A new genus of Triassic discinid brachiopod and re-evaluating the taxonomy of the group—evolutionary insights into autecological innovation of post-Palaeozoic discinids

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The discinid brachiopod from the Lower Triassic Osawa Formation in the Southern Kitakami Terrane, Japan, exhibited a unique morphological combination of a narrow pedicle track (listrium) and a V-shaped large depressed area, thereby suggesting an intermediate form between the Palaeozoic *Orbiculoidea* and the extant *Discinisca*. Based on these characteristics, we propose *Bronzoria recta* gen. et sp. nov., a genus that appeared in the late Permian and was widely distributed during the Triassic period. Morphological analysis of extant discinids revealed that the pedicle area showed an arrowhead-shaped median plate and a pair of semilunar plates, equivalent to the inner and outer listrial plates of Palaeozoic-type discinids, respectively. Consequently, there are great differences in the development of the pedicle area, i.e., the large pedicle area of extant discinids is suitable for robust pedicle attachment, whereas the narrow pedicle area of *Bronzoria* gen. nov. suggests a free-lying mode of life. Given the relationship between pedicle-related structures and the mode of life, we hypothesised that the evolution of the large depressed area preceded the development of the pedicle area. Subsequently, the large depressed area accommodated a larger pedicle, facilitating an autecological innovation for pedicle attachment, as observed in extant species.

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Introduction

Understanding the morphological stability of fossil organisms provides fundamental insights into the constraints of phenotypic evolution over geological timescales, a subject traditionally referred to as living fossils (e.g., Lidgard and Love 2018; Wood et al. 2020). Organisms with a conserved phenotype are often considered to have successful forms owing to the lack of necessity to change their forms in response to environmental changes. Functionally sophisticated morphology could be maintained with minimal phenotypic variations over the long term, as observed in the case of stabilomorphs (Kin and Błażejowski 2014). However, morphological conserva-

tion does not necessarily imply ecological conservation (e.g., Kin and Błażejowski 2014; Werth and Shear 2014). Even small morphological differences, which may seem minor, can produce significant genetic, anatomical, and functional variations. These variations can potentially provide new adaptation capabilities (e.g., Koehl 1996; Shiino and Kuwazuru 2010). Considering their long-term evolutionary history, it is crucial to understand why certain organisms maintain conservative morphologies and whether species with conservative morphology are ecologically conservative.

Lingulate brachiopods are a group with a static morphology that persists from the Cambrian to the present (Holmer and Popov 2000; Liang et al. 2023). Geologically, lingulates,
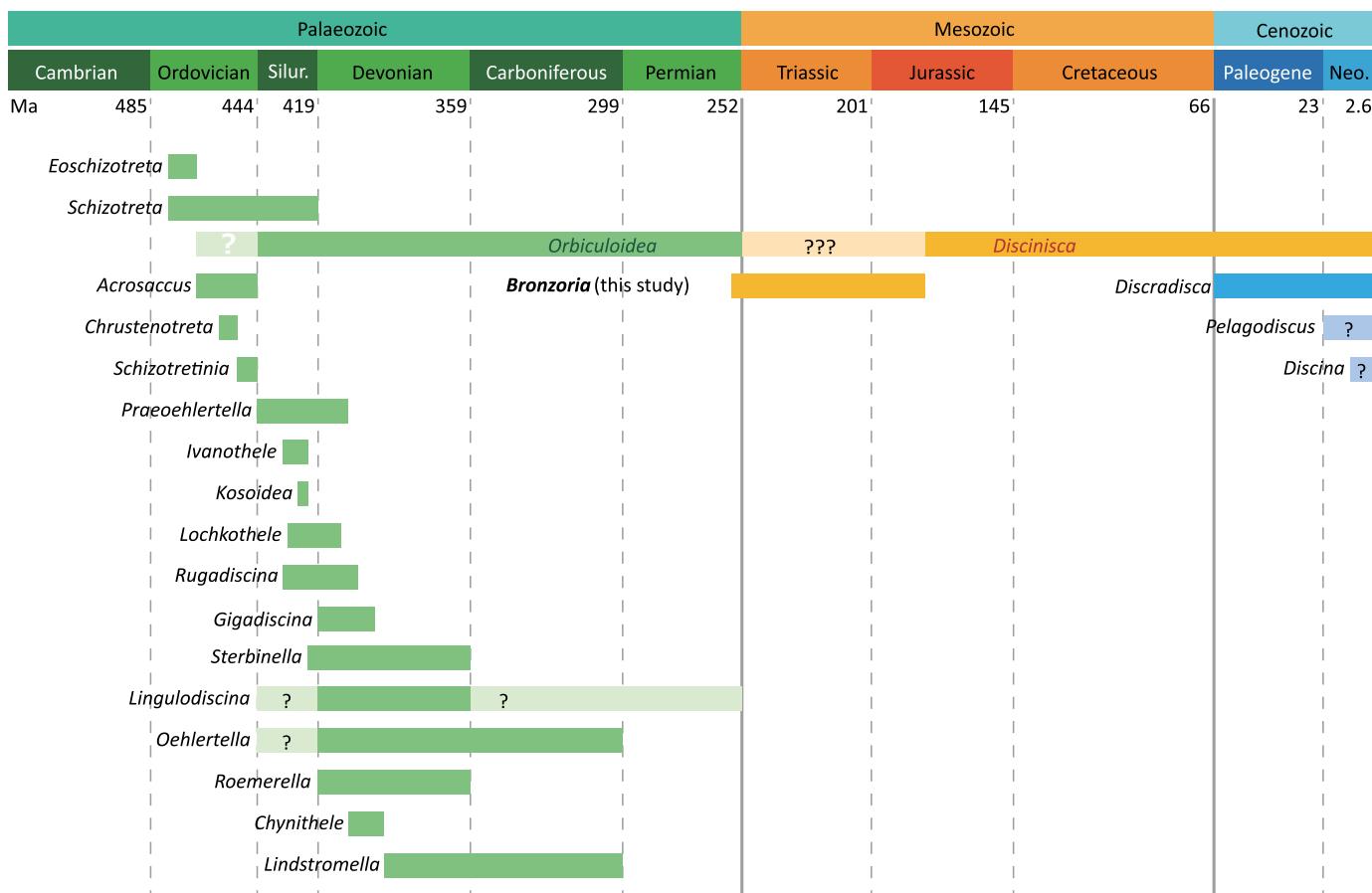
Fig. 1. Range chart of discinid genera. Based on Mergl and Massa (2005), Mergl (2006), and Curry and Brunton (2007). Abbreviations: Neo., Neogene; Silur., Silurian.

including lingulids and discinids, often occur in dysoxic/anoxic lithofacies and sometimes form monospecific assemblages (e.g., Dustira et al. 2013; Masunaga and Shiino 2021). To understand redox conditions, the fossil occurrences of lingulates have frequently been reported in geological studies described as "*Lingula*" for lingulid, "*Orbiculoidea*" for Palaeozoic discinid, and "*Discinisca*" for Mesozoic discinid. However, detailed information on their morphology and taxonomy has not been discussed (e.g., Souza et al. 2003). Recent anatomical information on lingulids, such as muscle scars and mantle canals, has allowed for a re-evaluation of the taxonomy of "*Lingula*", thereby leading to the conclusion that the true *Lingula* Bruguière, 1791, existed only since the Cenozoic (Emig 2003). It could be expected that discinids were taxonomically variable as well, but their static morphology of simple discoidal shells prevented the understanding of the diversity and evolution of discinids over time.

Among discinid brachiopods, it has been assumed that the extant genus *Discinisca* Dall, 1871, evolved from the Palaeozoic genus *Orbiculoidea* d'Orbigny, 1847, around the Permian/Triassic boundary, which suggests a monophyletic relationship based on fossil records (Holmer and Popov 2000; Fig. 1). Both *Discinisca* and *Orbiculoidea* exhibit a sedentary mode of life; however, the extant *Discinisca* differs from *Orbiculoidea* in having a thick pedicle protruding from

a large pedicle foramen for attachment to hard substrates (LaBarbera 1985; Mergl 2010). In the case of late Palaeozoic *Orbiculoidea*, having a smaller pedicle foramen located posteriorly, is interpreted as a free-lying mode of life (Masunaga and Shiino 2021). Based on the fossil records available thus far, evolution at the generic level has led to autecological innovation, specifically the acquisition of pedicle attachment to hard substrates. Otherwise, Mesozoic "*Discinisca*" may encompass a broader range of forms and adaptation capabilities than previously documented.

Understanding the autecological innovation of the pedicle attachment mode of life is to explore the morphology and taphonomy of Mesozoic discinids, which may bridge the gap between *Orbiculoidea* and extant *Discinisca*. Seilacher (1982) reported the Jurassic discinid *Discinisca papyracea* (Münster in Goldfuss, 1831) (= *Orbiculoidea papyracea* in Seilacher 1982), which shows cluster occurrences on ammonoid shells (Seilacher 1982). This clustering suggests the attachment of a pedicle protruding from a large arrowhead-shaped pedicle foramen in the ventral valve of *Discinisca papyracea* (see Seilacher 1982). Although reliable evidence exists regarding Jurassic discinids, whether Triassic discinids realised sessile pedicle attachment remains unclear. In addition, reports on fossil occurrences generally lack detailed taphonomic examinations.

Recently, we discovered discinid specimens in the Lower Triassic Osawa Formation in the Southern Kitakami Terrane, Japan, some of which were autochthonous (Ishizaki and Shiino 2023b). In a previous study (Murata 1973), the discinids from the Osawa Formation were identified as *Orbiculoidea* sp. cf. *O. sibirica*. However, some researchers have referred to them as *Discinisca* without formally describing their taxonomy (Radwański and Summesberger 2001). In this study, the taxonomy of Triassic discinid specimens from the Osawa Formation is re-examined, focusing on their ventral morphology. The ventral morphology

of the present specimens was compared with that of the extant *Discinisca* and *Discradisca* Stenzel, 1964. Based on the present and previous descriptions, the morphological characteristics of post-Palaeozoic discinid brachiopods were reviewed. Finally, we discuss the relationship between the adaptation capability of discinids and their habitats, specifically addressing the likely process of autecological innovation within a seemingly conservative morphology.
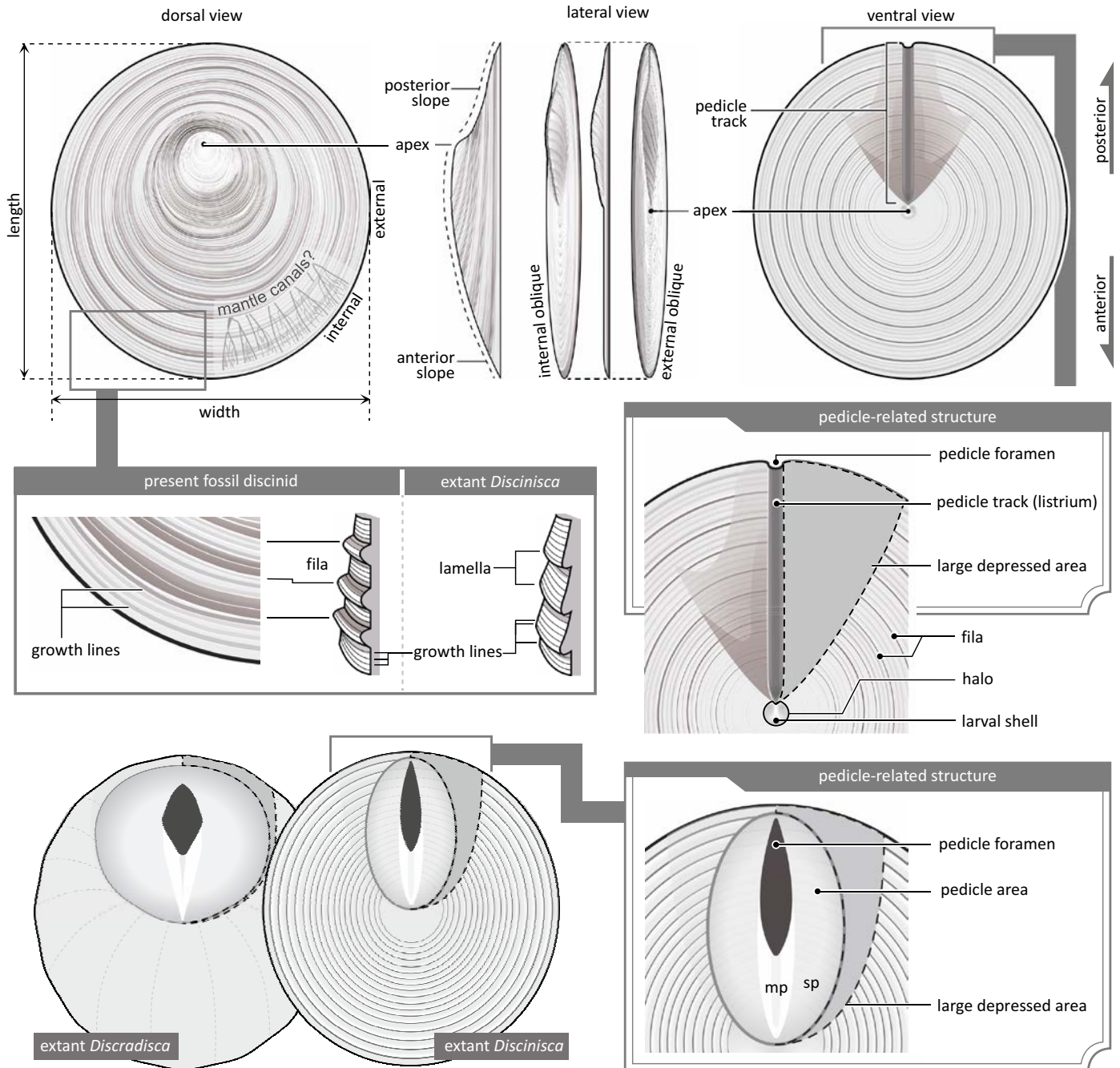
Fig. 2. Morphological terminology of discinid brachiopods. Based on the present fossil specimens and extant discinids of *Discinisca* and *Discradisca*. Abbreviations: mp, median plate (inner listrial plate); sp, semilunar plate (outer listrial plate).

UMUT, the University Museum, the University of Tokyo, Bunkyo-ku, Tokyo, Japan.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:DF44713F-9F10-442C-B922-99EE20BFACAE

Discinid terminology and diagnostic problems

Discinid brachiopods have been classified based on their convexity, with special reference to the anterior and posterior slopes, shape of the pedicle track, shell ornamentation, and pedicle-related structures (e.g., Mergl 2006, 2010; Zhang et al. 2014). Among these, there seems to be an inconsistency in the terminology of pedicle-related structures. Discinids generally have a slit-like opening just posterior to the ventral apex. This opening is for the pedicle, which is a crucial organ for anchoring or attaching individuals to the substratum (Rudwick 1970; James et al. 1992). In *Orbiculoidea*, the slit-like structure was sealed during growth, and the small pedicle foramen was positioned at the posterior end of the slit-like structure. This sealed structure forms a furrow-like surface called listrium (Williams and Rowell 1965; Holmer 1987). Since the external surface of the listrium is easily filled with sediment particles, many fossil discinids only exhibit an outline of the depression (e.g., Zhang et al. 2014). Instead, the term "pedicle track" is often used to describe the outline of the depression, regardless of the fossil preservation of the actual listrium (e.g., Zhang et al. 2014; Masunaga and Shiino 2021). Following previous studies, we adopted the term "pedicle track" as the outline of the listrium, and as the "listrium" when we see the plate-like shell inside the pedicle track. In Triassic discinids, a slit-like structure just posterior to the ventral apex extends to the posterior margin and is sometimes referred to as the "pedicle fissure" (Biernat 1995). Given the correspondence, the term "pedicle track" is used herein instead of the "pedicle fissure."

The extant genera *Discinisca*, *Discradisca*, and *Pelagodiscus* Dall, 1908, are characterised by a "large depressed area" around the pedicle track. Triassic discinids also have a depressed area called the "adherent area" around the pedicle track (Biernat 1995), which may be compared with a large depressed area or pedicle area. We here adopted "large depressed area" and avoided using "adherent area" due to less morphological information in previous photographs (Biernat 1995).

Schematic illustrations of the valve morphology and terminology adopted herein are based on Williams et al. (1997) (Fig. 2). In this study, the term "pedicle-related structure" includes "pedicle foramen", "pedicle track", "listrium", "pedicle area" and "large depressed area".

Geological setting

The Lower Triassic strata, which yield discinid brachiopods, are well exposed in the Tatezaki area of Minamisanriku Town, Miyagi Prefecture, Japan (Fig. 3). The strata of the study area correspond to the Osawa Formation of the Inai Group in the Southern Kitakami Terrane. The Inai Group in the study area, which is a Lower–Middle Triassic sequence, consists of four formations: the Hiraiso, Osawa, Fukkoshi, and Isatomae, in ascending order (Kamada 1989). The Osawa Formation in the study area is subdivided into three units (Fig. 4, unit-1 to unit-3 in ascending order; Ishizaki and Shiino 2023b). Unit-1 is characterised by alternating beds of poorly sorted silty sandstone and current-rippled sandstone, unit-2 is characterised by sandy faintly laminated mudstone and turbidite successions, and unit-3 is
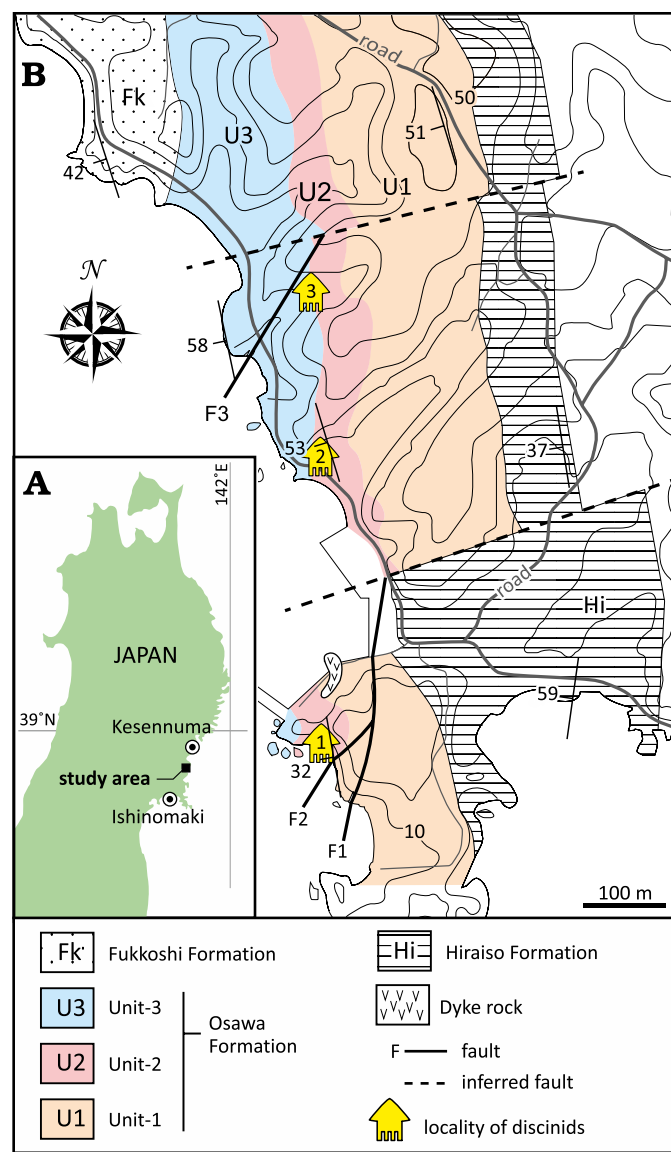

Fig. 3. **A**. Location of study area in the Tatezaki area, Japan. **B**. Geological map of the Tatezaki area, showing fossil localities (modified from Ishizaki and Shiino 2023b).
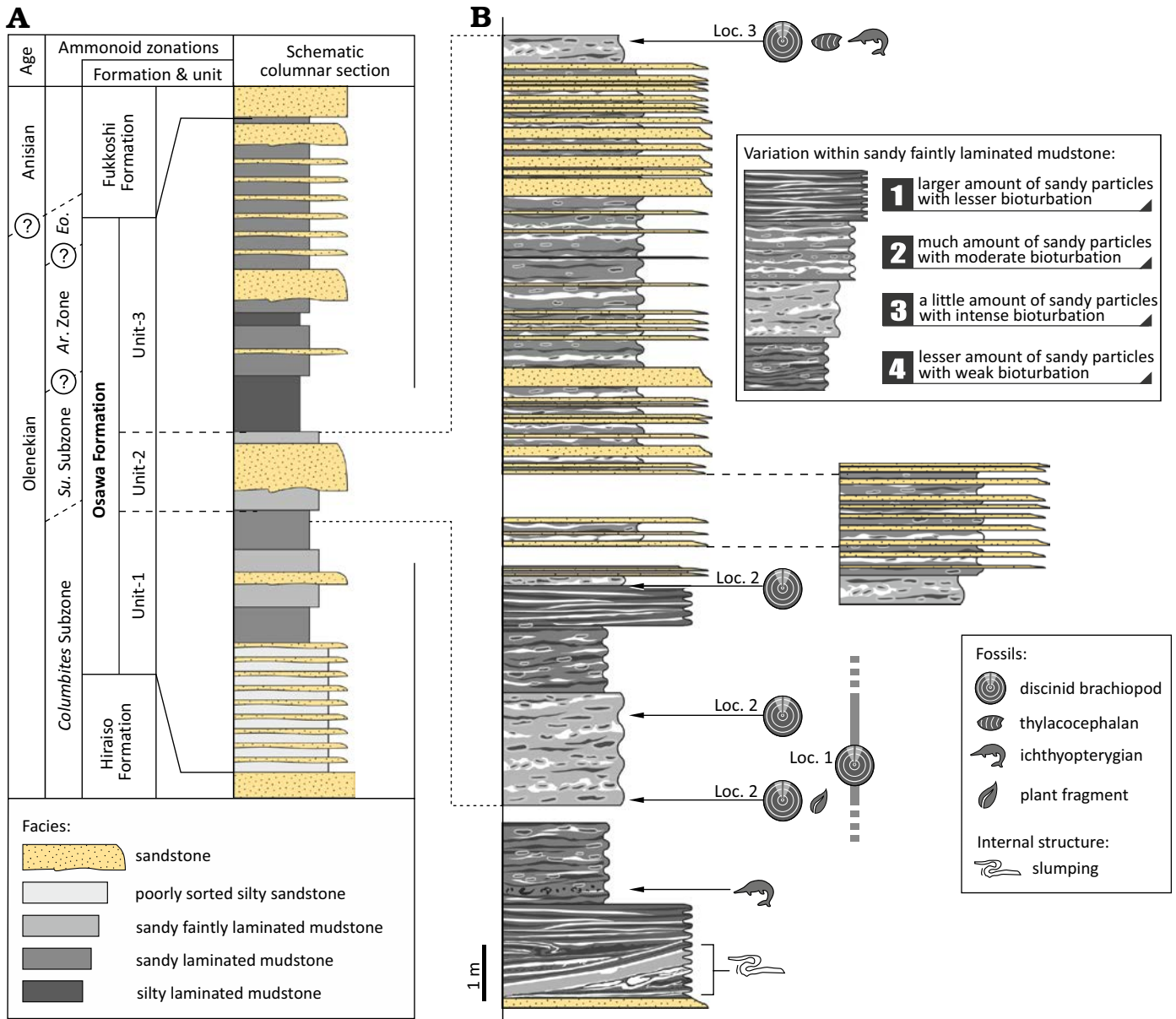
Fig. 4. **A**. Schematic columnar section and stratigraphic age based on Ishizaki and Shiino (2023b). **B**. Detailed columnar section of unit-2 based on the continuous outcrop at Locality 2. The stratigraphic horizons of localities 1 and 3 were inferred from Ishizaki and Shiino (2023b). Abbreviations: *Ar.*, *Arnautoceltites*; *Eo.*, *Eodanubites* Zone; *Su.*, *Subcolumbites*.

characterised by alternating beds of laminated mudstone and current-rippled sandstone (Kamada 1993; Ehiro et al. 2019; Ishizaki and Shiino 2023b). All units are thought to have been deposited in a prodelta setting (Ishizaki and Shiino 2023b).

The discinid specimens occurred at three localities in unit-2, and there were four stratigraphic horizons of fossil occurrences (Figs. 3, 4). A variety of ammonoid, bivalve, thylacocephalan, ichthyopterygian, coprolite, and plant fossils also occurs from unit-2. Based on biostratigraphic studies using ammonoids, the Osawa Formation has been correlated with the Spathian (upper Olenekian) (Ichikawa 1951; Onuki and Bando 1959; Bando 1964; Bando and Ehiro 1982; Ehiro et al. 2019; Shigeta 2022).

Material and methods

Fossil specimens.—For morphological analysis, 57 discinid specimens from unit-2 of the Osawa Formation were used. In addition, we used four specimens (IGPS 92672–92675) previously reported by Murata (1973). The external and internal morphologies of specimens were observed in colour and greyscale photographs using a Sony α7R IV digital camera (Sony Corporation, Japan). Prior to greyscale photography, the specimens were whitened with ammonium chloride. A total of 57 discinid specimens from the Tatezaki area are housed at the Tohoku University Museum (IGPS 112854–112910).

Extant specimens.—To compare the pedicle-related structures of fossils and extant discinids, two dead specimens

of *Discinisca laevis* (Sowerby, 1822) and 11 living specimens of *Discradisca stella* (Gould, 1862) were used. The specimens of *Discinisca laevis* are housed in the University Museum, the University of Tokyo (UMUT RB17215-1, -2), while those of *Discradisca stella* were collected from a tombolo (land-tied bar) on Hashira Island, Yamaguchi, Japan (34°00'56.6"N, 132°25'41.9"E; the sampling locality was followed that of Kato 1996). The beach of the tombolo is composed of boulders and gravel, and the interspaces are filled with coarse sand. The specimens attached to the underside of the boulders were slightly buried in the sand in the intertidal zone.

Discradisca stella was observed by removing the pedicle attached to a boulder, using a cutting knife. The ventral and dorsal valves were separated. After observing the relationship between pedicle and shell morphology, the soft parts were removed. Shell ornamentation in the pedicle area was observed. The external morphology of the specimen was examined in photographs using a Sony α7R IV digital camera (Sony Corporation, Japan) and images using a scanning electron microscope VE-8800 (Keyence, Japan).

Review.—Based on previous descriptions and the present morphological analysis, the morphological characteristics of post-Palaeozoic discinid brachiopods (four species of Triassic *Orbiculoidea* and 51 species of Mesozoic, Cenozoic, and extant discinid brachiopods) were reviewed. Here, we divided the morphology of post-Palaeozoic discinid brachiopods into two categories: dorsal and ventral forms.

In the dorsal valve, fossil species of *Discinisca* are traditionally subdivided into three types A, B, and C (Dall 1920). Type A features a large, lamellose shell ornamentation without costellae (e.g., *Discinisca lamellosa* [Broderip, 1833] and *Discinisca laevis*). In contrast, Type B exhibits a large, weakly lamellose shell ornamentation with faint, irregular costellae (e.g., *Discradisca strigata* [Broderip, 1833] and *Discradisca cumingi* [Broderip, 1833]). Type C is distinct for its small size and non-lamellose shell ornamentation with regular costellae (e.g., *Discradisca stella* and *Discradisca antillarum* [d'Orbigny, 1846]). Among these morphological characteristics, shell size is not a suitable morphological indicator, as each species can vary in size during growth and can be included in either large- or small-sized groups. Stenzel (1964) suggested dividing the genus based on the existence of costellae; therefore, some species in types B and C should be the derivative *Discradisca* rather than *Discinisca*. Recently, this suggestion has been followed, and costellae have been preferentially used for identification (Bitner and

Cahuzac 2013; Dulai and Hocht 2020; Ishizaki and Shiino 2023a). Following this method, we divided the discinid dorsal form based on striation morphology.

The ventral valves of discinids are not well documented in living individuals or fossils. Species with information on the ventral valve were classified based on the morphology of the pedicle-related structure, with special reference to the characteristics of *Orbiculoidea* and extant *Discinisca*. This study particularly focused on the size and shape of the pedicle track and the large depressed area.

Systematic palaeontology

Class Lingulata Gorjansky and Popov, 1985
Order Lingulida Waagen, 1885
Superfamily Discinoidea Gray, 1840
Family Discinidae Gray, 1840
Genus *Bronzoria* nov.

Zoobank LSID: urn:lsid:zoobank.org:act:D7CB0815-D9EB-44BE-8046-194F01627DA5

Type species: *Bronzoria recta* gen. et sp. nov., see below.

Species included: Only those discinid species with ventral morphology reported can be compared to *Bronzoria* gen. nov. and either included into the genus, or excluded from it. Members of *Bronzoria* gen. nov. are at the least *Orbiculoidea taskrestensis* Dagys in Dagys and Kurushin, 1985, *Bronzoria recta* gen. et sp. nov., *Discinisca sibirica* (Moisseiev, 1947), *Discinisca bosniaca* (Kittl, 1904), *Discinisca discoides* (Schlotheim, 1820), *Discinisca townshendi* (Davidson, 1851) (= *Discinisca babeana*? [d'Orbigny 1849]), *Discinisca rhaetica* (Andreae, 1893), *Discinisca zapfei* Radwański and Summesberger, 2001, and *Discinisca spitsbergensis* Biernat, 1995.

Etymology: From the *Bronzor* in the Japanese videogame Pokémon, modelled after the ancient circular bronze mirror. The pattern of concentric circles and the posterior slit on the ventral side of the *Bronzor* resembles the morphology of the present genus.

Diagnosis.—The shell convexity is convexoplane-convexoconcave. The dorsal apex is located subposteriorly. The ventral apex is located subcentral. In the posterior part of the ventral valve, there is a V-shaped large depressed area and a narrow pedicle track with a small pedicle foramen. The outer surface ornamentation shows smooth to concentric ridges of the fila and is not lamellose.

Remarks.—*Bronzoria* gen. nov. is similar to *Discinisca* in having a large depressed area (e.g., Holmer and Popov 2000). However, the present genus, which is characterised by a narrow pedicle track, differs from *Discinisca*,

Table 1. Diagnostic characters of three discinid genera.

| Pedicle-related structure	*Orbiculoidea*	*Bronzoria*	*Discinisca*
Large depressed area	–	V-shaped	wide, U-shaped
Pedicle track	elongate oval	narrow	U- or elliptical-shaped
Pedicle foramen	small	small	large, oval
Shell convexity	strongly dorsibiconvex-convexoplane	convexoplane-convexoconcave	dorsibiconvex-convexoconcave
Surface ornamentation	well-developed concentric fila	fine growth lines and fila	fine growth lines and lamellae
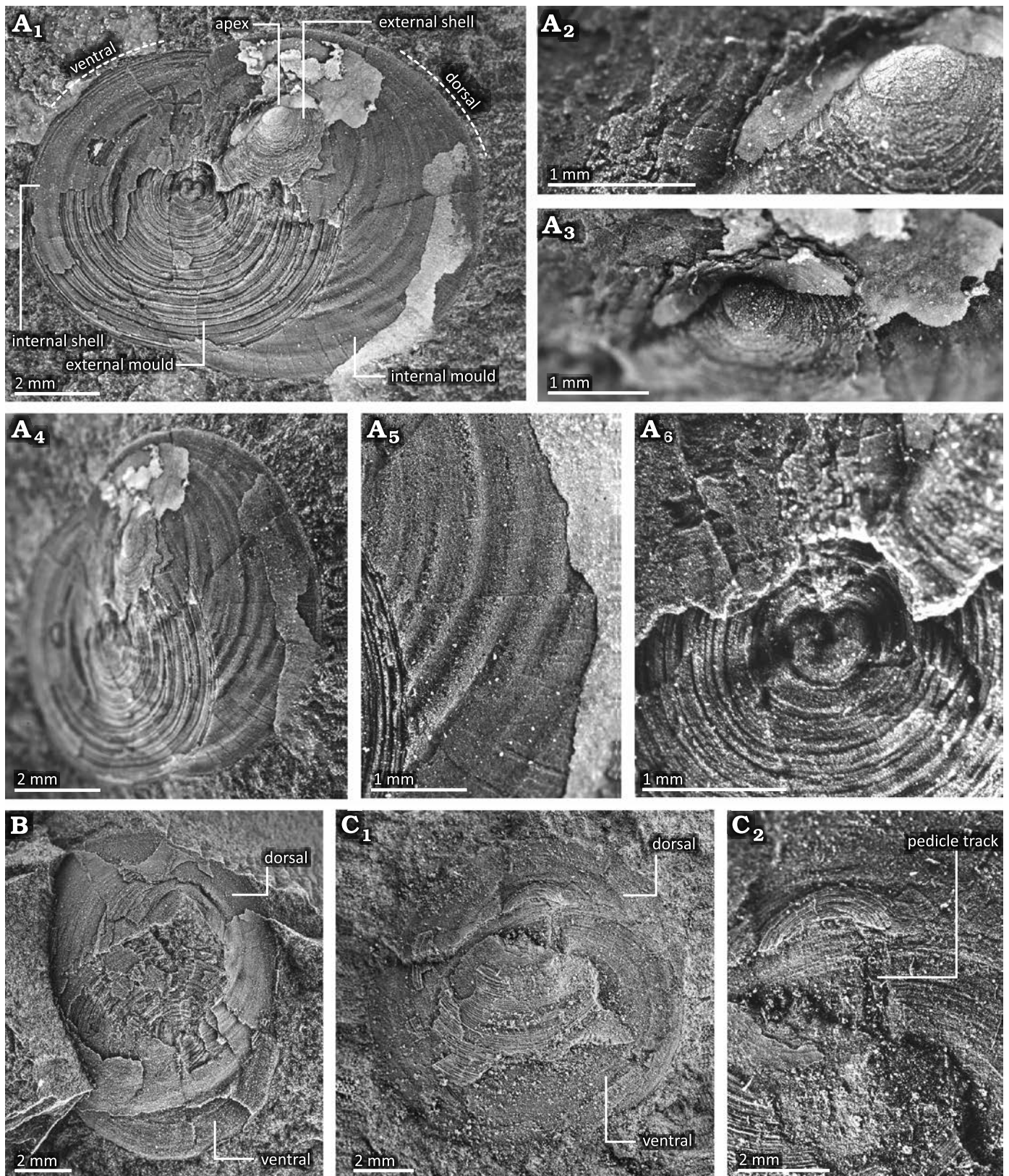
Fig. 5. Conjoined shell of discinid brachiopod *Bronzoria recta* gen. et sp. nov. from the Tatezaki area, Miyagi, Japan, Osawa Formation, Olenekian, Lower Triassic. **A**. IGPS 112854, holotype, internal surface of the dorsal valve and external surface of the ventral valve. The dorsal valve shows a smooth larval shell at its apex (A_2, A_3) and network-like thinner furrows on the internal mould (A_4, A_5). The centre of the ventral valve shows an external mould of the larval shell (A_6). **B**. IGPS 112855, internal mould of the dorsal valve and external mould of the ventral valve. **C**. IGPS 112856, external mould of the dorsal valve and internal mould of the ventral valve (C_1), and detail showing a pedicle track on the ventral valve (C_2).

which has a U-shaped or elliptical pedicle track (Table 1). *Bronzoria* gen. nov. also differs from *Discinisca* in that it lacks a lamellose shell. The present genus is similar to *Orbiculoidea* in having an elongate pedicle track with a small pedicle foramen (e.g., Mergl 2006; Zhang et al. 2014). However, the shape of the pedicle track in the genus is narrower than that of *Orbiculoidea*. A large depressed area is also unique to the present genus, which is not developed in *Orbiculoidea* (Table 1).

The internal posterior surface of the ventral valve is the potential attachment site of muscles (Holmer and Popov 2000). In this case, the presence of a large depressed area alters the valve opening and closure system, influencing the length and direction of muscle contractions. Additionally, the morphology of the pedicle track reflects the sedentary mode of life. Therefore, the morphological differences in pedicle-related structures among *Bronzoria* gen. nov., *Discinisca* and *Orbiculoidea* are considered to be generic-scale differences (Table 1).

Stratigraphic and geographic range.—The oldest species of this genus is *Bronzoria bosniaca* (Kittl, 1904) from the upper Permian, and the other species are from the Triassic and Middle Jurassic. The youngest species of this genus is *Bronzoria townshendi* (Davidson, 1851). Discinids assigned to *Bronzoria* have been reported from the United Kingdom, Spitsbergen, France, Germany, Austria, Slovenia, Bosnia, Siberia (Russia), and Japan (see SOM: table S1, Supplementary Online Material available at http://app.pan.pl/SOM/app69-Ishizaki_Shiino_SOM.pdf).

Bronzoria recta sp. nov.

Figs. 5–8.

1973 *Orbiculoidea* sp. cf. *O. sibirica* Moisseiev; Murata 1973: pl. 29: 16, 17.
2023 *Orbiculoidea* sp. cf. *O. sibirica* Moisseiev; Ishizaki and Shiino 2023b: fig. 12G.

ZooBank LSID: urn:lsid:zoobank.org:act:73725EC9-9A3E-41DF-85B5-6D3A6948E166

Etymology: From Latin *recta*, straight; a narrow and straight pedicle track is the most notable characteristic of this species.

Type material: Holotype: dorsal and ventral valves, originally conjoined shell, IGPS 112854 (Fig. 5A). Paratypes: four supposed conjoined shells, IGPS 92672, 112855–112857 (Figs. 5B, C, 6B, E); three dorsal valves, IGPS 112858–112860 (Fig. 6); two ventral valves, IGPS 112861–112862 (Figs. 7, 8); all from type locality and horizon.

Type horizon: Middle part of the Osawa Formation (unit-2: Spathian, Olenekian), Lower Triassic.

Type locality: Tatezaki area in Minamisanriku Town, Miyagi Prefecture, Japan (Fig. 3).

Material.—Eight articulated shells, 33 dorsal valves, 15 ventral valves and one unknown valve (dorsal or ventral) were collected (IGPS 112854–112910). We also used four specimens (IGPS 92672–92675) reported as *Orbiculoidea* sp. cf. *O. sibirica* by Murata (1973). Although the original height of the shell and the 3D morphology of the shell slope were not preserved due to deformation, the overall morphology was well preserved. The shells were thin and blackish in colour.

Diagnosis.—Convexoplane to convexoconcave shell with a low conical dorsal valve. Both dorsal and ventral valves have comparatively dense, regularly arranged fila on the outer surface. The dorsal valve has a convex anterior slope and a concave posterior slope. The dorsal apex is subposterior to the centre. The ventral apex is almost central, with a posterior slope curving dorsally. The pedicle track is narrow and straight, extending to the posterior margin along the midline of a V-shaped large depressed area.

Description.—The shell convexity is convexoplane–convexoconcave with a subcircular outline (Figs. 5–8). The length and width of the shell are 7–13 mm and 6–14 mm, respectively. The outline of the smaller specimens tends to be a true circle, while that of the larger specimens changes to a weak trapezoid with a short, straight posterior margin (Figs. 5, 6).

The dorsal valve is low conical in shape with 1.08–2.09 mm height, which is supposed to be lower than the original height. The apex is located posteriorly at one-third to one-fourth of its length from the posterior margin (Figs. 5, 6). The anterior slope is moderately convex (Fig. 6A$_2$, C$_2$). The posterior slope is overall concave (Fig. 6A–D), though its convexity changes during growth. The slope just posterior to the apex is moderately convex, and subsequently bent posteriorly to become a plane to a gently concave slope (Fig. 6A$_2$, A$_3$, C). The shell margin, including the posterior slope, is slightly bent ventrally (Fig. 6A$_2$, C). In this configuration, the position of the apex moves backwards, with the larval shell facing the posterior direction (Figs. 5A, 6A, C). The lateral slopes are gently convex and smoothly transition into the convex anterior slope and concave posterior slope. The external surface of the dorsal valve exhibits numerous, distinct, and slightly elevated concentric growth lines. These growth lines are somewhat discontinuous and are arranged at intervals of approximately 0.06–0.07 mm (Fig. 6A$_4$, D). Several growth lines are inserted into the anterior part. The growth lines periodically develop into higher-elevated concentric fila. The concentric fila interval is the broadest in the antero-median part, with 2–3 fila of 1 mm in length (Fig. 6A$_4$). Both the growth lines and concentric fila are faint around the apex, while they are distinct near the shell margin. The concentric fila are more continuous than the growth lines. The internal surface of the dorsal valve is comparatively smooth with broad concentric undulations (Fig. 6A$_3$). The undulations show low-height wavy outlines in cross sectional view, of which the width increases from 0.1 mm to 0.35 mm toward the shell margin (Figs. 5, 6). The larger specimen has a median septum just anterior to the apex (Fig. 6E). In the peripheral part of the internal surface, narrow and shallow furrows 0.02–0.04 mm in width extend radially (Fig. 5A$_5$). From these furrows, network-like thinner furrows branch and extend radially, all of which are similar to mantle canals (Mergl and Massa 2005; Williams et al. 1997).
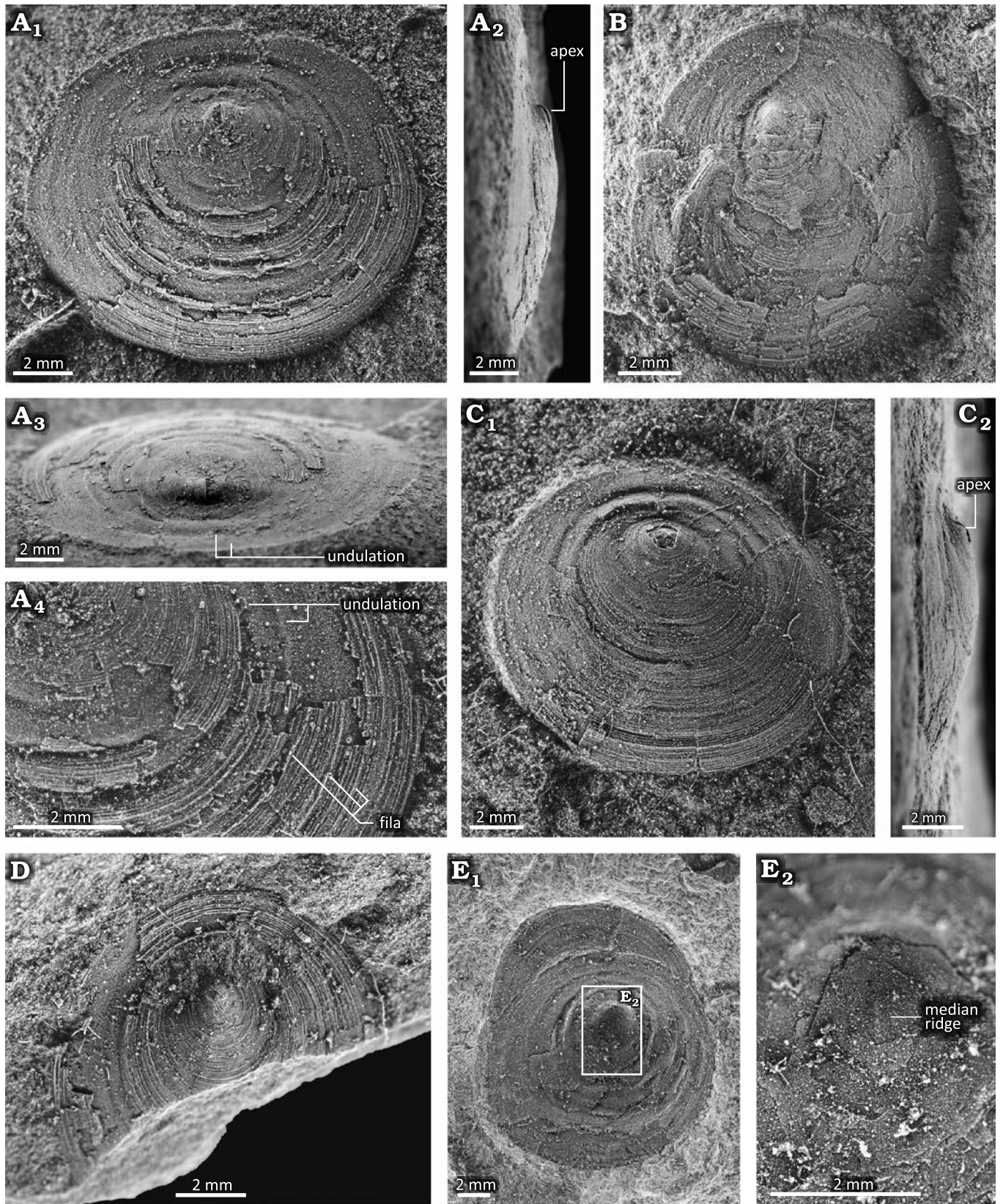
Fig. 6. Dorsal valve of discinid brachiopod *Bronzoria recta* gen. et sp. nov. from the Tatezaki area, Miyagi, Japan, Osawa Formation, Olenekian, Lower Triassic. **A**. IGPS 112858, internal mould with partially preserved external shell in the anterior half; dorsal (A$_1$), lateral (A$_2$), postero-oblique (A$_3$) views and detail (A$_4$). **B**. IGPS 112857, internal mould of the posterior half with external shell in part of the anterior half. The ventral shell is preserved anteriorly. **C**. IGPS 112859, external shell of anterior half and internal mould of posterior half; dorsal (C$_1$) and lateral (C$_2$) views. **D**. IGPS 112860, external shell in dorsal view. **E**. IGPS92672, internal surface of the dorsal valve (E$_1$) as described by Murata (1973), detail (E$_2$) shows a faint median ridge.
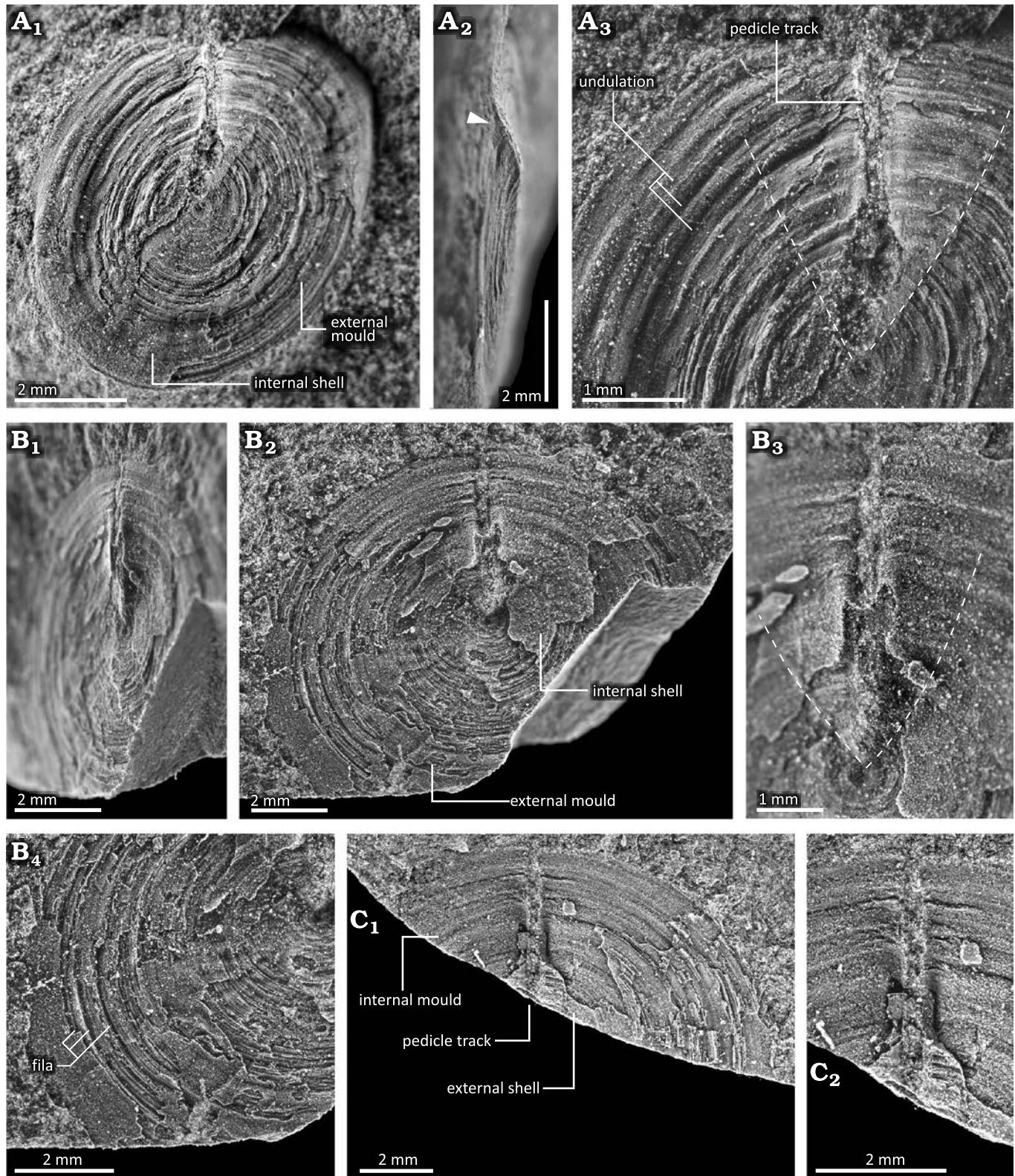
Fig. 7. Ventral valve of discinid brachiopod *Bronzoria recta* gen. et sp. nov. from the Tatezaki area, Miyagi, Japan, Osawa Formation, Olenekian, Lower Triassic. **A**. IGPS 112861, internal shell with a partially exposed external mould on the anterior right part (A_1).The white arrowhead in the lateral view (A_2) shows the posterior end of the ventral valve, which remains a furrow of the pedicle track. The area around the pedicle track posterior to the dashed line (A_3) is slightly elevated, forming V-shaped large depressed area in the external view. **B**. IGPS 112862b, internal shell around the pedicle track and external mould in the anterior half, in oblique (B_1) and dorsal (B_2) views. The area around the pedicle track posterior to the dashed line (B_3) is slightly elevated, similar to that in A_3. Anterior half of B_2 showing fila (B_4). **C**. IGPS 112862a, internal mould with partially preserved external shell at the anterior part around the listrium (C_1, counterpart of B). Detail showing a pedicle track (C_2).
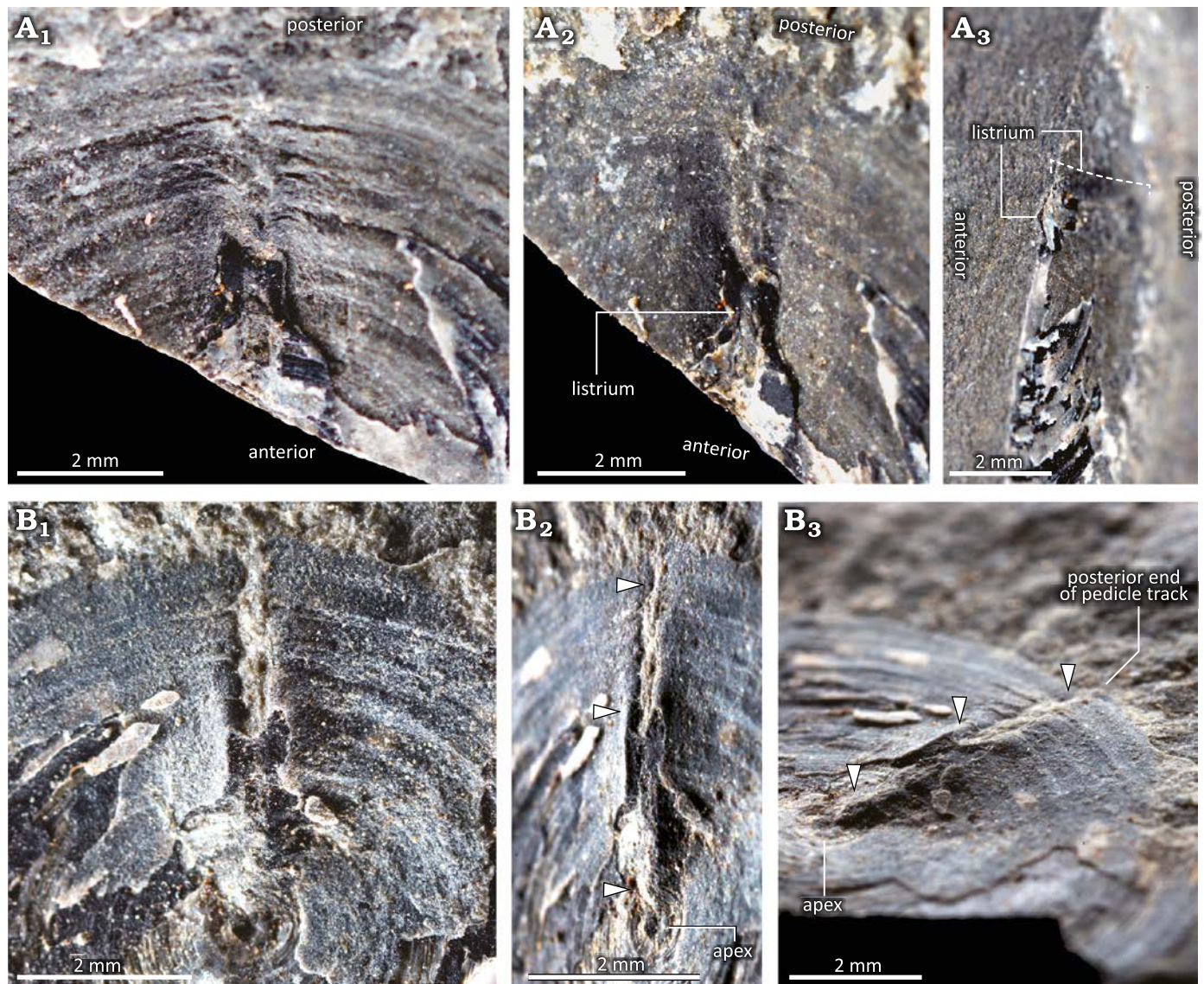
Fig. 8. Colour photographs of ventral morphology around the pedicle track of discinid brachiopod *Bronzoria recta* gen. et sp. nov. from the Tatezaki area, Miyagi, Japan, Osawa Formation, Olenekian, Lower Triassic. **A**. IGPS 112862a, internal mould with partially preserved external shell at the anterior part around the listrium (the same specimen as in Fig. 7C), in ventral (A_1), oblique (A_2), and anterior (A_3) views. **B**. IGPS 112862b, internal shell around pedicle track (the same specimen in Fig. 7B), in dorsal (B_1), oblique (B_2), and antero-oblique (B_3) views. Note that the listrium has a convex shape just posterior to the apex, a ridge shape in the middle, and a flat shape in the posterior area (B_2, B_3: three white arrowheads).

The ventral valve is flattened overall, and its apex is situated at the centre of the ventral valve (Figs. 5, 7). The margin of the ventral valve is slightly geniculated toward the ventral direction (Figs. $5A_1$, B, $7A_1$). The anterior and lateral slopes are flattened, while the posterior slope is concave, with its concavity change during growth (Fig. 7A, B). Along the median line, the posterior slope just posterior to the larval shell is strongly depressed and flattened (Figs. 7B, 8). In the posterior part, the posterior slope bends ventrally, forming a concave outline (Figs. 7B, 8). The peripheral part of the posterior slope is flattened with a geniculated margin. In the horizontal view, the concave area of the posterior slope exhibits a symmetric, V-shaped depression known as the large depressed area (Fig. $7A_3$, B_3). The angle of the V shape is approximately 70°. In the anterior part of the large

depressed area, the boundary with the lateral slope is geniculated, while in the posterior part is smooth (Fig. 7A, B). Similar to the dorsal valve, the external surface of the ventral valve exhibits numerous and distinct, slightly elevated concentric growth lines (Fig. 7A, B). These growth lines are irregular and arranged in approximately 0.02–0.04 mm intervals. The growth lines periodically develop into higher elevated and concentric fila, with intervals of 3–4 ridges of 1 mm in length (Fig. $7B_4$). The concentric growth lines and the fila of the ventral valve are elevated more vertically than those of the dorsal valve. Growth lines and fila are faint around the apex, while they become distinct near the shell margin.

The narrow, longitudinal pedicle track is positioned just posterior to the ventral apex, which is approximately

0.3 mm wide, extending to the posterior margin (Figs. 5C, 7, 8). On the external surface, the listrium is in the depressed area toward the midline of the posterior slope, although it is filled with muddy sediments (Figs. 7C, 8A). Thus, detailed information regarding the morphology and surface ornamentation of the listrium is unknown. The pedicle foramen is also invisible due to filled sediments. However, given that the pedicle track extends to the shell margin, the pedicle foramen is undoubtedly located at the posterior margin and opens outwards (Figs. 7A$_2$, B, 8). On the internal surface, the listrium has a shape different from that seen in the external view. An anterior part of the listrium is convex, corresponding to the depression observed on the external surface (Fig. 8B: arrowhead near the apex). In the middle part of the listrium, around the most depressed part on the posterior slope, the shells beside the pedicle track are elevated to the ridges; therefore, the middle part of the listrium appears depressed (Fig. 8B: arrowhead of the middle). In the posterior part, around the shell margin, the elevated ridges parallel to the listrium become weak and obscure (Fig. 8B: arrowhead near the posterior margin).

The larval shells are well-preserved in the dorsal and ventral valves, both of which have unique ornamentation with distinct boundaries (Fig. 5A). In the dorsal valve, the larval shell has a subcircular outline and was approximately 600 µm in diameter (Fig. 5A$_2$, A$_3$). All slopes of the larval shell are convex with a smooth surface. In the ventral valve, the larval shell has a subcircular outline, approximately 600 µm in diameter (Fig. 5A$_6$). In the best-preserved specimen, the outline of the larval shell is heart-shaped. Similar to the dorsal larval shell, the ventral larval shell has a smooth surface but shows a variety of convexities. The peripheral part of the anterior to postero-lateral slope is moderately concave. The postero-median part has a slit-like ridge 40 µm wide, extending from the centre to the posterior margin of the halo. The slit-like ridge changes wider and lower toward the posterior margin of the halo, connecting to the pedicle track. The central part of the larval shell is gently convex.

Remarks.—*Bronzoria recta* gen. et sp. nov. is similar to *Bronzoria sibirica* (Moisseiev, 1947), in having a subcircular outline approximately 10 mm in size with convexoplane convexity. In particular, the narrow, longitudinal pedicle track extending to the posterior margin with the V-shaped large depressed area in *Bronzoria sibirica* is extremely similar to that of the present species. Murata (1973) described this species as *Orbiculoidea* sp. cf. *O. sibirica* based on its size, flattened ventral valve, and narrow pedicle track. However, the position of the dorsal apex in *Bronzoria recta* gen. et sp. nov. is more anterior than that in *Bronzoria sibirica*, with its apex located posteriorly at one-fifth to one-ninth of its length (Dagys 1965). Moreover, the dorsal valve of the present species has a posterior slope with a concave outline, which differs from the gently convex posterior slope of *Bronzoria sibirica*. The dorsal convexity around the apex can be strongly related to the muscular system and the volume of soft parts

(Masunaga and Shiino 2021); therefore, this is not *Bronzoria sibirica* but a previously undescribed species.

In the Early Triassic, some discinid brachiopods exhibited a ventral morphology similar to that of *Bronzoria recta* gen. et sp. nov. (Kittl 1904; Wagner 1913; Dagys 1965). According to Radwański and Summesberger (2001), three discinid species are categorised as "slightly (?) older Triassic forms": *Bronzoria sibirica*, *Bronzoria bosniaca* (Kittl, 1904) and *Bronzoria major* (Wagner, 1913). *Bronzoria bosniaca* and *Bronzoria major* are characterised by a narrow, longitudinal pedicle track extending to the posterior margin with the V-shaped large depressed area, as observed in *Bronzoria recta* gen. et sp. nov. (Kittl 1904; Wagner 1913). These two species are also similar to this species in their low conical, convexoplane shell and the position of the dorsal apex, but they differ in their larger shell size (*Bronzoria bosniaca*: 30 mm in diameter, *Bronzoria major*: 43 mm in diameter) and wider intervals of the fila compared to the present species. A similar morphology of convexity has also been reported in the Late Triassic *Bronzoria rhaetica* (Andreae, 1893). However, the latter species differs from *Bronzoria recta* gen. et sp. nov. in its larger size (32 mm in diameter), a pedicle track widening toward the posterior margin, and a trapezoid outline with a long, straight posterior margin (Andreae 1893).

Stratigraphic and geographic range.—Osawa Formation, Spathian (upper Olenekian, Lower Triassic); probably within the Southern Kitakami Terrane, Japan.

Pedicle-related structure in extant and fossil discinids

Morphology of pedicle-related structures in extant discinids.—*Discinisca laevis* and *Discradisca stella* have a U-shaped large depressed area in the posterior half of the ventral valve (Fig. 9). A large pedicle area develops within this depression, but it is smaller than the large depressed area (Fig. 9A$_1$, A$_4$ B$_2$, C$_3$). The pedicle area is oval in *Discinisca laevis* (Fig. 9A, B), whereas it is heart-shaped in *Discradisca stella* (Fig. 9C).

In *Discinisca laevis*, the pedicle area is strongly concave with its external surface displaying growth lines (Fig. 9A$_4$, B$_3$). In contrast, the external surface, except for the pedicle area is characterised by concentric lamellae (Fig. 9A$_4$, B$_3$), showing a great disparity in surface ornamentation. The pedicle area is subdivided into two regions: a narrow, arrowhead-shaped median plate just anterior to the elongate oval pedicle foramen (Fig. 9A$_4$, B$_3$) and a pair of semilunar plates on the right and left sides (Fig. 9A$_4$, B$_3$). The former median plate is concave as it is a furrow-like depression (Fig. 9A$_4$, B$_3$). The growth lines on the median plate are correlated with the anterior curvature of the pedicle foramen (Fig. 9B$_3$).

In living *Discradisca stella*, the pedicle covers the entire external surface of the pedicle area. The pedicle area is
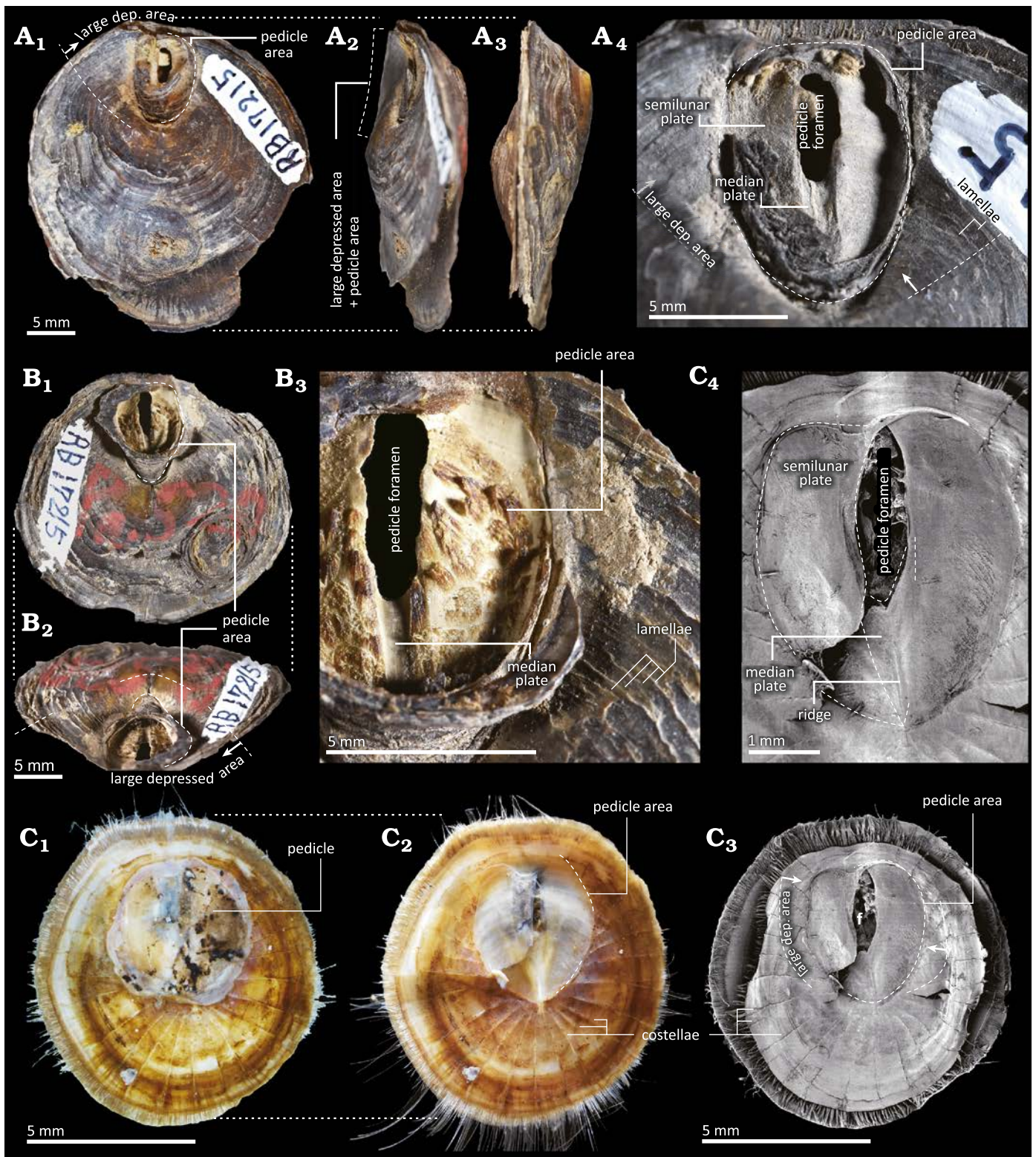
Fig. 9. Morphology of extant discinids. **A, B**. *Discinisca laevis* (Sowerby, 1822) from Calles, Peru, Recent. **A**. UMUT RB17215-1 in ventral (A_1), oblique lateral (A_2), and lateral (A_3) views, detail of the large depressed area (A_4). **B**. UMUT RB17215-2 in ventral (B_1) and oblique posterior (B_2) views, detail of the large depressed area (B_3). **C**. *Discradisca stella* (Gould, 1862) from Hashira Island, Yamaguchi, Japan, Recent. UMUT RB34200 in ventral view. Colour photographs with (C_1) and without (C_2) pedicle and SEM images (C_3, C_4) showing the relationship among pedicle-related structures. The shell outline in C_3 is slightly deformed owing to drying. Abbreviation: dep., depressed.

slightly concave and milky-white colour (Fig. $9C_2$). The external surface of the pedicle area appears smooth but exhib-

its faint growth lines (Fig. $9C_2$), while the outside of the external surface has radial ridges, the so-called costellae (Fig.

Fig. 10. Morphological types of post-Palaeozoic discinid brachiopods and selected Palaeozoic species. All discinids with type 1 ventral valves classified as *Bronzoria* gen. nov. The width of each stratigraphic unit not to scale. Each square and the position of the species name does not reflect its order of appearance; however, the order of the list is provided in the SOM. Abbreviations: *Disci.*, *Discinisca*; *Discr.*, *Discradisca*; Pa., Palaeozoic; *O.*, *Orbiculoidea*; *P.*, *Pelagodiscus*.

$9C_2$, C_3). The pedicle foramen is elongated oval located posteriorly in the pedicle area (Fig. $9C_3$). Similar to *Discinisca laevis*, the pedicle area of *Discradisca stella* shows an arrowhead-shaped median plate (Fig. $9C_4$) and a pair of semilunar plates (Fig. $9C_4$). The median plate is comparatively flat, with a thin ridge along the midline (Fig. $9C_4$).

Review of post-Palaeozoic discinid morphology.—The morphological characteristics of four species of the Triassic *Orbiculoidea* and 55 species of the Mesozoic, Cenozoic, and extant discinid genera are shown in SOM: table S1.

In previous studies, Triassic *Orbiculoidea* included *Orbiculoidea yangkangensis* Xu and Liu, 1983, *Orbiculoidea qieermaensis* Xu and Liu, 1983, *Orbiculoidea taskrestensis* Dagys in Dagys and Kurushin, 1985, and *Orbiculoidea win-*

snesi Gobbett, 1963. Of these, *Orbiculoidea winsnesi* was identified by Foster et al. (2017) using only the morphology of the dorsal valve, which seems doubtful for identifying it as *O. winsnesi* as it was originally described by Gobbett (1963) based on specimens from the middle Carboniferous. The four species of Triassic *Orbiculoidea* are characterised by subcircular outlines, low conical shapes, and fine concentric growth lines (Xu and Liu 1983; Dagys and Kurushin 1985; Foster et al. 2017). *Orbiculoidea yangkangensis* and *O. qieermaensis* have a biconvex shell with short, discontinuous costellae in their dorsal valve, while *O. taskrestensis* and *O. winsnesi* of Foster et al. (2017) have a convexoconcave shell. Their ventral valves, except for those of *O. winsnesi* described by Foster et al. (2017), exhibit different morphological characteristics of pedicle-related structure.

Orbiculoidea yangkangensis and *O. qieermaensis* are characterised by short, narrow pedicle tracks just posterior to the ventral apex without a V-shaped large depressed area (Xu and Liu 1983), as seen in *Bronzoria recta* gen. et sp. nov. These pedicle-related structural characteristics are typical of *Orbiculoidea*. In contrast, *O. taskrestensis* has a short, inverted triangle-shaped pedicle track just posterior to the ventral apex, with a V-shaped large depressed area (Dagys and Kurushin 1985), similar to *Bronzoria recta* gen. et sp. nov.

In this review, all species of discinid brachiopods, except *Orbiculoidea* are characterised by having convexoplane–convexoconcave shells with fine, concentric growth lines (see SOM: table S1). Among these, the ventral valves of three genera (*Discinisca*, *Discradisca*, and *Pelagodiscus*) definitely have a pedicle track within a large depressed area, although information regarding the ventral valve is lacking for many species. The dorsal form was subdivided into three types based on the development of the costellae (types A, B, and C), while the ventral form of the pedicle track and large depressed area was subdivided into three types (types 1, 2, and 3) (Fig. 10; see also SOM: table S1).

Among the 55 species from the late Permian to the present, there are 28 species of type A, 9 species of type B, and 18 species of type C (Fig. 10; see also SOM: table S1). The dorsal valve of type A, which is characterised by a lack of costellae, is 1.5–43 mm in size, with a subcentral to posterior (1/3–1/20 of the length from the posterior margin) apex position. The dorsal valve of type B, characterised by weak or partly visible costellae, is 6.5–24 mm in size, with a subcentral to posterior (1/3–1/10 of the length from the posterior margin) apex position. The dorsal valve of type C, characterised by distinct fine costellae, is 2.3–35 mm in size with a subcentral–posterior (central–1/7 of the length from the posterior margin) apex position. The dorsal valve is slightly larger than the ventral valve.

Ventral valve morphology was described in 24 species: type 1 for 9 species, type 2 for 9 species, and type 3 for 7 species.

The type 1 ventral valve has a narrow, longitudinal pedicle track on the midline of the V-shaped large depressed area, as seen in the present *Bronzoria recta* gen. et sp. nov. Some type 1 species exhibit pedicle track widening toward the posterior margin (see SOM: table S1). The external surface of the large depressed area exhibits fine concentric growth lines that are continuous with those in the peripheral part of the large depressed area. The pedicle foramen is invisible, possibly due to filled sediment.

The type 2 ventral valve has a pedicle area slightly inside the large depressed area. The pedicle area in smaller individuals is U-shaped, with its pedicle foramen opened posteriorly, while that in larger individuals shows an elliptical shape by closing the pedicle foramen (Mergl 2010). In larger individuals, the pedicle foramen is large and oval, with an arrowhead-shaped plate anterior to the pedicle foramen. The external surface of the pedicle area exhibits faint concentric growth lines, which differ greatly from those of

other areas with distinct growth lines. The ventral valve of *Discinisca papyracea* (Münster in Goldfuss, 1831) is illustrated as having a V-shaped pedicle area and costellae on the peripheral part of the large depressed area (Seilacher 1982). These features are different from those of type 2; however, the shape of the pedicle area is most similar to that of type 2. In *Discinisca elslooensis* Radwańska and Radwański, 2003, the pedicle area seems to be U-shaped, though the posterior parts of the specimens are broken (Radwańska and Radwański 2003). This leads to the possibility that the species belongs to the genus *Discina* Lamarck, 1819, which is characterised by a thick shell, short slit-like structure (= pedicle track of *Discina* in Holmer and Popov 2000; = pedicle slit of *D. elslooensis* in Radwańska and Radwański 2003), and a well-developed median septum in the ventral valve. However, we adopted the original descriptions of the authors and subdivided this species into type 2 based on the ventral valve.

The type 3 ventral valve has an oval to heart-shaped pedicle area, which is much wider than type 2. The pedicle foramen is also larger and wider than that in type 2. Similar to type 2, an arrowhead-shaped plate anterior to the pedicle foramen is present. The external surface of the pedicle area appears smooth but exhibits faint concentric growth lines, which differ greatly from those of the others with distinct growth lines and costellae.

Discussion

Occurrence and ecology of *Bronzoria recta* gen. et sp. nov.—All specimens occur in sandy faintly laminated mudstone layers in unit-2 of the Osawa Formation (Fig. 4: facies 1 and 3), with a large amount of small organic matter and plant fragments (Ishizaki and Shiino 2023b). There are four stratigraphic horizons of fossil occurrences, and the layers show slight variations in the amount of sandy particles and the intensity of bioturbation (Fig. 4). Among the layers, the lower two layers and the upper layer of fossil occurrences are characterised by a small amount of sandy particles with intense bioturbation (Fig. 4: facies 3), while the middle layer is characterised by a larger amount of sandy particles with less bioturbation (Fig. 4: facies 1).

The present specimens are autochthonous or parautochthonous elements with a preserved life posture based on the presence of conjoined valves and their occurrence of convex-up orientation (Ishizaki and Shiino 2023b). According to previous studies, extant species of *Discinisca* are present on hard substrates by way of pedicle attachment (e.g., Dall 1920). Due to this mode of life, extant species occasionally exhibit cluster assemblages on surfaces such as small pebbles and bioclasts when other attachment site is dispersed and restricted (Mergl and Massa 2005; Mergl 2010). However, in the present specimens, we did not find any other pebbles or bioclasts near the discinid specimens that could have been candidates for hard substrates for pedicle
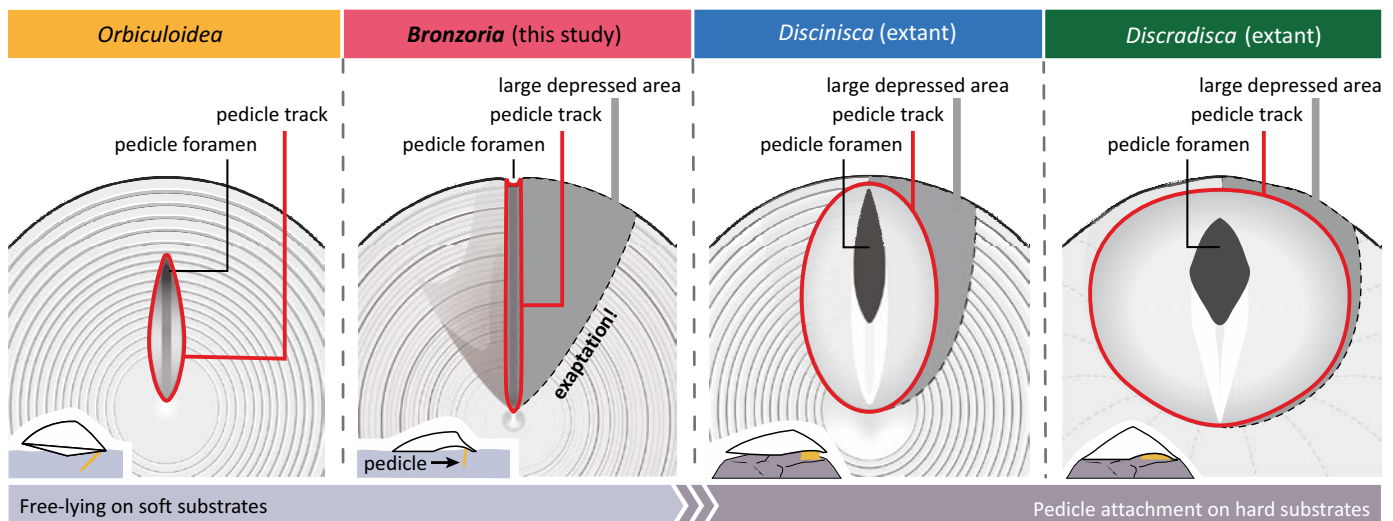
Fig. 11. Ventral morphology and related life postures of four discinid genera.

attachment in adult stage. Given that the specimens show a dispersed arrangement but are not densely colonised, the present species had a free-lying mode of life to muddy sediment, as observed in the Palaeozoic discinid *Orbiculoidea* (Mergl 2006; Masunaga and Shiino 2021).

Sedimentary analyses revealed that the habitat of the present species was near the fan lobe of the prodelta (distal outer shelf) (Ishizaki and Shiino 2023b). Muddy substrates were comparatively oxic because the sandy supply modified benthic redox conditions episodically. As a result, inhabitation by the opportunistic *Bronzoria recta* gen. et sp. nov. could have occurred during oxic episodes in the vicinity of the fan lobe, supplying a larger amount of food matter. However, the environment without the sandy supply was originally dysoxic (Ishizaki and Shiino 2023b).

Comparison of pedicle-related structures of fossil and extant discinids.—Although the terminology differs, the morphological combination of pedicle-related structures in extant discinids is very similar to that of the Palaeozoic discinid *Orbiculoidea*. Based on the present observation of extant discinids, the arrowhead-shaped median plate anterior to the pedicle foramen and the pair of semilunar plates are comparable to the inner and outer listrial plates, respectively (Masunaga and Shiino 2021; Fig. 11). As observed in extant discinids, the width of the arrowhead-shaped median plate is similar to that of the pedicle foramen. Given the pattern of the growth lines, the formation of the median plate is a result of stepwise secretions to seal the anterior part of the pedicle foramen as growth.

Following the morphological characteristics observed in extant discinids, we realised that *Bronzoria recta* gen. et sp. nov. has an extremely narrow pedicle area, as seen in the pedicle track. It is clear from the surface ornamentation that the pedicle area exists only within the pedicle track and does not reach a large depressed area. A similar morphology with a small pedicle foramen is abundant in Palaeozoic discinids,

such as *Acrosaccus* and *Orbiculoidea* (e.g., Holmer 1987; Mergl 2001; Masunaga and Shiino 2021), which may have a similar pedicle.

Morphology and adaptation capability of the pedicle-related structure.—Based on fossil occurrences, *Bronzoria recta* gen. et sp. nov. adopted a free-lying mode of life on muddy bottoms. This autecological property is similar to that of *Orbiculoidea* species such as *Orbiculoidea verum* Masunaga and Shiino, 2021. However, it has been suggested that most Mesozoic discinids were attached to hard substrates such as ammonite shells (Tate 1867; Boehm 1911; Seilacher 1982). Pedicle attachment to hard substrates such as shells and boulders is also common in extant discinids (e.g., LaBarbera 1985; Mergl 2010), which appears to contradict *Bronzoria recta* gen. et sp. nov. Understanding discinid adaptation requires examining the relationship between pedicle-related structures and the use of pedicles.

Extant *Discinisca* and *Discradisca* adopt a sessile mode of life by attaching with a thick, short pedicle onto a hard substrate (Emig 1997; Mergl 2010). Morphological observations of *Discradisca stella* revealed that the pedicle broadly covers a large depressed area, with the coated surface of the ventral valve exhibiting different ornamentation. This large depressed area accommodates a substantial amount of pedicle tissues as seen in pedicle area, ensuring a rigid attachment with no gap between the ventral valve and the substrate. In the present species, the ventral valve has no wide pedicle area but a narrow pedicle track, suggesting no feasibility for a sessile mode of life similar to extant discinids (Fig. 11).

In late Palaeozoic *Orbiculoidea*, the ventral valve typically has a narrow, long pedicle track with a pedicle foramen at the posterior end. The pedicle foramen, which is small (possibly less than a millimetre), suggests the presence of a thin, elongate pedicle. This pedicle indicates penetrating into firm but supple substrates and soft substrates, such as loose fine skeletal debris and mud, respectively (Mergl

2001; Masunaga and Shiino 2021). The direction of extension of the supposed pedicle may play a role in maintaining posture, even if the supposed pedicle is not as thick (Masunaga and Shiino 2021). Such a well-known relationship between the mode of life and the development of the pedicle track in *Orbiculoidea* fits the present conclusion that the present species adapted to soft substrates as a free-lying mode of life.

The narrow, long pedicle track is described in the other "*Discinisca*" from the Triassic and Jurassic (Fig. 10; see also SOM: table S1). Such type 1 morphology may reflect adaptation to soft substrates as a free-lying mode of life. In turn, discinids with type 2 ventral valves began to attach to ammonoid and bivalve shells from the Jurassic at the latest (Seilacher 1982). As a result, the morphology of a large depressed area would have been converted to host a larger volume of pedicle, making it possible for the animal to achieve a sessile mode of life, as observed in extant discinids (Fig. 11).

Acquisition and ecological significance of large depressed area.—Based on the morphological combination of pedicle-related structures, the type 1 ventral valve could be functional for the free-lying mode of life on soft substrates. A prime constraint of the free-lying mode of life is a narrow pedicle track (pedicle area). The supposed thickness of the pedicle shows a considerable degree of uniformity in its construction, regardless of the presence or absence of a large depressed area. However, the large depressed area is likely for functional pedicle attachment of the extant species of *Discinisca* and *Discradisca*, which provide a larger pedicle area and accommodate a thick pedicle between the ventral valve and the attachment substratum. This difference between the fossil and extant discinids suggests that the large depressed area may have evolved independently of the sessile mode of life.

Morphologically, the presence of a large depressed area alters the shell outline and convexity. The ventral valve of *Bronzoria* gen. nov. generally shows flat regions anteriorly and laterally, with the V-shaped large depressed area posteriorly, resulting in the formation of a concave valve. As the posterior space inside the shell is used as a storage of internal structures such as muscles and digestive tracts, the acquisition of the V-shaped large depressed area enables the reduction of the volume of the soft parts. This leads to the possibility that the oxygen consumption of *Bronzoria* gen. nov. was lower than that of the other discinids with no large depressed area, resulting in a lower metabolic rate.

The present review revealed that discinids bearing large depressed area persisted from the late Permian and thrived mainly in the Triassic (Fig. 10). Since the Guadalupian-Lopingian mass extinction event (Isozaki 1997), marine dysoxic-anoxic conditions have developed around the sea bottom, which lasted until the end of the Early Triassic (e.g., Hallam 1991; Twitchett and Wignall 1996; Chen et al. 2005; Dai et al. 2021). During this period, tolerance to poorly oxygenated conditions is required, as suggested previously (e.g., Twitchett et al. 2004). According to He et al. (2017), the end Permian to Early Triassic brachiopods in southern China decreased in size owing to anoxic, oligotrophic, and high-temperature environments. In addition to the decrease in size, a smaller amount of soft parts (by means of a large depressed area) could result from tolerance to an oxygen-poor environment. The present species *Bronzoria recta* gen. et sp. nov. was adapted to the dysoxic sea bottom as an opportunistic occurrence (Ishizaki and Shiino 2023b), which is consistent with the present interpretation.

In summary, the sedentary mode of life of discinids changed over time in response to changes in the benthic environment and related morphological evolution. First, Triassic-type discinids such as *Bronzoria* gen. nov., which enabled the reduction of soft parts, survived in the oxygen-poor environment of the end Permian to early Triassic owing to their lower metabolism. Subsequently, a large depressed area of the ventral valve could provide an extensive pedicle area, facilitating a robust attachment using pedicle, as seen in the extant discinids. In this scenario, the V-shaped large depressed area in *Bronzoria* gen. nov. is a trait of exaptation, leading to the hypothesis that the oxygen-poor environment of the Triassic resulted in the ecological innovation of discinids.

Remarks on the discinid diversity and evolution.—It is apparent that the acquisition of large depressed area results in the decrease of soft parts, possibly helping the adaptation to the oxygen-poor environment as discussed so far. From a morpho-functional viewpoint, the other discinid species with similar morphology to *Bronzoria* gen. nov. may also have the same adaptation capability, such as observed in Devonian discinids (e.g., a small, triangular depressed area of *Orbiculoidea tarda* [Barrande, 1879], in Mergl 2001: pl. 17: 4). However, the scenario is not so simply explained, as brachiopod morphology is designed to be a multi-functional body, which ensures consistency with any inferred autecological properties. There is a possibility to evolve similar morphology through entirely different pathways. In the case of a large depressed area, the concavity around the posterior part of the ventral valve enables not only the decrease of the amount of soft parts inside the shell but also the alteration of the direction of muscle contraction. Such a modification of the musculatory system has the potential for ecological differentiation (Shiino and Suzuki 2007; Masunaga and Shiino 2021), the hypothesis that has not yet been discussed.

Evolutionarily, a trait of exaptation exhibits a shift in function over time. If the habitat for discinids and its related environmental changes are closely similar, one would expect a corresponding pattern of morphological evolution. However, there is no evidence of ecological innovation as observed in *Bronzoria* gen. nov., even in species with similar morphology. The exaptation of a large depressed area would have caused unique environmental changes for *Bronzoria* gen. nov. that the Palaeozoic discinids have never experienced. Although we have no reliable methods to as-

certain evolutionary dynamic forces, careful examinations of morphology, ecology, environment, and their changes over time may provide plausible hypotheses to understand the evolution of discinids.

Conclusions

The current discinid brachiopod from the Lower Triassic Osawa Formation appears to exhibit a narrow pedicle track (listrium) and a V-shaped large depressed area, thus representing an intermediate form between *Orbiculoidea* and *Discinisca*. Based on these characteristics, we propose a new genus, *Bronzoria* gen. nov., which mainly includes discinids well-known from the Triassic. Morphological analysis of extant discinids revealed that the pedicle area consists of an arrowhead-shaped median plate and a pair of semilunar plates, which can be compared to the inner and outer listrial plates of Palaeozoic discinids, respectively. Based on the morphological relationship of pedicle-related structures, we hypothesised that the large depressed area has evolved regarding the tolerance of an oxygen-poor environment and has secondarily been diverted as a pedicle area, which provides a larger volume of pedicle with sufficient distance from the attachment site. The V-shaped large depressed area, as observed in *Bronzoria* gen. nov., is a case of exaptation for autecological innovation of the pedicle attachment mode of life.

Acknowledgements

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