

# INTERNAL MORPHOLOGY OF THE PALEOZOIC STROMATOPOROIDEA

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## INTRODUCTION

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

The skeleton of Paleozoic stromatoporoidea 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 stromatoporoidea, 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 stromatoporoidea (see Fig. 352.3; Fig. 355; Fig. 356.2) is reconstructed from observations of living hypercalcified sponges and from observations of the preserved growth surfaces of fossil stromatoporoidea. Where the terminal growth surface of stromatoporoidea 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. 317.1, and see Fig. 352.1–352.2).

When stromatoporoidea 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 p. 553), 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

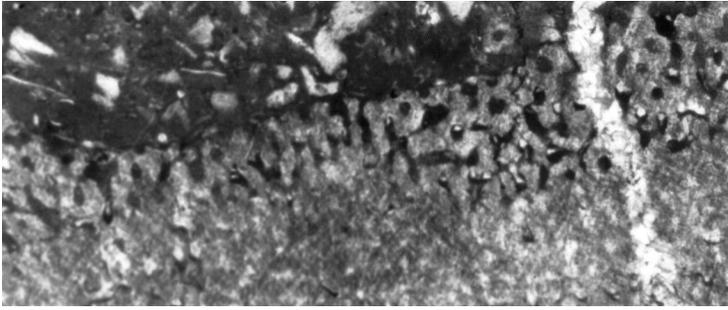
by pachysteale, pachystrome, and allotube, respectively (for definitions of these terms, see Glossary, p. 397–416).

The structural elements of the stromatoporoidea 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.

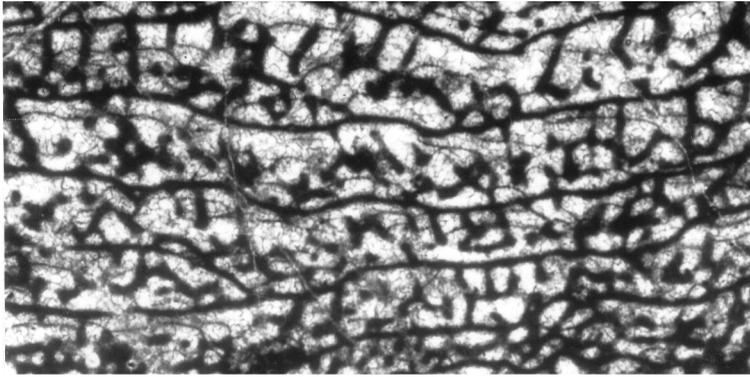
1. Domes and posts = cyst plates and pillars (Labechiida).
2. Floors and posts = laminae and pillars (Clathrodictyida, Stromatoporellida).
3. Posts and beams = pillars and colliculi (Actinostromatida).
4. Walls and floors = pachyestes and pachystromes in an amalgamate structure (Stromatoporida, Syringostromatida).

## SPACING OF STRUCTURAL ELEMENTS

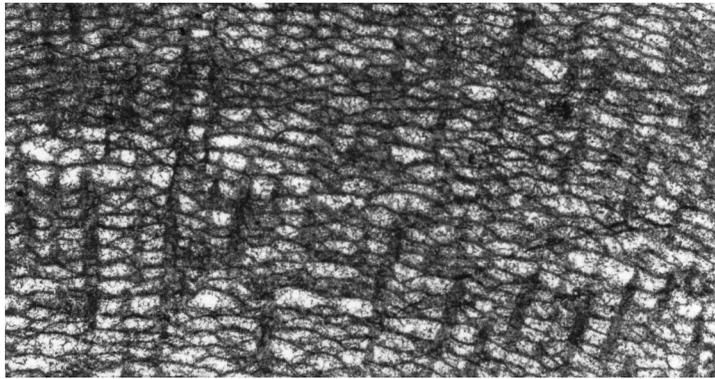
The spacing of elements has been used extensively as a specific character. For example, FLÜGEL (1959) used the spacing of pillars and laminae, plotted in what he called a species diagram, to distinguish between the many species of *Actinostroma*. Spacing is commonly expressed as the number of elements 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 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



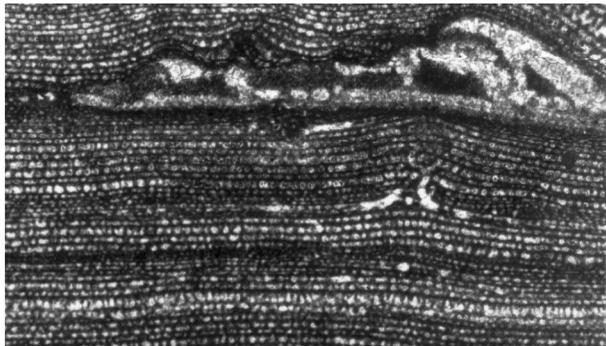
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FIG. 317. (For explanation, see facing page).

the specimen (see below). STEARN (1989a) 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, pachyστελεs, 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. 317.2) 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. 317.4), 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 Fig. 339.3) 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 megapillar spacing and diameter to assess the mode of the species 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 these 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 cyst-like microlaminae.

### CYSTS, CYST PLATES, AND DISSEPIMENTS

Cysts form important elements in the skeletons of stromatoporoids, archaeocyaths and other sponges, tabulates, scleractinians, rugosans, bryozoans, and rudist mollusks. In

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FIG. 317. 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 cyst plates 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, 1983a, SCRM 110-242, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a).

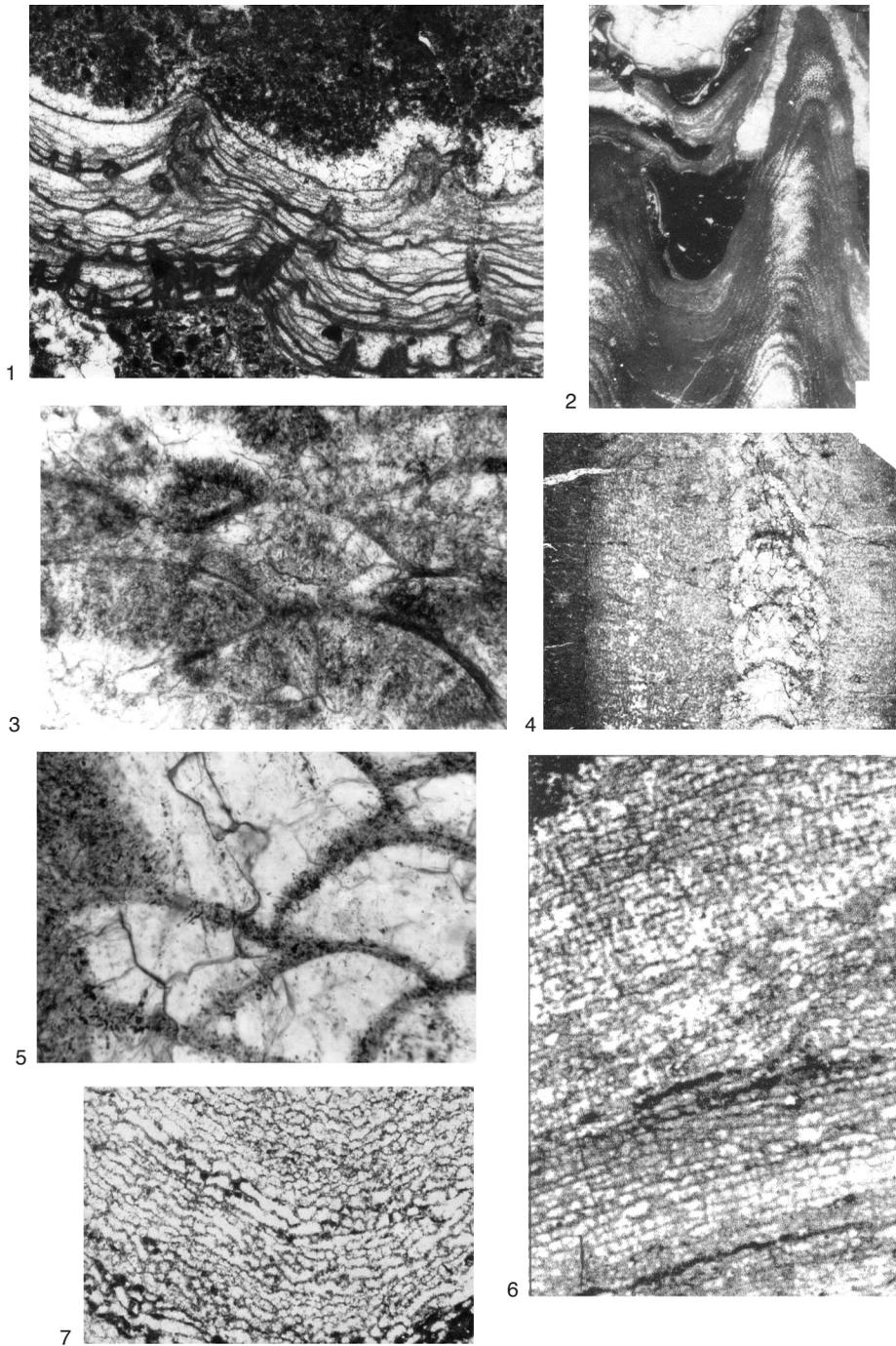


FIG. 318. 1, Longitudinal section through growth surface with mamelons; note denticles on cyst plates and spar-filled space above terminal cysts, possibly occupied at death by soft tissue; *Styloclycyon sinense* (DONG, 1964), SCRM 118-3, Famennian, Wabamun Formation, Normandville Field, northern Alberta, Canada,  $\times 10$  (Stearn, 2011a); 2, long, low cyst plates inflected into high mamelons in labechiids; *Pachystylostroma goodsellense* KAPP & STEARN, 1975, (Continued on facing page.)

nearly all of these organisms, the enclosing plate is convex upward, but its axis of symmetry may be inclined somewhat to the vertical (Fig. 317.3; Fig. 318.1; Fig. 318.3). 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. 318.3) that was described by GALLOWAY (1957) as part of the cyst plate. STEARN (1989b) suggested these zones were remnants of syntaxial aragonite rim cements. The absence of these zones on the cysts of post-Ordovician stromatoporoids (Fig. 318.5) suggests that the younger cyst plates were composed of calcite, probably of the high-magnesium variety.

### CURVATURE

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

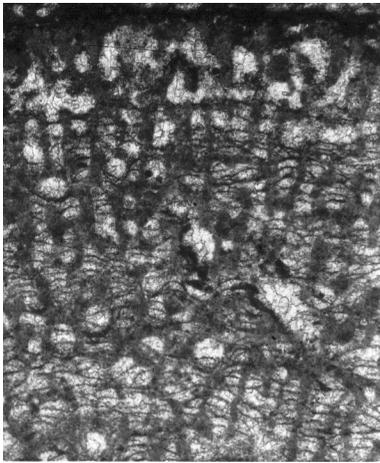
stromatoporoids take a variety of forms; the major types are as follows.

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. 318.2). 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. 318.6).
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. 318.4). The peripheral zone is occupied by small, imbricated cysts whose axes are inclined outward from the axis of the horseshoe cysts.

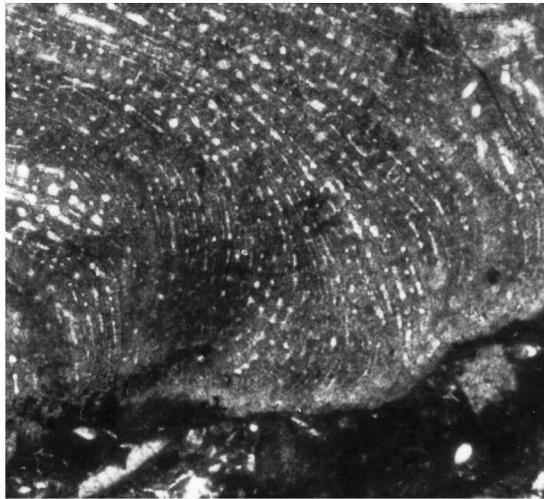
The wavy nature of the laminae of *Clathrodictionary* has suggested that the clathrodictionaryids evolved from labechiids by the joining of the cyst plates in horizontal rows. There is little direct evidence of this in transitional forms, however, and the first clathrodictionaryids to appear in Late Ordovician time include both forms with laminae that look like conjoined cyst plates

FIG. 318. Continued from facing page.

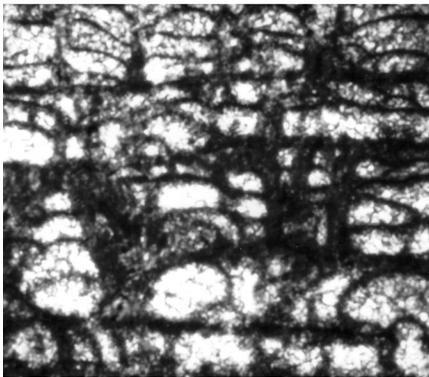
RM 14,004a, Middle Ordovician, Crown Point Limestone, Vermont, United States,  $\times 1.4$  (Kapp & Stearn, 1975); 3, cyst plates bordered with a zone of specks suggestive of fans of syntaxial aragonite crystals; *Aulacera nodulosa* BILLINGS, 1857, Nicholson 287, NHM P6001, Upper Ordovician, Vaureal Formation, Anticosti Island, Quebec, Canada,  $\times 50$  (Stearn, 2011a); 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,  $\times 55$  (Stearn, 2011a); 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 clathrodictionaryid; *Clathrodictionary* sp. cf. *microundulatum* NESTOR, 1964a, AM.FT 15211, Upper Ordovician, Ballingool Limestone, Bowan Park Group, New South Wales, Australia,  $\times 6.5$  (Webby, 1969).



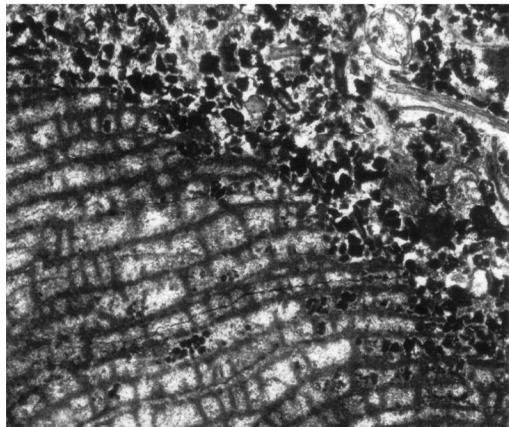
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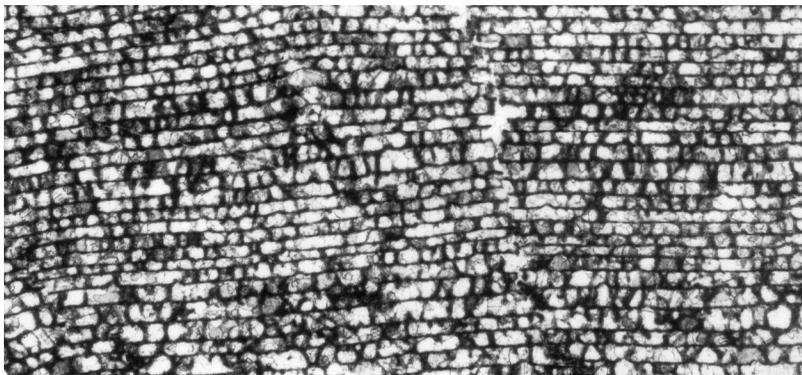
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FIG. 319. (For explanation, see facing page).

(*Clathrodictyon microundulatum*, Fig. 318.7), but also species of *Camptodictyon* NESTOR, COPPER, & STOCK, 2010, whose laminae are chevronlike, making cassiculate structures (*C. amzassense*, see Fig. 323.1).

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. 319.3; *Salairella*, Fig. 319.1). 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 stromatoporoid 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. 319.5). Very thin (approximately 20  $\mu\text{m}$ ) 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

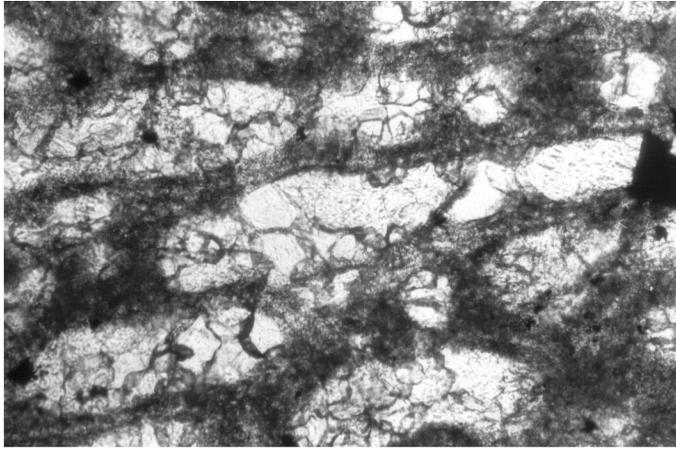
Few laminae continue across the whole skeleton; most merge laterally with others. At the lateral edges of skeletons, laminae may close off the gallery below by downward bending and merging with the underlying lamina, but in some fossils, they end abruptly, leaving the galleries open to the penetration of sediment (Fig. 319.2; Fig. 319.4). 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. 320.3).

## COMPACT AND TRIPARTITE LAMINAE

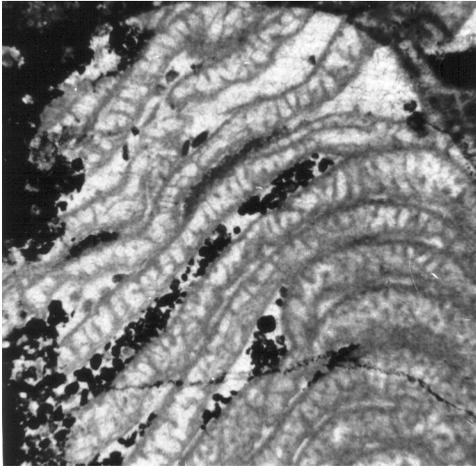
Laminae of the clathrodictyids are composed of a single layer of compact

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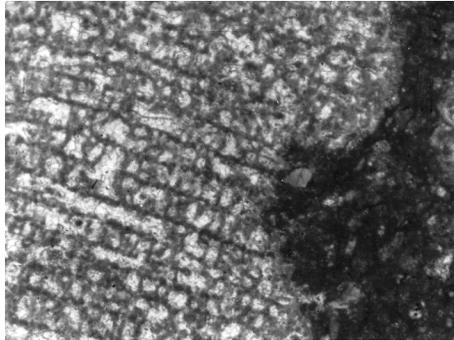
FIG. 319. 1, Abundant dissepiments occupying allotubes between pachystyles; *Salairella bullulosa* (STEARNS, 1966), GSC 18695, Frasnian, Mikkwa Formation, northern Alberta, Canada,  $\times 10$  (Stearn, 2011a); 2, lateral growth edge of stromatoporoid in which laminae seem to seal off galleries as they 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,  $\times 10$  (Stearn, 2011a); 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,  $\times 28$  (Stearn, 2011a); 4, lateral edge of stromatoporoid 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,  $\times 10$  (Stearn, 2011a); 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,  $\times 10$  (Stearn, 2011a).



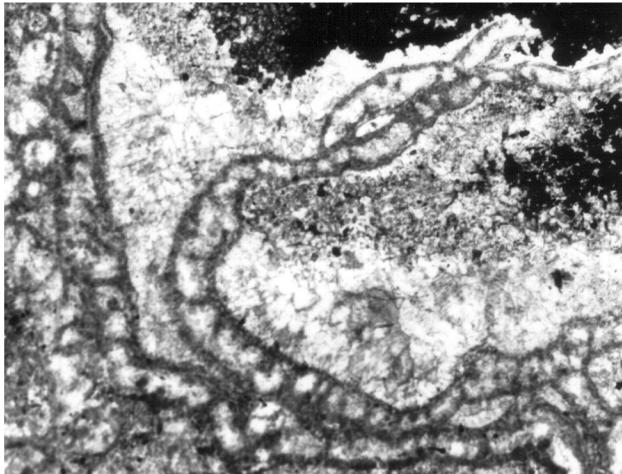
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FIG. 320. (For explanation, see facing page).

material. In some states of preservation, this may appear to be transversely fibrous or penetrated by fine transverse pores. This condition is common in specimens from the Ohio Valley Middle Devonian (GALLOWAY & ST. JEAN, 1957) but appears to be a result of diagenesis (see p. 524).

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. 320.1). 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.

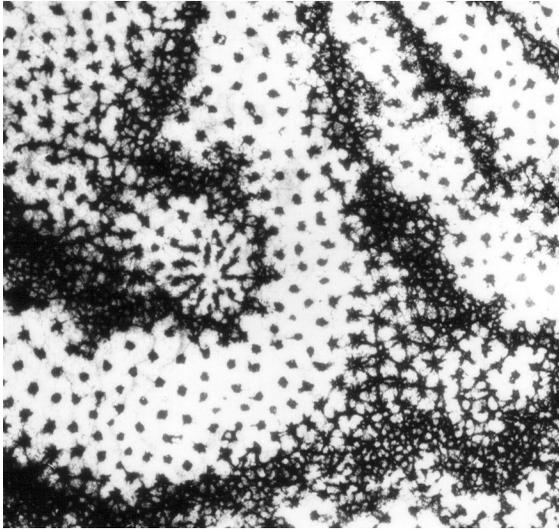
In some species with laminae consisting of upper and lower compact layers separated by a clear middle zone, sediment and epibionts penetrated this zone (Fig. 320.2). This phenomenon is best illustrated by species of *Simplexodictyon* in which, near the edge of the skeleton, the lateral layers of the 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 *Tienodictyon* grow out into a cavity that is now spar filled (Fig. 320.4, and see also Fig. 354.1–354.2). Epibionts in this clear zone suggest that it was a growth interruption surface, and on this basis KAŹMIERCZAK (1971) has interpreted all axial zones, whether light or dark, and all microlaminae as growth interruption surfaces.

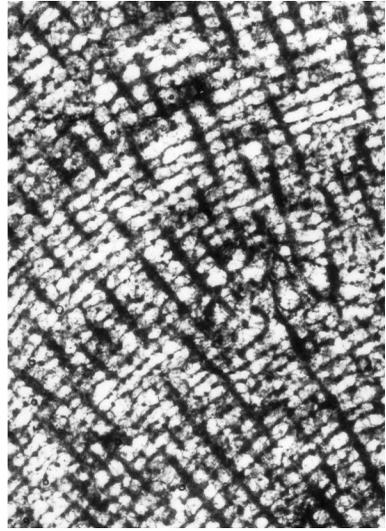
### COLLICULATE LAMINAE

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. 321.1). 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. 321.2 and see Fig. 329.2). The degree to which the colliculi are aligned tangentially, forming discrete laminae, is a morphologic character distinguishing such genera of the actinostromatids

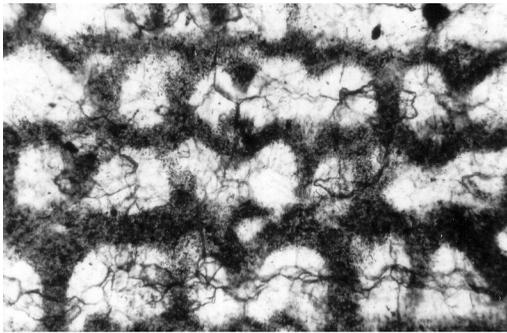
FIG. 320. 1, Tripartite laminae showing ordinicellular microstructure; *Stromatoporella granulata* NICHOLSON, 1873, Nicholson 329c, NHM P6021, Middle Devonian, Hamilton Formation, southwestern Ontario, Canada,  $\times 50$  (Stearn, 2011a); 2, laminae pairs separating into modules infiltrated with grains of sediment; *Simplexodictyon vermiforme* (STEARNS & MEHROTRA, 1970), SCRM 130-47, GSC 116, 284, Emsian–Eifelian, Ogilvie Formation, Yukon, Territory, Canada,  $\times 8$  (Stearn, 2011a); 3, lateral edge of stromatoporoid (growth condition or breakage?); *Aelodictyon stelliferum* STEARN, 1961, GSC 18684, Frasnian, Mikkwa Formation, northern Alberta, Canada,  $\times 8$  (Stearn, 2011a); 4, modules of laminae separating into spar-filled cavity; *Simplexodictyon* sp., AM.FT 15019, upper Silurian, Catombal Park Formation, New South Wales, Australia,  $\times 10$  (Stearn, 2011a).



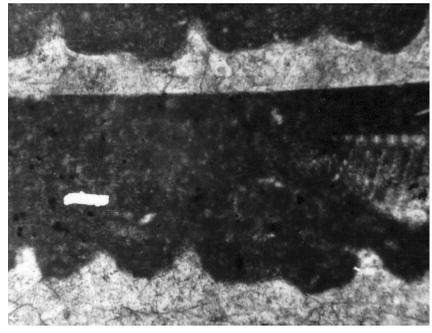
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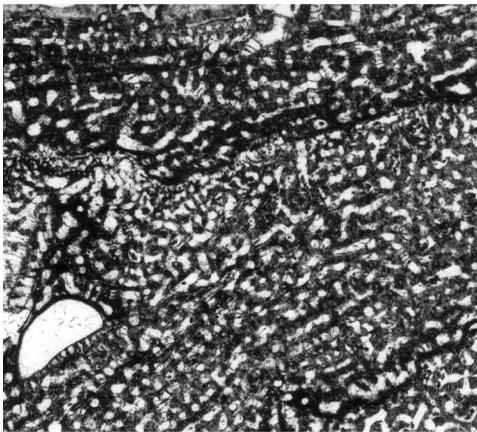
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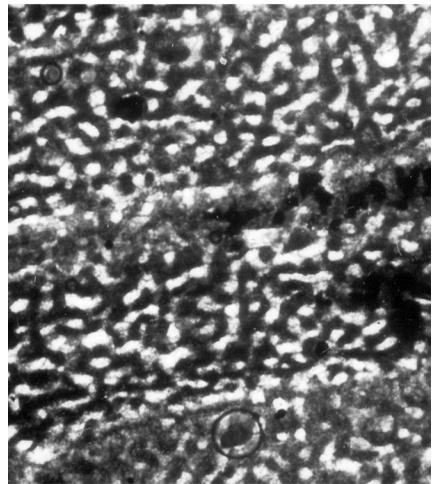
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FIG. 321. *For explanation, see facing page.*

as *Actinostroma*, *Plectostroma*, and *Bicolumnostratum*.

The network of pillars and colliculi exists on two scales in the 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 p. 524 and p. 542).

### 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. 321.3).

### 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, 1966a; see Fig. 419, 1a; Fig. 460a).

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, p. 172, pl. 3,2–3).

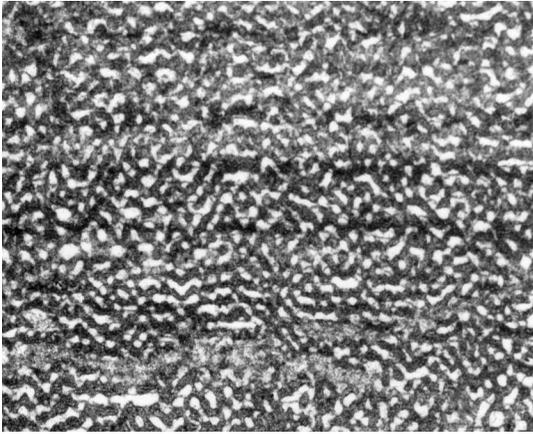
### PACHYSTROMES

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 (1886a, 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. 321.5–321.6). 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.

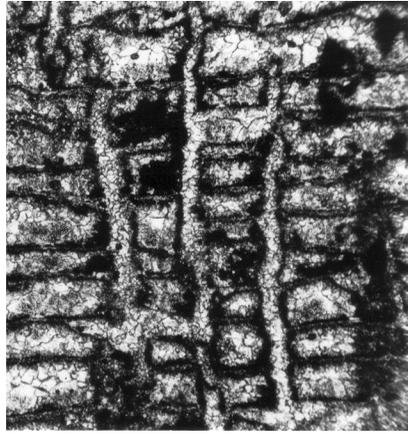
Typically, pachystromes are not extensive tangentially but join pachysteles in short segments. In a few genera of the Stromatoporida, such as *Lineastroma*, they are as extensive laterally as the laminae of

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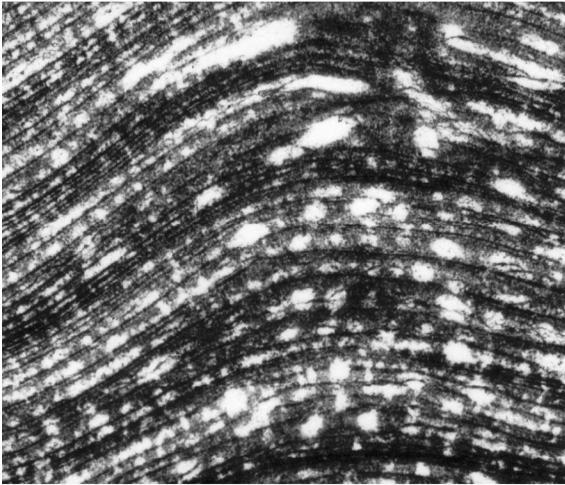
FIG. 321. 1, Colliculate laminae in tangential section; note stellate colliculi attached to pillars, uniting to form a hexactinellid network; *Actinostroma* cf. *clathratum* NICHOLSON, 1886a, GSC 48447, Givetian, Evie Lake reef, northeastern British Columbia, Canada,  $\times 10$  (Stearn, 2011a); 2, 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, 1886a, SCRM 67-274, Frasnian, Southesk Formation, Mount Haultain, western Alberta,  $\times 10$  (Stearn, 2011a); 3, Single-layer laminae inflected downward into tops of pillars; *Clathrodactyon striatellum* (D'ORBIGNY, 1849), Nicholson 243b, NHM P5664, Wenlock Limestone, Dudley, Shropshire, England,  $\times 50$  (Stearn, 2011a); 4, denticles on top surface of cyst plate; *Rosenella macrocystis* NICHOLSON, 1886a, Nicholson 280, NHM P5490, Wenlock, Gotland, Sweden,  $\times 50$  (Stearn, 2011a); 5, amalgamate structure dominated by pachystromes; note disturbance of growth caused by included organism on left; *Stromatopora cygnea* STEARN, 1963, GSC 18710, Frasnian, Mikikwa Formation, northern Alberta, Canada,  $\times 5$  (Stearn, 2011a); 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,  $\times 10$  (Stearn, 2011a).



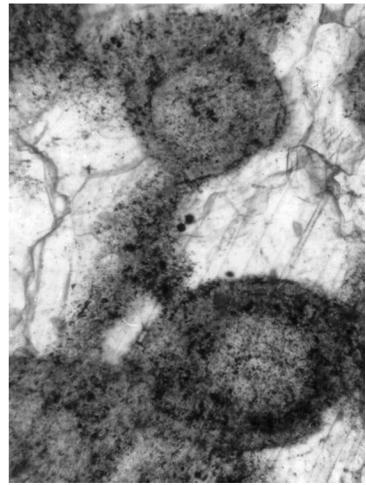
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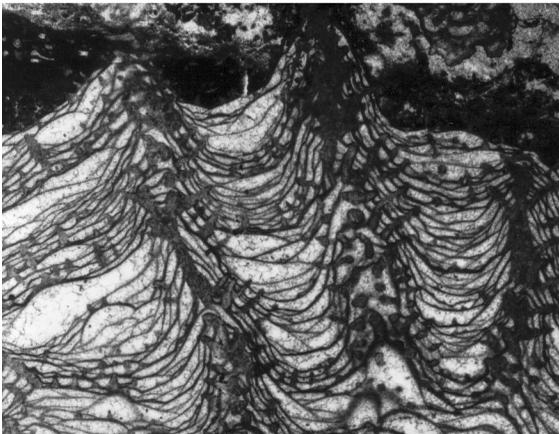
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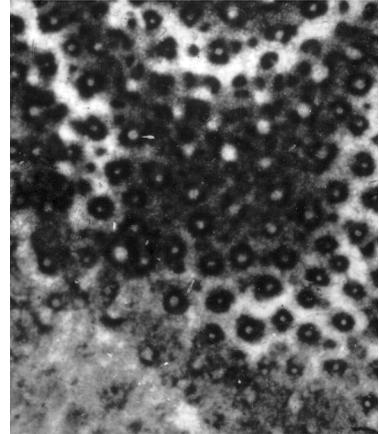
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FIG. 322. For explanation, see facing page.

the *Stromatoporellida*. In certain genera such as *Habrostroma*, thick pachystromes are associated with microlaminae on their upper surface (Fig. 322.3). In genera of 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. 322.1). 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. 322.1), *Ferestromatopora*, and *Arctostroma* (see Fig. 341.1).

### 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. 321.4; Fig. 322.5). 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 *Campodictyon*, another type of incipient pillar structure is formed. In *C. amzassense* (KHALFINA), the downwardly deflected edges of chevron-shaped laminae join to produce a vertical structure much like the pillars of younger stromatoporoids (Fig. 323.1).

### PILLARS

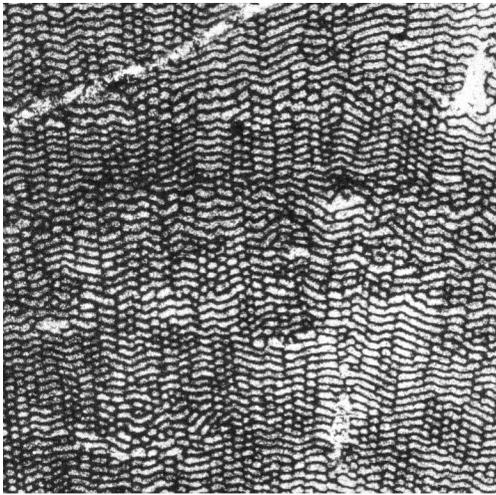
Pillars are post-shaped, longitudinal structural elements that extend between cyst plates, laminae (Fig. 319.5), or pachystromes, or constitute continuous structures around which the horizontal structures are formed (Fig. 321.2). In structures where the pillars are of two sizes (e.g., *Bifariostroma*), the larger are referred to as megapillars.

### LABECHIIDA

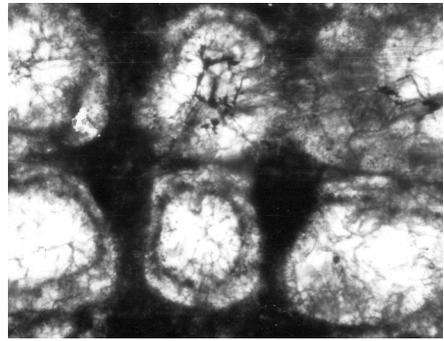
The tops of the pillars of labechiids, such as *Labechia*, *Pseudostylodictyon*, and *Stylostroma*, emerge on the growth surface as small pimples projecting into the covering sediment and are called papillae (see Fig. 326.1; and also see Fig. 316.1). Where microstructure is preserved, these pillars show growth lines of downward-opening cones (see Fig. 392*a,e*; Fig. 393*c,d*) in longitudinal section. In tangential sections (Fig. 322.4; see Fig. 392*b*), such pillars show concentric growth lines and a clear axis that NICHOLSON (1886*a*) 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 p. 533–538), they have been modified and

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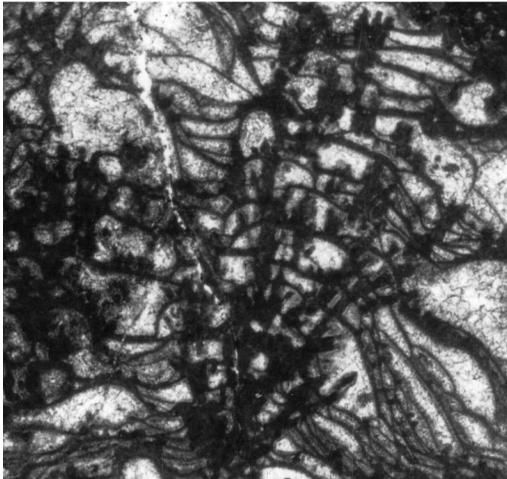
FIG. 322. 1, Cassiculate structure of oblique pachystromes; *Stromatopora* sp. cf. *polaris* (STEARNS, 1983*a*), SCRM 125-1, Emsian, Ogilvie Formation, Yukon Territory, Canada,  $\times 12$  (Stearn, 2011*a*); 2, pillars with centers removed in diagenesis; longitudinal section; *Stromatocerium rugosum* HALL, 1847, holotype, AMNH 590/x, Upper Ordovician, Black River Limestone, New York, United States,  $\times 20$  (Stearn, 2011*a*); 3, microlaminae within diffuse tissue of pachystromes; note also astrorhizal canals concentrated in upward inflection of pachystromes; *Habrostroma proximatum* (FAGERSTROM, 1961), holotype, UMMP 36177, Lower Devonian, Formosa Reef Limestone, southwestern Ontario, Canada,  $\times 10$  (Stearn, 2011*a*); 4, pillars in tangential section with zones of concentric growth; *Labechia conferta* (LONSDALE, 1839), Nicholson 264, NHM P5984, Wenlock Limestone, Dudley, Shropshire, England,  $\times 55$  (Stearn, 2011*a*); 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 and contemporary phases; *Stylostroma sinense* (DONG, 1964), RM 20.4916*a*, Famennian, Wabamun Formation, Nomandville field, northern Alberta, Canada,  $\times 5$  (Stearn, 2011*a*); 6, ring pillars in tangential section; *Stromatoporella granulata distans* PARKS, 1936, ROM 2246, Middle Devonian, Hamilton Formation, southwestern Ontario, Canada,  $\times 10$  (Stearn, 2011*a*).



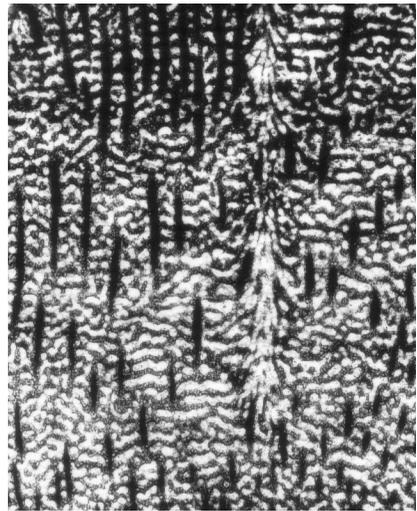
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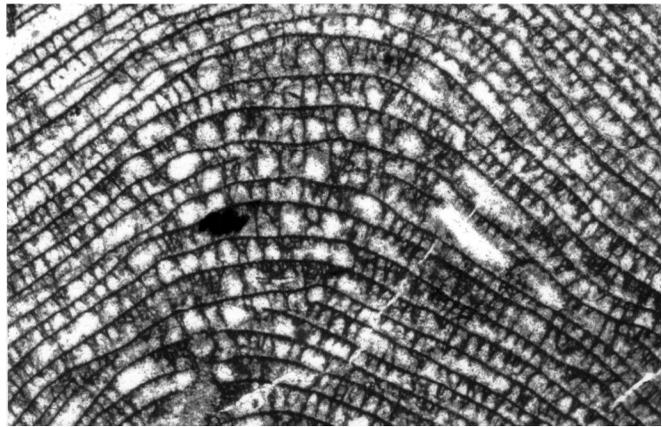
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FIG. 323. (For explanation, see facing page).

dissolved in diagenesis (Fig. 322.2), resulting in some taxonomic problems. For instance, opinion differs on the validity of the genus *Forolinia* NESTOR in which a structure of cyst plates 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. 323.3), but in most other stromatoporoidea, 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* (Fig. 395*b*) and several genera from Famennian rocks such as *Platiferostroma* (Fig. 398,1*b*) and *Vietnamostroma* (Fig. 400,2*b*).

#### ACTINOSTROMATIDA

Actinostromatid pillars give off colliculi that, forming a network, define laminae (Fig. 321.1–321.2). 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 section on Microstructure, p. 524).

#### CLATHRODICTYIDA

The pillars are compact in microstructure and confined to an interlaminae space.

In *Clathrodictyon*, laminae are inflected downward 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. 323.5) or branch complexly and spread out on the under surface of the overlying lamina (*Anostylostroma*, *Pseudodactinodictyon*). 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 interlaminae space directly but are tangled into complex structures in the interlaminae space (Fig. 317.2). Superposition of pillars from one gallery to the next is uncommon in the order but occurs in the family Gerrostromatidae (e.g., *Gerronostromaria*, p. 761, Fig. 420,1*a*).

#### STROMATOPORELLIDA

Like the laminae, the pillars of this order tend to have cellules or vacuoles. Pillars are confined to interlaminae 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.

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FIG. 323. 1, Incipient pillars formed by deflection of chevron laminae; longitudinal section; *Camptodictyon amzasense* (KHALFINA, 1960c), 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,  $\times 55$  (Stearn, 2011a); 3, pillars branching upward in labechiid, longitudinal section, *Stylodictyon sinense* (DONG, 1964), RM 20.4918a, Famennian, Wabamun Formation, Normandville field, northern Alberta, Canada,  $\times 10$  (Stearn, 2011a); 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,  $\times 5$  (Stearn, 2011a); 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,  $\times 10$  (Stearn, 2011a).

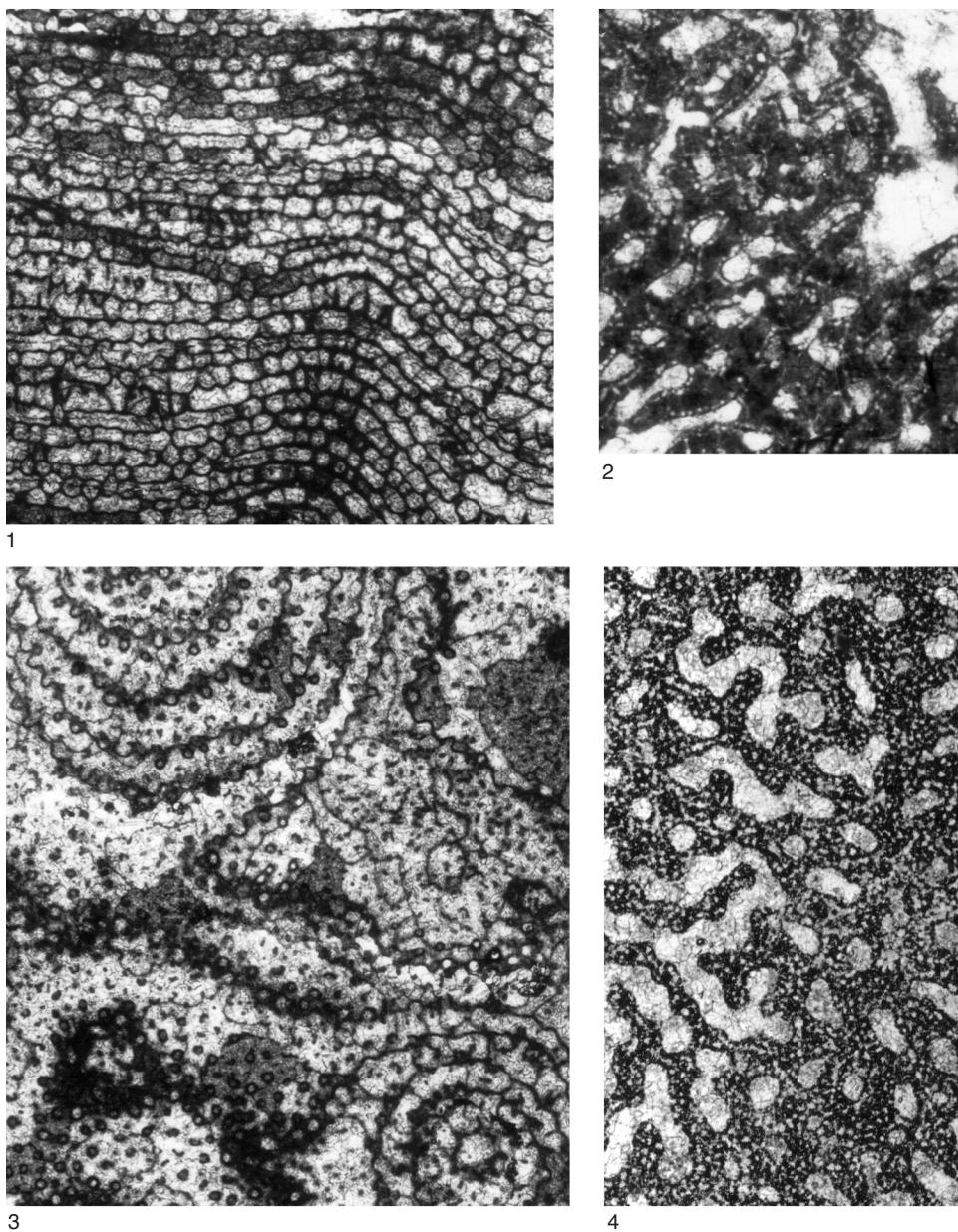


FIG. 324. 1, Ring pillars in longitudinal section; *Stromatoporella perannulata* GALLOWAY & ST. JEAN, 1957, GSC 108175, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a); 2, peripheral vacuoles on margins of pachyestes, tangential section; *Hermatoporella maillieuxi* (LECOMPTE, 1952 in 1951–1952), holotype, IRScNB-5760, Frasnian, Senzeille, Belgium,  $\times 18$  (Stearn, 2011a); 3, ring pillars in tangential section; *Stromatoporella perannulata* GALLOWAY & ST. JEAN, 1957, same specimen as 1,  $\times 10$  (Stearn, 2011a); 4, pachyestes with coarse cellular microstructure separated by allotubes; *Pseudotruperetostroma vitreum* (GALLOWAY, 1960), GSC 48453A, Givetian, Evie Lake reef, northeastern British Columbia, Canada,  $\times 25$  (Stearn, 2011a).

Where cut tangentially, such cones form rings known as ring pillars (Fig. 322.6; Fig. 324.1; Fig. 324.3). In *Trupetostroma*, the pillars are 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. 323.2; Fig. 324.2; and see Fig. 445–446). 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. 323.4).

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. 324.4; Fig. 325.3). Where the spaces enclosed are regular in shape,

the tangential section may resemble that of a favositid 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.

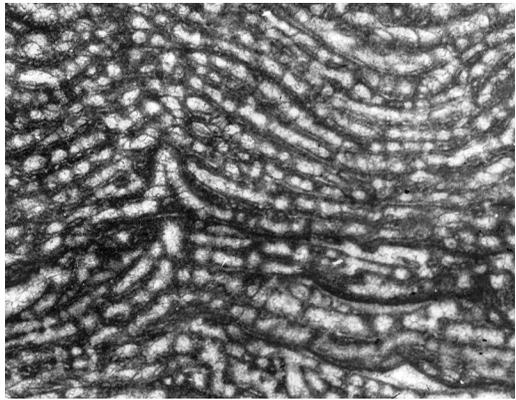
#### MAMELONS, COLUMNS, AND SUBCOLUMNS

Mamelons are round or irregular elevations on the terminal growth surface of stromatoporoids (Fig. 318.1,2; Fig. 322.5; Fig. 326.1; Fig. 326.3). 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. 325.4–325.5).

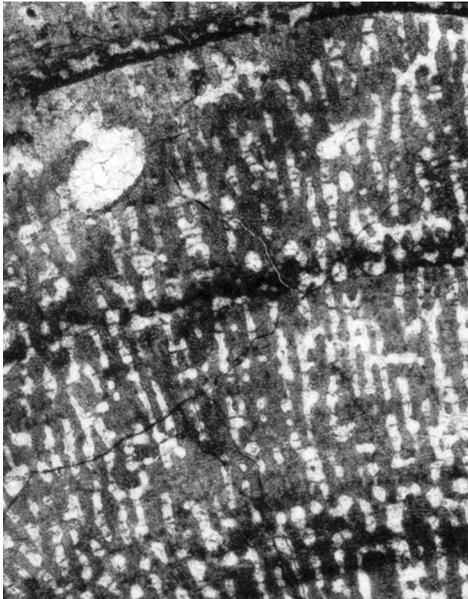
The position of mamelons commonly changed as the skeleton grew, so that in longitudinal section, the upward inflections and thickenings of the structural elements beneath them are scattered in the skeleton (Fig. 325.2). In genera in which mamelons are superposed (that is, that kept the same position as the skeleton grew), the upward inflection of the laminae below the surficial mamelons and the thickening of the



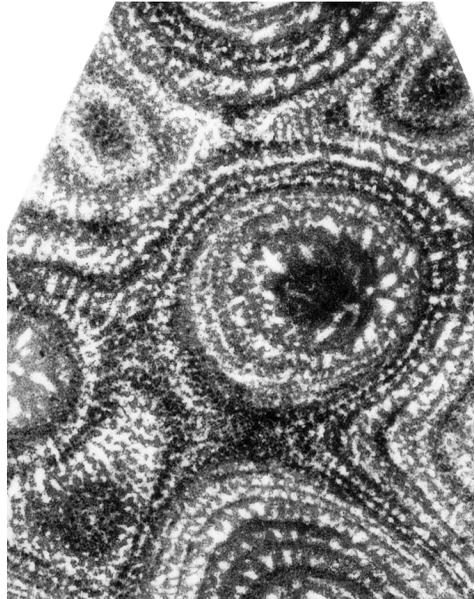
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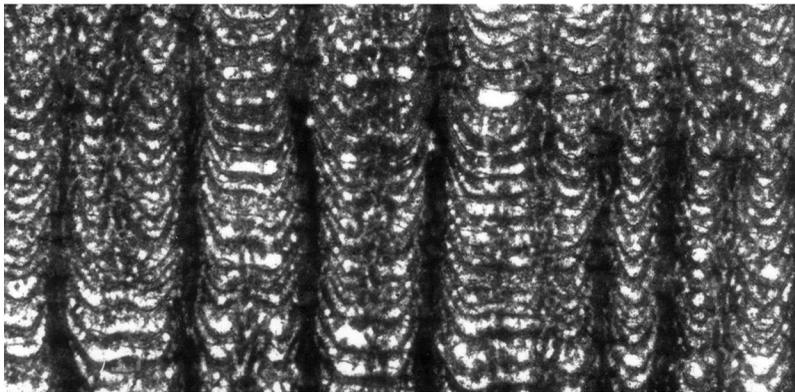
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FIG. 325. (For explanation, see facing page).

structural elements form a longitudinal element called a column, of denser skeletal material an order of magnitude bigger than a pillar (Fig. 322.5; Fig. 325.4–325.5; Fig. 327.1a–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. 325.4).

Columns commonly enclose astrorhizal canals, because astrorhizae may have been localized on the surficial mamelons. NICHOLSON (1891a) 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. 325.1).

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 acosmoreticulate or clinoreticulate pattern in some syringostromatid genera (see Glossary, p. 414).

### 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. 326.1; Fig. 326.3). 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 Fig. 356.1), ridges (*Goreau-iella*), or internal pathways (*Astrosclera*, see Fig. 357), 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 p. 570–573). 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. 327.2–327.3; PROSH & STEARN, 1996, p. 14).

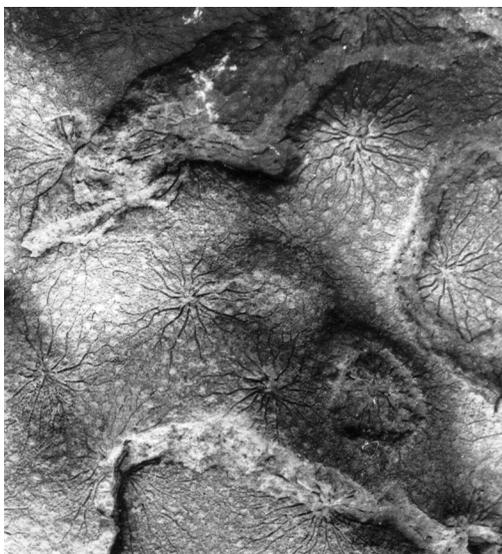
The diameter of the paths and canals is about 2 mm in Silurian species and averages slightly larger in Devonian species.

Astrorhizal systems are not evident in the skeletons of all stromatoporoid species, and STEARN (1982a) 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.

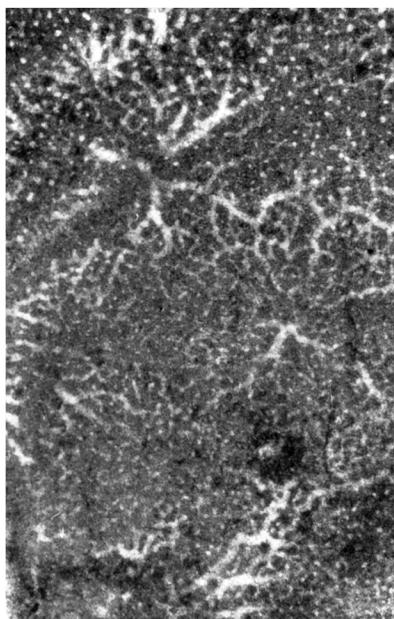
Astrorhizae are not common nor conspicuous in most labechiids but have been

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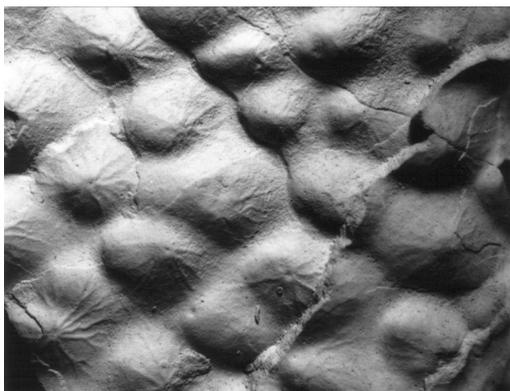
FIG. 325. 1, Isolated mamelon within a regular structure showing central astrorhizal canal; *Schistodictyon* sp., UWA 140802, Frasnian, Pillara Limestone, Canning Basin, Western Australia,  $\times 5.5$  (Stearn, 2011a); 2, mamelons isolated in regular structure, longitudinal section; *Sictostroma maclareni* STEARN, 1966, holotype, GSC 18674a, Frasnian, Kakisa Formation, northern Alberta, Canada,  $\times 10$  (Stearn, 2011a); 3, structure dominated with pachysteles separated by dissepiments; note also latilaminar growth and round boring of foreign organism; *Salairella prima* KHROMYKH, 1971, GSC 108899, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a); 4, mamelon columns in tangential section with astrorhizal canals; *Habrostroma proxilaminatum* (FAGERSTROM, 1961), holotype, UMMP 36177, Lower Devonian, Formosa Reef Limestone, southwestern Ontario, Canada,  $\times 5$  (Stearn, 2011a); 5, mamelon columns in which laminae are deflected upward and structural elements thickened reflecting contemporary phases, longitudinal section; *Syringostroma sherzeri* GRABAU in GRABAU & SHERZER, 1910, SCRM 22-7, Lower Devonian, Detroit River Limestone, southwestern Ontario, Canada,  $\times 10$  (Stearn, 2011a).



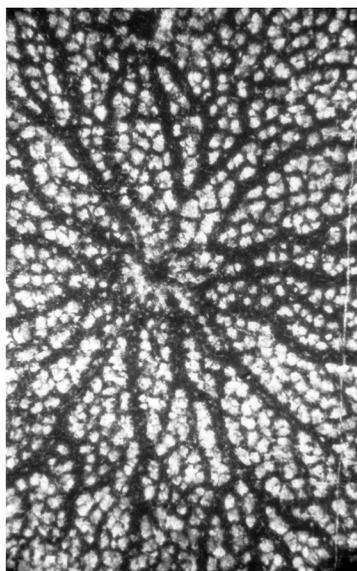
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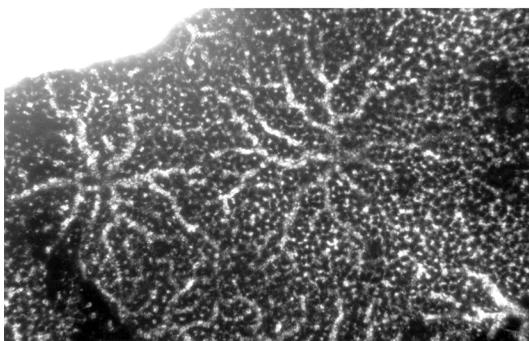
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FIG. 326. 1, Growth surfaces of three successive latilaminae in exfoliating, unidentified stromatoporoid (probably *Syringostroma* sp.), Devonian, Michigan; note astrorhizal grooves, some on mamelons and others between them, and emergence of columns as papillae on surfaces; RM 14,777, Middle Devonian, ?Alpena Limestone, Michigan, United States,  $\times 2.5$  (Stearn, 2011a); 2, branching astrorhizal canals in tangential section leading into galleries in dense skeleton of (Continued on facing page.)

detected in some of the earliest forms (KAPP & STEARN, 1975), and tangential sections of mid-Silurian genus *Cystocerium* NESTOR, 1976, show prominent stellate patterns (see Fig. 399*b-c*). They are well developed in densastromatids but generally inconspicuous in the open structure of actinostromatids such as *Actinostroma* (Fig. 327.2). 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 ASTRORHIZAE

Few stromatoporoids 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. 326.1); 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 stromatoporoids 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. 326.3).

### ASTRORHIZAL CANALS WITHIN THE SKELETON

Complete stellate astrorhizal systems are rarely shown in tangential section (Fig. 326.5), 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 stromatoporoids, these passages appear to open freely into the gallery space along their length (Fig. 326.2; Fig. 326.4; Fig. 328.1). In the sense that the astrorhizae drained all the choanocyte chambers within the soft tissue between the structural elements (see Fig. 356.2), the gallery space in the skeleton could be considered part of the astrorhizal system. In stromatoporoids 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 stromatoporoids with closely spaced elements (such as the densastromatids) are conspicuous.

FIG. 326. Continued from facing page.

*Gerronostromaria franklinensis* (STEARNS, 1990), SCRM 112-113, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada,  $\times 15$  (Stearn, 2011a); 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,  $\times 2$  (Stearn, 2011a); 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,  $\times 10$  (Stearn, 2011a); 5, extensive astrorhizal system with canals outlined by opaque matter, tangential section, *Parallepora dartingtonensis* CARTER, 1880, Nicholson 133 (compare NICHOLSON, 1886a, pl. 4, 1), NHM P5743, Middle Devonian, Devon, England,  $\times 10$  (Stearn, 2011a).

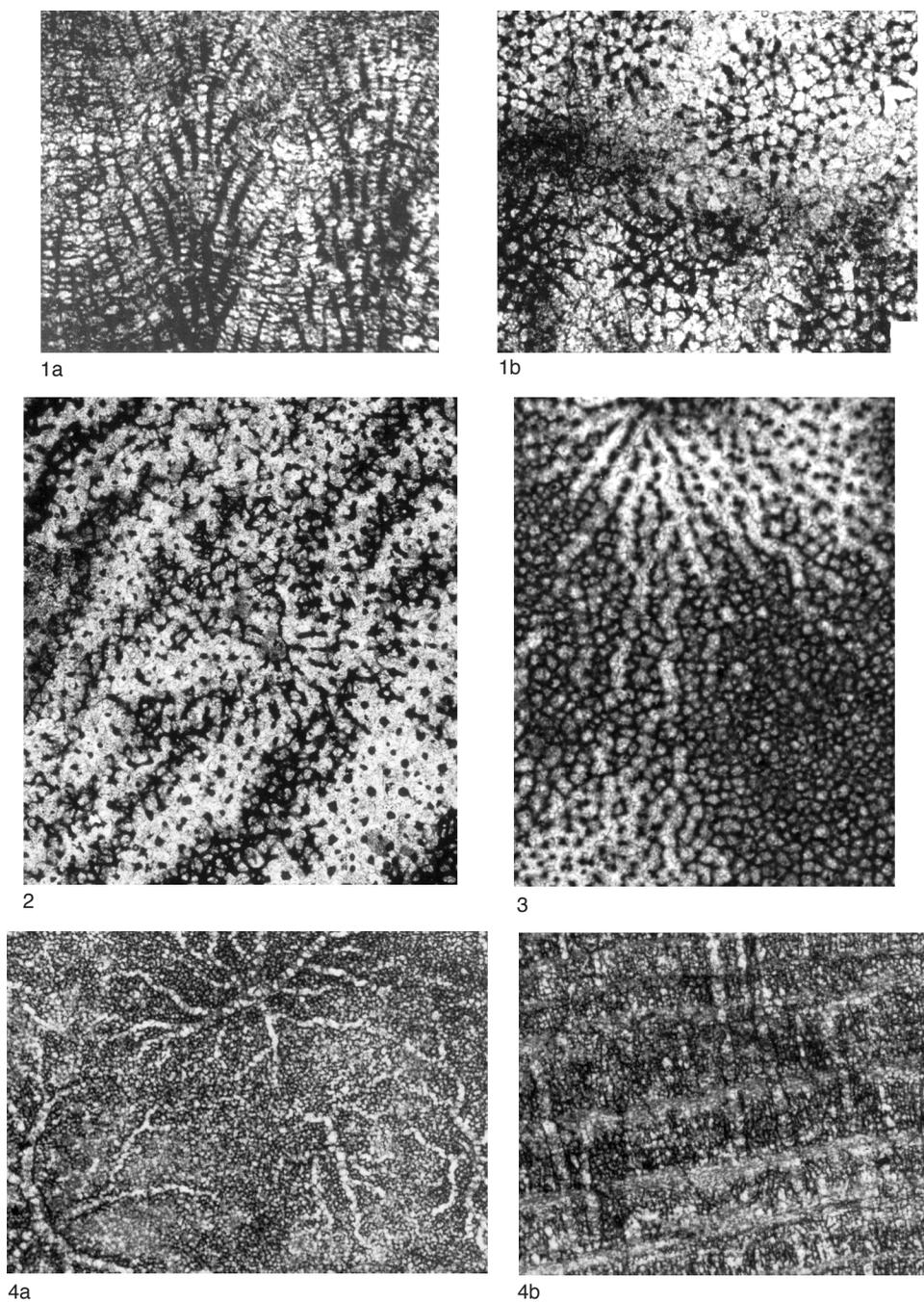


FIG. 327. 1a–b, Columns of pillars and microcolliculi in *Pseudolabechia granulata* YABE & SUGIYAMA, 1930, USNM 458898,  $\times 10$  (Stearn & others, 1999); 2, Astrorhizal paths in open skeleton of *Actinostroma expansum* (HALL & WHITFIELD, 1873), tangential section, GSC 65823A, Givetian, Dawson Bay Formation, Manitoba, Canada,  $\times 10$  (Stearn, 2011a); 3, astrorhizal paths in tangential section of *Atelodictyon* sp., UWA 140816, Frasnian Pillara Limestone, Canning Basin, Australia,  $\times 10$  (Stearn, 2011a); 4a, hidden astrorhizal systems containing skeletal elements, (Continued on facing page.)

There appears to be a complete gradation between astrorhizal systems in which the 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. 328.3). 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. 515). Relatively few species (STEARNS [1982a] 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. 327.4a–b). NESTOR (1966a) 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. 328.4). In some stromatoporoids, they are superposed in longitudinal series and may be joined in their axes by a single longitudinal passageway, such as longitudinal series of astrorhizae commonly, but

not always, occurring in mamelon columns (Fig. 328.2), or a set of passageways crossing the tangential structural elements (Fig. 328.4). Such longitudinal series of astrorhizae commonly, but not always, occur in mamelon columns (Fig. 328.2; Fig. 328.4).

#### ASTRORHIZAL TABULAE

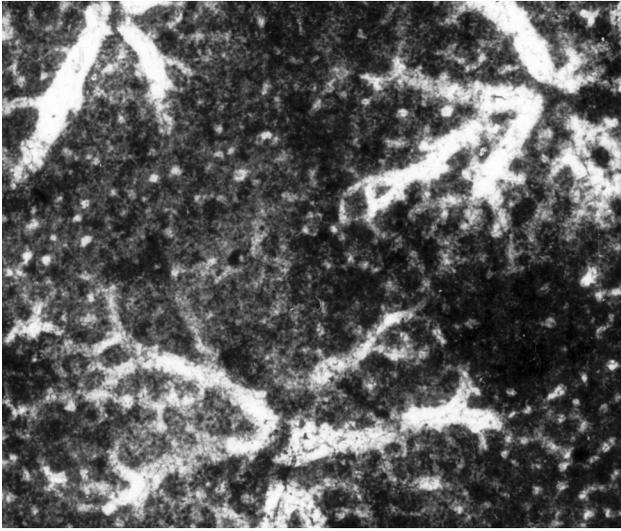
Astrorhizal passages within the skeleton may be divided into segments by thin, planar sheets of skeletal material like the tabulae of tabulate corals (Fig. 325.1; Fig. 329.1). These tabulae are commonly spaced distantly, at intervals several times the diameter of the tube. Rarely the partitions are curved and imbricate in larger passages, and then they resemble dissepiments. In STEARNS' (1982a) 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

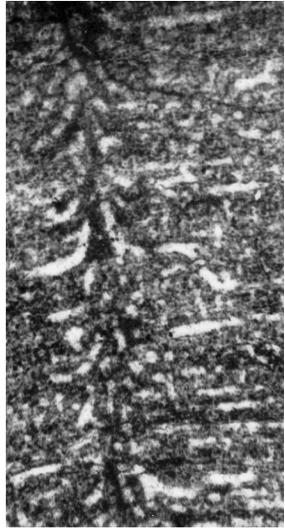
The tabulate axial canals of such genera as *Stachyodes*, *Amphipora*, and *Idiostroma*, can be modelled as longitudinal axial canals of astrorhizae, and the skeleton as a whole, as an isolated mamelon column. Support for this homology comes from rare specimens of *Stachyodes*, in which the fingerlike 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

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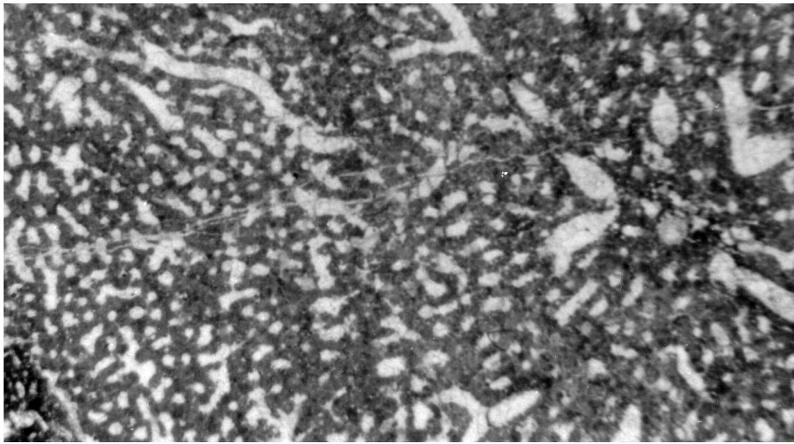
FIG. 327. (Continued from facing page).  
 tangential section; *Plectostroma* sp., AM.FT 15015, upper Silurian, Narragal Formation, New South Wales, Australia,  $\times 10$ ; 4b, vertical section of the same specimen as 4a, *Plectostroma* sp., showing superposed astrorhizal systems, AM.FT 15016, upper Silurian, Narragal Formation, New South Wales, Australia,  $\times 10$  (Stearn, 2011a).



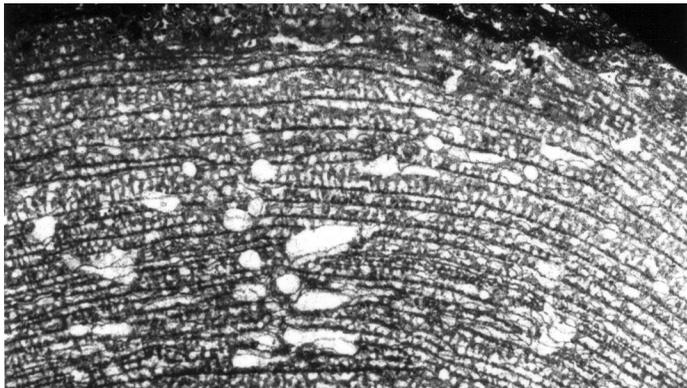
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FIG. 328. (For explanation, see facing page).

longitudinal axial canal of superposed astro-rhizae, and its function is problematic.

### GALLERIES, ALLOTUBES, AND AUTOTUBES

The spaces between structural elements were called galleries by GALLOWAY (1957) 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 stromatoporoids. 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 stromatoporoids 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 pseudo-zooidal tubes (GALLOWAY & ST. JEAN, 1957), then coenotubes and autotubes (NESTOR, 1966a, 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 stromatoporoids 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. 324.4 Fig. 325.3); autotubes are circular to subcircular (Fig. 329.3–329.4; Fig. 332.2). 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.

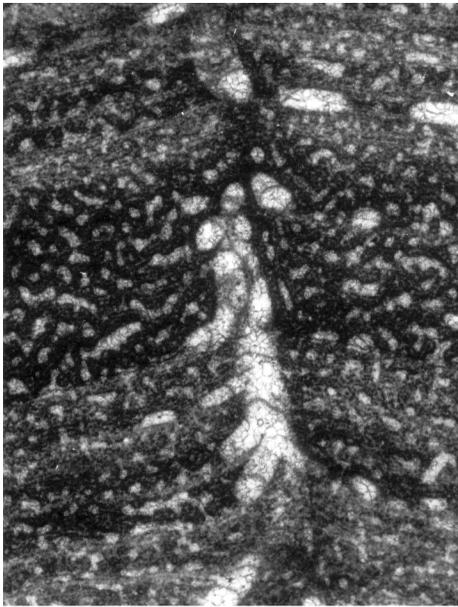
Spaces between the structural elements are, with few exceptions, filled with calcite spar in large cement crystals (see Fig. 335.1; Fig. 344.1). These spar-filled spaces must have been filled only with seawater below the living tissue and filled with spar cement as the skeleton became a fossil. The cysts in the Ordovician labechiids may be filled with sediment, but sediment within the galleries of later stromatoporoids 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. 317.1; also see p. 560). 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 stromatoporoids 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 stromatoporoid were successive phases; variations along the growth surface gave rise to contemporary phases (STEARNS, 1986).

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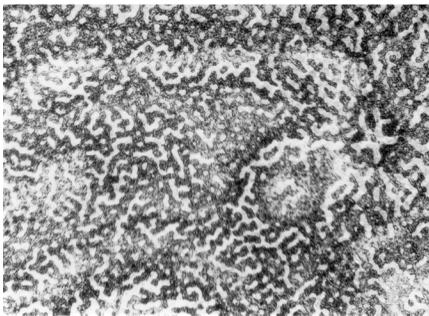
FIG. 328. 1, Astrorhizal systems with many branches opening into galleries, tangential section; *Gerronostromaria franklinensis* (STEARNS, 1990), GSC 95760, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada,  $\times 15$  (Stearns, 2011a); 2, superposed systems of astrorhizal canals, longitudinal section; *Habrostroma proxilaminatum* (FAGERSTROM, 1961), GSC 108905, Lower Devonian, Formosa reef, southwestern Ontario, Canada,  $\times 10$  (Stearns, 2011a); 3, astrorhizal canals almost entirely enclosed in skeletal tissue, tangential section; *Hermatoporella maillieuxi* (LECOMTE, 1952 in 1951–1952), IRScNB 5760, Frasnian, Senzeille, Belgium,  $\times 10$  (Stearns, 2011a); 4, Scattered astrorhizal tubes in longitudinal section, showing terminal growth phase at top and complex pillar structure; *Aelodictyon stelliferum* STEARNS, 1961, SCRM 67-800), Givetian–Frasnian, Flume Formation, Mount Haultain, western Alberta, Canada,  $\times 10$  (Stearns, 2011a).



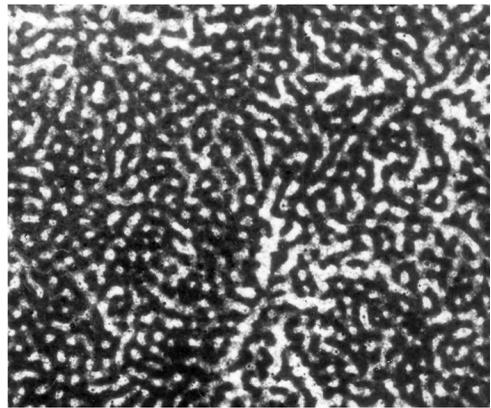
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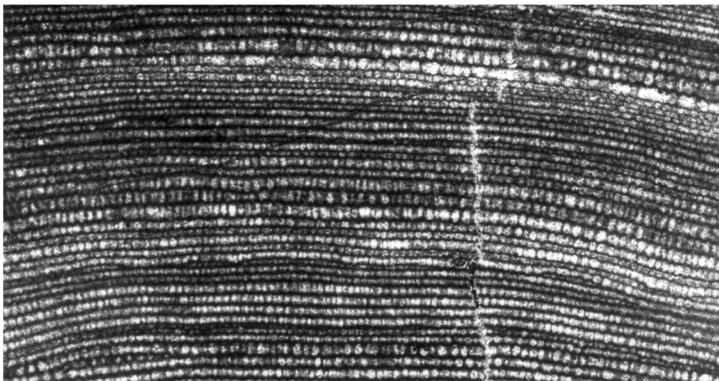
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FIG. 329. (For explanation, see facing page).

## 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. 317.4; Fig. 329.5). Where changes are rhythmic, 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. 330.1).

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. 328.4).

## BASAL PHASES

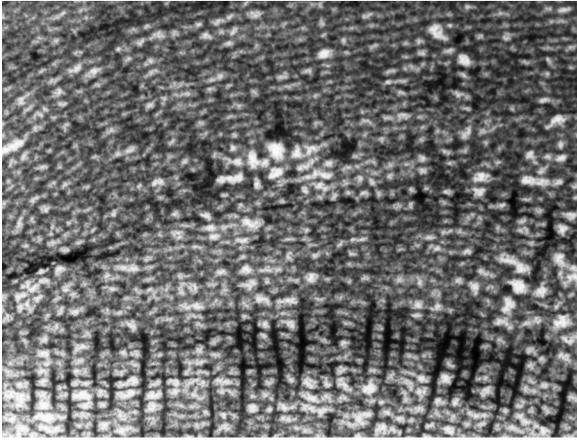
Many skeletons are characterized by basal phases formed as the organism spread across the sediment surface. These structures are generally formed of irregular, oblique, structural elements that have been described as stringy, but they have not received the attention they deserve. GALLOWAY (1957) referred 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. 329.2; Fig. 330.3). 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. 326.1). 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 p. 559–560).

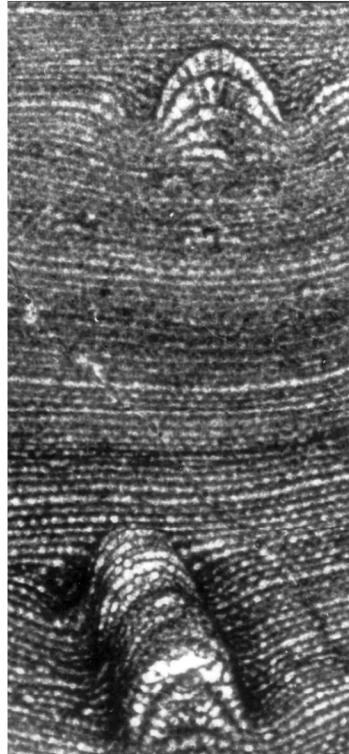
Although some writers (BOGOYAVLENSKAYA, 1984) have referred to progressive changes in successive phases as astogeny of the stromatoporoid colony, no convincing

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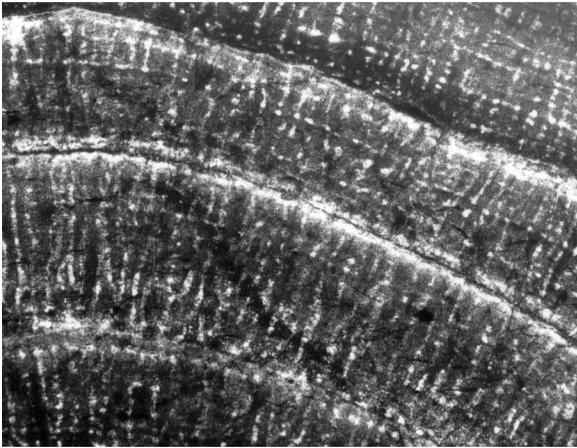
FIG. 329. 1, Superposed astrorhizal canal system with tabulae passing through a cassiculate network of cellular structural elements, longitudinal section; *Stromatopora hensoni* PROSH & STEARN, 1996, holotype, GSC 108890, Emsian–Eifelian, unnamed formation, Bathurst Island, arctic Canada,  $\times 10$  (Stearn, 2011a); 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,  $\times 10$  (Stearn, 2011a); 3, allotubes between pachystyles and traces of astrorhizae, tangential section; *Pseudotrurpetostroma vitreum* (GALLOWAY, 1960), GSC 104890, Givetian, Evie Lake reef, northeastern British Columbia, Canada,  $\times 6$  (Stearn, 2011a); 4, allotubes, autotubes, and astrorhizae, and astrorhizae, tangential section; *Syringostromella labyrinthea* STEARN, 1990, GSC 95779, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada,  $\times 8$  (Stearn, 2011a); 5, spacing phases, longitudinal section, *Clathrodictyon ellesmerense* STEARN, 1983a, SCRM 110-275, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a).



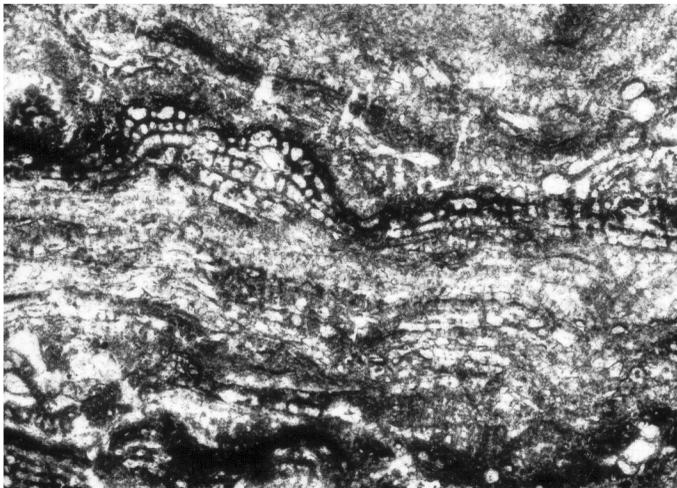
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FIG. 330. (For explanation, see facing page).

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. GALLOWAY and ST. JEAN (1961) thought they had discovered a larval stage they called the protocoenosteum 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 protocoenosteum 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. 322.5 Fig. 325.5). 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. 330.2).

#### 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 stromatoporoidea 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. 330.4). In enclosing foreign organisms, the stromatoporoidea 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 syringoporid tabulate corals whose tubes pervade some skeletons and whose growth apparently kept pace with the growth of the stromatoporoid (Fig. 331.1 Fig. 333.1). 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, stromatoporoidea grown through with syringoporids were long referred to as being in the caunopora-state. MISTIAEN (1984a) has noted that the walls of syringoporids encased in stromatoporoidea are missing a layer present in free-standing specimens and suggested that those growing in company with stromatoporoidea did not need as much support. YOUNG and NOBLE (1989) and MAY (1999) have discussed the relationship of syringoporids to stromatoporoidea. STEARN (1956) has described a similar relationship between a phaceloid amplexoid rugosan and a stromatoporoid. Certain species of stromatoporoid are more

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FIG. 330. 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,  $\times 10$  (Stearn, 2011a); 2, reaction of stromatoporoid to foreign intruder or trauma, longitudinal section; *Clathrodictyon ellesmerense* STEARN, 1983a, GSC 108858, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a); 3, latilaminar growth and distinct basal phases at base of each latilamina; *?Syringostromella discoidea* (LONSDALE, 1839), SCRM 50-17, Wenlock Limestone, Shropshire, England,  $\times 10$  (Stearn, 2011a); 4, interlayering of structures suggestive of algae and stromatoporoid alternating, longitudinal section; *Clathrocoilonia vexata* PROSH & STEARN, 1996, GSC 108881, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a).

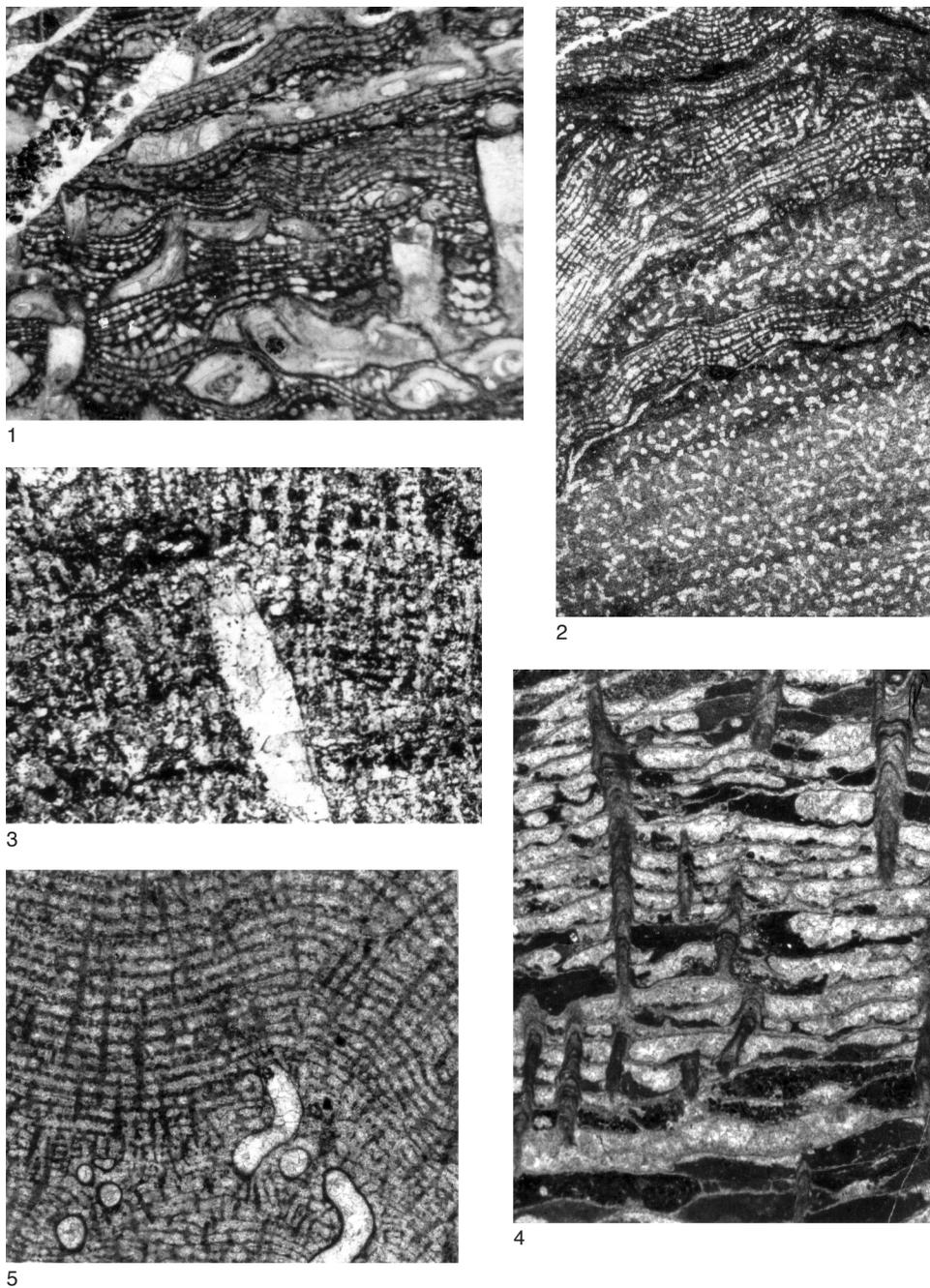


FIG. 331. 1, Syringoporid tubes intergrown with stromatoporoid (caunopore state), longitudinal section; *Gerronostromaria septentrionalis* (PROSH & STEARN, 1996), SCR 130-20, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 7$  (Stearn, 2011a); 2, intergrowth of two competing stromatoporoids alternating in dominance, longitudinal section; *Stromatopora polaris* STEARN, 1983a, below, *Gerronostromaria septentrionalis* (PROSH & STEARN, 1996), to left, SCR 110-342, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a); 3, *Trypanites* sp., boring in poorly preserved *Hermatoporella* cf. *pycnostylota* (STEARNS, 1962), longitudinal section, (Continued on facing page.)

likely to be associated with syringoporids 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.

Laminar tabulate corals are common along growth interruption surfaces. *Helio-lites*, 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. 331.4).

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. 331.2).

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. 331.3). 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. 333.2). 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. 331.5). These tubes resemble the various wormlike 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

FIG. 331. (Continued from facing page).

SCRM 67-272, Frasnian, Southesk Formation, Mount Haultain, western Alberta, Canada,  $\times 10$  (Stearn, 2011a); 4, *Cliefdenia* WEBBY, 1982, cyanobacterium in labechiid stromatoporoid, *Labechiella variabilis* (YABE & SUGIYAMA, 1930), UTGD 96366; Upper Ordovician, Benjamin Limestone, Tasmania, Australia,  $\times 7.5$  (Stearn, 2011a); 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,  $\times 8$  (Stearn, 2011a).

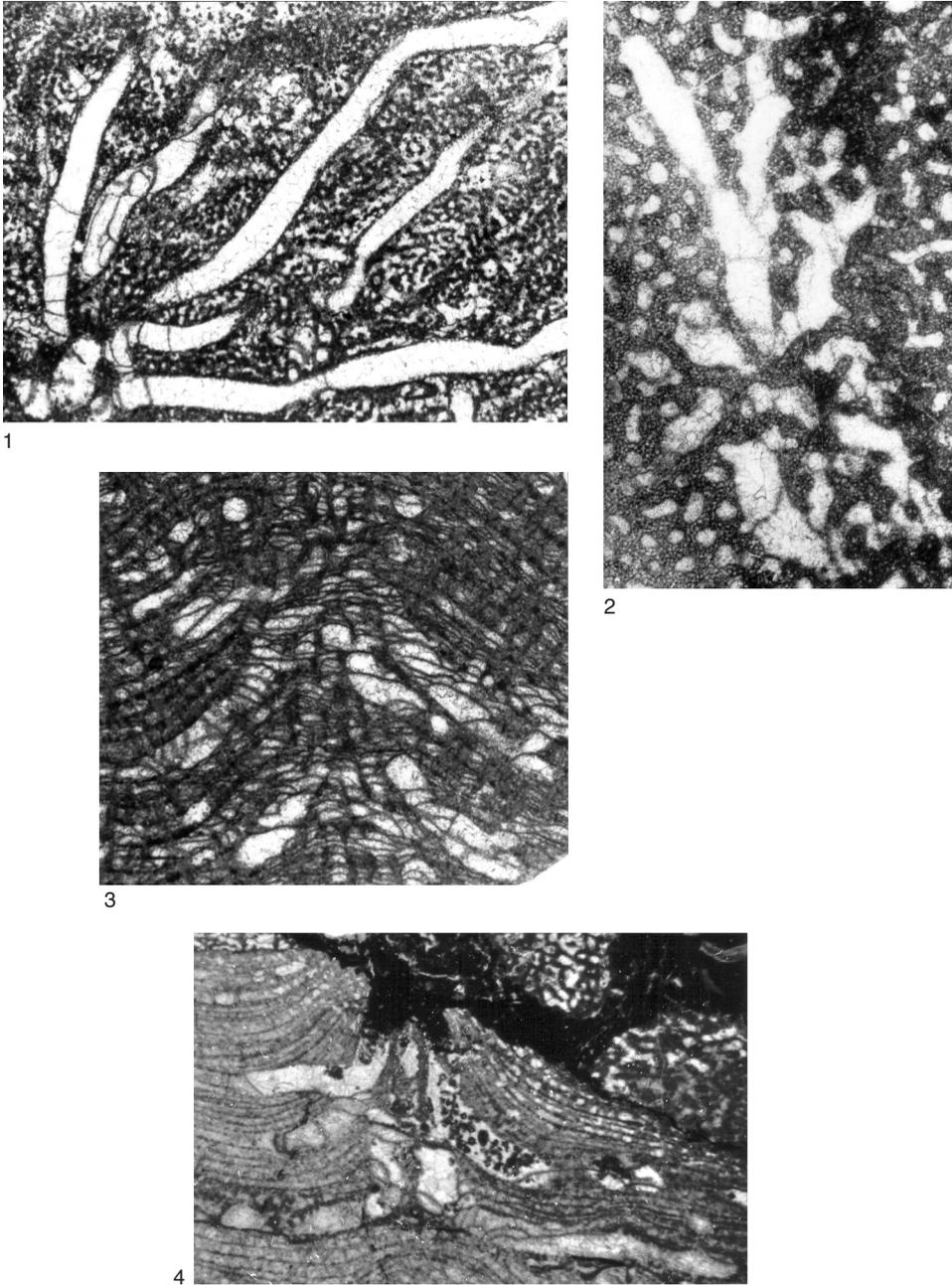
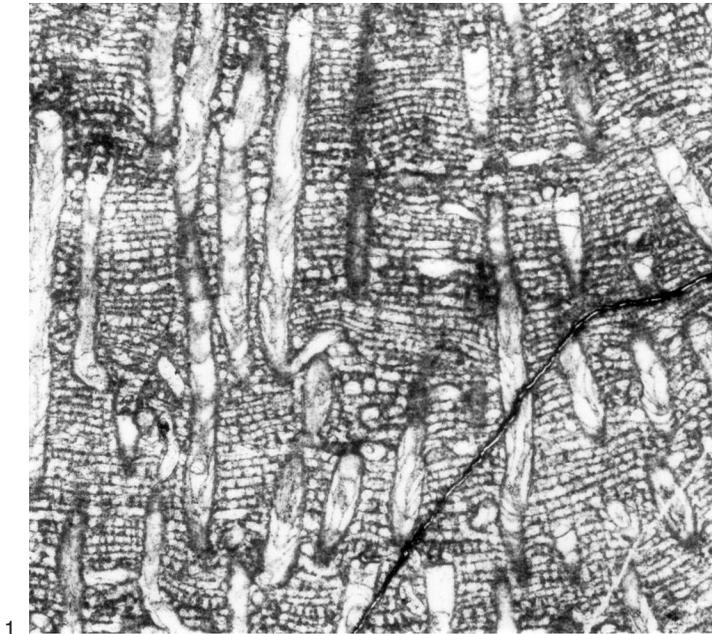
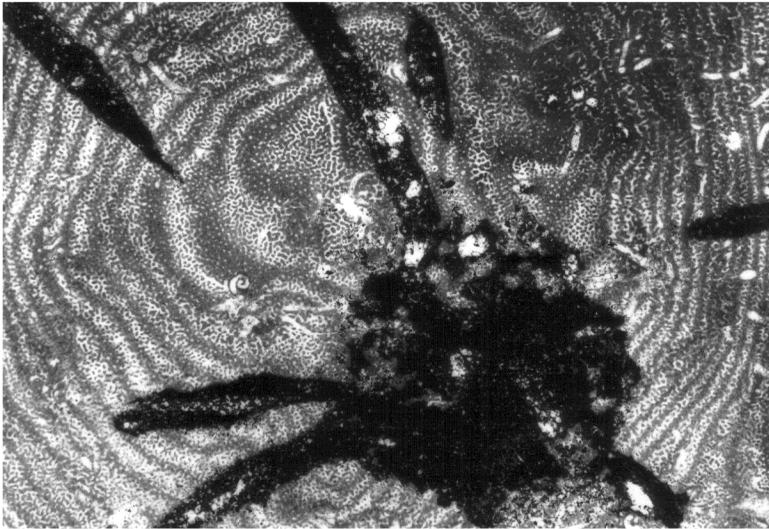


FIG. 332. 1, Large stellate canal system in tangential section, probably a foreign organism; *Atelodictyon* sp., UWA 140816, Frasnian, Pillara Limestone, Canning Basin, Western Australia,  $\times 10$  (Stearn, 2011a); 2, stellate canal system in tangential section, probably a foreign organism in *Salaivella prima* KHROMYKH, 1971; note also smaller astrorhizal canals and autotubes, GSC 108899, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 25$  (Stearn, 2011a); 3, canal system interpreted to be a foreign organism with prominent dissepiments, longitudinal section; *Trupestostroma* sp., UWA 140799, Frasnian, Pillara Limestone, Canning Basin, Western Australia,  $\times 10$  (Stearn, 2011a); 4, canal system of a foreign organism opening at surface, showing sediment infiltration, longitudinal section; *Petridiostroma* sp., GSC 54909, SCR 113-25, Emsian–Eifelian, Ogilvie Formation, Yukon Territory, Canada,  $\times 10$  (Stearn, 2011a).



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FIG. 333. 1, Stromatoporoid extensively intergrown with syringoporid (caunopora state), longitudinal section; *Gerronostromaria septentrionalis* (PROSH & STEARN, 1996), GSC 108862, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 10$  (Stearn, 2011a); 2, large complex boring of *Topsentopsis* sp. in tangential section in *Petridiostroma* sp., SCRM 126-131, Emsian–Eifelian, Truro Island, arctic Canada,  $\times 7$  (Stearn, 2011a).

*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. KAŻMIERCZAK (1969) drew attention to specimens with 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 astrorhizae 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 astrorhizae were integral to the stromatoporoid skeleton. STEARN (1972, 1975a) examined the idea further and reaffirmed that the integrated astrorhizae were certainly part of the stromatoporoid animal and most likely its exhalant canals; but the types bounded by walls of KAŻMIERCZAK could be traces of foreign organisms. By 1976, KAŻMIERCZAK had ascribed the stromatoporoids to the cyanobacteria and suggested that the astrorhizal 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 KAŻMIERCZAK in 1980 and 1981 using evidence from other specimens and scanning electron micrographs. In

1990, KAŻMIERCZAK and KEMPE compared the stromatolites of a crater lake in Indonesia with stromatoporoid skeletons. Although these cyanobacterial crusts do not show astrorhizae, 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 astrorhizae 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 astrorhizae, and none of the writers supporting the foreign organism hypothesis effectively confronted the evidence that astrorhizae are exhalant canals of an encrusting sponge (also see p. 572–573).

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. 332.1–332.4). The following features characterize such tubes and distinguish them from astrorhizae.

1. They are of larger diameter than most astrorhizae.
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 astrorhizae.

# MICROSTRUCTURE AND MINERALOGY OF PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

## INTRODUCTION

Microstructure is defined as the textures of the structural elements observed at magnifications greater than 20 $\times$ . The observation can be made with a light microscope using thin sections of standard thickness (a few tens of micrometers), using ultrathin sections (a few micrometers thick), or with a scanning electron microscope (SEM). Lower invertebrates, such as stromatoporoids, secrete carbonate skeletons of one or more of the following minerals: low magnesium calcite (<5 mole% Mg), high magnesium calcite (>5 and <20 mole% Mg), or aragonite. Almost all Paleozoic stromatoporoids are now preserved as low magnesium calcite. The basic principles of biomineralization have been reviewed by WEINER and DOVE (2003).

Stromatoporoids show a wide range of preservation states in Paleozoic rocks. They are rarely preserved in as much detail as brachiopods, bryozoans, or corals but are generally better preserved than mollusks. Even within a single fossil, the microstructure may range from a coarse calcite mosaic, formed by complete recrystallization, to finely detailed textures that appear little altered from the state in which they were secreted. The most extensive alteration of microstructure is usually around the edges of skeletons where pore waters, expressed from surrounding sediments, have been forced into the galleries. Wide variations in preservation potential exist between the different orders and within orders. This range in preservation states has been attributed to variations in microstructure, skeletal structure, diagenetic conditions, and original mineralogy. It suggests that determining the original mineralogy and microstructure of Paleozoic stromatopo-

roids may not be easy. Discussions of the microstructure of stromatoporoids before 1980 have been summarized by STEARN (1966, 1977, 1980).

The structural elements of the skeleton are generally composed of calcite crystals of smaller size than those of the galleries (Fig. 334.1–334.2; Fig. 335.1; STEARN, 1977; STEARN & MAH, 1987). Although galleries are almost universally filled with calcite, KANO and LEE (1997) have described Ordovician specimens with fluorite in the galleries. As observed in the light microscope, the structural elements are also distinguished by the presence of irregular opaque areas a few micrometers across called specks (Fig. 335.2). The specks were believed by NICHOLSON (1886a) to be fillings of minute pores or tubules. LECOMPTE (1951 in 1951–1952) believed they were cavities filled with organic matter, and GALLOWAY (1957) attributed them to deposits of infiltrating water. STEARN (1966) suggested they were carbonaceous concentrations from organic matter originally diffused throughout the skeletal material, a view similar to that of ST. JEAN (1967). CLARK (2005) found organic matrix remnants dispersed throughout the recrystallized calcite skeleton of an unidentified stromatoporoid. STEARN and MAH's (1987) investigations with the SEM showed that the specks were small cavities that they interpreted as filled with fluid inclusions (see p. 530, below).

## OBSERVATIONS OF MICROSTRUCTURES

### MICROSTRUCTURES IN STANDARD THIN SECTIONS

The microstructures observed in the light microscope have been classified into nine types of **skeletal material** (STEARNS & others, 1999).

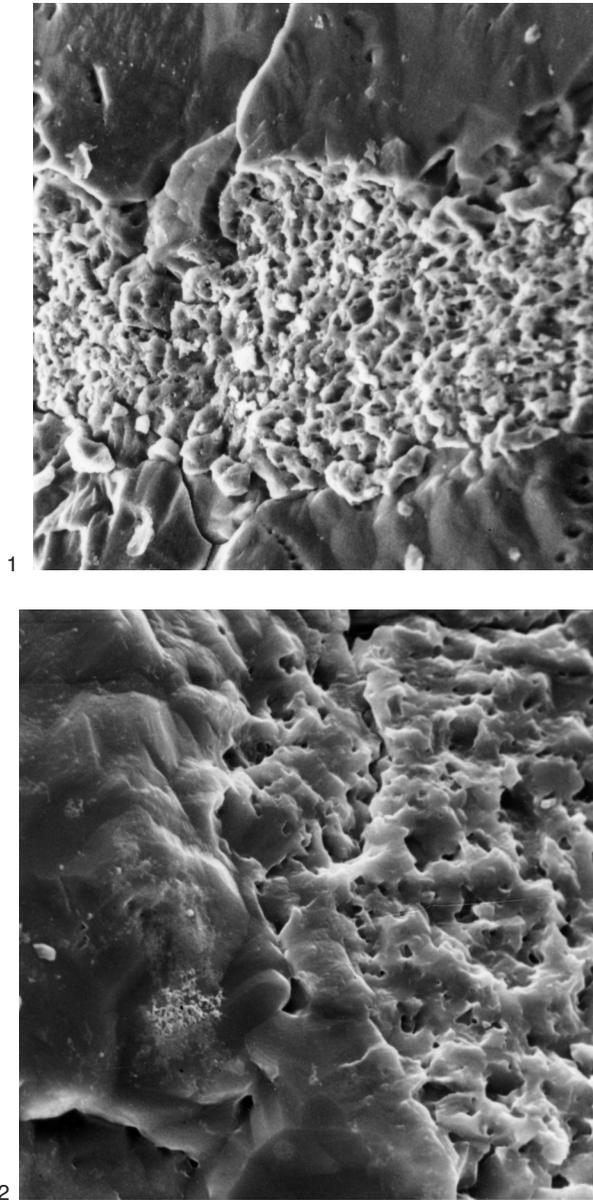
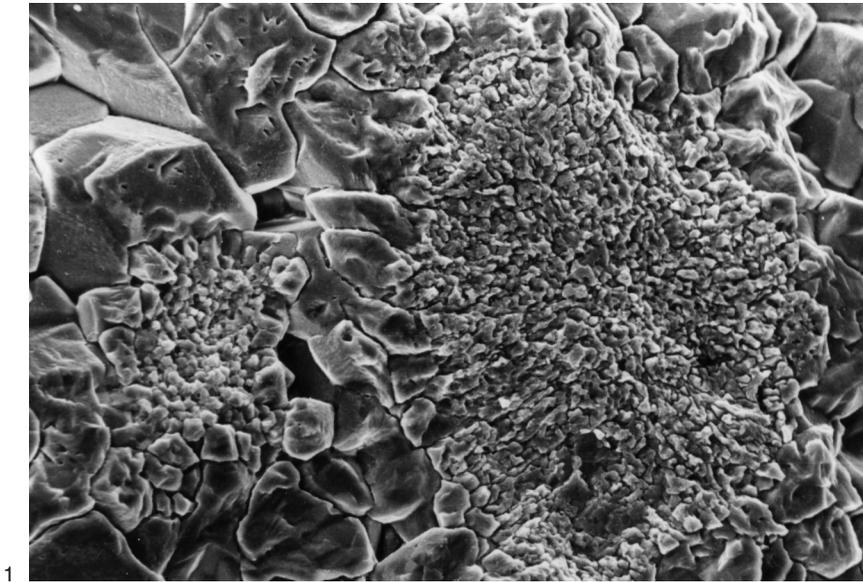
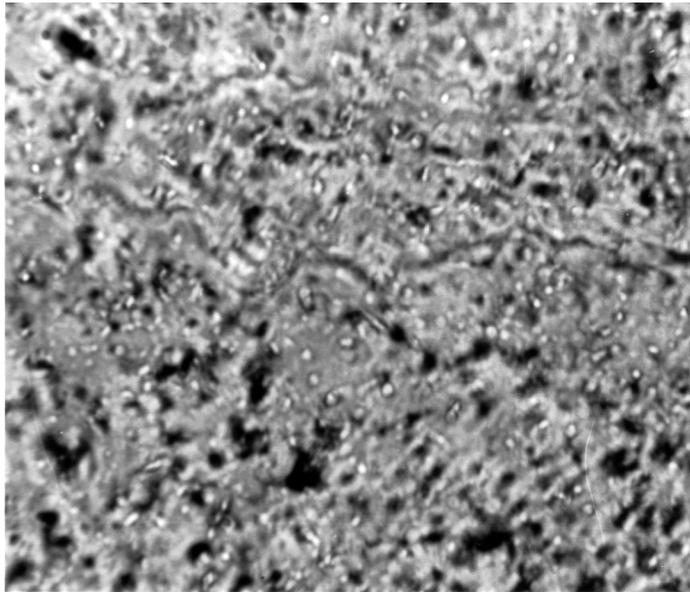


FIG. 334. 1, SEM, finely crystalline structural element with cavities bounded by solid cement crystals in galleries; *Anostylostroma* sp., SCRM 21-1, Emsian, Bois Blanc Limestone, Gorrie, southwestern Ontario, Canada,  $\times 700$  (Stearn, 2010b); 2, SEM, edge of structural element showing contrast of structure with cement crystals; *Actinostroma* sp., SCRM 90-26, Frasnian, Cerro Gordo Formation, Rockford, Iowa,  $\times 1900$  (Stearn, 2010b).



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FIG. 335. 1, SEM, cement crystals in galleries meeting at triple junctions and lack of rim cement, longitudinal section, *Stictostroma mccannelli* FAGERSTROM, 1961, UMMP ?36199, Emsian-Eifelian, Formosa Reef, southwestern Ontario, Canada,  $\times 590$  (Stearn, 2010b); 2, fluid inclusions in ultrathin section made by Jean Lafuste, *Clathrodictyon* sp., RM 14820, locality unknown,  $\times 1730$  (Stearn, 2010b).

### Compact

Specks are distributed evenly throughout the structural elements so that they have no regular internal structure (see Fig. 321.3). Minor, irregular differences in the density of the specks have been recognized as defining a variant of compact microstructure known as flocculent. Actinostromatids, labechiids, and clathrodicytids typically have compact structural elements.

### Fibrous

The specks and crystal boundaries are aligned. In laminae, this alignment is transverse (Fig. 336.2, Fig. 345.1); in pillars, it may curve upward and outward from the axis in a waterjet or feather structure, resembling that of the trabecula in cnidarians (Fig. 336.1–336.2). Fibrosity develops in stromatoporoids of compact microstructure and may be a diagenetic phenomenon in some. In a few stromatoporoids, coarse transverse fibrosity may reflect pores that penetrated the laminae from gallery to gallery. Such microstructure is rare (Fig. 337.1) and may be a diagenetic artefact of ordinicellular microstructure (see below). Fibrous microstructure may be considered a subdivision of compact microstructure.

### Striated

The specks are concentrated in short, rodlike bodies. This microstructure appears to be unique to *Stachyodes* (see Fig. 474*d*) and may be a diagenetic manifestation of originally microreticulate microstructure. These bodies are also suggestive of the simple bodies described as spicules by DA SILVA and others (2014).

### Tubulate

Clear, vermiform areas extend irregularly through the speckled tissue. This microstructure is rare and best shown in some species of *Clathrocoilona* (Fig. 435).

### Cellular

The speckled skeletal material is filled with closely spaced, irregularly distributed, subspherical, clear areas (cellules) that appear to have been voids in the structural element (Fig. 337.3; Fig. 338.1; Fig. 339.1; Fig.

343.1–343.2). This microstructure is typical of stromatoporids and syringoporids.

### Melanospheric

Specks are concentrated in closely spaced, irregularly distributed, subspherical, opaque areas separated by clearer areas (Fig. 338.2; Fig. 339.1). This is the negative of cellular microstructure.

### Microreticulate

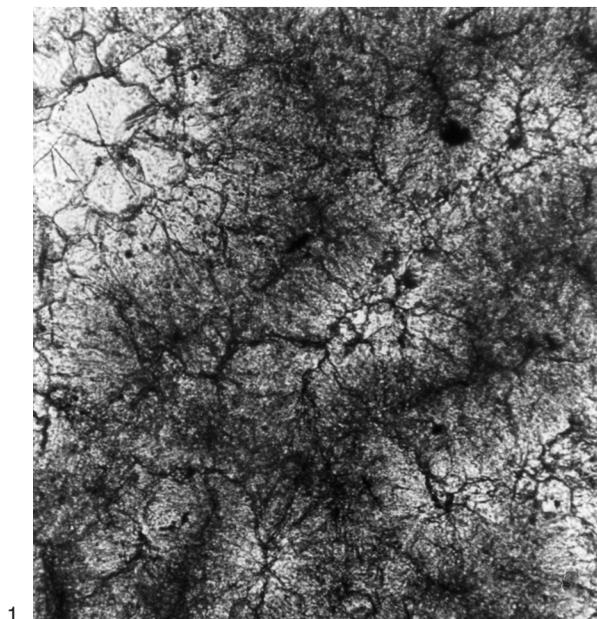
Structural elements contain rows of subspherical voids (cellules) separated by a fine, three-dimensional, rectilinear network of micropillars and microcolliculi (posts and beams) (Fig. 339.3; and see Fig. 472). Where the micropillars are perpendicular to the axis of laminae-pachystromes and the microcolliculi are parallel to the axes of laminae, microreticulate microstructure is distinguished as **orthoreticulate** (see *Parallelostroma*, Fig. 472*a–b*). Where the micropillars curve upward and outward from the axes of pillars or pachysteles, microreticulate microstructure is distinguished as **clinoreticulate** (Fig. 342.1*b*; Fig. 458*c*). Where orientation of micropillars and microcolliculi is without order, the microstructure is said to be **acosmoreticulate** (see STOCK, 1989, fig. 1, 2E, 2F). These microreticulate microstructures are typical of densastromatids and syringostromatids.

### Ordinicellular

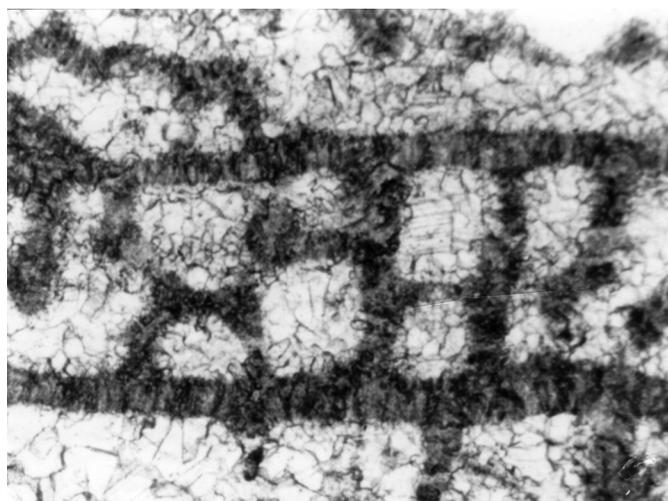
The axial planes of laminae are marked by a layer of subspherical, clear areas (cellules; Fig. 340.2); see *Stictostroma* (Fig. 439*c*) and *Stromatoporella* (Fig. 434). Where the divisions between the cellules are missing, a semicontinuous clear zone, or more opaque zone, makes the laminae appear to have three parts (**tripartite**). This microstructure is typical of the laminae of stromatoporellids.

### Vacuolate

Compact laminae and pillars contain scattered, subspherical voids larger than cellules (about 100  $\mu\text{m}$ ), as in *Trupetostroma* or *Paramphipora* (Fig. 340.2–340.3; Fig. 341.1–341.2; and see Fig. 443*b–d*, Fig. 481*b*).



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FIG. 336. 1, Transversely fibrous microstructure and center of calcification; *Amphipora* sp., GSC 54924, Emsian-Eifelian, Ogilvie Formation, Yukon Territory, Canada,  $\times 150$  (Stearn, 2010b); 2, transversely fibrous laminae and pillars, longitudinal section, *Hammatostroma albertense* STEARN, 1961, holotype, GSC 15318, Frasnian, Cairn Formation, western Alberta, Canada,  $\times 20$  (Stearn, 2010b).

In some preservation states, the borders of the structural elements are independent of crystal boundaries that are most clearly defined in the coarse mosaic of the galleries. The crystal boundaries extend from the galleries across the structural elements

without interruption, probably as a result of extensive aggrading neomorphism.

In addition to these microstructures that are found in several genera, there are many microstructures that are unique to a single genus or restricted to a few genera. For example, in the

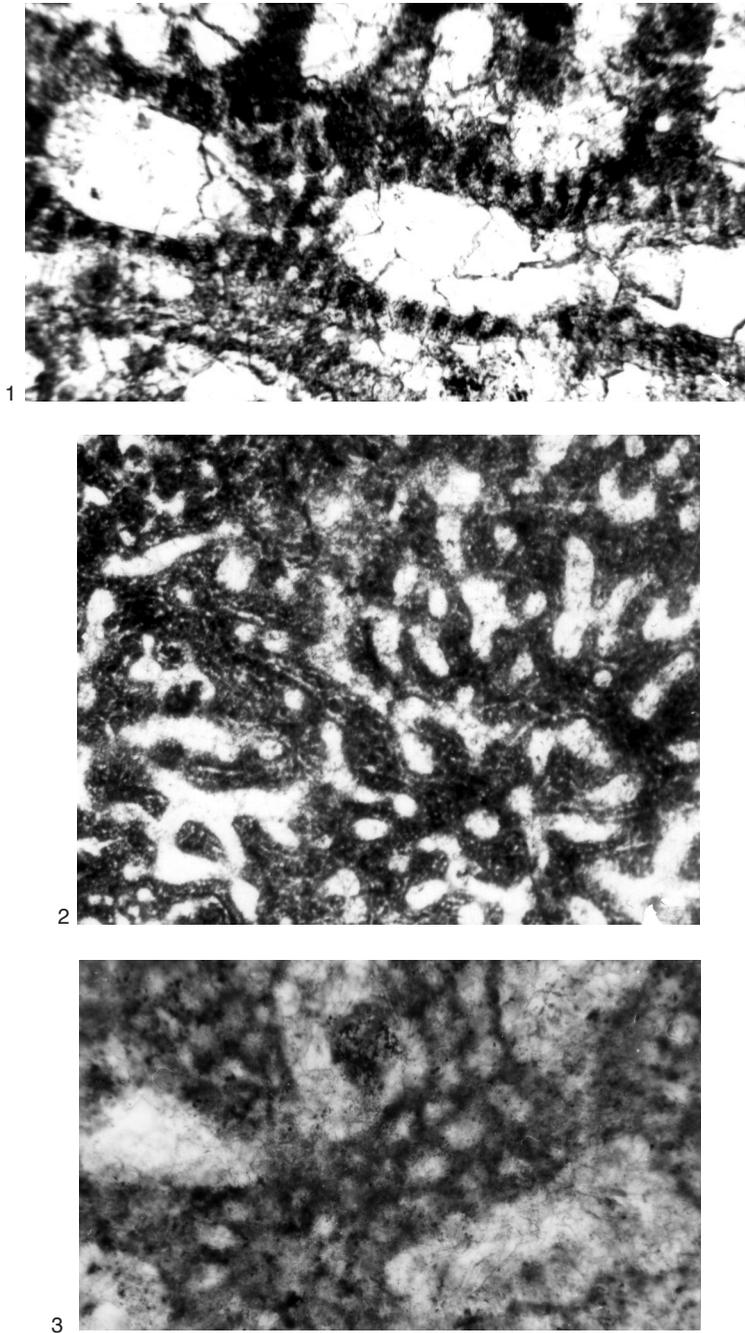


FIG. 337. 1, Transversely porous laminae and pillar, longitudinal section, *Gerronostromaria elegans* YAVORSKY, 1931, paratype, YPM.227561, Middle Devonian, Kuznetsk Basin, Russia,  $\times 100$  (Stearn, 2010b); 2, tubulate microstructure, tangential section, *Stictostroma? nunavutense* PROSH & STEARN, 1996, GSC 108876, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 25$  (Stearn, 2010b); 3, coarse cellular microstructure, tangential section, "*Stromatopora*" (*?Salairella*) *beuthii* (BARGATZKY, 1881a), Nicholson 62, ?NHM P5703, Middle Devonian, Hebborn, Rhineland, western Germany,  $\times 50$  (Stearn, 2010b).

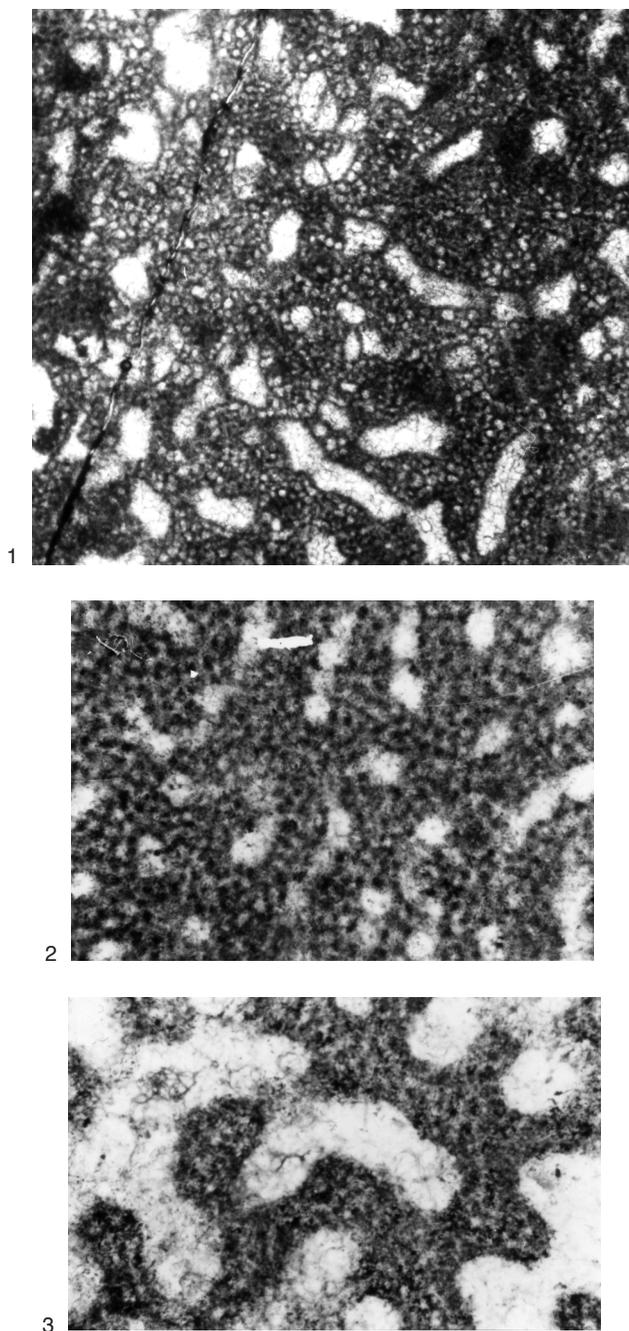


FIG. 338. 1, Coarse cellular microstructure, tangential section, *Syngstromella zintchenkovi* (KHALFINA, 1961d), GSC 108897, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 25$  (Stearn, 2010b); 2, tangential section of Figure 340.1, *Syngstromella carteri* NICHOLSON, 1891b, Nicholson 37, MNH P5678, Wenlock, Shropshire, England,  $\times 55$  (Stearn, 2010b); 3, tangential section of Figure 339.3, *Parallelostroma typica* (ROSEN, 1867), showing cellular-melanospheric appearance of cut ends of micropillars in pachyestes,  $\times 55$  (Stearn, 2010b).

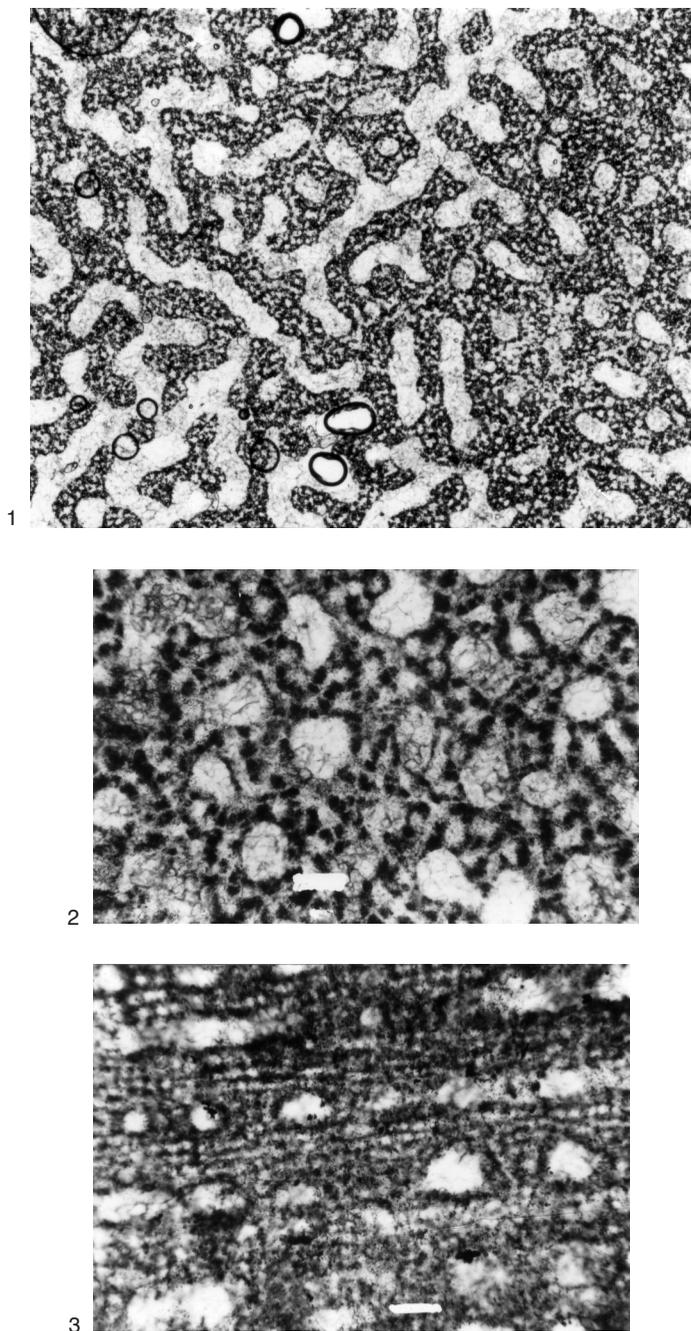


FIG. 339. 1, Cellular microstructure grading into melanospheric, tangential section, *Pseudotruperostroma vitreum* (GALLOWAY, 1960), GSC 48453A, Givetian, Evie Lake Reef, northeastern British Columbia, Canada,  $\times 25$  (Stearn, 2010b); 2, opaque (dark) cut ends of rodlike micropillars in pachyστεles in tangential section, *Parallelopora ostiolata* BARGATZKY, 1881a, holotype, Nicholson 125, NHM P5936, Middle Devonian, Büchel, Rhineland, western Germany; note also round autotubes,  $\times 55$  (Stearn, 2010b); 3, microreticulate microstructure showing thick laminae composed of thin microlaminae and micropillars, longitudinal section, *Parallelostroma typica* (ROSEN, 1867), holotype, Nicholson 59b, IG TUT Co3009, Ludlow, Saaremaa, Estonia,  $\times 50$  (Stearn, 2010b).

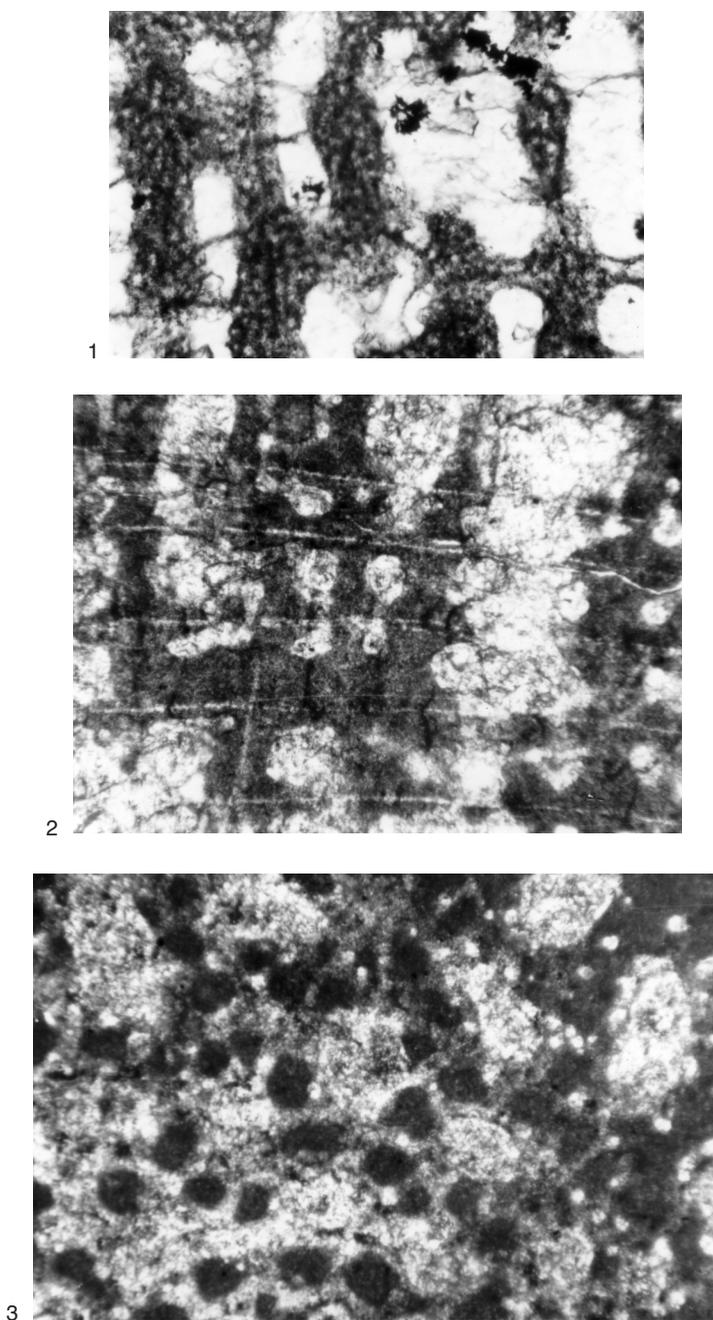


FIG. 340. 1, Cellular microstructure in pachyστεles, longitudinal section, *Syringostromella carteri* NICHOLSON, 1891b, Nicholson 37, MNH P5678, Wenlock, Shropshire, England,  $\times 55$  (Stearn, 2010b); 2, vacuoles (round holes) in compact pillars, longitudinal section, *Trupetostroma warreni* PARKS, 1936, ROM 1885A, holotype, Middle Devonian, Great Slave Lake, Northwest Territories, Canada; note superposed pillars interrupted by laminae, represented by a clear zone divided into cellules,  $\times 50$  (Stearn, 2010b); 3, vacuolate microstructure in compact structural elements, tangential section, *Trupetostroma warreni* PARKS, 1936, ROM 1885B, Middle Devonian, Great Slave Lake, Northwest Territories, Canada,  $\times 50$  (Stearn, 2010b).

type species of *Parallelopora*, the microreticulation is very coarse and the micropillars appear as dark (opaque) rods within the network of pachyestes (Fig. 339.2). In *Arctostroma* (Fig. 341.1–341.2) and *Ferestromatopora*, the irregular structural elements seem to be of compact microstructure but contain scattered dark nodes like melanospheres that are common in the structural elements of the order Stromatoporida. In addition, the skeletal elements enclose spherical vacuoles like those of *Trupetostroma* (Fig. 340.2–340.3).

#### MICROSTRUCTURES IN ULTRATHIN SECTIONS

In sections ground to a few micrometers in thickness, the specks appear at magnifications of about 1000 $\times$  as subspherical opaque areas if they are out of the the plane of focus, and as light areas if they are in focus (Fig. 335.2). This effect could be caused by the refraction of light around minute voids, such as fluid inclusions, as postulated by STEARN and MAH (1987).

#### MICROSTRUCTURES IN SCANNING ELECTRON MICROSCOPY

In thin sections of stromatoporoids several micrometers thick, the high birefringence of the calcite, in which the fossils are preserved, obscures the relationship between the crystals in the skeletal carbonates. The SEM permits observation of the skeletal textures at high magnifications but also clearly reveals the differences between the skeletal carbonate and the cement that fills galleries and canals.

The calcite that fills the galleries of stromatoporoids appears as coarse crystals more than 100  $\mu\text{m}$  across that have smooth surfaces, even when the surfaces examined have been prepared by etching. The crystals commonly meet at triple junctions (Fig. 344.1). These gallery fillings rarely show a rim of finer crystals bordering the structural elements (that is, syntaxial rim cements; Fig. 335.1), and, in many states of preservation, the boundary of the galleries is not sharply defined.

In contrast, the structural elements are composed of finer carbonate crystals (>10  $\mu\text{m}$ ) of irregular but elongate shape that are arranged in an overlapping pattern (Fig.

334.1–334.2), like the crystals described as bossulure by LAFUSTE (for example, LAFUSTE & FISCHER, 1971) from ultrathin sections in many corals. The alignment of elongate crystals may impart a crude fibrosity to the structural element observed in the SEM (STEARNS & MAH, 1987). It has been described in such Paleozoic stromatoporoids as *Hammatostroma* (Fig. 345.1), *Amphipora* (Fig. 345.2), and *Anostylostroma* (Fig. 334) but is by no means as common as in Mesozoic stromatoporoid-like genera. STEARN (1977) described specimens of *Stromatopora* with cellular microstructure, which showed traces of a radial arrangement of elongate crystals, suggesting they were remnants of spherules. These radial structures are rare, however (STEARNS & MAH, 1987), and may be a diagenetic product unrelated to original microstructure. In stromatoporoids of well-preserved cellular microstructure, the cellules are formed by calcite in coarser crystals than those in the more opaque areas of the structural elements and like those in the gallery filling (Fig. 346.1–346.2). This suggests that the cellules were originally voids subsequently filled with cement.

The specks seen in light microscope examination are shown in SEM to be cavities a few microns across that are the remnants of inclusions (mostly fluid) in the carbonate of the structural elements (Fig. 334.1–334.2; STEARN & MAH, 1987). Some of these cavities have rhombohedral shapes like negative carbonate crystals and like the rhombohedral cavities formed when aragonite botryoids are calcitized (Fig. 347.1–347.2; Fig. 348.1; AISSAOUI, 1985).

In Lower Devonian stromatoporoids from New York, RUSH and CHAFETZ (1991) discovered scattered rhombohedral crystals of microdolomite embedded in the calcite skeletal elements and brought into positive relief by the etching. The structural elements were marked by a finer crystallinity and abundance of cavities derived from fluid inclusions, but these cavities were not observed to have rhombohedral outlines. They did not comment on the significance of the fluid inclusions nor on the absence

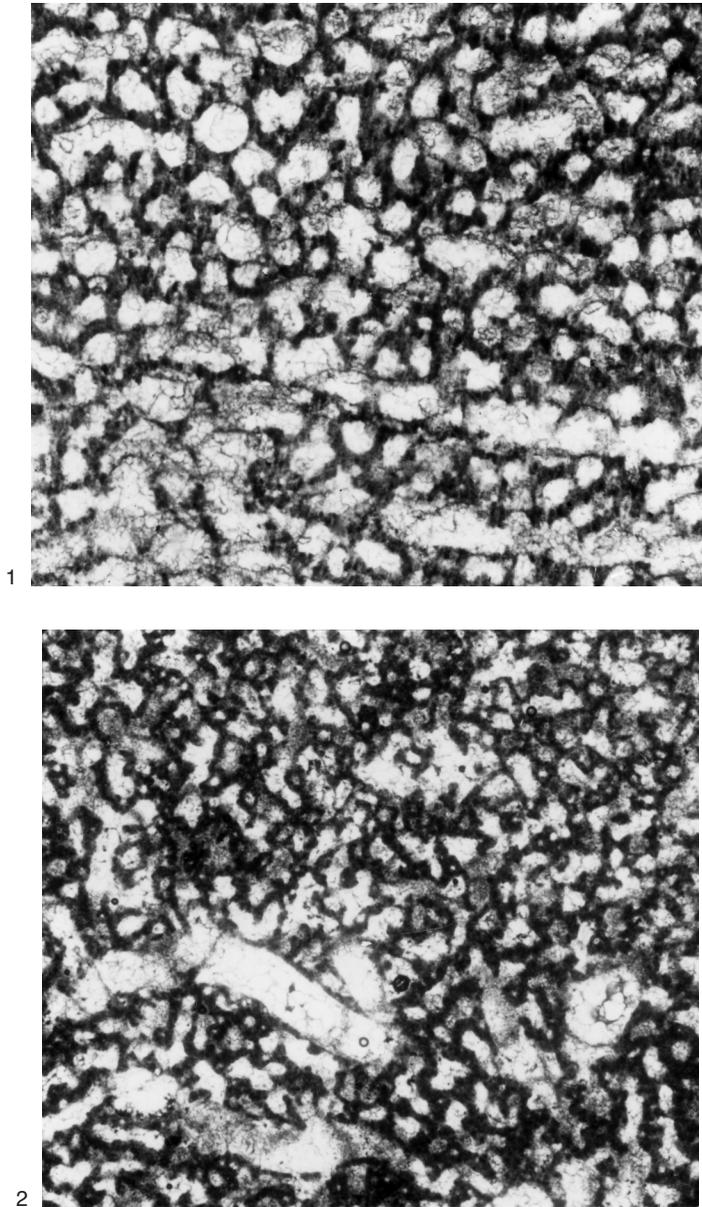


FIG. 341. 1, Vacuolate microstructure with traces of melanospheres, longitudinal section, *Arctostroma contextum* (STEARNS, 1963), holotype, GSC 16856, Frasnian, Milkwa Formation, Milkwa River, northern Alberta,  $\times 25$  (Stearn, 2010b); 2, compact irregular structural elements enclosing round vacuoles, tangential section, *Arctostroma contextum* (STEARNS, 1963), GSC 111384, Frasnian, Souris River Formation, Manitoba, Canada,  $\times 18$  (Stearn, 2010b).

of microdolomite in the extensive suite of stromatoporoids investigated by STEARN and MAH (1987), as they apparently did not see this earlier paper in their literature review. They concluded that these stromatoporoids originally secreted high magnesium calcite

(RUSH & CHAFETZ, 1988, 1991). Their observations were substantiated by YOO and LEE (1993), who found microdolomite in Middle Ordovician stromatoporoids and concluded that they were originally high magnesium calcite.

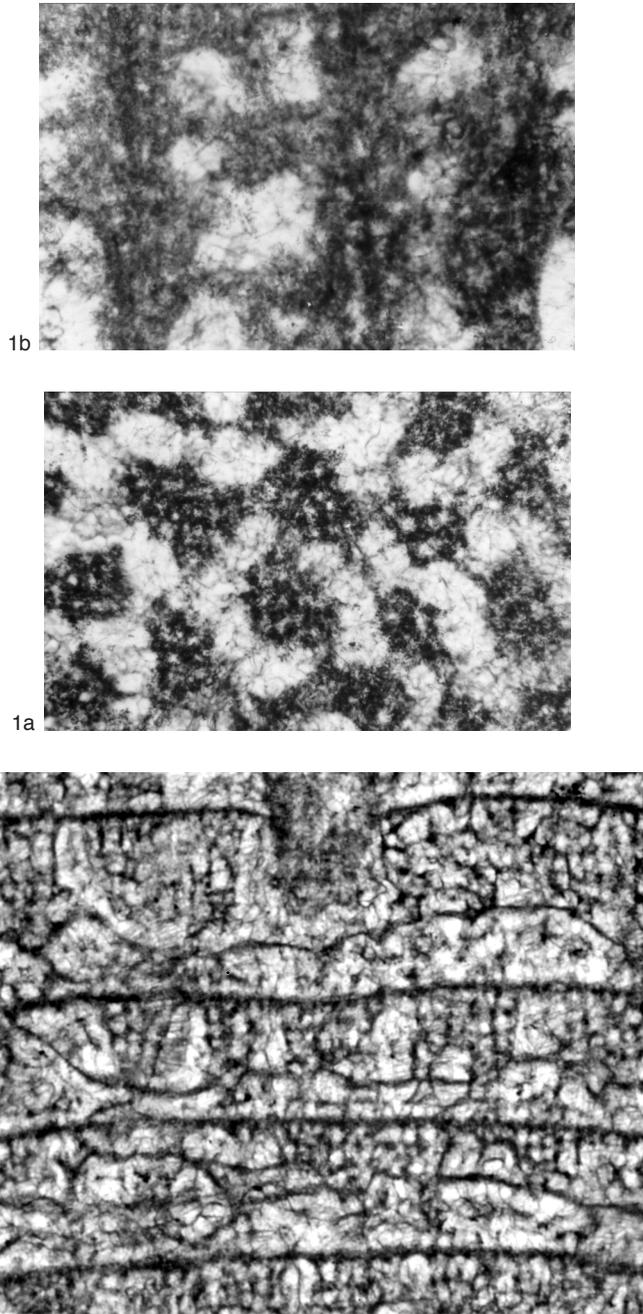


FIG. 342. *1a–b*, clinoreticular microstructure of pachyosteles, longitudinal and tangential sections, *Syringostroma nodulatum* (NICHOLSON, 1875), Nicholson 310, NHM P5604, Middle Devonian, Ohio, USA,  $\times 55$  (Stearn, 2010b); *2*, coarse clinoreticular microstructure in pachyosteles, longitudinal section, *Habrostroma alternum* WEBBY & ZHEN, 2008, holotype, AM FT.15128, Lower Devonian, Martins Well Limestone, Queensland, Australia,  $\times 50$  (Webby & Zhen, 2008).

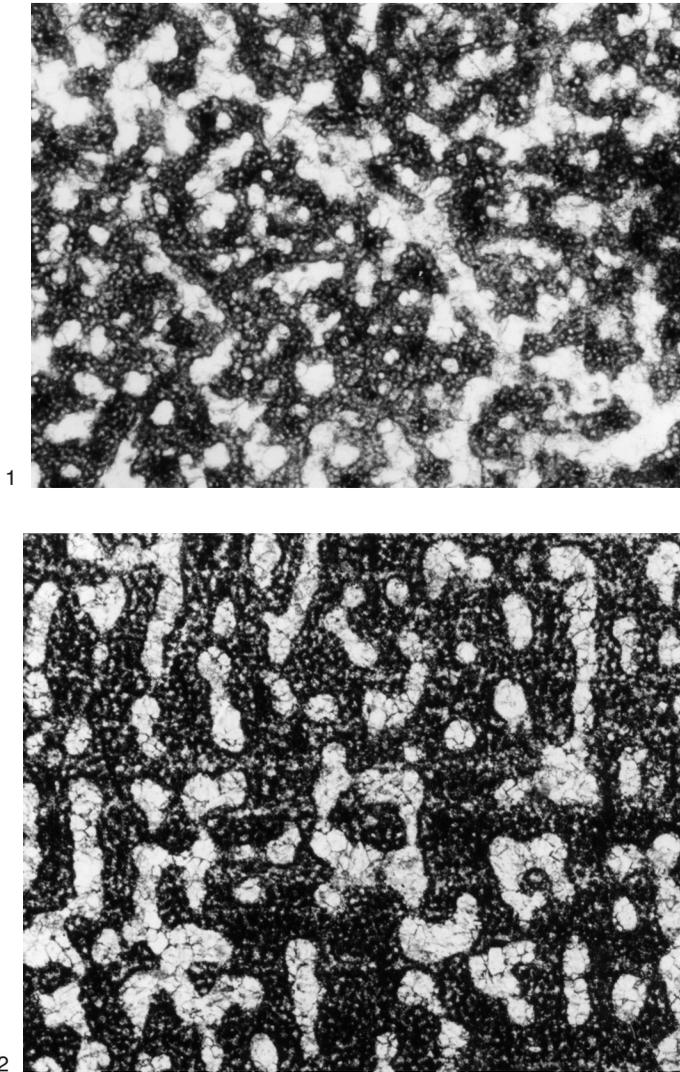


FIG. 343. 1, Cellular microstructure, tangential section, *Salirella prima* KHROMYKH, 1971, hypotype, GSC 108901, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada,  $\times 25$  (Stearn, 2010b); 2, coarse cellular microstructure in pachysteles, longitudinal section, *Pseudotrurpetostroma vitreum* (GALLOWAY, 1960), GSC 48453A, Givetian, Evie Lake Reef, northeastern British Columbia, Canada; note laminae outlined by line of cells,  $\times 25$  (Stearn, 2010b).

#### GEOCHEMISTRY AND MINERALOGY

Various studies have established the proportions of strontium and magnesium to be expected in fossil skeletons derived from aragonite and high magnesium calcite precursors (MARTIN, WILKINSON, & LOHMAN, 1986; BRAND, 1989a; MALLAMO, 1995;

MALIVA, 1998). The aragonite lattice, which is more receptive to the  $\text{Sr}^{++}$  ion, generally contains 7000–9000 parts per million (ppm) in the skeletons of organisms that now secrete this mineral. However, calcitized skeletons of such organisms lose some strontium in diagenesis and retain only 2000–4000 ppm  $\text{Sr}^{++}$ . In contrast, fossils of brachiopods that secreted low magnesium

calcite have  $\text{Sr}^{++}$  values generally below 1300 ppm and commonly below 1000 ppm. Most limestones have  $\text{Sr}^{++}$  values in the 400–700 ppm range (MALLAMO & STEARN, 1991). Calcites that contain  $\text{Sr}^{++}$  values in excess of 1000 ppm are likely to have had aragonite precursors, and those with values of 2000–3000 ppm must have had aragonite precursors.

Geochemical contrasts between skeletal material and galleries that have been filled with low magnesium calcite cements have been investigated by microprobe analysis (MALLAMO & STEARN, 1991; RUSH & CHAFETZ, 1991; MALLAMO, 1995). RUSH and CHAFETZ (1991) reported insignificant differences in magnesium and strontium between these two areas in Lower Devonian stromatoporoids. Magnesium values in the skeletal material were 2160 ppm and in the galleries 1800 ppm; strontium values were 1380 and 1140 ppm respectively.

MALLAMO and STEARN (1991) found strontium values comparable to those of the calcitized aragonite of scleractinian corals in the cyst plates of Ordovician labechiids. These values were much higher than those in the adjacent gallery-filling calcite, showing that they were likely a signal of aragonite skeletal mineralogy. MALLAMO (1995) also reported high  $\text{Sr}^{++}$  values in labechiids in the zone of diffused specks adjacent to cyst plates that were postulated by STEARN (1989b) to have been syntaxial aragonite cements (1800 ppm, compared to 240 ppm for adjacent clear galleries). Magnesium contents of the labechiids probed by MALLAMO (1995) was below 9000 ppm, considerably less than would be expected in high magnesium calcite. TOBIN and WALKER (1998) examined the alteration of stromatoporoid skeletons (labechiids) from Middle Ordovician rocks of Vermont, United States. They found that carbonate replacing stromatoporoids was low in  $\text{Mg}^{++}$ , had no microdolomite, and was variably but locally high in  $\text{Sr}^{++}$  (200–1600 ppm). The opposite was true of fossils believed to have secreted high magnesium calcite. They concluded that the labechiids secreted aragonite, as MALLAMO and STEARN

(1991) had concluded about a different suite and age of specimens.

SANDBERG (1983) proposed that oceanic water cycled between a so-called greenhouse condition that favored deposition of calcite and an icehouse condition that favored aragonite. The entire history of the stromatoporoids took place in seas that SANDBERG (1983) postulated favored calcite, but he was careful to point out that organisms could override the influence of the chemistry of the sea water they lived in by vital effects. However, STANLEY and HARDIE (1998) have extended the influence of SANDBERG's (1983) oscillating seawater chemistry, attributing it largely to changes in Mg/Ca ratios and extending its influence to the success or failure of so-called hypercalcifying organisms, which includes the stromatoporoids. They imply that stromatoporoids only secreted calcite and hence fit into SANDBERG's (1983) calcite depositional phase of the early and middle Paleozoic.

STANLEY (2006) has summarized the consequences of variations in the Mg/Ca ratio of sea water to several groups of organisms during geological time. SANDBERG's (1983) calcite seas correspond to times in the past (largely in the Cambrian to Mississippian and in the Cretaceous) when this molar ratio of sea water was lower than 2. The influence of seawater chemistry on the skeletal composition of marine animals is greatest for lower invertebrates, such as sponges and corals, and should be reflected in the skeletons of stromatoporoids. The Mg/Ca ratio in sea water also affects the proportion of Mg incorporated by these organisms in the calcite lattice, and therefore high-magnesium calcites are postulated to be favored by molar ratios above 2. The implications of these studies are that the Paleozoic stromatoporoids were composed of low-magnesium calcite, and the Mesozoic stromatoporoid-like genera were composed of aragonite or high-magnesium calcite. The dominantly fibrous nature of the skeletons of Mesozoic stromatoporoid-like fossils might suggest that they were originally aragonitic, but their similarity in preservation to Paleozoic stromatoporoids suggests that they shared a mineralogy. The evidence cited above

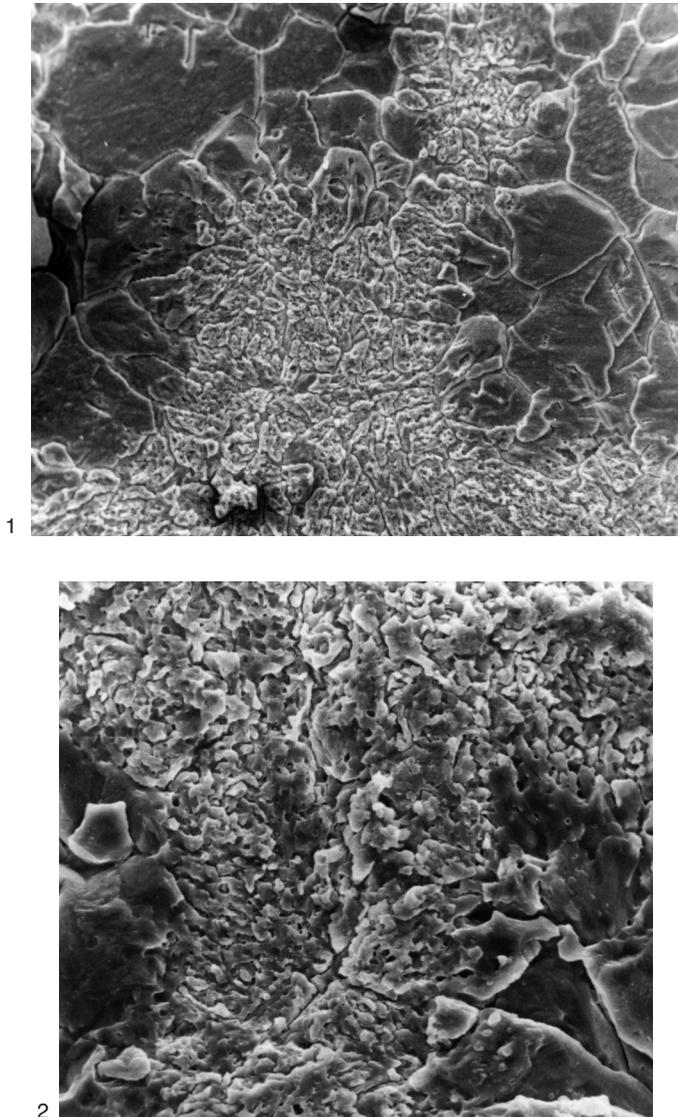
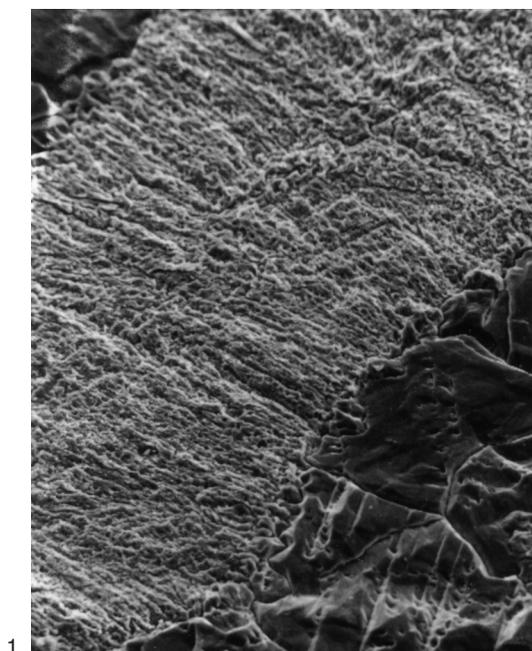


FIG. 344. 1, SEM, radial fibrosity in pillars and rim cements of fine crystals, tangential section, *Actinostroma clathratum* NICHOLSON, 1886a, SCRМ 96-09,  $\times 480$ , scale bar, 100  $\mu\text{m}$  (Stearn, 2010b); 2, SEM, fibrosity in pillars, longitudinal section, *Actinostroma clathratum*, SCRМ 96-09, hypotype, RM 14813, Frasnian, Duperow Formation, Esterhazy shaft, Saskatchewan, Canada,  $\times 800$  (Stearn, 2010b).

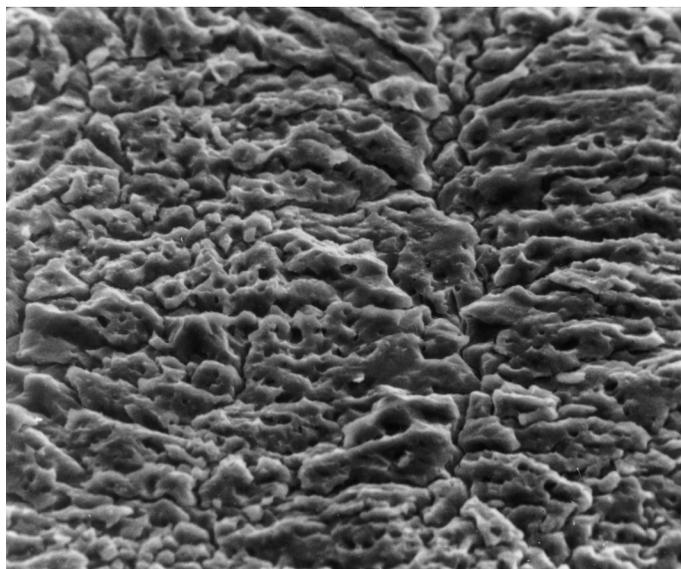
that Ordovician stromatoporoids secreted aragonite does not support the environmental control hypothesis, as the Mg/Ca ratio at that time is reconstructed as in the calcite field (STANLEY, 2006).

The  $\text{Sr}^{++}$  values of post-Ordovician stromatoporoids (including labechiids) analyzed by microprobe by MALLAMO

(MALLAMO & STEARN, 1991; MALLAMO, 1995) are all below 900 ppm, and most are below 400 ppm. Magnesium contents range from 2000 to 7000 ppm. These results confirm those of RUSH and CHAFETZ (1991) and strongly suggest that the precursor mineralogy of post-Ordovician stromatoporoids was calcite.



1



2

FIG. 345. 1, SEM, structural element showing fibrosity and central axis, longitudinal section, *Hammatostroma albertense* STEARN, 1961, SCRM 67-21, Frasnian, Cairn Formation, Mt. Haultain, western Alberta,  $\times 230$  (Stearn, 2010b); 2, SEM, coarse fibrosity and axial line in *Amphipora* sp., GSC 26144, Emsian-Eifelian, Ogilvie Formation, Yukon Territory, Canada,  $\times 750$  (Stearn, 2010b).

Comparison of post-Ordovician skeletal textures with those of better preserved fossils of animals that deposited high magnesium calcite (e.g., brachiopods)

suggests that stromatoporoids secreted high magnesium calcite that lost some of its original microstructure in conversion to low magnesium calcite.

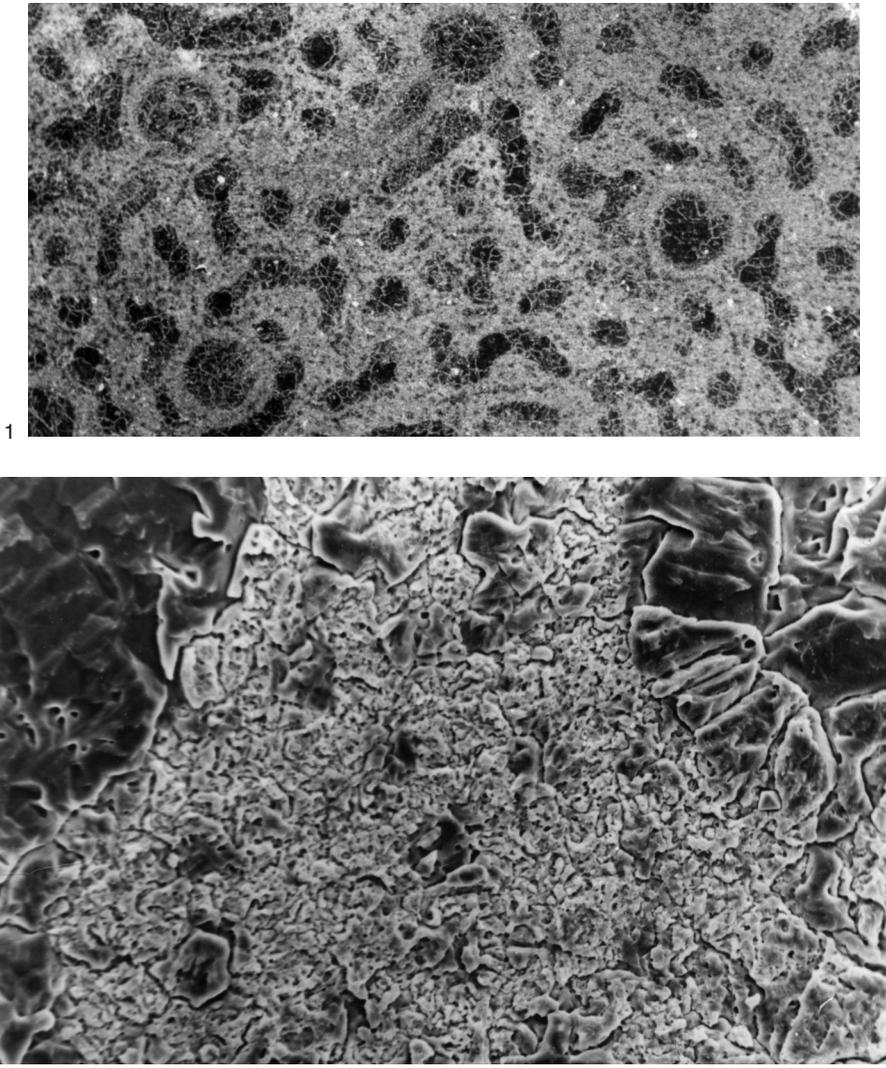


FIG. 346. 1, SEM, cellular microstructure of pachyστεles, tangential section, *Salairella buecheliensis* (BARGATZKY, 1881a), SCRM 116-1, Givetian, Blacourt Formation, Boulonnais, France,  $\times 34$  (Stearn, 2010b); 2, SEM, cellular microstructure, longitudinal section, *Salairella buecheliensis* (BARGATZKY, 1881a), SCRM 116-1, Givetian, Blacourt Formation, Boulonnais, France,  $\times 480$  (Stearn, 2010b).

Some studies of the geochemistry of living hypercalcified sponges have been applied to Paleozoic stromatoporoids. WEBB, WÖRHEIDE, and NOTHDURFT (2003) measured rare earth element geochemistry of living hypercalcified sponges and Devonian stromatoporoids and concluded that both resemble that of sea water. They concluded that these element distributions are consistent with a calcite skeleton in stromatoporoids. KAMBER and WEBB (2007)

used laser-ablation inductively coupled plasma-mass spectrometry to measure a wide suite of vital transition metals in Devonian limestones that included calcimicrobes and stromatoporoids. The stromatoporoid skeleton was enriched over the cement only in vanadium, whereas the calcimicrobe was enriched in vanadium, tin, copper, and zinc.

Some of these results from SEM studies and geochemistry are contradictory, but only

a few stromatoporoids have been analyzed for their trace elements. Much more work is required before the generalizations so far suggested can be confirmed.

#### COMPARISONS WITH MINERALOGY AND MICROSTRUCTURE OF MODERN HYPERCALCIFIED SPONGES

Comparisons with living sponges that secrete aspiculate basal skeletons have been used in the interpretation of the microstructure and mineralogy of Paleozoic stromatoporoids. The sponges *Calcifibrospongia* (see Fig. 181) and *Astrosclera* (see Fig. 154) are closest in macrostructure to that of the stromatoporoids. The skeleton of the former is composed of delicate structural elements composed of fibrous microcrystals of aragonite (Fig. 348.2) growing outward from their axes. The microstructure is trabecular, similar to that of the sclerodermites of scleractinian corals. The skeleton of *Astrosclera* (see Fig. 357) is composed of spherules of aragonite, about 20  $\mu\text{m}$  across, composed of radiating, fibrous crystals of aragonite. The spherules are secreted in cells and passed downward in the tissue to be cemented into the basal skeleton. In the bottom of this skeleton, the crystallites grow beyond the original boundaries of the spherules and join into a mosaic. STEARN (1975a) and WENDT (1984) suggested that stromatoporoids of cellular microstructure originally secreted spherulitic carbonate. Diagenetic changes then caused micritization of the centers of the spherules, resulting in melanospheric microstructures, and eventually replacement of the centers by coarser calcite spar, resulting in cellular microstructures. The lack of remnants of the spherulites in Paleozoic stromatoporoids, however, casts doubt on this interpretation (STEARNS & MAH, 1987).

The secretion of skeletons in such laminate stromatoporoids as clathrodictyids and stromatoporellids was compared by STEARN and PICKETT (1994) to that of the sphinctozoan sponges. The living genus

*Vaceletia* exhibits a sphinctozoan-like form, and it is now assigned to keratose demosponge order Dictyoceratida (see p. 273–276, Fig. 184). Its skeleton is composed of a very fine, nonfibrous mosaic of aragonite crystals, whereas some Triassic sphinctozoans are composed of aragonite and some of calcite.

Fibrous-spherulitic carbonate basal skeletons in modern sponges are not all aragonite. Both *Petrobiona* (see Fig. 206) and *Murrayona* (see Fig. 199), members of the class Calcarea, secrete fibrous and trabecular high-magnesium calcite whose texture locally resembles the fibrosity of some Paleozoic stromatoporoids. Some of the chaetetid-like living sponges secrete fibrous aragonite (*Ceratoporella*, see Fig. 156, Fig. 350) and others lamellar high-magnesium calcite (*Acanthochaetetes*, see Fig. 126). ROSENHEIM, SWART, and THORROLD (2005) measured trace elements in living *Ceratoporella* and showed that some of the ratios of Sr, Ba, and Ca could be correlated with temperature changes in the environment.

In conclusion, the mineralogy and microstructure of the carbonate of modern homologues to the stromatoporoids seem to be inadequate guides to the original mineralogy or microstructure of the stromatoporoids, as a wide range of conditions and compositions exists in the group.

#### DIAGENESIS AND INTERPRETATION OF MICROSTRUCTURES

In life, most stromatoporoids formed a basal skeleton in which the galleries, occupying more than half of the skeleton, were fluid filled. Possibly, as in modern scleractinians, the filling of the galleries with rim cements started during the life of the animal. The diagenesis of the fossil consisted of the filling of these internal cavities and the mineralogic and morphologic modification of the skeletal material. Most stromatoporoids lived in a reef environment and accumulated in sedimentary edifices noted for their porosity. Dolomitizing fluids had

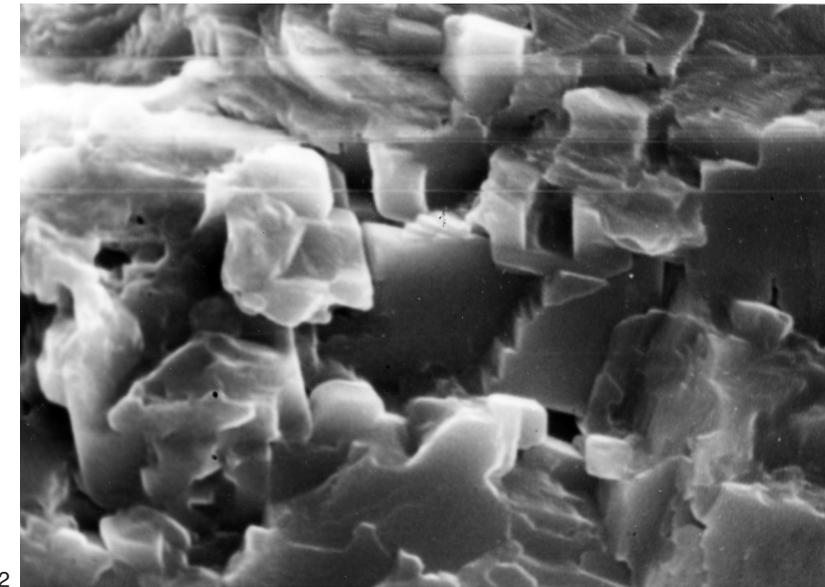
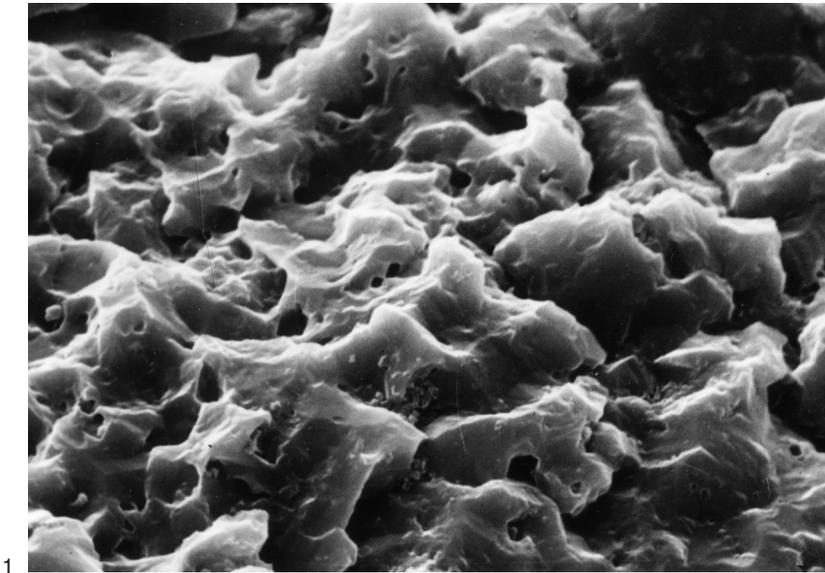


FIG. 347. 1, SEM, cavities in structural elements, some of rhombohedral outline, *Actinostroma* sp., RM 14811, Frasnian, Lime Creek Formation, Iowa, United States,  $\times 4800$  (Stearn, 2010b); 2, SEM, rhombohedral crystals and cavities, *Actinostroma* sp., RM 14811, Frasnian, Lime Creek Formation, Iowa, United States,  $\times 4700$  (Stearn, 2010b).

ready access to such masses. In many (for example, the edges of the Devonian reef complexes of Alberta), the effect of the flow of fluids through such porous and permeable masses has reduced the stromatoporoids that constructed the barrier to so-called ghosts in the pervasive sucrosic dolomite. Dolomiti-

zation may completely destroy the microstructure and obscure the macrostructure of stromatoporoids, but in many stromatoporoids from the Devonian of western Canada that have been dolomitized, fine details of both are revealed in dark-field illumination. Because the reef environments favored by

stromatoporoids are, by their ecological requirements, near to sea level, their skeletons may be exposed to diverse diagenetic environments, from vadose to both meteoric and marine phreatic. Petrographic studies to distinguish the influences of these various diagenetic environments have not been made on stromatoporoids.

Many of the microstructures observed in thin sections are diagenetic in origin, and paleontologists for the last 100 years have speculated on the original fabric, or fabrics, of the skeletal material and on the processes from which they have been derived. Viewpoints of early investigators are summarized by STEARN (1966, 1989b) and STEARN and MAH (1987).

Most of the studies of stromatoporoids have been directed naturally to well-preserved faunas and not to specimens that have been much affected by diagenesis (RIDING, 1974a). Details of microstructure and macrostructure are progressively lost, as aggrading neomorphism transforms the fossil into a mosaic of coarse, low magnesium calcite crystals. During this process, the twin laminae of calcite crystals may become evident and impose a fibrosity on the structural elements, particularly if the strata containing the fossils have been subject to deformation in mountain belts. In stromatoporoids with prominent pillars or pachyστεles, these may take on a waterjet fibrosity and grow to fill the interpillar space. Such structures were originally described by STEARN (1962) as a possible species of *Taleastroma* (*T.?* *confertum*) or *Syringostroma* (*S.?* *confertum*) (STEARNS, 1966). BIRKHEAD and MURRAY (1970) described similarly modified *Actinostroma* from the Swan Hills field. ZUKALOVA (1971) has illustrated similar structures under the name *Parallelopora perpetua* ZUKALOVA. Later, they were recognized as a diagenetic product of a variety of precursor species (STEARNS, 1975a).

Clathrodictyids, actinostromatids, and labechiids must have secreted a skeleton of randomly arranged microcrystals that results in a microstructure referred to as compact.

SEM studies have revealed little evidence that these crystals were fibrous in nature, and the fibrous fabrics evident in some specimens probably developed diagenetically.

The tubules within the compact elements of tubulate species resemble those of endolithic algae, such as *Ostreobium*, in the hard tissue of modern corals. However, the tubules in such genera as *Clathrocoilon* (0.04 mm) are an order of magnitude larger than those of boring algae. The recognition of questionable spicule traces in a Devonian stromatoporoid fragment (DA SILVA & others, 2011c, 2013) raises the possibility that the specimens referred to here as tubulate may have preserved irregularly shaped spicules.

The microstructure described as striated in the genus *Stachyodes* (Fig. 474) is suggestive of the apparently spiculate specimen described as a stromatoporoid by DA SILVA and others (2014). This opens a possibility requiring further study that *Stachyodes* is not a stromatoporoid, as herein defined, but a member of the Halichondrida and that the fragment described by these authors is of this genus. *Stachyodes* has several other features unique in the stromatoporoid that are discussed in later sections (see p. 824).

GALLOWAY (1957), GALLOWAY and ST. JEAN (1957), and ST. JEAN (1967) were influenced by the preservation of Middle Devonian stromatoporoids of the central United States to interpret the original fabric of the order Stromatoporida as full of hollow balls they called maculae. These appeared in thin sections in various preservation modes and orientations as: (1) opaque subspherical spots; (2) opaque annuli; or (3) light areas within a more opaque groundmass. STEARN (1966, 1989b) and STEARN and MAH (1987) explained these microstructures as diagenetic variants of originally cellular structural elements. They called the more opaque spots in a light groundmass melanospheres, rather than maculae, to distinguish them from the hollow balls (maculae) of GALLOWAY. STEARN (1989b) attributed melanospheric microstructure to the isolation of subspherical regions of inclusion-rich (speck-rich)

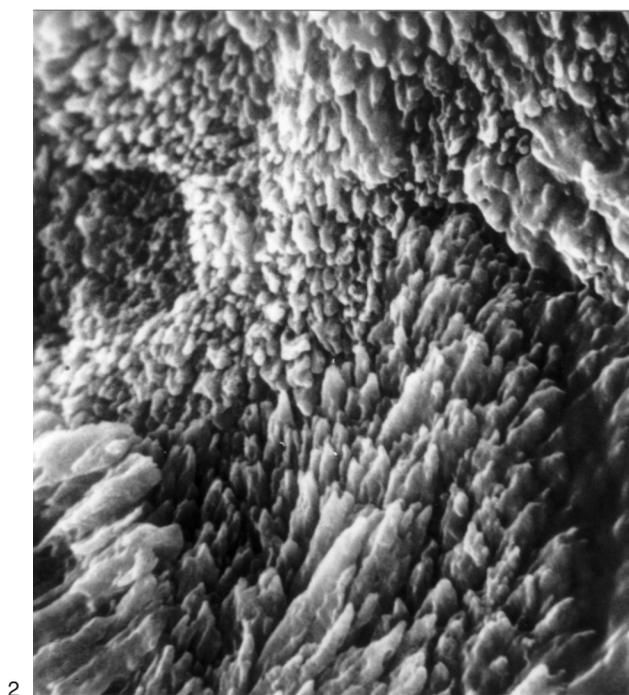
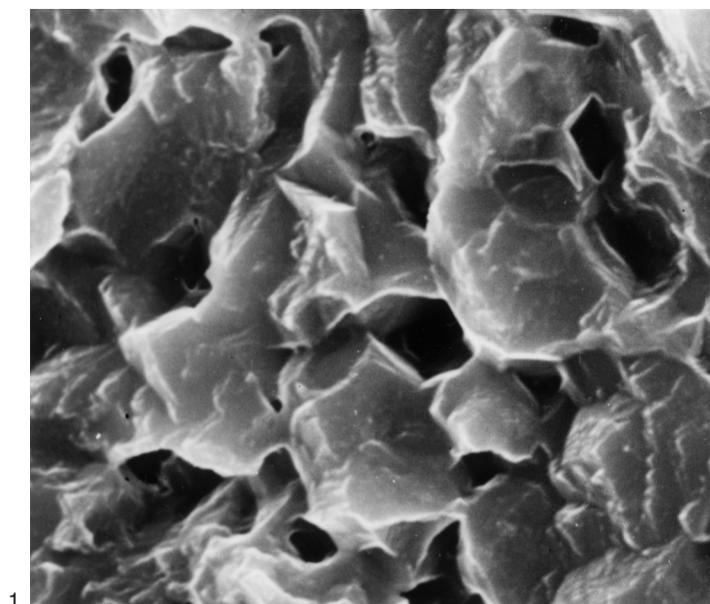


FIG. 348. 1, SEM, rhombohedral cavities in a structural element, *Actinostroma expansum* (HALL & WHITFIELD, 1873), SCRM 90-31, Frasnian, Shell Rock Formation, Iowa, United States,  $\times 7000$  (Stearn, 2010b); 2, SEM, fibrous aragonite skeleton of *Calcifibrospongia actinostromoides*, Recent, Bahama Island, SCRM 99-9,  $\times 7350$  (Stearn, 2010b).

carbonate between cellules by aggrading neomorphism.

In stromatoporoids termed microreticulate, the structural elements now contain what appear to be subspherical voids (cellules) arranged in longitudinal and tangential rows, as illustrated by *Parallelostroma* (Fig. 339.3). This microstructure may be conceived as being originally secreted as skeletal material: (1) containing regularly arranged cellules; or (2) composed of rectilinearly arranged micropillars and microcolliculi. The second viewpoint that the skeletal material of all stromatoporoids was laid down originally as a minute network (a replica of the macrostructure of *Actinostroma* but an order of magnitude smaller) was first stated by PARKS (1909) and can be followed through his later work (1936). This concept that the microstructure of the order Stromatoporida is basically a minute network of posts and beams was endorsed by KAŻMIERCZAK (1971), NESTOR (1974), and STOCK (1982, 1989). The first viewpoint that cellular microstructure is a separate, originally secreted microstructure, and the appearance of microreticulate stromatoporoids is the result of the regular superposition and horizontal alignment of cellules, can be followed through the works of NICHOLSON (1886a, 1889, 1891a, 1892), LECOMPTE (1951–1952), GALLOWAY (1957), and STEARN (1966, 1989b). Those who adopt the first viewpoint regard the arrangement of the voids as being of primary importance; those who favor the second viewpoint describe the microreticulate structure in terms of the dark material between the voids. In all but the most perfectly preserved specimens, the interpretation of the origin of the texture of specimens will be equivocal.

The hypothesis that all microstructures other than compact and fibrous are derived from original microcolliculi and micropillars (second viewpoint above) derives the other observed microstructures from this network as follows.

1. In **striated** microstructures, the micropillars (posts) dominate, and the microcolliculi are suppressed and commonly eliminated diagenetically. In rare specimens of *Stachyodes*

where the microcolliculi are preserved, traces of the original network can be seen.

2. **Ordinacellular** and its variant **tripartite** microstructure results where laminae are too thin to accommodate more than one layer of microgalleries.
3. **Tubulate** microstructure results from a peculiar preservation of tortuous microgalleries in basically ordinacellular tissue.
4. Where the microreticulum is irregular (acosmoreticular of STOCK, 1989) and neither micropillars nor microcolliculi align, the skeletal material appears **cellular**.
5. In tangential section, the cut ends of the micropillars define **melanospheres**, and in longitudinal section, they are the nodes between micropillars and microcolliculi.

The origin of microreticulate microstructure and its variants, orthoreticular and clinoreticular, is relevant to the phylogeny and classification of the stromatoporoids and is further discussed in Stromatoporellida, Stromatoporida, Syringostromatida, Amphiporida, and Genera With Uncertain Affinities (p. 781–836). The distinction between cellular and microreticular microstructures was used to separate the stromatoporoids into the orders Stromatoporida and Syringostromatida (STEARNS, 1993), and the difference between clinoreticular and orthoreticular is used in this volume to separate the families Coenostromatidae and Parallelostromatidae within the Syringostromatida. These microreticular microstructures are likely to have been derived from the finely reticular networks of the densastromatids. The origin of the cellular microstructures that characterize the Stromatoporida is more controversial. Some (STEARNS, 1993) postulated that they originated in late Llandovery time, in such genera as *Syringostromella* and *Stromatopora*, from clathrodityids before the appearance of microreticulate genera; others (STOCK, 1989) postulated that they are an irregular variant (acosmoreticular) of the microreticular microstructures that arose from the densastromatids.

# MORPHOLOGIC AFFINITIES OF THE PALEOZOIC STROMATOPOROIDEA TO OTHER FOSSIL AND RECENT GROUPS

COLIN W. STEARN

## INTRODUCTION

The Paleozoic stromatoporoids secreted a large calcareous skeleton of domical, laminar, bulbous, columnar, or branching form in common with many sessile, benthic, lower invertebrates such as the corals, hydrozoans, bryozoans, sponges, and encrusting foraminiferans; and also similar to some primitive members of the plant kingdom such as the green algae and cyanobacteria. In most of these groups, the skeleton is secreted of calcareous structural elements parallel and perpendicular to the growth surface—either forming a rectilinear, three-dimensional grid or making a less regular network of oblique and rectilinear elements—forming a continuous, space-enclosing framework. Reconstructions of the living stromatoporoïd animal (see Functional Morphology of the Paleozoic Stromatoporoïd Skeleton, p. 551–573) place the living tissue on the surface of this framework or penetrating it for only a few millimeters, as in many of the lower invertebrates listed above. The most significant way in which the stromatoporoïd skeleton differs from these is in the general lack of tubes, calices, or cups that housed individuals, such as polyps or zooids, and which indicate that the skeleton is secreted by associations of individuals; that is, it is colonial or clonal in nature. Instead, the skeleton is a largely uniform repetition of laminae, pillars, pachysteles, pachystromes, dissepiments, or tabulae, enclosing spaces initially occupied by soft tissue but ultimately abandoned as the organism grew upward, living only in the surficial layers and surface.

The nature of the stromatoporoïd skeleton was not revealed until thin sections were introduced in studies during the latter

part of the 19th century. Before this time, these fossils were considered to be related to corals or hydrozoans (for example, GOLDFUSS, 1826; and MILNE-EDWARDS & HAIME, 1851, who placed them with the chaetetes). ROSEN (1867), NICHOLSON and MURIE (1878), and SOLOMKO (1885) were among the first to place them with the sponges. LINDSTRÖM (1876) first suggested a relationship to the hydrozoans, and CARTER'S (1877) comparisons of stromatoporoïd skeletons with those of the Atlantic hydrozoan *Hydractinia* convinced NICHOLSON (1886a) that they were closely related. A list of paleontologists who acknowledged the Hydrozoa affinity of the stromatoporoïds would include most of those of the first three-quarters of the 20th century (see p. 545–546 below).

Although the hydrozoan hypothesis of the affinity of the stromatoporoïds was dominant through the latter part of the 19th century and the first 70 years of the 20th, some paleontologists maintained the sponge hypothesis. Among these was KIRKPATRICK (1912b), whose pioneering and beautiful work on the hypercalcified sponge *Merlia* (KIRKPATRICK, 1910a, 1911) was overshadowed by his subsequent unbelievable, and universally rejected, views on the nature of all rocks (KIRKPATRICK, 1913; GOULD, 1980). HEINRICH (1914b) also maintained that stromatoporoïds were sponges, but unfortunately he was killed in the First World War, after the publication of his dissertation. The sponge hypothesis was revived by the work of HARTMAN and GOREAU (1970) on Caribbean hypercalcified sponges and since has become the most widely accepted position. Yet only recently (BOL'SHAKOVA, 1993) has the work of HARTMAN and GOREAU (1970) on the hypercalcified sponges had an impact

on Russian stromatoporoid specialists. The position that the stromatoporoids were sponges is adopted herein and is more fully explored in the following section on functional morphology (see p. 544–549). The morphologic similarities of the Paleozoic stromatoporoids that have suggested to some that they belong in groups other than the hypercalcified sponges will be briefly considered in this section.

### FOSSIL GROUPS COMPARED TO PALEOZOIC STROMATOPOROIDS

#### FORAMINIFERA

DAWSON's (1879) interpretations of the structure of stromatoporoids in terms of the anatomy of rhizopod Foraminifera came to him via his interest in the Proterozoic pseudofossil *Eozoon*, which he believed to be a giant foraminiferan. Both *Eozoon* and the stromatoporoids are coarsely laminated structures, and, in both, DAWSON imagined he could make out the framework that is permeated completely by poorly organized cellular material in the Foraminifera. HICKSON (1934) studied the skeletal structure of *Gypsina plana*, a common encruster in reefs worldwide today, and compared it to that of stromatoporoids. PARKS (1935) compared the fine-chambered structure of *Gypsina* with that of some species of *Actinostroma* that would be placed in the densastromatids now, and of *Clathrodictyon*. In the cellular structure of the laminae of some of the latter and the microgalleries between the micropillars of the former, he saw cavities comparable in size and form to those of the foraminiferan, but he was puzzled by the lack of pores in the structural elements of most stromatoporoids and had problems accounting for the coarse textures and solid structural elements of most actinostromatids and clathrodictyids. He planned to elaborate on his hypothesis in a volume of his monograph on Devonian stromatoporoids that remained unpublished at his death. No paleontologist has since supported his hypothesis.

### ARCHAEOCYATHS AND SPHINCTOZOANS

YAVORSKY (1932) described several genera with laminar structures from the Cambrian of Siberia as stromatoporoids related to *Actinostroma* and *Clathrodictyon*. These forms were later established as the new genera *Praeactinostroma* and *Korovinella* by KHALFINA (1960b). Subsequent Soviet writers established the genus *Cambrostroma* and recognized *Clathrodictyon* (VLASOV, 1961) from the same lower Cambrian beds in the Altai region. GALLOWAY (1957) dismissed these forms as stromatoporoid ancestors on the basis that they could not have been collected from Cambrian beds, because they were too advanced. NESTOR's (1966b) examination of these forms showed they had porous structural elements, vase shapes, and empty central canals, unlike any stromatoporoid, but were similar in these features to archaeocyaths. Since then no paleontologists have included these Cambrian genera in the Stromatoporoidea.

HLADIL (2007) has compared some tubular microfossils that he identifies as early stages of Devonian amphiporid stromatoporoids with the early stages of archaeocyaths from the early Cambrian of Mongolia. The Devonian microfossils grew up from a basal disk, about 0.25 mm across, into a first chamber that may have septa or tubercles. The chamber then was extended upward into an expanding tube up to 2 mm long. Spongiform outgrowths were then formed in the tube and organized into an inner and outer wall. The similarity of these microfossils to the early stages of the much older archaeocyaths (at least 85 myr older than the oldest amphiporids) is close, but whether this similarity is sufficient to justify their being united into a single group that HLADIL (2007) suggests be called the Amphicyathida is doubtful. His suggestion that the strawlike adult amphiporids were supported by the buoyancy of gas bubbles in the upper parts of the stem is ingenious.

Another group of enigmatic, cystose, encrusting fossils from the lower Cambrian of Siberia has been thought to have connections to the stromatoporoids or archaeocyaths. These are classified by STEARN and others (1999) as the family Khasaktiidae SAYUTINA (1980). Although the title of SAYUTINA's paper suggests these forms are possible stromatoporoids, WEBBY (in STEARN & others, 1999, p. 59) described them as "probably not stromatoporoids" (see also ZHURAVLEV, DEBRENNE, & LAFUSTE, 1993; DEBRENNE & REITNER, 2001; PRATT & others, 2001; and see p. 576–577).

STEARNS and PICKETT (1994) have explored the similarity of some of the laminar stromatoporoids that secrete their skeletons in modules separated by growth pauses. They compared the modules of such sphinctozoan genera as *Cliefdenella* WEBBY, *Verticillites* DEFRENCE, and *Madonia* SENOWBARI-DARYAN & SCHÄFER, with those of *Stictostroma* PARKS, *Simplexodictyon* BOGOYAVLENSKAYA, and *Stromatoporella* NICHOLSON. Like some stromatoporoids, some sphinctozoans secreted a large, domical skeleton of superposed composite laminae, each consisting of upper and lower layers. The laminae are separated by complex pillars that cross the modules in both groups. This similarity in the way the skeleton is secreted does not imply that sponges of the sphinctozoan grade of construction are ancestors of these more advanced stromatoporoid genera but that the poriferan nature of both allowed for a convergent relationship. The secretion of the stromatoporoid skeleton in modules is further considered in the section on functional morphology (see p. 551–573).

### CHAETETIDS

In the 19th century, the chaetetids were considered to belong to the phyla Cnidaria or Bryozoa. The discoveries that chaetetiids had spicules (GRAY, 1980) and astrorhizae and that some of the living hypercalci-fied sponges, such as *Acanthochaetetes* and *Merlia*, had skeletons that resemble the honeycomb structure of the fossil chae-

tetids established that this group belongs in the phylum Porifera (see Introduction to the Fossil Hypercalci-fied Chaetetid-Type Porifera, p. 15–79). Typical stromatoporoid and chaetetid skeletons are not similar, but intermediate forms exist. The stromatoporoid skeleton is a continuous, irregular, three-dimensional meshwork; that of the chaetetids is ideally composed of walls separating adjacent, regularly cylindrical, or six-sided voids. In typical stromatoporoids, the spaces between the structural elements in tangential section are confluent, vermiform, and labyrinthine; in typical chaetetids, they are closed and subhexagonal to round in cross section. However, in some chaetetids (e.g., *Chaetetipora*, *Chaetetiporella*), the walls of the tubules break down, and the voids become confluent, appearing in cross section like the allotubes of stromatoporoids. In some Paleozoic stromatoporoids, such as *Salairella*, the voids between the vertical structural elements are closed (autotubes), and tangential sections may closely resemble those of chaetetids. The similarity between chaetetids and stromatoporoids also extends to the presence of astrorhizae in both groups (DEHORNE, 1920; CUIF & others, 1973; WEST & CLARK, 1984); this is a feature both share with a variety of encrusting sponges and Mesozoic stromatoporoid-like genera, and possibly the disjectoporids as well. The fibrous or trabecular microstructure of fossil chaetetids that may indicate an original aragonite mineralogy is not common in stromatoporoids but has been identified in such genera as *Amphipora* and *Tienodictyon*.

In summary, no single criterion easily separates the chaetetid skeleton from that of the stromatoporoids, and both have been recognized as merely grades of construction of hypercalci-fied sponges (WOOD, 1991b). However, typical exemplars of each group are unequivocally different.

### HYDROZOA AND DISJECTOPORIDS

In the first three-quarters of the 20th century, most paleontologists acknowledged the hydrozoan affinity of the

stromatoporoids (KÜHN, 1927, 1939b; LECOMPTE, 1951–1952, 1952a; GALLOWAY, 1957; FLÜGEL & FLÜGEL-KAHLER, 1968; KAŻMIERCZAK, 1971; BOL'SHAKOVA, 1973; FLÜGEL, 1975; BOGOYAVLENSKAYA & YANET, 1983; BOGOYAVLENSKAYA, 1984; MORI, 1984; BOGOYAVLENSKAYA & KHROMYKH, 1985; BOGOYAVLENSKAYA & YELKIN, 2011). The acceptance of the assignment of the Paleozoic stromatoporoids to the Hydrozoa in the 1870s set off a century of study of living hydrozoans in order to draw homologies between the living and fossil organisms. Because NICHOLSON (1886a) had divided the fossils into hydractinoid and milleporoid groups, attention was focused on modern *Hydractinia* and *Millepora*. The most extensive study of the former was by TRIPP (1929, 1932). These studies were summarized by KÜHN (1939b, p. 4–13) in the *Handbuch der Paläozoologie*. Less detailed comparisons between the fossils and hydrozoans can be found in LECOMPTE (1956), KAŻMIERCZAK (1971), FLÜGEL (1975), and BOGOYAVLENSKAYA (1984, chapter IV, fig. 9).

*Hydractinia* secretes a delicate skeleton of calcareous spines and a few horizontal plates or floors that form an edifice of two or three stories. The hydrozoan commonly encrusts gastropod shells. The spines have been compared to pillars of such stromatoporoids as *Actinostroma* and the floors to laminae of such genera as *Clathrodictyon*. The surface of the skeleton also rises into protuberances that have been likened to mamelons. The individuals of the colony are embedded in the surficial organic layer and do not make an impression on the skeleton. They are connected by canals by which they share nutrients in what is called the hydrorhizal system. These canals have been given particular attention, as they have some similarities to the astrorhizal systems of stromatoporoids. The canals form a continuous network connecting the individual polyps, and, unlike astrorhizae, they do not narrow away from the centers of confluence nor meld with interspaces in the structure

distally. The homology of astrorhizae with the exhalant systems of encrusting sponges is much more convincing and is further discussed in the chapter on Functional Morphology (see p. 551–573).

The supposed homology of the stromatoporoids of amalgamate structure with *Millepora* has received little attention in the literature, perhaps because it is even less convincing than that of *Hydractinia*. *Millepora* has an amalgamate network of entwining structural elements, but, unlike those of the stromatoporoids, these are composed of spherulitic carbonate and are penetrated by discrete, tabulated tubes of two sizes that housed the dimorphic polyps. These tubes were homologized by NICHOLSON (1886a) with the autotubes and allotubes of the stromatoporoids, and he called them zooidal tubes (NICHOLSON, 1886a, p. 49). GALLOWAY (1957) implied that the homology was not as certain as that postulated by NICHOLSON (1886a) and preferred to use the term pseudozooidal. Although astrorhizae are common in the amalgamate stromatoporoids, no similar structures are present in *Millepora* and its relatives.

The Mesozoic stromatoporoid-like genus *Milleporidium* has a structure that seems to be transitional from the hydrozoans to the stromatoporoids. The skeleton is dominated by tabulated tubes of two calibers that closely resemble the zooidal tubes of *Millepora* and suggests the dimorphism that characterizes this genus. The relationships of these Mesozoic forms, which are apparently transitional to hydrozoans, to the Paleozoic Stromatoporoidea and to the other Mesozoic stromatoporoid-like genera, is problematic.

The disjectoporoids of the late Paleozoic and early Mesozoic have commonly been recognized as hydrozoans (e.g., LECOMPTE, 1956, p. 138; FLÜGEL & SY, 1959) but share many features with Paleozoic stromatoporoids. They have a laminar and encrusting skeleton composed of an irregular, three-dimensional meshwork of longitudinal and tangential rods that are thickened where

they join to enclose rounded voids. The mesh may be traversed by longitudinal tubes and an irregular tangential canal system, which has been compared to the astrophorizae in Paleozoic stromatoporoids. Some thin sections of disjectoporids superficially resemble those of stromatoporoid genera, such as *Gerronostromaria* or *Actinostroma*, but it is the canal systems that suggest that the group is related to the Paleozoic stromatoporoids. Generally, these canals branch through the structure but do not form star-shaped clusters as in the stromatoporoids. In some Permian disjectoporids (e.g., *Radiotrabeculopora*), the structural elements merge in the interior of the skeleton to produce subcylindrical interspaces that resemble the tubules of chaetetids. Elsewhere the disjectoporids have been described (see Family Disjectoporidae, p. 311–320), they are tentatively placed in the order Inozoa of the calcareous sponges. Unfortunately, diagnostic spicules that would make classification easier only doubtfully occur in disjectoporids, although TERMIER and TERMIER (1977b, p. 61) recognized some units of “calcite monocrySTALLINES et carénées,” which they interpreted as altered triactine spicules. The disjectoporids are unlikely to be descendants of the early Paleozoic stromatoporoids (but see TERMIER & TERMIER, 1977b, p. 80), as they are separated from them in time by the Carboniferous period and are only superficially similar. They are more likely to be a result of convergent evolution in the calcareous sponges.

#### TABULATE CORALS (CNIDARIA)

The similarity of structural elements in some members of the order Tabulata (including heliolitid corals) and the Paleozoic stromatoporoids was discussed in detail by NESTOR (1981a). He noted that both groups have representatives that are composed of solid trabecular calcite, cyst plates, tabulated tubes, and finely reticulated so-called coenenchyme. Many of these features of the heliolitid corals are duplicated

in the stromatoporoid genera *Lophiostroma*, *Cystostroma*, and *Actinostromella*, according to NESTOR (1981a). He accounted for the absence of calices on the surface of the skeletons of stromatoporoids by the high position of their polyps on top of a thick layer of organic matter mantling the skeleton. Particular attention was paid by NESTOR (1981a) to the similarities between the solid skeletons of *Lophiostroma* and the heliolitid *Protaraea*. The similarity between tabulates and stromatoporoids that is evident in longitudinal section is much less convincing in tangential section. While it is true that both heliolitids and stromatoporoids were built of comparable structural elements, so are the skeletons of most of the lower invertebrates, and detailed comparisons of individual taxa do not therefore give a unique solution to the affinity of the stromatoporoids.

#### SCLERACTINIAN CORALS (CNIDARIA)

MORI (1982, 1984) drew attention to putative homologies between the skeletons of the scleractinian order of the modern corals and the Paleozoic stromatoporoids. He proposed that the latter be the class Stromatoporata of the phylum Coelenterata and contain the orders Stromatoporoidea and Sphaeractinoidea. The skeleton of *Acropora* is compared to that of *Gerronostromaria*; that of *Galaxea* with that of *Cystostroma*; and that of *Dendrophyllia* with that of *Parallelostroma*. MORI (1982) rejected the hypothesis that the astrophorizae are a poriferan exhalant system, citing evidence that structural elements are thickened near them, just as thickening occurs in the skeletons of scleractinians near the sites of polyps; that they are crossed by tabulae; and that their similarity to exhalant systems is not close. He concluded that they are tubes that contained zooids probably housing reproductive organs.

MORI's (1982) arguments in favor of placement of the stromatoporoids as a class of the Anthozoa comparable to the Scleractinia are based largely on comparisons

of structures that are common to many skeletonized lower invertebrates and do not provide a satisfactory answer to the function of the astrorhizae.

#### MESOZOIC STROMATOPOROID-LIKE GENERA

The gross similarity between the Paleozoic Stromatoporoidea and the Mesozoic stromatoporoid-like forms is so great that LECOMPTE (1956) united genera of the two groups in the same families (see also Post-Devonian Hypercalcified Sponges, p. 193–208). The principal similarities extend to practically all the macrostructural features found in the orders Stromatoporida, Actinostromatida, Clathrodictyida, and Syringostromatida. No forms comparable to genera of the Stromatoporellida, Amphiporida, or Labechiida are known in the Mesozoic group. The principal differences between the Mesozoic and Paleozoic groups can be summarized as follows.

1. Microstructure: The structural elements of the Mesozoic group are uniformly trabecular, that is, composed of fibrous carbonate (now calcite but likely pseudomorphic after aragonite), whereas such microstructure is rare in Paleozoic forms; cellular and melanospheric microstructures are unknown in the Mesozoic group.
2. Several of the Mesozoic forms contain spicule pseudomorphs, whereas none has been confirmed in Paleozoic forms.
3. The families Milleporellidae and Milleporidiidae, usually classified as so-called Mesozoic stromatoporoids, are composed largely of tabulated longitudinal tubes (in some genera they are composed of two calibers that suggest a dimorphism); they seem to have skeletons transitional from those of stromatoporoids to those of the Hydrozoa or other groups of the Cnidaria. They might also be placed in the chaetetes. KÜHN (1939b) placed them in the hydroids, entirely separate from the class Stromatoporoidea. The classification of these transitional forms was discussed and

illustrated by STEARN (1984) and requires further consideration.

Those genera that show spicules have been separated herein into various taxa of the Demospongiae; those devoid of spicular evidence are listed alphabetically (p. 308–309). The time gap between the last of the Paleozoic stromatoporoids and the Mesozoic stromatoporoid-like genera (more than two periods, even if *Circopora* is recognized as the first of these) suggests that they are not direct descendants of the Paleozoic stromatoporoids but, like the disjectoporida, are a poriferan group of convergent morphology. MISTIAEN (1984b, 1994) proposed that the Paleozoic stromatoporoids decreased in density toward the Late Devonian, owing to changes in water temperature and chemistry and eventually then lost their ability to secrete a carbonate skeleton. They were postulated to have persisted in late Paleozoic seas as soft-bodied animals and reappeared in the fossil record when conditions changed to greenhouse conditions in the Mesozoic.

#### CYANOBACTERIA

Since the beginning of life on Earth, bacteria, by secretion of carbonates and trapping of sediments, have constructed layered structures that have been mistaken for stromatoporoids. Before fossils were investigated using thin sections, these structures were given names like *Megastroma*, *Parastroma*, *Dictyostroma*, and *Neostroma*, which implied a relationship to the stromatoporoids. Most of these genera (see list in KÜHN, 1939b), when viewed in thin section, were shown to be indeterminate crusts formed by bacterial biofilms trapping sediments and building up laminated structures. They could be easily distinguished from the complex skeletons of structural elements secreted by the stromatoporoids.

However, KAŹMIERCZAK (1976, 1980, 1981) recognized, on the basis of some exceptionally preserved specimens, that the Paleozoic stromatoporoid skeletons composed of laminae, pillars, pachyστεles,

and pachystromes were also secreted by cyanobacteria. He proposed that the astro-rhizae were traces of the filamentous juvenile stages of colonial cyanobacteria (blue-green algae), because in the specimens he investigated they were filled with dark granules. He believed these granules were calcified cells of cyanobacteria and, because they resembled melanospheres within structural elements, that they were also composed of calcified cyanobacteria. KAŻMIERCZAK and KRUMBEIN (1983) identified rounded cavities seen in scanning electron micrographs in a specimen of *Ecclimadictyon* from the Silurian of Gotland as the remains of these cells. KAŻMIERCZAK and KEMPE (1990) described calcareous crusts formed of cysts by a cyanobacterium in an alkaline crater lake in Indonesia as a modern analogue of the Paleozoic stromatoporoids. They suggested that the similarity of these crusts to Paleozoic stromatoporoids indicated that the latter may have lived in seawater with greater alkalinity and carbonate saturation than modern seawater. Only KAŻMIERCZAK and his co-authors (cited above) have supported the cyanobacterial hypothesis, and several

authors have pointed to its weaknesses. RIDING and KERSHAW (1977) pointed out that KAŻMIERCZAK had failed to consider the more widely held theories on the origin of melanospheric microstructure and that the skeletal organization of the Paleozoic stromatoporoids indicated they were "higher organisms than cyanophytes" (RIDING & KERSHAW, 1977, p. 178). MONTY (1981) and SCRUTTON (1979) expressed similar views.

## CONCLUSIONS

Although the skeletal elements and microstructures of the Paleozoic stromatoporoids are common to many groups of lower invertebrates and mimicked by the cyanobacteria, if all the evidence is taken into account, rather than comparisons with specific taxa or exceptional specimens, their identity with encrusting hypercalcified sponges is entirely convincing. The long controversy over the place of this fossil group in the animal kingdom is essentially over. Comparisons in detail of various features of the stromatoporoids with those of the encrusting sponges can be found in the section on functional morphology (see p. 551–573).



# FUNCTIONAL MORPHOLOGY OF THE PALEOZOIC STROMATOPOROID SKELETON

COLIN W. STEARN

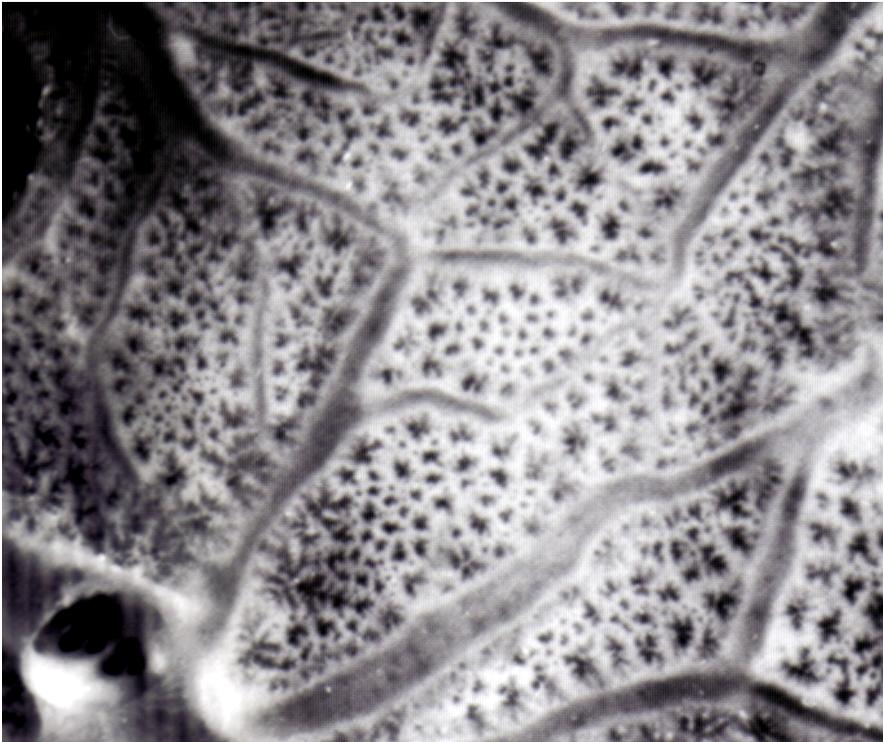
## INTRODUCTION

Interpretation of the life processes of long-dead fossil organisms proceeds by comparisons of their morphologic features with engineering models of their possible functions and by comparisons with living organisms of similar form whose functions can be observed directly (HICKMAN, 1988). For stromatoporoids, both methods are possible, as the laws of fluid mechanics can be applied to their canal systems, and living sponges have some morphologic features of fossil stromatoporoid skeletons.

Until 1970, the Paleozoic stromatoporoids had been considered by most paleontologists to be hydrozoans, but since that time the conviction that they were sponges has grown to a virtual certainty. Evidence for this assignment and evidence against their affinity to other groups, such as the Foraminifera, cyanobacteria, and corals, to which they had been assigned formerly, is presented in the section on morphologic affinities (p. 543–549). This discussion of their functional morphology is predicated on their placement in the phylum Porifera. Like sponges, the Paleozoic stromatoporoids were sessile, suspension-feeding acoelomate invertebrates that ingested very fine suspended food, such as bacteria, and also probably dissolved organic nutrients. They obtained this food through a water-processing system that included fine, widely distributed pores that pulled sea water into a set of inhalant canals leading to chambers lined with flagellated cells. These flagellated cells and cells in contact with the entering water current trapped a variety of microorganisms and detritus.

“Sponges are little more than highly elaborate manifolds of pipes with lots of small pores and one, or a few, large, commonly

apical openings on their surfaces” (VOGEL, 1994, p. 38). The laws governing the flow of fluids through these manifolds (and hence the morphology of the organism) are conveniently summarized by Steven VOGEL in the book, *Life in Moving Fluids* (2nd edit., 1994). Water is impelled through the tubes by flagellated cells (choanocytes) grouped in minute chambers. The helicoidal beating of the flagella draws water through sievelike villi arranged in a collar at their bases, where food is trapped and ingested. In order to enter the inhalant pores on the outer surface and be available for intracellular digestion in the sponge soft tissue, the nutrient particles can be no more than a few micrometers in diameter and are thought to be largely bacteria. The motion of the flagella also pumps the cleared water out through canals of increasing diameter to external orifices called oscula. The outflow velocity of a single osculum may be as high as 20 cm per second, and, although the contribution of each flagellum is almost infinitely small, the tens of thousands of them that contribute to the water flow allow a sponge to process water equal to its own volume every five seconds (REISWIG, 1974). The most familiar marine sponges are cylindrical or vase shaped, and water enters the outer surface of the vase and exits via an interior cavity (spongocoel) from an osculum at the top. However, the stromatoporoids must have resembled modern encrusting sponges in which openings for inhalant and exhalant water currents share different parts of the same upper surface. Such sponges, and many other features of sponge anatomy, are illustrated by DE VOS and others (1991) (Fig. 349.1). The relationships between the soft tissue and skeleton of most living sponges is not relevant to the understanding of the function of the skeleton of Paleozoic stromatoporoids,



1

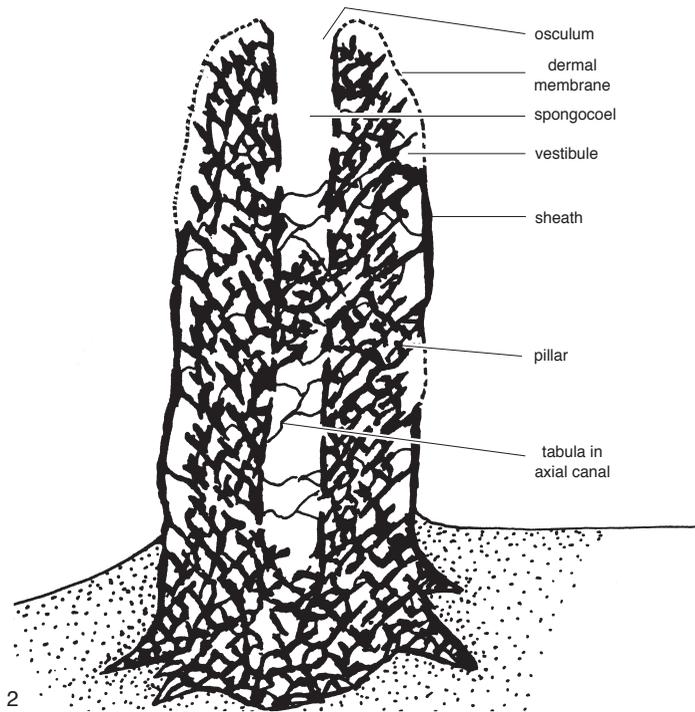


FIG. 349. (For explanation, see facing page).

because the great majority of living sponges support their tissues with spicules made of silica, which are bound together by organic compounds subject to decay on death. This structural design is unknown in Paleozoic stromatoporoids. Only the few encrusting sponges of the modern fauna that secreted a basal calcareous skeleton provide a model for these extinct organisms.

The work of Willard HARTMAN and Thomas GOREAU (1970, 1972, 1975) in the late 1960s on the living hypercalcified sponges of Jamaica supplied a specific living model for the extinct Paleozoic stromatoporoids. The skeleton of these sponges is either solid carbonate or the inner cavities, once occupied by soft tissue, are sealed off, abandoned, and fill with sea water as the sponge grows larger. Among the stromatoporoids, only the skeleton of the enigmatic *Lophiostroma* is solid; the rest must have secreted their skeletons, much as hypercalcified sponges such as *Acanthochaetetes* and *Calcifibrospongia* do today. In these genera, soft tissue occupies only the upper interskeletal spaces, and the spaces below this thin living layer contain only water.

## COLONIES OR INDIVIDUALS

Lack of evidence for multiple skeletal cavities, tubes, or enclosures suitable to house polyps in the stromatoporoid skeleton has convinced most paleontologists that the group cannot be closely related to clonal cnidarians such as hydrozoans, rugosans, or tabulates. A few paleontologists have modeled the astrorhizae as polyp sites (most recently BOGOYAVLENSKAYA, 1984), but this model does not explain their form, as discussed below (p. 572). The skeletons of several of the living hypercalcified sponges (*Ceratoporella*, *Merlia*, *Acanthochaetetes*) are divided into pseudocalices (small cavities in the upper surface containing units of the

filtering system (see Fig. 355; Fig. 356.1), but the stromatoporoid skeleton is distinctive in that it must have been essentially continuous across the growing surface.

This is not the place to review the long controversy over whether sponges should be considered individuals or modular organisms. HARTMAN and REISWIG (1973) and FRY (1979) have provided summary discussions. These three, and also FINKS (2003a, p. 213), regarded sponges as individuals with unitary control over their aquiferous systems. WOOD, ZHURAVLEV, and DEBRENNE (1992), following others, preferred to characterize most sponges, including stromatoporoids, as modular, and defined the repeated unit as the drainage area of a single osculum (Fig. 350). As applied to stromatoporoids, this would be the tissue and canals draining into a single astrorhizal system. However, the canal systems feeding an osculum may form a continuous, interconnected network over the surface of an encrusting sponge, and the so-called modules, defined on the basis of drainage areas, then have no boundaries in these sponges (Fig. 349.1). Also, in living sponges, reorganization of the oscular units of the aquiferous system in dimensions, spacing, and position may take place in a day. Such modules are in no way comparable to the individuals that form the skeletons of clonal animals in the Cnidaria, Bryozoa, or Hemichordata. In a few stromatoporoids, the astrorhizae, immobilized by encasement in the skeleton, maintained their position over long periods, becoming superposed as the skeleton grew; but in most stromatoporoids, the repeated reorganization of the aquiferous system is shown by the scattered distribution of canals observed in longitudinal sections. Evolutionary trends from individuals, through distinct modularity to integration of modules into a whole, have been traced through the Cnidaria (COATES & OLIVER, 1973) and Archaeocyatha (WOOD,

FIG. 349. 1, Surface of the living sponge *Spirastrella* showing network of exhalant canals (De Vos & others, 1991); 2, reconstruction of digitate stromatoporoid *Amphipora ramosa* (PHILLIPS, 1841) in axial section, showing position of peripheral sheaths and dermal membrane (uncalcified) enclosing vestibules; actual specimens are 3–4 mm in diameter (Stearn, 1997c).

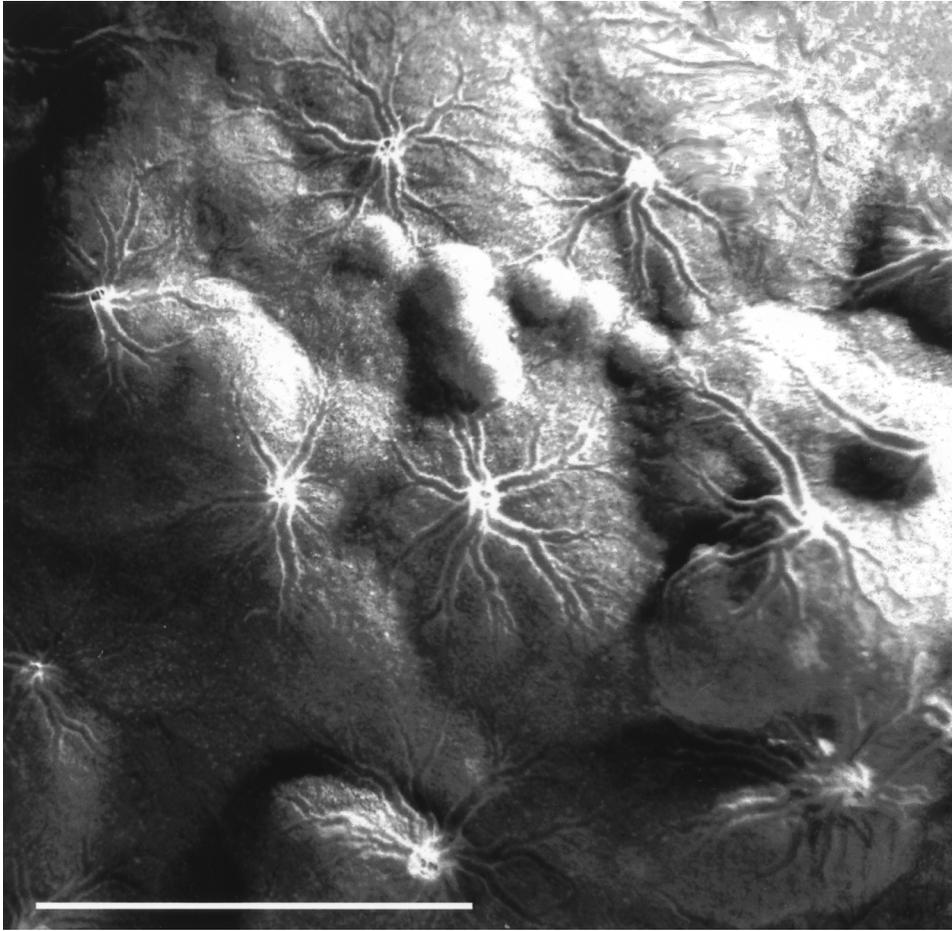


FIG. 350. Exhalant canal system, *Ceratoporella nicholsoni* (HICKSON, 1911), living specimen, Runaway Bay, Jamaica, scale bar, 2 cm (Stearn, 2010d; courtesy of H. Reiswig).

ZHURAVLEV, & DEBRENNE, 1992). No such trends are evident in the Paleozoic stromatoporoids. STEARN and PICKETT (1994) have used the term module more appropriately as a skeletal unit added repeatedly during growth (see p. 563–566, below).

### SPICULES

Nearly all Paleozoic stromatoporoid fossils differ from those of other sponges by their lack of spicules. Although both KIRKPATRICK (1912b) and TWITCHELL (1928–1929) reported seeing the remains of spicules in Paleozoic stromatoporoids, no reports of similar observations were published for

almost 100 years. DA SILVA and others (2013) have illustrated and analyzed spicules from a stromatoporoid fragment in the Devonian of the Ardennes. Although opaline spicules would be unstable in the calcium carbonate environment of the stromatoporoid skeleton, calcareous pseudomorphs apparently have survived in exceptional circumstances.

REITNER and WÖRHEIDE (2002, p. 59, fig. 12) have claimed that a specimen of “*Syringostroma cf. borealis* (NICHOLSON, 1875 [sic]),” from the Middle Devonian of Spain, is the only Paleozoic stromatoporoid showing spicules, in this case, “aster microscleres.” (The taxon referred to here is obscure, as

NICHOLSON described only a single species under the name *borealis* in 1891b from the Silurian of Estonia; a species now assigned to *Syringostromella*.) The Spanish specimen is here interpreted as showing coarsely cellular microstructure. Spicular pseudomorphs have been reported in late Paleozoic chaetetids and Mesozoic stromatoporoid-like genera (GRAY, 1980; WOOD & REITNER, 1986). However, the scarcity of specimens preserving spicule pseudomorphs among those examined through 150 years of study suggests that the great majority did not secrete spicules, or did not incorporate them in their calcareous skeletons.

The presence of spicules in a late Carboniferous sponge, *Newellia mira* (NEWELL), as reported by WOOD, REITNER, and WEST (1989), does not modify this statement, as this form (originally described with the stromatoporoid name *Parallelopora mira*) was never accepted by specialists as part of the Paleozoic stromatoporoid group. The relationship of spicules to basal skeletons in living hypercalcified sponges that are used as models for stromatoporoids is further considered in Microstructure section (p. 521–542).

## FUNCTION OF THE SKELETON AS A WHOLE

Why did stromatoporoids secrete a basal skeleton and why did they grow in forms shared by many clonal lower invertebrates that live in the reef environment? Because such organisms shared encrusting, tabular, domical, columnar, and dendroid shapes, we can conclude that the environmental and genetic controls on their growth were probably similar. The adaptations of these specific growth forms have been discussed by KERSHAW (1984, 1998), KERSHAW and BRUNTON (1999), KANO (1990), and several others and are summarized elsewhere (see section on external morphology, p. 419–486).

The major environmental factor affecting the growth form of stromatoporoids was rate of sedimentation (KERSHAW, 1993). It follows

that a major function of the skeleton was to raise the sponge above the sediment surface where particles would tend to clog the tiny incurrent pores. A modern sponge's defensive response to sediment is demonstrated when fine sediment is stirred up in storms, and the sponge closes its inhalant porocytes so that the filtration system does not clog (REISWIG, 1971). Because water is clearer higher in the water column, the stromatoporoid sponge gained by growing its top and side feeding surfaces above the turbid bottom waters. In areas of rapid sedimentation, rapid growth of the skeleton was necessary to keep the feeding surfaces from being buried, not just clogged. Why this group of sponges chose to support themselves above the accumulating sediment by means of a basal calcareous skeleton. That they did so over a period of 170 million years shows that this was a successful body plan and that the calcareous skeleton is a primitive shared characteristic of this unitary group.

KAZMIERCZAK, ITTEKOT, and DEGENS (1985) postulated that hypercalcified sponges and their ancestors secreted a basal skeleton, because they had to rid themselves of intracellular calcium ions. They believed that cyclic changes in calcium-ion concentrations in the marine environment caused deposition of laminae in stromatoporoids. REITNER and WÖRHEIDE (2002, p. 54) have postulated that Ca detoxification was a basic mineralization process in archaeocyaths and sphinctozoans and could be a model for all "irregular, micro-granular basal skeletons of 'stromatoporoid' and 'thalamid' grades of organization."

SCHUHMACHER and PLEWKA (1981) suggested that stromatoporoids built a skeleton of strength and weight to hold them on wave-swept reefs. They implied that the stromatoporoids had a skeleton of solid carbonate like that of the hypercalcified sponge *Ceratoporella*. Only *Lophiostroma*, a fossil that arguably may not be a stromatoporoid, had such a skeleton. In their porosity and bulk density, stromatoporoids were much like modern reef corals, and their extensive cavities were largely filled

with water and minor syntaxial cements in life. However, stromatoporoids, like corals, must have achieved stability in a turbulent environment by means of the rigidity of their skeleton. That they were commonly unable to maintain their position in storms is shown by the ubiquity of broken and displaced specimens.

MISTIAEN (1994) calculated that the average skeletal density of stromatoporoid skeletons increased from about 45% in Late Ordovician time to about 75% in early late Devonian (Frasnian) time and then decreased rapidly to the end of the Devonian as labechiids took over. He postulated that, at the close of the Devonian, they lost their skeletons entirely and persisted through the late Paleozoic and earliest Mesozoic as soft-bodied forms, before reappearing as the fossilized stromatoporoid-like forms (see also VACELET, 1985). He related these changes to cycles in chemistry and temperature of sea water as it passed through greenhouse and icehouse phases.

The competitive advantages of many of the clonal organisms that shared growth patterns and environments with stromatoporoids have been considered by COATES and JACKSON (1985), but the applicability of their conclusions, based on corals and bryozoans, to stromatoporoid sponges is in doubt (STEARNS, 1982b). These organisms are or were typically shallow water, sessile benthos living in reef and level-bottom environments. Such organisms today compete for space (settlement and growth sites), light, and food in hard substrate environments of considerable turbulence.

### SKELETAL FRAGMENTS AND PROPAGATION

The highly branched forms and rapid growth rates of many modern scleractinians allow them to overgrow and shade their competitors and to propagate new colonies by fragmentation during tropical storms. Rapidly growing, broken branches soon establish new growth if carried to suitable environments. The fragmentation

of stromatoporoids has been considered by KERSHAW and BRUNTON (1999), but there have been no suggestions that this is an adaptation for propagation, and only for dendroid forms, like *Amphipora*, would such breakage have a potential for dispersal.

Several writers have suggested that dendroid branches of such genera as *Amphipora* and *Stachyodes* were high, cylindrical mamelons broken off from tabular or domical bases (BOGOYAVLENSKAYA, 1985; WEBBY, 1993; KERSHAW & BRUNTON, 1999). Rare specimens of *Stachyodes* have been found with a laminar base and fingerlike mamelons (e.g., *S. fasciculata* HEINRICH [STEARNS, 1966, p. 118]), but for *Amphipora*, despite the many millions of stems that throng Devonian limestones, no putative bases with broken off mamelons have been demonstrated. The only conclusion is that *Amphipora* stems grew upright (Fig. 349.2) with some means of holding themselves vertical in the sediment and that dispersal and propagation by breakage from a tabular or domical base was highly unlikely (STEARNS, 1997c).

### LIGHT DEPENDENCE IN STROMATOPOROIDS

The scleractinians have had great success in modern reefs, becoming the dominant metazoans due to their ability to calcify rapidly with the aid of symbiotic dinoflagellates (identified largely as *Symbiodinium microadriaticum*). Organisms that live by such symbiosis are referred to as mixotrophs, because their metabolic needs are satisfied partly by the ingestion of food and partly by photosynthesis. Mixotrophs are particularly adapted to living in environments of low nutrient supply and productivity, and proof that the stromatoporoids belonged to this group would have important implications for mid-Paleozoic paleoceanography. The mechanism by which photosynthetic symbionts aid the calcification of reef corals is not completely understood, and the symbionts are not closely associated with the tissues that most actively secrete the skeleton

(CONSTANTZ, 1986; COHEN & MCCONNAUGHEY, 2003; WEINER & DOVE, 2003). However, this symbiosis allows their skeletons to extend at rates of a few millimeters per year. In contrast, the modern sponges used as models for the Paleozoic stromatoporoids, the hypercalcified sponges, do not have symbionts capable of aiding calcification, grow skeletons much more slowly, and have been relegated to dark, cryptic habitats in the competition for space on modern reefs. On what basis did the stromatoporoids compete with clonal rugosans, tabulates, and trepostome bryozoans with whom they grew on early Paleozoic reefs?

KERSHAW (1998) reviewed some of the published data on phototrophism in stromatoporoids. COWEN (1983, 1988), VACELET (1984), COATES and JACKSON (1987), YOUNG and SCRUTTON (1991), and WOOD (1993) speculated on the possibility that the reef-forming trio of the mid-Paleozoic rugosans, tabulates, and stromatoporoids had symbiotic algae that enhanced calcification and growth rate. The rate of calcification evident in the formation of vast Devonian reef tracts has been claimed to be evidence that rapid growth of these organisms was aided by symbiosis. As discussed below, we have no sure measure of the growth rate of any of these organisms, but because they lived in competition for living space over an interval of about 170 million years, their rates were probably roughly comparable, otherwise one would have excluded the others from a rapidly growing reef surface. However, unaided by intracellular symbionts, they all could have grown slowly relative to modern corals. The average rate of upward growth of Devonian reef tracts (that is, the thickness divided by the interval of accumulation) is of the order of a few millimeters per century, which could hardly be considered evidence for rapid growth of the reef builders. COATES and JACKSON (1987) did not consider stromatoporoids in their study but concluded that morphological criteria suggest that Siluro-Devonian tabu-

lates contained photosynthetic symbionts. COWEN (1988) used extensive surface area, thinness of living tissue, fast growth, and shallowness of habitat to conclude that stromatoporoids were photosynthetic, but none of these criteria is robust.

Living sponges have many unicellular symbionts, so many (up to 50% of the tissue) that some may be referred to as bacteriosponges (REISWIG, 1981), but they are not the type that aid calcification (Fig. 351). The only sponges harboring dinoflagellate symbionts like the corals are the clionids that bore into the hard tissue of modern corals, and their function in these sponges is problematic (VACELET, 1984). Most sponge symbionts are cyanobacteria that require light to grow and multiply. WILKINSON (1987) concluded that the photosynthesis of cyanobacteria within sponge tissue makes significant contributions to the energy requirements of sponges on a reef flat on the Great Barrier Reef. WILLENZ and HARTMAN (1989) reported that the soft tissue of *Ceratoporella* included nearly 20% bacteria. The lophocytes (collagen-secreting cells) ingest these bacteria for food, but other relationships between the bacteria and the sponge are in doubt. They may aid the sponges in using the dissolved organic matter in sea water (VACELET, 1984). We cannot know whether stromatoporoids shared the propensity of modern sponges to harbor symbionts, but there is no direct evidence that they did so.

In some specimens of stromatoporoids, KAŻMIERCZAK (1976, 1980) has illustrated granular fabrics that he interpreted as fossilized coccoid cyanobacteria. These were not interpreted as symbionts, but, on the basis of these specimens, he has attributed the whole class to the Cyanobacteria, a viewpoint that is rejected here (as is discussed previously in the section on morphologic affinities, p. 543–549).

## ISOTOPE FRACTIONATION

Modern mixotrophic corals secrete a carbonate skeleton that has a distinctive signature of carbon and oxygen isotopes,

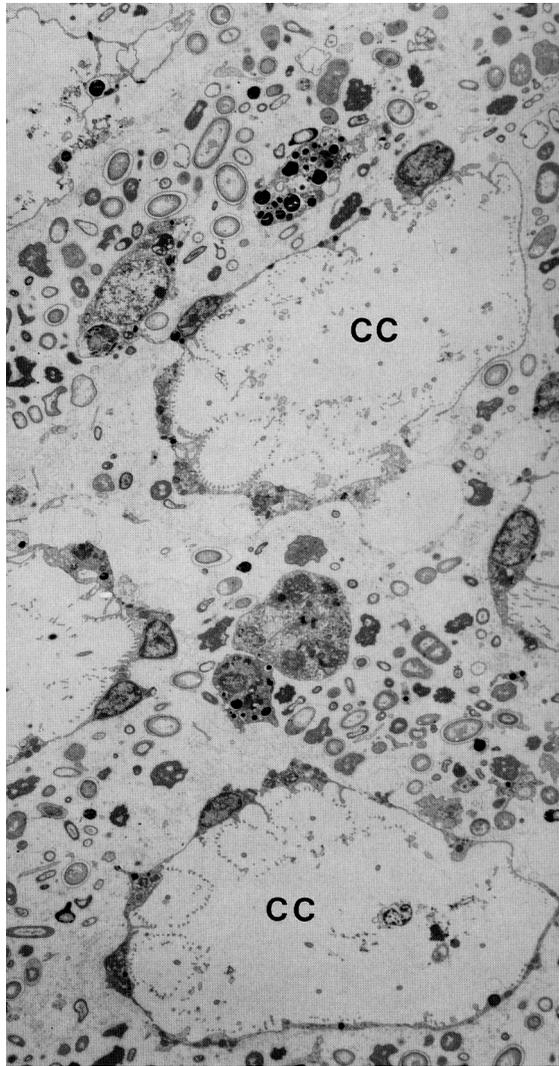


FIG. 351. Symbiotic cyanobacteria, *Ceratoporella nicholsoni* (HICKSON, 1911); Pear Tree Bottom, Jamaica; choanocyte chambers (cc),  $\times 2400$  (Stearn, 2010d; courtesy of Ph. Willenz).

owing to fractionation of algal photosynthesis.

SWART (1983) summarized the differences between the isotopic ratios in the skeletons of mixotrophic and nonmixotrophic corals. In mixotrophs, he found no correlation between the oxygen and carbon isotopes but a narrow range of values. MALLAMO (1995) has attempted to identify this signature in stromatoporoid skeletal material. Samples of the skeleton were extracted from Devo-

nian and Silurian stromatoporoids using a microdrill to avoid contamination by the gallery fillings. MALLAMO (1995) found  $\delta^{13}\text{C}$  (PDB) values in the 1.26 to 3.48 range and  $\delta^{18}\text{O}$  (PDB) in the  $-9.10$  to  $-4.22$  range. Photosynthesis preferentially fixes and removes  $^{12}\text{C}$ , increasing the  $^{13}\text{C}/^{12}\text{C}$  ratio in the skeleton (NORRIS, 1998). These values showed an enrichment in the  $^{13}\text{C}$  isotope and no correlation between the oxygen and carbon isotopes; both results suggest, but are

far from proving, that these stromatoporoids could have been mixotrophs. Suggestive also was the correspondence in isotopic signatures between a specimen of *Stromatopora* from Wenlock, England, and that of Triassic corals that SWART and STANLEY (1989) suggested were mixotrophs.

### GROWTH RATES AND GROWTH BANDS

If stromatoporoids were mixotrophs like scleractinians, their rate of calcification was probably rapid. Latilaminar growth (see p. 511–515), the rhythmic repetition of growth units (latilaminae) commonly separated by growth interruption surfaces, is common in stromatoporoids (see Fig. 329.2; Fig. 330.3). The thickness of these latilaminae is a few millimeters. The repetition of these units suggests that they are annual accretion units, but as yet no proof of their time value has been demonstrated (YOUNG & KERSHAW, 2005). On the basis of their observations on nonannual growth banding in domical skeletons of the hypercalcified sponge *Ceratoporella*, WILLENZ and HARTMAN (1985) have cautioned that the latilaminae of stromatoporoids should not be assumed to reflect annual cycles.

MEYER (1981) estimated vertical and horizontal growth rates in the Devonian stromatoporoids of Michigan on the basis of the relationships between favositid corals and the stromatoporoids that overgrew them. He assumed that bands defined by the spacing of tabulae in the corals were annual. Using this banding and steplike shape of the coral colony, he determined that the average lateral extension rate of 26 specimens of 3 species of stromatoporoids was between 10 and 23 mm per year. This was sufficient to allow the stromatoporoids to extend laterally over the corals, but their average vertical rate of growth was much lower, between 1.3 and 3 mm per year.

RISK, PAGANI, and ELIAS (1987) described six stromatoporoid thin sections that were repeatedly crossed by bands of microborings that they homologized with those of

endolithic algae in modern corals (*Ostreobium*). In modern corals, these algae form annual bands immediately below the growing surface. The assumption that the Devonian microborings represent a similar phenomenon yields a growth rate of about 10 mm per year, about the rate of growth of a domical scleractinian such as *Montastrea annularis*. The microborings are not confined to the structural elements of the skeleton but also cross galleries filled with carbonate spar cement. This suggests that they were not formed in the same way as the bands of endolithic algae in modern corals, which are bored soon after the skeleton is secreted and while the interskeletal chambers are empty. How these bands of borings formed is problematic, but they are unlikely to give a reliable growth rate. Similar microborings on the exterior of Ordovician rugose corals have suggested to ELIAS (1982) that they grew at about 20 mm per year.

GAO and COPPER (1997) measured the rates of growth of stromatoporoids from the early Silurian of Manitoulin Island, Canada, using the assumption that the latilaminae are annual additions. They found that the average thickness of the latilaminae in 6 genera ranged from 0.8 to 3.1 mm. They concluded that these results did not clearly indicate whether stromatoporoids were mixotrophic or not.

YOUNG and KERSHAW (2005) examined the spacing and nature of the boundaries of latilaminae in stromatoporoids but were unable to conclude whether they were annual or not. NESTOR, COPPER, and STOCK (2010) discussed the seasonal growth bands of stromatoporoids from Anticosti Island and concluded that growth rates of a few millimeters per year were probable.

These rates for stromatoporoids of a few millimeters per year are of the same order of magnitude as those of modern scleractinian corals, but they are much higher than those of living hypercalcified sponges such as *Ceratoporella*, which adds only 0.2 mm per year to its skeleton (WILLENZ &

HARTMAN, 1985). Since the discovery that hypercalcified sponges secrete a skeleton in isotopic equilibrium with ambient sea water and hence, owing to their slow growth, may preserve a record of ocean chemistry of the last several thousand years, many measurements of their growth rate have been made (WÖRHEIDE & others, 1997; SWART & others, 1998; WILLENZ & HARTMAN, 1999; LAZARETH & others, 2000; ROSENHEIM & others, 2004). These studies agree that the living hypercalcified sponges grow at rates of less than 1 mm per year and commonly in the 0.2 to 0.3 mm range. The rate for the hypercalcified sponge *Acanthochaetetes* is only 50 µm per year (REITNER & WÖRHEIDE, 2002). Whether comparisons of stromatopore growth rates to those of their modern analogues has any validity, or relevance to their metabolism, is open to question.

In summary, inadequate evidence suggests that stromatopore growth probably added vertically to their basal skeleton at from 2 mm to 10 mm per year but is equivocal as to their light dependence.

### STROMATOPOROID SKELETONS, LIGHT DEPENDENCE, AND REEF STRUCTURE

Light-dependent scleractinians compete for a “place in the sun.” For this they grow in upward-spreading forms to overshadow their neighbors. The fragility of such forms in storms is compensated for by their ability to repair rapidly and propagate by fragmentation. The stoutly branching *Acropora palmata* that forms the reef fronts in Caribbean reefs illustrates this reef facies. These enmeshing growth forms are responsible for the cavernous framework structures of modern coral reefs and the ability of such edifices to stand against the attack of storm waves. The common domical and tabular growth forms of the stromatopore growth forms resemble those of living hypercalcified sponges that are cryptic in habitat and are not adapted to competition with neighbors

for light. In mid-Paleozoic stromatopore reefs, the framework structure of modern reefs can rarely be demonstrated. FAGERSTROM (1987) placed stromatopore growth forms in his binder guild, but in mid-Paleozoic reefs, the stromatopore growth forms, where they appear to be in place, grew as isolated organisms, rarely uniting to bind and enclose coarse sediment nor construct a framework. KERSHAW (1998) concluded that field studies show that stromatopore growth forms grew on loose substrates rather than united into frameworks. Inability to form frameworks may account for the low marginal slopes of a few degrees in the profiles of mid-Paleozoic reefs, compared to the almost vertical underwater cliffs that are sustained by modern frame-builders around oceanic islands. These considerations suggest, but certainly do not prove, that the stromatopore growth forms did not compete with each other, or with other reef builders, for light.

### SOFT TISSUE WITHIN THE SKELETON

To what extent was the soft tissue confined to the surface of the skeleton and how much of the skeleton did it penetrate? The living hypercalcified sponges, stromatopore growth form analogs, exhibit a range of answers to these questions; in *Ceratoporella*, the soft tissue is entirely superficial; in *Astrosclera*, it fills spaces between skeletal elements deep below the surface. In most post-Ordovician stromatopore growth forms, the skeletal spaces are filled with calcite spar cement with textures typical of void-filling cements (see Microstructure, p. 521–542). There is no evidence in Paleozoic stromatopore growth forms that the lower parts of the skeleton were secondarily filled with carbonate by the animal, as in the living sponges *Vaceletia* and *Astrosclera*, in which living tissue continues to lay down skeletal material well below the surface.

In some specimens of stromatopore growth forms, the uppermost galleries are distinguished from the spar-filled galleries in the rest of the skeleton by their filling of fine sediment (Fig. 352.1; and see Fig. 317.1) (STEARN & PICKETT, 1994). These galleries probably contained

soft tissue when the organism suddenly died, while the interskeletal spaces below were water filled and sealed off from the soft tissue by tabulae, dissepiments, and laminae. The soft tissue decayed quickly, leaving the path open for sediment to enter before cement filled the empty spaces. Syntaxial cements in water-filled cavities of living corals indicate that abandoned and sealed-off parts of the skeleton may begin to be filled with cement while the coral is still alive at the surface of the skeleton.

At the final growth surfaces of stromatoporoids with laterally persistent laminae (Clathrodictyida, Stromatoporellida), usually only the layer of galleries below the incomplete last lamina has a sedimentary filling, rather than a cement filling. The soft tissue is unlikely to have penetrated deeper into the skeleton, and each completed lamina must have sealed off the interior. In most of the Stromatoporida, sediment surrounds the ends of the pachyestes to a depth of the highest dissepiment in the allotubes. In species with few dissepiments, sediment may penetrate the depth of the last latilamina (Fig. 352.2). In these stromatoporoids, the soft tissue presumably occupied the whole last latilamina, as appears to be the case in living *Calcifibrosporgia*.

### BASAL SKELETON SECRETION IN LIVING HYPERCALCIFIED SPONGES

Living hypercalcified sponges secrete their skeletons in three ways (WOOD, 1991b).

1. Basal: through a glucopolysaccharide layer below a basopinacoderm, much like the corals (e.g., *Ceratoporella*).
2. Intracellular: within archaeocytes as spherulites, which are cemented together to form structural elements (e.g., *Astrosclera*).
3. Collagenous: inside the soft tissue on an organic matrix (e.g., *Vaceletia*).

The stromatoporoids also appear to have secreted their skeletons using more than one

mechanism, certainly methods 1 and 3, and possibly also 2.

1. The secretion of the skeletal tissue of some stromatoporoids can be explained as a result of deposition from a basopinacoderm lying at the base of the soft tissue. The soft tissue in this model is entirely separate from, and superficial to, the skeleton. The modern hypercalcified sponge *Ceratoporella* illustrates this pattern. The skeleton of this sponge is secreted at the base of the soft tissue. It forms in an organic matrix beneath a layer of basopinacocytes that appears to control the deposition of the aragonite needles. In addition, monaxon siliceous spicules are formed in the soft tissue by sclerocytes and incorporated in the basal skeleton as it grows upward.

This method of secretion was adduced by STEARN (1975a) to explain skeleton formation in all stromatoporoids, but the model has problems with clathrodictyids and stromatoporellids, as explained below. It appears to be a satisfactory explanation for actinostromatids and labechiids, however (Fig. 352.3).

2. The open skeletal structure and spherulitic microstructure of the living hypercalcified sponge *Astrosclera* suggested to STEARN (1975a) that the skeletons of the Stromatoporida were formed as in this sponge. In *Astrosclera*, the skeleton consists of aragonite spherules a few micrometers in diameter. Each spherule is formed intracellularly in soft tissue and is passed down to the skeletal surface, where it is cemented in place. (Skeleton secretion in *Astrosclera* is described fully by WÖRHEIDE and others [1997]). Proof that skeletons of the order Stromatoporida were ever spherulitic is lacking, and in well-preserved specimens, the microstructure appears to have been originally porous (STEARNS & MAH, 1987). REITNER and WÖRHEIDE (2002) described the various groups of sponges that secrete spherulitic skeletons and conclude that the microstructure has no taxonomic

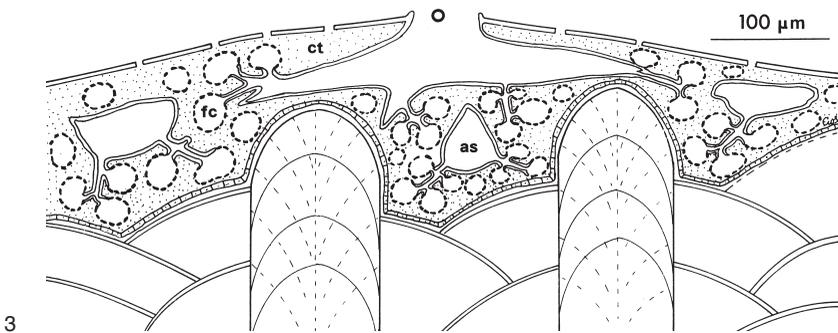
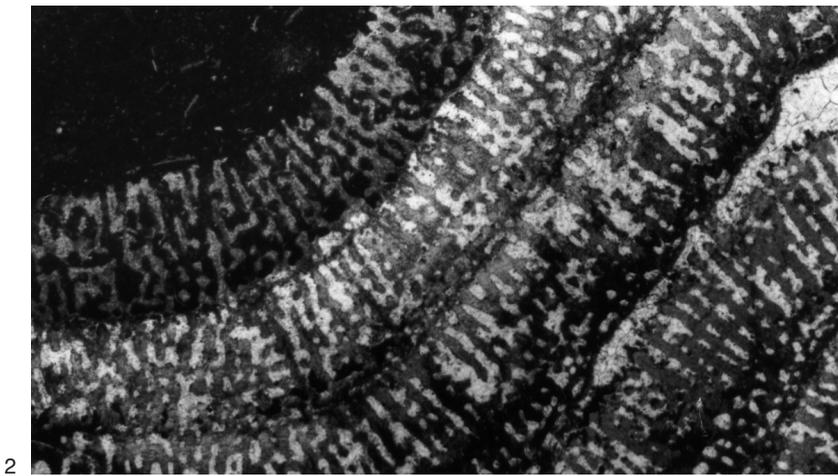
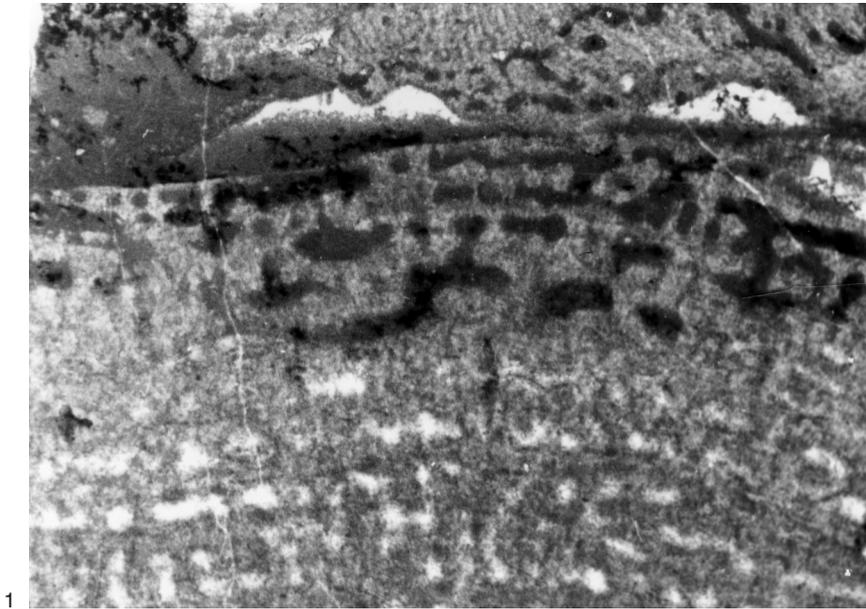


FIG. 352. (For explanation, see facing page).

significance. Whether any stromatoporoids skeletons were ever spherulitic or secreted intracellularly remains problematic (see Microstructure section, p. 521–542).

3. In stromatoporoids with skeletons dominated by laminae (the clathrodictyids and stromatoporellids), the laminae and pillars are commonly thinner within the terminal zone, where the galleries are filled with sediment (Fig. 352.1). This is the zone that was filled with soft tissue when the animal died. These thinner elements must have been in the process of formation within soft tissue when the animal died. The incomplete structural elements of these groups must have been secreted on an organic matrix inside the soft tissue of the surficial layer of the stromatoporoid (Fig. 353.1).

The wall of a new chamber in the modern sphinctozoan-type demosponge *Vaceletia* is formed just below the thin cell layer (exopinacoderm) that covers the last chamber. A collagenous template or organic matrix forms below this pinacoderm, and within this template, crystals of aragonite appear and grow into a felted layer to form a porous wall (VACELET, 1979b). The pillars within the chambers form by the mineralization of organic strands.

### GROWTH MODULES OF LAMINATE STROMATOPOROIDS

The laminae of stromatoporellids are tripartite; that is, they are divided axially by a light layer that may appear continuous or as a line of cellules. STEARN (1975a) explained the central light layer as being due to diage-

netic leaching of the axis of crystallization of a trabecular aragonite sheet by meteoric waters. KAŻMIERCZAK (1971) interpreted it as a growth interruption surface. The nature of this zone is clear in *Simplexodictyon* (Fig. 353.2; and see Fig. 320.2 and Fig. 320.4), in which the upper and lower laminar layers part and reunite and may be separated by sediment, epibionts, or calcite cement (POWELL, 1991). Each lamina in this genus is composed of two layers locally fused and locally separated. The fundamental unit secreted in successive growth modules within soft tissue consisted of (1) a floor that became the upper layer of an older lamina; (2) a roof that, as the next module was added, became the lower layer of the next tripartite lamina; and (3) the pillars and other structures enclosed between 1 and 2. This growth module is a laterally extensive chamber homologous to the chambers of the sphinctozoans. The modules must have been formed in soft tissue and added to the growing skeleton as units. In genera such as *Stictostroma*, *Stromatoporella*, and *Trupetostroma*, the axial light zone between the floor and roof of modules is divided into cellules or rounded, discontinuous spaces defining ordinicellular microstructure; that is, the floors and roofs are discontinuously fused, leaving cellules between them (see Fig. 320.1). Many species otherwise typical of the skeletal structure of *Stromatoporella* show only scattered areas of ordinicellular laminae or none at all. The irregularity of development of this ordinicellular microstructure has been attributed to preservational factors but may be caused by original lateral variation in the way in which the modules were fused into the skeleton.

FIG. 352. 1, Longitudinal section, ?*Trupetostroma* sp., showing thin, incomplete upper lamina and infiltration of sediment into uppermost galleries that are presumed to have been filled with soft tissue at death, NMV P.141665, Pragian-Emsian Buchan Caves Limestone, eastern Victoria, Australia,  $\times 16$  (Stearn, 2010d); 2, longitudinal section, *Syringostromella?* cf. *discoidea* (LONSDALE, 1839), SCRM 50-20, Much Wenlock Limestone, Wenlock Edge, Shropshire, England, showing latilamination and sediment penetrating galleries that were presumably filled with soft tissue through whole depth of last latilamina,  $\times 10$  (Stearn, 2010d); 3, diagrammatic reconstruction of longitudinal section, *Labechia*, showing skeleton of pillars and cyst plates secreted by a basal pinacoderm and soft tissue entirely on surface of skeleton; astrorhizal canals (*as*) lead from choanocyte chambers (*fc*) to an osculum (*o*); water enters choanocyte chambers from fine pores on surface through connective tissue (*ct*) in fine canals not shown on reconstruction; it is not clear whether additional skeleton is formed by formation of cysts within soft tissue and abandonment of sealed-off tissue, or by upward migration of basopinacoderm (Stearn, 1975a).

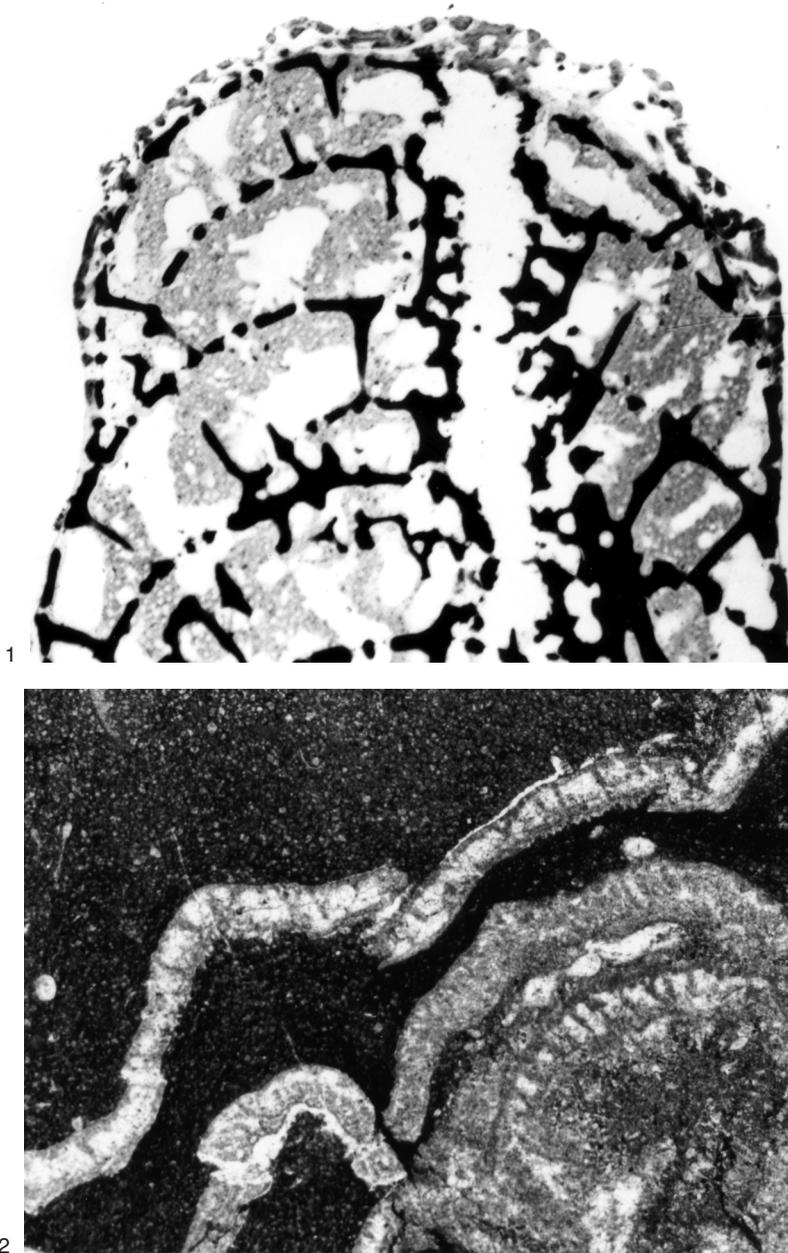


FIG. 353. 1, Cross section of soft tissue and skeleton of living sphinctozoan-type demosponge *Vaceletia* in process of secreting a new chamber in organic matrix of soft tissue; soft tissue does not completely fill chambers; empty spaces are canals; new, incompletely mineralized chamber appears irregular, probably as a result of some deformation during preparation,  $\times 35$  (Vacelet, 1979b; photo courtesy of J. Vacelet); 2, growth modules of upper and lower laminae and enclosed pillars separated from main skeleton and surrounded by sediment; *Simplexodictyon* sp., AM.FT 15018, upper Silurian, Catombal Park Formation, New South Wales, Australia,  $\times 10$  (Stearn, 2010d; courtesy of B. Webby).

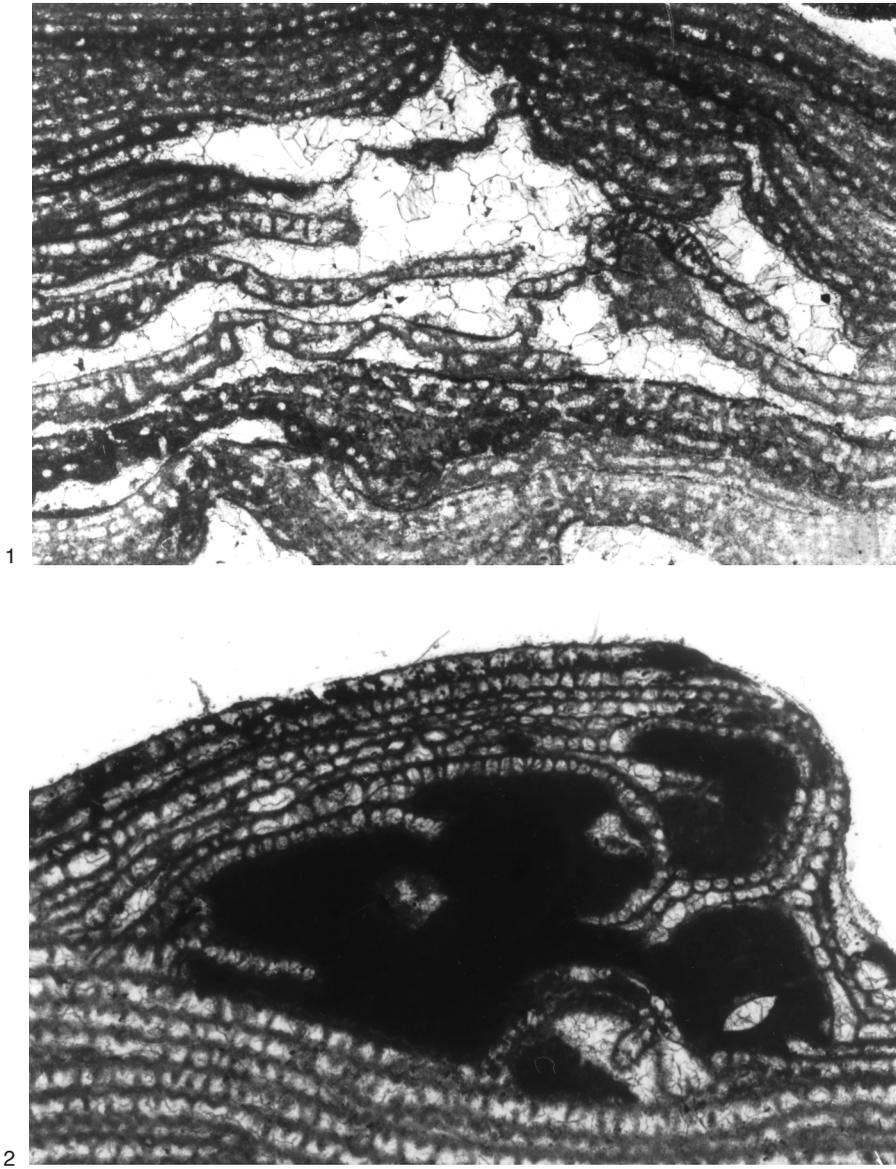


FIG. 354. 1, Growth modules consisting of upper and lower laminae and enclosed pillars projecting into a spar-filled cavity, presumably once filled with sediment; *Stictostroma maclareni* STEARN, 1966, SCRM 80-88, Frasnian, Kakisa Formation, Great Slave Lake area, Northwest Territories, Canada,  $\times 4.25$  (Stearn & Pickett, 1994); 2, laminae of a clathrodictyid, *Petridiostroma incrustatum* NESTOR, COPPER, & STOCK, 2010, separated from main skeleton and supported by sediment in a cavity; SCRM 133-1, Llandoverly, Jupiter Formation, Anticosti Island (specimen collected by P. Copper),  $\times 10$  (Stearn, 2010d).

Modules consisting of the upper and lower layers of two successive tripartite laminae and the intervening pillars may project laterally into spar-filled areas that were originally cavities (Fig. 354.1) in stromatoporellids, such as *Stictostroma* and *Stromatoporella*. The occurrence of these projections in genera of the Clathrodictyida, such as *Atelodictyon*, *Petridiostroma*, and *Hammatostroma*, indicates that this group also secreted skeletons in modules. The differences in appearance of laminae between the Stromatoporellida (1) and Clathrodictyida (2) may be due to the way in which the modules were added to the skeleton. In the Clathrodictyida (Fig. 354.2), which have single-layered laminae, the floors of the modules are the upper surfaces of the module below and no special floor is secreted (see STEARN & PICKETT, 1994, and particularly fig. 9A, for further discussion). The formation of some growth modules that project into the surrounding sediment in some laminate stromatoporellids may be difficult to reconstruct (Fig. 353.2; Fig. 354.2), but sediment must have accumulated between intervals of module construction in these specimens.

As noted above, most laminate stromatoporellids have smooth upper surfaces formed by the last lamina, and no sediment penetrates the last galleries that are sealed by this last lamina. In these specimens, modules in the process of calcification within soft tissue and insufficiently fused to the old skeleton have been disrupted and swept away when the soft tissue decayed. Only in exceptional circumstances, when the module was incomplete but sufficiently formed to be fused to the skeleton, was it left behind when the soft tissue decayed and was preserved by the infiltration of sediment into the incompletely sealed galleries.

A thin, calcareous sheath that envelops certain genera is a puzzling skeletal feature through which water must flow in freely. It is most conspicuous in *Amphipora* (STEARNS, 1997c) (Fig. 349.2; and see Fig. 475) but was noted by NICHOLSON (1886a, p. 59–60) on several domical and encrusting stro-

matoporellids and by NICHOLSON (1886a), ZUKALOVA (1971), and COCKBAIN (1984) on *Stachyodes*. In order for water to enter the interior of the fossil sponge, either this sheath must have been perforated by minute pores or it covered only parts of the animal that were nonfunctional. STEARN (1997c) has suggested that this sheath is similar to the dermal membrane that overlies the open space called the vestibule above the skeletal material in the hypercalcified sponges *Ceratoporella* and *Stromatospongia* (Fig. 355). The dermal membrane is minutely porous and allows water into the vestibule, where it is drawn into the choanocyte chambers. Stellate water canals within the vestibule isolate exhalant water from inhalant water and direct it to oscula that penetrate the dermal membrane. The calcification of the membrane as the inhalant surface becomes nonfunctional in older, damaged, or buried parts of the skeleton would produce a skeletal structure similar to the peripheral membranes in *Amphipora* and other genera.

The taxonomic and phylogenetic significance of the calcareous skeleton of hypercalcified sponges has been considered insignificant by some sponge workers who rely on arrangement and form of spicules and gene sequencing as guides to systematic relationships (e.g., VACELET, 1985; WOOD, 1990b; REITNER & WÖRHEIDE, 2002). They pointed out that the calcareous skeleton is secreted by various mechanisms (see above), in various mineralogies, and by genera belonging to various orders of sponges that are defined on the basis of their spicules and soft tissue organization. The basal skeleton therefore must be easy to secrete without much investment of biological energy; that is, it is facultative and therefore of little systematic value (WOOD, 1989). That the basal skeletons of demosponges, such as *Ceratoporella*, have an isotopic signature ( $\delta^{18}\text{O}$ ) that is close to that of ambient sea water, is taken as further proof of its facultative nature (see p. 560). The conclusion that the hypercalcified skeleton of these sponges is not only useless in establishing relationships, but may be

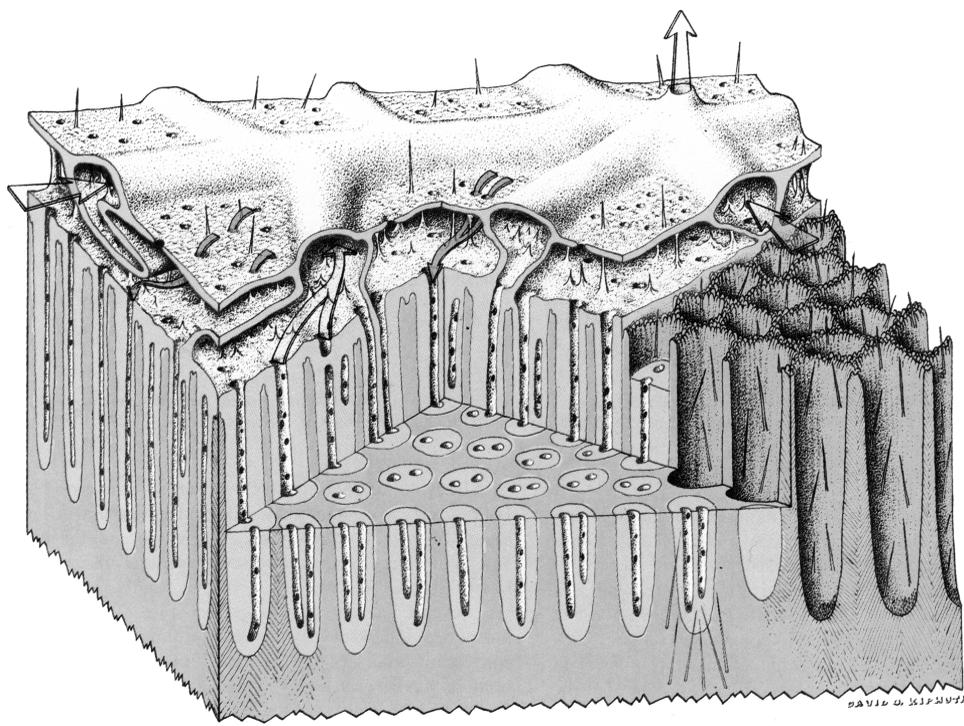


FIG. 355. Diagrammatic reconstruction of relationship between soft tissue and skeleton of *Ceratoporella nicholsoni* (HICKSON, 1911) showing flow of water into ostia, through vestibule, into choanocyte chambers and out via astrorhizal canals to osculum; scale bar, 1 mm (Willenz & Hartman, 1989; see also Fig. 3.2 and Fig. 156c).

misleading, is disturbing to paleontologists who have no choice but to base classification and phylogeny on these skeletal fossils. However, until some new key to unlocking the phylogeny of the Paleozoic stromatoporeids is found, paleontologists can proceed only as if features of the basal skeleton have systematic value.

### FUNCTIONS OF SPECIFIC STRUCTURAL ELEMENTS

Specific functions and adaptations cannot be ascribed to the skeletal architecture of stromatoporeids. Until more information is available about restriction of species to facies indicative of specific ancient environments, such speculation is idle. These sponges must have adapted various combinations of pillars, laminae, and dissepiments, involving structural

elements to lift their feeding surfaces from the substrate. Presumably, the structural elements were selected to optimize support, extension of the intake surface, passage of canals, isolation of inhalant from exhalant water, rigidity, energy cost, rate of growth, and resistance to parasites and predators. The specific advantages of such specialized structural elements as, for example, ring pillars in *Stromatoporella*, to survival of the species is presently unknown. Horizontal elements, such as dissepiments, laminae, and astrorhizal tabulae, were apparently secreted to seal off the unused part of the skeleton from the living tissue. Because the stromatoporeid sponge must have been physiologically incapable of lifting itself in its skeleton in growing, as cnidaria polyps do, the abandoned soft tissues must have been sealed off and left to decay.

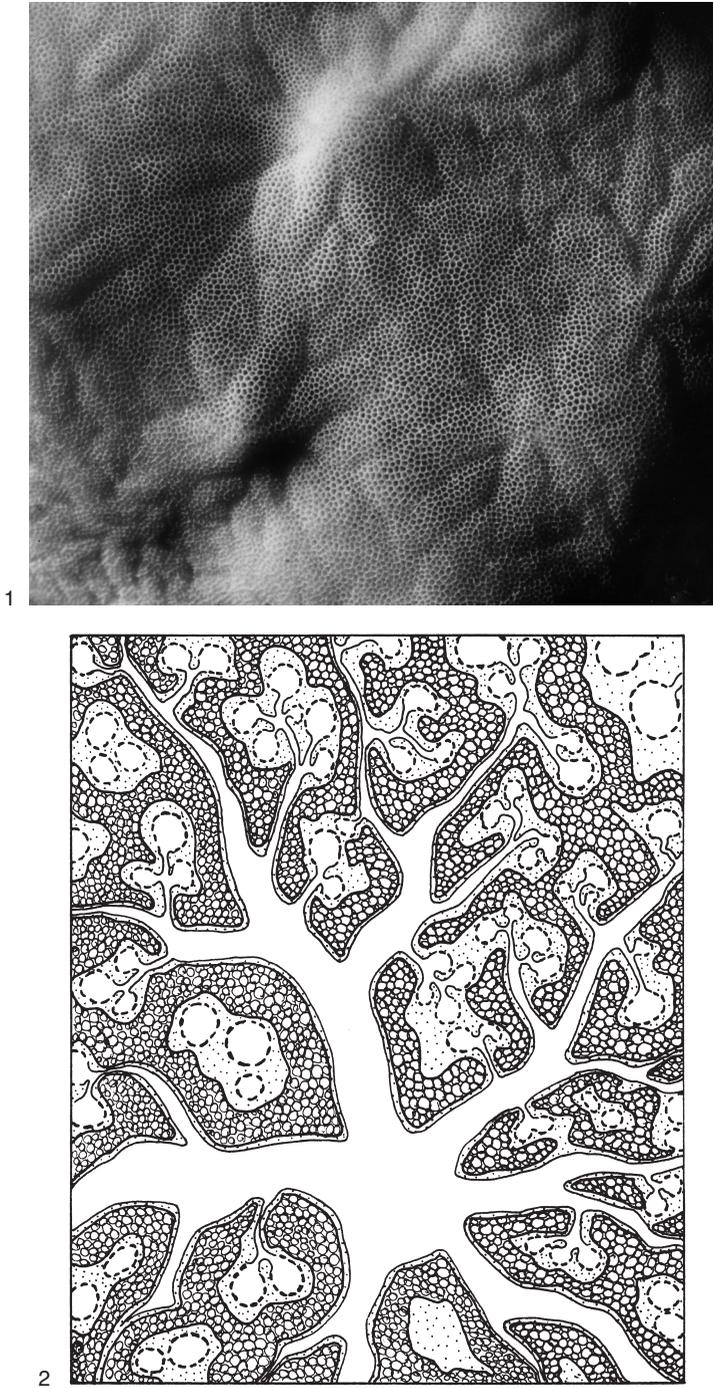


FIG. 356. 1, Surface of skeleton of *Ceratoporella nicholsoni* (HICKSON, 1911) showing astro-rhizal grooves branching and leading to mamelons on surface, SCRM 99-2, Runaway Bay, Jamaica,  $\times 3$  (Stearn, 1972); 2, reconstruction of tangential section of astro-rhizal system in a stromatoporoid, order Stromatoporida; branching canals connect to subspherical choanocyte chambers in gallery space; skeletal material is reconstructed as cellular; largest canals about 0.1 mm across (Stearn, 1975a).

Although the surfaces of modern sponges are attacked by organisms whose relatives would have been contemporaries of the stromatoporoids, no evidence of such predation has been described from these fossils and, if present, would be difficult to distinguish from mechanical damage.

The adaptive significance of only the astrorhizae, mamelons, and growth form have been investigated. Here the mamelons and astrorhizae are discussed (see p. 569–573); and the interpretation of growth form is presented elsewhere (see p. 419–486).

### MAMELONS

Many growth surfaces have these regularly spaced, radially symmetrical mounds with a few millimeters of relief (see also p. 481–483, Fig. 293.1–2). In typical skeletons, they are the sites of oscular openings of astrorhizae (Fig. 356.1; and see Fig. 326.1 and Fig. 326.3).

The function of mamelons is related to the need to separate the incoming from outgoing water streams to increase the efficiency of feeding. Water processed to remove microorganisms, nutrients, and oxygen exhaled from oscula should not be sucked back into inhalant pores (ostia) on the surrounding surface. FRY (1979) has summarized Bidder's Diameter of Supply concept to the spacing of oscula on the surface of encrusting sponges. The jet from an osculum should be able to diffuse water already cleaned away from the inhalant pores, and the sponge's anatomy and physiology is adapted to maximize this mechanism. Raising oscula on mamelons above the inhalant surface of an encrusting sponge is one strategy to achieve this, and in some living sponges, it results in the oscula being raised on high chimneys.

BOYAJIAN and LABARBERA (1987) investigated the effect of the flow of ambient sea water over mamelons on which astrorhizae were centered to explain the function and form of the mamelons on the growth surface. The stromatoporoid surface was

simulated by a model and the astrorhizae by radial grooves on its flanks. When water in a flume was passed over the model, the difference in velocity of the current near the base of the model mamelon (slowed by friction with the substrate) and that at the top caused a pressure differential defined by Bernoulli's Law, which pulled water marked by a dye stream up the astrorhizal grooves to the mamelon summit. BOYAJIAN and LABARBERA (1987) suggested that the experiment showed that the flow of water across mamelons would have helped the stromatoporoid in circulating water through the astrorhizal canals. As VOGEL (1994) explained, although this principle can be applied to the circulation of fluids in burrows of marine worms and gophers, its application to stromatoporoids is not as evident as the experiment suggests, for the following reasons.

1. Astrorhizae are not grooves open at their lower ends in the sides of mamelons as modeled, but enclosed tubes embedded in the skeleton. Although tubes were tried in the experiment, no results are reported.
2. Many stromatoporoids have astrorhizae without mamelons or between mamelons, i.e., the association of mamelons and astrorhizae is not as universal as implied in the experiment.
3. BOYAJIAN and LABARBERA (1987) suggested that mamelated surfaces should characterize stromatoporoids that lived in environments of low current velocities, where their circulatory system would need to be supplemented by the pressure differential, and pointed out that the mamelate hypercalcified sponge *Ceratoporella* lives in caves and at depth in Jamaican waters where currents are light. They suggested that ancient current conditions might be determined from mamelon and astrorhizal form. However, the reverse of this argument might be used; that is, in order for the mechanism proposed to be an effective aid to the circulation of sponges, a constant current must cross the surface, and the stronger the better. The occurrence

of mamelons on *Ceratoporella* could be taken to indicate that no relationship exists between currents and mamelons.

4. The flagella of sponges living in calm water seem quite capable of maintaining circulation in astrorhizae without the aid of this mechanism.
5. No relationship between the form or presence of astrorhizae or mamelons and the current regime of the environment of living or fossils sponges has been demonstrated.

Where mamelons and astrorhizae are associated in stromatoporoids, the association is more likely to be controlled by the need to separate incoming from outgoing water under still conditions than by an adaptation to take advantage of pressure differences caused by currents. Where the surface is swept by currents, the problem of recycling of water is much less.

### ASTRORHIZAE

For more than 150 years, the canal systems that shaped the astrorhizae have been considered the key to understanding the systematic position of the stromatoporoids (Fig. 356.2; and see p. 483, 485, Fig. 316.2–316.3, and Fig. 326–329). Note that astrorhizae are also known to occur on external surfaces of the basal skeletons (not internally) of chaetetid sponges (see p. 91–92, Fig. 60). The features of the astrorhizae in stromatoporoids that require explanation by a model of their functions are the following.

1. Most canals are not bounded by discrete walls but are represented by clear spaces (astrorhizal paths) through the skeletal elements communicating in three dimensions with the galleries. Some canals are bordered by a wall pierced with pores.
2. On growth surfaces, the traces of astrorhizal canals may be grooves or ridges.
3. The canals decrease in diameter regularly away from the centers of the astrorhizae. At the centers they are bent upward to join single, or multiple, ascending canals.

4. Most canals decrease in diameter distally until they cannot be distinguished from the galleries. Rarely the distal tips of the canals of adjacent astrorhizae join to form a network.
5. Astrorhizae may be superposed, forming columns, or they may be scattered in the skeleton.
6. Not all species or genera show them.
7. The canals may be crossed by simple tabulae.
8. Astrorhizae tend to be uniform in size, form, and spacing throughout the skeleton of a species; that is, they are distinctive of particular species.

Early in the history of the study of stromatoporoids, paleontologists (NICHOLSON & MURIE, 1878; SOLOMKO, 1885) recognized the similarity of the astrorhizae to the exhalant, water-gathering systems of sponges. CARTER (1877) reasoned that the canals were homologous to the hydrorhizal system of the hydrozoan *Hydractinia*. This system links the zooids of the hydroid and allows them to exchange nutrients by diffusion. His views convinced NICHOLSON (1886a) to abandon his former position that stromatoporoids were sponges and to ascribe them to the Hydrozoa. NICHOLSON'S influence was so great that, although a few continued to affirm the sponge model (KIRKPATRICK, 1912b; HEINRICH, 1914a; TWITCHELL, 1928–1929), the hydrorhizal model of the astrorhizae became orthodoxy for the next 85 years (e.g., KÜHN, 1927; LECOMPTE, 1951 IN 1951–1952, 1956; GALLOWAY, 1957; FLÜGEL & FLÜGEL-KAHLER, 1968; BOGOYAVLENSKAYA, 1984). Reasons for rejecting the hypothesis that astrorhizae are homologous to hydrozoan hydrorhizae have been reviewed by STEARN (1972). Hydrorhizal tubes should be of constant diameter along their length, always join into a continuous network, and conform at their branching points with the laws of fluid diffusion (LABARBERA & BOYAJIAN, 1991). The astrorhizae fulfill none of these requirements.

JORDAN (1969), KAŻMIERCZAK (1969), and NGUYEN HUNG (2001) have postulated that the astrorhizae are foreign organisms that have invaded the stromatoporoid skeleton. The integration of the canals into the skeleton and their uniformity within species makes this hypothesis unlikely. As explained in the Internal Morphology section (see p. 419–520), some radially branching tubes of astrorhizae formed within Devonian stromatoporoids do appear to be traces of a parasitic organism. They are characterized by: (1) greater diameters than normal astrorhizal canals (which may also be present in the same skeleton; KAŻMIERCZAK, 1969); (2) distinct walls; (3) abundant, closely spaced, curved dissepiments, rather than widely spaced tabulae (see Fig. 332.1). The affinity of the organism forming these walled tubes is unknown. KAŻMIERCZAK (1976) later changed his interpretation of astrorhizae to accord with his hypothesis that stromatoporoids belonged in the Cyanophyta. He proposed that the astrorhizae represent “. . . *in situ* developed new coccoid colonies . . .” (p. 51) and that modern counterparts can be found in the radially filamentous juvenile stages of colonial coccoid cyanophytes. The viewpoint that stromatoporoids were cyanophytes was effectively rebutted by RIDING and KERSHAW (1977) and LABARBERA and BOYAJIAN (1991).

Since the work on hypercalcified sponges of HARTMAN and GOREAU (1970), who revived and documented KIRKPATRICK’S (1912b) suggestion that astrorhizae proved the poriferan nature of stromatoporoids, most paleontologists have been convinced that these canal systems are homologous to the exhalant systems of encrusting sponges. If the astrorhizae carried the exhalant water from the stromatoporoid sponge, then their design should be optimized for this use by natural selection. The optimum design of such a system in organisms was defined as Murray’s Law, or  $Q = kd^3$ , where  $Q$  is the flow through a vessel and  $d$  is its radius (VOGEL, 1994). Murray’s Law describes a

bulk-flow transport system that minimizes the metabolic costs of moving fluid through the system and the metabolic costs of maintaining the system (ZIEGLER, 1995). Where a canal (such as an astrorhizal canal) branches into two or more tributaries, the relationship between their radii,  $d_n$ , is indicated as:

$$d_0^3 = d_1^3 + d_2^3 + \dots + d_n^3$$

That is, the sum of the cubes of the radii of the tributaries equals the cube of the radius of the vessel they join. Measurements by ZIEGLER (1995) show that the canal systems of two marine sponges are compatible with Murray’s Law and that it can be used to assess the sponge affinity of enigmatic fossils.

LABARBERA and BOYAJIAN (1991) considered three hypotheses to explain the function of astrorhizae: (1) the canals represent the traces of symbiotic organisms; (2) they represent diffusion canals; or (3) they carried a bulk flow of water to serve trophic-respiratory functions. Each of these hypotheses can be accepted or rejected on the basis of the anatomy of the branching points in the tributary system of the astrorhizae. If the canals are diffusion channels, such as postulated by those who favor a hydrozoan affinity, then the sum of the squares of the diameters of the daughter canals below a branch point should equal the square of the diameter of the canal into which they lead. If the bulk flow system was constructed so that both the resistance to flow and some cost associated with the volume of the system were minimized, then the sum of the cubes of the diameters of the daughters should equal the cube of the diameter of the canal to which they lead. By measuring the branching points in several specimens from the Devonian of Michigan, LABARBERA and BOYAJIAN (1991) showed that the diameters of the canals corresponded well with Murray’s Law and did not support the other hypotheses. They concluded that their study showed the astrorhizae were likely to be the exhalant canals of sponges.

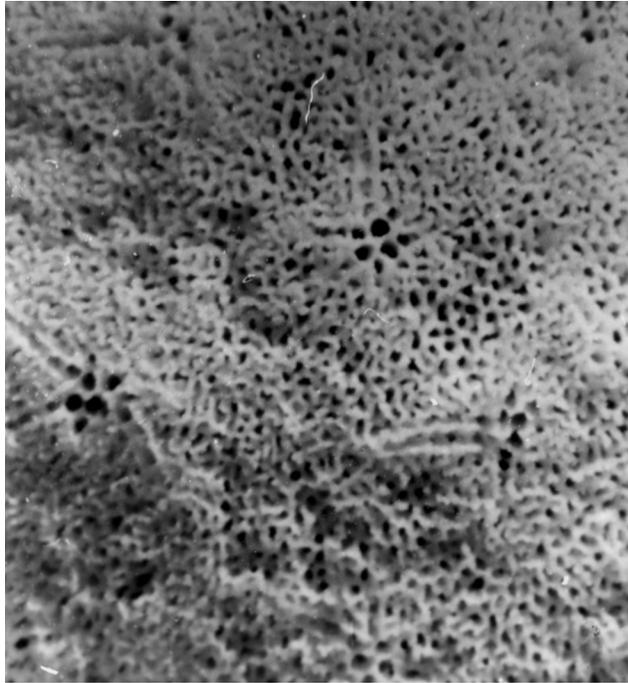


FIG. 357. Surface of skeleton, *Astrosclera willeyana* LISTER, 1900, showing astrorhizal canals on surface and penetrating into skeleton, SCRM 99-3, Guam, Anae Island,  $\times 10$  (Stearn, 2010d).

The living hypercalcified sponges provide models for the astrorhizal systems of stromatoporoids (Fig. 355; Fig. 356.2). In *Ceratoporella*, the soft tissue forms a thin (1.5 mm) layer on the surface of a domical solid skeleton of aragonite (Fig. 355; Fig. 356.1). WILLENZ and HARTMAN (1989) have described how water traverses the upper soft tissue surface through porocytes, with openings only a few micrometers across. The incoming water enters a vestibule cavity beneath the surface and passes by canals, into the choanocyte chambers located in regularly spaced depressions in the skeletal surface. Water cleaned of nutrients is impelled from the choanocyte chambers and gathered into tubes of steadily increasing diameter, joining others as tributaries that lead through the vestibules onto the surface to central oscula (Fig. 356.1). The astrorhizal canals leave vague depressions on the skeletal surface, because secretion of the skeleton

is inhibited beneath them (Fig. 355). No trace of these surficial astrorhizal canals is preserved in the skeleton as it is secreted. In *Goreauiella*, the canal system is similar but leaves ridges instead of depressions in the basal skeleton. In *Merlia*, the exhalant canals are entirely superficial and leave no trace on the skeleton. In *Astrosclera*, the skeleton has many internal cavities filled with soft tissue, and the astrorhizal canals reach downward into the cavities and are outlined by skeletal tissue (Fig. 357).

The preservation of open astrorhizal canals in the skeletons of many stromatoporoids indicates that they must have been functional in the soft tissue that occupied the upper layers of the skeleton, otherwise they would not have been accommodated by skeletal modifications. These open canals would have been points of entry to abandoned parts of the skeleton for destructive organisms, unless sealed off as the sponge grew upward. To seal them, the sponge

appears to have calcified the valvules, layers of tissue that extend across the canals in living hypercalcified sponges to regulate water flow, forming astrorhizal tabulae. The

level at which permanent astrorhizal tabulae were introduced in these canals may serve as an indicator of the depth of penetration of soft tissue in the skeleton.

