DESCRIPTION OF DIMORPHISM IN *STRIATOPORA FLEXUOSA* HALL

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ABSTRACT. *Striatopora* Hall comprises branching favositoid tabulate corals with thick, dilated walls near the outer surface of the colonies. Study of serial sections of the type species, *S. flexuosa* Hall, shows that individuals within colonies commonly originated in one of two positions, either near the axis of the colony or near the boundary between inner thin-walled and outer thick-walled zones. Corallites originating in the two positions are morphologically distinct and were produced alternately by corallites of the first type. Corallites of the second type did not reproduce asexually. Previous descriptions of *S. flexuosa* have been based on exteriors of colonies or on material other than the type specimens. Redescription of the type specimens based on thin section studies provides a better basis for understanding the genus.

Other named genera of morphologically comparable corals can be differentiated on the basis of wall microstructure or other features, or are possible subjective synonyms of *Striatopora*.

THE tabulate coral genus *Striatopora* Hall has been widely accepted since its first description in 1851, and specimens ranging in age from Silurian to Permian, from most continents, have been referred to it. Most workers have loosely conceived of the genus as a branching favositoid with a certain amount of wall dilation in individual corallites, especially near the surface of the colony. This concept was based on Hall's description and illustrations of the exterior of the Silurian type species, *S. flexuosa*. In recent years the accepted concept has been narrowed, good redescriptions of the type species have been published, and additional genera have been erected to include forms once referred to *Striatopora* sensu lato. Although the type species is now comparatively well known, much of the available descriptive information is based on specimens other than the syntypes, which have not previously been sectioned. The purpose of this paper is to describe the developmental pattern within colonies, to redescribe the type specimens so that there will be a satisfactory basis for understanding the genus, and to outline the problems connected with this and other morphologically similar genera.

Acknowledgements. The redescription was undertaken at the suggestion of Professor Dorothy Hill, Brisbane, Australia, who pointed out the need for a fuller understanding of *Striatopora flexuosa*. I am indebted to Professor Hill for her comments on an early draft of the description and generic discussion, many of which have been incorporated in the text. The manuscript also profited from review by Dr. Richard S. Boardman, U.S. National Museum, who suggested that the included analysis of colony growth be undertaken. The syntype collection is housed in the American Museum of Natural History (AMNH) and was loaned to me by Dr. Roger L. Batten. Topotype collections in the U.S. National Museum (USNM) were made available by Dr. Boardman. Photographs are by Robert H. McKinney (exteriors) and David H. Massie (thin sections). Publication is authorized by the Director, U.S. Geological Survey.

PATTERN OF GROWTH

After initial study of Hall's original specimens (see below), two topotype fragments of *S. flexuosa* were prepared by making two series of 8 and 10 thin sections, transverse to the branch axis at 1 mm. intervals. In these and other specimens, offsets (new corallites;

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'buds') were formed only in two positions, at the branch axis and near the boundary between the inner (thin-walled) and outer (thick-walled) zones.

Offsets originating at the branch axis (**a**-offsets in the following discussion) appear on the axial side of the thin-walled part of the protocorallite (**a** on Pl. 69, fig. 1, and Pl. 70, fig. 3). A polygonal bulge in the parental wall precedes the development of a new wall separating parent and **a**-offset (several examples can be seen in Pl. 71, figs. 1–6). Initially, **a**-offsets have thin walls with minimal light-coloured lamellar deposits.

Offsets appearing at the boundary between the inner and outer zones (**b**-offsets) also appear on the axial side of the protocorallite but seemingly form on the thick lamellar part of the parental wall (**b** on Pl. 69, fig. 1, and Pl. 70, fig. 3).

a- and **b**-corallites are morphologically distinct. Measured to the nearest millimetre, 14 **a**-corallites range in length from 5 to more than 9 mm., 6 mm. being the most common observed length; 15 **b**-corallites range from 2 to 4 mm. in length with 10 individuals being 3 mm. long. In addition, wall dilation is limited to the distal one-third to one-half of each **a**-corallite, whereas **b**-corallite walls are dilated along their entire length.

Within the studied material the pattern of colony development seems to be consistent. Each **a**-corallite gives rise to two offsets ('buds'). An **a**-offset is formed as the parent separates from the axis; a **b**-offset is formed as the parent becomes thick-walled. Both types are labelled in longitudinal sections illustrated on Plates 69 and 70. **b**-corallites do not produce offsets. The result of obtaining two offsets from each **a**-corallite and none from **b**-corallites is the **a**–**b** alternation which is so clearly shown in the illustrations. The lack of alternation at the top of the figured longitudinal sections is only apparent. Presumably each of the adjacent **a**-corallites produced **b**-corallites above the limits of the thin section.

If the described pattern of development were invariable, **a**- and **b**-offsets should appear in equal numbers. Counts were made in the two serial series with these results: in specimen USNM 146505 (Pl. 71, figs. 1–6), I identified 10 **a**-offsets and 10 **b**-offsets in the 5-mm. length illustrated; two other offsets are of uncertain origin. In the second specimen I found 8 **a**-, and 10 **b**-offsets in 5 mm. Although based on a small sample, these data do support the suggested alternation of **a**- and **b**-types. There are exceptions, however. On Plate 71, corallite 7 gives rise to **a**-offset 23 in fig. 4; 2 mm. higher in the branch (fig. 6), the same corallite gives rise to two more offsets which are completely separated from corallite 7 in a thin section taken 1 mm. higher. The upper offsets are probably **b**-types, although this is not certain from the section; neither is included in the previous offset count because no new wall was formed within the 5-mm. portion on which the count was based. Perhaps the 'extra' corallite was needed to fill space in the colony.

The dimorphism represented by **a**- and **b**-corallites was probably significant in the development of the living colony. **a**-polyps went through a longer development period. This may have been required for the attainment of full maturity, and **a**-polyps may have reproduced sexually as well as asexually. **b**-polyps apparently skipped early growth stages. They may have attained normal maturity for some functions, such as feeding or defence, but not for others, such as reproduction. Alternate production of **a**- and **b**-polyps permitted faster colony growth, which may have given the species certain advantages in food and/or oxygen intake or in some other way. Presumably both types of polyps competed for space with surrounding individuals but in somewhat different micro-environments.

The formation of **a**- and **b**-offsets is in some ways similar to lateral and peripheral offsetting, respectively, in rugose corals.

SYSTEMATIC DESCRIPTION

Genus STRIATOPORA Hall

Striatopora Hall 1851, p. 400; 1852, p. 156; Wells 1944, pp. 259–60 [part]; Hill and Stumm 1956, pp. 464 [part]; Lafuste 1959, pp. 85–87.

Type species. By monotypy, *S. flexuosa* Hall 1852, p. 156, pl. 40B, figs. 1*a–e*. Middle Silurian, Rochester Shale, Lockport, New York.

Diagnosis. Ramose favositoid coralla with cylindrical or slightly compressed branches. Corallites gently curve away from axial region, opening obliquely to surface on small branches, perpendicularly on large branches. Corallite walls thin axially, strongly dilated distally, distinctly lamellar. Corallites polygonal in cross-section, but lumen round because of dilation. Mural pores common. Septal spines project into lumen, expressed as septal ridges in calice. Tabulae complete.

Discussion. Several genera of ramose cerioid tabulates with greater or lesser dilation of distal corallite walls have been described, and it is not at all clear how they interrelate. Wells (1944) discussed the morphologic series *Favosites*→*Thamnopora*→*Striatopora*→*Trachypora* as one of increasing wall dilation with complete gradation in this character, but subsequent work indicates that the phylogenetic relationships are more complex than this would suggest. The genera were originally described without adequate analysis of similarities and differences and without knowledge of the morphology of even the type species of earlier genera. Some of these genera are briefly discussed below with emphasis on apparent differences from *Striatopora*.

Thamnopora Steininger (1833; see Lecompte 1939, pp. 102–4) has cylindrical or compressed branches; corallite walls are moderately dilated, the dilation increasing distally; septal spines are weak or lacking. Lecompte (1936, pp. 14–16), working with the Middle Devonian type material, and Lafuste (1958) have described the wall structure as fibrous, the fibres arranged more or less normal to the wall surface (radial-fibrous). Similar wall

EXPLANATION OF PLATE 68

Figs. 1–7, *Striatopora flexuosa* Hall. 1–4, Lectotype corallum, AMNH 1685:1, the original of Hall 1852, pl. 40B, fig. 1*a*. 1, Exterior of complete specimen (× 1), thin sections were taken from the distal end of the right-hand branch. 2, Enlargement of central portion of corallum (× 2). 3–4, Longitudinal and transverse thin sections (× 20), note the relatively thin walls in this 'young' portion of the colony. 5, Paralectotype, AMNH 1685:2; exterior (× 2); the original of Hall 1852, pl. 40B, fig. 1*b*. 6, Paralectotype, AMNH 1685:6; exterior (× 2); not illustrated by Hall; see also pl. 70, fig. 6. 7, Paralectotype, AMNH 1685:3; exterior (× 2); note that septal ridges are especially well preserved on this specimen; original of Hall 1852, pl. 40B, fig. 1*c*.

EXPLANATION OF PLATE 69

Figs. 1–5, *Striatopora flexuosa* Hall. Paralectotype, AMNH 1685:4; not illustrated by Hall; see also Pl. 70. 1–2, Longitudinal thin section (× 10) and detail of same (× 50), note mural pores, septal spines and lamellar wall-structure; **a**- and **b**- corallites are so labelled. 3–4, Transverse thin section (× 10) and detail of same (× 50), note septal spines and lamellar wall-structure. 5, Another transverse thin section (× 10), showing mural pores and excessive wall dilation.

structure is known in many Devonian species of '*Favosites*' (Swann 1947, Lafuste 1962) and *Thamnopora* is considered by many workers to be closely allied to that genus. Lafuste, however, has restudied the wall structure of *Favosites gotlandica* Lamarck, the Silurian type species, and describes it as lamellar (concentric) and 'apparently identical to that which has been observed in *Striatopora flexuosa* Hall . . . ' (Lafuste 1962, p. 106). Lafuste suggests that *Favosites* s.s. should include only forms with lamellar wall structure.

The type species of *Trachypora* Milne-Edwards and Haime (1851, pp. 158, 305, *T. davidsoni*, pp. 305–6, pl. 17, figs. 7, 7*a*, Upper Devonian) has widely spaced calice pits separated by a great deal of stereoplasm (possibly a symbiotic stromatoporoid, according to Lecompte, 1939, pp. 147–8), the outer surface of which is covered by vermiform marks. As far as I know, the type species has never been sectioned. Subsequent workers have based the genus on the excessive amounts of stereoplasm and the general external appearance. Hollard and Lafuste (1961, pp. 71–76) described the microstructure of *Trachypora* based on the American Middle Devonian *T. limbata* (Eaton). According to them, the heavily dilated walls of this species are lamellar and similar in structure to those of *Favosites gotlandica* and *Striatopora*.

The type species of *Cladopora* Hall (1851, p. 400; 1852, p. 137; *C. seriata* Hall, 1852, pp. 137–8, pl. 38, fig. 1 *a–m*) has recently been redescribed on the basis of thin sections (Stumm 1960; Oliver 1963). The species is of small diameter; corallites intersect the surface at a low angle, walls are only slightly thickened, mural pores are rare, and tabulae are lacking; no septa have been observed; the microstructure is lamellar.

Parastriatopora Sokolov (1949; 1955*b*, p. 32, based on *P. rhizoides*, p. 32, pl. 50, figs. 2–4) is diagnosed as follows: 'Fasciculate and finger-like coralla, formed by prismatic corallites, radially diverging from the axis of the corallum and opening normal to its surface. The stereoplasm zone is sharply demarcated at the periphery' (Sokolov 1955*b*, p. 32, translated by George Rabchevsky). The species description and subsequent usage of the genus by Russian workers emphasize the sharp separation of an inner thin-walled zone from an outer zone of heavily dilated walls. Illustrations make clear that dilation is strong, and that the two zones are sharply and smoothly separated. Sokolov also noted that septal spines are weakly developed (p. 32). Microstructure of *Parastriatopora rhizoides* was described and diagramed by Chudinova (1958) and Sokolov (1962).

Chudinova (1958, following in part Sokolov, 1955*a*) and Sokolov (1962) described three types of microstructure within their family Thamnoporidae or Pachyporidae (Chudinova 1958, pp. 30–31, figs. 8–10; pp. 36–37, 45, 53, 67–68; Sokolov 1962, p. 206, fig. 7 *a–c*; pp. 228–9):

1. 'Fibrous microstructure' has 'fibres' arranged parallel to the corallite walls (i.e. concentrically) without layering. This characterizes the Parastriatoporinae.
2. 'Concentric microstructure' has short 'fibres' arranged perpendicularly to the wall (i.e. radially); the fibres are thin, short, hard to discern, and in distinct concentric layers. This characterizes the Striatoporinae.
3. 'Radially-fibrous microstructure' has 'fibres' arranged perpendicularly to the wall (i.e. radially); the fibres are coarse, long and tend to fuse and obliterate the boundaries of the concentric layers. This characterizes the Thamnoporinae.

As indicated in previous paragraphs, the separation of a radial structure (3) from a concentric one (1 and 2) has been observed by several workers. The recognition of two types of concentric structure seems doubtful, as this will be very much a matter of preservation. This opinion is strengthened by present observations which indicate that the structure of typical *Striatopora* is closer to the Chudinova-Sokolov type 1 (their Parastriatoporinae) than to their type 2 (their Striatoporinae).

Chudinova separates the Parastriatoporinae from the Striatoporinae on the following characters in addition to microstructure: the Parastriatoporinae have a sharp break between an inner zone of little wall dilation and the outer dilated zone, they have more widely distributed mural pores, and their corallites open at right angles to the outer surface of the branch; the Striatoporinae show gradual increase in wall dilation with growth, fewer rows of mural pores, and corallites opening at an angle to the surface. These features are a questionable basis for even generic separation and seem quite inadequate for subfamily definition.

If wall structure can be shown to be primary, the following grouping of the discussed genera would be suggested by the available data: 1. radial-fibrous group, *Thamnopora* and many '*Favosites*'; 2. concentric group, *Favosites* s.s., *Striatopora* (and *Parastriatopora*), *Cladopora*, and *Trachypora*.

The problem of phylogenetic relationships is beyond the scope of the present paper which primarily is to redescribe the species and type specimens on which the genus *Striatopora* is based. It is clear that much remains to be done with all genera. The difficulties that result from long-distance interpretation of genera and type species are not to be easily overcome.

Striatopora flexuosa Hall

Plates 68–71

Striatopora flexuosa Hall 1851, p. 400 (nomen nudum); 1852, p. 156, pl. 40B, figs. 1 *a–e*; Wells 1944, p. 260, pl. 40, figs. 1–2; Hill and Stumm 1956, figs. 352, 5*a–b*; Lafuste 1959, pp. 85–87, text-figs. 1, 2, pl. 1, figs. 1–3.

External features. Coralla are ramose with cylindrical or compressed branches varying in diameter from 3 to 5 mm. The lectotype corallum bifurcates at intervals of from 11 to 22 mm.; bifurcation is common in other specimens, but none is complete from one

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EXPLANATION OF PLATE 70

Figs. 1–6, *Striatopora flexuosa* Hall. 1–2, Paralectotype, AMNH 1685:4, not illustrated by Hall; see also Pl. 69; thin section tangential to colony branch showing transverse sections of corallites in mature region (×10); detail (×50). 3–4, Paralectotype, AMNH 1685:5, not illustrated by Hall; longitudinal and transverse thin sections (×10). 5, Topotype, USNM 146506; detail of longitudinal thin section (×50) showing tunnel-like mural pores. 6, Paralectotype, AMNH 1685:6; longitudinal thin section (×10) of specimen illustrated on Pl. 68, fig. 6 (section was taken from the portion of the branch below the crack).

EXPLANATION OF PLATE 71

Figs. 1–6, *Striatopora flexuosa* Hall. Topotype, USNM 146505; serial transverse thin sections (×15) taken at right angles to the branch axis at 1 mm. intervals; figure 1 is the lowest section, 6 is the highest. Corallites are numbered for recognition in successive sections but numbers are omitted where their inclusion would cover important detail. Corallite origin is as follows: **a**-corallites, 13, 14, 15, 16, 17, 23, 24, 27, 28, 29; **b**-corallites, 8, 9, 10, 12, 18, 20, 21, 22, 25, 26; corallites of uncertain origin, 11(**b**?), 19(**a**?).

bifurcation to the next. Above bifurcations, branch diameters are commonly sub-equal, although unequal in some cases. The largest known specimen is the lectotype (Pl. 68, fig. 1) with a spread of 85 mm. between the ends of the two main branches.

Corallite boundaries are clearly defined. Calices are broad and shallow, normally deepest near the proximal margin. Calice walls slope gently from margin to pit; in slender corallum fragments, walls tend to be concave, rising to sharp ridges which separate corallites; in more robust fragments of coralla, outer parts of calice walls are gently convex so that the marginal ridges are subdued.

Where well preserved, calices are marked by low, broad septal ridges radiating from the axial pit; these are best developed on more robust fragments of coralla. In the few calices where septa can be counted with any degree of certainty, they are 12 in number.

The number of corallites was counted on the outer surface of five branch fragments with counts ranging from 2·9 to 4·5 corallites per mm. of branch length. This agrees with counts of 4·4 and 3·6 new buds per mm. in two serially sectioned branches. The variation between specimens indicates differences in rates of budding relative to rates of skeletal accretion and probably represents varying environmental conditions.

Internal features. Corallites originating near the axis of the corallum (**a**-corallites) extend upward and outward, initially at very small angles to the axis; distally, these corallites turn away from the axis and intersect the surface at angles of 60 to 80 degrees. **b**-corallites originate in the zone where the outward bending of earlier corallites takes place; these expand more rapidly and are initially at a high angle to the branch axis. Corallite walls consist of a very thin dark granular layer (epitheca of some workers) which separates corallites, and a light lamellar layer which is very thin near coralla axes, but which thickens with growth and is very thick peripherally. Mural pores are common at all stages of corallite growth; in thickened walls they appear as tunnels with lengths several times their diameters. In places, a low ridge surrounds the pore on one side of the wall (e.g. Pl. 70, fig. 5).

Tabulae are thin, complete, and irregularly spaced, composed of a dark, basal tissue overlain by varying thicknesses of light-coloured stereoplasm in lamellae continuous with those of the wall. They are commonly not at right angles to the axis or walls of the corallite but are inclined away from the branch axis.

Septa are irregular in their appearance and occurrence. They are rare in thin-walled parts of corallites, common in thick-walled parts. They appear to be low, broad ridges or spines projecting into the lumen, formed by the inward bending of the wall laminae, which are continuous around and through the septa.

Microstructure of the dark wall layer is obscure. The light tissue is distinctly lamellar parallel to the inner surface of the corallite wall.

Remarks. As the description indicates, two more or less distinct zones can be recognized in sections through or at right angles to the corallum axes. An inner zone is characterized by corallites having small total diameters, thin walls, occurring at low angles to branch axes, and being polygonal in internal cross-section. The outer zone has corallites having large total diameters, and thick walls; these corallites occur at high angles to branch axes and are circular in internal cross-section. Transverse sections of mature parts of corallites are seen in sections tangential to the branches (Pl. 70, figs. 1, 2).

Slender corallum fragments (diameters 3–4 mm.) apparently represent portions of colonies with minimal development of outer zone characters. The portion of the lectotype that was removed for thin sectioning was from a slender part of the right-hand branch (Pl. 68, fig. 1) near a growing tip and shows the characters of corallites in an early stage of 'maturity' (Pl. 68, figs. 3, 4). Although not sectioned, the oldest part of the holotype specimen is more robust, with larger corallites and thicker walls. The paralectotype illustrated on Plate 69 and Plate 70, figs. 1 and 2, is robust and shows full development of 'mature' characters. Note that the lectotype thin sections are illustrated at $\times 20$ whereas the others are at $\times 10$. Presumably corallite growth was continuous, and branch robustness and 'maturity' are a function of corallite age and environmental conditions.

Material. Lectotype, AMNH 1685:1; paralectotypes illustrated by Hall, 1685:2, :3; other paralectotypes, 1685:4–:8; 12 topotype fragments, USNM 114214; illustrated topotypes from the same collection have been renumbered USNM 146505 and 146506.

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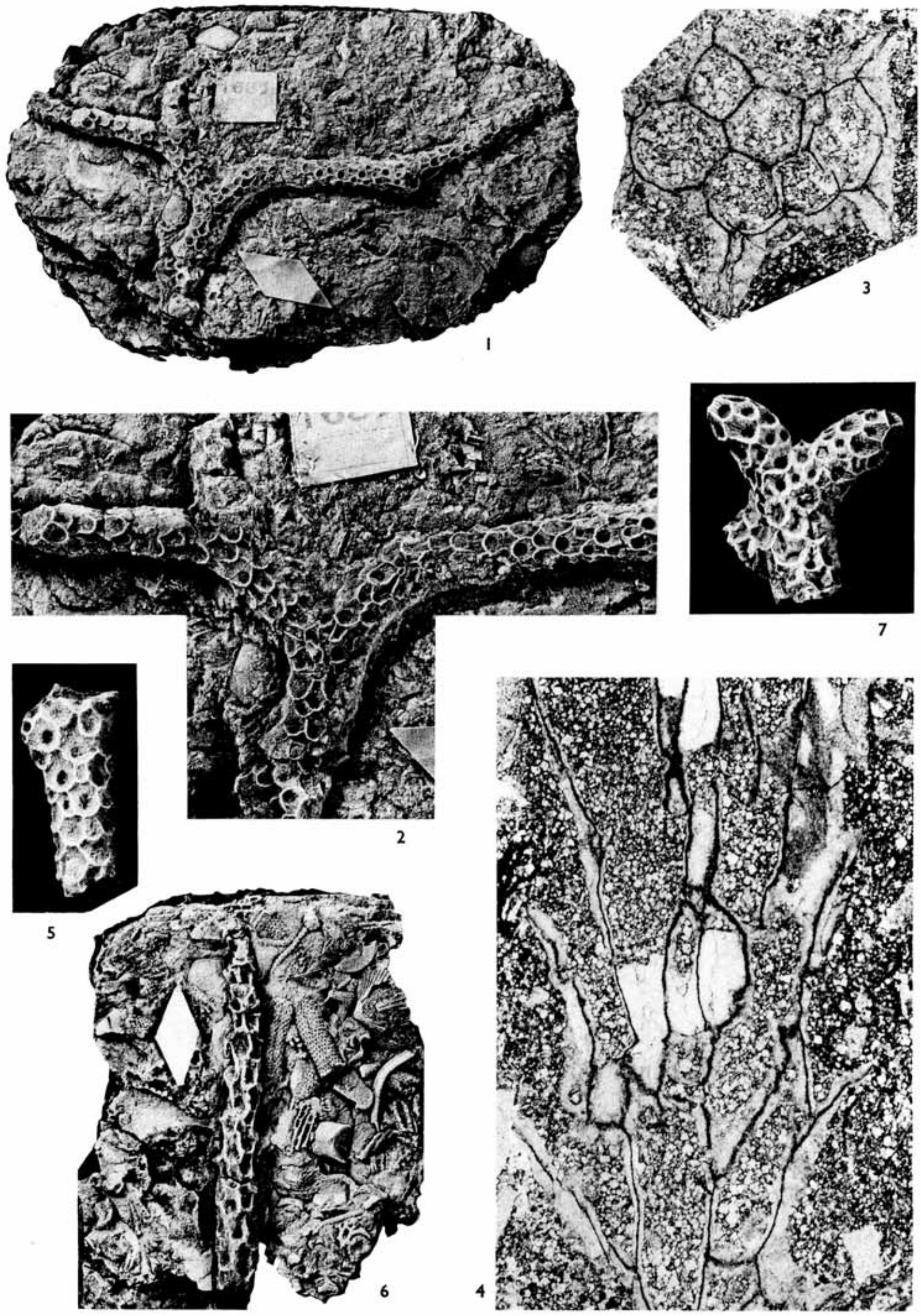

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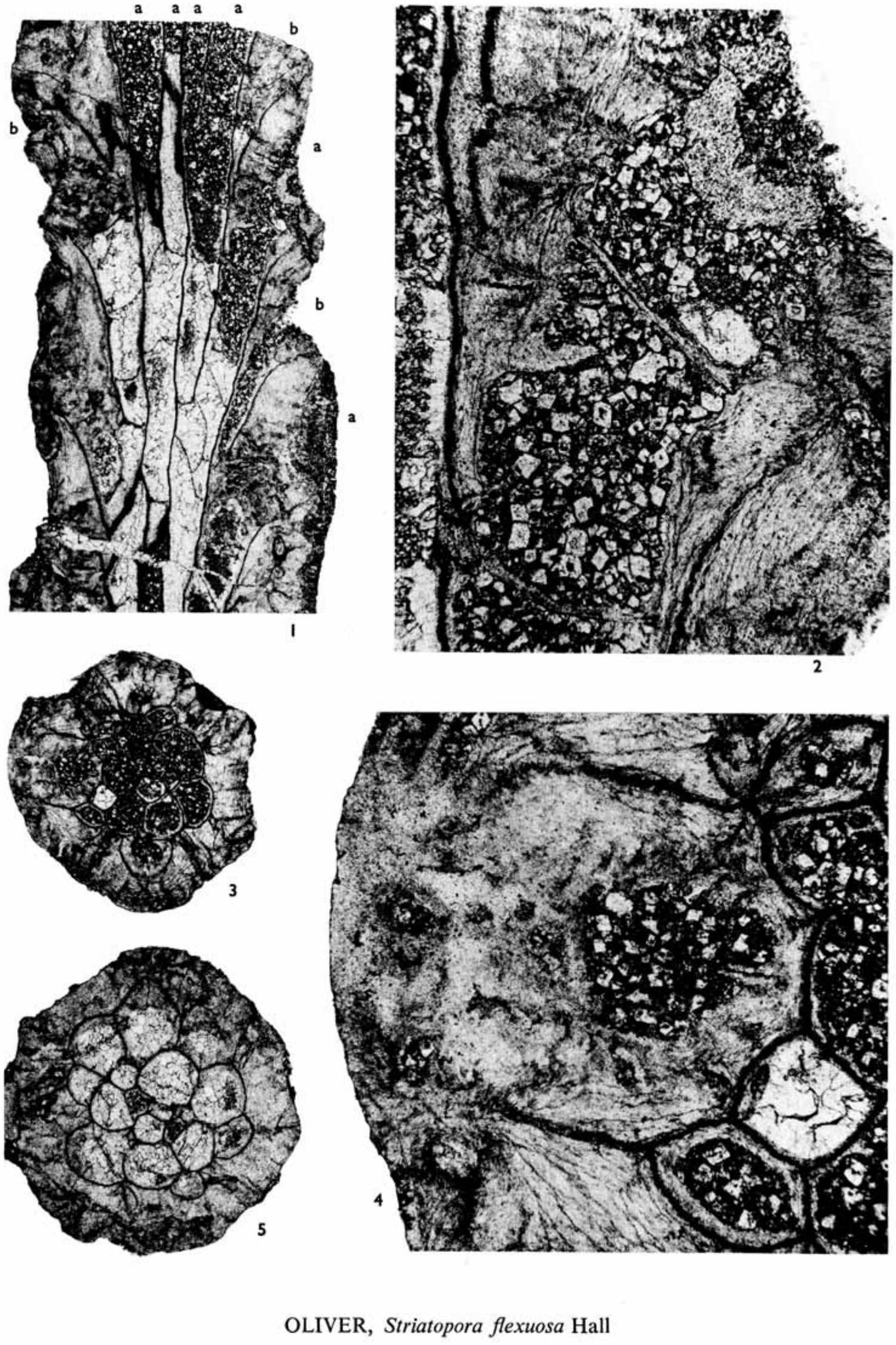

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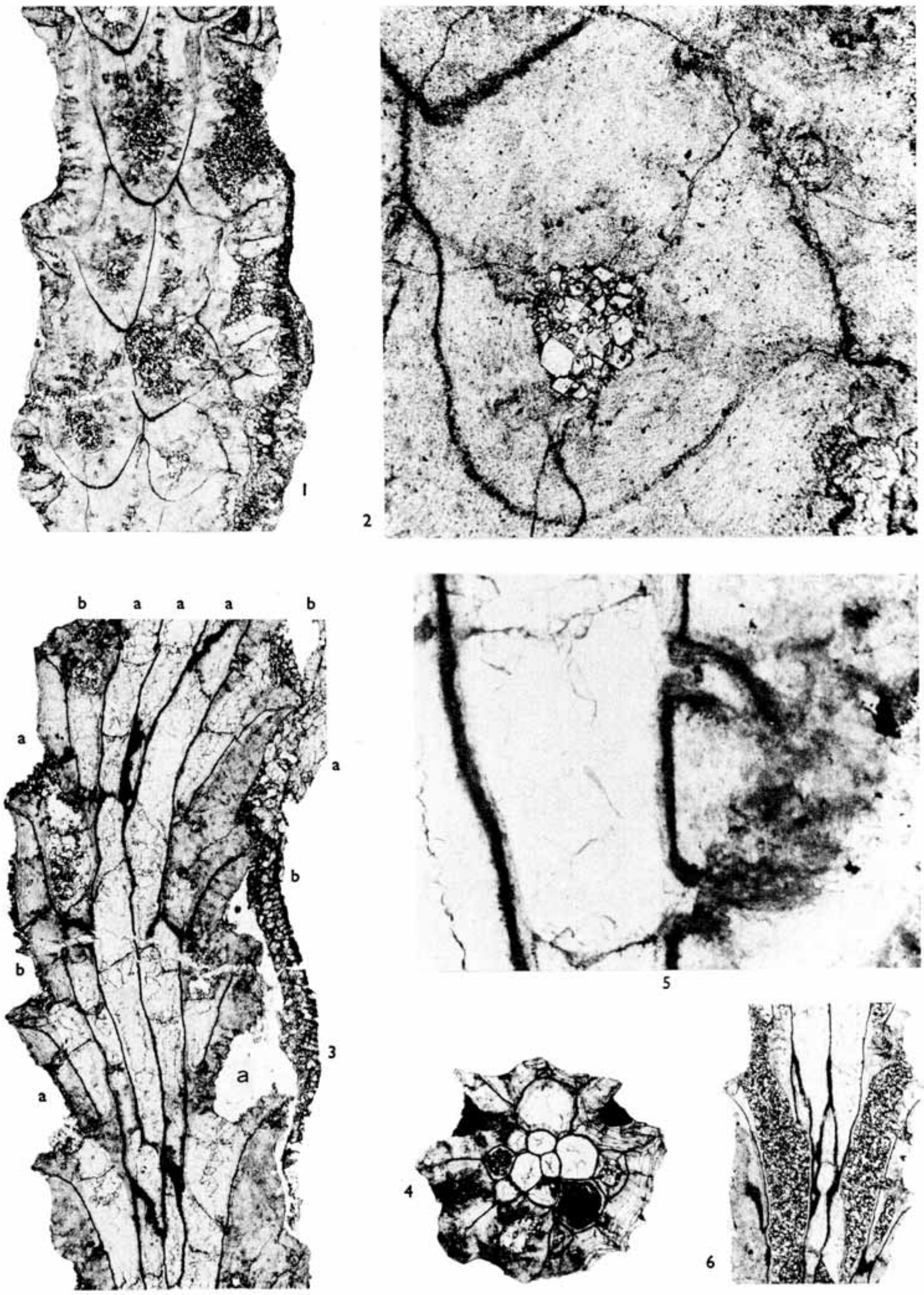

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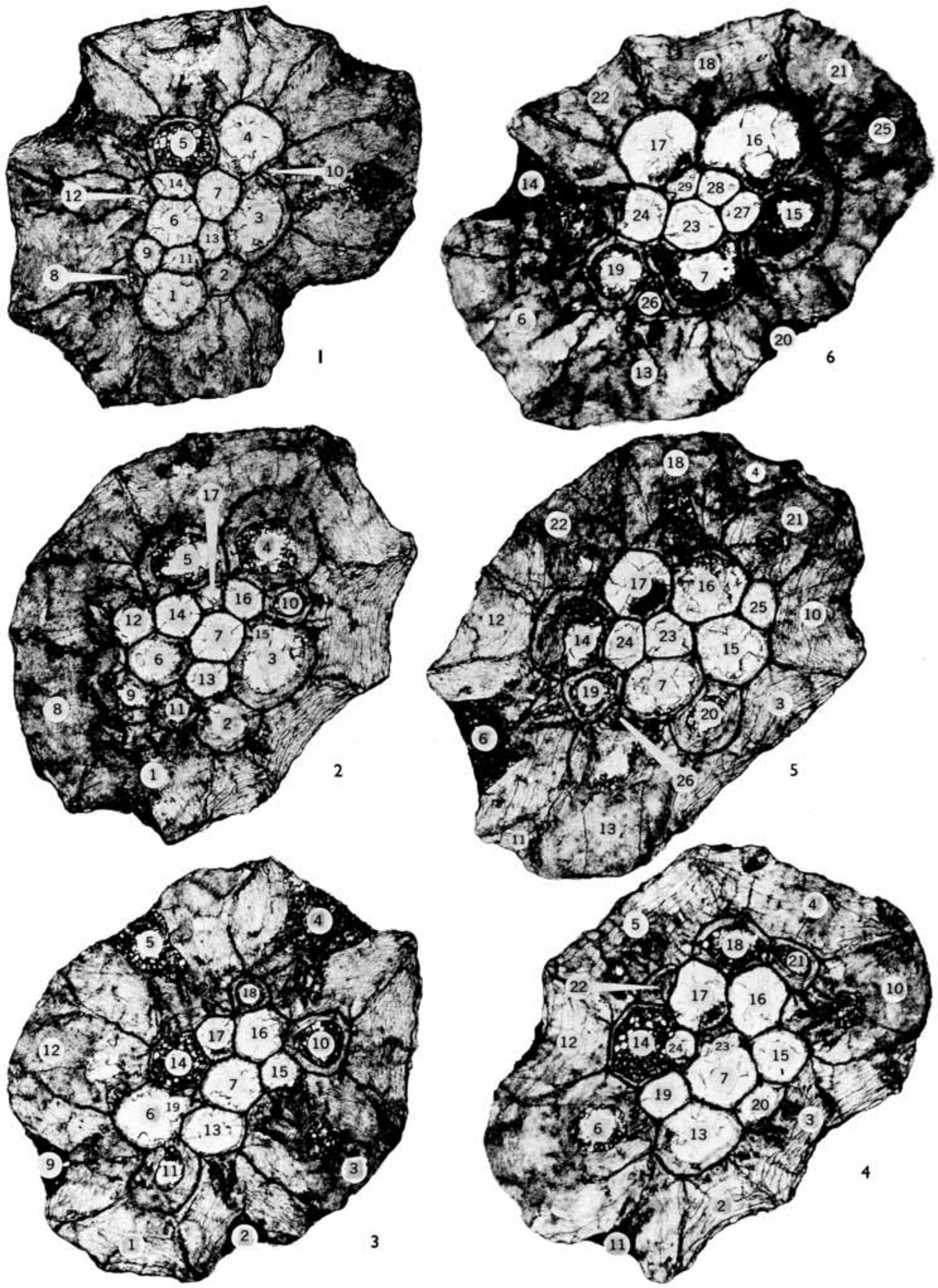

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