

Reexamination of Devonian Favositid Corals Described from the Fukuji Formation of Gifu Prefecture

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Abstract Favositid tabulate corals described by Kamei (1955) from the Early Devonian Fukuji Formation, Gifu Prefecture are reexamined. The assignments of the available specimens in the Kamei's original material using up to date taxonomic knowledge are as follows: *Favosites ichinotanensis* Kamei, 1955, *Mesofavosites igoi* (Kamei, 1955), *Sapporipora kamitakaraensis* Tsukada, 2005, *Plicatomurus flexuosus* (Kamei, 1955), *Squameopora hidensis* (Kamei, 1955), *Squameopora takarensis* (Kamei, 1955), *Squameofavosites fukujensis* (Kamei, 1955), *Squameofavosites sugiyamai* (Kamei, 1955), and *Squameofavosites* sp. indet. *Plicatomurus* was not previously known in Japan. On the basis of the emended generic diagnosis of *Squameopora*, its systematic position is transferred from the subfamily Favositinae to Pachyfavositinae.

Key words: Early Devonian, tabulate corals, Favositidae, Kamei's (1955) original specimens, Fukuji Formation, Gifu.

Introduction

The Early Devonian (Lochkovian to Emsian?) Fukuji Formation distributed in the Fukuji area of Okuhidaonsen-gou in Takayama-shi, Gifu Prefecture, Central Japan contains diverse and well-preserved marine fossils. In 1955, Dr. Tadao Kamei named many species of favositid tabulate corals, including *Favosites gotlandicus* [sic] Lamarck, 1816, *F. asper* d'Orbigny, 1850, *F. baculoides* Barrande, 1865, *F. flexuosus* Kamei, 1955, *F. ichinotanensis* Kamei, 1955, *F. forbesi sugiyamai* Kamei, 1955, *F. forbesi takarensis* Kamei, 1955, *F. aff. minor* Ozaki in Shimizu *et al.*, 1934, *F. hidensis* Kamei, 1955, *F. uniformis igoi* Kamei, 1955, and *Parafavosites fukujensis* Kamei, 1955. His pioneer work is the most important basic reference for Devonian favositids in Japan. They need taxonomic revisions, however, because of increasing our knowledge of the morphologic respects of over the half-century has provide further subdivision of “*Favosites*” and deletion of “*Parafavosites*”. The present work reconsiders the systematic positions of these

species based on a reexamination of the Kamei's (1955) original specimens. Nevertheless repository of the specimens was specified as in the collections of Department of Geology, Faculty of Science, Shinshu University (prefixed GISUL) in Matsumoto-shi, Nagano Prefecture, some of them including the types were unfortunately lost. Following specimens are now available: a specimen (GISUL 30103) of *F. asper*, a specimen (GISUL 30107) of *F. baculoides*, a specimen (GISUL 30109) of *F. flexuosus*, the paratype (GISUL 30113) of *F. ichinotanensis*, the syntypes (GISUL 30114a–c) and a specimen (GISUL 30115) of *F. forbesi sugiyamai*, the syntypes (GISUL 30116a–c) of *F. forbesi takarensis*, the paratype (GISUL 30120) and a specimen (GISUL 30122) of *F. hidensis*, the syntypes (GISUL 30123a, b) and a specimen (GISUL 30124) of *F. uniformis igoi*, and the holotype (GISUL 30126) of *P. fukujensis*.

Systematic Paleontology

Order Favositida Wedekind, 1937

Suborder Favositina Wedekind, 1937

Superfamily Favositoidea Dana, 1846

Family Favositidae Dana, 1846

Subfamily Favositinae Dana, 1846

Genus *Favosites* Lamarck, 1816

Type species: Favosites gothlandicus Lamarck, 1816.

***Favosites ichinotanensis* Kamei, 1955**

(Figs. 1-4-7)

Favosites ichinotanensis Kamei, 1955, p. 48, 49, pl. 3, figs. 1a-c; Kamei, 1961, p. 4; Kamei, 1962, p. 38.
[?] *Favosites* sp., Oyagi, 2000, p. 104 [head].

Types designated by Kamei (1955): Holotype, GISUL 30112 (missing). Paratype, GISUL 30113 (only a single thin section).

Description: Corallum probably globular, ce-roid; paratype has 37 mm in maximum observable diameter. Corallites prismatic, whose profiles indicate 3-5 sides in immature corallites, then shift mostly 6-8, rarely 12 sides in adult ones; arrangement of corallites is probably radial; corallite diameters range from 0.50 to 3.36 mm, with 2.97 mm mean in adult corallites; calices shallow to moderately deep; increases of new corallites relatively rare. Intercorallite walls differentiated into median dark line and stereoplasm, relatively thin, usually 0.09-0.15 mm in thickness; microstructure of intercorallite walls may be lamellar; mural pores rare, developed on corallite faces, circular in profile; diameter of typical mural pore is 0.17 mm; septal spines irregularly distributed, vary from nearly absent to abundant, thin rod-like, attaining 0.15 mm in length; most tabulae complete with weakly sagging (concave proximally) to nearly flat, but up-arched (concave distally), strongly oblique or sinuate forms rarely developed; incomplete tabulae occur as rare cases in peripheral zone of coral-

lum; spacing of tabulae is variable; closely spaced tabulae tend to occur in peripheral zone.

Discussion: With the exception of structure of the tabulae, the diagnostic feature of *Favosites ichinotanensis* is accurately documented by Kamei (1955). "The tabulae are thick" in his description seems a misinterpretation of post-depositional tabula thickening caused by outgrowth of inorganic calcite, and is eliminated herein.

Genus ***Mesofavosites*** Sokolov, 1951

Type species: Mesofavosites dualis Sokolov, 1951.

***Mesofavosites igoi* (Kamei, 1955)**

(Figs. 1-1-3; 2-1-5)

Favosites uniformis igoi Kamei, 1955, p. 54, pl. 1, figs. 3a-d, pl. 4, fig. 3; Kamei, 1961, p. 4; Kamei, 1962, p. 39.

[?] *Favosites* sp., Hamada and Itoigawa, 1983, p. 11, fig. 4.

[?] *Favosites hidensis* Kamei; Obata (ed.), 1994, p. 42.

Squameopora zhanwaensis fukujiensis Tsukada, 2005, p. 65, 66, pl. 5, figs. 3-7.

Types designated by Kamei (1955): Syn- types, GISUL 30123a (an isolated corallum preparing polished longitudinal and weathered transverse to oblique sections), 30123b (an isolated corallum preparing polished transverse and longitudinal sections).

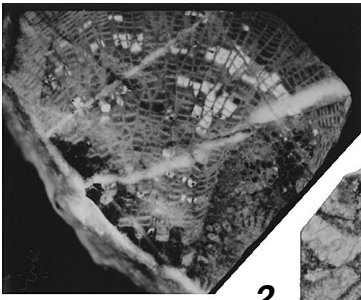
Other material examined by Kamei (1955): GISUL 30124 (a partly isolated corallum preparing polished transverse and longitudinal sections), 30125 (missing).

Lectotype designated here: GISUL 30123a.

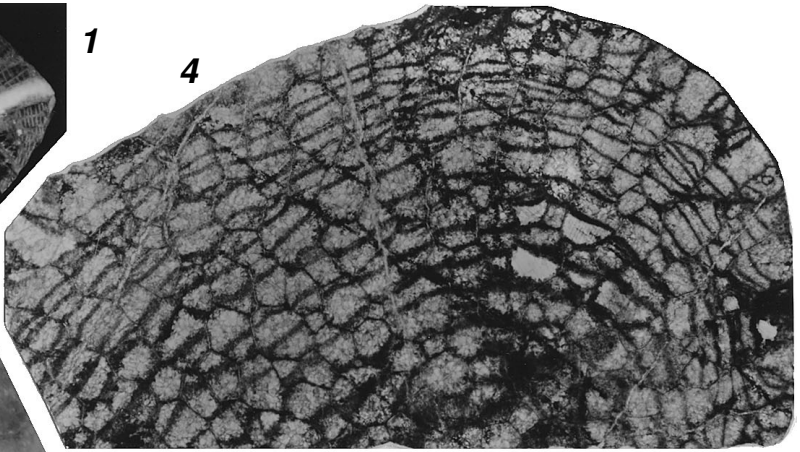
Paralectotype designated here: GISUL 30123b.

Emended diagnosis: Species of *Mesofavosites* with somewhat irregular shaped coralla indicating subspherical with projections to high bul-

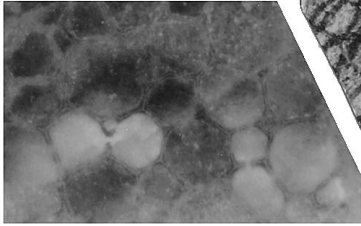
Fig. 1. 1-3, *Mesofavosites igoi* (Kamei, 1955), GISUL 30124, polished sections. 1, longitudinal section of corallum, $\times 1$. 2, transverse sections of corallites, $\times 5$. 3, longitudinal sections of corallites, $\times 5$. 4-7, *Favosites ichinotanensis* Kamei, 1955, paratype, GISUL 30113, thin sections. 4, oblique section of corallum, $\times 3$. 5, oblique sections of corallites, $\times 10$. 6, transverse sections of corallites, $\times 10$. 7, partial enlargement to show intercorallite wall structure, transverse section, $\times 75$.



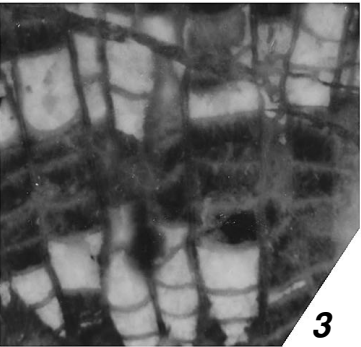
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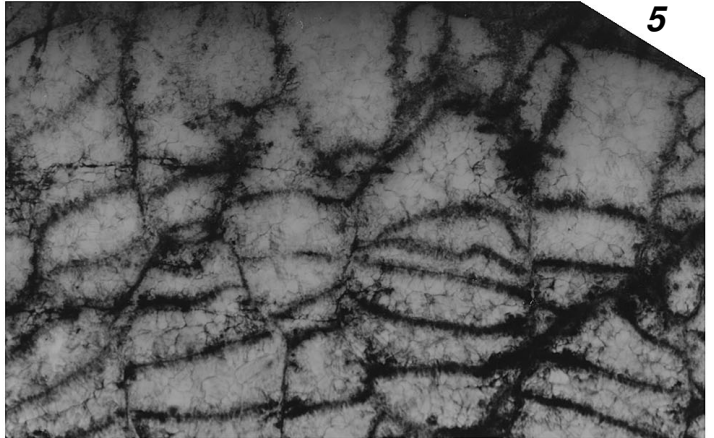
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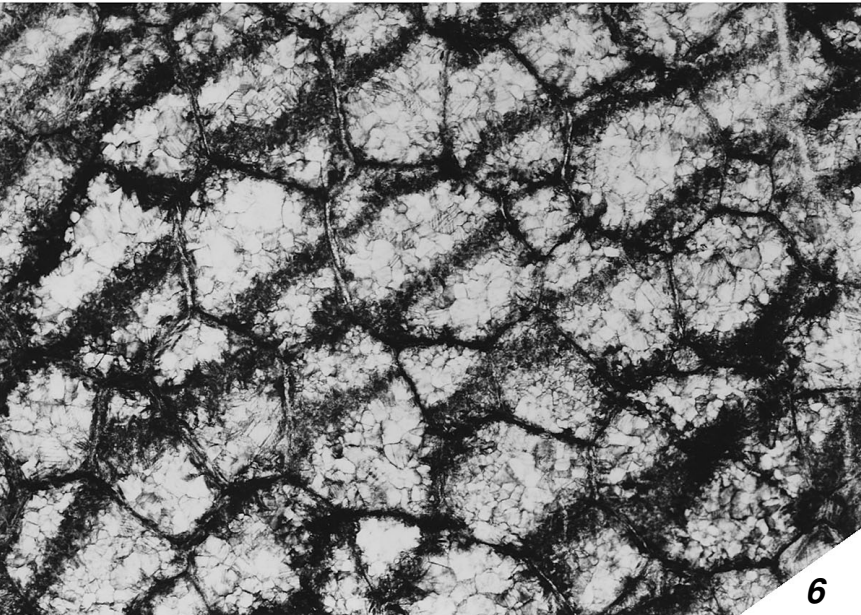
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bous; adult corallites are approximately 1.5 mm in diameter; mid-wall pores predominant; angle pores well developed; septal spines rare; 4–11 tabulae occur within 5 mm.

Description: Coralla indicate somewhat irregular outline; they are roughly subspherical with boss-like projections to high bulbous, cerioid; lectotype is 84 mm in diameter. Corallites prismatic with 3–5, rarely 6, sides in profiles of immature corallites and 6–8 sides in those of adult ones; arrangement of corallites radial, but bends caused by growth direction changes are commonly developed; approximate diameters of corallites range from 0.3 to 2.0 mm, rarely attaining 2.3 mm, with 1.5 mm mean in adult corallites; calices very shallow; increases of new corallites common, probably lateral. Intercorallite walls fairly uniform in thickness, approximately 0.1 mm; mural pores occur on corallite faces as mid-wall pores and at corallite corners as angle pores; most dominant type is mid-wall pores, but angle pores are also well developed; usual mural pores closed by pore plates; septal spines rare, short conical; tabulae mostly complete with nearly flat to weakly sagging, or incomplete in rare cases; spacing of tabulae is variable; there are 4–11 tabulae in 5 mm of corallite length.

Discussion: The present reexamination provides emendations on the original diagnosis about its corallite diameters and tabula counts. The possession of the angle pores is confirmed.

Detailed morphology including mural pores and septal spines of *Favosites uniformis* (Yang, 1948, p. 136–138, pl. 1, figs. 7a, b, 8a, b, 9a, b) from the Silurian of Yunnan in South China is ambiguous because of the Yang's (1948) description is too simple and illustrations use negative prints with low ($\times 3$) magnification. However, I can not detect the positive evidences support the Kamei's (1955) statement that the Fukuji repre-

sentatives are a variety of the Chinese species. Furthermore, the well-developed angle pores of the specimens suggest they are referable to *Mesofavosites*, rather than *Favosites*.

The features and dimensions of *Squameopora zhanwaensis fukujiensis* are consistent with those of *Mesofavosites igoi*, and the subspecies is here synonymized. On the other hand, *Squameopora zhanwaensis* Lin and Huang (1987, p. 212, pl. 43, figs. 2, 3, 4a, b) may approach *Mesolites* Mironova (1969; type species, *Pachyfavosites squamatus* Dubatolov, 1959).

Genus *Sapporipora* Ozaki in Shimizu,
Ozaki and Obata, 1934.

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

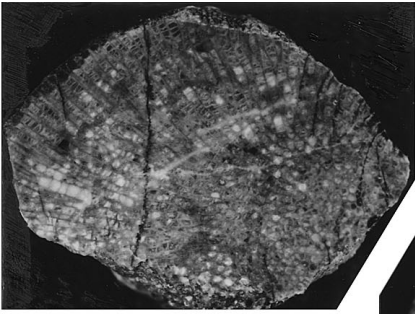
Sapporipora kamitakaraensis Tsukada, 2005
(Figs. 2–6–8)

Favosites asper d'Orbigny; Kamei, 1955, p. 45, 46, pl. 1, figs. 2a, b; Kamei, 1961, p. 4; Kamei, 1962, p. 39.
[?] *Favosites* sp., Obata (ed.), 1994, p. 39 [foot]; Hirata, 2006, p. 14, pl. 1, figs. 3-1, 2.
Sapporipora kamitakaraensis Tsukada, 2005, p. 67–69, pl. 8, figs. 3–5, pl. 9, figs. 1–5.

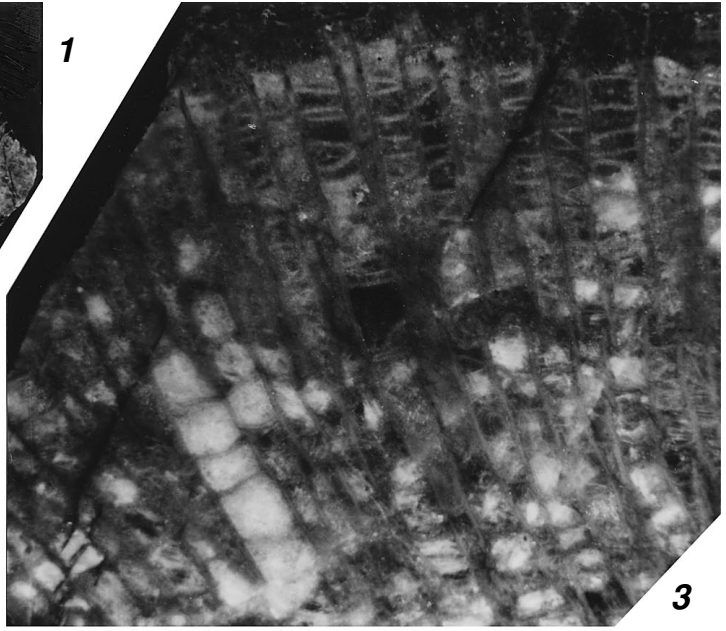
Material examined by Kamei (1955): GISUL 30103 (a partly isolated corallum preparing transverse and longitudinal polished sections). The specimen was referred to *Favosites asper*.

Description: Corallum massive, cerioid. Corallites prismatic to subprismatic with polygonal to rounded subpolygonal transverse sections; usual polygonal corallites have 6 sides; diameters of corallites are rather equal, approximately 0.8–1.6 mm, with 1.1 mm mean in adult corallites; increases of new corallites relatively rare. Intercorallite walls fairly uniform in thickness, lacks stereoplasmic thickening; mural pores nu-

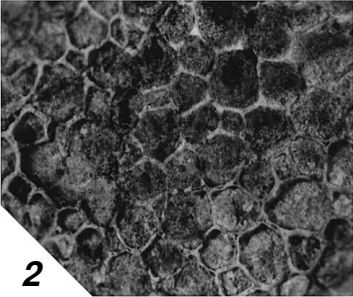
Fig. 2. 1–5, *Mesofavosites igoi* (Kamei, 1955). 1–4, lectotype, GISUL 30123a. 1, longitudinal polished section of corallum, $\times 1$. 2, weathered surface of corallum, $\times 5$. 3, longitudinal polished sections of corallites, $\times 5$. 4, transverse to oblique weathered sections of corallites, $\times 5$. 5, paralectotype, GISUL 30123b, transverse polished sections of corallites, $\times 5$. 6–8, *Sapporipora kamitakaraensis* Tsukada, 2005, GISUL 30103, polished sections. 6, oblique section of corallum, $\times 1$. 7, transverse sections of corallites, $\times 5$. 8, oblique to transverse sections of corallites, $\times 5$.



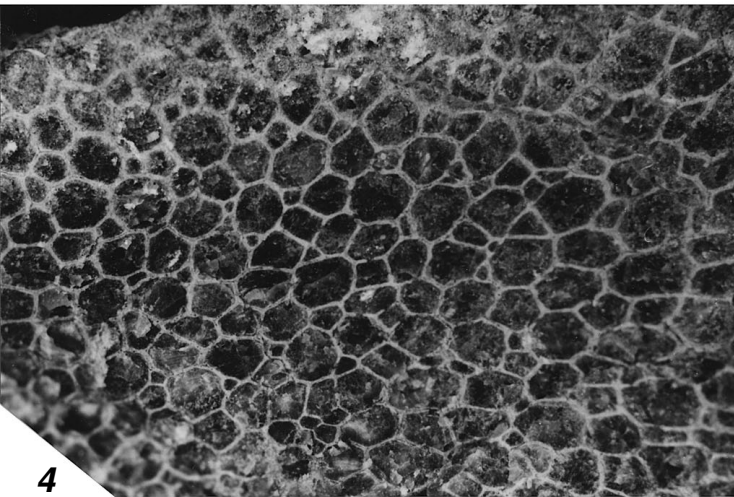
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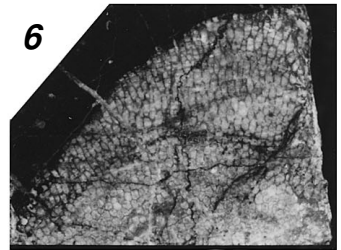
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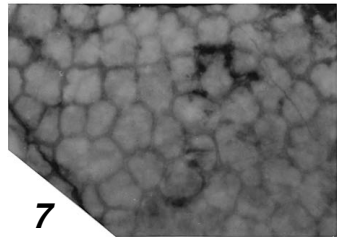
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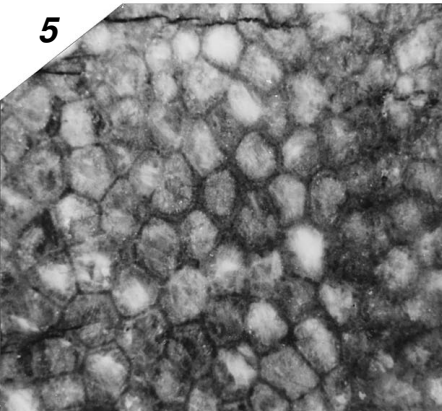
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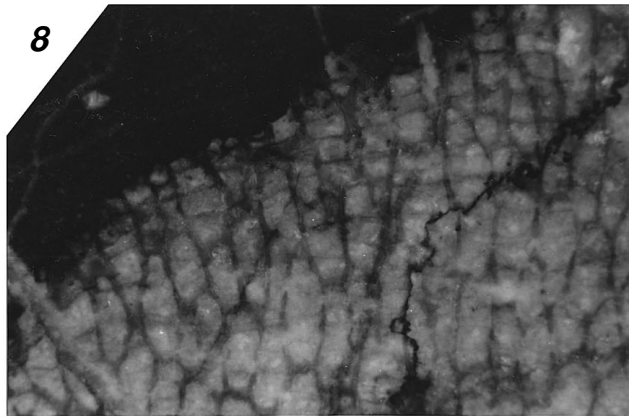
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merous, occur on corallite faces as mid-wall pores (and at corallite corners ?); diameters of mid-wall pores large in comparing with corallite diameters; septal spines short, sporadic; tabulae complete, nearly flat.

Discussion: Twenhofel (1914) created the genus *Paleofavosites* on the basis of the exclusive possession of the angle pores of a Wenlock (Middle Silurian) species, *Favosites asper*. Subsequent examinations by Stel and Oekentorp (1976) and Powell and Scrutton (1978) reveal that the angle pores in the type species are predominant, but the mid-wall pores and solenia are also developed though they are rare. Judging from this up to date knowledge, the well-developed mid-wall pores in the Fukuji specimen deny the Kamei's (1955) original assignment.

Although the corallite diameters of the present species are slightly larger than those of *Sapporipora kamitakaraensis*, the both species are closely similar and probably conspecific.

Subfamily Pachyfavositinae Mironova, 1965

Genus *Plicatomurus* Chang, 1959

Type species: *Plicatomurus solidus* Chang, 1959.

Plicatomurus flexuosus (Kamei, 1955)

(Figs 3-1-5)

Favosites flexuosus Kamei, 1955, p. 47, 48, pl. 3, figs. 2a-c; Kamei, 1961, p. 4; Kamei, 1962, p. 38; Tsukada, 2005, p. 62, 63, pl. 2, figs. 1-3.

Favosites hidensis Kamei; Masutomi and Hamada, 1966, pl. 21, fig. 3; Hamada and Itoigawa, 1983, p. 10 [title back]; Oyagi, 2003, p. 93 [upper left].

Squameopora takarensis (Kamei); Hirata, 2006, p. 16, pl. 2, figs. 6-1, 3, 4 [? 2].

Type designated by Kamei (1955): Holotype GISUL 30108 (missing).

Other material examined by Kamei (1955):

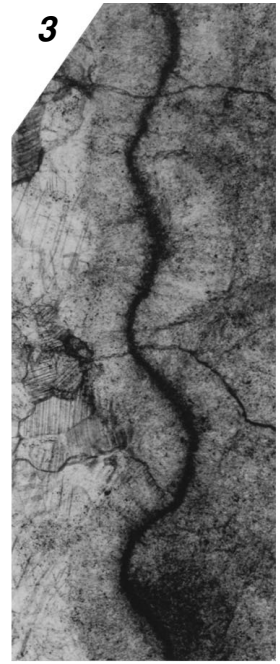
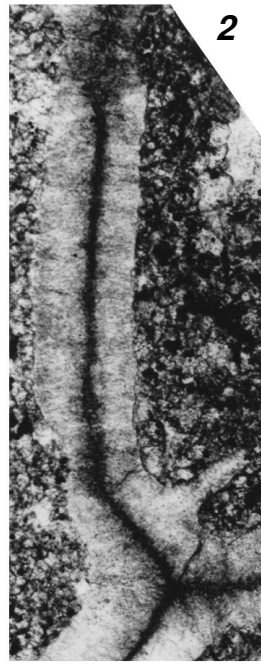
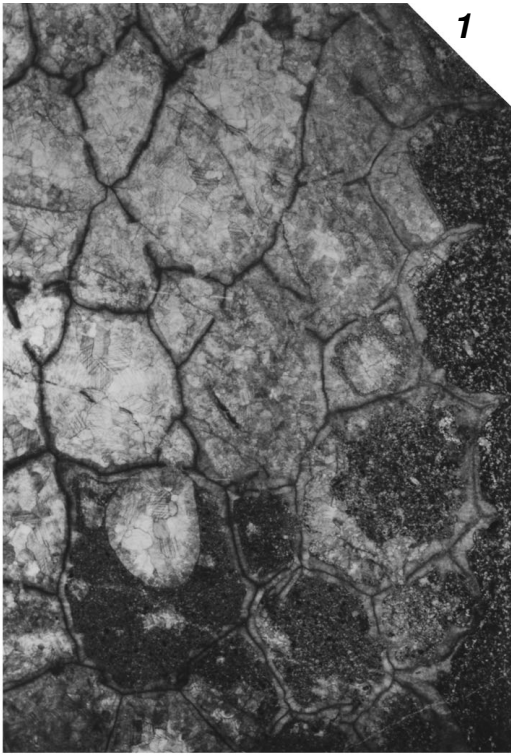
GISUL 30109 (only a thin section), 30110 (missing), 30111(missing).

Neotype designated here: GISUL 30109.

Emended diagnosis: Species of *Plicatomurus* having probably subcylindrical corallum, approximately 20 mm in diameter, with narrowly diverged corallites; adult corallite diameters approximately 2.37 mm; intercorallite walls wavy; thickened intercorallite walls in peripheral zone of corallum attain 0.46 mm; septal spines well developed, differentiated into conical to hemispherical and rod-like types; 3-5 tabulae occur within 2.5 mm.

Description: Corallum of neotype probably subcylindrical with approximate dimensions of 25 mm in maximum preserved length and 20 mm in maximum preserved diameter, cerioid. Corallites prismatic to subprismatic; their profiles indicate 3-5 sided in immature corallites, then shift 6-8 sided in adult ones; inflated or depressed corallite faces frequently occur, thus rounded polygonal or somewhat irregular transverse sections of corallites are recognized in addition to normal polygonal type; diameters of corallites range from 0.53 to 3.04 mm, with 2.37 mm mean in adult corallites; arrangement of corallites is narrowly divergent; calices shallow, to open obliquely upward; increases of new corallites lateral, commonly occurs at corallite corner. Intercorallite walls wavy in various degrees, and differentiated into median dark line and stereoplasm, the latter of which microstructure is rectradiate fibers; thickness of intercorallite walls is relatively thin, 0.10-0.21 mm, in inner (probably axial) portion of corallum, then gradually thickened in peripheral zone of corallum, where intercorallite wall thickness attains to 0.46 mm; stereoplasm at thickened intercorallite walls has growth lamellae that usually show weak plications by inference of waves of intercorallite walls and insertions of septal spines; mural pores nu-

Fig. 3. *Plicatomurus flexuosus* (Kamei, 1955), neotype, GISUL 30109, thin sections. 1, transverse sections of corallites, $\times 10$. 2, partial enlargement to show intercorallite wall structure and septal spine in inner portion of corallum, transverse section, $\times 75$. 3, partial enlargement to show intercorallite wall structure in inner portion of corallum, longitudinal section, $\times 75$. 4, partial enlargement to show intercorallite wall structure and septal spines in peripheral portion of corallum, transverse section, $\times 75$. 5, oblique section of corallum, $\times 5$.



merous, longitudinally elongated elliptical to circular profiles, forming a single row on corallite faces; diameters of typical mural pores are 0.22×0.31 mm and 0.26 mm; some mural pores closed by pore plates; septal spines well developed, differentiated into two types, namely conical to hemispherical septal spines with wide bases ranging 0.06–0.11 mm in length of protruded portions, and long attenuated rod-like ones having approximately 0.20 mm in length of protruded portions; transverse sections of adoral tabularia and calical pits indicate gear-like appearance owing to well-developed septal spines of the first type; tabulae complete or incomplete in rare cases; usual profiles of complete tabulae are nearly flat to weakly uparched or sagging; there are 3–5 tabulae in 2.5 mm of corallite length.

Discussion: An only single thin section (GISUL 30109) of the species is available now, that represents the neotype. Based on this specimen, some emendations of the specific diagnosis and description, including structure of the intercorallite walls and nature of the septal spines, are added. Among these respects, its gradually thickened intercorallite walls with the growth lamellae in the peripheral zone of the corallum support the assignment of this species to the subfamily Pachyfavositinae, and more restrictedly to the Late Silurian (or Early Devonian?) to Middle Devonian genus *Plicatomurus*. This report is the first record of the genus from Japan.

A favositid identified by Ozaki *in* Shimizu *et al.* (1934, p. 70, pl. 12, figs. 1–6, pl. 13, fig. 1) as *Favosites* cf. *forbesi* from the Silurian(?) of northwest Korea was erroneously synonymized with this species by Tsukada (2005) without any discussion. Its distinct septal ridges (see pl. 12, fig. 3) suggest that the Korean species belongs *Saffordophyllum* Bassler (1950; type species *S. deckeri* Bassler, 1950).

Genus *Squameopora* Preobrazhenskiy, 1967

Type species: *Favosites hidensis* Kamei, 1955.

Emended diagnosis: Coralla ramose with

slender branches; septal spines conical; no squamula developed; intercorallite walls moderately thick, thickening toward periphery; peripheral tabulae closely spaced. See Hill (1981, p. F546) for other diagnostic features of the genus.

Discussion: Hamada (1959) reconstructed a phylogenetic series of *Favosites* — *Squameopora* (=dendritic *Favosites* in his representation) — *Thamnopora* diverging in Early Devonian time. However, I can not agree with the Hamada's opinion because of the stock of *Thamnopora* Steininger (1831; type species *T. madreporacea* Steininger, 1831) extends to Silurian, e.g., *T. senzaii* Niko (2003) occurs in the Ludlow strata. Resemblance between *Squameopora* and *Thamnopora* is probably caused by convergent evolution. Mironova (1974) referred the type species of *Squameopora* to *Striatoporella* Rukhin (1938; type species *S. multiporifera* Rukhin, 1938, p. 63, 100, pl. 16, figs. 10, 11; Dubatolov, 1969, p. 80, 81, pl. 46, 1a, b, v, 2–4, pl. 47, fig. 6). Her assignment is incorrect. *Striatoporella* is clearly distinguished from *Squameopora* in its irregularly prismatic corallites. The thickened intercorallite walls of the type species suggest that *Squameopora* should be referred to the subfamily Pachyfavositinae. Except for the ramose corallum, *Squameopora* exhibits similar gross morphology of corallites and intercorallite wall structure with *Pachyfavosites* Sokolov (1952; type species, *Calamopora polymorpha tuberosa* Goldfuss, 1826) from the Eifelian (Middle Devonian) of Germany. The both genera may indicate close phylogenetic relationship.

Squameopora hidensis (Kamei, 1955)

(Figs. 4-1–6)

Favosites hidensis Kamei, 1955, p. 53, 54, pl. 3, figs. 4a–c, pl. 4, fig. 7; Hamada, 1959, p. 208, 209, pl. 14, figs. 1a–c, 2–8, 9a, b, 10, 11 [?12a, b]; Kamei, 1961, p. 4; Kamei, 1962, p. 38, 39; Shikama, 1964, pl. 20, fig. 6; Hamada, 1982, p. 6, pl. 3, fig. 18; Hamada, 1983, figs. 14a–c.

[non] *Favosites hidensis* Kamei; Masutomi and Hamada, 1966, pl. 21, fig. 3; Wakata, 1974, fig. 4 [p. 5], numberless fig. [p. 7]; Hamada and Itoigawa, 1983, p.10 [title back]; Obata (ed.), 1994, p. 42; Oyagi, 2003, p.

93 [upper right].

Squameopora hidensis (Kamei); Preobrazhenskiy, 1967, p. 7; Hill, 1981, p. F546, figs. 359.1a, b; Hirata, 2006, p. 16, pl. 2, figs. 5-1-3.

Striatoporella hidensis (Kamei); Mironova, 1974, p. 49.

[non] *Squameopora hidensis* (Kamei); Tsukada, 2005, p. 64, 65, pl. 3, figs. 4, 5, pl. 4, figs. 1-5, pl. 5, figs. 1, 2.

Types designated by Kamei (1955): Holotype, GISUL 30119 (missing). Paratype, GISUL 30120 (a ramose corallum preparing weathered longitudinal to transverse sections of branches).

Other material examined by Kamei (1955): GISUL 30121 (missing), 30122 (a fragmentary corallum, etched with hydrochloric acid).

Emended diagnosis: Branches subcylindrical to somewhat irregular; adult corallites approximately 1.1 mm in diameter; thickness of intercorallite walls attains 0.3 mm in peripheral zone; mural pores occur on corallite faces and near corallite corners; septal spines conical.

Description: Coralla ramose with slender subcylindrical to somewhat irregular shaped branches having 5–12 mm in usual diameter, cerioid. Corallites prismatic, growing longitudinally and parallel in axial zone of branches, then turning outward to open at acute, approximately 30°, to nearly right angle and forming shallow calices; transverse sections of corallites are 3–5 sided in immature and 5–8 sided in adult ones, whose diameters ranging 0.4–1.4 mm, with 1.1 mm mean in adult corallites; tabularia have rounded subpolygonal transverse sections; increases of new corallites frequent, lateral. Intercorallite walls weakly thickened even in axial zone, furthermore increase in their thickness, attaining approximately 0.3 mm, in peripheral zone; structure of intercorallite walls may be median line and stereoplasm; mural pores occur on corallite faces and near corallite corners (angle pores?); septal spines sporadic, short conical; tabulae complete with nearly flat to weakly sagging in profile; in peripheral zone, tabulae are closely spaced; no squamula developed.

Discussion: The present reexamination on the basis of more than 30 weathered and etched sections of the branches prepared from the

paratype and a specimen (GISUL 30122) is resulted in confirmation of an ambiguous point about presence or not presence of squamula in *Squameopora hidensis*, whose problem existed since the establishment of the genus. All specimens having squamulae figured by Tsukada (2005) from the Fukuji Formation must be omitted from this species. Without any discussion, Tsukada (2005) synonymized *S. sichuanensis* Lin and Huang (1987, p. 212, pl. 42, figs. 2a, b; *S. sichuanensis* [sic] in Tsukada, 2005, p. 64) from the Qinling [Qui Ling] Mountains of China and this species. In the same way, the Chinese species neither conspecific nor congeneric with *S. hidensis*. I think that these species having the squamulae belong to *Squameofavosites*.

Squameopora hidensis is characteristically found in greenish gray tuffaceous sandstone. This is in contrast to other Fukuji corals from which in argillaceous to micritic limestone. A habitat of *S. hidensis* probably was a high-energy hydrodynamic regime in a shelfal environment.

Squameopora takarensis (Kamei, 1955)

(Figs. 4-7-9; 5-3)

Favosites forbesi takarensis Kamei, 1955, p. 50–52, pl. 2, figs. 3a–c, 4a, b, 5a, b, pl. 4, figs. 4–6; Hamada, 1959, p. 205; Kamei, 1961, p. 4; Kamei, 1962, p. 39.

[non] *Favosites forbesi takarensis* Kamei; Maeda, 1958, p. 641.

Favosites hidensis Kamei; Wakata, 1974, fig. 4 [p. 5], numberless fig. [p. 7].

[non] *Squameopora takarensis* (Kamei); Hirata, 2006, p. 16, pl. 2, figs. 6-1-4.

Types designated by Kamei (1955): Syntypes, GISUL 30116a (a fragmentary corallum preparing polished nearly transverse and transverse sections), 30116b (a fragmentary corallum preparing polished oblique section), 30116c (a fragmentary corallum preparing weathered oblique section).

Lectotype designated here: GISUL 30116b.

Paralectotypes designated here: GISUL 30116a, 30116c.

Emended diagnosis: Similar to *Squameopora hidensis*, but it differs in having larger corallite

diameters, approximately 1.6 mm in adult ones.

Description: Coralla (=fragmentary branch?) subcylindrical having approximately 10–20 mm in diameter, cerioid. Corallites prismatic, growing longitudinally in axial zone of coralla, then turning outward to open at nearly right angle and forming shallow calices; transverse sections of corallites 3–5 sided in immature and 5–8, rarely 10, sided in adult ones, whose diameter ranging 0.5–1.9 mm, with 1.6 mm mean in adult corallites; tabularia have rounded subpolygonal transverse sections; increases of new corallites frequent, probably lateral. Intercorallite walls weakly thickened even in axial zone, furthermore increase in their thickness, attaining approximately 0.3 mm, in peripheral zone; structure of intercorallite walls is median line and stereoplasm; mural pores occur on corallite faces and near corallite corners (angle pores?), usually closed by pore plate; septal spines well developed, short conical; tabulae mostly complete or incomplete in rare cases; profiles of complete tabulae are nearly flat; in peripheral zone, tabulae are closely spaced; no squamula developed.

Discussion: This species was initially described as a new variety of *Favosites forbesi* Milne-Edwards and Haime (1851, p. 238, 239; 1885, p. 258, 259, pl. 60, figs. 2, 2a–g). In comparing the Fukuji specimens and the lectotype of *F. gothlandicus* forma *forbesi* figured by Jones (1936, p. 9–12, pl. 1, figs. 5, 6), there are suprageneric differences between them. The lectotype from the Wenlock (Early Silurian) limestone of Dudley, England apparently has characteristic diagnosis of *Favosites*, on the other hand morphology of this species, such as its corallum shape, rounded subpolygonal transverse sections of tabularia, thickened intercalate walls, and closely spaced peripheral tabulae, is indicative of *Squameopora*. There is thus no direct linking in

these two species.

The differences between *Squameopora hidensis* and *S. takarensis* are minor and only dimensional as noted in the above diagnosis, and may fall within a morphologic range of one species. However, more data are needed in order to formalize intraspecific variation.

Subfamily Emmonsinae Lecompte, 1952

Genus *Squameofavosites* Chernyshev, 1941

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

Squameofavosites fukujensis (Kamei, 1955)

(Figs. 5–5–7)

Parafavosites fukujensis Kamei, 1955, p. 55, 56, pl. 1, fig. 6, pl. 3, figs. 5a–c.

[?] *Favosites forbesi takarensis* Kamei; Maeda, 1958, p. 641.

Gephuropora fukujensis (Kamei); Kamei, 1961, p. 4, pl. 1, figs. 1a, b; Kamei, 1962, p. 39.

[?] *Favosites* sp., Wakata, 1974, fig. 3 [p. 5].

[partium] *Squameopora hidensis* (Kamei); Tsukada, 2005, p. 64, 65, pl. 4, figs. 1–5, pl. 5, figs. 1, 2 [non pl. 3, figs. 4, 5].

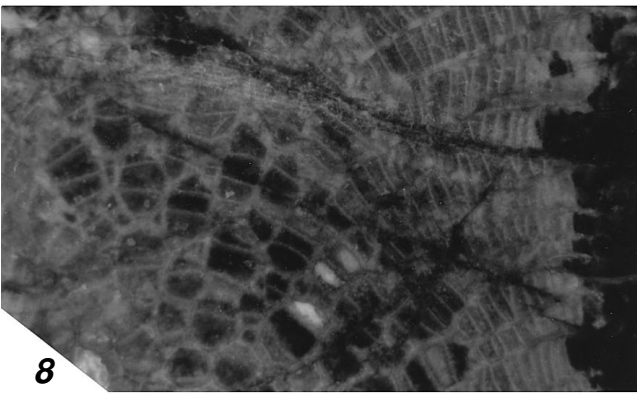
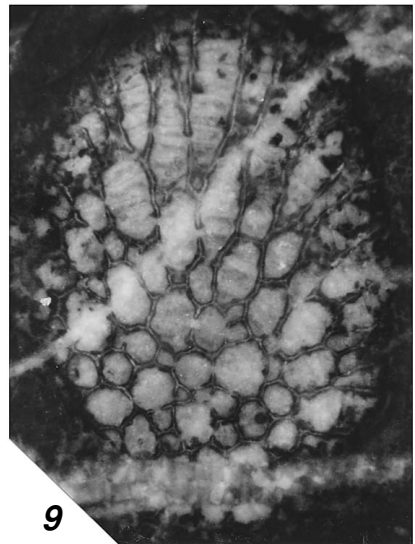
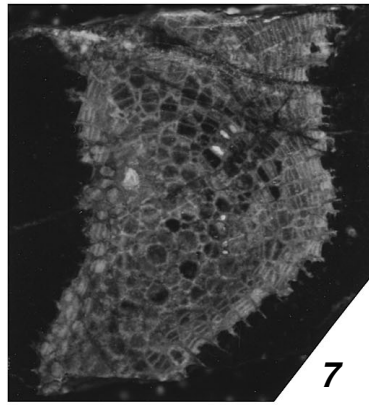
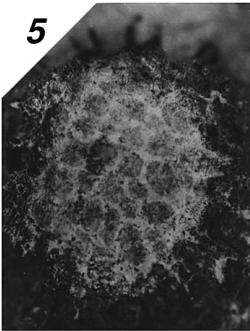
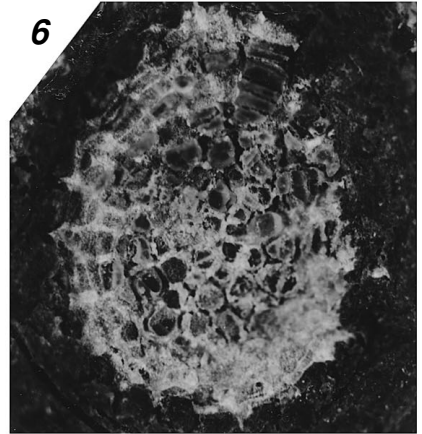
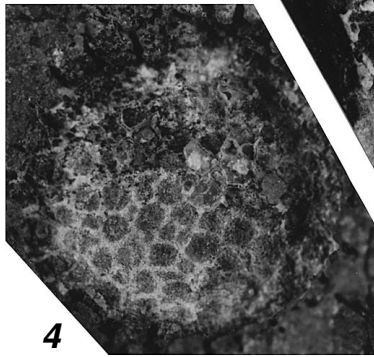
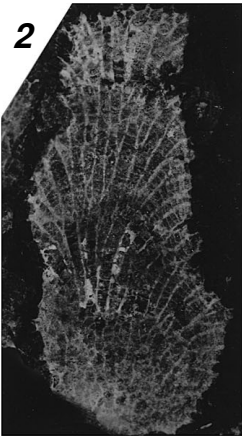
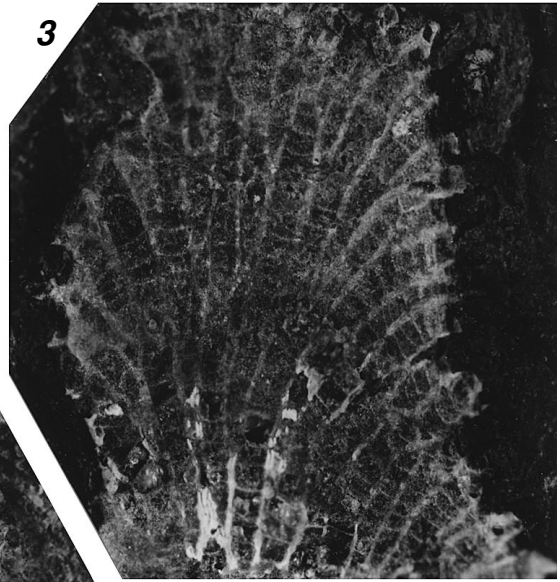
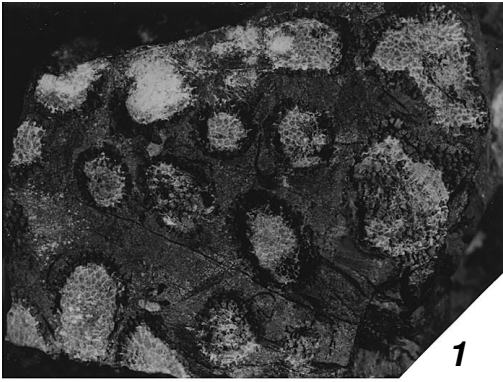
[partium] *Squameopora* cf. *zhanwaensis* Lin and Huang; Tsukada, 2005, p. 66, 67, pl. 6, figs. 1–5, pl. 7, figs. 1–6 [non pl. 7, fig. 7, pl. 8, figs. 1, 2].

Type designated by Kamei (1955): Holotype, GISUL 30126 (a fragment of corallum preparing polished transverse and weathered longitudinal sections).

Other material examined by Kamei (1955): GISUL 30127 (missing).

Emended diagnosis: Probably large species of *Squameofavosites* with parallel corallites having approximately 2.1 mm in diameter of adult corallites; increases common; squamulae thin, regularly and uniformly distributed; intercorallite

Fig. 4. 1–6, *Squameopora hidensis* (Kamei, 1955), paratype, GISUL 30120, weathered sections. 1, transverse section of fragmentary corallum, $\times 1$. 2, longitudinal section of branch, $\times 2$. 3, partial enlargement to show details of longitudinal sections of corallites, $\times 5$. 4, 5, 6, transverse sections of branches, $\times 5$. 7–9, *Squameopora takarensis* (Kamei, 1955), polished sections. 7, 8, lectotype, GISUL 30116b. 7, oblique section of corallum, $\times 2$. 8, partial enlargement to show details of transverse to longitudinal sections of corallites, $\times 5$. 9, paralectotype, GISUL 30116a, nearly transverse section of corallum, $\times 5$.



walls thin with numerous mid-wall and rare angle pores; 7–13 tabulae occur within 5 mm.

Description: Corallum probably large, cerioid; holotype is 76 mm in maximum preserved diameter. Corallites prismatic with 3–5 sides in immature and 5–8, rarely 9, sides in adult ones, parallel in arrangement; approximate diameters of corallites range from 0.5 to 2.4 mm, with 2.1 mm mean in adult corallites; calice not preserved; increases of new corallites common, lateral. Intercorallite walls thin, and may be differentiated into median line and stereoplasm; squamulae thin with uparched curvature, regularly and uniformly distributed through corallum; length of typical squamula is approximately 0.3 mm; mural pores numerous, subcircular in profile, usually occur on corallite faces as mid-wall pores, but angle pores at corallite corners rarely developed; mid-wall pores form 2 rows; approximate diameter of typical mid-wall pore is 0.2 mm; tabulae mostly complete, nearly flat, relatively uniform in spacing; there are 7–13 tabulae in 5 mm of corallite length. Commensality with a worm, *Helicosalpinx*, is recognized.

Discussion: Kamei (1955) wrote that “the characteristic cylindrical tubes which are hollow of small diameter (0.20 to 0.25 mm.), are irregularly distributed at the corner or in the middle of the walls; they have contorted form in longitudinally”. As noted by Kato (1975), the spiral tubes, figured in pl. 3, fig. 5b in Kamei (1955) and in pl. 1, fig. 1b in Kamei (1961), are produced by commensal worm *Helicosalpinx*, and it is also found in suprageneric taxa, including *Favosites*, *Thecia*, *Pachyfavosites*, *Thamnopora* and *Alveolites* (Oekentorp, 1969; Stel, 1976; Hill, 1981). Thus, there is no value of this structure at least generic level taxonomy. *Gephuropora* was established by Etheridge (1920) on the basis of *Columnopora duni* Etheridge (1920, p. 56–59, pl. 14, figs. 2–5,

pl. 15, figs. 1, 2). *Parafavosites* was established by Orlov (1930) on the basis of *P. ferganensis* Orlov (1930, p. 122–124, pl. 1, figs. 1, 2, pl. 2, figs. 1, 3; 1931, p. 502–504, figs. 1–3). The both genera are characterized by “straight tube-like structure”, that is of worms, *Phragmosalpinx* in the former case and *Chaetosalpinx* in the latter one (Sokolov, 1948; Oekentorp, 1968). Hill (1981) stated that *Gephuropora* and *Parafavosites* are invalid and they are probably congeneric with *Favosites*. On the other hand, Lin *et al.* (1988) have concluded that only *Gephuropora* is a valid genus diagnosed by the possession of squamulae, pinnatifid and unequally colored intercorallite walls. However, I cannot detect squamulae and pinnatifid intercorallite structure in the illustrations of Etheridge (1920). The unequally colored intercorallite walls are apparently resulted by recrystallization. This observation supports the Hill’s statement. Therefore, the Fukuji specimen is reassigned to the genus *Squameofavosites* based on the above mentioned description, especially its possession of the squamulae.

Squameofavosites sugiyamai (Kamei, 1955)

(Figs. 5-4; 6-1-4)

Favosites forbesi sugiyamai Kamei, 1955, p. 49, 50, pl. 2, figs. 1a–f, pl. 4, figs. 1, 2; Kamei, 1961, p. 4; Kamei, 1962, p. 39.

Favosites sp., Hamada, 1961, figs. 16, 27; Oyagi, 2000, p. 104 [lower left].

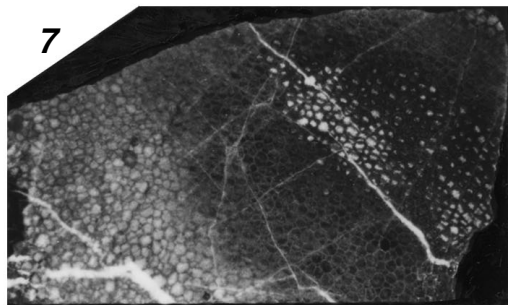
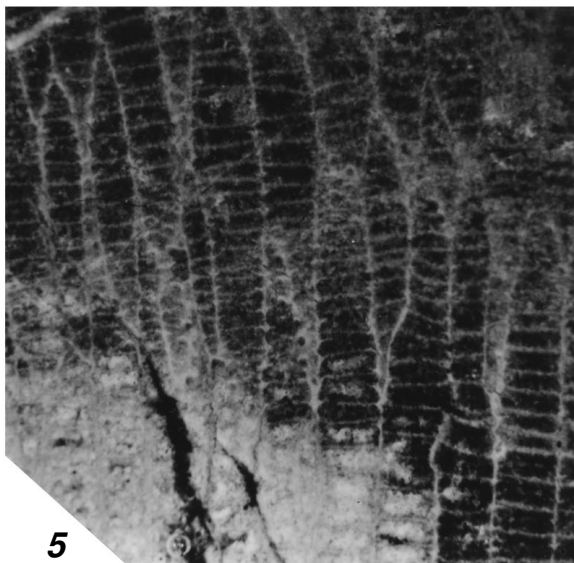
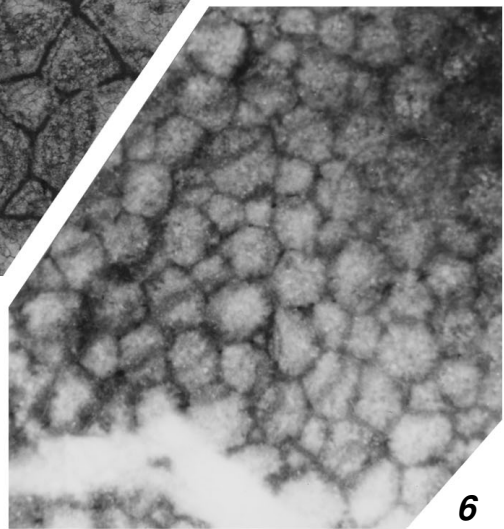
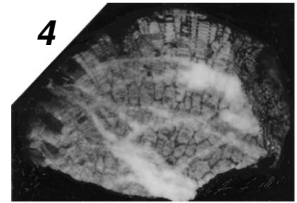
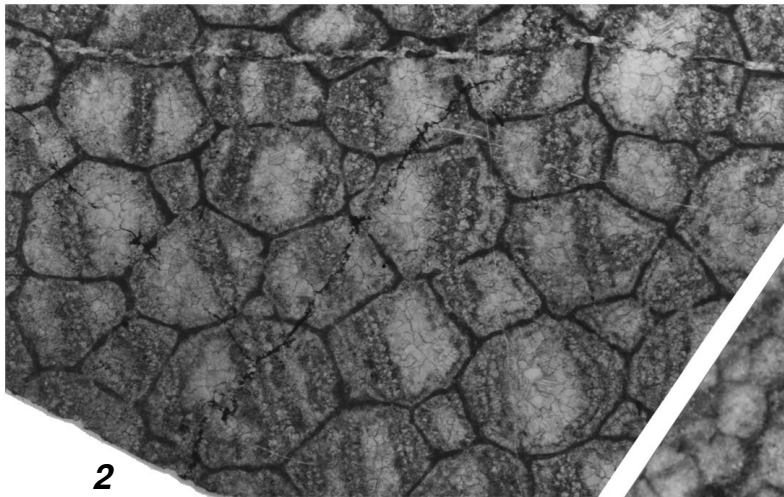
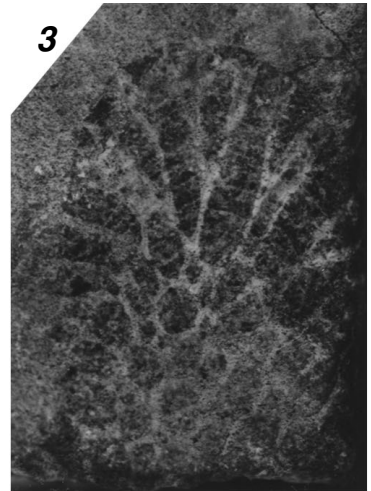
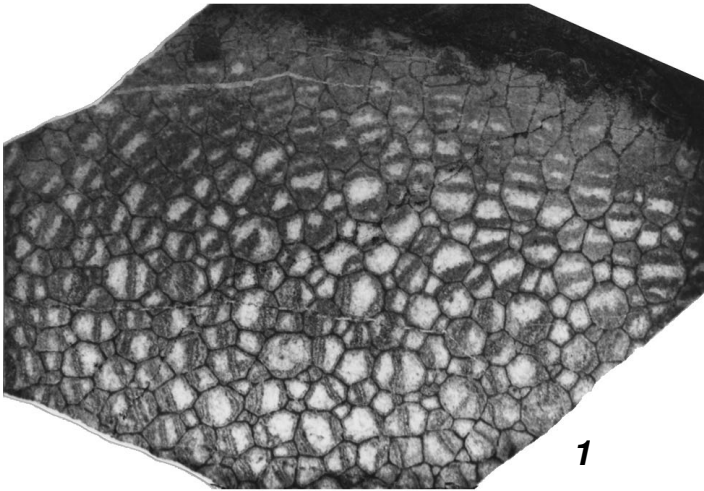
Squameofavosites sp., Masutomi and Hamada, 1966, pl. 21, fig. 4; Wakata, 1974, fig. 1 [p. 4]; Hirata, 2006, p. 18, pl. 3, figs. 8-1, 2.

[?] *Favosites* sp., Obata (ed.), 1994, p. 39 [head]; Oyagi, 2003, p. 92; Tokai Kaseki Kenkyukai (ed.), 1995, p. 28 [middle].

Favosites goldfussi d’Orbigny; Tsukada, 2005, p. 61, 62, pl. 1, figs. 1–6.

[partim] *Squameopora hidensis* (Kamei); Tsukada, 2005, p. 64, 65, pl. 3, figs. 4, 5 [non pl. 4, figs. 1–5, pl. 5,

Fig. 5. 1, 2, *Squameofavosites* sp. indet., GISUL 30107, thin sections. 1, oblique section of corallum, $\times 3$. 2, transverse sections of corallites, $\times 10$. 3, *Squameopora takarensis* (Kamei, 1955), paralectotype, GISUL 30116c, oblique weathered section of corallum, $\times 5$. 4, *Squameofavosites sugiyamai* (Kamei, 1955), paralectotype, GISUL 30114c, longitudinal polished section of corallum, $\times 1$. 5–7, *Squameofavosites fukujensis* (Kamei, 1955), holotype, GISUL 30126. 5, longitudinal weathered sections of corallites, $\times 5$. 6, transverse polished sections of corallites, $\times 5$. 7, transverse polished section of fragmentary corallum, $\times 1$.



figs. 1, 2].

[partim] *Squameopora* cf. *zhanwaensis* Lin and Huang; Tsukada, 2005, p. 66, 67, pl. 7, fig. 7, pl. 8, figs. 1, 2 [non pl. 6, figs. 1–5, pl. 7, figs. 1–6].

Squameofavosites sugiyamai (Kamei); Niko, 2006, p. 168.

Types designated by Kamei (1955): Syn-types, GISUL 30114a (an isolated corallum preparing polished longitudinal section), 30114b (a small fragment of corallum preparing polished transverse section), 30114c (an immature specimen of an isolated corallum preparing polished longitudinal section).

Other material examined by Kamei (1955): GISUL 30115 (partly silicified specimen of an isolated corallum, etched with hydrochloric acid).

Lectotype designated here: GISUL 30114a.

Paralectotypes designated here: GISUL 30114b, c.

Emended diagnosis: Species of *Squameofavosites* with radially arranged corallites of approximately 2.3 mm in adult corallite diameter; increases frequent; usual intercorallite walls thickened by contiguous robust squamulae; mid-wall pores numerous; angle pores common; 5–12 tabulae occur within 5 mm.

Description: Coralla depressed subspherical, cerioid; lectotype has 74 mm in diameter and 48 mm in height. Corallites prismatic with 3–6 sides in immature and 6–8 sides in adult ones, radially arranged; approximate diameters of corallites range from 0.5 to usually 2.6 mm, rarely attaining 3.2 mm, with 2.3 mm mean in adult corallites; calices probably shallow, perpendicularly oriented to corallum surface; increases of new corallites frequent, lateral. Intercorallite walls usually thickened, attaining approximately 0.2 mm, by contiguous squamulae; immature corallites partly lack squamula, where relatively thin (original?) intercorallite walls are observable; structure of

intercorallite walls may be median line and stereoplasm; squamulae robust, tongue-shaped with uparched curvature, making a pair between contiguous corallites; well-preserved squamula has approximately 0.3 mm in length; positions of mural pores are on corallite faces as mid-wall pores and at corallite corners as angle pores; mid-wall pores have longitudinally elongated elliptical to circular profiles, numerous and form 2–3 rows; angle pores have circular profiles, commonly occur; approximate diameters of typical mural pores are 0.2×0.3 mm and 0.3 mm; tabulae mostly complete, but incomplete ones are uncommonly developed; usual profiles of complete tabulae nearly flat to weakly sagging; spacing of tabulae moderate for the genus; there are 7–12 tabulae in 5 mm of corallite length.

Discussion: Although all thin sections of this coral are missing, observations on polished section and weathered surface of the lectotype, two polished sections of the paralectotypes and etched surface of a specimen (GISUL 30115) provide some importance emendations on the original description, especially septal elements. “The blunt septal spines” in Kamei (1955) must be amended to “squamulae”. This fact indicates that the specimens are referable to *Squameofavosites* rather than *Favosites*, and the Kamei’s (1955) statements, i.e., “the specimens represent a variety of *Favosites forbesi*” and “*F. forbesi takarensis* is the ancestral form of *F. forbesi sugiyamai*”, need revision.

Squameofavosites sp. indet.

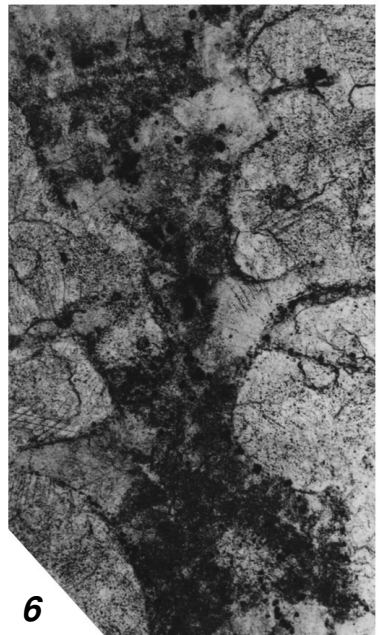
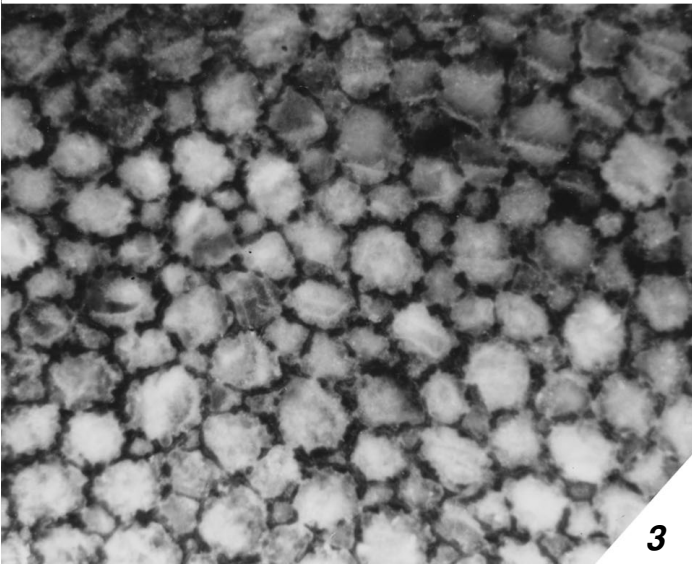
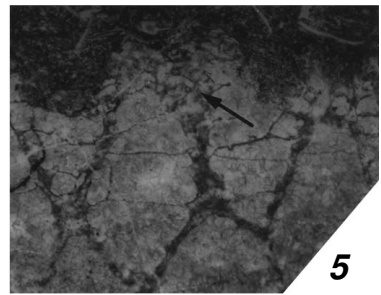
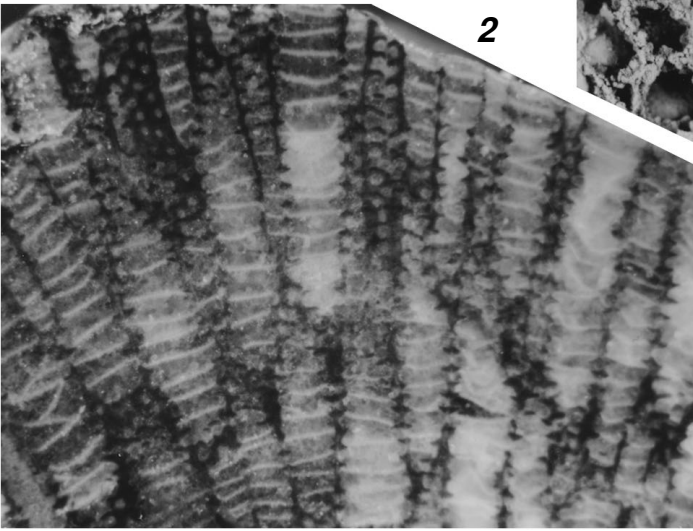
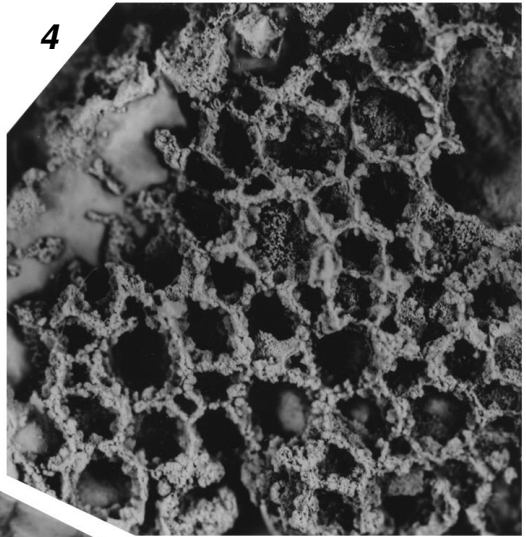
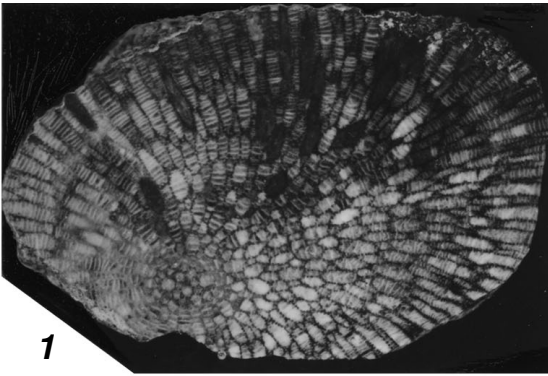
(Figs. 5-1, 2; 6-5, 6)

Favosites baculoides Barrande; Kamei, 1955, p. 46, 47, pl. 1, figs. 4a, b; Kamei, 1961, p. 4; Kamei, 1962, p. 39.

[?] *Favosites* sp. A, Tsukada, 2005, p. 63, pl. 2, figs. 4, 5, pl. 3, figs. 1–3.

Favosites gotlandicus [sic] Lamarck; Hirata, 2006, p. 14,

Fig. 6. 1–4, *Squameofavosites sugiyamai* (Kamei, 1955). 1–3, lectotype, GISUL 30114a, polished sections. 1, longitudinal section of corallum, ×1. 2, longitudinal sections of corallites, ×5. 3, transverse sections of corallites, ×5. 4, GISUL 30115, etched surface of corallum, ×5. 5, 6, *Squameofavosites* sp. indet., GISUL 30107, thin sections. 5, oblique sections of corallites, arrow indicates squamula, ×10. 6, partial enlargement to show intercorallite wall structure and squamulae, longitudinal section, ×75.



pl. 1, figs. 2-1, 2.

Material examined by Kamei (1955): GISUL 30106 (missing), 30107 (only a single thin section). These specimens were referred to *Favosites baculoides*.

Description: Corallum subspherical(?) having 22 mm in maximum preserved diameter, cerioid. Corallites prismatic with 3–9 sides in transverse section; diameters of corallites are 0.50–2.66 mm, 2.38 mm mean in adult corallites; calices shallow; increases of new corallites frequent. Intercorallite walls mostly thin, 0.03–0.05 mm, but partial intercorallite walls in peripheral zone indicate thickening, up to 0.20 mm, by contiguity of squamulae; mural pores occur on corallite faces and at corallite corners; usual mural pores closed by pore plates; tabulae complete, nearly flat.

Discussion: This coral is clearly different from a Silurian species, *Favosites baculoides* Barrande (1865 [nomen nudum]; Pocta, 1902, p. 242, 243, pl. 81, figs. 13–17, pl. 86, figs. 1–10, pl. 89, figs. 17, 18), in possessing the partly thickened intercorallite walls with the contiguous squamulae. There is a possibility that the examined specimen represents an intraspecific variation of *Squameofavosites sugiyamai*.

Acknowledgments

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