

A new species of *Parisicaris* (Microcarididae, Thylacocephala) from the upper Olenekian (Lower Triassic) Osawa Formation in the South Kitakami Belt, Northeast Japan

Masayuki Ehiro* and Harumasa Kano

The Tohoku University Museum, Sendai 980-8578 Japan,

*Corresponding author (e-mail: masayuki.ehiro.d4@tohoku.ac.jp)

Abstract: A new thylacocephalan species of the microcarid genus *Parisicaris*, *Parisicaris naoyai*, is described from the upper Olenekian (Lower Triassic) Osawa Formation in the South Kitakami Belt, Northeast Japan. It belongs to family Microcarididae and is associated with the thylacocephalan fauna, comprising the genera *Ankitokazocaris*, *Concavicularis*, *Kitakamicaris*, *Miyagicaris* and *Paraostenia*. The generic classification of family Microcarididae and the species composition of genus *Parisicaris* are also discussed.

Introduction

Thylacocephala is a class commonly considered to belong to subphylum Crustacea (e.g. Lange et al., 2001). Although it has a long stratigraphic record ranging from the Silurian (or Cambrian) to the Cretaceous and has a wide geographic distribution, only approximately 30 genera have been described at present (Schram, 2014; Ehiro et al., 2015, 2019). Before the mid-2010s, Triassic thylacocephalans had been reported mainly from various localities in southern Europe of Austria, Italy, Spain and Slovenia, whereas the occurrences of other regions are rare only from Madagascar and South China. In particular, the Early Triassic records are limited to Madagascar (Ehiro et al., 2015). However, over the past decade, information of Triassic thylacocephalans has increased markedly, and new occurrences from the Lower Triassic have been reported from Northeast Japan (Ehiro et al., 2015, 2019), Western Australia (Haig et al., 2015), southern China (Ji et al., 2017, 2021), Idaho, USA (Brayard et al., 2017, Charbonnier et al., 2019 and Laville et al., 2021), as well as Middle Triassic strata from southern China (Feldmann et al., 2015) and northern Italy (Teruzzi and Muscio, 2018). These informations suggest that thylacocephalans were already diversified and widely distributed in low- to mid-latitude areas worldwide during the Early Triassic (Ehiro et al., 2019).

Family Microcarididae is a major component of the Triassic thylacocephalan fauna; this family was present throughout the Triassic, and broadly distributed worldwide. In this study, we describe a new species of the microcarid genus *Parisicaris*, *Parisicaris naoyai*, from the Lower

Triassic (upper Olenekian) Osawa Formation distributed in the South Kitakami Belt of Northeast Japan, and discuss the generic classification of family Microcarididae and species composition of genus *Parisicaris*.

Geological setting and materials

Among the Japanese Islands, thylacocephalans have been reported only from the Lower Triassic Osawa Formation, distributed in the Minami-sanriku area (Miyagi Prefecture) of the South Kitakami Belt. The Osawa Formation is 250–350 m thick, and mainly composed of laminated mudstone. The late Olenekian ammonoids are abundant from the lower to upper parts (e.g. Bando and Shimoyama, 1974; Ehiro et al., 2016; Shigeta, 2022) and uppermost part of the formation (Ehiro, 2022). Thylacocephalans have been collected from three localities (Motoyoshi, Tatezaki A and Tatezaki B; Figure 1) in the lower to middle parts of the formation (Ehiro et al., 2015, 2019). However, most samples have been obtained from the Tatezaki B locality, with very few derived from other two localities. The fossil horizon of the Tatezaki B locality is considered to represent middle part of the Osawa Formation, and six species belonging to five genera have been described from an interval 2 to 4 m above the base of the sequence in this locality (Ehiro et al., 2019): *Ankitokazocaris bandoi* Ehiro and Kato (Ehiro et al., 2015), *Ankitokazocaris tatensis* Ehiro et al., 2019, *Concavicularis parva* Ehiro et al., 2019, *Kitakamicaris utatsuensis* Ehiro and Kato (Ehiro et al., 2015), *Miyagicaris costata* Ehiro et al., 2019 and *Ostenocaris* sp. In this fauna, *K. utatsuensis* is dominant, comprising more than 90% of the collection. The

stratigraphy and fossil assemblages of the Osawa Formation have been described in detail in the previous researches (Ehiro et al., 2015, 2016 and 2019).

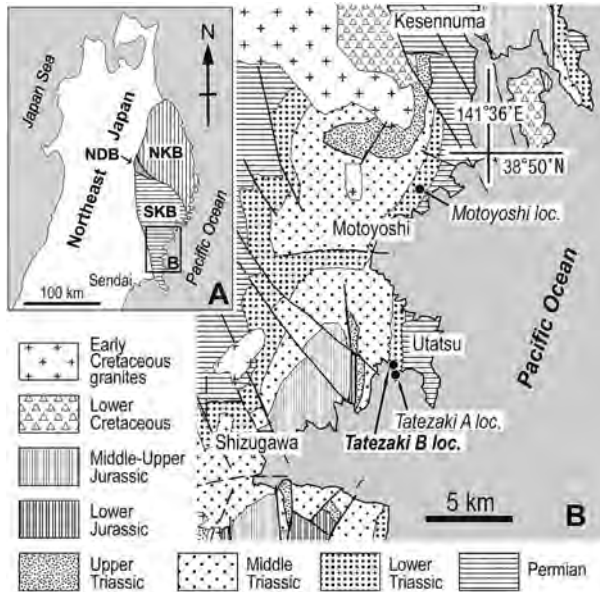


Figure 1. Index map showing the fossil locality (Tatezaki B locality) in the Utatsu area of the southern part of the Southern Kitakami Massif (South Kitakami Belt), Northeast Japan. NDB: Nedamo Belt; NKB: North Kitakami Belt; SKB: South Kitakami Belt.

Recently Laville et al. (2021) suggested that there is confusion between genus *Ostenocaris* Arduini et al., 1984 (originally described as *Ostenia* by Arduini et al., 1980) and *Paraostenia* Secrétan, 1985, stemming from the report of Arduini et al. (1980), in which some specimens with quite different morphology from *Ostenocaris* and more likely belonging to *Paraostenia*, were classified as *Ostenia cypriformis*. Therefore, Laville et al. (2021) suggested that some taxa attributed to *Ostenocaris*, including *Ostenocaris* sp. from the Osawa Formation, should be ascribed to *Paraostenia*. We agree that *Ostenocaris* sp. from the Osawa Formation belong to the genus *Paraostenia*. Laville et al. (2021) also raised questions concerning the taxonomy of some genera and species from the Osawa Formation, including *C. parva*, *K. utatsuensis* and *M. costata*. However, we do not agree with this latter proposal, as discussed later in this study.

The present specimens of Thylacocephala, described as *P. naoyai* sp. nov., were collected from the Tatezaki B locality in association with the thylacocephalan species, mentioned above. Therefore, the Osawa thylacocephalan fauna comprises seven species belonging to six genera: *A. bandoi*, *A. tatensis*, *C. parva*, *K. utatsuensis*, *M. costata*, *P.*

naoyai and *Paraostenia* sp.

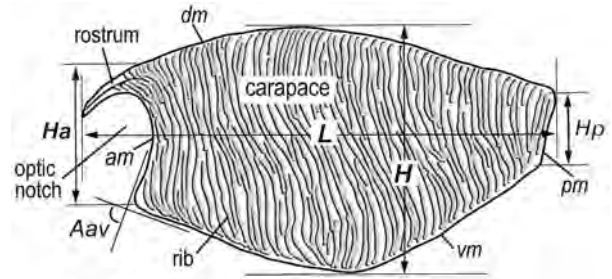


Figure 2. Morphological terminology and dimensions for the carapace in lateral view. Aav, angle (degree) of anteroventral process; am, anterior margin; dm, dorsal midline; H, Ha, Hp, maximum, anterior and posterior carapace height (mm), respectively; L, carapace length (mm); pm, posterior margin; vm, ventral margin.

The morphological terminology, dimensions and their abbreviations follow Ehiro et al. (2015; Figure 2), but using the term “dorsal midline” instead of “dorsal margin” following the observation and advocacy of Laville et al. (2021) that the thylacocephalan carapace (“shield” in Laville et al., 2021) is univalve, and not bivalve. Arduini (1988) reported that the carapace of Thylacocephala is univalve, as there is no hinge between the both sides of the carapace of “*Atropicaris*” in dorsal view (butterfly position), as also described by Laville et al. (2021). We agree with them because we also have some thylacocephalan specimens in butterfly position or equivalent to it, the dorsal midlines of them are only carinate without hinge lines (Figure 3); therefore, we used the terms “left side” and “right side” (of the carapace) rather than “left valve” and “right valve” (Ehiro et al., 2015, 2019).

Systematic description

The specimens described in this study are held in the Institute of Geology and Paleontology, Tohoku University, Sendai (IGPS; Tohoku University Museum) and the Utatsu Ichthyosaur Museum (UIM; Educational Committee of Minamisanriku Town, Miyagi Prefecture).

Class Thylacocephala Pinna, Arduini, Pesarini and Teruzzi, 1982

Family Microcarididae Schram, 2014

Included genera.— *Ferreccaris* Calzada and Mañé, 1993, *Kitakamicaris* Ehiro and Kato (Ehiro et al., 2015), *Microcaris* Pinna, 1974, *Miyagiacaris* Ehiro et al., 2019 and *Parisicaris* Charbonnier (Charbonnier et al., 2019).

Discussion.— Schram (2014) proposed the new family Microcarididae, as part of a working set of hypotheses

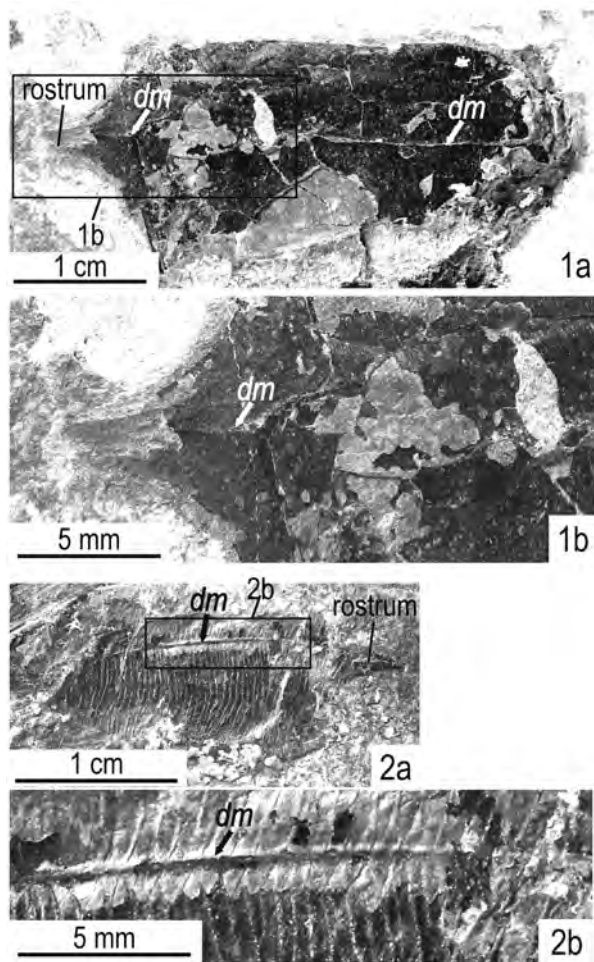


Figure 3. Dorsal views (in butterfly position) of thylacocephalan specimens from the Tatezaki B locality showing univalve nature of carapaces.

1, *Ankitokazocaris* cf. *bandoi* Ehiro and Kato in Ehiro et al., 2015, IGPS coll. cat. no. 112846; 1a, dorsal view; 1b, enlarged view of the dorsal midline of 1a; 2, *Kitakamicaris utatsuensis* Ehiro and Kato in Ehiro et al., 2015, IGPS coll. cat. no. 111456; 2a, dorsal view; 2b, enlarged view of the dorsal midline of 2a. *dm*, dorsal midline.

on the taxonomic subdivision of Thylacocephala, which included the Triassic genera *Atropicaris* Arduini and Brasca, 1984, *Ferrecaris* and *Microcaris*, and the Cretaceous genus *Thylacocephalus* Lange et al., 2001. The diagnostic characters listed by Schram (2014) are as follows: small to modest in size; thin pointed rostrum, anteriorly directed; carapace surface with rugations or terraces.

Hegna et al. (2014) compared the Cretaceous genus *Polzia* Hegna et al., 2014 with *Microcaris*. However, with the proposal of the new microcarid genus *Kitakamicaris* from the Triassic of Northeast Japan, Ehiro et al. (2015) claimed that

the genera *Thylacocephalus* and *Polzia* should be excluded from this family, because they have a distinct posterior spine, which can be compared to those of Cretaceous genera belonging to family Protozooidae Schrum, 2014 (e.g. *Protozoea* Dames, 1886 and *Pseuderichthus* Dames, 1886). Charbonnier et al. (2017) added the Cretaceous genus *Keelicaris* Charbonnier et al., 2017 and Jurassic genus *Rugocaris* Tintori et al., 1986, together with *Thylacocephalus*, to family Microcarididae on the grounds that they have remarkable ribs on the carapace, which are similar to other genera of Microcarididae. However, as noted by Ji et al. (2021), there remains some confusion about the classification of *Keelicaris* and *Thylacocephalus*. Later, Charbonnier et al. (2019) proposed a new microcarid genus, *Parisicaris*, from the Lower Triassic of Idaho, and excluded *Keelicaris*, *Rugocaris* and *Thylacocephalus* from the Microcarididae. Ehiro et al. (2019) added the new genus *Miyagicaris*, associated with *Kitakamicaris*, from the Lower Triassic of Northeast Japan.

Tintori et al. (1986) suggested that *Atropicaris rostrata* Arduini and Brasca, 1984 could be considered a junior synonym of *Microcaris minuta* Pinna, 1974, as these species have the same carapace outline and carapace ornamentation, differing only in size. Arduini (1988) rejected this view based mainly on the observations that *Microcaris* bears a well-developed, strong and pointed rostrum, whereas *Atropicaris* has a thin rostrum that ends in a spoon-like expansion; that the carapace of *Microcaris* is covered by fine, irregularly developed, straight transverse ribs, whereas *Atropicaris* shows strong, developed sigmoidal ribs; and that *Microcaris* and *Atropicaris* differ in the variability of their forms, with *Microcaris* specimens showing wide variability within a very small number of individuals, whereas *Atropicaris* is characterized by the near-homogeneity of its form. Tintori et al. (1986) reported that differences in ornamentation between *Atropicaris* and *Microcaris* depend exclusively on specimen size, but large specimens of *Microcaris* comparable to those of *Atropicaris* retained the same characteristics as smaller individuals. Recently, Ji et al. (2021) suggested that morphological differences between *Microcaris* and *Atropicaris* specified by Arduini (1988) resulted from preservation and intraspecific variability, and concluded that genus *Atropicaris* is a junior synonym of genus *Microcaris*, while accepting the specific validity of “*A.*” *rostrata* (as *Microcaris rostrata* [Arduini and Brasca]).

Microcaris minuta specimens described by Pinna (1974, 1976), Arduini (1988), and Dalla Vecchia and Muscio (1990) showed broad “intraspecific” variability in the carapace outline. Dalla Vecchia and Muscio (1990) divided these into forms designated A–D. Form A resembles a paratype described by Pinna (1974, p. 31, fig. 16), and has a broadly rounded anteroventral margin without a remarkable

anteroventral process. Form B is characterized by a largely obtuse anteroventral process and mountain-shaped convex venter. Form C is similar to form B in the carapace outline, but has somewhat sigmoidal ribs, similar to “*Atropicaris*.” The carapace outline of form D is similar to that of the holotype of *Microcaris minuta*, and has large, obtuse anteroventral process and nearly flat to broadly convex venter (Figure 4).

There are some common elements in morphology among the specimens belonging to *Microcaris* and “*Atropicaris*.” The carapace height/length (*H/L*) ratio of all forms of *Microcaris* and “*Atropicaris*” are within the range of 0.4–0.5, regardless of size (Figure 5A). The anteroventral process angles (*Aav* in Laville et al., 2021) are all large and obtuse, ranging from 100° to 140°, and become larger with increasing carapace size (Figure 5B). Therefore, it is difficult to discriminate *M. minuta* forms B and C and “*A.*” *rostrata*. Furthermore, some specimens reported by Dalla Vecchia (1993) as *Microcaris minuta* have a thin rostrum ending in a spoon-like expansion and somewhat sigmoidal ribs, both of which are characteristics shared by “*Atropicaris*.” Although some problems remain to be resolved and it is difficult to judge whether these morphological differences among the

Microcaris minuta specimens are the result of intraspecific variability, we tentatively follow Ji et al. (2021) and treat “*Atropicaris*” *rostrata* as a species of genus *Microcaris*.

Genus *Microcaris* (including *Atropicaris*) is clearly different from other genera of Microcarididae in having the following characters (Figures 4 and 6): the base of the rostrum is connected to the anterior margin of the carapace by subangular (not circular) corners; the angle of the anteroventral process (*Aav*) is large and obtuse (100°–140°); and the posterior margin is concave, with sharply pointed dorso- and ventroposterior processes. The holotype of *M. minuta* with a broadly convex venter seems to have a narrowly rounded dorso- and ventroposterior process. However, its posterior part is somewhat poorly preserved, and a specimen reported by Arduini (1988, pl. 16, fig. 2) with nearly the same carapace outline has a pointed dorsoposterior process (ventroposterior process is not well preserved).

The monotypic genus *Ferreccaris*, the type species of which is *Ferreccaris magransi* Calzada and Mañé, 1993, described from the Ladinian bed in Spain is distinguished from other genera of Microcarididae by its acute posterior margin.

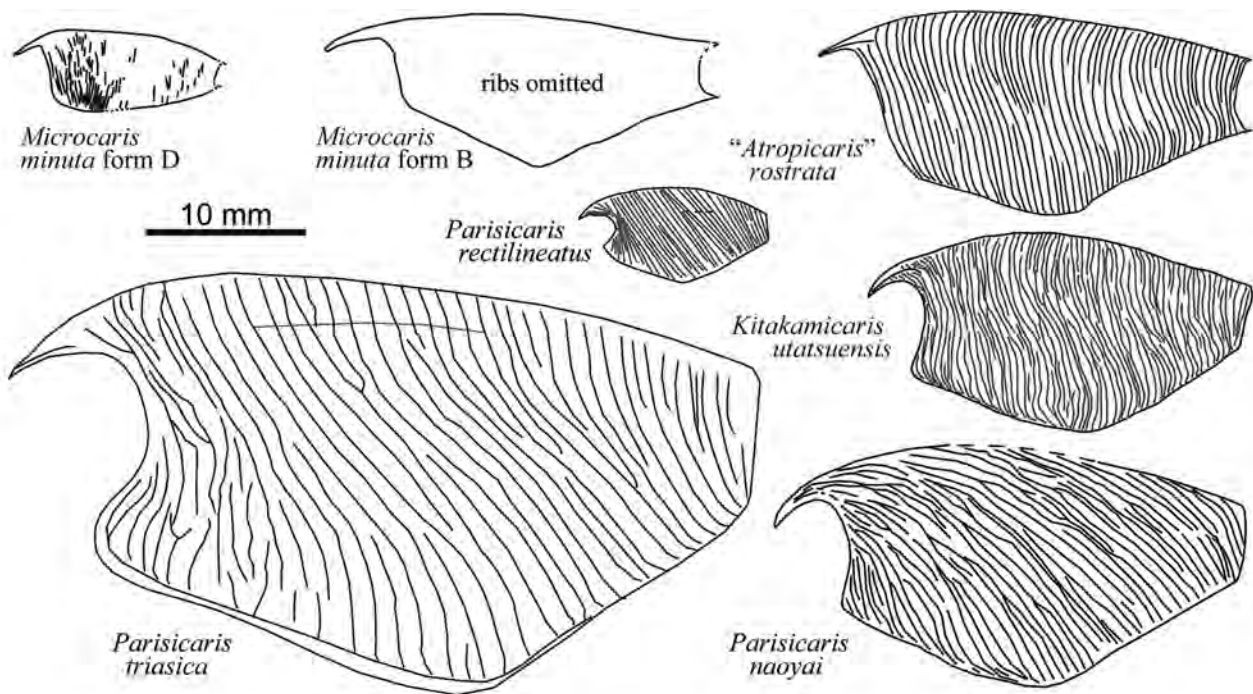


Figure 4. Sketched reconstructions of the carapaces of some species of Microcarididae.

Those of *Microcaris* and “*Atropicaris*” species were prepared from the figures of Arduini and Brasca (1984) and Arduini (1988); The posterior margin of *Microcaris minuta* form D was estimated from pl. 16, fig. 1 of Arduini (1988); those of *Parisicaris rectilineatus* and *Parisicaris triassica* are from Ji et al. (2021) and Laville et al. (2021), respectively. Scale bar is for all figures.

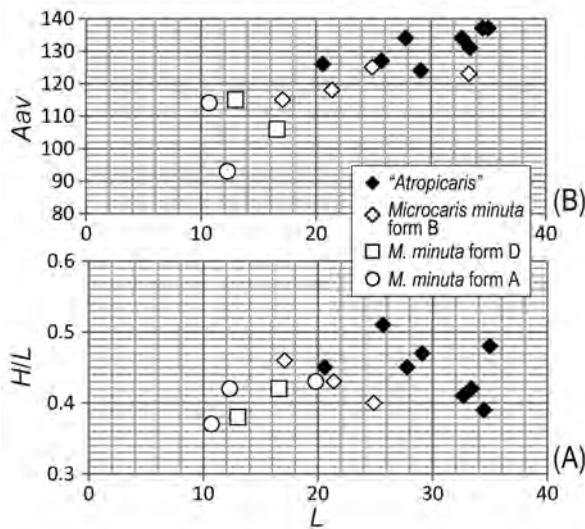


Figure 5. Plots of the (A) carapace height/length ratio (H/L) and (B) anteroventral process angle (Aav) to carapace length (L) for *Microcaris* and “*Atropicaris*” species.

However, specimens of *F. magransi* are poorly preserved and the outline of the posterior part is unclear (Calzada and Mañé, 1993, fig. 1). With the exception of the posterior end, the carapace outline and carapace ornamentation of *F. magransi* are very close to those of *M. rostrata* (Arduini and Brasca) and some specimens described as *M. minuta* by Dalla Vecchia (1993). Therefore, there remain questions about the validity of genus *Ferreccaris*.

Laville et al. (2021) claimed that the genera *Kitakamicaris* Ehiro and Kato (Ehiro et al., 2015) and *Parisicaris* Charbonnier (Charbonnier et al., 2019) are junior synonyms of *Ankitokazocaris* Arduini, 1990, and that *M. costata* Ehiro et al., 2019 may be a synonym of *K. utatsuensis* Ehiro and Kato (Ehiro et al., 2015). Laville et al. (2021) stated that *Kitakamicaris* and *Parisicaris* have a morphology diagnostic of *Ankitokazocaris*, and that the vertical ridges (ribs) that characterize these genera (*Kitakamicaris* and *Parisicaris*) may vary according to the sex, ontogeny or molting cycle of the organism, and can also be affected by the type of preservation.

However, there are obvious differences in carapace morphology between *Ankitokazocaris* and *Kitakamicaris-Parisicaris*. As noted in the emended diagnosis of genus *Ankitokazocaris* (Laville et al., 2021, p. 78), *Ankitokazocaris* has “a ventral margin subdivided into a sub-horizontal anterior part and a posterior part steeply descending anteroventrally,” whereas *Kitakamicaris* and *Parisicaris* (and other genera belonging to family Microcarididae) have a mount-like convex ventral margin, the anterior part of which is not sub-horizontal.

The bases for the second argument, outlined above, which deny the validity of surface ornamentation as a criterion of thylacocephalan classification, are hypothetical and lack reliable evidence. Laville et al. (2021, p. 80) stated only that “the outer layer of the shield is formed of sinuous, small and thin vertical ridges (Fig. 7E–G)” in the description of the shield ornamentation of *Ankitokazocaris acutirostris* Arduini, 1990. However, it is difficult to find any vertical ridges or ribs in these figures. Moreover, they described that “no transversal ridges were found in *A. acutirostris*” (p. 88). Likewise, they also stated that “with the reinterpretation of *Parisicaris* as *Ankitokazocaris*, we show that specimens of *Ankitokazocaris* can be preserved as a smooth shield, with only few ridges or with a fully ornamented shield” (p. 79). No specific evidence for these claims is provided, and their figure 10A–D for “*Ankitokazocaris* triassica” (p. 88) may be the only case. This specimen is a very poorly preserved *Parisicaris*, and there are no true *Ankitokazocaris* specimens with vertical ribs (including poorly developed), nor *Parisicaris* specimens originally having a smooth carapace.

For genus *Kitakamicaris*, we have more than 200 specimens of *K. utatsuensis*, including fragmental specimens, ranging in size (carapace length) from ca. 19 to 38 mm, which are considered to represent rather wide ontogenetic stages. The ratio of H/L ranges from 0.45 to 0.55, which show only a slight decreasing tendency with increasing size (Figure 6A). The Aav concentrated around 90°, mostly in the range of 87°–93°, and is also independent of size (Figure 6B). *Kitakamicaris utatsuensis* specimens ranging in size from smallest ($L =$ ca. 19 mm) to largest ($L =$ ca. 38 mm) are shown in Figure 7. There are almost no differences in carapace outline and rib pattern, except for a slight decreasing trend in the ratio of H/L with increasing size. In addition, the number of vertical ribs of *K. utatsuensis* specimens is constant throughout the ontogenetic stages (Figure 6C), although the rib measurements are rough estimates due to irregular rib bifurcation and poor preservation. All fragmental specimens also show remarkable ribbing; there are no smooth or poorly ribbed specimens.

Therefore, the hypothesis of Laville et al. (2021) that genera *Kitakamicaris* and *Parisicaris* are junior synonyms of *Ankitokazocaris* is unacceptable, and we consider both *Kitakamicaris* and *Parisicaris* to be valid genera.

Miyagiacaris costata Ehiro et al., 2019 has an acute (ca. 70°) Aav clearly different from that of *Kitakamicaris*. It is also characterized by strong, dendritically branched ribs in the anterior third of the carapace. Laville et al. (2021) suggested that the dendritic branching of ribs is ostensible, caused by deformation and fracturing. It is true that the holotype specimen of *M. costata* suffered some fracturing in its upper (dorsal) part and near posterior end; however, as

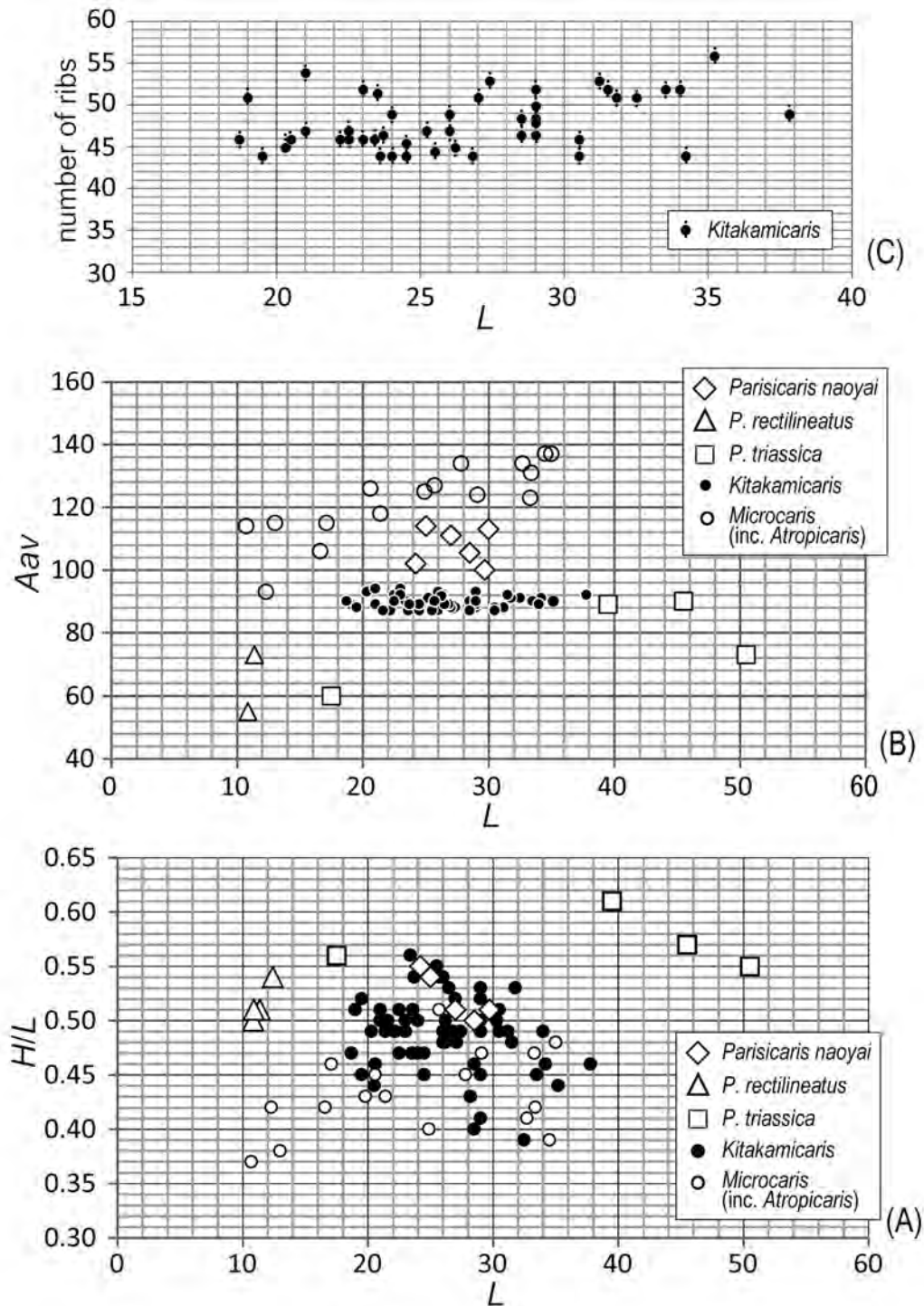


Figure 6. Plots of the (A) carapace height/length ratio ($H/L-L$) and (B) anteroventral process angle (Aav) to carapace length (L) for some genera and species of the Microcarididae, and (C) the primary rib number to L for *Kitakamicaris*.

H , L and Aav data for *Microcaris* (including “*Atropicaris*”) were estimated from figures of Arduini and Brasca (1984) and Arduini (1988). Those of *Pariscaris triassica* were obtained from Laville et al. (2021). H and L data for *Pariscaris rectilineatus* were obtained from Ji et al. (2021) and Aav data were estimated from figures of Ji et al. (2021). Data for *Kitakamicaris utatsuensis* and *Pariscaris naoyai* are provided in Appendices A and B, respectively.

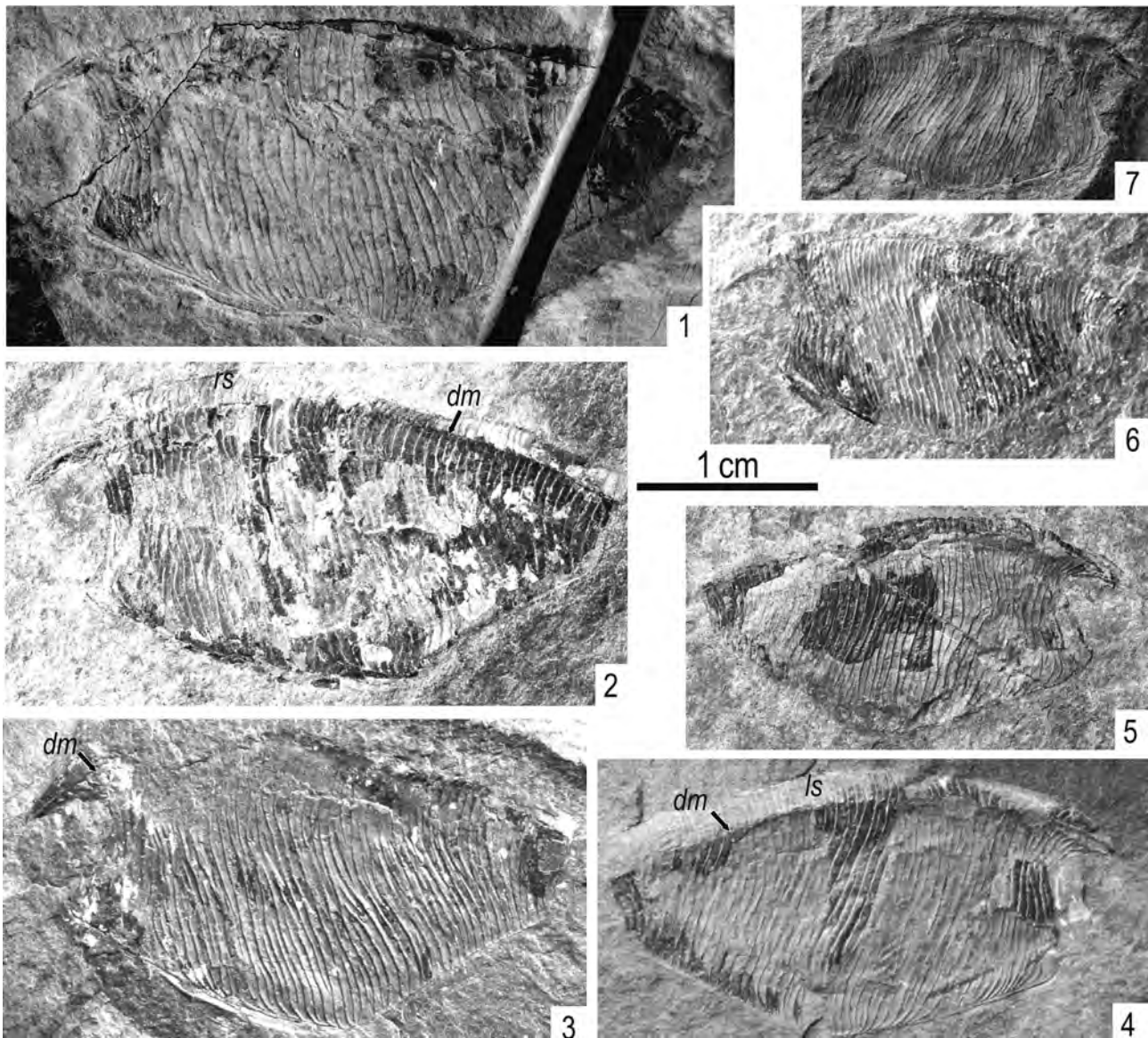


Figure 7. *Kitakamicaris utatsuensis* specimens of various sizes, sampled from an outcrop in the middle part of the Osawa Formation at the Tatezaki B locality, Utatsu, Minamisanriku Town.

1, IGPS coll. cat. no. 112783 (largest specimen); 2, UIM 30604; 3, IGPS coll. cat. no. 112786; 4, IGPS coll. cat. no. 111448 (holotype); 5, IGPS coll. cat. no. 112796; 6, IGPS coll. cat. no. 111453; 7, IGPS coll. cat. no. 111481 (smallest specimen). *dm*, dorsal midline; *ls*, left side; *rs*, right side. IGPS, Institute of Geology and Paleontology, Sendai; UIM, Utatsu Ichthyosaur Museum. Scale bar is for all figures.

shown in photographs and line drawings (Ehiro et al., 2019, fig. 10A–10D), the dendritic branching in the anteroventral region was clearly not affected by fracturing. This inference is supported by the smooth continuity of the lower part of the anterior margin and anterior half of the ventral margin.

Genus ***Parisicaris*** Charbonnier in Charbonnier, Brayard and

the Paris Biota Team, 2019

Type species.— *Parisicaris triassica* Charbonnier (Charbonnier et al., 2019)

Parisicaris Charbonnier (Charbonnier et al., 2019)

Microcaris (*Parisicaris*) Charbonnier (Charbonnier et al., 2019). Ji et al., 2021

Ankitokazocaris Arduini, 1990, Laville, Smith, Forel, Brayard and Charbonnier, 2021

Included species.— *Parisicaris naoyai* sp. nov., *P. rectilineatus* (Ji et al., 2021), *P. triassica* Charbonnier (Charbonnier et al., 2019).

Emended diagnosis.— The trapezoidal carapace has a relatively large, rounded optic notch, limited by a short thick rostrum, broadly fused with the carapace, and narrowly rounded, remarkable anteroventral process. In side view, the dorsal midline is broadly convex and the ventral margin is convex and mountain shape. The short, nearly straight posterior part is slightly inclined backward to the vertical axis, with narrowly rounded dorso- and ventroposterior processes. The carapace surface is ornamented by oblique, widely spaced ribs.

Discussion.— Charbonnier et al. (2019) proposed a new genus *Parisicaris* belonging to family Microcarididae, with *P. triassica* as the type species. A distinctive ventral notch at the anterior part of the ventral margin, which was deemed to be a diagnostic feature of the new genus, was later interpreted as an artifact of preparation (Laville et al., 2021). Ji et al. (2021) also pointed out that this feature was related to preservation. We agree with these opinions, although specimens of *Parisicaris* have other morphological features that allow its taxonomic identification. Laville et al. (2021) concluded that the genus *Parisicaris* is a junior synonym of *Ankitokazocaris* Arduini, 1990, because these two genera have the same morphological characteristics. As discussed above, this inference is based on hypotheses unsupported by specific evidence and erroneous identification, and is unacceptable.

Ji et al. (2021) considered *Parisicaris* to be a subgenus of *Microcaris* Pinna, 1974, and described a new species of *Microcaris*, *Microcaris rectilineatus* Ji et al., 2021, which resembles *P. triassica* in carapace outline and carapace ornamentation, from the late Olenekian of South China. They stated that the carapace outline and surface ornamentation of *P. triassica* and "*M.*" *rectilineatus* are similar to those of genus *Microcaris*. However, as described above, the carapace outline, particularly the angular shape of the optic notch and pointed dorso- and ventroposterior processes, and surface ornamentation characterized by dense, nearly vertical sigmoidal ribs of genus *Microcaris* are strikingly different from those of *P. triassica* and "*M.*" *rectilineatus* (Figure 4). We consider genus *Parisicaris* to be valid and that "*M.*" *rectilineatus* should belong to genus *Parisicaris* based on their similarities in carapace outline and surface ornamentation.

***Parisicaris naoyai* sp. nov.**

Figure 8.1–8.6

Material examined.— Eight specimens, IGPS coll. cat. nos. 1112810 (holotype) and 112811–112816, and UIM 30625.

Etymology.—The specific epithet is dedicated to Naoya Takahashi, who collected and donated specimens of present new species, including the holotype.

Diagnosis.— The small carapace is trapezoidal, with a thick rostrum widely fused with the carapace. The height of the carapace is approximately half of its length. The concave anterior margin is connected at an obtuse angle to the convex, mountain-shaped ventral margin. Widely spaced, slightly convex ribs incline forward, and develop over the entire carapace surface. Some ribs penetrate into the rostrum region, bending parallel to its extension direction.

Description.— Only the carapaces are preserved. The carapace is trapezoidal in lateral view, with a small but distinct, thick rostrum that is widely fused to it. The dorsal midline is broadly convex. The broad anterior margin (optic notch) is concave and composed of semicircular upper half and nearly straight lower half. The ventral margin is convex forming a mountain-shaped, nearly symmetrical, downward bend. The anteroventral process is narrowly rounded, forming an obtuse angle. The narrow posterior margin is nearly straight and inclined slightly backward, with narrowly rounded ventroposterior and dorsoposterior processes.

The maximum height is at a position close to the center of the venter where it bends. The carapace size ranges from ca. 24 to 31 mm in length and 12 to 16 mm in height, and the *H/L* ratio ranges from 0.47 to 0.52 (usually 0.51–0.52). The *Aav* ranges from 100° to 114°.

The entire carapace surface is covered by widely spaced fine ribs, many of which are single and run nearly in parallel from near the dorsal midline to the ventral margin; however, some ribs bifurcate, and some short ribs are intercalated between the primary ribs, mainly in the ventral region. A few ribs bifurcate at two or three points. Near the lower anterior margin, the ribs are diagonal to the nearly vertical anterior margin and run from the anterior margin to the venter. The ribs are slightly convex, and inclined forward at an angle of 40°–50° to the horizontal axis of the carapace in the main part and nearly 70° near the anterior and posterior margins. Near the base of the rostrum, three to five or more ribs bend parallel to the extending direction of the rostrum and penetrate into the rostrum region (Figures 8.1d, 8.2c, 8.3c and 8.5b). Although it is difficult to accurately calculate the number of primary ribs, because of their occasional branching and poor state of preservation, it is assumed to be 30–35, including short ribs near the anteroventral corner crossing the anterior margin.

Discussion.— The newly described species, *P. naoyai* resembles other species of the genus, i.e. *P. triassica* and

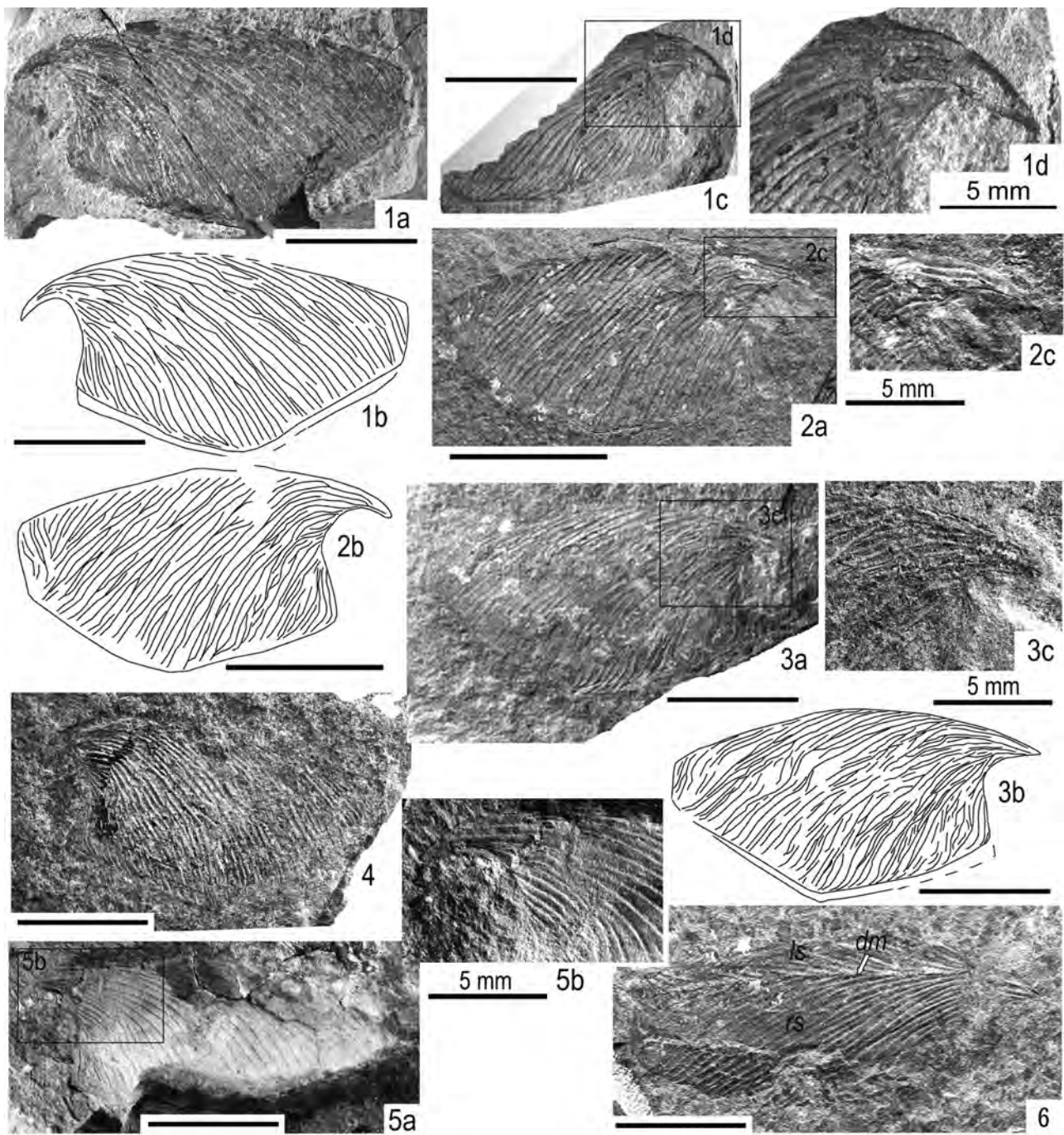


Figure 8. *Parisicaris naoyai* sp. nov., from the Osawa Formation in the South Kitakami Belt, Northeast Japan. All specimens were collected from the middle part of the formation at the Tatezaki B locality.

1, IGPS coll. cat. no. 112810 (holotype); 1a, left side view; 1b, interpretive drawing of 1a; 1c, counter part of 1a (fragmental); 1d, enlarged view of the rostrum of 1c; 2, IGPS coll. cat. no. 112814; 2a, right side view; 2b, interpretive drawing of 2a; 2c, enlarged view of the rostrum of 2a; 3, IGPS coll. cat. no. 112811; 3a, right side view; 3b, interpretive drawing of 3a; 3c, enlarged view of the rostrum of 3a; 4, UIM30625, left side view; 5, IGPS coll. cat. no. 112813; 5a, outer mold of right side; 5b, enlarged view of the rostrum of 5a; 6, IGPS coll. cat. no. 112815, dorsal view. Scale bars 1 cm, unless otherwise indicated.

P. rectilineatus, in having widely spaced, oblique ribs on the carapace. However, it is clearly distinguished from the latter two in having large *Aav* (100°–114°), upwardly curved ribs and ribs penetrating into the rostrum region.

Occurrence.— From an outcrop of the middle part of the Osawa Formation (upper Olenekian) to the north of Cape Tatezaki (Tatezaki locality of Ehiro et al., 2015; Tatezaki B locality of Ehiro et al., 2019), Utatsu, Minamisanriku Town, Miyagi Prefecture, Northeast Japan.

Acknowledgments

The authors express their deep gratitude to the Educational Committee of Minamisanriku Town and Abei-Gumi Co. Ltd. for their support during fieldwork. We also thank Naoya Takahashi for providing specimens including the holotype, and the members of the Tohoku University Museum for assistance in fieldwork. Hiroshi Nishi and an anonymous reviewer provided constructive comments and suggestions that helped us to improve the manuscript.

References

- Arduini, P., 1988, *Microcaris* and *Atropicaris*, two genera of the class Thylacocephala. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, vol. 129, p. 159–163.
- Arduini, P., 1990, Studies on Permo-Trias of Madagascar. 1. Thylacocephala from lower Trias of Madagascar. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, vol. 131, p. 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*, vol. 125, p. 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*, vol. 121, p. 360–370.
- Arduini, P., Pinna, G. and Teruzzi, G., 1984, *Ostenocaris* nom. nov. pro *Ostenia* Arduini, Pinna and Teruzzi, 1980. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, vol. 125, p. 48.
- Bando, Y. and Shimoyama, S., 1974, Late Schythian ammonoids from the Kitakami Massif. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 94, p. 293–312.
- Brayard, A., Krumenacker, L.J., Botting, J.P., Jenks, J.F., Bylund, K.G., Fara, E., Vennin, E., Olivier, N., Goudemand, N., Saucède, T., Charbonnier, S., Romano, C., Doguzhaeva, L., Thuy, B., Hautmann, M., Stephen, D.A., Thomazo, C. and Escarguel, G., 2017, Unexpected Early Triassic marine ecosystem and the rise of the Modern evolutionary fauna. *Science Advances*, vol. 3, e1602159.
- Calzada, S. and Mañé, R., 1993, Primera cita de un Tilacocefalo (Crustacea) en el Ladininiense español. *Trabajos del Museo Geológico del Seminario*, vol. 224, p. 13–17.
- Charbonnier, S., Brayard, A. and the Paris Biota Team, 2019, New thylacocephalans from the early Triassic Paris Biota (Bear Lake County, Idaho, USA). *Geobios*, vol. 54, p. 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*, vol. 188, no. 19.
- Dalla Vecchia, F.M., 1993, Segnalazion di crostacel Nell'unita Fonte Santa (Triassico Sup.) presso Filetino (Lazio, Italia). *Gortania - Atti del Museo Friulano di Storia Naturale*, vol. 14 (1992), p. 59–69.
- Dalla Vecchia, F.M. and Muscio, G., 1990, Occurrence of Thylacocephala (Arthropoda, Crustacea) from the Upper Triassic of Carnic Prealps (N. E. Italy). *Bollettino della Società Paleontologica Italiana*, vol. 29, p. 39–42.
- Dames, W., 1886, Ueber einige Crustaceen aus dem Kreideablagerungen des Libanon. *Zeitschrift der Deutschen Geologischen Gesellschaft*, vol. 38, p. 551–575.
- Ehiro, M., 2022, Latest Olenekian ammonoids from the uppermost part of the Osawa Formation (Inai Group) in the South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 26, p. 137–157.
- 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*, vol. 19, p. 269–282.
- Ehiro, M., Sasaki, O. and Kano, H., 2016, Ammonoid fauna of the upper Olenekian Osawa Formation in the Utatsu area, South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 20, p. 90–104.
- 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*, vol. 28, p. 320–333.
- Feldmann, R.M., Schweitzer, C.E., Hu, S.X., Huang, J.Y., Zhou, C.Y., Zhang, Q.Y., 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*, vol. 89, p. 1022–1037.
- Haig, D.W., Martin, S.K., Mory, A.J., McLoughlin, S., Backhouse, J., Berrell, R.W., Kear, B.P., Hall, R., Foster, C.B., Shi, G.R. and Bevana, J.C., 2015, Early Triassic (early Olenekian) life in the interior of East Gondwana: mixed marine–terrestrial biota from the Kockatea Shale, Western Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 417, p. 511–533.
- Hegna, T.A., Vega, F.J. and González-Rodríguez, K.A., 2014, First Mesozoic thylacocephalans (Arthropoda, ?Crustacea; Cretaceous) in the Western Hemisphere: new discoveries from the Muhi Quarry Lagerstätte. *Journal of Paleontology*, vol. 88, p. 606–616.
- Ji, C., Tintori, A., Jiang, D.Y. and Motani, R., 2017, New species of Thylacocephala (Arthropoda) from the Spathian (Lower Triassic) of Chaohu, Anhui Province of China. *PalZ*, vol. 91, p. 171–184.
- Ji, C., Tintori, A., Jiang, D., Motani, R. and Federico Confortini, F., 2021, New Thylacocephala (Crustacea) assemblage from the Spathian (Lower Triassic) of Majiashan (Chaohu, Anhui Province, South China). *Journal of Paleontology*, vol. 95, p. 305–319.
- Lange, S., Hof, C.H. J., Schram, F.R. and Steeman, A., 2001, New

- genus and species from the Cretaceous of Lebanon links the Thylacocephala to the Crustacea. *Palaeontology*, vol. 44, p. 905–912.
- 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*, vol. 127, p. 73–101.
- Pinna, G., 1974, I Crostacei della fauna Triassica di Cene in Val Seriana (Bergamo). *Atti Società italiana di Scienze naturali e del Museo civico di Storia naturale di Milano*, vol. 21, p. 7–33.
- Pinna, G., 1976, I crostacei Triassici dell'alta Valvestino (Brescia). *Natura Breaciana*, vol. 13, p. 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*, vol. 123, p. 469–482.
- Schram, F.R., 2014, Family level classification within Thylacocephala, with comments on their evolution and possible relationships. *Crustaceana*, vol. 87, p. 340–363.
- Secrétan, S., 1985, Conchyliocarida, a class of fossil crustaceans: relationships to malacostraca and postulated behavior. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, vol. 76, p. 381–389.
- Shigeta, Y., 2022, Revision of early Spathian (late Olenekian, Early Triassic) ammonoids from the Osawa Formation at Akaushi in the Motoyoshi area, South Kitakami Belt, Northeast Japan. *Paleontological Research*, vol. 26, p. 405–419.
- Teruzzi, G. and Muscio, G., 2018, Thylacocephalans from the Anisian (middle Triassic) of the Carnic Alps. *Gortania*, vol. 40, p. 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*, vol. 92, p. 239–250.

Appendix A. Measurements of *Kitakamicaris utatsuensis* Ehiro and Kato (Ehiro et al., 2015), all collected from the Olenekian Osawa Formation at the Tatezaki B locality in the Utatsu area, South Kitakami Belt, Northeast Japan. IGPS, Institute of Geology and Paleontology, Tohoku University, Sendai (Tohoku University Museum); UIM, Utatsu Ichthyosaur Museum. Dimensional abbreviations are provided in Figure 2. Rib numbers are rough estimates.

registered number	L	H	H/L	Ha	Hp	Aav	number of ribs
IGPS 111448	28.5	13.1	0.46	8.4	3?	90	48-49
111451	22.5	11.5	0.51	7.5	4.5	92	47+
111452	23.0	11.2	0.49	6.0	4?	94	50-51
111453	23.5	11.0	0.47	5.8?	3?		47-48
111454	24.0	11.2	0.47	6.5	4?		47-48
111457	32.5	12.7	0.39	9.5	4.0?	91	47+
111458	20.5	9?	0.44	6.5?	2.8		47+
111459	26.2	13.0	0.50	7.0	4.5	92	44?
111462	21.0	10.8	0.51	5.7	3?	89	54-55
111463	19.0	9.7	0.51	5.6	3?	89	47?
111464	30.3	15.2	0.50	9.0	5.8?		
111465	27.4	13.4	0.49	7.8	3.2?	88	52±
111466	35.2	15.5	0.44	10.3	4.5	90	51-52
111467	31.2	15.3	0.49	9.6	4.2	88	49
111469	22.2	10.8	0.49	7.5	2.7	87	47+
111471	21.4	10.5	0.49	7.6			
111472	28.2	12.0	0.43	6.0	3.0		
111474	29.0	15.4	0.53	7.7	4.0	91	46-47
111478	27.1	13.0	0.48	6.8	2.5	88	
111480	23.6	12.0	0.51	6.5	2.8?	87	41?
111481	18.7	8.7	0.47	5.7	2?	90	46+
111482	19.5	10.1	0.52	5.5	2?	88	43?
111486	27.0	14?	0.52	7.5		88	49-50
111487	20.3	10.0	0.49	7.2	3?	93	48+
111489	29.0	15.0	0.52	8.3	4.0	88	46-47
111490	26.8	13.2	0.49	8.0	3.7	89	44-45
112782	31.8	16.7	0.53	11.9	6.2	91	50-51
112783	37.8	17.2	0.46	9.5	6.0	92	45-48?
112784	30.5	14.8	0.49	8.5	4.5	88	46-47
112785	29.0	ca.13	0.45	ca.9.5	7.5		50
112786	30.5	15.5	0.51	8.0	5.0	87	43-44
IGPS 112787	26.0	14.0	0.54	7.0	3.0	87	
112788	26.0	12.5	0.48	7.0	3.5	93	47-48
112789	29.0	14.2	0.49	9.0	3?	89	50±
112790	31.5	15?	0.48	11.0	3.5	92	53±
112791	26.0	12.5	0.48	7.0	4.0	91	47±
112792	29.0	14.5	0.50	9.0	4.5	93	
112793	23.4	13.2	0.56	7.8	2.5?	90	49-50
112794	24.0	12.0	0.50	7.2	4.0	88	46-47
112795	24.0	12.0	0.50	8.5	3?	88	
112796	24.5	11.5	0.47	6.5	4.0	87	46-48
112797	25.2	13.5	0.54	9.0	4.2	91	45-46
112798	23.0	11.5	0.50	7.5	3.5?	92	46±
112799	29.0	12.0	0.41	6.0	3?	90	
112800	21.0	10.5	0.50	6.0	3.0	94	48±
112801	28.5	11.5	0.40	7.0	3.5	87?	52±
112802	26.0	12.7	0.49	7.0	4.0	89?	
112803	26.5	14.0	0.53	8.0?	4?	89	
112804	34.2	15.8	0.46	6.3		91	50
112805	22.5	10.6	0.47	7.3	3?	90	48-49
112806	24.5	13.2	0.45	7.8	2?	89	52
112807	23.7	12.8	0.54	7.1	4.0	89	46-47
112808	26.2	12.7	0.48	7.4	3.7	92	
112809	25.5	14.1	0.55	7.5	4?	87	45±
UIM 30604	33.5	15.2	0.45	8.7	3.7	90	46-47
30605	25.7	14.0?	0.54	9.0	3.5?	90	
30607	34.0	16.8	0.49	10.5	3.4	89	50-51
30608	20.6	9.5	0.46	5.5			
30609	21.6	11.0	0.50	6.8	3.5?	87	
30610	19.5	8.8	0.45	5.7			

Appendix B. Measurements of *Parisicaris naoyai* sp. nov. collected from the Olenekian Osawa Formation at the Tatezaki B locality in the Utatsu area, South Kitakami Belt, Northeast Japan. Rib numbers are rough estimates.

registered number	L	H	H/L	Ha	Hp	Aav	number of ribs
IGPS 112810	29.7	15.0	0.51	8.5	4.5	100	31-33
112811	28.5	14.3	0.5	8.7	3	106	29-31
112812	ca.25	13.5	0.54?	9.5	ca.4	114	
112813	ca.30			9.5		113	
112814	24.2	14.2	0.59	9.0	3.5?	102	35+
112815	32+						
112816	15+						
UIM 30625	27.0	14.5	0.51	9.8	3?	111	32