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CORALS FROM THE OMI LIMESTONE,
CENTRAL HONSHU, JAPAN

by

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(with 9 plates and 5 text-figures)

(Contribution from the Department of Geology and Mineralogy,
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The three coral species described below represent the first recorded occurrence of these species from the Omi Limestones exposed in the Omi district of Niigata Prefecture in central Honshu near the Japan Sea. They are; *Taisyakuphyllum rostfer* MINATO; *Pseudopavonia* cf. *P. taisyakuana* YABE, SUGIYAMA and EGUCHI; and *Chaetetes tangshanensis* CHU.

Chaetetes tangshanensis previously has been described by KANMERA (1961) from Carboniferous strata in central Kyushu, while the other two species have been described by several paleontologists from various localities in S.W. Honshu, Japan. However, the present study revealed additional details of morphology that escaped the attention of previous authors or were not preserved in previously described material. In particular, the singular morphology of *Taisyakuphyllum rostfer* and its ramifications as pertains to the mode of reproduction of this species has broad implications that merits redescription and discussion.

The authors wish to express their thanks to Professors S. NISHIDA, K. CHIHARA and Dr. Y. HASEGAWA, who kindly guided a geological excursion throughout the Omi district in October, 1966, at which time the fossil corals described here were collected. Messrs. H. TOGASHI and TAKEDA of the Denki-Kagaku Co., Ltd. and Mr. S. INOUE of the Nippon Sekkaiseki Kaihatsu Co. Ltd., both located in the Omi district, were also most helpful in arranging for transportation and the collection of fossils in this area. Acknowledgements are also do to Mr. S. KUMANO, who assisted in the preparation of the accompanying plates and text-figures.

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DESCRIPTION OF SPECIES

Genus *Pseudopavonia* YABE, SUGIYAMA and EGUCHI, 1943

Pseudopavonia cf. *P. taisyakuana* YABE, SUGIYAMA
and EGUCHI, 1943

Pl. 8, figs. 1, 2; pl. 9, fig. 2

- 1943 *Pseudopavonia taisyakuana*, YABE, SUGIYAMA et EGUCHI; A new Hexacoral-like Carboniferous coral (Preliminary note); Jour. Geol. Soc. Japan, v. 50, no. 600, pp. 242-245, figs. 1, 2.
- 1955 *Pseudopavonia taisyakuana*, MINATO: Japanese Carboniferous and Permian corals; Jour. Fac. Sci., Hokkaido Univ., ser. 4, no. 2, pp. 180, 181, pl. 41, figs. 1 a-b.
- 1957 *Pseudopavonia taisyakuana*, YOKOYAMA: Note on some Carboniferous corals from Taisyaku District, Hiroshima Prefecture, Japan; Jour. Sci. Hiroshima Univ., ser. c, v. 2, no. 1, pp. 73-82, pl. 12, figs. 1, 2; text-fig. 2.
- 1959 *Pseudopavonia taisyakuana izutoensis*, KAWANO: Two new Permian corals from Yamaguchi Prefecture; Trans. Proc. Palaeont. Soc. Japan, N. S., no. 36, pp. 181-184, pl. 20, figs. 1, 2.
- 1962 *Pseudopavonia taisyakuana*, YAMAGIWA: The Permo-Carboniferous corals from the Atetsu Plateau and the coral faunas of the same age in Southwest Japan; Mem. Osaka Univ. of Liberal Arts and Education, no. 10, p. 108, pl. 3, figs. 7, 8.

Material:—Portions of coralla intersected by thin sections of limestone blocks collected from the lower part of the Omi Limestone, Fukugakuchi, Tanomi, Omi District, Niigata Prefecture, Central Honshu, Japan. Thin sections UHR 18814, 18818.

Description; external form and growth habit:—Corallum massive, primarily thamnasteroid but locally aphroid; the corallum may appear to be asteroid in areas where solution has occurred, where septa are strongly geniculate and where corallites are obliquely cut. However, a primary asteroid condition is nowhere clearly present.

The corallum is fragmental and in matrix; the largest fragment observed is approximately 50 mm across, but it seems likely that the entire corallum was much larger. A holotheca several millimeters in thickness was at least locally present.

The thamnasteroid growth form and tendency for several small new corallites to appear in groups makes precise statements of corallite diameters impossible. Approximate values can be obtained by measuring the distance separating the columella of "adjacent" corallites. In the present specimens, this distance ranges from as little as 2.8 mm to 6.5 mm. The overall average, based on measurements from several thin sections, is 4.3 mm; however, in individual thin sections this average ranges from 3.9 to 4.8 mm.

Reproduction is by intermural increase, with new offsets commonly appearing, as noted, in groups. Immature corallites are recognizable by their smaller diameters, fewer septa, smaller and more narrow columella and more prominent zone of peripheral lonsdaleoid dissepiments. It is adjacent to these clusters of young corallites in particular that an aphroid condition is observed.

Septa and septal arrangement:—Septa are of two orders, and although it is possible that short tertiary septa may be present in the peripheral parts of some corallites, these were not observed. The distinction between primary and secondary septa is difficult to make inasmuch as the latter may be as wide or even wider than the former; in their thickest parts, septa range from 0.25 to 0.45 mm. In transverse sections, however, it is common to observe a more or less regular alternation in the lengths of primary and secondary septa; major septa extend to the edge of the axial structure while secondary septa are slightly (0.2 to 0.3 mm) shorter, leaving an open space in the tabularium between their axial ends and the column. Near the calice, however, there is a general tendency for all septa to withdraw from the columella and this distinction becomes difficult or impossible. Peripherally, all septa are in lateral contact and interseptal loculi are marked only by a dark line.

Only the cardinal septum extends into the axial column, and this condition appears to be consistently present throughout all stages of growth (i.e., neanic and ephebic; breaphic stages were not observed). In some corallites the median lamella of the axial column can be observed to be continuous with that of the cardinal septum, although the median line in the latter is poorly defined except in its axial part. Both the counter septum and alar septa commonly are slightly longer than

metasepta and are more consistently in contact with the axial column; they do not, however, penetrate this structure.

Septal arrangement is basically radial, but a vestige of tetrameral symmetry is retained in some corallites. In these specimens, metasepta adjacent to the cardinal septum are slightly shorter than others and parallel to the long cardinal septum. The fossula thus produced, however, is not prominent. Alar pseudofossulae are not developed.

This species has comparatively few septa for the genus; septal formulae range from K 3 A 4 C 4 A 3 K to K 5 A 3 C 3 A 5 K, giving totals of from 18 to 20 primary and secondary septa.

Septal microstructure:—Septal microstructure is not well preserved but can be observed to consist of simple trabeculae in the distal 1 to 2 mm or septa in which fibers are arranged in bundles approximately normal to the long axis of the septum. This structure is replaced peripherally by composite trabeculae arranged in two or more irregular tiers and rather variable in orientation. Microstructure of this type was described in detail and well illustrated in the description of *Pseudopavonia crassiseptata* by Kanmera (1941, p. 224). There are no significant differences between the microstructure observed in the present species and that described by KANMERA, although other differences in morphology are present and are discussed below.

Axial structure:—The axial structure consists of a solid columella that first appears as a slight axial swelling of the distal part of the cardinal septum. In mature corallites the columella is oval to subround and is up to 1 mm in alar diameter. Except in the late ephebic stages and in recrystallized portions of the corallum the microstructure of the columella can be observed to consist of a median lamella and radial, commonly bifurcating bundles ("rods") of trabeculae. Both the outer margin of the columella and the lateral margins of septa have a somewhat crenulated appearance due to the disposition of these structures.

Longitudinal sections:—Longitudinal sections show the tabularium to be equal to 1/4 and 1/3 the radius of mature corallites in width. Tabulae are spaced at between 10 and 15 per 3 mm and are subhorizontal adjacent to the columella, which

they intersect at approximately right angles. Adjacent to the dissepimental zone, however, tabulae may be anastomosing and inclined slightly axially; thus they may abut against the innermost dissepiments or merge gradually with the dissepimentarium. Dissepiments are steeply inclined toward the axis of corallites and variable in both size and shape; in the inner part of the dissepimentarium globose dissepiments whose longest dimension is approximately 0.5 mm are the most common type, but this varies from corallite to corallite.

Discussion:—The genus *Pseudopavonia* was based on corals collected from the Middle Upper Carboniferous *Fusulinella* zone near Taisayku, Hiroshima Prefecture, southern Honshu, Japan. The authors (YABE, SUGIYAMA and EGUCHI, 1943) initially suggested that this genus might represent a Paleozoic scleractinian coral due to what they interpreted as a "meandroid" growth habit. However, KANMERA (1961, p. 221–223) presented convincing arguments to the contrary on the basis of the morphology of *P. crassiseptata* and suggested that the genus is referable to the Rugosa. He noted that the type species nevertheless should be restudied before any final conclusions could be reached pertaining to the systematic position of this coral. The present authors have attempted to obtain the holotype materials from the Institute of Geology and Paleontology at Tohoku University, Sendai, Japan. Unfortunately, the original specimens and thin sections appear to have been lost or temporarily misplaced. As a result of our restudy of the illustration of type materials, however, we are also inclined to assign *Pseudopavonia* to the Order Rugosa, for the reasons discussed by KANMERA in 1961.

The known stratigraphic range of *Pseudopavonia* is somewhat in doubt. Although its presence in the Upper Carboniferous (S. I.) is now well documented, corals described as *Pseudopavonia taisyakuana izutoensis* by KAWANO (1959, p. 183, pl. 20, figs. 1, 2) from a known Permian formation in Yamaguchi Prefecture in southwest Honshu may represent reworked examples of this genus derived from lower (i.e., Upper Carboniferous) rocks. According to KAWANO the Permian Kane Formation in this area contains:

"... two limestone lenses, the lower is known as the Kooda limestone . . . and consists of limestone conglomerate or limestone breccia . . . the upper Izuto limestone is developed at about 300 meters north and is a lens measuring about 70 meters in thickness and one kilometer in length . . . north of the Abu limestone quarry, there occur abundant remains of crinoid stems, *Waagenophyllum* and *Pseudopavonia* . . ."

Although subject to confirmation by careful study of these deposits, the physical stratigraphy of the containing rocks thus suggests that the fossil assemblage may be reworked and in part relict. Moreover, the differences between this subspecies

and the type species, *P. taisyakuana* probably are not significant, even at the sub-species level.

The Omi specimens of *Pseudopavonia* were collected near the base of the Omi limestone in this area and apparently represent the Pre- *Profusulinella* zone. They differ from *P. crassiseptata* KANMERA (1961, p. 224, pl. 15, figs. 12, 13; pl. 17, figs. 1-7; pl. 18, figs. 1-9; text figs. 4, 5) primarily in their smaller size and fewer septa: *P. crassiseptata* is a comparatively large species in which corallite columellae are spaced at from 6 to 13 mm and with as many as 52 to 70 septa, including primary, secondary and tertiary septa. KANMERA's species also differs in having more strongly developed lonsdaleoid dissepiments, a larger columella, tertiary speta, axially joined septa, and better developed pinnate septal arrangement.

In contrast, there are few if any important differences between the Omi specimens and the type species, *P. taisyakuana*. Minor differences are attributable to the fact that only two poor illustration of the type specimen and a brief and very general description were published by YABE *et al.* in 1943. Pending the possible future rediscovery of the type material, the present authors have little choice but to assign the Omi specimens tentatively to the type species.

Genus ***Taisyakuphyllum*** MINATO, 1955

Taisyakuphyllum rostfer MINATO, 1955

Pl. 1, figs. 1-3; pl. 2, figs. 1-2; pl. 3, figs. 1-3; pl. 4, figs. 1-2;

Pl. 5, figs. 1-3; pl. 6, figs. 1-2; pl. 7, figs. 1-2; pl. 9, fig. 1; text-figs. 1-5.

1955 *Taisyakuphyllum rostfer* MINATO: Japanese Carboniferous and Permian corals;

- Jour. Fac. Science, Hokkaido Univ., Ser. IV, vol. 1X, no. 2, p. 143, pl. 22, fig. 12; pl. 25, fig. 4; pl. 34, fig. 8; text-fig. 15.
- 1960 *Taisyakuphyllum nakazawae* YAMAGIWA: The late Paleozoic corals from the Maizura zone, southwest Japan: Mem. Osaka Univ. of Liberal Arts and Education, no. 9, p. 77, pl. 1, figs. 4 a-g.
- 1962 *Taisyakuphyllum nakazawae* YAMAGIWA: The Permo-Carboniferous corals from the Atetsu Plateau and the coral faunas of the same age in southwest Japan: Mem. Osaka Univ. of Liberal Arts and Education, no. 10, Pt. 1, p. 106, pl. 2, figs. 1, 2.
- 1962 *Taisyakuphyllum fujimotoi* YAMAGIWA: *ibid.*, p. 107, pl. 2, figs. 3-10.
- 1962 *Taisyakuphyllum hashimotoi* YAMAGIWA: *ibid.*, p. 107, pl. 1, figs. 1-4.
- 1962 ?*Taisyakuphyllum* sp. indet.: YAMAGIWA: *ibid.*, p. 108, pl. 6, figs. 5, 6.

Material.—Limestone blocks containing numerous complete or partially preserved corallites representing all stages of growth from brephic to late ephebic. Approximately 45 longitudinal and transverse sections of individual specimens were studied in thin sections UHR 18815 (a), 18815 (b), 18817, 18819, 18861 (a), 18861 (b), 18863 (a), 18863 (b), 18864 (a), 18864 (b), 18865 (a), 18865 (f); in addition, three peels were made from 18865 (f) and a series of polished surfaces from a single block were studied (18865 b, c, e, and g). Lower part of the Omi Limestone, Fukukuchi, Tanomi, Omi District, Niigata Prefecture, central Honshu, Japan.

Description.—For clarity, the present redescription of this species is organized as follows; (1) external form and growth habit, (2) septa and mode of septal insertion, (3) axial structure, (4) longitudinal sections, (5) microstructure, (6) ontogeny and mode of reproduction. Discussions of described species of *Taisyakuphyllum*, the distribution and stratigraphic occurrence of this genus and the more general subject of reproduction among rugose corals follow the species description.

External form and growth habit.—MINATO (1955) described the type species of *Taisyakuphyllum* (*T. rostfer*) as a solitary form, primarily as the result of lack of evidence to the contrary. The original holotype material, from the collections of the late Prof. Y. OZAWA, consists of only two partial longitudinal sections and one transverse section, none of which show any indication of branching or budding.

Our collections from the Omi region, however, appear to indicate that this species may be colonial and loosely fasciculate; however, complete coralla are as yet unknown, coralites are rather irregularly disposed throughout the matrix of the limestone blocks studied and commonly are separated by considerable distances in the mature stages. Further, many specimens were broken prior to deposition

and thus do not reflect their original orientation within the corallum.

Several corallites nevertheless have been observed in which peripheral budding is clearly present (cf. thin section 18865 (f)). Moreover, small corallites representing very early stages of ontogeny are present in most transverse sections that typically are located immediately adjacent to large, fully mature specimens; these, however, seem to have already separated from the parent corallite through a process comparable to strobilization in modern corals. Accordingly it can be concluded that this species is at least in part characterized by an asexual generation in which both budding and strobilization occurred. In all observed specimens, however, branching is confined to what apparently constituted the lower portions of the corallum, where corallites are comparatively slender and densely distributed, while detached brephic and early neanic corallites are always associated with fully mature corallites in the upper portions (distal part) of the corallum.

The possibility that this species is also represented by a sexual generation consisting of large, cylindrical corallites can not entirely be discounted on the basis of the material studied, however; this conjecture is based upon the presence of a number of large cylindrical corallites, slightly curved and up to 22 mm or more in diameter, whose relationship to the loosely fasciculate specimens could not be established (e.g., corallite c, section 18815 a, b). The reader is referred to the discussion of reproduction among rugose corals for more details on this subject.

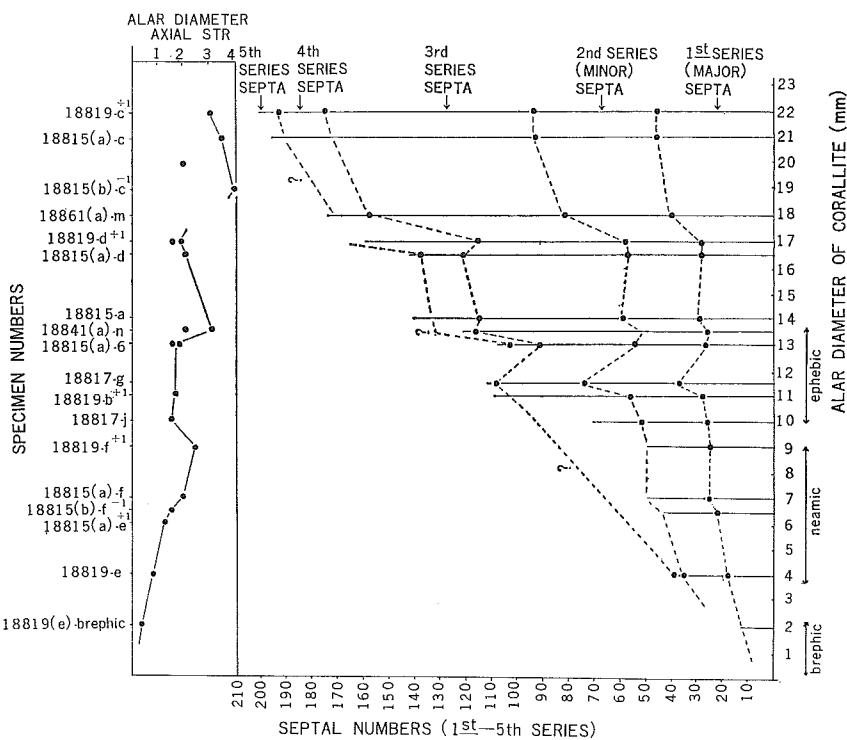
Inasmuch as all corallites are embedded in limestone, the direction of curvature can not be observed directly. If acceleration of septal insertion is related to curvature, then the strongly accelerated counter quadrants of this species suggest that the counter septum may have been located on the convex sides of corallites. External markings likewise are not visible, but in transverse sections the epitheca is very thin, 0.1 mm or less, and apparently smooth or marked only by faint septal grooves, ridges and growth lines. Rugae are absent, but longitudinal sections have a scalloped appearance due to invaginations possibly produced by peripheral budding and strobilization.

Septa and septal insertion:—The configuration of septa in this species is most unusual for rugose corals. The authors' restudy of the holotype of *T. rostfer* revealed that its septal pattern is basically similar to that of the Omi specimens, although only in part discernable. Numerous specimens of *Taisiyakuphyllum* collected by M. KATO from the Akiyoshi region of Honshu (as yet undescribed) were also studied and are also similar. However, the specimens from the Omi Limestone are exceptionally well preserved and for the first time offer an opportunity to observe and describe the mode of septal insertion in detail.

This description therefore is based primarily upon the new material from the Omi region. The numerous transverse sections studied range in diameter from

less than 2 mm to about 24 mm and represent stages of growth ranging from bryozoan through the late ephebic. The septal patterns for various stages of growth were determined by use of both standard and phase contrast microscopes as well as by inking of photographic enlargements and images reflected on a shadow-graph.

The major septa in all specimens are readily distinguished by their consistently greater lengths in all stages of growth. In the neanic and ephebic stages major septa commonly are between 5 and 8 mm in length and typically extend across the tabularium. Except for the counter septum, the major septa do not penetrate the amygdalophylloid axial structure in these stages, although the configuration of the column is such that it is clear that it is in part formed by septal lamellae that extend into the column in the early neanic stages. Metasepta adjacent to the cardinal septum commonly are sharply flexed toward the cardinal septum and are between



INSERTION OF MAJOR, MINOR AND AUXILLARY SEPTA
IN *Taisyakuphyllum*

Fig. 1

Diagram based on 18 stages of growth and septal counts in eleven specimens of *Taisyakuphyllum rostifer* increasing alar diameter of the axial structure in these specimens is shown at left. Note that 2nd series (minor) first appear at corallite diameters of 2-4 mm; 3rd series, between 4 and 8 mm; 4th series, at about 11 mm; 5th series, at about 14 mm.

2 and 4 mm shorter than other septa in the ephebic stages.

It must be said that the identification of the protosepta is problematical; however, it appears probable that it is the counter septum that extends as a median lamella into the amygdalophylloid column. The opposing cardinal septum is also long but does not reach the axial structure at any observed stage of growth. This tentative conclusion is based (1) a slight tendency toward pinnate arrangement in the cardinal quadrants, (2) the position of the alar septa and (3) the presence of what seem to be cardinal-lateral septa in the brephic and earliest neanic stages. If this interpretation is correct, septal insertion is marked in the counter quadrants, with approximately twice the number of septa being present in these quadrants throughout the ephebic stages. Typical septal formulae for the early neanic through the ephebic stages are shown in the following table (note that formulae are for major septa only):

Table 1. Representative septal formulae for various stages of growth in *Taisyakuphyllum rostfer*.

Specimen no.	alar diameter	septal formula	major septa	total septa	growth stage
NSB-e ⁻¹	2.0	K, KL1A2C2A1KL, K	12	12	earliest neanic
18815-e	4.0	K4A3C3A4K	18	38	neanic
18815-f	7.0	K7A4C4A6K	25	50	late neanic
18815-b	13.0	K5A6C6A6K	27	107	early ephebic
18861-m	18.0	K11A7C7A12K	41	176	middle ephebic
18815-c	21.0	K13A9C6A14K	46	196	ephebic

As shown in the table 1, major septa range from an observed minimum of about 12 to 46 in the ephebic stage. In the neanic stages, a regular alternation of major and minor septa is observable in both the axial and peripheral portions of corallites. When the ephebic stage is reached, a well developed septal steriowall appears in most specimens. Additionally, an unusual phenomenon occurs at this point in the ontogeny which renders all subsequent growth stages quite unique with respect to previously described patterns of septal insertion, viz., minor septa are augmented by a 3rd, 4th and even 5th series of paired "auxillary" septa. One

Table 2. Axial and peripheral septal counts in *Taisyakuphyllum rostfer*.

Specimen no.	alar diameter	major & minor septa in axial area	major, minor and auxillary septa in peripheral area
NSB-e ⁻¹	2.0	12	12 (major septa only)
18815-e	4.0	36	38
18815-b	13.0	54	107
18815-d	16.5	58	142
18815-c	21.0	88	196

result of this mode of septal insertion is that counts of major and minor septa in the axial region are greatly exceeded by peripheral septal counts, commonly by a factor of two or more. Some examples of axial and peripheral septal counts of both major, minor and "auxillary" septa are given for various stages of growth (Table 2).

Study of the configuration of septa in the ephebic stages of growth revealed that the peripheral auxillary septa which intervene between major septa almost invariably occur in groups of three, five or seven. It has been established that these groups are the result of a remarkably consistent mode of septal insertion in which minor septa are augmented by pairs of auxillary septa as the corallite diameter increases; the new septa appear adjacent to the corallite wall and are, for practical purposes, immediately fused with an adjacent (previously present) septum—the effect produced simulates septal *division* rather than septal *insertion*, or, more accurately, septal trifurcation inasmuch as two auxillary septa appear almost simultaneously. Indeed, on the basis of observable morphology, the possibility can not be precluded that septal division actually occurs. However, this explanation would require a configuration of the basal disc of the coral polyps that is entirely foreign to the inferred morphology of the soft parts of rugose corals and therefore must be considered as less likely.

Because the term "minor septum", or even "secondary", "tertiary" or "quaternary" septa do not accurately describe the process of septal insertion in this coral, an initial problem was the lack of a suitable septal notation. To avoid the possibly misleading connotation of these terms, it is expedient to refer to the septa of this species as constituting various *series*; major septa thus can be thought of as comprising *1st series* septa and minor septa comprise the *2nd series*. With few exceptions, only 1st and 2nd series series septa are present in the neanic growth stages, while only 1st series (major) septa are present in the brephic stage. The beginning of the ephebic stage is characterized by the appearance of a *3rd*, *4th* and *5th series* of auxillary septa. It is important to note, however, that while the 1st and 2nd series (i.e., major and minor) septa consist of single septa, all subsequent series are inserted as *pairs* of septa that appear almost simultaneously.

The basic pattern of septal insertion and septal notation used here to designate 1st and 2nd series septa as well as the 3rd, 4th and 5th series of paired auxillary septa is shown in text-fig. 2. Several points pertaining to this mode of septal insertion require elaboration, however. Examination of this diagram clarifies the observation that auxillary septa almost invariably appear in groups of three, five or seven; this is a consequence of their appearance as *pairs* following the insertion of 2nd series (minor) septa. It will also be noted that the 3rd and all subsequent pairs of auxillary septa that may appear are inserted on the counter (K, ct) side of 2nd series septa, although each pair tends to appear on alternatingly opposite sides of antecedent septa. Some variation is present in the insertion of 5th series auxillary septa, although the general rule stated above appears to hold. In one or

two examples, however, aberrations occur such as local reversals of this general pattern and/or insertion of two adjacent groups of three auxillary septa (i.e., one 2nd and two 3rd series septa) adjacent to each other without an intervening major septum.

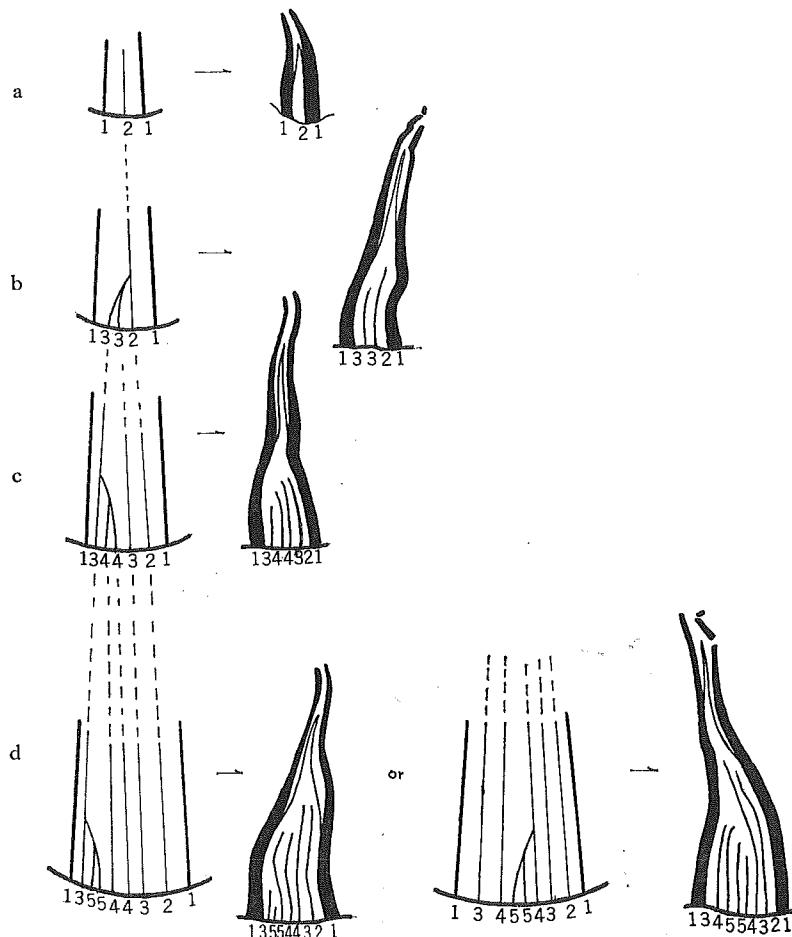


Fig. 2

Insertion of major and minor septa (1st and 2nd series) and subsequent pairs (3rd through 5th series) of auxillary septa in *Taisyakuphyllum*.

- 1st (major) and 2nd (minor) series only.
- First pair of auxillary septa appear (3rd series septa), resulting in group of three peripheral septa between major septa.
- Second pair of auxillary septa appear (4th series septa), resulting in group of five peripheral septa between major septa.
- Third pair of auxillary septa appear (5th series septa), resulting in group of seven peripheral septa between major septa.

In general, however, the pattern of septal insertion described is rather consistent in the specimens studied. Plots of septal counts against corallite diameter (fig. 1) also indicate a regular increase in the total number of septa with increasing diameter as well as regularity in the diameters at which auxillary septa occur; thus 2nd series (minor) septa first appear at corallite diameters of 2 to 4 mm, 3rd series septa between 4 and 10 mm, 4th series septa at approximately 11 mm and 5th series septa at about 14 mm.

A secondary pattern in the disposition of septa is also evident; in all specimens studied, 5th series septa, which occur only in the groups of seven auxillary septa, are restricted to the alar regions; 4th series septa may be present both adjacent to the alar septa and the cardinal and/or counter septa; 3rd series septa appear in all quadrants in the ephebic stages; finally, a simple alternation of 1st (major) and 2nd series septa commonly is retained, even throughout the ephebic stages, in the central parts of the counter quadrants.

Axial structure:—The axial structure is basically amygdalophylloid, and throughout the neanic stages in particular a one-to-one correspondence between the septal lamellae in the axial structure and the axial ends of major septa commonly can be discerned. The earliest preserved (brephic) stages unfortunately are without exception crushed, but at a diameter of about 2 mm (earliest neanic stage, in which 12 septa are present) the axial structure consists only of the expanded axial end of the counter septum; subsequently, it is augmented by the axial ends of major septa to form a true amygdalophylloid axial structure. In some specimens, a "wall" appears to intervene between the axial ends of septa and the central part of the column (cf. pl. 3, fig. 2); the orientation of the calcite fibers comprising this wall, as well as the configuration of the wall itself, indicates that it is formed by the flexed axial ends of major septa rather than by intersected tabulae; the latter can be easily distinguished by the position of calcite fibers relative to the dark line representing the under surface of the tabulae, which, in transverse sections of axially declining tabulae, are invariably on the axial side of an intersected tabulum.

The axial structure of this species increases in alar diameter from 0.1 mm or less in the earliest neanic stage to as much as 4 mm in the ephebic stage; it is commonly fusiform and elongated in the plane of the cardinal and counter septa throughout most stages of growth, but locally is oval, sub-round or compressed in the cardinal-counter plane. The axial end of the long counter septum extends, slightly expanded, into the axial structure throughout all but the latest ephebic stages, at which point there is a general withdrawal of septa and the column is isolated or aborted.

Because of the thickness of septa, which commonly are laterally in contact throughout most of their lengths in the ephebic stages, dissepiments are only rarely

observable in transverse sections and tabulae commonly can only be seen in the axial region. There is a marked tendency, however, for septa to become naotic in some specimens, especially in the cardinal quadrants.

Longitudinal sections:—Longitudinal sections consist essentially of (1) a greatly thickened peripheral region in which the numerous thick septa are intersected, (2) a narrow (2 mm or less in ephebic stages) tabularium and (3) a prominent and vertically continuous central columella. The latter is up to 4 mm across and occupies the central 1/4 to 1/5 of well oriented sections; it consists of numerous septal lamellae which, in longitudinal section, appear as distinct vertical or distally

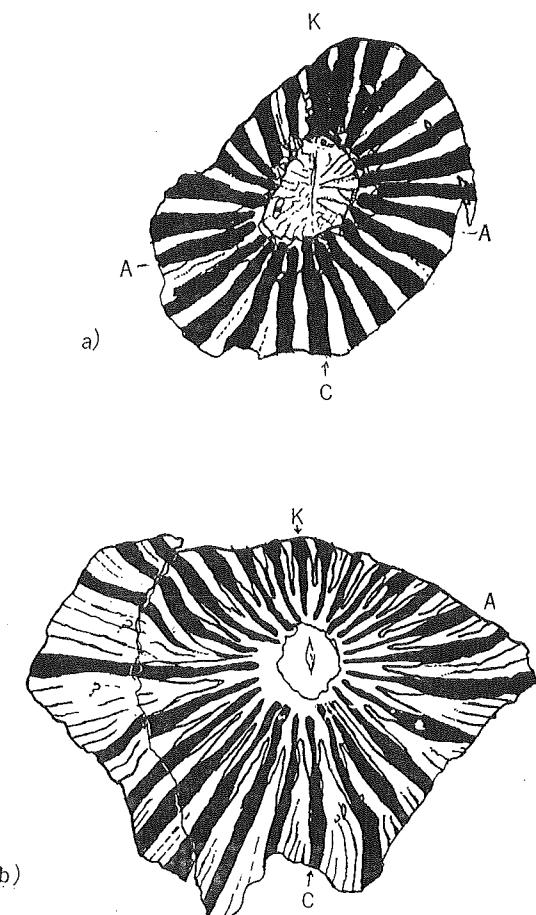


Fig. 3

radiating trabecular rods. The narrow tabularium is crossed by incomplete tabulae and a few clinotabulae, all of which are greatly thickened. From five to ten rows of dissepiments are present; these tend to be small (0.5 mm or less) and globose in the peripheral region but are steeply inclined axially, larger (2 mm or more) and elongated in the inner part of the dissepimentarium. Longitudinal sections of several large ephebic corallites (cf. Pl. 9, fig. 1) commonly have a "scalloped" marginal outline that may be the result of peripheral budding and strobilization of new corallites. In addition to the numerous brephic and earliest neanic specimens observable in transverse sections that are separated, even at this early stage, from the adjacent mature specimens, this is also suggested by the configuration of the invaginations themselves; in most cases, these correspond with a change in the orientation of the microstructure and typically are occupied by concentrations of dark organic material. In several longitudinal sections of corallites, an incipient row of dissepiments is developed adjacent to the described invaginations as well.

Longitudinal sections of corallites from what apparently constituted the basal

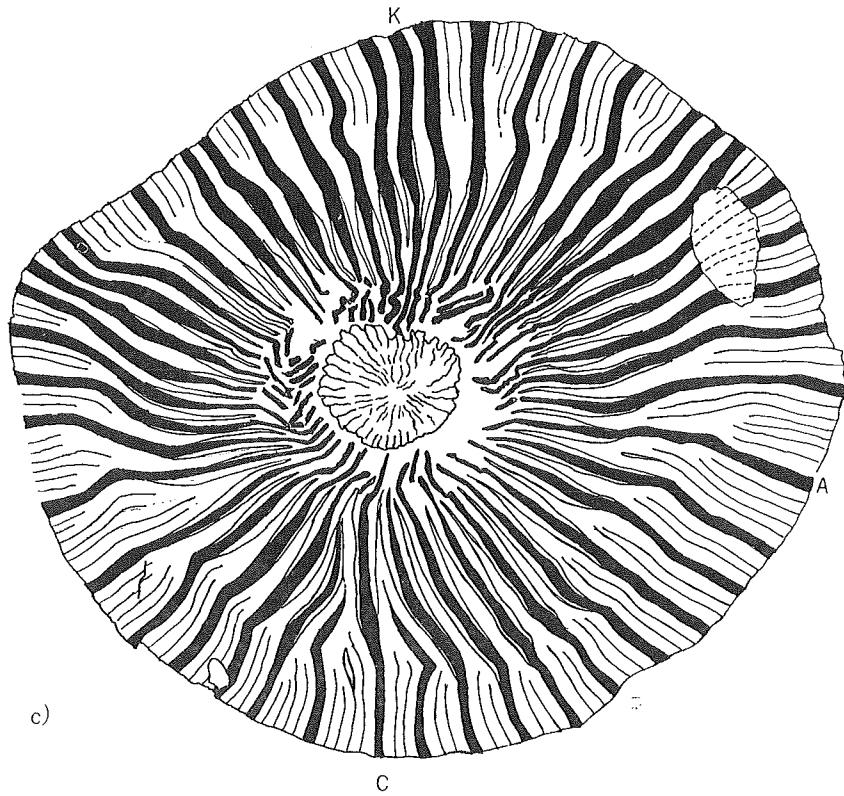


Fig. 4

portion of the corallum, conversely, are often branched. In these examples (cf. Pl. 9, fig. 1) one or more new corallites (" offsets ") arise from the peripheral portion of the calice of an antecedent corallite and in the early (brepthic and neanic) stages of growth share a common trabecular wall. In several examples, these can be observed to develop into fully mature corallites and are not separated from the parent specimen.

Septal microstructure.—The remarkable composite trabecular microstructure of *Taisiyakuphyllum rostfer* was first described by MINATO (1955) as a " septal grating." This type of microstructure subsequently was described and illustrated by KANMERA (1961) in his study of *Pusedopavonia* and related corals from Kyushu Island, Japan. Little need be added here except to note that a " septal grating " is well developed in all specimens of *T. rostfer* from the Omi region; this characteristic feature, as noted by Kanmera (1961) is the result of unusually distinct sutures between the calcite bundles (trabeculae) that comprise the septa. In transverse sections, trabeculae appear as bars whose orientation is normal to the long axis of septa, but this orientation may be altered locally by shearing and recrystallization. In longitudinal sections trabeculae are subhorizontal or inclined gently upward toward the axis of corallites.

Ontogeny and reproduction in Taisiyakuphyllum.—The limited holotype material precluded a description of both the growth habit and ontogeny of this species; however, the abundant material now available has raised almost as many questions as it has provided answers for. Nevertheless, a great deal can now be added to the limited previous knowledge of this species, especially as regards its reproduction. Various aspects of the growth habit, ontogeny and reproduction in *T. rostfer* are discussed above, but can be summarized as follows:

- (1) As suggested by YAMAGIWA (1960) and KANMERA (1961), *Taisiyakuphyllum* is at least in part a loosely fasciculate form. However, branching appears to be limited to slender corallites in the basal part of coralla and the distal portions consist of large, cylindrical unbranched corallites which may liberate peripherally budded juvenile specimens by strobilization. However, some large corallites may be completely solitary and reproduce only sexually; the production of eggs and/or sperm by these corallites raises the possibility that the independent brephic and early neanic specimens observed in the matrix surrounding adult specimens may in part represent the early growth stages of sexually-produced planula that have settled to the sea floor and begun the secretion of hard parts.
- (2) The growth form of *Taisiyakuphyllum* may be influenced by ecological conditions, and in particular by the degree of " crowding " of coralla. Although all of the specimens of *T. rostfer* from the Omi Limestone are basically cylindrical, adjacent corallites are commonly appressed and flattened against each other (cf. pl. 3 fig. 3), even beyond points where a common wall is present.

Moreover, among the undescribed specimens of *Taisyakuphyllum* from the Akiyoshi region, a wide variety of growth forms are present including polygonal and completely cerioid coralla, phaceloid corallites and loosely fasciculate forms.

Expectably, the internal morphology of individual corallites is affected by the growth form of the corallum; it has been observed, for example, that cerioid corallites are much smaller than loosely fasciculate forms and have fewer septa. In addition, the presence of 4th and 5th series septa is restricted to the larger cylindrical forms that form part of fasciculate coralla and to forms that may be solitary. It seems likely that some consistent relationship may be found between the growth form of coralla and the internal morphology of individual corallites, but inasmuch as the present study deals primarily with the Omi specimens, an evaluation of this factor must await a detailed description of the material from the Akiyoshi region.

- (3) The septal pattern and mode of septal insertion in *Taisyakuphyllum rostfer* can now be shown to be the result of the peripheral insertion of paired "auxillary" septa that give rise to groups of 3, 5, or even 7 septa between the major septa in adult corallites. Major septa (here designated as 1st series septa) appear at a diameter of about 2 mm; minor septa (2nd series) appear between diameters of 2 and 4 mm; the first pairs of auxillary septa (3rd series) appear between 4 and 10 mm; the second pairs of auxillary septa (4th series) appear at about 11 mm; and the third pairs of auxillary septa (5th series) appear at a diameter of about 14 mm (see also text-figs. 2-5).

Discussion:—The genus *Taisyakuphyllum* was proposed by MINATO, based on *T. rostfer* (1955, p. 143). The designated holotype, which has been restudied in connection with this report, was originally from the collections of the late Prof. OZAWA and consists of one transverse and two longitudinal sections labeled IV4, IV5 and IV6. This specimen was collected from Ofukudai, Yamaguchi Prefecture, Japan. A second specimen stated by MINATO to be conspecific had previously been collected from Tarosako in the Taisyaku Plateau area of Honshu. A third specimen, also from the Taisyaku Plateau in Hiroshima Prefecture, is among the collections of Professor FUJIMOTO and bears the label 1642.

As noted elsewhere, the poor preservation and other limitations of the type material prevented detailed description of the morphology of this species and completely precluded study of the ontogeny and growth form of this species. Consequently, subsequently collected examples of *Taisyakuphyllum* could not be meaningfully compared to the type species and were described as distinct species of this genus, including *T. nakazawae* YAMAGIWA (1960, p. 77, 1962, p. 106), *T. fujimotoi* (*ibid.*, 1962, p. 107), and *T. hashimotoi* (*ibid.*, 1962, p. 108).

Our restudy of the holotype of *Taisyakuphyllum rostfer* indicates that this coralite does not differ significantly in any respect from the Omi specimens; at a diameter of about 17 mm it possesses approximately 150 septa (peripheral count) that can be assigned to the 1st through the fourth series and thus corresponds to the middle ephibic stage of this species. The specimens from the Omi Limestone are therefore referred to the type species and here designated as homeotypes.

Similarly, the three forms described by YAMAGIWA as *T. nakazawae*, *T. fujimotoi* and *T. hashimotoi* can all be shown to correspond to various stages of growth of *T. rostfer*. Morphological differences cited by YAMAGIWA, including the absence of naotic septa in *T. nakazawae*, the presence of "quaternary" (3rd series) septa in *T. fujimotoi* and the numerous septa (up to approximately 200) of *T. hashimotoi* are characters that all fall well within the range of variability observable in the type specimen and the Omi homeotypes. It is also probable that the corallite described by YAMAGIWA (1962, p. 108) as *Taisyakuphyllum* sp. indet. can be referred to the type species inasmuch as the only difference in morphology noted is corallite size.

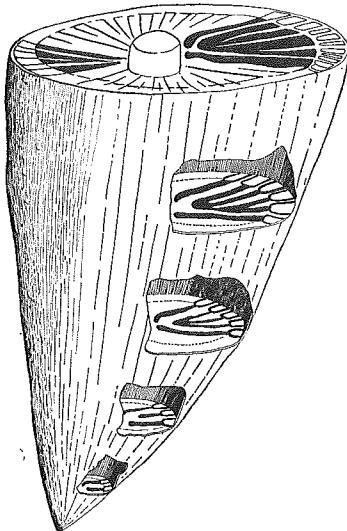


Fig. 5

Reconstruction of corallite of *Taisyakuphyllum rostfer* MINATO, showing the mode of development of septa in cross section.

Age and stratigraphic distribution of Taisyakuphyllum:—The corals described above as *Taisyakuphyllum rostfer* were collected from limestone rubble at the foot of a large quarry at the Tanomi mine, Fukugakuchi, Omi district, Niigata Prefecture, central Honshu, Japan. The quarry is in the lower part of the Omi Limestone.

Associated described species include *Pseudopavonia* cf. *P. taisyakuana* (YABE, SUGIYAMA and EGUCHI, 1943), and *Chaetetes tangshanensis* (CHU, 1928). Other poorly preserved rugose and tabulate corals are also present, including *Echigophyllum giganteum* YABE and HAYASAKA, 1924, *Clisiophyllum* (*Neoclesiophyllum*) sp. indet.

and " *Lonsdaleoides* " (?) sp. indet. The latter are listed here not only to complete the list of the coralline fauna but because *Echigophyllum* may have a bearing on the age of this fauna.

The Omi region, with the Kitakami Mountains of NE Honshu, is one of the classical areas of Carboniferous stratigraphy in Japan. Geological mapping in the Omi district by KAWADA (1954) and FUJITA (1958), as well as recent (as yet unpublished) studies by M. KATO of Hokkaido University and Y. HASEGAWA of Niigata University have provided comparatively detailed stratigraphic analyses of the Omi Limestone. Four major biostratigraphic units have been recognized which are, in ascending order, as follows: the Pre-*Profusulinella* (C_1) zone; the *Profusulinella* zone; the *Fusulinella-Fusulina* (C_2) zone; and the *Triticites* (C_3) zone.

No evidence of a physical stratigraphic break between any of these biostratigraphic units has been observed in the field, and they are therefore considered to represent a conformable sequence of limestones with a total thickness on the order of 660 m. Fusulinid zonation is well developed throughout these limestones and all of the named zones can be recognized virtually everywhere unfaulted and complete sections are exposed. Moreover, the basal limestones of the lower (Pre-*Profusulinella*, C_1) zone are physically traceable over a wide area and in many localities can be demonstrated to conformably overlie a greenish to purple basaltic tuff (" shalstein "). The limestones immediately above this gradational contact are also characteristically interbedded with thin tuffaceous layers; they are here considered to represent the lowermost Pennsylvanian, inasmuch as they physically underlie the *Profusulinella* zone and contain no fossils referable to the highly characteristic Viséan faunal assemblage of Japan.

The coral species cited above were not, as noted, collected *in situ*; however, the circumstantial evidence is strong that the limestone blocks collected were derived from the lowermost portion of the Omi Limestone by blasting in connection with the quarrying operation in this area. This conclusion is supported by the lithology of the limestone blocks and, as discussed below, the associated rugose and tabulate corals. In addition, neither *Profusulinella* nor fusulinidae from the *Fusulinella-Fusulina* zone were seen in any of the numerous thin sections examined.

The dominant coral species is *Taisiyakuphyllum rostfer*, which has not previously been reported from the Omi Limestone. Elsewhere in Japan, this species has been recognized by YOKAYAMA (1956) from the middle part of the *Millerella* zone in the Taisiyaku region of Honshu (fig. 5), presumably a correlative of the Pre-*Profusulinella* (C_1) zone in the Omi Limestone. However, *T. rostfer* also occurs in the Akiyoshi region (fig. 5) of Honshu in both the *Profusulinella* and *Fusulinell-Fusulina* zones (MINATO and KATO, 1957) and in the *Fusulinella-Fusulina* zone in the Atetsu region (fig. 5). In the latter, however, *T. rostfer* was described by YAMAGIWA (1960, 1962) as *T. nakazawai*, *T. hashimotoi* and *T. fujimotoi*.

Thus, although *T. rostfer* seemingly is limited to a restricted stratigraphic in-

terval in each of the regions in which it has been recognized, its overall geologic range appears to span the Lower Pennsylvanian C₁ zone through the Middle Pennsylvanian *Fusulinella-Fusulina* (C₂) zone.

Pseudopavonia taisyakuana is also reported here for the first time from the Omi Limestone. This species was first described from limestones of the *Fusulinella-Fusulina* zone in the Taisyaku region by YABE, SUGIYAMA and EGUCHI (1943) and confirmed by YOKOYAMA (1957). Subsequently, however, *P. taisyakuana* was discovered in limestones both underlying the *Profusulinella* zone and from the *Fusulinella-Fusulina* zone in the Akiyoshi limestone plateau by HASEGAWA (1963) and from limestones correlative to the *Profusulinella* zone in the Taisyaku region (M. KATO, personal communication). It therefore appears that this is also a comparatively long-ranging species with a known stratigraphic distribution similar to that of *Taisyakuphyllum rostfer*.

Echigophyllum giganteum YABE and HAYASAKA (1924) apparently is also a long-ranging species. Although stated by KAWADA (1954) to be restricted to the Pre-*Profusulinella* C₁ zone, according to Fujita (1958) it also occurs in the *Fusulinella-Fusulina* zone in the Omi Limestone. In the Atetsu district, moreover, this species is known to range from strata underlying the *Profusulinella* zone through the *Fusulinella-Fusulina* zone and is also present in the Akiyoshi limestone plateau in limestones below the *Profusulinella* zone. The known range of this species thus is comparable to that of both *Taisyakuphyllum rostfer* and *Pseudopavonia taisyakuana*, i.e., from the C₁ through the C₂ zones.

Chaetetes tangshanensis was originally described from the Moscovian of North China by CHU (1928); this species is also recorded herein for the first time from the Omi Limestone. Elsewhere in Japan, *C. tangshanensis* was described by KANMERA (1961) from strata he referred to the upper part of the *Fusulina* zone in the Yayamadake district of central Kyushu.

To summarize the forgoing, the precise stratigraphic position of *Taisyakuphyllum* and associated corals from the Omi Limestone remains, strictly speaking, equivocal. All of the associated species, with the sole exception of *Chaetetes tangshanensis*, can be shown to range from the Pre-*Profusulinella* C₁ through the *Fusulinella-Fusulina* C₂ zones at various localities in the Taisyaku, Omi, Akiyoshi and Atetsu regions of Japan. The apparent restriction of *C. tangshanensis* to the *Fusulina* zone in Kyushu must therefore be balanced against the well known tendency for tabulate coral species to be long-ranging and thus of limited stratigraphic value. The presence of this species in association with *Taisyakuphyllum* and *Pseudopavonia* in the Omi Limestone is not considered to be as significant as other lines of evidence that suggest a Pre-*Profusulinella* (C₁) age for the material collected, including the local physical stratigraphy, lithology, and absence of fusulinidae of any kind in the sections studied. However, an effort should be made to obtain conclusive evidence for the precise age of this coralline fauna.

Genus *Chaetetes* FISCHER von WALDHEIM in EICHWALD, 1829

Chaetetes tangshanensis CHU, 1928

Pl. 1, figs. 2–3; pl. 2, figs. 1–2; pl. 3, fig. 1; pl. 4, figs. 1–2;

Pl. 5, figs. 2–3; pl. 6, figs. 1–2; pl. 9, fig. 1

- 1923 *Alveolites tangshanensis*, GRABAU: Stratigraphy of China, Pt. 1, p. 256 (listed, nom. nud.)
- 1928 *Chaetetes tangshanensis* (GRABAU), CHU: Descriptions of two species of *Chaetetes* from the Moscovian of North China; Bull. Geol. Survey China, v. 7, p. 234, pl. 1, figs. 2 a–c.
- 1961 *Chaetetes tangshanensis*, KANMERA: Upper Carboniferous corals from the Yayanmadake Limestone, Kyushu; Mem. Fac. Sci. Kyushu Univ., Ser. D, v. X, 2, p. 228, pl. 16, figs. 10–13.

Material.—Portions of coralla intersected by thin sections of limestone blocks collected from the lower part of the Omi Limestone, Fukugakuchi, Omi District, Niigata Prefecture, central Honshu, Japan. Thin sections UHR 18815, 18817, 18861, 18864.

Description; external form and growth habit.—Corallum massive, locally consisting of small subhemispherical aggregates of corallites that radiate from a common center of growth; in general, however, growth habit in the sections studied is encrusting, in which the base of colonies are attached to the outer surfaces and within the calices of associated rugose corals. Encrusting portions of coralla are in general 5 mm or

less in height (thickness), but the non-encrusting coralla are as much as 15 mm across in sections where these are intersected more or less transversely. Individual corallites are as much as 5 mm in length, radially disposed, and straight or slightly flexuous. New coralites arise at intervals of 2 to 5 mm.

Transverse sections:—Corallites viewed in transverse sections are thick-walled and irregularly polygonal or sub-round. A few corallites might be described as pentagonal, hexagonal or elongate, no particular form appears to predominate. Although corallites appear quite uniform in diameter in well-oriented longitudinal sections, their varying orientations when intersected by transverse sections gives the effect of irregularity in size; for example, although the inner diameter (tabularium diameter) of most corallites falls between 0.2 and 0.25 mm in transverse sections, a few corallites reach 0.3 mm or slightly more in diameters. Corallite walls commonly are 0.15 to 0.17 mm thick, but locally as up to 0.2 mm across. Septal ridges and spines are absent, but a few projections of trabecular rods extend into the axial area in some corallites.

Longitudinal sections:—Because of the thickness of corallite walls, tabulae can be observed in only a few places in longitudinal sections; they are flat or slightly sagging, 0.03 to 0.04 mm in thickness and regularly disposed at intervals of between 0.3 and 0.25 mm (4 to 5 per 1 mm vertically).

Microstructure is not well preserved, but corallite walls appear to be imperforate and consist of outwardly radiating fine calcite fibers that are grouped into bundles, or trabeculae. In transverse sections from 6 to 8 such trabecular rods can be discerned in individual corallites due to partial recrystallization which produces dark "sutures" between them. Secondary deposits of skeletal material appear to be very minor or absent.

Remarks:—There are no significant differences between the morphology of these specimens and that of *Chaetetes tangshanensis* CHU (1928, p. 234, pl. 1, fig. 2 a-c), whose original specimen from the Tangshan Limestone of China was designated as the lectotype by KANMERA (1961, p. 228). Although CHU's specimens appear to be somewhat thinner-walled on the average (0.1–0.15 mm according to his table, 1928, p. 235), this character is variable in both his illustrations of the species and in the present material. The correspondence of all other characters, in particular the

regularity, spacing and attitude of tabulae, is very close. This species differs from *C. penchiensis* CHU, from the Moscovian Penchi Series of China, in having more numerous tabulae and much thicker walls, and from *C. radians* Fischer, from the Moscovian of Russia, in having smaller corallites, more closely spaced tabulae and thinner walls. *Chaetetes nagaiwaensis*, described by MINATO (1955, p. 190, pl. 19, fig. 1; pl. 38, fig. 3) from a slightly lower stratigraphic horizon (i.e., lower Pennsylvanian *Profusulinella* zone) in the Kitakami Mountains in NE Honshu, seems to be quite distinct from the present species and can be distinguished by its larger corallites (0.44–0.65 mm), irregularly spaced tabulae that are separated by intervals ranging from 0.11 to 0.24 mm, thinner corallite walls (0.05–0.06 mm) and general thickening of skeletal elements by steriplasmic deposits.

Distribution of Chaetetes in Japan.—Comparatively few species of *Chaetetes* have been described from Japan to date. For many years, virtually all chaetetid corals from the lower Pennsylvanian Nagaiwa Series in the Kitakami Mountains of NE Honshu were referred to *Chaetetes asiatica* YABE and HAYASAKA (1916), from the Middle Carboniferous Penchi basin in southern Manchuria (ONUKI, 1938; YABE, 1939; MINATO et al., 1953). However, neither a detailed description nor illustrations of this species was given by the original authors, and the type materials subsequently have been lost.

In order to resolve this taxonomic problem, chaetetid corals from previously collected localities in the Kitakami Mountains of NE Honshu were recollected by MINATO and described as *Chaetetes nagaiwaensis* (MINATO, 1955, p. 190, pl. 19, fig. 1; pl. 38, fig. 2) until such time as the holotype of *C. asiatica* may be found. The stratigraphic interval collected represents the *Profusulinella* zone in Japan.

Chaetetid corals from the slightly higher *Fusulinella* zone in the Omi district in western Honshu were first described by HAYASAKA (1924, p. 24) as *Chaetetes* sp. indet. Similarly, chaetetid corals described only as *Chaetetes* sp. were described by OZAWA (1925, p. 81) from the *Fusulinella* to *Yabeina* zone in the Akiyoshi Limestones of Yamaguchi Prefecture, southern Honshu. Corals from approximately the same horizon (*Beedeina higoensis* and *Fusulina ohtanii* subzones) in the Yayamadake Limestone of Kyushu Island of southern Japan were referred by KANMERA (1961, p. 228) to *Chaetetes tangshanensis* CHU.

Most recently, newly discovered chaetetid corals from southwestern Hokkaido, the northern island of Japan, were described by the present authors as *Chaetetes* sp. "A" (MINATO and ROWETT, 1967, p. 325). On the basis of associated fusulinidae and rugose corals these strata are believed to represent the *Fusulinella* zone. The present specimens, which appear to be examples of *Chaetetes tangshanensis* CHU, occur in the lower part of the Omi Limestone of Central Honshu and are thought

to have been derived from strata underlying the *Profusulinella* zone; the reader is also referred to the section on the age and stratigraphic distribution of *Taisyakuphyllum* in this connection.

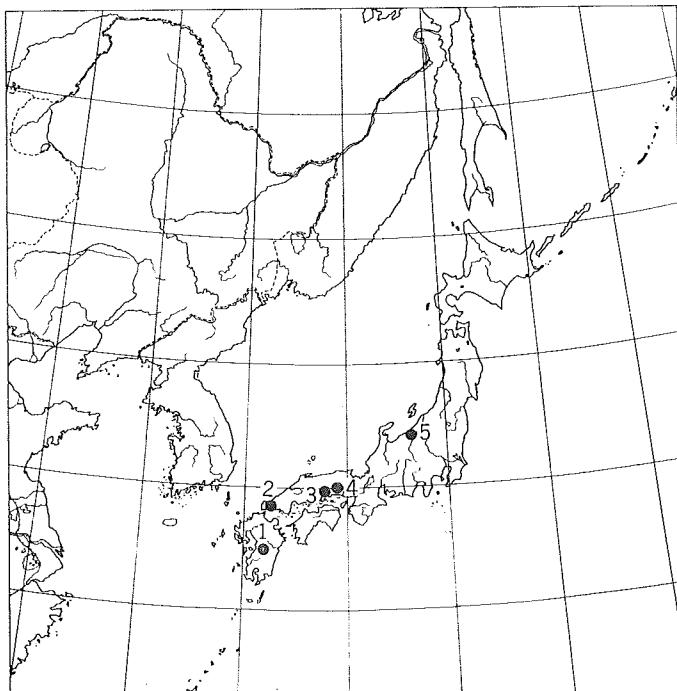


Fig. 5

1. Yayamadaka 2. Akiyoshi 3. Taishaku 4. Atetsu 5. Omi

Reproduction among the Rugosa; taxonomic and phylogenetic implications

The preceding discussion of the probable growth-form of the upper Paleozoic Tetracoral genus *Taisyakuphyllum* raises the broader question of reproduction among rugose corals in general. At the outset it should be started that while no final answers are as yet available, the discussion and isolation of some of the specific problems

may have some value.

As is inevitably the case in paleontological studies, any departure from recorded observations of living and reproducing organisms immediately enters the realms of almost pure speculation. This is particularly true as regards modes of reproduction, which involves primarily the soft anatomy of organisms and is not commonly reflected in the morphology of the hard, and thus preservable, parts. In discussing possible modes of reproduction among rugose corals, moreover, we are dealing with an extinct group of organisms whose last representatives lived almost two hundreds million years ago and which have no close living counterparts. Although it is tempting, and indeed necessary, to draw analogies from the several surviving groups of corals, especially Hexacorals and Octocorals, the dangers inherent in such an approach are all too obvious.

Still, speculation can also be based upon observable aspects of the morphology of fossil rugose corals and to some extent, at least, explained in terms of what is known about the life habits of living corals. Few paleontologists or zoologists would deny, for example, that longitudinal sections or closely spaced serial sections that show one fossil corallite arising from an antecedent individual ("protocorallite") constitutes acceptably good evidence that the species in question did reproduce—at least in part—by asexual gemmation or "budding". There are numerous carefully documented examples of this in paleontological literature, such as a comparatively recent study of budding in the Permian genera *Tschüssovskenia* and *Fisherina* by FEDOROWSKI (1965). General discussions of reproduction among Rugosa are, however, severely limited although various facets have been touched on by SMITH and RYDER (1927), DOBROLYUBOVA (1952), ROZKOWSKA (1953, 1960), HILL (1956) and FEDOROWSKI (1965). Notable studies of larval development in living corals were conducted by ATODA (1947, 1951 a, 1951 b, 1953).

It probably is reasonable, in the absence of direct evidence to the contrary, to assume that the forms of reproduction among rugose corals was fundamentally similar to that of living corals. Although this does not logically and absolutely follow, it is dictated by the observable anatomy and anatomical limitations of living corals and by the inferred anatomy of fossil corals. Thus it can be presumed that many rugose corals, like living coelenterates, may have undergone an "alternation of generations" that included sexually-and asexually-produced dimorphic equivalents. A term that has been applied for the morphological consequences of this is *dimorphism*.

It is well known, however, that among living coelenterates reproduction is quite varied. Forms having only the medusoid form reproduce sexually, while those having only the polypoid form reproduce either sexually or both sexually and asexually. In most living dimorphic species, sexual reproduction is confined to the medusoid stage and the polyp reproduces asexually. Thus we can not reasonably assume that for every sexually reproducing coral in the fossil record there was an

asexually reproductive dimorphic counterpart.

Among fossil rugose corals, solitary (simple) forms have long been supposed to represent a case in which there was no asexually-reproductive generation, i.e., these corals are thought to have reproduced sexually to produce subsequent generations of solitary forms that also reproduced sexually. Inasmuch as the formation of gametes (ova, sperm) is a function of the soft anatomy, there is, of course, no direct evidence of any kind that this was actually the case. However, the supposition is strengthened by the absence, except rarely, of obvious budding in solitary forms.

Asexual increase (vegetative increase, budding, or gemmation) in fossil corals is almost entirely confined to colonial forms. Based on the study of the preserved hard parts, many different types of budding have been described; EASTON (1944), for example, listed basal, fission, coenenchymal, interstitial, marginal, septal and tabular budding as terms that had been used up to that time; these terms in part correspond to axial, peripheral and intermural increase described by MOORE, HILL and WELLS (*in Hill*, 1956). While these terms by no means complete the list, the point of significance here is that asexual budding did occur, and in a considerable variety of ways, in colonial rugose corals. Even more importantly, a corallary question is raised by the following consideration: if each new individual arises by asexual budding from an antecedent corallite, what was the origin of the first corallite?

The answer that has been generally accepted to this query is that the first individual of a colony was produced *sexually*, presumably by some adjacent and co-existent sexually reproductive dimorphic equivalent. This forces the conclusion that colonial forms gave rise to a sexual generation by means of specialized polyps, much as in many living colonial hydrozoans.

Apparently, then, the presence of solitary rugose corals does not demand the presence of a subsequent asexually reproductive generation; however, we must logically assume, at least on the basis of the foregoing, that the presence of colonial rugose corals presupposes the co-existence of dimorphic (sexually reproductive) corals. While this is necessarily speculative, it is a point which has not, to the writer's knowledge, previously been considered.

Turning for a moment to solitary, and presumably sexually reproductive, rugose corals, another question presents itself. Were these corals hermaphroditic or bisexual? The bisexual nature of the sea anemone (e.g., *Metridium*) suggests that it is not impossible that solitary rugose corals may also have been bisexual. Clearly, however, if various pairs of described paleontological species (which actually are only morphospecies) do represent the "male" and "female" of a particular single species, there is nevertheless no conceivable way of establishing this among fossil corals. Similarly, we doubt whether solitary corals, even if found in close association with morphologically similar colonial forms, could be conclusively shown to be dimorphic equivalents, however strong the suspicion might be.

Aside from the fact that no technique exists for making such a determination, there is another factor that makes this, at least for the moment, an insoluble problem. It occurs to us that the sexually reproductive dimorphic equivalents of colonial rugosa may well have been medusoid rather than polypoid forms. This possibility presents itself in spite of the fact that the entire class Anthozoa, including the Order Rugosa, has invariably and traditionally been regarded as including only polypoid forms. If this were the case, the small and soft-bodied medusae budded from specialized coral polyps of colonial rugosa would hardly be expected to leave a recognizable fossil record. The objection to including a medusoid generation within the Anthozoa is, after all, only a semantic and taxonomic one.

It is legitimate and pertinent to consider the paleontological and stratigraphic significance of these considerations. Superficially, it may seem that the recognition and taxonomic distinction of dimorphic or even bisexual equivalents among fossil rugose corals would be of little importance, even if it were possible. If such equivalent forms existed, they must certainly have co-existed for a given species; it would thus seem to matter little stratigraphically whether or not they are given different (or similar) species names, for the stratigraphic utility of fossils depends upon their value as indicators of geologic age. To this extent, there can be no objection to this view. However, species are also established on the basis of phylogenetic considerations as well as morphological differences and examples of homeomorphs resulting from convergent evolutionary trends are not uncommon. In the larger view, the establishment of correct phylogenetic lineages is a far more important function of paleontology than either taxonomy or stratigraphy, and it can even be argued that the accuracy of latter ultimately depend upon the correctness of the former. In this sense, it is obvious that the interpretation of the phylogenetic relations of a group of associated solitary and colonial rugose corals might be greatly affected if dimorphism or bisexual equivalents were known, or even suspected.

It could be considered distressing to be unable to offer solutions for these problems, and there can be little doubt that some of the speculations indulged in above are far from the mark. However, these are problems confronting paleontologist that are unresolved after almost a century of descriptive taxonomy, and the first step toward their solution will have been taken when there is general recognition on the part of paleontologist of their importance.

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(Manuscript received May 10, 1967)

PLATE 1 AND EXPLANATION

Explanation of Plate 1

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18816(b) \times 10.0

Fig. 2 UHR. no. 18817 \times 5.0

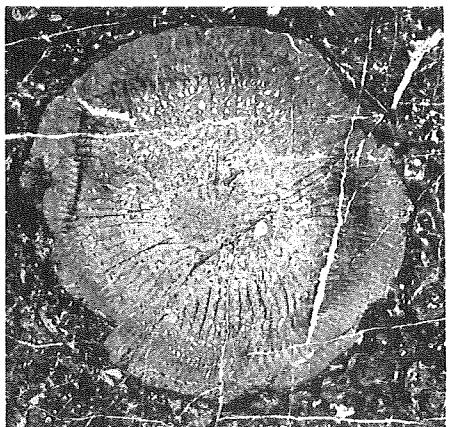
Fig. 3 UHR. no. 18815 \times 10.0

Chaetetes tangshanensis CHU

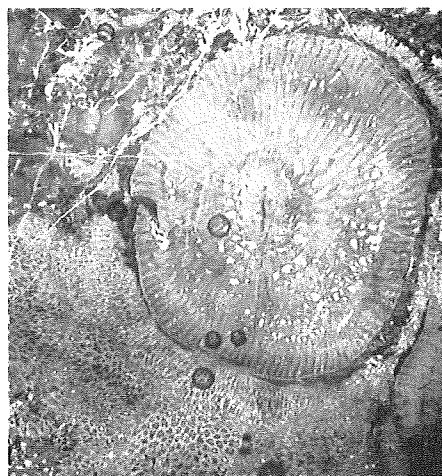
Fig. 2 UHR. no. 18817 \times 5.0

Fig. 3 UHR. no. 18815 \times 10.0

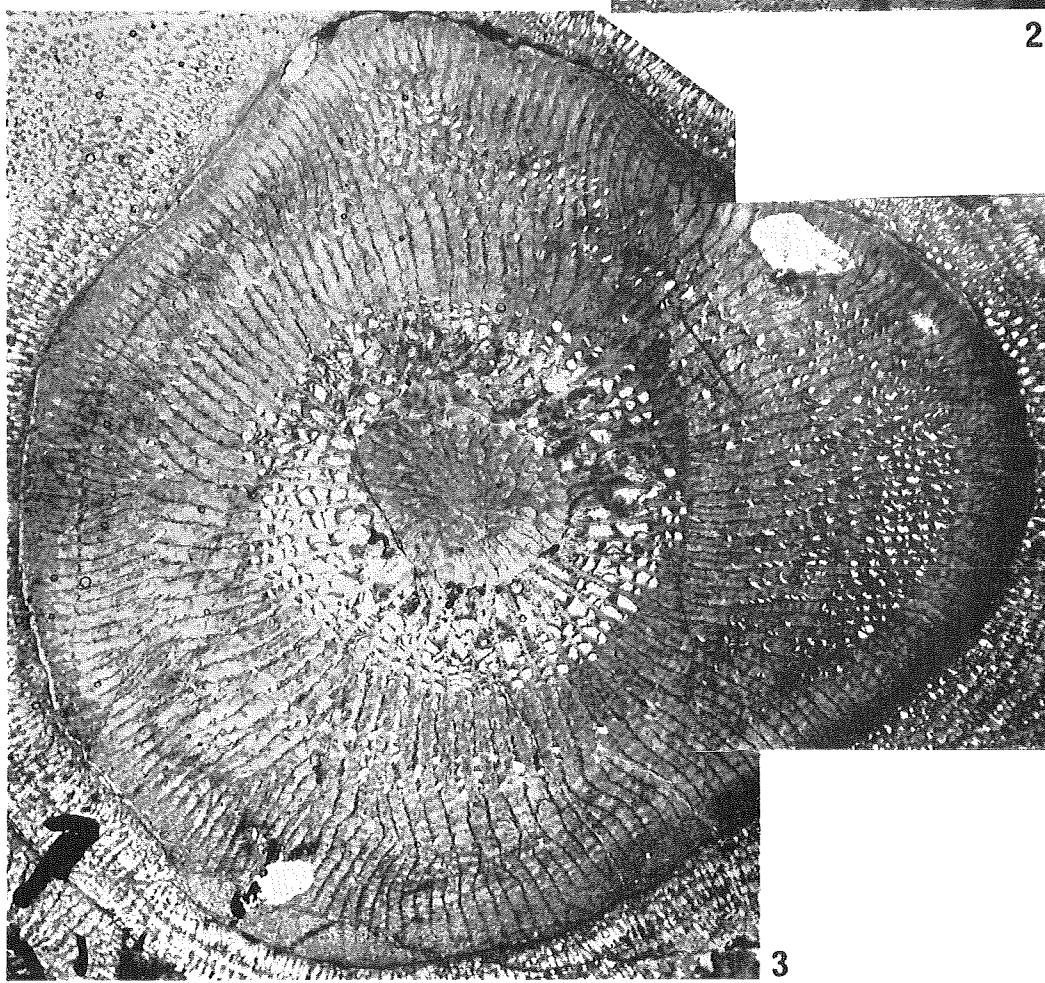
Plate 1



1



2



3

PLATE 2 AND EXPLANATION

Explanation of Plate 2

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18815 × 5.0

Fig. 2 UHR. no. 18815(a) × 5.0

Chaetetes tangshanensis CHU

Fig. 1 UHR. no. 18815 × 5.0

Fig. 2 UHR. no. 18815(a) × 5.0

Plate 2

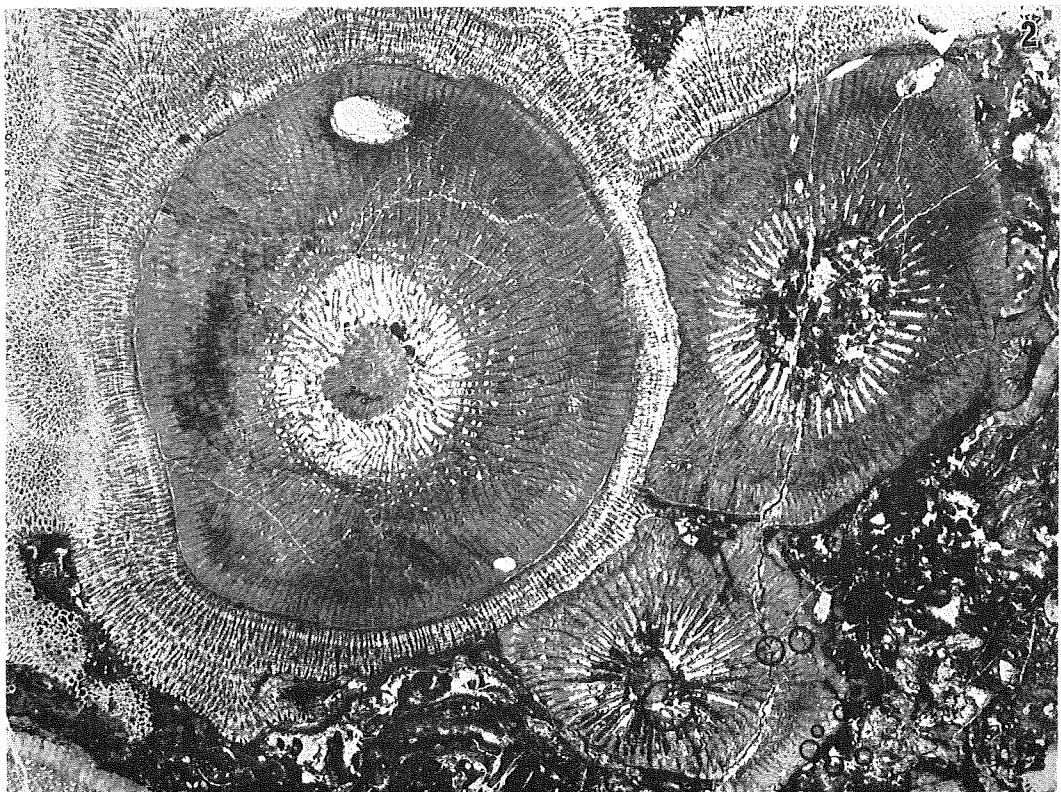
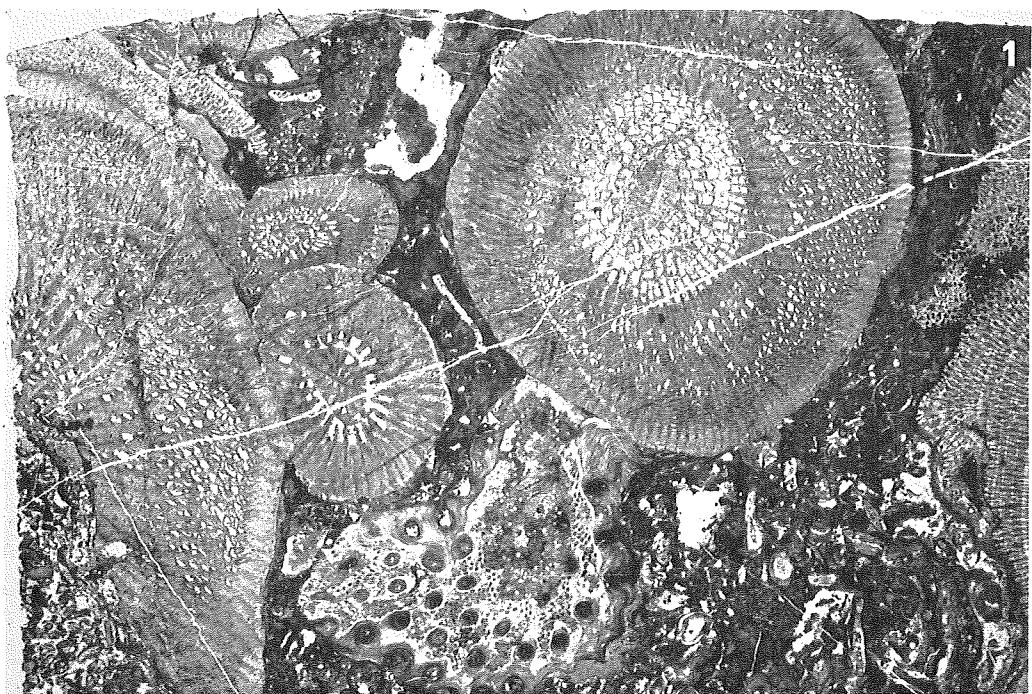


PLATE 3 AND EXPLANATION

Explanation of Plate 3

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18861(a) \times 5.0

Fig. 2 UHR. no. 18815(b) \times 10.0

Fig. 3 UHR. no. 18863(b) \times 10.0

Chaetetes tangshanensis CHU

Fig. 1 UHR. no. 18861(a) \times 5.0

Plate 3

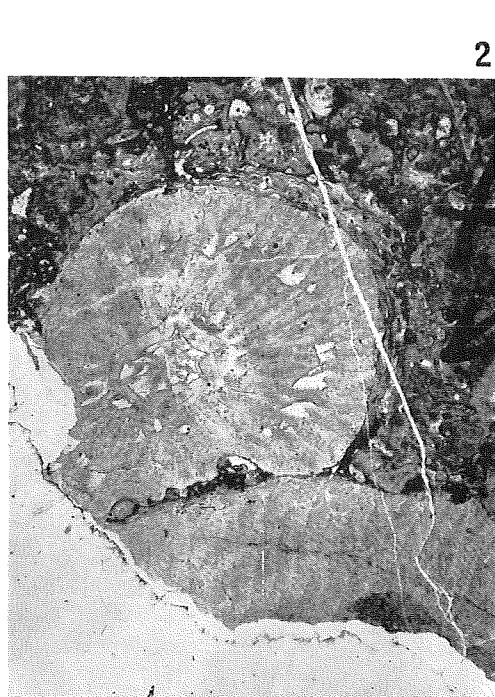


PLATE 4 AND EXPLANATION

Explanation of Plate 4

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18861 × 5.0

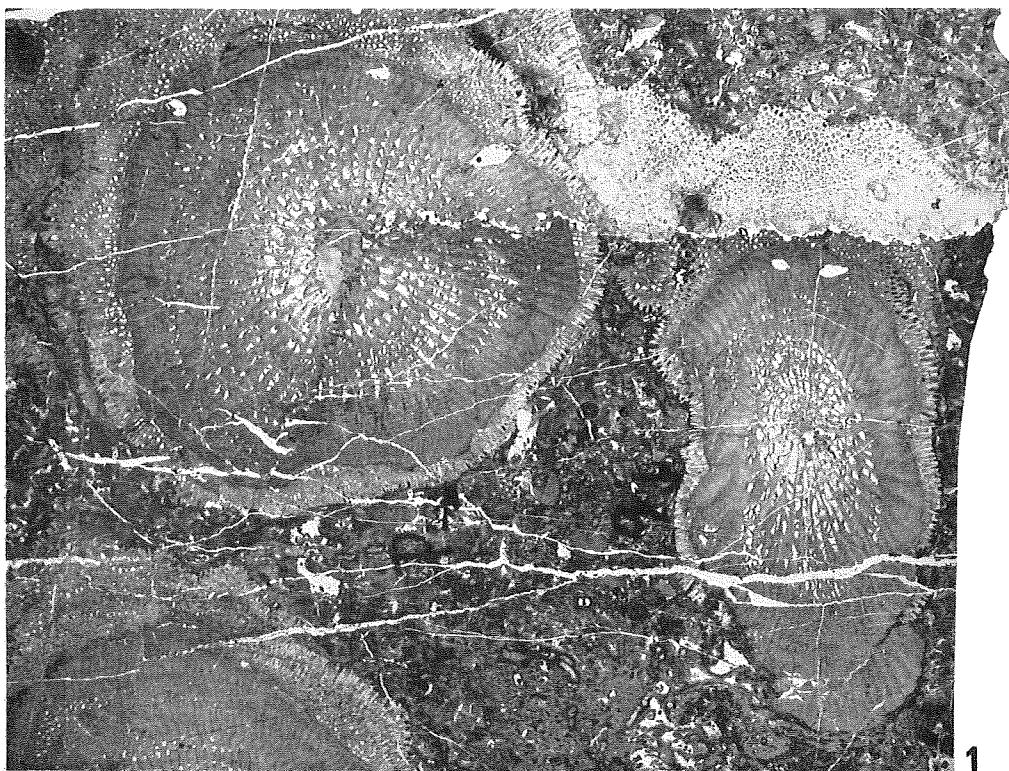
Fig. 2 UHR. no. 18817 × 5.0

Chaetetes tangshanensis CHU

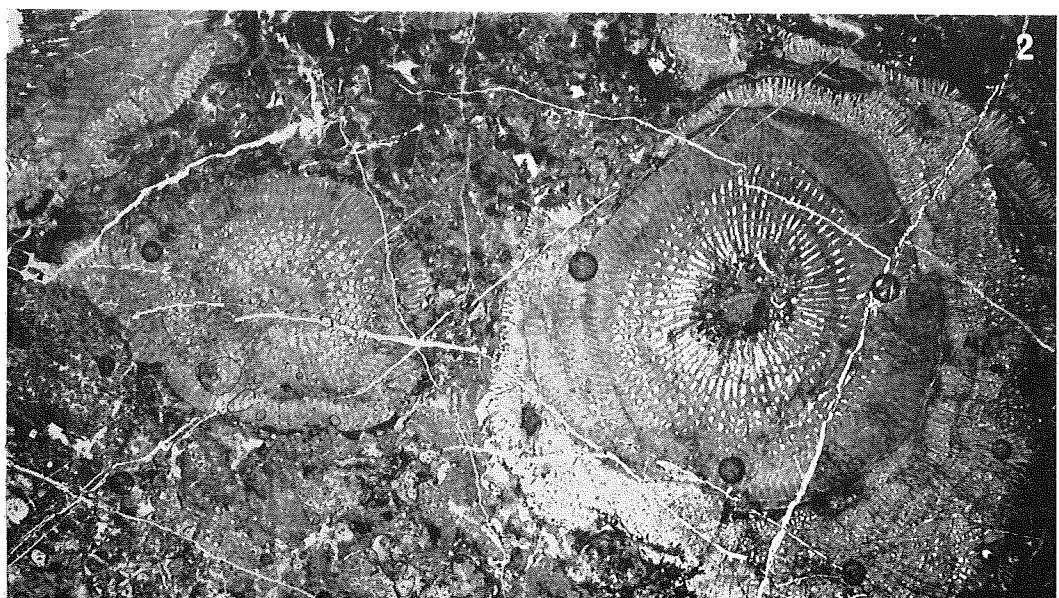
Fig. 1 UHR. no. 18861 × 5.0

Fig. 2 UHR. no. 18817 × 5.0

Plate 4



1



2

PLATE 5 AND EXPLANATION

Explanation of Plate 5

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18863(b) × 10.0

Fig. 2 UHR. no. 18864(a) × 5.0

Fig. 3 UHR. no. 18864(a) × 5.0

Chaetetes tangshanensis CHU

Fig. 2 UHR. no. 18864(a) × 5.0

Fig. 3 UHR. no. 18864(a) × 5.0

Plate 5

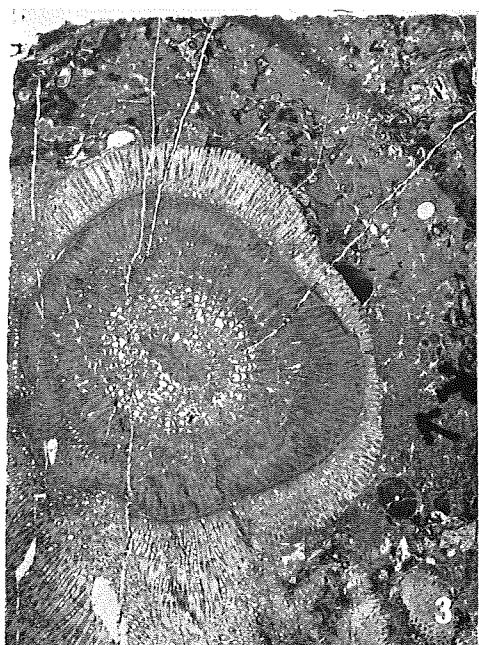
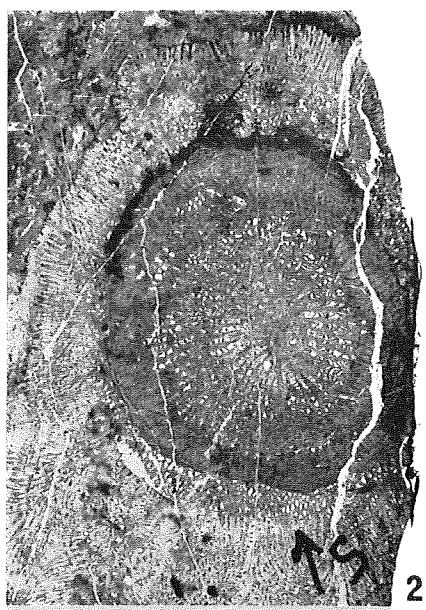


PLATE 6 AND EXPLANATION

Explanation of Plate 6

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18861(a) × 5.0

Fig. 2 UHR. no. 18817 × 5.0

Chaetetes tangshanensis CUH

Fig. 1 UHR. no. 18861(a) × 5.0

Fig. 2 UHR. no. 18817 × 5.0

Plate 6

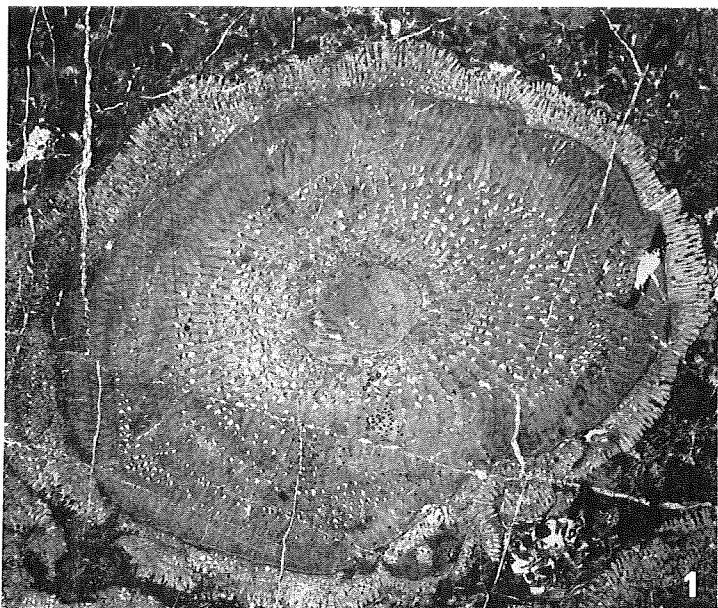


PLATE 7 AND EXPLANATION

Explanation of Plate 7

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18863(a) \times 10 0

Fig. 2 UHR. no. 18861(b) \times 10 0

Plate 7

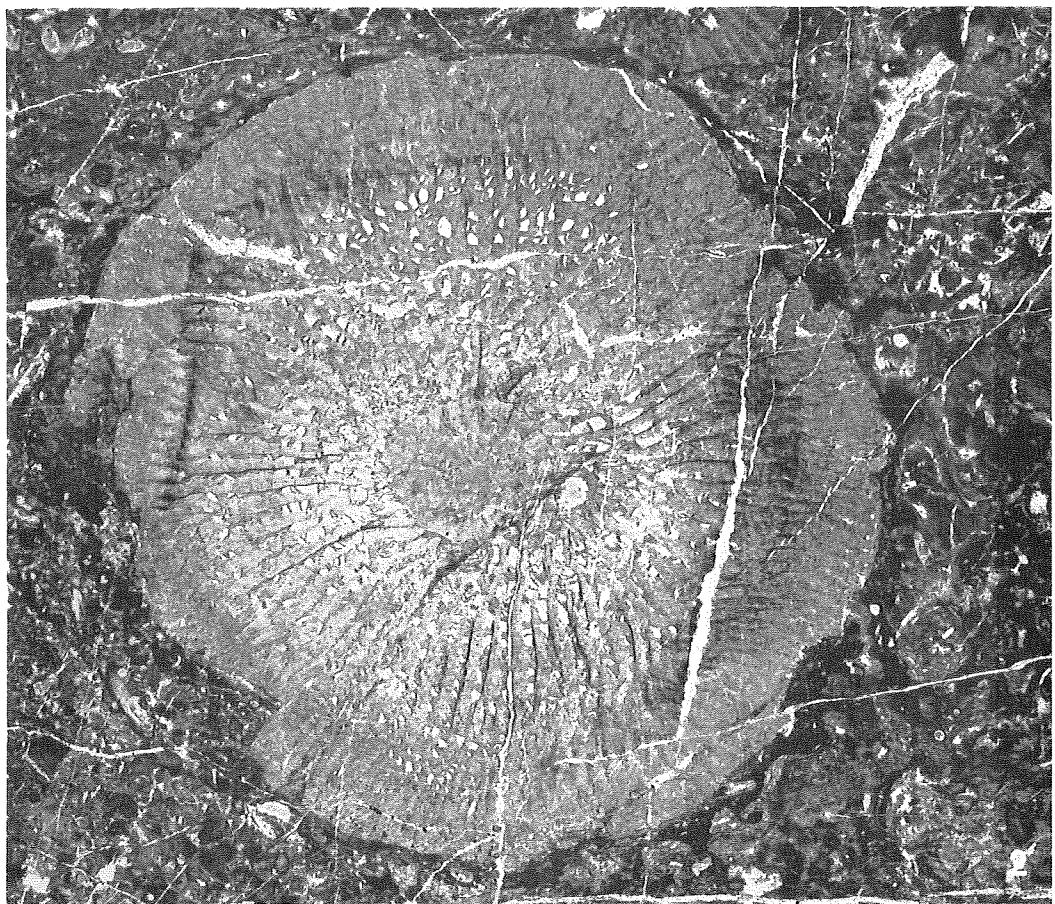
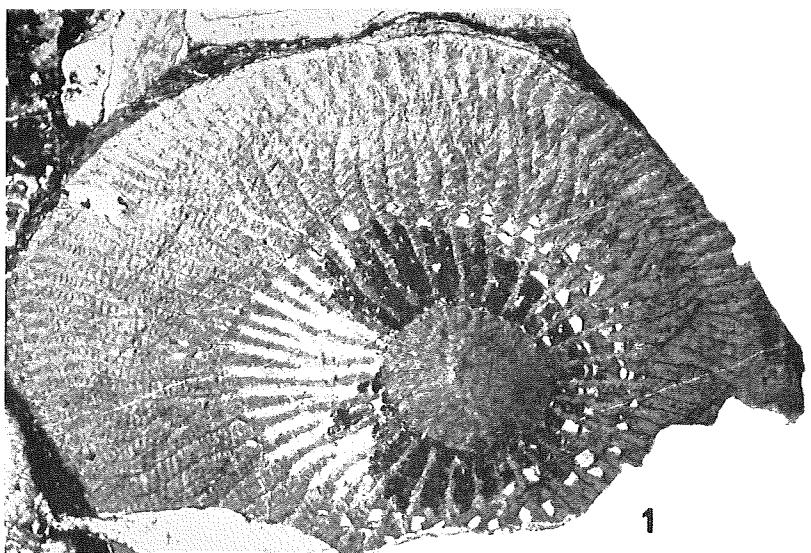


PLATE 8 AND EXPLANATION

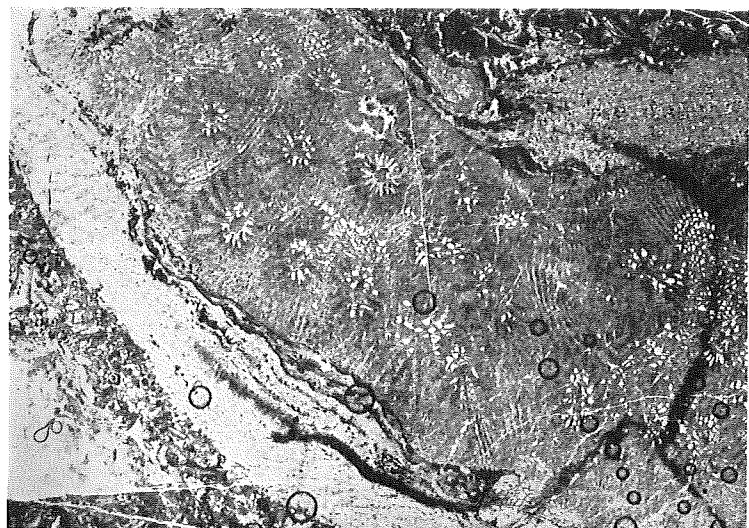
Explanation of Plate 8

Pseudopavonia cf taisyakuana YADE, SUGIYAMA and EGUCHI

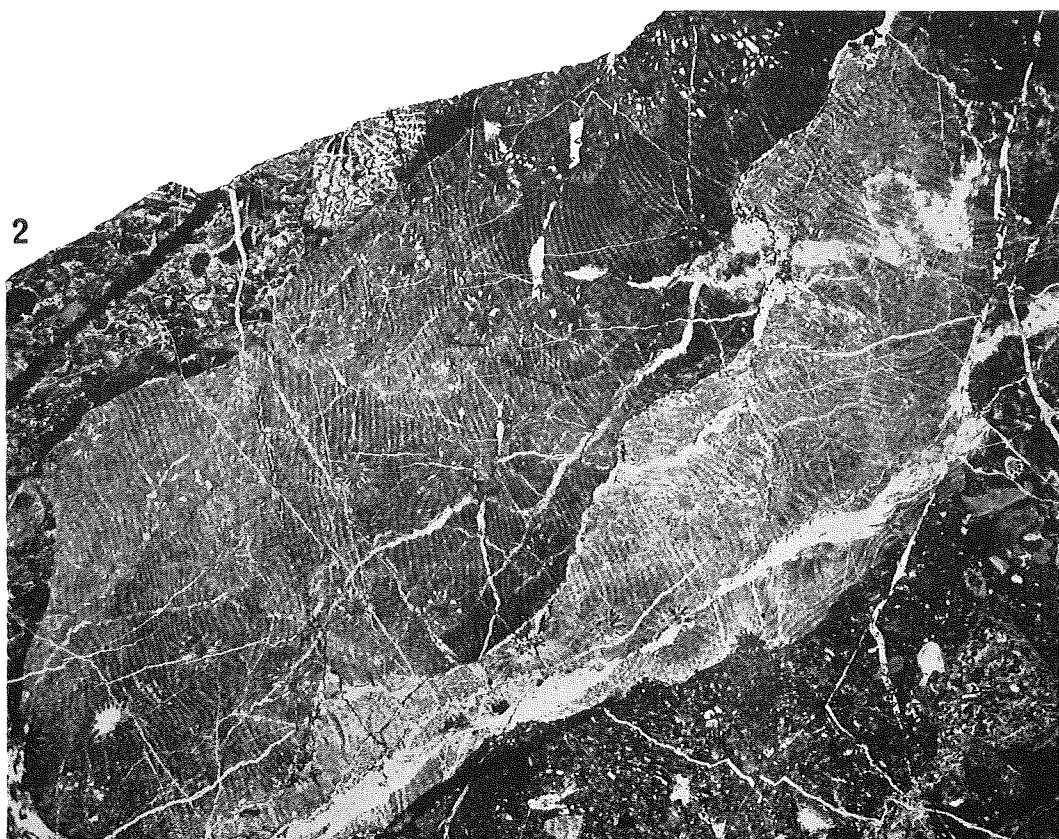
Fig. 1 UHR. no. 18818 × 5.0

Fig. 2 UHR. no. 18814 × 5.0

Plate 8



1



2

PLATE 9 AND EXPLANATION

Explanation of Plate 9

Taisyakuphyllum rostfer MINATO

Fig. 1 UHR. no. 18862 × 5.0

Pseudopavonia cf *taisyakuana* YABE, SUGIYAMA and EGUCHI

Fig. 2 UHR. no. 18818 × 5.0

Chaetetes tangshanensis CHU

Fig. 1 UHR. no. 18862 × 5.0

Plate 9

