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Devonian tabulate corals from pebbles in Mesozoic conglomerate, Kotaki, Niigata Prefecture, central Japan
Part 4: Auloporida

Shuji NIKO*, Yousuke IBARAKI** and Jun-ichi TAZAWA***

Abstract

As a fascicle of a serial work that describes tabulate corals in pebbles from the Kotaki area in Itoigawa, Niigata Prefecture, central Japan, this paper describes four Devonian species of auloporid tabulate corals, namely an auloporid *Aulopora chiharai* Niko, Ibaraki and Tazawa sp. nov., a palaeofavosiporid *Kanashiropora* sp. cf. *K. kozui* Niko, a syringoporid *Syringopora* sp. indet., and a multithecoporid *Syringoporella* sp. indet. *Aulopora chiharai* is distinguished from comparable species of the genus principally by its small corallite diameters and the possession of complete tabulae. *Kanashiropora* sp. cf. *K. kozui* represents the first record of the genus outside the type locality in the Fukuji area, Gifu Prefecture. *Aulopora chiharai, Syringopora* sp. indet., and *Syringoporella* sp. indet. are involved in stromatoporoids.

Key words: Devonian, auloporid tabulate corals, Kotaki area, Mesozoic conglomerate, *Aulopora chiharai* sp. nov.

Introduction

This paper is the fourth fascicle of a serial work on the Devonian tabulate coral fauna from the Kotaki area in Itoigawa, Niigata Prefecture, central Japan. This fauna is preserved in limestone and shale pebbles in a float block of conglomerate that most probably belongs

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to the Lower Jurassic Kuruma Group in the Hida-Gaien Belt (Niko et al., 2014). The present fascicle focuses into specimens of the order Auloporida. Their repository is the Fossa Magna Museum (abbreviation: FMM).

Systematic Paleontology

Subclass Tabulata Milne-Edwards and Haime, 1850
Order Auloporida Sokolov, 1947
Superfamily Auloporoidea Milne-Edwards and Haime, 1851
Family Auloporidae Milne-Edwards and Haime, 1851
Genus *Aulopora* Goldfuss, 1829

Type species.—Aulopora serpens Goldfuss, 1829.

Aulopora chiharai sp. nov.
Figs. 1-A–E

Etymology.—The specific name honors the late Dr. Kazuya Chihara in recognition of his contributions to the geology in the Hida-Gaien Belt.

Material.—Holotype, FMM6259, from which three thin sections were prepared. Six thin sections were studied from the three paratypes, FMM6260–6262. In addition, a single corallum, FMM6263, was also examined.

Diagnosis.—Species of *Aulopora* with coralla occurring inside stromatoporoids; corallite diameters small, 0.3–1.1 mm in proximal and 0.6–0.7 mm in distal portions; except for a levee-like projection at transposal portion of proximal-distal corallites, corallite walls mostly thin, 0.08–0.15 mm; septal spine absent; tabulae complete.

Description.—Coralla mat-like in growth form, occur inside stromatoporoids. Corallites small in diameter and uniserially arranged forming linear chains; anastomoses with adjoining corallites frequently developed; each corallite differentiated into adherent proximal and free distal portions; proximal corallites reptant, 1.0–1.8 mm in length, whose transverse sections are hemi-circular with relatively wide fringes in non-anastomosed corallites and sub-trapezoidal to rectangular in anastomosed corallites; diameters of proximal corallites are 0.3–1.1 mm; distal corallites cylindrical and upwardly directed with 100°–125° for proximal corallite; diameters of distal corallites are 0.6–0.7 mm; calical rims faintly inflated; calices very shallow; lumina (tabularia) subcircular in transverse section throughout all growth stages; daughter corallite arises near proximal-distal transposal portion of parent one. Corallite walls consist of epitheca and stereoplasm; wall thickness mostly thin, 0.08–0.15 mm, but it abruptly thickened on upper wall at transposal portion of proximal-distal corallites to form a levee-like projection, where wall thickness attains 0.33 mm; microstructure of

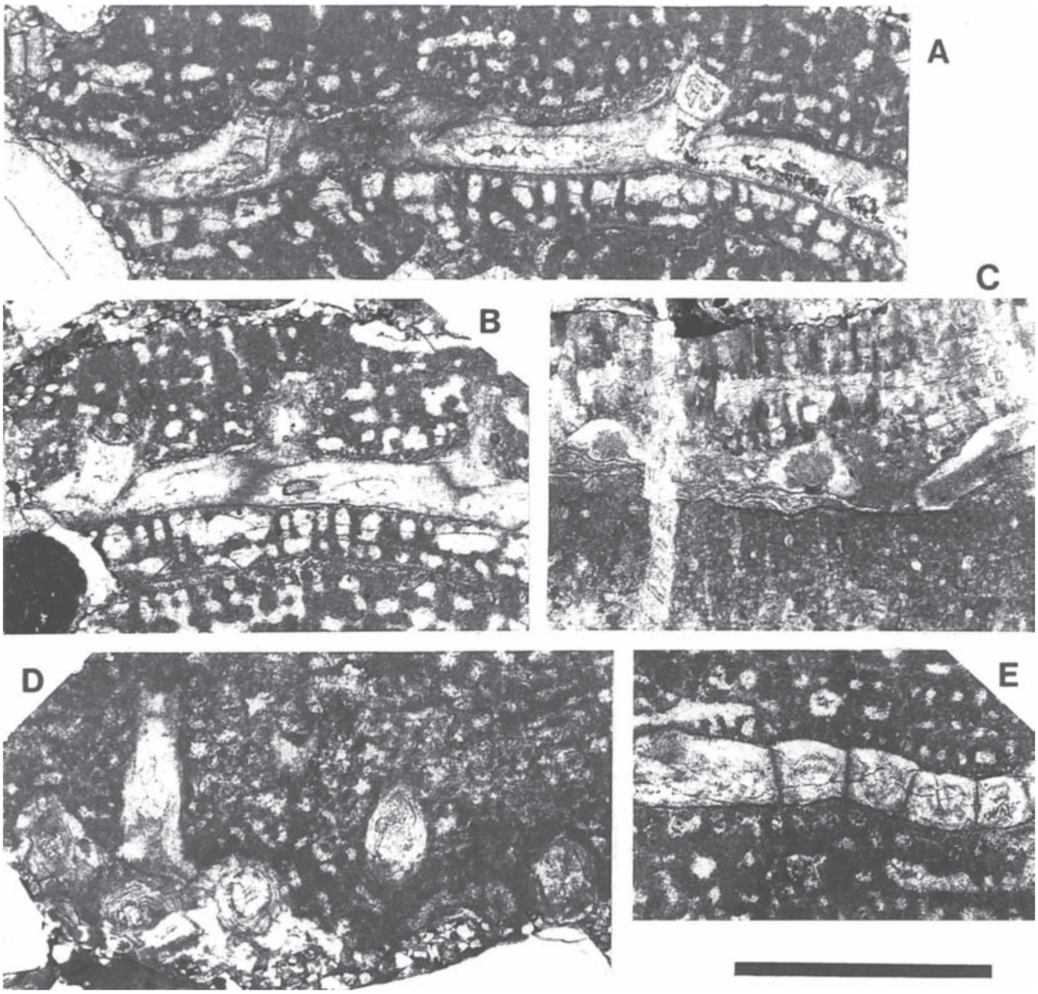

Fig. 1. *Aulopora chiharai* Niko, Ibaraki and Tazawa sp. nov., thin sections. **A, B**: holotype, FMM6259, longitudinal sections of corallites. **C**: paratype, FMM6261, transverse and longitudinal sections of non-anastomosed proximal corallites. **D**: paratype, FMM6260, longitudinal to transverse sections of distal corallites. **E**: paratype, FMM6262, transverse sections of anastomosed proximal corallites. Scale bar = 2.5 mm.

stereoplasm is not preserved; septal spine absent; tabulae rare in proximal and common in distal corallites, complete; profiles of tabulae vary from nearly flat to weakly concave proximally or distally; there are 2–4 tabulae in a single corallite.

Discussion.—The examined all specimens occur inside the skeletons of stromatoporoids. This fact indicates a possibility that there is a symbiotic relationship between them. Similar associations are also known in *Multithecopora* (Niko, 2001b; Niko and Senzai, 2006), *Syringopora* (i.e., Phillips, 1841; Stasińska, 1974; this report), *Syringopora*? (Mistiaen, 1984; Young and Noble, 1989; Young et al., 1991), and *Syringoporella* (i.e., Nowiński, 1992; Niko, 2001a; 2008; Zapalski, 2012; this report).

Aulopora chiharai sp. nov. is comparable with *A. mixta* Deng (1979, p. 158, pl. 3, fig. 4) and *A. sorasyamaensis* Niko (2001b, p. 74, 76, 77, figs. 1-1–7; 2-1–4; Niko and Senzai, 2006, p. 33, figs. 2-1–3). The former species described from the Middle Devonian Houershan Formation in Guizhou, South China. The latter species was named on the basis of specimens from the Lochkovian (lower Lower Devonian) Takaharagawa Member of the Fukuji Formation in the Fukuji area, Gifu Prefecture and subsequently discovered from the synchronous Oisedani Member in the Kamianama Formation in the Kuzuryu Lake-Ise River area, Fukui Prefecture. The new species is well differentiated from *A. mixta* and *A. sorasyamaensis* by its small corallite diameters and the possession of complete tabulae. In addition, these previously known species are not associated with stromatoporoids.

Family Palaeofavosiporidae Stasińska, 1976

Genus *Kanashiropora* Niko, 2001b

Type species.—*Kanashiropora kozui* Niko, 2001b.

Kanashiropora sp. cf. *K. kozui* Niko, 2001b

Figs. 2-A–C

Compare with:

Kanashiropora kozui Niko, 2001b, p. 82, 84, 86, figs. 5-1–5; 6-5, 6.

Material.—FMM6264, 6265. They were recovered from dark gray limestone pebbles.

Description.—Coralla phacelo-cerioid, probably massive. Corallites cylindrical in phaceloid and prismatic to subprismatic in cerioid portions. Transverse sections of corallites in cerioid portion are variable, indicating polygonal with 3–6 sides or sub-trapezoidal; corallite diameters 0.7–1.2 mm; no calice preserved. Walls thin to weakly thickened 0.10–0.19 mm in corallite and 0.19–0.44 mm in intercorallite walls; mural pores common, occur on corallite face, 0.17 mm in diameter; septal spine absent; tabulae uncommon, complete to rarely incomplete.

Discussion.—*Kanashiropora* was proposed by Niko (2001b) as a monotypic genus on the basis of a Lochkovian species, *K. kozui* Niko, 2001b, from the Takaharagawa Member. The present species from the Kotaki area is represented by two fragmentary specimens. Although their characters such as phacelo-cerioid coralla with mural pores and usually complete tabulae warrant the generic assignment, the available material is not complete to enough for a confident specific identification. This is the first record of *Kanashiropora* outside the type locality.

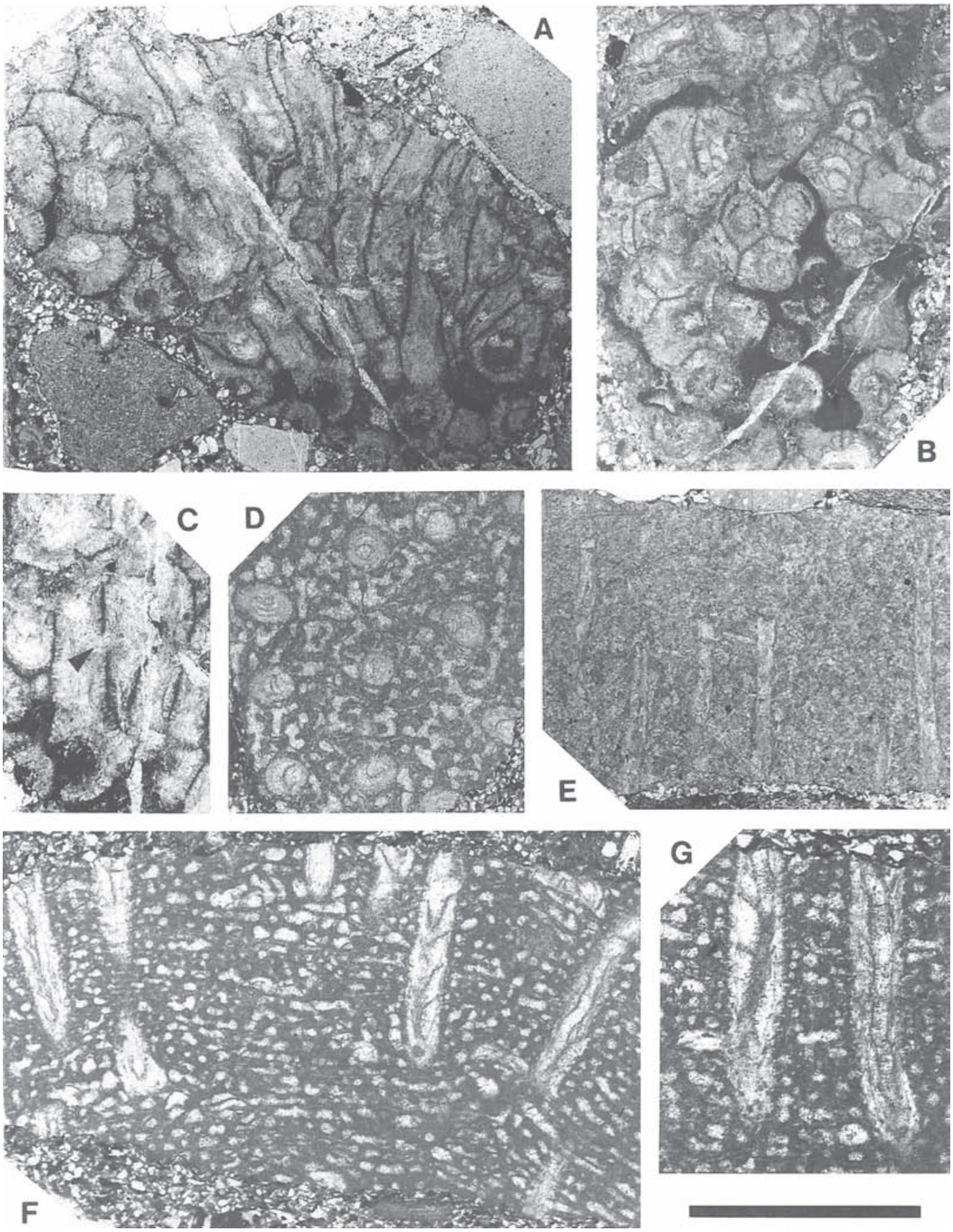

Fig. 2. **A–C**: *Kanashiropora* sp. cf. *K. kozui* Niko, 2001b, FMM6264, thin sections. A, longitudinal to transverse sections of corallites; B, transverse sections of corallites; C, partial enlargement of A, longitudinal sections of corallites, arrow indicates mural pore. **D, F, G**: *Syringopora* sp. indet., FMM6266, thin sections. D, transverse sections of corallites; F, G, longitudinal sections of corallites. **E**: *Syringoporella* sp. indet., FMM6272, thin longitudinal sections of corallites. Scale bar = 3.5 mm for A, B, D–F; 2.5 mm for C, G.

Superfamily Syringoporoidea Fromentel, 1861

Family Syringoporidae Fromentel, 1861

Genus *Syringopora* Goldfuss, 1826

Type species.—*Syringopora ramulosa* Goldfuss, 1826.

Syringopora sp. indet.

Figs. 2-D, F, G

Material.—FMM6266–6271. They were recovered from gray to milky white limestone pebbles composed almost entirely of skeletons of stromatoporoids.

Description.—Coralla phaceloid, occur inside stromatoporoids. Corallites cylindrical and narrow, 0.4–0.8 mm in diameter; connecting tubuli relatively rare, more than 0.9 mm in length; calice not preserved. Corallite walls thin to moderate, usually 0.04–0.19 mm in thickness; no apparent septal spine observable; tabulae well developed, infundibuliform forming relatively wide axial syrinx, whose diameter is approximately 26–38% of corresponding corallite diameter; horizontal diaphragms rarely recognized in syrinx.

Discussion.—The examined specimens refer to *Syringopora* rather than *Multithecopora* Yoh, 1927, *Syringoporella* Kettner, 1934, and *Syringoporinus* Sokolov, 1955, because of the possessions of infundibuliform tabulae and axial syrinx. The preservations of these specimens are not good enough to identify the species.

Family Multithecoporidae Sokolov, 1950

Genus *Syringoporella* Kettner, 1934

Type species.—*Syringopora moravica* Roemer, 1883.

Syringoporella sp. indet.

Fig. 2-E

Material.—FMM6272. It was recovered from gray limestone pebble composed almost entirely of skeletons of stromatoporoid.

Description.—Corallum phaceloid, occurs inside stromatoporoid. Corallites cylindrical and very narrow, 0.2–0.3 mm in diameter; connecting tubuli common, 0.4–0.7 mm in length; calical rims weakly inflated. Corallite walls thin, usually 0.04–0.08 mm; septal spine absent; tabulae rare, complete.

Discussion.—This fragmentary specimen is suggestive of *Syringoporella* but is not well preserved enough for a confident specific identification.

Acknowledgments

We would like to express our sincere gratitude to Mrs. Kanako Ito, who discovered examined tabulate corals herein and donated them to the Fossa Magna Museum. We also thank Drs. Atsushi Matsuoka and Isao Niikawa for their incisive reviews of an earlier version in this paper.

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Early Carboniferous (early Visean) brachiopod fauna from the middle part of the Arisu Formation in the Yokota area, South Kitakami Belt, Japan

Jun-ichi TAZAWA* and Yousuke IBARAKI**

Abstract

In this paper, we describe an early Carboniferous (early Visean) brachiopod fauna (the Odairayama fauna) from the middle part of the Arisu Formation in the Yokota area, South Kitakami Belt, northeastern Japan. The Odairayama fauna consists of six species in six genera: *Tomiproductus elegantulus, Marginatia burlingtonensis, Rhipidomella michelini, Cleiothyridina harkeri, Kitakamithyris hikoroitiensis* and *Asyrinxia nipponotrigonalis*. The age of the fauna is assigned to early Visean. Therefore, the middle part of the Arisu Formation is correlated with the lower Visean.

Key words: Arisu Formation, Brachiopoda, South Kitakami Belt, Visean, Yokota.

Introduction

Carboniferous rocks are well developed and exposed in the South Kitakami Belt, northeastern Japan. The Yokota area in the central part of the belt (i.e., Yokota-cho, Rikuzentakata City, Iwate Prefecture; Fig. 1) is a classical area for Carboniferous stratigraphy in Japan. Since the pioneering work of Minato (1941), the Carboniferous rocks in the Yokota area have been studied by Minato et al. (1953, 1979b), Saito (1966, 1968), Tazawa and Katayama (1979) and Kawamura (1985). Consequently, the Carboniferous strata in the Yokota area are classified into five formations, which are in ascending stratigraphic

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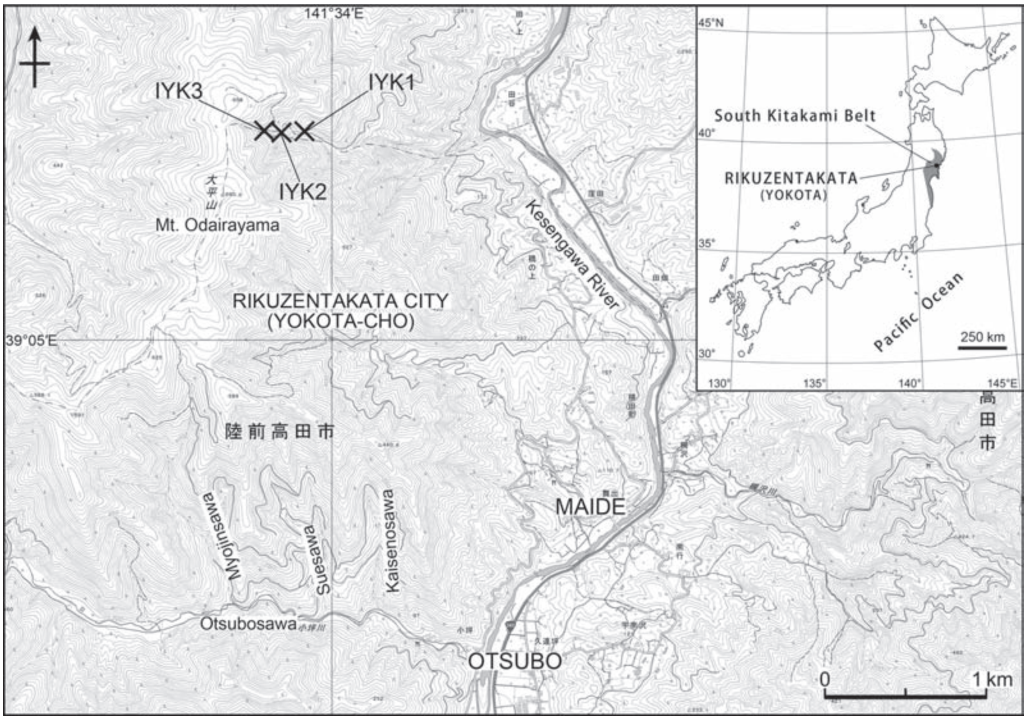

Fig. 1. Map showing the fossil localities IYK1, IYK2 and IYK3 at the northeastern slope of Mt. Odairayama in the Yokota area, South Kitakami Belt (using a digital topographic map of the Geospatial Information Authority of Japan).

order the Shittakazawa, Arisu, Odaira, Onimaru and Nagaiwa formations (Fig. 2). However, the ages of the lower three formations (Shittakazawa, Arisu and Odaira formations) are still uncertain, because of the lack of palaeontological data.

In the present study, we describe the brachiopods from the middle part of the Arisu Formation in the Yokota area, and discuss the age of the fossil fauna. The material was collected by Y. Ibaraki in 1996, in the course of his graduation thesis at the Department of Geology, Faculty of Science, Niigata University, under the supervision of J. Tazawa. The brachiopod specimens described herein are now registered and housed in the Faculty of Science, Niigata University, Niigata, Japan (prefix NU-B, numbers 2256 to 2265).

Stratigraphy and material

In the Yokota area, the Arisu Formation (330 m thick) is subdivided into a lower part (green to dark green andesitic lapilli tuff, 40 m thick), a middle part (sandstone with subordinate andesitic tuff and limestone, 260 m thick) and an upper part (black shale with a thin limestone bed in the topmost bed, 130 m thick). The brachiopod specimens were collected from dark grey fine-grained calcareous sandstone near (about 10 m below) the top

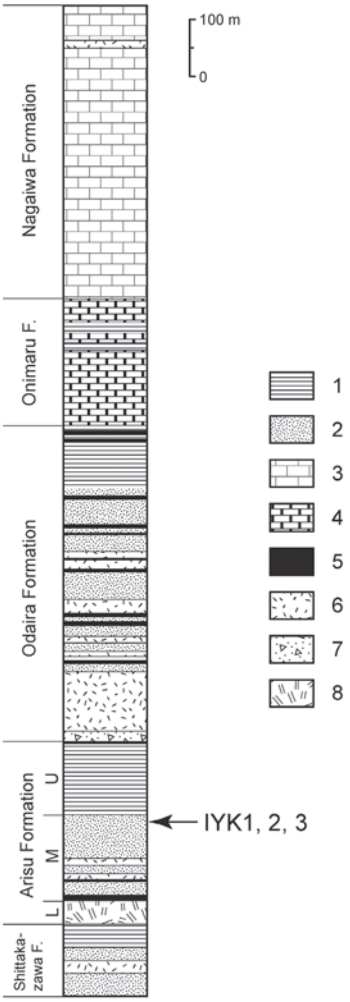

Fig. 2. Generalized columnar section of the Carboniferous formations in the Yokota area, showing the fossil horizons IYK1, IYK2 and IYK3 (adapted from Tazawa, 2017). L, lower part; M, middle part; U, upper part; 1, shale; 2, sandstone; 3, limestone of the Nagaiwa Formation; 4, limestone of the Onimaru Formation; 5, limestone of the Arisu and Odaira formations; 6, tuff, 7, tuff breccia; 8, lapilli tuff.

of the middle part of the Arisu Formation at three localities (IYK1, IYK2 and IYK3) on the northeastern slope of Mt. Odairayama in the Yokota area. The fossil horizon is equivalent to the E_0 Zone (Horizon) in unit Ⅲ of Minato et al. (1979b). The topographic and stratigraphic locations of the fossil localities and fossil contents are described below, and marked in Figs. 1 and 2.

IYK1: Northeastern slope of Mt. Odairayama (39°06′41″N, 141°33′53″E), dark grey calcareous sandstone, with *Tomiproductus elegantulus, Rhipidomella michelini* and *Kitakamithyris hikoroitiensis*.

IYK2: Northeastern slope of Mt. Odairayama (39°06′41″N, 141°33′47″E), dark grey calcareous sandstone, with *Tomiproductus elegantulus, Marginatia burlingtonensis* and *Cleiothyridina harkeri*.

IYK3: Northeastern slope of Mt. Odairayama (39°06′42″N, 141°33′42″E), dark grey calcareous sandstone, with *Marginatia burlingtonensis* and *Asyrinxia nipponotrigonalis*.

The Odairayama fauna

The brachiopod fauna described herein includes six species in six genera: *Tomiproductus elegantulus* (Tolmatchoff, 1924), *Marginatia burlingtonensis* (Hall, 1858), *Rhipidomella michelini* (Léveillé, 1835), *Cleiothyridina harkeri* Carter, 1987, *Kitakamithyris hikoroitiensis* Minato, 1951 and *Asyrinxia nipponotrigonalis* (Minato, 1951). The stratigraphic distribution of the brachiopod species of the fauna is summarized in Fig. 3.

Of the brachiopods listed above, *Tomiproductus elegantulus* is known from the lower Tournaisian to upper Visean (Sarytcheva et al., 1963; Nalivkin and Fotieva, 1973), *Marginatia burlingtonensis* from the upper Tournaisian to upper Visean (Weller, 1914; Tazawa, 2018c), *Rhipidomella michelini* from the upper Tournaisian to lower Bashkirian (Sarytcheva and Sokolskaya, 1952; Litvinovich et al., 1969; Tazawa, 2018c), *Cleiothyridina harkeri* from the upper Tournaisian to lower Visean (Abramov, 1970; Carter, 1987), *Kitakamithyris hikoroitiensis* from the upper Famennian to lower Visean (Tazawa, 2018b), and *Asyrinxia nipponotrigonalis* from the lower–upper Visean (Tazawa, 2018a). In summary, the age of the Odairayama fauna is identified as early Visean.

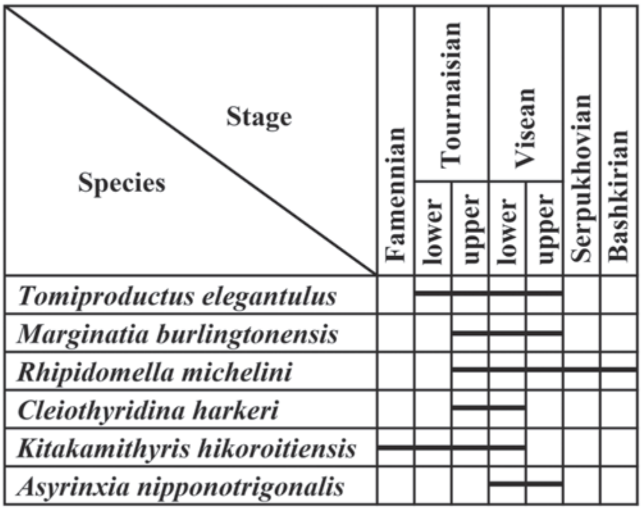

Fig. 3. Stratigraphic distributions of brachiopod species of the Odairayama fauna.

Discussion

Regarding the age of the Arisu Formation, Minato et al. (1953) proposed that unit Ⅲ (= middle and upper parts) of the Arisu Formation correlates with the upper Tournaisian of Europe and the Osagean of the USA, based on the abundant occurrence of *Syringothyris* in the D_0 Zone (lower part of unit Ⅲ). Minato and Kato (1979) later regarded the age of the Arisu Formation as late Tournaisian on the basis of brachiopods (*Syringothyris* spp., *Spirifer kozuboensis* and "*Athyris*" *lamellosa*), a crinoid (*Platycrinus asiaticus*) and a blastoid (*Nymphaeoblastus anossofi*) from the D_0 Zone. Tazawa (1985) considered that the upper part of the Arisu Formation correlates in lithology with the upper part of the lower Hikoroichi Formation of the Hikoroichi area (about 7 km east of the Yokota area); the latter is assigned to early Visean in age on the basis of the occurrence of a brachiopod (*Linoprotonia* sp). In the present study, the age of the middle part of the Arisu Formation is concluded to be early Visean, although the ages of the lower and upper parts of the Arisu Formation are uncertain.

Systematic descriptions

Order Productida Sarytcheva and Sokolskaya, 1959
Suborder Productidina Waagen, 1883
Superfamily Productoidea Gray, 1840
Family Buxtoniidae Muir-Wood and Cooper, 1960
Subfamily Buxtoniinae Muir-Wood and Cooper, 1960
Genus *Tomiproductus* Sarytcheva in Sarytcheva, Sololskaya, Besnossova and Maksimova, 1963

Type species.—*Productus elegantulus* Tolmatchoff, 1924.

Tomiproductus elegantulus (Tolmatchoff, 1924)
Fig. 4A

Productus elegantulus Tolmatchoff, 1924, p. 244, 579, pl. 14, figs. 5–7.
Tomiproductus elegantulus (Tolmatchoff). Sarytcheva in Sarytcheva et al., 1963, p. 202, pl. 31, figs. 1–11; pl. 32, figs. 1–7, text-figs. 88, 89; Nalivkin and Fotieva, 1973, p. 42, pl. 8, figs. 12, 13; Kalashnikov, 1974, p. 55, pl. 13, fig. 6; Bublichenko, 1976, p. 54, pl. 3, fig. 9; pl. 5, figs. 1, 2.

Material.—Two specimens from localities IYK1 and IYK2, internal moulds of two ventral valves, NU-B2262, 2263.

Remarks.—These specimens are referred to *Tomiproductus elegantulus* (Tolmatchoff, 1924), redescribed by Sarytcheva in Sarytcheva et al. (1963, p. 202, pl. 31, figs. 1–11; pl. 32, figs. 1–7, text-figs, 88, 89) from the lower–upper Tournaisian of the Kuznetsk Basin, central Russia, in the small size (length 20 mm, width 22 mm in the larger specimen, NU-B2262), strongly inflated ventral valve with a long trail, numerous fine costellae on entire surface of the ventral valve (numbering 10–12 in 5 mm on ventral trail) and weak concentric rugae on the ventral disc. *Tomiproductus minimus* (Demanet, 1921), redescribed by Nalivkin (1979, p. 91, pl. 13, fig. 26; pl. 31, figs. 1–11) from the upper Tournaisian–middle Visean of the northern Urals, is also a small-sized *Tomiproductus*, but it differs from *T. elegantulus* in having stronger rugae on the ventral trail. *Tomiproductus kollari* Carter (1990, p. 224, figs. 3.1–3.14), from the middle–upper Keokuk Limestone of Missouri, USA, differs from *T. elegantulus* in the larger size and coarser rugae on the ventral trail.

Distribution.—Lower Tournaisian–upper Visean: northeastern Japan (Yokota in the South Kitakami Belt), northern Russia (Pechora Basin), central Russia (western Urals and Kuznetsk Basin) and Kazakhstan (Altay Mountains).

Subfamily Marginatiinae Waterhouse, 2002

Genus *Marginatia* Muir-Wood and Cooper, 1960

Type species.—*Productus fernglenensis* Weller, 1909.

Marginatia burlingtonensis (Hall, 1858)

Figs. 4C, D

Productus flemingi var. *burlingtonensis* Hall, 1858, p. 598, pl. 12, fig. 3.

Productus burlingtonensis Hall. Weller, 1914, p. 104, pl. 9, figs. 1–10; Frech, 1916, p. 239, pl. 6, fig. 1; Tolmatchoff, 1924, p. 237, 575, pl. 14, figs. 8–11; Girty, 1929, p. 85, pl. 9, figs. 20–24.

Productus (*Productus*) *burlingtonensis* Hall. Nalivkin, 1937, p. 66, pl. 7, figs. 7–11.

Productus sp. Minato, 1951, p. 366, pl. 1, fig. 4.

Productus (*Dictyoclostus*) *burlingtonensis* Hall. Simorin, 1956, p. 136, pl. 9, figs. 1–3.

Marginatia burlingtonensis (Hall). Sarytcheva in Sarytcheva et al., 1963, p. 191, pl. 28, figs. 5–8, text-figs. 81, 82; Grechishnikova, 1966, p. 116, pl. 8, figs. 11–13; Litvinovich in Litvinovich et al., 1969, p. 213, pl. 35, figs. 2–4; Nalivkin and Fotieva, 1973, p. 39, pl. 8, fig. 1; Bublichenko, 1976, p. 50, pl. 2, fig. 12; pl. 4, fig. 6; pl. 5, figs. 4–6; pl. 6, fig. 9; Galitskaya, 1977, p. 83, pl. 22, figs. 6–10; Nalivkin, 1979, p. 94, pl. 32, figs. 1–10; pl. 34, figs. 3, 4; Lee et al., 1980, p. 368, pl. 148, fig. 10; Jin, 1985, p. 77, pl. 1, figs. 20–22; Carter, 1987, p. 39, pl. 9, figs. 1–8; Shi et al., 2005, p. 44, figs. 5D, I–K, M; Tazawa, 2006, p. 132, figs. 6.1–6.8; Tazawa, 2017, p. 335, figs. 6.3–6.5; Tazawa, 2018c, p. 44, fig. 23A–D.

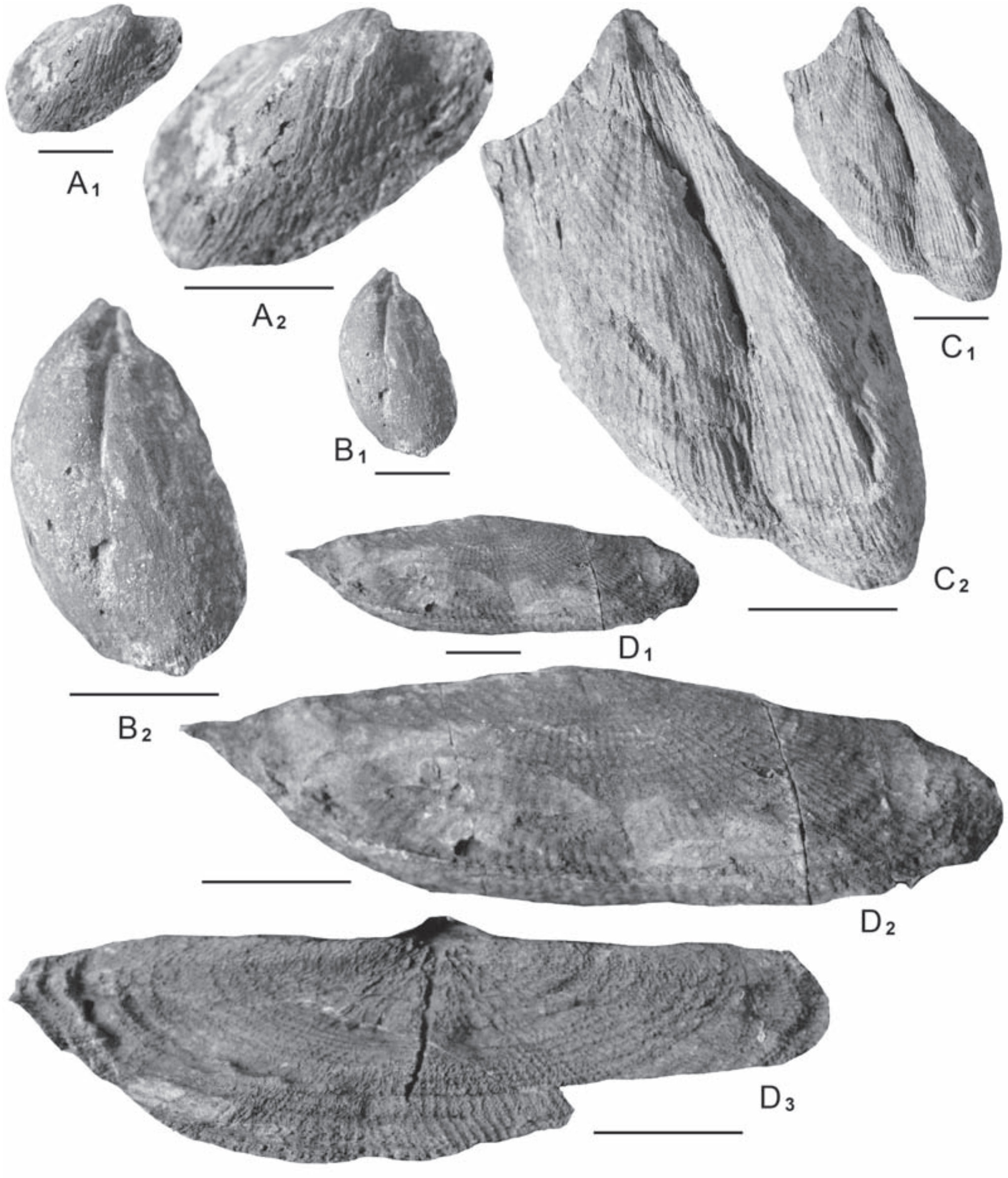

Fig. 4. Brachiopods of the Odairayama fauna (1). **A,** *Tomiproductus elegantulus* (Tolmatchoff), internal mould (A1, A2) of ventral valve, NU-B2262; **B,** *Rhipidomella michelini* (Léveillé), internal mould (B1, B2) of dorsal valve, NU-B2256; **C, D,** *Marginatia burlingtonensis* (Hall); internal mould (C1, C2) of ventral valve, NU-B2258; external mould (D1, D2) and internal mould (D3) of dorsal valve, NU-B2260. Scale bars are 1 cm.

Dictyoclostus sp. Hase and Yokoyama, 1975, pl. 18, fig. 1.

Marginatia sp. Tazawa, 1985, p. 459, figs. 2.3–2.7; Tazawa, 1989, p. 60, pl. 1, fig. 1; Tazawa, 2002, figs. 7.1, 7.2.

Material.—Four specimens from localities IYK2 and IYK3: (1) internal moulds of two ventral valves, NU-B2258, 2259; (2) external and internal moulds of a dorsal valve, NU-B2260; and (3) external mould of a dorsal valve, NU-B2261.

Remarks.—These specimens are more or less squashed, but can be referred to *Marginatia burlingtonensis* (Hall, 1858), redescribed by Weller (1914, p. 104, pl. 9, figs. 1–10) from the Burlington Limestone of the Mississippi Valley, USA, on the basis of the medium-sized (length 42 mm, width 24 mm in the best preserved ventral valve specimen, NU-B2258; length 22 mm, width 62 mm in the largest dorsal valve specimen, NU-B2261) and strongly geniculated both ventral and dorsal valves, with regular and strong reticulate ornament on the visceral disc of the dorsal valve. *Marginatia patersonensis* Roberts (1965, p. 63, pl. 10, figs. 1–5), from the lower and upper Visean of New South Wales, eastern Australia, differs from the present species in having finer costae and larger number of spines on the ventral valve. The type species, *Marginatia fernglenensis* Weller (1909, p. 299, pl. 12, figs. 14–17) from the Fern Glen Formation of Missouri, differs from *M. burlingtonensis* in having shallower ventral sulcus.

Distribution.—Upper Tournaisian–upper Visean: northeastern Japan (Hikoroichi and Yokota in the South Kitakami Belt), southwestern Japan (Hina in the Akiyoshi Belt), USA (Illinois, Iowa and Arkansas), western Canada (Alberta), Turkey (Taurus Mountains), central Russia (southern Urals and Kuznetsk Basin), Kazakhstan, Kyrgyzstan and northeastern China (Liaoning).

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

Type species.—*Terebratula michelini* Léveillé, 1835.

Rhipidomella michelini (Léveillé, 1835)
Fig. 4B

Terebratula michelini Léveillé, 1835, p. 39, pl. 2, figs. 14–17.

Orthis michelini (Léveillé). Davidson, 1861, p. 132, pl. 30, figs. 6–12.

Dalmanella michelini (Léveillé). Frech, 1900, p. 201, pl. 16, fig. 15.

Rhipidomella michelini (Léveillé). Rotai, 1931, p. 44, pl. 1, fig. 3; Demanet, 1934, p. 37, pl. 2, figs. 1–9; Sarytcheva in Sarytcheva and Sokolskaya, 1952, p. 26, pl. 1, fig. 7; Litvinovich, 1962, p. 177, pl. 1, fig. 1; Zang in Yang et al., 1962, p. 19, pl. 1, figs. 1–7; Ustritsky and Tschernjak, 1963, p. 68, pl. 1, figs. 11, 12; Yang, 1964, p. 58, pl. 1, fig. 1; Brunton, 1968, p. 17, pl. 3, figs. 1–25, text-fig. 5; Litvinovich in Litvinovich et al., 1969, p. 127, pl. 1, figs. 9, 10; Bublichenko, 1971, p. 29, pl. 2, figs. 9–12; Alexandrov and Solomina, 1973, p. 87, pl. 21, fig. 1; Kalashnikov, 1974, p. 21, pl. 3, figs. 7–9; Volgin and Kushnar, 1975, p. 21, pl. 1, figs. 1, 2; Lee and Gu, 1976, p. 231, pl. 131, figs. 1–6; Martinez Chacon, 1979, p. 63, pl. 3, figs. 12–15; pl. 4, figs. 1–15, text-figs. 6, 7; Lee et al., 1980, p. 330, pl. 145, fig. 4; Ding and Qi, 1983, p. 250, pl. 88, fig. 13; Zakowa, 1989, p. 115, pl. 3, fig. 5; pl. 7, fig. 7; Harper and Jeffrey, 1996, fig. 3a; Legrand-Blain in Legrand-Blain et al., 1996, p. 180, pl. 28, figs. 21, 22; Jiang, 1997, pl. 1, fig. 3; Bassett and Bryant, 2006, p. 502, pl. 1, figs. 1–4; pl. 6, figs. 11–17; Sun and Baliński, 2008, p. 519, fig. 26; Tazawa, 2018c, p. 52, figs. 26A–C, 30G.

Rhipidomella sp. Tazawa and Katayama, 1979, p. 170, pl. 11, figs. 1–7; Mori and Tazawa, 1980, text-figs. 3.4–3.6; Tazawa, 1984, p. 305, pl. 61, figs. 5–7.

Material.—One specimen from locality IYK1, internal mould of a dorsal valve, NU-B2256.

Remarks.—This specimen resembles the shells, described by Tazawa (2018c, p. 52, figs. 26A–C, 30G) as *Rhipidomella michelini* (Léveillé, 1835) from the middle and upper parts of the Hikoroichi Formation in the Hikoroichi area, South Kitakami Belt, in size, outline and internal structure of the dorsal valve. *Rhipidomella michelini* (Léveillé, 1835) is characterized by having a short hinge line and the widest part of shell at slightly anterior to midlength. *Rhipidomella altaica* Tolmatchoff (1924, p. 213, 569, pl. 13, figs. 5–7, 9, 10), from the Tournaisian of the Kuznetsk Basin, central Russia, differs from *R. michelini* in having longer hinge and the widest part at midlength of the shell.

Distribution.—Upper Tournaisian–lower Bashkirian: northeastern Japan (Hikoroichi, Shimoarisu and Yokota in the South Kitakami Belt), northern Russia (Taimyr Peninsula and Pechora Basin), UK (England, Wales and northern Ireland), Ireland, Poland, Belgium, France (French Pyrenees), Spain (Cantabrian Mountains), western Russia (Moscow Basin and Donetz Basin), Iran, central Russia (southern Urals), Kazakhstan, Uzbekistan, northwestern China (Xinjiang, Qinghai, Gansu and Ningxia), northern China (Inner Mongolia), northeastern China (Liaoning) and southwestern China (Guizhou and Yunnan).

Order Athyridida Boucot, Johnson and Staton, 1964

Suborder Athyrididina Boucot, Johnson and Staton, 1964

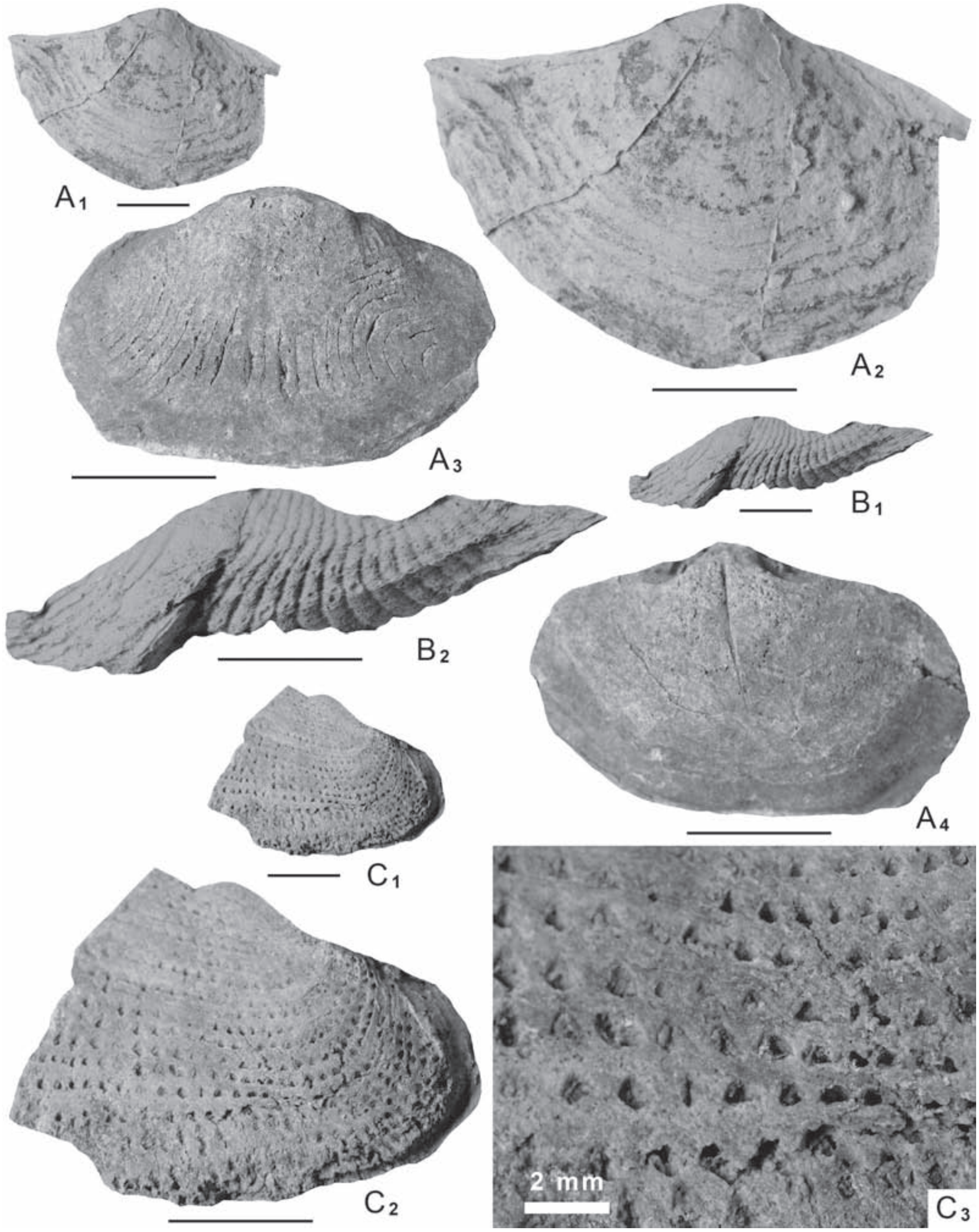

Fig. 5. Brachiopods of the Odairayama fauna (2). **A,** *Cleiothyridina harkeri* Carter, external latex cast (A_1, A_2) and internal mould (A_4) of dorsal valve, and internal mould (A_3) of ventral valve of conjoined shell, NU-B2265; **B,** *Asyrinxia nipponotrigonalis* (Minato), external latex cast (B_1, B_2) of dorsal valve, NU-B2264; **C,** *Kitakamithyris hikoroitiensis* Minato, external mould (C_1, C_2) of valve (ventral or dorsal uncertain), and enlarged one (C_3) showing biramose spine bases, NU-B2257. Scale bars are 1 cm, except for C_3.

Superfamily Athyridoidea Davidson, 1881
Family Athyrididae Davidson, 1881
Subfamily Cleiothyridininae Alvarez, Rong and Boucot, 1998
Genus *Cleiothyridina* Buckman, 1906

Type species.—*Atrypa pectinifera* Sowerby, 1840.

Cleiothyridina harkeri Carter, 1987
Fig. 5A

Cleiothyridina obmaxima (McChesney)? Nelson, 1961, pl. 4, figs. 5, 6; pl. 7, fig. 14; Abramov and Grigorjeva, 1986, pl. 15, figs. 17, 18.

Cleiothyridina obmaxima (McChesney). Abramov, 1970, p. 157, pl. 38, figs. 1–3.

Cleiothyridina harkeri Carter, 1987, p. 60, pl. 19, figs. 24–27.

Material.—One specimen from locality IYK2, internal mould of a conjoined shell, with external mould of the dorsal valve, NU-B2265.

Remarks.—This specimen can be referred to *Cleiothyridina harkeri* Carter, 1987, described by Carter (1987, p. 60, pl. 19, figs. 24–27) from the upper part of the Banff Formation of western Alberta, Canada, by the large, transverse shell (length about 25 mm, width about 36 mm), weakly uniplicate anterior commissure with shallow ventral sulcus and low dorsal fold, and external ornament consisting of numerous dense growth lamellae. *Cleiothyridina obmaxima* (McChesney), redescribed by Weller (1914, p. 475, pl. 79, figs. 1–11) from the Keokuk and Burlington formations of the Mississippi Valley, is also a large, transverse *Cleiothyridina,* but the American species differs from *C. harkeri* in having well developed sulcus and fold.

Distribution.—Upper Tournaisian–lower Visean: northeastern Japan (Yokota in the South Kitakami Belt), western Canada (Alberta) and northern Russia (Verkhoyansk Range).

Order Spiriferida Waagen, 1883
Suborder Delthyridina Ivanova, 1972
Superfamily Reticularioidea Waagen, 1883
Family Elythidae Fredericks, 1924
Subfamily Elythinae Fredericks, 1924
Genus *Kitakamithyris* Minato, 1951

Type species.—*Torynifer* (*Kitakamithyris*) *tyoanjiensis* Minato, 1951.

Kitakamithyris hikoroitiensis Minato, 1951
Fig. 5C

Torynifer (*Kitakamithyris*) *hikoroitiensis* Minato, 1951, p. 375, pl. 1, fig. 1.

Kitakamithyris hikoroitiensis Minato, 1952, p. 171, pl. 7, fig. 3; pl. 8, fig. 6; Minato et al., 1979a, pl. 16, fig. 1; Tazawa, 2018b, p 141, figs. 10E, 11B; Tazawa, 2018c, p. 72, figs. 20B, C, 21B, 29A, B.

Kitakamithyris semicircularis Minato, 1952, p. 171, pl. 7, fig. 6; pl. 8, fig. 5; pl. 10, fig. 3; Minato et al., 1979a, pl. 15, fig. 1.

Material.—One specimen from locality IYK1, external mould of a valve (ventral or dorsal uncertain), NU-B2257.

Remarks.—This specimen can be referred to *Kitakamithyris hikoroitiensis* Minato (1951), redescribed by Tazawa (2018b, p. 141, figs. 10E, 11B) from the upper part of the Choanji Formation (upper Famennian) at Choanji, by size, shape and external ornament of the shell, particularly in having large and sporadically arranged biramose spine bases (numbering 4–5 in 5 mm) on the valve. *Kitakamithyris semicircularis* Minato (1952, p. 171, pl. 7, fig. 6; pl. 8, fig. 5; pl. 10, fig. 3), from the Choanji and Arisu formations of the South Kitakami Belt, is deemed a junior synonym of *K. hikoroitiensis.* The type species, *Kitakamithyris tyoanjiensis* Minato, 1951, is readily distinguished from the present species by the smaller and densely arranged spine bases on the both valves.

Distribution.—Upper Devonian (upper Famennian)–lower Visean: northeastern Japan (Choanji, Hikoroichi, Yokota and Shimoarisu in the South Kitakami Belt).

Order Spiriferinida Ivanova, 1972
Suborder Spiriferinidina Ivanova, 1972
Superfamily Syringothyridoidea Fredericks, 1926
Family Syringothyrididae Fredericks, 1926
Subfamily Permasyrinxinae Waterhouse, 1986
Genus *Asyrinxia* Campbell, 1957

Type species.—*Spirifera lata* M'Coy, 1847.

Asyrinxia nipponotrigonalis (Minato, 1951)
Fig. 5B

Fusella nipponotrigonalis Minato, 1951, p. 372, pl. 2, fig. 5; Minato, 1952, p. 160, pl. 5, fig. 1; pl. 6, fig. 6; pl. 11, fig. 3; Minato et al., 1979a, pl. 22, fig. 4.

Fusella nipponotrigonalis var. *minor* Minato, 1952, p. 160, pl. 6, fig. 3.
Asyrinxia sp. Tazawa, 1981, p. 74, pl. 5, fig. 14.
Asyrinxia nipponotrigonalis (Minato). Tazawa, 2018a, p. 4, figs. 3.1, 3.2.

Material.—One specimen from locality IYK3, external mould of a dorsal valve, NU-B2264.

Remarks.—The single dorsal valve specimen from Yokota is medium in size (length 16 mm, width about 50 mm), transverse outline with alate cardinal extremities, moderately and unevenly convex in lateral profile, having a high smooth fold, and ornamented with numerous rounded simple costae (numbering 5–6 in 10 mm at anterior margin), some strong concentric rugae, and very fine concentric lamellae on the lateral slopes. This specimen resembles well the specimen (UHR16227), described by Minato (1952, p. 160, pl. 6, fig. 3) as *Fusella nipponotrigonalis* var. *minor* Minato, 1952 from the Jumonji Stage (= middle part of the Arisu Formation) and the Maide Stage (= middle part of the Odaira Formation) of the Yokota area, South Kitakami Belt, in size, shape and external ornament of the dorsal valve. *Fusella nipponotrigonalis* var. *minor* is deemed to be a synonym of *Fusella nipponotrigonalis* Minato (1951, p. 372, pl. 2, fig. 5), from the Jumonji Stage of the Shimoarisu and Yokota areas, South Kitakami Belt; and the latter is assigned to the genus *Asyrinxia* by Tazawa (2018a, p. 4).

Distribution.—Lower–upper Visean: northeastern Japan (Shimoarisu, Yokota and Nisawa in the South Kitakami Belt).

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Early Permian (Artinskian) brachiopods from the Ryozensan area, Mino Belt, southwestern Japan

Jun-ichi TAZAWA* and Kazuhisa OYAGI**

Abstract

A brachiopod fauna (the Ryozensan fauna), consisting of seven species in six genera, is described from the upper part of the Ryozensan Formation (Artinskian; *Pseudofusulina* Zone) in the Ryozensan area, northern Suzuka Mountains, Mino Belt, southwestern Japan. The brachiopods of the fauna are as follows: *Echinauris* sp., *Meekella* sp., *Enteletes stehlii* Cooper and Grant, *Acosarina rectimarginata* Cooper and Grant, *Acosarina* cf. *dunbari* Cooper and Grant, *Neospirifer* sp. and *Plectelasma* sp. Palaeobiogeographically, the Ryozensan fauna has a close affinity with the lower Permian brachiopod faunas of Kuzu, Kiryu and Hatahoko in the Mino Belt, Japan and West Texas, USA.

Key words: Brachiopoda, Permian, Mino Belt, Ryozensan, Japan.

Introduction

The Ryozensan area in the northern Suzuka Mountains, Mino Belt, southwestern Japan is famous for a Permian large limestone block and its karst topography. The stratigraphy of the Permian rocks in the Ryozensan area has been studied by Miyamura (1973), Miyamura et al. (1976), Harayama et al. (1989), Yamagata (2000) and Sano and Kojima (2000). Consequently, the Permian rocks, named as the Ryozensan Formation, are recognized as an early Permian (Sakmarian–Artinskian) limestone-basalt block (500–600 m thick) in a Jurassic accretionary complex, the Mino Belt. The limestone contains various fossils of marine

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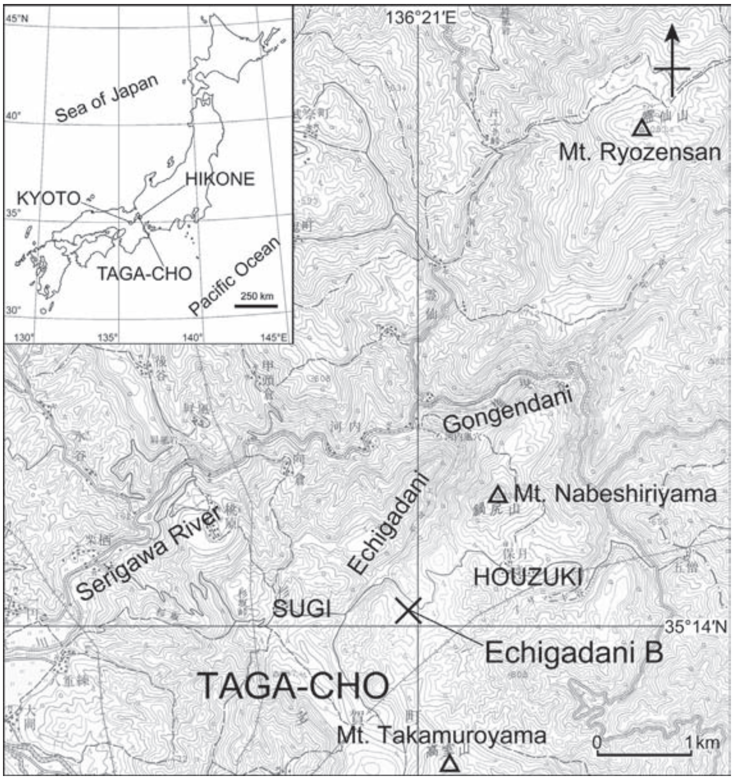

Fig. 1. Map showing the fossil locality Echigadani B in the Ryozensan area, Mino Belt, southwestern Japan (using the topographical map of "East Hikone" scale 1: 50,000 published by the Geospatial Information Authority of Japan).

invertebrates, such as fusulinids, corals, bryozoans, brachiopods, bivalves, gastropods, ammonoids, trilobites and crinoids (Oyagi, 1991). However, palaeontological studies on the fauna are poor. Only some fusulinids (Kobayashi and Furutani, 2009) and one species of trilobite (Kobayashi and Hamada, 1980) have been described until now. In the present paper, we describe a brachiopod fauna, consisting of seven species in six genera, from the upper part of the Ryozensan Formation (*Pseudofusulina* Zone). This is the first systematic study on the brachiopods of the Ryozensan Formation.

Material

The brachiopod specimens were collected by K. Oyagi from grey to dark grey limestone and light brown tuffaceous limestone of the Ryozensan Formation at locality Echigadani B (35°14′05″N, 136°20′56″E), upper Echigadani Valley, a tributary of the Serigawa River, 1 km SW of Houzuki, Taga-cho, Inukami-Gun, Shiga Prefecture, southwestern Japan (Fig. 1). The limestone blocks in the Sugi–Houzuki–Takamuroyama area, including the locality

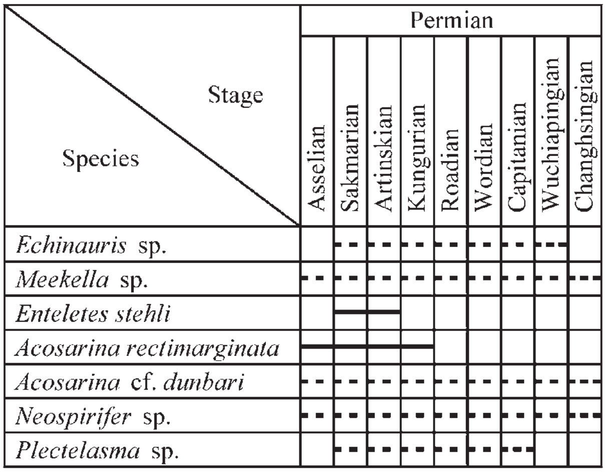

Fig. 2. Stratigraphic distribution of brachiopod species of the Ryozensan fauna. Broken line shows range of the genus.

Echigadani B, belong to the *Pseudofusulina* Zone, which is characterized by the occurrence of *Pseudofusulina vulgaris, P. krotowi, P. norikuraensis* and *P. kraffti* (Miyamura et al., 1976), and is assigned to the Artinskian in age (Sano and Kojima, 2000). The material was studied and described by J. Tazawa; and stored in the Taga Town Museum, Taga-cho, Shiga Prefecture, Japan (prefix TG-Inv, numbers 1064 to 1099).

The Ryozensan fauna

In this study, seven species in six genera are described from the upper part of the Ryozensan Formation of Echigadani, Ryozensan area. The species are as follows: *Echinauris* sp., *Meekella* sp., *Enteletes stehlii* Cooper and Grant, 1976, *Acosarina rectimarginata* Cooper and Grant, 1976, *Acosarina* cf. *dunbari* Cooper and Grant, 1976, *Neospirifer* sp. and *Plectelasma* sp.

Age

The stratigraphic distribution of the brachiopod species of the Ryozensan fauna is summarized in Fig. 2. Of the brachiopods listed above, *Enteletes stehlii* is known from the Sakmarian and Artinskian (Stehli, 1954; Cooper and Grant, 1976), and *Acosarina rectimarginata* from the Asselian to Kungurian (Cooper and Grant, 1976; Shen et al., 2011; Tazawa in Tazawa et al., 2012a). The other five species are uncertain for their species. However, at generic level, *Echinauris* is known from the Sakmarian to Wuchiapingian (Brunton et al., 2000), and *Plectelasma* from the Sakmarian to Capitanian (Cooper and Grant, 1976). Three genera (*Meekella, Acosarina* and *Neospirifer*) are long-ranging: *Meekella* occurs from the lower Carboniferous–upper Permian (Williams and Brunton, 2000), *Acosarina* from the upper Carboniferous–upper Permian (Harper, 2000), and *Neospirifer* from the lower–upper Permian (Carter, 2006). In summary, the age of the Ryozensan fauna is identified as Sakmarian–Artinskian. This conclusion is consistent with that of Sano and Kojima (2000), who considered the age of the upper part of the Ryozensan Formation to be Artinskian on the basis of the fusulinids listed by Miyamura (1973) and Miyamura et al. (1976).

Palaeobiogeography

In terms of palaeobiogeography, *Enteletes stehlii* is found from the Sakmarian–Kungurian of southwestern Japan (Hachiman in the Mino Belt) and West Texas, USA (see the distribution of this species in the chapter "Systematic descriptions"). *Acosarina rectimarginata* is found from the Asselian–Kungurian of central Japan (Kuzu and Hatahoko in the Mino Belt) and West Texas. *Echinauris* sp. resembles *Echinauris lateralis,* which is found from the Kungurian–Wordian of central Japan (Kiryu and Kuzu in the Mino Belt) and West Texas. *Meekella* sp. resembles *Meekella bisculpta,* from the Artinskian of Ko Muk, southern Thailand. *Acosarina* cf. *dunbari* resembles *Acosarina dunbari,* from the lower Wolfcampian of Nebraska, USA. *Neospirifer* sp. resembles *Neospirifer placidus,* from the lower Wolfcampian of West Texas. *Plectelasma* sp. resembles *Plectelasma kingi*, from the Wolfcampian of West Texas. Consequently, the Ryozensan fauna has a close affinity with the lower Permian brachiopod faunas of Kuzu, Kiryu and Hatahoko in the Mino Belt, Japan and West Texas, USA. This conclusion is consistent with those of Tazawa and Shen (1997), Shen et al. (2011) and Tazawa et al. (1998, 2013, 2016), who reported that the Permian brachiopod faunas of the Mino Belt are tropical faunas of the equatorial Panthalassa, not far from North America (West Texas).

Systematic descriptions

Order Productida Sarytcheva and Sokolskaya, 1959
Suborder Productidina Waagen, 1883
Superfamily Marginiferoidea Stehli, 1954
Family Costispiniferidae Muir-Wood and Cooper, 1960
Subfamily Costispiniferinae Muir-Wood and Cooper, 1960
Genus *Echinauris* Muir-Wood and Cooper, 1960

Type species.—*Echinauris lateralis* Muir-Wood and Cooper, 1960.

Echinauris sp.
Fig. 3A

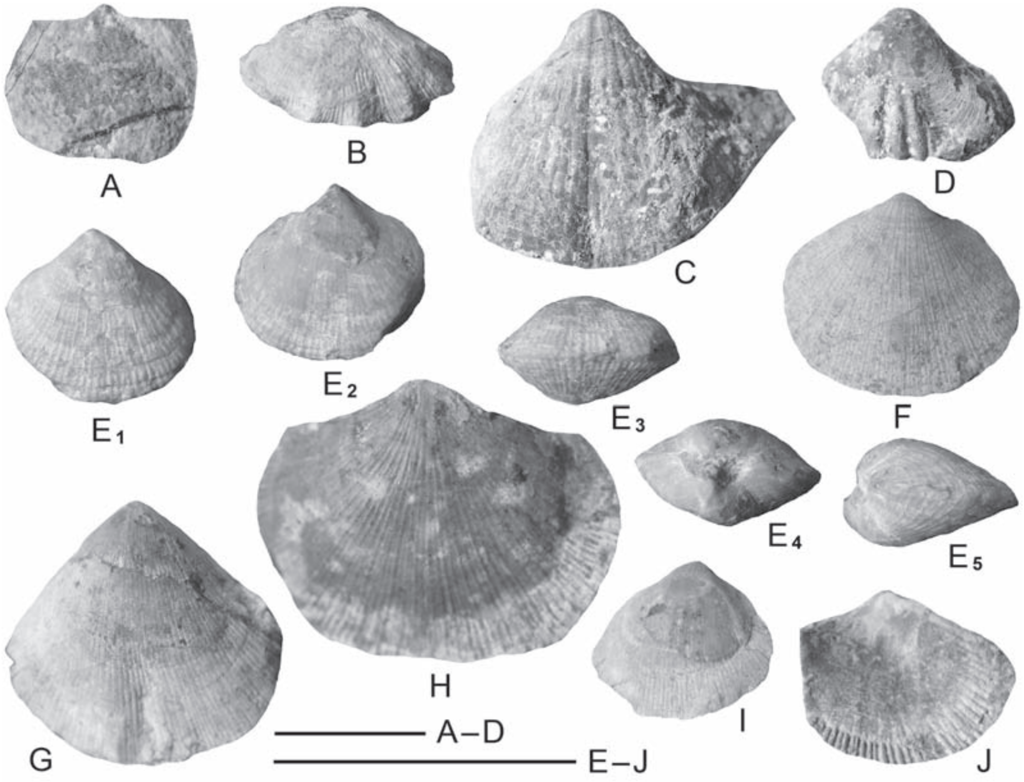

Fig. 3. Brachiopods of the Ryozensan fauna (1). **A,** *Echinauris* sp., external mould of dorsal valve, TG-Inv1057; **B,** *Meekella* sp., dorsal valve, TG-Inv1093; **C,** *Neospirifer* sp., ventral valve, TG-Inv1100; **D,** *Plectelasma* sp., dorsal valve, TG-Inv1101; **E, F,** *Acosarina rectimarginata* Cooper and Grant; E, ventral (E_1), dorsal (E_2), anterior (E_3), posterior (E_4) and lateral (E_5) views of conjoined shell, TG-Inv1090; F, dorsal valve, TG-Inv1095; **G–J,** *Acosarina* cf. *dunbari* Cooper and Grant, G, ventral valve, TG-Inv1085; H, dorsal valve, TG-Inv1088; I, ventral valve, TG-Inv1086; J, interior of dorsal valve, TG-Inv1092. Scale bars are 1 cm.

Material.—One specimen, external mould of a dorsal valve, TG-Inv1057.

Remarks.—This specimen can be assigned to the genus *Echinauris* by the small, transverse and gently concave dorsal valve (length 11 mm, width 13 mm), ornamented with numerous large, round dimples over the valve. The Ryozensan species resembles the type species, *Echinauris lateralis* Muir-Wood and Cooper (1960, p. 222, pl. 68, figs. 1–13) from the Road Canyon and Word formations of West Texas, in size, shape and external ornament of the dorsal valve. This species was described also from the lower Permian of Kuzu and Kiryu in the Ashio Mountains, central Japan (Tazawa in Tazawa et al., 2012a, b). But the poor preservation of the present material makes accurate comparison difficult.

Order Orthotetida Waagen, 1884

Suborder Orthotetidina Waagen, 1884

Superfamily Orthotetoidea Waagen, 1884

Family Meekellidae Stehli, 1954
Subfamily Meekellinae Stehli, 1954
Genus *Meekella* White and St. John, 1867

Type species.—*Plicatula striatocostata* Cox, 1857.

Meekella sp.
Fig. 3B

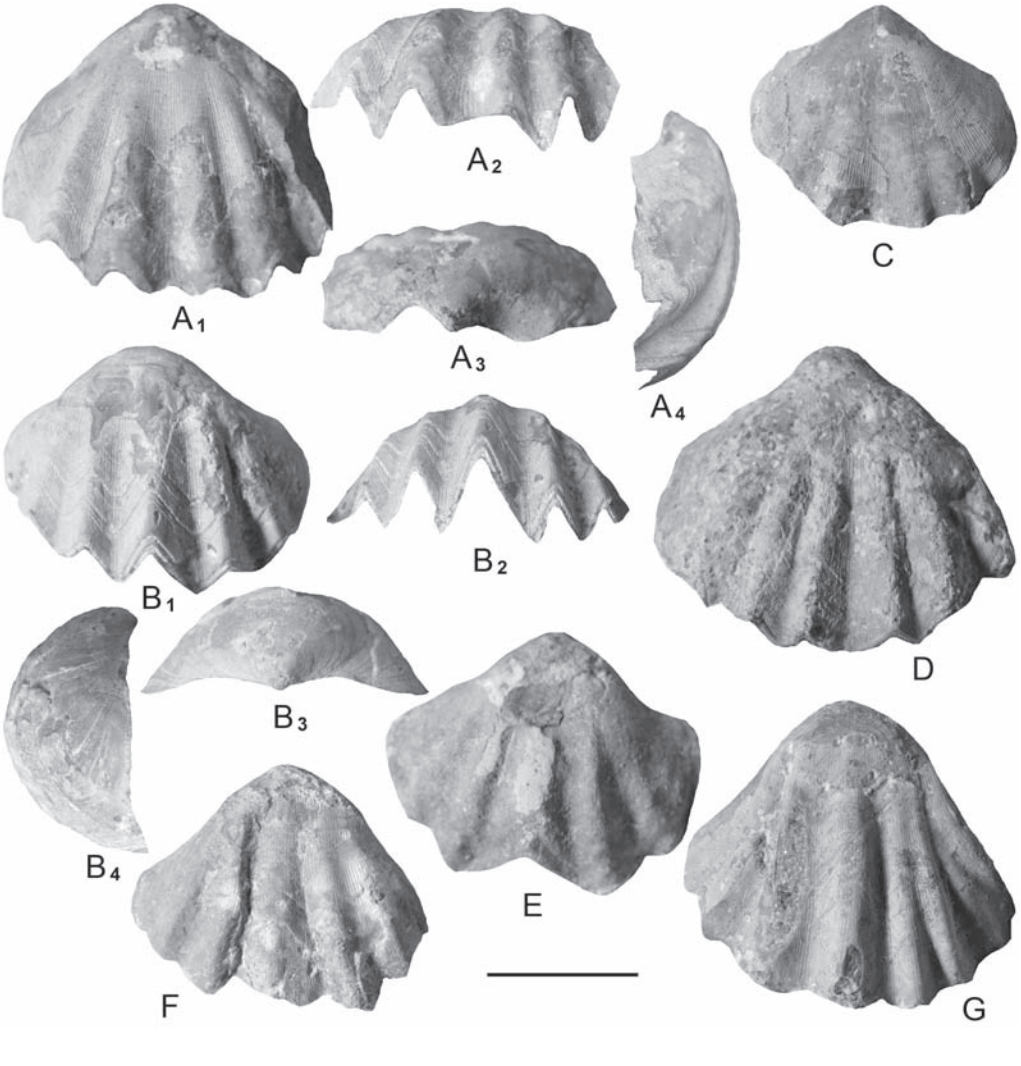

Fig. 4. Brachiopods of the Ryozensan fauna (2). **A–G,** *Enteletes stehlii* Cooper and Grant; A, ventral (A_1), anterior (A_2), posterior (A_3) and lateral (A_4) views of ventral valve, TG-Inv1070; B, dorsal (B_1), anterior (B_2), posterior (B_3) and lateral (B_4) views of dorsal valve, TG-Inv1064; C, ventral valve, TG-Inv1066; D, ventral valve, TG-Inv1061; E, dorsal valve, TG-Inv1062; F, dorsal valve, TG-Inv1059; G, dorsal valve, TG-Inv1060. Scale bar is 1 cm.

Material.—One specimen, a dorsal valve, TG-Inv1093.

Remarks.—This specimen is safely assigned to the genus *Meekella* by the external ornament, consisting of costae and costellae (numbering 4 costae in 10 mm, 3–4 costellae in 1 mm near the anterior margin). The Ryozensan species is small in size for the genus (length 9 mm, width 15 mm in the dorsal valve), and is characterized by the low rounded costae occurring near the anterior margin of the valve. The most comparable species, *Meekella bisculpta* Grant (1976, p. 58, pl. 10, figs. 1–35), from the Ratburi Limestone of Ko Muk, southern Thailand, differs from the present species in having more numerous costae with finer costellae on the dorsal valve.

Order Orthida Schuchert and Cooper, 1932
Suborder Dalmanellidina Moore, 1952
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, 1976
Figs. 4A–G

Enteletes dumblei Girty. Stehli, 1954, p. 295, pl. 17, figs. 13–18.
Enteletes stehlii Cooper and Grant, 1976, p. 2639, pl. 688, figs. 1–51.

Material.—Twenty specimens: (1) external and internal moulds of a ventral valve, TG-Inv1065; (2) twelve ventral valves, TG-Inv1061, 1063, 1066, 1070, 1097, 1098, 1099, 1102, 1103, 1104, 1105, 1106; and (3) seven dorsal valves, TG-Inv1058, 1059, 1060, 1062, 1064, 1067, 1068.

Description.—Shell medium in size for genus, roundly elliptical in outline, slightly wider than long, with greatest width at midlength; length 21 mm, width 25 mm in the largest specimen (TG-Inv1061). Ventral valve moderately and unevenly convex in lateral profile, strongly convex umbonal region and somewhat flattened venter; sulcus narrow and shallow. Dorsal valve strongly convex in lateral profile; fold narrow and low. External surface of both valves ornamented with costae and capillae; costae strong and rounded, numbering usually 3, rarely 4 on each side of sulcus and fold; 3–4 capillae in 1 mm at anterior margin of ventral valve. Internal structures of both valves not observed.

Remarks.—These specimens are referred to *Enteletes stehlii* Cooper and Grant (1976, p. 2639, pl. 688, figs. 1–51), from the Skinner Ranch and Bone Spring formations of West Texas, on account of the average-sized, slightly transverse and moderately biconvex shell, ornamented with 3–4 costae on each side of ventral costae and dorsal fold. *Enteletes gibbosus* Chronic (1953, p. 92, pl. 16, figs. 9–14), from the Copacabana Group (Wolfcampian) of southern Peru, differs from *E. stehlii* in having globose shell and ventral sulcus with V-shaped bottom and dorsal sulcus with sharp crest. *Enteletes costellatus* Cooper and Grant (1976, p. 2629, pl. 686, figs. 1–10), from the Hueco Formation of West Texas, differs from *E. stehlii* in having fewer and lower costae that originate just posterior to midlength of valve.

Distribution.—Sakmarian–Artinskian: southwestern Japan (Ryozensan in the Mino Belt) and western USA (Texas).

Family Schizophoriidae Schuchert and LeVene, 1929

Genus *Acosarina* Cooper and Grant, 1969

Type species.—Acosarina dorsisulcata Cooper and Grant, 1969.

Acosarina rectimarginata Cooper and Grant, 1976

Fig. 3E, F

Acosarina rectimarginata Cooper and Grant, 1976, p. 2624, pl. 674, figs. 1–46; Shen et al., 2011, p. 564, figs. 6.1–6.18; Tazawa in Tazawa et al., 2012b, p. 63, fig. 4.5.

Material.—Six specimens: (1) a conjoined shell, TG-Inv1090; (2) four ventral valves, TG-Inv1073, 1074, 1076, 1082 and (3) a dorsal valve, TG-Inv1095.

Description.—Shell small to medium in size for genus, transversely subelliptical in outline, with greatest width at midlength; hinge rather wide; sides rounded; anterior commissure rectimarginate; length 6 mm, width 7 mm in the best preserved specimen (TG-Inv1090); length 7 mm width 8 mm in the largest dorsal valve specimen (TG-Inv1095). Ventral valve moderately and unevenly convex in lateral profile, most convex in umbonal region; sulcus absent. Dorsal valve moderately convex in lateral profile, slightly more convex than ventral valve; fold absent. External surface of both valves ornamented with numerous rounded costellae and a few strong concentric lamellae; costellae numbering 4–5 in 1 mm anterior to midlength of ventral valve.

Remarks.—These specimens are referred to *Acosarina rectimarginata* Cooper and Grant (1976, p. 2624, pl. 674, figs. 1–46), from the Neal Ranch Formation (lower Wolfcampian) of West Texas, by size, shape and external ornament of both ventral and dorsal valves, particularly by the rectimarginate anterior commissure. The type species, *Acosarina dorsisulcata* Cooper and Grant, 1969, redescribed by Cooper and Grant (1976, p, 2621, pl. 667, figs. 1–26; pl. 673, figs. 1–6) from the upper Wolfcampian–lower Leonardian of West Texas, is readily distinguished from *A. rectimarginata* in having a median sulcus on the dorsal valve.

Distribution.—Asselian–Kungurian: central Japan (Kuzu and Hatahoko in the Mino Belt), southwestern Japan (Ryozensan in the Mino Belt) and USA (West Texas).

Acosarina cf. *dunbari* Cooper and Grant, 1976

Figs. 3G–J

cf. *Acosarina dunbari* Cooper and Grant, 1976, p. 2622, pl. 670, figs. 1–8.

Material.—Five specimens: (1) two ventral valves, TG-Inv1085, 1086; (2) two dorsal valves, TG-Inv1088, 1096; and (3) interior of a dorsal valve. TG-Inv1092.

Remarks.—These specimens can be assigned to the genus *Acosarina* by their small, transversely semioval and strongly biconvex shells (length 11 mm, width 13 mm in the largest specimen, TG-Inv1088) with rectimarginate anterior commissure and external ornaments consisting of numerous costellae (numbering 4–6 in 1 mm at near anterior margin) and a few concentric lamellae. The Ryozensan species resembles *Acosarina dunbari* Cooper and Grant (1976, p. 2622, pl. 670, figs. 1–8) from the Foraker Limestone (lower Wolfcampian) of Nebraska, USA, but differs from the American species in having finer costellae. The present species may be a new species, but the material is not adequate for establishing a new species.

Order Spiriferida Waagen, 1883
Suborder Spiriferidina Waagen, 1883
Superfamily Spiriferoidea King, 1846
Family Trigonotretidae Schuchert, 1893
Subfamily Neospiriferinae Waterhouse, 1968
Genus *Neospirifer* Fredericks, 1924

Type species.—*Spirifer fasciger* Keyserling, 1846.

Neospirifer sp.

Fig. 3C

Material.—One specimen, a ventral valve, TG-Inv1100.

Remarks.—This specimen is safely assigned to the genus *Neospirifer* by the transverse outline (length 17 mm, width about 30 mm), the greatest width at hinge and numerous sparsely bundled, rounded costae on the lateral slopes of the ventral valve. The Ryozensan species somewhat resembles *Neospirifer placidus* Cooper and Grant (1976, p. 2188, pl. 609, figs. 1–29), from the Neal Ranch Formation (lower Wolfcampian) of the Glass Mountains, West Texas, in the small to medium size, and in having sparsely bundled costae on the ventral valve. However, specific identification is difficult for the poorly preserved specimen.

Order Terebratulida Waagen, 1883
Suborder Terebratulidina Waagen, 1883
Superfamily Dielasmatoidea Schuchert, 1913
Family Dielasmatidae Schuchert, 1913
Subfamily Dielasmatinae Schuchert, 1913
Genus *Plectelasma* Cooper and Grant, 1969

Type species.—*Plectelasma kingi* Cooper and Grant, 1969.

Plectelasma sp.
Fig. 3D

Material.—One specimen, a dorsal valve, TG-Inv1101.

Remarks.—This specimen is safely assigned to the genus *Plectelasma* by the small size (length 16 mm, width 14 mm) and the plicated anterior margin of the dorsal valve. The Ryozensan species most resembles the type species, *Plectelasma kingi* Cooper and Grant, 1969, redescribed by Cooper and Grant (1976, p. 2904, pl. 755, figs. 53–80; pl. 778, figs. 18–23) from the Wolfcampian of the Glass Mountains, West Texas, but less elongate in outline.

Conclusions

In this study, brachiopods of seven species in six genera are described from the upper part of the Ryozensan Formation (Artinskian; *Pseudofusulina* Zone) at locality Echigadani B in the Ryozensan area, northern Suzuka Mountains, Mino Belt, southwestern Japan. The species are as follows: *Echinauris* sp., *Meekella* sp., *Enteletes stehlii* Cooper and Grant, *Acosarina rectimarginata* Cooper and Grant, *Acosarina* cf. *dunbari* Cooper and Grant, *Neospirifer* sp. and *Plectelasma* sp. The age of the Ryozensan fauna is identified as a Sakmarian–Artinskian, which is approximately consistent with that of Sano and Kojima (2000), an Artinskian, on the basis of fusulinids. In terms of palaeobiogeography, the Ryozensan fauna has a close affinity with those of Kuzu, Kiryu and Hatahoko in the Mino Belt, Japan and West Texas, USA. This conclusion is consistent with those of Tazawa and Shen (1997), Shen et al. (2011) and Tazawa et al. (1998, 2013, 2016), who reported that the Permian brachiopod faunas of the Mino Belt are tropical faunas of the equatorial Panthalassa, not far from North America (West Texas).

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Preliminary report of Carboniferous conodont fossils from the "Tsuchikurazawa Limestone", Kotaki, Itoigawa City, Niigata Prefecture, central Japan

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Abstract

Adetognathus unicornis (Rexroad and Burton) is the first representative of conodont fossils from the Carboniferous "Tsuchikurazawa Limestone" in the Itoigawa area, Niigata Prefecture, central Japan. The occurrence of this species indicates that the age of the limestone correlates with the late Serpukhovian (= late Chesterian) of the early Carboniferous, which is consistent with previous reports.

Key words: Conodont, Carboniferous, Kotaki Fomation, "Tsuchikurazawa Limestone," Hida Gaien Belt.

Introduction

Conodonts are minute fossils of extinct marine animals resembling spines, combs, or teeth (Briggs et al., 1983). Since the discovery of conodont-bearing animal fossils, they have been regarded as the earliest jawless fish (Purnell, 1995; Donoghue et al., 2000). Conodonts constitute the feeding apparatus of these animals and, in most cases, are the only parts of these animals preserved as fossils. Due to wide variation in their morphology, conodonts have been used in the biostratigraphy of Paleozoic and Triassic rocks in Japan (Igo and Koike, 1965; Koike, 1967).

The Kotaki Formation of the Hida Gaien Belt is distributed in and around the Tsuchikurazawa Valley, Kotaki, Itoigawa City, Niigata Prefecture in Japan (Nagamori et al.,

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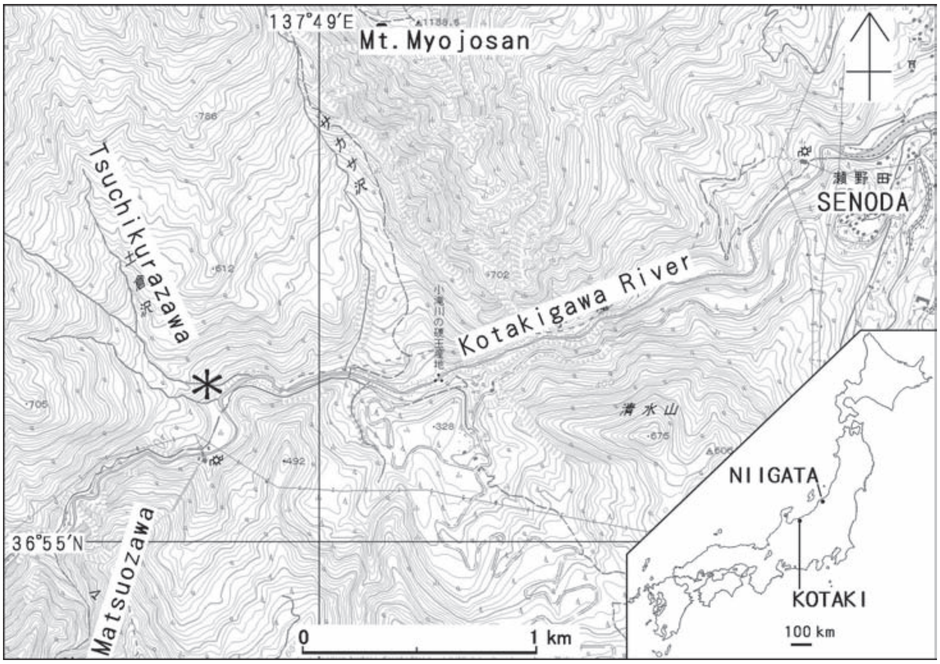

Fig. 1. This map represents the limestone block locality of the "Tsuchikurazawa Limestone" (asterisk). Topographic maps of Kotaki and Echigohiraiwa (scale 1:25,000), published by the Geospatial Information Authority of Japan, are used as a base map.

2010). This formation comprises pyroclastic rocks, sandstone, and mudstone, including mélange and chert (Nagamori et al., 2010). Because of large shear deformations, this formation was previously known as the Kotaki Complex (Kawai and Takeuchi, 2001); however, its name was changed to the Kotaki Formation based on similarities of its rock types with those of the adjacent Shiroumatake Formation (Nagamori et al., 2010). Radiolarian fossils from mudstone, siliceous shale, and chert date the formation to the Middle Permian (Tazawa et al., 1984; Kawai and Takeuchi, 2001). The mélange of this formation contains dark gray–black allochthonous limestone blocks—the "Tsuchikurazawa Limestone" (Nakazawa et al., 1998; Takenouchi, 2005). Over time, this limestone has yielded diverse Carboniferous fossils, including teeth of *Petalodus* and Cochliodontidae, which are considered the oldest shark remains found in Japan (Goto et al., 2011), and *Cyclus tazawai* Niko and Ibaraki, which is only the second-recorded cyclid crustacean in East Asia (Niko and Ibaraki, 2011). The occurrence of multiple taxa, such as foraminifers (Kamiya and Niko, 1996; Nakazawa et al., 1998), corals (Kamiya and Niko, 1996; Niko and Yamagiwa, 1998), brachiopods (Tazawa, 2004; Ibaraki et al., 2008, 2010; Ibaraki and Sato, 2013), and calcareous algae (Konishi, 1956), in this limestone dates it to the Early Carboniferous (Visean–Serpukhovian). Herein, we report the first conodont fossils found in the "Tsuchikurazawa Limestone".

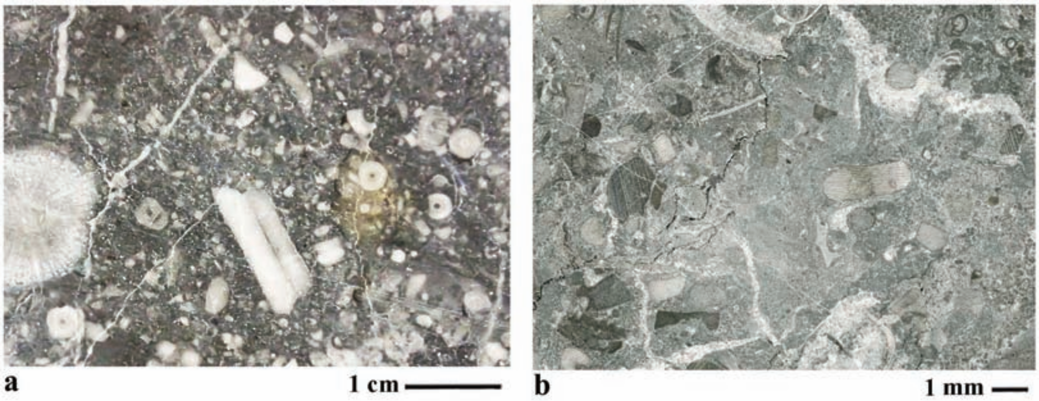

Fig. 2. Microlithology of the studied limestone blocks of the "Tsuchikurazawa Limestone." This limestone is composed of bioclasts, such as rugose corals and dominant small fragments of crinoids in the lime mud matrix, and limestone is determined to be bioclastic wackestone. **a**, Polished surface; **b**, thin section.

Materials and methods

Black limestone blocks originally collected from the Tsuchikurazawa Valley were deposited in the Fossa Magna Museum, and Y. I. handed over the limestone samples to Y. T., the first author of the present paper (Fig. 1 for details of the locality of the limestone). The limestone was examined by taking thin sections and polishing their surfaces (Fig. 2). Limestone comprising bioclasts (some millimeters or centimeters in size), such as rugose corals and dominant small fragments of crinoids in the black lime mud matrix, was determined to be bioclastic wackestone.

More than 5 kg limestone samples were treated with 5–10% acetic acid to recover conodont fossils. Limestone residues were sieved using a metal sieve with 105 μm mesh opening. The residues were dried and examined under a stereoscopic microscope (Nikon SMZ645). Under the microscope, conodonts were picked up using a thin brush, placed on slides, and photographed with a digital microscope (Keyence VH-Z100R).

Systematic paleontology

Family Cavusgnathidae Harris and Hallingsworth, 1933

Genus *Adetognathus* (Lane, 1967)

Type species.—*Cavusgnathus lautus* Gunnell, 1933

Remarks.—The P_1 element of this genus has a fairly deep median trough between two parapets, which continues to the posterior tip of the platform. These parapets are ornamented by nodes or ridges occupying the entire length of the lanceolate and slightly incurved platform. The short blade, which may or may not be slightly fixed, joins the outer parapet. *Adetognathus* is similar to an ancestral form of *Cavusgnathus*. The latter has a discrete fixed part on its blade, which in the case of *Adetognathus* is shorter or absent.

Adetognathus unicornis (Rexroad and Burton, 1961)

Fig. 3.1

Taphrognathus varians Cooper, 1947, p. 92, pl. 20, figs. 14–16.

Streptognathodus unicornis Rexroad and Burton, 1961, p. 1142, pl. 138, figs. 1–9; Collison et al., 1962, p. 27, charts 1, 4; Dunn, 1965, p. 1149, pl. 140, figs. 5, 6, 13, 14; Webster, 1969, p. 49, pl. 4, fig. 13.

Adetognathus unicornis (Rexroad and Burton); Lane, 1967, p. 930, pl. 119, figs. 16–25; Dunn, 1970, p. 316, pl. 61, figs. 20–22; Lane and Straka, 1974, figs. 33. 14–18; Kozitskaya et al., 1978, pl. 15, fig. 1, 2; Tynan, 1980, p. 1296, pl. 2, fig. 14; Nemirovskaya, 1983, p. 60, pl. 1, fig. 20; Grayson et al., 1985, p. 176, pl. 1, fig. 11; p. 178, pl. 2, fig. 10; Rexroad and Merrill, 1985, p. 56, pl. 1, figs. 1, 2, 8, 10, 17–19, p. 58, pl. 2, figs. 1–4, 40–54; Mapes and Rexroad, 1986, pl. 1, figs. 1–6; Grayson et al., 1990, pl. 2, figs. 25, 26; Morrow and Webster, 1992, pl. 1, figs. 10, 11; Weibel and Norby, 1992, p. 50, pl. 1, figs. 1–16; Nemyrovska, 1999, p. 95, pl. 11, fig. 11; Abplanalp et al., 2009, p. 95, fig. 7. 24–28.

? *Adetognathus unicornis* (Rexroad and Burton); Varker and Austin, 1975, p. 404, pl. 6, figs. 1, 2, 16–18.

Material.—A P_1 element and a probable M element. These specimens are deposited in the Earth Evolutionary Science, University of Tsukuba, Tsukuba, Ibaraki, Japan.

Revised diagnosis by Nemyrovska (1999).—Elongated narrow elements lacking a fixed blade. The largest denticle is present at the posterior end of the free blade and closest to the right (outer) parapet. The junction of the parapets forms the posterior tip.

Description.—The lanceolate platform of the dextral P_1 element occupies two-third of the entire length of the element. The entire length and height of the platform are 1.49 and 0.29 mm, respectively. The long, deep, median trough is the deepest at the anterior part. The parapets are ornamented by faint ridges. Each ridge is short and gentle. The free short blade continues to the outer parapet of the platform. The outer parapet is longer than the inner one. From a lateral view, the element is not arched and the basal and upper parts of the platform are thinly flanged. The blade is not fixed and bears six denticles. The prominent posterior huge cusp located in front of the platform is broken, while the other denticles are small and almost equal in size.

The probable M element comprises a huge broken cusp and posterior process with small denticles.

Remarks.—*Adetognathus unicornis* has been identified in the lower Carboniferous (upper Serpukhovian) strata of Eastern Europe and the Upper Mississippian (upper Chesterian)

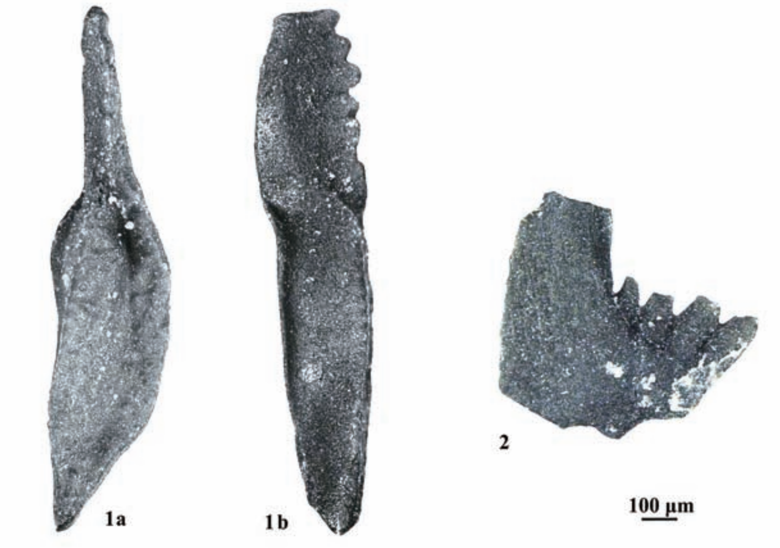

Fig. 3. *Adetognathus unicornis* (Rexroad and Burton) from the limestone blocks of the "Tsuchikurazawa Limestone." **1**, P1 element. **a**, oral view; **b**, lateral view. **2**, probable M element.

strata of North America. This species was once identified as *Taphrognathus varians* by Cooper (1947), but Rexroad and Burton (1961) evaluated morphological commonalities between *Cavusgnathus unicornis* and *Streptognathodus primus* and renamed the species as *Streptognathodus unicornis*. The generic reassignment to *Adetognathus* was recognized by Lane (1967) based on the following features: the fixed blade is short or completely absent; the blade junction is not always located in the median position on the platform; and the blade is continuous with the outer margin.

The P1 element of *Adetognathus unicornis* is different from that of *A. gigantus* and *A. lautus* due to the lack of a fixed blade and the presence of a huge, discrete denticle on the posterior end of the blade. *Adetognathus lautus* morphotype A, defined by Weibel and Norby (1992), is quite similar to *A. unicornis*, except for the location of the huge cusp, which is clearly inclined toward the outer parapet in the latter. The specimen reported in the present study is slightly different from *A. unicornis* specimens reported in other studies. The notch between the platform and blade is not deep because the ridges on both parapets of this specimen are lower and are less pronounced. However, because it shares almost all characteristics with *A. unicornis*, we identified it as *A. unicornis*.

Rexroad and Merrill (1985) have represented ramiform elements of the genus *Adetognathus*. An associated broken element (Fig. 3.2) is probably a part of the M element of *Adetognathus* due to its morphological similarities, but it remains uncertain whether the probable M element belongs to *Adetognathus unicornis*.

Biostratigraphic indications

Adetognathus unicornis (Rexroad and Burton) was recorded in Unit D of the Kinkaid Formation, the name of which was changed to the Grove Church Shale by Swann (1963), in the Mississippi Valley, Illinois (Rexroad and Burton, 1961). This is the uppermost part of both the Chester Series and the Mississippian System of Illinois, and the occurrence of this species is of stratigraphical importance. Collinson et al. (1962) used this species and established the *Streptognathodus unicornis* assemblage zone for the uppermost Mississippian. The zone was defined by the range of *A. unicornis*, but full range of the species in the Illinois Basin had not been determined because of the Mississippian–Pennsylvanian unconformity at the top of the Grove Church Shale. In southern Nevada, a more complete sequence was recognized across the Mississippian–Pennsylvanian boundary, where *A. unicornis* occurred in the Indian Springs and lower part of the Bird Spring Formations (Webster, 1969; Dunn, 1970). The species is associated with *Rhachistognathus muricatus* (Dunn) in the upper part of the Indian Springs Formation. Lane and Straka (1974) considered this association with *R. muricatus* to represent a new fauna (establishing *Adetognathus unicornis* and *Rhachistognathus muricatus* zones), which was absent in the Illinois Basin due to unconformity at the top of the Mississippian. This zonal scheme in North America has also been confirmed by other researchers (Grayson et al., 1985; Abplanalp et al., 2009). Nemyrovska (1999) established the *Gnathodus bilineatus bollandensis*–*Adetognathus unicornis* zone based on the occurrence of these species in the Donets Basin, Ukraine, Eastern Europe. Both species were associated with typical late Early Carboniferous (late Serpukhovian) conodonts, such as *Gn. bilineatus* (Roundy) and *Lochriea* spp., and the zone is easy to compare with other regions. According to Nemyrovska (1999), this zone corresponds to the *Adetognathus unicornis* and *Rhachistognathus muricatus* zones of North America, the upper part of the *Gn. bilineatus*–*Lochriea nodosus* zone of the Atetsu Limestone of Koike (1967), and the *Gn. bilineatus* zone of the Hina Limestone of Mizuno (1997). The latter two zones are the highest conodont zones of the Mississippian in the Akiyoshi Terrane. Together, these facts suggest that the occurrence of *A. unicornis* in blocks of the "Tsuchikurazawa Limestone" dates the limestone to the late Chesterian or late Serpukhovian of the early Carboniferous.

Our finding is consistent with those of previous paleontological works on the "Tsuchikurazawa Limestone". For instance, Abplanalp et al. (2009) suggested that the range of *A. unicornis* overlaps with the majority of zone 19 of the Mamet foraminiferal biozone framework. This biozone is characterized by the occurrence of *Eosigmoilina, Quasiarchaediscus, Biseriella,* and *Asteroarchaediscus* species, dating it to the late Chesterian (Mamet, 1975). *Asteroarchaediscus* was recorded in the "Tsuchikurazawa Limestone" by Niko and Yamagiwa (1998) and Nakazawa et al. (1998).

This is a preliminary report of the Carboniferous conodonts from the "Tsuchikurazawa Limestone". It is expected to find the early Carboniferous conodont fauna in the future research.

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Updated radiolarian zonation for the Jurassic in Japan and the western Pacific

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Abstract

An updated version from radiolarian zonal scheme in the 1990s for the Jurassic in Japan and the western Pacific is presented and vertical distributions of selected radiolarian species are illustrated. The major modifications are as follows: The *Bipedis horiae* Zone (JR0) is added below the *Parahsuum simplum* Zone (JR1). The base of the *Bipedis horiae* Zone (JR0) is defined by the last occurrence biohorizon of *Haeckelicyrtium breviora* Sugiyama and corresponds to the Triassic–Jurassic boundary. The base of the *Parahsuum simplum* Zone is dated within the Sinemurian. The *Tricolocapsa plicarum* Zone (JR4), *Tricolocapsa conexa* Zone (JR5), *Stylocapsa*(?) *spiralis* Zone (JR6), and *Pseudodictyomitra primitiva* Zone (JR8) are modified to the *Striatojaponocapsa plicarum* Zone (JR4), *Striatojaponocapsa conexa* Zone (JR5), *Kilinora spiralis* Zone (JR6), and *Loopus primitivus* Zone (JR8), respectively, in accordance to the change of generic assignment of zone-nominal species.

Key words: Jurassic, radiolaria, zonation, revision, Japan, western Pacific.

Introduction

Radiolarian zonation for the Jurassic and Lower Cretaceous using data from land sections in Japan and deep sea cores in the western Pacific was proposed in Matsuoka (1995a). Since then, taxonomic and biostratigraphic studies on Jurassic radiolarians have been actively carried out in Europe (e.g., Steiger, 1992; O'Dogherty et al., 2006, 2017), North

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America (e.g., Hull, 1997; Carter et al., 1998; Yeh, 2009; Pessagno et al., 2009), Asia (e.g., Sugiyama, 1997; Hori, 1999; Matsuoka et al., 2002), and Antarctica (Kiessling, 1999). International joint research on taxonomy and biostratigraphy of Jurassic radiolarians has been performed continuously (Carter et al., 2010; Goričan et al., 2006, 2013, 2018; O'Dogherty et al., 2009). The accumulation of new data in the last two decades requires a revision of the zonation and age assignments. Although revision of the zonation was briefly reported in Matsuoka (2006), detailed explanations have not been demonstrated yet. An updated version of the zonal scheme of Matsuoka (1995a) for the entire Jurassic in Japan and the western Pacific is presented in this paper.

A brief review of Jurassic radiolarian zonation in Japan and the western Pacific

Mesozoic radiolarian studies in Japan were carried out to clarify the geology of accretionary complexes since the 1970s. In the early 1980s several research groups started radiolarian biostratigraphic work at almost the same time so that several independent zonal schemes were proposed. A historical review on Jurassic radiolarian biostratigraphic research in Japan is given in Goričan et al. (2018).

Interval zones for the entire Jurassic were established by Matsuoka and Yao (1986). Deep sea cores in the western Pacific obtained from Leg 129 of the Ocean Drilling Program (ODP) contributed to testifying the zonal scheme for the Middle and Upper Jurassic established in Japan (Matsuoka, 1992). Combining data from land sections in Japan with data from the ODP materials, Matsuoka (1995a) proposed a zonal scheme for the Jurassic and Lower Cretaceous. A detailed data set for this zonation was presented in Matsuoka (1995b). The Jurassic succession includes the *Parahsuum simplum* Zone (JR1), *Trillus elkhornensis* Zone (JR2), *Laxtorum*(?) *jurassicum* Zone (JR3), *Tricolocapsa plicarum* Zone (JR4), *Tricolocapsa conexa* Zone (JR5), *Stylocapsa*(?) *spiralis* Zone (JR6), *Hsuum maxwelli* Zone (JR7), and *Pseudodictyomitra primitiva* Zone (JR8) in ascending order. In addition to these zones, the *Pseudodictyomitra carpatica* Zone (KR 1) includes the uppermost Jurassic as well. Most of these zones are introduced in a popular text book on radiolarians presented by De Wever et al. (2001). The zonal scheme has been widely utilized for the dating of marine sequences accumulated in the Panthalassa and Tethys (e.g., Matsuoka et al., 1998, 2002; Zamoras and Matsuoka, 2001, 2004; Li et al., 2016, 2018; Ito and Matsuoka, 2018).

Radiolarian zonation

As stated in "Introduction", much effort has been made on taxonomic and biostratigraphic research for Jurassic radiolarians. It is necessary to update zonal names and definition in accordance with the progress in radiolarian research for the last two decades. The updated zonal scheme for the Jurassic in Japan and the Pacific is summarized in Fig. 1. Vertical distributions of selected radiolarian species, especially zone-diagnostic taxa, are also illustrated in Fig. 1.

To define zones, radiolarian bio-events such as the evolutionary first appearance biohorizon (EFAB), first occurrence biohorizon (FOB), and last occurrence biohorizon (LOB) were used. The EFAB, which is the most synchronously reliable among various kinds of biohorizons, is selected as often as possible.

Bipedis horiae Zone
Code. JR0
Base. LOB of *Haeckelicyrtium breviora* Sugiyama.
Top. FOB of *Parahsuum simplum* Yao.
Remarks. Sugiyama (1997) established the *Haeckelicyrtium breviora–Bipedis horiae* Partial-range Zone (JR0A) and the *Bipedis horiae* Lowest occurrence Zone (JR0B) in the Sakahogi section of the Mino Terrane, central Japan. The *Bipedis horiae* Zone (JR0) of the present study is a zonal unit for the lowest portion of the Jurassic, combining JR0A and JR0B proposed by Sugiyama (1997). The LOB of *H. breviora* Sugiyama corresponds to the Triassic–Jurassic boundary (TJB) in the Sakahogi section (Sugiyama, 1997). Since species belonging to the genus *Bipedes* are common in marine sequences around the TJB, the phyletic analysis of *Bipedis* species can contribute to further refinement of this zone. The first occurrence of *B. horiae* Sugiyama has been reported only in the Sakahogi section so far, which is located just above the TJB.
Age. Hettangian to early Sinemurian.

Parahsuum simplum Zone
Code. JR1
Base. FOB of *Parahsuum simplum* Yao.
Top. FOB of *Trillus elkhornensis* Pessagno and Blome.
Remarks. Sugiyama (1997) showed the first occurrence of *Parahsuum simplum* Yao in the Sakahogi section, being higher than the FOB of *B. horiae*. The first occurrence biohorizon of *P. simplum* is located within the Sinemurian in Haida Gwaii, Canada (Carter et al., 1998).
Age. Late Sinemurian to middle Early Pliensbachian.

Trillus elkhornensis Zone
Code. JR2
Base. FOB of *Trillus elkhornensis* Pessagno and Blome.
Top. FOB of “*Laxtorum*” *jurassicum* Isozaki and Matsuda.
Remarks. Carter et al. (2010) reported that *Trillus elkhornensis* Pessagno and Blome first

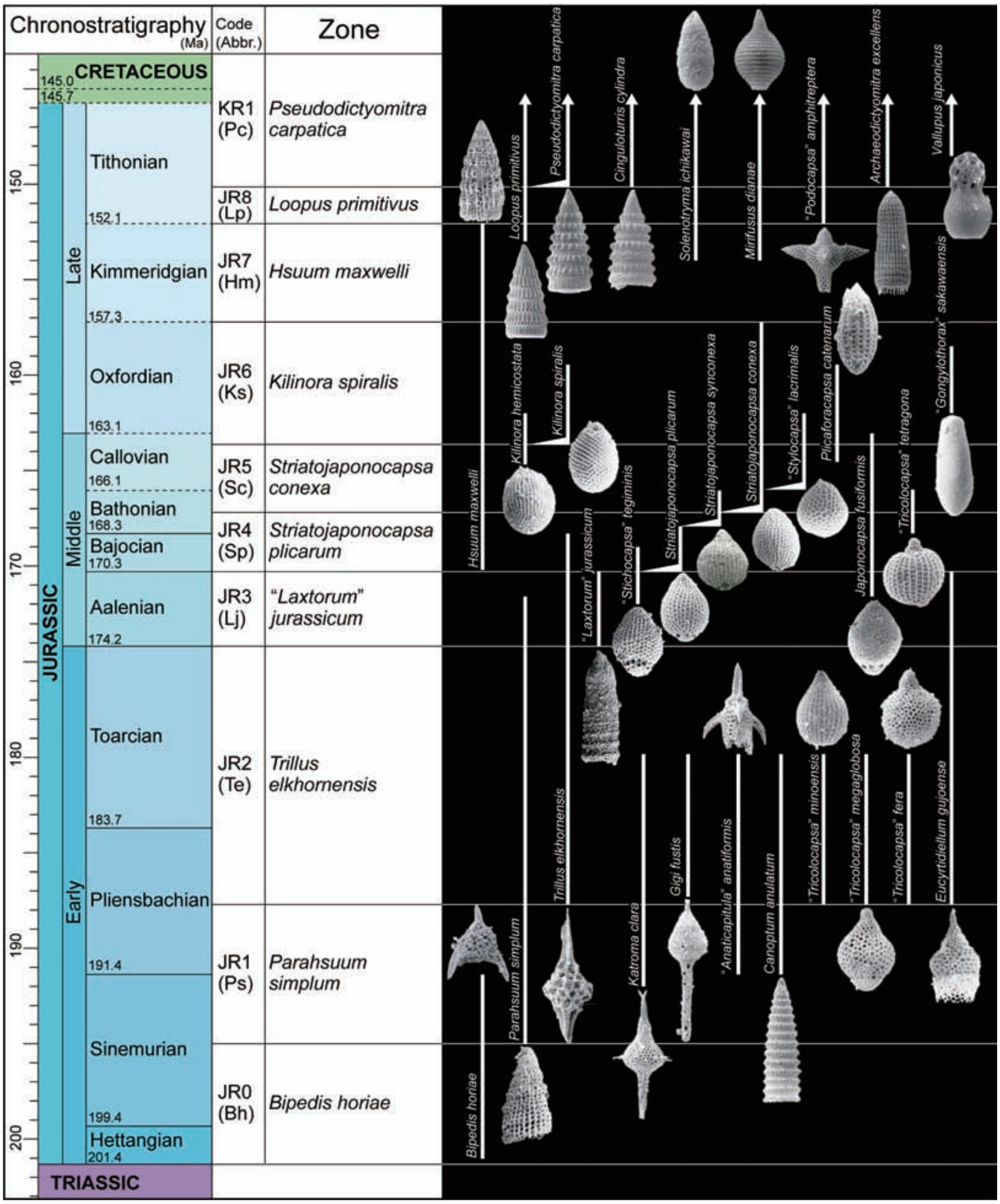

Fig. 1. Updated radiolarian zonation for the Jurassic in Japan and the western Pacific. Chronostratigraphy is based on Ogg et al. (2016). Images of index radiolarians are reprinted from authors' previous papers (Matsuoka, 1983, 1998, 2004) and unpublished data. Arrows in the range chart indicate that the vertical ranges extend beyond the Jurassic–Cretaceous boundary.

occurs in the *Hsuum mulleri–Trillus elkhornensis* Zone of middle Lower Pliensbachian.
Age. Middle Early Pliensbachian to Toarcian.

"Laxtorum" jurassicum Zone
Code. JR3
Base. FOB of *"Laxtorum" jurassicum* Isozaki and Matsuda.
Top. EFAB of *Striatojaponocapsa plicarum* (Yao).
Age. Aalenian.

Striatojaponocapsa plicarum Zone
Code. JR4
Base. EFAB of *Striatojaponocapsa plicarum* (Yao).
Top. EFAB of *Striatojaponocapsa conexa* (Matsuoka).
Remarks. *Striatojaponocapsa* was established by Kozur (1984), taking *Tricolocapsa plicarum* Yao as the type species. The evolutionary lineage from the ancestor *S. plicarum* to the descendant *S. conexa* was first demonstrated by Matsuoka (1983). O'Dogherty et al. (2006) described two new species of *Striatojaponocapsa* in the Austrian Alps; *S. synconexa* O'Dogherty, Goričan, and Dumitrica and *S. riri* O'Dogherty, Goričan, and Dumitrica. Hatakeda et al. (2007) examined in detail the evolutionary history of the *Striatojaponocapsa* lineage in continuous sections in Japan. They concluded that *S. plicarum* continuously and gradually changed into *S. synconexa*, then *S. synconexa* was rapidly replaced by *S. conexa* in a phyletic evolutionary process. In accordance with the change of generic assignment of the nominal species, the zonal name is changed to the *Striatojaponocapsa plicarum* Zone.
Age. Bajocian to early Bathonian.

Striatojaponocapsa conexa Zone
Code. JR5
Base. EFAB of *Striatojaponocapsa conexa* (Matsuoka).
Top. EFAB of *Kilinora spiralis* (Matsuoka).
Remarks. In relation to the change of generic assignment of the nominal species (Hull, 1997), the zonal name is changed to the *Striatojaponocapsa conexa* Zone.
Age. Late Bathonian to middle Callovian.

Kilinora spiralis Zone
Code. JR6
Base. EFAB of *Kilinora spiralis* (Matsuoka).
Top. LOB of *Striatojaponocapsa conexa* (Matsuoka).
Remarks. The genus *Kilinora* was established by Hull (1997) who took *Stylocapsa*(?) *spiralis*

Matsuoka as the type species. In accordance with the change of generic assignment of the nominal species, the zonal name is changed to the *Kilinora spiralis* Zone. The evolutionary lineage form the ancestor *Kilinora hemicostata* (Matsuoka) to the descendant *K. Spiralis* was first reported at several land sections in Japan (Matsuoka, 1983, 1995a). The same lineage was recognized at DSDP Site 534 in the north-western Central Atlantic as well (Matsuoka and Baumgartner, 1997).
Age. Late Callovian to Oxfordian.

Hsuum maxwelli Zone
Code. JR7
Base. LOB of *Striatojaponocapsa conexa* (Matsuoka).
Top. LOB of *Hsuum maxwelli* Pessagno.
Age. Kimmeridgian.

Loopus primitivus Zone
Code. JR8
Base. LOB of *Hsuum maxwelli* Pessagno.
Top. EFAB of *Pseudodictyomitra carpatica* Lozyniak.
Remarks. Yang (1993) established the genus *Loopus*, taking *Pseudodictyomitra primitiva* Matsuoka and Yao as the type species. In relation to the change of generic assignment of the nominal species, the zonal name is changed to the *Loopus primitivus* Zone. The evolutionary first appearance of *Pseudodictyomitra carpatica* was reported at Site 801 of ODP Leg 129 (Yang and Matsuoka, 1997; Matsuoka and Yang, 2000). Zügel (1997) showed the occurrence of *P. carpatica* in the lower Tithonian of the Solnhofen area, southern Germany.
Age. Early Tithonian.

Pseudodictyomitra carpatica Zone
Code. KR1
Base. EFAB of *Pseudodictyomitra carpatica* (Lozyniak).
Top. EFAB of *Cecrops septemporatus* (Parona).
Remarks. The Jurassic–Cretaceous boundary is located within this zone.
Age. Late Tithonian to early Valanginian.

Concluding remarks

The current status and future directions in Mesozoic radiolarian biochronological research are recently documented by Goričan et al. (2018). They stress the importance of detailed documentation of evolutionary first and last appearance in different radiolarian phylogenetic lineages. In the last two decades, some new taxa have been proposed and their biostratigraphic significance has been discussed. On the basis of the progress, this article updated Jurassic radiolarian zonation.

Generic assignment of many species, even zone-diagnostic species (i.e., "*Laxtorum*" *jurassicum*), is still debatable. Furthermore, phylogenetic relationships among Early and Late Jurassic radiolarians are not entirely clear compared to those of Middle Jurassic radiolarians. We expect this article to act as a stepping stone to further progress.

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