

Silurian Halysitids (Coelenterata: Tabulata) from the Gionyama Formation, Miyazaki Prefecture, Japan

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Abstract Diverse assemblages of halysitid tabulate corals occur in the upper Wenlock (upper Lower Silurian) G2 and the lower Ludlow (lower Upper Silurian) G3 Members of the Gionyama Formation in the Kuraoka area, Miyazaki Prefecture, southern Japan. Ten species were identified: *Halysites catenularius* (Linnaeus, 1767), *H. bellulus* Hamada, 1958, *H. delicatus* sp. nov., *H. intricatus* sp. nov., *H. kuraokensis* (Hamada, 1958), *H. kyushuensis* sp. nov., *H. tenuis* Hamada, 1958, *Falsicatenipora shikokuensis* Noda and Hamada, 1958, *Schedohalysites kitakamiensis* (Sugiyama, 1940), and *Catenipora nishioi* sp. nov. Among them, the Gionyama specimens of *H. catenularius* had been misidentified to *H. cratus* Etheridge, 1904 or *H. bellulus* in previous workers, in the same way *H. intricatus* had been erroneously subsumed in *H. süssmilchi* Etheridge, 1904, and *C. nishioi* represents the first undoubted record of the genus *Catenipora* in Japan. Reexamination of the original material confirms that a record of *Falsicatenipora japonica* (Sugiyama, 1940) from the Gionyama Formation is error.

Key words: Wenlock to Ludlow (late Early to early Late Silurian), *Halysites*, *Falsicatenipora*, *Schedohalysites*, *Catenipora*

Introduction

As the ninth installment in a series of our descriptive works concerning tabulate corals of the Silurian Gionyama Formation, this paper deals with halysitid specimens collected from the G2 and G3 Members at three localities (locs. 1–3) in the Kuraoka area, Miyazaki Prefecture, southern Japan. Detailed stratigraphic and geographic settings of the present material and its associated coral species are referable in previous publications, namely Niko (1998), Niko and Adachi (1999a, 1999b, 2000, 2002, 2004, 2008, 2012). Used abbreviations indicating repositories are as follows: NMNS (National Museum of Nature and Sciences, Tokyo) and UMUT (University Museum, the University of Tokyo).

Systematic Paleontology

Subclass Tabulata Milne-Edwards and Haime, 1850

Order Halysitida Sokolov, 1947

Family Halysitidae Milne-Edwards and Haime, 1849

Subfamily Halysitinae Milne-Edwards and Haime, 1849

Genus *Halysites* Fischer von Waldheim, 1828

Type species: *Tubipora catenularia* Linnaeus, 1767.

Halysites catenularius (Linnaeus, 1767)

(Figs. 1-1–5; 2-1–6)

See synonymy in Laub (1979, p. 274), Young and Noble (1987, p. 1135), and Môtus and Klaamann (1999,

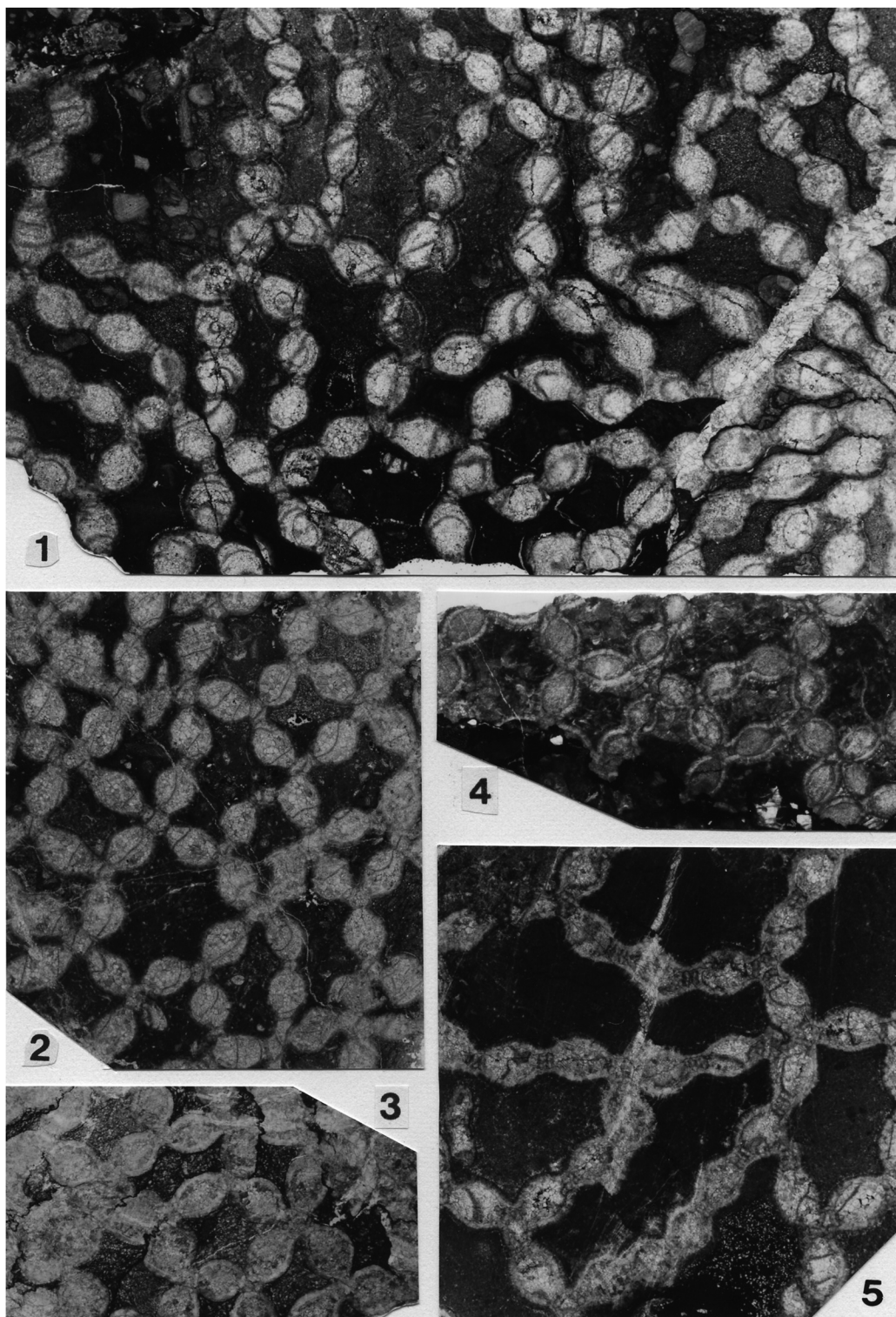


Fig. 1. *Halysites catenularius* (Linnaeus, 1767), transverse thin sections. 1, NMNS PA18246, $\times 5$. 2, NMNS PA18247, $\times 5$. 3, NMNS PA18249, $\times 5$. 4, NMNS PA18260, $\times 5$. 5, NMNS PA18245, $\times 5$.

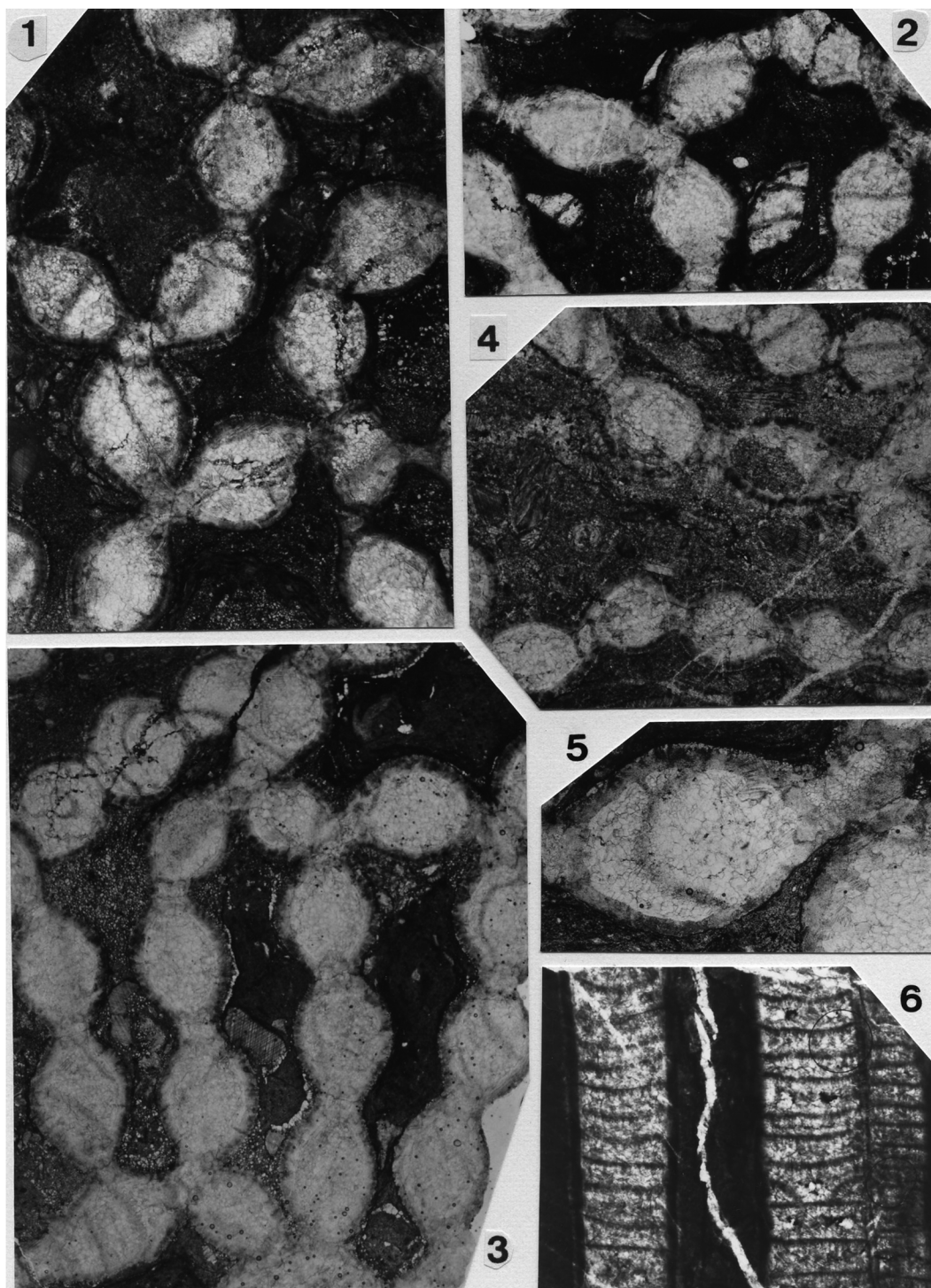


Fig. 2. *Halysites catenularius* (Linnaeus, 1767), NMNS PA18246, thin sections. 1–4, transverse sections, $\times 10$. 5, partial enlargement to show corallite (intercorallite) wall structure, transverse section, $\times 20$. 6, longitudinal section, $\times 10$.

p. 83), and added:

Halysites cratus Etheridge; Hamada, 1958, p. 101, 102, pl. 10, figs. 5, 6a, 6b; Adachi, 1979, fig. 1-7 [second from left in upper rank].

Halysites catenularius (Linnaeus); Nakai, 1981, p. 150, 151, pl. 16, fig. 4, pl. 19, figs. 2, 3, text-fig. 4c.

Acanthohalysites kuraokensis Hamada; Hamada and Itoigawa, 1983, p. 9, fig. 4.

Halysites bellulus Hamada; Tokai Kaseki Kenkyukai (ed.), 1995, p. 29 [head].

Halysites süssmilchi Etheridge; Oyagi, 2000, p. 223 [upper left]; Oyagi, 2003, p. 193 [head].

Halysitid gen. et sp. indet., Oyagi, 2000, p. 223 [upper right].

[?] *Halysitid* gen. et sp. indet., Ihara, 2001, figs. 1, 3.

Material examined: NMNS PA18233–18274.

Description: Coralla massive, halysitoid. Ranks exhibit variable length, ranging from very short to long; very short ranks consist of a single corallite, on the other hand the longest one consists of 12 corallites; lacunae exhibit also variable shapes; transverse sections of lacunae are small subpolygonal, elongate, sinuous, or irregularly lobated. Corallites inflated with subelliptical to nearly circular transverse sections; dimensions of usual corallites are 1.2–1.9 mm in length and 1.1–1.6 mm in width; form ratios (length/width) 0.97–1.21. Corallite walls moderate to thick, 0.19–0.25 mm in thickness; septa needle-like to high conical, occurrence of which spines ranges from almost absent to well-developed; tabulae complete with faintly sagging to horizontal profiles, or rarely incomplete and dissepiment-like; there are 10–13 tabulae in 5 mm of corallite length. Coenenchymal tubules present at all ranks and corallite junctions; tubule diaphragms complete.

Occurrence: Abundant in pebbles to cobbles of conglomeratic limestone (calcareous shale, NMNS PA18235; sandy shale, NMNS PA18240; argillaceous limestone, NMNS PA18234, 18239, 18246–18250, 18252, 18263, 18267, 18270; dark greenish gray, gray to black limestone, NMNS PA18237, 18238, 18241, 18244, 18245, 18251, 18253–18256, 18258, 18260, 18268, 18272, 18273) and dark gray to greenish gray limestone (NMNS PA18233, 18257, 18262, 18271) of the

upper Wenlock (upper Lower Silurian) G2 Member and right gray limestone (NMNS PA18236, 18242, 18243, 18259, 18261, 18264–18266, 18269, 18274) of the lower Ludlow (lower Upper Silurian) G3 Member at locality 1.

Discussion: *Halysites catenularius* shows considerable variations in length of the ranks, shapes of the lacunae and mode of occurrence of the septal spines. For this variable nature, not a few junior synonyms of this species were described, such as *H. cratus* Etheridge, 1904, *H. junior* Klaamann, 1961, and *H. priscus* Klaamann, 1966 (Laub, 1979, Young and Noble, 1987, Mötus and Klaamann, 1999). Further specific confusions in Japanese material are as follows: the portions consisting of the short ranks with the narrow and subprismatic lacunae were misidentified as *H. kuraokensis* (Hamada) or *H. bellulus* Hamada; and the portions of the long ranks with the elongated lacunae, on the other hand, were confused with *H. süssmilchi* Etheridge.

Previous records of *Halysites catenularius* in Japan include the Fukami Formation, Kumamoto Prefecture (Hamada, 1958, as *H. cratus*), the Gionyama Formation (Adachi, 1979, as *H. cratus*; Tokai Kaseki Kenkyukai (ed.), 1995, as *H. bellulus*) and the Yokokurayama Group, Kochi Prefecture (e.g., Nakai, 1981; Hamada and Itoigawa, 1983, as *H. kuraokensis*, Oyagi, 2000, as *H. süssmilchi*). In addition, a questionable occurrence in the Nabaehana Block, Wakayama Prefecture (Ihara, 2001) is known.

***Halysites bellulus* Hamada, 1958**

(Figs. 3-1-6)

Halysites bellulus Hamada, 1958, p. 103, 104, pl. 10, figs. 2-4; Ota, 1977, p. 22, pl. 7, fig. 2; Hamada, 1982, p. 4, pl. 2, fig. 15; Hamada, 1983, fig. 5.

[non] *Halysites bellulus* Hamada; Tokai Kaseki Kenkyukai (ed.), 1995, p. 29 [head] (= *H. catenularius*).

Material examined: NSMS PA18201–18216; UMUT PC7276 (holotype).

Description: Coralla probably thick tabular in growth form, halysitoid. Ranks short, consist-

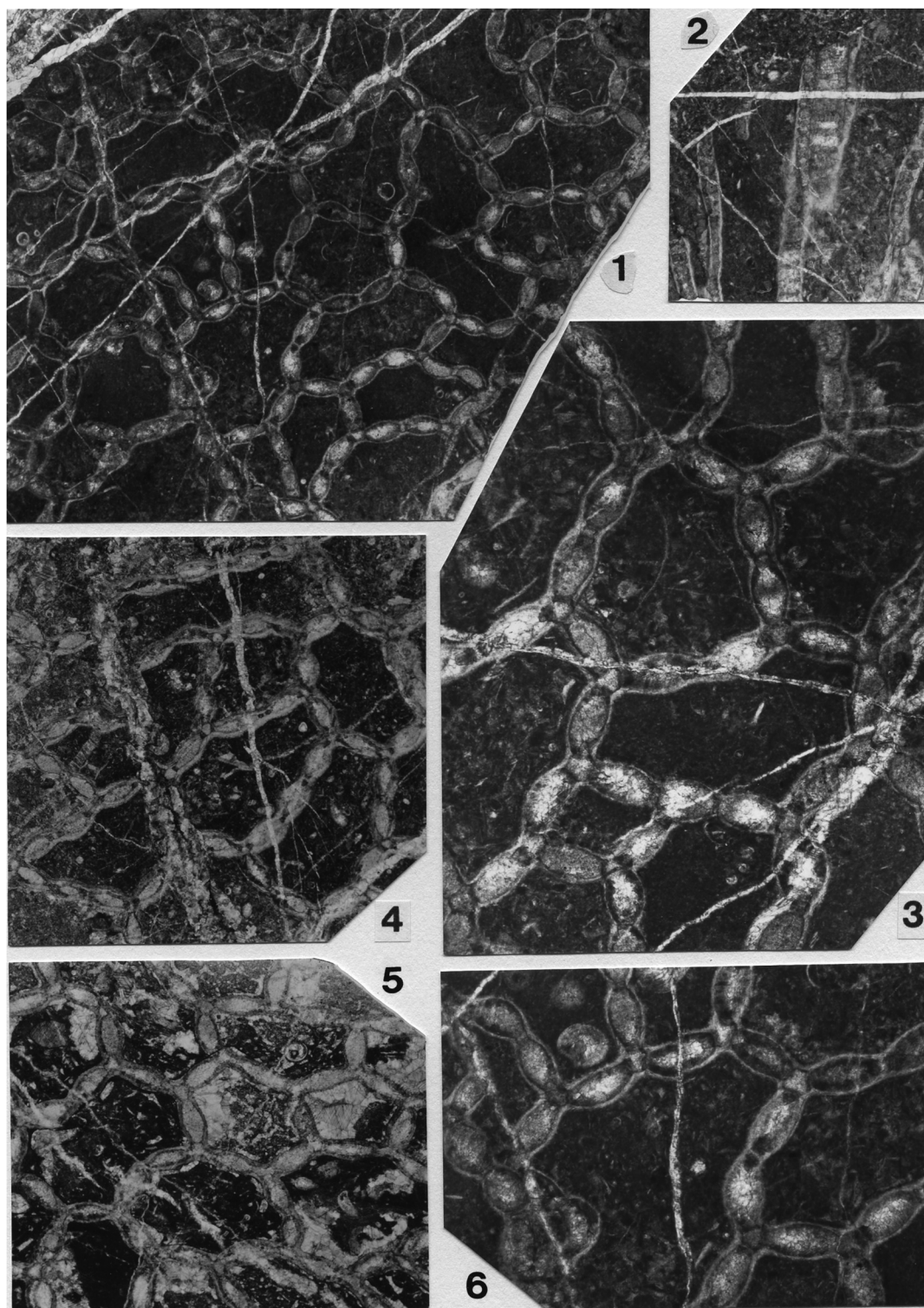


Fig. 3. *Halysites bellulus* Hamada, 1958, thin sections. 1–3, 6, holotype, UMUT PC7276. 1, transverse section, $\times 5$. 2, longitudinal section, $\times 5$. 3, 6, transverse sections, $\times 10$. 4, NMNS PA18206, transverse section, $\times 5$. 5, NMNS PA18210, transverse section, $\times 5$.

ing of one to two (rarely four) corallites; lacunae indicate subpolygonal transverse sections, whose shape variations are relatively small for the genus; diameters of lacunae are usually 1.6–3.8 mm. In transverse section, corallites are weakly inflated subrectangular (to subovate in rare cases) with 0.9–1.2 mm in length and 0.6–0.9 mm in width; form ratios (length/width) 1.19–1.78. Corallite walls thin to moderate, 0.06 to 0.19 mm in thickness, septal spines may be absent; tabulae complete and horizontal, numbering 4–6 in 2 mm of corallite length. Coenenchymal tubules present at all rank junctions and most corallite junctions; tubule diaphragms complete.

Occurrence: Common in dark greenish gray limestone (NMNS PA18207, 18213, 18216) of the G2 Member and light colored (greenish to brownish gray) limestone (NMNS PA18209–18212, 18214, 18215) of the G3 Member at locality 1 and light gray limestone (NSMN PA18201–18206) of the G3 Member at locality 3. The holotype (UMUT PC7276) was collected from light gray limestone of the G3 Member on the western slope of the Mt. Gionyama (Hamada, 1958).

Discussion: Although Hamada's (1958) description of *Halysites bellulus* was based on a single holotype from the G3 Member, our investigation reveals that this species occurs also in the G2 Member. *Halysites bellulus* is distinguished from *H. catenularius* (Linnaeus) by its short ranks, relatively small variations of transverse section of the lacunae, mostly subrectangular profiles of the corallites with smaller diameters, and the thinner corallite walls.

***Halysites delicatus* sp. nov.**

(Figs. 4–1–7)

Holotype: NMNS PA18280, from which five

thin sections were made.

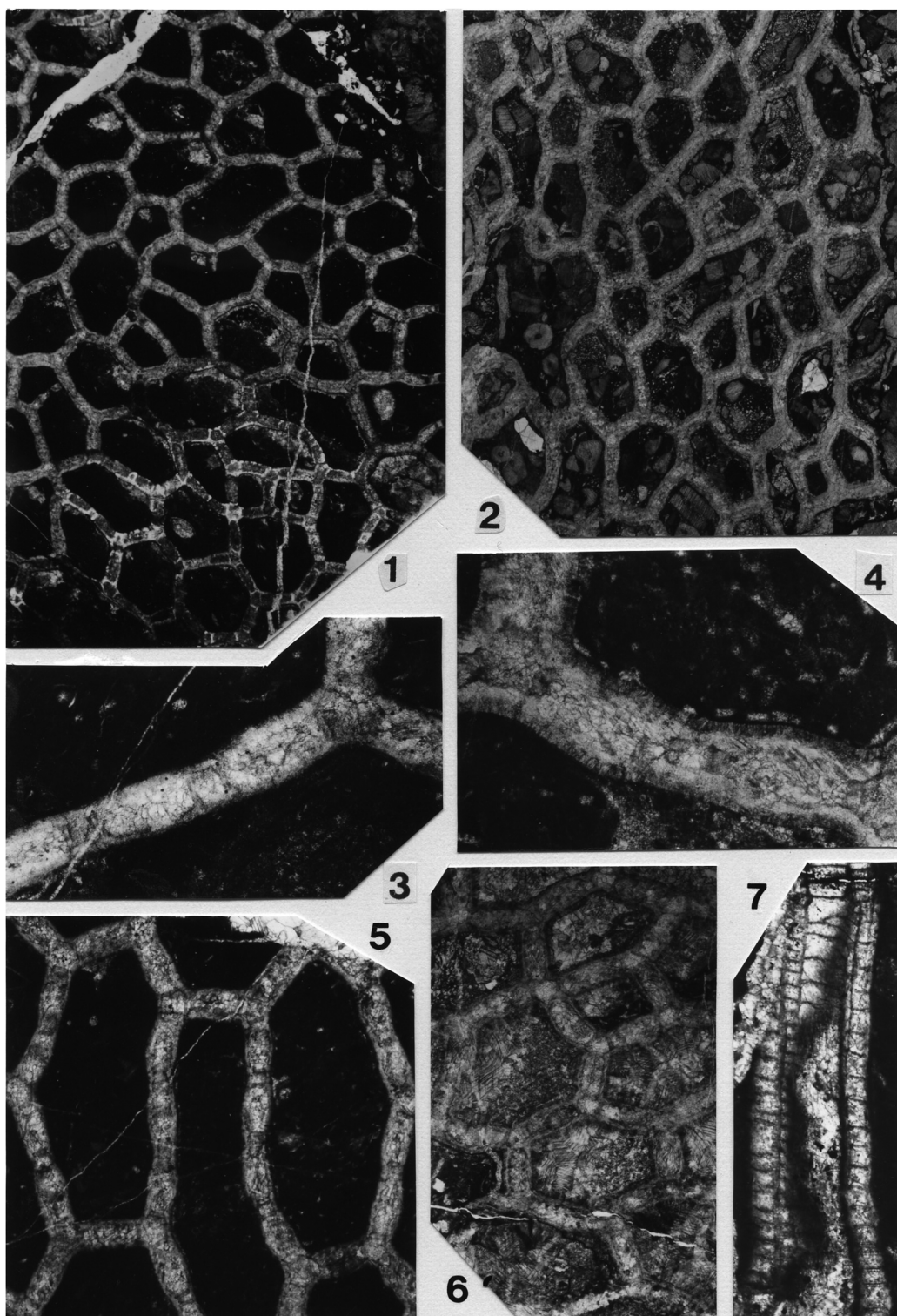
Paratypes: Six thin sections were studied from the four paratypes, NMNS PA18275, 18277, 18278, 18281.

Other material examined: NMNS PA18276, 18279.

Diagnosis: *Halysites* with mostly short ranks consisting of one to two corallites, narrow lacunae having polygonal transverse sections, and very small corallites indicating approximately 0.7 mm in length and 0.5 mm in width; transverse sections of corallites are faintly inflated subrectangular to rectangular profiles with approximately 1.46 in their form ratios (length/width); corallite walls thin to moderate, 0.07–0.12 mm; septa vary from almost absent to well-developed, short conical; coenenchymal tubules at corallite junctions have compressed rectangular to quadrate transverse sections.

Description: Coralla thick tabular in growth form, halysitoid; the largest specimen of corallum (holotype) attains 90 mm (imperfect) in width and 60 mm in height. Ranks mostly short, straight and composed of one to two corallites; in rare cases, somewhat longer and weakly curved ranks also recognized, in which up to four corallites occur; rank junctions correspond with corallite junctions; constrictions on sides of ranks at corallite junctions are weak, and partly disappear; lacunae narrow and nearly uniform, their transverse sections are polygonal with commonly four to six sides; diameters of usual lacunae are 0.8–2.2 mm. Corallites have faintly inflated subrectangular to rectangular profiles in transverse section; their dimensions are very small, 0.6–0.8 mm in length and 0.4–0.6 mm in width; mean length and width of corallites are respectively 0.7 and 0.5 mm; form ratios (length/width) 1.33–1.57, with 1.46 in mean; tabularia indicate elliptical to subrectangular transverse sections; no calice preserved; increase of new corallite is not

Fig. 4. *Halysites delicatus* sp. nov., thin sections. 1, 3–5, 7, holotype, NMNS PA18280. 1, transverse section, $\times 5$. 3, partial enlargement to show details of corallites and coenenchymal tubules, $\times 20$. 4, partial enlargement to show corallite (intercorallite) wall structure, $\times 30$. 5, transverse section, $\times 10$. 7, longitudinal section, $\times 10$. 2, paratype, NMNS PA18278, transverse section, $\times 5$. 6, paratype, NMNS PA18275, transverse section, $\times 10$.



detected in examined thin sections. Corallite walls thin to moderate, 0.07–0.12 mm in thickness; intercorallite walls (between tabularium and coenenchymal tubule) also thin, approximately 0.04 mm; septa vary from almost absent to well-developed in mode of occurrence, short conical, approximately 0.05 mm in their protrude portions into tabularia; tabulae complete or dissepiment-like in very rare cases; profiles of complete tabulae are horizontal to weakly concave; there are 4–6 tabulae in 2 mm of corallite length. Narrow coenenchymal tubules developed in both rank junctions and corallite ones; transverse sections of tubules are compressed rectangular to quadrate at corallite and hexagonal at rank junctions; measurements of usual tubules in transverse section are length 0.2–0.4 mm and width 0.3–0.4 mm at corallite junctions; tubule diaphragms complete, having nearly horizontal profiles.

Etymology: The specific name is derived from the Latin *delicatus*, meaning delicate, in reference to its corallite and rank shapes.

Occurrence: Relatively rare in pebbles to cobble (sandy shale, NMNS PA18278; calcareous shale, NMNS PA18276, 18277, 18281; argillaceous limestone, NMNS PA18275, 18279, 19280) in conglomeratic limestone of the G2 Member at locality 1.

Discussion: *Halysites delicatus* sp. nov. is distinguished from all other Silurian species in the genus by its very small corallite size. Except for this distinctive character, shapes of the corallites and lacunae of the new species are somewhat similar with those of *H. regulariformis* (Lin in Li and Lin, 1982, p. 81, pl. 25, figs. 8a, b) from the middle Silurian of Shanxi [Shaanxi] in North China.

Halysites intricatus sp. nov.

(Figs. 5-1-5)

Halysites süssmilchi Etheridge; Hamada, 1958, p. 102, 103, pl. 9, figs. 1–4; Shikama, 1964, pl. 20, fig. 9; Masutomi and Hamada, 1966, pl. 12, fig. 4; Adachi, 1979, fig. 1–7 [lower left]; Hamada, 1983, fig. 4; Tokai Kaseki Kenkyukai (ed.), 1995, p. 29 [middle].

Halysites sussmilchi [sic] Etheridge; Hamada, 1982, p. 4, pl. 2, fig. 12; Tashiro *et al.*, 1991, the first page of frontispieces [upper left].

Halysites suessmilchi [sic] Etheridge; Nakai, 1981, p. 151, 152, pl. 17, fig. 5, pl. 18, figs. 3, 4, text-fig. 4h.

Holotype: NMNS PA18230, from which four thin sections were made.

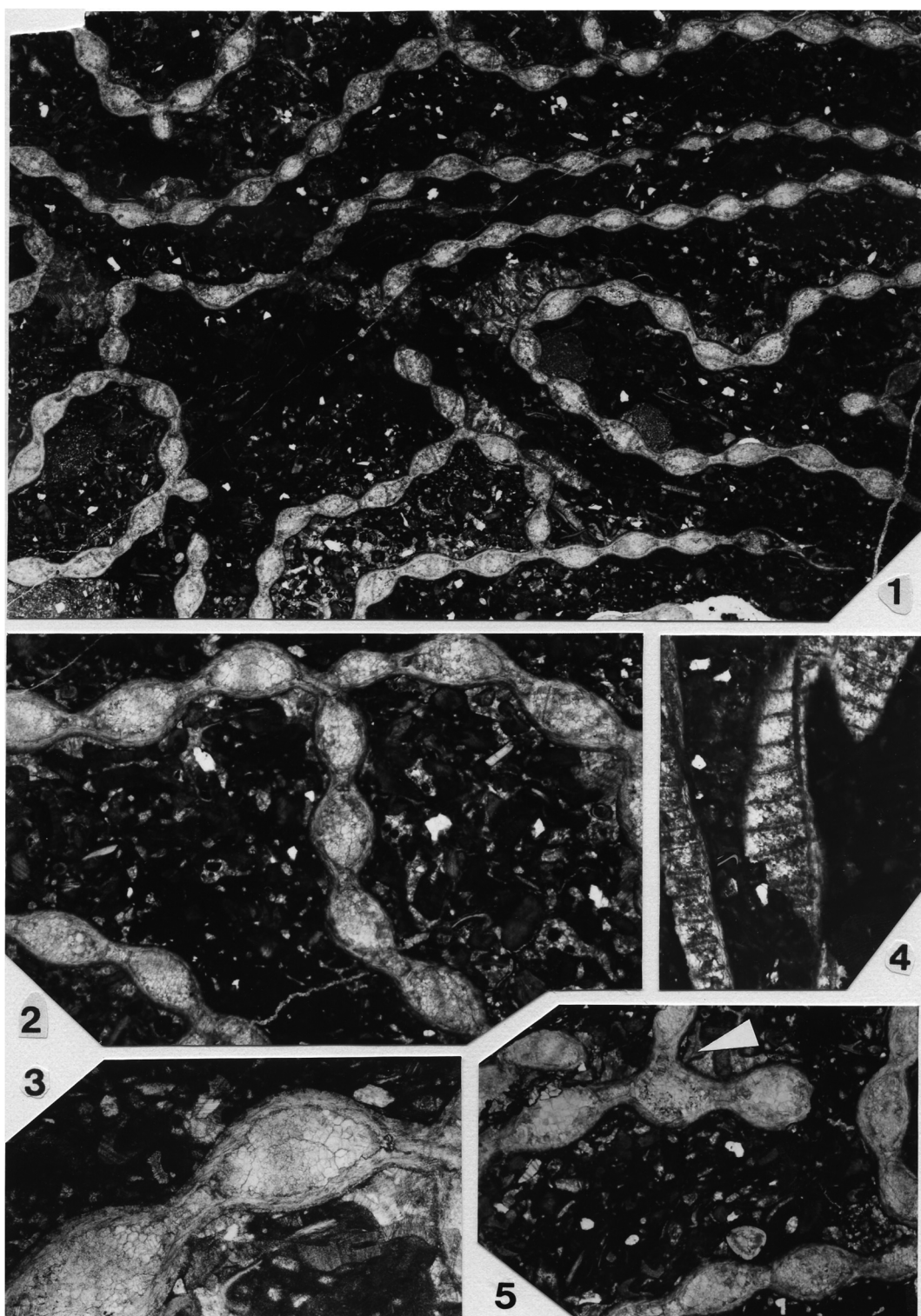
Paratypes: Two thin sections were studied from the two paratypes, NMNS PA18229, 18231.

Other material examined: A poorly preserved specimen, NMNS PA18232, was tentatively assigned to the new species.

Diagnosis: *Halysites* with wide variations in rank length, but most common ranks long to very long and sinuated; up to 21 corallites in a rank; transverse sections of lacunae are elongated labyrinthine and irregularly lobated; corallites have lenticular to subelliptical profiles and relatively small with approximate length and width are respectively 1.3 and 0.9 mm, form ratios (length/width) approximately 1.43; corallite walls moderate in thickness, 0.13–0.17 mm; septa may be absent; coenenchymal tubules in corallite junctions commonly have elongated rectangular transverse sections.

Description: Coralla massive, but growth forms cannot be determined since examined specimens are not complete, halysitoid; the largest corallum (holotype) attains 90 mm in width and 45 mm in height. Ranks exhibit wide variations in length, but are long to very long in most common cases; short ranks consist of a single corallum, whereas 21 corallites form a very long

Fig. 5. *Halysites intricatus* sp. nov., holotype, NMNS PA18230, thin sections. 1, transverse section, $\times 5$. 2, transverse section, $\times 10$. 3, partial enlargement of Fig. 5-2 to show details of corallites and coenenchymal tubules, $\times 20$. 4, longitudinal section, $\times 10$. 5, transverse section, arrow indicates rank junction at lateral corallite wall, $\times 10$.



rank without junction; arrangement of adjoining ranks are roughly parallel; in transverse section, ranks indicate sinuation with broad to strong curvatures; rank junctions occur at corallite junctions, or rarely at side of corallites; distinct and wide constrictions are developed on sides of ranks at corallite junctions; lacunae wide, have variable shapes indicating elongated labyrinthine and irregularly lobated shapes in transverse section. Corallites are relatively small and have lenticular to subelliptical profiles in transverse section, whose dimensions are 1.1–1.6 mm in length and 0.8–1.0 mm in width; their mean length and width are respectively 1.3 and 0.9 mm; form ratios (length/width) 1.16–1.75, with 1.43 in mean; tabularia are lenticular in transverse section; calice is not preserved in examined specimens; apparent offset of new corallites is not detected in sectioned parts of examined specimens. Corallite walls moderate in thickness, 0.13–0.17 mm, and differentiated into outer layer of epitheca and inner stereoplastic layer; internal- and micro-structure of stereoplasm are not preserved; intercorallite walls thin, approximately 0.03 mm in thickness; septa may be absent; tabulae complete, nearly flat; there are 13–19 tabulae in 5 mm of corallite length. Coenenchymal tubules present at all corallite and rank junctions; their transverse sections are elongated rectangular in usual cases to quadrat in relatively rare ones, having length 0.3–0.6 mm and width 0.3–0.5 mm; at rank junctions, they indicate elongated subrectangular with (or without) curvature, quadrate, indistinct sub-triangular and three-pointed shapes; tubule diaphragms complete.

Etymology: The specific name is derived from the Latin *intricatus*, meaning intricate, in reference to its rank shape.

Occurrence: Rare in pebbles to cobble (sandy shale, NMNS PA18229–18231; dark greenish gray limestone, NSM PA18232) of conglomeratic limestone of the G2 Member at locality 1.

Discussion: This species has been previously recorded as *Halysites süssmilchi* Etheridge

(1904, p. 26, 27, pl. 3, figs. 3, 4, pl. 7, figs. 1–3). However, the type specimen of *H. süssmilchi* from New South Wales in Australia is markedly different from the present Gionyama specimens in having the shorter ranks, which usually consist of the one to four corallites and define the less elongate lacunae. In this study a new species, *H. intricatus*, is erected based on the material from the Gionyama Formation. Except for the type stratum, *H. intricatus* is also documented from the Yokokurayama Group (e.g., Hamada, 1958; Nakai, 1981).

Halysites nitidus Lambe (1899, p. 71, pl. 4, figs. 2, 2a, b; Buehler, 1955, p. 49, pl. 8, figs. 4–7, pl. 9, fig. 1; Young *et al.*, 1991, p. 717, 718, figs. 3-1, 4-1–8) from Quebec in Canada is most similar to *H. intricatus*, but differs in having the well-developed and long septal spines. Yabe (1902, p. 35, 36, pl. 8, fig. 3, pl. 9, fig. 1) described a comparable species with *H. intricatus* from Gotland as *H. cf. süssmilchi*. The Yabe's (1902) species can be distinguished from the new species by its thicker corallite walls and well-developed septal spines.

Halysites kuraokensis (Hamada, 1958)

(Figs. 6-1–6)

Acanthohalysites kuraokensis Hamada, 1958, p. 101, pl. 8, figs. 1–3; Hamada, 1983, fig. 1; Oyagi, 2000, p. 247 [upper right]; Oyagi, 2003, p. 224 [lower left].

Halysites kuraokensis (Hamada); Nakai, 1981, p. 152, 153, pl. 18, figs. 1, 2, text-fig. 4f.

Halysites kuraokensis variety; Nakai, 1981, p. 153, 154, pl. 17, fig. 4.

[non] *Acanthohalysites kuraokensis* Hamada; Hamada and Itoigawa, 1983, p. 9, fig. 4 (= *H. catenularius*).

Acanthohalysites kuraokaensis [sic] Hamada; Adachi, 1979, fig. 1-7 [third from left in upper rank and lower right].

[?] *Acanthohalysites kuraokaensis* [sic] Hamada; Obata (ed.), 1994, p. 17 [head].

Material examined: NSMS PA18217–18228; UMUT PC7269 (holotype).

Description: Coralla massive, probably thick tabular in growth form, halysitoid. Ranks very short, mostly composed by a single corallite;

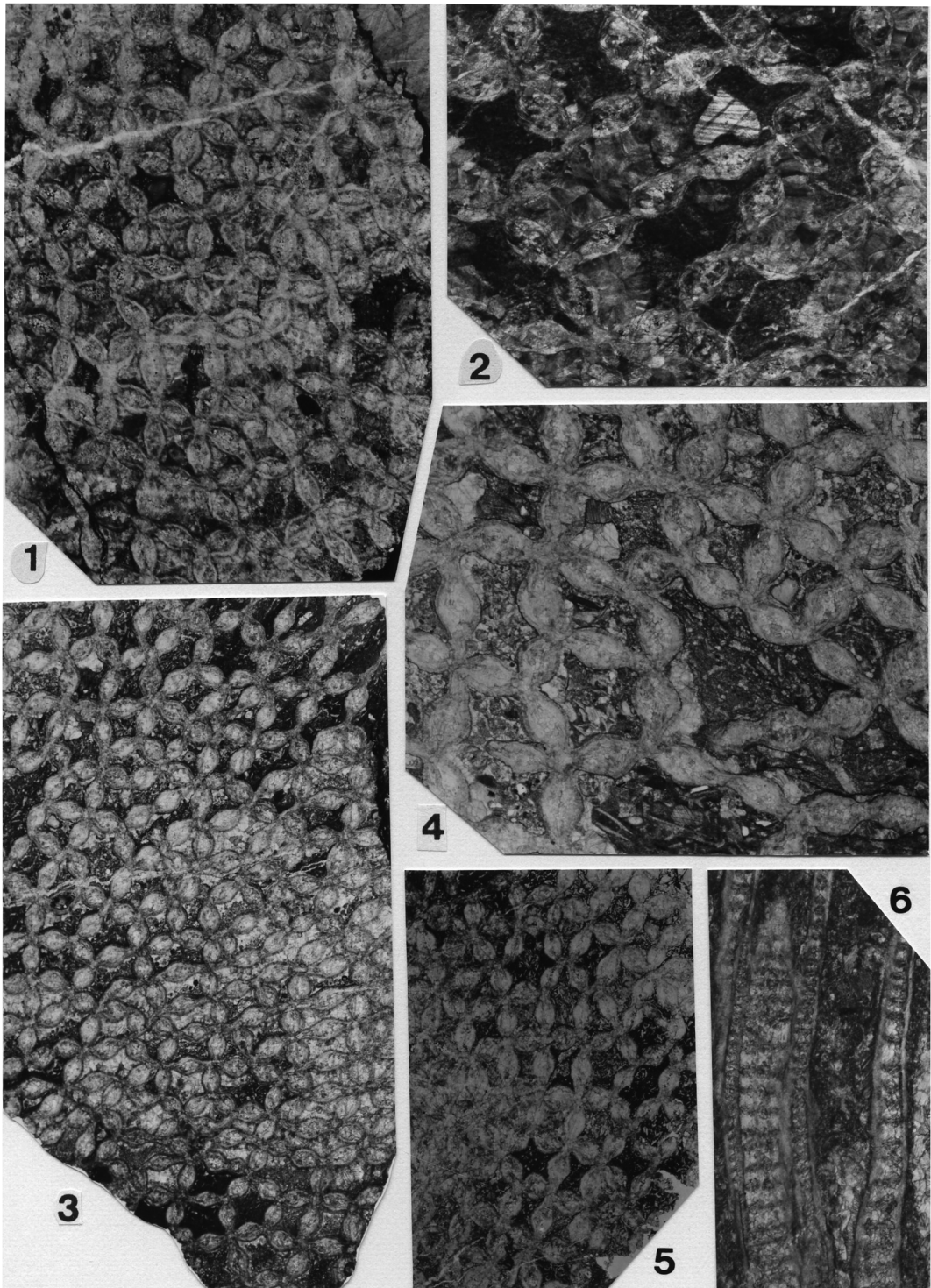


Fig. 6. *Halysites kuraokensis* (Hamada, 1958), thin sections. 1, NMNS PA18222, transverse section, $\times 5$. 2, holotype, UMUT PC7269, transverse section, $\times 10$. 3, 4, NSM PA18219. 3, transverse section, $\times 5$. 4, transverse section, $\times 10$. 5, NMNS PA18224, transverse section, $\times 5$. 6, NMNS PA18217, longitudinal section, $\times 10$.

lacunae narrow, having subpolygonal transverse sections with 0.4–2.0 mm in usual diameter. Corallites subelliptical (to subovate in rare cases) in transverse section with 0.7–1.0 mm in length and 0.6–0.8 mm in width; form ratios (length/width) 1.21–1.57. Corallite walls moderate in thickness, 0.10–0.17 mm; septal spines well-developed, short conical; tabulae complete and horizontal, numbering 5–7 in 2 mm of corallite length. Coenenchymal tubules present at rank junctions; in rarely developed longer ranks, coenenchymal tubules recognized also in all corallite junctions; tubule diaphragms complete, and more closely spaced than tabulae.

Occurrence: Common in pebbles to cobbles of conglomeratic limestone (calcareous shale, NMNS PA18224, 18225; argillaceous limestone, NMNS PA18219, 18222, 18223, 18226–18228; gray limestone, (NMNS PA18220) and gray to greenish gray limestone (NMNS PA18221) of the G3 Member at locality 1. The holotype (UMUT PC7269) was collected from lenticular gray limestone of the G2 Member at a road cut on the western foot of the Mt. Gionyama (Hamada, 1958).

Discussion: Although this species was proposed by Hamada (1958) as the tenth member of the genus *Acanthohalysites* (Hamada, 1957; type species, *Halysites australis* Etheridge, 1898), Laub (1979) synonymized the genus with *Halysites*. Because the presence or not presence of the septal spines in halysitids are variable even in the adjoining corallites, we follow this concept.

Based on the material from the Yokokurayama Group, Nakai (1981) described an unnamed variety that characterized by smaller diameters of the lacunae ($0.3\text{--}0.8 \times 0.6\text{--}1.75$ mm, averaging $0.75\text{--}1.25$ mm) and corallites ($0.6\text{--}0.8 \times 0.7\text{--}0.9$ mm) than those of *Halysites kuraokensis* (s. s.). We do not accept this sub-specific separation because of these smaller dimensions are sometimes visible in intra-colonial variation.

As stated above, taxonomic confusions between *Halysites kuraokensis* and *H. catenularius* (Linnaeus) are recognized. The former species, however, clearly differs in having the

smaller corallite diameters and the thinner corallite walls than those of the latter species.

Halysites kyushuensis sp. nov.

(Figs. 7-1–5)

Holotype: NMNS PA18282, from which six thin sections were made.

Diagnosis: *Halysites* with broadly curved ranks exhibiting very short to relatively long length; corallites small, approximately 1.0 mm in length and 0.9 mm in width; transverse sections of corallites well inflated, subelliptical to nearly circular having mean form ratios (length/width) of 1.13; corallite walls moderate in thickness, 0.13–0.17 mm; septal spines numerous, exceptionally long, attaining 0.27 mm; coenenchymal tubules elongated; at corallite junctions, tubules have rectangular transverse sections.

Description: Only a single specimen (holotype) of massive corallum is available for study; it has approximately 53 mm in maximum diameter and 42 mm in height, halysitoid; growth form cannot be determined since it is incomplete. Ranks broadly curved, whose length somewhat variable ranging from very short to relatively long; the former ranks consist of a single corallite and the latter ones consist of seven corallites; rank junctions occur at corallite junctions; deep and wide constrictions are developed on rank sides; lacunae also variable in transverse section; the most common lacunae have elongated and gently curved or subpolygonal sections. Corallites well inflated with subelliptical to nearly circular transverse sections; sizes of corallites are small, 0.8–1.1 mm in length and 0.7–1.0 mm in width; their mean length and width are respectively 1.0 and 0.9 mm; form ratios (length/width) 0.93–1.41, with 1.13 in mean; tabularia usually indicate subcircular transverse sections; no calice preserved; increase of new corallite is not detected in sectioned parts of the holotype. Corallite walls moderate in thickness, 0.13–0.17 mm, and differentiated into outer layer of epitheca and inner one of stereoplasm; thickness of intercoral-

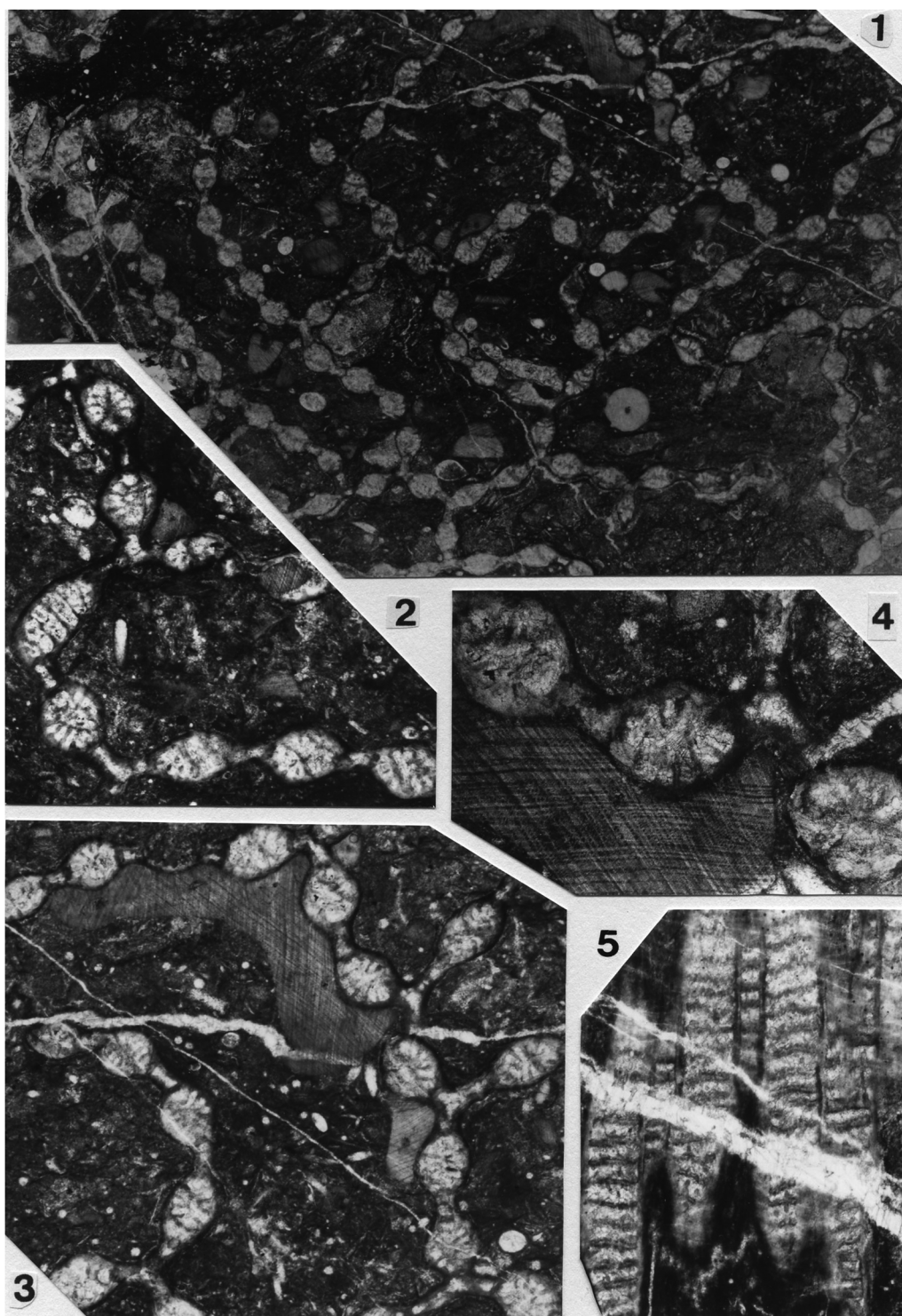


Fig. 7. *Halysites kyushuensis* sp. nov., holotype, NMNS PA18282, thin sections. **1**, transverse section, $\times 5$. **2**, **3**, transverse sections, $\times 10$. **4**, partial enlargement of Fig. 7-3 to show details of septal spines, $\times 20$. **5**, longitudinal section, $\times 10$.

lite walls is approximately 0.04 mm; microstructure of corallite and intercorallite walls are not preserved; septa numerous and composed of rod-like spines, whose length is exceptionally long for corallite sizes, attaining 0.27 mm in their protruded portions into tabularia; septal spines arrange in longitudinal rows; tabulae complete with faintly uparched, horizontal or faintly concaved profiles in longitudinal section; there are 6–8 tabulae in 2 mm of corallite length. Coenenchymal tubules present in all junctions, narrow; at corallite junctions, they indicate elongated rectangular in transverse sections with 0.5–0.9 mm in length and 0.3–0.4 mm in width; tubules at rank junctions indicate variable forms in transverse section, such as three-pointed star-like, more or less curved and strongly elongated rectangular, or sub-triangular shapes; tubule diaphragms complete.

Etymology: The specific name is taken from Kyushu. The type locality of the new species belongs to this province.

Occurrence: Very rare in argillaceous limestone pebble in conglomeratic limestone of the G2 Member at locality 1.

Discussion: Diagnosis of *Halysites kyushuensis* sp. nov. is distinctive. It clearly differs from all others assigned to the genus by having the small corallites with well inflated transverse sections, the exceptionally long septal spines, and the elongated coenenchymal tubules. As far as we know, no comparable species has been documented.

***Halysites tenuis* Hamada, 1958**

(Figs. 8–1–5)

Halysites tenuis Hamada, 1958, p. 103, pl. 9, figs. 5, 6, pl. 10, fig. 1; Shikama, 1964, pl. 20, fig. 8.

Material examined: UMUT PC7275 (holotype).

Occurrence: Very rare in light gray limestone of the G3 Member on the western slope of the Mt. Gionyama (Hamada, 1958).

Remarks: As indicated by Hamada (1958),

Halysites tenuis is diagnosed by its small corallite size and elongated transverse sections of the lacunae. Because no additional material was recovered during our collecting efforts, the holotype is still only representative of this species and there is no need to repeat its description here.

Genus *Falsicatenipora* Hamada, 1958

Type species: *Halysites japonica* Sugiyama, 1940.

***Falsicatenipora shikokuensis* Noda and Hamada in Hamada, 1958**

(Figs. 9–1–6)

Halysites shikokuensis Noda, 1952, p. 322 [nomen nudum].

Falsicatenipora shikokuensis Noda and Hamada in Hamada, 1958, p. 99, 100, pl. 6, figs. 4, 5, pl. 7, figs. 1–7; Kawamura, 1980, p. 280, pl. 1, figs. 1, 2, text-fig. 5a; Nakai, 1981, p. 144, 145, pl. 16, figs. 2–4, pl. 17, fig. 3, text-fig. 4b; Hamada, 1982, p. 4, pl. 2, fig. 8; Obata (ed.), 1994, p. 17 [bottom]; Oyagi, 2000, p. 223 [bottom]; Hirota, 2003, fig. 6.

Falsicatenipora cf. *shikokuensis* Noda and Hamada; Matsumoto and Kanmera, 1964, p. 16.

Catenipora shikokuensis (Noda and Hamada); Adachi, 1979, fig. 1–7 [lower right].

Falsicatenipora shikokuensis variety, Nakai, 1981, p. 145, 146, pl. 16, fig. 1.

[?] Halysitid gen. et sp. indet., Ihara, 2001, fig. 2.

Falsicatenipora sp., Oyagi, 2003, p. 193 [lower left].

Material examined: NSMS PA18185–18200, 18283–18291.

Emended diagnosis: Coralla dendritic, very large consisting of narrow branches. See Hamada (1958) for other characteristics including ranks (= chains in Hamada's terminology), corallites (= macrocorallites in ditto), lacunae (= fenestrules in ditto), coenenchymal tubule (= microcorallites in ditto), and internal structures.

Description: Coralla dendritic and very large; largest colony (NSMS PA18192) exceeds 80 cm in diameter; corallites arrange in halysitoid style in branches; branch diameters are small, usually 7–20 mm. Ranks mostly short with a

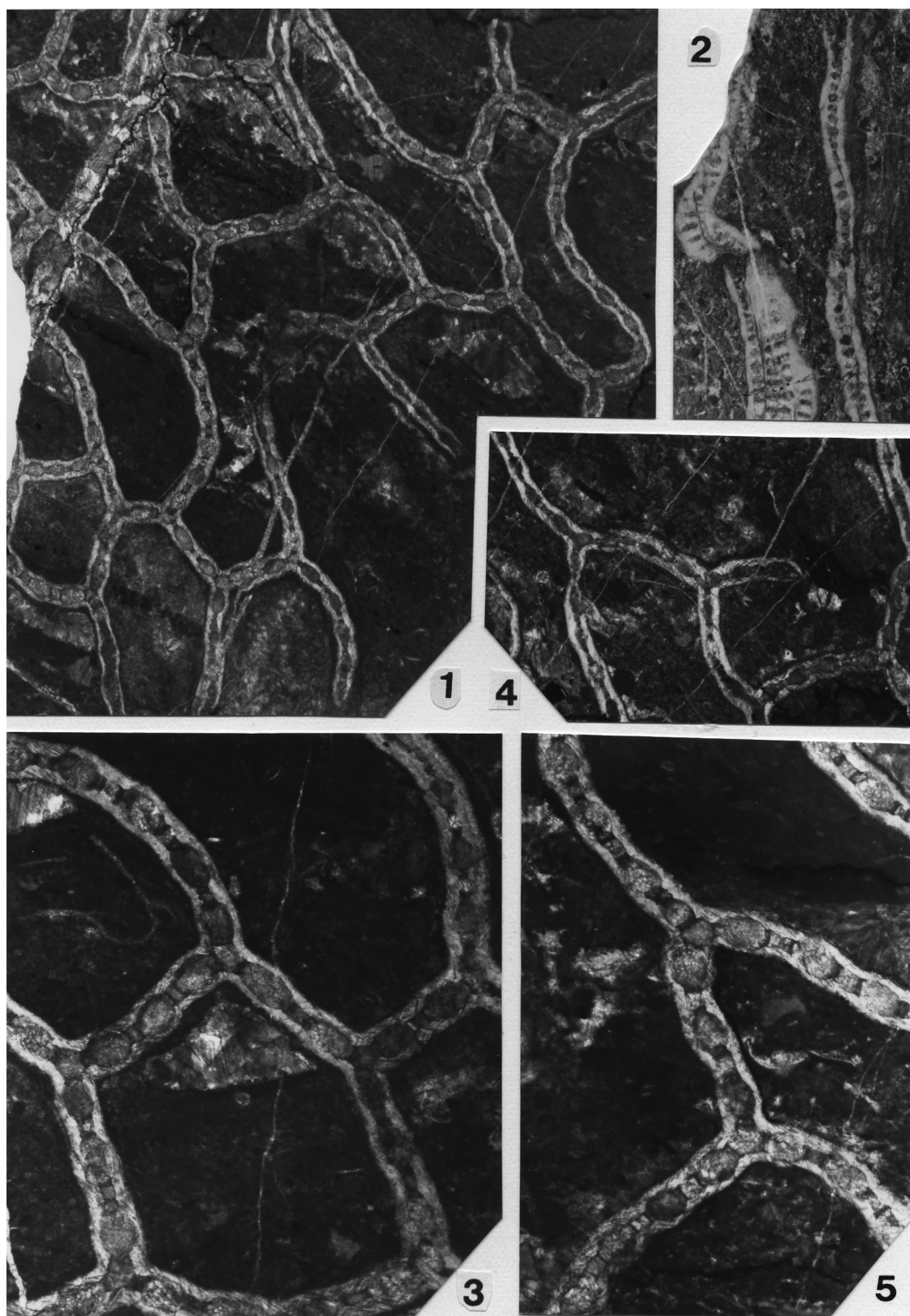


Fig. 8. *Halysites tenuis* Hamada, 1958, holotype, UMUT PC7275, thin sections. 1, transverse section, $\times 5$. 2, longitudinal section, $\times 5$. 3, 5, transverse sections, $\times 10$. 4, transverse section, $\times 5$.

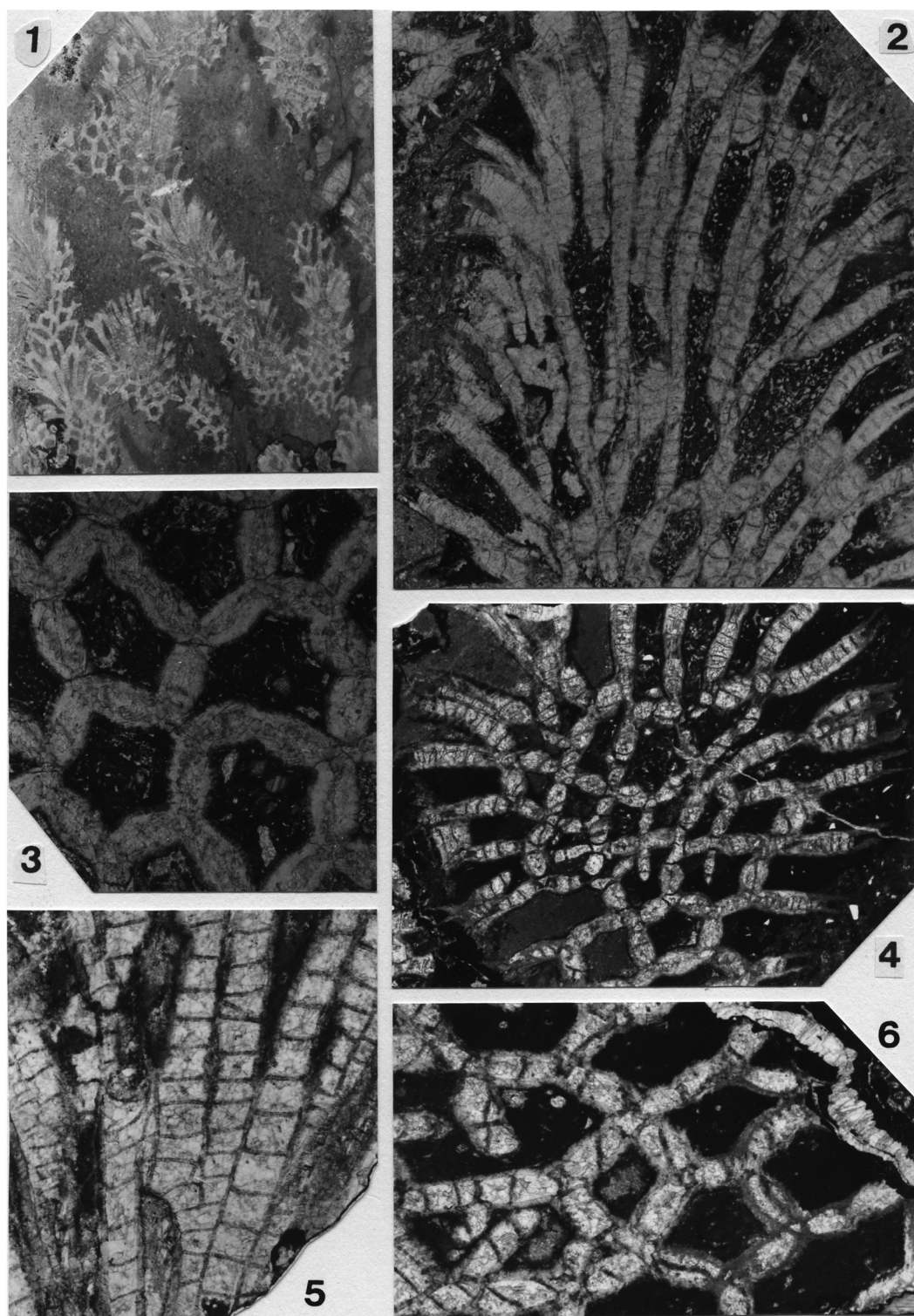


Fig. 9. *Falsicatenipora shikokuensis* Noda and Hamada, 1958. 1, 2, 4-6, NMNS PA18192. 1, longitudinal polished section, $\times 1$. 2, longitudinal thin section, $\times 5$. 4, transverse thin section of branch, $\times 5$. 5, longitudinal thin section, $\times 10$. 6, transverse thin section, $\times 10$. 3, NMNS PA18186, transverse thin section, $\times 10$.

single corallite, but longer ones consisting of up to tree corallites are recognized in rare cases; lacunae small, usually indistinct polygonal in transverse section with diameters of 0.6–3.0 mm. Corallite sub-rectangular, with 0.6–1.3 mm in length and 0.5–1.0 mm in width, giving from ratios (length/width) of 1.14–1.58. Corallite walls have 0.15–0.27 mm in thickness; occurrence of septal spines is variable, almost absent to well-developed, short; most tabulae complete and horizontal. Coenenchymal tubules having triangular to quadrate transverse sections are developed at rank junctions; apparent coenenchymal tubule is not detected at corallite junctions in examined rare examples.

Occurrence: Very abundant in pebbles to boulder of conglomerate (calcareous shale, NSMS PA18193, 18194; argillaceous limestone, NSMS PA18185–18191, 18195–18200, 18283–18291; dark gray limestone, NSM PA19192) of the G2 Member at locality 1.

Discussion: Because its fragile nature of the corallum, the original very large and dendritic colonies of *Falsicatenipora shikokuensis* have been misidentified as “small” and exhibiting “massive”, “hemispherical” or “cylindrical” growth forms. An unnamed variety from the Yokokurayama Group in Kochi Prefecture was defined by Nakai (1981), of which characters separating from *F. shikokuensis* (s. s.) are the hemispherical coralla and smaller sizes of the lacunae (0.7×1.6 to 1.0×2.3 mm) and the corallites ($0.45\text{--}0.5 \times 0.66\text{--}0.75$ mm). The former diagnosis is caused from this misidentification, and latter two fall into range of intra-specific variations. We consider that this sub-specific separation is not necessary.

The holotype of this species was collected from the Yokokurayama Group. Except for the Gionyama Formation and the type stratum, *F. shikokuensis* has been known to occur in the Okuhinotsuchi Formation, Iwate Prefecture (Kawamura, 1980). In addition, comparable forms of *F. shikokuensis* are recorded from the Fukami Formation (Matsumoto and Kanmera, 1964) and the Nabaehana Block (Ihara, 2001).

This species is a useful index fossil representing the late Wenlock in the Kurosegawa and Southern Kitakami Belts.

Genus *Schedohalysites* Hamada, 1957

Type species: *Halysites orthopteroides* Etheridge, 1904.

Schedohalysites kitakamiensis

(Sugiyama, 1940)

(Figs. 10-1-5; 11-1-7)

Halysites kitakamiensis Sugiyama, 1940, p. 129–131, pl. 27, figs. 4–9, pl. 28, figs. 3–8, pl. 30, fig. 14, text-figs. 6a, b; Noda, 1952, p. 322; Noda, 1955, p. 52; Ichikawa *et al.*, 1953, p. 15; Hamada, 1956, p. 134–140, pl. 9, figs. 1–6, text-fig. 1.

Halysites cf. *kitamiensis* [sic] Sugiyama; Saito and Kambe, 1954, fig. 1.

Halysites cf. *kitakamiensis* Sugiyama; Kambe, 1957, fig. 4.

Falsicatenipora japonica (Sugiyama); Hamada, 1958, p. 99, pl. 6, figs. 1, 2; Shikama, 1964, pl. 20, fig. 11.

Schedohalysites kitakamiensis (Sugiyama); Hamada, 1958, p. 100, 101, pl. 6, fig. 3, pl. 8, figs. 4, 5; Shikama, 1964, pl. 20, fig. 10; Hirata, 1966, pl. 2, figs. 7, 8; Masutomi and Hamada, 1966, pl. 12, fig. 3; Ishida, 1977, fig. 2; Adachi, 1979, fig. 1-7 [upper left]; Nakai, 1981, p. 146, 147, pl. 17, figs. 1, 2, pl. 19, fig. 1, text-fig. 4a; Hamada, 1982, p. 4, pl. 2, fig. 10; Hamada, 1983, fig. 3.

Schedohalysites sp., Nakai, 1981, p. 147, 149, pl. 16, fig. 5, text-fig. 4d; Oyagi, 2000, p. 247 [lower left].

[?] *Schedohalysites* sp., Hamada and Itoigawa, 1983, p. 8, fig. 1.

Halysites sp., Kashima, 1988, fig. 16-4.

Material examined: NSMS PA17419, 18162–18184; UMUT PC7251, 7264a, 7264b, 7265.

Description: Coralla may be dendritic and large; corallites arrange in halysitoid style in colony; usual diameters of cylindrical colonies (branches?) are 18–60 mm. Ranks exhibit wide variations in length, but are short to very short in most common cases; usual ranks consist of one to four corallites; lacunae also variable in shape, commonly their transverse sections are subpolygonal, but elongated or lobated profiles are not

rare. Corallites have weakly inflated subrectangular to rectangular shapes in transverse section, with 1.2–1.6 mm in length and 0.7–1.0 mm in width; form ratios (length/width) usually 1.19–2.06. Corallite walls variable in thickness, 0.08–0.21 mm; septa high conical, occurrence of which spines ranges from almost absent to common; tabulae complete with nearly horizontal profiles; there are 5–8 tabulae in 2 mm of corallite length. Coenenchymal tubules usually present at rank junctions, but their developments at corallite junctions are poor; tubule diaphragms complete.

Occurrence: Abundant in pebbles to cobbles of conglomerate (argillaceous limestone, NMNS PA18177, 18178, 18180; sandy limestone, NMNS PA18173; dark greenish gray to black limestone, NMNS PA19172, 18176, 18179, 18181–18183) and dark greenish gray limestone of the G2 Member at locality 1 (NMNS PA18174, 18175, 18184), and light colored (gray to pink or brown) and partly brecciated limestone of the G3 Member at locality 2 (NMNS PA17419, 18162–18166) and locality 3 (NMNS PA18167–18171). Four specimens (UMUT PC7251, 7264a, 7264b, 7265) were collected from light gray limestone of the G3 Member on the western slope of the Mt. Gioniyama (Hamada, 1958).

Discussion: *Schedohalysites kitakamiensis* shows wide morphologic variations in shapes of the ranks and lacunae, form ratios of the corallites, and thickness of the corallite walls. The development of the coenenchymal tubules in the rank and corallite junctions is also variable. On the basis of this character we conclude that a record of *Falsicatenipora japonica* (Sugiyama) from the Gioniyama Formation (Hamada, 1958) is error and resulted from misidentification of a fragmentary specimen (UMUT PC7251) of *S. kitakamiensis*. The Hamada's (1958, pl. 6, figs. 1, 2) specimen is re-illustrated herein (Fig. 11-5).

Furthermore, a similar taxon with the specimen was described by Nakai (1981) as *Schedohalysites* sp. from the Yokokurayama Group. This species is here subsumed into *S. kitakamiensis*.

The syntypes of *Schedohalysites kitakamiensis* were recovered from the Kawauchi Formation in the Southern Kitakami Belt (Sugiyama, 1940). As noted by Hamada (1958) many specimens of this species were collected at various localities also in the Kurosegawa Belt. Its stratigraphic distribution ranges from the upper Wenlock (upper Lower Silurian) to the lower Ludlow (lower Upper Silurian).

Subfamily Cateniporinae Hamada, 1957

Genus *Catenipora* Lamarck, 1816

Type species: *Catenipora escharoides* Lamarck, 1816.

Catenipora nishioi sp. nov.

(Figs. 12-1–5)

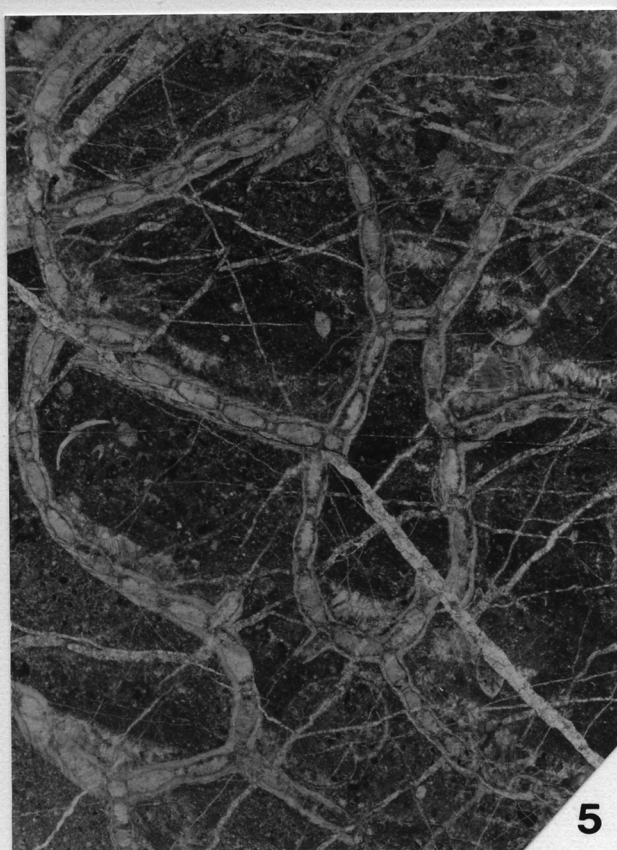
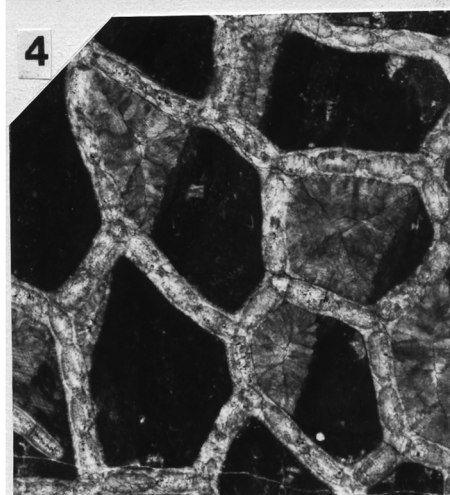
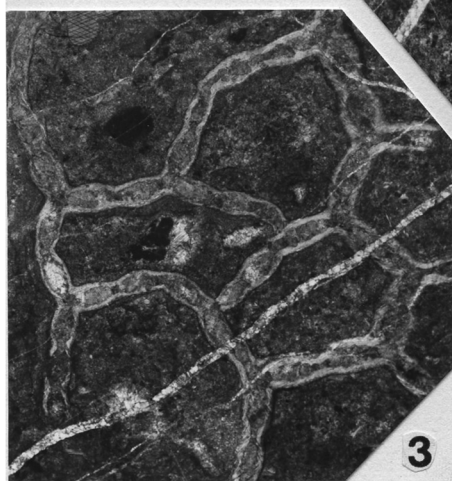
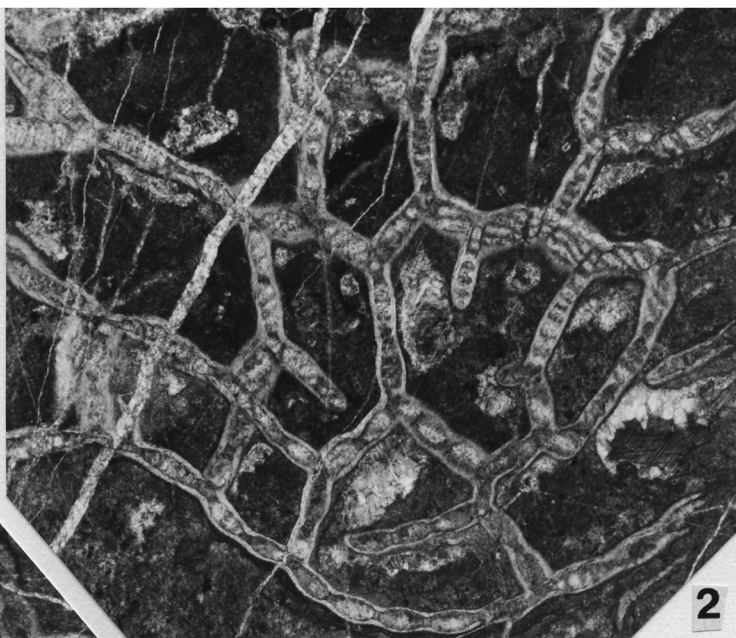
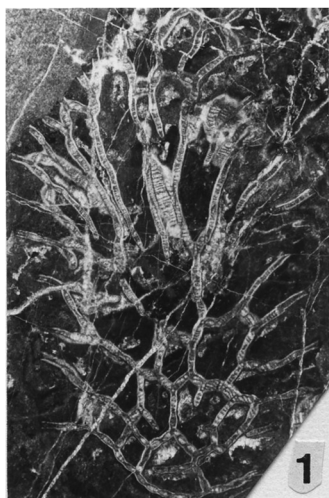
Catenipora? sp. indet., Hamada, 1958, p. 97, 98, pl. 6, fig. 6.

Holotype: NMNS PA17418, from which three thin sections were made.

Diagnosis: *Catenipora* with curved ranks that have variable length and made up of two to more than 18 corallites; constrictions on rank sides are shallow; usual lacunae indicate irregularly lobated or elongated subpolygonal profiles; transverse sections of corallites are subrectangular and approximately 1.6 mm in length and 1.1 mm in width; form ratios (length/width) approximately 1.47; corallite walls moderate to thick, 0.15–0.25 mm; septa common, relatively short; there are 4–5 tabulae in 2 mm.

Description: The holotype and only available specimen represents a fragment with

Fig. 10. *Schedohalysites kitakamiensis* (Sugiyama, 1940), thin sections. 1–3, NMNS PA18164. 1, oblique section of cylindrical colony (branch?), $\times 1.5$. 2, partial enlargement of Fig. 10-1 to show transverse to oblique sections of corallites, $\times 5$. 3, transverse section, $\times 5$. 4, NMNS PA18181, transverse section, $\times 5$. 5, NMNS PA18171, transverse section, $\times 5$.



approximately 70 mm in maximum diameter and 20 mm in height, halysitoid; corallum massive, but growth form cannot be determined since it is not complete. Ranks curved with weak to relatively strong curvatures; length of ranks is variable, ranges from short consisting of two corallites to long consisting of more than 18 corallites; rank junctions occur at corallite junctions; shallow constrictions are developed on sides of ranks at corallite junctions; transverse sections of lacunae are also variable, usually indicating irregularly lobated or elongated subpolygonal profiles. Corallites have weakly inflated subrectangular profiles in transverse section; dimensions of corallites are 1.3–1.8 mm in length and 0.9–1.2 mm in width; their mean length and width are respectively 1.6 and 1.1 mm; form ratios (length/width) 1.29–1.71, with 1.47 in mean; tabularia usually indicate elliptical transverse sections; no calice preserved; increase of new corallite is not detected in sectioned parts of the holotype. Corallite walls moderate to thick, 0.15–0.29 mm in thickness, and differentiated into outer layer of epitheca and inner one of stereoplasm; furthermore, stereoplasm differentiates into inner dark and outer transparent layers; intercorallite walls consist of three layers, including median transparent layer (= outer layer of stereoplasm) and dark layers on each side (= inner layer of ditto); thickness of intercorallite walls is thin, approximately 0.08 mm; microstructure of corallite (and intercorallite) walls is not preserved; apparent septum is not detected, it may be absent or enclosed in stereoplasm; tabulae complete with faintly uparched to horizontal profiles in longitudinal section; there are 4–5 tabulae in 2 mm of corallite length. No coenenchymal tubule is recognized at both rank and corallite junctions.

Etymology: The specific name honors Mr. Toshiaki Nishio (Gokase-cho, Miyazaki Prefecture). The holotype was collected by the second author (T.A.) under his co-operations.

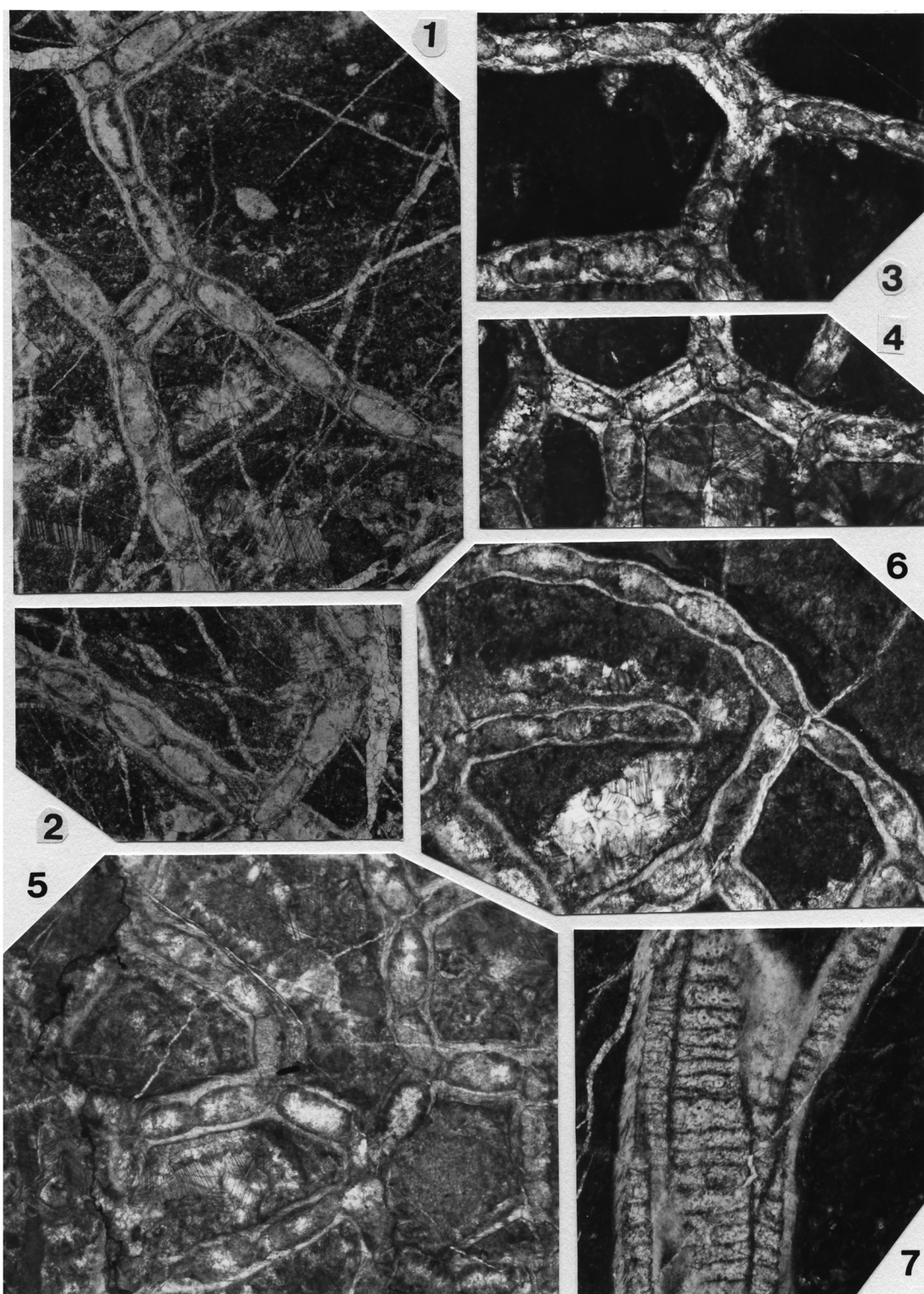
Occurrence: Very rare in sandy shale of the G2 Member at locality 1.

Discussion: A single, fragmentary and recrystallized corallum from the G2 Member of the Gionyama Formation was questionably placed in *Catenipora* by Hamada (1958). Although this specimen (UMUT PC7250) is missing, better preserved specimen in our collections shows details of the corallite walls and provides that enough information to define the genus and species levels. *Catenipora nishioi* sp. nov. represents the first undoubted record of the genus in Japan.

In shapes of its corallites and lacunae, number of corallites in a rank and relatively thin corallite walls, *Catenipora nishioi* resembles *C. gracilis* Hall (1851, p. 212, 213, pl. 29, figs. 1a, b; Buehler, 1955, p. 36–38, pl. 4, fig. 7, pl. 5, fig. 1) that was originally described by Hall (1851) on the basis of material from Wisconsin, North America and was also known from Canada (Lambe, 1899) and Norway (Kiær, 1930). The most apparent difference among these species is size of corallites, namely their mean length and width are respectively 2.0 and 1.5 mm in *C. gracilis* versus dittos of *C. nishioi* are approximately 1.6 and 1.1 mm. *Catenipora regnelli* Stasińska (1967, p. 52, pl. 2, figs. 2a, b, c) from Sweden and *C. wrighti* Klaamann in Kaljo and Klaamann (1965, p. 427, 428, pl. 2, figs. 7–11; Klaamann, 1966, p. 32–34, pl. 8, figs. 1–3, pl. 9, figs. 1, 2) from Estonia somewhat resemble *C. nishioi*, however the former two species differ from the new species by having numerous septal spines.

Falsicatenipora wangjiawanensis Lin (1975, p. 220, 221, pl. 70, figs. 2a, b) from the middle Silurian of Shaanxi in Chinling (Qing Ling), China exhibits the quite similar corallite morphologies, however B. Lin stated that *F. wangjiawanensis* has the triangular coenenchymal tubules at the rank junctions. In addition, the tabulae of the Chinese species are somewhat

Fig. 11. *Schedohalysites kitakamiensis* (Sugiyama, 1940), thin sections. **1, 2**, NMNS PA18171, transverse sections, $\times 10$. **3, 4**, NMNS PA18181, transverse sections, $\times 10$. **5**, UMUT PC7251, transverse section, $\times 10$. **6, 7**, NMNS PA18164. **6**, transverse section, $\times 10$. **7**, longitudinal section, $\times 10$.



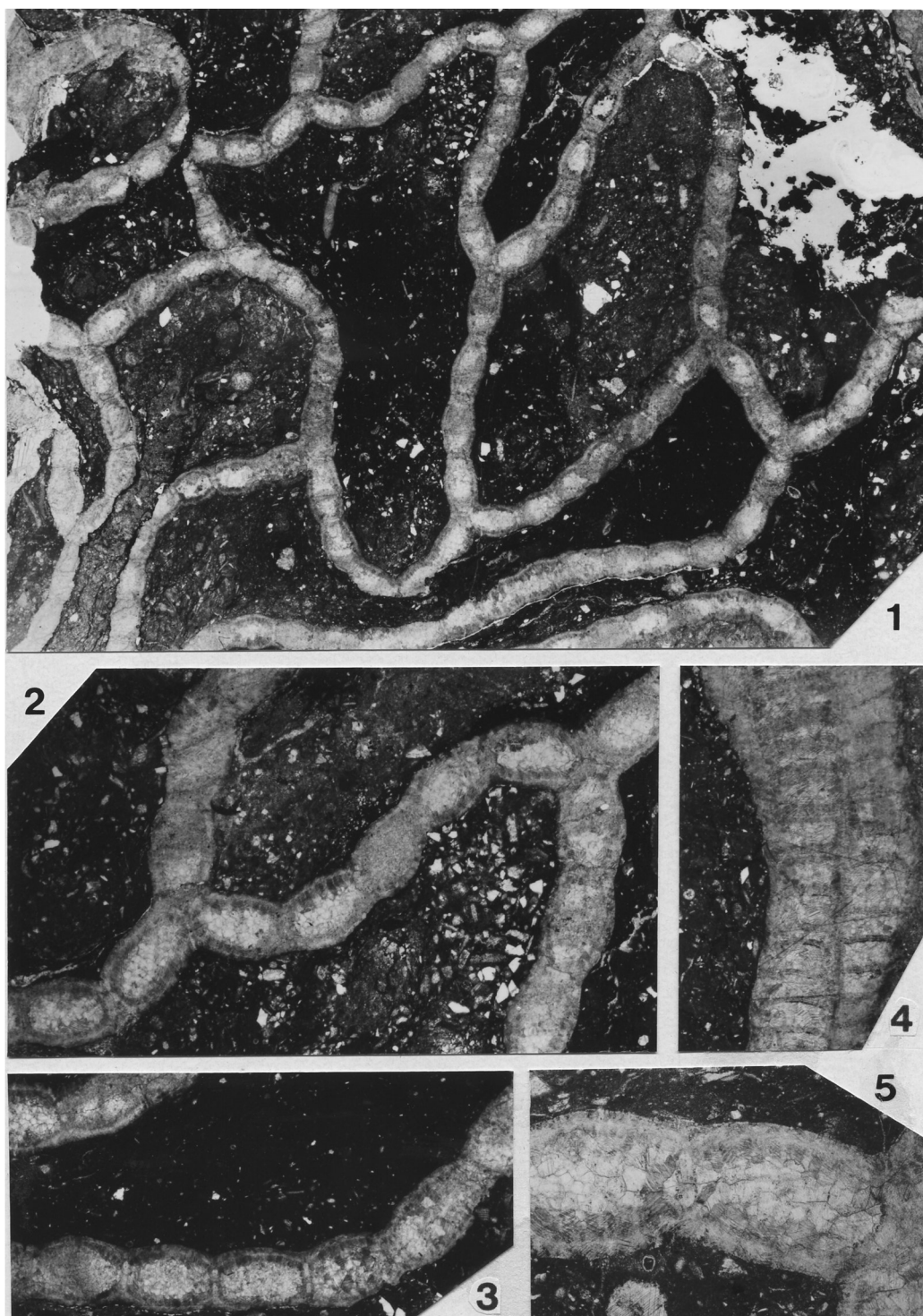


Fig. 12. *Catenipora nishioi* sp. nov., holotype, NMNS PA17418, thin sections. **1**, transverse section, $\times 5$. **2**, **3**, transverse sections, $\times 10$. **4**, longitudinal section, $\times 10$. **5**, partial enlargement to show corallite (intercorallite) wall structure, transverse section, $\times 20$.

more widely spaced than those of *Catenipora nishioi*. Number of the tabulae in 2 mm is 2–4, whereas that of *C. nishioi* indicates 4–5.

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We are grateful to the late Dr. Takashi Hamada, who provided guidance of morphology and taxonomy of halysitid corals. Field assistance was rendered by Mr. Toshiaki Nishio. Dr. Takenori Sasaki made the UMUT specimens available for our study. We also appreciate critical and helpful reviews of the manuscript by Dr. Hisayoshi Igo.

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