Tabulate Corals from the Lower Devonian Ohno Formation in the Hikoroichi area, Iwate Prefecture, Northeast Japan

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Abstract This study identifies diverse tabulate corals from the Lower Devonian Ohno Formation exposed in the Hikoroichi area, Iwate Prefecture, Northeast Japan. Stratigraphically, they are classified as three assemblages. *Schedohalysites kitakamiensis, Hillaepora gionensis, Striatopora* sp. cf. *S. sugiyamai*, from limestone pebbles in the basal conglomeratic limestone represent Assemblage 1, that is Ludlow (early late Silurian) in age. These three species are derived from the underling Kawauchi Formation. Assemblage 2 is composed of seven species, *Sapporipora*? sp., *Egosiella*? sp., *Acaciaporella*? sp., *Squameostriatopora tachibanai* sp. nov., *Thamnopora ohnoensis* sp. nov., *Alveolites* sp., *Crassialveolites* sp. cf. *C. niigataensis*, and occurs in "the Nameriishi Limestone" belonging to the Lower Member of the formation. Constituents of Assemblage 3 are the following seven species, *Pachyfavosites hikoroichiensis* sp. nov., *Syringopora sanrikuensis* sp. nov. They occur in greenish tuffaceous shale of the Lower Member. The age of the latter two assemblages is best constrained as Emsian (late Early Devonian).

Key words: South Kitakami Belt, Favositida, Heliolitida, Auloporida, Emsian

Introduction

The Ohno Formation in the South Kitakami Belt is a representative Devonian marine sequence in Japan. Since the first discovery of tabulate corals including Favosites cf. styriaca, Thamnopora cristata, and Alveolites sp., by Yabe and Sugiyama (1937), a considerable amount of species has been recorded from the formation, namely Favosites baculoides, F. cf. forbesi, F. cf. pseudosocialis, F. reticulatus, F. sp., Squameofavosites sp., Pachypora sp., Thamnopora sp. nov., Coenites sp., Heliolites bohemicus, H. sp., Thecostegites sp. (Sugiyama, 1941; Okubo, 1950; Onuki, 1956; Minato et al., 1959, 1979a). Murata and Mori (1973, figs. 1-1-3) discovered a Silurian tabulate coral, Schedohalysites kitakamiensis, from the basal part of the formation, but it was probably reworked from the Kawauchi Formation (see below). It is thought that "Favosites" sp. in Murata et al. (1974, pl. 1, fig. 5) also has originated in the underlining formation. Except for Thamnopora sp. (Minato et al., 1979a, pl. 7, fig. 1) and these derived fossils, unfortunately their taxonomic placements have not been verified because they are not figured or described yet. This precludes accurate chronologic and biogeographic competitions with other faunas. The present study provides the first detailed descriptions for the Ohno tabulate corals on the basis of new material collected from three collecting sites in the Hikoroichi area of Ofunato City, Iwate Prefecture, Northeast Japan (Fig. 1).

Repository: All specimens examined here are reposited in Department of Geology and Paleontology, National Museum of Nature and Science (prefixed NMNS), Tsukuba, Ibaraki Prefecture, Central Japan.

Geologic setting and locality

Yabe and Sugiyama (1937) divided the Middle Paleozoic rocks in the Hikoroichi area into five groups and named them Kawauchi, Takainari, Ōno, Nakazato, and Ōmori. The former two were assigned to the as the Silurian (Gotlandian) and other than groups regarded as the Devonian. In the recent definition given by Murata *et al.* (1974), the Ohno Formation comprises the uppermost Kawauchi, the uppermost Takainari and the Ōno groups. The

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Fig. 1. Map showing locations of Iwate Prefecture in Northeast Japan (A), the Hikoroichi area in Iwate Prefecture (B), and collecting sites of Assemblages 1–3 in the Hikoroichi area (C). Scale bar in inset at lower right corner is 500 m. Used base map is "digital Japan Basic Map" published by Geospatial Information Authority of Japan.

formation (approximately 450m thick) begins with conglomeratic limestone (= the uppermost part of the Kawauchi Group in Yabe and Sugiyama's scheme; Solenopora-limestone in Sugiyama, 1940), then it shifts to reddish tuffaceous shale (=the uppermost part of the Takainari group in Yabe and Sugiyama's scheme), greenish tuffaceous shale, alternating beds of acidic tuff and sandstone with a thin lens, up to 6m, of "the Nameriishi Limestone," and acidic to dacitic tuff (Okubo, 1950; Onuki, 1969; Minato et al., 1979a; Mori, 1989; Ehiro, 2017). On the basis of the present new observations at the Kusayami-zawa Valley, the Ohno Formation unconformable covers the Middle to Upper Silurian Kawauchi Formation. Relationship between the formation and the overlying Nakazato Formation is conformable (e.g., Ehiro, 2017).

Tabulate corals ware collected from angular pebbles in the basal conglomeratic limestone at an outcrop in a Kusayami-zawa Valley (Assemblage 1), float blocks of red spotted white limestone derived from "the Nameriishi Limestone" in a Sode-sawa Valley (Assemblage 2), and tuffaceous shale crops out along a road cut (Assemblage 3). All fossil-bearing horizons belong to the Lower Member in Mori (1989)'s stratigraphic subdivision (Fig. 2). Locality of Assemblage 3 is probably identical with that of *Thecostegites* sp. (Minato *et al.*, 1959; *= Ohnopora hayasakai* Minato and Minoura, 1977; *= Pernerocrinus hayasakai* in Minoura, 1987).

Systematic paleontology

Subclass Tabulata Milne-Edwards and Haime, 1850 Order Favositida Wedekind, 1937 Suborder Favositina Wedekind, 1937 Superfamily Favositoidea Dana, 1846 Family Favositidae Dana, 1846 Subfamily Favositinae Dana, 1846 Genus *Sapporipora* Ozaki *in* Shimizu, Ozaki and Obata, 1934

Type species: Sapporipora favositoides Ozaki *in* Shimizu, Ozaki and Obata, 1934.



Fig. 2. Generalized and simplified stratigraphic column of the Ohno Formation on the basis of research results by previous workers (Okubo, 1950; Onuki, 1969; Murata *et al.*, 1974; Minato *et al.*, 1979a; Mori, 1989; Kurihara *et al.*, 2005; Ehiro, 2017) and new information gained during the present study, showing horizons of Assemblages 1–3.

Sapporipora? sp. Figs. 3A, B

Material examined: NMNS PA20546, 20547.

Occurrence: Red spotted white limestones, Assemblage 2.

Description: Two fragments of poorly preserved coralla were examined; they are cerioid and attain 45 mm in diameter. Corallites prismatic with 4–6 sides; diameters of corallites are small, 0.4–0.7 mm. Intercorallite walls weakly thickened, 0.08–0.13 mm; mural pores may occur on corallite faces. No distinct septal spines observable. Tabulae complete and nearly horizontal.

Discussion: Although the examined specimens are poor in preservation, their narrow corallites and weakly thickened corallite walls suggest relationship with the Silurian? to Devonian genus *Sapporipora*. Subfamily Pachyfavositinae Mironova, 1965 Genus **Pachyfavosites** Sokolov, 1952 *Type species: Calamopora polymorpha* var. *tuberosa* Goldfuss, 1826.

Pachyfavosites hikoroichiensis sp. nov. Figs. 4A–F

urn: Isid:zoobank.org:act:C0FD0107-1E7B-42C7-8612-BD4E33ED0C5E

Type material: Holotype, NMNS PA20550. Paratypes, NMNS PA20548, 20552–20554, 20556, 20557.

Other material examined: NMNS PA20549, 20551, 20555.

Occurrence: Greenish tuffaceous shales, Assemblage 3.

Diagnosis: Species of *Pachyfavosites* with nodular to longitudinally elongated coralla; corallites large for the genus, 0.5–3.0 mm (2.7 mm mean near corallum periphery); intercorallite walls 0.20–0.53 mm in thickness; mural pores well develop mostly on corallite faces; septal spines well-developed, low conical; tabulae common, mostly complete; there are 3–8 tabulae in 5 mm.

Description: Coralla cerioid; the most usual corallum growth forms are nodular to subspherical, and longitudinally elongated types also recognized in rare cases; the holotype has 65 mm in diameter and 34mm in height; an elongated corallum of a paratype (NMNS PA20557) leaches 18mm in diameter and 66 mm in height. Corallites prismatic with 3-10 sides to rounded subprismatic; except for longitudinally elongated coralla where corallites indicate weak outward curvature, corallite arrangement is radial; diameters of corallites large for the genus, range from 0.5 mm to 3.0 mm with 2.7 mm mean near corallum periphery; calices shallow to very sallow: openings of calices are perpendicular for corallum surface in nodular and obliquely upward, approximately 50° for surface, in elongated types; lumina indicate rounded sub-polygonal transverse sections; increases of new corallites frequent, probably lateral. Intercorallite walls uniformly thickened, 0.20-0.53 mm and differentiated into thin median line and transparent stereoplasm; microstructure of stereoplasm is rect-radiate fibers; distinct growth lamellae in stereoplasm is not



Fig. 3. A, B, Sapporipora? sp., NMNS PA20547, thin sections; A, transverse sections of corallites, B, longitudinal sections of corallites. C–F, Acaciapora? sp., NMNS PA20558, thin sections; A, longitudinal section of corallum; D–F, transverse to longitudinal sections of corallites. Scale bar: 3 mm in A, B, D–F; 6 mm in C.

observable; mural pores well-developed, mostly occur on corallite faces and rarely near angles and form a single to rarely two row(s); profiles of pores are circular to longitudinally elongated; typical pores have 0.10-0.23, 0.21×0.27 mm in diameter; septal spines well-developed, low conical with wide bases; lengths of spines are 0.05-0.19 mm; tabulae common and complete or incomplete in very are cases; in longitudinal section, they exhibit nearly flat, weakly concave or convex, weakly to moderately oblique profiles; there are 3–8 tabulae in corallite length of 5 mm; some tabulae thickened, attaining 0.21 mm.

Etymology: The specific name derives from the Hikoroichi area, from which this new species was recovered.

Discussion: The absence of the distinct growth laminae in stereoplasm suggests that the Ohno



Fig. 4. Pachyfavosites hikoroichiensis sp. nov., thin sections. A–C, holotype, NMNS PA20550; A, transverse section of corallum, B, transverse sections of proximal corallites, C, longitudinal sections of distal corallites. D, paratype, NMNS PA20556, longitudinal section of corallum. E, paratype, NMNS PA20552, transverse sections of distal corallites. F, paratype, NMNS PA20554, transverse sections of distal corallites. Scale bar: 10 mm in A; 6 mm in B, D; 3 mm in C, E, F.

species places within *Pachyfavosites* rather than *Lamellaeoporella* (Smirnova *in* Cherkesova *et al.* 1968). *Pseudopachyfavosites* (Tchi, 1976) is diagnosed by the possessions of the pinnately arranged microstructure in stereoplasm and the squamulae-like septa. These characters are not developed in the species.

Pachyfavosites hikoroichiensis sp. nov. is comparable with two previously known species of the genus from Japan, namely P. katoi Niko (2007, p. 66, 68, figs. 6-1-5) from the Emsian to Eifelian (late Early to early Middle Devonian) Ozako Member of the Fukuji Formation in Gifu Prefecture and P. hidensiformis (Mironova, 1961, p. 149, 150, pl. 5, figs. 1a, b, v. g; Niko and Senzai, 2011, p. 29, 31, figs. 1-1-8) from the Lochkovian (early Early Devonian) part of the Oisedani Member, the Kamianama Formation in Fukui Prefecture. The type locality of the last species is the Lochkovian rocks of Salair, southwestern Siberia. After that it known to occur in the Yana River Basin, eastern Siberia (Dubatolov, 1969). The principal difference between P. hikoroichiensis and these known spices is mean corallite diameters; 2.7 mm in the new species versus 1.2 mm in P. katoi and 1.6 mm in P. hidensiformis.

An Eifelian species, *Pachyfavosites gurievskiensis* Dubatolov (1959, p. 66, 67, pl. 18, figs. 5a, b; Tchi, 1980, p. 156, pl. 72, figs. 3a, b) from the Kuznetsk Basin, southwestern Siberia (Dubatolov, 1959) and Jilin, Northeast China (Tchi, 1980), also resembles *P. hikoroichiensis*, but its small corallite diameters (up to 2 mm) and fewer septal spines distinguishes *P. gurievskiensis* from *P. hikoroichiensis*.

Superfamily Pachyporoidea Gerth, 1921 Family Pachyporidae Gerth, 1921 Genus *Acaciaporella* Tchi, 1980 *Type species: Acaciaporella jilinensis* Tchi, 1980.

> Acaciaporella? sp. Figs. 3C–F

Material examined: NMNS PA20558.

Occurrence: Red spotted white limestone, Assemblage 2.

Description: A single cerioidal corallum attached on brachiopod spine was available for study; it is short cylindrical having 7mm in diameter and 19 mm in length; no branching observable. Corallites prismatic with 3–8 sides; diameters of corallites are 0.6–2.2 mm; number of corallite consisting corallum is few for the family; calices very deep, oblique. Intercorallite walls strongly thickened, attaining 0.96 mm and differentiated into median line and stereoplasm; mural pores well developed on corallite faces and near corallite angles. Both spines and squamulae are recognized as septal element. Tabulae very rare, complete.

Discussion: The material clearly resembles the type species of *Acaciaporella* from Inner Mongolia, North China (Tchi, 1980) by its corallite number in transverse section of corallum, thickened intercorallite walls and the coexistences of septal spines and squamulae. However, previously known range of the genus is exclusively in the early Permian (Lin *et al.*, 1988).

Genus Egosiella Dubatolov in Sokolov, 1955

Type species: Egosiella safonoviensis Dubatolov *in* Sokolov, 1955.

Egosiella? sp. Figs. 5A–D

Material examined: NMNS PA20559-20563.

Occurrence: Red spotted white limestones, Assemblage 2 (NMNS PA20561–20563) and greenish tuffaceous shales, Assemblage 3 (NMNS PA20559, 20560).

Description: Coralla ramose, formed by cylindrical branches, and cerioid; anastomosed branches may present; diameters of branches are 3.2–4.9 mm. Corallites slender, probably prismatic; their transverse profiles are unclear by despairing median line; approximate corallite diameters 0.2–0.4 mm; proximal portions of corallite run parallel with branch axis and form axial zone, then distal corallites in peripheral zone curve outwardly to form oblique calices; transverse sections of lumina are nearly circular. Intercorallite walls thin, 0.02–0.09 mm, in axial zone and rapidly thickened attaining 0.33 mm in peripheral zone; distinct mural pore not observable. Tabulae probably absent.

Discussion: The preserved characters above correspond to those of the Middle Silurian to Middle Devonian genus *Egosiella*, but the present Ohno specimens are not complete to enough for the generic determination.



Fig. 5. A–D, *Egosiella*? sp., thin sections; A, NMNS PA20561, longitudinal to oblique sections of branches, B–D, NMNS PA20559, B, C, longitudinal sections of branches, D, longitudinal (off branch axis) section of branch, showing transverse sections of distal corallites. E, F, *Alveolites* sp., NMNS PA20611, thin sections; E, longitudinal section of corallum, F, transverse sections of corallites. Scale bar: 6 mm in A, B, E; 3 mm in C, D, F.

Genus *Hillaepora* Mironova, 1960 *Type species: Hillaepora spica* Mironova, 1960.

Hillaepora gionensis Niko and Adachi, 1999 Fig. 10E

Hillaepora gionensis Niko and Adachi, 1999, p. 112, figs. 1-1–5; Niko, 2003, p. 9, 10, figs. 1-5, 6.

Material examined: NMNS PA20564. Occurrence: Limestone pebble, Assemblage 1. Discussion: A single specimen of fragmentary branch is assigned to *Hillaepora gionensis* based on the following characters: branch relatively narrow with approximately 4 mm in reconstructed diameter and cerioid except for peripheral zone of branch, where distal corallites become free; corallite nearly straight to gradually bend outwardly; dimeters of corallites are small, 0.3–0.6 mm; intercorallite walls 0.10–0.25 mm in thickness; no septal spine observable; tabulae complete, rare.

Hillaepora gionensis was elected on the four type specimens from the Ludlow (early late Silurian) G3

Member of the Gionyama Formation in Miyazaki Prefecture (Niko and Adachi, 1999). This species also occurs from the Ludlow part of the Suberidani Group in Tokushima Prefecture (Niko, 2003).

Genus *Squameostriatopora* Tchi, 1980 *Type species: Squameostriatopora ferospina* Tchi, 1980.

Squameostriatopora tachibanai sp. nov. Figs. 6A–G

urn: Isid:zoobank.org:act:EF8B0F8A-0788-4E86-B83A-0410C29E82E9

Type material: Holotype, NMNS PA20565. Paratypes, NMNS PA20566, 20570.

Other material examined: NMNS PA20567–20569, 20571.

Occurrence: Red spotted white limestones, Assemblage 2 (NMNS PA20570–20571), and greenish tuffaceous shales, Assemblage 3 (NMNS PA20565–20569).

Diagnosis: Species of *Squameostriatopora* with large corallite diameters indicating 0.2–1.8 mm (1.5 mm mean near branch surface); intercorallite walls 0.15–0.49 mm in thickness; mural pores rarely occur on corallite faces; septal spines well developed, low conical; squamulae relatively rare, very long attaining 0.46 mm; tabulae sporadic, complete or incomplete; there are 0–4 tabulae in 5 mm.

Description: Only isolated branches are available for study; they are subcylindrical, 6-11 mm in diameter, cerioid. Corallites prismatic to sub-prismatic with somewhat irregular transverse sections having 4 to indistinct 9 sides; diameters of corallite are large for the genus, 0.2–1.8 mm, 1.5 mm mean near branch surface; each corallite run parallel with branch axis, then it gradually bent outward to form upwardly oblique calice; opening angles of calices for branch surface are 30°-65°; calical depths very deep to deep; lumina rounded sub-polygonal in transverse section; lateral increases of new corallites commonly occur in axial zone of branch. Intercorallite walls uniformly thickened and differentiated into median line and stereoplasm; in longitudinal section, walls exhibit weak sinus; microstructure of stereoplasm is rect-radiate fivers; thicknesses of walls are 0.15-0.49 mm; mural pores small, rarely

occur on corallite faces and have circular profiles; diameters of pores are 0.08–0.14 mm; septal element consists of well-developed spines and relatively rare squamulae; septal spines low conical, 0.06–0.10 mm in length; squamulae very long, 0.35–0.46 mm, and upwardly directed; tabulae sporadic, complete or incomplete in rare cases, directly transverse for corallite to more or less oblique; there are 0–4 tabulae in 5 mm of corallite length; some tabulae weakly thickened attaining 0.10 mm.

Etymology: The specific name honors the late Koichi Tachibana for recognition of his paleonto-logical and geological contributions in the South Kitakami Belt.

Discussion: Squameostriatopora is a very rare genus. Previously only the type species, *S. ferospina* Tchi (1980, p. 169, pl. 69, figs. 4a, b) from the Lower Devonian in Jilin have been known (Lin *et al.*, 1988). This species differs from *S. tachibanai* sp. nov. by its smaller corallite diameters; 0.4–0.7 mm versus attaining 1.8 mm in *S. tachibanai*. In addition, restricted distribution of its septal elements in the peripheral zone is not developed in the new species.

Genus *Striatopora* Hall, 1851 *Type species: Striatopora flexuosa* Hall, 1851.

> *Striatopora* sp. cf. *S. sugiyamai* Niko and Adachi, 1999 Fig. 10F

Compare with:

Coenites sp., Sugiyama, 1944, p. 46, pl. 3, figs. 2a, b.

Striatopora sp., Adachi and Niko, 1996, p. 70, figs. 4-3, 4.

Striatopora sugiyamai Niko and Adachi, 1999, p. 114, 116, figs. 2-1–7, 3-1; Niko, 2024a, p. 4, pl. 2, figs. 4–7.

Striatopora sp. cf. S. sugiyamai, Niko, 2003, p. 10, figs. 1-1-4.

Material examined: NMNS PA20572.

Occurrence: Limestone pebble, Assemblage 1.

Discussion: A single oblique section of fragmentary branch was examined. Its characters are as follows: diameter of branch is very small, 1.4 mm; corallites outwardly curved and have 0.2–0.4 mm in diameter; intercorallite walls thin in axial zone of branch, then rapidly increase in thickness, attaining



Fig. 6. Squameostriatopora tachibanai sp. nov., thin sections. A–C, E, F, holotype, NMNS PA20565; A, longitudinal section of branch, B, longitudinal sections of distal corallites, arrow indicates squamulae, C, longitudinal sections of proximal corallites, E, F, transverses to oblique sections of corallites; D, paratype, NMNS PA20570, transverse section of branch; G, paratype, NMNS PA20566, longitudinal sections of corallites, arrow indicates squamulae. Scale bar: 6 mm in A, D; 3 mm in B, C, E–G.

approximately 0.2 mm, to form peripheral stereozone; no septal spine observable; tabulae complete, common. The Ohno specimen agrees well with the type specimens of *Striatopora sugiyamai* from the G2 and G3 members of the Gionyama Formation in Miyazaki Prefecture except for its much smaller branch diameter. It thinks that this dimensional difference may be intraspecific variation, but the material is insufficient for a confident specific identification.

Striatopora sugiyamai and closely related species with it occur abundantly from the Wenlock and commonly from Ludlow in the Kurosegawa Belt in Southwest Japan (Niko and Adachi, 1999; Niko, 2003, 2024a).

Genus Thamnopora Steininger, 1831

Type species: Thamnopora madreporacea Steininger, 1831.

Thamnopora ohnoensis sp. nov. Figs. 7A–E

urn: Isid:zoobank.org:act:50218417-A31B-4274-8EBC-3AF22B8F0191

[?] *Thamnopora cristata* (Blumenbach). Yabe and Sugiyama, 1937, p. 418.

[?] *Thamnopora* sp. nov., Sugiyama, 1941, p. 548. *Thamnopora* sp., Minato *et al.*, 1979a, pl. 7, fig. 1.

Type material: Holotype, NMNS PA20578. Paratypes, NMNS PA20573, 20574, 20576, 20577, 20580, 20594, 20596, 20599, 20600.

Other material examined: NMNS PA20575, 20579, 20581–20593, 20595, 20597, 20598, 20601–20608.

Occurrence: Red spotted white limestones, Assemblage 2 (NMNS PA20583–20608) and greenish tuffaceous shales, Assemblage 3 (NMNS PA20573–20582).

Diagnosis: Species of *Thamnopora* with relatively small corallite diameters, 0.3–1.4 mm, 1.0 mm in mean near branch surface, and narrow peripheral zone; intercorallite walls 0.25–0.71 mm in thickness; peripheral stereozone absent; mural pores common, very small in diameter, up to 0.15 mm; septal spine relatively rare, low conical to needle-like; tabulae complete or incomplete, closely spaced; there are 5–13 tabulae in 5 mm.

Description: Coralla ramose with frequent anastomoses, cerioid; the largest specimen (holotype) has 102 mm in diameter and 55 mm in height; branches usually cylindrical; branching bifurcate or umbelliferous in rare cases; usual diameters of branches are 4–12 mm. Corallites prismatic with 4–9 sides; dented angles and faces of corallites commonly developed; there are 76–107 corallites in transverse section of branch; corallite diameters relatively small for the genus, 0.3-1.4 mm, with 1.0 mm mean near branch surface; in axial zone of branch, corallites run parallel with branch axis, then they turn outward to form narrow peripheral zone; calices shallow to very shallow and open nearly perpendicular for branch surface; transverse sections of lumina are circular to rounded subpolygonal; increases of new corallites occur frequently in axial and rarely in peripheral zones, lateral. Intercorallite walls uniformly thickened, 0.25-0.71 mm; peripheral stereozone not developed; structurally, walls differentiated into thin median dark line and stereoplasm; microstructure of stereoplasm is rect-radiate fibers; mural pores commonly occur on corallite faces; profiles of pores are circular to oval with very small diameters, indicating 0.06-0.13, 0.06×0.15 , 0.08×0.10 mm in typical ones; septal spine relatively rare, low conical to needle-like, and 0.08-0.23 mm in length; tabulae well-developed, mostly complete, but incomplete tabulae are not rare; complete tabulae variable in transverse section, ranging from directly transverse to more or less oblique for corallites, or concave proximally; spacing of tabulae close; there are 5–13 tabulae in corallite length of 5 mm.

Etymology: The specific name is derived from the type stratum named the Ohno Formation.

Discussion: Thamnopora ohnoensis sp. nov. is comparable with three Early Devonian species, including T. kolodaensis Dubatolov (1959, p. 83-85, pl. 24, figs. 3-5, 6a, b, v, 7) from the Lochkovian of the Kuznetsk Basin, southwestern Siberia, T. plumosa Yanet in Dubatolov et al. (1968, p. 86, 87, pl. 36, figs. 4a, b) from the Lochkovian of the Urals, and T. xinjiangensis Lin and Wang in Wang (1983, p. 228, 229, pl. 73, figs. 3a, b) from the Xinjiang Uygur Autonomous Region, Northwest China. Distinctive features of these species from T. ohnoensis are as follows: T. kolodaensis has the large mural pores, 0.2-0.3 mm, versus up to 0.15 mm in the new species; T. plumosa differs by its very small corallite diameters, 0.4-0.75 mm, versus attaining 1.4 mm in ditto; and septal spines are not observable in T. xinjiangensis.

Two closely related Givetian species, namely *Thamnopora angusta* Lecompte, 1939, p. 115, 116, pl. 16, figs. 17–20) from Belgium and *T. reedi* Dubatolov (1959, p. 107, 108, pl. 38, figs. 1a, b, v, g, 2, 3a,



Fig. 7. Thamnopora ohnoensis sp. nov., thin sections. A–C, holotype, NMNS PA20578; A, longitudinal section of corallum, B, longitudinal to oblique sections of corallites, C, transverse sections of corallites. D, E, paratype, NMNS PA20577; D, transverse to oblique sections of corallites, E, transverse section of branch. Scale bar: 10 mm in A; 3 mm in B–D; 6 mm in E.

b, v) from the Kuznetsk Basin, are also comparable with *T. ohnoensis*. However, their tabulae spacings are much wider than that of the new species.

Yabe and Sugiyama (1937)documented Thamnopora cristata (Blumenbach, 1803, p. 25, 26, pl. 3, fig. 12), whose type series known to occur from the Upper Devonian of Spain, in the faunal list of the Ohno Formation as mentioned above. The diagnostic characters of T. cristata cristata provided by Flügel and Flügel (1979, p. 52, 53, pl. 1, figs. 1-4) are 1) corallite diameters moderate up to 1.9mm, 2) intercorallite walls form peripheral stereozone, 3) septal spines absent, and 4) tabulae sparse having 3.0-4.5 mm in distance between adjacent tabulae. It thinks that there is no direct relationship between this species and at least the examined specimens of T. ohnoensis in the present study.

> Suborder Alveolitina Sokolov, 1950 Family Alveolitidae Duncan, 1872 Subfamily Alveolitinae Duncan, 1872 Genus *Alveolites* Lamarck, 1801

Type species: Alveolites suborbicularis Lamarck, 1801.

Alveolites sp. Figs. 5E, F

[?] Alveolites sp., Yabe and Sugiyama, 1937, p. 418.

Material examined: NMNS PA20609–20611.

Occurrence: Red spotted white limestones, Assemblage 2.

Description: Coralla thick tabular, alveolitoid; the largest specimen (NMNS PA20611) has 53 mm in diameter and 28 mm in height. Corallites reclined throughout all growth stages with nearly horizontal directions; transverse sections of corallites are crescentic to laterally elongated sub-elliptical and 0.7–0.9 mm in width and 0.2–0.3 mm in height. Intercorallite walls thin to relatively thin, 0.06–0.19 mm; mural pores occur at corallite angels. No septal spine and tabula observable.

Discussion: Alveolites sp. in faunal list of the Ohno Formation by Yabe and Sugiyama (1937) is probably conspecific with the present species. Unfortunately, the examined material here is not sufficient for a reliable specific determination. Stratigraphically, the genus *Alveolites* ranges the Middle Silurian to the Upper Devonian (Lin *et al.*, 1988).

Genus Crassialveolites Sokolov, 1955

Type species: Alveolites crassiformis Sokolov, 1952.

Crassialveolites sp. cf. *C. niigataensis* Niko, Ibaraki and Tazawa, 2015 Figs. 8A–E

Compare with:

Crassialveolites niigataensis Niko, Ibaraki and Tazawa, 2015, p. 19, 20, figs. 2-1–6.

Material examined: NMNS PA20612.

Occurrence: Red spotted white limestone, Assemblage 2.

Description: A single corallum is available for study; it is alveolitoid, low domical in growth form, 21 mm in diameter and 9 mm in height. Corallites very narrow for the family, sub-prismatic having fanshaped to sub-trapezoidal transverse sections, 0.5-0.7 mm in width and 0.3-0.4 mm in height; proximal corallites reclined with nearly horizontal growth direction, then distal ones turn upward; form ratios (width/ height) of corallites range from 1.2 to 1.8; lumina circular to oval in transverse section. Intercorallite walls uniformly thickened throughout, relatively thick in comparing with corallite diameters, 0.04-0.25 mm; structurally walls differentiated into median line and stereoplasm; mural pores commonly occur at corallite angles or narrow sides of corallite faces; profiles of pores are circular; diameters of pores are 0.02-0.03 mm; septal spine absent; tabulae complete, directly transverse for corallites; distribution of tabulae is variable ranging from almost absent to well-developed; there are 0-6 in 2mm of corallite length.

Discussion: The above features of the present Ohno specimen especially in the gross corallite shape and intercorallite wall nature are characteristic of *Crassialveolites niigataensis*, described by Niko *et al.* (2015) from the Middle Devonian pebbles in Mesozoic conglomerate of Niigata Prefecture. However, its thinner intercorallite walls (up to 0.25 mm) than those of the types of *C. niigataensis* (attaining 0.36 mm) preclude an identification between them. Furthermore, uneven distribution of the tabulae is not developed in a type series of *C. niigataensis*.



Fig. 8. Crassialveolites sp. cf. C. niigataensis Niko, Ibaraki and Tazawa, 2015, NMNS PA20612, thin sections. A, lon-gitudinal section of corallum, B, transverse sections of corallites, C, transverse to oblique sections of corallites, D, E, longitudinal to transverse sections of corallites. Scale bar: 6 mm in A; 2.5 mm in B; 3 mm in C, D.

Order Heliolitida Frech, 1897 Suborder Heliolitina Frech, 1897 Superfamily Heliolitoidea Lindström, 1876 Family Heliolitidae Lindström, 1876 Genus *Heliolites* Dana, 1846 *Type species: Astraea porosa* Goldfuss, 1826.

Heliolites sp. Figs. 9A, B

Material examined: NMNS PA20613.

Occurrence: Greenish tuffaceous shale, Assemblage 3.

Description: A single specimen of nodular corallum was examined; its diameter approximately 21 mm. Corallites cylindrical and surrounded by prismatic coenenchymal tubules; corallite diameters



Fig. 9. *Heliolites* sp., NMNS PA20613, thin sections. **A**, transverse section of corallum; **B**, transverse sections of corallites and coenenchymal tubes. Scale bar: 6 mm in A; 3 mm in B.

range from 1.2 to 1.5 mm; there are 2-5 tubules between adjacent corallites; tubule diameters 0.3-0.6 mm. Corallite walls relatively thin, 0.06 mm; no distinct septal element recognized; tabulae complete.

Discussion: Previous records of the genus *Heliolites* from the Ohno Formation include *H. bohemicus* Wentzel, 1895, by Okubo (1950) and *H.* sp. by (Sugiyama, 1941). Because it is unclear that what material was based on their identifications, comparisons between the present and these reported species are impossible. Stratigraphic range of the genus *Heliolites* is the Middle Ordovician to the Middle Devonian (Hill, 1981).

Suborder Halysitida Sokolov, 1947

Family Halysitidae Milne-Edwards and Haime, 1849 Subfamily Halysitinae Milne-Edwards and Haime,

1849

Genus Schedohalysites Hamada, 1957

Type species: Halysites orthopteroides Etheridge, 1904.

Schedohalysites kitakamiensis (Sugiyama, 1940) Figs. 10A–D

Schedohalysites kitakamiensis (Sugiyama, 1940): Niko, 2023, p. 76, figs. 2D–G [with earlier synonymy]. *Material examined*: NMNS PA20614, 20615. *Occurrence*: Limestone pebbles, Assemblage 1.

Discussion: Two fragmentally coralla were assigned to *Schedohalysites kitakamiensis* based on the following characters: coralla cateniform with elongated lacunas; ranks composed by 3–6 corallites; in transverse section, corallites weakly inflated with 1.0–1.3 mm in length and 0.6–0.8 mm in width; coenenchymal tubes between adjacent corallites sometimes absent; corallite wall thickness ranges from 0.08 to 0.17 mm; tabulae complete. This species dominantly occurs from the Ludlow limestone in the South Kitakami and Kurosegawa belts in Japan (e.g., Sugiyama, 1940; Hamada, 1956, 1958; Niko, 2015, 2023).

Order Auloporida Sokolov, 1947 Superfamily Auloporoidea Milne-Edwards and Haime, 1851

Family Palaeofavosiporidae Stasinska, 1976 Genus *Kanashiropora* Niko, 2001 *Type species: Kanashiropora kozui* Niko, 2001.

> *Kanashiropora okuboi* sp. nov. Figs. 11A–E

urn: Isid:zoobank.org:act:87398E2F-9094-4548-8E03-96C0F6F43CA5

Type material: Holotype, NMNS PA20617. Paratype, NMNS PA20616.



Fig. 10. A–D, Schedohalysites kitakamiensis (Sugiyama, 1940), thin sections. A, B, NMNS PA20615; A, transverse section of corallum, B, longitudinal section of corallum. C, D, NMNS PA20614, transverse sections of corallum. E, *Hillaepora gionensis* Niko and Adachi, 1999, NMNS PA20564, longitudinal thin section of branch. F, *Striatopora* sp. cf. S. sugiyamai Niko and Adachi, 1999, NMNS PA20572, oblique thin section of branch. Scale bar: 3 mm in A–C, E; 6 mm in D; 2.1 mm in F.

Occurrence: Greenish tuffaceous shales, Assemblage 3.

Diagnosis: Species of *Kanashiropora* with relatively large corallite diameters, mostly 0.4–1.9 mm, 1.3 mm in mean, and thickened intercorallite walls, 0.23–0.92 mm; mural pores rare; tabulae very rare, complete.

Description: Among the examined two specimens, a lager specimen, 18 mm in diameter and 29 mm in height, assigned the holotype and a smaller one, 20 mm in diameter and 10 mm in height, assigned the paratype; coralla phacelo-cerioid, high to low domical, and encrusting on rugose coral as substratum; intra-corallum lacunae frequently developed; connecting tubule absent. Early juvenile corallites alveolitoid-like with semi-circular to fun-shaped transverse sections; in cerioidal portions, transverse sections of corallites are prismatic with 4–8 sides to rounded subpolygonal; phaceloidal portions tend to occur vicinity of corallum periphery, where corallites usually free and cylindrical to subcylindrical; except for early juvenile corallites that have 0.9×0.6 , 1.4×0.8 mm in diameters of typical ones, corallite diameters relatively large for the genus, range from 0.4–1.9 mm with 1.3 mm mean; lumina narrowed by wall thickening and have nearly circular to subpolygonal transverse sections; calices upwardly oblique to perpendicular to corallum surface, very deep to deep; increase of new corallite commonly occur at lateral position. Intercorallite walls thickened and differentiated into median line and stereoplasm on its both sides; corallite walls composed by thin epitheca and inner thick stereoplasm; microstructure of stereoplasm is not preserved; thickness of intercorallite walls are 0.23–0.92 mm; mural pores rare, occur on corallite faces or near angles: profiles of pores are circular with 0.13–0.19 mm in diameter; septal spine absent; tabulae very rare, complete, and directly transverse to weakly uparched; some tabulae thick-ened, attaining 0.10 mm.

Etymology: This species is named in honor of the late Masahiro Okubo in recognition of his contributions in the geology of the Hikoroichi area.

Discussion: Until now Kanashiropora kozui Niko (2001, p. 82, 84, 86, figs. 5-1–5, 6-5, 6) from the Lochkovian Takaharagawa Member of the Fukuji Formation was an only representative of the genus. When compared with the type species, *K. okuboi* sp. nov. is characterized by its larger corallite diameters (0.4–1.9 mm with 1.3 mm mean versus 0.3–1.1 mm with 0.9 mm mean in *K. kozui*) and thicker intercorallite walls (0.23–0.92 mm versus 0.06–0.56 mm in ditto). A rareness of the mural pore developments in this new species also serves specific separation from *K. kozui* whose pores are abundant in the proximal and common in the distal portions.

Superfamily Syringoporoidea de Fromentel, 1861 Family Syringoporidae de Fromentel, 1861

Genus Syringopora Goldfuss, 1826

Type species: Syringopora ramulosa Goldfuss, 1826.

Syringopora sanrikuensis sp. nov. Figs. 12A–E

urn: Isid:zoobank.org:act:3D17C25B-DD9B-43E2-BAE4-770758AAB074

Type material: Holotype, NMNS PA20618.

Occurrence: Greenish tuffaceous shale, Assemblage 3.

Diagnosis: Species of *Syringopora* with corallite diameters of 1.5–2.4 mm, 2.2 mm in mean; spacing of corallites very close and coalescence of neighboring corallites frequently occurs; connecting tubuli well-developed, short; corallite walls thick, 0.38–0.52 mm; septal spines rare; tabulae numerous

and form intermittent axial syrinxes; positions of syrinxes central to sub-marginal.

Description: An only available specimen of phaceloid corallum assigned the holotype; it indicates tabular growth form with 49 mm in maximum observable diameter and 27 mm in height. Corallites cylindrical, moderate in diameter, 1.5-2.4 mm with 2.2 mm mean, and close in spacing; neighboring corallites frequently coalesce to form lax mass containing up to four corallites; distance (center-tocenter) between adjacent corallites are 1.6-2.7 mm; there are 15–18 corallites in 1 cm²; increase of new corallite is not developed in sectioned part; calices lacks external modification with relatively shallow pits; lumina circular in transverse section; connecting tubuli well-developed, having short lengths, 0.1-0.5 mm, and relatively large diameters, 0.7-1.2 mm. Corallite walls thick for the genus, 0.38-0.52 mm, and differentiated into thin epitheca and inner thick stereoplasm; no microstructure of stereoplasm preserved; in coalesced part, connecting tubuli replaced by mural tunnels; diameters of tunnels are 0.22-0.27 mm; septal spines rare, high conical to rod-like, and short, 0.08-0.13 mm; tabulae numerous, incomplete, and infundibuliform or dissepiment-like in rare cases; there are 5-11 tabulae in 5mm of corallite length; axial syrinxes intermittently formed by crowded tabulae, present at central to sub-marginal positions, and have circular to elliptical transverse sections; diameters of typical syrinxes are 0.4, 0.6, 0.5×0.7 , 0.4×0.8 mm.

Etymology: This species is named after Sankiku that is the old place name including the type locality.

Discussion: Syringopora sanrikuensis sp. nov. is similar to S. tarejaensis Chernyshev (1941, p. 33, 34, 56, pl. 12, figs. 1–3, text-fig. 10) from the Lower Devonian in the Taimyr Peninsular, the Far North of Russia and S. xuguitensis Tchi (1980, p. 178, 179, pl. 82, figs. 5a, b) from the Middle Devonian of Jilin, Northeast China. Distinctive features of S. sanrikuensis separating from latter two species are its moderate corallite diameters (approximately 2.2 mm versus 1.3–1.5 mm in S. xuguitensis), thick corallite walls (0.38–0.52 mm versus 0.1 mm in S. tarejaensis and 0.2 mm in S. xuguitensis), and septal spine occurrences (rare versus well-developed in S. tarejaensis and S. xuguitensis).



Fig. 11. Kanashiropora okuboi sp. nov., thin sections. A–C, holotype, NMNS PA20617, A, longitudinal section of corallum, B, longitudinal to transverse sections of corallites, C, transverse to oblique sections of corallites. D, E, paratype, NMNS PA20616, thin sections; D, longitudinal section of corallum, E, longitudinal to oblique sections of corallites. Scale bar: 6 mm in A, D; 3 mm in B, C, E.



Fig. 12. Syringopora sanrikuensis sp. nov., holotype, NMNS PA20618, thin sections. A, B, longitudinal sections of corallites, C, transverse section of corallum, D, E, transverse sections of corallites. Scale bar: 3 mm in A, B, D, E; 6 mm in C.

Syringopora sp. (Niko, 2012, p. 55, 57, figs. 6-1–7), described from the Lochkovian Takaharagawa Member in the Fukuji area, apparently distinguished from *S. sanrikuensis* by its larger corallite diameter attaining 3.8 mm and fewer connecting tubuli than those of the new species.

Assemblages and age

Identified tabulate corals and their inferred ages in each assemblage are as follows.

Assemblage 1: *Schedohalysites kitakamiensis*, Ludlow (see the discussions in the previous chapter, the same shall apply hereinafter); *Hillaepora* *gionensis*, Ludlow; *Striatopora* sp. cf. *S. sugiyamai*, Wenlock–Ludlow.

Assemblage 2: Sapporipora? sp., Silurian?– Devonian; Egosiella? sp., Middle Silurian–Middle Devonian; Acaciaporella? sp., early Permian; Squameostriatopora tachibanai sp. nov., Early Devonian; Thamnopora ohnoensis sp. nov., Lochkovian–Givetian; Alveolites sp., Middle Silurian–Late Devonian; Crassialveolites sp. cf. C. niigataensis, Middle Devonian.

Assemblage 3: *Pachyfavosites hikoroichiensis* sp. nov., Lochkovian–Eifelian; *Egosiella*? sp., see above; *S. tachibanai*, ditto; *T. ohnoensis*, ditto; *Heliolites* sp., Middle Ordovician–Middle Devonian; *Kanashiropora okuboi* sp. nov., Lochkovian; *Syringopora sanrikuensis* sp. nov., Early–Middle Devonian.

The age of Assemblage 1 can be considered as Ludlow. Among constituents of this assemblage, S. kitakamiensis is a characteristic tabulate coral of the underling Kawauchi Formation. Ehiro (2017) suggested that coral fossils in a basal slump bed (=conglomeratic limestone in this paper) are derived from the formation. The present detailed taxonomic and biostratigraphic examinations come to a similar conclusion. Although there are considerable dispersions in chronological ranges of species, the age of Assemblage 2 is probably constrained as Emsian taking into account the Nakazato Formation's age that ranges from Eifelian to Givetian (e.g., Cooper et al., 1982; Tazawa and Chen, 2001; Niko, 2024b). The formation has conformable relationship with the underlying Ohno Formation (e.g., Minato et al., 1979b). It is considerable that Assemblage 3 also suggests Emsian age because there are three common species with Assemblage 2 and the both assemblages are in close stratigraphic distance, approximately 45 m. Biostratigraphic study using radiolarians by Kurihara et al. (2005) provided Lochkovian (or Pragian) to Emsian for the age of a tuff bed that situates approximately 14m below of a horizon bearing tabulate corals of Assemblage 3. These micro- and macropaleontological results are not mutually contradictory.

Acknowledgements

The author is indebted to Masayuki Ehiro, who provided geological information of the Ohno Formation and helped in the field. I also thank Takuma Haga for his sport in registration in ZooBank. Masayuki Fujikawa reviewed the paper and offered kind suggestions.

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