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Abstract

A shell of discinid brachiopod was washed ashore on Ikarashi beach, Niigata, Japan. Because the detailed morphology of the extant discinids in Japan has not been previously examined, we described the external and internal structures of this specimen to provide insights into the taxonomy and biogeography of the present discinid. The specimen is a well-preserved dorsal valve characterised by the external ornamentations of concentric growth lines and fine, radiated ridges called costellae. The internal surface of the shell exhibits two distinct pairs of muscle scars (posterior adductor and anterior adductor I), two faint pairs of muscle scars (anterior adductor II and oblique lateral) and two supposed pairs of muscle scars (oblique posterior and oblique internal). Based on the external characters, the specimen evidently has diagnoses of the genus Discradisca, thus being identified as Discradisca sp. The most similar species to the present specimen is Discradisca stella Gould, but the dorsal value of Discradisca seems to share characters that are impossible to identify using both qualitative and quantitative methods. On the Japanese coast, there are three species if the original descriptions are correct, of which Discradisca stella and Discradisca sparselineata (Dall) show similar habitats and distributions. Given that the dysoxic, interstitial habitat of *Discradisca* could alter the secretion of shell during growth, a clue to reveal the taxonomic problem would be an ecomorphological viewpoint, specifically addressing the test of relationship between morphology and microhabitat.

Key words: flotsam, Discinidae, Japan Sea, Tsushima Current, beachcombing.

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Introduction

Beachcombing is crucial to exploring drifted objects that wash up on beaches, which provides basic information on geology and biology in terms of ocean current dynamics (e.g., Donovan, 2011; Seo and Tanangonan, 2014; Davies et al., 2022). Of these drifted objects, most benthic animals are dead with no evidence of the actual habitat, while they can be regarded as proof to expect a likely ecosystem under the shallow sea. The more minor the animal, the more important will be to discuss their diversity and distribution because of little evidence in the world.

Ikarashi beach, facing the Sea of Japan, is located 900 m northwest of Niigata University, Japan (Fig. 1) and consists of fine-grained sands with bioclasts. There are abundant drifted objects such as driftwoods and marine debris of Japan, Korea and Russia based on their notation (Ishizaki et al., 2023), possibly transported by the Tsushima Warm Current. Typically, planktonic animals show mere seasonality by means of the inflow of the Tsushima Warm Current (e.g., Matsuoka et al., 2001, 2002; Itaki, 2003; Itaki et al., 2003; Kurihara et al., 2006, 2007, 2008; Kurihara and Matsuoka, 2009, 2010), while some benthic animals appear to expand their distribution northwards along the coast of the Sea of Japan (e.g., Gallagher et al., 2015; Yoshioka, 2020). To understand the dynamics of biogeographic changes in benthic animals, periodic reports of the presence or absence of benthic animals are needed.

The linguliformean brachiopod, which was recently found in Ikarashi beach, appears to be a conical shape of dorsal valve with fine radial costellae, representing a species of the genus *Discradisca* Stenzel (1965). Discinid shells on beaches have been reported from the Sea of Japan since 2011 (Oki Marine Biological Station, 2011; Ogiso et al., 2014, 2019; Yoshioka, 2016, 2017, 2020), with no detailed morphological information. As a preliminary step to identify the discinid species, we described the external and internal morphology of this specimen, followed by perspectives of the morphological variation and the distribution of *Discradisca*.

Material and methods

1. Sampling locality

A discinid brachiopod shell was collected from Ikarashi beach, Niigata, Japan (Figs. 1, 2: 37° 52'14.8"N, 138° 55'30.6"E) at a lower tide (tide level of 14 cm) on 2 November 2022. At the locality 5 m from the shoreline beside the wharf, small shells 5–10 mm in size remained on the beach by the undertow and accumulated parallel to the shoreline (Fig. 2A, B). The shell assemblage consists mainly of small bivalves (e.g., *Protothaca jedoensis* (Lischke, 1874) and *Donax semigranosus* Dunker, 1877) and echinoderms *Scaphechinus mirabilis* Agassiz (1863) (Fig. 2C).



Fig. 1. Map showing the sampling locality of Ikarashi beach, Niigata, Japan.



Fig. 2. Photographs of the sampling locality. A. Photograph showing the sampling point and wharf. B. Shell assemblage on the beach. C. Magnified photograph of shell assemblage.

2. Brachiopod specimen

The discinid brachiopod specimen is a dorsal valve of *Discradisca* sp. cf. *D. stella* (Gould, 1862), showing well-preserved external ornamentations and internal structures associated with soft parts. The specimen is 11.1 mm length, 10.8 mm width and 3.7 mm height. Schematic illustrations of the valve morphology and terminology adopted herein are shown in Fig. 3. Among the terminology, primary radiated ridges are generally so-called costae,

while the secondarily branched ridges are costellae (Williams et al., 1997a). In the present specimen, we could not find any difference between costae and costellae, so we adopted costellae for all the radiated ridges.

The external and internal morphology of the specimen was observed in colour and greyscale photographs using a digital camera Sony a 7R IV (Sony Corporation, Japan). Prior to greyscale photographing, a whitening treatment with ammonium chloride was performed on the specimen.



Fig. 3. Schematic illustrations of Discradisca sp. cf. D. stella (Gould, 1862), showing terminology.

3. Distribution of Discradisca species

To examine the distribution of extant *Discradisca* in Japan, we listed all the reports of discovery available on published articles and short reports as formal references and websites of public institutions and private blogs as informal references. Several reports lack evidence of species identification; therefore, we declined to use the original description but adopted *D*. sp.

Results and discussion

1. Morphological descriptions

Figure 4 is a colour photograph showing a colour pattern, and Figures 5 and 6 are greyscale photographs showing morphology. The specimen of the external surface shows a geometric colour pattern by means of a combination of a concentric pattern (sahara colour: code #c49c64, straw colour: code #d3b47f) and radial pattern (bark brown: code #63390e) (Fig. 4A). The radial pattern of dark colour is shown in the interval of costellae but not on the costellae themselves (Fig. 4A, D, E). The colour pattern of the internal surface is comparatively pale (cherished gold colour: code #c1975a), while the area associated with the internal structure, such as muscle scars, shows a brown colour (bright tan colour: code #835121) (Fig. 4B, F).



Fig. 4. Colour photographs of *Discradisca* sp. cf. *D. stella* (Gould, 1862). A. External view. B. Internal view. C. Latelal view. D. Magnified image around the apex showing a larval shell (LS). E. Magnified image of costellae anterior to larval shell. F. Magnified image of the internal surface. LS: larval shell.

The dorsal valve shows a nearly circular outline with a conical shape (Figs. 4A, C, 5A). The anterior slope of the cone gently convex, while the posterior slope is slightly concave (Fig. 4C). The lateral slopes are slightly convex to flat and smoothly continue towards the convex anterior slope and the concave posterior slope. The dorsal apex is smooth and located very slightly posterior to the centre.

The external surface exhibits fine radial costellae and numerous concentric growth lines (Fig. 5A). There are three patterns of external ornamentations: central, transitional and peripheral areas (Fig. 5B). The central area, inside of approximately 2.3 mm diameter, is characterised by faint concentric growth lines with no radial costellae (Fig. 5B: central). The most central part is a larval shell 350 μ m in diameter, which has no ornamentation of either concentric growth lines or radial costellae (Figs. 4D, 5B, C: LS). The transitional area, inside of approximately 5.6 mm diameter except the central area, has concentric growth lines and comparatively faint, fine radial costellae (Fig. 5B: transitional). Both ornamentations of the posterior part are finer and more distinct than those of the anterior part. A new costella is occasionally inserted at which the interval of two radial costellae increased during growth (Fig. 5B: white arrowhead). In this case, the insertion of a new costella occurs when the distance between the two costellae reaches approximately 0.3 mm. In the case of shell up to



Fig. 5. External morphology of *Discradisca* sp. cf. *D. stella* (Gould, 1862). A. External view. B. Magnified image of costellae anterior to larval shell. Note that the new costella inserted at a point of white arrowhead. C. Magnified image around the apex showing a larval shell (LS). D. Magnified image of costellae posterior to larval shell. Note that a costella disappears at a point of white arrowhead. LS: larval shell, ir: irregular growth lines, gr: granule on costella.

5 mm in diameter (15.7 mm in circumference), the number of radial costellae is 57, and therefore, the average interval of the two costellae is 0.28 mm. The transitional area changes to the peripheral area with the straw-coloured boundary area of irregular growth lines with no radial costellae (Fig. 5B: ir). The peripheral area has distinct concentric growth lines and distinct, fine radial costellae (Fig. 5B: peripheral). The intersection of the concentric growth lines and radial costellae are distinctly granular (Fig. 5B, D: gr). Similar to the transitional area, the costellae are often inserted peripherally as two costellae always maintain the same interval. The costellae sometimes disappear when the two costellae become close to each

other by means of shell curvature (Fig. 5D: white arrowhead). In the case of shell up to 9.6 mm in diameter (30.2 mm in circumference), the number of radial costellae is 110, and therefore, the average interval of the two costellae is 0.28 mm.



Fig. 6. Internal morphology of *Discradisca* sp. cf. *D. stella* (Gould, 1862). A. Internal view. B. Magnified image around the median septum. C. Magnified image series of muscle scars. D. Magnified image of the left peripheral margin of A. MS: median septum, fr: furrows anterior to median septum, OP: oblique posterior, PA: posterior adductor, OI: oblique internal, A1: anterior adductor I, A2: anterior adductor II, OL: oblique lateral, VM: vascula media, VL: vascula lateralia, V-fr: V-shaped furrow.

The internal surface is smooth but exhibits several impressions that are associated with the internal structures (Fig. 6). A short median septum is located anterior to the inside of the apex (Fig. 6B: MS). A furrow-like structure extends from the anterior end of the median septum (Fig. 6B: fr). Muscle scars occur around the inside of the apex, showing a concentric arrangement. There are two distinct pairs, two faint pairs and two supposed pairs of muscle scars.

Two pairs of adductor muscle scars are distinct (Fig. 6C: PA, A1), the so-called posterior adductor and anterior adductor I (Williams et al., 1997b). The scars of posterior adductor muscles are subcircular in outline. The scar is smooth, while its margin is furrowed, forming a very slightly elevated platform. The right and left sides of the scar connect V-shaped furrows that extend from the inside of the apex, as if they are "speech bubbles" in shape (Fig. 6C: V-fr). The scars of anterior adductor I are located in the area lateral to the median septum (Fig. 6C: A1). The outline of the scar is longitudinally elongated, curved, and elliptical. The scar is slightly concave with its margin of weak furrow, similar to the posterior adductor. The furrow of the margin is the deepest antero-internally.

The two faint pairs of scars are the anterior adductor II and oblique lateral muscles (Fig. 6C: A2, OL). The scars of anterior adductor II and oblique lateral muscles are located at the area inside and anterolateral to the scars of anterior adductor I, respectively. The scar of anterior adductor II is longitudinally elongated and curved, elliptical outline, which arranges along the inner side of the anterior adductor I (Fig. 6C: A2). The scar of oblique lateral muscle seems to be posterolaterally elongated, with a short elliptical outline (Fig. 6C: OL). Both scars of anterior adductor II and oblique lateral muscles are slightly emphasised with those margins of weak furrows.

Based on the presence of faint margins with furrows, scars of oblique internal and oblique posterior muscles are assumed (Fig. 6C: OI, OP). The former is located just anterior to the scar of the posterior adductor muscle, and the latter is located between the right and left of the scars of posterior adductor muscles. Both scars are small and subcircular in outline. In discinid brachiopods, there would be a pair of scars for brachial retractor muscles laterally distant from the scars of oblique lateral muscles, but we could not identify it in the present specimen.

Only the proximal parts of the vascula media and lateralia are partially preserved as faint impressions (Fig. 6C: VM, VL). The vascula media extends from the area slightly anterior to the scars of anterior adductor I and seems to bend laterally along the visceral area (Fig. 6C: VM). The vascula lateralia laterally extends from the periphery of the visceral area around the scars of anterior adductor I (Fig. 6C: VL). Because the inner layer of the shell is partially removed, the distal network of the vascular system is unknown.

The margin of the shell exhibits a single lamella, which encloses small pebbles inside (Fig. 6D: white arrowhead).

2. Insights into morphological variation

The taxonomy of fossil and living discinid brachiopods is mainly based on the ornamentations of dorsal and ventral valves, the convexity of shells and the structure associated with the pedicle (e.g., Williams et al., 2000; Mergl, 2010; Masunaga and Shiino, 2021). In the case of *Discradisca*, the characteristics of radial costellae and concentric growth lines in the dorsal valve have been frequently adopted to identify their species (e.g., Bitner, 2010, 2014).

The characteristics of the present specimen fit with those of *Discradisca stella*, which has distinct, fine costellae and concentric growth lines in the dorsal valve (e.g., Bitner, 2010). However, this conclusion remains problematic because the relief of both ornamentations seems to be enhanced during growth. If the present animal died before the fully grown stage up to 5 mm, the morphology could be similar to that of *Discradisca sparselineata* (Dall, 1920), which is characterised by faint costellae.

Discradisca indica (Dall, 1920) is similar to *Discradisca stella* but differs in distinctly granular and more widely spaced costellae (e.g., Bitner, 2010). In the case of *Discradisca indica* shown in Bitner et al. (2008: Fig. 2B), the number of costellae is approximately 69 with a circumference of 11.7 mm, resulting in a 0.17 mm average interval of two costellae. This calculated value implied finer costellae than the present *Discradisca* sp. cf. *D. stella*, the taxonomic problem that is a future direction to explore detailed morphological analyses.



Fig. 7. Distribution of Discradisca in Japan.

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Table

Table Localit	1. Distribution of <i>Discradisca</i> in Japan. by number and name	Species	latitude (if described)	Depth or depth zone	Substrate and environment	Environment	Method	Sampling Date	Reference
-	Hakodate	Discradisca sparselineata							Dall (1920)
5	Kattoshi (Hokkaido)	Discradisca sp.			Underside of boulders and bioclasts	Sandy tidal flat and rocky coast			Laboratory of Animal Ecology, School of Agriculture, Hokkaido University (2018)
б	Asamushi (Aomori)	Discradisca sp.			1			,	Research Center for Marine Biology, Graduate School of Life Sciences, Tohoku
4	Ayukawa (Ishinomaki)	Discradisca rikuzenensis		37 m					University Hatai (1940)
ŝ	Tokyo bay	Discradisca stella							Dall (1920)
- ·		Discratisca sparsentienta						2001 0201	
•	rrayarna (Sagani Day)	Discratisca stena		E .	bivalve weopychodonie coch	- 4	OIII-net and nand travt institutes	0661-0061	
0	Hayama (Sagamı bay)	Discradisca sparselineata		mcl			Gill-net and hand traw! fishings	1963-1996	Ikeda and Kuramochi (1997)
9	Hayama (Sagami bay)	Discradisca sp.		200-300 m			Gill-net and hand trawl fishings	1963-1996	Ikeda and Kuramochi (1997)
r 3	Enoshima (Sagami bay)	Discradisca stella			:				Dall (1920)
~ ~	Hazu (Mikawa bay) Toha bav	Discratisca sparsetmeata Discratisca su		Intertidal Zone	Boulders -	LIGAL TIAT			Ishikawa et al. (2016) Toha Amarium (2014)
10	Shirahama (Wakayama)	Discradisca stella		Middle intertidal to subtidal zone	Underside of boulders				Kawamura et al. (2016)
Ξ	Osaka bay	Discradisca stella			Flat, underside of boulders	Rocky coast near mouth of Osaka bay		2006-2010	Association for the Research of Littoral Organisms in Osaka Bay (2012); Otani (2019)
Ξ	Osaka bay	Discradisca sp.		50 m	Molluscan shells				omoyasu ta (2020)
12	Tanoshiro coast (Awaji Island)	Discradisca stella						2020.07.18	Suzuki (2020)
5 S	Fukura (Awaji Island)	Discradisca stella							Dall (1920)
5	Awaji Island	Discradisca sparselmeata					•		Dall (1920)
14	Ushimado (Okayama)	Discradisca stella			Underside of boulders slightly buried in sand	Gravelly tidal flat an rocky coast	-		Ushimado Marine Institute, Okayama University
14-19	· Bisan-seto ocean area	Discradisca stella			Underside of boulders slightly buried in sand	Gravelly tidal flat an rocky coast	-		Tamano Marine Institute, Okayama University (1978); Wada and Yoshimatsu (2020a)
15	Okayama	Discrudisca sparsel neata		Middle intertidal to subidal zone	Flat, hard substrates such as boulders and bivalves	Mouth of bay, strait and tide pool			Fukuda (2010); Wada and Yoshimatsu (2020b)
16	Tamano (Okayama)	Discradisca sparselineata		Middle intertidal to subtidal zone	Flat, hard substrates such as boulders and bivalves	Mouth of bay, strait and tide pool	,		Fukuda (2010); Wada and Yoshimatsu (2020b)
17	Kurashiki (Okayama)	Discradisca sparsel meata		Middle intertidal to subtidal zone	Flat, hard substrates such as boulders and bivalves	Mouth of bay, strait and tide rool			Fukuda (2010); Wada and Yoshimatsu (7070h)
18 19 20	Hiro Island (Hiroshima, Shiwaku Islands) Kasaoka bay (Okayama) Hashira Island (Hashirajima, Yamaguchi)	Discrudisca . sp. cf. D. sparselineata Discradisca sp. Discradisca sparselineata	34°24'47,4"N, 133°43'53,4"E - -	21 m - -			Dredge -	2010.11.09 2016 -	Hirose et al. (2012) @menashi_sato (2016) Kato (1996)
21	Mouth of Kumanoe river (Miyazaki)	Discradisca sp.		Intertidal zone	Underside of gravel slightly buried in sand	Transitinal zone of rocky coast to sandy tidal flat			Miura et al. (2012)
22	Nobeoka bay (Miyazaki)	Discrudisca sp.		Intertidal zone	Underside of gravel slightly buried in sand	Transitinal zone of rocky coast to sandy tidal flat		,	Miura et al. (2012)

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Miura et al. (2012)	Miura et al. (2012)	Kumamoto Prefectural Rare Wild Fauna and Flora Review Committee (2009)	Dall (1920)	Dall (1920)	Osawa and Kurata (2016)	Yoshioka (2017)	Oki Marine Biological Station (2011)	Yoshioka (2017)	Yoshioka (2017)	Yoshioka (2016)	Yoshioka (2016)	Yoshioka (2016)	Yoshioka (2016)	Ogiso et al. (2014, 2019)	Ogiso et al. (2019)	Yoshioka (2016)	18- Yoshioka (2016, 2020)	Yoshioka (2016)	Yoshioka (2016)	This study	.11 Yoshimatsu (2014)
2010.5-9						2017.1.3	,	2016.12.27	2016.12.27	2016.7.1	2016.7.1	2016.7.1	2012.12.19	2014.10.7; 2018.7.31	2018.6.8	2016.6.6	2016.6.6; 20	2020 2016.6.3	2016.6.20	2022.11.02	2010.8-2012
						Beachcombing		Beachcombing	Beachcombing	Beachcombing	Beachcombing	Beachcombing	Beachcombing	SCUBA diving	SCUBA diving	Beachcombing	Beachcombing	Beachcombing	Beachcombing	Beachcombing	Kitahara's water bottle and plankton net
Transitinal zone of rocky coast to sand tidal flat with effec of blackish water	Transitinal zone of rocky coast to sand tidal flat													Rocky coast					,		
Underside of gravel slightly buried in sand	Underside of gravel slightly buried in sand					,				,				Underside of boulders slightly buried in sand of	Underside of boulders						
Intertidal zone	Intertidal zone		,							,				2.8-4.9 m	2 m						30 m (water column)
32°29'N,131°41'E	·							,		,										37°52'14.8"N, 138°55'30.6"E	
Discradisca sp.	Discradisca sp.	Discradisca sparselineata	Discradisca stella	Discradisca stella	Discradisca sp.	Discradisca sp.	Discradisca stella	Discradisca sp.	Discradisca sp.	Discradisca sp.	Discradisca sp.	Discradisca sp.	Discradisca sp.	Discradisca sperselineata	Discradisca stella	Discradisca sp.	Discradisca sp.	Discradisca sp.	Discradisca sp.	Discradisca sp.	Planktonic larvae of Disciradisca spp.
23 Iorigawa (Kadogawa bay)	24 Nojima (Miyazaki)	25 Kumarnoto	26 Nagasaki	27 Hirado (Nagasaki)	28 Sakaisuido (Shimane)	29 Yumigahama (Shimane)	30 Oki Islands	31 Karo coast (Tottori)	32 Kanzaki coast (Kyoto)	33 Tai coast (Wakasa bay)	34 Takasu coast (Fukui)	35 Komaiko coast (Ishikawa)	36 Masuhogaura (Ishikawa)	37 Tsukumo bay (Ishikawa)	38 Tara Island (Kuki, Notojima, Ishikawa)	39 Yaetsu beach (Toyama)	40 Hamakurosaki coast (Toyama)	41 Naoetsu coast (Niigata)	42 Ikarashi beach (Niigata)	42 Ikarashi beach (Niigata)	14-19 Bisan-seto area (Seto Island Sea)

3. Distribution of *Discradisca* species around Japan

All the discoveries of extant *Discradisca* at 42 localities in Japan are shown in Fig. 7 and Table 1. *Discradisca* has been frequently reported from the Bisan-seto area (locality number 14–19), while its distribution is almost whole along the Japanese coast (Fig. 7).

The living *Discradisca* always attach to a hard substratum such as boulders and bioclasts, almost all of which are slightly buried in sediments (Table 1). Oxygen-poor conditions may easily occur beneath the sediment-water interface (Bromley, 1996), which results in unique faunal characteristics. For example, linguliformean brachiopods, including discinids, could adapt to dysoxic environments as opportunists regardless of extant and fossil species (Chen et al., 2005; Peng et al., 2007; Masunaga and Shiino, 2021). Such a tolerance for oxygenic differences would realise the wide distribution along the Japanese coast, avoiding the severe competitive framework.

According to the original descriptions, three species have been reported from Japan: *Discradisca stella, Discradisca sparselineata* and *Discradisca rikuzenensis* Hatai (1940). It has been suggested that a colony consists of a single species, and occasionally neighbouring two colonies have different species (Ogiso et al., 2019). However, planktonic larva is not superior to swimming for selective settlement but depends mainly on passive settlement (Abelson, 1997; Shiino and Tokuda, 2016). If *Discradisca* species could form a monospecific colony, it leads to the possibilities of 1) sudden settlement close to the colony after free-spawning and 2) a difference in the spawning period that enables the dispersal of planktonic larvae via sea flows unique to the period.

In the former possibility, a new colony of a single species forms beside the original colony, resulting in the limited distribution of the species. This seems to be not the present case because the distributions of *Discradisca stella* and *Discradisca sparselineata* overlap with each other (Table 1). In the latter possibility, there is no evidence to explain the difference in spawning period among *Discradisca* species. Discinid larvae are planktotrophic, which enables them to persist in plankton for prolonged periods and travel over considerable distances (Williams et al., 1997b). According to Yoshimatsu (2014), planktonic larvae of *Discradisca* species area (Seto Island Sea), where adult individuals of *Discradisca stella* and *Discradisca sparselineata* also inhabit shallow seawater. The appearance of discinid larvae may include the two species of *Discradisca*.

Discradisca may have a wide variety of shell forms regarding the outline, convexity, number of radial costellae and intensity of external ornamentations. Given that the animal inhabits narrow, interstitial spaces, such as the underside of gravel (e.g., Kato, 1996), morphological variation could occur with regard to not only the difference in species but also the difference in microhabitats.

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* English translation from the original written in Japanese

A mixed Boreal-Tethyan-Panthalassan brachiopod fauna from the lower Permian (Asselian) of Miharanoro, Akiyoshi Belt, southwestern Japan

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Abstract

In this paper a brachiopod fauna (the Miharanoro fauna), consisting of 11 species in 9 genera, is described from the lower Permian limestone (Uyamano Formation) of Miharanoro in the Taishaku area, Akiyoshi Belt, southwestern Japan. The age of the Miharanoro fauna is identified as the Asselian (early Permian, Cisuralian). In terms of palaeobiogeography, the Miharanoro fauna is a mixed Boreal–Tethyan–Panthalassan fauna, and exhibits an affinity with the lower Permian fauna of Texas. Thus, the seamounts of the Akiyoshi Belt, including Taishaku, were probably located between the Sino-Mongolian–Japanese Province and North America (Texas) in Panthalassa during the Asselian.

Key words: Akiyoshi-type seamount, Asselian, Brachiopoda, Miharanoro, palaeobiogeography.

Introduction

The Akiyoshi Belt, southwestern Japan consists of a Permian accretionary complex, which is composed of lower Carboniferous-middle Permian limestone-basalt blocks (including the Omi, Atetsu, Taishaku, Akiyoshi and Hirao blocks; Fig. 1A) with contemporaneous cherts and upper Permian clastic rocks. The limestone-basalt blocks were seamounts with carbonate caps in Panthalassa during the early Carboniferous-middle Permian; they accreted to Proto-Japan during the late Permian (Kanmera et al., 1990; Isozaki, 1997). The locations of the seamounts during the early Carboniferous-middle Permian are, however, unclear because of a paucity of palaeobiogeographical studies on the

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Fig. 1. Maps showing the location and geology of fossil locality Miharanoro in the Taishaku area of the Akiyoshi Belt, southwestern Japan; **A**, geotectonic map of the southwestern Japan, MTL: Median Tectonic Line (based on Ishida et al., 2013); **B**, topographic map showing the fossil locality MHN1 in Miharanoro, Tojo-cho, Shobara City, Hiroshima Prefecture (using the electronic topographical map of the Geospatial Information Authority of Japan).

fossil biota from the limestone-basalt blocks and the surrounding clastic rocks in the Akiyoshi Belt.

The present study describes an early Permian brachiopod fauna (the Miharanoro fauna), consisting of 11 species in 9 genera from a limestone block at Miharanoro in the Taishaku area, Akiyoshi Belt, and discuss the age and palaeobiogeography of the fauna. In this study, Y. Ibaraki studied systematics in part (*Choristites*); and J. Tazawa studied systematics for the most part of the brachiopod species and palaeobiogeography of the Miharanoro fauna.



Fig. 2. Generalized columnar section of the limestone-basalt complex of the Taishaku area, Akiyochi Belt (compiled from Hase et al., 1974 and Ehiro and Ozawa, 2020).

Stratigraphy and material

The stratigraphy of the Carboniferous–Permian rocks of the Taishaku area, including Miharanoro, was studied and summarized by Hase et al. (1974). According to that study, the limestone–basalt block in the Taishaku area is divided into three formations, which are, in ascending stratigraphic order, the Dangyokei Formation (lower Carboniferous basaltic rocks, more than 150 m thick), the Eimyoji Formation (upper Carboniferous limestones, approximately 150 m thick), and the Uyamano Formation (lower–middle Permian limestones, 400–500 m thick). The brachiopod specimens, considered in the present study were collected by Isao Nishikawa in the 1950s and 1960s from light grey limestone of the lower part of the Uyamano Formation at locality MHN1 (34°51′20″N, 133°15′54″E, which is the same as locality 1 of Ehiro et al., 2014, fig. 1B), Miharanoro (i.e., Miharanoro, Tojo-cho, Shobara City, Hiroshima Prefecture) in the Taishaku area, Akiyoshi Belt, southwestern Japan (Figs. 1B and 2).

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Period, Epoc Age		Doundaria	rennsylvanian			Ciencolion	CISULALIAN		Guadalupian		
Species	Bashkirian	Moscovian	Kasimovian	Gzhelian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian	Wordian	Capitanian
Tubaria sp.		• • •		• • •	• • •	• • •					
Echinoconchus punctatus	\vdash				_					\square	
Karavankina typica						_				\square	
Compressoproductus flabellatus											
Spitzbergenia sp.					• • •	• • •	• • •	• • •	••••		
Rhipidomella sp.	·	• • •	• • •	• • •	• • • •	• • • •	• • • •	• • • •	• • •	•	••••
Enteletes stehlii											
Enteletes bowsheri											
Martinia cruenta											
Choristites fritschi											
Chorisitites sp.	• • • •	• • • •	• • • •	• • • •	• • • •						

Fig. 3. Stratigraphic distributions of brachiopod species of the Miharanoro fauna. Broken lines show those of the genera.

The Nishikawa brachiopod collection was initially studied by Hayasaka and Kato (1966) and subsequently by Nakamura and Nishikawa (1979): Hayasaka and Kato (1966) described a brachiopod species *Enteletes gibbosus* Chronic; and Nakamura and Nishikawa (1979) found a Boreal brachiopod genus *Spitzbergenia* (species uncertain) in the collection, and briefly noted palaeobiogeographical significance of the genus. Subsequently, most of the Nishikawa collection, excluding the specimens described by Hayasaka and Kato (1966) as *Enteletes gibbosus*, was made available to the senior author (J. T.) by Koji Nakamura. The brachiopod specimens studied in the present work are now registered (prefix FMM, numbers 6323–6376) and housed in the Fossa Magna Museum, Itoigawa City, Niigata Prefecture, Japan.

Miharanoro fauna

The brachiopod fauna (Miharanoro fauna) described herein consists of 11 species in 9 genera. The list of species is as follows: *Tubaria* sp., *Echinoconchus punctatus* (Sowerby), *Karavankina typica* Ramovš, *Compressoproductus flabellatus* Cooper and Grant, *Spitzbergenia* sp., *Rhipidomella* sp., *Enteletes stehlii* Cooper and Grant, *E. bowsheri* Cooper and Grant, *Martinia cruenta* Cooper and Grant, *Choristites fritschi* (Schellwien) and *Choristites* sp. Of these species, *Enteletes stehlii*, *Martinia cruenta* and *Choristites fritschi* are abundant; *Enteletes bowsheri* and *Choristites* sp. are common; and the other species are rare in the Miharanoro fauna.

Age

The stratigrapic distributions of the brachiopod species of the Miharanoro fauna are described in the section "Systematic descriptions" and summarized in Fig. 3. Of the brachiopod taxa listed above, *Enteletes bowsheri* is known only from the Asselian. *Echinoconchus punctatus* is known from the upper Tournaisian-Asselian and *Choristites fritschi* is known from the Moscovian-Sakmarian. In contrast, *Compressoproductus flabellatus* occurs from the Asselian-Kungurian, two species (*Karavankina typica* and *Martinia cruenta*) have a stratigraphic range of Asselian-Sakmarian, and *Enteletes stehlii* occurs from the Asselian-Artinskian. At the generic level, *Tubaria* is known from the Moscovian-Sakmarian (Grigorjeva et al., 1977; Klets, 2005; this study). Two of the genera (*Rhipidomella* and *Choristites*) have long stratigraphic ranges: *Rhipidomella* has a range of middle Devonian (Eifelian) to upper Permian (Tatarian; Harper, 2000); and *Choristites* is known from the lower Carboniferous (Mississippian)-lower Permian (Cisuralian; Carter, 2006).

In summary, the age of the Miharanoro fauna is identified as Asselian; thus, the lower part of the Uyamano Formation in Miharanoro is correlated with the Asselian. This conclusion is consistent with previous studies (Ehiro et al., 2014; Ehiro and Ozawa, 2020) on the fusulinoid-ammonoid fauna from the lower part of the Uyamano Formation of Miharanoro.

Palaeobiogeography

The geographic distributions of the brachiopod species of the Miharanoro fauna are described in the "Systematic descriptions" section. Echinoconchus punctatus is known from northeastern Japan (South Kitakami Belt), northern Russia (Verkhoyansk Range, Taimyr Peninsula and northern Urals), the UK (Scotland, England and Wales), Germany, Belgium, Spain, western Russia (Moscow Basin), central Russia (southern Urals), Kyrgyzstan, northwestern China (Xinjiang and Qinghai), northern China (Shanxi) and northeastern China (Liaoning). Karavankina typica is known from Slovenia. Four species (Compressoproductus flabellatus, Enteletes stehlii, E. bowsheri and Martinia cruenta) are known from the USA (Texas). Choristites fritschi is known from Spain, Slovenia, Austria, Kazakhstan, Uzbekistan and eastern China (Shandong). At the generic level, Tubaria is known from northern Russia (northern Urals, Pay-Khoy and Timan), Svalbard (Spitsbergen), western Russia (Moscow Basin and Donetz Basin), central Russia (southern Urals) and Uzbekistan (Muir-Wood and Cooper, 1960; Kalashnikov, 1993). Spitzbergenia is known from Arctic Canada (northern Yukon Territory), northern Russia (Verkhoyansk Range, Kolyma-Omolon Massif, Kanin Peninsula, northern Russian Platform and Novaya Zemlya), Svalbard (Spitsbergen and Northeast Island), Greenland and southern Mongolia (Grigorjeva et al., 1977; Brunton et al., 2000). Rhipidomella and Martinia are cosmopolitan (Harper, 2000; Carter and Gourvennec,



Fig. 4. Early Permian (Asselian) reconstruction map of the world (adapted from Ziegler et al., 1997), showing the location of the Aiyoshi-type seamounts (asterisk). AF: Africa, AN: Antarctica, AR: Arabia, AU: Australia, E: Eurasia; G: Greenland, IC: Indochina, IN: India, L: Lhasa, M: Mongolia, NA: North America, NC: North China, Q: Qangtang, SA: South America, SC: South China, SI: Sibumasu, T: Tarim.

2006). *Choristites* is known from Eurasia (Carter, 2006), mostly from Russia and northern China (Chao, 1929; Ivanov and Ivanova, 1937; Barchatova, 1970; He et al., 1995).

In summary, the Miharanoro fauna is a mixed Boreal-Tethyan-Panthalassan fauna, consisting of Boreal elements (*Tubaria* sp. and *Spitzbergenia* sp.), Tethyan elements (*Karavankina typica* and *Choristites fritschi*) and Panthalassan elements (*Compressoprodutus flabellatus, Enteletes stehlii, E. bowsheri* and *Martinia cruenta*). It is noteworthy that four species (*Compressoprodutus flabellatus, Enteletes stehlii, E. bowsheri* and *Martinia cruenta*). It is noteworthy that four species (*Compressoprodutus flabellatus, Enteletes stehlii, E. bowsheri* and *Martinia cruenta*) also occur in Texas. Moreover, mixed Boreal-Tethyan fauna occur in the Sino-Mongolian-Japanese Province (Shi and Tazawa, 2001) [=Inner Mongolian-Japanese Transition Zone (Tazawa, 1991); Northern Transitional Zone (Shi et al., 1995)], which occupied a vast area of the North China Block and the surrounding area. From the above data, it is concluded that the Akiyoshi-type seamounts, including the Taishaku (Miharanoro) one, were probably located between the Sino-Mongolian-Japanese Province and North America (Texas) in Panthalassa during the Asselian (Fig. 4).

In contrast, Ehiro and Ozawa (2020) proposed another hypothesis on the basis of a palaeobiogeographical study of the Miharanoro ammonoid fauna: the Akiyoshi-type seamounts were located in the equatorial region of Panthalassa (Mid-Panthalassan Realm) in the early Permian (Asselian). However, the ammonoid fauna consists of four indeterminate species, one taxon indeterminate at both generic and specific levels, and four new species; only one species (*Metapronorites timorensis*) was identified with certainty. Moreover, most of the genera of the Miharanoro fauna (*Agathiceras, Neoglaphyrites, Somoholites, Eoasianites*)

and *Metapronorites*) are cosmopolitan, occurring from the arctic to the equatorial regions and not restricted to the equatorial Panthalassa (Ehiro and Ozawa, 2020, p. 311–312). The material seems to be insufficient for the given conclusion.

Conclusion

The Miharanoro brachiopod fauna from the lower part of the Uyamano Formation of Miharanoro consists of 11 species in 9 genera: *Tubaria* sp., *Echinoconchus punctatus*, *Karavankina typica*, *Compressoproductus flabellatus*, *Spitzbergenia* sp., *Rhipidomella* sp., *Enteletes stehlii*, *E. bowsheri*, *Martinia cruenta*, *Choristites fritschi* and *Choristites* sp. The age of the Miharanoro fauna is identified as Asselian (early Permian, Cisuralian); thus, the lower part of the Uyamano Formation in Miharanoro is correlated with the Asselian. Palaeobiogeographically, the Miharanoro fauna is a mixed Boreal–Tethyan–Panthalassan fauna, and has an affinity with the lower Permian fauna of Texas. Thus, the Akiyoshi-type seamounts, including the Miharanoro (Taishaku) one, were probably located between the Sino-Mongolian–Japanese Province and North America (Texas) in Panthalassa during the Asselian.

Systematic descriptions

Order Productida Sarytcheva and Sokolskaya, 1959 Suborder Productidina Waagen, 1883 Superfamily Productoidea Gray, 1840 Family Productidae Gray, 1840 Subfamily Retariinae Muir-Wood and Cooper, 1960 Genus *Tubaria* Muir-Wood and Cooper, 1960

Type species.—Productus genuinus Kutorga, 1844.

Tubaria sp. Fig. 5A, B

Material.—Two specimens: (1) a ventral valve, FMM6323; and (2) a dorsal valve, FMM6324.

Remarks.—These specimens are fragmentarily preserved, but can be assigned to the genus *Tubaria* Muir-Wood and Cooper, 1960 by medium-size and transverse outline of the shell (length about 18 mm without tube-like anterior extension, width about 34 mm in the ventral valve specimen, FMM6323) and in havng an extended tubelike anterior margin. The



Fig. 5. A, B, *Tubaria* sp.; A₁, A₂, ventral view of ventral valve, FMM6323; B, dorsal view of dorsal valve, FMM6324; **C,** *Echinoconchus punctatus* (Sowerby), ventral view of ventral valve, FMM6330; **D**, *Karavankina typica* Ramovš, ventral view (D₁, D₂) of ventral valve, FMM6328; **E**, *Compressoproductus flabelatus* Cooper and Grant, ventral view (E₁, E₂) of ventral valve, FMM6329; **F**, *Spitzbergenia* sp., ventral (F₁, F₂), anterior (F₃) and lateral (F₄) views of ventral valve, FMM6350. Scale bars are 1 cm.

Miharanoro specimens resemble externally the type species, *Tubaria genuina* (Kutorga, 1844), redescribed by Sarytcheva (1971, p. 42, pl. 5, figs. 4–7; pl. 6, figs. 1–4, text-figs. 3–7) from the Asselian–Sakmarian of the southern Urals, central Russia, but the latter is larger in size. Accurate comparison is difficult owing to ill preservation of the Miharanoro specimens.

Superfamily Echinoconchoidea Stehli, 1954 Family Echinoconchidae Stehli, 1954 Subfamily Echinoconchinae Stehli, 1954 Genus *Echinoconchus* Weller, 1914

Type species.—Productus punctatus Sowerby, 1822.

Echinoconchus punctatus (Sowerby, 1822) Fig. 5C

- Productus punctatus Martin. Sowerby, 1822, p. 22, pl. 323, lower right figure; Davidson, 1861, p. 172, pl. 44, figs. 9–11, 16, 17.
- *Pustula punctata* (Martin). Thomas, 1914, p. 303, pl. 17, figs. 16–19, text-fig. 11; Tolmatchoff, 1924, p. 256, 584, pl. 16, fig. 9; Rotai, 1931, p. 58, pl. 4, figs. 1, 11.

Productus (Pustula) punctatus Martin. Yanishevsky, 1918, p. 47, pl. 3, figs. 7, 9.

- Echinoconchus punctatus (Martin). Chao, 1927, p. 67, pl. 6, figs. 7, 8, 15, 16; Sarytcheva in Sarytcheva and Sokolskaya, 1952, p. 103, pl. 18, fig. 120; Dedok and Tschernjak, 1960, p. 53, pl. 1, fig. 6; Ding in Yang et al., 1962, p. 51, pl. 19, figs. 1–4; Yang, 1964, p. 81, pl. 4, figs. 5, 6, 9, 10, text-fig. 7; Abramov, 1965, p. 38, pl. 3, fig. 2; Litvinovich et al., 1969, p. 164, pl. 9, figs. 5, 6; pl. 10, fig. 1; Abramov, 1970, p. 117, pl. 9, fig. 4; Alexandrow and Solomina, 1973, p. 93, pl. 22, figs. 1–3; Volgin and Kushnar, 1975, p. 46, pl. 4, fig. 1; Donakova, 1978, p. 208, pl. 1, figs. 5, 6; Nalivkin, 1979, p. 78, pl. 24, figs. 8, 9; Zhang et al., 1983, p. 288, pl. 127, fig. 11; pl. 128, fig. 2; Jin et al., 1985, p. 192, pl. 9, figs. 11, 12; Zhan and Wu, 1987, p. 207, pl. 48, fig. 38; Archbold and Stojamović-Kuzenko, 1995, pl. 62, fig. 10; Wang and Yang, 1998, p. 77, pl. 9, figs. 17, 18.
- Productus (Echinoconchus) punctatus (Martin) emend. Thomas. Paeckelmann, 1931, p. 152, pl. 15, figs. 7–10.
- Productus (Echinoconchus) punctatus (Martin). Nalivkin, 1937, p. 64, pl. 9, fig. 5.
- Echinoconchus punctatus (Sowerby). Muir-Wood, 1951, p. 102, pl. 4, fig. 2; Muir-Wood and Cooper, 1960, pl. 66, figs. 1, 2; pl. 82, figs. 8–10; pl. 83, figs. 1–4; pl. 88, fig. 11; pl. 125, fig. 5; Winkler Prins, 1968, p. 89, pl. 3, figs. 12–14; Nalivkin and Fotieva, 1973, p. 35, pl. 6, fig. 8; Kalashnikov, 1974, p. 48, pl. 9, figs. 1–3; Martinez Chacon and Legrand-Blain, 1992, p. 110,

pl. 3, figs. 15–18; Tazawa, 2017, p. 335, figs. 6.6, 6.7; Tazawa, 2018, p. 46, fig. 23G, H.

Productus-Echinoconchus-punctatus Martin. Pareyn, 1961, p. 197, pl. 23, figs. 1-4.

Productus (Echinoconchus) punctatus (Sowerby). Galitskaya, 1977, p. 62, pl. 16, figs. 1–5; pl. 18, fig. 1, text-fig. 7; Kalashnikov, 1980, p. 34, pl. 5, fig. 1.

Echinoconchus aohanensis Lee and Gu in Lee et al., 1980, p. 363, pl. 147, figs. 1, 2.

Material.-One specimen, a ventral valve, FMM6330.

Remarks.—This specimen can be referred to *Echinoconchus punctatus* (Sowerby, 1822), redescribed by Muir-Wood (1951, p. 102, pl. 4, fig. 2) and refigured by Muir-Wood and Cooper (1960, pl. 66, figs. 1, 2; pl. 82, figs. 8–10; pl. 83, figs. 1–4; pl. 88, fig. 11; pl. 125, fig. 5) from the upper Visean of England, in large size (length about 46 mm, width about 62 mm) and external ornament of the ventral valve consisting of regular strong concentric bands with rows of numerous slightly elongate spine bases. *Echinoconchus aohanensis* Lee and Gu (in Lee et al., 1980, p. 363, pl. 147, figs. 1, 2), from the lower Pennsylvanian of Liaoning, northeastern China, is deemed to be a junior synonym of *E. punctatus*. *Echinoconchus alternatus* (Norwood and Pratten, 1855), redescribed by Weller (1914, p. 138, pl. 17, figs. 1–7) from the Osagean of the Mississippi Valley, differs from *E. punctatus* in less transverse outline and in having broader concentric bands in the ventral valve. *Echinoconchus postpunctatus* Stepanov (in Mironova, 1967, p. 11, pl. 1, fig. 11), from the upper Carboniferous Kirovsky Horizon of the Urals, differs from *E. punctatus* in more elongate outline.

Distribution.—Lower Carboniferous (upper Tournaisian)-lower Permian (Asselian): southwestern Japan (Miharanoro in the Akiyoshi Belt), northeastern Japan (Hikoroichi and Yokota in the South Kitakami Belt), northern Russia (Verkhoyansk Range, Taimyr Peninsula and northern Urals), the UK (Scotland, England and Wales), Germany, Belgium, Spain, western Russia (Moscow Basin), central Russia (southern Urals), Kyrgyzstan, northwestern China (Xinjiang and Qinghai), northern China (Shanxi) and northeastern China (Liaoning).

Genus Karavankina Ramovš, 1969

Type species.—Karavankina typica Ramovš, 1969.

Karavankina typica Ramovš, 1969 Fig. 5D

Karavankina typica Ramovš, 1969, p. 254, 262, pl. 1, figs. 1-4.

Material.—One specimen, a ventral valve, FMM6328. *Remarks.*—This specimen can be referred to *Karavankina typica* Ramovš, 1969, from the Trogkofel Limestone of the Carnian Alps, Slovenia, by its small, strongly convex ventral valve (length 17 mm, width 19 mm) and in having regular concentric rugae with numerous very fine spine bases on the ventral valve. *Karavankina schellwieni* Ramovš (1969, p. 257, 264, pl. 2, figs. 1–4), from the same horizon and the same locality of Slovenia differs from *K. typica* in having no sulcus on the ventral valve.

Distribution.—Asselian-Sakmarian: southwestern Japan (Miharanoro in the Akiyoshi Belt) and Slovenia.

Superfamily Linoproductoidea Stehli, 1954 Family Linoproductidae Stehli, 1954 Subfamily Striatiferinae Muir-Wood and Cooper, 1960 Genus *Compressoproductus* Sarytcheva in Sarytcheva et al., 1960

Type species.—Productus compressus Waagen, 1884.

Compressoproductus flabellatus Cooper and Grant, 1975 Fig. 5E

Compressoproductus flabellatus Cooper and Grant, 1975, p. 1206, pl. 456, figs. 22–50; pl. 461, figs. 1–66; pl. 464, figs. 24–26.

Material.-One specimen, a ventral valve, FMM6329.

Remarks.—This specimen can be referred to *Compressoproductus flabellatus* Cooper and Grant, 1975, from the Cathedral Mountain Formation of Texas, in its small, roundly and transversely elliptical ventral valve (length 17 mm, width 18 mm) and in having numerous fine capillae (numbering 5 in 1 mm at about midlength) and somewhat irregular rugae on the ventral valve. *Compressoproductus parvus* Cooper and Grant (1975, p. 1207, pl. 459, figs. 9–31), from the Skinner Ranch Formation of Texas, differs from *E. flabellatus* in its elongate oval outline and in having more irregular rugae on the ventral valve. *Compressoproductus mongolicus* (Diener, 1897, p. 28, pl. 4, figs. 8–10), from the Capitanian–Wuchiapingian limestones of Chitichun in the Himalayas, is readily distinguished from *E. flabellatus* in having coarser capillae on the ventral valve.

Distribution.—Asselian-Kungurian: southwestern Japan (Miharanoro in the Akiyoshi Belt) and the USA (Texas).

Family Kansuellidae Muir-Wood and Cooper, 1960 Subfamily Auriculispininae Waterhouse, 1986 Genus *Spitzbergenia* Kotlyar in Grigorjeva et al., 1977

Type species.—Productus loveni Wiman, 1914.

Spitzbergenia sp. Fig. 5F

Spitzbergenia sp. Nakamura and Nishikawa, 1979, p. 165.

Material.-One specimen, a ventral valve, FMM6350.

Remarks.—This specimen is readily assigned to the genus *Spitzbergenia* Kotlyar in Grigorjeva et al., 1977 by numerous large, prominent spine bases and numerous fine costellae on flattened visceral disc of the ventral valve. The Miharanoro species resembles the type species, *Spitzbergenia loveni* (Wiman, 1914), originally described by Wiman (1914, p. 72, pl. 17, figs. 12–18) from the Spirifer Limestone of Spitsbergen, Svalbard and redescribed by Grigorjeva et al. (1977, p. 156, pl. 25, figs. 5–9, text-fig. 87) from the Selandersk Formation of Severo-Vostoknaya Zemlya (Nordaustlandet), Svalbard, in being relatively large size (length about 34 mm, width about 41 mm) and wider subrectangular outline of the ventral valve. But accurate comparison is difficult on the poorly preserved specimen. *Spitzbergenia gracilis* Kotlyar (in Grigorjeva et al., 1977, p. 157, pl. 25, fig. 10; pl. 26, figs. 1–5, text-fig. 88), from the Selandersk Formation of Severo-Vostoknaya Zemlya et al., 1977, p. 157, pl. 25, fig. 10; pl. 26, figs. 1–5, text-fig. 88), from the Selandersk Formation of Severo-Vostoknaya Zemlya et al., 1977, p. 157, pl. 25, fig. 10; pl. 26, figs. 1–5, text-fig. 88).

Order Orthida Schuchert and Cooper, 1932 Suborder Dalmanellidina Moore, 1952 Superfamily Dalmanelloidea Schuchert, 1913 Family Rhipidomellidae Schuchert, 1913 Subfamily Rhipidomellinae Shuchert, 1913 Genus *Rhipidomella* Oehlert, 1890

Type species.—Terebratula michelini Léveillé, 1835.

Rhipidomella sp. Fig. 6A



Fig. 6. A, *Rhipidomella* sp., ventral (A₁, A₂), dorsal (A₃), anterior (A₄), posterior (A₅) and lateral (A₆) views of conjoined shell, FMM6376; **B**, **C**, *Enteretes stehlii* Cooper and Grant; B, ventral (B₁, B₂) and dorsal (B₃) view of conjoined shell, FMM6339; C, ventral (C₁, C₂), dorsal (C₃), anterior (C₄), posterior (C₅) and lateral (C₆) views of conjoined shell, FMM6345; **D**-**F**, *Enteletes bowsheri* Cooper and Grant; D, dorsal view of conjoined shell, FMM6334; E, ventral (E₁) and anterior (E₂) views of conjoined shell, FMM6338. Scale bars are 1 cm.

Material.—One specimen, a conjoined shell, FMM6376.

Remarks.—This specimen can be assigned to the genus *Rhipidomella* Oehlert, 1890 on account of its small size (length 17 mm, width 19 mm), subcircular outline with short hinge, moderately biconvex profile with rectimarginate anterior margin and in having external ornaments consisting of numerous fine costellae (numbering 10–11 in 2 mm at about midlength of ventral valve) and irregular growth lines. *Rhipidomella hessensis* King (1931, p. 43, pl. 1, figs. 2–4), from the Hess Formation of the Glass Mountains, Texas, is also a large-sized *Rhipidomella* species, but the Texan species differs from the Miharanoro species in having more numerous tubercles on the both valves. *Rhipidomella corallina* (Waagen, 1884, p. 572, pl. 56, fig. 1), from the Wargal Formation of the Salt Range, Pakistan, differs from the present species in much larger size. The Miharanoro species may be a new species of *Rhipidomella*, but the poor material precludes that determination.

Superfamily Enteletoidea Waagen, 1884 Family Enteletidae Waagen, 1884 Genus *Enteletes* Fischer de Waldheim, 1825

Type species.-Enteletes glabra Fischer de Waldheim, 1830.

Enteletes stehlii Cooper and Grant, 1976b Fig. 6B, C

Enteletes stehlii Cooper and Grant, 1976b, p. 2639, pl. 688, figs. 1-51.

Material.-Eleven conjoined-valve specimens, FMM6339-6349.

Remarks.—These specimens are safely assigned to the genus *Enteletes* Fischer de Waldheim, 1825 by strongly biconvex shell and external ornament consisting of angular to subangular simple costae and numerous fine capillae. The Miharanoro species can be referred to *Enteletes stehlii* Cooper and Grant, 1976b, from the Skinner Ranch and Bone Spring formations of Texas, by its small, transverse and relatively low shell (length about 15 mm, width about 21 mm, thickness about 13 mm in the largest specimen, FMM6339). *Enteletes wolfcampensis* King, 1931, redescribed by Cooper and Grant (1976b, p. 2642, pl. 684, figs. 21–33; pl. 687, figs. 1–56) from the lower Wolfcampian of Texas, is also a small-sized *Enteletes* species, but differs from *E. stehlii* in being subequal and rotund outline. Hayasaka and Kato (1966, p. 281, pl. 34, figs. 1–4; pl. 35, figs. 1–4. text-figs. 1, 2) described *Enteletes gibbosus* Chronic, 1953 from the same locality of Miharanoro, southwestern Japan.

Distribution.—Asselian-Artinskian: southwestern Japan (Miharanoro in the Akiyoshi Belt) and the USA (Texas).

Enteletes bowsheri Cooper and Grant, 1976b, p. 2629, pl. 693, figs. 27-36.

Material.—Five specimens: (1) three conjoined shells, FMM6334–6336; and (2) two ventral valves, FMM6337, 6338.

Remarks.—These specimens are safely assigned to the genus *Enteletes* Fischer de Waldheim, 1825 by highly biconvex shell with external ornament consisting of strong simple costae and numerous fine capillae. The Miharanoro species can be referred to *Enteletes bowsheri* Cooper and Grant,1976b, from the Bursum Formation of Texas, by large, roundly elliptical shell (length about 37 mm, width about 50 mm in the largest specimen, FMM6334), with strong rounded costae which occur only anterior half of the both valves. This species is readily distinguished from the preceding species, *E. stehli* by its more strongly biconvex and globose outline. *Enteletes subcircularis* Cooper and Grant (1976b, p. 2640, pl. 675, figs. 36–39; pl. 676, figs. 1–30; pl. 685, figs. 1–27), from the Skinner Ranch, Hess and Bone Spring formations of Texas, is also a large-sized *Enteletes* species, but differs from the present species in having strong subangular costae extending to umbonal region. *Enteletes acutiplicatus* Hayasaka, 1932, redescribed by Hayasaka (1933, p. 23, pl. 8, fig. 19) from the Nabeyama Limestone of Nabeyama, Kuzu area in the Mino Belt, central Japan, is clearly distinguished from the Minaranoro species in having a few, very acute costae on the dorsal valve.

Distribution.—Asselian: southwestern Japan (Miharanoro in the Akiyoshi Belt) and the USA (Texas).

Order Spiriferida Waagen, 1883 Suborder Spiriferidina Waagen, 1883 Superfamily Martinioidea Waagen, 1883 Family Martiniidae Waagen, 1883 Subfamily Martiniinae Waagen, 1883 Genus *Martiniia* M'Coy, 1844

Type species.—Spirifer glaber Sowerby, 1820.

Martinia cruenta Cooper and Grant, 1976a Figs. 7A, B

Martinia cruenta Cooper and Grant, 1976a, p. 2266, pl. 644, figs. 54-57.



Fig. 7. A, **B**, *Martinia cruenta* Cooper and Grant; A, ventral (A₁), dorsal (A₂), anterior (A₃), posterior (A₄) and lateral (A₅) views of conjoined shell, FMM6374; B, ventral (B₁), dorsal (B₂), anterior (B₃), posterior (B₄) and lateral (B₅) views of conjoined sell, FMM6364. Scale bars are 1 cm.

Material.-Fifteen conjoined-valve specimens, FMM6361-6375.

Description.—Shell large in size for genus, transversely subrectangular in outline, with greatest width at midlength; cardinal extremities rounded: hinge wide, about two-thirds maximum width; length 47 mm, width 64 mm in the largest specimen (FMM6361); length 32 mm, width 53 mm in the best-preserved specimen (FMM6364). Ventral valve moderately convex in lateral profile, most convex in umbonal region; umbo small, strongly incurved; sulcus with U-shaped bottom, originating just posterior to midlength, shallow to moderately deep throughout its length, except for strongly depressed near anterior margin. Dorsal valve gently convex in lateral profile; fold originating just posterior to midlength, low to moderately high except for strongly elevated near anterior margin. External surface of both valves smooth except for very fine growth lines.

Remarks.—These specimens can be referred to *Martinia cruenta* Cooper and Grant, 1976a, from the Wolfcampian (Hess Formation?) of Texas, by being large, transverse outline and in having wide hinge and well developed sulcus-fold. *Martinia nipponica* Yanagida and Nishikawa (1984, p. 178, pl. 18, figs. 3, 4), from the Kawai Limestone (Asselian) of Kawai in the Akiyoshi Belt, southwestern Japan, has also conspicuous sulcus-fold, but differs from the



Fig. 8. A–D, *Choristites fritschi* (Schellwien); A, ventral (A₁), dorsal (A₂), posterior (A₃) and lateral (A₄) views of conjoined shell, FMM6351; B, ventral (B₁), dorsal (B₂) and posterior (B₃) views of conjoined shell, FMM6355; C, ventral view of ventral valve, FMM6354; D, dorsal view of dorsal valve, FMM6352. Scale bars are 1 cm.

present species in much smaller size and in having weak costae on each side of the dorsal fold.

Distribution.—Asselian-Sakmarian: southwestern Japan (Miharanoro in the Akiyoshi Belt) and the USA (Texas).

Superfamily Spiriferoidea King, 1846 Family Choristitidae Waterhouse, 1968 Subfamily Choristitinae Waterhouse, 1968 Genus *Choristites* Fischer de Waldhaim, 1825



Fig. 9. Serial sections of ventral valve, *Choristites fritschi* (Schellwien), FMM6366. Numbers are distance (mm) from posterior end of ventral beak.

Type species.—Choristites mosquensis Buckman, 1908.

Choristites fritschi (Schellwien, 1892) Figs. 8A–D, 9

Spirifer fritschi Schellwien, 1892, p. 43, pl. 5, figs. 4–8; Schellwien, 1900, p. 71, pl. 10, figs. 7–10; Tschernyschew, 1914, p. 21, pl. 5, fig. 4; Heritsch, 1931, p. 25, pl. 2, figs. 67–74.

Spirifer (Choristites) fritschi Schellwien. Ozaki, 1931, p. 38, pl. 2, fig. 6.

Spirifer (Munella?) fritschi Schellwien. Metz, 1936, p. 173, pl. 6, figs. 9, 10.

Choristites fritschi (Schellwien). Gauri, 1965, p. 45, pl. 7, figs. 1, 2, text-fig. 16; Besnossova, 1968, p. 182, pl. 28, figs. 1–5; Winkler Prins, 1970, p. 540, pl. 38, fig. 1.

Material.—Ten specimens: (1) two conjoined shells, FMM6351, 6352; and (2) eight ventral valves, FMM6353–6360.

Descriptions.—Shell medium to large in size for genus, transversely subsemicircular in outline, hinge equal to or slightly shorter than greatest width; length about 50 mm, width more than 60 mm in the largest specimen (FMM6351); length 36 mm, width 45 mm in the best preserved and average-sized specimen (FMM6354). Ventral valve moderately and unevenly convex in lateral profile, with maximum convexity at umbonal region; beak pointed and incurved; cardinal extremities blunt, angular; sulcus originating at beak, broad and shallow, and ornamented with 14–17 costae in anterior part of sulcus. Dorsal valve less convex than opposite valve; fold narrow and moderately high. External surface of both valves ornamented with numerous rounded costae, mostly irregularly bifurcated, numbering



Fig. 10. A-C, *Choristites* sp.; A, ventral view of ventral valve, FMM6326; B, ventral view of ventral valve, FMM6325; C, dorsal view of dorsal valve, FMM6327. Scale bars are 1 cm.

6–7 costae in 10 mm at about midlength of ventral valve. Interior of ventral valve with a pair of long, subparallel dental adminicula. Interior of dorsal valve not well preserved.

Remarks.—These specimens can be referred to *Choristites fritschi* (Schellwien, 1892), from the upper Carboniferous of the Carnian Alps, in large size, transverse outline and in having numerous rather fine, bifurcated costae on the both ventral and dorsal valves. *Choristites wangchchueni* Chao (1929, p. 45, pl. 3, fig. 1; pl. 6, fig. 7), from the Penchi Formation of Shanxi, northern China, is also a transverse subsemicircular *Choristites* species, but differs from *C. fritschi* in much smaller size and in having more numerous, finer costae on the both valves. *Choristites jigulensis* (Stuckenberg, 1905), redescribed by Sokolskaya (in Sarytcheva and Sokolskaya, 1952, p. 206, pl. 61, fig. 342) from the Moscovian-Gzhelian of the Moscow Basin, western Russia, differs from *C. fritschi* in having thicker costae on the both valves. The type species, *Choristites mosquensis* Buckman, 1908, redescribed by Sokolskaya (in Sarytcheva and Sokolskaya, 1952, p. 204, pl. 59, fig. 332), from the Moscovian-Kasimovian of the Moscow Basin, is readily distinguished from the present species by its longer outline.

Distribution.-Moscovian-Sakmarian: southwestern Japan (Miharanoro in the Akiyoshi

Belt), Spain, Slovenia, Austria, Kazakhstan, Uzbekistan (Fergana) and eastern China (Shandong).

Choristites sp. Fig. 10A-C

Material.—Three specimens: (1) two ventral valves, FMM6325, 6326; and (2) a dorsal valve, FMM6327.

Remarks.—These specimens can be assigned to the genus *Choristites* Fischer de Waldhaim, 1825, in having numerous simple, flat and thick costae on both valves. The Miharanoro species resembles *Choristites jigulensis* (Stuckenberg, 1905), redescribed by Barchatova (1970, p. 170, pl. 17, fig. 4; pl. 18, figs. 1, 2) from the Timansky Horizon (Orenburgian) of Timan, northern Russia, by its large size (length 72 mm, width more than 75 mm in the larger ventral valve specimen, FMM6325; length 54 mm, width more than 72 mm in the dorsal valve specimen, FMM6327), well developed sulcus-fold, and in having numerous thick costae (numbering 5–6 in 10 mm at about midlength of ventral valve) over the both valves. But accurate comparison is difficult for the ill preserved specimens.

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Report of the International Workshop on Renaissance Drilling on the Northwestern Pacific, 18–19 March 2023, Niigata, Japan

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Abstract

The International Workshop on Renaissance Drilling on the Northwestern Pacific was organized in Niigata during 18–19 March 2023, hosted by Niigata University and cosponsored by the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). A total of 30 participants from 4 countries attended the workshop. The scientific sessions were held on 18 March, followed by a discussion meeting on 19 March in the "Eki-nan" Campus TOKIMATE of Niigata University. This report summarizes the international workshop including the contents of scientific sessions in Niigata and post-meeting field activities during 20–22 March in Kochi.

Key words: International workshop, deep-sea drilling, pelagic clay, chert, radiolaria, fish debris, Jurassic-Cretaceous boundary.

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Introduction

The Pacific Ocean has been the largest ocean during the Mesozoic and Cenozoic and contains various types of sediments on the seafloor. Previous studies focused mainly on carbonate-bearing sediments to discuss the oceanic, biological, and geochemical evolution. However, chert and pelagic clay also have comparable, or complementary, information to that of carbonate. Radiolarians in chert were the main component of the pelagic siliceous sediments during the Mesozoic, and their diversity should have reflected local to global environmental changes. Recent studies on pelagic clay discovered that transient increase of the fish debris (teeth/bones) accumulation occurred repeatedly in the Pacific Ocean. For the complete understanding of the oceanic and biological evolution since the Mesozoic, it is essential to utilize the chert and pelagic clay as well as carbonate.

We submitted a drilling proposal for the International Ocean Discovery Program (IODP) in April, 2021 under the title of "The Renaissance of the oldest Pacific sediments: Trans-Pacific records of co-evolution of geochemistry, marine ecosystem, and sediment lithology in the pelagic realm." The proposal aims to recover the latest Jurassic to Cenozoic sediments on the Pacific abyssal plain (Site MM) and around Shatsky Rise (Site SR) (Fig. 1). Our primary objectives are (1) to elucidate the changes in marine biota across the Jurassic-Cretaceous boundary (JKB), (2) to understand the long-term transition from a Mesozoic chert-rich ocean to a Cenozoic chert-poor ocean including a change in diversity of radiolarians, and (3) to decipher the environmental change recorded as an enrichment of fish-remains, and rare-earth elements and yttrium (REY), in the pelagic clay during the Late Cretaceous and Cenozoic. The content of the proposal was presented at the 2021 annual meeting of the Geological Society of Japan (Matsuoka et al., 2021a) and at the Second International Symposium of the International Geoscience Programme Project 679 in Qingdao, China (Matsuoka et al., 2021b).

After receiving comments by the Scientific Evaluation Panel of the IODP in September, 2021, we realized the necessity of having an opportunity to discuss on deep sea drilling in the northwest Pacific to polish our scientific goals. We planned to organize an international workshop in the 2021 fiscal year but it had to be postponed due to the Covid-19 pandemic. The International Workshop entitled "Renaissance Drilling on the Northwestern Pacific" was performed in March 2023, having a chance to exchange ideas among a wide variety of scientists including stratigrapher, paleonotologists, geochemists, paleomagnetic specialists and so on. This report summarizes the workshop including the contents of scientific sessions in Niigata and post-meeting field activities in Kochi.



Fig. 1. Reconstructed track of the proposed sites. Yellow circles indicate paleopositions of the proposed sites in 10-million-year steps, with numbers showing the age in million years ago. The reconstruction was created by using GPlates software (http://www.gplates.org) based on the plate polygon and rotation data by Matthews et al. (2016). Background is modern global sea-surface chlorophyll *a* concentration (courtesy of SeaWiFS Project, NASA). White stars indicate terrestrial sections, Tokoro and Shimanto belts in Japan and Neuquén Basin in Argentina, that relate to the trans-Pacific records which this proposal targets.

Outline of the International Workshop

The scientific sessions of the workshop were held on 18 March at the "Eki-nan" Campus TOKIMATE of Niigata University. A total of 30 participants attended the meeting from 4 countries; China, Italy, Japan, and the United States of America. The program of the scientific sessions is shown in Fig. 2. They were composed of 16 oral presentations in three topics, namely Frontier Research on Pelagic Clay (Chairs: YASUKAWA, K. and TANAKA, E.), Co-evolution of Pelagic Life and Lithology (Chairs: KURODA, J. and MATSUOKA, A.), and Jurassic/Cretaceous Boundary (Chairs: MATSUOKA, A. and KURODA, J.). Two presentations in the Frontier Research on Pelagic Clay session were given on line by scientists in the U.S.A.

The workshop started with a welcome address and general introduction which included the following explanation and proposal of drilling sites (Fig. 3A). To study the turnovers of marine biota at pelagic sites in the Pacific Ocean across the JKB, both siliceous and calcareous fossils are required to be preserved. A promising sediment succession across the JKB could exist underneath the seafloor at the middle flank of Shatsky Rise. To investigate the transition from a Mesozoic chert-rich ocean to a Cenozoic chert-poor ocean, it is critical

Workshop Program on Saturday, 18th March

08:30-08:50	WELCOME & INTRODUCTION
Session 1. F	rontier Research on Pelagic Clay Chairs: K. YASUKAWA & E. TANAKA
08:50-09:15	YASUKAWA, Kazutaka University of Tokyo
	Pelagic clay revisited: Perspectives from a potential mineral resource and
	paleoceanographic archive
09:15-09:40	DUNLEA, Ann Woods Hole Oceanographic Institution (WHOI)
	Distinguishing the contributions of dust and volcanic ash to pelagic clay
09:40-10:05	SIBERT, Elizabeth Yale University
	Microfossils in Pelagic Clays: an overlooked but valuable tool for studying ecological
	response to global change
10:05-10:15	BREAK
10:15-10:40	IANAKA, Erika Kochi University Paconstruction of long-term denositional environmental changes using pelagis clav in the
	area around Minamitorizima (Marcus) Island
10:40-11:05	USUI Voichi Kanazawa University
10.40-11.05	Proposed Chikyu Shallow Core Program (SCORE) around Minamitorishima Island within
	the framework Cenozoic paleoceanography of North Pacific
11:05-11:30	IIJIMA, Koichi Japan Agency for Marine-Earth Science and Technology (JAMSTEC)
	Lithology and physical properties of pelagic sediment cores around Minamitorishima
	(Marcus) island
Session 2. C	O-evolution of Pelagic Life and Lithology Chairs: J. KURODA & A. MATSUOKA
11:30-11:55	KURODA, Junichiro University of Tokyo
	An overview of the sediments on the Shatsky Rise and its potential as a paleoenvironmental
	archive
11:55-13:30	LUNCH BREAK
13:30-13:55	MATSUOKA, Atsushi Niigata University
	Radiolarian evolution and lithological transition from chert to pelagic clay in the Pacific
13:55-14:20	KIMOTO, Katsunori JAMSTEC
11.00.11.15	Detection of density differences in radiolarian skeletons by micro-CT measurement
14:20-14:45	YOSHINO, lakashi toyo University
Section 7 1	Micro-CT technology and morphological analysis of radiolarian skeletons
Session 3. J	
14:45-15:10	LI, XIII Nanjing Institute of Geology and Palaeontology
15-10-15-30	BPEAK
15:30-15:55	ERBA Elisabetta University of Milan (UNIMI)
10.00 10.00	Calcareous panpofossil characterisation of the Jurassic-Cretaceous transition:
	western Pacific and global data
15:55-16:20	ITO, Tsuyoshi Geological Survey of Japan, AIST
	Radiolarian-bearing clasts within the Jurassic-Cretaceous neritic-terrestrial strata in East Asia
16:20-16:45	TAKETANI, Yojiro Fukushima Museum
	The Jurassic/Cretaceous boundary in the South Kitakami Terrane, northeast Japan
16:45-17:10	NAKADA, Kentaro Fukui Prefectural Dinosaur Museum
	The ammonite biostratigraphy around the Jurassic/Cretaceous boundary in Japan
17:10-17:35	SANO, Shinichi University of Toyoma
	Searching for a Jurassic/Cretaceous boundary in northern Central Japan
17:35-17:50	BREAK
17:50-18:30	JOINT DISCUSSIONS

Fig. 2. Program of the International Workshop on Renaissance Drilling on the Northwestern Pacific on 18 March in 2023 at the "Eki-nan" Campus TOKIMATE of Niigata University.



Fig. 3. Photographs of the workshop. **A**. The workshop was held in Lecture Room in the TOKIMATE on 18 March, **B**. Group photograph of the participants of the workshop, **C**. Separate meeting (Mesozoic chert session) on 19 March in Meeting Room A in the TOKIMATE.

to confirm the boundary layer from the chert/silica-rich sediments to the clayey/silica-poor sediments and to elucidate factors (e.g., environmental changes and/or physicochemical processes during early diagenesis) that caused the lithological transition. To verify the relationship among the enrichment of fish remains (and REY), paleoceanographic conditions, and geochemical cycles, a complete set of pelagic clay of the Cretaceous to Paleogene is required. For these purposes, we proposed drilling the southern foot of Shatsky Rise and north of Minamitorishima (Site SR and Site MM in Fig. 1, respectively).

At the end of the workshop on the first day, a group photograph was taken at Lecture Room (Fig. 3B). The welcome party was held in the evening of 18 March at Art Hotel Niigata Station located in the same building as the TOKIMATE.

In the morning session of 19 March, the participants were divided into two groups: Cenozoic pelagic clay session and Mesozoic chert session (including the JKB and chert-clay transition). In the pelagic clay session, scientific objectives were confirmed as reconstructing (1) long-term ecological record in pelagic clay, (2) plate tectonics and atmospheric circulations related to circum-Pacific, and (3) seafloor environmental changes through the Cenozoic. The participants agreed with the need for drilling of new reference sites in the western North Pacific which can be compared with other sites/areas (e.g., eastern North Pacific and South Pacific Gyre). In the chert session (Fig. 3C), one of the major discussion topics was stratigraphic correlations among deep-sea, neritic and terrestrial sequences around the JKB, which is essential for establishing a world-wide standard. It was pointed out that less altered deep-sea cores are advantageous not only biostratigraphy but also chemostratigraphy. The importance of micro-CT analysis for radiolarian skeletons was realized as a new method for evaluating physical property.

In the afternoon of 19 March, a special lecture on seismic survey for a successful drilling proposal was provided by PARK J. (Univ. Tokyo). The title was "Spatiotemporal scale of large-scale hydrothermal circulation system connecting ocean and mantle at the outer rise." The lecture included technical issues on the shipboard seismic survey and introduced a research topic on the sub-bottom reflection data from the outer rise along the Japan Trench, western North Pacific. After the special lecture, a joint discussion by all participants was performed and the results of each group were summed up.

Post-meeting activities

Post-meeting activities in Kochi Prefecture included a visit to the Kochi Core Center in Nankoku City on 20 March, rock sampling in the Birafu section in Kami City on 21 and 22 March and an excursion of the Yokonami mélange in Susaki City on 23 March (Fig. 4).



Fig. 4. Post-workshop activities in Kochi. **A.** Visit to the Kochi Core Center in Nankoku City on 20 March, **B.** Sampling in the Birafu section in Kami City on 21 and 22 March, **C.** Group photograph on the lower Cretaceous Yokonami chert in Susaki City on 23 March.

1. Visit to the Kochi Core Center

In the afternoon of 20 March, MATSUOKA, A. and ERBA, E. visited the center and had a look at the facilities including the core repository and several laboratories (Fig. 4A).

2. Rock sampling in the Birafu section

The upper Jurassic-lower Cretaceous Birafu Formation, one of equivalents of the Torinosu Group in the Chichibu belt is well exposed along the Nishinokawa River in the Birafu area, Kami City. Limestone and mudstone samples of the Birafu Formation were collected for radiolarian-calcareous nannofossil biostratigraphy and osmium isotope analysis along the river on 21 and 22 March (Fig. 4B).

3. Excursion of the Yokonami mélange

The Yokoyami mélange is well exposed in the east coast of the Yokonami Peninsula, Susaki City on 23 March. The mélange includes various rock types of ocean plate stratigraphy. An excursion was organized to observe the lower Cretaceous chert and upper Cretaceous hemipelagic-terrigenous sequences in the mélange (Fig. 4C).

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