# Late Silurian Favositida (Coelenterata: Tabulata) from the Hitoegane Formation, Gifu Prefecture

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**Abstract** Nine tabulate coral species belonging to the order Favositida occur in the Hitoegane Formation, Gifu Prefecture. The present Late Silurian (probably late Ludlow) fauna consists of *Favosites similis* Sokolov, 1952a, *Mesofavosites yoshikiensis* sp. nov., *Squameofavosites kamiyai* sp. nov., *Striatopora sukuna* sp. nov., *Hitoeganella hidensis* gen. et sp. nov., *Alveolites eguchii* sp. nov., *Alveolitella nectodigitata* sp. nov., *Coenites fukujiensis* Niko, 2003, and *Planocoenites gifuensis* sp. nov. *Favosites similis* indicates wide distribution, whose species has previously been recorded from Ludlow strata in Baltica, Kazakhstan and South China. The thickened tabulae of *Hitoeganella* form a peripheral stereozone as a major constituent. The new genus is somewhat similar in a morphology of the tabulae to *Kolymopora*, but the latter has the corner pores. *Alveolitella nectodigitata* is the first representative of the genus in Japan. The type locality of *C. fukujiensis* by the original designation needs to reconsider. Species of *Mesofavosites*, *Squameofavosites*, *Striatopora*, and *Alveolites* are closely allied respectively to Xinjiang Uygur (Tarim), Taimyr and Altai (Siberia), the Kuznetsk Basin (Siberia), and Kawauchi (Southern Kitakami Mountains) species. **Key words :** Late Silurian, tabulate corals, Favositida, *Hitoeganella* gen. nov., Hitoegane Formation, Gifu.

## Introduction

Late Silurian (probably late Ludlow) favositids are described from the Hitoegane Formation in the Hitoegane area, Yoshiki-gun, Gifu Prefecture, Central Japan as the second installment in a series describing the tabulate coral fauna of this formation. The coral specimens documented herein are from talus on an unnamed ridge, whose locality is identical with that for the previously described auloporids in Niko (2001). Used abbreviation of NSM showing the repository is the National Science Museum, Tokyo.

## Systematic Paleontology

Order Favositida Wedekind, 1937 Suborder Favositina Wedekind, 1937 Superfamily Favositicae Dana, 1846 Family Favositidae Dana, 1846

## Subfamily Favositinae Dana, 1846

## Genus Favosites Lamarck, 1816

*Type species: Favosites gothlandicus* Lamarck, 1816.

## Favosites similis Sokolov, 1952a

(Figs. 1-1-5)

- Favosites forbesi Milne-Edwards and Haime var. similis Sokolov, 1952a, p. 49, 50, pl. 18, figs. 3, 4; Kim, 1978, p. 46, 47, pl. 25, figs. 5a, b.
- Favosites similis; Klaamann, 1962, p. 36–38, pl. 6, figs. 1–6, text-figs. 5a, b; Kovalevskiy, 1965, p. 120, 121, pl. 25, figs. 3a, b, v; Keller, 1966, p. 123, 124, pl. 9, figs. 2a, b; Stasinska, 1967, p. 84, pl. 25, figs. 2a, b; Smirnova, 1970, p. 49, pl. 4, figs. 1a, b, 2a, b, v.

Favosites sp., Oyagi, 2003, p. 90 [upper left].

*Material examined*: Nineteen coralla, NSM PA15014–15027, 15313–15317.

Description: Coralla variable in growth form, columnar (rarely curved) to subspherical,

or thick discoid with low domical curvature, cerioid; maximum observed size 67 mm in diameter and 114 mm in height (NSM PA15018), and 98 mm in diameter and 43 mm in height (NSM PA15021); boss-like projections commonly recognized, among them a projection on a specimen (NSM PA15018) forms full-grown corallum. Corallites prismatic with 4-8 sides in transverse section; some corallites have depressed corallite corner; diameters of corallites are relatively small for genus, 0.42-1.69 mm, with 1.20 mm mean in adult ones; calical opening obliquely upward to right angle to corallum surface in columnar coralla, whereas subspherical coralla mostly have perpendicularly oriented calices; calical depth very shallow, 0.88-1.04 mm. Intercorallite walls usually thin, 0.04-0.07 mm, but partly thickened attaining 0.15 mm, differentiated into median dark line and stereoplasm, latter of which consists of rect-radiate fibers in microstructure; mural pores circular in profile, approximately 0.19 mm in diameter, well-developed on corallite faces (mid-wall pores) forming one or two rows; mural pores on corallite corners (corner pores) are also recognized as very rare cases; septal spines common to abundant, 0.10-0.17 mm in length; tabulae complete, concave proximally (sagging) to nearly flat; spacing of tabulae is somewhat variable, but closely spaced tabulae tend to occur in peripheral zone of coralla; there are 5–13 tabulae in 5 mm of corallite length.

*Occurrence*: Argillaceous limestone (NSM PA15022), calcareous shale (NSM PA15014–15021, 15023–15027, 15313–15314, 15316, 15317), and tuffaceous shale (NSM PA15315).

*Discussion*: The examined specimens from the Hitoegane Formation well agree to the widely distributed (Baltica, Kazakhstan, South China) Ludlow species *Favosites similis* except for their partly possession of the thickened intercorallite walls and the vary rare (malformed?) possession of the corner pores. These differences seemed to be too inconsistent and minor to warrant establishing a new species. *Favosites similis* is the most abundant favositicean coral in this formation, and was previously figured by Oyagi (2003) as an unnamed species of *Favosites* from the same locality.

## Genus Mesofavosites Sokolov, 1951

*Type species: Mesofavosites dualis* Sokolov, 1951.

Discussion: Stel and Oekentorp (1976) provided a detailed re-description of the type species of Paleofavosites Twenhofel, 1914, P. asper (d' Orbigny, 1850), which is characterized by having the mural pores at the corallite corners (corner pores) and a high population of the solenia. Subsequently, Powell and Scrutton (1978) detected the mural pores on the corallite faces (mid-wall pores) in this type species. These facts resulted in some considerations, such as 1) Priscosolenia Klaamann, 1964, is a junior subjective synonym of Paleofavosites (Stel and Oekentorp, 1976), 2) Mesofavosites is a junior subjective synonym of Paleofavosites (Powell and Scrutton, 1978), and 3) an important distinction between the Favositinae Dana, 1846, and Paleofavositinae Sokolov, 1950 [nom. correct. Hill, 1981] becomes extinct (Young and Elias, 1995). Among them, a synonymy Mesofavosites and Paleofavosites is not accepted. There is no solenium recognized in the previously known species of Mesofavosites and in the herein described Hitoegane species even in the small (less than 1 mm in diameter) corallites. The mid-wall pores are extremely rare (malformed?) in Paleofavosites, whereas Mesofavosites has the mid-wall pores as the most common mural pore type. I think that these features enough separate both forms in a generic level.

<sup>Fig. 1.</sup> *Favosites similis* Sokolov, 1952a. 1, NSM PA15018, longitudinal polished section of corallum, ×1. 2, 3, NSM PA15317. 2, longitudinal thin sections of corallites, ×10. 3, transverse thin sections of corallites, ×10. 4, NSM PA15016, transverse thin sections of corallites, ×10. 5, NSM PA15017, oblique and longitudinal thin sections of corallites, ×10.



# *Mesofavosites yoshikiensis* sp. nov. (Figs. 2-1–5; 3-2)

*Holotype*: NSM PA15320, from which eight thin and two polished sections were made.

*Other specimens*: Fifteen thin sections were studied from the six paratypes, NSM PA15318, 15319, 15321–15323, 15325. In addition, a single specimen, NSM PA15324, was also examined.

*Diagnosis*: Species of *Mesofavosites* with longitudinally elongated coralla, approximately 2.67 mm in adult corallite diameter; intercorallite walls strongly wavy, relatively thin, 0.07–0.13 mm; corner pores uncommon, their distribution restricted between immature and adult corallites; septal spines abundant, mostly low conical; tabulae widely spaced, 3–7 tabulae in 5 mm of corallite length.

Description: Coralla longitudinally elongate with height much greater than diameter, cerioid; holotype (largest specimen) indicates strongly curved clavate in growth form having  $63 \times 37$  mm in diameter and 110 mm in height; a lacuna with  $18 \times 9 \,\mathrm{mm}$  in diameter developed in holotype; branching not observed. Corallites roughly prismatic, gently curved away from axis of coralla; immature corallites have 3-6 sides, then ontogenetically shift usually 6-8 sided with partly indistinct polygonal profiles distally; depressed corallite faces commonly recognized; corallite diameters range from 0.62 to 3.04 mm, with 2.67 mm mean in adult ones; calical opening obliquely upward with approximately 40°-80° in angle on corallum side; depth of calices very shallow, usually 0.66-1.50 mm; increase of new corallites is lateral (and intracalicular?), frequent; thus corallite diameters are variable even in peripheral zone of coralla. Intercorallite walls strongly wavy in longitudinal and transverse sections, differentiated into median dark line and stereoplasm; thickness of intercorallite walls is relatively thin, 0.07-0.13 mm; peripheral stereozone absent; microstructure of stereozone not preserved; mural pores circular to longitudinally elongated subcircular profiles, occur on corallite faces as midwall pores and at corallite corners as corner pores; mid-wall pores common throughout all growth stages of corallites, forming 1 or 2 rows, 0.17-0.27 mm in diameter; corner pores uncommon: their distribution restricted to intercorallite walls between immature and adult corallites, approximately 0.25 mm in diameter; usual mural pores of both types closed by thin pore plates; solenium absent; septal spins abundant, low (or rarely high) conical with wide bases, 0.04-0.14 mm in length in protruded parts into tabularia; tabulae complete, usually nearly flat, but concave distally (uparched) ones frequently recognized near calice; spacing of tabulae widely distributed; there are 3-7 tabulae in 5 mm of corallite length; dissepiment-like plate (incomplete tabula?) occurs in calice as a solitary instance.

*Etymology*: The specific name is derived from a county named Yoshiki-gun. The type locality of this new species belongs to this county.

Occurrence: Calcareous shale.

Discussion: Mesofavosites yoshikiensis sp. nov. most closely approaches *M. baichengensis* Wang (1981, p. 43, pl. 23, figs. 3a, b) from the Middle to Upper Silurian of Xinjiang Uygur in Tarim, northwest China. Nevertheless, *M.* yoshikiensis can be distinguished from the Chinese species by being the widely spaced tabulae (3–7 tabulae in 5 mm of corallite length versus up to 20 in the peripheral coralla of *M. baichengensis*) and the somewhat thinner intercorallite walls (0.07–0.13 mm versus up to 0.2 mm in *M. baichengensis*). Mesofavosites orientalis Yü (1962, p. 48, pl. 10, figs. 1a, b, 2a, b), known from the Middle Silurian of the Qilian Shan Mountains in North China, and *M. tytschinskii* 

<sup>Fig. 2.</sup> *Mesofavosites yoshikiensis* sp. nov. 1, 2, 4, 5, holotype, NSM PA15320. 1, longitudinal polished section of corallum, ×1. 2, partial enlargement to show intercorallite wall structure, longitudinal thin section, ×75. 4, longitudinal thin sections of distal corallites, ×10. 5, transverse thin sections of corallites, ×10. 3, paratype, NSM PA15319, longitudinal thin sections of corallites, ×10.

## Silurian Corals from Gifu



Barskava (1962, p. 43, 45, pl. 1, figs. 5, 6), known from the Wenlock (Lower Silurian) of Central Taimyr in Siberia, are also comparable with M. yoshikiensis. These species differ from this new species in the following ways. The much thinner intercorallite walls (0.04-0.09 mm in M.orientalis and 0.03–0.08 mm in M. tytschinskii) with relatively weak waves, the closely spaced tabulae and the well-developed corner pores unlike in M. yoshikiensis. In addition, diameters of the adult corallites are slightly smaller in M. orientalis (2.3-2.5 mm) than M. yoshikiensis (approximately 2.67 mm). Mesofavosites was listed by Kato et al. (1980) from the Yokokurayama Group, Kochi Prefecture. Lacking of description concerning this Wenlock species precludes compression with M. yoshikiensis.

## Subfamily Emmonsiinae Lecompte, 1952

## Genus Squameofavosites Chernyshev, 1941

*Type species: Favosites hemisphericus bohemica* Počta, 1902; renamed *Squameofavosites cechicus* Galle, 1978.

## *Squameofavosites kamiyai* sp. nov. (Figs. 3-1–5; 4-1–6)

Favosites sp., Oyagi, 2003, p. 90 [upper right].

*Holotype*: NSM PA15498, from which seventeen thin and one polished sections were made.

*Other specimens*: Twenty-three thin sections were studied from the six paratypes, NSM PA15328, 15494–15496, 15499, 15501. In addition, five specimens, NSM PA15326, 15327, 15497, 15500, 15502, were also examined.

*Diagnosis*: Species of *Squameofavosites* with bulbous coralla, approximately 2.05 mm in adult corallite diameter; intercorallite walls thickened attaining 0.13–0.19 mm in peripheral zone

of coralla; in addition to common mid-wall pores, corner pores rarely recognized; squamulae roughly triangular, 0.10–0.33 mm in length; tabulae closely spaced, 14–20 tabulae in 5 mm of corallite length, in most part of corallites.

Description: Coralla subspherical in early growth stages, then grow into low to high bulbous forms, cerioid; holotype (fused cluster of two coralla?) has 92 mm in diameter and 45 mm in height; largest paratype (NSM PA15499) attains 72 mm in diameter and 96 mm in length; a paratype (NSM PA15501) encircling crinoid stem. Corallites prismatic except for most proximal corallites that attached to substrate (crinoid stem) with alveolitoid-like semi-circular transverse sections; arrangement of corallites radial; immature corallites have 3-5 sides, then ontogenetically shift usually 5-8 sided in profiles; corallite diameters range from 0.38 to 2.41 mm, with 2.05 mm mean in adult corallites; calical opening mostly perpendicular to corallum surface; calical depth very shallow, usually 0.40-1.18 mm; increase of new corallites is common, lateral. Intercorallite walls weakly wavy in proximal coralla, then nearly straight distally, differentiated into median dark line and stereoplasm; thickness of intercorallite walls usually thin, 0.03-0.11 mm, but gradually thickened attaining 0.13-0.19 mm in peripheral zone of coralla; microstructure of stereoplasm may be rect-radiate fibers; mural pores occur on corallite faces as mid-wall pores and at corallite corners as corner pores; mid-wall pores with longitudinally elongated subcircular to elliptic profiles, common, forming 1 or 2 rows,  $0.15 \times 0.23$  mm,  $0.18 \times 0.23$  mm in diameter of typical ones; corner pores with circular profiles, rare, 0.10-0.12 mm in diameter; septal elements represented by relatively long squamulae that are roughly triangular with uparched curvature and thickened bases, perpendicular to intercorallite

Fig. 3. 1, 3–5, Squameofavosites kamiyai sp. nov., thin sections. 1, 3, holotype, NSM PA15498. 1, near longitudinal section of corallum, ×5. 3, near transverse section of corallum, ×5. 4, paratype, NSM PA15499, transverse sections of corallites, arrow indicates corner pore, ×10. 5, paratype, NSM PA15501, longitudinal section of immature corallum, ×10. 2, *Mesofavosites yoshikiensis* sp. nov., paratype, NSM PA15323, near longitudinal section of immature corallum, ×10.



walls to slightly inclined upward, make a pair between contiguous corallites; some squamulae form eaves-like extensions from the upper rim of mid-wall pores; dimensions of squamulae are as follows, 0.10-0.33 mm in length, 0.10-0.29 mm in width of their bases, 0.67-1.30 in length/width ratio, 0.08–0.17 mm in thickness of their bases: spacing of squamulae sporadic except for peripheral zone of coralla where squamulae abundant, up to 11 squamulae in transverse section in each corallite; contiguous squamulae rarely fused; tabulae complete, but frequently adhere to squamulae, nearly flat; spacing of tabulae moderate in proximal corallites where 8-11 tabulae occur in 5 mm of corallite length, then ontogenetically shifts close in most part of corallites where 14-20 tabulae occur in ditto.

*Etymology*: The specific name honors Mr. Toshiaki Kamiya, who collected some paratypes of this coral.

*Occurrence*: Argillaceous limestone (NSM PA15500) and calcareous shale (NSM PA15326–13528, 15494–15499, 15501, 15502).

Discussion: Squameofavosites kamiyai sp. nov. differs from all other species of Squameofavosites except S. bohemicus forma taimyrica Mironova (1974, p. 51, pl. 1 figs. 1a, b, pl. 2, figs. 1a, b, v) by the morphologic combination consisting of the thickened intercorallite walls in the peripheral zone of coralla, the corner pores, and the closely spaced tabulae except for the proximal corallites. In S. bohemicus forma taimyrica from the Lower Devonian of Taimyr in arctic Siberia and the Altai in southern Siberia, however, the corner pores are well developed, unlike S. kamiyai, its corner pores are rare. A specimen assigned by Oyagi (2003) to Favosites, appears to belong to S. kamiyai. This new species records the oldest and first Silurian occurrence of Squameofavosites in Japan.

Superfamily Pachyporicae Gerth, 1921

Family Pachyporidae Gerth, 1921

Genus *Striatopora* Hall, 1851

*Type species: Striatopora flexuosa* Hall, 1851.

# Striatopora sukuna sp. nov.

(Figs. 5-1-9)

*Holotype*: NSM PA15503, from which fifteen thin sections were made.

*Other specimens*: Twenty-three thin sections were studied from the six paratypes, NSM PA15507–15512. In addition, four specimens, NSM PA15504–15506, 15513, were also examined.

*Diagnosis*: Species of *Striatopora* with slender branches, approximately 2.4 mm in diameter, 13–34 in number of corallites in transverse section of branch, usually 0.60–0.96 mm in corallite diameter near calical rim; calical opening oblique upward to nearly perpendicular to branch surface; intercorallite walls attain to 0.63 mm in thickness in peripheral stereozone; mural pores abundant, elliptical, typically  $0.14 \times 0.19$  mm in diameter; septal spines restricted to calices; tabulae sporadic.

*Description*: Coralla ramose with slender, roughly cylindrical branches of 1.7–3.7 mm (exceptionally attaining 4.0 mm near branching point), with 2.4 mm mean, in diameter, cerioid; branching uncommon, bifurcate; total corallum diameter and growth form unknown owing to fragile nature. Corallites prismatic with usually 4–8 sides, depressed corallite corners and/or faces frequently recognized; there are 13–34 corallites in transverse section of branch; diameters of corallites range from 0.24 to 1.21 mm, usually 0.60–0.96 mm near calical rim; each

Fig. 4. Squameofavosites kamiyai sp. nov. 1–5, holotype, NSM PA15498. 1, oblique polished section of colony (fused cluster of two coralla?), ×1. 2, longitudinal thin sections of corallites, ×10. 3, transverse thin sections of corallites, ×10. 4, oblique thin sections of corallites, ×10. 5, partial enlargement to show intercorallite wall structure and details of squamulae, longitudinal thin section, ×75. 6, paratype, NSM PA15499, partial enlargement to show intercorallite wall structure and details of squamulae, squamulae, transverse thin section, ×75.



corallite consists of narrowly divergent proximal portion of approximately 1.3 mm in length and outwardly curved distal portion of approximately 1.4-2.5 mm in length; proximal and distal portions respectively form axial and peripheral zones of branch; most distal corallites indicate rapid expansion in diameter forming funnelshaped calices that are mostly deep, subcircular transverse sections, and open oblique upward (not less than approximately 50° in angle) to nearly perpendicular to branch surface; increase of new corallites is lateral, frequent; an offset occurs on outer side of parent corallite at boundary between proximal and distal portions. Intercorallite walls variable in thickness with 0.06-0.23 mm in axial zone of branches and peripheral zone of immature branches; they are abruptly thickened attaining 0.63 mm in full-grown branches to form peripheral stereozone; thus transverse sections of tabularia shift from subpolygonal to subcircular; ratios of peripheral stereozone width per branch diameter are approximately 0.7; in immature branches, peripheral stereozone not developed, and in gerontic branches, it becomes somewhat obscure resulted by intercorallite wall thickening in axial zone; structural differentiation of intercorallite walls is distinct, median dark line and stereoplasm, latter of which consists of microlamellae; mural pores abundant on corallite faces, longitudinally elongated elliptical profiles with 0.14×0.19 mm in diameter in typical one; septal spines relatively rare, restricted to calice, long for corallite size, attaining 0.31 mm, but mostly enclosed in stereoplasm; tabulae complete, convex proximally to nearly flat; spacing of tabulae sporadic.

*Etymology*: The specific name is derived from a legendary lord named Sukuna, who ruled over the Hida area (ancient provincial name of the type locality) in the fourth century.

*Occurrence*: Argillaceous limestone (NSM PA15504, 15505, 15510, 15511, 15513) and calcareous shale (NSM PA15503, 15506–15509, 15512).

Discussion: Striatopora sukuna sp. nov. closely resembles S. peetzi Dubatolov (1956, p. 97-99, pl. 4, figs. 1a, b, 2a, b; 1959, p. 124-126, pl. 42, figs. 5a, b, v, g, 6) from the Lower Devonian of the Kuznetsk Basin in southern Siberia, but the latter species differs from this new species by being the larger branch diameter (3-5 mm versus approximately 2.4 mm in S. sukuna) and the somewhat smaller mural pores (0.12-0.15 mm versus typically  $0.14 \times 0.19$  mm in S. sukuna). Striatopora sukuna seems to have some affinities for S. anuvensis Mironova (1965, p. 133, 134, pl. 31, fig. 1) from the Ludlow of Altai in southern Siberia. However, S. anuyensis is distinguished from S. sukuna by the possession of the thinner intercorallite walls in the peripheral stereozone (0.25–0.35 mm versus attaining 0.63 mm in S. sukuna). Striatopora minuscula Chudinova (1964, p. 27, 28, pl. 10, figs. 1a, b, 2, 3a, b), known from the Lower Devonian of the Kuznetsk Basin (Chudinova, 1964), and Altai and Salair in southern Siberia (Mironova, 1974), is also similar to S. sukuna, but differs in its much larger branch diameters attaining 7 mm. Striatopora sugiyamai Niko and Adachi (1999, p. 114, 116, figs. 2-1-7; 3-1) from the Wenlock of the Gionyama Formation, Miyazaki Prefecture is readily distinguished from S. sukuna by its stellately arranged axial corallites.

# Family Parastriatoporidae Chudinova, 1959

## Genus Hitoeganella nov.

*Type species: Hitoeganella hidensis* sp. nov., by monotypy.

Diagnosis: Ramose coralla with cylindrical

<sup>Fig. 5. Striatopora sukuna sp. nov., thin sections. 1, 5–9, holotype, NSM PA15503. 1, longitudinal section of branch, ×10. 5, 6, 7, 8, transverse sections of branches, note variations of intercorallite wall thickness, ×10. 9, partial enlargement to show intercorallite wall structure, transverse section, ×75. 2, paratype, NSM PA15507, longitudinal section of branch, ×10. 3, 4, paratype, NSM PA15510. 3, longitudinal thin section of branch, note complete tabulae, ×14. 4, transverse and oblique sections of corallites near calical rims, ×14.</sup> 



to subcylindrical branches that differentiated into axial and peripheral zones by outwardly growth direction change of corallites; corallites relatively large having very shallow calices with nearly perpendicular orientation to branch surface; intercorallite walls very thin in axial zone, then abruptly thickened by contiguous septal spines and inflation of stereoplasm in peripheral zone; mural pores occur on corallite faces (mid-wall pores); axial zone lacks septal spine; tabulae thickened in peripheral zone; among them most distal tabulae exceptionally thickened, anastomosed, represening major constituent of peripheral stereozone.

*Etymology*: The generic name is derived from the type stratum named the Hitoegane Formation.

# Hitoeganella hidensis sp. nov. (Figs. 6-1–6; 7-1–7)

Parastriatopora hidensis Wakata, 1974, p. 6, fig. 8 [nomen nudum].

"Parastriatopora" like favositids, Kato, 1990, p. 308.

*Holotype*: NSM PA15520, from which 37 thin sections were made.

*Other specimens*: Seventy-one thin sections were studied from the seven paratypes, NSM PA15514–15516, 15521, 15524, 15527, 15531. In addition, 13 specimens, NSM PA15517–15519, 15522, 15523, 15525, 15526, 15528–15530, 15532–15534, were also examined.

Diagnosis: As for the genus.

*Description*: Coralla ramose, consisting of relatively thick, cylindrical to subcylindrical branches of 4.8–17.5 mm (exceptionally attaining 20.1 mm near branching point), usually 9.5–15.0 mm, in diameter, cerioid; branching rare, bifurcate; total corallum diameter and growth form unknown owing to fragile nature. Corallites pris-

matic with 3-6 sides in immature corallites, then ontogenetically shift to 6-8 sides in adult ones; depressed corallite corner rarely recognized; there are 22-74 corallites in transverse section of branch; corallite diameters relatively large for family, range from 0.38 to 2.55 mm, with 1.97 mm mean in adult corallites: each corallite usually consists of gradually divergent proximal portion forming axial zone of branch and outwardly directed distal portion forming peripheral zone of branch; length of proximal corallites variable, attains to approximately 4.8 mm; length of distal corallites also variable, 1.2-4.7 mm; inflation of corallites relatively rapid for family in proximal corallites, then decreased distally; calices very shallow, 0.65-1.03 mm in usual depth, nearly perpendicular to branch surface in opening; low but wide calical bosses commonly developed; increase of new corallites lateral, frequently occurs in axial zone of branch and rarely occurs in peripheral zone. Intercorallite walls weakly wavy in longitudinal section, very thin in axial zone, 0.03–0.06 mm, and abruptly thickened attaining 0.69 mm in peripheral zone by continuation of septal spines and inflation of stereoplasm; thus transverse section of tabularia shift from polygonal to stellated; thickened intercorallite walls represent a minor constituent of peripheral stereozone; structural differentiation of intercorallite walls is distinct, median dark line and stereoplasm, latter of which consists of microlamellae; mural pores circular in profile, occur on corallite faces as mid-wall pores, common in axial zone where they form a single row; in peripheral zone, mural pores become abundant forming 2-5 rows, but most of them narrowed or closed by thickened tabulae; diameters of mural pores are 0.17–0.31 mm; septal spines absent in axial zone, and numerous in peripheral zone, low conical with relatively wide bases, approximately 0.30

Fig. 6. *Hitoeganella hidensis* gen. et sp. nov., thin sections. 1, 2, 6, holotype, NSM PA15520. 1, 6, longitudinal sections of branches, ×5. 2, longitudinal sections of distal corallites, note exceptionally thickened tabulae, ×10. 3, paratype, NSM PA15531, longitudinal sections of proximal corallites, ×10. 4, paratype, NSM PA15521, longitudinal sections of distal corallites, note abundant mural pores, ×10. 5, paratype, NSM PA15524, transverse sections of most distal corallites, showing contiguous septal spines, ×10.



mm in length; tabulae complete, nearly flat, thin in axial zone, where 3–8 tabulae occur in 5 mm of corallite length; in peripheral zone, tabulae typically complete, rarely incomplete, weakly concave proximally to nearly flat, thickened by outward growth of microlamellae, where spacing of tabulae decreased, up to 21 ones occur in 2 mm of corallite length; most distal 2–5 tabulae exceptionally thickened attaining approximately 0.8 mm, anastomosed with adjoining tabulae, and represent a major constituent of peripheral stereozone; width of peripheral stereozone is narrower than that of peripheral zone of branches; ratios of peripheral stereozone width per branch diameter are variable, 0.2–0.7, usually 0.3–0.4.

*Etymology*: The specific name is derived from the ancient provincial name of the type locality.

*Occurrence*: Argillaceous limestone (NSM PA15514–15520, 15522–15534) and calcareous shale (NSM PA15521).

Discussion: A striking feature of Hitoeganella gen. nov. is the exceptionally thickened most distal tabulae representing a major constituent of the peripheral stereozone, whose diagnosis distinguishes this new genus from most other parastriatoporids. A Late Ordovician genus Kolymopora Preobrazhenskiy (1964; type species K. irjudiensis Preobrazhenskiy, 1964, p. 15, 16, pl. 3, figs. 1a, b, text-fig. 2) from northeastern Siberia somewhat resembles Hitoeganella. Among the known four species of Kolymopora, K. nikolaevi Preobrazhenskiy (1964, p. 17-19, pl. 3, fig. 3, pl. 4, figs. 1a, b, 2, text-fig. 3) most similar to H. hidensis in a morphology of the tabulae. However, Kolymopora including K. nikolaevi differs from Hitoeganella in having exclusively the corner pores.

Because of *H. hidensis* is the most abundant and conspicuous coral in the Hitoegane Formation, this species was figured by Wakata (1974) under an invalid name "*Parastriatopora hidensis*" and was mentioned by Kato (1990) as dendritic "*Parastriatopora*" like favositids. These reports lack description.

> Suborder Alveolitina Sokolov, 1950 Family Alveolitidae Duncan, 1872

Subfamily Alveolitinae Duncan, 1872

Genus Alveolites Lamarck, 1801

*Type species: Alveolites suborbicularis* Lamarck, 1801.

*Alveolites eguchii* sp. nov. (Figs. 8-1–3; 9-1, 2)

*Holotype*: NSM PA15535, from which three thin sections were made.

*Diagnosis*: Species of *Alveolites* with thick tabular corallum; corallites and tabularia have crescentic to elongated elliptic transverse sections; form ratios (width/height) of tabularia 3.2–4.8; intercorallite walls approximately 0.12 mm in thickness; mural pores rare, restricted to near calices; septal spines common, forming a single row on lower intercorallite walls; tabulae very rare, restricted to most proximal corallites.

*Description*: Corallum encrusting, multi-layered with film-like to lenticular lacunae, thick tabular in growth form, having approximately 84 mm in diameter and 26 mm in height in maximum observed size of holotype, alveolitoid; low boss-like projections commonly developed on corallum surface. Corallites reclined throughout all growth stages with nearly horizontal to slightly upward, up to 30° in angle to substrate, in growth direction; transverse sections of corallites and tabularia are crescentic to elongated elliptic; inflation of corallites is very gradual; corallite

Fig. 7. *Hitoeganella hidensis* gen. et sp. nov., thin sections. 1, 3, 5, 7, holotype, NSM PA15520. 1, 3, 5, transverse sections of branches, note variations of branch diameters and peripheral stereozone width, ×5. 7, partial enlargement to show intercorallite wall structure, ×50. 2, paratype, NSM PA15521, transverse section of branch, ×5. 4, paratype, NSM PA15515, transverse section of branch, ×5. 6, paratype, NSM PA15516, transverse section of branch, vacond, vacond, vacond, v



sizes approximately 0.7 mm in width and 0.2 mm in height near calical rim; tabularia have 0.55-0.69 mm, with 0.61 mm mean, in width and 0.10-0.25 mm, with 0.16 mm mean, in height; form ratios (width/height) of typical tabularia range from 3.2 to 4.8; distal ends of tabularia shift to deep calices that are strongly oblique with usually 30° in opening angle (from corallum bottom) to corallum surface; increase of new corallite not observable in sectioned corallum. Intercorallite walls evenly thickened except for most proximal corallites and calices, 0.06-0.17 mm, with 0.12 mm mean, in thickness; most proximal intercorallite walls differentiated into median dark line and stereoplasm, but this structural differentiation becomes indistinct by lacking median dark line as corallite growth; thus determination of accurate profiles of distal corallites is difficult; stereoplasm consists of rect-radiate fibers(?); mural pore rare, situate on narrow sides of corallite faces, uniserial, restricted to near calices, circular with approximately 0.10 mm in diameter; septal spines commonly occur on lower intercorallite walls at nearly midway of each corallite face, usually forming a single row; their protruded portions into tabularia are short, 0.04-0.06 mm, and robust with triangular profiles; tabulae very rare, recognized only in most proximal corallites, complete, rectangular to corallite.

*Etymology*: The specific name honors the late Dr. Motoki Eguchi, in recognition of his contribution to the taxonomic study of fossil corals.

Occurrence: Calcareous shale.

*Discussion*: Sugiyama (1940) referred a Ludlow species from the "*Halysites* limestone" of the Kawauchi [Kawauti] Formation, Iwate Prefecture in the Southern Kitakami Mountains to *Alveolites simplex* Barrande. Besides I cannot accept the Sugiyama's assignment, this Kawauchi species (Sugiyama, 1940, p. 128, 129, pl. 18, fig. 7, pl. 23, figs. 1–5, pl. 31, figs. 4, 5) is remarkably similar to *A. eguchii* sp. nov. in a tabular growth form of the corallum, cross sectional shape and size of the tabularia, and scarcity in the tabulae. The distinctive features of the new

species are as follows; 1) occurrence of the mural pores are restricted to near the calices, 2) the commonly possession of the septal spines, and 3) the tabulae occurs only in the most proximal corallites. *Alveolites simplex* Barrande in Počta (1902, p. 267, 268, pl. 116, figs. 2–4) from the Silurian of Bohemia differs from the both Japanese species, on being the well-developed tabulae.

## Genus Alveolitella Sokolov, 1952b

*Type species: Alveolites fecundus* Lecompte, 1939.

*Remarks*: The concept of *Alveolitella* found in Lin *et al.* (1988) is followed herein.

# Alveolitella nectodigitata sp. nov. (Figs. 9-3–5; 10-1–3)

*Holotype:* NSM PA15537, from which 26 thin sections were made.

*Other specimens*: Sixteen thin sections were studied from the four paratypes, NSM PA15536, 15538–15540.

*Diagnosis*: Species of *Alveolitella* with slender branches of usually 5.0–8.4 mm in diameter; usual form ratios (width/height) of calices 2.3–2.5; intercorallite walls attaining 0.42 mm in thickness; mural pores abundant; septal spines well-developed both on lower and upper intercorallite walls; tabulae uncommon.

*Description*: Coralla ramose with cylindrical branches whose diameters are slender for genus, 2.5–10.6 mm, usually 5.0–8.4 mm, alveolitoid except for cerioid-like axial zone of branches; branching common, bifurcate or umbelliferous in rare cases; partial anastomoses of branches frequently occur and form irregular mass attaining approximately 36 mm in diameter; total corallum diameter and growth form of corallum unknown owing to fragile nature. Corallites slender for genus, each corallite consists of longitudinally directed proximal portion forming axial zone of branches and outwardly curved distal portion forming relatively wide peripheral zone of branches; transverse sections of corallites are



Fig. 8. 1–3, Alveolites eguchii sp. nov., holotype, NSM PA15535, thin sections. 1, longitudinal section of corallum, ×5. 2, transverse sections of distal corallites, ×14. 3, longitudinal sections of distal corallites, ×14. 4, *Planocoenites gifuensis* sp. nov., paratype, NSM PA15550, partial enlargement to show intercorallite wall structure, longitudinal thin section, ×75.



Fig. 9. 1, 2, Alveolites eguchii sp. nov., holotype, NSM PA15535, thin sections. 1, longitudinal sections of most proximal corallites, note complete tabulae, ×14. 2, partial enlargement to show intercorallite wall structure of proximal corallites, transverse section, ×75. 3–5, Alveolitella nectodigitata sp. nov., thin sections. 3, 5, holo-type, NSM PA15537. 3, transverse sections of corallites near calical rims, ×14. 5, partial enlargement to show intercorallite wall structure of proximal corallites, transverse section of corallites near calical rims, ×14. 5, partial enlargement to show intercorallite wall structure of proximal corallites, longitudinal section, ×75. 4, paratype, NSM PA15538, transverse section of corallites near calical rims, ×14.

variable, sub-elliptical to indistinct polygonal with  $0.17 \times 0.25$ ,  $0.25 \times 0.63$ ,  $0.38 \times 0.44$  mm in diameters of typical ones in proximal corallites, and may be crescentic to elliptic in distal corallites; sizes of distal corallites approximately 1.1 mm in width and 0.4 mm in height; increase of new corallites is lateral, frequently occurs in proximal corallites; tabularia also variable in transverse section, subelliptic to subcircular, shift to deep calices that have crescentic to elongated elliptic transverse sections with 0.54–0.69 mm, 0.60 mm mean, in width and 0.21-0.27 mm, 0.25 mm mean, in height, giving 2.3-2.5 in usual form ratio (width/height); calical opening obliquely upward to downward in rare cases with  $25^{\circ}-151^{\circ}$ , usually  $30^{\circ}-40^{\circ}$ , in angle to branch surface. Intercorallite walls differentiated into median dark line and stereoplasm, latter of which consists of rect-radiate fibers; this structural differentiation becomes obscure in distal corallite, where determination of accurate corallite profiles is difficult; thickness of intercorallite walls is



Fig. 10. 1–3, Alveolitella nectodigitata sp. nov., thin sections. 1, 2, holotype, NSM PA15537. 1, partial enlargement of Fig. 10-2 to show details of corallites, ×14. 2, longitudinal section of branch, ×5. 3, paratype, NSM PA15536, transverse sections of branches, ×5. 4, *Planocoenites gifuensis* sp. nov., paratype, NSM PA15551, external view of corallum surface, silicone rubber cast, ×5.

0.06-0.13 mm in proximal corallites and gradually thickened attaining 0.42 mm in distal corallites that form somewhat obscure peripheral stereozone; mural pores uniserial abundant near corallite edges, large in comparing with corallite size, elliptical usually  $0.13 \times 0.21 \text{ mm}$  in diameter; septal spines well-developed both on lower and upper intercorallite walls; septal spines on lower intercorallite walls are low conical with approximately 0.05 mm in length of protruded part, usually forming two rows; septal spines on upper intercorallite walls are high conical with approximately 0.08 mm in length of protruded part, forming a single row at midway of each corallite face; tabulae uncommon, complete, nearly rectangular to corallites.

*Etymology*: The specific name is a combination of the Latin *necto* (=connect) and *digitus* (=finger) in reference of its branch shape.

Occurrence: Calcareous shale.

*Discussion*: This species is assigned to *Alveolitella* on the basis of its ramose coralla with the frequently anastomosed branches, cerioid-like axial zone of the branches, rect-radiate fibers in microstructure of the stereoplasm, and abundant mural pores. *Alveolitella nectodigitata* sp. nov. represents the first occurrence of the genus in Japan.

The Silurian record of *Alveolitella* is very rare. Previously only a Silurian species had been referred to *Alveolitella*, namely *A. zhifangensis* Wang (1981, p. 51, 52, pl. 30, figs. 5a, b) from the Upper Silurian of Xinjiang Uygur in Tarim, northwest China. The Chinese species is characterized by the large branch diameters attaining 20 mm unlike *A. nectodigitata*, its branch diameters are usually 5.0–8.4 mm.

Family Coenitidae Sardeson, 1896 Genus *Coenites* Eichwald, 1829 *Type species: Coenites juniperinus* Eichwald, 1829.

## *Coenites fukujiensis* Niko, 2003 (Figs. 11-1–4)

Coenites fukujiensis Niko, 2003, p. 19, 21, figs. 1-1-4; 2-1-4.

*Material examined*: Seven coralla, NSM PA15541–15547.

Occurrence: Calcareous shale.

Discussion: Previously this species was represented by an only known specimen (holotype) that had been kept in the repository of the Hikaru Memorial Museum with following locality data; "collected from a flat block in talus at the Kanashirozako Valley in the Fukuji area" and "probably derived from the Early Devonian Fukuji Formation". The holotype occurs in black limestone. Although lithology of matrix is different, the specimens from the Upper Silurian Hitoegane Formation are indistinguishable from the holotype in all observable characters. It is improbable that Coenites fukujiensis has such a long range. Confirmation of the type locality is essential on the basis of the supplementary specimen having lithologically identical one with the holotype.

## Genus Planocoenites Sokolov, 1952b

*Type species: Coenites orientalis* Eichwald, 1861.

# *Planocoenites gifuensis* sp. nov. (Figs. 8-4; 10-4; 12-1–7)

*Planocoenites* sp., Kamiya and Niko, 1998, p. 67, 69, figs. 1a-c, 2.

*Holotype*: NSM PA15549, from which three thin sections were made.

*Other specimens*: Nine thin sections and a single silicone rubber cast of an external mold were studied from the six paratypes, NSM PA15548, 15550–15554. In addition, two specimens, NSM PA15555, 15556, were also exam-

Fig. 11. Coenites fukujiensis Niko, 2003, NSM PA15547, thin sections. 1, oblique and transverse sections of branches, ×5. 2, transverse section of branch, ×14. 3, longitudinal section of branch, ×14. 4, oblique section of branch, ×14.





Fig. 12. *Planocoenites gifuensis* sp. nov., thin sections. 1, 2, 4, 7, holotype, NSM PA15549. 1, longitudinal section of corallum, ×5. 2, longitudinal sections of corallites, ×10. 4, partial enlargement of Fig. 12-2 to show details of corallites, ×14. 7, partial enlargement to show intercorallite wall structure, longitudinal section, ×75. 3, 5, paratype, NSM PA15550. 3, transverse sections of proximal corallites, ×10. 5, oblique and transverse sections of corallites, note septal spines on lower intercorallite walls, ×14. 6, paratype, NSM PA15551, longitudinal sections of corallites, note thickened intercorallite walls, ×14.

ined.

*Diagnosis*: Species of *Planocoenites* with approximately 1.5 mm thick in a lamella, and crescentic calical aperture with 1.4–2.0 in form ratio (width/height); angles of calical opening usually  $40^{\circ}$ – $60^{\circ}$  to corallum surface; intercorallite walls form indistinct peripheral stereozone, attaining 0.48 mm in thickness; mural pores frequent, 0.10–0.19 mm in diameter; septal spines rare; tabulae very rare.

Description: Coralla encrusting, composed of a single or multiple layers of film-like lamellae that have 0.8-2.6 mm, with 1.5 mm mean, in thickness of a lamella, consisting of less than four layers of corallites, alveolitoid; maximum observed size of largest corallum (paratype, NSM PA15548) attains approximately 89 mm in diameter. Corallites reclined; each corallite consists of prostrate proximal portion, 1.7-2.4 mm in length, having subtrapezoid to semicircular transverse sections, and upwardly directed distal portion, 2.2-3.3 mm in length, having fan-shaped to crescentic transverse sections: inflation of corallite diameters gradual; in longitudinal section of coralla, proximal corallite sizes are 0.3-0.9 mm in width and 0.1-0.6 mm in height, distal corallite sizes are 0.7-1.2 mm in width and 0.4-0.7 mm in height; tabularia usually have subcircular to subquadrate transverse sections proximally, crescentic transverse sections distally and shifting to mostly deep calices; calical opening oblique with 30°-75°, usually 40°-60°, in angle to corallum surface; calical apertures crescentic with 0.7-1.0 mm in width and 0.4-0.5 mm in height, giving form ratios (width/height) 1.4-2.0; increase of new corallites frequently occurs at basal part of distal corallites. Intercorallite walls differentiated into median dark line and stereoplasm, relatively thin in proximal corallites having 0.13-0.31 mm, then thickened to form indistinct peripheral stereozone; most distal intercorallite walls form visor-like structure with clavated longitudinal profiles, where their thickness attains to 0.48 mm; microstructure of stereoplasm is lamellar; mural pores occur on corallite faces, frequent for genus, circular in profile,

0.10–0.19 mm in diameter, forming a single row; septal spines rarely occur on lower intercorallite walls in calices, attain to 0.15 mm in length of protruded portion; tabulae vary rare, restricted to distal corallites, complete, roughly rectangular to corallite with weakly concave in profile.

*Etymology*: The specific name is derived from Gifu Prefecture.

Occurrence: Calcareous shale.

*Discussion*: Based on the two specimens, Kamiya and Niko (1998) preliminary documented as *Planocoenites* sp., whose report was the first record of the genus in Japan. Newly discovered specimens of this species lead some emendations that reflect upon the present diagnosis. Although most of these emendations are dimensional, the previous description "septal spine is not observable" in Kamiya and Niko (1998, p. 69) should be abandon. The septal spines of this species are rare, but they are undoubtedly present as shown in Fig. 12-5.

The morphologic combination of the lower opening angle of the calices with 40°-60°, the frequent occurrence of the mural-pores and the vary rare tabulae in *Planocoenites gifuensis* sp. nov. separates it from the more or less similar species, including P. oishinouchiensis Niko and Adachi (2002, p. 18, 20–23, figs. 8-4, 5; 9-1–5) from the lower Ludlow G3 member of the Gionyama Formation, Miyazaki Prefecture, P. ozakii Niko (2003, p. 21, 23, 24, figs. 2-5; 3-1-4) from the Lower Devonian of the Fukuji Formation, Gifu Prefecture, Placocoenites [sic] rotundus Sokolov and Tesakov (1963, p. 68, 69, pl. 11, figs. 6, 7) from the Wenlock (Lower Silurian) of Siberia, and Placocoenites [sic] rukhini Dubatolov (1972, p. 110, 111, pl. 29, figs. 1a, b, v, g, d, e, 2) from the Middle Devonian of Siberia.

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