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Internal morphology of the
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PART E, REVISED, VOLUME 4, CHAPTER 9C: INTERNAL MORPHOLOGY OF THE PALEOZOIC STROMATOPOROIDEA

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INTRODUCTION

The following is a general description of the structures common to many stromatoporoids and does not include all the variations in structures found within the class.

The skeleton of Paleozoic stromatoporoids was secreted as a base for the living tissue, to raise it above the substrate surface and the deleterious effects of accumulating sediment and overgrowing space competitors. In most stromatoporoids, living tissue occupied a film, probably only a few millimeters thick, over the growth surface of the skeleton, but in some, it occupied space within the upper few millimeters of the skeleton. Below the living soft tissue, the voids in the skeleton were filled with seawater while the organism was alive and filled with mineral spar as the skeleton became a fossil. This model of the stromatoporoid (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, Fig. 4,3, Fig. 7, Fig. 8,2) is reconstructed from observations of living hypercalcified sponges and from observations of the preserved growth surfaces of fossil stromatoporoids. Where the terminal growth surface of stromatoporoids that secreted discrete laminae or pachystromes is preserved, sediment does not fill the empty chambers left by the decay of soft tissues, beyond the few incomplete structures in the terminal phase (Fig. 1,1, and see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, Fig. 4,1–2).

When stromatoporoids were considered to be cnidarians and colonial, the term coenosteum (common or shared bone [Gk. *kainos* + *osteon*]) was appropriate to the whole skeleton, but now that the animals are widely considered to be sponges and individuals (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, p. 3), the implication of coloniality in the term makes it inappropriate. Unfortunately, several well-

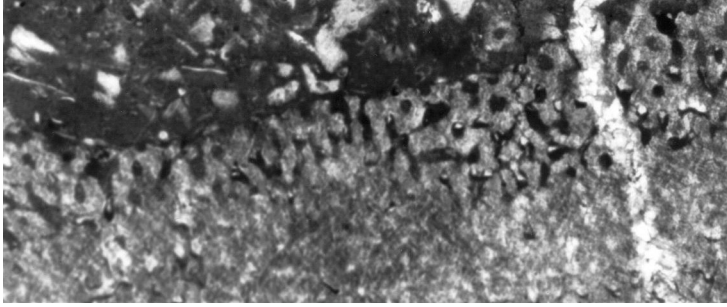
established terms still in use for skeletal elements, such as coenosteale, coenostrome, and coenotube, also share this legacy and are replaced here by pachysteale, pachystrome, and allotube, respectively (for definitions of these terms, see Glossary, *Treatise Online*, Part E, Revised, Volume 4, Chapter 8).

The structural elements of the stromatoporoid skeleton are similar to those found in space-filling frameworks in the skeletons of many lower invertebrates and in the homes of humans: posts, beams, walls, planar floors, and domed roofs. The various orders of the Stromatoporoidea are dominated by combinations of these elements.

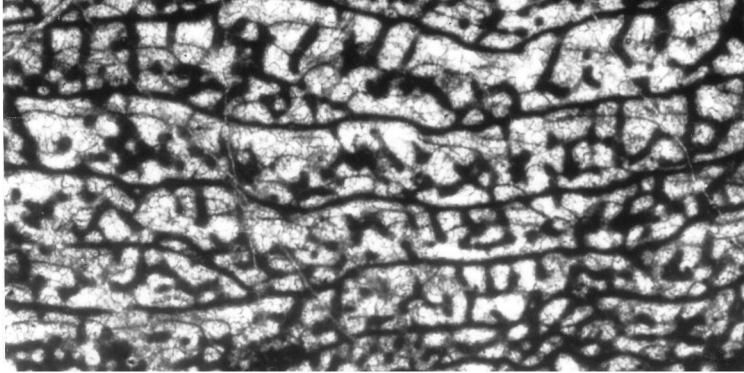
1. Domes and posts = cyst plates and pillars (Labechiida).
2. Floors and posts = laminae and pillars (Clathrodictyida, Stromatoporellida).
3. Posts and beams = pillars and colliculi (Actinostromatida).
4. Walls and floors = pachysteales and pachystromes in an amalgamate structure (Stromatoporida, Syringostromatida).

SPACING OF STRUCTURAL ELEMENTS

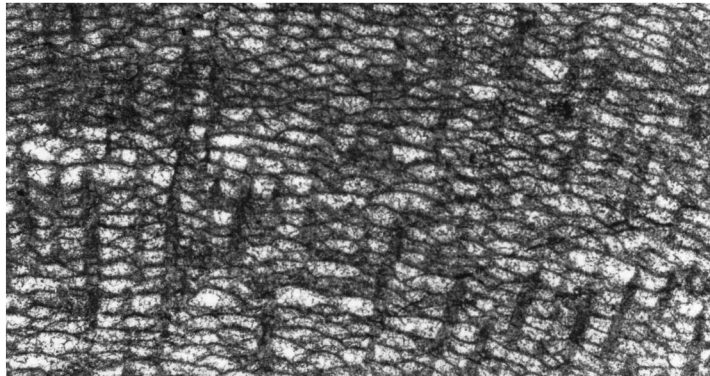
The spacing of elements has been used extensively as a specific character. For example, FLÜGEL (1959) used the spacing of pillars and laminae, plotted in what he called a species diagram, to distinguish between the many species of *Actinostroma*. Spacing is commonly expressed as the number of elements intersected along a transect of standard length. The standard length most used is 2 mm, but 5 mm and 1 mm have also been used. At least 10 counts are made on randomly placed transects in a longitudinal section by means of a calibrated microscope ocular. A mean and range are usually quoted. If more counts are made, standard deviations can be calculated, and means



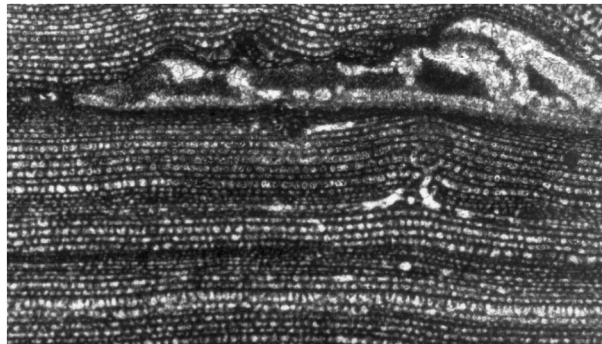
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FIG. 1. *For explanation, see facing page.*

and variance compared from specimen to specimen using standard statistical tests. Commonly the range of values is large, and the mean changes from phase to phase in the specimen (see below). STEARN (1989b) estimated that the Simpson coefficient of variability ($V = 100 \times \text{standard deviation} / \text{mean}$) ranges from about 5 to 30 and is commonly in the upper part of this range. The average spacing of pillars, laminae, pachysteles, and pachystromes is remarkably uniform throughout stromatoporoid history; this consistency suggests that it was controlled by a basic parameter of anatomy and physiology. Most structural elements are spaced about 8 in 2 mm, and the range rarely exceeds 5 to 11 in 2 mm. Stromatoporoids with widely spaced laminae (less than 5 in 2 mm, e.g., *Hammatostroma* and *Tienodictyon*, Fig. 1,2) have complex intergallery structures that may have functioned as laminae.

Pillar spacing generally closely approximates that of laminae, making equidimensional galleries. Where pillars are long, a grid is formed by the intersection of pillars and laminae.

Close spacing of tangential structural elements (10–20 in 2 mm) is characteristic of some Silurian and Early Devonian species of the clathrodictyids and actinostromatids. In the former (e.g., *Clathrodictyon ellesmerense*, Fig. 1,4), the spacing must reflect a finer internal anatomy, but in the latter it is a feature of microstructure. In the Densastromatidae, closely spaced tangential elements that appear in poorly preserved specimens are microlaminae and are not analogous to laminae but are diagenetic manifestations of microcolliculi of the microreticulate microstructure. The laminae in such genera as *Parallelostroma* (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9D, Fig. 6,3) appear

as clusters of 3 or 4 of these microlaminae in specimens where diagenesis has obscured the nature of the microreticulation and joined the microcolliculi into a continuous sheet.

The spacing of structural elements has been the metric most commonly used in the statistical evaluation of variation within skeletons and the comparison of specimens to assess their taxonomic distinctiveness. FAGERSTROM and SAXENA (1973) assessed the variation within a single specimen of *Syringostroma sherzeri*. They found that the coefficients of variation ranged from 14 to 22 for the features measured, and there were no significant differences in these parameters in different parts of the same skeleton. FAGERSTROM (1978), in further work on the statistics of *Syringostroma* species, used their megapillar spacing and diameter to assess the mode of their evolution and concluded that a choice could not be made between gradualism and punctuated equilibrium. FAGERSTROM (1981) used stromatoporoid morphometrics to unite and distinguish between species on the basis of the dimensions of their structures. The use of multivariate statistics to distinguish between closely related stromatoporoid species has been pioneered by STOCK and BURRY-STOCK (2001). They used cluster analysis and canonical correlation analysis to separate a collection of 103 specimens of *Habrostroma* into two species (*H. centrotum* and *H. consimile*) and to show that the collection could be most effectively separated on the basis of the abundance of cystlike microlaminae.

CYSTS, CYST PLATES, AND DISSEPIMENTS

Cysts form important elements in the skeletons of stromatoporoids, archaeocyaths

FIG. 1. 1, Terminal growth surface with last galleries filled with sediment, suggesting they could have been occupied by soft tissue when animal died; *Stromatopora* sp., NMV P141684, Lower Devonian, Buchans Cave Limestone, Victoria, Australia, $\times 10$; 2, complex pillar structure between widely separated laminae; *Hammatostroma albertense* STEARN, 1961, SCRM 67-671, Frasnian, Cairn Formation, Rocky Mountains, Alberta, Canada, $\times 10$; 3, structure of small cysts and long pillars, longitudinal section; *Labechia palliseri* STEARN, 1961, RM 20.4913a, Famennian, Palliser Formation, Rocky Mountains, western Alberta, Canada, $\times 10$; 4, closely spaced simple laminae showing variation in spacing; note foreign organism at growth interruption surface at top; *Clathrodictyon ellesmerense* STEARN, 1983, SCRM 110-242, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new).

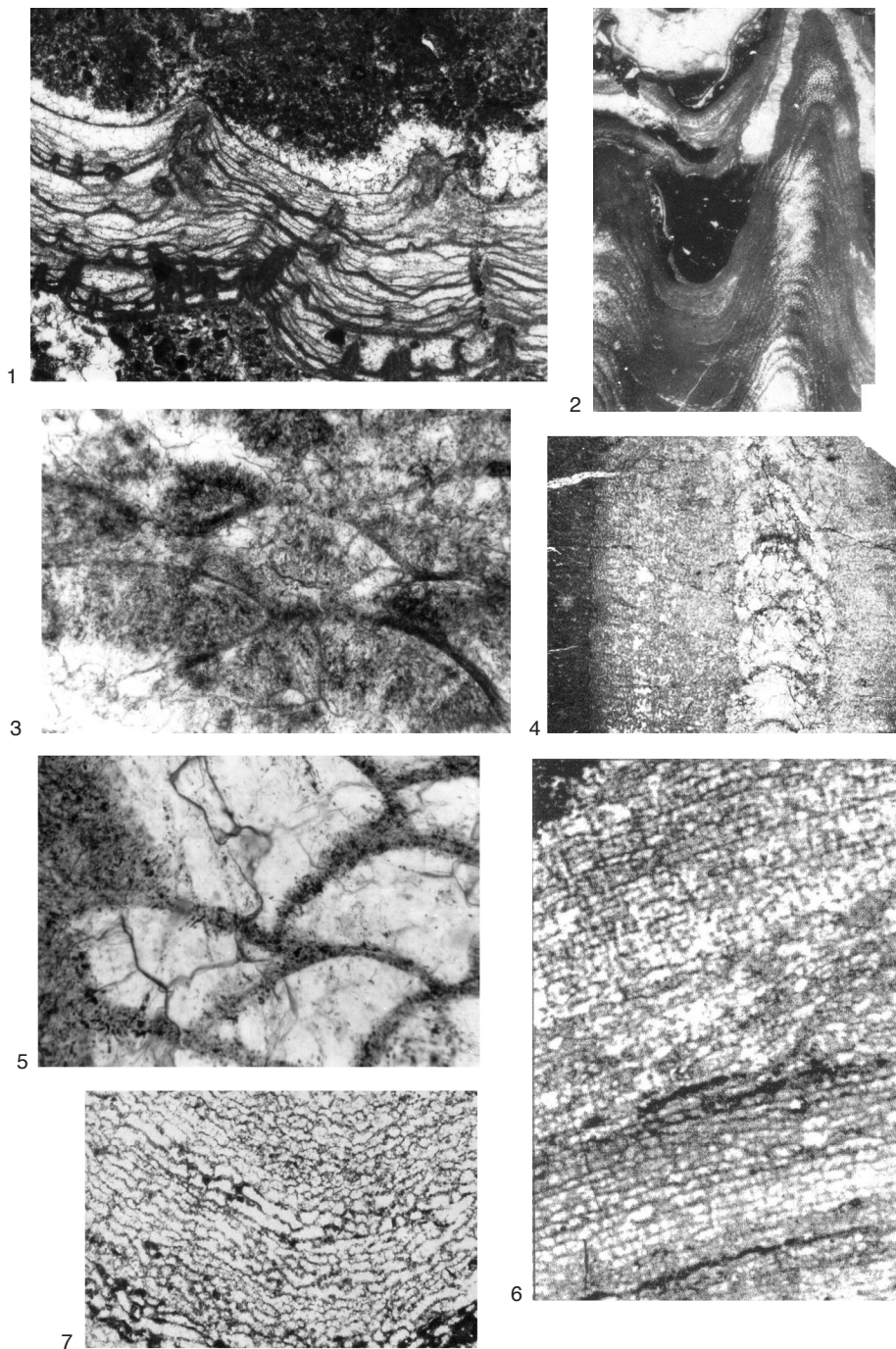


FIG. 2. 1, Longitudinal section through growth surface with mamelons; note denticles on cyst plates and spar-filled space above terminal cysts, possibly occupied at death by soft tissue; *Stylodictyon sinense* (DONG, 1964), SCRM 118-3, Famennian, Wabamun Formation, Normandville Field, northern Alberta, Canada, $\times 10$ (new); 2, long, low cyst plates inflected into high mamelons in labechiids; *Pachystylostroma goodsellense* KAPP & STEARN, 1975, (Continued on facing page.)

and other sponges, tabulates, scleractinians, rugosans, bryozoans, and rudist mollusks. In nearly all of these organisms, the enclosing plate is convex upward, but its axis of symmetry may be inclined somewhat to the vertical (Fig. 1,3; Fig. 2,1,3). This orientation suggests that it served a mass-bearing function in all of these organisms. Recognition of this geotropism is important for the orientation of thin sections of fossil specimens and may be the only reliable method of determining the growth vector in fragments of fossil skeletons. The space enclosed below the domelike plate is the cyst. Because cyst plates are the main structural elements used by the first stromatoporoids, they may be considered to be the most primitive of the structural elements.

Cyst plates appear as compact microstructures in the light microscope and in scanning electron micrographs as a uniform mosaic of small equant crystals. In Ordovician labechiids, they are bordered by a zone of speck-rich (inclusion-rich) carbonate (Fig. 2,3) that was described by GALLOWAY (1957) as part of the cyst plate. STEARN (1989a) suggested these zones were remnants of syntaxial aragonite rim cements. The absence of these zones on the cysts of post-Ordovician stromatoporoids (Fig. 2,5) suggests that the younger cyst plates were composed of calcite, probably of the high-magnesium variety.

CURVATURE

NESTOR (1964) has expressed the convexity of cyst plates by an isometry coefficient, the length/height ratio. Cysts in

stromatoporoids take a variety of forms; the major types are as follows.

1. The cyst plates of one of the earliest known stromatoporoid genera, *Pseudostylodictyon*, are extremely low and long (that is, the isometry coefficient is between 3 and 30) and are difficult to distinguish from imbricating microlaminae (Fig. 2,2). They have been called stratocysts by BOGOYAVLENSKAYA (1984).

2. In some Ordovician genera, typified by *Stratodictyon*, the cysts are small, densely spaced, and horizontally aligned (Fig. 2,6).

3. After Ordovician time, cyst plates are mostly of uniform size with isometry coefficients of 3 or less.

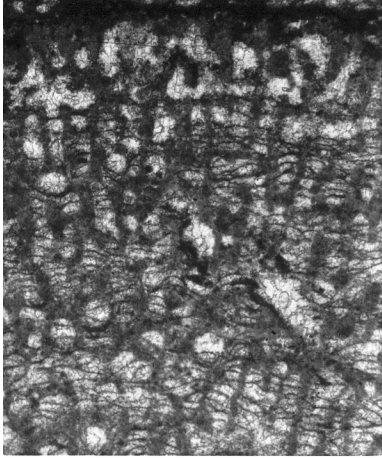
4. In many labechiids, phases of small cysts may alternate with those of larger cysts defining latilaminae.

5. In aulaceratids, the axis of the columnar skeleton is occupied by a line of large cysts, with cyst plates being horseshoe-shaped in longitudinal section (Fig. 2,4). The peripheral zone is occupied by small, imbricated cysts whose axes are inclined outward from the axis of the horseshoe cysts.

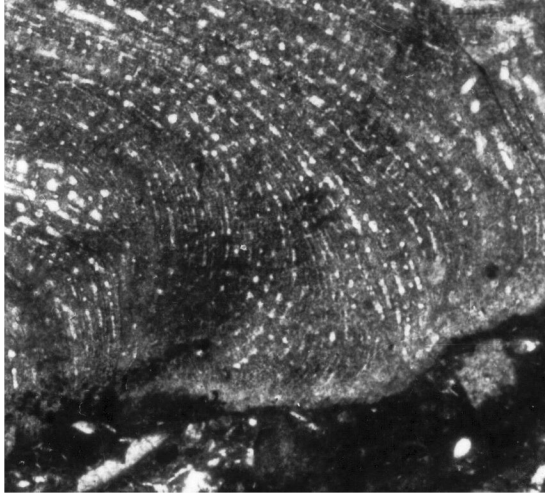
The wavy nature of the laminae of *Clathrodictyon* has suggested that the clathrodictyids evolved from labechiids by the joining of the cyst plates in horizontal rows. There is little direct evidence of this in transitional forms, however, and the first clathrodictyids to appear in Late Ordovician time include both forms with laminae that look like conjoined cyst plates (*Clathrodictyon microundulatum*, Fig. 2,7), but also species of *Camptodictyon* NESTOR, COPPER, & STOCK, 2010, whose laminae are

Fig. 2. Continued from facing page.

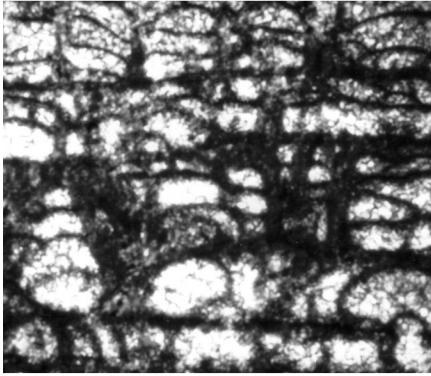
RM 14,004a, Middle Ordovician, Crown Point Limestone, Vermont, United States, $\times 1.4$ (Kapp & Stearn, 1975); 3, cyst plates bordered with a zone of specks suggestive of fans of syntaxial aragonite crystals; *Aulacera nodulosa* BILLINGS, 1857, Nicholson 287, NHM P6001, Upper Ordovician, Gamachian Formation, Anticosti Island, Quebec, Canada, $\times 50$ (new); 4, horseshoe-shaped, large cysts in axis of columnar growth form; *Aulacera denensis* WEBBY, 1991, UTGD 94652, Upper Ordovician, Chudleigh Group, Tasmania, Australia, $\times 1.75$ (Webby, 1991); 5, cysts in Silurian labechiid without fringe of specks as in 3, suggestive of a calcitic mineralogy; part of pillar on left; *Labechia conferta* (LONSDALE, 1839), Nicholson 264b, NHM P5984, Wenlock Limestone, Dudley, Shropshire, England, $\times 55$ (new); 6, small, tangentially aligned, cyst plates; *Stratodictyon ozakii* WEBBY, 1969, AMF:99377, Upper Ordovician, Fossil Hill Limestone, New South Wales, Australia, $\times 10$ (Webby, 1969); 7, undulant laminae resembling aligned cyst plates in clathrodictyid; *Clathrodictyon* sp. cf. *microundulatum* NESTOR, 1964, AM.FT 15211, Upper Ordovician, Ballingool Limestone, Bowan Park Group, New South Wales, Australia, $\times 6.5$ (Webby, 1969).



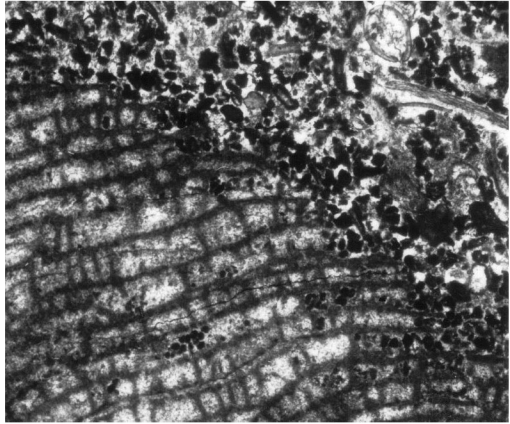
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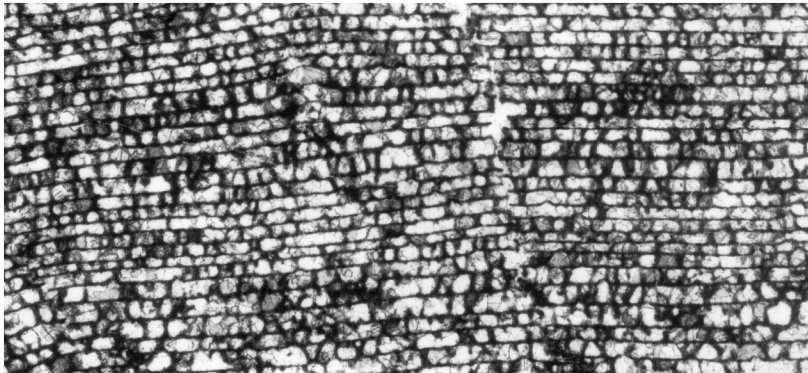
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FIG. 3. For explanation, see facing page.

chevronlike, making cassiculate structures (*C. amzassense*, see Fig. 7,1).

Dissepiments are the thin, curved structural elements that cross the galleries of clathrodictyids, actinostromatids, and stromatoporellids, and the autotubes and allotubes of stromatoporids and syringostromatids. They are usually remotely scattered in the structure and of little value for higher-level taxonomy but may be so abundant as to almost fill galleries and constitute a generic characteristic (e.g., *Pseudoactinodictyon*, Fig. 3,1,3). Dissepiments in the allotubes and autotubes of stromatoporids are not commonly aligned parallel to the growth surface across the skeleton, but where they are so aligned, they may be difficult to distinguish from microlaminae. The distinction between fine cassiculate laminae, dissepiments, and cyst plates may be difficult to see and may influence the classification of the genus. For example, in the genus *Actinodictyon*, the oblique structural elements traversed by the pillars have been referred to as dissepiments, cyst plates, or cassiculate laminae (NESTOR, 1976; MORI, 1978; STEARN, 1980). The position taken here is that they are laminae, and therefore the genus is referred to the Clathrodictyida.

Dissepiments are common in repair tissue or where the stromatoporooid animal isolated itself from an invading parasitic or predatory organism.

The thin irregular plates that cross many astrorhizal canals have been referred to as both dissepiments and tabulae. The latter term is used for them here.

LAMINAE

Laminae are tangentially extensive structural elements of intermediate thickness formed parallel to the growth surface in the labechiids, clathrodictyids, actinostromatids, and stromatoporellids (Fig. 3,5). Very thin (approximately 20 μm) tangential plates that are part of a lamina or an independent structural element are microlaminae. Thick, less extensive structures in the stromatoporids and syringostromatids are pachystromes.

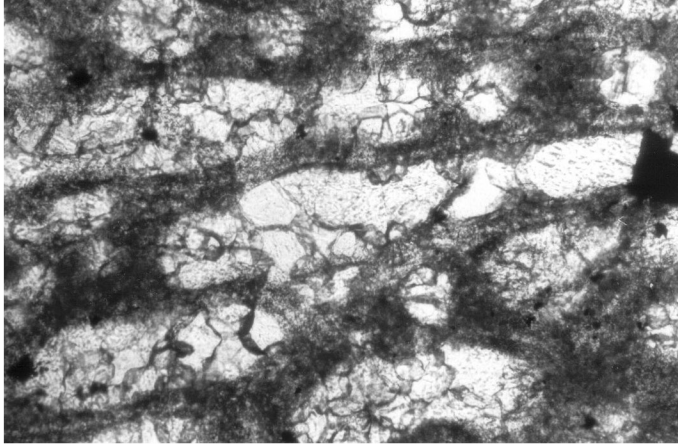
LATERAL CONTINUITY

Few laminae continue across the whole skeleton; most merge laterally with others. At the lateral edges of skeletons, laminae may close off the gallery below by downward bending and merging with the underlying lamina, but in some fossils, they end abruptly, leaving the galleries open to the penetration of sediment (Fig. 3,2,4). It is uncertain whether the opening of the gallery is the result of breakage of the skeletal margin and entry of sediment after the abandonment of that part of the skeleton by living material, or if the sediment has been incorporated in the soft tissue of the living animal (Fig. 4,3).

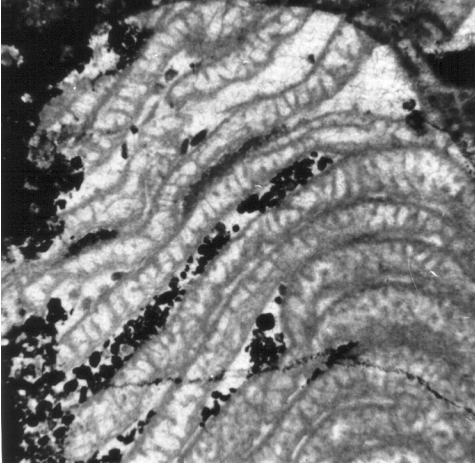
COMPACT AND TRIPARTITE LAMINAE

Laminae of the clathrodictyids are composed of a single layer of compact material. In some states of preservation, this may appear to be transversely fibrous or penetrated by fine transverse pores. This

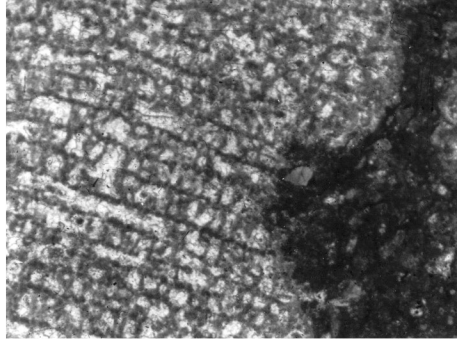
FIG. 3. 1, Abundant dissepiments occupying allotubes between pachystyles; *Salairella bullulosa* (STEARNS, 1966), GSC 18695, Frasnian, Mikkwa Formation, northern Alberta, Canada, $\times 10$ (new); 2, lateral growth edge of stromatoporooid in which laminae seem to seal off galleries as they move forward over the sediment; note also increased recrystallization zone at periphery where fluids in the sediment have entered fossil; *Parallelostroma microporum* (GIRTY, 1895), SCRM 112-145, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada, $\times 10$ (new); 3, abundant, highly curved dissepiments and pillars branching upward between distantly spaced laminae; *Pseudoactinodictyon juxi* FLUGEL, 1958, holotype, SMF XXV 1184a, Givetian, Massenkalk, Sauerland, Germany, $\times 28$ (new); 4, lateral edge of stromatoporooid against a grainstone matrix in which grains have penetrated gallery spaces and been incorporated in growing skeleton; *Anostylostroma laxum* (NICHOLSON, 1887), SCRM 112-14, GSC 95769, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada, $\times 10$ (new); 5, thin, single-layered, evenly spaced, compact laminae separated by pillars, many of which branch upward; *Schistodictyon* sp., GSC 108872, SCRM 110-210, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new).



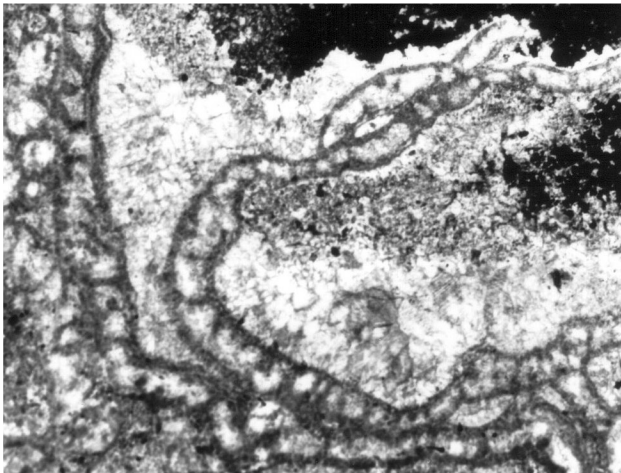
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FIG. 4. *For explanation, see facing page.*

condition is common in specimens from the Ohio Valley Middle Devonian (GALLOWAY & ST. JEAN, 1957) but appears to be a result of diagenesis (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9D, p. 4).

The members of the order Stromatoporellida are characterized by laminae of three layers (tripartite). GALLOWAY (1957, p. 354) referred to the axial layer as primary and the outer layers as secondary, but the terms are inappropriate as there is no evidence to show that one was secreted before the other or that the latter was of diagenetic (i.e., secondary) origin. In the best preserved specimens, the outer layers are compact and the middle zone is clear or divided into a series of equidimensional voids by transverse partitions (ordinicellular microstructure; Fig. 4, 1). The cellular nature of the middle zone may be more evident in tangential than in longitudinal sections. The clear middle zone of tripartite laminae can be traced laterally in some specimens into zones that are darker (in thin section more opaque) than the bordering parts of the laminae. This evidence indicates that laminae with a more opaque axis are a diagenetic variant of ordinicellular laminae. STEARN (1966) referred to this condition as tissue reversal.

In some species with laminae consisting of upper and lower compact layers separated by a clear middle zone, sediment and epibionts penetrated this zone (Fig. 4, 2). This phenomenon is best illustrated by species of *Simplexodictyon* in which, near the edge of the skeleton, the lateral layers of the tripartite laminae from above and below a gallery may join, sealing off the gallery but leaving the axial zone of the laminae open (POWELL, 1991). Similar laminae have been observed where laminae of *Stictostroma* and *Tienodic-*

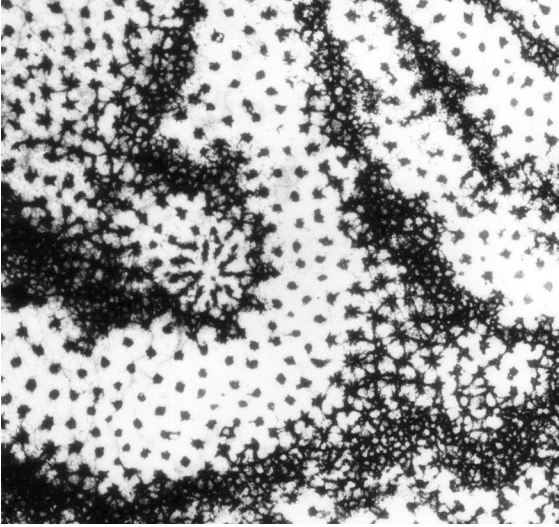
tyon grow out into a cavity that is now spar filled (Fig. 4, 4, and see also *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, Fig. 6, 1–2). Epibionts in this clear zone suggest that it was a growth interruption surface, and on this basis KAZMIERCZAK (1971) has interpreted all axial zones, whether light or dark, and all microlaminae as growth interruption surfaces.

COLLICULATE LAMINAE

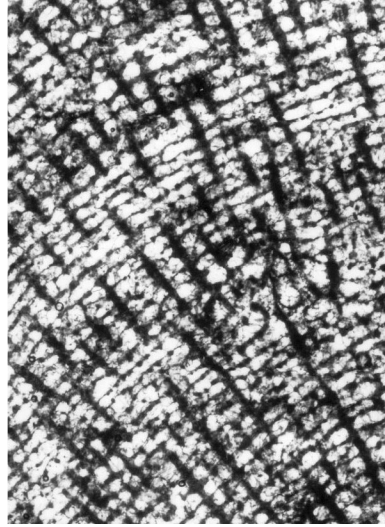
In the actinostromatids, laminae are composed of colliculi: beamlike outgrowths of the pillars that join adjacent pillars. Where the colliculi radiate from the pillars at the same level, they form a network, best studied in tangential sections (Fig. 5, 1). This network, which typically encloses triangular spaces, has been called a hexactinellid network, because it resembles the spicular network of hyalosponges. In species such as *Actinostroma clathratum*, the colliculi are thin and the network is open. In some species they are thick, thicken toward the pillars, and the holes or gaps in the network are small and round. In species with delicate colliculi, laminae in longitudinal section are discontinuous and outlined by subcircular masses of skeletal material, the cut ends of colliculi. In species with thick colliculi, the laminae in vertical section may appear to be continuous with widely spaced interruptions that represent the subcircular holes between the colliculi (Fig. 5, 2, and see Fig. 13, 2). The degree to which the colliculi are aligned tangentially, forming discrete laminae, is a morphologic character distinguishing such genera of the actinostromatids as *Actinostroma*, *Plectostroma*, and *Bicolumnostratum*.

The network of pillars and colliculi exists on two scales in the

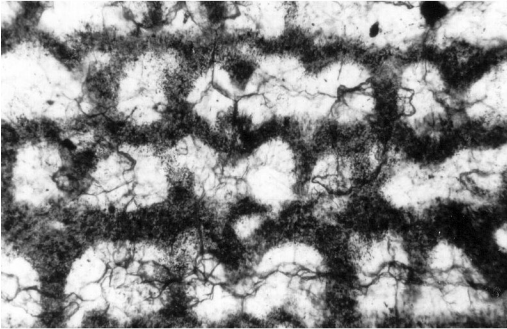
FIG. 4. 1, Tripartite laminae showing ordinicellular microstructure; *Stromatoporella granulata* NICHOLSON, 1873, Nicholson 329c, NHM P6021, Middle Devonian, Hamilton Formation, southwestern Ontario, Canada, $\times 21$ (new); 2, laminae pairs separating into modules infiltrated with grains of sediment; *Simplexodictyon vermiforme* (STEARNS & MEHROTRA, 1970), SCRM 130-47, GSC 116, 284, Emsian–Eifelian, Ogilvie Formation, Yukon, Territory, Canada, $\times 8$ (new); 3, lateral edge of stromatoporoid (growth condition or breakage?); *Aelodictyon stelliferum* STEARN, 1961, GSC 18684, Frasnian, Mikkwa Formation, northern Alberta, Canada, $\times 8$ (new); 4, modules of laminae separating into spar-filled cavity; *Simplexodictyon* sp., AM.FT 15019, upper Silurian, Narragal Limestone, New South Wales, Australia, $\times 10$ (new).



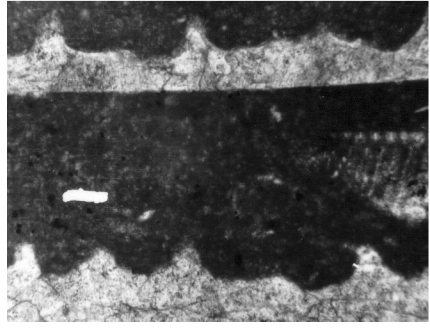
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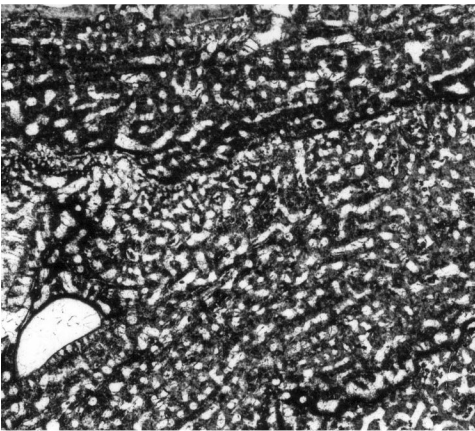
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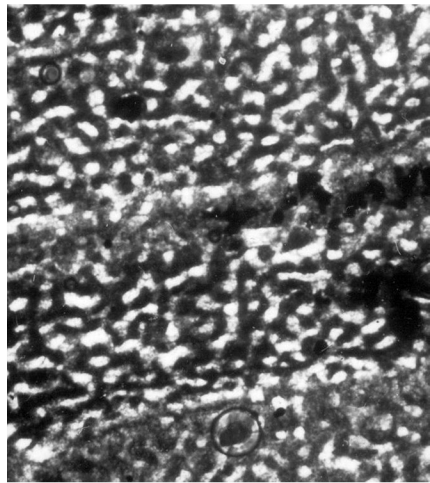
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FIG. 5. For explanation, see facing page.

stromatoporoids. As elements of the macrostructure, the pillars and laminae define such genera as *Actinostroma*. On a microstructural scale, micropillars and microcolliculi define a microreticulation within the structural elements in such genera as *Parallelostroma* that is further discussed in the chapter on Microstructure (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9D, p. 4, 22).

INFLECTED LAMINAE

In some stromatoporoids, the laminae are not planar but bent into imbricating chevrons. Such laminae characterize *Ecclimadictyon* and its relatives, which range from Late Ordovician to late Silurian time. These laminae, whose orientation is largely oblique to the direction of growth, have been called inflecting laminae (or inflexions) by BOGOYAVLENSKAYA (1984). The imbricating chevron structure is also found in the pachystromes of the cassiculate stromatoporoids, such as *Stromatopora*. Laminae may also be bent (inflected) upward into mamelons and mamelon columns and the bases of ring pillars (see below). They may also be inflected downward into the tops of pillars (Fig. 5,3).

PARALAMINAE

The structure of several genera with pervasively chevron-shaped laminae is traversed tangentially by thin, planar laminae parallel to the growth surface (*Plexodictyon*, *Ferestromatopora*) and called paralaminae (NESTOR, 1966).

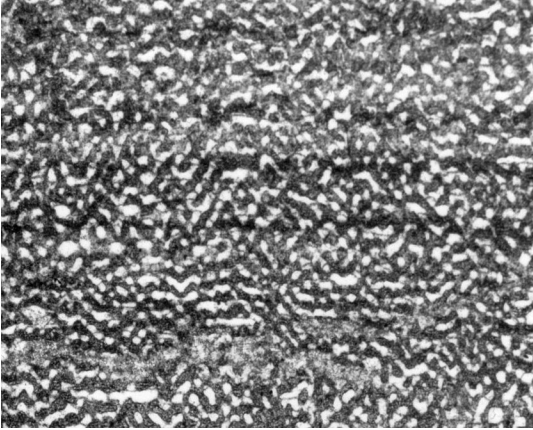
In the labechiid *Pachystylostroma*, the structure is composed dominantly of low cyst plates, but these are traversed by thick, dense laminae of compact microstructure that may show a coarse, transverse fibrosity, which has suggested the term palisade bands (KAPP & STEARN, 1975).

PACHYSTROMES

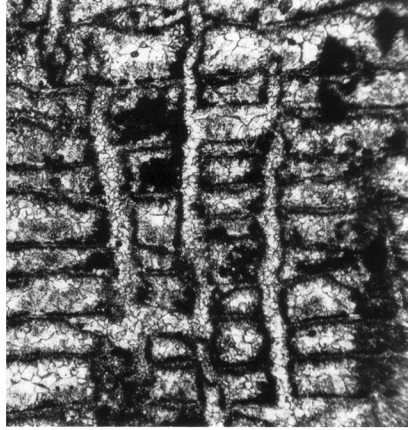
Pachystromes are the thick structural elements of the Stromatoporida and Syringostromatida secreted parallel to the growth surface. The assemblage of structural elements of these orders were characterized by NICHOLSON (1886, p. 34) as "continuously reticulated" and by GALLOWAY (1957, p. 350) as "amalgamated," that is, the longitudinal, oblique, and tangential structural elements grade into each other and are composed of the same skeletal material (Fig. 5,5-6). The distinction between laminae and pachystromes is not always clear. For example, the thick microreticulate tangential elements of *Parallelostroma* have been called laminae; but they grade into the pachysteles and are composed of similar skeletal material and could appropriately be called pachystromes.

Typically, pachystromes are not extensive tangentially but join pachysteles in short segments. In a few genera of the Stromatoporida, such as *Lineastroma*, they are as extensive laterally as the laminae of the Stromatoporellida. In certain genera such as *Habrostroma*, thick pachystromes are associated with microlaminae on their upper surface (Fig. 6,3). In genera of

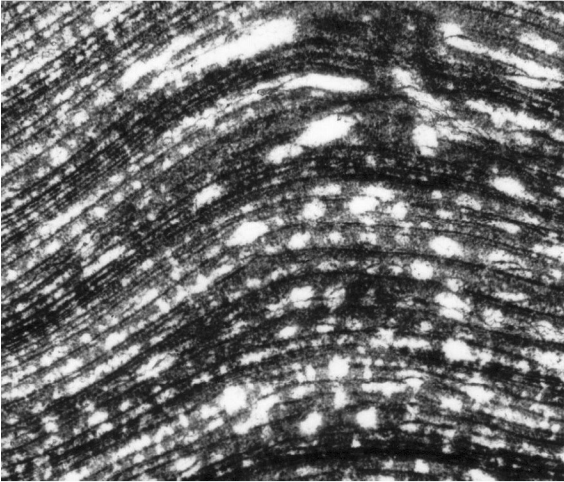
FIG. 5. 1, Colliculate laminae in tangential section; note stellate colliculi attached to pillars, uniting to form a hexactinellid network; *Actinostroma* cf. *clathratum* NICHOLSON, 1886, GSC 48447, Givetian, Evie Lake reef, north-eastern British Columbia, Canada, $\times 10$ (new); 2, colliculate laminae in longitudinal section; note that laminae in most places are reduced to a line of dots where ends of colliculi are cut; *Actinostroma clathratum* NICHOLSON, 1886, SCRM 67-274, Frasnian, Southesk Formation, Mount Haultain, western Alberta, $\times 10$ (new); 3, Single-layer laminae inflected downward into tops of pillars; *Clathrodiction striatellum* (D'ORBIGNY, 1849), Nicholson 243b, NHM P5664, Wenlock Limestone, Dudley, Shropshire, England, $\times 50$ (new); 4, denticles on top surface of cyst plate; *Rosenella macrocystis* NICHOLSON, 1886, Nicholson 280, NHM P5490, Wenlock, Gotland, Sweden, $\times 50$ (new); 5, amalgamate structure dominated by pachystromes; note disturbance of growth caused by included organism on left; *Stromatopora cygnea* STEARN, 1963, GSC 18710, Frasnian, Mikkwa Formation, northern Alberta, Canada, $\times 5$ (new); 6, amalgamate structure of pachystromes and pachysteles intergrading; parts of longitudinal section can be described as cassiculate structure; *Stromatopora concentrica* GOLDFUSS, 1826, IRScNB 6212a, Middle Devonian, Couvinian, Chimay, Belgium, $\times 10$ (new).



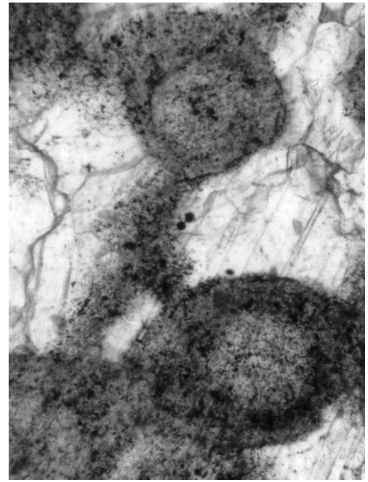
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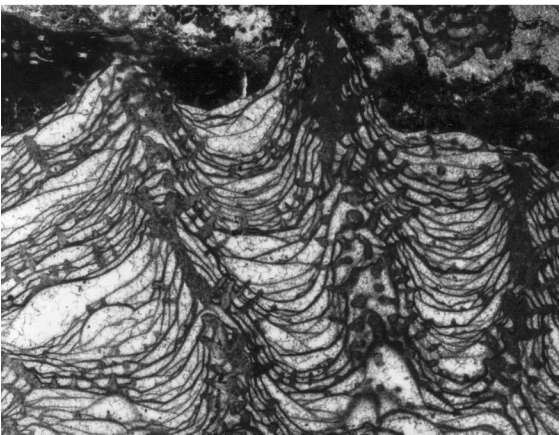
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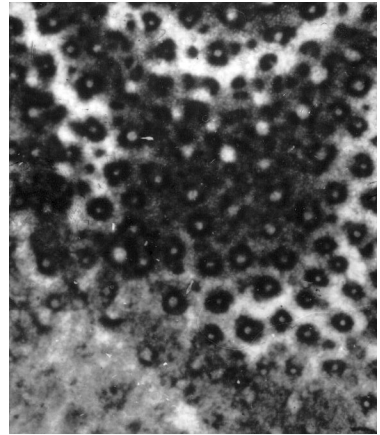
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FIG. 6. For explanation, see facing page.

microreticulate microstructure, the pachystromes may be traversed by several sets of microlaminae, apparently formed by the diagenetic alteration of aligned microcolliculi.

Oblique pachystromes have been characterized as chevron-shaped or tangled elements. The three-dimensional network formed by such oblique elements in longitudinal section is comparable in appearance to a chainlink fence whose wires enclose diamond-shaped voids and is termed cassiculate (Fig. 6, 1). The adjective can be used to describe the network as a whole or the pachystromes that form it. A network like this is particularly characteristic of such genera as *Stromatopora* (Fig. 6, 1), *Ferestro-matopora*, and *Arctostroma* (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9D, Fig. 8, 1).

INCIPIENT PILLARS, DENTICLES, AND CRENULATIONS

In the labechiids, the tops of the cyst plates may have small, pointed or blunt outgrowths that do not reach the cyst plate above. The pointed structures have been called denticles, and the blunt, finger-shaped ones have been called villi, but this latter term seems superfluous (Fig. 5, 4; Fig. 6, 5). In *Pseudostylodictyon*, GALLOWAY (1957) described crenulations, or upward inflections of the laminae that are hollow but otherwise are similar to denticles.

In some Late Ordovician species of *Camp-todictyon*, another type of incipient pillar

structure is formed. In *C. amzassense* (KHAL-FINA), the downwardly deflected edges of chevron-shaped laminae join to produce a vertical structure much like the pillars of younger stromatoporoids (Fig. 7, 1).

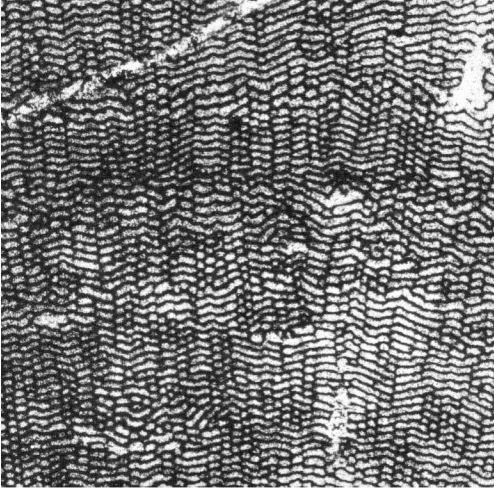
PILLARS

Pillars are post-shaped, longitudinal structural elements that extend between cyst plates, laminae (Fig. 3, 5), or pachystromes, or constitute continuous structures around which the horizontal structures are formed (Fig. 5, 2). In structures where the pillars are of two sizes (e.g., *Bifariostroma*), the larger are referred to as megapillars.

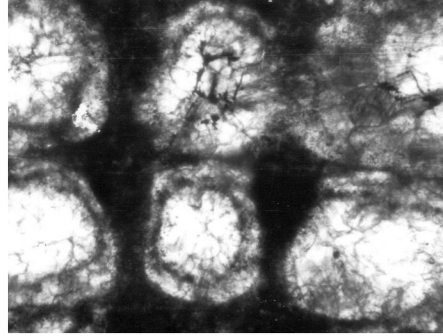
LABECHIIDA

The tops of the pillars of labechiids, such as *Labechia*, *Pseudostylodictyon*, and *Stylostroma*, emerge on the growth surface as small pimples projecting into the covering sediment and are called papillae (see Fig. 10, 1; and also see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9B, Fig. 44, 1). Where microstructure is preserved, these pillars show growth lines of downward-opening cones (Fig. 6, 4) in longitudinal section. In tangential sections, such pillars show concentric growth lines and a clear axis that NICHOLSON (1886) thought might have been hollow, but later workers have considered the axial spar to be a replacement. Because the pillars of labechiids were almost certainly made of aragonite (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9D, p. 13–18), they have been modified and dissolved in diagenesis (Fig. 6, 2), resulting

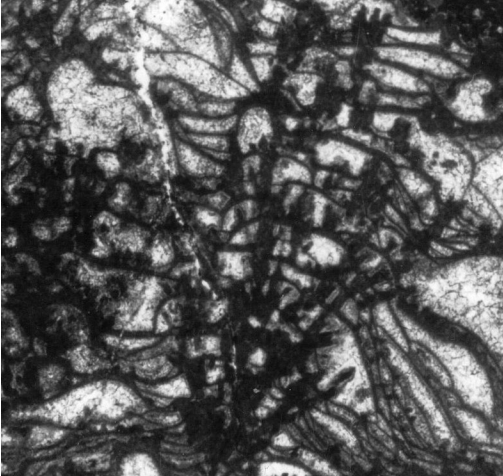
FIG. 6. 1, Cassiculate structure of oblique pachystromes; *Stromatopora* sp. cf. *polaris* (STEARNS, 1983), SCRM 125-1, Emsian, Ogilvie Formation, Yukon Territory, Canada, $\times 12$ (new); 2, pillars with centers removed in diagenesis; longitudinal section; *Stromatocerium rugosum* HALL, 1847, holotype, AMNH 590/x, Upper Ordovician, Black River Limestone, New York, United States, $\times 20$ (new); 3, microlaminae within diffuse tissue of pachystromes; note also astrorhizal canals concentrated in upward inflection of pachystromes; *Habrostroma proxilaminatum* (FAGERSTROM, 1961), holotype, UMMP 36177, Lower Devonian, Formosa Reef Limestone, southwestern Ontario, Canada, $\times 10$ (new); 4, pillars in tangential section with zones of concentric growth; *Labechia conferta* (LONSDALE, 1839), Nicholson 264, NHM P5984, Wenlock Limestone, Dudley, Shropshire, England, $\times 55$ (new); 5, denticles on upper surface of low cyst plates. Also note mamelons on terminal growth surface and thickening of pillars into mamelon columns below them; *Stylostroma sinense* (DONG, 1964), RM 20.4916a, Famennian, Wabamun Formation, Nomandville field, northern Alberta, Canada, $\times 5$ (new); 6, ring pillars in tangential section; *Stromatoporella granulata distans* PARKS, 1936, ROM 2246, Middle Devonian, Hamilton Formation, southwestern Ontario, Canada, $\times 10$ (new).



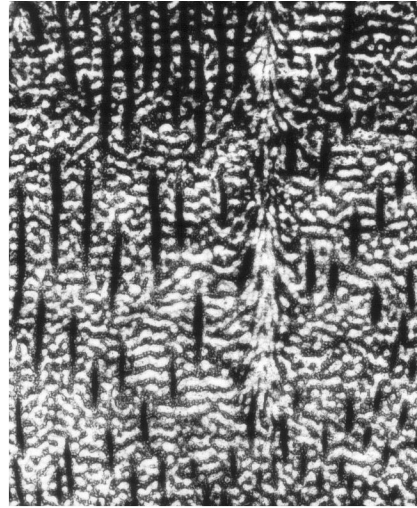
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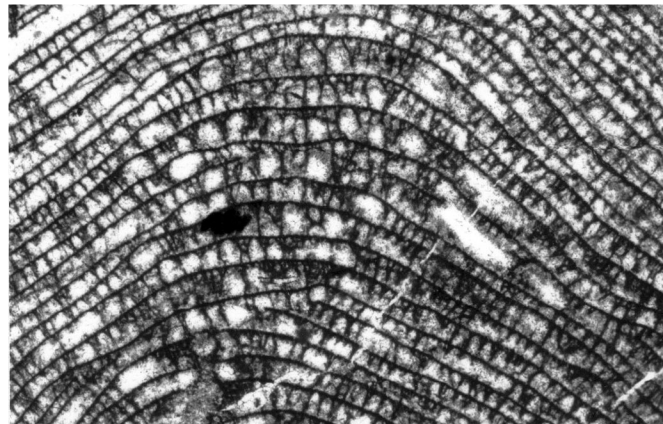
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FIG. 7. For explanation, see facing page.

in some taxonomic problems. For instance, opinion differs on the validity of the genus *Forolinia* NESTOR in which a structure of cysts is penetrated by a set of longitudinal voids that have been interpreted as both canals and as the loci of dissolved pillars (see STEARN & others, 1999, p. 13).

A few of the pillars of labechiids branch upward (Fig. 7,3), but in most other stromatoporoids, the increased number of pillars is by intercalation as the skeleton grows wider. In some labechiids, the pillars are walls with complex flanges but do not form a network in tangential section. Such pillars characterize the Ordovician *Stromatocerium* and several genera from Famennian rocks such as *Platiferostroma* and *Pennastroma*.

ACTINOSTROMATIDA

Actinostromatid pillars give off colliculi that, forming a network, define laminae (Fig. 5,1–2). The pillars of actinostromatids may show radial fibrosity in tangential section, and in rare specimens, the center of the pillars is dissolved away in diagenesis and appears clear. In most taxa of this order, the pillars are clearly the controlling structure around which the rest of the skeleton is formed and laminae laid down. (The pillars of the densastromatids are considered to be micropillars and are discussed in the chapter on Microstructure; see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9D, p. 4, 22).

CLATHRODICTYIDA

The pillars are compact in microstructure and confined to an interlaminar space. In *Clathrodictyon*, laminae are inflected down-

ward into the tops of the postlike pillars. In some species of the genus (for instance, *C. regulare*), tops of pillars cut by tangential sections in the funnel-shaped part appear to be annular. In most clathrodictyids, the pillars are short, post-shaped elements distinct from laminae, as in *Petridiostroma*. In advanced members of the order, the pillars divide once or twice at their upper ends (*Schistodictyon*, Fig. 7,5) or branch complexly and spread out on the under surface of the overlying lamina (*Anostylostroma*, *Pseudoactinodictyon*). Such complex pillars are subcircular in tangential section only near their bases but are vermiform or may form an irregular network below the overlying lamina at their tops where they branch. In some genera, they may join into chains (*Atelodictyon*). In genera such as *Hammatostroma* and *Tienodictyon*, the pillars do not cross the interlaminar space directly but are tangled into complex structures in the interlaminar space (Fig. 1,2). Superposition of pillars from one gallery to the next is uncommon in the order but occurs in the family Gerronostromatidae.

STROMATOPORELLIDA

Like the laminae, the pillars of this order tend to have cellules or vacuoles. Pillars are confined to interlaminar spaces, but in the Trupetostromatidae, they are superposed regularly and may appear to pass through the laminae. In *Stromatoporella*, the tripartite laminae are inflected upward to meet the lamina above, forming a cone or cylinder. Where cut tangentially, such cones form rings known as ring pillars (Fig. 6,6; Fig. 8,1,3). In *Trupetostroma*, the pillars are

FIG. 7. 1, Incipient pillars formed by deflection of chevron laminae; longitudinal section; *Camptodictyon amzassense* (KHALFINA, 1960), AMF.98976, Upper Ordovician, Vandon Limestone, New South Wales, Australia, $\times 5$ (Webby, 1969); 2, peripheral vacuoles on margins of pillars and laminae in stromatoporellid; *Hermatostroma schlueteri* NICHOLSON, 1892, holotype, Nicholson 386b, NHM P5527, Middle Devonian, Hebborn, western Germany, $\times 55$ (new); 3, pillars branching upward in labechiid, longitudinal section, *Stylodictyon sinense* (DONG, 1964), RM 20.4918a, Famennian, Wabamun Formation, Normandville field, northern Alberta, Canada, $\times 10$ (new); 4, postlike pillars traverse a cassiculate structure, longitudinal section; note also the superposed astrorhizal canals; *Taleastroma logansportense* (GALLOWAY & ST. JEAN, 1957), GSC 104078, Givetian, Evie Lake reef, northeastern British Columbia, Canada, $\times 5$ (new); 5, pillars dividing upward in several orders below single-layer laminae; longitudinal section, *Schistodictyon* sp., GSC-AWN-C-5849, Lower Devonian, Ogilvie Formation, Yukon Territory, Canada, $\times 10$ (new).

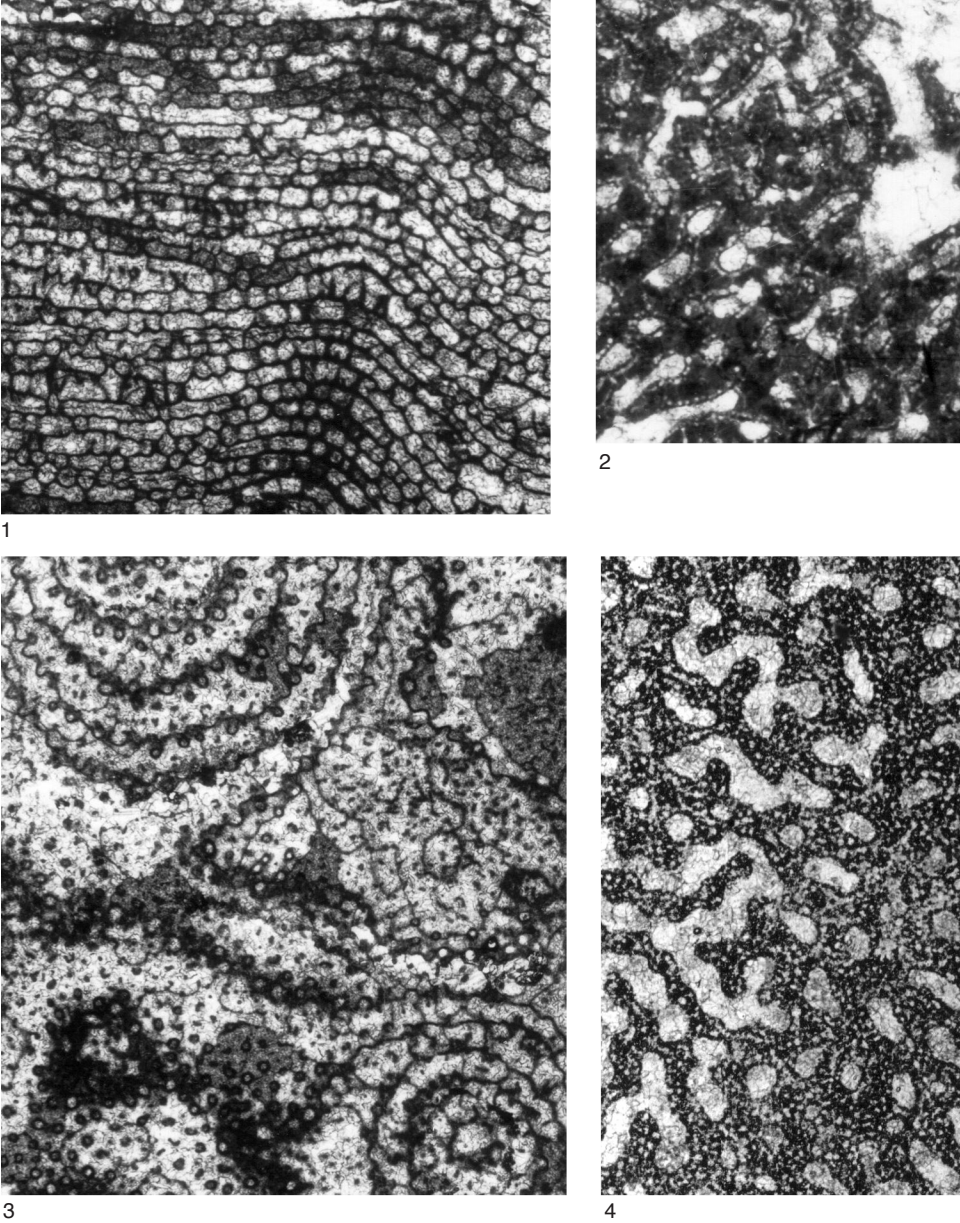


FIG. 8. 1, Ring pillars in longitudinal section; *Stomatoporella perannulata* GALLOWAY & ST. JEAN, 1957, GSC 108175, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new); 2, peripheral vacuoles on margins of pachyestes, tangential section; *Hermatoporella maillieuxi* (LECOMPTE, 1952), holotype, IRSNB-5760, Frasnian, Senzeille, Belgium, $\times 18$ (new); 3, ring pillars in tangential section; *Stomatoporella perannulata* GALLOWAY & ST. JEAN, 1957, same specimen as 1, $\times 10$ (new); 4, pachyestes with coarse cellular microstructure separated by allotubes; *Pseudotrurpetostroma vitreum* (GALLOWAY, 1960), GSC 48453A, Givetian, Evie Lake reef, northeastern British Columbia, Canada, $\times 25$ (new).

superposed spools with large, scattered cavities called vacuoles. Such a microstructure grades through that of *Hermatoporella* into that of *Hermatostroma*, in which the margins of the pillars are bordered by a row of peripheral vacuoles (Fig. 7,2; Fig. 8,2; and see *Treatise Online*, Part E, Revised, vol. 4, Chapter 16E, Fig. 12–13). These are enclosed by thin, curved walls, like dissepiments, that are supported a short distance from the pillars and laminae by small processes best seen in tangential section.

STROMATOPORIDA AND SYRINGOSTROMATIDA

Although the characteristic longitudinal structures of this order are pachysteles, true pillars are characteristic of some genera (*Atopostroma*, *Coenostroma*), and in most of the genera, some pillars are scattered between the dominant pachysteles. In *Taleastroma*, prominent postlike pillars traverse the dominantly cassiculate amalgamate structure (Fig. 7,4).

The pillars of the Stachyoditidae are much like those of the hermatostromatids in structure but are microreticulate in microstructure.

AMPHIPORIDA

Most of the structures of this cylindrical-branching order are amalgamate, but rodlike pillars may radiate outward and upward through the amalgamate structure from the axial canal.

PACHYSTELES

Pachysteles are longitudinal structural elements, mainly perpendicular to the growth surface, forming walls that enclose labyrinthine spaces like the walls or hedges of a maze. They may be vermiform and loosely joined in tangential section, or they may form a continuous network without loose edges (Fig. 8,4; Fig. 9,3). Where the spaces enclosed are regular in shape, the tangential section may resemble that of a

tabulate coral. Pachysteles are typical of the orders Stromatoporida and Syringostromatida, in which the microstructure is cellular or microreticulate, but similar structures were secreted in other orders that have compact tissue.

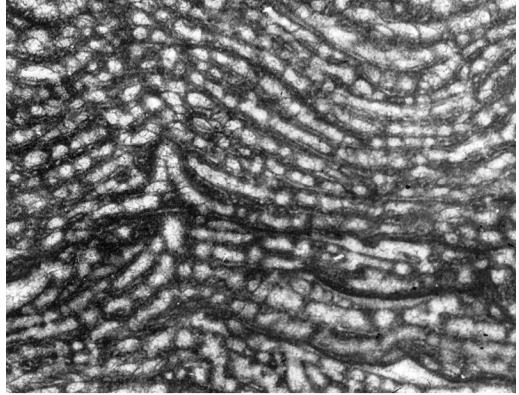
MAMELONS, COLUMNS, AND SUBCOLUMNS

Mamelons are round or irregular elevations on the terminal growth surface of stromatoporoids (Fig. 1,4; Fig. 6,5; and Fig. 10,1,3). Although the presence of such mounds is characteristic of stromatoporoids and useful in field identification of these fossils, only a minority of stromatoporoids have well-developed mamelons. Mamelons are usually a few millimeters in diameter and a few millimeters high, but in early labechiids, such as *Pachystylostroma*, they may be up to 30 mm high and narrow. Columnar growth forms in rare specimens of *Stachyodes* appear to have grown as high mamelons from a laminar base, but most stromatoporoids of columnar growth form show no evidence of having been broken from a laminar base. As mamelons are upward projections of the growth surface and laminae are secreted parallel to this surface, the location of mamelons is marked by upward inflections of laminae or pachystromes that are cut as circular structures in tangential section. In addition, structural elements, such as pillars and pachysteles, are commonly thickened beneath mamelons (Fig. 9,4–5).

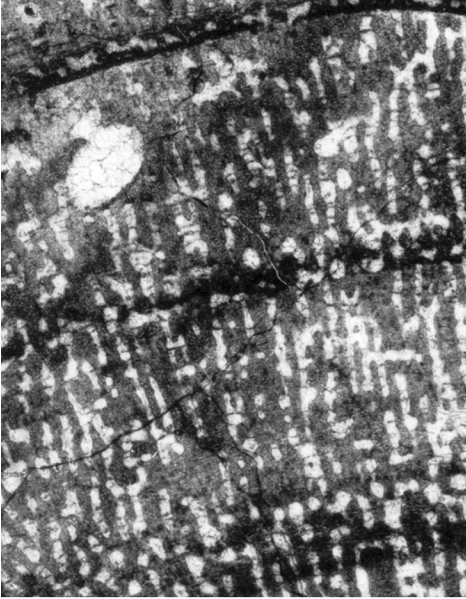
The position of mamelons commonly changed as the skeleton grew, so that in longitudinal section, the upward inflections and thickenings of the structural elements beneath them are scattered in the skeleton (Fig. 9,2). In genera in which mamelons are superposed (that is, that kept the same position as the skeleton grew), the upward inflection of the laminae below the surficial mamelons and the thickening of the structural elements form a longitudinal element



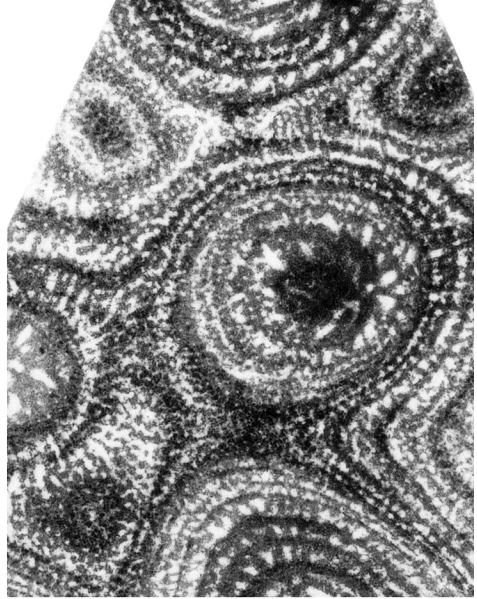
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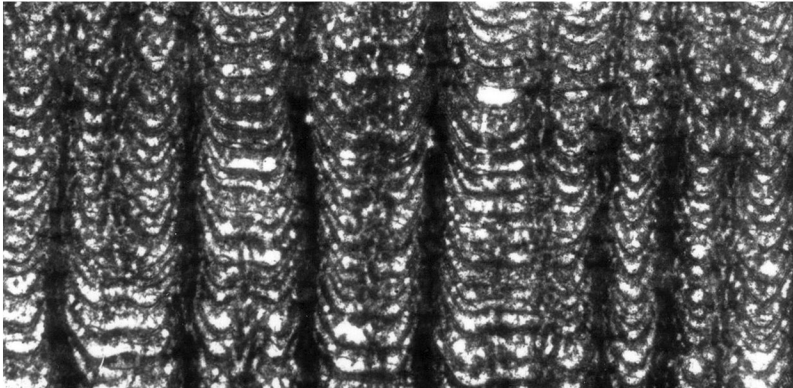
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FIG. 9. For explanation, see facing page.

called a column, of denser skeletal material an order of magnitude bigger than a pillar (Fig. 6,5; Fig. 9,4–5; Fig. 11,1a–b). In these structures, the pillars or pachysteles, because they are perpendicular to the upwardly inflected tangential elements, fan outward in longitudinal section and are radial in tangential section. In tangential section, such columns resemble spoked wheels, as concentric lines of the laminae cross the radial pillars (Fig. 9,4).

Columns commonly enclose astrorhizal canals, because astrorhizae may have been localized on the surficial mamelons. NICHOLSON (1890) referred to these structures as astrorhizal cylinders. A longitudinal axial astrorhizal canal, or set of axial canals, may occupy the centers of these columns (Fig. 9,1).

The term subcolumn has been used to refer to a columnar structure of subcircular cross section that consists of micropillars and microcolliculi arranged in an acsmoreticulate or clinoreticulate pattern.

ASTRORRHIZAL CANAL SYSTEMS

An astrorhiza is a set of radial branching grooves, ridges, or openings to the interior that join to form a stellate pattern on the terminal growth surface of stromatoporoids (Fig. 10,1,3). They have been considered to be diagnostic of the stromatoporoids but occur in other encrusting poriferans, such as chaetetids and other sponges, in which the inhalant and exhalant surfaces are the same. The astrorhizae of modern hypercalcified sponges are grooves (*Ceratoporella*, see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, Fig. 8,1), ridges (*Goreauia*), or internal

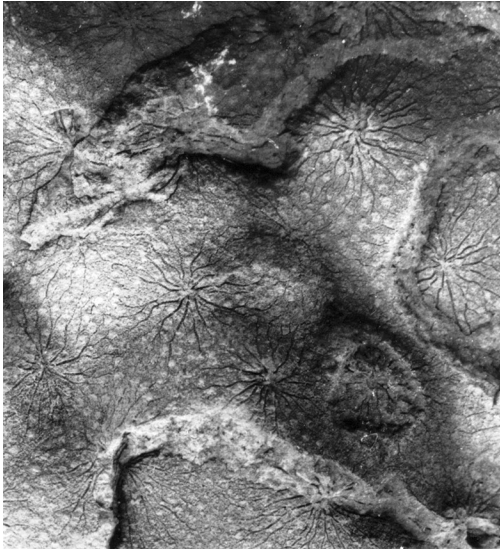
pathways (*Astrosclera*, see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, Fig. 9), localized by the soft-tissue exhalant canal system. The surficial grooves on the surface of modern representatives are produced by the modification of skeletal secretion below the canals, and those in stromatoporoids are, by analogy, assumed to have been occupied by similar tubes (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, p. 20–23). When the soft-tissue tubes were overgrown by the advancing skeleton, some were more or less encased (astrorhizal canals) or their positions were recorded in the skeleton by passages free of skeletal elements called astrorhizal paths (Fig. 11,2–3; PROSH & STEARN, 1996, p. 14).

The diameter of the paths and canals is about 2 mm in Silurian species and averages slightly larger in Devonian species.

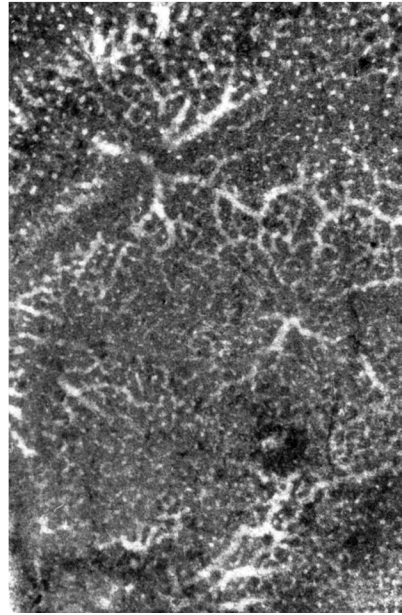
Astrorhizal systems are not evident in the skeletons of all stromatoporoid species, and STEARN (1982) estimated through a literature survey that only 35% of species and 45% of genera surveyed showed such canals. GALLOWAY (1957) stated that casual observation suggested that as few as 10% showed them. The preservation of the canals and paths within the skeleton may have depended on the thickness of the surficial soft tissue (that is, where it was thick, they did not influence the secretion of hard tissue below them); or on the size of the spaces between the structural elements and hence the ability of the skeleton to accommodate the canals without disruption of the regularity of the structure.

Astrorhizae are not common nor conspicuous in most labechiids but have been detected in some of the earliest forms (KAPP

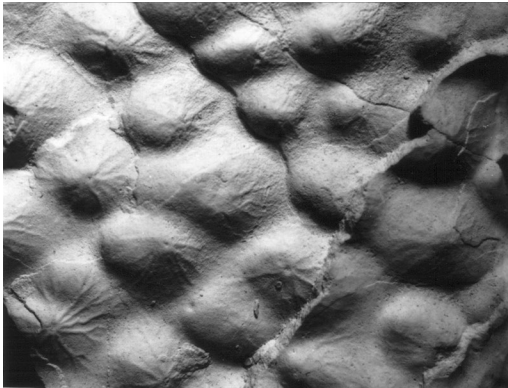
FIG. 9. 1, Isolated mamelon within a regular structure showing central astrorhizal canal; *Schistodictyon* sp., UWA 140802, Frasnian, Pillara Limestone, Canning Basin, Western Australia, $\times 5.5$ (new); 2, mamelons isolated in regular structure, longitudinal section; *Stictostroma maclareni* STEARN, 1966, holotype, GSC 18674a, Frasnian, Kakisa Formation, northern Alberta, Canada, $\times 10$ (new); 3, structure dominated with pachysteles separated by dissepiments; note also latilaminar growth and round boring of foreign organism; *Salairrella prima* KHROMYKH, 1971, GSC 108899, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new); 4, mamelon columns in tangential section with astrorhizal canals; *Habrostroma proxilaminatum* (FAGERSTROM, 1961), holotype, UMMP 36177, Lower Devonian, Formosa Reef Limestone, southwestern Ontario, Canada, $\times 5$ (new); 5, mamelon columns in which laminae are deflected upward and structural elements thickened, longitudinal section; *Syringostroma sherzeri* GRABAU in GRABAU & SHERZER, 1910, SCRM 22-7, Lower Devonian, Detroit River Limestone, southwestern Ontario, Canada, $\times 10$ (new).



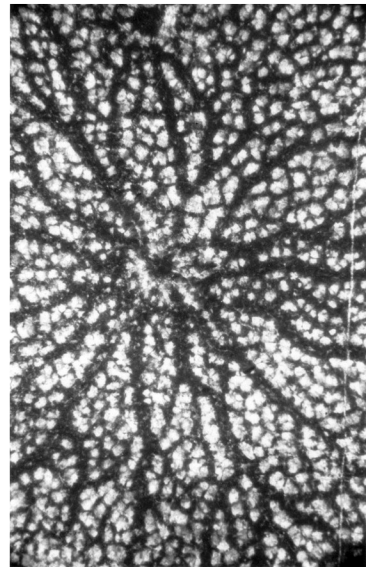
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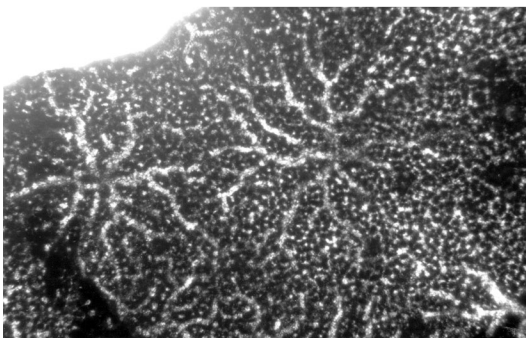
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FIG. 10. 1, Growth surfaces of three successive latilaminae in exfoliating, unidentified stromatoporoid (probably *Syringostroma* sp.), Devonian, Michigan; note astrorhizal grooves, some on mamelons and others between them, and emergence of columns as papillae on surfaces; RM 14,777, Middle Devonian, ?Alpena Limestone, Michigan, United States, $\times 2.5$ (new); 2, branching astrorhizal canals in tangential section leading into galleries in dense skeleton of (Continued on facing page.)

& STEARN, 1975), and tangential sections of mid-Silurian genus *Cystocerium* NESTOR, 1976, show prominent stellate patterns (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 16A–B, Fig. 13b–c). They are well developed in densastromatids but generally inconspicuous in the open structure of actinostromatids such as *Actinostroma* (Fig. 11,2). They are variably developed in clathrodictyids and stromatoporellids. The largest and most conspicuous astrorhizal systems are in the orders Stromatoporida and Syringostromatida, and nearly all species of the orders show these systems.

SURFICIAL ASTRORRHIZAE

Few stromatoporooids preserved in limestone show the terminal growth surface on which astrorhizae are expressed. The surface is most clearly revealed in specimens weathering free from argillaceous sedimentary rocks or specimens in which the layers will split apart along growth interruption surfaces.

Astrorhizae appear on the face of the growth surface as: 1) paths free of skeletal elements; 2) shallow grooves (Fig. 10,1); and 3) raised ridges. Whether they appear as ridges or grooves depends on whether they were accommodated in the skeleton by depression of the horizontal structural elements beneath them or arching of elements above them. They may be straight or sinuous. They decrease in diameter and branch, usually dichotomously, away from the axis of the star-shaped system. The stellate systems are commonly isolated from each other by skeletal tissue in which pathways cannot be distinguished, but in a few species, the ends of the channels of adjacent systems merge. Astrorhizae are commonly

centered on mamelons, but this association is not as universal as suggested by BOYAJIAN and LABARBERA (1987), and many stromatoporooids with mamelons have astrorhizae both on top of the mamelons and between them on the same growth surface. The centers of astrorhizae may show the orifices of one or more vertically directed canals on which the lateral passages converge (Fig. 10,3).

ASTRORRHIZAL CANALS WITHIN THE SKELETON

Complete stellate astrorhizal systems are rarely shown in tangential section (Fig. 10,5), because the canals, following the contour of the commonly domed growth surface, are not in one plane but bend downward, away from the center. The astrorhizae within the skeleton appear most clearly in tangential sections as branching, sinuous paths clear of structural elements radiating away from a central area. In most stromatoporooids, these passages appear to open freely into the gallery space along their length (Fig. 10,2,4; Fig. 12,1). In the sense that the astrorhizae drained all the choanocyte chambers within the soft tissue between the structural elements (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, Fig. 8,2), the gallery space in the skeleton could be considered part of the astrorhizal system. In stromatoporooids whose galleries are large and structure coarse, the astrorhizal systems are inconspicuous and must have been completely accommodated between the structural elements. In contrast, the astrorhizae in stromatoporooids with closely spaced elements (such as the densastromatids) are conspicuous.

There appears to be a complete gradation between astrorhizal systems in which the

Fig. 10. Continued from facing page.

Gerronostroma franklinense STEARN, 1990, SCRM 112-113, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada, $\times 15$ (new); 3, growth surface showing regular mamelons localizing astrorhizal ridges and with traces of a central astrorhizal canal; light from top of photograph; *Schistodictyon* sp., GSC Norris collection, AWN-C-5849, Lower Devonian, Ogilvie Formation, Yukon Territory, Canada, $\times 2$ (new); 4, many-branched astrorhizal canals leading into galleries in tangential section in *Pachystroma antiqua* NICHOLSON & MURIE, 1878, Nicholson 290, NHM P6003, middle Silurian, southwestern Ontario, Canada, $\times 10$ (new); 5, extensive astrorhizal system with canals outlined by opaque matter, tangential section, *Parallelopora dartingtonensis* CARTER, 1880, Nicholson 133 (compare NICHOLSON, 1886, pl. 4, 1), NHM P5743, Middle Devonian, Devon, England, $\times 10$ (new).

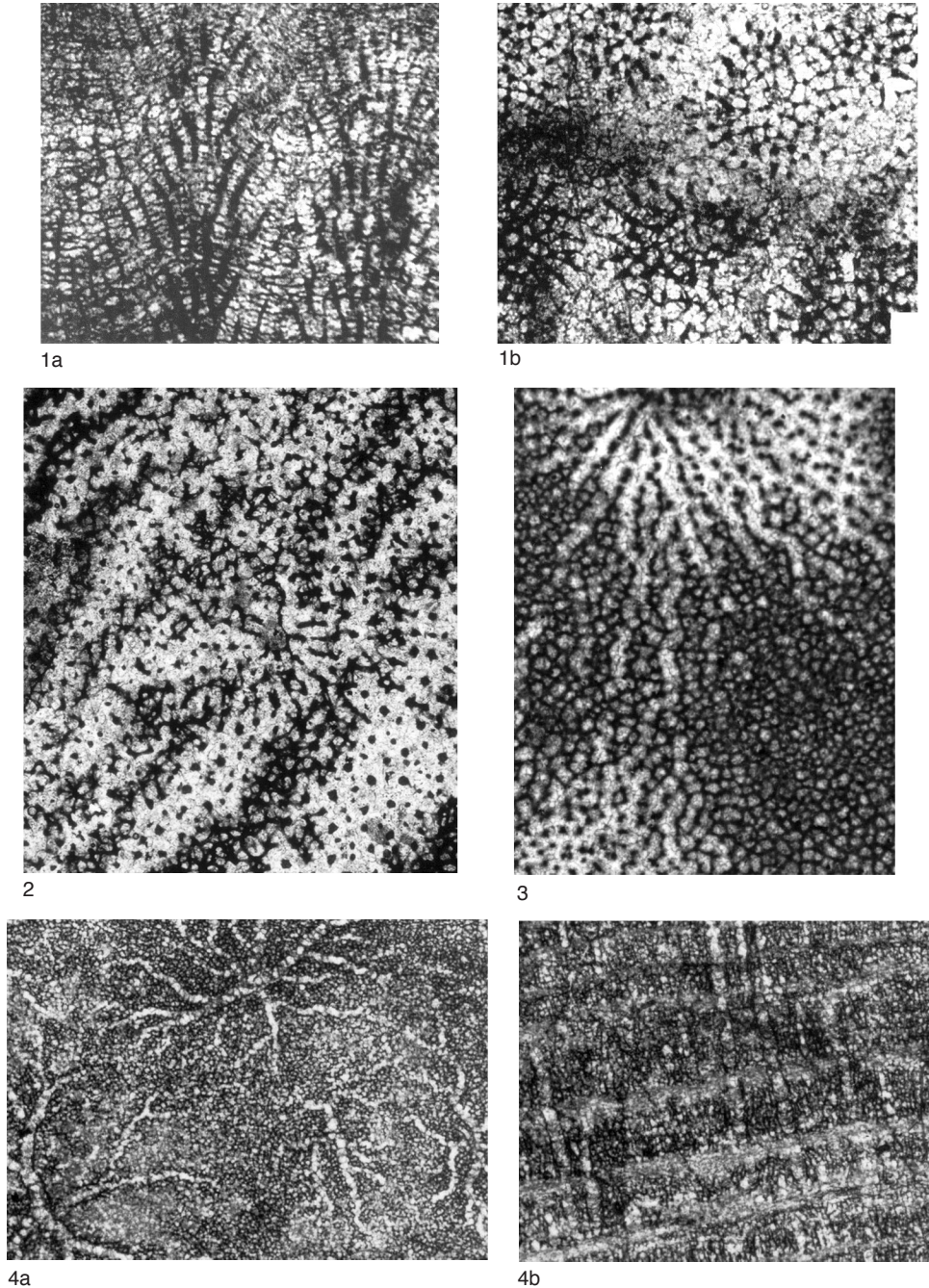


FIG. 11. 1a–b, Columns of pillars and microcolliculi in *Pseudolabechia granulata* YABE & SUGIYAMA, 1930, USNM 458898, $\times 10$ (Stearn & others, 1999); 2, Astrorhizal paths in open skeleton of *Actinostroma expansum* (HALL & WHITFIELD, 1873), tangential section, GSC- 65823A, Givetian, Dawson Bay Formation, Manitoba, Canada, $\times 10$ (new); 3, astrorhizal paths in tangential section of *Atelodictyon* sp., UWA 140816, Frasnian Pillara Limestone, Canning Basin, Australia, $\times 10$ (new); 4a, hidden astrorhizal systems containing skeletal elements, (Continued on facing page.)

paths are completely open to the galleries between the structural elements, systems in which pillars and pachysteles are more continuous and thickened beside the passageways that open into galleries only at intervals, and systems in which the passages appear as tubes almost entirely enclosed in skeletal tissue that is indistinguishable from that of other structural elements (Fig. 12,3). In the last state, the astrorhizae may be difficult to distinguish from the tubes of a foreign organism (see Foreign Organisms in Stromatoporoid Skeletons, p. 29 herein). Relatively few species (STEARNS [1982] suggested 5–10%) have passageways that appear to be isolated from the rest of the structure by a continuous wall. In some stromatoporoids (e.g., some species of *Plectostroma*), the astrorhizal passages are filled with delicate structural elements (Fig. 11,4a–b). NESTOR (1966) called these astrorhizae hidden or camouflaged [Russian = *zamaskirovannye*]. Such astrorhizae are produced where astrorhizal depressions on the surface of a lamina are filled in by growth of the skeletal elements crossing the overlying gallery.

In longitudinal section, astrorhizae are represented by round, oval, or elongate voids in the structure, depending on the angle at which the passage is cut by the section. Commonly such passages are scattered irregularly in the skeleton, indicating that the astrorhizal systems were developed randomly and the canals changed position on the growth surface as the skeleton grew (Fig. 12,4). In some stromatoporoids, they are superposed in longitudinal series and may be joined in their axes by a single longitudinal passageway or a set of passageways crossing the tangential structural elements. Such longitudinal series of astrorhizae commonly, but not always, occur in mamelon columns (Fig. 12,2,4).

ASTRORHIZAL TABULAE

Astrorhizal passages within the skeleton may be divided into segments by thin, planar sheets of skeletal material like the tabulae of tabulate corals (Fig. 9,1; Fig. 13,1). These tabulae are commonly spaced distantly, at intervals several times the diameter of the tube. Rarely the partitions are curved and imbricate in larger passages, and then they resemble dissepiments. In STEARNS' (1982) survey of illustrations of tangential sections, only 18% showed tabulae in the canals, which may reflect the poor preservation potential of these delicate plates or their rarity in the original skeletons.

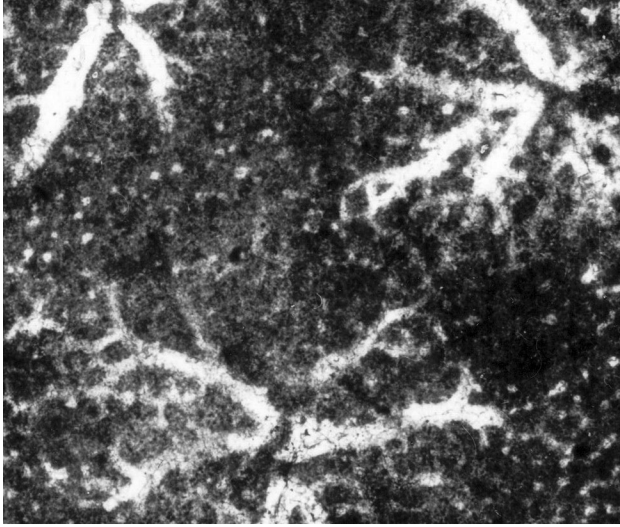
ASTRORHIZAE IN DENDROID GROWTH FORMS

The tabulate axial canals of such genera as *Stachyodes*, *Amphipora*, and *Idiostroma*, can be modelled as longitudinal axial canals of astrorhizae, and the skeleton as a whole, as an isolated mamelon column. Support for this homology comes from rare specimens of *Stachyodes*, in which the fingerlike stems emerge as high mamelons from a laminar base. The axial canal of *Stachyodes* also branches parallel to the parabolic laminae into canals like astrorhizae. In no dendroid genus has the surface revealed an astrorhizal groove system, but specimens showing the surface and particularly the growing tip, where such grooves would be expected, are very rare. The aligned stack of large, horseshoe-shaped, axial cysts in aulaceratids does not appear to be homologous to the longitudinal axial canal of superposed astrorhizae, and its function is problematic.

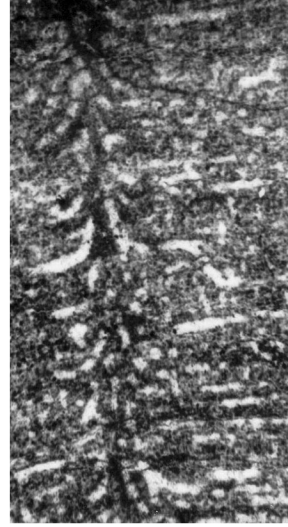
GALLERIES, ALLOTUBES, AND AUTOTUBES

The spaces between structural elements were called galleries by GALLOWAY (1957)

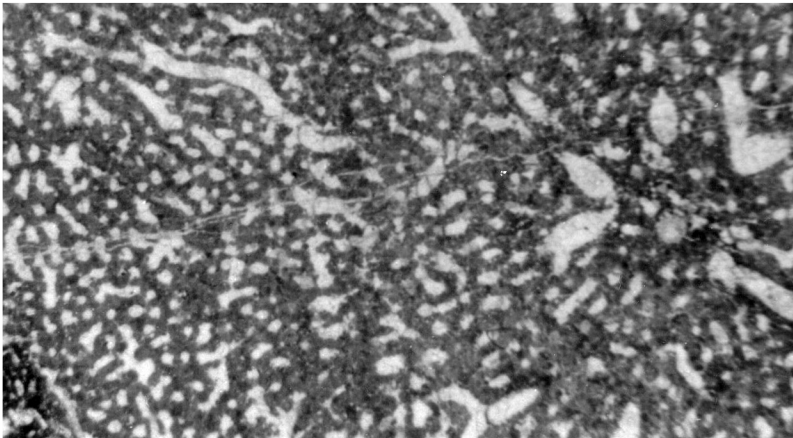
Fig. 11. Continued from facing page.
 tangential section; *Plectostroma* sp., AM.FT 15015, upper Silurian, Narragal Limestone, New South Wales, Australia, ×10; 4b, vertical section of the same specimen as 4a, *Plectostroma* sp., showing superposed astrorhizal systems, AM.FT 15016, upper Silurian, Narragal Limestone, New South Wales, Australia, ×10 (new).



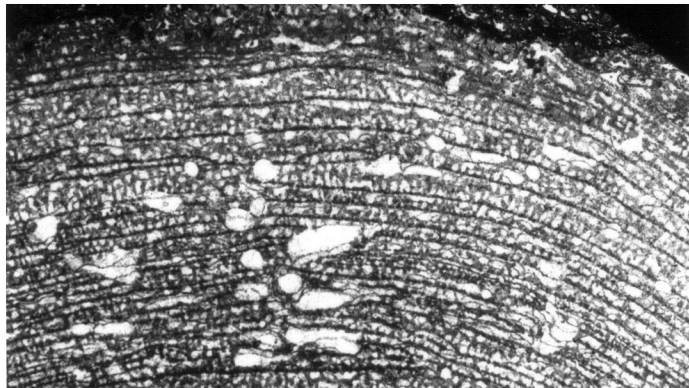
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FIG. 12. *For explanation, see facing page.*

in analogy to the galleries of a coal mine that are held open by unmined pillars that support the roof. The term is most appropriately used to describe the orders Clathrodictyida, Actinostromatida, and Stromatoporellida, where discrete pillars and laminae can be identified in most genera but can also be used for amalgamate stromatoporphs. GALLOWAY (1957) suggested that the spaces below cyst plates, such as those in the order Labechiida, should be called chambers, but the word cyst is used here.

In species where pachysteles are prominent, the spaces between them are vertically elongate and crossed by dissepiments or microlaminae. When most paleontologists referred the stromatoporphs to the hydrozoans, these vertical openings were thought to have contained zooids and were called zooidal tubes. When their homology to hydrozoan tubes became less certain, they were called pseudozooidal tubes (GALLOWAY & ST. JEAN, 1957), then coenotubes and autotubes (NESTOR, 1966, autotube after HUDSON's [1956] use for Mesozoic milleporidiids). Because the term coenotube (like the term coenosteum) implies a part of a colonial organism and the affinity of the stromatoporphs to the colonial hydrozoans is now considered unlikely, the term is replaced in this volume by allotube. Allotubes are meandriform, vermiform, or irregular in tangential section (Fig. 8,4; Fig. 9,3); autotubes are circular to subcircular (Fig. 13,3–4; Fig. 16,2). The shape and size of galleries is determined by the shape and spacing of the bounding structural elements and should only rarely need separate description.

Spaces between the structural elements are, with few exceptions, filled with calcite

spar in large cement crystals (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9D, Fig. 2,1, Fig. 11,1). These spar-filled spaces must have been filled only with seawater below the living tissue and filled with spar cement as the skeleton became a fossil. The cysts in the Ordovician labechiids may be filled with sediment, but sediment within the galleries of later stromatoporphs is rare, and in many specimens, its entry can be attributed to breakage that opened the margin of the skeleton. Rarely, the galleries near the final growth surface that have not been sealed have been infiltrated by sediment when the organism died (Fig. 1,1, also see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, p. 11). The presence of sediment within cysts and between cyst layers in Ordovician labechiids suggests that sediment rejecting and clearing mechanisms were not as well developed in these early forms as in later ones.

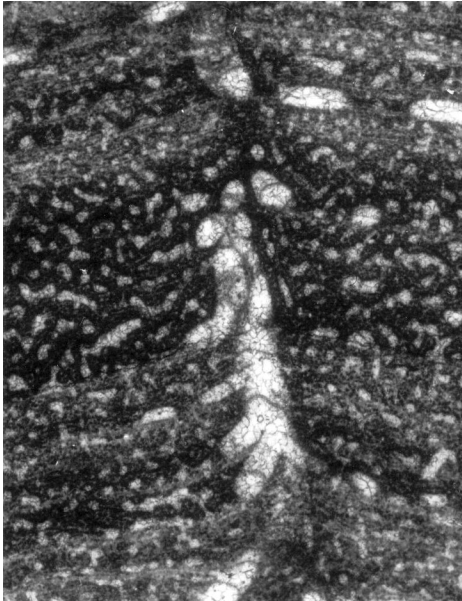
PHASES

The internal structure of stromatoporphs was not uniform throughout the skeleton but changed along the growth surface and as the organism grew. Assemblages of different skeletal structures formed at various stages in the growth of the stromatoporph were successive phases; variations along the growth surface gave rise to contemporary phases (STEARN, 1986).

SUCCESSIVE PHASES

Successive phases replace each other longitudinally. The most common successive phases are spacing phases in which the distance between the structural elements changes as the skeleton grows (Fig. 1,3; Fig. 13,5). Where changes are rhythmic,

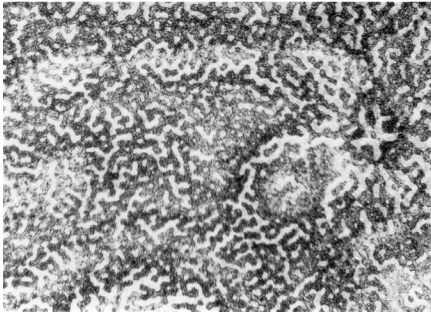
FIG. 12. 1, Astrorhizal systems with many branches opening into galleries, tangential section; *Gerronostroma franklinense* STEARN, 1990, GSC 95760, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada, $\times 15$ (new); 2, superposed systems of astrorhizal canals, longitudinal section; *Habrostroma proxilaminatum* (FAGERSTROM, 1961), GSC 108905, Lower Devonian, Formosa reef, southwestern Ontario, Canada, $\times 10$ (new); 3, astrorhizal canals almost entirely enclosed in skeletal tissue, tangential section; *Hermatoporella mailleuxi* (LECOMPTÉ, 1952), IRScNB 5760, Frasnian, Senzeille, Belgium, $\times 10$ (new); 4, Scattered astrorhizal tubes in longitudinal section, showing terminal growth phase and complex pillar structure; *Atelodictyon stelliferum* STEARN, 1961, SCRM 67-800, Givetian–Frasnian, Flume Formation, Mount Haultain, western Alberta, Canada, $\times 10$ (new).



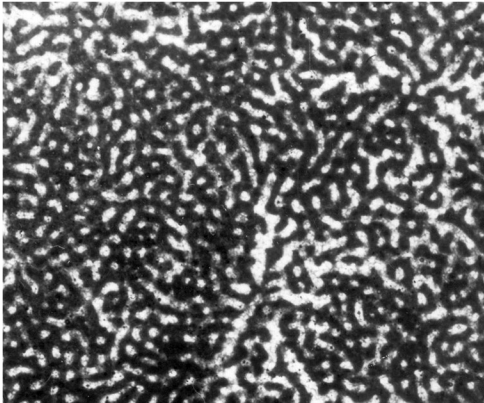
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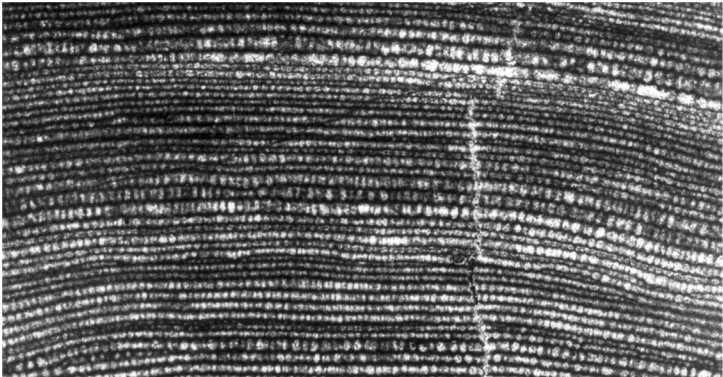
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FIG. 13. For explanation, see facing page.

they have been attributed to yearly environmental changes. Such changes may amount to 30% of the average value of the spacing parameter (such as the laminar spacing). Changes between some successive phases involve the appearance or disappearance of structural elements such as pillars and dissepiments and may be great enough to suggest that a specimen includes the characteristics of several different genera (Fig. 14,1).

YOUNG and KERSHAW (2005) made the most extensive study of successive phases in Paleozoic stromatoporoids on specimens from the Upper Ordovician of Manitoba and the Silurian of Gotland. They divided growth-related banding into density bands, reflected in the thickness and spacing of structural elements and growth interruption bands. They assessed the distinctness of the density banding on a scale of 0 to 5 and correlated internal banding with pulses in growth at the margins of the skeletons (raggedness). The relative thickness of the low- and high-density bands (L/H) in the two species that could be measured was 0.71 and 1.26. However, no firm conclusions were reached based on their limited data set on the taxonomic or paleoecologic significance of the measures of band thickness or distinctiveness.

TERMINAL PHASES

Terminal phases may have been formed by atypical structural elements when the organism modified its skeleton to resist deteriorating environmental conditions that led to its demise (Fig. 12,4).

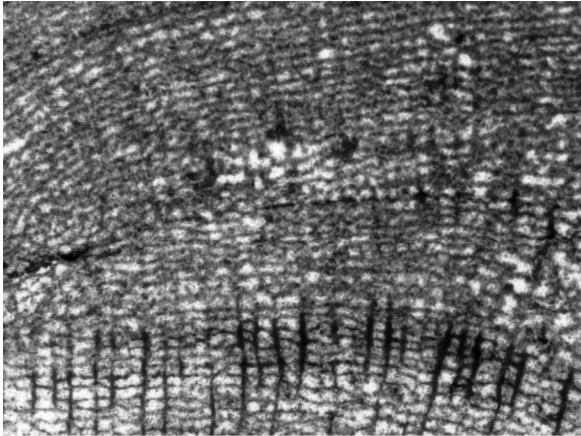
BASAL PHASES

Many skeletons are characterized by basal phases formed as the organism spread across the sediment surface. These structures are generally formed of irregular, oblique, structural elements that have been described as stringy, but they have not received the attention they deserve. GALLOWAY (1957) referred to basal phases as perithecata and related them to the epithecata of corals.

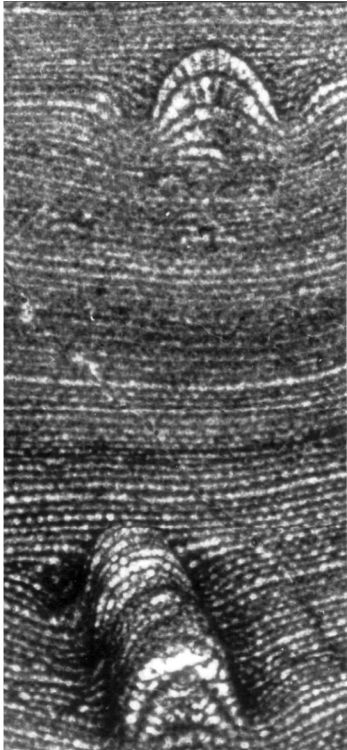
Units of growth characterized by rhythmic phase changes and bounded by surfaces of growth interruption are latilaminae (Fig. 13,2; Fig. 14,3). Weathered cross sections of stromatoporoids commonly show such concentric bands a few millimeters thick, and some split easily along the planes between the latilaminae (Fig. 10,1). Many latilaminae begin with distinctive basal phases and end with the intercalation of a sediment layer or the colonization of the growth surface by epibionts. BOGOYAVLENSKAYA (1984) referred to the succession of latilaminae as zonation. The interpretation of these latilaminae as units of annual accretion is discussed under Functional Morphology (see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, p. 9–10).

Although some writers (BOGOYAVLENSKAYA, 1984) have referred to progressive changes in successive phases as astogeny of the stromatoporoid colony, no convincing argument has been made that these changes are related to the life cycle of the stromatoporoid animal. The initial layers of growth (basal phase) of the stromatoporoid animal are not usually composed of labechiid-like cysts, as one might expect if they reflected on the early stages of stromatoporoid phylogeny.

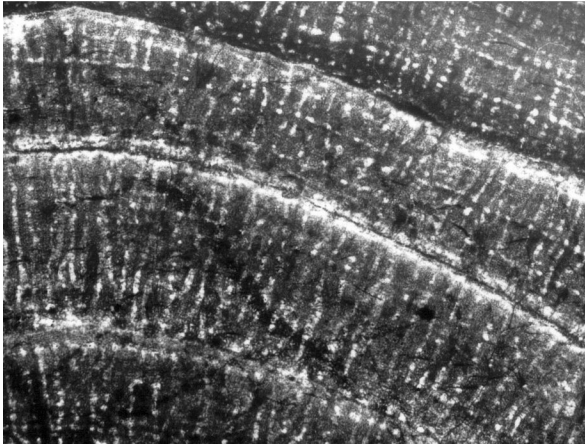
FIG. 13. 1, Superposed astrorhizal canal system with tubulae passing through a cassicate network of cellular structural elements, longitudinal section; *Stromatopora hensoni* PROSH & STEARN, 1996, holotype, GSC 108890, Emsian-Eifelian, unnamed formation, Bathurst Island, arctic Canada, $\times 10$ (new); 2, latilaminar growth, basal phases at start of each latilamina, colliculate laminae in longitudinal section cut as line of dots; *Actinostroma expansum* (HALL & WHITFIELD, 1873), SCRM 90-31, Frasnian, Shell Rock Formation, Iowa, United States, $\times 10$ (new); 3, allotubes between pachyestes, tangential section; traces of astrorhizae, cellular microstructure; *Pseudotruperetostroma vitreum* (GALLOWAY, 1960), GSC 104890, Givetian, Evie Lake reef, northeastern British Columbia, Canada, $\times 6$ (new); 4, allotubes, autotubes, and astrorhizae, tangential section; *Syringostromella labyrinthea* STEARN, 1990, GSC 95779, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada, $\times 8$ (new); 5, spacing phases; *Clathrodictyon ellesmerense* STEARN, 1983, SCRM 110-275, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new).



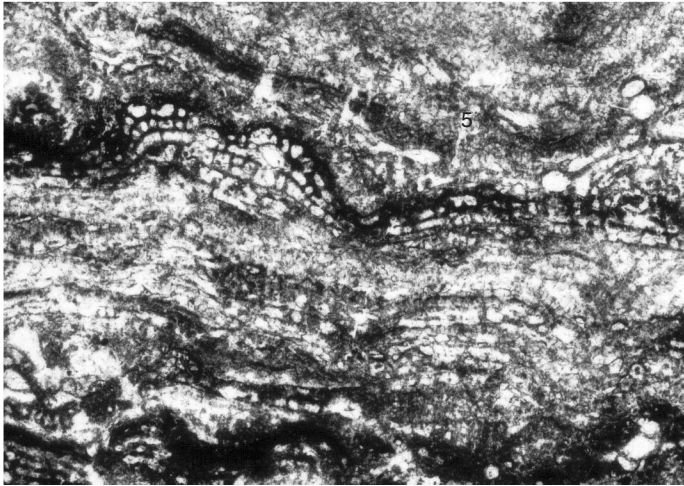
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FIG. 14. For explanation, see facing page.

GALLOWAY and ST. JEAN (1961) thought they had discovered a larval stage they called the protoconosteum in the form of a sphere surrounded by a few cysts, but considerable doubt has been thrown on this interpretation (KAPP & STEARN, 1975, p. 168). The so-called protoconosteas are found throughout the skeleton of labechiids, not just at the base, and are better accounted for as being caused by the reaction of the skeleton to foreign organism intrusion.

CONTEMPORARY PHASES

Contemporary phases replace each other tangentially and may have reflected the different functions of different parts of the skeleton.

The most common of these are mamelon phases in which structural elements thicken, laminae are inflected upward, and pillars diverge upward in mamelon columns (Fig. 6,5; Fig. 9,5). Other skeletal variations that took place parallel to the growth surface may be repair tissue secreted in local response to invading organisms, traumatic breakage by predators, or microenvironmental variations (such as sediment influx; Fig. 14,2).

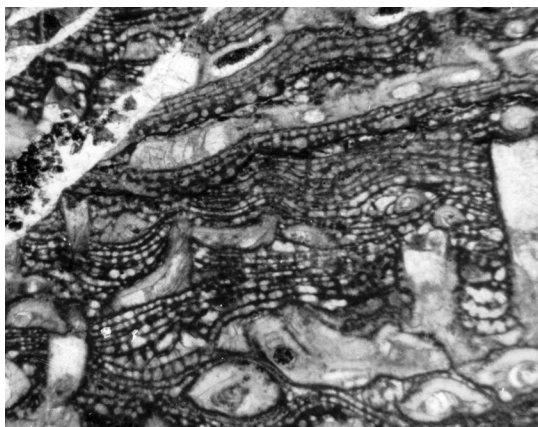
FOREIGN ORGANISMS IN STROMATOPOROID SKELETONS

Stromatoporoid skeletons may enclose tabulate corals, algae, rugose corals, and borings and tubes of unknown organisms. These associated organisms may have been competitors, commensals, parasites, or scavengers. SEGARS and LIDDELL (1988) and LEBOLD (2000) listed the organisms that grew as epibionts on Silurian stromatoporoids and could be incorporated as growth

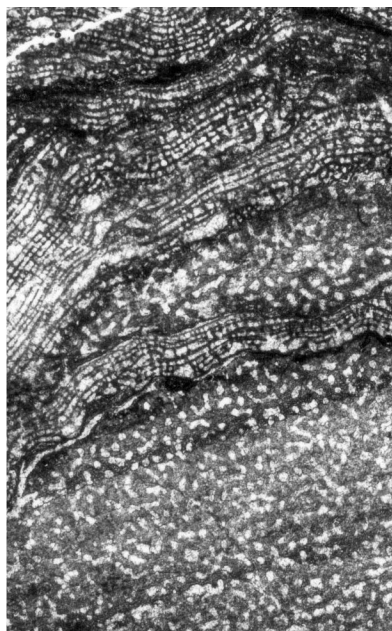
proceeded. Some may be difficult to distinguish from the different phases of a single stromatoporoid species, and some have been described as an integral part of the skeleton (Fig. 14,4). In enclosing foreign organisms, the stromatoporoids resemble many living sponges and in particular the hypercalcified sponges that are closely intergrown with serpulid worm tubes (HARTMAN & GOREAU, 1970).

The most common associated organisms are syringopoid tabulate corals whose tubes pervade some skeletons and whose growth apparently kept pace with the growth of the stromatoporoid (Fig. 15,1; Fig. 17,1). The tubes were thought to be integral parts of the skeleton in the 19th century, and specimens containing them were distinguished as the genera *Caunopora* PHILLIPS and *Diapora* BARGATZKY. Although these genera are now discredited, stromatoporoids grown through with syringopoids were long referred to as being in the caunopora-state. MISTIAEN (1984) has noted that the walls of syringopoids encased in stromatoporoids are missing a layer present in free-standing specimens and suggested that those growing in company with stromatoporoids did not need as much support. YOUNG and NOBLE (1989) and MAY (1999) have discussed the relationship of syringopoids to stromatoporoids. STEARN (1956) has described a similar relationship between a phaceloid amplexoid rugosan and a stromatoporoid. Certain species of stromatoporoid are more likely to be associated with syringopoids than others in the same collection. Whether these relationships were mutualistic, antagonistic, or tolerant is not clear from the fossil specimens, but that coral and sponge grew together is certain from their geometric relationships.

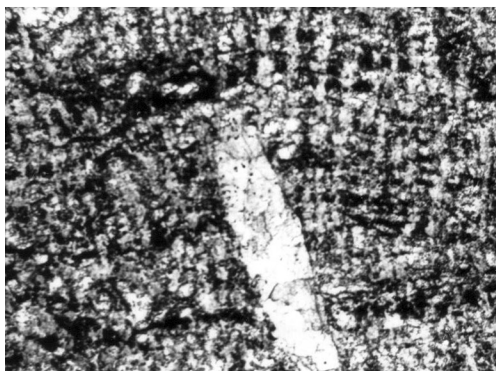
FIG. 14. 1, Successive phases with distinct pillars alternating with those in which the pillars are vague and indistinct; *Plectostroma salairicum* (YAVORSKY, 1930), SCRM 126-91, Emsian-Eifelian, unnamed formation, Truro Island, arctic Canada, $\times 10$ (new); 2, reaction of stromatoporoid to foreign intruder or trauma, longitudinal section; *Clathrodictyon ellesmerense* STEARN, 1983, GSC 108858, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new); 3, latilaminar growth and distinct basal phases at base of each latilamina; *?Syringostromella discoidea* (LONSDALE, 1839), SCRM 50-17, Wenlock Limestone, Shropshire, England, $\times 10$ (new); 4, interlayering of structures suggestive of algae and stromatoporoid alternating, longitudinal section; *Clathrocoilona vexata* PROSH & STEARN, 1996, GSC 108881, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new).



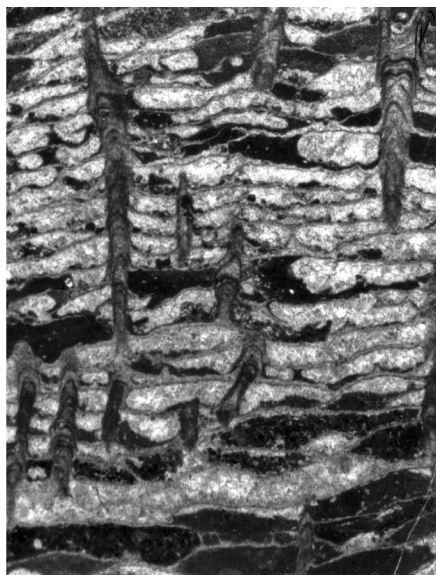
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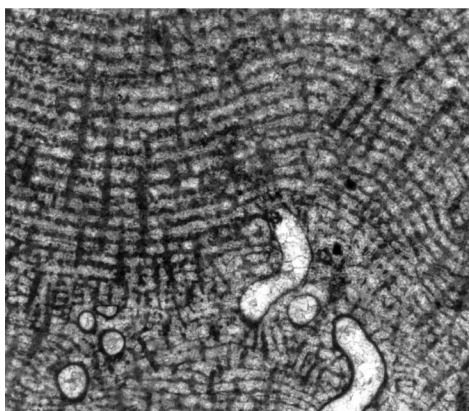
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FIG. 15. 1, Syringoporidae tubes intergrown with stromatoporoid (caunopore state), longitudinal section; *Gerronostroma septentrionalis* PROSH & STEARN, 1996, SCRM 130-20, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 7$ (new); 2, intergrowth of two competing stromatoporoids alternating in dominance, longitudinal section; *Stromatopora polaris* STEARN, 1983, below, *Gerronostroma septentrionalis* PROSH & STEARN, 1996, to left, SCRM 110-342, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new); 3, *Trypanites* sp., boring in poorly preserved *Hermatoporella* cf. *pycnostylota* (STEARNS, 1962), longitudinal section, (Continued on facing page.)

Laminar tabulate corals are common along growth interruption surfaces. *Heliolites*, in particular, commonly forms thin interlayers where stromatoporoid growth stopped and then resumed overgrowing the coral. *Alveolites* is also commonly intergrown with stromatoporoids, particularly in Devonian rocks. Among algae and *incertae sedis*, *Girvanella*, *Rothpletzella*, and *Wetheredella* are widely distributed associates along growth stoppage surfaces and can be confused with stromatoporoid structures (POWELL, 1991). The stromatolitic cyanobacterium *Cliefdenia* has been shown by WEBBY (1991) to have kept pace while growing within some Ordovician labechiids (Fig. 15,4).

The intergrowth of two or more stromatoporoid species to form a compound skeleton is common in some reefs. The contact between two species apparently competing for space may oscillate across the skeletal surface over considerable intervals of growth, as one and then the other alternately had the advantage (Fig. 15,2).

Destructive organisms that bored into the skeleton after or during growth may also modify it. Cylindrical cavities bored in the skeleton and filled with sediment have been referred to *Trypanites* (PEMBERTON, JONES, & EDGEcombe, 1988; TAPANILA & COPPER, 2002) (Fig. 15,3). TAPANILA, COPPER, and EDINGER (2004) measured the environmental and taxonomic controls on borings of *Trypanites* in corals and stromatoporoids. They showed that the abundance of borings was proportional to the density of the skeleton in aulaceratids, *Ecclimadictyon*, *Clathrodictyon*, and *Pachystroma*. NIELD (1984) has plotted the location of these vertical borings on stromatoporoid skeletons. TAPANILA and HOLMER (2006) have described stromatoporoids in which the lingulid brachiopod *Rowellella?* occupied *Trypanites* borings and

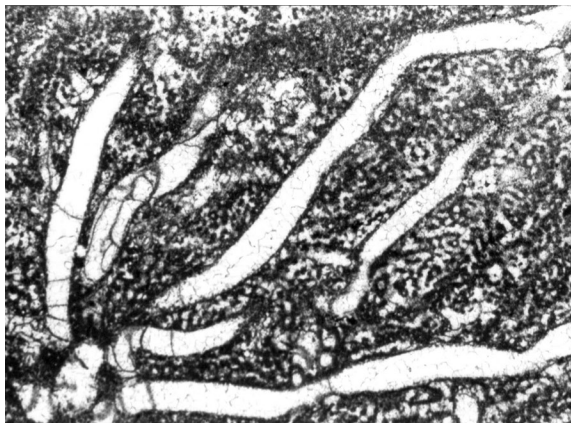
kept the cylindrical channel open as the stromatoporoid (*Clathrodictyon*) continued to grow around it. This trace fossil was named *Klematoica linguiformis*. Large cavities filled with sediment and spar with radiating, straight, tapering passages leading to the surface have been referred to *Topsentopsis* (Fig. 17,2). These resemble cavities formed at present by boring sponges, such as *Aka coralliphaga*, in scleractinian corals. TAPANILA (2006) synonymized *Topsentopsis* with the Mesozoic genus *Entobia* and described specimens from the Frasnian Guilmette Formation of Nevada. That no other borings of this form are preserved in fossils in the 100 million years separating these genera in time suggests that the identity of the two genera needs confirmation. RISK, PAGANI, and ELIAS (1987) have described microborings in a stromatoporoid skeleton as the product of endolithic algae. As the zones of these putative borings cross the spar filling of the galleries as well as the skeletal elements, their interpretation is in doubt. PLUSQUELLEC (1968), OEKENTORP (1969), and STEL (1976) have described helicoidal tubes in stromatoporoids, with or without walls and tabulae, under the generic names *Helicosalpinx* and *Torquaysalpinx* (Fig. 15,5). These tubes resemble the various worm-like borers in modern scleractinians such as sipunculans and polychaetes, but their affinity is in doubt.

BEUCK and others (2008) analyzed a large boring in *Densastroma pexisum* called *Osprioneides kampo* by computer tomography and were able to illustrate it in three dimensions.

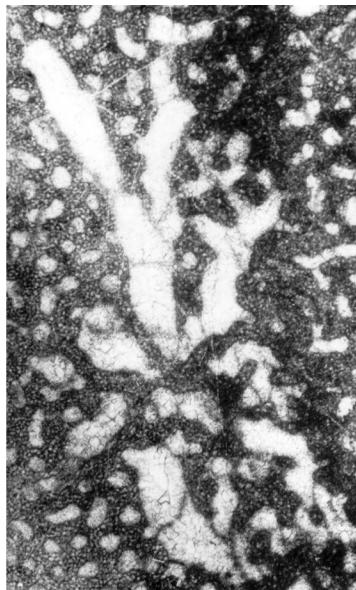
A continuing controversy has followed the suggestion that astrorhizae are not integral parts of the stromatoporoid skeleton but are instead foreign organisms. KAZMIERCZAK (1969) drew attention to specimens with

Fig. 15. Continued from facing page.

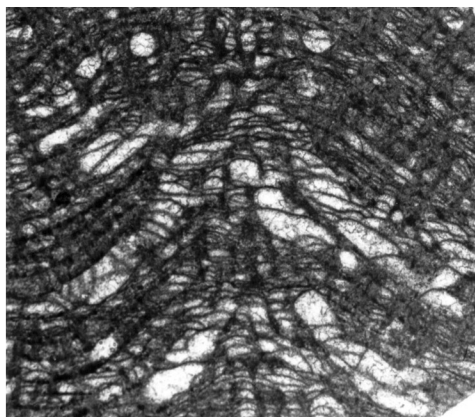
SCRM 67-272, Frasnian, Southesk Formation, Mount Haultain, western Alberta, Canada, $\times 10$ (new); 4, *Cliefdenia* WEBBY, 1982, cyanobacterium in labechiid stromatoporoid, *Labechiella variabilis* (YABE & SUGIYAMA, 1930), UTGD 96366; Upper Ordovician, Benjamin Limestone, Tasmania, Australia, $\times 7.5$ (new, courtesy of Barry Webby); 5, trochoidal boring with well-defined wall, longitudinal section, *Helicosalpinx* sp. in *Actinostroma expansum* (HALL & WHITFIELD, 1873), SCRM 67-273, Frasnian, Southesk Formation, Mount Haultain, western Alberta, Canada, $\times 8$ (new).



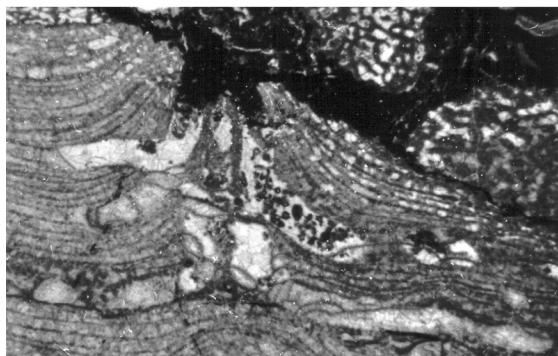
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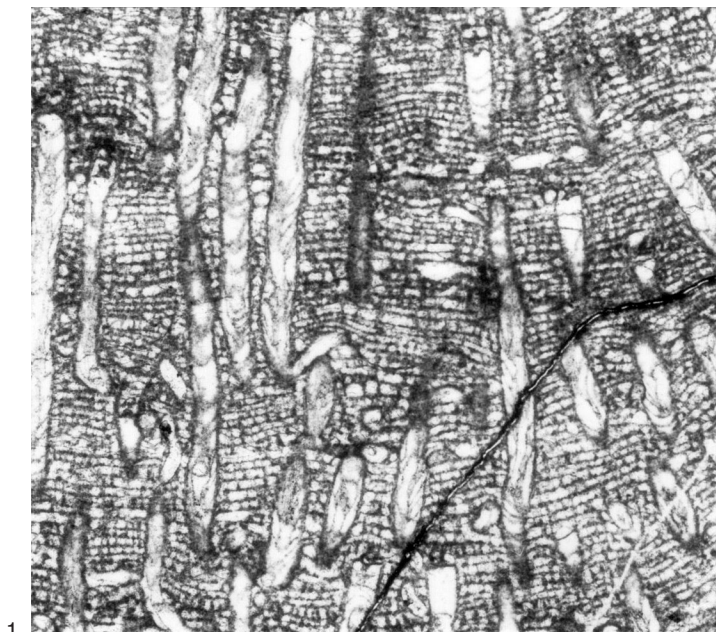


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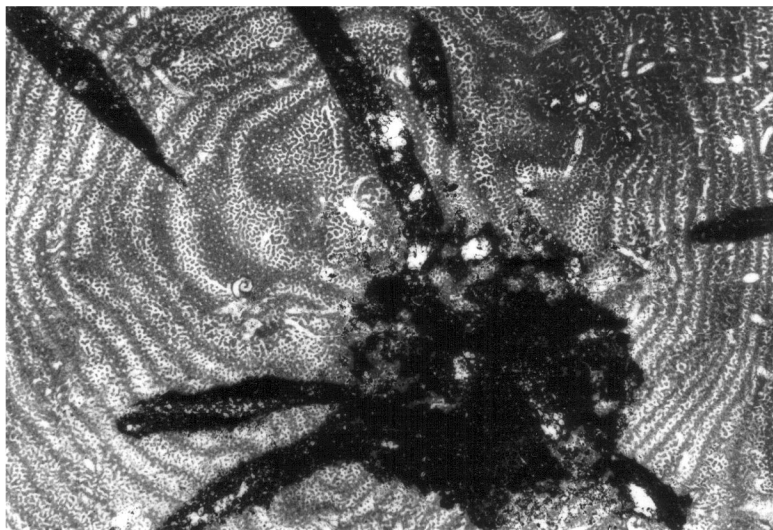


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FIG. 16. 1, Large stellate canal system in tangential section, probably a foreign organism; *Atelodictyon* sp., UWA 140816, Frasnian, Pillara Limestone, Canning Basin, Western Australia, $\times 10$ (new); 2, stellate canal system in tangential section, probably a foreign organism in *Salairella prima* KHRONYCH, 1971; note also smaller astrorrhizal canals and autotubes, GSC 108899, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 25$ (new); 3, canal system interpreted to be a foreign organism with prominent dissepiments, longitudinal section; *Trupetostroma* sp., UWA 140799, Frasnian, Pillara Limestone, Canning Basin, Western Australia, $\times 10$ (new); 4, canal system of a foreign organism opening at surface, showing sediment infiltration, longitudinal section; *Petridiostroma* sp., GSC 54909, SCR M 113-25, Emsian-Eifelian, Ogilvie Formation, Yukon Territory, Canada, $\times 10$ (new).



1



2

FIG. 17. 1, Stromatoporoid extensively intergrown with syringoporid (caunopora state), longitudinal section; *Geronostroma septentrionalis* PROSH & STEARN, 1996, GSC 108862, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, $\times 10$ (new); 2, large complex boring of *Topsentopsis* sp. in tangential section in *Petridiostroma* sp., SCRM 126-131, Emsian–Eifelian, Truro Island, arctic Canada, $\times 7$ (new).

two sizes of stellate canal systems and with different relationships of the canals to the galleries; some were confluent with them (integrated) and some separate (that is, bounded by walls). He proposed the hypothesis that both types were the products of the intervention of commensal or symbiotic foreign organisms and considered the possible plants and animals that could have occupied these tubes. JORDAN (1969), on the basis of stellate borings in the coral *Calceola*, suggested that the astrorrhizae of all stromatoporoids could be borings of a sponge, such as *Clionolithes* CLARKE. Many modern corals are bored by various species of the sponge genus *Cliona*. MORI (1970) rejected this interpretation and affirmed that the astrorrhizae were integral to the stromatoporoid skeleton. STEARN (1972, 1975) examined the idea further and reaffirmed that the integrated astrorrhizae were certainly part of the stromatoporoid animal and most likely its exhalant canals; but the separated type of KAZMIERCZAK could be traces of foreign organisms. By 1976, KAZMIERCZAK had ascribed the stromatoporoids to the cyanobacteria and suggested that the astrorrhizal canals were occupied by strands formed of “. . . linear cell masses of some . . . cyanophytes” (1976, p. 50). These ideas were rejected by RIDING and KERSHAW (1977) and LABARBERA and BOYAJIAN (1991). However, they were further elaborated by KAZMIERCZAK in 1980 and 1981 using evidence from other specimens and scanning electron micrographs. In 1990, KAZMIERCZAK and KEMPE compared the stromatolites of a crater lake in Indonesia with stromatoporoid skeletons. Although these cyanobacterial crusts do not show astrorrhizae, they speculated that “. . . such patterns could be easily produced by rhizoids or branched thalli of similar algae, overgrown by the calcifying cyanobacterial mat” (p. 1247). More recently, NGUYEN HUNG (2001) has revived the original idea that the astrorrhizae are foreign organisms without taking account of the negative views of the investigators cited above. He based his arguments on fan-shaped clusters of grooves

impressed on the epitheca of Carboniferous rugosan corals. Presumably the traces noted by NGUYEN HUNG (2001) are caused by an organism similar to that which excavated the grooves in JORDAN's (1969) specimens of *Calceola*. Neither of these occurrences show structures that closely resemble the integrated type of astrorrhizae, and none of the writers supporting the foreign organism hypothesis effectively confronts the evidence that astrorrhizae are exhalant canals of an encrusting sponge (also see *Treatise Online*, Part E, Revised, vol. 4, Chapter 9F, p. 22–23).

However, large walled tubes of the stellate form that do not empty into the galleries are common in some Early and Middle Devonian stromatoporoids and are apparently foreign organisms of commensal or parasitic nature (Fig. 16, 1–4). The following features characterize such tubes and distinguish them from astrorrhizae.

1. They are of larger diameter than most astrorrhizae.
 2. They are bounded by walls and not confluent with the galleries.
 3. They do not taper distally and may end bluntly or in a bulbous expansion.
 4. They are crossed by numerous flexuous dissepiments, many of which imbricate.
- These tubes require a taxonomic name to distinguish them from the astrorrhizae.

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