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Part E, Revised, Volume 4, Chapter 9D:
Microstructure and Mineralogy
of Paleozoic Stromatoporoidea

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PART E, REVISED, VOLUME 4, CHAPTER 9D: MICROSTRUCTURE AND MINERALOGY OF PALEOZOIC STROMATOPOROIDEA

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INTRODUCTION

Microstructure is defined as the textures of the structural elements observed at magnifications greater than 20×. 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. 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 stromatoporoids 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. 1,*1–2*; Fig. 2,*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. 2,*2*). The specks were believed by NICHOLSON (1886 in 1886–1892) 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 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** (STEARN & others, 1999).
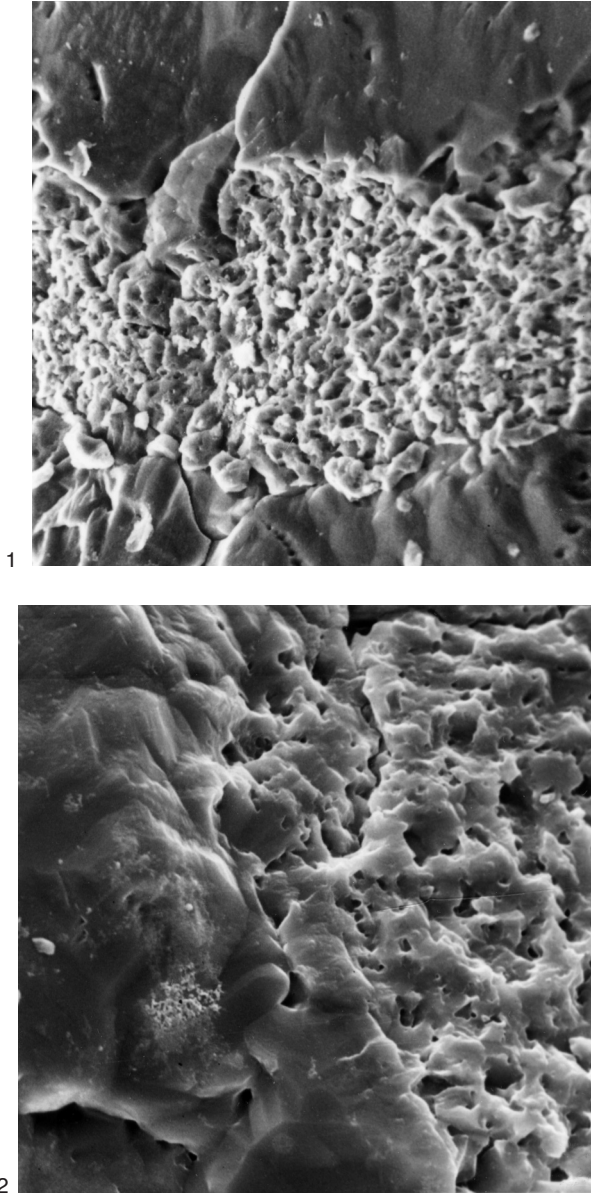
FIG. 1. *1,* SEM, finely crystalline structural element with cavities bounded by solid cement crystals in galleries; *Anostylostroma* sp., SCRM 21-1, Emsian, Bois Blanc Limestone, Gorrie, southwestern Ontario, Canada, ×700 (new); *2,* SEM, edge of structural element showing contrast of structure with cement crystals; *Actinostroma* sp., SCRM 90-26, Frasnian, Cerro Gordo Formation, Rockford, Iowa, ×1900, scale bar, 10 μm (new).
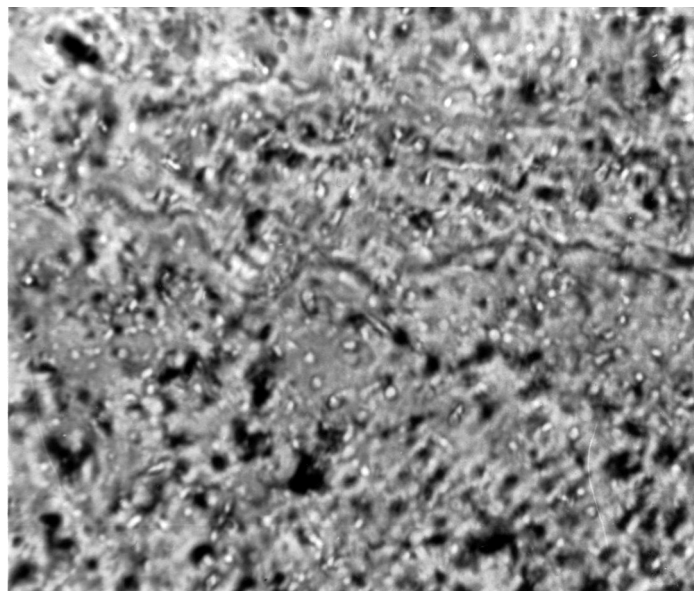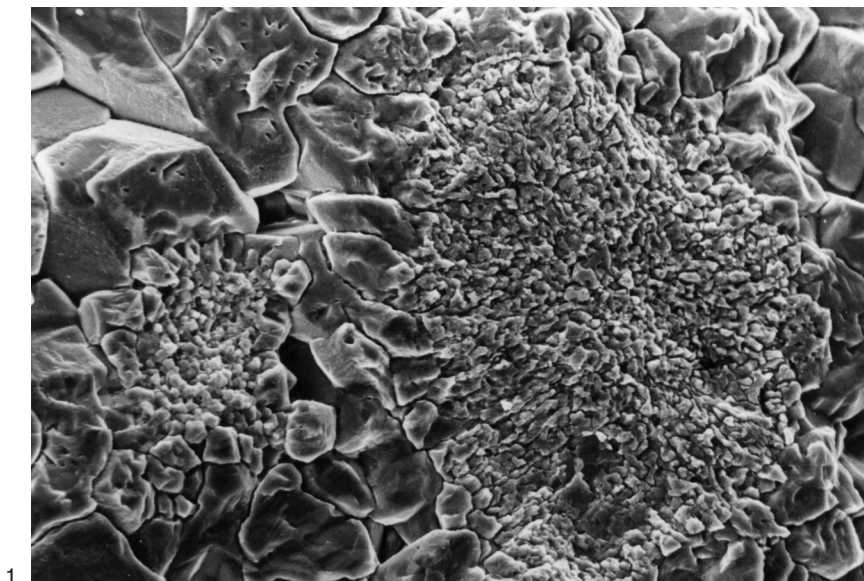
FIG. 2. *1,* SEM, cement crystals in galleries meeting at triple junctions and lack of rim cement, longitudinal section, *Stictostroma mccannelli* FAGERSTROM, 1961, UMMP ?36199, Emsian-Eifelian, Formosa Reef, southwestern Ontario, Canada, ×590 (new); *2,* fluid inclusions in ultrathin section made by Jean Lafuste, *Clathrodictyon* sp.*, RM 14820, locality unknown, ×1730 (new).

Compact

Specks are distributed evenly throughout the structural elements so that they have no regular internal structure (see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 5,*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 clathrodictyids typically have compact structural elements.

Fibrous—The specks and crystal boundaries are aligned. In laminae, this alignment is transverse; 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. 3,*1–2*). 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. 4,*1*) and may be a diagenetic artefact of ordinicellular microstructure (see below).

Striated

The specks are concentrated in short, rodlike bodies. This microstructure appears to be unique to *Stachyodes* and may be a diagenetic manifestation of originally microreticulate microstructure.

Tubulate

Clear, vermiform areas extend irregularly through the speckled tissue. This microstructure is rare and best shown in some species of *Clathrocoilona* (Fig. 4,*2*).

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. 4,*3;* Fig. 5,*1;* Fig. 6,*1;* Fig. 10,*1–2*). 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. 5,*2–3;* Fig. 6,*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. 6,*3;* Fig. 7,*1;* Fig. 9,*1a–b;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 16E, Fig. 39). 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 **orthoreticular**. Where the micropillars curve upward and outward from the axes of pillars or pachysteles, microreticulate microstructure is distinguished as **clinoreticular** (Fig. 9,*2*). Where orientation of micropillars and microcolliculi is without order, the microstructure is said to be **acosmoreticular.** 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. 7,*2;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 16E, Fig. 6*c*). 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 µm), as in *Trupetostroma* or *Paramphipora* (Fig. 7,*2–3;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 16E, Fig. 48*b*).
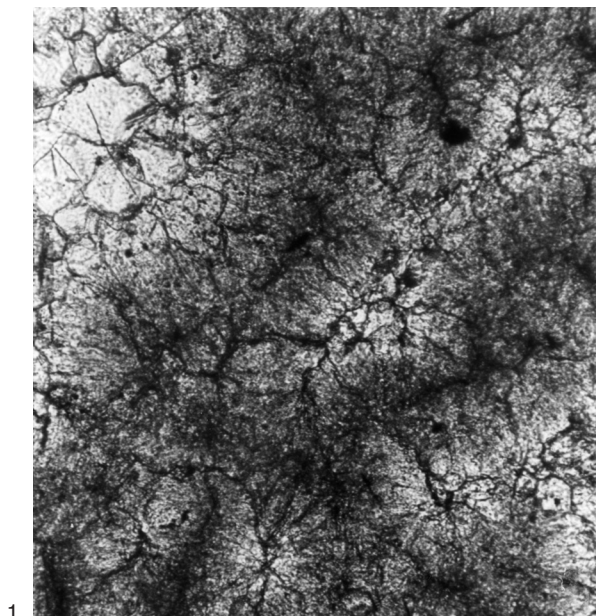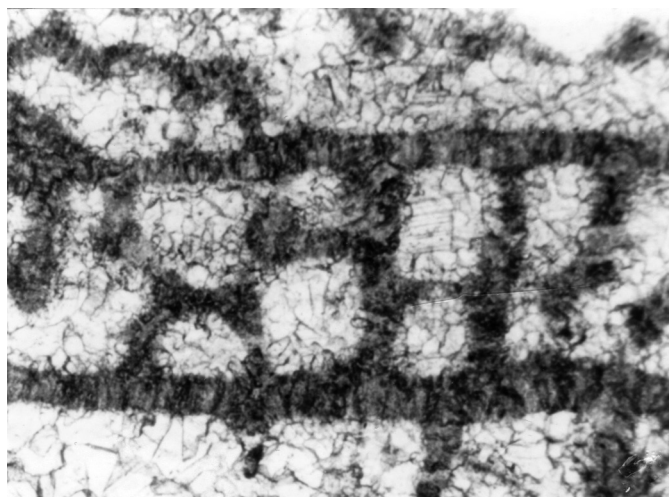
Fɪɢ. 3. *1,* Transversely fibrous microstructure and center of calcification; *Amphipora* sp., GSC 54924, Emsian-Eifelian, Ogilvie Formation, Yukon Territory, Canada, ×150 (new); *2,* transversely fibrous laminae and pillars, longitudinal section, *Hammatostroma albertense* Sᴛᴇᴀʀɴ, 1961, holotype, GSC 15318, Frasnian, Cairn Formation, western Alberta, Canada, ×20 (new).

In some preservation states, the borders of the structural elements are independent of crystal boundaries that are mostly 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
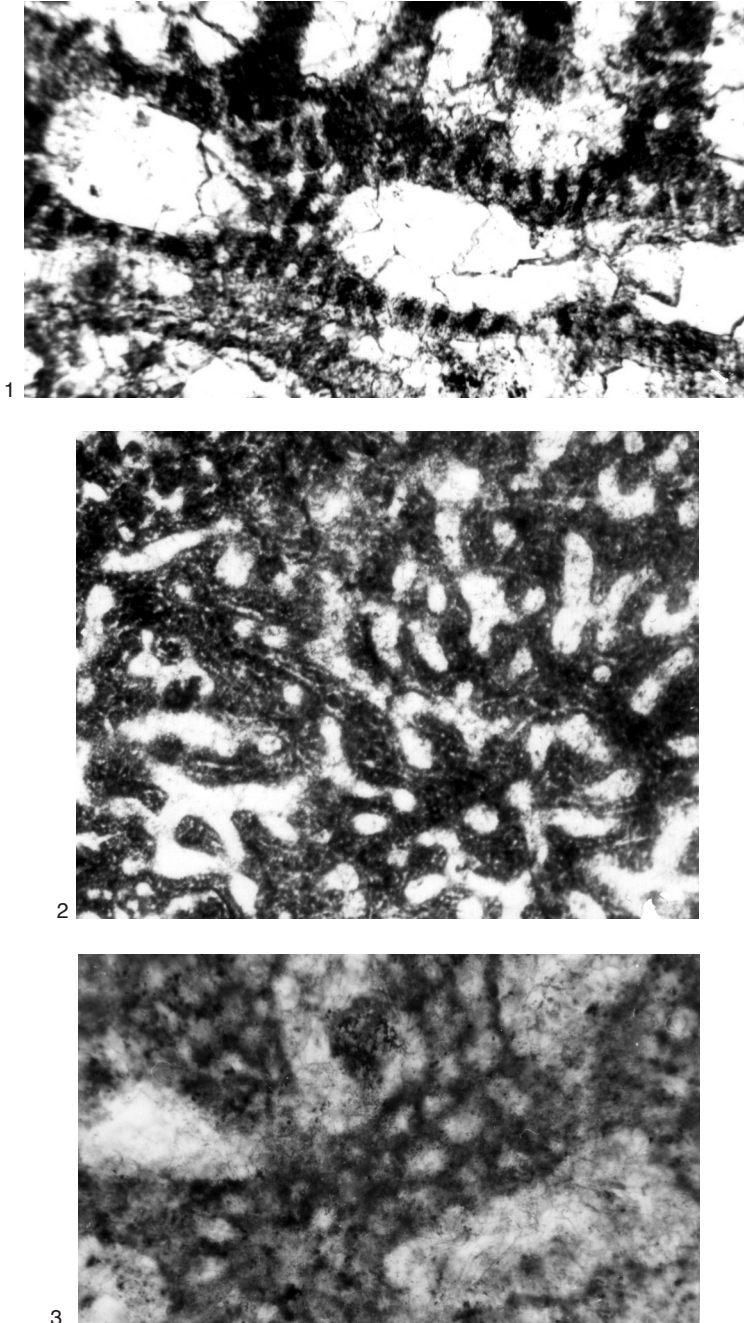
FIG. 4. *1,* Transversely porous laminae and pillar, longitudinal section, *Gerronstroma elegans* YAVORSKY, 1931, paratype, YPM.227561, Middle Devonian, Kuznetsk Basin, Russia, ×100 (new); *2,* tubulate microstructure, tangential section, *Stictostroma? nunavutense* PROSH & STEARN, 1996, GSC 108876, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×25 (new); *3,* coarse cellular microstructure, tangential section, *"Stromatopora" (?Salairella) beuthii* (BARGATZKY, 1881), Nicholson 62, ?NHM P5703, Middle Devonian, Hebborn, Rhineland, western Germany, ×50 (new).
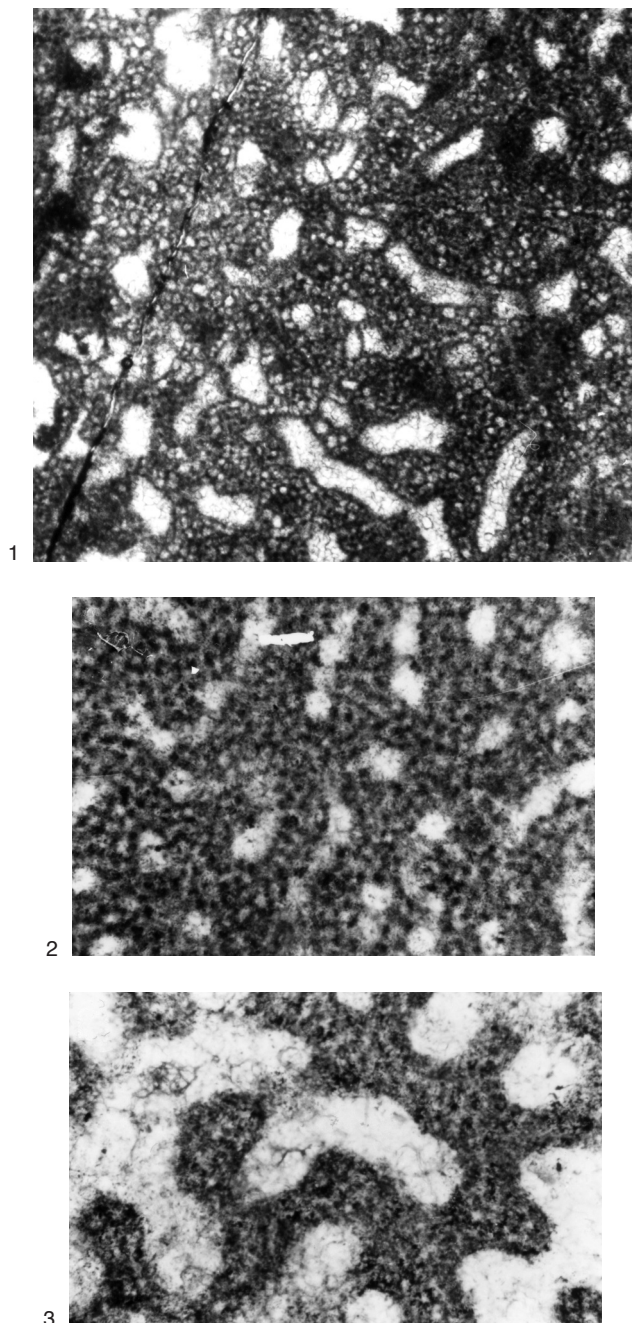
FIG. 5. *1,* Coarse cellular microstructure, tangential section, *Syringostromella zintchenkovi* (KHALFINA, 1961), GSC 108897, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×25 (new); *2,* tangential section of Figure 7,*1, Syringostromella carteri* NICHOLSON, 1891, Nicholson 37, MNH P5678, Wenlock, Shropshire, England, ×55 (new); *3,* tangential section of Figure 6,*3, Parallelostroma typica* (ROSEN, 1867), showing cellular-melanospheric appearance of cut ends of micropillars in pachysteles, ×55 (new).
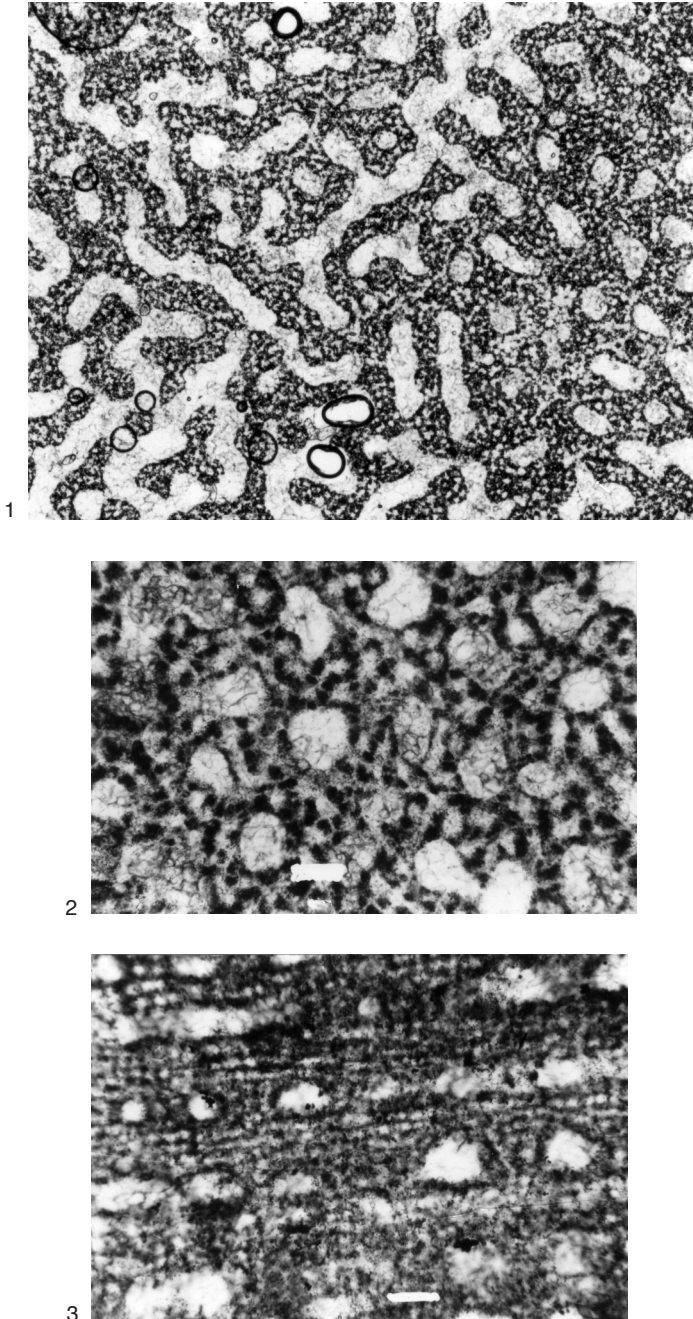
FIG. 6. *1,* Cellular microstructure grading into melanospheric, tangential section, *Pseudotrupetostroma vitreum* (GALLOWAY, 1960), GSC 48453A, Givetian, Evie Lake Reef, northeastern British Columbia, Canada, ×25 (new); *2,* opaque (dark) cut ends of rodlike micropillars in pachysteles in tangential section, *Parallelopora ostiolata* BARGATZKY, 1881, holotype, Nicholson 125, NHM P5936, Middle Devonian, Buechel, Rhineland, western Germany; note also round autotubes, ×55 (new); *3,* microreticulate microstructure showing thick laminae composed of thin microlaminae and micropillars, longitudinal section, *Parallelostroma typica* (ROSEN, 1867), holotype, Nicholson 59b, IGTTU Co3009, Ludlow, Saaremaa, Estonia, ×50 (new).
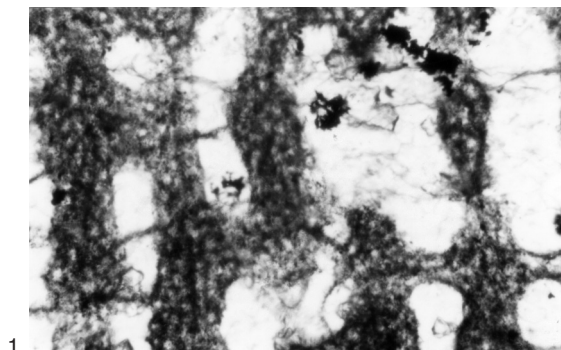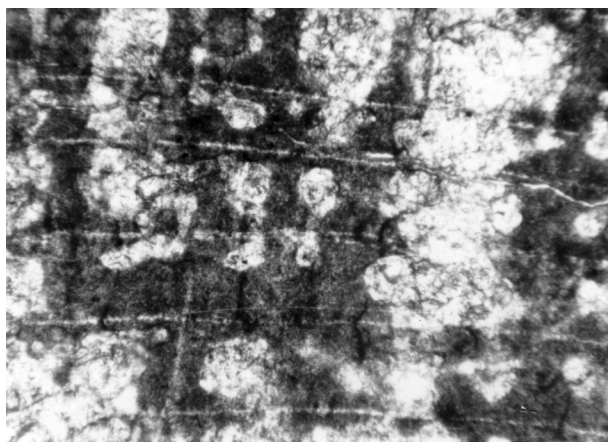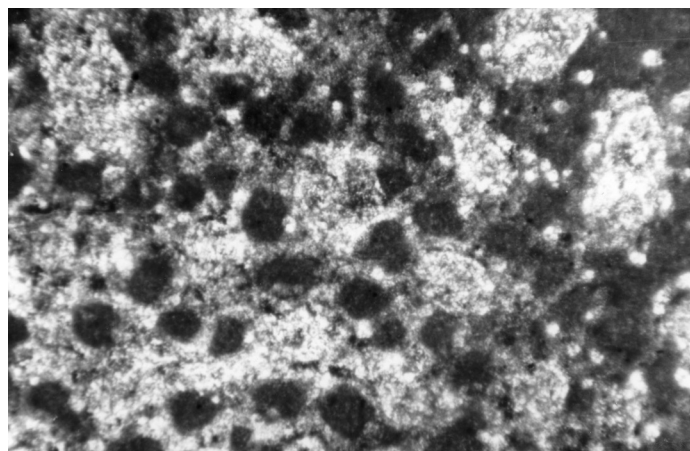
Fig. 7. *1,* Cellular microstructure in pachysteles, longitudinal section, *Syringostromella carteri* Nicholson, 1891, Nicholson 37, MNH P5678, Wenlock, Shropshire, England, ×55 (new); *2,* vacuoles (round holes) in compact pillars, longitudinal section, *Trupetostroma warreni* Parks, 1936, ROM 1885A, holotype, Middle Devonian, Great Slave Lake, Northwest Territories, Canada; note superposed pillars interrupted by laminae, represented by a clear zone divided into cellules, ×50 (new); *3,* vacuolate microstructure in compact structural elements, tangential section, *Trupetostroma warreni* Parks, 1936, ROM 1885B, Middle Devonian, Great Slave Lake, Northwest Territories, Canada, ×50 (new).

microstructures that are unique to a single genus or restricted to a few genera. For example, in the type species of *Parallelopora,* the microreticulation is very coarse and the micropillars appear as dark (opaque) rods within the network of pachysteles (Fig. 6,*2*). In *Arctostroma* and *Ferestromatopora* (Fig. 8,*1–2*), 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.*

MICROSTRUCTURES IN ULTRATHIN SECTIONS

In sections ground to a few micrometers in thickness, the specks appear at magnifications of about 1000✕ as subspherical opaque areas if they are out of the the plane of focus, and as light areas if they are in focus (Fig. 2,*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 µm across that have smooth surfaces, even when the surfaces examined have been prepared by etching. The crystals commonly meet at triple junctions (Fig. 11,*1*). These gallery fillings rarely show a rim of finer crystals bordering the structural elements (that is, syntaxial rim cements; Fig. 2,*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 µm) of irregular but elongate shape that are arranged in an overlapping pattern (Fig. 1,*1–2*), 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 (STEARN & MAH, 1987). It has been described in such Paleozoic stromatoporoids as *Hammatostroma, Amphipora,* and *Anostylostroma* (Fig. 2,*1;* Fig. 11,*2;* Fig. 12,*1–2*) 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 (STEARN & 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. 13,*1–2*). 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. 1,*1–2;* 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. 14,*1–2;* Fig. 15,*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
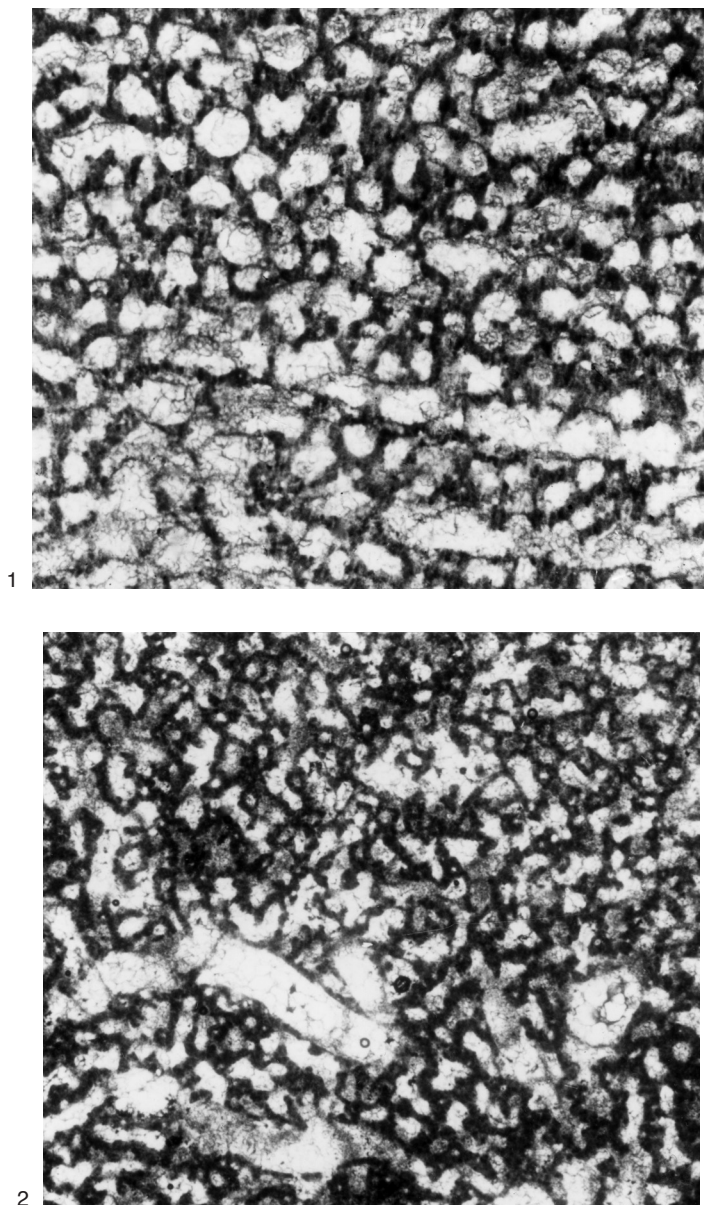
FIG. 8. *1,* Vacuolate microstructure with traces of melanospheres, longitudinal section, *Arctostroma contextum* (STEARN, 1963), holotype, GSC 16856, Frasnian, Mikkwa Fortmation, Mikkwa River, northern Alberta, ×25 (new); *2,* compact irregular structural elements enclosing round vacuoles, tangential section, *Arctostroma contextum* (STEARN, 1963), GSC 111384, Frasnian, Souris River Formation, Manitoba, Canada, ×18 (new).

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 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.
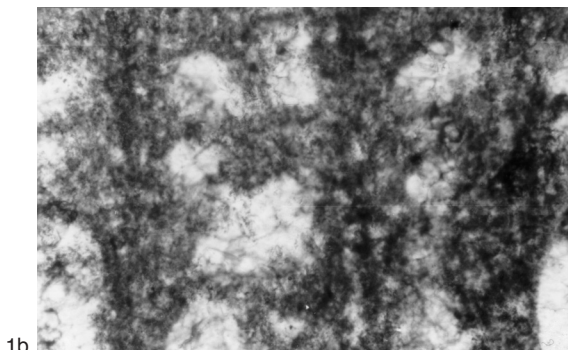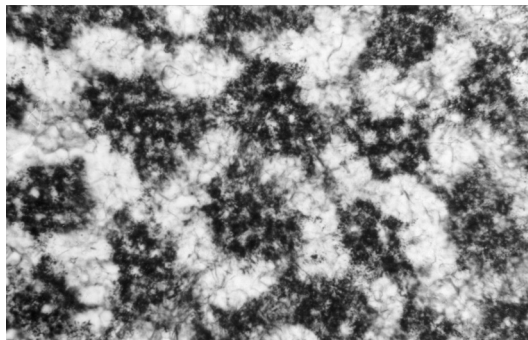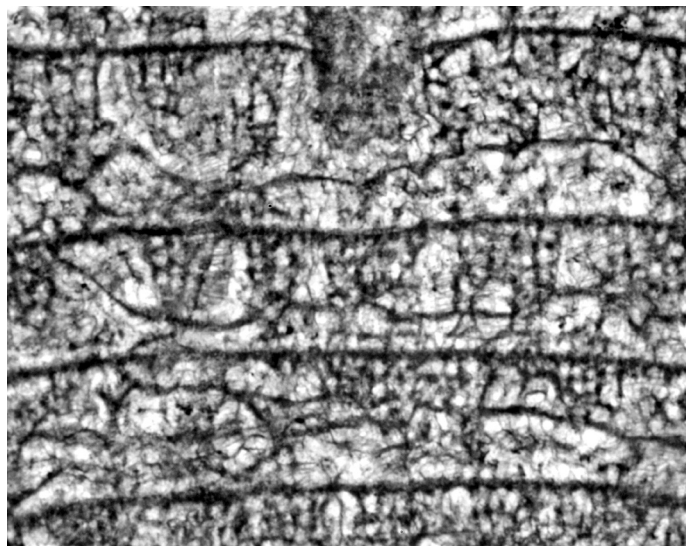
Fig. 9. *1a–b,* clinoreticular microstructure of pachysteles, longitudinal and tangential sections, *Syringostroma nodulatum* (Nicholson, 1875), Nicholson 310, NHM P5604, Middle Devonian, Ohio, USA, ×55 (new); *2,* coarse clinoreticular microstructure in pachysteles, longitudinal section, *Habrostoma alternum* Webby & Zhen, 2008, holotype, AM FT.15128, Lower Devonian, Martins Well Limestone, Queensland, Australia, ×50 (Webby & Zhen, 2008).
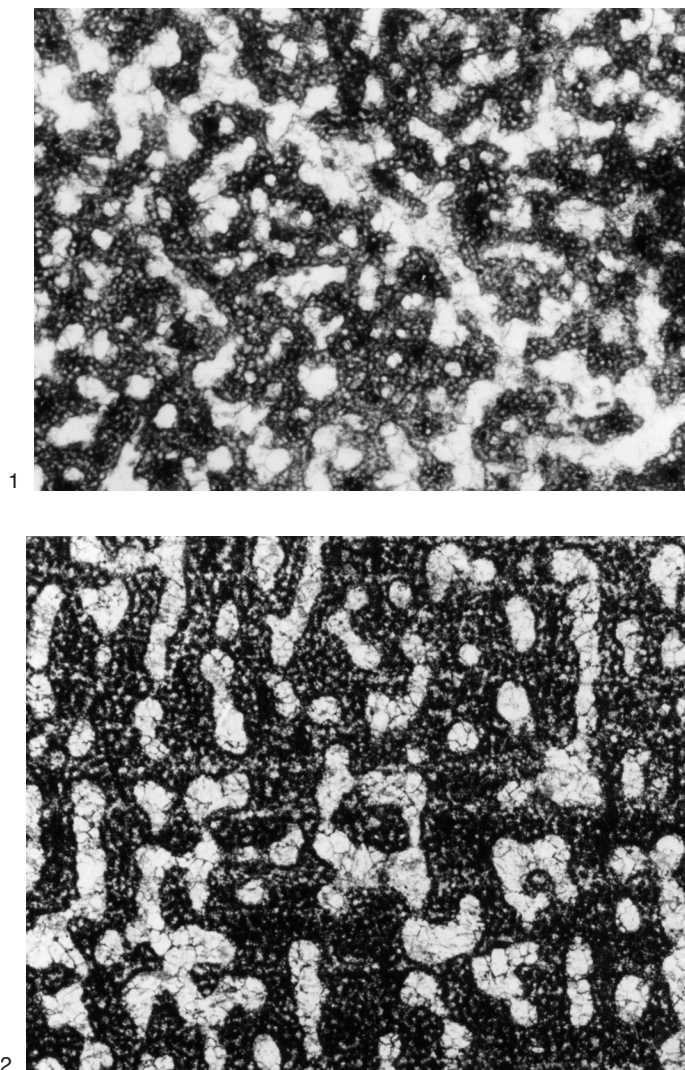
FIG. 10. *1,* Cellular microstructure, tangential section, *Salairella prima* KHROMYCH, 1971, hypotype, GSC 108901, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×25 (new); *2,* coarse cellular microstructure in pachysteles, longitudinal section, *Pseudotrupetostroma vitreum* (GALLOWAY, 1960), GSC 48453A, Givetian, Evie Lake Reef, northeastern British Columbia, Canada; note laminae outlined by line of cellules, ×25 (new).

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.

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, 1989; MALLAMO, 1995; MALIVA, 1998). The aragonite lattice, which is more receptive to the 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 Sr^{++}. In contrast, fossils of brachiopods that secreted low magnesium calcite have Sr^{++} values generally below 1300 ppm and commonly below 1000 ppm. Most limestones have Sr^{++} values in the 400–700 ppm range (MALLAMO & STEARN, 1991). Calcites that contain 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 Sr^{++} values in labechiids in the zone of diffused specks adjacent to cyst plates that were postulated by STEARN (1989) 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 Mg^{++}, had no microdolomite, and was variably but locally high in 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
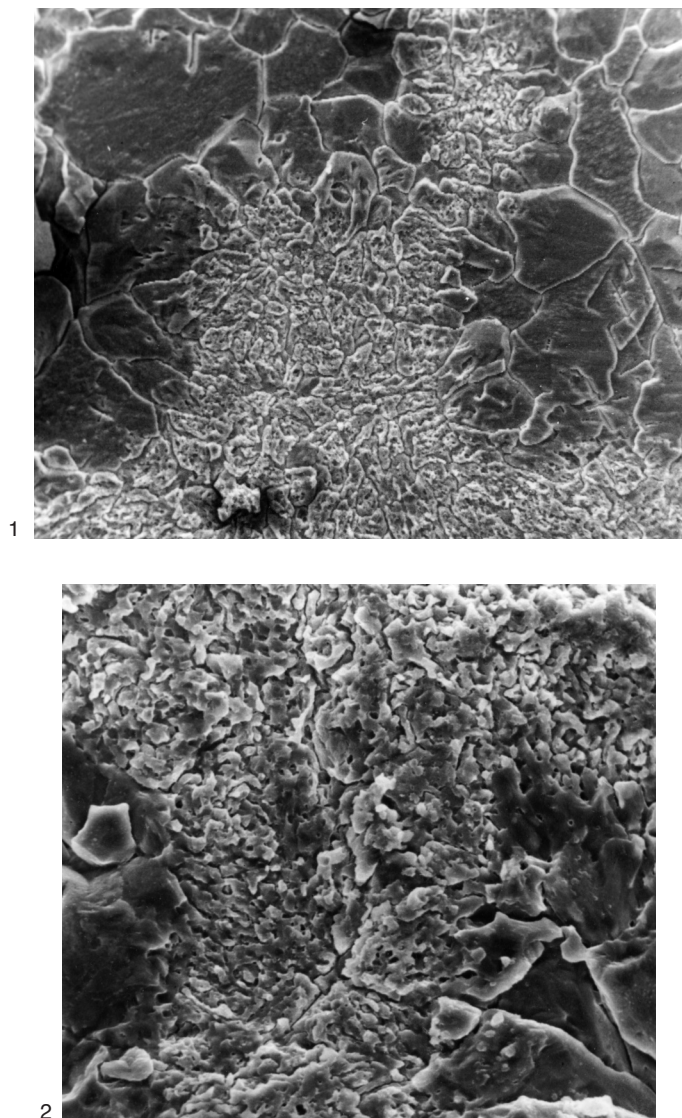
FIG. 11. *1,* SEM, radial fibrosity in pillars and rim cements of fine crystals, tangential section, *Actinostroma clathratum* NICHOLSON, 1886 in 1886–1892, SCRM 96-09, ×480, scale bar, 100 μm (new); *2,* SEM, fibrosity in pillars, longitudinal section, *Actinostroma clathratum*, SCRM 96-09, hypotype, RM 14813, Frasnian, Duperow Formation, Esterhazy shaft, Saskatchewan, Canada, ×800, scale bar, 10 μm (new).

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 that Ordovician stromatoporoids
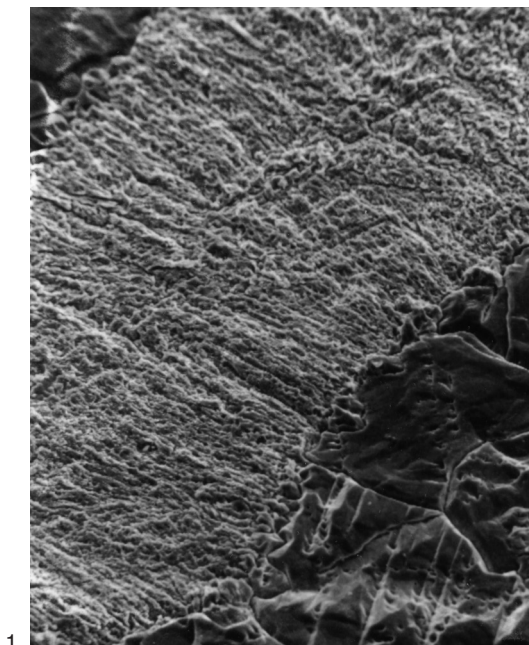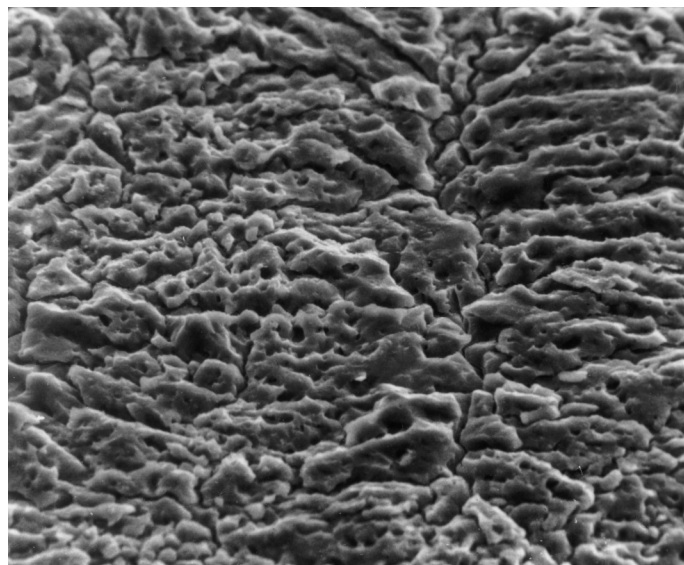
Fig. 12. *1,* SEM, structural element showing fibrosity and central axis, longitudinal section, *Hammatostroma albertense* Stearn, 1961, SCRM 67-21, Frasnian, Cairn Formation, Mt. Haultain, western Alberta, ×230 (new); *2,* SEM, coarse fibrosity and axial line in *Amphipora* sp., GSC 26144, Emsian-Eifelian, Ogilvie Formation, Yukon Territory, Canada, ×750 (new).

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 Sr^{++} values of post-Ordovician stromatoporoids (including labechiids) analyzed by microprobe by Mallamo (Mallamo & Stearn, 1991; Mallamo, 1995) are all
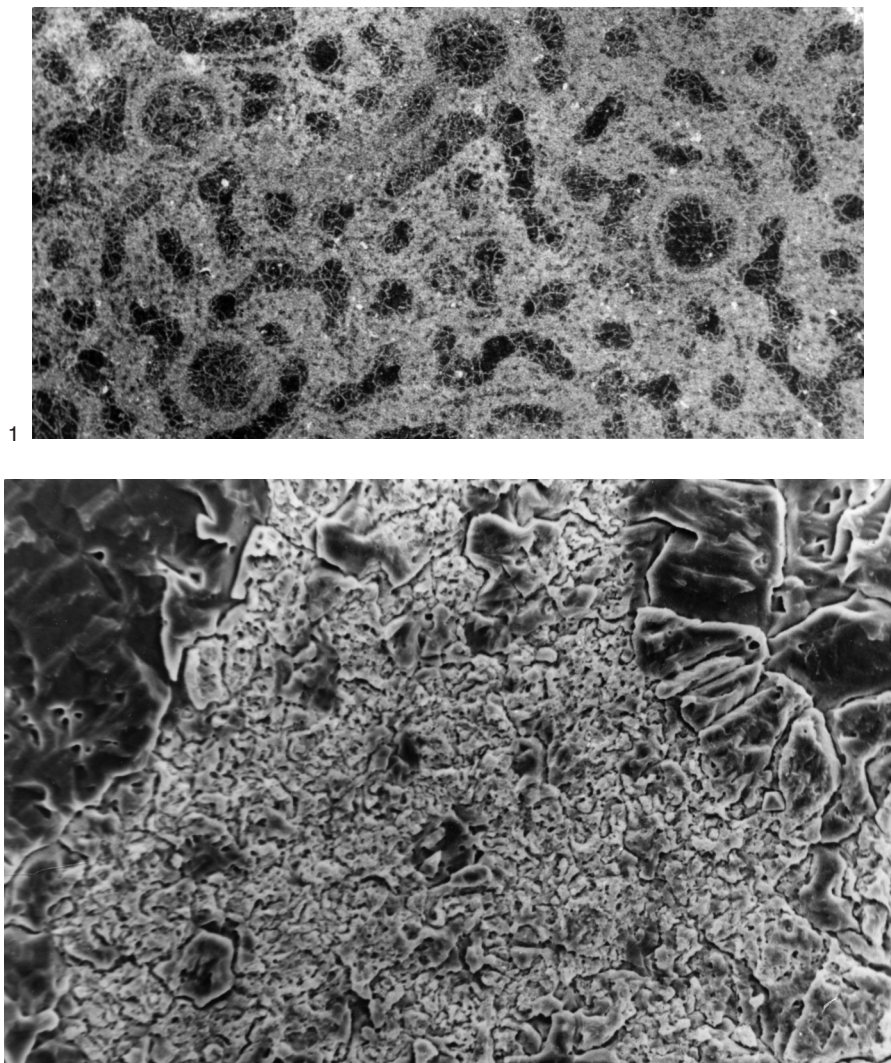
Fig. 13. *1,* SEM, cellular microstructure of pachysteles, tangential section, *Salairella buecheliensis* (Bargatzky, 1881), SCRM 116-1, Givetian, Blacourt Formation, Boulonnais, France, scale bar, 1 mm, ×34 (new); *2,* SEM, cellular microstructure, longitudinal section, *Salairella buecheliensis* (Bargatzky, 1881), SCRM 116-1, Givetian, Blacourt Formation, Boulonnais, France, ×480 (new).

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. 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.

Some studies of the geochemistry of living hypercalcified sponges have been

applied to Paleozoic stromatoporoids. WEBB, WORHEIDE, and NOTHDURFT (2003) measured rare earth element geochemistry of both 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 (see above) and geochemistry are contradictory, but only a few stromatoporoids have been analyzed for their trace elements, and 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* and *Astrosclera* 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. 15,*2*) growing outward from their axes. The microstructure is trabecular, similar to that of the sclerodermites of scleractinian corals. The skeleton of *Astrosclera* (see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9F, Fig. 9) is composed of spherules of aragonite, about 20 µm 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 (1975) 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 (STEARN & 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. In the living sphinctozoan *Vaceletia,* the skeleton is composed of a very fine, nonfibrous mosaic of aragonite crystals, but 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* and *Murrayona,* members of the class Calcispongiae, 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 *Treatise Online,* Part E, Revised, Volume 4, Chapter 9F, Fig. 2) and others lamellar high-magnesium calcite (*Acanthochaetetes*). ROSENHEIM, SWART, and THOROLD (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.
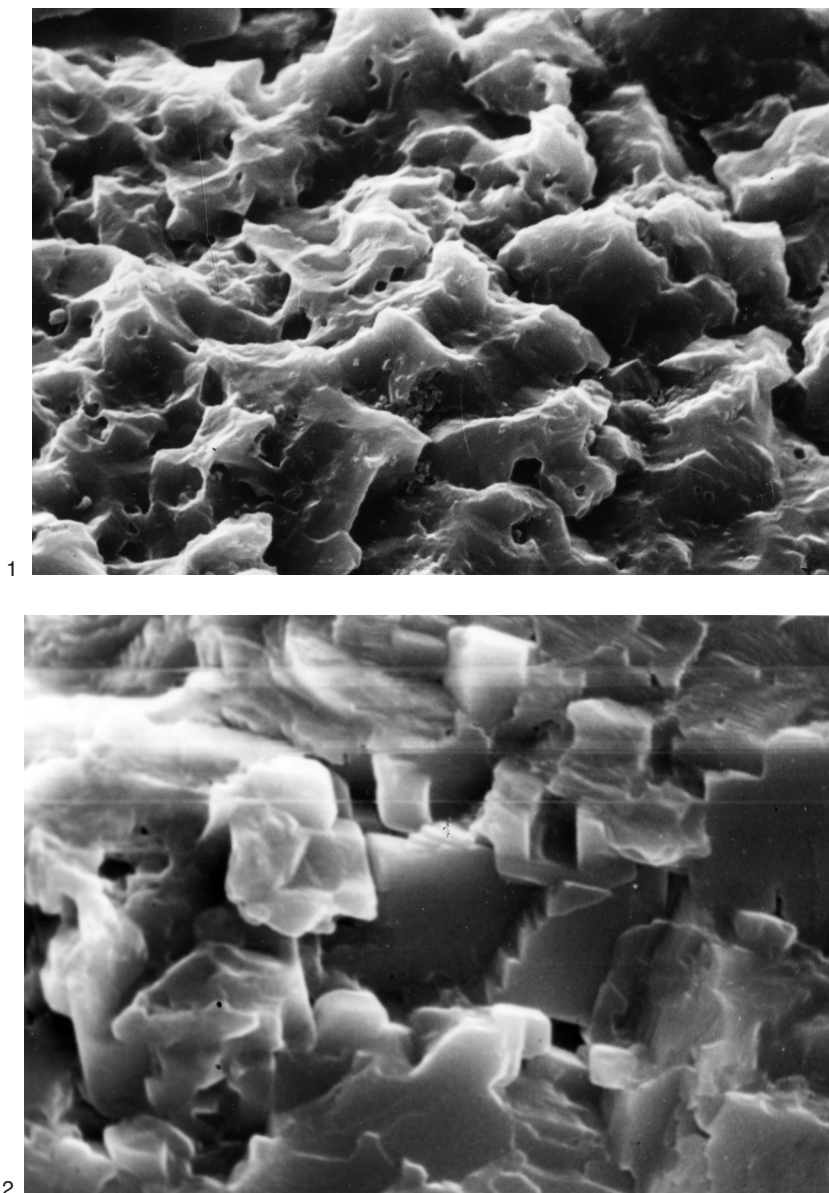
FIG. 14. *1,* SEM, cavities in structural elements, some of rhombohedral outline, *Actinostroma* sp., RM 14811, Frasnian, Lime Creek Formation, Iowa, United States, ×4800, scale bar, 10 μm (new); *2,* SEM, rhombohedral crystals and cavities, *Actinostroma* sp., RM 14811, Frasnian, Lime Creek Formation, Iowa, United States, ×4700, scale bar, 10 μm (new).

DIAGENESIS AND INTERPRETATION OF MICROSTRUCTURES

In life, most stromatoporoids formed a basal skeleton in which the galleries, occu-pying 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 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. Dolomitization 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, 1989) 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, 1974). 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 pachysteles, 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*) (STEARN, 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 (STEARN, 1975).

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 *Clathrocoilona* (0.04 mm) are an order of magnitude larger than those of boring algae.

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, 1989) 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 (1989) attributed melanospheric
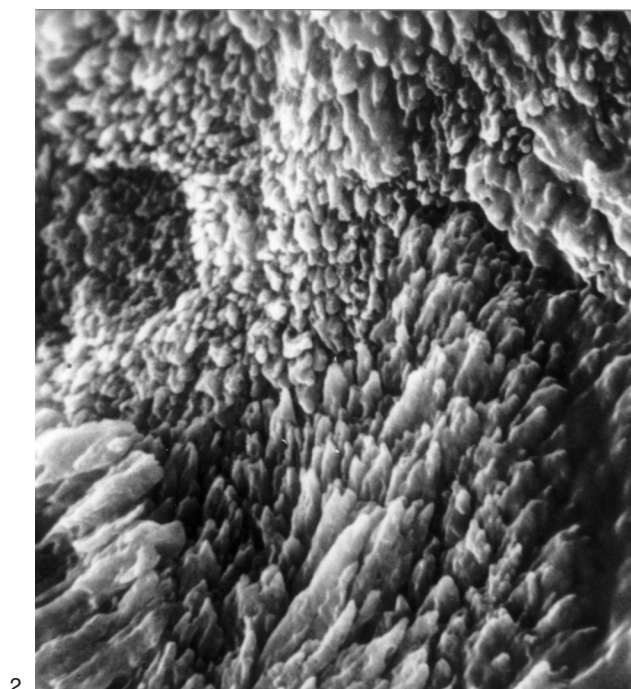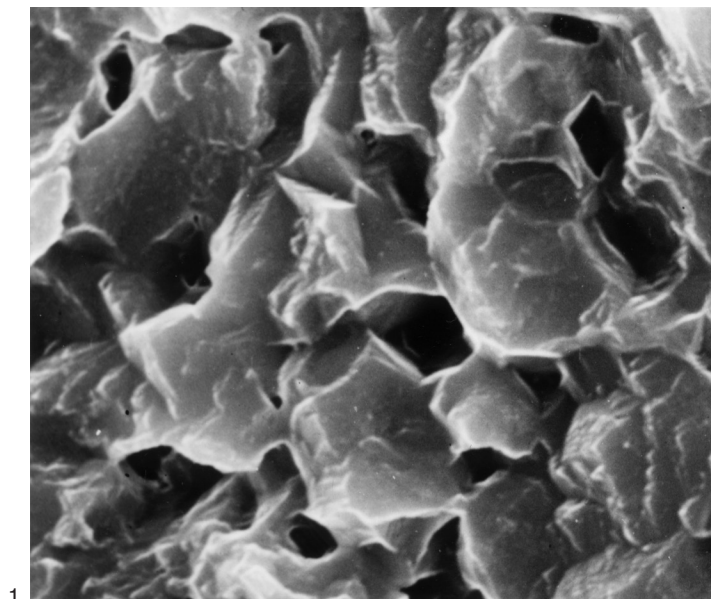
FIG. 15. *1,* SEM, rhombohedral cavities in a structural element, *Actinostroma expansum* (HALL & WHITFIELD, 1873), SCRM 90-31, Frasnian, Shell Rock Formation, Iowa, United States, ×7000, scale bar, 1 μm (new); *2,* SEM, fibrous aragonite skeleton of *Calcifibrospongia actinostromoides*, Recent, Bahama Island, SCRM 99-9, ×7350 (new).

microstrucure to the isolation of subspherical regions of inclusion-rich (speck-rich) 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. 6,*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 Kazmierczak (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 (1886–1891), Lecompte (1951–1952), Galloway (1957), and Stearn (1966, 1989). 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) **Ordinicellular** 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 ordinicellular 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 *Treatise Online,* Part E, Revised, Volume 4, Chapter 16E. The distinction between cellular and microreticular microstructures was used to separate the stromatoporids into the orders Stromatoporida and Syringostromatida (Stearn, 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 (Stearn, 1993) postulated that they originated in late Llandovery time, in such genera as *Syringostromella* and *Stromatopora,* from clathrodictyids 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.

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