain (locally called Grignone, the Big Grigna), a few kilometers North of Lecco (Lombardy, N. Italy) (Figure 1). The Northern Grigna was already famous for its invertebrate faunas, mostly molluscs and brachiopods from the Esino Limestone [24–27], as well as for the fishes and reptiles described in the middle of the XIX century from around the villages of Varenna and Perledo, on the northwest slope of the mountain [28–31], where the fossils were found during the quarrying of black limestone (Perledo-Varenna Formation) used for artistic works in churches or as fireplace profiles in the villas around Lario Lake.



**Figure 1.** Map of the section location yielding the thylacocephalans. The left star: Scudi Tremare in Northern Grigna, GPS:  $45^{\circ}56'25''$  N,  $9^{\circ}23'42''$  E. The right star: Rio Sacuz in Dolomites, GPS:  $46^{\circ}26'54''$  N,  $12^{\circ}04'59''$  E.

In the fall of 2003, a small excavation was started in the new site in order to check the significance of the fossiliferous level. Results were very promising, so during the 2004–2005 and 2007–2008 summers, larger excavations were performed, allowing the finds of more than 1500 fishes as well as a few crustaceans (Figure 2). So far, no remains of reptiles has been found, so that the fossiliferous level is commonly referred as “fish level”. Most fish specimens show poor preservation, but a few can be very nicely preserved and allow detailed description after careful preparation. The first new fish taxon, *Stoppania* was described by Lombardo et al. [20] while *Saurichthys* was reported by Tintori [21,22]. The only echinoderm was found at the very base of the fish level [23]. The presence of large crustaceans, though quite rare, was a surprise, as they are usually almost absent in many of the major Middle Triassic Lagerstätten, as in most Middle Triassic fossiliferous levels of Monte San Giorgio or in the late Ladinian of Xingyi (Guizhou Province, China). It must be pointed out that the

crustaceans studied in this paper are found in beds where no fish is present, and—apart from some small fragments—well preserved crustacean specimens are almost absent from the fish-bearing beds. At least in one case (uppermost surface of bed 48), we can consider the presence of a few crustaceans’ remains as being due to a sudden, catastrophic event even if no other organisms are present, as discussed later. On the other hand, in several other cases, thylacocephalans make most of the fossil assemblages, with very rare presence of other organisms ([10–13], AT pers. obs. on *Microcaris* from the Norian of northern Italy).

Fm	No	Stratigraphic column	Thick (cm)	Lithology	Fossil occurrence	
Buchenstein	50	[Stratigraphic column diagram]	26	Massive limestone with chert	<i>Daonella</i> ★	
				Massive limestone with chert	<i>Daonella</i> Ammonite Crustacean ★	
				Limestone	<i>Daonella</i> Ammonite Crustacean ★	
				Marly limestone	Ammonite Crustacean	
				Marly limestone	Peltopleuriform Coprolite	
	49		1			
	48		4			
	47		2.5			
	Formation	46	[Stratigraphic column diagram]	10	Massive limestone	Peltopleuriform unidentified bone ★
					Laminated limestone	
		45		1.5		
		44		3		Large ammonite <i>Saurichthys</i> ?
		43		2.5		
		42		2.5	Marly limestone	<i>Saurichthys</i> Peltopleuriform
		41	[Stratigraphic column diagram]	8	Laminated marly limestone	<i>Placopleurus</i> <i>Habroichthys</i> <i>Voltzia</i>
					marly limestone	<i>Saurichthys</i> <i>Habroichthys</i> ?
					Massive limestone	Peltopleuriformi <i>Ctenognathichthys</i> ?
		39		8		<i>Ctenognathichthys</i>
		38		5	Massive limestone	Peltopleuriform
		37		4.5	Massive limestone	<i>Saurichthys</i> Peltopleuriform
	Buchenstein	36	[Stratigraphic column diagram]	10	Massive limestone with chert	<i>Saurichthys</i> <i>Placopleurus</i> <i>Habroichthys</i> ? Scattered scales <i>Ctenognathichthys</i> ?
					Massive limestone with basal and top lamination	<i>Saurichthys</i> <i>Placopleurus</i> <i>Habroichthys</i> ? Peltopleuriform <i>Placopleurus</i>
		34		8.5	Laminated limestone	<i>Saurichthys</i> <i>Placopleurus</i> <i>Habroichthys</i> ? Peltopleuriform <i>Ctenognathichthys</i>
		33		6.5	Broadly laminated limestone	Scattered scales Plant remains
		32		6	Laminated limestone	<i>Saurichthys</i> <i>Habroichthys</i> Scattered peltopleuriform scales
		31		4	Massive limestone	<i>Ctenognathichthys</i> Brachiopod
		30		6	Massive limestone	Scattered bones and scales
29			3	Laminated limestone	Ammonite Terrestrial plants	
28			4	Massive limestone	Unspecified fishes Scattered scales	
27		[Stratigraphic column diagram]	17	Broadly laminated limestone with chert	<i>Stoppania gaetanii</i>	
					Starfish	

Figure 2. Occurrences of the newly described thylacocephalan material from the “fish level” in the Buchenstein Formation of Northern Grigna. The red stars represent the beds yielding the thylacocephalans.

Across the Grigna level, mass mortality surfaces yielding many small fishes are common, implying sudden changes in the environmental conditions, possibly related to the volcanic activity testified by the presence of thin to very thin ash layers ([32], AT pers. obs.) between the single limestone beds, characterizing the Buchenstein Fm. in this area.

Regarding the paleoenvironment, the Buchenstein Fm. in the Northern Grigna was deposited in a deep basin bordered by the carbonate platform of the Esino Limestone. To the north and west, the basin margins were quite close to the fossiliferous site (possibly 1–2 km), while the basin opened to the east-northeast without a known margin. The Buchenstein basin was separated from the partially coeval Perledo-Varenna Formation basin by about 5–7 km of shallow water carbonate platform (M. Gaetani, pers. comm.), making the bulk of the Northern Grigna mountain. Thus, we assume that shallow, well oxygenic bottom, rich in benthonic organisms, where close by the site, explain the presence of benthic crustaceans such as the thylacocephalans as well as necto-benthonic fishes (such as the quite common *Ctenognathichthys* and the much rarer *Stoppania*) who fed on shelled and/or incrusting organisms or calcareous algae. Since the fossiliferous level is made of thin biocalcarenites, we assume that the shallow water margins had a bioclastic sandy bottom, well adapted to support an assemblage of molluscs, echinoderms, crustaceans, corals, forams, and calcareous algae that formed the base of a quite complex food web that is known from the Esino Limestone. Regarding the Dolomite specimen, it comes from the scree in the lower part of the Buchenstein Fm. at Rio Sacuz (Sacuz Creek) near Selva di Cadore (Belluno, Italy). Although here, the sequence of this unit is somewhat different from that in Lombardy [33], being that the Sacuz Creek is more distant from the carbonate platform rim, the general paleoenvironment is considered to be the same. Research is underway in the area in the hope of finding a fossiliferous level corresponding to the “fish level” of the Northern Grigna.

### 3. Materials and Methods

In total, 12 specimens of thylacocephalan have been collected and are here described after mechanical preparation with very thin sharpened steel thread kept in a manual mandrel. Preparation was performed by the authors using a Wild M8 binocular microscope. The Rio Sacuz specimen was already quite weathered, and only a very light preparation along the margins was performed. Of the 12 specimens, 9 are ascribed to the genus *Ankitokazocaris* (7 belonging to a single species) and 3 to 3 different genera, respectively, hence recording—as usual—the dominance of one genus/species in a thylacocephalan assemblage.

Observations were made using a Wild M8 as well as an Olympus SZX10 binocular (Olympus, Japan) microscopes with photographic device and UltradePTH three-dimensional screen visual microscopy system KEYENCE VHX-6000 (Keyence, Japan) and Nikon COOLPIX S9700 (Nikon, Japan). To improve the contrast, some specimens have been photographed covered by ethylic alcohol. The element mapping analysis was performed under an SEM-coupled energy dispersive spectroscopy (EDS) detector.

Repository and institutional abbreviation. Specimens in this study are deposited in the Paleontological Museum collections of the Università degli Studi di Milano (PMUM). The referred material MFSN gp 20559-20560 are deposited at the Museo Friulano di Storia Naturale di Udine.

### 4. Systematic Paleontology

Thylacocephala Pinna et al., 1982

Genus. *Ankitokazocaris* Arduini, 1990.

Type species. *Ankitokazocaris acutirostris* Arduini, 1990 from the Dienerian to Smithian (Early Triassic) of Madagascar.

Other species. *A. chaohuensis* Ji et al., 2017; *A. bandoi* Ehiro et al., 2015; *A. parva* (Ehiro et al., 2019), *A. lariensis* sp.n.

Revised diagnosis. Small- to large-sized thylacocephalans; smooth bivalved carapace; dorsal margin gently convex; anterior rostrum sharp with well-developed and large optic



notch; ventral margin angular or nearly rounded; posterior margin short, straight and almost vertical; dorsal carina developed and nearly straight.

Occurrences. Dienerian to Smithian of Madagascar, Spathian (Early Triassic) of China and Japan, Early Ladinian (Middle Triassic) of northern Italy (this paper).

Remarks. *Ankitokazocaris* was first established based on material from Madagascar by Arduini [34] and diagnosed by the unique shape of the carapace. During the past decade, new material of this genus has been reported from multiple localities of Japan and South China [10–13]. Although it shows similar carapace shape outline with *Microcaris*, it is clearly distinct from the latter by the smooth carapace without remarkable ornamentation such as dense ridges as in the latter. Laville et al. [7] combined the two groups somehow and assigned *Microcaris triassica* (= *Parisicaris triassica* Charbonnier in Charbonnier and Brayard, 2019) to *Ankitokazocaris* due to the similar carapace shape. Laville [8] moved also *M. rectilineatus* Ji et al., 2021 to *Ankitokazocaris*. Furthermore, Laville et al. [7] again moved the ornamented *Kitakamicaris utatsuensis* Ehiro and Kato, 2015 to *Ankitokazocaris*. This assignment of prioritizing carapace outline without considering ornamentation seems to be highly unlikely and blurs the distinctions among the very few morphological characters useful to the separation of different taxa. Additionally, in Laville et al. (2021, figure 4), the general outline of smooth and ornamented *Ankitokazocaris* species appears quite different; in the ornamented ones, the angle of the ventral margin of the carapace is much sharper than in the smooth ones. We can also add further consideration because following Laville et al. [7] and Laville [8]’s line of thinking, *Ankitokazocaris* should be a junior synonym of *Microcaris*, although they did not consider the Middle–Late Triassic taxa.

Laville [8] erected the new genus *Gurgescaris* for *Ankitokazocaris bandoi* which he still considered as *Ankitokazocaris* in Laville et al. [7]. In Laville [8], *Gurgescaris* is diagnosed by the convex posterior margin. However, this feature is not obviously seen either in the photo of his paper or in the original description by Ehiro et al. [11], in which it was described as “narrow and slightly concave”. The carapace shape of *A. bandoi* still seems to resemble that of *Ankitokazocaris* in general ([34], pers. obs by C. J.). Therefore, the arguments of Laville [8] seem totally insufficient for erecting a new genus.

Microstructure and micro-ornamentation of the carapace are also important for the taxonomy of Eucrustacea and some Thylacocephala [35], although micro-ornamentation is not commonly detected, possibly also owing to the preservation in most of the known thylacocephalan assemblages. Broda et al. [35] pointed out that the use of just the carapace outline appears not useful in thylacocephalan taxonomy.

Given the fact that the taxonomy of Thylacocephala has been mostly based on the carapace shape and ornamentation morphology, and this group remains mysterious in many other aspects, here the previous [10,11,13,34] definition of *Ankitokazocaris* is followed.

*Ankitokazocaris lariensis* sp. nov.

Figure 3A–G, Figures 4 and 5

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Etymology. *Lariensis* from “Lario”, the old name of the Como Lake sitting at the western base of the Grigna Mountain, where the material was discovered.

Type material. Holotype, 48-575. Paratype, 49-1343, 48-1258, 49-1245, 49-1246, 49-1035, 49-498. Holotype, MPUM 13464. Paratype, MPUM 13465-13470.

Occurrence. Bed 48–49 of Scudo Tremare site, on the southern slope of the Northern Grigna Mountain a few kilometers north of Lecco (Lombardy, Italy), Buchenstein Formation, Early Ladinian (Middle Triassic).

Diagnosis. Medium sized *Ankitokazocaris* with a carapace length of 30–50 mm. Rostrum short and slender. Optic notch broad and slightly sinuous, occupied by the large oval compound eye. Dorso-lateral carina straight, nearly parallel to the straight ventral margin.

Description. The carapace is nearly triangular or trapezoidal in lateral view and shows remarkable variation on the proportions. Among this assemblage of eight specimens, the carapace has a length of 29–59 mm and the length/depth ratio varies between 1.7–2.2. The dorsal margin is gently convex and becomes nearly straight towards the posterior margin.

It is strongly convex and forms an angular margin on the anterior 1/3 of the dorsal margin in 48-1258, which has a deeper carapace. The ventral margin is round and angular, with the turning point at the posterior 1/3 or 1/4 of the carapace length. The angle formed by the two parts of the ventral margin is 100–130 degrees. The antero-ventral margin is nearly parallel to the dorsal margin. The postero-ventral margin is slightly shorter and forms an angle of 135–145 degrees with the posterior margin, which is nearly vertical. The optic notch is remarkably broad, and the shape is consistent among the assemblage. The rostrum is sharp and relatively short. The optic notch is shallow and slightly convex in the middle, forming a sinuous shaped margin. Ventrally, it forms an acute corner with antero-ventral margin, which is nearly symmetrical with the rostrum in some specimens (MPUM 13466, Figure 3E). The straight dorso-lateral carina is well developed nearly along the line from the tip of the rostrum to the end of the dorsal margin. It starts at the position posterior to the rostrum and ends before reaching the posterior margin, forming a crest on the carapace.

The compound eye is nearly completely seen on MPUM 13465 (Figures 3B and 4). It is oval-shaped, antero-dorsal to postero-ventrally oriented, and projecting from the carapace. The major and minor diameters of the eye are about 16 and 10 cm, respectively. No trace of stalk is seen, and the stalk is possibly absent based on the limited space between the eye and optic margin. The ommatidia can be observed under microscope (Figure 4). Unfortunately, no further details on the morphology can be observed under SEM.

The appendages are mostly not preserved except on MPUM 13464 and 13465 (Figure 3A,B). There are some long and slender fragments preserved next to the ventral margin, which are probably the raptorial appendages. Unfortunately, they are too poorly preserved to reveal the morphology.

Remarks. Eight specimens are discovered from two beds (No. 48–49) and clearly show interspecific variation on the carapace length/depth ratio (Table 1). Although all the specimens were compressed during preservation, the remarkable dorso-lateral carina on the carapace might shed some light on the three-dimensional shape of *A. lariensis* sp. nov. before it was buried. Probably, the carapace was not rounded in section originally but angulate along the carina. This is possibly similar to the *Concavicaris compi* and *C. playfordi*, which were preserved nearly three-dimensionally in concretion ([8], Figure 53).

The carapace of *A. lariensis* sp. nov. resembles that of other *Ankitokazocaris* species in the gently convex dorsal margin, angular ventral margin, and short and nearly vertical posterior margin without well-developed ornamentation such as ridges. It is different from most species of *Ankitokazocaris* in having a broader optic notch and larger-sized compound eyes. It is distinct from *A. chaohuensis* in the more posteriorly located angular position of the ventral margin. It strongly resembles the carapace shape of *A. bandoi* but is distinct from the latter in the more acute antero-ventral corner and convex margin in the middle of the optic notch.

*Ankitokazocaris* cf. *A. lariensis*

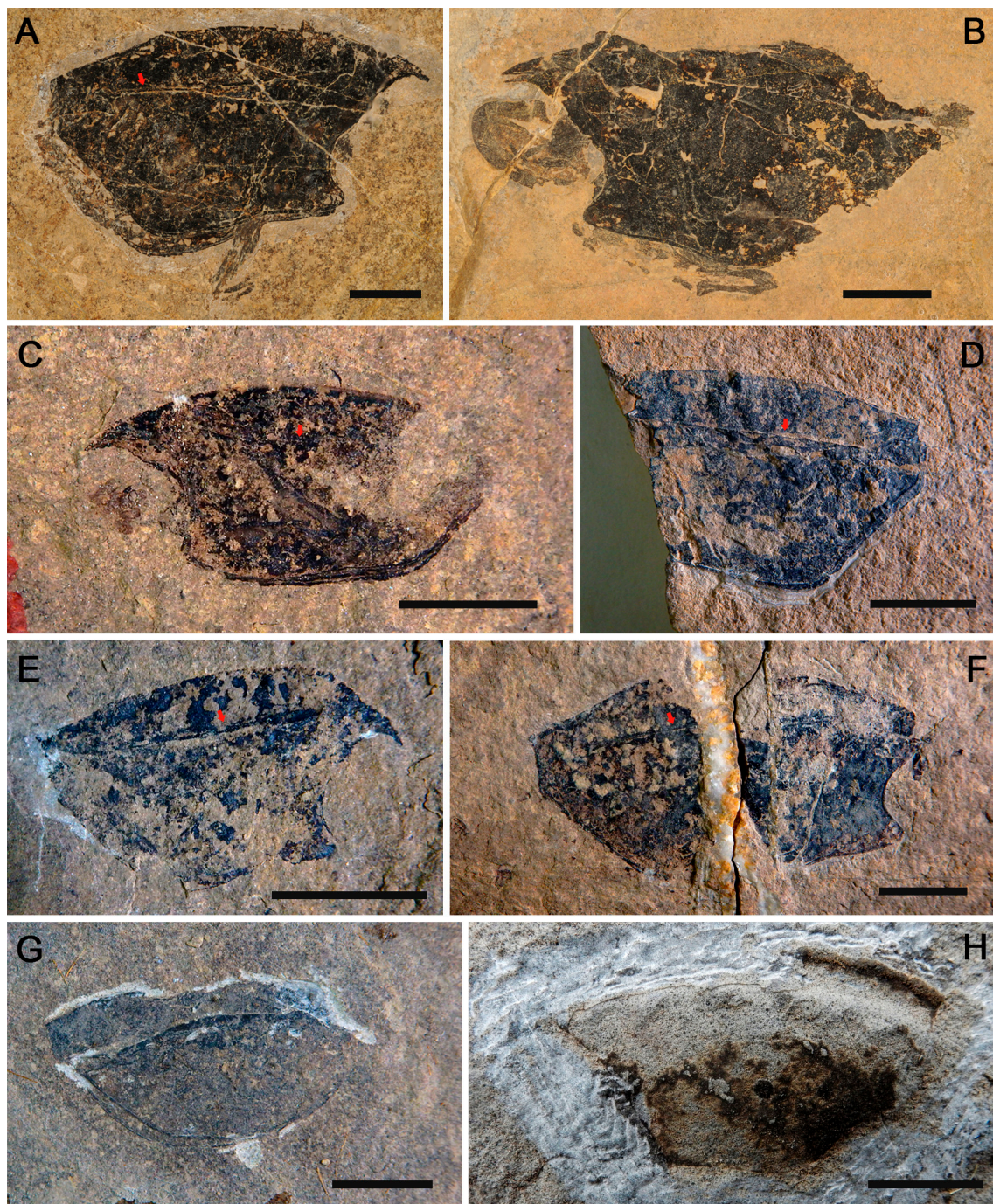
Figure 3H

Material. Specimen MVC-1 (Museo Vittorino Cazzetta, Selva di Cadore, Belluno, Italy).

Occurrence. Lower part of the Buchenstein Fm. (Livinallongo Fm. in Neri et al. [33]) at Rio Sacuz nearby Selva di Cadore (Belluno, Italy).

Description. The specimen shows the left side; its length is 34 mm, and the maximum height is 15 mm. The anterior margin appears as slightly concave up to a short rostrum but possibly the anterior tip is lacking due to the weathering. The dorsal margin is gently rounded. In the posterior half, the dorsal edge of the right valve seems to be present, showing a feeble crenulation on its inner side. The ventral margin has a short anterior part, while the postero-lateral one is longer, the two being connected through a round angle. The posterior edge is not very clear, but the truncation appears to be not sharp and vertical. A possible trace of the lateral carina is visible in the center of the valve.



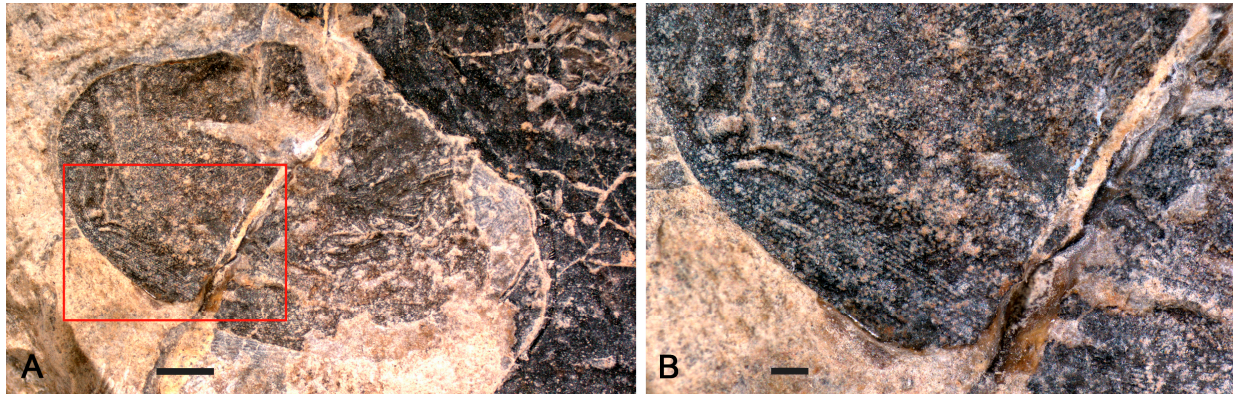


**Figure 3.** Thylacocephalans from Northern Grigna. (A–G), *Ankitokazocaris lariensis* sp. nov. (A) MPUM 13464. (B) MPUM 13465. (C) MPUM 13468. (D) MPUM 13469. (E) MPUM 13466. (F) MPUM 13467. (G) MPUM 13470. (H) *Ankitokazocaris* cf. *A. lariensis*, MVC-1. The red arrows indicate the dorso-lateral carina. Scale bars equal 1 cm.

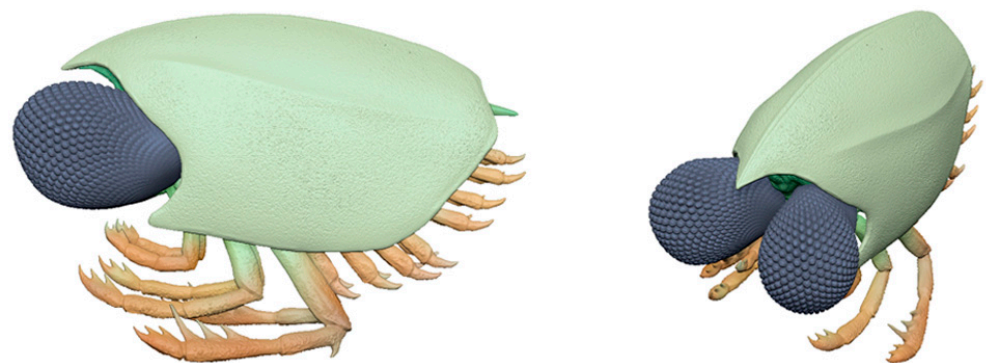
**Remarks.** This specimen—being from a loose slab in the scree below the actual outcrop—was quite weathered, and only a small part of the margins was still covered by a very thin rock layer. The general outline of the carapace is visible, although we consider this not enough to give a sound specific attribution. However, giving also the origin from the same stratigraphic unit as *A. lariensis* sp. n. (Buchenstein Fm.) and the similar age, we confidently consider this single specimen as very close to the species described from Lombardy. Only new and better-preserved material could solve the problematic identification. In the



case that it will be possible to confirm that the Dolomiti material belongs to the same species from the Northern Grigna, it would represent the first case of a thylacocephalan species found in two different sites a few hundred kilometers from each other.



**Figure 4.** Eye of *Ankitokazocaris lariensis* sp. nov. under microscope. (A) *Ankitokazocaris lariensis* sp. nov., MPUM 13465. (B) Enlargement of the rectangle area in (A). Scale bars equal 2 mm and 500  $\mu$ m, respectively.



**Figure 5.** Reconstruction of *Ankitokazocaris lariensis* sp. nov.

**Table 1.** Measurements of the thylacocephalans from the Ladinian of Grigna (mm). Abbreviations: *Anki.* = *Ankitokazocaris*, CL = length of carapace, CD = depth of carapace, ONL = optic notch length.

Specimen No.	Species Name	CL	CD	ONL	CL/CD
MPUM 13464	<i>Anki. lariensis</i> sp. nov.	51.25	26.9	19.85	1.9
MPUM 13466	<i>Anki. lariensis</i> sp. nov.	29.2	17.5	9.85	1.7
MPUM 13465	<i>Anki. lariensis</i> sp. nov.	59.1	27.3	20.45	2.2
MPUM 13468	<i>Anki. lariensis</i> sp. nov.	30.9	13.9	10.15	2.2
MPUM 13470	<i>Anki. lariensis</i> sp. nov.	>32.2	15.85	-	>2
MPUM 13469	<i>Anki. lariensis</i> sp. nov.	>31.4	20.1	-	-
MPUM 13472	<i>Austriocaris</i> sp.	>40.4	15.95	13.95	>2.5
MVC-1	<i>Anki.</i> cf. <i>A. lariensis</i>	34	15	16.4	2.3
MPUM 13473	? <i>Diplacanthocaris</i>	~45	~21	-	2.1
MPUM 13474	<i>Stoppanicaris grignaensis</i> sp. nov.	40	24	9.1	1.7

*Ankitokazocaris* sp. indet.

Figure 6A

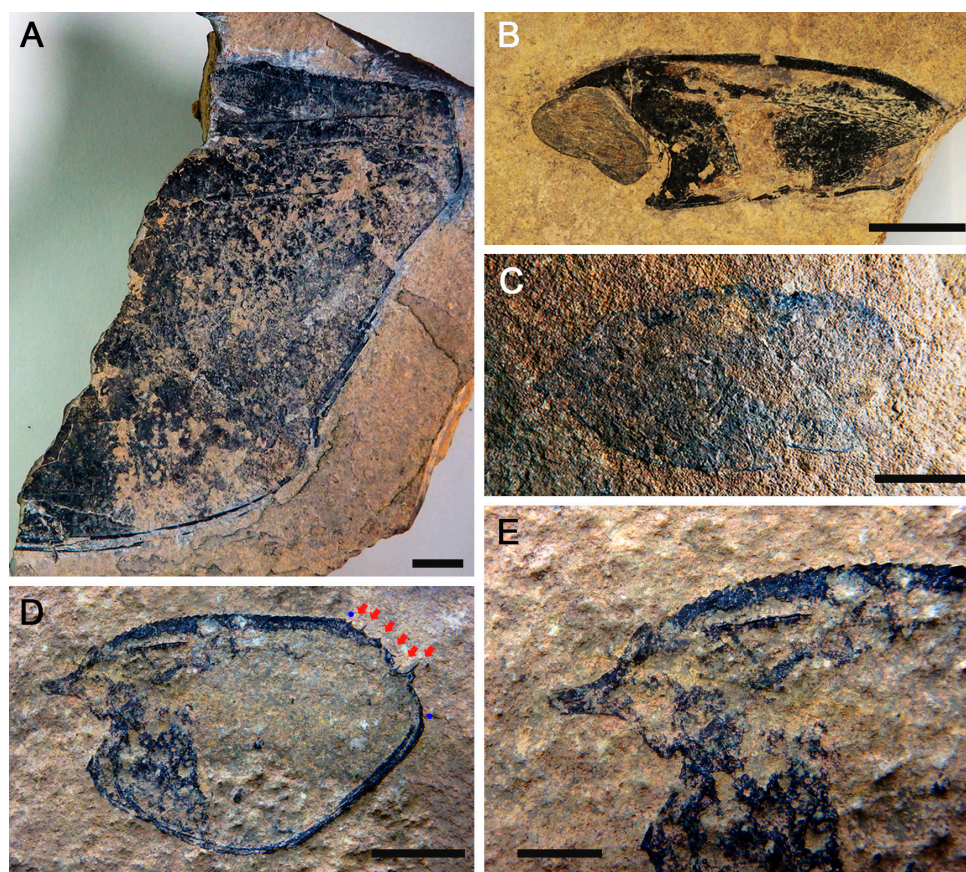
Material. MPUM13471.

Occurrence. Bed 53 of Scudo Tremare site, on the southern slope of the Northern Grigna Mountain a few km North of Lecco (Lombardy, Italy), Buchenstein Formation, Early Ladinian (Middle Triassic). This is the only fossil specimen found outside the so-called “fish bed”.



**Description.** The specimen is a partial carapace comprising only the posterior half. The posterior part of the dorsal margin is slight straight and formed an angle of around 100 degrees with the posterior region. The posterior margin is short and nearly vertical. The ventral margin is gently convex posteriorly and forms an angle of 135 degrees with the postero-ventral margin, which is straight. A dorsal carina is clearly developed along a line nearly perpendicular to the posterior margin and disappears before reaching the latter.

**Remarks.** This specimen is discovered from bed 53, a few cm above the fish level (Figure 2). The length of the carapace could reach 14 cm estimated by the preserved posterior part and the same proportion of the smaller *Ankitokazocaris* specimens from this site. It is likely the largest Triassic thylacocephalan carapace discovered so far based on published material. This raises the question of whether this specimen should be assigned to the same species as the rest of the population. The posterior part of the carapace strongly resembles that of *Ankitokazocaris lariensis* sp. nov. on the shape such as the angulate ventral margin and posterior dorso-upward margin without a spine, but we consider the specimen too incomplete, especially lacking the anterior part with the important optic notch. Therefore, it is temporarily assigned as *Ankitokazocaris* sp. until more complete material is discovered.



**Figure 6.** (A) *Ankitokazocaris* sp. gigantism specimen, MPUM 13471. (B) *Austriocaris* sp., MPUM 13472. (C) ? *Diplacanthocaris*, MPUM 13473. (D) *Stoppanicaris grignaensis*, MPUM 13474. The posterior margin is encompassed between the two blue dots. The red arrows indicate the indentations on the posterior margin. (E) Enlargement on the rostrum of (D). Scale bars equal 1 cm in (A–D) and 5 mm in (E).

Austriocarididae Glaessner, 1931

*Austriocaris* Glaessner, 1931

Type species. *Austriocaris carinata* Glaessner, 1931, from the Carnian of Polzberg (Austria).

*Austriocaris* sp.

Figure 6B



**Material.** MPUM 13472. It was discovered from a loose slab at the fossil site.

**Description.** The carapace, at least 40 mm long, has a remarkably elongate shape with the posterior part missing. The carapace length is more than 2.5 times the carapace depth based on the preserved part. The dorsal margin is gently and slightly convex from the tip of rostrum towards the posterior margin, which is broken off at the edge of the matrix. The ventral margin is nearly straight. However, the posterior part of ventral rim seems broken off from the rest of the carapace, as there is a big gap between them. Therefore, the postero-ventral margin is likely curved towards postero-dorsally, forming gently angulate ventral margin. The anterior margin is shallow and biconcave, formed by the short and sharp rostrum and the acute antero-ventral margin. The carapace is nearly smooth without distinct ornamentation. A dorso-lateral carina is well developed on the carapace along the line nearly parallel to the dorsal margin of the carapace. It starts at the level of 1/5 of the depth near the dorsal margin anteriorly near the optic margin and gradually reached the level of 1/3 at the crack of the matrix as the carapace is narrower posteriorly. A short carina is present from the level of the mid-line and extending postero-dorsally on the ventro-posterior part of the carapace. The left compound eye is preserved. The eye is irregularly rounded, kidney-shaped, with no trace of a stalk present. It is large and the small lenses are barely observable under microscope.

**Remarks.** This is the only specimen with a carapace shape of elongate rather than triangular or trapezoidal recovered in this assemblage. Although missing the posterior margin, the carapace shape strongly resembles that of *Austriocaris carinata* from Carnian beds of Austria [19], especially the biconcave anterior margin, which is not seen in other thylacocephalans. MPUM 13472 is different from *A. carinata* on the convex dorsal margin, which is nearly straight in the latter, and the position of the dorsal carina, which is less close to the dorsal margin. So far, this is the only specimen with this carapace shape discovered from this locality, and given its incompleteness, it is temporarily assigned as *Austriocaris* sp. before further material is recovered.

Order and Family uncertain

? *Diplacanthocaris* Ji et al., 2021

Figure 6C

**Material.** MPUM 13473.

**Occurrence.** Bed 44/45 Scudo Tremare site, on the southern slope of the Northern Grigna Mountain a few kilometers North of Lecco (Lombardy, Italy), Buchenstein Formation, Early Ladinian (Middle Triassic).

**Description.** This specimen is poorly preserved and missing the rostrum and optic notch. The carapace is nearly oval and has an estimated length of 45 mm. The dorsal margin is mostly gently convex and becomes nearly straight on the posterior 1/4. The anterior part of the ventral margin is broken and distorted. The ventral margin is rounded convex and becomes slightly concave posteriorly, where it forms a small spine with the dorsal margin. The carapace is smooth, without any remarkable ornamentation or microstructure.

**Remarks.** The carapace shape of this specimen strongly resembles that of *Diplacanthocaris chaohuensis* Ji et al., 2021 in the convex dorsal and ventral margins and especially on the short posterior spine. However, the carapace is clearly more elongate compared to that of the Early Triassic species from China.

*Stoppanicaris* gen. n.

LSID. urn: lsid:zoobank.org:act:3770D37B-CFF9-4CF2-8EA3-5286EEFFD9A5.

**Etymology.** From abbot Antonio Stoppani, born in Lecco in 1824—geologist, paleontologist, and popularizer—on the 200th anniversary of his birth. Stoppani worked in the Grigna mountain and published a large monography on fossils from the Ladinian carbonate platform heteropic to the Buchenstein Formation, from which our material comes, and *caris*, a general name for crustaceans.

**Occurrence.** Buchenstein Formation, Early Ladinian (Middle Triassic) of Scudo Tremare site (southern slope of the Northern Grigna Mountain a few km North of Lecco, Lombardy); Dont Formation, Pian delle Streghe, Bivera Mountain near Sauris (Udine, Friuli)

**Diagnosis.** Medium-sized thylacocephalan, with a carapace length of 40–60 mm. Subovoidal carapace with a gently curved dorsal margin and a well-rounded ventral and posterior ones. Rostrum short and slender. Optic notch small and semicircular. Carapace smooth, very thin but with thick rims. Dorso-lateral carina possibly present. Dorsal margin crenulated, ventral and posterior thickened rims with more- or less-developed spines. Posterior margin vertical or slightly forward inclined.

**Remarks.** Presence of a series of spines along the ventral and postero-ventral margins is not a common character in thylacocephalans. Usually, large spines (or better, projecting sharp corner) are recorded in both smooth and ornamented taxa but it seems this character being more common in Jurassic and Cretaceous taxa. Regarding Triassic, such spines are present in a new genus from the Anisian of Slovenia [18] or in *Austriacaris*. Regardless, those spines are totally different from the spinous margin of this new taxon, where more or less developed thorn are present all along the postero-ventral and the posterior margin. Additionally, as the carapace is not so well preserved, being mostly lacking in all the three considered specimens, it appears in contrast with the rather well-preserved carapace in the other taxa from the same sites. Thus, we consider this kind of carapace very thin and therefore difficult to be properly preserved.

*Stoppanicaris grignaensis* gen. et sp. n.

Figure 6D,E

LSID. urn:lsid:zoobank.org:act:0C4E0362-7626-4BF0-AEBD-2674F804F174.

**Etymology.** *grignaensis*, from the Northern Grigna mountain, where the holotype has been found.

**Type material.** Holotype, MPUM 13474, the only known specimen.

**Occurrence.** Bed 48 of Scudo Tremare site, on the southern slope of the Northern Grigna Mountain a few km North of Lecco (Lombardy, Italy), Buchenstein Formation, Early Ladinian (Middle Triassic).

**Diagnosis.** Same as the genus.

**Description.** The holotype is 40 mm long, its maximum height being 24 mm. It is preserved in lateral view apart from the rostral region that appears broken and turned by 90°. The general outline is almost oval with the optic notch apparently semicircular. The rostrum is broken and visible in dorsal (or ventral) view (Figure 6D,E). The rostrum itself is short and pointed. It is quite thick, as it is the large dorsal rim that shows a complete series of indentations, the single element being shorter and strong in the anterior region, then becoming smoother and smoother backward. The junction between the dorsal and the posterior margin is very gently rounded, and it is marked by the appearance of thin, sharp, and elongate spines. The posterior margin is forward inclined and bears at least six long spines. It is not clear if there are smaller spines in between the long ones. There is no sharp geometrical boundary between the posterior and the ventral margin, although the long spines make room for much shorter and stouter denticles. These latter denticles seem to be present only along the posterior half of the rounded ventral margin, although we cannot exclude that they are irregularly present also in the anterior half. The ventral beginning of the optic notch is marked by a short process. We presume that the notch is semicircular, but the displaced broken rostrum did not allow a precise restoration. The optic notch is small and there is no trace of the eye. The thickened marginal rim is present along the notch. Along the side of the carapace, only the most anterior and antero-dorsal regions are somewhat preserved, and a possible latero-dorsal carina is scanty visible.

*Stoppanicaris* sp.

We ascribe to this new genus the specimens described by Teruzzi and Muscio [36] as *Thylacocephala incertae sedis*, although the authors suggested they could belong to a new taxon. The two specimens (MFSN gp 20559-20560) are very fragmented, but they show strong resemblance to our new material in the way of preservation (only the thickened margin preserved) and in the presence of spines along the ventral and posterior margins. However, the Anisian specimens from the Friuli show a different posterior region outline that, in our opinion, could support the erection of a new species. However, as so far there

are no complete specimens, here the material described by Teruzzi and Muscio [36] is considered as *Stoppanicaris* sp.

## 5. Discussion

### 5.1. Comparison with Other (Middle) Triassic Thylacocephalan Fauna

Thylacocephalan assemblages during the Triassic can well be subdivided following the three major partitions, Early, Middle, and Late, the oldest ones being the richest known so far [8]. Moreover, in the Early Triassic, the assemblages yielding thylacocephalans were widespread along the Panthalassa and in the Tethys oceanic gulf, following the distribution of fish assemblages related to the post P/Tr crisis anoxic events [37]. Finding thylacocephalan specimens is usually not easy, owing to both their small size and relative rarity [13]. However, at least 12 nominal species have been described from four different areas (western US, Madagascar, China and Japan), which is around half of the remaining Middle–Late Triassic species. The latter show a Tethyan distribution and usually less diverse assemblages, apart from the one under study here. New assemblages from the Anisian have been recently studied [18] from the Slovenian Alps. We must also keep in mind that the Early Triassic lasted only 5 myr, while the remaining part of the Triassic was about 45 myr. Early Triassic blooming of the group was related to its possibility to live in poor bottom water conditions [13], possibly connected with the recovery after the huge P/Tr biological crisis.

The thylacocephalan assemblage from Grigna Mountain shows a quite high diversity compared to the other Triassic assemblages given that among only 13 specimens, we have at least four different genera. All the described specimens show a smooth carapace and medium to large size and possibly lived in shallow waters along the margin of a carbonate platform. We also suspect that the carapace lack of ornamentation could be related to the sandy bottom on which the thylacocephalans lived. Actually, the specimens, considering also the one from the Dolomites, are from beds made of thin calcarenite deposited in anoxic deep waters after being transported along the slope of the Buchenstein Formation basin from their original life habitat. Thus, all our specimens must be considered allochthonous.

### 5.2. Macro-Ornamentation in Triassic Thylacocephalan and Their Paleocological Implication

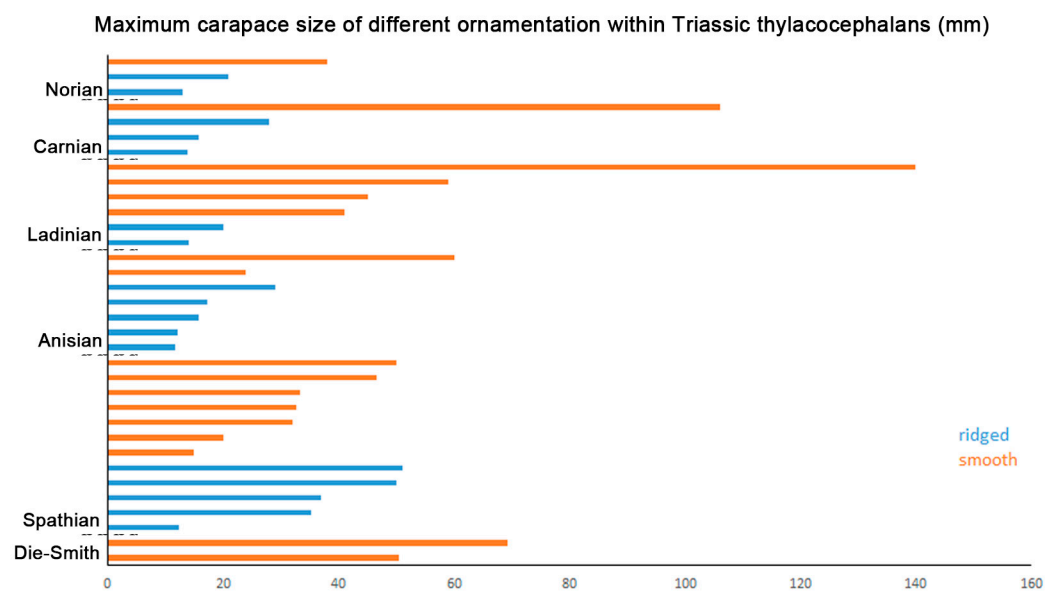
The quite large size of the *Ankitokazocaris* from this site could represent the results of a much better living environment and rich food source under high oxygen (see above) content in respect to most of the other Triassic thylacocephalans, which are mostly found in dark grey/black mudstones/shales. However, it must be noticed that *Ostenocaris cypriformis* from Early Jurassic of northern Italy has a carapace length up to 20 cm [38] and lived in a quite deep environment possibly not so rich in oxygen (39). *O. cypriniformis* is based on many specimens showing well-preserved large eyes and appendages, so they were possibly buried not far from the place they lived. This probably applies also to most other taxa recorded from the Triassic, as they are mostly found in laminated very dark to black mudstones/shales where bottom life was impossible owing to the lack of oxygen, but making preservation of delicate skeletal remains easier. This is also the case of the newly described Anisian faunas from Slovenia [18] that are represented mostly by specimens well under 20 mm in length, all of which show the typical ornamentation of Microcaridae. Large and smooth taxa were possibly more adapted to a life above sandy bottoms in shallow waters, under a somewhat high wave energy, while small, ornamented taxa are better suited for deeper environment with muddy bottom inside which they could move freely [39]. In this case, small size is probably more convenient for infaunal/semi-infaunal way of life.

For assemblages with abundant described specimens, the majority is often with one type of ornamentation while the other is rare. Take the two assemblages of Chaohu (South China) as an example, the carapace with similar ornamentation type appears consistent among individuals of the same population: nearly all the specimens from Bed 680 are *A. chaohuensis* with smooth carapace, while those from Bed 605 are mostly *M. rectilineatus*

with dense ridges on the carapace [10,13]. This also applied to the thylacocephalan faunas from the Early Triassic of Japan [12]. It appears that the different ornamentations of the carapace are correlative to different life environments.

### 5.3. Size Change and Gigantism of Thylacocephalans Through the Triassic and Their Implications

The maximum size of each species within different periods of Triassic is plotted based on published data (Figure 7). The species with vertical ridges on the carapace and those without remarkable ornamentation are shown in different colors to show the change among two morphological categories. The result suggests that the first recovered types of thylacocephalans were with smooth carapaces from the Dienerian to Smithian (mainly *Ankitokazocaris* from Madagascar), when the diversity of benthic invertebrates such as arthropods and mollusks remained relatively low, due to the unstable paleoenvironment during the post P/Tr recovery after the mass extinction [40]. They are rather large in size, which in this case might suggest less competition stress than other benthic groups [13]. Since Spathian, the diversity of thylacocephalans largely increased and many species started to develop well-ornamented carapaces such as *Microcaris* and *Kitakamicaris* [10,12]. During this period, both size and morphological variation appeared significant in multiple species, suggesting that they could have reached highest level of biodiversity during the Spathian (Early Triassic), as previously suggested [10,12,14]. Furthermore, the size of carapaces with ridges is generally larger during Spathian than in the subsequent periods.



**Figure 7.** Size range change of thylacocephalans through Triassic.

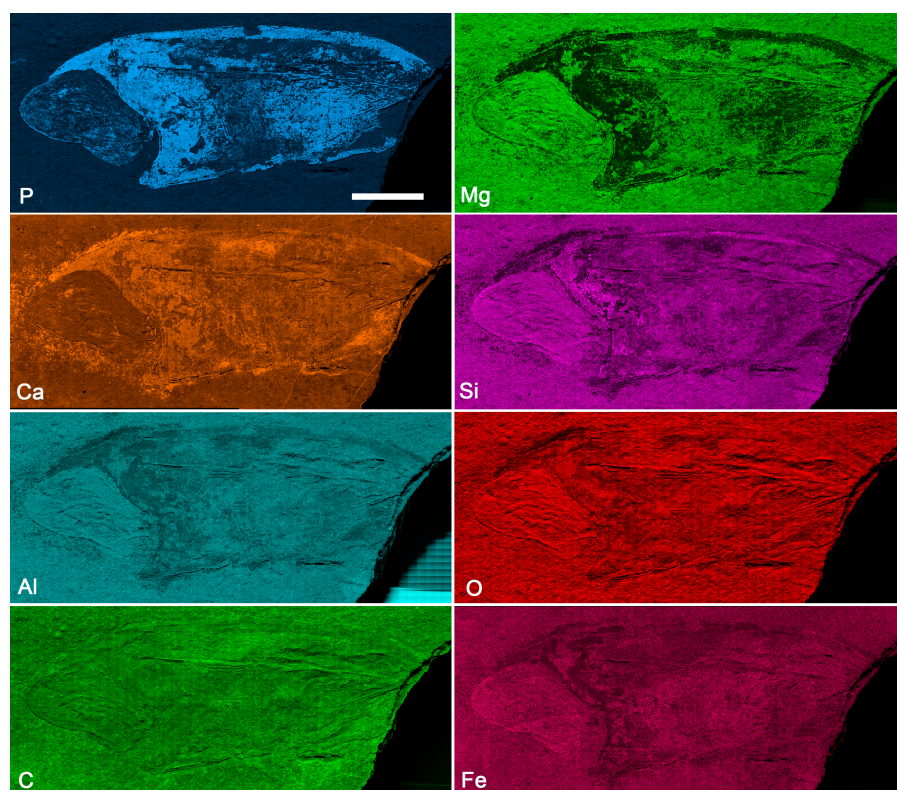
Since Anisian (Middle Triassic), the number of species decreased among both ridged and smooth carapaces. The size of species showing carapace with ridges became, on average, smaller [18] than those without remarkable ornamentation, which remained more or less around the same size, with the exception of few much larger species, such as *Austriocaris carinata* [19] and *Ankitokazocaris* sp. (this paper, MPUM 13471). It is worth mentioning that the specimen with carapace length of over 10 cm is usually represented by a single specimen, compared to the majority of the assemblage, which are much smaller. This might suggest that the paleoecological adaptation was slightly different among thylacocephalans of different size ranges. Above all, the taxa with ridges on the carapace are generally smaller than those with smooth carapaces based on published data and personal obs. (see Figure 7). This might provide new evidence on the interpretation of the different modes of life on the thylacocephalans. Thylacocephala have been reported to be bottom-feeders, and they might even burrow within the soft sediment [1,3]. The carapaces with vertical asymmetrical ridges, such as *Microcaris*, are better fitted to mov-



ing inside the sediment, and apparently, these kinds of thylacocephalans could tolerate a low oxygen environment, as they are mostly found in black laminated mudstone. The ones with smooth carapaces mostly lived above the oxic sediment because, like those studied herein, they are preserved in thin calcarenitic resedimented rocks. This could also be the reason that all the earliest thylacocephalans recorded after the EPME have smooth carapaces because they had lived above the anoxia bottom which had rare fossil record of burrower invertebrates. Additionally, the size decrease of ridged taxa could be related to the increase in the number of infaunal mollusks. This is in accordance with the benthic recovery process and paleoecological reconstruction of the marine invertebrates during Triassic e.g., [40,41].

#### 5.4. Element Mapping Analysis on the *Austriocaris*

The high percentage of phosphorus and calcium in the cuticle of the *Austriocaris* indicates the carapace mostly consists of apatite (Figure 8). This is in accordance with the interpretation of the material from Polzberg [42]. The phosphorus and calcium were merely detected from the matrix. The compound eyes instead show similar composition to the matrix which is rich in magnesium, silicon and aluminum, suggesting that no trace of primary composition or organic matter has been preserved and completely altered/ weathered during diagenesis. This might also be the reason that the lenses of the eyes can be barely observed under the microscope and no further detail can be revealed under SEM.



**Figure 8.** Element mapping results of the *Austriocaris* sp. MPUM 13472.

## 6. Conclusions

A new thylacocephalan fauna is described from the Early Ladinian (Middle Triassic) of Grigna, Northern Italy, with high diversity of at least four species of different genera: *Ankitokazocaris lariensis* sp. n., *Ankitokazocaris* sp., *Austriocaris* sp., *Diplacanthocaris chaohuensis*, *Stoppanicaris grignaensis* gen. et sp. n. The largest specimen of *Ankitokazocaris* has a carapace of over 14 cm long, which is likely the maximum size among all the thylacocephalans of the Triassic. The maximum size and ornamentation type of thylacocephalan species are compared and discussed among different periods of the Triassic. The results suggest that



taxa with ridges on the carapace are generally smaller than those with smooth carapaces. There may be a correlation between carapace morphology and their modes of life, such as inside or above the sediment with low oxygen level. Large and smooth taxa were possibly more adapted to a life above sandy bottoms in shallow waters under a somewhat high wave energy, while small, ornamented taxa are better suited for deeper environments with muddy bottoms inside which they could move freely. The EDS analysis of *Austriocaris* sp. reveals that the cuticle mainly consists of apatite, which is in accordance with previous interpretations.

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