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PALEOZOIC STROMATOPOROIDEA: GENERAL INTRODUCTION

COLIN W. STEARN

The stromatoporoids are a group of fossil organisms, now extinct, that lived during the Ordovician, Silurian, and Devonian periods and are preserved in rocks of these systems as large carbonate fossils in the shapes of plates, crusts, domes, fingers, and bulbs, consisting internally of a network of regularly repeating structural elements such as pillars, laminae, cysts, and walls. Although recognized as a class of sponges, these fossils, unlike most living sponges, are lacking in siliceous or evident calcareous spicules. A fragmentary, unique specimen from the Devonian of the Ardennes may be the exception to the generality of this statement (DA SILVA & others, 2011c; DA SILVA & others, 2014).

The previous volume of the *Treatise on Invertebrate Paleontology* that included a section on the stromatoporoids was published over 50 years ago as Part F (MOORE, 1956). At that time, the group was considered to belong in the phylum Coelenterata (subphylum Cnidaria). The section's author, Marius LECOMPTE, integrated the Mesozoic fossils that closely resemble the Paleozoic stromatoporoids into the order Stromatoporoidea. In this revised treatment, the Paleozoic fossils are considered to be a class of the Porifera, and the similar forms of the Mesozoic are divided into those fossils with spicules that can be assigned to taxa of living sponges and the aspiculate group that can be classified only on their calcareous basal skeletons. In this revised treatment of the Paleozoic Stromatoporoidea, they are placed in the hypercalcified sponges.

Consensus for the change from the Cnidaria to the phylum Porifera was largely due to discoveries during the past 50 years. The first was the detailed description by HARTMAN and GOREAU (1970) of the stromatoporoid-like hypercalcified sponges (they called them sclerosponges) from the northern coast of Jamaica. The second was the recognition that the exhalant current systems of these sponges were almost identical to, and probably analogous to, the radial canal systems on the surfaces of stromatoporoids. The third was the discovery of spicules in some of the Mesozoic so-called stromatoporoids by WOOD and REITNER (1986). Aspects of both these discoveries had been published before by KIRKPATRICK (1912b) but had attracted little attention among paleontologists (see p. 551–573 for further discussion). The rediscovery of the so-called sclerosponges demonstrated that the carbonate architecture like that of the Paleozoic stromatoporoids was duplicated in living sponges; the recognition of the remains of siliceous spicules, a unique skeletal feature of living sponges, in the carbonate skeletons of Mesozoic fossils of stromatoporoid architecture confirmed the close relationship between living sponges and fossils with similar carbonate skeletons.

The Stromatoporoidea are considered in this volume to be a class of the Porifera defined by characteristic internal structures of the basal skeleton and lack of spicules, but the term stromatoporoid also has been used to describe a grade of evolution of hypercalcified sponges that evolved in several lineages belonging to a range of other poriferan classes. The concept can be found in the works of VACELET (1985), REITNER (1987c), and WOOD (1987, 1990b, 1991a). For example, certain Cambrian archaeocyaths, a number of predominantly Paleozoic to Mesozoic agelasid demosponges (but that also includes modern *Astrosclera*), and Cenozoic demosponges (including modern *Vaceletia*, as well as modern *Calcifibrospongia*), have all been considered to be of stromatoporoid grade. According to WOOD (1991a, p. 119), this grade is characterized by " . . . a multioscular, 'compound,' 'colonial' or modular aquiferous system and a layered organization of radial and concentric skeletal elements . . . ." Division of the forms of this stromatoporoid grade into various higher taxa of the Porifera is not on the basis of their basal skeletons, which may mimic each other, but on their preserved spicules or, in living forms, on the basis of their soft tissues as well. The groups defined on the basis of their stromatoporoid architecture are therefore polyphyletic and should not be placed together as a taxonomic group. Although this architecture has evolved several times in disparate poriferan lineages, this does not prove that the group here recognized as the Paleozoic stromatoporoids is itself a polyphyletic collection of fossils of various poriferan classes; but this possibility needs to be addressed. For example, the labechiids have been considered to be a separate lineage from the rest of the stromatoporoids (HEINRICH, 1914a, 1916; KÜHN, 1927, 1939b; but see also discussions by NESTOR, 1966b; STEARN, 1982a; and WEBBY, 1993). That the class Stromatoporoidea is either polyphyletic or monophyletic can only be decided on the basis of evidence available from the basal skeletons of the group itself.

The formal class Stromatoporoidea applies only to a unified, nonspiculate group of lower Paleozoic–middle Paleozoic taxa, whereas the informal term stromatoporoid has been given a much wider application. Late Paleozoic to Mesozoic and Recent hypercalcified sponges that show features such as latilamination, laminar to bulbous or branching growth form, and astrorhizae have been considered to exhibit a stromatoporoid grade of organization, but these forms do not belong taxonomically in the class Stromatoporoidea. The late Paleozoic to Mesozoic forms are subdivided in this volume into the nonspiculate fossils of stromatoporoid architecture that are here referred to informally as stromatoporoid-like genera (see p. 307–310), and the Mesozoic taxa that have spicules or spicule pseudomorphs are included in the class Demospongiae (see p. 193–208).

As assignment to major divisions of the Porifera by zoologists is largely on the basis of spicule types, strict application of the grade concept to fossil sponges without preserved spicules means that such fossils cannot be placed in a taxonomy based on living forms and spiculate fossils. Without the aid of spicules, demonstrating that the Paleozoic stromatoporoids are a collection of other sponge classes is difficult, maybe impossible. VACELET (1985), WOOD (1990b), and REITNER and WÖRHEIDE (2002) have emphasized that the basal skeleton of hypercalcified sponges is facultative (see p. 533–538); that is, it is easy to secrete and is laid down by the sponge with little or no vital effect on the composition of the ions passing through the sponge tissues (see p. 566–567). They concluded that the basal skeleton in fossil sponges is invalid as a basis for classification, and without the evidence of spicules, the mid-Paleozoic fossils of stromatoporoid grade cannot be validly classified. However, for the group to be useful for interpreting biostratigraphy, paleoecology, paleogeography, and life history, they must be described and classified. The only basis available to the paleontologist to systematize the description of these fossils is their basal skeletons; that is all that remains of them. Similar failures to connect paleontological and zoological classifications are common in invertebrate paleontology where preservational factors stand in the way of ideal taxonomic solutions. Stromatoporoids are classified on the basis of the structural elements of their basal skeletons, because these incorporate the only criteria that are available to divide them into groups for description.

EXTERNAL MORPHOLOGY OF THE PALEOZOIC STROMATOPOROIDEA: SHAPES AND GROWTH HABITS

B. D. Webby and S. Kershaw

INTRODUCTION

Nicholson (1886a, 1889, 1891a, 1892), in his great pioneering work on British Paleozoic stromatoporoids about 120 years ago, was the first to differentiate clearly between basic shapes and growth habits in stromatoporoids, despite the overwhelmingly wide range of variability in external form they exhibit. He illustrated a number of forms, based mainly on rather incomplete, fragmentary skeletons, ranging from moundlike and laminar to dendroid and cylindrical forms (Fig. 273). Nicholson (1886a, p. 27) also recorded the presence of "a concentrically wrinkled imperforate epitheca" and noted a small centralized attachment area on some bases of moundlike and laminar stromatoporoids, comparable with the holothecate massive or laminar species of favositid and alveolitid tabulate corals. These overall similarities suggested to Nicholson (1886a) that stromatoporoids, like colonial corals, adopted similar modes of life, some being mainly free-living forms, and others living as habitual encrusters. Also, a few individual species were considered to have switched between free-living and encrusting modes of growth, depending on changes in environmental conditions. The cylindrical and dendroid stromatoporoids adopted another lifestyle category that Nicholson (1886a) compared with the growth of some ramose species of tabulate corals. Few later workers on stromatoporoids followed Nicholson's (1886a) lead of differentiating between basic shapes (descriptive features) and growth habit categories (mainly interpretative) in assessing their data on external form. It is important that descriptive and interpretative aspects of external growth form of stromatoporoid skeletons be recorded separately, and as far as possible through their growth histories.

The Stromatoporoidea have only been featured once previously in a *Treatise* volume; that was some 50 years ago, and in a coelenterate volume. At the time, Lecompte (1956) recognized the group as being an extinct, problematic, reef-forming order, exhibiting closest relationships to the coelenterate class Hydrozoa, and having a calcareous skeleton described as variable, composed of "irregular rounded masses, relatively thin sheetlike expansions, and branched or unbranched subcylindrical structures" (Lecompte, 1956, p. 108). In other words, the external morphology was typified by mainly domical and laminar shapes, as well as unbranched to branching forms. Lecompte (1956) also reported the layered appearance of latilaminae showing where the skeleton was broken or weathered, the presence of stellate grooves or ridges representing traces of astrorhizae on terminal growth surfaces, and astrorhizae, sometimes in association with mamelons (Lecompte, 1956, fig. 89–90, 92.1). Both astrorhizae and mamelons are now interpreted as integral parts of the exhalant water system (see Functional Morphology of the Paleozoic Stromatoporoid Skeleton, p. 551–573).

The calcareous skeleton of stromatoporoids represents a base that was precipitated from the underside of the thin, mantling veneer of living tissue, or from within the living part of the uppermost growth surface (Stearn, 1975b; and see p. 551–573). As it grew upward, the living tissue became progressively elevated above the substrate, and this facilitated the sponge's filter-feeding activities. The pattern of growth, however, was commonly disrupted by physical disturbance, such as sediment influx and

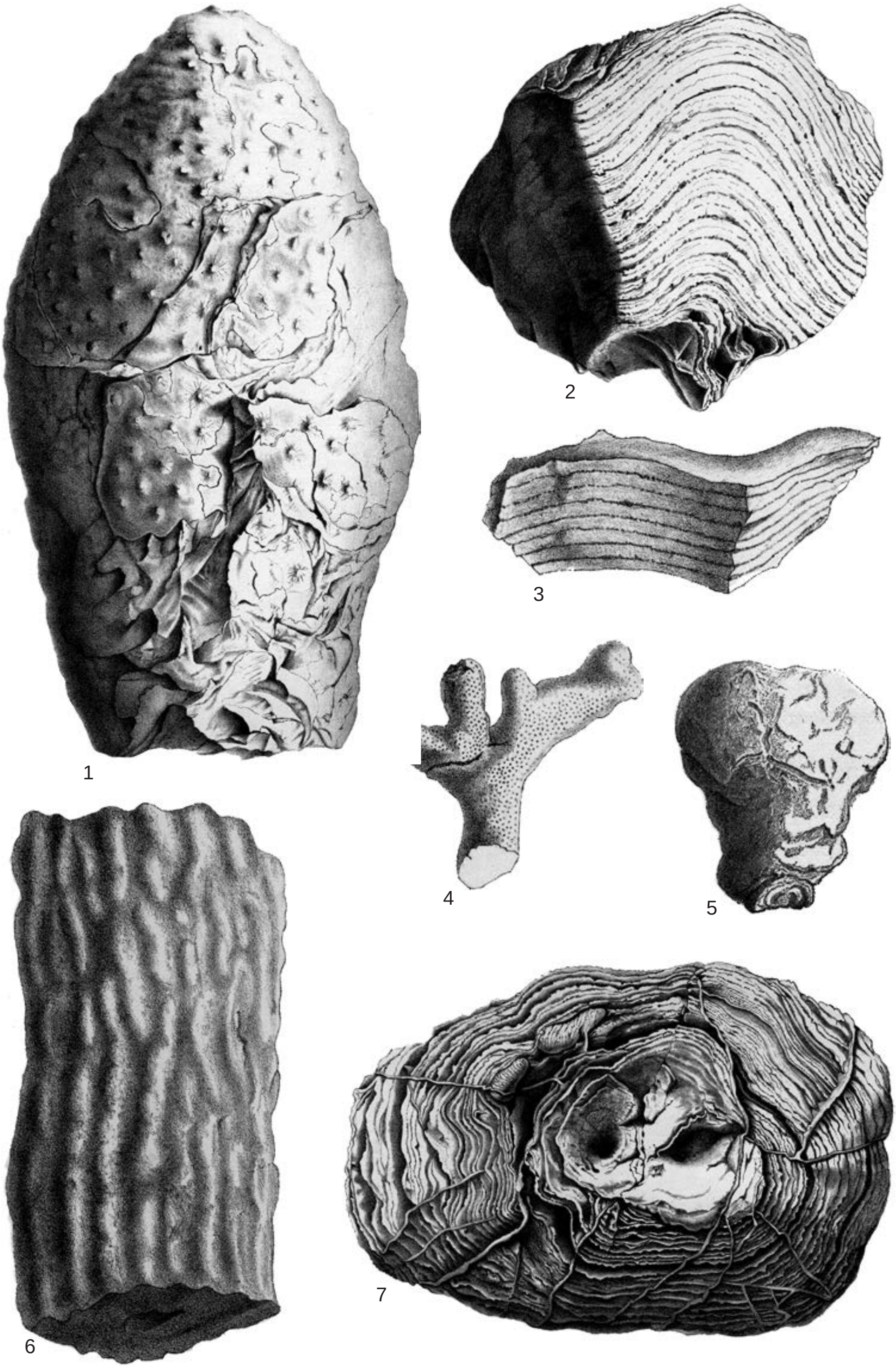

FIG. 273. *(For explanation, see facing page).*

turbulence, and sometimes by competition or predation pressures from associated organisms. The stromatoporoid animal produced a skeletal form that was governed largely by a combination of the sponge's functional and genetic makeup and its response to the environment. The external shape of the skeleton was, at least in part, an expression of the existing environmental controls, and therefore, of some potential for analyzing and interpreting paleoecological changes (Kershaw, 1984, 1990).

This contribution includes a full range of topics on the external morphology of stromatoporoids, the more descriptive parts being concerned with gross morphology (overall shapes) and surface features; some interpretative aspects of growth, development, and living habits are also considered, which impinge for the most part on the paleoautoecology of the group.

APPROACHES TO STUDY

Since the late 1960s, paleoecologists and sedimentologists have been largely responsible for advancing the studies of external stromatoporoid shapes, especially in developing field-based paleoecological and paleobiological approaches. The most common practice has been to study the stromatoporoid-bearing carbonate outcrops in the field and record the outcrop details of their shapes from exposed surfaces of broken or cut skeletons. Commonly, the skeletons are sectioned, usually longitudinally, in quarries and cliffs. This contrasts markedly with the main emphasis of work on stromatoporoids through nearly a century and a half, which has been taxonomically based, concentrating primarily on internal features using oriented thin sections to define and classify the taxa.

Where outcrops expose stromatoporoid morphologies in only two-dimensional views, it is commonly not easy to classify the three-dimensional shapes of skeletons; this applies particularly to reef-building forms (Kershaw, 1984). There are also practical difficulties in extracting large skeletons from matrices of well-lithified carbonate rocks intact, so, unfortunately, whole specimens are rarely collected. Where skeletons are intersected in cores of subsurface carbonate reefs, they are invariably incomplete, and their overall shape is often difficult to interpret from the core surfaces alone. Hence, some caution needs to be exercised in interpreting results of studies of external shapes of stromatoporoids, for example, based only on cores drilled in oil exploration work of subsurface reservoirs in Devonian carbonate reefs (Murray, 1966; Fischbuch, 1968; Noble, 1970; Embry & Klovan, 1971).

Stearn (1975b, 1982b) has previously reviewed aspects of studies of stromatoporoid shapes in applications by a number of workers through the late 1950s to 1970s of

Fig. 273. Representative stromatoporoid growth forms illustrated by H. A. Nicholson using lithographs and wood engravings that were published between 1886 and 1891; *1,* large, tall, bulbous form with external surface covered by small mamelons marking centers of astrorhizae in *Actinostroma stellulatum* Nicholson, Middle Devonian, Chircombe Bridge Quarry, Newton Abbott, Devon, England, ×0.5 (Nicholson, 1889, pl. 15, originally reproduced at ×1); *2,* incomplete specimen of a domical representative of *Stromatopora concentrica* Goldfuss, showing well-defined latilaminae on broken surfaces, but the overall shape is difficult to determine, Middle Devonian, Gerolstein, Germany, ×0.5 (Nicholson, 1891a, pl. 21,*1,* originally published at ×1); *3,* fragmentary specimen of presumed low profile (laminar or low domical) sample of *S. concentrica* that exhibits flat-lying latilaminae; from the same stratigraphic interval and locality as view *2,* ×1 (Nicholson, 1886a, pl. 11,*15,* ×1); *4,* portion of a branching, probably dendroid, stromatoporoid identified by Nicholson as *Stachyodes verticillata* McCoy; Middle Devonian, Hebborn, Paffrath district, Germany, ×1 (Nicholson, 1886a, pl. 8,*9,* ×1); *5,* bulbous, somewhat pyriform-shaped stromatoporoid that Nicholson assigned to *Parallelopora capitata* Goldfuss, same stratigraphic interval and locality as view *4,* ×1 (Nicholson, 1891a, p. 197, fig. 26, ×1); *6,* segment of the cylindrical stromatoporoid *Aulacera nodulosa* (Billings) exhibiting large, elongated nodes in slightly sinuous, vertical rows, Upper Ordovician, Cincinnati Group, Marion County, Kentucky, United States, ×1 (Nicholson, 1886a, pl. 8,*1,* ×1); *7,* undersurface view of stromatoporoid *Actinostroma clathratum* Nicholson that has been weathered and eroded to expose a concave central part, and flatter, outer part of concentric ridges representing growth layers; nature of central area suggests that initial growth developed on a topographic high of more lithified sediment and/or skeletal debris, Middle Devonian, Dartington, Devon, England, ×.05 (Nicholson, 1889, pl. 12,*1,* ×1).

paleoecological zonations in the Devonian reef facies of western Canada. FISCHBUCH (1962), for example, differentiated reef, forereef, and lagoonal facies on the basis of the stromatoporoid shapes and lithological types. Attempts were also made to apply concepts of gross shape differences to recognize bathymetric changes in these Devonian reefs, viewing the so-called massive stromatoporoids as best adapted to the most highly turbulent environment of the reef crest, in contrast to lamellar stromatoporoids that were considered to be more indicative of deeper, quieter, forereef settings. However, in the bank-type model of LAPORTE (1967), lamellar stromatoporoids were interpreted as occupying a position inshore from the massive stromatoporoids (see DOLPHIN & KLOVAN, 1970, p. 325). Although some workers established that shapes change in a systematic way across reef complexes (MURRAY, 1966; FISCHBUCH, 1968; LEAVITT, 1968), controversy remains on the issue of the environmental significance of laminar forms. STEARN (1975b, p. 1637) considered that acceptable conclusions could be drawn about the following: (1) that dendroid *Amphipora ramosa* occupied lagoonal environments, but probably did not act as a sediment baffle; (2) small, bulbous stromatoporoids lived in quiet waters; (3) large, domical (massive) forms of irregular shape were associated with the reef crest; and (4) the more robust dendroid genus, *Stachyodes,* was thought to have occupied positions on both sides of the reef crest. However, the status of laminar forms remains equivocal, not necessarily restricted to either quiet-water forereef or turbulent reef-crest settings. These laminar shapes are more likely to remain *in situ* in more turbulent conditions, but then they can also be reworked into forereef slopes.

STEARN (1982b) further questioned the validity of using shapes to interpret the paleoenvironments of Paleozoic reef complexes, given that, in terms of the shapes of modern reef organisms (e.g., scleractinian corals), such complex patterns of distribution existed and they were not specific guides to the environments. The patterns of distribution of stromatoporoid shapes across ancient reefs may similarly have rather doubtful paleoenvironmental significance, unless the analyses are properly focused on the documentation of individual species: the taxonomic identification based on internal structures, and the shape related to paleoenvironmental factors, as well as the genetic make up of the species. Ideally, environmental analyses using the shapes of stromatoporoids should be combined with taxonomic identification of species based on their internal features and an understanding of the genetic composition of the species.

KERSHAW's (1981) study of the taxonomically well-defined stromatoporoid species and the range of shapes they exhibit in one specific environmental setting (a Silurian biostrome in Gotland), allowing genetic inheritances to be differentiated from environmental influences in these species, is a good example of the type of research that is needed. The three most abundant species in the Gotland biostrome reflect two markedly different genetic responses by the species in the one biostromal habitat: one shows laminar to low domical shapes, and the other two exhibit high domical to bulbous forms. Each species also exhibits a range of specimen shapes within the biostrome that represents the ecophenotypic plasticity, or the individual responsiveness, of each species to the localized environmental fluctuations within the biostrome.

Stromatoporoids from shallower biostromal deposits, and deeper, level-bottom, argillaceous (marly) limestones, like those exposed along coastal sections in the Silurian of Baltoscandia (the successions on the Swedish island of Gotland and in northwestern Estonia) are uniquely well preserved and accessible. The skeletons can be relatively easily extracted whole for study in three dimensions in places, because they are preserved in thin carbonate units interbedded within a friable argillaceous matrix. These stromatoporoid-bearing Paleozoic carbonate sequences have proved particularly useful for establishing the range of skeletal morphotypes, and for defining models that employ stromatoporoid shapes in paleoenvironmental analyses (Kershaw, 1984, 1990; Kershaw & Keeling, 1994), though the results cannot be completely validated until the genetically related influences on these stromatoporoid species are more fully understood (Stearn, 1982b).

RECOGNIZING STROMATOPOROID SHAPES

GENERAL RELATIONSHIPS

Many workers have attempted to establish an acceptable terminology for classifying the chief skeletal shapes (e.g., Noble, 1970; Abbott, 1973; Kershaw & Riding, 1978, 1980; Stearn, 1983a, 1984; Kershaw, 1998), singling out a comparatively small number of major groups of forms. The scheme recognized by Kershaw (1998) included the terms: laminar, tabular, domical, columnar, bulbous, dendroid, expanding-conical, digitate, and irregular. Russian and Chinese workers have also restricted the number of names to more basic shapes. Bogoyavlenskaya (1984) identified laminar, approximately hemispherical, subspherical, irregular, subcylindrical, and dendritic; and Dong (2001) recognized broadly: massive (including a variety of spherical, hemispherical, columnar, or digitate) and tabular (single- to multilayered laminar or lens-shaped) forms. However, in a more detailed study of external forms of stromatoporoids from Middle Devonian reefs, Liu and Dong (1991) identified as many as 25 different shapes—massive forms (excluding columnar) that included both discrete (single-layered) and compound or composite (multilayered) types, as well as columnar, tabular (=laminar), dendritic (=dendroid) types, and encrusting types as a separate category—but most of these were just variations of more basic shapes. No completely consistent worldwide usage of terms for the description of external shapes has been adopted previously. It is hoped therefore that the following set of proposals for a Paleozoic stromatoporoid shape classification will be widely accepted.

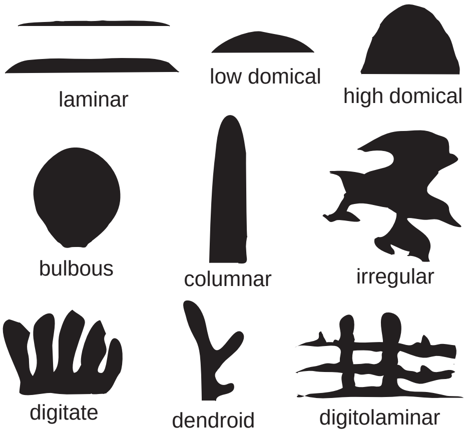

Fig. 274. Main shapes of Paleozoic stromatoporoids depicted as silhouettes in longitudinal section. Eight principal categories are recognized, and the domical shapes are further subdivided into two subgroups (see text for further discussion; Webby & Kershaw, 2011).

It is important here to characterize the bulk of Paleozoic skeletons consistently in terms of one or another of the six basic, geometrically distinct shapes (**laminar**, **domical**, **bulbous**, **columnar**, **digitate**, and **dendroid**), or as composites of these basic forms, for example, **digitolaminar** and **irregular** (Fig. 274). Most skeletons exhibit predominantly one type of external morphology through all mature stages of growth, but sometimes gradational relationships exist between two or more distinctly different shapes in the one skeleton, making such a classification difficult to apply. In a sense, the shapes are part of a continuum from laminar through various intermediates to columnar, digitate, and dendroid, reflecting differences in the relative rates of skeletal growth being secreted between its central axis and extremities by the mantling living tissue of the organism. The simple computer simulations presented by Swan and Kershaw (1994) are perhaps illustrative of the growth patterns.

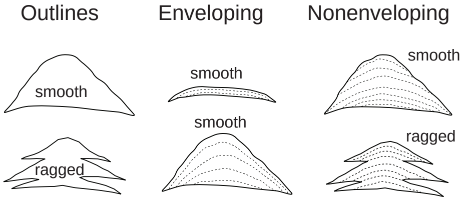

FIG. 275. Schematic representations in longitudinal section that illustrate relationships at lateral margins of stromatoporoid skeletons between smooth or ragged types of external surface growth and enveloping or nonenveloping styles of internal latilaminate growth (adapted from Kershaw, 1998, fig. 7, *partim*).

The term laminar should apply mainly to comparatively thin, laterally extensive, flattened to undulating, sheetlike forms. It should also include sheetlike skeletons that were classified previously as tabular bodies. Where possible, older, more mature stages of growth should be identified, because many stromatoporoid skeletons developed initially from a laminar base and then grew to maturity as different shapes (e.g., domical, columnar, digitate, or irregular). The term domical is recognized here as further subdivided into two groups: the **low domical** and **high domical** subgroups (Fig. 274). The high domical subgroup here combines the previously separated high and extended domical categories of KERSHAW and RIDING (1978) and KERSHAW (1990, 1998), and the separated high, extended and highly extended subdivisons of LUCZYNSKI (2005). LUCZYNSKI also proposed low and high subgroups for the bulbous category. The wider utility of LUCZYNSKI's subdivisions, however, have yet to be demonstrated. Irregular is a composite morphotype derived by renewed growth in different orientations after successive environmental disturbances on the sea floor. Digitolaminar is another composite shape involving alternations of laminar and columnar growth that may reflect episodic environmental events (possibly sudden changes in rates of sedimentation) or, in a few cases following WOOD (2000), may be related to an inherent growth style (see discussion of Primary Cavities, p. 475).

In general, domical to laminar forms are characteristically the most abundant (and the largest) Paleozoic stromatoporoid shapes; irregular and bulbous forms are also moderately common, and columnar, digitate, dendroid, and digitolaminar types are overall much less abundant. One other, distinctive, though very rare, shape is also known, restricted to Upper Devonian sequences: the inferred foliaceous shape recorded by WOOD (2000); see discussion on p. 457. Laminar to low domical forms are usually preserved intact with little or no evidence of transportation, whereas high domical and bulbous forms show a greater susceptibility to overturning and other sorts of disturbance due to current activity. Dendroid and columnar forms apparently grew in relatively quiet water environments, although they are mainly preserved as fragmentary stem or postlike skeletons, and their attachment bases are rarely found. The few specimens recognized as attachment bases suggest that the forms lived only partially stabilized on an unconsolidated substrate. The majority of these skeletons were broken from their bases and either locally toppled or swept away to other depositional sites, dependent on the intensity of the intermittent storm activity.

SMOOTH AND RAGGED SKELETAL MARGINS

KERSHAW and RIDING (1978) characterized all laminar and domical stromatoporoids as having either **smooth** or **ragged** skeletal outlines (Fig. 275). The mainly laminar and low domical forms developed a ragged appearance, as seen in longitudinal cross section, when successive influxes of sediment caused growth interruptions of the lateral margins of skeletons (KERSHAW, 1993, fig. 2c,e–f). For example, the well-developed ragged margins of stromatoporoids from certain level-bottom depositional settings were attributed to a pattern of episodic sedimentary influxes (KERSHAW, 1984). The structures are superficially like the rejuvenescences of corals (SCRUTTON, 1998) caused by episodes of stress-influenced growth, perhaps related to annual cyclicity. The rhythmic changes in stromatoporoids are apparently related to discontinuities that bounded latilaminae, but these have not been demonstrably shown to represent annual accretion events (see p. 551–573). Young and Kershaw (2005, pl. 1,*6;* pl. 4,*4,6*) illustrated a few examples of stromatoporoids that clearly show these skeletal relationships, each latilamina being bounded above and below by growth interruption surfaces that can usually be traced laterally into the ragged, sediment-filled, tongue- or wedgelike inclusions at the margin (Fig. 276, Fig. 277.1). High domical (stacked, inverted, saucer, bell, and mushroom shaped), bulbous, columnar, and irregular morphotypes (Kapp, 1974) occasionally also exhibit ragged margins, but such elevated shapes more commonly display smooth outlines.

Wood (2000, p. 700) suggested that raggedness (or production of laminar outgrowths) in Devonian stromatoporoids may, alternatively, be part of an inherent growth strategy. Wood referred to cases of laminar and domical stromatoporoid individuals that had responded to localized death of areas of their living surface by producing laterally updomed growth structures with accompanying large primary cavities over the substrate (Fig. 277.2; and see Fig. 282). Such features, and the characteristic raggedness, developed in response to the intrinsic growth style, with the episodic engulfment of sediment initiating the development of complex, variable, and elevated patterns of growth. The other ragged forms were subjected to episodic swamping of sediment onto flanks of their skeletons, and they mainly produced phases of lateral growth (Fig. 277.1). Kershaw, Wood, and Guo (2006) have shown them, in general, to include the ragged-margin Silurian stromatoporoids. They do not form large primary cavities, so laminar outgrowths did not grow above the substrate, although partial scouring did occur beneath skeletal margins; and in some places, whole skeletons were moved, with associated secondary subskeletal voids forming as a result of storm-generated events (Kershaw, 1980; and see section on Cavity Spaces, p. 475).

ENVELOPING AND NONENVELOPING STYLES

Relationships across successive latilaminae at the margins of the skeleton may be either enveloping or nonenveloping (Fig. 275). The **enveloping** condition occurred where a succeeding latilamina entirely overlapped a previous latilamina at the lateral margin (i.e., the skeleton is enveloping with smooth margins). The smooth enveloping form developed where the living surface of the stromatoporoid sponge completely mantled the top and lateral surfaces of the skeleton (Fig. 278). The condition was maintained as long as the sponge continued its upward and outward growth, and the lower parts of the lateral margin remained free of accumulating sediment. The **nonenveloping** condition occurred when the succeeding latilamina failed to completely overlap a preceding latilamina (i.e., the skeleton is nonenveloping, with either smooth or ragged margins). These nonenveloping associations formed when the living surface: (1) became more localized, possibly as sediment accumulated around the lower parts of lateral margins, thus restricting the overlap of successive growth units, as in smooth or ragged low-domical shapes; or (2) became more elevated and laterally limited to form high domical, bulbous, or columnar morphs, localizing the living surface to higher levels where nutrients and oxygen from the water column could be more readily accessed. Laminae may also exhibit enveloping-nonenveloping relationships, and along their edge zones, they were capable of sealing off adjoining gallery spaces from the associated sediment. The enveloping-nonenveloping terminology is, however, not always easy to apply, unless substantially complete stromatoporoid skeletons are collected and sectioned longitudinally (vertically) though their centers.

James and Bourque (1992, p. 328, fig. 9) depicted the enveloping and nonenveloping forms as resulting from different positions of the living surface of the organism at the time of growth. The nonenveloping,

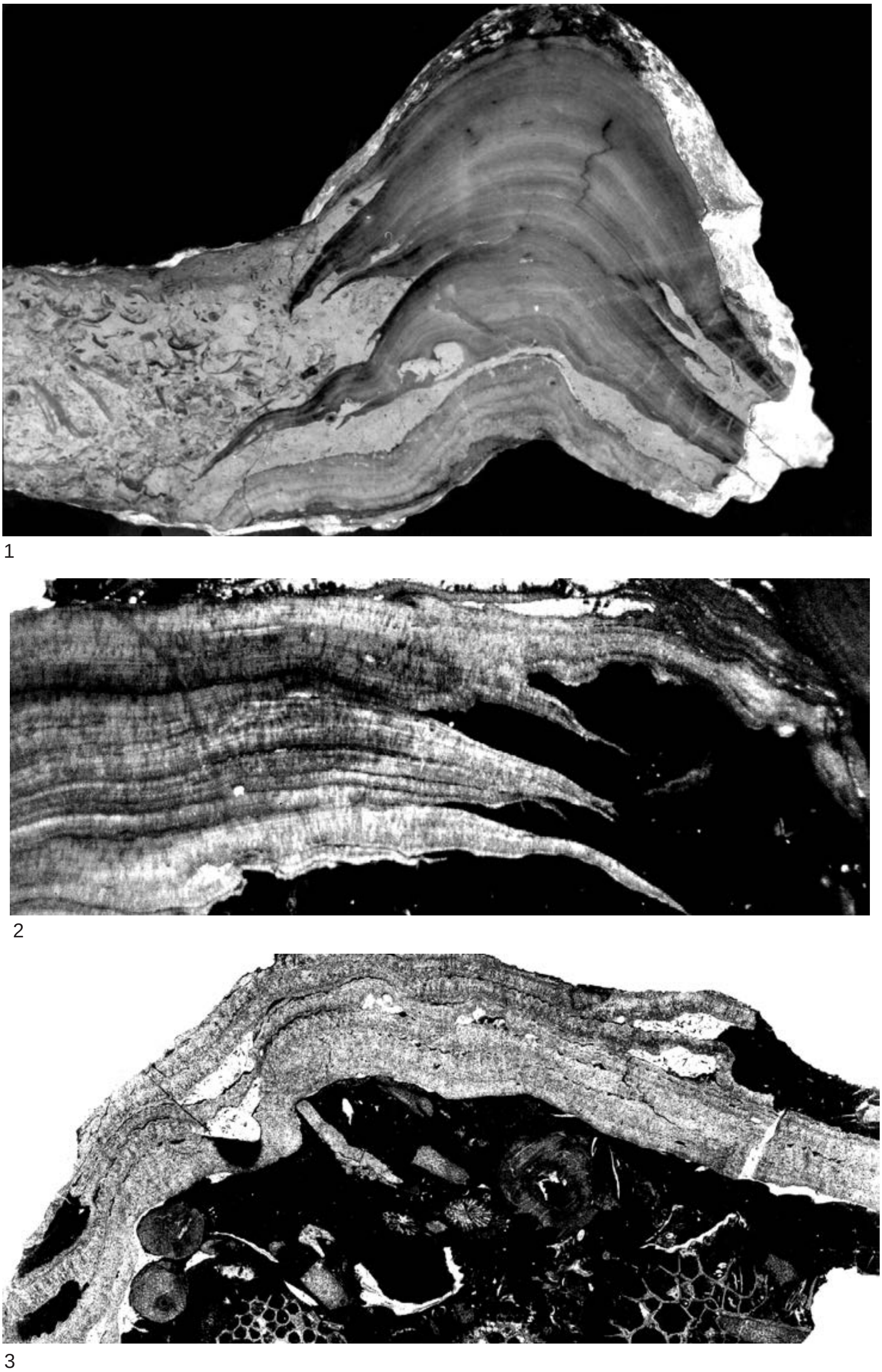

FIG. 276. *(For explanation, see facing page).*

ragged skeleton continued to maintain its living surface near the substrate, and remained more stable because it was being progressively buried by sediment as it grew, whereas the enveloping smooth skeleton was capable of maintaining a more elevated living surface, though it was less stable, and consequently more likely to be displaced. Most smooth-margined stromatoporoids, however, exhibit an enveloping style in their lower portions, and then a nonenveloping type in upper parts; consequently, they cannot be classified exclusively as belonging to either one type or the other. The reasons for this change are not entirely clear, but it seems that: (1) initial enveloping-type growth was mainly associated with stabilization and establishment of the skeleton on the substrate; and then, (2) the focus narrowed to topographically more elevated, nonenveloping growth, perhaps owing to lower parts suddenly becoming engulfed or swamped by sediment.

Most stromatoporoid growth forms can be subdivided broadly into two groups, based on: (1) whether they have a ragged margin with a nonenveloping style of growth; or (2) whether they show a smooth margin with enveloping and/or nonenveloping styles of growth. Many ragged types are laminar or low domical shapes, but they also include some high domical, and a few columnar or irregular forms. Smooth types are dominantly high domical, bulbous, and columnar shapes, as well as digitate and dendroid branching forms. What distinguishes most shapes with ragged margins from the shapes with smooth margins is the inclination of lateral ends of their latilaminae (and laminae): the latilaminae-laminae on the lateral flanks of ragged skeletons tend to be gently inclined, with angles up to 45° from the horizontal, whereas latilaminae-laminae at the lateral sides of smooth skeletons are characteristically inclined at angles greater than 45°, sometimes developing beyond 90° in bulbous forms so that the laminae curved inward, effectively becoming overhanging. Ragged margins developed because of growth interruptions between latilaminae, and episodic influxes of sediment accumulated as lateral tongues because the angle of repose of the sediment was less than 45°. Skeletons with smooth margins usually formed because sediment was unable to accumulate on steeply inclined lateral slopes; no sedimentation occurred on the adjoining substrate during the formation of the enveloping growth style, whereas episodic influxes of sediment were added to the adjacent sea floor during the production of a nonenveloping style.

The development of **coalescences** is another feature that was recorded by Kershaw (1990, p. 695, fig. 11) in the Silurian stromatoporoid species of the Kuppen biostrome on Gotland. A number of closely spaced, but initially separated, small specimens of one species merged as they grew to form a much larger, coalesced skeleton. Examples included one species that produced a large, low, domical form, and another that established itself as a large, high, domical form. Neighboring specimens belonging to other species did not participate

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Fig. 276. *1,* Superposed laminar and domical stromatoporoid skeletons, separated by a thin, continuous layer of sedimentary rock; the first (*Pachystroma hesslandi*) has a gently upwardly arched, laminar shape, and the second (*Densastroma pexisum*), a ragged, domical form, composed of superimposed low domical growths; longitudinal section, Visby Formation, Wenlock, Kneippbyn, Gotland, Sweden, ×1.5 (Kershaw & Riding, 1978, fig. 2); *2,* laminar stromatoporoid skeleton of *Densastroma pexisum* (Yavorsky), with very ragged (or frayed) lateral margin; note growth interruptions associated with tapering wedges of sedimentary rock may be traced into interior of specimen, where they define successive latilaminae. Longitudinal section, BU-V-I-SK120, Visby Formation, Wenlock, Ireviken, Gotland, ×3 (adapted from Young & Kershaw, 2005, pl. 4,*4*); *3,* laminar skeleton of stromatoporoid *Pachystroma hesslandi* (Mori) is draped over a mud- and bioclast-rich substrate, incorporating a few crinoid ossicles, a rodlike skeletal clast, and possibly an intraclast; note also inferred primary cavities with sparite and geopetal infills, and more bluntly wedged margins that apparently relate to growth interruption bands and intervening latilaminae within the skeleton; thin section, BU-V-I-46, Visby Formation, Ireviken, Gotland, ×3 (adapted from Young & Kershaw, 2005, pl. 1,*6*).

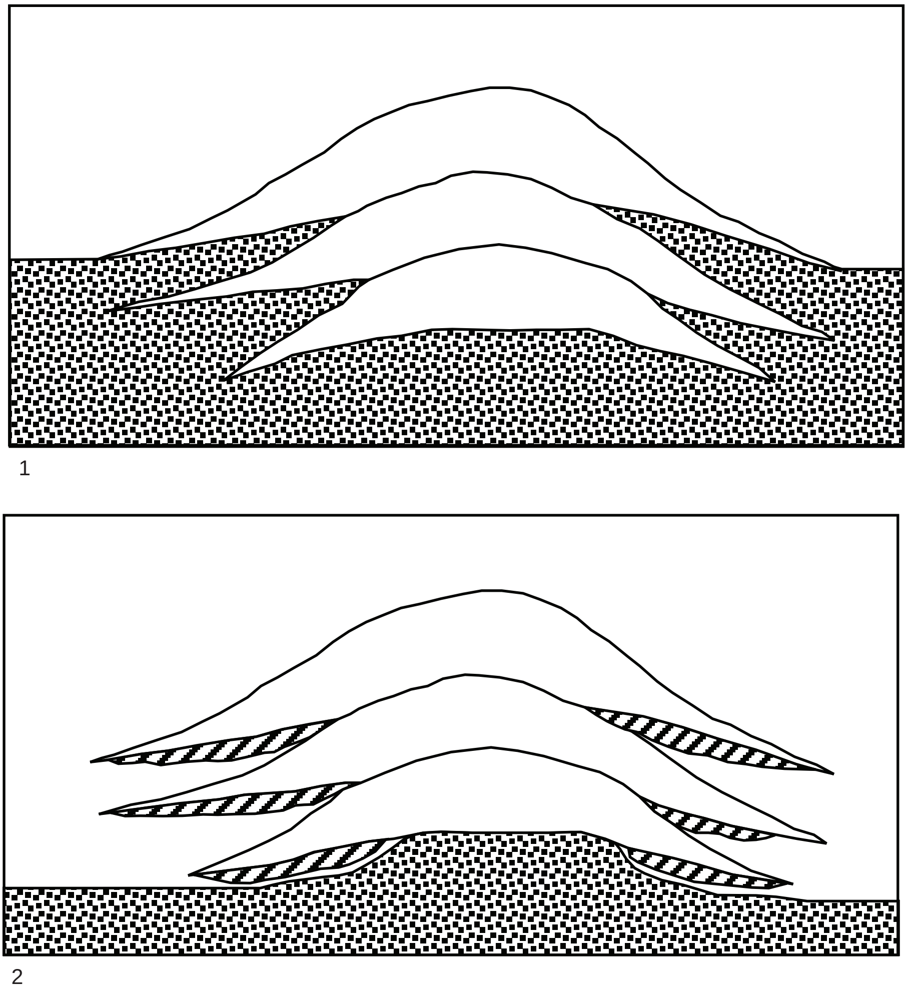

FIG. 277. Contrasting representations of how ragged margins of stromatoporoid skeletons may have formed. *1,* Marginal sediment wedges may be produced by periodic sediment swamping over lateral margins of the stromatoporoid, with consequent cessations of lateral growth. In recovery, after each phase of episodic sedimentation, the stromatoporoid grows laterally again over the newly accumulated sediment wedge. Each cycle of episodic sedimentation and renewed growth is repeated a number of times to produce the superimposed domical reconstruction shown; *2,* stromatoporoid developed three superposed low domical growths with ragged margins by the successive growth of raised, laterally extended outriggers above the substrate after each wholesale swamping episode. Apparently this type of growth developed in some stromatoporoids, for intrinsic reasons related to their genetic inheritance, and they can be identified because they created open undersurface sites (shelters or cavities) for the colonization of cryptic organisms (*oblique hachure*). Recognition of associated cryptic assemblages is therefore important in differentiating between the two growth styles of stromatoporoids (Webby & Kershaw, 2011).

in these coalescences; they were either species specific (KERSHAW, 1998, p. 523), or perhaps even infraspecific, given that coalescences in some living sponges (e.g., CURTIS, 1979) only occur between individuals with matching strain types.

PARAMETERIZATION OF SHAPES

A few simple parameterization schemes have been proposed to assess external shapes in stromatoporoids (and other skeletal forms), but each has limited value because of sampling problems, large specimen size, and preservation of stromatoporoids. There are only a few localities, like Gotland, where oriented, uniquely well-preserved material can be sampled, sectioned, and measured (see Kershaw & Riding, 1978; Kershaw, 1984). To be useful, whole specimens must be cut longitudinally along the growth axis, and this is seldom possible in more typical field occurrences. Selected specimens intersected on polished Devonian limestone blocks in public buildings of the city of Warsaw were the basis for Luczynski's (2005) study, not carefully oriented specimens from the field. Consequently, because solid limestones in the field or in public building facing stones limit the choice of orientation of section through a stromatoporoid, these approaches remain largely of theoretical value, but they are briefly outlined below.

Kershaw and Riding (1978) employed a triangular array to quantify, in two-dimensional profiles, the laminar, domical, and bulbous morphotypes (Fig. 279), on the basis that the three-dimensional shapes of stromatoporoid skeletons were approximately symmetrical about a vertical axis. The three parameters employed to measure the cross-sectional profiles were the vertical height (V), the basal length or diameter (B), and, arbitrarily at an angle of 25° to the vertical, the diagonal distance (D). This numerical scheme allowed the various morphs to be separated, using ratios of their vertical height to basal diameter, as follows: ratios of vertical height to basal diameter (V/B) of less than 0.1 grouped as the laminar forms, ratios between 0.1 and 0.5 classified as low domical, and ratios between 0.5 and 2.0 defined as high domical forms. The overall skeletal shape of the whole specimen could be determined using this method, but it remained impossible to quantify branching stromatoporoids using the given parameters.

Another comparatively simplified, shape-discriminating, parameterization method was introduced by Young and Scrutton (1991, fig. 2–3) and Scrutton (1993, 1994, 1998, fig. 23) for depicting similarly shaped, compound Paleozoic corals (and stromatoporoids). A triangular diagram was also used, but with a different set of parameters, allowing the branching forms to be included in the array. Their three parameters were based on measuring the widths (W), overall heights (H), heights to the widest point (N), and lengths around the perimeter of the skeleton (P) of specimens. In their triangular diagram, the corals were depicted as having a continuum of variation and clearly differentiated main shape fields. The range of variation and differentiation mirrored the distribution of stromatoporoid shapes, and even the growth-form categories bore close similarities. Furthermore, it was possible to plot laminar and domical forms with a concave base in fields of the triangular diagram below the base line (as negative values)—an additional advantage for plotting stromatoporoid shapes.

Luczynski (2005) proposed a number of other ways of measuring stromatoporoid shape based on Kershaw and Riding's (1978) parameterization method. The parameters not only took account of the dimensions of the whole skeleton, but also changes in shape during successive phases of growth. This also involved specimens presumed to be oriented longitudinally (or vertically) through central axes and, where latilaminae were visible, allowing the way successive latilaminae were added (either in enveloping or nonenveloping growth units) above the basal surface, and their relationship to inferred levels of accumulating sediment on the adjacent sea floor, to be determined. The changes in skeletal growth of a specimen could be recorded by measuring length and height parameters for each successive latilamina. In addition, the burial ratio, that is, the proportion of the skeleton buried under sediment at each phase of latilaminate growth, could be plotted, in addition to the final burial shape when all skeletal growth ceased (Luczynski, 2005). Another important consequence of these studies was to demonstrate how the

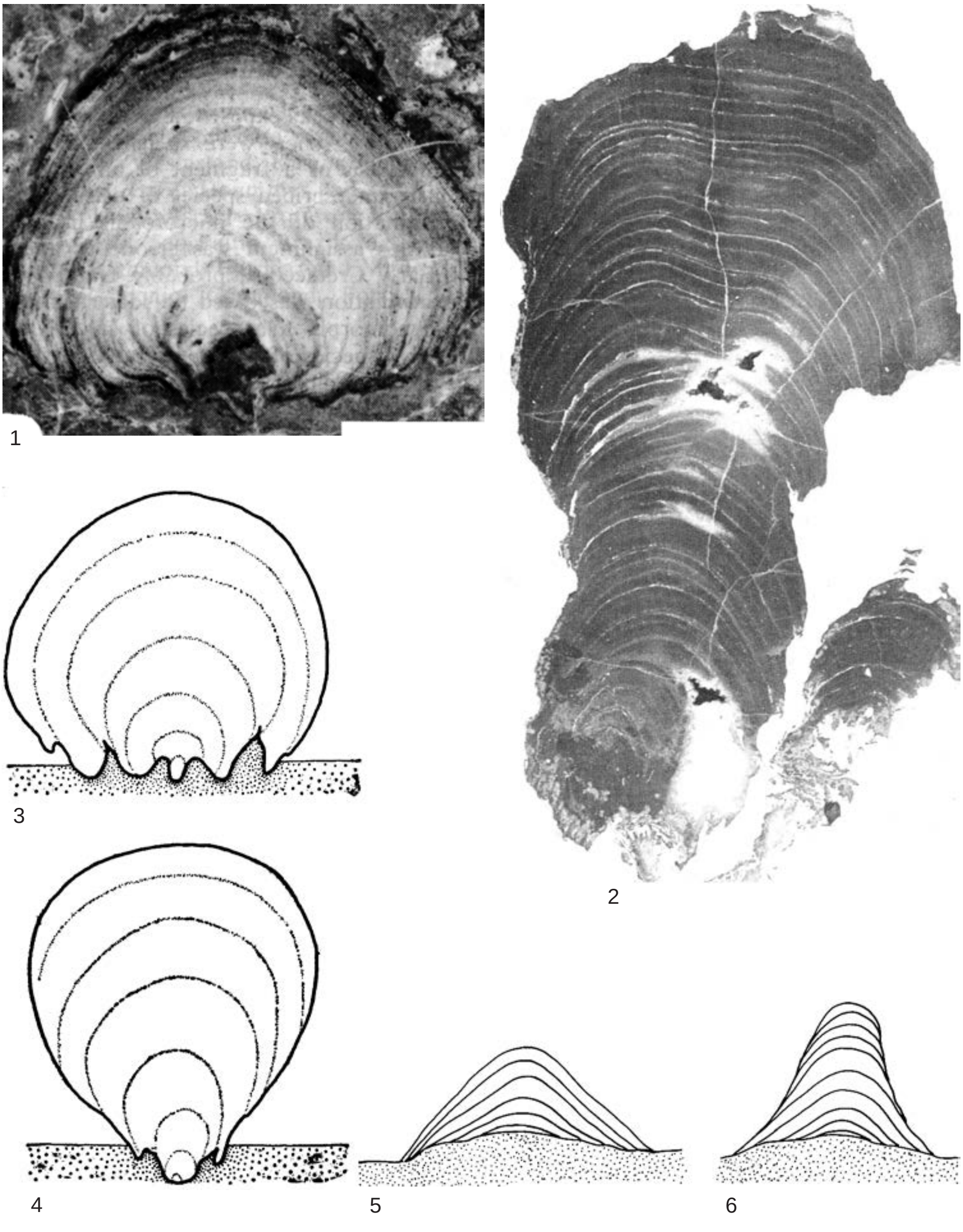

FIG. 278. Examples of some characteristic smooth-margined, bulbous, and domical stromatoporoid growth forms. *1,* Longitudinal section of typical smooth, bulbous stromatoporoid that shows concentrically arranged, internal skeletal banding (mainly enveloping, though toward the base it exhibits nonenveloping relationships); it occupied a somewhat irregular substrate, with its initial growth apparently centered on a small, rounded topographic high, perhaps of more lithified sediment and/or skeletal debris; *Stromatopora undata* RIABININ, Upper Devonian, Poland, ×0.75 (adapted from Kaźmierczak, 1976, fig. 1a; adapted by permission of Macmillan Publishers Ltd., *Nature*); *2,* large, high profile, relatively smooth stromatoporoid grew as an extended bulbous form; note latilaminae defining skeleton as a mainly nonenveloping form, suggesting that sediment accumulated in support of its *in situ* skeletal growth; longitudinal section, Lockport Group, Ludlow, Brockport, Monroe County, New York, United States, ×0.45 (adapted from Brett, 1991, fig. 7D); *3,* enveloping, *(Continued on facing page.)*

development of skeletons changes during growth, for example, from low domical to high domical and bulbous forms. However, currently none of the approaches toward using parameterization techniques allows the analysis of stromatoporoid form to be completely resolved. Consequently this remains an ongoing area of research.

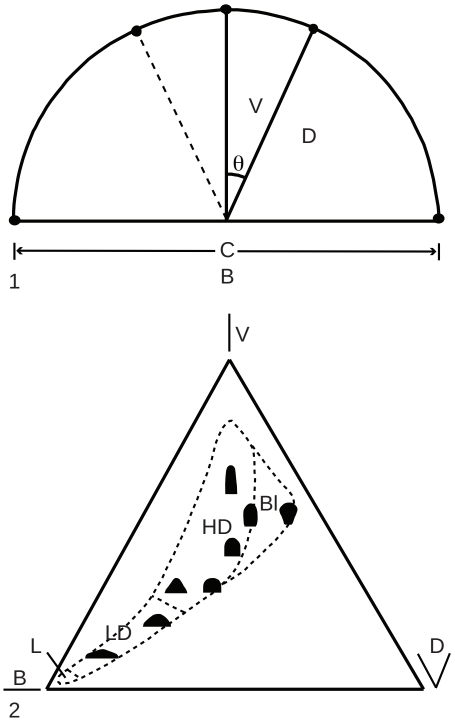

FIG. 279. Simplified parameterization approach for measuring and plotting stromatoporoid shapes, based on using skeletons oriented (or cut) in longitudinal section, as proposed by KERSHAW and RIDING (1978); *1,* three parameters are employed: basal (*B*), vertical (*V*), and diagonal (*D*). V and D are plotted from a central point (*C*), and the angle (θ) subtending D is set at 25 degrees (adapted from Kershaw & Riding, 1978, fig. 6); *2,* simple measurements of B, V, and D were plotted in a triangular diagram of stromatoporoid shapes, with the various fields being represented by the basic laminar (*L*), low domical (*LD*), high domical (*HD*), and bulbous (*Bl*) morphotypes (adapted from Kershaw & Riding, 1978, fig. 11).

SHAPE SUBDIVISIONS

JACKSON (1979) recognized six basic subdivisions of shape in sessile animals, and four of these—sheets, mounds, plates, and trees—are broadly applicable to the study of shapes in stromatoporoids (Fig. 280). Sheets differ from most other growth forms (except runners) in limiting the animal to the substrate surface, and hence, access to resources in the water column. Mounds give greater access to the water column and isolate most surface tissues from deleterious processes close to the substrate, though they may still maintain a major commitment to lateral spreading across the substrate. This gives mounds resistance to water movements and other sorts of bottom instability. Plates are rare growth forms in stromatoporoids; their raised, tierlike forms usually project laterally, more or less parallel to the substrate, from a limited area of attachment, but do not grow as tall as trees. Trees provide greater access to resources in the water column, and the soft tissues probably became well isolated from the substrate, but they have a much more limited area of attachment, with consequent loss of structural

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FIG. 278 *(Continued from facing page).*

bulbous form that formed presumably on a supportive though uneven substrate, little affected by transport of sediment (either by erosion or deposition) during growth. The base is shown as having a corrugated surface, perhaps including concentric growth ridges where they project downward, and these seem to coincide with the ends of successive latilaminae (adapted from Kaźmierczak, 1971, fig. 6b); *4,* nonenveloping, bulbous form with a narrow base that was capable of maintaining its *in situ* orientation, owing to the effect of progressive burial by sediment during growth (adapted from Kaźmierczak, 1971, fig. 6c); *5,* characteristic smooth, enveloping, domical form that was unlikely to have been affected by small-scale transport of sediment during growth (adapted from Kershaw, 1993, fig. 2A); *6,* typical smooth, nonenveloping, domical form that may have been produced while slow accumulation of sediment occurred but alternatively may have been capable of concentrating its growth axially, for some reason other than being related to sediment influx (adapted from Kershaw, 1993, fig. 2B).

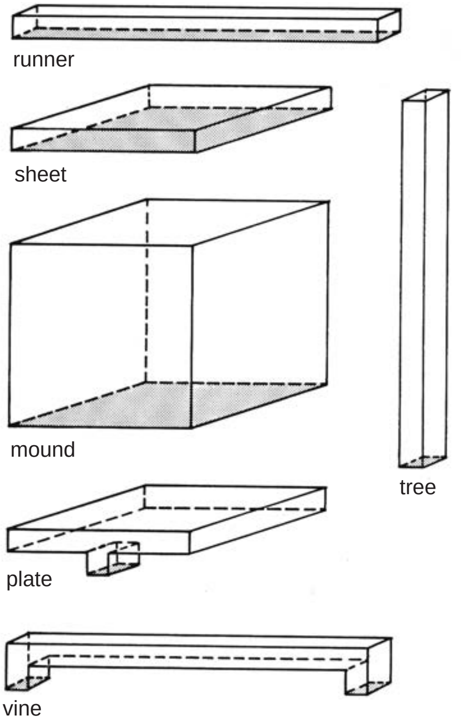

FIG. 280. Simple rectangular conceptions of the six basic sessile animal growth forms. Areas of attachment to substrate are *stippled* (adapted from Jackson, 1979, fig. 4).

integrity at their basal attachment. Sheets and mounds are the most common growth forms in stromatoporoids. Like a number of other groups of sessile animals, the stromatoporoids developed particularly variable growth forms that often formed composites of more than one major growth morphotype. Most commonly, these are sheet-mound combinations, but some comparatively rare composites of raised, tierlike plates and mounds may also occur. Here we have adopted these broad subdivisions for convenience in describing the main stromatoporoid shapes.

SHEETS

Sheets are defined as thin layers that spread laterally (tangentially) in all directions.

Laminar

The laminar morphotype is flat, thin, sheetlike layer that grew laterally outward with accretionary growth in all directions away from an initial settlement point. It may be only a few millimeters thick (Fig. 281.1), or may, provided a component of upward growth was maintained across the skeleton, form a tabular body to tens of centimeters in thickness (Fig. 281.2–281.3). It may spread freely across an unconsolidated substrate or encrust a hard surface such as another skeletal object. It usually remains in contact with the underlying surface but may, in places, be separated by primary, cement-filled cavities (Fig. 282). Irrespective of size and complexities of relationships with sediments, it is recommended that the general term laminar is preferred to all other names used to refer to sheetlike or platy structures, including the following: sheetlike, stratiform, lamellar, discoidal, platy, and tabular. These are all now regarded as obsolete. The laminar morphotype is the simplest and one of the most common stromatoporoid shapes, especially in reef complexes. It may have flattened, undulating, or wavy, up-domed or saucer-shaped (concave upward) orientations, dependent on the nature of the substrate. The shape exhibits smooth lateral margins when no episodic sedimentation is associated with growth (Fig. 281.2), or ragged lateral margins when sediment periodically interferes with growth (Fig. 281.3) (KERSHAW & RIDING, 1978); the terms smooth and ragged are features of lateral surfaces, not shapes. Note that the term encrusting does not apply, as it is not a shape; it signifies attachment to a surface, usually a hard (but not a soft) substrate. It is important, in addition, to emphasize that earliest growth stages of many stromatoporoids are laminar, as they grew from an initial laminar base, so the term should apply mainly to more mature stages of growth.

KERSHAW (1984) noted that laminar shapes were well suited to developing on unconsolidated muddy substrate, because the skeletal weight was low and evenly spread. The fact that they were able to develop intact suggests that there was little or no sedimentary influx for most of the time. However, they were more susceptible to

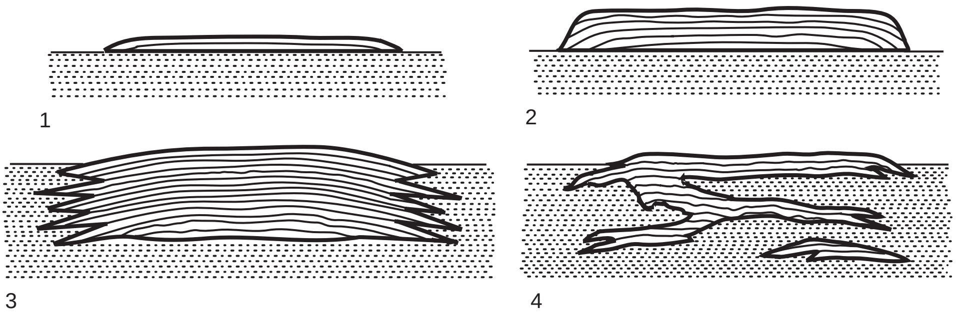

FIG. 281. The main laminar shapes dependent on the various interactions between growth, substrate, and sedimentary influx, particularly the possible effects of sedimentation on the development of the final form. The exception (see Fig. 282) is where sediment swamping causes partial mortality of a laminar skeleton, and parts were able regenerate to produce new outgrowths that spread laterally, but also tended to up-dome over newly accumulated sediment, producing primary cavities (not shown here); *1,* initial stages of predominant lateral spreading laminar growth (adapted from Kershaw, 1990, thin laminar morphotype part of fig. 7); *2,* successive laminar growth where the skeleton was able to maintain smooth lateral margins, perhaps because very limited sediment was accumulating on the substrate (adapted from Kershaw, 1990, thicker laminar, formerly tabular, morphotype part of fig. 7); *3,* laminar shape with ragged lateral margins where there may have been more frequent, small-scale influxes of sediment that disrupted growth, especially along lateral margins (adapted from Stearn, 1983a, fig. 1E); *4,* anastomosing pattern may have developed because persistent movement of sediment from place to place made it difficult for growth to be consistently maintained across entire growth surface; at any one time, parts of a skeleton remained alive, while other parts had become swamped by sediment (adapted from Stearn, 1983a, fig. 1A).

being overwhelmed by sedimentation than the domical shapes, especially at the margins. Laminar crusts formed also over large skeletal objects, though where the initial colonization occurred on smaller, ephemeral patches of hard substrate or skeletal debris, skeletons were likely to spread rapidly and widely to other areas with an unconsolidated substrate (KERSHAW, 1998, fig. 5). MEYER (1981) suggested lateral spreading rates of individual stromatoporoid growth of about 10–23 mm/yr.

Intermittent burial by influxes of sediment caused severe impacts on the lateral spread and vertical continuity of laminar growth, resulting in **anastomosing,** laminar to low domical sheets or crusts (Fig. 281.4). KERSHAW (1998, p. 522, fig. 7) noted that with such episodic patterns of rapid spread of sediment, the successive layers of such skeletons did not necessarily maintain continuity of growth across their entire surfaces; at one time parts may have remained alive, while other parts became swamped by sediment. Representatives of a species of *Lophiostroma,* possibly allied to *L. schmidtii,* illustrated by BOGOYAVLENSKAYA (1982b, p. 117, fig. 5; 1984, fig. 2), from the Silurian of Podolia, shows unusual examples of splayed or imbricated laminar sheets (Fig. 283.2) of large size (up to 2 m across) between sediment layers. These structures developed as a consequence of successive interactions of sediment influx and rapid spread of lateral growth (see Substrate Preferences, p. 460). Good examples of cavities have not yet been recorded from undersurfaces of anastomosing, laminar crusts of Silurian age.

The laminar stromatoporoids of the Middle Devonian reef complex of South Devon (KERSHAW & RIDING, 1980) exhibit some of the largest sizes, reaching dimensions of 5.5 m across and up to 0.20 m thick; however, they could not be identified taxonomically because of their state of recrystallization. Also, the laminar crusts of *Stachyodes australe* and *Clathrocoilona spissa* in different Upper Devonian reef habitats of the Canning Basin (Western Australia) are about 1.5 m across and often less than a centimeter thick (WOOD, 1998, 2000). They also exhibit remarkable developments of

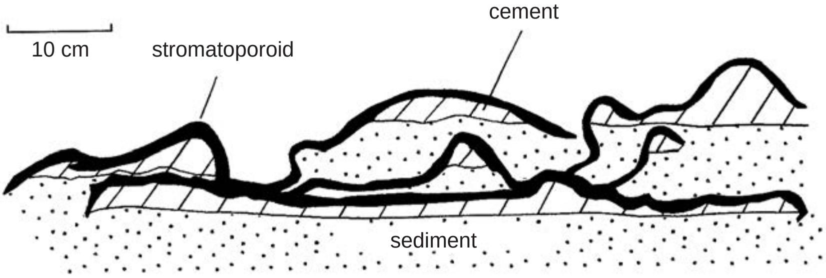

FIG. 282. Representation based on a tracing showing how a laminar stromatoporoid skeleton could possibly regenerate after partial mortality owing to sediment swamping. Both the initial laminar growth and the subsequent development of lateral outgrowths tend to up-dome over sediment-forming primary cavities that later became cement filled; Frasnian, Upper Devonian, Pillara Limestone, Bugle Gap, Canning Basin, Western Australia (adapted from Wood, 1999, fig. 6.20).

primary cavities on their undersurfaces (Fig. 282, Fig. 284.1–284.2; and see discussion of Primary Cavities, p. 475; after WOOD, 1998, fig. 2; 1999, fig. 6.19c, 6.20).

Euryamphipora platyformis KLOVAN, from the Devonian Redwater reef complex in Alberta, is another species with an unusual explanate growth form. The species is the only amphiporid taxon to exhibit a laminar shape, being variously interpreted as a horizontal, sheetlike form (KLOVAN, 1966; MISTIAEN, 1985; STEARN, 1997c, p. 842) and an erect, vertically elevated plate (COCKBAIN, 1984, fig. 10). However, MISTIAEN's (1985, p. 207, fig. 129, pl. 20,*9*) recognition of *Euryamphipora* sp., as a small, 1-mm-thick specimen encrusting a brachiopod shell (Fig. 283.3), seems to establish the taxon, with its complex internal amalgamate network of laminae and slightly zigzagged pillars, as a low-lying, laminar form.

Case studies show that laminar shapes are more commonly associated with more energetic Paleozoic reef regimes. Some also exhibit large sizes. For example, KERSHAW (1990, 1993, 1997) and KERSHAW and KEELING (1994) documented distribution patterns of stromatoporoid shapes from biostromal and biohermal habitats in Gotland. Detailed studies of the content and distribution of the two different biostromes at Kuppen and Grogarnshuvud (KERSHAW, 1990, 1997) demonstrated significant differences in proportions of low-profile (laminar to low domical) stromatoporoids relative to high-profile types (mainly the high domical to bulbous forms), whereas in the Holmhällar bioherm (KANO, 1989; KERSHAW & KEELING, 1994), only low-profile (laminar to low domical) and anastomosing forms were developed.

MOUNDS

Mounds are defined as three-dimensional domical and bulbous shapes that arose from combinations of lateral (tangential) and vertical (longitudinal) growth.

Domical

A domical shape is typically a skeletal mound combining outward (lateral) and upward growth from an initial laminar base; may appear as a simple hemisphere with a smooth, arcuately curved, upper part (Fig. 274), or may develop a more bell-shaped (campaniform) shape because of its ragged (zigzagged or skirted) extensions of lateral margins toward the base (Fig. 276.1, Fig. 277.1). Like laminar morphologies, the relationships at the base are largely dependent on substrate characteristics. The base may be relatively flat lying, but on soft substrates may vary from slightly convex downward, where lateral growth developed on an aggrading substrate, to convex upward, where the lateral growth formed while sediment was being winnowed away, more or less contemporaneously (Fig. 285; and see examples based on bryozoan colony shapes, in Spjeldnaes, 1996, fig. 2D–E). On firm substrates, the base may be convex upward, where lateral growth occurred over a preexisting local high or encrusted a large skeletal object with positive relief. The preferred term domical is more or less equivalent to the previous terms: hemispherical, domal, bun-shaped, bell-shaped, conical, mamelon, massive *partim,* and ?pyriform, which are now all regarded as obsolete.

In part, we follow Kershaw and Riding (1978), arbitrarily subdividing the low and high domical forms on the basis of whether their ratios of vertical height to basal diameter (V/B) are between 0.1 and 0.5, or 0.5 to 2.0, respectively. High domical shapes commonly develop from continued growth to maturity of a low domical skeleton; and this low domical stage may, or may not, have commenced initial growth from a laminar base. Hence, it is important in future growth analysis surveys that the nature of changes in skeletal shape within skeletons is evaluated through all stages of growth (Luczynski, 2005).

Smooth and ragged types of margins are well represented in the low domical morphs (Fig. 274; Fig. 276.1; Fig. 277; Fig. 278.5), whereas smooth associations are more commonly developed in the high domical subgroup (Fig. 278.6). Sometimes ragged domical shapes (some are composite domical types) developed asymmetrical appearances as they grew on the substrate, in association with unidirectional current activity (Fig. 286, Fig. 287.2). A divergence of views exists as to whether these asymmetrical skeletons grew inclined toward the direction of current flow (Broadhurst, 1966) or away from the current flow (Kapp, 1974).

The majority of stromatoporoids exhibit low-profile (that is, laminar to low domical) shapes. This is probably largely because they were hydrodynamically the most stable growth forms; that is, the most resistant to current activity in both reef and nonreef settings (Kershaw, 1998, p. 511). The high domical forms were mechanically less stable—that is, more prone to disturbance by current activity (unless sediment later accumulated around them)—but, because of their raised living surface, were better able to access nutrients higher in the water column.

The conical shape (apex upward) is distinctive (Fig. 288.1), although comparatively

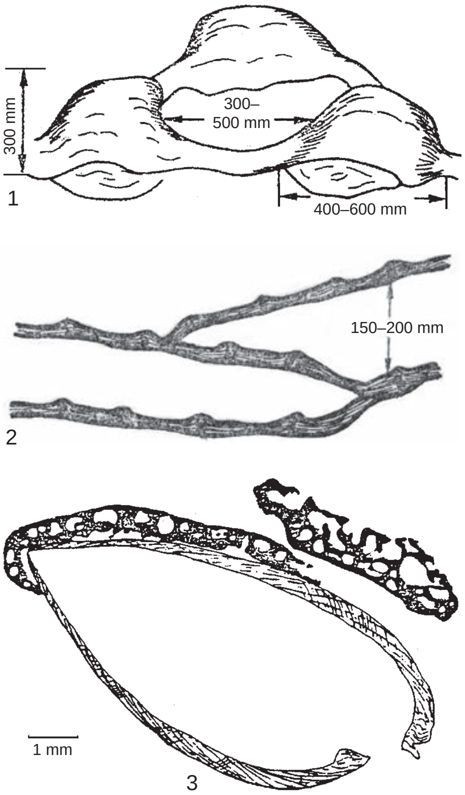

Fig. 283. *1,* Field sketch of a portion of a complex, composite intergrowth of domical and laminar forms of *Parallelostroma malinovzyensis* (Riabinin), Silurian, Podolia, Ukraine; interconnected, multiskeletal structures grew on substrate to large sizes, measuring up to 5 m^2 (adapted from Bogoyavlenskaya, 1982b, fig. 4); *2,* field sketch of a fragment of the anastomosing laminar sheets of a species of *Lophiostroma,* Silurian, Podolia, Ukraine; laminar shapes of such forms repeatedly split in response to episodic sediment swamping events and may extend to lengths of at least 1.2 m and heights of up to 0.6 m (adapted from Bogoyavlenskaya, 1982b, fig. 5); *3,* sketch of thin laminar growth of *Euryamphipora* sp., encrusting a slightly disarticulated brachiopod shell, including parts of both dorsal and ventral valves close to the anterior commissure; Dewal Formation, Givetian, Dewal section, Central Mountains, Afghanistan, based on specimen GFCL 4135 (thin sections: AF 76 D 83/4) (adapted from Mistiaen, 1985, vol. 2, fig. 128).

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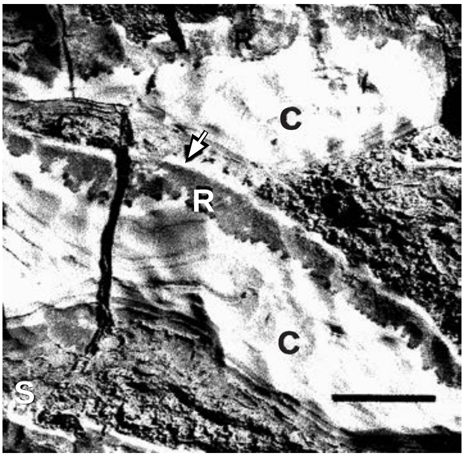

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FIG. 284. Unusual, widely spreading, thin, laminar stromatoporoid growth forms that produce large primary cavities; *1,* stromatoporoid *Stachyodes australe* (WRAY), slope-margin facies, Frasnian, Canning Basin reefs, Western Australia, exhibiting expansive, very thin, laminar crusts (continuous, wafer-thin, light colored bands shown in photo); laminar stromatoporoids are gently updomed over large primary cavities that largely became filled with lighter-colored, lens-shaped bodies of zoned calcite cement (also shown), and growths of cryptic calcimicrobe *Shuguria* also commonly preserved directly beneath stromatoporoid crusts, ×0.15 (adapted from Wood, 1999, fig. 6.19c; reproduced from *Reef Evolution,* Rachel Wood, 1999, p. 230, by permission of Oxford University Press); *2,* in more detail, an extensive, thin, gently doming, laminar sheet of *S. australe* (WRAY) as a thin, light-colored band (*arrowed*) that obliquely spans field of view, and more than 20 mm above dark-colored sedimentary rock (*S*) shown at bottom left. Originally, a large primary cavity formed in the space between and was first colonized by pendent growths of encrusting calcimicrobe *Shuguria* (*R*) as dark, sheetlike bands on underside of stromatoporoid, then the rest was infilled with light-colored, zoned, radiaxial calcite cement (*C*); Frasnian outcrop is in slope-margin facies, near Sheep Camp Yard, Geikie Gorge, on Fitzroy River, Canning Basin, Western Australia, scale bar, 20 mm (adapted from Wood, 1998, fig. 2D; reproduced with permission of and copyright Elsevier).

rare. It may be regarded as a subtype of the high domical forms, either where successive units (latilaminae) of skeletal growth were inclined sharply away from a central (vertical) axis (the enveloping condition), or where successively higher, more gently convex latilaminae became more withdrawn from lateral margins (the nonenveloping condition); see also discussion of columnar shape (p. 443).

The reef limestones of the Gotland succession generally have comparatively large, domical-shaped specimens (MORI, 1970). For example, the Kuppen biostrome, which has a high proportion of domical stromatoporoids relative to other shapes (KERSHAW, 1990), has low domical forms that are commonly up to 1 m across and 0.3 m high, and high domical shapes, typically up to 0.3 m across and 0.5 m in height. Few of them have a ragged appearance. Though many high domical shapes are toppled, the biostrome is interpreted to have been formed in a comparatively low to moderate energy regime, subject to episodic storms (KERSHAW & KEELING, 1994). Other reef deposits exhibit even larger high domical forms, such as the *in situ*, 1-m-high skeleton (Fig. 289) now exposed in a single *rauk* (sea stack) at Fågelhammar (KERSHAW & RIDING, 1978).

Domical stromatoporoids are the dominant growth forms of the marly, deeper, level-bottom Visby Formation (Silurian) of Gotland (KERSHAW, 1984), and they are of comparatively small size, normally 50 to 150 mm in diameter and up to 70 mm in height. About 20% of the skeletons have ragged lateral margins th at testify to the intermittent influxes of sediment during growth (Fig. 276.1). The mainly encrusting species *Petridiostroma simplex* also occurs in this habitat and produces another important shape variant of small, predominantly smooth, domical composites that may become interlinked by short lateral projections near their bases, giving them an irregularly lumpy, conjoint form overall (Fig. 290–291). Only a few laminar and bulbous shapes are additionally found in this habitat.

Another type of composite domical shape developed in the Silurian of Podolia. BOGOYAV-

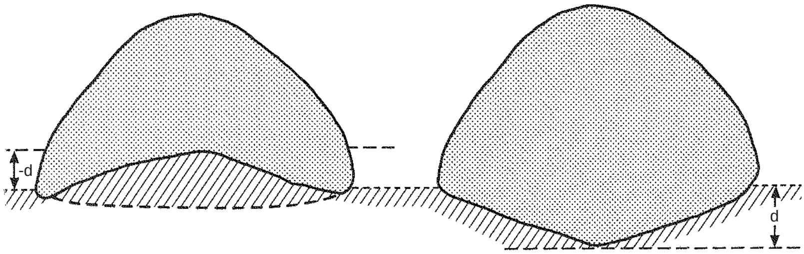


FIG. 285. Two longitudinally oriented sections, based on domical-shaped bryozoans, Lower Ordovician, Öland, Sweden, showing same basal morphology as many domical stromatoporoids that lived on soft substrates; specimen (left side) has a concave base; specimen (right side), a convex base. Growth of each example was initiated from a central point on base; sample on left then continued to grow outward and somewhat downward, to adjust for loss of sediment from surrounding substrate (*-d,* total amount of sediment removed during lifetime of its active growth); sample on right continued to grow outward and slightly upward to adjust to amount of sediment being added to surrounding substrate (*d,* total amount of sediment that must have been added during lifetime of its active growth) (Spjeldnaes, 1996, fig. 2D–E).

LENSKAYA (1982b, p. 117, fig. 3V, 4) illustrated this combination (Fig. 283.1) as an arrangement of three, conjoined, domical skeletons (each about 0.5 m in diameter and 0.3 m in height) that are linked by laminar projections (about 0.4 m in length) of *Parallelostroma malinovzyensis* (RIABININ). This large, partially coalescent growth form seems to have formed an approximately triangular array on the substrate.

Other domical variants are the ragged mushroom-type shapes that also formed as composites, first as an extended series of comparatively narrow growth units (latilaminae) forming a columnar base, and then overtopped abruptly by laterally expanded, convexly shaped, domical, upper growth units (Fig. 287.1; see also KAPP, 1974, fig. 1). This composite shape has a distinctive morphology but only occurs rarely. It reflects a rapid change from narrow columnar to laterally spreading growth. This apparently relates to a sudden change during growth, from a stressed to a less-stressed environmental condition, as the rate of sediment influx dramatically declined (see discussion of combinations of columnar and explanate patterns of growth, p. 455).

Large domical stromatoporoids also occur in Devonian reef facies. For example, KERSHAW and RIDING (1980) recorded a specimen from South Devon measuring 1.7 m across. WOOD (2000) reported other large examples from the Upper Devonian back reef community of the Canning Basin (Western Australia), including skeletons of *Actinostroma papillosum* that have a highly unusual, large, apparently composite (mound and plate-type), domical shape with extended lateral (tiered) platy outgrowths from domical centers (Fig. 292; see also Fig. 304). Overall skeletal dimensions are up to 1 m in width and 1 m in height. Primary cavities may be developed on undersurfaces of the successive, outwardly tapering extensions of these domical forms. It remains uncertain whether this complex form represents an intrinsic growth style or if the lateral outriggers with their accentuated raggedness developed as a consequence of repeated influxes of sediment (WOOD, 2000).

Other large domical stromatoporoids may exhibit upper surfaces that are covered by multiple peaks (or cones) that represent a part of the tops or sides of mamelon columns, as in a very large and complex, domical specimen of *Parallelostroma typicum* in the *rauk* (sea stack) area at Fågelhammar, in the Folhammarn nature reserve (see SANDSTRÖM, 1998) on Gotland (Fig. 289, Fig. 293.1). KERSHAW (1990, 1998) recognized many similar mamelated structures in species from the Gotland Silurian succession, including examples from the Kuppen biostrome (Fig. 293.2).

In a Middle Devonian reef core of the Rhenish Schiefergebirge in Germany, BRAUN

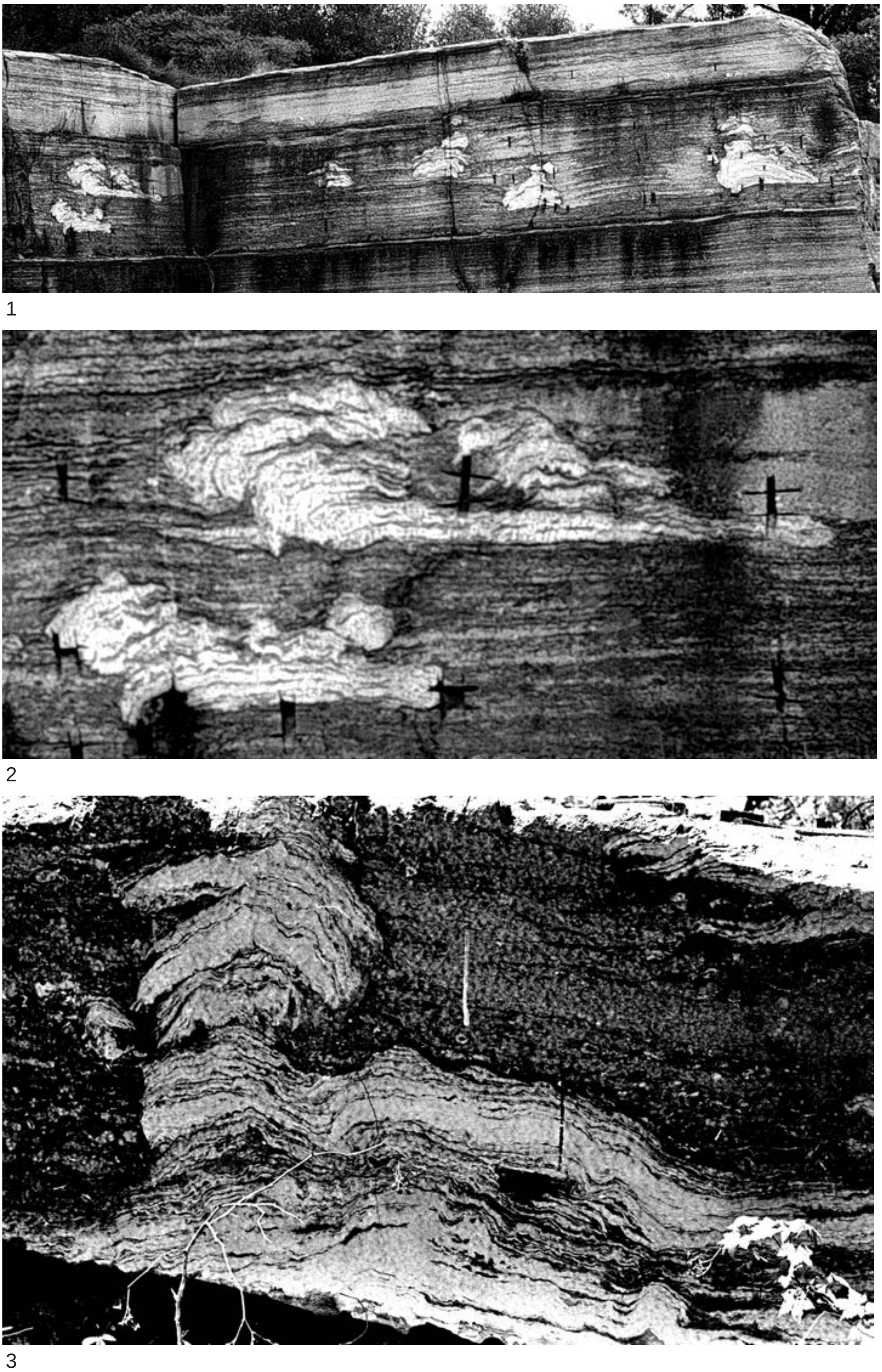


FIG. 286. *(For explanation, see facing page).*

and others (1994, p. 360, fig. 7) have recorded many large mamelated high domical to irregular specimens in the vertical and horizontal walls of a quarry (Fig. 293.3). Unfortunately, they regarded one of their growth forms as a mamelon morphotype. The term mamelon (see Glossary, p. 407, and also p. 481–483, 503–505) applies only to the upward skeletal extensions on the upper growth surface and should not be denoted as a stromatoporoid shape. The well-defined mamelon columns of specimens shown on the cut walls of the quarry are highlighted by distinctive, cone-in-cone, or zigzag-shaped, patterns of the latilaminae, but these represent internal (not external shape) features of the skeletons. Nevertheless, these large, prominently zigzag-mamelated skeletons are of interest, because, as shown by BRAUN and others (1994, p. 361, fig. 8b, 9, 10, pl. 5, 7, 8), in the central reef, they are more commonly reoriented than other high domical stromatoporoids, though in the interpreted reef growth center, an appreciable number of larger zigzag-mamelated specimens remain *in situ* or have only been slightly disturbed. Such structures have previously been termed protuberants by KERSHAW (1998, p. 522, fig. 7).

Bulbous

This form usually has a near-spherical outline, except for a relatively narrow, flattened base (Fig. 274, Fig. 278.1, 278.3–278.4). It is widest at the midpoint between bottom and top, and characteristically has a smooth outline as a consequence of an enveloping-type growth. Sometimes, with continued upward growth, a skeleton may develop as an extended bulbous form (Fig. 278.2). While many bulbous forms developed from a narrow laminar base, others appear to have grown from a single settlement point, such as a hard object on the substrate, with both upward and outward spreading from the initial attachment site. The shape was regarded by KERSHAW and RIDING (1978) as an end member of the more or less continuous laminar–domical–bulbous series. However, in terms of the three morphological variables of their parameterization scheme, the bulbous shape is only produced when the dimensions of the basal length remain low compared to the other (vertical and diagonal) dimensions. The term bulbous should take precedence over the more or less equivalent terms, such as globular, oblate, cabbage-shaped, nodular, subspherical, and spheroidal. All these latter should now be treated as obsolete.

The high center of gravity and narrow base resulted in the bulbous morphs being more susceptible to current activity (including overturning), and they seldom grew to larger sizes (greater than 0.3 m across), as did the laminar and domical forms. Overall, they occur less commonly than laminar and domical forms. The fact that some were able to grow to maturity and sustained little movement suggests they occupied relatively quiet-water environmental conditions, perhaps in back-reef habitats (KERSHAW & RIDING, 1980); though for such mature, enveloping-type skeletons to be preserved intact, it

FIG. 286. Cut walls showing many longitudinal sections of large, laminar to domical skeletons of the stromatoporoid *Pseudostylodictyon lamottense* (SEELY), Fisk quarry, Isle La Motte, Vermont, United States; exposures in the quarry are from middle part of Chazy Group, lower Crown Point Formation, Middle Ordovician, Darriwilian; *1,* large skeletons of *P. lamottense* occur at scattered intervals along two particular bedding planes spaced about 0.6 m apart, and some of the specimens have a noticeable asymmetry, with steeper slopes to the left. About 4.5 m sequence of the gently inclined, stromatoporoid-bearing limestone deposits shown in photo. KAPP (1974, fig. 5, 8) previously illustrated parts of this outcrop (Webby & Kershaw, 2011); *2,* enlarged view of two large, ragged, low domical skeletons of *P. lamottense* (also illustrated at left end of exposure in view *1*). Both show a similar asymmetry, with successive layers (latilaminae with ragged lateral ends) displaced toward their steeper sides that, according to KAPP (1974), probably represented the direction of current flow. The upper specimen has an overall length of 2 m (about 0.7 m in height), and the lower specimen is 1 m long at the base (about 0.4 m high) (Webby & Kershaw, 2011; KAPP [1974, fig. 8] previously provided a more generalized illustration that included these two skeletons); *3,* large, ragged, composite skeleton of *P. lamottense,* with lower half developing as laterally extended, undulating, laminar form, and upper half continuing into a narrowly constricted, high domical shape. Specimen is about 2 m long at the base and approximately 1.5 m high (Webby & Kershaw, 2011; based on photo kindly supplied by C. W. Stearn).

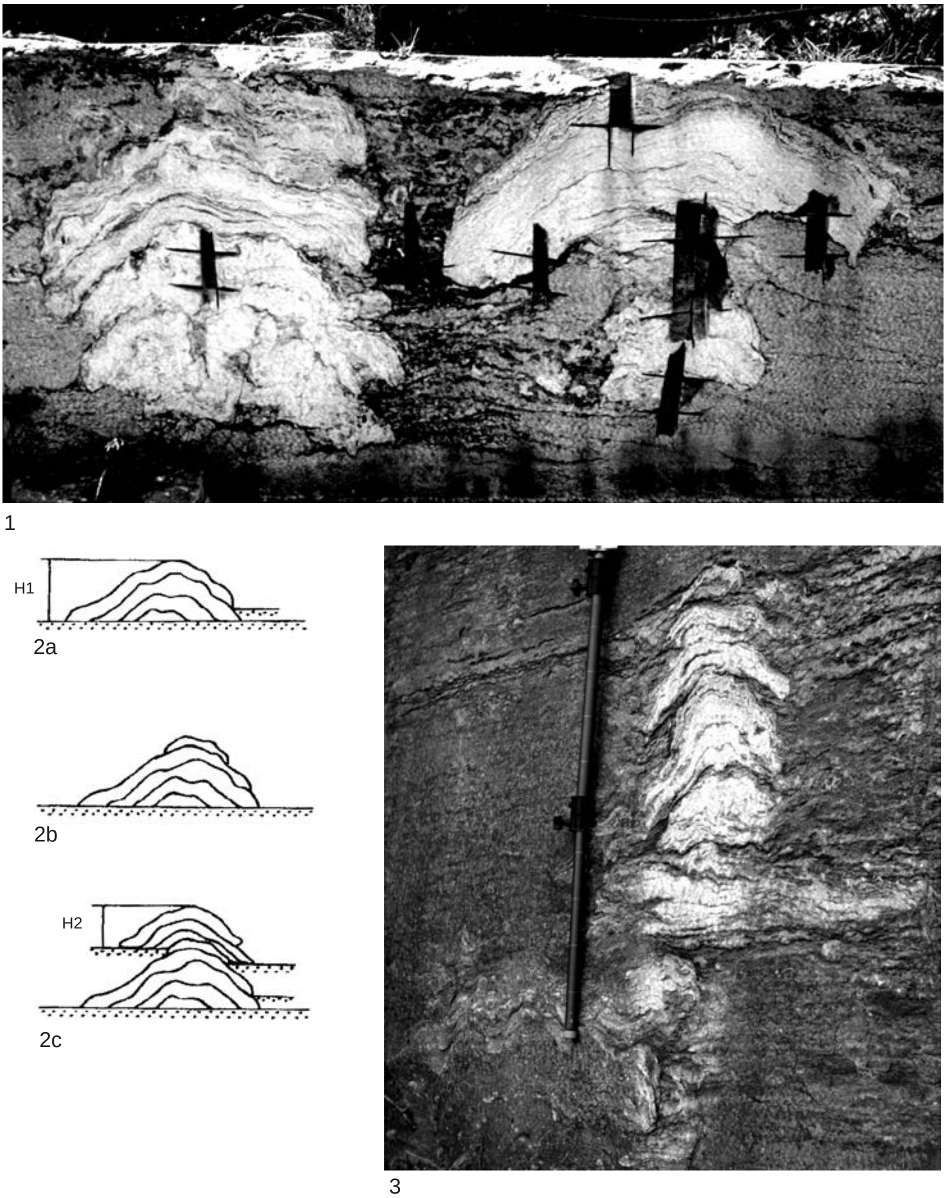


FIG. 287. *1,* Large, ragged, high domical and mushroom-shaped skeletons of *P. lamottense*, Goodsell quarry, lower Crown Point Formation, Chazy Group, uppermost Middle Ordovician, Darriwilian, Isle La Motte, Vermont, United States; mushroom-shaped form is a composite that may have developed when rate of sedimentary influx suddenly declined, although it is puzzling that the adjacent columnar form does not show the same pattern (Webby & Kershaw, 2011; similar image previously figured by KAPP [1974, fig. 1]); *2a–c,* diagrammatic representation of successive growth phases in a domical skeleton; *2a,* in first growth phase (*H1*), three domelike layers were added, maintaining contact on both sides with original substrate, but fourth layer was raised on one side because of small influx of sediment on that side; *2b,* sediment influx increased, causing most of skeleton to be buried, except a small area at top; *2c,* the small area then became site for a second growth expansion of new layers (*H2*), although the substrate levels were different on either side. *H1,* relief of skeleton during first growth phase; *H2*, relief achieved in second

(Continued on facing page.)

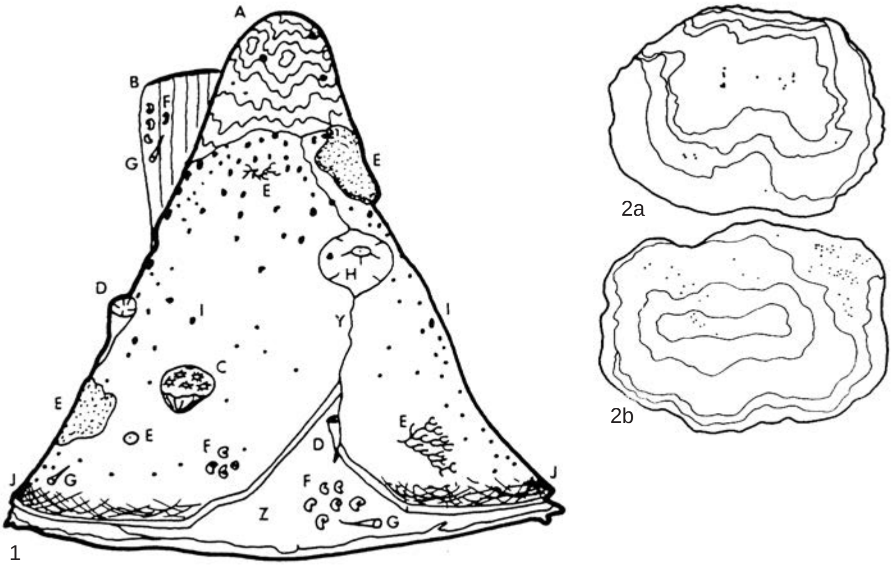


FIG. 288. Distribution of encrusters on high domical Silurian stromatoporoids, upper Visby Formation, Gotland, Sweden; *1,* sharply cone-shaped, high domical skeleton in lateral view showing varied distribution of mainly small, open surface epibionts; coverage of encrusters was greater toward top, suggesting progressive burial from base; *A,* stromatoporoid; *B,* halysitid coral; *C,* heliolitid coral; *D,* rugose coral; *E,* bryozoan; *F,* spirorbid worms; *G,* cornulitid; *H,* crinoid attachment base; *I, Trypanites; J, Allonema; Y,* hairline-type fracture; *Z,* exfoliated area, ×0.75 (adapted from Nield, 1986, fig. 3); *2a–b,* flattened undersurfaces of two high domical skeletons of specimens *a,* Hä6 and *b,* HäS8 that show patterns of clustering of tiny encrusting spirorbid worms, perhaps suggesting they colonized short-lived secondary cavities, ×0.23 (adapted from Nield, 1986, fig. 2A–B).

possibly requires their rapid engulfment in periodic sediment-laden storm surges.

The shape illustrated by STEARN (1983a, fig. 1F; 1984, fig. 1F) as bulbous expands upward from a narrow base and differs somewhat from typical bulbous morphs in having nonenveloping, ragged lateral edges. The shape is strictly obconical rather than bulbous. The skeletons appear to have grown in relationships with episodic sedimentation and maintained their stability as they progressively became engulfed. However, because this obconical shape only occurs rarely, it is perhaps best regarded as a subgroup of the more typical bulbous forms. An apparently obconical, or cuplike, skeleton of *Labechia conferta* was illustrated by NICHOLSON and MURIE (1878, fig. 5), and other species from the Halla and Sundre formations of Gotland also exhibit this shape (MORI, 1970; KERSHAW, 1998).

FIG. 287 *(Continued from facing page).*

growth phase. Such changes in growth are dependent on small-scale fluctuations in sedimentary input; local currents may have influenced the symmetry of vertical growth, for example, if they were maintained in one direction for a time, with a noticeable asymmetry developing as a consequence of successive layers being displaced in the direction of current flow (adapted from Kapp, 1974, fig. 6); *3,* large, ragged, predominantly columnar skeleton of *P. lamottense*, Fisk quarry, lower Crown Point Formation, Chazy Group, uppermost Middle Ordovician, Darriwilian, Isle La Motte, Vermont, United States; in detail, however, this complex skeleton has an irregular, steeply tilted (possibly disturbed), narrow base, then successive, 0.5 m long, laminar outgrowths, one undulating more to the left, and the other being more regularly layered and tapering to the right, followed by the upper, columnar part composed of stacked and ragged domical growths, about 0.3 m in diameter to the top; overall this complex, composite, stromatoporoid skeleton has a considerable number of laterally associated, sedimentary-rock–filled wedges and some internal sedimentary rock inclusions; the part of the monopod measuring stick shown in the photo is 1.05 m long (Webby & Kershaw, 2011; photo courtesy of Frank R. Brunton).

FIG. 289. High domical skeleton of *Parallelostroma typicum* (ROSEN) exposed on the coast, forming a small isolated *rauk* (sea stack), Hemse Group, Ludlow, Fågelhammar, Folhammarn nature reserve, Gotland, Sweden, showing areas of exfoliation of laterally exposed wavy latilaminae, especially in low to middle parts, although it retains a relatively smooth outer surface in the upper part; specimen is 1.35 m high; note also scale bar = 8 cm (Kershaw digitized photo no. DCP-9400; previously illustrated by Mori, 1970, pl. 28,*2*; Manten, 1971, fig. 223; Riding, 1981, fig. 42; Fagerstrom & West, 2011, fig. 1A–B).

TREES

Trees are defined as erect to inclined, unbranched columns, or branching (digitate or dendroid, rarely both branching types occurring in the same species). Treelike shapes are not common growth forms among Paleozoic stromatoporoids, and have limited real significance as taxonomic entities. Only a few taxonomic groupings have adopted predominantly treelike growth forms, among them, the small order Amphiporida, the moderate-sized family Aulaceratidae (order Labechiida), and the two small families, Idiostromidae (order Stromatoporellida) and Stachyodidae (order Syringostromatida). There are, in addition, a few genera with predominant treelike forms that are grouped within orders and families dominated by laminar and dendroid growth habits, e.g., clathrodictyid genera *Labechiina*, *Neobeatricea*, and stromatoporellid genus *Dendrostroma.* These may have taxonomic integrity, though some specialists may prefer to treat such forms as growth-form variations of related genera.

Columnar

This form is erect, unbranched, with lateral sides parallel to subparallel, and where the vertical height is more than twice the basal diameter (V/B > 2.0) or width (Fig. 274). In some cases, the unbranched columnar shapes may be linked to members of the laminar–domical–bulbous series of Kershaw and Riding (1978), with high domical and columnar forms developing from similar relatively narrow laminar bases (see Kershaw, 1998, fig. 7). Also, some extended bulbous forms are difficult to distinguish from columnar forms where they grow from a point rather than a laminar base (Fig. 278.2; and Harrington, 1987, fig. 6). Some columnar shapes represent broken fragments of larger branching growth forms, so some care is needed to establish that the skeletons were unbranched through all stages of their growth. The columnar growth form may exhibit smooth or ragged margins and either an enveloping or nonenveloping habit. Equivalent terms unbranched and subcylindrical are regarded as obsolete.

Both types of columnar shapes appear to have grown rapidly upward with limited lateral spreading. The smooth, enveloping forms (e.g., species of genus *Aulacera* of the family Aulaceratidae, order Labechiida) may have grown predominantly in quiet-water conditions but then were collapsed and completely engulfed by sediment in a major storm surge event (Fig. 294–295). In contrast, the ragged (irregularly notched, rejuvenated), nonenveloping forms may have grown in more episodic, turbulent (rough water) conditions, resulting in alternations between columnar (upward) growth, when the restricted growing surface was able to maintain pace with progressive burial by sediment, and pauses in sediment supply, when localized laminar outgrowths were able to develop (Fig. 287.3; see also Cuffey & Taylor, 1989, p. 297, fig. 2E). These two types of columnar growth responses developed from quite different sets of environmental conditions and probably from stromatoporoid organisms that had markedly different inherited growth programs.

The most striking examples of columnar stromatoporoids are the large, unbranched, postlike columns from the latest Ordovician (Hirnantian) successions of Anticosti Island, Canada (Petryk, 1981; Cameron & Copper, 1994). These are mainly referred to species of *Aulacera*. Most specimens (Fig. 294.1–294.2) are preserved as broken logs that are scattered randomly on bedding planes, or current aligned, typically 1–2 m in length and up to 0.3 m in diameter, although one specimen is 1.6 m long and only 0.13 m in diameter (Cameron & Copper, 1994, fig. 3C). The length-to-diameter ratios are estimated to range between 12:1 and 6:1. Most specimens show very limited taper along their lengths, but Plummer's (1843, fig. 8) originally figured, vertically fluted, 1-m-long specimen has a marked taper, from a point at one end to a maximum diameter of 6–7 cm at the other (see Fig. 406*h*).

During life, the aulaceratids are inferred to have grown vertically to at least a meter above the carbonate-mud substrate before being toppled by a storm event (Fig. 295). Some broken skeletal bases are preserved *in situ*, up to 0.25 m in height (part-embedded and part-exposed above the substrate), and occasionally grouped in nestlike clusters. They do not appear to develop a separately differentiated laminar base. The initial (basal) unit of growth, i.e., the part embedded in the substrate, has the same skeletal structure of large axial cyst plates

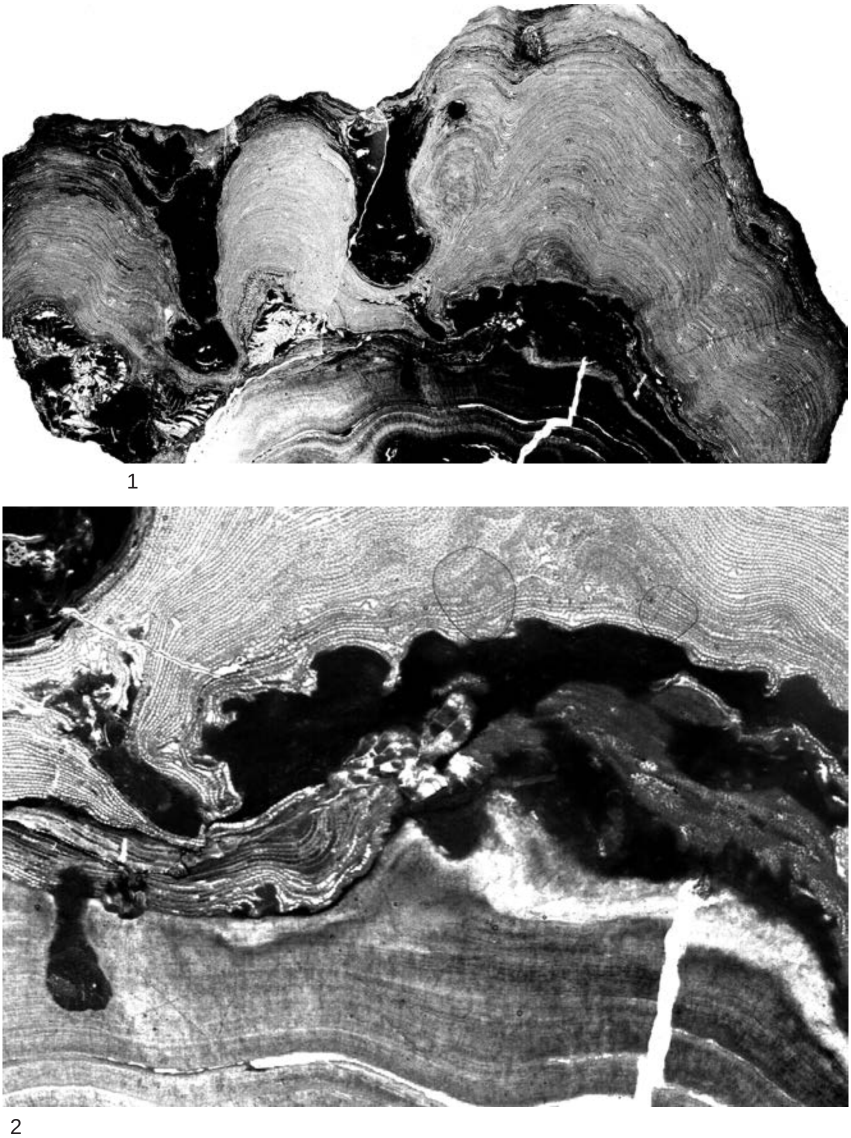


FIG. 290. *1,* longitudinal thin section of two stromatoporoid species, *Densastroma pexisum* (YAVORSKY) and *Petridiostroma simplex* (NESTOR), Visby Formation, Gotland, Sweden, sample 1-23, locality Ireviken 3 (Note: faint circles near base of right domical mass of *P. simplex* are air bubbles in thin section). *D. pexisum* is the gently updomed laminar stromatoporoid at the bottom, and *P. simplex* is the smooth, composite skeleton of three domical masses in middle to upper parts. Note that the three domical masses have laterally interconnected thin, irregular, laminar outriggers in their basal and topmost parts. Also note the complex and varied encrusting relationships between *P. simplex* and the underlying rugose coral and small bryozoan (left side; for details, see Fig. 291), as well as its relationships with the underlying, irregularly elongate tongue of dark sedimentary rock, ×0.9 (right side; for details, see view *2*); *2,* enlarged view of base of skeleton of *P. simplex* beneath right domical mass showing particularly complex and irregular arrangement of contacts with underlying dark sedimentary rock tongue. This suggests that either a large cavity originally existed beneath this part of the skeleton and that cavity was only later backfilled with sediment; or, alternatively, the sedimentary material predates the basal growth; i.e., it became lithified and irregularly eroded, perhaps even in part burrowed, before being overgrown by the stromatoporoid organism. Note well-defined, flask-shaped *Trypanites* boring in the upper part of the underlying, fine-textured, laminar skeleton of *D. pexisum* (lower left part of figure), ×3.6 (adapted from Kershaw, Wood, & Guo, 2006, fig. 3a).

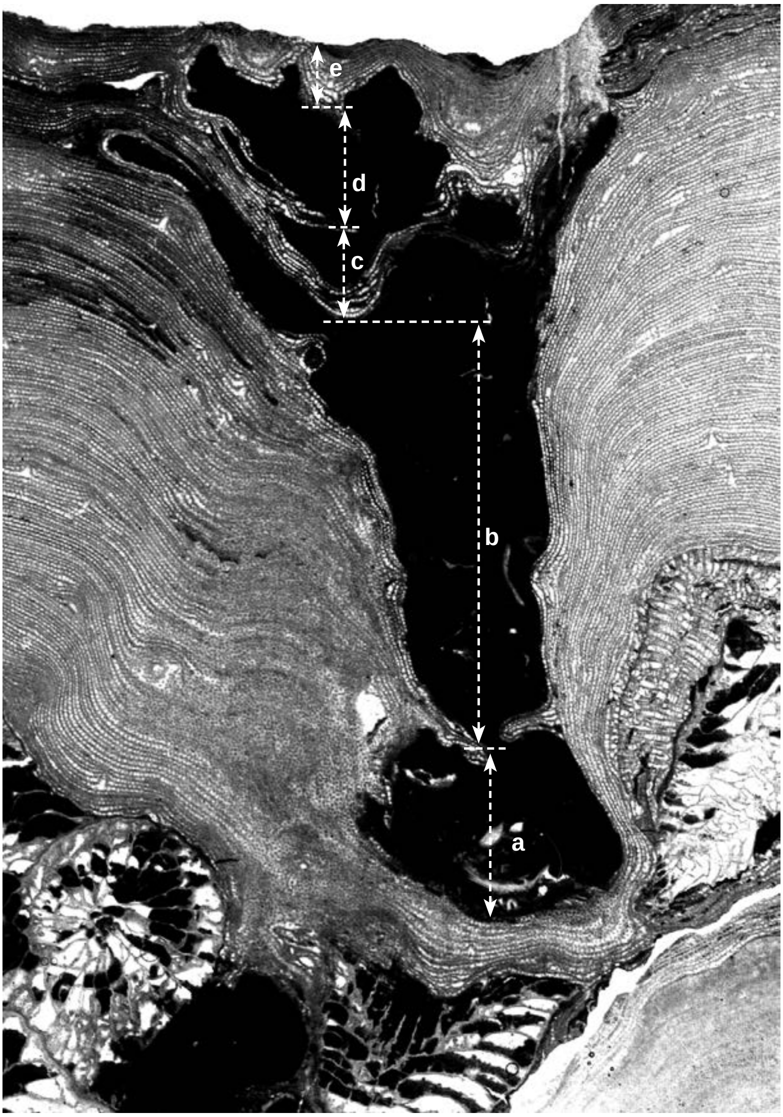


FIG. 291. Enlarged view of Figure 290.1 to show organism-organism and organism–sediment relationships associated with the left and central domical masses of the *P. simplex* skeleton. Note the encrusting basal contacts with the rugose coral to the left, and superposed coral and bryozoan colonies to the right. A delicate balance existed between the growth of the domical masses and the sedimentary infilling of intervening cavity spaces. The organism–sediment relationships may be traced through five separate phases (*a–e*), as follows: *a,* sediment infilling lower cavity, and then a pause in rate of sediment influx, allowing slender lateral offshoots, each with a few laminae to extend inward, almost closing off space; *b,* a more continuous period of sediment influx, allowing nonenveloping relationships of successive laminae to develop along sides of adjacent domical masses as cavity became progressively infilled; *c,* cessation of sedimentary input then permitted lateral spread of undulating, ragged strands of laminar growth, and in this case, the gap was bridged by a few irregular, sinuous laminae that formed across the cavity, although some localized swamping by sediment also continued to produce small, sediment-filled spaces; *d,* slightly increased rate of sedimentary input probably allowed the next, larger, sediment-filled cavity to form; *e,* in this last sediment-starved phase, lateral outriggers of growth were able to completely mantle the upper surface of skeleton, closing off all infilled cavity spaces between formerly separated left and central domical masses, ×5 (Webby & Kershaw, 2011).

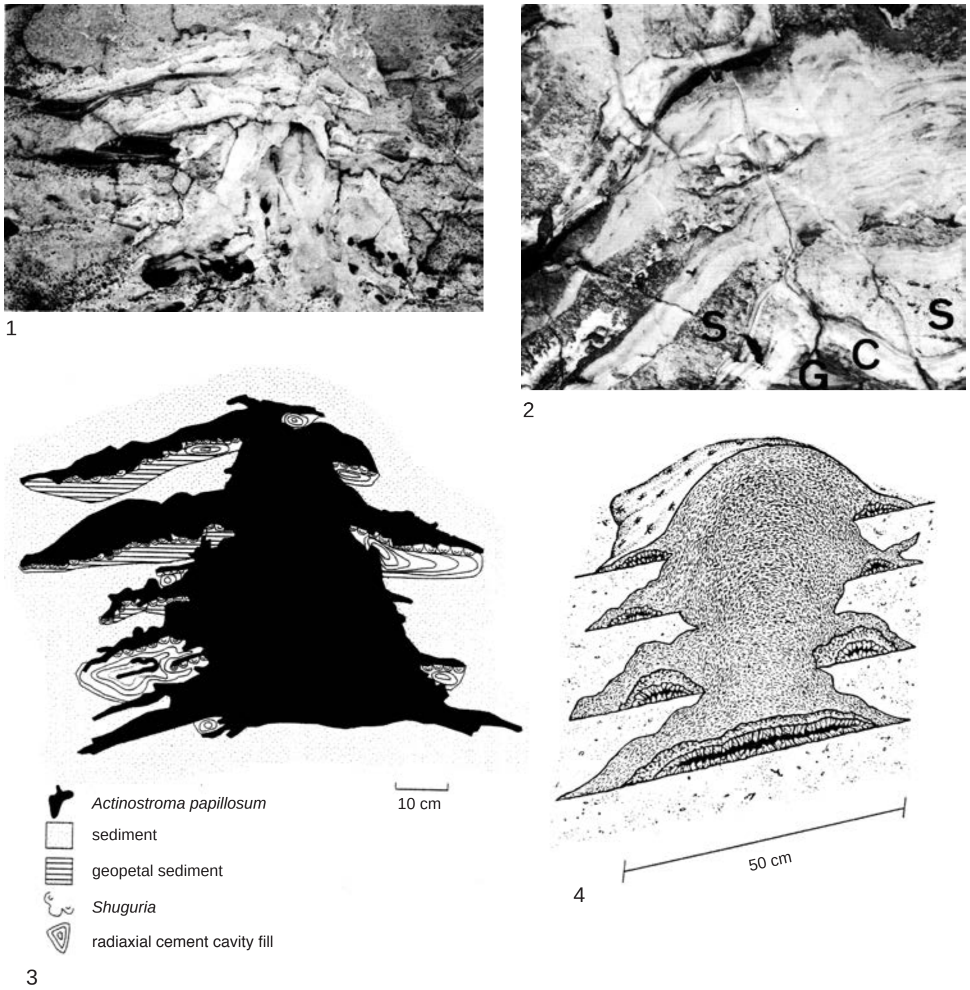


Fig. 292. Large, complex, free-standing, domical stromatoporoid that developed unsupported lateral outriggers off an elevated skeleton and was also colonized by cryptic organisms; these encrusted the sheltered sites beneath the extended outriggers, and the primary spaces were subsequently infilled by a combination of geopetal sediments and early marine cements. However, Wood (2000, p. 678) inferred that at any one time during growth, the overall relief above the substrate would rarely be more than about one-third the total height of skeleton. The stromatoporoid adopting this growth form is *Actinostroma papillosum* Bargatzsky, Frasnian, Upper Devonian, Pillara Limestone, Windjana Gorge, Canning Basin, Western Australia (see also Fig. 304; adapted from Wood, 1999, fig. CS 3.5b, copyright John Sibbick); *1,* a large domical specimen of *A. papillosum* Bargatzsky, ×0.05 (Wood, 2000, fig. 6A); *2,* part of a skeleton showing lateral outriggers of *A. papillosum* Bargatzsky with lower surfaces encrusted by *Shuguria* (*S*), and cavities filled with sedimentary rock that form geopetal structures (*G*), and fibrous cement (*C*), ×0.2 (Wood, 2000, fig. 6B); *3,* outline drawn from the same large domical specimen (see view *1*) to illustrate the nature of attached cryptic growth of *Shuguria* and cavities beneath lateral outgrowths containing geopetal structures and early marine cement (Wood, 2000, fig. 7A); *4,* schematic drawing depicting inferred mode of growth of large domical stromatoporoid, with its important role in generating cryptobiont-bearing cavity spaces (Wood, 2000, fig. 6C; drawing courtesy of John Sibbick).

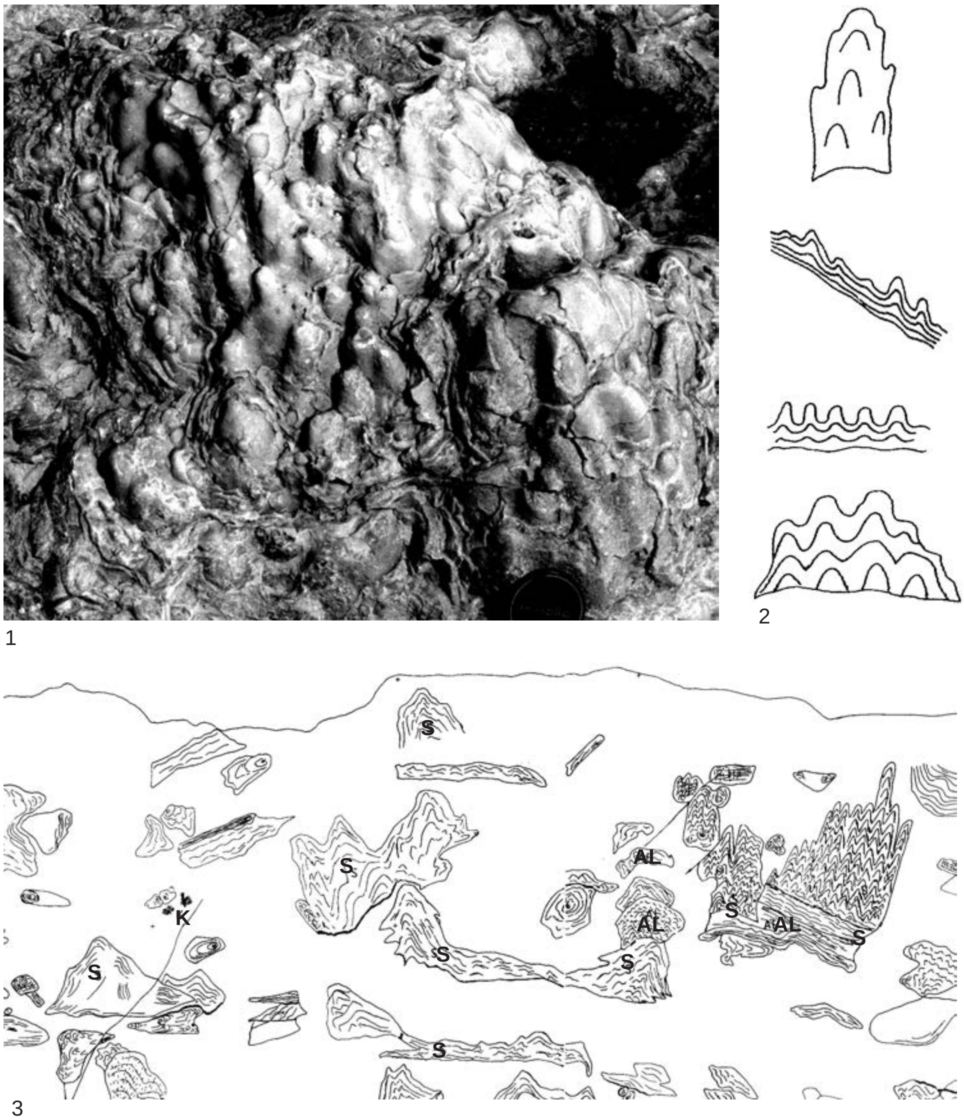


FIG. 293. *1,* Oblique view of part of a large, mamelated, domical specimen of *Parallelostroma typicum* (ROSEN), Hemse Group, Ludlow, Fågelhammar, Gotland, Sweden, showing smooth, conelike peaks of mamelons, and in some, inclined, exfoliated areas, examples of discontinuity surfaces between latilaminae, ×0.2 (Webby & Kershaw, 2011; similar specimen from same locality and stratigraphic level was illustrated by Mori, 1970, pl. 28,*3;* and by Fagerstrom & West, 2011, fig. 1C); *2,* diagrammatic sketches of mamelons on upper surfaces and their counterparts as mamelon columns in longitudinal section from the Kuppen Biostrome, Gotland; at the top are two examples of mamelons (or mamelon columns) that exhibit oblique relationships to lateral slopes; one is a large mamelon that shows very small, secondary cones on its slopes. The other two examples at the bottom show mamelon columns that developed on flat or updomed surfaces (adapted from Kershaw, 1990, part of fig. 7); *3,* tracing showing details of part of outcrop (mainly part of the reef growth center) at the center of 15-m-long cut wall A, Villmar reef complex, Givetian, Middle Devonian, Germany; detailed section is 4 m long and only top half (upper 1.5 m) of 3-m-high cut wall; it shows distributions of main components of reef: the bulk are stromatoporoids (only some are marked *S*), and others, much less common: one coral (*K*) and three laminar algae (*AL*); stromatoporoids include forms that are *in situ* (near horizontal in outcrop) and reworked forms (tilted in outcrop); shapes are mainly laminar, low, and high domical; additionally, there are prominently mamelated domical stromatoporoid skeletons—see upper right part of figure (adapted from Braun & others, 1994, part of pl. 5).

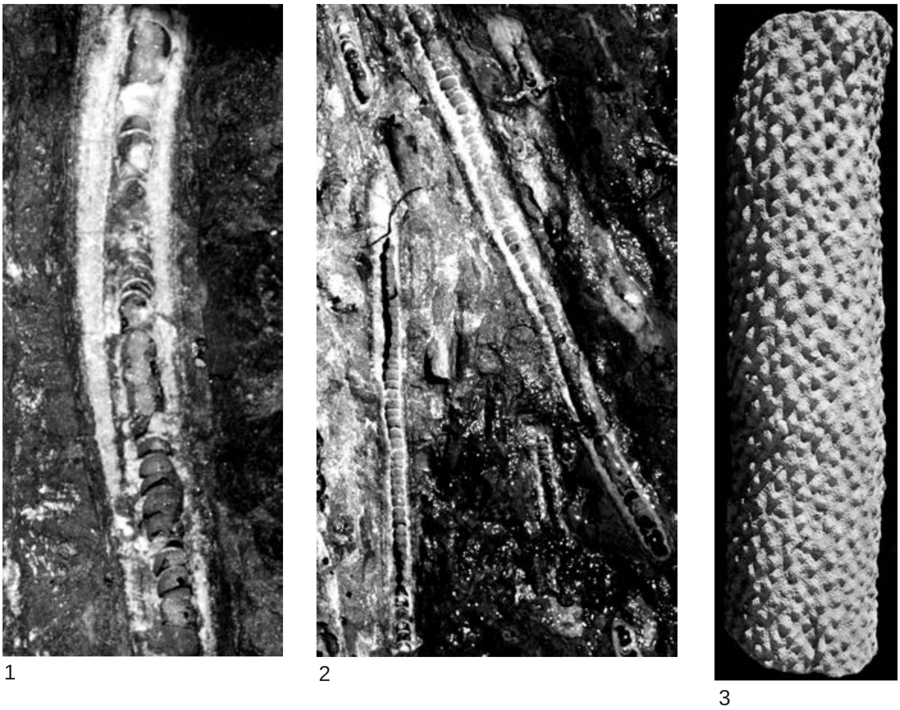


Fig. 294. Photographs of relatively slender, columnar, aulaceratid stromatoporoids, Vaureal Formation, Upper Ordovician, Anticosti Island, Canada. Specimens in views *1* and *2* are from exposed bedding surfaces, whereas specimen in view *3* has been isolated from the sedimentary rock; *1,* characteristic columnar shape of *Aulacera* sp., showing internal structures, especially arcuate axial cysts, of abraded specimen, Anse aux Fraises, western Anticosti Island, ×0.5 (Webby & Kershaw, 2011); *2,* toppled, current aligned, slender, columnar skeletons of *Aulacera* sp., exhibiting some internal axial and peripheral features in abraded specimens, Anse aux Fraises, western Anticosti Island, ×0.25 (Webby & Kershaw, 2011); *3,* columnar aulaceratid specimen, probably *Aulacera nodulifera* (Foerste, 1909), Anticosti coast, east of Rivière-aux-Saumons, showing the distinctive nodular external surface, AMF.134347, ×0.3 (Webby & Kershaw, 2011).

and lateral rows of small lateral cyst plates, as does the rest of the aulaceratid skeleton. Only one feature apparently helped to stabilize these large specimens on the unconsolidated substrate: a concretionary growth ring that probably developed by synsedimentary processes around the unmodified base (see Cameron & Copper, 1994, fig. 4). Bogoyavlenskaya, Vassiljuk, and Glebov (1990, p. 70), however, argued that the columnar skeletons of aulaceratids lacked traces of attachment, that they were spindle-like in shape, and hence, skeletons grew by adopting a rolling back-and-forth motion on nearshore substrates. This interpretation is discounted in favor of the group more typically exhibiting symmetrically arranged, erect, columnar shapes that represent upright growth, and internally composed of an axial core of large, superposed, horseshoe-shaped cyst plates and a surrounding, uniformly continuous, peripheral zone of smaller, imbricated cyst plates (see Bolton, 1988, pl. 2.5, fig. 4, 6; Webby, 1991, fig. 11A–C, 12A, E; Cameron & Copper, 1994, fig. 3e; and see also Fig. 318,*4*; Fig. 406*a–h*).

Outer lateral surfaces of the columnar aulaceratids on Anticosti Island show markedly different features. For example, they may be smooth, undulose, nodular (Fig. 294.3), or pustular. Some of these characters have been used to define the different taxonomic species of the genus. The aulaceratids of Anticosti Island are not closely associated

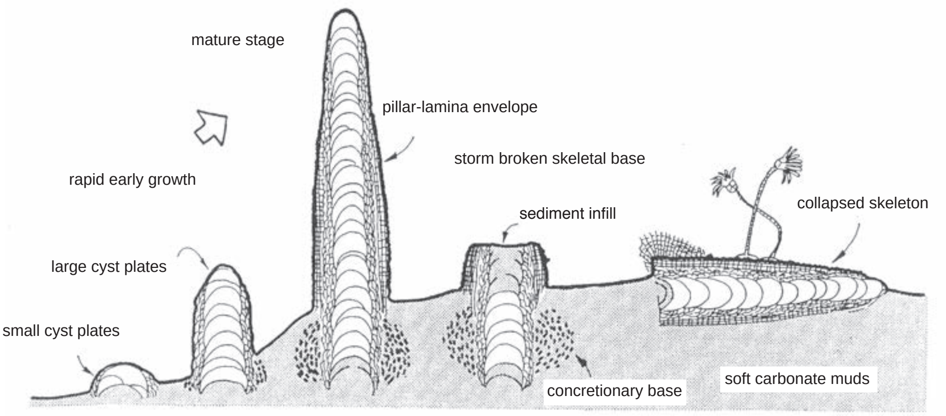


FIG. 295. Schematic reconstruction of life and death of large, columnar, aulaceratid stromatoporoids, Late Ordovician, Ellis Bay Formation, Anticosti Island, Canada (Cameron & Copper, 1994, fig. 4).

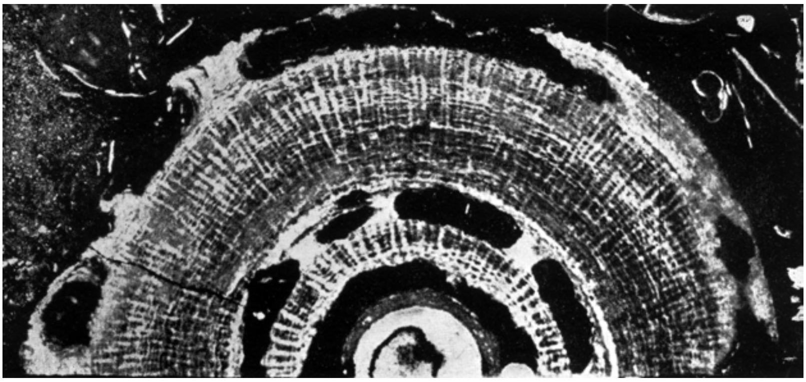
with reef complexes. They grew in forests on muddy, unconsolidated substrates in relatively undisturbed deeper water conditions above storm wave base and were subjected to periodic severe storm events (LONG & COPPER, 1987; CAMERON & COPPER, 1994; KERSHAW & BRUNTON, 1999). Other aulaceratid genera (e.g., *Ludictyon, Cryptophragmus)* exhibit unbranched, columnar shapes, but the nature of initial growth in these forms remains unknown.

A feature of a species of *Cryptophragmus* from western North America and the Siberian Platform (RAYMOND, 1914; GALLOWAY & ST. JEAN, 1961; BOGOYAVLENSKAYA, 1977a) is the presence of a mud or sparry, calcite sheath between the axial column with its large, superposed cysts and a lateral zone appearing as rows of small cyst plates (like the structure of *Cystostroma)* or a combination of cyst plates and pillars (as in *Labechia*). The lateral zone of *C. antiquatus* RAYMOND was interpreted by GALLOWAY and ST. JEAN (1961, p. 18) as representing "growth downward from the top of the column, after . . . the mud was deposited, making latilaminae" (Fig. 296). However, the latilaminae appear to be integral parts of the *Cryptophragmus* skeleton. The intervening mud (or sparry calcite) sheaths are between 1 and 2 mm thick, and may, in some specimens be repeated up to three times between successive latilaminae. Each mud sheath was implied by GALLOWAY and ST. JEAN (1961) to have been deposited during a nongrowing season. The problem remains how the mud sheaths formed as a relatively uniform layer on near-vertical slopes of the cylindrical skeleton. Possibly, with seasonal changes, there was partial mortality of the skeleton, allowing sediment-trapping, binding, or precipitating activities of microbial communities to preferentially mantle and then trap the mud on the outer surface before the next growing season allowed a new latilamina to be secreted over the mud layer. A study of better preserved specimens is needed to check whether the mud sheaths show evidence of mat or biofilm (microbial) communities or not.

The clathrodictyid genera *Labechiina* and *Neobeatricea* and problematic genera *Clavidictyon* and *Shirdagopora* also show predominantly columnar growth.

Digitate

The term digitate is preferred to describe shapes with subparallel, multibranched columns (Fig. 274; Fig. 297). Other related terms are multicolumnar, multiprotuberant, fingerlike, stachyodiform, and fasciculate, but these are all now regarded as obsolete. The term stachyodiform was restricted by COCKBAIN (1984, p. 9) to more robust-type



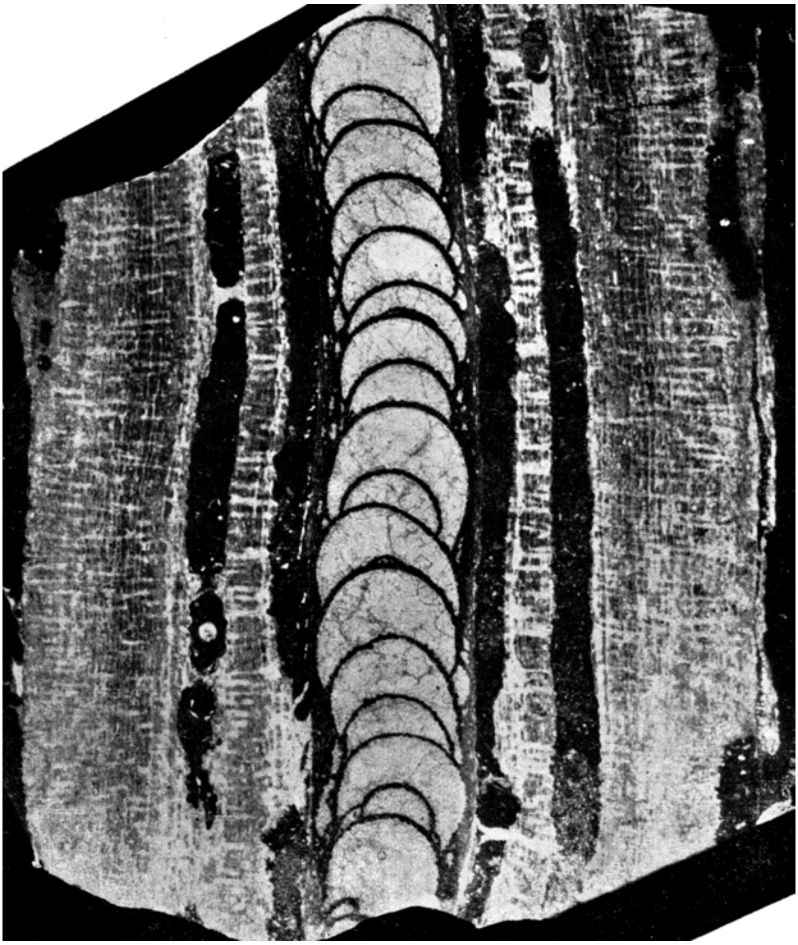


FIG. 296. *(For explanation, see facing page).*

branching forms (diameters greater than 5 mm) but was only applied to species of a few genera besides *Stachyodes*. Some of the examples of protuberant, multicolumnar growth reported by KERSHAW (1998, p. 522, fig. 7) represent digitate growth forms as described here.

Digitate shapes are characteristically erect, subparallel, close-spaced, fingerlike, or occasionally expanding-upward columns, off a laminar base. Comparatively smooth and nonenveloping types are commonly associated. In its simplest representation, the shape is depicted by the syringostromatid species *Syringostroma cylindricum* FAGERSTROM (BJERSTEDT & FELDMAN, 1985, fig. 6, 8), appearing as a number of discrete columns spreading upward and outward from a laminar base (Fig. 297.1). BJERSTEDT and FELDMAN (1985) identified a succession of growth forms (and taxa) through a 1.5-m-thick, upward-shoaling, Middle Devonian biohermal package that developed on a stabilized bindstone substrate at Kelleys Island, Ohio. The digitate growth form (they called it fasciculate) of *S. cylindricum* appeared in the topmost part of the bioherm, therefore representing the end member of their laminar→domical→irregular→digitate series of shapes.

Species of the syringostromatid genus *Parallelostroma,* from the Silurian of Podolia, also exhibit digitate growth (see BOGOYAVLENSKAYA, 1982b, p. 120, fig. 7; 1984, fig. 1c). The growth form of *P. kudrinzyensis* (RIABININ) has a very characteristic digitate shape arising off a laminar base (Fig. 297.2), and *P. typicum* (ROSEN)

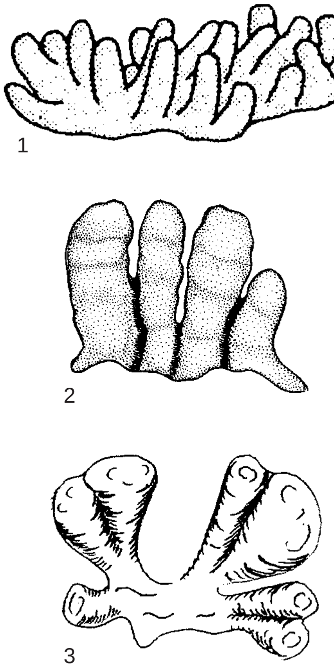


FIG. 297. Examples of stromatoporoids that exhibit digitate growth forms; *1,* schematic representation of digitate form of *Syringostroma cylindricum* FAGERSTROM, north lakeshore site of the stromatoporoid bioherm, lower Eifelian, Middle Devonian, uppermost Lucas Dolostone, uppermost Detroit River Group, Kelleys Island, Ohio, United States (adapted from Bjerstedt & Feldmann, 1985, see parts of fig. 6, 8, no scale); *2,* drawing of digitate morphotype of species *Parallelostroma kudrinzyensis* (RIABININ), of subparallel columns raised above a broad laminar base, Pridoli, upper Silurian, Skal'skiy horizon, Podolia, Ukraine, ×2.5 (adapted from Bogoyavlenskaya, 1984, fig. 1v, ×5); *3,* field sketch of digitate shape of *Parallelostroma typicum* (ROSEN), though it is not typical in being more openly radiating and with branches expanding outward; Ludlow, upper Silurian, Malinovetskiy horizon, Podolia (adapted from Bogoyavlenskaya, 1982b, fig. 7, no scale).

FIG. 296. Columnar labechiid *Cryptophragmus antiquatus* RAYMOND from beds equivalent to upper Pamelia formation, north of Aylmer, Quebec, Canada, in thin sections illustrating the specimen, with a narrow axial column of superposed, horseshoe-shaped cyst plates, and a broad lateral zone of very fine, outwardly radiating pillars intersecting very closely spaced rows of long, low cyst plates, as well as including three mud-filled (possibly in part sparry calcite) sheaths; *1,* transverse section of the columnar specimen showing main features of three mud-filled sheaths—two in inner part of the lateral zone and a third close to outer margin of this specimen. These concentrically arranged sheaths maintain parallel relationships with adjacent, much finer pillar and cyst plate structures, they have similar thicknesses, and in a few places, they show breaks in continuity of mud fill where a few, much thicker, hour-glass–shaped structures (possibly composed of sparry calcite) occur, ×4 (Raymond, 1914, pl. 2,*1*); *2,* longitudinal section exhibits similar features, although the outermost mud sheath appears to have a very limited continuity along length of specimen, ×4 (Raymond, 1914, pl. 2,*2*).

shows radiating columns that progressively expand away from the laminar base, with more vertically directed columns being larger than the more laterally directed columns (Fig. 297.3). Many species of the genus *Stachyodes* (family Stachyoditidae) exhibit a digitate growth form, and the skeletons usually have robust branch diameters of 5 mm or more. However, a few have a more completely integrated meshwork of columns and laminar elements, as shown in *S. fasciculata* HEINRICH from Middle Devonian reef complexes of Bergisches Land, Germany, and *S. costulata* LECOMPTE from the Upper Devonian Canning Basin reef complexes (COCKBAIN, 1984; WOOD, 2000). *S. fasciculata* has a laminar base and a more continuous laminar fusion of adjacent columns (STEARN, 1966, p. 118; see also p. 503), while *S. costulata* (Fig. 298, and see Fig. 304) exhibits more irregularly reticulated meshes of lateral bridges interlinking adjacent columns. These stachyodid species exhibiting combinations of the two morphologies (digitate and laminar) were capable of exhibiting more flexible growth strategies (perhaps they were less constrained by their genetic make up). It appears that the subparallel columnar growth was maintained during episodes of sediment swamping, and development of lateral offsets (laminar growth) relates to the pauses between the periodic influxes of sediment. Where meshworks of interlinked lateral bridges are more complete, the growth form should be described as digitolaminar (previously named digitate by KERSHAW, 1998, fig. 7); see further discussion of Digitolaminar shapes, p. 454).

The species *S. costulata* also exhibits, at widely spaced intervals, acutely dichotomous branches (Fig. 298.4), which suggests an even greater plasticity of growth in the species. This branching type is a feature of the more exclusively dendroid forms (see below), but in *S. costulata,* the dividing branches remained acutely aligned because so little space existed between the subparallel columns of its skeletal growth, as compared with more typical, open branching, dendroid forms.

Dendroid

The term dendroid is maintained for shapes that are typically produced by erect, open-spreading, laterally free, arborescent branches (Fig. 274, Fig. 299.1), and may have a smooth exterior and nonenveloping habit. The branching is usually dichotomous (Fig. 299.2–299.4), but offsets having the appearance of lateral buds may also be present (Fig. 299.5). The dendroid, thicketlike clusters grew initially from attachments to small skeletal grains on soft substrates, apparently developing some stability as they sank into muddy substrates under their own weight (adopting a mud-sticking strategy; BRETT, 1991, p. 330). Other terms have been used to identify this growth form, but they should now be regarded as obsolete (e.g., ramose, arborescent, twiglike, amphiporiform). The term amphiporiform has been applied only to slender-branching, *Amphipora*-like fossils with stemlike branches, usually less than 5 mm in diameter (COCKBAIN, 1984, p. 9).

The presence of dendroid branching has been used taxonomically to recognize some stromatoporoid genera of the Labechiida, Stromatoporellida, and Amphiporida. In the labechiid family Aulaceratidae, for example, about half the genera (*Sinodictyon, Thamnobeatricea, Alleynodictyon, Pararosenella*) exhibit dendroid (dichotomous or lateral) branching forms (others show columnar shapes). Other genera that developed mainly dendroid growth forms are: *Dendrostroma* (family Stromatoporellidae), *Idiostroma* (family Idiostromatidae), *Amphipora, Clathrodictyella, Novitella,* and *Paramphipora* (order Amphiporida), and the problematic genus *Praeidiostroma,* but this latter has been interpreted as a growth variant of the clathrodictyid genus *Gerronostromaria* (NESTOR, 2011, p. 6; also see systematic description, p. 761).

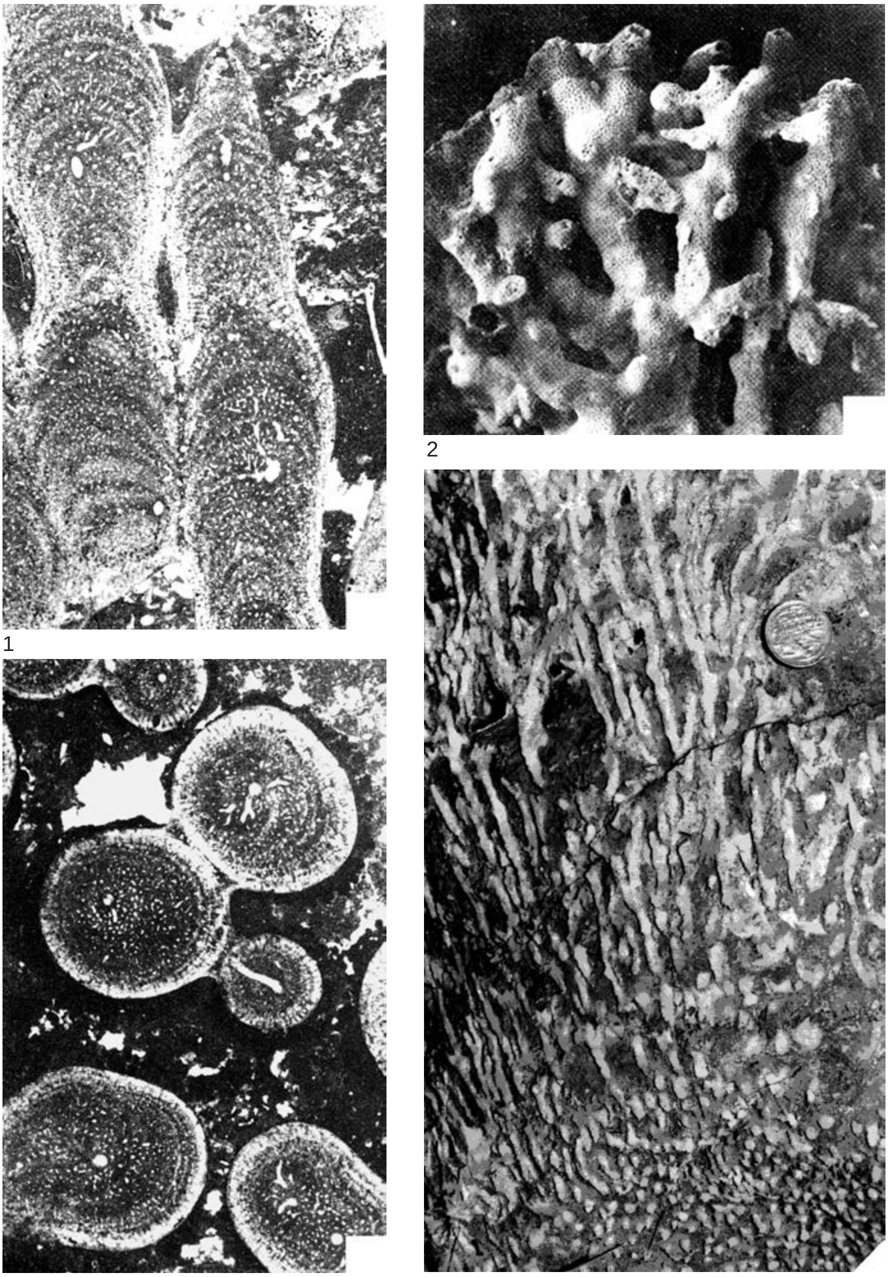


FIG. 298. Digitate shapes of *Stachyodes costulata* LECOMPTE, Frasnian, Upper Devonian, Canning Basin, Western Australia; *1,* longitudinal section, Pillara Limestone, Emanuel Range, fossil loc. no. NOB 33 (registered fossil no. GSWA F10625), ×3.2 (adapted from Cockbain, 1984, pl. 19A); *2,* general view of silicifed skeleton, Sadler Limestone, Emanuel Range Kudata Gap, fossil loc. no. NOB 32, showing dichotomous branching and lateral bridges (registered fossil no. GSWA F 7885), ×1.6 (adapted from Cockbain, 1984, pl. 19B); *3,* transverse section, Pillara Limestone, Emanuel Range, fossil loc. no. NOB 33 (registered fossil no. GSWA F10625), ×3.2 (adapted from Cockbain, 1984, pl. 19C); *4,* longitudinal section of a densely branching (digitate) thicket, Pillara Limestone, Baralama Spring; note also examples of dichotomous (dendroid) branching in middle upper part of figure, ×0.25 (adapted from Wood, 2000, pl. 3,*1*).

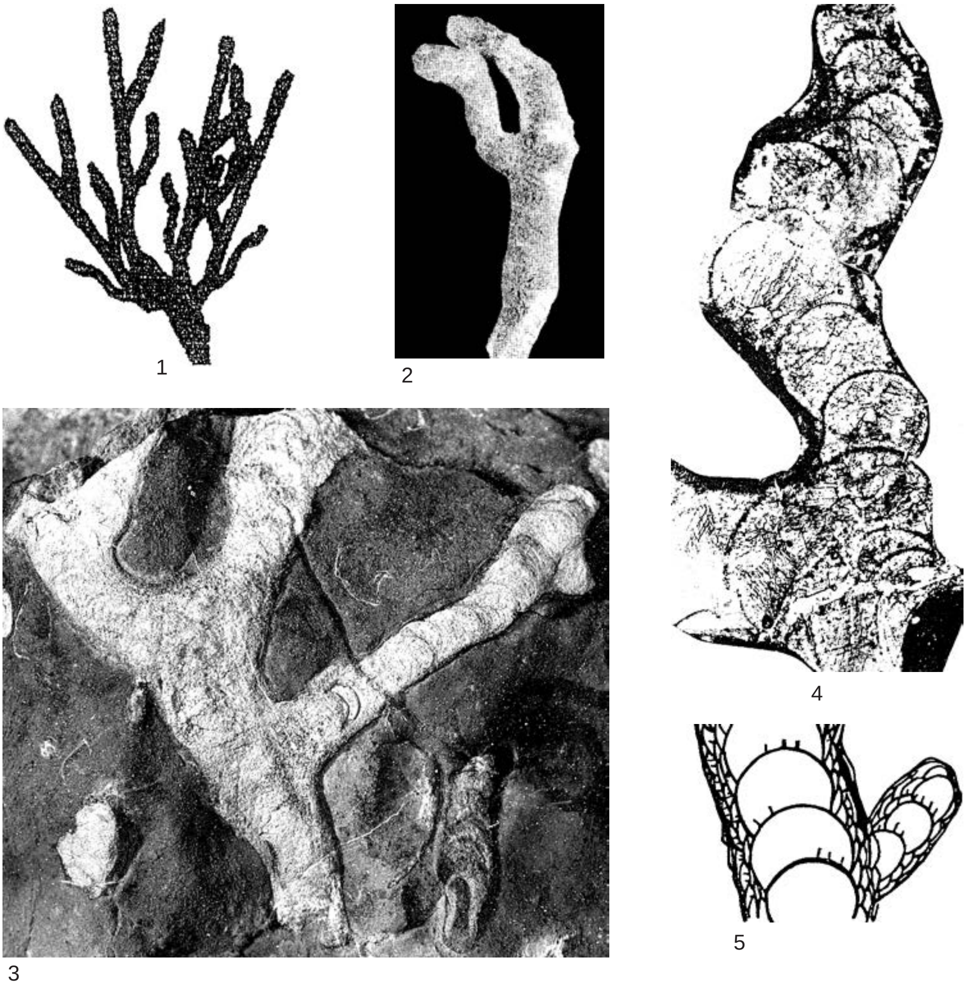


FIG. 299. Examples of branching, mainly dendroid-shaped stromatoporoids; *1,* hypothetical representation of skeleton of a slender, dendroid, amphiporid stromatoporoid (adapted from Kershaw & Brunton, 1999, fig. 3C); *2,* branching, silicified fragment of *Clavidictyon? sokolovi* (Riabinin), Hamra Formation, upper Ludlow, Burgsvik, Gotland, Sweden (loc. no 150), ×2 (Mori, 1970, pl. 22,*8)*; *3, Thamnobeatricea gouldi* Webby, Upper Ordovician, Sandbian, Gordon Group, Bubs Hill, Tasmania, showing typical lateral branching form, specimen no. UTGD90454, ×1 (Webby, 1991, fig. 16B); *4,* longitudinal section of incomplete, dichotomously branching specimen of *Pararosenella cylindrica* (Vassilyuk), Upper Devonian, Famennian, Donetsk Basin, Donbass, Ukraine, specimen no. 4, Sverdlovsk Mining Institute, ×5 (adapted from Bogoyavlenskaya, Vassilyuk, & Glebov, 1990, pl. 26,*1*); *5,* sketch showing a lateral branch (like a lateral bud) in a part of skeleton of *Pararosenella cylindrica;* incorrectly labelled as *Rosenella lissitzini* forma *cylindrica* Vassilyuk by Bogoyavlenskaya, Vassilyuk, & Glebov, 1990, p. 73 (adapted from Bogoyavlenskaya, Vassilyuk, & Glebov, 1990, fig. 7 *partim*).

COMBINATIONS

Digitolaminar

This composite shape comprises a complex, boxwork structure of laterally extensive, successive, platelike tiers (or floors) above a laminar base and separated to more coalescent, vertical, postlike columns (or lobes) that may be continuous or incomplete, the latter dependent on sediment-filled interruptions to vertical continuity (Fig. 274, Fig. 300–301, Fig.

315). The shape was termed digitate by Kershaw (1998, p. 520, fig. 7) and platy-multicolumnar by Wood (2000, p. 678), but the term digitate is inappropriate, because it exhibits the well-developed, laminar-shaped tiers, and the term platy-multicolumnar is not consistent with other basic descriptive shape terminology used here. Hence, the combined term digitolaminar is preferred to maintain conformity with the single laminar and digitate usages employed in this shape classification. The modern scleractinian coral, *Porites lichen* Dana, which is widely distributed in lagoons and reef slopes of the tropical Indo-Pacific from the Red Sea to Samoa, shows a strikingly similar growth form combination of laminar and digitate shapes (Fig. 300.1; see also Veron & Pichon, 1982, p. 43, fig. 61–62; and Veron, 1986, p. 228, fig. 3). The generalized digitolaminar shape is also exhibited within the growth form variations of the Silurian heliolitid coral, *Stelliporella parvistella* (Roemer) from Gotland and England (Young & Scrutton, 1991). This plastic species exhibits an extraordinarily wide range of growth forms (laminar, domical, bulbous to columnar, and branching), as well as alternations (or switches) between discrete units of laminar and digitate growth.

Examples of digitolaminar growth develop in a number of Paleozoic stromatoporoids. In *Ecclimadictyon stylotum* (Parks), the growth combination comprises successive growth units, each exhibiting a laminar tier from which a number of erect, bulbous to columnar lobes arise (Fig. 300.2–300.3). In the large, highly complex, composite growth form of *Actinostroma windjanicum* Cockbain, a boxwork structure develops from a centralized area of more or less parallel to slightly coalescent, vertical columns, and more laterally extensive, tiered, laminar outgrowths (Fig. 301, Fig. 304), as depicted by Wood (2000, p. 678, fig. 8–9). Another specimen identified by Riabinin (1953, p. 49, pl. 19, *1*) as *Stromatopora* n. sp., from the Silurian of Podolia, possibly another growth variant of *Parallelostroma typicum* (Rosen), also appears to show a digitolaminar phase of growth, with its broadly open, reticular form of lateral extensions and partially interconnected, postlike offshoots (Fig. 300.4). A digitolaminar habit also appears to be present in the specimens of *Stachyodes australe* described by Mistiaen (1991) and Lachkhem and Mistiaen (1994) that exhibit predominantly laminar crusts (Fig. 302), including the vertical to steeply inclined offshoots that may be preferably interpreted as representing columnar or chimneylike branches.

The units of growth that produced the composite digitolaminar shapes were probably capable of developing in two different ways, either: (1) the skeletal shapes were produced when marked changes in rates of sedimentation occurred, while both laminar and digitate types of growth were forming close to the substrate; or (2) the structures developed while rates of sediment influx were more uniform, with the laminar growth (with primary cavities) produced above the substrate, and the digitate growth close to the substrate. Consequently, the laminar part of the unit formed either on a substrate when sedimentation was reduced, or it was produced by lateral growth above the substrate, away from more continuous sediment influx on the sea floor. Presence of sparite cement beneath laminar growth portions of some lower Wenlock examples from Gotland suggest that primary cavities may have existed. The branching, digitate part of the growth, in contrast, probably formed near the substrate where moderate levels of sedimentary influx were maintained. These views are consistent with the suggestions made by Young and Scrutton (1991, p. 380–381) for the digitolaminar shapes displayed by the heliolitid coral *Stelliporella parvistella*. In their survey of a number of heliolitid corals, they noted that, whereas the others had marked genetic controls on their growth form variation, *S. parvistella* was a very plastic species that exhibited ecophenotypic responses, particularly to changes in the sedimentation rate. They

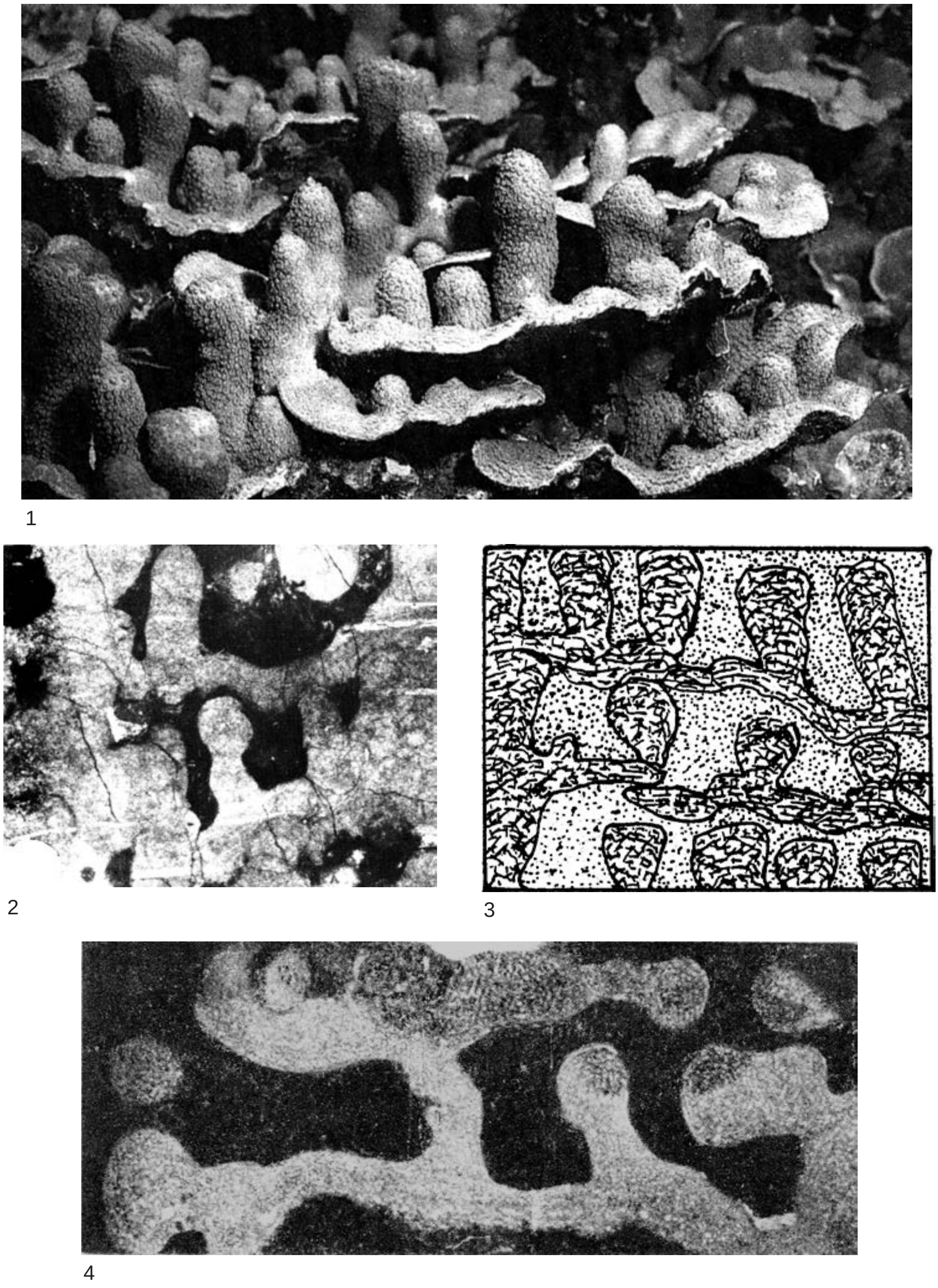


FIG. 300. Examples of Paleozoic digitolaminar stromatoporoids and a living scleractinian coral; *1,* digitolaminar-shaped skeleton of living, tropical, Indo-Pacific coral *Porites lichen* DANA (photo courtesy of Ron and Valerie Taylor, reproduced in Veron, 1986, p. 228, fig. 3); *2,* digitolaminar shape of skeleton of *Ecclimadictyon stylotum* (PARKS), Lake Aylmer Formation, upper Silurian, Marbleton area, southeastern part of Quebec Appalachians, Canada, ×2.8 (adapted from Hughson & Stearn, 1989, pl. 2L); *3,* thin section showing digitolaminar growth of *E. stylotum*

(Continued on facing page.)

commented: "A modest, nonlethal increase in sedimentation could stimulate branching (=digitate) growth," but growth returned "to tabular or domal (=laminar) form when sedimentation reverted to background rates" (YOUNG & SCRUTTON, 1991, p. 381). Similarly, WOOD (2000, p. 700) noted that digitolaminar forms were possibly "indicative of growth under stressed conditions, such as episodic siliciclastic-sediment input, and that episodic sediment swamping may have initiated the formation of elevated structures which provided escape from such a threat." However, some workers (e.g., C. W. STEARN, personal communication, September 2006) maintained that these rare, complex growth forms, with such regular, rhythmic, repetitions, must be genetically controlled.

Foliaceous

A few specimens of *Actinostroma* sp., from the Upper Devonian of the Canning Basin (Western Australia), were described by WOOD (2000, p. 680) as exhibiting an unusual, highly complex, "inferred, whorl-forming, foliaceous" shape (Fig. 303). WOOD (2000, fig. 18) reconstructed the growth form (Fig. 304; see the first of the four successive back-reef communities) as a large, elevated, free-standing shape, with a stacked, open, cuplike assembly of up to four, well-separated, thin, inwardly inclined, laminar layers or tiers (interpreted as parts of foliaceous whorls). The inferred shape was noted by WOOD as resembling the foliaceous growth form of the modern scleractinian coral, *Acropora palmata*.

Irregular (syn., massive *partim*)

This combination is not a geometrically distinct basic shape, and it is not easy to categorize, either by sampling whole specimens or, where this is not feasible because of their size, by accurately determining their three-dimensional form from oriented cross sections alone. Irregular shapes may vary in size from small to large, reaching sizes of more than a meter across and up to one meter in height. They commonly represent combinations of two or more basic growth forms, including the laminar, domical, bulbous, or even rarely, columnar forms (Fig. 274). The margins of skeletons are more often ragged than smooth. However, care must be taken when studying these irregular forms, because a good number prove to be composites of more than one growth form and may involve different species growing more or less contiguously with one another. The term irregular may sometimes be used with qualification to group shapes that cannot otherwise be accommodated into other main subdivisions, but adequate supplementary descriptions of the geometries and associations of these assigned forms should also be presented.

In some places, irregular shapes formed as *in situ* growths on hard substrates, where the stromatoporoid species encrusted irregular topographic highs of uneven rocky or reef areas or large skeletal objects. The irregular-shaped composites may have resulted from complex intergrowths of one, or more than one, stromatoporoid species or overgrowths of dead stromatoporoid surfaces, by the same or different encrusting stromatoporoid species. These shapes probably developed mainly in more turbulent conditions of the reef crest (STEARN, 1975b; BRAUN & others, 1994), though irregular combinations were capable of being formed in a variety of other environmental settings.

Irregular forms were also produced on unconsolidated substrates where skeletons, especially high-profile domical to bulbous

FIG. 300 *(Continued from facing page).*

(PARKS), with columnar lobes arising from successive laminar bases and intervening spaces surrounded by sediment (*dotted areas*), ×2.2 (adapted from Stearn, 1983a, fig. 6A); *4,* photograph of digitolaminar "*Stromatopora* sp." (probably a species of *Parallelostroma,* like *P. typicum*), Malinovetskiy horizon, upper Silurian, Ludlow, Zbruch River, Podolia, Ukraine; polished surface of specimen no. 105a in collection of O. I. Nikiforova, ×5 (adapted from Riabinin, 1953, pl. 19,*1*).

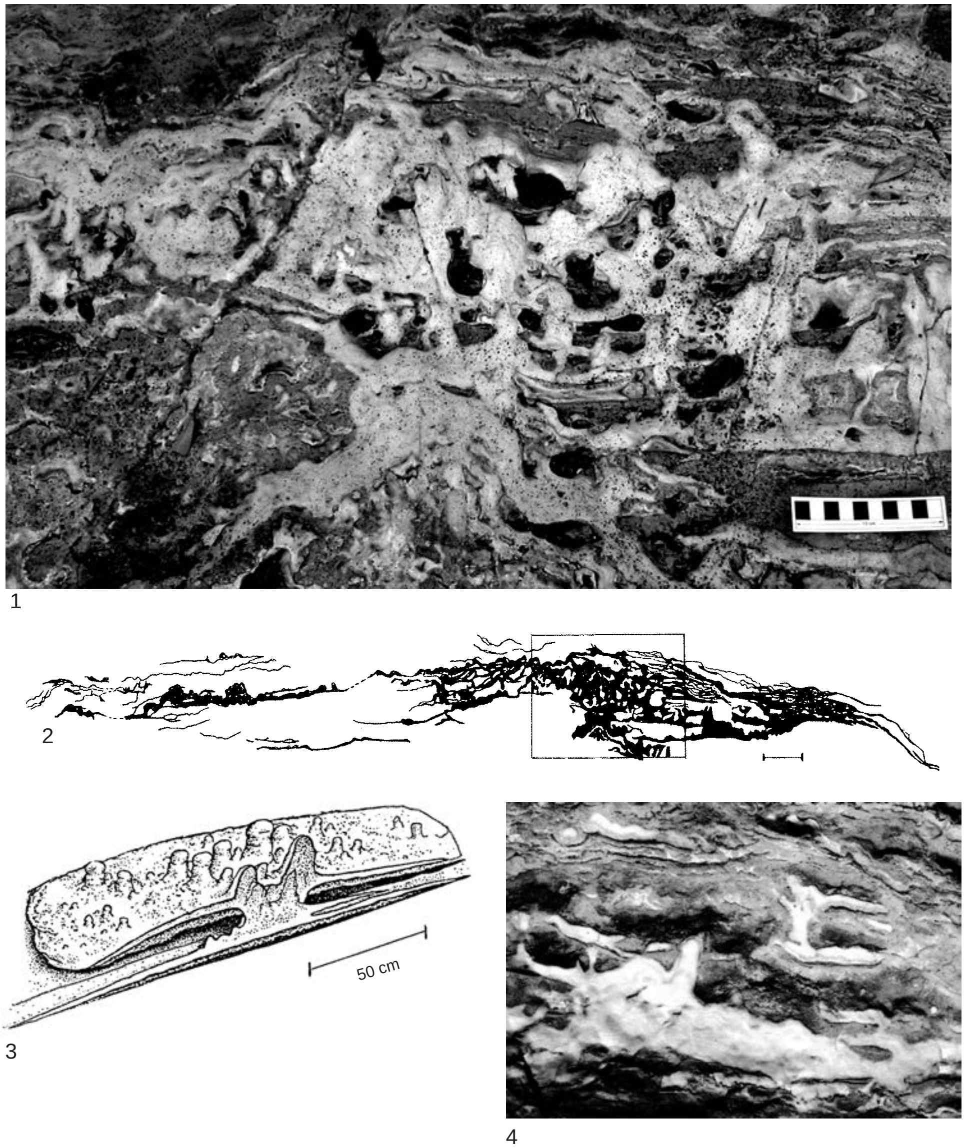


FIG. 301. Large, composite, digitolaminar stromatoporoid skeleton of *Actinostroma windjanicum* COCKBAIN, and other laminar stromatoporoid skeletons (possibly smaller specimens of the same species) with an incipient development of digitolaminar shape, Frasnian, Upper Devonian, Pillara Limestone (back reef facies), Windjana Gorge, Canning Basin, Western Australia; *1,* central columnar part of skeleton with extensive development of intersecting, stacked, lateral bridges (or domes) above substrate, leaving elevated undersurfaces as primary shelters or cavities available for encrusting *Shuguria*; scale bar, 10 cm (photograph courtesy of Rachel Wood; digitized photo IMG-0007); *2,* silhouette of very large, complete, digitolaminar-shaped skeleton of *A. windjanicum* from outcrop in gorge; note especially widely spread lateral outriggers (or plates), away from central part of specimen (*rectangular box*), shown in the outcrop photograph of view *1,* scale bar, 0.2 m (Wood, 2000, fig. 8B); *3,* reconstruction of the digitolaminar growth form based on the stromatoporoid *A. windjanicum* (Wood, 2000, fig. 9B; drawing courtesy of John Sibbick); *4,* other laminar skeletons may exhibit distinctive, columnar-shaped upgrowths off laminar bases; in a few places these upgrowths bear lateral offshoots, producing overall a rather rudimentary, digitolaminar shape, ×0.1 (Wood, 2000, fig. 15F).

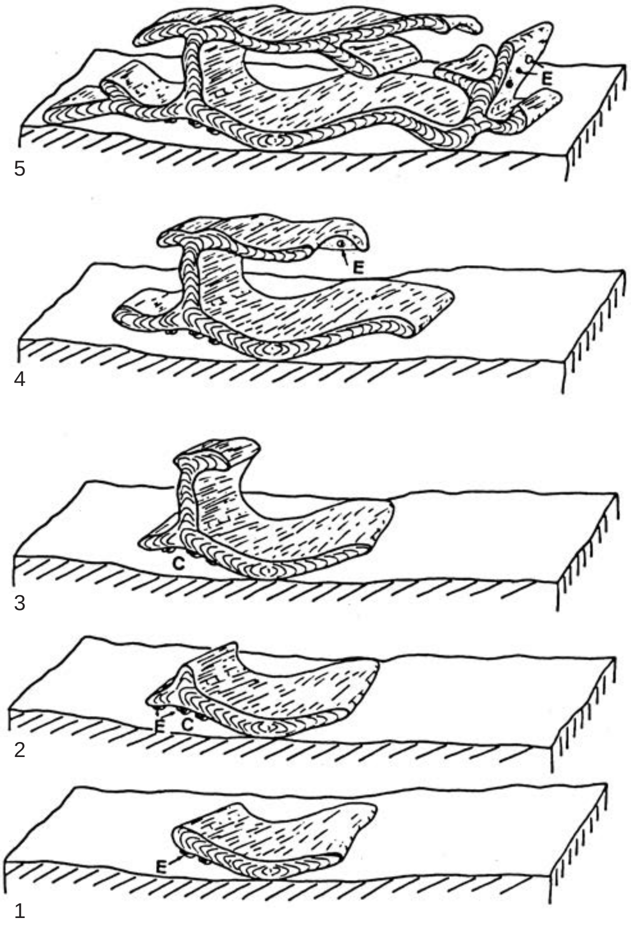


Fig. 302. Schematic representation of the morphology and five-stage growth development of *Stachyodes australe* (Wray). The sequence as interpreted by Lachkhem and Mistiaen (1994) comprises: (1) establishment as a free, recumbent, laminar sheet lying on the substrate, with a few cryptic organisms or so-called epizoans (*E*) becoming attached beneath a sheltered site; (2) initiation of vertical as well as continued lateral growth, with the sheltered site developing as a primary cavity (*C*) bearing a larger epizoan population; (3–4) extension of vertical growth and then lateral spread of an elevated outgrowth, with another sheltered site becoming available on its undersurface for colonization of cryptobionts (*E*); (5) continuation of the patterns of branching lateral, vertical, and oblique laminar growth, producing an anastomosing, wavy, sheetlike network, again with cryptobionts (*E*) colonizing some raised undersurfaces (Lachkhem & Mistiaen, 1994, fig. 4).

shapes, were affected by periodic current movements, causing them to be repeatedly tilted, rolled, and even, at times, partially fragmented, prior to successive resumptions of growth. Each disruptive event produced changes to the attitude of the skeleton, and hence a different orientation for the renewed growth. Sometimes thin layers of sediment were added during pauses between the renewed phases of growth, so in some cases, the regrowth could have included almost entirely ambitopic stromatoporoids (forms that largely occupied soft substrates). In other cases, a mixture of ambitopic and encrusting stromatoporoids may have been involved, even associations of different species. Consequently, shape analyses of skeletons that assumed irregularly shaped composites always need to be carried out with great care, and preferably in

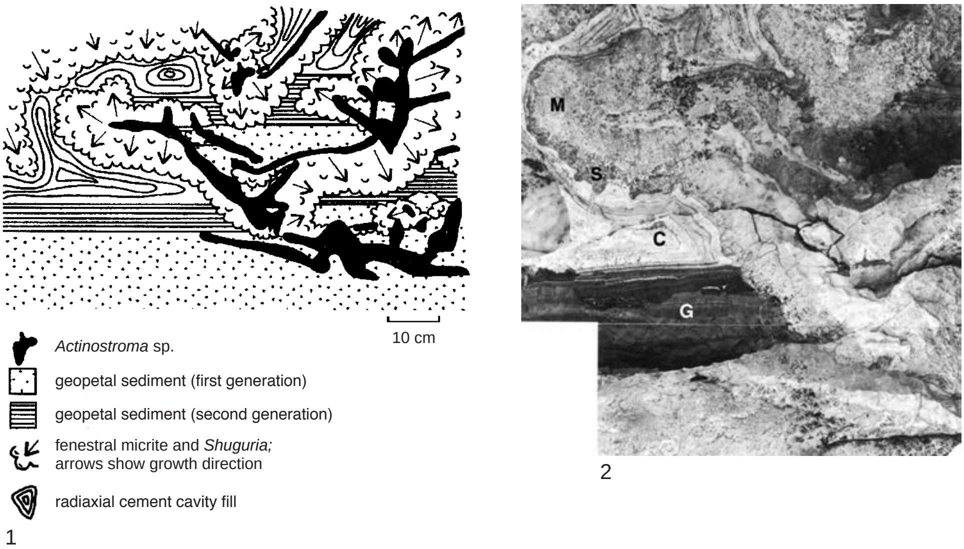


FIG. 303. Skeletal components for reconstructing the inferred foliaceous growth form of stromatoporoid *Actinostroma* sp., Frasnian, Upper Devonian, Pillara Limestone (back-reef facies), Windjana Gorge, Canning Basin, Western Australia, as shown in Figure 304.3 (Wood, 1999, fig. CS 3.5b); *1,* field tracing from a fallen block in gorge showing an incomplete skeleton of *Actinostroma* sp. It forms a complex, obliquely angled, open mesh of tierlike plates that WOOD (2000) infers to have been whorl-forming and foliaceous; lower surfaces of whorls were especially heavily encrusted by fenestral micrites and crusts or bushlike *Shuguria*, then one or two generations of geopetal sediment was added to remaining cavity spaces before final void-filling by banded calcite cements (adapted from Wood, 2000, part of fig. 11); *2,* longitudinal section through a series of stacked, whorl-like tiers (or plates) of the inferred foliaceous growth form of stromatoporoid *Actinostroma* sp. Note that the tiers or foliose plates are first encrusted by fenestral micrite (*M*), then by calcimicrobe *Shuguria* (*S*); large cavities that remain around plates are subsequently partly filled with dark-layered geopetal sedimentary rock (*G*) and the remaining void by banded radiaxial calcite cement (*C*), ×0.08 (Wood, 2000, fig. 12).

conjunction with the taxonomic identification of the species involved, based on their internal structures.

BJERSTEDT and FELDMANN (1985, p. 1044, fig. 6, 8) recognized an irregular shape as the penultimate member of their inferred stromatoporoid growth series through the upward-shoaling bioherm from the Middle Devonian of Ohio. The irregular shapes occur in the upper part of the bioherm, between the low domical (broadly hemispherical) and digitate (fasciculate) members of their growth series. The irregular skeletal shape is a more or less broadly arching combination of partly fused and partly anastomosing low, domical shapes, with sediment-filled, wedgelike invaginations around the margins of the structure. BJERSTEDT and FELDMANN (1985) considered the irregularity of these tongues of sediment to suggest that early growth became interrupted by episodes of high turbidity and/or influxes of sediment, and that some initial substrate instability may have existed as well, such as differential settling or sinking of skeletons into the soft substrate. Then, as the developing irregular skeletons grew upward, they may have become more prone to turbulence in the water column and hence developed more pronounced upper-surface irregularities in the skeletons.

SUBSTRATE PREFERENCES

Growth of the calcareous skeleton apparently commenced from a single point, where the larva first settled (STEARN, 1983a), then spread laterally in all directions across the substrate, unless constrained by proximity to other living organisms or influxes of sedi-

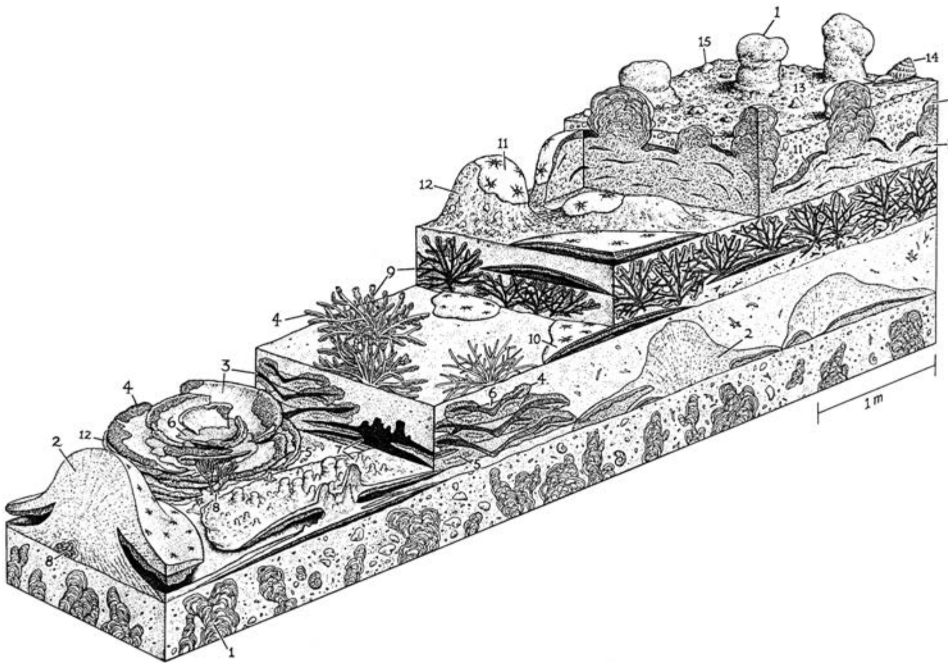


FIG. 304. Reconstruction of four successive back-reef communities based on data, Frasnian, Late Devonian, Windjana Gorge, Canning Basin, Western Australia: *1,* columnar growths of calcimicrobe *Rothpletzella*; *2,* domical stromatoporoid (*Actinostroma papillosum*); *3,* inferred whorl-forming foliaceous stromatoporoid (*Actinostroma* sp.); *4,* calcimicrobe *Shuguria*; *5,* fibrous cement; *6,* geopetal sediment; *7,* digitolaminar stromatoporoid (*Actinostroma windjanicum*); *8,* crinoids; *9,* digitate to dendroid stromatoporoid (*Stachyodes costulata*); *10,* laminar stromatoporoid (?*Hermatostroma* spp.); *11,* encrusting stromatoporoid (?*Clathocoilona spissa*); *12,* inferred microbialite; *13,* coarse siliciclastic sediment; *14,* gastropods; *15,* oncolites (Wood, 1999, fig. CS 3.5b; drawing courtesy of John Sibbick).

ment. A view favored by some workers (e.g., FAGERSTROM in KERSHAW, 1998, p. 514) is that stromatoporoids preferred to colonize dead skeletal material rather then living organisms. A wide range of hard and soft substrates were suitable, though in order to guarantee larval settlement, NESTOR (1984, p. 278) considered that the muds needed to be intermixed with at least 10% of skeletal grains to provide enough rigidity for settlement, and the more lithified the substrate, the better. According to NESTOR (1984), the most favorable hard-bottom sites were carbonate reefs, lithified sediments, and skeletal remains, but KERSHAW (1998, p. 513) has noted that the many examples of initial growth over soft substrates show little evidence of a hard object underlying the point of settlement. NICHOLSON (1886a, p. 27) referred to an initial attachment by "a narrow peduncle," but the structure has not been confirmed in Paleozoic stromatoporoids. BOGOYAVLENSKAYA's (1984, p. 7, fig. 1b) illustration of such a structure apparently belongs to a Mesozoic stromatoporoid (based on STEINER, 1932, p. 17). Stromatoporoids, like a wide range of other sedentary organisms (e.g., tabulate and rugose corals, certain brachiopod groups and bryozoans), as NICHOLSON (1886a) first recognized, adopted two different benthic lifestyles, depending on whether they occupied mainly hard or soft substrates (see also BRETT, 1991, p. 329). The terms used to differentiate between these lifestyles are: **ambitopic** (Latin, *ambo*, both; Greek, *topos*, place; see JAANUSSON, 1979a, p. 269–270), for organisms that were attached in early growth, but then lived essentially freely on unconsolidated substrates through their remaining life (Fig. 305.1–305.7), and

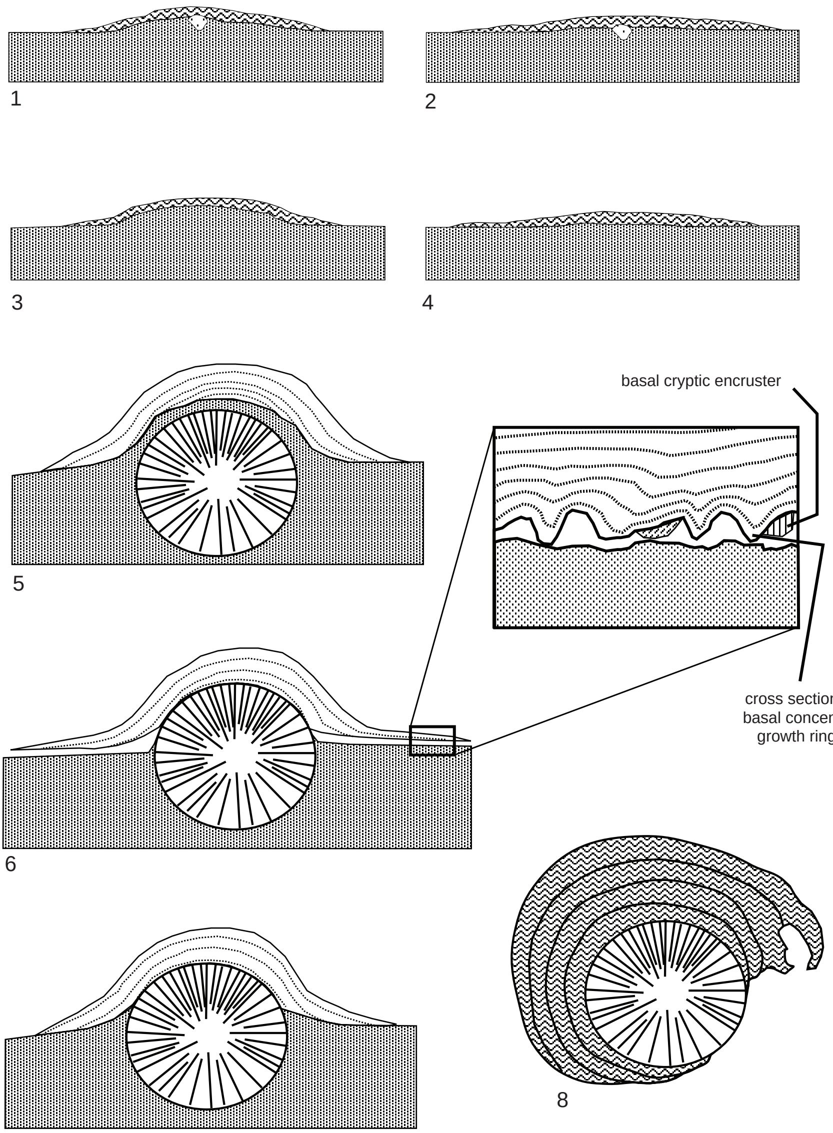


FIG. 305. Schematic representations of the likely range of interactions between stromatoporoids and the substrate during initial settlement of larvae and early skeletal growth, based on known examples of Paleozoic laminar, domical, and bulbous stromatoporoids. Identification of primary cavities is undoubted in Devonian stromatoporoids, but evidence remains equivocal for Ordovician and Silurian forms. *1–7,* ambitopic organisms, *8*, encrusting stromatoporoid; *1–2,* settlement on a small hard object, with and without a topographic high, then early growth spreading laterally over surrounding unconsolidated sediment; *3–4,* settlement on unconsolidated sediment, then early lateral spreading growth, with and without a topographic high (evidence of a tiny hard object for the initial larval settlement is lacking); *5,* establishment on a topographic high (possibly a large skeletal object) that has a thin layer of sediment draped over it; *6,* establishment directly on a hard skeletal object (no associated sediment), and then over the substrate, lateral outriggers develop, which have concentric growth rings on their undersurfaces, and small primary cavities form in spaces between rings (see details in enlargement); *7,* initiation occurs on a hard object and then lateral spread is over sediment without formation of primary cavities; *8,* initiation and subsequent growth is entirely encrusting over hard surface of a large bioclast (rugose coral) (adapted from Kershaw, 1998, fig. 5, and Kershaw, Wood, & Guo, 2006, fig. 1).

encrusting, for organisms that remained in occupation of hard substrates through most of their life (Fig. 305.8).

The majority of Paleozoic stromatoporoids seem to have adopted an ambitopic life habit during later stages of their growth, whereas only a relatively few of all the designated orders of the class have representatives that maintained encrusting habits through all stages of their growth history. In most cases, it is difficult to establish whether the encrusting lifestyle existed across the full range of the distribution of a species in time and place, but probably not. It seems likely that most species switched from encrusting to ambitopic life modes because of changing substrate characteristics, but they were probably controlled also, to a significant degree, by their inherited growth program. When the switch occurred during initial growth, the stromatoporoid is recognized as having an ambitopic lifestyle, but when the change occurred during later, more mature stages of growth, the stromatoporoid species should be regarded as having an encrusting mode of life. Though determinations of these changes tend to be somewhat arbitrary and conditional on the quality of preservation of whole skeletons, initial growth is usually taken to represent the first one, or perhaps two, recognizable sets of latilaminae at the base of the skeleton.

AMBITOPIC STROMATOPOROIDS

Most Paleozoic stromatoporoids grew like many tabulate corals, as almost completely free, unattached organisms on soft to partially consolidated substrates. As noted by JAANUSSON (1979a, p. 270), this contrasts with modern reef constructions that formed on hard substrates. For attachment of their free-living larvae, the stromatoporoid sponges probably required at least some small (or larger) skeletal grains, or reworked pieces of lithified mud, or microbial mat on the substrate, and then after initial settlement and metamorphosis as encrustations, they adapted through more mature stages of growth to a predominantly unattached, freely colonizing lifestyle over wide expanses of soft substrate (Fig. 305.1–305.2, 305.7).

A feature in some stromatoporoids is the broad, very thin, compact, concentrically wrinkled basal layer (Fig. 305.6, and see p. 468–474) and analogues in chaetetids and corals, that some authors (e.g., THAYER, 1975; BRETT, 1991) considered may have acted like a snowshoe. It maintained support for the stromatoporoid skeleton with its spread across a relatively large surface area of soft substrate, while also helping to stabilize the underlying substrate. However, this basal structure is rarely well preserved, and consequently remains poorly understood. Other skeletons do not appear to preserve any traces of a hard object for initial settlement, or the object is mantled by a thin layer of mud (Fig. 305.3–305.5), which may suggest these forms could grow directly on soft substrates without settling initially on hard objects (KERSHAW, 1998, p. 513), especially where there is some topographic expression. However, as alternatives: (1) the preserved hard objects may have been too small to be identified beneath the comparatively large skeletons, especially given how difficult whole specimens are to adequately sample and study; or (2) their absence may relate to the poor quality of preservation; perhaps the integrity of the hard objects was lost or destroyed due to differential compaction or selective dissolution (possibly originally aragonitic grains) along the interface between sediment and the overlying skeleton.

KERSHAW and BRUNTON (1999) recognized ambitopic stromatoporoids occupying a number of types of unconsolidated substrates, from calcareous sands to muds: (1) *Solenopora*-dominated, bank-type calcareous sands that, under steady current activity, caused low to high domical morphotypes to become partially buried; (2) cohesive, muddy substrates with associated flat-based laminar to low domical shapes that easily became displaced to other sites on the sea floor; (3) mixed mud and silt substrates that retained unbroken, *in situ* skeletons;

and (4) calcareous mudstone substrates that apparently became bioturbated, more consolidated (though possibly less cohesive), with associated columnar shapes that became broken. The bulk of these laminar to low domical stromatoporoids assisted very effectively in stabilizing extensive areas of unconsolidated substrate. This is supported by results of KERSHAW's (1998) modeling work on the effects of unattached stromatoporoid shapes in differing current velocities, across sand and mud substrates showing: (1) low domical stromatoporoids as relatively more stable than other forms; and (2) laminar to low domical shapes less susceptible than other forms to current scour and reorientation. The elevated shapes, especially those with smaller attachment bases (e.g., bulbous, columnar, and branching morphs), were more easily displaced on unconsolidated substrates. The large aulaceratid columnar shape, however, developed bulbous, ringlike, concretionary ballast at its base (CAMERON & COPPER, 1994), and this may have helped it sink under its own weight into the soft sediment, developing what BRETT (1991, p. 330) called a "mud-sticking" response.

Few attempts have been made to record substrate selectivity of stromatoporoid species, or to determine whether the stromatoporoid species of a particular assemblage maintained consistent relationships to the substrate types of a given habitat. Some writers (e.g., KERSHAW, 1998, p. 513) claimed that, in general, stromatoporoids did not apparently discriminate between specific substrates. However, in one detailed study of a Silurian assemblage of four species from Gotland, KERSHAW (1984) examined substrate relationships on a species-by-species basis and was able to show that preferential selection did exist. Three of the named species (*Densastroma pexisum, Pachystroma hesslandi, Eostromatopora impexa)* grew predominantly freely as ambitopic forms on the calcareous muddy substrate (though not exclusively, as they could facultatively encrust when settling by chance on a hard substrate). The other species, *Petridiostroma simplex* (NESTOR) is dominantly an encruster; see previous mention of this species (p. 436–437, Fig. 290–291) and discussion below (Fig. 306–307). The shapes of all four species varied from laminar to high domical, but the three ambitopic, muddy substrate-dominant species include forms with ragged margins and overall larger sizes, compared with *P. simplex,* which has a comparatively smooth margin and smaller size.

ENCRUSTING STROMATOPOROIDS

In the Gotland assemblage, *Petridiostroma simplex* encrusted the skeletons of other stromatoporoids, as well some corals, gastropods, and orthoconic nautiloids (MORI, 1968, p. 57, pl. IV,*2–3*, pl. 19,*1;* KERSHAW, 1984, pl. 20,*3–4,6,8;* cf. NESTOR, 1999a, p. 118, fig. 1b). It seems therefore, that this species had a different genetic inheritance from the other three ambitopic, muddy substrate-dominant species mentioned immediately above. *P. simplex* maintained a different growth program preferentially, but not exclusively, through its more mature stages of growth, favoring an encrusting mode of life, as a predominantly attached stromatoporoid (Fig. 290–291, Fig. 306). *P. simplex* is one of a number of stromatoporoid species that adopted a mainly encrusting mode of life, in preference to the majority of species that exhibited an ambitopic mode of life. It represented a minor, encrusting component (usually one or two species) of the level-bottom assemblage dominated by the ambitopic stromatoporoids that grew on the unconsolidated (muddy) substrate, but where there were also localized patches of skeletal debris representing a firm substrate for encrusters.

The encrusting stromatoporoids were more commonly represented in assemblages that occupied reef habitats (especially bioherms) with higher energy conditions and greater access to coarse skeletal debris, such as larger skeletal objects, intraclasts, or perhaps rigidly, microbially bound and/ or cemented (early lithified) pavements for their settlement and continued fixosessile growth. Some had no difficulty growing around vertically oriented solitary rugose corals (Kershaw, 1998, p. 514, fig. 5B), or overgrowing large gastropod or nautiloid shells (e.g., Fig. 308.2). It is not easy to prove whether stromatoporoids interacted in competitive, confrontational strategies with other living organisms on these hard substrates, or whether the successive overgrowths occurred dominantly as postmortem events over dead skeletal debris (Kershaw, 1998, p. 514; Fagerstrom & others, 2000, p. 10). Examples of repeated encrustations of different stromatoporoid genera (and species) are well known; see the specimen illustrated by St. Jean (1971, p. 1408, fig. 25), where species of three genera (*Stromatopora, Stromatoporella, Clathrocoilona*) took part in forming a multilayered composite of seven, successive, overgrowing laminar crusts.

Another multiple encrustation depicted by Nestor (1984, p. 268, fig. 1) includes stromatoporoids, a bryozoan, and a heliolitid coral, the stromatoporoid component, *Eostromatopora impexa,* being overgrown by *Clathrodictyon delicatulum* (in part directly encrusting and in part overgrowing a thin sediment tongue), and *C. delicatulum,* then substantially encrusted by *Petridiostroma simplex* (Fig. 307). This specimen is instructive because it emphasizes the need for caution in interpreting substrate contacts. Sometimes a thin layer of unconsolidated sediment may accumulate on the hard surface of the underlying stromatoporoid prior to the next overgrowth, so this overgrowing stromatoporoid may be ambitopic rather than an encrusting form. In the case of *C. delicatulum,* however, the growth was mixed, initially encrusting a hard substrate, then once established, it switched to an ambitopic mode and spread laterally over the unconsolidated substrate (see also Kershaw, 1998, p. 514, fig. 5A). Scrutton (1997, p. 180) reported similar examples of thin sediment layers occupying intergrowth relationships between successive tabulate coral colonies.

Many of the species of the Devonian stromatoporellid genus *Clathrocoilona* have been recognized as adopting an encrusting-type lifestyle, species such as *C. spissa, abeona, crassitexta lemisca, obliterata*, and *saginata* (Lecompte, 1951 in 1951–1952; Zukalova, 1971; Cockbain, 1984; Mistiaen, 1985; Cook, 1999). Some show striking examples of overgrowth relationships with other stromatoporoids (Fig. 308.1), rugose, and tabulate corals (Lecompte, 1951 in 1951–1952, pl. 27,*3–4,* pl. 28,*4;* St. Jean, 1971, fig. 23; Zukalova, 1971, pl. 14), and occasionally large nautiloid specimens (Cook & Wade, 1997). Cook and Wade (1997, p. 81) claimed that the growth of *C. spissa* "commenced and flourished while (the cyrtoconic) nautiloids were in an upright living position." The sheathlike overgrowth was apparently thickest along the ventral margin (Fig. 308.2) and thinner inside its open coil. Encumbered by this encrustation, it is unlikely that the nautiloid *Diademoceras submamillatum* (Whiteaves) could have been capable of more than limited motion above the substrate. These nautiloids are of variable heights (102 to 180 mm) and diameters (35 to 90 mm). Growth interruption surfaces within the stromatoporoid skeleton indicate repositioning of the nautiloid on the substrate. A thin section illustrated by Cook and Wade (1997, fig. 4B) shows a 12-mm-thick laminar encrustation of *C. spissa* on the ventral surface of the nautiloid. Wood (2000, p. 695, fig. 18) referred to domical or laminar stromatoporoids, most notably, *C. spissa,* that encrusted a community of moundlike structures (fenestral micrites that are inferred to be microbialites) in the Upper Devonian (Frasnian) reef flat and back reef settings of the Canning Basin (Fig. 304). These sheetlike, encrusting, stromatoporoid skeletons may be more than 1 m across and up to 80 mm thick. The species may also be intergrown within the mounds of fenestral micrites and with other stromatoporoids.

The lophiostromatid stromatoporoids are also of interest, being mainly an

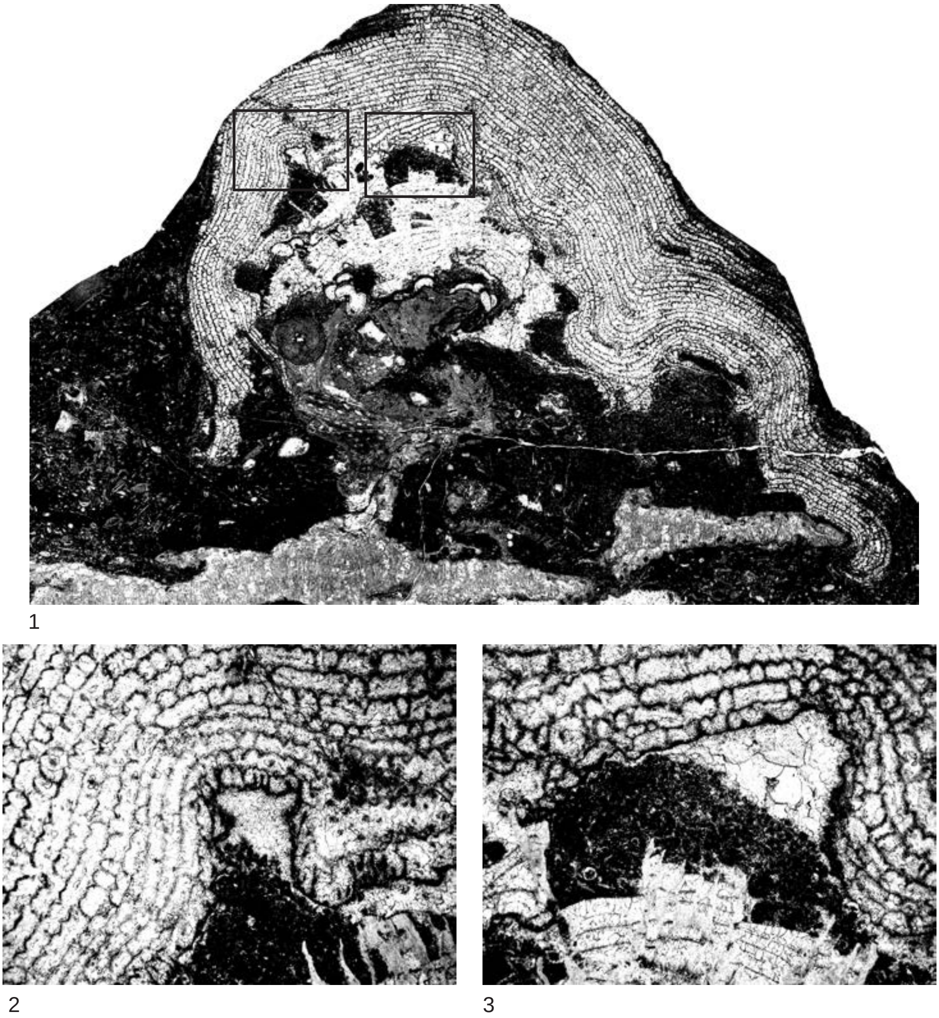


FIG. 306. Longitudinal thin section of another skeleton of stromatoporoid *Petridiostroma simplex* (NESTOR), Visby Formation, Gotland, Sweden, sample ST46; Ireviken 3; *1,* specimen grew as an irregularly undulating, laminar to low domical skeleton centered on a ball-like cluster of organisms, including a probable heliolitid coral colony (light colored at the top), calcimicrobes, a crinoid ossicle, and other bioclastic debris, as well as some sedimentary rock that is peloidal; *left and right boxes* are enlarged views 2 and 3, respectively, ×2.5; *2–3,* two enlarged areas at contact between *P. simplex* and underlying coral exhibit cavities with geopetal and calcite spar infills. It is uncertain whether cavities were primary or secondary; orientation of geopetal structures suggests whole skeleton of *P. simplex* may have been rotated clockwise about 45 degrees after initial burial, ×6 (adapted from Kershaw, Wood, & Guo, 2006, fig. 5).

encrusting group (WEBBY in STEARN & others, 1999). Only two genera (*Lophiostroma* and *Dermatostroma*) are assigned to the group. The type and best-known species of *Lophiostroma*, *L. schmidtii*, occurs in the Ludlow of various parts of Europe, notably Gotland, Estonia, and possibly Podolia (Ukraine) (NESTOR, 1966a; MORI, 1970; BOGOYAVLENSKAYA, 1984). In Gotland and Estonia, the skeletons of *L. schmidtii* are typically encrusting, laminar to low domical, and may form rather complex intergrowth associations with other stromatoporoids, tabulate corals, bryozoans, and calcareous algae (Nestor, 1984; Kershaw, 1990). They occur in reef habitats (e.g., biostromes), where larger skeletal remains or lithified sediments are available for overgrowth. According to Mori (1970, p. 143), individuals usually avoided marly bottoms, that is, they only exceptionally colonized soft substrates. On Gotland, the species size ranges vary from 9 mm to 0.5 m across and from 1 to 40 mm in thickness (Mori, 1970, p. 141).

Other occurrences of the same or a similar species of *Lophiostroma* from the biohermal deposits of the Malinovetskiy horizon in Podolia (Bogoyavlenskaya, 1982b, 1984) exhibit a markedly different skeletal shape, being composed of laterally extensive, composite growth in thin, splayed, or imbricated, anastomosing, laminar sheets (Fig. 283.2), with individual crusts up to 2 m across and 50 to 60 mm thick. Episodic sedimentation apparently played a significant part in the development of these anastomosing crusts. Initial growth may have encrusted a lithified substrate or associated skeletal objects, but then, following successive influxes of sediment, the stromatoporoid developed the free living, lateral-spreading, anastomosing, laminar growth form, that is, the species switched to an ambitopic (free-living) lifestyle over unconsolidated substrates. The successive interactions involved: (1) the organism first rejuvenating from small, surviving, less-elevated crusts after swamping with sediment and in places accompanying erosion; and then (2) rapid lateral spread to form a new laminar crust over all areas of the recently accumulated soft sediment and former substrate, acting to effectively stabilize and seal off these extensive areas beneath the laminar crust, which for a time represented a new sea floor. The switch from a more characteristic encrusting life habit of *L. schmidtii*, as seen in the Gotland and Estonian occurrences, to an ambitopic, anastomosing Podolian skeleton, seems to suggest that the species had a more plastic or flexible growth program than may have been suspected from study of Gotland and Estonian specimens alone. However, alternatively, Bogoyavlenskaya (1984, fig. 2c) incorrectly identified the large anastomosing specimens from Podolia as belonging to *L. schmidtii*. The specimens may, instead, belong to a different species of *Lophiostroma*, possibly *L. smotrischiense,* which was reported previously by Riabinin (1953) from the same stratigraphic interval (Malinovetskiy horizon). Further work is required to resolve the taxonomic status of these East European species. The other lophiostromatid genus is *Dermatostroma*. It only comprises a few species, and virtually all are small encrusting stromatoporoids that overgrew other organisms. For example, the Late Ordovician species *D. papillatum* encrusts the brachiopod *Hebertella,* and *D. scabrum* overgrows the bryozoan *Escharopora pavonia* (see Galloway, 1957; Galloway & St. Jean, 1961).

The following genera (including representatives of all the Paleozoic stromatoporoid

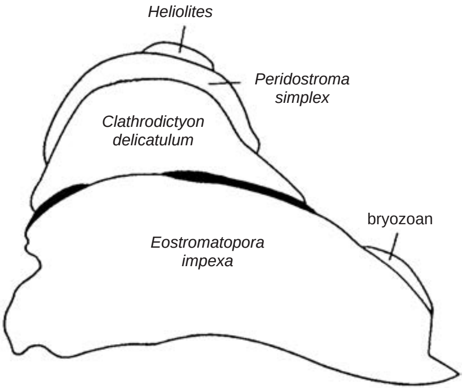


Fig. 307. Schematic longitudinal section of multiple encrustation of three different stromatoporoid species, a bryozoan, and a heliolitid coral, Jaani Stage, Wenlock, Suuriku, Estonia; of the three species, *Eostromatopora impexa* (Nestor*)* is overgrown by *Clathrodictyon delicatulum* Nestor, but much of the contact is separated by a thin layer of fine-grained sedimentary rock, suggesting it may be ambitopic, whereas *Petridiostroma simplex* completely overgrew *C. delicatulum,* supporting its predominantly encrusting role (adapted from Nestor, 1984, fig. 1).

1

2

FIG. 308. Examples of stromatoporoid *Clathrocoilona spissa* (LECOMPTE) that encrusted other stromatoporoids and large organisms such as nautiloids; this species seems to encrust other organisms directly without intervening layers of fine-grained sedimentary material; *1,* longitudinal thin section of a latilaminate specimen of *C. spissa* that encrusts discordantly the underlying latilaminate species of *Actinostroma;* from a paratype of the type species, specimen no. 7174, Givetian, Surice 51e, Dinant Basin, Belgium, ×3 (adapted from Lecompte, 1951 in 1952–1952, pl. 27,*4*); *2,* longitudinal thin section of specimen of laminar stromatoporoid *Clathrocoilona spissa* (LECOMPTE) encrusting the ventral side of nautiloid *Diademoceras submamillatum* (WHITEAVES); note the nautiloid also shows septa and part of the siphuncle; Papilio Formation, Middle Devonian, Storm Dam, Broken River area, northern Queensland, Australia; photo in negative relief, ×2.4 (adapted from Cook & Wade, 1997, fig. 4B).

orders) have been identified as having one or more encrusting stromatoporoid species.

Labechiida: *Cystistroma, Cystostroma, Labechia, Labechiella, Stratodictyon, Lophiostroma, Dermatostroma*
Clathrodictyida: *Atelodictyon, Clathrodictyon, Ecclimadictyon, Gerronostromaria, Hammatostroma, Plexodictyon*
Actinostromatida: *Plectostroma*
Stromatoporellida: *Clathrocoilina, Hermatostroma, Stictostroma, Stromatoporella, Synthetostroma, Trupetostroma*
Stromatoporida: *Ferestromatopora, Salairella, Stromatopora, Taleastroma*
Syringostromatida*: Habrostroma, Parallelostroma*
Amphiporida*: Euryamphipora*

The labechiids, clathrodictyids, stromatoporellids, and stromatoporids have proportionally greater numbers of encrusting species than the other groups. At present, it is only possible to speculate on the possible reasons for these different patterns. By analogy with the epitheca of some corals (SCRUTTON, 1998), the basal layer seems to be less commonly preserved in encrusting stromatoporoids, perhaps allowing them to more readily, opportunistically, overgrow other skeletal organisms on hard substrates (see further discussion of the basal layer below). The ambitopic stromatoporoids, on the other hand, may have needed to secrete a basal layer in order to seal off their undersurfaces from the deleterious effects of normal seawater (CLARK, 1976), or from being contaminated by small sedimentary particles or attacked by organisms associated with the substrate (STEARN, 1983a). However, some of the stromatoporoids that grew across finer muddy substrates do not preserve a basal layer either.

BASAL LAYER

The term **basal layer** was proposed by RIDING (1974b, p. 572) to represent the structurally modified basal part of a single skeletal crust of stromatoporoid *Stachyodes australe* (WRAY). It was previously interpreted as a crustose alga, named *Keega,* by Wray (1967). The layer normally overlies the sediment (or a cavity) directly, is usually less than 4 mm thick, and is composed of arcuate laminae and microlaminae as well as subhorizontal canals. In other stromatoporoids, the basal layer may be represented by initial growth over the substrate by skeletons that may exhibit latilaminae or not; the term does not apply to renewed (successive) growth within latilaminae. It only includes the start of growth in nonlaminate and latilaminate skeletons over areas of new (mainly unconsolidated) substrate, not the resumptions of growth within latilaminate skeletons, which are the basal phases of Stearn (1989a); see Glossary (p. 401) and Internal Morphology (p. 513–515).

Riding (1974b) did not regard the basal layer based on *S. australe* as strictly comparable to the thin, dense, wrinkled epithecal structure of Galloway (1957), but he did acknowledge that basal layers were present in other stromatoporoids, and Cockbain (1984) extended the list to a variety of typical laminar to domical stromatoporoids, including those with latilaminate skeletons. The basal layer is more typically a much thinner (less than 1 mm thick), compact skeletal structure, but it may occasionally develop thicker, irregularly reticulated or cystose structures above the dense basal surface, as in a few forms like *S. australe*. Both Riding (1974b) and Cockbain (1984) adopted the term basal layer in preference to epitheca and suggested it may have been an adaptation that aided rapid lateral spread of stromatoporoids (mainly ambitopic forms) across unconsolidated substrates.

Cockbain (1984) also recognized that a silicified specimen of *Actinostroma papillosum* with preservation of a recognizable basal layer had concentric wrinkles on its undersurface, this feature being long reported as associated with the basal layer. Whether the basal layer became well developed or not depended largely on variables such as the nature of the substrate and rate of spreading growth (Cockbain, 1984, p. 12). Kershaw (1998, p. 515) also preferred the use of the term basal layer, as it is a neutral term with no cnidarian connotations.

Nevertheless, many sponge workers have continued, in some cases, perhaps uncritically, to refer to the initial growth layer of stromatoporoids, and other hypercalcified sponges, as an epitheca, using Edwards and Haime's (1848, p. 46) long-established cnidarian term for Paleozoic stromatoporoids (see Rosen, 1867, p. 32; Nicholson, 1886a, p. 58; Stearn & others, 1999, p. 6), for Mesozoic stromatoporoids (see Wood, 1987, p. 87), and for those studying living hypercalcified sponge taxa (see Hartman, 1983, p. 121; Boury-Esnault & Rützler, 1997, p. 36, fig. 203). Stearn (1983b, p. 144–145) noted that stromatoporoids exhibit a "distinct epitheca . . . like that found in tabulate corals" and referred to the irregular basal structures as enclosing voids that had spread laterally along the substrate. Stearn (1983b, p. 145) added that these "epithecae" are rarely visible "in stromatoporoids enclosed in carbonate sediment but are conspicuous in stromatoporoids that weather free from argillaceous limestones and calcareous shales."

Two North American stromatoporoid workers (Galloway, 1957; Galloway & St. Jean, 1957; St. Jean, 1971, 1986), preferred the term peritheca to epitheca, although peritheca also has the drawback of an earlier use in coral terminology (Hill, 1935). Galloway (1957, p. 387) referred to stromatoporoid specimens that grew on a substrate of clay or lime mud, producing a less than one millimeter thick "wrinkled, thin, compact, lower layer." This was a finer and denser structure than the normal overlying skeletal elements, but he also noted some cases where the basal structure consisted of cyst plates. Galloway and St. Jean (1957, p. 45) additionally recorded occasional foreign bodies called protocoenostea, also interpreted as a part of the peritheca. Stearn's (1983b, p. 145) enclosing voids appear to be analogous to the spaces associated with Galloway's (1957, p.

387) cyst plates, and contrast markedly with the regular, laminated structures of mature (normal) phases of growth. St. Jean (1971, 1986), in his use of the term peritheca, emphasized its varied form, and (1971, fig. 34) added renewed growth between successive latilaminae as perithecal structures. Use of the term peritheca should now be discontinued.

In its original context as a term for cnidarians, epitheca represented a thin, calcareous skeletal structure (or investment) surrounding a corallite laterally, as an extension of the basal plate (Hill, 1935; Moore, Hill, & Wells, 1956). The structure may have a similar development in hypercalcified sponges, being related to initial primary growth of the basal surface of the rigid calcareous skeleton by incremental outward (lateral) spreading over the substrate, sometimes with concentrically wrinkled surfaces that have been represented as growth ridges. These latter may have sealed off the living parts of the mantling sponge from seawater, sedimentary particles, and/or boring organisms associated with the substrate, as in stromatoporoids. But in other hypercalcified sponge groups (e.g., living demosponges, such as *Ceratoporella, Acanthochaetetes, Astrosclera,* and *Calcifibrospongia*), where the living part of the sponge and its edge zone become raised well above the substrate, the epitheca is associated with lateral surfaces. Where these living forms exhibit a thin, compact epithecal layer, with concentric ridges resembling growth lines on lateral surfaces, Hartman and Goreau (1972, p. 135) and Hartman (1983, p. 121) have compared this structure to similar features in scleractinian corals. Though precise data are lacking on the structure and mode of formation of the epitheca, in extant hypercalcified sponges, it is currently regarded as a secondary structure (J. Vacelet, personal communication, 2007), not an initial primary growth layer, as in fossil representatives such as the stromatoporoids and chaetetids.

According to Wood (1998, p. 154), the epitheca (including holotheca) limited the ability of mid- to late Paleozoic tabulate corals to encrust, except for a few taxa (e.g., *Alveolites, Aulopora*) that opportunistically encrusted other skeletal metazoans. Similarly, she noted that most stromatoporoids did not settle actively on hard substrates, except for a few encrusting-type stromatoporoids that were capable of overgrowing repeatedly other large skeletal metazoans (tabulates and bryozoans). Wood (1998, p. 154), in consequence, considered it difficult to envisage that such stromatoporoids could have lived in "the highly turbulent, surf zone that reef corals and coralline algae occupy today," because they lacked the means to achieve "secure and permanent attachment to a hard substrate...." However, it is likely, judging from the record of abundant, large stromatoporoids in megabreccias derived from the Upper Devonian (Frasnian) reef margins of western Canada (Mountjoy, 1967; Srivastava, Stearn, & Mountjoy, 1972; Cook & others, 1972) that stromatoporoids did have a dominant role in building wave-resistant structures into the zone of turbulence, like counterparts in the modern reef.

Both the basal layer (or epitheca) of hypercalcified sponges and the epitheca of corals appear to have played pivotal roles in facilitating the initiation of calcification in the skeleton. Clark (1976) has proposed that for corals, based mainly on the work of Barnes (1972), the first stages of epithecal growth were confined within an envelope (fold or lappet) of soft tissue at the margins of the skeleton, preventing exposure to the surrounding seawater. In chaetetids, this similar thin, sheetlike epithecal growth is now termed a basal layer, and it is compositionally organic rich (R. R. West, personal communication, 2006; see p. 35, 43, Fig. 29, and also p. 88–89). The basal layer grew chiefly as a support for the rest of the skeleton, and as a barrier to seawater and extraneous small objects on its basal and/or perimeter sides.

In addition, archaeocyath workers (Debrenne & Zhuravlev, 1992b, p. 59; Debrenne, Zhuravlev, & Kruse, 2002, p. 1690, fig. 1–2) have also abandoned use of the term epitheca in favor of a new term, radicatus, and they regard this structure as a secondary growth layer (see Glossary, p. 397–416, and General Features of Archaeocyatha, p. 845–922).

Kershaw, Wood, and Guo (2006), in their study of stromatoporoids from level-bottom muddy substrates from the mid-Silurian Visby Formation of Gotland, concluded that the basal layer was not clearly differentiated from overlying laminae of the skeleton and no epithecal-type structures were found. Two main types of basal surface were depicted: smooth and corrugated (Fig. 305). The smooth growth developed initially on a topographic high formed by a bioclast (shell fragment) that had already been mantled by partially consolidated mud, and then spread laterally with no apparent disturbance to adjacent muds, perhaps because these too had already started to lithify (Fig. 305.5, 305.7, 309.1). Growth of this smooth type may be disrupted by periodic influxes of sediment, as shown in Figure 309.1. The corrugated growth type extended laterally, forming a concentrically arranged pattern of ridges and grooves, with the grooves sometimes interpreted as small-scale primary cavities Fig. 305.6). The ridge-and-groove structure is considered to have formed by the growing edge of the stromatoporoid pushing soft sediment into wavelike ridges as it grew, then it became well settled on the substrate as skeletal mass increased (Fig. 309.2–309.3, Fig. 310). A variant of the corrugated growth type also developed where episodic sedimentation interrupted its continuity of growth, producing intertonguing sediment wedges. In a longitudinal section across the corrugated basal surface of one specimen (Fig. 290.2), there is no evidence that an independent basal layer formed, though there are a number of downward-trending prolongations of the basal surface, including the first one or two laminae, that may be interpreted as representing an initial basal layer. However, a clearly defined basal layer is not that often differentiated, either because the structure is not preserved, or it never became secreted originally, as in some level-bottom muddy substrate occurrences (see Kershaw, Wood, & Guo, 2006).

Attempts to characterize early stages of skeletal development as ontogeny of the stromatoporoid organism, in terms of phylogeny, have not been successful (Galloway, 1957; Bogoyavlenskaya, 1984). Galloway (1957, p. 392), for example, found that the structurally modified initial growth in his skeletons preserved in limestones was "nearly always lost in freeing the specimens from the matrix," and he was equally unsuccessful in preparing specimens to show the initial growth of skeletons preserved in shale, probably because of weathering processes. Bogoyavlenskaya's (1984) efforts to demonstrate that the initial growth represented the first part of an ontogenetic (or astrogenetic) succession were similarly in vain. Stearn (1983a, 1989a, p. 46), in referring to the different growth changes through the skeleton, concluded that they were not part of an ontogenetic succession.

Stearn (1986, 1989a, p. 46) proposed a process-oriented approach to the study of variability of skeletal growth in stromatoporoids, employing phase changes, rather than using the more conventional basic descriptions of alternations in internal structures. He referred to rhythmic structural changes as units of growth that replaced each other on a number of occasions during the developmental (=growth) history of the skeleton. The successive phase changes were subdivided into basal, spacing, and terminal phases (Stearn & others, 1999; see also Internal Morphology, p. 511–515). He applied the term basal phase to initial growth, as well as to restarts of growth at bases of successive latilaminae within the stromatoporoid skeleton (Stearn, 1989a, p. 47); though no examples of characteristic units of growth representing a basal phase have been described. Here we prefer

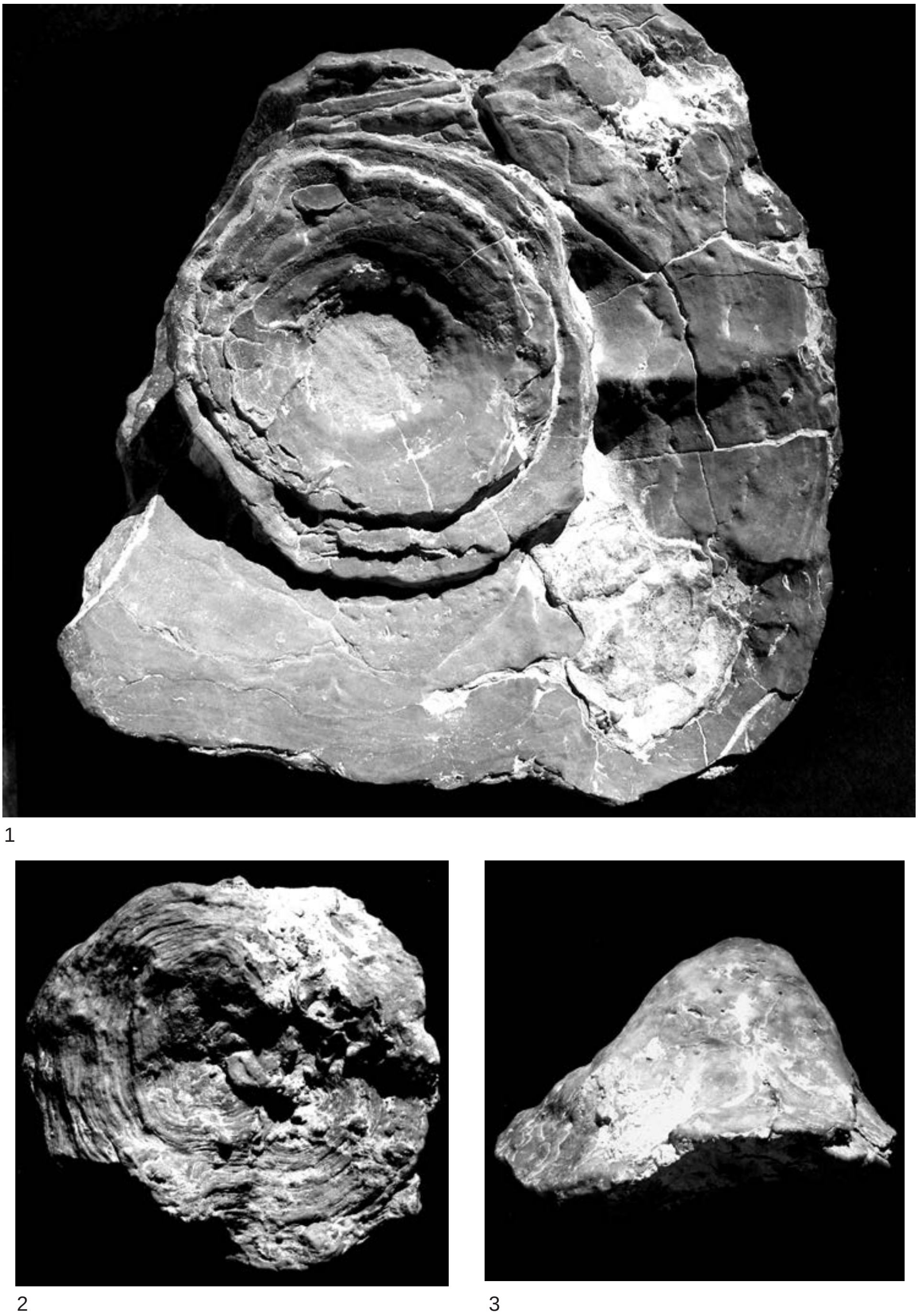


Fig. 309. *(For explanation, see facing page).*

to view the basal phase as more conceptual and interpretative than focused on the basic description of a skeletal structure. The feature (basal layer) developed as a product during the initial (basal) phase of growth, but no strictly comparable feature appears to accompany restarts of growth of successive latilaminae.

The basal layer of Paleozoic stromatoporoids remains inadequately known; a more intensive approach to the study of this structure is needed across main taxonomic groups, substrate types, lifestyles, and preservation states (for example, in response to processes such as differential compaction, dissolution and replacement, pressure solution, and weathering) and, as well, to a better understanding of its relationships to cavity spaces (see p. 475–480). As currently understood, the basal layer (syn., epitheca, peritheca) of Paleozoic stromatoporoids is a structurally modified unit, either a very thin, dense or compact, wrinkled layer representing the basal growth surface, or a composite layered interval comprising both the thin, dense layer and one or more, somewhat disordered, rows of small, irregular, cystlike plates, with sometimes even a few associated inclusions (though some of these are probably foreign bodies, like the protocoenostea of GALLOWAY & ST. JEAN, 1957, p. 45).

Where the stromatoporoid basal layer grew over the substrate, it sometimes developed broad concentric wrinkles on its undersurface. These may be: (1) related to the lateral growing edge pushing soft sediment into waves; or (2) they may have developed where each successive layer (laminae) at the base slightly overgrew the preceding layer along its lateral edge, producing a similar concentric pattern across the base; or (3) due to a more pronounced pattern of concentric rings, which sometimes developed between such layers when episodic sedimentation intervened (KERSHAW, WOOD, & GUO, 2006). These wrinkled basal surfaces have not been noted specifically at the bases of resumptions of internal growth in latilaminate skeletons, nor recorded apparently from the bases of encrusting-type stromatoporoids. The basal layer encompasses all the structural elements associated with the basal surface that rest on the substrate, as well as bases of upraised lateral outgrowths above the substrate, prior to the start of more orderly, layered, normal growth of the mature skeleton, irrespective of whether the skeleton is latilaminate or not. It may be concluded that basal layers are important in helping stromatoporoids colonize soft substrates by acting to seal off their bases (and sides) from entry of seawater, sedimentary particles, and invading organisms, both from underlying surfaces and from the adjacent water column.

FIG. 309. Views of the bases of typical domical stromatoporoids, Silurian, Gotland, Sweden; *1,* smooth basal surfaces beneath a ragged, domical, stromatoporoid skeleton, Hemse Group, Ludlow, Snoder, AMF.134348; specimen apparently commenced its growth on a topographic high and continued, successively, after each growth interruption to maintain its concave base. Consequently, overall the slightly curved to flattened surfaces are gently tilted outward; outer areas also show a few widely spaced, gentle undulations (or radial folds). The exposed smooth surfaces possibly formed from initial growth after each growth interruption over unconsolidated sediment and appear to be equivalent internally to bases of latilaminae; overall shape of skeleton is high domical but basically composed of superimposed, low, domical growths (in profile, it resembles ragged domical skeleton illustrated in middle to upper part of Figure 276.1), ×0.67 (Webby & Kershaw, 2011); *2–3,* basal and lateral views of a smooth, enveloping, high domical stromatoporoid, Visby Formation, Wenlock, Södra Backen; basal surface is gently undulating to flattened and has well-developed fine, concentric growth ridges, but the surface is not completely exposed because calcareous mudstones, encrusting organisms, and skeletal debris mask a few small areas of the surface, and growth ridges also in a few places have become a little weathered. Nevertheless, because an enveloping type of growth is represented, it appears that the successive latilaminae (and/or laminae) of the skeleton terminate on the basal surface, with their ends more or less coinciding with outer edges of successive concentric growth ridges, AMF. 134349, ×0.5 (Webby & Kershaw, 2011).

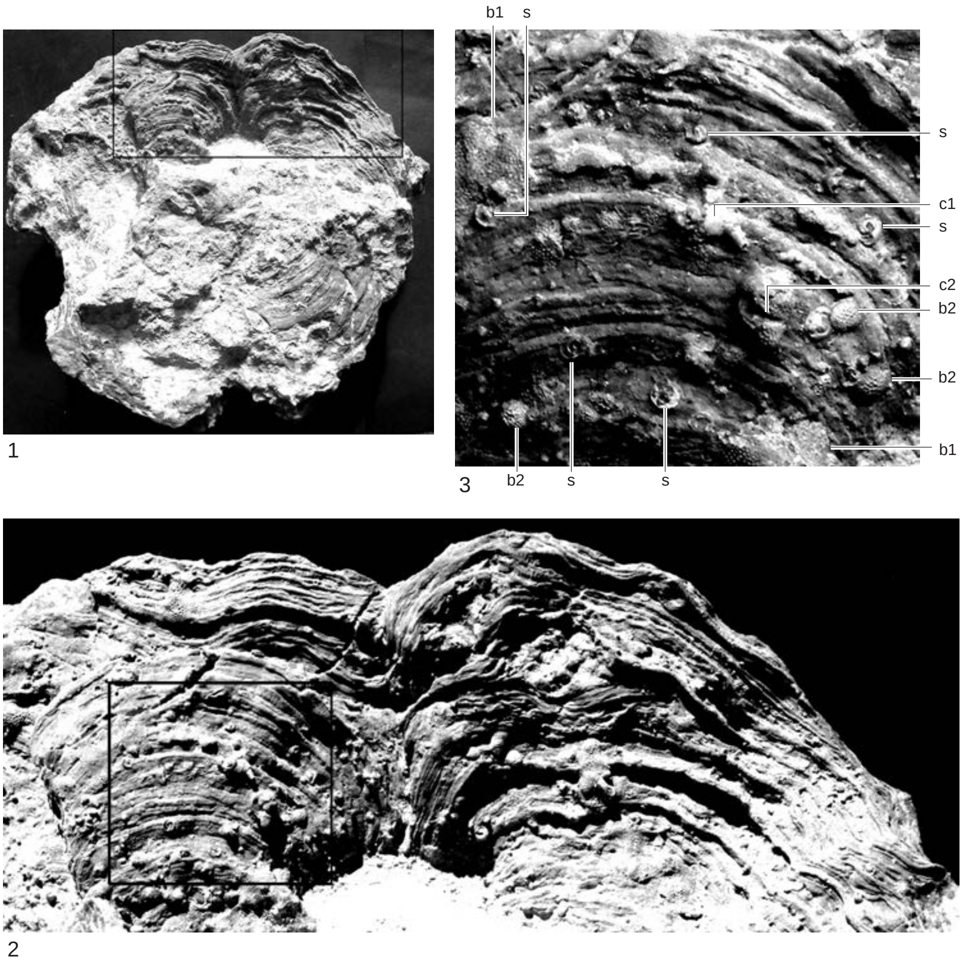


FIG. 310. Views at various magnifications of undersurface of a large, apparently coalescent, nonenveloping, low domical specimen of *Parallelostroma* sp., AMF.134350, Hamra Formation, Ludlow, Kättelviken, Gotland, Sweden. One area near margins of basal surface is well exposed and shows much detail of nature of corrugated base with growth rings and an abundance of cryptic encrusters (see views *2* and *3*); upper surface is undulose and encrusted by a variety of organisms, including small, solitary rugosans and auloporoid corals; *1,* general view of entire base of stromatoporoid *Parallelostroma* sp.; note the area outlined in black exhibits best-exposed part of basal surface (for more detail, see view *2*), ×0.25 (Webby & Kershaw, 2011); *2,* corrugated basal surface of part of skeleton of stromatoporoid *Parallelostroma* sp.; note the two convex-outward sets of concentric growth ridges and an intervening zone with a locally sinuous, concave-outward, as well as upwardly steplike trend of growth ridges that seems to have formed in response to coalescing growth of specimen; in outer part of zone, growth ridges have continuity through sinuous and steplike changes of direction—steplike rise is from right to left; basal growth ridges appear to equate with distal ends of successive latilaminae (and/or laminae) within skeleton; a large number of cryptic encrusters are scattered over corrugated basal surfaces; *box* shows location of part illustrated in view *3,* ×0.85 (Webby & Kershaw, 2011); *3,* enlargement depicting some of randomly distributed cryptic encrusters on corrugated underside of *Parallelostroma* sp. skeleton; they are completely randomly distributed over the corrugated basal surface; they did not preferentially occupy narrow groovelike hollows (potentially small primary occupation sites; see Fig. 305.6, inset) between individual growth ridges. Consequently, it is likely that these encrusters were predominantly colonizers of a large secondary shelter (overhang or cavity); *b1,* sheetlike bryozoan; *b2,* button-shaped bryozoan; *c1,* crinoid with articulated plates; *c2,* crinoid holdfast partly overgrown by bryozoan; *s, Spirorbis,* ×1.8 (Webby & Kershaw, 2011).

CAVITY SPACES

Spaces are mainly present beneath the stromatoporoid bases, but they may also develop at levels above initial bases, either representing secondary cavities that formed on lateral sides beneath ragged margins, in association with episodic sedimentation, or as primary cavities produced beneath upraised lateral outgrowths (or outriggers) of some larger, composite, Late Devonian growth forms (Wood, 1998, 2000; Kershaw, Wood, & Guo, 1999, 2006). Good examples of internal spar- and sediment-filled cavities may be associated with growth interruption surfaces (Fig. 276.3, Fig. 306; Stearn, 1983a, fig. 3; Young & Kershaw, 2005, pl. 1,*6*). The cavities exhibited in the illustrated specimen of the stromatoporoid *Pachystroma hesslandi* from the Silurian (Visby Formation) of Gotland (Fig. 276.3), are apparently, according to Kershaw, Wood, and Guo (2006, fig. 4), primary structures.

It is not always an easy matter to discriminate between primary and secondary cavities, because of the complex interactions between stromatoporoid growth and sedimentary processes (e.g., multiple phases of erosion and sedimentation). For example, a ragged, low domical skeleton may have lateral outgrowths, produced by intrinsic growth above the substrate, that create primary shelters for occupation of cryptobionts (Fig. 277.2). However, a similar ragged skeletal structure may result from growth that was interrupted by episodic sediment swamping of marginal areas of the skeleton (Fig. 277.1), and then much of the accumulated, unconsolidated sediment was removed in an erosive phase, leaving the successive lateral outgrowths exposed for colonization by crypt faunas (Fig. 277.2), but this time the reexposed sites are technically secondary shelters.

PRIMARY CAVITIES

Riding (1974b) first recognized that parts of the widely spreading laminar growth of Devonian stromatoporoids *Stachyodes australe* and ?*Hammatostroma* sp. maintained contact with the sediment surface, while other parts grew slightly upraised above the substrate, resulting in cavities that subsequently became cement filled (see illustrations in Riding, 1974b, pl. 86,*4;* Cockbain, 1984, pl. 18,*B,D*). Pratt (1989) also recognized small primary cavities in the Lower Devonian reefs of southwestern Ontario that include an encrusting, cryptic, tabulate coral and bryozoan fauna. These cavities were apparently produced by "sediment settling and shrinkage" (Pratt, 1989, p. 508).

Mistiaen (1991) and Lachkhem and Mistiaen (1994) also studied examples of *S. australe* from Upper Devonian (Frasnian) successions of the Ardennes (Belgium) and the Boulonnais area (northern France). These include specimens (up to 0.15 m long) with laminar sheets that grew across the substrate, as well as developing a broadly reticular mesh of vertical to inclined platy upgrowths that interconnect with raised, platelike, lateral outgrowths above the substrate. Lachkhem and Mistiaen (1994, fig. 4) identified primary cavities on the undersides of the platy upgrowths from the Ardennes that were colonized by cryptobionts, then infilled with early cement (Fig. 302). Skeletons were also recognized from the Boulonnais area (Mistiaen, 1991, fig. 2, pl. 1,*2*), indicating that *S. australe* may have been exposed to storm activity and overturning prior to final burial.

Wood (1998, 1999, fig. 6.20), studied a number of spectacularly large specimens of *Stachyodes australe* from marginal slope settings of the Upper Devonian Canning Basin, Western Australia, that were laminar platy crusts less than a centimeter thick and laterally extensive (up to 1.5 m wide); these thin sheets were typically upwardly arched over the substrate, forming primary cavities on their undersurfaces that were up to 0.3 m in height (Fig. 282, Fig. 284.1–284.2). This rather unique type of growth and cavity formation was largely a response to parts of the living surface becoming overwhelmed by episodic sedimentation, and this stimulated limited areas of living tissue at skeletal margins to produce upward-arching laminar growth, especially away from the sediment source. Cavities formed beneath the thin laminar outgrowths of stabilized stromatoporoids, with these crusts capable of extending laterally for distances of up to 1 m without coming into contact with the substrate (Wood, 1998, p. 154, 1999; Kershaw, Wood, & Guo, 2006). It was a novel and versatile solution for these stromatoporoids to maintain continued growth despite being subjected to periodic sedimentary events. The skeletons achieved a level of stability once the lateral outgrowths had developed into extensive dome-shaped crusts, affording them a measure of protection from further physical disturbance. These crusts then achieved some rigidity, as the underlying cavity spaces became infilled by geopetal sediment and early marine cement during burial processes (Fig. 282). There is little evidence of collapse of cavities associated with compaction or related breakage of the laminar crusts. The large primary framework cavities became attractive crypt dwelling sites. The invading cryptobionts included abundant pendent growths of the calcimicrobe *Shuguria,* a few lithistid sponges, spiny atrypid brachiopods, and ostracodes. Generations of geopetal sediment and pervasive early marine cements then filled the remaining space.

The widest range of complex laminar and domical stromatoporoids that developed primary cavities supporting cryptic communities, however, occurs in the back reef (and reef flat) settings of the Canning Basin (Wood, 2000). Three species of *Actinostroma*, a species attributed to *Hermatostroma*, and the digitate-dendroid growth form of *Stachyodes costulata,* were described by Wood (2000). Some of these are discussed briefly here (Fig. 304).

1. Skeletons of *Actinostroma papillosum* have a large size (up to 1 m in width and height), a broadly domical, ragged form, a tiered arrangement of tapering (up to 0.5 m long), lateral outgrowths from a centralized, updomed core, and open cavities on undersurfaces of the lateral outgrowths. These latter were colonized by the encrusting, cryptic growths of calcimicrobe *Shuguria* (Wood, 2000, p. 678; Fig. 292.1–292.4).

2. Spectacularly large (up to 5 m wide and 1.5 m high), complex, composite, digitolaminar *Actinostroma windjanicum* (Wood, 2000, fig. 9B) also developed shelters on undersides of extensive, vertically stacked, lateral outgrowths or plates (up to 1.5 m across and spaced 50 to 150 mm apart), and a digitate (or multicolumnar) central area, which was differentiated with partially separated to coalescent, lateral connecting bridges (sometimes looking like a boxwork structure). The lateral outgrowths arch upward or downward at distal ends, away from or toward the substrate, or form semi-enclosed overhangs, occupied by bushy growths of *Shuguria* above the substrate, which then became infilled with geopetal sediment and early cement (Fig. 301.1–301.4).

3. A third species of *Actinostroma* (*A.* sp.) interpreted by Wood (2000) as a complex, elevated, free-standing, foliaceous (whorl-forming to tiered) form (about 1 m in diameter and 0.6 m high), has successive encrustations of fenestral micrite (probably derived from microbes), cryptic *Shuguria,* and rare solitary rugosans that developed on the inclined foliose plates, especially undersurfaces, and intertier spaces, which were infilled by generations of geopetal sediment and early cement (Fig. 303.1–303.2).

4. Dense, multibranched (digitate to dendroid), monospecific thickets of *Stachyodes costulata*, up to 0.3 m in height (Fig. 298.1–298.4), have some interconnected, lateral bridges between adjacent branches. These latter may be preferentially encrusted on undersurfaces by *Shuguria* and contain geopetal structures as well (Wood, 2000).

In upper Silurian reefs of Gaspé Peninsula and the Brunswick area of eastern Canada, Bourque and Amyot (1989) and Noble

(1989) reported cavities partly or completely infilled by dark sedimentary rock and sparry calcite cement, that were, in places, occupied by cryptic faunas such as corals and brachiopods. However, these cavities occur beneath bases of laminar to irregularly low domical stromatoporoid skeletons that average only about 6 cm in diameter, and they are unusual in being separated by a thin, micritic, microbially generated veneer, rather than directly in contact with skeletal bases.

The primary cavities known to occur beneath stromatoporoid bases in the Silurian of Gotland are comparatively small structures (Kershaw, Wood, & Guo, 2006). They are represented by small, groovelike cavities that lie between concentric rings on the basal surfaces of stromatoporoids, occupying the muddy substrates of the Visby Formation. Additionally, Spjeldnaes (1975, fig. 2A–C) illustrated relationships between a Silurian bryozoan-dominated crypt fauna and the coral and stromatoporoid skeletons of the Visby Formation, that suggest cryptic bryozoans occupied undersurfaces of skeletal bases and sheltered sites beneath the tonguelike lateral outgrowths (or ragged margins) of possible domical stromatoporoids (Fig. 311.1–311.2). Spjeldnaes (1975) did not specifically identify whether his diagrammatic representations of domical growth forms were stromatoporoids or corals, but his figured outlines show typical stromatoporoid shapes. The bryozoans either colonized the sheltered (or shaded) undersurfaces areas as the vertically successive lateral outgrowths grew above the substrate, suggesting they were primary sites for settlement, or the successive outgrowths (or ragged margins) formed first during episodic buildup of sediments around the skeleton, and then much of the sediment was washed away, exposing the ragged margins with their undersurfaces available as secondary shelters. However, Kershaw, Wood, and Guo (2006) considered that encrusters rarely occupied the bases of ragged outgrowths in the Visby stromatoporoids, because their skeletons seldom prove to be unequivocally *in situ* forms.

SECONDARY CAVITIES

Other laminar to low domical stromatoporoids from the same deeper, level-bottom Visby Formation (Wenlock) of Gotland, have been recognized by Kershaw (1980, p. 327) as comparatively small (50 to 150 mm diameter), isolated skeletons that lived on a carbonate-mud substrate, "not a part of a reef framework where the growth could have created overhangs or primary cavities." These skeletons formed secondary cavities beneath their basal surfaces, either: (1) by partial scouring of unconsolidated deposits from beneath skeletal margins of *in situ* stromatoporoids; or (2) by movements of whole skeletons in storm-generated currents across an uneven substrate, and then imperfect (probably differential) settling to produce subskeletal voids for a cryptic community to colonize (Fig. 312). The sheltered undersides of stromatoporoid bases were occupied by a variety of encrusting bryozoans, tabulate corals, strophomenid brachiopods, and spirorbid worms.

Another Gotland survey (Nield, 1986) of encrusting faunas on mainly high domical upper Visby stromatoporoids noted a much greater diversity of encrusters on exposed apical and lateral surfaces than on skeletal bases (Fig. 288.1). The organisms on the bases were mainly spirorbid worms and tended to occur in clusters (Fig. 288.2), suggesting they may have been largely inhabitants of localized, short-lived (secondary) cavities. However, it is frequently impossible to differentiate unequivocally between the original cryptic, shade-loving (sciaphilic) forms of stromatoporoid bases and the open-surface encrusting forms that formed on the same bases after these high domical skeletons had been rolled and/or broken before final burial.

Another study of the diversity, distribution, and abundance of open-surface and cryptic encrusting communities of the upper Silurian (Ludlow) stromatoporoids from the

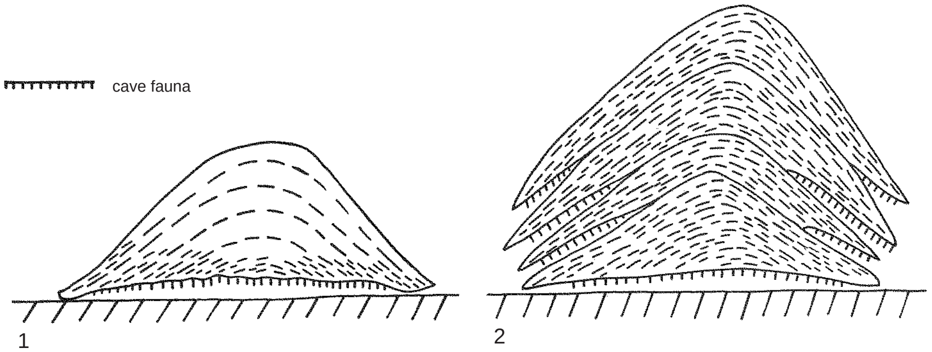


FIG. 311. A diagnostic cryptic bryozoan fauna was recognized by Spjeldnaes (1975) as encrusting undersurfaces of domical growth forms of stromatoporoid and coral bases in marly deposits of the Silurian Visby Formation, Gotland, Sweden; he noted the so-called cave fauna as occurring mainly on the bases of specimens but also, less commonly, beneath raised, lateral outriggers of certain specimens. Two of his diagrammatic longitudinal sections are reproduced here to show how Spjeldnaes (1975) conceived the distribution of the bryozoan cave fauna; *1,* smooth, enveloping, domical growth form that typically developed a slightly updomed basal surface over the substrate, leaving a cavity for colonization of the encrusting bryozoan cave dwellers (adapted from Spjeldnaes, 1975, fig. 2A); *2,* composed of four stacked, or superimposed, low domical growths, with the ragged margins resulting from lateral extensions (or outriggers) of the skeleton, like the example shown in Figure 277.2; cavity that formed beneath basal surface of this form was encrusted by cryptic organisms (mainly bryozoans), and sheltered undersurfaces of successive lateral outriggers were also colonized, although rather more spasmodically (adapted from Spjeldnaes, 1975, fig. 2B).

reef-forming Hamra Beds of Gotland was presented by Segars and Liddell (1988). The stromatoporoid skeletons were laminar, low domical, and bulbous shapes; more than 30 specimens were collected from the lower part of the reef where individuals were surrounded by argillaceous sediment. Segars and Liddell (1988) recorded the abundance and diversity of cryptic and open-surface encrusters on lower and upper surfaces, respectively. The encrusting organisms were also differentiated on whether they came from inner or outer parts of these surfaces. The encrusting (cryptic and open surface) bryozoans were the most diverse component (18 species), and occupied proportionally the most space. Other organisms included: spirorbids, crinoids, tabulates (cryptic and open surface), brachiopods (cryptic only), tentaculitids, and rugosans (open surface only).

Lower surfaces exhibit overall abundances of cryptobionts, declining from 18% coverage in outermost parts to 6.6% in the interiors, and the number of species dropping, correspondingly, from 29 to 18 toward the centers. Segars and Liddell (1988) suggested that the lower abundances in interiors relative to marginal areas reflected the lesser influences of currents scouring toward the center as compared to areas near the margins. Though they accepted Kershaw's (1980) proposal that the scouring process more commonly produced secondary cavities by removing sediment from areas in proximity of the margins, Segars and Liddell's (1988, fig. 4) reconstruction of the stromatoporoid specimen gave a misleading interpretation of how the cryptic colonization of the stromatoporoid skeletons took place (Fig. 313.1–313.2). They show a low domical stromatoporoid before death as almost completely undercut by secondary scouring processes, leaving it counterbalanced on a slender, centralized pedestal of presumed consolidated or cemented substrate, without apparently any evidence of collapse of this attachment support or of associated subsidence into the substrate. Yet, the stromatoporoids prior to sampling were "surrounded by argillaceous sediment [sic]" allowing easy removal of specimens (Segars & Liddell, 1988, p. 392), which suggests the original substrate was a uniform muddy,

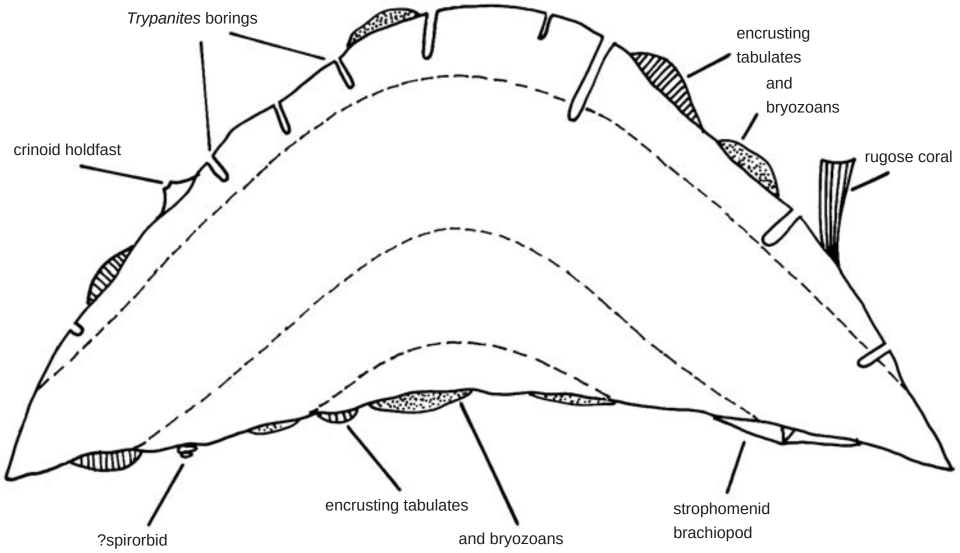


FIG. 312. Diagrammatic representation of a longitudinal section of a domical stromatoporoid showing differential distribution of encrusting and boring organisms on upper and lower surfaces; middle Silurian, Gotland, Sweden (Kershaw, 1980, fig. 3).

probably mainly unconsolidated (soft) sediment. The repeated winnowing processes of the sediment from beneath the rigid stromatoporoid bases allowed encrusting cryptic faunas to progressively colonize the skeletal undersurfaces, producing records of complete coverage, even beneath central interiors of the stromatoporoid specimens. This seems impossible to reconcile with the maintenance of a centralized pedestal of hard sedimentary rock (see SEGARS & LIDDELL, 1988, fig. 4) during the lifetime of the cryptobiont community.

An alternative explanation is required to explain the relationships, and one that is consistent with KERSHAW's (1980) earlier views. First, these stromatoporoids grew almost entirely on soft substrates, in contrast to the cryptic fauna that encrusted hard undersurfaces of stromatoporoid skeletons. A repeated series of episodic sedimentation, erosion, colonization, and early cementation events are required to explain the overall patterns of distribution, diversity, and abundance of cryptic encrusters on the stromatoporoid bases, as recorded by SEGARS and LIDDELL (1988). It seems likely that cryptic organisms first colonized the undersurface of the stromatoporoid when it was still actively growing, once the first cavities had formed by marginal scouring or winnowing of sediment from under the skeletal base, and/or after wholesale displacement of the skeleton in storm-generated activity across the substrate. The cavities existed long enough for a first wave of encrusters to settle and become well established, and then an episodic sedimentation, or combined sedimentation–early cementation event may have overwhelmed the initial population (Fig. 314.1–314.3). Successive phases of current scouring (or winnowing) and/or displacement movement were followed by waves of cryptic faunas again settling and thriving in the newly formed cavities (Fig. 314.3–314.5). These cycles of scouring at skeletal margins, and/or whole displacement of specimens that produced new cavities and cryptic recolonization, were preserved by further sedimentary events that caused the cavities to be sealed off and then infilled by early cements and geopetal sediments.

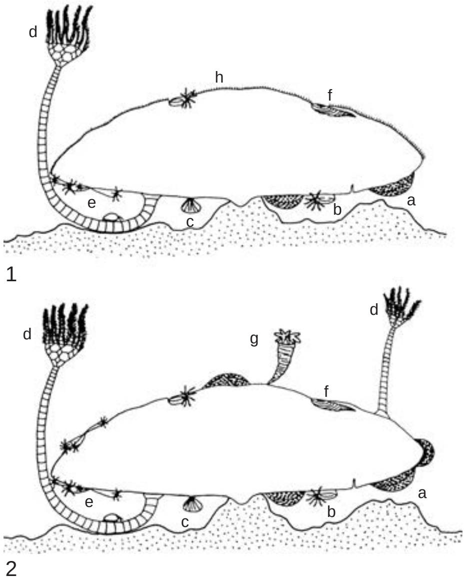


Fig. 313. Representation of record of epibionts that became encrusters on hard external surfaces of a smooth, low domical stromatoporoid, Ludlow, upper Silurian, Hamra Formation, Gotland, Sweden, both before its death and after death. The stromatoporoid was also shown as having an extensive, open, subskeletal cavity with a very small pedestal of sediment for attachment that was maintained for support of weight for some time (at least from before to after death), implying that the sediment was much lithified; see text for further discussion of this interpretation; *1,* encrusting epibionts on the stromatoporoid before death; note presence of living tissue mantling virtually entire upper surface of stromatoporoid; *2,* encrusting epibionts on stromatoporoid after death; note epibiont inhabitants now cover both upper and lower surfaces; *a,* bryozoans; *b,* spirorbids; *c,* brachiopods; *d,* crinoids; *e,* tabulate corals; *f,* tentaculitids; *g,* corals; *h,* area of surface with stromatoporoid living tissue (Segars & Liddell, 1988, fig. 4A–B).

The repetitions of these events occurred on the undersurfaces of a rigid stromatoporoid skeleton as it grew, and perhaps continued briefly after death, that is, prior to its final entombment in the succession. It is possible that the cavity infills of early cements and geopetal sediments imparted rigidity to areas immediately beneath many skeletons of individual stromatoporoids while they continued to grow.

LATERAL AND TERMINAL GROWTH SURFACES

Like the basal surfaces, the lateral margins of stromatoporoids need to be more carefully examined in the wider context of unraveling before-death interactions of growth in association with sediment and the water column, and after-burial impacts of diagenetic change. In general, the stromatoporoid organism was capable of sealing off its skeletal interior from intruding sedimentary particles and stopping sediment settling on the growth surface (Stearn, 1983b, p. 143; see also p. 493). However, sometimes growth interruptions occurred after sediment engulfed and necrotized parts of the growing surface. The cover of sediment then became a sediment inclusion as new, more continuous, lateral growth developed (Young & Kershaw, 2005). In broad outline, a wide range of marginal features occur, from smooth surfaces with no notching or raggedness, to extremely ragged or skirted margins, these latter exhibiting growth interruptions that are represented by sediment-filled tongues, or, less commonly, spar-filled cavities (Young & Kershaw, 2005, p. 643). Domical shapes are commonly bell shaped: smooth, convex tops that arch gently downward, becoming steeper on midslopes, then more flattened into ragged, lateral margins toward the base. Laminar forms are commonly extensive, flattened sheets with splayed, ragged, lateral margins, likely to develop at any successional level from bottom to top.

The main skeletal features capable of being preserved on upper surfaces are the mamelons, astrorhizae, and papillae. These are further detailed in the Internal Morphology and Functional Morphology of Paleozoic Stromatoporoidea (see p. 487–520, and p. 551–573). Only a few comments on surface characteristics of these features are included here. These structures were probably secreted from modified cells at the base of the organism's mantling sheet of living tissue, prior to

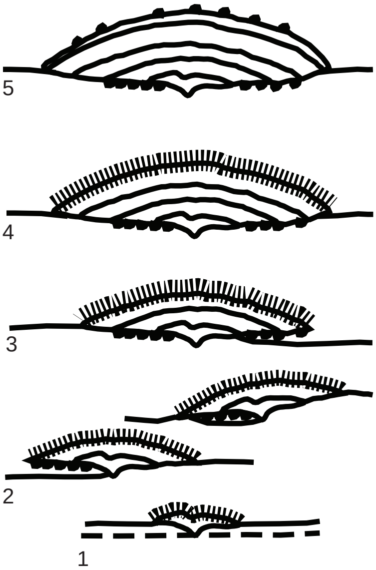


FIG. 314. This alternative model employs a stromatoporoid similar in shape to that represented by SEGARS and LIDDELL (1988), but it is based on the understanding that stromatoporoids of the Hamra Formation grew almost entirely on soft substrates. A rather different five-stage succession of events is proposed: stages *1–4*, growth of stromatoporoid, with its living tissue mantling the upper surface, and cryptobionts colonizing partially exposed areas of basal surfaces progressively during different stages, dependent on intermittent secondary scouring activity (before the death of the stromatoporoid); stage *5,* death of the stromatoporoid and the immediately following initial occupation of the upper surface by most of the encrusting epibiont organisms; meanwhile all the former encrusters of the basal surface had probably been overwhelmed by sediment influx and had probably died. The five-stage succession of events is summarized as follows; *1,* initiation of a small, low domical stromatoporoid, with upward and outward growth matching slow accumulation of sediment from a point coinciding with initial level of soft substrate (*dotted line*); *2,* larger, low domical stromatoporoid has grown, and on one side, soft muddy substrate has been scoured to form a large basal cavity for cryptic organisms to inhabit; first example (left side) is shown remaining upright, supported by substrate sediment to right side, or second example (right side) has become tilted to, in effect, cantilever the specimen over cavity (now supported on either side); *3,* with changed conditions—influx of sediment—the cavity on the left side may have been blocked off (or filled) by sediment, and then in another current scouring event, a new cavity (and site for cryptic organisms) may have been produced on right side; *4,* stromatoporoid continued to grow and then in another phase of sedimentary influx, cavity on right side was also blocked off, or filled; at this stage there had been two different generations of cryptic organisms that had lived and died on different parts of the stromatoporoid base. Many more cycles of episodic sedimentation and current scouring or movement of stromatoporoid individuals by storm-generated activity may have produced additional phases (or opportunities) for colonizing coverage of undersurfaces until the history of events was complete; *5,* after death, stromatoporoid skeleton was available for colonization by open surface encrusters, until final entombment of skeleton in sedimentary column (Webby & Kershaw, 2011).

termination of skeletal growth and probable death of the organism. Sometimes, a wide variety of hard-substrate-encrusting organisms colonized the terminal growth surface after death (for example, see SEGARS & LIDDELL, 1988, fig. 4B), and remained in occupation during a sediment-free interval on the terminal surface, until episodic sedimentation resumed and finally engulfed the skeleton completely.

The **mamelons** (LECOMPTE, 1956; GALLOWAY, 1957; STEARN & others, 1999; see Glossary, p. 407, and p. 503–505) are the updomed extensions or prolongations of the upper growing surface, being typically represented within the skeleton by vertically oriented mamelon columns. The terms mamelon and monticule were used interchangeably by NICHOLSON (1886a) in the first part of his monograph on the

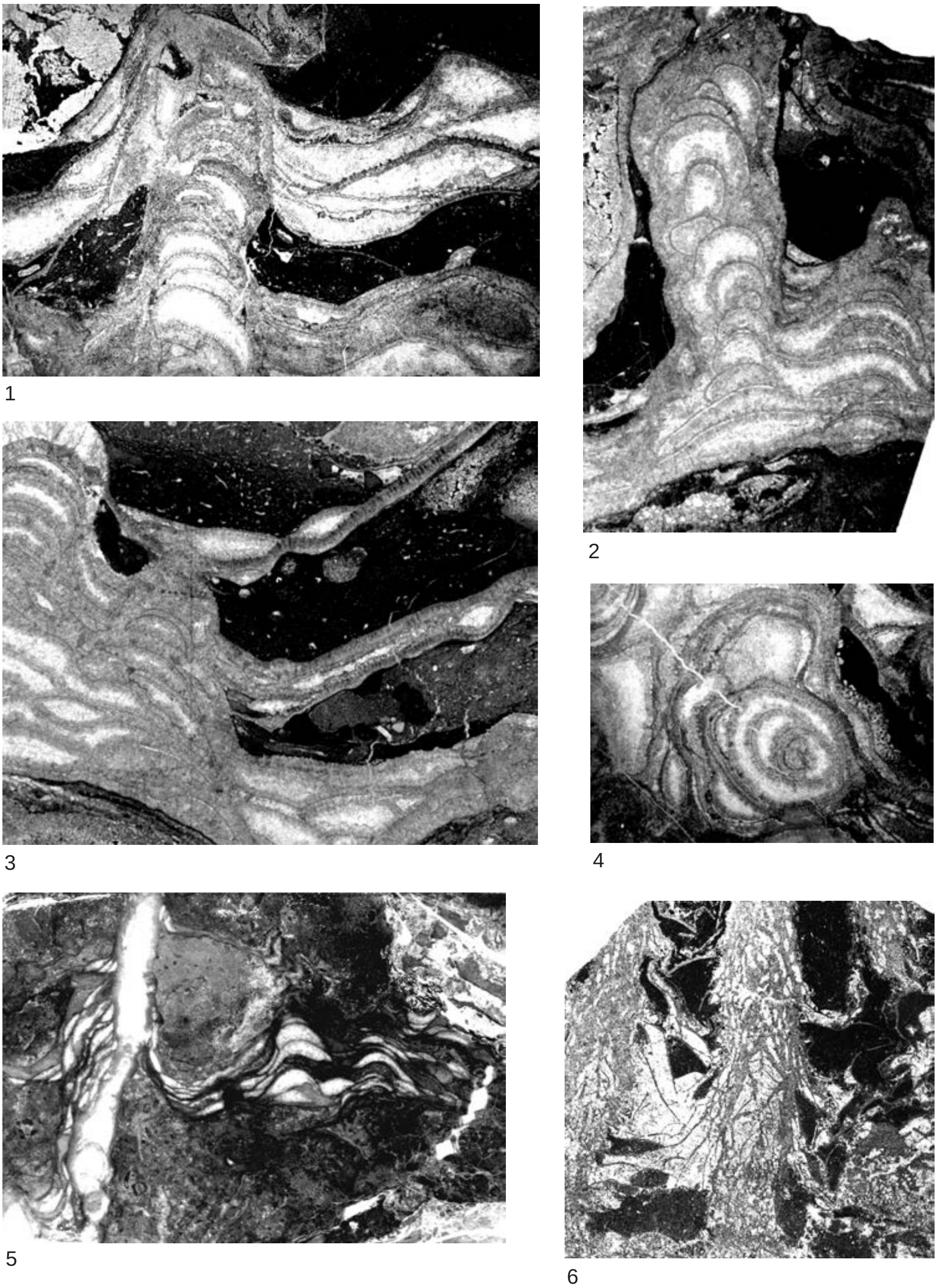


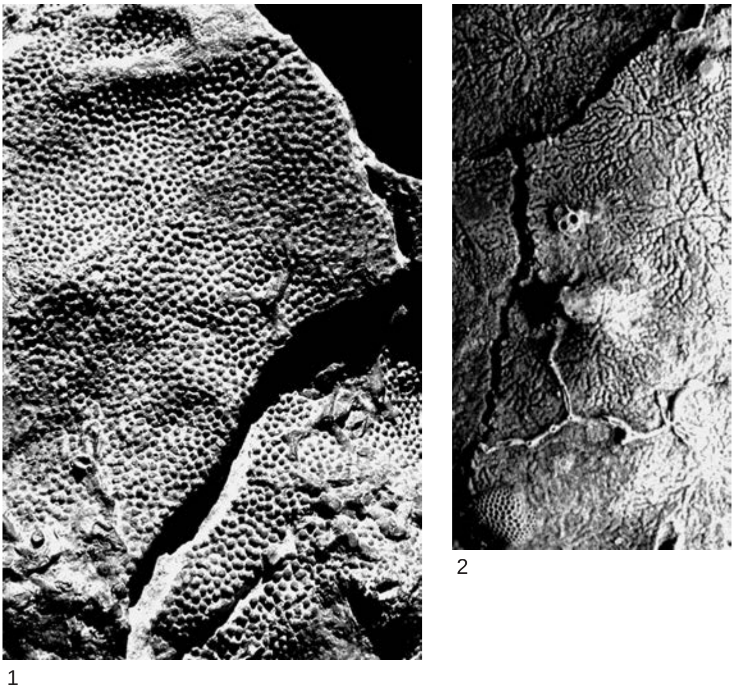
FIG. 315. Labechiid stromatoporoid skeletons in successions that exhibit digitolaminar shapes, lower Katian, Upper Ordovician; *1–5,* coarsely cystose species of *Rosenella*, with some affinities to *R. woyuensis* OZAKI, but it exhibits a more complex development of laterally extended, laminar growth units that may alternate in places with sediment-filled spaces, and commonly intersecting vertically persistent, mamelate-like, columnar upgrowths; just west of Boonderoo shearing shed, lower Fossil Hill Limestone, Cliefden Caves Limestone Group, central New South Wales, Australia, *(Continued on facing page.)*

British stromatoporoids, but in later parts, Nicholson (1889, 1891a, 1892) used only the term mamelon. Much later, Galloway (1957, p. 356) restored the use of monticule for a small mamelon. Kershaw (1990, p. 702, fig. 7; 1998, fig. 6) recognized that mamelons maintained vertical orientations, even though they occupied sites on steep slopes of cone-shaped, high domical types (Fig. 293.1), or tilted laminar shapes lying on a sloping substrate (Fig. 293.2). In both cases, the mamelons were aligned vertically upward toward the light or a particular upward pattern of current flow, though they were tilted with respect to the growing surface. The mamelons were usually evenly spaced across the upper surface of the skeleton, ranging from a few millimeters in height and diameter to exceptionally large dimensions, with vertical continuity up to 150 mm in height and 25 mm or more in diameter. Some Ordovician labechiids have comparatively extended mamelon columns, such as a *Rosenella* from New South Wales. This form has a composite digitolaminar shape (Webby, Zhen, & Percival, 1997, p. 170, pl. 2C; see also Fig. 315.1–315.5), and the mamelon columns are continuous vertically, up to 100 mm in height and about 10 mm in diameter, but the successive laminar phases are never more than about 3 cm apart, meaning that that columns probably did not rise as isolated columns more than that height above the sedimentary interface during growth. Such an example of digitolaminar growth demonstrates the ease with which environmental switches can occur in a few plastic, probably ecophenotypic species, of alternating phases of mainly coalesced, laterally extended laminar growth and the predominantly separated, erect, digitate upgrowths (multicolumnar protruberants of Kershaw, 1998, p. 522) that represent the mamelon columns. Another example of elevated mamelon columns is seen in large domical skeletons of *Pachystylostroma surculum* from the Mjøsa Limestone in Norway (Fig. 315.6). Some authors (Stearn, 1966; Webby, 1971; Cockbain, 1984) have noted that separated digitate skeletal growth tends to develop from extensions of mamelon columns off laminar bases.

Sometimes **astrorhizae** are associated with the mamelons of stromatoporoids (see Glossary, p. 400; see also p. 505–509 and Fig. 326.3). They may be represented by astrorhizal traces (grooves or ridges) that converge in a stellate pattern toward one or more osculum-like opening(s) at the summit of a mamelon, or they may also be present on smooth terminal growth surfaces of stromatoporoids where there are no clearly differentiated mamelons (Fig. 316.2–316.3; and see Fig. 326.1). Some stromatoporoids, like many labechiids, do not show traces of preserved astrorhizae, though they may exhibit mamelons. In the labechiids, astrorhizae are rarely preserved, because canals of

Fig. 315. *(Continued from facing page).*

AMF.12952; *1,* longitudinal section showing vertically upraised columnar growth that appears to have continued to grow, while the laminar growth units appear to have been disrupted at least twice by sediment incursions, ×2.5 (Webby, Zhen, & Percival, 1997, pl. 2C); *2,* longitudinal section illustrating that initial cystose growth of specimen developed over a relatively flat laminar base, then columnar growth took over as successive, large axial cyst plates were added to the column, ×2.5 (Webby & Kershaw, 2011); *3,* longitudinal section of skeleton also formed on a relatively flat laminar base, and again lower-lying laminar units appear to have been disrupted a number of times by sediment influxes, while broadly raised columnar area to left maintained a continuity of growth, ×2.5 (Webby & Kershaw, 2011); *4,* tangential section showing columnar nature of vertical growth, ×2.4 (Webby & Kershaw, 2011); *5,* longitudinal view illustrating remarkable continuity of a vertical column relative to lateral growth; note pattern of lateral extensions initially draping off main column, perhaps because sediment was already piled up against rapidly upgrowing column, ×0.75 (Webby & Kershaw, 2011); *6,* longitudinal section, *Pachystylostroma surculum* Webby, holotype, PMO 97112, Mjøsa Limestone, Bergevika, Norway, showing strongly mamelate nature of large domical skeleton, especially close to its upper surfaces, where many sediment-filled inclusions seem to occur; with respect to near-surface growth of such skeletons, they may be described also as locally digitolaminar, ×3.5 (Webby, 1979c, fig. 2C).



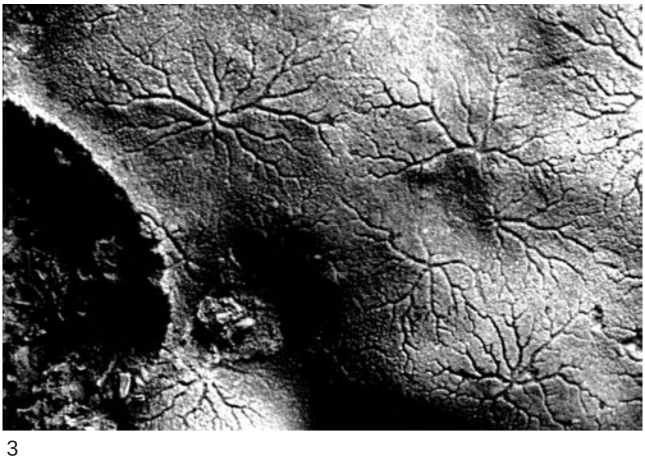


Fig. 316. *1,* Laminar skeleton of *Labechia conferta* (Londsdale), Silurian, Wenlock, Dudley, England, showing well-developed papillae representing tops of individual pillars on terminal growing surface; in places, papillae exhibit alignments into paired, slightly sinuous rows; rarely the paired rows vaguely radiated away from one or two centers; consequently, intervening grooves may be interpreted as original pathways for tubes of living tissue of astrorhizal system that failed to calcify; AMF.134351, a specimen originally presented to the Sydney University paleontology collection by T. W. Edgeworth David, now transferred to the Australian Museum, ×2 (Webby & Kershaw, 2011); *2–3,* two unidentified stromatoporoid skeletons, possibly *Eostromatopora* sp. (×2.5), and *Pachystroma hesslandi* (Mori) (×3), respectively, Visby Formation, Wenlock, Gotland, Sweden, showing terminal growing surfaces with well-preserved astrorhizal grooves, but no associated mamelons; note also the prominent encrusters in view *2*: a branching, reptant, auloporid coral, and a button-shaped bryozoan (Webby & Kershaw, 2011; views *2* and *3* courtesy of P. Copper).

the exhalant current system were probably almost completely confined to the living tissue that lay above the secreted structural elements of successive growing surfaces (Stearn, 1975b, fig. 4).

A few stromatoporoids exhibit small, raised, rounded surface cones or bosses on the terminal growing surface, named **papillae** (Galloway, 1957, p. 356; Mori, 1968, p. 17, fig. 5c; see Glossary, p. 410, and discussion of pillars, p. 499); these represent the tops of pillars, denticles, or pillarlike structures (they are not growth forms). They were originally termed tubercles by Nicholson (1886a, p. 60; see also Nestor, 1964a, 1966a) but this term is best abandoned, given its potential confusion with the spelling of the chaetetid term tubercule (defined as spinelike projections at junctions between two or more tubules). In stromatoporoids, papillae are well developed in some labechiids, most notably *Labechia (L. conferta*) and *Lophiostroma* (*L. schmidtii*), and some actinostromatids (Galloway & St. Jean, 1957, p. 149). In *L. conferta,* the papillae are usually separated and rounded (Fig. 316.1) but may be partially confluent, forming sinuous rows (Nicholson, 1886a, p. 60, pl. 3,*12–15*). The discrete structures recorded by Prosh and Stearn (1996, pl. 3,*3*) as protuberances are not like papillae (cf. Kershaw, 1998, p. 522), but domal inflexions of laminae that are apparently the result of the response from the stromatoporoid to a “foreign intruder or trauma” (see Fig. 330.2).

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INTERNAL MORPHOLOGY OF THE PALEOZOIC STROMATOPOROIDEA

Colin W. Stearn

INTRODUCTION

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

The skeleton of Paleozoic stromatoporoids was secreted as a base for the living tissue, to raise it above the substrate surface and the deleterious effects of accumulating sediment and overgrowing space competitors. In most stromatoporoids, living tissue occupied a film, probably only a few millimeters thick, over the growth surface of the skeleton, but in some, it occupied space within the upper few millimeters of the skeleton. Below the living soft tissue, the voids in the skeleton were filled with seawater while the organism was alive and filled with mineral spar as the skeleton became a fossil. This model of the stromatoporoid (see 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 stromatoporoids. Where the terminal growth surface of stromatoporoids that secreted discrete laminae or pachystromes is preserved, sediment does not fill the empty chambers left by the decay of soft tissues, beyond the few incomplete structures in the terminal phase (Fig. 317.1, and see Fig. 352.1–352.2).

When stromatoporoids were considered to be cnidarians and colonial, the term coenosteum (common or shared bone [Gk. *kainos* + *osteon*]) was appropriate to the whole skeleton, but now that the animals are widely considered to be sponges and individuals (see 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 coenostele, coenostrome, and coenotube, also share this legacy and are replaced here by pachystele, pachystrome, and allotube, respectively (for definitions of these terms, see Glossary, p. 397–416).

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

1. Domes and posts = cyst plates and pillars (Labechiida).
2. Floors and posts = laminae and pillars (Clathrodictyida, Stromatoporellida).
3. Posts and beams = pillars and colliculi (Actinostromatida).
4. Walls and floors = pachysteles 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

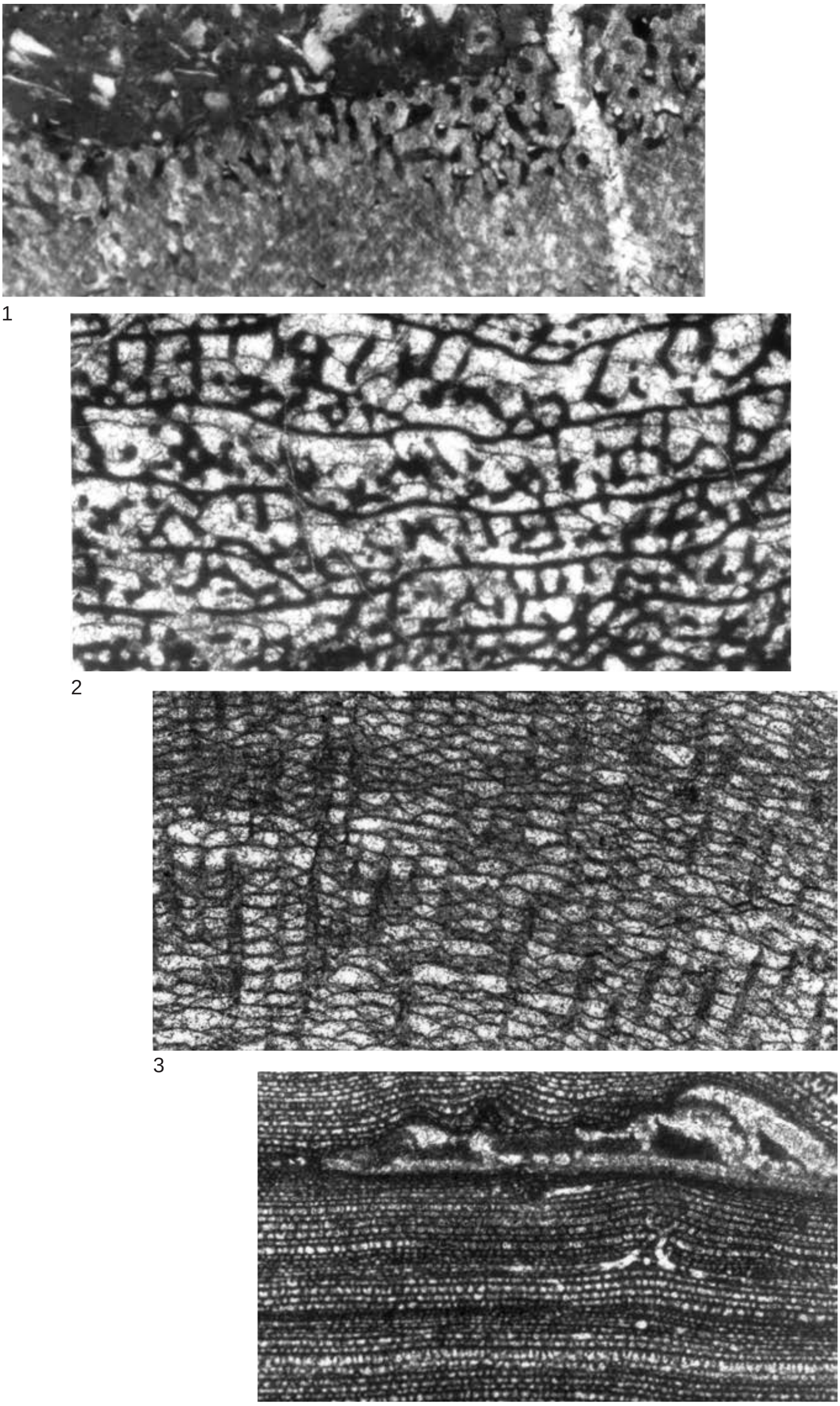

FIG. 317. *(For explanation, see facing page).*

the specimen (see below). STEARN (1989a) estimated that the Simpson coefficient of variability (V = 100 × standard deviation/mean) ranges from about 5 to 30 and is commonly in the upper part of this range. The average spacing of pillars, laminae, pachysteles, and pachystromes is remarkably uniform throughout stromatoporoid history; this consistency suggests that it was controlled by a basic parameter of anatomy and physiology. Most structural elements are spaced about 8 in 2 mm, and the range rarely exceeds 5 to 11 in 2 mm. Stromatoporoids with widely spaced laminae (less than 5 in 2 mm, e.g., *Hammatostroma* and *Tienodictyon*, Fig. 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

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, ×10; *2,* complex pillar structure between widely separated laminae; *Hammatostroma albertense* STEARN, 1961, SCRM 67-671, Frasnian, Cairn Formation, Rocky Mountains, Alberta, Canada, ×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, ×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, ×10 (Stearn, 2011a).

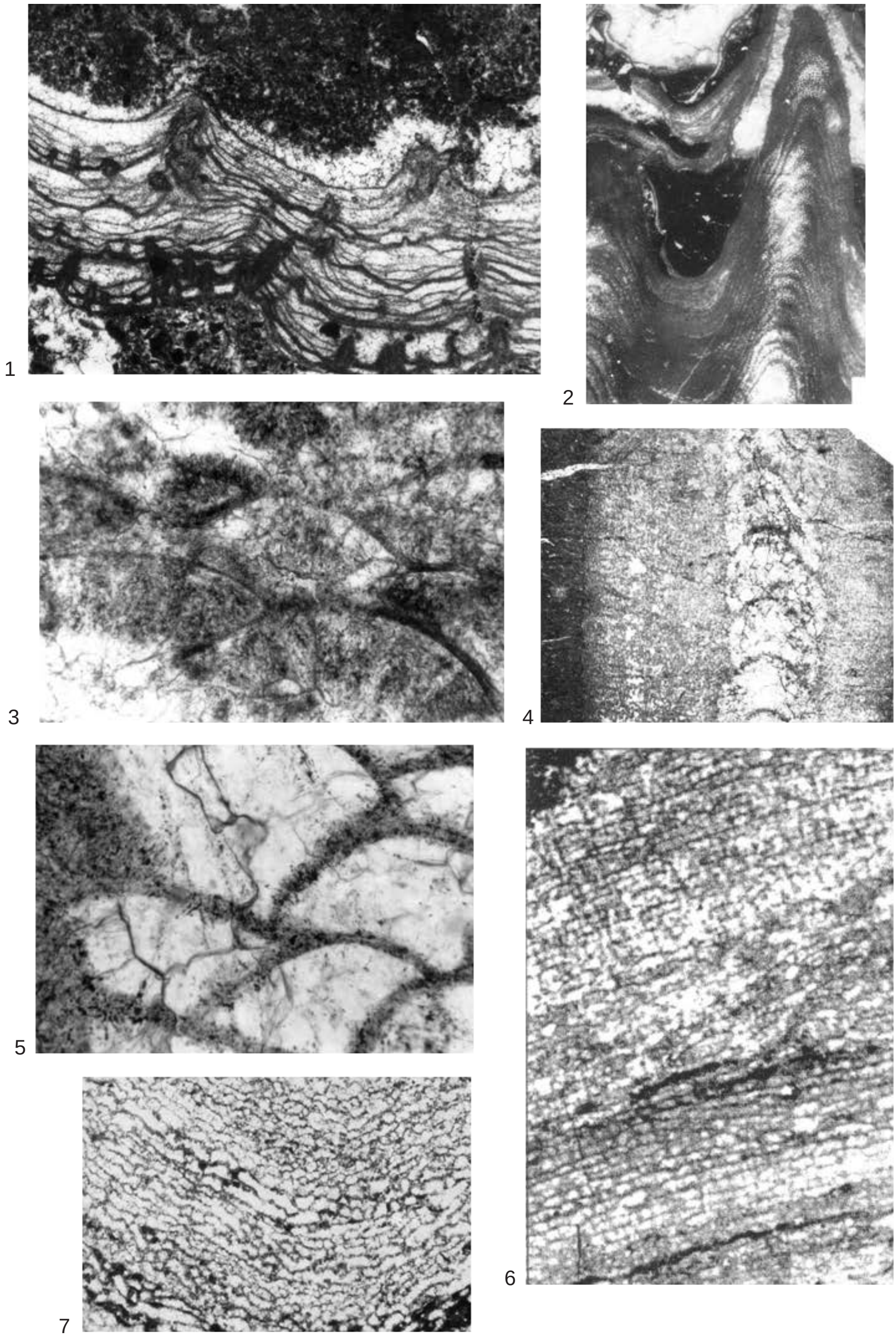

Fig. 318. *1,* Longitudinal section through growth surface with mamelons; note denticles on cyst plates and spar-filled space above terminal cysts, possibly occupied at death by soft tissue; *Stylodictyon sinense* (Dong, 1964), SCRM 118-3, Famennian, Wabamun Formation, Normandville Field, northern Alberta, Canada, ×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 *Clathrodictyon* has suggested that the clathrodictyids evolved from labechiids by the joining of the cyst plates in horizontal rows. There is little direct evidence of this in transitional forms, however, and the first clathrodictyids to appear in Late Ordovician time include both forms with laminae that look like conjoined cyst plates

Fig. 318. *Continued from facing page.*

RM 14,004a, Middle Ordovician, Crown Point Limestone, Vermont, United States, ×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, ×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, ×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, ×55 (Stearn, 2011a); *6,* small, tangentially aligned, cyst plates; *Stratodictyon ozakii* Webby, 1969, AMF.99377, Upper Ordovician, Fossil Hill Limestone, New South Wales, Australia, ×10 (Webby, 1969); *7,* undulant laminae resembling aligned cyst plates in clathrodictyid; *Clathrodictyon* sp. cf. *microundulatum* Nestor, 1964a, AM.FT 15211, Upper Ordovician, Ballingoole Limestone, Bowan Park Group, New South Wales, Australia, ×6.5 (Webby, 1969).

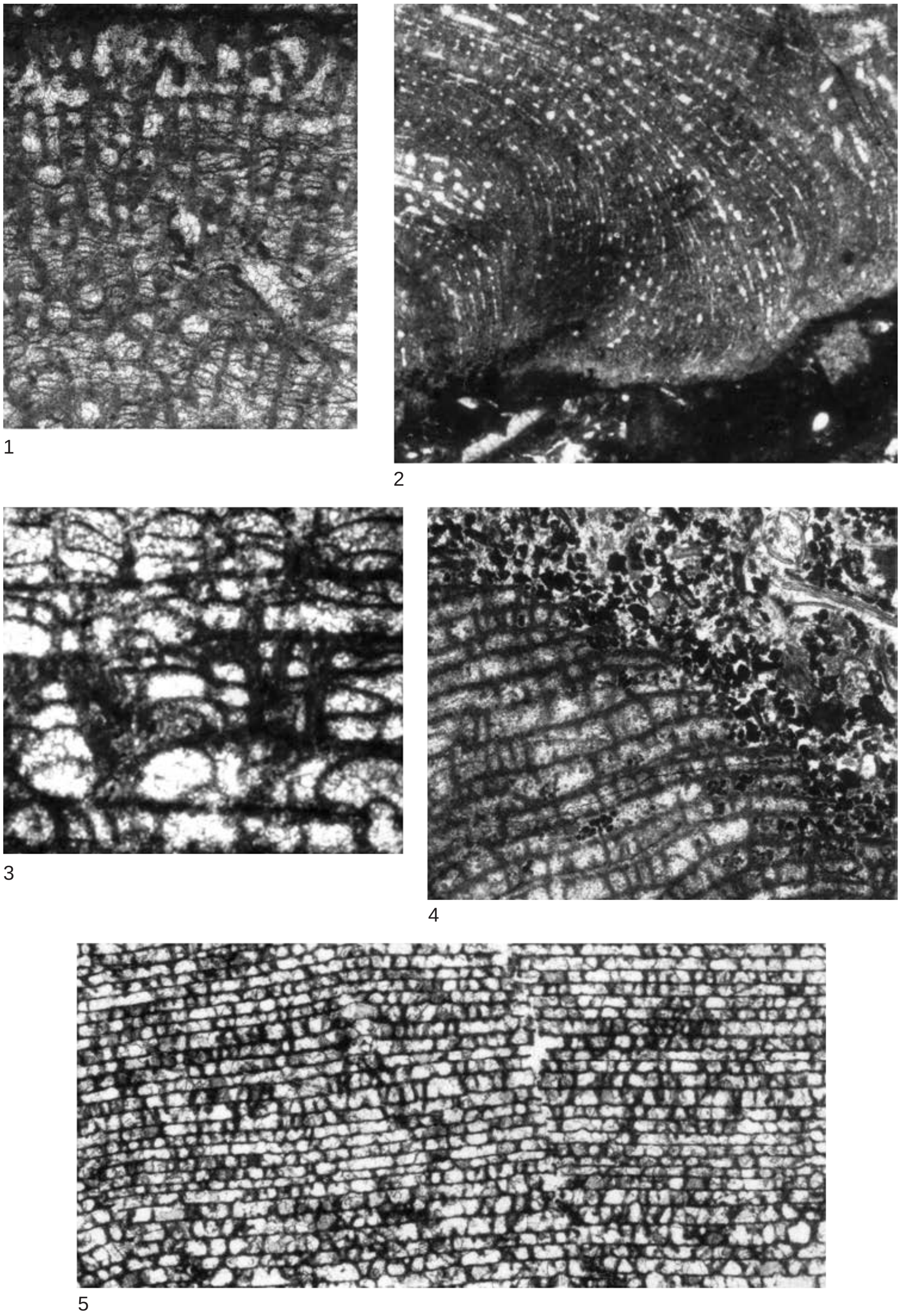

FIG. 319. *(For explanation, see facing page).*

(*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 µm) tangential plates that are part of a lamina or an independent structural element are microlaminae. Thick, less extensive structures in the stromatoporids and syringostromatids are pachystromes.

LATERAL CONTINUITY

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

Fig. 319. *1,* Abundant dissepiments occupying allotubes between pachysteles; *Salairella bullulosa* (Stearn, 1966), GSC 18695, Frasnian, Mikkwa Formation, northern Alberta, Canada, ×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, ×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, ×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, ×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, ×10 (Stearn, 2011a).

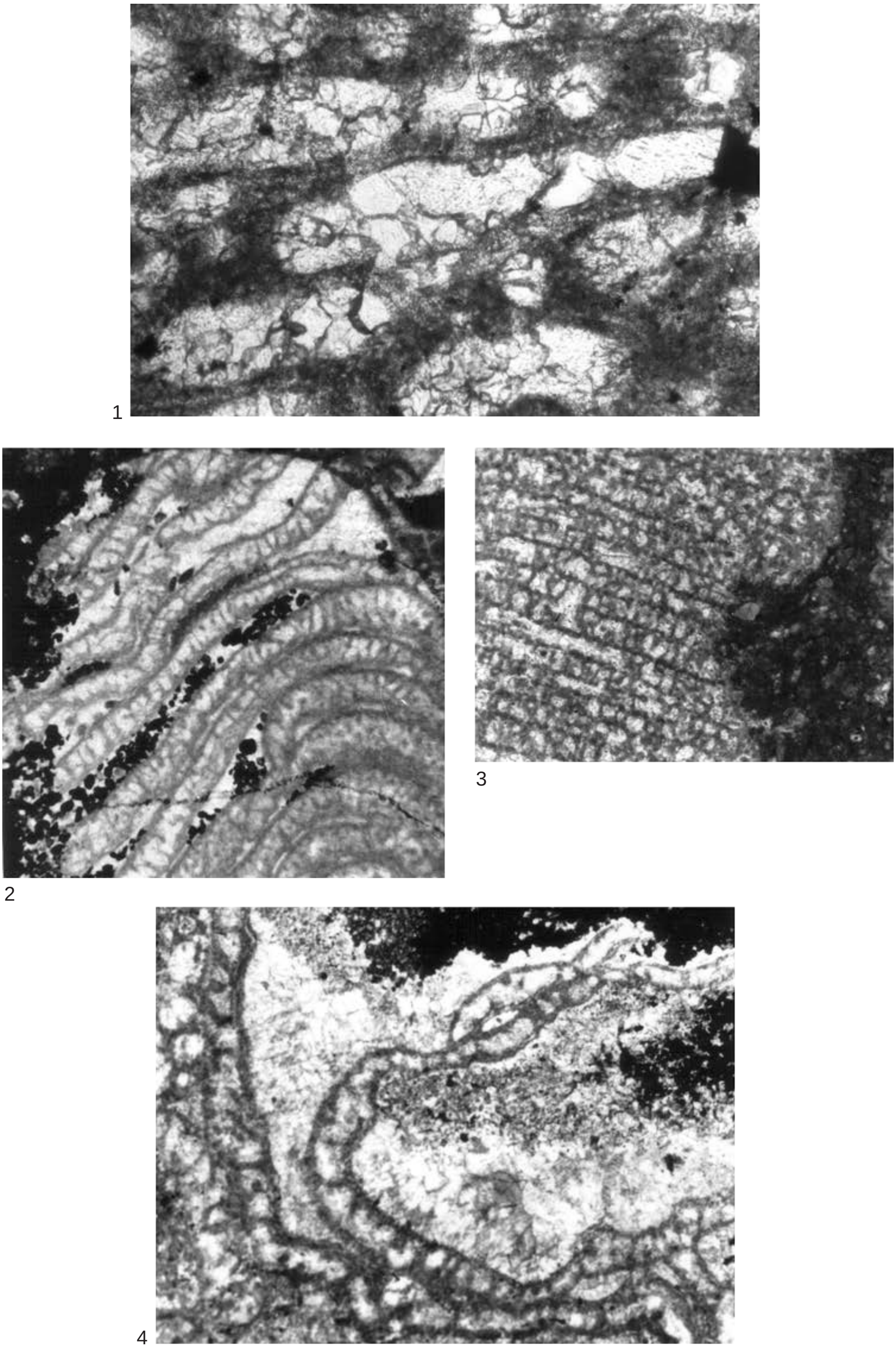

FIG. 320. *(For explanation, see facing page).*

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, ×50 (Stearn, 2011a); *2,* laminae pairs separating into modules infiltrated with grains of sediment; *Simplexodictyon vermiforme* (Stearn & Mehrotra, 1970), SCRM 130-47, GSC 116, 284, Emsian–Eifelian, Ogilvie Formation, Yukon, Territory, Canada, ×8 (Stearn, 2011a); *3,* lateral edge of stromatoporoid (growth condition or breakage?); *Atelodictyon stelliferum* Stearn, 1961, GSC 18684, Frasnian, Mikkwa Formation, northern Alberta, Canada, ×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, ×10 (Stearn, 2011a).

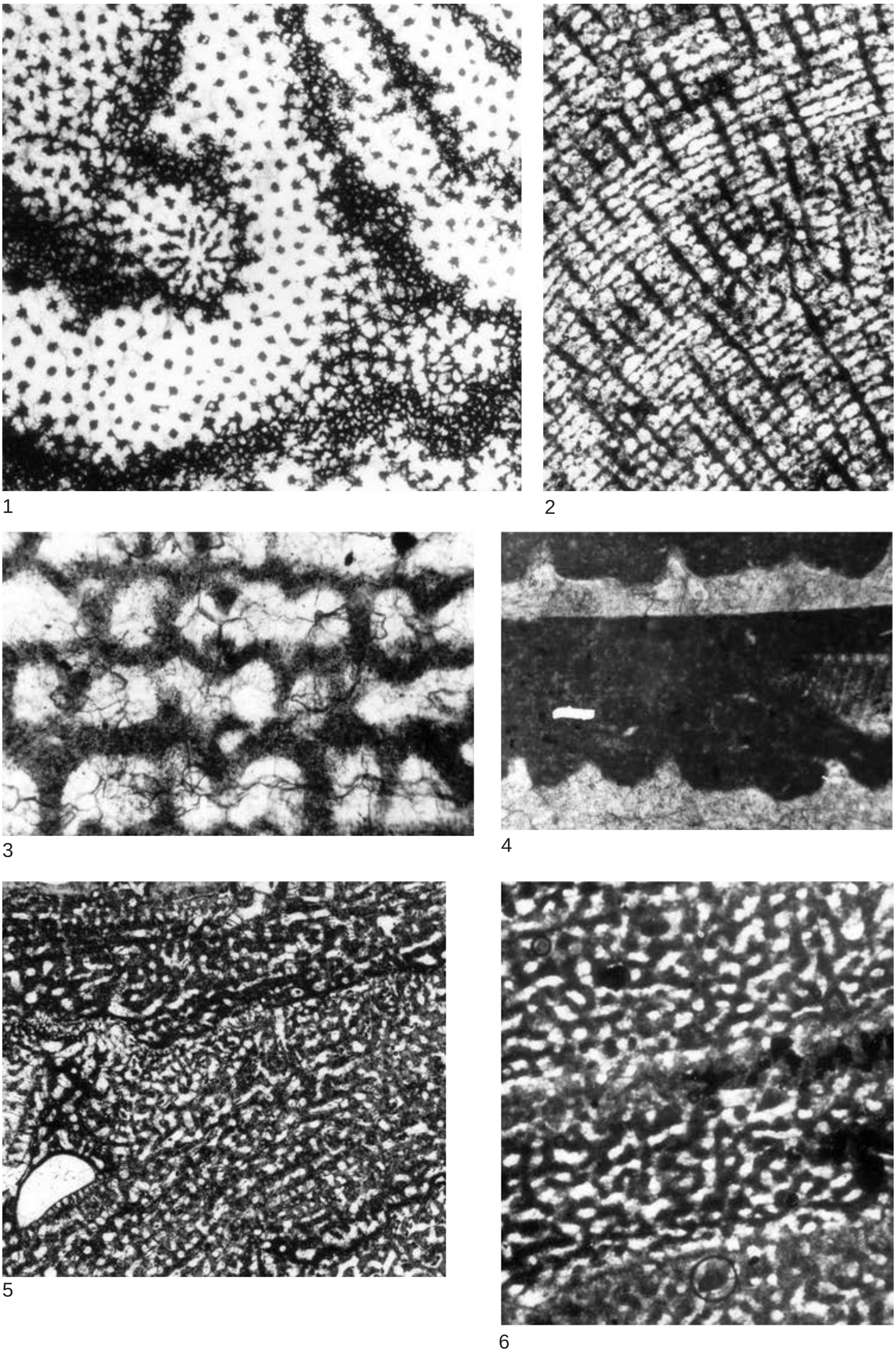

FIG. 321. *(For explanation, see facing page).*

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 inflectioning laminae (or inflexions) by Bogoyavlenskaya (1984). The imbricating chevron structure is also found in the pachystromes of the cassiculate stromatoporids, 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. 460*a*).

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

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, ×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, ×10 (Stearn, 2011a); *3,* Single-layer laminae inflected downward into tops of pillars; *Clathrodictyon striatellum* (d’Orbigny, 1849), Nicholson 243b, NHM P5664, Wenlock Limestone, Dudley, Shropshire, England, ×50 (Stearn, 2011a); *4,* denticles on top surface of cyst plate; *Rosenella macrocystis* Nicholson, 1886a, Nicholson 280, NHM P5490, Wenlock, Gotland, Sweden, ×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, Mikkwa Formation, northern Alberta, Canada, ×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, ×10 (Stearn, 2011a).

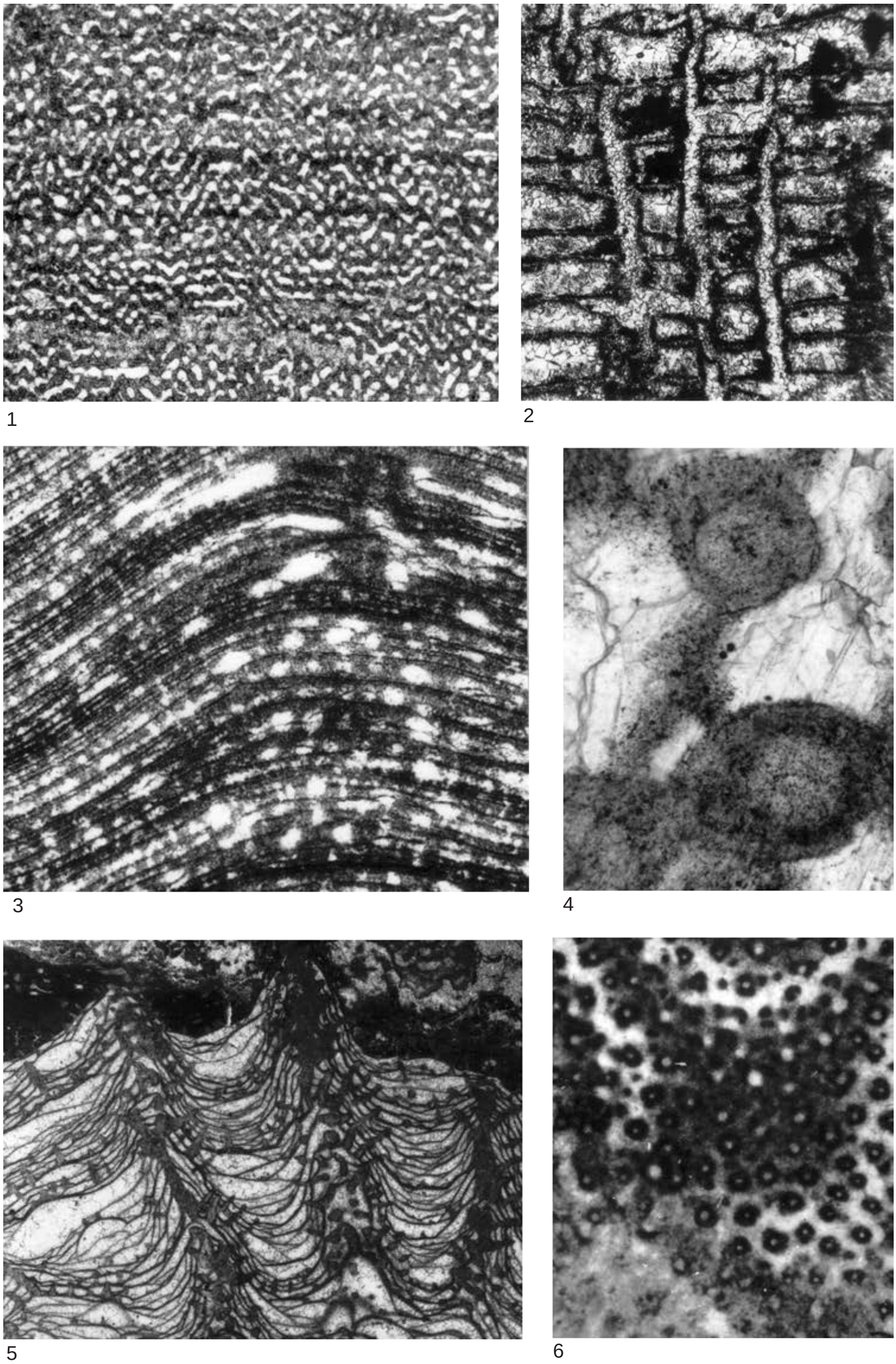

FIG. 322. *(For explanation, see facing page).*

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 *Camptodictyon,* 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 (1886a) 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

FIG. 322. *1,* Cassiculate structure of oblique pachystromes; *Stromatopora* sp. cf. *polaris* (STEARN, 1983a), SCRM 125-1, Emsian, Ogilvie Formation, Yukon Territory, Canada, ×12 (Stearn, 2011a); *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, ×20 (Stearn, 2011a); *3,* microlaminae within diffuse tissue of pachystromes; note also astrorhizal canals concentrated in upward inflection of pachystromes; *Habrostroma proxilaminatum* (FAGERSTROM, 1961), holotype, UMMP 36177, Lower Devonian, Formosa Reef Limestone, southwestern Ontario, Canada, ×10 (Stearn, 2011a); *4,* pillars in tangential section with zones of concentric growth; *Labechia conferta* (LONSDALE, 1839), Nicholson 264, NHM P5984, Wenlock Limestone, Dudley, Shropshire, England, ×55 (Stearn, 2011a); *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 20.4916a, Famennian, Wabamun Formation, Nomandville field, northern Alberta, Canada, ×5 (Stearn, 2011a); *6,* ring pillars in tangential section; *Stromatoporella granulata distans* PARKS, 1936, ROM 2246, Middle Devonian, Hamilton Formation, southwestern Ontario, Canada, ×10 (Stearn, 2011a).

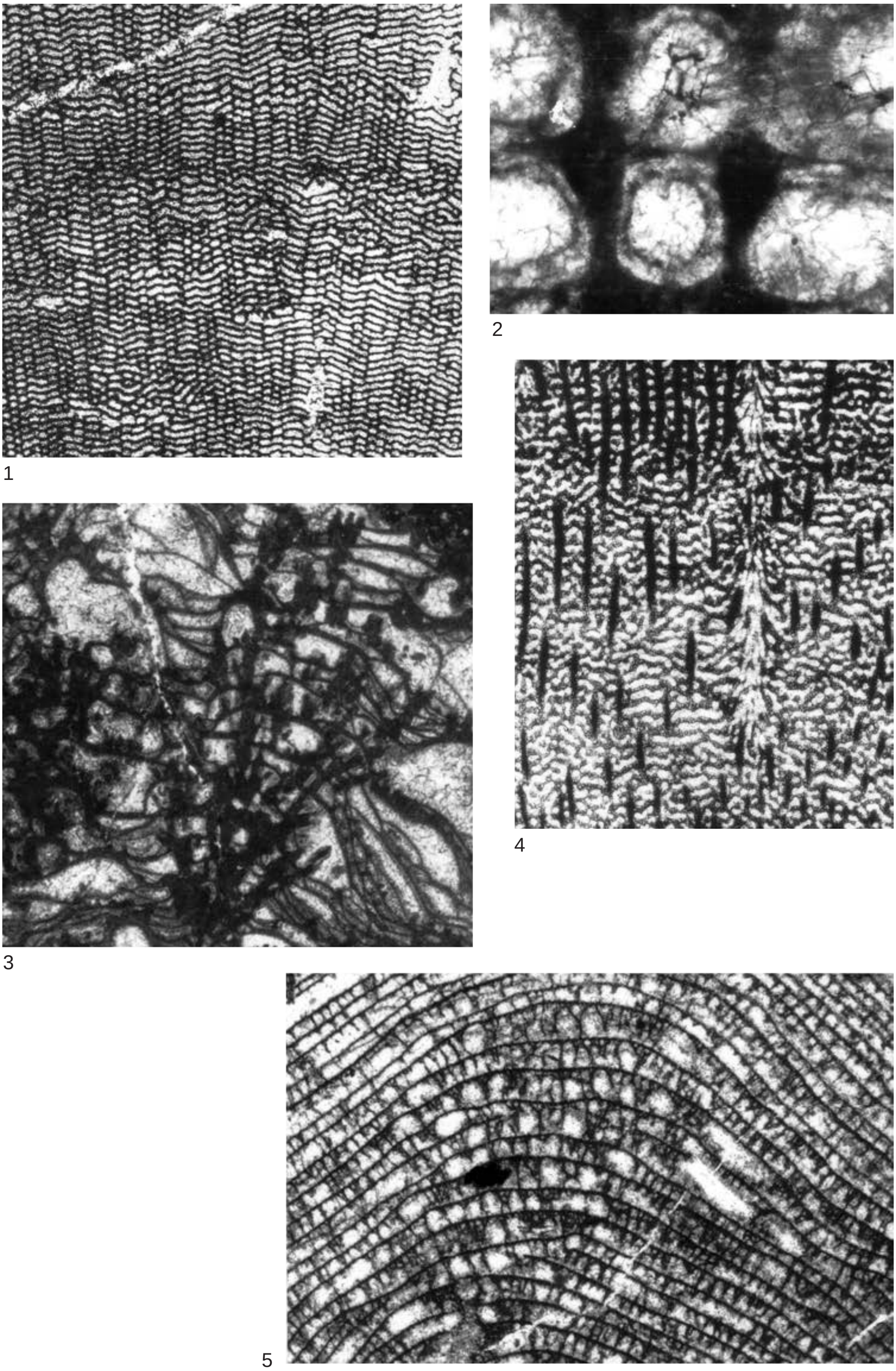

FIG. 323. *(For explanation, see facing page).*

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 stromatoporoids, the increased number of pillars is by intercalation as the skeleton grows wider. In some labechiids, the pillars are walls with complex flanges but do not form a network in tangential section. Such pillars characterize the Ordovician *Stromatocerium* (Fig. 395*b*) and several genera from Famennian rocks such as *Platiferostroma* (Fig. 398,*1b*) and *Vietnamostroma* (Fig. 400,*2b*).

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 interlaminar 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, Pseudoactinodictyon*). Such complex pillars are subcircular in tangential section only near their bases but are vermiform or may form an irregular network below the overlying lamina at their tops where they branch. In some genera, they may join into chains (*Atelodictyon*). In genera such as *Hammatostroma* and *Tienodictyon,* the pillars do not cross the interlaminar space directly but are tangled into complex structures in the interlaminar space (Fig. 317.2). Superposition of pillars from one gallery to the next is uncommon in the order but occurs in the family Gerronostromatidae (e.g., *Gerronostromaria,* p. 761, Fig. 420,*1a*).

STROMATOPORELLIDA

Like the laminae, the pillars of this order tend to have cellules or vacuoles. Pillars are confined to interlaminar spaces, but in the Trupetostromatidae, they are superposed regularly and may appear to pass through the laminae. In *Stromatoporella,* the tripartite laminae are inflected upward to meet the lamina above, forming a cone or cylinder.

FIG. 323. *1,* Incipient pillars formed by deflection of chevron laminae; longitudinal section; *Camptodictyon amzassense* (KHALFINA, 1960c), AMF.98976, Upper Ordovician, Vandon Limestone, New South Wales, Australia, ×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, ×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, ×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, ×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, ×10 (Stearn, 2011a).

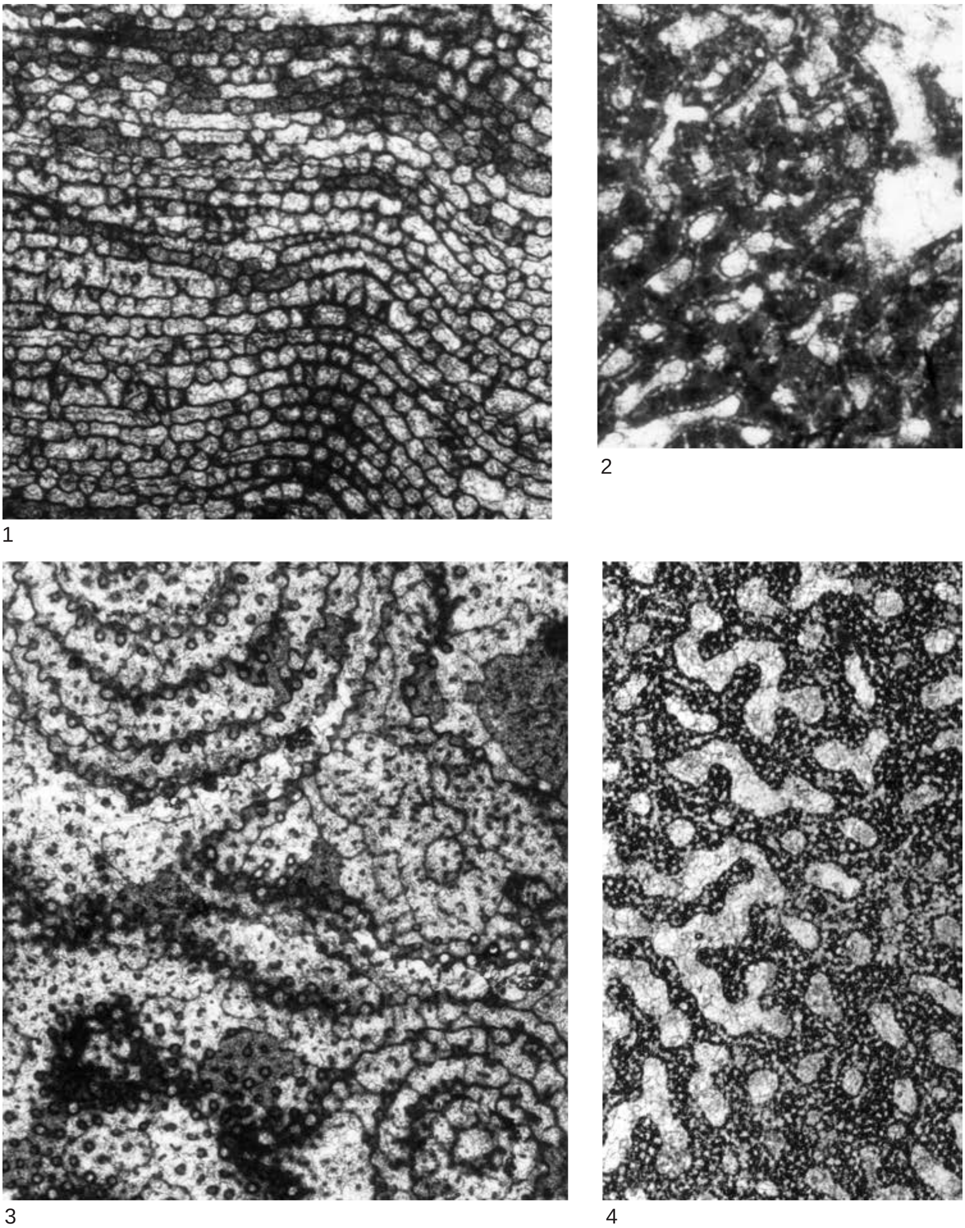

Fig. 324. *1,* Ring pillars in longitudinal section; *Stromatoporella perannulata* Galloway & St. Jean, 1957, GSC 108175, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×10 (Stearn, 2011a); *2,* peripheral vacuoles on margins of pachysteles, tangential section; *Hermatoporella maillieuxi* (Lecompte, 1952 in 1951–1952), holotype, IRScNB-5760, Frasnian, Senzeille, Belgium, ×18 (Stearn, 2011a); *3,* ring pillars in tangential section; *Stromatoporella perannulata* Galloway & St. Jean, 1957, same specimen as *1,* ×10 (Stearn, 2011a); *4,* pachysteles with coarse cellular microstructure separated by allotubes; *Pseudotrupetostroma vitreum* (Galloway, 1960), GSC 48453A, Givetian, Evie Lake reef, northeastern British Columbia, Canada, ×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

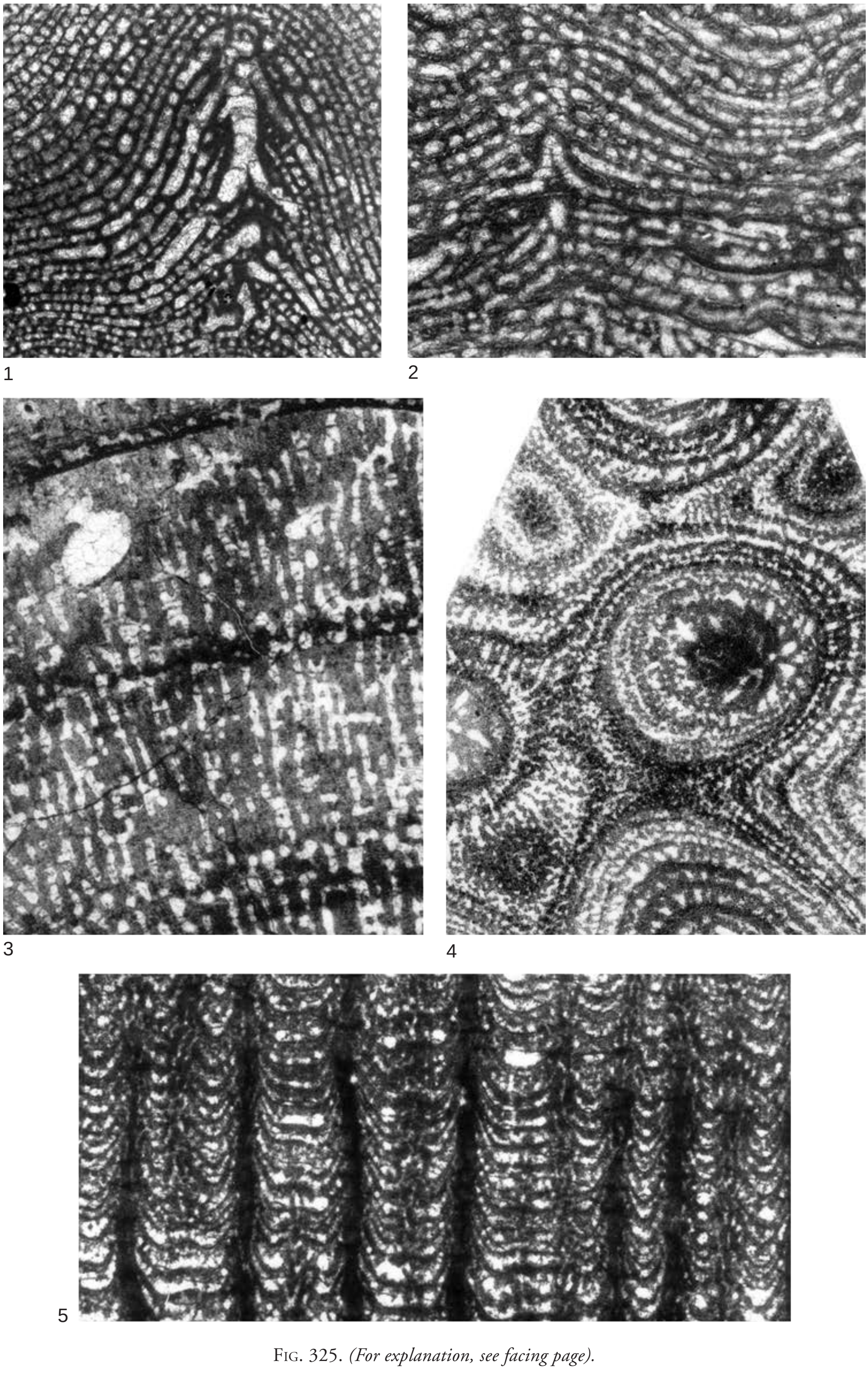

FIG. 325. *(For explanation, see facing page).*

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).

ASTRORHIZAL 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 (*Goreauiella*), 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

FIG. 325. *1,* Isolated mamelon within a regular structure showing central astrorhizal canal; *Schistodictyon* sp., UWA 140802, Frasnian, Pillara Limestone, Canning Basin, Western Australia, ×5.5 (Stearn, 2011a); *2,* mamelons isolated in regular structure, longitudinal section; *Stictostroma maclareni* STEARN, 1966, holotype, GSC 18674a, Frasnian, Kakisa Formation, northern Alberta, Canada, ×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, ×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, ×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, ×10 (Stearn, 2011a).

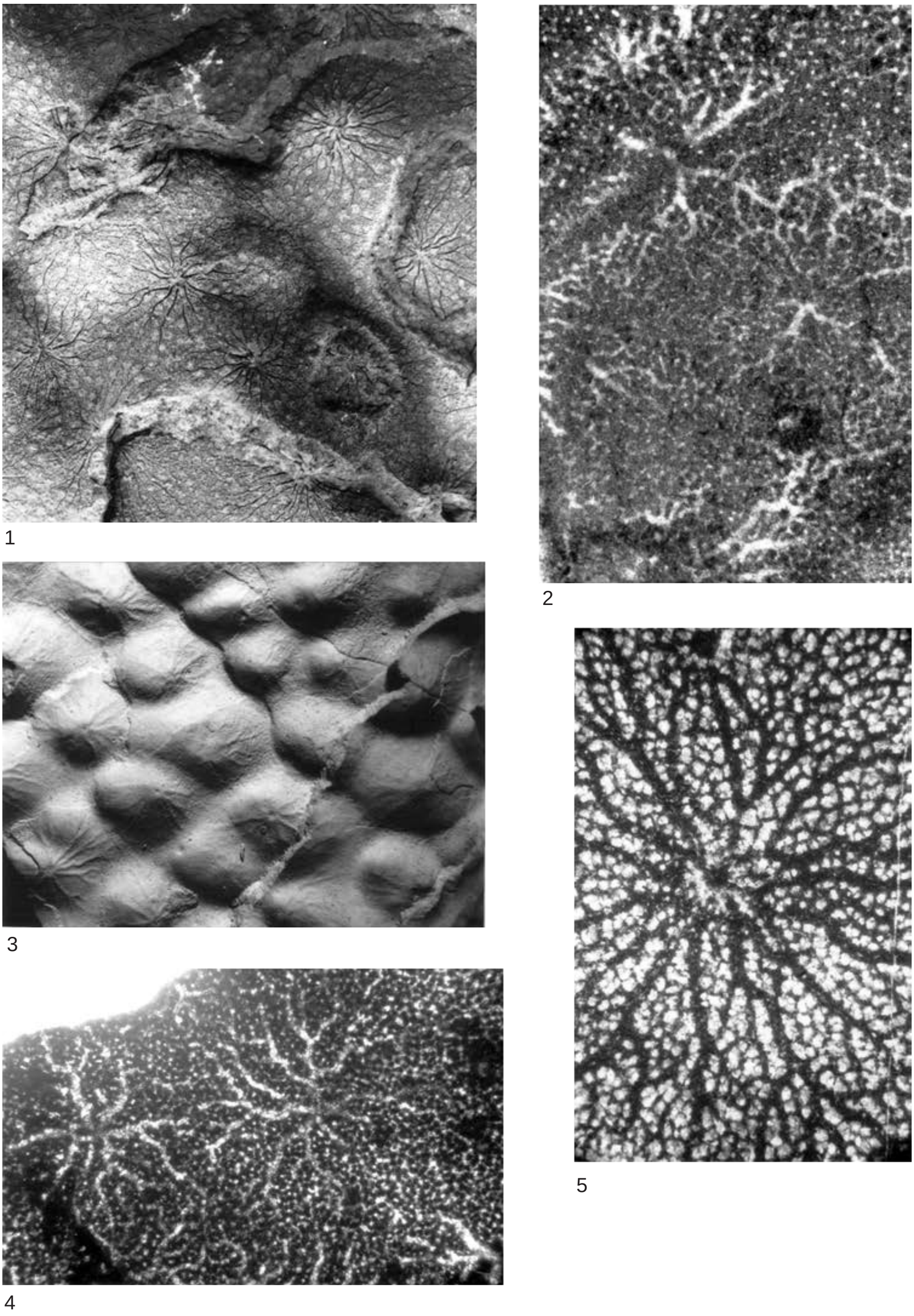

FIG. 326. *1,* Growth surfaces of three successive latilaminae in exfoliating, unidentified stromatoporoid (probably *Syringostroma* sp.), Devonian, Michigan; note astrorhizal grooves, some on mamelons and others between them, and emergence of columns as papillae on surfaces; RM 14,777, Middle Devonian, ?Alpena Limestone, Michigan, United States, ×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 (Stearn, 1990), SCRM 112-113, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada, ×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, Ogilviie Formation, Yukon Territory, Canada, ×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, ×10 (Stearn, 2011a); *5,* extensive astrorhizal system with canals outlined by opaque matter, tangential section, *Parallelopora dartingtonensis* Carter, 1880, Nicholson 133 (compare Nicholson, 1886a, pl. 4,*1*), NHM P5743, Middle Devonian, Devon, England, ×10 (Stearn, 2011a).

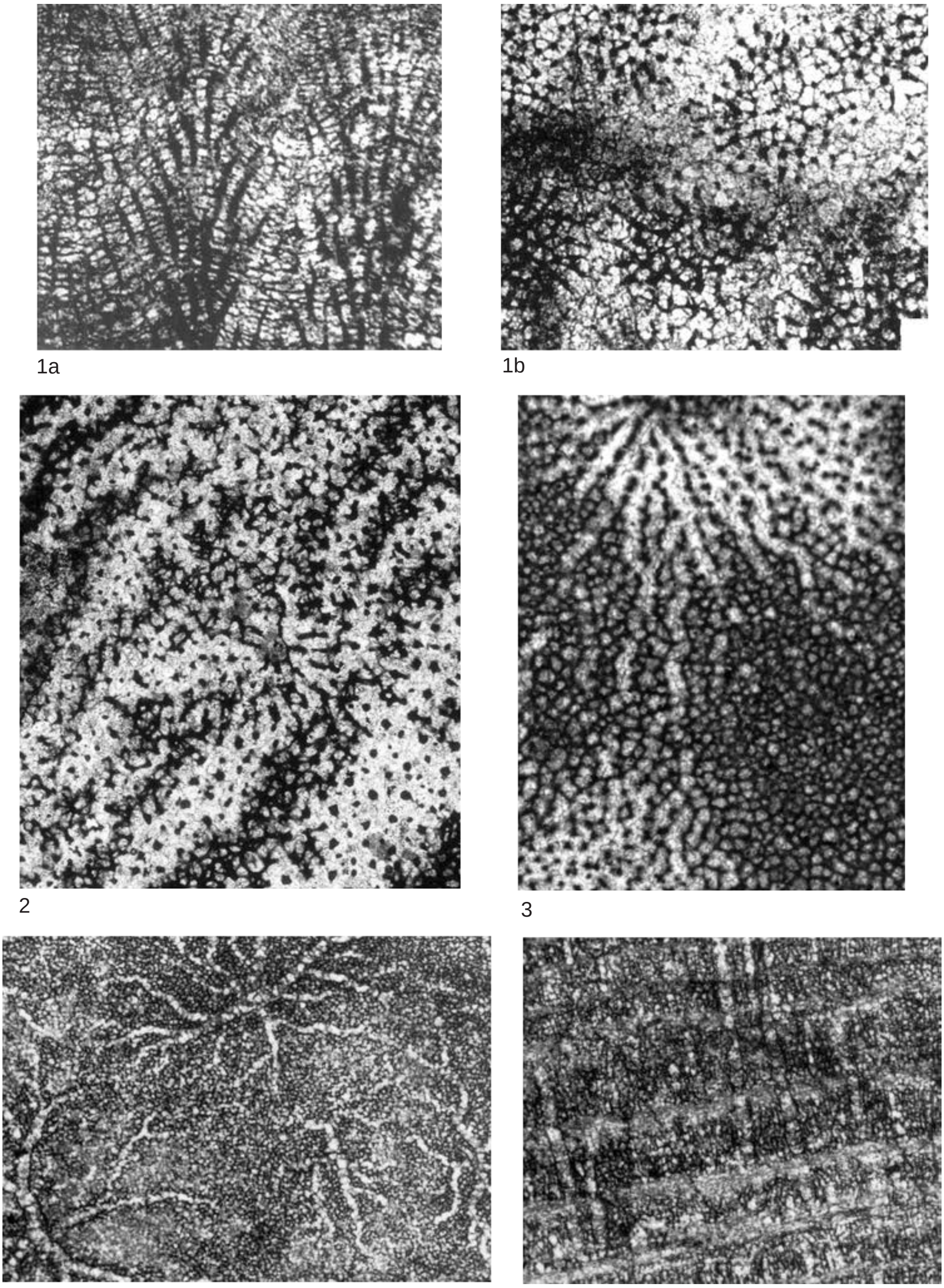

FIG. 327. *1a–b,* Columns of pillars and microcolliculi in *Pseudolabechia granulata* Yabe & Sugiyama, 1930, USNM 458898, ×10 (Stearn & others, 1999); *2,* Astrorhizal paths in open skeleton of *Actinostroma expansum* (Hall & Whitfield, 1873), tangential section, GSC 65823A, Givetian, Dawson Bay Formation, Manitoba, Canada, ×10 (Stearn, 2011a); *3,* astrorhizal paths in tangential section of *Atelodictyon* sp., UWA 140816, Frasnian Pillara Limestone, Canning Basin, Australia, ×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 (Stearn [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 Stearn's (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

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

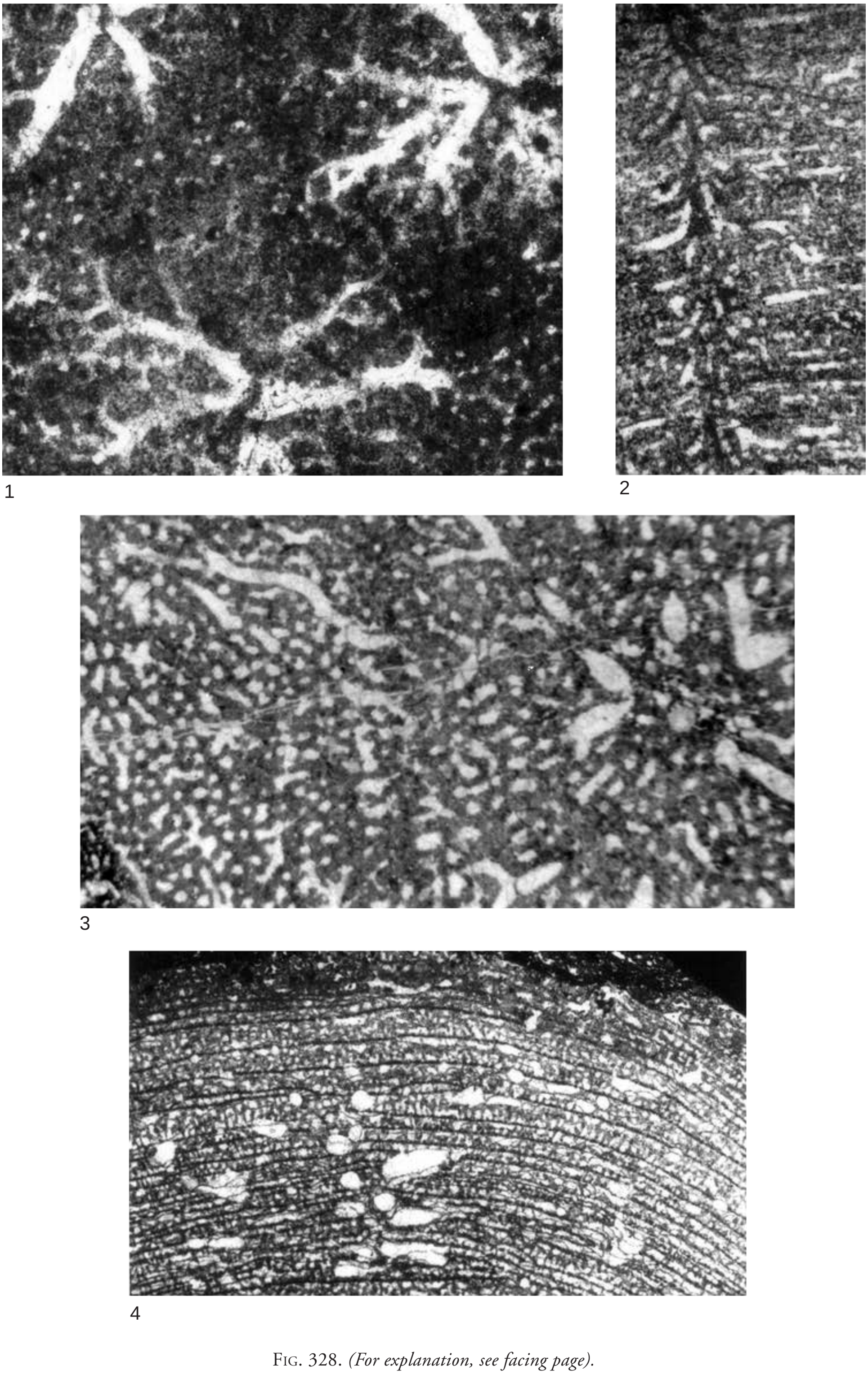

FIG. 328. *(For explanation, see facing page).*

longitudinal axial canal of superposed astrorhizae, and its function is problematic.

GALLERIES, ALLOTUBES, AND AUTOTUBES

The spaces between structural elements were called galleries by Galloway (1957) 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 stromatoporids. 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 pseudozooidal 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 (Stearn, 1986).

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

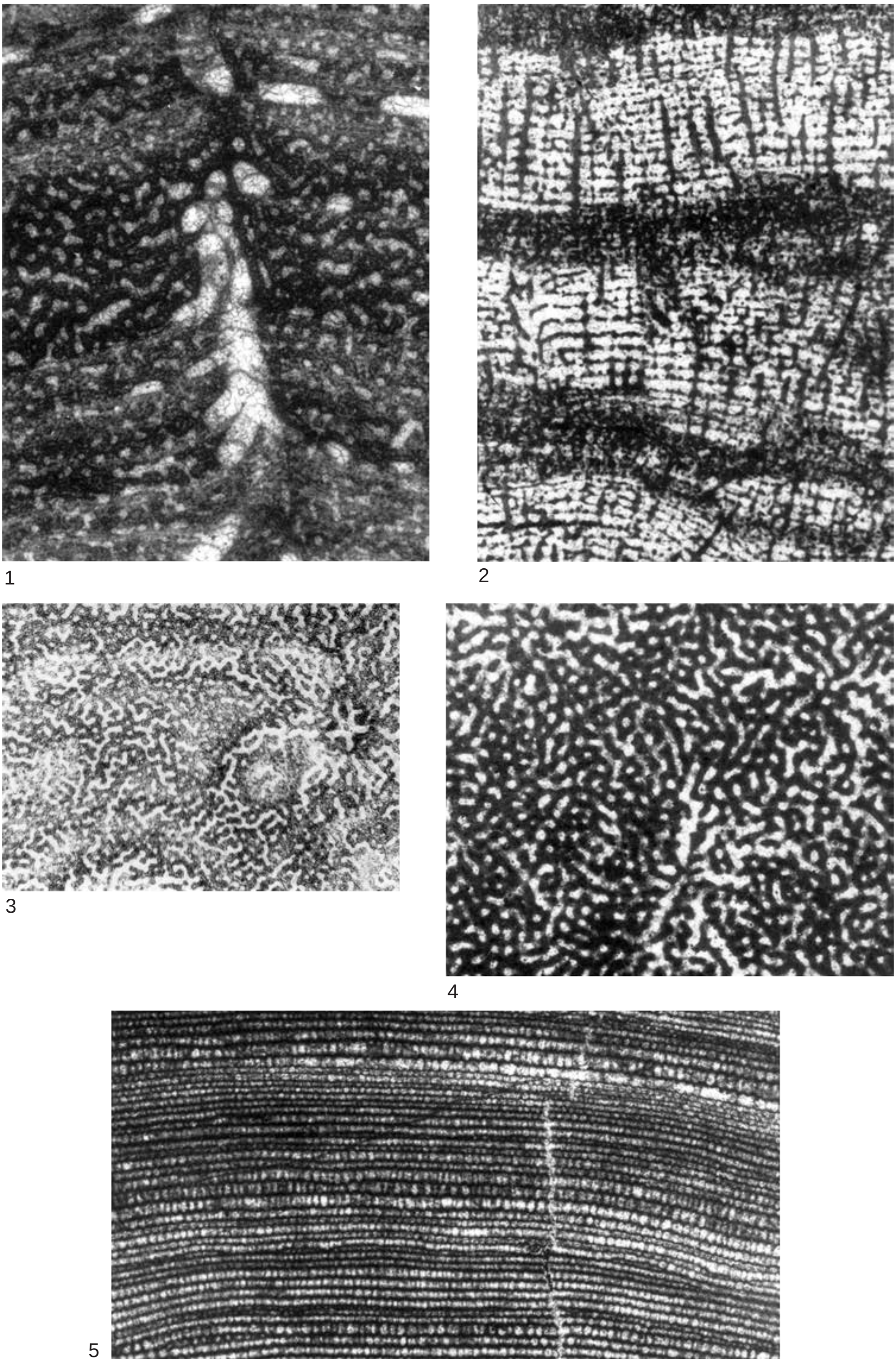

FIG. 329. *(For explanation, see facing page).*

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 peritheca and related them to the epitheca 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, ×10 (Stearn, 2011a); *2,* latilaminate 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, ×10 (Stearn, 2011a); *3,* allotubes between pachysteles and traces of astrorhizae, tangential section; *Pseudotrupetostroma vitreum* (Galloway, 1960), GSC 104890, Givetian, Evie Lake reef, northeastern British Columbia, Canada, ×6 (Stearn, 2011a); *4,* allotubes, autotubes, and astrorhizae, tangential section; *Syringostromella labyrinthea* Stearn, 1990, GSC 95779, Lochkovian, Stuart Bay Formation, Bathurst Island, arctic Canada, ×8 (Stearn, 2011a); *5,* spacing phases, longitudinal section, *Clathrodictyon ellesmerense* Stearn, 1983a, SCRM 110-275, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×10 (Stearn, 2011a).

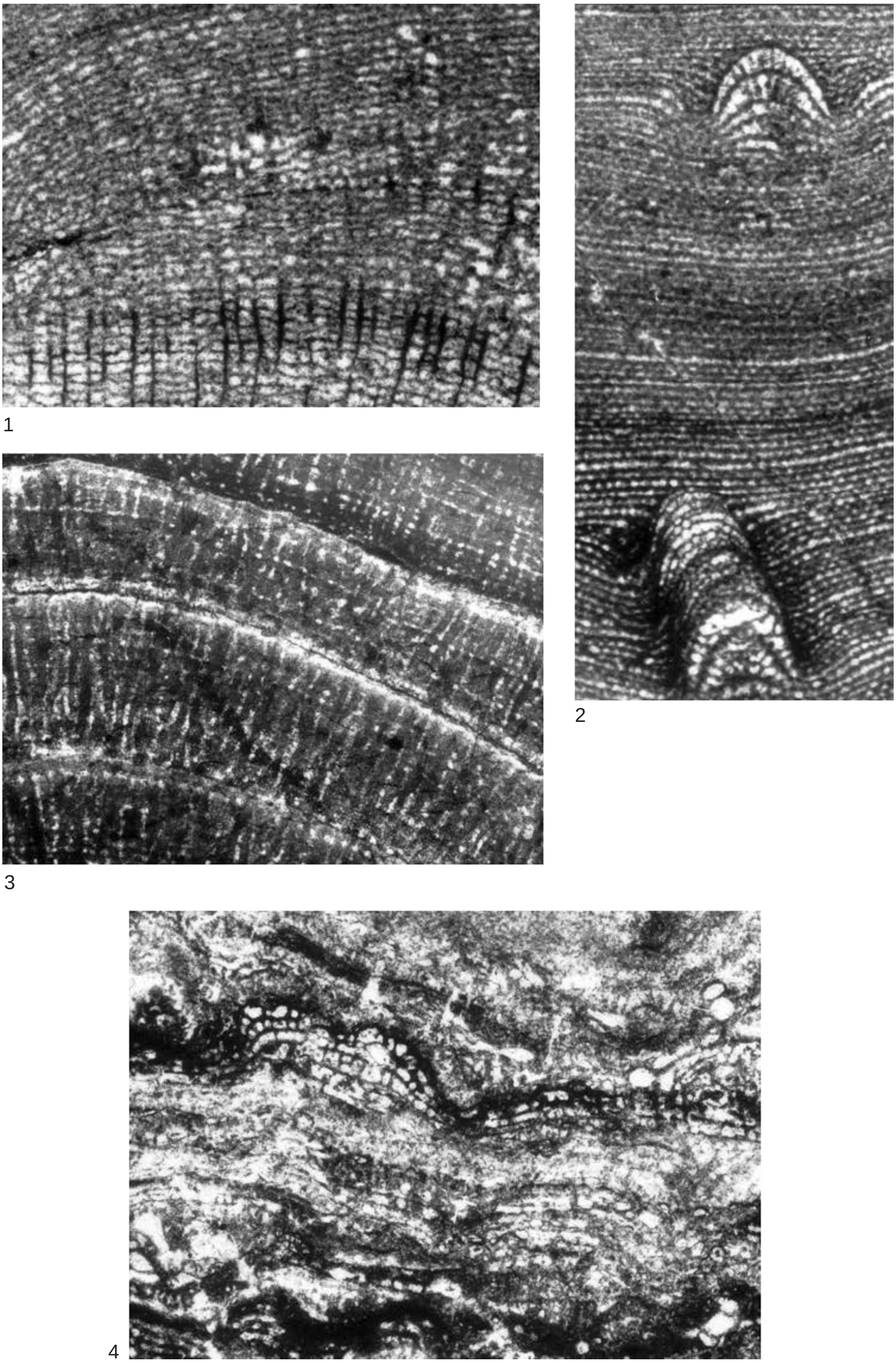

FIG. 330. *(For explanation, see facing page).*

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 protocoenostea 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 stromatoporoids and could be incorporated as growth proceeded. Some may be difficult to distinguish from the different phases of a single stromatoporoid species, and some have been described as an integral part of the skeleton (Fig. 330.4). In enclosing foreign organisms, the stromatoporoids resemble many living sponges and in particular the hypercalcified sponges that are closely intergrown with serpulid worm tubes (Hartman & Goreau, 1970).

The most common associated organisms are 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, stromatoporoids 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 stromatoporoids are missing a layer present in free-standing specimens and suggested that those growing in company with stromatoporoids did not need as much support. Young and Noble (1989) and May (1999) have discussed the relationship of syringoporids to stromatoporoids. Stearn (1956) has described a similar relationship between a phaceloid amplexoid rugosan and a stromatoporoid. Certain species of stromatoporoid are more

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, ×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, ×10 (Stearn, 2011a); *3,* latilaminate growth and distinct basal phases at base of each latilamina; *?Syringostromella discoidea* (Lonsdale, 1839), SCRM 50-17, Wenlock Limestone, Shropshire, England, ×10 (Stearn, 2011a); *4,* interlayering of structures suggestive of algae and stromatoporoid alternating, longitudinal section; *Clathrocoilona vexata* Prosh & Stearn, 1996, GSC 108881, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×10 (Stearn, 2011a).

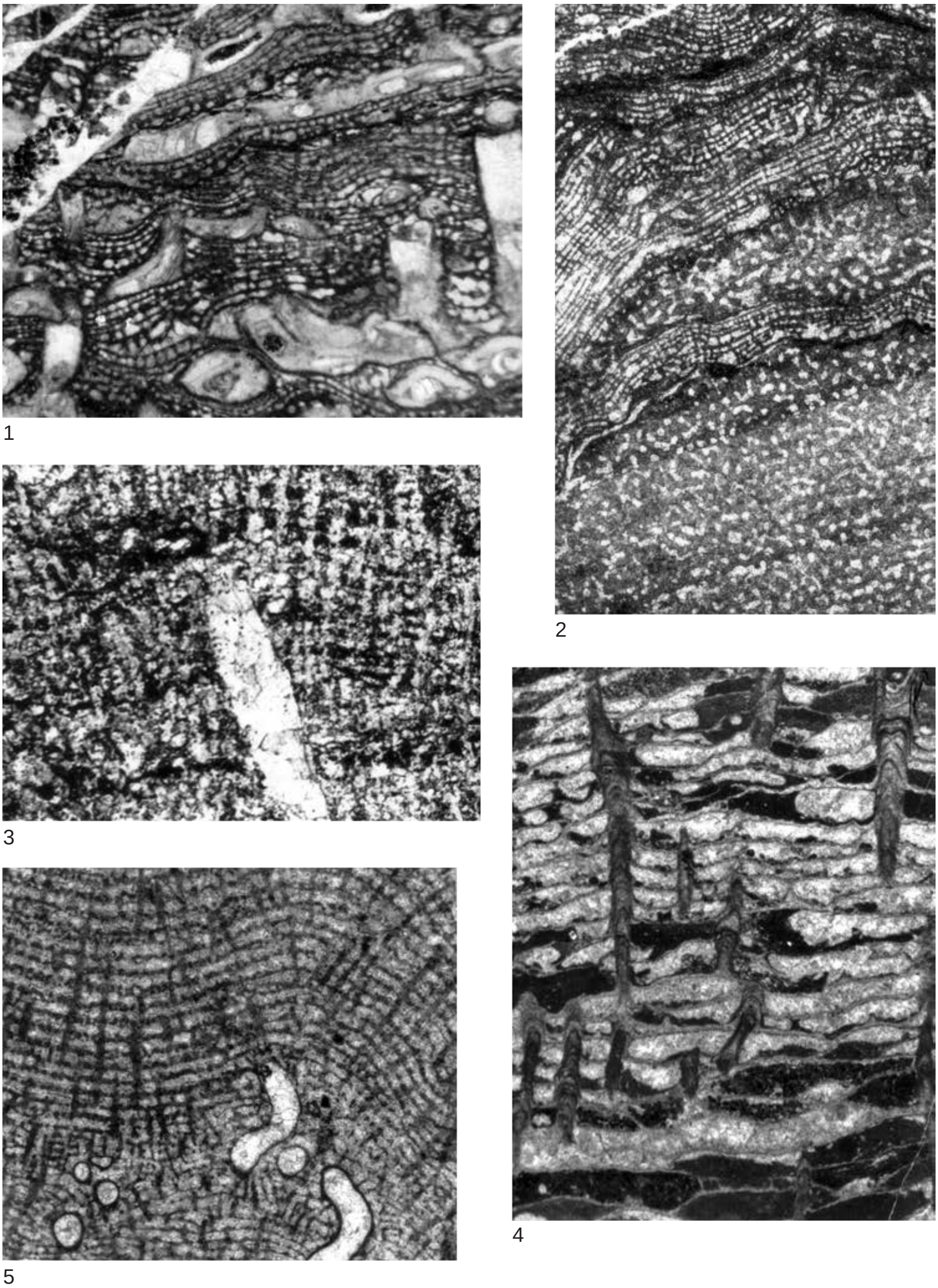

FIG. 331. *1,* Syringoporid tubes intergrown with stromatoporoid (caunopore state), longitudinal section; *Gerronostromaria septentrionalis* (PROSH & STEARN, 1996), SCRM 130-20, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×7 (Stearn, 2011a); *2,* intergrowth of two competing stromatoporoids alternating in dominance, longitudinal section; *Stromatopora polaris* STEARN, 1983a, below, *Gerronostromaria septentrionalis* (PROSH & STEARN, 1996), to left, SCRM 110-342, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×10 (Stearn, 2011a); *3, Trypanites* sp., boring in poorly preserved *Hermatoporella* cf. *pycnostylota* (STEARN, 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. *Heliolites*, in particular, commonly forms thin interlayers where stromatoporoid growth stopped and then resumed overgrowing the coral. *Alveolites* is also commonly intergrown with stromatoporoids, particularly in Devonian rocks. Among algae and *incertae sedis*, *Girvanella*, *Rothpletzella*, and *Wetheredella* are widely distributed associates along growth stoppage surfaces and can be confused with stromatoporoid structures (POWELL, 1991). The stromatolitic cyanobacterium *Cliefdenia* has been shown by WEBBY (1991) to have kept pace while growing within some Ordovician labechiids (Fig. 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, ×10 (Stearn, 2011a); *4, Cliefdenia* WEBBY, 1982, cyanobacterium in labechiid stromatoporoid, *Labechiella variabilis* (YABE & SUGIYAMA, 1930), UTGD 96366; Upper Ordovician, Benjamin Limestone, Tasmania, Australia, ×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, ×8 (Stearn, 2011a).

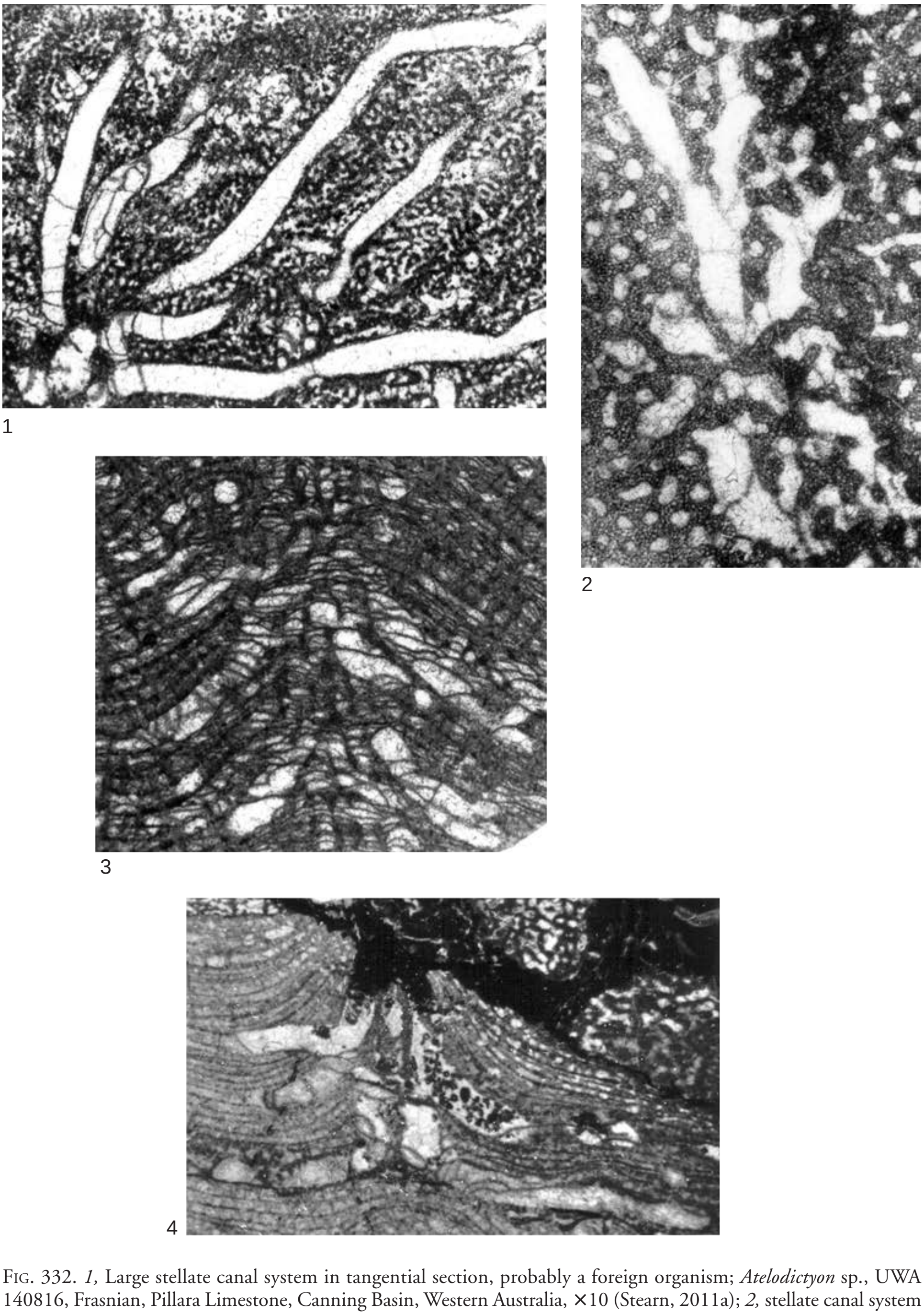

Fig. 332. *1,* Large stellate canal system in tangential section, probably a foreign organism; *Atelodictyon* sp., UWA 140816, Frasnian, Pillara Limestone, Canning Basin, Western Australia, ×10 (Stearn, 2011a); *2,* stellate canal system in tangential section, probably a foreign organism in *Salairella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

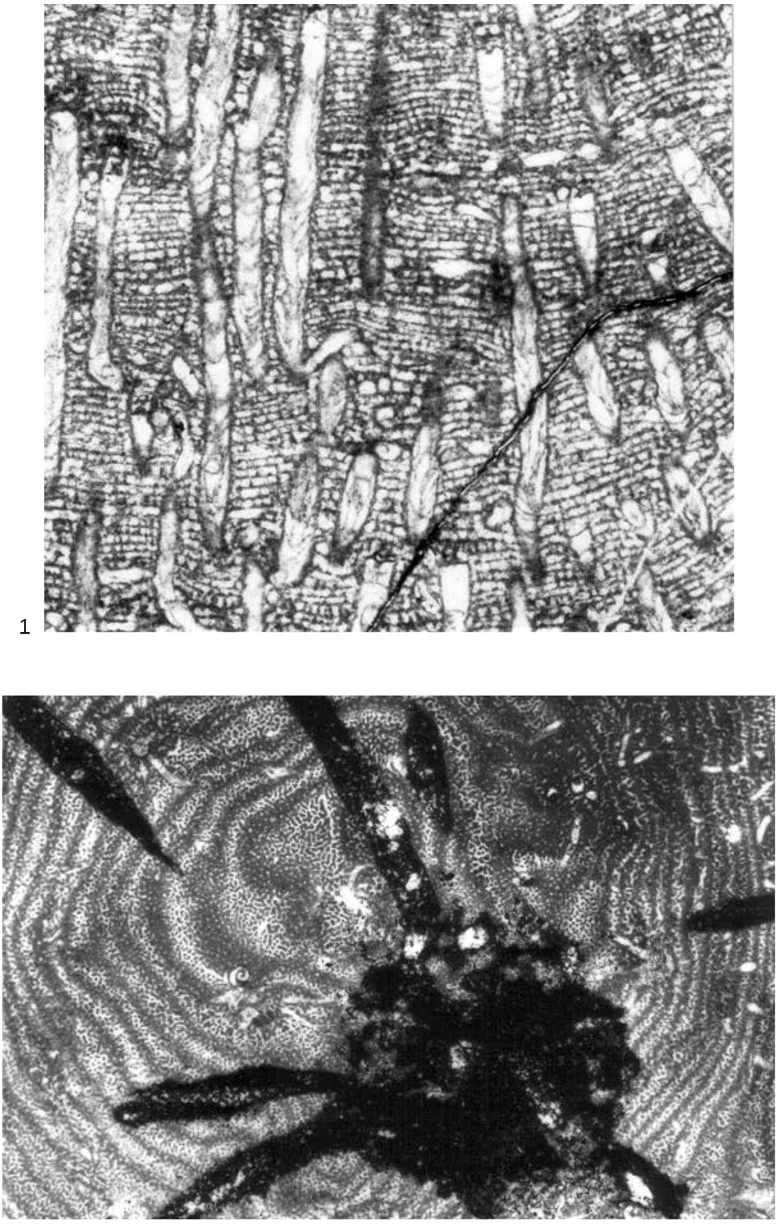

FIG. 333. *1,* Stromatoporoid extensively intergrown with syringoporid (caunopora state), longitudinal section; *Gerronostromaria septentrionalis* (PROSH & STEARN, 1996), GSC 108862, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×10 (Stearn, 2011a); *2,* large complex boring of *Topsentopsis* sp. in tangential section in *Petridiostroma* sp., SCRM 126-131, Emsian–Eifelian, Truro Island, arctic Canada, ×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. KAŹMIERCZAK (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 KAŹMIERCZAK could be traces of foreign orgamisms. By 1976, KAŹMIERCZAK 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 KAŹMIERCZAK in 1980 and 1981 using evidence from other specimens and scanning electron micrographs. In 1990, KAŹMIERCZAK 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×. 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 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. 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** (STEARN & others, 1999).

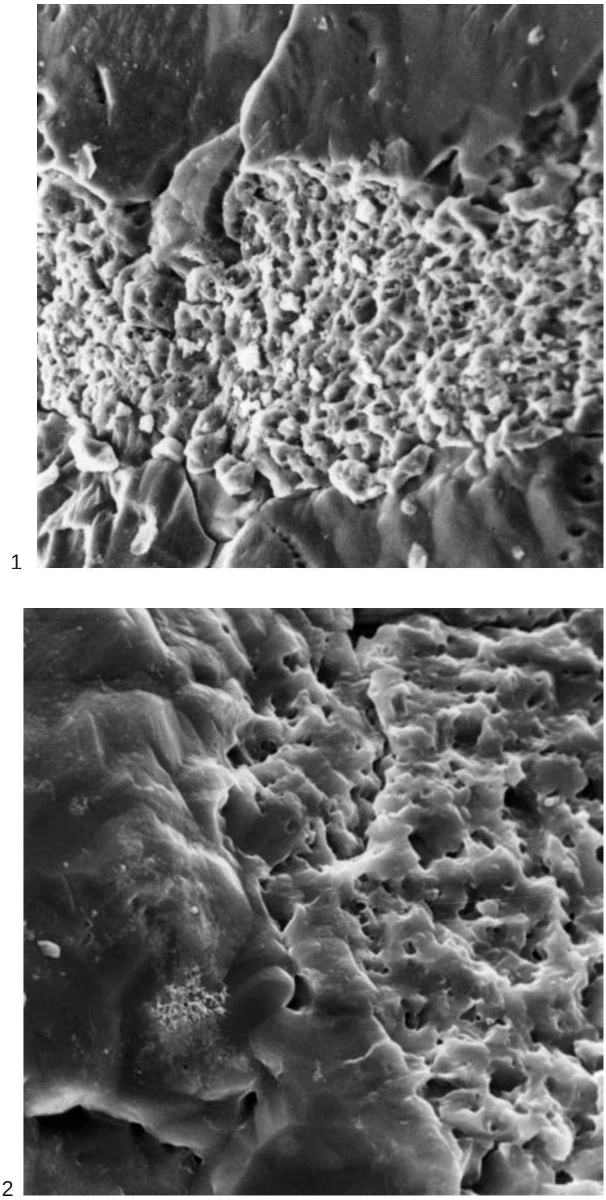

FIG. 334. *1,* SEM, finely crystalline structural element with cavities bounded by solid cement crystals in galleries; *Anostylostroma* sp., SCRM 21-1, Emsian, Bois Blanc Limestone, Gorrie, southwestern Ontario, Canada, ×700 (Stearn, 2010b); *2,* SEM, edge of structural element showing contrast of structure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

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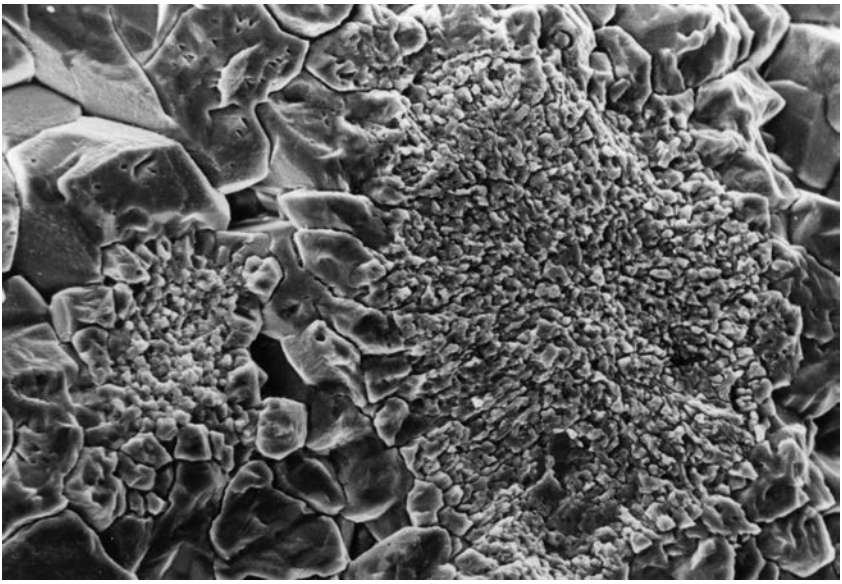

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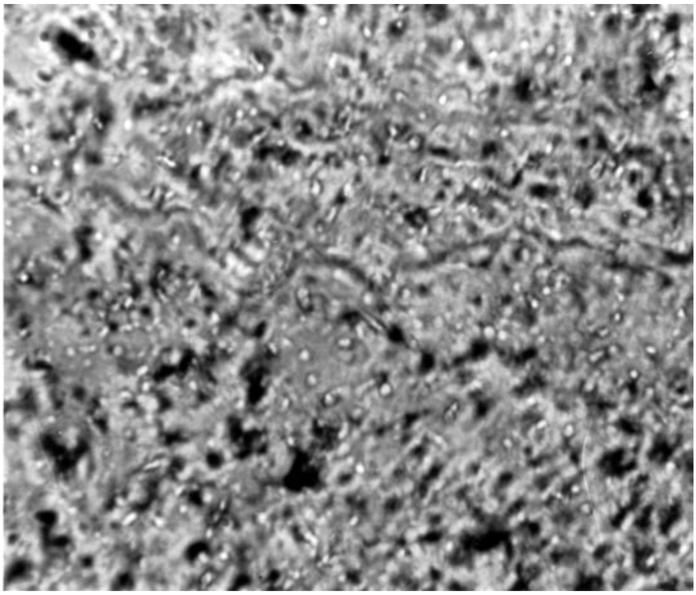


FIG. 335. *1,* SEM, cement crystals in galleries meeting at triple junctions and lack of rim cement, longitudinal section, *Stictostroma mccannelli* FAGERSTROM, 1961, UMMP ?36199, Emsian-Eifelian, Formosa Reef, southwestern Ontario, Canada, ×590 (Stearn, 2010b); *2,* fluid inclusions in ultrathin section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

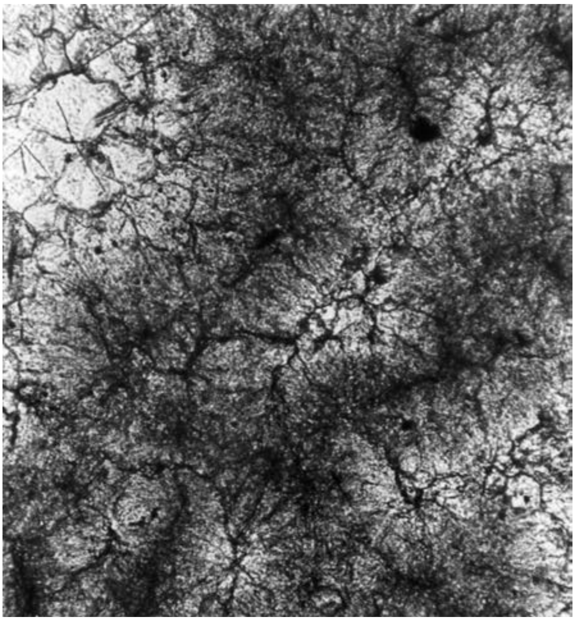
Structural elements contain rows of subspherical voids (cellules) separated by a fine, three-dimensional, rectilinear network of micropillars and microcolliculi (posts and beams) (Fig. 339.3; and see Fig. 472). Where the micropillars are perpendicular to the axis of laminae-pachystromes and the microcolliculi are parallel to the axes of laminae, microreticulate microstructure is distinguished as **orthoreticular** (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 **clinoreticular** (Fig. 342.1b; Fig. 458*c*). Where orientation of micropillars and microcolliculi is without order, the microstructure is said to be **acosmoreticular** (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 µm), 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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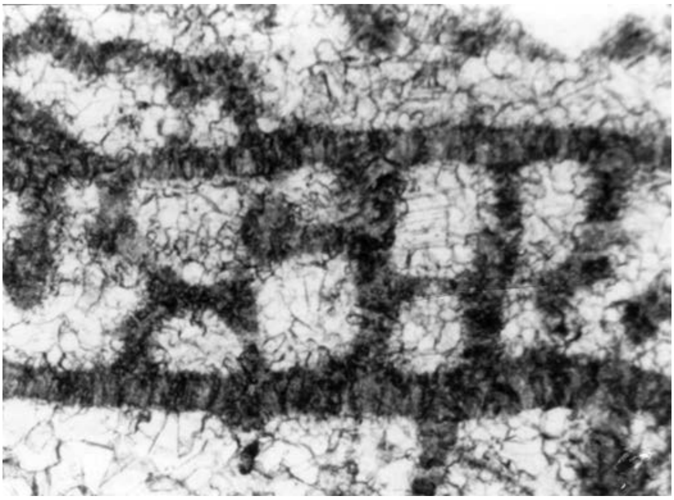
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FIG. 336. *1,* Transversely fibrous microstructure and center of calcification; *Amphipora* sp., GSC 54924, Emsian-Eifelian, Ogilvie Formation, Yukon Territory, Canada, ×150 (Stearn, 2010b); *2,* transversely fibrous laminae and pillars, longitudinal section, *Hammatostroma albertense* STEARN, 1961, holotype, GSC 15318, Frasnian, Cairn Formation, western Alberta, Canada, ×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

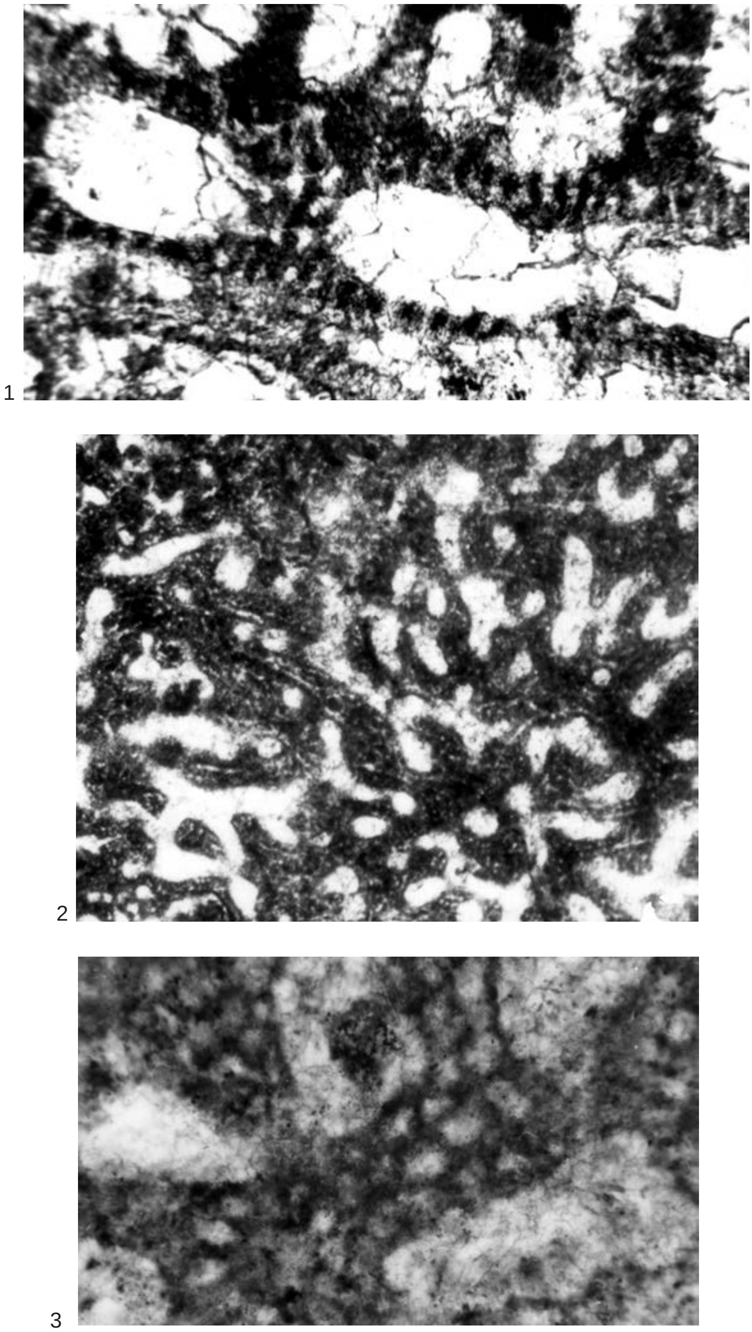


Fig. 337. *1,* Transversely porous laminae and pillar, longitudinal section, *Gerronostromaria elegans* Yavorsky, 1931, paratype, YPM.227561, Middle Devonian, Kuznetsk Basin, Russia, ×100 (Stearn, 2010b); *2,* tubulate microstructure, tangential section, *Stictostroma? nunavutense* Prosh & Stearn, 1996,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

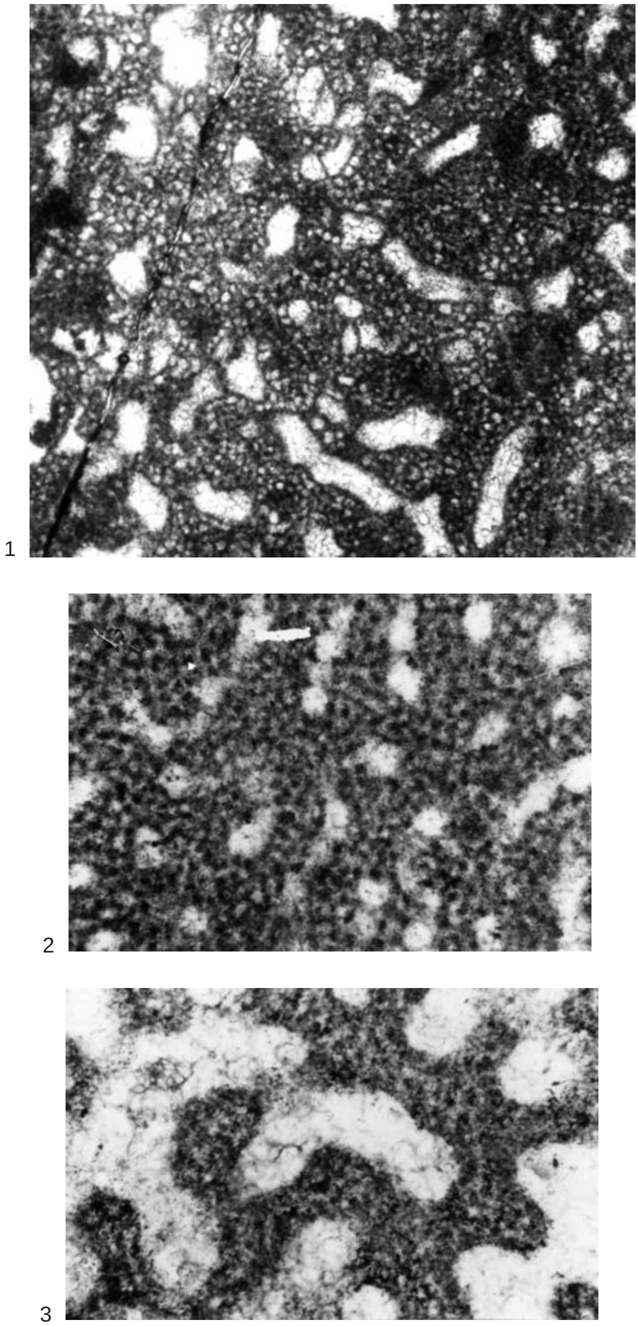


FIG. 338. *1,* Coarse cellular microstructure, tangential section, *Syringostromella zintchenkovi* (KHALFINA, 1961d), GSC 108897, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×25 (Stearn, 2010b); *2,* tangential section of Figure 340.1*, Syringostromella carteri* NICHOLSON, 1891b, Nicholson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

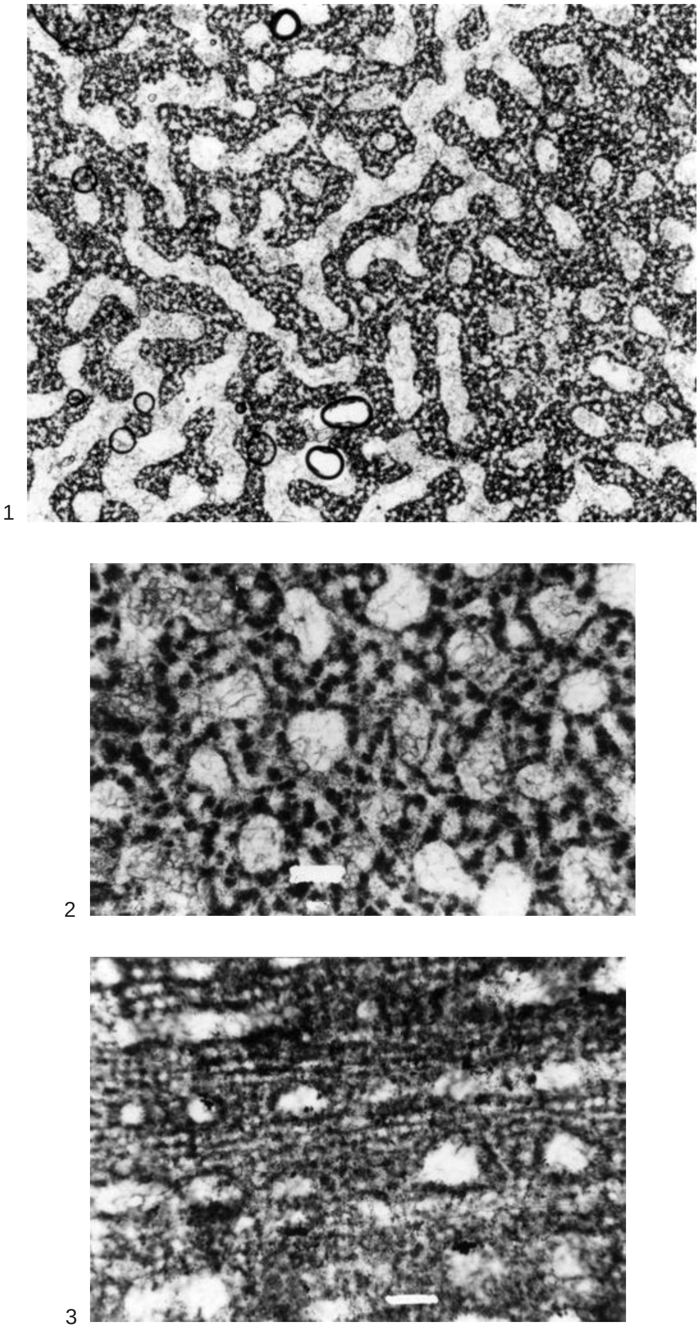
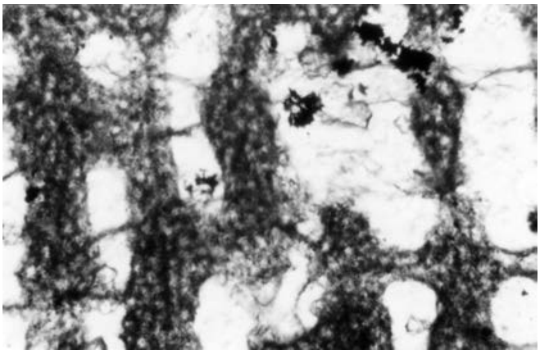


FIG. 339. *1,* Cellular microstructure grading into melanospheric, tangential section, *Pseudotrupetostroma vitreum* (GALLOWAY, 1960), GSC 48453A, Givetian, Evie Lake Reef, northeastern British Columbia, Canada, ×25 (Stearn, 2010b); *2,* opaque (dark) cut ends of rodlike micropillars in pachysteles in tangential section, *Parallelopora ostiolata* BARGATZKY, 1881a, holotype, Nicholson 125, NHM P5936, Middle Devonian, Büchel, Rhineland, western Germany; note also round autotubes, ×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, ×50 (Stearn, 2010b).



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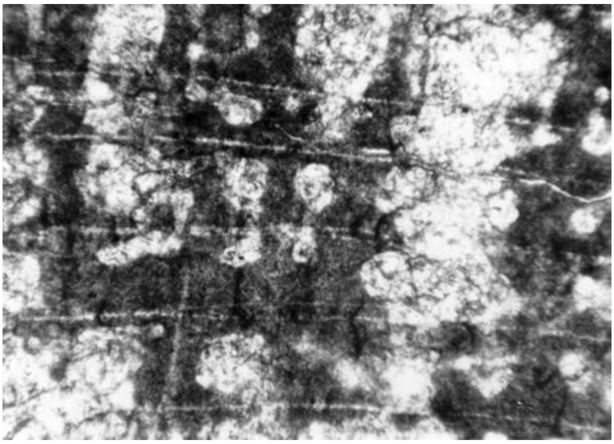

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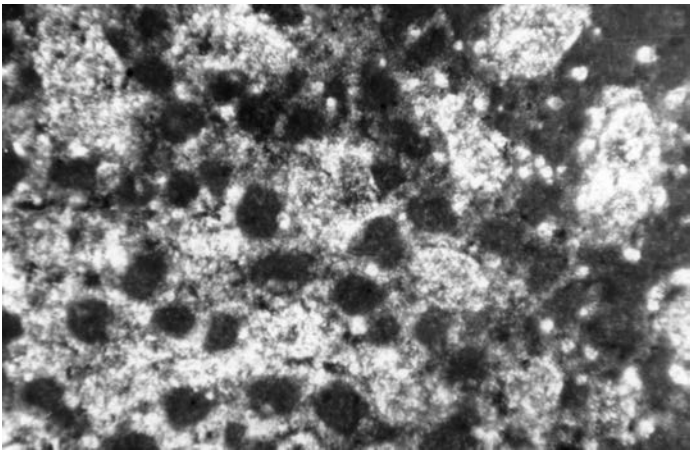

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FIG. 340. *1,* Cellular microstructure in pachysteles, longitudinal section, *Syringostromella carteri* NICHOLSON, 1891b, Nicholson 37, MNH P5678, Wenlock, Shropshire, England, ×55 (Stearn, 2010b); *2,* vacuoles (round holes) in compact pillars, longitudinal 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, ×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, ×50 (Stearn, 2010b).

type species of *Parallelopora,* the microreticulation is very coarse and the micropillars appear as dark (opaque) rods within the network of pachysteles (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× 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 µm 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 µm) 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 (Stearn & 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 (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. 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

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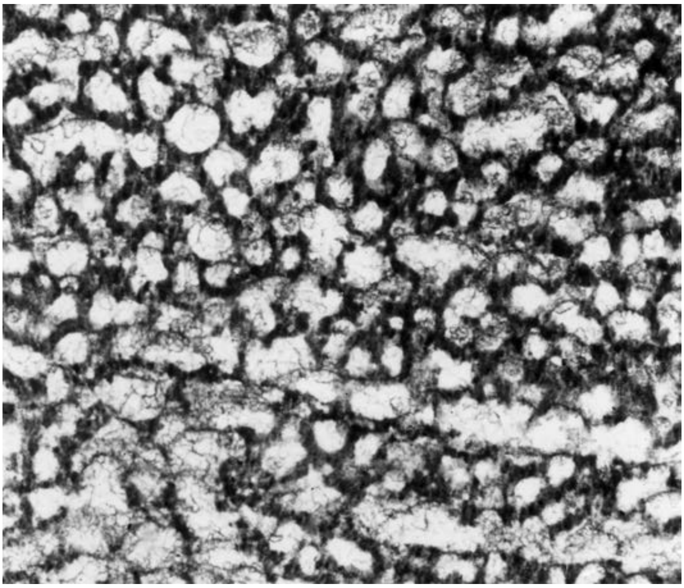

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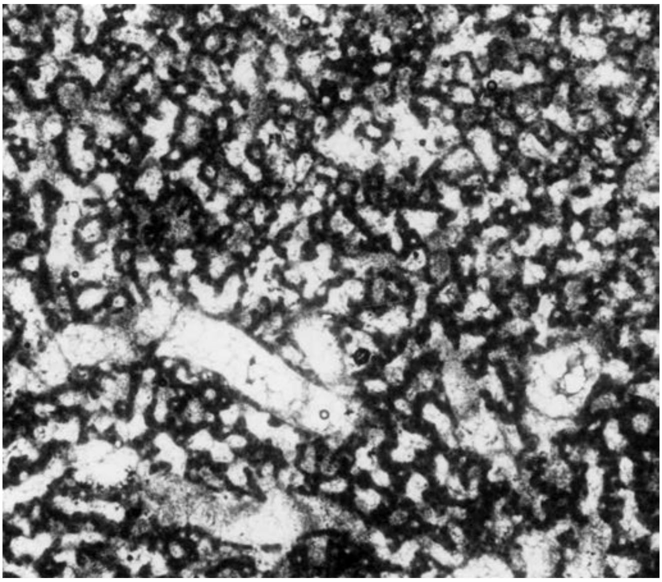

FIG. 341. *1,* Vacuolate microstructure with traces of melanospheres, longitudinal section, *Arctostroma contextum* (STEARN, 1963), holotype, GSC 16856, Frasnian, Mikkwa Fortmation, Mikkwa River, northern Alberta, ×25 (Stearn, 2010b); *2,* compact irregular structural elements enclosing round vacuoles,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

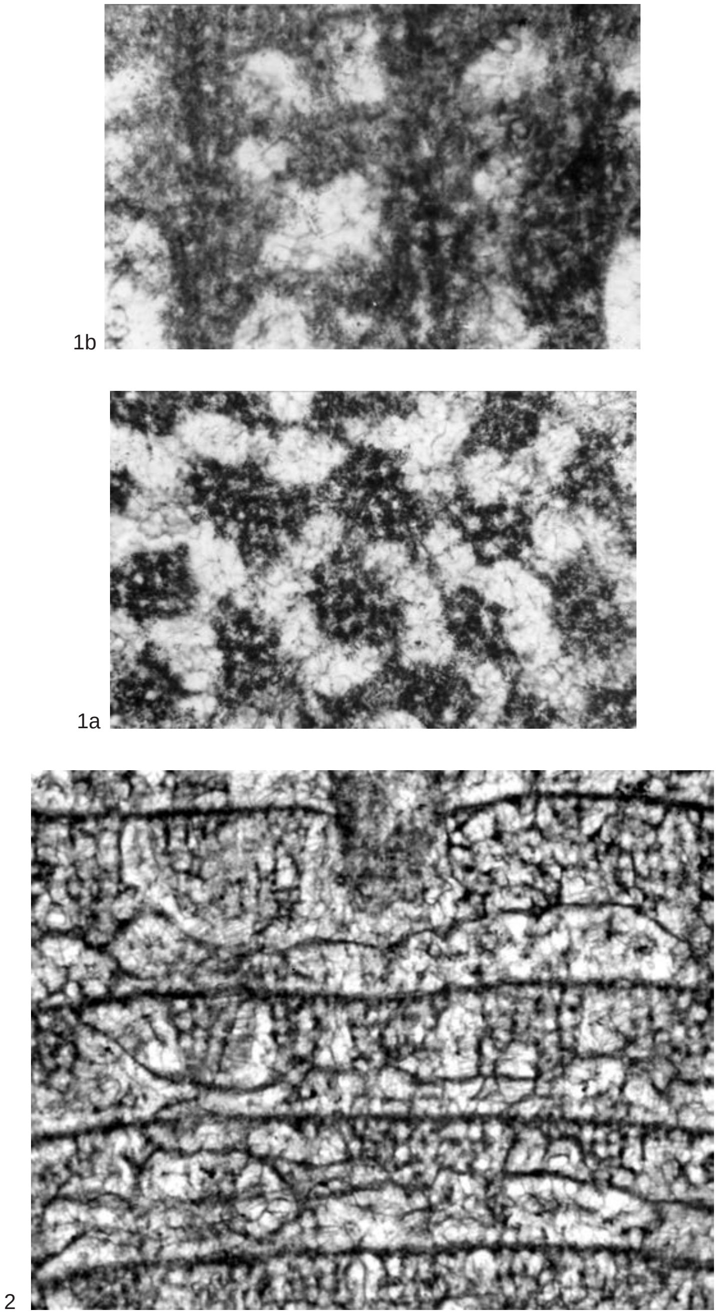

FIG. 342. *1a–b,* clinoreticular microstructure of pachysteles, longitudinal and tangential sections, *Syringostroma nodulatum* (NICHOLSON, 1875), Nicholson 310, NHM P5604, Middle Devonian, Ohio, USA, ×55 (Stearn, 2010b); *2,* coarse clinoreticular microstructure in pachysteles, longitudinal section,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

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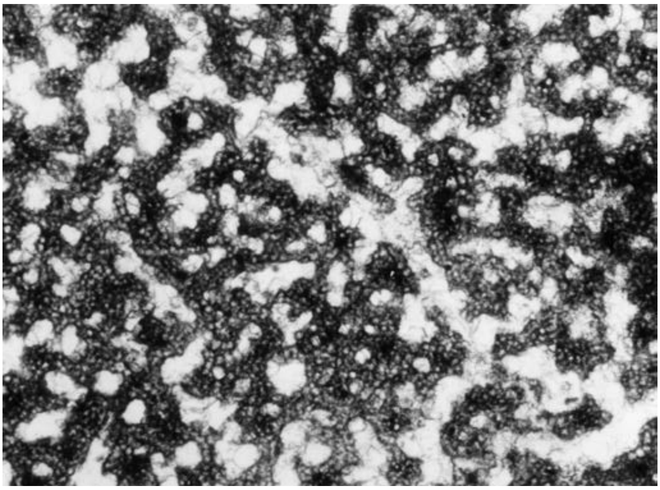

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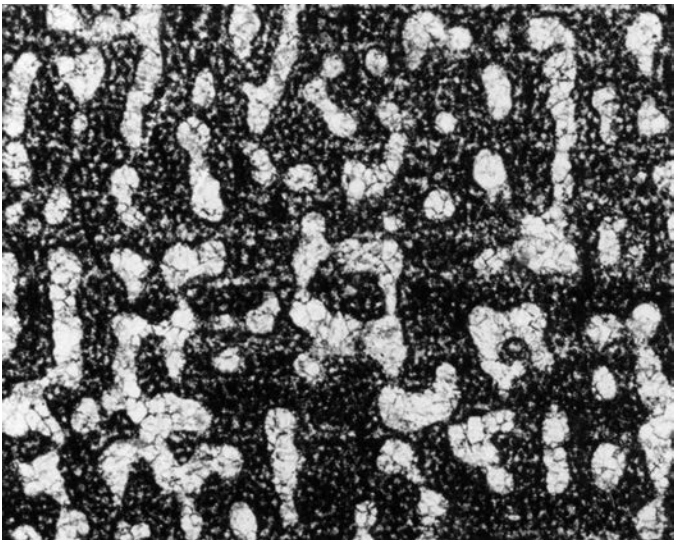

FIG. 343. *1,* Cellular microstructure, tangential section, *Salairella prima* KHROMYKH, 1971, hypotype, GSC 108901, Emsian, Blue Fiord Formation, Ellesmere Island, arctic Canada, ×25 (Stearn, 2010b); *2,* coarse cellular microstructure in pachysteles, longitudinal section, *Pseudotrupetostroma vitreum*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

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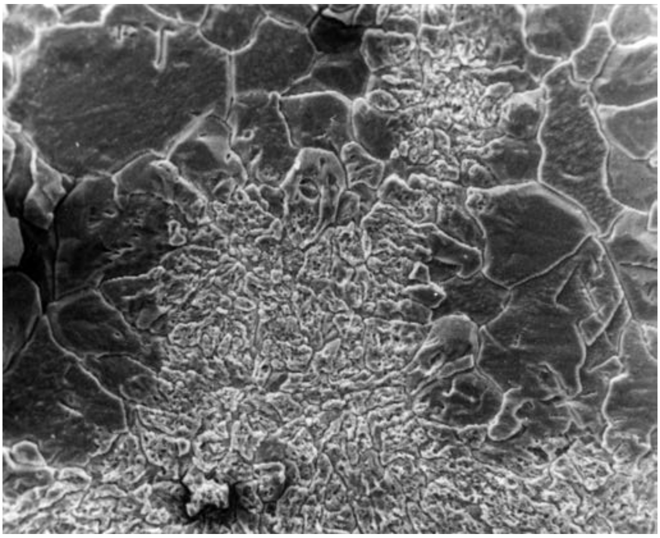

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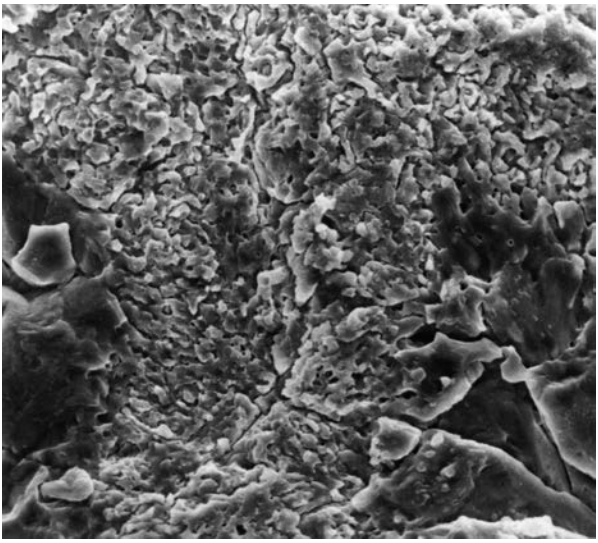
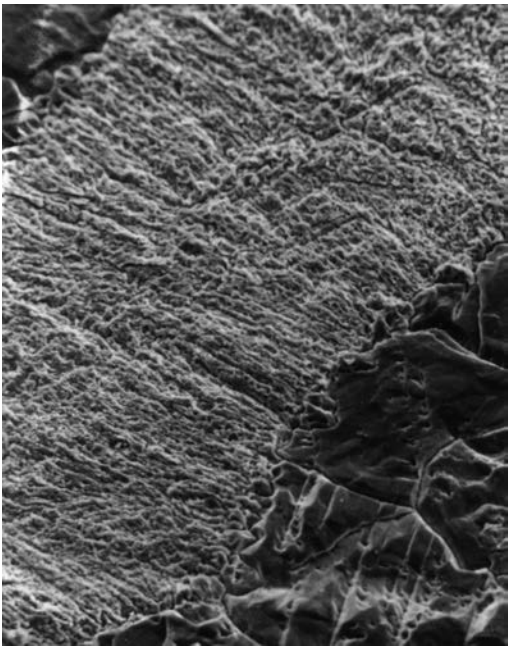


FIG. 344. *1,* SEM, radial fibrosity in pillars and rim cements of fine crystals, tangential section, *Actinostroma clathratum* NICHOLSON, 1886a, SCRM 96-09, ×480, scale bar, 100 µm (Stearn, 2010b); *2,* SEM, fibrosity in pillars, longitudinal section, *Actinostroma clathratum*, SCRM 96-09, hypotype, RM 14813, Frasnian, Duperow Formation, Esterhazy shaft, Saskatchewan, Canada, ×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 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.



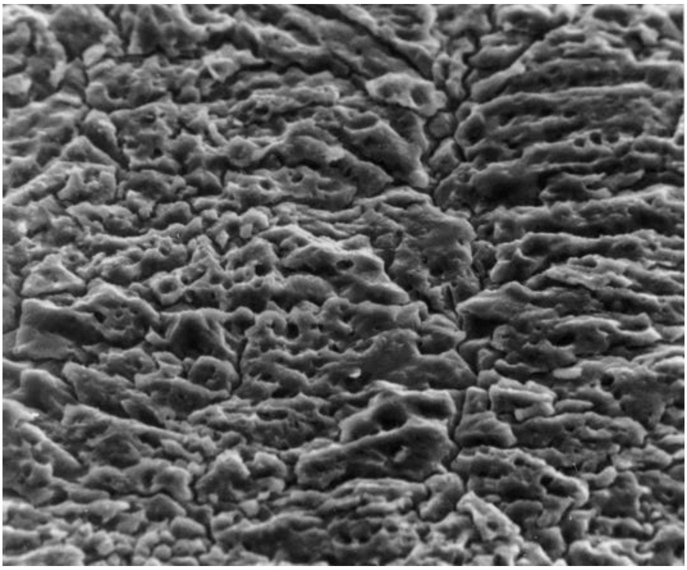


FIG. 345. *1,* SEM, structural element showing fibrosity and central axis, longitudinal section, *Hammatostroma albertense* STEARN, 1961, SCRM 67-21, Frasnian, Cairn Formation, Mt. Haultain, western Alberta, ×230 (Stearn, 2010b); *2,* SEM, coarse fibrosity and axial line in *Amphipora* sp., GSC 26144,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

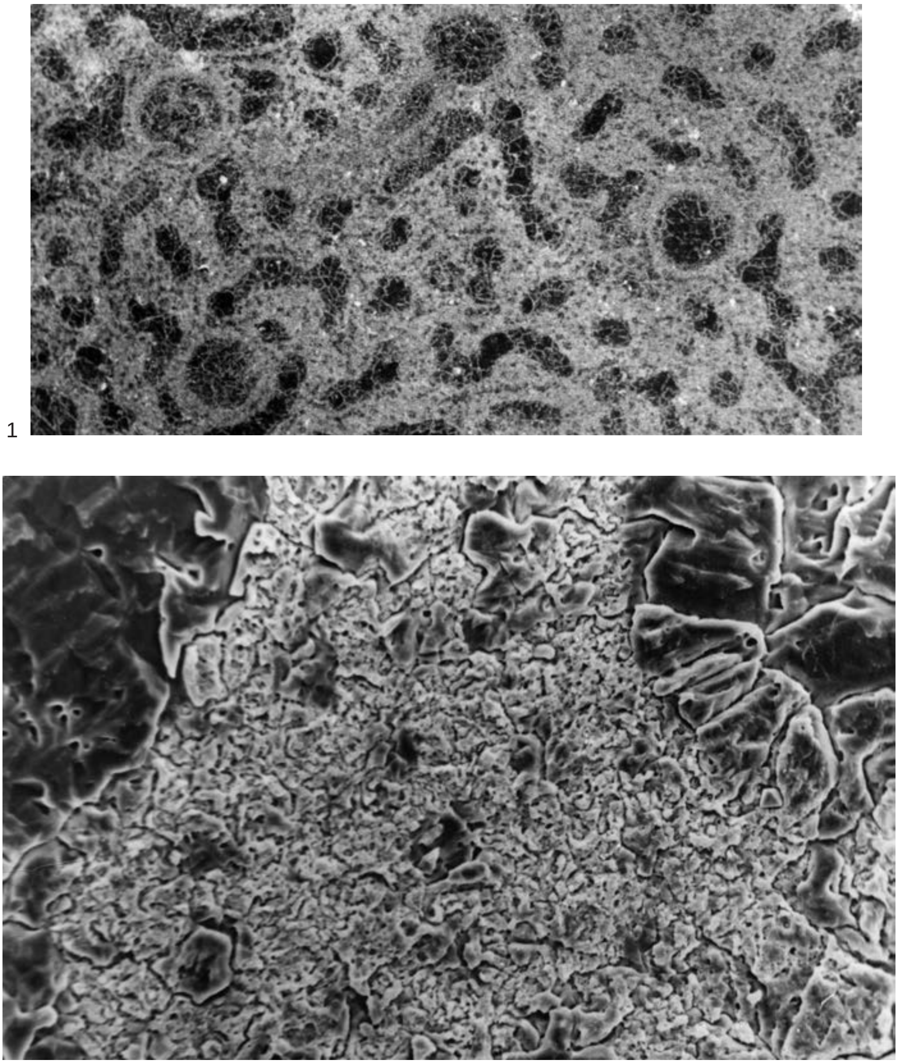


FIG. 346. *1,* SEM, cellular microstructure of pachysteles, tangential section, *Salairella buecheliensis* (BARGATZKY, 1881a), SCRM 116-1, Givetian, Blacourt Formation, Boulonnais, France, ×34 (Stearn, 2010b); *2,* SEM, cellular microstructure, longitudinal section, *Salairella buecheliensis* (BARGATZKY,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

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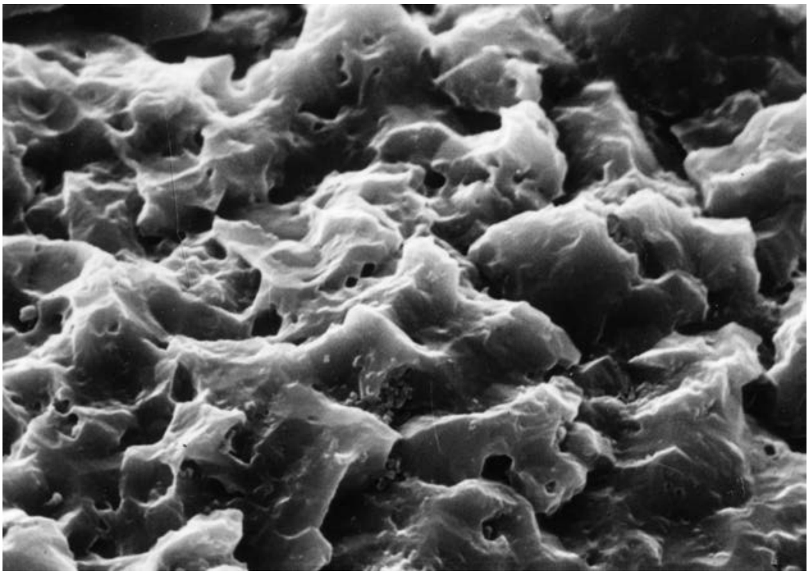

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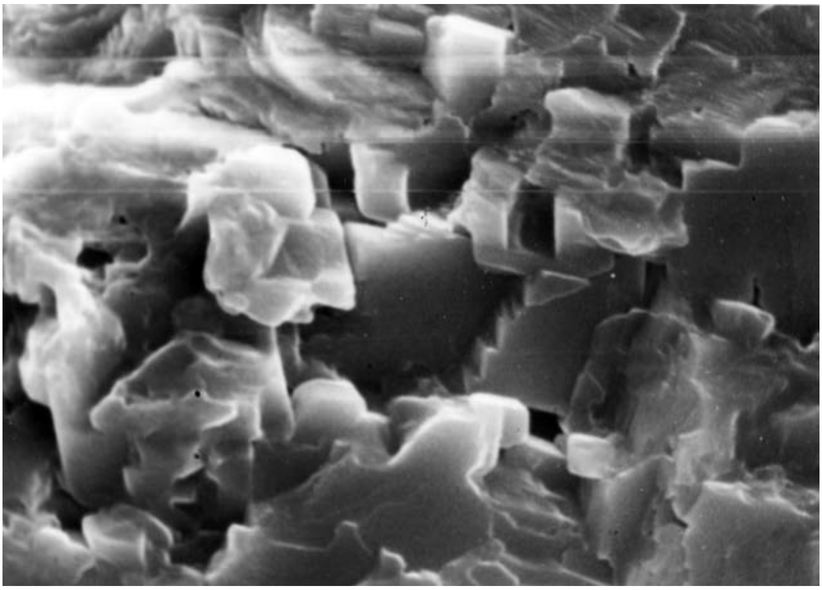

Fig. 347. *1,* SEM, cavities in structural elements, some of rhombohedral outline, *Actinostroma* sp., RM 14811, Frasnian, Lime Creek Formation, Iowa, United States, ×4800 (Stearn, 2010b); *2,* SEM, rhombohedral crystals and cavities, *Actinostroma* sp., RM 14811, Frasnian, Lime Creek Formation, Iowa, United States, ×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. 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, 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 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, 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 *Clathrocoilona* (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 microstrucure to the isolation of subspherical regions of inclusion-rich (speck-rich)

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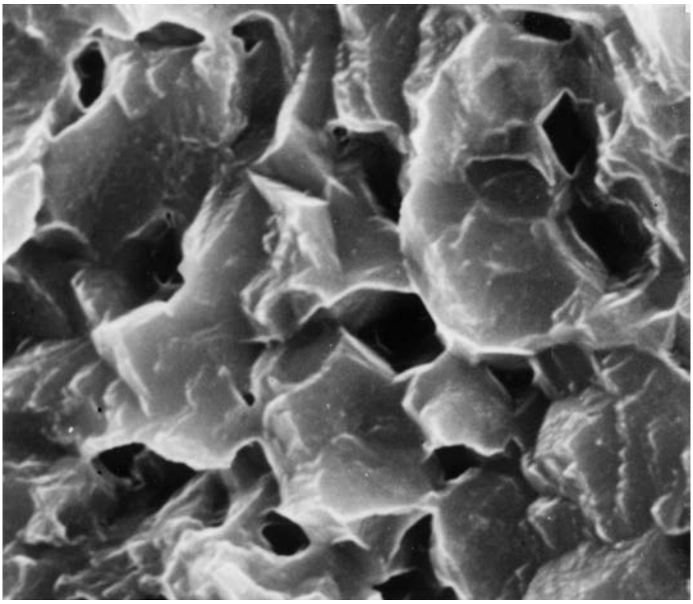

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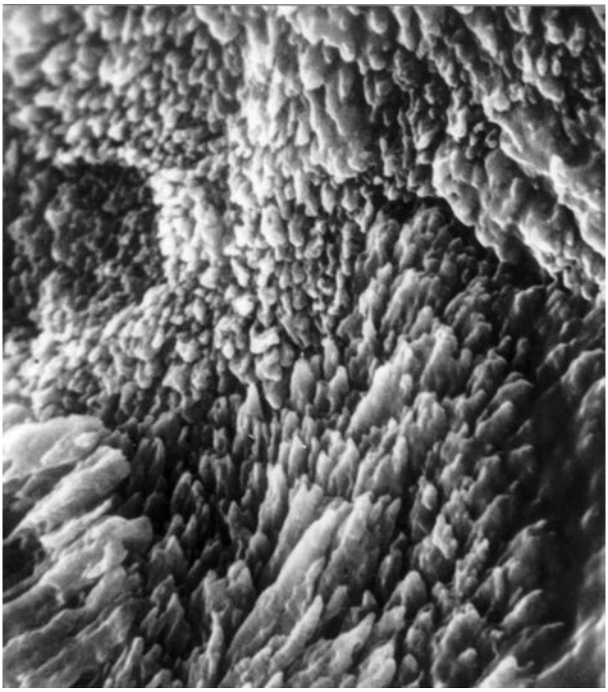


FIG. 348. *1,* SEM, rhombohedral cavities in a structural element, *Actinostroma expansum* (HALL & WHITFIELD, 1873), SCRM 90-31, Frasnian, Shell Rock Formation, Iowa, United States, ×7000 (Stearn, 2010b); *2,* SEM, fibrous aragonite skeleton of *Calcifibrospongia actinostromoides*, Recent, Bahama Island, SCRM 99-9, ×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 KAŹMIERCZAK (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. **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 Stromatoporellida, Stromatoporida, Syringostromatida, Amphiporida, and Genera With Uncertain Affinities (p. 781–836). 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.

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 stromatoporoid animal (see Functional Morphology of the Paleozoic Stromatoporoid 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 stromatoporoid 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 stromatoporoid 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 chaetetids). 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 stromatoporoid 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 stromatoporoids 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 stromatoporoids 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 stromatoporoids 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 tubercules. 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).

STEARN 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* DEFRANCE, 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 hypercalcified sponges, such as *Acanthochaetetes* and *Merlia*, had skeletons that resemble the honeycomb structure of the fossil chaetetids established that this group belongs in the phylum Porifera (see Introduction to the Fossil Hypercalcified 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 hypercalcified 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; KAŹMIERCZAK, 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), KAŹMIERCZAK (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 stromatoporids, 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 stromatoporids. 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 disjectoporids 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 astrorhizae 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 astrorhizae 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 chaetetids. 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 disjectoporids, 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, pachysteles, and pachystromes were also secreted by cyanobacteria. He proposed that the astrorhizae 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. KAŹMIERCZAK 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. KAŹMIERCZAK 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 KAŹMIERCZAK 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 KAŹMIERCZAK 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

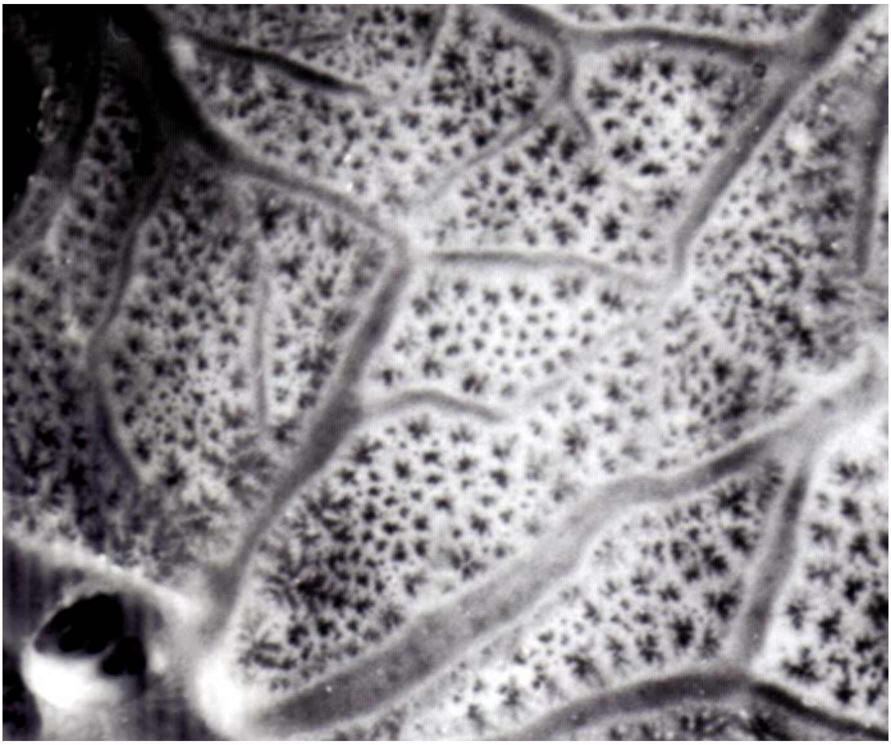
COLIN W. STEARN

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,



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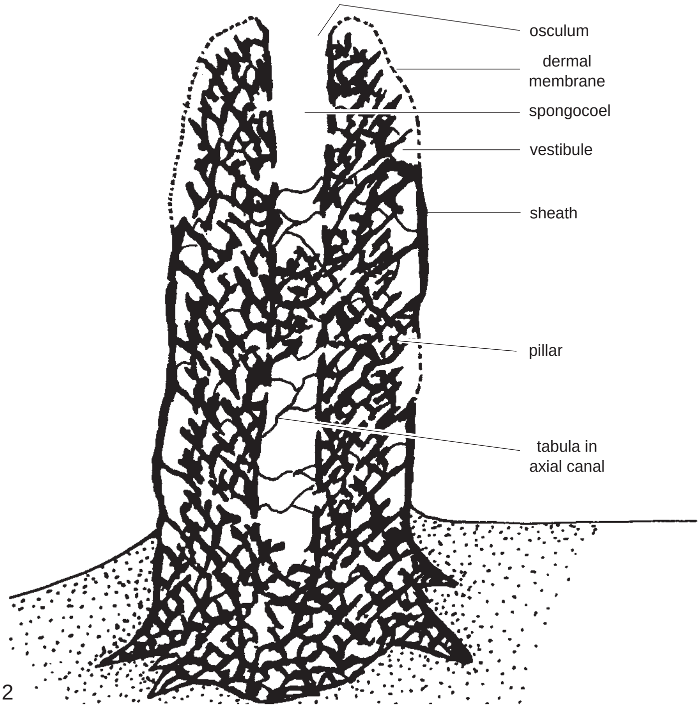

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FIG. 349. *(For explanation, see facing page).*

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).

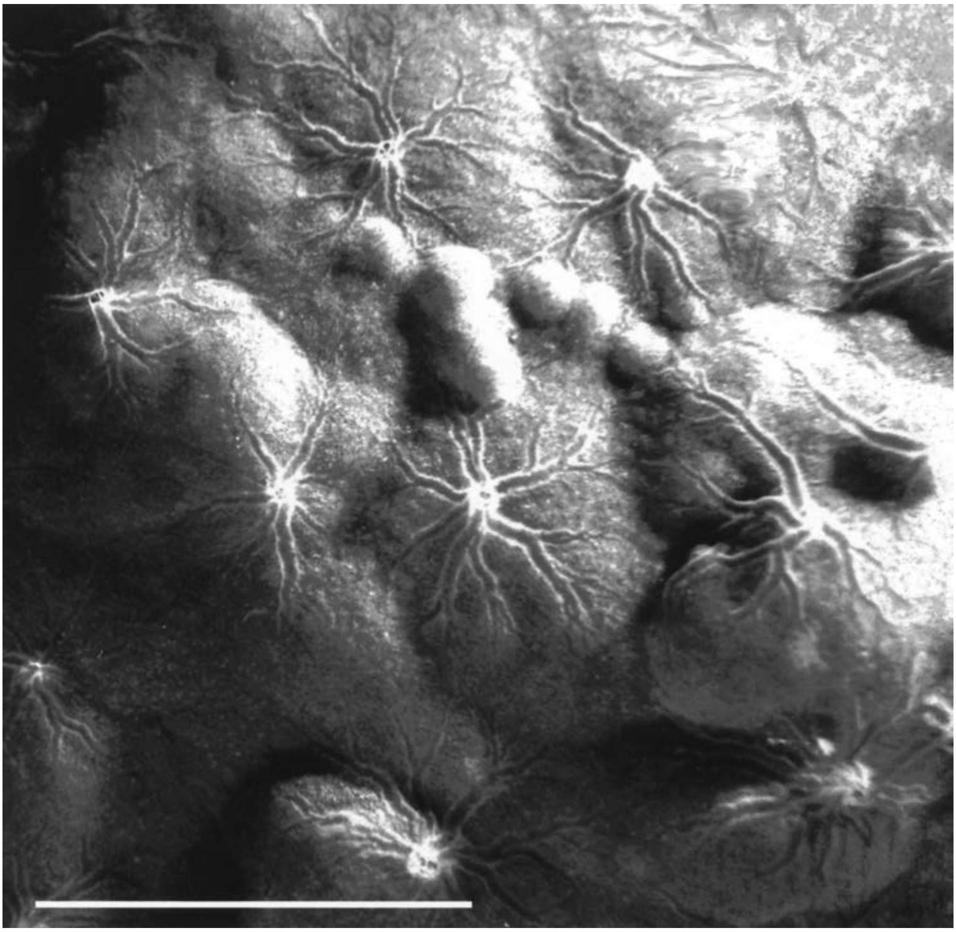

FIG. 350. Exhalant canal system, *Ceratoporella nicholsoni* (HICKSON, 1911), living specimen, Runaway Bay, Jamaica, scale bar, 2 cm (Stearn, 2010d; courtesy of H. Reiswig).

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, Ittekkot, 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 (Stearn, 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 [Stearn, 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 (Stearn, 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 tabulates 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, Kaźmierczak (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,

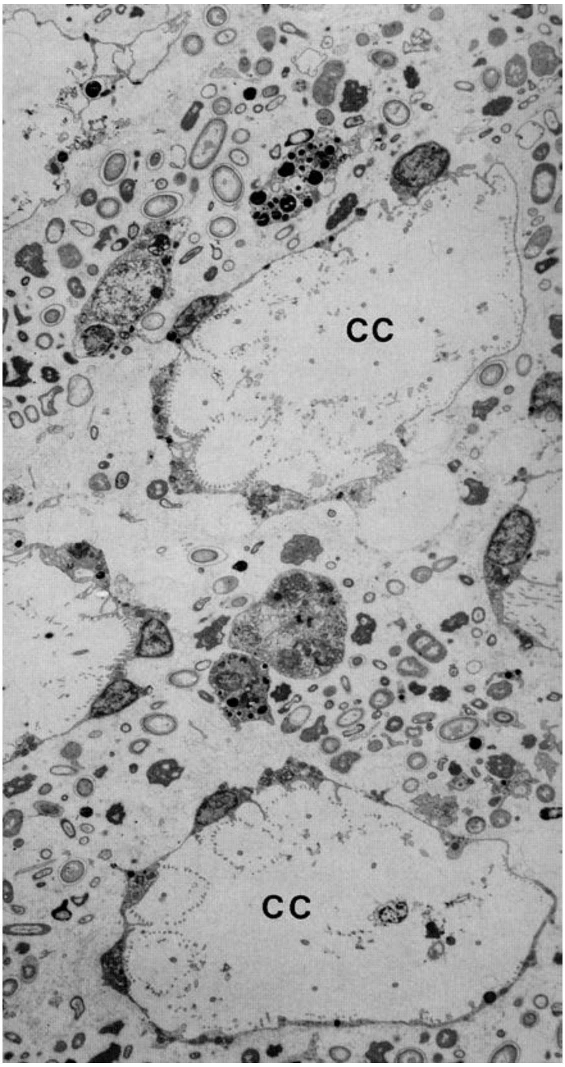

FIG. 351. Symbiotic cyanobacteria, *Ceratoporella nicholsoni* (HICKSON, 1911); Pear Tree Bottom, Jamaica; choanocyte chambers (*cc*), ×2400 (Stearn, 2010d; courtesy of Ph. Willenz).

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 Devonian and Silurian stromatoporoids using a microdrill to avoid contamination by the gallery fillings. MALLAMO (1995) found $\delta^{13}C$ (PDB) values in the 1.26 to 3.48 range and $\delta^{18}O$ (PDB) in the –9.10 to –4.22 range. Photosynthesis preferentially fixes and removes ^{12}C, increasing the $^{13}C/^{12}C$ ratio in the skeleton (NORRIS, 1998). These values showed an enrichment in the ^{13}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 stromatoporoid 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 stromatoporoids 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 stromatoporoids resemble those of living hypercalcified sponges that are cryptic in habitat and are not adapted to competition with neighbors for light. In mid-Paleozoic stromatoporoid reefs, the framework structure of modern reefs can rarely be demonstrated. Fagerstrom (1987) placed stromatoporoids in his binder guild, but in mid-Paleozoic reefs, the stromatoporoids, 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 stromatoporoids 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 stromatoporoids 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, stromatoporoid 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 stromatoporoids, 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 stromatoporoids 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 stromatoporoids, 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 pachysteles 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 *Calcifibrospongia*.

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 (Stearn & Mah, 1987). Reitner and Wörheide (2002) described the various groups of sponges that secrete spherulitic skeletons and conclude that the microstructure has no taxonomic

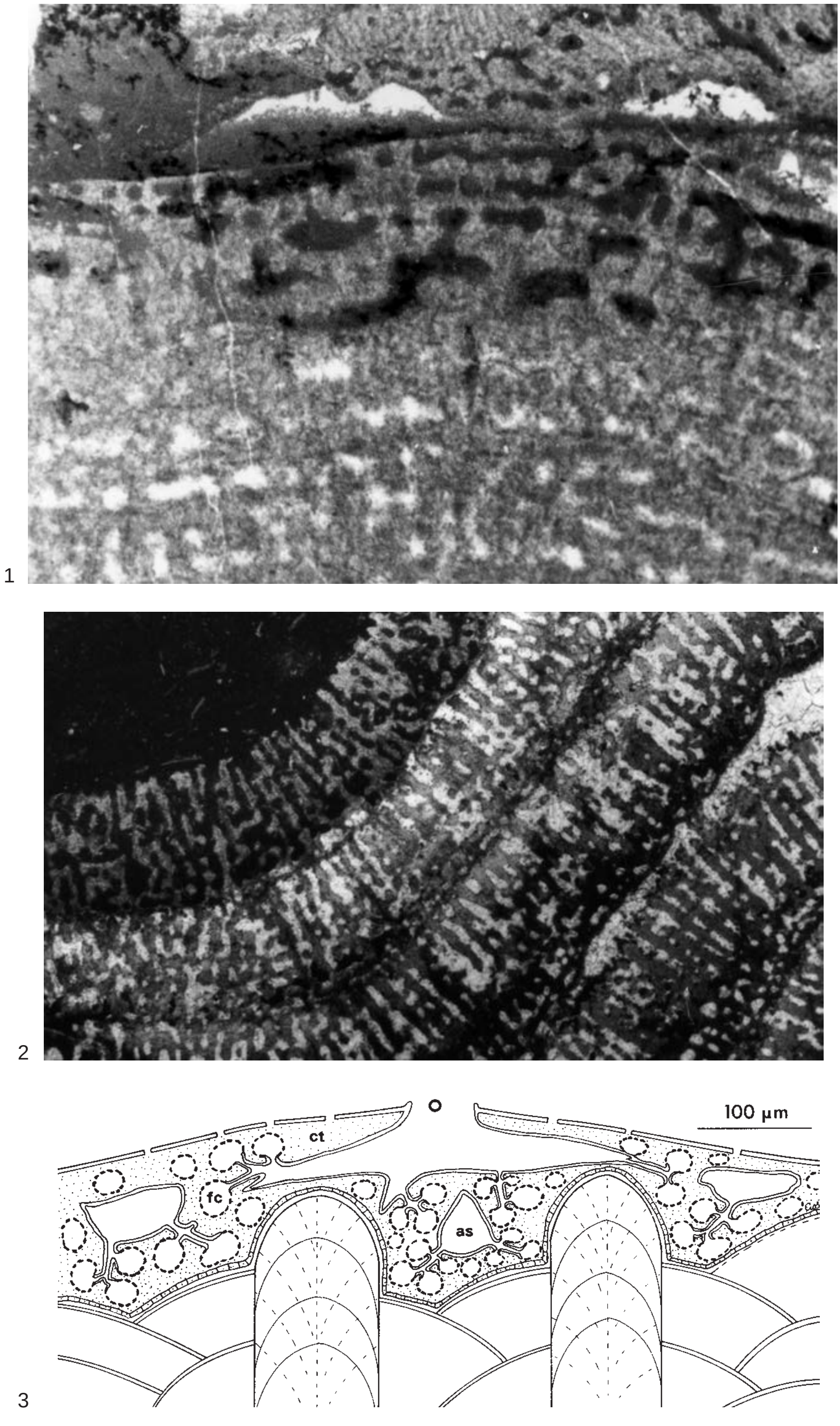

FIG. 352. *(For explanation, see facing page).*

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 diagenetic leaching of the axis of crystallization of a trabecular aragonite sheet by meteoric waters. Kaźmierczak (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,* Longtiudinal 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, ×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, ×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).

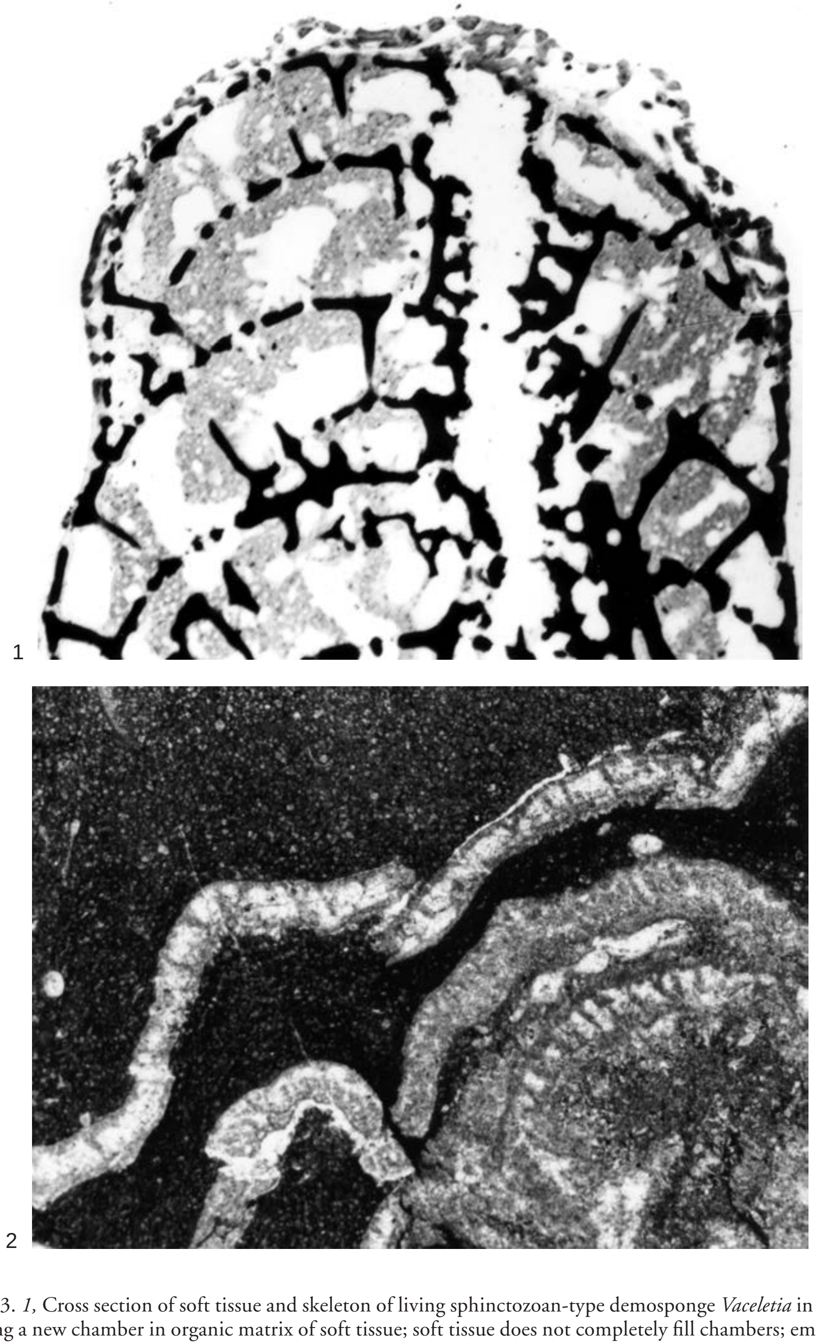

FIG. 353. *1,* Cross section of soft tissue and skeleton of living sphinctozoan-type demosponge *Vaceletia* in process of secreting a new chamber in organic matrix of soft tissue; soft tissue does not completely fill chambers; empty spaces are canals; new, incompletely mineralized chamber appears irregular, probably as a result of some deformation during preparation, ×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, ×10 (Stearn, 2010d; courtesy of B. Webby).

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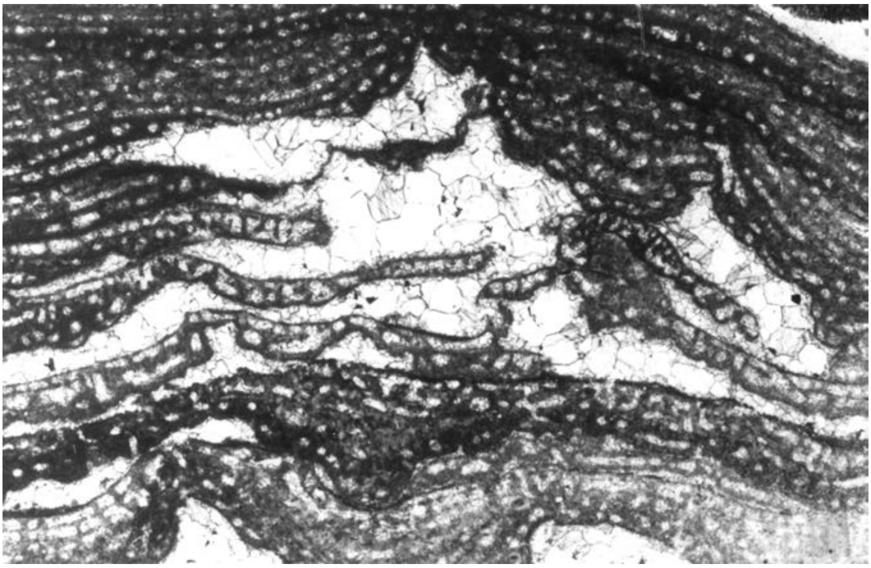

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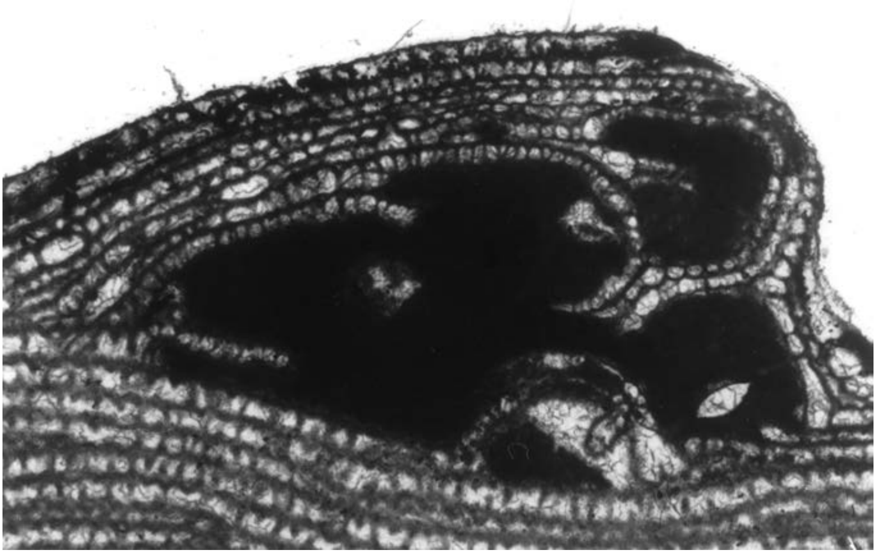

FIG. 354. *1,* Growth modules consisting of upper and lower laminae and enclosed pillars projecting into a spar-filled cavity, presumably once filled with sediment; *Stictostroma maclareni* STEARN, 1966, SCRM 80-88, Frasnian, Kakisa Formation, Great Slave Lake area, Northwest Territories, Canada, ×4.25 (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, Llandovery, Jupiter Formation, Anticosti Island (specimen collected by P. Copper), ×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 stromatoporoids 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 stromatoporoids 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* (Stearn, 1997c) (Fig. 349.2; and see Fig. 475) but was noted by Nicholson (1886a, p. 59–60) on several domical and encrusting stromatoporoids 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 ($\delta^{18}O$) 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

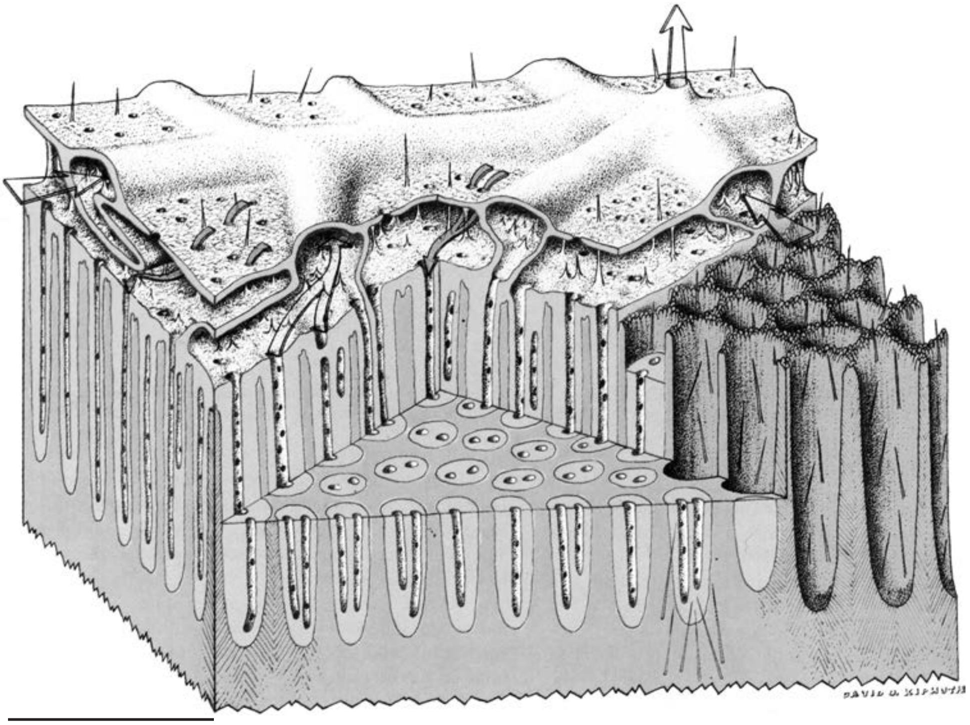

FIG. 355. Diagrammatic reconstruction of relationship between soft tissue and skeleton of *Ceratoporella nichsolsoni* (HICKSON, 1911) showing flow of water into ostia, through vestibule, into choanocyte chambers and out via astrorhizal canals to osculum; scale bar, 1 mm (Willenz & Hartman, 1989; see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

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 stromatoporoids 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 stromatoporoids. 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 stromatoporoid 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.

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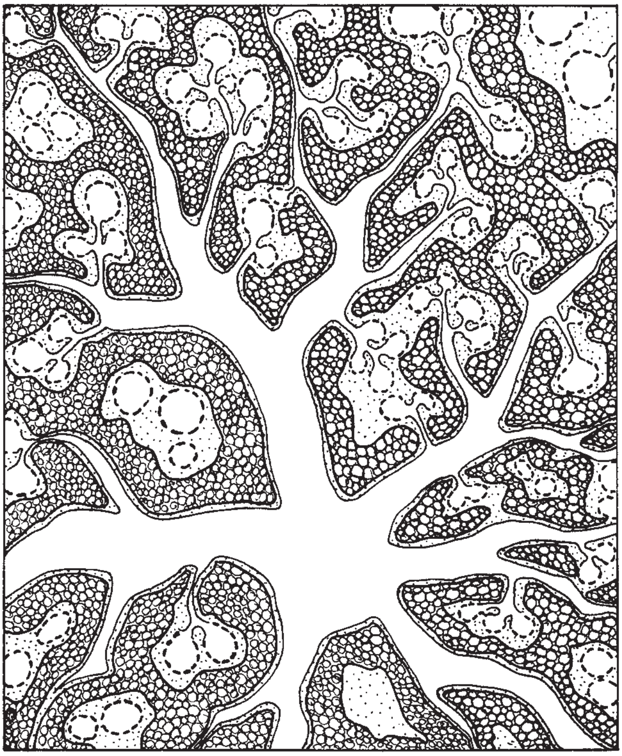

2

FIG. 356. *1,* Surface of skeleton of *Ceratoporella nicholsoni* (HICKSON, 1911) showing astrorhizal grooves branching and leading to mamelons on surface, SCRM 99-2, Runaway Bay, Jamaica, ×3 (Stearn, 1972); *2,* reconstruction of tangential section of astrorhizal 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), Kaźmierczak (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; Kaźmierczak, 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. Kaźmierczak (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:

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

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.

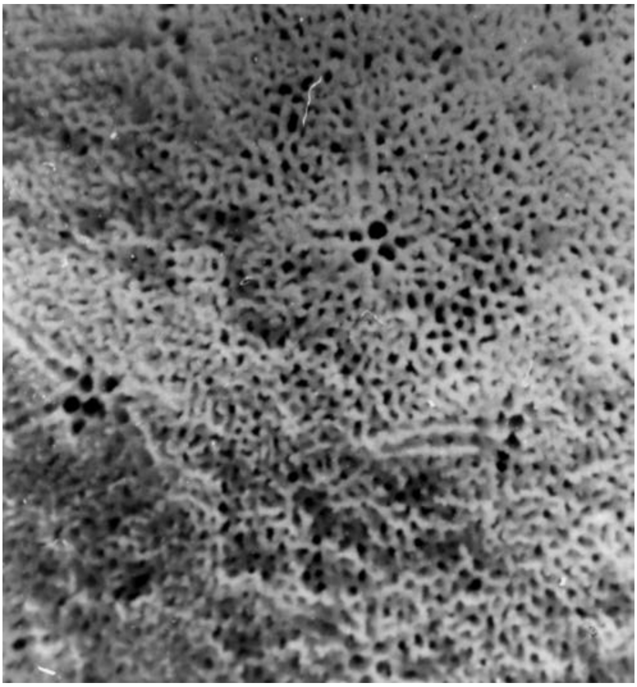

FIG. 357. Surface of skeleton, *Astrosclera willeyana* LISTER, 1900, showing astrorhizal canals on surface and penetrating into skeleton, SCRM 99-3, Guam, Anae Island, ×10 (Stearn, 2010d).

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.

EARLY EVOLUTION OF THE PALEOZOIC STROMATOPOROIDEA

B. D. WEBBY

PROBLEMATIC EARLY CAMBRIAN RECORD

Examples of early Cambrian fossil groups have long been known to exhibit stromatoporoid-like skeletal features (see early summaries in WEBBY, 1979a, p. 112–115; 1986, p. 148–151). However, all now appear to have been produced by organisms that are unrelated to indubitable members of the Ordovician-Devonian Stromatoporoidea, as outlined below.

ARCHAEOCYATHS WITH STROMATOROPOID-LIKE RESEMBLANCES

One small group of archaeocyaths belonging to the order Kazachstanicyathida KONYUSHKOV, 1967 (two suborders, two families, and three genera) developed comparable, well-integrated, modular, broadly thalamid (=sphinctozoan) to stromatoporoid-type structures [WOOD, ZHURAVLEV, & DEBRENNE, 1992; DEBRENNE & REITNER, 2001; and see *Korovinella sajanicum* (YAVORSKY, 1932) (Fig. 656,*1*); and *Altaicyathus notabilis* VOLOGDIN, 1932 (Fig. 657)].

These forms generally bear closer organizational resemblances to mid-Permian–Holocene verticillitinid (sphinctozoan) demosponge genera like *Stylothalamia, Menathalamia,* and *Vaceletia* (FINKS & RIGBY, 2004c, p. 712–719), only differing in tending to develop somewhat more fully integrated multioscular skeletal arrangements. In comparisons with typical Paleozoic stromatoporoids, the kazachstanicyathid genera *Korovinella* and *Altaicyathus* differ more fundamentally in developing perforate tabulae (equivalent to the cyst plates or laminae of stromatoporoids that are almost always nonporous), and the less fully integrated skeletal arrangements characteristically have lower skeletal densities and smaller sizes. The Paleozoic stromatoporoids established biomineralizing habits some 60 myr later than the archaeocyaths and were an independent group of sponges with a nonporous, nonspiculate skeleton. The Kazachstanicyathida merely represent the end product of a divergent line of descent within the class Archaeocyatha. This apparent convergence possibly relates to adaptive pressures associated with reef building in warm seas that developed for a short time during the early Cambrian (Botomian). The small archaeocyath group has no ancestral relationships to later stromatoporoids (NESTOR, 1966b; WEBBY, 1986). There is no evidence that any of these forms, or any other member of the Archaeocyatha (cf. VLASOV, 1961), gave rise to the stromatoporoids.

OTHER POSSIBLE CONVERGENCES

Coralomorph Genus *Yaworipora* ZHURAVLEV, 1999b (Tabulaconida)

Two early Cambrian (Toyonian) so-called species from the Kuznetskii Alatau, Altai Saian Fold Belt of southwestern Siberia, were illustrated by KHALFINA (in KHALFINA & YAVORSKY, 1974, p. 39, 270–271, pl. 1,*1–2*) without description (hence *nomina nuda*) and referred to the genus *Stromatocerium* (i.e., related to stromatocerid labechiids like those from the Ordovician). On this basis, KHALFINA and YAVORSKY (1967) argued that some Ordovician labechiid stromatoporoids were derived from stocks like the Cambrian species of so-called *Stromatocerium*. WEBBY (in STEARN & others, 1999, p. 18) tentatively associated KHALFINA's species in KHALFINA and YAVORSKY, 1974, with an unnamed stromatocerid genus (now described as *Vietnamostroma* NGUYEN, HUNG HUU, & MISTIAEN, 1998). However, ZHURAVLEV, DEBRENNE, and LAFUSTE (1993, p. 369) had previously recognized the resemblance between KHALFINA's Cambrian species in KHALFINA and YAVORSKY, 1974, and the early Cambrian coralomorph *Flindersipora* LAFUSTE in LAFUSTE and others, 1991, and ZHURAVLEV (1999b) has since revised KHALFINA's species in KHALFINA and YAVORSKY, 1974, combining the two species as the new coralomorph taxon, *Yaworipora khalfinae*. This Cambrian coralomorph has irregularly polygonal to meandroid corallites, and its tabulae are flattened to undulating and complete. The form has a general resemblance with corallites and tabulae as analogues of the pillars and cyst plates in stromatocerid stromatoporoids, but marked differences exist in preservational states of the two groups. The compound, modular, coralomorph colonies and stromatocerid stromatoporoid skeletons belong to completely unrelated groups of organisms, yet apparently each group was still capable of producing convergently similar skeletal structures in response to their respective growth in temporally discrete and independent reef-building episodes.

Coralomorph Genera *Khasaktia* SAYUTINA, 1980, *Vittia* SAYUTINA, 1980, and Others

These small, problematical early Cambrian genera were first described as members of a new family, the Khasaktiidae of SAYUTINA (1980), and suggested to have affinities with Paleozoic stromatoporoids (see also SAYUTINA in VORONIN & others, 1982, p. 66–68, pl. 8,*6–9,* pl. 9,*1–8;* SAYUTINA, 1983, p. 149–151, pl. 30,*1–5,* pl. 31,*5;* WEBBY, 1986, p. 150; WEBBY in STEARN & others, 1999, p. 59–61; and SCRUTTON, 1997, p. 196, for further discussions). Compared with stromatoporoids, these forms are a rather heterogeneous group, with structures that have finer and smaller sizes. The crustlike genera *Khasaktia* and *Vittia* were considered by ROZANOV and ZHURAVLEV (1992, p. 230) to to have been archaeocyath holdfasts (see also NESTOR in STEARN & others, 1999, p. 60), and some crusts of *Vittia* were noted (WEBBY, 1986, p. 150, fig. 2B) to be similar to certain labechiids, but the relationship is almost certainly to be convergent. The dendroid, multilayered *Edelsteinia* VOLOGDIN, 1940a, *Rackovskia* VOLOGDIN, 1940a, and *Drosdovia* SAYUTINA, 1980, were thought likely, especially based on their microstructures, to be coralomorphs (DEBRENNE, LAFUSTE, & ZHURAVLEV, 1990; ROZANOV & ZHURAVLEV, 1992; ZHURAVLEV, 2001c). However, RIDING (2001, p. 452) suggested *Edelsteinia* as an alga.

Others, for example, WRONA & ZHURAVLEV (1996 p. 31), PRATT & others (2001, p. 260), and DEBRENNE & REITNER (2001, p. 315) have recorded the family Khasaktiidae as a junior synonym of the family Tannuolaiidae VOLOGDIN, 1967. Their decision was apparently based on resemblances between VOLOGDIN'S (1967) new genus and type species, *Tannuolaia fonini,* from an early Cambrian sequence in southern Tuva (Russia), and SAYUTINA'S (1980) khasaktiid taxa described from the Siberian Platform and Mongolia, especially the close morphological similarities between *T. fonini* and the "khasaktiid" genus *Edelsteinia.*

However, relationships between the two families Tannuolaiidae and Khasaktiidae still need to be more fully explored. For example, VOLOGDIN (1967) interpreted the tannuolaiids as green algae (Chlorophyta), whereas SAYUTINA (1980) treated the superficially similar early Cambrian khasaktiids as skeletonized structures of stromatoporoid-type (likely to be derived from either sponge or cnidarian lines of descent) or, alternatively, having uncertain origins, as implied by BOGOYAVLENSKAYA (1984, 2001a). Also, SCRUTTON (1997, p. 196, 199) has reviewed some of the khasakiid taxa in terms of possible cnidarian relationships, indicating that they are unlikely to be related, apart from one genus, *Rackovskia,* which could be viewed as a zoantharian coral. SCRUTTON (1997) also commented on other forms such as *Khasaktia*, which he found difficult to assess: he preferred to keep an open mind on its relationships until this genus, and all the other problematical, skeletonized, early Cambrian life forms discussed here, were much more intensively studied to clarify their precise nature, origins, interrelationships, and patterns of diversification.

Bogoyavlenskaya (2001a, p. 46) also proposed the new order Khasaktiida of class *Incertae Sedis* (note the original "-ida"ending is here amended to an "-iida" ending to maintain consistency with the formalized family ending of the Khasaktiidae, discussed above). She only incorporated family Khasaktiidae, with the genera *Khasaktia* and *Vittia,* in her new order, and she also arbitrarily assigned a number of the major groups of stromatoporoids to this artificial grouping as well, including such orders as the Labechiida, Clathrodictyida, and Actinostromatida in her conception of class *Incertae Sedis.* Later, Bogoyavlenskaya (in Bogoyavlenskaya & Yelkin, 2011, p. 15–20) combined the khasaktiid order and the above-mentioned stromatoporoid orders again into one group, but this time she referred them all to the class Hydrozoa within the phylum Cnidaria (=Coelenterata). Again, this appears to have been a rather arbitrary change, though perhaps best explained in terms of her earlier views (see Bogoyavlenskaya, 1984, fig. 16) that all stromatoporoid orders had affinities to hydrozoans. For additional comments on other aspects of Bogoyavlenskaya's stromatoporoid-based classifications (Bogoyavlenskaya, 1984, 2001a; Bogoyavlenskaya & Yelkin, 2006, 2011; also see p. 581–583, 702).

Nevertheless, it remains unlikely that the problematical early Cambrian khasaktiids (based on *Khasaktia* and *Vittia*) were closely related to the Mid-Ordovician to Devonian stromatoporoids. The two groups do show convergently similar skeletal features, but they are phylogenetically remote from each other, given the approximately 60 myr gap in the record of occurrences. Also the khasaktiids have relatively restricted occurrences within Siberia, Mongolia, and West Antarctica, and they lack astrorhizal structures.

Problematical Genus *Maldeotaina*
Flügel & Singh, 2003

In another example from a richly fossiferous, nodular, limestone sample near the top of the Krol Formation (close to the Precambrian–Cambrian boundary) of northern India, two associations were recorded as including the presence of morphologically differentiated calcified sponges, with one (*Maldeotaina*) thought to include an example of stromatoporoid-like growth (Flügel & Singh, 2003, pl. 66,*1*). The form genus *Maldeotaina* comprises centimeter-sized nodules, including a stromatoporoid-like component that appears to have overgrown areas that were formerly voids (possibly original cavities). These exhibit lighter, spar-filled, vesicular, early marine cement botryoids, and each seems to be defined by a thin, dark, much-crenulated encrustation of microbial micrite. Flügel and Singh's (2003, p. 369) view, that this vesicular, inner part of the nodule was part of sponge "thalamid-type growth" is here rejected in favor of an interpretation that it was, more likely, formed mainly by the precipitation of early marine cements. The stromatoporoid-like overgrowth is a fine meshwork of rodlike and cystlike elements that resembles some examples of fine-textured labechiid stromatoporoids, and, in one part of the skeleton where it continued to grow, it developed a columnar growth form with an internal phase change to predominant cyst rows (Flügel & Singh, 2003, p. 366, pl. 66,*1*). In contrast to the *Maldeotaina* overgrowths, the skeletons of fine-textured labechiids, like members of the *Labechia prima* group and species of *Stratodictyon* (Kapp & Stearn, 1975; Webby, 1979a), exhibit less variability in their cystlike sizes and shapes; a more regular arrangement of cyst rows; rodlike (pillar) elements that do not show a tendency to become amalgamated in their outer zones; and do not exhibit similar patterns of encircling, encrusting meshworks around small nodules. Typically, labechiids form laminar skeletons and commonly have associated latilaminae. Consequently, the *Maldeotaina* overgrowth structure, though it superficially resembles fine-textured labechiid stromatoporoids, is likely to belong to some other early Cambrian form, perhaps a new variety of cyanobacterium or alga. Alternatively, the stromatoporoid-like part of the structure may represent another khasaktiid genus. Whichever alternative is favored, the simple, calcified skeleton lived more than 60 myr before phylogenetically unrelated, and convergently similar, labechiid stromatoporoids.

MID-CAMBRIAN TO EARLY ORDOVICIAN GAP IN THE RECORD

No stromatoporoid-like skeletal structures have been reported from reef or other habitats of the mid-Cambrian to Early Ordovician (Tremadocian). According to Rowland and Shapiro (2002, p. 119), the reef settings were almost entirely dominated by microbialite-building cyanobacteria, which had opportunistically invaded as metazoans disappeared, owing to seawater chemistry changes (a reduction in the Mg/Ca ratio prevented organisms that secreted high Mg calcite or aragonite skeletons [Stanley & Hardie, 1998]). Other factors, such as global warming, high levels of atmospheric CO_2, and the nutrient deficiencies of marine environments may have contributed also, directly or indirectly, to inhibiting the development of metazoan reef builders (Rowland & Shapiro, 2002, p. 95).

EARLY TO MID-ORDOVICIAN PULCHRILAMINIDA: AN INDEPENDENT, REEF-BUILDING HYPERCALCIFIED SPONGE

The small, geographically relatively restricted group of pulchrilaminid hypercalcified sponges appeared in North American (Laurentian) successions during the late Early Ordovician (Floian Stage; see Bergström & others, 2006), forming important frame-building contributors to reef mounds, especially the upper parts of the mounds, and in some forms, they also exhibit fine spicule-like elements aligned in palisade bands (Fig. 358). Best documented were the *Pulchrilamina*-bearing reef mounds in Texas and Oklahoma (Toomey & Ham, 1967; Toomey, 1970; Toomey & Nitecki, 1979; Toomey & Babcock, 1983; Webby, 1986, 2002, p. 140). *Pulchrilamina* has also been reported from bedded sequences of Floian age (Pratt & James, 1989), and reef-derived clasts of lower Mid-Ordovician (Dapingian) age (Pohler & James, 1989) in Newfoundland.

Also, in places, pulchrilaminids are represented mainly by sheetlike encrustations, and these may also be furnished with spicule-bearing palisade bands, as in the Lower Ordovician (upper Tremadocian–lower Floian) successions of Hubei Province, southern China (Zhu, Liu, & Li, 1993; Adachi, Liu, & Ezaki, 2011), and there are more doubtful records of pulchrilaminids, given that they lack the palisade-bearing, fine spicule-like elements occurring in the Middle Ordovician—the genus *Zondarella* Keller & Flügel, 1996, from the reef and biostromes of the Dapingian (lower Mid-Ordovician) of the Argentine Precordillera (that was possibly derived originally as a microcontinental block from near the Ouachita embayment in the southeastern United States; Thomas & Astini, 1996; Keller, 1999), and the genus *Ianilamina* Pickett & Zhen in Zhen & Pickett, 2008, from the lower Darriwilian (middle Mid-Ordovician) of central New South Wales, Australia, that formed as an isolated occurrence in a Darriwillian limestone lens of a volcanic arc setting in eastern Australia.

Toomey and Ham (1967, p. 984) reviewed the status of their enigmatic new genus *Pulchrilamina,* concluding that the genus should be assigned to *Incertae Sedis,* possibly a “primitive coelenterate,” akin to stromatoporoids. This view was formed when stromatoporoid workers were still interpreting stromatoporoids as hydrozoans. However, from the 1970s onward, as the views of Hartman and Goreau (1970, 1972, 1975) linking living hypercalcified sponges and fossil stromatoporoids gained acceptance, some workers did interpret *Pulchrilamina* as a sponge (e.g., Pratt & James, 1982). Nonetheless, few stromatoporoid specialists have included *Pulchrilamina* in their surveys of stromatoporoids since the 1970s, either because they were unaware of the existence of this small, comparatively restricted group, or because they doubted the group had links to stromatoporoids (e.g., Stearn, 1980; Bogoyavlenskaya, 1984; Bogoyavlenskaya & Lobanov, 1990; Khromykh, 1999a, 1999b).

Pulchrilamina was first described by Toomey and Ham (1967) as being formed of large, domical-shaped skeletons with wavy, sheetlike layers (laminations) and erect, upward, sharply pointed spines (spinose rods) that rise above the tops of individual layers into the intimately associated wedges or layers of mudrock; both sheets and centers of the spines are invariably replaced by sparry calcite. Later, Toomey and Nitecki (1979, fig. 13) identified small areas of the predominantly spar-replaced sheets as being composed of rows of gently wavy, cyst-like laminae that formed meshworks with the upright, spinelike rods, but they did not offer further comment on the possible significance of these morphological features.

Stearn (1972, p. 374) drew attention to *Pulchrilamina* in a comparison between gross structures of living hypercalcified sponges and Paleozoic stromatoporoids, such as the densely thickened Silurian genus *Lophiostroma*, apparently because it was thought to be composed of a solid mass of calcite. Nestor (1978) and Sayutina (1980) also gave credence to the linkage between *Pulchrilamina* and the skeletally dense, massively thickened members of the family Lophiostromatidae Nestor, 1966a, favoring a view that *Pulchrilamina* may have been the ancestor of the Stromatoporoidea, through a lophiostromatid line of descent. Stock (1983, p. 167) was another who commented on the close morphological similarities between skeletal structures of *Pulchrilamina* and the labechiids, recommending that further comparative studies of relationships were needed.

Studies of *Pulchrilamina* in the 1980s led to initial suggestions by Webby (1984a, p. 91; 1984b, p. 200) that the generalized growth form, latilaminae, cysts, and pillars were similar to later Ordovician labechiids. However, in a more detailed account, Webby (1986, p. 151–154, fig. 3–4) noted that, while there were mainly no substantial differences between the genus *Pulchrilamina* and members of the family Labechiidae, the pattern of long, slender, spinose rods (or spicules) extending above the tops of latilaminae in palisade bands was not typical of the Labechiidae. At this time (Webby, 1986, p. 154–155, fig. 5), *Pulchrilamina* was still depicted as a possible ancestor to other late Middle Ordovician genera of order Labechiida and the family Labechiidae. But later, Webby (1993, p. 58; 1994, p. 375) erected the family Pulchrilaminidae to accommodate the genus *Pulchrilamina*, retaining it with some reservations in the order Labechiida, because the long-low cysts had limited lateral continuity and the spinelike and sometimes tilted nature of the long, slender spicule-like elements suggested a much more loosely aggregated skeleton than in typical labechiids. Two other general concerns were discussed: (1) whether *Pulchrilamina* was truly ancestral to later members of the order Labechiida, given the above-stated morphological differences; or (2) whether, alternatively, the apparent close relationships arose merely as a consequence of convergences between pulchrilaminids and labechiids and were two unrelated groups (Fig. 358). A similar viewpoint was offered by Webby (in Stearn & others, 1999, p. 23) in recognizing the family Pulchrilaminidae as a doubtful member of the order Labechiida, or a small,

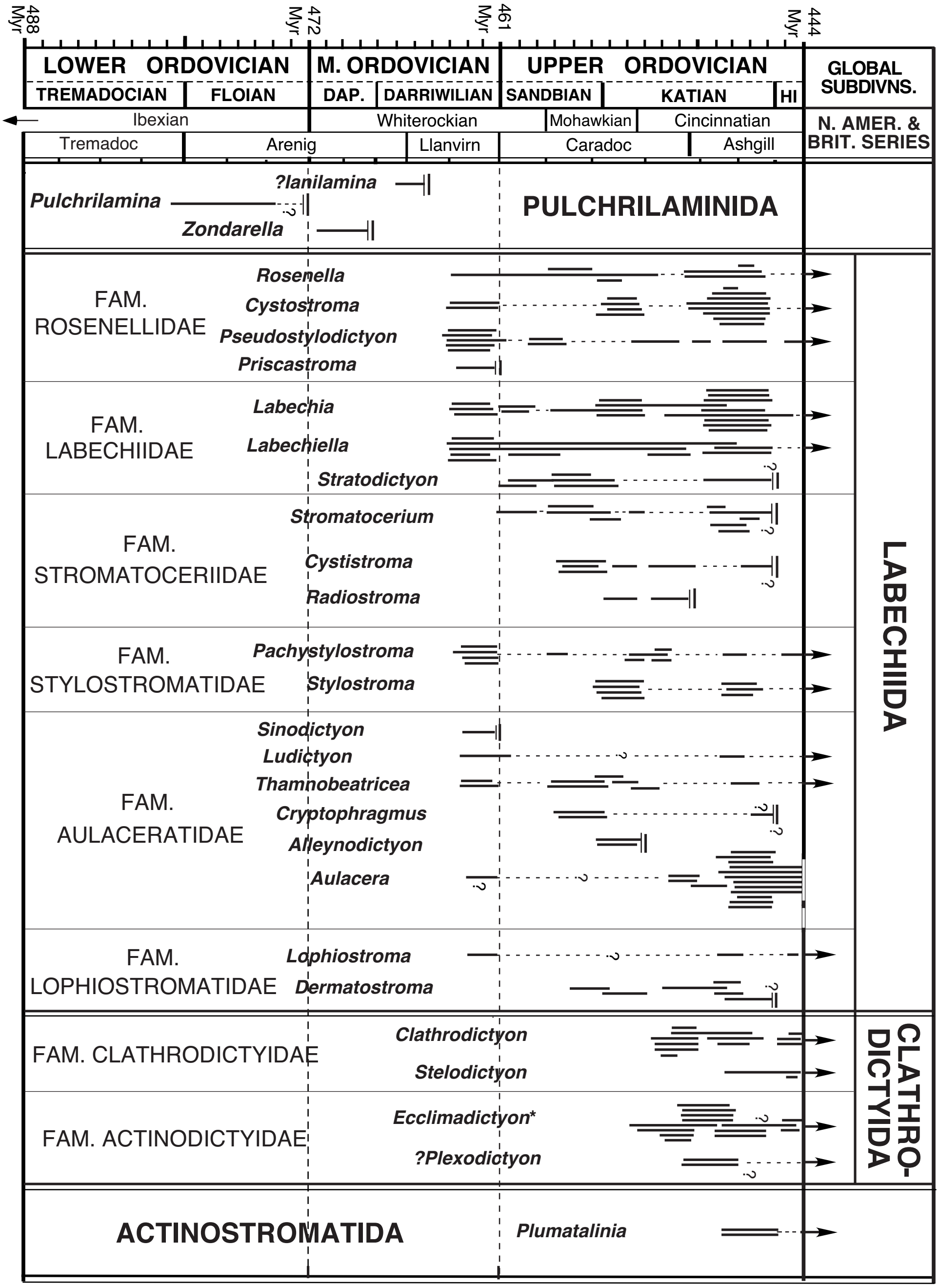

FIG. 358. *(For explanation, see facing page).*

unrelated, early, reef-forming group. By using a revised Ordovician time scale, WEBBY (2004b) suggested that a gap of about half the length of the Darrwilian stage (about 4 myr) separated the last appearance of mainly Laurentian pulchrilaminids and the first, sudden, mass appearances of labechiid stromatoporoids worldwide (distributed across paleoequatorial carbonate shelfal regions of North America, Siberia, northern China, Southeast Asia, and Australia). However, the recent discovery of the short-lived *Ianilamina* in the lower Darriwilian of Australia suggests now that there was no substantial gap in time between the last appearance of pulchrilaminids and the first appearances of indubitable labechiids.

WEBBY (p. 837–844) proposed the new order Pulchrilaminida to accommodate the eponymous family Pulchrilaminidae WEBBY, 1993. The order is regarded as a separate, independent group of hypercalcified sponges, placed in class Uncertain. Given its distinctive, slenderly tapering, rodlike, spicular elements that resemble styles, it may be more closely linked to spiculate sponge groups of the class Demospongiae than to nonspiculate stromatoporoid groups. In conclusion, it seems that much of the early history of pre-labechiid, spongelike forms, like the Pulchrilaminida, is not recorded in known fossils. The order Pulchrilaminida is a small clade with poriferan affinities that has a limited geographic spread and evolved as a reef-former in parts of North America, the Argentine Precordillera, and in southern China during the late Early Ordovician, surviving as reef-formers, at least to the end of the early Middle Ordovician. Additionally, there are records of pulchrilaminids as encrusters or matlike forms in most of the same places, but they also seem to have appeared earlier in the late Tremadocian of southern China, as well as surviving longer in certain places, like the isolated occurrence of problematic *Ianilamina* in a Darriwillian limestone lens of a volcanic arc setting in eastern Australia. Though it appears morphologically close to the Argentine *Zondarella* KELLER & FLÜGEL, 1996, it differs, according to PICKETT and ZHEN (in ZHEN & PICKETT, 2008, p. 66), in exhibiting "porous laminae," a feature that they believe implies a relationship with nonlabechiid ?clathrodictyid-type stromatoporoids. However, the genus *Ianilamina* has no direct link with the order Clathrodictyida, which first appeared some 10 myr later, during the Late Ordovician (Katian) age (see p. 590).

BOGOYAVLENSKAYA's (2001a, p. 46) proposal of the order Protolabechiida of class *Incertae Sedis* to accommodate a heterogenous assortment of labechiid, lophiostromatid, and pulchrilaminid families (and genera) is here rejected in favor of separating them into two clearly differentiated orders: the Pulchrilaminida and the Labechiida. Arguments against adopting the order Protolabechiida as a valid taxonomic subdivision are presented elsewhere (see separate sections on the taxonomy of the Labechiida, p. 709–754, and the Pulchrilaminida, p. 837–844).

FIG. 358. Chart showing temporal ranges of Ordovician stromatoporoids (orders Labechiida, Clathrodictyida, and Actinostromatida) and the problematical order Pulchrilaminida, worldwide, based on the sampled record. The named genera are represented with clusters of *vertical lines* representing approximate numbers of species and their ranges within a genus; *dotted vertical lines* represent gaps in the continuity of record, and the *double cross bars* depict inferred levels of extinction of individual genera; note the abbreviations of global subdivisions: *DAP* (Dapingian stage) and *HI* (Hirnantian stage). The pattern of first appearances commences with the major radiation of 12 labechiid genera in the late Middle Ordovician, then successive smaller pulses involving *Stratodictyon* and *Stromatocerium* near the mid–Late Ordovician boundary, followed by *Cystistroma*, *Cryptophragmus,* and *Dermatostroma* in the mid-Sandbian (early Upper Ordovician), then *Radiostroma, Stylostroma,* and *Alleynodictyon* near the Sandbian-Katian boundary. The clathrodictyids (4 genera) radiate later, during the mid–Late Ordovician (Katian), possibly from a *Cystostroma*-like ancestor; *asterisk,* the genus *Ecclimadictyon* is now separated into two genera, with the addition of newly designated genus *Camptodictyon* NESTOR, COPPER, & STOCK (2010, p. 84), including a distinctive Ordovician species. Also, the first actinostromatid (*Plumatalinia*) evolved in the late Katian, probably from a species of *Pseudostylodictyon* (adapted from Webby, 2004b, fig. 13.1; with permission of Columbia University Press, New York).

There is also a superficially similar hypercalcified spongelike organism of large size in the Table Head Formation of western Newfoundland, of lower Mid-Ordovician (Dapingian) age. It has a form that is not referable to stromatoporoids, chaetetids, secondarily altered lithistid sponges, or cryptalgal structures. This problematical taxon, described as *Lapidipanis terranovae* PAQUETTE, STEARN, & KLAPPA, 1983, exhibits a spherulitic microstructure that has led to the suggestion that it may have links with living (and Triassic) hypercalcified demosponge *Astrosclera* LISTER, 1900 (see p. 5). However, the spherules in *Lapidipanis* are larger than those found in *Astrosclera* (VACELET, 2002a, p. 825).

THE LABECHIIDA: RECORD OF EARLIEST STROMATOPOROIDS

In terms of the classification of the order Labechiida employed in this volume of the *Treatise on Invertebrate Paleontology,* it follows relatively closely the taxonomic framework used previously by WEBBY (see STEARN & others, 1999). The only significant differences are the exclusion of the family Pulchrilaminidae WEBBY, 1993, which was previously included with some uncertainty, and the Stromatoceriidae BOGOYAVLENSKAYA, 1969b, now divided into two families (comprising the revised Stromatoceriidae and Platiferostromatidae YAVORSKY in KHALFINA & YAVORSKY, 1973). The order Labechiida here comprises seven families: Rosenellidae (six genera), Labechiidae (three genera), Stromatoceriidae (three genera), Platiferostromatidae (five genera), Stylostromatidae (five genera), Aulaceratidae (seven genera), and Lophiostromatidae (two genera). Six of these, all except the Platiferostromatidae, have an Ordovician record (Fig. 358) for labechiids; see also the Paleozoic record of Labechiida (Fig. 362). The family Cystostromatidae KHROMYKH, 1974a, has not been accepted by other workers; its included taxa comprise a heterogeneous mixture of forms that should be assigned to at least three different labechiid families: Rosenellidae, Labechiidae, and Stromatoceriidae (and all of these family names have priority over KHROMYKH's Cystostromatidae). This latter family was referred by KHROMYKH (1999b) to the order Clathrodictyida, thus confusing its true identity. It does not show diagnostic features of clathrodictyids—that is the presence of single-layered, inflected to planar laminae and short to superposed pillars (see p. 755). Therefore the use of family Cystostromatidae and the order Cystostromatida (see KHROMYKH, 2001, p. 344) should be abandoned.

A well-constrained, globally based, stratigraphic framework (SADLER & COOPER, 2004; WEBBY, COOPER, & others, 2004; BERGSTRÖM & others, 2009; SADLER, COOPER, & MELCHIN, 2009) has become available to assess the origins and evolutionary development of the group. Earlier attempts to review this topic (WEBBY, 1979a, 1993; BOGOYAVLENSKAYA & LOBANOV, 1990; KHROMYKH, 1999b) were hampered by the difficulty of establishing precise ties between the local and regional range data and the available, globally based time scales.

BOGOYAVLENSKAYA (2001a, p. 48–49) and BOGOYAVLENSKAYA and YELTIN (2006, p. 188–189) adopted a classification of the order Labechiida that included six families, with four of these ("Rosenelliidae," Labechiidae, Aulaceratidae, and Stromatoceriidae) bearing some similarity to the familial subdivisions used in the present classification but with the two other families (Cystostromatidae and Tuvaechiidae) having markedly different conceptions. Nevertheless, the order was maintained with the scope of a major stromatoporoid group. However, BOGOYAVLENSKAYA and YELTIN (2011, p. 19) have since added a radically different proposal that greatly restricts the conception of the order Labechiida, in removing all the previously adopted families except the Labechiidae. This drastically alters the understanding of labechiids as a major, essentially unified, stromatoporoid group through the Mid-Ordovician to Late Devonian, comprised of a comparatively simple skeletal meshwork of cyst plates and rounded to flanged pillars, and/or denticles. The traditional conception must be maintained; and hence the Bogoyavlenskaya and Yeltin (2011) proposal must be rejected.

In a survey of Ordovician diversity trends, Webby (2004b) demonstrated that the labechiid stromatoporoids first appeared quite suddenly in the late Middle Ordovician (mid–late Darriwilian age), associated with a significant global evolutionary event. It involved the initial differentiation of 5 of the 7 labechiid families, with the appearance of 12 genera (i.e., representing a little less than half the known labechiid genera in the fossil record). It appeared that this event was concentrated in low paleolatitudes, mainly in shallow carbonate platform and shelf (including reef) sites of Laurentia, Siberia, and eastern Asia. Other metazoans, such as corals and bryozoans, and algal components also diversified rapidly at this time, and many new and complex reef community associations became established, as well as significant increases of bioeroders, encrusters, and bioturbators associated with the reef (Webby, 2002, 2004a). The reef-building phase is best developed in Laurentia, in particular, as seen in the eastern North American Chazyan reefs.

The globally distributed, mid-late Darriwilian, labechiid genera are distributed across five of the six known Ordovician families (see Fig. 358). The family Rosenellidae includes four genera (*Rosenella* from northern China [NC], Korea [K], and Malaysia [M]; *Cystostroma* from eastern North America [ENA]; *Pseudostylodictyon* from ENA and NC; and *Priscastroma* from Siberia); family Labechiidae includes two genera (*Labechia* from ENA and NC; and *Labechiella* from NC, K, and M), family Stylostromatidae includes one genus (*Pachystylostroma* from ENA), family Aulaceratidae includes four genera (*Aulacera*, *Thamnobeatricea*, *Sinodictyon,* and *Ludictyon* from NC); and family Lophiostromatidae includes one genus (*Lophiostroma* from NC). It should be noted that none of these early labechiid genera exhibits a circumpaleoequatorial distribution. A few occur in two main regions (e.g., *Pseudostylodictyon* and *Labechia* in ENA and NC), but all others (10 genera) have a largely restricted regional distribution, either in ENA, eastern or southeastern Asia (i.e., NC, or NC, K, and M), or in Siberia. It seems likely, therefore, that an initial simple, noncalcifying rootstock existed in warm shallow seas of most paleoequatorial regions, and then the mineralized skeletons of a number of different basic morphologies developed, most of them in comparative isolation to each other, either directly related to a globally widespread environmental perturbation or independently of it. The alternative is to suggest that one or two basic skeletonized morphologies of *Cystostroma-* or *Pseudostylodictyon*-type evolved first in the mid-Darriwilian and then spread circumequatorially over the next one to three million years, prior to the end of Mid-Ordovician time.

The events associated with the first appearances of stromatoporoid-bearing Chazyan reefs (Day Point to Crown Point formations) in eastern North America (Kapp & Stearn, 1975) were apparently mirrored by dramatic diversity changes in the contemporaneous, mainly level bottom communities of the Siberian Platform (Kanygin, 2001), and, by the first appearance of the labechiid genus *Priscastroma* Khromykh, 1999a, in the Moiero River basin section of that platform sequence. The stromatoporoid-bearing sequences in northern China and other parts of Asia were all of similar mid-upper Darriwilian age (Webby, 2004b, p. 114). Most of the early labechiid occurrences in northern China come from horizons in upper parts of the Machiakou Formation or its equivalents (Yabe & Sugiyama, 1930; Dong, 1982; Lin & Webby, 1989), and they broadly correlate with the middle upper Llanvirn interval, i.e., they represent a mid-upper Darriwilian age (see Chinese correlation chart in Chen & others, 1995).

Two additional genera, *Stratodictyon* (family Labechiidae from ENA and Australia [Tasmania and New South Wales]) and *Stromatocerium* (the type genus of the sixth labechiid family, the Stromatoceriidae from Australia [Tasmania]) have first appearances near the Middle–Upper Ordovician boundary. The Chazy Group succession apparently straddles the boundary with the Day Point and Crown Point formations in the uppermost Darriwilian and the overlying Valcour formation in the lowest Sandbian (see WEBBY, 2002, fig. 6). *Stratodictyon valcourensis* (KAPP & STEARN, 1975) first appears in the Valcour Formation of the upper Chazy Group and is therefore lower Sandbian in age (BERGSTRÖM & others, 2006). In Australia, there are records of *S. vetus* WEBBY, 1979b, in Tasmania and in New South Wales (PICKETT & PERCIVAL, 2001), and the New South Wales occurrence comes from a horizon a few hundred meters above the key zonal conodont marker, *Pygodus anserinus*, which identifies the boundary interval; hence the *S. vetus* outcrop is of lowest Sandbian age. The occurrence of *Stromatocerium bigsbyi* in Tasmania is associated with *S. vetus*, so this stromatoporoid-rich succession also is probably younger than previously thought (WEBBY, 1979b, fig. 1), still correlating with the upper part of the Chazy Group sequence but within beds now considered to lie just above the Middle–Upper Ordovician boundary.

The labechiid origins through the rest of the Late Ordovician are limited to a few new genera that appeared at intervals from late Sandbian to early Katian (early–mid Late Ordovician) time (BERGSTRÖM & others, 2006). These included *Cystistroma* (family Stromatoceriidae) and *Cryptophragmus* (family Aulaceratidae) from the late Sandbian, and *Dermatostroma* (family Lophiostromatidae), *Stylostroma* (family Stylostromatidae), *Radiostroma* (family Stromatoceriidae), and *Alleynodictyon* (family Aulaceratidae), from the early Katian (Fig. 358). All of these genera are likely to have been derived from one or another of the existing skeletonized, mid–late Darriwilian, labechiid taxa. A maximum of 20 labechiid genera occur in the Late Ordovician. At the species level, the labechiids also became most diversified in the Late Ordovician, as they spread more widely circumequatorially along platforms, shelf margins, and in island arcs than previously. Of particular note is the marked diversification of columnar aulaceratids, up to 13 species of *Aulacera* recorded from the uppermost Ordovician (upper Katian to Hirnantian) worldwide, prior to their end-Ordovician mass extinction. In North American successions in particular, the diversity decline of labechiid genera into the early Silurian is most noticeable (NESTOR & STOCK, 2001, fig. 1).

BOGOYAVLENSKAYA and LOBANOV (1990) adopted a different approach to determining early origins, using a combination of stratigraphic distributions, zoogeographic patterns, and apparent phylogenetic relationships. They reviewed the diverse labechiid assemblage in the Chazy Group, giving some of them different names from the taxa adopted here. For example, *Pseudostylodictyon* OZAKI, 1938, was subdivided into two genera (*Pseudostylodictyon* and *Parksodictyon* BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & LOBONOV, 1990); however, this discrimination based solely on one taxonomic character (presence or absence of mamelon columns) seems inadequate for recognizing such a genus-level subdivision and is rejected here (see p. 709–754). *Parkesodictyon* has been revised as a junior synonym of *Pseudostylodictyon*. Also, genus *Tuvaechia* BOGOYAVLENSKAYA, 1971b, which she used in preference to *Labechia* EDWARDS & HAIME, 1851, or *Labechiella* YABE & SUGIYAMA, 1930, for identifying some Chazy forms, is now considered to be a junior synonym of *Labechiella* (see p. 709–754). BOGOYAVLENSKAYA and LOBANOV's (1990, fig. 3) Middle Ordovician (Llanvirn–Llandeilo) was largely equivalent to the late Mid-Ordovician (mid–late Darriwilian interval) but is now established in the well-constrained global time scales of Bergström and others (2009) and Sadler, Cooper, and Melchin (2009) as representing a duration of about 5 myr, and the Late Ordovician interval is recognized as having a much longer duration of about 17 myr.

A summary of Bogoyavlenskaya and Lobanov's phylogenetic scheme for the mid–late Darriwilian interval comprised three main lines of descent. The first involved initial appearance of so-called "*Parksodictyon*" in the mid–late Darriwilian, then divergence into two branches involving *Pseudostylodictyon* and *Stratodictyon* in the latest Darriwilian; though the first appearance of *Stratodictyon* was probably later in the Sandbian (earliest Late Ordovician), given the earliest North American and Australian records (see earlier discussion, p. 583). The second line included the appearance of "*Tuvaechia*" (=*Labechiella*), with *Stromatocerium* as an offshoot in the latest Darriwilian, but again this offset probably did not occur until much later, in the earliest Late Ordovician. The third line of descent involved *Cystostroma* and *Pachystylostroma,* with these 2 genera appearing and diverging immediately, approximately latest Darriwilian time. The *Cystostroma* offshoot gave rise to many of the aulaceratid genera later in the Ordovician, and apparently to clathrodictyids as well. Overall, Bogoyavelskaya and Lobanov's (1990, fig. 3) phylogenetic tree is one of a steplike build up of new taxa through late Middle Ordovician to Late Ordovician time. They identified a maximum of 7 taxa by the end of the Middle Ordovician and a maximum of 12 genera in the mid-to-late Late Ordovician (late Katian), followed by rapid decline associated with the end-Ordovician extinction. Only 2 genera are recorded from the early Silurian.

Khromykh (1999b) also attempted to establish the main patterns of origins and early development of stromatoporoids, employing generalized stratigraphic distributions and inferred phylogenetic relationships to determine evolutionary trends, with global correlations using a broadly based time scale with subdivisions from a general stratigraphic scale using older (pre-1995) British standard series names. Khromykh (1999b) correlated the base of his Middle Ordovician with the base of the Llanvirn, which equates with a position in the current global Ordovician time scale similar to the middle of the Middle Ordovician series, i.e., in the lower half of the Darriwilian stage (Webby & others, 2004). Khromykh (1999b, table 1) provided stromatoporoid distribution data ranging from the topmost Mid-Ordovician (mid–upper Darriwilian) through to the mid–Upper Ordovician (mid-Katian stage = British late Caradoc), i.e., through about 15 myr of Earth history. Khromykh (1999b, fig. 1–2) presented a summary of the distribution of taxa from a phylogenetic point of view and a stratigraphic chart also showing the stepwise increase of generic diversity through late Mid- to mid–Late Ordovician time.

The mid–late Darriwilian record represents an interval of about 5 myr, and in Khromykh's (1999b) phylogenetic tree, the Siberian genus *Priscastroma* (type species *P. gemina,* with two varieties "a" and "b" (= forma A and B) were considered to be ancestral to other early stromatoporoids. The two varieties were recognized as the basis for a number of lines of descent, a main branch from *P. gemina* var. "a" leading to *Cystostroma*, then three separate offsets, in the first branch to *Stromatocerium, Pachystylostroma*, and "*Parksodictyon,*" this latter becoming *Pseudostylodictyon* by the end of the Middle Ordovician (end-Darriwilian), and a second branch in the early Late Ordovician producing *Rosenella* by the early Katian, and then *Clathrodictyon* on another branch in the mid-Katian. An additional side branch from *P. gemina* var. "a" gave rise to *Dermatostroma* in the early Katian, and the two offshoots from *P. gemina* var. "b" apparently produced *Labechia* in the latest Darriwilian and *Lophiostroma* in the early Sandbian. This overall coverage of labechiid and clathrodictyid genera (Khromykh, 1999b, fig. 2) included

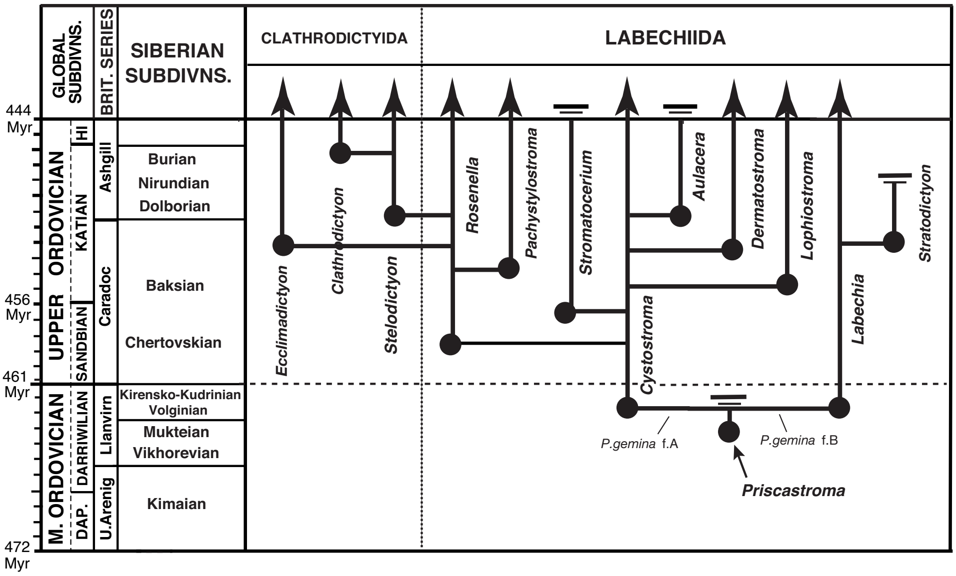

FIG. 359. Chart showing the inferred evolutionary relationships of 13 Mid–Late Ordovician stromatoporoid genera (10 labechiids, 3 clathrodictyids) from the Siberian Platform and Taymyr Peninsula (northeastern Siberia), based on data assembled by KHROMYKH (2010). The ranges of individual genera are shown by *thickened vertical lines* from their earliest records (denoted by *black circles*); *double cross bars* represent inferred levels of extinction, and *upwardly directed arrows* indicate taxa that have extended ranges above the Ordovician-Silurian boundary; note the abbreviations of global subdivisions: *DAP* (Dapingian stage) and *HI* (Hirnantian stage). The initial radiation of genus *Priscastroma* is based on type species *P. gemina,* which produced two variants (forma "A" and "B") thought by KHROMYKH (2010) to be ancestral to different lines of descent involving *Cystostroma* and *Labechia*, respectively. Two genera from the Upper Ordovician of Taimyr, *Nestoridictyon* KHROMYKH, 2001, and *Taymyrostroma* KHROMYKH, 2001, are excluded from this plot, because the first is considered to be a junior synonym of *Stromatocerium* (see p. 725), and *Taymyrostroma* has been classified by STEARN (2011b, p. 49–56; and see p. 829–836) in a stromatoporoid order and family with uncertain affinities (Webby, 2012b).

11 genera, which contrasts with the much larger total of genera known globally—some 24 genera plotted in Figure 358.

In a second contribution on the early evolution of stromatoporoids, KHROMYKH (2010) adopted a different approach, documenting the Ordovician and Silurian stromatoporoid generic records of the epicontinental so-called paleobasin successions of the Siberian Platform and the Taimyr Peninsula. Attention was focused on two important composite sections through the Ordovician (another included the Silurian record but is not considered here), including the Middle to Upper Ordovician succession in the Siberian Platform, and through the Upper Ordovician sequences of the other composite section in Taimyr. KHROMYKH (2010, fig. 2–3) compiled data in two stratigraphic columns, with details of the regional stratigraphic framework, tentative ties with global stage subdivisions, lithological details, thicknesses, stromatoporoid-bearing intervals, and first appearances of named genera. The total thickness of the Siberian Platform composite section is 130 m thick, and it has stromatoporoid-bearing limey deposits occupying about 38% of the total sequence, while the total thickness of the Taimyr composite section is 327 m thick and the stromatoporoid-bearing limey deposits comprises about the same proportion of the total sequence. In the Siberian Platform, the first appearances of sampled genera through the Mid–Upper Ordovician are as follows: *Priscastroma* and *Cysto-*

stroma in the mid–upper Darriwilian, then *Stromatocerium, Lophiostroma, Rosenella, Pachystylostroma,* and *Labechia* in Sandbian equivalents, followed by *Aulacera* in the mid-Katian. In the Taimyr Peninsula, first appearances of genera include the following, in stratigraphic order: from lower Katian (*Stratodictyon, Stelodictyon,* and *Ecclimadictyon*), to mid-Katian (*Dermatostroma*), and finally to Hirnantian (*Clathrodictyon*).

Most of the above-mentioned genera were included in an Ordovician-Silurian phylogenetic tree of KHROMYKH (2010, fig. 4) that displays only the generic data from the Siberian region. A compilation based on KHROMYKH's data is presented here, showing a phylogeny just for the Ordovician part of the Siberian record (see Fig. 359); its purpose is to allow comparisons between the generalized worldwide– and regional (Siberian)–based Ordovician plots presented in Figures 358 and 359. Based on the Siberian record, most of the genera, excepting *Labechia* and *Stratodictyon,* were derived directly or indirectly from *Cystostroma* (KHROMYKH, 2010, p. 691). *Cystostroma* initially gave rise to *Rosenella,* and then two side branches from *Rosenella* led directly to the first members of the Clathrodictyida; that is, *Ecclimadictyon* and *Stelodictyon* during the mid-Katian, and then *Clathrodictyon* was derived from *Stelodictyon* in the late Katian. All the other genera are members of the Labechiida (Fig. 359).

KHROMYKH (2010, p. 691) considered that all the Siberian taxa found in the Ordovician deposits had originated in the Siberian paleobasin; and he specifically named *Cystostroma*, *Dermatostroma, Pachystylostroma,* and *Stromatocerium* as genera that emerged earlier in the Siberian paleobasin than in other basinal regions elsewhere in the world. He did not discuss matters such as whether any of the Siberian faunal elements might have originated in other parts of the world, then migrated later into the Siberian region. Such a conclusion, however, must be drawn from comparing the patterns of first appearances of genera in the global and the Siberian charts (Fig. 358–359). For example, the labechiid genera *Pachystylostroma, Lophiostroma, Stratodictyon,* and *Aulacera* all exhibit earlier appearances, based on comparing the data plotted globally (Fig. 358) and regionally within Siberia (Fig. 359), and this implies that at least these four genera may have migrated initially into the Siberian region, rather than first evolving within the Siberian paleobasin. Also, the genus *Clathrodictyon* appeared much earlier in other parts of the world (Fig. 358) than in Siberia, and that genus was probably not derived from *Stelodictyon,* as shown in Figure 359, but its evolutionary pathway was probably in the opposite direction, from *Clathrodictyon* to *Stelodictyon*. In general, it is not easy to determine evolutionary patterns based only on one or two sets of regional data; a broader temporal and spatial approach is needed to achieve meaningful patterns of origins and dispersal worldwide.

In terms of the record of the earliest evolutionary relationships, KHROMYKH (2010, p. 687) has shown that the stromatoporoid *Priscastroma gemina,* with its two variants, *P. gemina* forma "A" and forma "B" (Fig. 359), comes from the upper Kochakan Formation, within the Mukteian horizon (or local stage) of the Moiero River basin section of the Siberian Platform, equating with the *Didymograptus murchisoni* graptolite Zone (within the middle-upper part of the Darriwilian stage). KHROMYKH (2010, p. 689) mentioned the possibility that the genus *Zondarella*, described previously from the early Mid-Ordovician (Dapingian) of Argentina (KELLER & FLÜGEL, 1996), might be ancestral to *Priscastroma,* but no evidence has emerged to indicate this taxon is present in critical Siberian sections; furthermore, it appears that the genus *Zondarella* has closer links to pulchrilaminids than to stromatoporoids (see above, p. 578).

Of significance are the appearances of a number of other distinctive, short-lived taxa in the Mukteian stage of the Moiero River basin section. In addition to *Priscastroma*, such forms as tabulate coral *Cryptolichenaria* SOKOLOV, 1955 (see KANYGIN, MOSKALENKO,

& YADRENKINA, 1988, p. 5; KANYGIN, 2001, p. 610) occur. Apparently, according to KANYGIN (2001, p. 610), such forms first appeared on the eve of the great "ecologic revolution" (a radiation event), but they did not leave direct descendants, only variants like the ones associated with *P. gemina*. These were responsible for producing the two main, long-lived lines of labechiid descent involving *Cystostroma* and *Labechia* (this last genus appeared in the late Mid-Ordovician in the paleobasin but is not recorded in the Moiero River composite section—see KHROMYKH, 2010, p. 689, fig. 2). The associated major taxonomic diversification event involved a number of marine benthic groups (e.g., stromatoporoids, corals, bryozoans, brachiopods, trilobites, ostracodes, and others) early in the next regional stage (early Volginian; see KANYGIN, 2001, p. 609–610, fig. 3; KHROMYKH, 2010, fig. 2; and Fig. 359), at a level some 25 m above the initial appearance of *Priscastroma*, in the overlying Moiero Formation of the Moiero River basin section. *Cystostroma* (e.g., *C. insuetum* NESTOR, 1976) occurs at this level and equates with the *Hustedograptus teretiusculus* graptolite Zone (see correlation chart in KANYGIN, MOSKALENKO, & YADRENKINA, 1988), which is correlative globally with the uppermost part of the Darriwilian stage. This Siberian sequence between the Muktiean and Volginian is here inferred to be stratigraphically equivalent to the Chazyan interval in eastern North America, that is, between the Day Point and Crown Point formations (lower to middle Chazy Group), where GALLOWAY and ST. JEAN (1961) and KAPP and STEARN (1975) described the earliest North American labechiid species of *Pseudostylodictyon lamottense* (SEELY, 1904) and *Cystostroma vermontense* GALLOWAY & ST. JEAN, 1961.

On the other hand, KHROMYKH (1999b, p. 229) has erroneously suggested that the lower part of the Chazy Group (Day Point Formation) should be correlated with higher levels (middle of the Moiero Formation), based on OXLEY and KAY's (1959, p. 825) field identification of "masses of *Stromatocerium*" in the lower part of the Day Point Formation. Others have attempted to find this stromatoporoid in the Day Point Formation, without success. For example, PITCHER (1964, p. 648), in his detailed survey of Chazyan reef assemblages, considered that most reports of *Stromatocerium* from the Day Point Formation probably referred to misidentified bryozoans. Clearly, the OXLEY and KAY determination has not been substantiated by the paleontological studies of Chazy stromatoporoids from Vermont and New York by GALLOWAY and ST. JEAN (1961) and KAPP and STEARN (1975). The genus *Stromatocerium* is instead characteristic of the disconformably overlying Black River Group (representing the upper part of the Sandbian stage) in the same region of eastern North America (GALLOWAY & ST. JEAN, 1955, 1961; HOFMANN, 1963, fig. 9; FISHER, 1968; KAPP & STEARN, 1975; BERGSTRÖM & others, 2009).

The major evolutionary event that occurred in shallow carbonate seas of different circumequatorial parts of the world during late Middle Ordovician (mid–late Darriwilian) time is represented by synchronous appearances of stromatoporoid-bearing Chazy reefs in eastern North America and the events and dramatic diversity changes recorded in mainly level bottom communities (including small stromatoporoid-bearing bioherms and biostromes) in the Siberian paleobasin (KANYGIN, 2001). Also, there were other stromatoporoid-bearing sequences in different parts of North America (Laurentia), and in Asian parts of northern China, Korea, and Malaysia (mainly parts of blocks associated with tropical East Gondwana) that contain genera of more or less the same mid–upper Darriwilian age (see Paleobiogeography of the Paleozoic Stromatoporoidea, p. 653–689).

The earliest appearances in Australia are in Tasmania and New South Wales, including records of *Labechia*, *Labechiella, Stratodictyon, Stromatocerium*, and ?*Aulacera*

(Webby, 1979a, 1991; Pickett & Percival, 2001), correlating with a level close to, but just above, the Middle–Late Ordovician boundary (basal Sandbian Stage).

In addition, a marked, "sudden dominance of stromatoporoids," was reported by Harper, Stouge, and Christiansen (2004, p. 157; 2005, p. 49) from the lower Middle Ordovician succession of "inshore" aspect, within the upper Cape Weber Formation of Albert Heim Bjerge, northeastern Greenland. The radiation of so-called stromatoporoids apparently occurred in the Dapingian (=early Whiterock) age, and this is much earlier than the confirmed major worldwide diversification of stromatoporoids (with its widespread appearances of earliest representatives of the order Labechiida) during mid- to late Darriwilian time (see previous discussion, p. 581–583; and see Webby, 2004b, p. 112–114). Stouge and others (2002, p. 122) also recorded "stromatoporoid bioherms" from a stratigraphically higher part of the Albert Heim Bjerge sequence, within the upper part of the Heimbjerge Formation, of late Darriwilian (=late Whiterock) age (see also Smith & Bjerreskov, 1994, p. 20 and chart 1). These preliminary field-based discoveries, especially the finds of so-called stromatoporoids from the Dapingian are of considerable interest, but none of the collected specimens has been subjected to rigorous, detailed study using thin sections (Svend Stouge, personal communication, February 2007). Until such studies are undertaken by specialists, it will remain a matter for speculation whether the Dapingian takeover of so-called stromatoporoids is a localized, early radiation event restricted to Greenland, or whether the collected hypercalcified fauna proves to represent a variety of other skeletonized groups that are unrelated to indubitable stromatoporoids.

LATE ORDOVICIAN ORIGINS OF CLATHRODICTYIDA

The order Clathrodictyida exhibited characteristic laminar skeletons (Nestor, 1994) and initially appeared during the Late Ordovician (early Katian). The genus *Ecclimadictyon* Nestor, 1964a, with its zigzag laminae, was first to appear, and then *Clathrodictyon* Nicholson & Murie, 1878, with its more gently inflected laminae, appeared a little later (Webby, 2004b). This was about 10 myr after the first appearances of labechiid stromatoporoids. The two genera became widely distributed through the latest Ordovician. Later, three additional genera, ?*Plexodictyon* Nestor, 1966a, *Camptodictyon* Nestor, Copper, & Stock, 2010, and *Stelodictyon* Bogoyavlenskaya, 1969a, appeared, but initially the first only maintained a distribution in New South Wales (NSW), the second, also in NSW and the Russian–Chinese Altai, and the third, in Estonia and Siberia. In terms of the origins of the clathrodictyids, Nestor (1994) has shown them diverging from the labechiid family Rosenellidae, early in the Mid-Ordovician. But there is no evidence of such an early clathrodictyid fossil record, so it is much more likely that a much later divergence occurred, possibly from rosenellids in the Late Ordovician, close to the boundary between Sandbian and Katian stages (formerly mid-Caradoc). Otherwise, perhaps a basically clathrodictyid morphology could have been derived from a *Cystostroma*-like ancestor at this time. Some qualifications remain, however, when it comes to explaining exactly the steps required for a simple labechiid ancestor, with denticles that grew upward off cyst plates, to have evolved into an early clathrodictyid, where the short, commonly superposed pillars arose as downward inflections of successive laminae (Webby, 1986, p. 157). This event may have coincided with the interval of the greatest circumequatorial spread of Ordovician reefs (Webby, 2002), when many other groups of organisms (e.g., rugose corals, echinoderms, bryozoans, rhynchonelliformean brachiopods, and vertebrates) were attaining significant peaks of global diversity (Webby & others, 2004).

Stearn (1980) and Nestor (1994) maintained that the most characteristic families of the order Clathrodictyida were the families

Clathrodictyidae Kühn, 1939b, featuring gently inflected laminae, and the Actinodictyidae Khalfina & Yavorsky, 1973 (formerly Ecclimadictyidae Stearn, 1980), exhibiting crumpled to chevron or zigzagged laminae. The Clathrodictyida are a major cosmopolitan group, and the two families show well-defined, parallel development through the Silurian and Devonian (Nestor, 1997), but it is difficult to maintain a differentiation into two families in Late Ordovician, because the early records of *Clathrodictyon*, *Ecclimadictyon,* and ?*Plexodictyon* show a range of gradations between forms with regular and crumpled types of laminae (Webby, 1986, p. 156–157). There is more plasticity among these early clathrodictyids, and Silurian-based classification simply does not work as well for classifying the Late Ordovician forms.

The stratigraphic record from the initial Late Ordovician appearances of *Clathrodictyon* and *Ecclimadictyon* is more or less continuous into the Silurian, but the species diversification remained rather low across the Ordovician-Silurian boundary (Nestor, Copper, & Stock, 2010, fig. 4), probably as a consequence of instability associated with the end-Ordovician glaciation (Webby, 2004b). However, the clathrodictyids were important contributors to reef growth during the initial warming phase of the late Hirnantian but did not diversify significantly through most of the earliest Silurian (Rhuddanian), until the significant radiation of clathrodictyids commenced in the mid-Llandovery (Aeronian) (Nestor, 1997; Nestor & Stock, 2001). The most comprehensive classifications of the Clathrodictyida are presented by Nestor (1997; Nestor in Stearn & others, 1999), with subdivisions into five families of mainly Siluro-Devonian taxa, updated to six families with the addition of the new family Anostylostromatidae (see p. 766).

LATE ORDOVICIAN ORIGINS OF ACTINOSTROMATIDA

One other stromatoporoid order may have had its origins in the Ordovician. Three workers in particular, Nestor (1960, 1964a, 1994), Bogoyavlenskaya (1969a, 1974, 2001a), and Stock (1983, 1994; Stock in Stearn & others, 1999), have been active in establishing the origins, relationships, and classification of the actinostromatids. The genus *Plumatalinia* Nestor, 1960, from the Late Ordovician (global late Katian = Pirgu stage of Baltoscandia) of Estonia, has been problematical because it shows morphological features that are typical of both labechiids and actinostromatids. Nestor (1960, 1964a) initially assigned the genus to the Labechiidae. Bogoyavlenskaya (1969b, p. 17, 25) subsequently recognized the Plumataliniidae (with sole genus *Plumatalinia*) as a new family of the order Labechiida, though she qualified her assignment to labechiids by noting that *Plumatalinia* could well be the ancestor of laminar stromatoporoids. Later she presented first a grouping in a stratigraphic chart, without specific discussion of the change showing the genus as ancestor of the order Actinostromatida and other descendants (Bogoyavlenskaya, 1974, p. 22), then formally justified the transfer (Bogoyavlenskaya, 1984, p. 70, 78, fig. 18) and has since maintained the family Plumataliniidae in order Actinostromatida (Bogoyavlenskaya, 2001a). Stock (1983, p. 168), on the other hand, treated *Plumatalinia* as a labechiid genus that probably gave rise to the Actinostromatida in the Late Ordovician or early Silurian, while Nestor (1994, fig. 2) viewed the family Plumataliniidae as a Late Ordovician offshoot from the family Labechiidae (though he retained *Plumatalinia* in the order Labechiida). Nestor also thought that the ancestral Late Ordovician plumataliniid line probably gave rise to all the descendant lines of Siluro-Devonian stromatoporoids belonging to the order Actinostromatida. He differentiated four families, the Actinostromatidae, Pseudolabechiidae, Densastromatidae, and Actinostromellidae.

Stock (1994) supported Bogoyavlenskaya's (1974, 1984) approach in transferring *Plumatalinia* from Labechiida, viewing it as the likely ancestor of actinostromatids. He offered two different evolutionary schemes for the development of the group, each showing *Plumatalinia* as the Late Ordovician ancestor and well prior to the initial radiation into two or three main lines of descent in the Silurian. In the more traditional evolutionary scheme, the three lines of descent are represented by families Actinostromatidae, Pseudolabechiidae, and Actinostromellidae, and the ancestral *Plumatalinia* was incorporated in the Pseudolabechiidae. First appearances of the Silurian genera were the actinostromatid *Plectostroma* in the late Llandovery and the pseudolabechiid *Desmostroma* and densastromatid *Densastroma* at the beginning of the Wenlock. This was a somewhat different arrangement from the scheme proposed by NESTOR (1994). STOCK (in STEARN & others, 1999, p. 36) later proposed the downgrading of family Plumataliniidae to subfamily Plumataliniinae of the family Pseudolabechiidae BOGOYAVLENSKAYA, 1969b, but in this volume the subfamily names have been abandoned; hence, Plumataliniidae becomes a junior synonym of the Pseudolabechiidae.

In terms of the stratigraphic relationships, it is important to note that there is a gap in the continuity of the actinostromatid record, representing an interval of about 3.5–4 myr, between the restricted Estonian record of *Plumatalinia* in the Late Ordovician (late Katian = Pirgu stage) and the appearance of genus *Plectostroma* NESTOR, 1964a, in the late Rhuddanian (early Llandovery). This latter genus belongs to the family Actinostromatidae (not the family Pseudolabechiidae), so no direct lines of descent are preserved through this critical Hirnantian to early Rhuddanian interval of extinction and recovery impacts associated with the end-Ordovician glaciation (e.g., NESTOR & STOCK, 2001).

Heldur NESTOR (personal communication, November 2006) has since kindly supplied some additional details about the original Estonian material (its preservation and occurrences) used to found the key taxon *Plumatalinia ferax*. A total of 15 specimens from 3 localities were used in the description of *P. ferax* presented in NESTOR (1964a). The material was collected from disused, overgrown farm quarries from the 19th and early 20th centuries. States of preservation vary considerably in the specimens studied and in some cases within a single specimen. The 3 states are represented by: (1) forms with long, low, flattened to wavy cysts (lacking longitudinal skeletal elements, as in simple labechiids), though they may show an incipient development of vertical canal-like interruptions; (2) forms with very fine, irregular skeletal meshwork between cyst plates and with columnlike structures in a few places; and (3) forms with a partially preserved fine microreticulate structure of columnlike structures and with a diffused outline. The microreticulate state is considered by NESTOR (personal communication, November, 2006) to be a primary structure, and therefore the resemblance is with microreticulate actinostromatids, though the particular microstructural type (acosmoreticular in *Plumatalinia*) differs from that found in other actinostromatid genera (*Densastroma* FLÜGEL, 1959, with orthoreticular and *Vikingia* BOGOYAVLENSKAYA, 1969a, with clinoreticular types; see STOCK in STEARN & others, 1999, and in Actinostromatida, p. 769–779).

WEBBY (1979a, p. 88; 1994, p. 375; WEBBY in STEARN & others, 1999, p. 13) originally considered that some of the fine subreticulate material may have been of secondary origin, pointing to similar features in other relatively poorly preserved labechiids, such as *Stratodictyon columnare* (WEBBY, 1969, pl. 118,*4–6*). Examples of this microreticulate state are also developed in other labechiids, typically in the columns of *Pseudostylodictyon poshanense* OZAKI (see *Pseudostylodictyon,* Fig. 391*a–b*), and apparently also in *Pachystylostroma mammillatum* (see WEBBY, 1979c, fig. 3E–F). Consequently, it seems that *Plumatalinia* genuinely occupies an intermediate position between labechiids like *Pseudostylodictyon* and actinostromatids. It may indeed be a kind of missing link between the two groups, but some caution still needs to be exercised in claiming this relationship when such variability exists between the morphologies of the two groups.

A brief review of patterns of Silurian origins and relationships in other, nonlabechiid, stromatoporoid groups such as the stromatoporellids, stromatoporids, syringostromatids, and amphiporids is elsewhere (see section on diversity trends, p. 593–597).

DIVERSITY TRENDS OF THE PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

INTRODUCTION

Diversity trends in paleontology have been almost universally measured by counting taxa and plotting the number of families, genera, or species against time. The assumption of taxon counting is that the division into named units is a measure of the overall differences or disparity between sets of organisms. For stromatoporoids, no attempt has been made, nor is it being made here, to measure trends in what has been called disparity; that is, changes of morphology with time, as opposed to changes in taxa. Information and references to the literature on the differences between these two metrics can be found in such articles as FOOTE (1997), EBEL (2000), MILLER (2000), and NARDINE, ROUGET, and NEIGE (2005). The division of diversity found in organisms into discrete taxa is subjective (STEARN, 1998), and this is a built-in weakness of taxon counting, but it can be minimized by using the taxonomy produced by a single paleontologist working with consistent principles, or a taxonomy agreed upon by a closely knit group of paleontologists working from common principles. Here, the latter approach is used, and the compilations of the four authors of the taxonomy of Paleozoic stromatoporoids (Colin W. STEARN, Barry D. WEBBY, Heldur NESTOR, & Carl W. STOCK; see Paleozoic Stromatoporoidea, p. 707; and Labechiida, p. 709–754) are the bases of this section (Fig. 360–361). Studies of diversity trends in the stromatoporoids have been published by NESTOR and STOCK (2001), COPPER (2002), WEBBY (2004b), and STOCK (2005). COPPER's (2002) diagram, which closely resembles Figure 360, was compiled from the review of stromatoporoid taxonomy by STEARN and others (1999). It differs from the figure shown here in the lack of diversity fall-off at the Silurian-Devonian boundary, but COPPER's figures for diversity are roughly comparable to those used here. In each of these studies, the genus is the taxon counted, and this procedure is followed here.

In tabulating the generic diversity of a group in various time intervals, one can record only the time slices in which the genus has been found, or one can make the assumption that, if the genus is found in slices 1 and 4, it must also have existed in slices 2 and 3. The latter method is called the range-through method. The ranges of some labechiid stromatoporoids illustrate one of the problems with this method of tabulation. For example, the genera *Pachystylostroma* and *Labechiella,* which are likely to be progenitors of Famennian genera, have breaks in the continuity of their records; the former through Lochkovian to Givetian (about 31myr) and the latter through the Llandovery to Wenlock (about 20 myr) (see Fig. 362). If the range-through method were used, it would exaggerate the diversity of labechiids in the Silurian system to some extent. For this reason, the range-through method is not used in this discussion, and the occurrence of a genus in a certain time slice has only been recognized when it has actually been recorded from rocks of the time interval.

Owing to divergences in opinion on taxonomic placement and on the age of certain collections, paleontologists do not agree on the precise generic diversity of stromatoporoids in the various time slices plotted in the figures. The figures on which the following discussion is based are attempts to reach consensus and are designed to show the relative rise and fall of diversity in stromatoporoid orders rather than the exact

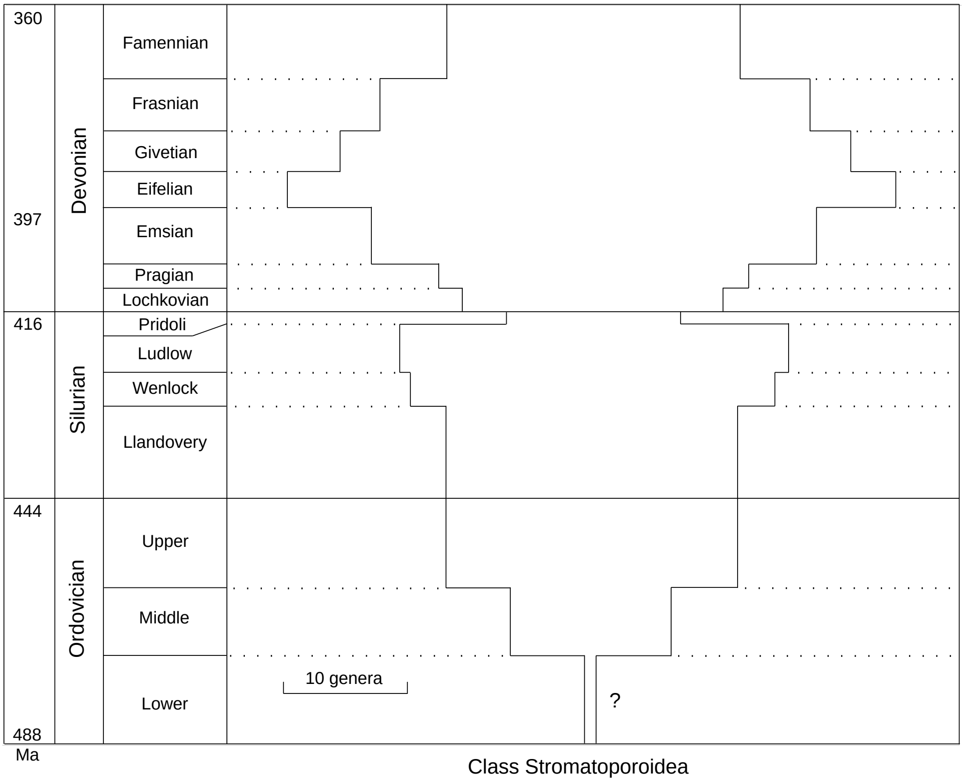

FIG. 360. Generic diversity of the class Stromatoporoidea. The vertical intervals are proportional to their time value in the geologic time scale according to GRADSTEIN, OGG, & SMITH (2004). Ages in millions of years (Ma) are indicated on the left; question mark in the Lower Ordovician denotes the author's view that the Pulchrilaminida is doubtfully ancestral to the class Stromatoporoidea. According to WEBBY (p. 575–592, p. 837–844), however, the new order Pulchrilaminida lacks close links to the Stromatoporoidea and, consequently, is best considered a completely independent hypercalcified sponge group of the class Uncertain. Note that in a more recent version of the time scale (COHEN & others, 2013), the base of the Ordovician is 485 Ma, base of the Silurian is 443 Ma, base of the Devonian is 419 Ma, base of the Middle Devonian is 393 Ma, and the top of the Devonian is 359 Ma (Stearn, 2010e).

number of genera in each time slice. The time scale used in calculations for Figure 360 is that published in 2004 by GRADSTEIN, OGG, and SMITH.

The causes for apparent changes in diversity in time have been widely discussed in the literature and are more fully discussed in the sections on evolution and extinction (see p. 575–592, and p. 599–612). Some of the factors affecting taxonomic diversity that have been recognized include: extent of exposure of rocks of various ages; extent of the seas depositing rocks of appropriate facies; number of paleontologists working on fossils of various ages; and all the environmental factors that affect the life history of any group and particularly the rates of origination and extinction of taxa. The last points are of primary concern in the interpretation of the past; however, they are not the focus of this chapter, which describes the changes of diversity in time, rather than the causes of these changes.

CLASS STROMATOPOROIDEA

The diversity of the stromatoporoids, like that of many marine invertebrates, diminished at or near the close of the three geological periods in which they thrived. The downward trend at the end of the Ordovician is recorded only in the labechiids (Fig.

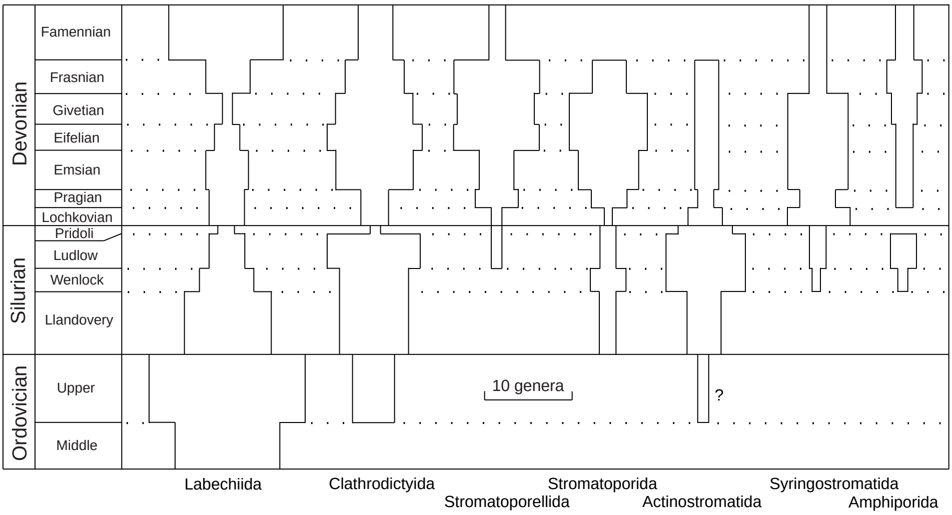

FIG. 361. Generic diversity of the orders of the class Stromatoporoidea, with the exception of the Pulchrilaminida. Time scale as in Figure 360. The extension of the Actinostromatida into the Upper Ordovician is based on the opinion of STOCK and NESTOR (personal communication, 2006) that the genus *Plumatalinia* is an actinostromatid, but WEBBY (see p. 590–592), on the basis of diagenetically altered skeletal material, believes the genus may be a poorly preserved labechiid, or that it occupies an intermediate position between the two groups (Stearn, 2010e).

361) and is compensated for by the rise of the clathrodictyids, stromatoporids, and actinostromatids. NESTOR and STOCK (2001) found that the crisis that abruptly affected other invertebrates at the end of the Ordovician is recorded by only gradual changes in the diversity of the stromatoporoids. From the Middle Ordovician until the end of the Ludlow, generic diversity of the order steadily increased (Fig. 360). The general decrease in diversity at the close of the Silurian reached its nadir in Pridoli time and was probably at least partially caused by the restriction of latest Silurian and earliest Devonian seas during this interval, leading to a consequent rarity of rocks of this age on the continental platforms. The extinction of the Paleozoic stromatoporoids at the close of the Devonian is fully discussed in the section on extinction patterns (see p. 599–612).

The greatest diversity of the class as a whole occurred in the middle of the periods (Fig. 360). In Ludlow and Wenlock times, diversity reached about 30 genera. The greatest diversity recorded in the compilation is 50 in Eifelian time, but values of more than 30 genera were maintained until the late Frasnian crisis.

From the high level of diversity during the Eifelian, the class declined toward its extinction at the end of the Devonian. The crisis at the end of the Frasnian, which has been much discussed as the Kellwasser Event (see section on extinction patterns, p. 599–612) is a prominent step in the decline, but the expansion of the labechiids in the Famennian compensated for the marked effect of the crisis on three of the orders (Stromatoporellida, Stromatoporida, Actinostromatida, Fig. 361). The generic diversity of the nonlabechiid stromatoporoids fell from 30 in Frasnian time to 11 in Famennian time.

LABECHIIDA

Both morphology and diversity history set the order apart from the rest of the stromatoporoids. Their origin is obscure, perhaps being with the enigmatic *Pulchrilamina* of the late Early Ordovician (Floian) of North America and *Zondarella* of the early Middle Ordovician of South America, separated by a gap representing about 4 million years from the first labechiids (Webby, 2004b), although a problematical *Zondarella*-like taxon named *Ianilamina* Pickett & Zhen (in Zhen & Pickett, 2008), which was found recently in the early Darriwilian of New Souh Wales, arguably closes the gap to the first labechiid appearances. They suddenly appear as a diverse group (12 genera) in rocks of Darriwilian (late Mid-Ordovician) age in North America and southeastern Asia. Their diversity increases to almost 20 genera by the end of the Ordovician, when they began a long decline through the Silurian Period to a minimum of 2 genera in Pridoli time. Their latest Ordovician decline in diversity has been attributed to two sharp cooling to warming events of the Hirnantian glaciation (Webby, 2004b). During the Middle Devonian diversity peak of the other orders, the labechiids appear to have been restricted to Europe and western Asia, as they do not occur in the varied stromatoporoid faunas of the vast reef tracts of North America, South China (e.g., Yang & Dong, 1979), or Western Australia, although they do appear in the early Middle Devonian of eastern Australia (Webby & Zhen, 1997). The sudden rise in diversity of the labechiids at the close of the Devonian (to about a dozen genera) is more fully discussed under the Kellwasser and Hangenberg extinction events that affected the whole class. Some feature of their adaptation allowed them to diversify, when the other orders were severely affected by the changes at the end of Frasnian time. However, they, like the other orders, could not survive events at the end of the Devonian Period, when the whole class became extinct.

NONLABECHIID ORDERS

The Clathrodictyida appeared about 10 million years after the labechiids in the later half of the Late Ordovician, but they did not reach their diversity maximum until the Ludlow. Their first representative was the typically Silurian genus *Ecclimadictyon*, rather than the structurally simpler (and presumably more primitive) genus, *Clathrodictyon*. The clathrodictyids are the most abundant and diverse stromatoporoids in middle Silurian reefs. They also thrived in the Middle Devonian, and about 11 genera are recorded from Eifelian rocks. The order was reduced slightly in diversity in Frasnian time and rendered almost extinct at its close.

The Stromatoporellida are largely a Devonian order and are represented in the Ludlow by the single aberrant genus *Simplexodictyon*, which seems unlikely to have been ancestral to the rest of the order. They probably arose from clathrodictyid stock. The diversity of the order shows a steady increase to a maximum of ten genera in Eifelian time, and this diversity was maintained until the late Frasnian crisis.

The Stromatoporida also reached their peak of diversity in the Devonian but are represented in the Silurian by several genera, beginning in the mid-Llandovery with *Lineastroma* and *Syringostromella.* Little change in the diversity of the order occurred until it began to increase in the Emsian. It reached its peak (nine genera) in the Givetian. The stromatoporids collapsed in the late Frasnian crisis, and the order is only doubtfully known from Famennian rocks.

The first of the actinostromatids is thought to have been *Plumatalinia,* which appears to be transitional to this order from the labechiids and is plotted in Figure 361 in the Ordovician (see Nestor, 1994, for discussion). The Actinostromatida reached their acme of diversity (about ten genera) during the middle of the Silurian period. Many of these genera had the closely spaced micropillars and microlaminae of the densastromatid family. Although the diversity of the actinostromatids decreased in the beginning of the Devonian, as the densastromatids died out or gave rise to the syringostromatids, the drop in diversity shown in Figure 361 misleads, if it is interpreted to imply the order was in decline in Devonian time, for the genus *Actinostroma* is abundant and ubiquitous in mid-Devonian carbonates. The generic diversity of the order remains at about three from Emsian time to the crisis at the end of the Frasnian.

The Syringostromatida apparently arose from actinostromatid ancestors in the middle Silurian. A few Silurian genera have been assigned to the order, but they are largely a Devonian group. They maintained a diversity of about seven genera for most of the period but became rare in Frasnian rocks and did not survive into the Famennian.

The sticklike Amphiporida first appear in middle Silurian rocks and are represented as one or two genera in most time intervals of the Silurian and Devonian, until they became both diverse and overwhelmingly abundant in Frasnian carbonates. Recently (MISTIAEN, 1997), *Amphipora* has been found in Famennian rocks, but compared with its ubiquity and abundance in Frasnian rocks, it is there very rarely.

EXTINCTION PATTERNS OF THE PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

INTRODUCTION

The Paleozoic stromatoporoids were greatly reduced in abundance and diversity in the middle of the Late Devonian epoch and became extinct at its end, in events that have been described as mass extinctions, owing to the disappearance of many groups of marine animals at the same time. These intervals of high rates of declining diversity in the Devonian period are clearly shown by graphs of family diversity published by RAUP and SEPKOSKI (1982): between the Frasnian and Famennian stages (F/F) and at the Devonian-Carboniferous boundary (D/C). Unfortunately, they have been named after intervals of dark shales and limestones in the western German succession, as the Kellwasser and Hangenberg events, on the unproven assumption that the anoxic environments that the sediments represent were worldwide in extent. Evidence of ubiquitous anoxia at these times is equivocal at best, so the terms should be confined to local use. No attempt is made in this chapter to review the vast literature on mass extinction, but possible causes common to events in which the stromatoporoids declined, and to other extinction events in life history, are discussed.

What is a mass extinction and at what level are such events to be separated from background extinction (HOFFMAN, 1989)? Are the causes of mass extinction different from, or did they operate on a different scale from, the causes that throughout geological time have carried away the great majority of organisms that have ever lived? HOFFMAN (1989) thought that no extraordinary causes needed to be postulated to explain mass extinctions but rather the coincidence of causes that operate all the time.

NEWELL (1967) suggested that there were six major episodes of accelerated extinction in the fossil record and favored a mechanism of regression to explain them. Most later work on characterizing mass extinctions has focused on the manipulation of various editions of SEPKOSKI's compilations (RAUP & SEPKOSKI, 1982; SEPKOSKI, 1996 [unpublished but see BAMBACH, KNOLL, & WANG, 2004, p. 523]; SEPKOSKI, 2002) to assess extinction patterns of the so-called big five events: (1) end-Ordovician; (2) Frasnian/Famennian; (3) end-Permian; (4) end-Triassic; and (5) end-Cretaceous. WANG (2003), WANG and MARSHALL (2004), and BAMBACH, KNOLL, and WANG (2004) concluded that the evidence for accelerated extinction as a cause of these diversity drops could only be established for three of these (1, 3, 5) and that the proportional decline in generic diversity for 2 and 4 was included in a continuum of background extinction rates. The D/C (Hangenberg) event that marks the final demise of the Paleozoic stromatoporoids is not one of the big five and is marked by only a minor decrease in the proportional diversity curve. BAMBACH, KNOLL, and WANG (2004) accounted for two-thirds of the diversity drop at the F/F boundary by origination failure and attributed only the remaining one-third to increase in extinction rate. The search for causes of marked diversity drops and extinctions in the fossil record now becomes as much one for mechanisms of origination failure as for catastrophic extinction disasters.

Most of the studies of mass extinctions have been based on counting of taxa (families and genera), but other methods for assessing the magnitude of extinction events have been proposed. MCLAREN (1983) emphasized the extent of biomass loss as a measure

Table 30. Commonly recognized sequence of conodont zones in the Late Devonian–earliest Carboniferous succession and showing stratigraphic levels of F/F (Kellerwasser) and D/C (Hangenberg) extinction events (adapted from Sandberg, Morrow, & Ziegler, 2002).

Lower Carboniferous	⋮
	sulcata
D/C	
Upper Devonian (Famennian)	*praesulcata*
	expansa
	postera
	tachytera
	marginifera
	rhomboidea
	crepida
	triangularis
F/F	
Upper Devonian (Frasnian)	*linguiformis*
	rhenana
	jamieae
	hassi
	punctata
	transitans
	⋮

of the significance of mass extinctions. In particular, he drew attention to the demise of the Devonian reef facies in the F/F event. Copper (1994) estimated that Frasnian reefs may have been ten times more extensive than modern ones and were reduced at the F/F event to insignificance. Droser and others (2000) rated extinctions on the basis of four paleoecological levels, ranging from community-level changes to disappearances of whole ecosystems. They rated the changes at the F/F event as second, third, and fourth levels, but it is not clear how they would rate the D/C extinctions. McGhee and others (2004) rated the Late Devonian crises (which they considered together) as fourth in ecological severity of the big five and third in loss of marine familial diversity. They emphasized that the Late Devonian crisis was "... triggered in large part by a precipitous decline in speciation rates at the end of the Frasnian" (McGhee & others, 2004, p. 295).

Much of the discussion of the mid-Paleozoic extinctions involve reconstructions of the positions of the continents in Late Devonian time. Although many paleogeographic maps have been published, the disposition of the continents at this time is still in doubt. Many paleontologists have rejected the widely distributed maps of Scotese and McKerrow (1990; and, for example, www.scotese.com) on the basis that both Siberia and Laurussia are too far north and Paleotethys too open. Streel and others (2000) adopted the map by Heckel and Witzke (1979), because it accounts for the distribution of palynomorphs better. McGhee (1996) discussed the uncertainties of mid-Paleozoic paleogeography at length.

The early literature on the mid-Paleozoic extinctions has been summarized in books by McGhee (1996), Hallam and Wignall (1997), and Hallam (2004). Koeberl and MacLeod (2002) have recently compiled a series of papers on mass extinctions (Geological Society of America Special Paper 356). Another series of papers presented at the Geological Society of America's symposium in 2003 was issued by Over, Morrow, and Wignall (2005) and contains an important paper by Stock (2005) on stromatoporoid originations and extinctions.

PHYSICAL EVIDENCE OF LATE DEVONIAN CONDITIONS

TIME SCALES AND BOUNDARIES

Certain hypotheses of Late Devonian extinctions depend on the coincidence, or lack of coincidence, of physical and biostratigraphic events. Unfortunately, the dates of these events are not known precisely, and they change as research progresses, making older theories invalid. The extinctions that decimated the stromatoporoids are commonly said to occur at the Frasnian-Famennian boundary and at the end of the Devonian period. But these extinctions do not define the boundaries, and proving they occurred at the boundaries is difficult. The boundaries are defined for the convenience of conodont workers at the beginnings of the *triangularis* (F/F) and *sulcata* (D/C) zones respectively. The precise boundaries are set in the Montagne Noir sections in France at certain convenient beds (for the D/C a ferruginous crust) that correspond closely to the conodont distributions. The commonly recognized sequence of conodont zones in the Late Devonian succession that are used to position events in the subsequent discussion are listed in Table 30 (SANDBERG, MORROW, & ZIEGLER, 2002). In most sections, the abrupt F/F changes in fauna occur just above the last beds bearing the youngest Frasnian conodont fauna of the *linguiformis* zone. WALLISER (1996) suggested that the D/C boundary is actually about half a million years younger than the Hangenberg shales that have been said to mark it. The age in years of the two events can only be estimated by making assumptions about the length of the conodont zones and extrapolating from dated ash beds or lavas. Commonly accepted values are 364 Ma and 354 Ma (GRADSTEIN & OGG, 1996; MCGHEE, 1996; STREEL & others, 2000), but dates as divergent as 376 Ma and 362 Ma have been suggested. The International Commission on Stratigraphy time scale of 2013 places the base of the Famennian (F/F) at 372.2 ± 1.6 Ma, and the base of the Carboniferous (D/C) at 358.9 ± 0.4 Ma (COHEN & others, 2013). SELBY and CREASER (2005) place the D/C boundary at 361 ± 2.5 Ma, on the basis of Re-Os dating of the Exshaw Shale.*

STRATIGRAPHIC EVIDENCE

Great significance has been placed by Europeans on the occurrence at the F/F and D/C horizons of black shales and limestones of the Kellwasser and Hangenberg formations. The Kellwasser dark shales actually are divided into two parts by some beds of limestone. Conodonts of the *linguiformis* zone (latest Frasnian) occur just below the Kellwasser interval. WALLISER (1996) has been particularly enthusiastic about a worldwide anoxia indicated by these black shales. However, this euxinic facies by no means universally interrupts the carbonate facies at the F/F horizon, and in western Canada and Australia, where the interval is extensively exposed, no anoxic interval interrupts the carbonate succession. In western Canada, dark, barren shales replace carbonates at the D/C horizon (Exshaw, Bakken, Chattanooga equivalents), but in much of eastern and arctic North America, long before the close of the Devonian period, the carbonate facies had given way to deltaic sandstones and siltstones. In the deltaic facies of the Upper Devonian there, black shales are so common that they are given no particular significance.

GELDSETZER, GOODFELLOW, and MCLAREN (1993) described the F/F contact on the Trout River in the Northwest Territories in detail. The beds below the contact are a stromatoporoid biostrome in the Kakisa Formation of *linguiformis* age. The contact is overlain by sandstone and is believed to represent an unconformity of lowermost *triangularis* age. In the southern Alberta Rockies (DAY & WHALEN, 2002), the F/F contact is underlain by stromatoporoid-bearing breccias in the Ronde Formation (of Kakisa age) and overlain by the Sassenach fine clastics (largely siltstones) in basinal sections and on the shelf succession by the Palliser carbonates, whose basal beds appear to be of *crepida* age; i.e., the whole *triangularis* zone is missing on the shelf where the Sassenach is absent, owing to regression at this time. Apparently a regression at the F/F boundary caused withdrawal of the sea from the shelf area into the basins and was followed by a transgression in mid-Famennian time.

In the Canning Basin of western Australia, the F/F boundary is not marked by any

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*It may be helpful to explain the understanding accepted by the author of certain terms used to described events at the F/F and D/C boundaries. Boundary is an instant in time between the two ages substantially defined by the plane between the two stages at the stratotype section in the Montagne Noir; its position in other sections is approximated by methods of correlation. Horizon is the plane in the stratotype section that separates the two stages, and its position in other sections is established by correlation with the stratotype. Events are changes in environment that have occurred at or near the boundary between the ages. Where the boundary can not be determined precisely in a section that is not the stratotype, the term interval is used for the thickness of beds in which it is believed to be contained. Boundary extinctions are based on those fossils that range up to a specific level, but not above it.

conspicuous change in the stratigraphy that is indicative of transgression or regression (see Cockbain, 1989; Becker & others, 1991). In southern China (Wang & others, 1991; Ma & others, 2002), dark shales interrupt the carbonate successions in the *linguiformis* zone of the shallow-water facies but are not conspicuous in the marly deposits of deeper-water basinal sections. No equivalents of the Hangenburg facies occur in the D/C in southern China, and the boundary is within a bed of bioclastic limestone (Hallam & Wignall, 1997). In Guilin (South China), karst features at the F/F boundary have been interpreted as evidence of regression (Chen & Tucker, 2004).

ISOTOPE VARIATIONS

At intervals suspected of recording extraordinary faunal events (so-called bioevents), geochemists note excursions from baseline values of the isotopes ^{13}C and ^{18}O. The most extensive compilation of these values for the whole of Phanerozoic time was that of Veizer and others (1999). Globally, average δ^{13}C values are low during the Devonian, compared to higher values in the Silurian and Carboniferous. Values also climb steadily through the Paleozoic toward the Permian. Values of δ^{18}O also dip (to about –2) during the Devonian but climb toward +2 in the Carboniferous near its end. Saltzman (2005) indicated only minor positive excursions of δ^{13}C values at the F/F boundary and larger ones at the D/C boundary, to about +5.

Global compilations are too broad to provide much information on immediate causes of Late Devonian extinctions. Isotope studies of local sections and short time intervals should be more helpful. In the western German sections, the black shale intervals show positive excursions of δ^{13}C (Hallam & Wignall, 1997). Joachimski and Buggisch (2002) examined conodont apatite for changes in C and O isotopes and reported δ^{13}C excursions of about +3‰ at the F/F boundary. They recorded positive swings in both δ^{18}O and δ^{13}C in late *rhenana* and early *triangularis* times. Geldsetzer, Goodfellow, and McLaren (1993) recorded zigzag excursions in both δ^{13}C and δ^{18}O across the F/F boundary on the Trout River. Wang and others (1991) reported δ^{13}C shifts from +1‰ to –2.5‰ at the southern China boundary and concluded that this indicates a reduction in surface water biomass. Streel and others (2000) summarized the evidence of δ^{13}C as equivocal at the F/F boundary, and Hallam and Wignall (1997) indicated that there are no excursions of carbon isotopes at the D/C boundary.

EVIDENCE OF IMPACTS

Evidence for the occurrence of asteroid or comet impacts at Late Devonian times of mass extinction comprises iridium anomalies, microtektites, impact breccia, and craters.

Two iridium anomalies have been recorded in the Late Devonian but have been dismissed as either being of insignificant magnitude to indicate a major event or as occurring at the wrong time. The first, at the F/F boundary in Guangxi, China (Wang & others, 1991) shows an Ir deflection of only about 0.21 ppbillion from that of adjacent strata. The second, at a bed rich in *Frutexites* fossils in the Famennian of Western Australia, is generally considered to be caused by organic concentration of platinum group elements, rather than by an impact, and is not at either the F/F or D/C horizons.

Microtektites, the small globules of fused rock that have been considered indicative of impact events, have been found at the F/F boundary in Europe (at Hony, Belgium; Claeys & others, 1996) and South China, but, as Walliser (1996) pointed out, these indicators are not uncommon in the insoluble residues extracted for conodont analyses throughout the Paleozoic. Since extraterrestrial matter of various calibers is continually raining through the atmosphere, the presence of some microtektites at any particular horizon is not, in itself, good evidence of a catastrophic event.

Craters and breccias provide more direct evidence of bolide impact. McGhee (1996, 2001) has proposed that the Siljan Crater in Sweden, the Flynn Crater in Tennessee, and the Alamo Crater and breccia in Nevada are evidence that impactors were the ultimate cause of the F/F extinctions. Although the Siljan, the largest of these craters at 52 km in diameter, was at one time thought to correspond in time to the F/F event, changes in the time scale have since placed all the craters at approximately the time of the *punctata* zone, which is about 3 million years before the close of the Frasnian. To account for the time difference, McGhee (2001) applied a lag-time multiple impacts hypothesis to explain how these bolides could have been the ultimate cause of environmental changes that brought about the extinctions. Tapanila and Ekdale (2004) reported that stromatoporoids overlie the breccia deposits from the Alamo event, and apparently the impact had no lasting effect on the stromatoporoid community. By 2006, McGhee recognized that all known impact events appeared to predate the F/F boundary, if the date of 376 Ma that he accepted was valid. However, recent studies of the Siljan crater using laser-argon dating (Reimold & others, 2005) give a date of 377 ± 2 Ma, which is outside the error limits of the 2013 date for F/F of the International Commission on Stratigraphy (372.2 ± 1.6 Ma). Hypotheses linking impacts and extinction are frequently modified as different dates for the events continue to be revised.

There is no sure evidence of an impact or volcanic event associated with the D/C boundary; however, estimates of the times of impacts of the Charlevoix crater in Canada (357 ± 15 Ma) and the Woodleigh crater in Australia (359 ± 4 Ma) are within the range of estimates of the D/C boundary on the International Stratigraphic Commission Scale (359 ± 2.5 Ma) (McGhee, 2006).

The Woodleigh structure in the Carnarvon Basin of western Australia has been proposed as evidence of a Late Devonian impactor large enough to form a crater 120 km across (Mory & others, 2000). The size, nature, and date of this structure is controversial, and discussions and replies can be followed through papers in Earth and Planetary Science Letters (for example, Reimold & Koeberl, 2000; Renne & others, 2002).

EVIDENCE OF GLACIATION

Traces of glaciation near the paleopoles have been recognized generally as evidence of worldwide cooling. Considerable discussion of the age of glacial deposits and glaciated surfaces in Brazil and North Africa has been summarized by Streel and others (2000). Although they postulated cooling as a cause of the F/F extinction event, there is no evidence of glaciation at that time. However, evidences of miospore distribution, diamictites, and glaciated surfaces of latest Famennian age (D/C) are cited by Streel and others (2000) as clear evidence of glaciation near the southern polar regions, close to Brazil and North Africa.

Fischer (1984) pointed out that important climatic changes were taking place near the close of Devonian time when he defined his supercycles. The change from Earth's greenhouse condition to the icehouse condition, the end of the warm seas and extensive reefs of the early and middle Paleozoic, and the beginning of widespread and prolonged glaciation in the southern hemisphere took place in the Famennian but must have been relatively gradual.

LATE DEVONIAN DECLINE OF STROMATOPOROID DIVERSITY

Not all investigators agree that the Paleozoic stromatoporoids became extinct at the end of the Devonian period. Mistiaen (1984b, 1994) has proposed that, with the changing ocean environments of the Sandberg Supercycle, the stromatoporoids merely lost the ability to secrete a carbonate skeleton until they reappeared as the Mesozoic

TABLE 31. Species and generic diversity of stromatoporoids (new).

Area	Author and date	Givetian			Frasnian			Famennian		
		sp.	gen.	s/g	sp.	gen.	s/g	sp.	gen.	s/g
Afghanistan	Mistiaen, 1985	34	19	1.8	18	10	1.8	3	3	1.0
Belgium	Lecompte, 1951 in 1951–1952*	56	11	5.1	61	11	5.5	4	3	1.3
Poland	Kaźmierczak, 1971	32	12	2.7	19	12	1.6	–	–	–
Czech Republic	Zukalova, 1971[§]	16	8	2.0	56	17	3.3	8	7	1.1
Western Australia	Cockbain, 1984	–	–	–	25	12	2.1	2	2	1.0
Western Canada	Stearn+	24	16	1.5	37	20	1.9	5	5	1.0

*Famennian data: Conil (1961); [§]Famennian data: Friakova and others (1985); + Stearn (2010f).

stromatoporoids. He suggested that the changing Late Devonian marine environment caused stromatoporoid skeletons to decrease in density during Famennian time and eventually to disappear at its end.

That stromatoporoids persisted into earliest Carboniferous time (Tournaisian) has also been reported. The stromatoporoids originally reported from the Tournaisian of China have since been reassigned to latest Famennian. SMITH (1932) described *Labechia carbonaria* from early Carboniferous beds in England, but SOKOLOV (1955, p. 111, pl. 90, see caption) considered the name to be preoccupied, interpreting it as a chaetetid, which he renamed as *L. smithi.* The cystose structure of labechiids is duplicated in many types of rugose and tabulate corals, and fragments of these can easily be mistaken for a labechiid stromatoporoid. At present, no post-Famennian stromatoporoids, in the sense of the term used here, are confirmed.

Most accounts of Late Devonian faunas describe the decline in diversity of not only the stromatoporoids but also of many other groups approaching the F/F crisis. STEARN (1982a) identified the peak of diversity of the stromatoporoids in Givetian reefs and outlined the decline in diversity through the Frasnian worldwide and in local sections (1982a, 1987). On a worldwide basis, STEARN (1987) recognized a Frasnian generic diversity of 37 and a late Famennian diversity of between 20 and 24 genera (see also Fig. 360–361).

The difference in taxonomic diversity between Givetian and Frasnian stromatoporoid faunas is not as obvious as between Frasnian and Famennian stromatoporoids, when monographic treatments of particular basins are tabulated. The number of species and genera in Givetian, Frasnian, and Famennian beds derived from various monographs (and therefore taxonomically consistent) for well-studied faunas within larger areas (i.e., not just local sections) is listed in Table 31.

Obviously, some paleontologists have different taxonomic philosophies and distinguish more morphologic variants as different species within genera; hence the wide variation shown in the ratio of species to genera (s/g) in Table 31. As a result, the number of genera appear to be the better measure of diversity for comparison between different studies. In most areas, the difference in generic diversity between Givetian and Frasnian faunas is insignificant. In Afghanistan, the taxonomic diversity decreases through the Devonian, but in the Czech Republic, it increases into the Frasnian. For the few areas where a comparison of Frasnian with Famennian faunas is possible, the drop in diversity from an average of about a dozen Frasnian genera to two or three in the Famennian is striking.

STOCK (2005) tabulated the diversity changes in seven Devonian successions from around the world and noted that in nearly all the sections, generic diversity fell during the Frasnian and into the Famennian. Origination and extinction of stromatoporoid genera were also tabulated from the taxonomic review of STEARN and others (1999). For the first four stages of the Devonian, originations exceeded extinctions, but from the Eifelian time to the end of the period, the rate of origination steadily declined and the rate of extinction increased, reaching a maximum in the Frasnian. STOCK (2005) also plotted overall generic diversity by stage through the Devonian. Diversity reached a peak in Eifelian time and declined slightly through Givetian to Frasnian time, but the difference between Emsian and Frasnian diversity is less than 10%, or only three genera. Famennian diversity was only half the diversity in the Eifelian.

The question of whether the decrease in diversity of stromatoporoid genera in Late Devonian time could be owing to the Signor-Lipps effect (SIGNOR & LIPPS, 1982) should be assessed. This effect produces an apparent decline in diversity toward abrupt extinctions and is caused by the decreased likelihood of collecting rare and poorly preserved species of fossils at the ends of their ranges. The effect is minimal for fossils of abundant animals and those with skeletons that are likely to be preserved, such as the stromatoporoids. It has largely been adduced in the interpretation of ranges of fossils in local sections rather than in regional and global diversity studies extending over tens of millions of years, as for the stromatoporoids.

Early and middle Famennian stromatoporoid faunas are known from the Czech Republic, Australia, and western Canada. They are much reduced in diversity from late Frasnian fauna but contain such typically Frasnian genera as *Amphipora, Stachyodes, Stromatoporella, Syringostroma, Gerronostroma*, and *Stromatopora.* In Australia (COCKBAIN, 1984), Famennian rocks contain *Clathrocoilona* and *Stromatopora* (STEARN, HALIM-DIHARDJA, & NISHIDA, 1987, suggested this is a *Trupetostroma*). By mid-Famennian time, stromatoporoids had recovered to the extent that they were building small reefs in the carbonates of western Alberta.

The most remarkable feature of the Famennian faunas in North America, Russia, Kazakhstan, Siberia, and southern China, however, is not the presence of survivors of the F/F decline but the abundance and diversity of the order Labechiida. The typical genus of these faunas is *Stylostroma,* but the labechiid root stock branched into as many as 13 genera in southern China. If these Chinese genera are subtracted from the Famennian generic diversity total, the decrease in diversity at the F/F interval becomes 86%. The distribution of the labechiid and nonlabechiid communities in the late Famennian has been discussed in the sections dealing with paleobiogeography (Paleobiogeography of the Paleozoic Stromatoporoidea, p. 653–689). Assemblages of nonlabechiids only, labechiids only, and mixed assemblages are separated geographically in late Famennian (Strunian) rocks, and they first appear to be localized around the equatorial Paleotethys ocean. On the basis of this distribution, STEARN (1987) suggested that the labechiids became dominant in the Famennian because they were more tolerant of cool water.

The abundance and diversity of the labechiids in latest Famennian rocks is more remarkable because the family is rare in nearly all other Devonian stromatoporoid faunas. WEBBY and ZHEN (1997) have reviewed the scattered occurrences in Lower and Middle Devonian rocks (Mid-Devonian England, Queensland; Lower Devonian Urals, Queensland, northeastern Russia), but the major monographs on Givetian and Frasnian stromatoporoids contain no mention of labechiids. STEARN (1983a) did describe a *Labechia* sp. from rocks of Emsian age in the Canadian Arctic, but ST. JEAN (1986) has suggested that this may be a misidentification of a cystose structure in *Syringodictyon.* YAVORSKY (1957) has described five species of *Labechia* from beds he identified as being of Frasnian age, southern Urals, and, if these beds are confirmed in age, they are a unique assemblage.

In summary, stromatoporoid diversity declined slightly from Eifelian time toward an ecological crisis at the end of the Frasnian stage; then the widespread reef facies of Frasnian time was greatly restricted and many genera became extinct. This drop was the result of a major decline in rate of origination since the middle of the Devonian Period and a less significant increase in the rate of extinction. During latest Devonian time, a few surviving Frasnian genera accompanied a resurgent labechiid order to form small reefs scattered in most of the continental blocks until the end of Famennian time. The remaining stromatoporoid stock went extinct at the D/C boundary. The F/F boundary marks an important ecological change, and the D/C boundary an important taxonomic one.

RESPONSE OF OTHER TAXA TO LATE DEVONIAN EVENTS

In assessing the nature of the environmental changes that determined faunal changes during F/F and D/C times, a survey of the changes in other taxonomic groups is useful. The numerous papers on the radical changes at the F/F boundary seem to have overshadowed and depreciated the changes that took place at the D/C boundary. Shallow-water faunas were not as much affected at the D/C boundary, but goniatites and hemipelagic ostracodes lost much of their diversity (Walliser, 1996).

Summaries of the groups affected by both episodes can be found in the works of Buggisch (1991), Walliser (1996), McGhee (1996), Hallam and Wignall (1997), and Hallam (2004), and these are not repeatedly cited in the following discussion. McGhee (1996) estimated that 14%–30% of families, 50%–60% of genera, and 70%–80% of species became extinct in the Late Devonian mass extinctions, between late *rhenana* and middle *triangularis* zones (i.e., the Kellwasser interval). McGhee and others (2004) place familial diversity loss of marine faunas at 21%.

The calcareous Foraminifera were in their initial interval of radiation in Givetian and Frasnian times, and their shells are common in Frasnian grainstones. They suffered a rapid decline at the F/F boundary from 30 to 2 genera. McGhee (1996) made much of the abundance of hexactinellid sponges in the Devonian shelf sediments of New York as evidence of invasion of deep cool-water taxa, but this occurrence is very local, perhaps unique, and can hardly have worldwide significance. Sorauf and Pedder (1986) considered the fate of the abundant Frasnian rugosans at the F/F boundary. They recorded that only 5 of the 47 genera of late Frasnian rugose corals survived into the Famennian. There is some evidence that deeper-water genera survived to radiate into shallow environments. Whether D/C events had a significant effect on rugosans is controversial. Tabulate corals were in decline in the Late Devonian and represented largely by branching forms such as *Thamnopora.* They were greatly reduced by the F/F change but little affected at the D/C boundary.

Bivalves and bryozoans both seem to have been little affected by either of the Late Devonian crises.

Cricoconarids had a precipitous decline at the F/F boundary, reducing from 6 genera to 1 genus. As they are generally regarded as pelagic in habitat and commonly preserved in dark shales, their decline is difficult to relate to some hypotheses of changing sea levels and rising anoxia. Ammonoids seem to have been facing crises throughout their history. As a result, investigators attach little significance to the fact that they declined in Frasnian time and recovered in the Famennian. However, about 85% of the goniatites became extinct at the end of the Devonian. Feist (1991) documented the general decline of the trilobites in the Frasnian from a high of diversity in the Eifelian. Very few new trilobite genera were added in Frasnian time, and the trilobites were never again a significant part of shallow-water faunas in late Paleozoic time.

Brachiopods have been regarded as holding the key to climate change at this time, owing to the work of Copper (1977, 1994) on South American faunas. The diversity of Frasnian brachiopods declined toward the F/F boundary; the number of genera reduced from 92 in the Frasnian to 23 in the Famennian. Thirty of the 33 families lost at this point were tropical forms. The orders Pentameroidea and Atrypoidea became extinct in Frasnian time (the latter in early *linguiformis* time). Orthids and strophomenids were greatly affected, but spiriferids and rhynchonellids were not. STIGALL RODE (in STIGALL RODE & LIEBERMAN, 2006) has studied changes in the brachiopod community at the Devonian biodiversity crisis using environmental niche modelling.

STREEL and others (2000) documented miospores. Their diversity shows a peak in the Givetian of about 58 species and a decline from Frasnian to Famennian from 51 to 23 species. Plant macrofossil diversity shows a similar decline. Chitinozoans survived the F/F boundary but, after a long decline, became extinct at the D/C boundary. Acritarch diversity collapsed at the end of the Devonian rather than at the F/F horizon. Ostracode history gives no clear signal, and their distribution and decline has been interpreted in various ways.

In summary, most fossil groups responded to Late Devonian environmental change by decreasing in diversity; most survived the two (or more) crises, but the stromatoporoids did not. The extinctions, largely at the family and lower taxonomic levels, extended over a considerable period of time; MCGHEE (2001) suggested from late *rhenana* to mid-*triangularis* times.

CAUSES OF LATE DEVONIAN EXTINCTIONS

Paleontologists have suggested many causes to explain mass extinctions. MCLAREN (1983) suggested that we should recognize a hierarchy of causes leading us to some ultimate cause; that is, if anoxia is the immediate cause of the extinction of shallow-water faunas, was the anoxia caused by transgression, was the transgression caused by ice-cap melting, was the melting caused by climate change, and was the warming caused by an increase in CO_2 in the atmosphere? The problems of identifying causes and distinguishing them from triggers in the interpretation of the stratigraphic record has been examined by CLELAND (2001) and commented on by KILTY (2002) and BAILEY (2002). BAILEY (2002, p. 953) concluded that in stratigraphic interpretation: "The attempt to establish causality within reasonable doubt is for the most part futile and when attempted likely to be misleading." Earth systems are so complex and interrelated that retracing the whole chain of causation for events of hundreds of millions of years ago seems impossible, and we should be cautious of simplistic solutions.

In the search for causes of mass extinctions, the most powerful tool is selectivity: the difference in ecologic requirements between the organisms becoming extinct and those surviving. For example, if species that lived in the tropics become extinct, while cool-water species survive and occupy formerly tropical environments, then cooling temperatures are almost certainly part of the complex of causes.

Although many discrete causes of Late Devonian diversity decline have been suggested, they can be grouped into three general hypotheses: (1) extraterrestrial influences, impactors, or cosmic rays; (2) sea level changes and accompanying anoxia; (3) climate change, notably cooling, shown by and giving rise to Southern Hemisphere glaciation.

BOLIDE IMPACT HYPOTHESES

Extraterrestrial matter continually impacts the atmosphere, and larger particles rain down on the Earth's surface. The evidence for this is usually widely distributed in marine sediments and is unlikely to have significant effect on marine life. The search for extraterrestrial causes, or triggers, for mass extinction is a search for anomalies in the rate at which this evidence is introduced into the marine record. The extent of the anomaly required for an extensive extinction has not been clearly defined but is usually stated in terms of the diameter of the impactor; i.e., a 10 km impactor should do the job. The question of how many microtektites, or shocked quartz grains, demand our attention as causes or triggers, goes unanswered. The search for these signatures of impact at the F/F and D/C has yielded little evidence and that which has been adduced has been efficiently refuted (Hallam, 2004, p. 76).

The evidence for bolide impact has been reviewed above and, apart from the occurrence of breccias, is not compelling. Coincidence of impact date of major sites with biostratigraphic events is difficult to establish. McGhee (2001) suggested that multiple impacts in early to middle Frasnian time (approximately *transitans* zone) would have produced an anomalous warm period in the general cooling trend of Late Devonian time associated with the transition from greenhouse to icehouse conditions. He proposed that the immediate cause of F/F extinctions was the abrupt return to the general cooling of oceans as the anomalously high CO_2 concentrations caused by the impacts was absorbed in the rapidly spreading plant community. Application of the multiple impact hypothesis to Late Devonian extinctions seems to be a final attempt to rescue the bolide hypothesis from rejection.

Suggestions that radiation from space may have caused mass extinctions can be traced back to Schindewolf (1954), who suggested that cosmic rays from a supernova explosion caused the end-Permian extinction. A similar hypothesis has been proposed more recently by Adrian Melott (see Hecht, 2003) that gamma rays from an exploding star caused the Late Ordovician event. Shaviv and Veizer (2003) have drawn attention to the probable effect of cosmic ray flux as a determinant of Phanerozoic climate but do not apply their model to extinction causes.

ANOXIA, TRANGRESSION, AND REGRESSION

The coincidence of the Kellwasser and Hangenburg intervals of dark shales and limestones with the extinctions in Europe has convinced many geologists there that the spread of anoxia over continental shelves through transgression was an immediate cause of the biota changes. A corollary hypothesis is that the mid-Paleozoic oceans were chronically unventilated at depth, and it was this anoxic water spreading over the carbonate shelves that poisoned so many animals adapted to shallow, oxygenated waters (such as stromatoporoids). The hypothesis is also connected to the burial of large quantities of organic carbon in these dark shales and consequent drawdown of atmospheric CO_2 and decrease in temperature. Joachimski and Buggisch (2002) attributed positive excursions in $\delta^{13}C$ as evidence of 20%–30% increase in burial of organic carbon in the ocean and hence a drawdown of atmospheric CO_2. Murphy, Sageman, and Hollander (2006), who studied two black shale intervals in the Devonian of New York that they correlated with the Lower and Upper Kellwasser horizons, recorded in them a positive $\delta^{13}C$ excursion of 4‰ to 5‰. On the basis of this and changes in the C:N:P ratio of buried organic matter, they postulated that eutrophication of the water column was important in causing extinctions. Bratton, Berry, and Morrow (1999) studied the geochemistry of an anoxic interval in the Great Basin of the southwestern United States and concluded that it marked neither the end of the Frasnian nor the *linguiformis* zone, but ended about 0.1 million years before the F/F boundary. The interpretation of the positive shift in $\delta^{13}C$ at the F/F boundary in some sections has been difficult to explain. Erwin (2006) discussed various alternatives for similar changes at the end-Permian extinction.

McGhee (1996) pointed out that intervals of dark, organic-rich shales, much like the Hangenburg and Kellwasser, are common at many levels within the Late Devonian successions around the world, and the great majority have not been associated with extinctions or radical faunal changes. In addition, local anoxia is easy to accept, but worldwide oceanic anoxia is more difficult to model.

If the incursions of anoxic water onto shelves is taken as evidence of rise of sea level, then sea level must have fallen rapidly thereafter to account for the widely recognized regression at the beginning of Famennian time (STREEL & others, 2000; JOACHIMSKI & BUGGISCH, 2002; STOCK, 2005). In western Canada, for example, the F/F boundary appears to be associated with a disconformity formed by widespread regression from the carbonate shelf environments. Such regression would have restricted shallow-water habitats and might have led to increased competition between shallow-water benthic organisms and thus extinctions. BUGGISCH (1991) has constructed a complex cyclic model of rising and falling sea levels and anoxic shelves to explain the upper and lower Kellwasser intervals. His sequence can be summarized as follows: transgression → anoxia on shelves → organic carbon sequestering → decrease in atmospheric CO_2 → icehouse → glaciation → regression → erosion of organic C → increase in atmospheric CO_2 → greenhouse → increased organic production → transgression, and so on. MAY (1997) postulated that the Kellwasser and five other previous Devonian bioevents were all caused by rapid transgression of anoxic waters over the shelves. RACKI (1998) reminded us that rapid sea level changes can also be caused by tectonic events such as rifting, but commonly the postulated sea level changes are attributed to Late Devonian glaciation.

STOCK (2005) attributed the fall in diversity of stromatoporoid faunas in Frasnian time to the transgression of the Transcontinental Arch in North America and consequent mixing of faunas from the Eastern Americas realm and Old World realms. Whether the arch was an effective barrier to stromatoporoids from Eifelian to late Frasnian time, or if its flooding had more than a local effect on world faunas, remains to be proven.

HALLAM (HALLAM & WIGNALL, 1997; HALLAM, 2004) strongly supported anoxia as a cause of mass extinctions. He postulated that a late Frasnian regression was followed by a Famennian transgression flooding the continents with anoxic waters that until then had been confined to the deep oceans.

In a similar hypothesis, KUMP, PAVLOVA, and ARTHUR (2005) suggested that during intervals of oceanic anoxia, the chemocline separating sulfidic deep waters from oxygenated surface waters could have risen to the surface, killing much marine life and introducing lethal doses of H_2S into the atmosphere in Late Devonian time. Another hypothesis advanced by BAMBACH, KNOLL, and SEPKOSKI (2002) postulated that large quantities of CO_2 introduced into the atmosphere from an anoxic ocean's depths would more seriously affect invertebrates of lower metabolism and activity (such as stromatoporoids) than those with higher metabolic rates and would lead to less successful survival of such an event. The release of methane (CH_4) from hydrates in the deep continental shelves by fall of sea level or rise of temperature has been proposed to account for the positive excursions of $\delta^{13}C$ at extinction boundaries (ERWIN, 1993, 2006) and deleterious effects on the environment by increasing the greenhouse effect.

In conclusion, oscillations of sea level in Late Devonian time have certainly been documented, but their effects as controls on diversity and extinction are not obvious.

GLACIATION IN THE SOUTHERN HEMISPHERE

When rapid transgressions and regressions occur in the geological record, stratigraphers turn to the growth and melting of continental ice sheets for explanation. The spread of ice beginning in mid-Carboniferous time over much of the southern hemisphere in the icehouse phase of the late Paleozoic has been accepted since early in the 20th century, but the identification of Late Devonian glaciation has been controversial. The evidence of diamictites and striated surfaces in northeastern Brazil dated palynologically has recently been reviewed by STREEL and others (2000). They concluded that glaciation there, and possibly in North Africa, is well supported by stratigraphic evidence in the D/C interval but not at the end of the Frasnian. Still, to justify the extinctions in the F/F interval, they postulated a short glacial interval within a generally warm climate. The general cause of the cooling that brought on the glaciations is so-called sinking of the greenhouse gas CO_2, in both marine organisms and rapidly spreading land vegetation. STREEL and others (2000) pointed out that, at present, the productivity in plant-matter mass on land is three times that of the sea, but this does not mean that it was so in Devonian time.

GLOBAL COOLING

The fractionation of oxygen isotopes is dependent on temperature, and excursions in $\delta^{18}O$ have been used as a proxy for temperature. GONG and XU (2003) warned, however, that ^{18}O excursions can also be caused by changes in sea-water salinity. Temperature has also been used as a proxy for the extent of continental ice sheets, and the extent of ice has been used as a proxy for sea level. For example, STREEL and others (2000) suggested that the $\delta^{18}O$ positive excursions at the F/F horizon can be correlated with a drop of sea level of 180 m, owing to the trapping of water in polar ice. In contrast, JOACHIMSKI and BUGGISCH (2002) suggested that $\delta^{18}O$ values of –1‰ indicate warm sea temperatures of about 26° C at this time. For comparison, recall that the steady decrease of water temperatures from Eocene time to the present leading to the Ice Age is represented by a $\delta^{18}O$ from about 0‰ to +4‰. VEIZER and others (1999) correlated a positive swing of ^{18}O with Late Ordovician glaciation and suggest that the rise in the Late Devonian may be correlated with a similar phenomenon at that time. The extensive $\delta^{18}O$ determinations on mid-Paleozoic brachiopods published by BRAND (1989b) gave unrealistic seawater temperatures in the 36° C to 54° C range, which have been largely dismissed by later investigators as being influenced by diagenesis of his samples.

On the basis of oxygen isotopes from conodonts, JOACHIMSKI and BUGGISCH (2002) denied evidence of extensive Late Devonian ice sheets. The ocean temperatures for late Frasnian time derived from $\delta^{18}O$ values of –1‰ are warm, about 32° C; the two excursions in the oxygen isotope curves near the F/F horizon indicate temperatures falling to about 26° C. This decrease in temperature is comparable to that which accompanied the Pleistocene glaciation (4–8° C). However, they attributed the Late Devonian extinctions to general and episodic cooling and ultimately to the burial of organic carbon in so-called sinks and decrease in atmospheric CO_2. JOACHIMSKI, VON BITTER, and BUGGISCH (2006) discussed the significance of $\delta\ ^{18}O$ to sea level changes in the Pennsylvanian cyclothems and suggested that a change of +1.7‰ would be equivalent to a temperature decrease of 7° C, if explained solely by temperature, and could have resulted in sea level falls of more than the 120 m experienced during Pleistocene glaciations.

The hypothesis that global cooling was one of the main causes of Late Devonian extinctions, which was first clearly stated by COPPER (1986), has been supported since by more and more evidence. COPPER's conclusions grew out of studies of South American brachiopods (1977). These cold-water faunas displaced the tropical brachiopods in Late Devonian time, clearly signalling a cooling event. Originally, COPPER (1986) suggested that the cooling was caused by the movement of the continents and closing of the Frasnian equatorial ocean (Paleotethys). Later, COPPER (1994) suggested that reefs and calcareous plankton have a great capacity to sink CO_2 and cause climatic change.

That global cooling, CO_2 in the atmosphere, sea level changes, and even glaciation are connected with the burial of organic carbon at the beginning of the Icehouse Earth is a common thread in many recent hypotheses. The increase in removal of C_{org} from recycling to the atmosphere, as evidenced by organic-rich sediments and positive $\delta^{13}C$ excursions, is most commonly attributed to the spread of plants upon the land (Algeo & Sheckler, 1998) but may also have been related to ocean anoxia, slowing the decay of marine organic matter and sequestering it in black shales.

McGhee (2006) based his discussion of extinction hypotheses on a model of falling global temperatures, starting at the beginning of the Givetian and culminating in late Famennian glaciation. The ultimate cause of the cooling was falling atmospheric CO_2 content, owing to the rise of vascular plants. McGhee postulated that this steady cooling trend was interrupted by a brief, sharply defined, warmer greenhouse interval in late Frasnian time, caused by impacts or volcanic phenomena (flood basalts), whose collapse led to F/F extinctions. The climatic changes could have been episodic to explain the series of pulses that McGhee identified in late Frasnian extinctions. Similar episodic extinction events have not been identified in the history of the stromatoporoids.

Stearn (1987) suggested that general cooling of Late Devonian climates led first to widespread F/F decline in diversity and abundance of the stromatoporoids, the rise of the cool-water tolerant labechiids, and eventually to the demise of the whole class (D/C). Copper (1994) has suggested that the greater effect of F/F events on the corals than on the stromatoporoids means that the former were more sensitive to environmental change than the latter.

Clarke (1993) commented on the role of temperature alone in causing extinction of marine organisms. He emphasized changes in seasonality in interrupting reproductive cycles as being more important than changes in temperature. The latter are more likely to cause changes in the distribution of organisms than their extinction. He noted that humans, as warm-blooded animals, may see colder temperatures as detrimental, while many marine invertebrates thrive in frigid waters.

Not all models of Late Devonian temperatures postulate overall steady cooling of the atmosphere during this interval, and several postulate warm seas in Frasnian and Famennian time. Until a detailed temperature curve is agreed upon, hypotheses linking temperature and extinction will continue to be subject to modification. Twitchett (2006) has summarized studies of mass extinctions and concluded that climate change is the only reasonable explanation for most of these events.

CONCLUSIONS

That changing conditions as the Devonian Period came to an end were challenging to shallow-water faunas is clearly evident; that they were catastrophic is harder to prove (Hallam, 2004). The appeal of the so-called New Catastrophism has led many to seek an extraordinary event or events and a unique cause to explain the deteriorating marine environment of Late Devonian time. In consideration of Gould's (1985, 1989) proposal that contingency and, in particular, randomly caused episodes of mass extinction are the fundamental controls on the history of life, paleontologists have concentrated on the study of these time intervals. Certainly, the attention given by media and public to the abrupt extinction of the dinosaurs coincident with an extraordinary astronomical event has focused attention on other similar incidents in life history and suggested similar abrupt scenarios. But there is no reason why each of the big five extinction events should have the same cause; on the contrary, marked differences in the stratigraphic record at the five boundaries suggest just the opposite. The evidence for each event must be weighed separately. For example, although the coincidence in time with extinction events at the end of the Cretaceous and Permian of extensive flood basalts in India and Siberia, respectively, has been suggested as a cause of the extinctions, no such extensive extrusions coincide with the Devonian extinctions. The evidence for each extinction event in the geologic record must be weighed separately.

Extinctions at all hierarchical levels: orders, families, genera, and species, took place continuously throughout life history, as the changing environmental determinants became inhospitable to this or that organism. As the cycles of change in limiting environmental parameters such as (in the marine environment) temperature, salinity, oxygenation, nutrient level, depth, and illumination, took place, different organisms with different sensitivities to these parameters became extinct. When conditions adverse to marine life in a few of the parameters coincided in time, several groups became extinct; at those rare times when adverse conditions coincided in most of them, then what has been called a mass extinction occurred. If this is the case, then not only are such episodes inevitable at random times in the history of life, but they have no immediate single cause, only multiple causes. The model is further complicated by the intimate interrelationships of the ecological determinants, so that looking for a single trigger in this web of causes is frustrating. JABLONSKI (2000, and references therein) argued that large-scale ecologic systems (such as the mid-Paleozoic reef complexes) have an inherent resistance to perturbations and require an external extraordinary event to disrupt them. A hypothesis of multiple coincident causes has also been discusssed by ERWIN (1993, 2006).

All the major mechanisms of Late Devonian extinction that have been proposed have evidence in their favor and evidence against them. That we will ever be able to reconstruct the events of hundreds of millions of years ago seems unlikely. What seems likely is that some combination and interaction of climate change, anoxia, sea level variation, and sinking of carbon dioxide resulted in environmental instability beyond the capability of much of the warm-water marine benthos to accommodate. Whether extraterrestrial influences had any effect as a trigger remains to be proven. RACKI (2005) has summarized many of these arguments and provided an extensive bibliography.

Only a likely scenario can be postulated. Deteriorating marine conditions associated with temperature fall slowly affected the rate of origination of stromatoporoids from Givetian to Famennian time. The ultimate cause of such global climatic change is unlikely to be determined from paleontological or stratigraphical studies. This decline in originations was intensified into widespread extinctions in the F/F and D/C intervals by changes in sea level, causing habitat loss and locally catastrophic flooding of anoxic waters onto shelf environments. By the end of the Devonian, stromatoporoids were unable to withstand further stress and became extinct.

BIOSTRATIGRAPHY OF THE PALEOZOIC STROMATOPOROIDEA

B. D. WEBBY, C. W. STEARN, and HELDUR NESTOR

INTRODUCTION

Although all life forms have a limited existence in time, some are more valuable than others for recognizing a particular time interval. Such species have short stratigraphic ranges and wide distribution, and are, therefore, potentially useful in distinguishing short intervals of time. Also, for groups to be potentially valuable for dating, they must have been studied and understood taxonomically. In addition, students of groups of fossils that are valuable in biostratigraphy must be able to agree on a consistent taxonomy. The stromatoporoids only partly meet these requirements. Only within the past three decades has the broadening of the species concept allowed the recognition of species from one region to another. Previous research was concentrated on distinguishing new taxa by refining the differences between specimens, and the species established in one continent or country were rarely identified in other parts of the world. For example, STEARN (1979) compared monographic descriptions of Frasnian faunas from the Ardennes (Belgium), Poland, and the Czech Republic, and showed that the taxonomic principles used by the investigators to distinguish species led to the conclusion that none of the 132 species of stromatoporoids were common to all three areas, even though they are separated presently by only a few hundred kilometers in Europe.

Faunas that do not have common species cannot be correlated. Not until a broader species concept, and an appreciation of the degree of variation inherent in stromatoporoid species are accepted, can the true biostratigraphic potential of the group be fully assessed. Yet, despite this realization, some stromatoporoid species and assemblages have been recognized as having wide distribution and short duration, and they therefore have considerable potential for zonation and correlation.

Stromatoporoids occur commonly in Ordovician, Silurian, and Devonian carbonate successions but have seldom been used primarily as biostratigraphic indicators. They occupied mainly warm, well-circulated, shallow, marine, carbonate shelves, especially the reef and shoal habitats of equatorially disposed continental platform and island-arc settings. In reef and shoal facies, stromatoporoids are often the only fossils available for biostratigraphic studies. Notwithstanding their prominence in many Paleozoic carbonate successions, they have remained comparatively poorly understood. Taxonomic approaches have long been founded on differentiating a species on the basis of a single, or a few specimens, rather than evaluating the variation that existed among many individuals of a particular species. In addition, some taxonomists have used traits (such as astrorhizae, e.g., BOGOYAVLENSKAYA, 1965b, and subsequently) for essential specific characters and for guides to phylogeny and classification, which are regarded as trivial by other research workers, making their taxa difficult to recognize in other parts of the world.

The basic framework of a modern-type of stromatoporoid taxonomy was presented by NICHOLSON (1886a, p. 2) some 120 years ago. He stressed the necessity for investigation of diagenetic alteration across a large number of specimens and assessment of the range of variability in populations of the species with use of adequate numbers of collected samples. However, NICHOLSON's approaches were not adopted by many stromatoporoid workers, at least not until the last few decades. Too many workers have been intent on multiplying the numbers of species based on differences between a few, often fragmentary specimens. A more rigorous approach is required for sampling and studying a stromatoporoid species. This entails using a larger number of specimens as the basis for fully describing the range of diagnostic morphological features: the variability of form and attributes of the species that arose from diagenetic alteration.

Three promising approaches to biostratigraphic correlation using Ordovician–Devonian stromatoporoids are the following.

1. Compilation of range charts (both at genus and species levels).
2. Establishment of sets of laterally adjacent successions of species-based zonal assemblages (NESTOR, 1982, 1990b, 1999b).
3. Development of a succession of species-based zonal assemblages tied to the zonation of conodonts (STEARN, 1997a, 2001).

Continuity of rigorous taxonomic work through the Ordovician to the Devonian stratigraphic record is needed to provide the basis for more precise biostratigraphic analyses, using one or more of the abovementioned approaches, hopefully leading to recognition of many more diagnostic, zonally restricted, but widely distributed stromatoporoid species. Each of the three biostratigraphic approaches is further discussed below.

RANGE CHARTS

KÜHN (1939b, p. 14–15) assembled one of the earliest broad-scale compilations of the stratigraphic distribution of important stromatoporoid genera. Another, more comprehensive, tabular representation of Paleozoic and Mesozoic stromatoporoid species was presented by YAVORSKY (1951). This was useful for generalized correlation across the former Soviet Union (mainly Russia), with many of the species listed by YAVORSKY exhibiting series-length (or epoch-duration) time ranges (that is, restricted either to the middle Silurian, Middle Devonian, or Upper Devonian). YAVORSKY (1929, 1955, 1957, 1961, 1962, 1963, 1965, 1967), RIABININ (1936, 1937, 1939, 1941, 1951, 1953), and GORSKY (1938) also demonstrated the value of stromatoporoids as generalized guide fossils for regional geological exploration work in the Ordovician, Silurian, and Devonian successions of the former Soviet Union.

LECOMPTE (1951 in 1951–1952), in a monographic treatment of the Devonian stromatoporoid species from the Ardennes of Belgium, also included a tabular presentation of species data—recognizing about half of the 115 species as being confined to 1 of the 5 main stratigraphic subdivisions (Couvinian 1 substage, Couvinian 2 substage, Givetian stage, Frasnian 1 substage or Frasnian 2 substage)—but he did not provide any further biostratigraphic details. Similar tables of the species distribution were presented by RIABININ (1951, 1953) for the local stages (horizons) of the Silurian in Estonia and Podolia (Ukraine).

The view that the stromatoporoids were biostratigraphically important fossils was first clearly proposed by GALLOWAY and ST. JEAN (1957, p. 31, 85) in their monographic treatment of Middle Devonian stromatoporoids from the central United States. They suggested that stromatoporoids were likely to prove to be zonal fossils, as useful in the Devonian as the trilobites were in the Cambrian, or the graptolites in the Ordovician! FLÜGEL (1959, table 25) emphasized the stratigraphic importance of stromatoporoid genera. His range chart, based mainly on GALLOWAY's (1957) taxonomy, showed that many of the genera were restricted to either the Ordovician or the Devonian. FLÜGEL stressed that a number of genera and species could be viewed as index fossils for the Devonian, especially the Middle Devonian. FLÜGEL (1962) also presented a general review of the biostratigraphic significance of stromatoporoid faunas in the Silurian and Devonian.

In the 1960s and 1970s, Silurian stromatoporoid faunas of different regions were described, and the stratigraphic distribution of species was recorded. This description and stratigraphic placement opened the possibility of using stromatoporoids in local stratigraphy and increased their value for correlating stratigraphic sequences. NESTOR (1964a, table 2, 5; 1966a, table 2, 4) published range charts of genera and species distributed in regional stages of the Upper Ordovician and Silurian of Estonia and commented on the occurrences of some species from other areas. MORI (1968, table 1; 1970, table 1) published range charts of stromatoporoid species in the stratigraphic units of the Wenlock and Ludlow strata on Gotland (Sweden), and roughly correlated the stratigraphic successions of Gotland and Estonia using the assemblages of species in common. MORI (1978, table 1) also presented the stratigraphic distribution of Silurian stromatoporoids from the Oslo area, Norway, and compared them with the Gotland and Estonian stromatoporoid successions. BOL'SHAKOVA (1973, p. 19–20) recorded the stratigraphic distribution of stromatoporoid species in the Silurian sequence of Podolia. BOGOYAVLENSKAYA (1973a) described the Silurian stromatoporoids from different districts of the Urals and used common species for correlation of stratigraphic units.

In North America, Ordovician–Silurian stromatoporoids of Anicosti Island, eastern Canada, were described by NESTOR, COPPER, and STOCK (2010, fig. 4–5), and other Silurian stromatoporoids were documented from eastern Quebec and from Somerset Island of Arctic Canada (SAVELLE, 1979). All of these works included range charts. Also, NESTOR (1976) authored a monograph on Ordovician and Silurian stromatoporoids from the Siberian platform and additionally distinguished a succession of species assemblages.

The stratigraphic ranges of species have also been used to establish correlations of the Devonian rocks. MISTIAEN (in BRICE & others, 1977) presented a table of ranges for the Ferques section in the Boulonnais area of northern France and compared the occurrences with those in the Ardennes of Belgium and in other countries. In addition, MISTIAEN (1980) described the species from the Ferques section, recognized 13 levels characterized by distinctive stromatoporoid faunas, and compared the faunas with those in the stratigraphic sections through the Givetian interval of the Ardennes described by LECOMPTE (1951 in 1951–1952). MISTIAEN (1982) also analyzed the distribution of faunas around the Givetian-Frasnian boundary in the Boulonnais, Ardennes, Poland, and the Czech Republic. In 1988, he recognized there were 3 stromatoporoid-based Givetian zones and 2 in the Frasnian part of the Boulonnais section.

MISTIAEN (1985) also showed the distribution of Devonian stromatoporoid species in the reefal complexes of the Central Mountains of Afghanistan. He presented tables showing distributions of stromatoporoid species in a number of stratigraphic sections, as well as the overall Devonian ranges of taxa, with ties to the main global conodont, graptolite, and other biozonations. The Middle Devonian fauna in particular is closely related to counterparts in the Ardennes (LECOMPTE, 1951 in 1951–1952) and the Boulonnais area (MISTIAEN in BRICE & others, 1977; MISTIAEN, 1980, 1982, 1988). The correspondence of European stratigraphic ranges with those of Afghan taxa confirmed that the stromatoporoids were both members of the same comparatively wide-ranging, provincial Old World Realm. Less close relationships exist with other so-called Old World faunas in other regions, such as the Czech Republic (ZUKALOVA, 1971; MAY, 2005), the Kuznetsk Basin (Siberia), southern China, and Australia. MISTIAEN (1985, fig. 17–18) was able to determine the age relationships of the discrete reefal complexes to within a Devonian stage, based on the overlapping stratigraphic ranges of the stromatoporoid faunas (36 species belonging to 19 genera), at least through the Emsian to early Frasnian interval.

The documentation of stromatoporoid faunas in China commenced mainly following the discoveries of abundant faunas during the nationwide geological surveys and stratigraphic work from 1949 onward (YANG & DONG, 1962). Through the 1970s and 1980s, numerous species were described from the Middle Ordovician to Upper Ordovician, lower Silurian, and especially from the rich assemblages through the Devonian of southern China (DONG & YANG, 1978; YANG & DONG, 1979; DONG, 1982; DONG & WANG, 1982; DONG & WANG, 1984; WANG, DONG, & FU, 1986; WANG, 1988; DONG, 2001). Some of these assemblages were useful for correlation and/or for establishing age relationships of particular stromatoporoid-bearing successions. Several of the above-cited publications included tabular presentations of species ranges: for example, through the Middle Ordovician to Devonian successions of the Xinjiang Autonomous Region (northwestern China) by DONG and WANG (1984), and the Devonian sequences in southern China: parts of Guangxi province by YANG and DONG (1979) and Sichuan province by WANG (1988).

NESTOR and STOCK (2001) presented range charts of the distribution of genera in North America and Baltoscandia as part of a discussion of the extinction of stromatoporoid faunas leading up to the end-Ordovician glaciation, and then their recovery through the early Silurian (Llandovery), including their generalized spread into other regions, such as Ireland, Novaya Zemlya, the Siberian Platform, and the Yangtze Platform.

Where stromatoporoid generic ranges were well understood, for example, in the Devonian (as shown by STEARN, 1979, fig. 1), the data could be plotted in a range chart for broad-scale correlation work. In this chart, most of the Devonian is divided into stage-age subdivisions (the exception being the Lower Devonian series-epoch couplet). Many Devonian genera are long ranging, through more than one stage-age interval, but a few short-ranging (key) genera are also represented, such as *Araneosustroma,* encompassing the Lower Devonian series; *Pseudoactinostroma* in the Eifelian stage; *Columnostroma* in the Givetian; and *Bullulodictyon, Arctostroma, Styloporella,* and *Euryamphipora,* in the Frasnian. Other slightly longer-ranging genera also have correlation potential because their first and/or last appearances coincide with particular stage (or series) boundaries. Remarks on the patterns of development of the Lower Devonian faunal successions were also presented by WEBBY, STEARN, and ZHEN (1993, fig. 4). In the figure, first and last appearances of key, short-lived genera characterize boundaries between the Lochkovian, Pragian, and lower Emsian. The scheme provides a broad basis for identifying diagnostic stromatoporoid assemblages to stage level.

We here present a set of range charts to show the stratigraphic distribution of genera worldwide (Fig. 362–364). Although the genus is, in taxonomic usage, a more artificial concept than species, it provides a reasonable means of attaining broadly based global correlations employing stratigraphic ranges.

The first stromatoporoids were the labechiids (Fig. 362; see p. 709–753); they remained the dominant group through the Mid–Late Ordovician, but declined through the Silurian, with few persisting into the Early–Mid-Devonian, and then showed a resurgence during the Late Devonian. In general, the genera do not seem to have much biostratigraphic potential (Fig. 362), though within the Ordovician the assemblages exhibit some successional changes, from associations of morphologically simpler families Rosenellidae, Labechiidae, and Aulaceratidae taxa in the Darriwilian, to the more complex, skeletal meshworks of some genera of the families Stromatoceriidae, Platiferostromatidae, and Stylostromatidae, with mamelon columns and flanged pillars in the Late Ordovician and early to mid-Silurian. A number of labechiids in the Late Devonian (Famennian), such as the platiferostromatids (*Platiferostroma*, *Vietnamostroma*) and more specialized stylostromatids (*Pennastroma,*

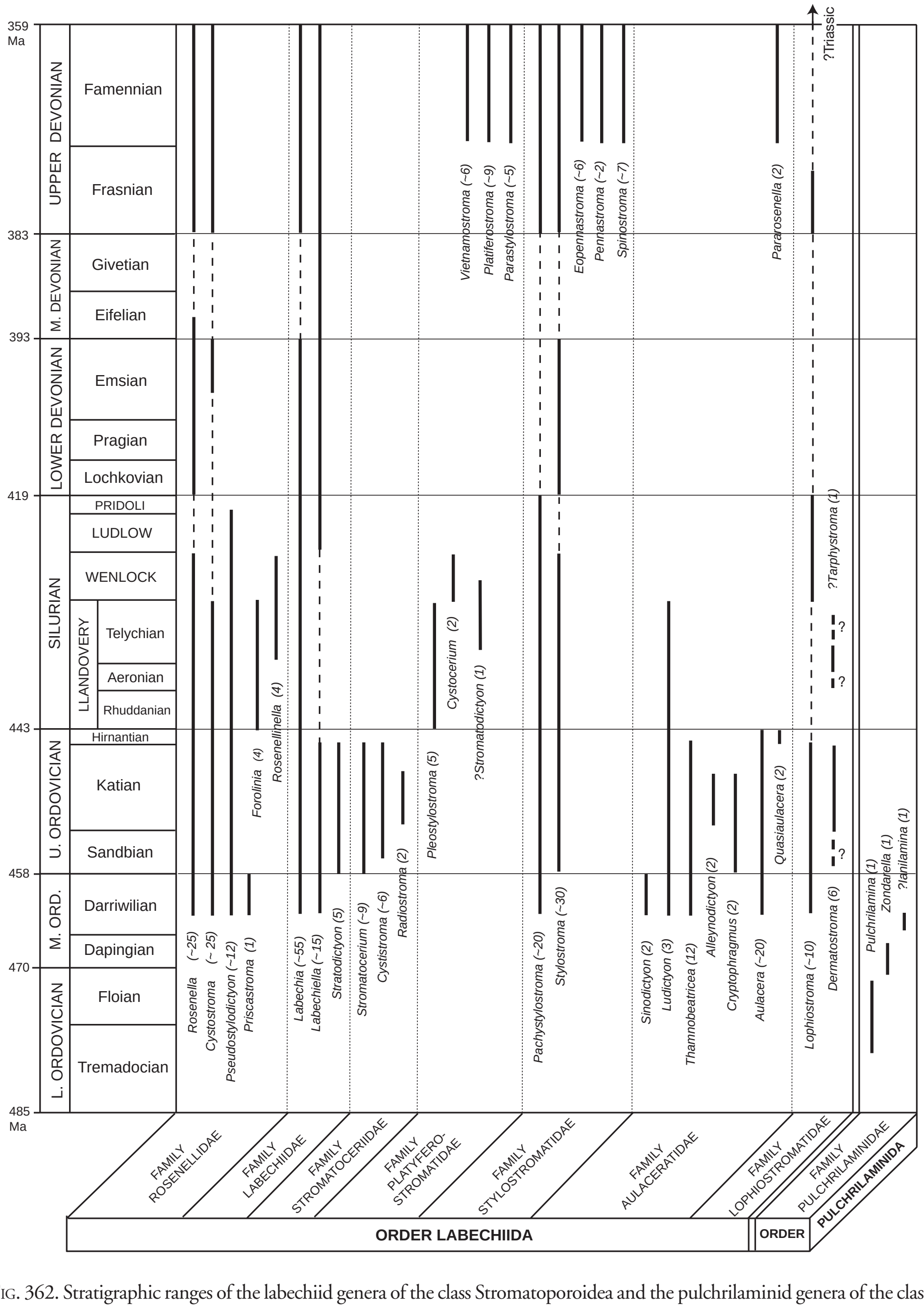


FIG. 362. Stratigraphic ranges of the labechiid genera of the class Stromatoporoidea and the pulchrilaminid genera of the class Uncertain (see Class Uncertain, Order Pulchrilaminida, p. 837–844); *fine dashed lines* depict apparent gaps in the continuity of the record; *thick dashed line* with a question mark signifies a doubtful extension of a taxon range (e.g., range of *Dermatostroma);* note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history; *Lophiostroma* is the only labechiid genus to have a possible post-Paleozoic record, here shown with an *upwardly directed arrow* and of ?Triassic age (see Boiko, 1970a). Note also that Stearn and Stock (p. 310) listed *Lophiostroma* as an excluded taxon for calcareous crusts in the upper Paleozoic of Japan (adapted from Webby, Stearn, & Nestor, 2012; time scale after Gradstein & others, 2012).

Spinostroma), show further differences that may have some correlation potential.

Two of the present authors (STEARN and WEBBY) have very different explanations for the late Silurian to Mid-Devonian decline then Late Devonian resurgence of the labechiids. STEARN considers that some of the genera, for example, *Labechia, Stylostroma,* and *Pachystylostroma,* have such long and discontinuous ranges as to suggest that their Late Devonian representatives are not directly descended from their Ordovician precursors, but evolved anew from some persistent rootstock; in other words, they represent Elvis taxa (ERWIN & DROSER, 1993). The almost complete absence of labechiids from the Eifelian–Givetian interval, when other stromatoporoids reached their greatest diversity, supports this hypothesis. STEARN also suggests that the uncommon Mid-Devonian occurrences of labechiids may be misidentifications of simple cystose structures common in the space-filling strategies of other fossil organisms (rugosans, tabulates, hydrozoans, bryozoans, mollusks) (ST. JEAN, 1986, p. 1053, commenting on STEARN, 1983a).

On the other hand, WEBBY prefers to regard the patterns of disappearances and reappearances of labechiid genera through the Silurian to Late Devonian as representing Lazarus taxa—that the gaps in the continuity of the labechiid records are artifacts of their relatively poor preservation and low diversity. A number of labechiids were found in well-exposed and dated reefal sequences of Lockhovian–Pragian and Emsian–Eifelian ages of the Broken River region of Queensland by WEBBY and ZHEN (1997); that is, from intervals that were previously represented by gaps in the continuity of the labechiid record. These Lochkovian–Pragian (species of *Cystostroma* and *Labechiella*) and late Emsian–early Eifelian labechiids (species of *Stylostroma* and *Rosenella*) form a sparse, poorly preserved component of associations that are dominated by richly diverse and well-preserved nonlabechiid stromatoporoids. In other words, the poorly preserved minor component of labechiids was only found at the various localities because of the high quality of the exposures available for study. It is considered likely that the labechiid component may be difficult to find in less well-preserved successions, leaving only the dominantly, less altered nonlabechiids for study. The Broken River example is instructive in demonstrating that labechiids were continuing to live in associations with Early to earliest Mid-Devonian nonlabechiids, and they may yet prove to form part of a more or less continuous line of labechiid descent from Ordovician precursors into the Late Devonian. More intensive collecting and study of sequences (especially Devonian carbonate) is expected to bridge the gaps in continuity of the labechiid record prior to the Late Devonian.

The clathrodictyids have their roots in the Late Ordovician (*Clathrodictyon, Ecclimadictyon*) (Fig. 363; and see Clathrodictyida, p. 755–768). They reached their peak of diversity in Silurian time were numerous also in the Early and Middle Devonian, but only a few persisted to the end of the Devonian. Many genera are relatively long ranging and almost cosmopolitan (*Clathrodictyon, Ecclimadictyon, Gerronostromaria, Petridiostroma*), but some rare and peculiar forms (*Bullulodictyon, Gerronodictyon, Belemnostroma*) also occur. The representatives of the families Clathrodictyidae and Gerronostromatidae are widespread in both Silurian and Devonian rocks, but most of the representatives of the family Actinodictyidae are restricted to the Silurian. On the other hand, the representatives of the families Atelodictyidae and Tienodictyidae mostly occur in Devonian rocks. They include such genera as *Anostylostroma, Atelodictyon, Pseudoactinodictyon,* and others that are valuable for correlation.

The generic diversity of the actinostromatids peaked in the middle of the Silurian, when a rapid evolutionary radiation took place in the families Pseudolabechiidae, Actinostromellidae, and Densastromatidae

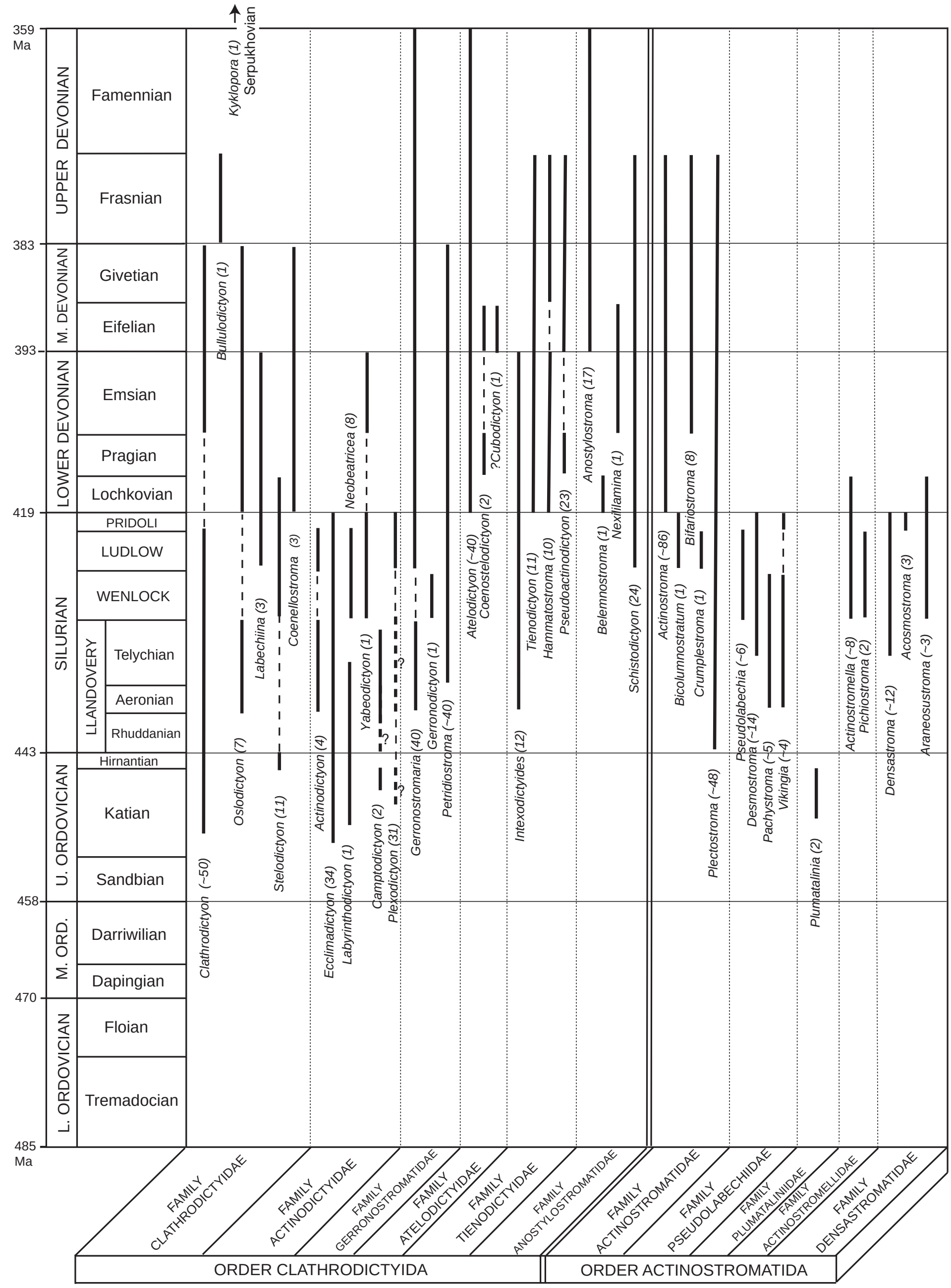


FIG. 363. Stratigraphic ranges of clathrodictyid and actinostromatid stromatoporoid genera of the class Stromatoporoidea; *thick dashed lines with question marks* signify doubtful extensions of taxon ranges; *fine dashed lines* depict apparent gaps in the continuity of record; note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history; *Kyklopora* is the only genus that has a restricted post-Devonian record, with a limited occurrence in the lower Carboniferous (Serpukhovian stage), according to NESTOR (see p. 755) (adapted from Webby, Stearn, & Nestor, 2012; time scale after Gradstein & others, 2012).

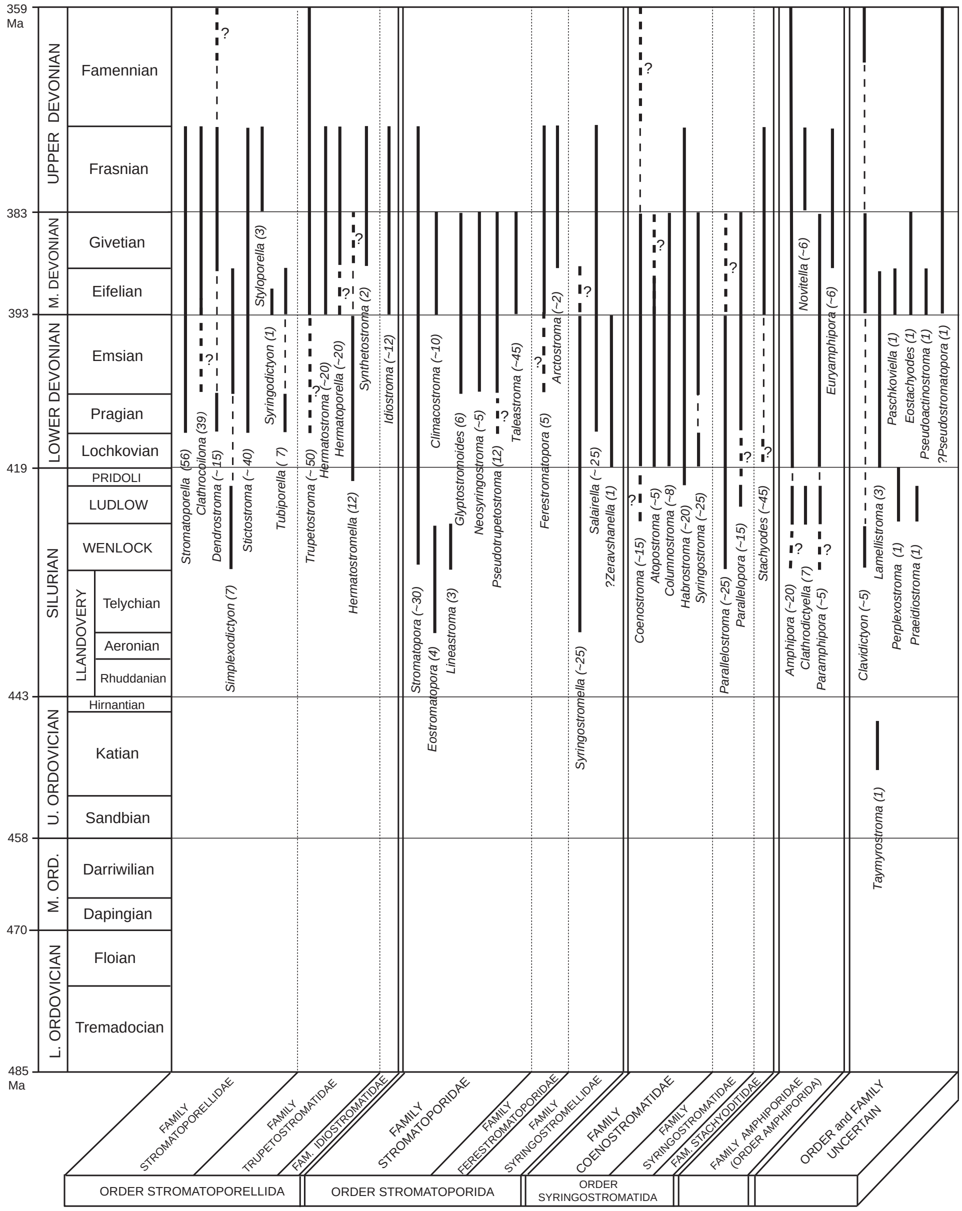


FIG. 364. Stratigraphic ranges of stromatoporellid, stromatoporid, and syringostromatid stromatoporoid genera, as well as representatives of order and family Uncertain of the class Stromatoporoidea; *thick dashed lines with question marks* signify doubtful extensions of taxon ranges; *fine dashed lines* depict apparent gaps in the continuity of record; note that the numbers in brackets are the estimated numbers of species for each genus; ranges of genera are depicted for convenience as mainly commencing and terminating at series and/or stage boundary intervals, but such a representation may not be significant in terms of life history (adapted from Webby, Stearn, & Nestor, 2012; time scale after Gradstein & others, 2012).

(Fig. 363; see p. 769–779). Only a few genera (*Actinostromella, Araneosustroma*) of these families range into the Lochkovian. Comparatively short-ranging genera include stratigraphically valuable species, for example, index species of such Baltoscandian stromatoporoid communities as *Vikingia tenuis, Araneosustroma stelliparratum,* and *Actinostromella vaiverensis* (Nestor, 1999b). Three of the most common genera of actinostromatids (*Actinostroma, Bifariostroma, Plectostroma*) belong to the family Actinostromatidae and are the main representatives of actinostromatids in the Devonian.

The orders Stromatoporellida, Stromatoporida, and Syringostromatida mainly include Devonian taxa with a few genera (*Simplexodictyon, Stromatopora*, *Syringostromella, Parallelostroma*) originating in the Silurian (Fig. 364; see p. 781–824). Among the stromatoporellids, such genera as *Clathrocoilona, Stictostroma, Stromatoporella, Trupetostroma*, and *Hermatostroma* are the most characteristic of this almost cosmopolitan fauna. Most of the common stromatoporellid genera extend through the Eifelian–Frasnian acme of stromatoporoid diversity. Rather similar are the ranges of the stromatoporids. Such genera as *Climacostroma, Glyptostromoides, Neosyringostroma, Taleastroma*, and *Pseudotrupetostroma* appear to have biostratigraphic potential, but the genus *Stromatopora* itself has a very long range from the Ludlow to Famennian. Some earlier records of *Stromatopora* are now treated as representatives of *Lineastroma* and *Eostromatopora* (Nestor, 1999a). The family Syringostromatidae was characteristic of the Early Devonian and Eifelian. The acme of the family Coenostromatidae was also in the Early Devonian, but *Parallelostroma* appeared earlier in the Wenlock and *Habrostroma* in the Pridoli. *Atopostroma* may prove to be an excellent indicator of Lower Devonian rocks, though the presence of the genus in a reefal deposit of Givetian age in Afghanistan (Mistiaen, 1985) remains an anomaly. Difficulties in recognizing the genera of the Amphiporidae limit their usefulness for biostratigraphy (Fig. 364; see p. 824–829).

It should also be noted that there are two “stromatoporoid” genera with post-Devonian records, one supposedly a labechiid referred to the genus *Lophiostroma,* implying it formed part of an extended range until the Triassic (see Fig. 362; see p. 751–752), and the other is the clathrodictyid genus *Kyklopora* (see p. 755–757) recorded only from the Carboniferous (Upper Mississippian, Serpukhovian Stage, see Fig. 363); no earlier record of this form is known. It remains uncertain whether these post-Devonian records represent convergences derived from different “stromatoporoid-type” stocks (e.g., Introduction to Post-Devonian Hypercalcified Sponges, p. 193–208) during the upper Paleozoic to Mesozoic (i.e., an Elvis taxon of Erwin & Droser, 1993), or, whether, at least in the case of *Lophiostroma*, it reappeared in the Triassic as a Lazarus taxon at the end of its range in a long-lived, more or less continuous line of descent from Middle Ordovician precursors.

BIOSTRATIGRAPHIC STANDARDS BASED ON CONCURRENT COMMUNITY SUCCESSIONS

Nestor (1982, 1984, 1990b) adopted a novel approach to establishing a biostratigraphic standard for Late Ordovician to Silurian stromatoporoid faunas in the Baltic-Scandinavian region, based on the spread of assemblages across a full range of onshore to offshore environments, from lagoonal, to shoal and reef, to open shelf, and into some slope habitats (Fig. 365). Later, Nestor (1999b) linked the associations (communities) of stromatoporoids with the standard benthic assemblages (BA1–BA5) of Boucot (1975). The complete spectrum of laterally equivalent associations was particularly well developed in the Silurian rocks.

Associations of taxa in the open shelf, reef, and shoal facies, representing BOUCOT's BA2–4 assemblages, were more diverse, temporally shorter-ranging, and spatially more widely distributed. The more cosmopolitan, open shelf taxa were considered by NESTOR (1999b) to have the greater potential for use in the stromatoporoid biostratigraphy, because they had geographically wider ranges. Examples in the Llandovery include the *Clathrodictyon boreale–Ecclimadictyon microvesiculosum* community, which is moderately diverse, spans two regional stages, and spreads laterally into both open shelf and shoal lithofacies. Its two name-bearing species have been recorded from the same interval in many parts of the world, including Anticosti Island (Canada; NESTOR, COPPER, & STOCK, 2010, p. 22). The succeeding *Clathrodictyon variolare* community is also diverse, characteristic of the open shelf, and has a short time range (only part of one regional stage); and typical elements of the community (*C. variolare, Ecclimadictyon fastigiatum* [=*Camptodictyon penefastigiatum* NESTOR, COPPER, & STOCK, 2010], *Stelodictyon conodigitatum*) are widely recognized elsewhere (e.g., Norway, Novaya Zemlya, Anticosti Island, Iowa, Alabama). The stromatoporoid assemblages at opposite ends of the environment spectrum—in the lagoon (BA 1) and the deeper marginal shelf to slope (BA 4/5)—were the least diverse and had the longest ranges in time.

A community-based approach was also applied by NESTOR (1999b) to establish the Late Ordovician stromatoporoid faunal succession in Baltoscandia, but no lateral equivalents were recognized, as in the Silurian succession. The six temporally distinct Late Ordovician examples comprise: (1) the reef (shoal)-type assemblages with labechiids in the Oandu stage of Estonia and Mjøsa Formation of Norway (early Katian); (2) the first clathrodictyids with some labechiids in the above-storm-base, open-shelf assemblages of the Vormsi to early Pirgu (i.e., from mid- to late Katian) in Estonia; and (3) some clathrodictyids and labechiids again in the reef (shoal)-type assemblages of the late Pirgu to Porkuni (late Katian to Hirnantian) interval of Estonia and Norway.

The development of NESTOR's (1999b) laterally equivalent, community-based correlation scheme was based primarily on the more complete Silurian successional record of stromatoporoid faunas across the Baltic-Scandinavian region. This record was derived largely from the major documentation of the Silurian stromatoporoid faunas by NESTOR (1964a, 1964b, 1966a) in Estonia, and by MORI (1968, 1970, 1978) from the Island of Gotland (Sweden) and the Oslo region of Norway. In Estonia, NESTOR (1964a, 1964b, 1966a) recognized 65 valid Silurian stromatoporoid species belonging to 20 genera, he revised RIABININ's (1951) earlier work on the faunas and outlined a broadly based, fivefold, stromatoporoid species-based, assemblage zonation that more or less paralleled the existing tabulate coral zonation. The Llandovery (Juuru, Raikküla, and Adavere regional stages) was divided into three stromatoporoid zones. Broadly based zonal indices for the Wenlock (Jaani to Jaagarahu stages) and Ludlow (Paadla and Kuressare stages) intervals were characterized by a species name bearer and other diagnostic index fossils. The units including reefs, such as those included in the Llandovery (upper Juuru), Wenlock (Jaagarahu), and Ludlow (Paadla) stages, were particularly rich in species. However, the lack of detailed studies of Silurian stromatoporoids in other areas prior to the late 1960s prevented these broadly based stromatoporoid zonal indices being used for wider-ranging correlation, except for one example establishing a tie, based on stromatoporoids between the lower Ludlow Paadla stage of Estonia and the Malinovetsky Horizon of Podolia, southwestern Ukraine (NESTOR, 1966a, p. 73).

The Silurian stromatoporoids that occur abundantly through the Gotland reefal and nonreefal successions in Sweden were studied by MORI (1968, 1970). Sixty-eight species belonging to 24 genera were described. The ranges of the species were relatively short,

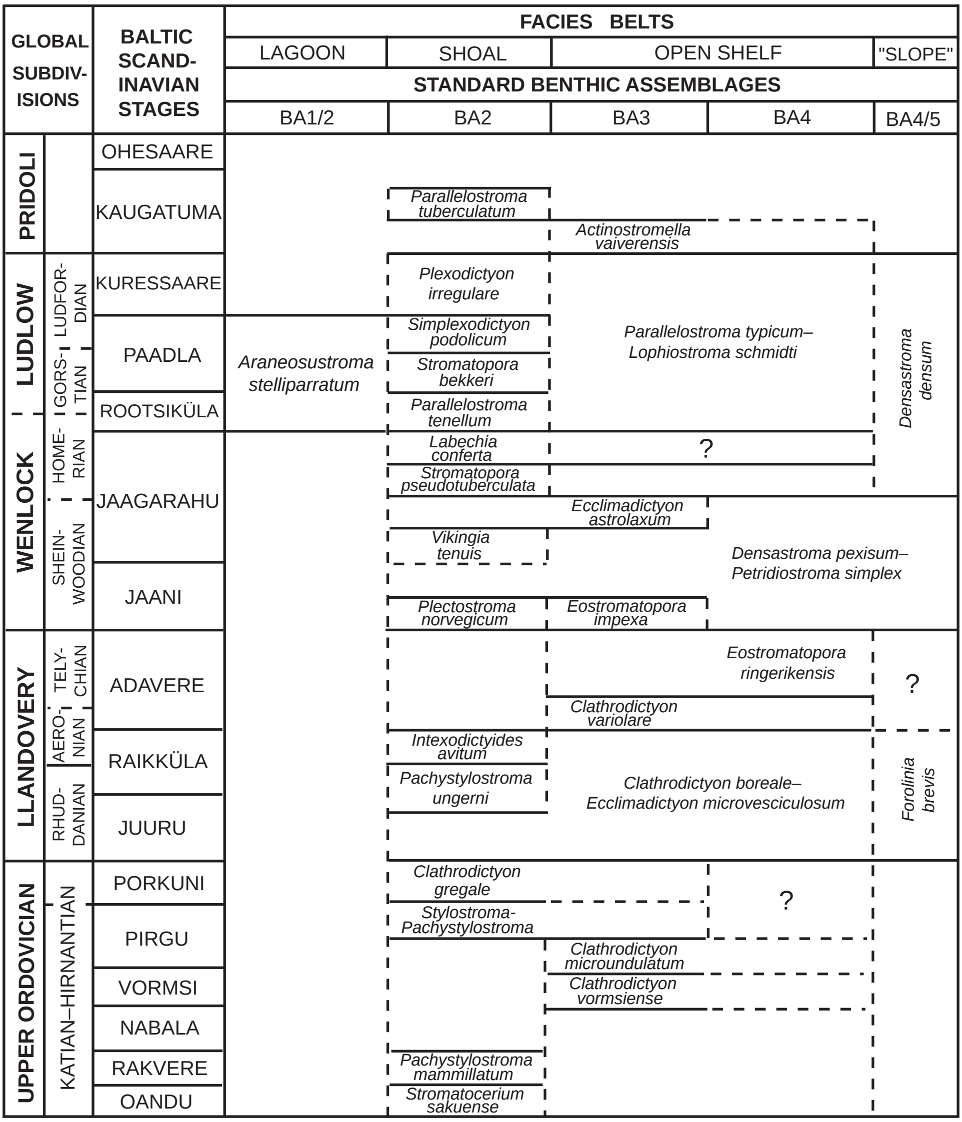


FIG. 365. Diagrammatic representation of biostratigraphically useful, laterally equivalent, stromatoporoid assemblages of Upper Ordovician–Silurian sequences of Baltoscandia across the main facies belts of Nestor's (1990b) Paleobaltic basin, and Boucot's (1975) Standard Benthic Assemblages (BA) (adapted from Nestor, 1999b).

confined to one or two stratigraphic units within the Wenlock or Ludlow (see MORI, 1968, table 1; 1970, table 1), possibly due to facies constraints. Nevertheless, approximately one-third of these species are known to occur also in Estonia and provide a useful means of biostratigraphic correlation, at a number of different levels, through respective Wenlock and Ludlow successions (see MORI, 1968, table 2; 1970, table 4).

In addition, MORI (1978) undertook a comparative survey of Silurian stromatoporoid assemblages from the Oslo region (Norway) in order to reveal their relationships to contemporaneous occurrences in Estonia and Gotland. Of the 15 species, 10 are from the Llandovery, 3 are from the Wenlock, and the remaining 2 are probably from the Ludlow. Two-thirds of the species are found in other areas of the Baltic (Estonia, Gotland). However, Mori's (1978, table 1) stratigraphic distribution chart shows that not all these common occurrences are strictly coeval.

Through the past three decades, Nestor (1982, 1984, 1990a, 1999b) has refined the biostratigraphy of the Baltic Silurian on the basis of community associations. He noted that parallel shallower and deeper-water communities could be differentiated within the respective stromatoporoid zonal successions and suggested that the succession of shallower associations may prove suitable as a zonal standard for use in Balto-Scandinavia and further afield. In 1982, Nestor defined five superposed, shorter-ranging, shallow-water associations (*Eostromatopora impexa, Vikingia tenuis, Ecclimadictyon astrolaxum, Labechia conferta,* and *Parallelostroma tenullum* communities), and two laterally equivalent, longer-ranging, deeper-water associations (*Densastroma pexisum* and *D. densum* communities) in the Wenlock and Ludlow (Fig. 365). Additionally, he identified a restricted nearshore association dominated by *Araneosustroma stelliparratum* in the late Wenlock of Estonia that represents a lateral equivalent of the normal shallow-water association of the *P. tenullum* community on Gotland. A detailed log of the stromatoporoid species, through the 29-m-thick, lower Wenlock biostratigraphic reference section of Vattenfallet, close to Visby (Gotland), identifying representatives of the *Eostromatopora impexa* community in the upper Visby Marl, and members of the *Vikingia tenuis* community in overlying beds of the Högklint Limestone (Fig. 365), was also contributed (Nestor, 1979).

A more complete listing of the distribution of stromatoporoid taxa in the Silurian of Estonia was presented in Nestor (1990a), together with a more comprehensive subdivision of the community-based zonation of stromatoporoids across lower energy lagoonal, high-energy shoal (or reefal), lower energy, open shelf, and slope facies belts (Nestor, 1984, 1990a). In the latter work, the complete list of the Upper Ordovician and Silurian stromatoporoid species from Estonia and Sweden was published, including 104 species belonging to 25 genera. The genera, except for *Clathrodictyon* and *Ecclimadictyon*, exhibit only moderate levels of species diversification. Species of *Clathrodictyon* and *Ecclimadictyon,* especially those from the Llandovery interval, have records of 13 and 10 species, respectively; that is, they were relatively much more diverse than the rest. This suggests that the taxa have been oversplit, and that it would be useful, at least for biostratigraphic purposes, to have them reevaluated using a broader species concept, as in the study undertaken recently by Nestor, Copper, and Stock (2010).

An updated version of the community-based biostratigraphic standard of the Baltic-Scandinavian Silurian stromatoporoids was presented by Nestor (1999b), with the addition of supplementary data from Norway. As a result, 22 different successive and concurrent Silurian stromatoporoid communities were defined (see Fig. 365). The succession is most completely developed in the onshore, high-energy shoal (or reef) facies that occupies the position of Boucot's (1975) Benthic Assemblage BA2, with the species represented by the most diverse, short-ranging forms. Nestor (1999b) further noted that some 99 species have now been recorded through the Baltic-Scandinavian Late Ordovician to Silurian succession in the shoal reef (BA2 position), as compared with 49 species in the inner open shelf (BA3 position). The combined, relatively diverse, short-ranging shoal and inner open shelf assemblages provide the best composite basis for establishing the biostratigraphic standard, with potential use for correlating sequences well beyond the Baltic-Scandinavian region.

Nestor's (1999b) Silurian reef and shoal assemblages were the most diverse, and though the taxa exhibited the shortest time ranges, they unfortunately had mainly narrower spatial distributions. Therefore, these shorter-range, more specialized, reef and shoal species were not as useful for establishing interregional correlations, but they were still important for determining the spatial and temporal relationships of reefs and shoals in the Baltic-Scandinavian region and, less commonly, based on a few species, farther afield. NESTOR (1990b) also demonstrated in a global biogeographic survey of Silurian stromatoporoid genera that very limited evidence of provincialism exists. Consequently, the impact of provincialism on species-based correlations is probably minimal.

NESTOR's (1999b) approach to establishing a laterally equivalent, community-based, biostratigraphic standard, using the Silurian stromatoporoid succession in the Baltic-Scandinavian, is a good model for application to other continental platform regions of the world, for example, in North America and China. In these regions, as in Balto-Scandinavia, there is a wide range of well-exposed Paleozoic stromatoporoid-bearing carbonate successions available for study across a range of onshore to offshore environments and the potential to closely tie such regional, community-based stromatoporoid zonal indices to well-established and highly resolved zonal schemes based on other fossil groups such as conodonts and graptolites (see below).

LINKAGES WITH OTHER ZONATIONS

The comparison of zonal successions based on different fossil organisms is an essential part of the work of the biostratigrapher. An unrivaled succession of 28 named conodont zones has been established for worldwide correlation of Devonian rocks (ZIEGLER & KLAPPER, 1985), but zonal schemes based on stromatoporoid taxa remain at a much more rudimentary stage of development. STEARN's (1997a, 2001) biostratigraphic work on the stromatoporoid assemblages of the Devonian reef-bearing carbonate succession in Western and Arctic Canada has already demonstrated the group's value for correlation across North America and their potential for wider-ranging, perhaps global, correlation of the reef facies. Because diagnostic conodonts rarely occur in reefs, precise stratigraphic relationships must be established between the stromatoporoid assemblages and the diagnostic conodont zones of the laterally equivalent strata. Conodont work in Western and Arctic Canada by UYENO (1974, 1990, 1991), UYENO and KLAPPER (1980), and others permits the age relationships of the stromatoporoid-bearing reefs to be assigned to a particular part of the conodont zonal succession (Fig. 366).

STEARN (1997a, 2001) regarded all ten stromatoporoid assemblages spanning the Devonian as having value for correlation in North America, and more than half the assemblages (those extending through the Lower Devonian, lowermost and uppermost Givetian, and Famennian intervals) as having wider, intercontinental, correlation potential. STEARN (2001) included a range chart showing the ranges of diagnostic species for each assemblage. This work involved adopting a broader species concept than previously and placing a large number of previously described species (about 50%) in synonomy. His approach recognized that the complex skeletons of stromatoporoids exhibit a far wider variability than was thought previously. The assemblages define some time units that range through entire stage divisions and others that are of substage duration. Most of the listed species (STEARN, 2001, fig. 1) have comparatively short time ranges.

PROSH and STEARN (1996) presented in greater detail the Emsian–early Eifelian records of stromatoporoid ranges (a fauna comprising 25 species in 22 genera) from Arctic Canada, with ties to the well-established, standardized, conodont zonation. Nearly half the Arctic species are common to other regions (eastern North America, Asiatic Russia, southeastern

Australia, and China). More than half the species span more than one conodont zone (within the Emsian–earliest Eifelian interval), but one third of the species exhibit very short stratigraphic ranges, of approximately one conodont zone.

Additionally, Prosh and Stearn (1993, 1996) asserted that a number of the species from Arctic Canada allowed precise correlation with faunas described by Galloway and St. Jean (1957) and Fagerstrom (1982) from the midcontinental United States. In particular, occurrences of four stromatoporoid species [*Stromatoporella perannulata* Galloway and St. Jean; *Stictostroma gorriense* Stearn; *Habrostroma proximlaminatum* (Fagerstrom); and *Parallelopora campbelli* Galloway & St. Jean] in the Blue Fiord succession of the Arctic, which is well dated by conodonts, and in the Detroit River Group of the Michigan Basin, have led to the proposal that the Detroit River Group is entirely Emsian, rather than Eifelian, in age, and the conodont dating for this group has been misinterpreted (Prosh & Stearn, 1993, 1996). However, Klapper and Oliver (1995) disputed this correlation on the basis that the conodonts of the Detroit River Group and correlatives in eastern North America are of Middle Devonian age, and two of the four stromatoporoid species have ranges extending up into the Eifelian. They claimed the stromatoporoid species had diachronous relationships—that they needed a long time to migrate from the Arctic to the eastern regions of America because of biogeographic barriers (but see Prosh, 1995, for counterarguments).

In summary, Stearn (1997a, 2001) has suggested that the Devonian succession of Arctic and Western Canada could be divided into ten biozones on the basis of distinctive stromatoporoid faunas (Fig. 366). He proposed that the stromatoporoids of these ten assemblages could form the basis of correlation between reef successions on the continental and perhaps intercontinental scale. The restriction of certain species to narrow time intervals and their wide geographic extent gave hope, in his view, that stromatoporoid biostratigraphy would be as effective in the reef facies as the graptolites have proven to be in the black shale facies. At present, this goal has not been attained and will not be until the data on stratigraphic distribution are brought together with a consistent taxonomy and within the context of a much more complete knowledge of global patterns of provincial change through Devonian time.

OTHER BIOSTRATIGRAPHIC RECORDS

ORDOVICIAN AND SILURIAN

Webby (1969) introduced three informal subdivisions based on diagnostic coral and stromatoporoid assemblages for correlation of the Upper Ordovician island-arc carbonate successions of the Molong Volcanic Belt, central New South Wales (NSW), Australia. Fauna I included a number of distinctive labechiids, and Faunas II and III were characterized by the first appearances of clathrodictyids and continued presence of other labechiids. Pickett (1985a) recognized an older, pre-Fauna I assemblage (with earlier labechiids) in the adjacent Junee-Narromine Volcanic Belt, and Pickett and Percival (2001) later replaced Webby's numbered stromatoporoid assemblages with four, formalized, composite coral/sponge assemblage zones, in ascending order: *Foerstephyllum-Billingsaria-*Stratodictyon; Hillophyllum-Tetradium-*Rosenella; Propora-*Ecclimadictyon-Cliefdenella*; and *Favistina-Halysites-Plasmoporella* (asterisks denote the stromatoporoids). These assemblage zones have not been applied outside central NSW, though generalized correlations between the informally numbered NSW faunal assemblages and the Tasmanian associations (see below) have been previously made (see Webby, 1979b; Webby in Webby & others, 1981, p. 9–10; Webby, 1991; Webby in Young & Laurie, 1996, p. 83–84). The two lower coral-sponge assemblage zones span Australasian regional stages from Gisbornian (=global Sandbian Stage)

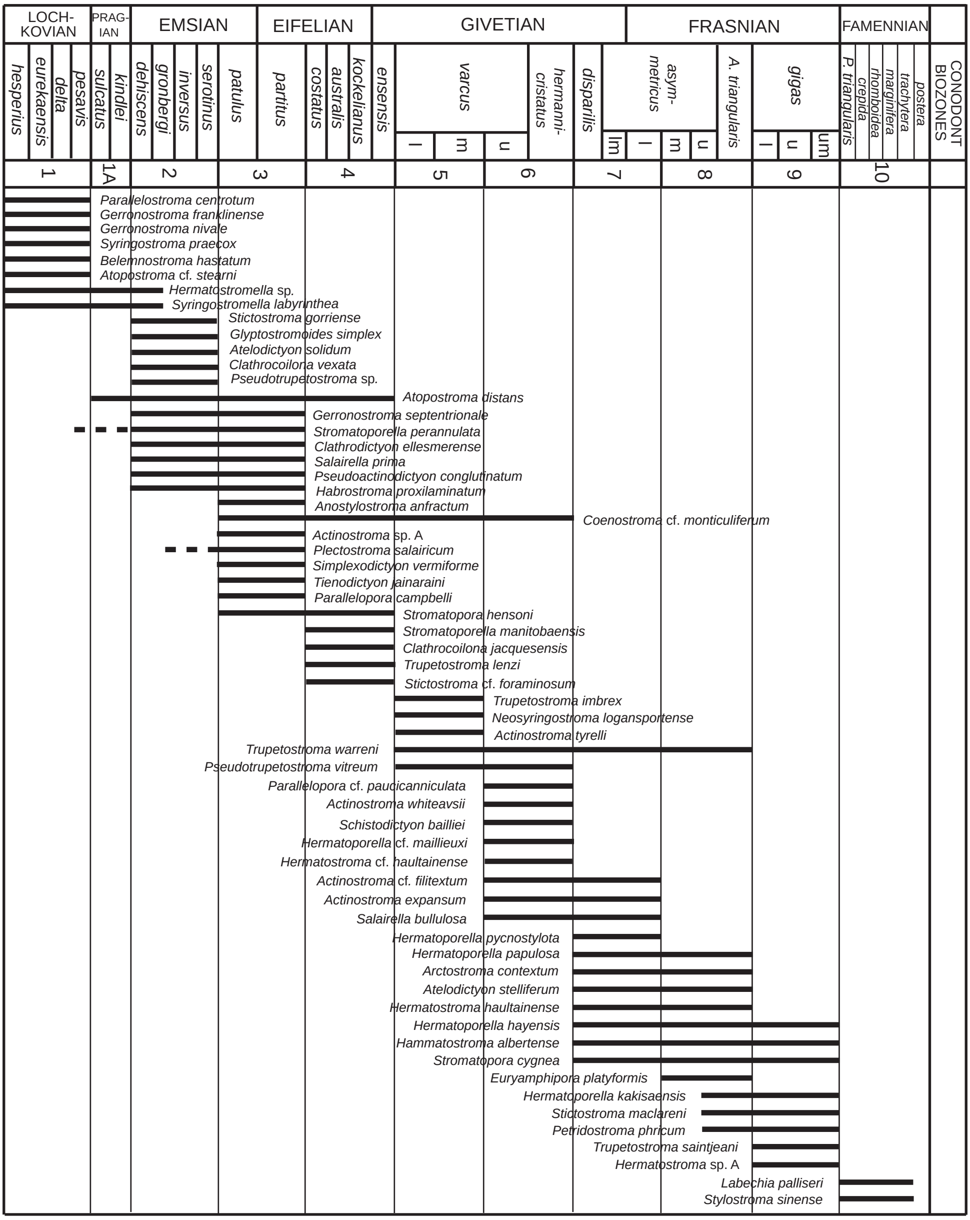


FIG. 366. Diagram depicting stratigraphic ranges of diagnostic stromatoporoid species that form the basis for establishment of ten stromatoporoid assemblage zones through Devonian successions of Arctic and Western Canada by Stearn (2001), and ties to the standardized conodont zonation of Klapper and Ziegler (1979), Klapper and Johnson (1980), Orchard (1989), and Uyeno (1990, 1991).

to lowermost Eastonian, and the two upper zones range between the middle and upper Eastonian. These latter three Eastonian zones equate with lower-middle parts of the global Katian Stage (WEBBY & others, 2004; BERGSTRÖM & others, 2006).

Stromatoporoids are important constituents of the Ordovician carbonate succession

(Gordon Group) on the Tasmanian Shelf (Webby, 1979b, 1991). The two lower faunal assemblages exhibit abundant and varied labechiids, and similarly span the Gisbornian and lower part of the Eastonian, and the two upper assemblages, composed of labechiids and abundant clathrodictyids, have a mid-late Eastonian age. A general similarity exists in the stromatoporoid successional patterns of the Tasmanian Shelf and offshore NSW island arc, but few species are common to the stromatoporoid assemblages of the two regions (Webby in Webby & others, 2000).

Kapp and Stearn (1975) recognized three assemblage zones through the Day Point and Crown Point formations of the Chazy Group of Vermont (eastern North America) that effectively outline the rapid initial evolutionary expansion of the oldest indubitable reef-forming labechiid stromatoporoids during late Mid-Ordovician (late Darriwilian) time. Zone I of the upper Day Point to basal part of the Crown Point Formation contains only *Pseudostylodictyon lamottense*. The base of Zone II is characterized by appearances of the genera *Labechia* and *Pachystylostroma* (a total of five species) within the lower Crown Point. A further stage of diversification of *Pachystylostroma*, and the appearance of *Stratodictyon,* marked the succeeding Zone III, which spanned from the middle Crown Point through the Valcour Formation. Webby (1979b, p. 240) noted that, although the main expansion of the Labechiida in North America and Tasmania appeared to be "strikingly rapid," the earliest part of the initial diversification in the Day Point and lower Crown Point formations of the Chazy Group apparently preceded the appearance of the earliest Tasmanian assemblage, in the Cashion Creek Limestone of Gisbornian age (Webby, 1991).

Bolton (1988) recorded the stratigraphic distribution of Ordovician stromatoporoid species across central and eastern Canada. His discoveries of new records of *Ecclimadictyon* established that the clathrodictyid stromatoporoids made their first appearances in North America during the Edenian; in global terms, early Katian (=Australasian mid-Eastonian, or British late Caradoc), as the group first appeared in Australia, northern China (Lin & Webby, 1988), and in Baltoscandia.

Stearn (1997b) outlined the main Silurian faunal assemblages represented in Canadian rocks at the generic level. He distinguished five assemblages and listed their distinguishing genera: (1) early Llandovery; (2) late Llandovery (Telychian); (3) Wenlock; (4) Ludlow; and (5) Pridoli. These faunas were cross referenced to a large correlation chart for the whole country.

DEVONIAN

Although stratigraphic position of Devonian stromatoporoids was indicated for species described in the first half of the twentieth century, no synthesis of stratigraphic ranges into a biostratigraphic scheme was attempted. Lecompte (1951 in 1951–1952) did not attempt any zonation or correlation of the Devonian species data from the Ardennes, but he found that about half of the species he distinguished were confined to one of the five intervals of stage (Givetian) or half-stage durations (Couvinian 1 & 2, Frasnian 1 & 2). The first paper written specifically on the biostratigraphy of stromatoporoids is that of Flügel (1962). He considered that the group had a potential for use in stratigraphy after reviewing the distribution of the major faunas that had been described until that time. In a subsequent review of the whole group (Flügel, 1975), he did not include a section on biostratigraphy but emphasized paleobiogeography and paleoecology.

Starting in the 1950s, Zukalova documented the stratigraphic distribution of stromatoporoids in the Givetian and Frasnian from the Moravian Karst, Czech Republic (1958, 1974). In 1971, she described the taxonomy of all the stromatoporoid species and recorded the ranges of all the 66 species of stromatoporoids (Zukalova, 1971, table 7). Later, the Givetian to Famennian stromatoporoid succession was divided into 7 biozones (Galle & others, 1988), and the ranges of the stromatoporoids in Moravia were plotted and keyed to conodont zones, but no attempt was made to apply this zonation to correlation problems beyond the Czech Republic.

Stearn (1975b) attempted to divide a local section on Mount Haultain in the Rocky Mountains of Alberta into vertically successive assemblages on the basis of the overlapping ranges of stromatoporoid species. He interpreted these assemblages largely in terms of changing conditions on the reef front, but he also suggested that two zones, those of *Stromatopora parksi* and *Stictostroma mclareni,* could be useful for regional correlation.

For a 1979 review, Stearn compiled the stratigraphic position of Devonian species and used these to plot the ranges of Devonian genera. He distinguished three major faunal intervals. The Gedinnian to Emsian faunal interval was characterized by forms transitional from the Silurian, the Eifelian to Frasnian interval by the maximum stromatoporoid diversity, and the Famennian to Strunian interval by the return of the labechiids, and particularly *Stylostroma.* The Strunian, since ICS-IUGS ratification of the Devonian-Carboniferous boundary in 1990, has been adopted as the uppermost part of the Famennian (Oliver & Chlupac, 1991; Ogg, 2004).

Lessovaya (in Kim & others, 1978; Lessovaya, 1984) delineated in detail the ranges of Lower and Middle Devonian stromatoporoids in Uzbekistan and adjacent areas. She plotted the ranges of species across the boundary between these series. Also, Lessovaya (1982) distinguished the characteristic stromatoporoid assemblages of the Lochkovian, Pragian, and Kitabian (=Emsian) stages in the southern Tian Shan.

Mistiaen (1999), Mistiaen and Gholamalian (2000), and Mistiaen (in Brice, Mistiaen, and Rohart, 1999) have demonstrated that the Devonian stromatoporoid species from the Kerman and Chahriseh regions of central Iran are closely similar to Frasnian assemblages in Afghanistan (five out of the eight species in common), as well as to assemblages in Old World regions of Europe; for example, with ties based on three species in common to the *Syringostromella*? *cooperi* Zone of the Boulonnais area of northern France (Mistiaen, 1988; Mistiaen in Brice, Mistiaen, & Rohart, 1999).

In the Devonian of the Michigan Basin, Fagerstrom (1982, p. 64) identified three local stromatoporoid assemblage zones, named after relatively common species; in ascending order, *Anostylostroma columnare, Syringostroma sherzeri,* and *Amphipora nattresi,* but they were considered to be of little value for regional correlations.

Cockbain (1984) outlined a threefold assemblage zonal scheme for the Middle to Upper Devonian Canning Basin reef complexes of Western Australia, which comprise the *Anostylostroma ponderosum–Stromatopora cooperi* and the *Stachyodes costulata–Clathrocoilona spissa* zones. They are characteristic of the Sadler and Pillara limestones respectively (spanning from near the Givetian-Frasnian boundary into the Frasnian), and the overlying *Clathrocoilona saginata–Stromatopora lennardensis* Zone of the Windjana Limestone (Famennian). The *Stachyodes costulata–Clathrocoilona spissa* Zone has also been identified in the Gneudna Formation of the Carnarvon Basin (Cockbain, 1985) some 1200 km away, suggesting that this zonal scheme may have some potential for wider, intracontinental correlation. Note that *Syringostromella*? *cooperi* Lecompte, 1952 (in Lecompte, 1951–1952), recognized in northern France (see two previous paragraphs, above), and *Stromatopora cooperi* Lecompte, 1952 (in Lecompte, 1951–1952) in the Canning Basin, represent the same species and zonal index. It is remarkable therefore that this same species, either singly or coupled with another zonal indicator species, is available within a part of the Frasnian for use in even wider-range, intercontinental correlation, such as between northern Europe and Western Australia.

Krebedünkel (1995) has published detailed logs of outcrop sections in the Gladbach-Paffrath basin of western Germany, which include the listing of stromatoporoid species found in each bed. A chart (1995, fig. 12) showed the ranges of the species he identified in the Givetian and Frasnian strata. Plotted on another chart (1995, fig. 20) were the occurrences of species common to Europe, Russia, North America, Asia (China), and Australia.

Bogoyavlenskaya (2001b) summarized the occurrence of stromatoporoids on the Russian Platform in terms of the Devonian conodont zonation. She also illustrated the changes in diversity of these faunas throughout the Devonian; by far, the most diverse faunas are of Frasnian age. No attempt was made to establish stromatoporoid-based zones or to use stromatoporoid ranges for correlation.

PALEOECOLOGY OF THE PALEOZOIC STROMATOPOROIDEA

STEPHEN KERSHAW

INTRODUCTION

The study of stromatoporoid paleoecology allows workers to investigate both the fundamental environmental controls on these hypercalcified sponges and their wider paleoenvironmental significance in Paleozoic sedimentary rocks. The two principal objectives are as follows.

1. To determine how stromatoporoids lived, what controlled them, and how they varied through geological time.
2. To apply stromatoporoids to address interpretations of paleoenvironments at a variety of spatial scales (from individual fossils to entire reef systems).

The second main objective is the principal focus here, with treatment of paleoenvironmental controls of stromatoporoid distribution, aspects of community-scale ecology, and the role of stromatoporoids in wider (global) applications, such as changing sea level. For further information on the shapes, growth habits, and individual paleoenvironmental controls of Paleozoic stromatoporoids, see sections on external morphology (p. 419–486) and functional morphology (p. 551–573). These sections contain data on substrate preferences and growth banding and refer to case studies that may be studied in conjunction with the information presented here.

KEY ASPECTS

Interpreted as sponges, stromatoporoids were filter feeders presumed to have been subject to processes influencing supply of detrital organic matter. Modern hypercalcified sponges have little tolerance of fine sedimentary material (WÖRHEIDE, 1998), so fossil stromatoporoids are presumed to be similar. However, Paleozoic stromatoporoids are found commonly in fine-grained, carbonate, sedimentary rock, which may include substantial amounts of siliciclastic, muddy material, though stromatoporoids are rare in clastic-only sedimentary rocks. Stromatoporoids are therefore presumed to have developed mechanisms to overcome the clogging effects of such sedimentary material. Evidence that this was achieved by growth above the substrate, thereby forming primary cavities, is clear in Devonian stromatoporoids, but equivocal in the majority of Ordovician and Silurian examples. That stromatoporoids were able to survive so well on muddy substrates may have played a significant part in their success in middle Paleozoic settings, up to the Frasnian–Famennian extinction event. Evidence from individual stromatoporoids shows they often appeared to recover well from both episodic sedimentation (by growth from unaffected portions of skeletons), and also from disturbance (by reoriented growth attitudes) (Fig. 367). Figure 368 shows the full range of results in stromatoporoids of processes that affected the sea floor when stromatoporoids were alive. Figure 369 shows the results of experimental work on the stability of major growth forms of stromatoporoids on different substrates and current regimes that may influence interpretations of their paleoecology.

Modern hypercalcified sponges grow at very slow rates (DUSTAN & SACCO, 1982; BENAVIDAS & DRUFFEL, 1986) and ecologically often occur as a cryptic fauna, subordinate to corals in reef facies. In contrast, stromatoporoids dominated Silurian and Devonian reef facies and built skeletons that were commonly tens of centimeters in diameter. The largest published stromatoporoid in the Devonian of Poland is 8.5 m in diameter (RACKI & SOBSTEL, 2004), but an even larger specimen of *Actinostroma*

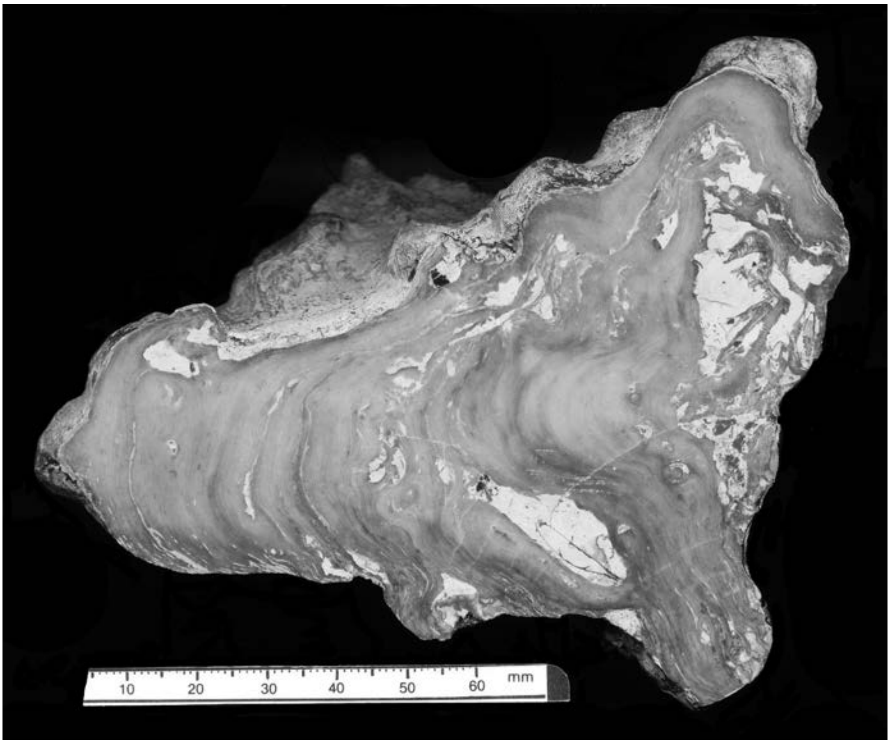


FIG. 367. Longitudinal section of a specimen of *Petridiostroma linnarssoni*, Visby Formation, lower Wenlock, Gotland, that was collected in the field occupying a sideways orientation on the bedding surface; specimen shows interdigitated sediment through the skeleton, which may be interpreted as indicating small-scale episodic sedimentation between the successive phases of upward growth of the organism while it occupied a muddy environment. Then a sudden reorientation occurred, with a rotation of 90° to the left, as a result of storm action, and in the following recovery, the skeleton can be seen to have resumed growth on upper slopes in its final orientation prior to final burial (Kershaw, 2012; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

expansum, 30 m wide and about 1.5 m thick, occurs in the Nora Member of the Shell Rock Formation (mid-Frasnian) near Rockford, Iowa (Carl Stock, personal communication, 2005). These large sizes imply that stromatoporoids grew at rates as least as fast as modern corals, yet there is no evidence that stromatoporoids contained symbiotic photosynthetic algae (notwithstanding the views of KAŹMIERCZAK, 1976; KAŹMIERCZAK & KRUMBEIN, 1983; and KAŹMIERCZAK & KEMPE, 1990, that stromatoporoids were cyanobacteria). Furthermore, modern sponges can grow well in nutrient-rich waters, in contrast to modern reefs (and, by analogy, fossil reefs), which are found in low-nutrient settings. Consequently, with respect to growth rate and nutrient requirements and the implications for their ecology, the modern hypercalcified sponges are only partially analogous to fossil stromatoporoids.

Stromatoporoids are most abundant in carbonate platform settings of various types, less abundant in siliciclastics, reefs, and related facies, and they probably responded favorably to low-nutrient conditions. They were apparently stenohaline (therefore normal marine) organisms.

OVERVIEW OF FEATURES

The following sections identify features of stromatoporoid paleoecology and present the current state of knowledge. Figures

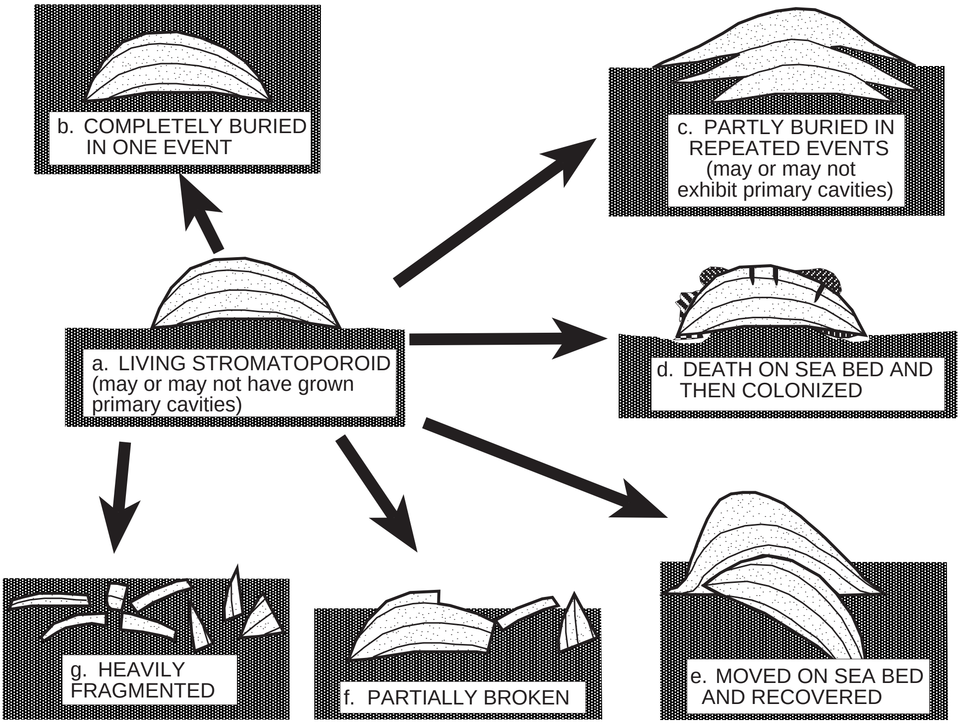


FIG. 368. Fossil stromatoporoid skeleton geometries demonstrating events affecting sea bed during life and in early postmortem, prior to final burial. *a,* Living stromatoporoid prior to burial; *b,* completely buried; *c,* partial burial with flank recovery, but the flanges of skeleton may have grown into the water to form original cavities (see p. 419–486); *d,* death without burial may be suspected for cases with epifauna but may instead have been buried then exhumed; *e,* dislocation during life is recorded in changes of growth attitude; *f–g,* variations of degree of damage to stromatoporoids on the sea floor, either during life or soon after death, and such taphonomic information may be valuable in paleoenvironment reconstruction (Kershaw, 2012).

368–372 give key information about the paleoenvironmental controls on stromatoporoids.

GROWTH FORM DEVELOPMENT

Stromatoporoid early growth often formed sheetlike skeletons across the substrate, and subsequent growth was concentrated in central areas, producing a smooth, nonenveloping profile (KERSHAW & RIDING, 1978); uncommonly, others are fully enveloping (see p. 425). The resulting basal surfaces of skeletons display concentric ridges where successive overlapping layers touch the substrate, enhanced into minor ragged edges, which may be due to a little sedimentary material collected on the edges as successive layers grew. Form usually changed as individuals grew: early growth of a stromatoporoid was commonly laminar, with later growth focused in central regions to form a domical shape. Some samples, which have a final bulbous form, are observed in longitudinal section to have gone through laminar and then domical forms in the process. Therefore, determination of growth form should take into account such changes in growth form history within individual specimens, where they are visible in cut sections; individuals of the same species within an assemblage may display different growth forms if they died before the final form could develop, and species-level taxonomy is crucial in such investigations. An example of the history of a single specimen in relation to

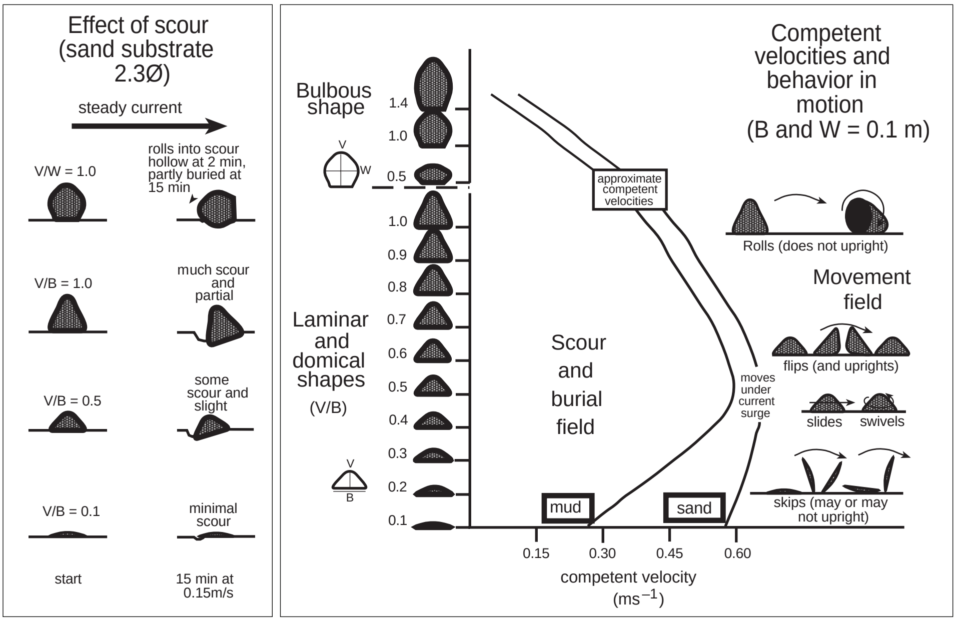


FIG. 369. Results of experimental work on model stromatoporoids illustrating the range of behavior of simple-shaped forms under steady and surge current influence on sand and mud substrates. Models were not fixed to the substrate, emulating fossil stromatoporoids. The data show that stromatoporoids are more stable on muddy substrates; this is circumstantial evidence that may partly account for their common occurrence on such substrates. Stability is inherent in the common low- to mid-domical shapes, and the slow currents used in these experiments serve to emphasize the important role of obstructions, which prevented movement of fossil stromatoporoids in reefs in many cases. Responses of more complex forms were not tested, and divergence from this simple pattern is expected; *V,* maximum vertical dimension; *B,* maximum basal dimension; *W,* maximum width in bulbous forms (therefore not the base); ø (phi), grain size of the sediment from international standards of grain size (Kershaw, 1998; reproduced with kind permission of the Palaeontological Association).

environmental influences is given in Figure 367.

PHOTOTROPISM AND DEPTH

Circumstantial evidence that stromatoporoids were photoresponsive employs size and growth rates in relation to modern coral-dominated reef systems (BAARLI, JOHNSON, & KEILEN, 1992; WOOD, ZHURAVLEV, & DEBRENNE, 1992), morphology (KLOVAN, 1964), and association with algae (e.g., BAARLI, JOHNSON, & KEILEN, 1992). In contrast, although modern sponge biomass (noncalcified types only) may be 50% bacteria (WILLENZ & HARTMAN, 1989), these are not photosensitive. In Devonian stromatoporoid morphotype data, laminar and tabular forms are more common in fore reefs than in other large domical-bulbous-irregular forms. Laminar forms grew better in the finer sediment, deeper water facies of the Canadian Leduc reefs (and also occur in back-reef facies), while massive and subspherical forms (domical, bulbous, and irregular) dominate reef facies and are less common in fore reefs (KLOVAN, 1964). Geopetally constrained, fore-reef, paleoslope data in the Canning Basin reef-rimmed shelves (PLAYFORD, 1980; PLAYFORD & COCKBAIN, 1989) imply depths comparable to modern reef systems. The earliest laminar stromatoporoids are Ordovician in age and may have occupied deeper water (approximately 30 m depth) habitats (BOURQUE & AMYOT, 1989, p. 255); such laminar shapes could have existed in deeper, poorly lit environs,

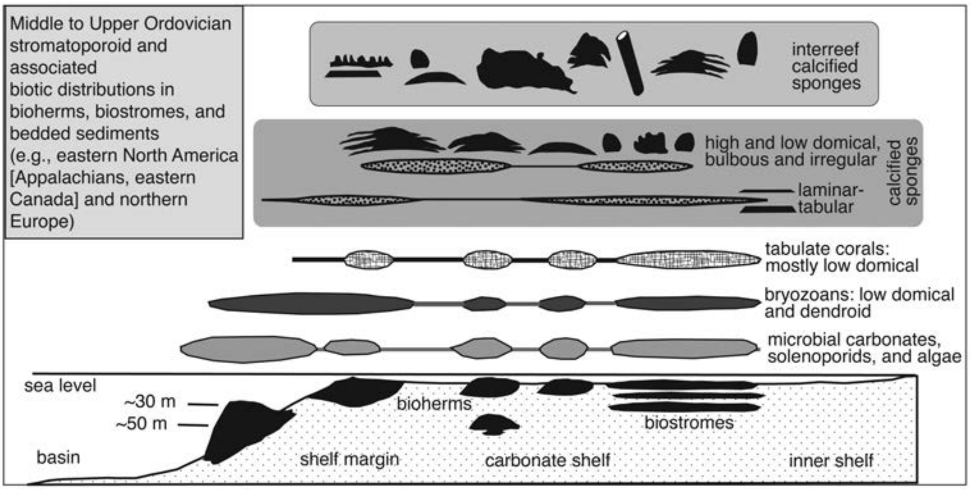


FIG. 370. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Ordovician carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Ordovician labechiid-dominated stromatoporoid morphotypes exhibit a wide range across carbonate banks. Stromatoporoids commonly occur with solenoporid-rich rudaceous carbonates. Level-bottom community dwellers (e.g., Mid-Ordovician [Chazyan] *Pseudostylodictyon* and Upper Ordovician *Aulacera*) are the largest stromatoporoids. Note: the stromatoporoids are commonly associated with facies rich in microbial carbonates, algae, and solenoporids (compiled from various sources; see Kershaw & Brunton, 1999; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

as do some modern corals. Arguments favoring algal (=?microbial) symbiosis (e.g., Cowen, 1988) are circumstantial, and papers that record relatively deeper water, laminar forms (Klovan, 1964, at Redwater; Krebs, 1974, in Europe; Kobluk, 1975, at Miette—see Wilson, 1975, p. 144) do not contain sufficient species-morphotype information to demonstrate flattening at depth within a species. Also, low profile is common in stromatoporoids and may relate instead to sedimentation rate and substrate type, similarly poorly investigated.

PALEOENVIRONMENTAL DISTRIBUTION

Stromatoporoids with diameters up to tens of centimeters grew in deeper facies, lagoons, and small reefs, and up to several meters in larger reefs and mounds, and they occupy up to 90% of reef volume (Machel & Hunter, 1994, p. 162). Stromatoporoids were limited in deeper facies and in mud mounds, occurring uncommonly as small individuals (e.g., Bourque & Raymond, 1989). Siliceous sponges played a role in deeper water mounds (e.g., Brunton & Dixon, 1994) and have been postulated as major elements of stromatactoid-rich mud mounds by Bourque and Gignac (1983, 1986), but none of these are the calcified forms typified by the stromatoporoid skeleton. In contrast, stromatoporoids may be major elements of framestones, bafflestones, bindstones, and debris in both biostromes and bioherms (e.g., Watts, 1988a; Sønderholm & Harland, 1989; Riding & Watts, 1991; James & Bourque, 1992; de Freitas, Dixon, & Mayr, 1993; Kershaw, 1993; Machel & Hunter, 1994). Absence of a rigid frame is common in stromatoporoid reefs, and, except where bound by microbial growth (e.g., Devonian platform-margin reef limestones of the Canning Basin), presumably they could not withstand high-energy conditions (de Freitas, Dixon, & Mayr, 1993). They usually did not build up high

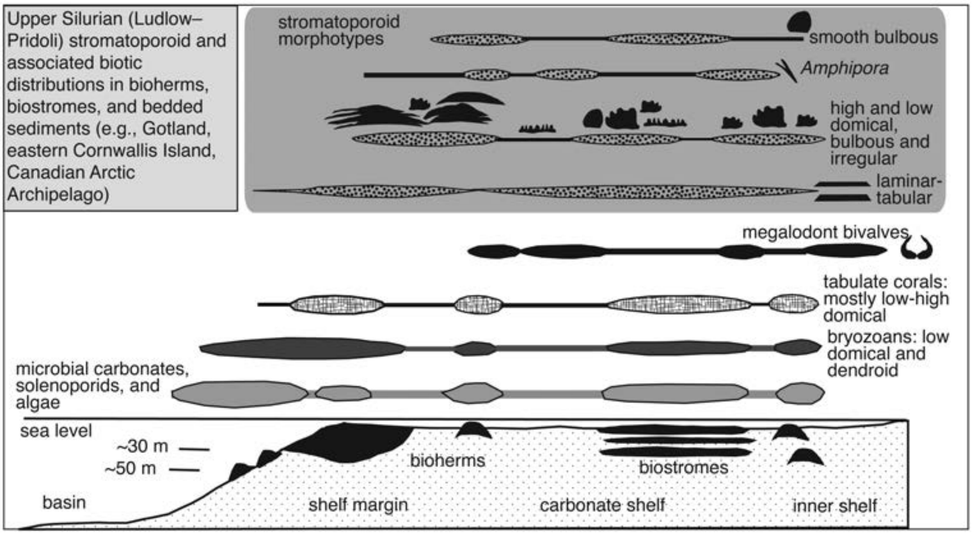


FIG. 371. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Silurian carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Late Silurian, predominantly nonlabechiid morphotypes occur in a wider range of niches than Ordovician stromatoporoids and have a greater range of skeletal architecture and taphofacies variation. A wider variety of forms are evident in Silurian than in Ordovician bioherms; in Silurian biostromes, there are predominantly smooth, bulbous-to-high domical forms. Note: Silurian and Devonian reef-dwelling stromatoporoids both have a spatial and temporal association with photosymbiotic megalodontid bivalves and microbial carbonates, algae, and solenoporids (compiled from various sources; see Kershaw & Brunton, 1999; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

reef profiles. Unbound stromatoporoid buildups are discrete objects (RIDING, 1981) made of closely juxtaposed fossils, called cluster reefs by RIDING (1990).

Nevertheless, stromatoporoids apparently grew best in the shallower, more turbulent waters of Paleozoic reefs, outcompeting corals and other organisms, and forming low diversity stands in the climax stages of reef development (e.g., WILSON, 1975), which is true in many biohermal reefs (e.g., the Silurian Högklint reefs of Gotland, Sweden: RIDING & WATTS, 1991; Devonian reefs in South Devon, United Kingdom: SCRUTTON, 1977a, 1977b); but some exceptionally stromatoporoid-rich assemblages formed as biostromes in lower-energy, shelf-ramp settings conditions in Silurian and Devonian platforms. Furthermore, MONTY, BERNET-ROLLANDE, and MAURIN (1982) drew attention to the fact that although stromatoporoids are major reef-builders in the Devonian, they are not abundant in all cases. Presumption of shallow water may not always be justified. Summaries of the distribution of stromatoporoids in Ordovician, Silurian, and Devonian facies are provided in Figures 370–372 respectively.

STROMATOPOROID TAPHONOMY

Impact damage to stromatoporoids can be observed both in Paleozoic-age events and in the presently occurring erosion of modern outcrops; recently eroded stromatoporoid clasts found in quarries and cliffs are similar in nature to their Silurian counterparts. Breakage is governed by form, degree of fixation to the Paleozoic seabed, the degree to which latilaminae are developed, and the amount of diagenetic alteration of skeletons, especially along latilaminae. Skeletal breakage, as well as attitude in outcrop, may influence form recognition. Furthermore, the common effect of pressure

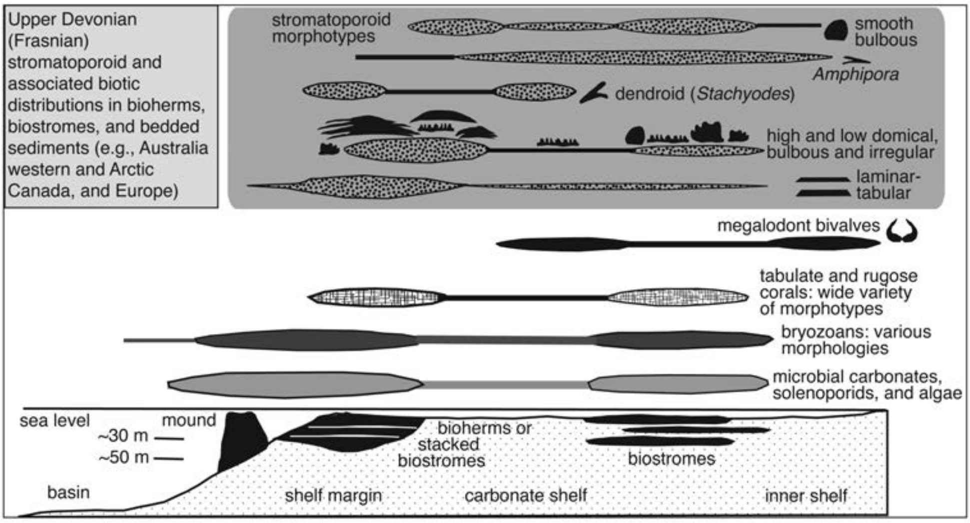


FIG. 372. Occurrence of stromatoporoid morphotypes and associated reef and interreef (level-bottom) faunas across Devonian carbonate shelves. Thicknesses of fill patterns represent approximate relative abundances. Upper Devonian, predominantly nonlabechiid morphotypes have the widest range of morphotype distribution, skeletal architecture, and taphofacies. Late Devonian stromatoporoid morphotypes tend to have a wider variety of irregular forms and a greater tendency for encrusting than Silurian forms. Note: Silurian and Devonian reef-dwelling stromatoporoids both have a spatial and temporal association with photosymbiotic megalodontid bivalves and microbial carbonates, algae, and solenoporids (compiled from various sources; see Kershaw & Brunton, 1999; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

solution degrades the margins of stromatoporoids, so that marginal damage may not be preserved. Stromatoporoid taphonomy is, of course, crucial in paleoenvironmental analyses and underlies much of the analogy drawn between modern coral reefs and Devonian stromatoporoid reefs. Examples of the importance of taphonomic aspects are: (1) a delicate branching species of the genus *Amphipora* occurs as fragmented branches across Devonian reef complexes, and its preferred growth site is poorly understood; it is not known whether it was restricted to quieter waters of back-reef settings, or if it grew over a reef complex; (2) the very thin laminar genus *Lophiostroma,* in Ludlow biostromes on Gotland, is commonly found as fragments, because it is less robust than other stromatoporoids in the assemblage, affecting its preservation potential relative to other stromatoporoids. Most studies have been qualitative, but quantitative work (e.g., Kobluk, 1974; Kobluk, Bottjer, & Risk, 1977; Kershaw, 1990), especially where fragments are identified and size-classed, has much potential (Kershaw & Brunton, 1999); if, for example, the fragments show differences in taxonomic distribution from the in-place stromatoporoids, inferences can be made about fragmentation and transport in a stromatoporoid-bearing deposit.

STRATIGRAPHIC GROWTH FORM TRENDS

Ordovician and Silurian stromatoporoid growth forms are conservative, but expand to a modern-looking form distribution in the Devonian (Andrichuk, 1958; Fischbuch, 1962). However, stromatoporoids lack the branching habit of the modern dominant reef coral *Acropora*. Ordovician and Silurian reefs are similar in structure and function, and differ mainly in taxonomic composition (Copper, 1988, p.

137). Many upper Silurian reefs resemble Devonian platform margin systems and include important elements of microbial binding (e.g., BOURQUE & AMYOT, 1989). Devonian reefs (e.g., GISCHLER, 1995) may contain substantial submarine cement; the presence of cement in Devonian reefs appears to have enhanced the preservation of primary cavities in stromatoporoids, in contrast to the Silurian (as discussed in p. 425).

PALEOENVIRONMENTAL ANALYSIS

GENERAL RELATIONSHIPS

Growth form was controlled by environmental (extrinsic) and genetic (intrinsic) factors (NICHOLSON, 1886a, p. 27–29; GALLOWAY, 1957, p. 374; KISSLING & LINEBACK, 1967; FISCHBUCH, 1968, fig. 23; LEAVITT, 1968, p. 323; MORI, 1968, 1970; KAPP, 1974, 1975; CORNET, 1975; HOGGAN, 1975; KOBLUK, 1975; KERSHAW, 1981, 1984, 1990; COCKBAIN, 1984; KANO, 1989, 1990). Most species are limited to a narrow morphospace that varies depending on interaction between paleoenvironment and morphospecies. Short-lived events are also recorded, particularly sedimentation and movement effects during life (Fig. 368). However, since these effects do not influence the basic shape (a domical stromatoporoid that reoriented several times in life so that its shape is rounded is still intrinsically domical), then underlying controls on form, if they can be identified, may provide important data on the overall character of the paleonvironment.

Several studies illustrate the selective advantage of dominantly lateral growth in stromatoporoids (MEYER, 1981; BJERSTEDT & FELDMANN, 1985; HARRINGTON, 1987; KANO, 1990; KERSHAW, 1990). STEARN's (1982b) comparison of stromatoporoids with modern coral growth forms, which may provide analogues, revealed no parallel patterns; and the forms of modern reef animals are not even useful guides to modern reef environments, thereby emphasizing the care needed for interpretation of stromatoporoids. NESTOR (1984) discussed the range of controls on stromatoporoids. A general summary, derived from many sources, is presented in Figure 373, which summarizes a diverse range of aspects of stromatoporoid paleoecology (see also p. 423–485).

Large stromatoporoids reflect long periods of growth (YOUNG & KERSHAW, 2005) and highlight their ability to survive events affecting the seabed. Depending on the nature of the assemblage, stromatoporoids have potential to reveal regional and even global processes. Examples of Paleozoic stromatoporoid assemblages demonstrate the range of process-response relationships in order to emphasize their value in paleoenvironmental analysis at these different scales; these are demonstrated in the Ordovician, Silurian, and Devonian systems, and summarized in Figures 370–372.

COMMUNITY-SCALE ECOLOGY—OUTCROP SCALE

Here, selected examples from the literature and outcrops illustrate characters and problems of interpretation of stromatoporoid assemblages at relatively small scale in outcrop studies. The small-scale approach is most commonly adopted by field geologists investigating the factors that may have been responsible for controlling growth (further examples are presented on p. 423–485).

Middle Ordovician Stromatoporoids, Chazy Group, Vermont, USA

Large stromatoporoids appear in Middle Ordovician level bottom and mound environments at the start of Paleozoic stromatoporoid dominance in many shallow marine facies (WEBBY, 1986, 1994; FLÜGEL & FLÜGEL-KAHLER, 1992, p. 178), although stromatoporoid abundance varies within the Ordovician buildups (DESROCHERS & JAMES, 1989). KAPP (1974, 1975) and KAPP and STEARN (1975) noted that laminar to high domical forms are abundant in the

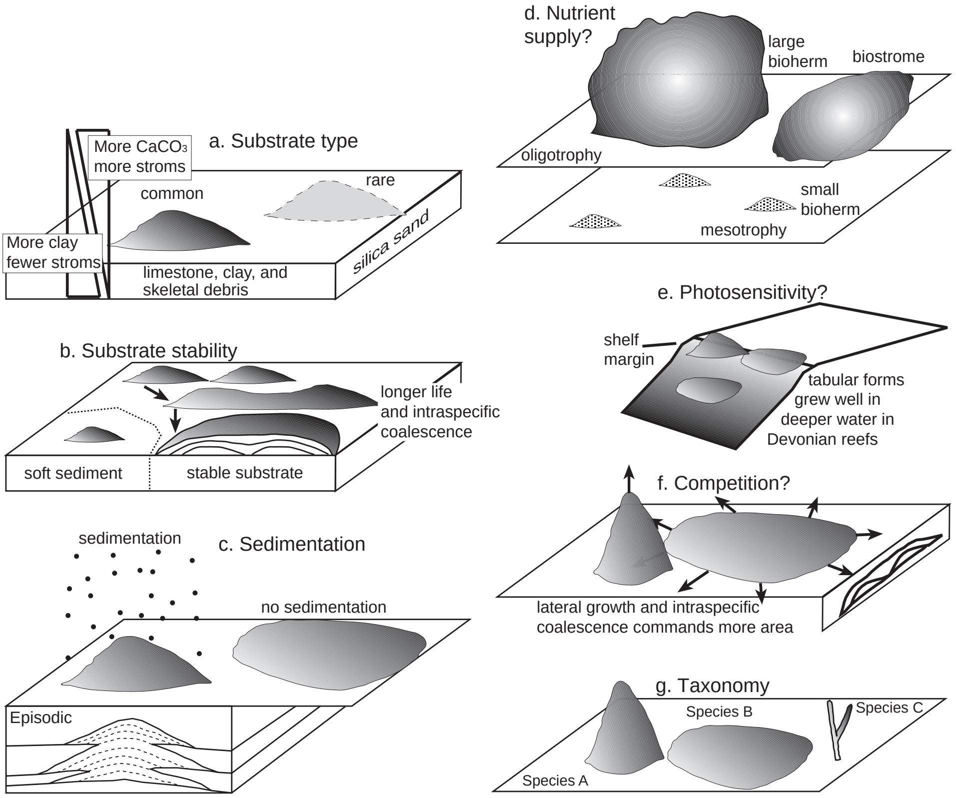


FIG. 373. Diagram summarizing stromatoporoid growth controls, which encompass the range of environmental boundaries that may be expected to have operated on Paleozoic stromatoporoids. *a,* Stromatoporoids are found mostly associated with calcareous sediments low in clay and are rare in coarser siliciclastic sediments; *b,* stromatoporoids grew most successfully on stabilized sediments of skeletal debris and were smaller on clay-rich limestones; coalescence of neighboring individuals of the same species is a likely means of increasing size; *c,* sedimentation is suspected to be a major control on stromatoporoid growth; stromatoporoids that grew in conditions of little sediment deposition grew larger; *d,* stromatoporoid-dominated reefs may have grown in low-nutrient conditions, by analogy with modern reefs that are best developed in such oligotrophic environments; *e,* stromatoporoids in deeper water environments commonly developed a laminar or tabular form, which may be due to photoresponsive tissue; however, there is no unequivocal evidence that stromatoporoids possessed a photoresponsive capability; *f,* whether or not stromatoporoids developed a competitive ability is unclear; no proof of competitive interactions has been published (Fagerstrom & others, 2000); *g,* stromatoporoid growth form was influenced by taxonomy in at least some species, with a predominance of lower profile forms (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

Middle Ordovician Crown Point Formation, Lake Champlain area, Vermont, and have a component of taxonomic control on form; *Pseudostylodictyon lamottense* (SEELY) grew into high domical shapes (see Fig. 287), whereas species of *Pachystylostroma* and *Labechia* were laminar (KAPP, 1974, p. 1235). *Pachystylostroma* and *Labechia* are present only in mounds, whereas *Pseudostylodictyon* occurs mainly in level bottom sediments. Stromatoporoids occupy the greatest biovolume of mound faunas, but are low in diversity within individual mounds dominated by single stromatoporoid species, or different species may dominate in different mounds (KAPP, 1975, p. 201).

Only *P. lamottense* formed large stromatoporoids (KAPP, 1974) as stacked, ragged domes due to episodic sedimentation (see Fig. 286–287) and may have grown quickly, because it is also the only species in the level bottom facies able to grow high enough to survive episodic sedimentation. Kapp (1974, p. 1236) noted that individuals began on small substrate irregularities, and although not stated in her papers, the indications are that they could grow directly on the sediment surface, a feature noted also by Kano and others (1994) in Middle Ordovician stromatoporoids of Korea. In Vermont, individuals are isolated and grew on several bedding planes (Fig. 374; and see Fig. 286.1); early growth showed lateral expansion with some enveloping latilaminae, then upward growth was apparently stimulated by episodic sedimentation to generate ragged forms (see Fig. 282.2–286.3; Fig. 287).

Specimens may be closely spaced, less than one meter apart (Kapp, 1974), and commonly asymmetrical (Fig. 374; and see Fig. 286.2), with growth axes of neighboring stromatoporoids commonly pointing in different directions, interpreted by Kapp as a result of variable local current vectors. Asymmetry is maintained through the vertical thickness, so for currents to be the cause, they would have to be peculiar to each stromatoporoid throughout its life, and the many intervening episodes of sediment deposition; asymmetry may be better explained by chance development of the growth form of individual stromatoporoids. Overall, the Vermont examples give considerable information about stromatoporoid paleobiology and autecology but also raise questions about the controls of form.

Silurian Level Bottom Stromatoporoids, Gotland, Sweden

Figure 375 summarizes features of an assemblage of small stromatoporoids from Gotland, but the principles apply to most level bottom stromatoporoid assemblages. *Densastroma pexisum* grew taller and apparently survived episodic sedimentation better than other species in the assemblage, leading to its higher abundance and lower degrees of raggedness (Kershaw, 1984). Note, however, the reappraisal of the nature of ragged margins in stromatoporoids (Kershaw, Wood, & Guo, 2006), reinterpreting at least some of them as flanges extending outward into the water column and not necessarily directly linked to episodic sedimentation (see p. 424), which, therefore, reduces the certainty of application of ragged margins as sedimentation rate indicators. Some tabulate coral species are likewise better adapted to episodic sedimentation (e.g., Gibson & Broadhead, 1989). An environmental energy index, using proportion of overturned stromatoporoids, could be used only broadly, because experimental work shows that domical stromatoporoids were usually restored to an upright position following disturbance (Fig. 369); nearly all stromatoporoids are upright in the muddy limestones, less so in coarser beds, interpreted as storm events (Kershaw, 1984).

Middle Devonian Level Bottom Stromatoporoids, Hope's Nose, Devon, UK

Low profile (laminar and low domical) stromatoporoids colonized coarse crinoidal grainstones and presumably helped to stabilize the substrate. The lack of ragged forms suggests periods of no sedimentation while they grew in well-aerated water, followed by sudden episodic deposition that overwhelmed them (Fig. 376).

Upper Devonian Bioherm, Lion Quarry, Southern Belgium

Figure 377 illustrates laminar and domical stromatoporoids in a Frasnian bioherm, in which large laminar and domical stromatoporoids occur together at particular levels, separated by layers containing small laminar stromatoporoids and layers with coarse debris. The larger stromatoporoids presumably grew in episodes of reduced deposition and relative substrate stability, interspersed with energetic events. These features are consistent with the interpretation of Monty, Bernet-Rollande, and Maurin (1982), that this bioherm lacks a frame and possibly formed in deeper water.

COMMUNITY-SCALE ECOLOGY—ANALYSIS OF ASSEMBLAGES

Stromatoporoid Diversity Indices as Paleoenvironmental Tools—Silurian and Devonian Examples

Quantification of modern organic diversity is achieved using diversity indices (e.g., PIELOU, 1966) but is problematic in fossils because of difficulties in precision of species definitions, time-averaging of communities, and taphonomy. FAGERSTROM (1983) applied diversity concepts qualitatively to Emsian and Eifelian stromatoporoid assemblages, where diversity in reefs is greater than in level bottom communities, and Eifelian reef organisms are strongly endemic; also reef environments are likely to have greater origination and extinction rates and consequently could play an important role in evolution of reef builders. COCKBAIN (1989) similarly noted higher species numbers in reef (25 taxa) compared to shelf (6 taxa) environments in Middle to Upper Devonian successions of Western Australia. In contrast, Devonian reefs in Nevada have lower diversity, with *Hammatostroma* abundant as tabular and bulbous shapes, although such reefs are considered as biostromes (HOGGAN, 1975). BRUNTON and COPPER (1994) categorized early Silurian reef biotas into groups, depending on numbers of species, and revealed a low diversity in reef cores, with up to 70% of volume being composed of only four species. COPPER (1988) drew attention to the lower diversity of modern reef communities in areas under great stress, whereas the rest of a reef complex usually exhibits a higher diversity.

Although such general observations are valuable, numerical diversity indices, such as Shannon's Information Function (H) applied by STEARN (1975b) to the Devonian Ancient Wall stromatoporoid assemblages, provide a better comparative tool for paleoecological and paleoenvironmental work. Species diversity indices are calculated from relative abundance of individuals of each species, not just numbers of species, and greatest diversity lies in assemblages with equal numbers of each species. Approaches to diversity analysis were discussed by KREBS (1972), who noted that different methods have different advantages. Shannon's Information Function (H) is particularly applicable to assemblages of organisms in cases where there is no assumption of the shape of the distribution; furthermore H should be applied to random samples. STEARN (1975b) argued that stromatoporoids, being fossils that cannot be identified in the field, provide a good approximation to randomness in collection, since the collector is not influenced by selection of specimens with particular skeletal structures, especially in cemented limestones where internal structure is difficult to see. Nevertheless, truly random samples need to be collected using a grid system and random number tables, as applied by KERSHAW (1990). KREBS (1972, p. 455) pointed out in a footnote that the Shannon Function is correctly called the Shannon-Wiener Function, and sometimes incorrectly referred to as the

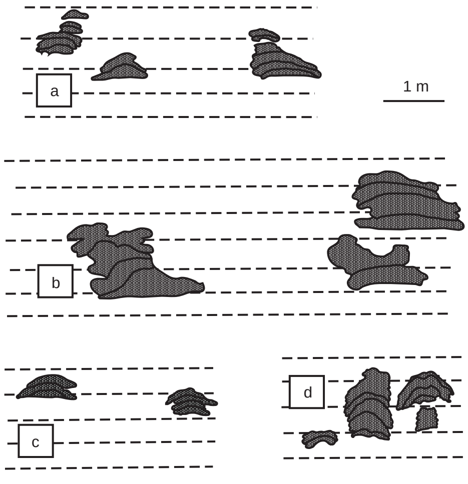
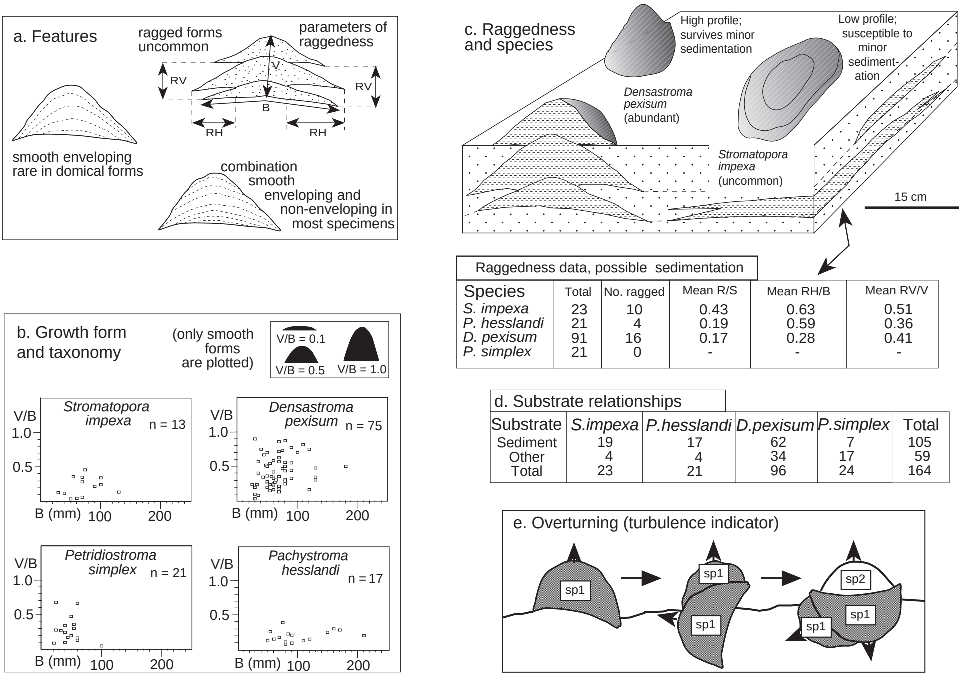


FIG. 374. Sketches of stromatoporoid vertical sections. Growth was apparently principally on soft sediment; individuals began growth at different levels and have ragged margins, suggesting that episodic sedimentation controlled growth initiation and development. Growth is biased in left or right directions. *a–c,* Fisk Quarry; *d,* Goodsell Quarry (drawn from photographs in Kapp, 1975).



Raggedness data, possible sedimentation

Species	Total	No. ragged	Mean R/S	Mean RH/B	Mean RV/V
S. impexa	23	10	0.43	0.63	0.51
P. hesslandi	21	4	0.19	0.59	0.36
D. pexisum	91	16	0.17	0.28	0.41
P. simplex	21	0	-	-	-

d. Substrate relationships

Substrate	*S.impexa*	*P.hesslandi*	*D.pexisum*	*P.simplex*	Total
Sediment	19	17	62	7	105
Other	4	4	34	17	59
Total	23	21	96	24	164

FIG. 375. Comparative stromatoporoid autecology in the Visby Formation, lower Wenlock, Gotland, Sweden, based on data from KERSHAW (1984). *a,* Features of stromatoporoids in this assemblage; *b,* morphological variation between species; *c,* selective advantage of a high profile form in this environment; *d,* species selection of substrate type; *e,* broad indication of frequency of dislocating currents shown by episodic overturning and recovery by species 1, and use of the upturned base of the first growth of species by species 2 (the horizontal arrows show the successive stages of growth development of the sample from left to right). Note that the raggedness data in view *c* may reflect sedimentation and/or growth to form primary cavities. *V,* maximum vertical dimension; *B,* maximum basal dimension; *V/B,* ratio of V to B, as an approximate measure of shape; *R/S,* ratio of number of ragged-margined to number of smooth-margined specimens; *RV,* vertical extent of raggedness; *RH,* horizontal extent of raggedness; *RH/B,* ratio of RH to B as an measure of horizontal extent of raggedness; *RV/V,* ratio of RV to V as a measure of vertical raggedness (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

Shannon-Weaver Function. As an attempt to demonstrate its utility, Figure 378 provides diversity indices calculated using the Shannon-Wiener Function (H) for a range of published species distributions of stromatoporoids from well-documented Silurian and Devonian examples, assembled by KERSHAW (1990). H was chosen by KERSHAW (1990), following its application by STEARN (1975b), in order to attempt to compare diversities of different stromatoporoid assemblages, using the same index. However, in the examples of Figure 378, comparisons are probably fully valid only *within* and not *between* datasets, because of uncertainty about whether the data collection methods were all random; therefore, these data give only a general guide to stromatoporoid diversity.

According to STEARN (1975b), the Shannon-Wiener Function (H) is calculated according to the formula:

$$H = -\sum_{i=1}^{S} p_i \log_e p_i$$

where S = number of species in the sample, and p_i is the proportion of the ith species of the sample (Table 32).

KREBS (1972, p. 455) used Log_2, although as long as a uniform approach is applied, comparisons of H values between samples collected by the same method will be valid. H is most easily calculated

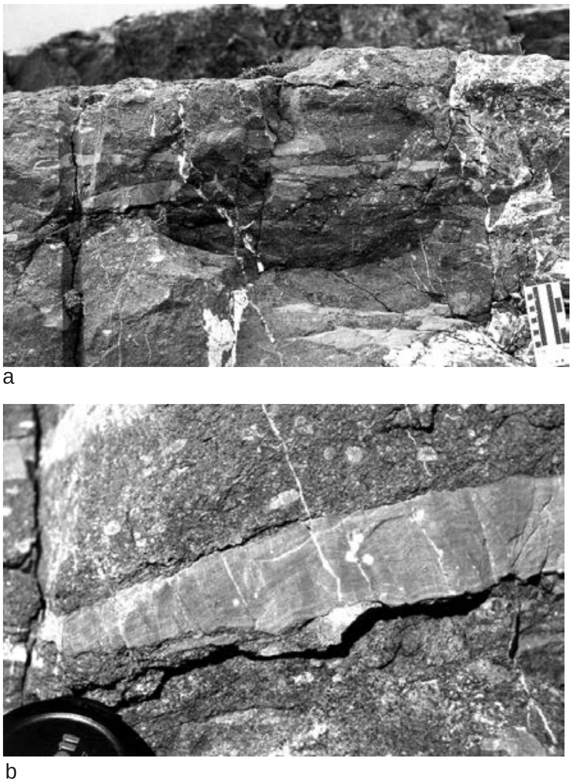


FIG. 376. Laminar stromatoporoids at Hope's Nose, Givetian, South Devon, United Kingdom. *a–b,* Growth of low profile stromatoporoids on mobile substrates made of crinoidal debris suggests a stabilizing effect provided by the stromatoporoids. The stromatoporoids probably grew in low-moderate energy conditions, because laminar forms are readily overturned by current flow (see Fig. 369); view *b* shows that themargin of stromatoporoid is modified by pressure solution, visible part of lens cap is 4 cm wide (Kershaw, 2012; for a color version, see *Treatise Online,* Number 31: paleo.ku.edu/treatiseonline).

using a spreadsheet, and an example is given below, for the marginward Peechee Member stromatoporoid assemblage collected by KOBLUK (1975), plotted on Figure 378, upper right (when viewed in a horizontal orientation).

Although H is calculated as a negative number, its sign is simply changed to positive for ease of expression. In Figure 378, the point plotted in relation to Table 32 is accompanied by text (2/76; 68%) that summarizes the data relating to that point, explained also in the key (Fig. 378, lower right when viewed in a horizontal orientation). The remainder of Figure 378 was constructed using spreadsheets, as above. Data plotted from STEARN (1975b, p. 1644) were taken from his summary. Diversity index data depend on sampling procedure, but also on quality of taxonomy; in the Högklint Formation of Gotland,

TABLE 32. Example of method of calculation of species diversity H index, used in Figure 378. The example comes from the reef marginward Peechee Member stromatoporoid sample collected by Kobluk (1975).

Species	No. of specimens	P_i	$\mathrm{Log}_e\, p_i$	$P_i\, \mathrm{Log}_e\, p_i$
1	52	0.684	–0.380	–0.2598
2	26	0.342	–1.073	–0.3669
total	76	1	–H	–0.6267
			H (rounded)	0.627

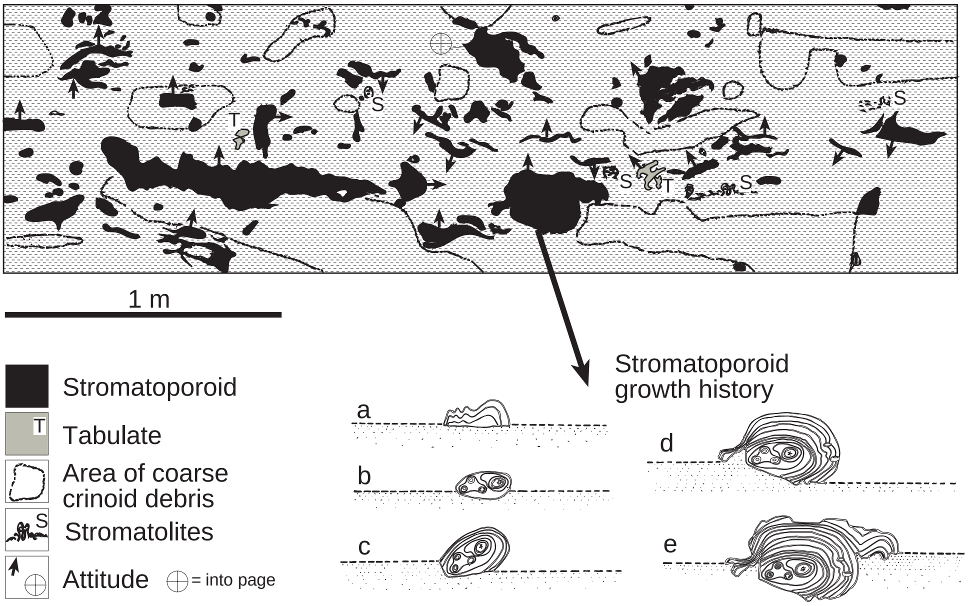


FIG. 377. Small area of vertical surface of reef, Lion Quarry, Frasnes, southern Belgium. A mixture of whole and fragmented stromatoporoids appear to occur in rhythms separated by coarser debris; stromatoporoids demonstrate growth on a probable loose substrate, with a prominent lateral growth aspect. The complex form of one specimen is interpreted as episodically reoriented in sequence *a–e.* Temporal energy reduction is indicated by occurrence of thin laminar stromatoporoids associated with microbial heads and mats. This diagram illustrates the problems of growth form classification, with some forms being more readily classifiable than others (see p. 431–461). In the *Attitude* box of legend, *into page* means that the specimen is lying on its side with its apex pointing away from the reader (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

for example, many stromatoporoids are so strongly recrystallized that they are unidentifiable (MORI, 1968), reducing the utility of the diversity index for that formation in comparison with others.

In Figure 378, only data for stromatoporoids are given, and total biotic diversity must differ from the indices, except in assemblages composed almost entirely of stromatoporoids. Such assemblages have many stromatoporoid species and thus a high diversity of stromatoporoids, but other components of such assemblages may be represented only by a few species each of tabulate and rugose corals, brachiopods, crinoids, and rarely other fossils. STEARN (1975b, p. 1637–1639) attributed progressive stromatoporoid diversity reduction at the Ancient Wall to increasing severity of the reef crest environment, as relief increased on the reef front, and the same conclusion may be drawn for data given by KOBLUK (1975) for both lagoon and reef margin communities of the Miette Complex (Fig. 378). Similarly, H, calculated for Devonian stromatoporoids of southern Belgium (CORNET, 1975), shows that large bioherm complexes sited in open water have a slightly lower stromatoporoid diversity than shelf biostromes and back-reef settings, and these biostromes are much richer in

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FIG. 378. *(Continued from facing page).*
UC(U), Lower and Upper Cairn Formation respectively; *MP* and *UP,* Middle and Upper Peechee Member, respectively; *b,* H is calculated from stromatoporoid data from named sites by Cornet (1975); *c,* MORI's (1968, 1970) data are from the range of stratigraphic units on Gotland; data from Kano (1989) and Kershaw (1990) focus on specific sites and stratigraphic units within the Gotland sequence. [1]Note that for the Gotland data set, the Högklint stromatoporoids are mostly poorly preserved and probably are underrepresented on the diagram (adapted from Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).

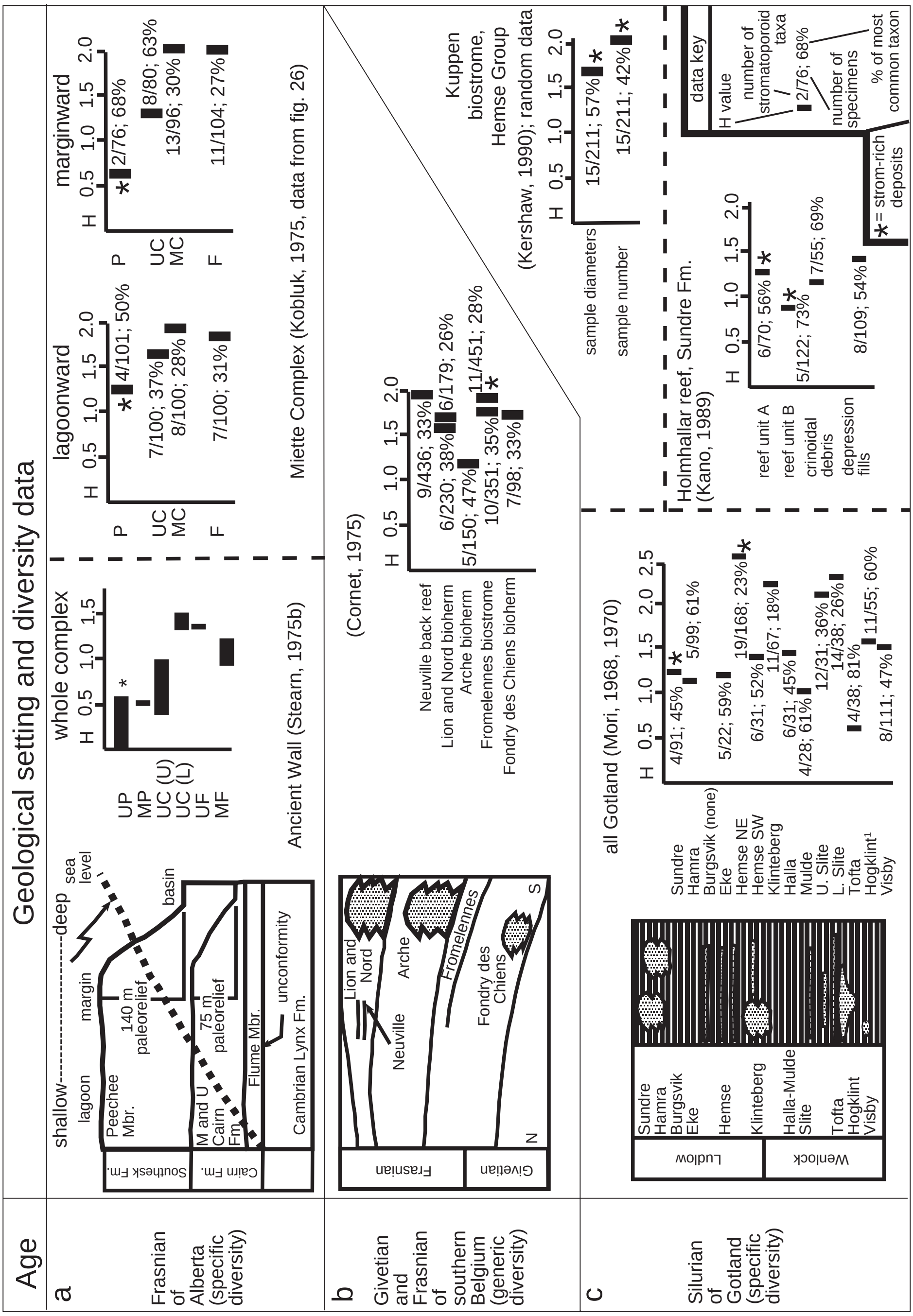


FIG. 378. Shannon-Wiener index (H) for stromatoporoid assemblages from published data for Silurian and Devonian locations. The diversity index is calculated using a combination of numbers of species and numbers of specimens of each species, as explained in the text. *a,* Data were compiled by Kershaw (1998) from the plots of Stearn (1975b, p. 1644) and information in Kobluk (1975, fig. 26)*; F,* Flume Member; *MF,* Middle Flume Member; *P,* Peechee Member; *UF,* Upper Flume Member; *UC(L)* and *(Continued on facing page).*

stromatoporoids. In Figure 378, data from Gotland (Mori, 1968, 1970) show that stratigraphic units dominated by stromatoporoid-rich platform biostromes (Slite, Klinteberg, and Hemse units) have the highest diversities of stromatoporoid faunas, while the lowest values are recorded for very shallow, high stress settings, such as the Tofta Formation (where salinity may have played a part in diversity control), and deeper muddy environments of the Mulde Formation. Kano's (1989) work on the abundant stromatoporoid faunas of the upper Ludlow Holmhällar site, Gotland (where facies are only partly exposed and the reef shape indeterminable), shows diversity differences through the reef complex. Ludlow reefs on Gotland (Fig. 379) are composed almost completely of stromatoporoids (Kershaw, 1981, 1990; Kano, 1989, 1990; Mori, 1970); although diversity of all fossil groups is low, stromatoporoid diversity is high [see Fig. 378c, from Mori's (1970) data, and see the next section on Stromatoporoid Biostromes]. Most are biostromes, implying stable conditions of low sedimentation and possible sea level still-stands (Kershaw & Keeling, 1994; Kershaw, 1994b), in contrast to bioherms (see discussion in Fig. 380). Stromatoporoid faunas mostly comprise large, low profile forms, many coalesced from smaller individuals, and emphasize the competitive advantage of a lateral growth habit, commonly seen in Ordovician to Devonian reef-builders.

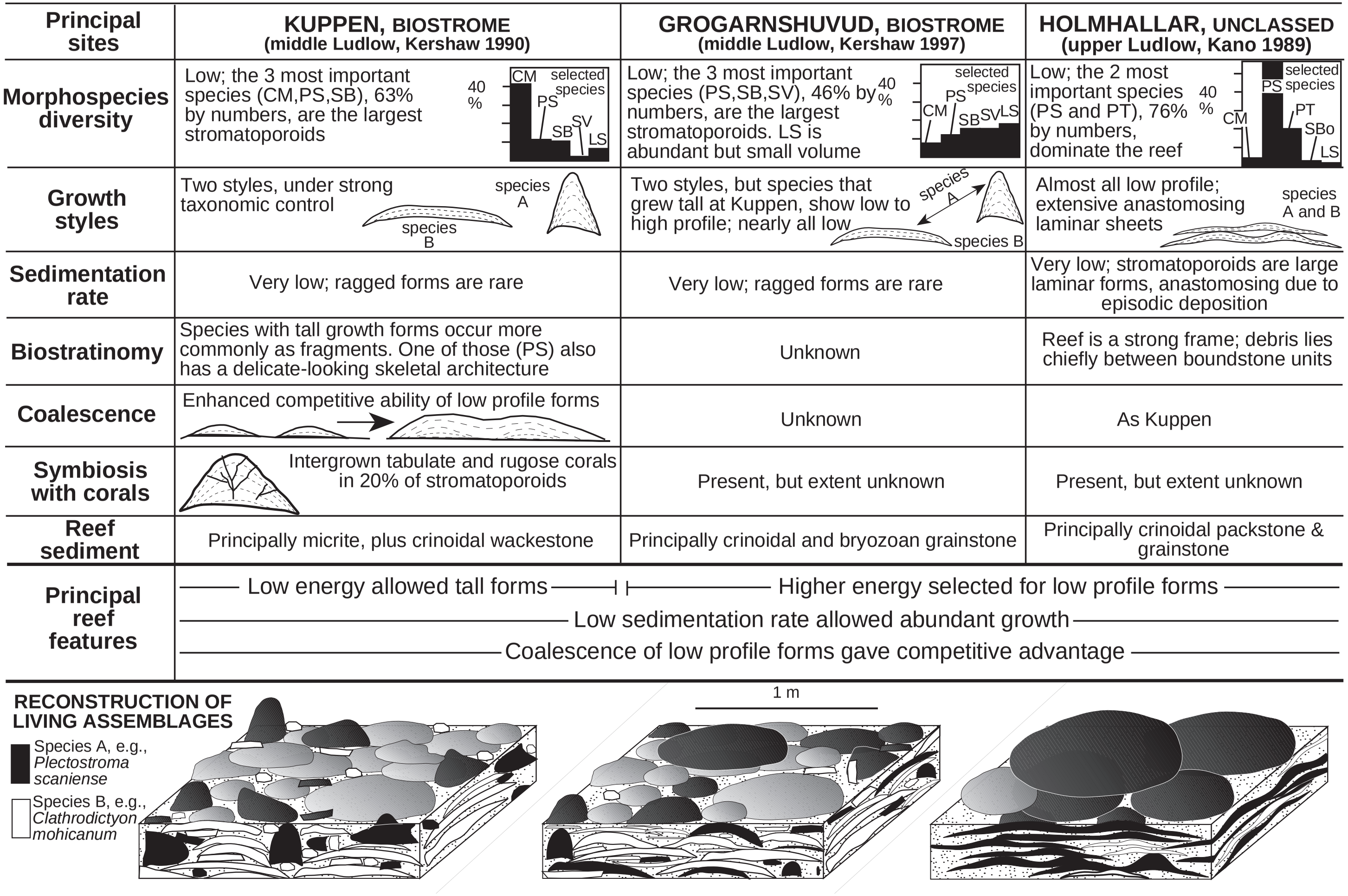
The sum of available data suggests that low stress environments (where platform biostromes were formed) were the optimum settings for stromatoporoids. In a truly random sample, collected using random numbers on a sampling grid (Kershaw, 1990), albeit time-averaged for a single biostrome, stromatoporoid size is emphasized by comparing diversity of the same samples, expressed both as numbers and size (≈basal diameter) of individuals. The use of a diversity index based on a measure of the size of specimens of each species, rather than numbers of individuals of each species, is a novel approach. H is lower for basal diameters than for numbers of specimens, emphasizing the ability of large stromatoporoids to occupy larger areas of sea floor, and suggests that the competitive ability of stromatoporoid taxa is related to the amount of sea floor they were able to occupy.

Stromatoporoid Biostromes

Dense accumulations of stromatoporoids in biostromal deposits occur in Wenlock to Devonian deposits, apparently occurring in platform interior settings. Figure 379 summarizes data from three well-exposed Silurian sites, in order to compare features of the stromatoporoid assemblages. Environmental and stromatoporoid parameters combined to produce dense accumulations of stromatoporoids with a limited range of growth forms. Sample size is, of course, important to gain an accurate picture of diversity. Using a much larger sample than that collected by Mori (1970), two examples studied by Kershaw (1990, 1997) presented in Figure 379 and expanded by Sandström and Kershaw (2008), show that the stromatoporoid assemblages of the Hemse Group biostromes are in fact widely distributed as a low-diversity accumulation, with three species being most abundant.

Work on Devonian examples described later (p. 649; Da Silva, Kershaw, & Boulvain, 2010, 2011b) also supports the need

Fig. 379. Parameters of stromatoporoid-dominated Ludlow reef communities from Gotland, Sweden, with principal reef features highlighted (see two Hemse Group biostromes and an unclassified reef from the Sundre Formation). These reef structures are ideal settings for stromatoporoids because of abundance and diversity of taxa; they formed in ramp-shelf settings. Together with many Devonian stromatoporoid-rich biostromes, they represent platform features not associated with barrier formation at platform margins; platform margin reefs are much less dominated by stromatoporoids. *CM, Clathrodictyon mohicanum*; *PS, Plectostroma scaniense*; *SB, ?Stromatopora bekkeri; SV, Stromatopora venukovi; LS, Lophiostroma schmidti*; *PT, Parallelostroma typicum, SBo, Syringostromella borealis* (Kershaw, 1998; reproduced with kind permission from the Palaeontological Association).



Principal sites	**KUPPEN,** BIOSTROME (middle Ludlow, Kershaw 1990)	**GROGARNSHUVUD,** BIOSTROME (middle Ludlow, Kershaw 1997)	**HOLMHALLAR,** UNCLASSED (upper Ludlow, Kano 1989)
Morphospecies diversity	Low; the 3 most important species (CM,PS,SB), 63% by numbers, are the largest stromatoporoids	Low; the 3 most important species (PS,SB,SV), 46% by numbers, are the largest stromatoporoids. LS is abundant but small volume	Low; the 2 most important species (PS and PT), 76% by numbers, dominate the reef
Growth styles	Two styles, under strong taxonomic control	Two styles, but species that grew tall at Kuppen, show low to high profile; nearly all low	Almost all low profile; extensive anastomosing laminar sheets
Sedimentation rate	Very low; ragged forms are rare	Very low; ragged forms are rare	Very low; stromatoporoids are large laminar forms, anastomosing due to episodic deposition
Biostratinomy	Species with tall growth forms occur more commonly as fragments. One of those (PS) also has a delicate-looking skeletal architecture	Unknown	Reef is a strong frame; debris lies chiefly between boundstone units
Coalescence	Enhanced competitive ability of low profile forms	Unknown	As Kuppen
Symbiosis with corals	Intergrown tabulate and rugose corals in 20% of stromatoporoids	Present, but extent unknown	Present, but extent unknown
Reef sediment	Principally micrite, plus crinoidal wackestone	Principally crinoidal and bryozoan grainstone	Principally crinoidal packstone & grainstone
Principal reef features	Low energy allowed tall forms	Higher energy selected for low profile forms	
	Low sedimentation rate allowed abundant growth		
	Coalescence of low profile forms gave competitive advantage		

FIG. 379. *(For explanation, see facing page).*

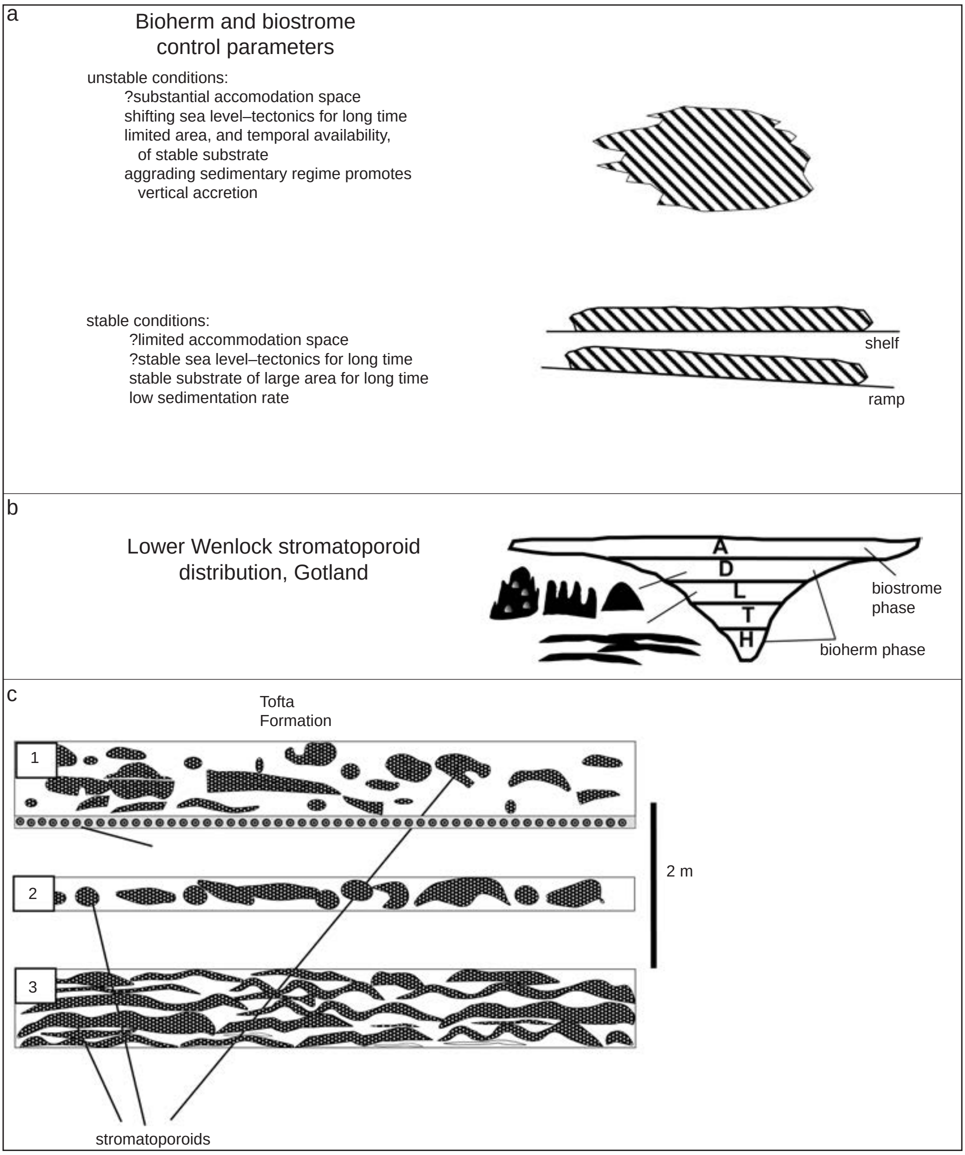


FIG. 380. Application of concepts of bioherm and biostrome in Silurian stromatoporoid reef facies. *a,* Form differences between bioherms and biostromes, demonstrating the dimensions in vertical section. Note that within these two forms, the constructing biota may consist of in-place frames, eroded debris, or a mixture of the two. Thus the biostrome and the bioherm are simply geometric objects without implication of their constructors; *b,* schematic vertical section of Högklint reef from the lower Wenlock of Gotland, Sweden, showing vertical change in form from bioherm upward into biostrome, within the same reef mass. Stromatoporoid general growth forms are added, illustrating the environmental change (relative sea-level fall) throughout the history of the reef; *H,* halysitid tabulate corals most abundant; *T,* tabulate corals of all types most abundant; *L,* laminar stromatoporoids most abundant; *D,* domical stromatoporoids most abundant; *A,* calcified algae most abundant (Kershaw, 1998; reproduced with kind permission from the Palaeontological Association); *c,* stylized examples of three biostromes from the lower Wenlock of Gotland, Sweden, showing the constructors, stromatoporoids and corals (not differentiated); *1,* contains a mixture of debris and in-place constructors; *2,* contains only debris; *3,* contains laminar-frame constructors. These illustrations demonstrate the range of constructional elements within biostromes, thereby showing that some biostromes are most appropriately classified as reefs (based on data from Kershaw, 1994b).

for large sample size in stromatoporoid studies. Biostromes are probably the richest stromatoporoid faunas, representing ideal conditions for their growth, characterized by low sedimentation rates and, presumably, widespread availability of suitable substrate.

Devonian Reef Communities and Barrier Reefs

Stromatoporoids are very abundant in Devonian reef systems, where *Amphipora* is the most abundant volumetrically (e.g., Cockbain, 1984). Although Middle Devonian reefs contain the first interpreted barriers and reef systems, and the best known of these are the occurrences in the Canning Basin (Playford & Lowry, 1966; Playford, 1980) and western Canada (e.g., Klovan, 1964; Jamieson, 1969), these mainly lack evidence of an identifiable reef core: for example, the Miette complex of Alberta (Noble, 1970, p. 540; see Fig. 378a), and the southern Belgium bioherms (Monty, Bernet-Rollande, & Maurin, 1982). Devonian reef crests typically contain relatively small numbers of stromatoporoids, with other elements, such as *Renalcis*, being equally or more important reef constructors. In the Canning Basin, the crest zone is narrow, 100–200 m wide (Wilson, 1975, p. 137), and without biozonation; whereas fore-reef slopes of up to 30° were generated by microbial constructors (Playford & Lowry, 1966, p. 71), compared to 5° slopes where reefs are not present on platform margins.

Sporadic efforts have been made using taxonomic and growth form data to apply an integrated approach to illustrate aspects of stromatoporoid community ecology (e.g., Cornet, 1975; Hoggan, 1975). Kobluk (1975) attempted a community reconstruction using crude statistical measures of association between growth forms and species, but his data did not relate species to growth forms and environments. He noted (p. 243) that some stromatoporoid morphologies occur together and others do not. Kobluk (1975, p. 259) extended life-table analysis to stromatoporoids using basal diameter as a proxy for relative age in the Devonian Miette Reef complex in Canada. Data were time-averaged within a bed, growth forms rather crudely classified, and although species/growth form data were not available, the results produced the broad conclusion that most stromatoporoids are small, with a relatively low chance of growing large. This observation is consistent with studies in other sites and ages, presumably largely attributable to fluctuating energy levels and sediment deposition rates. A feature of stromatoporoids influenced by such processes is that, as their skeletons grew, their forms commonly changed from an initial laminar shape to domical, then sometimes to bulbous, so it is important to plot growth form against size (e.g., basal diameter, see Kershaw, 1990). If this can be related to taxa, then there is a much more useful data set available for the interpretation of controls on stromatoporoid growth form, although little information is yet available.

In the most comprehensive survey so far attempted of Frasnian stromatoporoids of Belgium (Da Silva, Kershaw, & Boulvain, 2010, 2011b), the branching stromatoporoid *Stachyodes* was shown to represent approximately half of the assemblage, measured both by numbers of samples and by area of the rock occupied in vertical rock faces. Ten genera were found altogether, but only one or two genera are abundant in any one bed. These results emphasize not only the relatively low diversity of stromatoporoid assemblages, but also their importance in development of Devonian reef facies.

REGIONAL AND GLOBAL SCALE SYNECOLOGY

Stromatoporoids in Devonian Global Facies Patterns

Although reef facies may be difficult to unravel in tectonically complex terrains (Scrutton, 1977b), Devonian reefs formed mostly at platform margins (e.g., Playford, 1980, in the Canning Basin; and Scrutton, 1977a, in the United Kingdom). Significant buildups worldwide contain similar fossil assemblages (across all phyla) (e.g., Belgium, Germany [Eifel region], Alberta, Canning Basin; WILSON, 1975, p. 119). STOCK (2005) recorded provincialism of earlier Devonian stromatoporoid faunas, changing to cosmopolitanism at genus level through the Frasnian, and restriction in the Famennian. Furthermore, STOCK (2005) noted a decrease in generic diversity in the Frasnian, interpreted by him as caused by sea level rise, allowing mixing of faunas by submerging of barriers; PROSH and STEARN (1996) recognized Devonian stromatoporoid cosmopolitanism commencing earlier in the Emsian, and migration being facilitated by Early Devonian transgression across epeiric shelves. Rapid widespread migration also promotes the use of stromatoporoids as biostratigraphic tools, due to more restricted stratigraphic ranges (PROSH & STEARN, 1996), in contrast to the traditional view that stromatoporoids lack stratigraphically restricted ranges.

Stromatoporoid growth forms aid recognition of facies patterns in the Devonian Iberg reef in Germany (GISCHLER, 1995); the patterns suggest influence of southeastern trade winds and provide interpretation of the reef as an atoll. Although GISCHLER (1995, p. 185) suggested that the southeast-facing (windward) portion containing massive stromatoporoids and bulbous corals was wave-resistant, the reef rim itself is hardly preserved. Wave resistance on the constructor organisms of Devonian reefs is relatively low, so early cementation (BURCHETTE, 1981; MOUNTJOY & RIDING, 1981; WATTS, 1988b; GISCHLER, 1995) and microbial stabilization were important features. Care is therefore required in interpreting wave resistance in Devonian reef systems; the analogy between modern coral reefs and their Devonian counterparts is not reliable. KOBLUK's (1978) application of the Waltherian concept to the Miette reef near Jasper, Alberta, using statistically constrained stromatoporoid assemblages, is affected by taphonomic disturbance of the reef biota, even locally (e.g., FISCHBUCH, 1970), and reconstruction of the original assemblages is difficult.

Stromatoporoid Reefs and Sea Level Change

Stromatoporoid reefs are generally assumed to indicate shallow waters. While this is normally true for rimmed shelves and patch reef bioherms, distinguishing between ecological upward reef growth and sea level change to generate reef aggradation cannot always be achieved, and controls on biostromes remain problematic. Stromatoporoids in sequence stratigraphic analysis of Middle Devonian platform sediments of the Great Basin, United States, suggest that biostromes could grow in both transgressive and regressive settings (ELRICK, 1996, p. 403–405), which adds to the debate outlined by BRUNTON and COPPER (1994, p. 74) that reefs grow better in trangressive regimes than in regressive settings.

If stromatoporoid biostromes formed in transgressive (as well as regressive) settings, then water depth (=accommodation space), as long as sea level rise was not fast, was probably not as important as the nature of the substrate in controlling their occurrence with low sedimentation rate. Availability of suitable substrate also controlled individual stromatoporoid development, and because stromatoporoid substrate tolerance is so broad (see p. 419–480 and p. 555–567), perhaps it is not surprising that biostromes provide the richest stromatoporoid faunas. Some stromatoporoid biostromes are demonstrably shallow; two examples are: approximately 10 m water depth suggested for many European Devonian examples (BURCHETTE, 1981, p. 119); and 10–30 m water depth for upper Llandovery of Michigan (JOHNSON & MCKERROW, 1991, p. 156) and the Upper Ordovician of southern China (JOHNSON, RONG, & FOX, 1989, p. 47). In contrast, coral-dominated Silurian biostromes form in deeper water, prior to shallowing

(Desrochers & Bourque, 1989), and stromatoporoids and corals aided stabilization of steep off-reef slopes in lower Silurian biostromes of Greenland during pauses in subsidence (Sønderholm & Harland, 1989, p. 361–365), further illustrating that conditions of stability favored biostromal growth. Nestor (1995) also noted that stable environments promoted development of flattened lenticular bioherms and biostromes in the Silurian of Baltica, as in Devonian biostromes in Belgium (Tsien, 1974). There is much work to do here, because although some reefs apparently formed in regressive settings, others present conflicting data. Middle Ludlow biostromes of southeastern Gotland have been regarded as exhibiting shallow water characteristics (low mud, abundant grainstones, abundant syntaxial cement on crinoid grains, eroded biostrome tops, stacked rocky shorelines; Keeling & Kershaw, 1994; Kershaw & Keeling, 1994). However, these biostromes contain almost no algae, otherwise common in shallow Silurian facies; that they may have grown in deepening water on flooding surfaces and acquired their shallow water features during later regression is supported by the recognition of an oceanic S-state during this interval (Jeppsson, 1990; Jeppsson, Aldridge, & Dorning, 1995), one feature of which is slightly higher sea level. Clearly, no reliance can be placed on biostromes as general indicators of regressive systems. Whether stromatoporoid-rich deposits can be related to suggestions of orbitally forced sea level change for the Givetian and Frasnian (e.g., Marshall, Rogers, & Whiteley, 1996, p. 461) is another topic requiring further study.

CONCLUSIONS

Though stromatoporoids have complex paleoecological aspects, they are valuable tools in paleoenvironmental interpretation, at various scales. There is much more detailed work required to fully realize their potential, but the information presented here should provide a basis for investigators to apply stromatoporoids in their analyses of paleoenvironments.

ACKNOWLEDGMENTS

Steve Kershaw's work on stromatoporoids began under supervision from Robert Riding. Discussions on various aspects of calcified sponge paleobiology and their facies, with Ron West (Manhattan, Kansas), Colin Stearn (Montreal), Lennart Jeppsson (Lund), Mike Keeling (ex-Brunel), Frank Brunton (Kingston, Ontario), and Barry Webby (Macquarie, NSW) have substantially enhanced ideas presented here. Field work on Gotland was facilitated by the Allekvia Field centre, now sadly closed, and its administrators at Lund University are warmly thanked.

PALEOBIOGEOGRAPHY OF THE PALEOZOIC STROMATOPOROIDEA

CARL W. STOCK, HELDUR NESTOR, and B. D. WEBBY

INTRODUCTION

Data points on the accompanying maps represent occurrences of stromatoporoids as best determined by the authors. We used simplified versions of the base maps of GOLONKA (2002) for plotting the data. One point may represent several localities in one larger area (e.g., Frasnian of Alberta) and may represent several different stratigraphic levels in one area (e.g., within Frasnian of Iowa). Most points represent faunas that have been described in the literature, but a few others are superficial reports of stromatoporoid occurrences or unpublished records known to one of the authors. The exact location of some data points has been easy to determine (e.g., Michigan), whereas others have proved problematic using the Golonka base maps (e.g., Ulachan–Sis Range; Donets Basin). We relied heavily on the work of STEARN and others (1999) to determine which genera are present at each data point, but where the responsible author had more detailed and/or up-to-date information, that information was employed. Great significance should not be paid to small latitudinal changes in geographic ranges between adjacent stages and ages, as they may result from different placement of symbols within the same geographic locality.

Stromatoporoids lived in shallow, tropical to subtropical seas; thus, the extent of their geographic distribution through time can be viewed in terms of distance from the equator. The obvious interpretation would be that the warmer the Earth, the larger the latitudinal range of stromatoporoids; however, some exceptions to this generalization have been observed.

On continental portions of tectonic plates, as eustatic sea level rose, epeiric seas formed in low-lying areas, providing new, more extended regions for stromatoporoid habitation. Increases in eustatic sea level result from the melting of glacial ice as a byproduct of global warming, and/or from an increase in the rate of seafloor spreading, which raises the level of the seafloor, causing seawater to spill onto low-lying parts of continents (e.g., LIEBERMAN, 2000, p. 86).

There is no uniform agreement among biogeographers where it comes to the delineation of synchronous areas containing different assemblages of taxa, known as biogeographic units (CECCA, 2002, p. 81). Among paleontologists, KAUFFMAN (1973), working with Cretaceous bivalves, determined that a realm is a biogeographic unit containing more than 75% endemic taxa (i.e., at least 75% of the genera present are found in no other realm), an approach accepted in theory by BOUCOT (1975) for Paleozoic brachiopods. OLIVER (1977) found percentages of endemism for rugose coral genera in the Early and Middle Devonian ranged from 33% in the Siegenian (Pragian) to 92% in the late Emsian. Similar data are presented here, because it is at the level of genus that the group is most clearly defined and characterized, thanks in part to the recent work of STEARN and others (1999) and herein (Labechiida, p. 709–754; Clathrodictyida, p. 755–768; Actinostromatida, p. 769–779;

Stromatoporellida, Stromatoporida, Syringostromatida, Amphiporida, and Genera With Uncertain Affinities, p. 781–836).

ORDOVICIAN

B. D. Webby

A number of reviews of global and regional aspects of Ordovician stromatoporoid biogeography have been presented by Webby (1980, 1992; in Webby & others, 2000) and by Lin and Webby (1989), and see Webby in Nestor and Webby (2013). Also Bogoyavlenskaya and Lobanov (1990), Bogoyavlenskaya (2001a), and Bogoyavlenskaya and Yelkin (2006) have discussed various biogeographic relationships during the initial global spread of Ordovician stromatoporoids. In most cases, these studies have been hampered by the lack of a well-constrained, unified timescale to establish close ties for precisely correlating the stromatoporoid-bearing assemblages, especially on a global basis. Only now, with the more reliable and well-calibrated, internationally based, Ordovician stratigraphic framework and time scale (Sadler & Cooper, 2004; Webby, Cooper, & others, 2004), can more reliable age determinations of assemblages be made across different regions and paleolatitudes of the globe.

In the 1980 survey of the distribution of Ordovician stromatoporoids, Webby argued that: (1) the earliest known stromatoporoids (labechiids) appeared in the Chazy Group successions of eastern North America (Kapp & Stearn, 1975), and in near-age equivalents of Tasmania and Scotland (Webby, 1977, 1979b), with a comparatively low-diversity assemblage (up to five genera) during the upper Llanvirn–Llandeilo interval, now recognized as representing the middle to latter part of the Darriwilian age (=late Middle Ordovician); (2) the main diversification occurred a little later, during the early Caradoc or early part of Sandbian age (=early Late Ordovician), with a tripling of the generic diversity, and establishment of a separate northern China province marked by first appearances of four endemic genera (*Lophiostroma, Aulacera, Ludictyon, Sinodictyon*); (3) in the middle Caradoc to early Ashgill (=late Sandbian to middle Katian ages), the first clathrodictyid stromatoporoids (and the first cliefdenellid sphinctozoan sponges) appeared in Australian and Eurasian sequences, forming apparently a separate provincial element; and (4) during the middle–late Ashgill (middle Katian to Hirnantian, or latest Ordovician) the development of single, more cosmopolitan, mixed, American–Eurasian assemblage developed, as the labechiids declined, though the cylindrical *Aulacera* and the clathrodictyids remained important. This succession of events now needs revision in terms of the more precise stage-level correlations (see below).

The review of Ordovician stromatoporoid and coral assemblages presented by Webby (1992) revealed a markedly different global biogeographic pattern based on the 22 known stromatoporoid, 120 tabulate, and 67 rugose coral genera. The focus was mainly on the more diverse assemblages, through what is now regarded as most of Late Ordovician time (a period of about 15 myr), because there was a marked lack of precision in establishing stage-level correlations. If smaller time intervals had been used, it is probable that samples from some regions would not have been large enough to provide meaningful results. On the other hand, by taking a larger interval, some degree of masking of biogeographic relationships was inevitable, especially where lithospheric plates moved significant distances across paleolatitudes during the Late Ordovician, and/or where major global cooling and warming events were taking place, as within the interval of the end-Ordovician glaciation (Webby, 1984a). Nevertheless, a broad, twofold, biogeographic subdivision of assemblages was recognized, with the stromatoporoids associated with compound rugose and tabulate corals of the North American–Siberian

Realm having an essentially broad, bandlike, paleoequatorial spread. The other, more restricted, southern, intermediate paleolatitude association included corals (solitary rugosans and some halysitine and heliolitine tabulate corals), but no accompanying stromatoporoids. This latter association represents the cooler, more temperate Euroasiatic Realm. The North American–Siberian Realm has a wide, circumglobal spread, equatorally extending to about 30° N and S of the paleoequator, remaining within the influence of warm equatorial currents. In most places, the typical stromatoporoid-compound rugose coral and *Tetradium* coral biofacies of the North American–Siberian Realm were considered to be associated with warm tropical waters of normal salinity, but in a few places, evaporites may also occur in association with this biofacies. Additionally, the assemblages of stromatoporoids and corals contributed to the development of frame-building Mid–Late Ordovician reefs, and their distribution has been shown to exhibit a direct relationship to paleomagnetically determined low paleolatitudes, with stromatoporoid growth usually extending to about 30° N and S of the paleoequator (Webby, 1980, 1984a, 2002).

Other studies have been more regionally focused. For example, Bol'shakova and Ulitina (1985) depicted the distribution and provincial relationships of Late Ordovician (Ashgill) stromatoporoids in three different tectonic belts of Outer Mongolia, and Lin and Webby (1989) compared the Australian and Chinese Ordovician stromatoporoid and coral distributions in terms of their biogeographic significance. The stromatoporoids were also employed as just one component in a comprehensive biogeographic analysis of the whole described Australasian Ordovician biota (as part of a survey by a team of experts involving 17 fossil groups), to assess relationships with provincially significant biotas of equatorial Gondwanan and other adjoining regions, set in the context of available paleogeographic reconstructions, based on paleomagnetic data and tectonic considerations, such as known data about plate margins and the differentiation of discrete terranes (Webby & others, 2000).

A comparative survey between the Australian and Chinese stromatoporoid faunas by Lin and Webby (1989) was also undertaken, showing that the earliest (Llanvirn to lower Caradoc, i.e., upper Darriwilian to Sandbian) Chinese assemblages differed markedly from counterparts in eastern Australia. However, this particular comparison has proven, with recent application of the more reliable, internationally based, stratigraphic framework, to be not entirely valid, because the respective successions were of different ages. Higher in the respective successions, the ages were correctly determined (mid-Caradoc–Ashgill, i.e., mainly Katian), and the Australian (especially the New South Wales island-arc occurrences) and Chinese stromatoporoid taxa exhibit remarkably similar biogeographic relationships, even down to species level. For example, *Rosenella woyuense, Labechiella regularis,* and *Pseudostylodictyon poshanense* are northern Chinese (and Kazakhstani) provincial elements that also occur in the lower Eastonian (=lower Katian) successions of New South Wales. In addition, northwestern Chinese (and southwestern Siberian–Altai–Shoria Mt. regions) have the distinctive species *Ecclimadictyon amzassensis* (now assigned to genus *Camptodictyon* Nestor, Copper, & Stock, 2010, p. 84) and *Labechiella variabilis* that are also represented in the middle–upper Eastonian (=mid-Katian) sequences of New South Wales. On the other hand, the correlative Tasmania Shelf successions have members of the genera *Thamnobeatricea, Pachystylostroma,* and *Aulacera* that suggest closer biogeographic ties with North America (Laurentia).

Later, Webby (in Webby & others, 2000, p. 69–70), in outlining again the biogeographic affinities of Australian Ordovician stromatoporoids, concluded that the assemblages in the New South Wales island-arc complexes consistently had closest affinities with associations in southeastern Asia and China, excluding most of the South China Platform, whereas the Tasmanian Shelf faunas seemed to develop rather mixed provincial relationships, dominantly Asian, except for two separate intervals: first in the Gisbornian (early Sandbian) and second during the late Eastonian (mid-Katian), when distinctive invasions of Laurentian stocks occurred.

Bogoyavlenskaya and Lobanov (1990) supported the view that the earliest labechiid assemblages appeared in the Chayzan (late Darriwilian–early Sandbian) reefal complexes of eastern North America (Kapp & Stearn, 1975), and that the early dispersal of stocks from eastern North America (Laurentia) may have extended more widely than previously thought, not only across the Iapetus Ocean, but well beyond, to the basins of the Uralian and Mongolian fold belts across Asia (Bogoyavlenskaya & Lobanov, 1990, fig. 6). They reported occurrences of the Chazy-type labechiid, *Pseudostylodictyon kayi,* in the Garevska Formation of the western slopes of the Urals, and a similar form from north of the Betpak-Dala desert region of Kazakhstan, which greatly extends the range of this species into Asia. However, there were equally significant early diversification centers for labechiid stromatoporoids, such as northern China (and perhaps Siberia), and these may have been even more important in providing early stocks that were capable of migrating into other parts of Asia (see discussion on p. 582–583).

Bogoyavlenskaya (2001a) also provided a generalized outline of the global spread of Ordovician stromatoporoids within a broadly based framework of three biogeographic divisions: a North Atlantic belt for the faunas distributed across North America and Europe; the Ural-Mongolian belt across Middle Asia; and a Pacific belt, encompassing the faunal assemblages of China and Australia. In addition, Bogoyavlenskaya and Yelkin (2006, p. 190, fig. 4) proposed the southern part of the Siberian platform as a center of origin for the stromatoporoids and showed in a world map how they inferred the early (Mid-Ordovician) stocks may have dispersed globally from the Siberian so-called center to the main regions of: (1) North America and Western Europe; (2) Eastern Europe (Russian platform); (3) China-Kazakhstan; and (4) Australia. An attempt was also made to recognize new endemic and relict endemic elements of the faunas and to differentiate more cosmopolitan and more regional components of the faunas. However, these surveys employed poorly constrained stratigraphic frameworks and made little effort to take account of contemporary plate tectonic approaches or the different available paleogeographic reconstructions that combine paleomagnetic and faunal data.

In the present review of the distribution of Ordovician stromatoporoids, the occurrences are plotted on a simplified plate tectonic base map for the late Middle to Late Ordovician (between 464 and 443 myr) produced by Golonka (2002, see fig. 7), following the approach adopted by all authors of this biogeography section. However, it is important to note that a part of the Ordovician map reconstruction covering the area of the northern China Block (extending from Inner Mongolia to Korea) shows a questionable paleoposition. Webby (2002), in a global survey of Ordovician reefs, demonstrated that the Late Ordovician stromatoporoid and coral reefs on the platform margins of northern China (region of Ordos Basin in Shaanxi and Inner Mongolia), occupied an anomalously high paleolatitude (42° N), and this may have implications also for the positioning of East Gondwana (see discussion below). In commenting on the global spread of reefs during the late Mid–Late Ordovician, Kiessling (2002, p. 636) calculated the tropical spread as being between 34° S and 25° N, though he acknowledged that the paleopositions for northern China and (Outer) Mongolia (Amuria), where rich

Table 33. Geographical distribution of stromatoporoid (labechiid only) assemblages in the Darriwilian Stage (Middle Ordovician). The seven middle Darriwilian–upper Darriwilian sites are represented in Figure 381 by *black circles* (numbered as indicated here); †genera that were the only forms that apparently did not survive into the Late Ordovician (Stock, Nestor, & Webby, 2012).

Genera (Labechiida)	Vermont, New York 4	Slopes of W. Urals 14	Siberian Platform 16	Kazakhstan 19	Malaysia: Langkawi Is. 24	Korean Peninsula 25	N. China: Anhui-Liaoning 26
Rosenella					+		+
Cystostroma	+				+?		
Pseudostylodictyon	+	+		+			+
Priscastroma†			+				
Labechia	+				+?		+
Labechiella					+	+	+
Pachystylostroma	+						
Aulacera							+
Ludictyon							+
Sinodictyon†							+
Thamnobeatricea							+
Lophiostroma							+

Ashgill coral and stromatoporoid associations and local reefs occur (Bol'shakova & Ulitina, 1985), were anomalous. Overall, the spread of Ordovician stromatoporoids has been found to be within limits of near 30° N and S of the paleoequator (Webby, 1980). Kiessling (2001a) recognized the tropical reef zone as significantly narrower during the Ordovician than in the Silurian and Devonian. However, Kiessling's (2002, p. 636) data indicate rather conflictingly that the late Middle to Late Ordovician reefs spread across 59° of paleolatitude, whereas the spread during the Llandovery was 55° of paleolatitude, so the main expansion of tropical reefs was actually from the Wenlock onward, not starting immediately after the end of the Ordovician.

Whereas Golonka (2002) has shown northern China attached to the northeastern margins of East Gondwana during the Ordovician, and it probably remained more or less in contact with Gondwana until it rifted away in the latest Devonian, the Li and Powell (2001) and Cocks and Torsvik (2002) reconstructions represented northern China as a discrete offshore terrane during the Late Ordovician (not a part of East Gondwana). Li and Powell (2001) regarded northern China as being peri-Gondwanan, and between 20° and 30° N paleolatitude, whereas Cocks and Torsvik (2002) considered the terrane as being more isolated, near the paleoequator, becoming a part of the peri-Gondwanan collage of terranes during only the latest Ordovician. Both of these latter reconstructions, and the latest published global maps of Torsvik and Cocks (2013a, fig. 12, and 2013b, fig. 2.12, 2.14, 2.15), which show representations of north China, south China, and Tarim as discrete, peri-Gondwanan island-type continental blocks that occupy positions in low paleolatitudes, even straddling the paleoequator, rather than having a close association with Gondwana. Perhaps it is also significant that these offshore, paleoequatorial, peri-Gondwanan sites exhibit somewhat more diversified Middle–Late Ordovician stromatoporoid faunas.

The geographical distribution of the Ordovician stromatoporoid genera is compiled in three tables, representing the late Middle Ordovician (mid–late Darriwilian) associations (Table 33), the early Late Ordovician (Sandbian) assemblages (Table 34), and the latest Late Ordovician (Katian and

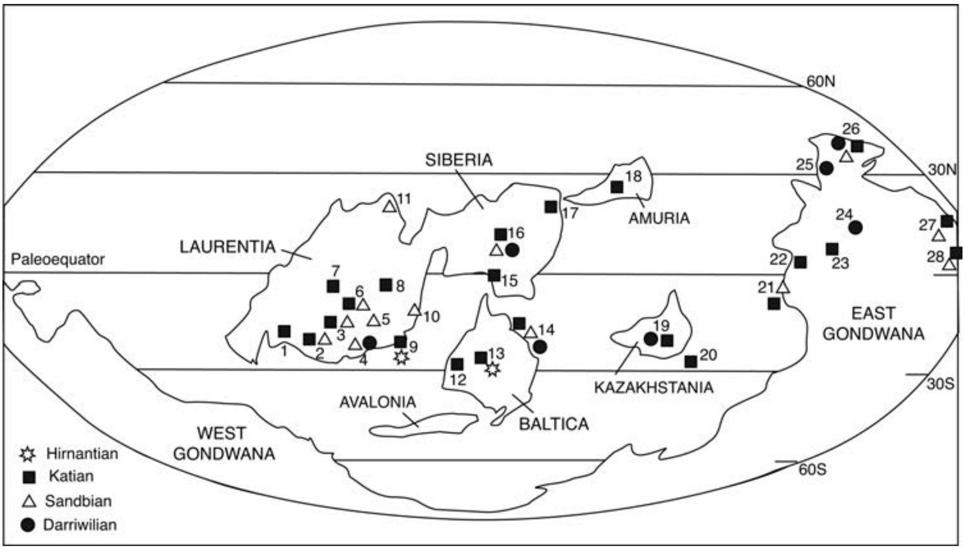


FIG. 381. Ordovician paleobiogeographic map based on GOLONKA's (2002) reconstruction showing the distribution of Middle Ordovician–Upper Ordovician stromatoporoid assemblages. Note the clustering of Ordovician sites in low paleolatitudes, mainly between 30° N and S. Nevertheless, GOLONKA's "East Gondwana" is not likely to have been part of such a large, undivided block through Ordovician time, given that some parts, such as North China, South China, and Tarim, now seem to be confirmed (e.g., TORSVIK & COCKS, 2013) as remaining discrete, peri-Gondwanan blocks throughout this time interval. Key to symbols: *black circles,* mid–late Darriwilian; *open triangles,* Sandbian; *black squares,* Katian; *open, seven-pointed stars,* Hirnantian; localities: *1,* Texas and New Mexico; *2,* Alabama, Kentucky, and Tennessee; *3,* Ohio, Indiana, Iowa, and Michigan; *4,* Vermont, New York, and Pennsylvania; *5,* southern Quebec; *6,* southern Ontario; *7,* Manitoba; *8,* islands of northern Hudson Bay and Ungava Bay; *9,* Anticosti Island; *10,* Scotland; *11,* Chukchi Peninsula; *12,* southern Norway; *13,* Estonia; *14,* western slopes of Urals; *15,* Taimyr Peninsula; *16,* Siberian Platform; *17,* Altai-Sayan region; *18,* Tuva and Mongolia; *19,* Kazakhstan; *20,* Central Asia; *21,* Tarim (Xinjiang); *22,* Qinghai (northwestern China); *23,* Zhejiang and Jiangxi (southeastern China); *24,* Langkawi Island (Malaysia); *25,* Korean Peninsula; *26,* Anhui, Liaoning, Hebei, and Shaanxi (northern China); *27,* central New South Wales (Australia); *28,* Tasmania (Stock, Nestor, & Webby, 2012).

Hirnantian) associations (Table 35). The distribution of the stromatoporoid localities is plotted on the simplified base map (Fig. 381).

MIDDLE DARRIWILIAN–LATE DARRIWILIAN

All available evidence points to the earliest stromatoporoids (the labechiids) appearing rather suddenly in association with a significant metazoan biodiversification event in low paleolatitudes. This event produced many new community assemblages, best characterized by the Chazy-type reefs of eastern North America, on the Laurentian Platform (PITCHER, 1971; KAPP, 1974, 1975; WEBBY, 2002, p. 145, fig. 6). The labechiids are first recorded from seven main sites worldwide (numbered: 4, 14, 16, 19, 24, 25, and 26 [Table 33]), involving the differentiation of five of the seven known families of labechiids and containing more than half of the known genera (WEBBY, 2004b; and see Early Evolution of Ordovician Paleozoic Stromatoporoidea, p. 575–589).

Stromatoporoids are most common in the Crown Point Formation of the Lake Champlain area of New York and Vermont, where four labechiid genera are known. They occur as large, isolated, meter-size, skeletal masses of variable growth form, like microatolls (KAPP, 1974) or may develop in prominent, frame-building roles of the Chazy-type reefs (Pitcher, 1964; Kapp, 1975). *Pseudostylodictyon* (*P. lamottense*) appeared in the Day Point Formation and is therefore the earliest stromatoporoid to be seen in North American successions (Kapp & Stean, 1975). Its ancestors were thought by Kapp and Stearn to be derived from an encrusting sponge that began to precipitate a carbonate (aragonite) skeleton, probably earlier in the Middle Ordovician. Species of *Labechia* and *Pachystylostroma* in succeeding beds of the Crown Point Formation apparently evolved from this *Pseudostylodictyon* stock (Kapp & Stearn, 1975). *Pachystylostroma* was initially an endemic genus. The genus *Cystostroma* has also been recorded from the Crown Point succession (Galloway & St. Jean, 1961), in the same area. All these stromatoporoid diversification and reef-building events occurred in on-shelf sites, in warm, shallow, subtidal seas of the Laurentian Platform (Webby, 2002).

The most diverse associations of early labechiids are recorded from a number of localities of the widely distributed, moderately thick (up to 270 m) sequence of massively bedded limestones (in places mottled and dolomitic) of the Machiakou Formation on the North China Platform (extending to parts of Anhui, Shandong, Shaanxi, Hebei, Liaoning, and Jilin provinces). None of the rich stromatoporoid collections from the Machiakou Formation have been precisely located in respective sequences, so it is not yet possible to establish a meaningful faunal succession or understanding of evolutionary relationships based on first appearances within the respective successions. However, it is likely that most of them come from the upper parts of the respective Machiakou sequences, correlating with middle Darriwilian–late Darriwilian. A total of nine labechiid genera have been recorded from the region, and they all appear to have evolved in on-shelf, warm, shallow, subtidal locations of the North China Platform. A few genera have localized distributions, such as *Pseudostylodictyon* and *Lophiostroma* from Shandong (Yabe & Sugiyama, 1930; Ozaki, 1938), *Sinodictyon* from Liaoning (Yabe & Sugiyama, 1930), and *Thamnobeatricea* from Anhui (Dong, 1982), whereas *Rosenella, Aulacera,* and *Ludictyon* occur in both Shandong and Anhui (Ozaki, 1938; Dong, 1982). The genera *Labechiella* and *Labechia* have the widest distribution across northeastern China (Liaoning, Shandong, Anhui, Shaanxi). All these genera, with the exception of *Pseudostylodictyon* and *Labechia,* were initially endemic to the northern China region. The previous recognition of this assemblage as a separate northern China province (Webby, 1980) is probably no longer justified, given that, with improved assessments of age, the marked northern Chinese diversification can be more confidently recognized as commencing, like the first appearances of the less diverse Laurentian Chazy assemblages, at the very beginning of the record of skeletonized labechiid faunas.

The Korean Peninsula is recognized in the Middle Ordovician as being a part of the North China Block, and it includes stromatoporoid-bearing sequences (Fig. 381, site no. 25). *Labechiella* has been recorded from both North and South Korea (Yabe & Sugiyama, 1930; Kano & others, 1994; Kano & Lee, 1997). The South Korean material comes from the Yeongheung Formation of the Yeongweol area and is of mid-Darriwilian age (Kano & others, 1994; Choi & Lee, 1998). These latter sequences probably accumulated in more open marine platform conditions than those with the more diverse faunas in northern China.

Labechiids from the Langkawi Islands of Malaysia (Webby, Wyatt, & Burrett, 1985) are associated with Unit J of the lower Setul Limestone, a succession now renamed the Kaki Bukit Limestone Formation (Cocks, Fortey, & Lee, 2005). The assemblage of four stromatoporoid genera (Fig. 381, site no. 24) were earlier suggested to have a pre-Chazyan Whiterockian age (Wongwanich & others, 1983; Stait & Burrett, 1984). However, more complete correlation

TABLE 34. Geological distribution of stromatoporoid (labechiid only) assemblages in the Sandbian stage (Upper Ordovician). The 13 Sandbian-age sites are represented by *open triangles* in Figure 381; *genera that made their first appearances in the Sandbian (Stock, Nestor, & Webby, 2012).

Genera (Labechiida)	Alabama, Kentucky, Tennessee, Pennsylvania 2	Ohio, Indiana, Iowa, Michigan 3	Vermont, New York, Pennsylvania 4	Southern Quebec 5	Southern Ontario 6	Girvan, Scotland 10
Rosenella			+	+		
Cystostroma	+			+?		
Pseudostylodictyon						
Labechia	+			+	+	+
Labechiella						
**Stratodictyon*			+			
**Stromatocerium*	+	+	+	+	+	
**Cystistroma*	+	+	+	+	+	
Pachystylostroma					+	
**Stylostroma*						
Aulacera			+	+		
**Cryptophragmus*	+	+	+	+	+	
Thamnobeatricea			+	+	+	
**Dermatostroma*					+	

of the Langkawi Ordovician sequence, as presented by LAURIE and BURRETT (1992), indicates that Unit J is more likely Darriwilian in age, though possibly not latest Darriwilian. Consequently, these stromatoporoid ranges coincide closely with the range of occurrences from northern China. From a biogeographic standpoint, the Langkawi assemblage is associated with the Sibumasu terrane, according to COCKS, FORTEY, and LEE (2005, p. 715), either as a part of the peri-Gondwanan collage of small terranes, close to East Gondwana, or it was separated by a larger ocean from Gondwana. The similarities between the northern China and Sibumasu stromatoporoid assemblages suggest close late Mid-Ordovician biogeographic links, with occupation of rather similar low paleolatitudes in shallow, subtidal, warm-water seas.

Three other middle Darriwilian–late Darriwilian sites have been recorded in Eurasia (Table 33), each represented by one labechiid genus. The first is site no. 14, with the occurrence of *Pseudostylodictyon* from the Garevka Formation of the western slopes of the Urals (BOGOYAVLENSKAYA & LOBANOV, 1990; KHROMYKH, 1999b, table 1). It probably comes from a position on the margins of the Baltica (eastern European) paleocontinent (COCKS & FORTEY, 1998, fig. 1). A similar occurrence of *Pseudostylodictyon* is recorded from a second site (no. 19) by BOGOYAVLENSKAYA and LOBANOV (1990), from a similar stratigraphic level in the northern Betpak–Dala desert region of Kazakhstan. This site is another along the line of interconnected basins of the Uralian–Mongolian belt across Asia (BOGOYAVLENSKAYA & LOBANOV, 1990, p. 83, fig. 6). The third site (no. 16) is from the Moiero River basin section of the Siberian Platform and represents the first appearance of a labechiid, the genus *Priscastroma*, with basically very simple cystose elements (KHROMYKH, 1999a, 1999b). The age relationships of this occurrence are clearly established within the upper Kochakan Formation (Muktei horizon), which correlates with the middle–upper part of the Darriwilian stage (WEBBY, COOPER, & others, 2004; see also p. 575–592). According to FORTEY and COCKS (2003), the Siberian paleocontinent remained in a low-latitude, tropical position, lying astride the paleoequator during Mid-Ordovician time (COCKS & TORSVIK, 2002; FORTEY & COCKS, 2003).

TABLE 34 (*continued from facing page*).

Genera (Labechiida)	Russia: Chukchi Peninsula 11	Slopes of western Urals 14	Siberian Platform 16	Tarim: southern Xinjiang 21	Northern China: Hebei 26	Macquarie Arc: New South Wales 27	Tasmanian Shelf 28
Rosenella							
Cystostroma		+	+	+?			
Pseudostylodictyon	+						
Labechia	+			+	+	+	+
Labechiella				+	+	+	
**Stratodictyon*						+	+
**Stromatocerium*	+		+		+		+
**Cystistroma*							
Pachystylostroma				+			
**Stylostroma*				+			
Aulacera							
**Cryptophragmus*							
Thamnobeatricea							
**Dermatostroma*							

The earliest stromatoporoids were exclusively labechiids and achieved a circum-paleoequatorial distribution during the mid–late Darriwilian. Within the present resolution of dating of the various successions, it is not possible to say that any one region evolved its skeletonized faunas earlier than another. The northern China faunas were the most diverse and endemic, but this region did not necessarily act as a center of origin for the rest. It seems more likely that a simple, noncalcifying, wide-ranging, root stock existed earlier in the warm, shallow, circumpaleoequatorial seas and provided the sources for the development of mineralized skeletons of a number of different morphologies in at least three main regions–northern China, Laurentia, and Siberia (see further discussion on p. 575–589). *Pseudostylodictyon* appears to represent the most basic skeletonized genus, both in Laurentia and northern China, and may be ancestral to a number of lines of descent in the two regions: for example, leading to *Pachystylostroma* and *Labechia* in Laurentia, and to *Rosenella*, the cylindrical forms (*Thamnobeatricea, Ludictyon, Sinodictyon,* and *Aulacera*), and perhaps even to *Labechiella* and *Lophiostroma* in northern China.

SANDBIAN

The stromatoporoid assemblages of the Sandbian Stage (=lower–midddle Caradoc) were entirely labechiids, and they were associated with a second, less intense, diversification that spread more widely across low paleolatitudes (WEBBY, 2004b). The global distribution of Sandbian genera is shown in Table 34. A number of regions show labechiid faunas for the first time, such as Scotland, Chukchi Peninsula (northeastern Russia), Xinjiang (northwestern China), and eastern Australia (New South Wales, Tasmania). A sixth labechiid family, the Stromatoceriidae, appeared in addition to the continued representation of the five families that had evolved previously in the Darriwilian. A number of genera, the labechiid *Stratodictyon*, stromatocerids *Stromatocerium, Cystistroma*, stylostromatid *Stylostroma*, aulaceratid *Cryptophragmus,* and lophiostromatid *Dermatostroma* made their first appearances during this interval. No clearly recognizable provincialism existed during the interval. Some genera that previously existed as endemics in northern China made their first appearances in Laurentia. Overall, the most diverse assemblages are recorded from sites in Laurentia. Only a few genera are recognized as endemic during the Sandbian interval: *Cryptophragmus, Dermatostroma,* and *Cystistroma,* in eastern Laurentia; and *Stylostroma* in Tarim (northwestern China).

In the north-central Appalachians (Pennsylvanian, New York, Vermont; site no. 4; Table 34 and Fig. 381), a localized, early Sandbian appearance of genus *Stratodictyon* (*S. valcourensis*) is recorded (KAPP & STEARN, 1975) from the uppermost part of the Chazy succession (Valcour Formation), and then, elsewhere in the region, other genera (*Rosenella*, *Stromatocerium, Cystistroma, Cryptophragmus, Thamnobeatricea,* and *Aulacera*) appear in the succeeding Black River Group beds—part of the Turinian stage (lower Mohawkian Series) of the North American Middle Ordovician; now recognized as equivalent to the lower part of the internationally ratified Upper Ordovician series (see WEBBY, COOPER, & others, 2004). The genera *Stromatocerium, Cystistroma,* and *Cryptophragmus* are the most widely distributed forms across the on-shelf regions of the eastern Laurentian platform (sites no. 2–6; see Table 34 and Fig. 381). The Girvan area of Scotland is likely also to have been a part of the Laurentian margin during Sandbian time (WOODCOCK in FORTEY & others, 2000), and includes an isolated occurrence of *Labechia* (WEBBY, 1977) from within the Stinchar Limestone Formation (site no. 10; see Fig. 381), from a stratigraphic level close to the base of the Sandbian (equivalent to uppermost Chazy in Vermont and New York). The Chukchi Peninsula of northeastern Russia also had links with Laurentia, remaining close to Alaska and the northwest of Canada throughout the Paleozoic (GOLONKA, 2002). The Sandbian stromatoporoid assemblage from this region (site no. 11) comes from the Isseten Formation of the Chegitun River Basin (ORADOVSKAYA, 1988), and includes *Stromatocerium*, *Labechia,* and *Pseudostylodictyon* (KHROMYKH, 1977, 1999b).

Other Russian localities, from the western slopes of the Urals (BOGOYAVLENSKAYA, 1973b) and in the Moiero River Basin section of the Siberian Platform (NESTOR, 1976), include rather sparse Sandbian faunas. BOGOYAVLENSKAYA (1973b) reported an occurrence of *Cystostroma* from the so-called Middle Ordovician, part of the Trypyl River section from the western slopes of the Urals (site no. 14), and she also claimed an occurrence of *Ecclimadictyon* from the Uls River section on the western slopes of the northern Urals as being of Middle Ordovician age. However, this stratigraphic determination is likely to be erroneous, as no clathrodictyid stromatoporoids appeared elsewhere in the global record before the middle of the Upper Ordovician (that is, early in the Katian Stage; see discussion on p. 575–590). In upward continuation of the Siberian Moiero River Basin section, which included the mid–late Darriwilian genus *Priscastroma* (site no. 16), NESTOR (1976) recorded two genera, *Cystostroma* from a horizon close to the Mid–Late Ordovician boundary (Krivoluk horizon; see KANYGIN, MOSKALENKO, & YADRENKINA, 1988) and *Stromatocerium* from the succeeding Mangazey horizon, also of Sandbian age.

DONG and WANG (1984) have described stromatoporoids of probable Sandbian age from two horizons within the Malieciken Group of the Altun Mountains in northwestern China, Xinjiang (site no. 21; see Fig. 381). The Altun Mountains are associated with the southeastern part of the Tarim terrane (LI, ZHANG, & POWELL, 1996; FORTEY & COCKS, 2003) or paleoplate (CHEN & others, 2001). Two stromatoporoid-bearing horizons comprise a lower, dominated by *Labechia* and *Stylostroma*, and an upper, having the same genera, and, in addition, *Labechiella, Pachystylostroma,* and *Cystostroma(?)*. The Kunlun Mountains in the southwestern part of the Tarim terrane also include a stromatoporoid-bearing horizon of the Malieciken Group, including *Labechia* and *Labechiella*. Dong and Wang (1984) commented on the uncertainties of the age determinations, suggesting that these Tarim assemblages were slightly younger than the mid–late Darriwilian (Majiagou Formation equivalent) assemblages of northern China. That implies a Sandbian age, though, given the early appearance of *Stylostroma* (not recorded elsewhere until later, i.e., early Katian), these assemblages may conceivably be younger. However, Chen (in Wang & others, 1996, p. 70, 83) reported a contrary view, with what appears to represent the same two stromatoporoid-bearing horizons in a sequence given a different stratigraphic name but from the same Altun Mountains, that underlie a graptolite- and conodont-dated sequence of mid-Darriwilian–lower Sandbian age, suggesting the stromatoporoid-bearing horizons may be older. Clearly, in this remote region, much remains to be done to clarify the stratigraphic and tectonic relationships. Given the morphological development of the Altun labechiid faunas, it is unlikely that they represent assemblages as old, or older, than those of the Majiagou Formation in northern China; therefore, following Dong and Wang (1984), they are preferably regarded here as having a Sandbian age.

Another Chinese Sandbian association (site no. 26) with *Labechia* and *Labechiella* is recognized from the Fengfeng Formation at Fengfeng, near Handan city, southern Hebei province, North China Platform (An in Lai & others, 1982; Lin & Webby, 1989, p. 209). The Fengfeng Formation occupies a position directly overlying the Majiagou Formation (Zhou & Fortey, 1986; Chen & others, 1995; Wang & others, 1996).

In eastern Australia, the earliest known stromatoporoids are found in sequences that are close to the Mid–Upper Ordovician boundary. In two areas in central New South Wales (site no. 27), the Gunningbland area of the Junee-Narromine Volcanic Belt and the Wahringa area of the northern Molong Volcanic Belt, small assemblages of characteristic labechiids have been described (Pickett & Percival, 2001; Percival, Webby, & Pickett, 2001), representing occurrences that include the genera *Stratodictyon*, *Labechia, Labechiella* (some skeletons being preservationally gradational into *Stromatocerium*), and *Aulacera(?)*. Both stromatoporoid-bearing successions accumulated in shallow-water limestones on the fringes of partially emergent offshore volcanic islands of the Macquarie Arc (formerly Macquarie Volcanic Belt; Webby, 1976). The Gunningland and Wahringa assemblages are established as having a Sandbian (=Australian Gisbornian) age.

The early stromatoporoid assemblages in Tasmania (site no. 28) occur in the carbonate successions of the lower Gordon Group of the Florentine Valley and Mole Creek areas on the Tasmanian Shelf (Webby, 1979b, 1991), from what may have been a remnant of the main East Gondwanan margin, or a microcontinent (Webby, 1987). The genera comprise *Rosenella*, *Labechia, Stratodictyon*, *Stromatocerium,* and *Thamnobeatricea*. The abundant Tasmanian species, *Stromatocerium bigsbyi,* bears a near identical *Labechiella regularis*–type morphology to skeletons in the Wahringa Limestone Member of central New South Wales, except for a much greater tendency for its solid pillars to be secondarily replaced, becoming calcite spar–filled "hollow" pillars. These lower Tasmanian stromatoporoid-bearing units are also regarded as having a Sandbian age.

KATIAN

The widest geographical spread of Ordovician stromatoporoids occurred during the Katian Stage (=middle Caradoc to middle Ashgill). This Late Ordovician interval has a duration of about 8 myr, which is much longer than the preceding Sandbian Stage (Gradstein & others, 2004, 2012). The global distribution is represented by the occurrences of genera from 22 sites, shown in Table 37 and Figure

TABLE 35. Geological distribution of stromatoporoid assemblages in the Katian and Hirnantian stages (Upper Ordovician). The 22 Katian-age sites are represented by most of the columns in the table and depicted in Figure 381 by *black squares.* Also, 2 Hirnantian-age sites are represented by 2 extra columns at the right extreme side of the table (and are shown in Fig. 381 by *open, seven-pointed stars);* genera that made their first appearances in the Katian and Hirnatian are indicated with an asterisk (*) and hash mark (#), respectively (Stock, Nestor, & Webby, 2012).

Order Genus	Texas, New Mexico 1	Kentucky, Tennessee 2	Ohio, Indiana 3	Southern Ontario 6	Northern and southern Manitoba 7	Northern Hudson and Ungava Bays 8	Anticosti Island 9	Baltica: southern Norway 12	Baltica: Estonia 13	Slopes of western Urals 14	Taimyr Peninsula 15
Labechiida											
Rosenella											+
Cystostroma		+		+	+	+			+	+	+
Pseudostylodictyon	+						+				
Labechia	+	+	+	+		+		+			+
Labechiella											+
Stratodictyon											
Stromatocerium		+	+		+					+	+
Cystistroma		+				+?			+		
**Radiostroma*								+			
Pachystylostroma				+				+			
**Stylostroma*								+			
Aulacera		+	+		+	+	+				
#*Quasiaulacera*							+				
**Alleynodictyon*											
Cryptophragmus											
Ludictyon											
Thamnobeatricea											
Lophiostroma											+
Dermatostroma		+	+								
Clathrodictyida											
**Clathrodictyon*					+		+	+	+	+	
**Stelodictyon*											+?
**Ecclimadictyon*				+	+			+		+	+?
Camptodictyon											
Plexodictyon											
Labyrinthodictyon											
Actinostromatida											
**Plumatalinia*									+		

381, and shows almost complete differentiation of labechiids, with appearances of 2 more short-ranging genera (*Radiostroma, Alleynodictyon*), as well as the initial diversification of clathrodictyid stromatoporoids during the early–mid-Katian. Three clathrodictyid genera, *Clathrodictyon, Ecclimadictyon,* and *Stelodictyon* make their appearances. Their differentiation into two families (Clathrodictyidae, Actinodictyidae) is difficult to sustain in Katian occurrences, because these early genera exhibit such a wide range of forms between those showing regular and crumpled types of laminae (see also p. 575–592). A number of regions, such as Norway, Estonia, Taimyr Peninsula, Altai-Sayan Belt, Tuva, Mongolia, Qinghai (Qaidam Platform) and Zhejiang (southern China), exhibit stromatoporoid faunas for the first time. The wide distribution of stromatoporoids (both labechiids and clathrodictyids) seems to have coincided with the maximum circumequatorial spread of Ordovician reefs (WEBBY, 2002). The appearance also of the genus *Plumatalinia* may mark the beginnings

TABLE 35 (*continued from facing page*).

Order Genus	Siberian Platform 16	Altai-Sayan Fold Belt 17	Tuva, Mongolia 18	Kazakh-stan 19	Central Asia 20	Tarim: northern Xinjiang 21	Chaidam: Qinghai 22	Southern China: Zhejiang 23	Northern China: Shaanxi 26	Macquarie Arc: New South Wales 27	Tasman-ian Shelf 28	Anti-costi Island 9	Baltica: Estonia 13
Labechiida													
Rosenella	+									+	+		
Cystostroma	+	+	+		+					+	+		
Pseudostylodictyon			+							+	+		
Labechia	+	+	+	+			+	+		+	+	+	
Labechiella	+	+	+	+	+		+		+	+	+		
Stratodictyon	+		+							+			
Stromatocerium	+		+			+	+				+?		
Cystistroma	+									+			
**Radiostroma*													
Pachystylostroma		+	+								+		+
**Stylostroma*											+		
Aulacera	+										+	+	
#*Quasiaulacera*												+	
**Alleynodictyon*									+	+	+		
Cryptophragmus	+												
Ludictyon			+										
Thamnobeatricea											+		
Lophiostroma	+		+			+							
Dermatostroma													
Clathrodictyida													
**Clathrodictyon*			+					+	+	+	+	+	+
**Stelodictyon*								+		+?			+
**Ecclimadictyon*				+?	+?		+	+	+	+	+	+	+
Camptodictyon		+								+			
Plexodictyon										+?			
Labyrinthodictyon												+	
Actinostromatida													
**Plumatalinia*													

of the actinostromatid stromatoporoids; the genus first appeared in Estonia during the late Katian, and possibly is a kind of missing link between labechiids, much as *Pseudostylodictyon* and the Silurian actinostromatids, but some qualifications about this relationship need to be maintained (see discussion on p. 589–590).

Katian stromatoporoids are widely distributed across Laurentia and have been documented by a number of workers, such as GALLOWAY and ST. JEAN (1961) and BOLTON (1988), from the most westerly occurrences (site no. 1) in Texas and New Mexico to Anticosti Island (site no. 9). All seven Laurentian sites (no. 1–3, 6–9) exhibit labechiids, and a few of these, additionally, include records of the first clathrodictyid stromatoporoids (*Clathrodictyon, Ecclimadictyon*); e.g., from sites in southern Ontario, Manitoba, and Anticosti Island (BOLTON, 1988). For example, in the Central Appalachian areas of Tennessee and Kentucky, labechiid genera *Labechia, Cystostroma, Stromatocerium, Cystistroma,* *Aulacera,* and *Dermatostroma* have been reported (GALLOWAY & ST. JEAN, 1961). Sequences in different parts of Manitoba have included records of the labechiids *Cystostroma, Stromatocerium,* and *Aulacera,* and clathrodictyids *Clathrodictyon* and *Ecclimadictyon*, and on Anticosti Island within the Vaureal Formation, there are numerous records of *Aulacera* (some giant sized) and rare *Clathrodictyon* [see BOLTON (1988), and *Pseudostylodictyon* (NESTOR, COPPER, & STOCK, 2010, fig. 4–5)]. *Dermatostroma* appears to be the only endemic genus in the Katian record of Laurentia.

Stromatoporoids play an important part as contributors to reefs in the Katian successions of the Oslo region, southern Norway; site no. 12 (HARLAND, 1981; WEBBY, 2002). In areas near Lake Mjøsa (SPJELDNAES, 1982), the lower Katian stromatoporoid assemblage includes *Labechia, Pachystylostroma,* and *Stylostroma,* and the possibly endemic genus *Radiostroma* (WEBBY, 1979c), though NESTOR and STOCK (2001, p. 334, fig. 1) have listed it as being present also in North America. Additionally, stromatoporoids have been recorded from the uppermost Katian; for example, from the informal Norwegian stage 5a interval, at Stavnestangen in the Ringerike area, with *Stylostroma, Pachystylostroma, Labechia*, *Clathrodictyon,* and *Ecclimadictyon* (KALJO, KLAAMANN, & NESTOR, 1963; NESTOR, 1999b). In Estonia (site no. 13), two temporally distinct and approximately correlative, stromatoporoid associations also occur: the lower Katian (=Oandu regional stage) with occurrences of *Cystostroma* and *Cystistroma*, and the uppermost Katian (=Vormsi and Pirgu regional stages; see HINTS & MEIDLA, 1997), with records of *Cystostroma, Cystistroma, Clathrodictyon,* and *Plumatalinia* (NESTOR, 1999b). All these records developed in shallow shoal to open shelf conditions of the extensive epicontinental sea, which covered much of the western side of Baltica (JAANUSSON, 1982; COCKS & FORTEY, 1998).

The Katian stromatoporoids from the western slopes of the Urals include the records BOGOYAVLENSKAYA (1973b) assigned to the Rassokha horizon (and equivalents); these comprise *Cystostroma, Stromatocerium,* and probably both *Clathrodictyon* and *Ecclimadictyon* (despite her probably mistaken recognition of *E. geniculatum* as having a Middle Ordovician age; see BOGOYAVLENSKAYA, 1973b, p. 22–23), and given that elsewhere, BOGOYAVLENSAKYA (1984, p. 69) has listed *Ecclimadictyon*, like *Clathrodictyon,* as having an Upper Ordovician–Silurian range.

A number of Upper Ordovician (Katian) stromatoporoids have been recorded by KHROMYKH (2001) from sections along the Paranaya and the lower Taimyr rivers within the southern (carbonate) facies belt of the Taimyr Peninsula (site no. 15). They include the labechiid genera *Cystostroma, Rosenella, Labechia, Labechiella, Stromatocerium*, and *Lophiostroma*, and, apparently, the clathrodictyids *Ecclimadictyon* and *Clathrodictyon* (these forms are mentioned, but not described), and genus *Taymyrostroma*, with uncertain relationships within the class Stromatoporoidea (see Order and Family Uncertain on p. 837). This southern belt is considered to be a part of the Siberian plate, probably marginal to it during the Late Ordovician (FORTEY & COCKS, 2003, p. 270). Katian assemblages from the main cratonic areas of the Siberian Platform (site no. 16), from main localities along major waterways such as the Moiero and Podkammennaya Tunguska rivers, as well as other areas (e.g., the Verkhoyansk-Kolyma Fold Belt of northeastern Siberia), include *Rosenella, Cystostroma, Labechiella, Stromatocerium, Cystistroma, Aulacera, Cryptophragmus,* and *Lophiostroma* (YAVORSKY, 1955, 1961; NESTOR, 1976; BOGOYAVLENSKAYA, 1977a). The Verkhoyansk-Kolyma Fold Belt incorporates a number of terranes that apparently remained close to the margins of the Siberian plate through the Cambrian and Ordovician, but rifted away during Middle Paleozoic time, according to GOLONKA (2002). Because faunal connections remained closely linked to Siberia through the Late Ordovician, the stromatoporoid data for the Siberian craton and the northeastern fold belt region has been combined in site no. 16 (Fig. 381), though at least one record, that of *Stratodictyon* (Bogoyavlenskaya, 1973b), is restricted to the northeastern fold-belt region (Sette Daban Range).

In the Altai-Sayan Fold Belt of southwestern Siberia, specifically the Gornaya Shoriya and the Gorny Altai regions (site no. 17), stromatoporoids were first recognized by Khalfina (1960c), including *Rosenella, Labechiella,* and a distinctive clathrodictyid, later determined to be *Ecclimadictyon amzassensis,* but recently reassigned to the genus *Camptodictyon* Nestor, Copper, & Stock, 2010. The biogeographically important species, now determined to be *C. amzassense,* is found in three areas of the fold belt in Gornaya Shoria, the central part of Gorny Altai, and in the intervening Uymen'-Lebed Zone (Sennikov & others, 1988). Sampled localities lie along an arcuate, paleogeographically defined, carbonate platform that developed within the fold belt during Katian time (Yolkin & others, 2001, p. 16). A markedly close species-level biogeographic tie exists between the occurrences of *C. amzassensis* in the Altai-Sayan region (those considered to be the same species from localities in the Chinese Altai Mountains of far northwestern Xinjiang, only 600 km to the south [Dong & Wang, 1984; Lin & Webby, 1988, p. 233]) and records of *C. amzassensis* from the peri-Gondwanan, Macquarie Arc terrane of central New South Wales (Webby, 1969, 1976). Other species-level links also exist between the Altai-Sayan and New South Wales regions among labechiids with common occurrences, such as *Rosenella* (*R. woyuensis*) and *Labechiella* (*L. regularis*), adding weight to the closeness of the biogeographic connection. This accords with the views of Fortey and Cocks (2003, fig. 15), that the Altai-Sayan region had developed as an isolated terrane and had moved to a peri-Gondwanan, low paleolatitude, position by Late Ordovician (Katian) time.

The Tuva Mountains of southern Russia and Mongolia have been linked in a separate Tuva-Mongol Arc during the Early Paleozoic (Şengör & Natal'in, 1996), though, as Fortey and Cocks (2003) have indicated, because the faunas of both regions maintained such close Siberian affinities, debate continues as to whether the arc terrane was part of Siberia or independent of it. The integration may have occurred in the Ordovician, or the arc remained a separate entity, but close to Siberia, during Ordovician time. Alternatively, the Tuva-Mongolia region has been regarded by Golonka (2002, p. 25), following Zonenshain, Kuzmin, and Natapov (1990), as being represented by the Amuria terrane that formed off Siberia by "collision between microcontinents" during the latest Cambrian to Early Ordovician. The Katian stromatoporoids of Tuva and Mongolia are combined in site no. 18, though in Tuva only three genera are recorded (Bogoyavlenskaya, 1971b), whereas a more diverse fauna occurs in Mongolia (Bol'shakova & Ulitina, 1985), including *Cystostroma, Pseudostylodictyon, Rosenella, Labechia, Labechiella, Stratodictyon(?), Ludictyon, Lophiostroma,* and *Clathrodictyon*. Bol'shakova and Ulitina (1985) have recognized that across Mongolia there were three regional collections, each exhibiting a different mix of faunal components, but overall suggesting closer zoogeographic links to Siberia and Central Asia than to North America and Europe, as might be expected.

Stromatoporoids have rarely been reported from Kazakhstan (site no. 19) or Central Asia (Tadjikistan, Uzbekistan, Kyrgyzstan; site no. 20). *Labechiella* is known from the Dulankarian horizon (mid-Katian) of southern Kazakhstan (Khalfina, 1958) and the Zeravshan Range of Tadjikistan (Karimova & Lessovaya, 2007), and *Cystostroma* is reported from Kyrgyzstan (Yavorsky, 1961). Previously, Webby (1992) concluded that such Central Asian Late Ordovician sequences contained predominantly solitary rugose and tabulate coral faunas (rarely stromatoporoids), representing cooler water assemblages of the southern mid-paleolatitude Euroasiatic Realm, but it is possible that a short-lived phase of global warming may have been responsible for some rare appearances in mid-paleolatitudes; for example, as a consequence of the Boda event in the late Katian (Fortey & Cocks, 2005).

The Katian stromatoporoid distributions within China are differentiated, based on available paleogeographic reconstructions, into four sets of assemblages, represented by sites no. 21 (Tarim), no. 22 (Qaidam), no. 23 (southern China), and no. 26 (northern China), respectively. The first is an assemblage of *Labechia, Stromatocerium,* and *Lophiostroma* (Lin & Webby, 1989) from the Houcheng area of northwesterm Xinjiang (site no. 21) and recorded from a sequence considered by Chen and others (1992, p. 171) to be part of the cratonic Yining Basin; this latter occupied a position near the outer (northern) margin of the Tarim plate (Chen & Rong, 1992).

Two other stratigraphically distinct assemblages (Lin & Webby, 1988) occur in a section south of Golmud City, Qinghai province (site no. 22). The lower unit contains *Labechiella* and *Stromatocerium*, and the upper includes *Labechia* and *Ecclimadictyon*. The genus *Stelodictyon* was not recorded from the upper assemblage (cf. Nestor, 1999b, p. 128). Paleogeographically, these occurrences occupy a position toward the southern margin of the Chaidam (or Qaidam) Platform, which probably represented another small and discrete, peri-Gondwanan terrane (Chen & Rong, 1992; Metcalfe, 1996).

The southeastern part of the southern China plate became an uplifted extension of the Cathaysian land during the Late Ordovician, separating the broad, stable, Yangtze Platform from the transitional Jiangnan belt, with its basinal and slope facies, and more localized platform areas marginal to the Cathaysian land; the marginal areas include a variety of shallow carbonate reefs and slope deposits that are mainly exposed across parts of the Zhejiang and Jiangxi provinces (Chen & Rong, 1992; Webby, 2002). These deposits (site no. 23) contain late Katian stromatoporoids, the labechiid *Pachystylostroma*, and the clathrodictyids *Clathrodictyon, Ecclimadictyon,* and *Stelodictyon* (Lin & Webby, 1988; Bian, Fang, & Huang, 1996).

A number of Katian stromatoporoid assemblages occur in successions along the southern and western margins of the uplifted Ordos Platform (northern China plate; site no. 26); some come from shelf-edge reefs (Ye & others, 1995; Zhou & Ye, 1996). In Shaanxi province, the stromatoporoids occur in two stratigraphically distinct horizons, the lower (Taoqupo Formation) with *Clathrodictyon* and *Ecclimadictyon* (some forms appear to have been mistakenly identified as *Forolinia* by Ye & others, 1995, pl. 8,*3*), and the upper (Beigoushan Formation) with *Labechia*, *Labechiella, Clathrodictyon,* and *Ecclimadictyon* (Lin & Webby, 1988, 1989; Ye & others, 1995). *Clathrodictyon* is also recorded from Inner Mongolia (Lin & Webby, 1988).

Varied assemblages of stromatoporoids occur in the early to mid-Katian (=Eastonian) successions of the central New South Wales Macquarie Arc (site no. 27) and the Tasmanian Shelf (site no. 28) in eastern Australia. Three stratigraphically distinct assemblages are recognized in the central New South Wales carbonate successions (Webby, 1969; Webby & Morris, 1976), across Macquarie Arc remnants (Molong and Junee-Narromine volcanic belts), as follows: (1) exclusively labechiid associations from the lower Cliefden Caves Limestone Group and equivalents with *Pseudostylodictyon, Stratodictyon, Rosenella, Labechiella, Cystistroma,* and *Alleynodictyon*; (2) labechiids (*Pseudostylodictyon, Labechia, Cystostroma*, *Alleynodictyon*) and first clathrodictyids (*Ecclimadictyon, Clathrodictyon, Camptodictyon, Stelodictyon[?],* and *Plexodictyon[?]*) from the upper Cliefden Caves Limestone Group and equivalents; and (3) labechiid *Pseudostylodictyon*, along with clathrodictyids *Ecclimadictyon, Camptodictyon,* and *Plexodictyon(?),* from the upper Ballingoole Limestone (upper Bowan Group) and equivalents.

The Katian assemblages in the Gordon Group limestones of the Tasmanian Shelf (Webby & Banks, 1976; Webby, 1991) are counterparts to the New South Wales assemblages 1 and 2 noted above; they comprise: (1) the labechiid associations of *Pseudostylodictyon, Rosenella, Labechia, Labechiella, Stylostroma, Thamnobeatricea*, and *Alleynodictyon* from the Dogs Head to Overflow Creek formations (middle–upper Chudleigh Subgroup) of the Mole Creek section and correlatives; and (2) labechiids (*Cystostroma, Labechia, Labechiella*, *Stromatocerium[?], Stylostroma, Pachystylostroma, Aulacera*) and the first clathrodictyids (*Clathrodictyon, Ecclimadictyon*) from the Den Formation (uppermost Chudleigh Subgroup) of the Mole Creek section and equivalents. In terms of biogeographic relationships, it should be noted that *Stylostroma, Pachystylostroma*, *Thamnobeatricea,* and *Aulacera* are found in Tasmania but have not been recorded from the New South Wales arc faunas. Also, at the species level, there are important differences, because none of the Tasmanian species of *Clathrodictyon* or *Ecclimadictyon* is conspecific with counterparts in New South Wales. On the other hand, the distinctive *C. amzassensis*, which is recorded in the Altai-Sayan, Chinese Altai, and New South Wales regions, has not been recognized in Tasmania. *Alleynodictyon* is apparently the only endemic genus to occur across eastern Australia.

In terms of the early clathrodictyid stromatoporoids (Webby in Webby & others, 2000, p. 70), it seems that the main stocks involved in the initial dispersal were the genera *Clathrodictyon* and *Ecclimadictyon*. These genera show a marked range of variability between their more characteristic regular, or more crumpled, types of laminae (see further discussion on p. 575–592). Both genera achieved a comparatively rapid circumequatorial distribution during the early Katian (=late Caradoc). In contrast, *Camptodictyon* was restricted to arc-related settings in the Russian and Chinese Altai and New South Wales; *Stelodictyon* and *Plexodictyon(?)* maintained a limited spread between the peri-Gondwanan New South Wales arc, southern China, and Baltica; and *Plexodictyon(?)* possibly also spread to Laurentia (see Nestor & Stock, 2001, fig. 1). These latter genera achieved more cosmopolitan distributions in the Silurian.

HIRNANTIAN

Only a few sites worldwide exhibit Hirnantian stromatoporoids. The Hirnantian was a relatively short interval of time (about 1.5 myr), dominated by glacioeustatic sea-level changes, glaciation during the early to middle part, and global warming in the last part (Brenchley, 2004; Finnegan & others, 2011). The documented records of Hirnantian stromatoporoids (two right-hand columns, Table 37) are limited to localities on Anticosti Island, eastern Canada (site no. 9), and the Porkuni horizon of Estonia (site no. 13). On Anticosti Island, the stromatoporoid genera occur in the Ellis Bay Formation and are dominantly the cylindrical labechiid *Aulacera* and the clathrodictyids *Clathrodictyon* and *Ecclimadictyon* (Bolton, 1988; Cameron & Copper, 1994), as well as *Labyrinthodictyon* Nestor, Copper, & Stock (2010, p. 74). In the Arina Formation (Porkuni stage) of Estonia, the stromatoporoids include the labechiid *Pachystylostroma* (rare) and clathrodictyid genera *Clathrodictyon, Ecclimadictyon,* and *Stelodictyon* (Nestor, 1964a, 1999b). There are also records of *Aulacera* from the Stonewall Formation of southern Manitoba (Bolton, 1988) and abundant *Pachystylostroma* in a carbonate bank from the informal Norwegian stage 5b interval at Ullerntangen in the

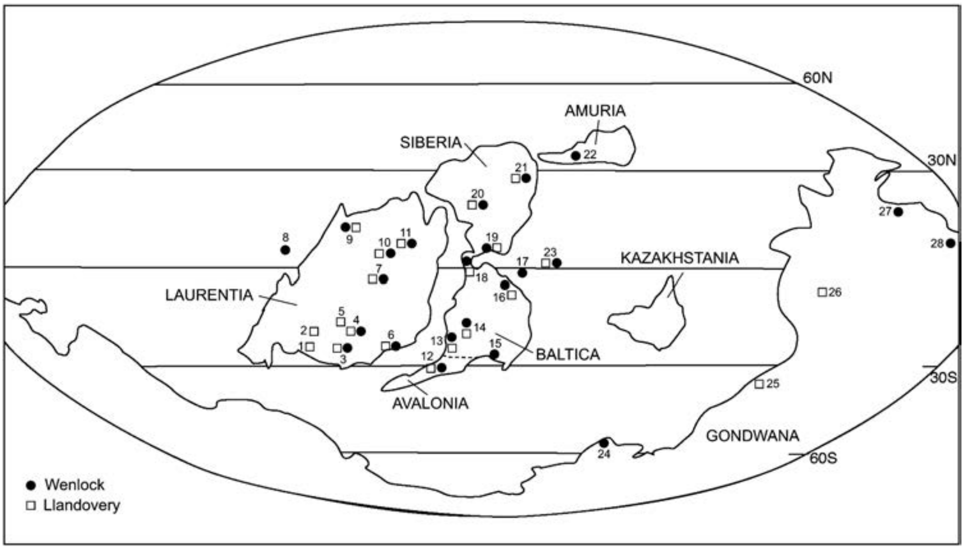


FIG. 382. Geographical distribution of stromatoporoids in the lower Silurian (Llandovery, Wenlock). The names of the localities are shown in Tables 37 and 38; *dashed line* separates cratons of Avalonia and Baltica (Stock, Nestor, & Webby, 2012).

Ringerike area, Norway (HANKEN & OWEN, 1982, p. 128) that represent additional, confirmed Hirnantian localities.

SILURIAN

HELDUR NESTOR

The present review of the biogeography of the Silurian stromatoporoids is mainly based on publications containing systematic descriptions and photos of species that enabled, in case of need, reinterpretation of generic identifications according to the taxonomic nomenclature used in the present paper. In some cases, trustworthy species lists and range charts from biostratigraphic publications were taken into account. Insufficiently precise stratigraphic datings prevented the use of older publications, e.g., most of RIABININ's and YAVORSKY's data, though contributions by RIABININ (1951, 1953) have been retained (see listings in next paragraph).

The Silurian stromatoporoids treated herein have been studied from the following districts: Ontario, Hudson Bay, and other, scattered localities of North America (PARKS, 1907, 1908, 1909); eastern Quebec (PARKS, 1933; STEARN & HUBERT, 1966); Anticosti Island (BOLTON, 1981; NESTOR, COPPER, & STOCK, 2010); New York and Virginia (STOCK, 1979; STOCK & HOLMES, 1986); Baffin Island (PETRYK, 1967); Somerset Island (SAVELLE, 1979); northern Greenland (POULSEN, 1941); England (NICHOLSON, 1886a, 1889, 1891a, 1892); Ireland (NESTOR, 1999a); Norway (MORI, 1978); Gotland Island (MORI, 1968, 1970); Estonia (RIABININ, 1951; NESTOR, 1964a, 1966a, 1990b); Podolia (RIABININ, 1953; BOL'SHAKOVA, 1973; BOGOYAVLENSKAYA, 1969a; BOGOYAVLENSKAYA in TSEGELNJUK & others, 1983); Bohemia (MAY, 2005); Urals (BOGOYAVLENSKAYA, 1973a, 1976); Novaya Zemlya (NESTOR, 1981b, 1983); Siberian Platform (NESTOR, 1976; KHROMYKH in TESAKOV & others, 1980, 1985); Altai and Salair (KHALFINA, 1961b); Tuva (BOGOYAVLENSKAYA, 1971b, 1976); Mongolia (BOL'SHAKOVA & ULITINA, 1985; BOL'SHAKOVA & others, 2003), northern China (DONG, 1984; DONG & WANG, 1984); southern China (DONG & YANG, 1978; YANG & DONG, 1980; WANG in JIN & others, 1982); Central Asia (Tian Shan) (LESSOVAYA, 1962, 1971, 1972, 1978b; LESSOVAYA & ZAKHAROVA, 1970); Turkey (WEISSERMEL, 1939); Iran (FLÜGEL, 1969); Japan (SUGIYAMA, 1939, 1940); northern Queensland (WEBBY & ZHEN, 1997); New South Wales (BIRKHEAD, 1976, 1978).

Biogeography of the Silurian stromatoporoids was considered earlier in papers by KALJO, KLAAMANN, and NESTOR (1970) and NESTOR (1990a). NESTOR and STOCK (2001) summarized data on the distribution of the stromatoporoid genera in the Llandovery. BOGOYAVLENSKAYA (1981) considered distribution of the Pridoli stromatoporoids in the former U.S.S.R. Unpublished data on stromatoporoids from Severnaya Zemlya (NESTOR's data from 1983) and from Alabama, Ohio, Oklahoma, Iowa, and northern Michigan (STOCK and NESTOR's data from 1998–1999) are also used in the present review.

The main districts of stromatoporoid occurrences are plotted on the simplified base maps of GOLONKA (2002) (Fig. 382–383). Geographical distribution of the Silurian stromatoporoid genera is represented in Tables 36–39.

LLANDOVERY

During the Llandovery, stromatoporoids were widespread in epicontinental seas and continental shelves of the Laurentia, Baltica, and Siberia cratons, which were situated close together in low paleolatitudes, within subtropical to tropical climatic zones (Fig. 382) and associated with carbonate sedimentation. Only a few occurrences of Llandovery stromatoporoids have been recorded from the marginal areas of eastern Gondwana (southern China, Iran), which also are placed in low paleolatitudes. The occurrences of Llandovery stromatoporoids ranged from ~30° N (Tuva) to ~35° S (Iran).

After a gradual extinction of the Ordovician labechiid-dominated stromatoporoid fauna, only a few genera survived, and the early Silurian fauna became clathrodictyid dominated (NESTOR & STOCK, 2001). In most regions, the early Llandovery (Rhuddanian) is represented by a hiatus in the stromatoporoid succession. Abundant, but low-diversity, stromatoporoid fauna has been recorded from Estonia and Anticosti, where only four genera, *Clathrodictyon, Ecclimadictyon, Pachystylostroma,* and *Forolinia,* are present. The first two, belonging to the order Clathrodictyida, became the most common cosmopolitan elements of the Llandovery stromatoporoid fauna. Labechiids maintained an accessory role and were more common in the Siberian and Chinese faunas. During the Llandovery, a marked generic diversification and areal extension of stromatoporoid faunas took place. The earliest representative of the family Actinostromatidae, genus *Plectostroma,* appeared in Estonia in the late Rhuddanian. In the Aeronian (middle Llandovery), among Clathrodictyida, representatives of Tienodictyidae (*Intexodictyides*) were added in the sections of Estonia, Anticosti, Michigan, Baffin Island, as well as gerronostromatids (*Gerronostromaria, Petridiostroma*) in the sections of Baffin Island, Anticosti, and Norway. At the same time, first representatives of the order Stromatoporida appeared: *Eostromatopora* (Stromatoporidae) in Baffin Island and *Syringostromella* (Syringostromellidae) in northern Michigan. In the late Llandovery (Telychian), the first densastromatids (*Densastroma*) and pseudolabechiids (*Desmostroma, Pachystroma*) were added in Michigan, Iowa, Baffin Island, Anticosti, Estonia, and Gotland.

Thus, during the second half of the Llandovery, a gradual diversification and expansion of stromatoporoid faunas took place. The center of origination of the new taxa shifted from the margins of the Iapetus Ocean (Anticosti, Norway, Estonia) to the Michigan Basin and the Canadian Arctic, where the earliest representatives of Gerronostromatidae (*Gerronostromaria, Petridiostroma*), Stromatoporidae (*Eostromatopora*), and Syringostromellidae (*Syringostromella*) continued to be represented in the Aeronian and extended their area

TABLE 36. Distribution of stromatoporoid genera in the Llandovery (+, general occurrences of Llandovery genera; *x,* records of more restricted upper Llandovery occurrences; *?,* uncertain or doubtful generic entries; *quotation marks,* questionable occurrences) (adapted from Stock, Nestor, & Webby, 2012).

Order Genus	Alabama 1	Oklahoma 2	Ohio 3	Michigan, Ontario 4	Iowa 5	Eastern Quebec 6	Hudson Bay 7	Northwestern Canada 9	Baffin Island 10	Northern Greenland 11
Labechiida										
Forolinia	+					+				
Labechia										
Ludictyon										
Pachystylostroma				+		+				+
Pleostylostroma										
Rosenella										
Stylostroma										
Tarphystroma						+				
Clathrodictyida										
Actinodictyon							x		x	
Camptodictyon						+				
Clathrodictyon	x	+	+	+	+	+			+	+
"Clavidictyon"				+	+	+				
Desmidodictyon						+				
Ecclimadictyon		+	+	+	x	+			+	+
Gerronostromaria				?	x		?		x	
Intexodictyides				+	+	+			+	
Neobeatricea							x			
Oslodictyon				x	x	x		x		
Petridiostroma				x	x	+				
"Plexodictyon"			+				x			
Stelodictyon	?			+	x					
Actinostromatida										
Densastroma				x	x					
Desmostroma					x	x				
Pachystroma				x	x	x				
Plectostroma							x		x	
Stromatoporida										
Eostromatopora									x	
Lineastroma										
Stromatopora							?			
Syringostromella				+	x		x			
Syringostromatida										
"Parallelopora"										

of occupation in the Telychian to other districts of Laurentia and Baltica. The most conservative Llandovery stromatoporoid faunas were in Siberia and southern China, where labechiids (*Labechia, Pachystylostroma, Forolinia, Rosenella, Stylostroma, Ludictyon, Pleostylostroma*) maintained an important role, along with *Clathrodictyon* and *Ecclimadictyon.* Actinostromatids and stromatoporids were quite rare, with the exception of *Plectostroma* (Siberian Platform, Altai, Tian Shan) and *Lineastroma* (Siberian Platform), belonging to the families Actinostromatidae and Stromatoporidae, respectively. It is worth mentioning that the first probable syringostromatid—*"Parallelopora"* (originally described as *Gerronostromaria dragunovi* YAVORSKY, 1961)—is also recorded from the Llandovery of the Siberian Platform (KHROMYKH in TESAKOV & others, 1985).

In summary, at the generic level, the provincialism of the Llandovery stromatoporoids is rather weakly expressed. Paleobiogeographic peculiarities of stromatopo-

TABLE 36 (*continued from facing page*).

Order Genus	Ireland 12	Norway 13	Estonia, Gotland 14	Western Urals 16	Novaya Zemlya 18	Severnaya Zemlya 19	Siberian Platform 20	Altai, Salair, Tuva 21	Tian Shan 23	Iran 25	Southern China 26
Labechiida											
Forolinia		+	+		x				+		+
Labechia			+	+		+	+	+	+		+
Ludictyon											+
Pachystylostroma	x		+				x				+
Pleostylostroma											+
Rosenella			x				x				+
Stylostroma							x				+
Tarphystroma											
Clathrodictyida											
Actinodictyon											
Camptodictyon			+								
Clathrodictyon		+	+		+	+	+	+	+		+
"Clavidictyon"							+				+
Desmidodictyon											
Ecclimadictyon		+	+			+		+	+	+	?
Gerronostromaria	x										
Intexodictyides			+					?			+
Neobeatricea							x				
Oslodictyon		x	x						x		
Petridiostroma	x	+	x					x			
"Plexodictyon"											+
Stelodictyon				+							
Actinostromatida											
Densastroma			x								
Desmostroma			x								
Pachystroma			x								
Plectostroma			+	+			+	x	x		
Stromatoporida											
Eostromatopora	x	x									
Lineastroma							x				
Stromatopora											
Syringostromella											
Syringostromatida											
"Parallelopora"							x				

roid faunas in different regions depend on the presence of temporary endemics, i.e., genera making their first appearance in one region and spreading afterward into other areas.

WENLOCK

In the beginning of the Wenlock, the Silurian marine transgression reached its maximum extent. Vast areas of Siberia and eastern Gondwana were covered with warm, tropical epicontinental seas. Wide inland seas (Michigan, Illinois, Hudson, and Williston basins) were located in the interior of Laurentia. Extensive platform margin seas (Baltic and Petchora basins) were situated at the opposite margins of the Baltica craton, as well as in the present-day Canadian Arctic. Therefore, the Wenlock stromatoporoid faunas were the most widespread during the entire Silurian. Extensive stromatoporoid-dominated reef tracts and complexes have been recorded from the margins of the Michigan and Hudson

TABLE 37. Distribution of stromatoporoid genera in the Wenlock (+, occurrences of Wenlock genera; *?*, uncertain or doubtful generic entries) (Stock, Nestor, & Webby, 2012).

Order Genus	Kentucky, Indiana	Michigan, Ontario	Eastern Quebec	Hudson Bay	Alaska	Baffin Island	England	Norway	Gotland, Estonia	Podolia
	3	4	6	7	8	10	12	13	14	15
Labechiida										
Cystocerium										
Labechia	+						+		+	+
Lophiostroma	+	+	+							
Pachystylostroma									+	
Rosenella		+							+	
Rosenellinella										
Clathrodictyida										
Actinodictyon									+	
Clathrodictyon	+	+	+	+			+		+	+
"Clavidictyon"										
Ecclimadictyon		+	+				+	+	+	+
Gerronodictyon										
Gerronostromaria										
Neobeatricea										
Petridiostroma	+						+		+	+
Stelodictyon		+		+			+	+	+	+
Yabeodictyon			+						+	
Actinostromatida										
Actinostromella									+	
Araneosustroma									+	?
Densastroma	+		+				?		+	+
Desmostroma	+								+	+
Pachystroma		+	+						+	
Pichiostroma	?									
Plectostroma							+		+	
Plumatalinia									?	
Pseudolabechia										+
Vikingia					+				+	+
Stromatoporellida										
Simplexodictyon	+								+	
Stromatoporida										
Eostromatopora	+								+	
Lineastroma						+				+
Stromatopora							+	+	+	+
Syringostromella								+	+	+
Syringostromatida										
Columnostroma										
"Parallelopora"									+	
Parallelostroma						+			+	

TABLE 37 (*continued from facing page*).

Order Genus	Western Urals 16	Eastern Urals 17	Novaya Zemlya 18	Severnaya Zemlya 19	Siberian Platform 20	Altai, Salair, Tuva 21	Mongolia 22	Tian Shan 23	Bohemia 24	Northern Queens-land 27	New South Wales 28
Labechiida											
Cystocerium				+	+						
Labechia			+		+	+					+
Lophiostroma				+							+
Pachystylostroma		+			+						
Rosenella			?			+					
Rosenellinella											
Clathrodictyida											
Actinodictyon		+	+	+	+	+					
Clathrodictyon					+	+	+	+			+
"Clavidictyon"				+	+		+				+
Ecclimadictyon	+	+	+	+	+		+	+		+	+
Gerronodictyon		+									
Gerronostromaria											?
Neobeatricea			+		+						
Petridiostroma	+	+	+		+	+	+	+			
Stelodictyon			+	+	+		+		+		+
Yabeodictyon				+	+						
Actinostromatida											
Actinostromella											
Araneosustroma			+	+							
Densastroma					+		?				+
Desmostroma							+	+			
Pachystroma				+							
Pichiostroma											
Plectostroma				+	+	+		+			
Plumatalinia					?						
Pseudolabechia		+									
Vikingia			+	+	+						
Stromatoporellida											
Simplexodictyon				?	+	+	?	+		+	
Stromatoporida											
Eostromatopora					?						
Lineastroma				+	+						+
Stromatopora					+			?			
Syringostromella			+	+	+	+		+	+		?
Syringostromatida											
Columnostroma						+					
"Parallelopora"					+						
Parallelostroma			+	+	+						+

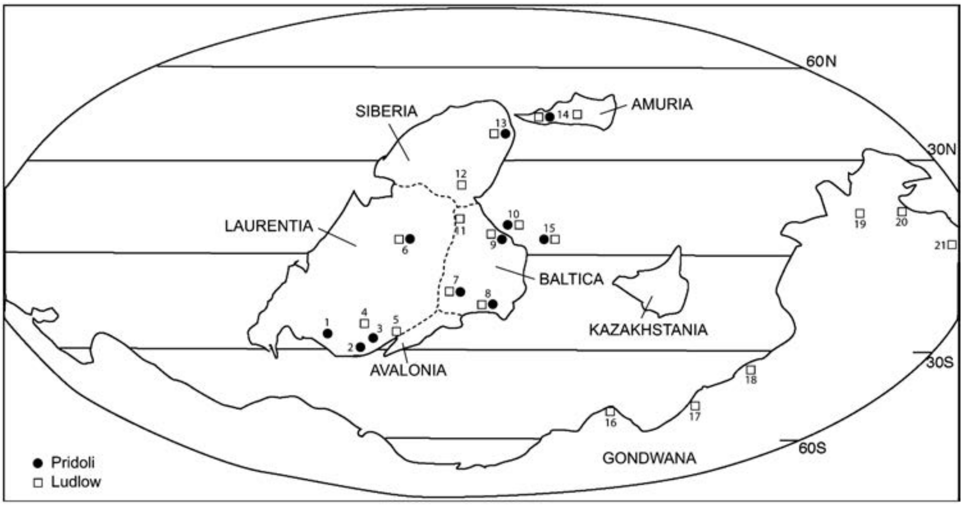


FIG. 383. Geographical distribution of stromatoporoids in the upper Silurian. The names of the localities are shown in Tables 39 and 40; *dashed lines* separate named cratons that during the late Silurian were merged to form the Laurussia paleocontinent (Stock, Nestor, & Webby, 2012).

basins, Gaspé region, Baltic area, Podolia, western and northern Urals, Arctic islands, Siberian Platform, Central Asia (Tian Shan) and the Verkhoyan-Kolyma region (COPPER, 2002). The Wenlock stromatoporoid occurrences range from ~35° N (Mongolia) to 50–55° S (Bohemia), according to the base maps of GOLONKA (2002), used herein. The paleomaps of TORSVIK and COCKS (2013b), however, show a more convincing Wenlock relationship, with Bohemia in a more northerly position (27–28° S) (see also NESTOR & WEBBY, 2013, fig. 7.10), almost connected to a part of the African margin of Gondwana.

During the Wenlock, diversification of stromatoporoid faunas continued. The most remarkable event was the appearance of the genus *Simplexodictyon,* the earliest representative of the order Stromatoporellida, recorded from Kentucky, Estonia, Gotland, Altai, Tian Shan, northern Queensland; i.e., from all of the main paleocontinents (Table 37). Except for doubtful records of *"Parallelopora"* from the Llandovery of the Siberian Platform (KHROMYKH in TESAKOV & others, 1985), the first confirmed representative of the order Syringostromatida, genus *Parallelostroma*, was distributed in the Wenlock in many regions: Baffin Island, Gotland, Podolia, Novaya Zemlya, Severnaya Zemlya, Siberian Platform, and New South Wales. Wide geographical distribution of new phylogenetic stocks demonstrates good intercommunication of the Wenlock stromatoporoid faunas of different paleocontinents and lack of biogeographic provincialism.

In the Wenlock stromatoporoid fauna, clathrodictyids maintained their leading position. *Petridiostroma* and *Stelodictyon* gained a cosmopolitan status beside *Clathrodictyon* and *Ecclimadictyon,* already widespread in the Llandovery. A very unusual taxon, *Gerronodictyon*, was specific for the eastern Urals and may be treated as a real endemic genus. A rapid diversification took place in the order Actinostromatida. Actually, it had started already in the latest Llandovery. First, actinostromellid genera *Actinostromella* and *Pichiostroma* appeared in the Gotland sections and Kentucky section respectively. *Araneosustroma,* of the family Densastromatidae, was also added, as well as *Pseudolabechia* and *Vikingia* of the family Pseudolabechiidae. *Densastroma* and *Plecto-*

stroma became the most widespread genera among the order Actinostromatida.

Representatives of Stromatoporida (*Eostromatopora, Lineastroma, Stromatopora, Syringostromella*), which had already appeared in the late Llandovery, but had a restricted distribution, expanded their area of distribution considerably during the Wenlock.

In summary, the present, rather uneven, data from different regions do not provide evidence of the existence of faunal provinces in the Wenlock stromatoporoids. However, the species lists from the western and eastern slopes of the Urals (Bogoyavlenskaya, 1973a, 1976) contain only a few common species, suggesting that the eastern Urals represented a Silurian island-arc setting, and that it was situated further away from the Baltica paleocontinent.

LUDLOW

The Ludlow epoch was characterized by the final closure of the Iapetus Ocean, which evoked progressive upheaval of the Laurentia, Baltica, and Siberia paleocontinents, sea-level lowstands, and regressions. The epi- and intracontinental basins of North American and Siberian platforms became largely restricted marine, evaporitic, and unfavorable for inhabitation of stromatoporoids. It was a time of decline in prominence of shallow shelf coral-stromatoporoid reefs, but expansion of microbial-sponge reefs in off-shelf and slope settings (Copper, 2002). The main stromatoporoid localities of Ludlow age are situated on the platform margins (Fig. 383): Gaspé Peninsula (North America); Baltic area, Podolia, and Ural-Novaya Zemlya district (eastern European Platform); Kureika River (Siberian Platform). Some new stromatoporoid localities were added in the Ludlow: Turkey, Inner Mongolia, and Japan (Kitakami Mountainland). The occurrences of the Ludlow stromatoporoids range from ~45° N (Mongolia, Inner Mongolia) to ~50° S (Bohemia, Turkey), using the base maps of Golonka (2002), but the latitudinal range decreases to about 40° N and S, which seems more realistic if the paleomaps of Torsvik and Cocks (2013b) are employed.

The Ludlow stromatoporoid fauna was almost as diverse as that of the Wenlock. It was still dominated by clathrodictyids and actinostromatids, but representatives of the Labechiida became very rare. In the order Clathrodictyida, genus *Plexodictyon sensu stricto (s.s.)* became almost as widespread and cosmopolitan as *Clathrodictyon, Ecclimadictyon,* and *Petridiostroma*, but more remarkable is the addition of *Schistodictyon* in the stratigraphic sections of northern China, Tian Shan, Bohemia, and New South Wales, whereas this genus does not appear from the Laurussian cratons (Laurentia, Baltica, Siberia).

Compared with the Wenlock, there were no remarkable changes in the generic content or distribution of actinostromatids, stromatoporids, and syringostromatids. In the order Stromatoporellida, *Hermatostromella* (originally *Amnestostroma*) was added to the widespread *Simplexodictyon* in the region of the eastern Urals. The presence of the fine-columnar to dendroid stromatoporoids *Amphipora sensu lato (s.l.)* and *Clathrodictyella* deserve special mention as the earliest representatives of the very specific order Amphiporida, which became widespread in the Devonian. *Clavidictyon s.s.* and *Praeidiostroma* may belong to the same order, but their systematic position remains in dispute.

The generally cosmopolitan nature of the stromatoporoid fauna remained during the Ludlow, though a restricted distribution of some specific taxa points to a certain tendency to endemism or provincialism. First, the eastern Urals were characterized by the presence of *Gerronodictyon, Praeidiostroma, Hermatostromella* (syn. *Amnestostroma*) and specific species of *Stelodictyon, Gerronostromaria, Clathrodictyella,* and *Amphipora* (syn. *Stellopora*). Second, *Schistodictyon*, which is common to northern China, Tian Shan, New South Wales, and Bohemia, is not

TABLE 38. Distribution of stromatoporoid genera in the Ludlow (+, occurrences of Ludlow genera; *?*, uncertain or doubtful generic entries) (Stock, Nestor, & Webby, 2012).

Order Genus	Michigan, Ontario	Eastern Quebec	Somerset Island	Gotland, Estonia	Podolia	Western Urals	Eastern Urals	Novaya Zemlya
	4	5	6	7	8	9	10	11
Labechiida								
Labechiella								
Lophiostroma				+	+			
Rosenella	?							
Clathrodictyida								
Clathrodictyon	+	+		+	+	+		+
Ecclimadictyon	+	+		+	+	+	+	+
Gerronodictyon							+	
Gerronostromaria		?				+	+	
Intexodictyides								
Neobeatricea		+						
Oslodictyon				+				
Petridiostroma				+	+	+	+	
Plexodictyon			+	+		+	+	+
Schistodictyon								
Stelodictyon	+				+		+	
Yabeodictyon			+	+		+		+
Actinostromatida								
Actinostromella		+		+	+			
Araneosustroma				+			+	
Bicolumnostratum					+			
Crumplestroma								
Densastroma		+		+	+	+		+
Desmostroma					+			
Pichiostroma								
Plectostroma	+	+	+	+	+			+
Pseudolabechia				+				+
Stromatoporellida								
Hermatostromella							+	
Simplexodictyon			+	+	+		+	+
Stromatoporida								
Stromatopora		+		+	+			
Syringostromella	+			+	+		+	
Syringostromatida								
"Parallelopora"				+				
Parallelostroma		+		+	+	+		+
Amphiporida								
Amphipora s.l.			+	+			+	
Clathrodictyella					+		+	+
Uncertain affinities								
Clavidictyon s.s.								
Praeidiostroma							+	

recorded from North America, Siberian, and eastern European platforms. Third, the genus *Lophiostroma* (order Labechiida, family Lophiostromatidae) reappears in the Ludlow of Gotland, Estonia, Podolia, and Bosporus district of Turkey, although this genus had only been present previously in the Ordovician.

TABLE 38 (*continued from facing page*).

Order Genus	Siberian Platform 12	Altai, Salair, Tuva 13	Mongolia, northern China 14	Tian Shan 15	Bohemia 16	Turkey 17	Iran 18	Japan 19	Northern Queensland 20	New South Wales 21
Labechiida										
Labechiella								+		
Lophiostroma						+				
Rosenella										+
Clathrodictyida										
Clathrodictyon	+		+				+			+
Ecclimadictyon	+		+	?					+	+
Gerronodictyon										
Gerronostromaria										
Intexodictyides				+						+
Neobeatricea										
Oslodictyon										+
Petridiostroma		+	+	+				+		
Plexodictyon		+	+							+
Schistodictyon			+	+	+					+
Stelodictyon		+								
Yabeodictyon				+						
Actinostromatida										
Actinostromella										+
Araneosustroma										
Bicolumnostratum										
Crumplestroma		+								
Densastroma	+		+					?		+
Desmostroma			+							?
Pichiostroma		+	?							
Plectostroma			+	+						
Pseudolabechia										
Stromatoporellida										
Hermatostromella	?									
Simplexodictyon		+	+	+					+	+
Stromatoporida										
Stromatopora	+		+	+				+		
Syringostromella		+	+	+						
Syringostromatida										
"Parallelopora"										
Parellelostroma	+		+	+						+
Amphiporida										
Amphipora s.l.				+				+		+
Clathrodictyella				+						
Uncertain affinities										
Clavidictyon s.s.								+		
Praeidiostroma										

PRIDOLI

In the Pridoli, the regressive trend of development continued in many parts of the world, and occurrences of stromatoporoids became less common (Fig. 383). Stromatoporoids have not been described from the Pridoli of the Gondwana supercontinent or the Siberian craton, except Salair. In North America,

TABLE 39. Distribution of stromatoporoid genera in the Pridoli (+, occurrences of Pridoli genera; ?, uncertain or doubtful generic entries) (Stock, Nestor, & Webby, 2012).

Order Genus	Alabama 1	Virginia 2	New York 3	Somerset Island 6	Estonia 7	Podolia 8	Western Urals 9	Eastern Urals 10	Salair 13	Mongolia 14	Tian Shan 15
Labechiida											
Labechia									+		
Lophiostroma						+					
Pachystylostroma					+						
Rosenella						+					
Clathrodictyida											
Ecclimadictyon								+			+
Intexodictyides											?
Labechiina									+		
Petridiostroma	+		?								
Plexodictyon		+		+		+	+	+		+	+
Schistodictyon											+
Yabeodictyon				+							
Actinostromatida											
Acosmostroma		+	+								
Actinostromella	+				+						
Bicolumnostratum			+			+					
Densastroma					+	+		+			+
Desmostroma						+					?
Plectostroma					+	+				+	
Vikingia						+					
Stromatoporellida											
Simplexodictyon						+					
Stromatoporida											
Stromatopora			+			+				+	
Syringostromella	?					+		+		+	?
Syringostromatida											
Parallelostroma	+	+	+		+	+	+	+	+	+	+
Amphiporida											
Amphipora s.l.						+	+	+			+
Clathrodictyella						+	+	+			+
Uncertain affinities											
Perplexostroma						+					
Praeidiostroma								+			

the findings are restricted to the foreland basin of the Appalachians (Alabama, Virginia, New York), and to arctic Canada (Somerset Island). The richest stromatoporoid localities are situated around the Baltica paleocontinent (Estonia, Podolia, Urals), and in Tian Shan, which were located within the tropical climatic zone. The latitudinal range of stromatoporoids stayed the same as in Ludlow time.

There is almost no change in the taxonomic content of the Pridoli stromatoporoid fauna in comparison with the Ludlow fauna. Labechiids are represented by single findings of the most common genera: *Labechia*, *Lophiostroma, Pachystylostroma*, and *Rosenella*. In the order Clathrodictyida, the role of the family Clathrodictyidae decreased drastically, and the most common genera, *Clathrodictyon* and *Stelodictyon,* are practically lacking. *Plexodictyon* (family Actinodictyidae) became the most numerous and widespread genus of clathrodictyids. *Parallelostroma* (order Syringostromatida) also gained a prevalent position and practically cosmopolitan distribution. Amphiporids (*Amphipora s.l.* and *Clathrodictyella*) occur abundantly in the sections of Podolia, Urals, and Tian Shan, forming specific biogenic interbeds, but recorded data are insufficient to allow patterns of endemism for provincialism of the Pridoli stromatoporoid faunas to be ascertained.

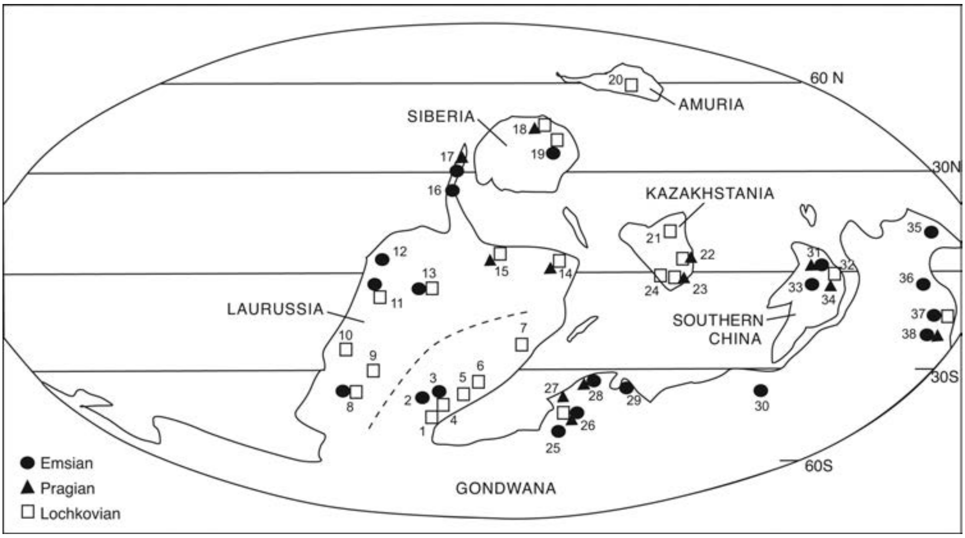


FIG. 384. Geographic distribution of Lower Devonian stromatoporoids; *dashed line* separates the two realms; localities 1–7 are in the Eastern Americas Realm, and localities 8–38 are in the Old World Realm. Key to localities: *1,* Virginia; *2,* Michigan; *3,* southern Ontario; *4,* New York; *5,* Maine; *6,* Gaspé, Quebec; *7,* Podolia, Ukraine; *8,* Nevada; *9,* Idaho; *10,* southern British Columbia; *11,* Yukon Territory and Northwest Territories; *12,* eastern Alaska; *13,* Arctic Canada; *14,* southern and eastern Urals; *15,* northern and western Urals; *16,* Kolyma Basin; *17,* Ulachan-Sis Range; *18,* Altai-Sayan and Salair; *19,* Kuznetsk Basin; *20,* Mongolia; *21,* Tian Shan; *22,* Central Asia; *23,* Turkestan and Zeravshan Range; *24,* Uzbekistan; *25,* southern Spain; *26,* northern Spain; *27,* northwestern France; *28,* Czech Republic; *29,* Carnic Alps, Austria; *30,* Afghanistan; *31,* Vietnam; *32,* Yunnan; *33,* Guangxi; *34,* Sichuan; *35,* Inner Mongolia; *36,* northern Queensland; *37,* New South Wales; *38,* Victoria (Stock, Nestor, & Webby, 2012).

Investigators of different groups of fossils have stressed the extremely low degree of provincialism of the Silurian faunas in comparison with the Ordovician and Devonian. Boucot and Johnson (1973) distinguished two faunal provinces for the brachiopods: (1) Silurian Cosmopolitan Province, embracing continents of the present Northern Hemisphere and Australia; and (2) Malvinokaffric Province, including southern parts of South America and Africa. In the Silurian, the Malvinokaffric Province was situated in the cold, high southern latitudes, uninhabited by stromatoporoids. In the second half of the Silurian, from the late Wenlock onward, the provincialism of brachiopods increased slightly. Therefore, Boucot and Johnson (1973) divided the Cosmopolitan Province into the Circum-Atlantic and Uralian-Cordilleran subprovinces. The analysis of the distribution of stromatoporoids confirms the almost cosmopolitan character of the early Silurian fauna of stromatoporoids and its slightly increasing provincialism in the late Silurian (particularly in the Ludlow), but too unequal information from different regions prevents recognition of clearly defined provinces or subprovinces for the stromatoporoids.

DEVONIAN

Carl W. Stock

The Devonian Period is divided into three epochs: Early, Middle, and Late. In ascending order, the Early Devonian contains three stages/ages: Lochkovian, Pragian, Emsian; the Middle Devonian contains two: Eifelian and Givetian; and the Late Devonian two: Frasnian and Famennian. Stromatoporoids reached their peak abundance during the Givetian and Frasnian (Stock, 1990), suffered a near-extinction at the close of the Frasnian, and were extinct by

TABLE 40. Devonian stromatoporoid genera in time and space ; *?,* hiatus with no specimens of the genus confirmed within the time interval (and consequently not included in generic totals); *Prev.,* genera originating prior to the Devonian; *O,* Old World Realm; *E,* Eastern Americas Realm. Use of *O* and/or *E* for the Frasnian and Famennian represent areas formerly in both of those realms (new).

Order Genus	Prev.	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Labechiida								
Rosenella	x	O	?	O	O	?	O	O
Cystostroma	x	?	?	O	?	?	O	O
Labechia	x	O	?	O	?	?	O	O
Labechiella	x	?	O	O	O	O	O	O
Stromatocerium	x	?	?	O				
Platiferostroma								O
Parastylostroma							O	O
Stylostroma	x	O	?	O	?	?	O	O
Pachystylostroma	x	?	?	?	?	?	?	O
Pennastroma								O
Spinostroma								O
Pararosenella								O
Lophiostroma	x	?	?	?	?	?	O	
Vietnamostroma								O
Clathrodictyida								
Clathrodictyon	x	?	?	O	OE	OE		
Bullulodictyon							O	
Coenellostroma				O	O			
Oslodictyon	x	O						
Stelodictyon	x	E						
Yabeodictyon	x	?	?	O				
Gerronostromaria	x	?	O	O	OE	OE	O	O
Petridiostroma	x	OE	?	?	OE	OE		
Atelodictyon		O	O	O	OE	OE	OE	O
Coenostelodictyon		O						
?*Cubodictyon*					O			
Intexodictyides	x	E	O	O				
Tienodictyon				O	O			
Anostylostroma					OE	OE	O	O
Belemnostroma		O						
Hammatostroma						O	OE	
Nexililamina				O	O			
Pseudoactinodictyon				OE	OE	OE	O	
Schistodictyon	x	?	O	O	OE	OE	O	
Actinostromatida								
Actinostroma		O	O	O	O	OE	OE	
Bifariostroma				O	O	O	O	
Plectostroma	x	O	O	O	O	O	O	
Actinostromella	x	O						
Araneosustroma	x	O						
Stromatoporellida								
Stromatoporella			O	OE	OE	OE		
Clathrocoilona				O	O	OE	OE	
Dendrostroma						OE	O	
Simplexodictyon	x	?	?	O	O			
Trupetostroma					OE	OE	OE	
Stictostroma				OE	OE	OE	OE	
Syringodictyon					E			
Styloporella							O	
Tubuliporella			O	?	O			
Hermatostroma					O	OE	OE	
Hermatoporella						O	OE	
Hermatostromella	x	O	O	O				

TABLE 40 (*continued from facing page*).

Order Genus	Prev.	Lochkovian	Pragian	Emsian	Eifelian	Givetian	Frasnian	Famennian
Synthetostroma						O	O	
Idiostroma					O	OE	O	
Stromatoporida								
Stromatopora	x	O	O	O	O	OE	O	O
Climacostroma					O	O		
Glyptostromoides				O	O	O		
Neosyringostroma				O	O	OE		
Pseudotrupetostroma				O	O	O		
Taleastroma					OE			
Ferestromatopora						OE	O	
Arctostroma						O	OE	
Syringostromella	x	OE	O	O				
Salairella			O	O	O	O	O	
Syringostromatida								
Syringostroma		O	?	OE	OE	E		
Atopostroma		OE	?	O				
Columnostroma		E	O	?	E	O		
Coenostroma	x	E	?	O	OE	OE		
Parallelopora				OE	OE	O		
Habrostroma	x	OE	O	OE	OE	OE		
Parallelostroma	x	OE	O					
Stachyodes					O	OE	OE	
Amphiporida								
Amphipora	x	O	O	O	OE	OE	OE	O
Euryamphipora							O	
Novitella							O	
Vacuustroma				O	?	O	O	
Total genera	27	24	17	37	39	37	35	17

the end of the Devonian. One exception is *Kyklopora,* from the the Upper Mississippian of the Donets Basin, Ukraine, which may be a clathrodictyid descendant (see Clathrodictyida, p. 755–758) or may derive from a different line of descent from post-Devonian stromatoporoid-type hypercalcified sponges (see p. 193–208). Generic diversity peaked in the Eifelian but was high from the Emsian through Frasnian (Table 40).

In Devonian paleogeography, a new tectonic plate developed. The Ordovician–Silurian Laurentia, Baltica, and Avalonia plates merged to form the Laurussia plate (see GOLONKA, 2002), known to some as the Euramerica plate (e.g., JOHNSON, KLAPPER, & SANDBERG, 1985).

DISTRIBUTION OF DEVONIAN DATA

The Lower Devonian map is based on the latest Silurian–Early Devonian map of GOLONKA (2002, fig. 11), and the Middle and Upper Devonian maps are founded on the Middle–Late Devonian map of GOLONKA (2002, fig. 13). The total latitudinal range and the northernmost and southernmost occurrences of Devonian stromatoporoids by stage are given in Table 40.

The southernmost occurrence of Lochkovian stromatoporoids is in Virginia (Fig. 384, no. 2), and the northernmost is in Mongolia (Fig. 384, no. 17), for a range of 105°. The Pragian range is 90°, with extremes in northern Spain (Fig. 384, no. 23) and Altai-Sayan and Salair (Fig. 384, no. 15). The range remained at 90° in the Emsian, but shifted slightly southward, with southern Spain being southernmost (Fig. 384, no. 22) and the Ulachan-Sis Range and the Kuznetsk Basin being equally northernmost (Fig. 384, no. 14, 16).

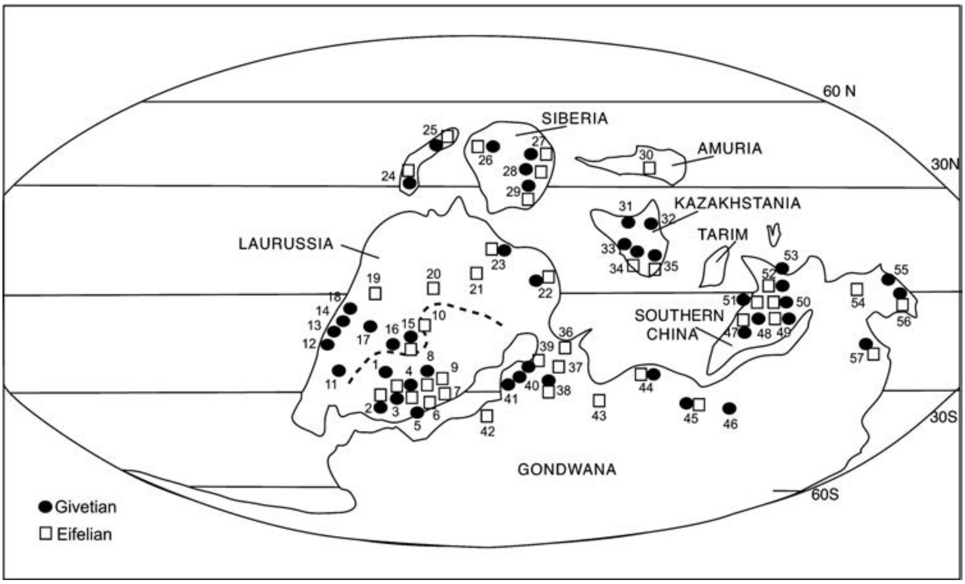


FIG. 385. Geographic distribution of Middle Devonian stromatoporoids. The *dashed line* separates the two realms; localities 1–10 are in the Eastern Americas Realm, and all the known localities (11–57) worldwide are in the Old World Realm. Key to localities: *1,* Iowa; *2,* Missouri; *3,* Illinois; *4,* Indiana; *5,* Kentucky; *6,* Ohio; *7,* New York; *8,* Michigan; *9,* southern Ontario; *10,* northern Ontario; *11,* Nevada; *12,* northern California; *13,* Oregon; *14,* Washington; *15,* Manitoba; *16,* Saskatchewan; *17,* Alberta; *18,* northern British Columbia; *19,* Yukon and Northwest Territories; *20,* Arctic Canada; *21,* Russian Platform; *22,* southern Urals; *23,* northern Urals; *24,* Omolon; *25,* Ulachan-Sis; *26,* Sette-Daban Range and Far East; *27,* Altai-Sayan and Salair; *28,* Kuznetsk Basin; *29,* western Siberian Platform; *30,* Mongolia; *31,* Karaganda; *32,* Tian Shan; *33,* southern Kazakhstan; *34,* Uzbekistan; *35,* Zeravshan Range, Isfar, and Kashkadar; *36,* Poland; *37,* Czech Republic; *38,* Germany; *39,* Belgium; *40,* France; *41,* northern Spain; *42,* Morocco; *43,* Turkey; *44,* Caucasus; *45,* Afghanistan; *46,* Xizang (Tibet); *47,* Hunan; *48,* Guizhou; *49,* Sichuan; *50,* Yunnan; *51,* Guangxi; *52,* Vietnam; *53,* Northeast China; *54,* Qinghai; *55,* Xinjiang; *56,* northeastern Thailand; *57,* northern Queensland (Stock, Nestor, & Webby, 2012).

Eifelian stromatoporoids range from Morocco (Fig. 385, no. 40) to the Ulachan-Sis and Sette-Daban Ranges (Fig. 385, no. 23–24) for a total of 82°. The Givetian range is slightly smaller (80°), with the same northern extreme as in the Eifelian and the southern extreme in Kentucky (Fig. 385, no. 7).

The total range for the Frasnian (78°) is down slightly from the Givetian, but the extremes have shifted slightly, with the northernmost occurrence being in the Ulachan-Sis Range (Fig. 386, no. 16) and the southernmost occurrence being in both Nevada and Afghanistan (Fig. 386, no. 2, 43). The southern extent of Famennian stromatoporoids was limited to Germany (Fig. 386, no. 34), but the northernmost occurrence of stromatoporoids remained in the Ulachan-Sis Range, resulting in a total paleolatitudinal spread of 70°.

Examination of Table 41 reveals that in five of the seven stages, the northern limit of the total range extends further from the paleoequator than does southern limit. In only the Emsian is the paleolatitudinal limit to the south greater than the northern limit—the limits are equal in the Pragian. This sort of asymmetry was noted on older plate reconstructions of SCOTESE (1986), by STOCK (1990) for the Devonian stromatoporoids, and PEDDER and OLIVER (1990) for Emsian rugose corals. STOCK (1990) concluded that the absence of a large land mass in the northern hemisphere, relative to the large land mass in the southern hemisphere, may have led to warmer sea temperatures in the north, allowing an asymmetry

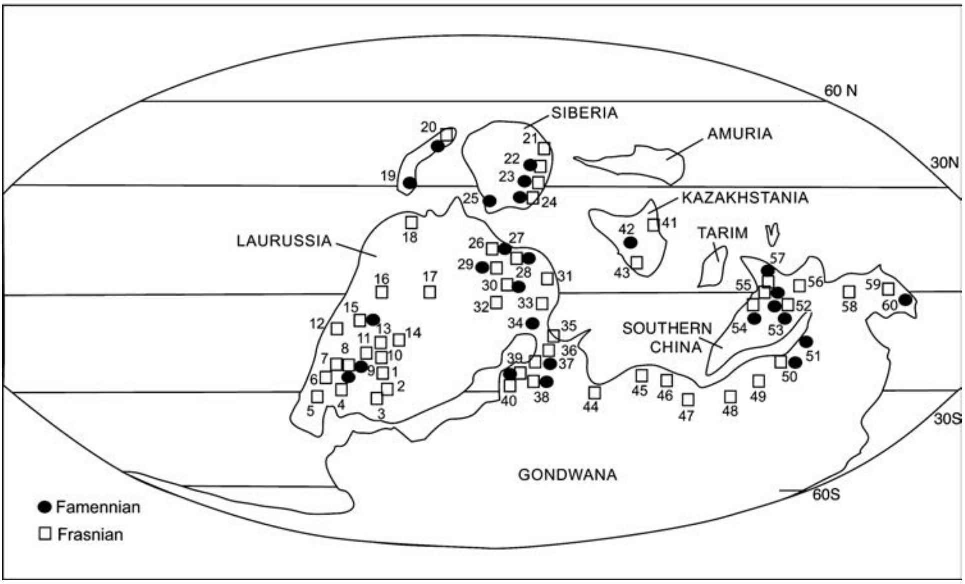


FIG. 386. Geographic distribution of Upper Devonian stromatoporoids. Key to localities: *1,* Nebraska; *2,* Iowa; *3,* Missouri; *4,* New Mexico; *5,* Sonora; *6,* Arizona; *7,* Nevada; *8,* Utah; *9,* Wyoming; *10,* North Dakota; *11,* Montana; *12,* Washington; *13,* Saskatchewan; *14,* Manitoba; *15,* Alberta; *16,* Northwest Territories; *17,* Arctic Canada; *18,* northern Alaska; *19,* Omolon; *20,* Ulachan-Sis; *21,* Altai-Sayan; *22,* Kuznetsk Basin; *23,* western Siberian Platform; *24,* Yogorsk Peninsula; *25,* Novaya Zemlya; *26,* Bolshaya Zelenets and Dolgi Islands; *27,* Voivo-Vozh; *28,* northern Urals; *29,* Pechora Basin and Timan; *30,* Russian Platform; *31,* southern Urals; *32,* St. Petersburg region; *33,* Lower Volga and Volgograd; *34,* Donets Basin; *35,* Poland; *36,* Czech Republic; *37,* Belgium; *38,* Germany; *39,* France; *40,* northern Spain; *41,* Tian Shan; *42,* Kazakhstan; *43,* Uzbekistan; *44,* Turkey; *45,* Caucasus; *46,* Iran; *47,* Afghanistan; *48,* Xizang; *49,* Carnarvon Basin; *50,* Canning Basin; *51,* Bonaparte Basin; *52,* Sichuan; *53,* Guizhou; *54,* Hunan; *55,* Guangxi; *56,* Yunnan; *57,* Vietnam; *58,* northeastern China; *59,* Qinghai; *60,* Xinjiang (Stock, Nestor, & Webby, 2012).

of the tropical and subtropical climates in which the stromatoporoids dwelled. He also suggested that the Siberian plate might have been plotted too far north, as that is where the northernmost data points were located. In the GOLONKA (2002) plate reconstructions, Siberia remains fairly far north—up to 55° N—but not as far north as with SCOTESE (1986)—60–80° N. The northernmost landmass on GOLONKA's (2002) reconstructions is in the Lower Devonian, where the Amuria plate extends to 65° N.

Another aspect revealed by the data in Table 41 is that the total latitudinal range of stromatoporoids decreased through the Devonian. A first hypothesis might be that the Earth cooled throughout the Devonian, resulting in shrinking of the tropical and subtropical climates toward the equator. Generally speaking, global cooling accompanies a fall in eustatic sea level, and global warming accompanies a rise in eustatic sea level (e.g., FRAKES, FRANCIS, & SYKTUS, 1992); however, JOHNSON and SANDBERG (1988) indicated that, following relatively low eustatic sea level during the Early Devonian, sea level rose throughout the Eifelian and Givetian, peaking near the end of the Frasnian, with a precipitous fall in association with the Frasnian–Famennian boundary. According to JOACHIMSKI and others (2002), global temperature rose irregularly through the Middle Devonian, with an abrupt fall near the end of the Givetian, followed by a general rise during the Frasnian, followed by another abrupt fall near the end of the Frasnian. During the Famennian, Earth cooled, and eustatic sea level fell,

TABLE 41. Paleolatitudinal ranges of Devonian stromatoporoids by stage (Stock, Nestor, & Webby, 2012).

Age	Northernmost	Southernmost	Total
Famennian	45°	25°	70°
Frasnian	45°	33°	78°
Givetian	45°	35°	80°
Eifelian	45°	37°	82°
Emsian	40°	50°	90°
Pragian	45°	45°	90°
Lochkovian	60°	45°	105°

due at least in part to the onset of glaciation (e.g., CROWELL, 1999). Thus, the latitudinal contraction toward the paleoequator of the geographic range of stromatoporoids through the Devonian appears to contradict what would be expected of global warming and rise of eustatic sea level for at least the Eifelian through the Frasnian. A factor that could explain at least some of the apparent contradiction in the range of stromatoporoids, and the increase in temperature and sea level, is the loss of appropriate habitat.

The Laurussia plate developed in two stages (see Fig. 382–384) with a collision (an accretion event) of the Siberian, Baltica, Avalonian, and Laurentian cratons by the Ludlow, and then in the Early Devonian, the Siberian craton was rifted from the rest of Laurussia to again become an isolated craton, while the remains of Laurussia continued to approach Gondwana (in association with a partial closure of the Rheic Ocean). Stromatoporoids in southern Laurussia—including the area of present-day eastern United States (see spread of localities 1–9 on Fig. 385)—represent some of their southernmost occurrences. During the Middle and Late Devonian, the Acadian Orogeny took place in southeastern Laurussia, resulting in a northwestwardly prograding wedge of siliciclastic sediments. The introduction of siliciclastics caused increases in turbidity and substrate instability, both prohibitive for stromatoporoid habitation, and stromatoporoids withdrew from the eastern United States (STOCK, 1997b). In addition, on the Gondwanan margin of Morocco, stromatoporoids invaded the region for a comparatively short time in the Middle Devonian (Eifelian) (see Fig. 385). A noticeable post-Lochkovian latitudinal contraction can be seen in the distribution of stromatoporoids from the higher southern paleolatitudes between Early Devonian (Lochkovian) to Late Devonian (Famennian) time (see map series, Fig. 384–386).

PALEOBIOGEOGRAPHIC UNITS

Most workers have divided the marine biota of the Devonian into three realms (e.g., BLODGETT, ROHR, & BOUCOT, 1990): (1) Malvinokaffric Realm—southern high latitude areas; (2) Eastern Americas Realm (EAR)—southeastern North America and northwestern South America; and (3) Old World Realm (OWR)—all separate marine habitats. These realms became established primarily on the basis of distributions of brachiopods (e.g., JOHNSON & BOUCOT, 1973) and rugose corals (e.g., OLIVER, 1977). Apparently, it was too cold for stromatoporoids in the Malvinokaffric Realm and the South American part of the Eastern Americas Realm. The barrier separating the OWR from the EAR was located in Laurussia (Fig. 384–385) and consisted of the Transcontinental Arch, which extended from Arizona and New Mexico to Minnesota and Wisconsin, and to the Canadian Shield, including most of central Canada, and probably extended into Greenland and the Baltic Shield, as a kind of so-called Laurussian inter-realm barrier (e.g., WITZKE, 1990).

The existence of two tropical to subtropical realms was in place at the beginning of the Devonian until late in the Middle Devonian. An exception to this is the total absence of stromatoporoids from the Pragian of the EAR, and North American parts of the OWR, first noted by STOCK (1990). There are two possible explanations for this absence. The Pragian to early Emsian is a time that coincides with extreme sea-level fall, at the end of SLOSS's (1963) Tippecanoe cratonic sequence, when much of North America was exposed to the erosion of its most recently deposited sediments (see also Devonian sea-level curve of JOHNSON, KLAPPER, and SANDBERG, 1985, fig. 12). Additional erosion in the Mesozoic and Cenozoic, especially by glacial ice during the Quaternary, also could have contributed to the removal of Pragian sedimentary rocks. The erosional hypothesis is given credence by two recent descriptions of Jurassic kimberlites on the Canadian Shield that contain Devonian normal marine carbonate xenoliths (Cookenboo, Orchard, & Daoud, 1998; McCracken, Armstrong, & Bolton, 2000).

Most researchers agree that the discrimination between the OWR and EAR ended during an episode of sea-level rise in the middle–late Givetian, known as the Taghanic Onlap, cycle IIa of Johnson and Sandberg (1988). At this time, it is believed that the Laurussian inter-realm barrier was breached, allowing the mixing of OWR and EAR faunas. Seven genera, known from only the OWR during the Eifelian, invaded the EAR during the Givetian, but only one genus migrated from the EAR to the OWR at the same time (Table 40). Oliver and Pedder (1989) stated that the mixing of OWR and EAR rugose coral faunas during the Taghanic Onlap resulted in the extinction of all former EAR families and genera. Boucot (1990) saw a similar pattern for brachiopods at the same time. Eight stromatoporoid genera found in both the OWR and EAR during the Givetian became extinct in the areas of the former EAR during the Frasnian, but eight OWR-EAR Givetian genera remained in both areas in the Frasnian (Table 40).

The Frasnian–Famennian extinction profoundly affected the stromatoporoids; a total of 24 Frasnian genera became extinct before the Famennian (Table 40). During the Famennian, stromatoporoids were absent from the area of the former EAR; Stock (1997b) concluded that the influx of siliciclastic sediments produced during the Acadian Orogeny and global cooling contributed to this absence.

Table 42. Degrees of endemism of stromatoporoid genera through the Devonian; *OWR,* Old World Realm; *EAR,* Eastern Americas Realm; *NA,* not applicable, as stromatoporoids absent from area of EAR (Stock, Nestor, & Webby, 2012).

Age	OWR Endemic	EAR Endemic	Cosmopolitan
Famennian	17 (NA)	0 (NA)	0
Frasnian	24 (69%)	0 (0%)	11
Givetian	14 (54%)	1 (4%)	22
Eifelian	21 (57%	2 (11%)	16
Emsian	31 (84%)	0 (0%)	6
Pragian	17 (NA)	0 (NA)	0
Lochkovian	15 (75%)	4 (20%)	5

During the Famennian, stromatoporoids retreated from many areas of Laurussia and Gondwana (Fig. 386). Stearn (1987) delineated three stromatoporoid faunas in the Famennian: (1) dominantly labechiids; (2) labechiids and clathrodictyids; and (3) mainly clathrodictyids, without labechiids, a more Frasnian-like assembly of genera. He suggested that labechiids might have been better adapted to cooler water than were the typically Devonian nonlabechiids. Bogoyavlenskaya (1982a) described two Famennian stromatoporoid communities: (1) western slopes of the Urals, Novaya Zemlya, Donets Basin, several other parts of Russia, and southeastern China (e.g., Guangxi, Guizhou, Hunan); and (2) eastern slopes of the Urals, central Kazakhstan, and western Europe (France, Belgium, Germany, Czech Republic). At the time of publication, several of Bogoyavlenskaya's localities were thought to contain strata of earliest Carboniferous (Tournaisian) age; her so-called Etroeungtian (or Strunian) fauna, is presently equated with the late Famennian interval—a subdivision that remains to be defined at a level toward the base, or higher, within the *expansa* Zone of the Upper Devonian–Lower Carboniferous conodont succession (see Extinction Patterns of the Paleozoic Stromatoporoidea, p. 600, Table 30; adapted from Sandberg, Morrow, & Ziegler, 2002). They since have been placed in the Famennian. Faunas 1 and 2 of Stearn (1987) coincide with Bogoyavlenskaya's (1982a) community 1, and his fauna 3 coincides with her community 2. Hamilton (1970) stated that, in Russia, the Famennian strata of the western slopes of the Urals, Novaya Zemlya, the Yogorsk Peninsula, Bolshaya Zelenets Island, and Dolgi Island were deposited in relatively shallow, miogeosynclinal environments, whereas strata on the eastern slopes of the Urals were deposited in deeper, eugeosynclinal environments. Stock (1990) noted that areas of shallower water contained dominantly labechiid and mixed stromatoporoid faunas (Stearn's [1987] faunas 1 and 2) and areas of deeper water contained dominantly nonlabechiids (Stearn's [1987] fauna 3). Stock (2005) suggested that global cooling associated with Famennian glaciations (e.g., Crowell, 1999), which probably made a significant contribution to nonlabechiid stromatoporoid extinctions at the end of the Frasnian, continued to adversely affect those genera most typical of the Lochkovian–Frasnian.

Table 42 summarizes the level of endemism of the Devonian stromatoporoid genera in the OWR and EAR by age. For the OWR, endemism ranged from 54% in the Givetian to 84% in the Emsian. In only the Lochkovian (75%) and Emsian (84%) was the 75% endemism criterion of Kauffman (1973) attained; however, in all ages, the minimum criterion of 33% of Oliver (1977) was exceeded.

Whereas the OWR contains an endemic stromatoporoid fauna, this is not the case for the EAR, where endemism ranged from 0% in the Emsian to 20% in the Lochkovian (Table 42). Clearly, the stromatoporoids do not support the EAR as a separate realm. Perhaps, the EAR existed as a province within one tropical to semitropical realm during the Devonian. The OWR covered a much greater area than did the EAR, and no doubt contained several provinces that have the same level of genus endemism as the EAR. This having been said, it is interesting to note that stromatoporoids in order Labechiida were absent from the EAR throughout the Devonian (Table 40).

CONCLUSIONS

Carl W. Stock, Heldur Nestor,
& B. D. Webby

In their paper on Devonian world paleogeography, Heckel and Witzke (1979, p. 116) stated, "Stromatoporoids are the most widely reported benthonic group confined to Devonian warm water between 35° N. and 40° S." Although the exact paleolatitudinal ranges plotted here do not always match those of Heckel and Witzke (1979), we still find a paleoequatorially centered, paleogeographic distribution of stromatoporoids in the Devonian, as well as in the Ordovician and Silurian. Examination of the full time range of stromatoporoids indicates several trends in terms of geographic range and endemism.

PALEOLATITUDINAL RANGE

Latitudinal ranges given here are understood to be approximations, limited by geographic uncertainties in the determination of collecting localities and time averaging used in constructing the base maps. The paleolatitudinal range of stromatoporoids in the mid–late Darriwilian and Sandbian was 55° and 75° in the Katian. In the Hirnantian, the range contracted to 10°, but it increased through most of the Silurian, with 65° in the Llandovery, 75–80° in the Wenlock, and 95° in the Ludlow. After a contraction of 75° in the Pridoli, a maximum range of 105° was attained in the Lochkovian. This maximum is heavily dependent on the far northern location of Amuria, as plotted by Golonka (2002); were that locality omitted, the Lochkovian range would have been 90°, the same as that determined for the Pragian and Emsian. The remainder of the Devonian shows a gradual decrease in paleolatitudinal range, with 82° in the Eifelian, 80° in the Givetian, 78° in the Frasnian, and 70° in the Famennian.

For 9 of the 15 time intervals documented here, there is an asymmetry to the paleolatitudinal range of stromatoporoids; the northern limit of their extent is at least 10° further from the paleoequator than it is south of the paleoequator. This is true for the mid–late Darriwilian through the Katian, the Pridoli through the Lochkovian—the latter dependent on the position of Amuria—and the Eifelian through the Famennian. A steeper climatic gradient may have existed in the Devonian of the southern hemisphere, relative to the northern hemisphere, due to the presence of the large landmass of Gondwana in the south and the presence of mostly ocean in the north (see p. 681). More than not, this paleolatitudinal asymmetry is associated with times of abundance for stromatoporoids (e.g., Katian, Eifelian–Frasnian), but it is not for the Wenlock and Ludlow. Symmetry to near symmetry of paleolatitudinal ranges in the Llandovery and Pragian–Emsian are associated with times of relatively low genus diversity, as well as low sea level associated with latest Ordovician–early Silurian glaciation (GRAHN & CAPUTO, 1992; FINNEGAN & others, 2011) and the end of SLOSS's (1963) Tippecanoe sequence in the Early Devonian.

PALEOGEOGRAPHIC ANOMALIES

There were three times when the paleogeographic ranges of stromatoporoids displayed anomalous patterns. The first of these was in the Hirnantian, when stromatoporoids were restricted to just two areas—southern Laurentia (28° S; Anticosti Island); and western Baltica (30° S; Estonia) (Fig. 381). Their limited distribution may be explained by the shortness of duration of the stage, the cooling effects of ocean waters, and extinction associated with the end-Ordovician glaciation (WEBBY, 2004b).

The second is the complete absence of stromatoporoids from Gondwana during the Pridoli (Fig. 383), and the third is the complete disappearance of stromatoporoids from the Eastern Americas Realm during the Pragian (Fig. 384). With the exception of the Hirnantian, there are no obvious reasons to explain these anomalies. They could in part be artifacts of collecting—either given that not all potential stromatoporoid faunas of these ages have been sampled—or stromatoporoid-bearing strata of these ages may have been eroded, as postulated for the Pragian (see p. 686).

ENDEMISM

Provincialism is often characterized in a region by the appearance of significant endemicity of genus-level categories. In stromatoporoids, it developed to only a very limited degree through Middle–Late Ordovician and Early–Middle Devonian time. In the Ordovician, stromatoporoids were mainly confined paleoequatorially (Fig. 381) within the North American–Siberian Realm, but they did not show any marked regional (or provincial) differentiation through successive Middle–Upper Ordovician stage intervals.

There is no genus-level endemism among the Silurian stromatoporoids (see p. 681), a pattern that accords with the conclusions of BOUCOT and JOHNSON (1973) for the brachiopods of the warmer paleolatitudes. The Lochkovian–Givetian paleoequatorial Old World and Eastern Americas Realms are recognized, based on other taxa (e.g., brachiopods, corals), but no differentiation of the paleobiogeography can be recognized using the stromatoporoids alone (see p. 686).

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TECHNIQUES OF STUDY: COLLECTION, PREPARATION, AND ANALYSIS OF THE PALEOZOIC STROMATOPOROIDEA

Colin W. Stearn

FIELD OBSERVATIONS AND COLLECTING

COLLECTING IN CARBONATES OF THE REEF FACIES

Most stromatoporoids are preserved in carbonate sediments formed within a reef environment. They are, therefore, most common in unbedded or poorly bedded limestones and dolomites of the reef facies, or in bedded carbonates deposited in adjacent lagoonal or foreslope deposits. In such carbonates, the fossils do not weather free of the matrix and must be extracted, usually in fragments, by breaking the rock. Where the rock is broken in fragments in quarrying, this may not be difficult, but in natural outcrops where the unbedded reefal facies commonly forms smooth-surfaced domes, it may be almost impossible with a geologist's hammer. Where a specimen must be extracted to satisfy a sampling scheme, a portable circular saw with a cement-cutting blade can be used to make grooves around the sample and allow a cold chisel to chip it out. The saw, however, generates much rock dust, therefore the operator should wear a protective mask. Generally, in such host rocks, the collector must be satisfied with fragments that will provide enough material for the two thin sections required for identification.

In many reef outcrops, the shapes of stromatoporoids can be observed only in a random cross section. Because the whole specimen can rarely be collected, the impression of shape that such sections allow should be recorded in notes or by taking photographs before collection. The study of stromatoporoids in cores from reef reservoirs in the subsurface involves similar problems, although the regularity of the core surface may make estimates of shape in three dimensions easier. Samples must be cut from the core with a rock saw. Core storage agencies will generally allow only a small sample to be cut out of the core (for example, a cubic inch every linear foot or 15 ml/0.3 m).

In areas of cold climate, such as high altitudes and latitudes, carbonate outcrops are commonly covered with a thin tufa that obscures fossils. Fresh rock faces recently exposed by frost wedging that show the rock texture better can usually be found in these areas, but the surface may have to be broken with a hammer to reveal the fossils within. Reef textures and fossils are most clearly revealed in outcrops repeatedly abraded by flooding rivers, tides and waves, and winds charged with sand.

COLLECTING IN FOREREEF SLOPES

The carbonates deposited at the margins of Paleozoic reef complexes are commonly affected by pervasive dolomitization that reduces stromatoporoids to so-called ghosts. The faunas of these margins are commonly much better preserved in debris blocks that have slumped from the steep reef front onto the forereef slope (Mountjoy & others, 1972; Conaghan & others, 1976). Reef blocks several meters across may have traveled several kilometers downslope into basinal deposits and now constitute beds of megabreccia. Well-preserved stromatoporoid faunas have been described from such debris flow deposits (Scrivastava, Stearn, & Mountjoy, 1972; Polan & Stearn, 1984).

The depositional slope on which benthic organisms (such as stromatoporoids in position of growth) grew can be estimated by measuring growth axes. If it is assumed that the growth axis of domical and dendroid stromatoporoids is on average vertical (that is, they are geotropic or phototropic), then the divergence between the axis and a line perpendicular to the bedding will indicate the slope on which they grew. The orientation of the growth axis can be determined if the stromatoporoid is exposed in more than one plane and its pole measured with a simple device. A dowel that can be oriented along the growth axis and fixed at one end temporarily with plasticine is attached at right angles at the free end to a flat disk whose strike and dip can be measured with a Brunton compass. From these data, the poles of the bedding and growth axes can be plotted on a stereonet. In deformed beds, the post-depositional tilt of the beds must be compensated for by modifying the poles of growth by the strike and dip of the bed using a stereonet.

ORIENTATION

Kobluk (1974) measured the azimuths of dendroid stromatoporoids on bedding planes in the Miette Reef Complex in Alberta, Canada. He analyzed the results by a chi-square test to show that the stems had a preferred northwest orientation. Kobluk, Bottjer, and Risk (1977) measured the proportion between domical stromatoporoids of various sizes that were in growth position and those that were disoriented. They found no difference in mean size between those that were turned over and those in growth position. The toppled or upright position of stromatoporoids has also been measured by Kershaw (1981) at the Kuppen biostrome in Gotland, Sweden, and by Kershaw and Riding (1980) in Devon, England.

MARLS

In argillaceous limestone successions (marls), stromatoporoids may weather free or be easily extracted from the soft matrix. Such successions are found in the Silurian rocks of Scandinavia and Britain. There the growth forms of stromatoporoids are much easier to study, and surfaces of the skeletons can be examined in detail. Many of the studies of the relationship of growth form, environment, and taxonomy have been made in these areas (for example, Kershaw 1981, 1984, 1993; Kershaw & Keeling, 1994) and are discussed elsewhere (see External Morphology of Paleozoic Stromatoporoids, p. 419–486).

STATISTICALLY CONTROLLED SAMPLING

Although various research workers have advocated a statistical approach to the study of the distribution of stromatoporoid taxa or shapes in reefs, local conditions rarely make random sampling, a requirement of most statistical tests, possible over a large area. Stromatoporoids on extensively exposed horizontal bedding planes have been divided into quadrats and surveyed as to shape and size over areas of several tens of square meters. Quarry faces and mountain cliffs may expose large vertical sections of a reef deposit but are only rarely accessible for random sampling over extensive horizontal or vertical distances.

Estimates of the proportion or density of various growth forms or types of organisms on a face or bedding plane can be made by drawing random lines, or stretching strings randomly, across a face. The constituents along the line are identified. Either the total length of the line lying upon each constituent is summed, or the line is marked at a regular interval (e.g., every 5 cm), the constituent beneath each mark is recorded, and the number of occurrences is taken as a measure of the relative abundance of each constituent. The latter method, a form of point counting, is the quicker of the two (Polan & Stearn, 1984). Line intercept transects were also used by Edinger and others (2002) in their survey of Onandaga reefs. Sandström (1998) drew sketches of outcrops on Gotland at 1:5 scale and point counted these sketches to quantify the identity and shape of the stromatoporoids. Because stromatoporoids can rarely be identified taxonomically on external appearance alone, methods like these that depend on identification without collection and processing do not give information for plotting the distribution of species in a reef.

MAPPING

Detailed maps of the distribution of stromatoporoid shapes and taxa on small representative areas of biostromes and bioherms have been made by many investigators. Only studies in which the occurrence of stromatoporoids is essential, rather than incidental, are mentioned here. KERSHAW (1984, 1990) and KANO (1989, 1990) have published maps showing the distribution of stromatoporoids in the reefs of Gotland. SCHNEIDER and AUSICH (2002) have mapped the distribution of various framebuilders, including stromatoporoids, in the lower Silurian Brassfield Formation of Ohio, USA. FAGERSTROM and BRADSHAW (2002) drew maps of the distribution of Early Devonian stromatoporoids in the reef facies at Reefton, New Zealand. Stromatoporoids are prominent in the maps of Late Ordovician patch reefs in Alabama presented by STOCK and his colleagues (STOCK & BENSON, 1982; CROW & others, 2001).

GENERAL

The usual precautions of labeling and cataloguing that apply to all fossils are not discussed here. Because specimens broken from carbonates rarely are complete or show details of surfaces, wrapping of individual specimens is usually unnecessary, but pieces broken from a single large specimen should be kept together if an approximation of the abundance of the individual taxa in a collection is to be obtained from the contents of the collection bag.

A collection of papers on various laboratory techniques for preparation of fossils published as Paleontological Society Special Publication 4 (FELDMAN, CHAPMAN, & HANNIBAL, 1989) contains descriptions of many procedures relevant to stromatoporoids. A similar collection of papers was assembled earlier by KUMMEL and RAUP (1965).

THIN SECTIONS

SIZE AND THICKNESS

Since NICHOLSON introduced the method about 1875, stromatoporoid workers have used thin sections viewed in transmitted light to identify these fossils (WELLS in FELDMAN, CHAPMAN & HANNIBAL, 1989). Two sections are required to define the skeletal elements in three dimensions; one parallel to the growth surface (tangential) and the other perpendicular to it (longitudinal). Large thin sections are better than small ones, because they show the local variation of structural elements in the various phases of the skeleton. LECOMPTE (1951–1952) studied sections that were up to 5 cm × 10 cm. However, such large sections are very difficult to make uniformly thin enough to show microstructure clearly. Such sections are also difficult to store. The most useful size for thin sections is 44 mm × 75 mm, as commercially available cabinets for storing 22 mm × 75 mm slides can be modified to hold them. Sections ground to standard petrographic thickness of 30 µm are too thin to show structural elements clearly. The appropriate thickness of the section can only be determined experimentally as it depends on the particular type of preservation but should be such that the structural elements are translucent, their microstructure is clear, their edges are in sharp focus in photographs at ×10 magnification, and the crystal boundaries in the galleries are sharp. Most illustrations that appear out of focus are taken of thin sections that are too thick. Unfortunately, sections of the holotypes of older taxa are commonly too thick to show microstructure clearly.

ADHESIVES

Until the middle of the 20th century, thin sections were made exclusively with Canada Balsam (a resin made from balsam firs). If the adhesive is properly cooked, such sections are archival, and many in collections of the late 1800s are in pristine condition. In the 1950s, thermoplastics, such as Lakeside 70, were used to cement the specimen to the slide. These were convenient but were difficult to clear of bubbles. Covering agents used at this time included the commercial product Permount, which proved unsatisfactory because it became opaque after about 20 years. Beginning about 1960, epoxy cements such as Araldite became the choice of many preparators, as, once set, they were impervious to heat or chemicals. Plastic solutions that were allowed to flow over the surface and set were also used to form a clear membrane on the thinned specimen in place of a cover glass. About 1990, adhesives that set by the action of ultraviolet radiation became generally available and proved to be a great convenience for thin-section preparation. The adhesive film between the specimen and glass slide is set by ultraviolet light shone through the glass slide for a few minutes. It sets only under the specimen where not exposed to the air and the excess cement around the specimen can be wiped off with methanol. If the cover glass is to be permanently attached, the same adhesive can be used. Canada Balsam remains the most reliable, long lasting, and easily removable cement for cover glasses.

IMPREGNATION

In stromatoporoids that have been dolomitized, the galleries and pores of the stromatoporoid skeleton are empty, and they trap air bubbles and abrasive in the cements used in making thin sections. The pores must be filled before the specimen is cemented to the glass to exclude these undesirable contaminants. In the traditional method, the specimen is immersed in a low-viscosity, slow-setting epoxy treated with hardener and is placed in a chamber in which pressure can be reduced by a vacuum pump (Wells in Feldman, Chapman, & Hannibal, 1989, gave trade names of products). As ambient pressure is reduced, the air escapes from the pores, and the epoxy takes its place. Unfortunately, the low pressure produced by the vacuum pump may evaporate the more volatile constituents of the epoxy mixture, and the proper proportions of hardener and resin that ensure setting may be modified. If the pores are not interconnected, the impregnating epoxy may fail to reach them all. Stearn (1996) proposed a method using melted paraffin wax to fill the pores on the polished surface and diamond-faced laps to eliminate loose abrasive. Excess wax is scraped from the surface with a blade, and the specimen is cemented to the glass with an ultraviolet-setting adhesive such as Locktite.

SERIAL SECTIONS

Successive, parallel, thin sections or polished surfaces cut through a fossil specimen allow it to be reconstructed in three dimensions. Computer programs are available to assist in combining the multiple images into a three-dimensional reconstruction. This technique may involve the destruction of the specimen by grinding it away to produce the successive polished surfaces, or closely spaced thin sections may be prepared by repeatedly cementing the specimen to a microscope slide and slicing it off as close to the slide as possible. The spacing of the sections is as close as the thickness of the blade. This latter procedure was used by Stearn (1997c) to prepare a set of serial thin sections to act as neotypes for *Amphipora*. Another method of preparing three-dimensional reconstructions of large specimens of corals that could be applied to stromatoporoids was described by Hammer (1999). He placed successive polished sections of the tabulate coral *Catenipora* on a scanner and used a computer program to produce a three-dimensional image of its growth.

A nondestructive technique using computer tomography to delineate the interior of a stromatoporoid has been tested by Beuck and others (2008). The C-T scan allowed the authors to reconstruct the trace of a boring in a stromatoporoid skeleton from Gotland in three dimensions. Differences between the physical properties of the boring and stromatoporoid skeleton allowed its reconstruction, but the method does not reveal the internal structure of the stromatoporoid.

REFLECTED LIGHT

Nearly all thin sections of stromatoporoids are best observed in transmitted light at magnifications of ×10 to ×50, but some dolomitized specimens show much more detail in reflected light against a white background. Lights are directed at the thin section surface, about 45° from the plane of the section. Photography under these conditions is difficult, as the level of the light reflected and contrast are low.

ULTRATHIN SECTIONS

In sections of several tens of micrometers thickness, the high birefringence of calcite makes resolution of the crystal boundaries within the structural elements difficult. To examine this aspect of the microstructure of corals, LAFUSTE (1970) introduced the technique of polishing the face of the specimen that is to be adhered to the slide and grinding it carefully to a thickness of two or three micrometers. At this thickness, the interference colors of calcite under crossed polars are grey and yellow. LAFUSTE's work in the 1970s and 1980s was largely applied to tabulate and rugosan corals and convinced him that his slides showed the preservation of original biocrystals. Many of the elongate calcite crystals had a shape he referred to as dented (*bosselure*) with small embayments down their length. The technique was applied to stromatoporoids by STEARN and MAH (1987) to investigate the nature of the specks in structural elements (see Fig. 335.2). MISTIAEN (1994) illustrated many ultrathin sections of stromatoporoids in his discussion of the density of the skeleton.

STATISTICAL EVALUATION OF TAXONOMIC DIFFERENCES

Relatively little work has been done on specifying the variability of the stromatoporoid skeleton statistically or on using the parameters that define this variability to distinguish between species or other taxa. FAGERSTROM and SAXENA (1973) used statistical tests to assess whether the variability within a single section of *Syringostroma sherzeri* was representative of the whole of the skeleton. FAGERSTROM (1982) made extensive measurements of the structural elements of specimens and calculated similarity coefficients to distinguish between and to group taxa of stromatoporoids from the Detroit River Group. STEARN (1989b) recorded the intraspecific variability of stromatoporoids and related organisms in terms of Simpson's coefficient of variability. The most extensive use of statistics to distinguish between species has been by STOCK and BURRY-STOCK (STOCK & BURRY-STOCK, 1998, 2001; STOCK, 1991, 1997a) who have applied multivariate procedures to separate species in large collections from the Lower Devonian of New York. They used cluster analysis in an exhaustive study of 103 specimens of *Habrostroma* to distinguish the two species, *H. centrotum* and *H. consimile,* and to rate by canonical correlation analysis which of the skeletal features were most useful in distinguishing them (STOCK & BURRY-STOCK, 2001). Research into stromatoporoid phylogeny using concepts of cladogenesis has been limited, probably owing to the small number of skeletal characters that these fossils present for analysis. The only cladogram of stromatoporoid genera published so far is based on 16 characters of the labechiids (WEBBY, 1994). WOLNIEWICZ (2010) has used an image analysis computer program that performs measurements of skeletal elements of stromatoporoids, distinguishing the structures from the sparry calcite filling galleries. The program's software allows rapid analysis of the measurements taken from photographs and is more objective than traditional measurements taken by an operator using a microscope. He has also written on the value of the usual measurements for stromatoporoid taxonomy (WOLNIEWICZ, 2013).

CATHODOLUMINESCENCE

If thin sections are uncovered, their microstructure can be investigated under the microscope by cold cathode luminescence. This technique is particularly suitable for assessing the degree of alteration of the skeleton and delineating the crystal boundaries (Kershaw, 1994a). The reasons why certain calcite crystals luminesce with different colors is still unclear, but most carbonate workers believe it is due to slight impurities in their crystal lattices. Kershaw's studies (1994a) confirmed that different stromatoporoids secreted skeletons of aragonite or high magnesium calcite with various proportions of magnesium.

Attempts (by this author) to detect organic matter within the skeleton of stromatoporoids by stimulating fluorescence in ultraviolet light under the microscope showed no response from thin sections. Stromatoporoids, like scleractinian corals, seem to have been able to secrete skeletal carbonates free of organic matter. However, Clark (2005) reported organic matrix dispersed through a stromatoporoid skeleton.

SCANNING ELECTRON MICROSCOPY

The relationship between the arrangement of crystals and the structure and microstructure of the stromatoporoid skeleton can be studied on polished surfaces that have been etched or on broken surfaces with the scanning electron microscope (SEM). The technique was described by Stearn (1977). Although other workers polished the specimen highly and etched it with weak acids such as acetic or formic, Stearn (1977) found that good results were obtained by grinding with 600 grain silicon carbide and etching with 10% hydrochloric acid for 10 seconds. The specimen surface is then coated with a metallic film (usually gold-palladium) or carbon and placed in the SEM. The relief produced by the differential etching is imaged by the microscope at magnifications up to the tens of thousand times, but for most microstructural studies, magnifications of a few hundred times are most useful (see Fig. 335.1; Fig. 344–348). To test whether textures seen in etched specimens are artifacts of the preparation process, specimens may be fractured and the broken surface examined. Some investigators, to insure that the fracture is random and not guided by fine pores and cracks, have soaked the specimen in a penetrating liquid of very low viscosity (such as ethyl ether) and immersed it in liquid nitrogen to freeze the liquid before fracturing the specimen (Stearn & Mah, 1987).

Direct comparison of transmitted light images with scanning electron micrographs of the same part of the specimen is difficult. Stearn (1977) described a technique of cutting a disk about 5 mm in diameter from a thin section with an abrasive jet charged with alumina, such as those used to excavate small fossils. The disk is photographed at high and low powers in transmitted light and marked with a reference mark (such as a scratch or depression) that will appear in the electron microscope. It is then prepared for the SEM in the usual way, and the area that was photographed at high power is located in the scanning electron image by reference to the mark. However, comparison of light microscope and SEM images is not easy, because the specimen in the SEM is tilted at an angle, chosen by the operator, to the electron beam, foreshortening its image in the direction of tilt, and the photograph is an inverted mirror image of the scanning electron micrograph. Scanning electron micrographs of stromatoporoids have been published by Stearn (1977, 1989b), Stearn and Mah (1987), and Rush and Chafetz (1991).

GEOCHEMISTRY

The original skeletal composition of Paleozoic stromatoporoids and related living hypercalcified sponges has been studied through analysis of the structural elements for strontium, magnesium, lead, and rare earth elements. Results of these studies are further discussed in the section on skeletal microstructure and mineralogy (see p. 521–542). The results have been obtained largely through microprobe x-ray fluorescence and laser-ablation plasma mass spectrometry.

Biologically secreted aragonite is enriched in strontium and may contain up to 9000 ppm Sr^{2+}. Rush and Chafetz (1991) supported their conclusion that the original mineralogy of Devonian stromatoporoids was high magnesium calcite with microprobe analyses of Sr^{2+} and Mg^{2+}. Mallamo (1995; Mallamo & Stearn, 1991) made cross plots of Sr^{2+} and Mg^{2+} from microprobe analyses of living corals, recently calcitized corals, and stromatoporoids of various ages. He found that high values of Sr^{2+} in the structural elements of Ordovician labechiids relative to that of the gallery cements justified the conclusion of an original aragonite mineralogy. Younger stromatoporoids do not show the elevated Sr^{2+} and probably secreted high magnesium calcite.

Rosenheim and others (2004) found that the strontium-calcium ratio in living *Ceratoporella* was an indication of the temperature at which the aragonite skeleton was secreted, but this method has not been applied to fossils. Webb, Worheide, and Nothdurft (2003) measured the distribution of rare earth elements (REE) in stromatoporoids from the Devonian of the Canning Basin, Australia, and the living sponge *Acanthochaetetes*. The proportion of REE in the stromatoporoid was similar to that of sea water and suggested that its skeletal composition was originally calcite. Lazareth and others (2000) measured lead in recent *Ceratoporella* to assess its relationship to environmental changes.

Identification of microdolomite by morphology in scanning electron micrographs as an indication of original magnesium calcite composition in Ordovician stromatoporoids has led to contradictory results (Yoo & Lee, 1993; Tobin & Walker, 1998).

ISOTOPE STUDIES

Norris and Corfield (1998) collected a series of papers on the use of isotopes in paleontology.

To isolate a carbonate sample for isotope analysis of the skeleton from that of the galleries, a micropositioning stage driven by stepping motors and connected to a computer is used (Dettman & Lohmann, 1995). A structural element in a polished thin section is drilled out with a dental drill 20 µm wide to a depth of 50 µm. To get a sample large enough for the mass spectrometer (10 µg), about 4 mm along the length of the structural element (e.g., a lamina) must be drilled out.

Mallamo (1995) has applied analyses of oxygen and carbon isotopes in the stromatoporoid skeleton to the problem of whether the organisms were photosymbiotic. Because photosynthesis preferentially fixes ^{12}C, it increases the $^{13}C/^{12}C$ ratio in the skeleton but has only a minor effect on the oxygen isotopes (Swart, 1983). Frykman (1986) plotted the C and O isotopes in stromatoporoids from Gotland but did not discuss the significance of the results for these fossils.

The proportion of O isotopes in the skeletons of modern corals is sensitive to temperature, and changes in the ratio of $^{18}O/^{16}O$ across the growth axis have been used to define annual increments. Boehm and others (2000) have applied this technique to the skeletons of living hypercalcified sponges, but so far application of this technique to stromatoporoids to determine paleotemperatures has not been reported.

PHOTOGRAPHY

In 19th century works, the illustrations are engravings produced by lithography. While most of these illustrations are fair representations of the thin sections from which they were drawn, writers (e.g., Stearn, 1993) have commented that they cannot find the part illustrated in the plate in the type thin sections. In some publications (e.g., PARKS, 1936; GALLOWAY & ST. JEAN, 1955, 1957; GALLOWAY, 1960), the photographs are retouched, typically by whiting out details that the author decided were of secondary origin. The microstructures of such illustrations are rarely accurate representations of the nature of the specimen and in worst cases are misleading. Such retouching has not been practiced in recently published papers.

Standard methods of photomicrography have been used in illustrating stromatoporoids. Although various magnifications have been used, the standard magnification of 10 for macrostructure and 25 for microstructure has been widely adopted and allows easy comparison between taxonomic descriptions. To increase depth of focus and uniformity of focus across the picture, the thin section can be placed in an enlarger and projected onto film. The image from the enlarger can best be captured on slow orthochromatic emulsions (for example, the now unobtainable Kodak 7302 or 5302), but such products are now difficult to find as manufacturers are discontinuing production of black and white films. To increase depth of focus in producing the negative, the initial magnifications should be kept low, typically ×3, and the ×10 image produced by enlarging the negative ×3.3 onto paper. To save effort, some paleontologists have published negative prints produced by projecting the thin section directly onto printing paper rather than film. To compare such illustrations with those produced as photomicrographs, one must make a mental adjustment that the darker areas on the photograph would be lighter (less opaque) when the section is seen under the microscope.

Recording images with a digital camera or scanning photographs produced from film and paper allows the image to be stored in various memory devices, such as hard disks, zip drives, compact discs, or memory cards and manipulated for size, brightness, and contrast on a computer. As a result, these digital techniques have largely replaced film and paper methods, and all the illustrations in this volume have, at some stage, been digitized, although many were originally recorded on film and later scanned. So far, paleontologists have not confronted the problem that electronic manipulation of images may mislead readers as to the true state of the specimens, to the same extent that retouching photographs could mislead an earlier generation.

CLASSIFICATION OF THE PALEOZOIC STROMATOPOROIDEA

COLIN W. STEARN

INTRODUCTION

The Paleozoic stromatoporoids have been considered, among other groups, to be an order of the class Hydrozoa (e.g., NICHOLSON, 1886a; LECOMPTE, 1956; BOGOYAVLENSKAYA, 1969b, 1984), a subphylum of the phylum Porifera (e.g., STEARN, 1972), and a class of the Porifera (e.g., STEARN & others, 1999; and p. 707–836). Recently, the most commonly adopted rank for this group has been a class of the Porifera.

BASIS OF CLASSIFICATION

In sorting or classifying fossils, the paleontologist decides which of the features of morphology or life history of the group are important, and which are trivial. An important influence on classification has been the living group to which the fossil group has been assigned. Although the first writers describing the stromatoporoids suggested they were sponges (see Morphologic Affinities, p. 543–549), the consensus from the 1870s to the 1970s was that they were Hydrozoa and that the morphology of that living group should be the guide to assessing the relative importance of features of the fossil for classification. Thus NICHOLSON's classification (1886a), which was followed for a century by many writers, was based on the division of the fossils of the four families into groups that resembled the living hydroids *Hydractinia* (Hydractinoidea) and those that resembled *Millepora* (Milleporoidea). Comparison with these living hydroids also influenced the classification used by LECOMPTE (1956) in volume F of the *Treatise on Invertebrate Paleontology* and KÜHN (1939b). TRIPP (1929), BOGOYAVLENSKAYA (1984), and BOGOYAVLENSKAYA and YELKIN (2011) made detailed comparisons between living hydroids and fossil stromatoporoids.

The selection of a single morphological feature as the basis for classification has appealed to several paleontologists. HEINRICH (1914b) divided stromatoporoids into families in which the microstructure was homogeneous (Actinostromatidae) and in which it was porous or tubular (Stromatoporidae). The sensitivity of the skeleton to diagenesis has discouraged other writers from reliance on microstructure for classification (LECOMPTE, 1956; STEARN, 1966). BOGOYAVLENSKAYA (1965b, 1969b) proposed that the form of the astrorhizae should be the basis of major divisions of the stromatoporoids, but she did not use this criterion in practice. Other classification schemes have been based on the overall morphological similarity of the groups rather than a single feature. STEARN (1980, p. 881–882) called such schemes phenetic and explained that in them the higher taxonomic groups (for instance, orders) ". . . are conceived as being groupings of lower taxa (e.g., families) which share more morphological features in common than they share with taxa (other families) of another higher taxon (another order)." While it is easy to formulate diagnoses for higher taxa distinguished by single or few distinguishing features, it may be difficult to diagnose higher taxa based on overall similarity.

The methods grouped as cladistics depend on a compilation of a series of character states that together express overall similarity and comparison of these states to an outgroup. For the stromatoporoids, cladistics has been applied only to the labechiids. Webby (1994) used 16 derived characters to produce a cladogram and division of the order into 4 families. The small number of morphological features of the stromatoporoids that can be factored into cladistic analysis appears to have limited the further application of this methodology.

The ideal classification will faithfully reflect the phylogeny of the Paleozoic stromatoporoids. Ideally each higher taxon should be monophyletic, that is, derived from a single ancestor. Many taxonomists assume that overall similarity of morphology is a reliable guide to ancestry (like begets like). Textbooks discuss exceptions to this principle caused by convergent evolution. Stearn's (1993, fig. 4) revision of the order Stromatoporida is an example of a classification based on overall similarity as a guide to a reconstructed phylogeny.

TREATISE CLASSIFICATION

The classification used in this volume has been slightly modified from that published by Stearn and others (1999). The main changes in higher taxa from that classification are as follows.

1. Addition of the family Platiferostromatidae.
2. Deletion of the subfamilies Pseudolabechiinae and Plumataliniinae from the family Pseudolabechiidae.
3. Substitution of the name Coenostromatidae for Syringostromatidae in the order Syringostromatida.
4. Introduction of a new family to the Clathrodictyida: the Anostylostromatidae.
5. Transfer of the family Pulchrilaminidae from the class Stromatoporoidea and order Labechiida to the separate class Uncertain and order Pulchrilaminida (see below).

The classification is based on the overall similarity of structural elements in the skeletons but emphasizes microstructures of these elements and phylogeny of the taxa. The authors assume and hope that the major groups are monophyletic, but monophyly is difficult to prove.

- Phylum Porifera Grant, 1836
  - Class Stromatoporoidea Nicholson & Murie, 1878
    - Order Labechiida Kühn, 1927
      - Family Rosenellidae
      - Family Labechiidae
      - Family Stromatoceriidae
      - Family Platiferostromatidae
      - Family Stylostromatidae
      - Family Aulaceratidae
      - Family Lophiostromatidae
    - Order Clathrodictyida Bogoyavlenskaya, 1969b
      - Family Clathrodictyidae
      - Family Actinodictyidae
      - Family Gerronostromatidae
      - Family Tienodictyidae
      - Family Anostylostromatidae
      - Family Atelodictyidae
    - Order Actinostromatida Bogoyavlenskaya, 1969b
      - Family Actinostromatidae
      - Family Pseudolabechiidae
      - Family Actinostromellidae
      - Family Densastromatidae
    - Order Stromatoporellida Stearn, 1980
      - Family Stromatoporellidae
      - Family Trupetostromatidae
      - Family Idiostromatidae
    - Order Stromatoporida Stearn, 1980
      - Family Stromatoporidae
      - Family Ferestromatoporidae
      - Family Syringostromellidae
    - Order Syringostromatida Bogoyavlenskaya, 1969b
      - Family Coenostromatidae
      - Family Parallelostromatidae
      - Family Stachyoditidae
    - Order Amphiporida Rukhin, 1938
      - Family Amphiporidae
    - Order and Family Uncertain
  - Class Uncertain
    - Order Pulchrilaminida Webby, 2012a
      - Family Pulchrilaminidae

Seven of the formally named orders unite stromatoporoids of similar, but not unique, skeletal architecture and microstructure that can reasonably be considered to be a clade. The labechiids are characterized by an architecture based on cyst plates but include forms that also incorporate laminae and pillars. Their early appearance in the Middle Ordovician and the persistence of conservative morphologies in the order to the end of the Devonian suggest that they are the basic stock from which the other orders evolved. In the Late Ordovician, they grade into the actinostromatids, whose skeletal network is based on pillars of a range of sizes giving off colliculi to form lacy laminae. The clathrodictyids appeared after the labechiids in early Late Ordovician time, possibly from noncalcified ancestors, and built skeletons of single-layer, compact laminae, combined with a wide variety of pillars that spanned the spaces between them. The stromatoporellids had laminae that are more complex, typically thick and divided into layers. STEARN and PICKETT (1994) suggested that they, and the clathrodictyids, may have formed their skeleton in modules like that of the sponges informally grouped as sphinctozoans. The stromatoporids arose at the end of early Silurian time, probably from clathrodictyid ancestors, and were characterized by amalgamate skeletons formed of pachysteles and pachystromes of cellular microstructure. *Eostromatopora*, which is of obscure microstructure, may have been an ancestor. Structural elements with cellules are not confined to the stromatoporids, however; elements of similar microstructure also occur in the stromatoporellids. The syringostromatids are typically a Devonian group but are believed to have evolved in middle Silurian time from the actinostromatids. They built skeletons of pachysteles, pachystromes, and columns typically of microreticulate microstructure. NESTOR and STOCK (personal communication, 2006) are of the opinion that the order Syringostromatida should be divided into an order with clinoreticular microstructure derived from the Pseudolabechiidae and an order with orthoreticular microstructure derived from the Actinostromellidae or Densastromatidae. The amphiporids are a small group of abundant fossils, most of which are digitate, columnar, or dendritic in form, and composed of a network of compact, fibrous, or vacuolate elements. The order Pulchrilaminida is a small, independent, Early to Mid-Ordovician group of hypercalcified sponges assigned to class Uncertain (see Early Evolution of the Paleozoic Stromatoporoidea, p. 575–592; and Class Uncertain, Order Pulchrilaminida, p. 837–844).

HISTORICAL REVIEW
1826–1980

The classifications of Paleozoic stromatoporoids published before 1980 have been reviewed by LECOMPTE (1956) and STEARN (1980); no purpose would be served by repeating these summaries of older work. Few papers have been published that cover the whole class and provide diagnoses of each higher taxon. The literature on classification since 1980 will be discussed in the following section.

LECOMPTE's (1956) critiques of previous viewpoints on classification were based on his convictions that: (1) the stromatoporoids were hydroids; (2) microstructures were of little value in their classification; and (3) the Mesozoic stromatoporoid-like forms should be integrated into the families of Paleozoic stromatoporoids. None of these convictions are held by the writers of this section of the volume (see p. 417–836). He outlined the classifications used by NICHOLSON (1886a), HEINRICH (1914b), DEHORNE (1920), STEINER (1932), and KÜHN (1939b) before proposing a new classification of 10 families (plus an uncertain group). He also included in the stromatoporoids the Cambrian forms (YAVORSKY, 1932) of the former Soviet Union that have generally been excluded from the Stromatoporoidea by most specialists (e.g., NESTOR, 1966b; and see p. 575–577). LECOMPTE's classification was criticized (ST. JEAN, 1957) and then largely ignored by paleontologists. Its neglect was partly owing to the publication soon after of GALLOWAY's 1957 classification, which proved more acceptable to those working with this group, including YANG and DONG (1962), who used it in their first comprehensive survey of Chinese stromatoporoids. YAVORSKY, who contributed five major monographs on stromatoporoids of the former Soviet Union through the 1950s and 1960s, also found it difficult to use LECOMPTE's classification, preferring to use a simpler scheme for the Paleozoic forms (YAVORSKY, 1962) based on NICHOLSON's four original families: Actinostromatidae, Labechiidae, Stromatoporidae, and Idiostromatidae.

STEARN (1980) also briefly reviewed the history of classification of the Paleozoic stromatoporoids from the beginning and proposed a modification of the GALLOWAY (1957) classification to include the many new genera proposed from the Soviet Union. His classification was based on overall similarity and minimized the influence of microstructures in defining higher taxa. Major modifications of STEARN's (1980) classification made in this *Treatise* involve the giving of a larger place to microstructure in the criteria of classification, as well as the following modifications.

1. Splitting off of the Stylostromatidae and Stromatoceriidae from the Labechiidae.
2. Removing the Lophiostromatida as an order to a family of the Labechiida.
3. Removal of the Ecclimadictyidae as a family and placing some of these genera in the family Actinodictyidae.
4. Recognition of the families Gerronostromatidae, Atelodictyidae, and Anostylostromatidae in the Clathrodictyida.
5. Removal of the Syringostromatidae from the Stromatoporida to a separate order with new families Coenostromatidae, Parallelostromatidae, and Stachyoditidae.
6. Recognition of the amphiporids as a separate order and removal from the Clathrodictyida.

1980–2009

An extensive analysis of stromatoporoid morphology, interpretation, and classification from a Soviet Union perspective was published in 1984 by BOGOYAVLENSKAYA, based on earlier papers (BOGOYAVLENSKAYA, 1969b, 1974). This was followed in 1985 by a catalogue of genera and species of the stromatoporoids by BOGOYAVLENSKAYA and KHROMYKH. BOGOYAVLENSKAYA compared the classifications of NICHOLSON (1886a), KÜHN (1939b), LECOMPTE (1956), GALLOWAY (1957), and KHALFINA and YAVORSKY (1973) in a table. BOGOYAVLENSKAYA's own classifcation reflected her belief that the stromatoporoids were hydrozoans and that the Mesozoic stromatoporoid-like fossils should be included in the subclass. Her classification of 1984 did not include Mesozoic genera, however. She formulated a phylogeny diagram showing an interpretation of the relationship between the taxa. The following is a summary of her higher taxa.

Subclass Stromatoporata
  Order Labechiida
      Family Aulaceratidae
      Family Stratodictyidae
      Family Tuvaechiidae
      Family Labechiidae
      Family Stromatoceriidae
  Order Clathrodictyida
      Family Clathrodictyidae
      Family Plexodictyidae
      Family Actinodictyidae
      Family Stromatoporellidae
      Family Coenellostromatidae
  Order Actinostromatida
      Family Plumataliniidae
      Family Pseudolabechiidae
      Family Densastromatidae
      Family Actinostromatidae
      Family Atelodictyidae
  Order Gerronostromatida
      Family Gerronostromatidae
      Family Simplexodictyidae
      Family Tienodictyidae
  Order Syringostromatida
      Family Parallelostromatidae
      Family Clathrocoilonidae
      Family Pichiostromatidae
      Family Syringostromatidae
      Family Hermatostromatidae
  Order Stromatoporida
      Family Stromatoporidae
      Family Ferestromatoporidae
  Order Incertae Sedis
      Family Cleifdenellidae [*sic*]
      Family Amphiporidae
      Family Lophiostromatidae

As might be expected, many of BOGOYAVLENSKAYA's higher taxa are recognized in the classification adopted here. The major changes for the *Treatise* classification are as follows.

1. Removal of the Tuvaechiidae as a separate family.
2. Recognition of the Stromatoporellida as a separate order, not a family.
3. Placing of the Gerronostromatida as a family in the Clathrodictyida.
4. Placing of the Simplexodictydae in the Stromatoporellida, with the exception of *Anostylostroma,* which is a clathrodictyid.
5. Reinterpretation of the Syringostromatida based on the typical genus and removal of the genera grouped in the Clathrocoilonidae and Hermatostromatidae to the Stromatoporellida.
6. Assignment of the genus *Pichiostroma* to the Actinostromellidae and removal of the family.
7. Removal of the Cliefdenellidae from the Stromatoporoidea (WEBBY & LIN, 1988).
8. Recognition of the Amphiporida as a separate order.
9. Assignment of the Lophiostromatidae to the Labechiida.

BOGOYAVLENSKAYA and LOBANOV (1990) reviewed the morphological relationships, phylogeny, and paleogeography of many genera of the labechiids. They proposed another family be established in this order, the Cystostromatidae, to include the genera *Cystostroma* and *Pachystylostroma.*

WEBBY (1979a, 1986, 1993) has written extensively on the early history of the stromatoporoids and the classification and phylogeny of the labechiids. In 1979, he reviewed the genera of the labechiids and clathrodictyids that accompany them in Ordovician rocks and the speculations of GALLOWAY (1957), NESTOR (1966b), BOGOYAVLENSKAYA (1969b), and KAŹMIERCZAK (1971) that the former gave rise to the latter in Late Ordovician (Katian) time. WEBBY (1979a) considered the labechiiids to be an undivided family, but later (WEBBY, 1986) recognized a division of the labechiids into the Rosenellidae, Aulaceridae, Lophiostromatidae, and Labechiidae and speculated on the origin of the group from *Pulchrilamina* (which he included in the Labechiidae) and part of the Cambrian Khasaktiidae, which he included in the Stromatoporoidea (WEBBY, 1986, fig. 10). By 1993, WEBBY had increased the number of families in the order Labechida to six with the addition of the Pulchrilaminidae (doubtfully assigned) and the Stylostromatidae (WEBBY, 1993, 1994). WEBBY's evolving views on the classification of the labechiids are recorded by his doubtful inclusion of the pulchrilaminids in the labechiids (STEARN & others, 1999) and his later exclusion of them from the order to an indeterminate position (WEBBY, 2004b). They are now separated in this *Treatise* volume into a small, independent order of hypercalcified sponges of stromatoporoid-like appearance with uncertain phylogenetic relationships (see p. 837–844). NESTOR (in STEARN & others, 1999, p. 60) regarded two of the khasaktiid genera as being possibly parts of archaeocyath holdfasts. In this volume, the family Khasaktiidae does not have a relationship with members of the class Stromatoporoidea; see discussion of the family Khasaktiidae (p. 576–577).

WEBBY (1994, p. 379) noted that the morphological gradations between first-appearing clathrodictyid (Late Ordovician) genera—*Clathrodictyon* on the one hand and *Ecclimadictyon* and *Plexodictyon(?)* on the other—do not support the differentiation of these genera into separate families during their early developmental history. WEBBY, STEARN, and ZHEN (1993) used the classification of STEARN (1980) in their description of non-labechiid Lower Devonian stromatoporoids from the state of Victoria, Australia.

The Chinese viewpoint on classification has been formulated largely by DONG, who wrote numerous reports on Chinese Paleozoic stromatoporoids during the 1980s and 1990s. In 1983, he recognized nine different pillar microstructures and described the form of pillars of many genera. In 1987, DONG presented an extensive summary of the group, including sections on the significance of morphologic features, microstructures, and principles of classification. This handbook reviewed the classification of NICHOLSON (1886a), KÜHN (1927), LECOMPTE (1956), GALLOWAY (1957), BOGOYAVLENSKAYA (1965b, 1969b), and KHALFINA and YAVORSKY (1973). DONG's (1987) classification is basically a modification of STEARN's (1980) classification with the following differences.

1. The family Platiferostromatidae was established within the Labechiida to receive, in most part, Famennian stromatoporoid genera from China.
2. The family Gerronostromatidae was established within the Actinostromatida to receive genera, which are regarded herein, largely on the basis of microstructure, as being of different orders (e.g., *Atopostroma* [Syringostromatida], *Amnestostroma* = *Hermatostromella* [Stromatoporellida], *Clathrostroma* = *Gerronostromaria* [Clathrodictyida]).
3. The family Cubodictyonidae in the Actinostromatida was established to contain the single genus *Cubodictyon*. NESTOR (in STEARN & others, 1999) placed the genus provisionally in the Clathrodictyida (family Atelodictyidae) and suggests it may not be a stromatoporoid.
4. The new order Idiostromatida was established to accommodate three families: Idiostromatidae, Amphiporidae, and Stachyoditidae. This is an unwarranted return to the concept of NICHOLSON (1886a) and GALLOWAY (1957) that digitate, columnar, and dendroid growth forms can be used as a criterion for separation of higher taxa.

The same classification was presented by DONG in 1988. The stromatoporoids were placed in the phylum Porifera, STEARN's (1980) classification was criticized, and the modifications listed above proposed. Diagnoses of the various taxa were formulated in which little significance is given to microstructure as a guide to taxonomic affinity. In DONG's (2001) monographic treatment of the stromatoporoids of China, these same higher taxa are used in the classification.

STEARN (1993) revised his classification of the order Stromatoporida by dividing it into two orders separated by microstructure and phylogeny by splitting off the Syringostromatida. The stromatoporids were postulated to have arisen from clathrodictyid or labechiid ancestors in late early Silurian time, while at a similar time, the syringostromatids evolved from actinostromatids, from which they derived their microreticulate microstructure. Only a single family was recognized in the Syringostromatida.

The section on Paleozoic stromatoporoids in *The Fossil Record 2* (RIGBY & others, 1993) is based on the classifications of LECOMPTE (1956) and STEARN (1980) and does not introduce new taxa.

In 1994, STOCK reviewed the origin, evolution, and classification of the Actinostromatida. The phylogeny of the order is traced from the Late Ordovician genus *Plumatalinia* through the early Silurian *Plectostroma* to its diversification in middle Silurian time. Although suggesting that not all genera fit into these divisions, he recognized only three families in the order: Pseudolabechiidae, Actinostromellidae, and Actinostromatidae.

NESTOR has published several versions of his classification of Paleozoic stromatoporoids as phylogenetic diagrams without diagnoses. In the first series of these, which appeared in 1974, the main divisions were recognized as the superfamilies Labechiacea, Clathrodictyacea, Actinostromacea, and Stromatoporacea. This classification differed from his subsequent ones, largely in the inclusion of the Stromatoporellidae and Hermatostromatidae in the clathrodictyids and the Syringostromatidae in the actinostromatids. In his monograph on the Silurian of the Moiero River, NESTOR (1976) removed the lophiostromatids to the superfamily Lophiostromatacea, recognized the Actinodictyidae and Synthetostromatidae in the clathrodictyids, and the Yavorskiinidae in the Stromatoporacea. In a diagram of 1994, NESTOR recognized the superfamilies as orders and proposed the following subdivisions of these orders.

- Order Lophiostromatida
  - Family Lophiostromatidae
- Order Stromatoporellida
  - Family Hermatostromatidae
  - Family Synthetostromatidae
  - Family Stromatoporellidae
- Order Clathrodictyida
  - Family Clathrodictyidae
  - Family Amphiporidae
  - Family Tienodictyidae
  - Family Ecclimadictyidae
- Order Labechiida
  - Family Rosenellidae
  - Family Aulaceratidae
  - Family Stromatoceriidae
  - Family Plumataliniidae
- Order Actinostromatida
  - Family Pseudolabechiidae
  - Family Actinostromatidae
  - Family Densastromatidae
  - Family Actinostromellidae
- Order Stromatoporida
  - Family Pseudotrupetostromatidae
  - Family Yavorskiinidae
  - Family Stromatoporidae

In NESTOR's 1997 paper and his contribution to the classification of the clathrodictyids in 1999 (in STEARN & others, 1999), he substituted the name Actinodictyidae for the Ecclimadictyidae, added the Gerronostromatidae and Atelodictyidae, and removed the Amphiporidae. In the classification adopted herein, he also added the new family Anostylostromatidae.

In 1996, KHROMYKH outlined his concept of the clathrodictyids, emphasizing the similarity of structural elements in various higher taxa and the necessity to maintain the uniformity in microstructure of such taxa. He reintroduced from his 1974 paper (see KHROMYKH, 1974b) the superfamily Cystostromacea, which no other paleontologists have used, and divided it into various families, one of which, the Clathrodictyidae, is subdivided in the 1996 paper into the subfamilies Clathrodictyinae, Tienodictyinae, Ecclimadictyinae, and Actinodictyinae. Although NESTOR (1997) used the term Actinodictyidae as a substitute for the Ecclimadictyidae, KHROMYKH (1996)regarded the two groups of genera as separate entities.

In the *Systema Porifera*, no attempt was made by COOK (2002) to present a classification of the Paleozoic stromatoporoids.

Taking account here of the classification of BOGOYAVLENSKAYA and YELKIN (2011) and incorporating their higher taxa in synonymies of the taxonomic sections of the *Treatise* is not practical owing to fundamental differences in the bases of their taxonomy and that of the *Treatise* authors. BOGOYAVLENSKAYA and YELKIN based their wide-ranging revisions on assumptions that the Paleozoic stromatoporoids (and the disjectoporids and Mesozoic stromatoporoid-like genera) were Hydrozoa and that the astrorhizae, whose form they used as defining characterisitics of higher taxa, housed polyps rather than being canal systems of sponges. See discussion herein of the interpretation of the astrorhizae and their significance in taxonomic definitions in sections on internal morphology and functional morphology (p. 487–520 and p. 551–573).

PALEOZOIC STROMATOPOROIDEA

C. W. Stearn, B. D. Webby, Heldur Nestor, and Carl W. Stock

Class STROMATOPOROIDEA Nicholson & Murie, 1878

[Stromatoporoidea Nicholson & Murie, 1878, p. 241] [=class Stromatoporoidea Stearn & others, 1999, p. 11; =subphylum Stromatoporata Stearn, 1972, p. 385; =subclass Stromatoporata Nestor, 1978, p. 18; Bogoyavlenskaya, 1984, p. 66]

Invertebrate organisms of poriferan affinities with calcareous, basal skeletons, of laminar, domical, bulbous, branching to columnar form; internally composed of regular, continuous network of tangential and longitudinal structural elements; normally without preserved spicules; either interconnected laminae or cyst plates and pillars; or an amalgamated network in which tangential, longitudinal, and oblique elements are poorly differentiated; skeletons may be interrupted by a system of astrorhizae: canal-like voids that branch between structural elements and converge toward centers on growth surfaces. [Almost complete unanimity exists among contemporary stromatoporoid workers for the use of Nicholson and Murie's (1878) prior taxonomic name, the Stromatoporoidea, and the informal group name stromatoporoids. Bogoyavlenskaya (1984, 2001a) and Bogoyavlenskaya and Yelkin (2011), however, have preferred to maintain Stearn's (1972) term Stromatoporata and the informal term stromatoporates for the group.] *Middle Ordovician (Darriwilian)–Lower Carboniferous (Serpukhovian), ?Triassic.*

LABECHIIDA: SYSTEMATIC DESCRIPTIONS

B. D. WEBBY

Order LABECHIIDA Kühn, 1927

[*nom. correct.* BOGOYAVLENSKAYA, 1969b, p. 16, *pro* order Labechioidea KÜHN, 1927, p. 547] [=Lophiostromatida NESTOR, 1978, p. 18; =Lophiostromatida STEARN, 1980, p. 888; =Protolabechiida BOGOYAVLENSKAYA, 2001a, p. 46, *partim;* =Cystostromatida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & YELKIN, 2011, p. 18; =Aulaceratida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & YELKIN, 2011, p. 19; =Stromatoceriidae BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & YELKIN, 2011, p. 19; =Tuvaechiida BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & YELKIN, 2011, p. 19]

Stromatoporoids with cysts usually defined by long, low to upwardly convex, blister-like plates, and intersected by continuous, upwardly inflected pillars with rounded, irregular or flanged cross sections, and/or denticles confined to tops of cyst plates; in a few latilaminate forms, skeletal layers become much thickened; mamelons and mamelon columns may occur; astrorhizae rarely well developed; microstructure usually compact and imperforate. [The ordinal conception of the Labechiida was drastically restricted by BOGOYAVLENSKAYA (in BOGOYAVLENSKAYA & YELKIN, 2011, p. 19), in her major revision of the classification of Paleozoic and Mesozoic stromatoporoids, to just one family: the Labechiidae. This radical change in the scope and importance of the order greatly limits its usefulness as a major group. It fragments what had previously been regarded an almost natural grouping of taxa and is difficult to justify. The proposal should be abandoned in favor of the subdivisions used, more or less continuously, since the 1980s (see Classification of the Paleozoic Stromatoporoidea, p. 699–705). These earlier schemes included first the recognition of five labechiid families by BOGOYAVLENSKAYA (1984), then four family subdivisions were employed by NESTOR (1994), and more recently, six family subdivisons by WEBBY (in STEARN & others, 1999). Here, with a little additional fine tuning, this older, more traditional approach is followed, with the subdivion of the order into seven separate families (see also discussion on p. 582)]. *Middle Ordovician (Darriwilian)–Upper Devonian, ?Triassic.*

INTRODUCTION TO ORDER LABECHIIDA

GENERAL RELATIONSHIPS

The order Labechiida is regarded as having sufficiently common morphological features to warrant assignment within the class Stromatoporoidea (WEBBY, 1979a, 1993), rather than being separated from so-called more advanced stromatoporoid orders because of their characteristic cyst plates and limited preservation of astrorhizae (HEINRICH, 1914b; KÜHN, 1927, 1939b; TRIPP, 1929). STEARN (1982a) also favored the view that the stromatoporoids were essentially a unified, homogeneous group because a good level of morphological continuity existed between labechiids and other Paleozoic stromatoporoids. However, opinions remain divided about the role and/or significance that particular ancestral labechiid genera played in the derivation of new stromatoporoid groups like the Clathrodictyida and Actinostromatida (WEBBY, 1993, 1994). Also, there appears to be little evidence that close links existed between Ordovician–Devonian stromatoporoids and a number of examples of early Cambrian stromatoporoid-like structures. Fuller discussions of these matters are presented elsewhere (see p. 575–592).

A separation of the Labechiida into two very unequally sized orders, the Labechiida and Lophiostromatida, was adopted for a time (NESTOR, 1978; STEARN, 1980), but not all workers accepted this subdivision, given the very small size of the latter group (based largely on the type species *Lophiostroma schmidtii*). A relatively large morphological gap appears to separate the two groups, but it is preferable here to maintain the separation of the two groups only up to the family level. Further studies of the lophiostromatids are needed to resolve their taxonomic relationships.

The order Protolabechiida BOGOYAVLENSKAYA, 2001a, represents a heterogeneous grouping of three families, two of which belong to the order Labechiida: Stratodictyidae, previously merged as part of family Labechiidae (WEBBY in STEARN & others, 1999, p. 13), and the family Lophiostromatidae, as well as the Pulchrilaminidae, now included in the independent order Pulchrilaminida (see description on p. 837–844). None of these family groups is closely related to one another, nor, as the name implies, are any of BOGOYAVLENSKAYA's (2001a) protolabechiids close to roots of either the Labechiida (see p. 582–589) or the Pulchrilaminida (see p. 837–838).

BOGOYAVLENSKAYA's (2001a, p. 46) diagnosis of the order Protolabechiida (translation courtesy of Heldur NESTOR) is as follows: "Structure, zonal laminate. Horizontal elements represented by stratocysts [=long, low cysts herein] in some cases inflecting into mamelons [=mamelon columns herein]. Vertical elements—denticles, sometimes sporadic. Astrorhizae may be diagnosed." The problem with this definition is that comparatively few of these morphological features are common to the three groups. For example, taking the characteristic longitudinal structural elements of each family group, as follows: (1) representatives of family Labechiidae (including the stratodictyid-like forms) have pillars that are continuous across cyst plates and occasionally emerge on upper surfaces as papillae (shortened denticle-like elements are rarely developed); (2) members of the Lophiostromatidae commonly feature thickened skeletal layers that updome into pillarlike upgrowths and papillae on upper surfaces (denticles usually lacking); and (3) in family Pulchrilaminidae, the longitudinally directed structures are long, slender, spinose rods that may appear to be loosely aggregated and may extend upward well above their prominent latilaminae (denticles, mamelons, and astrorhizae apparently not formed). In consequence, none of these family groupings can be satisfactorily accommodated within order Protolabechiida BOGOYAVLENSKAYA, 2001a; see BOGOYAVLENSKAYA and YELKIN (2006, p. 186; 2011, p. 16, 18); and hence use of this particular ordinal grouping should be abandoned.

IMPLICATIONS OF DIFFERENT PRESERVATIONAL FEATURES

The poor preservation of many early (Ordovician–early Silurian) labechiids may be attributed to their skeletons of cysts and pillars (or denticles) being composed of relatively high volumes of void space and the instability of aragonite that they probably secreted, making them rather more susceptible to alteration by diagenesis than many other, skeletally more dense stromatoporoid groups (STEARN, 1972; MALLAMO & STEARN, 1991; MISTIAEN, 1994; TOBIN & WALKER, 1998). It is generally agreed that solid dark pillars may be formed as primary structures in both *Labechia* and *Stromatocerium*. But two different explanations have been offered to explain the other types of so-called pillars found in *Stromatocerium* and related forms; that is, the structures that have been commonly termed hollow [but they are filled with sparry calcite] (or tubelike) pillars and wall-less rods.

First, KAPP and STEARN (1975, p. 167, see especially fig. 3) noted that, in addition to the presence of solid dark pillars, sometimes a pillar may develop as a tubelike hollow wall (or plate) with a light-colored, spar-filled center by secondary dissolution of the center of a once-solid pillar (or by a process of eruption of superposed denticles), or sometimes the entire pillarlike structure (including the tube wall) may become replaced as a wall-less rod or plate. The selective process of subaerial leaching of skeletal material seems the best way to explain this differential type of transformation of pillars, with both hollow and solid often being preserved in the same skeleton (Webby, 1979a, p. 96), like the partial dissolution of septal structures and tabulae with sparry calcite infilling of molds recognized in the well-known Ordovician genus *Tetradium* (now interpreted as a florideophyte alga [replacement name *Prismostylus* Okulitch, 1935a] by Steele-Petrovich, 2011, p. 802), also thought to represent original aragonite frameworks (Semeniuk, 1971; Webby, 1990).

Second, Nestor (1964a, 1976), in a very different interpretation, again based on structures found in *Stromatocerium*, argued that secondary diagenetic processes were not capable of selectively destroying the centers of the pillarlike elements. Nestor (1964a, p. 17, see especially fig. 2b–d) preferred to interpret the tubelike, so-called pillars as primary structures, suggesting a three-stage process of development of upwardly inflected, superposed, conical updomes of cyst plates into short, superposed tubes, then these in turn became united into longer, open, tube-walled structures that intersected successive cyst plates. Other workers (e.g., Kaźmierczak, 1971; Khromykh, 1999b) have adopted views similar to those of Nestor, namely that the longitudinal structural elements are primary hollow tubes or plates.

Nestor (1964a, p. 17, fig. 3) also regarded the tube-walled, so-called pillars as transforming originally into rather complicated shapes: in outline these were rounded, angular, elongate, meandriform, and flanged. In 1976, Nestor further noted some individual skeletons of *Stromatocerium* that exhibited all three different kinds of longitudinal structural elements (tube-walled, wall-less rods, and solid). He referred to the primary cavities in the centers of the tube walls as being the best passageways for movement of solutions, and suggested that, in life, they may have been occupied by soft tissue (Nestor, Copper, & Stock, 2010, p. 58).

Nestor, Copper, and Stock (2010, p. 57–60) have also applied the term pore tubes from archaeocyath sponge nomenclature of Debrenne, Zhuravlev, and Kruse (p. 887) to the tubelike longitudinal elements of labechiids. However, the archaeocyath structures are confined in rows of small, fine, obliquely to sigmoidally shaped slots within inner walls, whereas the so-called pore tubes of labechiids represent longitudinally oriented tubes that are localized, apparently randomly, within the body of a skeleton; hence, this latter type of structure bears little resemblance to an archaeocyath pore tube. Consequently, use of pore tubes as a term in labechiids should be abandoned (see p. 411).

Currently there are two ways of approaching the study of Ordovician–early Silurian Labechiida. The first treats many of the differences in skeletal structures (especially pillars) as substantially being the result of secondary alteration; consequently the taxonomic differences between groups of taxa included in the family Labechiidae and the family Stromatoceriidae may not be that significant. The second approach argues that virtually all differences in appearance of hollow, so-called pillars, including the range of shapes that these structures depict in tangential section, are taxonomically important. The later (post–middle Silurian) labechiids, most notably the Late Devonian (late Famennian) forms, exhibit solid pillars with little evidence of diagenetic or other effects, perhaps because they developed calcitic skeletons originally. Consequently, taxonomic study of these forms is rather more straightforward, and certainly less controversial.

Family ROSENELLIDAE
Yavorsky in Khalfina & Yavorsky, 1973

[Rosenellidae Yavorsky in Khalfina & Yavorsky, 1973, p. 32] [=Cystostromatidae Khromykh, 1974a, p. 28, *partim*]

Simple, small to large, highly arched, upward to flattened cyst plates; longitudinal elements limited to denticles or crenulations. *Middle Ordovician (Darriwilian)–Upper Devonian.*

KHROMYKH (1999b) has maintained the separation of the Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973, and Cystostromatidae KHROMYKH, 1974a, despite the fact that his diagnoses of the respective families are virtually identical. For the Rosenellidae (1999b, p. 226), the key features are: "moderately convex cyst plates," "denticles or short, extremely scarce superposed pillars," and microstructure "compact." For the Cystostromatidae (1999b, p. 223) the characters are: "cyst plates of various convexity," vertical elements "either absent or include denticles, sometimes short pillars," and microstructure "compact fibrous." Both families are tied to their respective type genera *Rosenella* and *Cystostroma*, but the two genera are related to each other, exhibiting similar diagnostic features at the family level; consequently the two families are combined, and the original family name Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973, is retained on grounds of priority. KHROMYKH (1974b, 1996, 1999b) assigned these families to the order Clathrodictyida, characterized by simple cysts, whereas typical clathrodictyids are composed of single-layered, continuous laminae that may be downwardly inflected into short pillars (see STEARN, 1980; NESTOR, 1994, 1997; STEARN & others, 1999; and see p. 755). No other stromatoporoid worker has followed KHROMYKH's approach.

BOGOYAVLENSKAYA (in BOGOYAVLENSKAYA, VASSILYUK, & GLEBOV, 1990), and BOGOYAVLENSKAYA (in BOGOYAVLENSKAYA & LOBANOV, 1990), added further nomenclatural confusion when she proposed new families with the same names (Rosenellidae and Cystostromatidae), and subsequent misspellings of Rosenellidae (see BOGOYAVLENSKAYA, 2001a, p. 48; BOGOYAVLENSKAYA & YELKIN, 2006, p. 189; BOGOYAVLENSKAYA & YELKIN, 2011, p. 18). Key features of her diagnoses of the two families are similar. In BOGOYAVLENSKAYA (2001a, p. 48), these conceptions of her new families were proposed as emendments to the original definition of the family Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973, and to KHROMYKH's family Cystostromatidae, respectively. However, it seems that all the groupings and revised groupings of these closely related taxa should be rejected in favor of the original YAVORSKY in KHALFINA and YAVORSKY (1973) classification of the Rosenellidae, where he first recognized the importance of grouping simple cystose genera like *Rosenella*, *Cystostroma*, and *Rosenellinella* into one family. The group is united by its primitive features and seems to have a position near the root of the stromatoporoids.

Rosenella NICHOLSON, 1886a, p. 84 [**R. macrocystis* NICHOLSON, 1886a, p. 84, pl. 7,*12–13*; OD; NICHOLSON, 1886c, p. 20, pl. 1,*8*; NICHOLSON, 1886a, included a description of the genus and figures and the name of the species, without description (the type species is illustrated in both papers). The figures are not photos but lithographs prepared on stone, based on NICHOLSON's accurate original drawings. The figures of *R. macrocystis* in NICHOLSON (1886a) included longitudinal and tangential views of the type, and the figure in NICHOLSON (1886c) included another longitudinal section from a slightly different aspect]. Skeleton commonly composed of large-sized, overlapping, gently convex-upward cyst plates; in a few places alternating with flatter, thickened bands; with or without denticles. *Middle Ordovician (Darriwilian)–Upper Devonian:* China (Anhui, Shandong), Malaysia, *Darriwilian;* Australia (New South Wales, Tasmania), China, Mongolia, Russia (Gornaya Shoriya), USA (New York), *Sandbian–Katian;* China (Guizhou), Estonia, *lower Silurian;* Australia (New South Wales), Canada (Ontario), Sweden (Gotland), Russia (Tuva), *Wenlock;* Ukraine (Podolia), *upper Silurian;* Australia (northern Queensland), *Lower Devonian–Middle Devonian (lower Eifelian);* China (Sichuan), Russia (Urals, Kuznetsk Basin, Vaigach Island, Pay Khoy), Ukraine (Donets Basin), Vietnam, *Upper Devonian.*——FIG. 387,*1a–c*. **R. macrocystis*, Wenlock limestone, Visby, Gotland (specimen collected by G. J. Hinde; precise locality and stratigraphic level unknown); holotype, NHM P.5490, Nicholson's slides no. 280, 280a–d; *a*, longitudinal section of slide 280 showing long, low cyst plates with small denticles on their tops, especially thicker cyst plates, ×5; *b*, tangential section of slide 280d showing tiny, dark-colored, solid, dot-shaped denticles (best seen in lighter-colored areas where spar-filled gallery spaces are preserved); whereas a few denticles preserved as darker rings with lighter centers (near center of figure) and, in darkest areas (lower part of figure), equivalent, dot-shaped, lighter colored, replacement structures (voids or hollow denticles) are represented within an intersected, thick, cyst plate, ×10; *c*, tangential section of slide 280a shows many finely preserved, darker, dot-shaped denticles, ×10

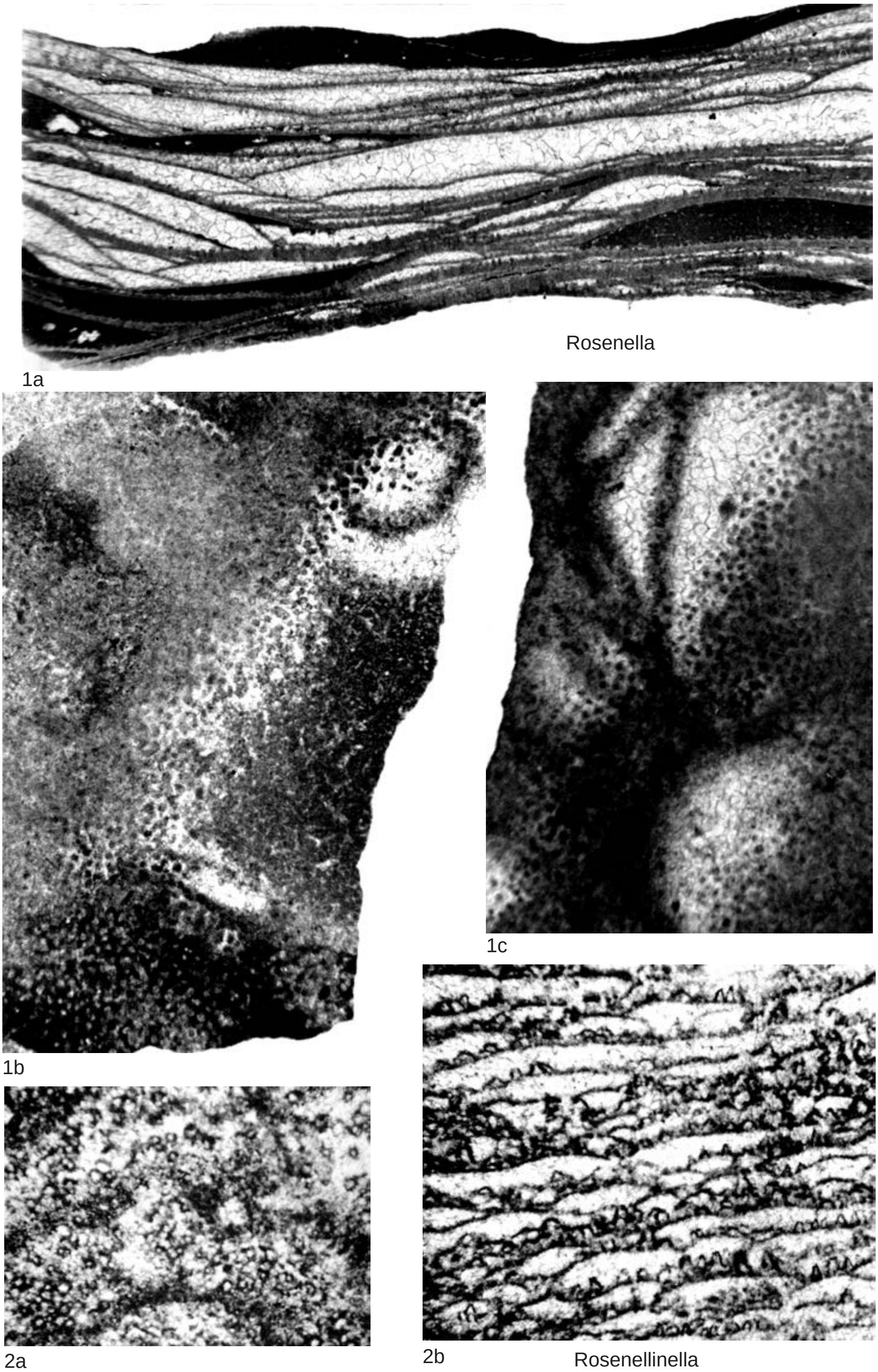


FIG. 387. Rosenellidae (p. 712–719).

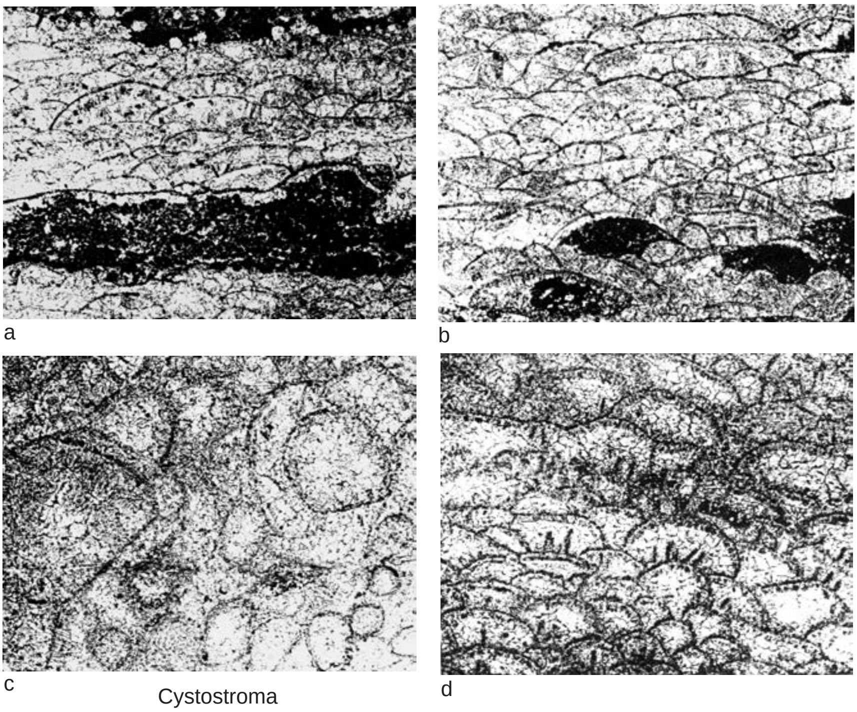


FIG. 388. Rosenellidae (p. 714).

(Webby, 2012c; photos of Nicholson's slides 280, 280a–280d, rephotographed by Webby in 1989).

Cystostroma GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 421 [**C. vermontense* GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 421, pl. 31,*1*, pl. 32,*1*; OD; GALLOWAY & ST. JEAN, 1961, p. 12, pl. 1,*1a–c, non* fig. 2 (illustrations of the types in GALLOWAY & ST. JEAN in GALLOWAY, 1957, are drawings, whereas GALLOWAY & ST. JEAN, 1961, includes photos of the types)]. Skeleton has moderately convex-upward cyst plates of comparatively small size, forming an imbricated pattern, with or without denticles. [STEARN (1980) and WEBBY (1993) considered *Bullulodictyon* YAVORSKY, 1967, to be a junior synonym of *Cystostroma,* given particularly the vesicular nature of horizontal elements resembling rows of cyst plates, but NESTOR (in STEARN & others, 1999, p. 24; and see p. 755) transferred the taxon to Clathrodictyida after reexamination of type material revealing paths of numerous astrorhizae largely simulating the vesicular structure.] *Middle Ordovician (Darriwilian)–Upper Devonian:* USA (Vermont), *Darriwilian;* Australia (New South Wales, Tasmania), Canada (Ontario), Central Asia, China (Xinjiang), Estonia, Russia (Urals, Siberian platform, Tuva), USA (Tennessee, Kentucky), *Sandbian–Katian;* Russia (Urals), *lower Silurian;* Australia (northern Queensland), Russia (northeastern Siberia), *Emsian;* China (Sichuan), Russia (Urals, ?North Caucasus), ?Uzbekistan, *Upper Devonian.*——FIG. 388*a–c*. **C. vermontense*, middle Chazy Group, Darriwilian, Isle La Motte, Vermont; holotype, YPM.450460, including slides 300-17, 300-18, 300-25 (note, photos of slides were retouched by original authors), ×10; *a*, longitudinal section of slide 300-17 showing latilaminae with imbricated cyst plates separated by dark bands of sedimentary rock; *b*, longitudinal section of slide 300-18 exhibiting rather varied range of sizes and shapes of moderately convex, imbricated cyst plates; *c,* tangential section of slide 300-25 showing wide range of sizes of approximately rounded, obliquely intersected cyst plates; two factors are responsible for variations: overall size and relative heights of tangential cuts across individual cysts (Galloway & St. Jean, 1961, pl. 1,*1a–1c*).——FIG. 388*d. C. simplex* GALLOWAY & ST. JEAN in GALLOWAY (1957, p. 421), Carter Limestone, Upper Ordovician, Mill Creek, south of Nashville, Tennessee; holotype, YPM.222148, including slide 299-60, ×10; longitudinal section showing highly convex cysts and scattered, well-defined, sharply pointed, denticles on tops of cyst plates, formerly differentiated as villi by GALLOWAY (1957, p. 359), see p. 416 (retouched photo, Galloway & St. Jean, 1961, pl. 1,*3a*).

Forolinia Nestor, 1964a, p. 31 [**Rosenella pachyphylla* Nicholson, 1886c, p. 21, pl. 1,*6, 7*; OD]. Skeleton formed of large, gently arched to flattened cyst plates, in places resembling laminae; some thickened to form palisade bands (like superposed cyst plates) that may be perforated by short, longitudinally oriented, cylindrical voids, possibly representing leached-out small pillars and/or superposed denticles; tops of some cyst plates exhibit small, dark, rounded denticles, and a few unthickened cyst plates may show a three-layered microstructure of transversely fibrous layers above and below dense median layer. [This genus bears close similarities to *Rosenella*, especially to the type species, *R. macrocystis*. Compare the respective tangential sections of the *Rosenella* type species (Fig. 387,*1b*) with the *Forolinia* type species (Fig. 389*b*). The main basis for distinguishing between the two taxa is that *Forolinia* develops much thicker palisade bands containing perforated, slenderly cylindrical, spar-filled voids (or hollow pillars); these latter are considered to be diagenetically altered replacement structures like those developed in a number of early labechiid genera, as outlined above. At least one of the species included recently in genus *Forolinia*—described as *F. lenticularis* Nestor, Copper, & Stock (2010, p. 59, pl. 2a–f, 4c–d)—should be included in the genus *Labechia.* In particular, this species is closely related to representatives of the *Labechia prima* species group (see p. 720).] *lower Silurian:* China (Guizhou), Estonia.——Fig. 389*a–c*. **F. pachyphylla* (Nicholson), Llandovery, Adavere stage, Päri outcrop (20th century Kattentack fossil locality), Estonia; holotype, NHM P.5629 (Nicholson's slides 283, 283a–e; note that sections 283 and 283a have been partially damaged); *a*, longitudinal section of slide 283, showing latilaminae consisting of much thickened, flattened to gently curved, palisade bands that alternate with layers composed of large to small, flattened to gently convex, spar-filled cysts; one very large, lens-shaped fill of sedimentary material that probably represents a growth interruption; and palisade bands showing lighter colored, longitudinally oriented, cylindrical voids, with tops of individual palisade bands exhibiting solid, rounded, denticles, ×7.5; *b*, tangential section of slide 283b showing a large, speckled area of numerous small, light-colored dots on a dark background of an intersected palisade band; these dot-shaped, replacement structures (voids) represent superposed, hollow denticles (or pillars) below upper surfaces (i.e., within thickened palisade bands), whereas the tiny, rounded, dark denticles scattered in lighter, spar-filled, gallery spaces are dark-colored solid structures that have evidently not been replaced on upper surfaces of cyst plates, ×7.5; *c*, longitudinal section of slide 283a shows part of skeleton with latilaminate alternations between thickened palisade bands, and long-low, very slightly convex, cyst plates, as well as zones with large, light-colored, calcite-spar–filled voids, and lenses filled with dark sedimentary material, ×5 (Webby, 2012c; Nicholson's slides 283, 283a–b, rephotographed by Webby in 1989).

Priscastroma Khromykh, 1999a, p. 801 [178] [**P. gemina* Khromykh, 1999a, p. 801, fig. 1a–b, 2a–e; M]. Skeleton of irregularly wavy to flattened walls, though in places enclose discrete, chevron-shaped cyst plates; in tangential sections where intersected, these may appear as ring structures; also in a few places, short, dark, solid, cone-shaped elements of finely reticulate (possibly secondary) skeletal material partially filling cyst spaces; in other areas, successive, undulating walls only make contacts at irregular intervals, leaving laterally extensive, calcite-spar–filled gallery spaces with few partitions; walls may have a fibrous microstructure; no pillars, denticles, or astrorhizae recorded. [This simple genus bears only a few diagnostic features: for example, the chevron-shaped cyst plates within individual latilaminae resemble patterns in rosenellid labechiids. Other characters such as the small (possibly secondary) columnlike thickenings and the fibrous microstructure may support Khromykh's view (1999a) that the genus was a member of the Lophiostromatidae (see p. 749–753). However, it bears little resemblance to other early lophiostromatids like *Lophiostroma shangtungensis* Yabe & Sugiyama, 1930 (see Ozaki, 1938), from a similar Middle Ordovician (Darriwilian) stratigraphic horizon in Shandong Province, northern China, which chararacteristically exhibits much thickened skeletons and long pillarlike columns.] *Middle Ordovician (Darriwilian):* Siberian platform, Russia.——Fig. 390*a–e*. **P. gemina*, upper Kochakan Formation, Muktei horizon, right bank of Moiero River, 1 km upstream from the mouth of Bugarikta River tributary, central Siberia, holotype, CSGM, T-781/7 (no. 367/1); *a–b,* views of longitudinal section, *a,* ×4; *b,* ×8 (Khromykh, 1999a, fig. 2a, 2d); *c,* paratype CSGM, T-781/7-1 (no. 367/2), tangential section showing a few ring structures intersected near apices of chevron-shaped cyst plates, ×8 (Khromykh, 1999a, fig. 2c); *d–e,* sketches of longitudinal sections of holotype (no. 367/1) and paratype (no. 367/2), respectively, showing irregular distribution of fine serrations on upper and lower surfaces of walls; *d,* a few small patches of darker, finely reticulate secondary material in localized places beneath updomed cyst plates, ×20; *e,* ×15 (Khromykh, 1999a, fig. 1a–b).

Pseudostylodictyon Ozaki, 1938, p. 208 [**P. poshanense* Ozaki, 1938, p. 208, pl. 24,*2;* M; holotype, pl. 25,*1a–e*] [=*Parksodictyon* Bogoyavlenskaya in Bogoyavlenskaya & Lobanov, 1990, p. 85 (type, *Pseudostylodictyon? kayi* Galloway & St. Jean in Galloway, 1957, p. 425, OD)]. Skeleton with cyst plates, commonly long-low (resembling laminae) in specimens lacking mamelon columns and in others (including type species), upwardly inflected into mamelon columns; denticles (less commonly crenulations) locally prominent on upper surfaces of cyst plates and may be present in mamelon columns as well as in interspaces. [The type species of *Parksodictyon* Bogoyavlenskaya in Bogoyavlenskaya & Lobanov, 1990 (*Pseudostylodictyon kayi* Galloway & St. Jean in

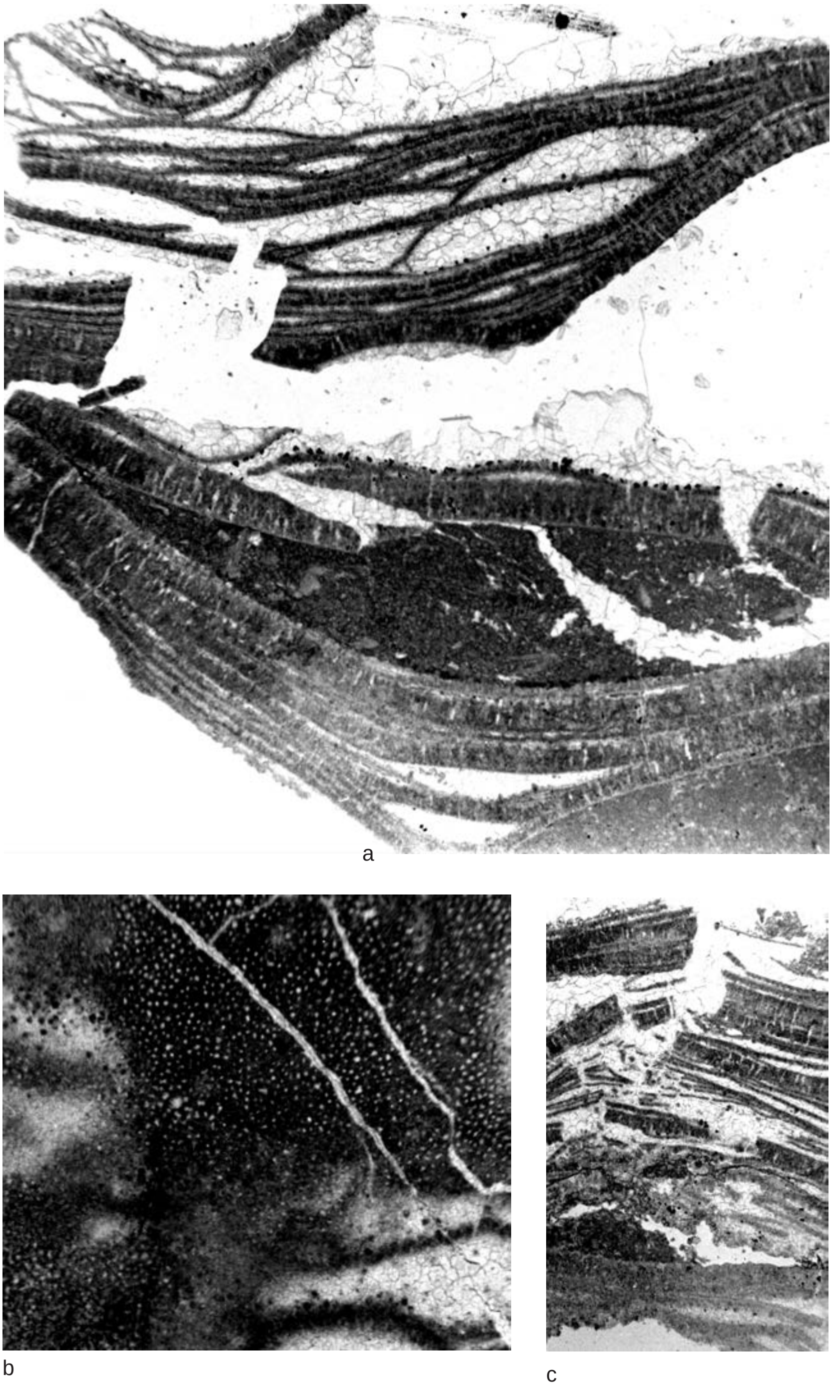


FIG. 389. Rosenellidae (p. 715).

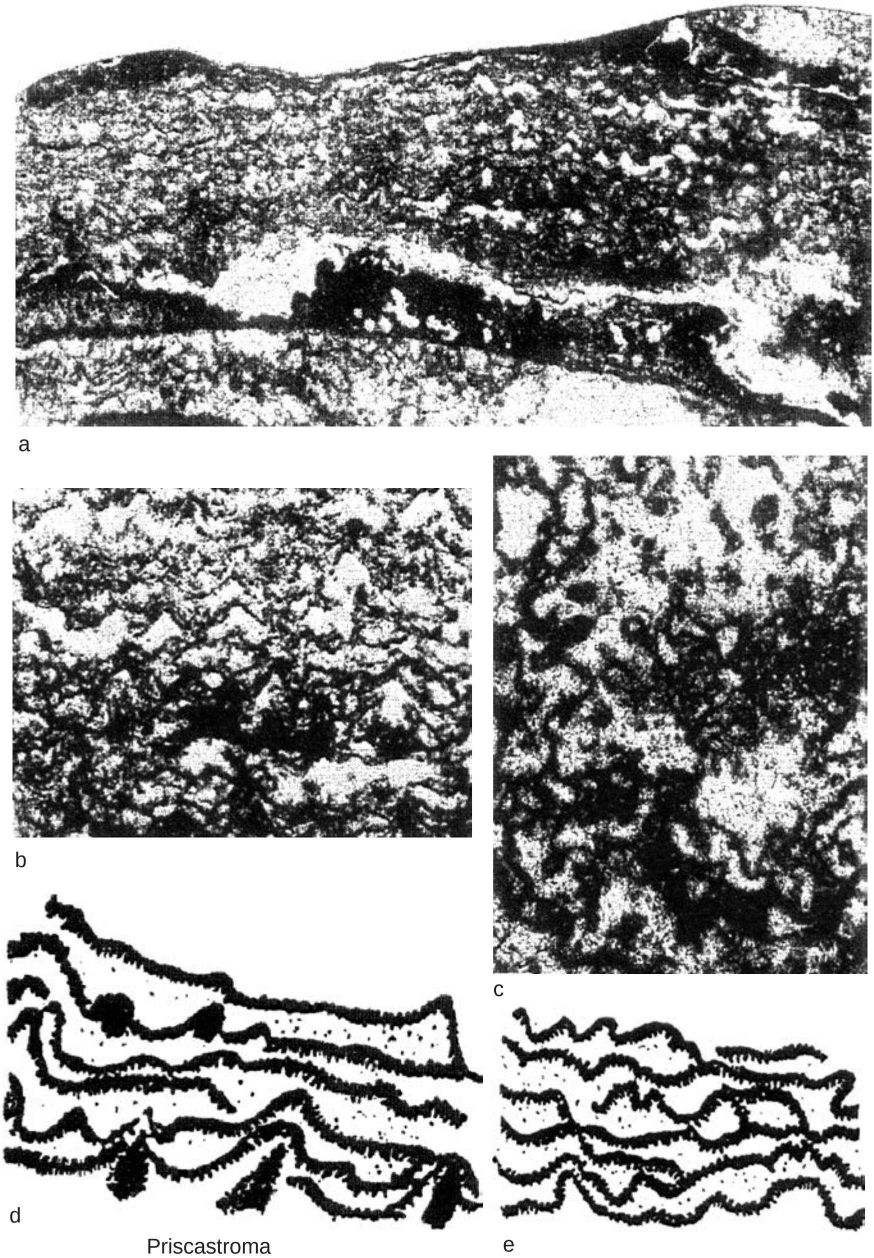


FIG. 390. Rosenellidae (p. 715).

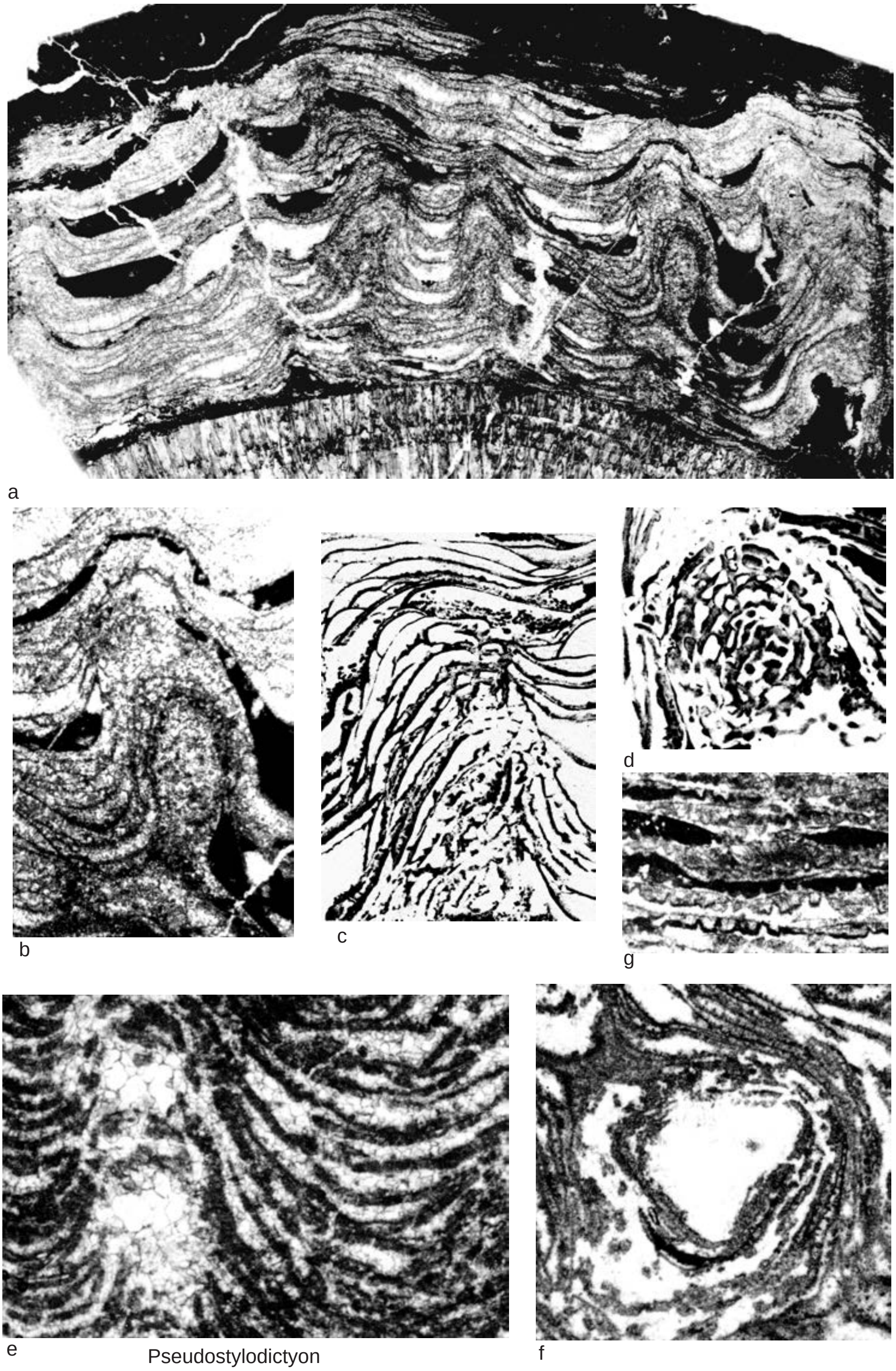


FIG. 391. Rosenellidae (p. 715–719).

GALLOWAY, 1957), is a junior subjective synonym of *Pseudostylodictyon lamottense* (SEELY, 1904), according to KAPP and STEARN (1975, p. 171). Most of the morphological features of the two species are the same, and both come from similar stratigraphic levels in the Chazy Group and localities on the Isle La Motte, Vermont (United States). Moreover, the characteristic presence or absence of mamelon columns is not regarded as a basis for generic subdivision. Accordingly, it is inappropriate to retain *Parksodictyon* as a separate genus.] *Middle Ordovician (Darriwilian)–upper Silurian:* China (Shandong), USA (Vermont, New York), *Darriwilian;* Australia (New South Wales, Tasmania), ?Kazakhstan, Russia (Chukotsk Peninsula, Urals), USA (Texas), *Sandbian–Katian;* Norway, *lower Silurian;* Sweden (Gotland), *middle Silurian;* Australia (New South Wales), China (Inner Mongolia), *middle Silurian–upper Silurian.*——FIG. 391*a–d.* **P. poshanense,* Darriwilian, Majiagou Group, north of Woyu, Boshan County, Shandong Province; holotype, NIGP no. 121556a; *a*, longitudinal section of holotype showing overall skeleton of type species in overgrowth relationship with possible lichenariid coral; skeleton shows superposed latilaminate growth best in interspaces between well-developed, variably spaced, mamelon columns, where dark sedimentary rock infills (originally inclusions of mud) intervene successively; cyst plates of variable size and shape, with cyst plates updomed over mamelon columns and broadly flattened to sagging across interspaces, ×2.5 (Webby, 2012c; photos of OZAKI's type thin section in Nanjing collection; see also OZAKI, 1938, pl. 25,*1b*); *b*, enlarged view of right side of holotype showing mamelon column with associated denticles, and also a vague impression of one or two, more continuous, upwardly and outwardly radiating, pillarlike structures, ×5 (Webby, 2012c; photos of OZAKI's type thin section in Nanjing collection; see also OZAKI, 1938, pl. 25,*1b*); *c–d*, longitudinal and tangential sketches based on type material showing mamelon columns with weakly developed pattern of concentrically arranged cyst plates, outwardly radiating structures, mainly denticles and a few incomplete pillars, ×8 (Ozaki, 1938, pl. 25,*1d–1e*).——FIG. 391*e–g. P. lamottense* (SEELY), lower Crown Point Formation, Chazy Group, Darriwilian, Isle La Motte, Vermont; *e*, specimen RM 14.000 (slide RM 14.000a) from Fisk quarry (Isle La Motte), longitudinal section showing cyst plates that are upwardly inflected adjacent to mamelon column and flattened to slightly concave across interspaces, ×10; *f*, specimen RM 14.021 (slide RM 14.021b) from Fisk quarry, Isle La Motte, longitudinal section across a mamelon column, some cyst plates that simulate laminae, and denticles; *g*, specimen RM 14.001 (slide RM 14.001a) from Goodsell quarry, Isle La Motte, longitudinal section showing rows of hollow denticles on upper surfaces of slightly wavy, long, low, cyst plates, ×10 (KAPP & STEARN, 1975, pl. 1,*1–3*).

Rosenellinella YAVORSKY, 1967, p. 16 [**R. venusta*; OD]. Skeleton of long, low cyst plates that typically form in gently wavy to flattened rows; some (including type species) exhibit numerous crenulations represented by calcite spar-filled blebs at tops of cyst plates (only rarely seen to involve upward flexure of cyst plate itself); in tangential sections these small structures appear as rings with light-colored centers; others show thickened rows of cyst plates with palisade banding, and their upper surfaces have small, solid, dark denticles. [All four recorded species of *Rosenellinella* have been described from one region in Tuva, southern Russia, based on few specimens, and through a limited stratigraphic interval; consequently, as noted by BOGOYAVLENSKAYA (1971b, p. 37), they may prove on further study to represent a single taxon.] *lower Silurian–middle Silurian:* Russia (Tuva).——FIG. 387,*2a–b.* **R. venusta*; Wenlock, Elegest River; *a*, specimen CNIGR 7351/556, tangential section showing numerous, small, rounded, spar-filled blebs, ×10; *b*, holotype, CNIGR 7351/555, longitudinal section showing main features of cyst plates and crenulations, ×10 (Yavorsky, 1967, pl. 3,*3–4*).

Family LABECHIIDAE Nicholson, 1879

[*nom. correct.* NICHOLSON, 1886a, p. 74, *ex* Labechidae NICHOLSON, 1879b, p. 28] [=Stratodictyidae BOGOYAVLENSKAYA, 1977a, p. 6; =Tuvaechiidae BOGOYAVLENSKAYA, 1984, p. 6]

Simple, upwardly convex to flattened cyst plates of variable size and rounded pillars exhibiting a range of morphologies, from somewhat sporadically developed small pillars and denticles to, more commonly, more continuous, large, solid pillars, and occasionally where closely spaced, forming chainlike rows. *Middle Ordovician (Darriwilian)–Upper Devonian.*

The group unites genera that characteristically exhibit solid, rounded, large or small pillars. Other features are not taxonomically diagnostic; for example, whether the pillars as seen in tangential sections are separated or occasionally develop in chainlike rows, or whether the cyst plates form imbricated, vesicle-shaped cysts or are more flattened. The genus *Tuvaechia* (based on type species *Labechia regularis* YABE & SUGIYAMA, 1930) is regarded as a junior synonym of *Labechiella* (based on type species *Labechia serotina* NICHOLSON, 1886c). The only taxonomically significant difference is at the species level (e.g., between the two type species, one with separated pillars and the other showing chainlike rows). Consequently, not only is the genus *Tuvaechia* a junior synonym of *Labechiella*, but Bogoyavlenskaya's (1984) family Tuvaechiidae is also a junior synonym of family Labechiidae Nicholson, 1879b.

Bogoyavlenskaya's (1977a) family Stratodictyidae, with *Stratodictyon* Webby, 1969, as type genus, is based mainly on the presence of the distinctive long, low cyst rows (what she has called stratocysts; see p. 414). However, similar, elongate, long, low cyst plates are recorded by her in a number of other genera (Bogoyavlenskaya, 1984, p. 11) that belong to other families, recorded here in the rosenellids (*Rosenella, Pseudostylodictyon*), stromatocerids (*Stromatocerium*), and stylostromatids (*Pachystylostroma, Stylostroma*). Therefore, the Stratodictyidae also cannot be maintained as a separated valid group on the basis of stratocysts. Bogoyavlenskaya's (2001a; and see Bogoyavlenskaya & Yelkin, 2011, p. 18) incorporation of the Stratodictyidae in her order Protolabechiida seems to add further confusion to current taxonomic nomenclature, given that the relevant part of her 2001a diagnosis of that new order states (p. 46): "Vertical elements—denticles, sometimes sporadic," when *Stratodictyon,* the type genus of Stratodictyidae, exhibits characteristic small pillars (see p. 723).

Labechia Edwards & Haime, 1851, p. 155, 279 [**Monticularia conferta* Lonsdale, 1839, p. 688, pl. 16,*5,5a*; M; only external surfaces of one (or possibly two) of Lonsdale's syntypes from Benthall Edge and/or Gleedon Hill were illustrated initially, and that material is presumed lost; then Edwards and Haime (1855, p. 269, pl. 62,*6,6a–c*) figured external surfaces of a topotype from Benthall Edge (specimen placed in MNHM, Paris); later, Smith (1932, pl. 1,*1–2*) chose a specimen from Wenlock Limestone, Benthall Edge as the neotype (BGS no. 28183, Nottingham), because it had been presented originally by R. I. Murchison to the Geological Society of London, and Smith thought it might have represented one of Lonsdale's syntypes; however Smith's neotype has remained unsectioned and unstudied, hence it is probably invalidly designated; Nicholson (1886a, 1886c, 1889, 1891a) was the first to study thin sections based on specimens from Dudley, Benthall, and Ironbridge, including the Dudley specimen NHM P.5984, with nine thin sections (no. 264, 264a–h) apparently cut from it, but that specimen is missing]. Skeleton composed of long, stout, rounded pillars to more sporadically developed, less continuous, small pillars, and an intricate mesh of cyst plates with moderately upward convexity; pillars may terminate as papillae on upper surface and may show upwardly converging cone-in-cone banding in longitudinal section (concentric rings in tangential section). [The genus includes a wide range of longitudinal structural elements, from those with a patchy development of small short pillars that are grouped in the *Labechia prima* species group to those with long and stout, rounded pillars of the *L. conferta* species group (Webby, 1979a, p. 90). Representatives of the *L. prima* group commonly show aligned rows of small to moderately sized, low-convexity cyst plates that, in places, alternate with irregularly laterally continuous bands of spar with loss of original structural elements, perhaps because they were originally poorly calcified bands; finer-textured *Stratodictyon* Webby, 1969, exhibits similar patterns of aligned rows of low-convexity cyst plates. Members of the *L. conferta* group, on the other hand, have interspaces between pillars filled by a meshwork of cysts that are characteristically coarser, more vesicular and more imbricated.] *Middle Ordovician (Darriwilian)–Upper Devonian (Famennian):* Canada (Quebec), China (Shandong), ?Korea, USA (New York, Vermont), *Darriwilian;* Australia (Tasmania), Canada (Ontario, Akpatok Island, Newfoundland), China (Xinjiang), Mongolia, Norway, Kazakhstan, Russia (Urals, Gornaya Shoriya, Tuva), Scotland, USA (Alabama, Tennessee, Virginia, Kentucky, Indiana, Ohio, Michigan), *Sandbian–Katian;* China (Guizhou), Estonia, Russia (Siberian platform, Tuva), *lower Silurian;* Central Asia, England, Sweden (Gotland), Russia (Russian and Siberian platforms, Urals, Kolyma, Tuva), Ukraine (Podolia), USA (Indiana), *middle Silurian;* Russia (Siberian platform, Urals, Altai Mountains), Sweden (Gotland), *upper Silurian;* Canada (Ellesmere Island), China (Sichuan, Guizhou, Hunan), Russia (Kolyma), *Lower Devonian;* Canada (Alberta), Russia (Russian platform, Novaya Zemlya, Vaigach Island, Urals, northern Caucasus), Ukraine (Donets basin), *Frasnian–Famennian.*——Fig. 392*a–b*.**L. conferta* (Lonsdale), Wenlock Limestone, Dudley, England, ×5, NHM P.5984, Nicholson's thin sections no. 264, 264g; *a*, longitudinal section showing solid, vertically aligned pillars with thickening close to skeletal base and in places a cone-in-cone appearance, as well as well-imbricated series of upwardly convex cyst plates; note also thin film of dark matter (possibly originally sediment) and a small, domelike, growth-banded bryozoan colony, near bottom center of field of view (Webby, 2012c; Nicholson's thin section 264g, rephotographed by Webby in 1989); *b*, tangential section (part of Nicholson thin section no. 264) showing round pillars, some with lighter- or darker-colored centers where apices of compositionally distinct cone-in-cone layers are intersected, and cyst plates are represented by offsets between pillars (Webby, 2012c; part of Nicholson's

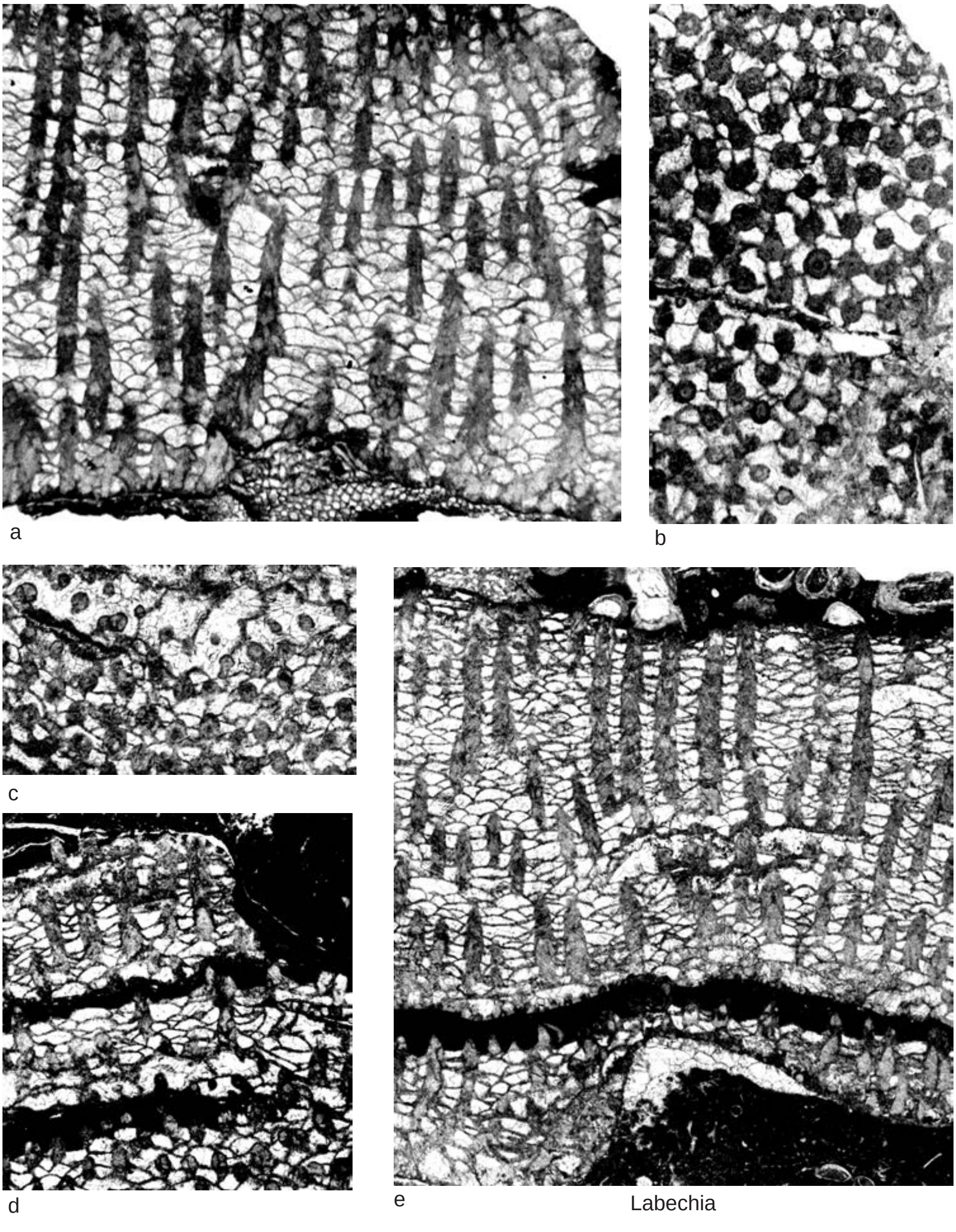


FIG. 392. Labechiidae (p. 720–722).

thin section 264, rephotographed by Webby in 1989).——FIG. 392*c–e*. *L. conferta* (LONSDALE), probably from same Dudley locality and stratigraphic level; specimen AMF.134351, originally presented by T. W. Edgeworth David to Sydney University, ×5 (Webby, 2012c); *c*, tangential section showing rounded pillars with a wide range of diameters; *d*, longitudinal section showing successive latilaminae and pillars extending as papillae into darker sedimentary material above successive tops of latilaminae; *e*, longitudinal section showing initial latilaminate growth over an uneven (possibly unconsolidated) substrate, and a small cavity (now represented as a calcite-spar–filled space) at the base that possibly formed when the initial growth spread (and uparched) over the substrate; note well-developed

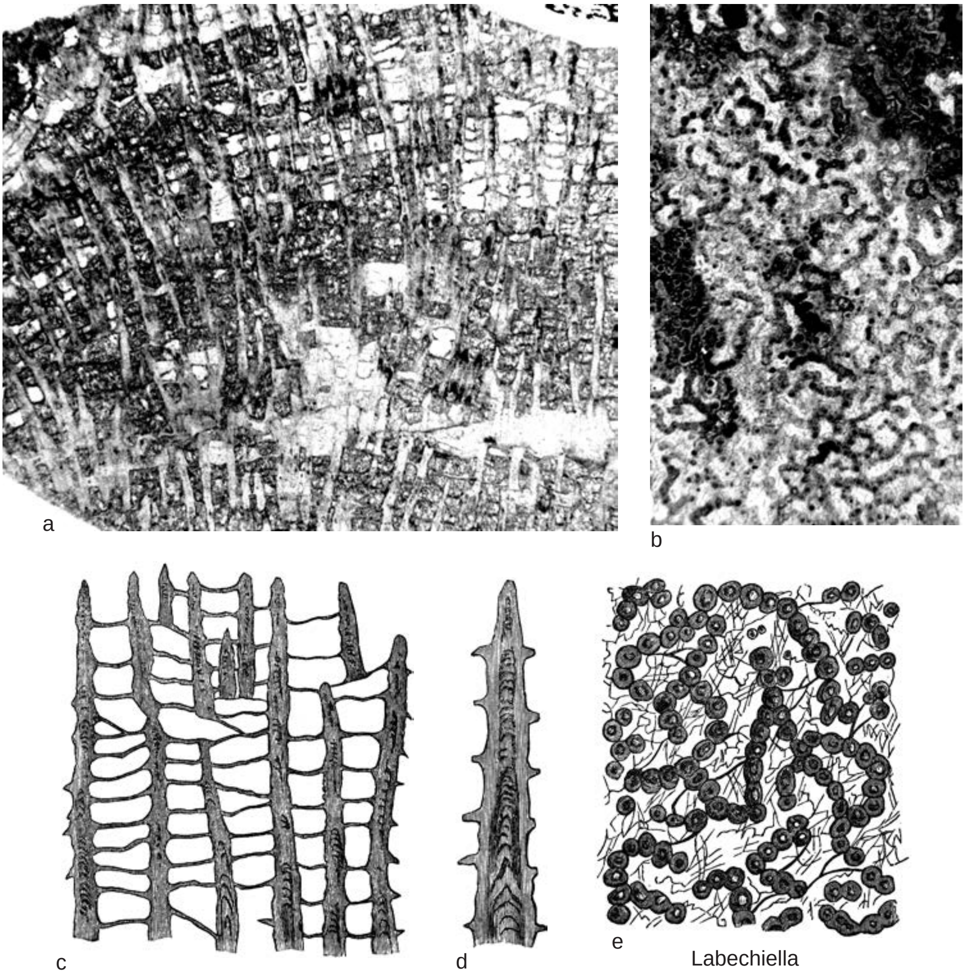


FIG. 393. Labechiidae (p. 722–723).

papillae occur at tops of both latilaminae (papillae on terminal surface of this specimen are illustrated in Fig. 316.1) (Webby, 2012c).

Labechiella Yabe & Sugiyama, 1930, p. 54 [**Labechia serotina* Nicholson, 1886c, p. 15, pl. 2,*3,4;* OD] [=?*Columna* Ivanov in Ivanov & Myakova, 1955, p. 13 (type, *C. sokolovi,* OD), *non* Perry, 1811 (mollusk), *nec* Signoret, 1877 (hemichordate), *nec* Cooper, 1892 (mollusk); =*Tuvaechia* Bogoyavlenskaya, 1971b, p. 34 (type, *Labechia regularis* Yabe & Sugiyama, 1930, p. 56, OD)]. Skeleton of longitudinally aligned, continuous pillars, in places closely spaced even in contact, and acutely branching; pillars in transverse section have rounded outline and, where in contact, form incomplete, chainlike rows (approximating a vermicular appearance); in longitudinal section may show upwardly converging cone-in-cone banding with lighter axial canals; cyst plates flattened, rarely vesicular. [Yabe and Sugiyama (1930, p. 54) introduced *Labechiella* as a subgenus of *Labechia* but misinterpreted the flattened cyst plates of *L. serotina* as being bars and recognized *L. regularis* Yabe & Sugiyama, 1930, p. 56, Ordovician, Liaoning Province, China, as an independent species. Then, nine years later, Sugiyama (1939, p. 443–444) used the same binominal, *Labechiella regularis,* duplicating the name based on different material from the Silurian of Japan. This action ignored common practices adopted under the International Code of Zoological Nomenclature and caused some confusion (Galloway, 1957; Flügel & Flügel-Kahler, 1968; Webby, 1979a; Mori, 1994). Apparently realizing the error, Sugiyama (1940, p. 111–112) substituted the name *Labechiellata* (printed on an errata slip in Sugiyama, 1940, no pagination), which avoided his genus *Labechiella*

Sugiyama, 1939, p. 443 (type, *Labechiella regularis* Sugiyama, 1939, p. 444) becoming a junior homonym of *Labechiella* Yabe & Sugiyama, 1930 (Mori, 1994, p. 677). However, given the presence of flat-lying cyst plates in Sugiyama's Japanese species (a key feature of genus *Labechiella* Yabe & Sugiyama, 1930), it was evident that *Labechiellata* Sugiyama, 1940, was also a junior synonym of *Labechiella* Yabe & Sugiyama, 1930 (Webby in Stearn & others, 1999, p. 14). Furthermore, given broad acceptance of the genus-level status of *Labechiella* Yabe & Sugiyama, 1930 (Galloway, 1957; Flügel & Flügel-Kahler, 1968; Webby, 1979a), it was apparent that Sugiyama's (1939) *L. regularis* being a junior homonym of the well-established *L. regularis* (Yabe & Sugiyama, 1930) required an alternative name; consequently *Labechiella sugiyami* Webby (1979a, p. 92) was proposed. Reinterpretation of the type material of *L. sugiyami* by Mori (1994) has since revealed that Sugiyama's holotype is part of rugose coral *Mazaphyllum* Crook, 1955. With name reversions, the Sugiyama taxon becomes the cystiphyllid rugosan *Labechiellata regularis* (Sugiyama, 1939). *Labechiellata* Sugiyama, 1940, is therefore excluded from the Stromatoporoidea]. *Middle Ordovician (Darriwilian)–Upper Devonian:* China (Anhui, Liaoning, Shandong), Korea, Malaysia, *Darriwilian;* Australia (New South Wales, Tasmania), China (Xinjiang), Kazakhstan, Mongolia, Russia (?Altai Mountains, Chukotsk Peninsula, Siberian platform, eastern Siberia, Tuva), USA (Alabama), *Sandbian–Katian;* Russia (Urals), *upper Silurian;* Australia (Queensland), *Lower Devonian;* England, Russia (Urals, ?Altai Mountains, ?Salair), *Middle Devonian;* China (Sichuan, Hunan), *Upper Devonian.*——Fig. 393*a–e*. **L. serotina* (Nicholson), Middle Devonian limestone, Teignmouth, near Torquay, England; holotype, NHM P.5988 (Nicholson's thin sections no. 268, 268a–d); *a,* longitudinal section (thin section 268a) showing long, continuous, moderate- to large-sized, subparallel pillars, with, in places, acutely shaped branching and closely spaced pillars where chainlike rows have been intersected obliquely; cyst plates mainly thin, flattened to slightly inclined at rather irregular, relatively widely spaced intervals, ×5 (Webby, 2012c; Nicholson section 268a, rephotographed by Webby in 1989); *b,* tangential section showing rounded, interlinked pillars in slightly sinuous, incomplete, chainlike rows, ×5 (Webby, 2012c; Nicholson's section 268c, rephotographed by Webby in 1989); *c,* sketch of longitudinal section showing large, regular boxwork of columnar-shaped pillars and platelike cyst plates, and in places, upwardly converging, conelike banding along pillar axes, referred to as axial canals, ×12 (Nicholson, 1891a, p. 162, fig. 19B); *d,* enlarged longitudinal section showing a single upwardly tapering pillar, with detail of axial cone-in-cone banding, ×25 (Nicholson, 1891a, fig. 19C); *e,* sketch of tangential section showing pillars arranged in sinuous, mainly incomplete, chainlike rows, and darker and lighter centers of the rounded pillars, ×12 (Nicholson, 1891a, fig. 19A).

Stratodictyon Webby, 1969, p. 647 [**S. ozakii;* OD]. Skeleton of flattened, undulating to mamelonate latilaminae, with dominantly fine-textured internal features; tangential skeletal elements uniformly more conspicuous than longitudinal structures; cyst plates commonly thin, closely and regularly spaced in rows that enclose long, low cysts, or very sporadically, rows may be more imbricated with irregular distribution; small- to moderate-sized, short pillars, and/or their shorter counterparts (denticles), have patchy distribution in longitudinal section but apparently more evenly spread, preserved as rounded, dark dots in tangential section; also rather inconspicuous astrorhizae may occur. *Upper Ordovician (Sandbian–Katian)*: Australia (New South Wales, Tasmania), Russia (Tuva, northeastern Russia), USA (Alabama, New York).——Fig. 394*a–d*. **S. ozakii*, lower part of Fossil Hill Limestone, lower Eastonian, Licking Hole Creek area, central New South Wales; *a–b,* holotype, AMF.99377 (AMFT.15020, 15021), longitudinal and tangential sections showing part of latilaminate skeleton with rows of long, low cyst plates and scattered short pillars, in tangential section, represented by fine, rounded, dark dots, ×10 (Webby, 1969, pl. 119,*4–5*); *c,* paratype, AMF.99382 (AMFT.15023), tangential section showing pillars mainly as rounded black dots, and a few light-colored (spar-filled) astrorhizal tracts, ×10 (Webby, 1969, pl. 120,*2*); *d,* topotype IGTUT 477, enlarged view of longitudinal section showing cysts arranged in rows bounded by rather thin, laterally continuous, lamina-like cyst plates, but in a few places these elements are downwardly inflected to close off cystlike (lenticular) spaces, and short, dark pillars of variable lengths and thicknesses are represented, as well as small areas where skeletal structures are barely recognizable because of spar replacement, ×25 (Webby, 2012c; preparation and photography courtesy of Heldur Nestor).——Fig. 394*e*. *S. columnare* Webby, Fossil Hill Limestone near west Boonderoo shearing shed, central New South Wales; holotype, AMF.99378, exhibiting a fine-textured latilaminate skeleton very similar to that of *S. ozakii* but additionally producing moderately large, vertically persistent mamelon columns that also include areas of spar replacement toward their axes, ×5 (Webby, 1969, pl. 118,*4*).

Family STROMATOCERIIDAE Bogoyavlenskaya, 1969

[Stromatoceriidae Bogoyavlenskaya, 1969b, p. 16] [=Cystostromatidae Khromykh, 1974a, p. 28, *partim*]

Coarse-textured labechiids with skeletal mesh of large, erect, post- to platelike pillars, cyst plates of large to moderate sizes, and shapes that vary from flattened or low convexity elements simulating laminae to both moderately convex and concave cyst plates; usually flattened to concave across narrower interspaces but may be convex upward in near proximity to mamelon

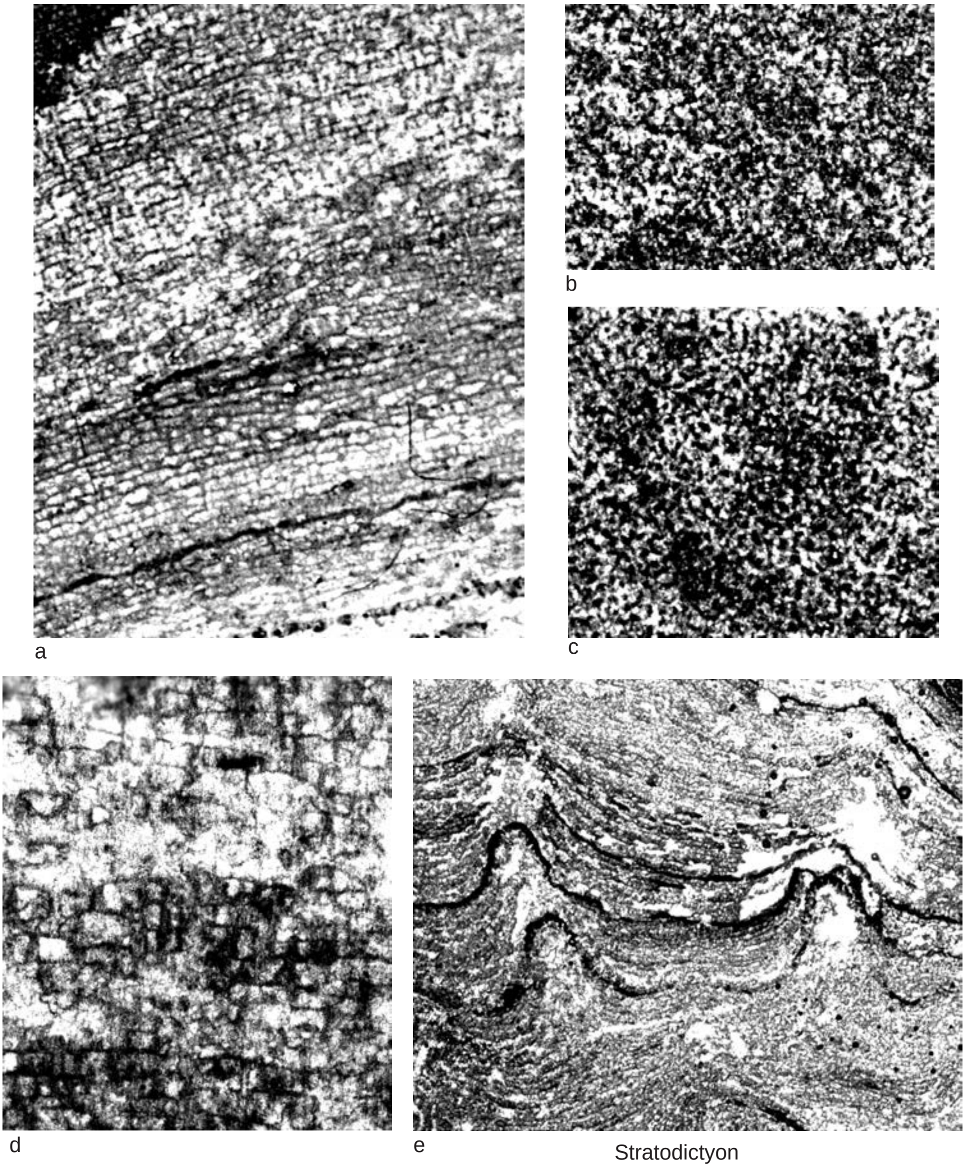


FIG. 394. Labechiidae (p. 723).

columns or across wider interspaces; in tangential outline, pillars may be irregularly rounded to elongate, serrated, meandriform or star shaped, or may even develop partially closed polygonal meshworks; intersections between rows of cyst plates and pillars may vary from approximately right-angle relationships to inclined at angles of at least 45° to alignment of erect pillar centers; denticles may be present on tops of cyst plates and locally on outer walls of pillars; astrorhizae not positively confirmed. *Upper Ordovician (Sandbian–Katian).*

Stromatocerium HALL, 1847, p. 48 [**S. rugosum* HALL, 1847, pl. 12,*2;* M] [?=*Nestoridictyon* KHROMYKH, 2001, p. 348 (type, *N. webbyi*, OD)].

Pillars large, continuous, with interiors preserved as sparry calcite infills (rarely solid); angular-oval to meandriform with lateral offsets to star-shaped (rarely regularly rounded) outlines in tangential section; in places, short, denticle-like flanges occur on outer walls of pillars; cyst plates large, of low convexity; in places, radially arranged pillars but not apparently incorporated into mamelon columns. [The genus includes a comparatively wide range of forms with rather different longitudinal structural elements, recognized presently as belonging to three species groups: (1) *S. rugosum* group (including type species), which is characterized by having pillars that in tangential section show vermicular to irregularly radiating outlines, rarely exhibit denticles, and apparently not associated with mamelon columns (Galloway & St. Jean, 1955); (2) *S. bigsbyi* group, based on *S. bigsbyi* Webby, 1979b, p. 248, characterized by pillars that in tangential section are oval to angular (rarely more complex), they lack denticles (were it not for the predominant sparry calcite pillar infills, such a form might be more appropriately assigned to *Labechiella*); and (3) *S. michiganense* group (including *S. michiganense*, *S. platypilae* Galloway in Galloway & St. Jean, 1961, and *S. pergratum* Nestor, 1976; =*S. moierense* Bogoyavlenskaya, 1977a), which exhibits pillars with meandriform, platelike offsets that in places become partially closed polygonal meshworks.] *Upper Ordovician (Sandbian–Katian):* Australia (Tasmania), Canada (Manitoba, Ontario, Quebec), China (Xinjiang, Qinghai) ?Mongolia, Russia (Taimyr Peninsula, Urals, Chukotsk Peninsula, Siberian platform, Tuva), USA (New York, Ohio, Kentucky, ?Michigan).——Fig. 395*a–d*. **S. rugosum,* Upper Ordovician Black River Group, Watertown, New York, holotype, AMNH 590/5A, B, C, E; *a,* longitudinal section (thin section 590/5A) showing a coarse, gridlike pattern of laterally continuous, flattened to gently undulating cyst plates, and moderately large, subparallel, calcite-spar–filled pillars usually growing apart, but in a few places they become more closely associated with lateral flanges or offsets, seemingly interconnecting them together in composite structures; *b,* tangential section (thin section 590/5C) showing varied slender, composite pillar outlines, from elongate to vermicular (with or without flanges), even sometimes radiating outward from a center; *c,* tangential section (thin section 590/5E) through another radial center with thicker, elongate to vermicular patterns; *d,* longitudinal section (thin section 590/5B) showing similar features to those exhibited in view *a*, ×10 (Galloway & St. Jean, 1955, fig. 2,3,5,6).

Cystistroma Etheridge, 1895, p. 134 [**Labechia(?) (Cystistroma) donnellii* Etheridge 1895, p. 134, pl. 14,*1–6;* pl. 15,*1–2;* pl. 16,*1–3;* M]. Coarse-textured skeletal mesh of large pillars and cyst plates; pillars, long, stout, may radiate upward and outward but rarely branch; in tangential section including oval, irregular, elongated, and, in places where tiny, outwardly directed, spinelike denticles are intersected, show serrated outlines; pillar interiors commonly preserved as sparry calcite infills; a few denticles also occur on tops of large, undulating to sagging cyst plates; away from intersecting pillars, cyst plates may be more gently convex. *Upper Ordovician (upper Sandbian–Katian):* Australia (New South Wales), Canada (Ontario, Quebec), Estonia, Russia (?Urals, Siberian platform), USA (New York, Kentucky, Michigan).——Fig. 396*a–g*. **C. donnellii*, lower part of Fossil Hill Limestone, lower Eastonian, Fossil Hill, near Belubula River, Boonderoo property, central New South Wales, Australia; *a–c*, lectotype, MMF907, 14517; *a,* longitudinal section showing general appearance of skeletal meshwork with large, spar-filled pillars and flattened to gently concavely shaped cyst plates, ×2 (Pickett, 1970, pl. 1,*1*); *b*, tangential section showing spinelike denticles on outer walls of spar-filled pillars; tiny spar-filled dots and rods in central dark area of sedimentary matrix are difficult to interpret but are unlikely to represent denticles associated with an obliquely intersected cyst plate, ×10 (Pickett, 1970, pl. 2,*1*); *c*, longitudinal section that shows scattered, spar-filled denticles on both the outer surfaces of large pillars and the upper surface of a cyst plate, ×10 (Pickett, 1970, pl. 2,*2*); *d–e*, topotype, AMF.98995 (variant A), tangential and longitudinal sections showing large pillars with oval outlines in tangential section and cyst plates that mainly drape across interspaces between adjacent pillars; localized areas of the pillars and cyst plates of this better preserved specimen exhibit brown, compact, specked material, ×5 (Webby, 1969, pl. 122,*7,* pl. 123,*1*); *f–g*, topotype, AMF.99005 (variant B), longitudinal and tangential sections showing pillars with more angular to bladelike outlines in tangential section and more complete alternation of skeletal elements, especially the pillars, replaced by calcite spar, ×5 (Webby, 1969, pl. 123,*2–3*).

Radiostroma Webby, 1979c, p. 208 [**R. tenue* Webby, 1979c, p. 210, fig. 5B–E; M]. Pillars long, slender, erect, vanelike, commonly fused at centers of closely associated, narrow, mamelon columns; in tangential section, pillars commonly stellate shaped, but in a few places more complex, partially closed, polygonal meshworks occur; denticles randomly developed on tops of cyst plates, and in places denticle-like spines may be present on free outer edges of bladelike pillars; cyst plates extend as thin, commonly undulate to concave-upward elements between pillars. *Upper Ordovician (Katian):* Norway.——Fig. 397*a–d*. **R. tenue*, Mjøsa Limestone, north of Bergvika, Lake Mjøsa; holotype, PMO 97113; *a,* longitudinal section showing pillars with long, slender, vertical vanelike plates (looking spinelike where a plate is intersected at right angles), and cyst plates that typically drape successively off pillars, either sagging across narrower interspaces or undulating where one or more cyst plates are involved across

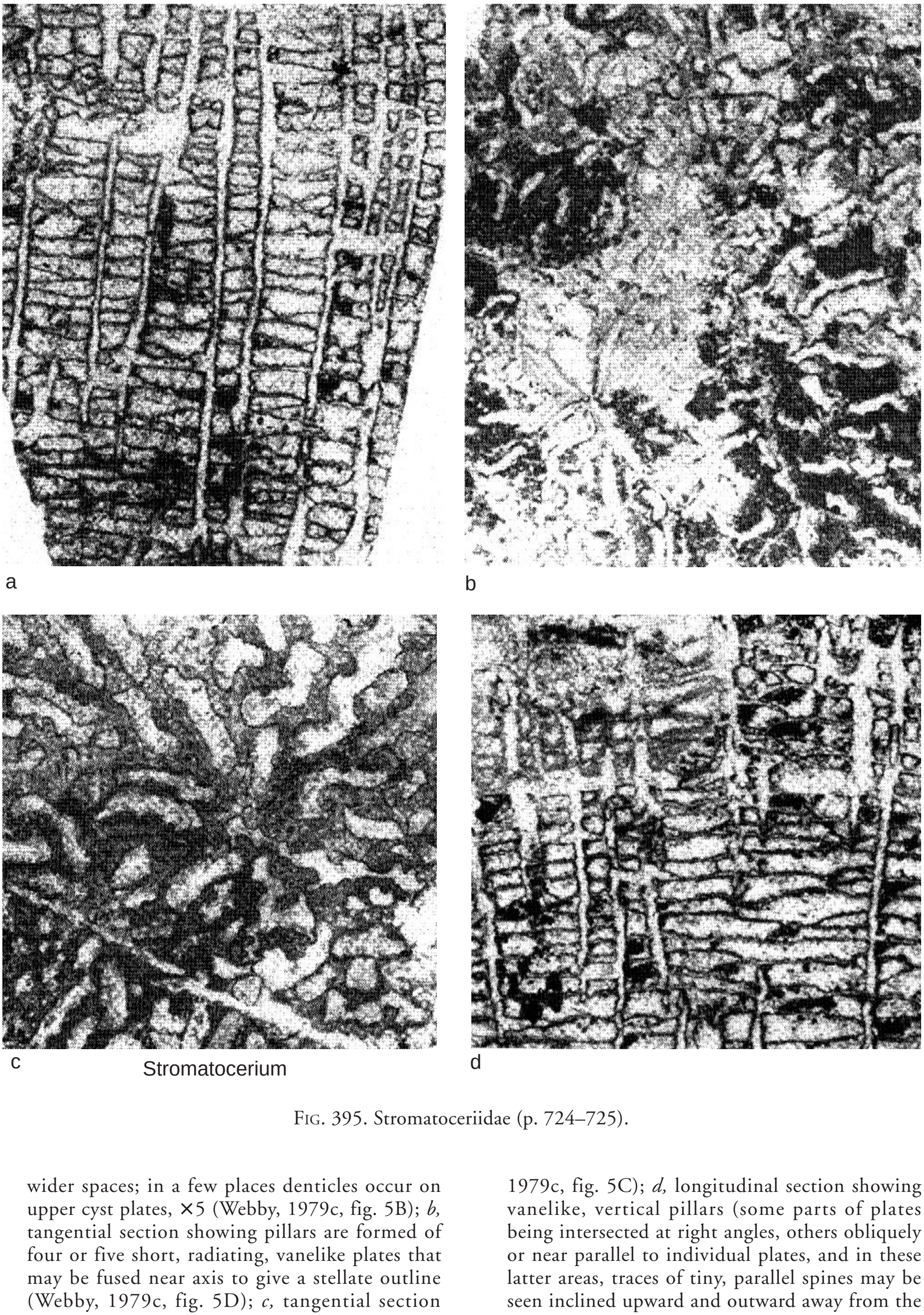


FIG. 395. Stromatoceriidae (p. 724–725).

wider spaces; in a few places denticles occur on upper cyst plates, ×5 (Webby, 1979c, fig. 5B); *b,* tangential section showing pillars are formed of four or five short, radiating, vanelike plates that may be fused near axis to give a stellate outline (Webby, 1979c, fig. 5D); *c,* tangential section showing complex pillars with their outwardly radiating, vanelike plates, but also in places, one or two concentrically arranged, closely spaced cyst plates intersect these vanelike plates, producing centers with fine meshworks of tiny, complete and incomplete, polygonal spaces, ×5 (Webby, 1979c, fig. 5C); *d,* longitudinal section showing vanelike, vertical pillars (some parts of plates being intersected at right angles, others obliquely or near parallel to individual plates, and in these latter areas, traces of tiny, parallel spines may be seen inclined upward and outward away from the pillar centers to about 25 degrees; also in places, well-defined, spar-filled denticles are exhibited on tops of cyst plates, and the spar-replaced cyst plates also seem to have been disrupted (perhaps even perforated) in places, ×10 (Webby, 1979c, fig. 5E).

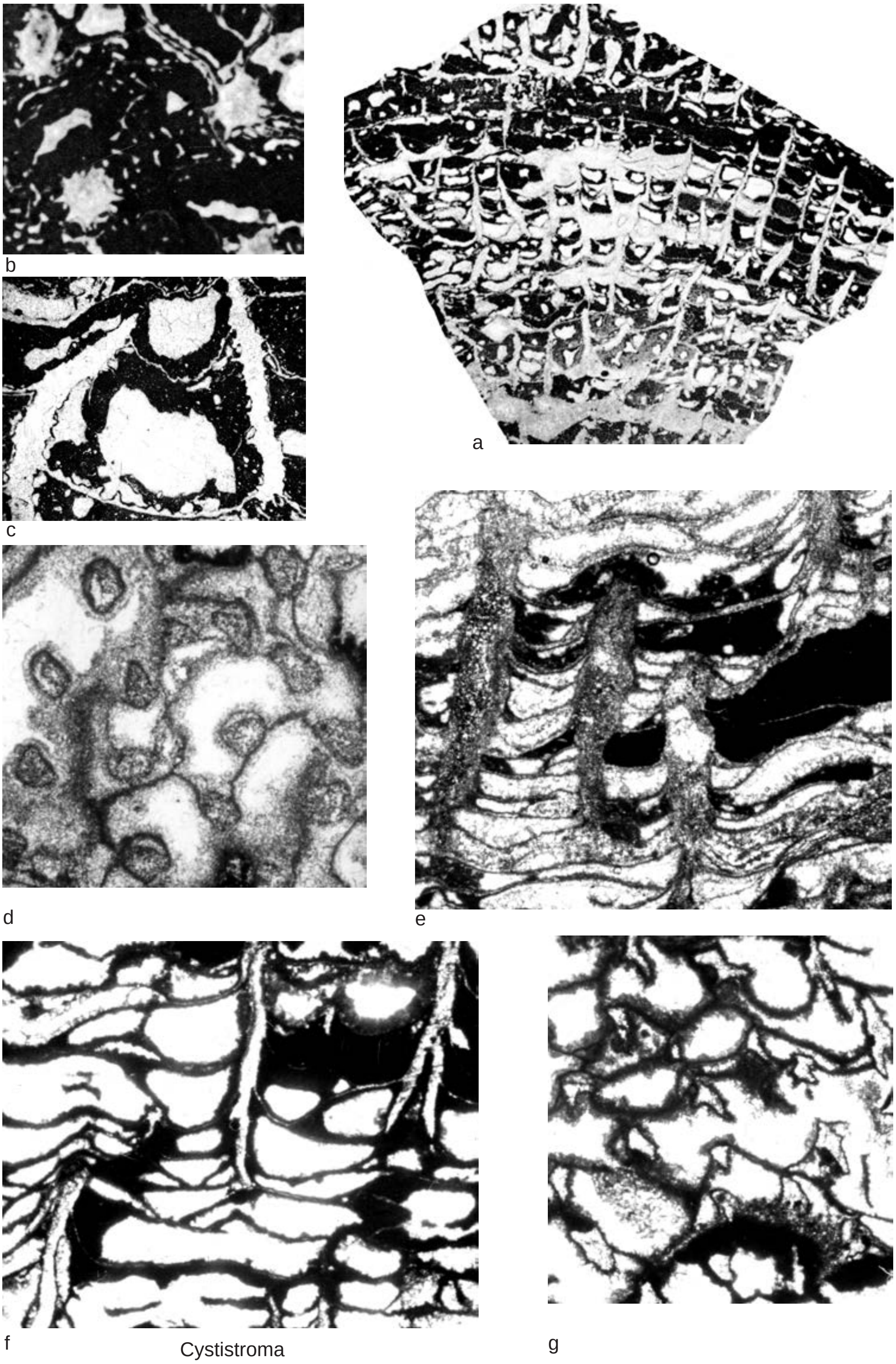


FIG. 396. Stromatoceriidae (p. 725).

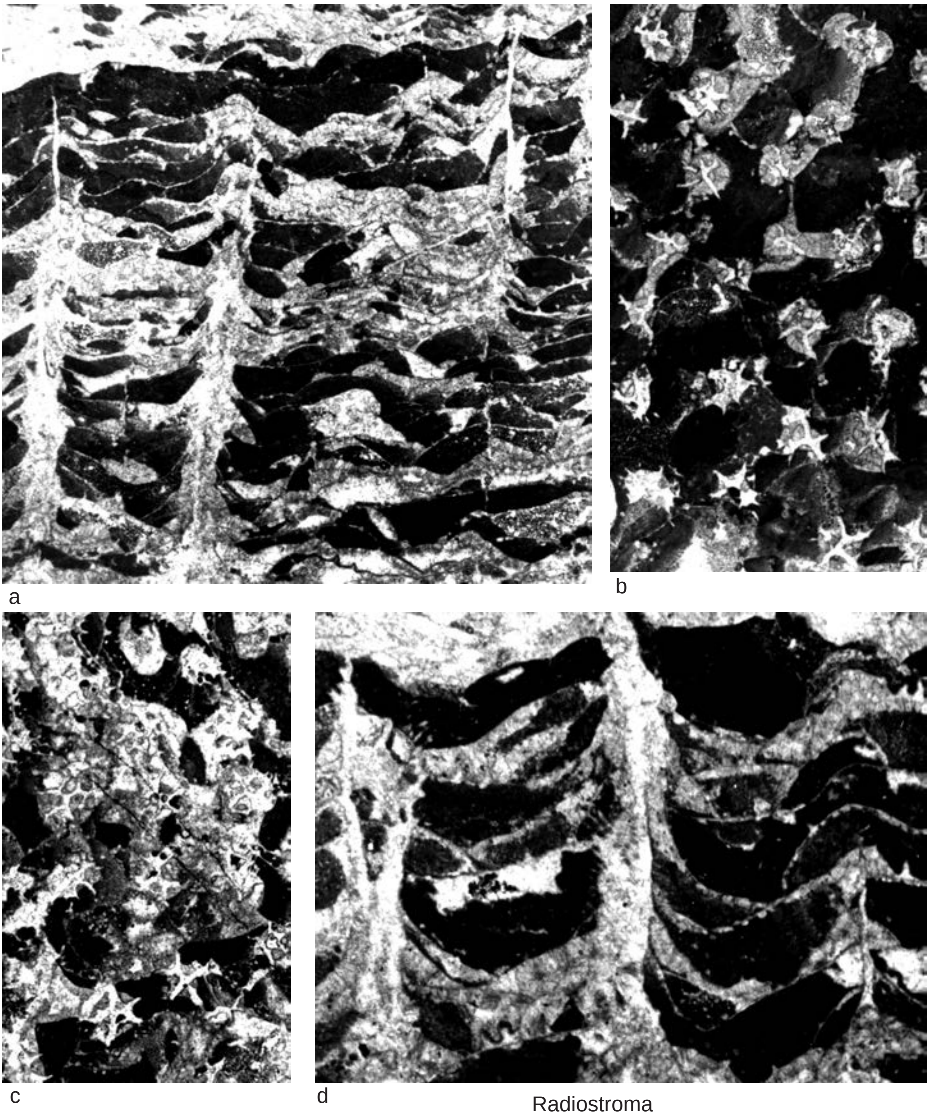


FIG. 397. Stromatoceriidae (p. 725–726).

Family PLATIFEROSTROMATIDAE Khalfina & Yavorsky, 1973

[Platiferostromatidae KHALFINA & YAVORSKY, 1973, p. 32]

Pillars long, solid, erect and branching, platelike elements, with tangential sections that show a variety of outlines from rounded, angular, triangular, star-shaped, meandriform, and anastomosing to zigzagged shapes, even locally, incomplete polygonal networks; cyst plates also exhibit a range of form from long, low, extended elements, simulating laminae, to more numerous, variably sized, blisterlike, imbricated cyst plates, with minimal upflexing of cyst rows adjacent to pillars; astrorhizal centers and pathways may be present, but their taxonomic significance remains uncertain. *Silurian (Llandovery)–Upper Devonian (Famennian).*

Platiferostroma Khalfina & Yavorsky, 1973, p. 32 [**Stromatocerium hybridum* Dong, 1964, p. 284 [294], pl. 2,*3–8;* OD; some discrepancies exist between catalogue numbers marked on thin sections of types of *P. hybridum* housed in Nanjing collections, and published registration numbers cited in descriptions and captions of plates published by Dong (1964); a few details are noted below]. Pillars long, continuous, intermittently branched, platelike, elements that may be moderately widely spaced and/or of varying thickness, dependent on orientation of pillarlike plates where intersected in longitudinal section, and proximity to a branch; in tangential section outlines are mainly irregularly elongate to meandriform, though a few, small, rounded or more complexly flanged offsets, even incompletely fused polygonal meshworks, may also be shown; cyst plates are thin and enclose numerous, variably sized (mainly small), convex-upward, imbricated cysts across interspaces between pillars, with rows not noticeably upflexed adjacent to pillars. *Upper Devonian (Famennian):* Australia (Bonaparte basin), China (Guangxi, Guizhou, Sichuan, Hunan), Vietnam, Russia (Northern Caucasus, Novaya Zemlya), Ukraine (Donets basin), Uzbekistan.——Fig. 398,*1a–d.* **P. hybridium* (Dong), lower part of Shizixu Formation, between Huangjin and Muliu, Luocheng County, Guangxi Province, ×5; *a,* holotype, NIGP Kw044-3 (14167), longitudinal section showing pillars of variable thickness, and in places, forklike branches and small- to moderate-sized, upwardly convex cyst plates (this specimen is recorded as a paratype; Dong, 1964, pl. 2,*5*); *b,* paratype, NIGP Kw044-2 (14170), tangential section showing dark-colored, irregular, elongate, flanged, meandering, sinuous, and rarely small-rounded outlines of pillars and patchy development of finer, obliquely intersected cyst plates (this specimen is recorded as part of the holotype; Dong, 1964, pl. 2,*4*; 2001, pl. 19,*2*); *c,* doubtful holotype, NIGP Kw044-3 (14168), oblique section showing mainly elongate to irregularly meandering pillars and cyst plates (Webby, 2012c; courtesy of Dong De-yuan); *d,* paratype, NIGP Kw044-2 (14169), longitudinal section showing long pillars that are thickened and branched in places, and vaguely aligned, imbricated rows of small, upwardly convex cyst plates (this figure was recorded as part of holotype; Dong, 1964, pl. 2,*3*; 2001, pl. 19,*1*).

Cystocerium Nestor, 1976, p. 41 [**C. sincerum* Nestor, 1976, p. 42; OD]. Pillars long, stout, sporadically branching, platelike structures; in tangential section showing rounded, angular, oblong, and vermicular shapes; walls of long, low cyst plates, thin and simulate laminae; astrorhizae represented by stellate pattern of radiating, wall-less pathways. [*Cystocerium* exhibits some similarities to *Parastylostroma* Bogoyavlenskaya, 1982a, but it has a much denser concentration of branching, pillarlike elements than is characteristic of *Parastylostroma*.] *Silurian* (*Wenlock*)*:* Russia (Siberian platform).——Fig. 399*a–b.* **C. sincerum,* Moiero River section, Siberian Platform, holotype, IGTUT 166-29 (Co3217); *a,* longitudinal section showing latilaminate skeleton, prominent solid pillars that frequently branch and rapidly thicken from slender initial offshoots, and rather thin, long, low cyst plates; *b,* tangential section exhibiting highly variable shapes and sizes of pillar outlines within skeleton, from small-rounded to larger-triangular to irregular-oblong and vermicular, and a few, well-defined, calcite-spar–filled, wall-less, astrorhizal pathways, ×10 (Nestor, 1976, pl. 9,*1a–b*).——Fig. 399*c–d. C. stellatum* Nestor, Wenlock, Moiero River section (different locality and slightly higher stratigraphic level), Siberian Platform, holotype, IGTUT, 166-30 (Co3216); *c,* tangential section exhibiting wall-less pathways radiating and branching from astrorhizal centers and pillars with regularly rounded to subangular outlines; *d,* longitudinal section showing more regularly aligned pillars with fewer branches and more narrowly spaced long, low cyst plates, ×10 (Nestor, 1976, p. 43, pl. 9,*2a–b*).

Parastylostroma Bogoyavlenskaya, 1982a, p. 36 [**Stromatocerium irregularis* Vassilyuk, 1966, p. 44; OD]. Pillars are long, solid, rod- to platelike, longitudinal elements, and in places, branched; in tangential sections, outlines of pillars may be rounded, elongate, or meandering with short, lateral offsets; rare denticles occurring on tops of cyst plates; in most places, cyst plates are thin, flattened (long, low), or more gently convex to wavy; cyst plates usually maintain a relatively flattened to slightly sagging disposition between pillars; no astrorhizae seen. [The relationships between *Parastylostroma* and *Vietnamostroma* are discussed herein (see p. 732)]. *Upper Devonian (Famennian):* Russia (Northern Caucasus, Novaya Zemlya), Ukraine (Donets basin), Uzbekistan.——Fig. 400,*1a–b.* **P. irregularis* (Vassilyuk), Famennian sequence, Porfirtovaya ravine, near Novotroitskoye village, Donbass, Ukraine, holotype, DPI 12/130, longitudinal and tangential sections, ×5 (Vassilyuk, 1966, pl. 32,*8a–b*).

Pleostylostroma Wang, 1982, p. 24 [**Labechia shiniulanense* Wang, 1978a, p. 14, pl. 2,*1a–b*; OD]. Pillars are long, erect, moderately closely spaced, platelike elements that are of variable thickness dependent on orientation of longitudinal section and incidence of branches; in tangential section, pillars exhibit irregularly rounded to elongated, or triangular to starlike shapes; cyst plates vary from small and incomplete to larger and complete cystlike elements across pillar interspaces; cyst plates have variable convexity and in many places show overlapping relationships but are not regularly imbricated; cyst plates usually thin; cyst rows extending without conspicuous sagging or updoming between pillars; in tangential section, cyst plates show approximately rounded outlines; no denticles or astrorhizae. [This genus exhibits a superficial resemblance to stromatocerid genus *Radiostroma* Webby, 1979c, but it has thicker, solid, platelike pillars rather than the thin, bladed,

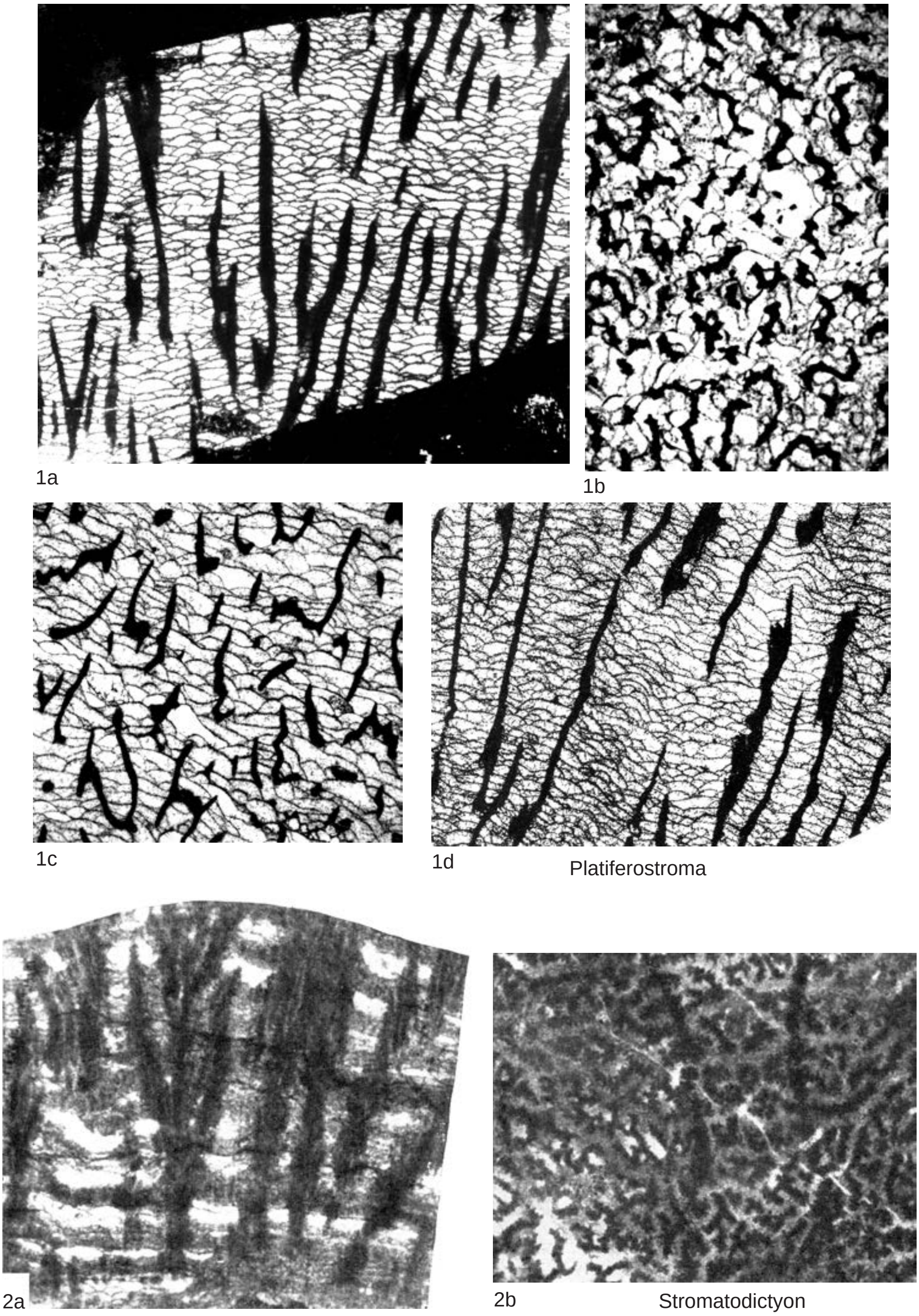


FIG. 398. Platiferostromatidae (p. 729–732).

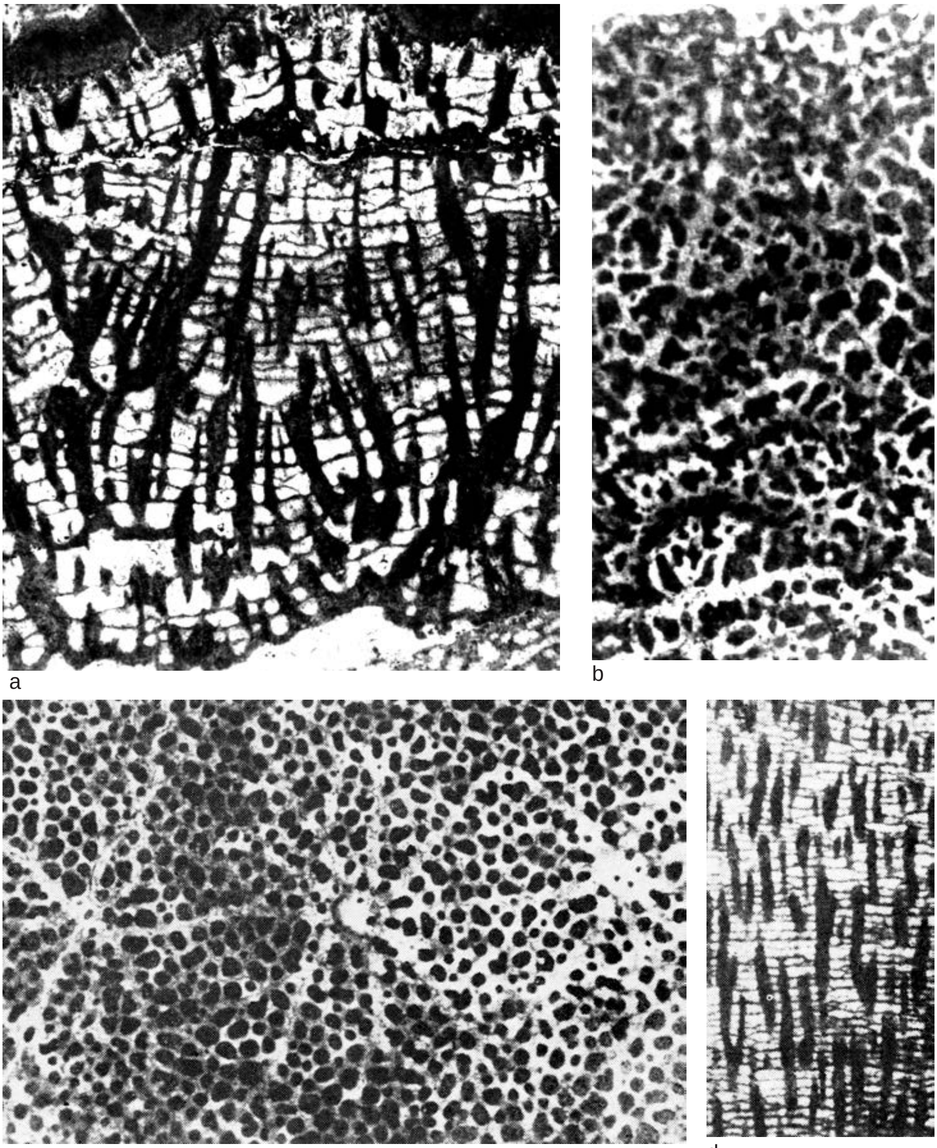


FIG. 399. Platiferostromatidae (p. 729).

or flanged pillars of *Radiostroma;* and smaller, nondenticulate, cystose elements that are not markedly inflected upwardly against adjacent pillars, in contrast to the cysts of *Radiostroma* that are larger, denticulate, and become steeply inclined close to adjacent pillars.] *lower Silurian (Llandovery):* China (Sichuan).——FIG. 401*a–d.* **P. shiniulanense* (WANG), Shiniulan Formation, Shiniulan, Guanyinqiao, Qijiang County, holotype, CIGMR, Gsf 105-5 (Ss1001); *a,* longitudinal section showing long, slender pillars, thickened only in a few places, in proximity to a branch, and with moderately upflexed, blisterlike, imbricated cyst plates of variable size; *b,* tangential section exhibiting solid pillars with round, elongate to subtriangular outlines, and thin cyst plates that enclose irregularly rounded, spar-filled spaces; *c,* tangential section showing solid pillars with elongated to subtriangular and subrounded outlines, in part aligned radially, and small, subrounded cyst plates in interspaces; *d,* longitudinal section exhibiting thicker pillars, where platelike or branching forms are intersected obliquely, and cyst plates upwardly arch and are of markedly different sizes, ×5 (Wang, 1982, pl. 1,*3–6*).——FIG. 401*e–f. P. coalitum* WANG, 1982, Shiniulan Formation, Shimenkair, Qijiang County; holotype, CIGMR, Sf1-3 (Ss1069); *e,* longitudinal section showing thinner, erect, platelike pillars and very thin, gently convex, cyst plates; *f,* tangential section showing that pillars may sometimes develop more complex polygonal to starlike outlines representing outwardly flanged, platelike pillars, ×5 (Webby, 2012c, courtesy of Wang Shu Bei; see also WANG, 1982, pl.1,*7–8*).

?**Stromatodictyon** KHALFINA, 1972, p. 148 [**S. repentinium* KHALFINA, 1972, p. 152, pl. C-12, fig. 4-5, M]. Skeleton with broad, continuous, longitudinally branched, irregular to bladelike or flanged pillars (with somewhat ragged margins) that are intersected by banded, laminar (or latilaminar) elements composed of an alternating lower part, with a laterally somewhat discontinuous, comparatively finer, denser meshwork of cystose layers and/or microlaminae and short micropillars or denticles, and with an upper part of large, spar-filled chambers that are bounded by large, flattened to sagging cyst plates. In tangential section, coarser, interconnected, open and closed meshworks are represented that comprise darker, irregularly rounded to bladed or flangelike pillars and lighter areas with irregularly branching to sinuous spar-filled canals, including astrorhizal structures, as well as some irregular to more rounded spar-filled cystlike cavities. [The genus was incompletely described, and no holotype specimen number was printed in the original publication, but the genus does seem to be a distinctive labechiid, here tentatively included in the family Platiferostromatidae. Previously the genus was referred to the order Actinostromatida (included in the subfamily Plumataliniinae BOGOYAVLENSKAYA, 1969b, family Pseudolabechiidae BOGOYAVLENSKAYA, 1969b) by STOCK (in STEARN & others, 1999, p. 37), but since excluded (see Actinostromatida, p. 769–779). *Stromatodictyon* has slight resemblances to *Cystocerium* NESTOR, 1976, with its well-developed, dense, branching pillars, but these pillars are more distinctively flanged, micropillars and denticles may be associated at the margins of the pillars, and a much finer development of cystose elements occurs within laminar layers of the skeleton. *Stromatodictyon* may also be compared to another genus, *Tarphystroma* NESTOR, COPPER, & STOCK (2010, p. 62), which these authors tentatively included in the Lophiostromatidae (the genus is similarly treated herein as a questionable member of the family Lophiostromatidae; see p. 753); however, compared to *Stromatodictyon*, with its characteristically branching, flanged pillars and traces of marginal micropillars and denticles, *Tarphystroma* has markedly different, comparatively short, stout, longitudinally oriented, cone-in-cone type, bundled upgrowths.] *Silurian (upper Llandovery–lower Wenlock)*: Russia (Siberian Platform).——FIG. 398,*2a–b.* **S. repentinium*, Moiero River section; holotype may exist in CSGM but has not been found, presumed lost; *fide*, V. G. Kromykh, personal communication, November 2011); *a,* longitudinal section of holotype, ×10 (Khalfina, 1972, pl. 12,*4*); *b,* tangential section of holotype, ×5 (Khalfina, 1972, pl. 12,*5*).

Vietnamostroma NGUYEN HUU HUNG & MISTIAEN, 1998, p. 63 [**V. vietnamense* NGUYEN HUU HUNG & MISTIAEN, 1998, p. 64, pl. 5,*1a–e;* OD]. Pillars long, complex, platelike to flanged and, in places, multibranched; tangential sections show meandering to anastomosing outlines with zigzag offsets; these latter commonly developing areas with open, incompletely partitioned, polygonal meshworks, even becoming partially closed meshes in a few forms; cyst plates thin, long, low, simulating laminae; astrorhizae may be present. [This genus, like *Parastylostroma* BOGOYAVLENSKAYA, 1982a, exhibits long, low, rather flattened, cyst plates but differs in having pillars that are longitudinally more complexly flanged and multibranched, and in showing in outlines that they are more meandriform to anastomose, or incompletely partitioned meshworks. The pillars of a few Late Devonian species such as *V. kueichowense* (DONG, 1964), *V. kwangsiense* (DONG, 1964), and *V. chaetetiporoides* WANG (1988) even exhibit patchy clustering of completely closed polygonal outlines, resembling meshworks seen in some Ordovician stromatocerids, e.g., members of the *Stromatocerium michiganense* species group (see especially *S. michiganense* PARKS in GALLOWAY & ST. JEAN, 1961, p. 64, pl. 9,*3b*). BOGOYAVLENSKAYA (1973b, p. 22) and NESTOR (1976, p. 25) have suggested that Late Devonian species exhibiting these features were more likely to be chaetetids, but these views are rejected in favor of maintaining their relationships within labechiids, and herein, members of family Platiferostromatidae.] *Upper Devonian (Famennian)*: China (Guizhou, Sichuan), Vietnam.——FIG. 400,*2a–b.* **V. vietnamense*, upper part of the Cù Bai Formation,1 km northeast of Phong Nha Cave, Phong Nha area, Quang province, Vietnam; holotype, FN.743/2, RIGMR; *a,* longitudinal section showing long, slender, erect, many-branched, platelike pillars, as well as rows of long, low cyst plates, ×10; *b,* tangential section exhibiting incomplete meshworks of irregular to sinuous, platelike pillars with numerous, short, lateral, zigzagged offsets, obliquely intersected cyst plates, and patterns of broadly ramifying and branching astrorhizal pathways, ×10 (Webby, 2012c, courtesy of Nguyen Huu Hung & Bruno Mistiaen).——FIG. 400,*2c–d. V. kueichowense* (DONG, 1964), p. 286 [295], pl. 3,*7–8,* pl. 4,*1–2,* lower part of Gelaohe Formation, Famennian, between Wuliqiao and Biaoli, Dushan County, Guizhou Province, holotype, NIGP, Gy311-1 (14156-14157); *c,* tangential section showing variety of anastomosing, meandering, partially and completely fused meshworks of

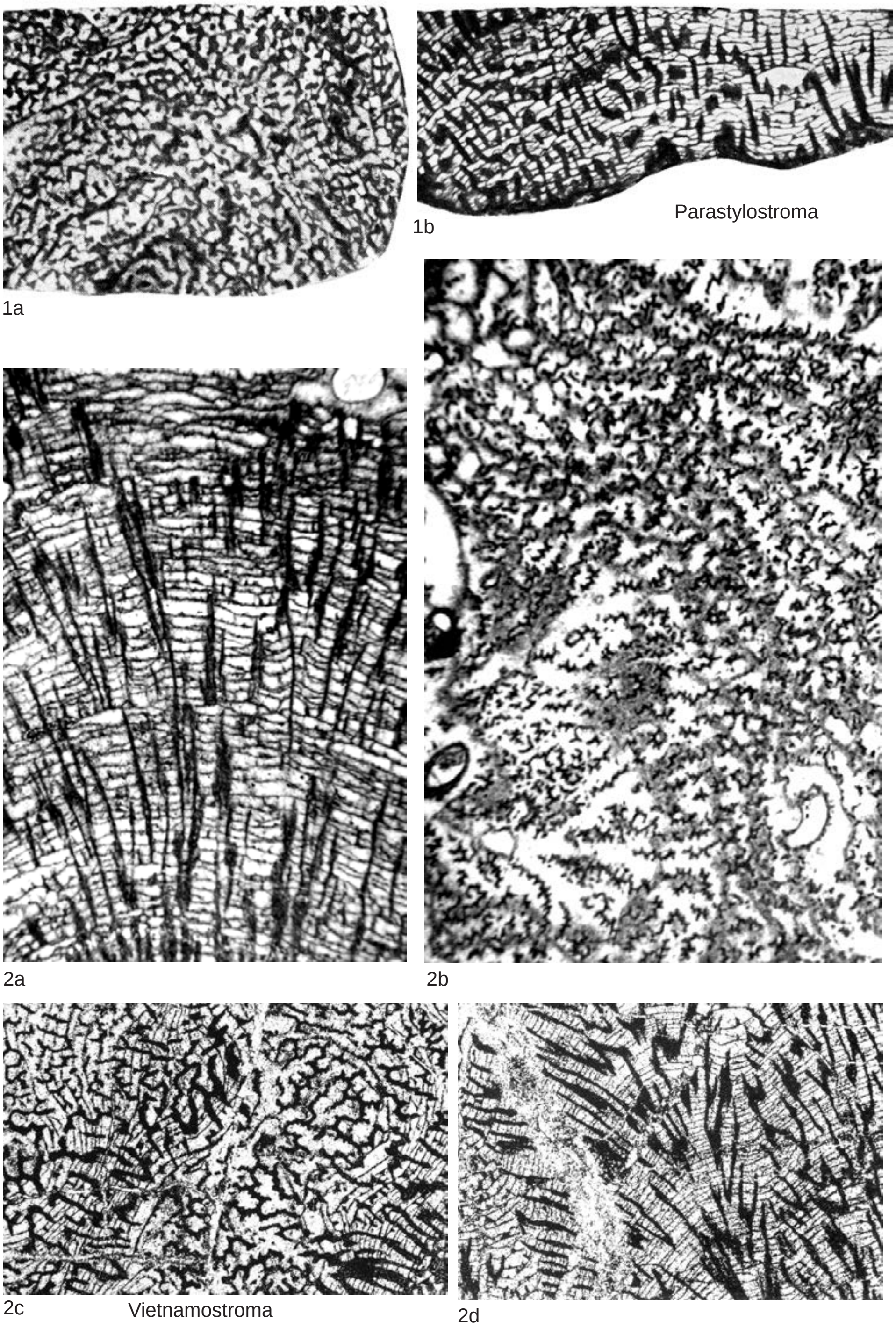


FIG. 400. Platiferostromatidae (p. 729–734).

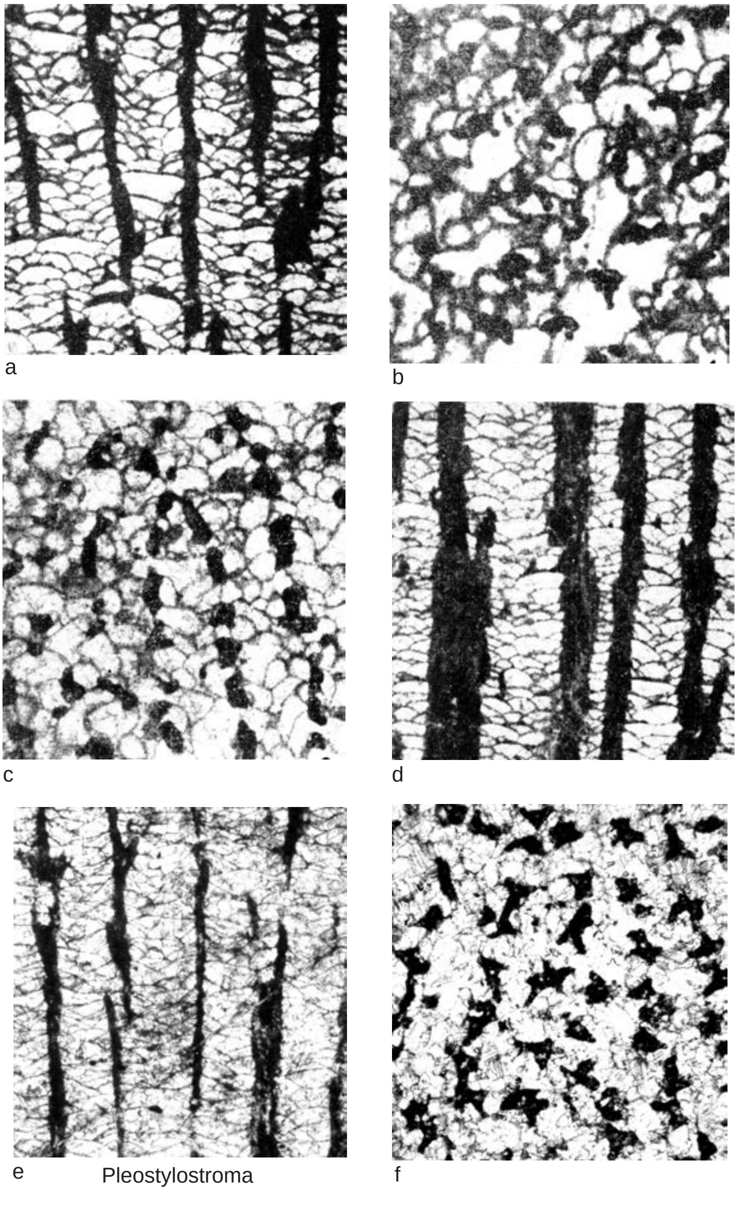


FIG. 401. Platiferostromatidae (p. 729–732).

platelike, zigzag-shaped pillars across broad centers, identified by the near-parallel, curved lines of cyst plates, ×5; *d,* longitudinal section showing flanged or platelike pillars that produce offsetting branches as they radiate upward and outward from weakly developed centers, defined by weakly updomed, closely spaced, long, low cyst rows, ×5 (Dong, 2001, pl. 19,*3–4*).

Family STYLOSTROMATIDAE Webby, 1993

[Stylostromatidae WEBBY, 1993, p. 58]

Strongly mamelonate with longitudinal elements ranging from discrete, simple, rounded, outwardly radiating branched pillars to more platelike, flanged or pinnately arranged, composite pillars in mamelon columns; cyst plates range widely in size and shape, commonly low convexity to flattened, and upwardly arching into closely spaced rows across mamelon columns (and composite pillars); denticles commonly formed on tops of cyst plates and locally superposed to form short pillars; markedly latilaminate skeletons may exhibit successive phases of thickened skeletal material. *Middle Ordovician (Darriwilian)–Upper Devonian (Famennian).*

Stylostroma GORSKY, 1938, p. 15 [**S. crassum;* OD] [=*Mamelolabechia* KHROMYKH, 1977, p. 44 (type, *Pseudolabechia tuberculata* YAVORSKY, 1955, p. 66–67, OD)]. Skeleton mamelonate with pillars commonly restricted to mamelon columns, as simple, postlike, and upwardly and outwardly radiating, branching elements; pillars may be clustered in multibranched arrays, developing stellate or other less regular patterns tangentially, or may be more loosely interconnected where branching is more open and at less frequent intervals; denticles, or less commonly, short, unbranched, superposed pillars may occupy interspaces between columns; cyst plates commonly of small to moderate size and low convexity in regular cyst rows, but sometimes more cystose and imbricated patterns occur, especially across interspaces. [The type species of *Stylostroma* (*S. crassum*) is characterized by having upwardly and outwardly radiating pillars that branch repeatedly within broad mamelon columns, giving an approximately stellate appearance of platelike forms where pillar branches remain fused toward the axis, but the pillars have a postlike form where unbranched, especially away from centers. *S. tuberculata* (YAVORSKY) is at the other end of the range of morphological forms assigned to this genus. It shows more open and much less frequent branching in mamelon columns, and these pillars mainly exhibit postlike structures. A complete gradation of morphological forms exists between end members, here referred to as the *S.crassum* and *S. tuberculata* species groups. No clear-cut, age-related subdivision exists between the two morphological types: the simpler, mainly postlike *S. tuberculata* morphologies are not restricted to the Ordovician-Silurian record, nor are the more complexly fused *S. crassum*-type morphologies limited to the Late Devonian. Consequently, it remains preferable not to divide the genus into two, as favored by KHROMYKH (1977), with *Mamelolabechia* reserved for the Ordovician–Silurian species, and *Stylostroma* for the Late Devonian species. Additionally, a number of Chinese Ordovician species of *Stylostroma* have been retained in *Pseudolabechia* YABE & SUGIYAMA, 1930, by DONG and WANG (1984), and DONG (2001), but should be excluded from that genus, as the type species is an actinostromatid (see MORI, 1968, 1970; STOCK in STEARN & others, 1999; and see p. 771–776). Apart from some differences in preservation of the early forms, all the species of *Stylostroma* exhibit mamelon columns and pillars that branch and splay upward and outward from their centers, and cyst rows that range from long, low to imbricated, blisterlike profiles.] *Upper Ordovician (Sandbian)–Upper Devonian:* Australia (Tasmania), China (Xinjiang), Norway, *Sandbian–Katian;* China (Guizhou), *lower Silurian;* Russia (Siberian platform), *middle Silurian;* Australia (northern Queensland), *Lower Devonian;* Canada (Alberta), China (Sichuan, Guizhou, Guangxi, ?Hunan), Kazakhstan, Russia (northern Caucasus, Novaya Zemlya, Urals, northeastern Siberia), Ukraine (Donets basin), *Upper Devonian.*——FIG. 402*a–i.* **S. crassum*, southern shore of Melkaya Bay (loc. 401), Samolet Peninsula, probably upper Famennian, Novaya Zemlya, Russia; holotype, CNIGR, 5767/6; *a–c,* slide 5767/6b, low to high magnification longitudinal sections; *a,* ×2; *b,* ×5; *c,* ×10; *d–e,* slide 5767/6c, longitudinal sections, ×5; *f–h,* slide 5767/6a, low to high magnification sections; *f,* ×2; *g,* ×5; *h,* ×10; *i,* topotype, tangential section, ×5; this latter specimen was termed an autotopotype by GORSKY (1938), probably to signify its special significance as collected from the type locality by the original author of the species (Gorsky, 1938, p. 15, pl. 2,*2–7,* pl. 3,*2*).

Eopennastroma WANG, 1978c, p. 104 [**E. sinense*; OD]. Skeleton usually exhibits moderately upraised, relatively narrow (mamelon-like) columns and broad intercolumnar spaces; pillars centered in columns and comprising relatively long, slender, platelike axial structure with associated open branches or weakly bundled elements; shorter lateral offsets occurring in places off main axial plates; abundant, small, closely spaced, imbricated cyst plates usually dominate columnar areas, but in a few places they extend outward in rows across intercolumnar spaces, alternating with large, nearly complete cyst plates with gently convex to flattened, or concave-shaped profiles; denticles occur sporadically on tops of cyst plates; becoming short pillars in places where associated with rows of small cyst plates; in oblique-tangential section, pillars appear dominantly as elongated to curved plates with short lateral offsets. [Platelike pillars in *Eopennastroma* are markedly less densely clustered than in *Pennastroma*. The holotype of *Eopennastroma* is not illustrated in a section that is precisely oriented tangentially. However, WANG (1978c, p. 105) designated two other species, *E. guizhouense* WANG, 1978c, and *E. multicystosum* WANG, 1978c, from the same locality and horizon as the type species that do exhibit pillar shapes set within columns and completely encircled by outwardly directed cyst plates, demonstrating that they are well-oriented tangential sections. The pillar shapes in *E. guizhouense* include one example that has four unequal branches (with lateral offsets) diverging

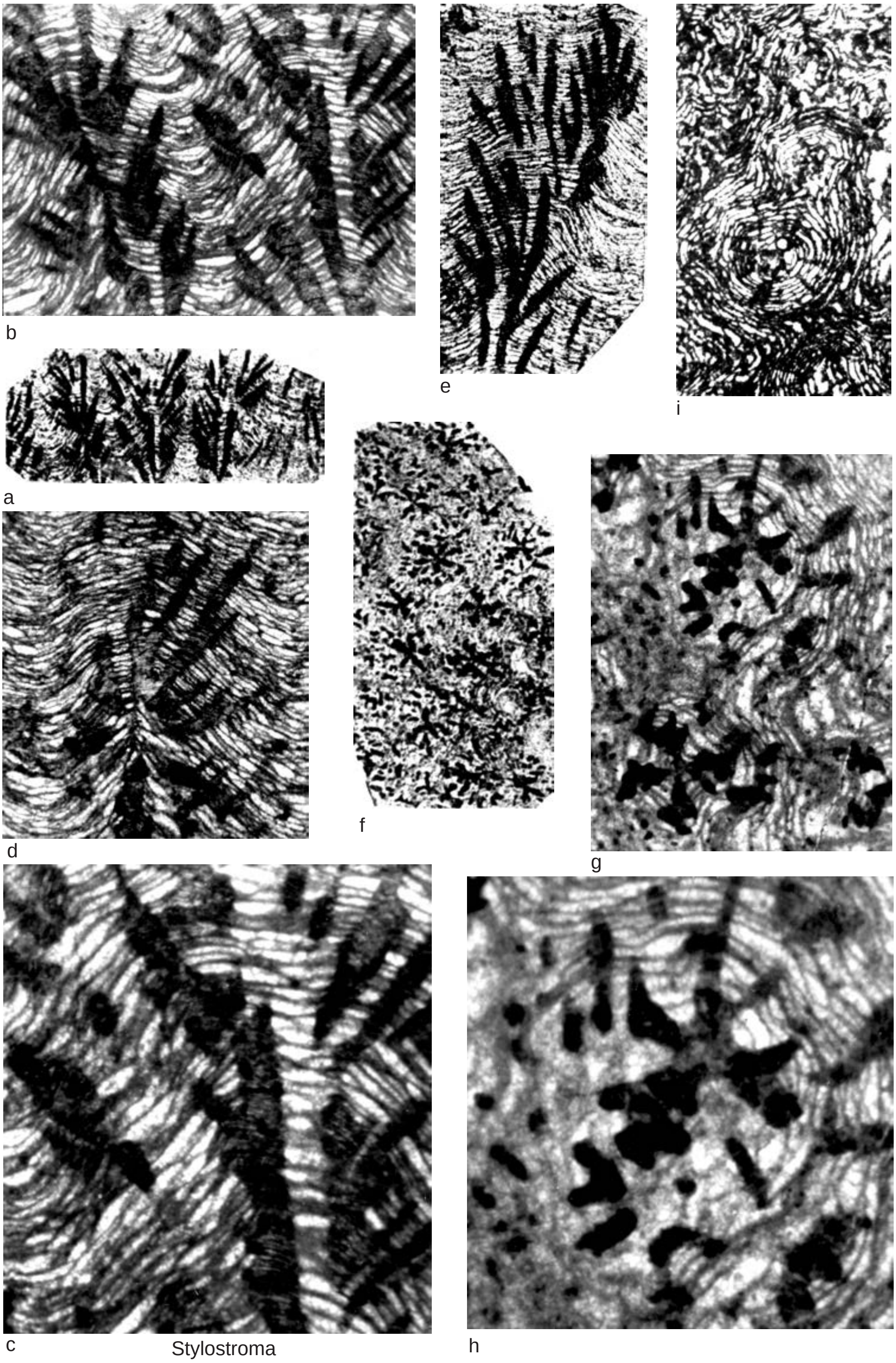
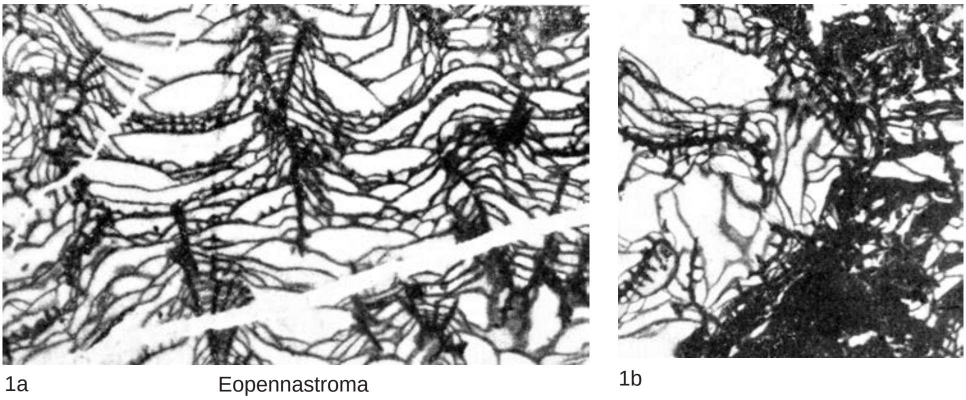
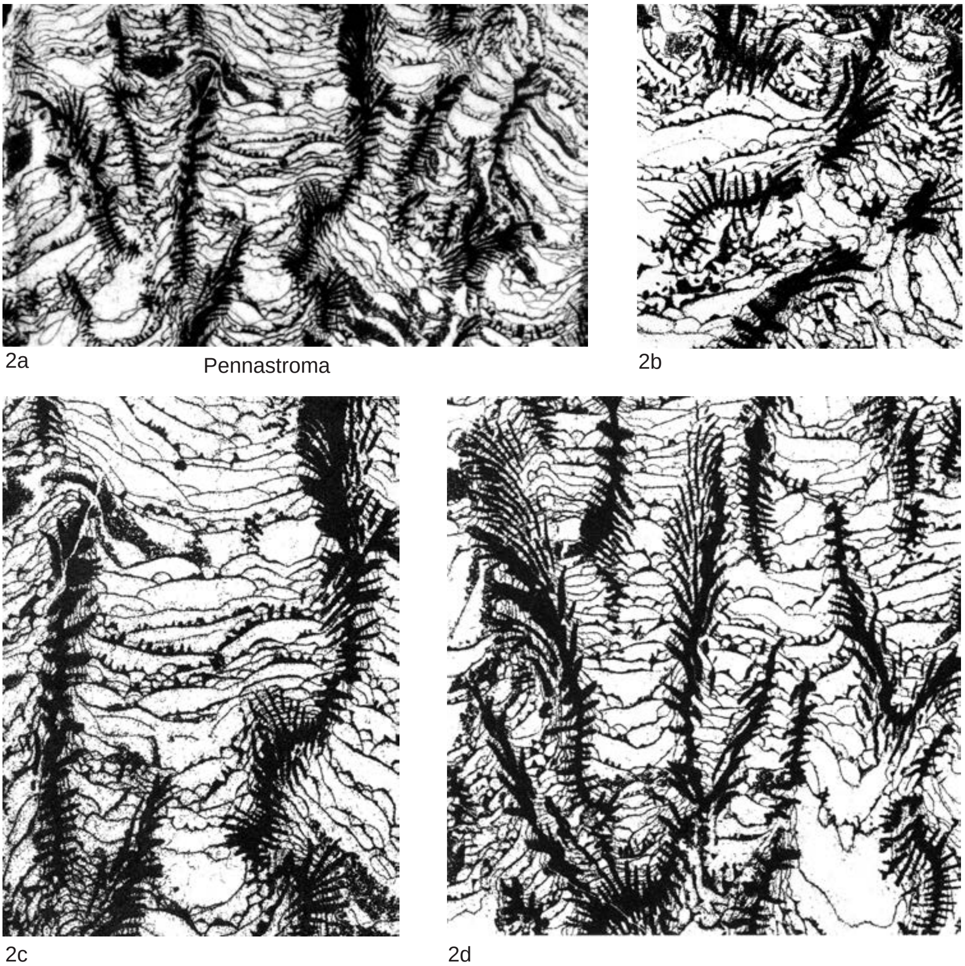


FIG. 402. Stylostromatidae (p. 735).



Eopennastroma



Pennastroma

FIG. 403. Stylostromatidae (p. 735–738).

from a center to one side of a column (Wang, 1978c, pl. 27,*4b*), and in *E. multicystosum,* several examples of gently arcuate, slender, single, stipelike structures with spiny lateral offsets occur (Wang, 1978c, pl. 28,*1b*). It seems therefore that *Eopennastroma* has a pillar outline that is more bar shaped than outwardly radiating (stellate) from centers of the columns.] *Upper Devonian (Famennian):* China (Guangxi, Guizhou).——Fig. 403,*1a–b.* **E. sinense*, lower part of Gelaohe Formation, Pinglang, Duyun, Guizhou Province, holotype, CIGMR, no. GS–70, 71, longitudinal and partially tangential to oblique sections, ×5 (Webby, 2012c, courtesy of Wang Shu Bei; see also Wang, 1978c, pl. 27,*3a–b*).

Pachystylostroma Nestor, 1964a, p. 23 [**Stromatopora ungerni* Rosen, 1867, p. 75, pl. 9; OD]. Skeleton usually moderately to strongly mamelonate; cysts of variable size; cyst plates alternating between thicker, gently wavy laminae; mamelon columns sometimes lacking; where present have simple, upwardly and outwardly branching pillars, and in some cases axial thickening of skeletal elements; denticles commonly developed on upper surfaces of thickened laminae, less common on tops of individual cyst plates; locally, successive, close-spaced laminae may appear palisade-like where intersected by short, superposed pillars. [The main feature of this genus that allows it to be distinguished from *Stylostroma* is the presence of thickened, wavy laminae. Nestor (1964a) recognized the following three species groups: (1) *P. ungerni* species group that exhibits strongly compacted mamelon columns; (2) *P. contractum* species group that has weakly developed mamelon columns; and (3) *P. estoniense* species group that shows well-developed, slender mamelon columns incorporating well-differentiated branching pillars.] *Middle Ordovician (Darriwilian)–Upper Devonian:* USA (Vermont, New York), *Darriwilian;* Australia (Tasmania), Canada (Ontario), Norway, Estonia, Russia (Altai-Sayan, Tuva), USA (Alabama), *Sandbian–Hirnantian;* Estonia, Ireland, *Llandovery;* Russia (Siberian platform), Sweden (Gotland), *Wenlock;* Estonia, *Ludlow–Pridoli*; China (Sichuan), Russia (Novaya Zemlya, Vaigach Island, Urals), *Upper Devonian.*——Fig. 404*a–c.* **P. ungerni* (Rosen), Hilliste Formation, Suuremõisa, Hiiumaa Island, Estonia; *a–b,* lectotype, IGTUT 112-2 (Co3011), longitudinal and tangential sections, ×5 (Nestor, 1962, pl. 2,*1–2*; 1964a, pl. 4,*4–5*); *c,* paralectotype, IGTUT 112-2 (Co3012), longitudinal section, note uneven base of skeleton in part overgrowing fragment of halysitid coral and large area of calcite spar fill, ×5 (Webby, 2012c, courtesy of Heldur Nestor).

Pennastroma Dong, 1964, p. 296 [**P. yangi*; OD]. Pinnately arranged, composite, platelike pillars developing within rather narrowly centralized, upwardly arching (possibly mamelon) columns as upwardly and outwardly splayed elements on either side of a more continuous, centralized, platelike structure, or grading into areas where central plate has mainly lateral, yard-arm–type offsets, best represented in obliquely oriented sections; in other areas these composite pillars may either branch, maintain their rather sinuous courses, or develop breaks in upward continuity; broad, intercolumnar spaces composed dominantly of large, complete to near complete, weakly convex to flattened, or concave cyst plates; in places these may alternate with one or more rows of small, imbricated cyst plates that seldom extend entirely across an intercolumnar space; successive rows of tiny, imbricated cyst plates are most commonly intermeshed with pillar offsets within uparching columns; denticles (and short pillars) of intercolumnar spaces are usually confined to tops of more complete cyst plates. [This genus differs from *Stylostroma* in displaying more concentrated, centralized, columnar areas with innumerable well-developed lateral (yard arm) offsets from its platelike pillars. However, Mistiaen, Hou, and Wu (1997) questioned the validity of the genus *Pennastroma* based on a study of material from Famennian deposits in the Etaoucun section of the Guilin region, Guangxi province. They identified their species as belonging to *Stylostroma,* claiming that features—in longitudinal sections, pectinate and penniform aspects of the pillars, and in tangential sections, the V-shaped outlines of pillars—were not diagnostic, therefore arguing that Dong's (1964) original genus *Pennastroma* was a junior synonym of *Stylostroma* Gorsky, 1938. But Mistiaen, Hou, and Wu (1997) did not study (or revise) the original type material of *Pennastroma* (*P. yangi*) housed in Nanjing, nor use comparative material from the original type locality (Luocheng area, Guangxi province), nor attempt to compare their species with species of *Stylostroma* (more than 10 species) already described from the Famennian of southern China (Dong, 1964; Wang, 1978b, 1978c, 1988). The case for relegating *Pennastroma* to junior synonomy within *Stylostroma* is, therefore, not based on comparisons between the same or similar type material and should be rejected. It remains, however, a matter of concern that so few, well-oriented, tangential sections have been used to describe *Pennastroma* and related taxa, preventing their three-dimensional form from being fully evaluated. *Upper Devonian (Famennian):* Australia (Bonaparte basin), China (Guangxi, Guizhou, Hunan), ?Uzbekistan.——Fig. 403,*2a–d.* **P. yangi*, lower part of Shizixu Formation, between Huangjin and Muliu, Luocheng district, northern part of Guangxi Province, holotype, NIGP, Kw047-2 (14160-14162); *a,* longitudinal section, thin section no. 14162, ×2; *b,* obliquely oriented section, thin section no. 14161, ×3.5; *c,* enlarged longitudinal section, thin section no. 14162, ×2; *d,* longitudinal section, thin section no. 14160, ×3.5 (Webby, 2012c, courtesy of Dong De Yuan; see also Dong, 1964, pl. 4,*3–5*).

Spinostroma Wang, 1978b, p. 131 [**S. diversum;* OD] [=*Sichuanostroma* Wang, 1978b, p. 133 (type, *S. robustum* Wang, 1978b, p. 133, pl. 42,*3,* OD)]. Pillars large, erect, rather compact, solid, rodlike to

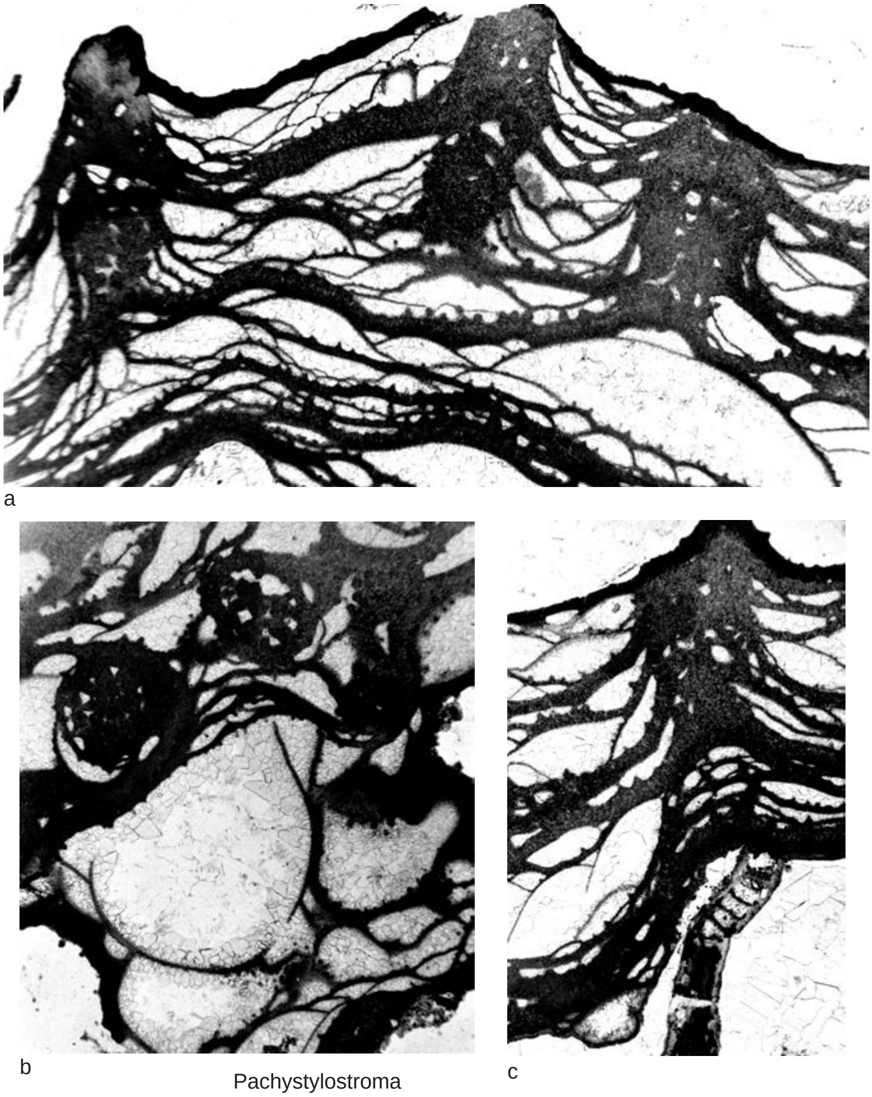


FIG. 404. Stylostromatidae (p. 738).

narrowly elongated, platelike structural elements, and may be irregularly thickened along margins where associated lateral offsets occur; these latter may be directed outward and upward in places, having a spinose appearance; where main pillars become more thickened and rounded, lateral offsets may become obscured; in tangential section, pillar outlines vary from subrounded to angular or more elongated and irregular, with associated, short, zigzagged lateral offsets; cyst plates are large, thin, sagging to flattened, and complete or incomplete across pillar interspaces, but near the pillars, much smaller cysts become clustered and inclined; a few thicker cyst plates may also occur across interspaces, and tops of these are more likely to show denticles than elsewhere. [The genus *Sichuanostroma* WANG, 1978b, is a junior synonym of *Spinostroma,* only differing in the presence of more dilated, pillarlike elements. On the other hand, *Spinostroma* is distinguished from *Pennastroma* by having a more thickened, rodlike or platelike (narrowly elongated) pillar structure that largely masks the lateral offsets except at their spinose tips, in contrast to *Pennastroma,* which has conspicuous, upwardly and outwardly splayed elements (lateral offsets) on either side of a widely elongated, platelike, pillar structure.] *Upper Devonian (Famennian)*: China (Sichuan), Russia (Novaya Zemlya).——FIG. 405*a–d*. **S. diversum,* lower part of Changtanzi

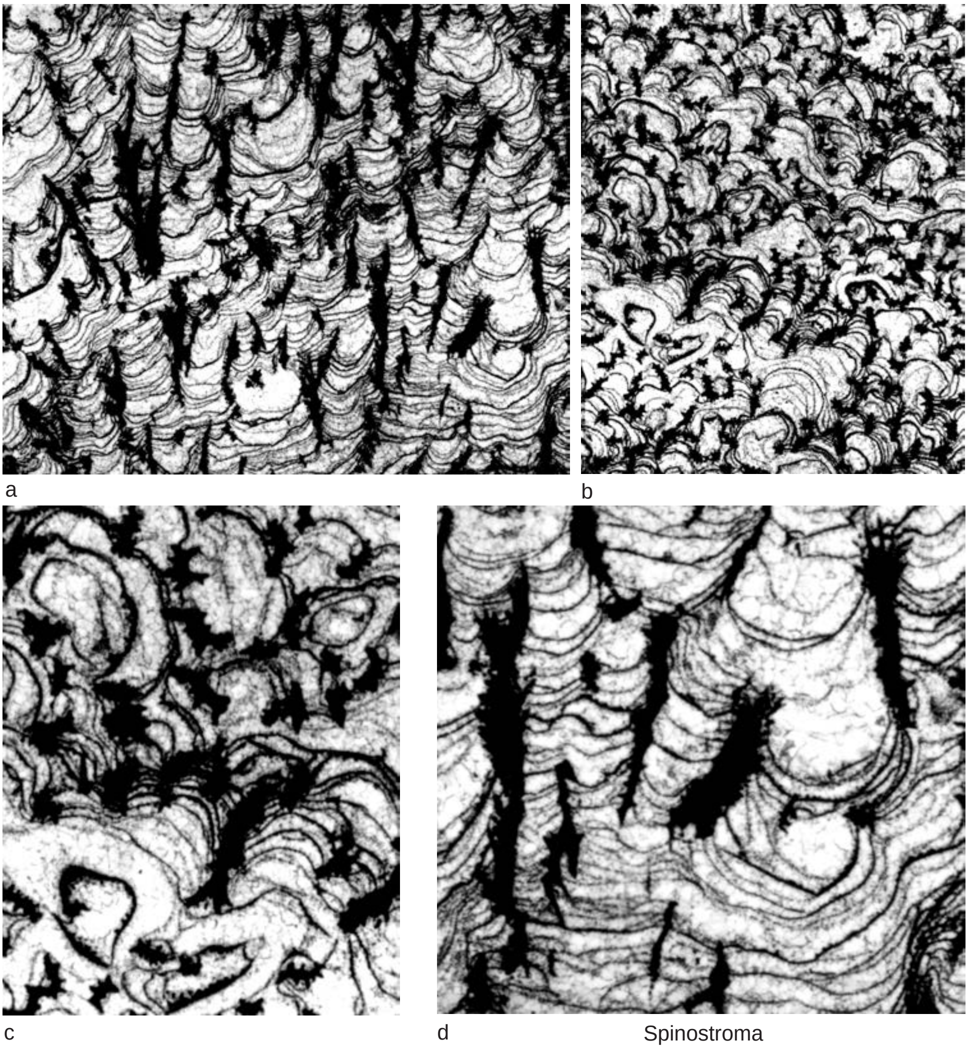


Fig. 405. Stylostromatidae (p. 738–740).

Formation, Shawozi, Ganxi, Sichuan Province; holotype, CIGMR, no. Ss2025; *a–b,* longitudinal and tangential sections, ×2; *c–d,* detailed tangential and longitudinal sections, ×5 (Webby, 2012c, courtesy of Wang Shu Bei; see also Wang, 1978b, pl. 41,*2a–b*).

Family AULACERATIDAE Kühn, 1927

[Aulaceratidae Kühn, 1927, p. 548] [=Beatriceidae Ulrich in Bassler, 1915 (rarely used family-group name and not replaced prior to 1961, so has not been adopted; Art. 40, ICZN, 1985, p. 81); =Beatricidae Raymond, 1931b, p. 178; =Aulaceridae Bogoyavlenskaya, 1969b, p. 16, *nom. null.*]

Branched dendroid to unbranched, columnar skeletons, with differentiated axial and lateral zones; axial columns of large, stacked or overlapping cyst plates, in a few places denticulate; lateral zones with rows of small imbricated cyst plates and sporadically distributed short pillars or denticles; pillars commonly simple, rounded, but in one genus represented by composite, fused, outwardly radiating, platelike elements. *Middle Ordovician (Darriwilian)–Upper Devonian (Famennian).*

Aulacera Plummer, 1843, p. 293, fig. 1 [**A. plummeri* Galloway & St. Jean in Galloway, 1957, p. 422;

SD GALLOWAY & ST. JEAN in GALLOWAY, 1957, p. 422] [=*Beatricea* BILLINGS, 1857, p. 344 (type, *B. nodulosa*, SD MILLER, 1889, p. 155)]. Large, unbranched, columnar skeleton, differentiated into axial column and lateral zone; axial column comprised of a single series of large, stacked cyst plates; lateral zone has multiple rows of smaller, imbricated cyst plates, and sporadic development of short, rounded pillars. *Middle Ordovician (Darriwilian)–Upper Ordovician (Hirnantian):* China (Anhui), *Darriwilian;* Australia (Tasmania, ?New South Wales), Canada (Anticosti Island, Akpatok Island, Hudson Bay, Ontario, Manitoba, British Columbia), Russia (Siberian Platform, Novaya Zemlya), USA (Indiana, Kentucky, Ohio), *Sandbian–Hirnantian.*——FIG. 406*a–h.* **A. plummeri* GALLOWAY & ST. JEAN, Saluda Formation, Elkhorn Creek, 6.4 km south of Richmond, Indiana; *a–c,* holotype, YPM.222149, including slides 285-46, 299-35, 299-36, 300-9; *a,* external view exhibiting upward enlargement and gently raised spiraling ridges, ×0.38 (Galloway & St. Jean in Galloway, 1957, pl. 37,*1a*); *b,* longitudinal section showing axial column and lateral zones with latilaminae and calcite-filled lacunae, ×1 (Galloway & St. Jean in Galloway, 1957, pl. 37,*1b*); *c,* longitudinal section of slide 300-9 showing lateral zone, ×15 (Galloway & St. Jean in Galloway, 1957, pl. 37,*1c*); *d–g,* topotype (and hypotype), YPM.222147, including slides 282-58, 299-40; *d–e,* sketches of transverse and longitudinal sections of topotype, ×2 (Galloway & St. Jean in Galloway, 1957, pl. 32,*3*); *f–g,* ×10; *f,* transverse section of slide 299-40 showing cyst plates of lateral zone with small pillars restricted to outer part (Galloway & St. Jean 1961, pl. 3,*1a*); *g,* longitudinal section of slide 282-58 showing rows of cyst plates and, additionally, in the outer part of lateral zones, upwardly and outwardly inclined pillars (Galloway & St. Jean, 1961, pl. 3,*1b*); *h,* sketch of PLUMMER's (1843) originally named genus *Aulacera*, Richmond Group of Indiana, magnification approximate, at least ×0.25 (Schuchert, 1919, fig. 1).

Alleynodictyon WEBBY, 1971, p. 10 [**A. nicholsoni* WEBBY, 1971, p. 11; OD]. Slender, branching, columnar skeleton with outwardly radiating, platelike pillars in outer margin of axial column and lateral zone; axial column exhibiting large, upwardly convex cyst plates with a few scattered denticles on upper surfaces; rows of small, long, low cyst plates occupy lateral zone, being flattened to concave outwardly between radiating pillars and gently convex outwardly in areas lacking pillars. *Upper Ordovician (Katian):* Australia (New South Wales, Tasmania).——FIG. 407*a–e.* **A. nicholsoni*; *a–c,* Daylesford Limestone, lower Bowan Park Group, Paling Yards Creek, 7 km southeast of Cudal, New South Wales, holotype, AMF.98943, transverse, centered-longitudinal and offset-longitudinal sections; *d–e,* silicified specimens, middle Regan's Creek Limestone, southeast of Cargo; *d,* paratype, AMF.98941, interior view of outer part of axial column showing some intersections between large, uparching cyst plates and inner ends of vertical, platelike pillars; *e,* paratype, AMF.98946, top view showing broadly uparched cyst plates of axial column and more densely fused lateral zone of platelike pillars and small cyst plates, ×4 (Webby, 1971, pl. 5,*1–5*).

Cryptophragmus RAYMOND, 1914, p. 8 [**C. antiquatus*; OD]. Unbranched, cylindrical skeleton composed of narrow axial column with large, stacked axial cyst plates and a few small cyst plates at margins, and an outer, sheathlike lateral zone exhibiting regular skeletal meshwork of small pillars intersected by laterally persistent, thin, undulating-to-flattened cyst plates (resembling laminae). *Upper Ordovician (Sandbian–Katian)*: Canada (Ontario, Quebec), Russia (?Siberian platform), USA (New York, Pennsylvania, Virginia, Tennessee, Alabama, Indiana).——FIG. 408*a–h.* **C. antiquatus*, upper Pamelia Limestone, near hilltop beyond quarry on continuation of Broad Street, Aylmer, Quebec (holotype), and Carden township, Ontario (paratypes); *a,* holotype, GSC 5390, lateral view of unsectioned specimen, ×1 (Raymond, 1914, pl. 1,*1*); *b,* paratype, GSC 4329e, offset-longitudinal section of lateral zone showing numerous, tiny, dotlike, spar-replaced pillars, ×3 (Raymond, 1914, pl. 3,*4*); *c,* paratype, GSC 4329c, and a fragment that was cut from GSC 4329c, now catalogued as YPM.222170, including slide 308-31 (this slide, however, is missing and presumed lost), transverse section showing spar-replaced pillars and cyst plates, ×10 (Galloway & St. Jean, 1961, pl. 2,*3c*); *d,* paratype, GSC 4329h, tangential section showing alternation between latilaminae and a mud-rock sheath, and spar-filled pillars, the outermost surface of which are markedly papillate, ×3 (Raymond, 1914, pl. 4,*2*); *e–f,* paratypes, GSC 4329a–b, longitudinal and transverse sections of best-preserved and most complete specimens, ×4 (Raymond, 1914, pl. II,*1–2*; see also Fig. 296.1–296.2); *g,* paratype, GSC 4329i, slightly oblique transverse section showing papillae surmounting spar-replaced pillars, ×3 (Raymond, 1914, pl. IV,*1*); *h,* paratype, GSC 4329, lateral view of uncut specimen exhibiting bulblike enlargement toward apical end, ×0.6 (Raymond, 1914, pl. I,*2*).

Ludictyon OZAKI, 1938, p. 219 [**L. vesiculatum* OZAKI, 1938, p. 219, pl. 33,*3a–c,* pl. 34,*3;* OD; NIGP, holotype, thin sections no.121555a–b]. Skeleton unbranched and broadly cylindrical with poorly defined axial and lateral zones; no clearly differentiated axial column; commonly large, stacked to overlapping cyst plates of axial zone alternate successively with rows of small, long, low, imbricated cyst plates; denticles may occur on upper surfaces of larger, axial cyst plates and also on smaller cyst plates laterally. *Middle Ordovician (Darriwilian)–lower Silurian:* China (Shandong, Anhui), *Darriwilian;* ?Mongolia, *Upper Ordovician;* China (Guizhou), *lower Silurian.*——FIG. 409*a–c.* **L. vesiculatum,* Majiagou Group, west of Beizhuang, Zhangqiu county, Shandong Province, holotype, NIGP, slides 121555a–b; *a,* longitudinal section

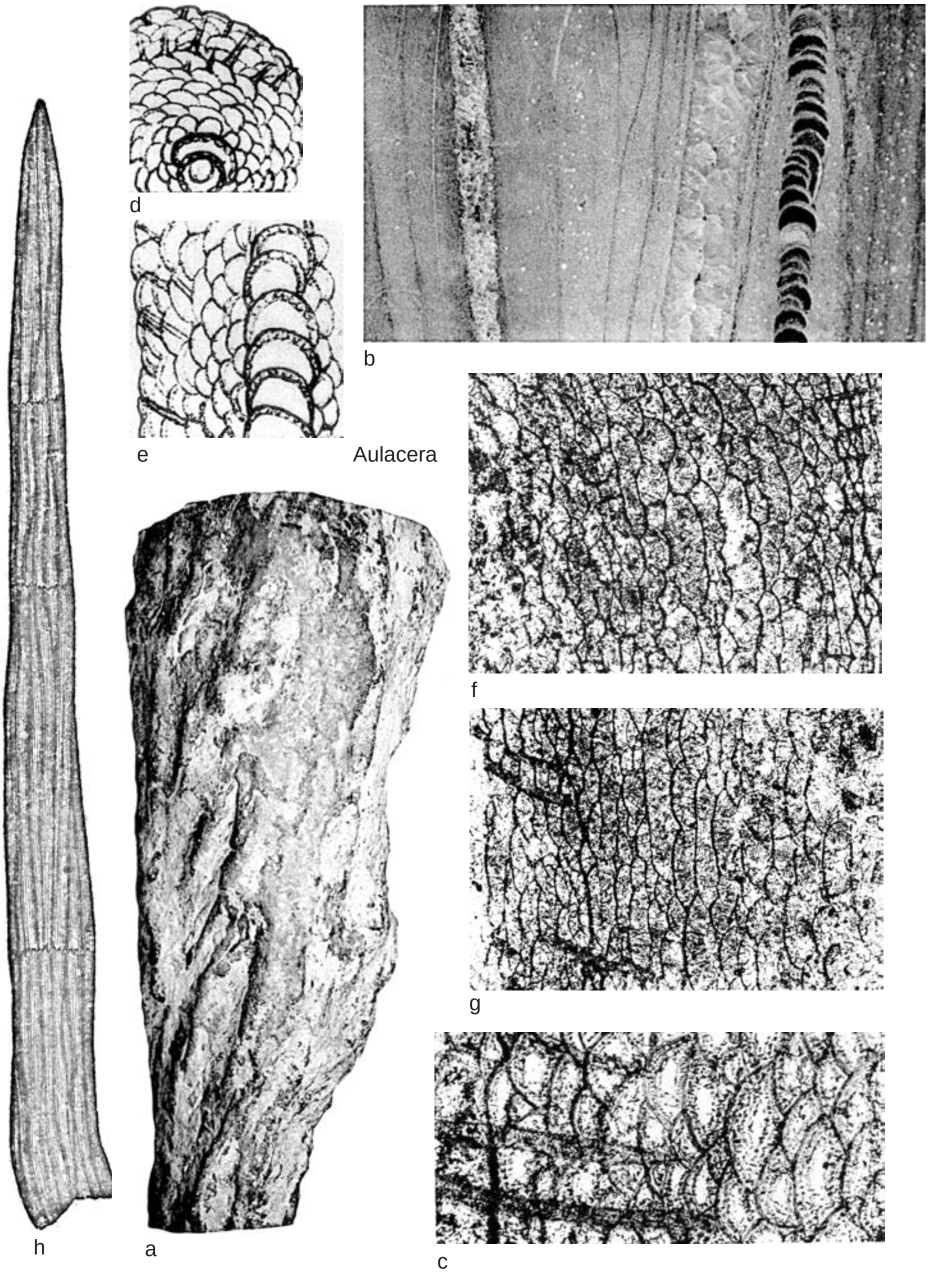


FIG. 406. Aulaceratidae (p. 740–741).

(121555a), ×2; *b,* partially transverse to oblique section (121555b), ×5; *c,* enlarged part of longitudinal section (121555a) depicting a few poorly defined denticles on tops of cyst plates, ×5 (Webby, 2012c, photos of OZAKI's type thin sections in Nanjing collection; see also OZAKI, 1938, pl. 33,*3b–c*).

Pararosenella VASSILYUK & BOGOYAVLENSKAYA in BOGOYAVLENSKAYA, VASSILYUK, & GLEBOV, 1990, p. 75 [**Rosenella lissitzini* forma *cylindrica* VASSILYUK, 1966, p. 46, pl. 32,*1–7*; OD; Donets Polytechnical Institute (DPI), Ukraine, no. 12/141]. Dichotomously branching, columnar skeleton with single row of large doughnut-shaped axial cyst plates of

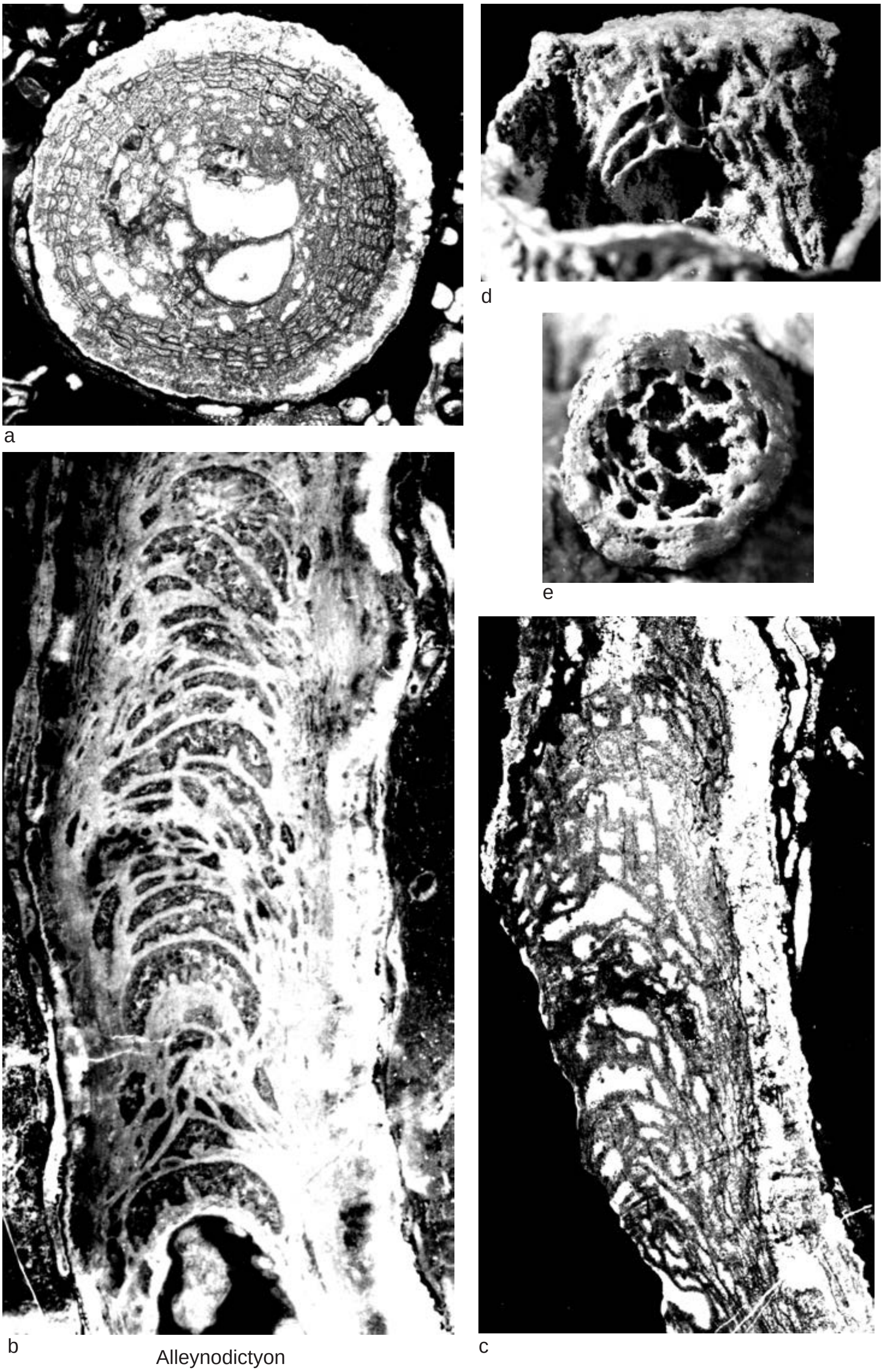


FIG. 407. Aulaceratidae (p. 741).

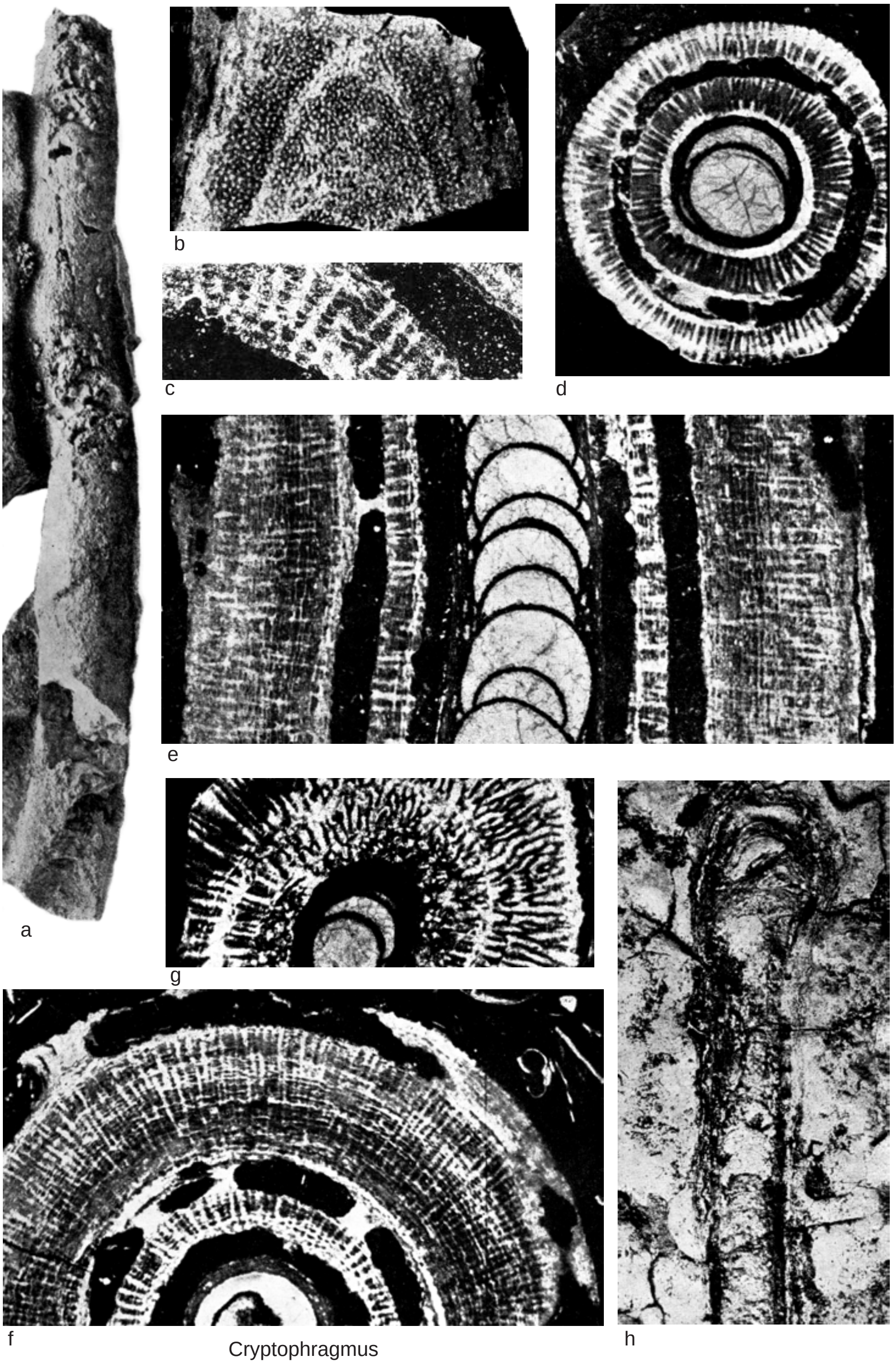


FIG. 408. Aulaceratidae (p. 741).

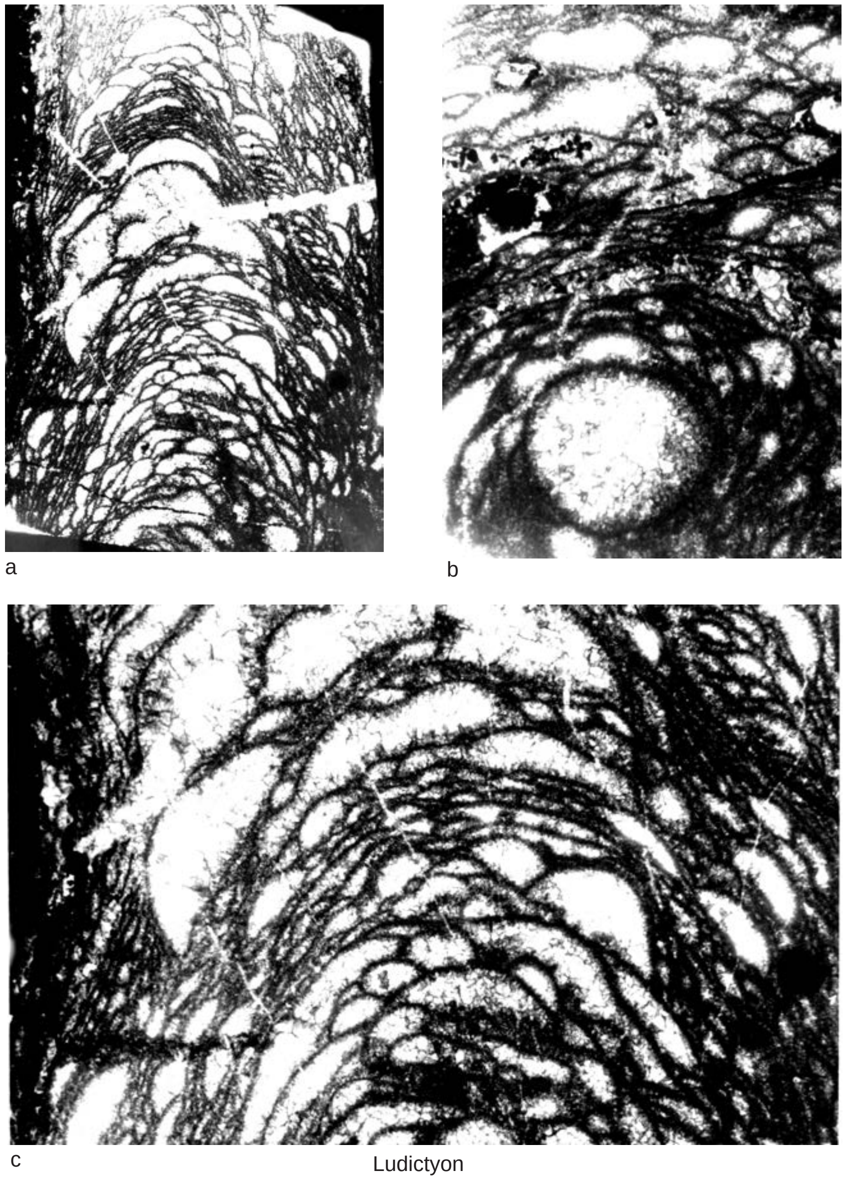


FIG. 409. Aulaceratidae (p. 741–742).

high convexity; branches are usually dichotomous but may be rarely as lateral offsets; denticles limited to tops of some axial cyst plates; lateral zone very incomplete, composed of very few small cyst plates filling spaces at margins between bulbous axial cyst plates and angles of dichotomous branches. *Upper Devonian (Famennian):* Russia (northern Caucasus), Ukraine (Donets basin).——FIG. 410,*1a–h*. **P. cylindrica* (VASSILYUK), Famennian sequence, Porfirtovaya ravine, near Novotroitskoye village, Donbass, Ukraine; *a–c,* holotype, DPI, 12/141; *a–b,* transverse sections showing parts of skeleton with dichotomous branching and very large axial cyst plates, thickened outer wall with tiny lateral cyst plates in places; *c,* transverse section of top of one axial cyst plate showing presence of denticles (Vassilyuk, 1966, pl. 32,*2a,b,v*); *d–h,* other figured material from type locality as basis for subspecies, not specifically designated by author but probably has status as paratypes; *d–e,*

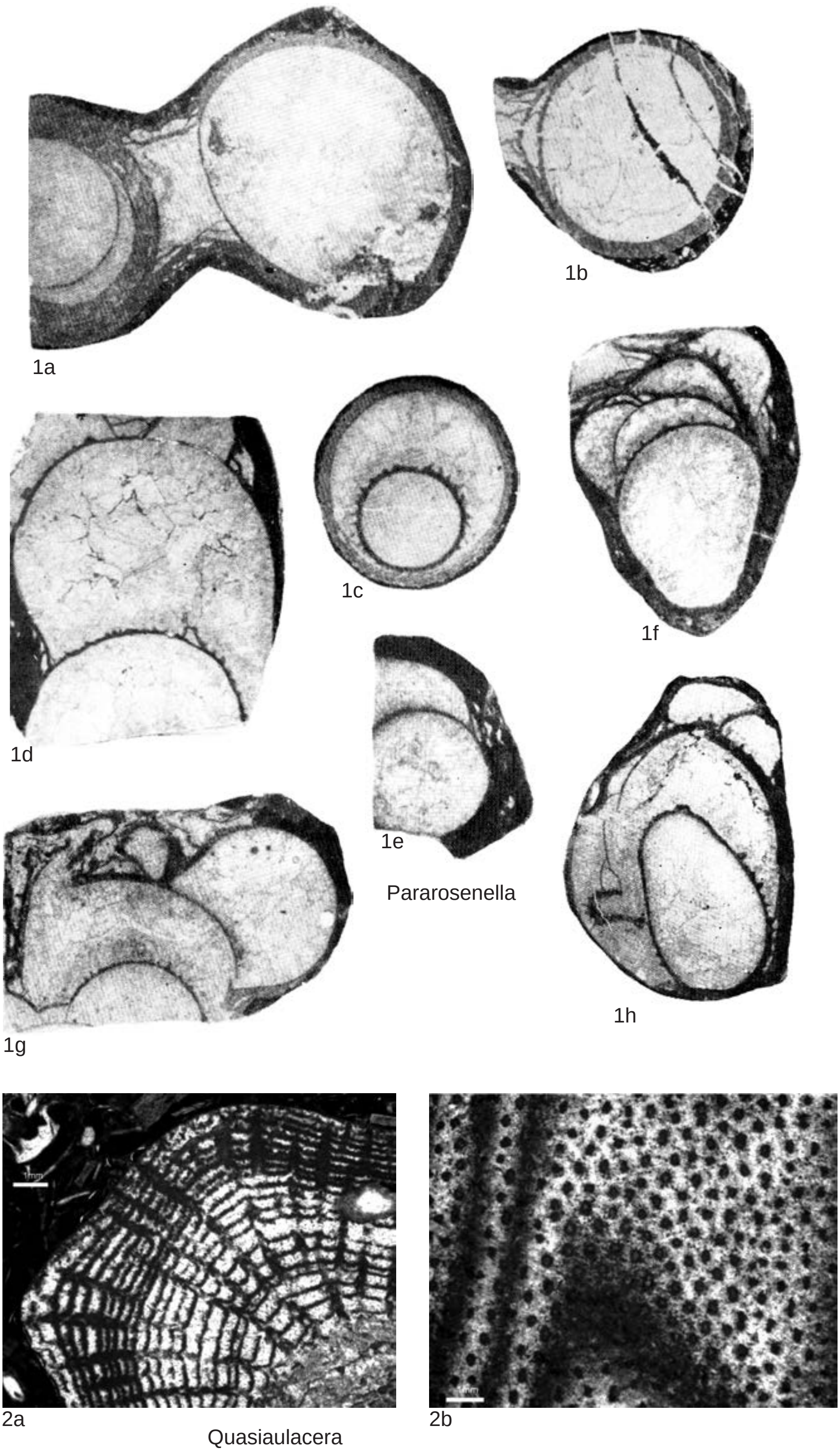


FIG. 410. Aulaceratidae (p. 742–749).

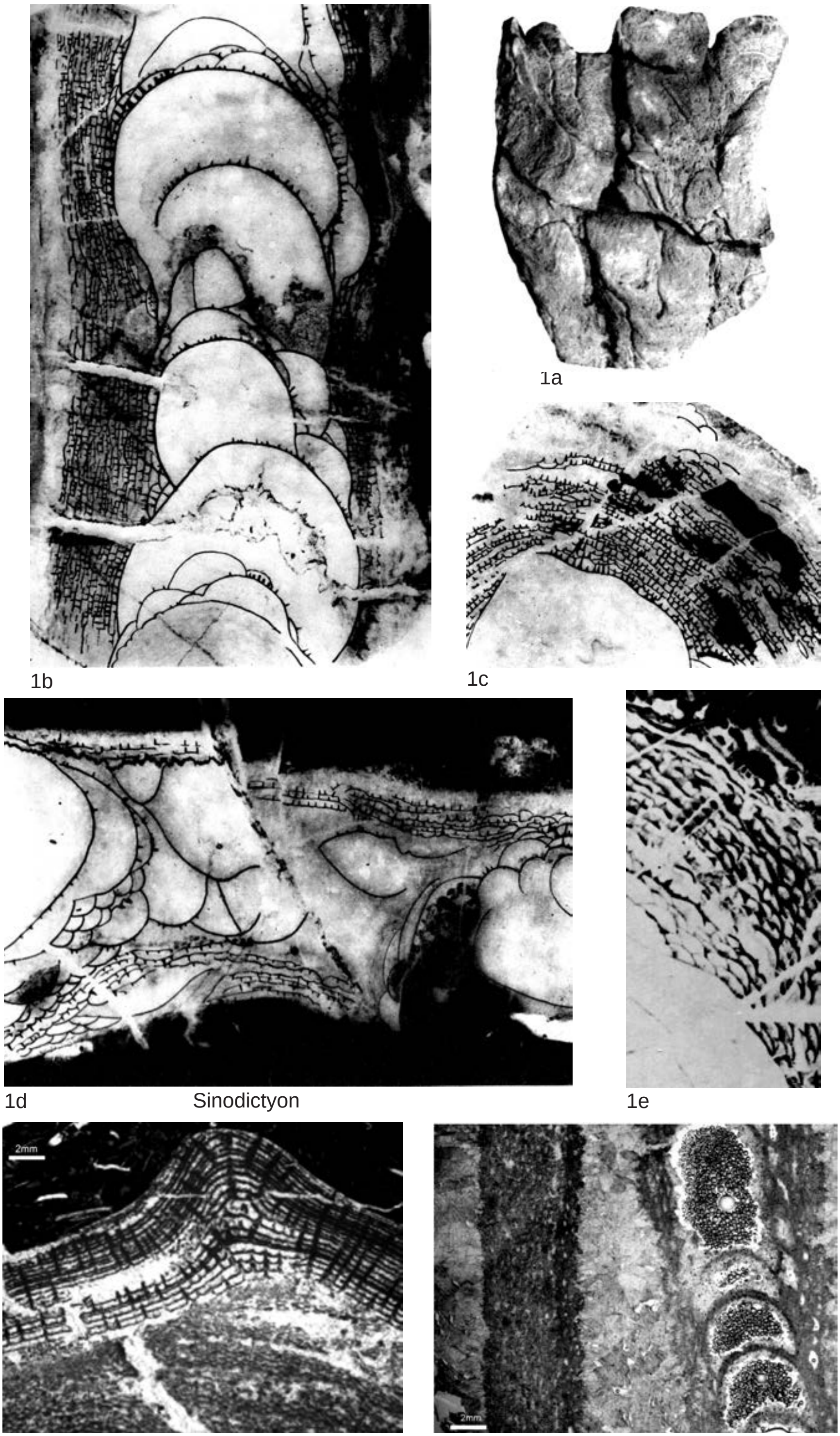


FIG. 411. Aulaceratidae (p. 748–749).

Fig. 412. Aulaceratidae (p. 749).

longitudinal and transverse sections of specimen showing bulbous shape of axial cyst plates, a few localized, very small, lateral cyst plates associated with outer wall; *f,* transverse-oblique section of another specimen showing comparatively large denticles; *g–h,* approximately longitudinally and transversely oriented sections of a third specimen; and see other examples of dichotomous and lateral branching of *P. cylindrica* (see Fig. 299.4–299.5), ×5 (Vassilyuk, 1966, pl. 32, fig. 1a–b, 3a–b, 4–7).

Quasiaulacera Copper, Stock, & Jin, 2013, p. 670 [**Q. occidua* Copper, Stock, & Jin, 2013, p. 671; OD]. Large to very large, columnar, nonbranching skeleton, and longitudinally fluted externally. Skeleton of three layers: axial column with large cyst plates occupying about 30%–50% of skeleton, surrounded by envelope of small cyst plates, ultimately covered by outer layer of multiple, thin, concentric laminae, penetrated by thick, radiating, superposed pillars. Axial cyst plates occur in a single, stacked row. *Upper Ordovician (Hirnantian):* Canada (Anticosti Island).——Fig. 410,*2a–b.* **Q. occidua,* upper Lousy Cove Member, 5–8 m below Laframboise Member, Ellis Bay Formation, type locality A972, tidal flat outcrops adjacent to Laframboise Creek, ~300 m NNW of Pointe Laframboise, western Anticosti Island, holotype, GSC 129346, transverse *(a)* and tangential *(b)* sections, ×5 (scale bar, 1 mm) (Copper, Stock, & Jin, 2013, fig. 6.2, 7.2).——Fig. 411,*2a–b.* **Q. occidua; 2a,* holotype, GSC 129346, transverse section from NNW of Pointe Laframboise, western Anticosti Island, type locality A972, ×2.5 (scale bar, 2 mm) (Copper, Stock, & Jin, 2013, fig. 6.3); *2b,* juvenile specimen, GSC 129722, longitudinal section showing large axial cyst plates, from upper Lousy Cove Member, Ellis Bay Formation (locality A1163), eastern Anticosti Island, Quebec, Canada, ×2.5 (scale bar, 2 mm) (new, courtesy of Paul Copper, Carl Stock, and Jisua Jin).

Sinodictyon YABE & SUGIYAMA, 1930, p. 52 [**S. columnare;* OD]. Skeleton branching (fasciculate) to cylindrical with large cyst plates with denticles axially, and rows of smaller, long, low cyst plates with denticles and short, rounded pillars laterally. [In their original description of *S. columnare*, YABE and SUGIYAMA (1930) allocated the same registration number to more than one specimen. Here, where such specimens are reillustrated, an additional lower case letter is added to that number to avoid any confusion. All these specimens are presumed to be syntypes. Also, note that most of YABE and SUGIYAMA's illustrations have been crudely overdrawn in black ink over photos to emphasize the skeletal structures. *Middle Ordovician (Darriwilian):* China (Shandong, Liaoning).——FIG. 411,*1a–e*. **S. columnare*, Majiagou Group, slopes of hill near Chenxing wharf, Wuhuzui, Fuxian County, Liaoning Province; *a,* syntype, IGPS 37676a, lateral view of a broadly fasiculate skeleton, ×0.6 (Yabe & Sugiyama, 1930, pl. 19,*5*); *b,* syntype, IGPS, 37676b, longitudinal section, ×5 (Yabe & Sugiyama, 1930, pl. 19,*3*); *c,* syntype, IGPS 37678, transverse section, ×5 (Yabe & Sugiyama, 1930, pl. 18,*10*); *d,* syntype, IGPS 37676c, obliquely cut section, ×5 (Yabe & Sugiyama, 1930, pl. 19,*4*); *e,* specimen from Chien-shih-hui-yao-tzu locality, western coast of Liaoning Bay, Jinxian County (about 25 km south of Yabe and Sugiyama's 1930 type locality); sketch of transverse section showing differentiation of cyst plates, particularly rows of smaller cyst plates in lateral zone, a few with associated short pillars, ×8 (Ozaki, 1938, p. 219, pl. 34,*2*; specimen not traced, possibly in NIGP).

Thamnobeatricea RAYMOND, 1931b, p. 180 [**T. parallela;* OD] [=*Cladophragmus* RAYMOND, 1931b, p. 182 (type, *C. bifurcatus* RAYMOND, 1931b, p. 182, pl. 3,*1–4*, OD); =*Rosenellina* RADUGIN, 1936, p. 92 (type, *R. wellenformis* RADUGIN, 1936, pl. 2,*8,9,11*, OD)]. Unbranched or branched cylindrical skeleton with axial column composed of large, variably sized cyst plates, commonly but not always spanning axial column, and very narrow lateral zone of small cyst plates; lateral offsets or dichotomous branches may occur; pillars mentioned as occurring in lateral zone but needs confirmation; denticles may occur on upper surfaces of cyst plates. *Middle Ordovician (Darriwilian)–Upper Ordovician (Katian)*: China (Anhui), *Darriwilian;* Australia (Tasmania), Canada (Ontario), Russia (Siberian platform, Gornaya Shoria), USA (Alabama, Pennsylvania, Tennessee, Kentucky), *Sandbian–Katian.*——FIG. 412*a–d*. **T. parallela,* middle of Stones River Group, Sandbian–Katian, large quarry north of Bellefonte-Miles Gap road, west of Bellefonte, Pennsylvania; *a–b,* holotype, MCZ 9302; *a,* lateral view showing a number of lateral offsets, ×0.3 (Raymond, 1931b, pl. 2,*9*); *b,* longitudinal section of part of one of branches showing large axial column and very narrow lateral zone, ×2.67 (Raymond, 1931b, pl. 2,*4*); *c,* paratype, MCZ 9304, showing ornamentation of fine longitudinal ridges, ×1.33 (Raymond, 1931b, pl. 2,*5*); *d,* specimen MCZ, thin section no. 127, showing large axial cyst and very small lateral cyst plates (at right) associated with base of lateral offset [RAYMOND's other paratypes are listed as MCZ 9303, 9305 (see his pl. 2,*6–7*)], ×3.5 (Raymond, 1931b, pl. 2,*8*).

Family LOPHIOSTROMATIDAE Nestor, 1966

[Lophiostromatidae NESTOR, 1966a, p. 58]

Encrusting laminar, latilaminate, composed of much thickened, tangential skeletal layers almost completely filling interskeletal space, sharply undulated skeletal layers forming pillarlike upgrowths appearing as papillae on upper surface; discrete longitudinal and tangential elements rare. [Only two genera, *Lophiostroma* and *Dermatostroma,* are regarded as valid, and one other, the genus *Tarphystroma,* is tentatively included in the family. *Solidostroma* KHROMYKH, 1974a, from the Lower Devonian of northeastern Siberia, was originally described as a member of the Lophiostromatidae but currently has uncertain status, doubtfully included as a junior synonym of *Euryamphipora* KLOVAN, 1966 (see p. 826). *Priscastroma* KHROMYKH, 1999a, from the Middle Ordovician of the Siberian Platform, was considered to be an early representative of the group (KHROMYKH, 1999b, p. 223), but it is not a typical member of the family given its very thin, long-low to irregularly undulating to zigzag-shaped elements, resembling cyst plates, with these mainly separated by an abundance of unfilled interskeletal spaces; consequently this genus is here transferred to family Rosenellidae (see p. 715). *Taymyrostroma* KHROMYKH, 2001, from the Upper Ordovician, Taimyr Peninsula, has also been assigned to the lophiostromatids (KHROMYKH, 2001, p. 347), but this genus remains inadequately described and illustrated; here it is regarded as convergent toward younger (Siluro-

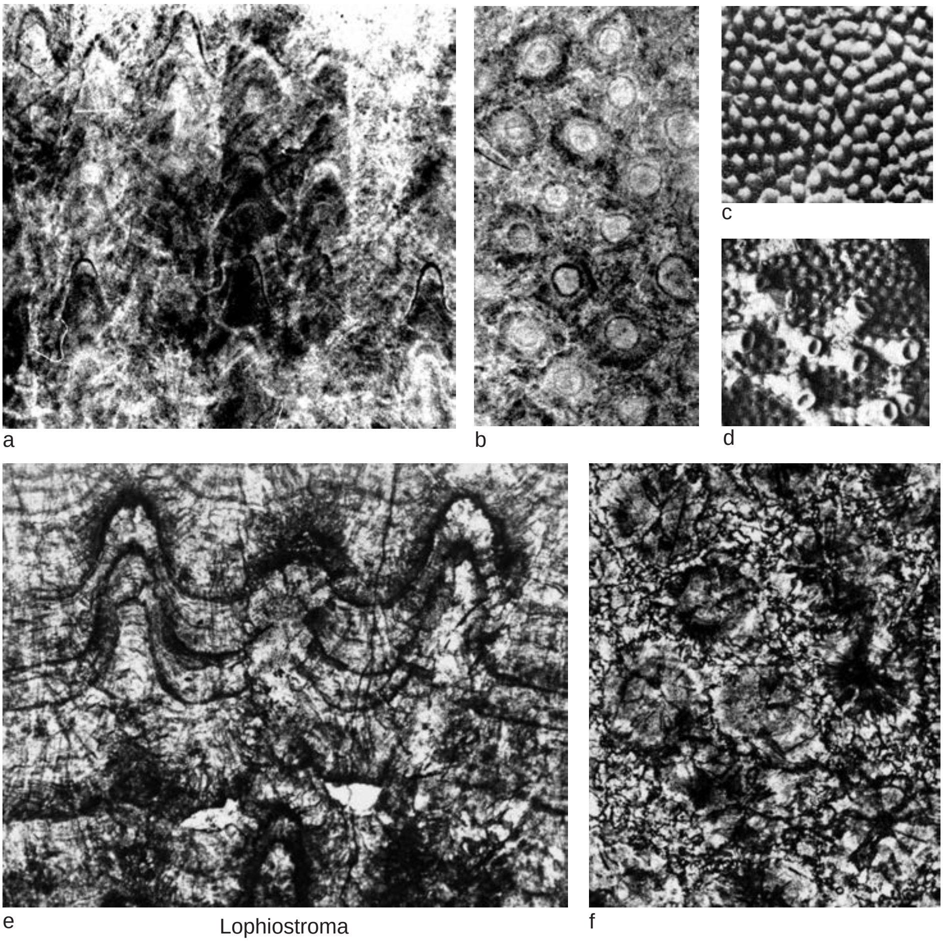


Fig. 413. Lophiostromatidae (p. 750–752).

Devonian) clathrodictyid genera, such as *Intexodictyides* and *Atelodictyon* and is best grouped elsewhere (see p. 829–836) within the stromatoporoid order and family uncertain.] *Middle Ordovician (Darriwilian)–Upper Devonian (Frasnian), ?Triassic.*

Lophiostroma Nicholson, 1891a, p. 160 [**Labechia? schmidtii* Nicholson, 1886c, p. 16, pl. 2,*6–8;* OD] [=*Chalazodes* Parks, 1908, p. 33 (type, *C. granulatum* Parks, 1908, p. 36, OD)]. Skeleton commonly latilaminate and laminar, consists of, dominantly, much thickened, superposed, sheetlike layers, sharply and regularly undulating into columnar, pillarlike upgrowths, giving a kind of cone-in-cone structure; these upgrowths expressed as papillae on upper surfaces; sheetlike layers almost entirely occupy interiors and do not represent true laminae, only rarely discernible cysts preserved; compact microstructure has a transverse fibrosity within sheetlike layers. [Nicholson's original spelling of the species name with its double "ii" termination is retained, in accordance with ICZN Art. 33.4 (1999) rather than *schmidti* (see Galloway, 1957, p. 439; Nestor, 1966a, p. 60; Flügel & Flügel-Kahler, 1968, p. 381; Mori, 1970, p. 141), which is deemed to be an incorrect subsequent spelling. A number of Upper Paleozoic–Triassic stromatoporoid-like forms have been described as species of *Lophiostroma,* but their affinities remain in doubt. Stearn and Stock (see p. 310) recognized two of them as "calcareous crusts" coming from the Carboniferous and Permian of Japan (Yabe & Sugiyama, 1931b; Sugiyama, 1939) but excluded them completely from a close association with the genus, even suggesting one was a brachiopod, based on a restudy by Mori (1980). A third species from the Triassic of the southeastern Pamirs was described by Boiko (1970a) as *Lophiostroma boletiformis*. It

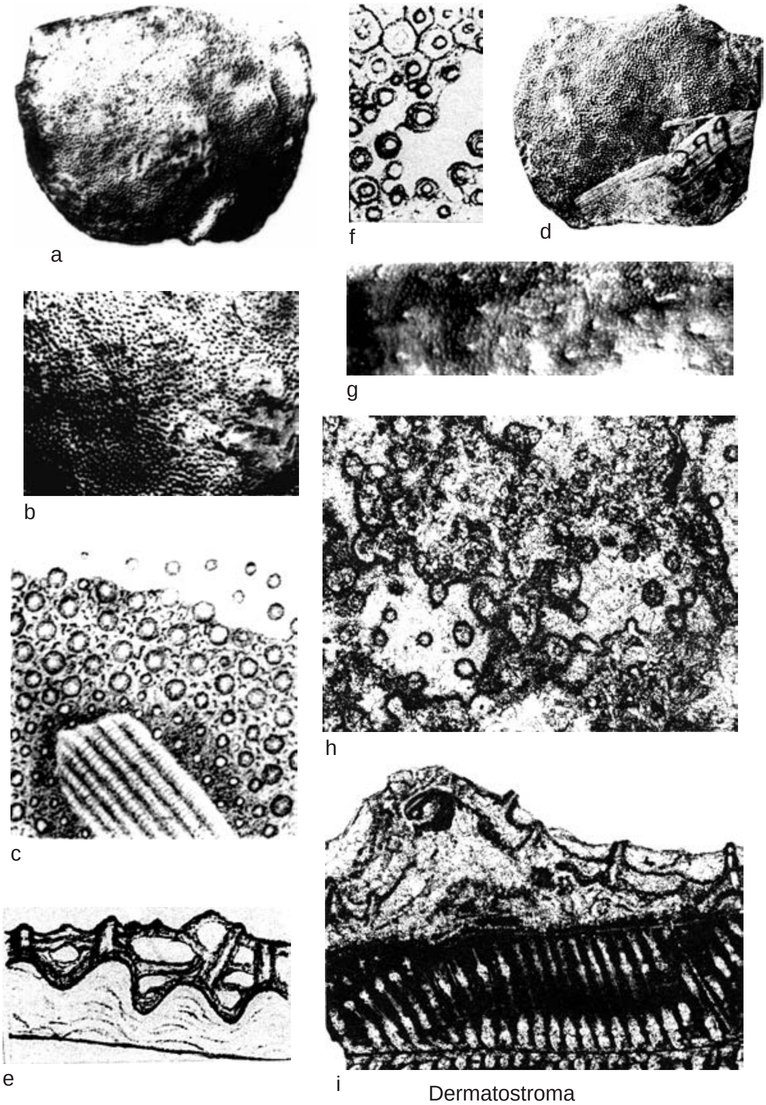
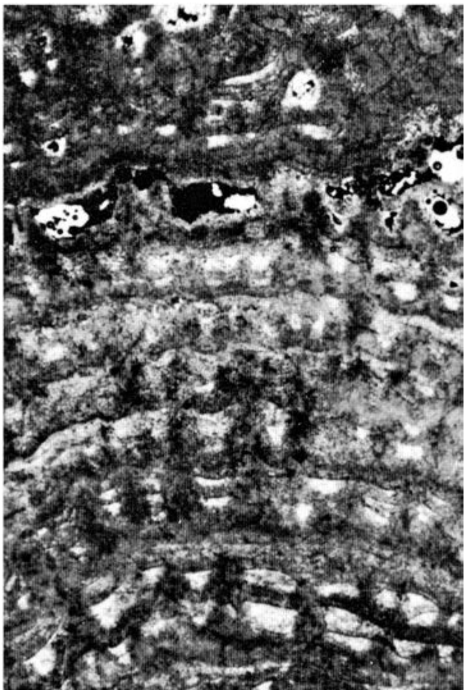


FIG. 414. Lophiostromatidae (p. 752–753).

was based on a single specimen with clearly discernable zigzagged upper and lower boundaries of the sheetlike latilaminae and longitudinally oriented, dark, columnar to cone-shaped upgrowths that align and may be superposed across the upwardly bent parts of the latilaminar boundaries, but other parts of the skeleton are composed of spar-filled calcite that is nondiagnostic, making it difficult to confirm this early Mesozoic species unquestionably as a member of the genus.] *Middle Ordovician (Darriwilian)–Upper Devonian (Frasnian), ?Triassic:* China (Shandong), *Darriwilian;* Mongolia, Russia (Siberian platform), *Upper Ordovician;* Canada (Ontario, Quebec), England, Sweden (Gotland), Estonia, Turkey, USA (Michigan, Kentucky), Ukraine (Podolia), *middle Silurian–upper Silurian;* Russia (Kuznetsk basin), *Frasnian;* Tadjikistan (southeastern Pamirs), *?Triassic.*——FIG. 413*a–f.* **L. schmidtii* (NICHOLSON), Paadla stage, Ludlow, Pilguse (=Hoheneichen) locality, 33 km west of Kuressaare, Saaremaa, Estonia; *a–b,* holotype, NHM, P.5606, longitudinal and tangential sections, ×7.5 (Webby, 2012c; Nicholson's slides 279a, 279, rephotographed by Webby in 1989); *c,* topotype,



Tarphystroma

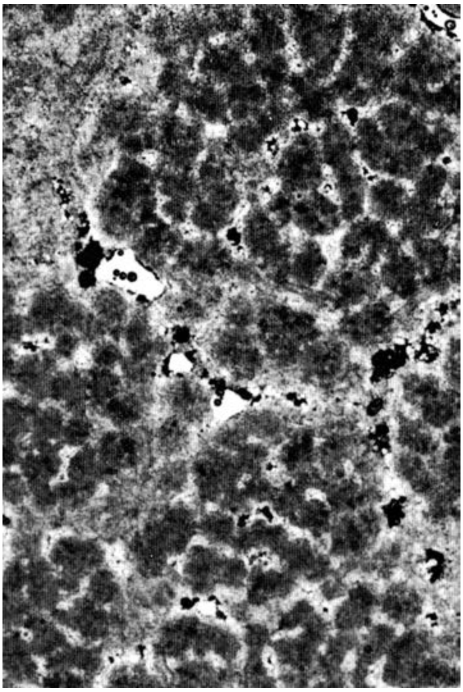


Fig. 415. Lophiostromatidae (p. 753).

IGTUT 114-49 (Co3178), showing papillae representing tops of pillarlike upgrowths, ×2 (Nestor, 1966a, p. 60, pl. 23,*3*); *d,* specimen SMNH, B10-X (GIK-195), Ludlow Hamra Formation of loc. 150 (south of Burgsvik) Gotland, showing papillose upper surface, with addition of an encrusting auloporoid coral, ×2 (Mori, 1970, p. 28, pl. 19,*2*); *e–f,* specimen IGTUT 114-48 (Co3177), from another Paadla age locality at Riiumägi, Saaremaa, longitudinal and tangential sections showing better preserved details of internal features of skeleton than in designated holotype, ×10 (Webby 2012c, photos courtesy of Heldur Nestor; see also Nestor, 1966a, p. 60, pl. 23,*1–2*).

Dermatostroma Parks, 1910, p. 29 [**Stromatopora papillata* James, 1878, p. 2; OD]. Skeleton encrusting and laminar; at most only exhibits a few rows of irregular, undulating to even, long, low cyst plates (some simulating laminae), and intersected by short, solid pillars, rounded to polygonal in tangential section; tops of pillars preserved as papillae. [This problematical genus needs further revision. Some of the species originally included by Parks (1910), but not including the type species, have a skeleton consisting of layers of vertically oriented prismatic crystalline material. Dixon, Bolton, and Copper (1986) have demonstrated that these are heliolitine corals. Others, previously inferred to be independent species, overgrow parts of skeletons of *Aulacera* (see descriptions in Galloway & St. Jean, 1961, p. 74–78) and should be excluded because they probably represent outer parts of aulaceratid skeletons (“outer lamellar layer,” Cameron & Copper, 1994, p. 17; see also discussion by Nestor, 1976, p. 35). The regular laminae and aligned denticles (so-called pseudopillars) of *Dermatostroma concentricum* Galloway & Ehlers in Galloway & St. Jean (1961, pl. 11,*4a–c*) are remarkably similar to structures termed the outer lamellar layer of the new aulaceratid genus *Quasiaulacera* Copper, Stock, & Jin, 2013 from Anticosti Island (see p. 748–749, Fig. 410,*2a–b,* 411,*2a–b;* and also Cameron & Copper, 1994, p. 17, fig. 2b, 2d). The authentic, coarse-textured forms like type species *D. papillatum* and species *D. scabrum* usually develop only as very thin encrusting sheets and in this respect bear close resemblances to thinner latilaminar growths of stromatocerids like *Stromatocerium bigbysi* Webby (1979b, p. 248, fig. 5A–B).] *Upper Ordovician (?Sandbian, Katian)*: Canada (Ontario), USA (Ohio, Kentucky, Indiana, Tennessee, Iowa).——Fig. 414*a–c.* **D. papillatum* (James), Maysvillian, middle Katian, Cincinnati, Ohio, holotype, FMNH (formerly Walker Museum, no. 160); *a,* external surface of brachiopod shell (?*Hebertella*) partially encrusted by sheetlike skeleton, ×1; *b,* more magnified view showing finely papillate surface of skeleton, ×1.7; *c,* sketch of part transversely and part obliquely cut section of skeleton, intersecting a few rounded tips of papillae (top right), and pillarlike extensions within encrusting skeleton and small area of apparent radial ribbing of brachiopod shell (bottom center), ×10 (Parks, 1910, p. 30, pl. 23,*8–10*).——Fig. 414*d–i. D.*

scabrum (James, 1879); *d–f,* Richmondian, upper Katian, Kentucky end of bridge, Madison, Indiana, hypotype YPM.222150 (including slide 299-50); *d,* brachiopod shell (?*Hebertella*) partially encrusted by sheetlike skeleton, ×1 (Galloway & St. Jean, 1961, pl. 13,*1*); *e–f,* sketches of longitudinal and tangential sections of skeleton encrusting brachiopod shell with pillars and showing a polygonal shape near base of skeleton, ×10 (Galloway, 1957, pl. 33,*2;* originally labeled *D. papillatum* but later transferred to *D. scabrum*, see Galloway & St. Jean, 1961, p. 70); *g,* Katian, Warren County, southwestern Ohio, specimen (USNM 40080) showing sheetlike skeleton with small mamelons and smaller papillae encrusting part of bivalve shell (*Byssonychia*), ×1.7 (Parks, 1910, pl. 24,*3*); *h–i,* middle Katian, Leipers Formation, Mt. Parnassus, Columbia, Tennessee, hypotype divided into two: MUO spec. 821 (not studied, possibly lost), and a small fragment of the hypotype studied and labeled YPM.450501, with addition of slide 302-10; this latter shows rounded outlines of pillars in tangential section and encrusting skeletal growth over bryozoan colony (*Escharopora*), cyst plates simulating laminae that define a broadly raised mamelon column, and short pillars in longitudinal section, ×10 (Galloway & St. Jean, 1961, pl. 10,*2a–b*).

?**Tarphystroma** Nestor, Copper, & Stock, 2010, p. 62 [**T. tuberosum* Nestor, Copper, & Stock, 2010, p. 62, pl. 5a–5b, 6a–f; fig. 3c, 9a–b; M]. Low domical skeleton with comparatively closely spaced, variably thickened, planar to undulating composite skeletal layers that resemble composite laminae or latilaminae, with associated upwardly extending, stout, relatively short longitudinal elements with the appearance of columnar to slightly cone-in-cone–type upgrowths; these latter may be superposed across up to three or four successive latilaminae but more commonly appear as shorter upgrowths that may, at certain levels, only extend partially or entirely through one latilamina, and tops may form tubercles. Each latilamina may be differentiated into two parts, comprising a lower, mainly laterally continuous, variably thickened, dark skeletal layer, but in a few places, successive microlaminae are preserved with a vague microreticulation over short distances laterally; and in upper part, a series of spar-filled gallery spaces occur between intervening columnar upgrowths and are bounded above and below by medium-to-large, concave-to-flattened cyst plates; and in a few places, additional cyst plates may subdivide individual spar-filled gallery spaces. In tangential section, rounded to irregular, close-spaced upgrowths coalesce together to form large, rounded to variably shaped, mamelon-like bundles or clusters, up to 5 mm in diameter; also extensive lighter interspaces occur around lateral margins of mamelon-like bundles, and within these areas, there are spar-filled radial to vermiform-shaped astrorhizal canals and other irregular spar-filled cavities. In many places, skeletal structures are rather dense and poorly defined, but in localized areas of latilaminae, longitudinal elements may show flocculent to finely microreticulated microstructures. [The genus is based on limited material, with only the holotype being illustrated. Consequently, Nestor, Copper, and Stock (2010, p. 62) have had difficulty placing the genus within existing families, suggesting tentatively that it be included in the family Lophiostromatidae, because, like *Lophiostroma* Nicholson, 1891a, it has a "comparatively dense general architecture" and a vaguely similar pattern of cone-in-cone–type, columnar, longitudinal elements arising above undulating skeletal layers (Nestor, Copper, & Stock, 2010, p. 62). However, *Tarphystroma* shows a markedly more complicated skeletal pattern, as seen in tangential section, with mamelon-like bundles or clusters of upgrowths, as well as astrorhizae. Another genus, *Stromatodictyon* Khalfina, 1972 (see p. 732), though it remains poorly known, exhibits distinctive, long, branching, bladed to flanged pillars, which contrast markedly with the comparatively short, columnar, knoblike, cone-in-cone type of longitudinal elements seen in *Tarphystroma*.] *Silurian (middle Llandovery)*: Canada (Anticosti Island).——Fig. 415*a–b*. **T. tuberosum*, holotype GSC127868; longitudinal and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, p. 116, pl. 5a–b).

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Paleontological Research Institution, Ithaca, New York, Paula M. Mikkelsen, Editor and Director of Publications: *Aulacera*, Fig. 406*a–g; Cystostroma*, Fig. 388*a–d; Dermatostroma*, Fig. 414*d,f,h,i.*

American Museum of Natural History Library, Mary DeJong, Reference Librarian; and approval of coauthor J. J. St. Jean, Jr., Chapel Hill, North Carolina: *Stromatocerium,* Fig. 395*a–d.*

Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, Catherine Weisel, Museum Projects Coordinator: *Thamnobeatricea*, Fig. 412*a–d.*

Norwegian Journal of Geology, Geological Survey of Norway, Trondheim, Per Terje Osmundsen, Editor: *Radiostroma*, Fig. 397*a–d.*

Estonian Academy Publishers, Tallinn, Estonia, Ülo Niine, Director, and author Heldur Nestor: *Cystocerium*, Fig. 399*a–d.*

Stockholm Contributions in Geology, Stockholm, Sweden, Jan Backman, Editor: *Lophiostroma,* Fig. 413*d.*

Nanjing Institute of Geology & Palaeontology, Chinese Academy of Sciences, Nanjing, China, Yang Qun, Deputy Director of Academic Affairs; as well as help of author Dong De Yuan and Chen Xu: *Pseudostylodictyon,* Fig. 391*a–b; Platiferostroma*, Fig. 398,*1a–d; Pennastroma,* Fig. 403,*2a–d; Ludictyon,* Fig. 409*a–c.* Photographs of Dong's and Ozaki's thin sections of types were provided during a visit in 1993, and some were used here instead of earlier printed figures.

Chengdu Institute of Geology & Mineral Resources, Wang Shu Bei, author, Chengdu, China: *Pleostylostroma,* Fig. 401*a–f; Eopennastroma,* Fig. 403,*1a–b; Spinostroma,* Fig. 405*a–d.* A few new photographs of Wang's thin sections of types were also supplied in Nanjing and used here instead of older printed figures.

Scientific Reports of Tohoku University, Institute of Geology & Paleontology, Sendai, Japan, K. Osuki, Director; also Kei Mori and J. Nemoto: *Sinodictyon,* Fig. 411,*1a–d.*

Pleiades Publishing Inc., Moscow, Russia, Doklady Earth Sciences, vol. 365, no. 2, author V. G. Khromykh, 1999, New genus of the earliest stromatoporoids, p. 178–180, fig. 1a–b, 2a,c,d; and with approval of author, V. G. Khromykh, Institute of Petroleum Geology & Geophysics Siberian Branch, Russian Academy of Science, Novosibirsk: *Priscastroma,* Fig. 390*a–e.*

New South Wales Department of Primary Industries: Geological Survey of New South Wales, Bruce Ward, Manager of Publishing Communications; and author John Pickett: *Cystistroma,* Fig. 396*a–c.*

I also acknowledge the opportunity to photograph many of H. A. Nicholson's stromatoporoid type specimens in the Natural History Museum, London during 1979, and, additionally, Nguyen Huu Hung and Bruno Mistiaen kindly supplied new photographs of the holotype of *Vietnamostroma* (see Fig. 400,*2a–b*). Heldur Nestor also provided photos of *Stratodictyon* (Fig. 394*d*), *Pachystylostroma* (Fig. 404*c*), and a topotype of *Lophiostroma* (Fig. 413*e–f*), as well as granted permission (with his colleagues, Paul Copper and Carl Stock) for use of photos of *Tarphystroma* (Fig. 415*a–b*), and, with Jisuo Jin, assisted in contributing the images of *Quasiaulacera* (Fig. 410,*2a–b*, 411,*2a–b*). Mike Boroczki, Director of the NRC Research Press, Ottawa, Canada, also approved use of the *Tarphystroma* images.

CLATHRODICTYIDA: SYSTEMATIC DESCRIPTIONS

Heldur Nestor

Order CLATHRODICTYIDA Bogoyavlenskaya, 1969

[Clathrodictyida Bogoyavlenskaya, 1969b, p. 17; *emend.*, Nestor in Stearn & others, 1999, p. 23] [=Gerronostromatida Bogoyavlenskaya, 1969b, p. 19]

Skeleton consists of continuous, single-layer, inflected to planar laminae and short to superposed pillars; microstructure compact; interspaces are galleries. [Clathrodictyids were separated from actinostromatids by Kühn (1939a) as an independent family. Bogoyavlenskaya (1969b) elevated the group to the ordinal rank, defining it as being represented by stromatoporoids with inflected laminae and poorly differentiated pillars. The stromatoporoids with well-differentiated planar laminae and rod-shaped pillars were distinguished by her as the separate order Gerronostromatida. Nestor in Stearn and others (1999) reclassified gerronostromatids as a family within the order Clathrodictyida.] *Upper Ordovician (Katian)–Carboniferous (Serpukhovian).*

Family CLATHRODICTYIDAE Kühn, 1939

[*nom. correct.* Lecompte, 1956, p. 128, *pro* Clathrodictyonidae Kühn, 1939a, p. 340; *emend.,* Bogoyavlenskaya, 1969b, p. 17] [=Coenellostromatidae Bogoyavlenskaya, 1977c, p. 14]

Skeletal elements weakly differentiated; laminae irregularly inflected, bending down into short pillars; galleries open, lenticular or irregular in longitudinal section. [Bogoyavlenskaya (1969b) restricted the scope of Clathrodictyidae to the forms having inflected laminae. Later, Bogoyavlenskaya (1977c) established a new family Coenellostromatidae, merged with Clathrodictyidae by Nestor in Stearn and others (1999).] *Upper Ordovician (Katian)–Carboniferous (Mississippian, Serpukhovian).*

Clathrodictyon Nicholson & Murie, 1878, p. 220 [**C. vesiculosum*; OD; holotype NHM P5495]. Growth form domical to laminar; laminae irregularly wrinkled; pillars short, in many cases oblique or funnel shaped, rodlike at base; galleries lenticular or irregular in longitudinal section; astrorhizae common. *Upper Ordovician (Katian)–Middle Devonian:* Australia (New South Wales, Tasmania), Canada (Anticosti), China (Inner Mongolia, Guangxi, Shaanxi, Zhejiang), Estonia, Norway, *Katian–Hirnantian;* Canada (Anticosti, Arctic islands, Hudson Bay, eastern Quebec), central Asia (Tien Shan), China (Quizhou), Estonia, Greenland, Norway, Russia (Altai, Arctic islands, Siberian Platform, Tuva, western Urals), Ukraine (Podolia), United States (Missouri, Ohio), *Llandovery;* Canada (Arctic islands, Hudson Bay, Manitoba, Ontario, eastern Quebec), central Asia (Tien Shan), England, Estonia, Greenland, Norway, Russia (Altai, Pechora Basin, northeastern Siberia, Siberian Platform, Tuva), Sweden (Gotland), United States (Kentucky), *Wenlock;* Australia (New South Wales), Canada (Ontario), central Asia (Tien Shan), Estonia, Iran, Russia (Altai, Arctic islands, Pechora Basin, Siberian Platform, western Urals), Sweden (Gotland), Ukraine (Podolia), *Ludlow;* Canada (Arctic islands), *Emsian;* China (Yunnan), England, Russia (Urals, northeastern Siberia), United States (Ohio), *Middle Devonian.*——Fig. 416,*1a–b*. **C. vesiculosum,* Clinton, Llandovery, Yellow Springs, Ohio, United States, holotype NHM P5495; longitudinal and tangential sections, ×10 (Nestor, 2011).

Bullulodictyon Yavorsky, 1967, p. 17 [**B. patokense*; OD; holotype CNIGR 7351/557]. Growth form laminar; laminae moderately inflected, zonally indefinite; pillars very weakly differentiated; galleries lenticular, of different sizes; astrorhizae large, frequent. *Upper Devonian (Frasnian)*: Russia (Pechora Basin).——Fig. 416,*2a–b*. **B. patokense*, River Bol’shoi Potok, holotype CNIGR 7351/557; longitudinal and tangential sections, ×10 (Yavorsky, 1967, pl. 3,*5,7*).

Coenellostroma Bogoyavlenskaya, 1977c, p. 14 [**C. kaljanum* Bogoyavlenskaya, 1977c, p. 15; OD; holotype UGM 1089a]. Growth form domical; laminae wrinkled, inflected downward into funnel-shaped pillars; galleries arch shaped in longitudinal, meandroid or subhexagonal in tangential section; astrorhizae large, superposed, frequent. *Lower Devonian–Middle Devonian*: Russia (Eastern Urals).——Fig. 416,*3a–b*. **C. kaljanum,* Karpinskiĭ Horizon, Middle Devonian, Kal’ia village, Severoural’skiĭ District, holotype, UGM 1089a; longitudinal and tangential sections, ×10 (Nestor, 2011).

Kyklopora Bogoyavlenskaya, 1982a, p. 37 [**K. kalmiusensis;* OD; holotype UGM 15/57/103]. Growth form laminar; laminae abruptly wrinkled;

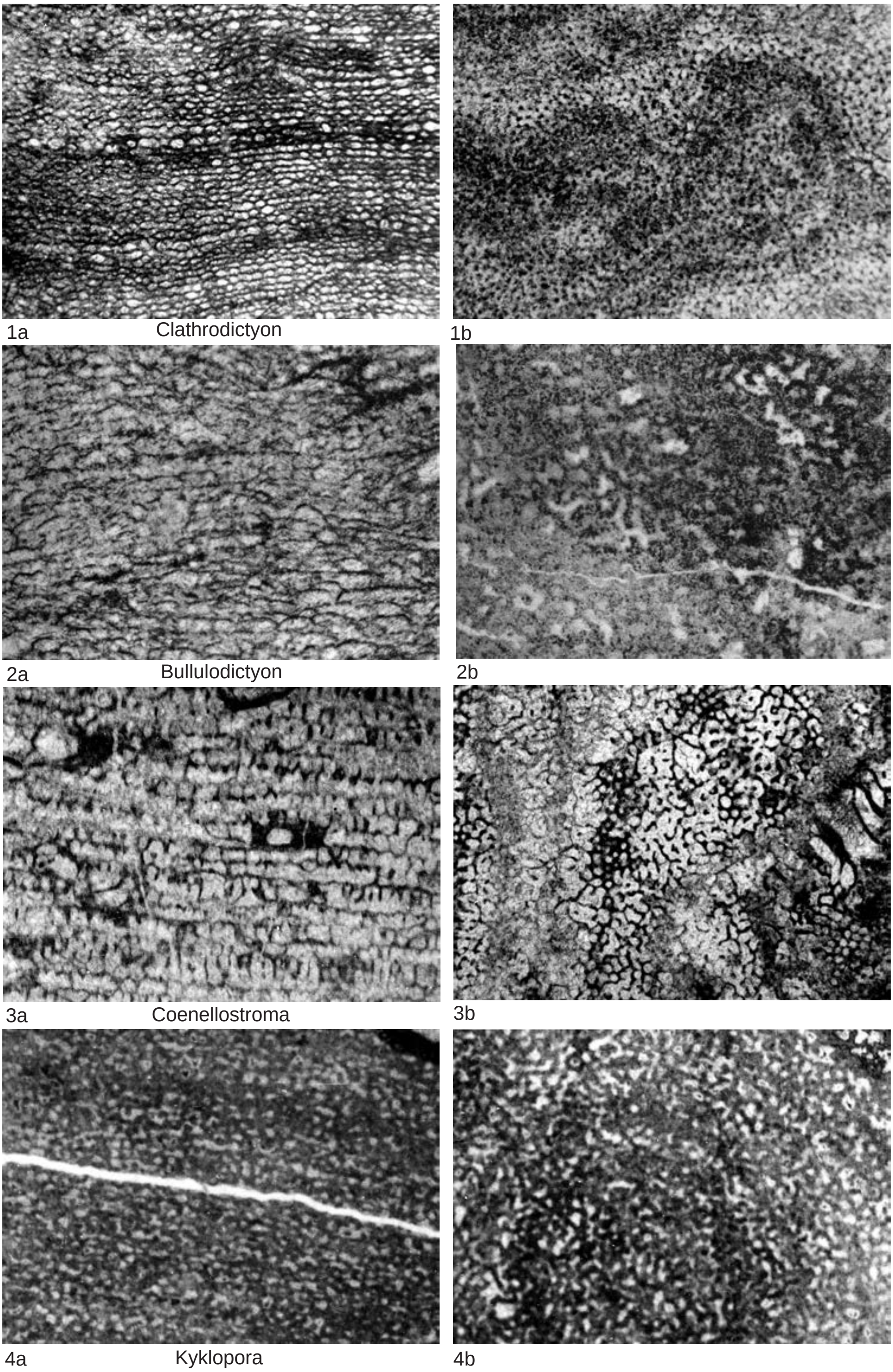


FIG. 416. Clathrodictyidae (p. 755–757).

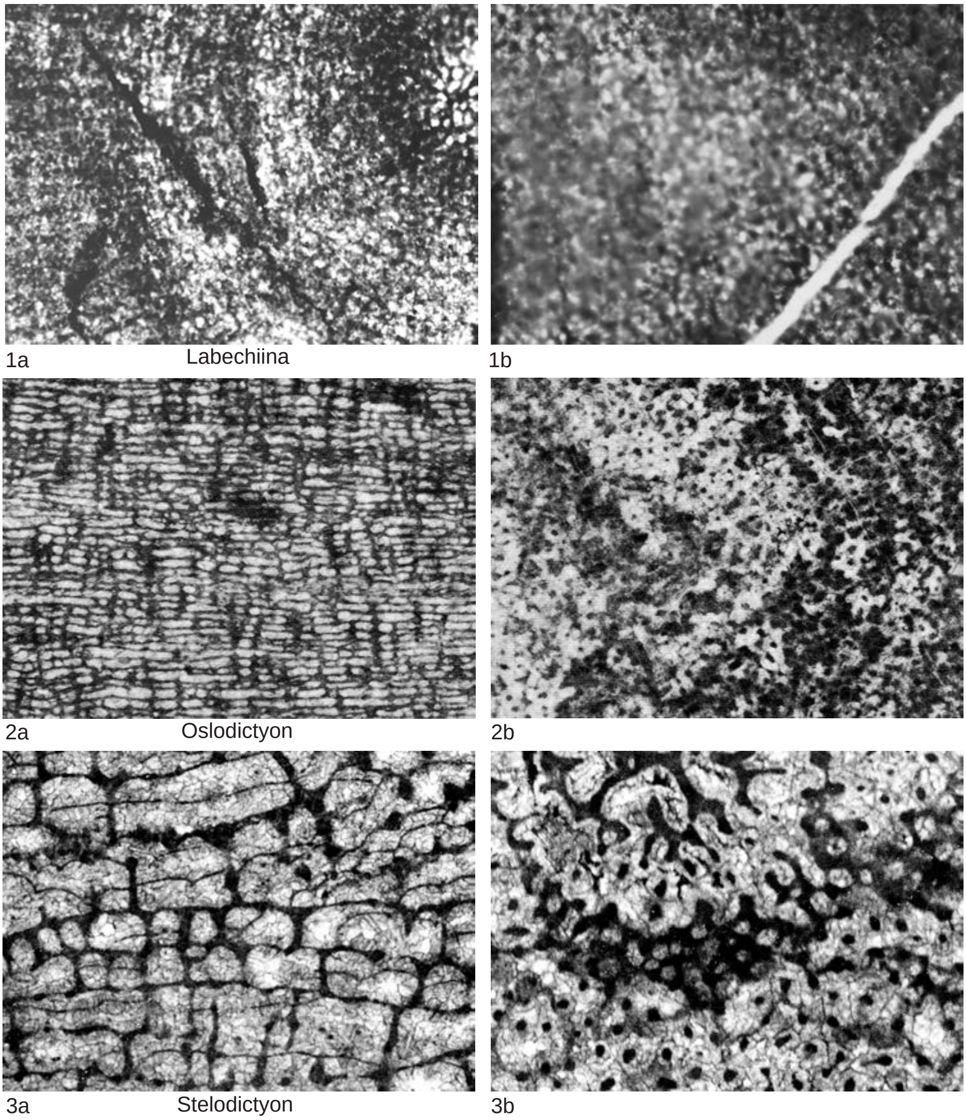


FIG. 417. Clathrodictyidae (p. 757–758).

pillars very weakly differentiated; galleries irregular; astrorhizae obscure. *Carboniferous (Mississippian, Serpukhovian):* Russia (Donetsk Basin).——FIG. 416,*4a–b*. **K. kalmiusensis*, Kal'mius River at Zhelvakovaia, holotype, UGM 15/57/103; longitudinal and tangential sections, ×10 (Nestor, 2011).

Labechiina KHALFINA, 1961b, p. 55 [**L. cylindrica* KHALFINA, 1961b, p. 56, holotype, CSGM 401/50; OD]. Growth form columnar, without axial canal; laminae moderately wrinkled, thin, bending downward into short pillars; long, stout megapillars well developed, densely spaced. *Silurian–Lower Devonian*: Canada (Mackenzie District), *Silurian;* Russia (Salair), *Lower Devonian.*——FIG. 417,*1a–b*. **L. cylindrica*, Sukhaia Suite, Lochkovian, Aleksandrovka, Salair, holotype CSGM 401/50; transverse and tangential sections, ×10 (Nestor, 2011, courtesy of V. G. Khromykh).

Oslodictyon MORI, 1978, p. 134 [**O. henningsmoeni* MORI, 1978, p. 135, holotype, PMO 45420; OD] [=*Distylostroma* KOSAREVA in BOGOYAVLENSKAYA & KHROMYKH, 1985, p. 75 (type, *D. crassum*, *nom. nud.*)]. Growth form domical to laminar; laminae moderately wrinkled, bending downward into short pillars; long, stout megapillars are present; astrorhizae obscure. *Silurian (Llandovery)–*

Middle Devonian: Canada (Anticosti), Estonia, Norway, *Llandovery;* Urals, *Silurian*; Canada (Arctic islands), Russia (northeastern Siberia), *Lower Devonian;* Russia (Salair), *Middle Devonian.*——FIG. 417,*2a–b*. **O. henningsmoeni*, Rytteråker Formation (7b), Llandovery, Vesleøya, Ringerike, Norway, holotype PMO 45420; longitudinal and tangential sections, ×10 (Mori, 1978, fig. 9A–B).

Stelodictyon BOGOYAVLENSKAYA, 1969b, p. 17 [**S. iniquum;* OD; holotype UGM 990/61a]. Growth form domical or laminar; laminae microundulate at junctions of funnel-shaped pillars, may be penetrated by pores; galleries arch shaped in longitudinal section, open in tangential section; astrorhizae rare, irregular. *Upper Ordovician (Hirnantian)–Lower Devonian (Lochkovian)*: Estonia, *Hirnantian;* Canada (Manitoba, Ontario), England, Russia (western Urals, Siberian Platform), Sweden (Gotland), Ukraine (Podolia), *Wenlock;* Russia (Urals), *Ludlow;* United States (New York), *Lochkovian.*——FIG. 417,*3a–b*. **S. iniquum*, Isovskaia Suite, Ludlow, Is River, Isovskoĭ District, Middle Urals, holotype UGM 990/61a; longitudinal and tangential sections, ×10 (Nestor, 2011).

Family ACTINODICTYIDAE Khalfina & Yavorsky, 1973

[Actinodictyidae KHALFINA & YAVORSKY, 1973, p. 26; *emend.,* NESTOR in STEARN & others, 1999, p. 25] [=Ecclimadictyidae STEARN, 1980, p. 890; =Plexodictyidae BOGOYAVLENSKAYA, 1981, p. 30]

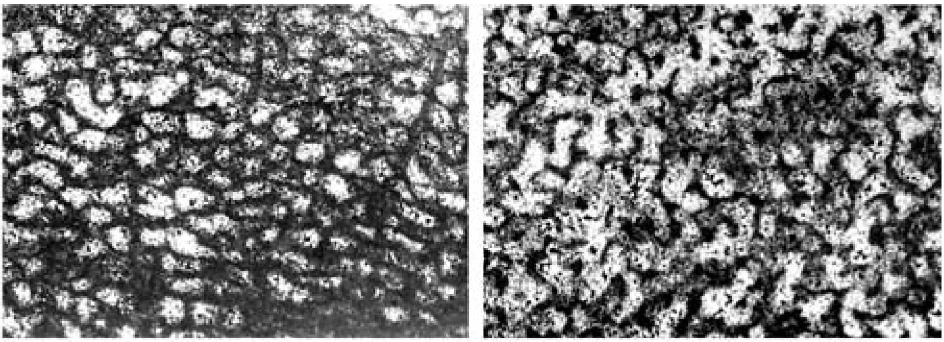
Skeletal elements very weakly differentiated; laminae crumpled (zigzag), forming cassiculate network; pillars indistinct or oblique; galleries labyrinthine, subangular in longitudinal section; megapillars and paralaminae may be present. [KHALFINA and YAVORSKY (1973) restricted the family Actinostromatidae to the genera having long megapillars, in addition to crumpled laminae. BOGOYAVLENSKAYA (1981) erected a new family Plexodictyidae, based on the presence of crumpled laminae and paralaminae. STEARN (1980) treated the presence of megapillars and paralaminae as genus-level characters and combined all genera with crumpled laminae, including *Actinodictyon* and *Plexodictyon*, into the newly erected family Ecclimadictyidae, which by priority became a junior synonym of Actinodictyidae (NESTOR in STEARN & others, 1999).] *Upper Ordovician (Katian)–Lower Devonian (Emsian).*

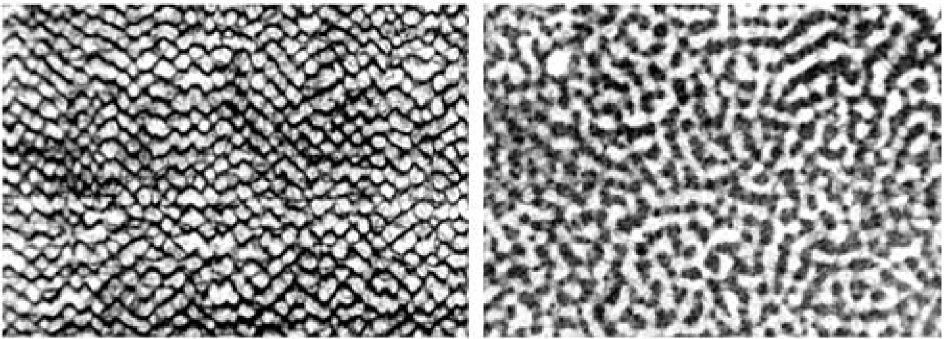
Actinodictyon PARKS, 1909, p. 30 [**A. canadense* PARKS, 1909, p. 32; SD BASSLER, 1915, p. 15, holotype GSC 9123]. Growth form columnar; laminae irregularly crumpled, fused with dissepiments, intersected by scattered, crooked megapillars; galleries very irregular, labyrinthine; astrorhizae obscure. *Silurian:* Russia (Pechora Basin); Canada (Hudson Bay), *Llandovery;* Australia (New South Wales), *Ludlow.*——FIG. 418,*1a–b*. **A. canadense*, lower Silurian, Southampton Island, Hudson Bay, holotype GSC 9123; transverse and tangential sections, ×10 (Nestor, 2011).

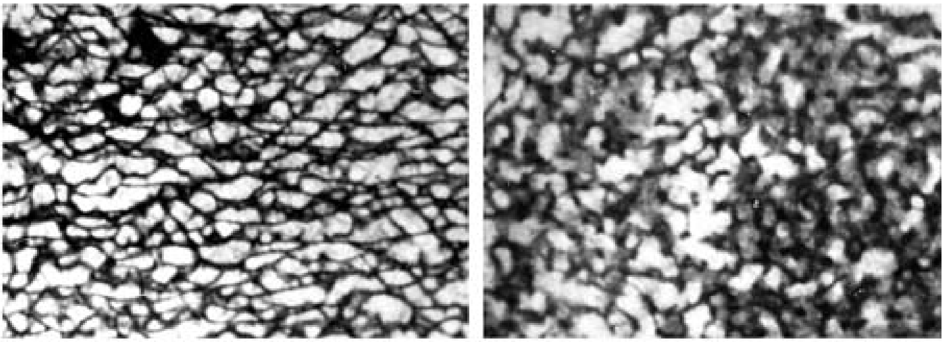
Camptodictyon NESTOR, COPPER, & STOCK, 2010, p. 83–84 [**C. penefastigiatum* NESTOR, COPPER, & STOCK, 2010, p. 84–85; OD; holotype, GSC 128021]. Growth form laminar to domical; laminae chevronlike folded to smoothly microundulating; pillars imperfect, oblique inflexions of laminae, partly superposed, forming longer zigzag-shaped pseudopillars; galleries labyrinthine, round, oval or meandriform in longitudinal section, often superposed forming subvertical rows, separated from each other by zigzag pseudopillars; astrorhizae inconspicious. *Upper Ordovician (Katian)–lower Silurian (Telychian):* Russia (Gornaia Shoriia, Altai), Australia (New South Wales), *Katian;* Canada (Anticosti and Baffin islands), Estonia, *Llandovery.*——FIG. 419,*3a–b*. **C. penefastigiatum,* Goéland Member, Jupiter Formation, Aeronian, Gull Cape, Anticosti, holotype GSC 128021; transverse and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, pl. 21c–d).

Desmidodictyon NESTOR, COPPER, & STOCK, 2010, p. 85–86 [**D. exoticum* NESTOR, COPPER, & STOCK, 2010, p. 86–87; OD; holotype, GSC 129268]. Growth form fasciculate or digitate; subcylindrical stems lacking axial canal, but possessing a broad axial zone with irregularly twisted rodlike pillars and colliculi; very narrow, reduced peripheral zone consists of small number of minutely crumpled laminae. *Silurian (Llandovery):* Canada (Anticosti Island), *Rhuddanian.*——FIG. 419,*4a–b*. **D.exoticum,* Merrimack Formation, Rhuddanian, Jupiter River at 24 mile bridge, Anticosti, holotype, GSC 129268; transverse and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, pl. 22a–b).

Ecclimadictyon NESTOR, 1964a, p. 60 [**Clathrodictyon fastigiatum* NICHOLSON, 1887, p. 8; OD; holotype NHM P5773]. Growth form laminar to domical; laminae crumpled, forming cassiculate network; pillars oblique or indistinct; galleries labyrinthine, subangular in longitudinal section; astrorhizae fasciculate, irregular. *Upper Ordovician (Katian)–Silurian:* Australia (New South Wales, Tasmania), China (Quinghai, Xinjiang, Zhejiang), Estonia, Kazakhstan, Russia (Urals, Altai, Gornaia Shoria), *Katian–Hirnantian;* Canada (Anticosti, Arctic islands, eastern Quebec), central Asia (Tien Shan), China (Guizhou, Hubei, Sichuan), Estonia, Greenland, Iran, Norway, Russia (Arctic islands), United States (Iowa, Michigan, Missouri, Ohio, Oklahoma), *Llandovery;* Australia (New South Wales), Canada (eastern Quebec, Ontario), central Asia (Tien Shan), England, Estonia, Norway, Russia (Altai, Arctic islands, Siberian Platform, Urals), Sweden (Gotland), Ukraine (Podolia),


1a Actinodictyon 1b


2a Ecclimadictyon 2b


3a Neobeatricea 3b

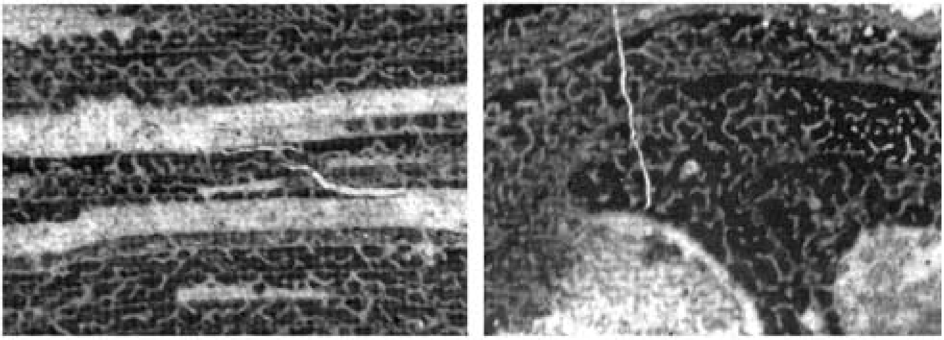

4a Labyrinthodictyon 4b

FIG. 418. Actinodictyidae (p. 758–761).

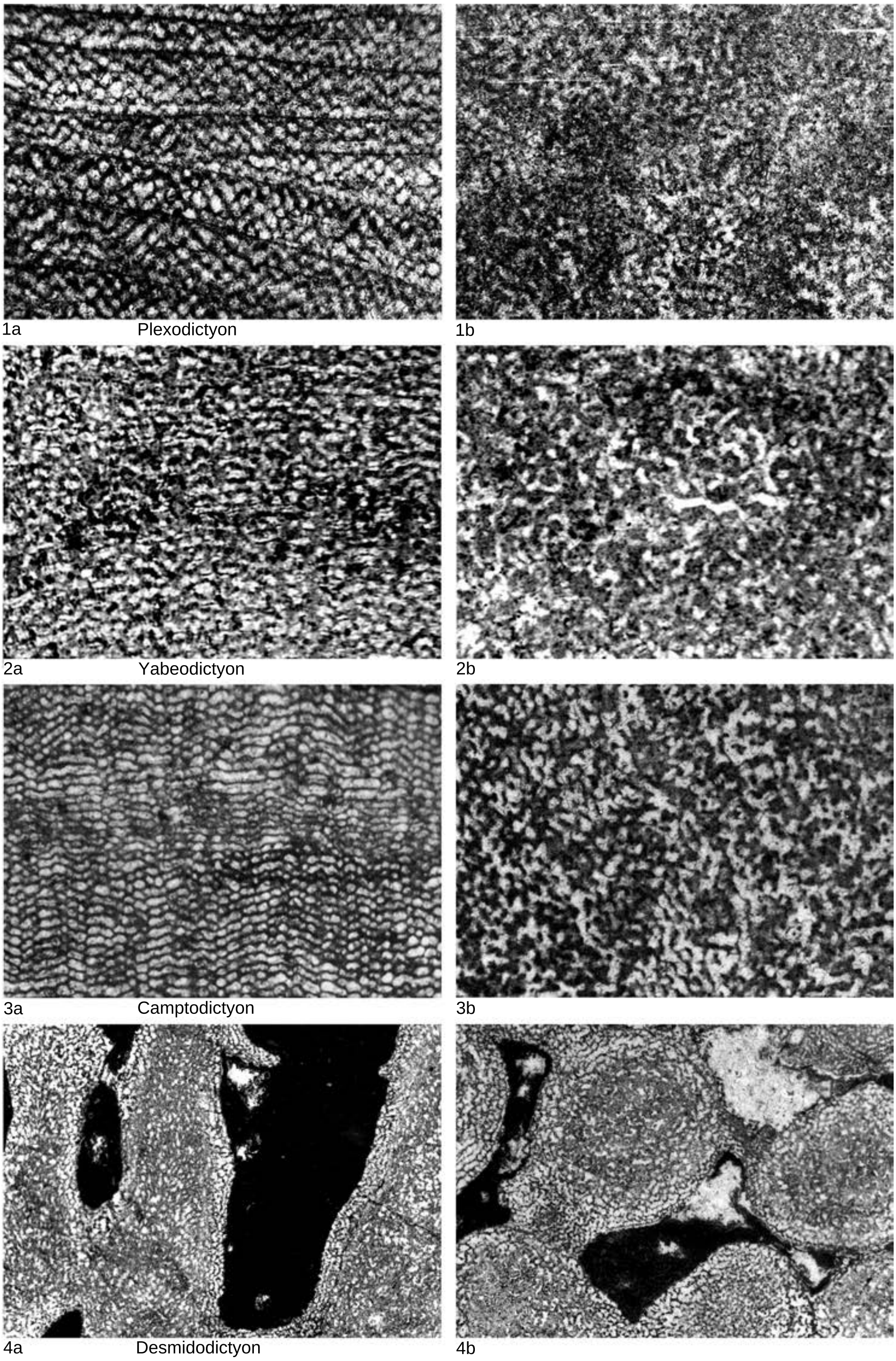


FIG. 419. Actinodictyidae (p. 758–761).

United States (Michigan), *Wenlock;* Canada (eastern Quebec, Ontario), China (Inner Mongolia), Norway, Russia (Arctic islands, Urals), Sweden (Gotland), *Ludlow;* Russia (Urals), *Pridoli;* Russia (Pechora Basin, northeastern Siberia, Tuva), *Silurian.*——FIG. 418,*2a–b.* **E. fastigiatum* (NICHOLSON), Much Wenlock Limestone Formation, Wenlock, Ironbridge, Shropshire, holotype NHM P5773; longitudinal and tangential sections, ×10 (Nestor, 2011).

Labyrinthodictyon NESTOR, COPPER, & STOCK, 2010, p. 74–75 [**L. angulosum*; OD; holotype, GSC 127961]. Growth form laminar to domical; skeleton consists of planar paralaminae and irregular interlaminar meshwork, formed by tangled , oblique and tortuous, randomly oriented plate- or rodlike skeletal elements; astrorhizae unknown. [NESTOR, COPPER, and STOCK (2010) erroneously placed the description of this genus under the heading of the family Clathrodictyidae.] *Upper Ordovician:* Canada (Anticosti Island), *Hirnantian;* Australia (New South Wales), *Katian.*——FIG. 418,*4a–b.* **L. angulosum,* Prinsta Member, Ellis Bay Formation, Hirnantian, Table Head, Anticosti, holotype, GSC 127961; transverse and tangential sections, ×10 (Nestor, Copper, & Stock, 2010, pl. 16a–b).

Neobeatricea RUKHIN, 1938, p. 95 [**Beatricea tenuitextilis* YAVORSKY, 1929, p. 92; OD; holotype CNIGR 2595/20]. Growth form columnar, without axial canal; laminae irregularly crumpled, intertwined with flat dissepiments; short pillars indistinguishable, megapillars absent; astrorhizae rare, with short unbranched canals. *Silurian*: Russia (Siberian Platform, Urals), *Wenlock;* Canada (Quebec), *Ludlow;* Russia (northeastern Siberia, Novaya Zemlya, Pechora Basin), *Silurian.*——FIG. 418,*3a–b.* **N. tenuitextilis* (YAVORSKY), Silurian, Rusanov valley, Novaya Zemlya, northern island, holotype CNIGR 2595/20; longitudinal and tangential sections, ×10 (Nestor, 2011).

Plexodictyon NESTOR, 1966a, p. 20 [**P. katriense* NESTOR, 1966a, p. 21; OD; holotype IGTUT 114-18 (Co 3132)]. Growth form laminar or domical; laminae crumpled, forming regular cassiculate network traversed by planar paralaminae; astrorhizae rare, tubular. [A few superficially similar species from the Upper Ordovician and Llandovery (Silurian) may represent another genus.] ?*Upper Ordovician, Silurian (?Llandovery, Ludlow–Pridoli)*: Australia (New South Wales, Queensland), ?*Upper Ordovician;* China (Guizhou, Hubei), *?Llandovery;* Australia (New South Wales, Queensland), Canada (Arctic islands), central Asia (Tien Shan), China (Inner Mongolia), Estonia, Sweden (Gotland, Scania), Russia (Arctic islands, northeastern Siberia, Pechora Basin, Urals), Ukraine (Podolia), United States (Michigan, Virginia), *Ludlow–Pridoli.*——FIG. 419,*1a–b.* **P. katriense*, Paadla Stage, Ludlow, Katri, Saaremaa Island, Estonia, holotype IGTUT 114-18 (Co 3132); longitudinal and tangential sections, ×10 (Nestor, 2011).

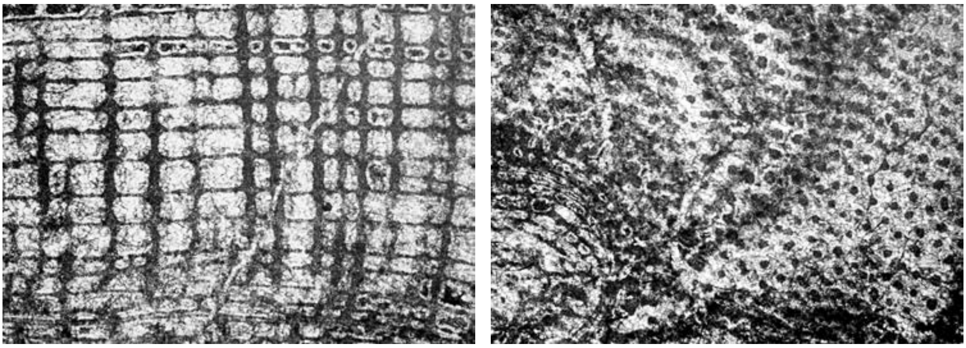
Yabeodictyon MORI, 1968, p. 67 [**Y. balticum* MORI, 1968, p. 68; OD; holotype SMNH Cn 68177 (GIK-35)] [=*Neoclathrodictyon* LESSOVAJA, 1971, p. 116 (type, *N. flexibilis,* OD)]. Growth form domical or laminar; laminae crumpled, intersected by long megapillars; galleries labyrinthine; astrorhizae common, small. [NESTOR (1976, p. 59) treated *Neoclathrodictyon* as a junior synonym of *Yabeodictyon.*] *Silurian (Llandovery)–Lower Devonian (Emsian):* Canada (Arctic islands, eastern Quebec), Russia (Siberian Platform), Sweden (Gotland), *Wenlock;* Canada (Arctic islands), central Asia (Tien Shan), Russia (Urals, ?Salair), *Ludlow–Pridoli;* Canada (Hudson Bay), Russia (Pechora Basin), *Silurian*; central Asia (Tien Shan), *Emsian.*——FIG. 419,*2a–b.* **Y. balticum*, Slite Beds, Wenlock, Slite, Gotland, holotype SMNH Cn 68177 (GIK-35); longitudinal and tangential sections, ×10 (Nestor, 2011).

Family GERRONOSTROMATIDAE Bogoyavlenskaya, 1969

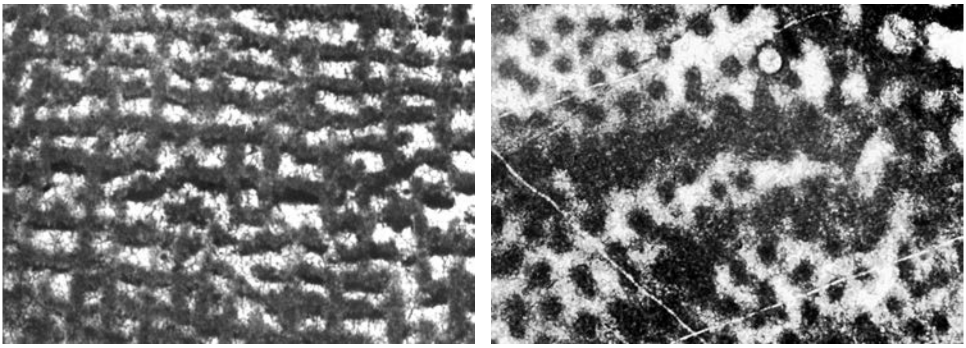
[Gerronostromatidae BOGOYAVLENSKAYA, 1969b, p. 19; *emend.,* NESTOR in STEARN & others, 1999, p. 28] [=Clathrostromatidae KHALFINA & YAVORSKY, 1971, p. 118]

Skeletal elements very well differentiated; laminae continuous, planar (straight); pillars simple, rodlike, short or long (superposed); galleries open, subrectangular in longitudinal section; astrorhizae rare, irregular. [BOGOYAVLENSKAYA (1969b) originally incorporated stromatoporoids with single-layer and tripartite laminae both in the present family. STEARN (in STEARN & others, 1999) removed those with tripartite laminae into the family Stromatoporellidae and thus restricted the scope of Gerronostromatidae. KHALFINA and YAVORSKY (1971) established a new family Clathrostromatidae, which differs from Gerronostromatidae by the presence of short pillars in addition to the long ones. This feature is not considered to be diagnostic of the family level by other investigators.] *Silurian (Llandovery)–Upper Devonian (upper Famennian).*

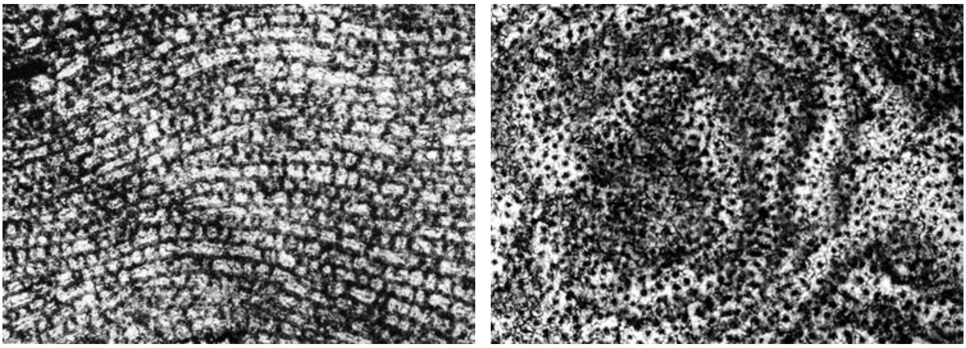
Gerronostromaria NESTOR, 2011, p. 6, *nom. nov. pro Gerronostroma* YAVORSKY, 1931, p. 1392, *nom. nud.* [**Gerronostroma elegans* YAVORSKY, 1931, p. 1393; OD; holotype CNIGR 3338/3] [=*Clathrostroma* YAVORSKY, 1960, p. 132 (type, *C. stolbergense,* OD)]. Growth form domical or bulbous; laminae planar, continuous; pillars rodlike, mostly long or superposed; galleries rectangular in longitudinal section; astrorhizae rare, fasciculate. [YAVORSKY (1931) established a new genus *Gerronostroma* without designation of the type species, and therefore, according to the IZCN Code (1999), Article 13.3, its name is invalid and requires replacement. YAVORSKY



1a Gerronostromaria 1b



2a Gerronodictyon 2b



3a Petridiostroma 3b

FIG. 420. Gerronostromatidae (p. 761–763).

(1960) established the new genus *Clathrostroma*, differing from *Gerronostroma* by the presence of both short and long (superposed) pillars. The presence of partly short and partly long pillars is not considered here to be a generic character.] *Silurian (Llandovery)–Upper Devonian (upper Famennian)*: Canada (Arctic islands), *Llandovery;* Canada (Quebec), Russia (Pechora Basin, Urals), *Ludlow–Pridoli;* Canada (Arctic islands), central Asia (Tien Shan), Russia (Kuznetsk Basin, northeastern Siberia, Urals), *Lower Devonian*; Afghanistan, Australia (Queensland, Victoria), central Asia (Tien Shan), Russia (Kuznetsk Basin, northeastern Siberia, Pechora Basin, Urals), United States (Indiana, Ohio), *Middle Devonian*; Canada (Alberta), Germany, Russia (Kuznetsk Basin, Russian Platform), *Upper Devonian*; Germany, Russia (southern Urals), *upper Famennian.*——FIG. 420,*1a–b*. **G. elegans* (YAVORSKY), Middle Devonian, Bachat village, Kuznetsk Basin, holotype CNIGR 3338/3; longitudinal and tangential sections, ×10 (Nestor, 2011).

Gerronodictyon Bogoyavlenskaya, 1969b, p. 20 [**G. incisum;* OD; holotype UGM 990/189a]. Growth form domical or irregular; laminae thick, discontinuous; pillars rodlike, mostly superposed, unequally situated; astrorhizae rare, fasciculate. *Silurian (Wenlock)*: Russia (Urals).——Fig. 420,*2a–b.* **G. incisum,* Pavdinsk Horizon, Wenlock, Is River, Isovskoĭ District, Middle Urals, holotype UGM 990/189a; longitudinal and tangential sections, ×10 (Nestor, 2011).

Petridiostroma Stearn, 1992, p. 531, *nom. nov. pro Petrostroma* Stearn, 1991, p. 617, *non* Döderlein, 1892 [**Simplexodictyon simplex* Nestor, 1966a, p. 25; OD; holotype IGTUT 114-20 (Co3134)] [=*Faciledictyon* Lessovaja, 1991, p. 28 (type, *Simplexodictyon torosum* Lessovaja, 1972, p. 49, OD)]. Growth form laminar to domical; laminae planar, continuous; pillars short, rodlike to spool shaped; galleries open, rectangular, oval to arch-shaped in longitudinal section; astrorhizae rare, inconspicuous. [Stearn (1991) and Lessovaja (1991) in the same year published the morphologically identical genera *Petrostroma* and *Faciledictyon*. The former name has priority, as it was published in July, while the latter appeared in November.] *Silurian (Telychian)–Middle Devonian:* Estonia, Norway, Sweden (Gotland), Canada (Anticosti), *Telychian;* central Asia (Tien Shan), Estonia, Russia (Urals), Sweden (Gotland), United States (Kentucky), *Wenlock;* Russia (Pechora Basin, northeastern Siberia), *Silurian*; Australia (Victoria), Canada (Arctic islands), central Asia (Tien Shan), Czech Republic (Bohemia), Russia (northeastern Siberia, Salair, Urals), United States (New York), *Lower Devonian*; Canada (Ontario), central Asia (Tien Shan), Germany, Russia (Kuznetsk Basin, northeastern Siberia, Pechora Basin, Urals), United States (Ohio), *Middle Devonian.*——Fig. 420,*3a–b.* **P. simplex* (Nestor), Jaani Stage, Wenlock, Liiva, Saaremaa Island, Estonia, holotype IGTUT 114-20 (Co3134); longitudinal and tangential sections, ×10 (Nestor, 2011).

Family TIENODICTYIDAE

Bogoyavlenskaya, 1965

[Tienodictyidae Bogoyavlenskaya, 1965c, p. 37, *emend.,* Stearn, 1980, p. 890; Nestor, 1997, p. 327; Nestor in Stearn & others, 1999, p. 30; **Nestor, 2011, p. 10**] [=Dualestromatidae Khalfina & Yavorsky, 1973, p. 27]

Skeletal elements well differentiated; laminae continuous, planar; branching or oblique longitudinal skeletal elements, together with dissepiments, form tangled network in interlaminar space; galleries irregular, astrorhizae weakly developed. *Silurian (Llandovery)–Upper Devonian (Frasnian).*

Tienodictyon Yabe & Sugiyama, 1941b, p. 139 [**T. zonatum;* OD; holotype TUM 65229]. Growth form domical, structure laminate; laminae planar; interlaminar space divided into two zones, longitudinal skeletal elements in lower zone very irregular, connected with processes into tangled network, in upper zone, isolated pillars occur, circular in cross section; galleries irregular; dissepiments abundant in upper zone; astrorhizae indistinct. *Lower Devonian–Upper Devonian (Frasnian)*: Australia (northern Queensland), Russia (northeastern Siberia), *Lower Devonian;* Australia (northern Queensland), Canada (Northwest Territories), China (Yunnan), Russia (eastern Urals, Kuznetsk Basin, Salair), *Middle Devonian*; Czech Republic (Moravia), *Frasnian.*——Fig. 421,*1a–b.* **T. zonatum*, Middle Devonian, Nanshan, Paichiaying, eastern Yunnan, China, holotype TUM 65229; oblique longitudinal and tangential sections, ×10 (Nestor, 2011).

Hammatostroma Stearn, 1961, p. 939 [**H. albertense* Stearn, 1961, p. 940; OD; holotype GSC 15318]. Growth form domical to laminar; laminae planar or irregularly wavy, transversely fibrous; interlaminar spaces occupied by tangled, irregular structure, forming discontinuous, crumpled additional laminae in the middle part; galleries irregular; astrorhizae inconspicuous. *Lower Devonian–Upper Devonian (Frasnian):* Austria (Carnic Alps), *Lower Devonian;* China (Guangxi), *Givetian;* Canada (Alberta, Saskatchewan), China (Guangxi), Czech Republic (Moravia), Poland, Russia (Arctic islands, Timan, Urals), United States (Iowa), *Frasnian.*——Fig. 421,*2a–b.* **H. albertense*, Cairn Formation, Frasnian, Isaac Creek, Rocky Mountains, Alberta, holotype GSC 15318; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of T. E. Bolton).

Intexodictyides Nestor, 2011, p. 8, *nom. nov. pro Intexodictyon* Yavorsky, 1963, p. 34, *nom. nud.* [**Intexodictyon perplexum* Yavorsky, 1963, p. 36; OD; lectotype CNIGR 7351/469]. Growth form domical; laminae thin, planar; longitudinal skeletal elements (pillars) thin, irregularly branching, forming a fine tangled network in interlaminar space; additional inflected lamina locally developed in interlaminar space or below the planar lamina. [Yavorsky (1963) erected the new genus *Intexodictyon* without designation of the type species, and therefore, according to the IZCN Code (1999), Article 13.3, its name is invalid and requires replacement.] *Silurian (Llandovery)–Lower Devonian:* Canada (Arctic islands, eastern Quebec), China (Quizhou), Estonia, United States (northern Michigan), *Llandovery;* Russia (northeastern Siberia, Pechora Basin, Tuva), *Silurian*; China (Inner Mongolia), Russia (Kuznetsk Basin), *Lower Devonian.*——Fig. 421,*3a–b.* **I. perplexum* (Yavorsky), upper Silurian, R. Iblagas, Magadan, northeastern Siberia; lectotype CNIGR 7351/469; longitudinal and tangential sections, ×16 (Nestor, 2011).

Pseudoactinodictyon Flügel, 1958, p. 137 [**P. juxi;* OD; holotype SMF XXV-1184] [=*Dualestroma* Khalfina, 1968b, p. 61 (type, *Stromatoporella*

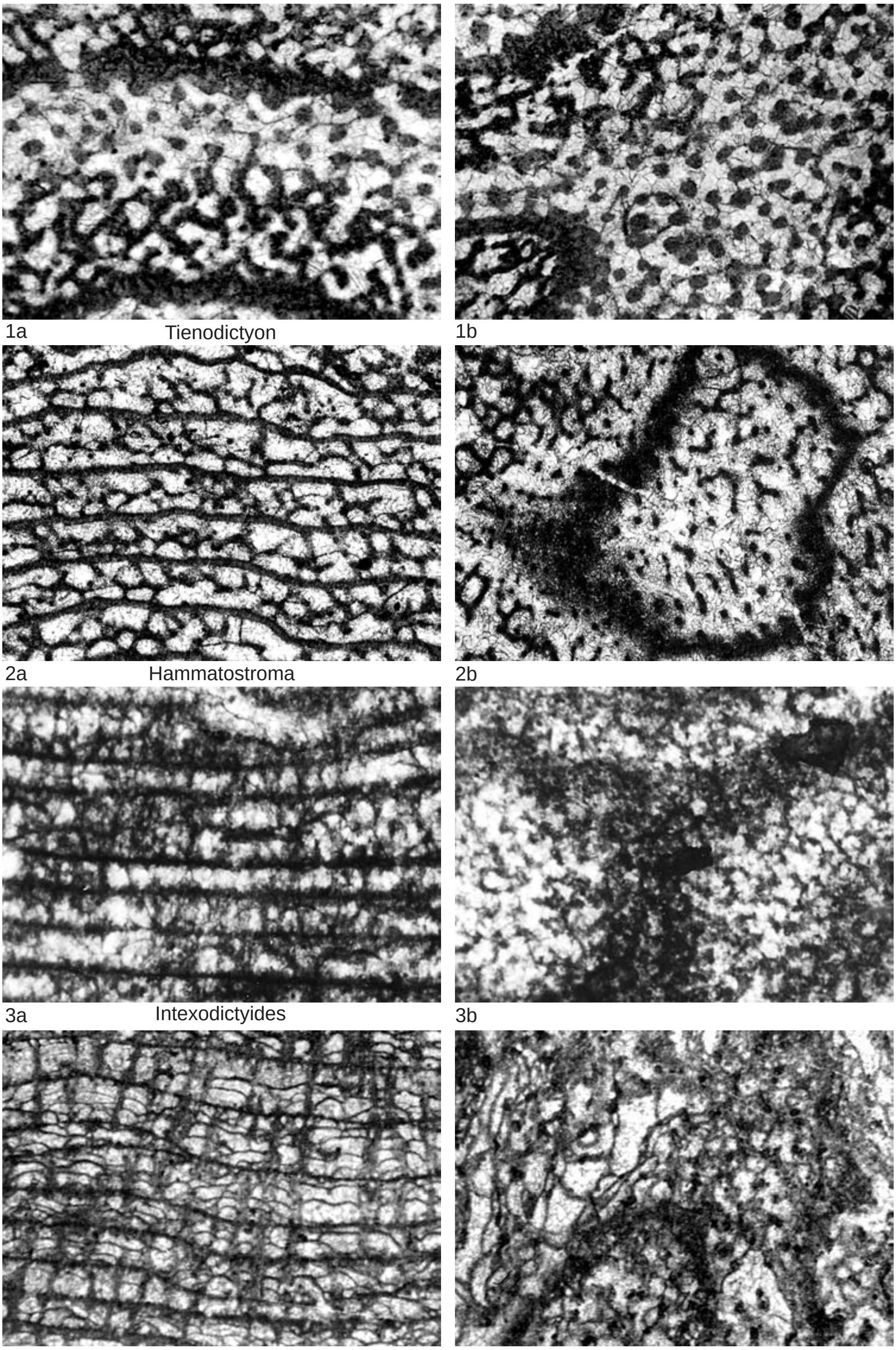


FIG. 421. Tienodictyidae (p. 763–766).

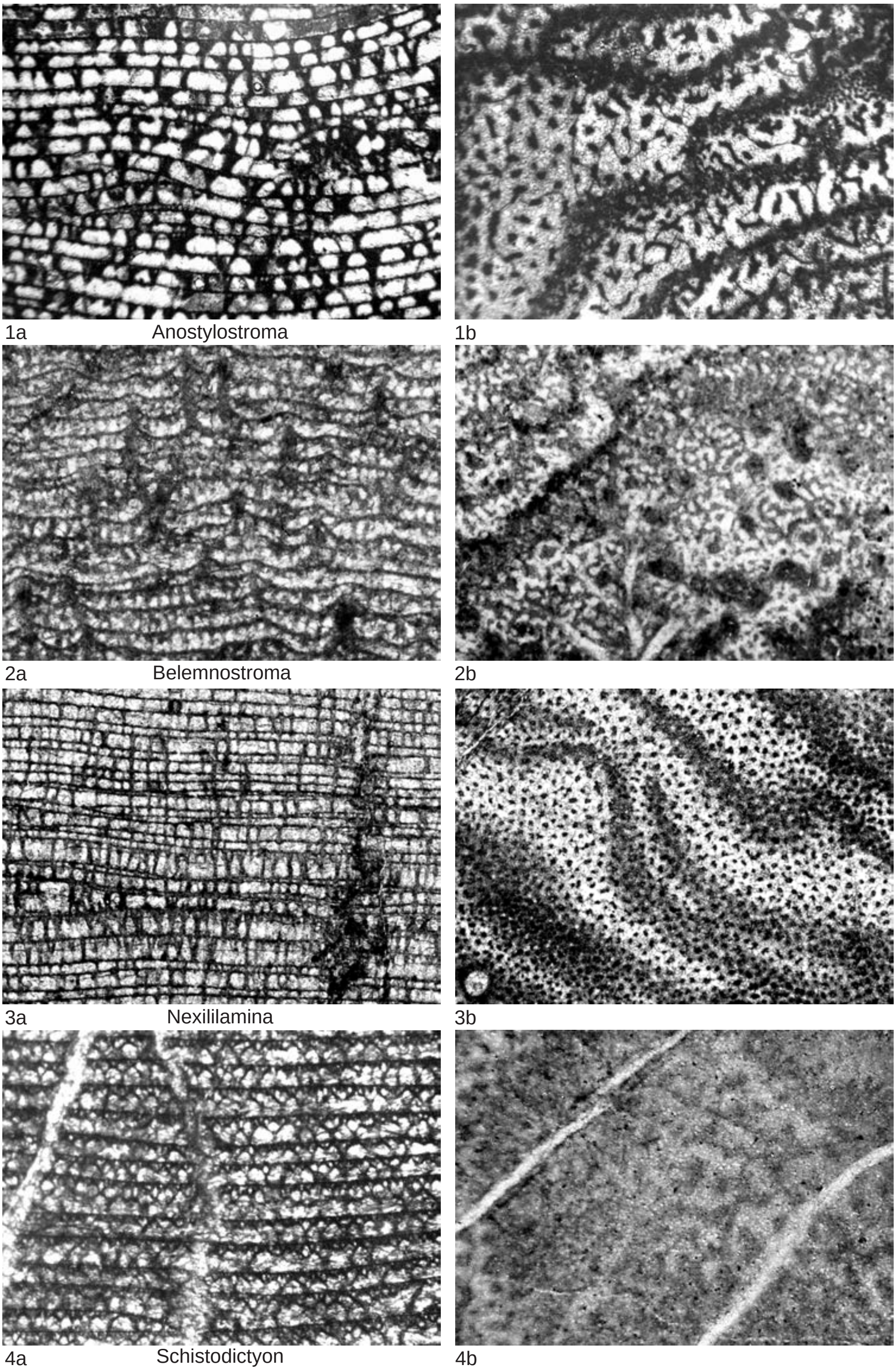


FIG. 422. Anostylostromatidae (p. 766).

dualis Khalfina, 1961d, p. 332, OD); =*Intexodictyonella* Yavorsky, 1969b, p. 102 (type, *Stromatoporella undata* Yavorsky, 1950, p. 258, OD)]. Growth form laminar to domical; laminae planar; pillars short, partly superposed, locally crooked or oblique, expanding at tops; wide interlaminar spaces filled with abundant convex dissepiments; astrorhizae irregular. [Flügel (1958) originally published negative prints of *Pseudoactinodictyon* with low magnification that complicated identification of the genus. Therefore, the species *Stromatoporella dualis* Khalfina, 1961d, and *Stromatoporella undata* Yavorsky, 1950, were distinguished as new genera *Dualestroma* and *Intexodictyonella,* respectively]. *Lower Devonian (Pragian)–Upper Devonian (Frasnian)*: Australia (Victoria), United States (?Michigan), *Pragian;* Australia (northern Queensland), Canada (Alberta, Ontario), China (Yunnan), Czech Republic (Moravia), England, France (Boulonnais), Germany (Sauerland), Poland, Russia (Kuznetsk Basin, southern Urals), United States (Ohio), *Middle Devonian;* Belgium, Canada (Alberta, Arctic islands), China (Guangxi), Germany (Sauerland), Russia (Russian Platform), *Frasnian.*——Fig. 421,*4a–b.* **P. juxi*, holotype SMF XXV-1184, "Massenkalk," Givetian, Delsten-Milchenbach, Sauerland, Germany; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of E. Schindler).

Family ANOSTYLOSTROMATIDAE
Nestor, 2011

[Anostylostromatidae Nestor, 2011, p. 10] [type genus, *Anostylostroma* Parks, 1936, p. 44]

Skeletal elements well differentiated; laminae continuous, planar; pillars expanding and branching at tops. [The genera included herein in the family Anostylostromatidae were formerly included in the family Tienodictyidae (Stearn & others, 1999).] *Silurian (Ludlow)–Upper Devonian (upper Famennian).*

Anostylostroma Parks, 1936, p. 44 [**A. hamiltonense* Parks, 1936, p. 46; OD; *emend.,* Stearn, 1991, p. 612, holotype ROM 16536 (2240)]. Growth form laminar to domical; laminae thin, planar, penetrated by scattered pores; pillars thick, expanding and branching at tops, oblong to vermiform in tangential section; galleries irregular; dissepiments common; astrorhizae rare, small. *Middle Devonian–Upper Devonian (upper Famennian)*: Canada (Arctic islands), China (Guangxi), Russia (eastern Urals, Kuznetsk Basin), United States (Indiana, Missouri), *Middle Devonian;* Kazakhstan, Russia (Pechora Basin), *Frasnian;* China (Guangxi), France, Germany (Aachen), Russia (Pechora Basin), *upper Famennian.*——Fig. 422,*1a–b.* **A. hamiltonense*, Long Lake, Alpena, Michigan, Hamilton Formation, holotype ROM 16536 (2240); longitudinal and tangential sections, ×10 (Nestor, 2011).

Belemnostroma Stearn, 1990, p. 504 [**B. hastatum* Stearn, 1990, p. 505; OD; holotype GSC 95772]. Growth form laminar to domical; laminae planar, inflected upward at megapillars; ordinary, short pillars expanding and branching at top; thicker megapillars, circular in cross section, penetrate through several laminae; astrorhizae inconspicuous. *Lower Devonian (Lochkovian)*: Canada (Arctic Islands).——Fig. 422,*2a–b.* **B. hastatum*, Loc. B24A near Polar Bear Pass, Bathurst Island, Stuart Bay Formation, holotype GSC 95772; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of C. W. Stearn).

Nexililamina Mallett, 1971, p. 241 [**N. dipcreekensis;* OD; *emend.,* Webby & Zhen, 1997, p. 35, holotype UQF 47608]. Growth form laminar to domical; laminae planar with few pores; pillars of two types: superposed, long, spool-shaped (megapillars) and simple, short, rodlike, expanding and branching at top, rounded to angular in cross section; dissepiments scattered; astrorhizae apparently lacking. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Australia (northern Queensland).——Fig. 422,*3a–b.* **N. dipcreekensis,* Martins Well, Broken River, Dip Creek Limestone, holotype, UQF 47608; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of B. D. Webby).

Schistodictyon Lessovaja in Lessovaja & Zakharova, 1970, p. 47 [**S. posterium;* OD; holotype GMU 240/2-9/74]. Growth form domical; laminae thin, planar; pillars upward forking or funnel shaped, branching in longitudinal section once or twice before reaching overlying lamina, pillars vermicular, irregular to circular in cross section; galleries irregular; astrorhizae rare. *Silurian (Ludlow)–Upper Devonian (Frasnian):* Australia (New South Wales, northern Queensland), central Asia (Tien Shan), *Ludlow–Pridoli;* Australia (New South Wales, northern Queensland), Russia (Kuznetsk Basin), *Lower Devonian;* Belgium, Canada (Ontario), United States (Michigan, Missouri, Ohio), Russia (southern Urals, Kuznetsk Basin), *Middle Devonian;* Canada (Arctic islands), Russia (Kuznetsk Basin), Turkey, *Frasnian.*——Fig. 422,*4a–b.* **S. posterium*, Isfara River, Tien Shan, Isfarinsk Horizon, Pridoli, holotype GMU 240/2-9/74; longitudinal and tangential sections, ×10 (Nestor, 2011).

Family ATELODICTYIDAE
Khalfina, 1968

[Atelodictyidae Khalfina, 1968a, p. 148; *emend.,* Stearn & others, 1999, p. 29] [=Aculatostromatidae Khalfina & Yavorsky, 1973, p. 27]

Skeletal elements well differentiated; laminae continuous, planar; pillars blade shaped, laterally joined in chains or walls; galleries labyrinthine in tangential section,

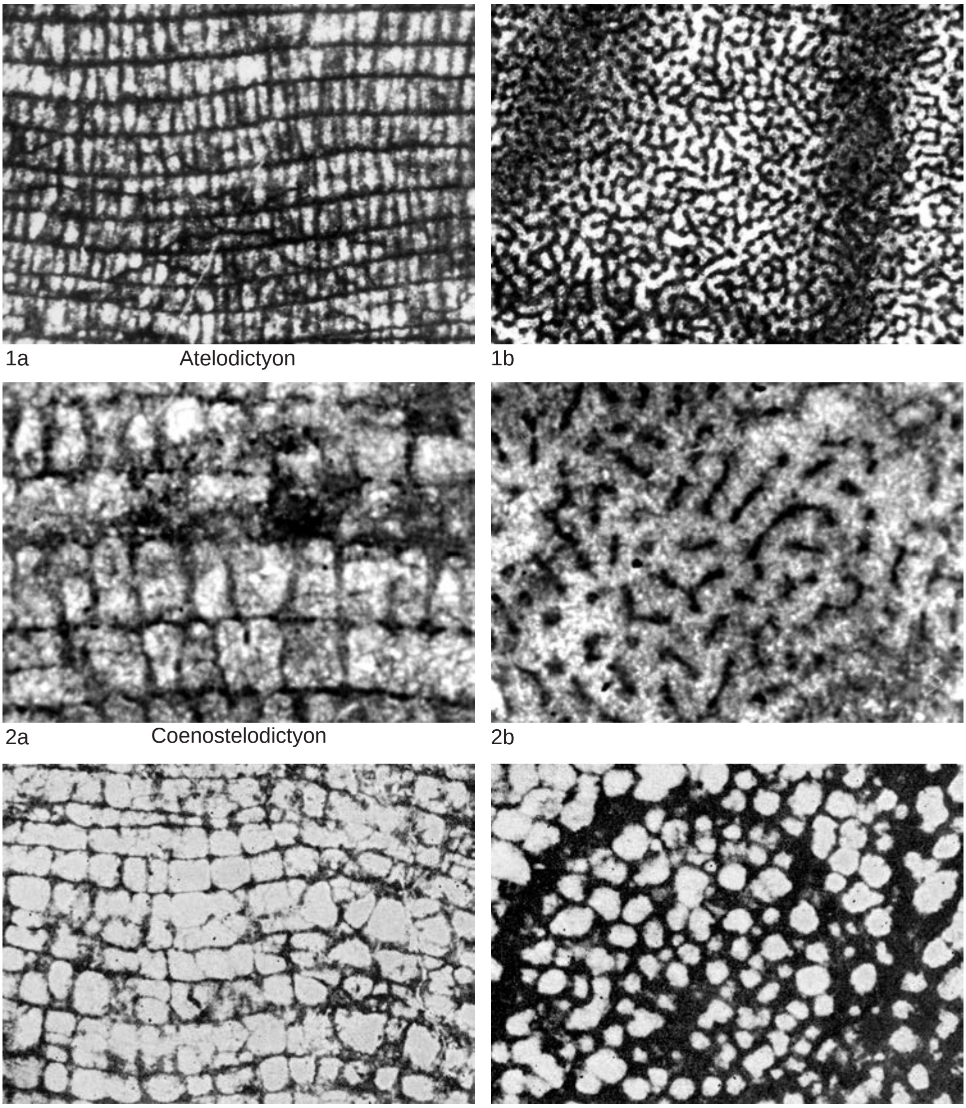


FIG. 423. Atelodictyidae (p. 767–768).

subrectangular in longitudinal section; astrorhizae rare. [STEARN (1991) transferred the genus *Atelodictyon* from Actinostromatida to Clathrodictyida, as it has continuous and not colliculate laminae. The so-called hexactinellid structure occurs in the interlaminar space of *Atelodictyon* and not at the level of lamina, as in actinostromatids. The representatives of the family Aculatostromatidae KHALFINA & YAVORSKY, 1973, have quite analogous interlaminar structure and continuous laminae. Therefore, the latter family is synonymous with Atelodictyidae.] *Lower Devonian–Upper Devonian (upper Famennian).*

Atelodictyon LECOMPTE, 1951 in 1951–1952, p. 124 [**A. fallax* LECOMPTE, 1951 in 1951–1952, p. 125; OD; holotype IRScNB 7411] [=*Aculatostroma*

Khalfina, 1968b, p. 62 (type, *Syringostroma verrucosum* Khalfina, 1961d, p. 342, OD)]. Growth form laminar or domical; laminae continuous, planar, thin; pillars bladelike, laterally joined in chains, short to superposed; galleries labyrinthine in tangential section, rectangular in longitudinal section; astrorhizae rare. [The original figures of *Syringostroma verrucosum* (Khalfina, 1961d, pl. D13,*3a–b*), designated as the type species of the genus *Aculatostroma* Khalfina, 1968b, clearly demonstrate that it has continuous laminae and so-called hexactinellid structure in the interlaminar space. Therefore, *Aculatostroma* is treated as a junior synonym of *Atelodictyon.*] *Lower Devonian–Upper Devonian (upper Famennian):* Australia (northern Queensland, Victoria), central Asia (Tien Shan), Russia (Kuznetsk Basin, northeastern Siberia), *Lower Devonian;* Afghanistan, Austria, Belgium, China (Quizhou), France (Boulonnais), Poland, Russia (Kuznetsk Basin, northeastern Siberia, Urals), United States (Indiana), *Middle Devonian;* Canada (Alberta), Czech Republic (Moravia), Poland, Russia (Kuznetsk Basin, northeastern Siberia, Russian Platform), United States (Iowa), *Upper Devonian;* Belgium, Germany, Kazakhstan, *upper Famennian.*——Fig. 423,*1a–b*. **A. fallax*, Couvinian, Eifelian, Dinant Basin, Belgium, holotype IRScNB 7411; longitudinal and tangential sections, ×10 (Nestor, 2011, courtesy of C. W. Stearn).

Coenostelodictyon Yavorsky in Khalfina & Yavorsky, 1971, p. 118 [**Clathrodictyon krekovi* Yavorsky, 1955, p. 50; OD; holotype CNIGR 7351/62]. Growth form laminar; laminae thin, planar, slightly inflected at the junctions with pillars; pillars bladelike, circular at base, mainly isolated but laterally joined in chains at top; galleries open in tangential section, subrectangular in longitudinal section; astrorhizae unknown. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Russia (Kuznetsk Basin), *Pragian;* China (Yunnan), *Eifelian.*——Fig. 423,*2a–b*. **C. krekovi* (Yavorsky), Krekov Horizon, Pragian, River Chernovoĭ Bachat, Kuznetsk Basin, holotype CNIGR 7351/62; longitudinal and tangential sections, ×20 (Nestor, 2011).

?Cubodictyon Yang & Dong, 1979, p. 45 [88] [**C. sinense;* OD; holotype NIGP Bd 644-4]. Growth form domical or irregular; laminae thin, continuous, wrinkled on a small scale; longitudinal elements, walls of subhexagonal chambers; astrorhizae unknown. [The presence of chamberlike structures in interlaminar spaces shows that the relationship of the genus with stromatoporoids is problematic.] *Middle Devonian (Eifelian):* China (Guangxi).——Fig. 423,*3a–b*. **C. sinense*, Beiliu Formation, holotype NIGP Bd 644-4; longitudinal and tangential sections, ×10 (Yang & Dong, 1979, pl. 20,*5–6*).

ACTINOSTROMATIDA: SYSTEMATIC DESCRIPTIONS

Carl W. Stock

Order ACTINOSTROMATIDA Bogoyavlenskaya, 1969

[Actinostromatida Bogoyavlenskaya, 1969b, p. 18]

Skeleton network of pillars or micropillars, and horizontal colliculi or microcolliculi that form hexactinellid pattern in tangential sections of most genera; microstructure compact to microreticulate. *Upper Ordovician (Katian)–Upper Devonian (Frasnian).*

Family ACTINOSTROMATIDAE Nicholson, 1886

[*nom. correct.* Lecompte, 1956, p. 127, *pro* Actinostromidae Nicholson, 1886a, p. 75]

Skeleton consists of well developed, parallel pillars, usually more prominent than colliculi; microstructure compact. *lower Silurian (Llandovery)–Upper Devonian (Frasnian).*

Actinostroma Nicholson, 1886a, p. 75 [**A. clathratum* Nicholson, 1886b, p. 226; OD] [=*Rosenia* Waagen & Wentzel, 1887, p. 943 (type, *Stromatopora astroites* Rosen *sensu* Bargatzky, 1881a, p. 284); =*Bullatella* Bogoyavlenskaya, 1977b, p. 13 (type, *B. crassa* Bogoyavlenskaya, 1977b, p. 14, OD); =*Auroriina* Bogoyavlenskaya, 1977b, p. 16 (type, *A. primigenia* Bogoyavlenskaya, 1977b, p. 17, OD)]. Pillars thick, usually long, continuous; colliculi horizontally aligned. [Nicholson (1886a, 1886b) published the type species before he published the initial description of the genus. Stock in Stearn and others (1999) noted that there are two groups of species within *Actinostroma* that are atypical. One group has complexly arranged colliculi and mostly short pillars, as in *A. verrucosum* (Goldfuss, 1826). The other group has simple colliculi and mostly short pillars, as in *A. stellulatum* Nicholson, 1886b.] *Lower Devonian (Lochkovian)–Upper Devonian (Frasnian):* Russia (Kuznetsk Basin), Uzbekistan, *Lower Devonian;* Canada (Arctic islands), Russia (eastern Urals), *Lochkovian;* Australia (New South Wales, Queensland), Czech Republic, *Pragian;* Australia (New South Wales, Queensland), Austria, Czech Republic, Mongolia, Russia (northeastern Siberia, Ulakhan-Sis Range), Spain, *Emsian;* China (Hunan, northeastern China), Italy, Russia (Pechora Basin, Salair, Siberia, Urals), Vietnam, *Middle Devonian:* Australia (Queensland), Austria, Belgium, China (Guangxi, Xinjiang), Czech Republic, Germany, Mongolia, Russia (Altai, Kuznetsk Basin, Siberia), Slovenia, Spain, Uzbekistan, *Eifelian;* Afghanistan, Australia (Queensland), Austria, Belgium, Canada (Manitoba, Northwest Territories), China (Guangxi, Guizhou, Hunan, Sichuan, Xizang, Yunnan), Czech Republic, France, Germany, Poland, Russia (Kuznetsk Basin, Omolon Massif, Pechora Basin, Salair, Siberia, Ulakhan-Sis Range, Urals), Thailand, United States (Indiana), Uzbekistan, Vietnam, *Givetian;* Russia (Pechora Basin, Russian Platform), Turkey, *Upper Devonian;* Australia (Western Australia), Belgium, Canada (Alberta, Manitoba, Northwest Territories, Saskatchewan), China (Guangxi, Sichuan, Yunnan), Czech Republic, France, Germany, Iran, Mexico (Sonora), Poland, Russia (Kuznetsk Basin, northeastern Siberia, Russian Platform, St. Petersburg, Timan), United States (Alaska, Iowa, Montana, Nevada, Utah), Uzbekistan, Vietnam *Frasnian.*——Fig. 424*a–d.* **A. clathratum* Nicholson; *a–b,* lectotype, Givetian, Gerolstein, Eifel, Germany, NHM P5774; *a*, longitudinal section, showing long pillars and horizontally aligned colliculi; isolated dots, as in center of figure, represent cross sections of colliculi; *b*, tangential section, showing pillar cross sections as isolated dots, and dark bands with poorly preserved colliculi and pillars forming hexactinellid network, ×10; *c–d*, hypotype, Mason City Member, Shell Rock Formation, Frasnian, Nora Springs, Iowa, USNM 307172; *c*, longitudinal section; *d*, tangential section, better preserved than view *b;* hexactinellid network best displayed in lower half of figure, ×10 (Stock, 2012).

Bicolumnostratum Stock in Stock & Burry-Stock, 1998, p. 191 [**Actinodictyon mica* Bogoyavlenskaya, 1969a, p. 20; OD; holotype, Bogoyalenskaya, 1969a, p. 20, pl. 4,*2a–b,* UGM 26-M 113 67, Ekaterinburg, Sverdlovsk]. Pillars mix of two types, some long, continuous and thick, others short and thin; colliculi not horizontally aligned. *upper Silurian (Ludlow–Pridoli):* Ukraine (Podolia), *Ludlow;* United States (New York), *Pridoli.*——Fig. 425*a–d.* **B. micum* (Bogoyavlenskaya); *a–b,* holotype, Sokol Beds, Malinovtsy Horizon, Ludlow, Podolia, Ukraine, UGM 26-M 113 67; *a,* longitudinal section; *b,* tangential section, ×30 (Bogoyavlenskaya, 1969a); *c–d,*

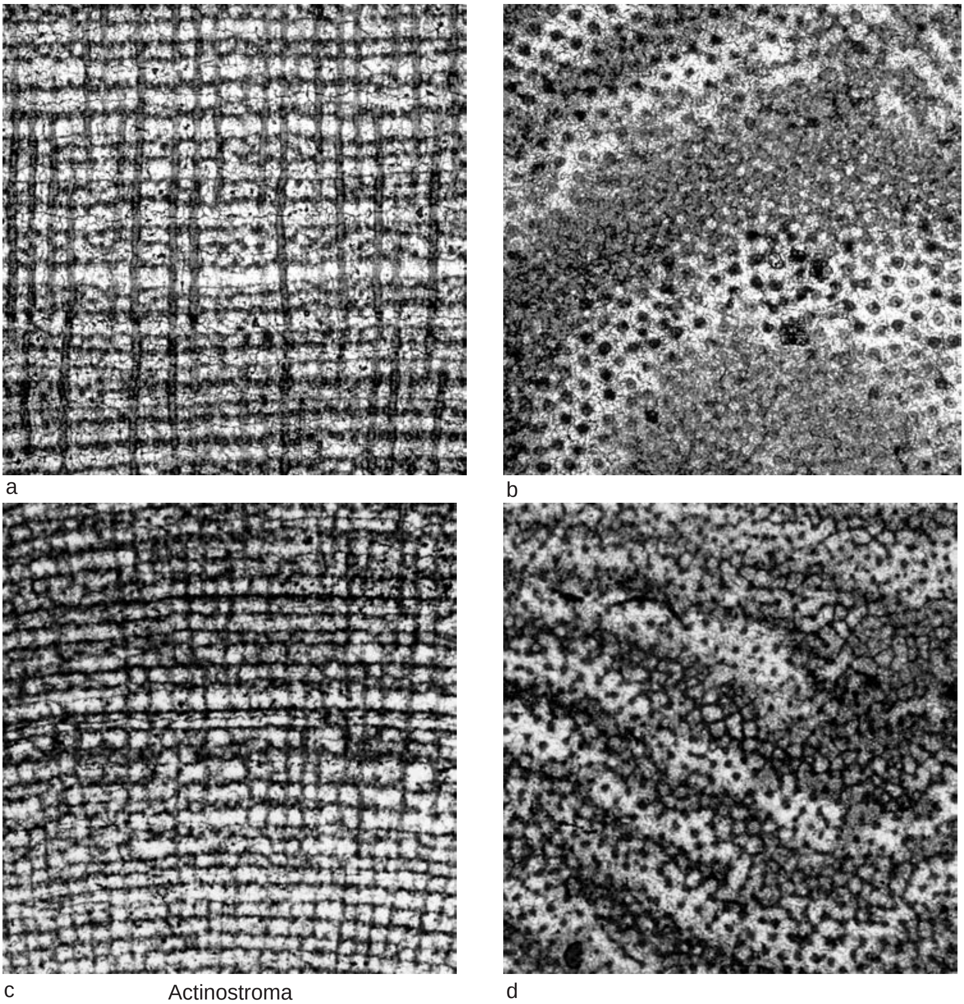


FIG. 424. Actinostromatidae (p. 769).

hypotype, Cobleskill Member, Rondout Formation, Pridoli, Cobleskill, New York, USNM 492553; *c*, longitudinal section, black dots represent air bubbles in thin section mounting medium; *d*, tangential section, black dots represent cross sections of well developed pillars, from which extend colliculi, ×30 (Stock, 2012).

Bifariostroma KHALFINA, 1968a, p. 149 [**Actinostroma bifarium* NICHOLSON, 1886b, p. 231; OD]. Pillars mix of two types, some long, continuous, and thick, others short and thin; colliculi horizontally aligned. *Lower Devonian (Emsian)–Upper Devonian (Frasnian):* Austria, Spain, *Emsian;* Italy, *Middle Devonian;* Belgium, Spain, Uzbekistan, *Eifelian;* Belgium, China (Guangxi, Sichuan), Czech Republic, France, Poland, Germany, *Givetian;* Afghanistan, Belgium, Czech Republic, Poland, Russia (Timan), *Frasnian.*——FIG. 426,*1a–b.* **B. bifarium* (NICHOLSON); lectotype, Givetian, Büchel bei Bensberg, Paffrath-Mulde, Germany, NHM P5639; *a*, longitudinal section, Nicholson slide 165c, apparent cellules in pillars and some colliculi represent diagenetic alteration of original compact microstructure; *b*, tangential section, Nicholson slide 165b; hexactinellid pattern best developed in center to lower center of figure, ×10 (Stock, 2012).

Crumplestroma KHALFINA, 1972, p. 148 [**C. lacerilaminatum;* OD]. Skeleton consists of long pillars and steplike offsets of colliculi interrupted by paralaminae, thicker than colliculi. *upper Silurian (Ludlow):* Russia (Altai).——FIG. 426,*2a–b.* **C.*

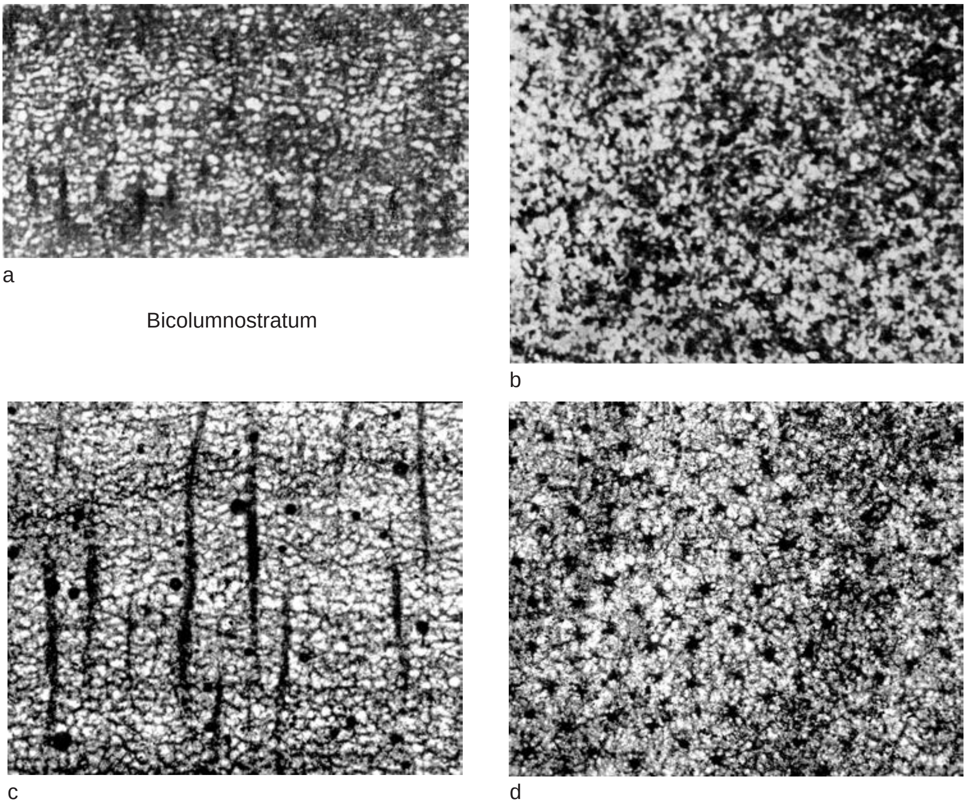


FIG. 425. Actinostromatidae (p. 769–770).

lacerilaminatum; holotype, photomicrographs, CSGM no. unknown; *a*, longitudinal section showing crumpled paralaminae between which pillars and colliculi developed; *b*, tangential section, poorly developed hexactinellid pattern in upper half of figure, ×10 (Khalfina, 1972, pl. C-II,*1–2*).

Plectostroma NESTOR, 1964a, p. 78 [**Actinostroma intertextum* NICHOLSON, 1886b, p. 233; OD]. Pillars long, continuous; colliculi not horizontally aligned, in many cases not perfectly horizontal. *lower Silurian (Llandovery)–Upper Devonian (Frasnian):* Russia (Altai, Salair), *Silurian;* Estonia, Russia (Siberian Platform, Tuva, Urals), Sweden (Gotland), Uzbekistan, *Llandovery;* China, *middle Silurian;* Canada (Northwest Territories), Estonia, Mongolia, Norway, Russia (Kuznetsk Basin, Urals), Sweden (Gotland), United Kingdom, *Wenlock;* China, Russia (Kuznetsk Basin, Pechora Basin, Urals), *upper Silurian;* Canada (Quebec), Estonia, Mongolia, Russia (Altai, Novaya Zemlya), Sweden (Gotland, Scania), Ukraine (Podolia), *Ludlow;* Canada (Quebec), Estonia, Mongolia, Ukraine (Podolia), *Pridoli;* Russia (northeastern Siberia), Uzbekistan, *Lower Devonian;* Canada (Arctic islands), Uzbekistan, *Lochkovian;* Australia (Victoria), *Pragian;* Canada (Arctic islands, Northwest Territories), Czech Republic, Spain, *Emsian;* Russia (Salair), *Middle Devonian;* Canada (Arctic islands, Northwest Territories), China (Guangxi), Czech Republic, Russia (Altai), Uzbekistan, *Eifelian;* China (Guangxi), Czech Republic, France, *Givetian;* Vietnam, *Frasnian.*——FIG. 426,*3a–b.* **P. intertextum* (NICHOLSON); holotype, Wenlock, Ironbridge, England, NHM P5620; *a*, longitudinal section, Nicholson slide 188b, latilaminar phases with short pillars low in figure and long pillars high in figure; *b*, tangential section, Nicholson slide 188, showing well developed hexactinellid pattern, ×10 (Stock, 2012).

Family PSEUDOLABECHIIDAE Bogoyavlenskaya, 1969

[Pseudolabechiidae BOGOYAVLESKAYA, 1969a, p. 17]

Skeleton contains pillars and colliculi, or micropillars and microcolliculi, clustered

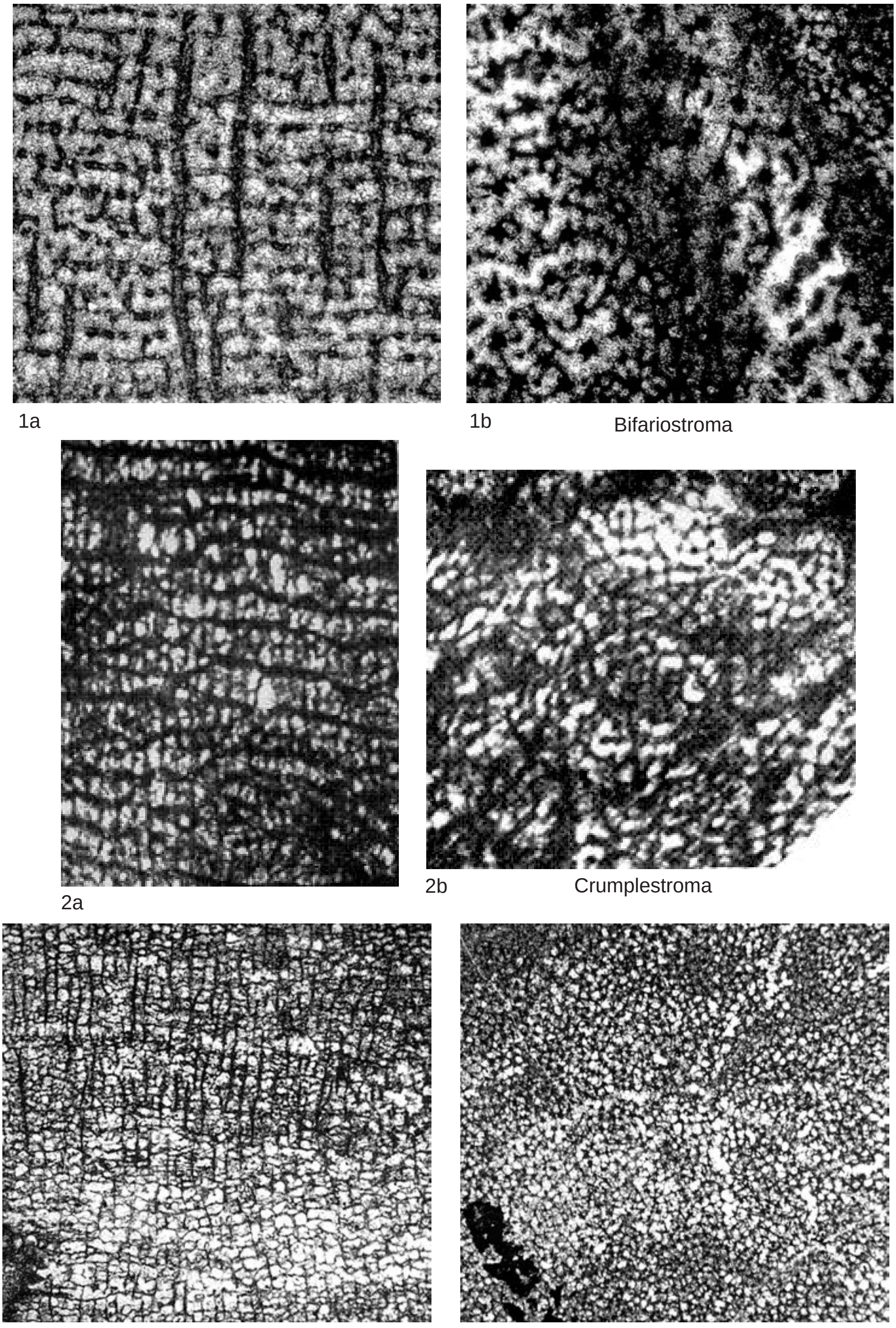
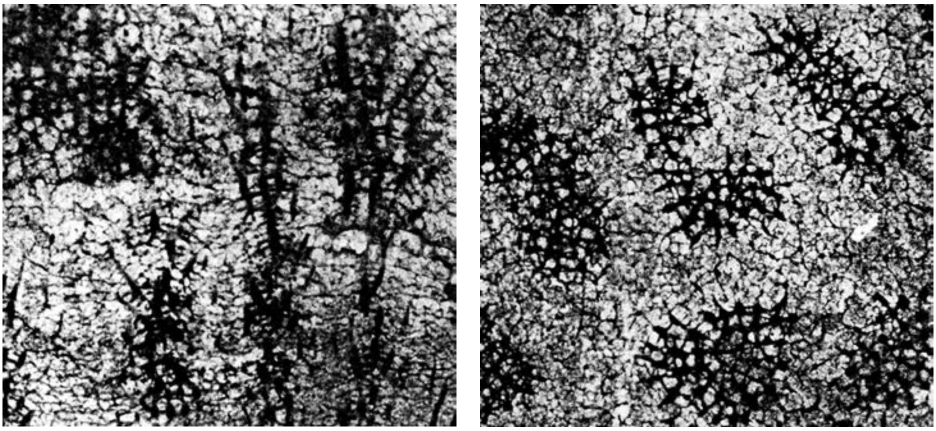
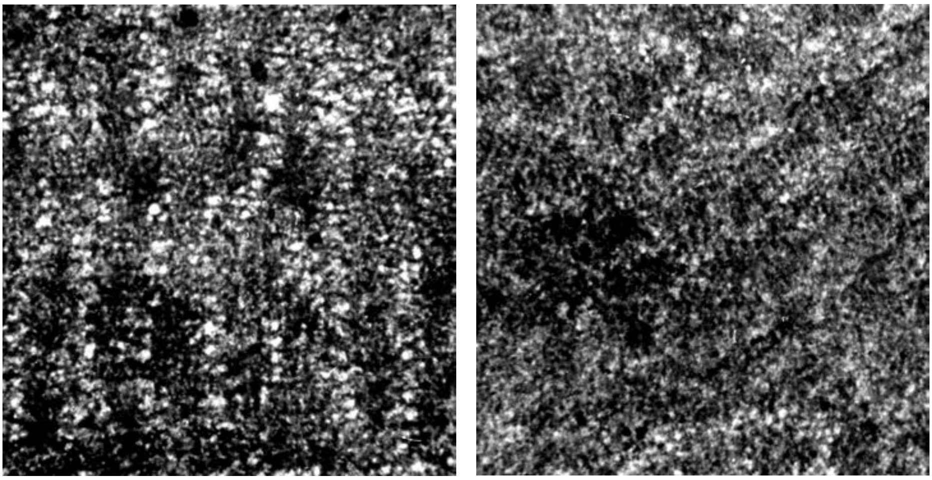


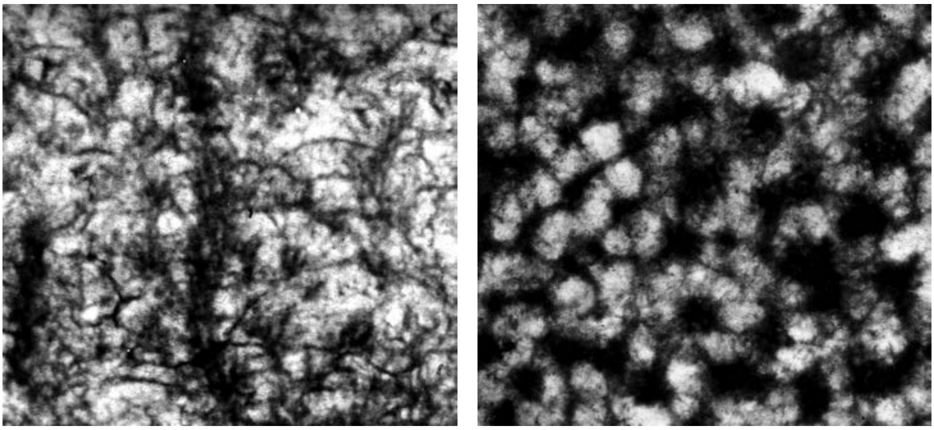
FIG. 426. Actinostromatidae (p. 770–771).



1a Pseudolabechia 1b



2a Desmostroma 2b



3a Vikingia 3b

FIG. 427. Pseudolabechiidae (p. 774–776).

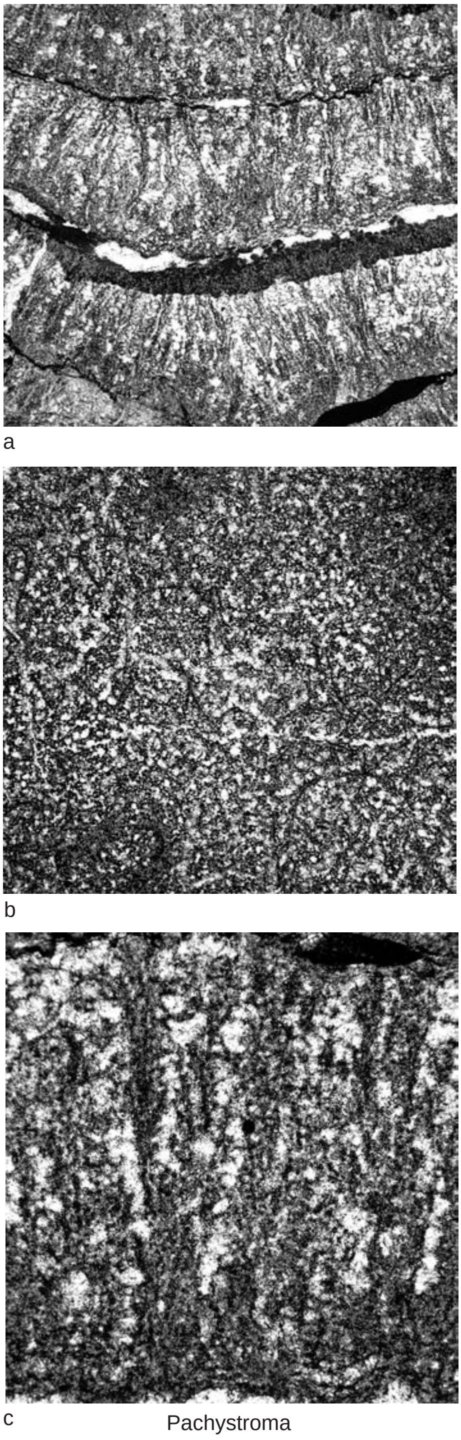


Fig. 428. Pseudolabechiidae (p. 775).

in columns or subcolumns respectively; pillars or micropillars diverge upward; areas between columns or subcolumns contain microlaminae and may contain few pillars; colliculi or microcolliculi occur in only columns or subcolumns; microstructure compact or microreticulate. *lower Silurian (Llandovery)–upper Silurian (Pridoli).*

Pseudolabechia Yabe & Sugiyama, 1930, p. 59 [**P. granulata*; OD]. Vertical skeletal elements with pillars diverging upward in columns, horizontal elements with colliculi in columns; microstructure compact. *middle Silurian (Wenlock)–upper Silurian (Ludlow):* Russia (Urals), Ukraine (Podolia), *Wenlock;* Estonia, Russia (Novaya Zemlya), Sweden (Gotland), *Ludlow.*——Fig. 427,*1a–b*. **P. granulata*; holotype, Hemse Beds, Ludlow, Gotland, Sweden, TUM 720, photomicrographs; *a*, longitudinal section; *b*, tangential section, ×10 (Yabe & Sugiyama, 1930, pl. XXII,*11–12*).

Desmostroma Bol'shakova, 1969, p. 28 [**D. columnatum* Bol'shakova, 1969, p. 30; OD] [=*Hexastylostroma* Dong, 1984, p. 71 (type, *H. neimongolense*, OD)]. Clinoreticular subcolumns constitute more than half volume of skeleton; intercolumnar structures acosmoreticular. [*Desmostroma* was first published as a new genus in 1969 (p. 30, pl. 5,*1a–b*), with type species *D. columnatum,* holotype PIN 2336/629. However, Bol'shakova (1973, p. 82) again published *Desmostroma* as a new genus, with type species *D. columnum,* labeled as a so-called holotype, PIN 2336/628; however the illustrated "holotype" was cited as PIN 2336/628 in the text but PIN 2336/548 is listed in the figure caption of plate 12, fig. 2a–b (on p. 111). Notably, a copy of Bol'shakova (1973) that was presented to B. D. Webby about 1993 included a handwritten amendment of the specimen number in her text on p. 83, with the 628 part of the number crossed out and replaced by 548, so it was consistent with the original number in her figure caption. However this designation of *D. columnum* as the type species of *Desmostroma* does not represent a valid type fixation.] *lower Silurian (Llandovery)–upper Silurian (Pridoli):* Sweden (Gotland), United States (Iowa), *Llandovery;* Kirghizstan (Tien Shan), Mongolia, Sweden (Gotland), Ukraine (Podolia), United States (Kentucky), *Wenlock;* China (Inner Mongolia), *upper Silurian;* Australia (New South Wales), China (Inner Mongolia), Sweden (Gotland), Ukraine (Podolia), *Ludlow;* Russia (Urals), Ukraine (Podolia), *Pridoli.*——Fig. 427,*2a–b*. **D. columnatum*; holotype, Mukshinsky Horizon, Wenlock, Podolia, Ukraine, PIN 2336/629; *a*, longitudinal section; *b*, tangential section, ×30 (Stock, 2012, photos courtesy of Heldur Nestor).

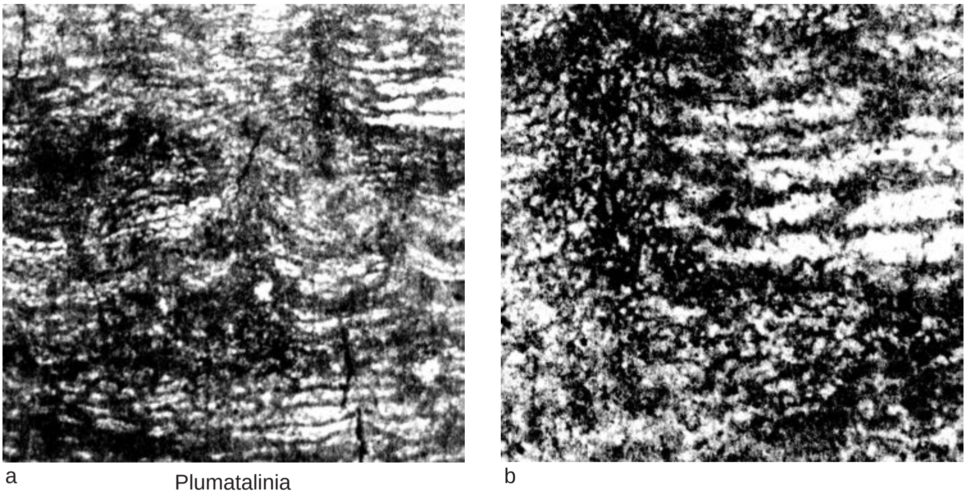


FIG. 429. Plumataliniidae (p. 776).

Pachystroma NICHOLSON & MURIE, 1878, p. 223 [**P. antiqua;* OD]. Skeleton latilaminate, irregular; clinoreticular subcolumns consist of fused micropillars and constitute about half volume of skeleton; microlaminae occur in intersubcolumnar space; thickened acosmoreticular structure developed at base of latilaminae. *lower Silurian (Llandovery)–middle Silurian (Wenlock):* Canada (Ontario), Estonia, United States (Michigan), *Llandovery;* Canada (Ontario, Quebec), United States (Kentucky), *Wenlock.*——FIG. 428*a–c.* **P. antiquum*; holotype, Niagara Limestone, Wenlock, Thorold, Ontario, Canada, NHM P6003; *a*, longitudinal section, note conspicuous latilamination; *b*, tangential section, ×10; *c*, longitudinal section, ×30 (Stock, 2012).

Vikingia BOGOYAVLENSKAYA 1969a, p. 19 [**Actinodictyon*? *vikingi* NESTOR, 1966a, p. 62; OD]. Longitudinal skeletal elements composed of clinoreticular subcolumns with distinct to fused micropillars and microcolliculi, and constitute less than half volume of skeleton; intersubcolumnar structures cyst plates. *lower*

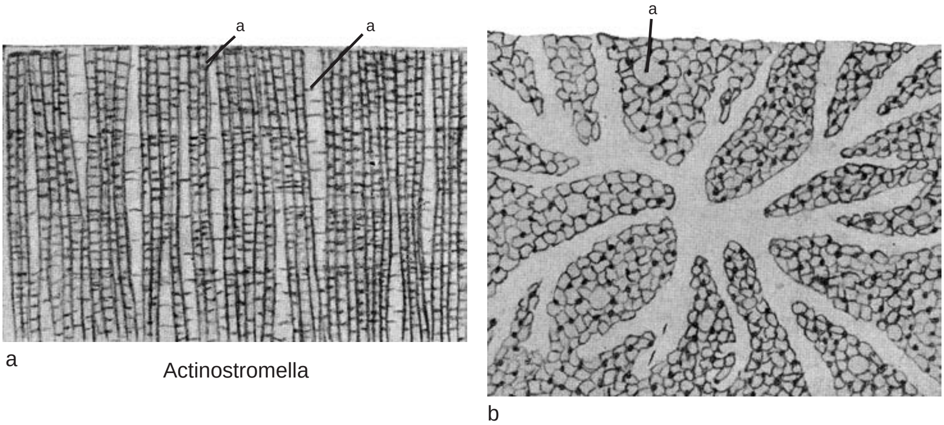


FIG. 430. Actinostromellidae (p. 776–777).

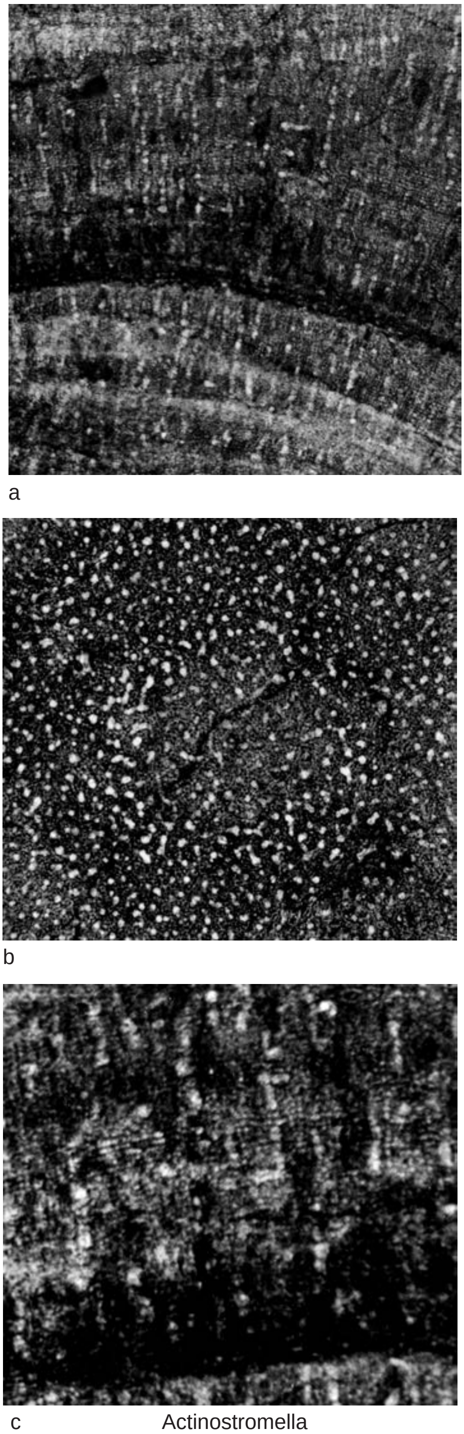


FIG. 431. Actinostromellidae (p. 776–777).

Silurian (Llandovery)–upper Silurian (Pridoli): Russia (Siberian Platform), Ukraine (Podolia), United States (Iowa), *Llandovery;* Estonia, Russia (Novaya Zemlya, Siberian Platform), Sweden (Gotland), Ukraine (Podolia), United States (Alaska), *Wenlock;* Ukraine (Podolia), *Pridoli.*——FIG. 427,*3a–b.* **V. vikingi* (NESTOR); holotype, Jaagarahu Stage, Wenlock, Estonia, IGTUT 114-51 (Co3146); *a*, longitudinal section; *b*, tangential section, ×30 (Stock, 2012, courtesy of Heldur Nestor).

Family PLUMATALINIIDAE Bogoyavlenskaya, 1969

[Plumataliniidae BOGOYAVLENSKAYA, 1969b, p. 17]

Skeleton contains micropillars and microcolliculi, clustered in subcolumns; areas between subcolumns contain cyst plates or microlaminae; microstructure of subcolumns acosmoreticular. *Upper Ordovician* (*Katian*).

Plumatalinia NESTOR, 1960, p. 225 [**P. ferax* NESTOR, 1960, p. 226; OD]. Skeleton of acosmoreticular subcolumns, and cyst plates or microlaminae. *Upper Ordovician (Katian):* Estonia.——FIG. 429*a–b.* **P. ferax*; holotype, Pirgu Stage, late Katian, IGTUT 111-1 (Co3001); *a*, longitudinal section, ×10; *b*, longitudinal section, enlargement of upper right portion of view *a,* ×25 (Stock, 2012, courtesy of Heldur Nestor).

Family ACTINOSTROMELLIDAE Nestor, 1966

[Actinostromellidae NESTOR, 1966a, p. 50] [=Pichiostromatidae BOGOYAVLENSKAYA, 1981, p. 31]

Skeleton a microreticulate mass pierced by elongate, vertical spaces. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian).*

Actinostromella BOEHNKE, 1915, p. 162 [**A. tubulata* BOEHNKE, 1915, p. 163; OD]. Micropillars long, connected by microcolliculi that may or may not align horizontally; longitudinal spaces autotubes. [The holotype, and only known specimen of *A. tubulata* BOEHNKE, 1915, is from Silurian glacial erratics in eastern Prussia (=Kaliningrad District). All type material was lost during the Second World War. Subsequent authors did not report *A. tubulata* from other localities, so no potential neotype specimens are available. Silurian-age glacial erratics in northern Poland, Germany, and Kaliningrad District, Russia most likely originated in Sweden (Gotland), Estonia, or the floor of the Baltic Sea. Therefore, *A. vaiverensis* NESTOR, 1966a, from western Estonia (Saarema) is used here as the

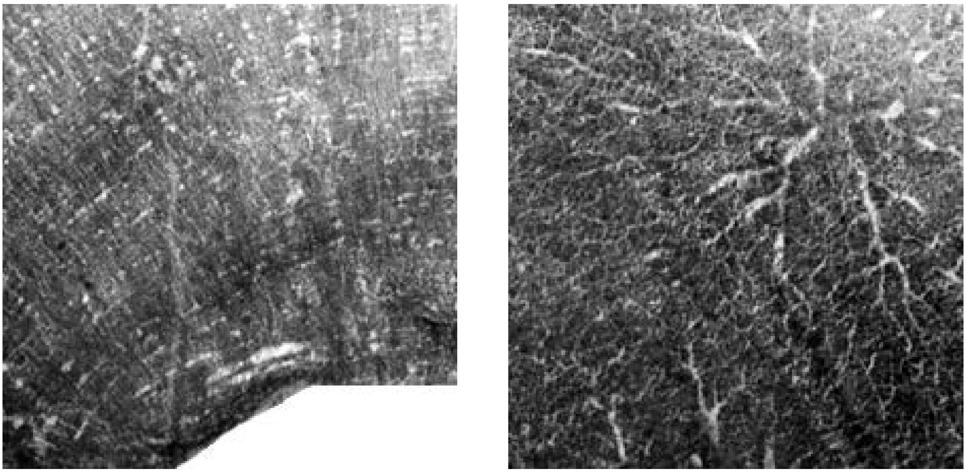


FIG. 432. Actinostromellidae (p. 777).

reference species.] *middle Silurian (Wenlock)–Lower Devonian (Lochkovian)*: Sweden (Gotland), *Wenlock;* Australia (New South Wales), China (Inner Mongolia), Sweden (Gotland), Ukraine (Podolia), *Ludlow;* Canada (Quebec), Estonia, United States (Alabama, New York), *Pridoli;* China (Inner Mongolia), *Lochkovian.*——FIG. 430*a–b*. **A. tubulata*; holotype, glacial erratic, Kaliningrad District, Russia, specimen no. unknown, micrographs, lower case *a* on photos indicates what BOEHNKE (1915) called zooidal tubes (=autotubes); *a*, longitudinal section; note some colliculi are horizontally aligned, but others are not; *b*, tangential section, magnification unknown, reproduced here at same size as original publication (Boehnke, 1915, fig. 6–7).——FIG. 431*a–c*. *A. vaiverensis* NESTOR; holotype, Kaugatuma stage, Pridoli, Saarema, Estonia, IGTUT 114-42 (Co3159); *a*, longitudinal section, note change in density of macrostructures associated with base of a latilamina about two-fifths above base of photomicrograph; *b,* tangential section, ×10; *c*, longitudinal section, note horizontal alignment of microcolliculi, ×20 (Stock, 2012, courtesy of Heldur Nestor).

Pichiostroma BOGOYAVLENSKAYA, 1972a, p. 28 [**P. pichiense*; OD]. Skeleton microreticulate, pierced by vertical slitlike spaces. *middle Silurian (Wenlock)–upper Silurian (Ludlow)*: United States (?Kentucky), *Wenlock;* Russia (Tuva), Ukraine (Podolia), *Ludlow.*——FIG. 432*a–b*. **P. pichiense*; holotype, Ludlow, Tuva, Russia, UGM 2808/3, *a*, longitudinal section; *b*, tangential section, ramifications of extensive astrorhizae may be responsible for slitlike spaces noted in longitudinal section, ×10 (Stock, 2012, courtesy of Heldur Nestor).

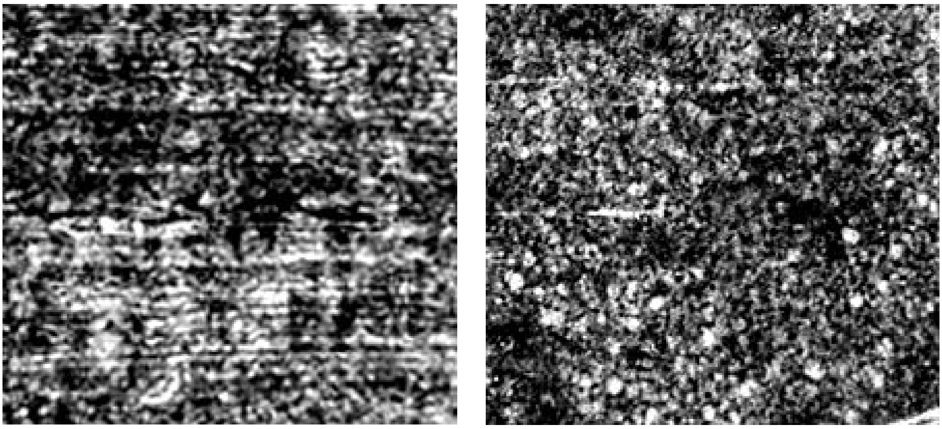
Family DENSASTROMATIDAE Bogoyavlenskaya, 1974

[Densastromatidae BOGOYAVLENSKAYA, 1974, p. 22]

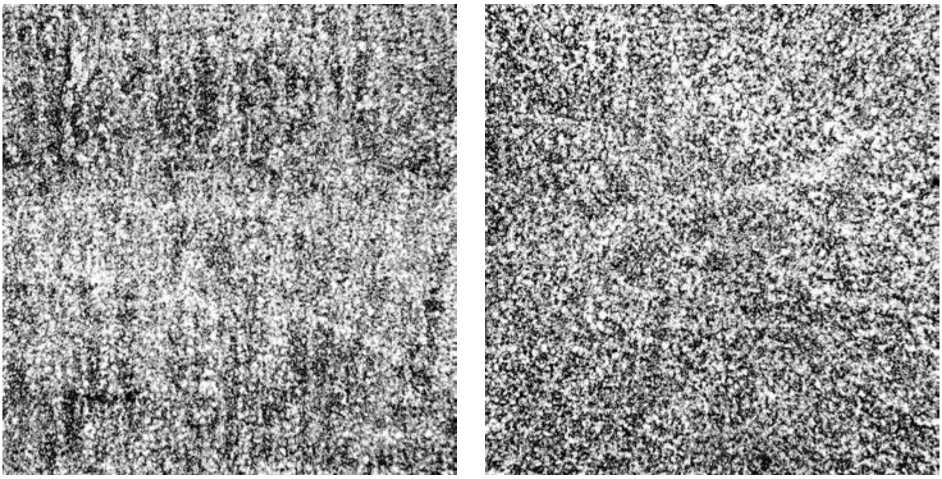
Skeleton microreticulate, uninterrupted by accessory spaces. *lower Silurian (Llandovery)–Lower Devonian (Lochkovian).*

Densastroma FLÜGEL, 1959, p. 196 [**Stromatopora astroites* ROSEN, 1867, p. 62; OD] [=*Pycnodictyon* MORI, 1970, p. 103 (type, *P. densum,* OD)]. Microcolliculi horizontally aligned, giving impression of microlaminae; micropillars short; forming orthoreticular pattern. *lower Silurian (Llandovery)–upper Silurian (Pridoli)*: Sweden (Gotland), United States (Iowa), *Llandovery;* Canada (Quebec), Estonia, Sweden (Gotland), Ukraine (Podolia), United States (Kentucky), *Wenlock;* China (Inner Mongolia), *upper Silurian;* Australia (New South Wales), Canada (Quebec), Estonia, Russia (Siberian Platform, Urals), Sweden (Gotland), Ukraine (Podolia), Uzbekistan, *Ludlow;* Canada (Quebec), Estonia, Russia (Urals), Ukraine (Podolia), *Pridoli.*——FIG. 433,*1a–b*. **D. astroites* (ROSEN); lectotype, Ludlow, Saarema, Estonia, IGTUT 115-1 (Co3181); *a*, longitudinal section; *b*, tangential section, ×30 (Stock, 2012, courtesy of Heldur Nestor).

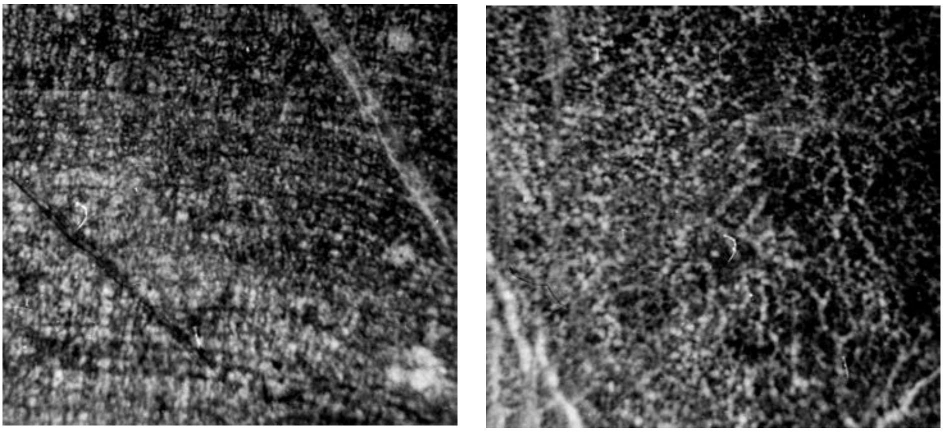
Acosmostroma STOCK in STOCK & BURRY-STOCK, 1998, p. 195 [**A. ataxium*; OD]. Skeleton acosmoreticular, to which micropillars added in some species. *upper Silurian (Pridoli)*: United States (New York, Tennessee, Virginia).——FIG. 433,*2a–b*. **A. ataxium*; holotype, Glasco Member, Rondout Formation, Alligerville, New



Densastroma



Acosmostroma



Araneosustroma

FIG. 433. Densastromatidae (p. 777–779).

York, USNM 248115; *a*, longitudinal section; *b*, tangential section, ×30 (Stock, 2012).

Araneosustroma Lessovaya, 1970, p. 80 [**A. fistulosum* Lessovaya, 1970, p. 81; OD] [=*Petschorostroma* Bogoyavlenskaya, 1983, p. 84 (type, *P. kozhmiense,* OD)]. Microreticulate structure orthoreticular to acosmoreticular, in some species combined with microlaminae; microcolliculi horizontally aligned at some levels, not aligned at other levels; in some species, micropillars clustered into indistinct, narrow subcolumns, giving impression of closely packed microreticulate pillars. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian)*: Estonia, Russia (Novaya Zemlya), Sweden (Gotland), Ukraine (Podolia), *Wenlock;* Estonia, Russia (Novaya Zemlya, Urals), Sweden (Gotland), Ukraine (Podolia), *Ludlow;* Ukraine (Podolia), *Pridoli;* Uzbekistan, *Lochkovian.*——Fig. 433,*3a–b.* **A. fistulosum*; holotype, Bursykhirman Horizon, Lochkovian, Uzbekistan, GMU 9994-6/149; *a*, longitudinal section; *b*, tangential section, ×20 (Stock, 2012, courtesy of Heldur Nestor).

STROMATOPORELLIDA, STROMATOPORIDA, SYRINGOSTROMATIDA, AMPHIPORIDA, AND GENERA WITH UNCERTAIN AFFINITIES: SYSTEMATIC DESCRIPTIONS

COLIN W. STEARN

Order STROMATOPORELLIDA Stearn, 1980

[Stromatoporellida STEARN, 1980, p. 891]

Stromatoporoids with extensive, thick, prominent laminae, marked by an axial zone or zones (light or dark, ordinicellular, cellular, or tubulate) and short, generally simple pillars confined to an interlaminar space. *Silurian (Pridoli)–Upper Devonian (Famennian).*

Family STROMATOPORELLIDAE Lecompte, 1951

[Stromatoporellidae LECOMPTE, 1951 in 1951–1952, p. 152] [=Simplexodictyidae LESSOVAJA, 1972, p. 47; =Stictostromatidae KHALFINA & YAVORSKY, 1973, p. 26 [148]; =Diplostromatidae STEARN, 1980, p. 890; =Clathrocoilonidae BOGOYAVLENSKAYA, 1984, p. 73]

Genera of stromatoporellids with short pillars, not superposed from one interlaminar space to another. *Silurian (Wenlock)–Devonian (Frasnian, ?upper Famennian).*

Stromatoporella NICHOLSON, 1886a, p. 92 [**Stromatopora granulata* NICHOLSON, 1873, p. 94; OD; =*Stromatopora (Coenostroma?) granulata* NICHOLSON & MURIE, 1878, p. 218–219, pl. 1; =*Stromatoporella granulata* NICHOLSON, 1886a, p. 93; neotype, NHM P6021 (Nicholson No. 329), MELVILLE, 1982, p. 126] [=*Stictostromella* GALLOWAY & ST. JEAN in FRITZ & WAINES, 1956, p. 92 (no type specified, but *Stictostroma eriense* PARKS, 1936, p. 81, implied), genus proposal withdrawn, p. 126; =*Pseudostictostroma* FLEROVA, 1969, p. 26 (type, *P. mitriformis,* OD); =?*Cancellatodictyon* KHALFINA & YAVORSKY, 1971, p. 119 (type, *Stromatoporella granulata sensu* YAVORSKY, 1951, p. 14, SD KHALFINA & YAVORSKY, 1971, p. 119); =*Pseudostromatoporella* KAŹMIERCZAK, 1971, p. 76 (type, *Stictostroma huronense* PARKS, 1936, p. 83, OD)]. Extensive, thick laminae and short pillars confined to interlaminar space, not superposed, many formed by upward inflection of laminae into cones (ring pillars), others simple, spool-shaped posts; microstructure of laminae ordinicellular but appearing in various states of preservation as transversely porous, tripartite, cellular, tubulate, or fibrous. Pillars cellular to fibrous. [The wide range of microstructures shown by the laminae may be partially accounted for by diagenesis but is likely also to be influenced by original variation. Controversy over the definition of the genus has focused on the correlation, or lack of it, between the ring pillars and the microstructures. Summaries of these discussions can be found in the work of ST. JEAN (1962, 1977), STEARN (1966), KAŹMIERCZAK (1971), and MISTIAEN (1985).] *Lower Devonian (Pragian)–Upper Devonian (Frasnian)*: Australia (Victoria), Czech Republic (Bohemia), *Pragian;* Afghanistan, Australia (Queensland), Canada (Arctic Island, Ontario), Russia (Salair), USA (Kentucky), *Emsian–Eifelian;* Belgium, Canada (Ontario, Manitoba), China (Sichuan), Germany (Eifel), Russia (Altai-Salair, Kuznetsk Basin), Spain (Calabria), USA (Indiana, Kentucky), *Eifelian;* Canada (Ontario), Russia (Kuznetsk Basin, Tyrgan), USA (Michigan), Ukraine, *Givetian;* Belgium (Ardennes), Kazakhstan, Poland, *Frasnian;* England (Devon), Germany (Büchel), Mongolia, Russia (Kuznetsk Basin, Urals), USA (Missouri, Indiana, Kentucky, Michigan), *Middle Devonian.*——FIG. 434*a–d.* **S. granulata* (NICHOLSON), Hamilton Formation, Arkona, Ontario, holotype, NHM P6021; *a,* longitudinal section, Nicholson slide 329b, ×10; *b,* tangential section showing ring pillars, Nicholson slide 329, ×10; *c,* tangential section, Nicholson slide 329a, showing cellular nature of pillars, ×70; *d,* longitudinal section, Nicholson slide 329c, showing ordinicellular laminae, ×60 (Stearn, 2011b).——FIG. 434*e. S. perannulata* GALLOWAY & ST. JEAN, Blue Fiord Formation, Ellesmere Island, arctic Canada, GSC no. 108175, tangential section showing ring pillars, ×10 (Prosh & Stearn, 1996).

Clathrocoilona YAVORSKY, 1931, p. 1394 [**C. abeona*; OD; holotype, CNIGR 3338/8a,b (KOSAREVA, 1976)]. Laminae extensive, thick (of thickness comparable to gallery height) of tripartite, ordinicellular, microreticulate or tubulate microstructure. Pillars postlike, commonly spool shaped, confined to interlaminar spaces, not superposed, compact or obscurely cellular. Commonly irregular, incrusting in growth, with algal interlayers. [The laminae may appear to be stranded, showing less opaque zones. Several layers of cellules in the laminae may give the appearance of microreticulation. In tangential section, the thick skeletal material may appear to be tubulate (described as felted by KOSAREVA, 1976). The genus has been confused with *Synthetostroma,* but in this genus the pillars are well superposed.] *Lower Devonian (?Emsian), Middle Devonian (Eifelian)–Upper Devonian (Frasnian)*: Austria (Carnic Alps), Canada (Arctic Island), Russia (northeastern Siberia, Salair), *?Emsian;* Belgium (Ardennes), Canada (Arctic Island, Manitoba), Central Asia (Altai), Germany (Eifel), Russia

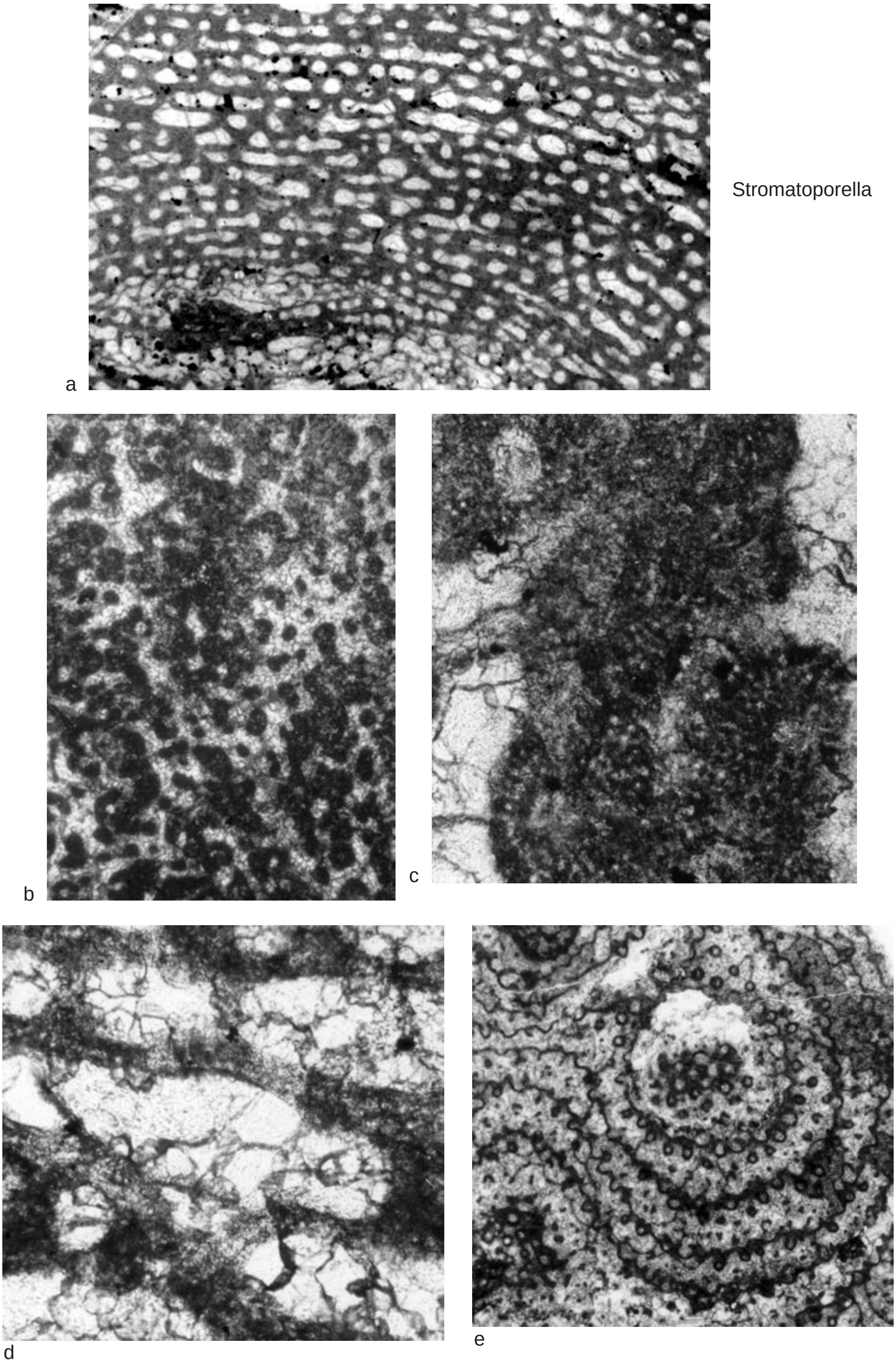


FIG. 434. Stromatoporellidae (p. 781).

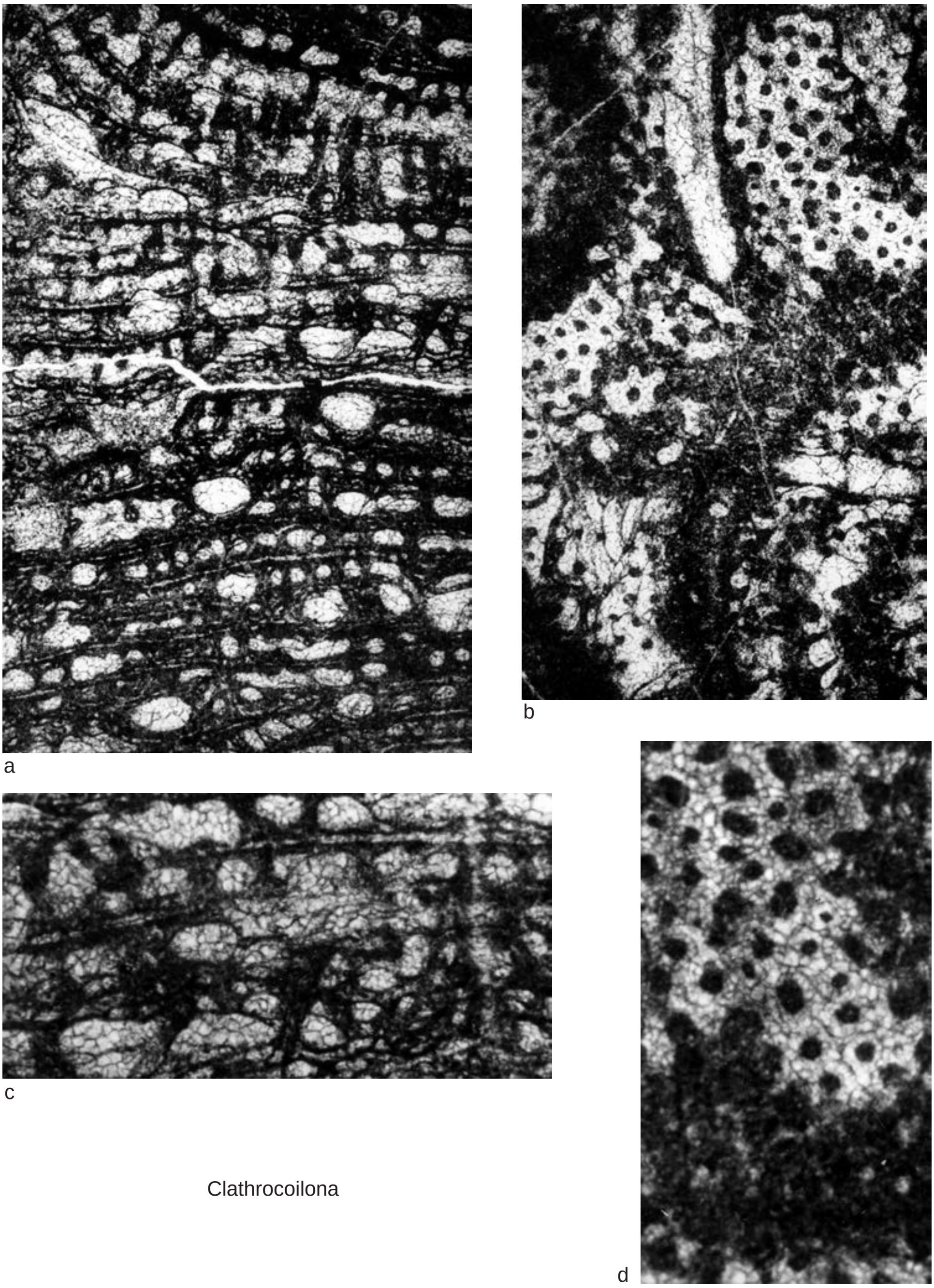


FIG. 435. Stromatoporellidae (p. 781–784).

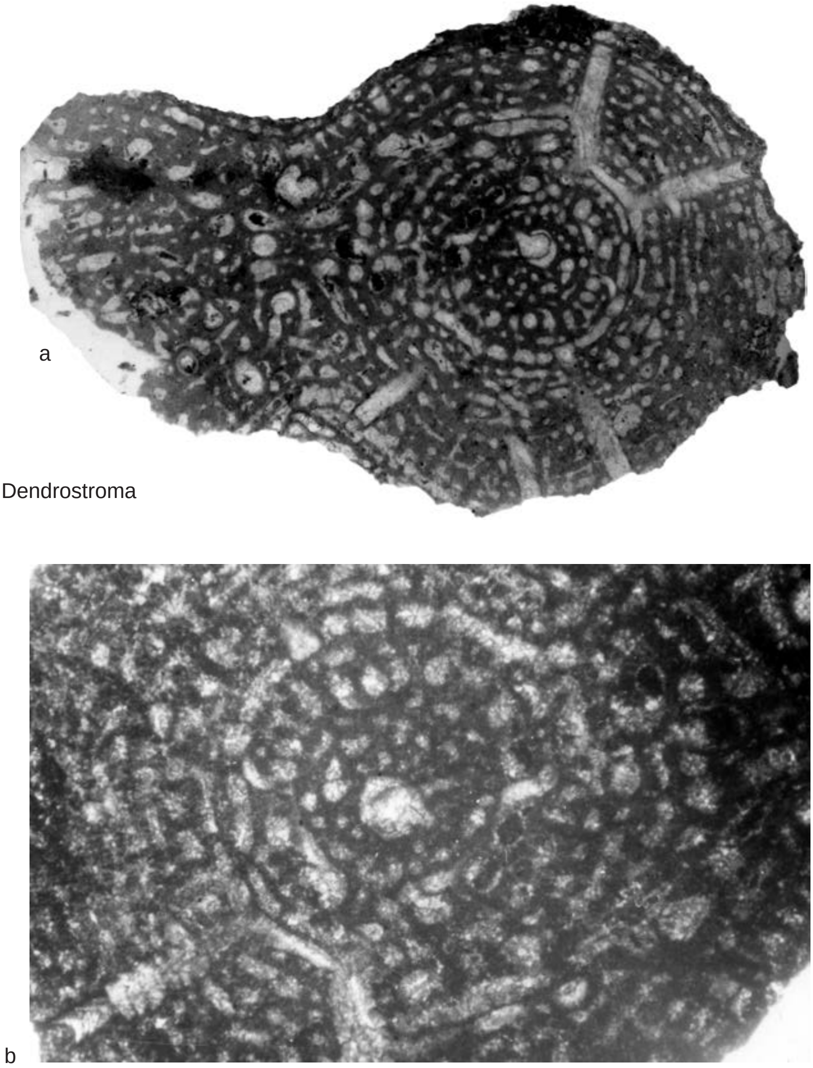


FIG. 436. Stromatoporellidae (p. 784–785).

(northeastern Siberia, Salair), *Eifelian;* Belgium (Ardennes), Canada (northern Alberta, Manitoba), Czech Republic (Moravia), France (Boulonnais), Iran (central), USA (Indiana, Michigan), *Givetian;* Australia (Queensland), China (Guangxi, Sichuan), Czech Republic (Moravia), Germany (Eifel), Russia (Kuznetsk Basin, northeastern Siberia, Salair), *Middle Devonian;* Australia (Canning Basin), Belgium (Ardennes), Canada (Alberta, Manitoba), Czech Republic (Moravia), France (Boulonnais), Russia (Russian platform, Kuznetsk Basin), USA (Iowa), *Frasnian.*——FIG. 435*a–d.* **C. abeona*, Middle Devonian, Kuznetsk Basin, Russia, holotype, CNIGR 3338/8; *a*, longitudinal section, ×10; *b*, tangential section, ×10; *c,* longitudinal section showing thick, tripartite laminae, ×25; *d*, tangential section showing round pillars, ×25 (Stearn, 2011b).

Dendrostroma LECOMPTE, 1952 in 1951–1952, p. 320–321 [**Idiostroma oculatum* NICHOLSON, 1886a, p. 101; OD; holotype, NHM P6073 (Nicholson No. 403)]. Dendroid skeleton with axial tube; laminae distinct, thick, extensive, compact to fibrous, commonly obscurely tripartite with axial dark or light zone; pillars postlike, confined to interlaminar spaces, not superposed, compact to fibrous. *Lower Devonian (Pragian)–Upper Devonian (Frasnian, ?upper Famennian)*: Australia (?Victoria), *Pragian;* Canada (Manitoba), Czech Republic, France (Boulonnais), Germany (Eifel), Russia

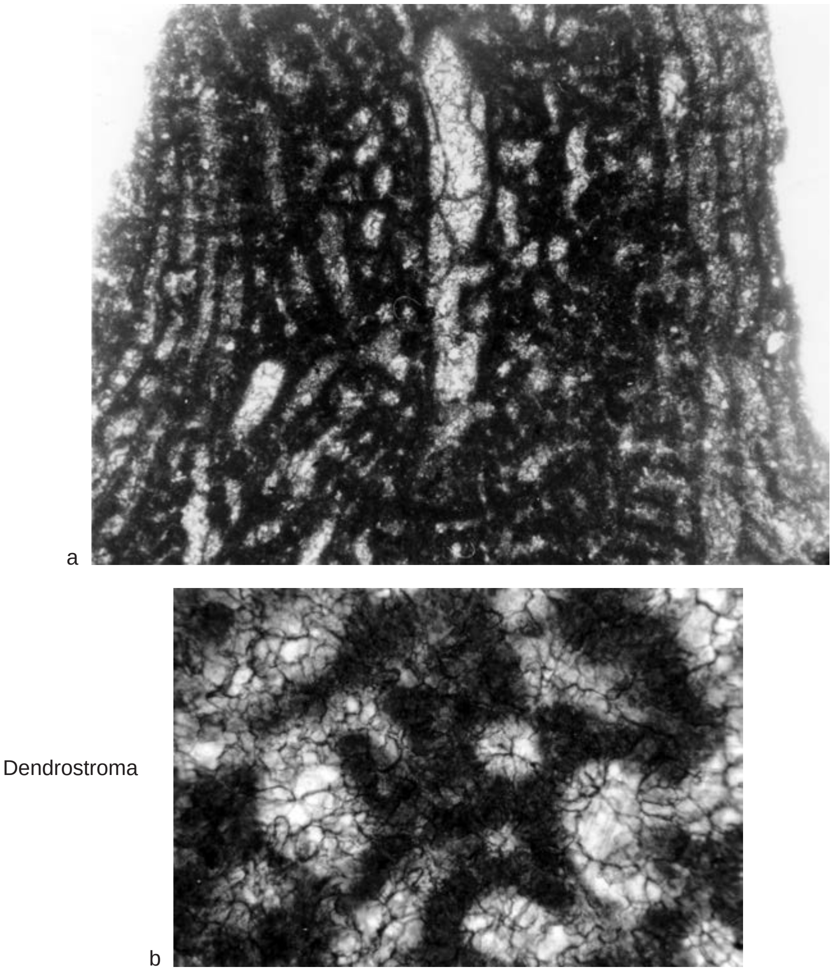


FIG. 437. Stromatoporellidae (p. 784–785).

(northeastern Siberia), USA (Michigan), *Givetian;* Germany (Eifel), India (Himalaya), Russia (Urals), Vietnam, *Middle Devonian;* Australia (Canning Basin, Carnarvon Basin), Czech Republic, Iran (Kerman), Russia (Kuznetsk Basin), *Frasnian;* ?Kazakhstan, Russia (?Donetsk Basin), *?upper Famennian.*——FIG. 436*a–b*. **D. oculatum* (NICHOLSON), Middle Devonian, Büchel, Germany, holotype, NHM P6073; *a,* complete transverse section of dendroid skeleton showing central and radiating canals and continuous laminae, ×6; *b*, transverse section of columnar skeleton showing short pillars, ×10 (Stearn, 2011b).——FIG. 437*a–b*. **D. oculatum* (NICHOLSON), Middle Devonian, Büchel, Germany, holotype, NHM P6073; *a*, longitudinal axial section showing axial canal with tabulae, ×10; *b*, tangential section showing fibrous microstructure, ×50 (Stearn, 2011b).

Simplexodictyon BOGOYAVLENSKAYA, 1965b, p. 110 [**Clathrodictyon regulare* var. nov. YAVORSKY, 1929, p. 83; OD; CNIGR 2595/30(6); =*C. regulare podolica* YAVORSKY, 1955, p. 43; see STEARN, 1991, for full discussion of the type. Although some authors have attributed the varietal name *podolica* to YAVORSKY, 1929, it was not formally proposed until 1955] [=*Diplostroma* NESTOR, 1966a, p. 27–28 (type, *Clathrodictyon pseudobilaminatum* KHALFINA, 1961b, p. 47); =*Nuratadictyon* LESSOVAJA, 1972, p. 48 (type, *N. duplexolaminum,* OD)]. Laminae extensive, composed of two compact layers separated (in the same skeleton) by either or all of 1) spar cement, 2) sediment, 3) epibionts, 4) a line of cellules; or fused into a single layer. Pillars compact, simple, postlike, commonly incomplete or oblique. *Silurian (Wenlock)–Middle Devonian (Eifelian):* Estonia (Saaremaa), Russia (Moiero River, Siberian

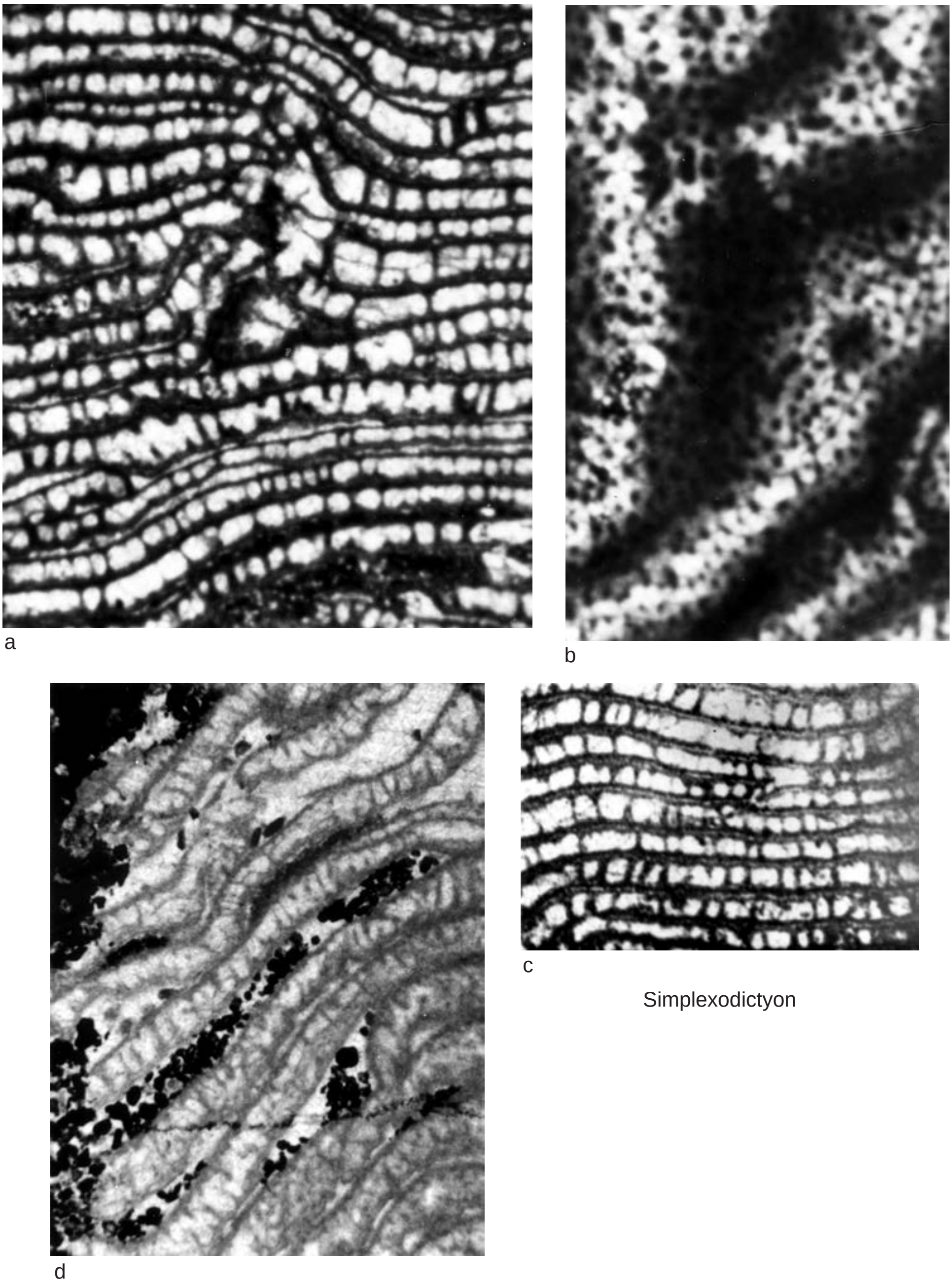


FIG. 438. Stromatoporellidae (p. 785–787).

platform), USA (Kentucky), *Wenlock;* Australia (Queensland), Central Asia (Tien Shan), Estonia, Russia (Salair, Altai), Ukraine (Podolia), *Ludlow;* Australia (Victoria, northern Queensland), *Emsian;* Canada (Arctic Island, Yukon), *Eifelian.*——FIG. 438*a–c.* **S. podolicum* (YAVORSKY), holotype, Ludlow, Smotrich River, Ukraine; *a*, longitudinal section, ×10; *b*, topotype, tangential section, ×10 (Stearn, 2011b); *c,* longitudinal section, ×10 (Yavorsky, 1929).——FIG. 438*d. S. vermiformis* (STEARN & MEHROTRA, 1970), Eifelian, Blue Fiord Formation, Cameron Island, Canada, GSC

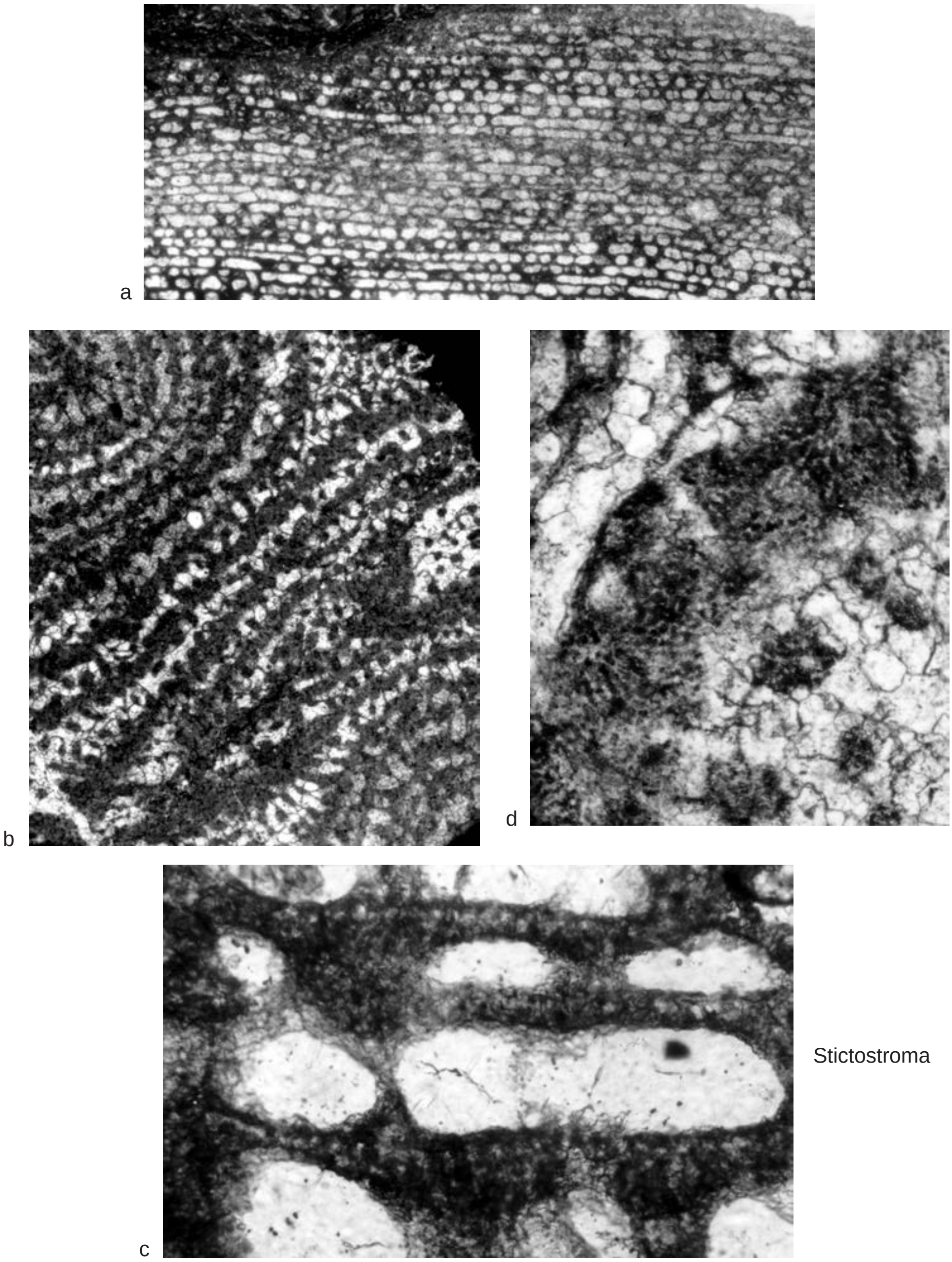


FIG. 439. Stromatoporellidae (p. 787–789).

116284, longitudinal section, showing separated laminae, ×10 (Stearn, 2011b).

Stictostroma PARKS, 1936, p. 78 [**Stromatopora mammillata* NICHOLSON, 1873, p. 94; OD; *non* SCHMIDT, 1858; holotype, ROM 9360; =*Stromatopora mamilliferum* GALLOWAY & ST. JEAN, 1957, p. 125; =*Stictostroma gorriense* STEARN, 1995a, p. 26, designated the type in a ruling by ICZN (1996). The type specimen that PARKS (1936) designated as *Stromatopora mammillata* NICHOLSON, 1873, and renamed *S. mamilliferum* GALLOWAY & ST. JEAN by GALLOWAY and ST. JEAN (1957) to avoid homonymy,

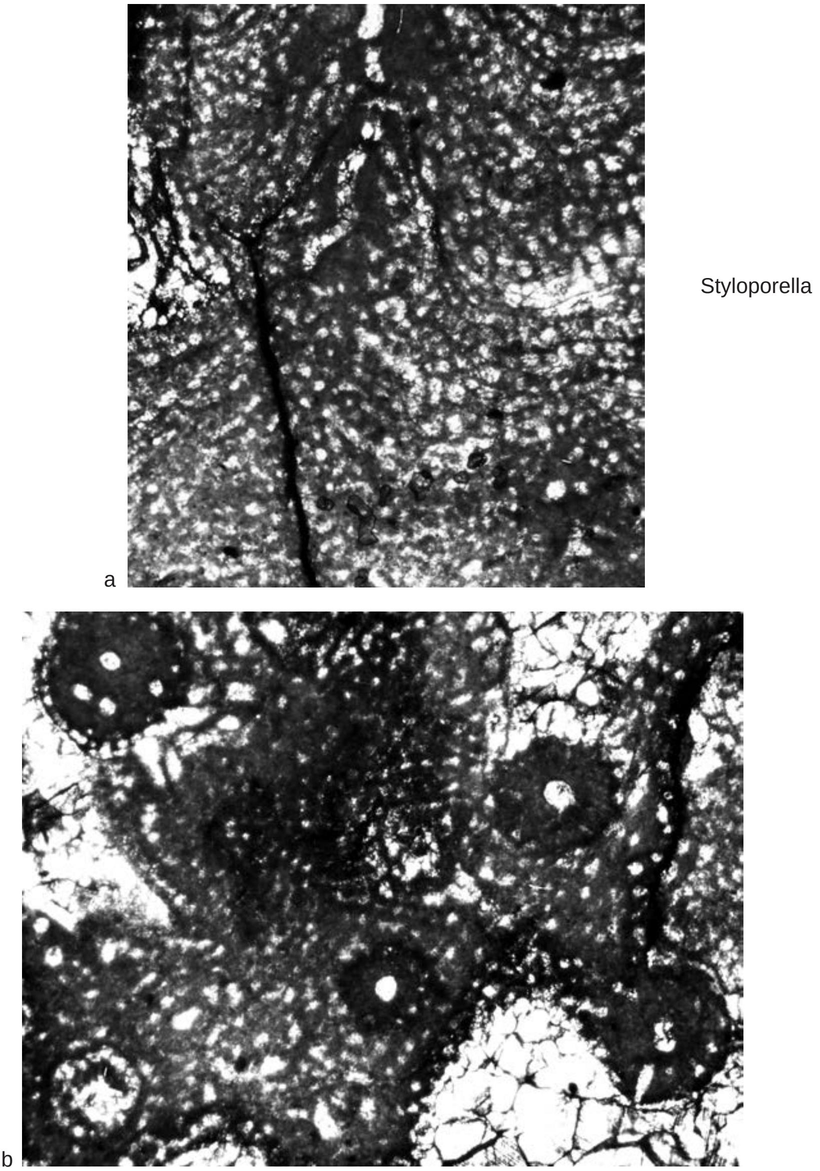


FIG. 440. Stromatoporellidae (p. 789).

had unknown internal structure, because NICHOLSON's (1873) types were not sectioned. PARKS's (1936) descriptions were based on specimens from Gorrie, Ontario, recognized as holotypes by ICZN Opinion 1843, Case 2109 (1996), because NICHOLSON's (1873) specimens, when sectioned, were indeterminate in diagnostic internal structure]. Laminae thick, extensive, ordinicellular in microstructure but commonly appearing transversely porous, tripartite, fibrous, rarely tubulate; pillars confined to interlaminar spaces, not systematically superposed, postlike, only rarely ring pillars, cellular where best preserved, commonly fibrous. *Lower Devonian (Pragian)–Upper Devonian (Frasnian)*: Czech Republic (Bohemia), *Pragian;* Australia (Victoria), Canada (Arctic Island, Northwest Territories, Ontario), New Zealand (Reefton), *Emsian;* Australia (Queensland), Belgium (Ardennes), Canada (Manitoba, Ontario), Czech Republic, western Germany (western), Russia (Kuznetsk Basin, Salair), USA (Michigan, Ohio), *Eifelian;* Afghanistan, Belgium (Ardennes), Canada (British Columbia, Ontario), France (Boulonnais), Germany (Sauerland), Russia (Kuznetsk Basin), USA (Missouri), *Givetian;* Canada (northern Ontario), China (Guangxi), Russia (Omolov, Kuznetsk Basin, Urals), USA (Missouri), Vietnam, *Middle Devonian*; Belgium (Ardennes), Canada (Alberta), China (Xizang), France (Boulonnais), Iran (Kerman), Russia (Kuznetsk Basin), USA (Iowa), *Frasnian.*——FIG. 439*a–d.* **S. gorriense* STEARN, holotype, ROM 9360, Bois Blanc Formation, Gorrie, Ontario; *a*, longitudinal section 2149, ×10; *b*, tangential section 2152, ×10; *c*, longitudinal section 2151, showing microstructure of laminae, ×55; *d*, tangential section 2150, showing microstructure of pillars, ×55 (Stearn, 2011b).

Styloporella KHALFINA, 1956, p. 62 (as subgenus of *Stromatoporella*, elevated to generic rank by KHALFINA, 1961d, p. 338) [**Stromatoporella (Styloporella) grata* KHALFINA, 1956, p. 62; OD; holotype, SOAN 402/67b]. Similar to *Stromatoporella* but with structural elements thickened into astrorhizal columns with prominent axial canals where laminae inflected upward. *Upper Devonian (Frasnian)*: Russia (Kuznetsk Basin, eastern Siberia).——FIG. 440*a–b.* **S. grata*, holotype, SOAN 402/67b, Kuznetsk Basin; *a*, longitudinal section showing column with axial canal, ×10; *b*, tangential section showing cross sections of columns, ×10 (Stearn, 2011b).

Syringodictyon ST. JEAN, 1986, p. 1050 [**Stromatopora tuberculata* NICHOLSON, 1873, p. 92–93; OD; NHM P5627 (type specimen never illustrated in thin section)]. Laminae extensive, thick, inflected upward in invaginating cones into vertically extensive columns with narrow openings. Pillars formed by superposition of upward extensions of laminae, other pillars scarce. [The difference between *Syringodictyon* and *Tubuliporella* is in the size and nature of the vertical tubes formed by the upwardly inflected laminae—small and formed of invaginating cones in the former, and large and continuous in the latter—and in the absence of ring pillars between the columns in the former.] *Middle Devonian (lower Eifelian)*: Canada (southern Ontario).——FIG. 441*a–c.* **S. tuberculatum* (NICHOLSON), topotypes, Onondaga Formation, Empire Beach; *a*, longitudinal section showing columns of skeletal material, topotype, YPM222128; *b*, longitudinal section, showing inverted cones of laminae inflected into columns, topotype, YPM222129; *c*, tangential section showing cross sections of columns and lack of other pillars, topotype, YPM222128, ×10 (St. Jean, 1986).

Tubuliporella KHALFINA, 1968a, p. 150 [**T. lecompti*; OD (as *T. lecomti*, *lapsus calami)*]. Similar to *Stromatoporella,* but some ring pillars superposed, forming vertical open channels crossed by thin dissepiments. *Lower Devonian–Middle Devonian (Eifelian)*: Russia (Altai), *Lower Devonian;* Australia (Victoria), *Pragian;* Russia (Kuznetsk Basin, Altai, Salair), *Eifelian.*——FIG. 442*a–c.* **T. lecompti*, holotype, CSGM409/3a, Salair, Eifelian, Shandinskie Stage; *a,* longitudinal section, ×10; *b*, tangential section, ×10; *c,* tangential section through a mamelon, ×10 (Khalfina, 1968a).

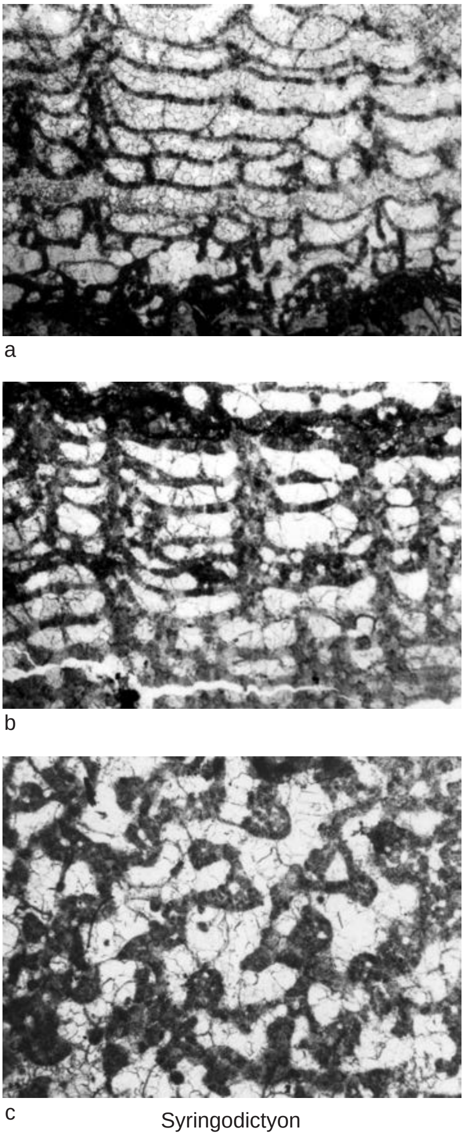


FIG. 441. Stromatoporellidae (p. 789).

Family TRUPETOSTROMATIDAE
Germovsek, 1954

[*nom. correct.* STEARN & others, 1999, p. 43 *pro* Trupetostromidae GERMOVSEK, 1954, p. 361] [=Hermatostromatidae NESTOR, 1964a, p. 13; =Synthetostromatidae KHROMYKH, 1969, p. 35; =Imponodictyidae KHALFINA & YAVORSKY, 1971, p. 119]

Stromatoporellids with superposed, postlike pillars or, rarely, pachysteles and

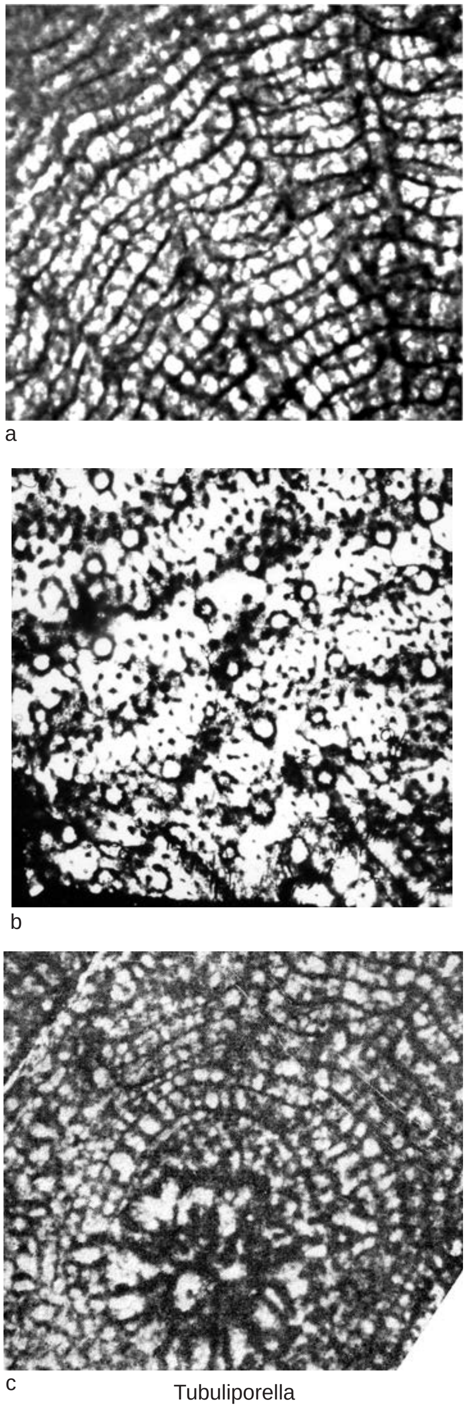


FIG. 442. Stromatoporellidae (p. 789).

tripartite or ordinicellular laminae forming a grid in longitudinal section. [Many of the genera of this family contain species that have compact-vacuolate microstructure and some that are cellular. Microstructure is therefore not considered diagnostic of the family.] *Silurian (Pridoli)–Upper Devonian (Famennian).*

Trupetostroma PARKS, 1936, p. 55 [**T. warreni*; OD; holotype, ROM 12197 (thin sections only), specimen DU677, referred to by PARKS as the type, is lost] [=*Flexiostroma* KHALFINA, 1961d, p. 345 (type, *F. flexuosum* KHALFINA, 1961d, p. 346, OD, see also STOCK, 1982, p. 666); =*?Imponodictyon* KHALFINA & YAVORSKY, 1971, p. 119 (type, *Stromatoporella loutouguini* var. *postera* KHALFINA, 1956, p. 60, OD)]. Laminae extensive, thick, typically ordinicellular but commonly showing a central clear zone or opaque axis, pierced by large pores joining the galleries above and below. Pillars short, expanded above and below at laminae, systematically superposed across successive laminae, forming grid with laminae; microstructure vacuolate, cellular, compact. *?Lower Devonian, Middle Devonian (Eifelian)–Upper Devonian (Famennian)*: China (Guangxi), *?Lower Devonian;* Australia (Broken River), China (Guangxi, Guizhou, Hunan, Yunnan), Czech Republic (Bohemia), Mongolia, Poland (Holy Cross), Russia (Kuznetsk Basin, Salair, South Urals), USA (Missouri), *Middle Devonian;* Canada (Arctic Island, Northwest Territories), China (Guangxi), Russia (Magadan), USA (Indiana), *Eifelian;* Belgium (Ardennes), Canada (Manitoba, Northwest Territories, northeastern British Columbia), China (Guangxi, Yunnan), Germany (Sauerland), Russia (Kuznetsk Basin, Salair, Urals), Vietnam, *Givetian;* Australia (Canning Basin), Belgium (Ardennes), Canada (Alberta, Manitoba, Saskatchewan), China (Guangxi, Guizhou), Russia (Kolymy, West pre-Urals), Vietnam, *Frasnian;* Kazakhstan, *Famennian;* China (Guangxi), Poland (Sudetes Mountains), *upper Famennian.*——FIG. 443*a–d*. **T. warreni,* holotype, ROM 12197, Presqu'ile Dolomite, Great Slave Lake, Canada; *a,* longitudinal section showing thin laminae and superposed pillars, ×10; *b*, tangential section showing large circular pores through cut laminae, ×10; *c,* longitudinal section showing compact vacuolate pillars and tripartite laminae, ×30; *d*, tangential section showing vacuolate pillars, round in cross section; a lamina is cut obliquely on right side, ×30 (Stearn, 2011b).

Hermatostroma NICHOLSON, 1886a, p. 105 [**H. schlueteri* NICHOLSON, 1886a, p. 105–106; OD; NICHOLSON, 1892, p. 215–219, holotype, NHM P5527] [=*Argostroma* YANG & DONG, 1979, p. 45 (type, *A. typicum*, OD); MISTIAEN (1985, p. 189–190) showed that *Argostroma* is a diagenetic phase of

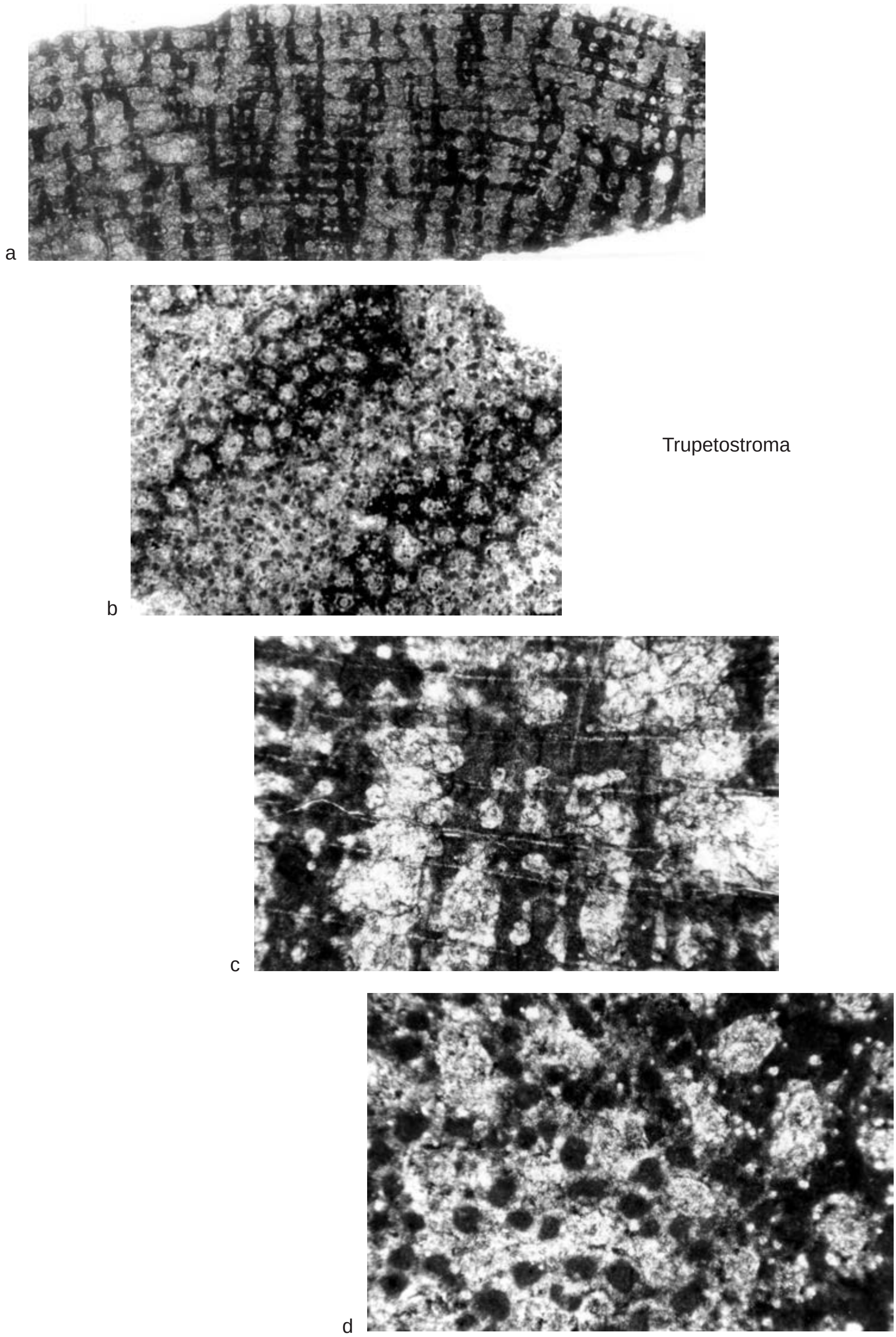


FIG. 443. Trupetostromatidae (p. 790).

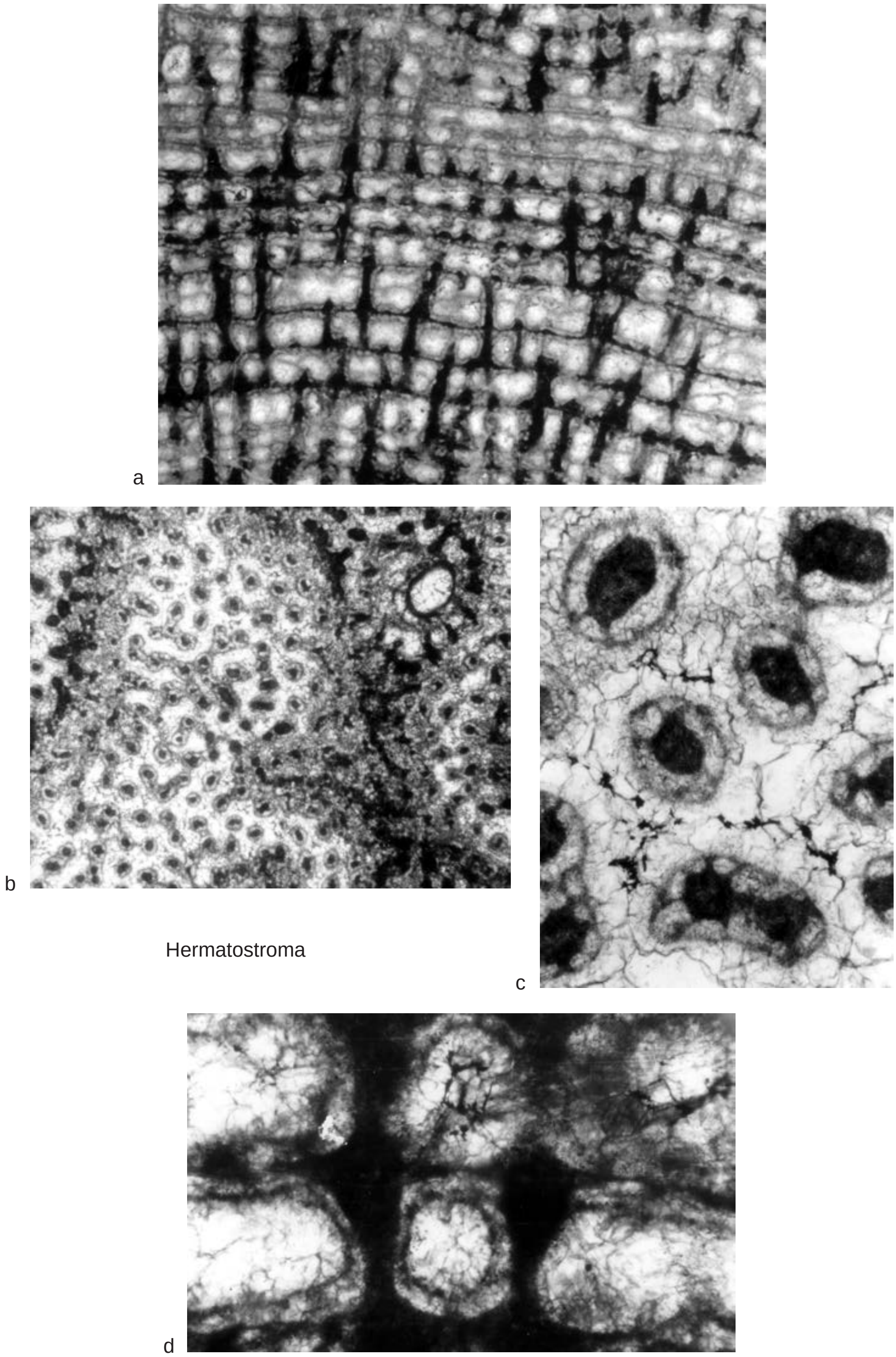


FIG. 444. Trupetostromatidae (p. 790–794).

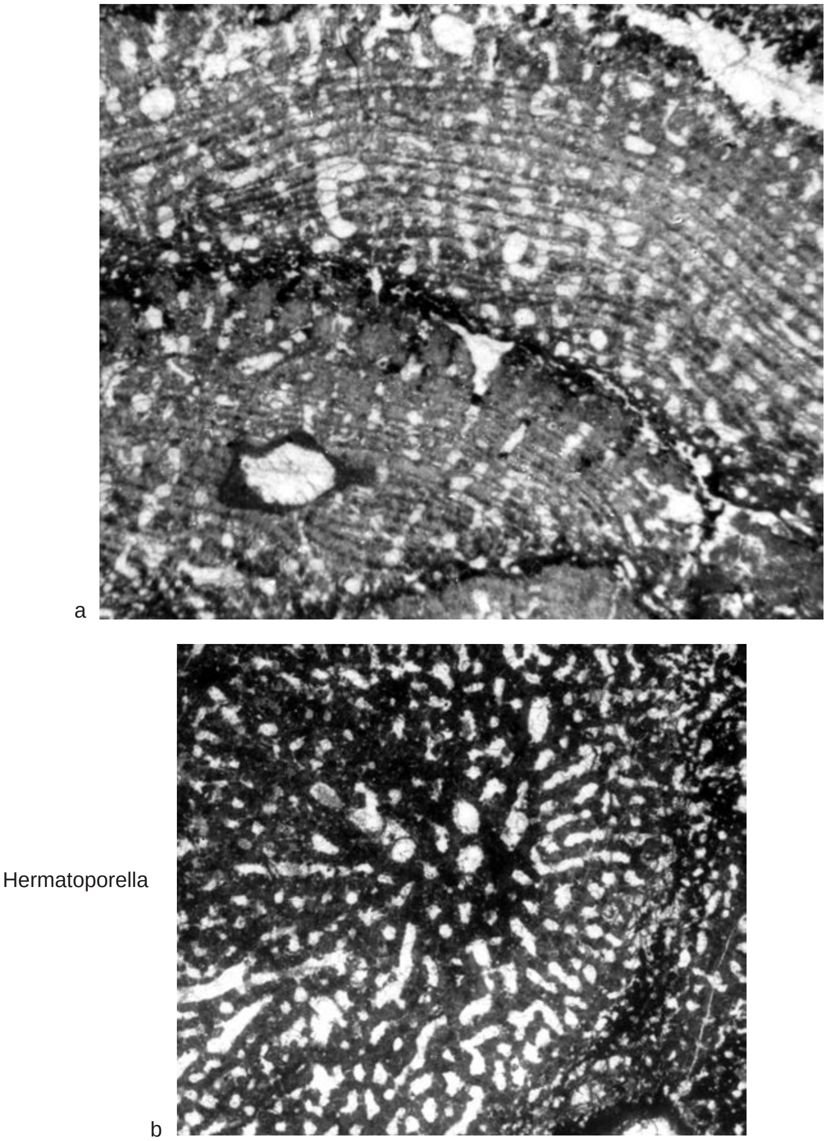


FIG. 445. Trupetostromatidae (p. 794–796).

Hermatostroma]. Laminae extensive, prominent, tripartite with central dark zone, or light zone and more opaque lateral zones, penetrated by large pores between the pillars; pillars spool shaped, confined to interlaminar spaces, regularly superposed in longitudinal section, subcircular in tangential section, surrounded by peripheral cyst plates or bordered by peripheral vesicles. Microstructure compact, vacuolate, cellular. [*Hermatostroma* may grade into *Trupetostroma* through forms with lines of vacuoles along the pillar edges.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian)*: Australia (Queensland), Russia (Kuznetsk Basin), *Eifelian;* Australia (Canning Basin, Queensland), Belgium (Ardennes), China (Guangxi, Guizhou, Yunnan), France (Boulonnais, Ancenis), Poland (Holy Cross Mountains), Thailand, *Givetian;* Czech Republic (Bohemia), England (Devon), Germany (Eifel), China (Guangxi, Sichuan, Yunnan), USA (Missouri), *Middle Devonian;* Australia (Canning Basin), Belgium (Ardennes), Canada (Alberta, Manitoba, Saskatchewan), China

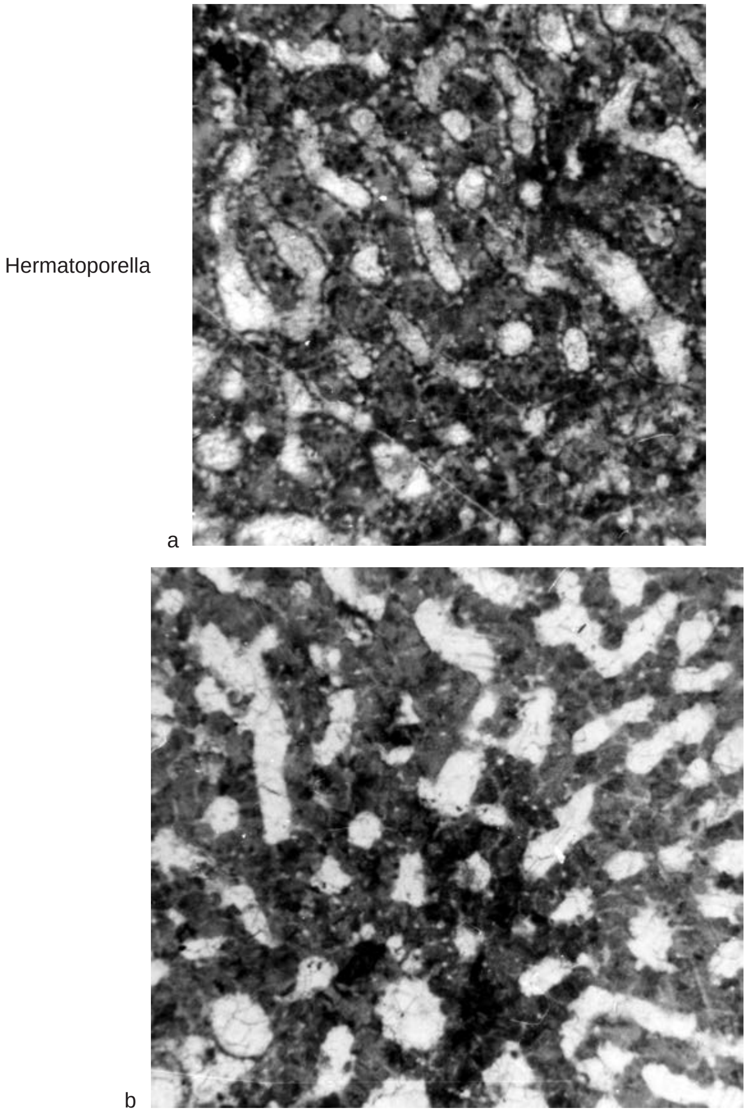


FIG. 446. Trupetostromatidae (p. 794–796).

(Sichuan, Yunnan), Czech Republic (Moravia), Germany, Poland (Holy Cross Mountains), Russia (northeastern Siberia), USA (Iowa), *Frasnian.*——FIG. 444*a–d.* **H. schlueteri*, holotype, NHM P5527, Middle Devonian, Hebborn, Paffrath District, Germany; *a*, longitudinal section, showing grid of pillars and laminae; *b*, tangential section, showing pillars, round in cross section, ×10; *c*, longitudinal section showing peripheral vesicles and compact pillars, ×50; *d,* tangential section, showing peripheral vesicles, ×50 (Stearn, 2011b).

Hermatoporella KHROMYKH, 1969, p. 34 [**Trupetostroma maillieuxi* LECOMPTE, 1952 in 1951–1952, p. 237–239; OD; holotype, IRScNB 5760a]. Irregular grid formed by pachysteles and microlaminae intersecting pachysteles, locally replaced by aligned dissepiments; pachysteles superposed systematically, with peripheral vacuoles in parts of type, in tangential section forming a labyrinthine network, rarely cut as isolated subcircular masses; microstructure compact, vacuolate, or cellular. *Middle Devonian (?Eifelian, Givetian)–Upper Devonian (Frasnian)*: Morocco, *?Eifelian;* Canada (Northwest Territories, northeastern British Columbia), Russia (Omolon, South Urals), Vietnam, *Givetian;* China (Guizhou), Russia (Salair), *Middle Devonian;* Australia

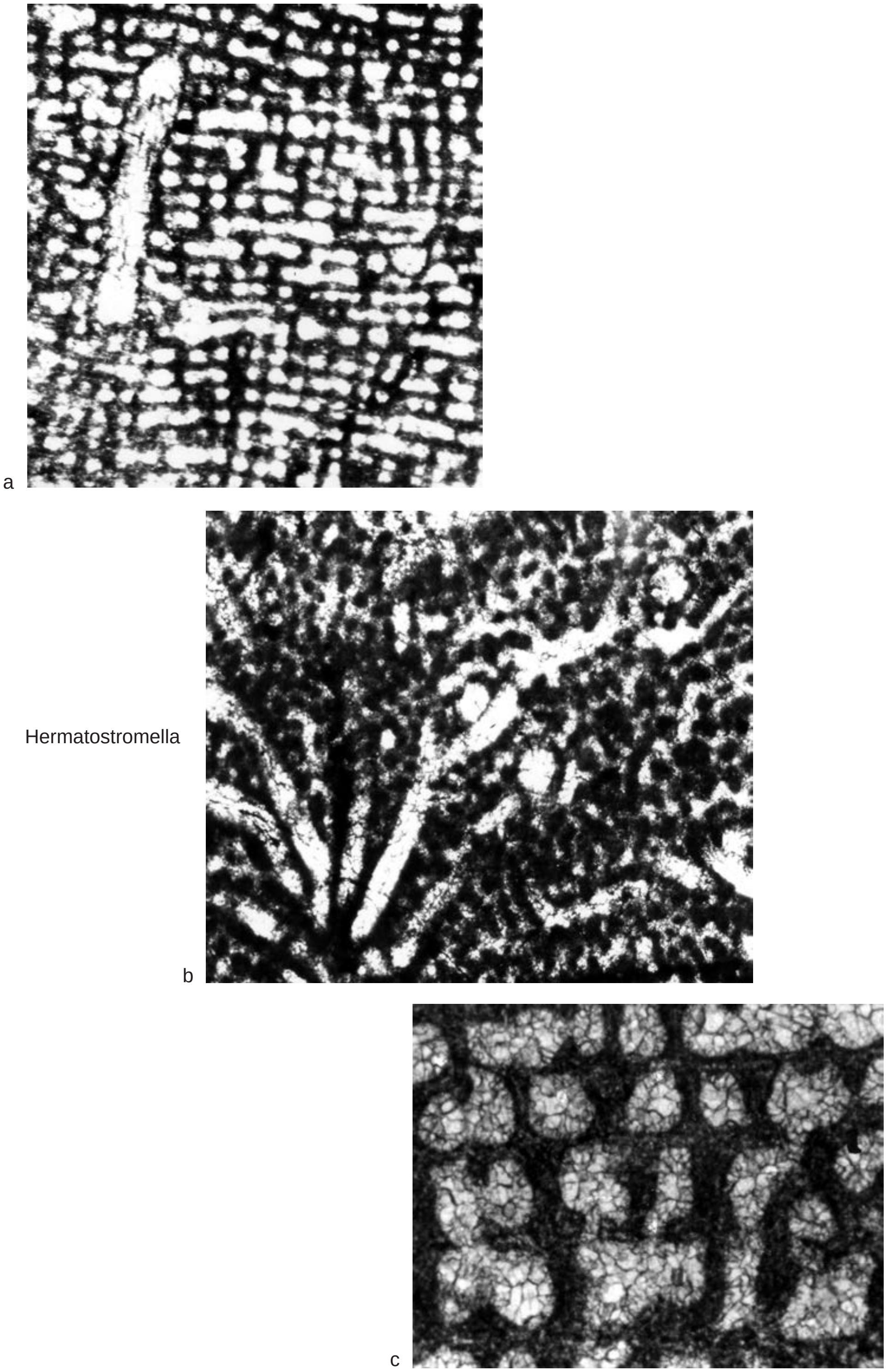


FIG. 447. Trupetostromatidae (p. 796–797).

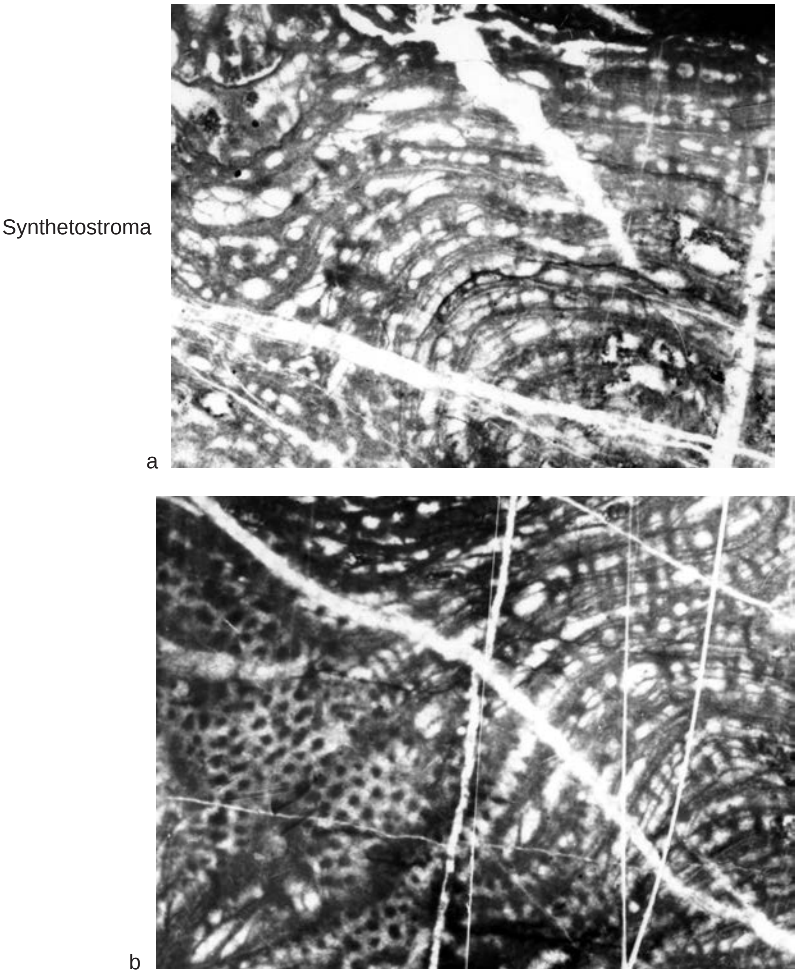


FIG. 448. Trupetostromatidae (p. 17).

(Canning Basin), Belgium (Ardennes), Canada (Alberta, Northwest Territories, Saskatchewan), China (Xinjiang), Czech Republic (Moravia), Iran (Kerman), Russia (North Urals, South Urals), USA (Iowa, Missouri), Vietnam, *Frasnian*.——FIG. 445*a–b*. **H. maillieuxi* (LECOMPTE), holotype, IRScNB 5760a, Fromelennes Assise, Frasnian, Senzeille, Belgium; *a*, longitudinal section showing pachysteles and microlaminae, ×10; *b*, tangential section showing pachysteles around an astrorhizal center, ×10 (Stearn, 2011b).——FIG. 446*a–b*. **H. maillieuxi* (LECOMPTE), holotype, IRScNB a 5760, Fromelennes Assise, Frasnian, Senzeille, Belgium; *a*, tangential section showing peripheral vacuoles at edges of pachysteles, ×25; *b*, tangential section showing vacuolate microstructure of pachysteles but lack of peripheral vacuoles, ×25 (Stearn, 2011b).

Hermatostromella KHALFINA, 1961a, p. 52 [**H. parasitica*; OD; holotype, CSGM 401/33] [=*Amnestostroma* BOGOYAVLENSKAYA, 1969b, p. 22 (type, *Syringostroma federovi* YAVORSKY, 1929, p. 109, OD; STEARN & others, 1999, p. 45); =*Gerronostromina* KHALFINA & YAVORSKY, 1971, p. 119 (type, *Gerronostroma kitatense* YAVORSKY, 1961, p. 12, OD; STEARN & others, 1999, p. 45)]. Laminae and pillars subequal in thickness forming grid; laminae extensive, locally with axial dark or light zone, or ordinicellular; pillars postlike, locally appearing continuous, locally superposed and interrupted by lighter central zone in laminae, mostly discrete and subcircular in tangential section; microstructure compact, vacuolate, rarely cellular. [The most extensive discussion of this genus is that of KHROMYKH (1974a) who emphasized as diagnostic characters the equal thickness of pillars and laminae, the dark or light central line in the laminae, the superposed pillars, and the cellular microstructure. *Amnestostroma* is intermediate between *Hermatostromella* and *Trupetostroma*; however, the features of the type species are basically those of *Hermatostromella* and therefore difficult to justify as a separate genus. See STEARN and others (1999, p. 45) for discussion.] *Silurian (Pridoli)–Lower Devonian (Emsian), Middle Devonian (?Givetian)*: Russia (eastern Siberia, Urals), *Pridoli;* Canada (Arctic Island), Central Asia (Tien Shan), Russia (Salair, Urals), *Lochkovian;* Australia (Victoria), *Pragian;* Australia (New South Wales), *Emsian;* Russia (eastern Siberia, Altai Sayan), Central Asia (Tien Shan), *Lower Devonian;* Queensland, *?Givetian.*——FIG. 447*a–b.* **H. parasitica*, holotype, CSGM 401/33a, Tom'chumyshskii Horizon, Lower Devonian, Salair, Russia; *a*, longitudinal section, ×10; *b*, tangential section, showing astrorhizal canals, ×10 (Stearn, 2011b).——FIG. 447c. *H. federovi* (YAVORSKY), type species of *Amnestostroma*, holotype, CNIGR 2595, showing cellular microstructure, ×25 (Stearn, 2011b).

Synthetostroma LECOMPTE, 1951 in 1951–1952, p. 193 [**S. actinostromoides* LECOMPTE, 1951 in 1951–1952, p. 194; OD; holotype, IRScNB7296]. Laminae extensive, continuous, composed of multiple microlaminae or imbricating dissepiments giving tangled appearance, commonly with central lighter zone or zones. Pillars postlike, confined to interlaminar spaces but systematically superposed. Microstructure compact. [The genus differs from *Clathrocoilona* with which it has been confused (NESTOR, 1966a; KAŹMIERCZAK, 1971; KOSAREVA, 1976) in having well-superposed pillars that appear to be continuous.] *Middle Devonian (Givetian)–Upper Devonian (Frasnian)*: Belgium (Ardennes), *Givetian;* Czech Republic, *Frasnian.*——FIG. 448*a–b.* **S. actinostromoides*, holotype, IRScNB7296a, Givetian, Surice, Belgium; *a*, longitudinal section showing multiple-stranded laminae and superposed pillars, ×10; *b*, partly tangential and partly longitudinal section showing pillars round in cross section, ×10 (Stearn, 2011b).

Family IDIOSTROMATIDAE
Nicholson, 1886

[*nom. correct.* GALLOWAY, 1957, p. 440, *pro* Idiostromidae NICHOLSON, 1886a, p. 98]

Family diagnosis as for genus. [The family name came to be used for any dendroid genus, although the original diagnosis noted that growth form was not a diagnostic feature; it originally included disparate genera that are now assigned to three different orders.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian).*

Idiostroma WINCHELL, 1867, p. 99 [**Stromatopora caespitosa* WINCHELL, 1866, p. 91; OD; lectotype, UMMP 32401A (slides W2-17,18), GALLOWAY & EHLERS, 1960, p. 63]. Growth form dendroid with axial tabulated canal and, in some species, subsidiary canals. Axial zone of amalgamate structure in transverse section, passing outward into peripheral zone of well-defined continuous or superposed pachysteles, intervening allotubes crossed by dissepiments and concentric laminae. Laminae variably expressed by alignment of opaque dissepiments to form microlaminae, by well-defined opaque microlaminae passing through pachysteles, and/or by tripartite laminae with central light zone. Laminae forming parabolas parallel to successive growth surfaces in longitudinal section. Microstructure coarsely and irregularly vacuolate. [Vacuolate microstructure, tripartite laminae, and the tendency for the dominance of concentric laminae over pachysteles are distinguishing features of the lectotype, but parts of it resemble *Stachyodes* in microstructure. NICHOLSON's (1886a) description of the genus, which was widely accepted by later workers, was based on *I. roemeri* NICHOLSON, in the absence at that time of adequate descriptions of the type species.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* Germany (Sauerland), *Eifelian;* Australia (Queensland), China (Guizhou, Guangxi, Hunan, southern Tien Shan, Xizang), Mongolia, Spain (Cantabria), USA (Iowa, Michigan), Vietnam, *Givetian;* Uzbekistan, China (Sichuan), Germany, Russia (Urals), *Middle Devonian;* Australia (Canning Basin), Canada (northern Alberta), Uzbekistan, China (Sichuan), Czech Republic (Moravia), western Germany, *Frasnian.*——FIG. 449*a–c.* **I. caespitosum* (WINCHELL), lectotype, UMMP 32401A, Petoskey Formation, Little Traverse Bay, Michigan; *a*, axial section showing central canal, ×10; *b*, cross section of skeleton showing axial canal and vacuolate pachysteles, ×10; *c*, cross section of laminae showing vacuolate microstructure, ×25 (Stearn, 2011b).——FIG. 450*a–c. I. roemeri* NICHOLSON, 1886a, holotype, NHM P6076, Middle Devonian, Hebborn, Germany; *a*, cross section showing extensive laminae and radial pachysteles, ×10; *b*, longitudinal section, ×10; *c*, longitudinal section showing microstructure of peripheral vesicles and tripartite laminae, Nicholson section 406c, ×50 (Stearn, 2011b).

Order STROMATOPORIDA
Stearn, 1980

[Stromatoporida STEARN, 1980, p. 892]

Stromatoporoids with cellular or obscurely cellular microstructure and structure dominated by pachysteles and pachystromes forming amalgamate networks. *Silurian (upper Llandovery)–Upper Devonian (Frasnian).*

Family STROMATOPORIDAE
Winchell, 1867

[Stromatoporidae WINCHELL, 1867, p. 98] [=Angulatostromatidae KHALFINA, 1968a, p. 151]

Genera of the Stromatoporida dominated by pachystromes, laminae, and/or cassiculate structure. *Silurian (upper Llandovery)–Upper Devonian (Frasnian).*

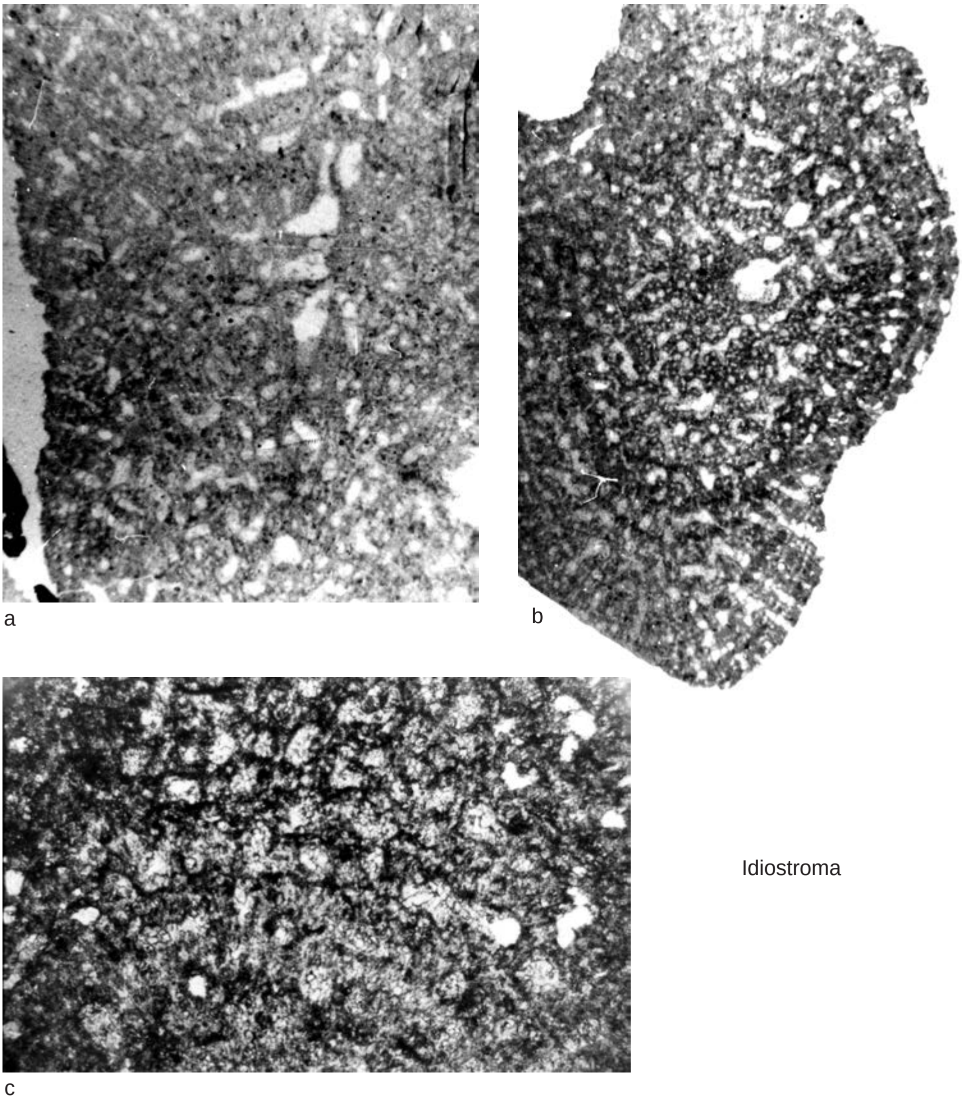


FIG. 449. Idiostromatidae (p. 797).

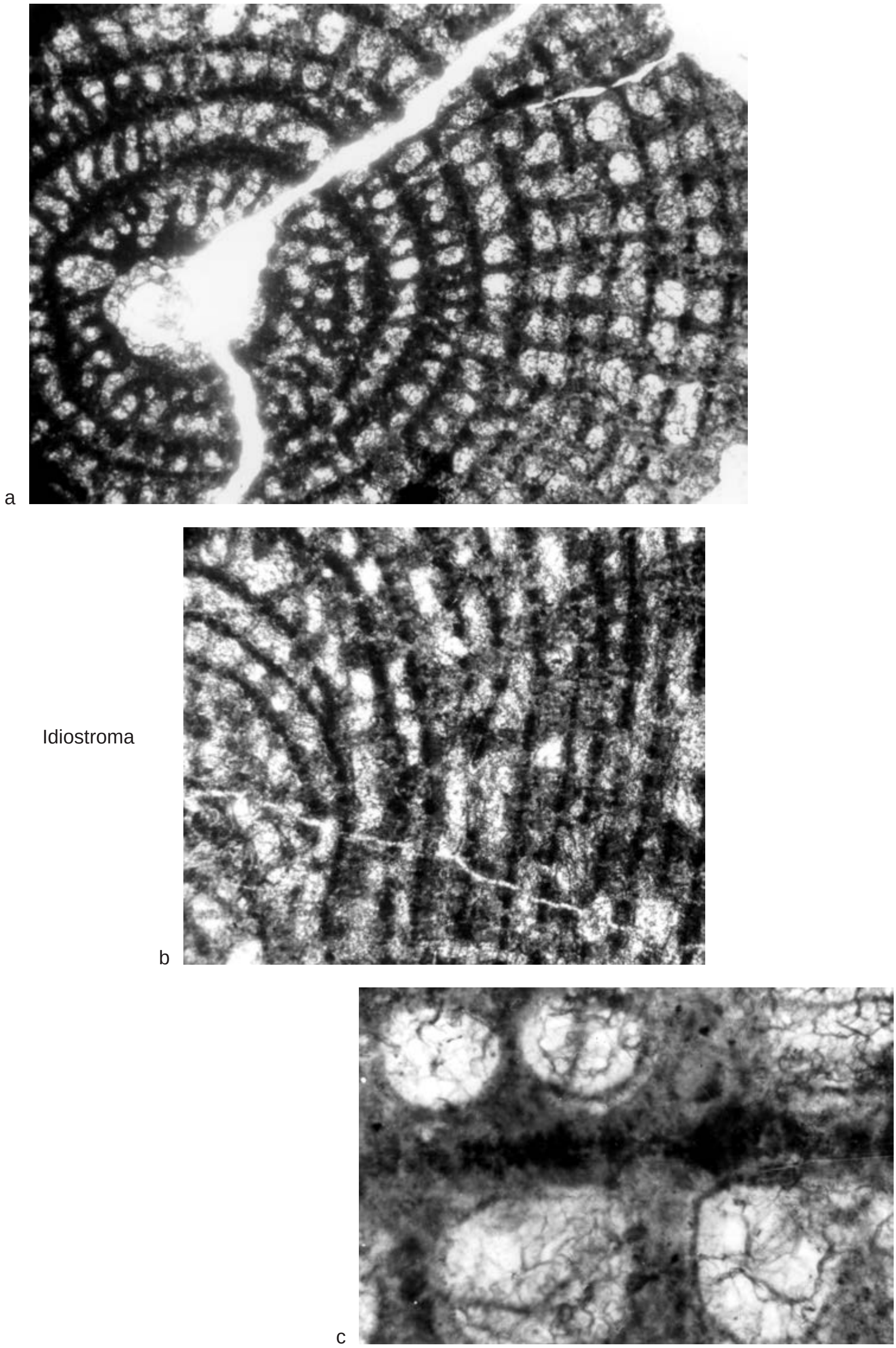
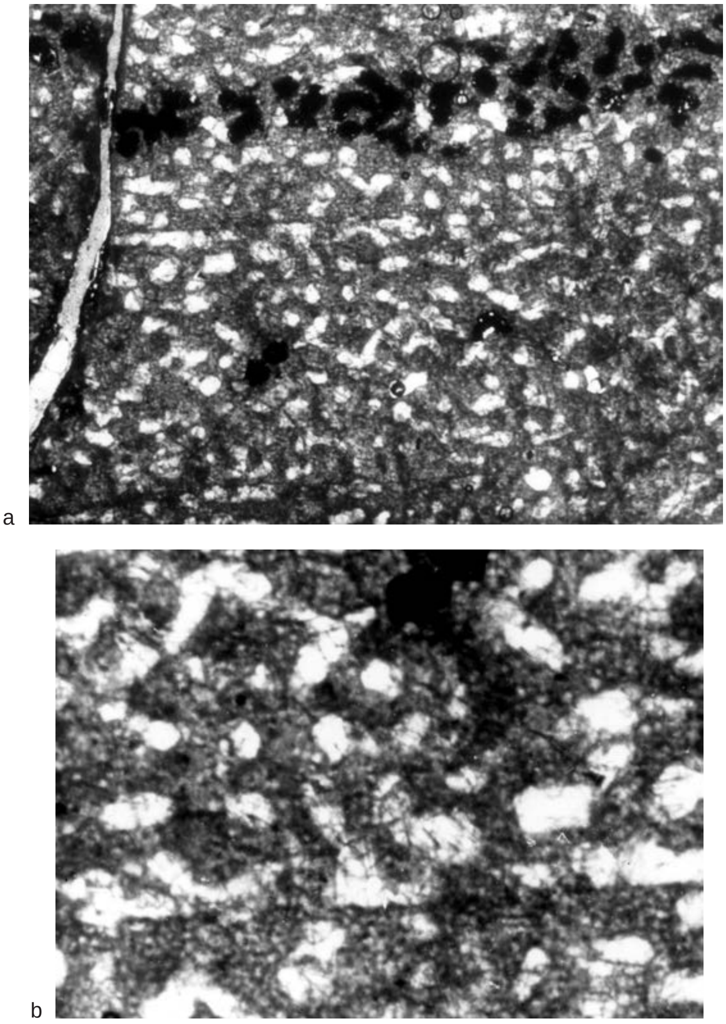


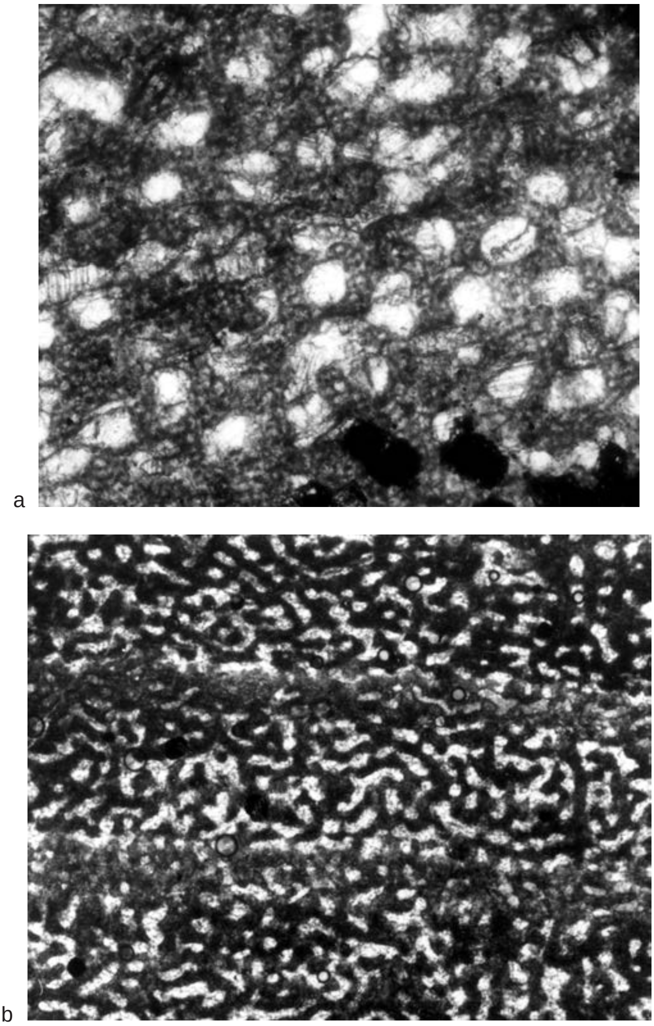
FIG. 450. Idiostromatidae (p. 797).



Stromatopora

FIG. 451. Stromatoporidae (p. 800–801).

Stromatopora GOLDFUSS, 1826, p. 21 [**S. concentrica* GOLDFUSS, 1826, p. 22; OD; holotype, IPB 80] [=*Angulatohtroma* KHALFINA, 1968a, p. 152, *lapsus calami pro Angulatostroma* (type, *Stromatopora angulata* YAVORSKY, 1947, p. 10, OD)]. Skeleton of cellular, cassiculate, oblique pachystromes and scattered dissepiments, in some successive phases including short pachysteles; structural elements in tangential section cut as labyrinthine network or discrete vermiform elements. [Problems concerning the type and definition of the genus have been discussed by STEARN (1993)]. *Silurian (Wenlock)–Upper Devonian (Frasnian)*: Czech Republic (Bohemia), Russia (Kuznetsk Basin, Lena River, Vaigach Island), Ukraine (Podolia), *Wenlock;* Czech Republic (Bohemia), Estonia, Russia (Vaigach Island, Siberian platform), USA (New York), *Ludlow–Pridoli;* Australia (Victoria, New South Wales), Canada (Arctic Island), China (Guangxi), Spain (south), *Lower Devonian;* Australia (Queensland), Belgium (Ardennes), Canada (Arctic Island, Northwest Territories), China (Sichuan, Guangxi, Yunnan), Morocco, New Zealand (Reefton), Russia (Kuznetsk Basin, Petchora Basin, Salair), USA (Missouri), *Middle Devonian;* Belgium (Ardennes), Canada (Alberta, Saskatchewan, Northwest Territories), Poland (Holy Cross Mountains), Russia (Novaya Zemlya), *Frasnian.*——FIG. 451*a–b.* **S. concentrica,* holotype, IPB 80, Middle Devonian, Gerolstein, Eifel, Germany; *a,* longitudinal section

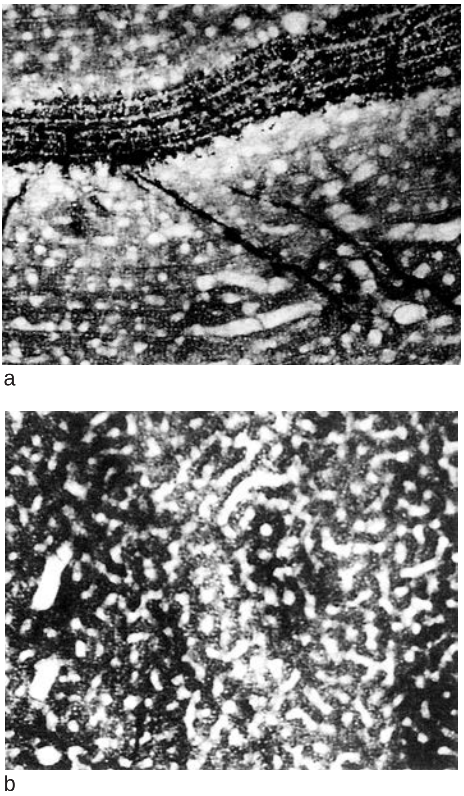


Stromatopora

FIG. 452. Stromatoporidae (p. 800–801).

showing cassiculate structure, ×10; *b*, longitudinal section showing cellular microstructure, ×25 (Stearn, 2011b).——FIG. 452*a–b*. **S. concentrica; a,* holotype, longitudinal section cut for LECOMPTE (1952 in 1951–1952) showing microstructure, ×25; *b,* specimen IRScNB 6212a of LECOMPTE (1952 in 1951–1952), Eifelian, Chimay, Ardennes, Belgium, longitudinal section showing latilamination and cassiculate structure, ×10 (Stearn, 2011b).

Climacostroma YANG & DONG, 1979, p. 72 [**C. guangxiense*; OD; holotype, NIGP 33129, 33130] [=*Lineastroma* KHALFINA & YAVORSKY, 1973, p. 31, *partim* (type, *Stromatopora vorkutensis* YAVORSKY, 1961, p. 39, of STEARN, 1993, p. 213) see *Lineastroma* below and STEARN (in STEARN & others, 1999, p. 47) for further discussion]. Structure dominated by thick, discontinuous pachystromes associated with microlaminae. Pachysteles short, confined to space between pachystromes, not superposed, forming a closed network in tangential section. Microstructure cellular. *Middle Devonian:* Belgium (Ardennes), Canada (Northwest Territories), China (Guangxi, Sichuan), Poland (Holy Cross Mountains), Russia (Pechora Basin, South Urals, Kuznetsk Basin), USA (Missouri).——FIG. 453*a–b*. **C. guangxiense*, holotype, 331229-30, Guangxi, China; *a*, longitudinal section, ×10; *b,* tangential section, ×10 (Dong, 2001).



Climacostroma

Fig. 453. Stromatoporidae (p. 801).

Eostromatopora Nestor, 1999a, p. 120 [**Stromatopora impexa* Nestor, 1966a, p. 44–45; OD; holotype, IGTUT Co3168]. Structure amalgamate, structural elements occupying most of skeleton, pierced by thin, tangential, vermiform canals and short, curved autotubes and allotubes with tabulae. Tangential canals in irregular layers simulating galleries and vaguely defining thick, irregular pachystromes. Microstructure compact or obscurely cellular. [This earliest representative of the order Stromatoporida appears to be the only genus without clear cellular microstructure.] *Silurian (upper Llandovery–Wenlock)*: Canada (Arctic Island), Ireland, Norway, *Telychian;* Estonia, Sweden (Gotland), *Wenlock.*——Fig. 454*a–c. *E. impexa* (Nestor), holotype, IGTUT Co3168, Jaani Formation, Saaremaa, Estonia; *a,* longitudinal section, ×10 (Nestor, 1966a); *b,* tangential section, ×10; *c,* tangential section showing poorly defined microstructure, ×10 (Stearn, 2011b).

Glyptostromoides Stearn, 1983a, p. 553 [**Glyptostroma simplex* Yang & Dong, 1979, p. 66; OD; holotype, NIGP33083-4] [=*Glyptostroma* Yang & Dong, 1979, p. 65 (based on *Stromatopora beuthii sensu* Yavorsky, 1955, p. 106; *non S. beuthii* Bargatzky, 1881a)]. Structure in longitudinal section cassiculate, formed by network of oblique structural elements penetrated by thick, cellular, long pachysteles; in tangential section, pachysteles merging into labyrinthine network with oblique structural elements. [The type species of *Glyptostromoides* was designated by Yang and Dong (1979) as *Stromatopora beuthii* Bargatzky, and they referred to the citation of this species by Yavorsky (1955). However, the type specimens of *S. beuthii* had been identified as a species of the much different genus *Hermatostroma* Nicholson by Lecompte (1952 in 1951–1952, p. 253) and Stearn (1980, p. 898–899). *Glyptostroma* therefore became a junior synonym of *Hermatostroma* and the generic grouping distinguished by Yang and Dong required a new name.] *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Canada (Arctic Island), *Emsian;* Spain (Cantabria), *Emsian–Eifelian;* China (Guangxi), Russia (Kuznetsk Basin, Salair), *Middle Devonian;* Canada (British Columbia), Russia (Kuznetsk Basin), *Givetian.*——Fig. 455*a–d. *G. simplex* (Yang & Dong); *a–b,* holotype, NIGP33083-4, Middle Devonian, Guangxi, China; *a,* longitudinal section, ×10; *b,* tangential section, ×10 (Yang & Dong, 1979); *c,* hypotype, GSC108894, Blue Fiord Formation, Ellesmere Island, arctic Canada, longitudinal section, ×10; *d,* drawings of type specimen, ×10 (Stearn, 1993).

Lineastroma Khalfina & Yavorsky, 1973, p. 31 [**Stromatopora vorkutensis* Yavorsky, 1961, p. 39; OD; holotype, CNIGR 7354/420; the type is synonymized with *Stromatopora sibirica* Riabinin, 1928, p. 1046, and *Stromatopora elegestica* Riabinin, 1937, p. 16; Nestor, 1976, p. 78; if the synonymy is confirmed by comparison of the type specimens, then *L. sibirica* Riabinin, 1928, is the type species.] Structure of prominent, extensive but interrupted pachystromes and short, mostly longitudinal but locally oblique pachysteles, mostly confined to space between pachystromes, only locally superposed or more continuous longitudinally; in tangential section cut as isolated dots or irregular vermiform masses, rarely joined. Microstructure finely and inconspicuously cellular. [Stearn (1993) included both forms with postlike pillars and pachysteles in the genus, which resulted in a widely split temporal range, with a gap of late Silurian and Early Devonian. Transferring the species that have pachysteles forming a closed network in tangential section to *Climacostroma* makes better sense of the stratigraphic distribution of *Lineastroma* and *Climacostroma.*] *middle Silurian*: Russia (Siberian platform, Pre-Urals, Tuva), Ukraine (Podolia).——Fig. 456*a–b. *L. vorkutense* (Yavorsky), holotype, CNIGR 7354/420, Pre-Urals, Russia; *a,* longitudinal section, ×10; *b,* tangential section, ×10 (Khalfina & Yavorsky, 1973).

Neosyringostroma Kaźmierczak, 1971, p. 117 [**Hermatostroma logansportense* Galloway & St. Jean, 1957, p. 219; OD; holotype, YPM222127]. Long pillars of cellular-melanospheric microstructure pass through amalgamate structure of

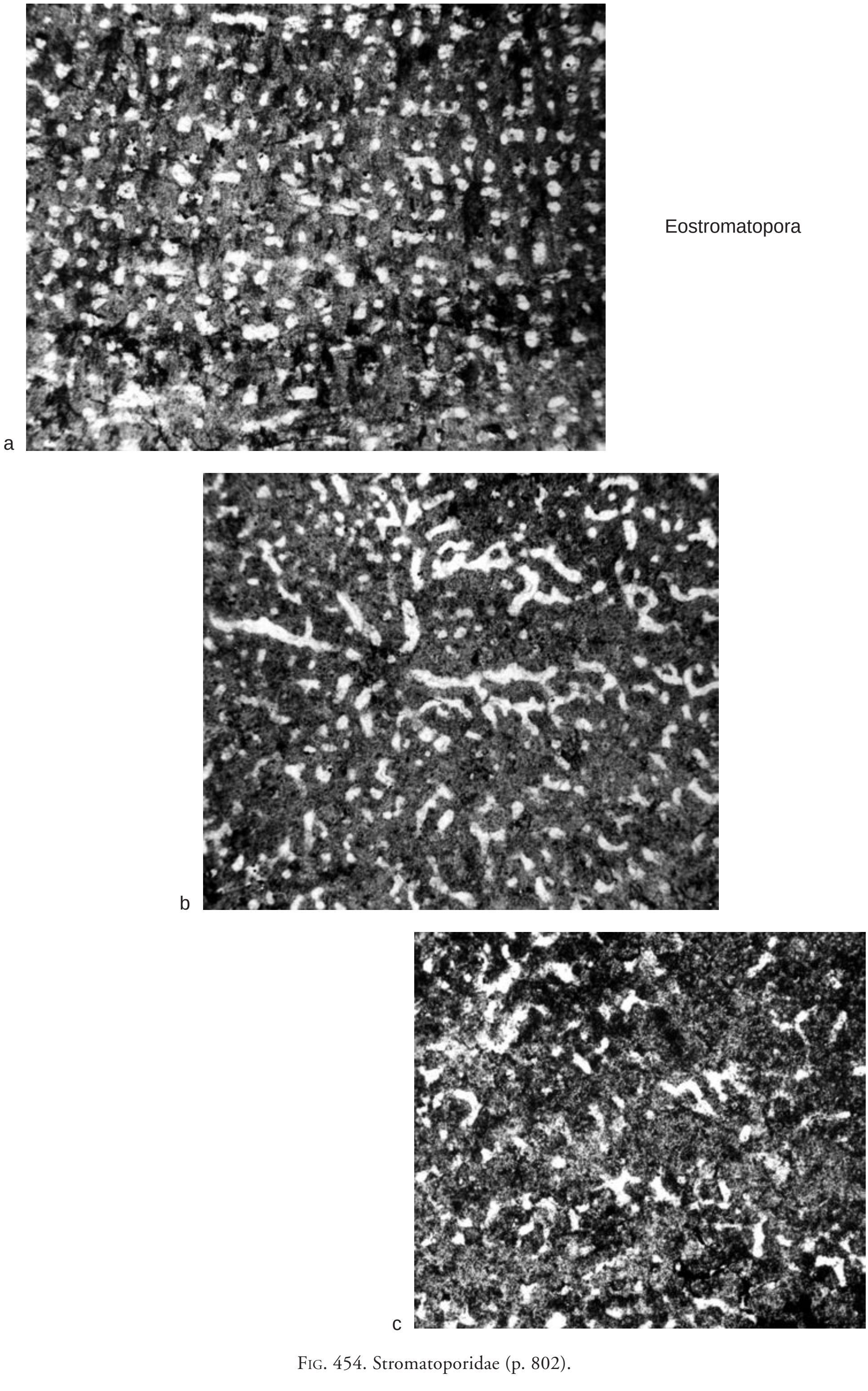


FIG. 454. Stromatoporidae (p. 802).

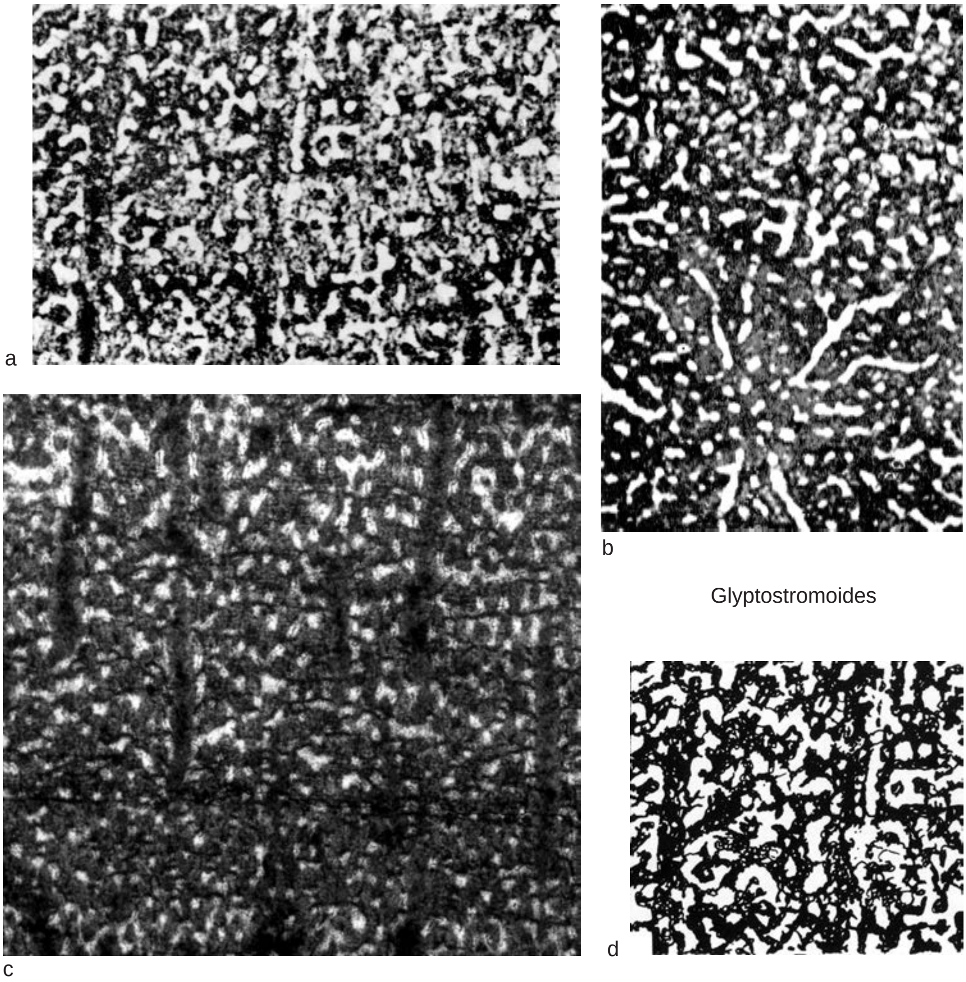


FIG. 455. Stromatoporidae (p. 802).

short pachysteles, pachystromes, and cassiculate structural elements, commonly chevron shaped in longitudinal section. In tangential section, pillars circular within amalgamate structural elements. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Spain (Cantabria), *Emsian–Eifelian;* Afghanistan, *?upper Emsian;* Belgium (Ardennes), Russia (Kuznetsk Basin), *Eifelian;* China (Guangxi, Guizhou, Hunan), *Middle Devonian;* Afghanistan, Canada (British Columbia, Manitoba), Poland, USA (Indiana), *Givetian.*——FIG. 457*a–d.* **N. logansportense* (GALLOWAY & ST. JEAN), hypotype, GSC 104075 (illustrated as *Taleastroma logansportense* in QI & STEARN, 1993), Slave Point Formation, Evie Lake Field, northeastern British Columbia, Canada; *a*, longitudinal section, ×10; *b*, tangential section, ×10 (Qi & Stearn, 1993); *c–d*, holotype, original illustrations highly retouched; *c*, longitudinal section; *d*, tangential section, ×10 (Galloway & St. Jean, 1957).

Pseudotrupetostroma KHALFINA & YAVORSKY, 1971, p. 120 [**Stromatopora pellucida artyschtensis* YAVORSKY, 1955, p. 100; OD; holotype (apparently lost), CNIGR 7351/132, elevated to species rank by KHALFINA and YAVORSKY (1971, p. 120)]. Pachysteles confined to interlaminar space, commonly well superposed, very coarsely cellular. Tangential elements fine microlaminae coated with coarsely cellular material like that of pillars. In tangential section, longitudinal elements (pachysteles) cut as a closed network or as vermiform isolated masses. [The type specimen of *P. artyschtense* is apparently lost, but as originally defined as a variety, it had the same specimen and type number as the species *S. pellucida* Yavorsky from the same locality and was very similar in form (*fide* Nestor, personal communication, 2003). The figures of the variety from Yavorsky, 1955, and of the species *S. pellucida* are therefore used here to illustrate the genus.] *Lower Devonian (?Pragian, Emsian)–Middle Devonian (Givetian)*: Australia (Victoria), *?Pragian;* Australia (New South Wales, Victoria), Spain (Moreno Mountains), *Emsian;* Canada (Arctic Island), *Emsian–Eifelian;* Russia (Kuznetsk Basin), *Eifelian;* Russia (Salair), *Middle Devonian;* Australia (Queensland), Canada (northeastern British Columbia, Northwest Territories), China (Guizhou), Russia (Kuznetsk Basin, Salair), *Givetian.*——Fig. 458*a–c*. ***P. artyschtense** (Yavorsky), holotype, 7351/132, Givetian, Artyschta River, Kuznetsk Basin, Russia; *a–b*, longitudinal and tangential sections, ×10; *c*, longitudinal section, ×25 (Yavorsky, 1955).——Fig. 458*d–e*. *P. pellucida* Yavorsky, holotype, CNIGR 7351/132, locality as for *P. artyschtense; d*, tangential section, ×10; *e*, longitudinal section, showing coarsely cellular microstructure, ×25 (Yavorsky, 1955).

Taleastroma Galloway, 1957, p. 448 [**Stromatopora cumingsi* Galloway & St. Jean, 1957, p. 182; OD; holotype, YPM222129]. Structure amalgamate with small, round galleries, dominated by thick pachystromes, commonly showing microlaminae and traces of microreticulation. Pillars penetrate the structure, of melanospheric microstructure, commonly with clear axes, probably originally cellular. Round ends of pillars cut tangentially within amalgamate, melanospheric structural elements. [*Taleastroma* is similar to *Neosyringostroma* but has more prominent pachystromes. The clear zones in the pillar axes, which are exaggerated in the retouched original illustration, may be diagenetic in origin.] *Middle Devonian*: Belgium (Ardennes), Germany (Hebborn), USA (Indiana).——Fig. 459*a–b*. **T. cumingsi* (Galloway & St. Jean), Logansport Limestone, holotype, YPM222129, unretouched; *a*, longitudinal section, ×10; *b*, tangential section, ×10 (Stearn, 2011b).

Family FERESTROMATOPORIDAE Khromykh, 1969

[Ferestromatoporidae Khromykh, 1969, p. 30]

Stromatoporids of melanospheric to obscurely cellular microstructure composed of oblique structural elements forming a closely spaced, cassiculate network. [The microstructure commonly appears to be finely melanospheric or compact and vacuolate. Uncertainty about its microstructure is reflected in the original description of Yavorsky (1955) and in the discussion of Flügel and Flügel-Kahler (1968).] *Lower Devonian (?Emsian), Middle Devonian–Upper Devonian (Frasnian).*

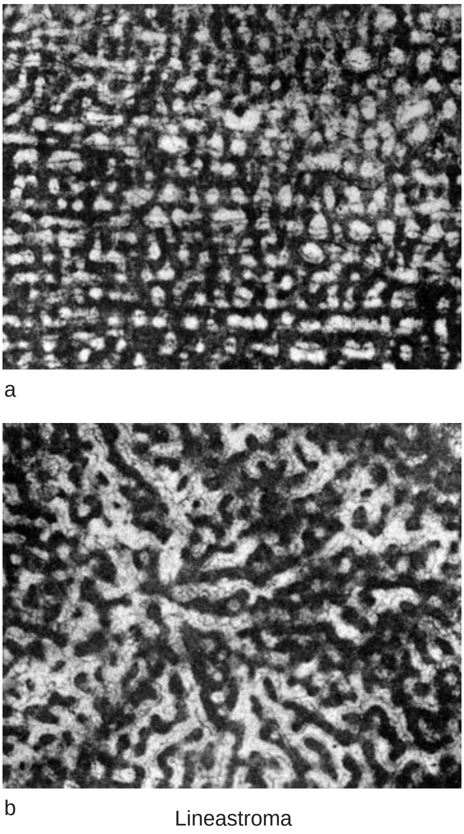


Fig. 456. Stromatoporidae (p. 802).

Ferestromatopora Yavorsky, 1955, p. 109 [**F. krupennikovi*; OD; holotype, CNIGR 7351/165]. Structural elements largely oblique, forming cassiculate network traversed by thin, continuous paralaminae, forming a labyrinthine network in tangential section. Pachysteles absent. Microstructure obscurely cellular, commonly melanospheric. *Lower Devonian (?Emsian), Middle Devonian–Upper Devonian (Frasnian)*: Canada (Arctic Island), *?Emsian;* China (Sichuan, Guangxi), *Middle Devonian;* Germany (Rhineland), Poland (Holy Cross Mountains), Russia (Kuznetsk Basin, Salair), USA (Missouri), *Givetian;* Canada (Alberta), Poland (Holy Cross Mountains), Russia (eastern Siberia), *Frasnian.*——Fig. 460*a–c*. **F. krupennikovi*, holotype, CNIGR 7351/165, Givetian, near Safonov, southwest of Kuznetsk Basin, Russia; *a*, longitudinal section, ×6; *b*, tangential and oblique section, ×12; *c*, longitudinal section showing microstructure, ×25 (Yavorsky, 1955).

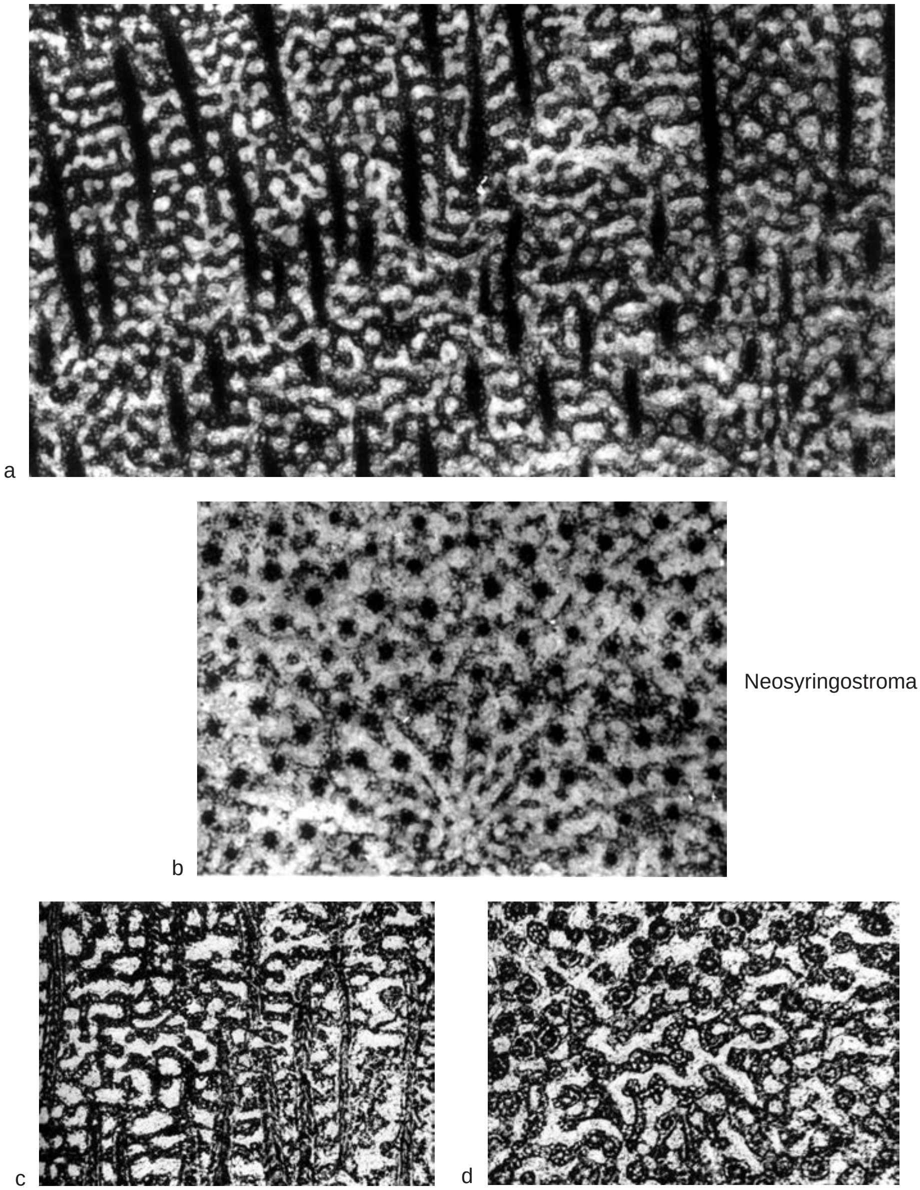


FIG. 457. Stromatoporidae (p. 802–804).

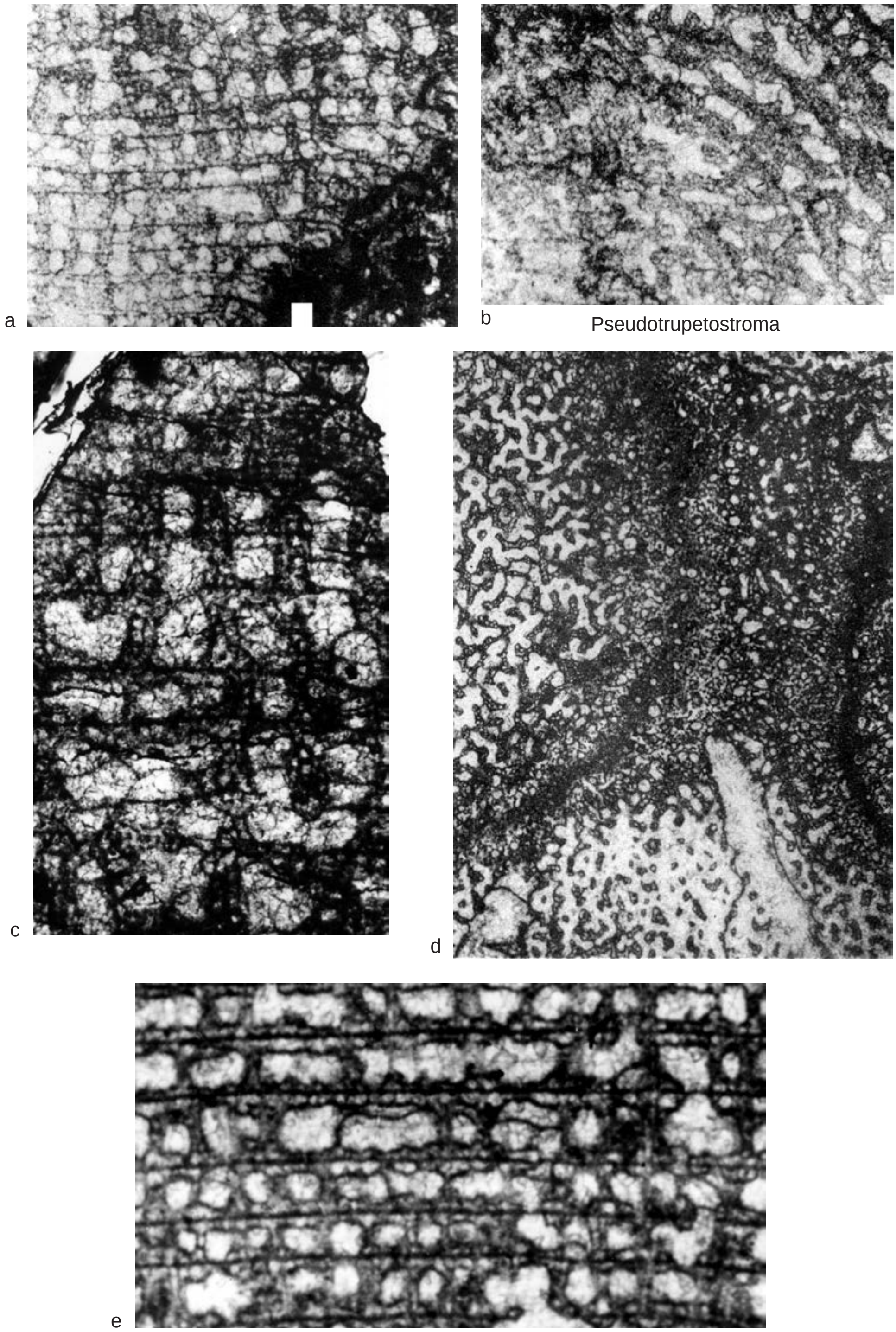


FIG. 458. Stromatoporidae (p. 804–805).

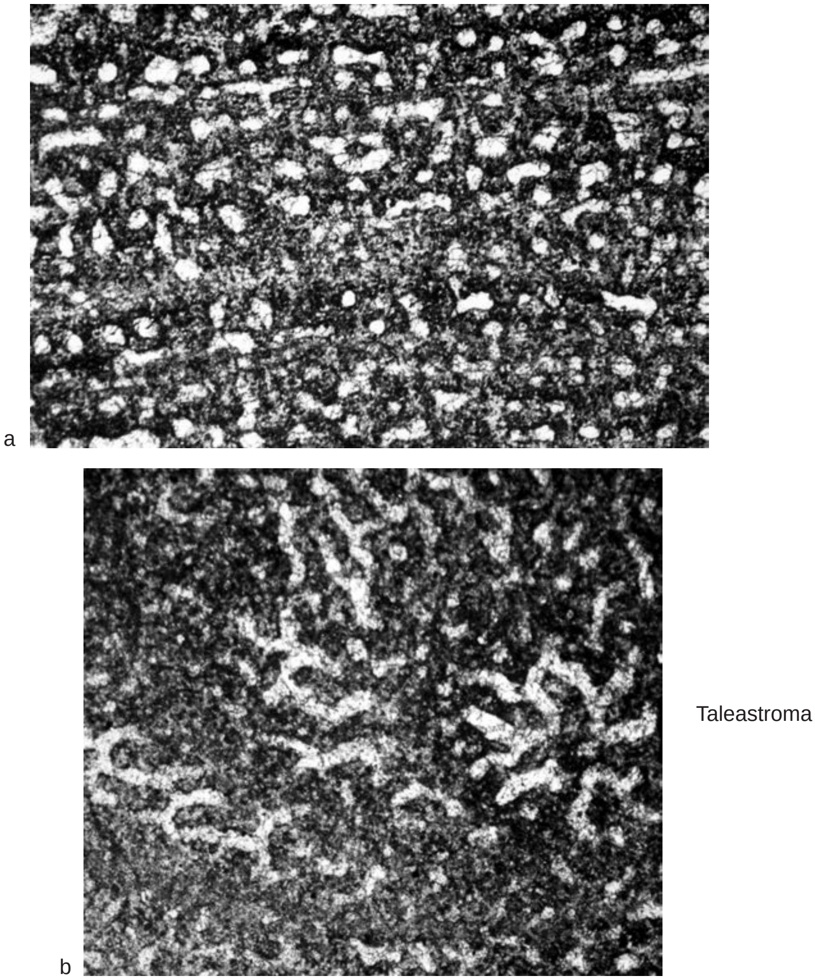


Fig. 459. Stromatoporidae (p. 805).

Arctostroma Yavorsky, 1967, p. 30 [**A. ignotum*; OD; holotype, CNIGR No. unknown; =*Ferestromatopora contexta* Stearn, 1963, p. 666; Stearn, 1980, p. 898]. Oblique structural elements forming continuous cassiculate network in longitudinal section, enclosing galleries arched at top; neither pachysteles nor pachystromes prominent, but structural elements may align tangentially locally; structural elements cut as labyrinthine network in tangential section. Microstructure cellular, commonly altered to melanospheric with vertical alignment of melanospheres. [Nestor (personal communication, 2009) asserted that until the identity of the two species is proven, *A. ignotum* should remain the type species.] *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* Australia (Queensland), Belgium (Ardennes), *Givetian;* Australia (Canning Basin), Canada (Alberta, Manitoba, Saskatchewan), China (Guangxi), Germany (Rhineland), Russia (western Pre-Urals), *Frasnian.*——Fig. 461*a–b.* **A. contextum* (Stearn), holotype, GSC 29150, Mikkwa Formation, Frasnian, Mikkwa River, northern Alberta, Canada; *a*, longitudinal section, ×10; *b*, longitudinal section showing microstructure, ×25 (Stearn, 2011b).——Fig. 461*c–e. A. ignotum*; holotype, Frasnian, western Pre-Urals, Tshernysheva Mountains, Russia; *c–d*, longitudinal and tangential sections, ×10; *e*, longitudinal section, showing microstructure, ×25 (Yavorsky, 1967).

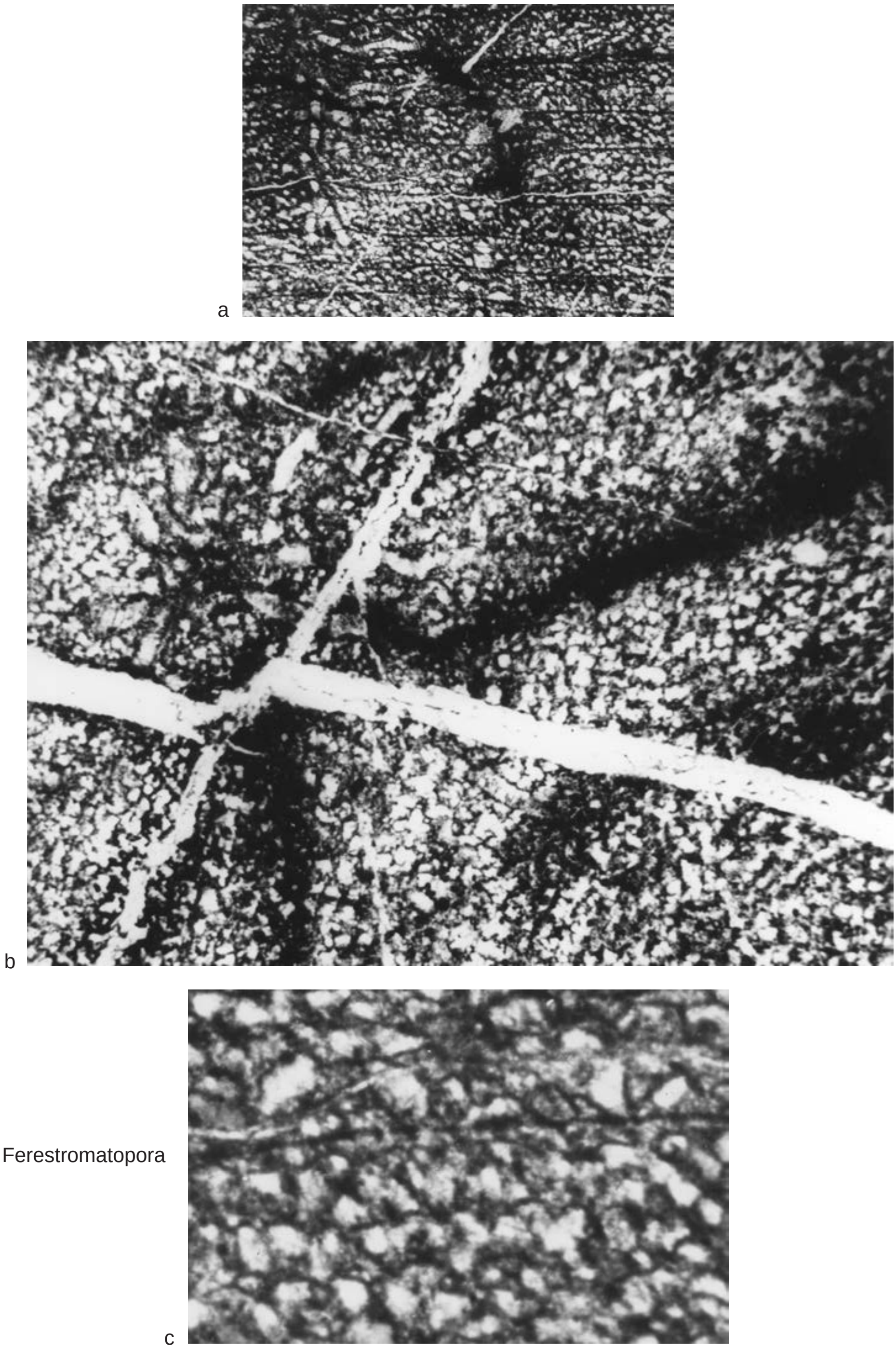


FIG. 460. Ferestromatoporidae (p. 805).

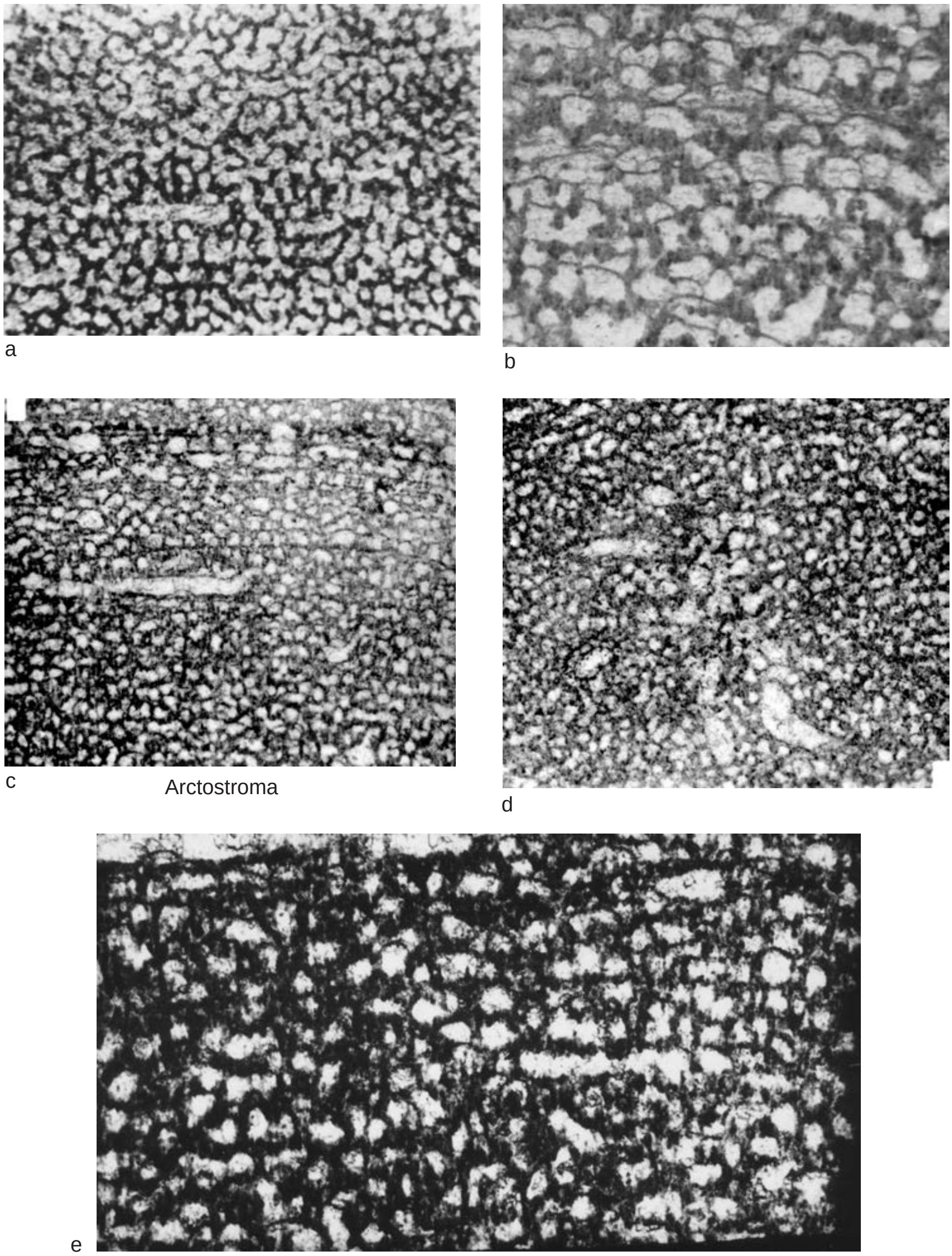


FIG. 461. Ferestromatoporidae (p. 808).

Family SYRINGOSTROMELLIDAE Stearn, 1980

[Syringostromellidae STEARN, 1980, p. 892]

Stromatoporida with structure dominated by pachysteles and dissepiments. *Silurian (upper Llandovery)–Upper Devonian (Frasnian).*

Syringostromella NESTOR, 1966a, p. 47 [**Stromatopora borealis* NICHOLSON, 1891b, p. 315; OD; holotype, NHM. P5894] [=*Yavorskiina* KHALFINA, 1968a, p. 148, *nom. nud.*]. Pachysteles long, continuous,

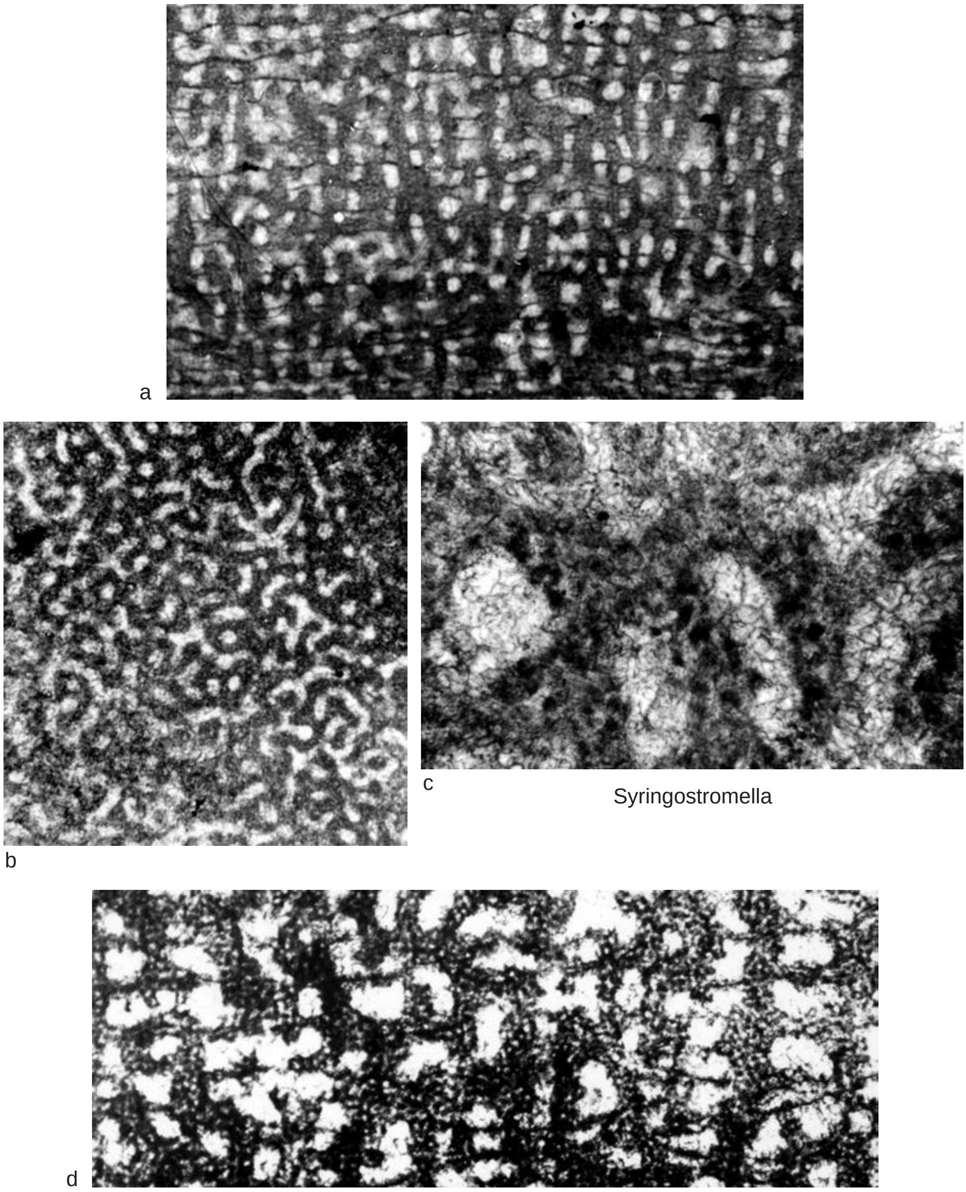


FIG. 462. Syringostromellidae (p. 810–812).

joining and dividing in longitudinal section; pachystromes rudimentary or absent, dissepiments common. In tangential section, pachysteles vermiform or loose labyrinthine network. Microstructure cellular, some species may appear microreticulate. *Silurian (upper Llandovery)–Lower Devonian, Middle Devonian (?Eifelian)*: Canada (Hudson Bay), *Telychian;* Canada (eastern Quebec), England (Wenlock), Japan, Russia (Moiero River, Tuva), Sweden (Gotland), Ukraine (Podolia), *Wenlock;* Canada (Chaleurs Bay), Turkestan Mountains, Estonia, Kazakhstan, Russia (Siberia), Sweden (Gotland), Ukraine (Podolia), *Ludlow;* China (Inner Mongolia), Mongolia, Ukraine (Podolia), Russia (eastern slope of Urals), USA (New York), *Pridoli;* Canada (Arctic Island), *Lochkovian;* Czech Republic (Bohemia), *Pragian;* Australia (Victoria), Canada (Arctic Island), Russia (Salair), *Lower*

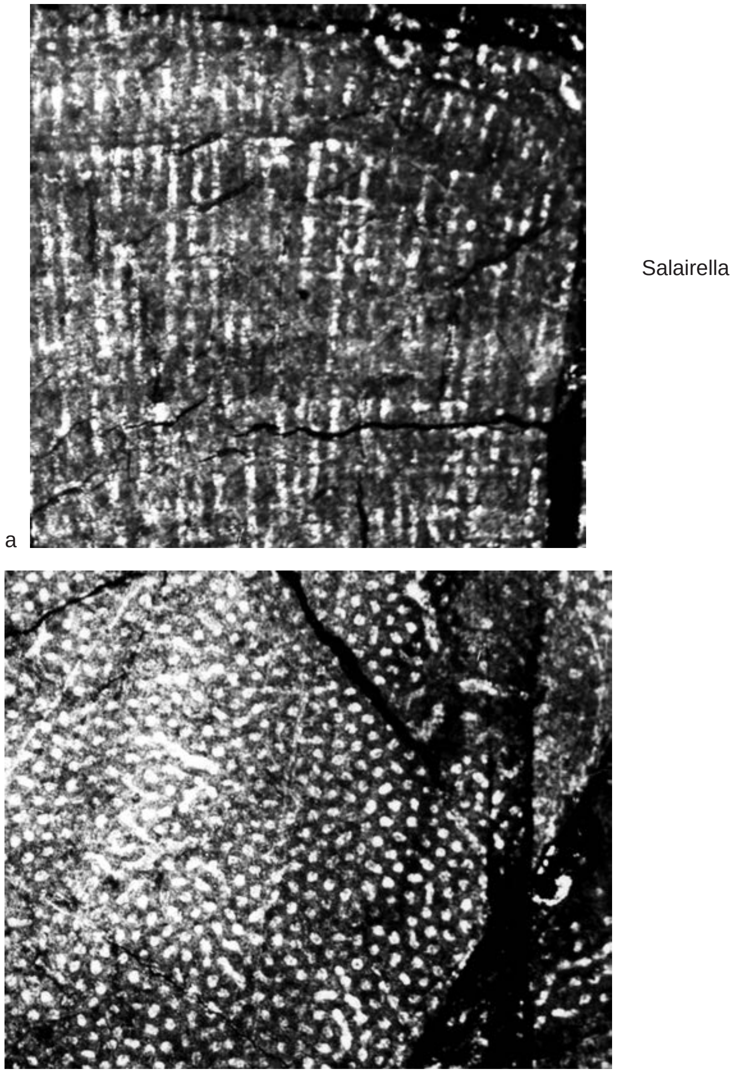


FIG. 463. Syringostromellidae (p. 812–813).

Devonian; Russia (Siberia, Omolov), *?Eifelian.*——FIG. 462*a–d.* **S. borealis* (NICHOLSON); *a–c*, holotype, NHM. P5894, Ludlow, Oesel Island, Estonia; *a*, longitudinal section showing long pachysteles, ×10; *b*, tangential section showing allotubes and autotubes, ×10; *c*, tangential section of pachysteles showing melanospheric microstructure, ×50 (Stearn, 2011b); *d,* topotype, IGTUT Co 3176, longitudinal section showing cellular microstructure and long pachysteles, ×25 (Nestor, 1966a).

Salairella KHALFINA, 1961d, p. 330 [**S. multicea* KHALFINA, 1961d, p. 331; OD; holotype, CSGM 402/37] [=*Lecomptella* KHALFINA, 1972, p. 151 (type, *Stromatopora racemifera* KHALFINA, 1961d, p. 327, OD); =?*Tubuliporellina* KOSAREVA in BOGOYAVLENSKAYA & KHROMYKH, 1985, p. 93 (type, *T. crispa*, ?SD)]. Pachysteles long, joining and dividing in longitudinal section, pachystromes rudimentary to absent, dissepiments common in autotubes between pachysteles. In tangential section, most pachysteles joined in closed network enclosing autotubes. Microstructure finely cellular. [Although the genus *Tubuliporellina* was attributed by BOGOYAVLENSKAYA and KHROMYKH to KOSAREVA (1968), a generic diagnosis was not published until that in BOGOYAVLENSKAYA and KHROMYKH in 1985, and the proposed type species was only illustrated at that time but not described. The status of the genus is therefore in doubt.] *Lower Devonian (Pragian)–Upper Devonian (Frasnian)*: Austria (Carnic Alps), Czech Republic (Bohemia), Mongolia, Russia (Salair, eastern Siberia), *Lower Devonian;* Australia (Victoria), Czech Republic (Koneprusy), *Pragian;* Australia (New South Wales), Canada (Arctic Island), *Emsian;* Altai, Zeravshan Mountains, Czech Republic (Bohemia), Russia (Salair, Kuznetsk Basin), *Eifelian;* China (Guangxi, Yunnan), Russia (eastern slope of Urals, Salair), *Middle Devonian;* Australia (Queensland), Belgium (Ardennes), Russia (Kuznetsk Basin), USA (Missouri), *Givetian;* Australia (Queensland), Belgium (Ardennes), Canada (Alberta, Manitoba), Russia (Russian platform), *Frasnian.*——FIG. 463*a–b.* **S. multicea*, holotype, CSGM 402/37, Podshandinskie stage, Gur'evska district, Salair, Russia; *a*, longitudinal section, ×10; *b*, tangential section, showing prominent autotubes, ×10 (Stearn, 2011b).

?**Zeravshanella** LESSOVAJA, 1986, p. 36 [**Z. cavernosa;* OD; holotype, GMU 270/7a-33/412]. Long pachysteles, highly irregular in outline in both longitudinal and tangential sections; tangential structural elements amalgamate, irregular, resembling those of *Glyptostromoides* and dissepiments. [Further study may show this genus to be based on a diagenetically altered specimen of *Syringostromella;* however, the microstructure of this genus resembles that of the Ferestromatoporidae. The name was first published by LESSOVAJA (1978a) as a *nomen nudum* in a caption to plate 1,*1.* The name is very similar to *Zeravschanella* LYASHENKO, 1969, a tentaculatid.] *Lower Devonian:* Tien Shan.——FIG. 464*a–b.* **Z. cavernosa*, holotype, GMU 270a-33/412, Kushnovin horizon (approximately Pragian), Mount Bursykhirman, Zeravshan Range, Uzbekistan; *a*, longitudinal section, ×10; *b*, tangential section, ×10 (Stearn, 2011b).

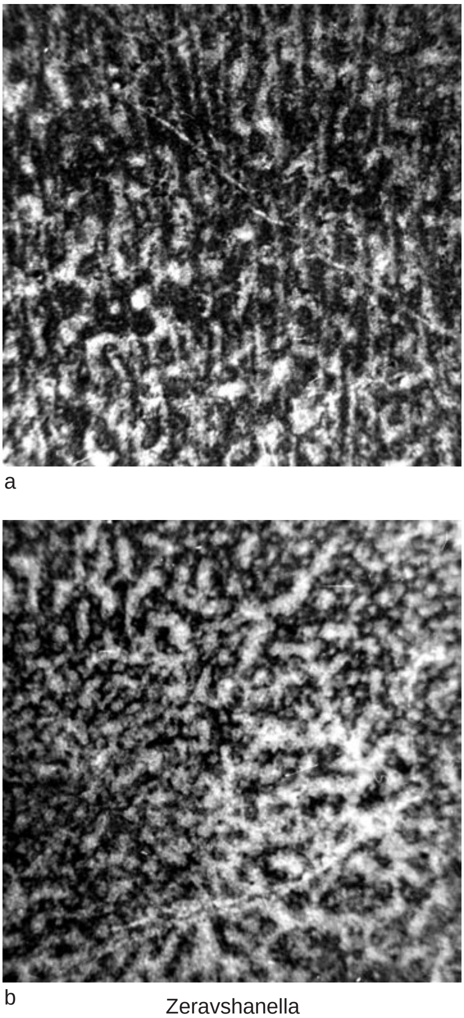


FIG. 464. Syringostromellidae (p. 813).

Order SYRINGOSTROMATIDA Bogoyavlenskaya, 1969

[Syringostromatida BOGOYAVLENSKAYA, 1969b, p. 21]

Stromatoporoids of microreticulate microstructure and skeleton composed of discrete structural elements rather than amalgamate networks, including commonly dominant pachystromes and microlaminae, pachysteles and pillars. [Microstructure alone does not define the order; several genera of the Stromatoporida also show traces of this microreticulation. The grouping of genera in the Syringostromatida is based partly on phylogenetic considerations that suggest that the order arose in Wenlock time from the actinostromatids: the Coenostromatidae from the Pseudolachiidae and the Parallelostromatidae from the Densastromatidae (NESTOR, 1974).] *Silurian (Wenlock)–Middle Devonian (Givetian), Upper Devonian (?Famennian).*

Family COENOSTROMATIDAE Waagen & Wentzel, 1887

[*nom. correct.* STEARN & others, 1999, p. 53, *pro* Coenostromidae WAAGEN & WENTZEL, 1887, p. 925] [=Syringostromidae LECOMPTE, 1951 in 1951–1952, p. 195]

Syringostromatida of laminar, bulbous, and domical growth form with structure dominated by longitudinal structural elements (pachysteles and pillars) of clinoreticular and acosmoreticular microstructure. *Silurian (Pridoli)–Upper Devonian (Frasnian).*

Coenostroma WINCHELL, 1867, p. 99 [**Stromatopora monticulifera* Winchell, 1866, p. 91; SD

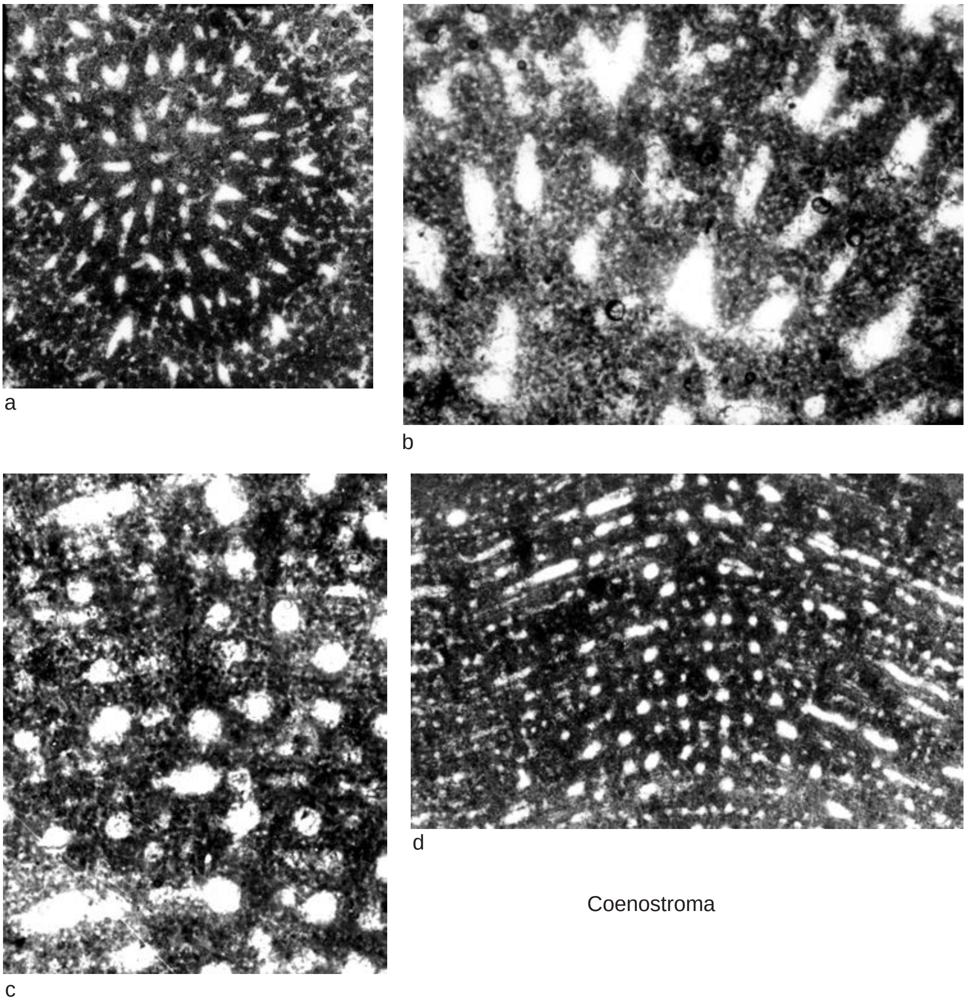
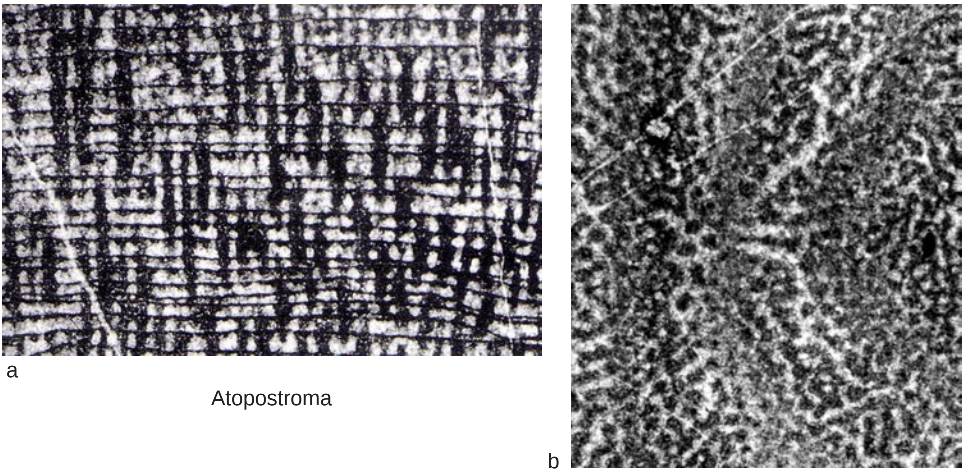


Fig. 465. Coenostromatidae (p. 813–814).

Miller, 1889, p. 157; lectotype, UMMP 32409A, Galloway & Ehlers, 1960, p. 51] [=?*Parallelostromella* Kosareva, 1968, p. 80 (type, *P. collina* Kosareva, 1968, p. 80–81, OD, *nom. nud.*, published without a diagnosis)]. Extensive, thick pachystromes, superposed pachysteles, and pillars forming an imperfect grid in longitudinal section; galleries small, irregular; microstructure of structural elements obscurely clinoreticular, locally with microlaminae in pachystromes. In tangential section, structural elements forming irregular network, or, in some species, longitudinal elements appear as dots (i.e., they are pillars). [Some of the species presently included in *Coenostroma* are acosmoreticular in microstructure and could form the basis of a new genus.] *Lower Devonian (Lochkovian)–Middle Devonian (Givetian), Upper Devonian (?Famennian)*: USA (New York), *Lochkovian;* Australia (Victoria), *Emsian;* Canada (southern Ontario), Germany (Eifel), Russia (Kuznetsk Basin, northeastern Siberia, ?Salair), *Eifelian;* Australia (Queensland), Canada (Manitoba, Northwest Territories), Czech Republic, Poland (Holy Cross Mountains), Russia (Kuznetsk Basin), USA (Michigan), *Givetian;* China (Guangxi), *Middle Devonian;* Russia (Novaya Zemlya), Australia (Canning Basin), *?Famennian.*——Fig. 465*a–d.* **C. monticuliferum* (Winchell), Gravel Point Formation, Traverse Group, Petosky, Michigan, USA; *a–c*, lectotype, UMMP 32409A; *a*, tangential section, ×10; *b*, tangential section showing cellular microstructure, ×25; *c*, longitudinal section showing traces of microreticulate microstructure, ×25; *d*, paralectotype, UMMP 32409B, longitudinal section, ×10 (Stearn, 2011b).



Atopostroma

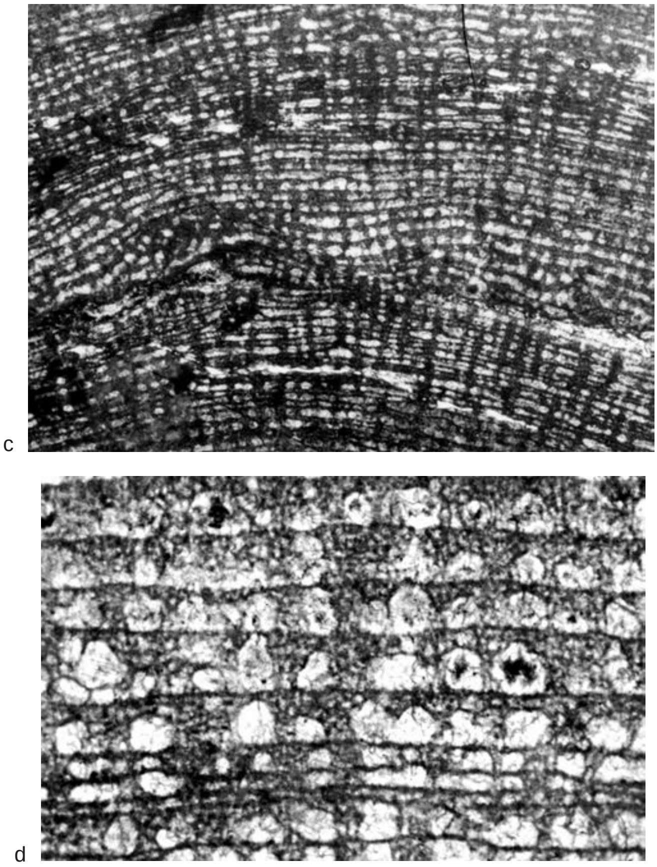


FIG. 466. Coenostromatidae (p. 816).

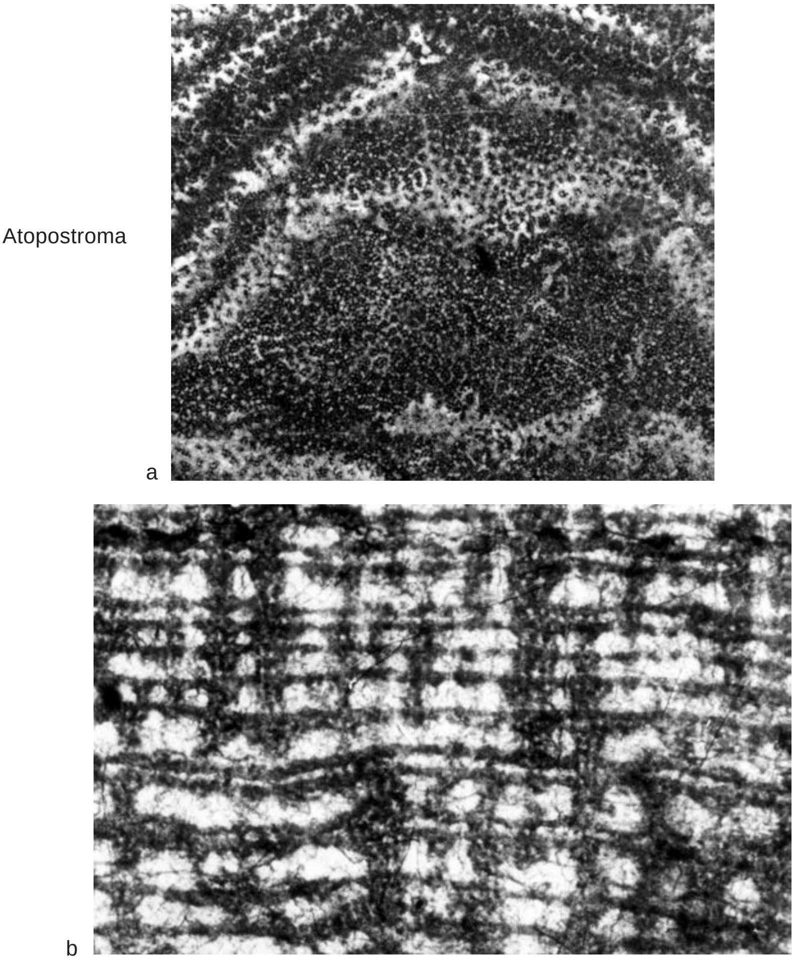


FIG. 467. Coenostromatidae (p. 816).

Atopostroma Yang & Dong, 1979, p. 74 [**A. tuntouense*; OD; holotype, NIGP Bd343-9]. Laminae regular, extensive, formed of a single microlamina with skeletal material from pillars spread irregularly below; pillars typically superposed, narrow, subcircular in tangential section at base, composed of orthoreticular to clinoreticular skeletal material. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian, ?Givetian)*: Canada (Arctic Island), USA (New York), *Lochkovian;* Czech Republic (Bohemia), *Pragian;* Australia (New South Wales, Victoria), Canada (Arctic Island, Northwest Territories, Yukon), China (Sichuan, Yunnan, Guangxi), *Emsian;* Canada (Arctic Island), Russia (Kuznetsk Basin), *Eifelian;* Afghanistan, *?Givetian.*——FIG. 466*a–b*. **A. tuntouense*, holotype, NIGP Bd343-9, Yujiang Formation, Emsian, Guangxi, China; *a*, longitudinal section, ×10; *b*, tangential section, ×10 (Dong, 2001).——FIG. 466*c*. *A.* n. sp., = *A. tuntouense* Stearn, 1990, p. 496 (see Webby, Stearn, & Zhen, 1993, p. 171–172), hypotype, GSC95786, Stuart Bay Formation, Bathurst Island, arctic Canada, longitudinal section, ×10 (Stearn, 2011b).——FIG. 466*d*. *A. stearni* Webby & Zhen, 2008, holotype, Martin Wells Limestone, Queensland, Australia, AM.F 134883, longitudinal section, showing microstructure, ×35 (Webby & Zhen, 2008).——FIG. 467*a–b*. *A. n. sp.* (=*A. tuntouense* Stearn, 1990, p. 496), hypotype, GSC95786, Stuart Bay Formation, Bathurst Island, arctic Canada; *a*, tangential section, ×10; *b,* longitudinal section showing microstructure, ×25 (Stearn, 2011b).

Columnostroma Bogoyavlenskaya, 1972b, p. 33 [**Coenostroma ristigouchense* Spencer, 1884, p. 599; OD; specimen repository unknown, type slide 309, NHM. P5591]. Pillars (subcolumns) long,

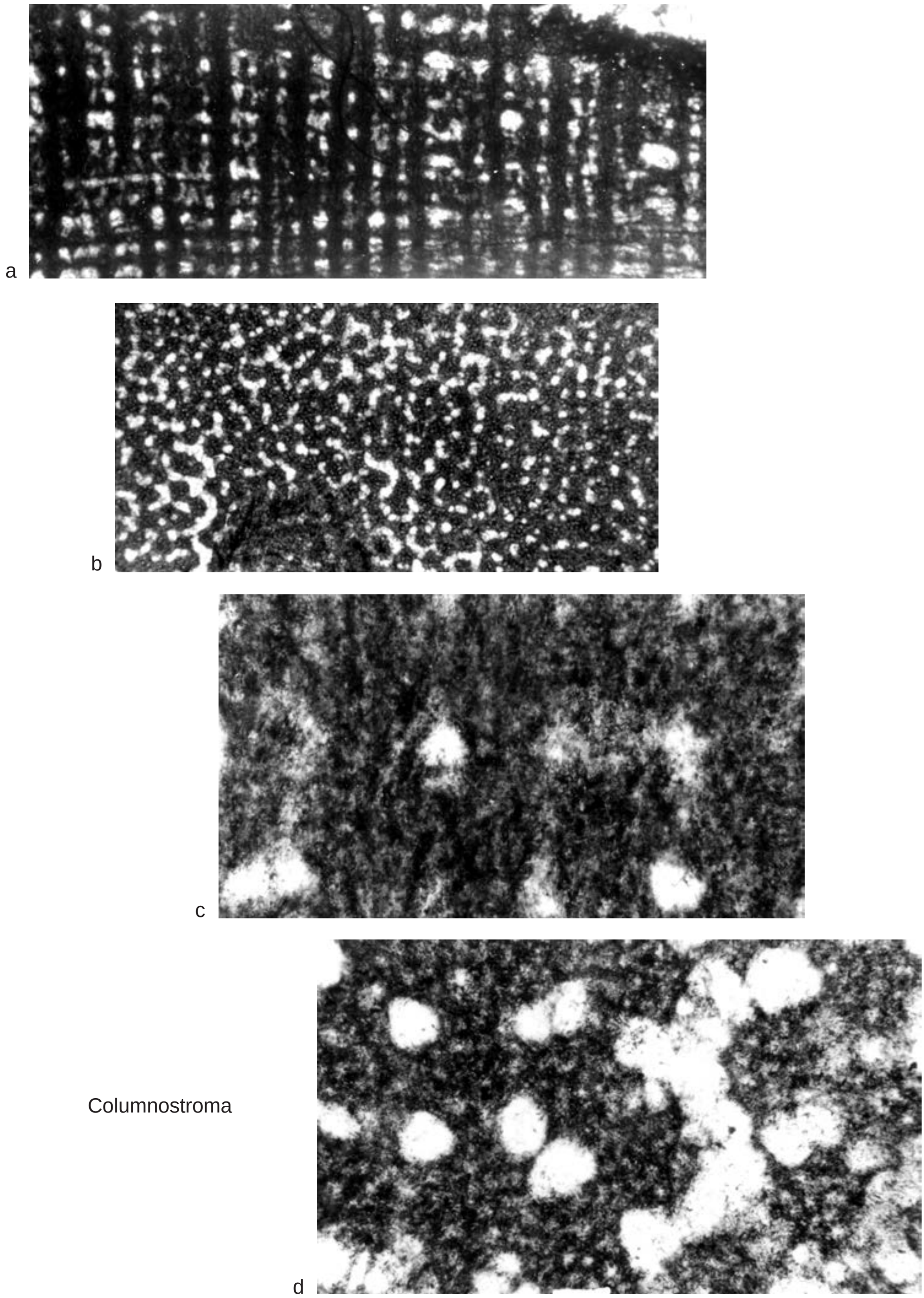


FIG. 468. Coenostromatidae (p. 816–818).

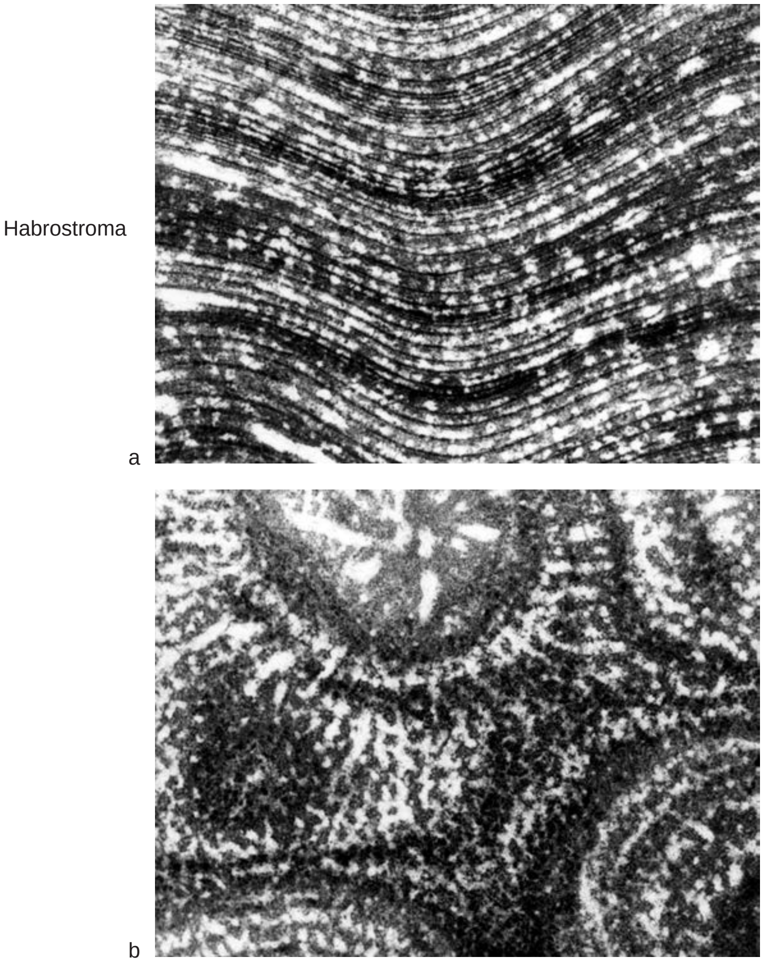


Fig. 469. Coenostromatidae (p. 818–819).

continuous, rarely joining or dividing, clinoreticular, round in tangential section and joined by radial processes (colliculi) forming colliculate laminae or locally thicker pachystromes; dissepiments common; pillars (subcolumns) separated by autotubes. *Lower Devonian (Lochkovian)–Middle Devonian (Givetian)*: Canada (New Brunswick), *Lochkovian;* Australia (Victoria), *Pragian;* Russia (eastern Urals), *Lower Devonian;* Canada (Hudson Bay), USA (Indiana, Ohio), *Emsian–Eifelian;* England (?Devon), Russia (northern Urals, eastern slope of Urals, Kuznetsk Basin), *Givetian.*——Fig. 468*a–d.* **C. ristigouchense* (Spencer), holotype, NHM. P5591, ?Lochkovian, Dalhousie, New Brunswick, Canada; *a*, longitudinal section (section is thick), ×10; *b*, tangential section showing round pillars (subcolumns) joined by radial processes, ×10; *c*, longitudinal section showing clinoreticular nature of pillars (subcolumns), ×50; *d*, tangential section of microstructure, ×50 (Stearn, 2011b).

Habrostroma Fagerstrom, 1982, p. 11 [**Stromatopora proxilaminata* Fagerstrom, 1961, p. 8; OD; holotype, UMMP 36177]. Pachysteles short, irregular, largely confined between pachystromes, forming an irregular network of cellular skeletal tissue with diffuse boundaries in tangential section; pachystromes prominent, of similar cellular-to-acosmoreticular material containing one or more microlaminae. [This genus has been difficult to define, and at the beginning of its range near the Silurian-Devonian boundary, it is difficult to distinguish from *Parallelostroma* (Fagerstrom, 1982; Stock & Holmes, 1986; Stock, 1989).] *Silurian (Pridoli)–Upper Devonian (Frasnian)*: Estonia, USA (New York, Virginia), *Pridoli;* Canada (Arctic Island), USA (New York, Virginia), *Lochkovian;*

Australia (Victoria), *Pragian;* Australia (New South Wales), Canada (Arctic Island), *Emsian;* Belgium (Ardennes), Canada (Arctic Island, southern Ontario), Poland, Russia (Kuznetsk Basin, Russian platform, Urals), USA (Indiana, Missouri, Ohio), *Eifelian;* Belgium (Ardennes), China (Guizhou), Germany (Sauerland), USA (Indiana), *Givetian;* Canada (northern Alberta, Northwest Territories), France, Iran (Kerman), Russia (St. Petersburg), *Frasnian.*——FIG. 469*a–b.* **H. proxilaminatum* (FAGERSTROM), holotype, UMMP36177, Formosa Reef Limestone, 4 km north of Formosa, Ontario, Canada; *a*, longitudinal section, ×10; *b*, tangential section, ×10 (Stearn, 2011b).——FIG. 470*a–b.* **H. proxilaminatum* (FAGERSTROM), holotype, UMMP36177, Formosa Reef Limestone, 4 km north of Formosa, Ontario, Canada; *a*, longitudinal section showing microstructure and microlaminae, ×25; *b*, tangential section showing diffuse skeletal material of pillars, ×25 (Stearn, 2011b).

Syringostroma NICHOLSON, 1875, p. 251 [**S. densum*; SD NICHOLSON, 1886a, p. 98; holotype, NHM. P5598] [=*Stylodictyon* NICHOLSON & MURIE, 1878, p. 221–222 (type, *Syringostroma columnaris* NICHOLSON, 1875, p. 263, OD); GALLOWAY, 1957, p. 450; STEARN, 1966, p. 116]. Pachysteles short, irregular, coarsely cellular, without well-defined boundaries, irregular in shape in tangential section; subcolumns long, continuous, clinoreticular, round in tangential section; pachystromes persistent, thick, appearing cellular or acosmoreticular, containing one or more microlaminae; dissepiments rare. [A great majority of species that have been assigned to this genus do not have the prominent subcolumns characteristic of the type species and should be assigned to other genera, notably *Coenostroma* and *Habrostroma* (STEARN, 1993).] *Lower Devonian (Lochkovian)–Middle Devonian (Givetian)*: Canada (Arctic Island), *Lochkovian;* Canada (southern Ontario, Hudson Bay), USA (Michigan, Ohio), *Emsian–Eifelian;* USA (Missouri), *Middle Devonian;* USA (Indiana, Ohio), *Givetian.*——FIG. 471*a–c.* **S. densum; a–b,* holotype, NHM. P5598, Corniferous limestone (Columbus Limestone), Kelley's Island, Lake Erie, Ohio, USA; *a*, longitudinal section, ×10; *b*, tangential section, showing round cut ends of subcolumns, ×10; *c*, topotype, YPM 452617, longitudinal section showing loosely open microreticular microstructure, ×50 (Stearn, 2011b).

Family PARALLELOSTROMATIDAE Bogoyavlenskaya, 1984

[Parallelostromatidae BOGOYAVLENSKAYA, 1984, p. 73]

Syringostromatida of laminar, bulbous, and domical growth forms with structure dominated by pachystromes and microlaminae; microstructure largely orthoreticular. *Silurian (Wenlock)–Middle Devonian (Givetian), Upper Devonian (?Frasnian).*

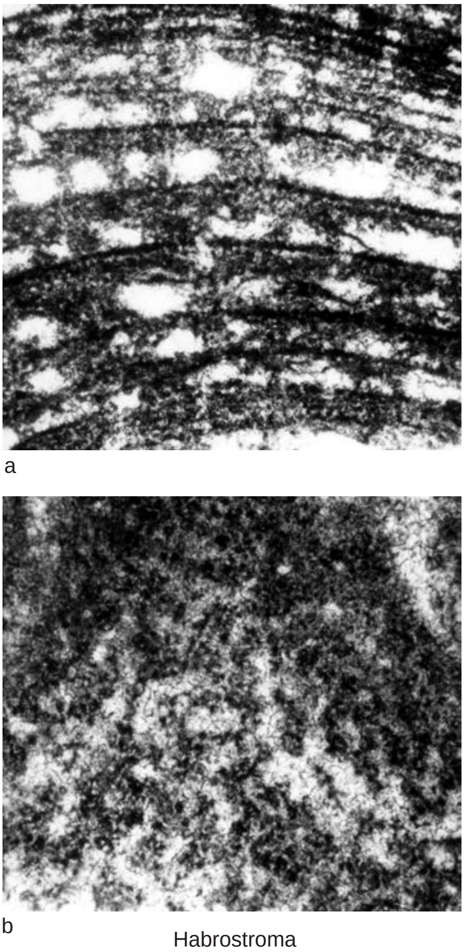


FIG. 470. Coenostromatidae (p. 818–819).

Parallelostroma NESTOR, 1966a, p. 52 [**Stromatopora typica* ROSEN, 1867, p. 58; OD; holotype, IGTUT Co3009]. Pachystromes thick, composed of orthoreticular skeletal material enclosing multiple microlaminae and micropillars; short autotubes separate pachysteles at their base. Pachysteles of orthoreticular microstructure, largely confined to space between pachystromes, some superposed; in tangential section forming closed network penetrated by autotubes. *Silurian (Wenlock)–Lower Devonian, ?Middle Devonian, Upper Devonian (?Frasnian)*: Mongolia, Russia (Pechora Basin, Pre-Urals), Ukraine (Podolia), *Wenlock;* Canada (Quebec), China (Inner Mongolia) Estonia, Russia (eastern Urals),

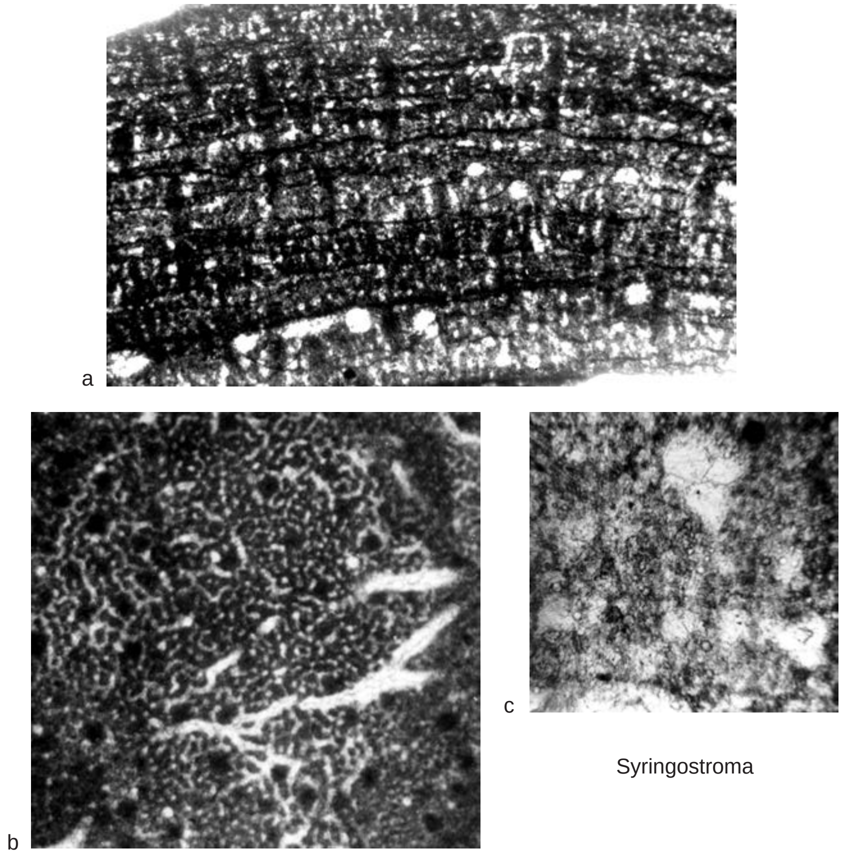


FIG. 471. Coenostromatidae (p. 819).

Sweden (Gotland), Ukraine (Podolia), USA (New York), *Ludlow–Pridoli;* Canada (Arctic Island), Estonia, Ukraine (Podolia), USA (New York), *Lochkovian;* China (Guangxi, Inner Mongolia, Sichuan), Russia (eastern Urals), *Lower Devonian;* China (Guangxi), Russia (western Urals, Arctic Island), ?*Middle Devonian;* China (Guangxi), ?*Frasnian.*——FIG. 472*a–d.* **P. typicum* (ROSEN), holotype, IGTUT Co3009, Ludlow, Saaremaa, Estonia; *a*, longitudinal section, ×10; *b*, tangential section, ×10; *c*, longitudinal section showing orthoreticular microstructure, ×25; *d*, tangential section showing autotubes between pachysteles, ×25 (Stearn, 2011b).

Parallelopora BARGATZKY, 1881a, p. 291 [**P. ostiolata* BARGATZKY, 1881a, p. 292; OD; holotype, IPB 571b, also NHM. P5936 (slides 125); type illustrated by NICHOLSON (1886a, pl. 2), LECOMPTE (1952 in 1951–1952, pl. 51)]. Pachysteles long, continuous, branching and joining in longitudinal section, in tangential section mostly joined into closed network, enclosing autotubes; pachystromes suppressed or absent; dissepiments abundant. Microstructure of pachysteles coarsely microreticulate (orthoreticular), apparently formed of closely spaced, opaque micropillars and more widely spaced, short microcolliculi. *Silurian (upper Ludlow)–Middle Devonian (Givetian)*: Sweden (Scania, Gotland), *upper Ludlow;* Czech Republic (Bohemia), *Pragian;* Australia (Victoria), Canada (Arctic Island), *Emsian;* Canada (Arctic Island), Czech Republic (Bohemia), Morocco, USA (Indiana), *Eifelian;* Belgium (Ardennes), Canada (Manitoba), France (Boulonnais), Germany (Eifel, Rhineland, Sauerland), Russia (Kuznetsk Basin), *Givetian;* China (Guangxi, Hunan, Sichuan), Germany (Eifel), Russia (South Urals), *Middle Devonian.*——FIG. 473*a–d.* **P. ostiolata*, holotype, slides NHM. P5936, Middle Devonian, Büchel, Eifel, Germany; *a*, longitudinal section of Nicholson's sample of holotype, ×10; *b*, tangential section, showing continuous network of pachysteles, ×10; *c*, longitudinal section showing microstructure of micropillars, ×50; *d*, tangential section showing coarsely melanospheric microstructure, ×50 (Stearn, 2011b).

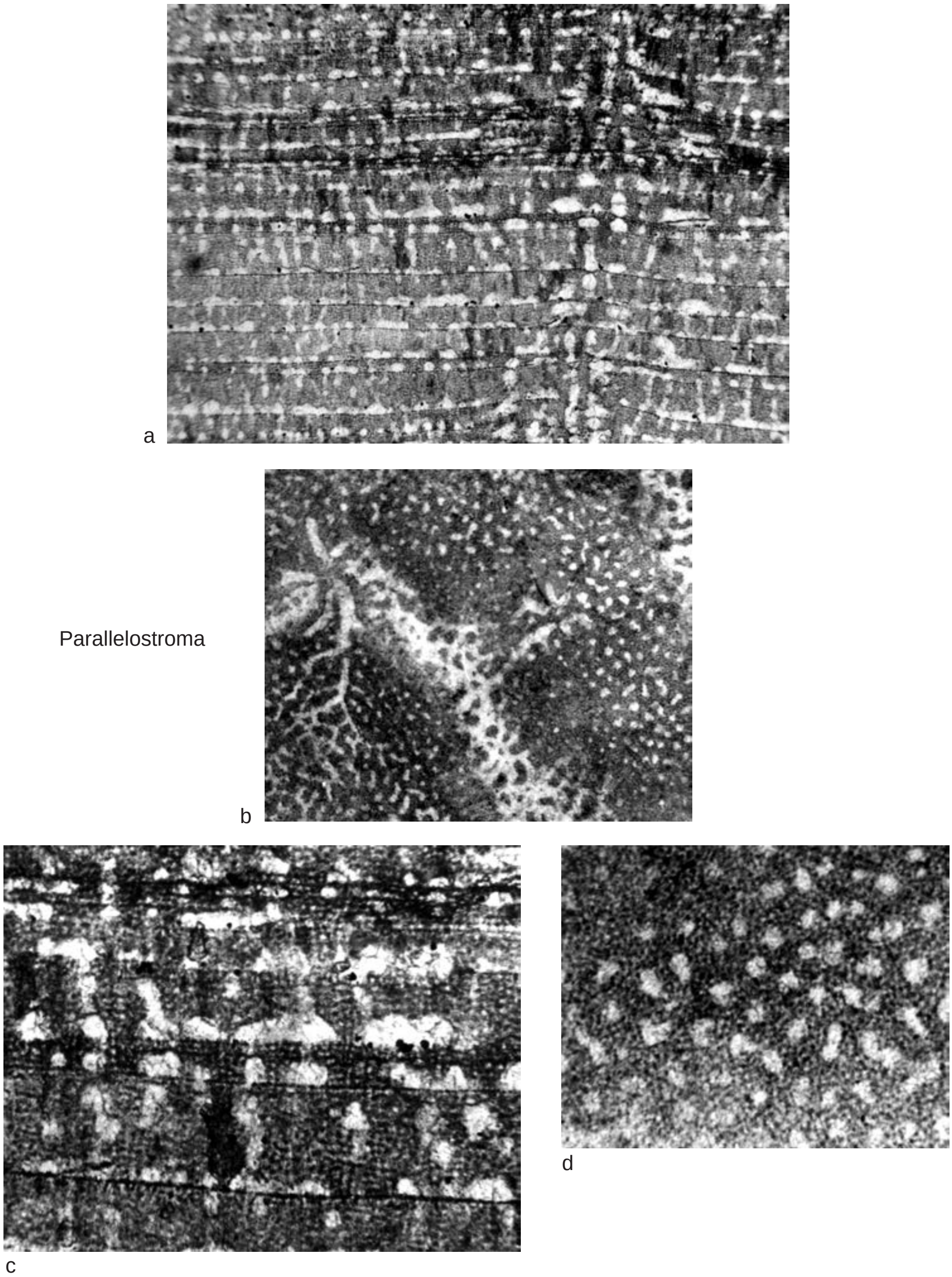


FIG. 472. Parallelostromatidae (p. 819–820).

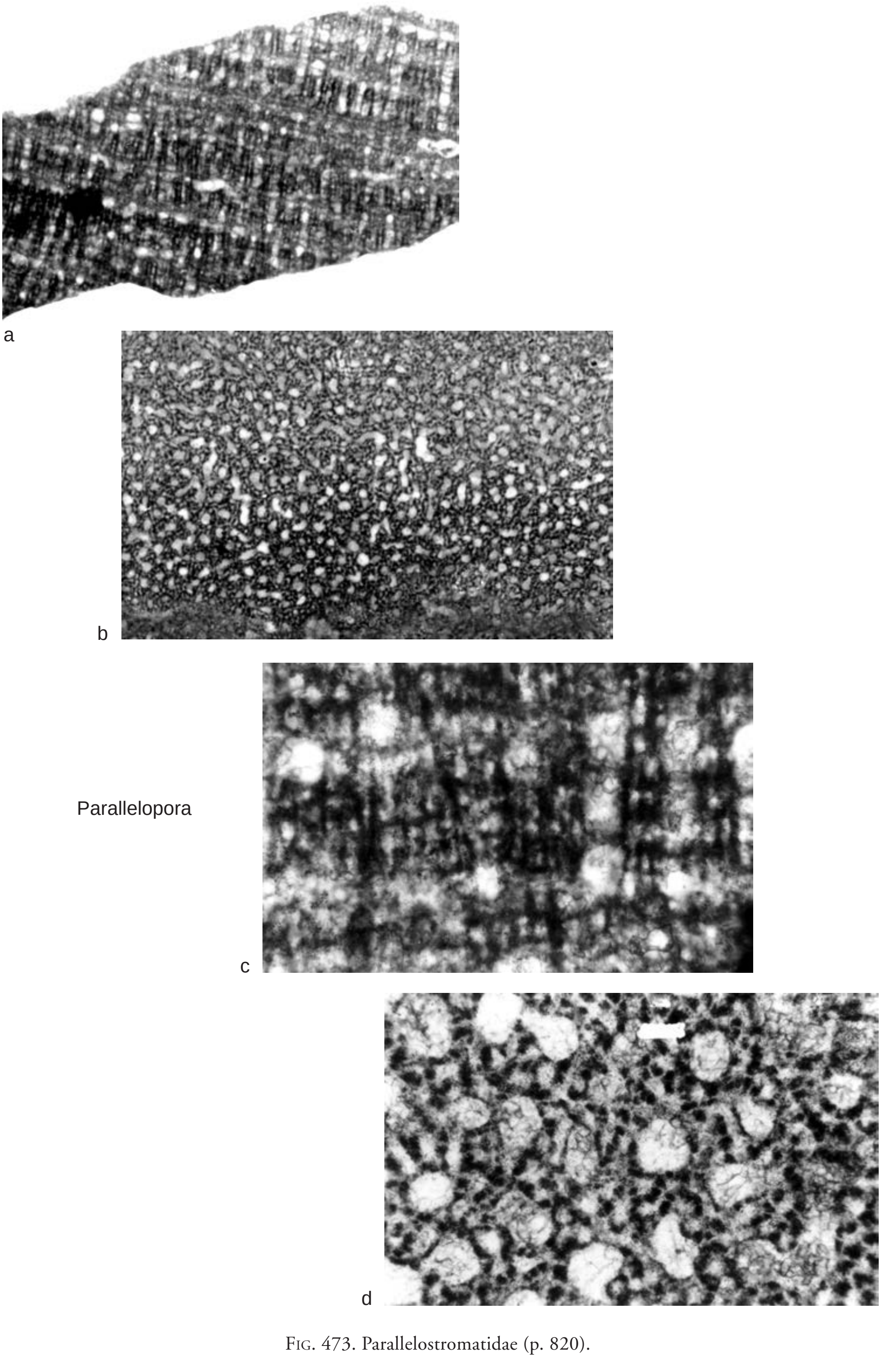


FIG. 473. Parallelostromatidae (p. 820).

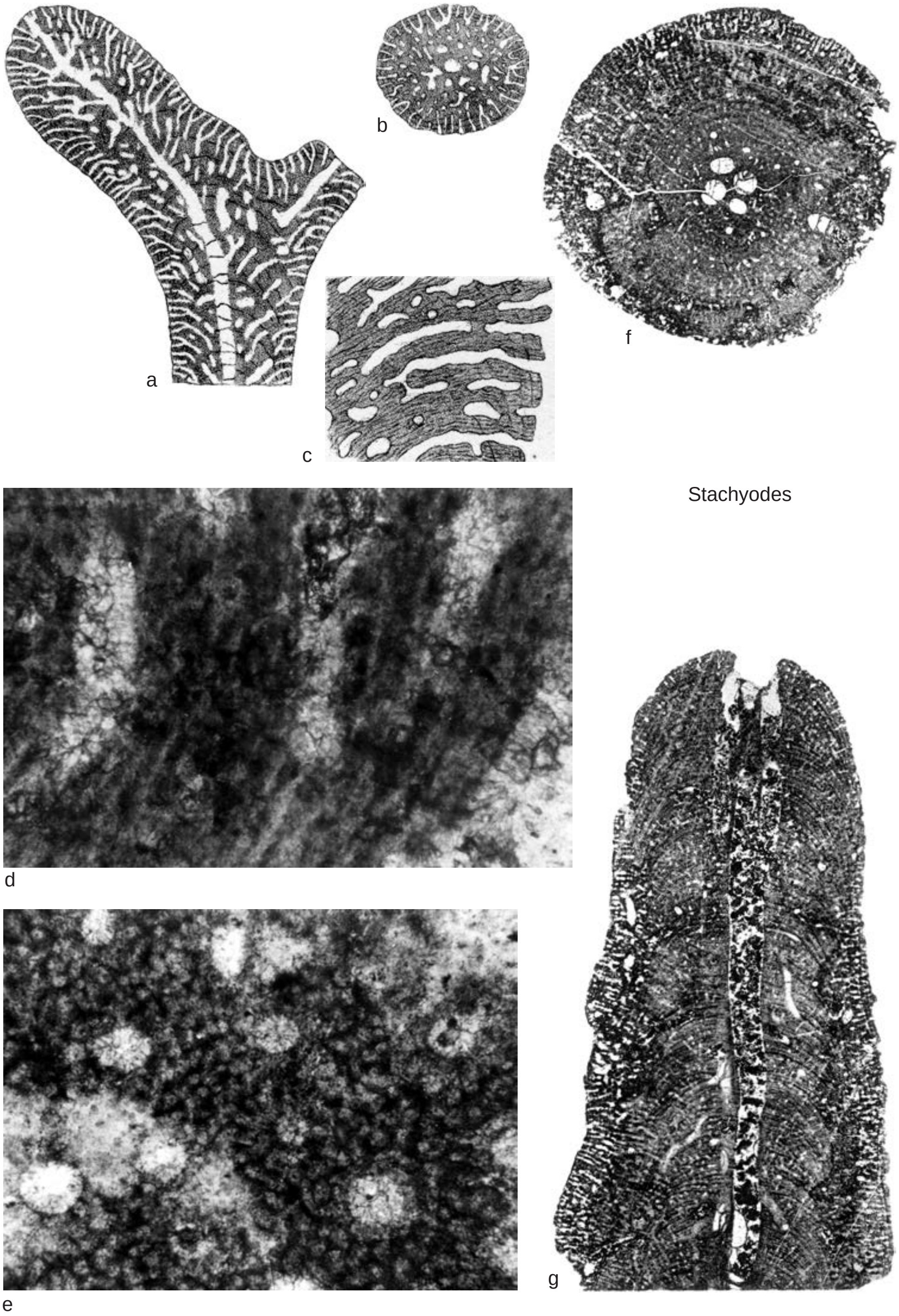


FIG. 474. Stachyoditidae (p. 824).

Family STACHYODITIDAE Khromykh, 1967

[*nom. correct.* Khromykh, 1969, p. 36, *pro* Stachyodidae Khromykh, 1967, p. 67]

Syringostromida of almost exclusively dendroid growth form with structure of prominent pachysteles separated by allotubes and microlaminae. Microstructure obscurely microreticulate. *Lower Devonian (?Lochkovian), Middle Devonian (Eifelian)–Upper Devonian (Frasnian, ?Famennian).*

Stachyodes Bargatzky, 1881b, p. 688, *non* Wright & Studer, 1889, p. 55, an alcyonarian according to Mistiaen (1985, p. 192) and *nomen oblitum* [**S. ramosa* Bargatzky, 1881b, p. 691; OD; holotype specimen lost; synonymized by Nicholson, 1886a, p. 107, with *Stromatopora verticillata* M'Coy, 1850, p. 377, type specimen at Cambridge University, apparently lost] [=*Sphaerostroma* Gürich, 1896, p. 127 (type, *S. exiguum* Gürich, 1896, p. 128, OD); =*Stachyodella* Delage & Hérouard, 1901, p. 162, see Mistiaen, 1985, p. 192 for discussion of synonymy; =*Keega* Wray, 1967, p. 18 (type, *K. australe*, OD), see Riding, 1974b, for discussion of synonymy]. Growth form in most species dendroid, rarely laminar or combination of laminar growing into erect branches; with axial canal, or canals, crossed by tabulae. Smaller canals and pachysteles separated by allotubes radiating upward and outward to periphery in dendroid forms. Structure defined by canals, allotubes, and autotubes cut in axial parts of transverse sections as round and irregular voids and at periphery as irregular radial canals opening at margin (and covered in best-preserved specimens by an enveloping, thin, skeletal sheath). Peripheral allotubes separating irregular, radial pachysteles. Structure traversed by dark microlaminae parallel to successive growth surfaces, forming concentric rings only in peripheral zone of transverse sections, and parabolas in longitudinal sections. Structural elements thick, occupying most of the skeleton, microreticulate in well-preserved specimens, more commonly appearing striated, with vacuoles in some species, commonly recrystallized to diagenetic fibrous microstructures. [*Stachyodes* differs from most stromatoporoid genera in the consistency of its dendoid growth form, its central canal exiting at the top, its lack of strorhizae, the peripheral membrance in well-preserved specimens, and the obscure but striated nature of its microstructure. The last of these suggests that it may be a non-stromatoporoid sponge with poorly preserved spicules. Further study of teh specimen described by Da Silva and others (2014) should determine whether it could be assigned to *Stachyodes.* In the absence of both possible type specimens, most research workers have accepted Nicholson's interpretation that *S. ramosa* and *S. verticillata* are the same species and have recognized the genus on the basis of his descriptions and illustrations.] *Lower Devonian (?Lochkovian), Middle Devonian (Eifelian)–Upper Devonian (Frasnian, ?Famennian)*: Australia (New South Wales), *?Lochkovian;* Afghanistan, Kara-Kalpak, China (Guangxi, Sichuan, Hunan), England (Devon), Germany (Eifel), Russia (Kuznetsk Basin, Pechora Basin, Urals, Pre-Urals), Uzbekistan, *Middle Devonian;* Belgium (Ardennes), Tien Shan, China (Qinghai), Germany (Sauerland), Russia (Kuznetsk Basin), Vietnam, *Eifelian;* Afghanistan, Australia (Canning Basin, Queensland), Belgium (Ardennes), Canada (Alberta, British Columbia, Manitoba), China (Guangxi, Guizhou, southern Qinghai), Czech Republic (Moravia), Germany (Eifel), Russia (Kuznetsk Basin), Thailand, USA (Missouri), *Givetian;* Afghanistan, Australia (Canning Basin, Queensland), Belgium (Ardennes), Canada (Alberta, Saskatchewan), Tien Shan, Zeravshan Ridge, China (Guangxi, Guizhou, Yunnan), Czech Republic (Bohemia), France (Boulonnais), Germany (Rhineland), Iran (Kerman), Poland (Holy Cross Mountains), Russia (northeastern Siberia, Pechora Basin, Timan), USA (Iowa, Missouri), Vietnam, *Frasnian;* Russia (western Pre-Urals), *?Famennian.*——Fig. 474*a–g.* **S. verticillata* (M'Coy); *a–e*, Middle Devonian, Hebborn, Eifel, Germany, Nicholson's slide 397, NHM. P6069; *a–b,* axial and transverse section, ×1; *c*, longitudinal section of peripheral zone showing pachysteles and striation, ×12 (Nicholson, 1886a); *d–e*, longitudinal and tangential sections showing striated microstructure of pachysteles, ×50 (new); *f–g*, axial and transverse sections of hypotype, IRScNB5254, Givetian, Olloy, Ardennes, Belgium, ×3 (Lecompte, 1952 in 1951–1952).

Order AMPHIPORIDA Rukhin, 1938

[*nom. transl.* Webby, Stearn, & Zhen, 1993, p. 174, *ex* Amphiporidae Rukhin, 1938 p. 90]

Stromatoporoids of dominantly dendroid form composed of compact to fibrous, single layer skeletal elements, commonly arranged in irregular amalgamate networks but also in pillars radiating upward and outward from growth axis, with or without axial canals, obscure laminae, and peripheral sheaths enclosing skeleton. *?middle Silurian, upper Silurian (Ludlow)–Upper Devonian (upper Famennian).*

Family AMPHIPORIDAE Rukhin, 1938

[Amphiporidae Rukhin, 1938, p. 90]

Diagnosis as for order. *?middle Silurian, upper Silurian (Ludlow)–Upper Devonian (upper Famennian).*

Amphipora Schulz, 1883, p. 245 [**Caunopora ramosa* Phillips, 1841, p. 19, SD Stearn, 1997c, p. 839; holotype lost, neotype, NHM. P0308, sections A1 to A6] [=*Haraamphipora* Rukhin, 1938, p. 93 (type, *H. pachyroides*, OD); =*Vicinustachyodes* Yavorsky, 1961, p. 56 (type, *V. mirabilis*, OD); =*Vicinostachyodes*

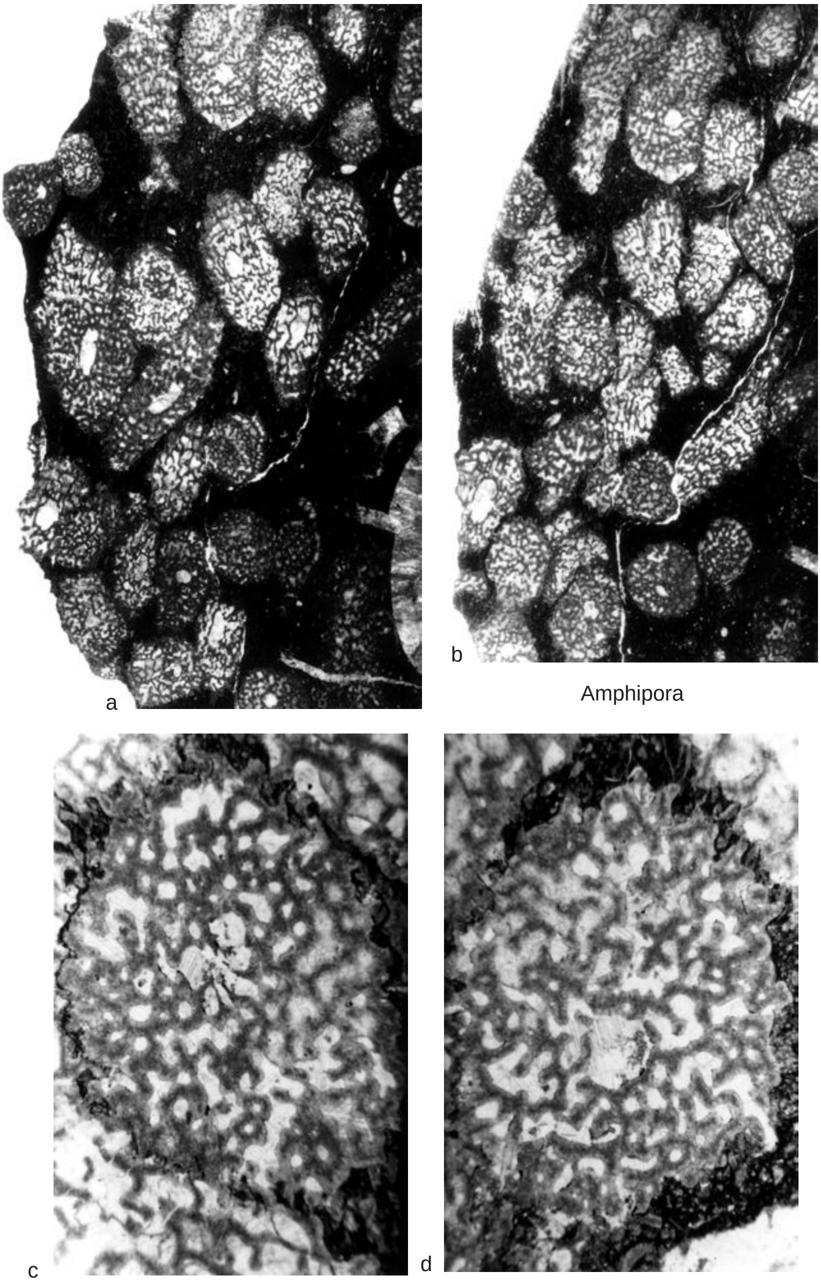


FIG. 475. Amphiporidae (p. 824–826).

YAVORSKY, 1967, p. 38, *lapsus calami pro Vicinustachyodes*; =*Stellopora* BOGOYAVLENSKAYA, 1972b, p. 27 (type, *Amphipora intexta* YAVORSKY, 1957, p. 62, OD), see WEBBY, STEARN, & ZHEN, 1993, p. 174–176 for discussion of date; =*Taeniostroma* DONG & WANG, 1982, p. 29 (type, *T. yunnanense*, OD); =*Columndictyon* DONG & WANG, 1982, p. 29 (type, *C. regulare* DONG & WANG, 1982, p. 30, OD); =*Tianshanostroma* DONG & WANG, 1984, p. 269 (type, *T. xinjiangense* DONG & WANG, 1984, p. 269–270, OD); =*Qinghaipora* DONG, 1991, p. 75 (type, *Q. gracilenta*, OD)] [STEARN (1997c) discussed the choice of a neotype and the variations in the neotype suite that justify placing in synonymy the genera listed above.] Skeleton dendroid, branching dichotomously, with axial canal locally absent, locally with well-defined wall, locally poorly defined, opening into interskeletal network of voids and irregular canals by pores. Skeletal network formed by pillars radiating upward and outward obliquely from axis, and short elements extending from and joining them to form an irregular structure that may, in transverse sections, define open or closed spaces. Peripheral sheaths sporadically developed in most species, as an imperforate, thin, skeletal wall supported beyond skeletal network by extensions of skeletal elements. Microstructure compact, fibrous. [The plethora of Middle and Upper Devonian occurrences and published species make the listing of their distribution impractical here.] *?middle Silurian, upper Silurian (Ludlow)–Upper Devonian (upper Famennian):* Russia (Belyj Island), *?middle Silurian;* Estonia, Russia (Urals, Kuznetsk Basin, central Siberia, Timan), Sweden (Gotland), Tien Shan, *Ludlow;* Canada (Arctic Island), China (Xinjiang), Russia (central and eastern Siberia, Salair, Kuznetsk Basin), Tien Shan, USA (Alaska), *Lower Devonian;* cosmopolitan at lower paleolatitudes, *Middle Devonian*; cosmopolitan at lower paleolatitudes, *Frasnian;* China (Guangxi), Russia (Pechora Basin), *Famennian;* Belgium, northeastern France, Germany (Sittard), *upper Famennian* or *Strunian.*——Fig. 475*a–d*. **A. ramosa* (Phillips), neotype, NHM. P0308, Chercombe Bridge Limestone, near Newton Abbott, Devon, England; *a–b*, two sections through neotype suite, ×2.5; *c–d*, two transverse sections across neotype stem showing variations in skeletal network and central canal, ×10 (Stearn, 2011b).——Fig. 476*a–b*. **A. ramosa* (Phillips), neotype, NHM. P0308, Chercombe Bridge Limestone, near Newton Abbott, Devon, England; *a*, longitudinal section from neotype suite showing axial canal, pillars, and peripheral sheath on only one side, ×10; *b*, axial to tangential section of stem from neoparatype, NHM. P0310, showing peripheral sheaths and well-developed pillars, ×10 (Stearn, 2011b).

Clathrodictyella Bogoyavlenskaya, 1965a, p. 42 [**Amphipora turkestanica* Lessovaja, 1962, p. 117; OD; holotype, GMU 46/489]. Similar to *Amphipora* in axial canal and peripheral sheaths, but in axial section, structural elements are gently arched, crumpled laminae or cysts, arranged in parabolic series transverse to axial canal. *Silurian (Ludlow):* Russia (eastern Urals), Uzbekistan (Tien Shan).——Fig. 477*a–b*. **C. turkestanica* (Lessovaja), holotype, GMU 46/489, Bankovyi horizon, eastern slope of Urals, axial and transverse sections, ×10 (Stearn, 2011b).

Euryamphipora Klovan, 1966, p. 14 [**E. platyformis*; OD; holotype, GSC 19834] [=*?Solidostroma* Khromykh, 1974a, p. 30 (type, *S. congesta,* OD)]. Growth form tabular, platelike; structure amalgamate in longitudinal section, with peripheral sheaths, may have long pillars evident in sections parallel to plate axes. [Klovan (1966) and Mistiaen

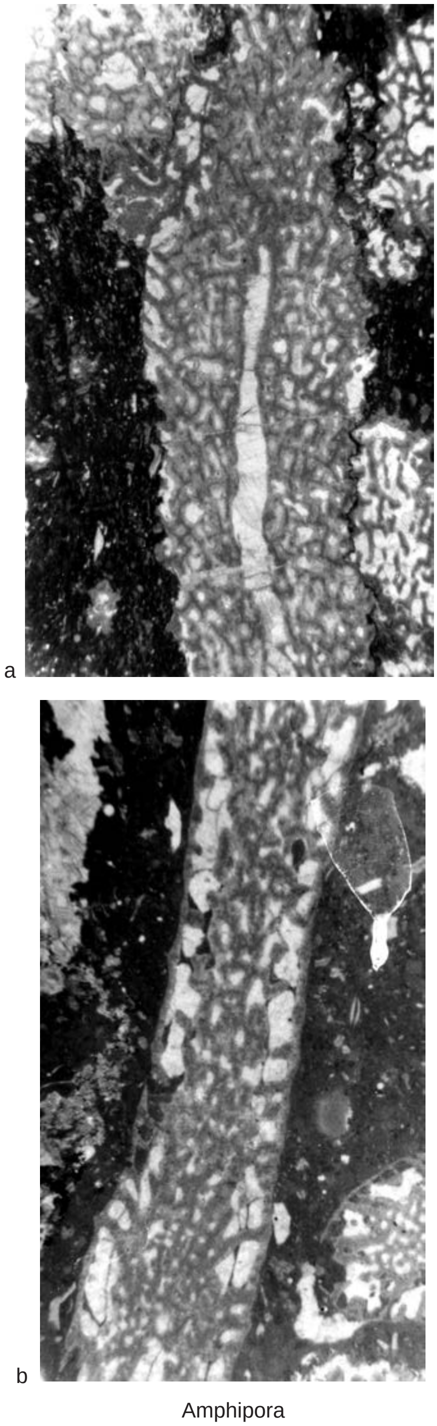


Fig. 476. Amphiporidae (p. 824–826).

Fig. 477. Amphiporidae (p. 826).

(1985) described the genus as growing as a horizontal plate; Cockbain (1984) reconstructed the skeleton as a vertical plate.] *Middle Devonian (Givetian)–Upper Devonian (Frasnian)*: Australia (Queensland), France (Boulonnais), *Givetian;* Afghanistan, Australia (West Australia), Canada (Alberta, Saskatchewan), *Frasnian.*——Fig. 478*a–b.* **E. platyformis*, holotype, GSC 19834, Leduc Formation, Redwater Field, Alberta, Canada; *a*, longitudinal section showing laminar growth form, ×5; *b*, longitudinal section showing amalgamate appearance and flexing of skeleton, ×10 (Stearn, 2011b).——Fig. 479*a–b.* **E. platyformis*, holotype, GSC 19834, Leduc Formation, Redwater Field, Alberta, Canada; *a*, longitudinal section showing peripheral sheaths, ×10; *b*, tangential section showing pillars at edge of skeleton and amalgamate structure, ×10 (Stearn, 2011b).

Novitella Bogoyavlenskaya in Bogoyavlenskaya & Dan'shina, 1984, p. 22 [**Paramphipora tchussovensis* Yavorsky, 1955, p. 159; OD; holotype, CNIGR 7351/136]. Similar to *Amphipora* but with prominent, gently arched laminae in axial sections. *Upper Devonian (Frasnian)*: Russia (Tsaritsin, now Volgograd region, eastern and western Urals).——Fig. 480*a–b.* **N. tchussovensis*

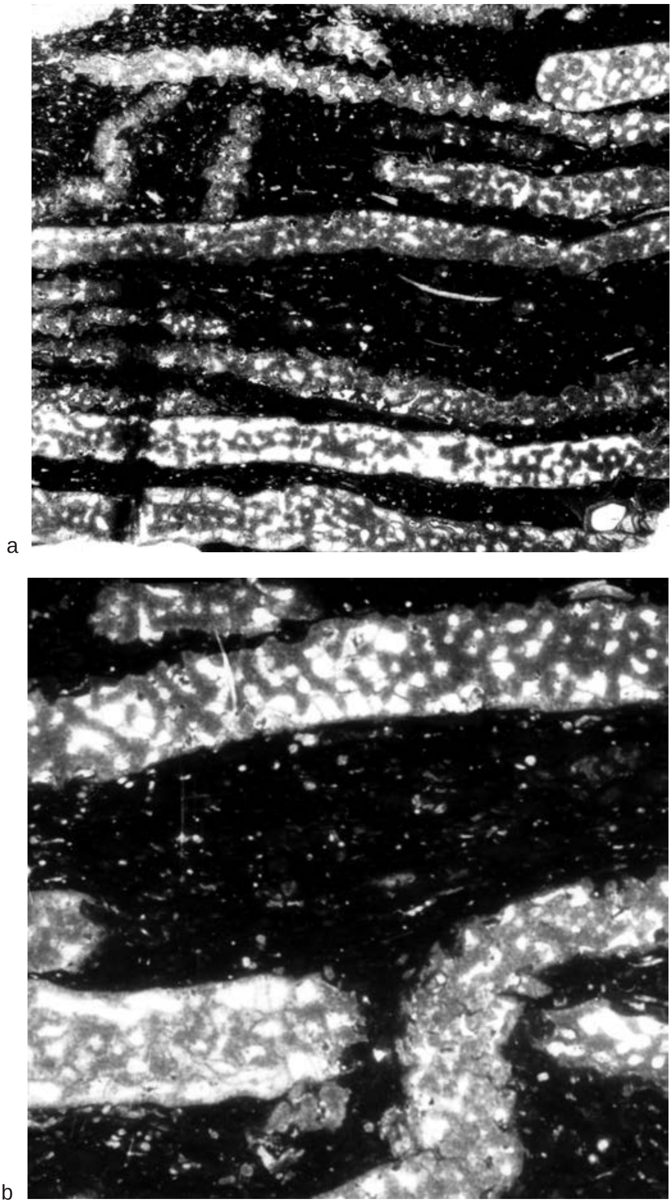
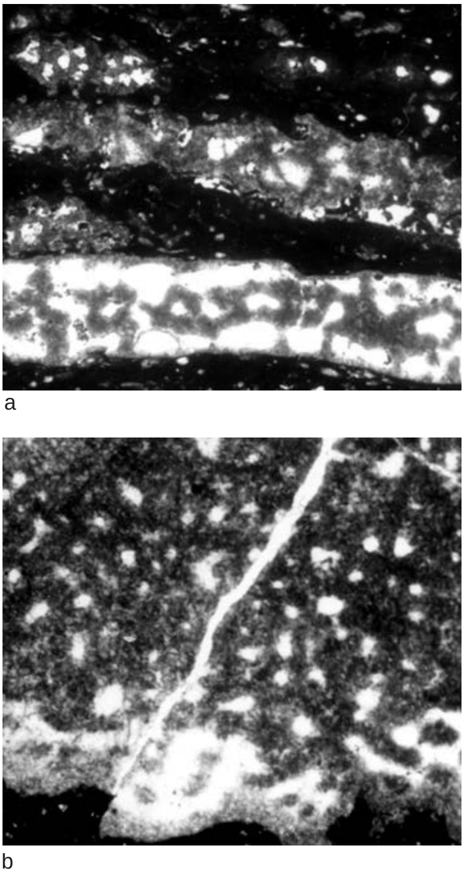


FIG. 478. Amphiporidae (p. 826–827).

(YAVORSKY), CNIGR 7351/136, Askynian horizon, Chusovaya River, western slope of Urals, transverse and axial to oblique transverse sections, ×10 (Yavorsky, 1955).

Paramphipora YAVORSKY, 1955, p. 154 [**P. mirabilis*; OD; holotype, CNIGR 7351/236] [=*Vacuustroma* NGUYEN HUNG & MISTIAEN, 1997, p. 193 (type, *V. michelini* NGUYEN HUNG & MISTIAEN, 1997, p. 198, OD)]. Similar to *Amphipora* in structure but with skeletal elements of vacuolate microstructure without central axis. [Although several writers (KLOVAN, 1966; STEARN, 1966, 1997c; FLÜGEL & FLÜGEL-KAHLER, 1968; COCKBAIN, 1984; MISTIAEN, 1988) have questioned the validity of YAVORSKY's genus because it was based on the absence of an axial dark line in the skeletal elements that they considered subject to diagenesis, YAVORSKY insisted (1968, 1969a, 1971) that it was equally distinguished by vacuolate microstructure. Since the only characters separating both *Paramphipora* and *Vacuustroma* from *Amphipora* are the lack of the axial line and the presence of vacuoles, the latter *(Vacuustroma)* is listed as a junior synonym here. Nearly all the more than 60 species that have been ascribed to *Paramphipora* are found in Russia and China only. Because the diagnoses and types of these species have not been individually examined to see whether they conform to YAVORSKY's definition, the list of occurrences is based on the original generic assignments and should be regarded as tentative.] *Silurian (?Wenlock, Ludlow)–Upper Devonian:* Russia (Belyj Island), *?Wenlock;* Russia (northwestern Kuznetsk Basin, Salair, western Pre-Urals, Ulachan Sis), *Ludlow;* Russia (northeastern Siberia, Salair), Uzbekistan, Vietnam, *Lower Devonian;* Kara Kalpaksk, China (Guizhou, Guangxi), Russia (Tyrgan), Turkey, *Middle Devonian;* France (Boulonnais), Russia (Lochitina Sea, northern Pre-Urals, western Pre-Urals, Kuznetsk Basin, Pechora Basin, Urals, River Chusovaya), Vietnam, *Frasnian;* Russia (Pechora Basin, western Pre-Urals), *?Famennian;* Russia (Urals, River Ai), Vietnam, *Givetian;* China (Guangxi), *Upper Devonian.*——FIG. 481*a.* **P. mirabilis*, holotype, CNIGR 7351/236, Ludlow, River Chernevaya, Salair, axial to tangential sections showing vacuolate skeletal material, ×10 (Yavorsky, 1955).——FIG. 481*b–e. P. michelini* (NGUYEN HUNG & MISTIAEN), Beaulieu Formation, Frasnian, Boulonnais, France; *b*, holotype, transverse section, GFCL 1507, showing vacuolate microstructure, ×20; *c*, holotype, drawing of transverse section, ×13; *d*, hypotype, drawing of transverse section, GFCL 1490, ×13; *e*, paratype, drawing of axial section, GFCL 149, ×13 (Nguyen Hung & Mistiaen, 1997).



Euryamphipora

FIG. 479. Amphiporidae (p. 826–827).

ORDER AND FAMILY UNCERTAIN

Clavidictyon SUGIYAMA, 1939, p. 441 [**C. columnare*; OD; holotype, Tôhoku University, Sendai, 60,813]. Columnar, without axial canal, amalgamate in axial zone but with well-defined laminae and short pillars confined to interlaminar space in peripheral zone. Compact microstructure. [Some characteristics suggest affinity to the clathrodictyids, others to the amphiporids.] *middle Silurian–Upper Devonian (upper Famennian)*: Japan, *middle Silurian;* USA

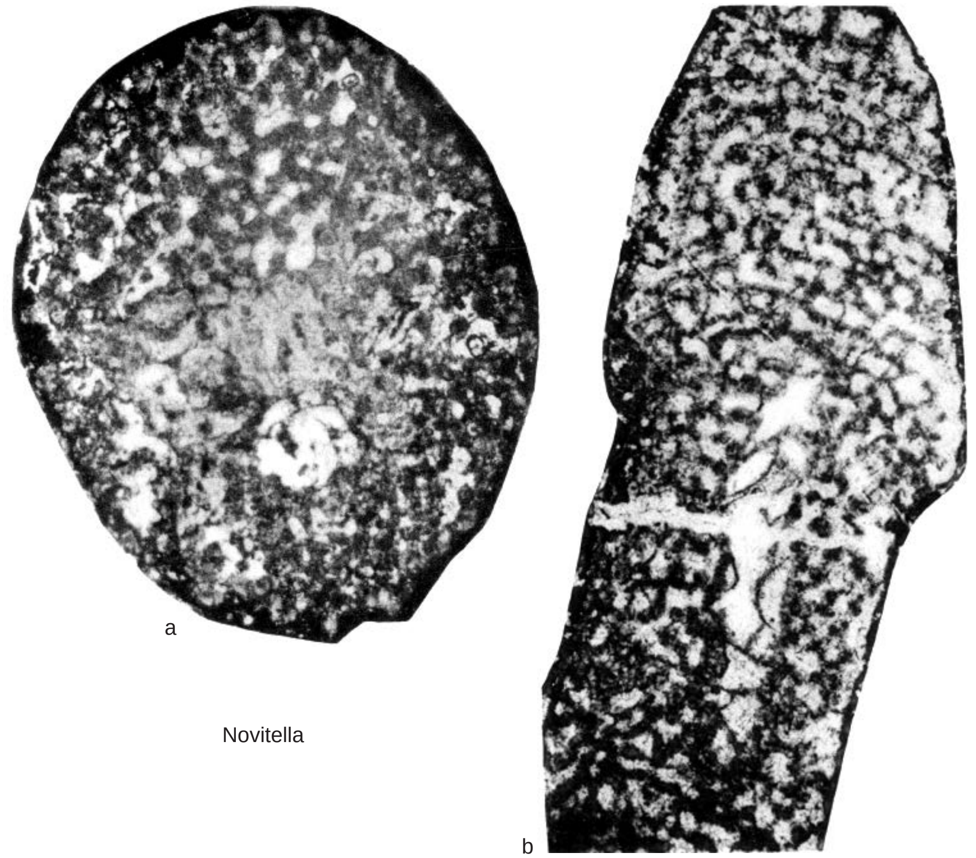


FIG. 480. Amphiporidae (p. 827–829).

(Michigan), *Middle Devonian;* China (Guangxi), *upper Famennian.*——FIG. 482*a–c.* **C. columnare*, holotype, 60,813, middle Silurian, Hikororoiti-mura, Japan; *a*, longitudinal sections, from type slide, ×6; *b*, transverse section, showing few laminae, ×10; *c*, transverse section showing well-defined laminae, ×10 (Stearn, 2011b).

Eostachyodes Dong & Wang, 1982, p. 28 [**E. compacta;* OD; holotype, NIGP 61351–61352]. Columnar growth form, without axial canal, structural elements in axial zone completely amalgamate, peripheral zone with pachystele-like elements; microstructure fibrous or melanospheric. [Dong and Wang (1982) placed the genus in the Idiostromatidae. Dong (1988) placed it in the Stachyoditidae. It differs from *Stachyodes* in lacking an axial canal, the extreme difference between axial and peripheral parts of the skeleton, and in its microstructure.] *Middle Devonian:* China (Yunnan).——FIG. 483,*1a–c.* **E. compacta*, holotype, NIGP61351-52, Gumu Formation, Wenshan, longitudinal and transverse sections, ×5 (Dong, 2001).

Lamellistroma Bogoyavlenskaya, 1977b, p. 17 [**L. lamelliferum* Bogoyavlenskaya, 1977b, p. 18; OD; holotype, SOAN 1089/101]. Thin, compact pillars and laminae forming regular, closely spaced grid. Pillars round in tangential section. [Bogoyavlenskaya (1977b) placed this genus in the family Densastromatidae, but Stearn (1980) placed it in synonymy with *Actinostroma*. Other possibilities are *Coenostroma, Gerronostroma,* or *Densastroma.*] *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*: Russia (eastern Urals), *Lochkovian;* Russia (eastern trans-Urals), *Pragian–Emsian;* Russia (eastern Urals), *Eifelian.*——FIG. 483,*2a–b.* **L. lamelliferum,* holotype, 1089/101,Tal'tiiskii horizon, Eifelian, River Saumy, eastern slope of Urals, Russia, longitudinal and tangential sections, ×10 (Stearn, 2011b).

Paschkoviella Kosareva, 1979, p. 43 [**P. aequicrassa*; OD; holotype, location of type specimen uncertain]. Spool-shaped pillars, superposed, and extensive laminae, locally with axial light zone. Microstructure finely porous. *Middle Devonian (Eifelian)*:

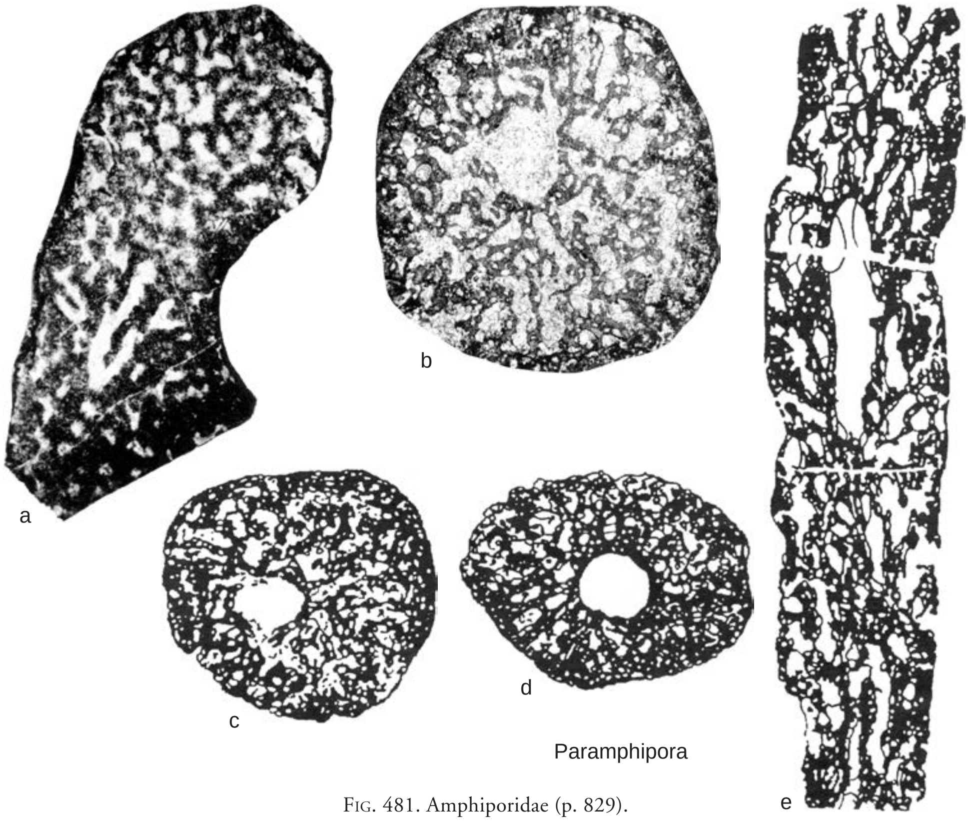


FIG. 481. Amphiporidae (p. 829).

Russia (River Zolotukha).——FIG. 483,*3a–b*. **P. aequicrassa;* holotype, longitudinal and tangential sections, ×10 (Kosareva, 1979).

Perplexostroma BOGOYAVLENSKAYA, 1981, p. 32 [**Stromatopora dzvenigorodensis* RIABININ, 1953, p. 51; OD; VNIGRI 153]. Pillars long, sinuous, anastomosing; tangential elements largely dissepiments. [This genus is probably synonymous with *Vikingia* on the basis that the type species *S. dvenogorodensis* RIABININ is a species of *Vikingia* comparable to *V. tenuis* (NESTOR), and the specimens illustrated by BOGOYAVLENSKAYA (1981, pl. 23,*2;* pl. 24,*1*) are not conspecific with the designated type species.] *Silurian (Ludlow–Pridoli)*: Ukraine (Podolia).——FIG. 484,*1a–b*. **P. dzvenigorodense* (RIABININ), holotype, VNIGRI 153, lower Ludlow, River Dneister, longitudinal and tangential sections, ×10 (Riabinin, 1953).

Praeidiostroma BOGOYAVLENSKAYA, 1971a, p. 108 [**P. praecox*; OD; holotype, SOAN 38a/982]. Dendroid growth form with axial canal branching into smaller canals. Pillars and laminae thin, long, apparently compact. [The type species appears to be a dendroid form of *Gerronostroma* with an axial canal.] *Silurian (Ludlow)*: Russia (eastern slope of Urals).——FIG. 485,*1a–b*. **P. praecox*, holotype, 38a/982, axial and transverse sections, ×10 (Stearn, 2011b).

Pseudoactinostroma LESSOVAJA, 1970, p. 81 [**P. hamidulense* LESSOVAJA, 1970, p. 82; OD; holotype, GMU 13/493]. Pillars confined to interlaminar space, compact, branching and joining, locally forming intermediate laminae; laminae extensive, widely spaced, formed of colliculi from pillars, making hexactinellid network in tangential section. [The laminae are much like those of an actinostromatid.] *Middle Devonian (Eifelian):* Central Asia (Zeravshan Mountains).——FIG. 484,*2a–b*. **P. hamidulense*, holotype, 38a/982, longitudinal and tangential sections, ×10 (Stearn, 2011b).

?**Pseudostromatopora** DONG, 1991, p. 70 [**P. yushuensis* DONG, 1991, p. 71; OD; holotype, NIGP 91933]. Structure irregular of dominant pachysteles, locally forming amalgamate network, cut as isolated masses of irregular outline in tangential section, separated by allotubes, cellular to diffuse in microstructure; tangential elements largely dissepiments. [The genus is a homonym of *Pseudostromatopora* SIMIONESCU, 1926, a bryozoan, and requires a new name.] *Middle Devonian–Upper Devonian*: China (Qinghai, Tibet).——FIG.

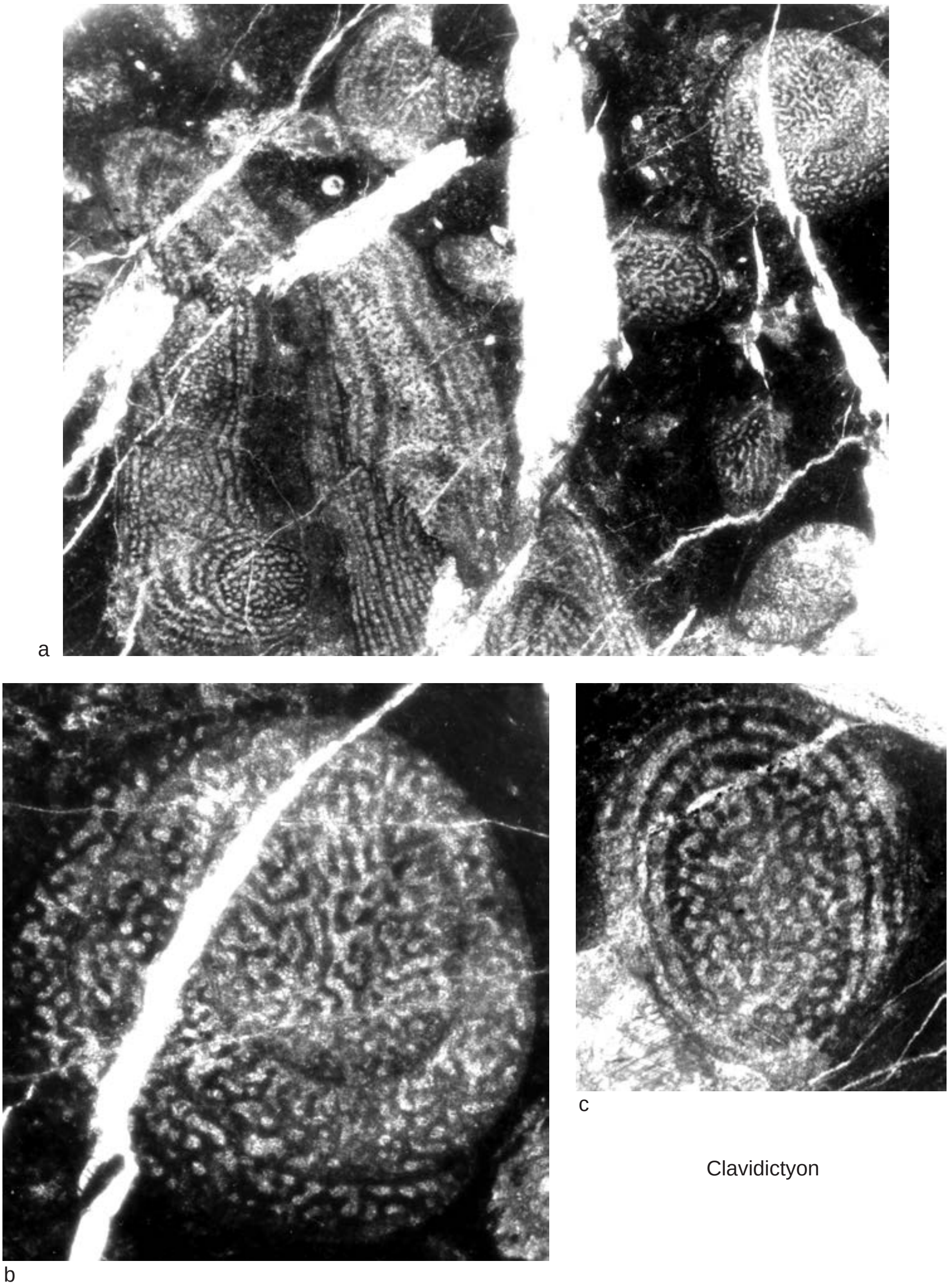


FIG. 482. Uncertain (p. 829–830).

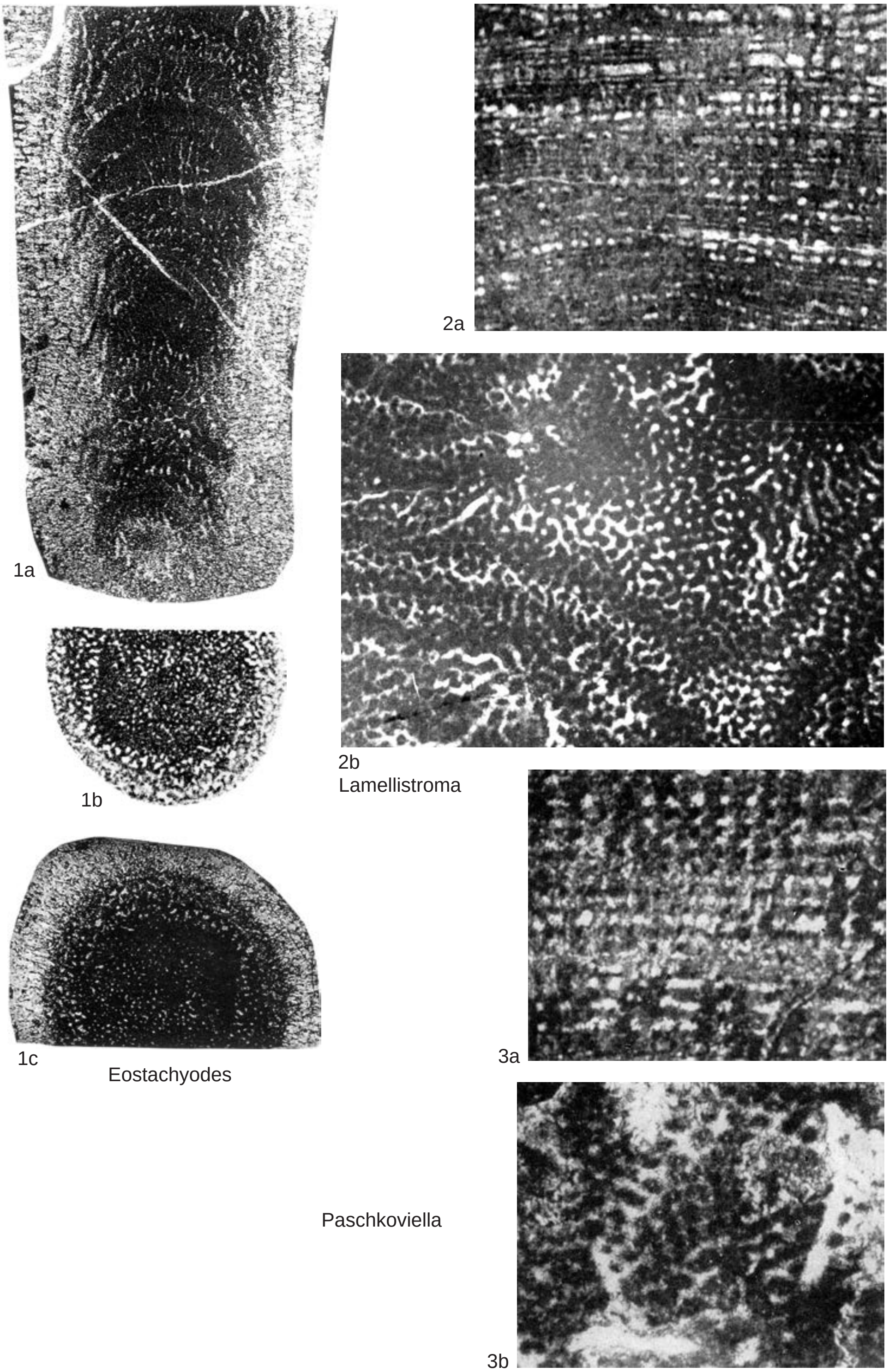
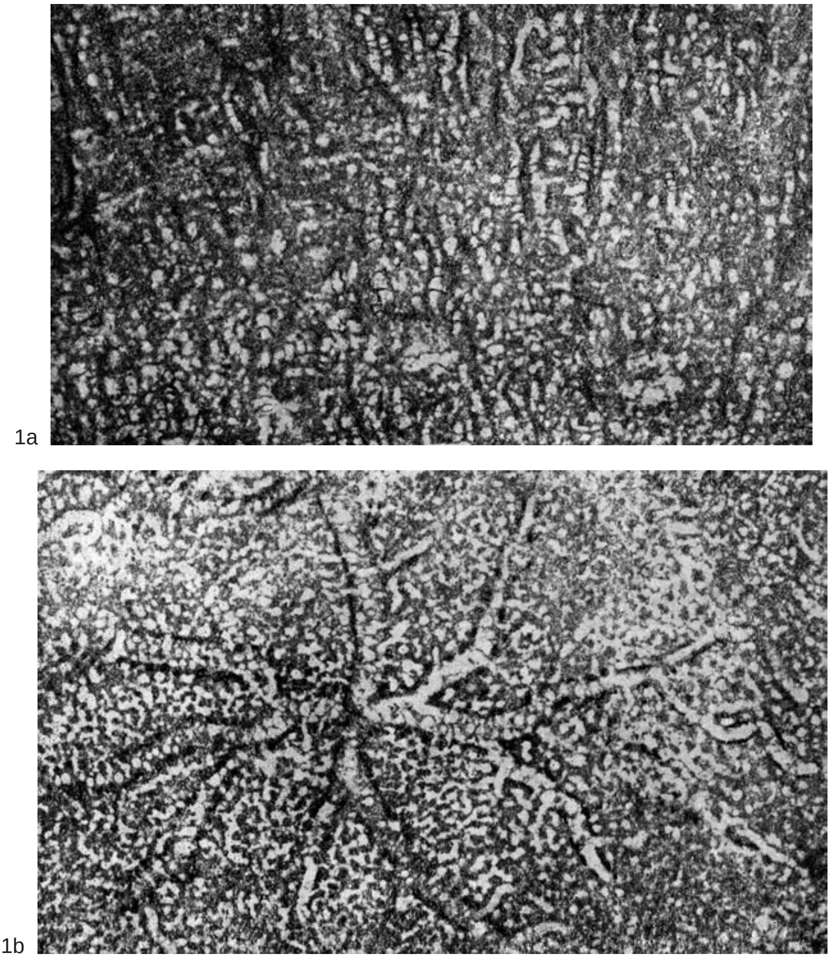
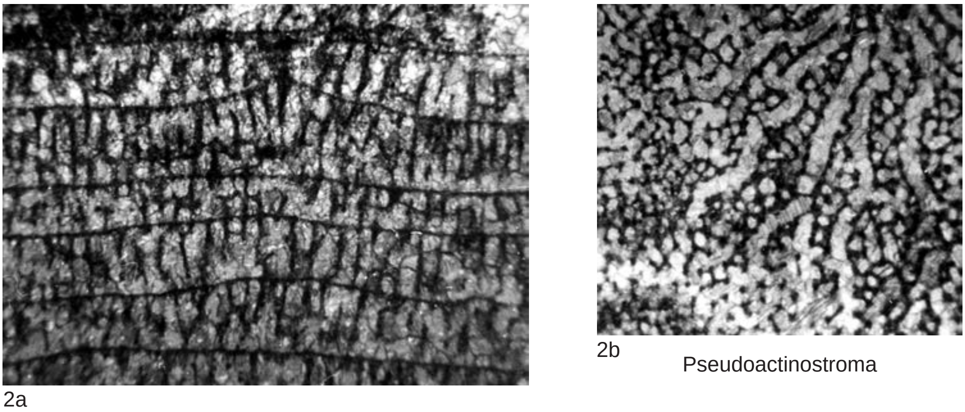


FIG. 483. Uncertain (p. 830–831).



Perplexostroma



Pseudoactinostroma

FIG. 484. Uncertain (p. 831).

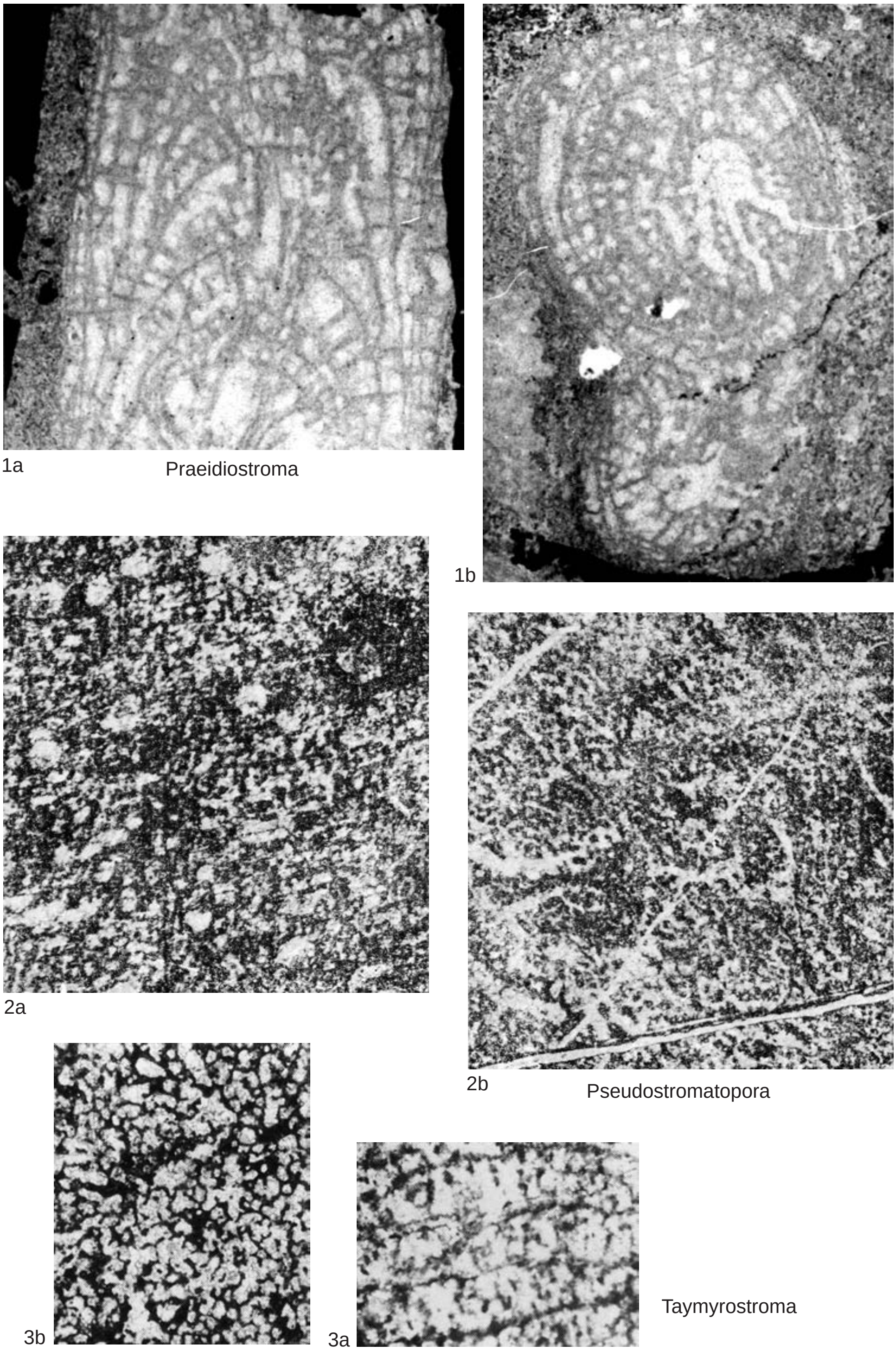


FIG. 485. Uncertain (p. 831–836).

485,*2a–b*. **P. yushuensis*, holotype, 91933ab, Xiongqin Formation, southern Qinghai, China, longitudinal and tangential sections, ×10 (Dong, 2001).

Taymyrostroma Khromykh, 2001, p. 13 [**T. taymyrensis;* OD; holotype, TsGM 2022/4]. Laminae thin, compact, single layer, extensive; longitudinal structural elements (possibly pillars) highly irregular, confined to interlaminar space, rarely extending directly across interlaminar space, forming a tangled mass in longitudinal section; thin, compact, in tangential section forming an irregular, fine meshwork enclosing rounded galleries; astrorhizae well developed, superposed. [Although placed in the Lophiostromatidae by Khromykh (2001), this genus is unlike the other genera in the family or any other late Ordovician stromatoporoid in its complex pillar structure between extensive thin laminae. In these features, it shows convergence with such younger genera such as *Intexodictyides* and *Atelodictyon.*] *Upper Ordovician (Katian):* Russia (Taimyr Peninsula).——Fig. 485,*3a–b*. **T. taymyrensis*, holotype, CSGM 2022/4, left bank of Parnaya River, Siberia, Burskii horizon, Nyun'skaya Subformation; *a,* longitudinal section, ×10; *b,* tangential section, ×10 (Khromykh, 2001).

CLASS UNCERTAIN, ORDER PULCHRILAMINIDA: SYSTEMATIC DESCRIPTIONS

B. D. WEBBY

Class UNCERTAIN
Order PULCHRILAMINIDA Webby, 2012

[Pulchrilaminida WEBBY, 2012a, p. 1]

Large, laminar, domical to columnar skeleton represented by thin latilaminae of mainly calcite spar–replaced skeletal elements that intercalate with mudrock layers; internally main skeletal elements preserved as erect, slender, upwardly tapering, spinose rods (walled but with spar-replaced centers); typically extending from tops of latilaminae into overlying mudrock layers; weakly developed meshworks also preserved in localized areas where rods combine with undulating rows of long, low cysts, or sometimes latilaminae exhibit intermingling wispy, threadlike elements; no astrorhizae known. *Lower Ordovician (upper Tremadocian)–Middle Ordovician (lower Darriwilian).*

This small group of large, hypercalcified, frame-building organisms occupies an important place in the development of Lower Ordovician–Middle Ordovician reefs in North America, the Argentine Precordillera, and southern China (WEBBY, 2002; ADACHI, LIU, & EZAKI, 2011), but its affinities remain to be fully evaluated. The group has no apparent links with Cambrian hypercalcified sponges, but in exhibiting skeletons of large size, frayed lateral margins, and well-developed latilaminae, it shares certain resemblances with the nonspiculate Ordovician–Devonian labechiid stromatoporoids (and other stromatoporoids). The pulchrilaminids, however, differ morphologically in having a more loosely aggregated meshwork of skeletal elements, including slender, upwardly tapering, spinose rods that are spiculelike and may represent diagenetically altered styles. They therefore seem best regarded as a separate, independent group of hypercalcified sponges. Relationships with known spiculate sponge groups remain uncertain. Previously the family Pulchrilaminidae WEBBY, 1993, was doubtfully incorporated in the order Labechiida (WEBBY, 1993, 1994, 2004b; WEBBY in STEARN & others, 1999) but is excluded herein.

BOGOYAVLENSKAYA (2001a, p. 46), adopted a different approach in introducing the order Protolabechiida to accommodate members of three families: the Lophiostromatidae NESTOR, 1966a, Stratodictyidae BOGOYAVLENSKAYA, 1977a, and Pulchrilaminidae WEBBY, 1993. But this is a heterogeneous grouping that bears little relation to the key morphological features of both pulchrilaminids and the other families. In this *Treatise* volume, the families Lophiostromatidae and Stratodictyidae are maintained as parts of the order Labechiida (see p. 709–754). BOGOYAVLENSKAYA's family Stratodictyidae is recognized as a part of the family Labechiidae NICHOLSON, 1879b (based on genus *Stratodictyon* WEBBY, 1969), and a part of the family Rosenellidae YAVORSKY in KHALFINA & YAVORSKY, 1973 (based on genus *Pseudostylodictyon* OZAKI, 1938, and its junior synonym *Parksodictyon* BOGOYAVLENSKAYA in BOGOYAVLENSKAYA & LOBANOV, 1990), of the Labechiida. None of the characters used by BOGOYAVLENSKAYA (2001a) to define the order Protolabechiida is diagnostic specifically of that order (for English translation of BOGOYAVLENSKAYA'S [2001a] diagnosis of order Protolabechiida, provided by Heldur Nestor, see p. 710). All listed morphological characters are present also in representatives of the order Labechiida. Consequently, the Protolabechiida is regarded in part as a junior synonym of the Labechiida. However, the family Pulchrilaminidae has fundamentally different diagnostic characters and must be separated from labechiids, including BOGOYAVLENSKAYA's two other protolabechiid families. The uniquely pulchrilaminid features are: (1) long, slender, spinose, spiculelike rods (usually erect but sometimes tilted) that characteristically protrude above tops of latilaminae into overlying mudrock, or more randomly spaced, oblique-to-erect threadlike elements; and (2) may, in localized areas (usually upper parts of latilaminae), combine in loosely aggregated meshworks with rows of finer, undulating cyst plates.

Family PULCHRILAMINIDAE Webby, 1993

[Pulchrilaminidae WEBBY, 1993, p. 58]

Characters as for order. [The pulchrilaminid skeleton is distinguished by its large size (commonly up to 300 mm in width and 500 mm in height), thin latilaminae, and mainly erect (in a few places tilted), slender, upwardly tapering, spinose (spiculelike) rods. The latilaminae vary from 0.1 to 3.0 mm in thickness and are characteristically bounded by growth interruptions, probably mainly caused by regular, episodic sedimentation events, resulting in the intercalated mudrock layers. The latilaminae are commonly frayed at lateral margins to give a markedly ragged appearance to the skeleton. Even the thinnest latilaminae (0.1–0.2 mm thick) were able to support the bases of long, slender, tapering, spinose rods in upright orientations, and they extend into overlying layers of mudrock (maintaining their orientation in the mud to a height of at least 0.5 mm) without much evidence of visible support (apart from a few wispy films of broken or incomplete cyst plates). Cyst plates generally are not well preserved in the *Pulchrilamina* skeleton, mainly occurring in localized areas near tops of latilaminae as rows of fine, closely spaced, undulating, platelike elements forming meshworks with the slender, upright, spinose rods. Only a few examples of rods tilted out of parallel alignments suggest that the overall structural meshwork of rods and cysts was rather weakly developed, with the cyst plates providing very limited support, unlike the larger, more compact and rigid skeletal frameworks of labechiid stromatoporoids. The intermingling, threadlike elements in some growth layers of *Zondarella* resemble the slender threads of a possible unnamed cyanobacterium (or possibly alga) that intergrew with the labechiid stromatoporoid *Cystostroma* in the Upper Ordovician Gordon Group, Tasmania (WEBBY, 1991, fig. 10a–c), which raises the possibility that *Zondarella* may have sometimes developed as an intergrowth of pulchrilaminid and cyanobacterial crusts. *Ianilamina* is another problematic genus that exhibits slender threadlike strands but differs in developing porous laminae]. *Lower Ordovician (upper Tremadocian)–Middle Ordovician (lower Darriwilian).*

Pulchrilamina TOOMEY & HAM, 1967, p. 983 [**P. spinosa* TOOMEY & HAM, 1967, p. 983, pl. 128,*1–4;* M; holotype, thin section, U.S. National Museum, Washington, no. USNM 155300, remains unfigured; three paratypes, USNM no. 155303, 155304, 155315, all longitudinal sections, have been figured (TOOMEY & HAM, 1967, pl. 128,*1–4*]. Large, strongly latilaminate, laminar, domical-to-columnar skeleton; latilaminae commonly ragged or frayed toward lateral margins, bounded top and bottom by growth interruptions, and alternating between wedges of mudrock; internally exhibit upwardly tapering long, slender, spinose (spiculelike) rods, characteristically protruding beyond tops of latilaminae into overlying mudrock; a few may be tilted out of an orderly, subparallel alignment; also, more localized rows of long, thin, low, undulating cyst plates may be preserved, forming meshworks in combination with the rodlike elements, but these appear, in a few places, to be rather loosely aggregated with some cyst plates not entirely fused to rods; in most areas, latilaminae are mainly replaced by spar, including crystalline calcite mosaics; no astrorhizae have been confirmed. *Lower Ordovician (upper Tremadocian–Floian):* Canada (Newfoundland), United States (Texas, Oklahoma), southern China (Guizhou, Hubei, Anhui).——FIG. 486*a–c*. **P. spinosa*; El Paso Group, McKelligon Canyon Formation, southern Franklin Mountains, western Texas, and Arbuckle Group, Kindblade Formation, Oklahoma; field photographs of outcrops showing growth form of skeletons; *a,* photograph of part of a reef mound, Kindblade Formation, dipping at 45° N, with exposure of individually

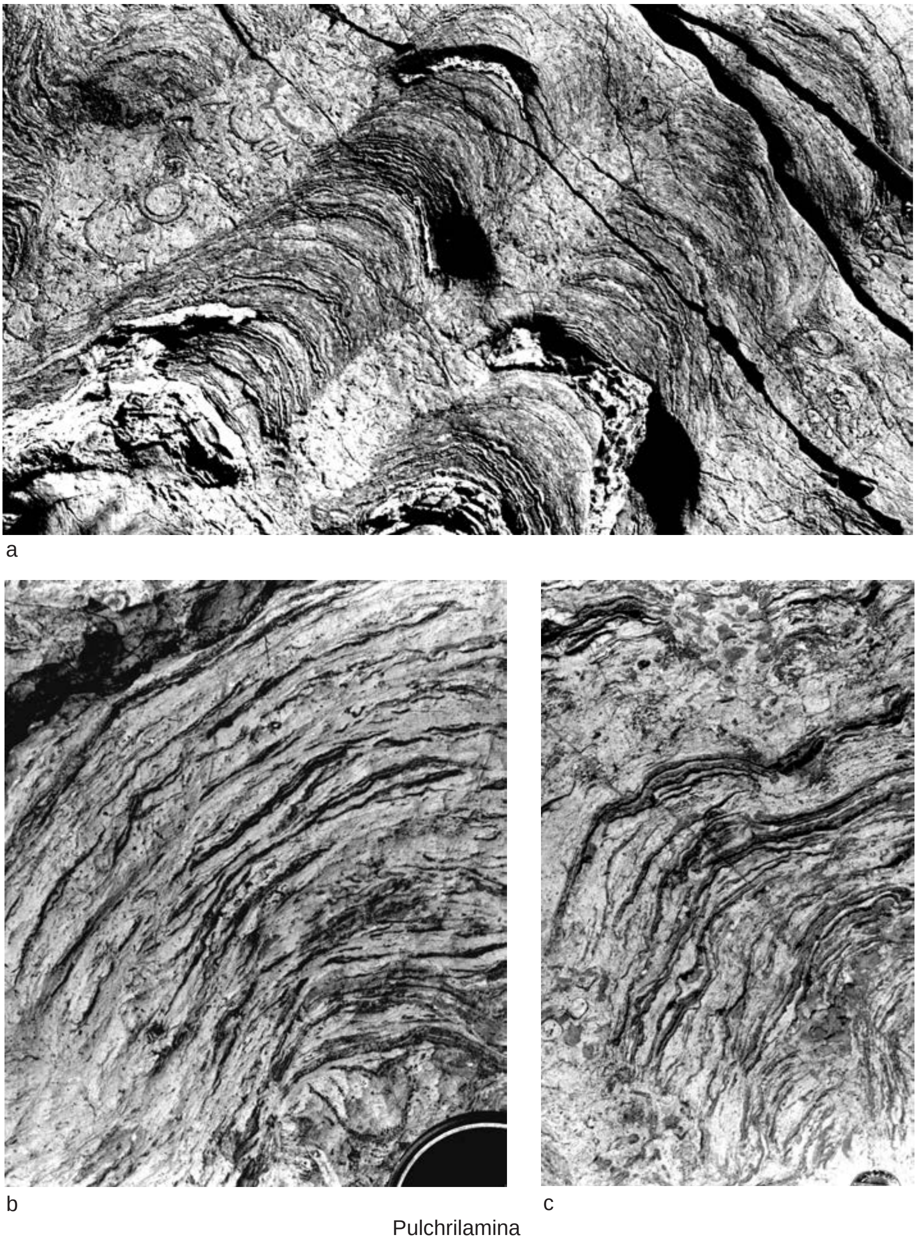


FIG. 486. Pulchrilaminidae (p. 838–841).

large *Pulchrilamina* skeletal mounds that exhibit a columnar shape and lateral margins that sometimes have a ragged appearance, but in other places have apparently been cut by narrow erosion channels and infilled by calcarenite deposits; structures exposed along Interstate Highway 35, southern Arbuckle Mountains, Oklahoma, ×0.24 (Webby, 2012a); *b,* more detailed characteristics of domical *Pulchrilamina* skeleton showing distinctive, slightly undulating laminae that appear to individually taper toward lateral margins of specimen (see area at lower left); exposed in reef mound, main biohermal interval, McKelligon Canyon Formation, southern Franklin Mountains, ×0.46 (Webby, 2012a); *c,* part

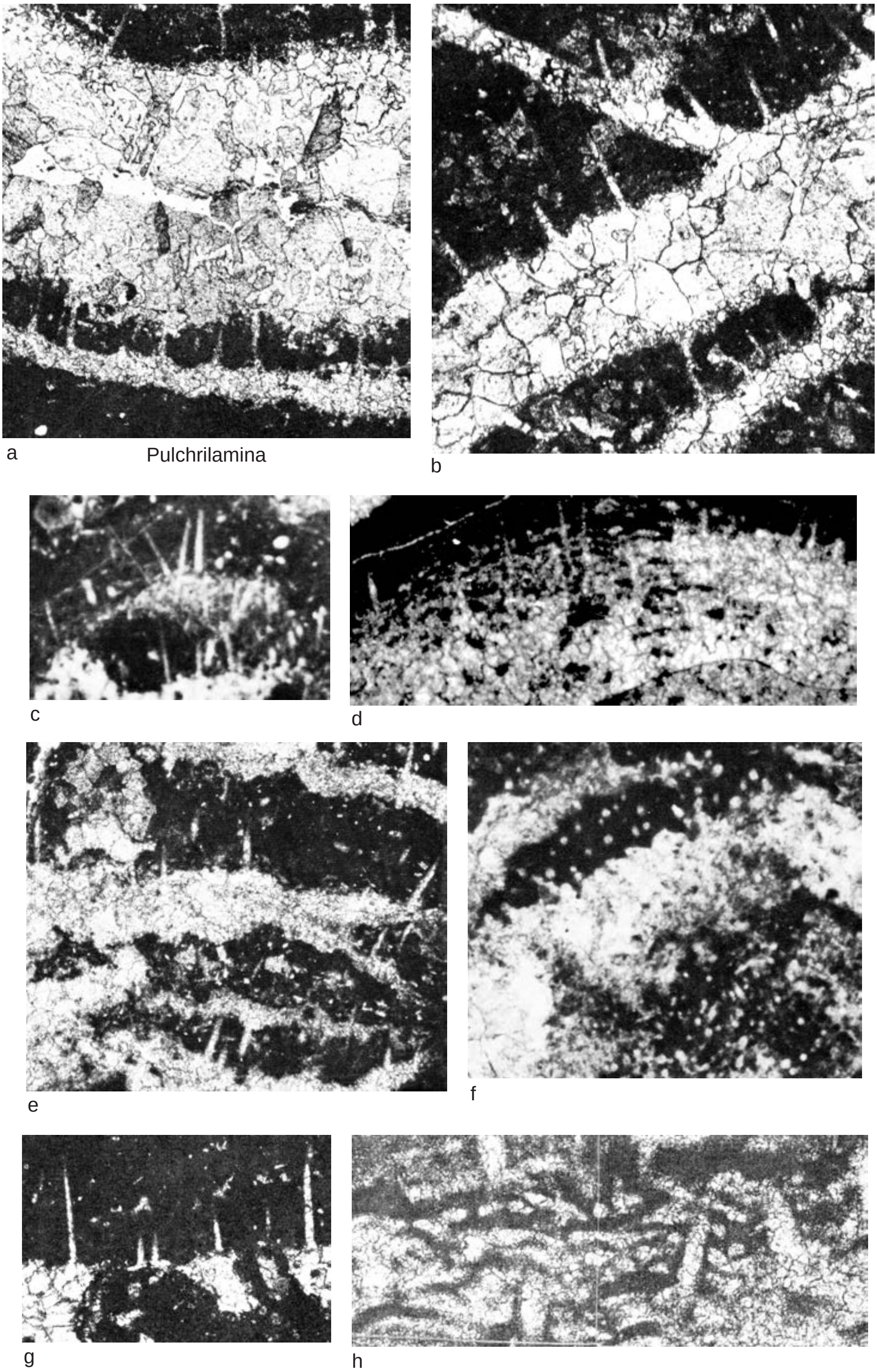


FIG. 487. Pulchrilaminidae (p. 838–841).

of domical *Pulchrilamina* skeleton, laminae (see area at lower left) on lateral margin appearing to be sharply truncated by an erosion channel; main biohermal interval, McKelligon Canyon Formation, southern Franklin Mountains, ×0.33 (for additional locality details, see TOOMEY & BABCOCK, 1983, p. 51–91, Stop 2) (Webby, 2012a).——FIG. 487*a–h*. **P. spinosa,* thin sections of type and other specimens; *a,* paratype, USNM 155315, ~137 m above base of Kindblade Formation, Mill Creek section, Arbuckle Mountains, Murray County, Oklahama, thin, lowermost, spar-filled latilamina and vertical spinose rods, continuous through a dark, mudrock inclusion into much thicker, overlying latilamina (completely replaced by mosaic calcite), ×20 (Toomey & Ham, 1967, pl. 128,*4*); *b,* paratype, USNM 155304, main mound section, lower part, McKelligon Canyon Formation, southern Franklin Mountains, western Texas, completely recrystallized main latilamina, and irregularly distributed, vertical, slightly tapering-upward, spinose rods that protrude upward into overlying mudrock, ×30 (Toomey & Ham, 1967, pl. 128,*3*); *c,* longitudinal section of specimen, MC-38-MB, D. V. LeMone collection, University of Texas, El Paso, McKelligon Canyon Formation, southern Franklin Mountains, divergent spinose rods, suggesting they formed in a loosely aggregated skeleton of weakly developed, very fine horizontal elements, unlike labechiid structures, ×20 (Webby, 1986, fig. 4B; reproduced with the permission of Oxford University Press: "Problematic Fossil Taxa," 1986, edited by A. Hoffman & M. H. Nitecki, p. 153, fig. 4B); *d,* longitudinal section, thin section no. PP22967, Toomey's collection, Field Museum of Natural History, Chicago, same horizon in Mill Creek section as view *a,* finely preserved meshwork of long, slender, spinose rods and undulating rows of long-low cyst plates in upper part of latilamina, ×40 (Webby, 1986, fig. 3E; reproduced with the permission of Oxford University Press: "Problematic Fossil Taxa," 1986, edited by A. Hoffman & M. H. Nitecki, p. 153, fig. 3E); *e,* longitudinal section of unnumbered specimen, mound horizon, lower portion of McKelligon Canyon Formation, southern Franklin Mountains, part of latilamina forking into two (right center of photo), and a markedly spinose rod that projects up into dark mudrock above upper splay of that latilamina (right center), ×20 (Toomey & Nitecki, 1979, fig. 12a; reproduced with permission of the Managing Editor of *Fieldiana,* Harold Voris, Field Museum of Natural History, Chicago); *f,* tangential section, thin section no. PP22845, Toomey's collection, Field Museum of Natural History, Chicago, mound horizon in lower part of McKelligon Canyon Formation, southern Franklin Mountains, showing round shapes of intersected spinose rods, ×20 (Webby, 1986, fig. 3C; reproduced with the permission of Oxford University Press: "Problematic Fossil Taxa," 1986, edited by A. Hoffman & M. H. Nitecki, p. 153, fig. 3C); *g,* longitudinal section of portion of paratype, USNM no. 155304, same horizon and locality as view *b;* very long, slender, upwardly tapering spinose rods from section of underlying latilamina that is only partially differentiated by spar-replacement structures (Toomey & Ham, 1967, pl. 128,*1*); *h,* enlarged longitudinal section of unnumbered specimen from same locality and horizon as view *e,* showing greater detail of meshwork of vertical rods (spar-replaced but not wall-less vertical structures) and undulating horizontal rows of variably sized cyst plates, from tiny vesicles to more moderately sized, elongate, low-convexity structures, ×80 (Toomey & Nitecki, 1979, fig. 13a; reproduced with permission of the Managing Editor of *Fieldiana,* Harold Voris, Field Museum of Natural History, Chicago.).

?Ianilamina PICKETT & ZHEN in ZHEN & PICKETT, 2008, p. 63 [**I. kirkupensis* PICKETT & ZHEN in ZHEN & PICKETT, 2008, p. 64, fig. 5A–H,J; M; Londonderry Geoscience Centre, Geological Survey of New South Wales, Australia, holotype, thin sections no. MMF29887a-b and five paratypes, MMF44870a-b, MMF35560a-b, MMF44875a-b, MMF44876, and MMF 44879; eight thin sections]. Skeleton laminar to broadly domical in shape, and composed of successive, comparatively thin latilaminae (incremental units) that are discontinuous laterally and subdivided into a lower part of thicker, poorly differentiated, vaguely meshwork-like areas of threadlike strands, flocculent structures and calcite spar replacement textures, and an upper part defined by a very thin, darker, densely porous lamina. In addition, succession of latilaminae may be interrupted by darker mudrock layers, lighter-colored spar-filled cavities and encrustations of organisms like cyanobacteria, sponges, and bryozoans. [The presence of porous laminae is not characteristic of other pulchrilaminid genera; therefore, the genus is only doubtfully referred to the group. Other features of *Ianilamina* are similar to *Zondarella*; however, *Zondarella* shows a few traces of very fine, rounded, dotlike shapes suggestive of spinose rods, but these still require to be positively confirmed; see further discussion of *Ianilamina* in PICKETT and ZHEN (in ZHEN & PICKETT, 2008, p. 64, 66)]. *Middle Ordovician (lower Darriwilian):* Australia (New South Wales).——FIG. 488*a–f*. **I. kirkupensis;* limestone lens from base of Goonumbla Volcanics, Kirkup property, near Gunningbland, central New South Wales; *a–c,* paratype MMF 44875a, longitudinal section showing different enlargements of the same thin section; *a,* general view of domical skeleton with extensive, thin latilaminae that encrusts an anthaspidellid sponge (lower right), ×1.2 (Zhen & Pickett, 2008, fig. 5B); *b,* enlarged view of upper right part of view *a* showing successive latilaminae with a mainly dark flocculent appearance, except where capped by even darker, crustlike laminae and in an area near the middle where latilaminae have been largely replaced by lighter sparry calcite infills, ×6.8 (Zhen & Pickett, 2008, fig. 5E); *c,* detailed view of small area in upper left part of view *b* showing regular latilaminar elements but may

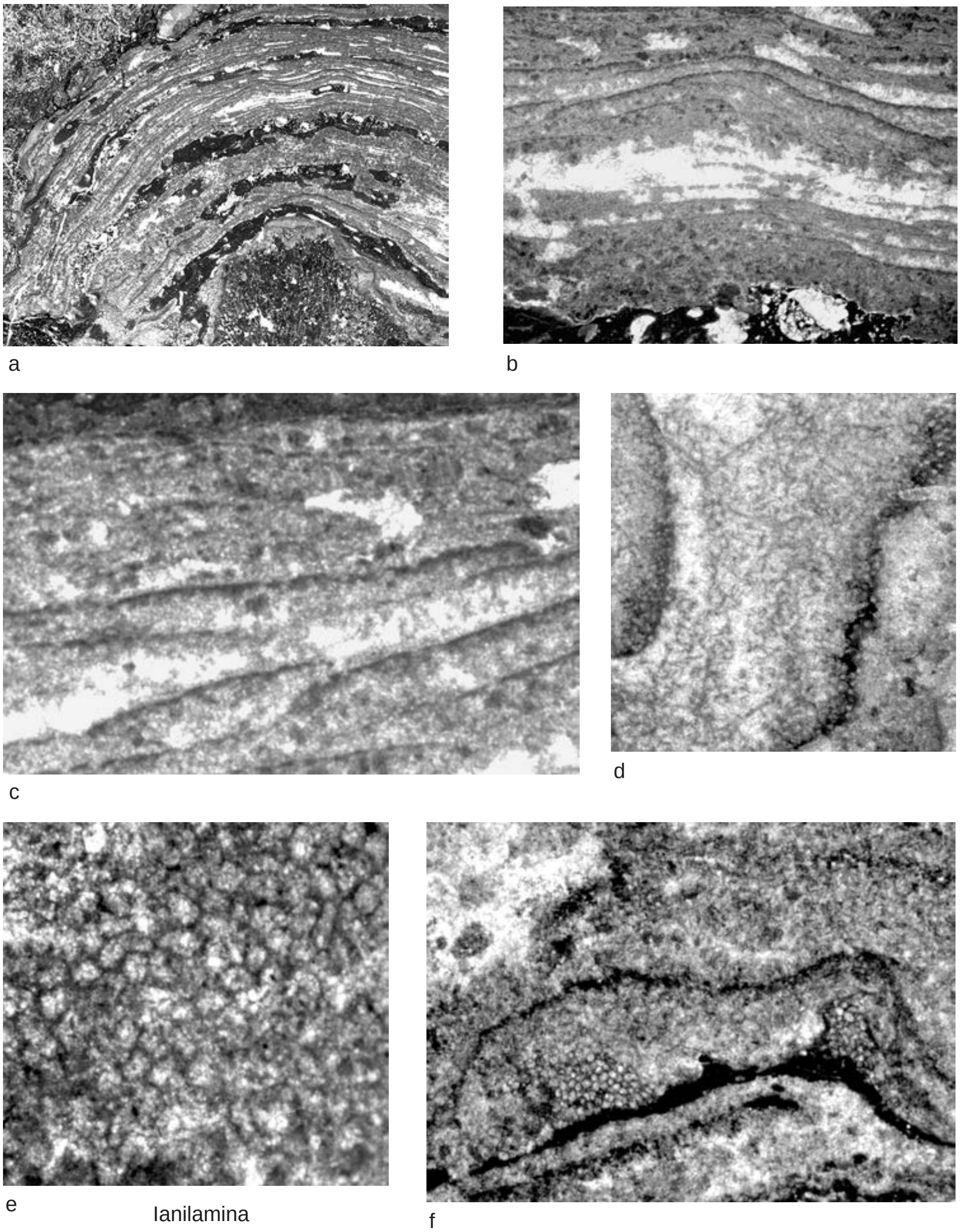


FIG. 488. Pulchrilaminidae (p. 841–843).

have only limited lateral continuity, as shown by a number of terminations where an upper lamina curves downward to a meet an underlying lamina abruptly; each crustlike lamina commonly exhibits a row of very small disruptions that represent pores; vaguely threadlike strands are only shown in a few small areas within latilaminae, whereas irregular, elongated areas with sparry calcite replacements are more common, ×16.7 (Webby, 2012a); *d,* oblique-tangential section of paratype MMF 44875b through a latilamina showing porous laminae along latilaminae boundaries and threadlike to vaguely cellular elements within the body of central latilaminar unit, ×8 (Zhen & Pickett, 2008, fig. 5F); *e,* tangential section of holotype MMF 29887b, illustrating details of the pores within a

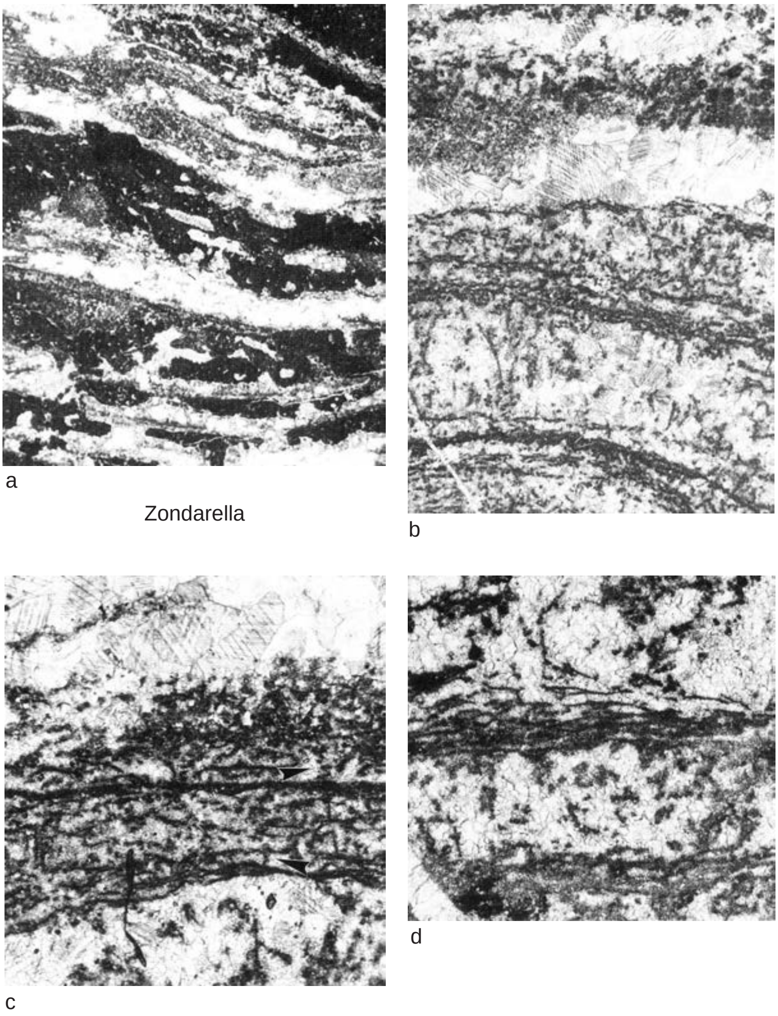


FIG. 489. Pulchrilaminidae (p. 843–844).

single lamina, ×40 (Zhen & Pickett, 2008, fig. 5J); *f,* longitudinal view of paratype MMF 44876 showing two small encrusting, rounded to irregular possible bryozoan colonies that grew above a dark mudrock sliver between underlying and overlying latilaminae of *Ianilamina,* ×10 (Zhen & Pickett, 2008, fig. 5G).

Zondarella KELLER & FLÜGEL, 1996, p. 188 [**Z. communis* KELLER & FLÜGEL, 1996, p. 188, pl. 47,*1,7,9;* pl. 48,*1–3;* M; Institute of Paleontology, University of Erlangen, Germany, no. RA 641; no illustrations of types or other material have yet been illustrated in tangential section]. Large, mainly domical to laminar skeleton characteristically composed of stacked, sheetlike growth layers, in places simulating latilaminae; both irregularly undulating, horizontal dark laminae, sometimes recognizable as less continuous discrete, elongated low convexity cyst plates or less continuous horizontal, spaced-out rows of colliculi-like rods, and more localized, randomly spaced, intermingling, oblique-to-vertical, threadlike elements (possibly rods) may occur and may alternate with bands filled with calcite spar and/or darker mudrock matrix. [Photos of tangential sections of specimens of *Z. communis* from the type locality (kindly provided courtesy of Marcelo Carrera, Córdoba, Argentina in 1999, 2008) show a pattern of very fine, rounded, dotlike shapes representing probable rods. Compared with the dotlike appearance of spinose rods in *Pulchrilamina spinosa* (see tangential section: Fig. 2*f*), these are much finer (about half the diameter), and they are more closely spaced]. *Middle*

Ordovician (Dapingian): Argentina (Precordillera), Canada (?Newfoundland).——FIG. 489*a–d*. **Z. communis*; upper San Juan Formation, Las Lajas section, 24 km southwest of San Juan, Argentine Precordillera; *a,* holotype, longitudinal section, showing nature of latilaminate growth layers and a number of intercalations of dark layers composed of sedimentary matrix, ×3.5 (Keller & Flügel, 1996, pl. 47,*7*); *b,* holotype, longitudinal section, contrasting zones of horizontal laminar and intermingling, oblique-to-vertical skeletal features in lower to middle parts, and zones of largely coarse, recrystallized sparite and fine matrix in the upper part, ×8.5 (Keller & Flügel, 1996, pl. 47,*9*); *c,* holotype, longitudinal section, showing more continuous dark lines bounding latilaminae, and incomplete, slightly undulating laminae that are interrupted by a few short vertical elements (*small arrowheads*) within the latilaminae, ×16 (Keller & Flügel, 1996, pl. 48,*1*); *d,* longitudinal section, specimen no. RA 542, *Z. communis,* Los Berros section, San Juan Formation; darker bands showing well-defined, elongated, low-convexity cyst plates, ×16 (Keller & Flügel, 1996, pl. 47,*2*).

ACKNOWLEDGMENTS

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GENERAL FEATURES OF THE ARCHAEOCYATHA

F. DEBRENNE, A. YU. ZHURAVLEV, and P. D. KRUSE

INTRODUCTION

The Archaeocyatha represent the first substantial diversification of the phylum Porifera, to which they are now generally assigned as a distinct class. They flourished in carbonate shelf and reef environments of the early Cambrian; a depauperate stock persisted into the late Cambrian. They were the first Paleozoic metazoans to engage in extensive bioconstruction, in some regions building reef complexes rivalling those of the present. Their exquisite, morphologically varied, calcareous skeletons provide the basis for a more or less precise biozonation, particularly well developed for the Siberian region. *In situ* archaeocyaths are known from all continents except South America, where archaeocyaths have recently been reported in allochthonous blocks.

HISTORICAL OVERVIEW

Archaeocyaths were first discovered along the shores of Forteau Bay in southern Labrador, Canada by the hydrographer Captain H. W. BAYFIELD, who later (BAYFIELD, 1845) reported them as the coral *Cyathophyllum*. Specimens were renamed by BILLINGS (1861) as *Archeocyathus* (subsequently spelled *Archaeocyathus*), destined to become the eponymous genus for the entire group.

BORNEMANN (1884, 1886) was the first to undertake a regional monographic study of archaeocyaths—from Sardinia—and to establish them as a group of high taxonomic rank: the class Archaeocyatha. The taxonomic affinities of archaeocyaths have been debated since that time (Fig. 490). TAYLOR (1910, p. 177) was the first author to recognize and elaborate on their distinctiveness, considering them as intermediate between Porifera and Coelenterata.

Thereafter, archaeocyaths were seldom compared with sponges and were established as a separate phylum by VOLOGDIN and ZHURAVLEVA (1947) and OKULITCH and DE LAUBENFELS (1953). These authors emphasized the differences between archaeocyaths and sponges, among which the total absence of spicules in archaeocyaths was thought particularly significant. Nevertheless, while paleontologists generally accepted the concept of an independent phylum (e.g., ZHURAVLEVA, 1960b, p. 79; DEBRENNE, 1964, p. 106–107; HILL, 1965, p. 49, 1972, p. 50), some prescient sponge specialists (VACELET, 1964, p. 109; ZIEGLER & RIETSCHEL, 1970) remained opposed. The rediscovery of living sponges capable of secreting massive calcareous skeletons has since confirmed the archaeocyaths as members of the phylum Porifera.

The first higher subdivisions of Archaeocyatha were established by TAYLOR (1910, p. 105), who distinguished five families based on intervallum structure. OKULITCH (1935b) and the BEDFORDS (R. BEDFORD & J. BEDFORD, 1936, 1937, 1939; R. BEDFORD & W. R. BEDFORD, 1934, 1936) subsequently united the families into orders according to their style of ontogenetic development. VOLOGDIN (1936, 1937a, 1937b) proposed two classes, Regularia and Irregularia, on the basis of morphological differences of the secondary calcareous skeleton, as now understood. Initially, VOLOGDIN was not supported by his contemporaries. OKULITCH (1943, 1955a, p. 8) established three classes: (1) one walled, with central cavity empty; (2) two walled; and (3) central cavity full. At that time, about 400 species of archaeocyaths had been described, of which over 230 were due to VOLOGDIN's studies on material from the former USSR (Siberian Platform, Altay-Sayan, Tuva, Urals, Kazakhstan) and

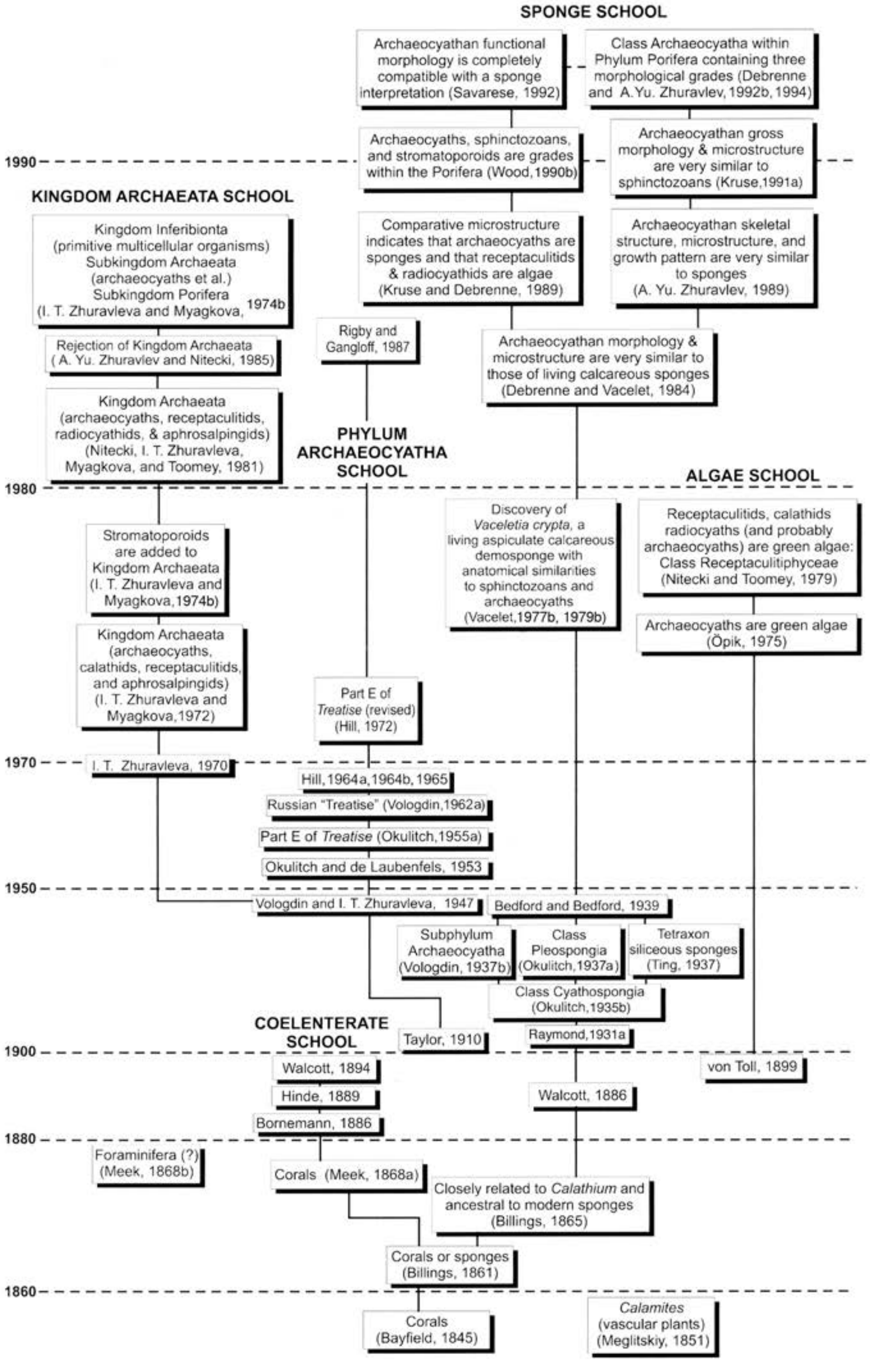

FIG. 490. History of phylogenetic interpretations of archaeocyaths (adapted from Rowland, 2001).

Mongolia. Rich collections from a diversity of localities provided him with much material for the study of morphology and the elaboration of a theoretical approach to classification. However, it was ZHURAVLEVA (1955b) who established a firmer basis for the distinction of the Regularia and Irregularia from her study of skeletal ontogeny. She also defined orders and families based on intervallar and wall structures respectively—criteria still broadly applied in the current classification. In 1960, she corrected the names Regularia and Irregularia to Regulares and Irregulares (as subclasses), to avoid confusion with the major subdivisions of the Echinoidea and Cystoidea (ZHURAVLEVA, 1960b, p. 80, 267).

Since the early 1960s, the archaeocyathan genus has become a taxonomic category whose definition has achieved general consensus among specialists. It is based upon variations of skeletal elements, particularly within designated categories of wall construction and the presence or absence of supplementary elements. An increase in the number of described genera from this time reflects both the publication of regional monographs and a tendency to oversplit taxa on criteria not now considered to be of generic significance.

By the mid-1970s, the Regulares had been intensively investigated. Their elegant porous skeleton proved to be an ideal model for the application of VAVILOV's (1922) principle of homologous series in hereditary variability, thus strengthening the basis for classification (ROZANOV in ROZANOV & MISSARZHEVSKIY, 1966, p. 73; ROZANOV, 1973, p. 50, 1974). VAVILOV's principle postulates that within a particular clade, such as a family, constituent species and genera display a common, but limited set of homologous character states that have parallels in closely related clades. Morphological attributes of as yet undiscovered clade members may thereby be predicted. Archaeocyathan evolution was used to establish four early Cambrian stages in Siberia (ROZANOV, 1973, p. 80). Comprehensive studies by ZHURAVLEVA, DEBRENNE, ROZANOV, and others were the basis for the successful revision of the *Treatise on Invertebrate Paleontology*, Part E, by HILL (1972).

The 1970s and 1980s were a period of accumulation of comprehensive regional material. Monographic compilations treated archaeocyaths from throughout the former USSR, Western Europe, Morocco, China, Australia, Antarctica, South Africa, and western and eastern North America, including Greenland.

The rediscovery of sponges having massive calcareous skeletons, with or without spicules, transformed conceptions of the affinities of groups such as archaeocyaths, sphinctozoans, stromatoporoids, and others. One of the most striking finds was of *Vaceletia crypta* (VACELET), an extant chambered demosponge with a massive calcareous skeleton devoid of spicules (VACELET, 1977b). Such discoveries forced a reconsideration of the nature of archaeocyaths (DEBRENNE & VACELET, 1984; PICKETT, 1985b; ZHURAVLEV, 1985).

This accumulation of regional data, together with the new actualistic model of archaeocyathan functional morphology, culminated in a thorough revision of taxonomy, ontogeny, ecology, biostratigraphy, and biogeography by DEBRENNE, ZHURAVLEV, and ROZANOV (1989), DEBRENNE, ROZANOV, and ZHURAVLEV (1990), and DEBRENNE and ZHURAVLEV (1992b). This work resulted in a drastic decrease in the total number of genera in the group, from 587 before 1989 to 298. Aspects of the relationship between archaeocyaths and sponges were also extensively discussed, affirming the Archaeocyatha as a class within the phylum Porifera. These publications, together with the earlier compilation of HILL (1972) and the summary revision of DEBRENNE, ZHURAVLEV, and KRUSE (2002), form the basis for the present work.

SYSTEMATIC POSITION AMONG METAZOA

On the basis of superficial similarities, archaeocyaths have been attributed to a variety of groups, including corals, sponges, protists, and algae, regarded as an independent phylum, or united with aphrosalpingoids (actually thalamid sponges) and receptaculitaleans (algae or lower invertebrates) as a separate kingdom (ZHURAVLEVA & MYAGKOVA, 1987, p. 174). A historical compendium of the systematic attributions of Archaeocyatha is provided by DEBRENNE and ZHURAVLEV (1992b, table I). Extant sponges with a nonspiculate skeleton (*Acanthochaetetes wellsi* HARTMAN & GOREAU, *Vaceletia crypta* [VACELET], and others) show similarities to archaeocyaths in architecture, skeletal structure (both primary and secondary), functional morphology, and evolutionary trends (DEBRENNE & VACELET, 1984; PICKETT, 1985b; ZHURAVLEV, 1985, 1989, 1993; DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 152; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 197; KRUSE, 1990a; SAVARESE, 1992, 1995; WOOD, ZHURAVLEV, & DEBRENNE, 1992). Such similarities favor a close taxonomic relationship between archaeocyaths and calcified sponges.

VACELET (1985) drew a comparison between Archaeocyatha and Hexactinellida in that both groups have a complicated skeleton, which in hexactinellides is probably due to their syncytial organization and relatively advanced conductive system (BERGQUIST, 1985). DEBRENNE and ZHURAVLEV (1994) proposed that shared similarities with regard to immune reactions and modes of asexual reproduction, particularly intracalicular budding and the interpreted presence of crypt cells, support a closer affinity of Archaeocyatha with demosponges than with other classes of Porifera. These hypotheses remain to be confirmed.

MORPHOLOGY

The archaeocyathan skeleton is typically a narrow conical cup with porous outer and inner walls, connected by longitudinal partitions (septa and others). This architecture is distinctive of the archaeocyaths, though structures mimicking septa are known, for example, in the Early Devonian thalamid sponge *Radiothalamos* PICKETT & RIGBY (1983) and its allies. As well, archaeocyaths exhibit almost the entire range of growth forms found in calcified sponges: thalamid (sphinctozoan) (ZHURAVLEV, 1989; DEBRENNE & WOOD, 1990), stromatoporoid (ZHURAVLEV, 1990a), and chaetetid (DEBRENNE, KRUSE, & ZHANG, 1991) (Fig. 491). Organisms with these skeletal morphologies were previously considered as separate groups of cnidarians, sponges, or even algae. However, studies of living representatives have established their individual systematic positions and hence their polyphyletic origin (VACELET, 1979b, 1983; VAN SOEST, 1984; REITNER & ENGESER, 1985; WOOD, 1987; WOOD & REITNER, 1988; DEBRENNE, 1991). Each group had been described with its own nomenclature; to avoid confusion, a synonymized nomenclature was proposed by ZHURAVLEV, DEBRENNE, and WOOD (1990).

The remarkable similarity of thalamid archaeocyaths and extant thalamid demosponges (*Vaceletia* PICKETT) has been frequently noted (DEBRENNE & VACELET, 1984; ZHURAVLEV, 1985; KRUSE, 1990a). A great diversity of morphological elements (SENOWBARI-DARYAN & SCHÄFER, 1986; RIGBY, FAN, & ZHANG, 1989a; SENOWBARI-DARYAN, 1990; BOĬKO, BELYAEVA, & ZHURAVLEVA, 1991, pl. 42,*3*) has been observed in thin sections of thalamid sponges, which are referable mainly to the demosponges, although a minority are calcareans. These structures are similar to some archaeocyathan elements (e.g., syringes, taenialike structures). The presence of outer wall microporous sheaths in the two groups is especially significant for functional morphology. Some Carboniferous and Mesozoic chaetetid sponges have continuous tabulae (WEST & CLARK, 1984) and porous calicles. In *Chaetetes* FISCHER VON WALDHEIM, the fiber bundles forming the tabulae result from the progressive bending of fibers issuing from the longitudinal axis; they converge at the center of the functional cavity but do not coalesce, and a central pore may be present. On the contrary, chaetetid archaeocyathan tabulae

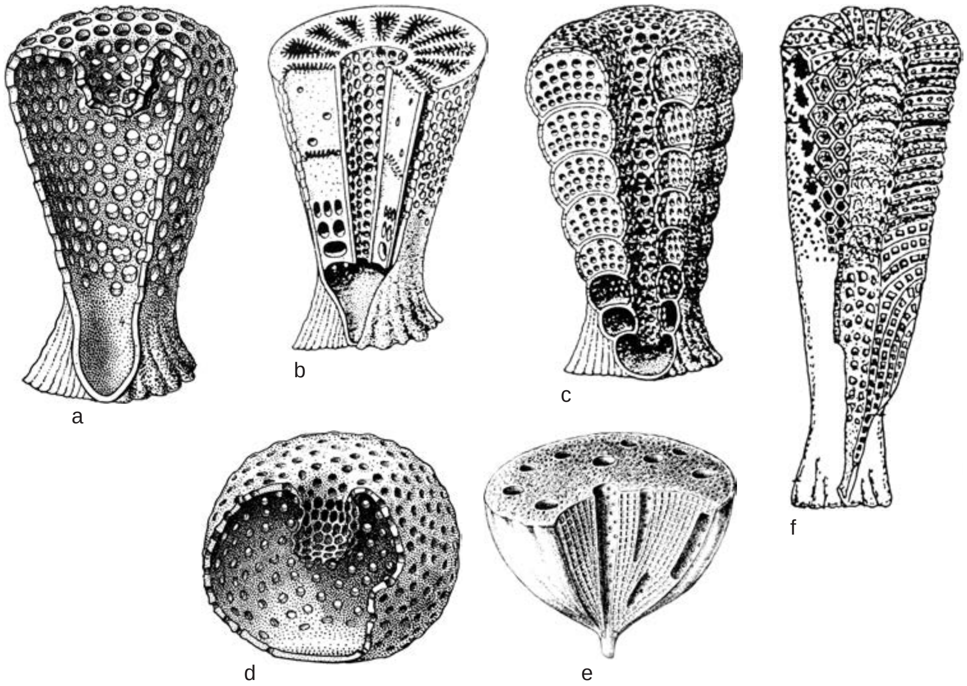

FIG. 491. Archaeocyathan architecture; *a,* one-walled conical; *b,* two-walled conical; *c,* multichambered conical (thalamid); *d,* single-chambered subspherical (Debrenne, Rozanov, & Zhuravlev, 1990); *e,* chaetetid; *f,* syringoid (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

are produced by the secondary skeleton and are continuous. Both might correspond to an externalization of the soft tissue in the skeleton, but are nevertheless convergent. The facultative presence of intracalicular (septal) spines and astrorhizae has been reported in some genera of chaetetid demosponges and chaetetid archaeocyaths (WEST & CLARK, 1983; DEBRENNE & ZHURAVLEV, 1994).

MORPHOLOGY OF PRIMARY SKELETON

Archaeocyathan taxonomy is derived from ontogenetic studies, which have established the order of appearance and complication of the various structural elements constituting the archaeocyathan cup (R. BEDFORD & J. BEDFORD, 1939; ZHURAVLEVA, 1960b). On the principle that ontogenetically earlier appearing features are accorded higher taxonomic rank, orders are delineated by architecture of the cup; suborders by the basic intervallar structures present, and for modular forms, mode of increase (Fig. 492); superfamilies by the outer wall type; families by the inner wall type; genera by specified variants of wall and intervallar structures; and species by variation in shape, size, and number of skeletal constituents.

Six orders and 12 suborders are thus recognized within the class (DEBRENNE, ZHURAVLEV, & ROZANOV, 1989; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990; ZHURAVLEV, 1990a; DEBRENNE, 1991; DEBRENNE & ZHURAVLEV, 1992b) (Fig. 491):

- Monocyathida (one-walled conical cup)
- Ajacicyathida (archaeocyathan architecture: two-walled cup with septa as radial partitions)
  - Dokidocyathina (intervallum with septa bearing one longitudinal pore row)
  - Ajacicyathina (intervallum with septa bearing several longitudinal pore rows)
  - Erismacoscinina (intervallum with septa and plate tabulae)

Putapacyathida (archaeocyathan architecture: two-walled cup with plate tabulae only)

Capsulocyathida (thalamid cup with inner wall of invaginal type)

  Capsulocyathina (cup single-chambered and subspherical, or multichambered without septa)

  Coscinocyathina (cup multichambered, intervallum with septa)

Archaeocyathida (archaeocyathan architecture: two-walled cup with radial partitions other than septa)

  Loculicyathina (pseudocolonies by interparietal budding, intervallum with pseudosepta)

  Anthomorphina (pseudocolonies by external budding, intervallum with pseudosepta and membrane tabulae)

  Archaeocyathina (pseudocolonies by external budding and/or longitudinal subdivision, intervallum with taeniae, pseudosepta, or dictyonal network)

  Dictyofavina (branching or massive pseudocolonies by intercalicular budding, intervallum with calicles)

  Syringocnemina (pseudocolonies by longitudinal fission, intervallum with syringes)

Kazachstanicyathida (thalamid and stromatoporoid architecture)

  Kazachstanicyathina (initial chambers hollow and elongate, pillars in subsequent chambers)

  Altaicyathina (initial chambers subspherical, pillars in all chambers).

Architecture

The architecture of a two-walled cup is determined by the development of its component longitudinal platelike elements. No other sponge group is known that exhibits an archaeocyathan architecture. This architecture, characterized by (pseudo)septa, (pseudo)taeniae, tabulae, syringes, and/or dictyonal network, is typical of Ajacicyathida and Archaeocyathida.

The chaetetid architecture (intervallum with calicles), ontogenetically proceeds from a typical archaeocyathan development with taeniae, which, with growth, is transformed into calicles (Fig. 491e). The syringoid architecture (Fig. 491f) is developed from the chaetetid. Like the chaetetid, syringoid forms are not exclusive to the archaeocyaths, being known, for example, among Permian sphinctozoan sponges (e.g., *Tebagathalamia* in SENOWBARI-DARYAN & RIGBY, 1988).

The rare, thalamid architecture consists of a succession of chambers that are initially subspherical (Fig. 491c), but in some forms become more laterally elongate (see Fig. 513b). Chambers generally contain longitudinal elements (pillars). Growth proceeds by the distal addition of chambers. It is a typical architecture of sphinctozoan demosponges and calcareans.

Cup Size and Shape

Across the above categories, the typical solitary conical cup may expand slowly or rapidly to generate a spectrum of shapes from subcylindrical, through narrowly and widely conical, to discoid. Increase in the rate of expansion with growth produces a bowl-shaped cup. A typical ajacicyathide conical cup is of the order of 5–15 mm in diameter and several centimeters in height, but exceptionally may attain a height of 1.5 m. Discoid cups such as in the archaeocyathide *Okulitchicyathus* ZHURAVLEVA may attain a diameter of half a meter but are generally several centimeters in diameter.

Transverse or longitudinal folding may complicate the basic conical cup shape. Where this is regular and affects both walls, as in some Ajacicyathida, it is treated as a generic criterion (e.g., *Orbicyathus* VOLOGDIN with periodic, synchronous, transverse folds of both walls giving rise to undulose longitudinal section; *Orbiasterocyathus* ZHURAVLEVA with both walls longitudinally folded, resulting in stellate transverse section). The plicate wall, in which each intersept is individually folded to form a sharp mid-interseptal longitudinal ridge, is also a generic criterion,

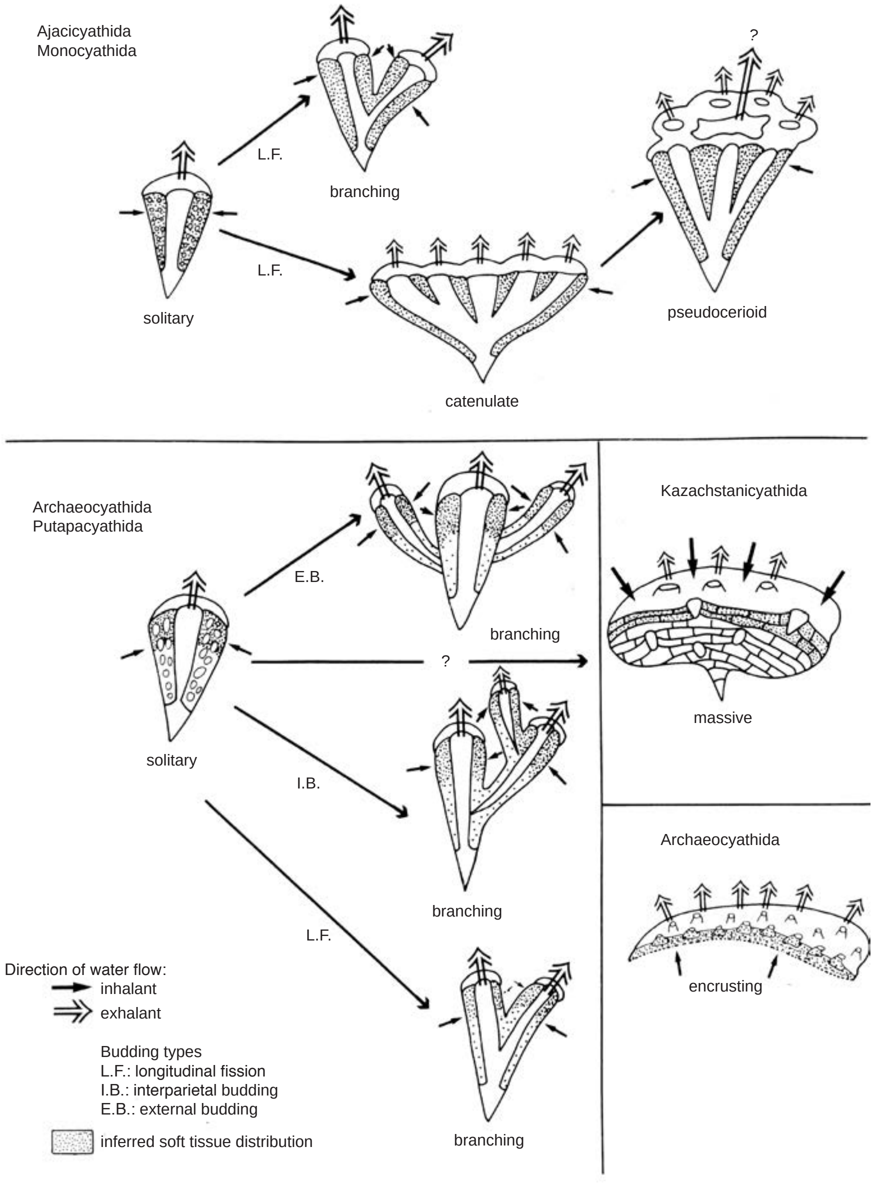

FIG. 492. Development of modular archaeocyath types based on module organization and mode of proliferation; possible evolutionary pathways from an ancestral solitary cup are indicated (Wood, Zhuravlev, & Debrenne, 1992).

e.g., *Rozanovicoscinus* DEBRENNE with plicate outer wall (Fig. 492, Fig. 493a).

In Archaeocyathida, only the outer wall may be folded, with transverse folds generating an undulose longitudinal section, e.g., *Pycnoidocoscinus* R. BEDFORD & W. R. BEDFORD (Fig. 494c).

Subspherical cups may show a variety of regularly or irregularly arranged prominences and indentations, as in *Capsulocyathus* ZHURAVLEVA (Fig. 493b, Fig. 493d). In conical cups, such as those of *Batschykicyathus* ZHURAVLEV, prominences are evenly arranged in single planes, several

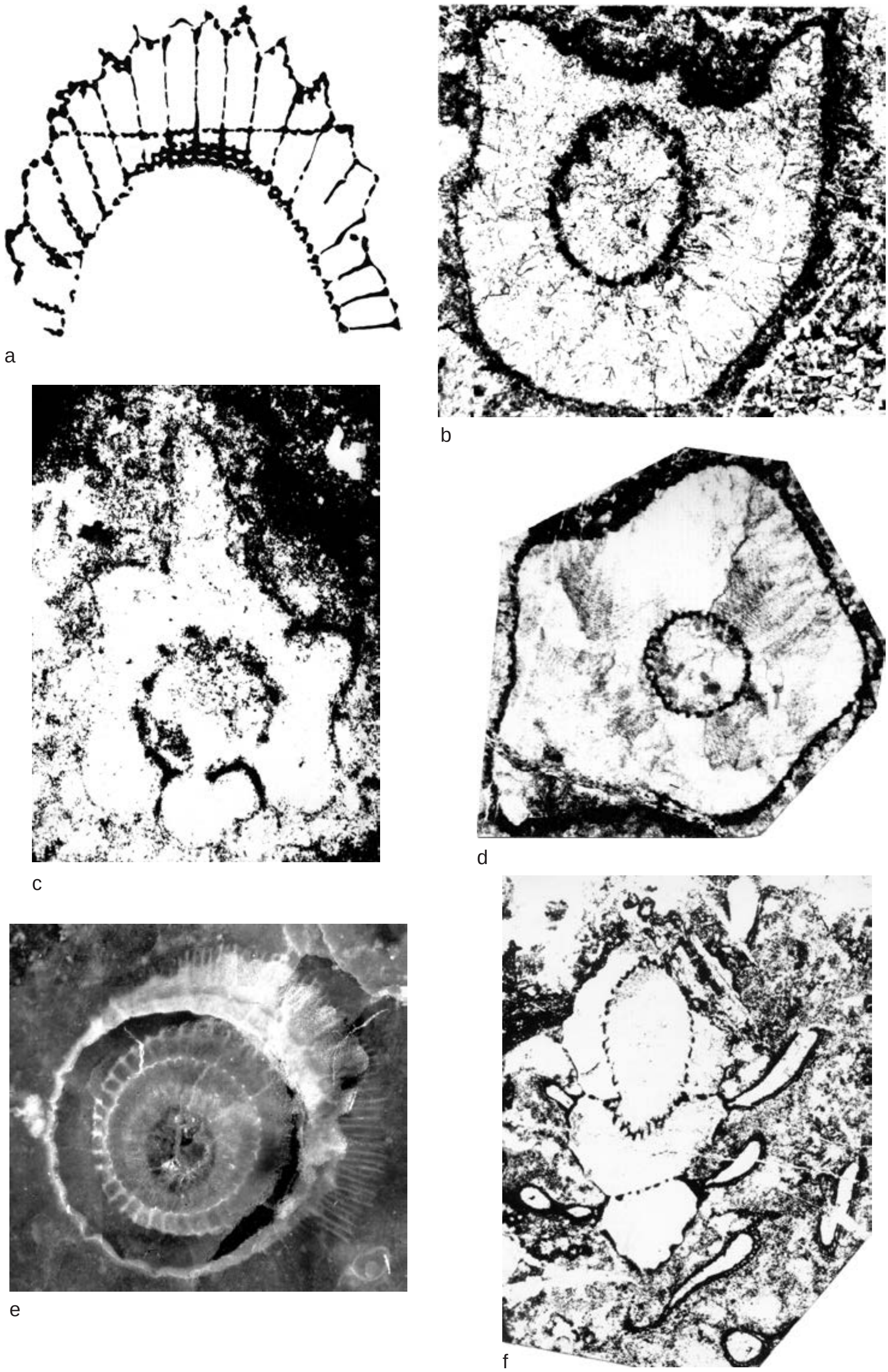

FIG. 493. *(For explanation, see facing page).*

to a cup (Fig. 493c). The distinctively shaped cup of *Yukonensis* Özdikmen (Fig. 493e–f) consists of a subcylindrical cup with periodic constrictions, each with an accompanying umbrella-like corolla of hollow shafts and connecting membranes.

Cup Modularity

As with sponges generally, archaeocyaths were probably not true colonial organisms. However, it is possible to apply the concept of sponge modularity to archaeocyaths and hence to treat a single central cavity with its surrounding elements as analogous to the osculum of a sponge (Koltun, 1988) or to an aquiferous unit space in stromatoporoid sponges (Wood, 1987). Hence an archaeocyathan skeleton that is not a single cup is described as modular (Fig. 492) (previously, colonial).

Modularity is common in the Archaeocyathida, Putapacyathida, and Kazachstanicyathida and also occurs in some members of most other orders (e.g., branching *Archaeolynthus polaris* [Vologdin] in Monocyathida).

Modularity in archaeocyaths is understood in terms of the individual aquiferous unit: that portion of an archaeocyathan cup with a number of inhalant openings converging on a single exhalant opening (osculum) (Wood, Zhuravlev, & Debrenne, 1992). Most archaeocyaths are therefore solitary, their conical cups bearing a single osculum represented by the central cavity orifice. Some, however, are multioscular and thus modular, generating branching, catenulate, pseudocerioid, massive, and encrusting forms (Fig. 495).

Proliferation of modules is by several methods: longitudinal fission and external, interparietal, and intercalicular budding (Debrenne, Zhuravlev, & Kruse, 2002; longitudinal subdivision, external and intervallar budding respectively of Wood, Zhuravlev, & Debrenne, 1992). Longitudinal fission produces branching, catenulate and pseudocerioid morphology (Fig. 492, Fig. 495a–c; see Fig. 523b). In external budding, a bud arises on the outer wall of the cup, whereas in interparietal budding, the bud arises within the intervallum. Both produce branching modularity (Fig. 492, Fig. 519d). Intercalicular budding generates buds inside a single calicle to produce branching and massive morphology (see Fig. 523a). As well, some encrusting and massive morphologies could form by individualization of additional aquiferous units within a modular skeleton (Fig. 492, Fig. 495d–e).

Living organisms exhibit a wide spectrum of degrees of bodily integration, and archaeocyaths are no exception. In considering the archaeocyaths, Wood, Zhuravlev, and Debrenne (1992) categorized branching and laminar modularity as having low integration, as constituent modules were either isolated or discrete yet connected. Catenulate and pseudocerioid forms, with adjacent confluent units having no separating wall, were considered to be of medium integration. Highly integrated forms were the massive and encrusting types, notably among the Kazachstanicyathida, that lack separating walls or septa between aquiferous units. Massive forms present thalamid-stromatoporoid and chaetetid architectures (see Fig. 513b).

Fig. 493. Archaeocyathan cup shapes; *a,* longitudinally plicate cup of *Rozanovicoscinus stellatus* Gravestock, Botoman, Ajax Limestone, Mount Aroona, South Australia, Australia, oblique section, NL82013, MNHN, ×7 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* subspherical cup of *Capsulocyathus irregularis* (Zhuravleva), Botoman, Salaany Gol Formation, Salaany Gol, Tsagaan Oloom province, western Mongolia, oblique longitudinal section, 3302/3023, PIN, ×16 (Voronin & others, 1982); *c,* regularly bulging outer wall in *Batschykicyathus angulosus* Zhuravlev, Atdabanian, Pestrotsvet Formation, Bachyk Creek, Lena River, Sakha (Yakutia), Russia, transverse section, paratype, 3848/504, PIN, ×22 (Zhuravlev, Zhuravleva, & Fonin, 1983); *d,* same as view *b,* transverse section, 3302/3025, PIN, ×17 (Voronin & others, 1982); *e,* multichambered cup and corolla (at top and right) of *Yukonensis yukonensis* (Handfield), Botoman, Adams Argillite, Tatonduk River, Alaska, United States, transverse section, locality USGS 5156C, collection not located, ×24 (Debrenne, Zhuravlev, & Kruse, 2012b); *f, Yukonensis yukonensis* (Handfield), cup with shafts of successive corollas (at right), Botoman, Mackenzie Mountains, Northwest Territories, Canada, oblique longitudinal section, 90149, GSC, ×7 (Voronova & others, 1987).

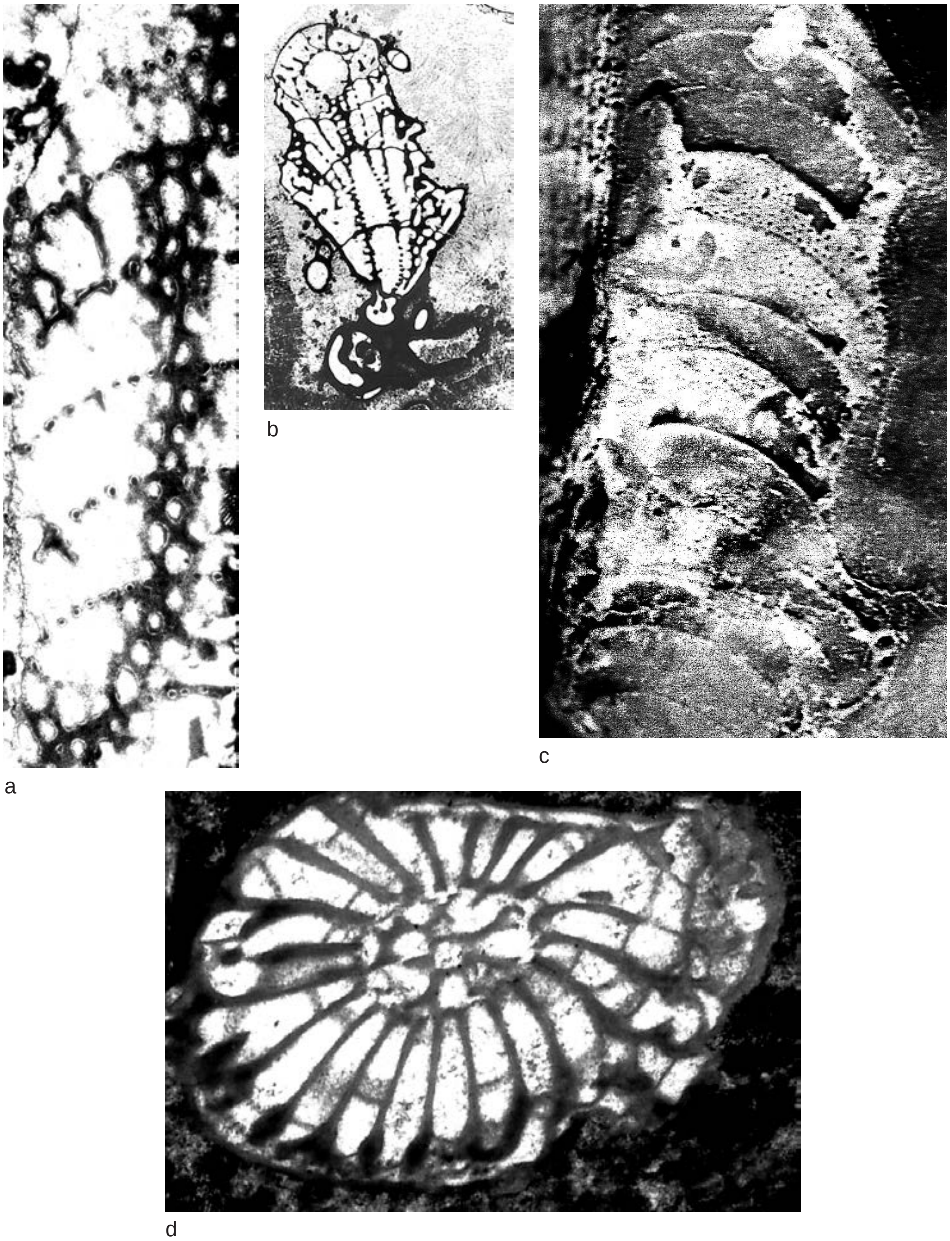

Fig. 494. Transverse folds and pseudoseptal porosity; *a,* irregular pseudoseptal porosity in *Cellicyathus* sp., Botoman, Chara Formation, Peleduy River, Sakha (Yakutia), Russia, longitudinal section (outer wall to left), 4451/18, PIN, ×20 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* coarsely porous pseudosepta in *Cambrocyathellus proximus* (Fonin), Tommotian, Pestrotsvet Formation, Lena River, Sakha (Yakutia), Russia, longitudinal section, 4451/8, PIN, ×4.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* transverse outer wall folds and finely porous pseudosepta in *Pycnoidocoscinus pycnoideum* R. Bedford & W. R. Bedford, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to right), paratype, P991, SAM, ×5 (Debrenne, 1974a); *d,* aporose pseudosepta in *Anthomorpha margarita* Bornemann, Botoman, Matoppa Formation, Cuccuru Contu, Sardinia, Italy, transverse section, paratype, M84138, MNHN, ×10 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

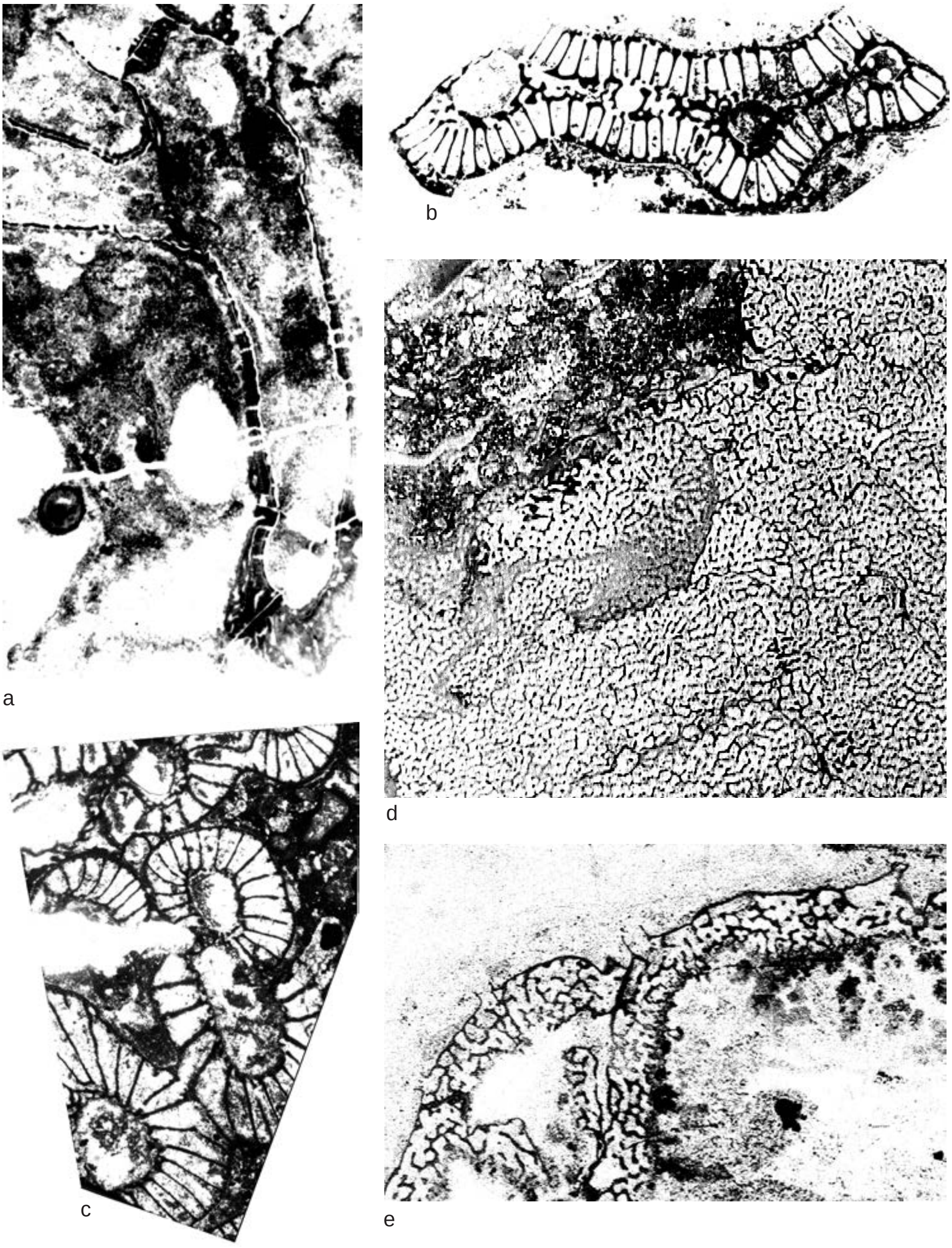

FIG. 495. Modularity in archaeocyaths; *a,* longitudinal subdivision in branching *Archaeolynthus polaris* (Vologdin), Tommotian, Pestrotsvet Formation, Zhurinskiy Mys, Lena River, Sakha (Yakutia), Russia, longitudinal section, 3848/564, PIN, ×7.5 (Wood, Zhuravlev, & Debrenne, 1992); *b,* catenulate *Pluralicyathus heterovallum* (Vologdin), Toyonian, Torgashino Formation, Uymen' River, East Sayan, Altay Sayan, Russia, transverse section, institution and collection number not known, ×2 (Wood, Zhuravlev, & Debrenne, 1992); *c,* pseudocerioid *Densocyathus sanashticolensis* Vologdin, Botoman, Verkhnemonok Formation, Sanashtykgol Spring, West Sayan, Altay Sayan, Russia, transverse section, 4327/7, PIN, ×5 (Wood, Zhuravlev, & Debrenne, 1992); *d,* massive *Zunyicyathus grandis* (Yuan & Zhang), Botoman, Jindingshan Formation, Jindingshan, Guizhou, China, transverse section, 85103, MNHN, ×5 (Debrenne, Kruse, & Zhang, 1991); *e,* encrusting *Retilamina amourensis* Debrenne & James, Botoman, Forteau Formation, Mount St Margaret, Newfoundland, Canada, longitudinal section, paratype, 62127, GSC, ×5 (Debrenne & James, 1981).

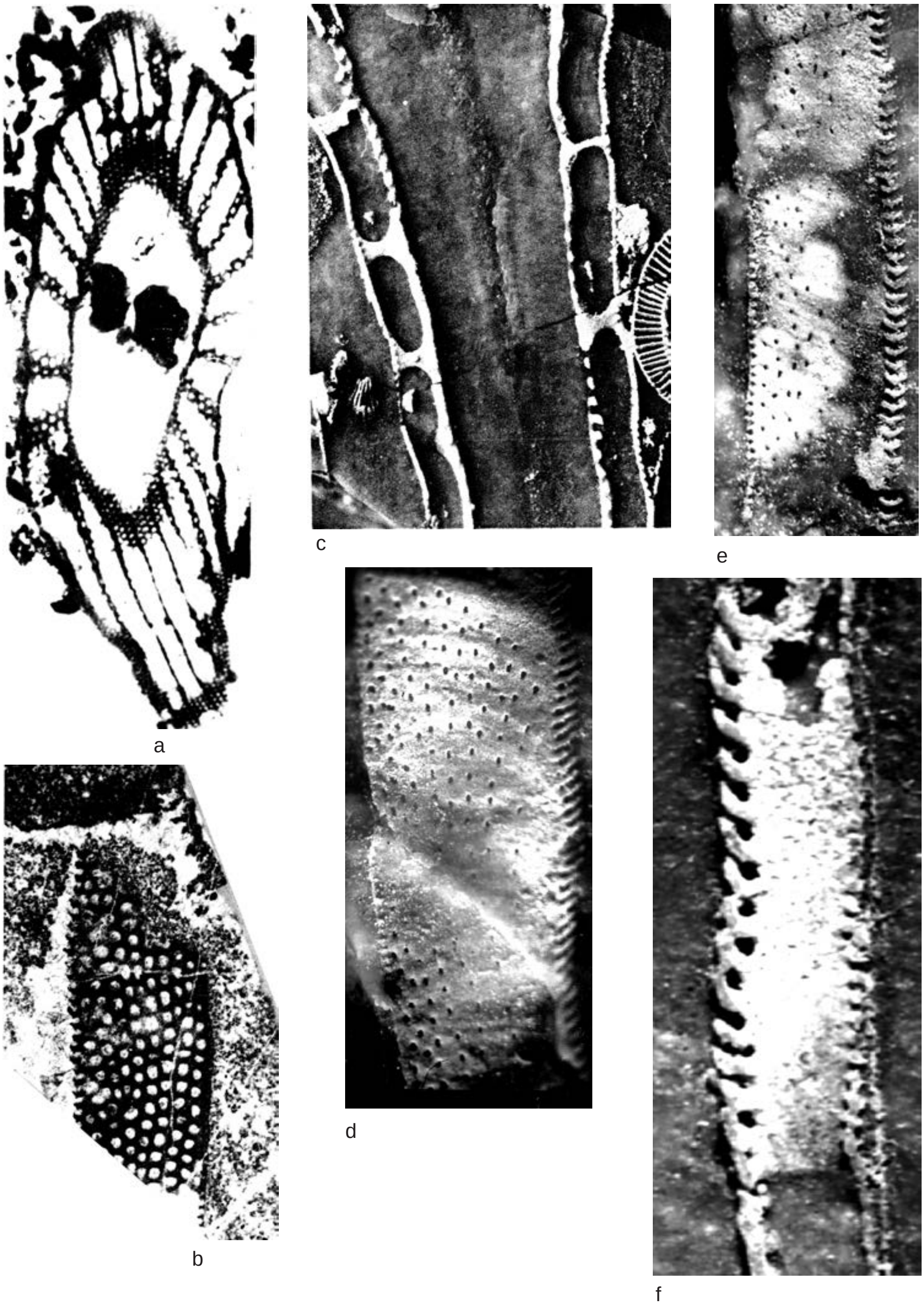

FIG. 496. Septal porosity in Ajacicyathida; *a,* completely porous septa in *Nochoroicyathus sunnaginicus* (ZHURAVLEVA), Tommotian, Pestrotsvet Formation, Aldan River, Sakha (Yakutia), Russia, oblique section, 2411-35/4, PIN, ×6.5 (Debrenne & Voronin, 1971); *b,* completely porous septa in *Gordonicyathus xandarus* (KRUSE), Botoman, Mount Wright Volcanics, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to right), FT.8475, holotype, F.83827, AM, ×12 (Kruse, 1982); *c,* septa bearing a single longitudinal pore row in *(Continued on facing page.)*

MORPHOLOGY OF MONOCYATHIDA, AJACICYATHIDA, PUTAPACYATHIDA, AND CAPSULOCYATHIDA

Wall and intervallum structures are sufficiently different between the above orders and the Archaeocyathida and Kazachstanicyathida to warrant separate treatments. Discussions by DEBRENNE, ROZANOV, and ZHURAVLEV (1990) and DEBRENNE and ZHURAVLEV (1992b) provide the basis for the following outline.

INTERVALLUM STRUCTURES

One or a combination of a variety of radial, transverse, and longitudinal skeletal structures may be present within the intervallum of two-walled cups. Those directly connecting both walls are first-order intervallar structures, whose presence or absence represents ordinal or subordinal taxonomic criteria. Those developed upon or between these are second-order intervallar structures, generally of genus- and species-level taxonomic value.

Septa

Septa are radial-longitudinal partitions linking inner and outer walls in conical cups; in nonconical cases, such as catenulate cups, they are not strictly radial, but nevertheless retain a perpendicular orientation to the walls. Most septa are planar, but a minority are wavy, as, for example, in *Leptosocyathus curviseptum* VOLOGDIN. In some taxa, septa may bifurcate toward the outer wall.

With cup growth, new septa are inserted at the outer wall as a rudimentary plate when the number of interseptal wall pores reaches a maximum for the species. This plate then grows more or less rapidly toward the inner wall (ZHURAVLEVA, 1960b).

Septal porosity has been widely accepted as a generic criterion ever since it was first espoused by DEBRENNE and VORONIN (1971). Two broad styles of septal porosity are thus recognized: completely porous and aporose to sparsely porous, based on the work of ROZANOV (1973), who documented two corresponding pathways of ontogenetic porosity development. In the first, an initial netlike (large-pored) porosity results in completely porous septa with generally ordered longitudinal rows of pores covering the entire septal area; in the second, initial porosity rapidly reduces or disappears with growth, producing mature septa in which pores are restricted in their distribution or even virtually absent. Netlike (pore diameter much greater than lintel width) and finely porous (pore diameter subequal to lintel width) variants are noted by DEBRENNE, ROZANOV, and ZHURAVLEV (1990) among completely porous septa, and sparsely porous (with consistent presence of rare pores), scattered porous (with porosity of only part of a septum), and perforate (with stirrup pores, together with scattered solitary pores, in median area of a septum) variants among aporose to sparsely porous septa, but these have only species-level significance (Fig. 496).

In the case of septa with stirrup pores only (among the most aporose septal porosities known), early ontogenetic stages show septa with an initial single row of pores adjacent to either or both walls. With cup growth, this pore row gradually migrates into the wall to form a row of stirrup pores (arrested initial stage of septal development

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FIG. 496. *(Continued from facing page).*
Dokidocyathus simplicissimus TAYLOR, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section, lectotype, T1589A-B, SAM, ×3.5 (Taylor, 1910); *d,* sparsely porous septa in *Thalamocyathus tectus* DEBRENNE, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to left), 165, PU, ×10 (Debrenne, 1973); *e,* sparsely porous septa in *Thalamocyathus trachealis* (TAYLOR), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to left), paralectotype, T1585, SAM, ×10 (Debrenne, 1973); *f,* stirrup pores at junction of septa and inner wall in *Stapicyathus stapipora* (TAYLOR), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to right), paratype, 86782, PU, ×12 (Debrenne, 1974b).

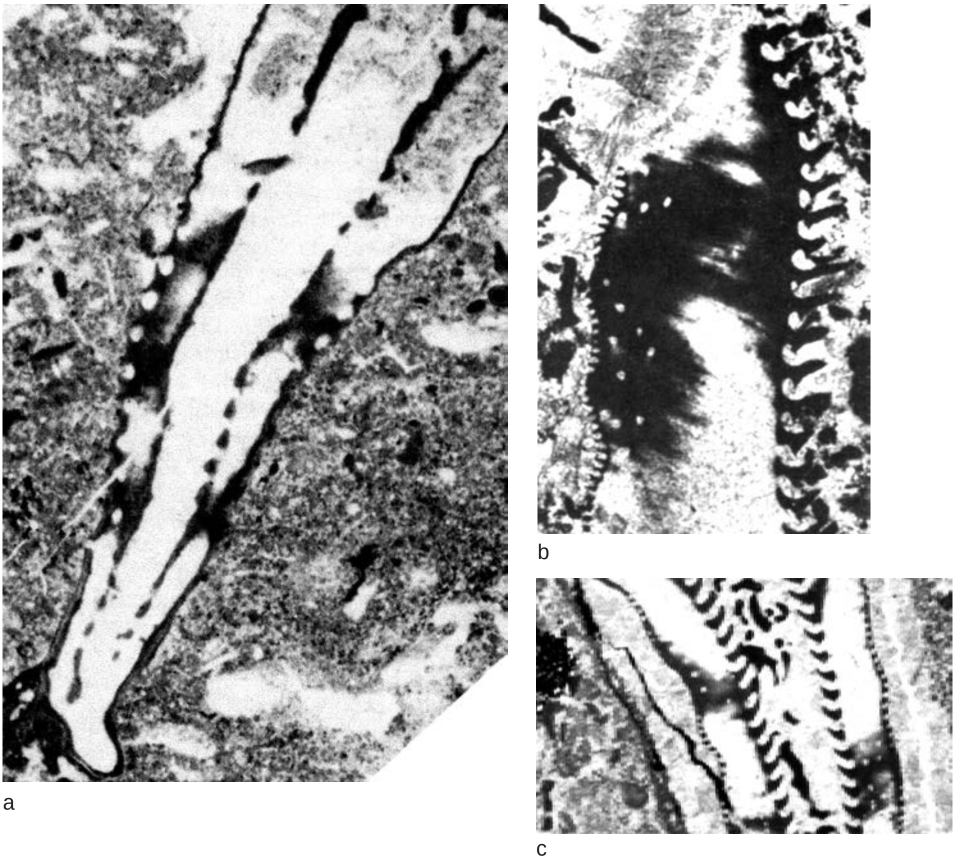

FIG. 497. Ontogenetic development of aporose to sparsely porous septa; *a,* arrested initial stage of pore development, in which a single pore row initially wholly within the septum migrates centrifugally during ontogeny to become a stirrup pore row along the outer wall, *Kisasacyathus caecum* (GRAVESTOCK), Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia, longitudinal section of apex, paratype, P21481, SAM, ×15 (Gravestock, 1984); *b,* adult septal porosity concentrated adjacent to outer wall in *Sagacyathus stonyx* KRUSE, Botoman, Mount Wright Volcanics, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left) FT.8492, paratype, F.83568, AM, ×10 (Kruse, 1982); *c,* same, juvenile septal porosity across entire septum, longitudinal section, FT.8491, holotype, F.83576, AM, ×10 (Kruse, 1982).

of GRAVESTOCK [1984]) (Fig. 497a). In fact, this same ontogenetic lateral migration of pores also operates in septa with scattered porosity of several pores adjacent to one wall (Fig. 497b–c).

KRUSE (1982), supported in part by GRAVESTOCK (1984), considered that the distinction between these two styles of septal porosity was independent of pore size and that septal coefficient (pore diameter:lintel width) is arbitrary and without biological significance. He proposed that pore distribution, rather than pore size, was diagnostic.

ROZANOV (1973) related the observed ontogenetic reduction of septal porosity to the stratigraphic succession of archaeocyath taxa. Species with aporose to sparsely porous septa are descended from completely porous ancestors by heterochronic acceleration. Thus, Tommotian and Atdabanian forms with completely porous septa were gradually supplanted by less porous Botoman and Toyonian forms.

Alternatively, ZHURAVLEV (1986a) reported an influence of facies upon septal porosity: genera with aporose to sparsely porous septa

(*Leptosocyathus* VOLOGDIN, *Plicocyathus* VOLOGDIN, *Robustocyathellus* KONYUSHKOV) were predominant in reef facies, while their completely porous analogues (*Tennericyathus* ROZANOV, *Tumulocyathus* VOLOGDIN, *Rotundocyathus* VOLOGDIN) occupied back-reef facies. Septal porosity may therefore be an ecological adaptation. This proposal draws some support from the flume tank testing of skeletal models, by which SAVARESE (1992) concluded that porous septa are advantageous at low free-stream velocities, whereas aporose septa are better adapted to higher-energy environments. A compilation of field data from Mexico, South Australia, and Mongolia by DEBRENNE and ZHURAVLEV (1996) provides some further support.

Synapticulae

Synapticulae are second-order, rodlike structures that link adjacent septa, perpendicularly to obliquely, to provide structural support. They are typically of circular cross section, thickening slightly toward each septum. Associated septa tend to be bifurcating, with netlike porosity; synapticulae are rarely associated with aporose to sparsely porous septa, and never with pectinate tabulae. Where septa are wavy, synapticulae tend to link opposing septal crests. Synapticulae are generally randomly arranged. In some cases, synapticulae are concentrated at discrete transverse planes to form synapticular tabulae, which may include additional linking lintels (Fig. 498f).

With the sole known exception of the erismacoscinine *Muchattocyathus* ROZANOV, all synapticulate genera within the orders here considered belong to the Ajacicyathina. They are restricted to the Atdabanian and Botoman stages and equivalent strata. The presence or absence of synapticulae is a genus-level criterion.

Interseptal Plates

These porous plates link adjacent septa. They are known from the beginning of the Tommotian stage, in *Nochoroicyathus sunnaginicus* (ZHURAVLEVA). Their taxonomic value is low.

Plate Tabulae

Plate tabulae are porous, flat to slightly arched transverse plates connecting the walls of two-walled cups. Unlike tabular walls (see below), walls in forms with plate tabulae are independent, with tabula and wall connecting at a high angle. Plate tabulae are characteristic of the Erismacoscinina, Putapacyathida, and some Loculicyathina. They may be densely or sparsely distributed, but in either case tend to be evenly spaced. In Erismacoscinina, they are usually located at the same level in all or several interseptal loculi.

Tabular porosity in erismacoscinines may consist of normal pores (pore diameter not greater than interpore distance), retiform (large, subpolygonal) pores, heterogeneous pores, or slitlike pores (DEBRENNE, ROZANOV, & ZHURAVLEV, 1990) (Fig. 498a–b). Only the last has generic significance.

In the more common case of plate tabulae with normal porosity, pores are arranged in septa-parallel rows where septa are completely porous, or irregularly where septa are aporose to sparsely porous. In the former, the largest pores are near the septa, since tabular pores are often associated with septa or walls by means of stirrup pores. Within any loculus, pore diameter is almost constant, and because a loculus is necessarily trapezoidal in transverse section, the number of septa-parallel pore rows increases toward the outer wall.

Slitlike tabulae have two septa-parallel rows in each loculus, with component pores being elongate, parallel to the cup walls (Fig. 498e).

Plate tabulae in Putapacyathida are typically planar and generally bear pores of irregular size and shape. These tabulae are often associated with redimiculi.

Tabular walls are characteristic of the Coscinocyathina: each tabula is downturned so that it is smoothly continuous with the outer and/or inner wall—except that [other than *Yukonensis yukonensis* (HANDFIELD)] no genus with only an inner tabular wall is known (Fig. 498c).

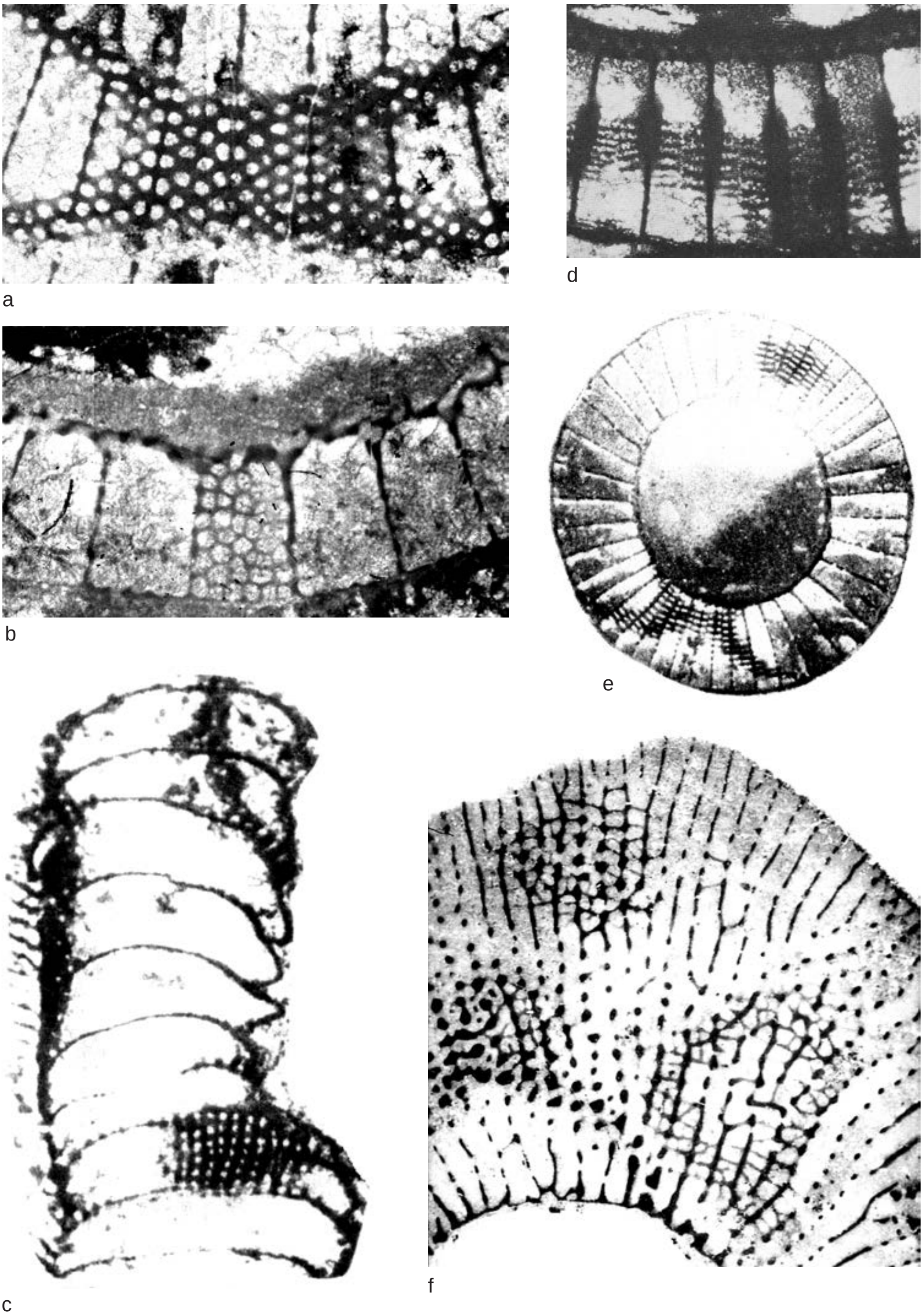

FIG. 498. Tabulae and tabula-like structures; *a,* regularly porous tabulae in *Erismacoscinus oymuranensis* ZHURAVLEV, Atdabanian, Pestrotsvet Formation, Oy-Muran, Lena River, Sakha (Yakutia), Russia, transverse section, 4220/13, PIN, ×24 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* retiform tabulae in *Erismacoscinus* sp., Botoman, Uba Formation, Tyrga River, Altay Mountains, Altay Sayan, Russia, transverse section, 4327/32, PIN, ×17 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications

(Continued on facing page.)

No tabular-walled form is known that is also plicate. Contrastingly, pseudoclathrate wall structure is known only in forms with tabular walls.

The distinctive tabulae of *Yukonensis yukonensis* (HANDFIELD) (Capsulocyathina) comprise coplanar radial rods linked by lintels; rods are directed upward at a low angle from the inner to the outer wall and actually constitute a continuation of the inner wall (Fig. 493e–f).

Pectinate Tabulae

Each interseptal loculus of a pectinate tabula comprises girdling bolsters from which coplanar spines project, giving the appearance of opposed combs (Fig. 498d). Spines may bear secondary spinules along their length (plumose) or on the tip only (bushy), but spinules are generally absent. In some cases, the tips of these secondary spinules coalesce. Archaeocyaths with pectinate tabulae were at one time considered to be a separate suborder, Nochoroicyathina ZHURAVLEVA in VOLOGDIN, 1956 (ZHURAVLEVA, 1960b), but observation of the irregular, sporadic occurrence of pectinate tabulae (spacing of which may range from 0.1 mm to 30 mm in a single cup), their anomalously late appearance in ontogeny, and the co-occurrence of otherwise identical forms with and without pectinate tabulae eventually led to their rejection as a high-level taxonomic criterion. Pectinate archaeocyaths are now placed in the Ajacicyathina (DEBRENNE, ZHURAVLEVA, & ROZANOV, 1973).

Synapticular Tabulae

F. DEBRENNE, M. DEBRENNE, and ROZANOV (1976) documented synapticular tabulae in some species of *Afiacyathus* VORONIN (their *Axiculifungia* F. DEBRENNE & M. DEBRENNE). Such tabulae are constructed of coplanar synapticulae, in several adjacent intersepts or around the entire circumference of the cup (Fig. 498f). Additional linking lintels may be present, as in *A. tabulatus* DEBRENNE, or absent, as in *A. compositus* (DEBRENNE). Initially accorded genus-level significance, synapticular tabulae are now regarded as a species-level criterion only.

WALL TYPES

Wall with Simple Porosity

Wall with simple porosity describes a simple perforate plate, generally 0.05–0.15 mm thick, in which the pores are typically arranged in alternating longitudinal rows. In any one species, pore size and the number of pore rows per intersept tend to vary within narrow limits (see Fig. 514a); in septate, two-walled forms, the number of rows increases immediately before the insertion of a new septum. In most two-walled species, there are more pore rows per intersept in the outer wall than in the inner, and the latter tend to be larger. Those with only a single inner wall pore row are distinguished on this basis from otherwise similar forms at the generic level, e.g., *Rotundocyathus* VOLOGDIN (one pore row) versus *Nochoroicyathus* ZHURAVLEVA (several pore rows) in Ajacicyathidae. Stirrup pores, in which a pore row coincides with a septum, may be present in inner walls, either alone or together with additional interseptal pore rows (Fig. 496f). In the former case, they constitute a generic criterion. Inner wall pores formed by flexure of the inner edges of the septa are also distinguished at the genus level, e.g., *Kisasacyathus* KONYUSHKOV. Exceptionally, pores may be irregularly arranged.

FIG. 498. *(Continued on facing page).*
Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* tabular outer wall in *Clathricoscinus vassilievi* (VOLOGDIN), Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, longitudinal section (outer wall to right), 20-7 NR-62, institution not known, ×12 (Zhuravleva & others, 1967); *d,* pectinate tabula in *Nochoroicyathus mirabilis* ZHURAVLEVA, Tommotian, Pestrotsvet Formation, Zhurinskiy Mys, Lena River, Sakha (Yakutia), Russia, transverse section, 4327/34, PIN, ×24 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* slitlike tabulae in *Retecoscinus sakhaensis* ZHURAVLEV, Tommotian, Medvezh'ya Formation, Moyero River, Krasnoyarsk region, Russia, transverse section, 1181 334b/1-b, PIN, ×8 (Zhuravleva, 1960b); *f,* tabula-like structure in *Afiacyathus tabulatus* DEBRENNE, Atdabanian, Amouslek Formation, Amouslek, Morocco, transverse section, M80254, MNHN, ×6 (F. Debrenne, M. Debrenne, & Rozanov, 1976).

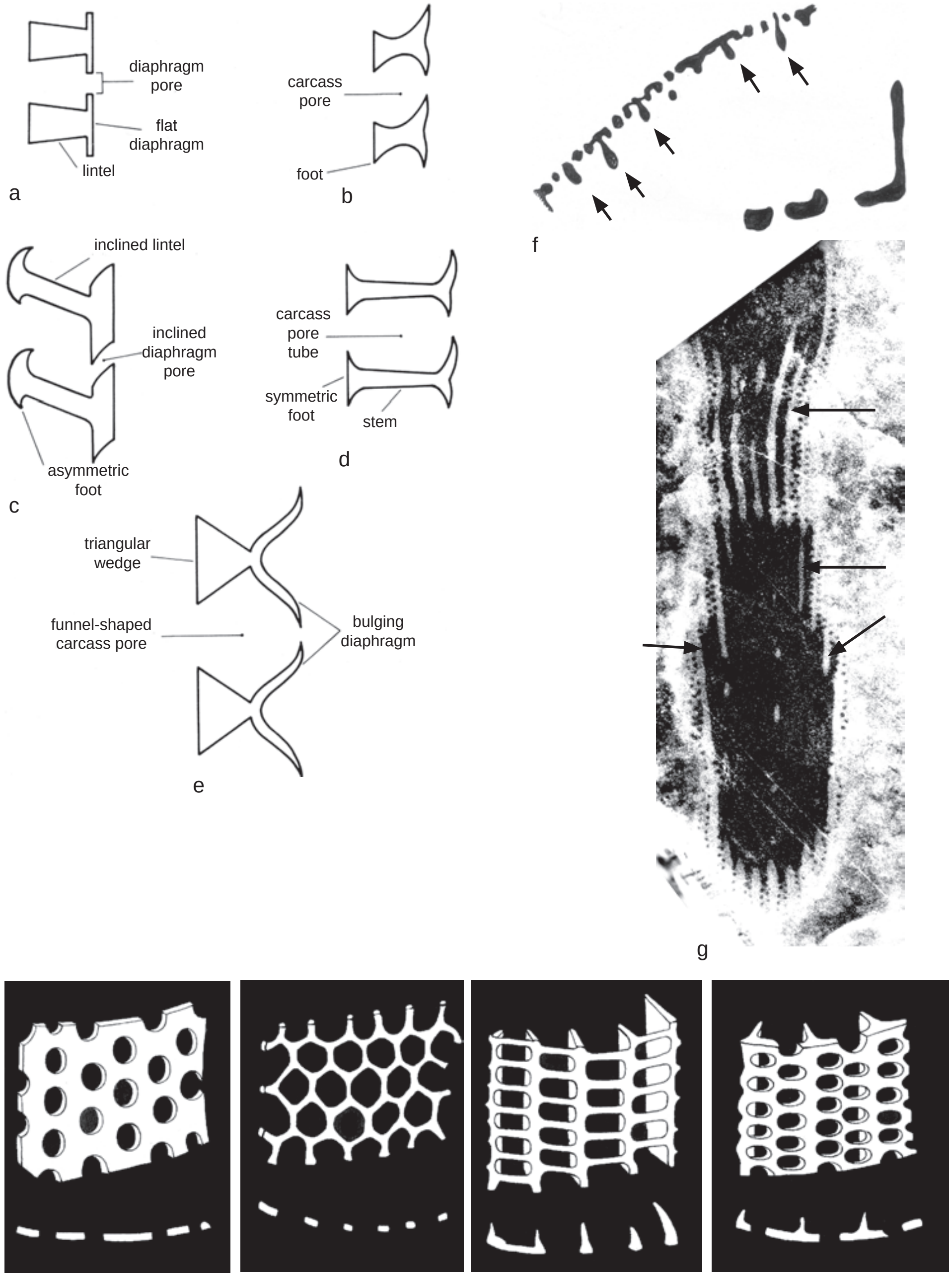

FIG. 499. Outer wall simple pores and redimiculi; *a–e,* schematic sections of varieties of flat (*a–d*) and convex (*e*) diaphragm pores in longitudinal section, intervallum to left (Gravestock, 1984); *f,* outer wall redimiculi (*arrows*) of *Dokidocyathus lenaicus* ROZANOV, Atdabanian, Pestrotsvet Formation, Oy-Muran, Lena River, Sakha (Yakutia), Russia, transverse section (outer wall at top), GIN3461/15, PIN, ×10; *g,* same, outer wall redimiculi (*arrows*) and intervallar flattened rods, tangential longitudinal section, 3848/585, PIN, ×6.5; *h–k,* schematic reconstructions of varieties of outer wall simple pores: *h,* normal pores, *i,* netlike pores, *j,* slitlike pores, *k,* elliptical pores (*f–k,* Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

While pore size tends to increase slightly with cup growth, the ratio of pore diameter to the width of the intervening lintels remains more or less constant. This can be a useful measurement for distinguishing species. By definition, pore diameter equals or exceeds wall thickness (see discussion of walls with canals below). Pores may be cylindrical, funnel shaped or, in outer walls, bear thin skeletal diaphragms constricting the external orifice to a central hole (Fig. 499a–e). Funnel-shaped and diaphragm pores were promoted as family-group characters by ZHURAVLEVA and ELKINA (1974), but due to their inconsistent development within species, and even within individual cups, they are now regarded as a variant of simple porosity, without value above the species level.

Pore orifices are generally rounded to subquadrate or subhexagonal in shape, but in rare instances may be slitlike (Fig. 499h–k). The slitlike condition is distinguished from all other pore shapes as a generic criterion, as in *Svetlanocyathus* MISSARZHEVSKIY and ROZANOV (Fig. 499j). In a few cases, outer walls are penetrated by pores of two distinct size ranges (*Cryptoporocyathus* ZHURAVLEVA, *Kyarocyathus* KRUSE).

Simple walls may bear spines, protruding externally from an outer wall, into the central cavity from an inner wall, or within the plane of the pore orifice in either wall. Spines have a narrow base relative to bracts (see following section) and taper to a point at the free end. Redimiculi adorn the intervallum side of one or both walls in some forms (Fig. 499f–g).

Intersepts of either wall may be consistently crenulate [smoothly convex, as in *Nochoroicyathus kokoulini* KORSHUNOV and *Rotundocyathus floris* (VORONIN)] or plicate (folded to form a sharp mid-interseptal ridge, separating planar to subplanar lateral flanks, as in *Rozanovicoscinus* DEBRENNE) (Fig. 493a).

Wall with Bracts or Scales

Pores of an otherwise simple wall may be partially constricted by bracts or scales (Fig. 500). Bracts cover a single pore; scales cover two or more laterally adjacent pores. Scales are planar or curved (S-shaped or V-shaped). Laterally adjacent bracts may mutually fuse across several pores of a horizontal file. Such fused bracts are reminiscent of annuli, but remain incomplete; forms with fused bracts are categorized together with those bearing bracts or scales. Fused bracts are planar or S-shaped. Bracts and scales may also bear spines.

The present taxonomy is based on a conception of bracts that is more restrictive than previously employed: namely, it is based primarily on bracts that exhibit a cupped shape. The bract is thereby taken here to have an area of attachment to the wall that is sufficiently broad as to almost span the width of the associated pore, and this attachment area possesses a discernible curvature around the pore rim. Conversely, structures with narrower attachment areas, which typically taper to a point, are regarded as spines and, hence, are non-diagnostic at the genus level.

Bracts or scales may also be supplementary additions to canals (see discussion of walls with canals below) or other wall types. The presence of such supplementary bracts is accorded genus-level status in the present taxonomy, but may prove in future to be a species-level character only (see discussion of innovations in archaeocyathan taxonomy, p. 907–908).

Distinctive arcuate bracts on the inner wall canals of *Kordecyathus* MISSARZHEVSKIY are likewise treated as modified cupped bracts; they arch to link the lower and upper canal rims and may narrow toward upper rims. As these bracts are attached to the central cavity side of a wall with canals, they are regarded as supplementary.

The distinction between spines (see previous discussion of walls with simple porosity) and bracts may nevertheless be difficult to determine in some instances. It is acknowledged that some genera assigned here to families with simple inner walls have spines that may yet prove upon reassessment to be cupped bracts. Examples of potentially relevant genera are in the suborder Ajacicyathina: (i) in the simple outer-walled Ajacicyathidae, *Orbicyathellus* OSADCHAYA, *Robustocyathellus* KONYUSHKOV, and *Nochoroicyathellus* OSADCHAYA, which may each be better assigned to the bractose Densocyathidae; and (ii) in the tumulose outer-walled Tumulocyathidae, *Isiticyathus* KORSHUNOV and *Kotuyicyathellus* OSADCHAYA, which might

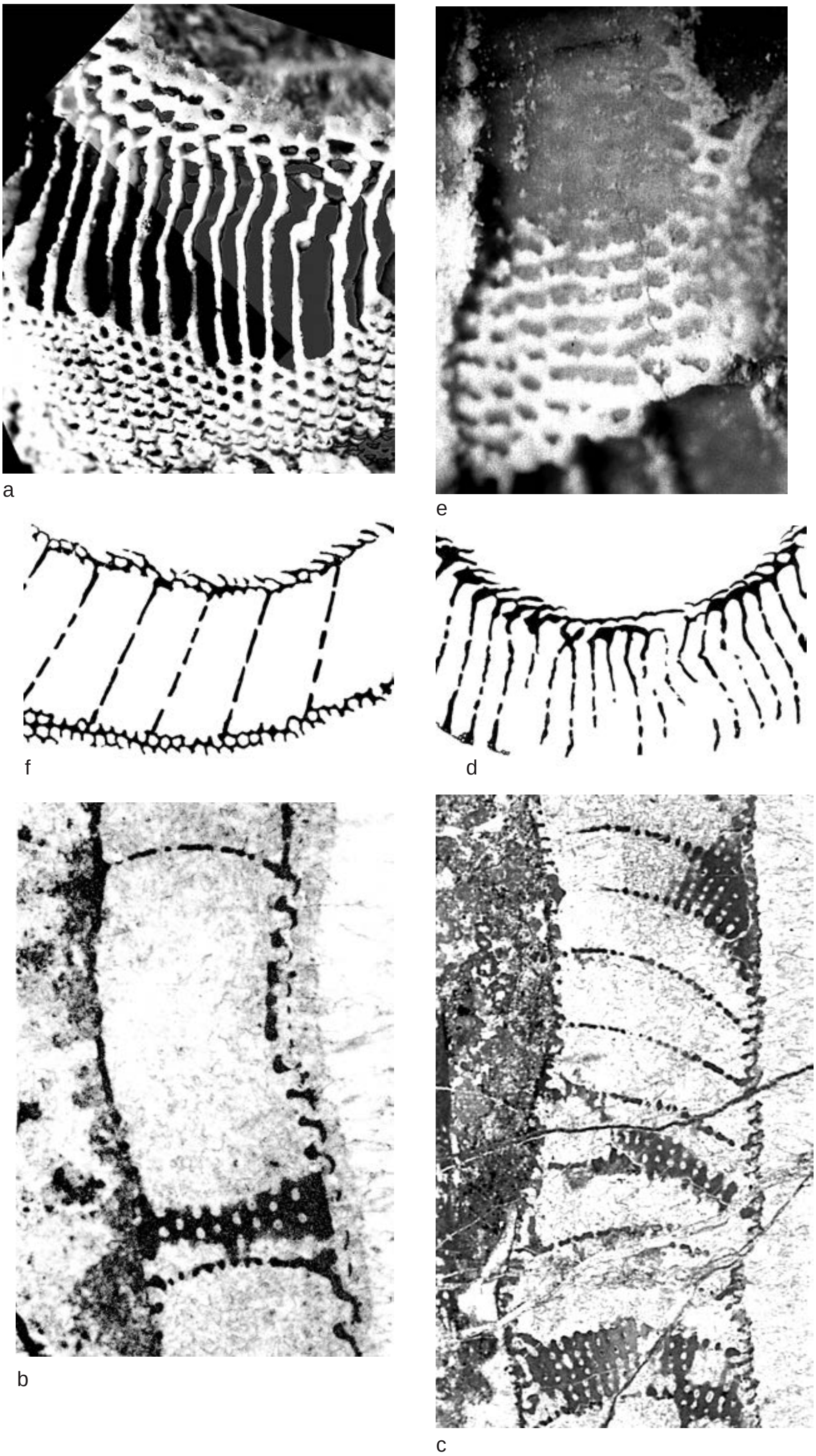

FIG. 500. *(For explanation, see facing page).*

belong in the Sanarkocyathidae. Similarly, in the suborder Erismacoscinina there are: (i) the simple-walled Asterocyathidae, with *Antoniocoscinus* Zhuravlev, that might belong in the bractose Rudanulidae; and (ii) in the Rozanovicyathidae, the genus *Rozanovicyathus* Korshunov, that might require redefinition within a revised, bractose inner-walled family.

An alternative proposal, not employed in the present taxonomy, is to treat bracts together with spines as simple-walled forms and to retain separate families only for those genera with inner wall scales. The consequence of this would be to transfer all such bractose genera to their corresponding simple inner-walled family. Thus, for example, in the ajacicyathine family Densocyathidae, genera such as *Dailycyathus* Debrenne, *Deceptioncyathus* Gravestock, and *Khirgisocyathus* Voronin would be transferred to the Ajacicyathidae.

These issues will continue to be a matter of debate among specialists. Indeed, there is no consensus among the present authors concerning the delimitation of bracts and spines. The definition of bracts given above and applied in the present taxonomy is the majority view (Debrenne and Kruse). However, unpublished observations by Zhuravlev highlight variation among late Atdabanian–early Botoman *Coscinocyathus* Bornemann on the Siberian Platform. Within this region, southern populations of *Coscinocyathus isointervallumus* Zhuravleva (1960b) display well-developed bracts, each supporting a spine, on their inner wall pores, whereas in otherwise morphologically similar northern populations (identified by Zhuravlev [1990b] as *C. marocanoides* Zhuravleva [in Datsenko & others, 1968]), the inner wall pores bear a spine supporting a second-order spinule. This variation may be treated as either intra- or interspecific. Such examples illustrate the necessity for comprehensive revisions based on large, sufficiently representative population samples in order to more completely understand the taxonomic value of the various elements termed bracts and spines.

For the present, in the absence of additional relevant published data, we follow with few modifications the systematic principles outlined by Debrenne, Zhuravlev, and Kruse (2002, p. 1544–1546).

Wall with Annuli

Either wall may bear regularly spaced planar, S-shaped, or V-shaped annuli. Commonly, each inner wall intersept of an annulate form has only a single, longitudinal pore row; less commonly, there are several. Annuli are much more common on the inner wall than the outer: outer wall annuli are known only in the atabulate family Sigmocyathoidea, in which all three known constituent genera bear S-shaped annuli. V-shaped annuli may be upright or inverted (a genus-level distinction), or may bear a short, arête-like carina, extending from the apex of each V, and coplanar with one limb of the V (Fig. 501).

Fig. 500. Bracts and scales; *a,* probable upwardly projecting cupped bracts on outer wall of *Russocyathus rodionovae* Zhuravleva, Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, external view of cup in longitudinal section (outer wall at bottom), 4137/14-4, PIN, ×14 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* downwardly projecting cupped bracts on inner wall of *Polycoscinus cymbricensis* (Kruse), Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.12784, holotype, FT.8270, 8271, 8581, 8582, 12784, AM, ×16 (Kruse, 1982); *c,* upwardly projecting S-shaped scales on inner wall of *Xestecyathus zigzag* Kruse, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.12793, holotype, F.83405, AM, ×10 (Kruse, 1982); *d,* horizontal to upwardly projecting curved scales, fused into pseudoannuli on inner wall of *Rectannulus* sp., Botoman, Usa Formation, Kuznetsk Alatau, Russia, transverse section, 4327/76, PIN, ×7 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* upwardly projecting planar fused bracts on inner wall of *Cadniacyathus asperatus* R. Bedford & J. Bedford, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, internal view of cup in longitudinal section, lectotype, 86616(1), USNM, ×14 (Debrenne, 1974b); *f,* upwardly projecting S-shaped scales on inner wall of *Tennericyathus malycanicus* Rozanov, Atdabanian, Pestrotsvet Formation, Malykan, Lena River, Sakha (Yakutia), Russia, transverse section, GIN2034/14, PIN, ×12 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

Most annuli have smooth inner rims; in a minority of genera these are denticulate, e.g., *Sagacyathus* KRUSE (Fig. 501e).

Wall with Canals

By definition, canal length is greater than diameter. Inner wall canals may be noncommunicating (Fig. 502), or communicating with their neighbors via porelike openings along their length (Fig. 503). These two conditions are considered sufficiently distinct in their hydrodynamic properties to warrant placement in separate family-level taxa. Only noncommunicating canals are known for the outer wall.

Like simple pores, canals are typically arranged in alternating longitudinal rows, and forms with a single canal row per inner wall intersept are distinguished at the genus level from those with several canal rows per inner wall intersept. In yet other genera, each inner wall canal row coincides with a septum to form stirrup canals. Some genera have spongiose inner walls constructed of waved, anastomosing, communicating canals, e.g., *Kiwicyathus* DEBRENNE & KRUSE (Fig. 503b). Genera such as *Ethmophyllum* MEEK have complex, doubly zoned inner walls, with anastomosing, waved canals arising from the fluted inner edges of the septa, so that the wall has an overall upright V-shaped appearance (Fig. 503c–e).

Exceptionally, canals may span several intersepts, e.g., *Gnaltacyathus* KRUSE (Fig. 502b). Some genera (e.g., *Ethmocyathus* R. BEDFORD & W. R. BEDFORD) bear inner wall canals formed by flexure of the inner edges of the septa. Canals may be straight, S-shaped, or V-shaped, branching or nonbranching, discrete or anastomosing, and may project horizontally, obliquely upward, or obliquely downward with respect to the wall.

Some canal-bearing genera also bear supplementary structures, generally bracts, attached to the free ends of their canals; if canals and supplementary structures are obliquely, but oppositely, oriented, an overall upright or inverted V-shaped appearance is imparted to the wall. In practice, care is needed to distinguish this condition from true V-shaped canals. A spine or small plate may arise from the apex of each constituent canal-bract couplet in some such forms, e.g., the outer wall of *Ethmophyllum* MEEK (Fig. 503c).

Wall with Microporous Sheaths

Microporous sheaths are much more common on the outer wall than on the inner; examples of the latter are *Membranacyathus* ROZANOV and *Bipallicyathus* ZHURAVLEV. They are typically supported on an otherwise simple porous wall with constituent framework (or carcass) pores with a diameter of 0.15–0.25 mm, but exceptionally they are supported on S-shaped canals in *Hupecyathellus* ROZANOV.

ROZANOV (1973) first elaborated the important distinction between the two major variants of the microporous sheath: attached and independent (his erbocyathoid and pretiosocyathoid types respectively) (Fig. 504). These two variants represent a suprafamilial criterion.

Attached sheaths are generally a feature of walls in which the framework pores are funnel shaped, widening toward the exterior so that the lintels are externally narrow and arête-like (see Fig. 514b). Finer rodlike or

FIG. 501. Annuli; *a,* upwardly projecting S-shaped annuli on inner wall of *Stillicidocyathus sigmoideus* (R. BEDFORD & J. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, internal view of cup in longitudinal section, holotype, 86750, PU, ×4.5 (Debrenne, 1970a); *b,* upright V-shaped annuli on inner wall of *Thalamocyathus trachealis* (TAYLOR), Botoman, allochthonous, Whichaway Nunataks, Antarctica, oblique section, S8413-5, NHM, ×5 (Hill, 1965); *c,* upright V-shaped annuli on inner wall of *Aporosocyathus gnaltaensis* KRUSE, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.14168, paratype, F.83604, AM, ×10 (Kruse, 1982); *d,* schematic section of inverted V-shaped annuli on inner wall of *Svetlanocyathus primus* MISSARZHEVSKIY & ROZANOV, Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, longitudinal section (outer wall to right), ×9 (Missarzhevskiy & Rozanov, 1962); *e,* upright V-shaped annuli bearing denticulate rims on inner wall of *Sagacyathus stonyx* KRUSE, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, oblique section, FT.8499, paratype, FT.8498–8500, AM, ×3.5 (Kruse, 1982); *f,* ?horizontally projecting planar annuli bearing short beams that support microporous sheath on inner wall of *Compositocyathus muchattensis* (ZHURAVLEVA), Atdabanian, Pestrotsvet Formation, Mukhatta Creek, Lena River, Sakha (Yakutia), Russia, transverse section, holotype, 205/47a, TsSGM, ×10 (Zhuravleva & Zelenov, 1955).

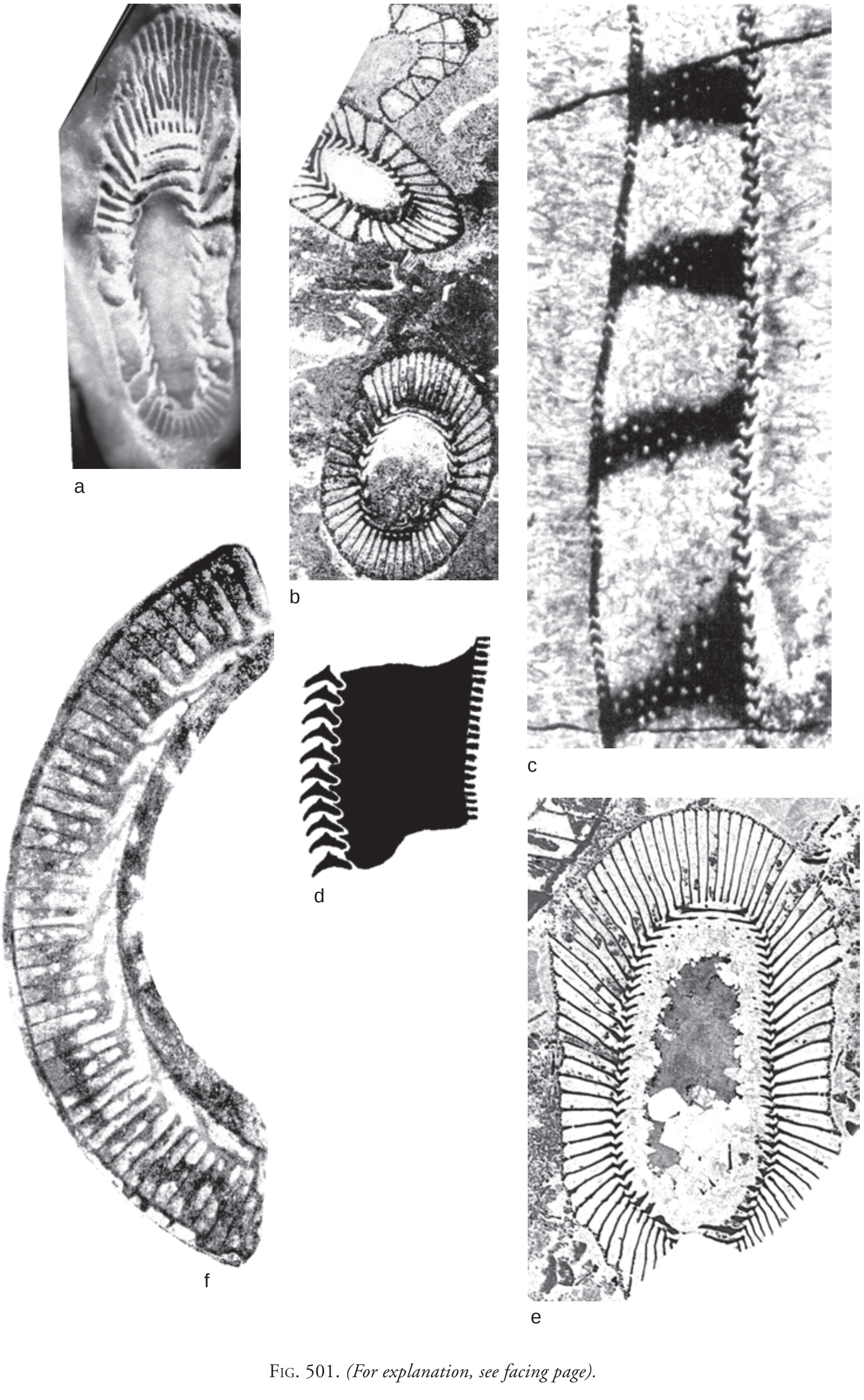

FIG. 501. *(For explanation, see facing page).*

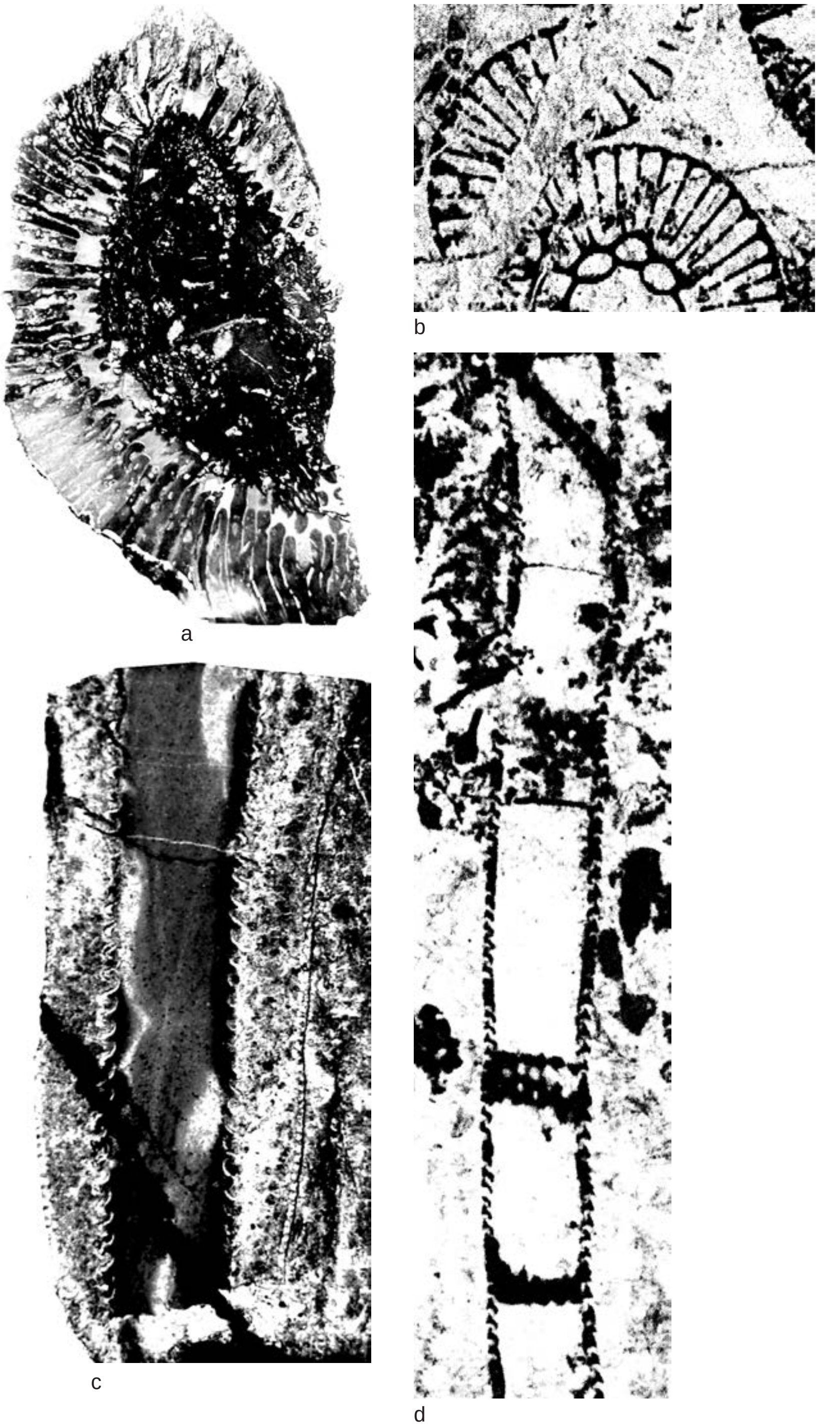

FIG. 502. *(For explanation, see facing page).*

tapering lintels delineating the sheath micropores thereby radiate centripetally inward from the outer margins of the framework pores to form a more or less continuous sheet of micropores. Continuous sheaths cover the entire surface of the wall (Fig. 504b, Fig. 505a–d); discontinuous sheaths cover each framework pore separately (Fig. 504c, Fig. 505e–g). A common pattern of attached sheaths for any one framework pore is of a central micropore surrounded by a circlet of six similarly sized micropores (i.e., about seven micropores), but a greater or lesser number of micropores may be developed in different taxa (Rozanov, 1973; Kashina, 1979). A unique tylocyathoid-type of attached sheath is shown by *Tylocyathus* Vologdin, in which the sheath is supported on longitudinally subrectangular framework pores, with two rows of micropores per framework pore; each micropore bears an S-shaped bract (Fig. 505j).

Independent sheaths are invariably continuous, supported by short perpendicular rods arising from the lintels of the framework pores (Fig. 504a, Fig. 505h–i). There is no direct participation of the pore lintels in this sheath variant, and pores need not be funnel shaped. The common micropore pattern is one of more or less regular, alternating rows. Micropores may be rounded or subpolygonal.

Wall with Tumuli

Tumuli are hollow, porous, hemispherical to prolately ellipsoidal domes covering the pores of outer walls; they are not known on inner walls. Tumulose walls exist in two variants: with simple or multiperforate tumuli (Fig. 506). Simple tumuli have a single small pore, usually located toward the lower side of the tumulus (Fig. 506b–c). In some cases, bracts have been incorrectly identified as tumuli, e.g., *Tumulifungia* Zhuravleva, which actually bears cupped bracts on the outer wall. True tumuli will have similar morphology in either transverse or longitudinal section, and only rarely will the single pore be intersected.

Multiperforate tumuli, in contrast, possess many small pores, typically covering the entire surface of the tumulus (Fig. 506d–e).

Other Types of Wall

Other distinctive wall types are the clathrate type, with closely spaced longitudinal ribs (Fig. 506f); and the pseudoclathrate type, with longitudinal ribs and transverse linking lintels, together supported by short rods (Fig. 506a).

UPPER SURFACE STRUCTURES

Certain skeletal elements were evidently developed only once in the ontogeny of some cups, since they are always observed crowning the tops of cups but are never found within cups.

Peltae

Peltae are unique to the Monocyathida. They are horizontal, slightly convex plates developed as a continuation of the wall. Two broad types, nonporous and porous, can be recognized, but the distinction is accorded little taxonomic importance, even at species level. Earlier authors (e.g., Zhuravleva, 1963b; Okuneva & Repina, 1973; Vologdin, 1977) recognized many more

Fig. 502. Noncommunicating canals; *a,* horizontal to upwardly projecting straight canals on inner wall of *Inessocyathus spatiosus* (Bornemann), Botoman, Matoppa Formation, San Pietro, Sardinia, Italy, transverse section, topotype, M84074, MNHN, ×2.3 (Debrenne, 1964); *b,* horizontal to upwardly projecting straight canals, each canal spanning several intersepts on inner wall of *Gnaltacyathus nodus* Kruse, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, transverse section, FT.8495b, holotype, FT.8453, 8454, 8495b, AM, ×8 (Kruse, 1982); *c,* horizontal to upwardly projecting S-shaped canals on inner wall of *Rasetticyathus acutus* (Bornemann), Botoman, Matoppa Formation, Monte Cuccurinu, Sardinia, Italy, longitudinal section, M84036, MNHN, ×10 (Debrenne, 1972); *d,* horizontal to upwardly projecting S-shaped canals, bearing supplementary bracts externally on outer wall and inverted V-shaped canals on inner wall of *Porocoscinus rudens* (Kruse), Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.8295, holotype, F.83933, AM, ×8.5 (Kruse, 1982).

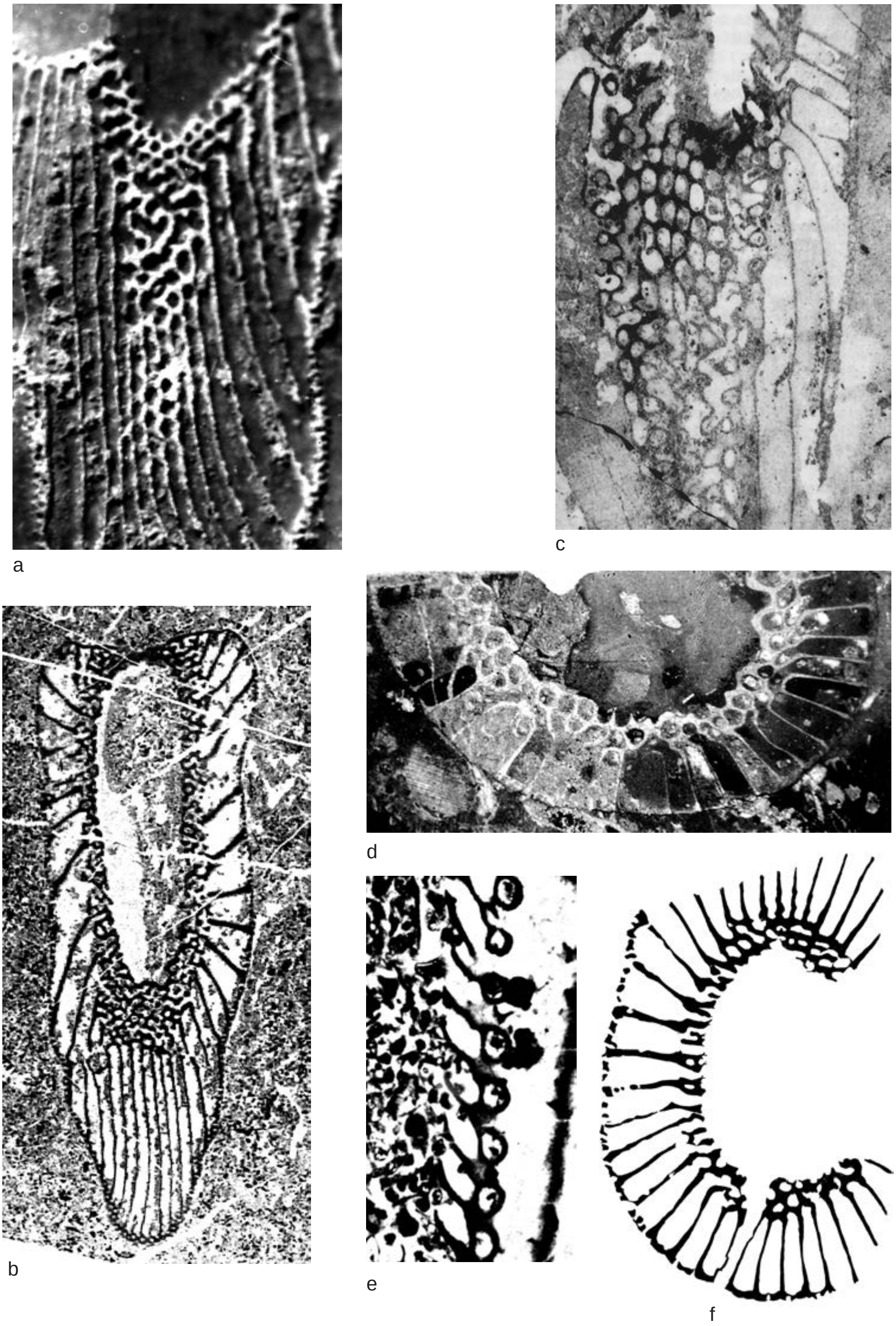

FIG. 503. *(For explanation, see facing page).*

variants, but these were based on differing orientations of section through the cup.

Nonporous peltae possess a central sag, bearing an orifice. The orifice may support a concave, finely perforated, saclike membrane directed into the inner cavity (Fig. 507.1). Nonporous peltae are known in some *Archaeolynthus* TAYLOR, *Palaeoconularia* CHUDINOVA, *Tumuliolynthus* ZHURAVLEVA, and *Propriolynthus* OKUNEVA.

Porous peltae are present in some other species of *Archaeolynthus* TAYLOR, *Palaeoconularia,* and *Propriolynthus*, and in some *Sajanolynthus* VOLOGDIN & KASHINA and *Melkanicyathus* BELYAEVA. Their porosity invariably matches that of the cup wall. Thus, in *Propriolynthus vologdini* (YAKOVLEV) and *Melkanicyathus operculatus* (MASLOV), the marginal area of the pelta bears bracts oriented in a reverse sense to those of the wall (Fig. 507.2b). *Archaeolynthus cipis* (VOLOGDIN) has spines on the wall and pelta (Fig. 507.2a).

Rims

Rims are restricted to two-walled cups. They include types in which the outer wall curves toward the inner wall; for example, in *Cordilleracyathus blussoni* HANDFIELD (Fig. 507.3) and species of *Irinaecyathus* ZHURAVLEVA, *Tegerocyathus* KRASNOPEEVA, *Plicocyathus* VOLOGDIN, and *Sekwicyathus* HANDFIELD. This type of rim is favored in genera with aporose to sparsely porous septa. Alternatively, the rim is the result of growth of the inner wall, complicated by fringelike skeletal processes (e.g., in *Nochoroicyathus sunnaginicus* [ZHURAVLEVA] and *Formosocyathus bulynnikovi* VOLOGDIN). In a third type, the rim is a horizontal plate covering the intervallum, as observed, for example, in *Nochoroicyathus* ZHURAVLEVA, *Baikalocyathus* YAZMIR, *Dokidocyathus* TAYLOR (Fig. 507.4), and *Siderocyathus* DEBRENNE & GANGLOFF.

MORPHOLOGY OF ARCHAEOCYATHIDA AND KAZACHSTANICYATHIDA

INTERVALLUM STRUCTURES

Intervallar structures in these two orders are more diverse than in those orders previously discussed.

Taeniae

Taeniae are homologous to septa in the other orders but are not limited to a single plane. Rather, component lintels diverge in orientation so that taeniae appear wavy. Most Archaeocyathida have taeniae, at least in early ontogeny. Some genera exhibiting taeniae throughout cup development were formerly described as bearing buttresses or struts adjacent to one or both walls, as in *Aruntacyathus* KRUSE (=*Spirocyathella* VOLOGDIN) by KRUSE and WEST (1980) (Fig. 508a) and *Spirillicyathus* R. BEDFORD & J. BEDFORD by GRAVESTOCK (1984) (Fig. 508b), or as wavy and dichotomous taeniae in *Pycnoidocyathus* TAYLOR by FONIN (1985) (Fig. 508c).

FIG. 503. Communicating canals; *a,* horizontal to upwardly projecting straight stirrup canals, branching toward central cavity, on inner wall of *Zonacyathus retezona* (TAYLOR), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section, paralectotype, T1591, SAM, ×7 (Taylor, 1910); *b,* horizontal to upwardly projecting straight stirrup canals on inner wall of *Kiwicyathus nix* DEBRENNE & KRUSE, Botoman, Mt. Egerton, Byrd Glacier, Antarctica, longitudinal section, holotype VC19, VU, ×4.5 (Debrenne & Kruse, 1986); *c,* subspherical chambered canals each with base commencing in intervallum, canals subdivided by stipules on outer wall, and anastomosing, horizontal to upwardly and laterally projecting waved canals, arising from fluted inner edges of septa, on inner wall of *Ethmophyllum whitneyi* MEEK, Botoman, Rosella Formation, Kechika Mountains, British Columbia, Canada, longitudinal section (outer wall to right), 69269, GSC, ×7; *d,* same specimen, transverse section, ×7 (Mansy, Debrenne, & Zhuravlev, 1993); *e,* detail of anastomosing, horizontal to upwardly and laterally projecting waved canals, arising from fluted inner edges of septa, on inner wall of *Ethmophyllum whitneyi* MEEK, Botoman, Atan Group, Good Hope Lake, British Columbia, Canada, longitudinal section (intervallum to right), 25333, GSC, ×9 (Handfield, 1971); *f,* downwardly projecting straight canals, bearing supplementary bracts or annuli on central cavity side, on inner wall of *Irinaecyathus schabanovi* ROZANOV, Toyonian, Elanskoe Formation, Elanskoe, Lena River, Sakha (Yakutia), Russia, oblique transverse section, GIN4434/9, PIN, ×3 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

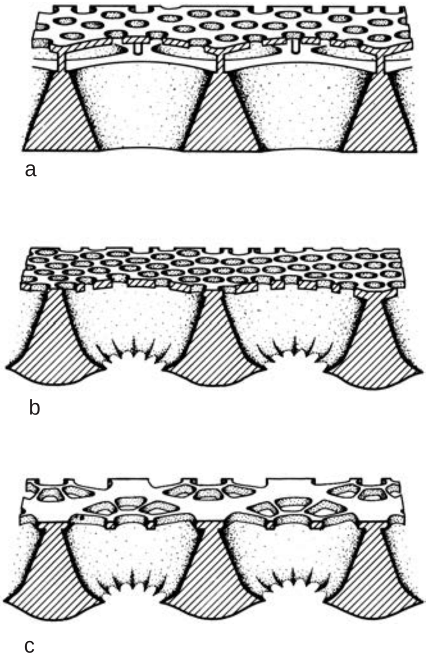

FIG. 504. Schematic sections of types of microporous sheath; *a,* independent sheath supported on short pillars; *b,* attached sheath, continuous over external surface; *c,* attached sheath, discontinuous, restricted to framework pore openings (Gravestock, 1984).

True taeniae are present only in adult cups of Archaeocyathina. Two taenial porosity types—coarsely porous and finely porous—are recognized, but porosity may vary between the two types in a single cup. In such cases, larger pores tend to be nearer the outer wall. Synapticulae are typically associated with taenial cups, but are not regularly arranged.

Pseudosepta

All other radial-longitudinal, platelike elements are ontogenetic derivatives of taeniae. Pseudosepta develop ontogenetically from taeniae as ordered, planar, porous partitions. They comprise regularly arranged lintels yet differ from true septa in their developmental pathway. Pseudosepta differ from septa in having no regularity in size or shape of their pores (Fig. 494a).

Pseudosepta may be coarsely or finely porous in Loculicyathina and Archaeocyathina, or aporose in Loculicyathina and Anthomorphina (Fig. 494b–d).

Synapticulae are not typically associated with pseudosepta.

Pseudotaenial and Dictyonal Network

Pseudotaenial structure comprises taeniae with regularly distributed synapticulae linking taeniae at each interpore lintel (Fig. 509a). Pseudotaeniae are invariably coarsely porous. They characterize the Archaeocyathina.

Pseudotaenial structure is morphologically transitional between true taeniae and dictyonal network. This latter comprises equidimensional synapticulae and radial and longitudinal taenial lintels, together forming an orthogonal network of rods, which may arch between the inner and outer wall in some taxa (Fig. 509c) and remain planar in others (Fig. 509b).

FIG. 505. Microporous sheaths; *a,* continuous attached sheath on outer wall of *Erugatocyathus krusei* GRAVESTOCK, Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, tangential section, holotype, P21599, SAM, ×38 (Gravestock, 1984); *b–d,* continuous attached sheath on outer wall of *Erugatocyathus howchini* GRAVESTOCK, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia; *b,* tangential section, paratype, P21630, SAM, ×38; *c–d,* holotype, P21590-1, SAM, ×38; *c,* oblique section through outer wall; *d,* longitudinal section (intervallum to left) (Gravestock, 1984); *e–g,* partially discontinuous attached sheath on outer wall of *Erugatocyathus mawsoni* GRAVESTOCK, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia; *e,* tangential section, paratype, P21473-2, SAM, ×38; *f,* transverse section, intervallum to left, paratype, P21474-2, SAM, ×38; *g,* tangential section, paratype, P21466-2, SAM, ×38 (Gravestock, 1984); *h–i,* independent sheath on outer wall of *Agyrekocyathus dissitus* (KRUSE), Botoman, Mount Wright Volcanics and Cymbric Vale Formation, Mount Wright, New South Wales, Australia; *h,* transverse section, FT.8176, paratype, F.83942, AM, ×15; *i,* oblique section through outer wall, FT.8179, paratype, F.87962, AM, ×15 (Kruse, 1982); *j,* attached microporous sheath, each micropore bearing a cupped bract, on outer wall of *Tylocyathus bullatus* (ZHURAVLEVA), Botoman, Lenyaka Formation, Schamanikha River, Kolyma River basin, Russia, tangential section, specimen 3900/53, PIN, ×24 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

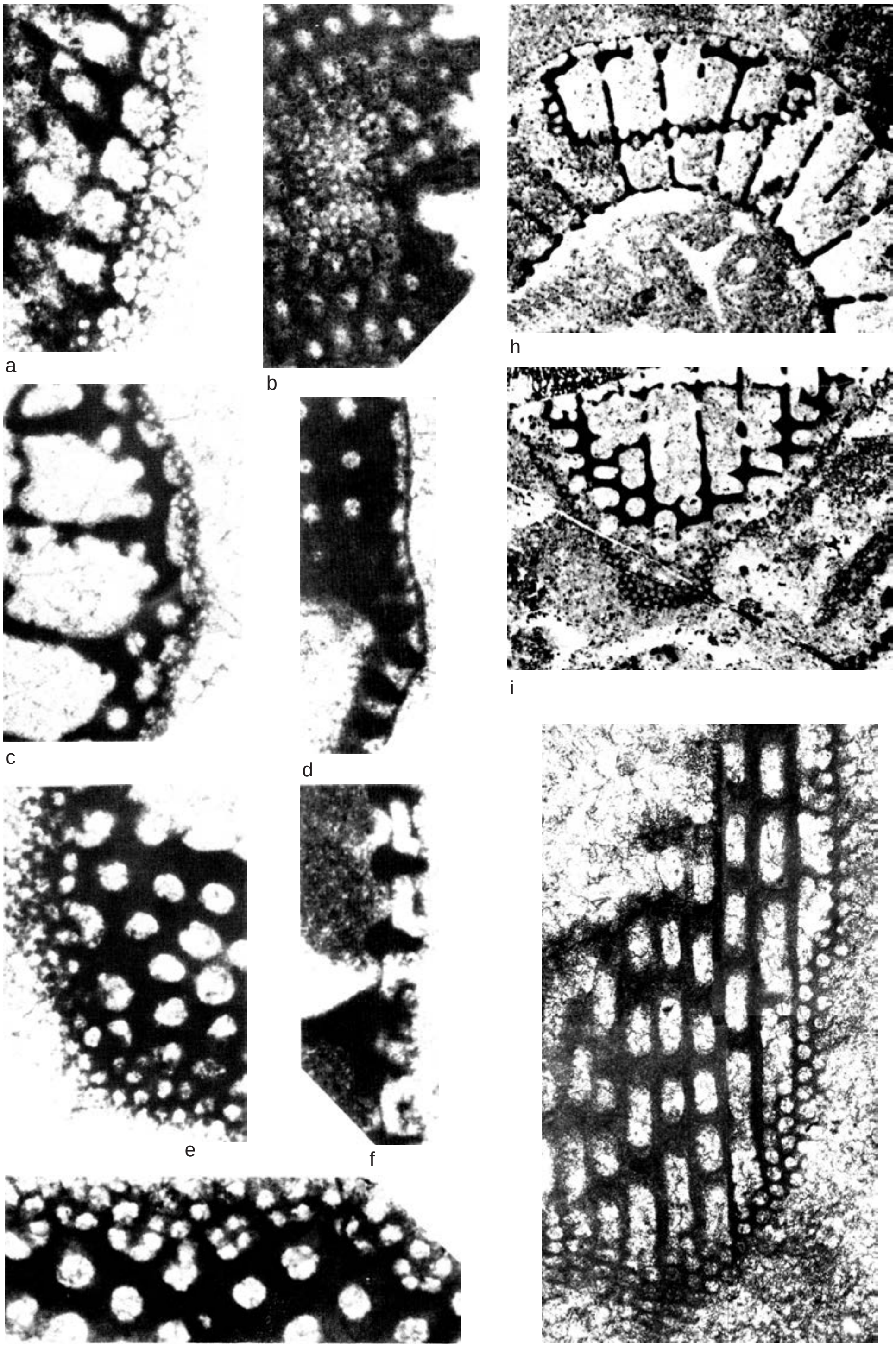

FIG. 505. *(For explanation, see facing page).*

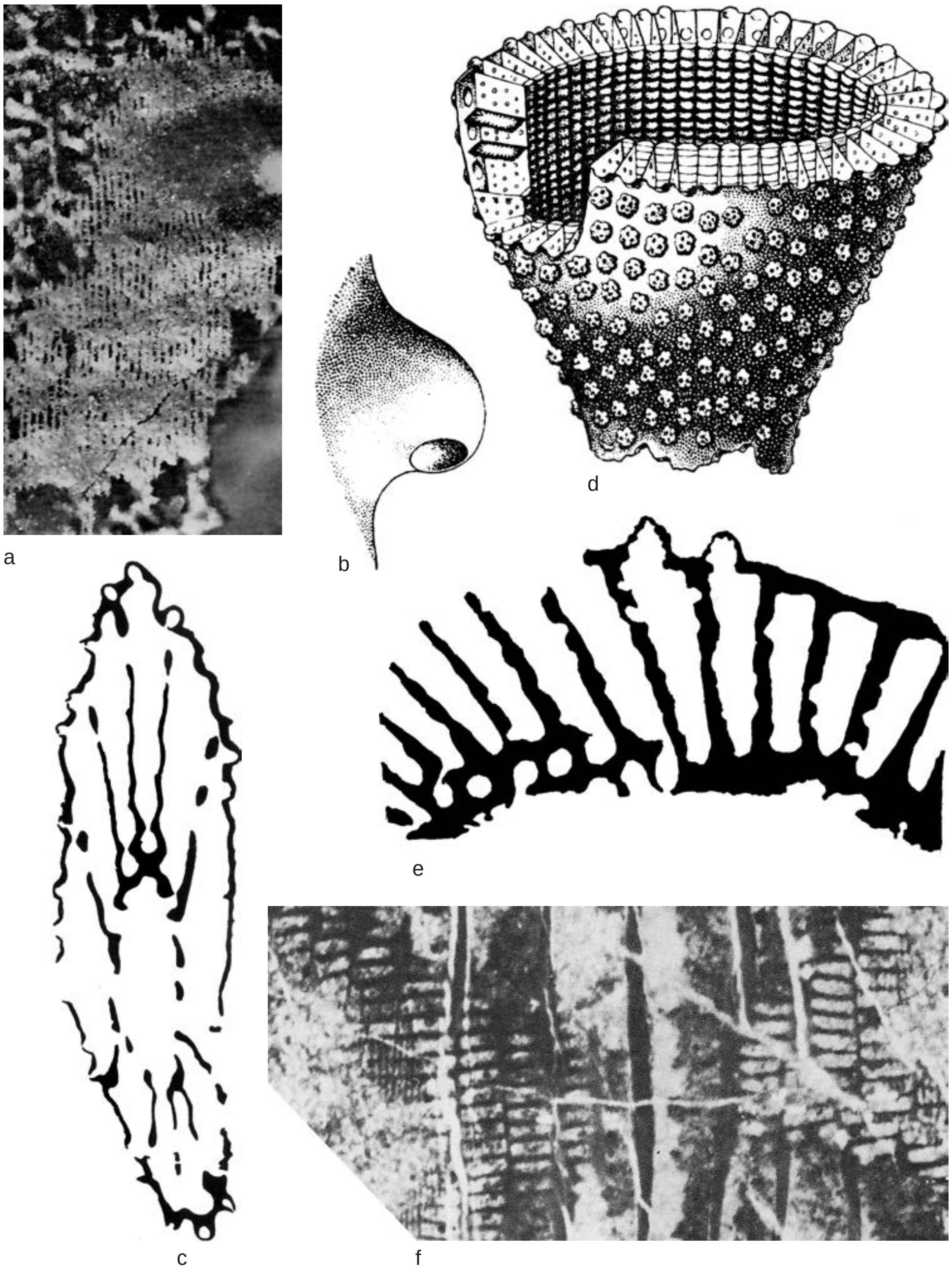

Fig. 506. Tumuli, clathri, and pseudoclathri; *a,* pseudoclathrate outer wall of *Clathricoscinus* sp., Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, external view, 4327/5, PIN, ×12 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* detail of simple tumulus on outer wall of *Tumulocyathus kotuyikensis* (Zhuravleva), ×100 (Zhuravleva, 1960b); *c,* simple tumuli on plicate outer wall of *Plicocyathus rozanovi* (Handfield), Botoman, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, oblique longitudinal section, 90125, GSC, ×12 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *d,* multiperforate tumuli on outer wall

(Continued on facing page.)

Calicles

By analogy with other sponges of chaetetid architecture, longitudinal tubelike elements in archaeocyaths are termed calicles (West & Clark, 1983). Calicles develop ontogenetically from taeniae and are diagnostic of the Dictyofavina (Fig. 510.1). They are tetragonal or hexagonal in cross section. Hexagonal calicles bear one or several longitudinal pore rows per facet, whereas tetragonal calicles invariably bear only one.

Syringes

Syringes (Zhuravleva & Myagkova, 1981) are diagnostic of the Syringocnemina. These are stacked radial tubes of hexagonal cross section, transverse across much of the intervallum, but typically curving downward near the inner wall (Fig. 510.3).

Like taeniae, syringes can be coarsely or finely porous, corresponding to one or several radial pore rows per component facet, respectively. The number of pore rows per facet (one versus several) is a generic criterion in this suborder. In most genera, this number is invariant for all facets. However, in *Pseudosyringocnema* Handfield and *Williamicyathus* Zhuravlev, porosity of the two transverse facets differs from that of the four lateral facets comprising each syrinx, with one pore row per transverse facet and several pore rows per lateral facet (Fig. 510.2).

The syringes of *Syringothalamus* Debrenne, Gangloff, & Zhuravlev bear a single radial row of coarse pores per facet. In oblique section, these could potentially be confused with pseudotaenial or dictyonal network.

Tabulae

Pectinate tabulae are not known in these two orders. Most Archaeocyathina possess segmented tabulae, generally formed by the outer wall, and a few Loculicyathina (*Mikhnocyathus* Maslov) have plate tabulae. Only *Anthomorpha* Bornemann and its allies (Anthomorphina) bear independent (membrane) tabulae. Membrane tabulae show some similarity to pectinate tabulae in Ajacicyathida, in that they are developed separately in each intersept. They are pierced by two poorly delineated radial rows of irregular pores per loculus, which are identical in morphology to that of the outer wall (Fig. 511).

The more common segmented tabulae tend to be irregularly spaced along the length of the cup, and between different cups, even from the same locality. A few genera, such as *Claruscoscinus* Handfield, *Pycnoidocoscinus* R. Bedford & W. R. Bedford, and *Gabrielsocyathus* Debrenne, show regular spacing of segmented tabulae. However, although these genera mimic Coscinocyathina and Kazachstanicyathida in this regard, their segmented tabulae develop late in ontogeny; this is not the case in these two ordinal taxa.

Segmented tabulae are extensions of the outer and/or inner wall, and so reflect the porosity of the parent wall. Thus, segmented tabulae of simple porosity accompany simple outer walls. Such tabulae are finely porous (Fig. 512a) or coarsely porous (Fig. 512b), according to wall porosity. In some *Pycnoidocoscinus* R. Bedford & W. R. Bedford (outer wall basic simple), the tabular pores are slitlike (Fig. 512c).

Likewise, in Archaeocyathoidea (outer wall concentrically porous), tabular porosity is concentric (Fig. 512d), and in Metacyathoidea (outer wall compound), it is compound (Fig. 512f).

However, in the case of concentrically porous and compound walls, the tabular porosity is inconsistently conserved in some

Fig. 506. *(Continued from facing page).*
of *Lenocyathus lenaicus* Zhuravleva, schematic external view of cup, ×2.5 (Zhuravleva, 1960b); *e,* multiperforate tumuli on outer wall of *Torosocyathus provisus* Kashina, Botoman, Usa Formation, Kuznetsk Alatau, Russia, transverse section (outer wall at top), GIN3878-4, PIN, ×45 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *f,* clathrate outer wall of *Clathrithalamus mawsoni* Debrenne & Kruse, Botoman, Skackleton Limestone, Holyoake Range, Nimrod Glacier, Antarctica, tangential section, holotype, MG511, GNS, ×20 (Debrenne & Kruse, 1986).

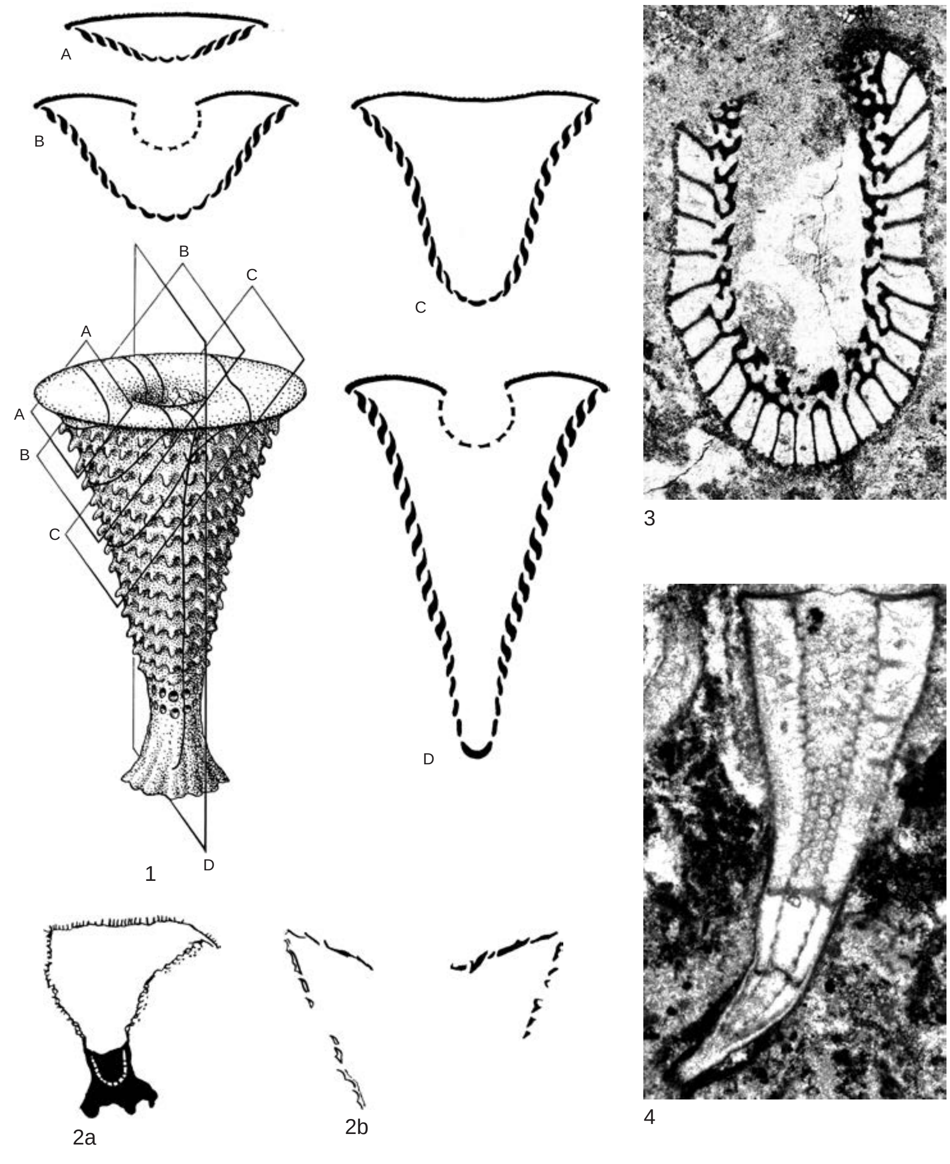

Fig. 507. Upper surface structures of cup; *1,* schematic reconstruction of nonporous pelta on cup of *Propriolynthus vologdini* (Yakovlev) with various possible sections, section B corresponding to *Globosocyathus bellus* Okuneva; *2a–b,* porous peltae; *2a,* porous pelta with spines on cup of *Archaeolynthus cipis* (Vologdin), Botoman, Usa Formation, Sukhie Solontsy, Batenev Range, Kuznetsk Alatau, Russia, longitudinal section, holotype, 1924-43, PIN, ×16; *2b,* porous pelta with bracts on cup of *Melkanicyathus operculatus* (Maslov), Atdabanian, Usa Formation, Bol'shaya Erba, East Sayan, Altay Sayan, Russia, longitudinal section, 1923-41-2, PIN, ×16; *3,* rim in which outer wall curves toward inner wall, *Cordilleracyathus blussoni* Handfield, Botoman, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, oblique longitudinal section, 90140, GSC, ×8; *4,* rim as horizontal plate covering intervallum in *Dokidocyathus* sp., Botoman, Terekla Formation, Kurogan-Sakmara zone, western flank of Southern Urals, Russia, longitudinal section, 4327/38, PIN, ×20 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

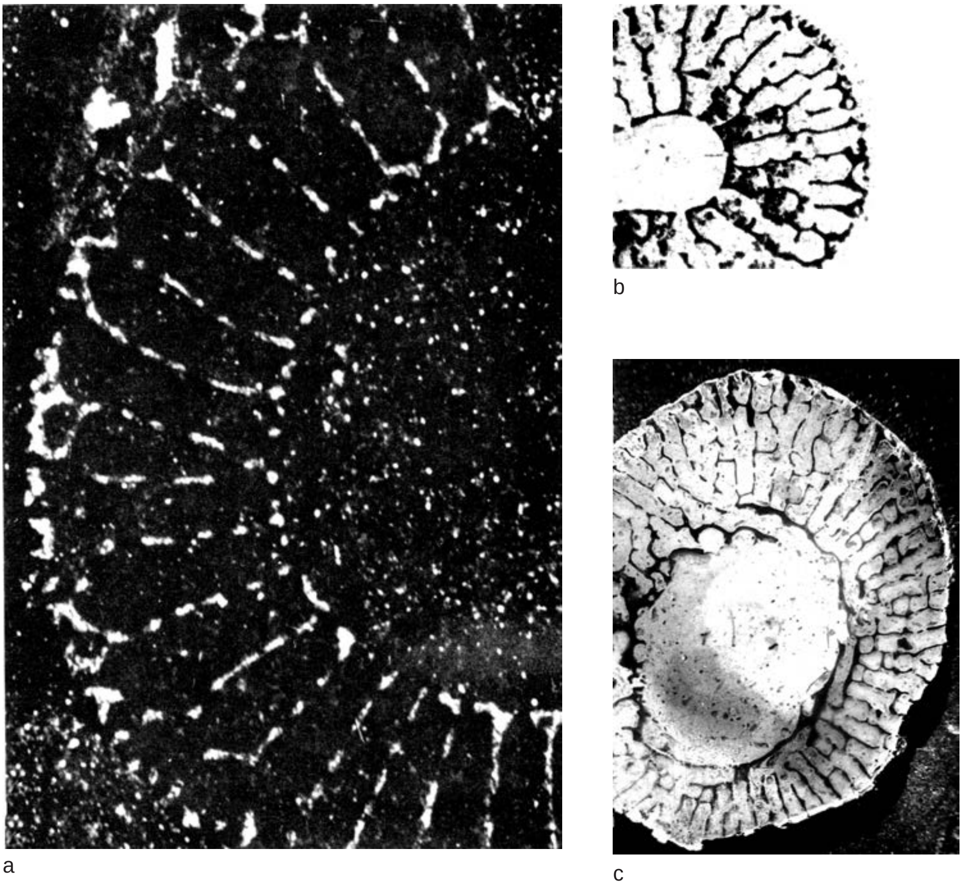

FIG. 508. Taeniae; *a,* taeniae with strutlike bifurcation adjacent to both walls in *Spirocyathella toddi* (KRUSE), Atdabanian, Todd River Dolostone, Ross River, Northern Territory, Australia, transverse section, FT.9947, specimen F.132942, AM, ×12 (Kruse & West, 1980); *b,* taenial bifurcation in intervallum and adjacent to outer wall (strutlike) in *Spirillicyathus tenuis* R. BEDFORD & J. BEDFORD, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia, transverse section, P21411-2, SAM, ×5 (Gravestock, 1984); *c,* taenial bifurcation in intervallum of *Pycnoidocyathus sekwiensis* HANDFIELD, Botoman, Sekwi Formation, Caribou Pass, Northwest Territories, Canada, transverse section, 12362, GSC, ×2 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

taxa. In *Archaeopharetra* R. BEDFORD & W. R. BEDFORD, for example, concentric porosity can cover only the outer portion of a tabula, or can be completely absent. In some *Dictyosycon* ZHURAVLEVA, also with concentrically porous outer wall, segmented tabulae are nevertheless constructed only of coplanar, rodlike, intervallar elements (Fig. 512e).

Tabulae with canals are known in *Maiandrocyathus* DEBRENNE & *Beltanacyathus* R. BEDFORD & J. BEDFORD (GRAVESTOCK, 1984), both Beltanacyathoidea (outer wall with subdivided canals).

Astrorhizae and Tubuli

Astrorhizae are recognized as a diagnostic feature of choanocyte-bearing organisms (HARTMAN, 1983; BOYAJIAN & LABARBERA, 1987). It is quite possible that many archaeocyaths had astrorhizal canals embedded in the soft tissue, as in some extant demosponges with nonspiculate

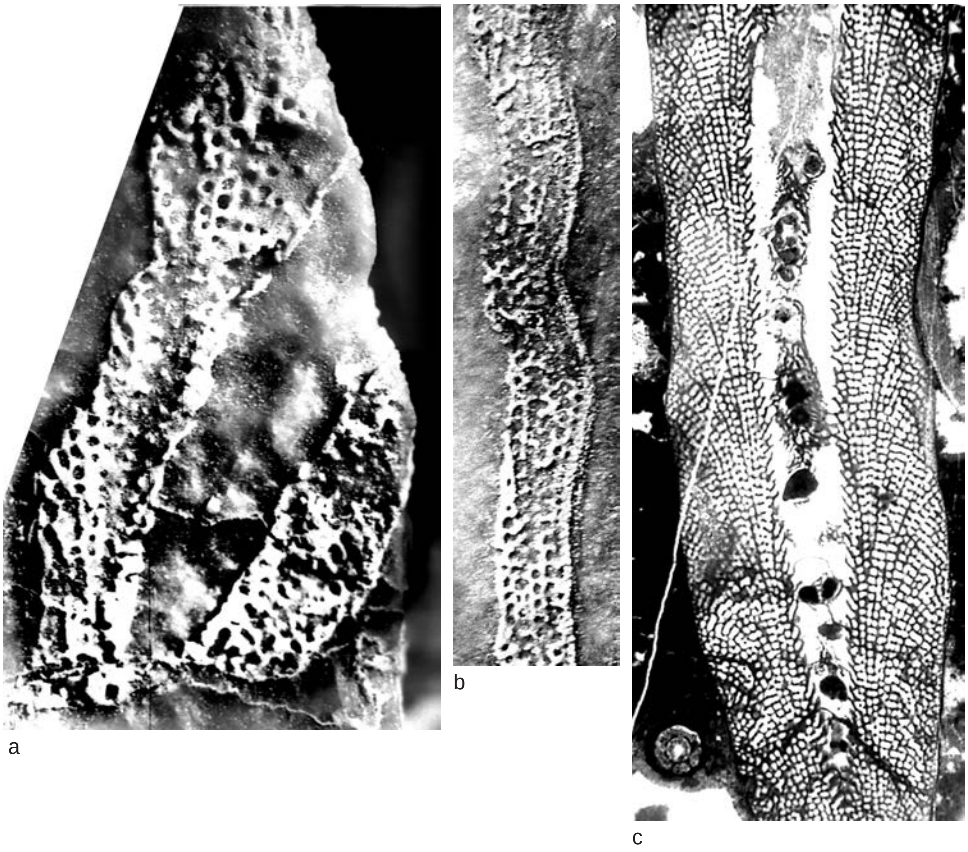

FIG. 509. Pseudosepta, pseudotaeniae, and dictyonal network; *a,* coarsely porous pseudotaeniae in *Archaeocyathus decipiens* R. BEDFORD & J. BEDFORD, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section, holotype, 86670-247, PU, ×5.3 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* pseudosepta in *Graphoscyphia graphica* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to right), paralectotype, P947-68, SAM, ×6 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* dictyonal network in *Fenestrocyathus complexus* HANDFIELD, Botoman, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, longitudinal section, paratype, 25390, GSC, ×4.5 (Handfield, 1971).

FIG. 510. Calicles and syringes; *1,* calicles of hexagonal cross section in *Usloncyathus araneosus* (GRAVESTOCK), Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, transverse section, paratype, P21663-3, SAM, ×10 (Gravestock, 1984); *2a–d,* schematic reconstructions of varieties of syrinx; *2a,* several pore rows per facet, as in *Syringocnema*, *Kruseicnema*, *Fragilicyathus*, *Tuvacnema*; *2b,* one pore row per transverse facet and several pore rows per lateral facet, as in *Pseudosyringocnema*; *2c,* one pore row per facet, as in *Syringothalamus*; *2d,* complex syrinx with one pore row per transverse facet and several pore rows per lateral facet, as in *Williamicyathus* (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *3,* syringes of hexagonal cross section with several pore rows per facet, *Syringocnema favus* TAYLOR, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to right), FT.9486, specimen F.83936, AM, ×10 (Kruse, 1982).

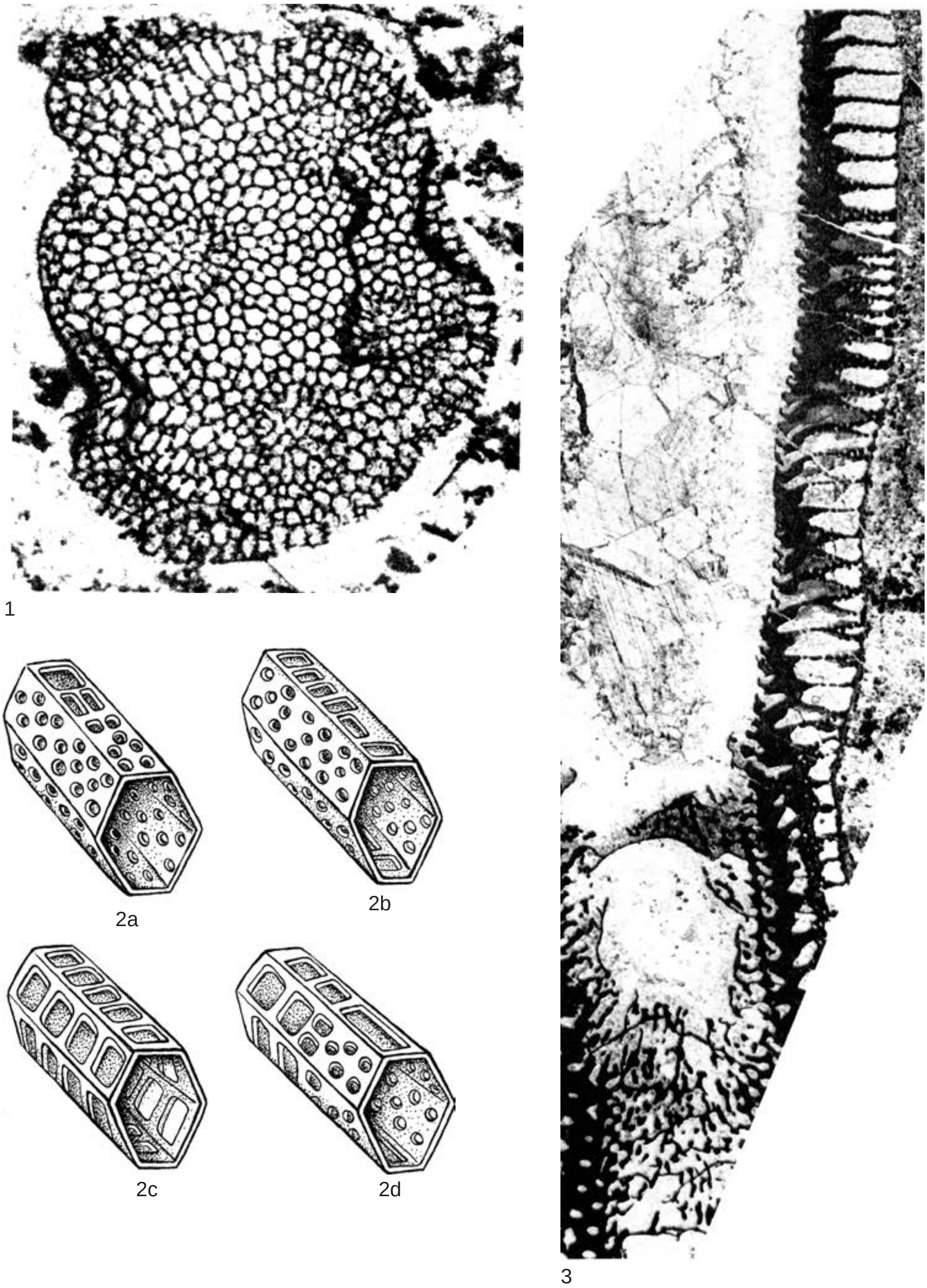

FIG. 510. *(For explanation, see facing page).*

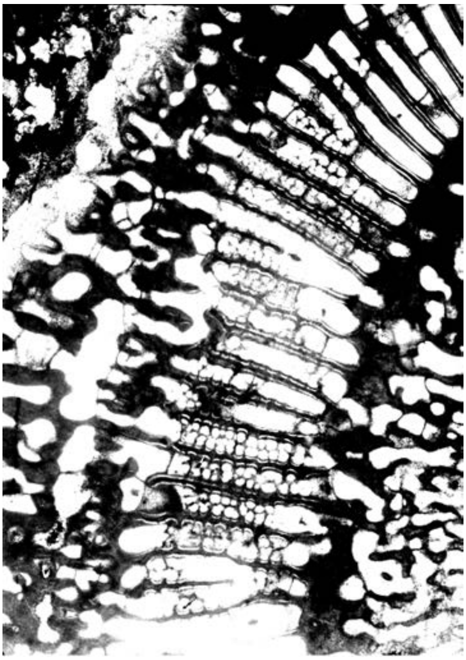

FIG. 511. Membrane tabulae with two radial rows of irregular pores per loculus in *Shiveligocyayhus plenus* FONIN, Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, transverse section (outer wall to left), 1915/814, PIN, ×9.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

skeletons. Traces of this system were perhaps replicated in the secondary calcareous skeleton of some *Archaeocyathus yichangensis* YUAN & ZHANG (Fig. 513a). However, in only three species, *Palaeoconularia triangulata* (YAZMIR), *Altaicyathus vologdini* (YAVORSKY) (Fig. 513b), and *Landercyathus lewandowskii* DEBRENNE & GANGLOFF (Fig. 513d), have traces of the astrorhizal canals been retained in the primary calcareous skeleton. Other species of *Altaicyathus* VOLOGDIN (Fig. 513c) and *Retilamina* DEBRENNE & JAMES (Fig. 495e) lack astrorhizae but possess chimneylike outpockets on the outer wall. Such a chimney might become a new central cavity during ontogeny. It is thus possible to consider these as homologous to astrorhizae.

Juvenile *Archaeocyathus* BILLINGS cups may also have tubelike structures on the outer wall, but, unlike chimneys, these are incurrent rather than excurrent adaptations. They are homologous to the exaulos of thalamid sponges *sensu* FINKS (1983).

Some cups contain porous, longitudinal, tubular structures in the central cavity (Fig. 494d). These structures were called tubuli by FONIN (1963) and are part of the secondary skeleton. Tubuli can be located anywhere within the central cavity; when located at its upper part, they act as excurrent adaptations. Tubuli could thus be related to excurrent canals of the cup, like similar structures in inozoan calcareans or in lithistide demosponges. All the above mentioned features (astrorhiza, chimney, exaulos, tubulus) can be well developed, or completely missing, in individuals of the same species.

Pillars

Pillars are longitudinal, rodlike elements directly linking adjacent tabulae. They characterize sponges with a stromatoporoid

FIG. 512. Segmented tabulae; *a,* finely porous segmented tabula in *Claruscoscinus mactus* (FONIN), Toyonian, Usa Formation, Matur River, Kuznetsk Alatau, Altay Sayan, Russia, oblique transverse section (outer wall at top), 2851/28, PIN, ×12; *b,* coarsely porous segmented tabula in *Cellicyathus* sp., Botoman, Chara Formation, Olekma River, Russia, oblique transverse section (outer wall at top), 4451/30, PIN, ×16 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* slitlike pores in segmented tabula of *Pycnoidocoscinus pycnoideum* R. BEDFORD & W. R. BEDFORD, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, oblique transverse section (outer wall at top), paratype, P991, SAM, ×9 (Debrenne, 1974a); *d,* concentric porosity in segmented tabula of *Markocyathus clementensis* DEBRENNE, Botoman, Puerto Blanco Formation, Caborca, Sonora, Mexico, oblique transverse section, 90178, GSC, ×18; *e,* coplanar rodlike intervallar elements in segmented tabulae of *Dictyosycon* sp., Atdabanian, Altay Sayan, Russia, oblique transverse section, 4451/21, PIN, ×11; *f,* compound porosity in segmented tabulae of *Tabulacyathellus bidzhaensis* MISSARZHEVSKIY, Atdabanian, Salaany Gol Formation, Khasagt-Khayrkhan Range, Tsagaan Oloom province, western Mongolia, oblique longitudinal section, 4451/39, PIN, ×18 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

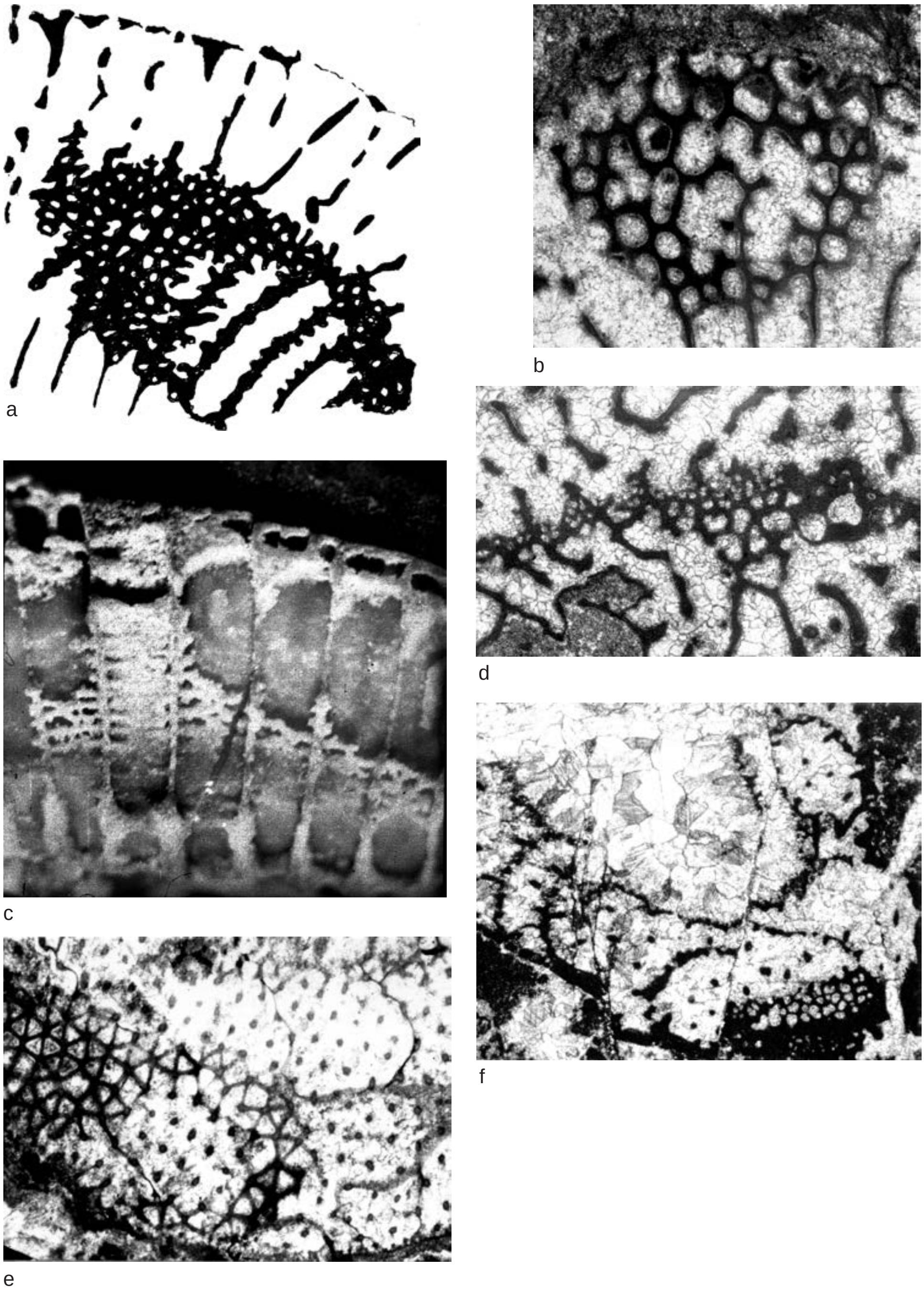

FIG. 512. *(For explanation, see facing page).*

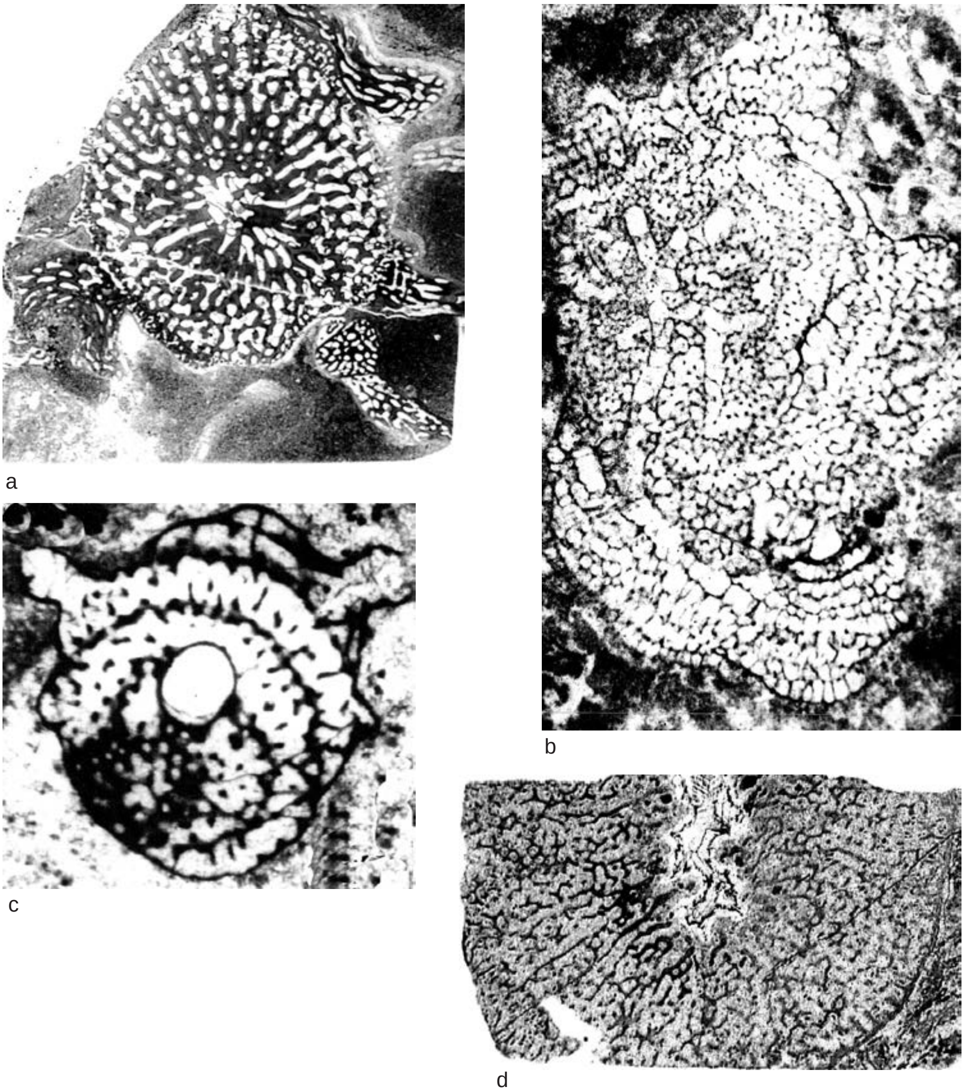

FIG. 513. Astrorhizae and chimneys; *a,* canals in secondary skeleton, possibly replicating astrorhizal canals in original soft tissue, in central cavity of *Archaeocyathus yichangensis* YUAN & ZHANG, Toyonian, Tianheban Formation, Yichang, Hubei, China, transverse section, M85082, MNHN, ×3.3 (Debrenne, Gandin, & Zhuravlev, 1991); *b,* astrorhizal canals in primary skeleton of *Altaicyathus vologdini* (YAVORSKY), Botoman, Torgashino Formation, East Sayan, Altay Sayan, Russia, longitudinal section, 4451/52, PIN, ×10; *c,* chimneys on outer wall of *Altaicyathus* sp., Botoman, Adams Argillite, Tatonduk River, Alaska, United States, 2549, UAM, ×20; *d,* astrorhizal canals in primary skeleton of *Landercyathus lewandowskii* DEBRENNE & GANGLOFF, Botoman, Valmy Formation, Iron Canyon, Nevada, United States, oblique longitudinal section, 38115, UCMP, ×5.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

or thalamid architecture, and, among archaeocyaths, the Kazachstanicyathida (with composite architecture). They may be superposed in successive chambers, but otherwise show no regularity of arrangement (Fig. 513b–c, Fig. 516c). In *Korovinella* RADUGIN, pillars can bifurcate at their distal ends. Ontogenetically, pillars probably develop in a proximal direction from the chamber ceiling.

OUTER WALL TYPES

Observations on outer wall morphology by GRAVESTOCK (1984), and modifications by DEBRENNE and ZHURAVLEV (1992b), are the basis for the present account.

Simple Walls

Simple walls are united in possessing simple pores. Several subtypes are recognized.

Simple wall–Rudimentary.—In this wall type, the outer edges of intervallar elements open directly to the exterior. There may be some thickening of the marginal intervallar elements, but effectively there is no distinct outer wall. True rudimentary outer walls characterize some Dictyofavina (*Usloncyathus* FONIN, *Zunyicyathus* DEBRENNE, KRUSE, & ZHANG) and Syringocnemina (*Auliscocyathus* DEBRENNE) (Fig. 515a).

Simple wall–Basic.—Basic simple walls incorporate the marginal intervallar elements, but with additional linking lintels (Fig. 514c, Fig. 515b). This wall type is found in the Archaeocyathina only (DEBRENNE & ZHURAVLEV, 1992b).

Simple wall–Cambroid.—This is the new designation for the so-called simple wall of *Cambrocyathellus*-type of DEBRENNE and ZHURAVLEV (1992b, p. 49). Restricted to the Loculicyathina, this simple wall subtype is most similar to the simple wall of Monocyathida, Ajacicyathida, Putapacyathida, and Capsulocyathida. It is a continuous plate pierced by simple pores. Constituent pores may be rounded, irregularly rounded, or irregularly quadrate (Fig. 515c–f).

Pore orifices may bear flat to convex diaphragms, as, for example, in *Loculicyathus membranivestites* VOLOGDIN. Stirrup pores are rare. There may be one or several pore rows per intersept, but where there is only one, pores gently zigzag along the row (Fig. 515f).

Simple wall–Anthoid.—Found only in the Anthomorphina, this is the proposed new name for so-called simple wall of *Anthomorpha*-type of DEBRENNE and ZHURAVLEV (1992b, p. 49). It comprises transverse lintels linking adjacent pseudosepta to form a single row of slightly subquadrate large pores (Fig. 516a). In some cases, additional lintels define several poorly expressed discontinuous pore rows per intersept (Fig. 516b).

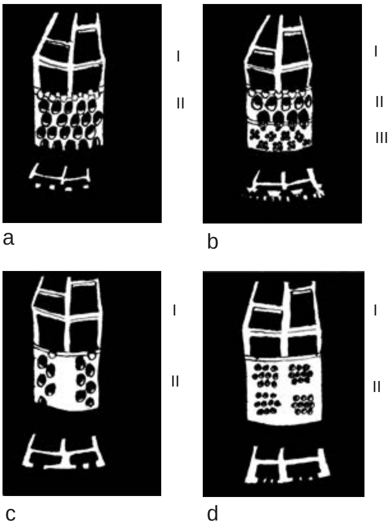

FIG. 514. Schematic reconstructions of outer walls; *a,* outer wall with simple pores in Ajacicyathida; *b,* outer wall with attached microporous sheath in Ajacicyathida; *c,* basic simple outer wall in Archaeocyathida; *d,* concentrically porous outer wall in Archaeocyathida; *I,* distal elements of intervallum; *II,* outer wall; *III,* microporous sheath (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

Microporous membranes superficially similar to the attached microporous sheath in Ajacicyathida can be intermittently developed (Fig. 494d). The structure of these is identical to that of membrane tabulae.

Simple wall–Altoid.—Not unlike the anthoid wall subtype, the altoid simple wall is found in Kazachstanicyathida (*Altaicyathus* VOLOGDIN and *Korovinella* RADUGIN). In this wall, lintels link the distal ends of pillars to form a continuous plate pierced by frequent polygonal pores (Fig. 516c). This is the so-called simple wall of *Altaicyathus*-type of DEBRENNE and ZHURAVLEV (1992b, p. 49).

Concentrically Porous Walls

This wall type is found in Archaeocyathina and Syringocnemina. It consists of a continuous membrane bearing irregularly

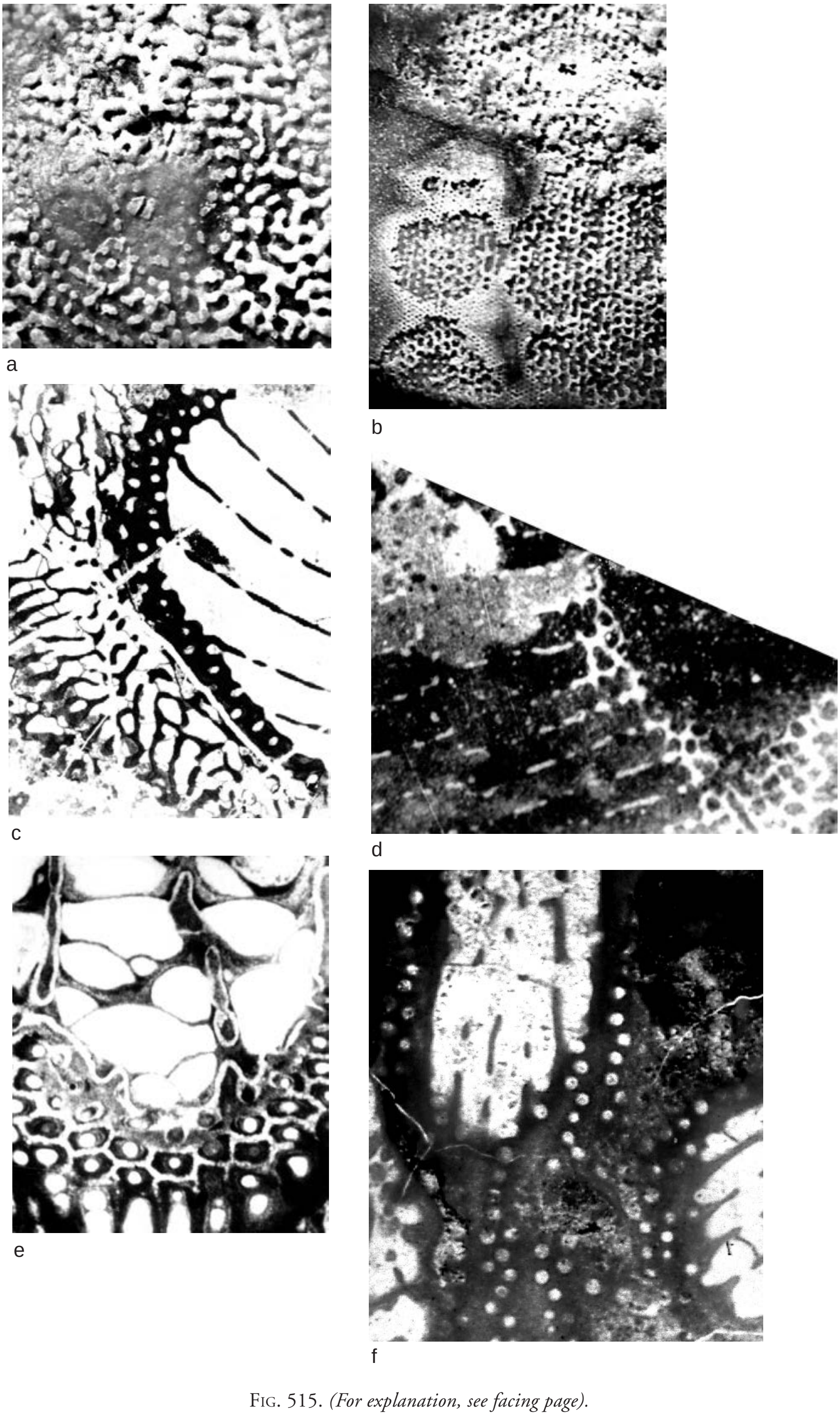

FIG. 515. *(For explanation, see facing page).*

arranged pores clustered within intervallar cells, bounded in Archaeocyathina by pseudotaeniae and synapticulae or by taeniae and linking transverse rods (Fig. 514d); and, in Syringocnemina, by individual syringes (Fig. 516e). There is no clear organization of pores into longitudinal rows.

GRAVESTOCK (1984) introduced the term centripetal for this wall type, but because that term is also used to describe wall development, the wall type is here termed concentrically porous. Prior to GRAVESTOCK (1984), this wall type was commonly described as simple, comparable to the simple outer wall in Monocyathida, Ajacicyathida, Putapacyathida, and Capsulocyathida (e.g., ZHURAVLEVA, 1960b; YAROSHEVICH, 1966), or as double (e.g., KRASNOPEEVA, 1961; OSADCHAYA & others, 1979; FONIN in VORONIN & others, 1982). Thus, some genera were described twice: with simple outer wall (*Archaeocyathus* BILLINGS, *Archaeopharetra* R. & W. R. BEDFORD) and with microporous sheath ("*Syringsella*" KRASNOPEEVA, "*Salanycyathus*" FONIN).

Compound Walls

In compound walls (GRAVESTOCK, 1984), a discontinuous porous membrane is attached to marginal intervallar cells. Two variants are accorded genus-level significance: walls with incipient subdivision of intervallar cells (Fig. 517c) and walls with completely subdivided pores (Fig. 516d, Fig. 517a).

In the first variant, thick spines arise from pore lintels but are not completely connected; in the second, the spines are completely connected to form irregular micropores. Compound walls are present in Archaeocyathina and Dictyofavina.

Pustular Walls

This wall type is known in Putapacyathida (*Chabakovicyathus* KONYUSHKOV), Loculicyathina (*Sakhacyathus* DEBRENNE & ZHURAVLEV), Archaeocyathina (*Naimarkcyathus* WRONA & ZHURAVLEV), and Syringocnemina (*Kruseicnema* DEBRENNE, GRAVESTOCK, & ZHURAVLEV). It is characterized by pustulae with a single central pore (Fig. 517d). In the last two genera, the pustulae are low cones, but in *Chabakovicyathus* KONYUSHKOV, they are hemispherical domes. Pustulae are similar to simple tumuli in Monocyathida, Ajacicyathida, and Capsulocyathida, which, however, differ in having the pore located toward the bottom.

Walls with Canals

Three types of outer wall canals are known in Archaeocyathida and Kazachstanicyathida:

1. Straight oblique canals, as in *Fragilicyathus* BELYAEVA and *Warriootacyathus* GRAVESTOCK (Fig. 517b).
2. Subdivided canals, as in *Beltanacyathus* R. BEDFORD & J. BEDFORD (Fig. 517e); these are short oblique canals with incipient or complete subdivision of external orifices by short protrusions of the canal wall. DEBRENNE and ZHURAVLEV (1992b) interpreted the outer walls of *Ataxiocyathus* DEBRENNE and *Maiandrocyathus* DEBRENNE as extreme developments of such protrusions

FIG. 515. Outer walls in Archaeocyathida; *a,* rudimentary simple outer wall in *Auliscocyathus multifidus* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longitudinal section, 245, PU, ×6; *b,* basic simple outer wall, *Graphoscyphia graphica* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longitudinal section, paralectotype, 85, PU, ×5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* simple outer wall with rounded pores of cambroid type, *Ardrossacyathus endotheca* R. BEDFORD & J. BEDFORD, Botoman, Parara Limestone, Ardrossan, South Australia, Australia, tangential section, topotype, P32041, SAM, ×6 (Zhuravlev & Gravestock, 1994); *d,* simple outer wall with irregularly rounded pores of cambroid type, *Okulitchicyathus discoformis* (ZHURAVLEVA), Tommotian, Pestrotsvet Formation, Zhurinskiy Mys, Lena River, Sakha (Yakutia), Russia, tangential section, 4451/59, PIN, ×20; *e,* simple outer wall with irregularly quadrate pores of cambroid type, *Neoloculicyathus sibiricus* (SUNDUKOV), Atdabanian, Pestrotsvet Formation, Oy-Muran, Lena River, Sakha (Yakutia), Russia, tangential section, 4451/1, PIN, ×20; *f,* simple outer wall with one row of pores of cambroid type per intersept, *Cambrocyathellus proximus* (FONIN), Tommotian, Pestrotsvet Formation, Titirikteekh Creek, Lena River, Sakha (Yakutia), Russia, tangential section, 4451/5, PIN, ×20 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

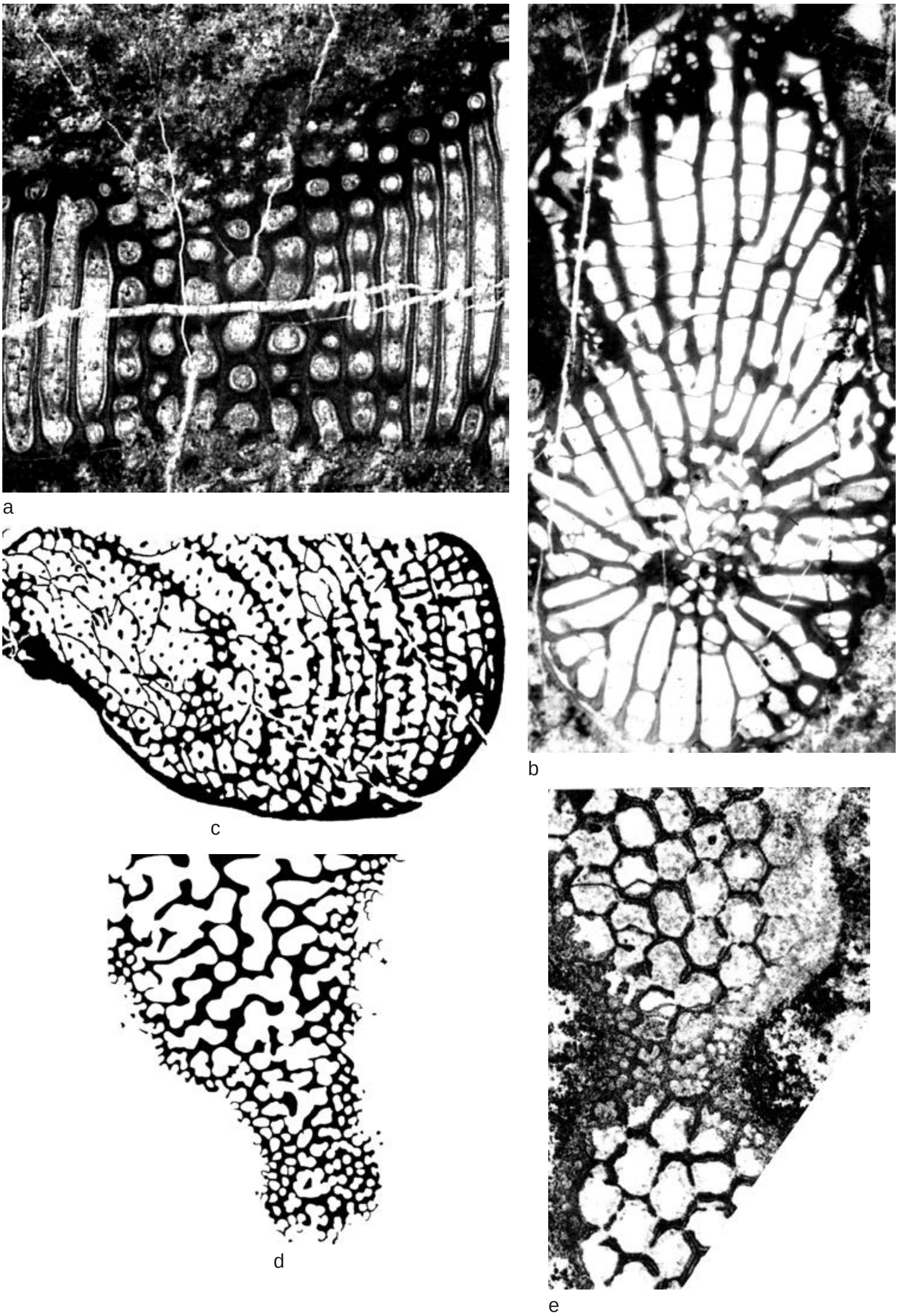

FIG. 516. *(For explanation, see facing page).*

to form an additional microporous sheath with elongate irregular pores (Fig. 517f).

3. S-shaped canals, as in *Tchojacyathus* ROZANOV (Fig. 518.1) and canals with supplementary bracts, having a V-shaped appearance, as in *Chankacyathus* YAKOVLEV (Fig. 518.2).

Tabellar Walls

This wall type is known only in *Taeniaecyathellus* ZHURAVLEVA (Archaeocyathina). It comprises longitudinal ribs linked by transverse lintels (Fig. 518.4). FONIN (1963) provided the first comprehensive description of this wall type. However, due to the common occurrence of an adherent pellis, FONIN oriented the longitudinal ribs (his tabellae) and transverse lintels (his metulae) perpendicular to their true orientation.

Aporose Walls

This outer wall is not comparable to other wall types in that it is characteristic of early ontogenetic stages in all suborders of Archaeocyathida and Kazachstanicyathida, except Loculicyathina, which never passes through an aporose outer wall stage. One possible exception is *Chouberticyathus* DEBRENNE (Archaeocyathina) (Fig. 518.3). The aporose outer wall is usually a laminated structure, similar to epitheca of other calcified sponges.

INNER WALL TYPES

Inner walls are less diverse than outer walls, as in all orders of Archaeocyatha.

Simple Walls

Simple inner walls in Archaeocyathida and Kazachstanicyathida typically comprise a single longitudinal pore row per intersept. Forms with several pore rows per intersept are the exception. Pores may be rounded, elliptical, or subquadrate (Fig. 519a–c). Rarely, pore lintels bear spines (e.g., in *Copleicyathus* R. BEDFORD & J. BEDFORD, *Spinosocyathus* ZHURAVLEVA).

Walls with Bracts, Fused Bracts, or Pore Tubes

In Archaeocyathina and Syringocnemina, there is a structural continuum between these otherwise disparate wall types, so they are treated collectively in these suborders. Taken together, these wall types are analogous to the bracts and scales grouping in the much less morphologically plastic orders Monocyathida, Ajacicyathida, and Capsulocyathida (see previous section on walls with bracts or scales, p. 863). Due to the absence of septa, Putapacyathida possess an intermediate type of such structures.

Fused bracts have often been described as scales or annuli but are distinguished from these latter by their undulating outline, indicative of their constituent, semi-independent units. All formerly recognized so-called scales in this order are here regarded as fused bracts. Fused bracts are planar or S-shaped. With the exception of *Taeniaecyathellus* ZHURAVLEVA inner walls, all these variant walls possess only one longitudinal pore row per intersept.

FIG. 516. Outer walls in Archaeocyathida and Kazachstanicyathida; *a,* simple outer wall with pores of anthoid type, *Anthomorpha margarita* BORNEMANN, Botoman, Matoppa Formation, Serra Scoris, Sardinia, Italy, tangential section, M84144, MNHN, ×10; *b,* simple outer wall with pores of anthoid type, *Tollicyathus nelliae* (FONIN), Botoman, Shangan Formation, Ulug-Shangan River, Tuva, Russia, oblique transverse section, 4451/12, PIN, ×10; *c,* outer wall with simple pores of altoid type, *Altaicyathus notabilis* VOLOGDIN, Botoman, Verkhneynyrga Formation, Altay Mountains, Altay Sayan, Russia, oblique transverse section, 290/2957, TsNIGRm, ×9; *d,* compound outer wall with completely subdivided pores, *Spirillicyathus pigmentus* R. BEDFORD & J. BEDFORD, Atdabanian, Mount Scott Range, South Australia, Australia, tangential section, P21747, SAM, ×10 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* concentrically porous outer wall, *Syringocnema favus* TAYLOR, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, tangential section, FT.9487, specimen, F.83936, AM, ×4 (Kruse, 1982).

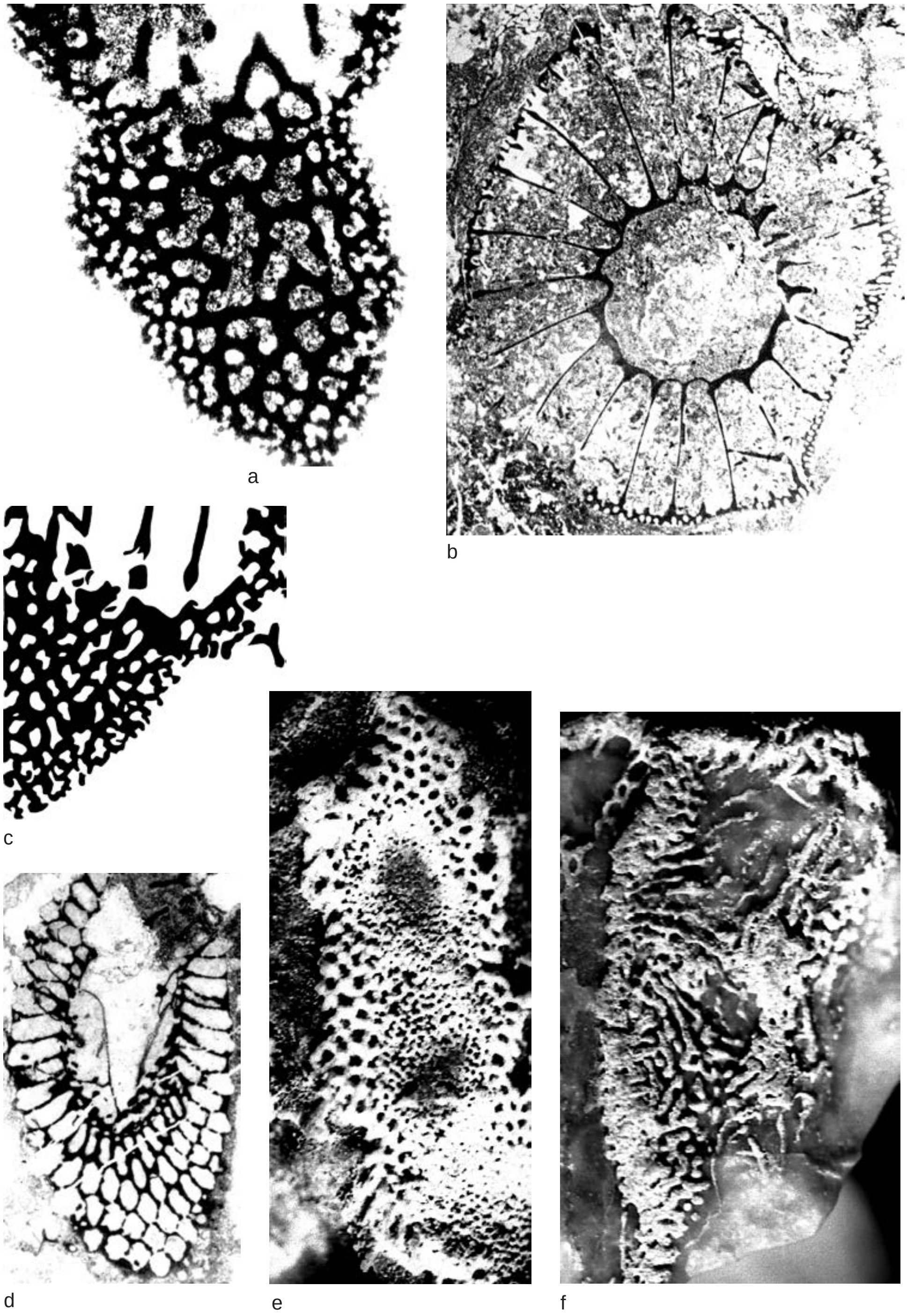

FIG. 517. *(For explanation, see facing page).*

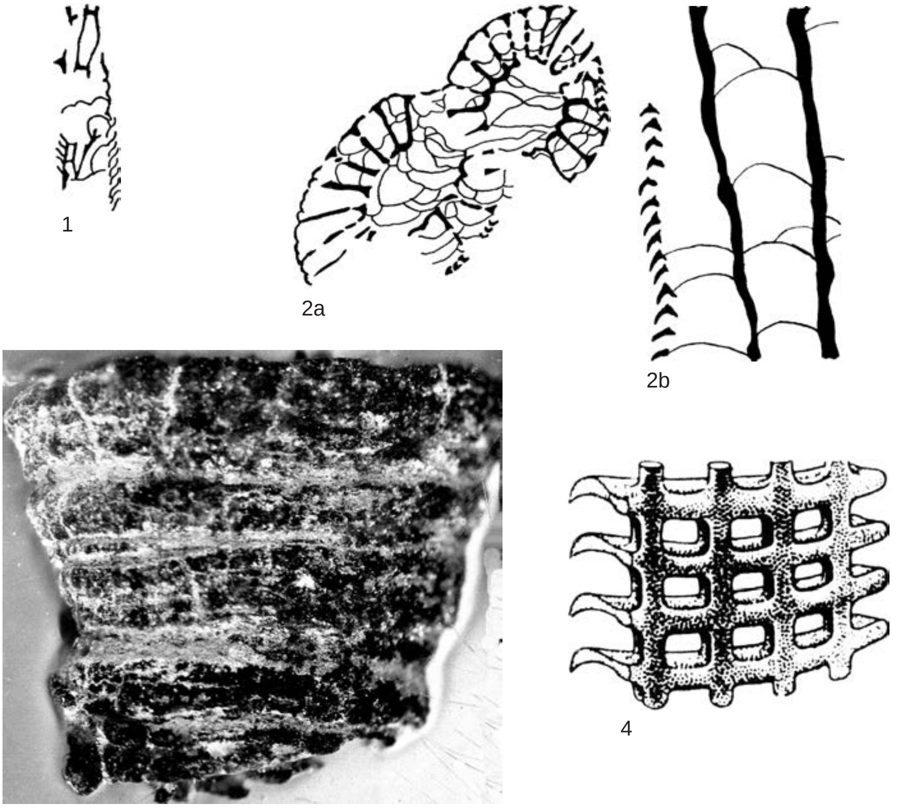

FIG. 518. Outer walls in Archaeocyathida; *1,* horizontal to upwardly projecting S-shaped canals on both walls of *Tchojacyathus validus* ROZANOV, Atdabanian, Uba Formation, Tyrga River, Altay Mountains, Altay Sayan, Russia, longitudinal section (outer wall to left), GIN3447/7-8, PIN, ×3.5; *2a–b,* horizontal to upwardly projecting straight canals, bearing supplementary bracts externally, on outer wall of *Chankacyathus strachovi* YAKOVLEV; *2a,* Botoman, Dmitrievka Formation, Kar'ernaya Hill, Far East, Russia, transverse section, 133/52, PGU, ×3.5; *2b,* Botoman, Khanka Lake area, Far East, Russia, longitudinal section (outer wall to left), 1768-12b, PGU, ×17; *3,* imperforate (possibly rudimentary) outer wall in *Chouberticyathus clatratus* DEBRENNE, Botoman, Issafen Formation, Tizi Oumeslema, Morocco, external view of outer wall, M80272, MNHN, ×8.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *4,* schematic reconstruction of tabellar outer wall in *Taeniaecyathellus tectus* FONIN, external view, ×85 (Fonin, 1963).

FIG. 517. Outer walls in Archaeocyathida; *a,* compound outer wall with completely subdivided pores, *Copleicyathus scottensis* GRAVESTOCK, Atdabanian, Mount Scott Range, South Australia, Australia, tangential section, holotype, P21423-1, SAM, ×19 (Gravestock, 1984); *b,* horizontal to upwardly projecting straight canals in outer wall, *Warriootacyathus wilkawillinensis* GRAVESTOCK, Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, transverse section, paratype, P21806-2, SAM, ×2 (Gravestock, 1984); *c,* compound outer wall with incipient subdivision of intervallar cells, *Jugalicyathus tardus* GRAVESTOCK, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia, tangential section, holotype, P21747, SAM, ×7.5; *d,* pustular outer wall, *Kruseicnema gracilis* (GORDON), Botoman, Parara Limestone, Minlaton 1 drillhole, Yorke Peninsula, South Australia, Australia, oblique longitudinal section, P32047, SAM, ×5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* subdivided canals in outer wall, *Beltanacyathus wirrialpensis* (TAYLOR), Atdabanian, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longitudinal section, holotype of junior synonym *ionicus* R. BEDFORD & J. BEDFORD, 86718-275, PU, ×7 (Debrenne, 1974a); *f,* subdivided canals in outer wall, *Maiandrocyathus insigne* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longitudinal section, holotype, P986-168, SAM, ×4.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

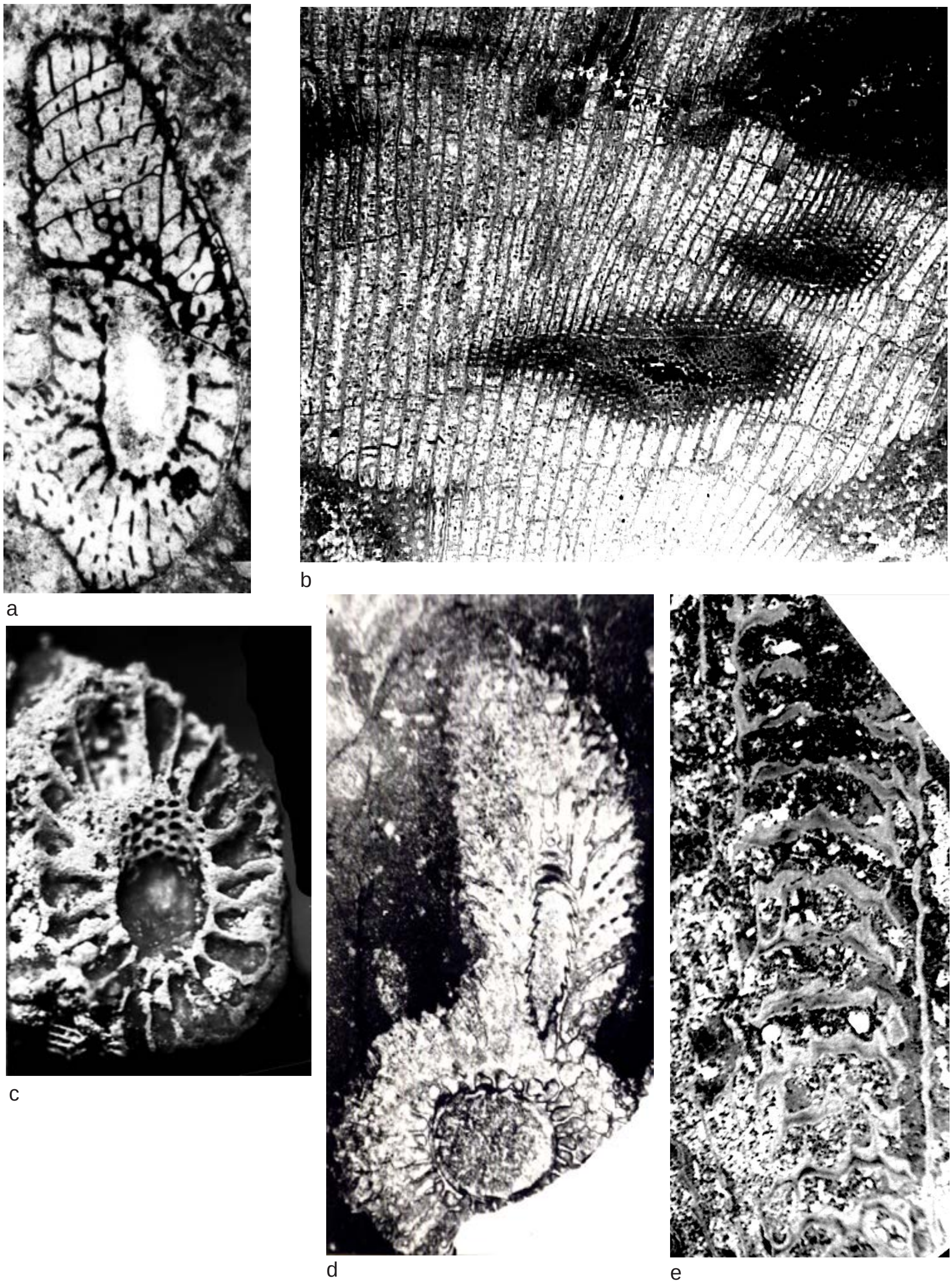

Fig. 519. Inner walls in Archaeocyathida; *a,* inner wall with rounded simple pores, *Cambrocyathellus tuberculatus* (Vologdin), Atdabanian, Salaany Gol Formation, Zuune-Arts, Tsagaan Oloom province, western Mongolia, oblique transverse section, 4451/10, PIN, ×7.5; *b,* inner wall with elliptical simple pores in *Anthomorpha margarita* Bornemann, Botoman, Matoppa Formation, Cuccuru Contu, Sardinia, Italy, tangential section, M84253, MNHN, ×5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* inner wall with subquadrate simple pores, *Paranacyathus parvus* (R. Bedford & W. R. Bedford), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, oblique transverse view, holotype, P992, SAM, ×6 (Debrenne, 1974c); *d,* annulus-like

(Continued on facing page.)

In the present suborders, fused bracts typically develop into oblique canals during ontogeny. They may in turn fuse to form annulus-like structures (Fig. 519d). Fused and nonfused bracts and pore tubes can arbitrarily appear in the same or different cups of the same species.

Pore tubes are generally described as straight (Fig. 520a), but a minority are clearly S-shaped (e.g., in *Sigmofungia* R. Bedford & W. R. Bedford, Fig. 520b), while others are intermediate, with both types intergradational (e.g., in *Fenestrocyathus* Handfield).

Walls with Canals

Inner wall canals are known only in Loculicyathina and Anthomorphina, and stirrup canals only in Anthomorphina. Canals are straight in *Shiveligocyathus* Missarzhevskiy and S-shaped in *Tchojacyathus* Rozanov.

Uniquely, the inner wall of *Eremitacyathus* Zamarreño & Debrenne has a single continuous opening along each intersept, bounded by longitudinal plates (Fig. 520c). These openings are treated as canals.

Compound Walls

Compound inner walls bear similarity to compound outer walls. As in the latter, the pore subdivision of inner walls can be incipient (e.g., *Changicyathus* Debrenne & Zhuravlev, *Metaldetes* Taylor) (Fig. 520e) or complete (e.g., *Archaeosycon* Taylor, *Pycnoidocoscinus* R. Bedford & W. R. Bedford) (Fig. 520d).

However, some compound inner walls differ structurally from the compound outer wall. Thus, while in Metacyathoidea the inner wall pore subdivision mirrors that of the outer wall, in *Archaeosycon* and *Pycnoidocoscinus* the inner wall is formed from the superposition of wall and tabular structure.

SKELETAL MICROSTRUCTURE

PRIMARY SKELETON

The well-preserved primary archaeocyathan skeleton shows a uniformly microgranular microstructure comprising a mosaic of interlocking isometric polyhedral microgranules with randomly oriented c-axes (Hinde, 1889; Taylor, 1910, p. 162; Hill, 1964b). There are no spicules. Hinde (1889) described the archaeocyathan microstructure as minutely granular, and some 70 years later, Zhuravleva (1960b, p. 22) reported a mosaic of grains. All these observations relied on normal thin sections, which permit a maximum magnification of about 300× only. From 1970, two new methods were introduced: polished ultrathin sections (thickness 3 µm) and scanning electron microscopy. Both techniques permit greater magnification (up to 4000×, although 2000× is generally sufficient for microstructural studies). The first result obtained by the new methods was a more precise definition of the microgranules (Lafuste & Debrenne, 1970): these are uniformly polyhedral crystallites, the surfaces of which are embossed by irregular cupules and protruberances (Fig. 521.1–2).

Surveys of various archaeocyath taxa from different regions and ranging in age from Tommotian to Botoman demonstrate a general uniformity of microstructure among the Archaeocyatha in time, space, and systematic position (Fig. 521.3–4) (Debrenne, Zhuravlev, & Rozanov, 1989, p. 40; Kruse & Debrenne, 1989; Debrenne, Rozanov, & Zhuravlev, 1990, p. 60). The maximum size of microgranules is within the range of 0.5–20 µm, but more commonly 4–8 µm (Kruse & Debrenne, 1989). Some difference has been observed

Fig. 519. *(Continued from facing page).*

structures developed from upwardly projecting S-shaped fused bracts on inner wall of *Syringothalamus crispus* Debrenne, Gangloff, & Zhuravlev, Botoman, Poleta Formation, Westgard Pass, California, United States, oblique transverse section, B4008, UCMP, ×5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* upwardly projecting straight pore tubes on inner wall of *Pycnoidocyathus sekwiensis* Handfield, Botoman, Sekwi Formation, Caribou Pass, Northwest Territories, Canada, tangential section, holotype, 25384, GSC, ×4 (Handfield, 1971).

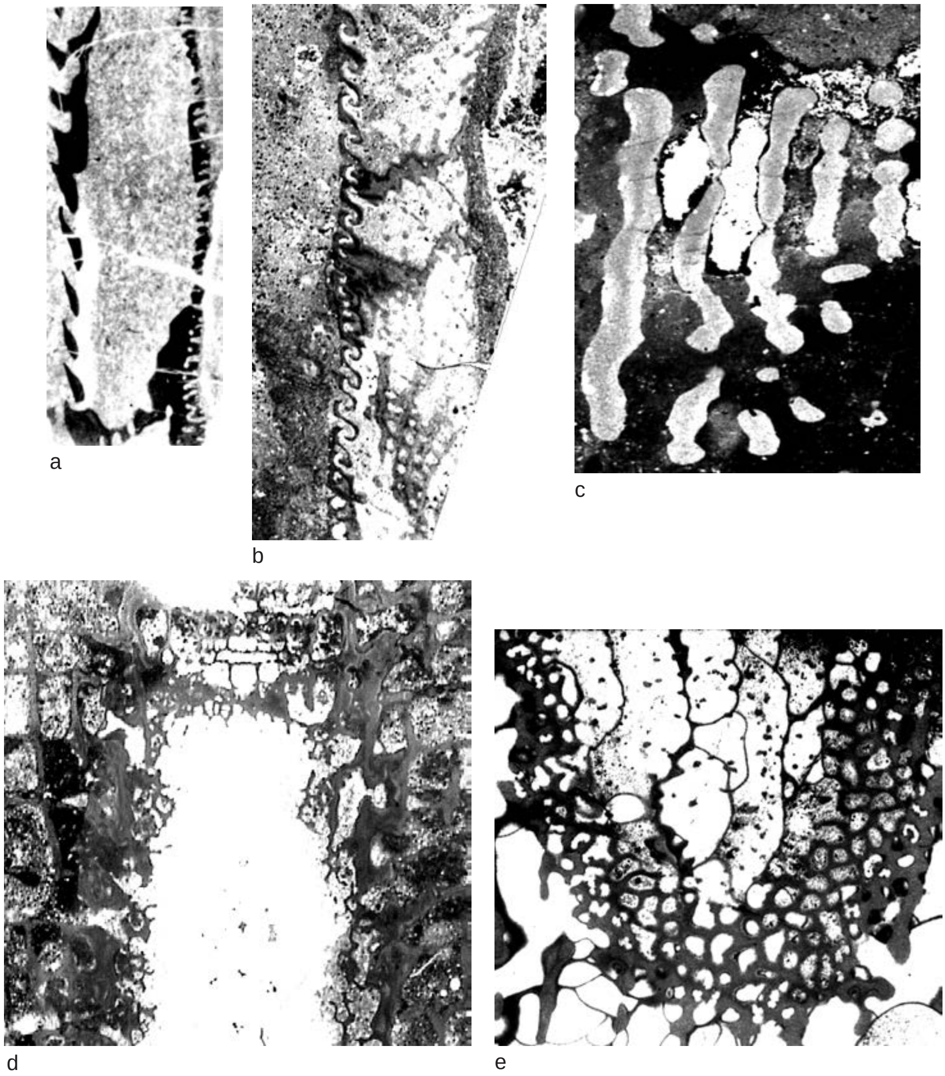

Fig. 520. Inner walls in Archaeocyathida; *a,* upwardly projecting straight pore tubes on inner wall of *Beltanacyathus digitus* Gravestock, Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, longitudinal section (outer wall to right), paratype, P21825, SAM, ×3 (Gravestock, 1984); *b,* upwardly projecting S-shaped pore tubes on inner wall of *Sigmofungia undata* (Debrenne), Botoman, Puerto Blanco Formation, Cerro Rajon, Sonora, Mexico, longitudinal section (outer wall to right), holotype, M83098, MNHN, ×5.5 (Debrenne, Gandin, & Rowland, 1989); *c,* longitudinally continuous canal-like openings in inner wall of *Eremitacyathus fissus* Debrenne, Atdabanian, Pedroche Formation, Las Ermitas, Cordoba, Spain, tangential section, holotype, M84016, specimen Spe 10-1a, MNHN, ×12; *d,* compound inner wall with complete pore subdivision in *Archaeosycon billingsi* (Walcott), Botoman, Forteau Formation, Treasure Reef, Labrador, Canada, tangential section, 62119, GSC, ×7.5; *e,* compound inner wall with incipient pore subdivision in *Metaldetes profundus* (Billings), Botoman, Forteau Formaton, Mount St. Margaret, Newfoundland, Canada, tangential section, 103937, GSC, ×10 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

between Monocyathida (one-walled cups) and Ajacicyathida: component granules in the former measure 1.7 × 1.1 µm, versus 4 × 3 µm in the latter (LAFUSTE & DEBRENNE, 1982; DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, pl. 10,*1–4*; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, pl. 10,*1–4*).

SECONDARY SKELETON

Investing the primary skeleton of some archaeocyath cups is a later-formed secondary skeleton, termed stereoplasm by VORONIN (1963). Although observed occasionally in other suborders, it is most characteristic of the Archaeocyathina. The secondary skeleton envelops the external surface of the cup (Fig. 511, Fig. 521.2), either as a thin sheet (pellis), as thicker encrustations of the cup apex (radicatus), or otherwise protruding from the cup (buttresses) (Fig. 522). Within the cup, it infills spaces between primary skeletal elements, as bubblelike vesicles in the intervallum and/or central cavity (Fig. 521.3), or as tubular structures (tubuli) in the central cavity (Fig. 494d, Fig. 513a). There is continuity between exostructures, endostructures, and intervallar structures. Secondary skeleton is typically laminated, indicating repeated episodic accretion. It has no fixed morphology and is no longer accorded taxonomic significance.

Secondary skeleton in archaeocyaths was apparently of dual origin. On the one hand, it was initiated while the archaeocyath was still alive, forming canals similar to the crypts of *Merlia normani* KIRKPATRICK. On the other hand, while the cells responsible for this process die, early diagenesis may modify the secondary skeleton even as the organism continues to function normally in the upper part of the cup. Microstructural differences delimit the early diagenetic skeleton (REITNER & ENGESER, 1987).

LAFUSTE and DEBRENNE (1977) were the first to document the microstructure of the secondary skeleton, in *Archaeocyathus atlanticus* BILLINGS from Labrador. Like the primary skeleton, the secondary skeleton is microgranular, but finer than the former, in the size range of 0.5–4 µm, but commonly 2–3 µm. Slight variations in microgranule size define the laminations. Additionally, rims of palisading crystallites, 0.75 × 2.0 µm in size, were identified by these authors, separating the primary and secondary skeletons of *Archaeocyathus atlanticus* BILLINGS from the same area. Less distinct palisades were observed between individual laminations of the secondary skeleton. Palisades were also present in *Archaeosycon billingsi* (WALCOTT) from the same locality (DEBRENNE & JAMES, 1981).

Vesicles are an aspect of the secondary calcareous skeleton characteristic of many sessile organisms, namely sponges, corals, rudists, bryozoans, brachiopods (e.g., *Richthofenia* KAYSER), and some cirripedes (SEILACHER & SEILACHER-DREXLER, 1986). The widespread occurrence of vesicles in cups of Archaeocyathida (Fig. 521.3) is considered to be indicative of the progressive withdrawal of the living matter toward the distal end of the cup with growth (VOLOGDIN, 1962a; ZIEGLER & RIETSCHEL, 1970), by analogy with the living *Vaceletia crypta* (VACELET), with the soft body being restricted to the uppermost millimeters of the cup (DEBRENNE & VACELET, 1984). A similar ratio of skeleton to living tissue is observed in many extant nonspiculate skeleton-bearing sponges and Mesozoic stromatoporoids (WOOD, 1987). Conversely, Ajacicyathida and Putapacyathida are generally devoid of vesicles, suggesting that the living matter occupied virtually the entire cup throughout growth in these orders (DEBRENNE, 1991).

Of the diverse functions proposed for the secondary skeleton (see DEBRENNE & ZHURAVLEV, 1992b, p. 56–57), those relating to anchoring a cup to the substrate (buttresses; GRAVESTOCK, 1983) and sealing vacated portions of a cup (vesicles) seem the best founded. The secondary skeleton also prevents the introduction of parasitic organisms and epibionts into dead parts of the skeleton, heals injuries to the skeleton, and may assist in the regulation of water flow through the skeleton. When secondary layers fill skeletal injuries, no gaps are observed between them and the

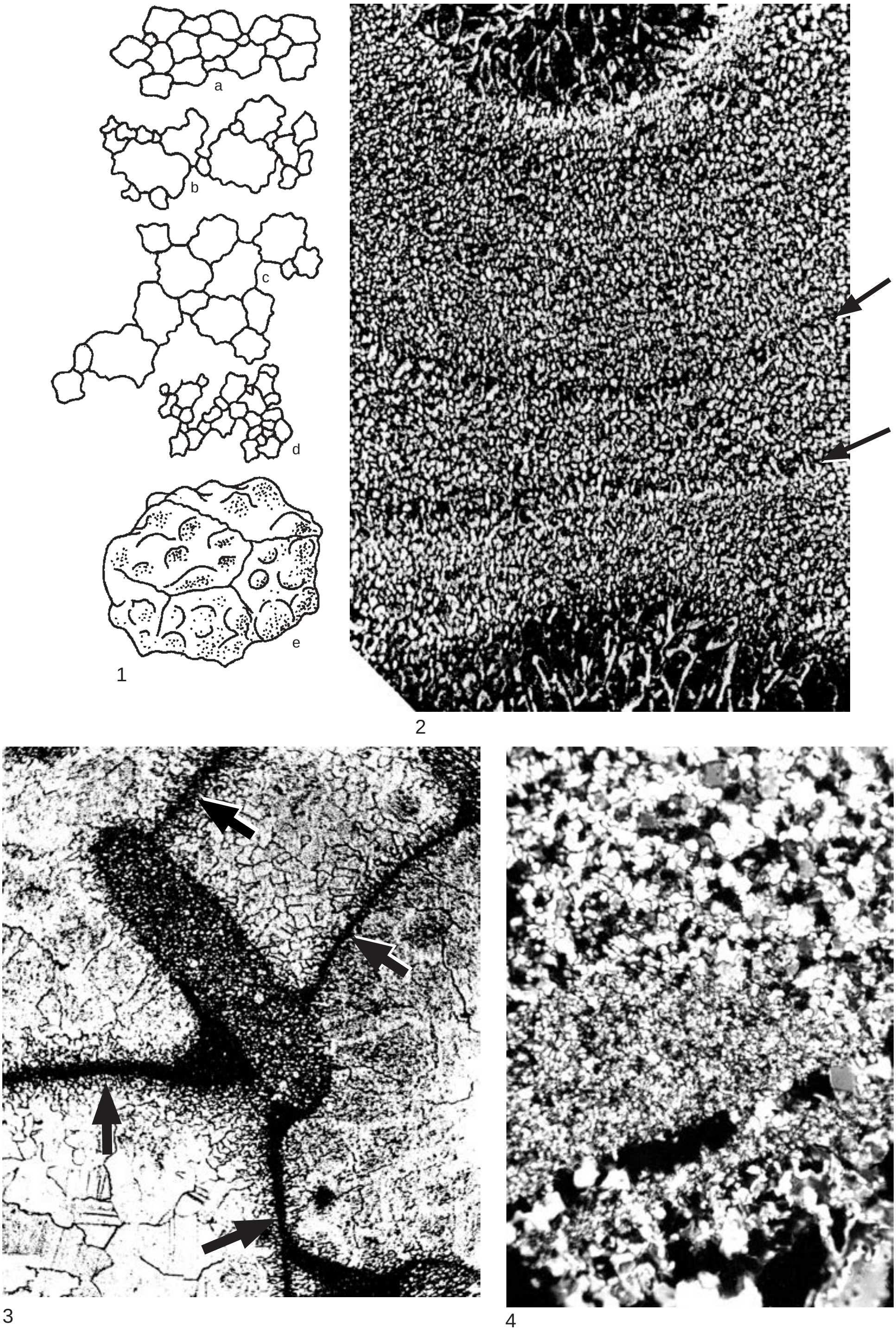

FIG. 521. *(For explanation, see facing page).*

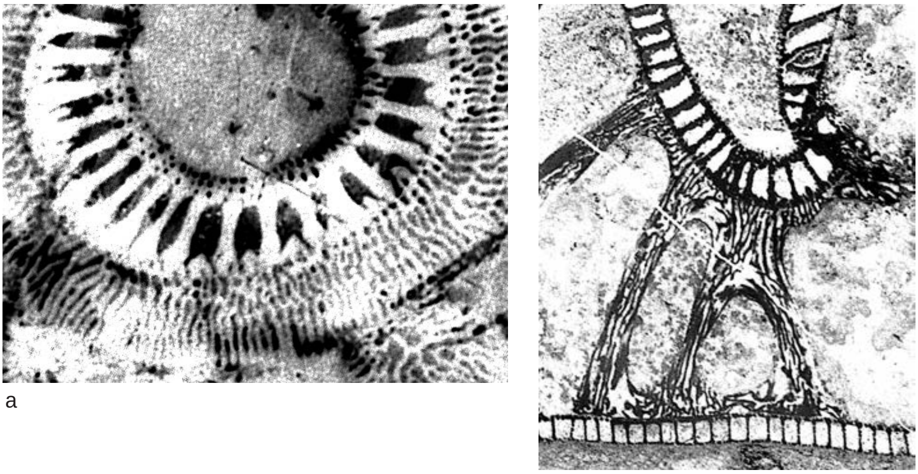

FIG. 522. Buttresses; *a,* successive development of exocyathoid and tersioid buttresses upon a *Somphocyathus coralloides* TAYLOR cup, Atdabanian, Wilkawillina Limestone, Wirrealpa, South Australia, Australia, transverse section, 86673-376, PU, ×5; *b,* tersioid buttresses upon a *Polycoscinus cymbricensis* (KRUSE) cup (top) abutting a *Coscinoptycta convoluta* (TAYLOR) cup (bottom), Botoman, White Point Conglomerate, Emu Bay, Kangaroo Island, South Australia, Australia, transverse section, M82007-9, MNHN, ×7 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

primary skeleton (DEBRENNE & ROZANOV, 1978). These functions imply facultative secretion by the host cup, and not by any foreign organism. They were evidently responsible for the development of complex exocyathoid structures. Exocyathoid structures look superficially like independent archaeocyathan cups, but their contiguity with the parent cup may be interpreted as a process of anchoring the cup on the substrate, as demonstrated by GRAVESTOCK (1983) (Fig. 522).

Putative archaeocyathan spicules (triactines, tetractines) in archaeocyaths from Atdabanian reefs of Australia, figured and discussed by REITNER (1992, p. 293, pl. 59,*1–10*; REITNER & MEHL, 1995), were discounted as archaeocyathan by DEBRENNE and ZHURAVLEV (1992b), who emphasized that such spicules invariably occur within the secondary skeleton. In fact, any fine allochthonous material from the immediate environment may be incorporated into the archaeocyathan secondary skeleton: these authors illustrated trilobite fragments likewise trapped in this manner (DEBRENNE & ZHURAVLEV, 1992b, pl. 35,*2*) in Toyonian reefs of China to demonstrate that the so-called archaeocyathan spicules are adventitious. No undoubted spicules have been recorded from the primary skeleton of archaeocyaths. In other groups of calcified sponges,

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FIG. 521. Archaeocyathan microstructure; *1a–e,* microstructure in ultrathin section, ×1700; *a, Archaeolynthus* TAYLOR; *b, Nochoroicyathus* ZHURAVLEVA (Debrenne, 1983); *c,* primary skeleton of *Archaeocyathus* BILLINGS; *d,* secondary skeleton of *Archaeocyathus* (Lafuste & Debrenne, 1977); *e,* schematic reconstruction of microgranule comprising archaeocyathan skeleton (Debrenne, 1983); *2,* primary skeletal element of a taenia (center) limited by secondary palisading tissue (*arrows*) and further invested above and below by laminae of secondary thickening (stereoplasm) with fine-grained external limit; coarsely crystalline darker areas at top and bottom are cement, *Archaeocyathus atlanticus* BILLINGS, Botoman, Forteau Formation, Mount St. Margaret, Newfoundland, Canada, SEM image of transverse section, 62107, GSC, ×200 (Debrenne & James, 1981); *3,* portions of taeniae (primary skeleton; center, top right and bottom right) invested by secondary vesicles (dark; *arrows*); cavities occluded by calcite spar mosaic (pale), *Archaeocyathus atlanticus* BILLINGS, Botoman, Forteau Formation, Taylors Gulch, Labrador, Canada, transverse section, M83136, MNHN, ×70; *4,* same, contact of coarser-crystalline primary taenia (above) and finer-crystalline secondary vesicle (below), ultrathin transverse section, ×350 (Lafuste & Debrenne, 1977).

the spicules are incorporated into the primary skeleton as they are secreted in the earliest stage of biomineralization (Wendt, 1980). The apparent absence of genuine spicules among archaeocyaths favors comparison with the Demospongiae, as Calcarea and Hexactinellida invariably possess spicules, whereas demosponges can construct a calcareous or keratose nonspiculate skeleton (e.g., *Vaceletia* Pickett, Pacific population of *Astrosclera* Lister, Dictyoceratida, Dendroceratida) (Vacelet, 1979b).

BIOMINERALIZATION AND DIAGENESIS

The uniformity of archaeocyathan microstructures implies some measure of organic matrix-mediated mineralization (Lowenstam, 1981), whereby mineral nucleation and growth occur in contact with a precursor organic template (Debrenne & Vacelet, 1984). Matrix mediation is suggested by the reactions of archaeocyathan cups in close proximity, the younger of which tend to distort in response to their encroachment upon the older; this implies an initially unmineralized growing edge. In support of this, Brasier (1976) observed that archaeocyaths in the Wilkawillina Limestone (South Australia) were often distorted where juveniles had attached, suggesting that the disturbed portion of the organism was originally elastic. This hypothesis is preferred to the so-called biologically induced mineralization assumed by some authors (Lowenstam, 1981; Barskov, 1984), which results in component crystal habits similar to those produced by inorganic precipitation. In the case of the Archaeocyatha, the presence of embossed surfaces is in favor of organic secretion, as mineral precipitation generates only planar surfaces; the interlocking granules, despite the fact that axes have random orientation, are therefore most probably the result of an organic matrix-mediated process, albeit at a primitive stage.

Microgranular microstructures are shared by several fossil groups: cribricyaths, some calcareous algae, probable calcified cyanobacteria (*Renalcis* Vologdin and others), some foraminifers, some calcified sponges and hydrocorals (Fenninger & Flajs, 1974; Flajs, 1977; Jones, 1979; Rozanov, 1979; Wendt, 1979, 1984; Rozanov & Sayutina, 1982; Boyko, 1984). In all these groups, granules differ in size and shape, being much smaller and less embossed than in archaeocyaths. No conclusions can be drawn concerning possible affinities between these groups on the basis of microstructure alone. The microgranular structure is a primitive one and may have given rise to a variety of more elaborate secretion products in the course of evolution.

Altogether, this microstructure is finer than that expected from the neomorphism of aragonite, so an original calcitic mineralogy is assumed. Comparative petrographic study of Labrador reef fabrics and faunas by James and Klappa (1983) led these authors to conclude that archaeocyaths were probably originally of magnesium calcite composition. This conclusion is supported by the common occurrence of microdolomite inclusions in the skeleton, an increased magnesium content, synsedimentary marine epitaxial fibrous cement developed in optical continuity with skeletal elements, and less altered carbon and oxygen isotope signatures (Brasier & others, 1994; Zhuravlev & Wood, 2008).

BIOLOGY OF ARCHAEOCYATHA

INFERRED CHOANOCYTES

The presence of choanocyte chambers in archaeocyaths can only be indirectly demonstrated. Balsam and Vogel (1973) pioneered the empirical study of archaeocyathan functional morphology using generalized metal models in flume tanks. These authors, and subsequently Zhuravlev (1989, 1993) and Savarese (1992, 1995), concluded that the archaeocyathan cup was admirably suited to passive filtration. Due to the velocity gradient induced within the cup, water entered the cup through the outer wall pores, passed through the intervallum, and exited via the inner wall pores and central cavity. This is the water flow direction in sponges. Hypotheses suggesting a passive ingress of water into the cup through the central cavity or intervallum and its egress through the outer wall (Vologdin, 1962a; Zhuravleva, 1974c) are inconsistent with the principles of hydrodynamics.

The absence of septa in sponges was one of the major arguments of Okulitch and de Laubenfels (1953) against the assignment of archaeocyaths to Porifera. However, Ziegler and Rietschel (1970) noted that the presence of septa only means that the water flow did not stream diffusely through the soft tissue, but was channelled. This proposal has been confirmed by Savarese (1992), who found that his septate models did not leak fluid from the outer wall, enhancing the excurrent fluid flow through the central cavity. Thus, certain Devonian and Triassic thalamid sponges also developed septalike structures (Ott, 1974; Pickett & Rigby, 1983). It is thus clear why the intervallar rods of dokidocyathine archaeocyaths are arranged in regular longitudinal rows (Gravestock, 1984; Debrenne & Rozanov, 1985; Zhuravlev, 1989) rather than arbitrarily: they form a structure which is indeed a septum with a single longitudinal row of pores.

In summary, the archaeocyathan skeleton was to some degree suited to passive filtration—although, as in extant sponges with nonspiculate skeletons, this need not exclude active filtration and, indeed, given the now established poriferan nature of the group, choanocytes are inferred to be present.

An auxiliary observation, favoring the presence of choanocyte chambers in archaeocyaths, concerns forms having an outer wall consisting of an attached microporous sheath mantling funnel-shaped pores. As in extant demosponges, only a choanocyte chamber system could prevent the blockage of such a porous structure by external particles (Rigby & Potter, 1986).

IMMUNE RESPONSES

Archaeocyaths display a wide range of skeletal reactions in response to the proximity of other species (Brasier, 1976; Debrenne & Zhuravlev, 1992b, 1994; Wood, Zhuravlev, & Debrenne, 1992) (Fig. 523). These are comparable with the allograph, autograph, and xenograph immune behaviors of demosponges (van de Vyver & Buscema, 1985; Ilan & Loya, 1990). The development of archaeocyathan secondary calcareous laminations might be analogous to the formation of a collagen barrier between demosponge bodies (van de Vyver & Buscema, 1985).

Partial atrophy and maintenance of spatial separation due to juvenile attachment or proximity to adjacent adult cups (Kruse, 1990a) have been recognized to be more pronounced among the Ajacicyathida than the Archaeocyathida or Kazachstanicyathida, that is, there is a spectrum of allogenic incompatibility in the class (Wood, Zhuravlev, & Debrenne, 1992). The greater incompatibility demonstrated by the Ajacicyathida hinders mutual encrustation, and thereby greatly limits the ability of ajacicyathides to construct rigid reef framework. Conversely, allogenic reactions are minimal among the Archaeocyathida and Kazachstanicyathida, and these orders played a much greater bioconstructional role in reefs.

These inferences alone cannot be used as a definitive argument in favor of the taxonomic proximity of archaeocyaths and demosponges; data on immune responses in calcified sponges are lacking, thus precluding comparison. Furthermore, the comparison of secondary calcareous skeleton with collagen barriers can only be a working hypothesis at present. Nevertheless, it is interesting to note the similarities in interspecific interactions within the two groups.

ASEXUAL REPRODUCTION IN CHAETETID ARCHAEOCYATHS

The modularity of chaetetid archaeocyaths results from two processes: in

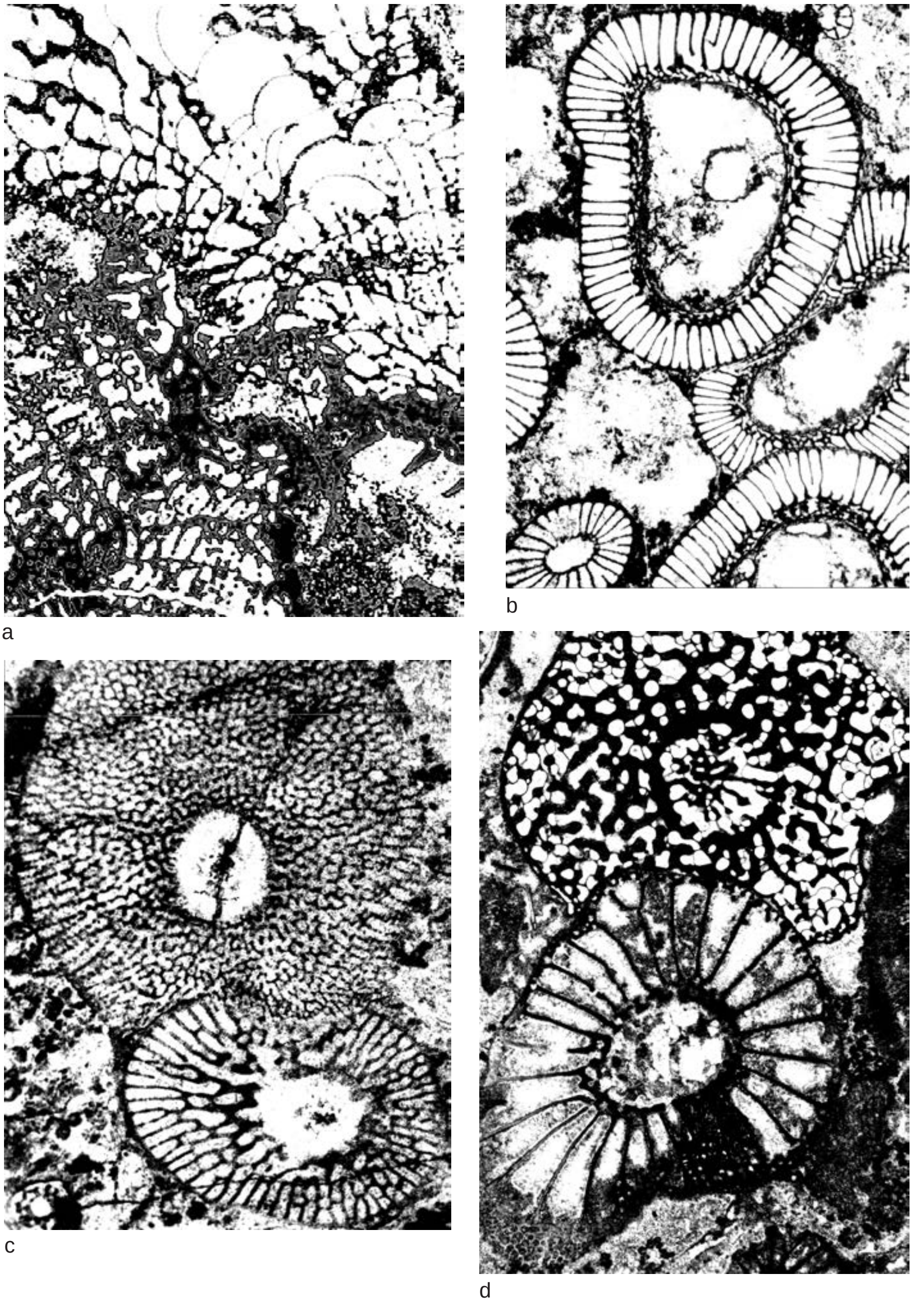


Fig. 523. Modularity and immune responses; *a,* intercalicular budding on surface of skeleton of *Gatagacyathus mansyi* Debrenne & Zhuravlev, Botoman, Poleta Formation, Mount Lida, Nevada, United States, oblique longitudinal section, M83138, MNHN, ×10 (Debrenne & Zhuravlev, 1994); *b,* interaction of modules in pseudocerioid *Sajanocyathus ussovi* Vologdin, Botoman, Verkhnemonok Formation, West Sayan, Altay Sayan, Russia, transverse section, 4451/55, PIN, ×2.7; *c,* interaction of *Keriocyathus arachnaius* Debrenne & Gangloff (Archaeocyathida; top) and *Siderocyathus duncanae* Debrenne & Gangloff (Ajacicyathida; bottom), *(Continued on facing page).*

Gatagacyathus DEBRENNE & ZHURAVLEV, by external budding evolving into a branching modular form (Fig. 523a); and in *Usloncyathus* FONIN (Fig. 510.1) and *Zunyicyathus* DEBRENNE, KRUSE, & ZHANG (Fig. 495d), by the separation of new aquiferous units within a thin sheath of soft tissue covering the skeleton (DEBRENNE & ZHURAVLEV, 1994). In chaetetid sponges, two similar budding modes have been noted by WEST and CLARK (1983): calicular longitudinal fission and addition of new calicles at the periphery. A third mode of asexual reproduction is observed in most chaetetid archaeocyaths: the arising of small buds connected with a single calicle. The cavity of the parent calicle extends into the atrium of the offspring bud and the parent calicle's facets become the bud's inner wall, as in *Zunyicyathus grandis* (YUAN & ZHANG), *Gatagacyathus mansyi* DEBRENNE & ZHURAVLEV, *Usloncyathus araneosus* (GRAVESTOCK), *U. obtusus* (GRAVESTOCK), and *Zunyicyathus pianovskajae* (ZHURAVLEVA) (ZHURAVLEVA & others, 1970, p. 45; DEBRENNE, KRUSE, & ZHANG, 1991; DEBRENNE & ZHURAVLEV, 1994). This process may correspond to the intercalicular budding of WEST and CLARK (1983). In living chaetetid demosponges, peculiar buds are connected with certain calicles (VACELET, 1991; VACELET & others, 1992). These buds are spectacular in *Acanthochaetetes wellsi* HARTMAN & GOREAU (REITNER, 1991a; WOOD, 1991a). A similarity in skeletal structure of chaetetid archaeocyaths and chaetetid demosponges, together with an even greater similarity in the nature of their budding, suggests the presence of crypt cells in some archaeocyaths.

SYMBIONTS

Microscopic ovoid and rodlike bodies, 0.25 mm in diameter, observed in samples from early Cambrian reefs of Sardinia, were interpreted by CAMOIN, DEBRENNE, and GANDIN (1989) as bacteria and bacterial aggregates. They occur within all three major components of these bioconstructions: archaeocyaths, calcimicrobes, and sediment. As bacteria, they have been considered responsible for the precipitation of the micritic sedimentary matrix (BURNE & MOORE, 1987), as well as participating in the calcification of archaeocyathan skeleton. Within archaeocyathan skeletons, the putative bacteria are generally clustered, but within interskeletal spaces (pores or loculi) cemented by calcite spar, they are generally isolated and only rarely clustered.

The observation of putative bacteria within the skeletal elements of archaeocyaths might suggest a symbiotic relationship similar to that practiced by many extant sponges (VACELET, 1975). However, precise studies by SURGE and others (1997) of carbon stable isotope ratios in archaeocyathan skeletons collected from shallow-water and deep-water bioherms in the Ajax Limestone (South Australia) showed no significant variation in isotope ratio within either category of bioherm, but they did reveal a significant difference between shallow and deep samples. The observed difference parallels the upward increase in $\delta^{13}C$ in present oceans. These authors concluded that the archaeocyathan skeleton was precipitated in equilibrium with seawater and that archaeocyaths therefore did not possess photosymbionts. This need not preclude the presence of chemotrophic or heterotrophic symbionts.

Evidence for the presence of photosymbionts is necessarily indirect: the so-called thin-tissue syndrome and the lack of correlation between archaeocyathan abundance and high nutrient supply, as indicated, for example, by phosphate-enriched strata (COWEN, 1988;

FIG. 523. *(Continued from facing page).*

Botoman, Valmy Formation, Iron Canyon, Nevada, United States, transverse section, collection number not known, UCMP, ×6.8; *d,* interaction of *Archaeocyathus* sp. (Archaeocyathida; top) and *Tegerocyathus edelsteini* (VOLOGDIN) (Ajacicyathida; bottom), Toyonian, Torgashino Formation, East Sayan, Altay Sayan, Russia, transverse section, 4451/73, PIN, ×4.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

Rowland & Gangloff, 1988; Talent, 1988; Rowland & Shapiro, 2002; cf. Wood, Zhuravlev, & Debrenne, 1992; Wood, 1995, 1999). Many archaeocyaths did possess a large skeletal surface area mantled by a thin veneer of soft matter amenable to photosymbionts. However, such forms tended to be mud dwellers favoring turbid waters, presumably inimical to photosymbionts (Zhuravleva, 1972a; Kruse, Zhuravlev, & James, 1995; Zhuravlev, 2001c). Similarly, the plot of archaeocyathan generic diversity through time matches that of phosphatic-shelled genera (lingulates+tommotiids+mobergellans+protoconodonts), suggesting that there is indeed a positive correlation between archaeocyathan diversity and phosphate input (Zhuravlev, 2001b).

SYSTEMATICS OF ARCHAEOCYATHA

HISTORY OF CLASSIFICATION

The first major step in archaeocyathan studies was by Bornemann (1884, 1886, 1891a, 1891b). In contrast to North American discoveries up to that time, the material he collected in Sardinia from 1868 onward was plentiful and well preserved. Bornemann distinguished most of the fundamental skeletal elements. His interpretations of their nature and significance in some ways foreshadowed modern concepts (longitudinal radial partitions, now Ajacicyathina; horizontal partitions, now Coscinocyathina; vegetative stages as the basis of different Archaeocyathina), which are the basis of the present systematics (Debrenne, 1996, p. 35). Importantly, he recognized the distinctiveness of the group in creating a separate class, Archaeocyathinae, ostensibly allied to sponges and cnidarians (Bornemann, 1884).

Taylor (1910) was the first to organize genera into families to create the beginnings of an archaeocyath systematics. These families were based on differences in intervallar structures, now the basis for subordinal categories, such as Dokidocyathina (his Dictyocyathidae), Ajacicyathina (Archaeocyathidae), Archaeocyathina (Spirocyathidae), Syringocnemina (Syringocnemidae), and Coscinocyathina (Coscinocyathidae).

Subsequently, archaeocyathan systematics were strongly influenced by Okulitch (1935b, 1943), Vologdin (1936, 1937b, 1940a, 1940b), and the Bedfords (R. Bedford & W. R. Bedford, 1934, 1936; R. Bedford & J. Bedford, 1936, 1937, 1939). Archaeocyaths were recognized as a subphylum of the Porifera and divided into classes Regulares and Irregulares, based on differences in skeletal ontogeny. Concurrently, Ting (1937) and Simon (1939) viewed the group as merely a superfamily in the suborder Tetracladina of siliceous sponges. Their opinion derived from the observation that some Australian archaeocyaths were silicified and that *Archaeocyathus minganensis* Billings had spicules. That species, however, is a true Ordovician anthaspidellid sponge, the type species of the genus *Archaeoscyphia* (Hinde, 1889). They also criticized those systematists who followed Taylor (1910); in their opinion, wall structures, and not intervallar structures, should form the framework for archaeocyathan systematics.

Developments up to the early 1950s were summarized by Okulitch (1955a).

It was Zhuravleva's (1960b, p. 48–51) classification that laid the basis for the modern systematics of so-called regular archaeocyaths (Monocyathida, Ajacicyathida, Tabulacyathida [=Putapacyathida, p. 1019], Capsulocyathida). She applied ontogenic principles and demonstrated from the order of appearance and complication of skeletal structures that intervallar elements had hierarchical primacy over outer wall structures that, in turn, had primacy over inner wall structures. Thus, suborders were established on intervallar features, superfamilies on outer wall features, and families on inner wall features. This scheme was further developed by Debrenne (1964, p. 112–117), Hill (1965, p. 46–49; 1972, p. 50–103) and Rozanov (1973, p. 85–86). Only Krasnopeeva (1953, 1978) persisted with systematics in the style of Ting, while Konyushkov

(1978) attempted to construct a system based on purely theoretical ideas concerning the integration of soft tissue in various archaeocyathan groups. ROZANOV (1973) introduced VAVILOV's (1922) principle of homologous variability, which facilitated the recognition of features of equal weight in related lineages (ROZANOV & MISSARZHEVSKIY, 1966, p. 73; ROZANOV, 1973, p. 80).

The taxonomy of so-called irregular archaeocyaths (Archaeocyathida, Kazachstanicyathida) has proven more difficult, due to the abundance of secondary calcareous skeleton, which tends to obscure primary features, as well as to the lesser diversity of skeletal features in this group. At least five independent schemes have been established (see DEBRENNE & ZHURAVLEV, 1992b, tables 7–8). KRASNOPEEVA (1953, 1969, 1980) considered that all Irregulares possess intervallar tubes (class Syringoidea), whereas all one-walled archaeocyaths represented the initial stages of development of two-walled cups. ZHURAVLEVA (1960b, p. 267–315), by analogy with her Regulares scheme, distinguished among the Irregulares: one-walled cups (order Rhizacyathida), two-walled cups (Archaeocyathida), and forms with tubular intervallum (Syringocnematida). The Archaeocyathida were subdivided into forms without tabulae (Archaeocyathina) and with tabulae (Archaeosyconiina). This proposal was adopted in the *Treatise on Invertebrate Paleontology* classification of HILL (1972, p. 103–130), with the nomenclatural change of Rhizacyathida to Thalassocyathida. DEBRENNE (1970a, 1974a) employed the combination of intervallar elements and attempted to establish homologous series, as in the Regulares. Later, FONIN (1981, 1985, p. 35) and GRAVESTOCK (1984, p. 23) used skeletal ontogenetic data, but they arrived at different results.

As archaeocyaths are generally studied using thin sections, or incomplete silicified or dolomitized cups, overestimation of the taxonomic value of certain features can become inevitable. The suborders Globosocyathina and Nochoroicyathina were proposed on this basis. The former was established on oblique thin sections of Monocyathida with peltae (Fig. 507.1), whereas the latter was described from occasional thin sections intersecting pectinate tabulae. At the same time, all regular septate archaeocyaths with porous tabulae were assigned to a single suborder, Coscinocyathina, independently of skeletal ontogeny. It was subsequently demonstrated that such archaeocyaths represented at least two different groups (now suborders Erismacoscinina and Coscinocyathina of the orders Ajacicyathida and Capsulocyathida, respectively). In the ontogeny of Erismacoscinina, tabulae appeared after septa and were independent of the cup wall, whereas in the Coscinocyathina, the cup is distinguished by a thalamid architecture with later development of septa (ZHURAVLEV, 1986a). The tabula presence/absence problem in irregular taenial archaeocyaths creates even more difficulties. In some cases, as in *Metacyathellus caribouensis* (HANDFIELD) or *Pycnoidocoscinus serratus* (KAWASE & OKULITCH) as redescribed from Canada by ZHURAVLEV (in VORONOVA & others, 1987, p. 38, 40), tabulae are scarce and similar in construction to the outer wall. The chance of missing such structures in transverse thin section is therefore great, and consequently pairs of twin genera have been established, for example, *Sigmofungia-Palmericyathellus*, *Metaldetes-Metacoscinus,* and *Archaeocyathus-Claruscyathus*, the synonymy of which need to be confirmed. As well, forms with frequent tabulae do not constitute a single discrete group: in *Altaicyathus* VOLOGDIN, cup development begins with a spherical chamber with pillars, while in *Korovinella* RADUGIN, it begins with a one-walled cup with tabula, differences that substantiate the distinction of Kazachstanicyathina and Altaicyathina. On the other hand, in *Paracoscinus* R. BEDFORD & W. R. BEDFORD and similar forms, tabulae appear later than the other intervallar elements, and cup development is similar to that in typical Archaeocyathida and comparable with that in Ajacicyathida.

A further problem is the interpretation of juvenile taenial archaeocyaths. For example, Hill (1972, p. 131–132) doubted the reality of *Rhizacyathus* R. Bedford & J. Bedford as an independent genus, whereas Gravestock (1984, p. 40) demonstrated from Australian material that many one-walled or even two-walled irregular cups were juveniles of various genera of Irregulares. Indeed, while mature one-walled regular archaeocyaths are readily distinguishable from one-walled juvenile stages of two-walled regular species, all described one-walled, and even some two-walled irregular archaeocyaths, are identical in size and morphology to the initial stages of the Irregulares present in the same locality.

All these inconsistencies were recognized during a major revision of the archaeocyaths by Debrenne, Zhuravlev, and Rozanov (1989; Debrenne, Rozanov, & Zhuravlev, 1990; Debrenne & Zhuravlev, 1992b), which allowed these authors to compile a completely new systematics for irregular archaeocyaths and to significantly rework the systematics of regular archaeocyaths. Their scheme is adopted here with further modification. Their revision has led to the rejection of the customary subdivision of archaeocyaths into (sub)classes Regulares and Irregulares, now superseded by six orders, based on structural differences and skeletal ontogeny: Monocyathida, Ajacicyathida, Putapacyathida, Capsulocyathida, Archaeocyathida, and Kazachstanicyathida. The two most diverse orders are Ajacicyathida and Archaeocyathida, approximately corresponding to the former subdivision into Regulares and Irregulares, respectively.

CURRENT PRINCIPLES OF CLASSIFICATION

The present archaeocyathan systematics are based on three principal datasets: (1) skeletal ontogeny; (2) morphological functional analysis; and (3) limits of homologous variability. The ontogenetic observations allow the determination of the order of appearance of skeletal elements and of stabilization of adult features, and thence, in accordance with principles of heterochrony, the use of these data for the establishment of the taxonomic hierarchy. Morphological functional analysis, coupled with paleoecological observations, provides the basis for the discrimination of genotypic from phenotypic features. Finally, knowledge of the series of homologous variability allows us to establish those features of equal taxonomic weight in different evolutionary lineages, and even to forecast the features of taxa that could conceivably exist. Data on skeletal microstructure and paleogeographic and stratigraphic distribution are consistent with the systematics derived on the three above-mentioned criteria.

Skeletal Ontogeny

Archaeocyathan skeletons preserve much information on the ontogeny of individual species. As ontogenetic patterns are recapitulated in the stratigraphic distribution of related species and genera, their significance is assured. The intensive study of archaeocyathan skeletal ontogeny commenced as early as Bornemann (1886) and was continued by Taylor (1910, p. 82), the Bedfords (R. Bedford & W. R. Bedford, 1934, 1936; R. Bedford & J. Bedford, 1936, 1937, 1939), Okulitch (1935b, 1943, p. 32), Vologdin (1957a, 1959b) and especially by Zhuravleva (1960b, p. 40) and Rozanov (1973, p. 27). These data were summarized and supplemented by significant new observations, especially on Capsulocyathida, Archaeocyathida, and Kazachstanicyathida, by Debrenne, Zhuravlev, and Rozanov (1989, p. 80; Debrenne, Rozanov, & Zhuravlev, 1990, p. 65; Debrenne & Zhuravlev, 1992b, p. 76). The following generalizations are applicable to archaeocyathan skeletal ontogeny.

1. There are three major types of skeletal ontogeny among two-walled archaeocyaths:

a. The septal type begins with a juvenile conical cup resembling one-walled archaeocyaths (Monocyathida) and proceeds via the initial development of a centripetal inner wall, open below the lowermost rods of the septa supporting it, and by the initial parts of the septa, irrespective of their adult morphology, bearing a single longitudinal row of pores. The septal type is restricted to the orders Ajacicyathida and Archaeocyathida. In succeeding ontogeny, the distinction between these two orders appears: multiporous septa begin to develop in ajacicyathides, but multiporous taeniae in archaeocyathides. The initial multiporous septa in the ajacicyathide suborders Ajacicyathina and Erismacoscinina are always retiform. Archaeocyathide taeniae can persist until maturity or evolve into pseudosepta (as in Loculicyathina and Anthomorphina), into a pseudotaenial or dictyonal network (Archaeocyathina), or into calicles (Dictyofavina). In turn, calicles can be reorganized into syringes (Syringocnemina).

b. The second type of skeletal ontogeny is the thalamid type, in which the juvenile cup is subspherical in shape, the inner wall is of invaginal type and is a continuation of the outer wall, and the inner wall is closed at the base. Such juvenile cups characterize the order Capsulocyathida.

c. The Kazachstanicyathida have their own distinctive type of ontogeny: initial chambers are empty (Kazachstanicyathina) or contain pillars (Altaicyathina), and the entire skeletal ontogeny is limited to the successive accretion of similar chambers.

The nature of cup ontogeny in the order Putapacyathida is still uncertain.

2. The relative rapidity of stabilization of outer wall features was greater than for other skeletal elements. In late Atdabanian and Botoman forms, the outer wall could acquire the characteristic structures of a given species even at the one-walled stage in Ajacicyathina, before the appearance of tabulae in Erismacoscinina, and before the appearance of septa in Coscinocyathina.

Characteristics of first-order intervallar elements (septa, plate, and segmented tabulae) are established earlier than those of the inner wall. Exceptionally, in forms with aporose septa and a complex outer wall, mostly of late Atdabanian and Botoman age, the sequence is reversed due to heterochrony.

Overall, stabilization of cup features thus occurred in the following sequence: outer wall—intervallar elements of the first order—inner wall.

Intervallar elements of the second order (pectinate and membrane tabulae, synapticulae, and spines) could appear at any stage after the initiation of development of the first-order intervallar elements, this varying even in different individuals of the same species. Pectinate tabulae could appear after all other elements had acquired the features characteristic of species.

The shapes of cup elements (pore outlines, additional elements on the inner wall) typical of a given species of Ajacicyathida or Capsulocyathida were stabilized earlier than the size of those elements.

Spines or bracts always preceded fused bracts, scales, annuli, or canals developed on the inner wall in adult forms (ROZANOV, 1973; GRAVESTOCK, 1984; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 67–74).

3. The secondary calcareous skeleton, as well as traces of the aquiferous system (astrorhizae, exaules, tubuli), could appear irregularly at any stage of development but always after the primary calcareous skeleton.

These morphogenetic observations suggest that, on the basis of architecture, archaeocyaths can be subdivided into the presently accepted six orders. Aspects of intervallar development allow further division into the twelve aforementioned suborders. As the order of stabilization of cup elements during ontogeny suggests the primacy of outer wall features over inner wall features, outer wall structure defines the superfamily level, and inner wall structure defines the family level.

Functional Morphology

BALSAM and VOGEL (1973) pioneered the empirical study of archaeocyathan functional morphology using generalized metal models of the archaeocyathan skeleton in flume tanks. They concluded that the porous, upright skeleton was admirably suited to passive filtration in ambient flow and that water must enter the cup through the outer wall pores, pass to the central cavity via the inner wall pores, and ultimately exit the osculum at the top of the central cavity. Further research on fossil material (ZHURAVLEV, 1989, 1993; DEBRENNE & ZHURAVLEV, 1992b, p. 96, 1994, 1996; WOOD, ZHURAVLEV, & DEBRENNE, 1992; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; RIDING & ZHURAVLEV, 1995; ZHURAVLEV & WOOD, 1995) and with models (SIGNOR, SAVARESE, & DENNY, 1989; SAVARESE, 1992, 1995) has focused on the significance of specific skeletal elements in archaeocyathan functional morphology.

These results have led to the synonymy of many species, genera, and higher taxa, which were found to reflect phenotypic variations only. The two former major archaeocyathan subdivisions, the classes Regulares and Irregulares, were rejected as they proved to represent two generalized archaeocyathan adaptations only. It has been postulated that the majority of the former regular archaeocyaths (Monocyathida and Ajacicyathida) were adapted mainly to soft, shifting substrates and low ambient energy (WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; RIDING & ZHURAVLEV, 1995; DEBRENNE & ZHURAVLEV, 1996) and/or turbidity (ZHURAVLEV, 1999a). Ajacicyathide cups were relatively material-efficient structures (SIGNOR, SAVARESE, & DENNY, 1989) and so facilitated more rapid growth. In contrast, the bulk of former irregular archaeocyaths (Archaeocyathida) were presumably restricted to lithified substrates and high ambient energy (WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; RIDING & ZHURAVLEV, 1995; DEBRENNE & ZHURAVLEV, 1996). According to ZHURAVLEV and WOOD (1995), the two thalamid orders (Capsulocyathida and Kazachstanicyathida) were, with few exceptions, obligate cryptobionts. Together with ontogenetic data that indicate closer relationships between Monocyathida, Ajacicyathida, and Archaeocyathida, a subdivision according to adaptive strategies does not permit a Regulares-Irregulares distinction.

The archaeocyathine adaptation to lithified substrates and high ambient energy prompted strong development of the secondary calcareous skeleton in order to anchor the cup. Aspects of the secondary skeleton that served this function, such as an elaborated radicatus, secondary thickenings, and buttresses, were in the past overstated as criteria for the establishment of genera (e.g., *Retecyathus* VOLOGDIN, a junior synonym of *Archaeocyathus* BILLINGS with less developed secondary thickenings) and even orders (e.g., Somphocyathida, established for Ajacicyathida with buttresses). In addition, observations show that secondary calcareous skeleton served to cicatrize damaged skeleton, isolate extraneous bodies on the growing surface, seal off abandoned parts of the cup, and protect from neighboring organisms (DEBRENNE & ZHURAVLEV, 1992b, p. 62).

On a smaller scale, features such as cup shape, modularity, septal and tabular porosity, orientation of inner wall elements, presence of synapticulae and pectinate tabulae, number of wall pores per intersept, development of double inner walls, and stirrup pores were analyzed in order to clarify their systematic significance as generic criteria.

Among these, platelike cup shape and outer wall transverse bulging were found to lack generic significance, as the first relates to substrate softness, and the second depends on the degree of development of segmented tabulae. Nevertheless, the mutual longitudinal (e.g., *Orbiasterocyathus* ZHURAVLEVA) or transverse folding of both walls (e.g., *Orbicyathus* VOLOGDIN) warrants generic status, as this generates two cup shapes that maintain a constant locular volume during growth and thus maintain the outer-inner wall pore area ratio. In some genera, this ratio may be regulated by the development of longitudinal outer wall plication (as, for example, in *Rozanovicoscinus* DEBRENNE).

In contrast, outer wall transverse bulging (as in *Batschykicyathus* ZHURAVLEV) did not maintain this ratio. A thalamid wall, however, which is also expressed in outer and inner wall bulging, does not represent a single feature and must be treated together with the entire set of features of the thalamid architecture.

As modular organization confers many ecological advantages in reef-building settings, such as indeterminate growth leading to larger size, greater powers of regeneration, and the ability to encrust and gain secure attachment to substrates, modularity was one of the main pathways of archaeocyathan evolution (WOOD, ZHURAVLEV, & DEBRENNE, 1992). As such, it developed independently and repeatedly in all major archaeocyathan lineages (suborders). Some atypical budding types, such as intercalicular budding, suggest close affinities between archaeocyaths and demosponges (DEBRENNE & ZHURAVLEV, 1994). Although certain types of modular organization and development are restricted to particular archaeocyathan suborders, the same features are widespread among other sponges and even other sessile animals. Consequently, only species can be defined with certainty by this feature.

Archaeocyathan models must be treated with caution as they do not take account of soft tissue mantling the skeleton. Nonetheless, such models provide some constraints on functional morphology. Thus, flume experiments with archaeocyathan skeletal models predict that archaeocyaths with completely porous septa would filter more effectively under low current speeds, while those with aporose septa would be advantaged under high free-stream velocities (SAVARESE, 1992). Such a conclusion is confirmed by ecological observations: archaeocyathan communities living in low-energy environments were dominated by individuals with porous septa (e.g., deeper facies of the Pestrotsvet Formation, Siberian Platform [ZHURAVLEV, 1986a]; upper Sellick Hill Formation, South Australia [DEBRENNE & GRAVESTOCK, 1990]), while those that developed in high-energy environments are dominated by species with aporose septa (e.g., reef-core facies of Pestrotsvet Formation, Siberian Platform [ZHURAVLEV, 1986a]; oncoid archaeocyathan rudstone of Salaany Gol Formation, Mongolia [WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993]). The restriction of the latter to warmer waters with normal salinity (DEBRENNE & ZHURAVLEV, 1996) may also be explained by the greater filtration rates correlated with increased water temperature, as observed among extant sponges (RIISGARD, 1993). Septal porosity thus indicates two modes of adaptation: archaeocyaths possessing completely porous septa are generalists, while those with aporose septa are specialists. Septal porosity is thus a genotypic rather than a phenotypic feature and may be used as a generic criterion if all individuals of the same species consistently show the same type of septal porosity. However, the advantage of aporose septa in tall cups encountering higher ambient currents may lead to a loss of septal porosity during ontogeny. In such cases (ROZANOV, 1973, p. 38, 70; GRAVESTOCK, 1984, p. 37), this feature would have intraspecific value only. Further, in some ajacicyathines with inner walls of communicating canals, the enhanced soft tissue communication thereby provided apparently compensated for a reduction of porosity in the septa. The majority of such genera thus either lack septal pores (e.g., *Ethmophyllum* MEEK, *Stephenicyathus* ZHURAVLEV) or possess a transitional porosity varying between the porous and aporose states in different populations (e.g., *Formosocyathus* VOLOGDIN, *Irinaecyathus* ZHURAVLEVA, *Tegerocyathus* KRASNOPEEVA).

Similarly, a temperature gradient is observed in the distribution of genera possessing pectinate tabulae, which are restricted to warmer waters, whereas synapticulate genera are more eurythermic (ZHURAVLEVA, 1981; DEBRENNE & ZHURAVLEV, 1996). This mutual paleogeographic substitution of synapticulae and pectinate tabulae is further confirmation of the homology of these elements, which, while functionally interchangeable, are not completely identical. Possibly, synapticulae add some rigidity to the skeleton, as they are present only in archaeocyaths with coarsely porous septa or similar structures.

The number of pore rows per intersept is another feature that reflects the differing functions of the outer and inner walls. Thus, a general trend to (1) reduce the mutual friction between currents outflowing the intervallum; and (2) to increase the speed of the cental cavity outflow in order to avoid water recycling; would and did lead to the dominance of a uniporous interseptal state of the inner wall. Thus, among 187 genera of Ajacicyathina and Erismacoscinina listed by DEBRENNE, ROZANOV, and ZHURAVLEV (1990, table 9), genera with a uniporous inner wall comprise 58% of the total. Chronologically, this ratio increased from 0% in the early Tommotian to 67% in the middle Toyonian. The transition from the multiporous interseptal state of the inner wall to the uniporous state is thus a significant functional threshold for the archaeocyathan filtration system that warrants use as a generic criterion. However, the number of pore rows per intersept of the outer wall has no effect on current inflow, and so this feature lacks generic value. For the inner wall, stirrup pores and canals were significant only if there were no additional intervening pores.

Many other features of the inner wall, such as the shape of the primary elements (annuli and canals) and the development of fused bracts and fused ethmophylloid-type canals, presumably served to increase the initial velocity of the cumulative exhalant jet. The progressive development of such structures was among the major evolutionary trends in Ajacicyathida and Coscinocyathina (ZHURAVLEV, 1993). However, in Archaeocyathida, whose aquiferous system was restricted to the uppermost few millimeters of the soft tissue, the same elements probably play a protective function only, and intraspecific variability in the development of spines, bracts, and even fused bracts is observed (DEBRENNE & ZHURAVLEV, 1992b, p. 55).

Another trend is revealed by the appearance on the inner wall of various structures (spines, narrow bracts) that probably served a protective function. Their presence is the rule rather than the exception, and taxonomically, such structures, attached to otherwise simple pores, should be grouped as elements of the simple inner wall type. Subsidiary elements (spines, bracts, annuli, and microporous membranes) covering the primary elements on the central cavity side typically present a high intraspecific variability (ZHURAVLEVA, 1960b, p. 160; REPINA & others, 1964, p. 214) and could be considered of equivalent significance.

The orientation of spines and narrow bracts and the development of modified bracts, canals, scales, and annuli upon them would be expected to reduce mutual friction between currents (ZHURAVLEV, 1993). However, the significance, and thus the taxonomic value of the shape of these structures, is difficult to evaluate without the testing of models.

Homologous Variability

The principle of homologous (parallel) series in hereditary variability was advanced by VAVILOV (1922). He proposed that the variability of related taxa is not merely an arbitrary set of traits, but a repetition of the same limited set of features. Thus, species of the one genus have similar series of variability, genera of the one family potentially contain a parallel set of species bearing the same features, and so on. The principle implies the operation of genetic constraints on morphological variability, which are shared among allied genera or families. It means that the number of possible features in a given group of organisms is limited, so that the whole set of characters of a yet undiscovered form can be predicted.

VAVILOV's Principle was successfully applied to regular archaeocyathan genera by ROZANOV (ROZANOV & MISSARZHEVSKIY, 1966, p. 73; ROZANOV, 1973, p. 50, 1974), and the history of this application is documented by

DEBRENNE, ZHURAVLEV, and ROZANOV (1989, p. 77; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 89). Archaeocyaths provide an excellent example of VAVILOV's concept: the first of ROZANOV's tables of homologous variability (ROZANOV & MISSARZHEVSKIY, 1966, fig. 45) forecast many genera of regular archaeocyaths, which were subsequently discovered in various localities and described by different specialists. A corresponding table of homologous variability for irregular archaeocyaths was first given by DEBRENNE and ZHURAVLEV (1992b, table 5).

Homologous features include the diverse types of outer and inner walls and intervallar structures. For example, a pustular outer wall occurs in Loculicyathina, Archaeocyathina, Syringocnemina, and Putapacyathida, while a somewhat similar tumulose outer wall is known in Monocyathida, Dokidocyathina, Ajacicyathina, Erismacoscinina, and Capsulocyathina. Similarly, inner walls with scales or fused bracts are known in all suborders (except Coscinocyathina) of two-walled archaeocyaths, and so on.

Homologous series can be established through recurrences. The concept of recurrences (DEBRENNE & ZHURAVLEV, 1992b, p. 87), or repeating polymorphic sets, was introduced by MEYEN (1988) under the term refrains. According to MEYEN, the existence of recurrences can be attributed to a certain inherited genotypic unity. In the case of archaeocyaths, recurrences can be represented by identical vectors corresponding to a certain order in the appearance of structures during skeletal ontogeny; for example, simple pores, then bracts, then canals on the inner wall in a set of related archaeocyathan lineages. Thus, the structures belonging to the same recurrence are homologous.

The table of homologous variability may serve as a key for the determination of genera, as a prognosis of taxa that may conceivably exist and as a basis for the estimation of the systematic value of a character. This does not mean that every empty cell of the table will eventually be occupied, but that any new form found and described will be accommodated within such a table. Such consistency permits the construction of taxonomic keys (KERNER, VIGNES LEBBE, & DEBRENNE, 2011).

Innovations in Archaeocyathan Taxonomy

Archaeocyathan taxonomy (see Archaeocyatha systematics descriptions, p. 923–1084) takes account of developments up to and including the most recent revision, that of DEBRENNE, ZHURAVLEV, and KRUSE (2002). Two significant taxonomic innovations are additionally introduced here.

Role of supplementary wall features.—DEBRENNE, ZHURAVLEV, and KRUSE (2002) introduced the concept of supplementary features in walls comprising a combination of different wall types. These authors applied it mainly among ajacicyathine genera bearing walls with canals, most notably the Ethmocyathidae (inner wall with noncommunicating canals) and Sajanocyathidae (inner wall with communicating canals) among the Bronchocyathoidea (outer wall with simple pores), and the Ethmophylloidea (outer wall with canals). Studies of several of these genera had disclosed that some taxa did not possess straight or V-shaped canals as commonly described, but in fact bore a combination of straight canals with terminal bracts. These bracts were termed supplementary by DEBRENNE, ZHURAVLEV, and KRUSE (2002).

In the systematic descriptions of the Archaeocyatha (p. 923–1084), this concept is extended consistently to combination walls of all types, not only those with component bracts. In any wall comprising two different wall types, the fundamental wall type is the element adjacent to the intervallum, whereas the supplementary wall type is the constituent facing the exterior (on outer walls) or the central cavity (on inner walls). The fundamental wall type remains the family-level criterion; the supplementary elements are of genus-level significance only.

The major outcomes of this innovation are the following.

1. In Ajacicyathina, synonymy of Hupecyathelloidea (outer wall with canals and independent microporous sheath) with Ethmophylloidea, the independent microporous sheath of the former is now treated as supplementary. Hupecyathellidae becomes a junior subjective synonym of Carinacyathidae.
2. In Erismacoscinina, synonymy of Lunulacyathoidea (outer wall with spinose screen and bracts or scales) with Polycoscinoidea (outer wall with attached microporous sheath), the bracts or scales of the former are now treated as supplementary. Lunulacyathidae becomes a junior subjective synonym of Polycoscinidae.
3. In Erismacoscinina, synonymy of Schumnyicyathoidea (outer wall with noncommunicating canals and attached microporous sheath) with Porocoscinoidea (outer wall with noncommunicating canals), the attached microporous sheath of the former is now treated as supplementary. Schumnyicyathidae becomes a junior subjective synonym of Tatijanaecyathidae.

Tabulacyathida versus Putapacyathida.—Vologdin (1956) erected the order Tabulocyathida (subsequently corrected by Hill [1972] to Tabulacyathida) based on his tabulate, nonseptate genus *Tabulacyathus* Vologdin, 1932. Subsequently, Debrenne, Zhuravlev and Rozanov (1989); Debrenne, Rozanov, and Zhuravlev (1990); and Debrenne (1991) retained Tabulacyathina as a suborder within the Ajacicyathida. The taxon was restored to ordinal status by Debrenne, Zhuravlev, and Kruse (2002).

Regrettably, in erecting the nominate genus *Tabulacyathus* and its type species *T. taylori,* Vologdin (1932, p. 30–33, fig. 24 and pl. 7,*3*) figured two specimens in the type series of *T. taylori* but failed to designate either as holotype. Furthermore, as subsequently established by Zhuravleva, Konyushkov, and Rozanov (1964, p. 124–126), the two specimens figured by Vologdin (1932) were of different taxa. These authors designated the specimen figured by Vologdin (1932, fig. 24) with a tabular outer wall as "holotype" (i.e., lectotype, in accordance with Article 74 of the International Code of Zoological Nomenclature, ICZN, 1999), and Konyushkov (in Zhuravleva, Konyushkov, & Rozanov, 1964, p. 102–104) assigned the second specimen (with plate tabulae between independent walls) to his new genus and species *Galinaecyathus lebedensis.*

Debrenne, Zhuravlev, and Rozanov (1989, p. 67–68) and Debrenne, Rozanov, and Zhuravlev (1990, p. 94) reported that the designated lectotype of *T. taylori* is "more or less" similar to *Altaicyathus notabilis* Vologdin (1932, p. 27), described from the same locality in the same publication. If the identification of these two species were to be accepted, *Tabulacyathus* and Tabulacyathidae should be transferred to Altaicyathina and synonymized with *Altaicyathus* and Altaicyathidae, respectively. Hence, on the basis of page precedence and a claimed better accord with the original generic diagnosis, these authors invalidly argued for the lectotype designation to be reversed and diagnosed their Tabulacyathina accordingly.

From examination of the type material of *T. taylori* in 1990, A. Yu. Zhuravlev concludes that the lectotype could represent any of several similar taxa. Consequently, *Tabulacyathus* (together with its derivatives Tabulacyathidae and Tabulacyathida) is here removed from the order formerly named Tabulacyathida and treated as a *nomen dubium.*

The ordinal taxon Putapacyathida Vologdin (1961) now embraces the remaining genera formerly united in Tabulacyathida.

EVOLUTIONARY TRENDS

The major temporal trends in archaeocyathan evolution were: (1) oligomerization (increase in size of outer wall pores within fixed limits)—compensation (formation of microporous sheaths, thus decreasing pore sizes)—renewed oligomerization (Rozanov, 1973, p. 62); (2) increased modularity (Wood, Zhuravlev, & Debrenne, 1992); (3) reduction of septal porosity (Gravestock, 1984; Wood, Zhuravlev, & Debrenne, 1992); (4) development of annular and oblique upwardly projecting structures on the inner wall (Zhuravlev, 1993); and (5) transition from a multiporous interseptal state of the inner wall to a uniporous state. These are all consistent with the evolution of archaeocyaths as filter feeders (Zhuravlev, 1989, 1993; Savarese, 1992).

BIOSTRATIGRAPHY

The first archaeocyathan zonation was proposed by Vologdin (1940b, 1957a, 1957b, 1961), based mainly on faunas of the Altay Sayan Fold Belt of Siberia. Unfortunately, his schemes were supported neither by evolutionary patterns within the group nor by an accurate lithostratigraphy.

The archaeocyathan zonation of Zhuravleva (1960b), based on the relatively continuous lower Cambrian sections of the Siberian Platform, was honed by Zhuravleva, Korshunov, and Rozanov (1969); Rozanov and others (1969); and Varlamov and others (1984) to form the basis of the current archaeocyathan zonation for Siberia. This comprehensive scheme, and its associated stages, are the only ones officially approved in the former USSR and now in Russia (Spizharskiy & others, 1983; Spizharski & others, 1986; Astashkin & others, 1991). The scheme comprises four lower Cambrian stages, in ascending order: Tommotian (with three archaeocyath zones), Atdabanian (four zones), Botoman (one zone at the base), and Toyonian (one medial zone).

Tommotian

Tom.1. *Nochoroicyathus sunnaginicus* Zone
Tom.2. lower *Dokidocyathus regularis* Zone
Tom.3. upper *Dokidocyathus regularis* Zone
Tom.4. *Dokidocyathus lenaicus–Tumuliolynthus primigenius* Zone

Atdabanian

Atd.1. *Retecoscinus zegebarti* Zone
Atd.2. *Carinacyathus pinus* Zone
Atd.3. *Nochoroicyathus kokoulini* Zone
Atd.4. *Fansycyathus lermontovae* Zone

Botoman

Bot.1. *Carinacyathus squamosus–Botomocyathus zelenovi* Zone
Bot.2. unzoned
Bot.3. unzoned

Toyonian

Toy.1. unzoned
Toy.2. beds with *Irinaecyathus grandiperforatus*
Toy.3. unzoned

This Siberian Platform zonation is supplemented by archaeocyathan zonations developed for other regions of the former USSR in accordance with the then prevailing national stratigraphic rules. Such local zones (lonas) were established for the Russian Far East and Altay Sayan, so that the Botoman and Toyonian stages each have three zones (Repina & others, 1964; Zhuravleva, Repina, & Khomentovskiy, 1967; Borodina & others, 1973; Okuneva & Repina, 1973; Belyaeva & others, 1975; Osadchaya & others, 1979; Belyaeva, 1988; Astashkin & others, 1995).

The composite Siberian scheme does not take account of evolutionary events within monophyletic lineages of the group, or even of the complete stratigraphic ranges of constituent taxa. Its component zones are Oppel zones *sensu* Hedberg (1976), that provide convenient, relatively rich fossil assemblages that are easily traceable between sections. Some zone boundaries were subsequently recognized as markers of significant evolutionary events within the group (Rozanov, 1973). Thus, for example, the base of the first Atdabanian zone represents the mass appearance of archaeocyaths with complex walls, and the base of the first Botoman zone was thought to mark the rise of a variety of advanced wall types (e.g., attached microporous sheaths on the outer wall, communicating canals on the inner wall). Some of these proposals were subsequently confirmed, whereas others were not. Nevertheless, by default, the Siberian scheme became the reference zonation for determining the ages of faunas in other regions of the globe up to the 1980s. It remains the most comprehensive archaeocyathan zonation available, and the Siberian

Platform zonation is the basis for the listed age ranges of individual genera in the present Archaeocyatha, Cribricyatha, and Radiocyatha systematic sections.

In the 1980s and 1990s, early Cambrian archaeocyathan zonations based on the same approaches were proposed for other regions, namely Australia (GRAVESTOCK, 1984; ZHURAVLEV & GRAVESTOCK, 1994), Spain (PEREJÓN, 1984, 1994), North America (VORONOVA & others, 1987; MANSY, DEBRENNE, & ZHURAVLEV, 1993; MCMENAMIN, DEBRENNE, & ZHURAVLEV, 2000), Morocco (DEBRENNE & DEBRENNE, 1995), and Mongolia (ZHURAVLEV, 1998). In China, several discrete archaeocyathan assemblages are recognized (YUAN & ZHANG, 1981; YUAN & others, 2001; YANG & others, 2005).

Although archaeocyathan zonations now embrace the principal regions of archaeocyathan distribution, they are still primarily of regional use only. From the very beginning, the number of zones has exceeded their correlation potential. Interprovincial correlation is still effected at the genus level; there are no species in common between the principal areas of archaeocyathan development, namely the Siberian Platform (including Kolyma Uplift) and the bordering part of the Russian Far East (Yudoma–Maya Depression and Shevli terrane); Altay Sayan together with Mongolia and Transbaikalia; South Urals; Kazakhstan; Central-East Asia (Tajikistan, Uzbekistan, and Tarim of China); Morocco; Spain-Germany-Poland (BIAŁEK & others, 2007); France, together with southwestern Sardinia; South China; Laurentian part of present North America and Koryakia; and Australia and Antarctica with South African, Falkland Islands (STONE, THOMSON, & RUSHTON, 2012), and Argentine (GONZÁLEZ & others, 2013) allochthonous clasts.

Nevertheless, the value of archaeocyaths as index fossils remains, in that within any one region the archaeocyathan assemblages maintain the same species composition within the same lithofacies, irrespective of distance. Thus, a correlation of Australia and Antarctica, eastern and western Laurentia, or Altay Sayan and Mongolia is available at the zonal level (DEBRENNE & KRUSE, 1989; WRONA & ZHURAVLEV, 1996; ZHURAVLEV, 1998; MCMENAMIN, DEBRENNE, & ZHURAVLEV, 2000), whereas other lower Cambrian fossil groups thus far provide only a tentative correlation within these same regions (THEOKRITOFF, 1982; PALMER & REPINA, 1993; PALMER & ROWELL, 1995; LANDING & BARTOWSKI, 1996; LANDING, 1998). Furthermore, certain distinct, stratigraphically restricted archaeocyathan genera are useful for correlation of lower Botoman strata between such remote regions as Western Europe, southern China, and Australia (*Rudanulus, Porocoscinus*); as well as Altay Sayan, Mongolia, and Laurentian North America (*Krasnopeevaecyathus, Polythalamia, Claruscoscinus, Altaicyathus*); western Europe, Altay Sayan, and Australia (*Aptocyathus*); and Australia and North America (*Sigmofungia, Pseudosyringocnema*). Early Atdabanian assemblages in Morocco, western Europe, Kazakhstan, Altay Sayan, and Mongolia are characterized by *Urcyathus, Retecoscinus, Agyrekocyathus,* and *Uslonсyathus*, and allied species of *Tegerocyathus, Archaeocyathus,* and *Pycnoidocyathus* are present in middle Toyonian strata worldwide. In general, at least three archaeocyathan assemblages—early Atdabanian, early Botoman, and middle Toyonian—are useful for global correlation of lower Cambrian strata (especially in conjunction with other fossil groups).

Regrettably, regional zonations are not necessarily comprehensively applicable within their own geographic ambit, due to lithofacies variation among archaeocyathan assemblages. This is illustrated particularly in the key Lena-Aldan River area of the southeastern Siberian Platform, where correlation between lithofacies has proven difficult. Whereas species composition, and even proportions of individuals, may vary little for hundreds of kilometers within the same lithofacies, correlation between adjacent lithofacies only a few kilometers apart may be impossible. This pattern is particularly well expressed during the late Tommotian–early Atdabanian interval, where a transitional phase of especially rapid turnover is evident within reef paleocommunities. The rapidity of this reorganization was related to the dispersion of reef biota into a variety of environments from extremely shallow, agitated waters to relatively deep, calm conditions below fair-weather wave base. Eventually, such communities had no species in common. As a result, two different archaeocyathan zones were established for the base of the Atdabanian stage in the area of its type section, and correlation of these is still under debate. Thus, even similar archaeocyath genera are rare in *Dictyosycon-Khasaktia* boundstone developed in the *Leptosocyathus polyseptus* Zone, as compared to *Renalcis-Epiphyton* mudmounds of the *Retecoscinus zegebarti* Zone (Zhuravleva, Korshunov, & Rozanov, 1969; Varlamov & others, 1984; Zhuravlev & Naimark, 2005). Other early Cambrian animal groups, for example, trilobites (Palmer, 1998; Pegel, 2000; Álvaro & others, 2003), were probably similar in this respect.

Correlation difficulties are compounded in the mobile belts of the Altay Sayan and Mongolia. From the beginning, it has been suggested that archaeocyathan assemblages containing the simplest genera should be the oldest, independently of any lithofacies restriction (Rozanov & Missarzhevskiy, 1966). As a result, assemblages that include forms with attached microporous sheath, inner wall communicating canals, and other complicated cup elements have been assigned to younger horizons. Thus, for example, an assemblage of morphologically complex taxa (*Alataucyathus jaroschevitschi*, *Tabulacyathellus bidzhaensis*, *Pretiosocyathus subtilis*) from the Salaany Gol Formation of Mongolia has been treated as latest Atdabanian or even early Botoman (Voronin & others, 1982; Astashkin & others, 1995). However, subsequent analysis of Mongolian reef taxa, as well as new data on continuous sections in the Altay Sayan (Tuva, East Sayan, Kuznetsk Alatau) and Transbaikalia, have revealed a rich species pool already present by the earliest Atdabanian stage in these regions as well (Zhuravleva & others, 1997a, 1997b; Osadchaya & Kotel'nikov, 1998; Zhuravlev, 1998; Dyatlova & Sycheva, 1999). The aforementioned *Alataucyathus jaroschevitschi–Tabulacyathellus bidzhaensis–Pretiosocyathus subtilis* assemblage in these mobile belts has proven to be earliest Atdabanian.

It is noteworthy that taxonomic disparity among the environmentally much more heterogeneous paleocommunities of the Altay Sayan, Russian Far East, and Mongolia is greater than that among their less diverse Siberian Platform counterparts (Zhuravlev & Naimark, 2005). These regions spanned a number of different volcanic arcs (West Sayan, Altay, Far Eastern Gerbikan–Nel'kan River area), accretionary wedges, microcontinents, and seamounts (East Sayan, Kuznetsk Alatau), whereas on the Siberian Platform, reef communities occupied a relatively simple, ramplike margin of a broad, epeiric platform (Sukhov, 1997; Kheraskova & others, 2003). Comparison of community and taxonomic diversity for the Siberian Platform and these mobile belts reveals that seascape heterogeneity, significantly more varied in the latter, was the underlying determinant. Thus, in the Altay Sayan and Russian Far East, different zonations were applied to lithologically different Botoman successions, such as carbonate (East Sayan, Kuznetsk Alatau), volcanic-carbonate (Tuva), and volcanic-siliciclastic-carbonate (Altay, West Sayan) (Osadchaya & others, 1979).

Analogous dissimilarity of archaeocyathan assemblages, even within the same basin, has also been noted in the Stansbury Basin of South Australia, where Atdabanian-Botoman archaeocyaths of Yorke Peninsula are totally different from the coeval fauna of Fleurieu Peninsula (Debrenne & Gravestock, 1990; Zhuravlev & Gravestock, 1994; Gravestock & others, 2001), and in the Ossa-Morena tectonosedimentary zone of Iberia, where seven Ovetian (Atdabanian-?Botoman) archaeocyathan biostratigraphic zones established by Perejón (1984, 1994); and Perejón and Moreno-Eiris (2006) could, to a certain extent, represent coeval paleocommunities developing in different environments.

The influence of lithofacies needs to be taken into account also with respect to other early Cambrian fossil groups, including trilobites, acritarchs, mollusks, hyoliths, and small skeletal fossils (Zhuravlev, 1995; Palmer, 1998). Considered in isolation, any one group can provide a basis for a provisional correlation chart only. Global correlation charts based purely on archaeocyath, trilobite, or acritarch assemblages differ as a result (Debrenne & Zhuravlev, 1992b, fig. 43; Vidal, Moczydłowska, & Rudavskaya, 1995, fig. 9; Geyer & Shergold, 2000; Zhuravlev & Riding, 2001; Shergold & Geyer, 2003). Archaeocyathan assemblages are thereby commonly regarded as relatively young, whereas trilobite assemblages are assumed to be relatively old, and acritarch assemblages, significantly older. For example, some trilobite assemblages from the Holyoake Range of Antarctica have been correlated with Atdabanian assemblages of the Siberian Platform, whereas archaeocyaths from the same localities have been interpreted as Botoman (Debrenne & Zhuravlev, 1992b; Palmer & Rowell, 1995). The underlying problem is that none of these assemblages has a definite analogue on the Siberian Platform, and reliance on such broad entities as the superfamily Fallotaspidoidea or suborder Syringocnemina cannot yield precise correlation.

Robust correlation requires a synthesis of data from several fossil groups.

In the current provisional global chronostratigraphic scheme (Peng & Babcock, 2011), archaeocyaths range through the Terreneuvian Series (Stage 2) to Cambrian Series 2 (Stage 4) interval, and single species are restricted to each of Cambrian Series 3 (Guzhangian Stage) and the Furongian Series (Paibian Stage).

PALEOECOLOGY

Archaeocyaths were adapted to a narrow range of temperature, salinity, and depth, but, in concert with calcimicrobes, were among the earliest widespread metazoan reef builders.

TEMPERATURE

Archaeocyaths were stenothermal organisms, corresponding to intertropical climatic conditions (Zhuravleva, 1981; Debrenne & Courjault-Radé, 1994). Paleogeographic reconstructions indicate that the regions farthest from the paleoequator were Morocco and southern Europe to the south, and possibly Yangtze (southern China) and an enigmatic (nonconfirmed) locality in Korea to the north (Courjault-Radé, Debrenne, & Gandin, 1992, fig. 1). The Moroccan–southern European and Chinese archaeocyathan assemblages are characterized by (1) low generic diversity; (2) a predominance of morphologically simple, solitary forms with highly porous septa (*Nochoroicyathus* Zhuravleva) or additionally with plate tabulae (*Erismacoscinus* Debrenne), even during late Atdabanian–Botoman time; (3) an almost complete lack of forms with aporose septa during the Atdabanian-Botoman; (4) the absence of forms with pectinate tabulae; and (5) a prevalence of forms with synapticulae (*Afiacyathus* Voronin, *Sibirecyathus* Vologdin) (Perejón, 1984; Debrenne & Gandin, 1985; Debrenne & Jiang, 1989; Debrenne, Gandin, & Debrenne, 1993; Yang & others, 2005; Perejón & Moreno-Eiris, 2006).

SALINITY

Archaeocyaths were stenohaline organisms. Increased salinity impoverished archaeocyathan communities; only the simplest forms, with simple walls and porous septa, tolerated more saline conditions. Archaeocyaths could survive in lime muds deposited during brief salinity decreases, although not in evaporitic environments.

Such a trend has been observed on the Siberian Platform, particularly in the *Cari-*

nacyathus pinus Zone (Atdabanian). Along the Lena River, westward shallowing and associated salinity increase is accompanied by a drastic drop in species diversity and changes in the distribution of archaeocyathan skeletal features (DEBRENNE & ZHURAVLEV, 1996, fig. 1).

The same salinity intolerance is observed in South Australia in the direction of the formerly lagoonal northern Lake Torrens area (upper Andamooka Limestone), by comparison with the correlative marine Wirrealpa Limestone in the Flinders Ranges.

Siberian and Australian archaeocyathan communities inhabiting equivalent high-salinity environments comprise species of the same genera (*Nochoroicyathus* ZHURAVLEVA) with similar morphological features (highly porous septa and spinose walls), despite the great distance separating these regions. Taxonomic similarity among archaeocyathan communities was thus dependent upon environmental as well as phylogenetic and dispersive factors.

BATHYMETRY

The depth zonation proposed by ZHURAVLEVA and ZELENOV (1955)—cited in the revision of Part E of the *Treatise on Invertebrate Paleontology* (HILL, 1972, fig. 26) and still occasionally quoted—of archaeocyathan growth between 10 and 100 m depth is no longer accepted for normal archaeocyathan-calcimicrobial buildups. The use of calcimicrobes as depth indicators was rejected by RIDING (1975) on the basis of uncertainties in both growth limits and taxonomic affinities of the claimed calcimicrobial depth indicators.

Archaeocyaths were stenobathic organisms. They lived anchored in soft substrates in intertidal to subtidal zones but probably did not occupy the subphotic zone. Their preference for shallow water is evidenced by (1) their development mainly in carbonate-dominated lithofacies; (2) their common association with ooid and bioclast limestones; (3) their association with siltstone and quartz arenite exhibiting oscillation and interference ripples and other tidal-flat features, indicating nearshore settings; (4) their common occurrence interbedded with a variety of hemispheroidal stromatolites and oncoids (ROWLAND, 1981; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; PEREJÓN & others, 2000; HICKS & ROWLAND, 2009; GANDIN & DEBRENNE, 2010); and (5) the coexistence of macroboring organisms in Labrador patch reefs (JAMES & KOBLUK, 1978).

On the Siberian Platform, there is a progressive basinward disappearance and eventual termination of archaeocyaths in bioherms. In the Tommotian stage, only solitary *Archaeolynthus* TAYLOR and *Nochoroicyathus* ZHURAVLEVA have been reported from the outer shelf facies (KHOMENTOVSKIY & KARLOVA, 1986; PEL'MAN & others, 1990). The Atdabanian distal assemblage was more diverse, as it reflects the general archaeocyathan diversification at that time. *Propriolynthus* OKUNEVA, *Batschykicyathus* ZHURAVLEV, *Nochoroicyathus* ZHURAVLEVA, *Tumulocyathus* VOLOGDIN, *Geocyathus* ZHURAVLEVA, *Jakutocarinus* ZHURAVLEVA, *Japhanicyathus* KORSHUNOV, *Fansycyathus* KORSHUNOV & ROZANOV, and *Coscinocyathus* BORNEMANN were present, for example, in the middle Atdabanian (*Carinacyathus pinus* Zone) in the facies seaward of a carbonate barrier. But again, this assemblage was poor by comparison with the reef belt proper and deeper backreef facies; it completely lacked any modular or irregular forms. Additionally, the distal archaeocyathan assemblage was restricted mainly to biohermal cavities. Archaeocyaths were completely absent from the deepest buildups, which were stromatactis-bearing mudmounds (ZHURAVLEV, 2001c).

From the abundance of spicules (hexactinellide, calcarean, and heteractinide), it seems that basinward, spiculate sponges dominated over calcified sponges during the early Cambrian (DEBRENNE & ZHURAVLEV, 1996). In the Flinders Ranges of South Australia (JAMES & GRAVESTOCK, 1990), on the Siberian Platform, and in Mongolia (ZHURAVLEV, 2001c; ZHURAVLEV & NAIMARK, 2005), these spicule-archaeocyath assemblages appear to be restricted to deeper water settings. Elsewhere in South Australia, isolated bioherms in the upper Sellick Hill Formation and lower Fork Tree Limestone were deposited in deep water on a mildly unstable ramp adjoining a shallow shelf (Alexander & Gravestock, 1990). They contain an oligotypic fauna dominated by ajacicyathides, with extensive development of exocyathoid buttresses (Debrenne & Gravestock, 1990). This community appears relatively undifferentiated in comparison to the coeval shallower water community in the uppermost Kulpara Formation and lowermost Parara Limestone (Zhuravlev & Gravestock, 1994).

The striking characteristic of these deeper communities is the extreme development of secondary skeletal structures in practically all species. A similar behavior has been observed in the deepest bioherms of the Tommotian stage of the Siberian Platform (Kruse, Zhuravlev, & James, 1995), but in archaeocyathide archaeocyaths (*Dictyocyathus* Bornemann) only.

Toward the shallower limit of the archaeocyathan depth range, episodic erosional events can be demonstrated for archaeocyathan settings in only a few cases: the Punta Manna Member of the Nebida Formation, Sardinia (Selg, 1986; Debrenne, Gandin, & Pillola, 1989) and the upper Tommotian portion of the Tyuser Formation, Khara-Ulakh Mountains, Siberian Platform (Zhuravleva, 1966). In the latter, a distinctive archaeocyathan strategy consists of *Dictyocyathus* Bornemann encrusting the biohermal surface (Debrenne & Zhuravlev, 1996, fig. 2).

WATER ENERGY AND TURBIDITY

As passive filter feeders, archaeocyaths were more adapted to habitats with reduced turbulence and increased currents and nutrient supply, as are extant calcified sponges (Wilkinson & Evans, 1989). The dominance of certain morphological features within some archaeocyathan communities might be due to local environmental conditions such as turbulence, detrital input, or volcanic ashfall (Pratt & others, 2001; Zhuravlev, 2001c).

Clathrate outer walls, associated with complex inner walls, have been ascribed to volcanogenic facies (e.g., Verkhnemonok Formation of West Sayan; Ust'toka unit of Dzhagdy Range, Russian Far East; Cymbric Vale Formation of New South Wales, Australia) (Repina & others, 1964; Belyaeva & others, 1975; Kruse, 1982). However, where present in these facies, archaeocyaths are preserved in pure limestone. Although *Botomocyathus* Zhuravleva, the most widespread clathrate genus, was typical of Siberian Platform areas where volcanic rock was totally absent, a significant input of siliciclastic and sometimes of tuffaceous particles, combined with agitated water conditions, characterized many of these areas.

Putapacyathida also show an association with volcanogenic facies (West Sayan and New South Wales) (Debrenne, Rozanov, & Zhuravlev, 1990, table 9).

Other types of complex outer and inner walls (e.g., in *Ethmophyllum* Meek, *Sekwicyathus* Handfield, *Aulocricus* Debrenne, *Cordilleracyathus* Handfield) were, with few exceptions, typical of Laurentia, especially throughout the Cordillera. A significant terrigenous input has been noted for most localities there (Morgan, 1976; Debrenne, Gandin, & Rowland, 1989; Mount & Signor, 1992; Mansy, Debrenne, & Zhuravlev, 1993). These complex outer wall systems [downwardly oriented bract, intrapore spine(s), or V-shaped canal] could be interpreted as a resistant screen preventing the clogging of pores by terrigenous particles.

In the Achchagyy Tuoydakh–Churan profile along the Lena River, Siberia, modular forms and species with sparsely porous to aporose septa were evidently more frequent in shallower platform areas with greater current activity. In contrast, species with compound outer and inner walls were dominant eastward, in deeper environments with gentler ambient currents. Seemingly, the compound outer wall enhanced the inhalant flow by narrowing the pore area, while complex inner walls enhanced the initial velocity of the exhalant water jet, reducing the possibility of recycling the used water (Debrenne & Zhuravlev, 1996, fig. 1).

ARCHAEOCYATHAN INTERACTIONS

Archaeocyathan skeletons display a variety of reactions in response to the proximity of other species (Brasier, 1976; Kruse, 1990a; Debrenne & Zhuravlev, 1992b, p. 163, 1994; Wood, Zhuravlev, & Debrenne, 1992). These range from a simple intraspecific competition between two individuals with antagonistic rejection and atrophy of the weaker (Ajacicyathida-Ajacicyathida; Fig. 523b), to an acute rejection and resorption (Archaeocyathida-Ajacicyathida). The competitive superiority of the Archaeocyathida over the Ajacicyathida was presumably due to the former's possession of a more mobile aquiferous system (Debrenne & Zhuravlev, 1992b, p. 99), related to their morphofunctional dissimilarity in distribution of soft tissue. On contact, the archaeocyathide cup overgrew the ajacicyathide and usually completely suppressed it by ultimately obscuring it with secondary thickening (Fig. 523c–d).

Archaeocyathides were more compatible with each other in both conspecific and interspecific interactions than were other orders. Their relationships may be interpreted as mutualism. In Archaeocyathida-Archaeocyathida interactions, secondary skeletal layers were generally developed on both individuals in the immediate area of contact. Complete fusion could be achieved in the interaction of several branching units of the same archaeocyathide modular form.

The dominance of solitary forms among the Ajacicyathida is the consequence of their high degree of individualization, which is itself tied to the pattern of soft tissue distribution in the cup. Being passive filter feeders using an elaborate skeletal sieve system, ajacicyathides could presumably pump at fairly low exhalant and inhalant velocities. Consideration of similar extant sponges (Reiswig, 1971) shows that such forms were resistant to the occlusion of their incurrent system. Among the Archaeocyathida, the sealing of all basal ostia by secondary skeleton was also a response to high sedimentation rates in order to prevent sediment infiltration into the choanoderm (Debrenne & Zhuravlev, 1992b, p. 62; Krautter, 1994).

Modular archaeocyathides and dendritic renalcid calcimicrobes (*Gordonophyton* Korde*, Tubomorphophyton* Korde) evidently outcompeted solitary ajacicyathides, but even the modular archaeocyathides were locally subdued by the renalcids. In turn, ajacicyathides, as well as their superiors, were able to outcompete chambered and tubular renalcids and stromatolite-associated noncalcified microbes (Zhuravlev, 2001c).

Massive modular Kazachstanicyathida were especially successful, because of the considerable flexibility of their aquiferous system (Debrenne & Zhuravlev, 1992b, pl. 38,*5*).

BIOCONSTRUCTION

The bioconstructional capacity of archaeocyaths has been documented in many recent works, representing all regions and spanning their appearance in the Tommotian to their virtual demise in the Toyonian (Zhuravleva, 1960b, p. 59, 1966, 1972a; James & Kobluk, 1978; James & Klappa, 1983; Gandin & Debrenne, 1984, 2010; Rowland, 1984; Rowland & Gangloff, 1988; Debrenne, Gandin, & Rowland, 1989; James, Kobluk, & Klappa, 1989; Rees, Pratt, & Rowell, 1989; James & Gravestock, 1990; Debrenne, Gandin, & Zhuravlev, 1991; Kennard, 1991; Kruse, 1991; Wood, Zhuravlev, & Chimed Tseren, 1993; Kruse, Zhuravlev, & James, 1995; Riding & Zhuravlev, 1995; Kruse & others, 1996; Zhuravlev, 1996, 2001c; Wood, 1999; Copper, 2001; Pratt & others, 2001; Rowland & Shapiro, 2002;

Kiessling, Flügel, & Golonka, 2003). The resultant bioconstructions (meter-scale mounds) all had the same basic plan and can be categorized into component domains occupied by associations of lime mud, archaeocyaths, renalcid calcimicrobes, and/or cement. Whereas the frame-building capacity of solitary archaeocyaths was low, modular archaeocyaths did produce genuine framework, particularly in the later early Cambrian. Additionally, both types provided substrate for the frame-building renalcids and/or cement, as well as furnishing additional opportunities for cavity development.

Calcimicrobial-archaeocyathan bioconstructions may be termed reefs *sensu lato*, but most are strictly bioherms, having topographic relief and biogenic framework, but of uncertain capacity for wave resistance. The majority probably grew in mesotrophic to mildly eutrophic waters, with the relative dominance of archaeocyaths or renalcids and other associated organisms determined by nutrient and terrigenous siliciclastic input, wave energy, sedimentation rate, and depth (Wood, Zhuravlev, & Debrenne, 1992; Wood, Zhuravlev, & Chimed Tseren, 1993). Sedimentologically, archaeocyathan reefs were similar to later Phanerozoic reefs in possessing synoptic relief, synsedimentary cements, and growth-framework cavities housing cryptobionts (James & Klappa, 1983; Kruse, Zhuravlev, & James, 1995; Zhuravlev & Wood, 1995). Among the archaeocyaths, Ajacicyathida were highly competitive, and their incompatibility often involved spatial separation between adjacent cups, preventing them from becoming good binders (Debrenne & Zhuravlev, 1992b, p. 164; Wood, Zhuravlev, & Debrenne, 1992). Their elaborate skeletal sieve system allowed them to proliferate on mud substrates, in habitats with low turbulence and a high sedimentation rate, where the probability of pore clogging was high (Wood, Zhuravlev, & Debrenne, 1992; Wood, Zhuravlev, & Chimed Tseren, 1993). They populated the immediate periphery and the internal cavities of reefs where calcareous mud is dominant (Debrenne, Gandin, & Debrenne, 1993). In contrast, in Archaeocyathida and Kazachstanicyathida, the development of secondary skeleton, distal localization of living tissue, and greater integration favored modularity over individualization and hence a greater tolerance to the proximity of other species. This enhanced their bioconstructional capability as binders and bafflers (Wood, Zhuravlev, & Debrenne, 1992). Such capacities allowed the archaeocyathides to constitute up to 99% of the total archaeocyathan population in some bioherms (Debrenne, Gandin, & Gangloff, 1990).

Within early Cambrian reefs, the two groups engaged in competition for space, with resultant suppression of weaker individuals (Debrenne & Zhuravlev, 1992b; Wood, Zhuravlev, & Debrenne, 1992; Kruse, Zhuravlev, & James, 1995; Zhuravlev & Wood, 1995; Zhuravlev, 1996). Direct overgrowth of one organism by another led to incomplete or even pathological development of the primary skeleton, extreme production of secondary skeleton, especially along mutual contacts, and/or dwarfing or complete immuration of the weaker competitor.

Together with archaeocyaths, coralomorphs (e.g., *Cysticyathus* Zhuravleva, *Hydroconus* Korde), radiocyaths, cribricyaths, and especially renalcid calcimicrobes (e.g., *Renalcis* Vologdin, *Epiphyton* Bornemann) were common constituents in early Cambrian reefs. Archaeocyath-coralomorph and archaeocyath-radiocyath interactions show no hierarchy. All these organisms used each other as a substrate.

Exceptionally, cribricyaths appear to have considerably disrupted archaeocyathan growth (Debrenne & Zhuravlev, 1992b, pl. 38,*6*), suggesting that cribricyaths facultatively behaved as parasites on archaeocyaths. This observation contradicts the view that cribricyaths may have been a type of archaeocyathan larva (Zhuravleva &

OKUNEVA, 1981; BELYAEVA, 1985; BELYAEVA & ZHURAVLEVA, 1990).

The relationship between archaeocyaths and renalcid calcimicrobes was more varied. Renalcids were tiny, dendritic (*Epiphyton* BORNEMANN, *Gordonophyton* KORDE, *Tubomorphophyton* KORDE), chambered (*Chabakovia* VOLOGDIN, *Renalcis* VOLOGDIN, *Tarthinia* DROZDOVA), fanlike (*Bija* VOLOGDIN), or tubular (*Batinevia* KORDE, *Girvanella* NICHOLSON & ETHERIDGE, *Razumovskia* VOLOGDIN) calcareous organisms. Their simple morphology and common facultative occurrence in reef cavities imply that they were calcified bacteria, probably cyanobacteria (RIDING, 2001). Conversely, their distinct microgranular microstructure, typical of eukaryotes (ROZANOV & SAYUTINA, 1982), the appearance of obligate cryptobionts (ZHURAVLEV & WOOD, 1995), and the lack of vital effects on carbon isotopic values (SURGE & others, 1997) do not favor a cyanobacterial assignment.

All these factors tended to displace the ajacicyathides toward marginal, at times harsh, environments (extremely shallow, deep, agitated, or turbid).

This engendered three principal associations: modular archaeocyaths and *Gordonophyton-Tubomorphophyton* occupying optimal niches; solitary ajacicyathides and *Renalcis-Tarthinia* in intermediate locales; and skeletal and nonskeletal stromatolites in marginal settings (ZHURAVLEV, 2001c).

Branching forms (e.g., *Cambrocyathellus* ZHURAVLEVA) were mainly bafflers, whereas encrusting (e.g., *Retilamina* DEBRENNE & JAMES) and massive examples (e.g., *Korovinella* RADUGIN) were binders. Colonization by encrusting and massive archaeocyaths required a hard substrate.

Reefs were either dominantly renalcid calcimicrobial or (rarely) dominated by metazoans (ZAMARREÑO, 1977; GANDIN & DEBRENNE, 1984; SELG, 1986; STEPANOVA, 1986; DEBRENNE, GANDIN, & ROWLAND, 1989; REES, PRATT, & ROWELL, 1989; DEBRENNE & GRAVESTOCK, 1990; JAMES & GRAVESTOCK, 1990; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; MORENO-EIRIS, 1994). Indeed, historically, Tommotian archaeocyaths initially invaded purely calcimicrobial reefs, which had first proliferated in the preceding basal Cambrian Nemakit–Daldynian stage.

Reefs were presumably initiated during episodes when mud input slowed or ceased, allowing localized cementation or stabilization of seafloor mud (KRUSE, ZHURAVLEV, & JAMES, 1995; RIDING & ZHURAVLEV, 1995; ROWLAND & SHAPIRO, 2002). The large monospecific domains that formed the bulk of many biohermal communities suggest that archaeocyathan larvae were of viviparous origin, as they apparently did not travel far after release. This reproductive strategy is typical of sponges and other sessile organisms subject to high disturbance (AYLING, 1980; HOPPE, 1988).

The early Cambrian reef ecosystem was largely composed of generalists and opportunistic filter- and suspension-feeders, which were dependent upon a relatively high supply of nutrients. Many reefs were dominated by only one or two archaeocyathan species, implying that these communities were the result of rapid colonization and subsequent growth from one or a few larval spat falls (WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993). Such trophic organization is similar to some other Paleozoic reefs, but contrasts fundamentally with some Mesozoic and most Cenozoic (both fossil and living) reefs, which are dominated by mixo- and phototrophs adapted to low-nutrient conditions (WOOD, 1993, 1995, 1999).

ZHURAVLEV (2001c) has proposed an ecological succession for these early Cambrian reefs: (1) settlement on muddy substrate of solitary ajacicyathides tolerant of turbid conditions (pioneer stage); (2) encrusting of resulting floatstone-rudstone by modular archaeocyaths to produce framework (stabilization stage); (3) strengthening of framework by binding *Renalcis* VOLOGDIN and occupation of reef cavities by an array of monocyathides, capsulocyathides, cribricyaths, and boring organisms (diversification stage); (4) either via intrinsic reef growth or extrinsic sea level fall, growth into the marginal peritidal or surf zone, with development of a species-impoverished, commonly monospecific, archaeocyathan community (e.g., *Protopharetra*-"*Paranacyathus*" community in the Poleta Formation at Stewart's Mill, Nevada, United States; Rowland & Shapiro, 2002). Despite their small size, a number of early Cambrian reefs represent such complete ecological successions. Others were initiated and dominated by calcimicrobes, with archaeocyaths as subordinate dwellers contributing only modestly to reef construction.

Cryptic cavities have provided archaeocyaths with a hard substate since their inception. Cavities and cavity dwellers have been described in reefs (Kobluk & James, 1979), among them a large variety of archaeocyaths, some of which are thought to have been obligate cryptobionts, e.g., thalamid forms such as *Polythalamia* Debrenne & Wood (Capsulocyathida) and *Altaicyathus* Vologdin (Kazachstanicyathida), and archaeocyaths of chaetetid organization, such as *Usloncyathus* Fonin (Zhuravlev & Wood, 1995).

Cryptic niches are not limited to reefs. A remarkable cryptic community in the Ovetian (Atdabanian) Pedroche Formation of southern Spain comprises archaeocyaths and other cryptobionts encrusting the walls and ceilings of crevices formed during synsedimentary fracturing of Neoproterozoic andesite (Vennin & others, 2003). These cavity dwellers additionally represent the earliest known metazoan rocky community.

It may be that archaeocyathan-calcimicrobial competitive interactions, in which dendritic renalcids were dominant, contributed to the eventual near-total elimination of archaeocyaths from the Cambrian reef biota in the Toyonian stage (Zhuravlev, 1996).

PALEOBIOGEOGRAPHY

Global archaeocyathan distribution was fundamentally controlled by the availability and mutual proximity of normal-marine carbonate depositional tracts. Resulting biogeographic patterns were influenced by rapid tectonic changes, particularly those accompanying rifting (Lieberman, 1997; Zhuravlev & Maidanskaya, 1998; Debrenne, Maidanskaya, & Zhuravlev, 1999), as well as by evolution within the group, leading to the frequent appearance of short-lived, specialized, endemic taxa (Naimark & Rozanov, 1997).

Among global paleogeographic reconstructions proposed for the early Cambrian (e.g., Rozanov, 1984; Zonenshain, Kuzmin, & Kononov, 1985; Scotese & McKerrow, 1990; Courjault-Radé, Debrenne, & Gandin, 1992; Kirschvink, 1992; McKerrow, Scotese, & Brasier, 1992; Storey, 1993; Dalziel, Dalla Salda, & Gahagan, 1994; Torsvik & others, 1996; Kirschvink, Ripperdan, & Evans, 1997; Lieberman, 1997; Smith, 2001; Golonka, 2002; Meert & Lieberman, 2008; Rino & others, 2008), those that best fit the archaeocyathan distribution portray a post-supercontinental world (Rodinian or Pannotian) with the major epicontinental basins within the intertropical zone. The inferred pathways of archaeocyathan migration, coupled with the use of the Jaccard similarity coefficient applied to the total local Cambrian faunas, calculated for Nemakit-Daldynian–early Tommotian, early Atdabanian, and late Atdabanian–Botoman intervals, support those paleogeographic reconstructions suggesting the existence of East and West Gondwana in the early Cambrian, as proposed by Moores (1991) and Kirschvink (1992), with their subsequent collision by the late early Cambrian (Cawood, 2005; Paulsen & others, 2007), the rifting of Laurentia from the Australian-Antarctic margin, and the drift of suspect terranes toward Siberia (Debrenne, Maidanskaya, & Zhuravlev, 1999). Terrane theory, with the prospect of more complex models incorporating suspect terranes and drifting microcontinents (Coney, Jones, & Monger, 1980), provides further options for the reconstruction of archaeocyathan paleobiogeography.

Archaeocyaths appeared within the transitional Anabar–Sinsk tract of the Siberian Platform at the beginning of the Tommotian stage and had dispersed to the Altay Sayan Fold Belt (East Sayan and Kuznetsk Alatau) and Far East (Shevli Basin) only by the very end of this stage. The Siberian Platform, the first center of archaeocyathan diversification (ROZANOV, 1980), was located at low latitudes, mostly south of the paleoequator and was geographically inverted relative to its present position (COCKS & TORSVIK, 2007).

A longstanding puzzle has been the relatively late appearance of archaeocyaths in suitable lithofacies in Altay Sayan, Transbaikalia, Mongolia, and other nearby areas, together with the organization of archaeocyathan assemblages in distinct circumplatformal belts according to age and composition. Three sets of terranes are currently recognized in the archaeocyath-bearing regions of present Central Asia: Kazakhstan terrane group (Kazakhstan-Turkmenistan-Tajikistan-Kyrgyzstan), Altay Sayan–Transbaikalia-Mongolia terranes, and Far East terranes (KHAIN & others, 2003; KHERASKOVA & others, 2003; SENNIKOV & others, 2004; COCKS & TORSVIK, 2007; GORDIENKO & others, 2007). Overall, Central Asia is a complex of accretionary (Altay, Sayans, Transbaikalia, Mongolia, Kazakhstan) and collisional terranes (northern China, southern Mongolia, Dzhungaria, southern Tien Shan, northern Pamir). Their appearance has been linked to the postulated development of several paleooceans (ZONENSHAIN, KUZMIN, & KONONOV, 1985; KHERASKOVA & others, 2003), of which the earliest Paleoasian Ocean was probably never wide. Intense tectonism, including volcanism, took place in the latest Ediacaran and earliest Cambrian along the northern periphery of East Gondwana, where a rift-to-drift transition involved a number of Central Asian microcontinents (e.g., Zavkhan, Tuva-Mongolia, South Gobi, North Tien Shan). Tectonic and sedimentological analyses suggest that these blocks drifted from northwestern East Gondwana toward Siberia during that interval (KHERASKOVA & others, 2003; COCKS & TORSVIK, 2007). Paleomagnetic and paleontological data have further confirmed and constrained this scenario (ZHURAVLEV & MAIDANSKAYA, 1998; METELKIN & KAZANSKIY, 2002; MIKHAL'TSEV, KAZANSKIY, & SENNIKOV, 2002).

Other regions were not suitable for archaeocyathan colonization at that time, with phosphate-rich sedimentation prevailing in northern peri-East Gondwana terranes (Yangtze, Mongolia, and Kazakhstan) and West Gondwana (West Africa and Iberia [PARRISH & others, 1986; VIDAL, MOCZYDŁOWSKA, & RUDAVSKAYA, 1995; CULVER & others, 1996]), extensive evaporite basins in subequatorial parts of Siberia (Turukhansk-Irkutsk-Olekma tract) and northern West Gondwana (Oman–southern Iran–Saudi Arabia, northern Pakistan [WOLFART, 1983; ASTASHKIN & others, 1991]), and mainly fluviatile and deltaic siliciclastic sediments elsewhere (HOLLAND, 1971, 1974; GANDIN, MINZONI, & COURJAULT-RADÉ, 1987; ROZANOV & ŁYDKA, 1987; COOK, 1988; LANDING & others, 1988; FRITZ & others, 1991; BORDONARO, 1992; PILLOLA & others, 1994).

During the first half of the Atdabanian Stage, when marine transgression generated widespread carbonate sedimentation in the Altay Sayan Fold Belt, Mongolia, Iberia, Germany, Poland, Morocco, and Australia (SHERGOLD & others, 1985; MORENO-EIRIS, 1987; ASTASHKIN & others, 1991, 1995; ELICKI, 1995; GEYER, LANDING, & HELDMAIER, 1995; BIAŁEK & others, 2007; ÁLVARO & others, 2010), archaeocyaths of Siberian affinity (e.g., *Sibirecyathus* VOLOGDIN, *Geocyathus* ZHURAVLEVA, *Retecoscinus* ZHURAVLEVA, *Capsulocyathus* VOLOGDIN, *Dictyocyathus* BORNEMANN) reached western Europe (Normandy, Spain) and Morocco, where a new center of diversification developed and endemic forms appeared. ROZANOV'S (1984) and MCKERROW, SCOTESE, and BRASIER'S (1992) paleogeographic reconstructions showing a close proximity of Siberia to the northern West Gondwana margin are consistent with a postulated Siberian-Euro-Moroccan archaeocyathan dispersal pathway. Avalonia was unsuitable for archaeocyaths due to its temperate location (LANDING & MACGABHANN, 2010).

By the terminal Atdabanian and initial Botoman stages, continued transgression had finally initiated carbonate accumulation and hence archaeocyathan proliferation on Yangtze, Australia, and Laurentia. Archaeocyaths migrated along the northern periphery of West Gondwana from the European-Moroccan center of diversification, and via Mongolia and Kazakhstan, to populate Yangtze. (Note that archaeocyaths reported from intervening Sinai and Iran by OMARA [1972], BASAHEL and others (1984), MEL'NIKOV and others [1986], and LASEMI and AMIN-RASOULI [2007] should be discounted, as the Iranian so-called archaeocyaths are eocrinoids, spiculate demosponges, microbialites, and ooids, whereas the Sinai material could be the enigmatic, tubelike *Cloudina* GERMS. As well, putative Himalayan archaeocyaths have proved to be microstromatolites [DEBRENNE, GANGLOFF, & ZHURAVLEV, 1990]). A number of genera, for example, *Rasetticyathus* DEBRENNE, *Porocoscinus* DEBRENNE, *Rudanulus* DEBRENNE, and *Spirillicyathus* R. BEDFORD & J. BEDFORD, were restricted or almost exclusive to Yangtze, western Europe–Morocco, and/or Australia (DEBRENNE & JIANG, 1989). By the end of the Botoman Stage, archaeocyaths had dispersed from Australia to Antarctica, where some 50% of species were in common with the former (DEBRENNE & KRUSE, 1986, 1989; WRONA & ZHURAVLEV, 1996; KRUSE & SHI in BROCK & others, 2000).

Australia became one of the principal Botoman centers of diversification (ROZANOV, 1980; DEBRENNE & ZHURAVLEV, 1992b, fig. 40c). Archaeocyathida with outer wall canals (*Warriootacyathus* GRAVESTOCK) and subdivided canals (*Beltanacyathus* R. BEDFORD & J. BEDFORD, *Ataxiocyathus* DEBRENNE, *Maiandrocyathus* DEBRENNE), as well as erismacoscinines with attached microporous sheath (*Polycoscinus* R. BEDFORD & J. BEDFORD), were restricted entirely to this center of diversification. A possible independent center of diversification, the Russian Far East, was proposed by BELYAEVA (1987). Some centers of diversification are also characterized by the presence of peculiar forms difficult to place in the classification system, for example, *Eremitacyathus* ZAMARREÑO & DEBRENNE in Spain, *Retilamina* DEBRENNE & JAMES in North America.

By the late Atdabanian, the Cordilleran margin of Laurentia crossed the paleoequator, providing suitable conditions for archaeocyathan settlement. At the same time, Laurentia and Siberia moved toward each other, facilitating faunal migration. The first Laurentian archaeocyaths probably originated from Australian stock: *Metaldetes* TAYLOR, *Metacyathellus* DEBRENNE & ZHURAVLEV, *Sigmofungia* R. BEDFORD & W. R. BEDFORD, and *Pycnoidocoscinus* R. BEDFORD & W. R. BEDFORD are known only from these two regions (MANSY, DEBRENNE, & ZHURAVLEV, 1993). By the end of the Botoman Stage, the distance between Laurentia and Siberia was not great, facilitating migration of common genera and perhaps even species (*Tegerocyathus* KRASNOPEEVA, *Krasnopeevaecyathus* ROZANOV, *Polythalamia* DEBRENNE & WOOD, *Claruscoscinus* HANDFIELD). Laurentia, in turn, became a center of diversification (ROZANOV, 1980; DEBRENNE & ZHURAVLEV, 1992b, fig. 40c).

Further northward movement of Laurentia allowed archaeocyaths and other reef-building organisms to spread to the Appalachian margin, while simultaneously they were significantly reduced along its Cordilleran margin (DEBRENNE, MAIDANSKAYA, & ZHURAVLEV, 1999; MCMENAMIN, DEBRENNE, & ZHURAVLEV, 2000).

Early Cambrian transgression attained its maximum in the Botoman Stage, leading to the relative isolation of those regions inhabited by archaeocyaths. Archaeocyathan endemicity was thus greatest at that time. The percentage of endemic genera in the various centers of diversification was 22% in Europe-Morocco, 21% in Australia-Antarctica and 38% in Laurentia (DEBRENNE & ZHURAVLEV, 1992b, p. 96). Similarly, archaeocyathan gamma diversity, which expresses the degree of provinciality, was highest in the Botoman and indicates that geographic isolation was among the major factors controlling archaeocyathan diversification. A further factor was environmental heterogeneity, as revealed by beta diversity analysis. Again, beta diversity was highest in the Botoman (ZHURAVLEV & NAIMARK, 2005, fig. 2a, 3). On this collective basis, an early Cambrian paleogeographic division, based on archaeocyaths, into Afro-Siberian-Antarctic and American-Koryakian provinces was suggested (ZHURAVLEV, 1986a) and since employed by other authors (GANGLOFF, 1990; DEBRENNE & ZHURAVLEV, 1992b, fig. 40d). This broad division has been confirmed by cluster analysis of more current generic distribution data, by which KRUSE and SHI (in BROCK & others, 2000) recognized two archaeocyathan realms, Eurasian and Lauraustral, the former embracing Siberia-Mongolia, Central–East Asia, and Europe-Morocco provinces, and the latter the Australia-Antarctica and North America–Koryakia provinces.

Intraprovincial lithofacies-based subdivision has been proposed by OSADCHAYA (1979) for the Altay Sayan Fold Belt. She recognized carbonate-, mixed siliciclastic-carbonate-, and mixed volcanic-carbonate-dominant provinces, the last two of which have recognizable counterparts in Mongolia (ZHURAVLEV, 1998).

The appearance of new centers of diversification does not seem to be associated only with regional isolation; the high Botoman endemism is also due to the rapid diversification of certain superfamilies (e.g., Ethmophylloidea in Laurentia, and Polycoscinoidea and Beltanacyathoidea in Australia). In addition, diverse and distinct genera appeared in both regions among the Metacyathoidea. All these superfamilies were characterized by complicated outer wall structures, which might have provided an improved screen, preventing the clogging of pores by particles, as discussed above. Thus, inferred unsuitable conditions might have increased the specialization rate within these taxa and consequently contributed to endemicity.

On the whole, the Atdabanian–Botoman witnessed the greatest extent of carbonate platforms in the entire early Cambrian, facilitating extensive calcimicrobial-archaeocyathan reef building within the belt extending 30° to either side of the paleoequator (DEBRENNE & COURJAULT-RADÉ, 1994).

The middle Botoman peak of the early Cambrian transgression was marked by extensive accumulation of black shale and black, thin-bedded limestone in low latitudes: Siberia, some microcontinents of the Altay Sayan Fold Belt, Transbaikalia, Russian Far East, Kazakhstan, Iran, Turkey, South Australia, Yangtze (CHEN & others, 1982; SHERGOLD & others, 1985; ASTASHKIN & others, 1991, 1995; HAMDI, 1995). These deposits reflected an anoxic-dysoxic event adversely affecting archaeocyathan communities (ZHURAVLEV & WOOD, 1996). Seemingly, archaeocyaths survived this event in refugia, some of which were island arcs, in West Sayan and Tuva of the Altay Sayan Fold Belt, the Dzhagdy Basin of the Russian Far East, Kazakhstan, and some regions of Australia, where the most complete Botoman record of archaeocyathan assemblages is preserved. The late Botoman archaeocyathan fauna included abundant Erbocyathoidea, Tercyathoidea, Claruscoscinidae, and Kazachstanicyathida.

The late Botoman–Toyonian probably coincides with the major early Cambrian regression, variously termed in different regions the Hawke Bay, Daroca, or Toyonian regression. The Toyonian sedimentary record is characterized by widespread *Skolithos* piperock in Iberia, Morocco, eastern Laurentia, and other intertidal siliciclastic tracts of Baltica, the Midde East, and Laurentia. Sabkha conditions prevailed over large areas of Siberia, Australia, and Yangtze (PALMER & JAMES, 1980; BERGSTRÖM &

Ahlberg, 1981; Brangulis & others, 1986; Cook, 1988; Mel'nikov & others, 1989; Astashkin & others, 1991; Fritz & others, 1991; McCollum & Miller, 1991; Mansy, Debrenne, & Zhuravlev, 1993; Gozalo & others, 2007; Lasemi & Amin-Rasouli, 2007; Álvaro & Clausen, 2008). Together with the preceding anoxic-dysoxic event, this regression decimated the archaeocyaths and other invertebrate reef dwellers by substantially reducing the shallow marine platform area.

During the middle Toyonian, low-diversity archaeocyathan communities consisting mainly of surviving *Tegerocyathus* Krasnopeeva, *Archaeocyathus* Billings, and *Pycnoidocyathus* Taylor species became widespread (Debrenne & Zhuravlev, 1992b, fig. 40d).

A general foundering of carbonate and mixed-sedimentary ramps at the beginning of the middle Cambrian (Amgan stage) led to the virtual extinction of the archaeocyaths. This foundering was expressed in the accumulation of deeper-water (including black) shale in the Siberia, northern Mongolia–Transbaikalia, Russian Far East, and Kazakhstan terranes (Astashkin & others, 1991, 1995; Kheraskova & others, 2003). The postulated transition from coldhouse to greenhouse conditions during the late early to late middle Cambrian was probably also a major factor in this extinction (Zhuravlev & Wood, 2008; Landing & MacGabhann, 2010; Landing, 2011). Prior emission of greenhouse gases from the Botoman-age Kalkarindji continental flood basalt province of northern Australia offers a potential trigger for this warming (Glass & Phillips, 2006; Hough & others, 2006). In addition, drift of the European-Moroccan margin of Gondwana toward higher, temperate latitudes, beyond the limits of carbonate development (Courjault-Radé, Debrenne, & Gandin, 1992), no doubt hindered the reestablishment of archaeocyathan populations within this region. The same probably held true for Australia, due to a counterclockwise rotation of Gondwana (Kirschvink, 1992). Thus, Antarctica alone remained in low paleolatitudes, so furnishing both known species of post–early Cambrian archaeocyaths (Debrenne, Rozanov, & Webers, 1984; Wood, Evans, & Zhuravlev, 1992).

SYSTEMATIC DESCRIPTIONS: ARCHAEOCYATHA

F. DEBRENNE, A. YU. ZHURAVLEV, and P. D. KRUSE

Phylum PORIFERA Grant, 1836

Class ARCHAEOCYATHA Bornemann, 1884

[*nom. correct.* VOLOGDIN, 1937b, p. 464, *pro* Archaeocyathinae BORNEMANN, 1884, p. 706] [=class Archaeocyathinae TAYLOR, 1910, p. 105; =class Cyathospongia OKULITCH, 1935b, p. 88; =class Archaeocyathi R. BEDFORD & W. R. BEDFORD, 1936, p. 9; =subphylum Archaeocyatha VOLOGDIN, 1937b, p. 464 (Porifera); =class Pleospongia OKULITCH, 1943, p. 1; =phylum Archaeocyatha OKULITCH, 1955a, p. 8; =phylum Archaeocyathi KRASNOPEEVA, 1955, p. 17; =subphylum Euarchaeocyatha ZHURAVLEVA, 1960b, p. 79, *nom. transl.* ZHURAVLEV & others in SOKOLOV & ZHURAVLEVA, 1983, p. 6, *ex* class Euarchaeocyathi ZHURAVLEVA, 1960b, p. 79; =Salpingidea VOLOGDIN & YAZMIR, 1967, p. 1377; =phylum Archaeocyatha HILL, 1972, p. 2; =Euarchaeocyatha ZHURAVLEVA & MYAGKOVA, 1979, p. 521] [equivalent to superfamily Archaeocyathaceae SIMON, 1939, p. 5]

Skeleton nonspiculate, calcareous cup of microgranular microstructure and (with few exceptions) original magnesium calcite composition. Cup generally of archaeocyathan architecture with one or two porous walls bounding inner or central cavity respectively; porous to aporose septa, pseudosepta, taeniae, pseudotaeniae, pseudotaenial network, dictyonal network, syringes, and/or tabulae may form in intervallum; a minority are of chaetetid (intervallum with calicles) or thalamid architecture (cup consisting of successive chambers). Solitary or modular. Secondary calcareous skeleton may be present. [For an explanation of zonal terms used herein, see General Features of the Archaeocyatha, p. 909–912.] *Cambrian (Terreneuvian–Furongian).*

Order MONOCYATHIDA Okulitch, 1935

[*nom. correct.* OKULITCH, 1955a, p. 9, *pro* order Monocyathina OKULITCH, 1935b, p. 90] [=Archaeolynthida ZHURAVLEVA, 1957, p. 174; =Tectocyathida VOLOGDIN in VOLOGDIN & YAZMIR, 1966, p. 948; =suborder Globosocyathina OKUNEVA, 1969, p. 74; =suborder Monocyathina DEBRENNE, 1970a, p. 24; =Tecticyathida VOLOGDIN, 1977, p. 93]

Cup one walled, solitary or low modular; pelta may be present. [Within each (sub) order, superfamilies and constituent families are arranged in order of wall type.] *lower Cambrian (Tom.1–Bot.3).*

Family MONOCYATHIDAE R. Bedford & W. R. Bedford, 1934

[Monocyathidae R. BEDFORD & W. R. BEDFORD, 1934, p. 2] [=Rhabdocnemidae OKULITCH, 1943, p. 45, *nom. nov. pro* Rhabdocyathidae VOLOGDIN, 1931, p. 52, invalid family-group name based on junior homonym; =Archaeolynthidae ZHURAVLEVA, 1949, p. 550; =Monocyathinae ZHURAVLEVA, 1963b, p. 74, *nom. transl. ex* Monocyathidae R. BEDFORD & W. R. BEDFORD, 1934, p. 2; =Rhabdocyathellidae ZHURAVLEVA, 1963b, p. 114; =Capsolynthidae OKUNEVA, 1969, p. 75; =Crassicyathidae VOLOGDIN, 1977, p. 79; =Spinicyathidae VOLOGDIN, 1977, p. 103]

Wall with simple pores. *lower Cambrian (Tom.1–Bot.3).*

Archaeolynthus TAYLOR, 1910, p. 158 [**Monocyathus porosus* R. BEDFORD & W. R. BEDFORD, 1934, p. 2; SD R. BEDFORD & W. R. BEDFORD, 1936, p. 20; lectotype, R. BEDFORD & W. R. BEDFORD, 1934, fig. 1; ZHURAVLEVA, 1963b, fig. 39d; HILL, 1965, pl. 2,*1;* DEBRENNE, 1969a, pl. 1,*3;* DEBRENNE, 1974b, pl. 19,*1;* SD HILL, 1965, p. 52, NHM S4140, London] [=*Ventriculocyathus* VOLOGDIN, 1928, p. 31, *nom. nud.;* =*Ventriculocyathus* VOLOGDIN, 1931, p. 51 (type, *V. caulius,* M), for discussion, see HILL, 1965, p. 63; =*Monocyathus* R. BEDFORD & W. R. BEDFORD, 1934, p. 2 (type, *M. porosus,* SD R. BEDFORD & W. R. BEDFORD, 1936, p. 20; lectotype, HILL, 1965, pl. 2,*1;* SD HILL, 1965, p. 52, S4140, NHM, London); =*Rhabdocnema* OKULITCH, 1937a, p. 252, *nom. nov. pro Rhabdocyathus* VON TOLL, 1899, p. 45, *non* BROOK, 1893, cnidarian (type, *R. sibiricus,* M), for discussion, see HILL, 1965, p. 51; =*Rhabdocyathella* VOLOGDIN, 1937b, p. 474 (type, *R. lebedevae,* M), for discussion, see HILL, 1965, p. 53; =*Capsolynthus* OSADCHAYA in ZHURAVLEVA & others, 1967, p. 26 (type, *C. helenae,* OD); =*Corticicyathus* VOLOGDIN, 1977, p. 46 (type, *C. aequiporosus,* OD); =*Crassicyathus* VOLOGDIN, 1977, p. 79 (type, *C. canaliculatus,* OD); =*Tegminicyathus* VOLOGDIN, 1977, p. 98 (type, *T. simplex,* OD); =*Tytthocyathus* VOLOGDIN, 1977, p. 98 (type, *T. jenisseicus,* OD); =*Spinicyathus* VOLOGDIN, 1977, p. 103 (type, *S. cipis,* OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 94; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 133]. Wall pores of uniform size. *lower Cambrian (Tom.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Australia, Antarctica, Morocco, Iberia.——FIG. 524,*1a–b.* **A. porosus* (R. BEDFORD & W. R. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, NHM S4140; *a,* external

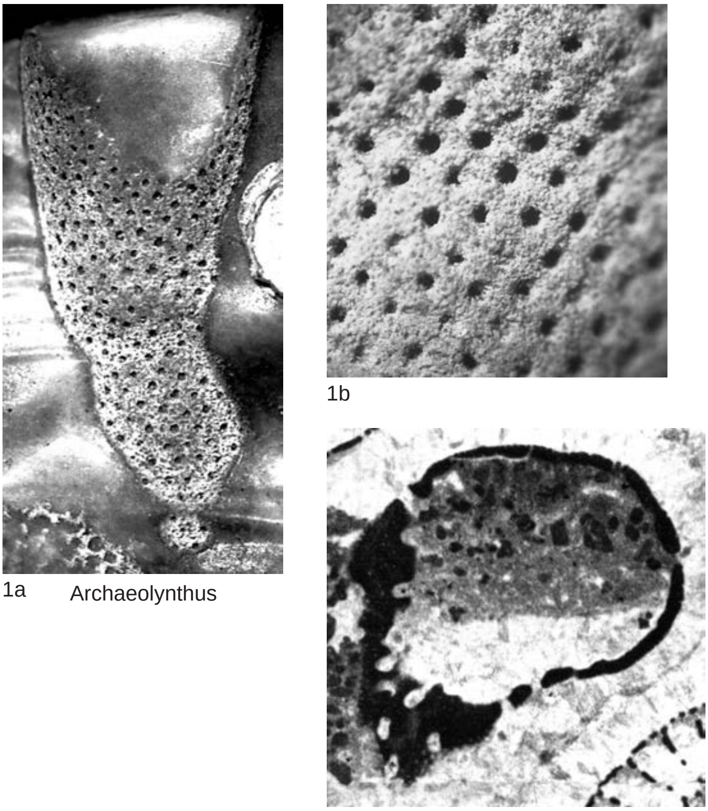


Fig. 524. Monocyathidae (p. 923–924).

longitudinal view of cup, ×5 (Hill, 1965); *b,* detail of porosity in external tangential view, ×10 (Debrenne, 1974b).

Kyarocyathus Kruse, 1982, p. 144 [**K. duplus*; OD; holotype, Kruse, 1982, fig. 7H–J, AM FT.8240, FT.8244, Sydney]. Wall pores of two distinct sizes. *lower Cambrian (Bot.1–Bot.2):* Mongolia, Australia.——Fig. 524,*2*. **K. duplus*, Mount Wright Volcanics, Botoman, Mt. Wright, New South Wales, Australia, AM FT.8240, FT.8244, oblique transverse section, ×10 (Kruse, 1982).

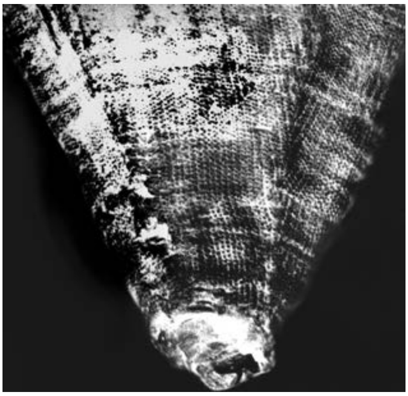
Family PALAEOCONULARIIDAE Chudinova, 1959

[Palaeoconulariidae Chudinova, 1959, p. 53] [=Debrennecyathidae Vologdin in Vologdin & Yazmir, 1966, p. 948, invalid family-group name based on unavailable genus name; =Debrennecyathidae Vologdin, 1977, p. 100]

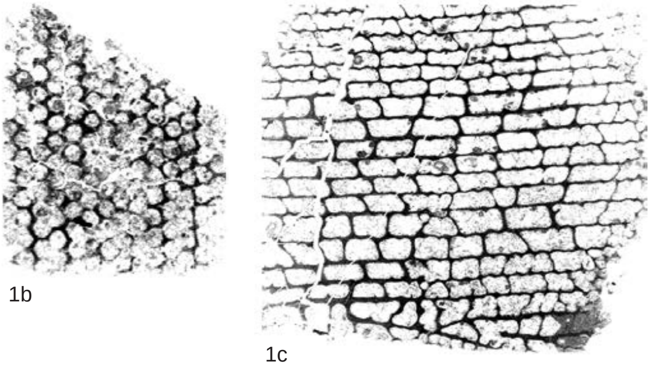
Wall with attached microporous sheath. *lower Cambrian (Atd.4–Bot.3).*

Palaeoconularia Chudinova, 1959, p. 53 [**P. prima*; OD; holotype, Chudinova, 1959, fig. 1–2, PIN 1577/1, Moscow] [=*Laminaecyathus* Yazmir in Vologdin & Yazmir, 1966, p. 948 (type, *L. triangulatus*, OD); =*Debrennecyathus* Vologdin in Vologdin & Yazmir, 1966, p. 948, *nom. nud.*, unavailable genus-group name without associated nominal species; =*Debrennecyathus* Vologdin, 1977, p. 101 (type, *D. pulcher*, OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 122; Debrenne, Rozanov, & Zhuravlev, 1990, p. 154]. Wall with reticulate carcass pores and attached microporous sheath. *lower Cambrian (Bot.1–Bot.3):* Altay Sayan, Tuva, Mongolia, Transbaikalia.——Fig. 525,*1a–c*. **P. prima*, Verkhnemonok Formation, Botoman, Karakol River, West Sayan, Altay Sayan, Russia, holotype, PIN 1577/1; *a,* external longitudinal view of cup, ×2; *b,* tangential section of microporous sheath, ×6; *c,* tangential section of carcass pores, ×11 (Chudinova, 1959).

?Butakovicyathus Zhuravleva, 1980, p. 175 [**B. butakovi;* OD; holotype, Zhuravleva, 1980, pl. 30,*1–2*, TsSGM 569, Novosibirsk]. Wall carcass pores of two distinct sizes with attached

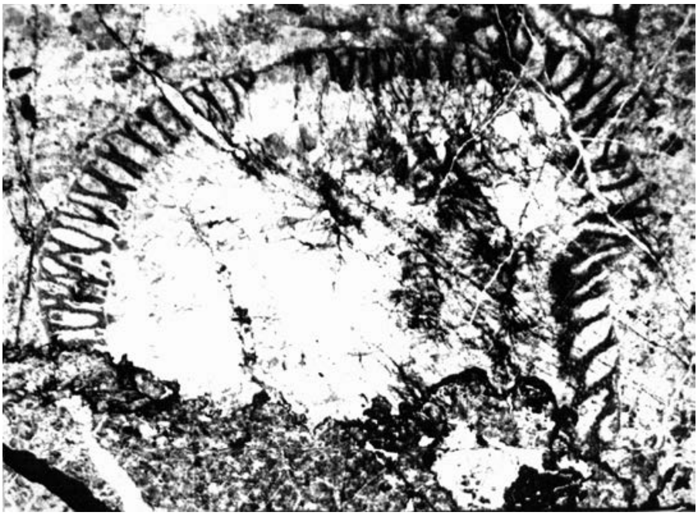


1a Palaeoconularia



1b

1c



2 Butakovicyathus

FIG. 525. Palaeoconulariidae (p. 924–926).

microporous sheath. [The single available section does not provide certainty as to wall structure.] *lower Cambrian (Atd.4–Bot.1):* Altay Sayan.——FIG. 525,*2*. **B. butakovi*, Krol Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia, holotype, TsSGM 569, transverse section, ×12 (Zhuravleva, 1980).

Family TUMULIOLYNTHIDAE
Rozanov, 1966

[Tumuliolynthidae ROZANOV in ROZANOV & MISSARZHEVSKIY, 1966, p. 77] [=Papulicyathidae VOLOGDIN, 1977, p. 62; =Verrucicyathidae VOLOGDIN, 1977, p. 63; =Orthocyathidae VOLOGDIN, 1977, p. 96]

Wall with simple tumuli. *lower Cambrian (Tom.2–Bot.3).*

Tumuliolynthus ZHURAVLEVA, 1963b, p. 101 [**Rhabdocyathus tubexternus* VOLOGDIN, 1932, p. 64; OD; holotype, VOLOGDIN, 1932, pl. 5,*1a*, TsNIGRm 209a/2957, St. Petersburg] [=*Papulicyathus* VOLOGDIN, 1977, p. 62 (type, *P. longus,* OD); =*Verrucicyathus* VOLOGDIN, 1977, p. 64 (type, *V. tumefactus,* OD), for discussion, see KRUSE, 1982, p. 144; =*Isthmocyathus* VOLOGDIN, 1977, p. 70 (type, *I. articulatus,* OD); =*Mammaticyathus* VOLOGDIN, 1977, p. 71 (type, *M. kyzasicus*, OD); =*Orthocyathus* VOLOGDIN, 1977, p. 97 (type, *O. bateniensis*, OD), *non Cyathophyllum (Orthocyathus)* MERRIAM, 1974, p. 34 (type, *Prismatophyllum flexum* STUMM, 1938, p. 483, OD), cnidarian; for discussion, see DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 165]. Wall with simple tumuli. *lower Cambrian (Tom.2–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Urals, Australia, Antarctica, Falkland Islands (allochthonous), Morocco, Iberia.——FIG. 526,*1*. **T. tubexternus* (VOLOGDIN), Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Altay Sayan, Russia, holotype, TsNIGRm 209a/2957, transverse section, ×3 (Vologdin, 1932).

Family SAJANOLYNTHIDAE
Rozanov, 1989

[Sajanolynthidae ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 79] [=Sajanolynthidae KASHINA in ROZANOV, 1973, p. 85, *nom. nud.*]

Wall with multiperforate tumuli. *lower Cambrian (Bot.1).*

Sajanolynthus VOLOGDIN & KASHINA, 1972, p. 152 [**S. desideratus;* OD; holotype, VOLOGDIN & KASHINA, 1972, pl. 20,*1*, KGU 19/1, Krasnoyarsk] [=*Pustulicyathus* VOLOGDIN, 1977, p. 94 (type, *P. tectus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 129; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 159]. Wall with multiperforate tumuli. *lower Cambrian (Bot.1):* Altay Sayan, Far East.——FIG. 526,*2*. **S. desideratus*, Torgashino Formation, Botoman, Uyar River, East Sayan, Altay Sayan, Russia, holotype, KGU 19/1, transverse section, ×15 (Vologdin & Kashina, 1972).

Family GLOBOSOCYATHIDAE
Okuneva, 1969

[Globosocyathidae OKUNEVA, 1969, p. 75] [=Propriolynthidae ROZANOV, 1973, p. 85, *nom. nud.;* =Tumuloglobosidae ROZANOV, 1973, p. 85, *nom. nud.;* ?=Tecticyathidae VOLOGDIN, 1977, p. 93]

Wall with bracts or scales. *lower Cambrian (Atd.2–Bot.1).*

Propriolynthus OKUNEVA, 1967, p. 133 [**Archaeolynthus vologdini* YAKOVLEV, 1956, p. 855; OD; lectotype, YAKOVLEV, 1956, pl. 1,*1,* SD OKUNEVA, 1967, p. 133, not located] [=*Globosocyathus* OKUNEVA, 1969, p. 75 (type, *G. bellus,* OD); =*Tumuloglobosus* OKUNEVA in OKUNEVA & REPINA, 1973, p. 93 (type, *T. crassus,* OD); =*Subiculicyathus* VOLOGDIN, 1977, p. 49 (type, *Archaeolynthus vologdini* YAKOVLEV, 1956, p. 855, OD); ?=*Tecticyathus* VOLOGDIN, 1977, p. 93 (type, *Archaeolynthus peltathus* MASLOV, 1961, p. 121, OD); =*Propricyathus* OKUNEVA in VOLOGDIN, 1977, p. 100 (type, *P. maritimus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 125; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 156]. Wall with pores bearing downwardly projecting, cupped bracts. *lower Cambrian (Atd.2–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East.——FIG. 526,*3a–b*. **P. vologdini* (YAKOVLEV), Dmitrievka Formation, Botoman, Spassk-Chernigovka area, Far East, Russia, specimen PGU 30-x_2; *a,* oblique longitudinal section, ×3; *b,* tangential section, ×15 (Okuneva, 1967).

Melkanicyathus BELYAEVA, 1969, p. 88 [**M. limitatus;* OD; holotype, BELYAEVA, 1969, pl. 38,*2–3,* DVGU 212/5, Khabarovsk] [=*Phymatocyathus* VOLOGDIN, 1977, p. 72 (type, *P. orillatus,* OD); =*Scyphocyathus* VOLOGDIN, 1977, p. 96 (type, *Rhabdocnema operculatum* MASLOV, 1960, p. 1117, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 118; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 151]. Wall with pores bearing upwardly projecting, cupped bracts. *lower Cambrian (Bot.1):* Altay Sayan, Far East.——FIG. 526,*4a–b*. **M. limitatus*, Ust'toka unit, Botoman, Bol'shoy Mel'kan River, Dzhagdy Range, Far East, Russia, holotype, DVGU 212/5; *a,* oblique transverse section, ×6; *b,* longitudinal section, ×6 (Belyaeva, 1969).

Family FAVILYNTHIDAE
Debrenne, 1989

[Favilynthidae DEBRENNE in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 79] [=Favilynthidae DEBRENNE, 1974b, p. 98, *nom. nud.*]

Wall with canals. *lower Cambrian (Atd.1–Bot.3).*

Favilynthus DEBRENNE in ZHURAVLEVA, 1974a, p. 138 [**Monocyathus mellifer* R. BEDFORD & W. R.

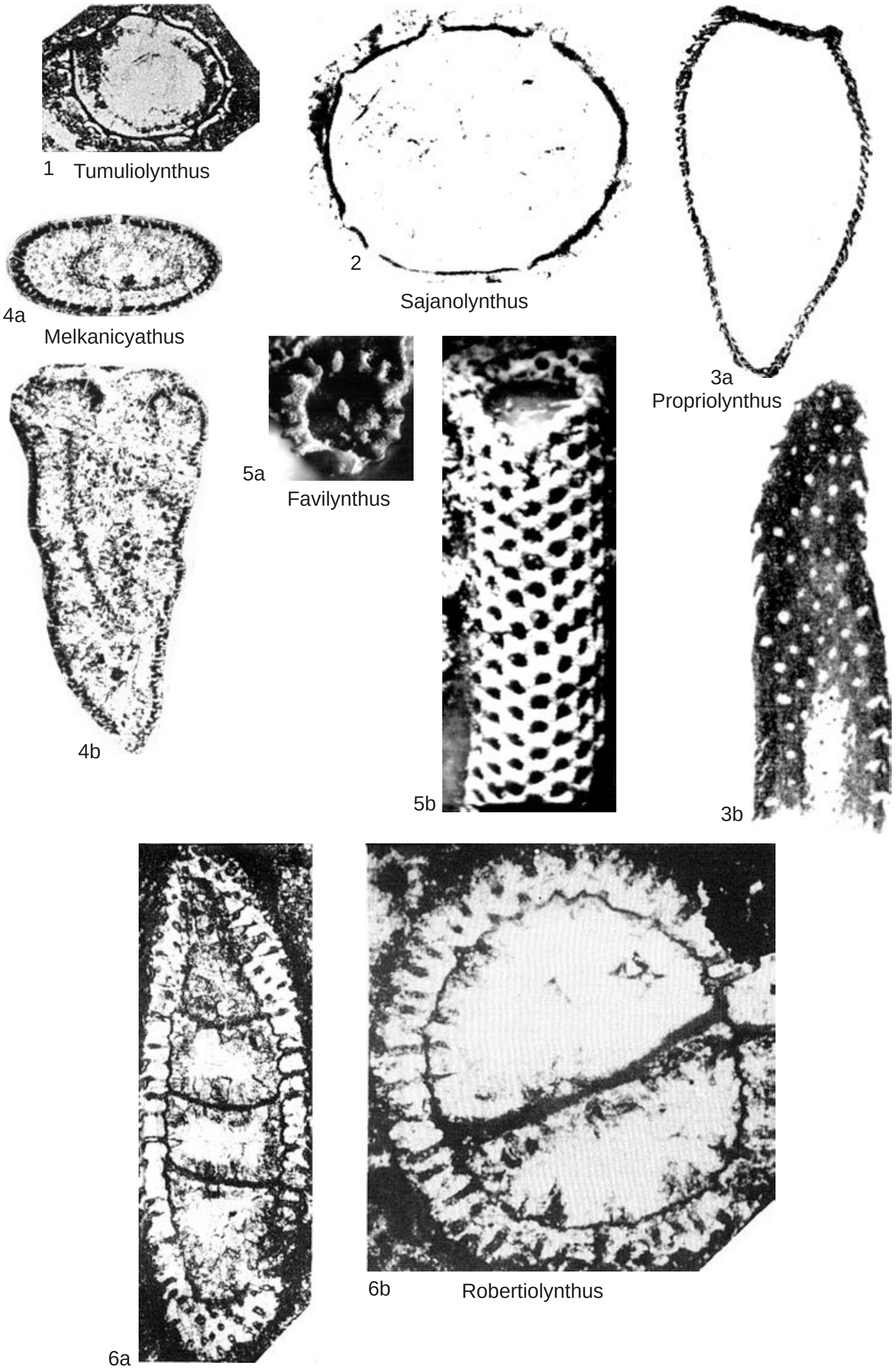


FIG. 526. Tumuliolynthidae, Sajanolynthidae, Globosocyathidae, and Favilynthidae (p. 926–928).

Bedford, 1936, p. 12; OD; holotype, R. Bedford & W. R. Bedford, 1936, fig. 49; Zhuravleva, 1963b, fig. 42; Debrenne, 1974b, pl. 19,_5–6_, SAM P932-47, Adelaide]. Wall with horizontal to upwardly projecting, straight canals. _lower Cambrian (Atd.1–Bot.3):_ Altay Sayan, Tuva, Mongolia, Far East, Australia, Antarctica, Falkland Islands (allochthonous).——Fig. 526,_5a–b._ *_F. mellifer_ (R. Bedford & W. R. Bedford), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; _a,_ external transverse view, holotype, SAM P932-47, ×6; _b,_ external longitudinal view, topotype, USNM PU9, ×6 (Debrenne, 1974b).

Robertiolynthus Zhuravlev in Voronova & others, 1987, p. 19 [*_R. handfieldi_; OD; holotype, Voronova & others, 1987, pl. 1,_1_, GSC 90116, Ottawa] [=_Veolynthus_ Boyarinov & Konyaeva in Zhuravleva & others, 1997a, p. 26 (type, _V. jucundus_, OD)]. Wall with horizontal to upwardly projecting, straight canals bearing supplementary bracts externally. _lower Cambrian (Bot.1–Bot.2):_ Altay Sayan, Canada.——Fig. 526,_6a–b._ *_R. handfieldi_, Sekwi Formation, Botoman, Mackenzie Mountains, Northwest Territories, Canada; _a,_ holotype, GSC 90116, longitudinal section, ×19; _b,_ paratype, GSC 90117, transverse section, ×19 (Voronova & others, 1987).

Order AJACICYATHIDA
R. Bedford & J. Bedford, 1939

[_nom. correct._ Okulitch, 1955a, p. 10, _pro_ order Ajacicyathina R. Bedford & J. Bedford, 1939, p. 70] [?=order Somphocyathina Okulitch, 1943, p. 47, _nom. nud.;_ =Somphocyathida Okulitch, 1955a, p. 19; =Nochoroicyathida Zhuravleva in Vologdin, 1956, p. 879; =Dokidocyathida Vologdin, 1957a, p. 178; =Bronchocyathida Zhuravleva in Vologdin, 1957a, p. 180; =Bosceculida Krasnopeeva, 1960, p. 41; =Ethmophyllida Vologdin, 1961, p. 178; =Cyclocyathellida Vologdin, 1961, p. 179]

Cup two walled, solitary or low modular; inner wall of centripetal type of development; intervallum with septa, with or without plate tabulae. _lower Cambrian (Tom.1–Toy.3)._

Suborder DOKIDOCYATHINA
Vologdin, 1957

[_nom. transl._ Zhuravleva, 1960b, p. 95, _ex_ order Dokidocyathida Vologdin, 1957a, p. 178]

Intervallum with septa bearing single longitudinal pore row. _lower Cambrian (Tom.2–Bot.3)._

Superfamily DOKIDOCYATHOIDEA
R. Bedford & W. R. Bedford, 1936

[_nom. correct._ Debrenne, Zhuravlev, & Rozanov, 1989, p. 80, _pro_ Dokidocyathacea Debrenne, 1970a, p. 24, _nom. transl. ex_ Dokidocyathidae R. Bedford & W. R. Bedford, 1936, p. 12]

Outer wall with simple pores. _lower Cambrian (Tom.2–Bot.3)._

Family DOKIDOCYATHIDAE
R. Bedford & W. R. Bedford, 1936

[Dokidocyathidae R. Bedford & W. R. Bedford, 1936, p. 12]

Inner wall with simple pores. _lower Cambrian (Tom.2–Bot.3)._

Dokidocyathus Taylor, 1910, p. 146 [*_D. simplicissimus_; M; lectotype, Taylor, 1910, pl. 16, photos 91–92; Zhuravleva, Konyushkov, & Rozanov, 1964, pl. 4,_2–3;_ Rozanov, 1973, pl. 14,_1;_ Debrenne, 1974b, pl. 20,_3;_ SD Debrenne, 1970a, p. 33, SAM T1589A-B, cups F-G, Adelaide] [?=_Velicyathus_ Debrenne, 1964, p. 125 (type, _V. levillaini_, OD); =_Dokidolynthus_ Debrenne, 1974b, p. 101 (type, _Dokidocyathus lenaicus_ Rozanov in Zhuravleva, Konyushkov, & Rozanov, 1964, p. 83, OD); ?=_Kamyshovaecyathus_ Yazmir in Zhuravleva, 1974a, p. 183, _nom. nud.,_ based on type species not then available; ?=_Kamyshovaecyathus_ Yazmir in Yazmir, Dalmatov, & Yazmir, 1975, p. 38 (type, _K. immanis,_ OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 104; Debrenne, Rozanov, & Zhuravlev, 1990, p. 141]. Outer and inner walls with simple pores. _lower Cambrian (Tom.2–Bot.3):_ Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Urals, Australia, Antarctica, Morocco, Iberia.——Fig. 527,_1._ *_D. simplicissimus_, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1589A-B, cups F-G, oblique transverse view, ×2.5 (Taylor, 1910).

Family DOKIDOCYATHELLIDAE
Debrenne, 1964

[Dokidocyathellidae Debrenne, 1964, p. 112]

Inner wall with bracts or scales. _lower Cambrian (Atd.2–Bot.1)._

Dokidocyathella Zhuravleva, 1960b, p. 100 [*_D. incognita_; OD; holotype, Zhuravleva, 1960b, fig. 73, pl. 5,_3,_ TsSGM 205/8, Novosibirsk]. Inner wall with pores bearing upwardly projecting, S-shaped scales. _lower Cambrian (Atd.2–Bot.1):_ Siberian Platform, Altay Sayan, Tuva, Far East.——Fig. 527,_2._ *_D. incognita_, Pestrotsvet Formation, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 205/8, transverse section, ×10 (Zhuravleva, 1960b).

Incurvocyathus Rozanov in Rozanov & Missarzhevskiy, 1966, p. 50 [*_I. voronovae;_ OD; holotype, Rozanov & Missarzhevskiy, 1966, pl. 1,_4–5_, PIN 4597/57, Moscow]. Cup with regular transverse folds affecting both walls; inner wall with pores bearing possibly upwardly projecting, S-shaped scales. _lower Cambrian (Atd.2–Bot.1):_ Altay Sayan, Tuva.——Fig. 527,_3a–b._ *_I. voronovae_, Shangan Formation, Botoman, East Tannu-Ola Range, Tuva, Russia, holotype, PIN 4597/57; _a,_ longitudinal section (outer wall to left), ×8; _b,_ detail of longitudinal section (outer wall to left), ×8 (Rozanov & Missarzhevskiy, 1966).

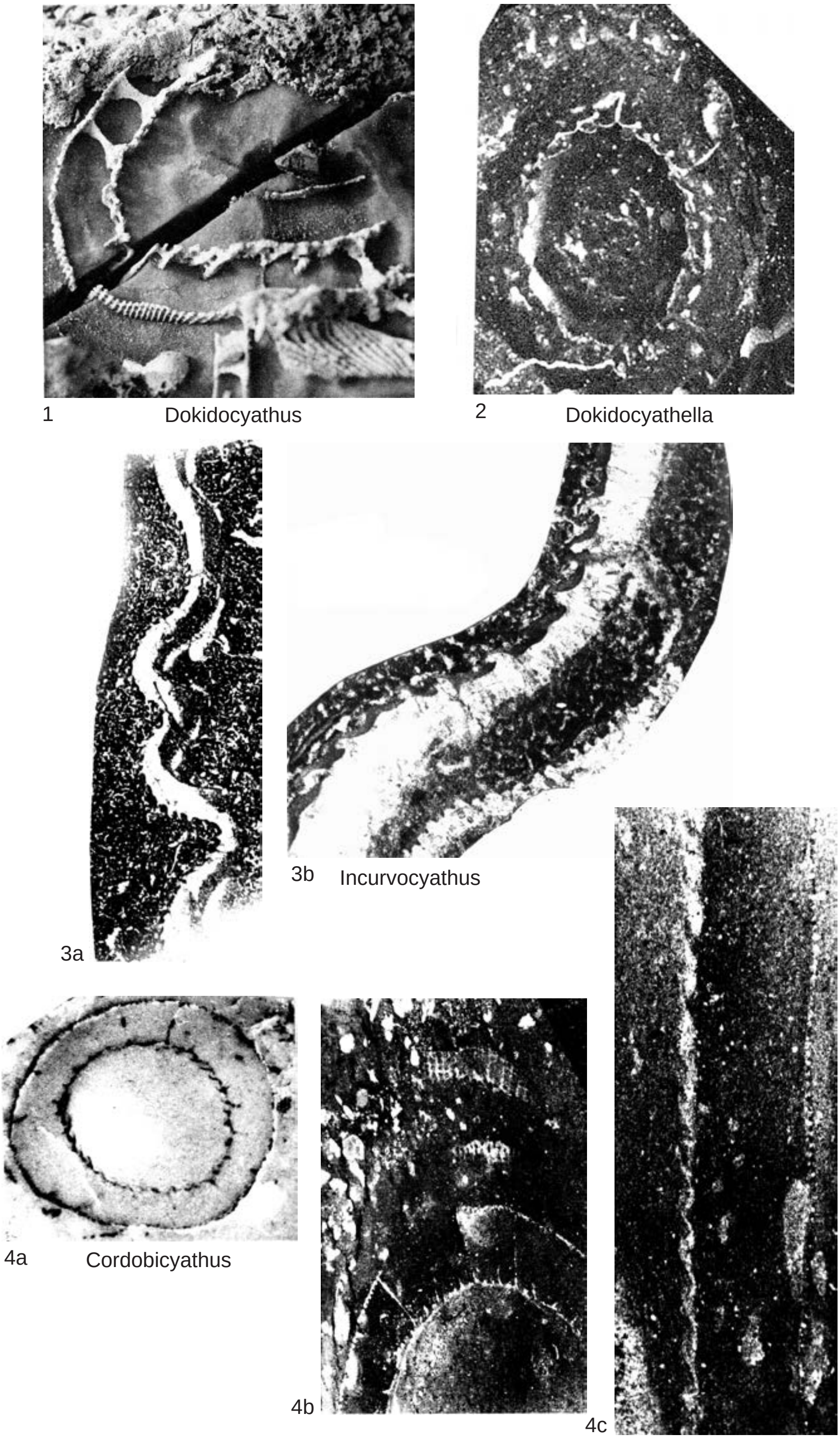


FIG. 527. Dokidocyathidae, Dokidocyathellidae, and Cordobicyathidae (p. 928–930).

Family CORDOBICYATHIDAE
Perejón, 1975

[Cordobicyathidae PEREJÓN, 1975a, p. 136]

Inner wall with annuli. *lower Cambrian (Atd.2).*

Cordobicyathus PEREJÓN, 1975a, p. 136 [**C. deserti*; OD; holotype, PEREJÓN, 1975a, pl. 3,*1–3*, CE 3-74-2, Madrid]. Inner wall with upwardly projecting, S-shaped annuli. *lower Cambrian (Atd.2):* Iberia, Germany, Poland.——FIG. 527,*4a–c*. **C. deserti*, Pedroche Formation, Atdabanian, Las Ermitas, Cordoba, Andalusia, Spain, holotype, CE 3-74-2; *a,* transverse section, ×6.5 (Perejón, 1975a); *b,* oblique section, ×6.5; *c,* detail of longitudinal section (outer wall to right), ×15 (Debrenne, Zhuravlev, & Kruse, 2002).

Superfamily KIDRJASOCYATHOIDEA
Rozanov, 1964

[*nom. transl.* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 80, *ex* Kidrjasocyathidae ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 95] [=Kidrjasocyathacea ROZANOV, 1973, p. 85, *nom. nud.*]

Outer wall with independent microporous sheath. *lower Cambrian (Atd.2–Bot.1).*

Family KIDRJASOCYATHIDAE
Rozanov, 1964

[Kidrjasocyathidae ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 95]

Inner wall with simple pores. *lower Cambrian (Atd.2–Bot.1).*

Kidrjasocyathus ROZANOV, 1960b, p. 43 [**K. uralensis*; OD; holotype, ROZANOV, 1960b, fig. 1, pl. 1,*1a–b;* ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 10,*3*, PIN 4297/9, Moscow]. Inner wall with simple pores. *lower Cambrian (Atd.2–Bot.1):* Altay Sayan, Urals.——FIG. *528a–c*. **K. uralensis*, Terekla Formation, Botoman, Kidryassovo, western flank of southern Urals, Russia, holotype, PIN 4297/9; *a,* transverse section, ×9; *b,* detail of transverse section (outer wall to right), ×20 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* sketch of transverse section, ×20 (Rozanov, 1960b).

Superfamily KALTATOCYATHOIDEA
Rozanov, 1964

[*nom. transl.* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 80, *ex* Kaltatocyathidae ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 92] [=Kaltatocyathacea ROZANOV, 1973, p. 85, *nom. nud.*]

Outer wall with simple tumuli. *lower Cambrian (Atd.1–Bot.1).*

Family KALTATOCYATHIDAE
Rozanov, 1964

[Kaltatocyathidae ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 92]

Inner wall with simple pores. *lower Cambrian (Atd.1–Bot.1).*

Kaltatocyathus ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 92 [**K. kaschinae*; OD; holotype, ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 9,*7*, PIN 4297/47, Moscow] [=*Aroonacyathus* GRAVESTOCK, 1984, p. 46 (type, *A. gregarius*; OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 114; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 147]. Inner wall with simple pores. *lower Cambrian (Atd.1–Bot.1):* Altay Sayan, Transbaikalia, Far East, Australia.——FIG. 529. **K. kaschinae*, Bazaikha Formation, Atdabanian, Bazaikha River, East Sayan, Altay Sayan, Russia, holotype, PIN 4297/47, transverse section, ×19 (Zhuravleva, Konyushkov, & Rozanov, 1964).

Superfamily PAPILLOCYATHOIDEA
Rozanov, 1989

[Papillocyathoidea ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 80] [=Papillocyathacea ROZANOV, 1973, p. 85, *nom. nud.*].

Outer wall with multiperforate tumuli. *lower Cambrian (Atd.4–Bot.1).*

Family PAPILLOCYATHIDAE
Rozanov, 1989

[Papillocyathidae ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 80] [=Papillocyathidae ROZANOV, 1973, p. 85, *nom. nud.*]

Inner wall with simple pores. *lower Cambrian (Atd.4–Bot.1).*

Papillocyathus ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 94 [**P. vacuus*; OD; holotype, ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 10,*1–2*, PIN 4297/48-2, Moscow]. Inner wall with simple pores. *lower Cambrian (Atd.4–Bot.1):* Altay Sayan.——FIG. *530a–b*. **P. vacuus*, Balakhtinson Formation, Botoman, Kazyr River, East Sayan, Altay Sayan, Russia, holotype, PIN 4297/48-2; *a,* transverse section, ×20; *b,* longitudinal section (outer wall to right), ×20 (Zhuravleva, Konyushkov, & Rozanov, 1964).

Superfamily SOANICYATHOIDEA
Rozanov, 1964

[*nom. transl.* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 80, *ex* Soanicyathidae ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 97] [=Soanicyathacea ROZANOV, 1973, p. 85, *nom. nud.*]

Outer wall with bracts or scales. *lower Cambrian (Atd.2–Bot.1).*

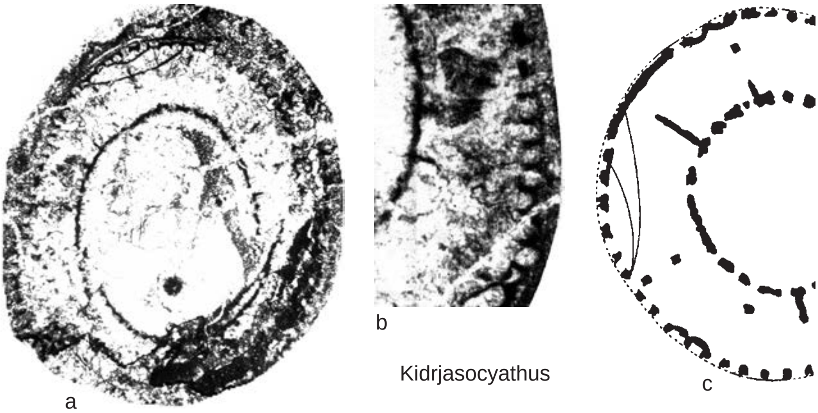


FIG. 528. Kidrjasocyathidae (p. 930).

Family SOANICYATHIDAE Rozanov, 1964

[Soanicyathidae ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 97]

Inner wall with bracts or scales. *lower Cambrian (Atd.2–Bot.1).*

Subtilocyathus VOLOGDIN, 1960, p. 422 [**Archaeocyathus subtilis* VOLOGDIN, 1932, p. 41; OD; lectotype, VOLOGDIN, 1932, fig. 32a–b, pl. 7,*7,* pl. 8,*5b,* SD DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1557, TsNIGRm 50a/2957, St. Petersburg] [=*Soanicyathus* ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 98 (type, *S. admirandus,* OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 133; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 162]. Outer and inner walls with pores bearing upwardly projecting, cupped bracts. *lower Cambrian (Atd.2–Bot.1):* Altay Sayan, Tuva, Mongolia.——FIG. 531,*1a–b*. **S. subtilis* (VOLOGDIN), Verkhneynyrga Formation, Botoman, Lebed’ River, Altay Mountains, Altay Sayan, Russia, lectotype, TsNIGRm 50a/2957; *a,* transverse section, ×4; *b,* detail of transverse section, ×20 (Vologdin, 1932).

Batschykicyathus ZHURAVLEV in ZHURAVLEV, ZHURAVLEVA, & FONIN, 1983, p. 23 [**B. angulosus*; OD; holotype, ZHURAVLEV, ZHURAVLEVA, & FONIN, 1983, pl. 3,*4*, PIN 3848/501, Moscow]. Outer wall regularly bulging in transverse files; outer and inner walls with pores bearing upwardly projecting, cupped bracts. *lower Cambrian (Atd.4):* Siberian Platform.——FIG. 531,*2*. **B. angulosus*, Pestrotsvet Formation, Atdabanian, Bachyk Creek, Lena River, Sakha (Yakutia), Russia, holotype, PIN 3848/501, oblique longitudinal section, ×10 (Zhuravlev, Zhuravleva, & Fonin, 1983).

Family ZHURAVLEVAECYATHIDAE Rozanov, 1989

[Zhuravlevaecyathidae ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 81] [=Zhuravlevaecyathidae ROZANOV, 1973, p. 85, *nom. nud.*]

Inner wall with annuli. *lower Cambrian (Bot.1).*

Zhuravlevaecyathus ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 98 [**Z. pulchellus*; OD; holotype, ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 11,*5–6*, PIN 4297/54, Moscow]. Outer wall with pores bearing upwardly projecting, cupped bracts; inner wall with possibly upwardly projecting, S-shaped annuli. *lower Cambrian (Bot.1):* Altay Sayan.——FIG. 531,*3a–b*. **Z. pulchellus*, Verkhnemonok Formation, Botoman, Abakan River, West Sayan, Altay Sayan, Russia; *a,* holotype, PIN 4297/54, transverse section, ×4; *b,* paratype, PIN 4297/55, detail of transverse section, ×3.5 (Zhuravleva, Konyushkov, & Rozanov, 1964).

Superfamily KYMBECYATHOIDEA Debrenne, Rozanov, & Zhuravlev, 1989

[Kymbecyathoidea DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 81]

Outer wall with canals. *lower Cambrian (Atd.4–Bot.3).*

Family KYMBECYATHIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Kymbecyathidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 81]

Inner wall with simple pores. *lower Cambrian (Atd.4–Bot.3).*

Fig. 529. Kaltatocyathidae (p. 930).

Kymbecyathus Debrenne & Kruse, 1986, p. 241 [**K. avius*; OD; holotype, Debrenne & Kruse, 1986, fig. 6A–B, VU VC9, Wellington]. Outer wall with horizontal to upwardly projecting, straight canals; inner wall with simple pores. *lower Cambrian (Atd.4–Bot.3):* Australia, Antarctica.——Fig. 532*a–b*. **K. avius*, Shackleton Limestone, Botoman, Crackling Cwm, Byrd Glacier, Antarctica, holotype, VU VC9; *a,* transverse section, ×3 (Debrenne & Kruse, 1986); *b,* oblique longitudinal section, ×3 (Debrenne, Zhuravlev, & Kruse, 2002).

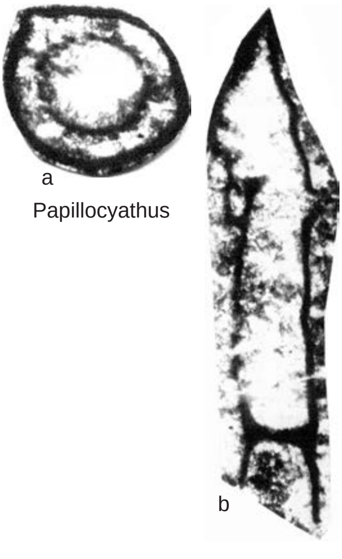


Fig. 530. Papillocyathidae (p. 930).

Suborder AJACICYATHINA R. Bedford & J. Bedford, 1939

[*nom. transl.* Zhuravleva, 1960b, p. 106, *ex* order Ajacicyathina R. Bedford & J. Bedford, 1939, p. 70] [=Nochoroicyathina Zhuravleva in Vologdin, 1956, p. 879, *nom. transl.* Zhuravleva, 1960b, p. 198, *ex* Nochoroicyathida Zhuravleva in Vologdin, 1956, p. 879; =Schidertycyathina Krasnopeeva, 1969, p. 63; =Boscekulcyathina Krasnopeeva, 1969, p. 63]

Intervallum with septa; pectinate tabulae or synapticulae may be present. *lower Cambrian (Tom.1–Toy.3).*

Superfamily BRONCHOCYATHOIDEA R. Bedford & J. Bedford, 1936

[*nom. transl.* Zhuravlev in Voronova & others, 1987, p. 20, *ex* Bronchocyathidae R. Bedford & J. Bedford, 1936, p. 25] [=Ajacicyathoidea R. Bedford & J. Bedford, 1939, p. 73, *nom. correct.* Debrenne & Kruse, 1986, p. 242, *pro* Ajacicyathacea Zhuravleva, 1960b, p. 106, *nom. transl. ex* Ajacicyathidae R. Bedford & J. Bedford, 1939, p. 73; =Nochoroicyathacea Zhuravleva in Vologdin, 1956, p. 879, *nom. transl.* Zhuravleva, 1960b, p. 198, *ex* Nochoroicyathidae Zhuravleva in Vologdin, 1956, p. 879; =Irinacyathacea Zhuravleva in Debrenne, 1972, p. 174, *nom. neg.*; =Aldanocyathacea Zadorozhnaya, Osadchaya, & Repina, 1973, p. 129, *nom. transl.* Korshunov, 1983a, p. 96, *ex* Aldanocyathinae Zadorozhnaya, Osadchaya, & Repina, 1973, p. 129; =Irinaecyathacea Zhuravleva in Zhuravleva & Elkina, 1974, p. 44; =Inessocyathacea Zhuravleva in Zhuravleva & Elkina, 1974, p. 45]

Outer wall with simple pores. *lower Cambrian (Tom.1–Toy.2).*

Family AJACICYATHIDAE R. Bedford & J. Bedford, 1939

[Ajacicyathidae R. Bedford & J. Bedford, 1939, p. 73] [=Nochoroicyathidae Zhuravleva in Vologdin, 1956, p. 879; =Kisasacyathidae Konyushkov, 1972, p. 137; =Aldanocyathidae Zadorozhnaya, Osadchaya, & Repina, 1973, p. 129]

Inner wall with simple pores. *lower Cambrian (Tom.1–Toy.2).*

Ajacicyathus R. Bedford & J. Bedford, 1939, p. 73 [**Archaeocyathus ajax* Taylor, 1910, p. 118; OD; lectotype, Taylor, 1910, pl. 1, photo 1a, pl. 7, photo 39 (lower part); Hill, 1965, pl. 1,*6;* Debrenne, 1974b, pl. 21,*2–4;* SD Debrenne, 1970a, p. 27, SAM T1550A, Adelaide] [=*Loculicyathellus* Debrenne, 1969a, p. 310 (type, *Archaeocyathus floreus* R. Bedford & W. R. Bedford, 1934, p. 2, OD), *nom. transl.* Debrenne, 1974b, p. 115, *ex Loculicyathus (Loculicyathellus)* Debrenne, 1969a, p. 310; =*Ajacicyathus (Juricyathus)* Debrenne, 1974b, p. 110 (type, *Archaeocyathus aequitriens* R. Bedford & J. Bedford, 1937, p. 35, OD); =*Ambistapis* Kruse, 1982, p. 161 (type, *A. integer*, OD)]. Inner wall with several rows of simple pores per intersept; stirrup pores may be present; septa aporose to sparsely porous. *lower Cambrian (Atd.1–Toy.2):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East, Australia, Antarctica, Sardinia, France, Canada.——Fig. 533,*1a–b*. **A. ajax* (Taylor), Ajax Limestone, Botoman,

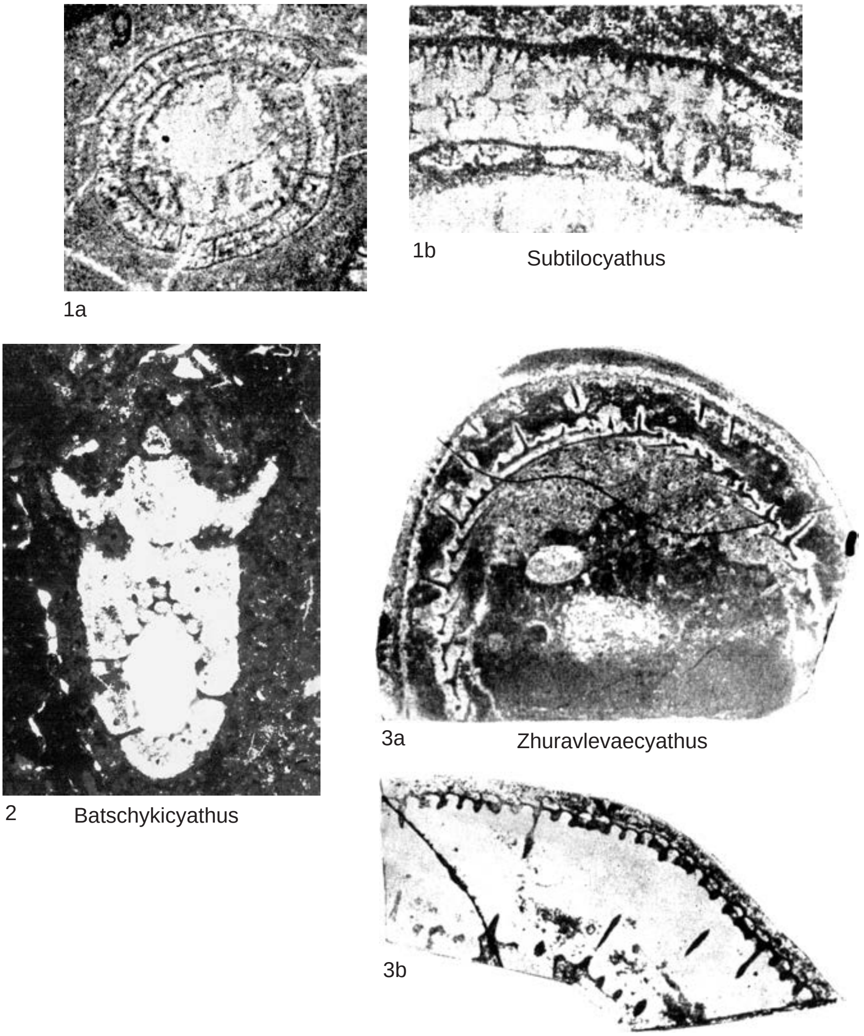


FIG. 531. Soanicyathidae and Zhuravlevaecyathidae (p. 931).

Ajax Mine, South Australia, Australia, lectotype, SAM T1550A; *a,* oblique longitudinal view, ×1 (Taylor, 1910); *b,* detail of septum and inner wall in longitudinal view (outer wall to right), ×10 (Debrenne, 1974b).

Davidicyathus DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 139 [**?Loculicyathus racemiferus* GRAVESTOCK, 1984, p. 48; OD; holotype, GRAVESTOCK, 1984, fig. 32H, 32L, SAM P21452, Adelaide]. Outer wall with two sizes of pores, the smaller either isolated or clustered over the larger; inner wall with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Atd.4):* Australia.——FIG. 533,*2a–c*. **D. racemiferus* (GRAVESTOCK); *a–b,* Wilkawillina Limestone, Atdabanian, Wilkawillina Gorge, South Australia, Australia, holotype, SAM P21452, *a,* transverse section, ×4; *b,* longitudinal section, ×9.5 (Gravestock, 1984); *c,* Ajax Limestone, Atdabanian, Mount Scott Range, South Australia, Australia, SAM P21455-1, tangential section of outer wall, ×15 (Debrenne, Zhuravlev, & Kruse, 2012b).

Dentatocyathus OKUNEVA, 1972, p. 57 [**D. maritimus*; OD; holotype, OKUNEVA, 1972, pl. 10,*7*, PGU 202, Khabarovsk]. Outer wall longitudinally plicate; inner wall with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Bot.1):* Altay Sayan, Tuva, Mongolia,

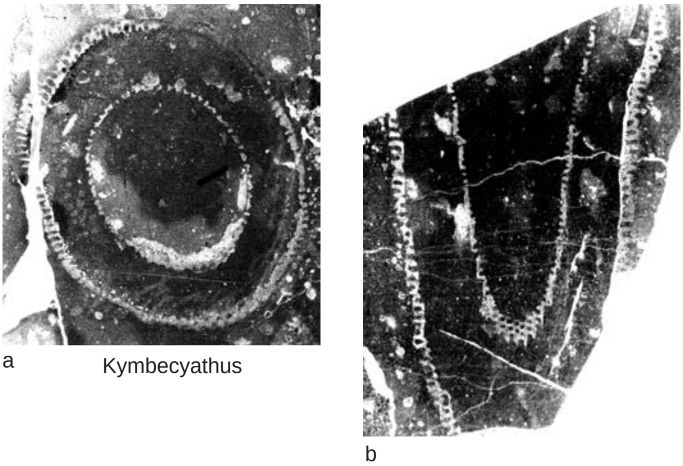


Fig. 532. Kymbecyathidae (p. 932).

Far East.——Fig. 534,*1a–b*. **D. maritimus*, Dmitrievka Formation, Botoman, Knorring Hill, Spassk-Chernigovka area, Far East, Russia, holotype, PGU 202; *a,* transverse section, ×5; *b,* detail of transverse section (outer wall to right), ×10 (Okuneva, 1972).

Iljinicyathus Zhuravleva, 1972b, p. 155 [**I. ulanbatoriensis*; OD; holotype, Zhuravleva, 1972b, pl. 21,*1–3*, TsSGM 755/1, Novosibirsk]. Cup in which inner wall shows periodic transverse folds; inner wall with several rows of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Atd.4):* Mongolia.——Fig. 534,*2a–b*. **I. ulanbatoriensis*, formation not known, Atdabanian, northern Mongolia, holotype, TsSGM 755/1; *a,* transverse section, ×4; *b,* longitudinal section (outer wall to right), ×5 (Zhuravleva, 1972b).

Kisasacyathus Konyushkov, 1972, p. 137 [**K. microtumulatus*; OD; holotype, Konyushkov, 1972, pl. 16,*1*, PIN 4755/7, Moscow] [=*Prethmophyllum* Debrenne, 1974c, p. 174 (type, *Archaeocyathus subacutus* R. Bedford & W. R. Bedford, 1934, p. 2, OD)]. Inner wall with one row of simple pores per intersept, formed by fluting of inner edges of septa; septa aporose to sparsely porous. *lower Cambrian (Atd.4–Bot.3):* Altay Sayan, Tuva, Mongolia, Far East, Australia, Antarctica.——Fig. 534,*3a–b*. **K. microtumulatus*, Verkhnemonok Formation, Botoman, Kizas River, West Sayan, Altay Sayan, Russia; *a,* holotype, PIN 4755/7, oblique longitudinal section, ×6; *b,* paratype, PIN 4755/8, transverse section, ×6 (Konyushkov, 1972).

Nochoroicyathus Zhuravleva, 1951, p. 78 [**N. mirabilis*; OD; holotype, Zhuravleva, 1951, fig. 1a–b, PIN 1168, Moscow, not located] [=*Ajacicyathellus* Debrenne, 1958, p. 64 (type, *A. hollardi*, M); =*Ascocyathus* Vologdin, 1960, p. 422 (type, *Archaeocyathus arteintervallum* Vologdin, 1931, p. 84, OD); =*Howellicyathus* Vologdin, 1961, p. 180, *nom. nud.*; =*Howellicyathus* Vologdin, 1962a, p. 126 (type, *Coscinocyathus howelli* Vologdin, 1940b, p. 88, OD); =*Pachecocyathus* Perejón, 1971, p. 81 (type, *P. cabanasi*, OD); =*Aldanocyathus* Voronin in Debrenne & Voronin, 1971, p. 30 (type, *Ajacicyathus sunnaginicus* Zhuravleva, 1960b, p. 115, OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 120; Debrenne, Rozanov, & Zhuravlev, 1990, p. 153]. Inner wall with several rows of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Tom.1–Bot.3):* Siberian Platform, Kolyma, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Urals, Kazakhstan, Australia, South China, Morocco, Iberia, France, Sardinia, Germany, Serbia.——Fig. 534,*4a–c*. **N. mirabilis*; *a,* Pestrotsvet Formation, Tommotian, Nokhoroy Creek, Lena River, Sakha (Yakutia), Russia, holotype, PIN 1168, transverse section, ×6 (Zhuravleva, 1951); *b–c,* Medvezh'ya Formation, Tommotian, Kotuy River, Krasnoyarsk region, Russia; *b,* TsSGM 205/87, detail of septum in longitudinal section (outer wall to left), ×6; *c,* specimen TsSGM 205/88, detail of transverse section at inner wall, ×20 (Debrenne, Zhuravlev, & Kruse, 2002).

Orbiasterocyathus Zhuravleva in Repina & others, 1964, p. 183 [**O. geri*; OD; holotype, Repina & others, 1964, pl. 11,*6*, TsSGM 4272/5, Novosibirsk]. Cup in which both walls are longitudinally folded, resulting in stellate transverse section; inner wall with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Atd.3–Atd.4):* Altay Sayan.——Fig. 534,*5*. **O. geri*, Adiak Formation, Atdabanian, Terensu River, Gornaya Shoria, Altay Sayan, Russia, holotype,

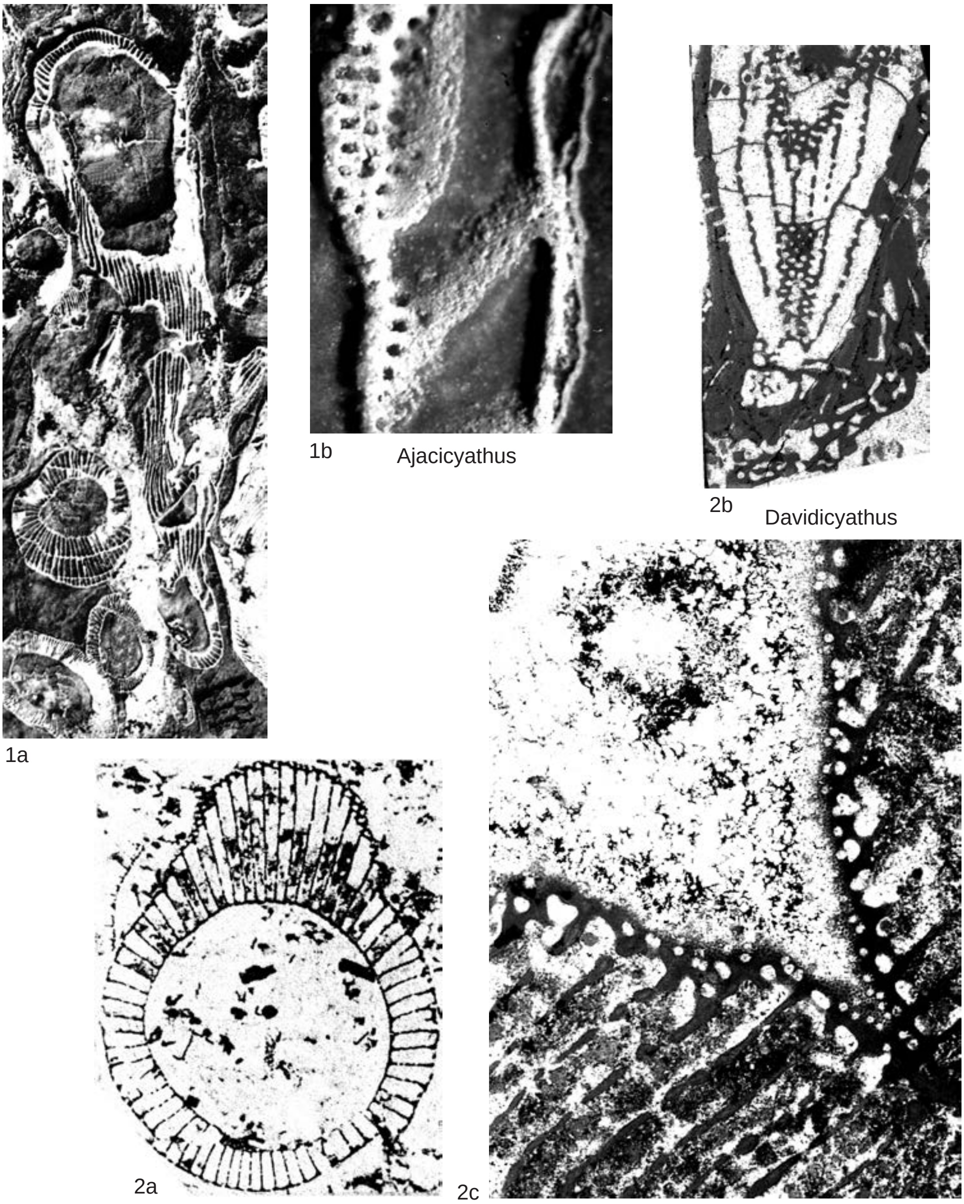


FIG. 533. Ajacicyathidae (p. 932–933).

TsSGM 4272/5, transverse section, ×4 (Repina & others, 1964).

Orbicyathellus OSADCHAYA in ZADOROZHNAYA, OSADCHAYA, & REPINA, 1973, p. 133 [**O. bogradi*; OD; holotype, ZADOROZHNAYA, OSADCHAYA, & REPINA, 1973, pl. 19,*1–2*, TsSGM 424/1, Novosibirsk]. Cup in which both walls show periodic, synchronous transverse folds; inner wall with stirrup pores only; septa aporose to sparsely porous. *lower Cambrian (Atd.1–Atd.4):* Siberian Platform, Altay Sayan, Mongolia.——FIG. 535,*1a–b*. **O. bogradi*, Usa Formation, Atdabanian, Bograd, Batenev Range, Kuznetsk Alatau, Russia, holotype, TsSGM 424/1; *a,* oblique longitudinal section, ×4.5; *b,* tangential section of inner wall, ×12 (Zadorozhnaya, Osadchaya, & Repina, 1973).

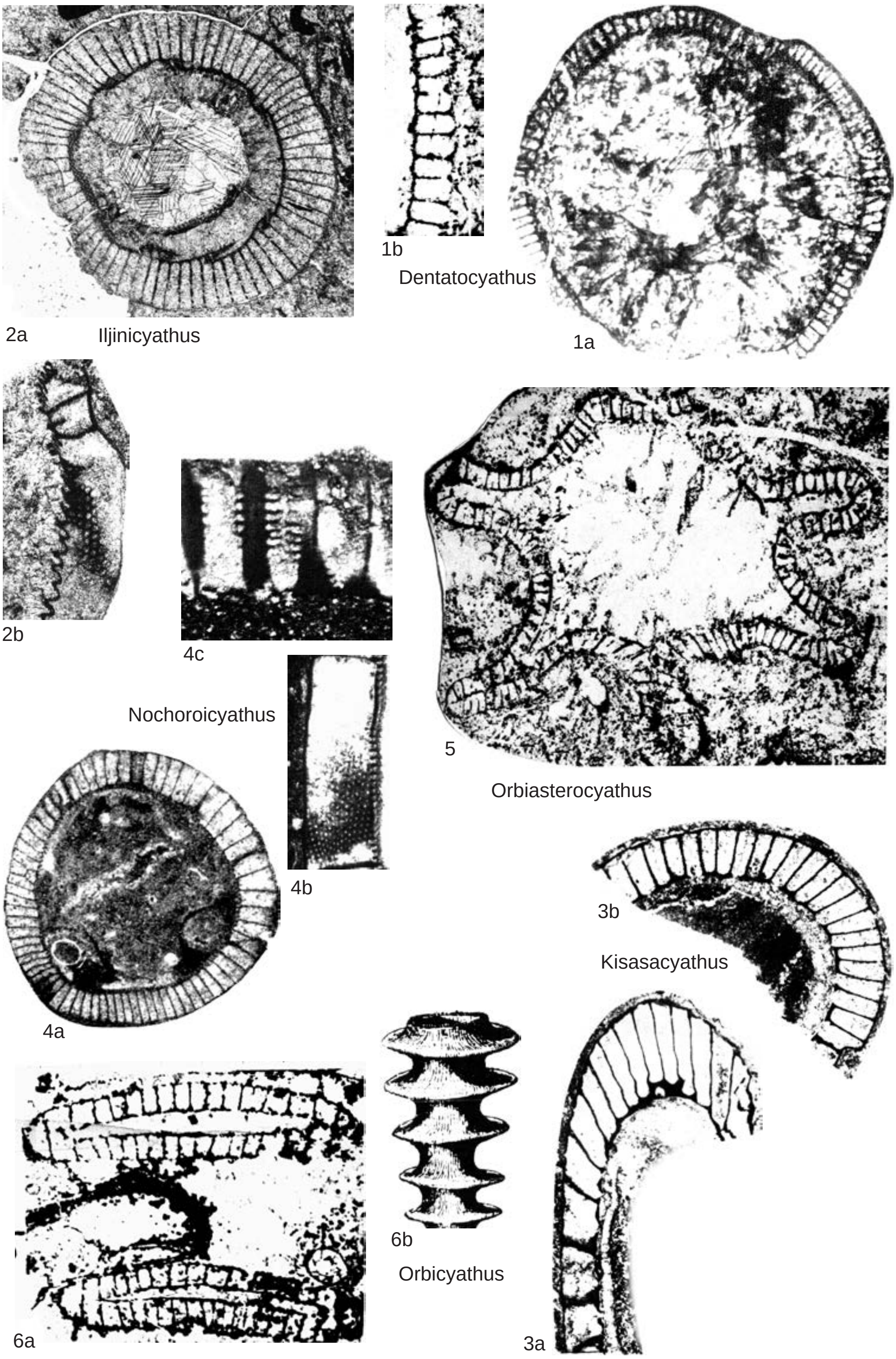


FIG. 534. Ajacicyathidae (p. 933–938).

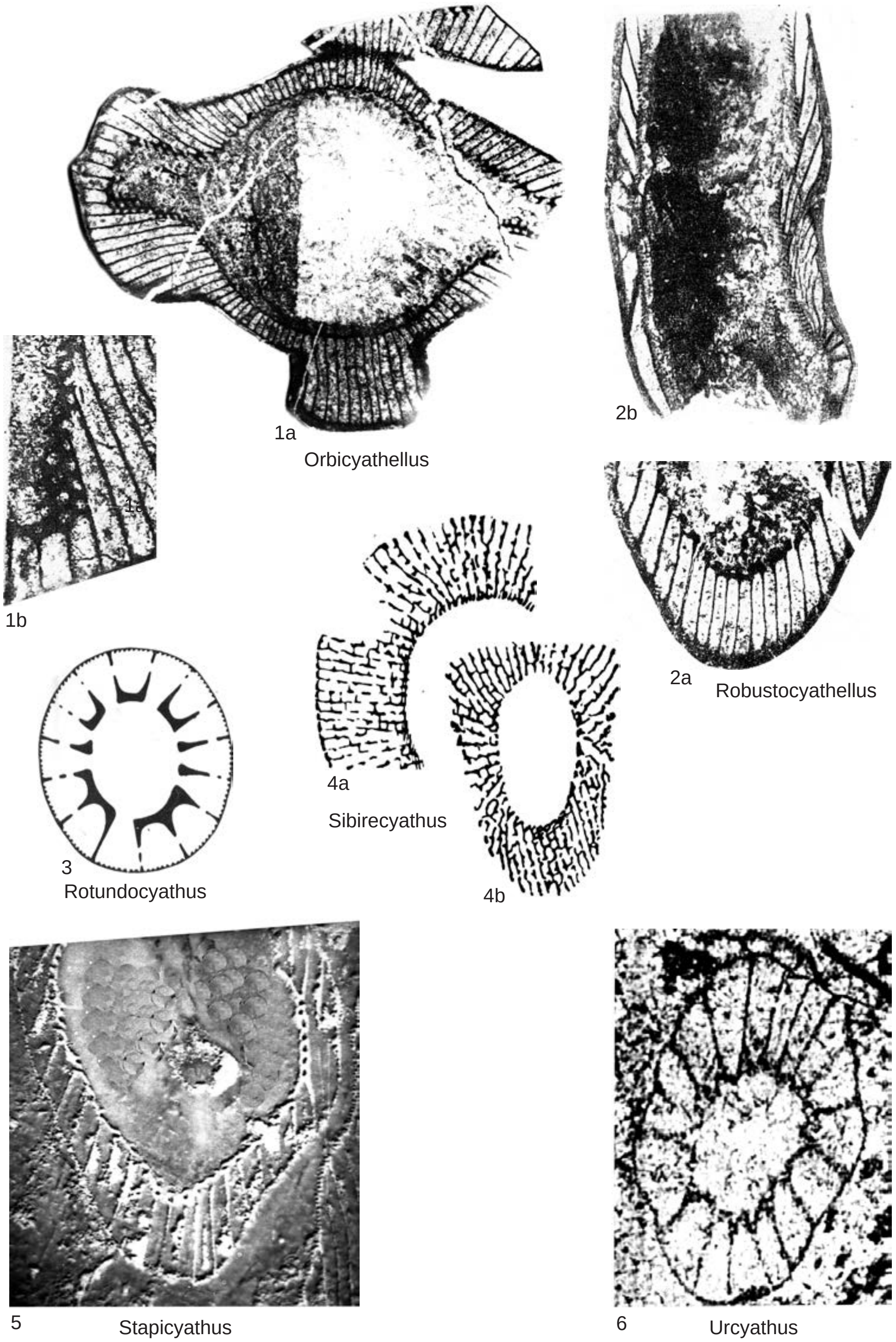


FIG. 535. Ajacicyathidae (p. 935–938).

Orbicyathus VOLOGDIN, 1937b, p. 468 [**O. mongolicus*; M; holotype, VOLOGDIN, 1937b, pl. 2,*4*, not located]. Cup in which both walls show periodic, synchronous transverse folds; inner wall with several rows of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Tom.4–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Morocco.——FIG. 534,*6a–b*. **O. mongolicus*, Burgasutay Formation, Atdabanian, Seer' Mountains, Ikh nuuruuundyn hotgor, western Mongolia, holotype; *a,* longitudinal section, ×3; *b,* schematic reconstruction of cup, ×2 (Vologdin, 1937b).

Robustocyathellus KONYUSHKOV, 1972, p. 133 [**R. spinosus*; OD; holotype, KONYUSHKOV, 1972, pl. 13,*1*, not located]. Inner wall with one row of simple pores per intersept; septa aporose to sparsely porous. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Tajikistan, South China, Canada.——FIG. 535,*2a–b*. **R. spinosus*, Verkhnemonok Formation, Botoman, Kizas River, West Sayan, Altay Sayan, Russia, holotype; *a,* oblique longitudinal section, ×6; *b,* longitudinal section, ×3 (Konyushkov, 1972).

Rotundocyathus VOLOGDIN, 1960, p. 422 [**R. rotaceus*; OD; holotype, VOLOGDIN, 1960, fig. 1zh, not located]. Inner wall with one row of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, South China, Morocco, Iberia, France, Sardinia.——FIG. 535,*3*. **R. rotaceus*, Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Altay Sayan, Russia, holotype, transverse section, ×1 (Vologdin, 1960).

Sibirecyathus VOLOGDIN, 1937b, p. 468 [**S. naletovi*; M; holotype not designated, collection not located]. Inner wall with one row of simple pores per intersept; septa completely porous, linked by synapticulae. *lower Cambrian (Tom.3–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, South China, Morocco, Iberia, France, Sardinia, Germany.——FIG. 535,*4a–b*. **S. naletovi*, Burgasutay Formation, Botoman, Seer' Mountains, Ikh nuuruuundyn hotgor, western Mongolia, *a,* unlocated syntype, transverse section, ×4; *b,* unlocated syntype, oblique longitudinal section, ×4 (Vologdin, 1937b).

Stapicyathus DEBRENNE, 1964, p. 127, *nom. transl.* DEBRENNE, 1970a, p. 43, *ex Archaeocyathellus (Stapicyathus)* DEBRENNE, 1964, p. 127 [**Archaeocyathus stapipora* TAYLOR, 1910, p. 118; OD; lectotype, TAYLOR, 1910, pl. 7, photos 37a, 38D, 38G; DEBRENNE, 1974b, pl. 24,*1;* SD DEBRENNE, 1970a, p. 43, SAM T1591, Adelaide] [=*Sivovicyathus* KONYUSHKOV, 1972, p. 134 (type, *S. abakanensis,* OD); =*Nochoroicyathellus* OSADCHAYA in OSADCHAYA & others, 1979, p. 154 (type, *N. activus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 132; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 161]. Inner wall with stirrup pores only; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Australia, Antarctica, South Africa (allochthonous).——FIG. 535,*5*. **S. stapipora* (TAYLOR), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1591, oblique longitudinal section, ×4 (Taylor, 1910).

Urcyathus VOLOGDIN, 1940b, p. 64 [**U. asteroides*; OD; holotype, VOLOGDIN, 1940b, pl. 14,*5,* not located] [=*Pectenocyathus* KASHINA in REPINA & others, 1964, p. 211 (type, *P. torgaschinicus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 139; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 166]. Inner wall longitudinally plicate, with several rows of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Atd.2):* Altay Sayan, Tuva, Mongolia, Iberia, Germany.——FIG. 535,*6*. **U. asteroides*, Gavrilovskoe Formation, Atdabanian, Gorskino, Salair, Russia, holotype, oblique transverse section, ×9 (Vologdin, 1940b).

Family DENSOCYATHIDAE Vologdin, 1937

[Densocyathidae VOLOGDIN, 1937b, p. 471] [=Leptosocyathidae VOLOGDIN, 1961, p. 178; =Tennericyathidae ROZANOV in ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, p. 34]

Inner wall with bracts or scales. *lower Cambrian (Atd.1–Bot.3).*

Densocyathus VOLOGDIN, 1937b, p. 471 [**D. sanaschticolensis;* M; holotype not designated, collection not located]. Inner wall with several rows of pores per intersept, bearing upwardly projecting, S-shaped scales; septa aporose to sparsely porous. *lower Cambrian (Bot.1–Bot.3):* Altay Sayan.——FIG. 536,*1*. **D. sanaschticolensis*, Verkhnemonok Formation, Botoman, Sanashtykgol Spring, West Sayan, Altay Sayan, Russia; unlocated syntype, transverse section of modular skeleton, ×5 (Vologdin, 1937b).

Cadniacyathus R. BEDFORD & J. BEDFORD, 1937, p. 36 [**C. asperatus;* OD; lectotype, R. BEDFORD & J. BEDFORD, 1937, fig. 152; DEBRENNE, 1974b, pl. 27,*2;* SD DEBRENNE, 1970a, p. 30, USNM PU86616(1), Washington, D.C.]. Inner wall with several rows of pores per intersept, bearing upwardly projecting, planar fused bracts; septa aporose to sparsely porous. *lower Cambrian (Bot.3):* Australia, ?Antarctica.——FIG. 536,*2*. **C. asperatus*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, USNM PU86616(1), oblique transverse view, ×3 (Debrenne, Zhuravlev, & Kruse, 2002).

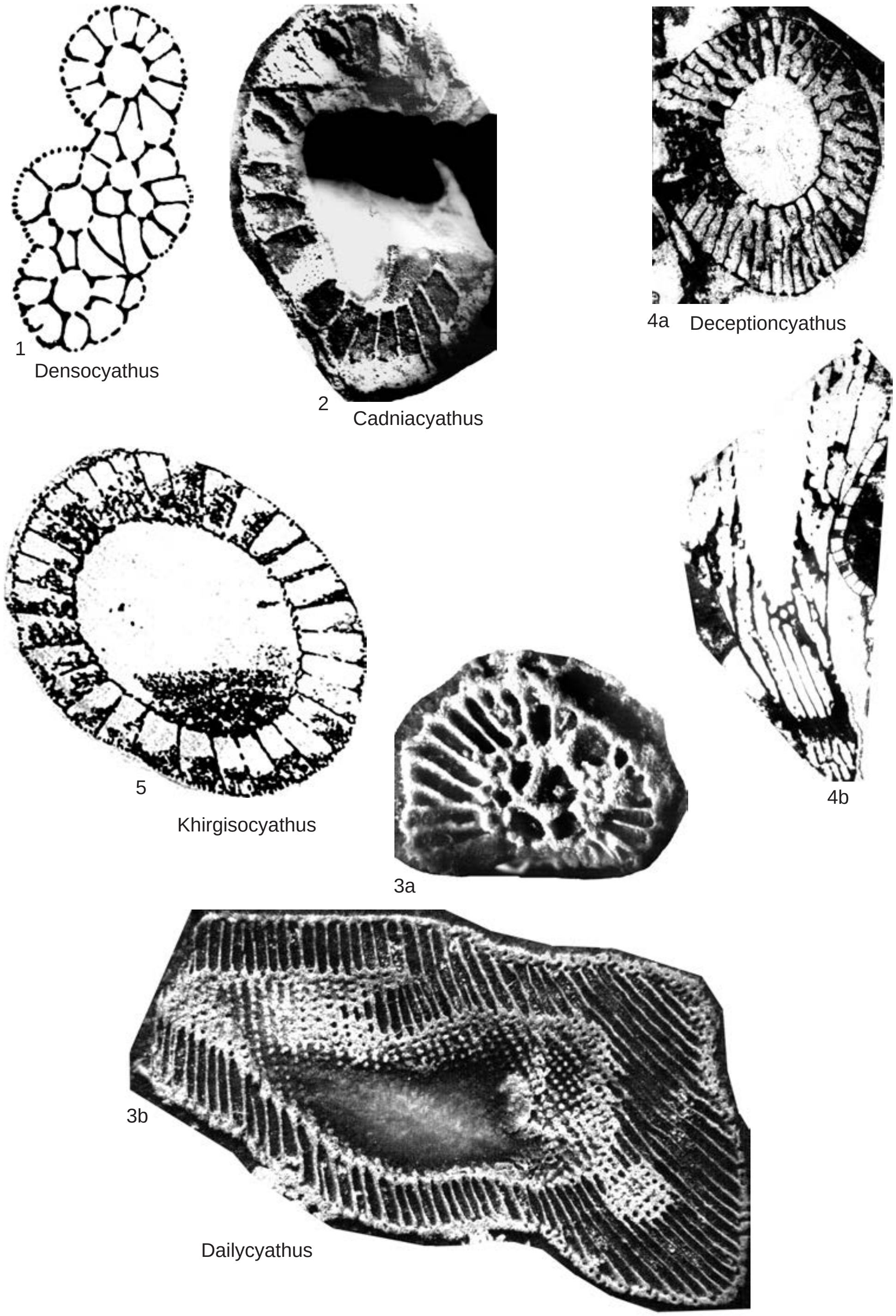


FIG. 536. Densocyathidae (p. 938–940).

Dailycyathus Debrenne, 1970a, p. 32 [**Paranacyathus margarita* R. Bedford & J. Bedford, 1937, p. 34; OD; lectotype, R. Bedford & J. Bedford, 1937, fig. 138b–c; Debrenne, 1970a, pl. 1,*5;* SD Debrenne, 1970a, p. 32, USNM PU87214, specimen 304, Washington, D.C.] [=*Joanaecyathus* Gravestock, 1984, p. 53 (type, *J. cupulosus*, OD; =*Paranacyathus margarita* R. Bedford & J. Bedford, 1937, p. 34), for discussion, see Debrenne, Rozanov, & Zhuravlev, 1990, p. 139]. Inner wall with one row of pores per intersept, bearing upwardly projecting, cupped bracts; septa aporose to sparsely porous. *lower Cambrian (Atd.4–Bot.3):* Altay Sayan, Mongolia, Tarim, South China, Australia.——Fig. 536,*3a–b*. **D. margarita* (R. Bedford & J. Bedford), Ajax Limestone, Atdabanian, Paint Mine, South Australia, Australia; *a,* lectotype, USNM PU87214, specimen 304, transverse view near cup base, ×5; *b,* paralectotype, USNM PU87215, tangential view of inner wall, ×5 (Debrenne, 1970a).

Deceptioncyathus Gravestock, 1984, p. 53 [**D. synapticulosus*; OD; holotype, Gravestock, 1984, fig. 34H–J, SAM P21504-1, Adelaide]. Inner wall with one row of pores per intersept, bearing upwardly projecting cupped bracts; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.4):* Australia.——Fig. 536,*4a–b*. **D. synapticulosus*, Ajax Limestone, Atdabanian, Mount Scott Range, South Australia, Australia, holotype, SAM P21504-1; *a,* transverse section, ×2; *b,* longitudinal section, ×2 (Gravestock, 1984).

Khirgisocyathus Voronin, 1988, p. 5 [**K. primus*; OD; holotype, Voronin, 1988, pl. 2,*1*, PIN 3301/511, Moscow]. Inner wall with several rows of pores per intersept, bearing upwardly projecting cupped bracts; septa completely porous. *lower Cambrian (Atd.2):* Mongolia.——Fig. 536,5. **K. primus*, Ichituin Formation, Atdabanian, Boro-Khairkhan-Obo Mountain, Khan-Khukhiy Range, Mongolia, holotype, PIN 3301/511, oblique transverse section, ×9 (Voronin, 1988).

Leptosocyathellus Osadchaya in Osadchaya & others, 1979, p. 119 [**L. mirandus*; OD; holotype, Osadchaya & others, 1979, pl. 5,*3*, VSEGEI 11594, St. Petersburg]. Inner wall with stirrup pores only, bearing upwardly projecting, S-shaped scales; septa completely porous. *lower Cambrian (Atd.2–Atd.4):* Altay Sayan, Iberia.——Fig. 537,*1a–b*. **L. mirandus*; *a,* Usa Formation, Atdabanian, Krutoy Log, Batenev Range, Kuznetsk Alatau, Russia, holotype, VSEGEI 11594, transverse section, ×8.5; *b,* Usa Formation, Atdabanian, Srednyaya Mountain, Batenev Range, Kuznetsk Alatau, Russia, VSEGEI C-69, oblique longitudinal section, ×8 (Osadchaya & others, 1979).

Leptosocyathus Vologdin, 1937b, p. 470 [**L. curviseptum*; OD; holotype, Vologdin, 1937b, fig. 14, not located; =*Leptocyathus curviseptatus* Vologdin, 1940a, p. 146] [=*Leptocyathus* Vologdin, 1937b, p. 468, *nom. null.*, *non Leptocyathus* Milne-Edwards & Haime, 1850, a scleractinian; =*Halysicyathus* Debrenne, 1965, p. 144 (type, *H. multifurcus,* OD)]. Inner wall with one row of pores per intersept, bearing upwardly projecting, S-shaped scales; septa aporose to sparsely porous. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Tajikistan, Australia, Antarctica, Morocco, Iberia.——Fig. 537,*2a–c*. **L. curviseptus*, Burgasutay Formation, Botoman, Seer' Mountains, Ikh nuuruundyn hotgor, western Mongolia; *a,* holotype, transverse section, ×1; *b,* holotype, oblique transverse section of inner wall, ×1 (Vologdin, 1937b); *c,* topotype, PIN 3156/3000, transverse section, ×9 (Debrenne, Zhuravlev, & Kruse, 2002).

Natalijaecyathus Kotel'nikov, 1995, p. 23 [**N. vadibalaensis*; OD; holotype, Kotel'nikov, 1995, fig. 1d, pl. 2,*7,* TsNIGRm 12890/4, St. Petersburg]. Inner wall with stirrup pores only, bearing upwardly projecting, S-shaped scales; longitudinal bars may be present, bisecting stirrup pores; septa completely porous. *lower Cambrian (Atd.2):* Tuva.——Fig. 537,*3a–b*. **N. vadibalaensis*, Il'chir Formation, Atdabanian, Vadi-Bala Creek, Tapsa River, Tuva, Russia, holotype, TsNIGRm 12890/4; *a,* oblique transverse section, ×5.5; *b,* detail of oblique transverse section, ×9 (Kotel'nikov, 1995).

Rectannulus Debrenne, 1977a, p. 106 [**R. willefertae*; OD; holotype, Debrenne, 1977a, pl. 6,*2–3*, MNHN M80026, specimen IRH4-2b, Paris]. Inner wall with stirrup pores only, bearing horizontal to upwardly projecting, S-shaped scales; scales may be fused into pseudoannuli; septa sparsely to completely porous. *lower Cambrian (Atd.4–Bot.1):* Morocco.——Fig. 538,*1a–b*. **R. willefertae*, Issafen Formation, Botoman, Jbel Irhoud, Morocco, holotype, MNHN M80026, specimen IRH4-2b; *a,* detail of transverse section, ×5 (Debrenne, 1977a); *b,* oblique longitudinal section, ×5 (Debrenne, Zhuravlev, & Kruse, 2012b).

Tennericyathus Rozanov in Zhuravleva, Korshunov, & Rozanov, 1969, p. 35 (Rozanov in Rozanov & others, 1969, p. 182, *nom. nud.*) [**T. malycanicus*; OD; holotype, Zhuravleva, Korshunov, & Rozanov, 1969, pl. 4,*5;* Rozanov, 1973, pl. 9,*4*, PIN 4297/79, Moscow, not located] [=*Memoriacyathus* Yazmir in Zhuravleva, 1974a, p. 215, *nom. nud.*; =*Memoriacyathus* Yazmir in Yazmir, Dalmatov, & Yazmir, 1975, p. 47 (type, *M. burjaticus*, OD); =*Raropectinus* Debrenne & Rozanov, 1983, p. 735, *nom. nov. pro Rarocyathus* Osadchaya in Osadchaya & others, 1979, p. 155, *non* Vologdin & Jankauskas, 1968, p. 203, cribricyath (type, *R. rarus,* OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 135; Debrenne, Rozanov, & Zhuravlev, 1990, p. 163]. Inner wall with several rows of pores per intersept, bearing upwardly projecting, S-shaped scales; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East.——Fig. 538,*2*. **T. maly-*

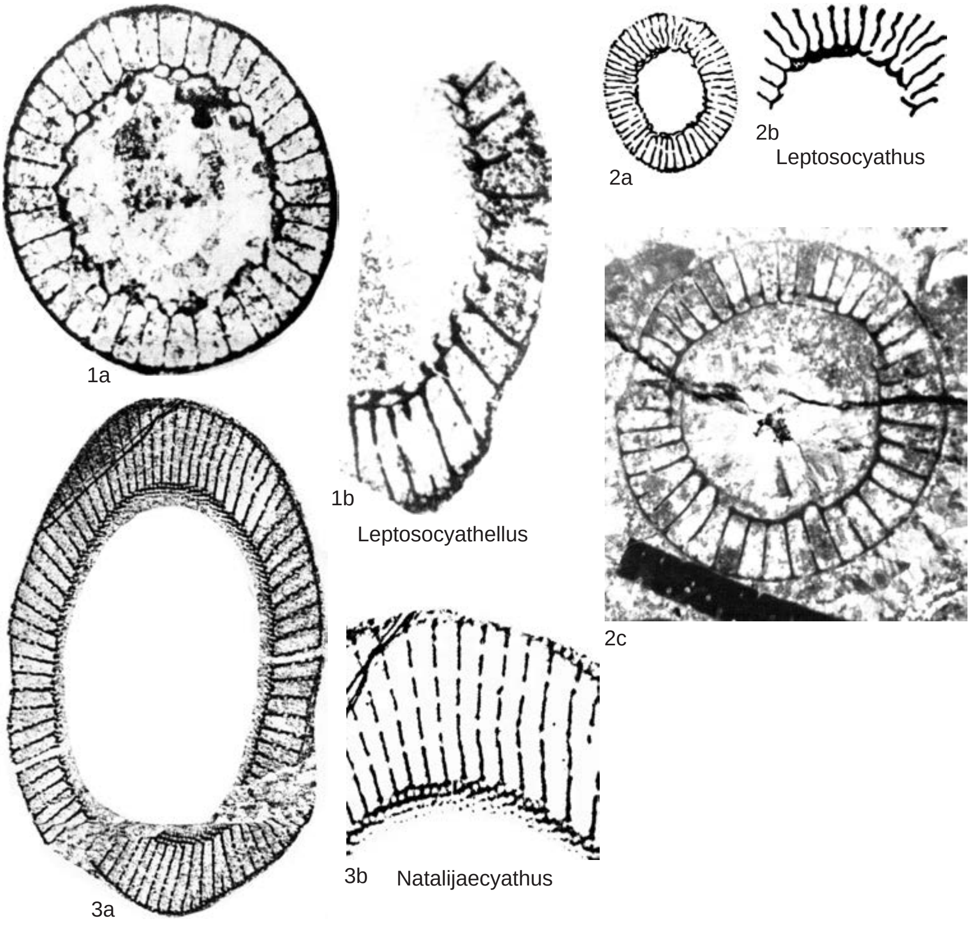


FIG. 537. Densocyathidae (p. 940).

canicus, Pestrotsvet Formation, Atdabanian, Malykan, Lena River, Sakha (Yakutia), Russia, holotype, PIN 4297/79, detail of oblique transverse section, ×15 (Zhuravleva, Korshunov, & Rozanov, 1969).

Family BRONCHOCYATHIDAE R. Bedford & J. Bedford, 1936

[Bronchocyathidae R. BEDFORD & J. BEDFORD, 1936, p. 25] [=Stillicidocyathidae TING, 1937, p. 367; =Thalamocyathidae ZHURAVLEVA, 1954, p. 28; =Cyclocyathellidae ZHURAVLEVA, 1960c, p. 74; =Trininaecyathidae DEBRENNE, 1964, p. 114; =Compositocyathidae ZHURAVLEVA in ZHURAVLEVA & others, 1967, p. 52; =Glaessnericyathidae DEBRENNE, 1970a, p. 35]

Inner wall with annuli. *lower Cambrian (Atd.1–Bot.3).*

Thalamocyathus GORDON, 1920, p. 687 [**Archaeocyathus trachealis* TAYLOR, 1910, p. 125; SD TING, 1937, p. 368, by elimination; lectotype, TAYLOR, 1910, pl. 8, photo 47(8); HILL, 1965, pl. 7,*1*; DEBRENNE, 1973, pl. 1,*6;* SD DEBRENNE, 1969b, p. 262; SAM T1555A, Adelaide] [=*Bronchocyathus* R. BEDFORD & J. BEDFORD, 1936, p. 25 (type, *Archaeocyathus trachealis* TAYLOR, 1910, p. 125, OD); =*Thalamopectinus* DEBRENNE, 1973, p. 8 (type, *T. arterialis*, OD; =*Archaeocyathus trachealis* TAYLOR, 1910, p. 125), for discussion, see DEBRENNE & KRUSE, 1989, p. 27; =*Gordonicyathella* YAZMIR in ZHURAVLEVA, 1974a, p. 160, *nom. nud.*; =*Gordonicyathellus* YAZMIR in YAZMIR, DALMATOV, & YAZMIR, 1975, p. 48 (type, *G. solidus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 136; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 164]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Bot.3):* Altay Sayan, Tuva, Mongolia, Transbaikalia, South China, Australia, Antarctica, South Africa (allochthonous), Falkland

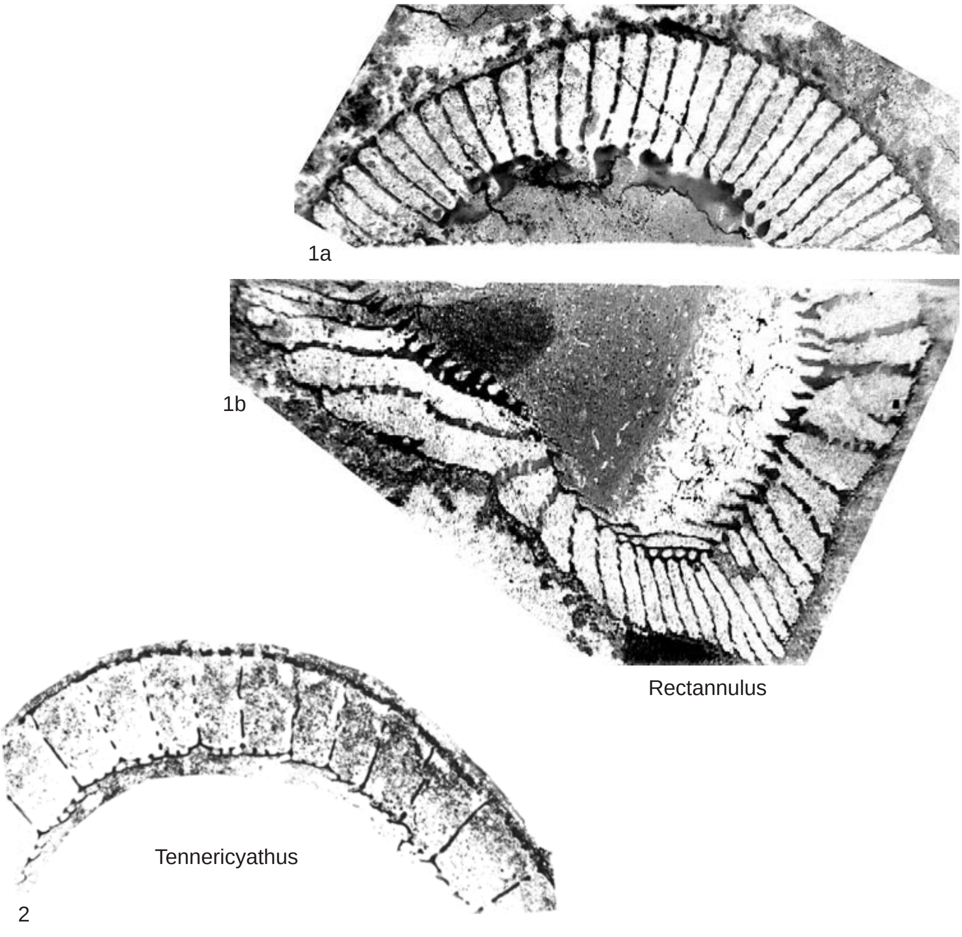


FIG. 538. Densocyathidae (p. 940–941).

Islands (allochthonous).——FIG. 539,*1a–b*. **T. trachealis* (TAYLOR), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1555A; *a,* transverse view, ×3.5 (Debrenne, 1973); *b,* external longitudinal view of cup, ×8 (Taylor, 1910).

Compositocyathus ZHURAVLEVA, 1960b, p. 159 [**Thalamocyathus muchattensis* ZHURAVLEVA in ZHURAVLEVA & ZELENOV, 1955, p. 71; OD; holotype, ZHURAVLEVA & ZELENOV, 1955, pl. 2,*1–2;* ZHURAVLEVA, 1960b, pl. 10,*3–5,* TsSGM 205/47a-b, Novosibirsk]. Inner wall with one pore row per intersept and planar annuli bearing short beams that support supplementary microporous sheath; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Transbaikalia.——FIG. 539,*2a–b*. **C. muchattensis* (ZHURAVLEVA), Pestrotsvet Formation, Atdabanian, Mukhatta River, Lena River, Sakha (Yakutia), Russia; *a,* holotype, TsSGM 205/47b, longitudinal section (outer wall to left), ×7 (Zhuravleva & Zelenov, 1955); *b,* topotype TsSGM 323, oblique transverse section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Conannulofungia YUAN in YUAN & ZHANG, 1980, p. 383 [**C. jinshaensis*; OD; holotype, YUAN & ZHANG, 1980, pl. 2,*1a–f*, NIGP 51288, Nanjing]. Inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli linked to septa by ribs; septa completely porous, linked by synapticulae. *lower Cambrian (Bot.1–Bot.2):* South China.——FIG. 540,*1a–c*. **C. jinshaensis*, Minxinsi (Minghsingssu) Formation, Botoman, Yankong, Guizhou, China; *a–b,* holotype, NIGP 51288; *a,* transverse section, ×4; *b,* longitudinal section near inner wall, ×4 (Yuan & Zhang, 1980); *c,* specimen MNHN M85006, longitudinal section near inner wall, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

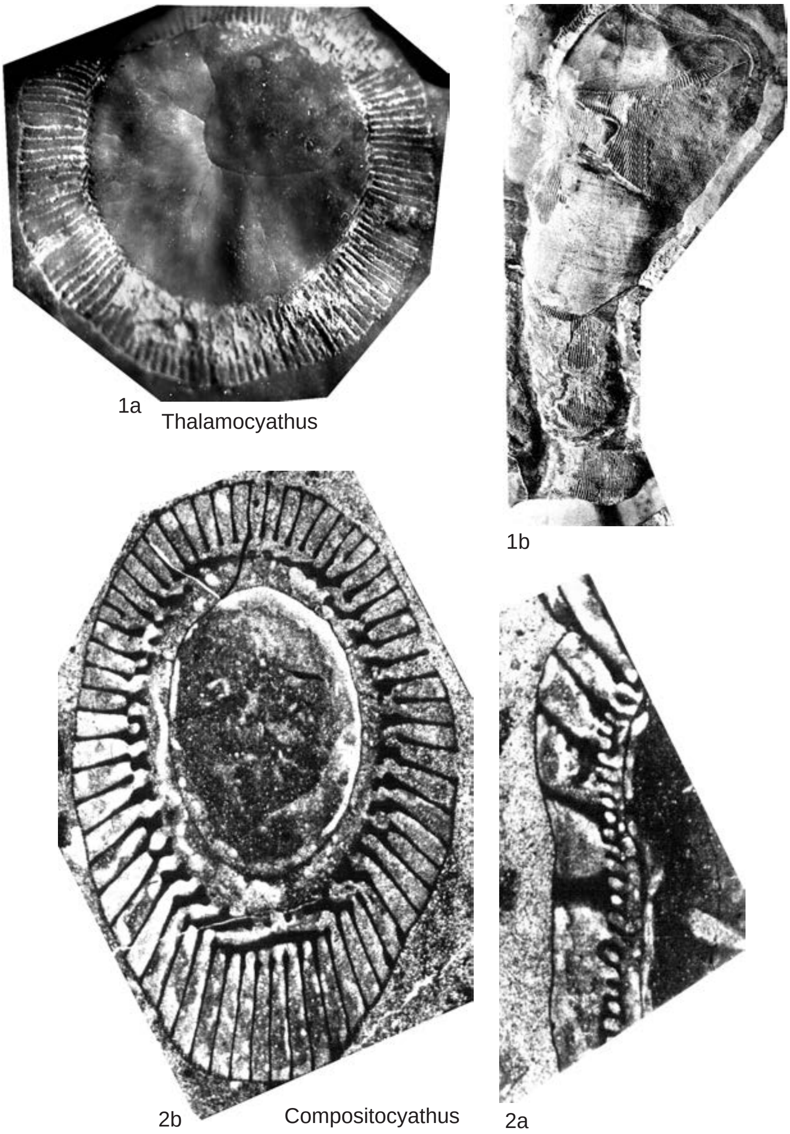


FIG. 539. Bronchocyathidae (p. 941–942).

Cyathocricus DEBRENNE, 1969a, p. 318 [**Archaeocyathus tracheodentatus* R. BEDFORD & W. R. BEDFORD, 1934, p. 2; OD; lectotype, R. BEDFORD & W. R. BEDFORD, 1934, fig. 5; DEBRENNE, 1969a, pl. 5,*4–5;* SD DEBRENNE, 1969a, p. 319, NHM S4148, London; =*Ethmophyllum dentatum* TAYLOR, 1910, p. 129; lectotype, TAYLOR, 1910, pl. 16, photo 89; DEBRENNE, 1970a, pl. 1,*1;* SD DEBRENNE, 1974b, p. 132, SAM T1606C-D, Adelaide] [=*Cricopectinus* DEBRENNE, 1970a, p. 32 (type, *C. dentulus*, OD)]. Inner wall with one pore row per intersept and commonly horizontally projecting waved annuli that may mutually coalesce; denticles may be present on annular rims; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (?Atd.4–Bot.3):* Altay Sayan, Tuva, Far East, Australia, Antarctica, ?Morocco.——FIG. 540,*2a–c*. **C. dentatus* (TAYLOR), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1606C-D; *a,* transverse view, ×6; *b,* oblique longitudinal view, ×5 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* oblique longitudinal view, ×4 (Taylor, 1910).

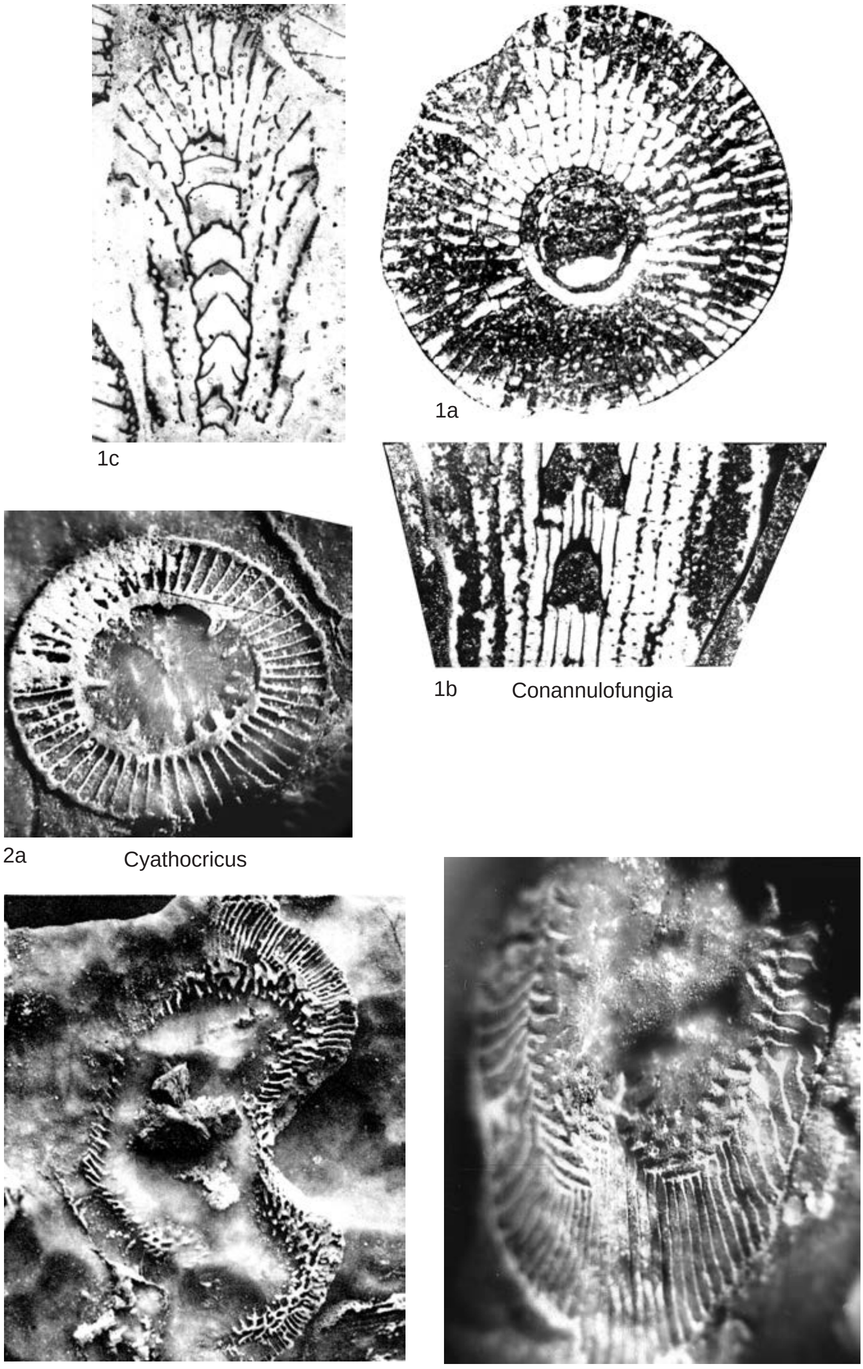


FIG. 540. Bronchocyathidae (p. 942–943).

Cyclocyathella VOLOGDIN in ZHURAVLEVA, KRASNOPEEVA, & CHERNYSHEVA, 1960, p. 105 [**Cyclocyathus yakovlevi* VOLOGDIN, 1931, p. 49; OD; lectotype, VOLOGDIN, 1931, pl. 4,*7–8;* SD DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1569, TsNIGRm 44a/2956, St. Petersburg] [=*Cyclocyathus* VOLOGDIN, 1928, p. 30, *nom. nud.*, *non* MILNE-EDWARDS & HAIME, 1850, p. liv, scleractinian, *nec* DUNCAN & THOMPSON, 1867, p. 1, rugose coral; =*Cyclocyathus* SIMON, 1939, p. 27 (type, *C. yakovlevi* VOLOGDIN, 1931, p. 49)]. Inner wall with one pore row per intersept and inverted V-shaped annuli; septa completely porous. *lower Cambrian (Atd.2):* Altay Sayan, Tuva, Far East.——FIG. 541,*1a–c*. **C. yakovlevi* (VOLOGDIN), Torgashino Formation, Atdabanian, Kameshki, East Sayan, Altay Sayan, Russia; *a,* paralectotype, TsNIGRm 45/2956, transverse section, ×6; *b,* paralectotype, TsNIGRm 47a/2956, longitudinal section, ×6; *c,* schematic sketch of septum in longitudinal section (outer wall to left), ×8 (Vologdin, 1931).

Denaecyathus ZHURAVLEVA in ZHURAVLEVA & others, 1967, p. 57 [**D. biporosus*; OD; holotype, ZHURAVLEVA & others, 1967, pl. 17,*5–6*, TsSGM 325/17, Novosibirsk]. Inner wall with several pore rows per intersept and upright, V-shaped annuli; septa aporose to sparsely porous. *lower Cambrian (Bot.1)*: Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East.——FIG. 541,*2a–c*. **D. biporosus*, Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia; *a,* holotype, TsSGM 325/17, oblique transverse section, ×5; *b,* paratype, TsSGM 325/16, oblique longitudinal section (outer wall at bottom), ×5; *c,* holotype, TsSGM 325/17, oblique transverse section (outer wall to left), ×5 (Zhuravleva & others, 1967).

Gordonicyathus ZHURAVLEVA, 1959, p. 426 [**Thalamocyathus gerassimovensis* KRASNOPEEVA, 1955, p. 95; OD; holotype not designated, collection not located] [=*Sichotecyathus* OKUNEVA in OKUNEVA & REPINA, 1973, p. 138 (type, *S. orientalis*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 109; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 144]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Australia.——FIG. 541,*3*. **G. gerassimovensis* (KRASNOPEEVA), Verkhnemonok Formation, Botoman, Gerasimov Spring, Monok River, West Sayan, Altay Sayan, Russia, unlocated syntype, oblique transverse section, ×7 (Krasnopeeva, 1955).

Gordonifungia ROZANOV in REPINA & others, 1964, p. 193 [**G. batinensis*; OD; holotype, REPINA & others, 1964, pl. 11,*1*, PIN 4297/24, Moscow]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.3–Bot.1):* Altay Sayan, ?Morocco.——FIG. 542,*1*. **G. batinensis*, Usa Formation, Atdabanian, Verkhnyaya Erba, Batenev Range, Kuznetsk Alatau, Russia, holotype, PIN 4297/24, oblique transverse section, ×4 (Repina & others, 1964).

Morenicyathus PEREJÓN, 1975b, p. 169 [**M. arruzafai*; OD; holotype, PEREJÓN, 1975b, pl. 6,*5–6;* PEREJÓN, 1975c, pl. 6,*8–9*, CE 62-14, Madrid; =*Archaeocyathellus (Protocyathus) cordobae* SIMON, 1939, p. 74; holotype, SIMON, 1939, pl. 2,*11*, SM 26-179e, Frankfurt am Main] [=*Kellericyathus* ROZANOV, 1973, p. 61, *nom. nud.*; =*Denaecyathellus* OSADCHAYA in OSADCHAYA & others, 1979, p. 122 (type, *D. makarichus*, OD); =*Kellericyathus* ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 114 (type, *K. altaicus*, OD)]. Inner wall with several pore rows per intersept and upright, V-shaped annuli; septa completely porous. *lower Cambrian (Atd.2–Atd.3):* Kolyma, Altay Sayan, Iberia.——FIG. 542,*2a–b*. **M. cordobae* (SIMON) [=*M. arruzafai* PEREJÓN], Pedroche Formation, Atdabanian, Las Ermitas, Cordoba, Andalusia, Spain, holotype, CE 62-14; *a,* oblique transverse section, ×4; *b,* detail of longitudinal section (outer wall to left), ×8 (Perejón, 1975c).

Pseudotennericyathellus OSADCHAYA in OSADCHAYA & others, 1979, p. 120 [**Tennericyathus latus* OSADCHAYA in ZADOROZHNAYA, OSADCHAYA, & REPINA, 1973, p. 134; OD; holotype, ZADOROZHNAYA, OSADCHAYA, & REPINA, 1973, pl. 19,*3;* OSADCHAYA & others, 1979, pl. 5,*1–2*, TsSGM IGiG424, Novosibirsk]. Inner wall with several pore rows per intersept and upwardly projecting, S-shaped annuli; septa completely porous. *lower Cambrian (Atd.2–Atd.4):* Altay Sayan, Mongolia.——FIG. 542,*3a–b*. **P. latus* (OSADCHAYA), Usa Formation, Atdabanian, Bograd, Batenev Range, Kuznetsk Alatau, Russia, holotype, TsSGM IGiG424; *a,* transverse section, ×9; *b,* longitudinal section (outer wall to left), ×9 (Osadchaya & others, 1979).

Sagacyathus KRUSE, 1982, p. 178 [**S. stonyx*; OD; holotype, KRUSE, 1982, fig. 15D–H, AM F.83576, Sydney]. Inner wall with one pore row per intersept and upright, V-shaped annuli bearing denticulate rims; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Atd.4–Bot.3):* Altay Sayan, Mongolia, Far East, Australia.——FIG. 542,*4a–c*. **S. stonyx*, Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia, holotype, AM F.83576; *a,* transverse section AM FT.8487, ×6; *b,* oblique longitudinal section AM FT.8486, ×4; *c,* longitudinal section AM FT.8490, ×4 (Kruse, 1982).

Stillicidocyathus TING, 1937, p. 367 [**Coscinocyathus aulax* TAYLOR, 1910, p. 139; OD; lectotype, TAYLOR, 1910, pl. 10, photo 57; SD DEBRENNE, 1969b, p. 263, SAM T1605A-B, Adelaide] [=*Glaessnericyathus* DEBRENNE, 1970a, p. 35 (type, *Bronchocyathus sigmoideus* R. BEDFORD & J. BEDFORD, 1936, p. 25, OD), for discussion, see GRAVESTOCK, 1984, p.

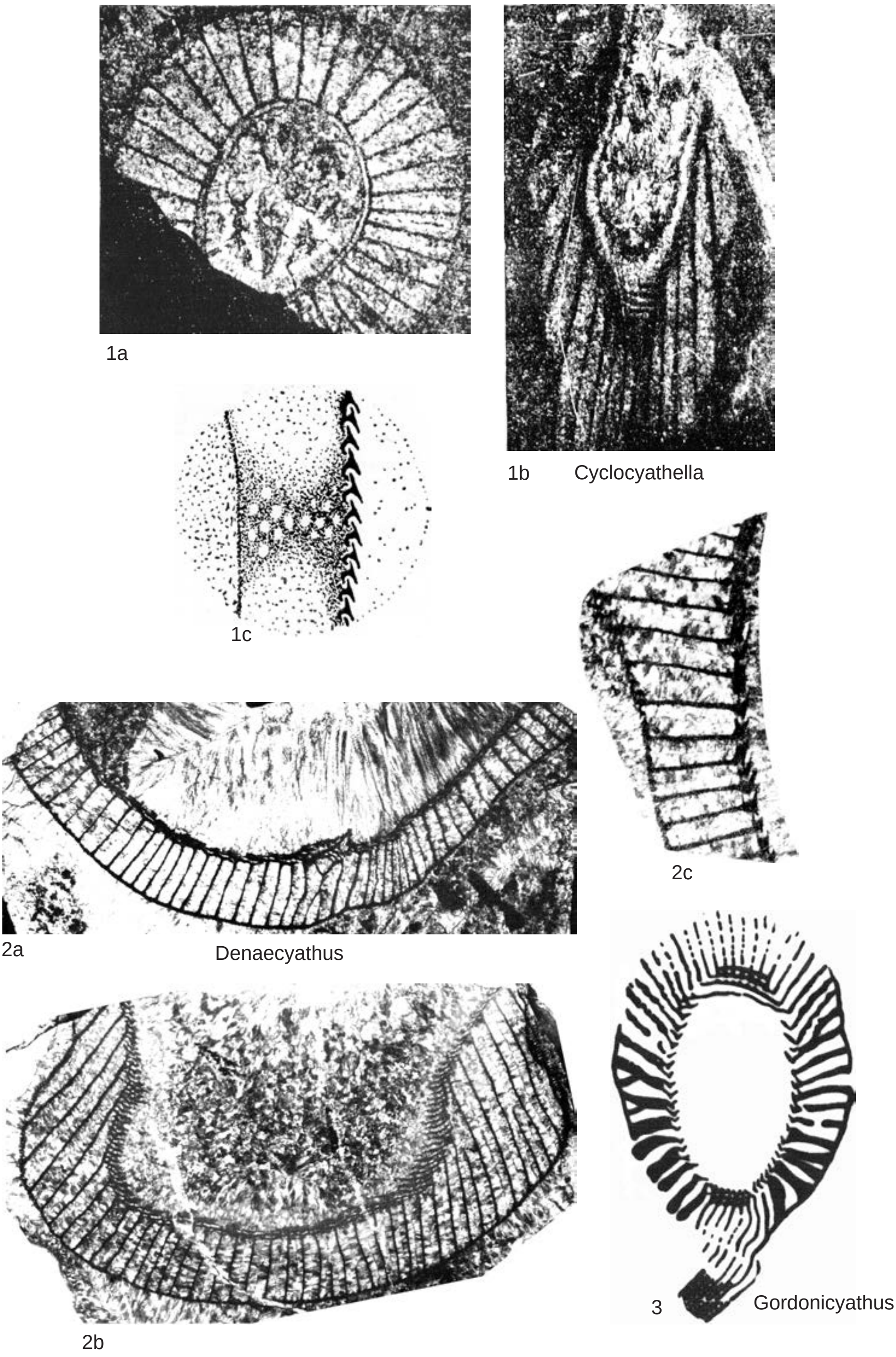


FIG. 541. Bronchocyathidae (p. 945).

69; Debrenne, Zhuravlev, & Rozanov, 1989, p. 133; Debrenne, Rozanov, & Zhuravlev, 1990, p. 162]. Inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1–Bot.3):* Altay Sayan, Tuva, Mongolia, Australia, Antarctica, South China, Iberia, Sardinia.——Fig. 543,*1*. **C. aulax* (Taylor), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1605A-B, longitudinal view, ×7 (Taylor, 1910).

Svetlanocyathus Missarzhevskiy & Rozanov, 1962, p. 43 [**S. primus*; OD; holotype, Missarzhevskiy & Rozanov, 1962, pl. 3,*2a–v;* Rozanov, 1973, pl. 1,*5*, PIN 4297/19-20, Moscow]. Outer wall with slitlike, simple pores; inner wall with one pore row per intersept and inverted V-shaped annuli; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Altay Sayan, Tuva.——Fig. 543,*2*. **S. primus*, Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia, holotype, PIN 4297/19-20, oblique transverse view, ×5 (Debrenne, Zhuravlev, & Rozanov, 1989).

Taylorcyathus Vologdin, 1955, p. 143 [**Cyclocyathus subtersiensis* Vologdin, 1940b, p. 63; OD; holotype not designated, collection not located] [=*Tersicyathus* Vologdin, 1955, p. 143 (type, *Cyclocyathus tersiensis* Vologdin, 1931, p. 87, OD); =*Thalamocyathellus* Osadchaya in Osadchaya & others, 1979, p. 155 (type, *T. inclinatus*, OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 134; Debrenne, Rozanov, & Zhuravlev, 1990, p. 163; =*Pospelovicyathus* Konyaeva in Zhuravleva & others, 1997a, p. 49 (type, *P. gravis*, OD)]. Inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Australia, Iberia, France, Sardinia.——Fig. 543,*3*. **T. subtersiensis* (Vologdin), Gavrilovskoe Formation, Atdabanian, Belaya Gorka, Salair, Russia, topotype, PIN 4754/50, oblique transverse section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Taylorfungia Perejón, 1989, p. 180 [**Thalamocyathus synapticulosus* Zhuravleva, 1955a, p. 41; OD; holotype, Zhuravleva, 1955a, pl. 5,*1*, PIN 495, Moscow, not located]. Inner wall with one pore row per intersept and upwardly projecting, planar to S-shaped annuli; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.2–Atd.3):* Altay Sayan.——Fig. 543,*4*. **T. synapticulosa* (Zhuravleva), Usa Formation, Atdabanian, Bol'shaya Erba (Potekhino), Batenev Range, Kuznetsk Alatau, Russia, holotype, PIN 495, oblique transverse section, ×8 (Zhuravleva, 1955a).

Trininaecyathus Zhuravleva, 1960b, p. 218 [**T. macroporus*; OD; holotype not located; paratypes, Zhuravleva, 1960b, pl. 18,*6–8,* fig. 122, TsSGM 205/100, 205/101, Novosibirsk]. Inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli bearing denticulate rims; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1):* Siberian Platform.——Fig. 543,*5*. **T. macroporus*, Perekhod Formation, Botoman, Botoma River, Sakha (Yakutia), Russia, paratype, TsSGM 205/100, oblique transverse section, ×8 (Zhuravleva, 1960b).

Family ETHMOCYATHIDAE
Debrenne, 1969

[Ethmocyathidae Debrenne, 1969a, p. 322] [=Ethmopectinidae Debrenne, 1970a, p. 25; =Zonacyathellidae Zhuravleva in Zhuravleva & Elkina, 1974, p. 65; =Baikalocyathinae Zhuravleva in Zhuravleva & Elkina, 1974, p. 68; =Inessocyathidae Zhuravleva in Zhuravleva & Elkina, 1974, p. 106; =Hyptocyathidae Kruse, 1978, p. 29; =Gnaltacyathidae Kruse, 1982, p. 166; =Baikalopectinidae Gravestock, 1984, p. 66]

Inner wall with noncommunicating canals. *lower Cambrian (Atd.1–Bot.3).*

Ethmocyathus R. Bedford & W. R. Bedford, 1934, p. 2 [**E. lineatus;* M; holotype, R. Bedford & W. R. Bedford, 1934, fig. 8; Hill, 1965, pl. 4,*2;* Debrenne, 1969a, pl. 5,*1–3;* Debrenne, 1974b, pl. 27,*1;* NHM S4149, M, London] [=*Ethmopectinus* Debrenne, 1970a, p. 34 (type, *E. walteri,* OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 106; Debrenne, Rozanov, & Zhuravlev, 1990, p. 142]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept, formed by flexure of inner edges of septa; supplementary screen of planar rings on central cavity side; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.3):* Australia, Antarctica, Falkland Islands (allochthonous).——Fig. 544,*1a–b*. **E. lineatus*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, NHM S4149; *a,* longitudinal view of inner wall, ×7; *b,* oblique longitudinal view of inner wall (to left) and septa (to right), ×15 (Debrenne, 1969a).

Afiacyathus Voronin, 1962, p. 26 [**A. lativallum*; OD; holotype, Voronin, 1962, pl. 4,*4–5*, PIN 1914/74-80a, Moscow, not located] [=*Axiculifungia* F. Debrenne & M. Debrenne in F. Debrenne, M. Debrenne, & Rozanov, 1976, p. 102 (type, *Ajacicyathus compositus* Debrenne, 1961, p. 9, OD)]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.2–Bot.1):* Tuva, Morocco, South China, Iberia, Sardinia, ?Poland.——Fig. 544,*2a–b*. **A. lativallum*, Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia, holotype, PIN 1914/74-80a; *a,* oblique transverse view, ×2; *b,* oblique longitudinal view, ×2 (Voronin, 1962).

Baikalocyathus Yazmir in Zhuravleva, 1974a, p. 55 [**Ethmophyllum rossicum* Zhuravleva, 1960b, p. 164; OD; holotype, Zhuravleva, 1960b, pl. 11,*2*, TsSGM 205/51, Novosibirsk] [=*Nochoroicyathella* Korshunov, 1983b, p. 110 (type, *N. fragilis*, OD); =*Baikalopectinus* Gravestock, 1984, p. 66 (type,

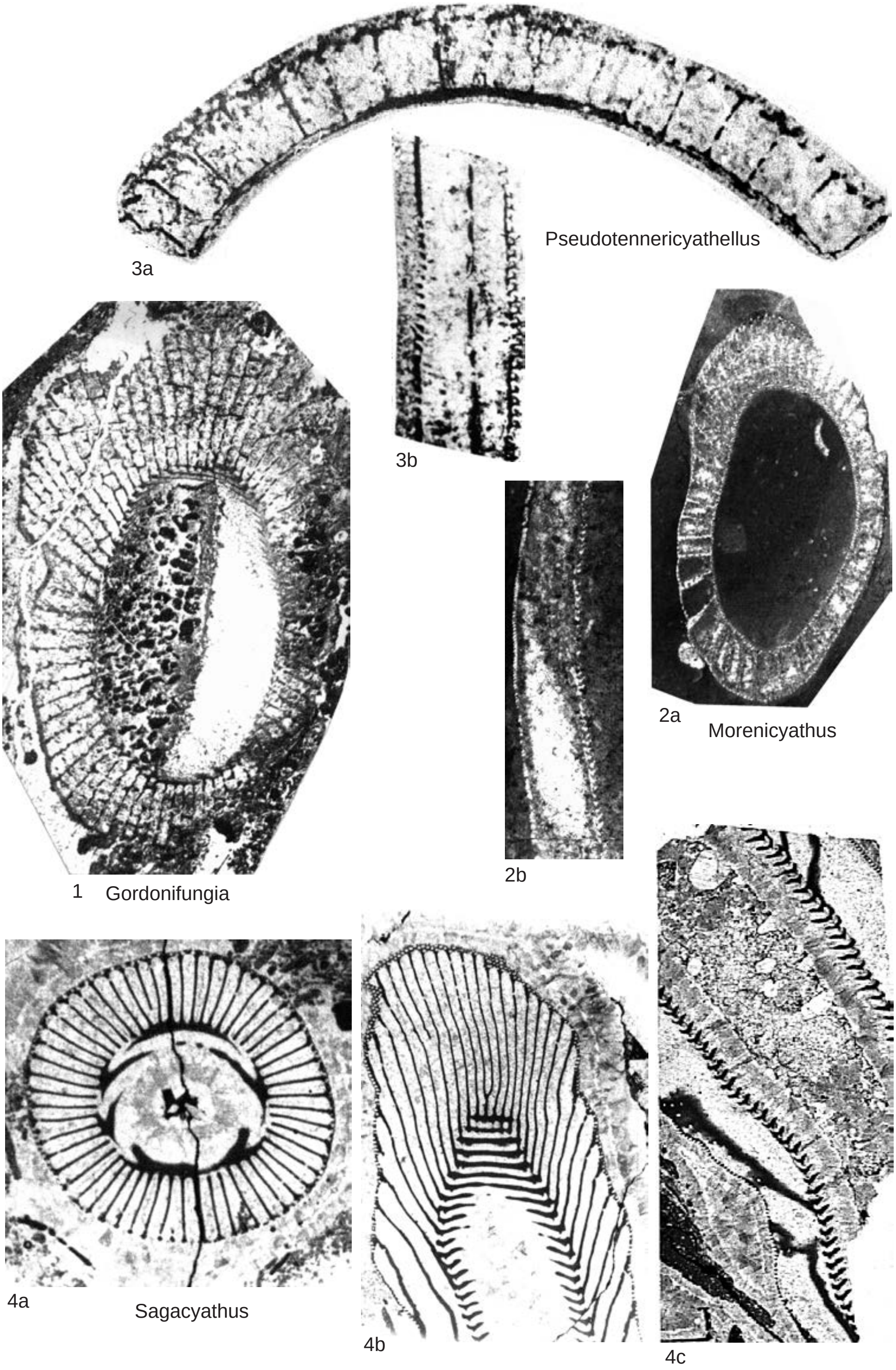
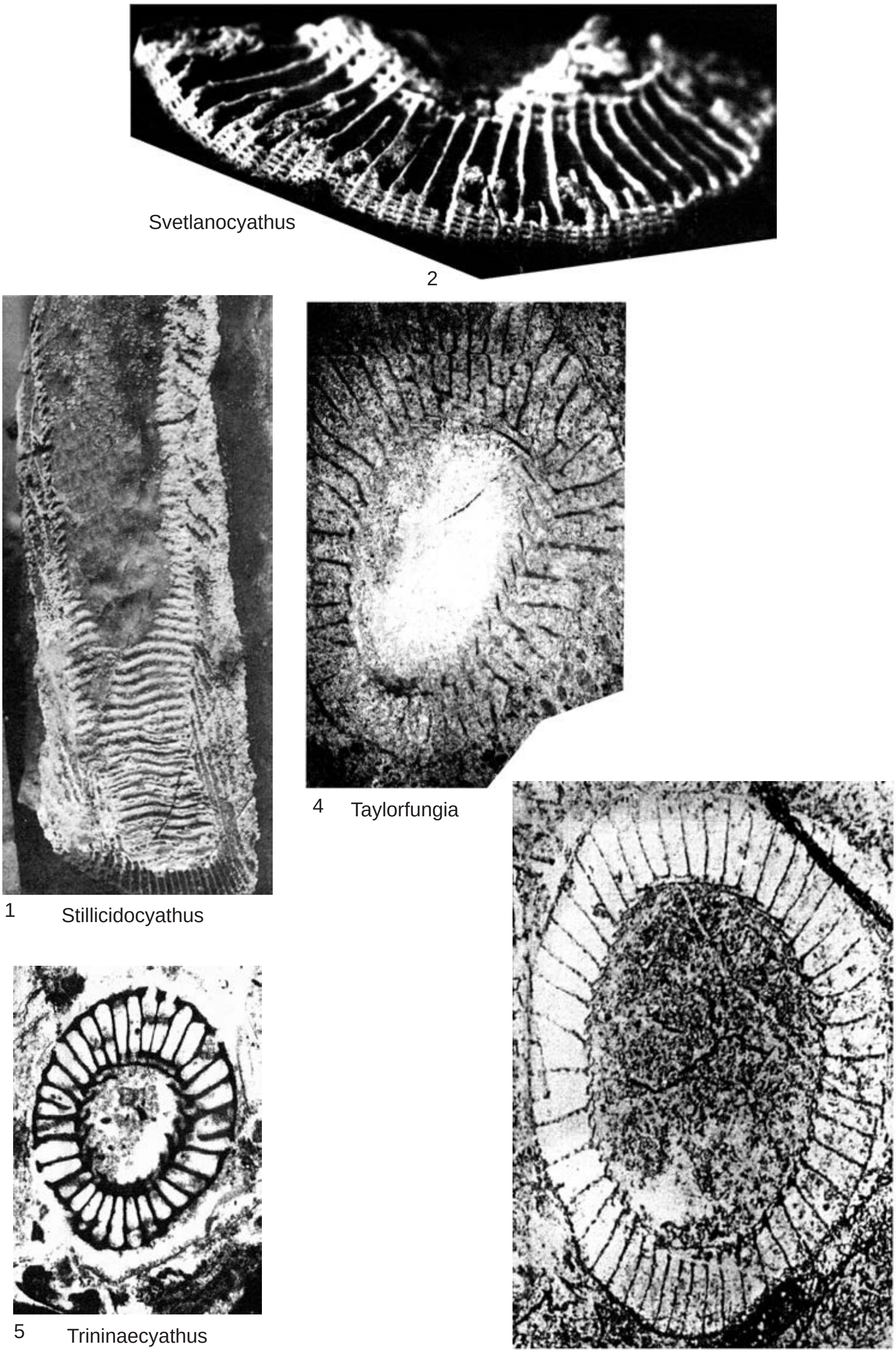


FIG. 542. Bronchocyathidae (p. 945).



Svetlanocyathus
2

4 Taylorfungia

1 Stillicidocyathus

5 Trininaecyathus

3 Taylorcyathus

FIG. 543. Bronchocyathidae (p. 945–947).

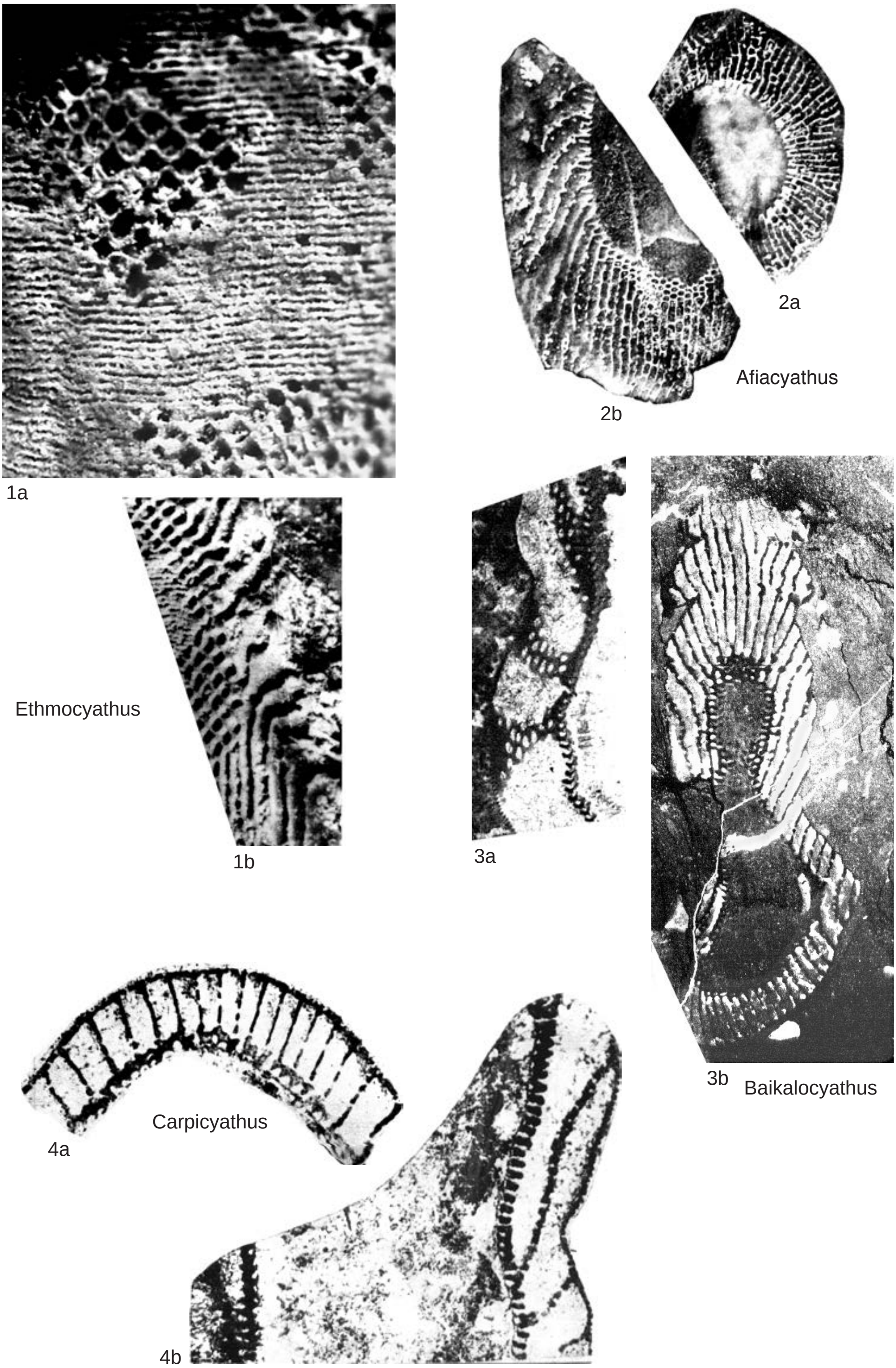


FIG. 544. Ethmocyathidae (p. 947–951).

B. capulus, OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 95; Debrenne, Rozanov, & Zhuravlev, 1990, p. 134]. Inner wall with one row of downwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Kolyma, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Australia, ?Morocco.——Fig. 544,*3a–b.* **B. rossicus* (Zhuravleva); *a,* Pestrotsvet Formation, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 205/51, detail of longitudinal section of septum (outer wall to left), ×10 (Zhuravleva, 1960b); *b,* Pestrotsvet Formation, Atdabanian, Mukhatta River, Lena River, Sakha (Yakutia), Russia, paratype, TsSGM 205/52, oblique longitudinal section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Carpicyathus Osadchaya in Zhuravleva & others, 1967, p. 51 [**C. mysticus*; OD; holotype, Zhuravleva & others, 1967, pl. 14,*3–6*, VSEGEI 9594, St. Petersburg]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa completely porous. *lower Cambrian (Atd.2–Bot.2):* Altay Sayan, Tuva, Transbaikalia, Morocco.——Fig. 544,*4a–b.* **C. mysticus*, Shangan Formation, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia, holotype, VSEGEI 9594; *a,* transverse section, ×1.5; *b,* longitudinal section, ×3.5 (Zhuravleva & others, 1967).

Degeletticyathus Zhuravleva in Zhuravleva, Korshunov, & Rozanov, 1969, p. 36 [**Ethmophyllum? galuschkoi* Zhuravleva, 1960b, p. 169; OD; holotype, Zhuravleva, 1960b, pl. 11,*7*, TsSGM 205/56, Novosibirsk] [=*Degeletticyathellus* Zhuravleva in Zhuravleva & Elkina, 1974, p. 66 (type, *D. lebedevae,* OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 103]. Inner wall with horizontal to upwardly projecting, straight stirrup canals only; septa aporose to sparsely porous. *lower Cambrian (Atd.2–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Tajikistan, Australia, Morocco.——Fig. 545,*1a–b.* **D. galuschkoi* (Zhuravleva), Oy-Muran reef massif, Botoman, Lena River, Sakha (Yakutia), Russia; *a,* specimen TsSGM 323/40, transverse section, Oy-Muran, ×5 (Zhuravleva, Korshunov, & Rozanov, 1969); *b*, holotype, TsSGM 205/56, longitudinal section of septum (outer wall to left), Mukhatta River, ×5 (Zhuravleva, 1960b).

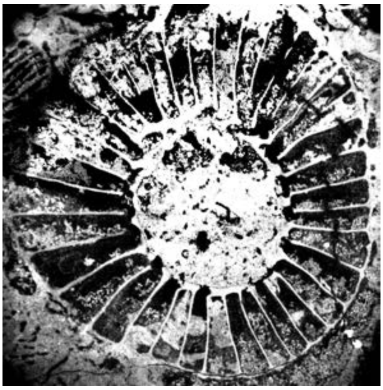
Frinalicyathus Debrenne, Rozanov, & Zhuravleva in Zhuravleva & Elkina, 1974, p. 73 [**Leptosocyathus altaicus* Rozanov in Repina & others, 1964, p. 190; OD; holotype, Repina & others, 1964, pl. 4,*2*, PIN 4297/21, Moscow] [=*Pseudodegeletticyathellus* Osadchaya in Osadchaya & others, 1979, p. 123 (type, *P. ladae*, OD), for discussion, see Debrenne, Rozanov, & Zhuravlev, 1990, p. 143]. Inner wall with downwardly projecting, straight stirrup canals only, bearing supplementary scales on central cavity side; septa completely porous. *lower Cambrian (Atd.1–Atd.4):* Altay Sayan, Mongolia.——Fig. 545,*2.* **F. altaicus* (Rozanov), Verkhneynyrga Formation, Atdabanian, Tyrga River, Altay Mountains, Altay Sayan, Russia, holotype, PIN 4297/21, transverse section, ×3 (Repina & others, 1964).

Gnaltacyathus Kruse, 1982, p. 166 [**G. nodus*; OD; holotype, Kruse, 1982, pl. 3,*2–4*, AM FT.8453, 8454, 8495b, Sydney]. Inner wall with horizontal to upwardly projecting, straight canals, each canal spanning several intersepts; septa completely porous. *lower Cambrian (Bot.1–Bot.3):* Tuva, ?Mongolia, Australia.——Fig. 545,*3a–b.* **G. nodus*, Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia, holotype, AM FT.8453, 8454, 8495b; *a,* transverse section, AM FT.8495b, ×8; *b,* longitudinal section, AM FT.8454, ×8 (Kruse, 1982).

Hyptocyathus Kruse, 1978, p. 30 [**H. licinus*; OD; holotype, Kruse, 1978, fig. 2–3, AM F.83402, Sydney]. Inner wall with downwardly projecting, straight stirrup canals only, bearing upwardly projecting, branching canals on central cavity side; septa aporose to sparsely porous. *lower Cambrian (Bot.3):* Australia.——Fig. 546,*1a–c.* **H. licinus*, Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia, holotype, AM F.83402; *a,* oblique transverse section, AM FT.14171, ×4; *b,* longitudinal section, AM FT.14173, ×4; *c,* tangential section of inner wall, AM FT.14174, ×15 (Kruse, 1978).

Inessocyathellus Belyaeva in Zhuravleva & Elkina, 1974, p. 78 [**I. synapticulosus*; OD; holotype, Zhuravleva & Elkina, 1974, pl. 7,*3*, DVGU, Khabarovsk]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa aporose to sparsely porous, linked by synapticulae. *lower Cambrian (Bot.3):* Far East.——Fig. 546,*2a–b.* **I. synapticulosus*, Ust'toka unit, Botoman, Verkhneurminsk Spring, Dzhagdy Range, Far East, Russia, holotype, DVGU, Khabarovsk; *a,* transverse section, ×10; *b,* oblique longitudinal section, ×10 (Zhuravleva & Elkina, 1974).

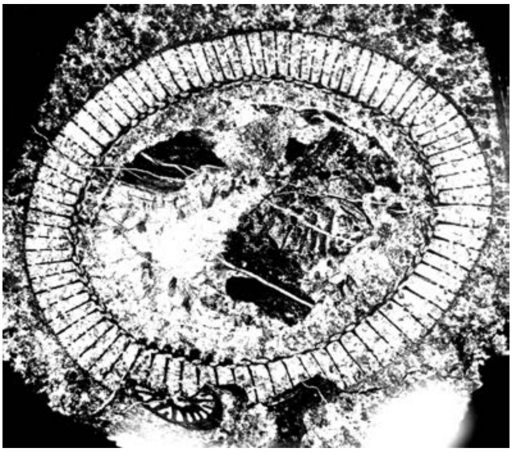
Inessocyathus Debrenne, 1964, p. 143 [**Archaeocyathus spatiosus* Bornemann, 1886, p. 59; OD; lectotype, Bornemann, 1886, pl. 15,*1a;* SD Debrenne, 1964, p. 143, not located; topotype, Debrenne, 1964, pl. 9,*1–2*, MNHN M84074, specimen SPi-13, Paris] [=*Voroninicyathus* Zhuravleva in Zhuravleva & Elkina, 1974, p. 79 (type, *Inessocyathus karakolicus* Voronin, 1969, p. 103, OD); =*Rowanpectinus* Gravestock, 1984, p. 67 (type, *R. clarus*, OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 112; Debrenne, Rozanov, & Zhuravlev, 1990, p. 146]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East, Australia, South China, Morocco, Iberia, France, Sardinia, Germany.——Fig. 546,*3a–b.* **I. spatiosus* (Bornemann), Matoppa Formation, Botoman, San Pietro, Sardinia, Italy; *a,* lectotype, transverse section, ×2.5 (Bornemann, 1886); *b,* topotype,



1a

Degeletticyathus

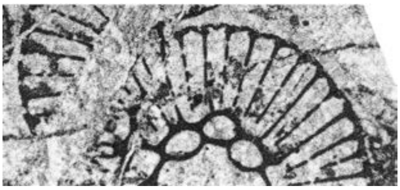
1b



2 Frinalicyathus

3a

Gnaltacyathus



3b

FIG. 545. Ethmocyathidae (p. 951).

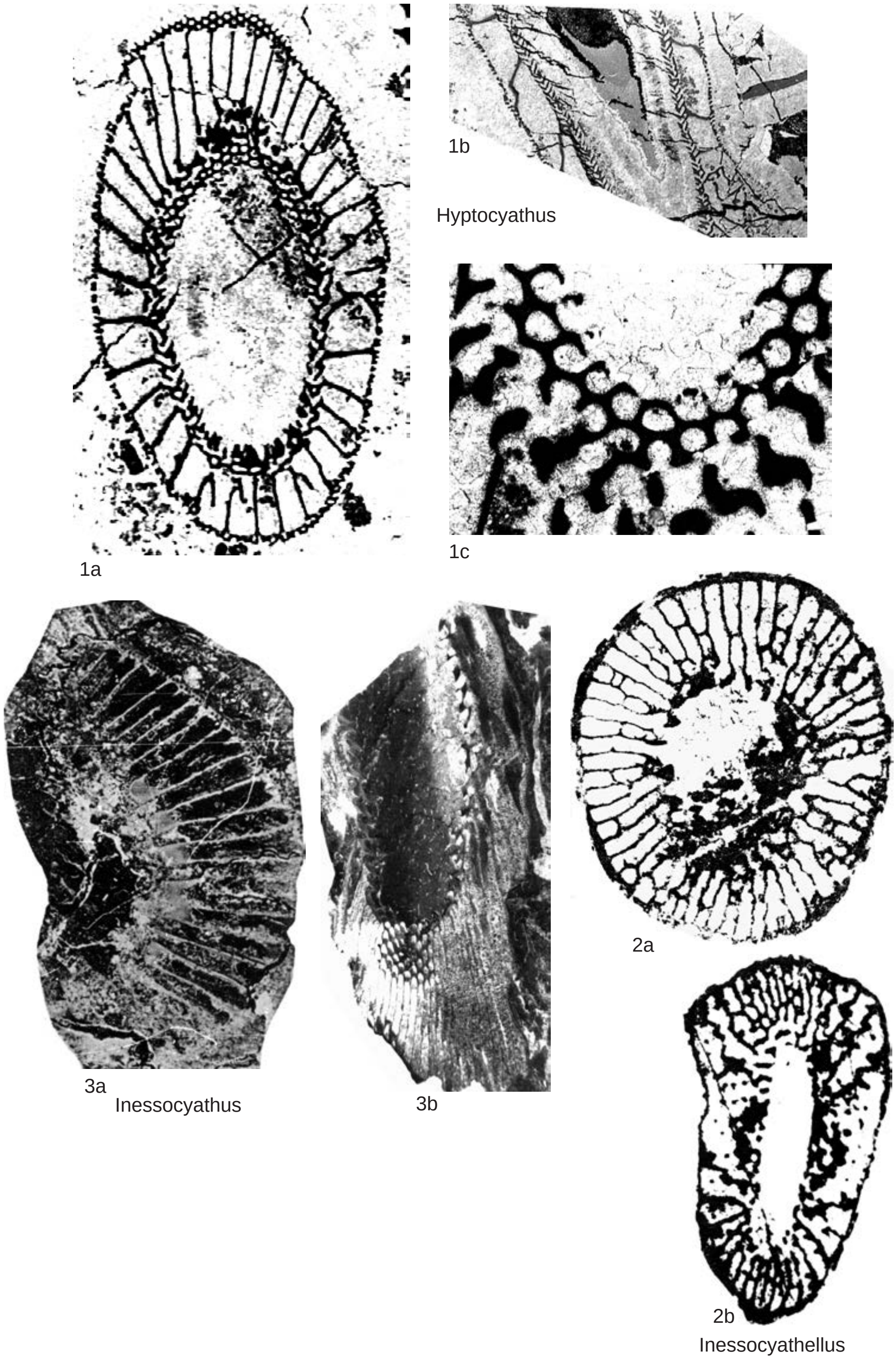


FIG. 546. Ethmocyathidae (p. 951–954).

MNHN M84074, specimen SPi-13, longitudinal section, ×2.5 (Debrenne, Zhuravlev, & Kruse, 2002).

Mackenziecyathus Handfield, 1971, p. 43 [**M. bukryi*; OD; holotype, Handfield, 1971, pl. 5,*1a–d*, GSC 25334, Ottawa] [=*Ussuricyathus* Okuneva in Okuneva & Repina, 1973, p. 113 (type, *U. kropotkini*, OD)]. Inner wall with horizontal to upwardly projecting straight stirrup canals only, bearing supplementary scales on central cavity side; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1):* Altay Sayan, Tuva, Mongolia, Far East, Canada, United States.——Fig. 547,*1a–c*. **M. bukryi*, unnamed Sekwi Formation equivalent (map unit 5 of Handfield, 1971), Botoman, Coal River, Yukon Territory, Canada, holotype, GSC 25334; *a,* transverse section, ×4; *b,* longitudinal section (outer wall to right), ×4; *c,* tangential section of inner wall, ×4 (Handfield, 1971).

Rasetticyathus Debrenne, 1971, p. 193 [**R. iglesiensis*; OD; holotype, Debrenne, 1971, fig. 1–2, not located; =*Archaeocyathus acutus* Bornemann, 1886, p. 50; holotype not designated; for discussion, see Debrenne, Rozanov, & Zhuravlev, 1990, p. 157]. Inner wall with one row of horizontal to upwardly projecting, S-shaped canals per intersept; septa aporose to sparsely porous; synapticulae may be present. *lower Cambrian (Bot.1–Bot.2):* South China, Morocco, Iberia, Sardinia.——Fig. 547,*2*. **R. acutus* (Bornemann) [=*R. iglesiensis*], Matoppa Formation, Botoman, Monte Cuccurinu, Sardinia, Italy, holotype, transverse section, ×16 (Debrenne, 1972).

Terraecyathus Zhuravleva in Zhuravleva & Elkina, 1974, p. 104 [**T. lathentis*; OD; holotype, Zhuravleva & Elkina, 1974, pl. 23,*2*, TsSGM 442/37, Novosibirsk] [=*Sericyathus* Voronin, 1988, p. 7 (type, *S. tartsinicus*, OD)]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept; septa completely porous. *lower Cambrian (Atd.1–Bot.1):* Altay Sayan, Tuva, Mongolia, Morocco.——Fig. 547,*3a–b*. **T. lathentis*; *a,* Adiak Formation, Atdabanian, Tom' River, Gornaya Shoria, Altay Sayan, Russia, holotype, TsSGM 442/37, transverse section, ×5 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* Usa Formation, Botoman, Bograd, Batenev Range, Kuznetsk Alatau, Russia, paratype, TsSGM 442/38, longitudinal section of septum (outer wall to left), ×5 (Zhuravleva & Elkina, 1974).

Ussuricyathellus Voronin, 1988, p. 6 [**U. bellus*; OD; holotype, Voronin, 1988, pl. 1,*4*, PIN 3175-920/a-2, Moscow]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept; septa aporose to sparsely porous. *lower Cambrian (Bot.1–Bot.3):* Mongolia, Australia.——Fig. 547,*4*. **U. bellus*, Burgasutay Formation, Botoman, Seer' Mountains, Ikh nuuruundyn hotgor, western Mongolia, holotype, PIN 3175-920/a-2, transverse section, ×5 (Voronin, 1988).

Zonacyathellus Zhuravleva in Zhuravleva & Elkina, 1974, p. 66 [*?*Zonacyathus monoporosus* Zhuravleva in Zhuravleva & others, 1967, p. 66; OD; holotype, Zhuravleva & others, 1967, pl. 23,*2;* Zhuravleva & Elkina, 1974, pl. 3,*2*, TsSGM 325/35, Novosibirsk]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Tuva.——Fig. 547,*5*. **Z. monoporosus* (Zhuravleva), Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia, holotype, TsSGM 325/35, longitudinal section, ×5 (Zhuravleva & others, 1967).

Family SAJANOCYATHIDAE Vologdin, 1956

[Sajanocyathidae Vologdin, 1956, p. 879] [=Formosocyathidae Zhuravleva, 1957, p. 175; =Irinacyathidae Zhuravleva in Debrenne, 1972, p. 173, *nom. neg.*; =Irinaecyathidae Zhuravleva in Zhuravleva & Elkina, 1974, p. 67; =Diplocyathidae Debrenne, 1974b, p. 123]

Inner wall with communicating canals. *lower Cambrian (Atd.1–Toy.2).*

Sajanocyathus Vologdin, 1940b, p. 81 (Vologdin, 1937b, p. 471, *nom. nud.*) [**S. ussovi*; OD; lectotype, Vologdin, 1940b, pl. 22,*8;* SD Zhuravlev, 2001a, p. 92, PIN 4754/2, Moscow] [=*Sayanocyathus* Vologdin, 1937b, p. 479, *nom. nud.* (type, *Sayanocyathus ussovi* Vologdin, 1937b, p. 479, M)]. Inner wall with several rows of anastomosing, horizontal to upwardly and laterally projecting, waved canals per intersept; septa aporose to sparsely porous. *lower Cambrian (Bot.1–Toy.2):* Siberian Platform, Altay Sayan, ?Antarctica, ?northeastern China (Hinggan), ?Sardinia, Canada, United States.——Fig. 548,*1*. **S. ussovi*, Verkhnemonok Formation, Botoman, Sanashtykgol River, West Sayan, Altay Sayan, Russia, lectotype, PIN 4754/2, transverse section of modular skeleton, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

Chakassicyathus Zhuravleva & Osadchaya in Zhuravleva & Elkina, 1974, p. 93 [**Ethmophyllum pseudoratum* Zhuravleva in Zhuravleva & others, 1967, p. 62; OD; holotype, Zhuravleva & others, 1967, pl. 21,*2*, TsSGM 325/28b, Novosibirsk]. Inner wall with one row of downwardly projecting, straight porous canals per intersept, bearing supplementary bracts or annuli on central cavity side; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Altay Sayan, Tuva.——Fig. 548,*2*. **C. pseudoratus* (Zhuravleva), Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia, holotype, TsSGM 325/28b, oblique longitudinal section, ×5.5 (Zhuravleva & others, 1967).

Emucyathus Kruse & Moreno-Eiris, 2013, p. 23 [**E. elinorae*; OD; holotype, Kruse & Moreno-Eiris, 2013, fig. 15a–c, SAM P48475, Adelaide]. Inner wall with horizontal to upwardly projecting, straight stirrup canals only; septa completely porous. *lower Cambrian (Bot.3):* Australia.——Fig. 548,*3a–c*. **E. elinorae,* White Point Conglomerate, Botoman,

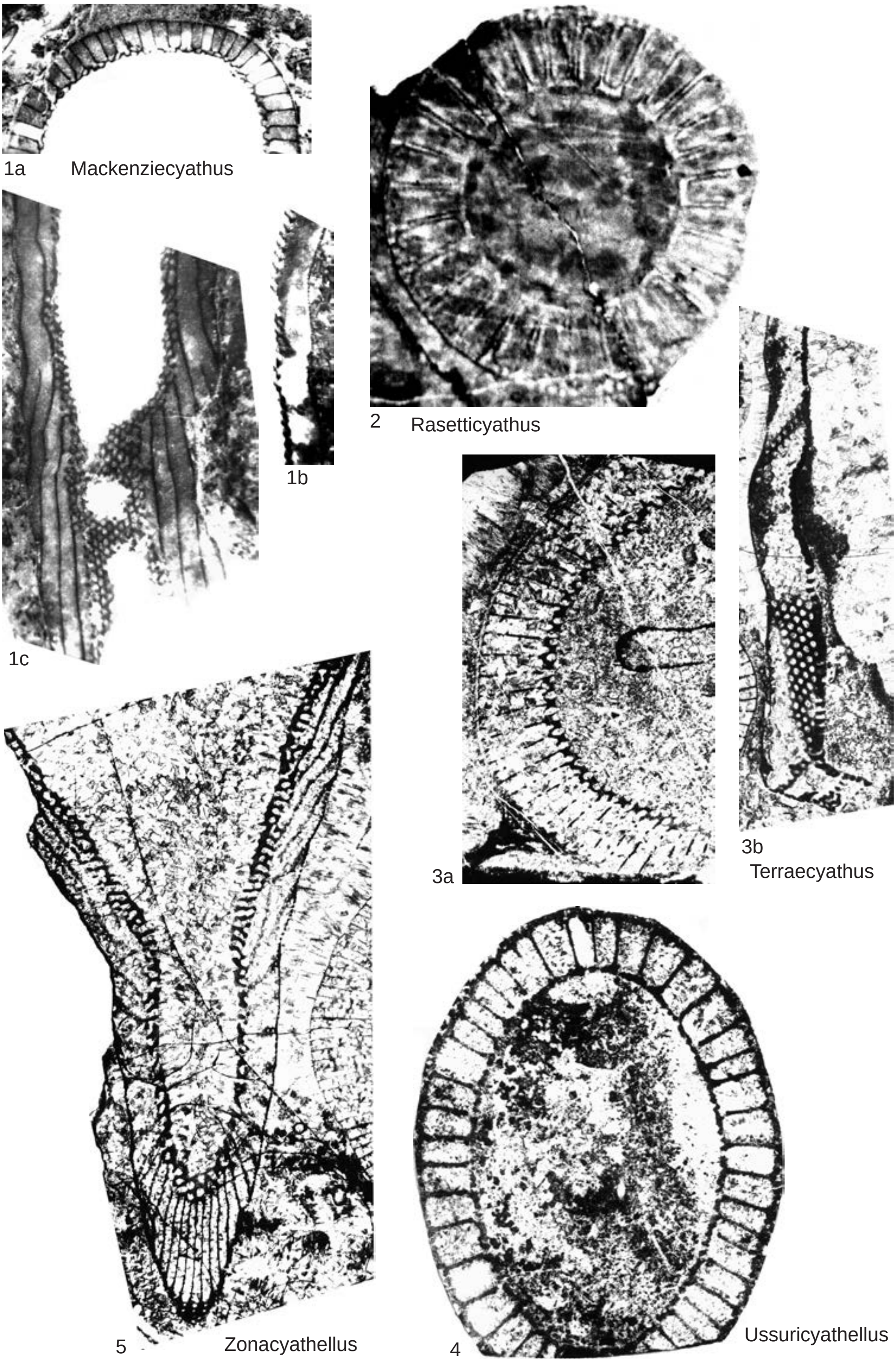


FIG. 547. Ethmocyathidae (p. 954).

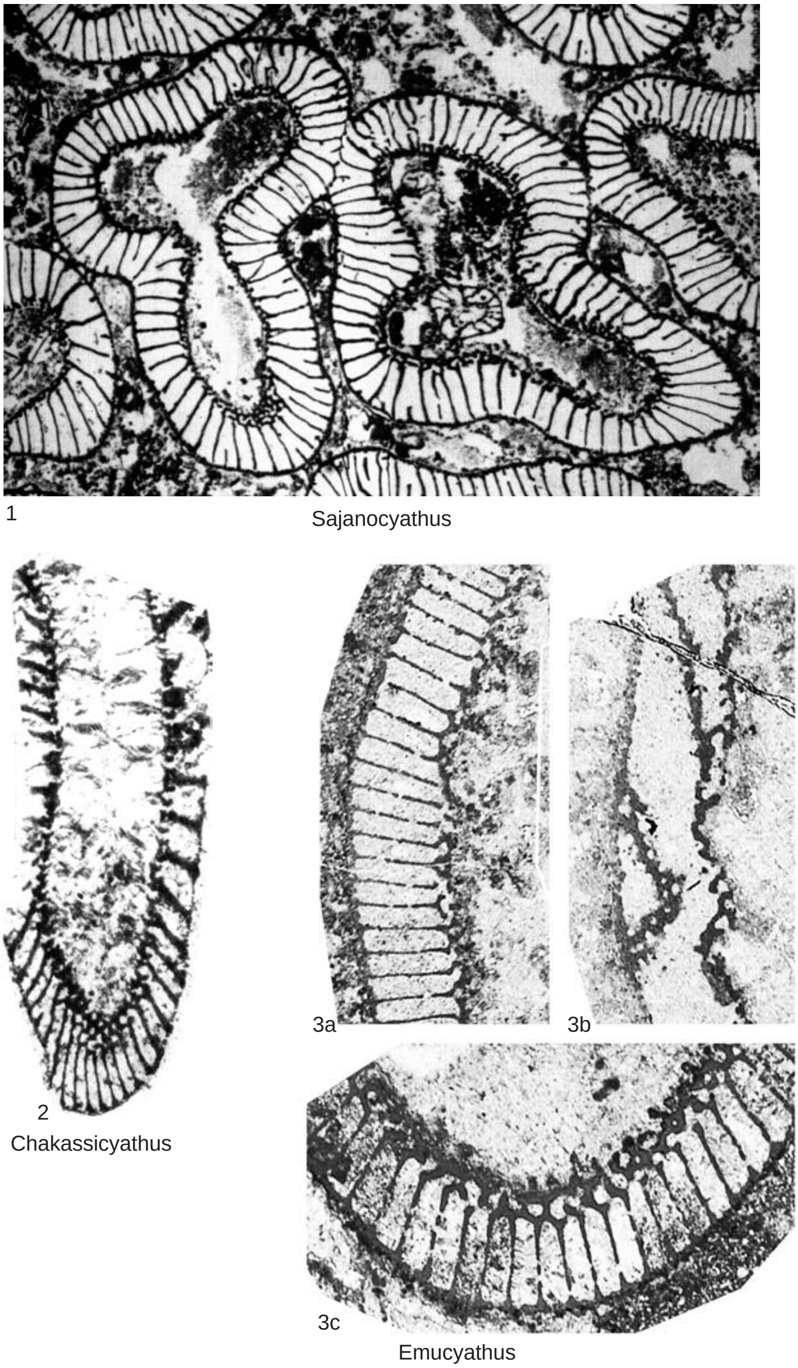


FIG. 548. Sajanocyathidae (p. 954–956).

Cape d'Estaing, South Australia, Australia; *a–b,* holotype, SAM P48475; *a,* transverse section (outer wall to left), ×8; *b,* longitudinal section (outer wall to left), ×8; *c,* paratype, SAM P48476, oblique transverse section (outer wall at bottom), ×8 (Kruse & Moreno-Eiris, 2013).

Formosocyathus VOLOGDIN, 1940b, p. 90 (VOLOGDIN, 1937b, p. 471, *nom. nud.*) [*F. *bulynnikovi*; OD;

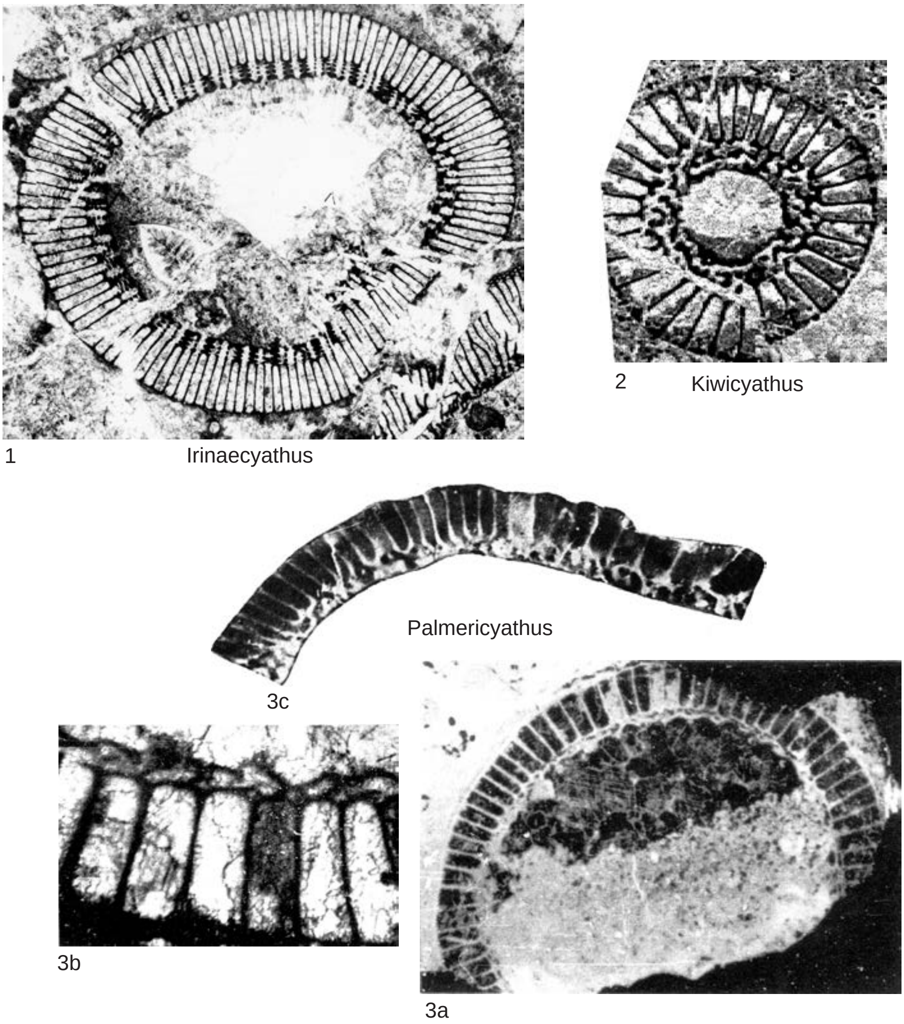


FIG. 549. Sajanocyathidae (p. 957–959).

holotype not designated, collection not located]. Inner wall with one row of anastomosing, horizontal to upwardly and laterally projecting, waved canals per intersept; supplementary spines, annular structures, and/or microporous sheath may be present on central cavity side; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.2):* Altay Sayan, Tuva, Mongolia, Transbaikalia.——FIG. 550,*3a–b*. **F. bulynnikovi*, Verkhnemonok Formation, Botoman, Sanashtykgol River, West Sayan, Altay Sayan, Russia, unlocated syntype; *a,* transverse section (outer wall at top), ×6; *b,* longitudinal section (outer wall to left), ×6 (Vologdin, 1940b).

Irinaecyathus Zhuravleva in Zhuravleva & Elkina, 1974, p. 87 [**Ethmophyllum grandiperforatum* Vologdin, 1940a, p. 160; OD; lectotype, Vologdin, 1940a, fig. 75, pl. 46,*1,* SD Zhuravleva & Elkina, 1974, p. 88, collection not located] [=*Kandatocyathus* Kashina in Osadchaya & others, 1979, p. 156 (type, *K. kalleganovi,* OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 112; Debrenne, Rozanov, & Zhuravlev, 1990, p. 146]. Inner wall with one row of downwardly projecting, straight porous canals per intersept, bearing supplementary bracts or annuli on central cavity side; septa sparsely to completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1–Toy.2):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East.——FIG. 549,*1*. **I. grandiperforatus* (Vologdin), Burgasutay Formation, Botoman, Seer' Mountains, Ikh nuuruundyn hotgor, western Mongolia, topotype, PIN 4327/24-2042/5, transverse section, ×5 (Debrenne, Zhuravlev, & Kruse, 2002).

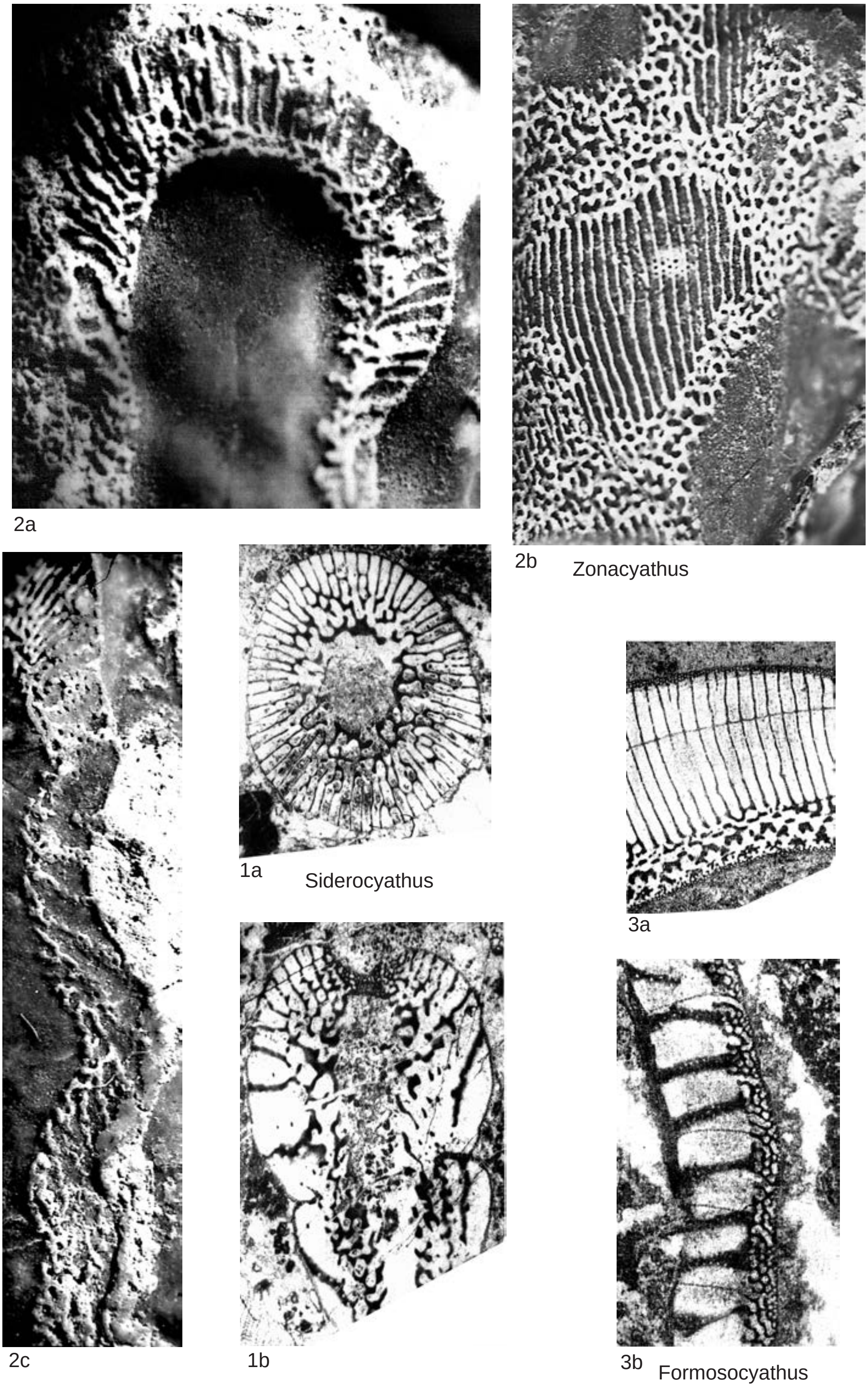


FIG. 550. Sajanocyathidae (p. 956–959).

Kiwicyathus DEBRENNE & KRUSE, 1986, p. 250 [**K. nix*; OD; holotype, DEBRENNE & KRUSE, 1986, fig. 15A–B, VU VC19, Wellington]. Inner wall with horizontal to upwardly projecting, straight porous stirrup canals only; septa aporose to sparsely porous. *lower Cambrian (Bot.3):* Antarctica.——FIG. 549,*2*. **K. nix*, Shackleton Limestone, Botoman, Mt. Egerton, Byrd Glacier, Antarctica, holotype, VU VC19, transverse section, ×6 (Debrenne & Kruse, 1986).

Palmericyathus HANDFIELD, 1971, p. 44 [**Ethmophyllum lineatum* GREGGS, 1959, p. 66; OD; holotype, GREGGS, 1959, pl. 14,*2*, GSC 14315, Ottawa; =*Ethmophyllum americanum* OKULITCH in COOPER & others, 1952, p. 30; holotype, COOPER & others, 1952, pl. 7,*3–4*, USNM 111816, Washington, D.C. (for discussion, see DEBRENNE, 1987, p. 270)]. Inner wall with anastomosing, horizontal to upwardly and laterally projecting, waved stirrup canals only; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Canada, United States, Mexico.——FIG. 549,*3a–c*. **P. americanus* (OKULITCH); *a–b,* Puerto Blanco Formation, Botoman, Caborca, Sonora, Mexico, holotype, USNM 111816; *a,* transverse section, ×8; *b,* detail of transverse section (outer wall at bottom), ×25 (Cooper & others, 1952); *c,* [=*P. lineatus* (GREGGS)], Laib Formation, Botoman, Salmo, British Columbia, Canada, holotype, GSC 14315, transverse section (outer wall at top), ×6 (Greggs, 1959).

Siderocyathus DEBRENNE & GANGLOFF in DEBRENNE, GANDIN, & GANGLOFF, 1990, p. 87 [**S. duncanae*; OD; holotype, DEBRENNE, GANDIN, & GANGLOFF, 1990, pl. 1,*7*, USNM 443555, specimen IR1-3, Washington, D.C.]. Inner wall with one row of short, noncommunicating, horizontal to upwardly projecting canals per intersept, continuing into central cavity as communicating waved canals bearing supplementary bracts on central cavity side; septa aporose to sparsely porous, linked by synapticulae. *lower Cambrian (Bot.1):* United States.——FIG. 550,*1a–b*. **S. duncanae*, Valmy Formation, Botoman, Iron Canyon, Nevada, United States, holotype, USNM 443555, specimen IR1-3; *a,* transverse section, ×5; *b,* longitudinal section, ×5 (Debrenne, Gandin, & Gangloff, 1990).

Zonacyathus R. BEDFORD & J. BEDFORD, 1937, p. 36 [**Archaeocyathus retevallum* R. BEDFORD & W. R. BEDFORD, 1934, p. 2; OD; holotype, R. BEDFORD & W. R. BEDFORD, 1934, fig. 6; HILL, 1965, pl. 4,*3;* DEBRENNE, 1969a, pl. 4,*4;* NHM S4147, M, London; =*Archaeocyathus retezona* TAYLOR, 1910, p. 121; OD; lectotype, TAYLOR, 1910, pl. 6,*31;* DEBRENNE, 1974b, pl. 26,*4–5;* SD DEBRENNE, 1974b, p. 124, SAM T1577A, Adelaide] [=*Diplocyathellus* DEBRENNE, 1977b, p. 1222, *nom. nov. pro Diplocyathus* DEBRENNE, 1974b, p. 124, *non* ALLMAN, 1888, p. 16, cnidarian (type, *Archaeocyathus retezona* TAYLOR, 1910, p. 121; OD)]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept, canals branching and becoming porous toward central cavity; septa sparsely to completely porous; stirrup canals may be present. *lower Cambrian (?Bot.1, Bot.2–Bot.3):* ?Siberian Platform, Australia.——FIG. 550,*2a–c*. **Z. retezona* (TAYLOR), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; *a–b,* [= *Z. retevallus* (R. BEDFORD & W. R. BEDFORD)] holotype, NHM S4147; *a,* oblique longitudinal view, ×5 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* tangential view of inner wall, ×5 (Hill, 1965); *c,* topotype, USNM PU86606, longitudinal view (outer wall to right), ×5 (Debrenne, 1974b).

Family BIPALLICYATHIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Bipallicyathidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 82]

Inner wall with attached microporous sheath. *lower Cambrian (Atd.2).*

Bipallicyathus ZHURAVLEV in VORONIN & others, 1982, p. 78 [**B. manifestus*; OD; holotype, VORONIN & others, 1982, pl. 15,*6a–b*, PIN 3302/3305, Moscow] [=*Kashinaecyathus* YAROSHEVICH, 1990, p. 25 (type, *K. salairicus,* OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 173]. Inner wall with one pore row per intersept and attached microporous sheath; septa completely porous. *lower Cambrian (Atd.2):* Altay Sayan, Mongolia.——FIG. 551,*1a–c*. **B. manifestus*, Salaany Gol Formation, Atdabanian, Khasagt-Khayrkhan Range, Tsagaan Oloom province, western Mongolia; *a,* paratype, PIN 3302/3006, oblique transverse section, ×8; *b–c,* holotype, PIN 3302/3305; *b,* longitudinal section, ×7; *c,* detail of inner wall, ×17 (Voronin & others, 1982).

?**Heckericyathus** ZHURAVLEVA, 1960b, p. 220 [**Ethmophyllum heckeri* ZHURAVLEVA in ZHURAVLEVA & ZELENOV, 1955, p. 69; OD; holotype, PIN 1161, Moscow, not located; paratypes, ZHURAVLEVA & ZELENOV, 1955, pl. 1,*3–4*, TsSGM 205/102, 205/103, Novosibirsk] [=*Heckerocyathus* ZHURAVLEVA in VOLOGDIN, 1957a, p. 180, *nom. nud.*]. Inner wall with one pore row per intersept and independent microporous sheath, each micropore bearing a supplementary bract; septa completely porous; pectinate tabulae may be present. [Inner wall bears supplementary elements atypical of other members of family.] *lower Cambrian (Atd.1–Atd.4):* Siberian Platform, Transbaikalia, Far East.——FIG. 551,*2a–c*. **H. heckeri* (ZHURAVLEVA), Pestrotsvet Formation, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia; *a,* paratype, TsSGM 205/102, transverse section, ×8 (Zhuravleva & Zelenov, 1955); *b–c,* paratype, TsSGM 205/103; *b,* detail of septum in longitudinal section (outer wall to right), ×16; *c,* detail of inner wall in oblique longitudinal section, ×16 (Debrenne, Zhuravlev, & Kruse, 2002).

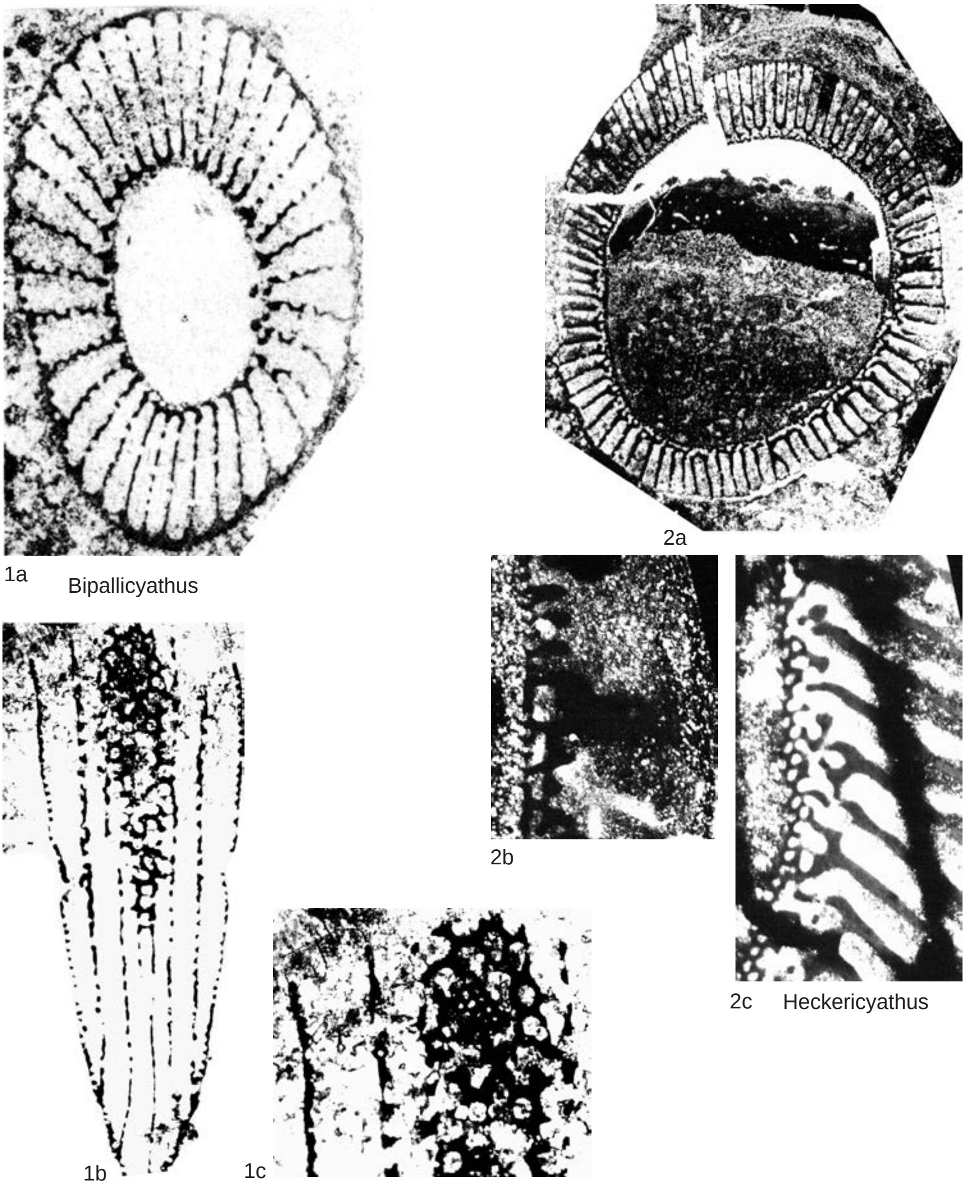


FIG. 551. Bipallicyathidae (p. 959).

Superfamily PRETIOSOCYATHOIDEA
Rozanov, 1969

[*nom. correct.* DEBRENNE, ZHURAVLEV, & KRUSE, herein, *pro* Pretiosocyathacea ROZANOV, 1969, p. 112]

Outer wall with independent microporous sheath. *lower Cambrian (Atd.1–Bot.2).*

Family ROBERTOCYATHIDAE
Rozanov, 1969

[Robertocyathidae ROZANOV, 1969, p. 112]

Inner wall with simple pores. *lower Cambrian (Atd.2–Bot.1).*

Robertocyathus ROZANOV, 1969, p. 112 [**R. polaris*; OD; holotype, ROZANOV, 1969, pl. 42,*1–2*, PIN

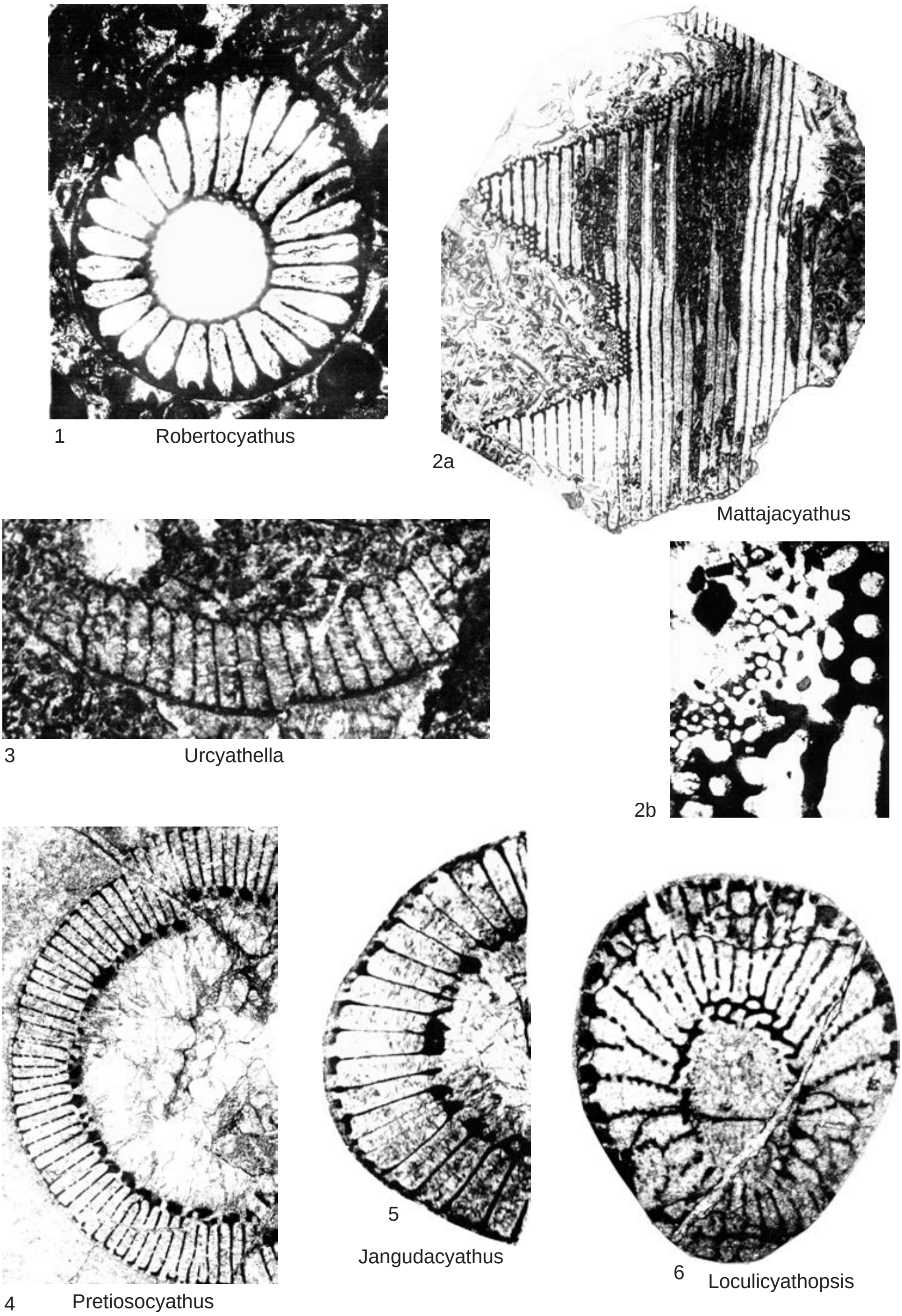


FIG. 552. Robertocyathidae and Pretiosocyathidae (p. 960–962).

4297/96, Moscow]. Inner wall with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Australia, Morocco, Iberia.——FIG. 552,*1.* **R. polaris*, Erkeket Formation, Botoman, Khorbusuonka River, Olenek Basin, Sakha (Yakutia), Russia, holotype, PIN 4297/96, transverse section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Mattajacyathus ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 118 (ROZANOV, 1973, p. 61, *nom. nud.;* ROZANOV in DEBRENNE & ROZANOV, 1983, p. 735, *nom. nud.*) [**Robertocyathus arduus* ROZANOV, 1969, p. 113; OD; holotype, ROZANOV, 1969, pl. 42,*3–4;* ROZANOV, 1973, pl. 5,*1*, PIN 4297/97, Moscow]. Cup in which both walls show periodic, synchronous transverse folds; inner wall with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Bot.1):* Siberian Platform.——FIG. 552,*2a–b.* **M. arduus* (ROZANOV), Erkeket Formation, Botoman, Khorbusuonka River, Olenek Basin, Sakha (Yakutia), Russia, holotype, PIN 4297/97; *a,* longitudinal section, ×7; *b,* detail of outer wall in tangential section, ×15 (Debrenne, Zhuravlev, & Kruse, 2002).

Urcyathella ZHURAVLEVA in MUSATOV & others, 1961, p. 25 [**U. tercyathoides*; OD; holotype, MUSATOV & others, 1961, pl. 3,*8–9*, TsSGM 264/26, Novosibirsk]. Inner wall longitudinally plicate, with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Atd.4–Bot.1):* Altay Sayan.——FIG. 552,*3.* **U. tercyathoides*, Balakhtinson Formation, Atdabanian, Kazyr River, East Sayan, Altay Sayan, Russia, holotype, TsSGM 264/26, transverse section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Family PRETIOSOCYATHIDAE Rozanov, 1969

[Pretiosocyathidae ROZANOV, 1969, p. 112]

Inner wall with noncommunicating canals. *lower Cambrian (Atd.1–Bot.1).*

Pretiosocyathus ROZANOV in ROZANOV & MISSARZHEVSKIY, 1966, p. 55 [**P. subtilis*; OD; holotype, ROZANOV & MISSARZHEVSKIY, 1966, pl. 4,*4;* ROZANOV, 1973, pl. 11,*3*, PIN 4297/65, Moscow] [=*Cosmocyathus* YAZMIR in ZHURAVLEVA, 1974a, p. 96, *nom. nud.*; =*Cosmocyathus* YAZMIR in YAZMIR, DALMATOV, & YAZMIR, 1975, p. 63 (type, *C. perforatus*, OD); =*Pretiosocyathellus* OSADCHAYA in OSADCHAYA & others, 1979, p. 133 (type, *P. toltschiensis*, OD); =*Grandicyathus* KORSHUNOV, 1983b, p. 109 (type, *G. lectus*; OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 125; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 156]. Inner wall with horizontal to upwardly projecting, straight stirrup canals only; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Tajikistan.——FIG. 552,*4.* **P. subtilis*, Usa Formation, Atdabanian, Bol'shaya Erba, Batenev Range, Kuznetsk Alatau, Russia, holotype, PIN 4297/65, transverse section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Jangudacyathus YAZMIR in YAZMIR, DALMATOV, & YAZMIR, 1975, p. 62 (YAZMIR in ZHURAVLEVA, 1974a, p. 180, *nom. nud.*) [**J. simplex*; OD; holotype, YAZMIR, DALMATOV, & YAZMIR, 1975, pl. 23,*5*, BGU 0138/21, Ulan-Ude]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Transbaikalia.——FIG. 552,*5.* **J. simplex*, Uran Formation, Botoman, Yanguda River, Vitim Highlands, Transbaikalia, Russia, holotype, BGU 0138/21, transverse section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Loculicyathopsis BOYARINOV in ZHURAVLEVA & others, 1997a, p. 61 [**L. septospinosus;* OD; holotype, ZHURAVLEVA & others, 1997a, pl. 11,*9*, ZSGGU 2329/62, Novokuznetsk]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous. *lower Cambrian (Atd.2):* Altay Sayan.——FIG. 552,*6.* **L. septospinosus*, Usa Formation, Atdabanian, Malaya Belokamenka River, Kiya River, Kuznetsk Alatau, Russia, holotype, ZSGGU 2329/62, oblique transverse section, ×5 (Zhuravleva & others, 1997a).

Superfamily ERBOCYATHOIDEA Vologdin & Zhuravleva, 1956

[*nom. correct.* DEBRENNE & KRUSE, 1986, p. 251, *pro* Erbocyathacea ZHURAVLEVA, 1960b, p. 187, *nom. transl. ex* Erbocyathidae VOLOGDIN & ZHURAVLEVA in VOLOGDIN, 1956, p. 879] [=Bosceculcyathacea KRASNOPEEVA, 1959, p. 7, *nom. transl.* HILL, 1972, p. 77, *ex* Bosceculcyathidae KRASNOPEEVA, 1959, p. 7; =Kordecyathoidea MISSARZHEVSKIY, 1961, p. 21, *nom. transl.* MISSARZHEVSKIY in REPINA & others, 1964, p. 218, *ex* Kordecyathidae MISSARZHEVSKIY, 1961, p. 21, *nom. correct. pro* Kordecyathacea DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 82]

Outer wall with attached microporous sheath. *lower Cambrian (Atd.1–Toy.3).*

Family ERBOCYATHIDAE Vologdin & Zhuravleva, 1956

[Erbocyathidae VOLOGDIN & ZHURAVLEVA in VOLOGDIN, 1956, p. 879, *nom. nov. pro* Polycyathidae VOLOGDIN, 1928, p. 35, invalid name based on junior homonym] [=Ladaecyathidae DEBRENNE, 1964, p. 114]

Inner wall with simple pores. *lower Cambrian (Atd.1–Toy.3).*

Pluralicyathus OKULITCH, 1950c, p. 503, *nom. nov. pro Polycyathus* VOLOGDIN, 1928, p. 32, *non* DUNCAN, 1876, p. 433, cnidarian [**Polycyathus heterovallum* VOLOGDIN, 1928, p. 36; SD SIMON, 1939, p. 34; lectotype, VOLOGDIN, 1928, pl. 2,*1,2,4,5;* SD

DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1586, TsNIGRm 1/a-t/2617, St. Petersburg] [=*Erbocyathus* ZHURAVLEVA, 1950, p. 857, *nom. nud.; =Erbocyathus* ZHURAVLEVA, 1955a, p. 44, *nom. nov. pro Polycyathus* VOLOGDIN, 1928, p. 32 (type, *Polycyathus heterovallum,* SD SIMON, 1939, p. 34), *non* DUNCAN, 1876, p. 433, cnidarian; application by DEBRENNE, ZHURAVLEV, and KRUSE (2003) to suppress *Pluralicyathus* and conserve *Erbocyathus* rejected by ICZN (2005); =*Neocyathus* VOLOGDIN, 1960, p. 422 (type, *Archaeocyathus laevus* VOLOGDIN, 1940b, p. 57, OD)]. Inner wall with several rows of simple pores per intersept; septa aporose to sparsely porous. *lower Cambrian (Bot.1–Toy.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East, Uzbekistan.——FIG. 553,*1a–b*. **P. heterovallum* (VOLOGDIN); *a,* Torgashino Formation, Toyonian, Uyar River, East Sayan, Altay Sayan, Russia, unlocated specimen, transverse section, ×8.5 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* Khomustakh Formation, Toyonian, Amga River, Sakha (Yakutia), Russia, specimen TsSGM 205/71, section of modular skeleton, ×1 (Zhuravleva, 1960b).

Ladaecyathus ZHURAVLEVA, 1960a, p. 43 [**Tegerocyathus limbatus* ZHURAVLEVA, 1955a, p. 46; OD; holotype, ZHURAVLEVA, 1955a, pl. 5,*3–4*, PIN 494, Moscow, not located]. Inner wall with several rows of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.4–Bot.3):* Siberian Platform, Kolyma, Altay Sayan, Transbaikalia, Far East, Australia, Antarctica, Morocco.——FIG. 553,*2a–b*. **L. limbatus* (ZHURAVLEVA), Usa Formation, Botoman, Mt. Martyukhina, Batenev Range, Kuznetsk Alatau, Russia; *a,* holotype, PIN 494, transverse section, ×6.5 (Zhuravleva, 1955a); *b,* TsSGM 273/4d, longitudinal section of septum (outer wall to left), ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Milaecyathus DEBRENNE & ZHURAVLEV, 2000, p. 49 [**Ladaecyathus melnikovae* ZHURAVLEV in VORONIN & others, 1982, p. 79; OD; holotype, VORONIN & others, 1982, pl. 16,*2,5*, PIN 3302/300v, Moscow]. Inner wall with stirrup pores only; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Atd.2):* Altay Sayan, Mongolia.——FIG. 553,*3a–b*. **M. melnikovae* (ZHURAVLEV), Salaany Gol Formation, Atdabanian, Salaany-Gol River, Khasagt-Khairkhan Range, Tsagaan Oloom province, western Mongolia, holotype, PIN 3302/300v; *a,* transverse section, ×5 (Voronin & others, 1982); *b,* detail of outer wall in tangential section, ×25 (Debrenne, Zhuravlev, & Kruse, 2002).

Family PEREGRINICYATHIDAE Zhuravleva, 1967

[Peregrinicyathidae ZHURAVLEVA in ZHURAVLEVA & others, 1967, p. 74]

Inner wall with annuli. *lower Cambrian (Bot.1–Bot.2).*

Peregrinicyathus ZHURAVLEVA in ZHURAVLEVA & others, 1967, p. 75 [**P. dorotheae*; OD; holotype, ZHURAVLEVA & others, 1967, pl. 28,*1*, TsSGM 325/54, Novosibirsk]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Tuva.——FIG. 554,*1a–b*. **P. dorotheae*, Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia; *a,* holotype, TsSGM 325/54, transverse section, ×4.5 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* paratype, TsSGM 325, specimen 1, thin section 1, sample 314-7, OR-64, detail of oblique transverse section (outer wall to left), ×8 (Zhuravleva & others, 1967).

Family VOLOGDINOCYATHIDAE Yaroshevich, 1957

[Vologdinocyathidae YAROSHEVICH, 1957, p. 1015] [=Bosceculcyathidae KRASNOPEEVA, 1959, p. 7; =Kordecyathidae MISSARZHEVSKIY, 1961, p. 21; =Schidertycyathidae KRASNOPEEVA, 1969, p. 63; =Gumbycyathidae DEBRENNE & KRUSE, 1986, p. 253]

Inner wall with noncommunicating canals. *lower Cambrian (Bot.1–Toy.2).*

Vologdinocyathus YAROSHEVICH, 1957, p. 1015 [**V. erbiensis*; OD; holotype, YAROSHEVICH, 1957, fig. 1a–v, TsSGM 499/1a-b, Novosibirsk] [=*Tegerocyathella* KONYUSHKOV, 1967, p. 109 (type, *T. borovikovi*, OD); =*Larecyathus* KASHINA, 1979, p. 46, *nom. nud.*; =*Larecyathus* KASHINA in OSADCHAYA & others, 1979, p. 145 (type, *L. infinitus,* OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 139; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 167]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa aporose to sparsely porous. *lower Cambrian (Bot.3–Toy.2):* Altay Sayan, Tuva, Mongolia, Kazakhstan, Uzbekistan, Antarctica, Greenland.——FIG. 554,*2a–b*. **V. erbiensis*, Usa Formation, Toyonian, Bol'shaya Erba, Batenev Range, Kuznetsk Alatau, Altay Sayan, Russia, holotype, TsSGM 499/1a-b; *a,* detail of transverse section, ×30; *b,* detail of septum in longitudinal section (outer wall to left), ×50 (Debrenne, Zhuravlev, & Kruse, 2002).

Gumbycyathus KRUSE, 1982, p. 168 [**G. pythoni;* OD; holotype, KRUSE, 1982, pl. 4,*1–5,* AM F.83930, Sydney]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa completely porous. *lower Cambrian (Bot.1–Bot.3):* Mongolia, Australia.——FIG. 555,*1a–d*. **G. pythoni,* Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia, holotype, AM F.83930; *a,* transverse section (outer wall to right), AM FT.8457, ×6; *b,* detail of longitudinal section (outer wall to left), AM FT.8455, ×8; *c,* detail of outer wall in tangential section, AM FT.8458, ×8; *d,* detail of

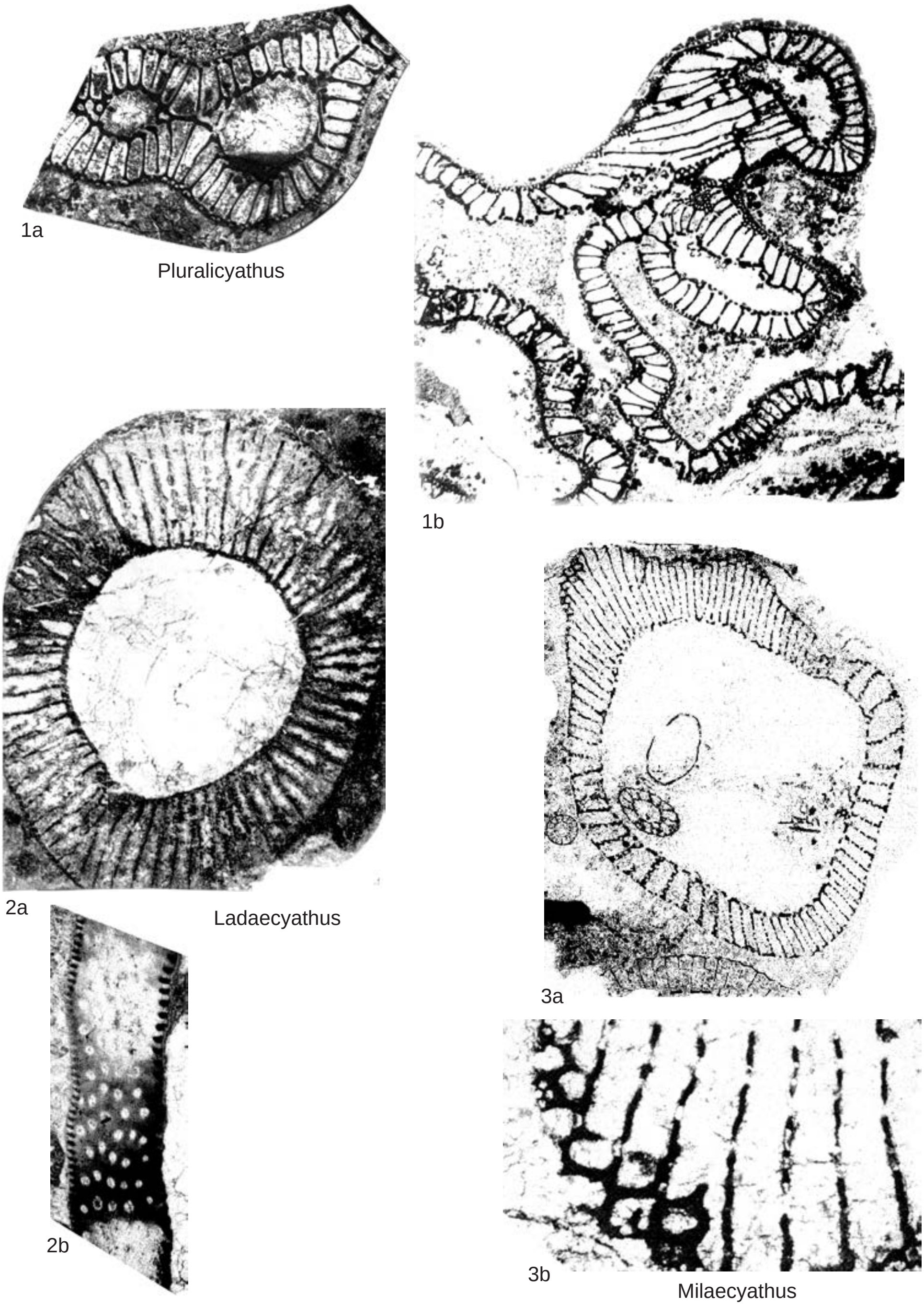


FIG. 553. Erbocyathidae (p. 962–963).

inner wall in tangential section, AM FT.8456, ×8 (Kruse, 1982).

Inacyathella Debrenne, 1977a, p. 109 [**I. pulchra*; OD; holotype, Debrenne, 1977a, pl. 8,*3–4*, MNHN M80037, Paris]. Inner wall with one row of horizontal to upwardly projecting, S-shaped canals per intersept; septa completely porous. *lower Cambrian (Bot.1):* Morocco.——Fig. 554,*3a–b*. **I. pulchra*, Issafen Formation, Botoman, Jbel Irhoud, Morocco, holotype, MNHN M80037; *a,* oblique transverse section, ×3.5 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* detail of septum in longitudinal section (outer wall to left), ×10 (Debrenne, 1977a).

Kordecyathus Missarzhevskiy, 1961, p. 21 [**K. shiveligensis;* OD; holotype, Missarzhevskiy, 1961, pl. 1,*3*, PIN 1914/73M/1, Moscow, not located]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1–Bot.2):* Tuva, Mongolia.——Fig. 554,*4a–b*. **K. shiveligensis*, Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia, holotype, PIN 1914/73M/1; *a,* detail of transverse section (outer wall at top), ×8 (Missarzhevskiy, 1961); *b,* oblique longitudinal section, ×3 (Debrenne, Zhuravlev, & Kruse, 2002).

Sanarkophyllum Debrenne & Kruse, 1986, p. 254 [**Formosocyathus antarcticus* Hill, 1964c, p. 616; OD; holotype, Hill, 1964c, fig. 1(4a), An 62/1B/p, not located]. Inner wall with one row of downwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa aporose to sparsely porous. *lower Cambrian (Bot.3):* Antarctica.——Fig. 555,*2a–d*. **S. antarcticum* (Hill), Shackleton Limestone, Botoman; *a,* Plunket Point, Beardmore Glacier, Antarctica, holotype, An 62/1B/p, oblique transverse section, ×2 (Hill, 1964c); *b–d,* Holyoake Range, Nimrod Glacier, Antarctica, specimen GNS MG509; *b,* transverse section, ×4; *c,* oblique longitudinal section, ×3.5; *d,* detail of repeated longitudinal section (outer wall to left), ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Syringocyathus Vologdin, 1940b, p. 82 (Vologdin, 1937b, p. 471, *nom. nud.*) [**S. aspectabilis;* OD; lectotype, Vologdin, 1940b, pl. 23,*3;* SD Zhuravlev, 2001a, p. 92, PIN 4754/3, Moscow] [=*Schidertycyathus* Krasnopeeva, 1959, p. 3 (type, *S. borucaevi,* M); ?=*Bosceculcyathus* Krasnopeeva, 1959, p. 7 (type, *B. agyrekensis,* OD); ?=*Boscekulcyathus* Krasnopeeva, 1959, p. 7, *nom. null.; =Schidertycyathellus* Konyushkov, 1967, p. 108 (type, *S. borukaevi,* OD); =*Syringocyathellus* Kashina in Osadchaya & others, 1979, p. 149 (type, *S. kazachstani,* OD), for discussion, see Debrenne, Rozanov, & Zhuravlev, 1990, p. 162]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept; septa completely porous, linked by interseptal plates. *lower Cambrian (Bot.3–Toy.2):* Altay Sayan, Tuva, Kazakhstan, Uzbekistan.——Fig. 555,*3*. **S. aspectabilis*, Verkhnemonok Formation, Botoman, Abakan River, West Sayan, Altay Sayan, Russia, lectotype, PIN 4754/3, oblique transverse section, ×5 (Vologdin, 1940b).

Family TEGEROCYATHIDAE Krasnopeeva, 1972

[Tegerocyathidae Krasnopeeva, 1972, p. 145]

Inner wall with communicating canals. *lower Cambrian (Bot.1–Toy.3).*

Tegerocyathus Krasnopeeva, 1955, p. 90 (Krasnopeeva, 1953, p. 52, 56, *nom. nud.*) [**Ethmophyllum abakanensis* Vologdin, 1940b, p. 69; holotype not designated, collection not located; Zhuravleva, 1960b, p. 192, invalidly nominated *Ethmophyllum edelsteini* Vologdin, 1931, p. 47, as type species] [=*Tegerocoscinus* Krasnopeeva, 1972, p. 145 (type, *T. tchesnokovensis*, OD); =*Alexandricyathus* Kashina in Osadchaya & others, 1979, p. 142 (type, *A. ultrus*, OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 134; Debrenne, Rozanov, & Zhuravlev, 1990, p. 163]. Inner wall with one row of horizontal to upwardly projecting, straight porous canals per intersept; septa sparsely to completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1–Toy.3):* Siberian Platform, Altay Sayan, Mongolia, Uzbekistan, Antarctica, Greenland, United States.——Fig. 556,*1a–b*. **T. abakanensis* (Vologdin), Verkhnemonok Formation, Botoman, Abakan River, West Sayan, Altay Sayan, Russia, unlocated syntype; *a,* transverse section, ×5; *b,* longitudinal section, ×5 (Vologdin, 1940b).

Krasnopeevaecyathus Rozanov in Repina & others, 1964, p. 208 [**K. tyrgaensis*; OD; holotype, Repina & others, 1964, pl. 21,*3–4*), PIN 4297/26-27, Moscow] [=*Krishnanicyathus* Vologdin, 1964b, p. 358 (type, *K. elegans*, OD); =*Ethmosyringocyathus* Konyushkov, 1972, p. 138 (type, *E. primus*, OD)]. Inner wall longitudinally plicate, with several rows of anastomosing, horizontal to upwardly projecting, waved canals per intersept; septa completely porous. *lower Cambrian (Bot.2):* Altay Sayan, United States.——Fig. 556,*2*. **K. tyrgaensis*, Verkhneynyrga Formation, Botoman, Tyrga River, Altay Mountains, Altay Sayan, Russia, holotype, PIN 4297/26-27, oblique transverse section, ×3.5 (Repina & others, 1964).

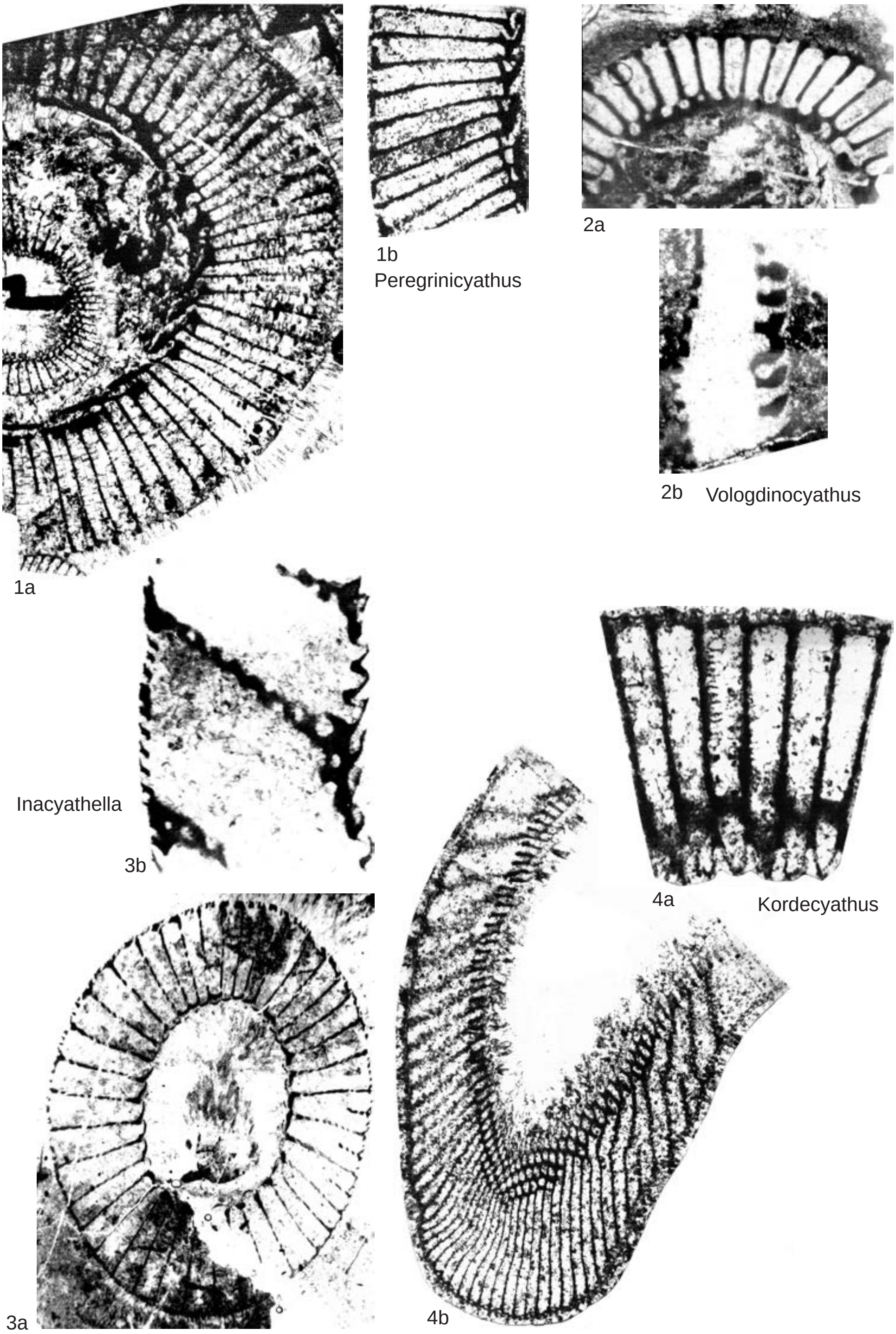


Fig. 554. Peregrinicyathidae and Vologdinocyathidae (p. 963–965).

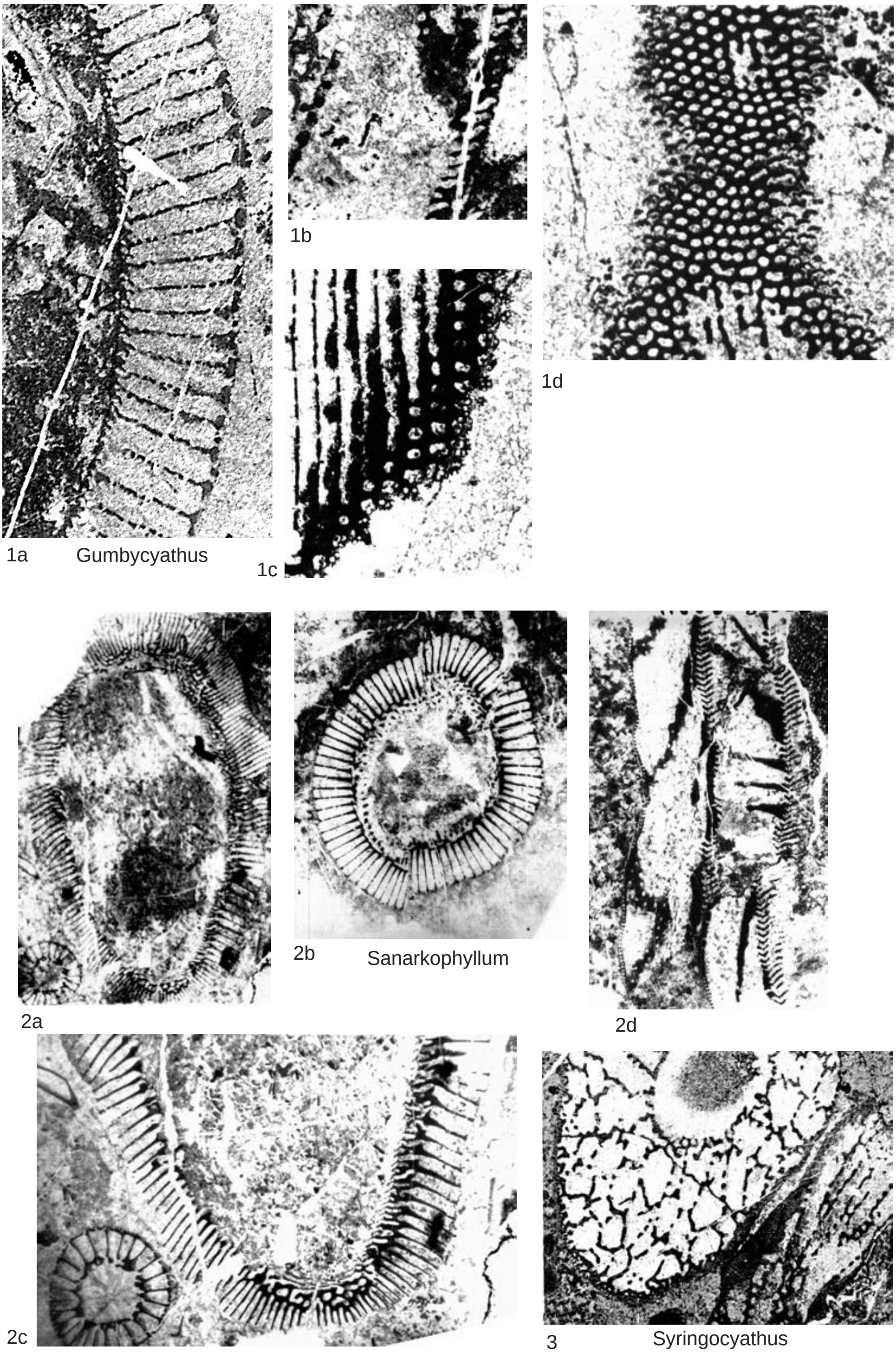


FIG. 555. Vologdinocyathidae (p. 963–965).

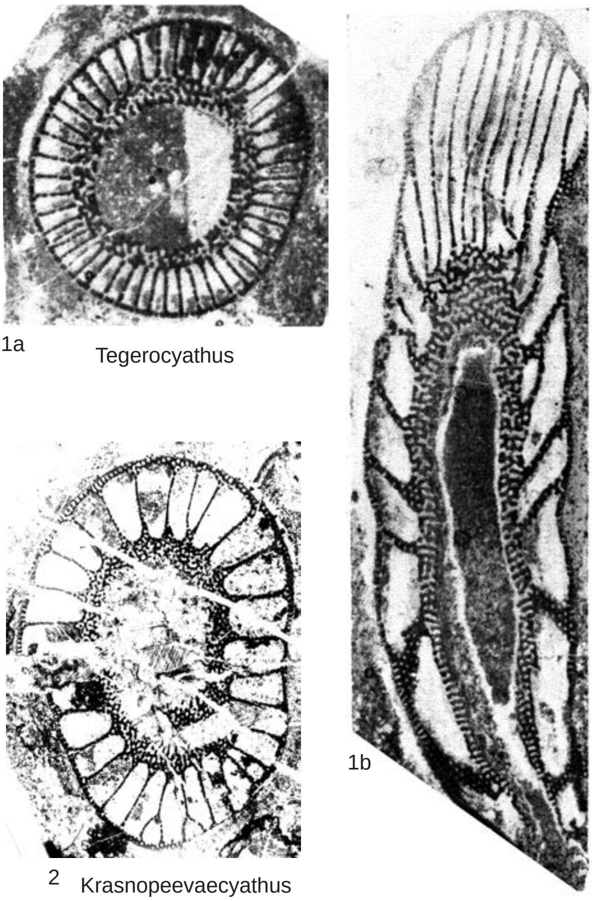


FIG. 556. Tegerocyathidae (p. 965).

Superfamily TUMULOCYATHOIDEA Krasnopeeva, 1953

[*nom. correct.* ZHURAVLEV & ROZANOV in VORONOVA & others, 1987, p. 21, *pro* Tumulocyathacea DEBRENNE, 1964, p. 113, *nom. transl. ex* Tumulocyathidae KRASNOPEEVA, 1953, p. 56] [=Geocyathacea DEBRENNE, 1964, p. 114, *nom. nud.*, *nom. transl.* ROZANOV, 1973, p. 86 *ex* Geocyathidae DEBRENNE, 1964, p. 114]

Outer wall with simple tumuli. *lower Cambrian (Tom.2–Bot.3).*

Family TUMULOCYATHIDAE Krasnopeeva, 1953

[Tumulocyathidae KRASNOPEEVA, 1953, p. 56] [=Kotuyicyathidae ROZANOV in ROZANOV & others, 1969, p. 186, *nom. nud.*]

Inner wall with simple pores. *lower Cambrian (Tom.2–Bot.3).*

Tumulocyathus VOLOGDIN, 1937b, p. 470 [**T. pustulatus*; M; holotype not designated, collection not located] [=*Kotuyicyathus* ZHURAVLEVA, 1960b, p. 226 (type, *K. kotuyikensis*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 138; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 165; =*Tumulocyathoides* BOYARINOV & KONYAEVA in ZHURAVLEVA & others, 1997b, p. 123 (type, *T. kiyaensis*, OD)]. Inner wall with one row of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Tom.2–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Australia.——FIG. 557,*1*. **T. pustulatus*; Salaany Gol Formation, Atdabanian, Salaany Gol, Khasagt-Khayrkhan Range, Tsagaan Oloom province, western Mongolia, specimen PIN 3302/710, oblique transverse section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Isiticyathus KORSHUNOV, 1972, p. 60 [**?Tumulifungia ultra* KORSHUNOV in ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, p. 38; OD; holotype, ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, pl. 10,*2;*

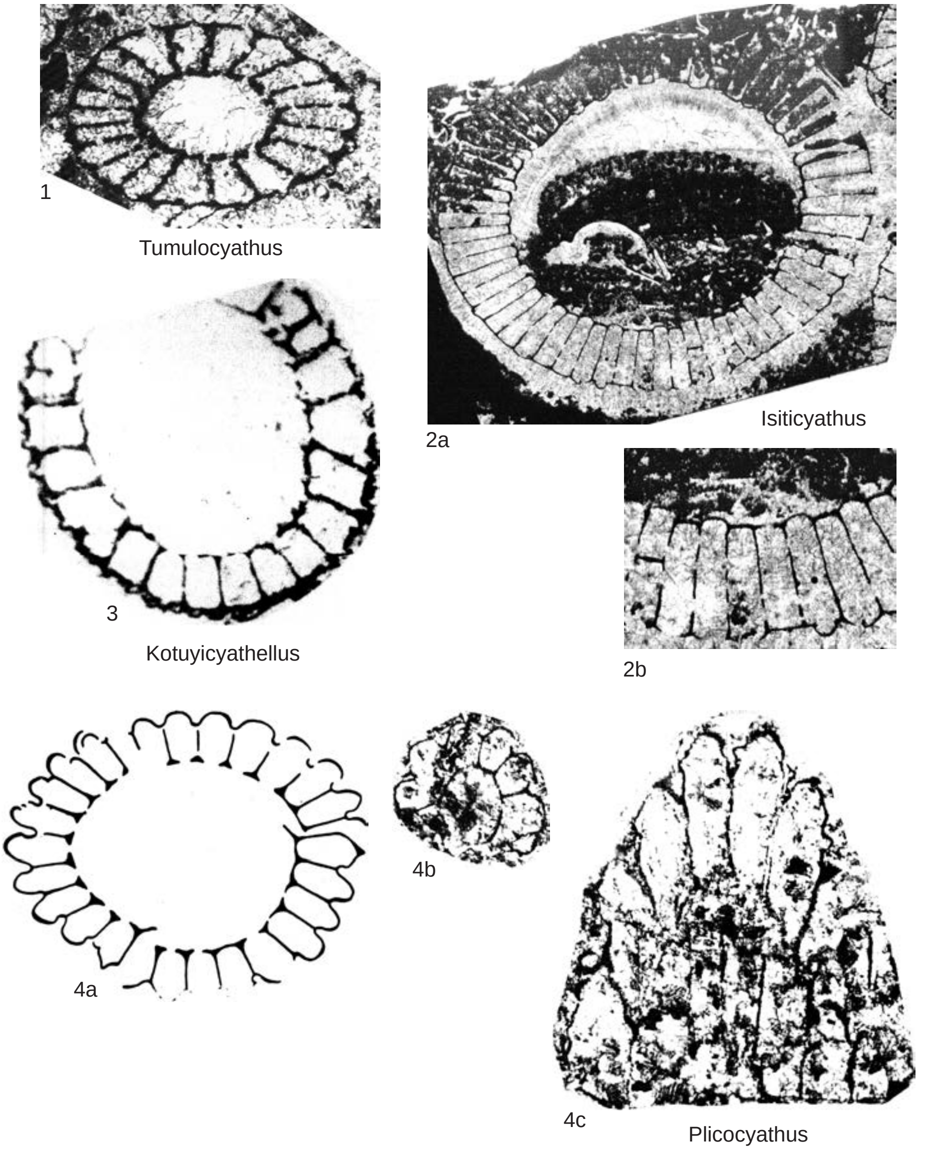


FIG. 557. Tumulocyathidae (p. 968–970).

KORSHUNOV, 1972, pl. 8,*6*, TsSGM 323/45, Novosibirsk]. Inner wall with one row of simple pores per intersept; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.4–Bot.1):* Siberian Platform, Transbaikalia.——FIG. 557,*2a–b*. **I. ultra* (KORSHUNOV), Oy-Muran reef massif, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 323/45; *a,* transverse section, ×8 (Zhuravleva, Korshunov, & Rozanov, 1969); *b,* detail of transverse section (outer wall at bottom), ×13 (Debrenne, Zhuravlev, & Kruse, 2002).

Kotuyicyathellus OSADCHAYA in OSADCHAYA & others, 1979, p. 157 [**K. minus*; OD; holotype, OSADCHAYA & others, 1979, pl. 25,*5*, VSEGEI 11594, St. Petersburg] [=*Borocyathus* VORONIN, 1988, p. 8 (type, *B. khairkhanicus,* OD)]. Inner wall with several rows of simple pores per intersept; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Bot.1):* Siberian Platform, Altay Sayan, Mongolia, Far East.——FIG. 557,*3*. **K. minus*, Usa Formation, Atdabanian, Krutoy Log, Batenev Range, Kuznetsk

Alatau, Russia, holotype, VSEGEI 11594, transverse section, ×15 (Osadchaya & others, 1979).

Plicocyathus Vologdin, 1960, p. 424 [**P. krassnyi*; OD; holotype, Vologdin, 1960, fig. 1m, PIN 4754/45, Moscow] [=*Tumulocyathellus* Zhuravleva, 1960b, p. 174, *nom. transl.* Repina & others, 1964, p. 194, *ex Tumulocyathus (Tumulocyathellus)* Zhuravleva, 1960b, p. 174 (type, *Tumulocyathus admirabilis* Vologdin, 1940b, p. 72, OD); for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 123; Debrenne, Rozanov, & Zhuravlev, 1990, p. 155; =*Torosocyathellus* Osadchaya in Osadchaya & others, 1979, p. 128 (type, *T. torosus*, OD)]. Outer wall longitudinally plicate; inner wall with stirrup pores only; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Kolyma, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Morocco, Iberia, Canada, United States, Mexico.——Fig. 557,*4a–c*. **P. krassnyi*; *a,* Ust'toka unit, Botoman, Gerbikan River, Dzhagdy Range, Far East, Russia, holotype, PIN 4754/45, sketch of transverse section, ×5 (Vologdin, 1960); *b–c,* Ust'toka unit, Botoman, Onnetok River, Dzhagdy Range, Far East, Russia, specimen DVGU 6M; *b,* transverse section, ×10; *c,* oblique transverse section, ×10 (Belyaeva & others, 1975).

Family SANARKOCYATHIDAE Hill, 1972

[Sanarkocyathidae Hill, 1972, p. 79] [=Sanaricyathidae Rozanov, 1969, p. 107, name based on invalid generic name *Sanaricyathus* Rozanov, 1969, p. 108, *nom. null. pro Sanarkocyathus* Zhuravleva, 1963a, p. 118]

Inner wall with bracts or scales. *lower Cambrian (Atd.3–Bot.1).*

Sanarkocyathus Zhuravleva, 1963a, p. 118 [**S. mamaevi;* OD; holotype, Zhuravleva, 1963a, fig. 2, TsSGM 99/1, Novosibirsk] [=*Sanaricyathus* Rozanov, 1969, p. 108, *nom. null.*]. Inner wall with one row of pores per intersept, bearing possibly upwardly projecting, S-shaped scales; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Urals, Altay Sayan.——Fig. 558,*1*. **S. mamaevi,* Sanarka Formation, Botoman, Sanarka River, eastern flank of southern Urals, Russia, holotype, TsSGM 99/1, oblique transverse section, ×6 (Zhuravleva, 1963a).

Neokolbicyathus Konyaeva in Zhuravleva & others, 1997b, p.131 [**N. azhuravlevi;* OD; holotype, Zhuravleva & others, 1997b, pl. 4,*3*, ZSGGU 2329/83, Novokuznetsk]. Inner wall with stirrup pores only, bearing upwardly projecting, S-shaped scales; septa aporose to sparsely porous. *lower Cambrian (Atd.4–Bot.1):* Altay Sayan, Far East, Canada.——Fig. 558,*2*. **N. azhuravlevi*, Usa Formation, Atdabanian, Malaya Belokamenka River, Kiya River, Kuznetsk Alatau, Russia, holotype, ZSGGU 2329/83, oblique transverse section, ×8 (Zhuravleva & others, 1997b).

Ringifungia Korshunov in Zhuravleva, Korshunov, & Rozanov, 1969, p. 38 [**R. vavilovi;* OD; holotype, Zhuravleva, Korshunov, & Rozanov, 1969, pl. 10,*4–5*, TsSGM 323/47, Novosibirsk]. Inner wall with one row of pores per intersept, bearing upwardly projecting, S-shaped scales; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.3):* Siberian Platform.——Fig. 558,*3*. **R. vavilovi*, Perekhod Formation, Atdabanian, Ulakhan-Taryng Creek, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 323/47, oblique transverse section, ×8 (Zhuravleva, Korshunov, & Rozanov, 1969).

Family GEOCYATHIDAE Debrenne, 1964

[Geocyathidae Debrenne, 1964, p. 114] [=Jakutocyathidae Korshunov, 1972, p. 65; =Eladicyathidae Perejón, 1977, p. 550]

Inner wall with annuli. *lower Cambrian (Atd.1–Bot.1).*

Geocyathus Zhuravleva, 1960b, p. 234 [**Thalamocyathus botomanensis* Zhuravleva in Zhuravleva & Zelenov, 1955, p. 71; OD; holotype, Zhuravleva & Zelenov, 1955, pl. 2,*3–4*, TsSGM 205/115a-b, Novosibirsk; =*T. botomaensis* Zhuravleva, 1960b, p. 234, *nom. null.*] [=*Jakutocyathus (Jakutocyathus)* Zhuravleva, 1960b, p. 230 (type, *J. (J.) latini*, OD); =*Eladicyathus* Perejón, 1977, p. 550 (type, *E. beticus*, OD); for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 108; Debrenne, Rozanov, & Zhuravlev, 1990, p. 144]. Inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Altay Sayan, Transbaikalia, Far East, Iberia.——Fig. 558,*4a–b*. **G. botomanensis* (Zhuravleva), Perekhod Formation, Atdabanian, Botoma River, Sakha (Yakutia), Russia, holotype, TsSGM 205/115a-b; *a,* transverse section, ×15; *b,* longitudinal section, ×15 (Zhuravleva & Zelenov, 1955).

Family KONJUSCHKOVICYATHIDAE Debrenne & Zhuravlev, 2000

[Konjuschkovicyathidae Debrenne & Zhuravlev, 2000, p. 49]

Inner wall with noncommunicating canals. *lower Cambrian (Bot.1–Bot.3).*

Konjuschkovicyathus Debrenne & Zhuravlev, 2000, p. 49 [**Jakutocyathus spinosus* Konyushkov, 1972, p. 140; OD; holotype, Konyushkov, 1972, pl. 14,*6*, not located; paratypes, Konyushkov, 1972, pl. 14,*5*, PIN 4755/5; Konyushkov, 1972, pl. 16,*3*, PIN 4755/6, Moscow]. Inner wall with downwardly projecting, straight stirrup canals only, bearing supplementary bracts on central cavity side; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1–Bot.3):* Altay Sayan, Transbaikalia.——Fig. 558,*5a–b*. **K. spinosus* (Konyushkov), Verkhnemonok Formation, Botoman, Malyy Karakol River, West Sayan, Altay

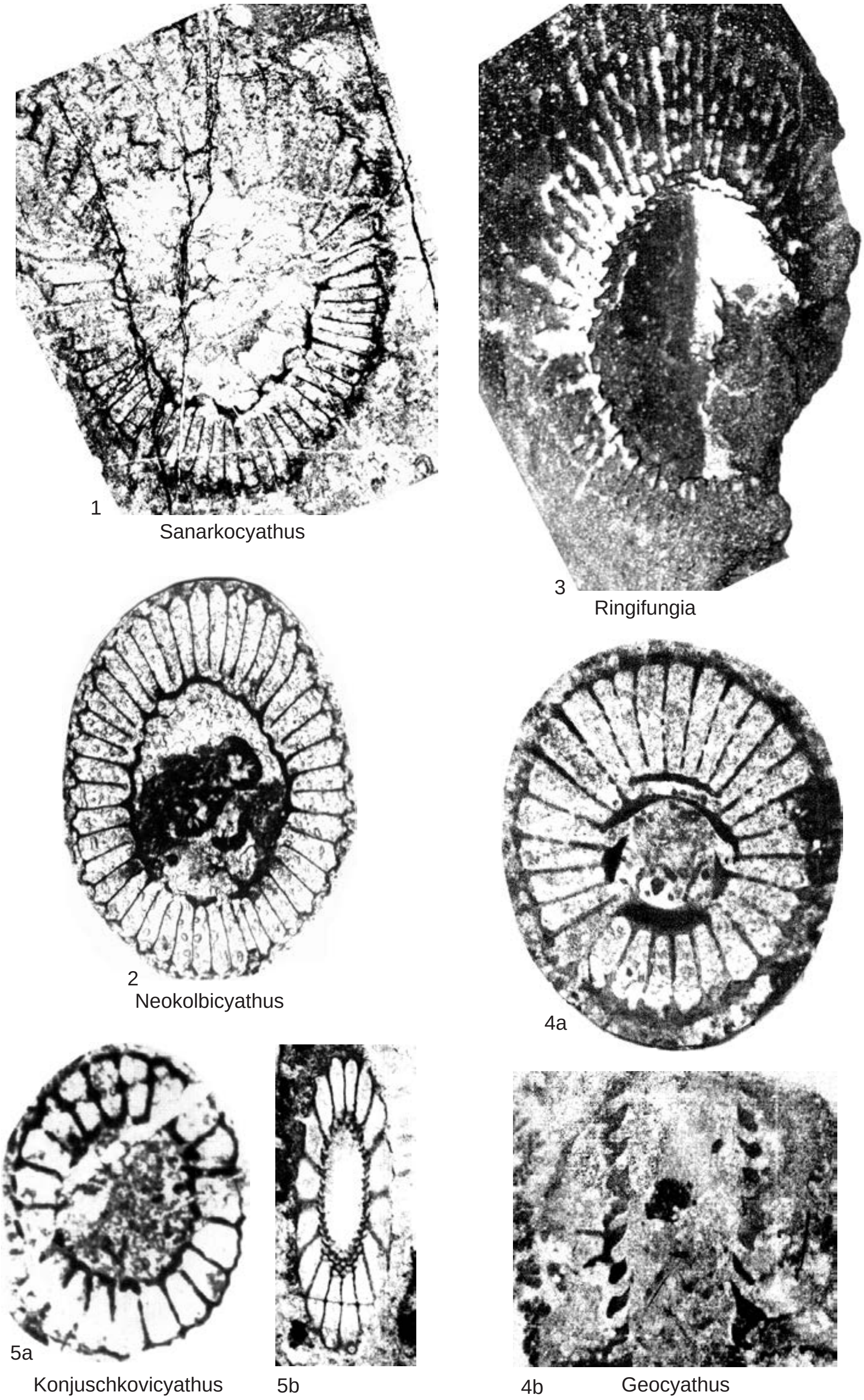
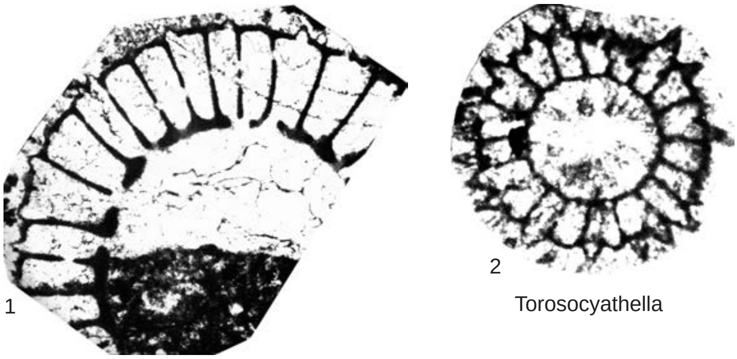
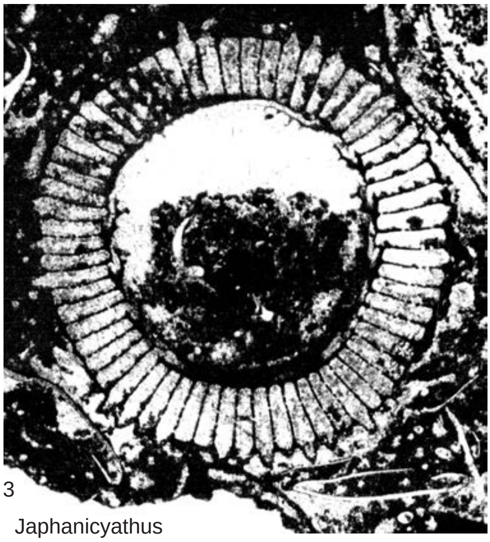


FIG. 558. Sanarkocyathidae, Geocyathidae, and Konjuschkovicyathidae (p. 970–973).

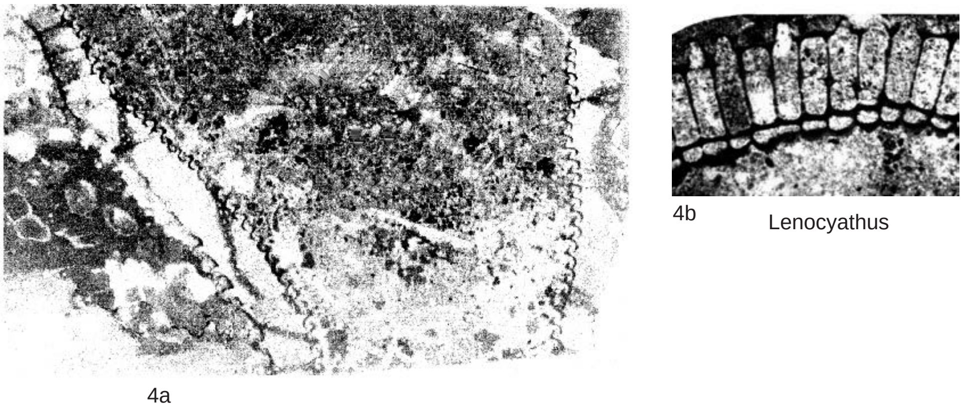


Torosocyathella

Torosocyathus



Japhanicyathus



Lenocyathus

FIG. 559. Torosocyathidae, Japhanicyathidae, and Lenocyathidae (p. 973).

Sayan, Russia; *a,* holotype, transverse section, ×10; *b,* paratype, PIN 4755/6, oblique longitudinal section, ×10 (Konyushkov, 1972).

Superfamily LENOCYATHOIDEA Zhuravleva, 1956

[*nom. correct.* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 83, *pro* Lenocyathacea ZHURAVLEVA, 1960b, p. 224, *nom. transl. ex* Lenocyathidae ZHURAVLEVA in VOLOGDIN, 1956, p. 879] [=Rewardocyathacea ROZANOV, 1973, p. 86, *nom. nud.*]

Outer wall with multiperforate tumuli. *lower Cambrian (Atd.1–Bot.1).*

Family TOROSOCYATHIDAE Debrenne, Zhuravlev, & Kruse, 2002

[Torosocyathidae DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1594] [=Rewardocyathidae ROZANOV, 1973, p. 86, *nom. nud.*; =Rewardocyathidae ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 83, *nom. nud.*, based on unavailable genus-group name]

Inner wall with simple pores. *lower Cambrian (Atd.1–Bot.1).*

Torosocyathus KASHINA in VOLOGDIN & KASHINA, 1972, p. 153 [**T. provisus;* OD; holotype, VOLOGDIN & KASHINA, 1972, pl. 20a,*1*, KGU 19/729a, Krasnoyarsk] [=*Rewardocyathus* ROZANOV, 1973, p. 59, 75, 161, *nom. nud.*]. Inner wall with stirrup pores only; septa completely porous. *lower Cambrian (Atd.1–Bot.1):* Altay Sayan, Mongolia.——FIG. 559,*1*. **T. provisus*, Balakhtinson Formation, Atdabanian, Uyar River, East Sayan, Altay Sayan, Russia, holotype, KGU 19/729a, detail of transverse section, ×12 (Vologdin & Kashina, 1972).

Torosocyathella KOTEL'NIKOV, 1995, p. 27 [**T. osadchajae*; OD; holotype, KOTEL'NIKOV, 1995, pl. 2,*5*, TsNIGRm 12890/9, St. Petersburg]. Inner wall with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Atd.2):* Tuva.——FIG. 559,*2*. **T. osadchajae*, Il'chir Formation, Atdabanian, Vadi-Bala, Tapsa River, Tuva, Russia, holotype, TsNIGRm 12890/9, transverse section, ×20 (Kotel'nikov, 1995).

Family JAPHANICYATHIDAE Rozanov, 1989

[Japhanicyathidae ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 83] [=Japhanicyathidae ROZANOV, 1973, p. 86, *nom. nud.*]

Inner wall with annuli. *lower Cambrian (Atd.2–Bot.1).*

Japhanicyathus KORSHUNOV in ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, p. 45 [**J. genurosus*; OD; holotype, ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, pl. 17,*1–2*, TsSGM 323/67, Novosibirsk]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Bot.1):* Siberian Platform, Far East.——FIG. 559,*3*. **J. genurosus*, Oy-Muran reef massif, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 323/67, transverse section, ×8 (Zhuravleva, Korshunov, & Rozanov, 1969).

Family LENOCYATHIDAE Zhuravleva, 1956

[Lenocyathidae ZHURAVLEVA in VOLOGDIN, 1956, p. 879]

Inner wall with noncommunicating canals. *lower Cambrian (Atd.2–Bot.1).*

Lenocyathus ZHURAVLEVA in ZHURAVLEVA & ZELENOV, 1955, p. 73 (ZHURAVLEVA, 1954, p. 12, *nom. nud.*) [**L. lenaicus*; OD; holotype, ZHURAVLEVA & ZELENOV, 1955, pl. 2,*5–6*, TsSGM 205/117, Novosibirsk]. Inner wall with one row of horizontal to upwardly projecting, S-shaped canals per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Bot.1):* Siberian Platform, Far East, Morocco.——FIG. 559,*4a–b*. **L. lenaicus*, Pestrotsvet Formation, Atdabanian, Yudyay, Botoma River, Sakha (Yakutia), Russia, holotype, TsSGM, 205/117; *a,* longitudinal section, ×7; *b,* detail of transverse section (outer wall at top), ×20 (Debrenne, Zhuravlev, & Kruse, 2002).

Superfamily ANNULOCYATHOIDEA Krasnopeeva, 1953

[*nom. correct.* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 83, *pro* Annulocyathacea ZHURAVLEVA, 1960b, p. 171, *nom. transl. ex* Annulocyathidae KRASNOPEEVA, 1953, p. 56]

Outer wall with bracts or scales. *lower Cambrian (Tom.2–Bot.3).*

Family TUMULIFUNGIIDAE Rozanov, 1989

[Tumulifungiidae ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 83] [=Tumulifungiidae ROZANOV, 1973, p. 85, *nom. nud.*]

Inner wall with simple pores. *lower Cambrian (Tom.2–Bot.3).*

Tumulifungia ZHURAVLEVA in DATSENKO & others, 1968, p. 144 (ZHURAVLEVA in ZHURAVLEVA & others, 1967, p. 68, *nom. nud.*) [**T. datzenkoi*; OD; holotype, DATSENKO & others, 1968, pl. 4,*2–3*, TsSGM 277/30, Novosibirsk]. Outer wall with upwardly projecting cupped bracts; inner wall with one row of simple pores per intersept; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East, Morocco, Iberia.——FIG. 560,*1*. **T. datzenkoi*, Shumnoy Formation, Botoman, Sukharikha River, Krasnoyarsk region,

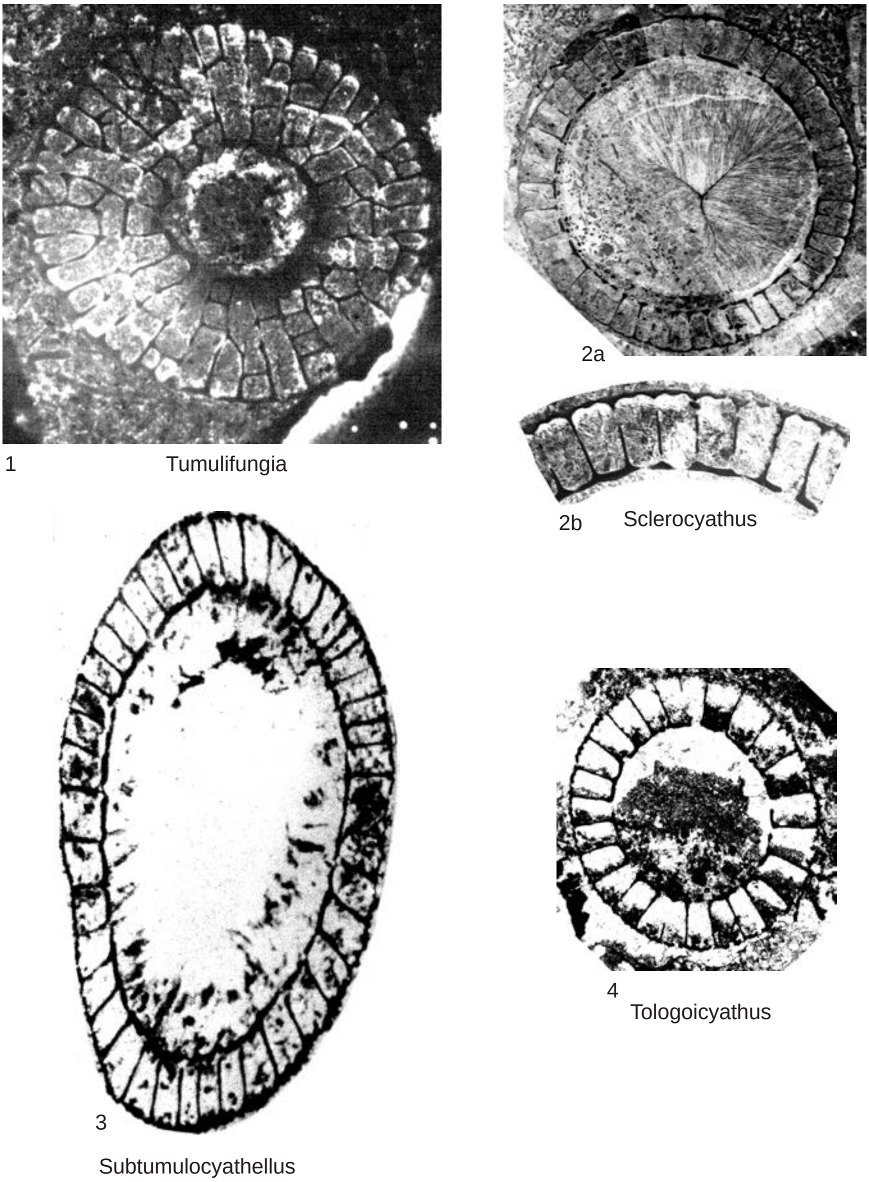


FIG. 560. Tumulifungiidae (p. 973–975).

Russia, holotype, TsSGM 277/30, transverse section, ×11 (Datsenko & others, 1968).

Sclerocyathus VOLOGDIN, 1960, p. 424 [**S. scrofulosus*; OD; holotype, VOLOGDIN, 1960, fig. 1z-i, PIN 4754/1, Moscow]. Outer wall with upwardly projecting, cupped bracts; inner wall with one row of simple pores per intersept; septa completely porous. *lower Cambrian (Tom.2–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East, Iberia.——FIG. 560,*2a–b*. **S. scrofulosus*, Bayan-Kol Formation, Atdabanian, Yenisey River, Shagonar Mountains, Tuva, Russia, holotype, PIN 4754/1; *a,* transverse section, ×4; *b,* detail of transverse section, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

Subtumulocyathellus OSADCHAYA in OSADCHAYA & others, 1979, p. 129 [**S. vulgaris*; OD; holotype, OSADCHAYA & others, 1979, pl. 11,*1*, VSEGEI

11594, St. Petersburg] [=*Arturocyathus* ROZANOV, 1973, p. 61, 162, *nom. nud.*; =*Arturocyathus* ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 95 (type, *A. borisovi* ROZANOV, 1973, p. 162, OD)]. Outer wall with upwardly projecting, cupped bracts; inner wall with stirrup pores only; septa aporose to sparsely porous. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East.——FIG. 560,*3*. **S. vulgaris*, Usa Formation, Atdabanian, Krutoy Log, Batenev Range, Kuznetsk Alatau, Russia, holotype, VSEGEI 11594, oblique transverse section, ×10 (Osadchaya & others, 1979).

Tologoicyathus VORONIN, 1988, p. 9 [**T. ichituinicus*; OD; holotype, VORONIN, 1988, pl. 2,*3*, PIN 3301/516, Moscow]. Outer wall with upwardly projecting, cupped bracts; inner wall with several rows of simple pores per intersept; septa completely porous. *lower Cambrian (Tom.4–Bot.1):* Mongolia, Far East.——FIG. 560,*4*. **T. ichituinicus*, Ichituin Formation, Atdabanian, Boro-Khairkhan-Obo Mountain, Khan-Khukhiy Range, Mongolia, paratype, PIN 3301/515, transverse section, ×5 (Voronin, 1988).

Family ANNULOCYATHIDAE Krasnopeeva, 1953

[Annulocyathidae KRASNOPEEVA, 1953, p. 56]

Inner wall with annuli. *lower Cambrian (Atd.2–Bot.3).*

Annulocyathus VOLOGDIN, 1937b, p. 468 [**A. pulcher*; M; lectotype, DEBRENNE, ZHURAVLEV, & KRUSE, 2002, fig. 32E; SD DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1597, PIN 4754/5, Moscow]. Outer wall with upwardly projecting, cupped bracts; inner wall with one pore row per intersept and upright V-shaped annuli; septa completely porous. *lower Cambrian (Bot.1):* Altay Sayan, Far East.——FIG. 561,*1a–b*. **A. pulcher*, Verkhnemonok Formation, Botoman, Sanashtykgol River, West Sayan, Altay Sayan, Russia, lectotype, PIN 4754/5; *a,* transverse section, ×11 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* sketch of longitudinal section (outer wall to left), ×5.5 (Vologdin, 1937b).

Annulocyathella VOLOGDIN, 1962a, p. 123 [**Annulocyathus lavrenovae* KRASNOPEEVA, 1955, p. 99; OD; holotype, KRASNOPEEVA, 1955, pl. 3,*2;* VOLOGDIN, 1962a, fig. 86, not designated; =*Anulocyathus lavrenovi* KRASNOPEEVA, 1937, p. 33; holotype, KRASNOPEEVA, 1937, pl. 4,*38–39,41,43–44;* pl. 16,*109;* pl. 19,*118*, not designated]. Outer wall with upwardly projecting, cupped bracts; inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa aporose to sparsely porous. *lower Cambrian (Atd.4–Bot.3):* Altay Sayan.——FIG. 561,*2a–b*. **A. lavrenovae* (KRASNOPEEVA), Usa Formation, Botoman, Bol'shaya Erba, Batenev Range, Kuznetsk Alatau, Russia; *a,* unlocated syntype, oblique transverse section, ×8; *b,* unlocated syntype, sketch of longitudinal section (outer wall to left), ×8 (Krasnopeeva, 1955).

Annulofungia KRASNOPEEVA, 1955, p. 99 (KRASNOPEEVA, 1953, p. 56, *nom. nud.*) [**Anulocyathus taylori* KRASNOPEEVA, 1937, p. 34; OD; holotype, KRASNOPEEVA, 1937, pl. 4,*46–47;* pl. 18,*115–116;* pl. 22,*130;* pl. 24,*137*, not designated, collection not located] [=*Kiyafungia* BOYARINOV in ZHURAVLEVA & others, 1997b, p. 130 (type, *K. concinna,* OD)]. Outer wall with upwardly projecting, cupped bracts; inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous, linked by synapticulae. *lower Cambrian (Atd.4–Bot.1):* Altay Sayan.——FIG. 561,*3a–b*. **A. taylori* (KRASNOPEEVA), Usa Formation, Botoman, Mt. Aydachikha, Batenev Range, Kuznetsk Alatau, Russia, unlocated specimen; *a,* longitudinal section, ×6; *b,* transverse section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Hemithalamocyathus TING, 1937, p. 367 [**Archaeocyathus sibiricus* TOLL, 1899, p. 40; M; lectotype, TOLL, 1899, pl. 6,*5;* SD DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1598, TsNIGRm 24a/11533, St. Petersburg]. Outer wall with upwardly projecting, cupped bracts; inner wall with several pore rows per intersept and upright, V-shaped annuli; septa completely porous. *lower Cambrian (Atd.4–Bot.1):* Altay Sayan.——FIG. 561,*4*. **H. sibiricus* (TOLL), Torgashino Formation, Torgashino, Krasnoyarsk region, East Sayan, Altay Sayan, Russia, unnumbered paralectotype, oblique longitudinal section (outer wall to left), ×10 (Toll, 1899).

Family JAKUTOCARINIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Jakutocarinidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 83]

Inner wall with noncommunicating canals. *lower Cambrian (Atd.1–Bot.3).*

Jakutocarinus ZHURAVLEVA, 1960b, p. 232 [**Jakutocyathus (Jakutocarinus) jakutensis*; OD; holotype, ZHURAVLEVA, 1960b, pl. 20,*2*, TsSGM 205/113, Novosibirsk]. Outer wall with upwardly projecting, cupped bracts; inner wall with several rows of downwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia.——FIG. 562,*1*. **J. jakutensis*, Pestrotsvet Formation, Atdabanian, Mukhatta River, Sakha (Yakutia), Russia, holotype, TsSGM 205/113, detail of oblique transverse section (outer wall at top), ×15 (Debrenne, Zhuravlev, & Kruse, 2002).

Kosticyathus DEBRENNE & ZHURAVLEV, 2000, p. 49 [**Porocyathus sheglovi* KONYUSHKOV, 1972, p. 138; OD; holotype, KONYUSHKOV, 1972, pl. 16,*4–5*, PIN 4755/9, Moscow]. Outer wall with upwardly projecting, cupped bracts; inner wall with one row of downwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity

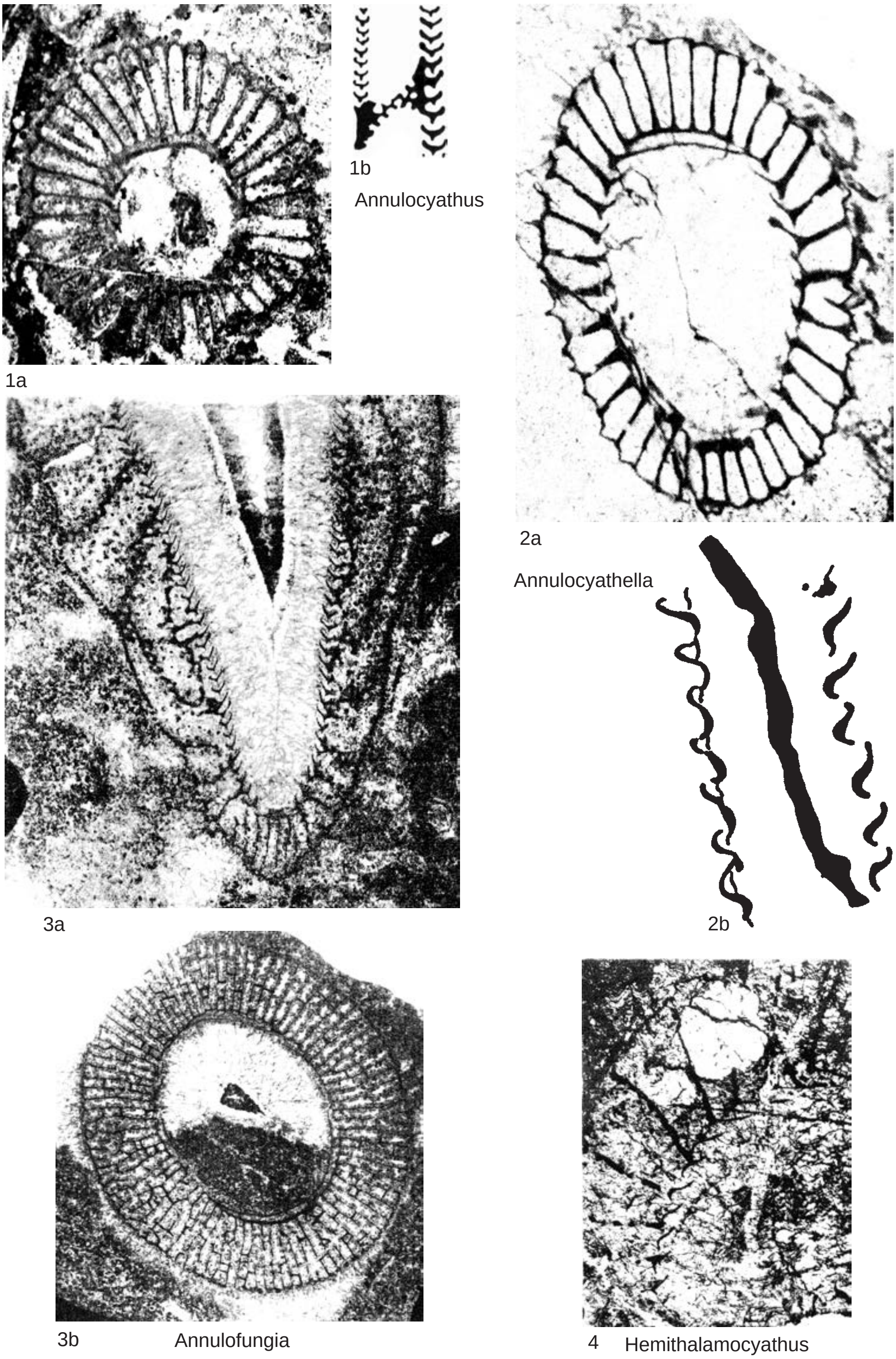


FIG. 561. Annulocyathidae (p. 975).

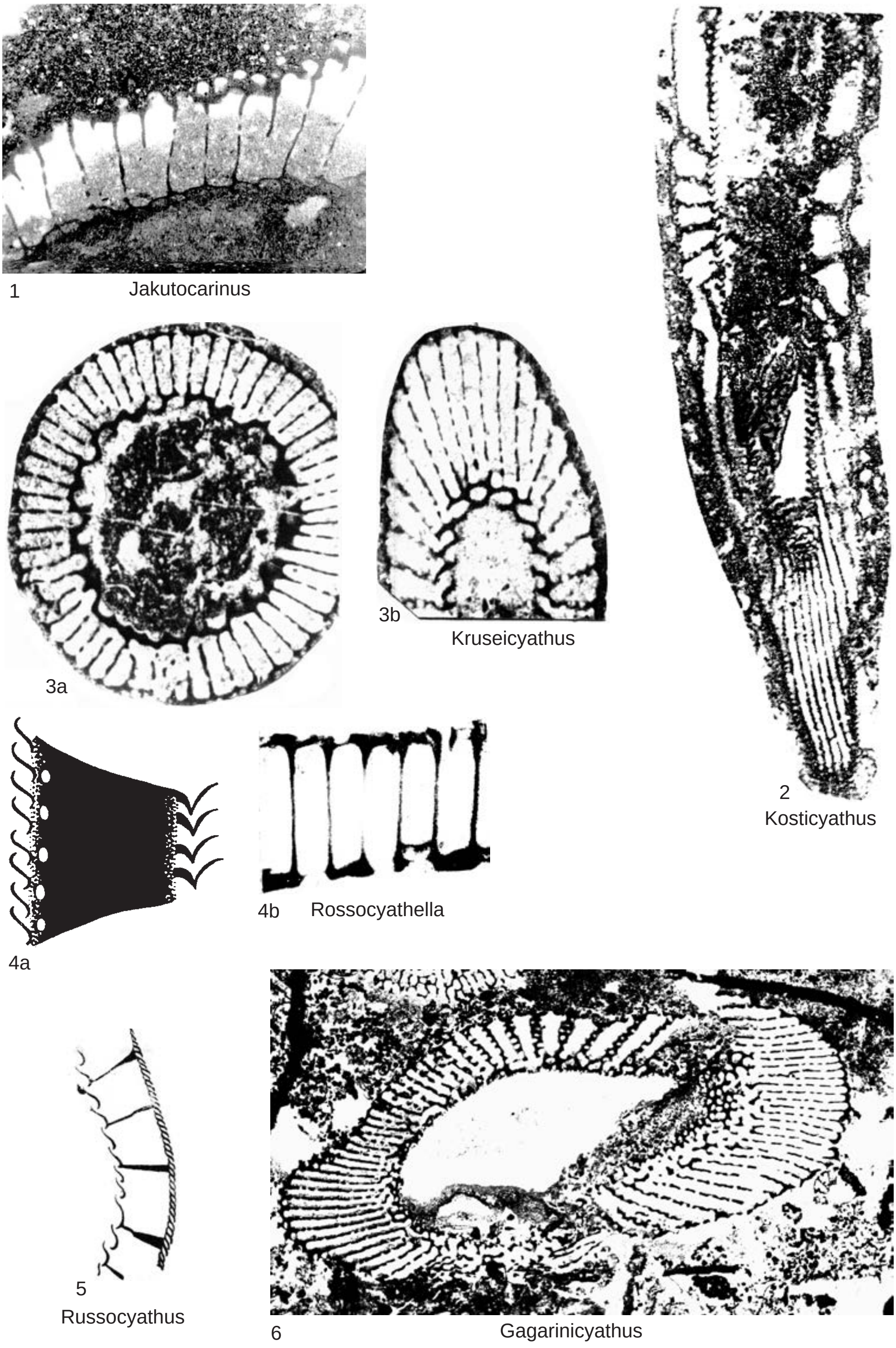


FIG. 562. Jakutocarinidae and Gagarinicyathidae (p. 975–978).

side; septa completely porous. *lower Cambrian (Bot.1–Bot.3):* Altay Sayan.——FIG. 562,*2*. **K. sheglovi* (KONYUSHKOV), Verkhnemonok Formation, Botoman, Malyy Karakol River, West Sayan, Altay Sayan, Russia, holotype, PIN 4755/9, longitudinal section, ×6 (Konyushkov, 1972).

Kruseicyathus BOYARINOV & KONYAEVA in ZHURAVLEVA & others, 1997b, p. 134 [**K. notabilis*; OD; holotype, ZHURAVLEVA & others, 1997b, pl. 4,*5*, ZSGGU 2329/86, Novokuznetsk]. Outer wall with upwardly projecting, cupped bracts; inner wall with horizontal to upwardly projecting, S-shaped canals, each canal spanning several intersepts; septa completely porous. *lower Cambrian (Bot.1):* Altay Sayan.——FIG. 562,*3a–b*. **K. notabilis*, Usa Formation, Botoman, Malaya Belokamenka River, Kiya River, Kuznetsk Alatau, Russia; *a,* paratype, ZSGGU 2329/85, transverse section, ×10; *b,* holotype, ZSGGU 2329/86, oblique longitudinal section, ×10 (Zhuravleva & others, 1997b).

Rossocyathella ZHURAVLEVA, 1960b, p. 178 [**R. ninaekosti*; OD; holotype, ZHURAVLEVA, 1960b, pl. 12,*5*, PIN 1038, Moscow, not located]. Outer wall with upwardly projecting, cupped bracts; inner wall with one row of downwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Siberian Platform, Altay Sayan, Tuva.——FIG. 562,*4a–b*. **R. ninaekosti*, Perekhod Formation, Botoman, Botoma River, Sakha (Yakutia), Russia, holotype, PIN 1038; *a,* sketch of longitudinal section (outer wall to left), ×40; *b,* detail of transverse section (outer wall at bottom), ×15 (Zhuravleva, 1960b).

?Russocyathus ZHURAVLEVA, 1955b, p. 628 [**R. basaichensis*; OD; holotype, ZHURAVLEVA, 1955b, fig. 1E, 2v; REPINA & others, 1964, pl. 19,*2*, PIN 1039, Moscow, not located]. Outer wall with probable upwardly projecting, cupped bracts; inner wall with one row of probable horizontal to upwardly projecting, S-shaped canals per intersept; septa aporose to sparsely porous. [Limited type material does not provide certainty as to orientation of cup and hence as to presence or absence of canals and/or bracts in walls.] *lower Cambrian (Atd.3–Bot.1):* Altay Sayan, Tuva.——FIG. 562,*5*. **R. basaichensis*, Torgashino Formation, Atdabanian, Torgashino, Krasnoyarsk region, East Sayan, Altay Sayan, Russia, holotype, PIN 1039, sketch of oblique longitudinal section, ×20 (Zhuravleva, 1955b).

Family GAGARINICYATHIDAE
Debrenne, Rozanov, & Zhuravlev, 1989

[Gagarinicyathidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 84]

Inner wall with communicating canals. *lower Cambrian (Atd.3–Bot.1).*

Gagarinicyathus ZHURAVLEVA in DATSENKO & others, 1968, p. 146 [**G. ethmophylloides*; OD; holotype, DATSENKO & others, 1968, pl. 5,*1*, TsSGM 277/36, Novosibirsk]. Outer wall with upwardly projecting, cupped bracts; inner wall with one row of horizontal to upwardly projecting, straight porous canals per intersept; septa completely porous. *lower Cambrian (Atd.3–Bot.1):* Siberian Platform.——FIG. 562,*6*. **G. ethmophylloides*, Shumnoy Formation, Botoman, Sukharikha River, Krasnoyarsk region, Russia, holotype, TsSGM 277/36, oblique longitudinal section, ×4.5 (Datsenko & others, 1968).

Superfamily ETHMOPHYLLOIDEA
Okulitch, 1937

[*nom. transl.* ZHURAVLEV in VORONOVA & others, 1987, p. 23, *ex* Ethmophyllidae OKULITCH, 1937b, p. 358] [=Carinacyathoidea KRASNOPEEVA, 1953, p. 52, *nom. transl.* ZHURAVLEV in VORONOVA & others, 1987, p. 23, *ex* Carinacyathidae ZHURAVLEVA, 1960b, p. 240, *nom. correct. pro* Carinocyathidae KRASNOPEEVA, 1953, p. 52; =Fansycyathacea KORSHUNOV & ROZANOV in ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, p. 46; =Hupecyathelloidea ROZANOV, 1969, p. 111, *nom. correct.* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 84, *pro* Hupecyathellacea ROZANOV, 1969, p. 111]

Outer wall with canals. *lower Cambrian (Atd.1–Toy.1).*

Family FALLOCYATHIDAE
Rozanov, 1969

[Fallocyathidae ROZANOV in ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, p. 47] [=Sekwicyathidae ROZANOV, 1973, p. 85, *nom. nud.*]

Inner wall with simple pores. *lower Cambrian (Bot.1–Bot.2).*

Fallocyathus ROZANOV in ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, p. 47 [**F. dubius*; OD; holotype, ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, pl. 18,*5–6;* pl. 19,*2*, PIN 4297/84, Moscow]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with several rows of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1):* Siberian Platform, Iberia.——FIG. 563,*1*. **F. dubius*, Oy-Muran reef massif, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, PIN 4297/84, oblique transverse section, ×12 (Zhuravleva, Korshunov, & Rozanov, 1969).

Sekwicyathus HANDFIELD, 1971, p. 34 [**S. nahanniensis*; OD; holotype, HANDFIELD, 1971, p. 34, pl. 2,*5*, GSC 25317, Ottawa; ?=*Archaeocyathus nevadensis* OKULITCH, 1935b, p. 101]. Outer wall with subspherical chambered canals each with base commencing in intervallum, canals subdivided by stipules (imparting overall inverted V-shaped appearance to outer wall); inner wall with several rows of simple pores per intersept; septa aporose to sparsely porous. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Iberia, Canada, United States.——FIG. 563,*2a–c*. **S. nahanniensis*; *a,* Sekwi Formation, Botoman, Mackenzie Mountains, Northwest Territories, Canada, holotype, GSC 25137, oblique longitudinal section, ×15 (Handfield, 1971); *b,* Atan Group, Botoman, Gataga River,

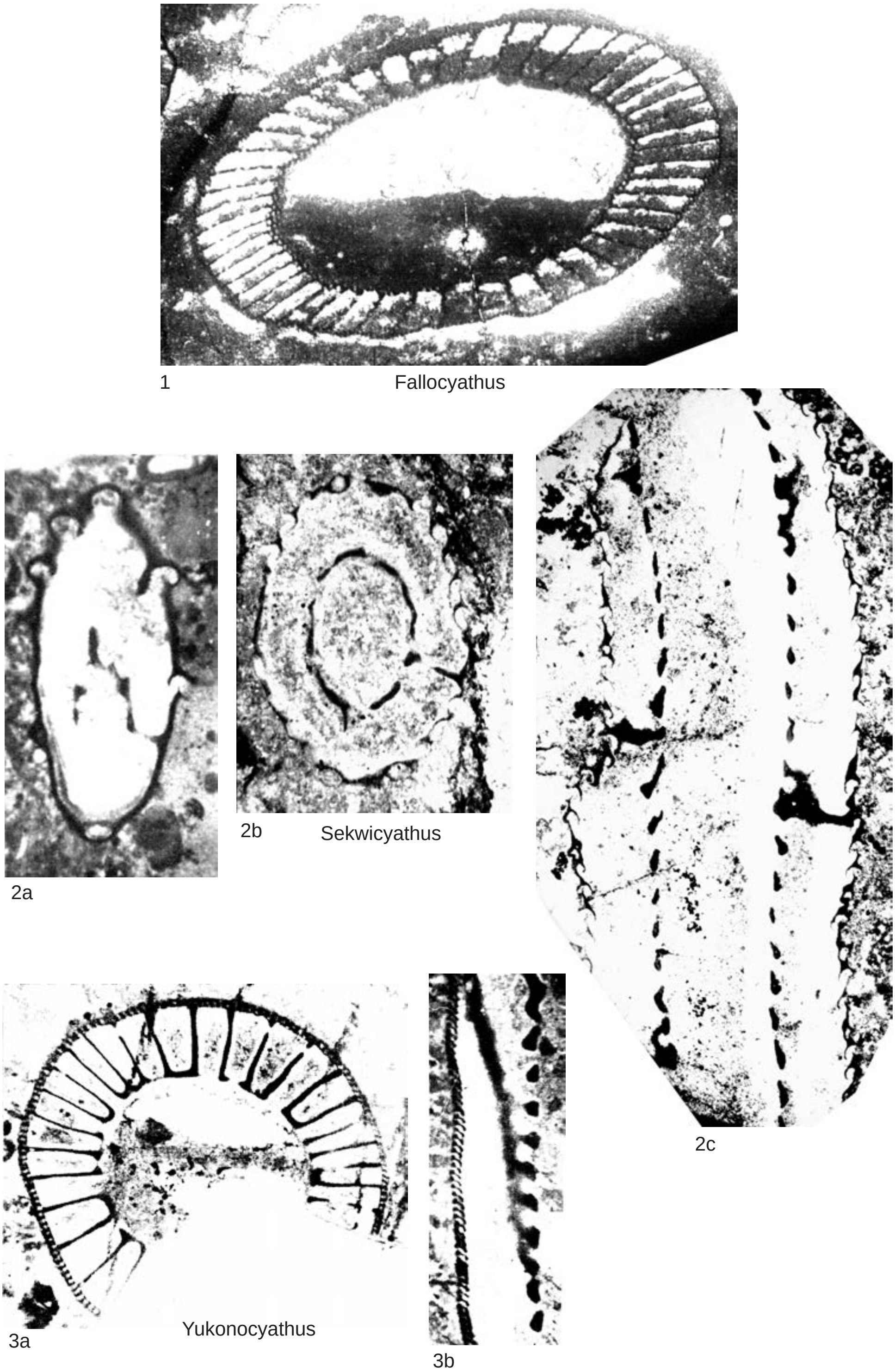


FIG. 563. Fallocyathidae (p. 978–980).

British Columbia, Canada, specimen GSC 69260, transverse section, ×10 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* Sekwi Formation, Botoman, Mackenzie Mountains, Northwest Territories, Canada, specimen GSC 90132, longitudinal section, ×10 (Voronova & others, 1987).

Yukonocyathus Handfield, 1971, p. 51 [**Y. francesi*; OD; holotype, Handfield, 1971, pl. 8,*1a–c*, GSC 25351, Ottawa]. Outer wall with horizontal to upwardly projecting, S-shaped canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of simple pores per intersept, formed by fluting of inner edges of septa; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Canada, United States.——Fig. 563,*3a–b*. **Y. francesi*, Sekwi Formation, Botoman, Frances Lake, Yukon Territory, Canada, holotype, GSC 25351; *a,* transverse section, ×6; *b,* longitudinal section (outer wall to left), ×6 (Handfield, 1971).

Family GLORIOSOCYATHIDAE Rozanov, 1969

[Gloriosocyathidae Rozanov, 1969, p. 108]

Inner wall with bracts or scales. *lower Cambrian (Atd.1–Bot.1).*

Gloriosocyathus Rozanov, 1969, p. 108 [**G. permultus*; OD; holotype, Rozanov, 1969, pl. 40,*3*, PIN 4297/95, Moscow]. Outer wall with horizontal to upwardly projecting, S-shaped canals; inner wall with one row of pores per intersept, bearing upwardly projecting, S-shaped scales; septa completely porous. *lower Cambrian (Bot.1):* Siberian Platform, Iberia.——Fig. 564,*1*. **G. permultus*, Erkeket Formation, Botoman, Khorbusuonka River, Olenek Basin, Sakha (Yakutia), Russia, holotype, PIN 4297/95, oblique transverse section, ×10 (Debrenne, Zhuravlev, & Kruse, 2002).

Gandinocyathus F. Debrenne & M. Debrenne in Gandin, F. Debrenne, & M. Debrenne, 2007, p. 41 [**G. gravestocki*, OD; holotype, F. Debrenne, Gandin, & M. Debrenne, 1993, pl. 3,*1*, MNHN M84234, Paris]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of pores per intersept, bearing upwardly projecting, cupped bracts; septa completely porous. *lower Cambrian (Atd.3–Bot.1):* South China, Sardinia.——Fig. 564,*2*. **G. gravestocki*, Matoppa Formation, Botoman, Matoppa Valley, Sardinia, Italy, holotype, MNHN M84234, oblique longitudinal section, ×10 (F. Debrenne, Gandin, & M. Debrenne, 1993).

Nalivkinicyathus Boyarinov & Osadchaya in Osadchaya & Ganachkova, 1986, p. 170 [**Porocyathellus cyroflexus* Boyarinov & Osadchaya in Osadchaya & others, 1979, p. 132; OD; holotype, Osadchaya & others, 1979, pl. 8,*1–2;* Osadchaya & Ganachkova, 1986, pl. 18,*1–2*, VSEGEI 11594, St. Petersburg] [=*Nalivkinicyathus* Osadchaya in Debrenne & Rozanov, 1983, p. 735, *nom. nud.*, *nom. nov. pro Porocyathellus* Boyarinov & Osadchaya in Osadchaya & others, 1979, p. 131, *non* Debrenne, 1977a, p. 107, archaeocyath]. Outer wall with downwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall upright V-shaped appearance to outer wall); inner wall with one row of pores per intersept, bearing upright, V-shaped scales; septa completely porous. *lower Cambrian (Atd.1–Bot.1):* Altay Sayan, Iberia.——Fig. 564,*3a–b*. **N. cyroflexus* (Boyarinov & Osadchaya), Usa Formation, Atdabanian, Krutoy Log, Batenev Range, Kuznetsk Alatau, Russia, holotype, VSEGEI 11594; *a,* transverse section, ×4; *b,* detail of septum in longitudinal section (outer wall to right), ×12 (Osadchaya & others, 1979).

Family KIJACYATHIDAE Zhuravleva, 1964

[Kijacyathidae Zhuravleva in Repina & others, 1964, p. 195] [=Fansycyathidae Korshunov & Rozanov in Zhuravleva, Korshunov, & Rozanov, 1969, p. 47]

Inner wall with annuli. *lower Cambrian (Atd.2–Bot.3).*

Kijacyathus Zhuravleva, 1959, p. 424 [**K. chomentovskii*; OD; holotype, Zhuravleva, 1959, fig. 2b–g, PIN 1431, Moscow, not located]. Outer wall with horizontal to upwardly projecting, S-shaped canals; inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous. *lower Cambrian (Atd.3–Bot.1):* Altay Sayan, Mongolia, Far East.——Fig. 565,*1a–b*. **K. chomentovskii*, Usa Formation, Atdabanian, Kiya River, Kuznetsk Alatau, Russia, holotype, PIN 1431; *a,* transverse section, ×8 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* detail of septum in longitudinal section (outer wall to left), ×13 (Zhuravleva, 1959).

Aporosocyathus Kruse, 1978, p. 32 [**A. mucroporus*; OD; holotype, Kruse, 1978, fig. 4A–B, AM FT.15203, 15204, Sydney]. Outer wall with horizontal to upwardly projecting, S-shaped canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one pore row per intersept and upright, V-shaped annuli; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.2–Bot.3):* ?Mongolia, Australia, Antarctica, ?Canada.——Fig. 565,*2a–b*. **A. mucroporus*, Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia, holotype, AM FT.15203, 15204; *a,* oblique transverse section, AM FT.15204, ×6 (Kruse, 1978); *b,* detail of longitudinal section (outer wall to right) AM FT.15203, ×8 (Kruse, 1982).

Fansycyathus Korshunov & Rozanov in Zhuravleva, Korshunov, & Rozanov, 1969, p. 48 [**F. lermontovae*; OD; holotype, Zhuravleva, Korshunov, & Rozanov, 1969, pl. 17,*7;* Rozanov, 1973, pl. 20,*2*, PIN 4297/83, Moscow]. Outer wall with horizontal

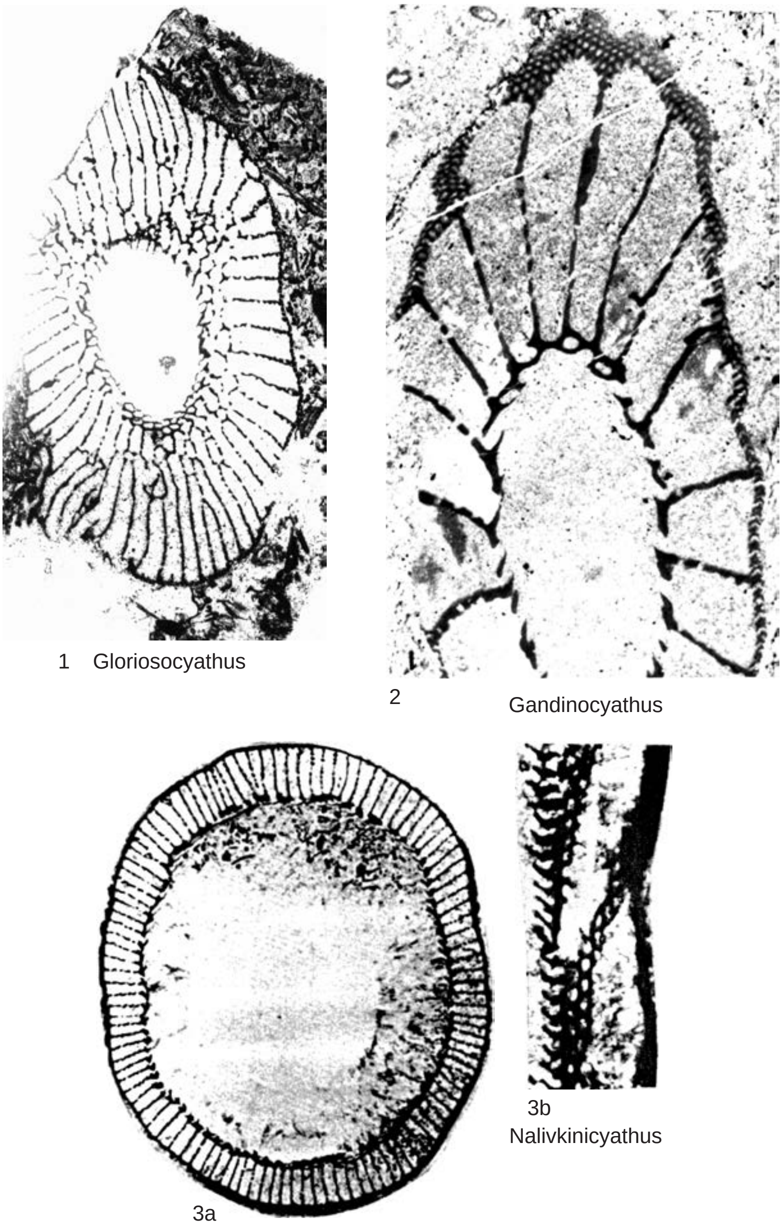


FIG. 564. Gloriosocyathidae (p. 980).

to upwardly projecting, S-shaped canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.2–Bot.1):* Siberian Platform.——FIG. 565,*3. *F. lermontovae*, Oy-Muran reef massif, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, PIN 4297/83, longitudinal section, ×12 (Zhuravleva, Korshunov, & Rozanov, 1969).

Flexanulus DEBRENNE, 1975, p. 335 [**F. oosthuizeni*; OD; holotype, DEBRENNE, 1975, fig. 3a–b, SAM(C) K4495 B-12a, Cape Town]. Outer wall with horizontal to upwardly projecting, S-shaped canals, each with base commencing in intervallum,

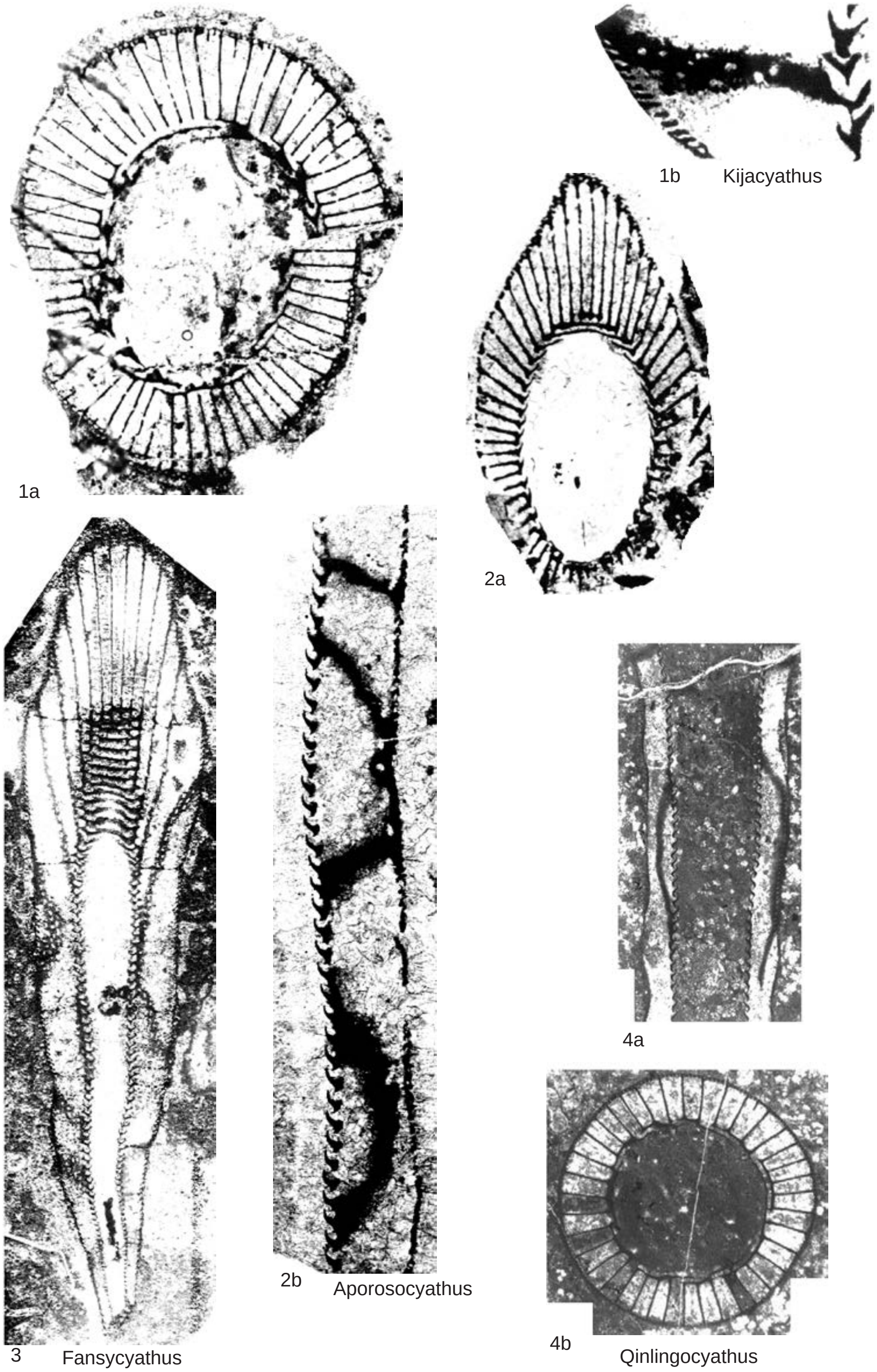


FIG. 565. Kijacyathidae (p. 980–984).

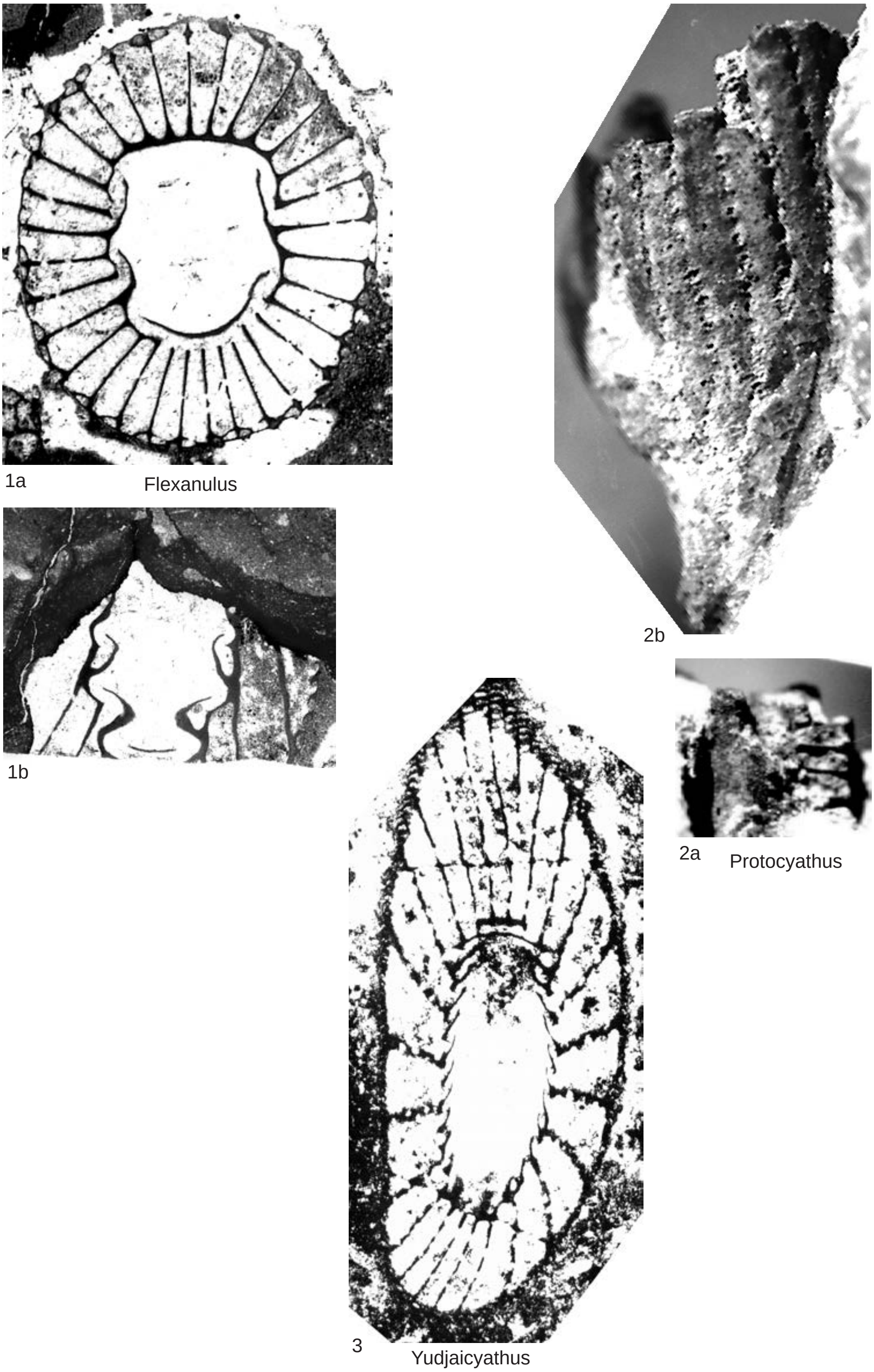


FIG. 566. Kijacyathidae (p. 981–984).

bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa aporose to sparsely porous. *lower Cambrian (Bot.3):* Antarctica, Falkland Islands (allochthonous), South Africa (allochthonous).——FIG. 566,*1a–b*. **F. oosthuizeni*, Dwyka Subgroup, Botoman (allochthonous in Permian), Zwartskraal, South Africa, holotype, SAM(C) K4495 B-12a; *a,* transverse section, ×10; *b,* longitudinal section, ×10 (Debrenne, 1975).

Protocyathus FORD, 1878, p. 124 [**P. rarus*; M; holotype, FORD, 1878, fig. 1a–b, NYSM 52, Albany]. Outer wall with horizontal to upwardly projecting, straight stirrup canals only; inner wall with stirrup pores only, bearing horizontal planar to waved annuli, one per several horizontal pore files; septa aporose to sparsely porous. *lower Cambrian (Bot.1–Bot.2):* Canada, United States.——FIG. 566,*2a–b*. **P. rarus*, Brown's Pond Formation, Botoman, Troy, New York, United States, holotype, NYSM 52; *a,* detail of septum and inner wall in longitudinal view (outer wall to left), ×15; *b,* longitudinal view of outer wall, ×15 (Debrenne, Zhuravlev, & Kruse, 2002).

Qinlingocyathus YANG & YUAN, 2012, p. 599 [**Q. astomus*; OD; holotype, YANG & YUAN, 2012, fig. 7B–E, NIGP FVI-1a (8)a,b, Nanjing]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa aporose to sparsely porous. *lower Cambrian (Atd.3):* South China.——FIG. 565,*4a–b*. **Q. astomus*, Xiannudong Formation, Fucheng, Nanzhen, Shaanxi, China, holotype, NIGP FVI-1a (8)a,b; *a*, longitudinal section, ×5; *b*, transverse section, ×6 (Yang & Yuan, 2012; copyright ©2012 Elsevier Masson SAS, all rights reserved).

Yudjaicyathus ZHURAVLEV in ZHURAVLEV, ZHURAVLEVA, & FONIN, 1983, p. 25 [**Y. astashkini*; OD; holotype, ZHURAVLEV, ZHURAVLEVA, & FONIN, 1983, pl. 4,*1*, PIN 3848/505, Moscow]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.3–Atd.4):* Siberian Platform.——FIG. 566,*3*. **Y. astashkini*, Pestrotsvet Formation, Atdabanian, Bachyk Creek, Lena River, Sakha (Yakutia), Russia, holotype, PIN 3848/505, oblique longitudinal section, ×14 (Zhuravlev, Zhuravleva, & Fonin, 1983).

Family CARINACYATHIDAE Krasnopeeva, 1953

[*nom. correct.* ZHURAVLEVA, 1960b, p. 240, *pro* Carinocyathidae KRASNOPEEVA, 1953, p. 56] [=Porocyathidae ZHURAVLEVA in VOLOGDIN, 1957a, p. 179; =Hupecyathellidae ROZANOV, 1969, p. 111]

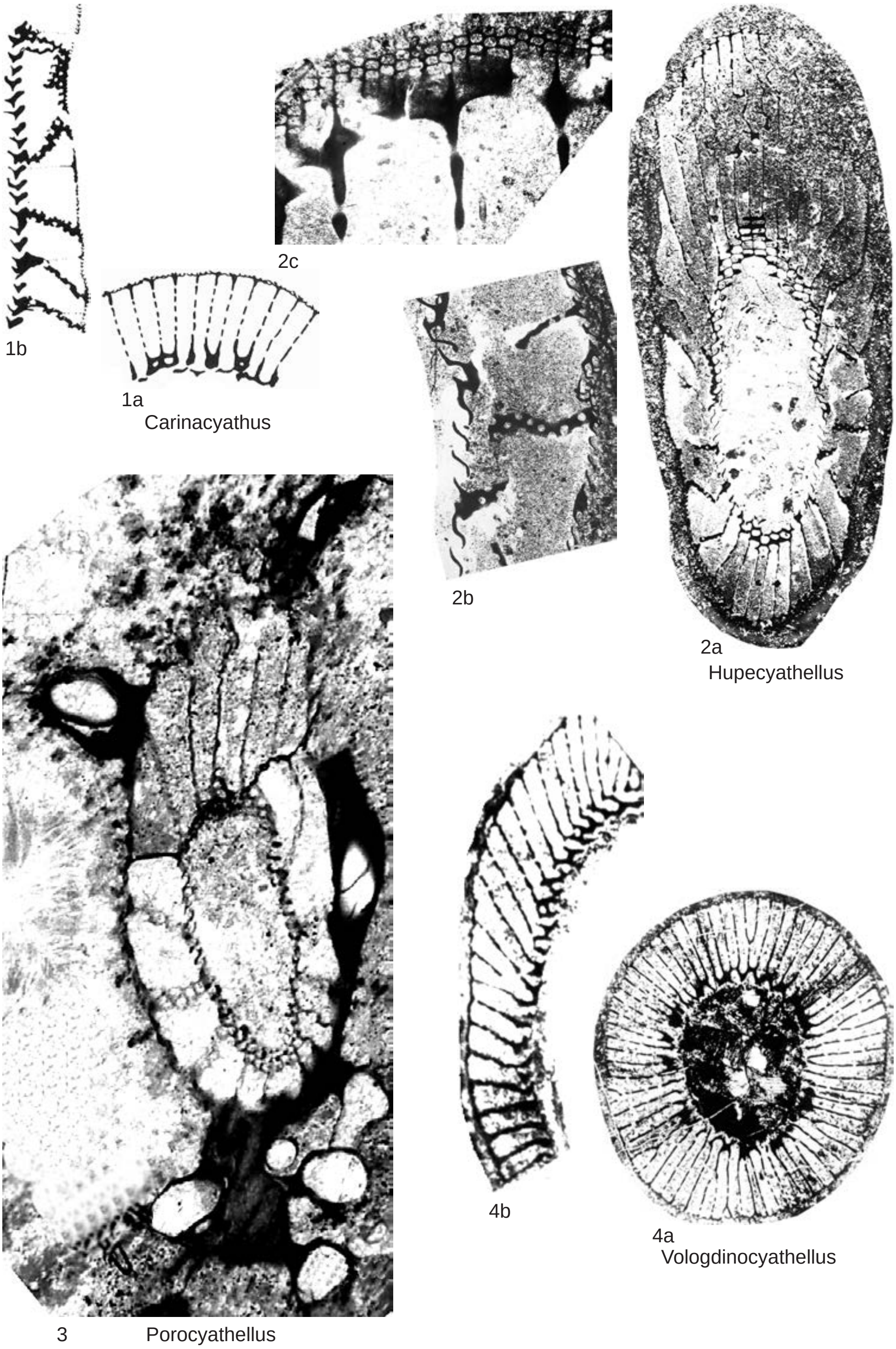
Inner wall with noncommunicating canals. *lower Cambrian (Atd.1–Bot.3).*

Carinacyathus VOLOGDIN, 1932, p. 37 [**C. loculatus*; M; holotype, VOLOGDIN, 1932, fig. 28, pl. 10,*5;* M; VOLOGDIN, 1940b, fig. 77, pl. 27,*7*, TsNIGRm 45a/2957, St. Petersburg] [=*Carinocyathus* VOLOGDIN, 1937b, p. 471, *nom. null.*; =*Porocyathus* ZHURAVLEVA in VOLOGDIN, 1957a, p. 179, *nom. nud.*; =*Porocyathus* ZHURAVLEVA, 1960b, p. 180 (type, *P. pinus*, OD); =*Fossilicyathus* KORSHUNOV, 1983b, p. 111 (type, *F. evidens*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 98; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 136]. Outer wall with downwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall upright V-shaped appearance to outer wall); inner wall with one row of downwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Kolyma, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East.——FIG. 567,*1a–b*. **C. loculatus*, Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Altay Sayan, Russia, holotype, TsNIGRm 45a/2957; *a,* transverse section (outer wall at top), ×10; *b,* longitudinal section (outer wall to right), ×10 (Vologdin, 1932).

Hupecyathellus ROZANOV in DATSENKO & others, 1968, p. 149 [**H. schuberti*; OD; holotype, DATSENKO & others, 1968, pl. 14,*1–3;* ROZANOV, 1973, pl. 7,*1*, PIN 4297/75, Moscow]. Outer wall with downwardly projecting, S-shaped canals, bearing supplementary independent microporous sheath externally; inner wall with several rows of horizontal to upwardly projecting, S-shaped canals per intersept; septa completely porous. *lower Cambrian (Bot.1):* Siberian Platform.——FIG. 567,*2a–c*. **H. schuberti*, Shumnoy Formation, Botoman, Sukharikha River, Krasnoyarsk region, Russia, holotype, PIN 4297/75; *a,* oblique longitudinal section, ×5; *b,* detail of septum in longitudinal section (outer wall to right), ×7; *c,* detail of outer wall in tangential section, ×17 (Datsenko & others, 1968).

Porocyathellus DEBRENNE, 1977a, p. 107 [**P. bouddi*; OD; holotype, DEBRENNE, 1977a, pl. 6,*1*, MNHN M80025, IRH 2 1aL, Paris]. Outer wall with horizontal to upwardly projecting, S-shaped canals; inner wall with several rows of horizontal to upwardly projecting, S-shaped canals per intersept; septa completely porous. *lower Cambrian (Bot.1):* Morocco.——FIG. 567,*3*. **P. bouddi*, Issafen Formation, Botoman, Jbel Irhoud, holotype, MNHN M80025, IRH 2 1aL, oblique longitudinal section, ×10 (Debrenne, 1977a).

Vologdinocyathellus KONYUSHKOV, 1972, p. 136 [**V. schischlovi*; OD; holotype, KONYUSHKOV, 1972, pl. 15,*2*, not located]. Outer wall with horizontal to upwardly projecting, S-shaped canals; inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous. *lower Cambrian (Bot.1):* Altay Sayan.——FIG. 567,*4a–b*. **V. schischlovi*, Verkhnemonok Formation, Botoman, Bol'shoy Karakol River, West



1b

1a Carinacyathus

2c

2b

2a Hupecyathellus

3 Porocyathellus

4b

4a Vologdinocyathellus

FIG. 567. Carinacyathidae (p. 984–987).

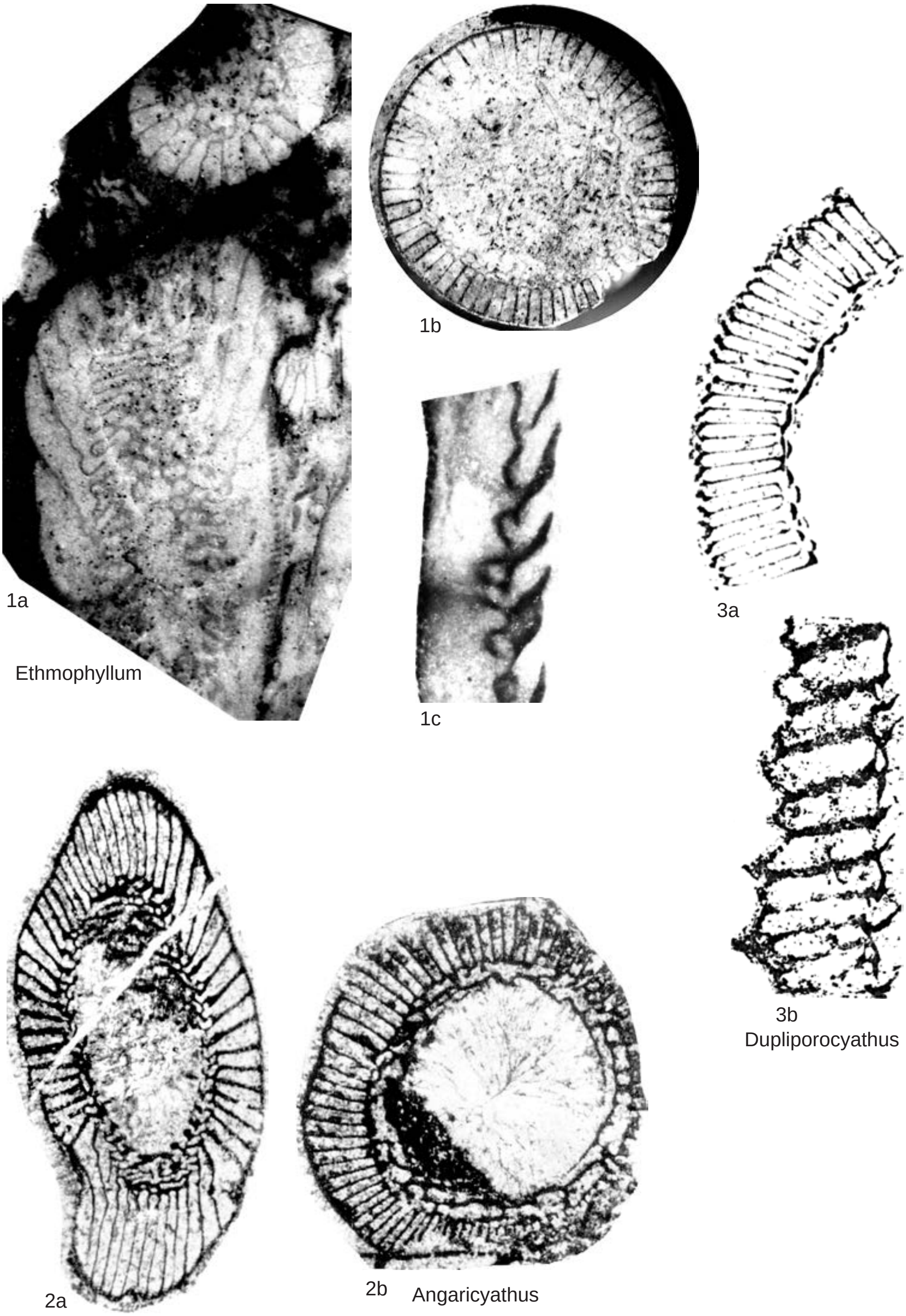


FIG. 568. Ethmophyllidae (p. 987).

Sayan, Russia; *a,* holotype, transverse section, ×4; *b,* unnumbered paratype, oblique longitudinal section, ×4 (Konyushkov, 1972).

Family ETHMOPHYLLIDAE Okulitch, 1937

[Ethmophyllidae Okulitch, 1937b, p. 358] [=Archaeocyathellidae Simon, 1939, p. 73; =Dupliporocyathidae Yazmir in Yazmir, Dalmatov, & Yazmir, 1975, p. 58; =Kolbicyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1988, p. 97]

Inner wall with communicating canals. *lower Cambrian (Atd.4–Toy.1).*

Ethmophyllum Meek, 1868a, p. 64 [**E. whitneyi*; OD; lectotype, Okulitch, 1943, pl. 3,*15;* Hill, 1965, pl. 4,*1;* SD Okulitch, 1943, p. 66, USNM 15307 1,1b, thin sections A, Washington, D.C.]. Outer wall with subspherical, chambered canals, each with base commencing in intervallum, canals subdivided by stipules (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of anastomosing, horizontal to upwardly and laterally projecting, waved canals per intersept, arising from fluted inner edges of septa; septa aporose to sparsely porous. *lower Cambrian (Atd.4–Bot.2):* Canada, United States.——Fig. 568,*1a–c.* **E. whitneyi*, Poleta Formation, Botoman, Silver Peak, Nevada, United States; *a–b,* lectotype, USNM 15307 1,1b, thin sections A; *a,* longitudinal section, ×5; *b,* transverse section, ×5; *c,* topotype, MCZ 9314, detail of septum in longitudinal section (outer wall to left), ×9 (Debrenne, Zhuravlev, & Kruse, 2002).

Angaricyathus Zhuravleva, 1965, p. 7 [**A. cyrenovi*; OD; holotype, Zhuravleva, 1965, pl. 2,*1*, TsSGM 215, specimen 2, thin section 1, Novosibirsk]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of anastomosing, horizontal to upwardly and laterally projecting, straight to waved canals per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Toy.1):* Transbaikalia, ?Sardinia.——Fig. 568,*2a–b.* **A. cyrenovi*, Kacha Formation, Toyonian, Kookta River, Transbaikalia, Russia; *a,* holotype, TsSGM 215, specimen 2, oblique longitudinal section, ×6; *b,* paratype, TsSGM 215, specimen 4, transverse section, ×6 (Zhuravleva, 1965).

Aulocricus Debrenne, 1987, p. 270 [**A. arellani*; OD; holotype, Debrenne, 1987, pl. 1,*7*, USNM 111823, Washington, D.C.]. Outer wall with horizontal to upwardly projecting, straight canals, subdivided by stipules and bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with anastomosing, horizontal to upwardly and laterally projecting, straight stirrup canals only, bearing supplementary planar annuli on central cavity side; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* Canada, United States, Mexico.——Fig. 569,*1a–b.* **A. arellani*, Puerto Blanco Formation, Botoman, Caborca, Sonora, Mexico; *a,* holotype, USNM 111823, transverse section, ×10; *b,* paratype, USNM 414812, longitudinal section, ×10 (Debrenne, 1987).

Cordilleracyathus Handfield, 1971, p. 49 [**C. blussoni*; OD; holotype, Handfield, 1971, pl. 7,*2*, GSC 25345, Ottawa]. Outer wall with horizontal to upwardly projecting, S-shaped canals, subdivided by stipules and bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of anastomosing, horizontally to upwardly and laterally projecting, S-shaped canals per intersept, formed by fluting of inner edges of septa, bearing supplementary scales on central cavity side; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Atd.4–Bot.2):* Koryakia, Canada, United States, Mexico, ?Greenland.——Fig. 569,*2a–c.* **C. blussoni*, Sekwi Formation, Botoman, Caribou Pass, Northwest Territories, Canada; *a,* holotype, GSC 25345, detail of tangential section (outer wall at bottom, inner wall at top), ×12; *b,* paratype, GSC 25348, transverse section, ×10; *c,* paratype, GSC 25347, detail of longitudinal section (outer wall to right), ×12 (Handfield, 1971).

?Dupliporocyathus Yazmir in Yazmir, Dalmatov, & Yazmir, 1975, p. 59 (Yazmir in Zhuravleva, 1974a, p. 119, *nom. nud.*) [**D. tumulosus*; OD; holotype, Yazmir, Dalmatov, & Yazmir, 1975, pl. 21,*5–7*, BGU 0138/17, Ulan-Ude]. Outer wall longitudinally plicate, canal shape and orientation uncertain; inner wall with one row of downwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa aporose to sparsely porous. [Limited type material does not provide certainty as to inner wall structure: canals with supplementary bracts, or V-shaped scales.] *lower Cambrian (Atd.4):* Transbaikalia.——Fig. 568,*3a–b.* **D. tumulosus*, Oldyndy Formation, Atdabanian, Ul'dzuytuy Creek, Vitim Highlands, Russia, holotype, BGU 0138/17; *a,* transverse section, ×10; *b,* oblique longitudinal section, ×10 (Yazmir, Dalmatov, & Yazmir, 1975; reproduced from Debrenne & others, 2002. ©Kluwer Academic/Plenum Publishers, New York, p. 1593, Figure 31H–I with kind permission of Springer Science and Business Media).

Kolbicyathus Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1988, p. 97 [**Vologdinocyathus kolbiensis* Zhuravleva, 1959, p. 425; OD; holotype, Zhuravleva, 1959, fig. 2d; TsSGM 282/2, Novosibirsk]. Outer wall with horizontal to upwardly projecting, S-shaped canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with horizontal to upwardly projecting, straight stirrup canals only, bearing supplementary bracts on central cavity side; septa completely porous; pectinate tabulae may be present. *lower*

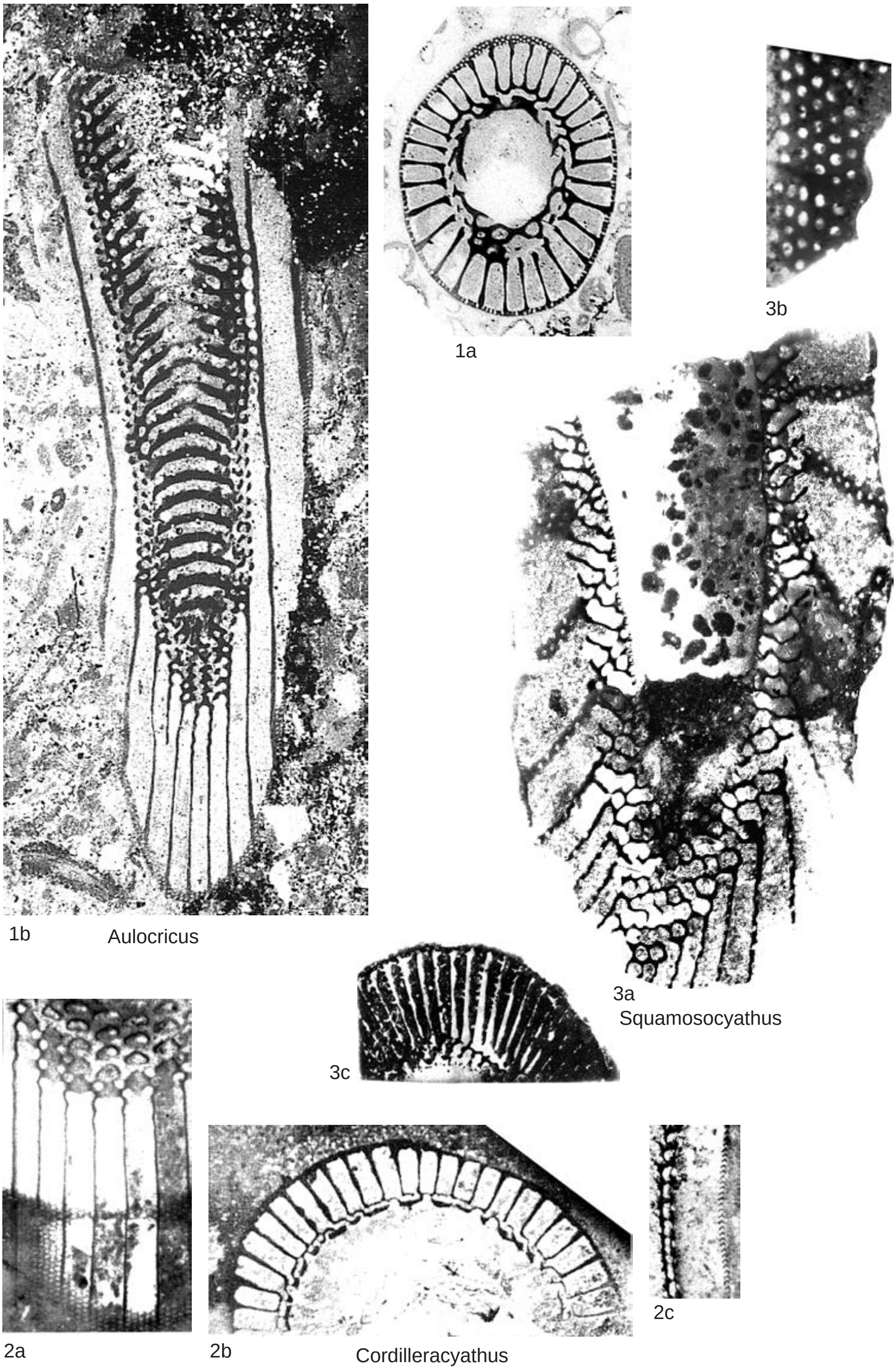


FIG. 569. Ethmophyllidae (p. 987–990).

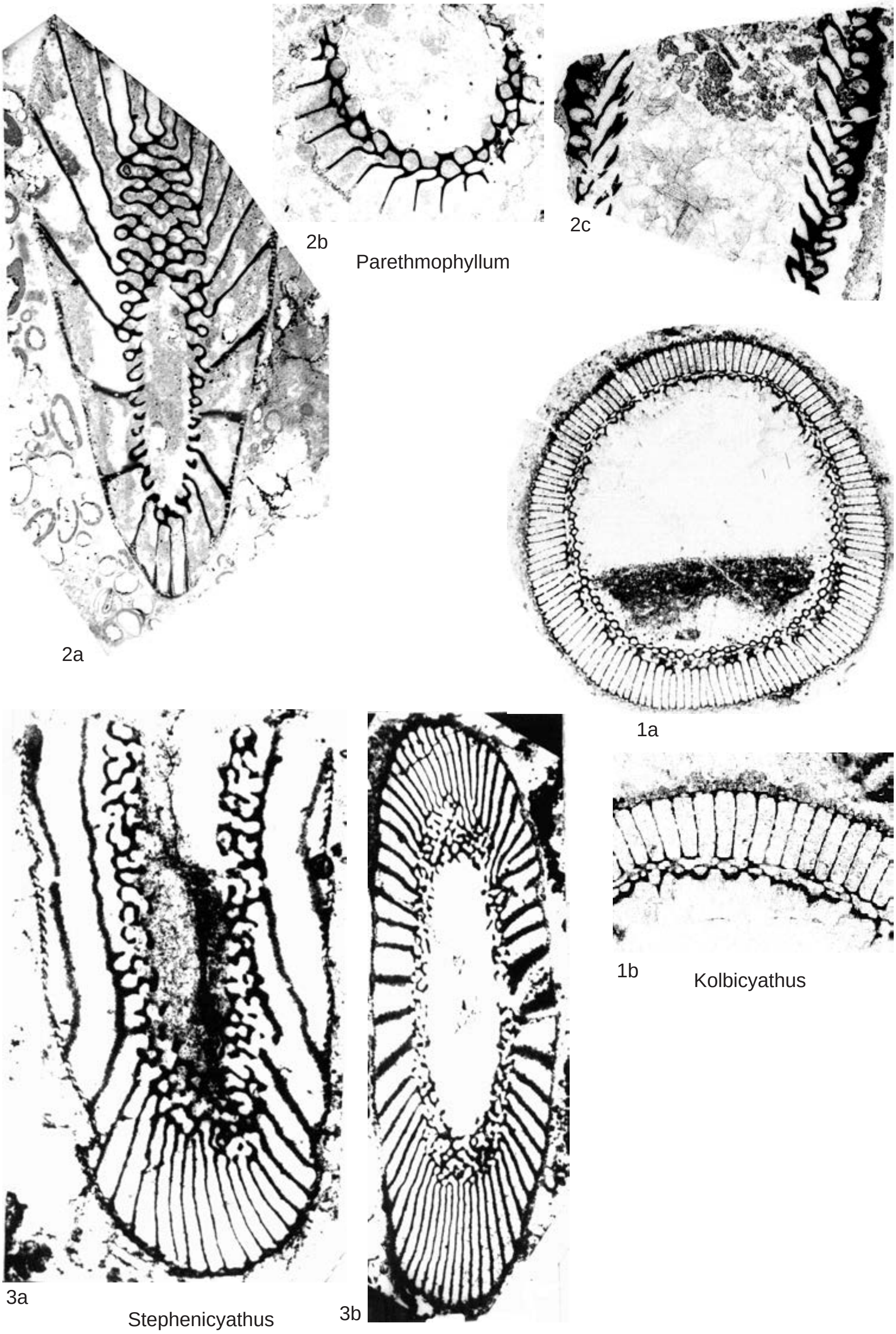


FIG. 570. Ethmophyllidae (p. 987–990).

Cambrian (Bot.1): Altay Sayan, Mongolia.——FIG. 570,*1a–b*. **K. kolbiensis* (ZHURAVLEVA), Usa Formation, Botoman, Petrovka, Kiya River, Kuznetsk Alatau, Russia, holotype, TsSGM 282/2; *a,* transverse section, ×5; *b,* detail of same, ×15 (Debrenne, Zhuravlev, & Kruse, 2002).

Parethmophyllum DEBRENNE, 1987, p. 270 [**Ethmophyllum cooperi* OKULITCH in COOPER & others, 1952, p. 29; OD; holotype, COOPER & others, 1952, pl. 7,*1–2;* DEBRENNE, 1987, pl. 1,*2,4*, USNM 111814, Washington, D.C.]. Outer wall with horizontal to upwardly projecting, straight canals; inner wall with one row of anastomosing, horizontal to upwardly and laterally projecting, straight to waved canals per intersept, formed by fluting of inner edges of septa, bearing supplementary bracts on central cavity side; septa aporose to sparsely porous. *lower Cambrian (Bot.1):* United States, Mexico.——FIG. 570,*2a–c*. **P. cooperi* (OKULITCH), Puerto Blanco Formation, Botoman, Caborca, Sonora, Mexico; *a,* paratype, USNM 111813, oblique longitudinal section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002); *b–c,* holotype, USNM 111814; *b,* transverse section, ×6; *c,* longitudinal section, ×6 (Debrenne, 1987).

Squamosocyathus ZHURAVLEVA, 1960b, p. 183 [**S. taumatus*; OD; holotype, ZHURAVLEVA, 1960b, pl. 13,*5a–b*, TsSGM 205/66a-b, Novosibirsk]. Outer wall with horizontal to upwardly projecting straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of horizontal to upwardly projecting, straight porous canals per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.3–Bot.1):* Siberian Platform, ?Altay Sayan.——FIG. 569,*3a–c*. **S. taumatus*, Perekhod Formation, Atdabanian; *a,* Botoma River, Sakha (Yakutia), Russia, paratype, TsSGM 205/67, longitudinal section, ×6 (Zhuravleva, 1960b); *b–c,* Yudyay, Lena River, Sakha (Yakutia), Russia; *b,* holotype, TsSGM 205/66a-b, detail of septum in longitudinal section (outer wall to left), ×12 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* paratype, TsSGM 205/68, transverse section, ×6 (Zhuravleva, 1960b).

Stephenicyathus ZHURAVLEV in VORONOVA & others, 1987, p. 26 [**S. rowlandi*; OD; holotype, VORONOVA & others, 1987, pl. 6,*1*, GSC 90145, Ottawa]. Outer wall with horizontal to upwardly projecting, straight canals, subdivided by stipules and bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of anastomosing, horizontal to upwardly projecting, waved canals per intersept, formed by fluting of inner edges of septa; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1):* Canada, United States.——FIG. 570,*3a–b*. **S. rowlandi*, Sekwi Formation, Botoman, Mackenzie Mountains, Northwest Territories, Canada; *a,* paratype, GSC 90146, longitudinal section, ×12; *b,* holotype, GSC 90145, oblique longitudinal section, ×5 (Voronova & others, 1987).

Superfamily TERCYATHOIDEA Vologdin, 1939

[*nom. correct.* DEBRENNE & KRUSE, 1986, p. 256, *pro* Tercyathacea ZHURAVLEVA, 1960b, p. 184, *nom. transl. ex* Tercyathidae VOLOGDIN in SIMON, 1939, p. 11] [=Piamaecyathacea ZHURAVLEVA, 1960a, p. 44, *nom. transl.* ZHURAVLEVA, 1960b, p. 50, *ex* Piamaecyathidae ZHURAVLEVA, 1960a, p. 44]

Outer wall clathrate. *lower Cambrian (Atd.4–Toy.1).*

Family PIAMAECYATHELLIDAE Rozanov, 1974

[Piamaecyathellidae ROZANOV in BORODINA, 1974, p. 157] [=Piamaecyathellidae ROZANOV, 1973, p. 86, *nom. nud.*]

Inner wall with simple pores. *lower Cambrian (Bot.2).*

Piamaecyathellus ROZANOV in REPINA & others, 1964, p. 217 [**P. simplex*; OD; holotype, REPINA & others, 1964, pl. 23,*5*, PIN 4297/28, Moscow]. Inner wall with several rows of simple pores per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.2):* Altay Sayan.——FIG. 571,*1*. **P. simplex*, Verkhneynyrga Formation, Botoman, Kyzyl-Tash, Bol'shaya Isha River, Altay Mountains, Altay Sayan, Russia, holotype, PIN 4297/28, transverse section, ×5 (Repina & others, 1964).

Family BOTOMOCYATHIDAE Zhuravleva, 1955

[Botomocyathidae ZHURAVLEVA, 1955b, p. 628] [=Botomacyathidae ZHURAVLEVA in VOLOGDIN, 1956, p. 879, *nom. null.*]

Inner wall with annuli. *lower Cambrian (Atd.4–Bot.3).*

Botomocyathus ZHURAVLEVA, 1955b, p. 629 (ZHURAVLEVA, 1954, p. 12, *nom. nud.*) [**B. zelenovi*; OD; holotype, ZHURAVLEVA, 1955b, fig. 2e, TsSGM 205/69, Novosibirsk] [=*Botomacyathus* ZHURAVLEVA in VOLOGDIN, 1956, p. 879, *nom. null.*]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Atd.4–Bot.1):* Siberian Platform, Altay Sayan, Far East.——FIG. 571,*2a–c*. **B. zelenovi*, Perekhod Formation, Botoman, Botoma River, Sakha (Yakutia), Russia; *a–b,* holotype, TsSGM 205/69; *a,* oblique longitudinal section, ×6; *b,* detail of outer wall in tangential section, ×16; *c,* paratype TsSGM 205/70, detail of longitudinal section (outer wall to right), ×10 (Debrenne, Zhuravlev, & Kruse, 2002).

Clathrithalamus DEBRENNE & KRUSE, 1986, p. 256 [**C. mawsoni*; OD; holotype, DEBRENNE & KRUSE, 1986, fig. 21A–C, GNS MG511, Lower Hutt]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa aporose to sparsely porous; pectinate tabulae may be present. *lower Cambrian (Bot.3):* Antarctica.——FIG. 571,*3a–c*. **C. mawsoni*, Shackleton Limestone, Botoman, Holyoake Range, Nimrod

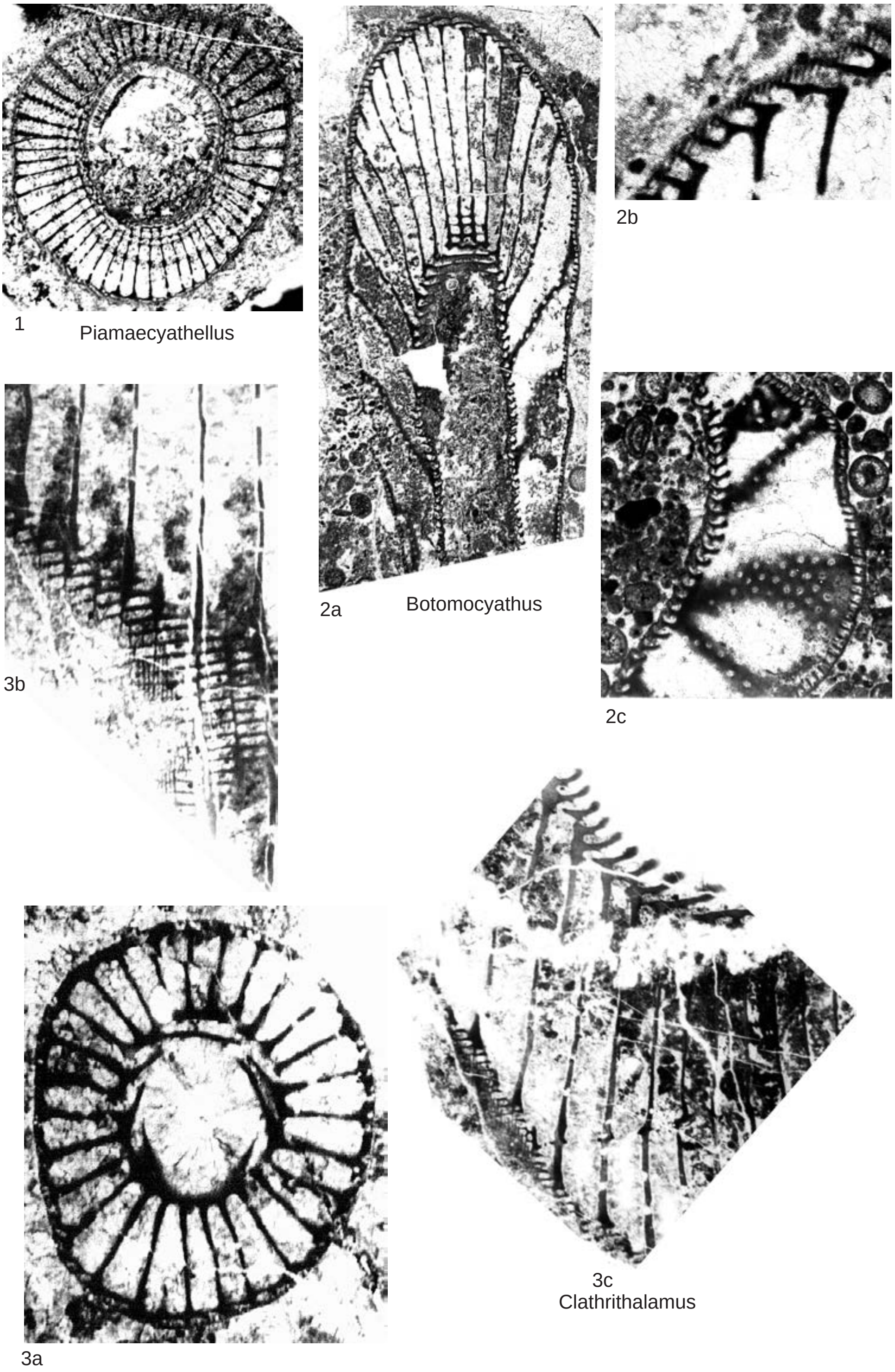


FIG. 571. Piamaecyathellidae and Botomocyathidae (p. 990–992).

FIG. 572. Olgaecyathidae (p. 992).

Glacier, holotype, GNS MG511; *a,* transverse section, ×5 (Debrenne & Kruse, 1986); *b,* detail of outer wall in tangential section, ×16 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* detail of oblique longitudinal section, ×7 (Debrenne & Kruse, 1986).

Family OLGAECYATHIDAE Borodina, 1974

[Olgaecyathidae BORODINA, 1974, p. 158]

Inner wall with noncommunicating canals. *lower Cambrian (Bot.2).*

Olgaecyathus BORODINA, 1974, p. 158 [**O. fistulosus*; OD; holotype, BORODINA, 1974, pl. 16,*8*, TsSGM 429/2, Novosibirsk]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.2):* Altay Sayan.——FIG. 572. **O. fistulosus*, Verkhnemonok Formation, Botoman, Kazly River, West Sayan, Russia, holotype, TsSGM 429/2, oblique longitudinal section, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

Family TERCYATHIDAE Vologdin, 1939

[Tercyathidae VOLOGDIN in SIMON, 1939, p. 11] [=Tercyathidae VOLOGDIN, 1937b, p. 459, *nom. nud.*, invalid family-group name based on unavailable genus name; =Piamaecyathidae ZHURAVLEVA, 1960a, p. 44]

Inner wall with communicating canals. *lower Cambrian (Bot.1–Toy.1).*

Tercyathus VOLOGDIN in SIMON, 1939, p. 40 (VOLOGDIN, 1932, p. 55, *nom. nud.*, without designated type species) [**T. duplex* VOLOGDIN, 1932, p. 56; OD; lectotype, VOLOGDIN, 1932, pl. 13,*2;* SD BORODINA, 1974, p. 154, TsNIGRm 71a-g/2957, St. Petersburg] [=*Piamaecyathus* ZHURAVLEVA, 1960a, p. 45 (type, *P. sajanicus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 135; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 164; =*Rugocyathus* VOLOGDIN, 1962d, p. 13 (type, *R. venustus*, M), *nom. nud.*]. Inner wall with one row of anastomosing, horizontal to upwardly and laterally projecting, straight to waved canals per intersept; supplementary spines, annular structures and/or microporous sheath may be present on central cavity side; septa sparsely to completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.1–Toy.1):* Altay Sayan.——FIG. 573,*1a–c*. **T. duplex*, Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Russia; *a,* lectotype, TsNIGRm 71a-g/2957, longitudinal section of inner wall (central cavity to right), ×6 (Vologdin, 1932); *b,* unlocated specimen, longitudinal section, ×6; *c,* unlocated specimen, transverse section, ×6 (Repina & others, 1964).

Clathricyathellus BORODINA, 1974, p. 150 [**Clathricyathus robustus* VOLOGDIN, 1932, p. 53; OD; lectotype, VOLOGDIN, 1932, pl. 12,*6;* SD BORODINA, 1974, p. 151, TsNIGRm 68a/2957, St. Petersburg] [=*Lebedicyathus* BORODINA, 1974, p. 164 (type, *L. duplicatus*, OD)]. Inner wall with one row of downwardly projecting, straight porous canals per intersept; supplementary spines, annular structures, and/or microporous sheath may be present on central cavity side; septa completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.3):* Altay Sayan.——FIG. 573,*2a–b*. **C. robustus* (VOLOGDIN), Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Russia; *a,* lectotype, TsNIGRm 68a/2957, oblique transverse section, ×4; *b,* paralectotype, TsNIGRm 69a/2957, longitudinal section, ×4 (Vologdin, 1932).

Clathricyathus VOLOGDIN in SIMON, 1939, p. 25 (VOLOGDIN, 1932, p. 50, *nom. nud.*, without designated type species) [**C. firmus* VOLOGDIN, 1932, p. 50; OD; lectotype, VOLOGDIN, 1932, pl. 10,*12;* SD BORODINA, 1974, p. 150, TsNIGRm 65, 65a-v/2957, St. Petersburg] [=*Clathrocyathus* VOLOGDIN, 1937b, p. 469, *nom. null.*]. Inner wall with one row of amalgamating, downwardly projecting, straight canals per intersept, continuing into larger, horizontal to upwardly projecting, confluent canal system on central cavity side; septa completely porous;

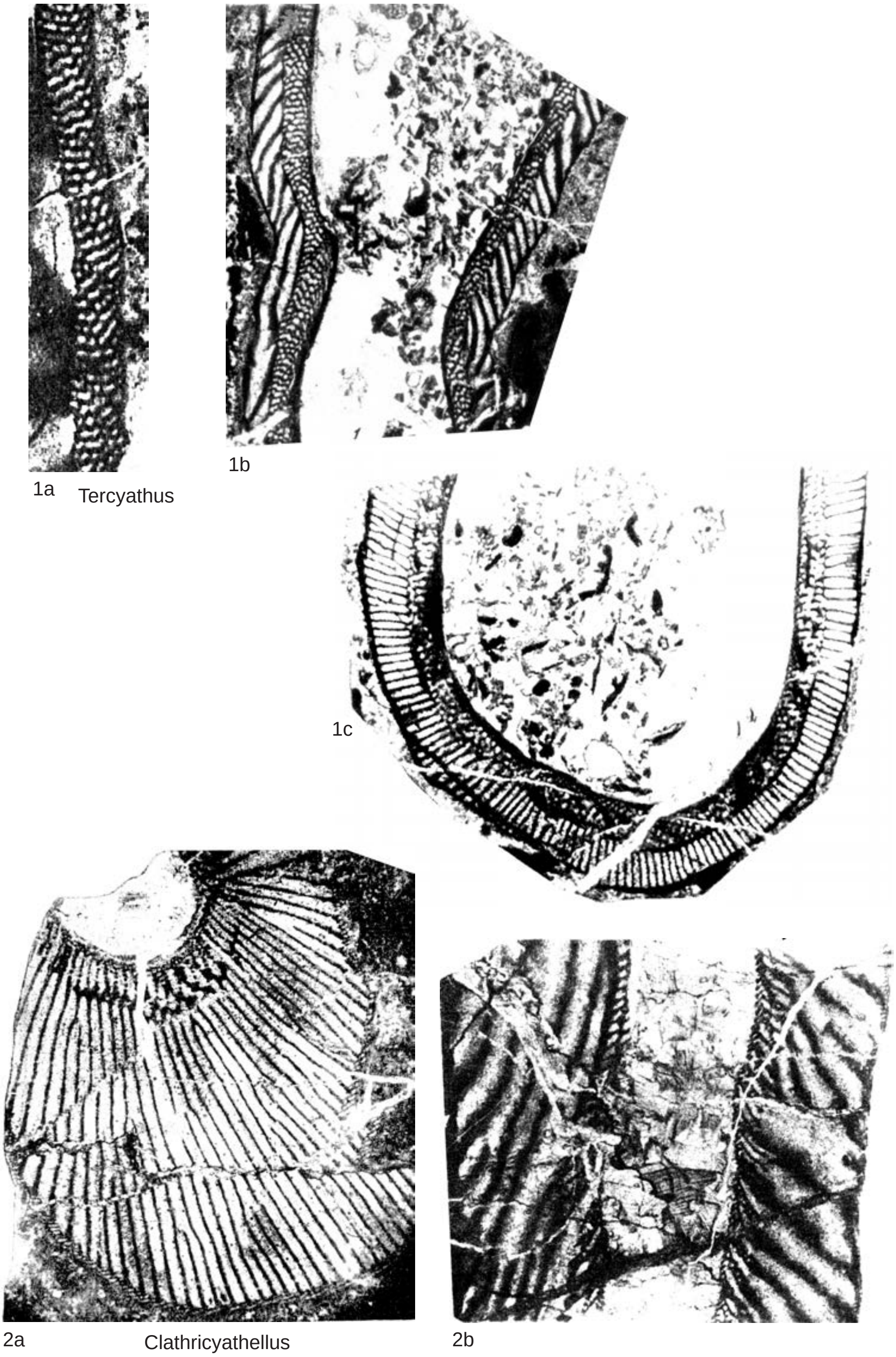


FIG. 573. Tercyathidae (p. 992).

Fig. 574. Tercyathidae (p. 992–994).

pectinate tabulae may be present. *lower Cambrian (Bot.3):* Altay Sayan.——Fig. 574,*1a–b*. **C. firmus*, Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Russia, lectotype, TsNIGRm 65, 65a-v/2957; *a,* transverse section, ×7; *b,* oblique longitudinal section, ×7 (Vologdin, 1932).

Tercyathellus Borodina, 1974, p. 155 [**T. capisterium*; OD; holotype, Borodina, 1974, fig. 13, pl. 10,*3*, TsSGM 429/1, Novosibirsk] [=*Kazlycyathus* Borodina, 1974, p. 163 (type, *K. flexuosus,* OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 135; Debrenne, Rozanov, & Zhuravlev, 1990, p. 164]. Inner wall with several rows of anastomosing, horizontal to upwardly and laterally projecting, straight to waved canals per intersept, continuing into larger, horizontal to upwardly projecting, confluent canal system on central cavity side; septa sparsely to completely porous; pectinate tabulae may be present. *lower Cambrian (Bot.2):* Altay Sayan.——Fig. 574,*2*. **T. capisterium*, Verkhnemonok Formation, Botoman, Kazly River, West Sayan, Russia, holotype, TsSGM 429/1, oblique transverse section, ×8 (Borodina, 1974).

Superfamily SIGMOCYATHOIDEA
Krasnopeeva, 1953

[*nom. correct.* Debrenne & Kruse, 1986, p. 255, *pro* Sigmocyathacea Debrenne, 1970a, p. 25, *nom. transl. ex* Sigmocyathidae Krasnopeeva, 1953, p. 56, as Sygmocyathidae, *nom. null.*]

Outer wall with annuli. *lower Cambrian (Bot.3).*

Family SIGMOCYATHIDAE
Krasnopeeva, 1953

[*nom. correct.* Zhuravleva, 1960b, p. 49, *pro* Sygmocyathidae Krasnopeeva, 1953, p. 56, *nom. null.*, based on erroneous spelling of generic name]

Inner wall with annuli. *lower Cambrian (Bot.3).*

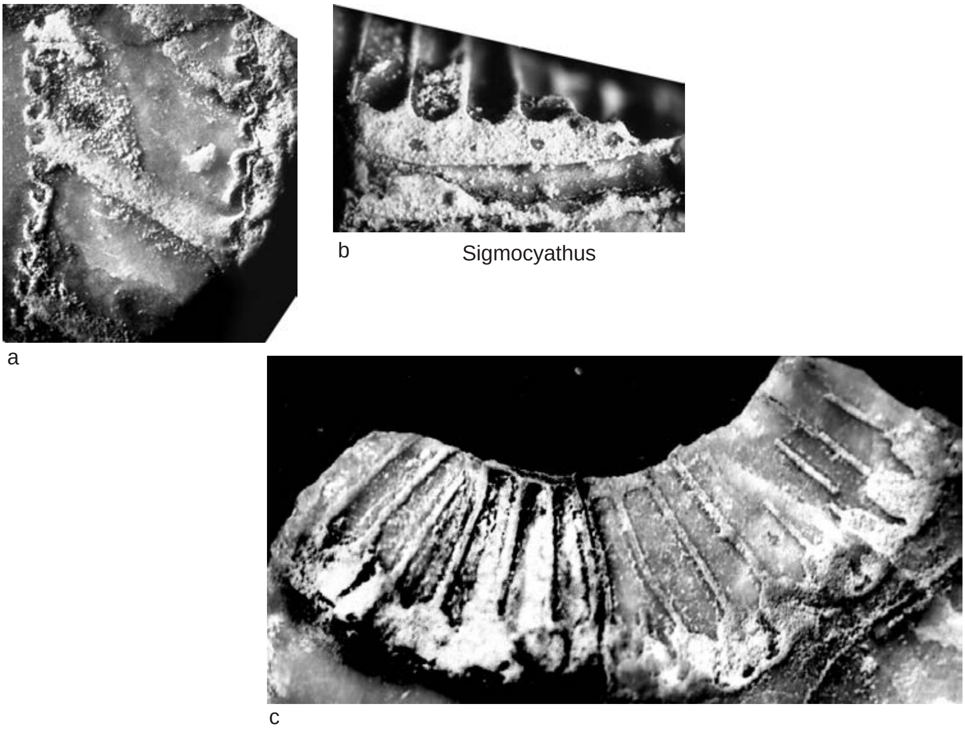


Fig. 575. Sigmocyathidae (p. 995).

Sigmocyathus R. Bedford & J. Bedford, 1936, p. 23 [**Coscinocyathus didymoteichus* Taylor, 1910, p. 140; OD; lectotype, Taylor, 1910, pl. 10, photo 58; Debrenne & Rozanov, 1972, pl. 43,*1,3*; Rozanov, 1973, pl. 4,*3;* SD Debrenne, 1970a, p. 42, SAM T1606B-D, Adelaide] [=*Hemistillicidocyathus* Ting, 1937, p. 368 (type, *Coscinocyathus didymoteichus* Taylor, 1910, p. 140, OD)]. Outer wall with upwardly projecting, S-shaped annuli; inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa aporose to sparsely porous. *lower Cambrian (Bot.3):* Australia, ?Antarctica.——Fig. 575*a–c*. **S. didymoteichus* (Taylor), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1606B-D; *a,* longitudinal view of septum (outer wall to left), ×8; *b,* external view of outer wall, ×8 (Debrenne & Rozanov, 1972); *c,* transverse view, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Didymocyathus Debrenne & Rozanov, 1972, p. 236 [**D. hillae*; OD; holotype, Debrenne & Rozanov, 1972, pl. 42,*2–3;* pl. 43,*2;* pl. 44,*1,* USNM PU299, Washington, D.C.]. Outer wall with upwardly projecting, S-shaped annuli; inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa completely porous. *lower Cambrian (Bot.3):* Australia, ?Antarctica.——Fig. 576*a–c*. **D. hillae*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; *a,* holotype, USNM PU299, longitudinal view of septum (outer wall to left), ×5 (Debrenne, Zhuravlev, & Kruse, 2002); *b–c,* topotype, USNM PU296; *b,* longitudinal view of outer wall, ×5; *c,* longitudinal view of inner wall, ×5 (Debrenne & Rozanov, 1972).

Family WRIGHTICYATHIDAE Kruse, 1978

[Wrighticyathidae Kruse, 1978, p. 34]

Inner wall with communicating canals. *lower Cambrian (Bot.3).*

Wrighticyathus Kruse, 1978, p. 34 [**W. nexus*; OD; holotype, Kruse, 1978, fig. 7A–E, AM F.83298, Sydney]. Outer wall with upwardly projecting, S-shaped annuli; inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous. *lower Cambrian (Bot.3):* Australia.——Fig. 577*a–c*. **W. nexus*, Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia, holotype, AM F.83298; *a,* transverse section, AM FT.8268, ×4 (Kruse, 1978); *b,* longitudinal section, AM FT.8265, ×4 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* detail of outer wall in longitudinal section, AM FT.8264, ×10 (Kruse, 1978).

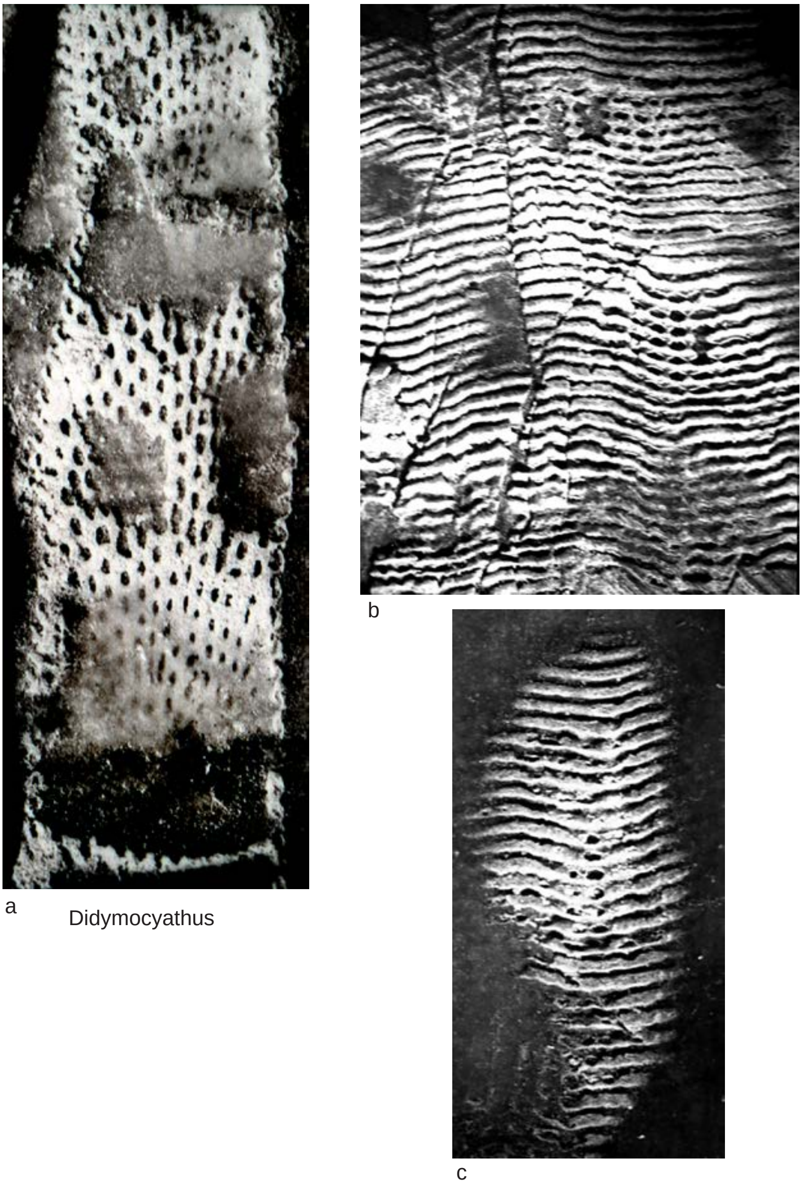


FIG. 576. Sigmocyathidae (p. 995).

Suborder ERISMACOSCININA Debrenne, Rozanov, & Zhuravlev, 1989

[Erismacoscinina DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 85] [?=Erismacoscinina ZHURAVLEV, 1988, p. 105, *nom. nud.*]

Intervallum with septa and plate tabulae; synapticulae may be present. *lower Cambrian (Tom.2–Bot.3).*

Superfamily SALAIROCYATHOIDEA Zhuravleva, 1956

[*nom. transl.* ZHURAVLEV, 1988, p. 105, *ex* Salairocyathidae ZHURAVLEVA in VOLOGDIN, 1956, p. 879] [=Erismacoscinacea DEBRENNE, 1964, p. 166, *nom. transl.* DEBRENNE, 1970a, p. 25, *ex* Erismacoscinidae DEBRENNE, 1964, p. 166]

Outer wall with simple pores. *lower Cambrian (Tom.2–Bot.3).*

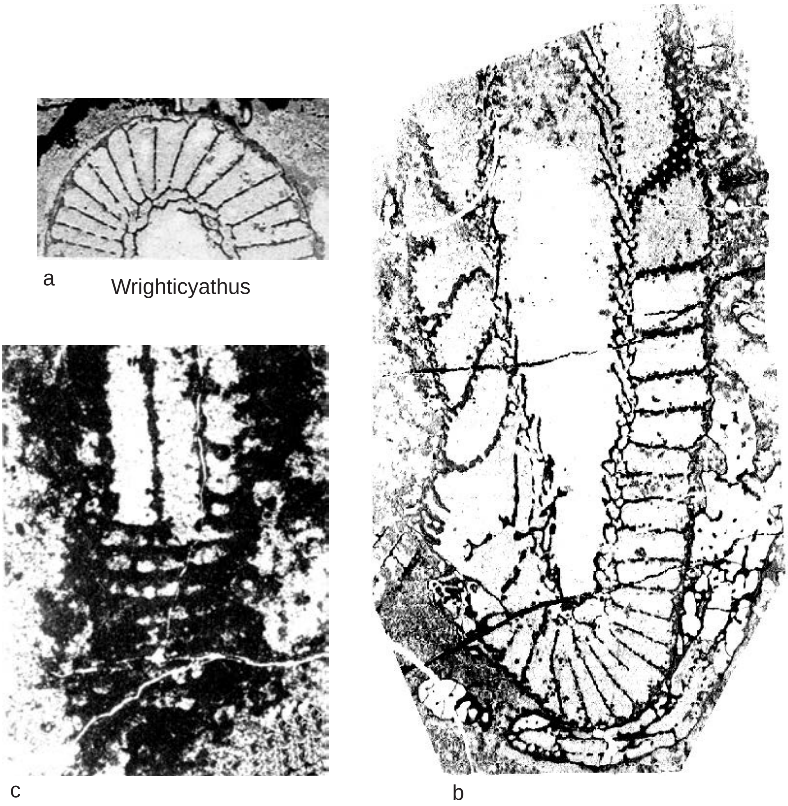


FIG. 577. Wrighticyathidae (p. 995).

Family ASTEROCYATHIDAE Vologdin, 1956

[Asterocyathidae VOLOGDIN, 1956, p. 879] [=Erismacoscinidae DEBRENNE, 1964, p. 166; =Syringocoscinidae VOLOGDIN & YAZMIR, 1967, p. 1375]

Inner wall with simple pores. *lower Cambrian (Tom.2–Bot.3).*

Asterocyathus VOLOGDIN, 1940b, p. 92 [**A. salairicus*; OD; holotype not designated, collection not located]. Inner wall longitudinally plicate, with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.1–Atd.2):* Altay Sayan, Tuva, Mongolia.——FIG. 578,*1*. **A. salairicus*, Gavrilovskoe Formation, Atdabanian, Belaya Gorka, Gorskino, Salair, Russia, unlocated syntype, oblique transverse section, ×5 (Vologdin, 1940b).

Antoniocoscinus ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1988, p. 98 [**Coscinocyathus vsevolodi* KORSHUNOV in ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, p. 51; OD; holotype, ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969, pl. 20,*2,4;* KORSHUNOV, 1972, pl. 15,*5;* pl. 16,*5*), TsSGM 323/84, Novosibirsk]. Inner wall with one row of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.4–Bot.3):* Siberian Platform, Tuva, Transbaikalia, South China, Morocco, Iberia, Sardinia.——FIG. 578,*2a–b*. **A. vsevolodi* (KORSHUNOV), Oy-Muran reef massif, Botoman, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 323/84; *a,* transverse section, ×4 (Debrenne, Zhuravlev, & Kruse, 2012b); *b,* detail of longitudinal section (outer wall to left), ×10 (Korshunov, 1972).

Erismacoscinus DEBRENNE, 1958, p. 65 [**E. marocanus*; M; holotype, DEBRENNE, 1958, pl. 3,*12,14–16;* DEBRENNE, 1964, pl. 20,*1–2,* MNHN M80139, specimen H2, Paris] [=*Pluralicoscinus* DEBRENNE, 1963b, p. 135 (type, *P. alanisensis*, OD); =*Syringocoscinus* YAZMIR in VOLOGDIN & YAZMIR, 1967, p. 1376 (type, *S. angulatus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 105; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 141; =*Churanocyathus* SUNDUKOV, 1984, p. 14 (type, *C. aculeatus*, OD)]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Tom.2–Bot.3):* Siberian Platform, Kolyma, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Urals, Tajikistan, Australia, Antarctica, ?Falkland

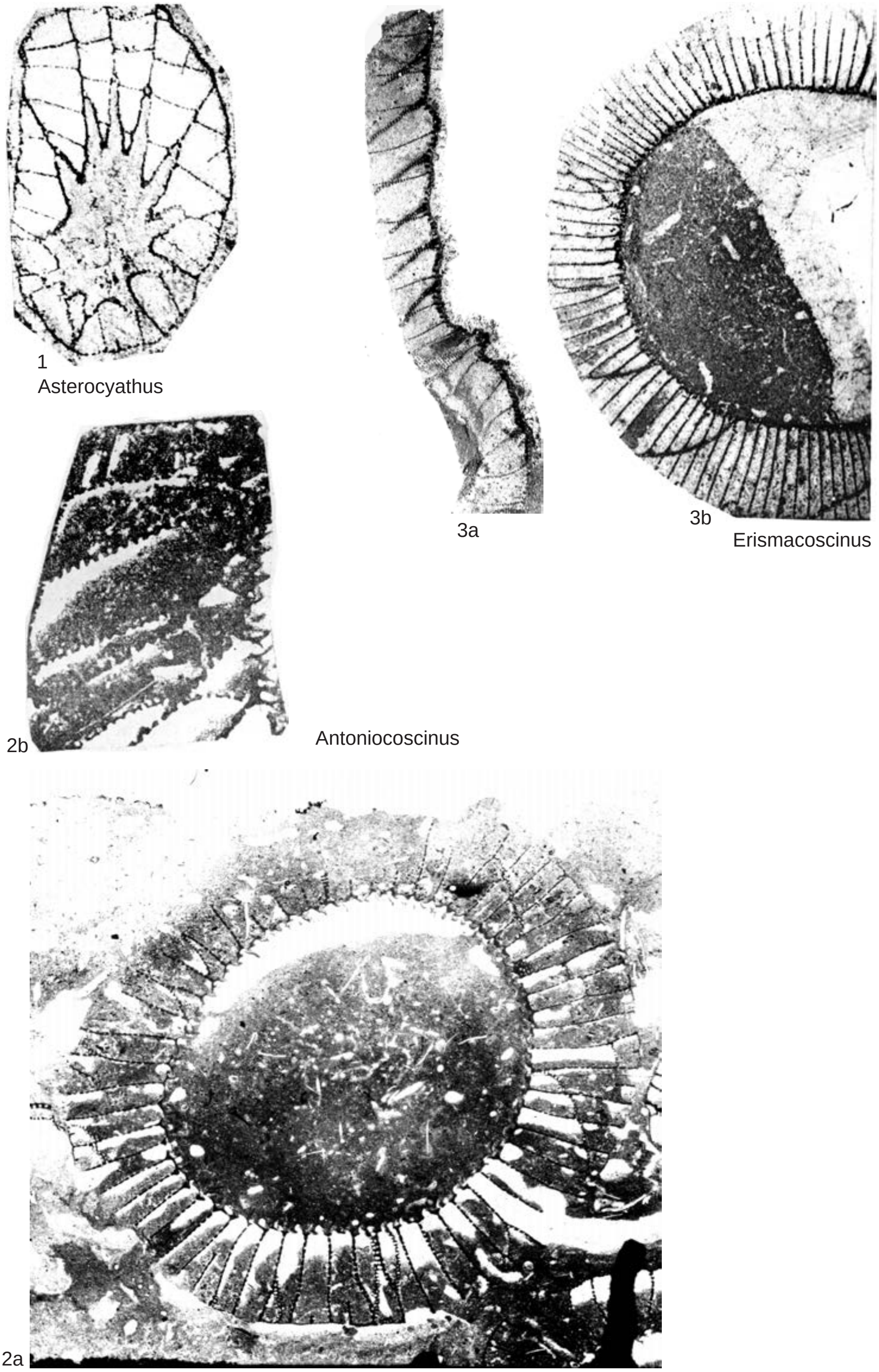


FIG. 578. Asterocyathidae (p. 997–999).

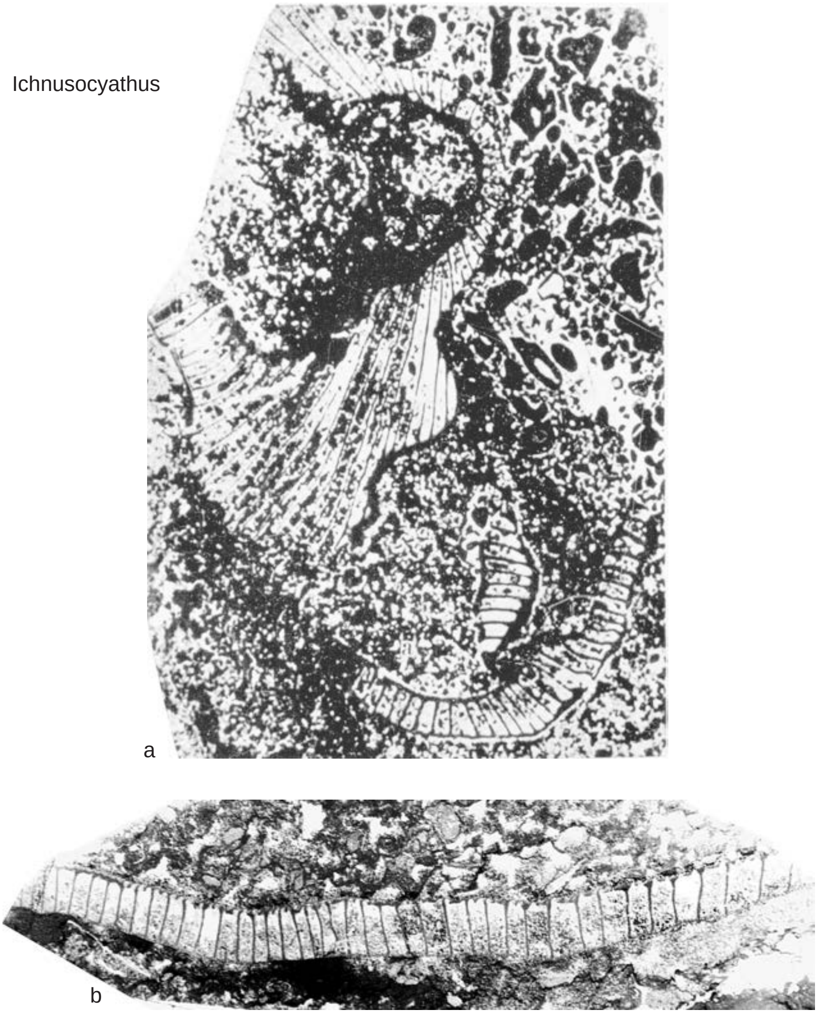
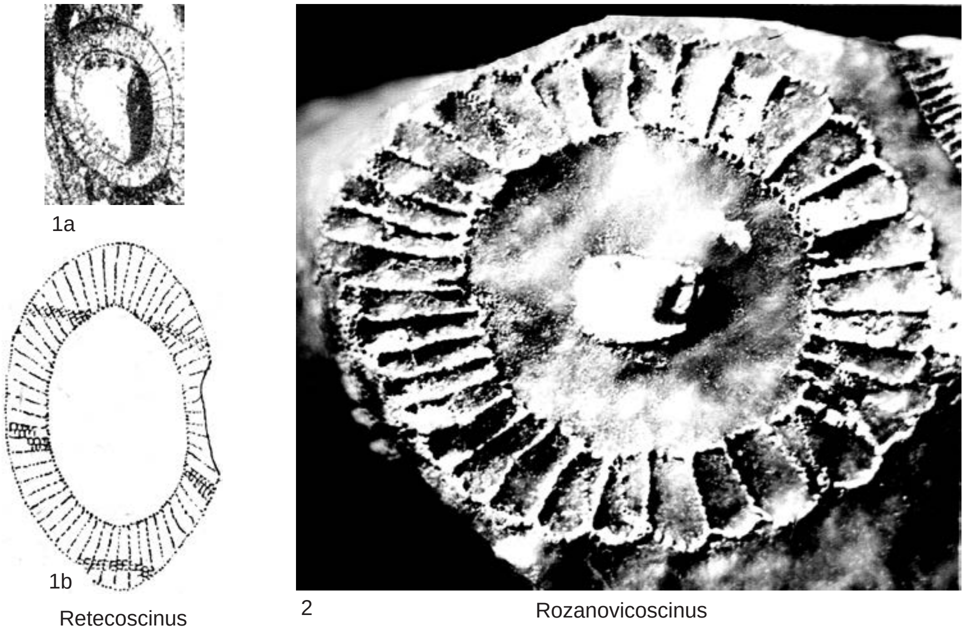


FIG. 579. Asterocyathidae (p. 999).

Islands (allochthonous), Tarim, South China, Morocco, Iberia, France, Sardinia, Germany.——FIG. 578,*3a–b*. **E. marocanus*, Amouslek Formation, Atdabanian, Jbel Taïssa, Morocco, holotype, MNHN M80139, specimen H2; *a,* longitudinal section (outer wall to left), ×4; *b,* transverse section, ×4 (Debrenne, 1958).

Ichnusocyathus DEBRENNE, 1977a, p. 103 [**Archaeocyathus ichnusae* MENEGHINI, 1881, p. 201; OD; lectotype, BORNEMANN, 1886, pl. 13,*3–4;* SD DEBRENNE, 1964, p. 129, not located]. Inner wall with several rows of simple pores per intersept; septa aporose to sparsely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Morocco, Sardinia.——FIG. 579*a–b*. **I. ichnusae* (MENEGHINI), Matoppa Formation, Botoman, Monte Gloria, Canal Grande, Sardinia, Italy; *a,* lectotype, oblique section, ×4 (Bornemann, 1886); *b,* topotype, MNHN M84258, specimen RFB 14/1, transverse section, ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

Retecoscinus ZHURAVLEVA, 1960b, p. 247 [**Coscinocyathus retetabulae* VOLOGDIN, 1931, p. 75; OD; lectotype, VOLOGDIN, 1931, pl. 22,*1e;* SD DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1617, TsNIGRm 94a/2956, St. Petersburg]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with slitlike pores. *lower Cambrian (Tom.3–Bot.1):* Siberian Platform, Altay Sayan, Far East, Morocco, Iberia, France, Germany.——FIG.



Retecoscinus

Rozanovicoscinus

FIG. 580. Asterocyathidae (p. 999–1000).

580,*1a–b*. **R. retetabulae* (VOLOGDIN), Usa Formation, Atdabanian, Nizhnyaya Ters' River, Kuznetsk Alatau, Russia, lectotype, TsNIGRm 94a/2956; *a,* transverse section, ×2; *b,* unlocated specimen TsNIGRm, sketch of oblique transverse section, ×2.5 (Vologdin, 1931).

Rozanovicoscinus DEBRENNE, 1970a, p. 41 [**R. fonini*; OD; holotype, DEBRENNE, 1970a, pl. 2,*1*, USNM PU86614, Washington, D.C.]. Outer wall longitudinally plicate; inner wall with several rows of simple pores per intersept; septa aporose to sparsely porous; tabulae with normal pores. *lower Cambrian (Atd.4–Bot.3):* Australia.——FIG. 580,*2*. **R. fonini*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, USNM PU86614, transverse view, ×5 (Debrenne, 1970a).

Family RUDANULIDAE
Debrenne, Rozanov, & Zhuravlev, 1989

[Rudanulidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 85]

Inner wall with bracts or scales. *lower Cambrian (Bot.1–Bot.3).*

Rudanulus DEBRENNE in ZHURAVLEVA, 1974b, p. 79 [**Coscinocyathus petersi* R. BEDFORD & W. R. BEDFORD, 1934, p. 3; OD; holotype, R. BEDFORD & W. R. BEDFORD, 1934, fig. 13; DEBRENNE, 1969a, pl. 10,*4–5;* M, NHM S4158, London]. Outer wall longitudinally plicate; inner wall with several rows of pores per intersept, bearing upwardly projecting, S-shaped scales; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1–Bot.3):* Australia, South China.——FIG. 581,*1a–c*. **R. petersi* (R. BEDFORD & W. R. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, NHM S4158; *a,* transverse view, ×8 (Debrenne, 1969a); *b,* longitudinal view, ×8; *c,* detail of transverse view, ×16 (Debrenne, Zhuravlev, & Kruse, 2012b).

Pilodicoscinus DEBRENNE & JIANG, 1989, p. 826 [**P. yuani*; OD; holotype, DEBRENNE & JIANG, 1989, pl. 2,*6*, MNHN M85002, specimen 2-13, Paris]. Cup in which outer wall shows periodic transverse folds; inner wall with several rows of pores per intersept, bearing upwardly projecting, cupped bracts; septa aporose to sparsely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* South China.——FIG. 581,*2*. **P. yuani*, Tsanglangpu Formation, Botoman, Yangchang, Yunnan, holotype, MNHN M85002, specimen 2-13, longitudinal section, ×7.5 (Debrenne & Jiang, 1989).

Yhecyathus BELYAEVA & YUAN, 1995, p. 140 [**Y. futchinensis*; OD; holotype, BELYAEVA & YUAN, 1995, fig. 1d, NIGP NF$_6$H$_1$, Nanjing]. Cup with regular transverse folds affecting both walls; inner wall with several rows of pores per intersept, bearing upwardly projecting, cupped bracts; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* South China.——FIG. 581,*3*. **Y. futchinensis*, Xiannudong Formation,

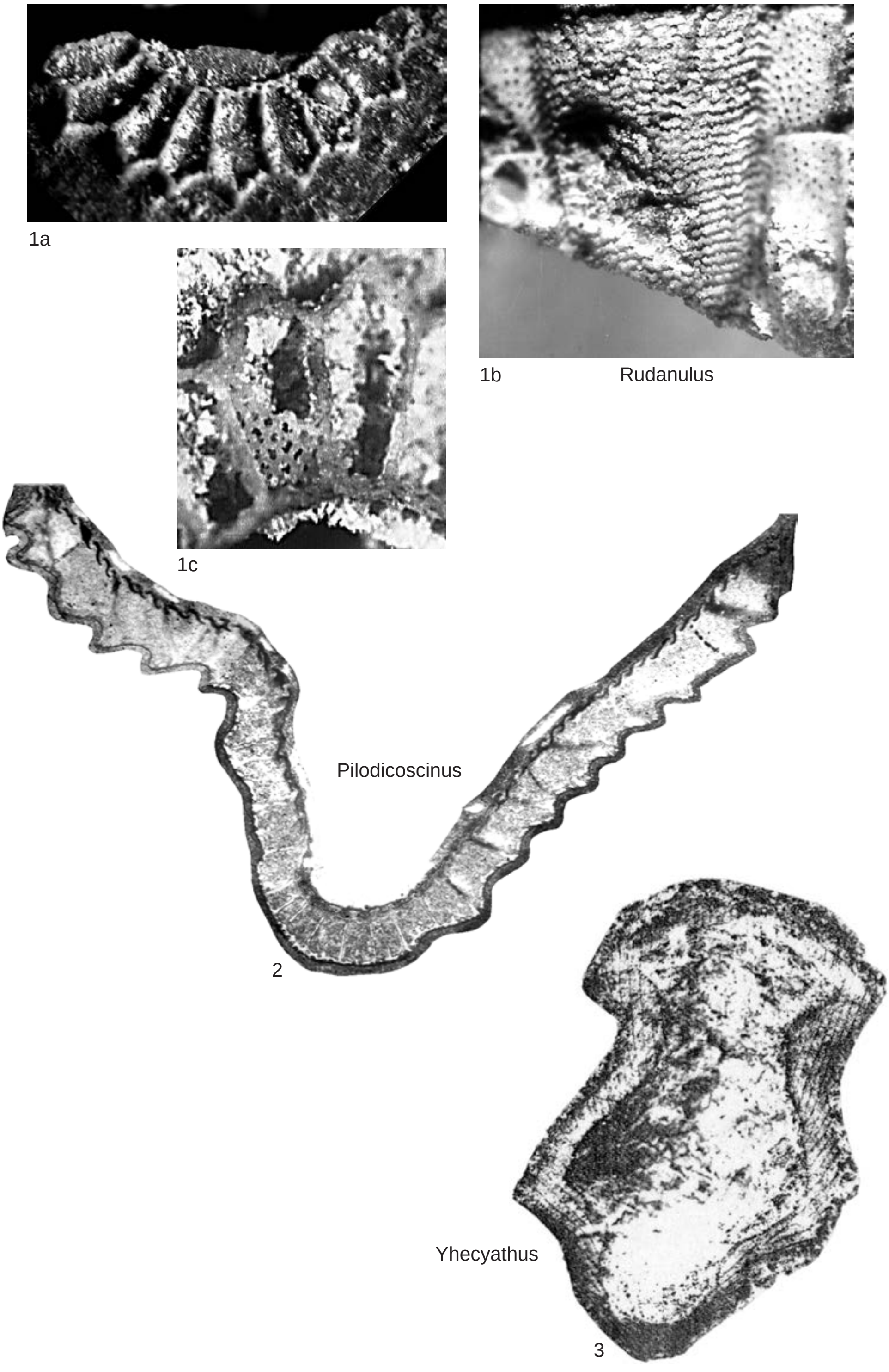


FIG. 581. Rudanulidae (p. 1000–1003).

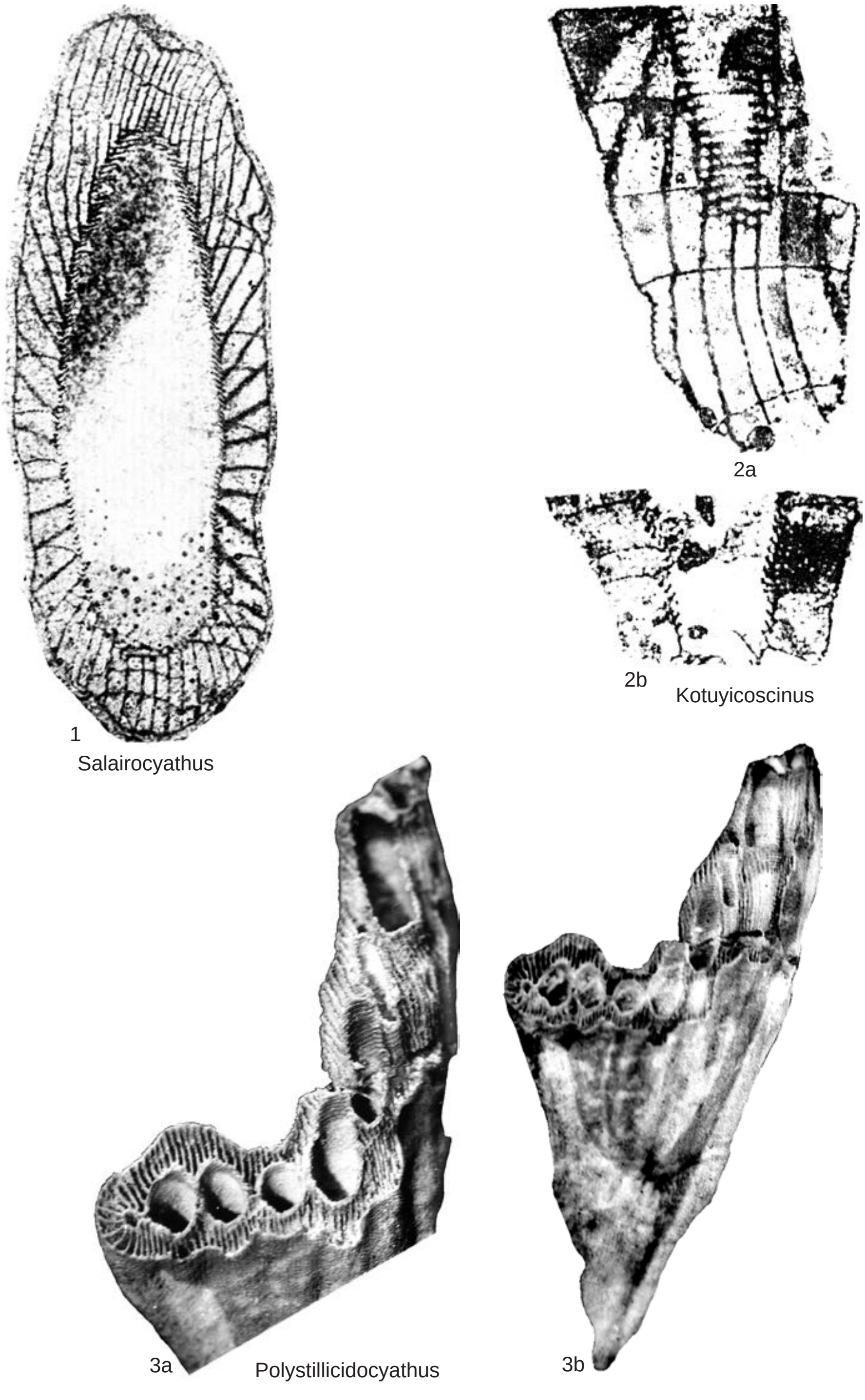


FIG. 582. Salairocyathidae (p. 1003).

Botoman, Fuchin, Shaanxi, China, holotype, NIGP NF$_6$H$_1$, oblique longitudinal section, ×2 (Belyaeva & Yuan, 1995).

Family SALAIROCYATHIDAE Zhuravleva, 1956

[Salairocyathidae ZHURAVLEVA in VOLOGDIN, 1956, p. 879]

Inner wall with annuli. *lower Cambrian (Atd.2–Bot.1).*

Salairocyathus VOLOGDIN, 1940b, p. 89 [**S. zenkovae*; OD; holotype not designated, collection not located] [=*Rimotabulocyathus* YAROSHEVICH, 1990, p. 26 (type, *R. bulynnikovi*, OD)]. Inner wall with one pore row per intersept and upright V-shaped annuli; septa completely porous; tabulae with slitlike pores. *lower Cambrian (Atd.2):* Altay Sayan.——FIG. 582,*1*. **S. zenkovae*, Gavrilovskoe Formation, Atdabanian, Belaya Gorka, Salair, Russia, unlocated syntype, oblique longitudinal section, ×6 (Vologdin, 1940b).

Kotuyicoscinus SUNDUKOV, 1983, p. 16 [**K. minaevae*; OD; holotype, SUNDUKOV, 1983, pl. 1,*7*, SNIIGGiMS 1580/2, Novosibirsk]. Inner wall with several pore rows per intersept and upwardly projecting, S-shaped annuli; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.2–Atd.3):* Siberian Platform.——FIG. 582,*2a–b*. **K. minaevae*, Kyndyn Formation, Chomp-Yurekh Creek, Kotuy River, Krasnoyarsk region, Russia; *a,* holotype, SNIIGGiMS 1580/2, oblique longitudinal section, ×9; *b,* paratype, SNIIGGiMS 1580/1, longitudinal section, ×9 (Sundukov, 1983).

Polystillicidocyathus DEBRENNE, 1959a, p. 14 [**P. erbosimilis*; OD; holotype, DEBRENNE, 1959a, fig. 1; DEBRENNE, 1964, pl. 17,*1–2*, MNHN M80166, specimen Ki140, Paris]. Inner wall with one pore row per intersept and upright, V-shaped annuli; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Altay Sayan, Morocco.——FIG. 582,*3a–b*. **P. erbosimilis*, Issafen Formation, Botoman, Tizi Oumeslema, Morocco; holotype, MNHN M80166, specimen Ki140, modular skeleton; *a,* oblique transverse view, ×4; *b,* longitudinal view, ×3 (Debrenne, 1964).

Family CRASSICOSCINIDAE Debrenne, Rozanov, & Zhuravlev, 1988

[Crassicoscinidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1988, p. 98]

Inner wall with noncommunicating canals. *lower Cambrian (Atd.4–Bot.1).*

Crassicoscinus ROZANOV & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1988, p. 98 [**Coscinocyathellus vulgaris* ROZANOV in REPINA & others, 1964, p. 227; OD; holotype, REPINA & others, 1964, pl. 24,*2*, PIN 4297/29, Moscow]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.4–Bot.1):* Altay Sayan.——FIG. 583,*1*. **C. vulgaris* (ROZANOV), Uba Formation, Atdabanian, Verkhnyaya Tyrga River, Altay Mountains, Russia, holotype, PIN 4297/29, transverse section, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

Crucicyathus GRAVESTOCK, 1984, p. 74 [**C. repandus*; OD; holotype, GRAVESTOCK, 1984, fig. 42A–B, D, SAM P21585, Adelaide]. Outer wall longitudinally plicate; inner wall with several rows of horizontal to upwardly projecting, S-shaped canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.4):* Australia.——FIG. 583,*2a–b*. **C. repandus*, Ajax Limestone, Atdabanian, Mount Scott Range, South Australia, Australia, holotype, SAM P21585; *a,* longitudinal section, ×3.5; *b,* transverse section, ×3 (Gravestock, 1984).

Dentatocoscinus ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1988, p. 98 [**Asterotumulus sektensis* KORSHUNOV & ZHURAVLEVA, 1967, p. 10; OD; holotype, KORSHUNOV & ZHURAVLEVA, 1967, pl. 2,*5*, TsSGM 247/11, Novosibirsk]. Outer wall longitudinally plicate; inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept, bearing supplementary bracts on central cavity side; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Siberian Platform.——FIG. 583,*3*. **D. sektensis* (KORSHUNOV & ZHURAVLEVA), Sekten Formation, Botoman, Tuora-Sis Range, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 247/11, detail of oblique transverse section, ×9 (Korshunov & Zhuravleva, 1967).

Superfamily KASYRICYATHOIDEA Zhuravleva, 1961

[*nom. transl.* DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1620, *ex* Kasyricyathidae ZHURAVLEVA in MUSATOV & others, 1961, p. 29]

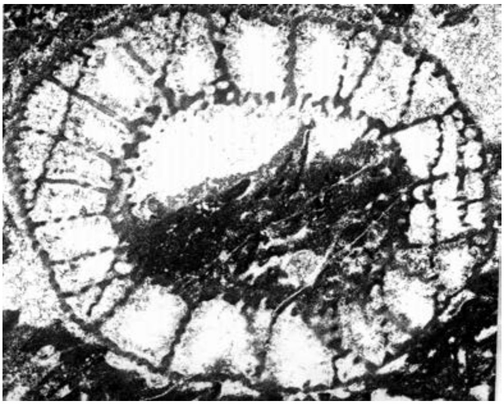
Outer wall with independent microporous sheath. *lower Cambrian (Atd.1–Bot.3).*

Family AGYREKOCYATHIDAE Konyushkov, 1967

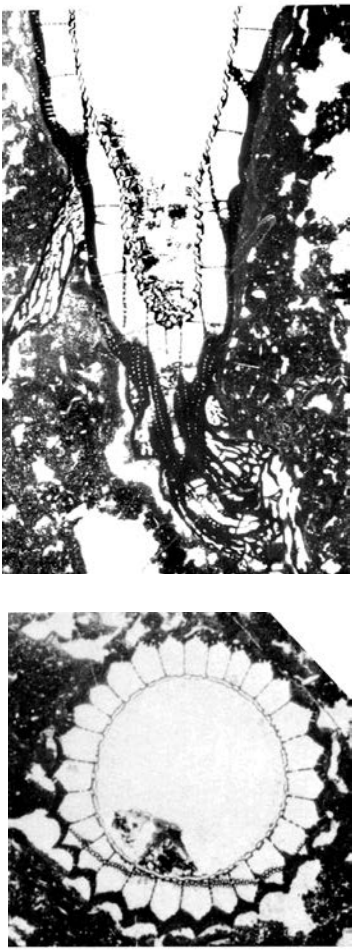
[Agyrekocyathidae KONYUSHKOV, 1967, p. 110]

Inner wall with simple pores. *lower Cambrian (Atd.1–Bot.1).*

Agyrekocyathus KONYUSHKOV, 1967, p. 110 [**A. malovi*; OD; holotype, KONYUSHKOV, 1967, pl. 1,*10*, TsNIGRm 8722/6, St. Petersburg] [=*Mennericyathus* DEBRENNE & ROZANOV in ZHURAVLEVA, 1974a, p. 216 (type, *Tomocyathus kundatus* ROZANOV in ROZANOV



1 Crassicoscinus



2a

2b

Crucicyathus

3 Dentatocoscinus

FIG. 583. Crassicoscinidae (p. 1003).

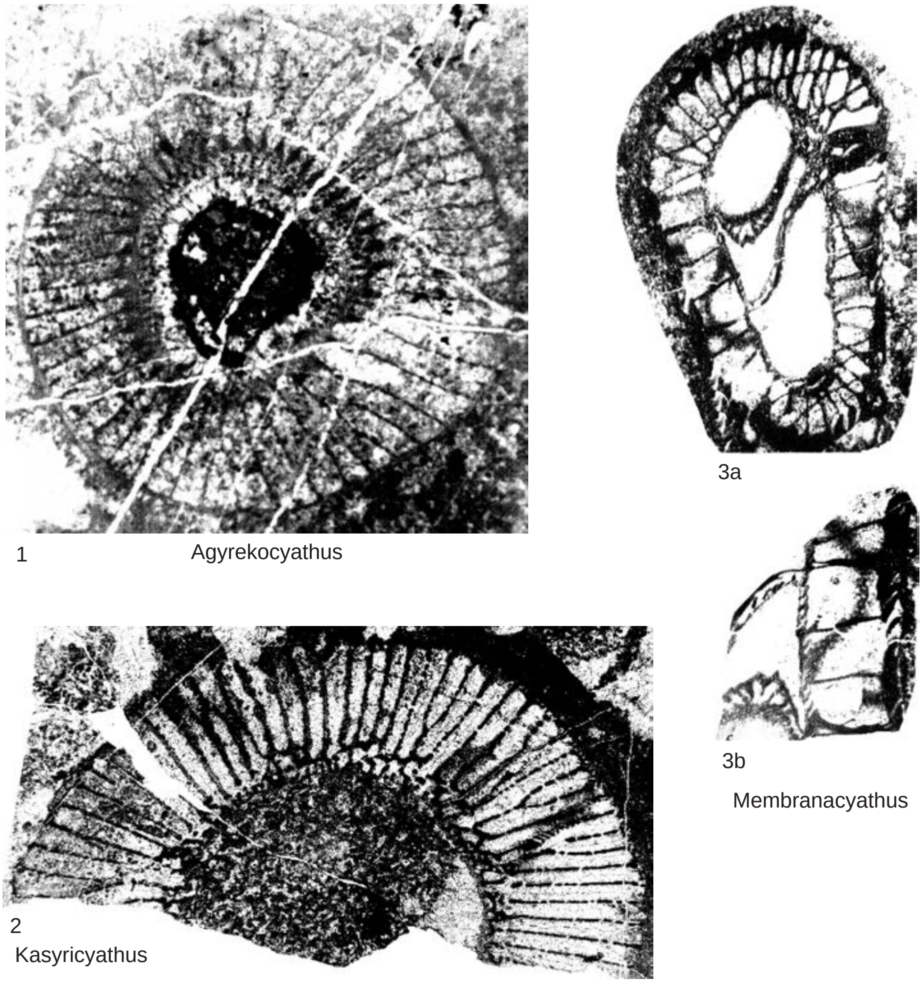


FIG. 584. Agyrekocyathidae, Kasyricyathidae, and Membranacyathidae (p. 1003–1007).

& MISSARZHEVSKIY, 1966, p. 63, OD)]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.1–Bot.1):* Siberian Platform, Altay Sayan, Mongolia, Far East, Kazakhstan, Tajikistan, Australia, Antarctica, Morocco, Iberia, Sardinia.——FIG. 584,*1*. **A. malovi*, Boshchekul' Formation, Atdabanian, Agyrek Mountains, northern Kazakhstan, holotype, TsNIGRm 8722/6, transverse section, ×5 (Debrenne, Zhuravlev, & Kruse, 2002).

Family XESTECYATHIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Xestecyathidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 86]

Inner wall with bracts or scales. *lower Cambrian (Bot.3).*

Xestecyathus KRUSE, 1982, p. 193 [**X. zigzag*; OD; holotype, KRUSE, 1982, pl. 14,*1–7*, AM F.83405, Sydney]. Inner wall with several rows of pores per intersept, bearing upwardly projecting, S-shaped scales; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* Australia.——FIG. 585*a–c*. **X. zigzag*, Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, holotype, AM F.83405; *a,* tangential section of inner wall, AM FT.8526, ×5; *b,* transverse section, AM FT.8527, ×5; *c,* longitudinal section, AM FT.12793, ×5 (Kruse, 1982).

Family KASYRICYATHIDAE Zhuravleva, 1961

[Kasyricyathidae ZHURAVLEVA in MUSATOV & others, 1961, p. 29]

Inner wall with communicating canals. *lower Cambrian (Bot.1).*

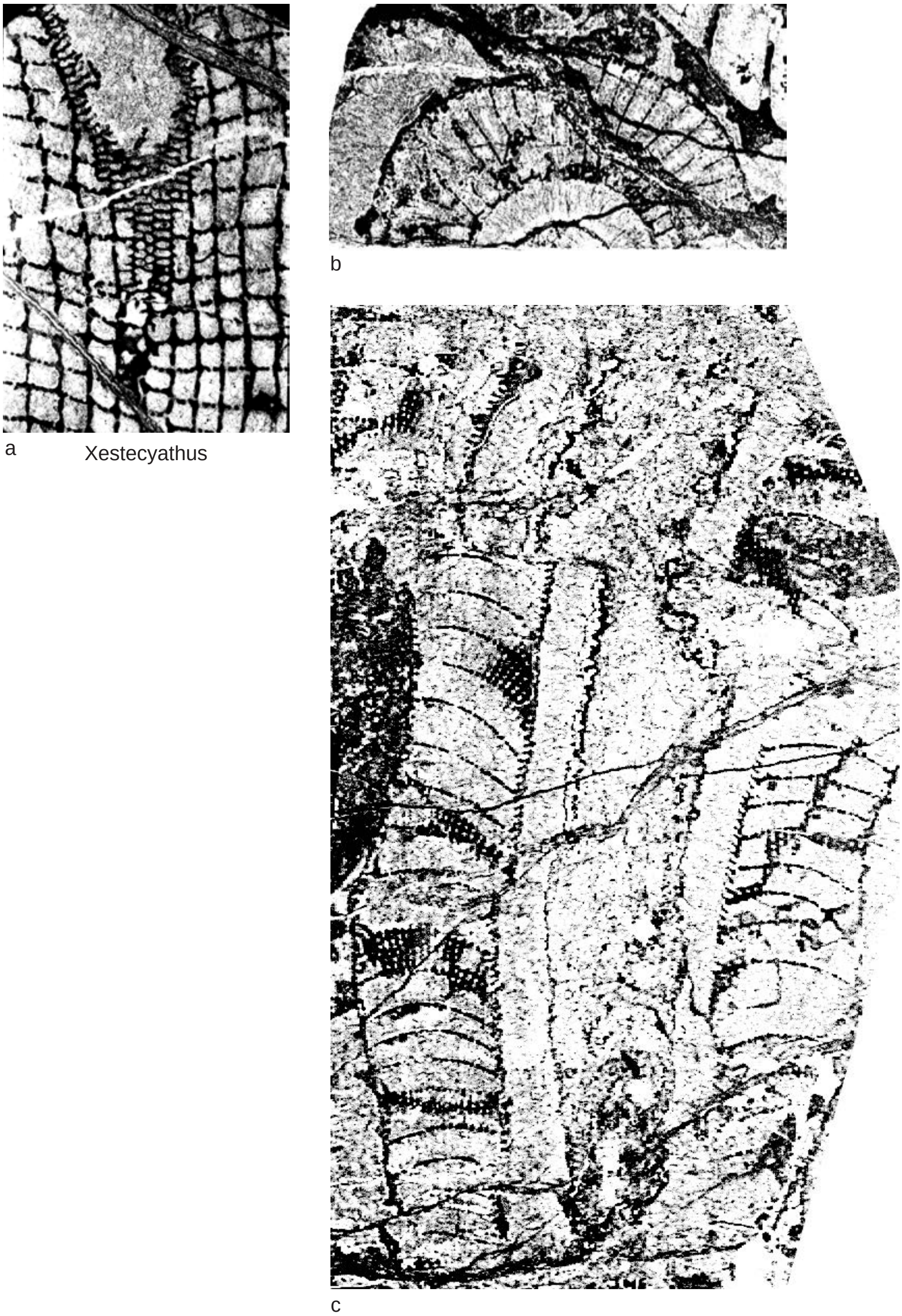


FIG. 585. Xestecyathidae (p. 1005).

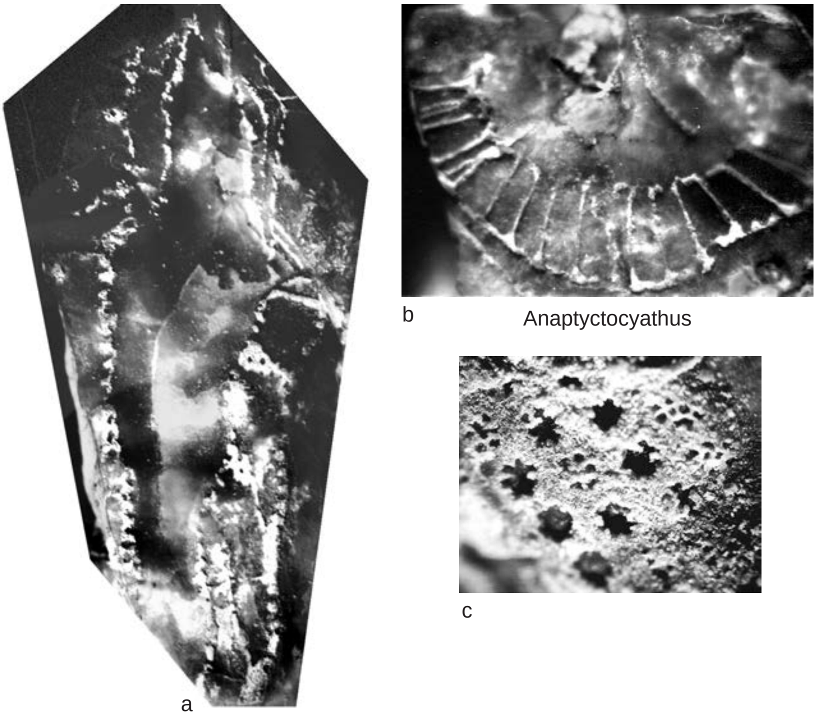


Fig. 586. Anaptyctocyathidae (p. 1008).

Kasyricyathus Zhuravleva in Musatov & others, 1961, p. 30 [**K. schirokovae*; OD; holotype, Musatov & others, 1961, pl. 6,*3–4*, TsSGM 264/36, Novosibirsk]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Altay Sayan.——Fig. 584,*2*. **K. schirokovae*, Balakhtinson Formation, Botoman, Kazyr River, East Sayan, Russia, holotype, TsSGM 264/36, transverse section, ×8 (Musatov & others, 1961).

Family MEMBRANACYATHIDAE
Debrenne, Zhuravlev, & Kruse, 2002

[Membranacyathidae Debrenne, Zhuravlev, & Kruse, 2002, p. 1622]

Inner wall with microporous sheath. *lower Cambrian (Atd.1–Atd.2).*

Membranacyathus Rozanov, 1960a, p. 664 [**M. repinae*; OD; holotype, Rozanov, 1960a, fig. 1zh-z; Rozanov, 1973, pl. 13,*2*, PIN 4297/15, Moscow]. Inner wall with several rows of pores per intersept and continuous microporous sheath; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.1–Atd.2):* Altay Sayan.——Fig. 584,*3a–b*. **M. repinae*, Adiak Formation, Atdabanian, Mrassu River, Gornaya Shoria, Russia, holotype, PIN 4297/15; *a,* oblique transverse section, ×4.5 (Rozanov, 1960a); *b,* detail of longitudinal section (outer wall to left), ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

Superfamily
POLYCOSCINOIDEA
Debrenne, 1964

[*nom. transl.* Debrenne, Zhuravlev, & Kruse, 2002, p. 1623, *ex* Polycoscinidae Debrenne, 1964, p. 194] [=Anaptyctocyathoidea Debrenne, 1970a, p. 25, *nom. correct.* Debrenne & Kruse, 1986, p. 260, *pro* Anaptyctocyathacea Debrenne, 1970a, p. 25; =Lunulacyathacea Debrenne, 1973, p. 18, *nom. nud.*; =Lunulacyathoidea Debrenne in Debrenne, Zhuravlev, & Rozanov, 1989, p. 87]

Outer wall with attached microporous sheath. *lower Cambrian (Atd.3–Bot.3).*

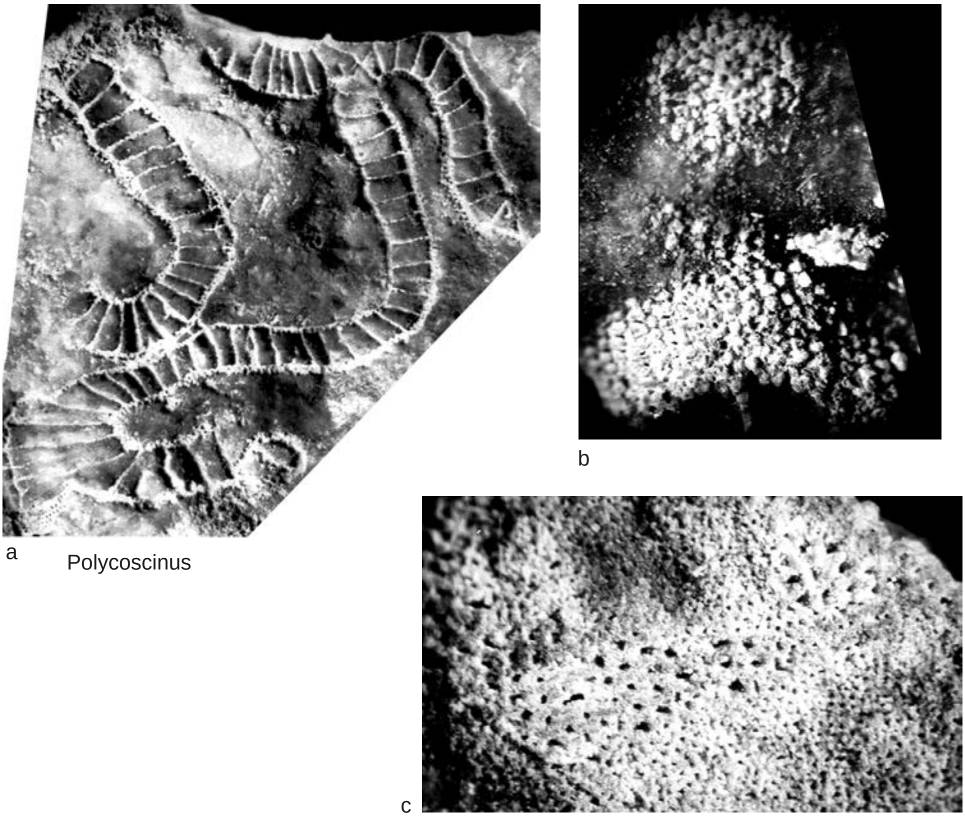


FIG. 587. Polycoscinidae (p. 1008–1009).

Family ANAPTYCTOCYATHIDAE Debrenne, 1970

[Anaptyctocyathidae DEBRENNE, 1970a, p. 25]

Inner wall with simple pores. *lower Cambrian (Atd.4–Bot.3).*

Anaptyctocyathus DEBRENNE, 1969a, p. 340, *nom. transl.* DEBRENNE, 1970a, p. 28, *ex Alataucyathus (Anaptyctocyathus)* DEBRENNE, 1969a, p. 340 [**Coscinocyathus cribripora* R. BEDFORD & W. R. BEDFORD, 1934, p. 3; OD; lectotype, R. BEDFORD & W. R. BEDFORD, 1934, fig. 15; DEBRENNE, 1969a, pl. 11,*1,3;* DEBRENNE, 1973, pl. 2,*6;* SD DEBRENNE, 1969a, p. 340, NHM S4160, London]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.4–Bot.3):* Australia, Antarctica.——FIG. 586*a–c*. **A. cribripora* (R. BEDFORD & W. R. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, NHM S4160; *a,* longitudinal view, ×5; *b,* transverse view, ×5; *c,* detail of outer wall, ×15 (Debrenne, Zhuravlev, & Kruse, 2002).

Family POLYCOSCINIDAE Debrenne, 1964

[Polycoscinidae DEBRENNE, 1964, p. 194] [=Lunulacyathidae DEBRENNE, 1973, p. 18, *nom. nud.*; =Lunulacyathidae DEBRENNE in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 87]

Inner wall with bracts or scales. *lower Cambrian (Atd.3–Bot.3).*

Polycoscinus R. BEDFORD & J. BEDFORD, 1937, p. 37 [**P. contortus*; OD; holotype, R. BEDFORD & J. BEDFORD, 1937, fig. 157; DEBRENNE, 1973, pl. 3,*7;* M; USNM PU87217, specimen 222, Washington, D.C.] [=*Erugatocyathus* DEBRENNE, 1969a, p. 334 (type, *Coscinocyathus papillatus* R. BEDFORD & W. R. BEDFORD, 1934, p. 3, OD), *nom. transl.* DEBRENNE, 1970a, p. 33, *ex Tomocyathus (Erugatocyathus)* DEBRENNE, 1969a, p. 334)]. Inner wall with several rows of pores per intersept, bearing downwardly projecting, cupped bracts; septa sparsely to completely porous; tabulae with normal pores. *lower Cambrian (Atd.3–Bot.3):* Australia, Antarctica, Falkland Islands (allochthonous).——FIG. 587*a–c*. **P. contortus*, Ajax Limestone, Atdabanian, Paint Mine, South Australia,

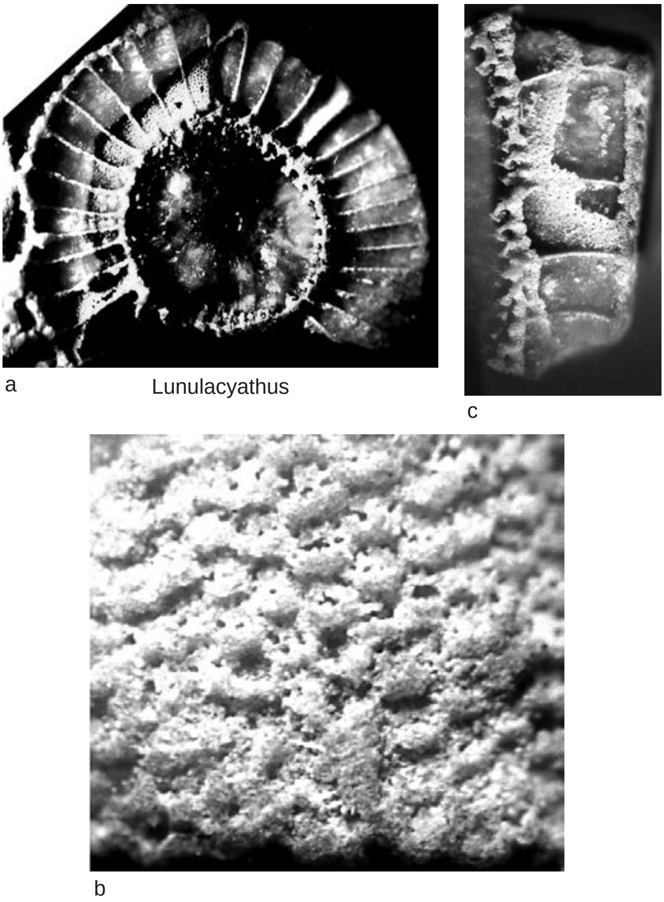


FIG. 588. Polycoscinidae (p. 1009).

Australia, holotype, USNM PU87217, specimen 222; *a,* transverse view of modular skeleton, ×3; *b,* detail of inner wall, tangential view, ×9; *c,* detail of outer wall, tangential view, ×15 (Debrenne, Zhuravlev, & Kruse, 2002).

Lunulacyathus DEBRENNE, 1973, p. 17 [**Coscinocyathus minimiporus* R. BEDFORD & J. BEDFORD, 1937, p. 37; OD; lectotype, R. BEDFORD & J. BEDFORD, 1937, fig. 155; DEBRENNE, 1973, pl. 4,*6;* SD DEBRENNE, 1973, p. 17, USNM PU86705, Washington, D.C.]. Outer wall with attached microporous sheath and supplementary cupped bracts; inner wall with several rows of pores per intersept, bearing downwardly projecting, cupped bracts; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* Australia.——FIG. 588*a–c.* **L. minimiporus* (R. BEDFORD & J. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, USNM PU86705; *a,* transverse view, ×8; *b,* detail of outer wall in longitudinal view, ×30 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* longitudinal view (outer wall to right), ×8 (Debrenne, Zhuravlev, & Kruse, 2012b).

Family VERONICACYATHIDAE Debrenne, Zhuravlev, & Kruse, 2002

[Veronicacyathidae DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1625]

Inner wall with noncommunicating canals. *lower Cambrian (Atd.4–Bot.3).*

Veronicacyathus DEBRENNE, 1973, p. 19 [**V. frondeus* DEBRENNE, 1973, p. 20; OD; holotype, DEBRENNE, 1973, pl. 2,*4–5;* pl. 3,*1;* pl. 4,*8*, USNM PU86731, specimen 200, Washington, D.C.; =*Coscinocyathus tatei* ETHERIDGE, 1890, p. 18; lectotype, ETHERIDGE, 1890, pl. 3,*2–4;* DEBRENNE, ZHURAVLEV, & GRAVESTOCK, 1993, fig. 3–4; SD DEBRENNE, ZHURAVLEV, & GRAVESTOCK, 1993, p. 182, choice following elimination of all other specimens by TATE, 1892, p. 188, SAM T1245, Adelaide][=*Bractocyathus* KRUSE, 1978, p. 41 (type, *B. labiosus;* OD)]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept, bearing spines projecting radially across orifice

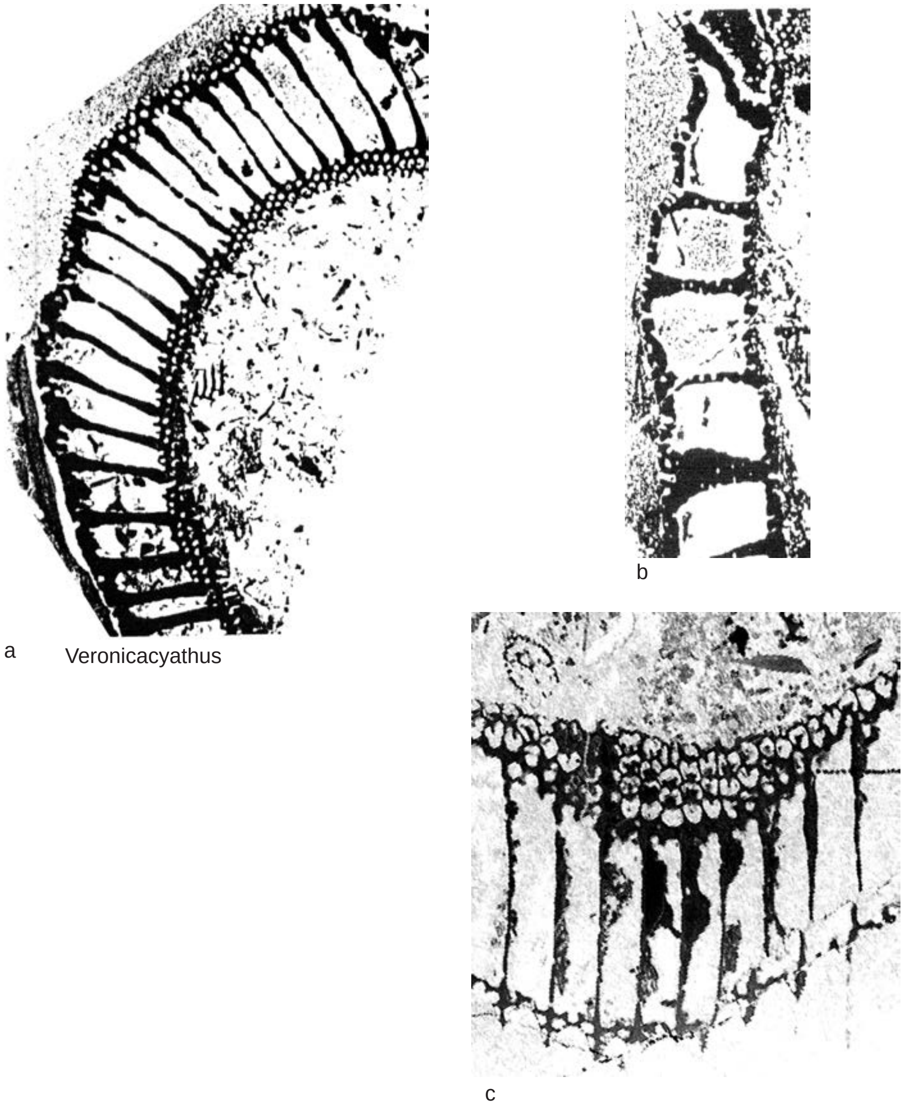


FIG. 589. Veronicacyathidae (p. 1009–1010).

to form screen; septa aporose to sparsely porous; tabulae with normal pores. *lower Cambrian (Atd.4–Bot.3):* Australia, Antarctica.——FIG. 589*a–b*. **V. tatei* (ETHERIDGE), Parara Limestone, Botoman, Pavy Gully, Ardrossan, South Australia, Australia, lectotype, SAM T1245; *a,* transverse section, ×3; *b,* longitudinal section (outer wall to left), ×3 (Debrenne, Zhuravlev, & Gravestock, 1993).——FIG. 589*c, V. labiosus* (KRUSE), Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia; topotype, AM FT.10077, detail of inner wall, tangential section, ×6 (Kruse, 1982).

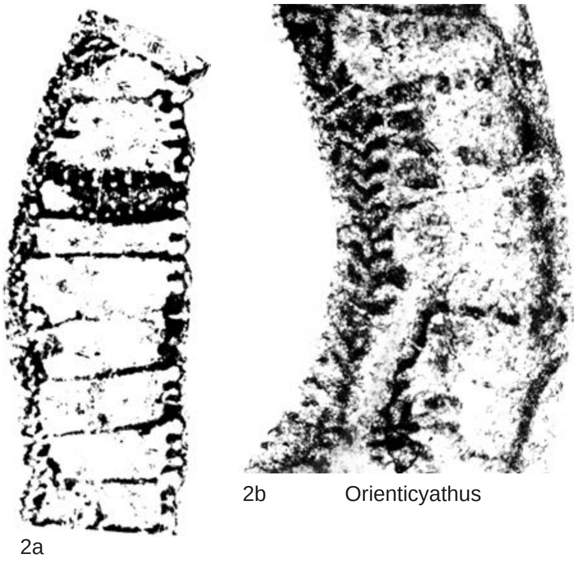
Family ZONACOSCINIDAE
Debrenne, 1971

[Zonacoscinidae DEBRENNE, 1971, p. 194]

Inner wall with communicating canals. *lower Cambrian (Bot.1).*

Zonacoscinus DEBRENNE, 1971, p. 194 [**Z. tumulosus*; OD; holotype, DEBRENNE, 1971, fig. 3; DEBRENNE, 1972, pl. 4,*5–6*, MNHN M84037, specimen Ci 15U 21-2, Paris]. Inner wall with

Zonacoscinus



Orienticyathus

FIG. 590. Zonacoscinidae (p. 1010–1011).

several rows of horizontal to upwardly projecting, straight canals per intersept, canals branching toward central cavity; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Sardinia.——FIG. 590,*1*. **Z. tumulosus*, Matoppa Formation, Botoman, Monte Cuccurinu, Sardinia, Italy, holotype, MNHN M84037, specimen Ci 15U 21-2, transverse section (outer wall at top), ×10 (Debrenne, 1972).

Orienticyathus BELYAEVA, 1969, p. 95 [**O. mamontovi*; OD; holotype, BELYAEVA, 1969, pl. 36,*1–2*, DVGU 6M/K8/3-3, Khabarovsk]. Inner wall with several rows of upright, V-shaped canals per intersept; septa completely porous; tabulae with normal pores; synapticulae may be present. *lower Cambrian (Bot.1):* Far East.——FIG. 590,*2a–b*. **O. mamontovi*, Ust'toka unit, Botoman, Gerbikan River, Dzhagdy Range, Far East, Russia; *a,* holotype, DVGU 6M/K8/3-3, detail of transverse section (outer wall to right), ×13; *b,* paratype, DVGU 6M/K8/3-2, detail of longitudinal section (outer wall to right), ×13 (Debrenne, Zhuravlev, & Kruse, 2002).

Superfamily ETHMOCOSCINOIDEA Zhuravleva, 1957

[*nom. transl.* DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 87, *ex* Ethmocoscinidae ZHURAVLEVA in VOLOGDIN, 1957a, p. 181] [=Tumulocoscinacea ZHURAVLEVA, 1960b, p. 265, *nom. nud., nom. transl.* ROZANOV, 1973, p. 86, *ex* Tumulocoscininae ZHURAVLEVA, 1960b, p. 265; =Tumulocoscinoidea ZHURAVLEVA, 1960b, p. 265, *nom. transl.* ROZANOV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 86, *ex* Tumulocoscininae ZHURAVLEVA, 1960b, p. 265]

Outer wall with simple tumuli. *lower Cambrian (Atd.2–Bot.3).*

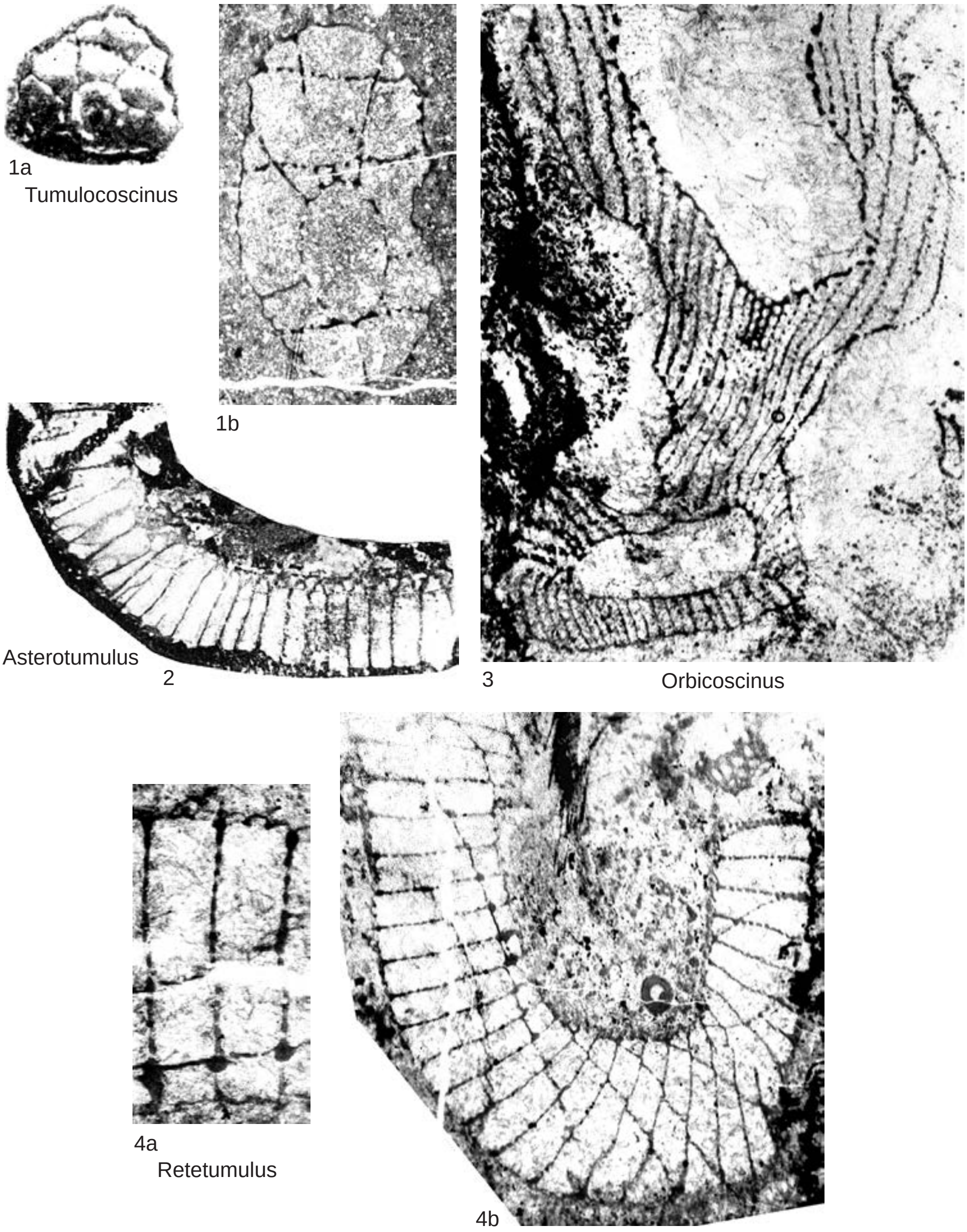


FIG. 591. Tumulocoscinidae (p. 1012–1013).

Family TUMULOCOSCINIDAE
Zhuravleva, 1960

[*nom. transl.* DEBRENNE, 1970a, p. 25, *ex* Tumulocoscininae ZHURAVLEVA, 1960b, p. 265]

Inner wall with simple pores. *lower Cambrian (Atd.2–Bot.1).*

Tumulocoscinus ZHURAVLEVA, 1960b, p. 265 [**T. atdabanensis*; OD; holotype, ZHURAVLEVA, 1960b, pl. 3,*3b;* pl. 23,*10*, PIN 1161, Moscow, not located]. Inner wall with several rows of simple pores per intersept; septa aporose to sparsely porous; tabulae with normal pores. *lower Cambrian (Atd.2–Bot.1):* Siberian Platform, Altay Sayan.——FIG. 591,*1a–b*. **T. atdabanensis*, Perekhod Formation, Atdabanian;

a, Yudyay, Lena River, Sakha (Yakutia), Russia, holotype, PIN 1161, transverse section, ×12 (Zhuravleva, 1960b); *b,* Achagyy-Taryng Creek, Lena River, Sakha (Yakutia), Russia, specimen TsSGM 323/91, oblique longitudinal section, ×15 (Zhuravleva, Korshunov, & Rozanov, 1969).

?Asterotumulus Kashina in Repina & others, 1964, p. 229 [**A. receptori*; OD; holotype, Repina & others, 1964, pl. 15,*3*, TsSGM KGU1313/61, Novosibirsk]. Outer wall with probable tumuli; inner wall longitudinally plicate, with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. [Limited type material does not provide certainty as to which wall is outer and which inner, thereby creating uncertainty as to whether accepted outer wall bears tumuli or bracts.] *lower Cambrian (Atd.3–Bot.1):* Altay Sayan.——Fig. 591,*2.* **A. receptori*, Bazaikha Formation, Atdabanian, Bazaikha River, East Sayan, Russia, holotype, TsSGM KGU1313/61, transverse section, ×7 (Repina & others, 1964).

Orbicoscinus Debrenne, 1977a, p. 111 [**O. schaerti*; OD; holotype, Debrenne, 1977a, pl. 10,*4*, MNHN M80045, specimen IRH24-1c, Paris]. Cup in which both walls show periodic, synchronous transverse folds; inner wall with one row of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Morocco.——Fig. 591,*3.* **O. schaerti*, Issafen Formation, Botoman, Jbel Irhoud, holotype, MNHN M80045, specimen IRH24-1c, longitudinal section, ×5 (Debrenne, 1977a).

Retetumulus Debrenne, 1977a, p. 112 [**R. dutuiti*; OD; holotype, Debrenne, 1977a, pl. 10,*1*, MNHN M80042, specimen IRH34-3f, Paris]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with slitlike pores. *lower Cambrian (Bot.1):* Morocco.——Fig. 591,*4a–b.* **R. dutuiti*, Issafen Formation, Botoman, Jbel Irhoud, Morocco, holotype, MNHN M80042, specimen IRH34-3f; *a,* detail of outer wall (at top) in transverse section, ×20 (Debrenne, 1977a); *b,* oblique transverse section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Family ETHMOCOSCINIDAE
Zhuravleva, 1957

[Ethmocoscinidae Zhuravleva in Vologdin, 1957a, p. 181]

Inner wall with noncommunicating canals. *lower Cambrian (Bot.3).*

Ethmocoscinus Simon, 1939, p. 28 [**Coscinocyathus papillipora* R. Bedford & W. R. Bedford, 1934, p. 4; OD; holotype, R. Bedford & W. R. Bedford, 1934, fig. 18; Hill, 1965, pl. 8,*7;* Debrenne, 1969a, pl. 3,*3,* NHM S4164, M, London]. Inner wall with several rows of horizontal to upwardly projecting, S-shaped canals per intersept; canals may be fused to form pseudoannuli; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* Australia.——Fig. 592,*1a–b.* **E. papillipora* (R. Bedford & W. R. Bedford), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, NHM S4164; *a,* detail of outer wall in longitudinal view, ×7; *b,* transverse view, ×4 (Hill, 1965).

Superfamily COSCINOPTYCTOIDEA
Debrenne, Rozanov, & Zhuravlev, 1989

[Coscinoptyctoidea Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989, p. 86]

Outer wall with multiperforate tumuli. *lower Cambrian (Atd.1–Bot.3).*

Family GEYERICOSCINIDAE
Debrenne & Zhuravlev, 2000

[Geyericoscinidae Debrenne & Zhuravlev, 2000, p. 50]

Inner wall with simple pores. *lower Cambrian (Atd.1–Bot.1).*

Geyericoscinus Debrenne & Zhuravlev, 2000, p. 50 [**Coscinocyathus equiporus* Debrenne, 1959b, p. 8; OD; lectotype, Debrenne, 1959b, pl. 1,*4;* Debrenne, 1964, pl. 28,*4;* SD Debrenne, 1963a, p. 23, MNHN M80081, specimen TAI 1-5-4T, Paris]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.1–Bot.1):* Morocco.——Fig. 592,*2a–b.* **G. equiporus* (Debrenne), Amouslek Formation, Atdabanian, Jbel Taïssa, lectotype, MNHN M80081, specimen TAI 1-5-4T; *a,* transverse section, ×5 (Debrenne, 1959b); *b,* detail of transverse section (outer wall at bottom), ×15 (Debrenne, 1964).

Family COSCINOPTYCTIDAE
Debrenne, Rozanov, & Zhuravlev, 1989

[Coscinoptyctidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989, p. 86]

Inner wall with bracts or scales. *lower Cambrian (Bot.3).*

Coscinoptycta Broili, 1915, p. 121, *nom. nov. pro Coscinoptycha* Taylor, 1910, p. 141, *non* Meyrick, 1881, p. 700, insect [**Coscinoptycha convoluta* Taylor, 1910, p. 141; SD Simon, 1939, p. 26; lectotype, Taylor, 1910, fig. 7–8, pl. 11, photo 60; SD Debrenne, Zhuravlev, & Kruse, 2002, p. 1630, SAM T1594-6, Adelaide]. Cup in which both walls show synchronous transverse folds; inner wall with several rows of pores per intersept, bearing probably downwardly projecting, cupped bracts; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.3):*

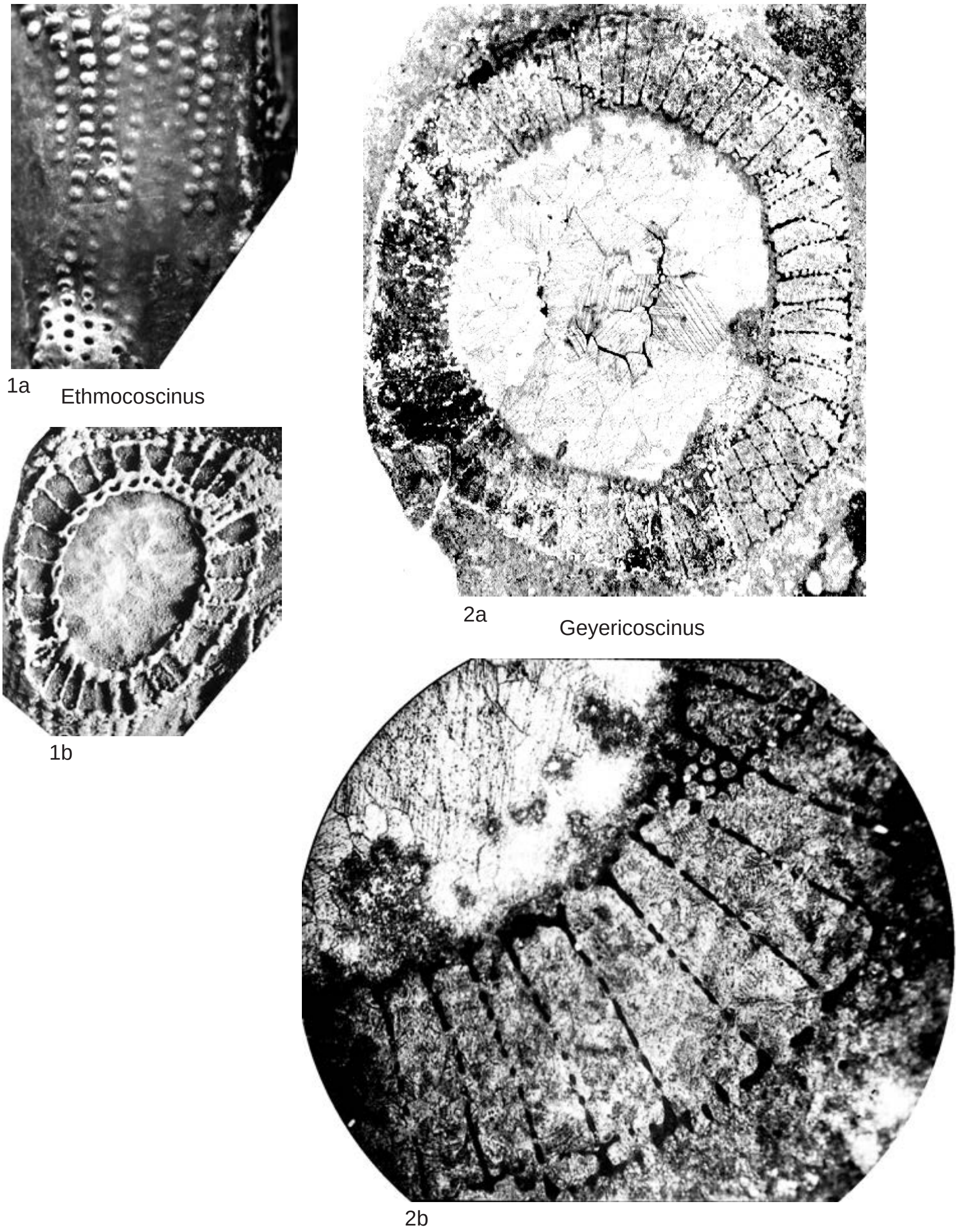


FIG. 592. Ethmocoscinidae and Geyericoscinidae (p. 1013).

Australia, Antarctica.——FIG. 593*a–c*. **C. convoluta* (TAYLOR), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1594-6; *a,* detail of outer wall in tangential section, ×7; *b,* transverse section (outer wall at bottom), ×4; *c,* detail of transverse section (outer wall at top), ×9 (Debrenne, Zhuravlev, & Kruse, 2002).

Family JEBILETICOSCINIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Jebileticoscinidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 86]

Inner wall with noncommunicating canals. *lower Cambrian (Bot.1).*

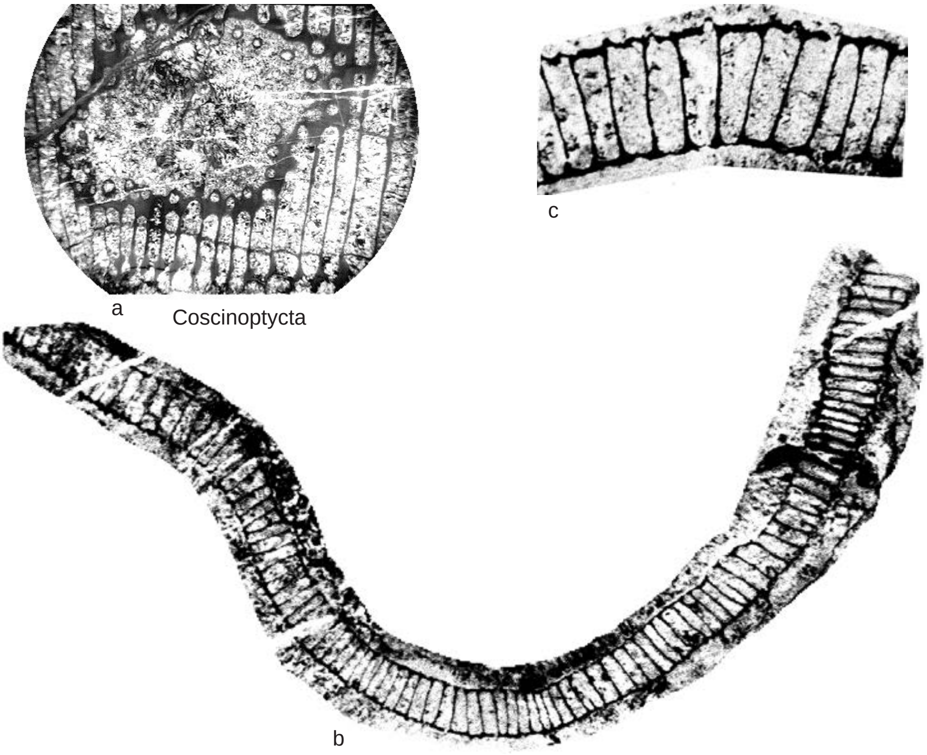


FIG. 593. Coscinoptyctidae (p. 1013–1014).

Jebileticoscinus DEBRENNE, 1977a, p. 114 [**J. huvelini*; OD; holotype, DEBRENNE, 1977a, pl. 11,*2*, MNHN M80048, specimen IRH4-1d, Paris] [=*Pachycoscinus* DEBRENNE, 1977a, p. 117 (type, *P. hollardi*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1630]. Inner wall with several rows of horizontal to upwardly projecting, straight canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Morocco.——FIG. 594,*1*. **J. huvelini*, Issafen Formation, Botoman, Jbel Irhoud, Morocco, holotype, MNHN M80048, specimen IRH4-1d, longitudinal section, ×4 (Debrenne, 1977a).

Irhoudicoscinus DEBRENNE, 1977a, p. 117 [**I. destombesi;* OD; holotype, DEBRENNE, 1977a, pl. 12,*3–4*, MNHN M80052, specimen IRH2-1a, Paris]. Inner wall with one row of horizontal to upwardly projecting, straight canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Morocco.——FIG. 594,*2*. **I. destombesi*, Issafen Formation, Botoman, Jbel Irhoud, Morocco, holotype, MNHN M80052, specimen IRH2-1a, oblique transverse section, ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

Superfamily SIGMOCOSCINOIDEA R. Bedford & J. Bedford, 1939

[*nom. correct.* DEBRENNE & KRUSE, 1986, p. 264, *pro* Sigmocoscinacea DEBRENNE, 1970a, p. 25, *nom. transl. ex* Sigmocoscinidae R. BEDFORD & J. BEDFORD, 1939, p. 76]

Outer wall with bracts or scales. *lower Cambrian (Bot.1–Bot.3).*

Family SYLVIACOSCINIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Sylviacoscinidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 87]

Inner wall with simple pores. *lower Cambrian (Bot.1–Bot.3).*

Sylviacoscinus DEBRENNE in ZHURAVLEVA, 1974b, p. 119 [**Coscinocyathus sylvia* R. BEDFORD & J. BEDFORD, 1937, p. 37; OD; holotype, R. BEDFORD & J. BEDFORD, 1937, fig. 156, USNM PU86706, specimen 221, M, Washington, D.C.]. Outer wall with upwardly projecting,

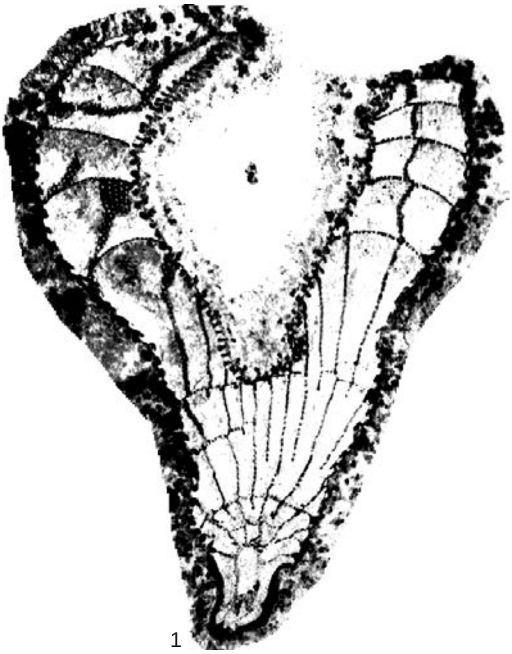


FIG. 594. Jebileticoscinidae (p. 1015).

denticulate, curved scales; inner wall with one row of simple pores per intersept; septa aporose to sparsely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* Australia.——FIG. 595*a–c*. **S. sylvia* (R. BEDFORD & J. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, USNM PU86706, specimen 221; *a,* detail of outer wall, longitudinal view, ×15; *b,* transverse view, ×7; *c,* detail of inner wall, internal longitudinal view, ×9 (Debrenne, Zhuravlev, & Kruse, 2002).

Family SIGMOCOSCINIDAE R. Bedford & J. Bedford, 1939

[Sigmocoscinidae R. BEDFORD & J. BEDFORD, 1939, p. 76]

Inner wall with annuli. *lower Cambrian (Bot.3).*

Sigmocoscinus R. BEDFORD & J. BEDFORD, 1936, p. 24 [**S. sigma*; OD; lectotype, R. BEDFORD & J. BEDFORD, 1936, fig. 98; SD HILL, 1965, p. 111, USNM PU86686, specimen 235, Washington, D.C.]. Outer wall with upwardly projecting, S-shaped scales; inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* Australia, Antarctica.——FIG. 596,*1a–d*. **S. sigma*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, USNM PU86686, specimen 235; *a,* transverse view, ×8; *b,* detail of inner wall, internal longitudinal view, ×11; *c,* detail of outer wall, longitudinal view, ×11; *d,* longitudinal view, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

?**Statanulocyathus** DEBRENNE, 1975, p. 342 [**S. oosthuizeni*; OD; holotype, DEBRENNE, 1975, fig. 7a–b, SAM(C) K44945, Cape Town]. Outer wall with upwardly projecting, cupped bracts; inner wall with one row of pores per intersept, bearing upwardly projecting, cupped bracts; upwardly projecting, arcuate annuli at each tabula; septa completely porous; tabulae with normal pores. [Inner wall structure comprises bracts together with unusual, hypertrophied annuli, the appropriate taxonomic treatment of which is uncertain.] *lower Cambrian (Bot.3):* South Africa (allochthonous).——FIG. 596,*2*. **S. oosthuizeni*, Dwyka Subgroup, Botoman (allochthonous in Permian), Zwartskraal, South Africa, holotype, SAM(C) K44945, oblique longitudinal section, ×10 (Debrenne, 1975).

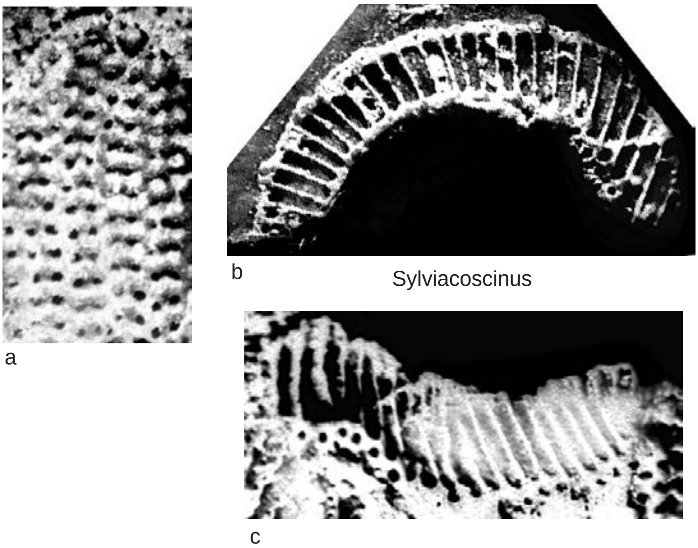


Fig. 595. Sylviacoscinidae (p. 1015–1016).

Superfamily POROCOSCINOIDEA
Debrenne, 1964

[*nom. transl.* Debrenne, Zhuravlev, & Kruse, 2002, p. 1633, *ex* Porocoscinidae Debrenne, 1964, p. 190] [=Rozanovicyathacea Korshunov in Zhuravleva, Korshunov, & Rozanov, 1969, p. 54; =Schumnyicyathoidea Debrenne, Zhuravlev, & Rozanov, 1989, p. 87, *nom. transl.* Debrenne, Zhuravlev, & Kruse, 2002, p. 1635, *ex* Schumnyicyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989, p. 87]

Outer wall with canals. *lower Cambrian (Atd.1–Bot.3).*

Family ROZANOVICYATHIDAE
Korshunov, 1969

[Rozanovicyathidae Korshunov in Zhuravleva, Korshunov, & Rozanov, 1969, p. 54]

Inner wall with simple pores. *lower Cambrian (Bot.1).*

Rozanovicyathus Korshunov in Zhuravleva, Korshunov, & Rozanov, 1969, p. 54 [**R. alexi*; OD; holotype, Zhuravleva, Korshunov, & Rozanov, 1969, pl. 23,*1,3*, TsSGM 323/93, Novosibirsk]. Outer wall with horizontal to upwardly projecting, S-shaped canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of simple pores per intersept; septa completely porous; tabulae with slitlike pores. *lower Cambrian (Bot.1):* Siberian Platform.——Fig.597,*1.* **R. alexi*, Mukhatta Formation, Botoman, Mukhatta River, Sakha (Yakutia), Russia, holotype, TsSGM 323/93, transverse section, ×5 (Zhuravleva, Korshunov, & Rozanov, 1969).

Family TATIJANAECYATHIDAE
Korshunov, 1976

[Tatijanaecyathidae Korshunov, 1976, p. 149] [=Schumnyicyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989, p. 87]

Inner wall with annuli. *lower Cambrian (Bot.1).*

Muchattocyathus Rozanov in F. Debrenne, M. Debrenne, & Rozanov, 1976, p. 103 (Rozanov, 1973, p. 61, *nom. nud.*) [**M. sibiricus*; OD; holotype, F. Debrenne, M. Debrenne, & Rozanov, 1976, pl. 1,*5*, PIN 4597/142, Moscow] [=*Tatijanaecyathus* Korshunov, 1976, p. 149 (type, *T. laetus,* OD), for discussion, see Debrenne, Zhuravlev, & Rozanov, 1989, p. 120; Debrenne, Rozanov, & Zhuravlev, 1990, p. 152]. Outer wall with downwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall upright V-shaped appearance to outer wall); inner wall with one pore row per intersept and upwardly projecting, S-shaped annuli; septa completely porous, linked by synapticulae; tabulae with normal pores. *lower Cambrian (Bot.1):* Siberian Platform.——Fig. 597,*2.* **M. sibiricus*, Oy-Muran reef massif, Botoman, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, PIN 4597/142, oblique transverse section, ×7 (F. Debrenne, M. Debrenne, & Rozanov, 1976).

Schumnyicyathus Zhuravleva in Datsenko & others, 1968, p. 164 [**S. validus*; OD; holotype, Datsenko & others, 1968, pl. 9,*3*, TsSGM

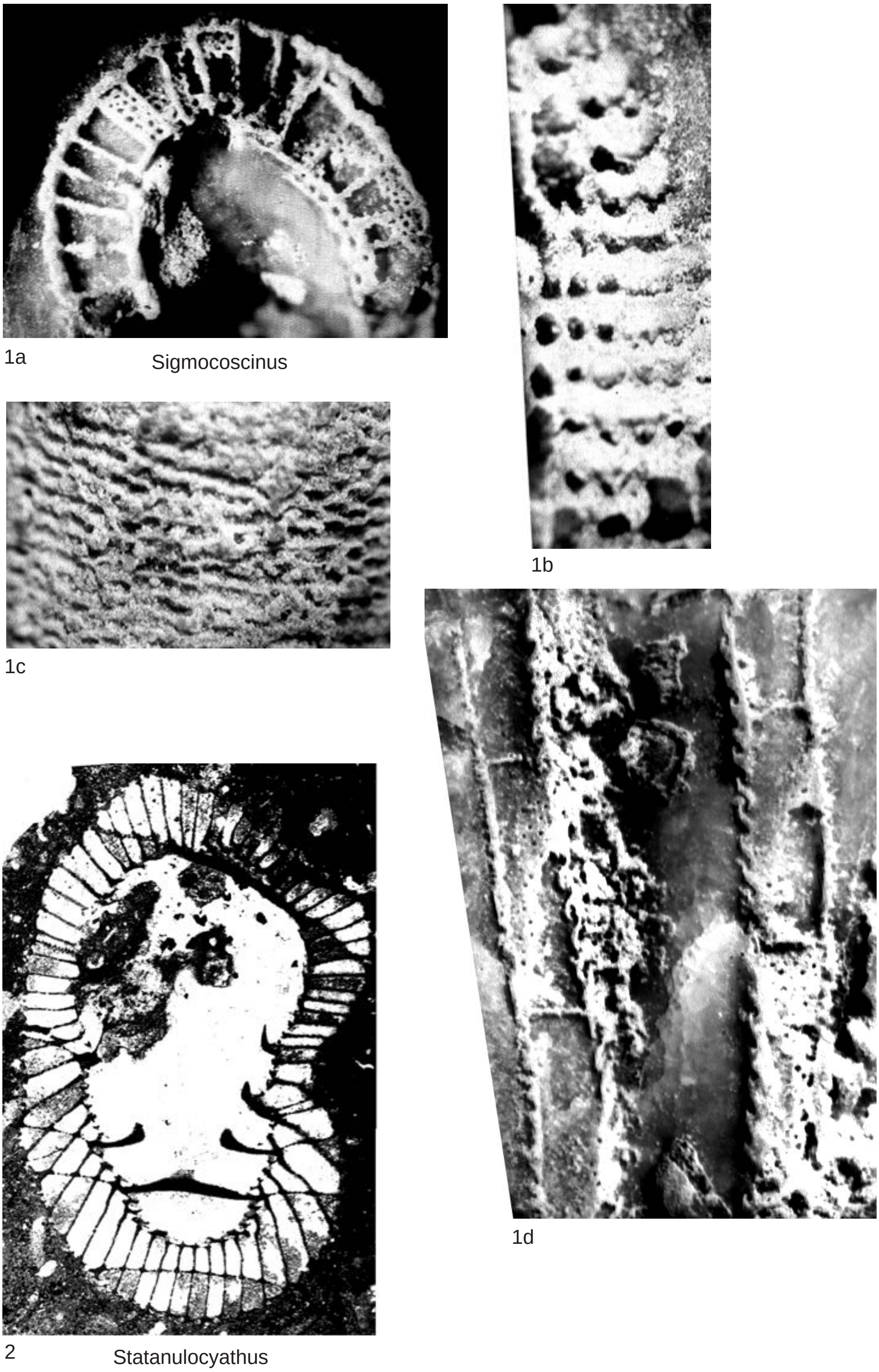


FIG. 596. Sigmocoscinidae (p. 1016).

278/72, Novosibirsk]. Outer wall with horizontal to upwardly projecting, S-shaped canals and supplementary attached microporous sheath; inner wall with several pore rows per intersept and upwardly projecting, S-shaped annuli; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Siberian Platform.——FIG. 597,*3a–b*. **S. validus*, Shumnoy Formation, Botoman, Sukharikha River, Krasnoyarsk region, Russia; *a,* holotype, TsSGM 278/72, transverse section, ×12; *b,* paratype, TsSGM 278/73, oblique longitudinal section, ×12 (Datsenko & others, 1968).

Family POROCOSCINIDAE Debrenne, 1964

[Porocoscinidae DEBRENNE, 1964, p. 190]

Inner wall with noncommunicating canals. *lower Cambrian (Atd.3–Bot.3).*

Porocoscinus DEBRENNE, 1964, p. 190 [**P. flexibilis*; OD; holotype, DEBRENNE, 1964, pl. 28,*1–3*, MNHN M84108, specimen S Sc 5-4b, Paris] [=*Coscinoteichus* DEBRENNE, 1964, p. 180 (type, *C. minimiporus*, OD); =*Chengkoucyathus* YUAN, 1974, p. 81 (type, *C. shabaensis*, OD); =*Flexicyathus* KRUSE, 1978, p. 40 (type, *F. rudens*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 124; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 155; DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1635]. Outer wall with horizontal to upwardly projecting, S-shaped canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with several rows of inverted V-shaped canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1–Bot.3):* Australia, Antarctica, South China, Iberia, Sardinia.——FIG. 598,*1a–b*. **P. flexibilis*, Matoppa Formation, Botoman, Serra Scoris, Sardinia, Italy, holotype, MNHN M84108, specimen S Sc 5-4b; *a,* transverse section (outer wall at top), ×8 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* longitudinal section (outer wall to left), ×8 (Debrenne, 1964).

Geniculicyathus DEBRENNE, 1960, p. 118 [**G. varius*; M; holotype, DEBRENNE, 1960, fig. A, MNHN M80154, specimen HD40, Paris]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with several rows of horizontal to upwardly projecting, S-shaped canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.3):* Morocco.——FIG. 598,*2a–b*. **G. varius*, Amouslek Formation, Atdabanian, Jbel Taïssa, Morocco, holotype, MNHN M80154, specimen HD40; *a,* transverse section, ×4; *b,* longitudinal section, ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

Tubicoscinus DEBRENNE in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 137 (DEBRENNE, 1970b, p. 207, *nom. nud.*, proposed conditionally, ICZN Art. 15) [**Coscinocyathus tuba* BORNEMANN, 1884, p. 704; OD; holotype, BORNEMANN, 1886, pl. 15,*2a;* DEBRENNE, 1964, pl. 18,*1–2*, GML 930, Halle]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of horizontal to upwardly projecting, slightly S-shaped canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Iberia, Sardinia.——FIG. 598,*3a–b*. **T. tuba* (BORNEMANN), Matoppa Formation, Botoman, San Pietro, Sardinia, Italy, holotype, GML 930; *a,* longitudinal section, ×7 (Bornemann, 1886); *b,* detail of same, ×14 (Debrenne, 1964).

Superfamily MOOTWINGEECYATHOIDEA Kruse, 1982

[*nom. transl.* DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 87, *ex* Mootwingeecyathidae KRUSE, 1982, p. 194]

Outer wall clathrate. *lower Cambrian (Bot.3).*

Family MOOTWINGEECYATHIDAE Kruse, 1982

[Mootwingeecyathidae KRUSE, 1982, p. 194]

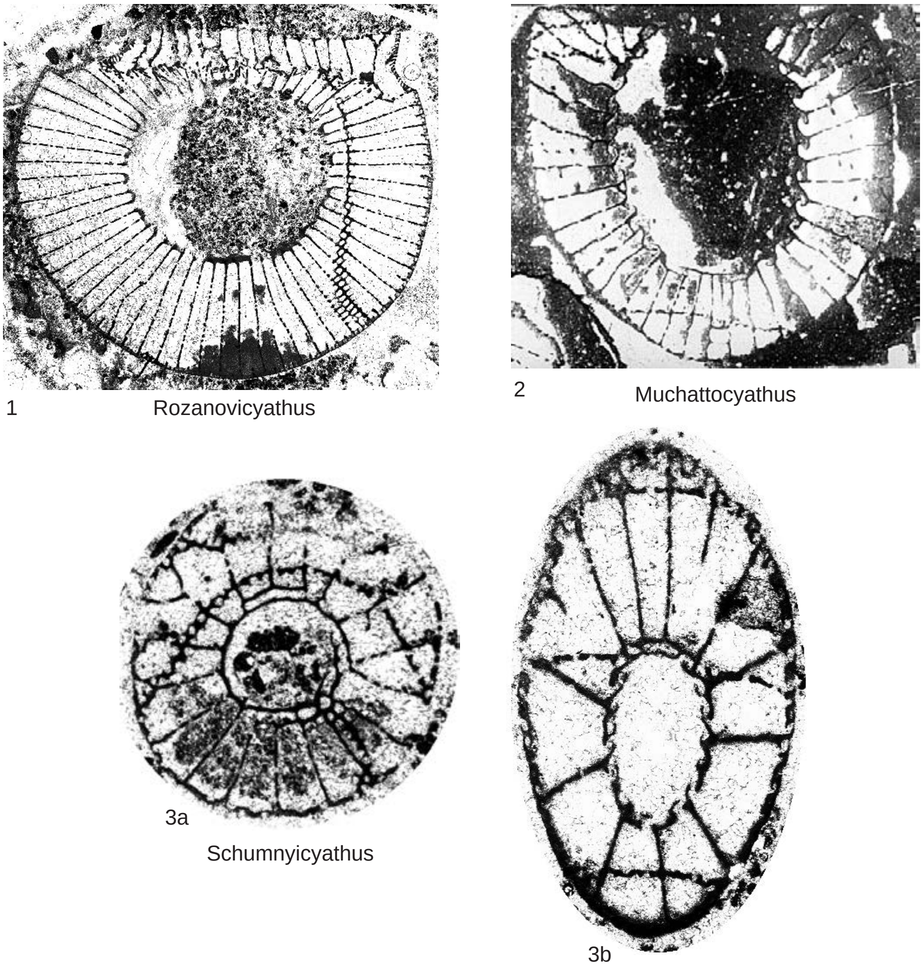
Inner wall with bracts or scales. *lower Cambrian (Bot.3).*

Mootwingeecyathus KRUSE, 1982, p. 195 [**M. mootwingeensis*; OD; holotype, KRUSE, 1982, fig. 20–21, pl. 15,*4–11*, AM F.83344, Sydney]. Inner wall with several rows of pores per intersept, bearing upwardly projecting, S-shaped scales; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* Australia.——FIG. 599*a–d*. **M. mootwingeensis*, Cymbric Vale Formation, Botoman, Mt. Wright, New South Wales, Australia, holotype, AM F.83344; *a,* oblique longitudinal section, AM FT.14162, ×8; *b,* detail of outer wall in tangential section, AM FT.8175, ×30; *c,* transverse section, AM FT.14163, ×7; *d,* detail of inner wall, transverse section, AM FT.14163, ×30 (Kruse, 1982).

Order PUTAPACYATHIDA Vologdin, 1961

[Putapacyathida VOLOGDIN, 1961, p. 177]

Intervallum with plate tabulae; redimiculi may be present on intervallum side of either or both walls. *lower Cambrian (Bot.1–Bot.3).*



1 Rozanovicyathus

2 Muchattocyathus

3a Schumnyicyathus

3b

FIG. 597. Rozanovicyathidae and Tatijanaecyathidae (p. 1017–1019).

Superfamily ALPHACYATHOIDEA R. Bedford & J. Bedford, 1939

[Alphacyathoidea R. BEDFORD & J. BEDFORD, 1939, p. 72, *nom. transl.* DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV & ROZANOV, 1989, p. 88, *ex* Alphacyathidae R. BEDFORD & J. BEDFORD, 1939, p. 72] [=Aptocyathacea KONYUSHKOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 102, *nom. nud., nom. transl.* ROZANOV, 1973, p. 85, *ex* Aptocyathidae KONYUSHKOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 102)]

Outer wall with simple pores. *lower Cambrian (Bot.1–Bot.3).*

Family ALPHACYATHIDAE R. Bedford & J. Bedford, 1939

[Alphacyathidae R. BEDFORD & J. BEDFORD, 1939, p. 72] [=Aptocyathidae KONYUSHKOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 102]

Inner wall with simple pores. *lower Cambrian (Bot.1–Bot.3).*

Alphacyathus R. BEDFORD & J. BEDFORD, 1939, p. 72 [**Dictyocyathus annularis* R. BEDFORD & W. R. BEDFORD, 1936, p. 13; OD; lectotype, R. BEDFORD & W. R. BEDFORD, 1936, fig. 55; ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, fig. 53; SD DEBRENNE, 1969a, p. 305, SAM P942, Adelaide; =*Dictyocyathus simplex* TAYLOR, 1910, p. 144; lectotype, TAYLOR, 1910, fig. 34; SD DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1638, SAM T1598A, B, Adelaide]. Inner wall with stirrup pores at each tabula and one file of simple, intertabular pores; tabulae with normal pores; longitudinal lintels form septumlike plates in some intertabulae. *lower Cambrian (Bot.3):* Australia.——FIG. 600,*1a–c*. **A. simplex* (TAYLOR), Ajax Limestone, Botoman, Ajax Mine, South Australia; *a,* lectotype, SAM T1598, longitudinal view, ×12; *b,* paralectotype, USNM PU86714, specimen 225, transverse view, ×12 (Debrenne,

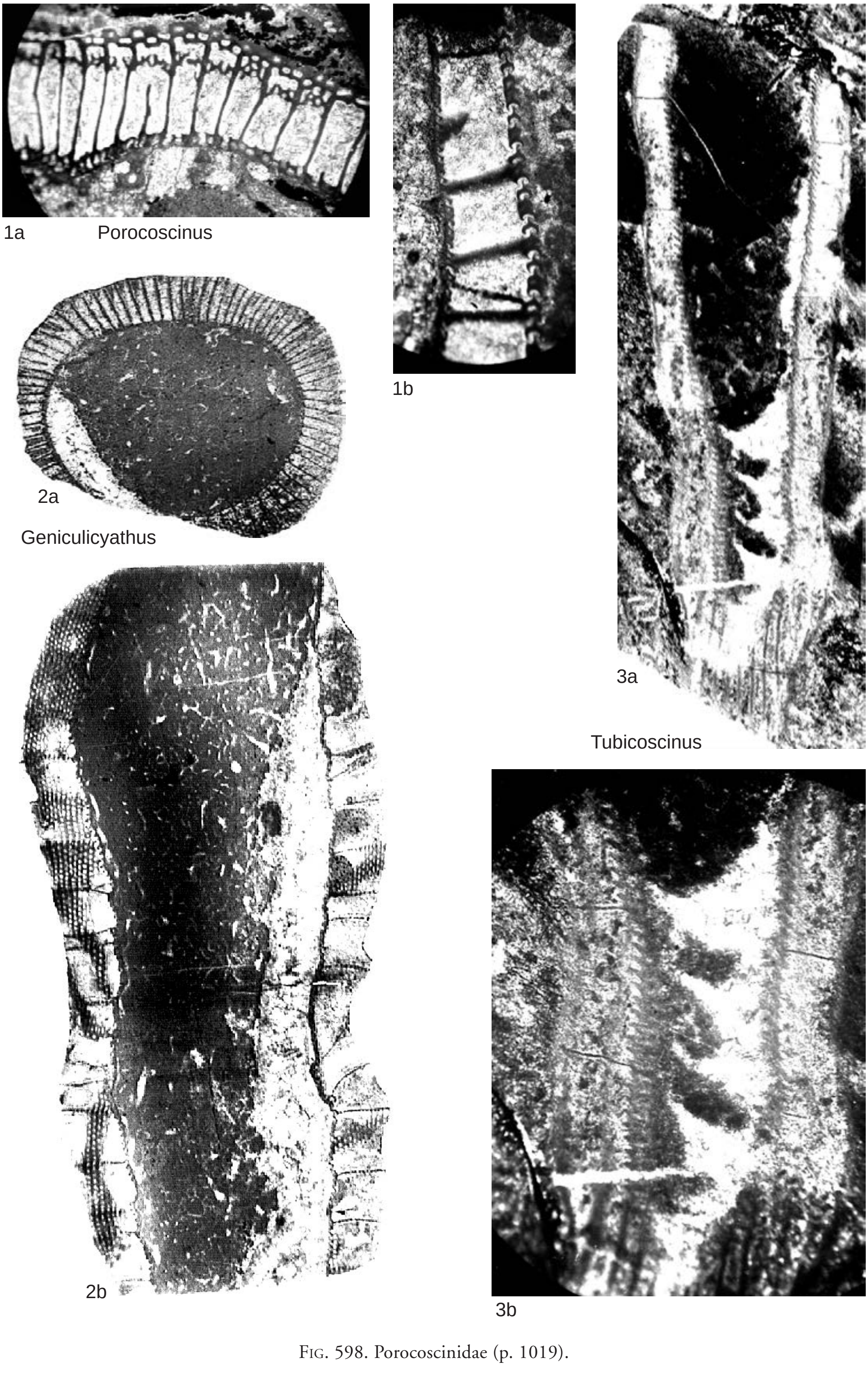


FIG. 598. Porocoscinidae (p. 1019).

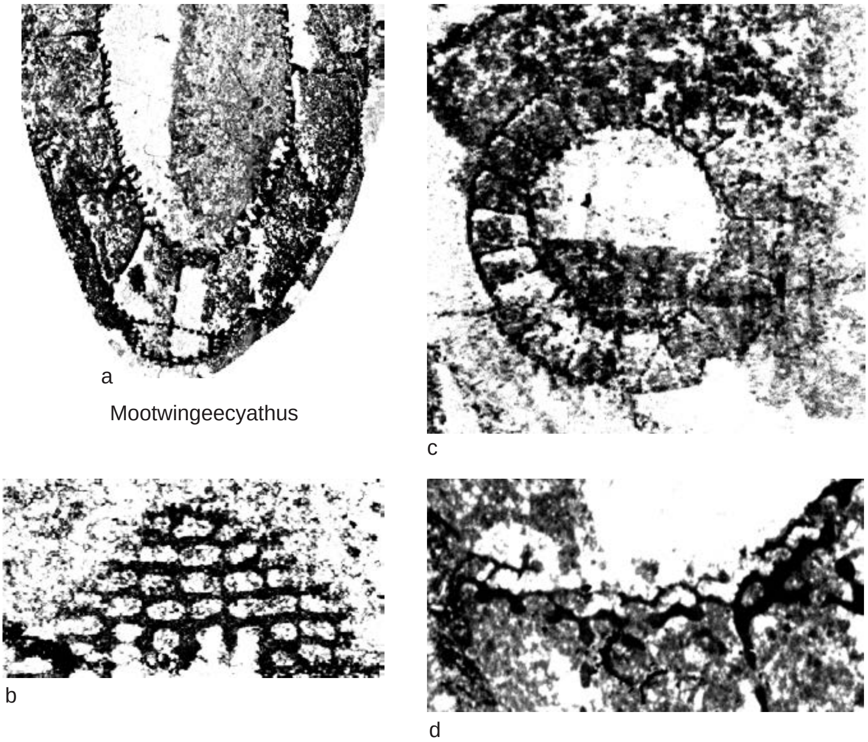


FIG. 599. Mootwingeecyathidae (p. 1019).

Zhuravlev, & Kruse, 2002); *c,* paralectotype, NHM S4822, longitudinal view, ×12 (Debrenne, Zhuravlev, & Kruse, 2012b).

Aptocyathus Vologdin, 1937b, p. 471 [**A. gordoni*; M; lectotype, SD Zhuravleva, Konyushkov, & Rozanov, 1964, p. 106, collection IK Bazhenova, specimen 28-4048, thin section 3/10, not located] [=*Aptocyathella* Konyushkov in Zhuravleva, Konyushkov, & Rozanov, 1964, p. 111 (type, *A. prima*, OD); =*Galinaecyathus* Konyushkov in Zhuravleva, Konyushkov, & Rozanov, 1964, p. 102 (type, *G. lebedensis*, OD); =*Arthrocyathus* Vologdin, 1977, p. 61 (type, *A. articulatus,* OD)]. Inner wall with several files of simple pores per intertabulum; tabulae with normal pores. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Urals, Australia, Iberia, Sardinia.——Fig. 600,*2a–b*. **A. gordoni*, Verkhnemonok Formation, Botoman, Sanashtykgol River, West Sayan, Altay Sayan, Russia; *a,* topotype, possibly of type series, PIN 4754/42, transverse section of modular skeleton, ×10 (Vologdin, 1940b); *b,* unlocated syntype, sketch of transverse and longitudinal sections of modular skeleton, ×10 (Vologdin, 1937b).

Superfamily PUTAPACYATHOIDEA R. Bedford & J. Bedford, 1936

[*nom. transl.* Debrenne, 1970a, p. 24, *ex* Putapacyathidae R. Bedford & J. Bedford, 1936, p. 24; *nom. correct.* Debrenne, Zhuravlev, & Kruse, 2002, p. 1638 (*pro* Putapacyathacea)]

Outer wall with attached microporous sheath. *Lower Cambrian (Bot.3).*

Family PUTAPACYATHIDAE R. Bedford & J. Bedford, 1936

[Putapacyathidae R. Bedford & J. Bedford, 1936, p. 24]

Inner wall with bracts or scales. *lower Cambrian (Bot.3).*

Putapacyathus R. Bedford & J. Bedford, 1936, p. 24 [**P. regularis*; OD; holotype, R. Bedford & J. Bedford, 1936, fig. 97; Zhuravleva, Konyushkov, & Rozanov, 1964, fig. 68; Hill, 1965, pl. 9,*1,* USNM PU86699-115, M, Washington, D.C.]. Inner wall with several files of

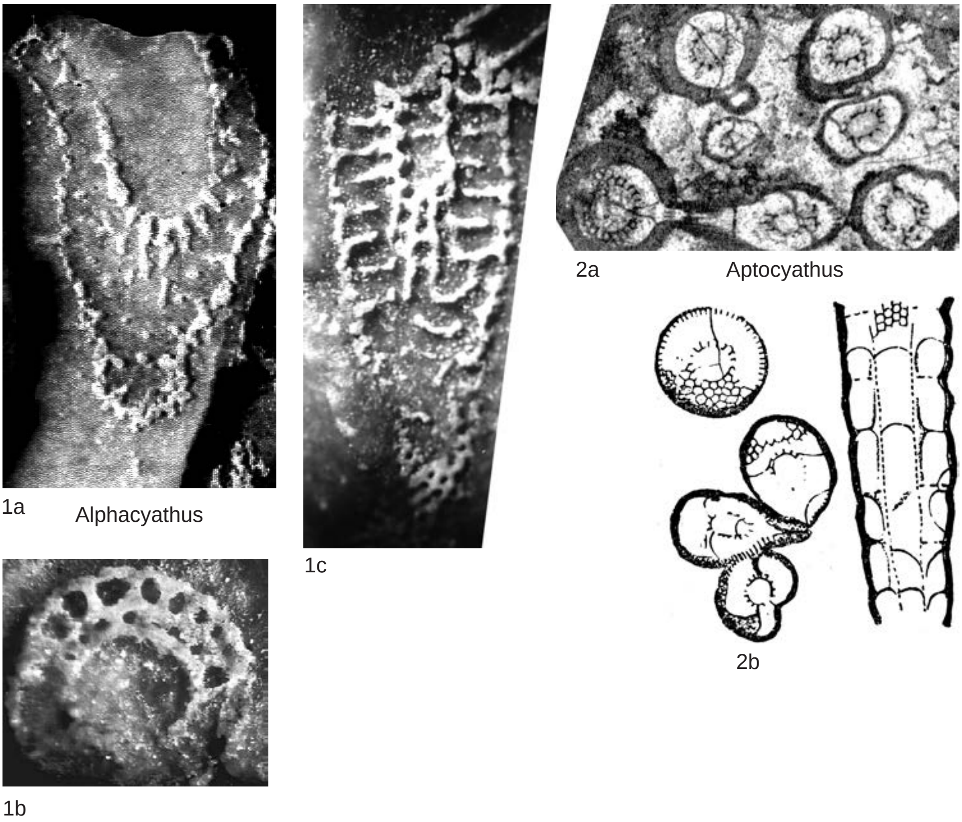


FIG. 600. Alphacyathidae (p. 1020–1022).

pores per intertabulum, bearing downwardly projecting cupped bracts; tabulae with normal pores; sporadic septa may be present. *lower Cambrian (Bot.3):* Australia.——FIG. 601*a–c.* **P. regularis*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, USNM PU86699-115; *a,* transverse view, ×6; *b,* oblique longitudinal view, ×6 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* internal longitudinal view of inner wall, ×4.5 (Hill, 1965).

Superfamily HUPECYATHOIDEA Debrenne, Rozanov, & Zhuravlev, 1990

[Hupecyathoidea DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 121]

Outer wall with canals. *lower Cambrian (Atd.4).*

Family HUPECYATHIDAE Debrenne, Rozanov, & Zhuravlev, 1990

[Hupecyathidae DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 121]

Inner wall with bracts or scales. *lower Cambrian (Atd.4).*

Hupecyathus DEBRENNE, 1964, p. 198 [**H. sphinctoides*; OD; holotype, DEBRENNE, 1964, pl. 15,*7*, MNHN M80258, specimen Ki135, Paris]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with several files of pores per intertabulum, bearing upwardly projecting, cupped bracts; tabulae with normal pores, linked by pillars. *lower Cambrian (Atd.4):* Morocco.——FIG. 602*a–b.* **H. sphinctoides*, Amouslek Formation, Atdabanian, Ouijane, holotype, MNHN M80258, specimen Ki135; *a,* transverse section, ×6; *b,* detail of longitudinal

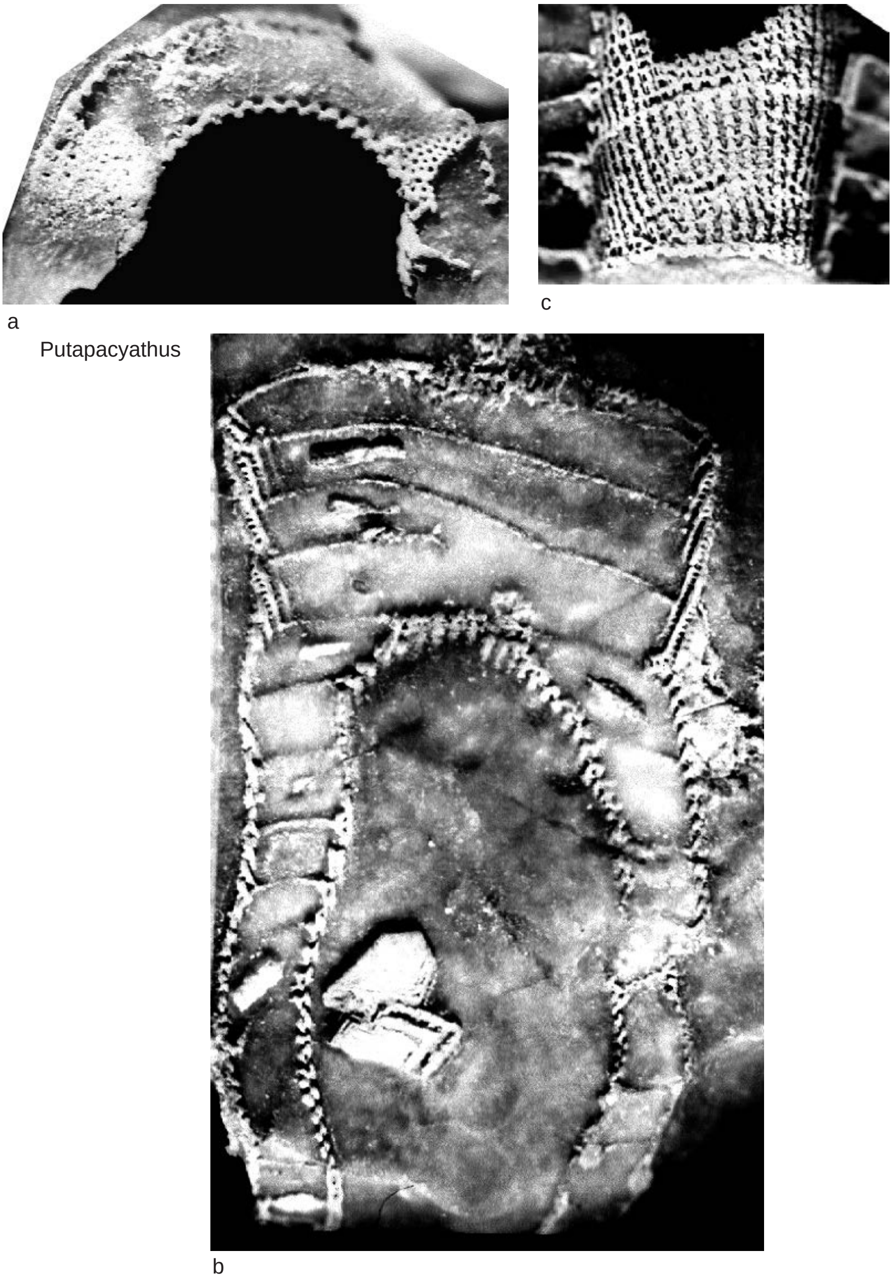


FIG. 601. Putapacyathidae (p. 1022–1023).

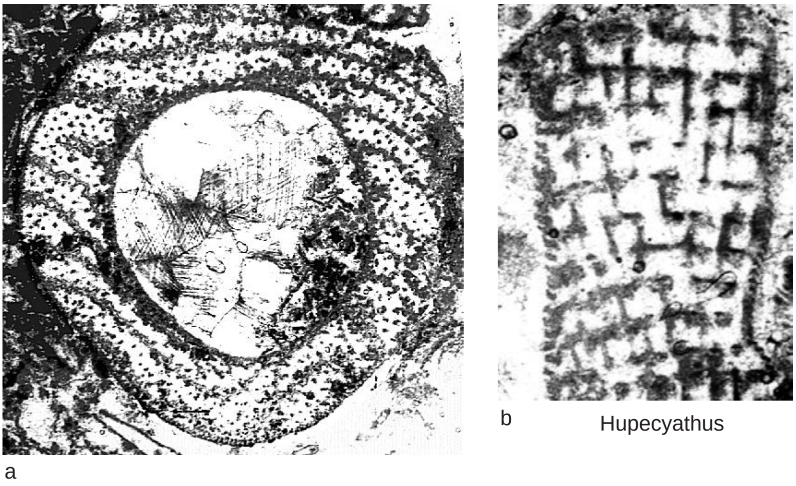


FIG. 602. Hupecyathidae (p. 1023–1025).

section (outer wall to right), ×13 (Debrenne, 1964).

Superfamily CHABAKOVICYATHOIDEA Rozanov, 2002

[Chabakovicyathoidea ROZANOV in DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1639] [=Chabakovicyathacea ROZANOV, 1973, p. 85, *nom. nud.*]

Outer wall pustular. *lower Cambrian (Bot.1).*

Family CHABAKOVICYATHIDAE Rozanov, 2002

[Chabakovicyathidae ROZANOV in DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1639] [=Chabakovicyathidae ROZANOV, 1973, p. 85, *nom. nud.*]

Inner wall with simple pores. *lower Cambrian (Bot.1).*

Chabakovicyathus KONYUSHKOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 114 [**C. tumulatus*; OD; holotype, ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 14,*6,* not located]. Inner wall with several files of simple pores per intertabulum; tabulae with normal pores. *lower Cambrian (Bot.1):* Urals.——FIG. 603*a–b*. **C. tumulatus*, Terekla Formation, Botoman, Terekla River, western flank of southern Urals, Russia; *a,* longitudinal section, specimen PIN 4327/80, ×16 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* holotype, oblique transverse section, ×28 (Zhuravleva, Konyushkov, & Rozanov, 1964).

Order CAPSULOCYATHIDA Zhuravleva, 1964

[*nom. transl.* ZHURAVLEV & ROZANOV in VORONOVA & others, 1987, p. 29, *ex* Capsulocyathina ZHURAVLEVA in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 59] [=Coscinocyathida ZHURAVLEVA, 1955a, p. 10; =Clavicyathida VOLOGDIN, 1977, p. 110]

Thalamid cup, single or multichambered; inner wall of invaginal type of development; septa and/or plate tabulae may be present in intervallum of multichambered cups. *lower Cambrian (Tom.1–Bot.3).*

Suborder CAPSULOCYATHINA Zhuravleva, 1964

[Capsulocyathina ZHURAVLEVA in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 59] [?=Uralocyathina DEBRENNE, 1964, p. 113]

Cup single chambered and subspherical, or multichambered without septa. *lower Cambrian (Tom.1–Bot.3).*

Family CRYPTOPOROCYATHIDAE Zhuravleva, 1960

[Cryptoporocyathidae ZHURAVLEVA, 1960b, p. 92] [=Cryptaporocyathidae ZHURAVLEVA, 1963b, p. 117, *nom. null.*; =Capsulocyathidae ZHURAVLEVA in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 60; =Gerbicanicyathidae BELYAEVA, 1969, p. 90; =Vasicyathidae VOLOGDIN, 1977, p. 104; =Clavicyathidae VOLOGDIN, 1977, p. 110; ?=Complicatocyathidae YAROSHEVICH, 1990, p. 23]

Outer wall with simple pores. *lower Cambrian (Tom.1–Bot.3).*

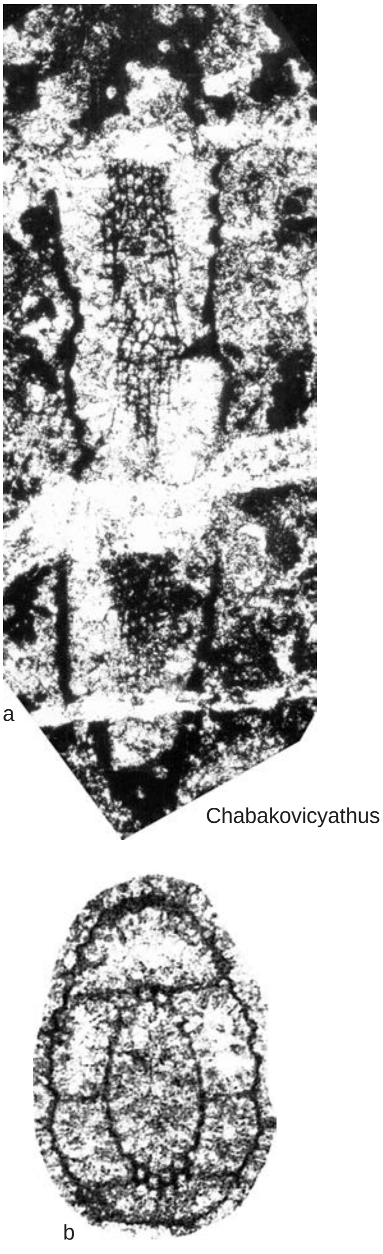


FIG. 603. Chabakovicyathidae (p. 1025).

Cryptoporocyathus ZHURAVLEVA, 1960b, p. 92 [**C. junicanensis*; OD; holotype, ZHURAVLEVA, 1960b, pl. 4,*9;* ZHURAVLEVA, 1963b, pl. 12,*3*, not located; paratype, TsSGM 205/6, Novosibirsk] [=*Cryptaporocyathus* ZHURAVLEVA, 1963b, p. 117, *nom. null.*]. Cup single chambered; outer wall pores of two distinct sizes; inner wall simple. *lower Cambrian (Tom.1–Tom.4):* Siberian Platform.——FIG. 604,*1a–b*. **C. junicanensis*; *a,* Medvezh'ya Formation, Tommotian, Moyero River, Krasnoyarsk region, Russia, holotype, oblique section, ×20; *b,* Pestrotsvet Formation, Tommotian, Aldan River, Sakha (Yakutia), Russia, paratype, TsSGM 205/6, section of outer wall (inner cavity at bottom), ×16 (Debrenne, Zhuravlev, & Kruse, 2002).

Capsulocyathus VOLOGDIN in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 61 (VOLOGDIN, 1962c, p. 75 [type, *C. capsulifer*, OD], *nom. nud.*, not described, figured or separately diagnosed until VOLOGDIN, 1977, p. 76, fig. 44, wherein a holotype was invalidly nominated from material other than type or topotype material) [**C. subcallosus* ZHURAVLEVA in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 62; OD; holotype, ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 1,*8(3),* TsSGM 283/5, Novosibirsk] [=*Capsulicyathus* VOLOGDIN, 1977, p. 75 (type, *C. capsulifer*, OD), *nom. van.*; =*Mesocyathus* VOLOGDIN, 1977, p. 95 (type, *M. plasticus*, OD); =*Vasicyathus* VOLOGDIN, 1977, p. 104 (type, *V. urniformis*, OD); =*Clavicyathus* VOLOGDIN, 1977, p. 110 (type, *C. clavellatus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 97; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 135]. Cup single chambered; outer and inner walls with simple pores. *lower Cambrian (Tom.3–Bot.3):* Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Urals, Morocco, Iberia, Sardinia.——FIG. 604,*2*. **C. subcallosus*, Bazaikha Formation, Atdabanian, Bazaikha River, East Sayan, Altay Sayan, Russia, holotype, TsSGM 283/5, longitudinal section, ×6 (Zhuravleva, Konyushkov, & Rozanov, 1964).

?**Complicatocyathus** YAROSHEVICH, 1990, p. 23 [**C. rozanovi*; OD; holotype, YAROSHEVICH, 1990, pl. 12,*1*, TsSGM 901/5a, Novosibirsk]. Cup with regular transverse folds affecting both walls, forming empty multichambered cups; outer and inner walls with simple pores. [Limited type material does not provide certainty as to whether cup is multichambered.] *lower Cambrian (Atd.2):* Altay Sayan.——FIG. 604,*3*. **C. rozanovi*, Gavrilovskoe Formation, Atdabanian, Gavrilovskoe, Salair, Russia, holotype, TsSGM 901/5a, longitudinal section, ×3 (Yaroshevich, 1990).

Gerbicanicyathus BELYAEVA, 1969, p. 90 [**G. emili*; OD; holotype, BELYAEVA, 1969, pl. 37,*1*, DVGU 55/68, Khabarovsk]. Cup multichambered; outer and inner walls with simple pores. *lower Cambrian (Bot.1–Bot.2):* Far East.——FIG. 605,*1*. **G. emili*, Ust'toka unit, Botoman, Gerbikan River, Dzhagdy Range, Far East, Russia, holotype, DVGU 55/68, oblique longitudinal section, ×8 (Belyaeva, 1969).

Mirandocyathus BELYAEVA, 1974, p. 121 [**M. artus*; OD; holotype, BELYAEVA, 1974, pl. 3,*8*, DVGU 13M/572/3, Khabarovsk]. Cup multichambered; outer wall with simple pores; inner wall with pores bearing downwardly projecting, cupped bracts.

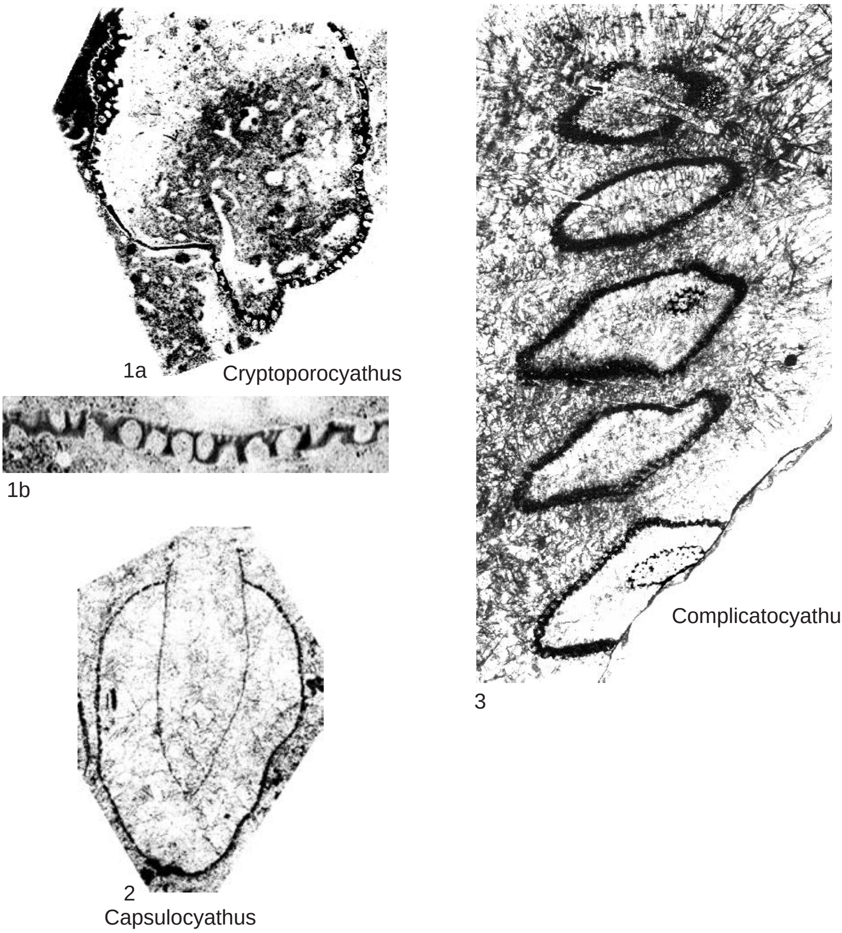


FIG. 604. Cryptoporocyathidae (p. 1026).

lower Cambrian (Bot.1): Far East.——FIG. 605,*2.* **M. artus*, Ust'toka unit, Botoman, Gerbikan River, Dzhagdy Range, Russia, holotype, DVGU 13M/572/3, longitudinal section, ×7 (Belyaeva, 1974).

Polythalamia DEBRENNE & WOOD, 1990, p. 436 [**P. americana*; OD; holotype, DEBRENNE & WOOD, 1990, fig. 1B, USNM 434924, specimen GA5.18F, Washington, D.C.]. Cup multichambered, globose chambers propagating linearly or glomerately; outer wall with few or no pores; inner wall with simple pores. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Tuva, Mongolia, United States.——FIG. 605,*3.* **P. americana*, Valmy Formation, Botoman, Galena Canyon, Nevada, United States, holotype, USNM 434924, specimen GA5.18F, longitudinal section, ×20 (Debrenne & Wood, 1990; ©Cambridge University Press).

Family URALOCYATHELLIDAE Zhuravleva, 1964

[Uralocyathellidae ZHURAVLEVA in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 72]

Outer wall with independent microporous sheath. *lower Cambrian (Bot.1).*

Rhabdolynthus ZHURAVLEVA, 1960b, p. 91 [**R. conicus*; OD; holotype, ZHURAVLEVA, 1960b, pl. 4,*8;* ZHURAVLEVA, 1963b, pl. 9,*11–12*, TsSGM 205/5, Novosibirsk] [=*Uralocyathella* ZHURAVLEVA in ZHURAVLEVA, KRASNOPEEVA, & CHERNYSHEVA, 1960, p. 99 (type, *U. repinae*, OD); =*Miricyathus* VOLOGDIN, 1977, p. 88 (type, *M. aseptatus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 127; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 157]. Cup single chambered; outer wall with independent microporous sheath; inner wall with simple pores. *lower Cambrian*

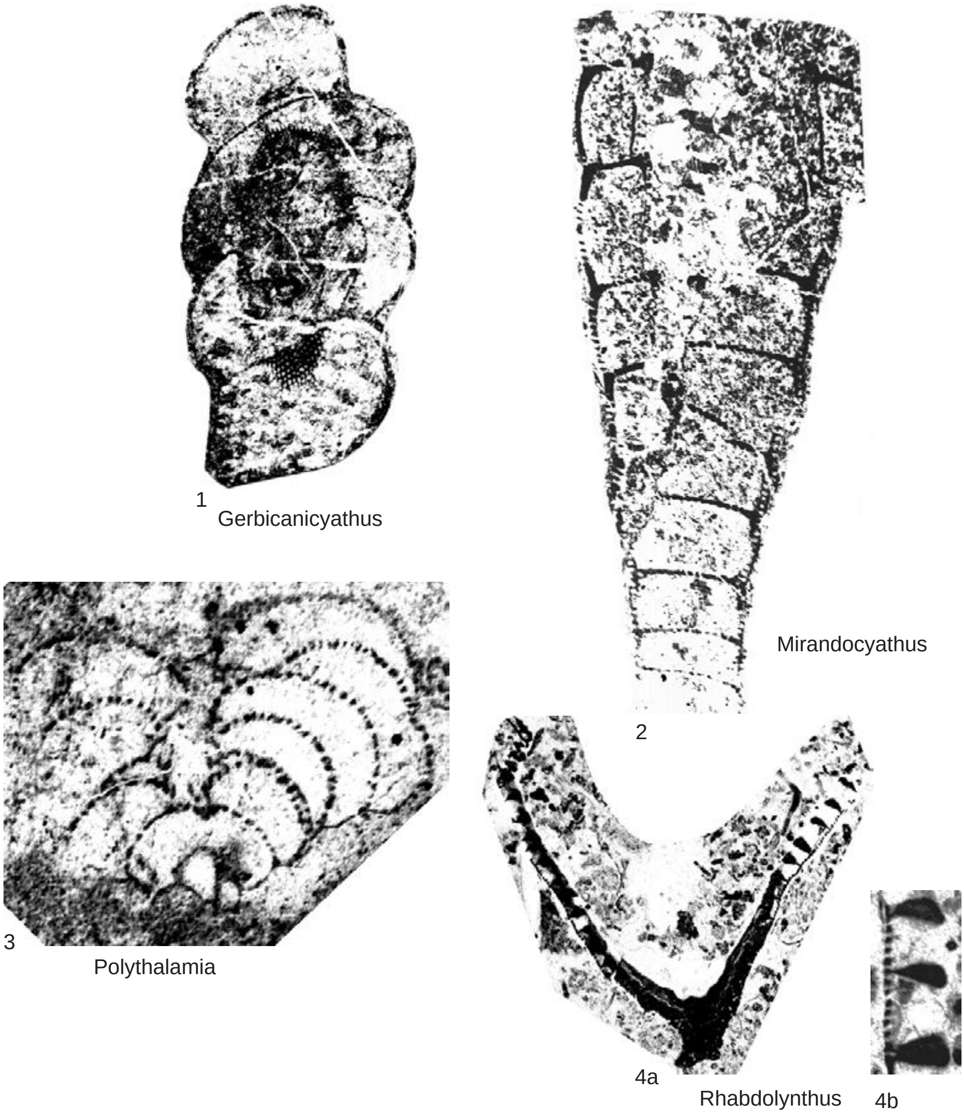


FIG. 605. Cryptoporocyathidae and Uralocyathellidae (p. 1026–1028).

(Bot.1): Siberian Platform, Altay Sayan.——FIG. 605,*4a–b*. **R. conicus*, Perekhod Formation, Botoman, Atdaban, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 205/5; *a,* longitudinal section, ×4; *b,* detail of wall in longitudinal section (inner cavity to right), ×7.5 (Zhuravleva, 1963b).

Family TYLOCYATHIDAE Zhuravlev, 1988

[Tylocyathidae ZHURAVLEV, 1988, p. 106]

Outer wall with attached microporous sheath. *lower Cambrian (Tom.4–Bot.3).*

Tylocyathus VOLOGDIN, 1977, p. 102 (VOLOGDIN in VOLOGDIN & YAZMIR, 1966, p. 948, *nom. nud.*) [**T. inaequilateralis;* OD; holotype, VOLOGDIN, 1977, pl. 1,*7*, PIN 1924-41, Moscow; =*Uralocyathella bullata* ZHURAVLEVA in MUSATOV & others, 1961, p. 19; OD; holotype, MUSATOV & others, 1961, pl. 1,*7*, TsSGM 264/7, Novosibirsk]. Cup single chambered; outer wall with attached microporous sheath, each micropore bearing a supplementary bract; inner wall with simple pores. *lower Cambrian (Bot.1–Bot.3):* Altay Sayan, Far East.——FIG. 606,*1*. **T. bullatus* (ZHURAVLEVA), Balakhtinson Formation, Botoman, Kazyr River, East Sayan, Altay Sayan, Russia, holotype,

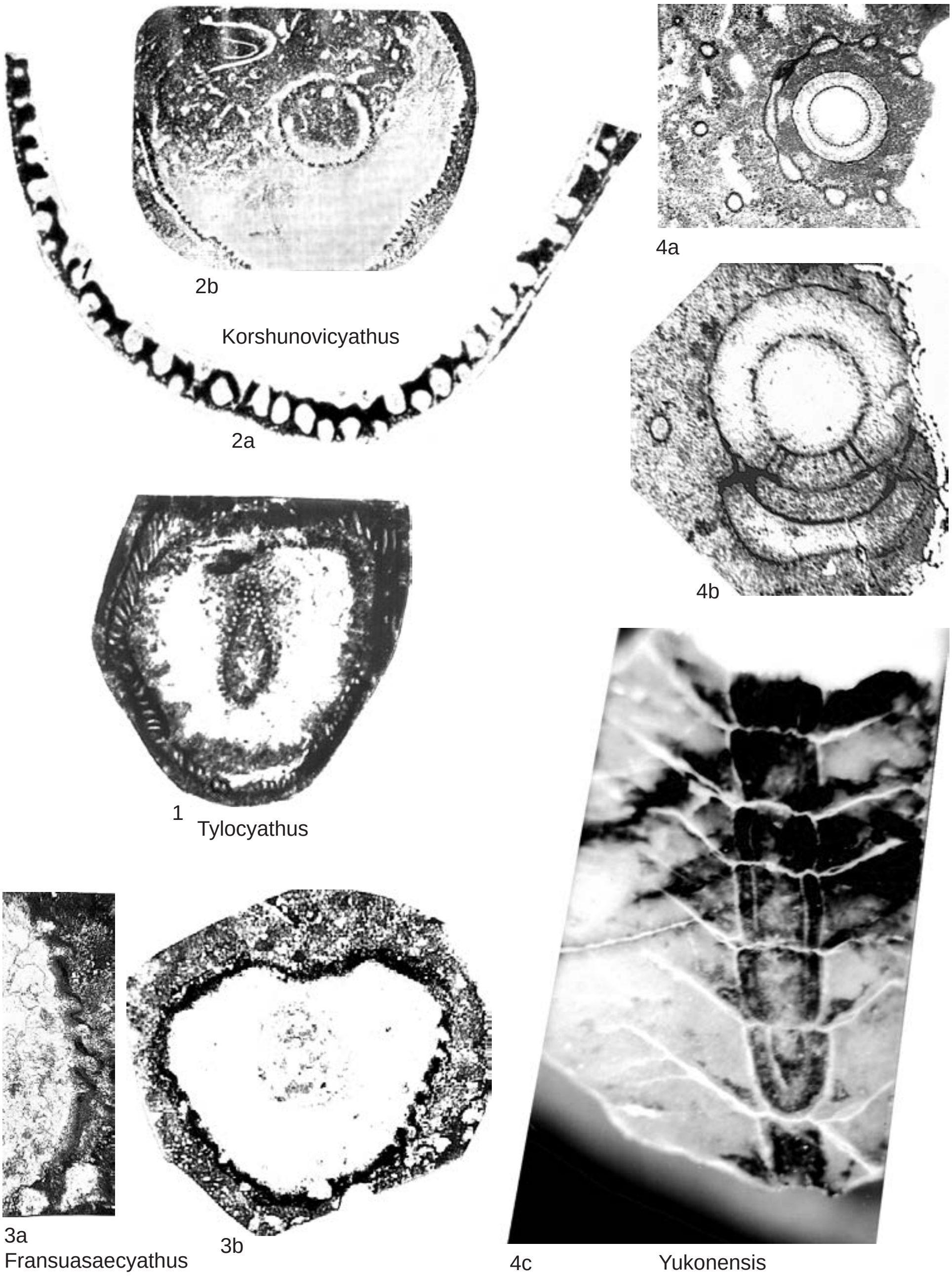


FIG. 606. Tylocyathidae and Fransuasaecyathidae (p. 1028–1030).

TsSGM 264/7, oblique longitudinal section, ×5.5 (Musatov & others, 1961).

Korshunovicyathus Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1988, p. 99 [**Cryptaporocyathus melnikovi* Korshunov & Zhuravleva, 1967, p. 5; OD; holotype, Korshunov & Zhuravleva, 1967, pl. 1,*1*, TsSGM 247/1, Novosibirsk]. Cup single chambered; outer wall with attached microporous sheath; inner wall with simple pores. *lower Cambrian (Tom.4–Atd.1):* Siberian Platform.——Fig. 606,*2a–b*. **K. melnikovi* (Korshunov & Zhuravleva); *a,* Tyuser Formation, Atdabanian,

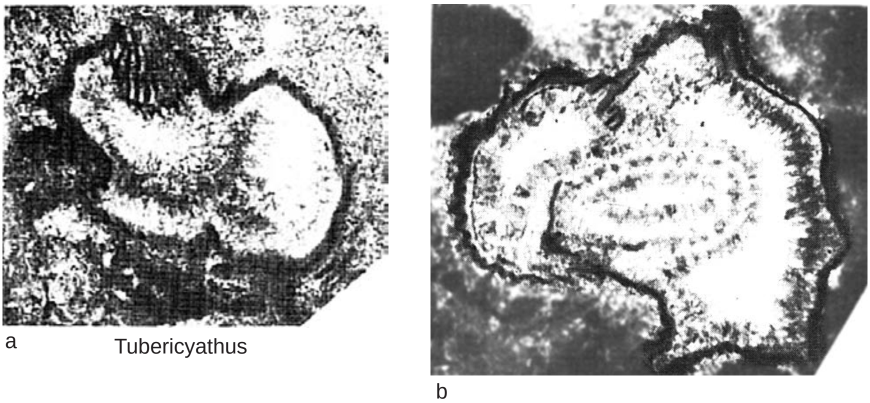


Fig. 607. Tubericyathidae (p. 1030).

Ulakhan-Ald'arkhay Creek, Lena River, Tuora-Sis Range, Sakha (Yakutia), Russia, holotype, TsSGM 247/1, detail of transverse section, ×20 (Korshunov & Zhuravleva, 1967); *b,* Pestrotsvet Formation, Atdabanian, Isit', Lena River, Sakha (Yakutia), Russia, specimen PIN 4220/117, transverse section, ×8 (Debrenne, Zhuravlev, & Rozanov, 1988).

Family FRANSUASAECYATHIDAE
Debrenne, 1964

[Fransuasaecyathidae Debrenne, 1964, p. 113] [=Acanthopyrgidae Handfield, 1971, p. 31]

Outer wall with simple tumuli. *lower Cambrian (Atd.1–Bot.3).*

Fransuasaecyathus Zhuravleva, 1960b, p. 103 [**F. subtumulatus*; OD; holotype, Zhuravleva, 1960b, pl. 5,*5*, TsSGM 205/10, Novosibirsk] [=*Bullicyathus* Vologdin, 1977, p. 105 (type, *B. pyxidatus*, OD); =*Marginicyathus* Vologdin, 1977, p. 107 (type, *M. cardiosimilis*, OD)]. Cup single chambered; outer wall with simple tumuli; inner wall with simple pores. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Mongolia, Transbaikalia, Far East.——Fig. 606,*3a–b*. **F. subtumulatus*, Perekhod Formation, Atdabanian, Yudyay, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 205/10; *a,* detail of wall in oblique longitudinal section, ×20; *b,* oblique longitudinal section, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

Yukonensis Özdikmen, 2009, p. 216, *nom. nov. pro Acanthopyrgus* Handfield, 1967, p. 209, *non* Descamps & Wintrebert, 1966, p. 28 (type, *Geloius finoti* Bolivar, 1905, p. 285, OD), insect [**Acanthopyrgus yukonensis* Handfield, 1967, p. 209; OD; holotype, Handfield, 1967, pl. 23,*1,4*, GSC 21059, Ottawa]. Cup multichambered with a tabula of rods linked by synapticulae and an external thorny corolla at each chamber junction; outer wall with simple tumuli; inner wall with simple pores. *lower Cambrian (Bot.1):* Canada, United States.——Fig. 606,*4a–c*. **Y. yukonensis* (Handfield); *a–b,* Adams Argillite, Botoman, Tatonduk River, Alaska, United States; *a,* transverse section, locality USGS 5156-CO (A1), collection not located, ×6 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* transverse section, locality USGS 5156-CO (A4), collection not located, ×10 (Nitecki & Debrenne, 1979); *c,* Sekwi Formation, Botoman, Mackenzie Mountains, Yukon Territory, Canada, holotype, GSC 21059, longitudinal section, ×4.5 (Debrenne, Zhuravlev, & Kruse, 2012b).

Family TUBERICYATHIDAE
Debrenne, Rozanov, & Zhuravlev, 1989

[Tubericyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989, p. 89] [=Tubericyathidae Vologdin, 1977, p. 31, *nom. nud.*]

Outer wall with bracts or scales. *lower Cambrian (Bot.1).*

Tubericyathus Vologdin, 1977, p. 90 [**T. clathratus*; OD; holotype, Vologdin, 1977, fig. 57, pl. 13,*9*, PIN 1924/38, Moscow] [=*Arminocyathus* Vologdin, 1977, p. 113 (type, *A. fungiformis*, OD)]. Cup single chambered; outer wall with pores bearing upwardly projecting, cupped bracts; inner wall with simple pores. *lower Cambrian (Bot.1):* Altay Sayan, Mongolia.——Fig. 607*a–b*. **T. clathratus*, Usa Formation, Botoman, Sukhie Solontsy Valley, Batenev Range, Kuznetsk Alatau, Russia; *a,* holotype, PIN 1924/38, oblique longitudinal section, ×10; *b,* paratype, PIN 1924/39, oblique transverse section, ×10 (Vologdin, 1977).

Suborder COSCINOCYATHINA
Zhuravleva, 1955

[*nom. transl.* Zhuravleva, 1960b, p. 245, *ex* order Coscinocyathida Zhuravleva, 1955a, p. 25]

Cup multichambered; intervallum with septa. *lower Cambrian (Atd.1–Bot.3).*

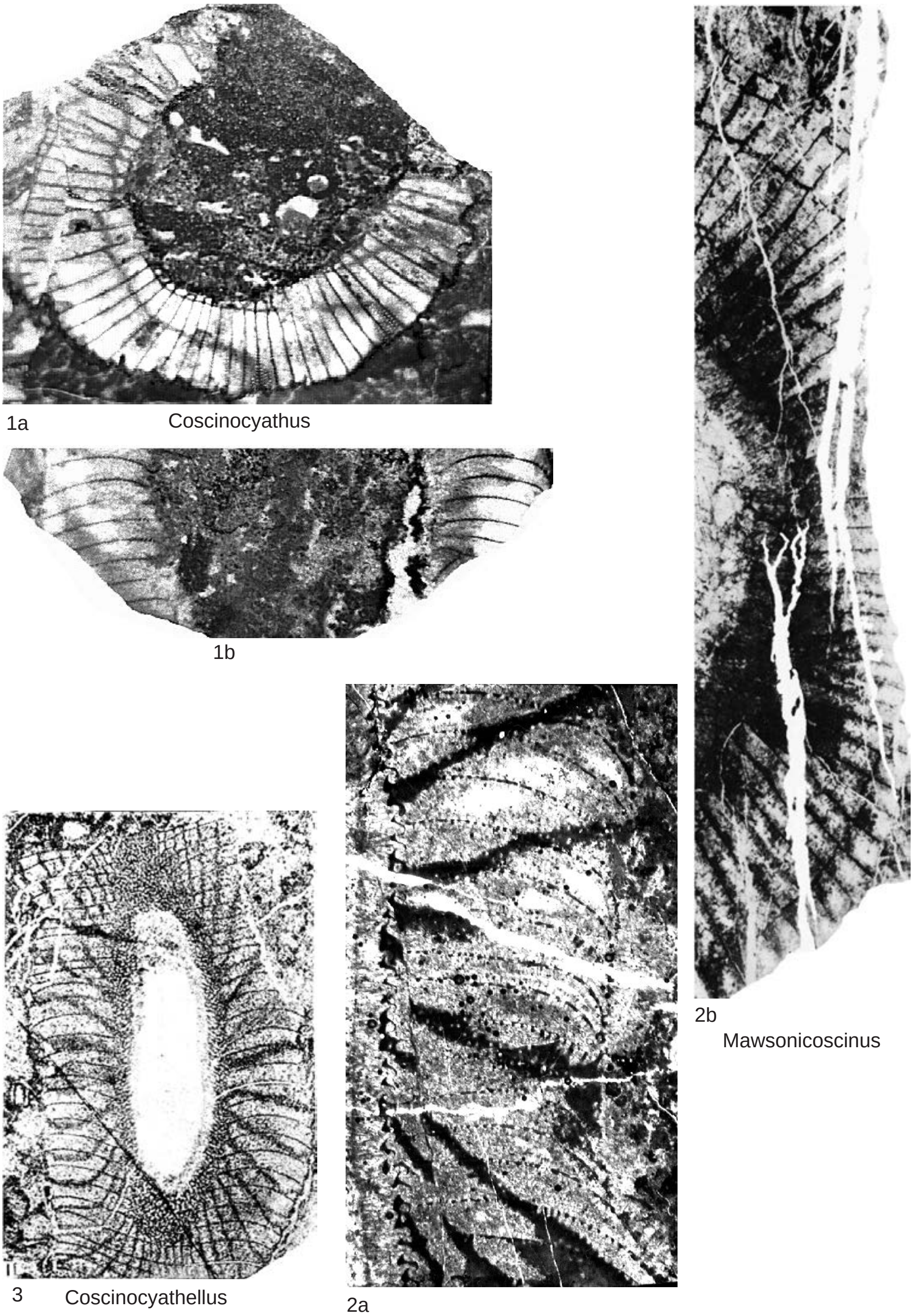


FIG. 608. Coscinocyathidae, Mawsonicoscinidae, and Coscinocyathellidae (p. 1032).

Superfamily COSCINOCYATHOIDEA Taylor, 1910

[*nom. correct.* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 89, *pro* Coscinocyathacea ZHURAVLEVA, 1960b, p. 245, *nom. transl. ex* Coscinocyathidae TAYLOR, 1910, p. 137] [=Mawsonicoscinoidea DEBRENNE & KRUSE, 1986, p. 258]

Outer wall tabular with simple pores. *lower Cambrian (Atd.2–Bot.3).*

Family COSCINOCYATHIDAE Taylor, 1910

[Coscinocyathidae TAYLOR, 1910, p. 137] [=Poletaevacyathidae VOLOGDIN, 1962a, p. 125].

Inner wall with simple pores. *lower Cambrian (Atd.2–Bot.3).*

Coscinocyathus BORNEMANN, 1884, p. 704 [**C. dianthus*; SD by exercise of ICZN plenary powers by MELVILLE, 1974, p. 155, following application by DEBRENNE, 1970b, p. 207, negating SD of *C. tuba* BORNEMANN, 1884, p. 704 by TING, 1937, p. 360 (now type of *Tubicoscinus* DEBRENNE in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 137); lectotype, BORNEMANN, 1886, pl. 17,*2–7;* DEBRENNE, 1964, pl. 21,*1–2;* SD DEBRENNE, 1964, p. 169, GML An597, Halle] [=*Poletaevacyathus* VOLOGDIN, 1959b, p. 88 (type, *P. obrutchevi*, M)]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.2–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Tajikistan, Morocco, Iberia, Sardinia.——FIG. 608,*1a–b*. **C. dianthus*, Matoppa Formation, Botoman, Canal Grande, Sardinia, Italy, lectotype, GML An597; *a,* transverse section, ×4; *b,* longitudinal section, ×4 (Bornemann, 1886).

Family MAWSONICOSCINIDAE Debrenne & Kruse, 1986

[Mawsonicoscinidae DEBRENNE & KRUSE, 1986, p. 258]

Inner wall with noncommunicating canals. *lower Cambrian (Bot.3).*

Mawsonicoscinus DEBRENNE & KRUSE, 1986, p. 259 [**M. sigmoides*; OD; holotype, DEBRENNE & KRUSE, 1986, fig. 22, GNS MG513, Lower Hutt]. Inner wall with one row of horizontal to upwardly projecting, S-shaped canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.3):* Antarctica, ?Falkland Islands (allochthonous).——FIG. 608,*2a–b*. **M. sigmoides*, Shackleton Limestone, Holyoake Range, Nimrod Glacier, holotype, GNS MG513; *a,* longitudinal section (outer wall to right), ×3.5; *b,* transverse section, ×3.5 (Debrenne & Kruse, 1986).

Family COSCINOCYATHELLIDAE Zhuravleva, 1956

[Coscinocyathellidae ZHURAVLEVA in VOLOGDIN, 1956, p. 879]

Inner wall with communicating canals. *lower Cambrian (Bot.1–Bot.3).*

Coscinocyathellus VOLOGDIN, 1940b, p. 91 (VOLOGDIN, 1937b, p. 471, *nom. nud.*) [**C. parvus*; OD; lectotype, VOLOGDIN, 1940b, pl. 29,*1;* SD ZHURAVLEV, 2001a, p. 92, PIN 4754/4, Moscow]. Inner wall with several rows of horizontal to upwardly projecting, straight to waved canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1–Bot.3):* Altay Sayan.——FIG. 608,*3*. **C. parvus*, Verkhnemonok Formation, Botoman, Sanashtykgol River, West Sayan, Russia, lectotype, PIN 4754/4, oblique longitudinal section, ×8 (Vologdin, 1940b).

Superfamily CALYPTOCOSCINOIDEA Debrenne, 1964

[*nom. correct.* DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 89, *pro* Calyptocoscinacea DEBRENNE, 1964, p. 115]

Outer wall tabular with independent microporous sheath. *lower Cambrian (Atd.1–Bot.1).*

Family TOMOCYATHIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Tomocyathidae DEBRENNE, ROZANOV, & ZHURAVLEV in DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 89]

Inner wall with simple pores. *lower Cambrian (Atd.1–Atd.3).*

Coscinocyathella VOLOGDIN, 1959b, p. 87–88 (VOLOGDIN, 1957d, p. 699, *nom. nud.*) [**C. nikitini*; M; holotype, VOLOGDIN, 1957d, fig. 1(11), PIN 1800/1,1a, M, Moscow] [=*Tomocyathus* ROZANOV, 1960a, p. 664 (type, *T. operosus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 100; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 138]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.1–Atd.3):* Altay Sayan, Tuva, Mongolia.——FIG. 609*a–b*. **C. nikitini*, Usa Formation, Atdabanian, Kiya River, Kuznetsk Alatau, Russia, holotype, PIN 1800/1,1a; *a,* transverse section, ×4; *b,* longitudinal section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Family CALYPTOCOSCINIDAE Debrenne, 1964

[Calyptocoscinidae DEBRENNE, 1964, p. 115]

Inner wall with independent microporous sheath. *lower Cambrian (Bot.1).*

Calyptocoscinus Debrenne, 1964, p. 196 [**Coscinocyathus cornucopiae* Bornemann, 1884, p. 704; OD; lectotype, Bornemann, 1886, pl. 16,*1;* SD Debrenne, 1964, p. 196, GML block B, Halle, requires restudy]. Inner wall with several rows of pores per intersept and independent microporous sheath; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Sardinia.——Fig. 610*a–e*. **C. cornucopiae* (Bornemann), Matoppa Formation, Botoman, Monte Gloria, Canal Grande, Italy, topotype, MNHN M84106; *a,* oblique transverse section, ×6; *b,* transverse section, ×5; *c,* detail of inner wall, longitudinal section (central cavity to right), ×30; *d,* detail of transverse section (outer wall at bottom), ×10; *e,* longitudinal section, ×5 (Debrenne, 1964).

Superfamily ALATAUCYATHOIDEA

Zhuravleva, 1955

[*nom. correct.* Debrenne, Zhuravlev, & Rozanov, 1989, p. 89, *pro* Alataucyathacea Zhuravleva, 1960b, p. 264, *nom. transl. ex* Alataucyathidae Zhuravleva, 1955b, p. 626] [=Mrassocyathoidea Vologdin in Zhuravleva, Krasnopeeva, & Chernysheva, 1960, p. 130, *nom. correct.* Debrenne, Zhuravlev, & Rozanov, 1989, p. 85, *pro* Mrassucyathacea Zhuravleva & Rozanov in Repina & others, 1964, p. 230, *nom. transl. ex* Mrassocyathidae Vologdin in Zhuravleva, Krasnopeeva, & Chernysheva, 1960, p. 130, as Mrassucyathidae *nom. null.*]

Outer wall tabular with multiperforate tumuli. *lower Cambrian (Atd.1–Atd.2).*

Family ALATAUCYATHIDAE

Zhuravleva, 1955

[Alataucyathidae Zhuravleva, 1955b, p. 626] [=Mrassocyathidae Vologdin, 1956, p. 879, *nom. nud.*; =Alataucyathinae Zhuravleva, 1955b, p. 626, *nom. transl.* Zhuravleva, 1960b, p. 264, *ex* Alataucyathidae Zhuravleva, 1955b, p. 626; =Mrassocyathidae Vologdin in Zhuravleva, Krasnopeeva, & Chernysheva, 1960, p. 130, *nom. correct.* Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989, p. 86 *pro* Mrassucyathidae Vologdin in Zhuravleva, Krasnopeeva, & Chernysheva, 1960, p. 130]

Inner wall with simple pores. *lower Cambrian (Atd.1–Atd.2).*

Alataucyathus Zhuravleva, 1955b, p. 626 [**A. jaroschevitschi*; OD; holotype, Zhuravleva, 1955b, fig. 1a, 2g–d, PIN 1040, Moscow, not located] [=*Mrassocyathus* Krasnopeeva in Vologdin, 1956, p. 879, *nom. nud.*; =*Mrassocyathus* Krasnopeeva, 1960, p. 43 (type, *M. micropora*, OD); =*Mrassucyathus* Krasnopeeva in Zhuravleva, Krasnopeeva, & Chernysheva, 1960, p. 130 (type, *M. schoriensis*, OD), *nom. null.*]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Atd.1–Atd.2):* Altay Sayan, Tuva, Mongolia.——Fig. 611*a–b*. **A. jaroschevitschi*; *a,* Usa Formation, Atdabanian, Mt. Martyukhina, Kuznetsk Alatau, Russia, holotype, PIN 1040, oblique longitudinal section, ×4; *b,* Usa Formation, Atdabanian, Sukhie Solontsy Valley, Batenev Range, Kuznetsk Alatau, Russia, unlocated specimen, neither holding institution nor collection number known, transverse section, ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

Fig. 609. Tomocyathidae (p. 1032).

Superfamily CLATHRICOSCINOIDEA

Rozanov, 1964

[*nom. correct.* Zhuravlev, 1988, p. 105, *pro* Clathricoscinacea Debrenne, 1964, p. 115, *nom. transl. ex* Clathricoscinidae Rozanov in Repina & others, 1964, p. 223]

Outer wall tabular and pseudoclathrate. *lower Cambrian (Bot.1–Toy.1).*

Family CLATHRICOSCINIDAE

Rozanov, 1964

[Clathricoscinidae Rozanov in Repina & others, 1964, p. 223]

Inner wall with simple pores. *lower Cambrian (Bot.1–Toy.1).*

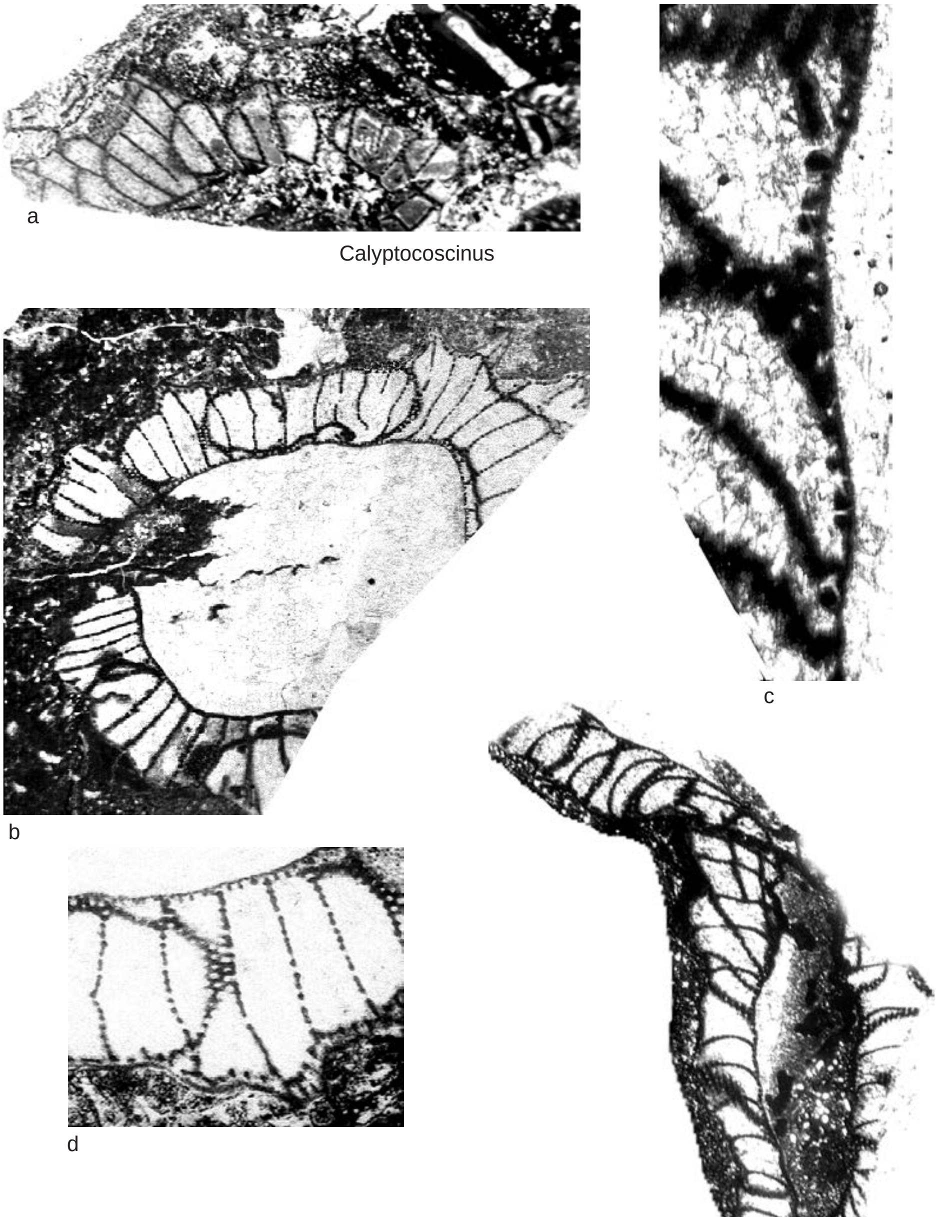


FIG. 610. Calyptocoscinidae (p. 1033).

Clathricoscinus ZHURAVLEVA, 1955b, p. 627 [**Coscinocyathus infirmus* VOLOGDIN in ZHURAVLEVA, 1955b, p. 627; OD; holotype, ZHURAVLEVA, 1955b, fig. 2a, PIN 1040, Moscow; collection not located] [=*Asterocyathellus* VOLOGDIN, 1962a, p. 126 (type, *A. compositus*, OD), for discussion, see DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 99; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 136]. Inner wall with several rows of simple pores per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1–Toy.1):* Kolyma, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, South China.——Fig. 612,*1a–b*. **C. infirmus* (Vologdin), Usa Formation, Botoman, Bol'shaya Erba, Batenev Range, Kuznetsk Alatau, Russia, syntype, PIN 1040; *a,* transverse section, ×10; *b,* tangential section of outer wall (at top), ×10 (Debrenne, Zhuravlev, & Kruse, 2002).

Family LANICYATHIDAE Debrenne, Rozanov, & Zhuravlev, 1989

[Lanicyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989, p. 90]

Inner wall with noncommunicating canals. *lower Cambrian (Bot.1).*

Lanicyathus Belyaeva in Belyaeva & others, 1975, p. 87 [**L. albus*; OD; holotype, Belyaeva & others, 1975, pl. 19,*3;* pl. 37,*2–3*, PIN DVIMS5157/6, Moscow]. Inner wall with several rows of horizontal to upwardly projecting, straight to waved canals per intersept; septa completely porous; tabulae with normal pores. *lower Cambrian (Bot.1):* Far East.——Fig. 612,*2a–b*. **L. albus*, Ust'toka unit, Botoman, Lan River, Dzhagdy Range, Far East, Russia, holotype, PIN DVIMS5157/6; *a,* longitudinal section, ×7; *b,* transverse section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Order ARCHAEOCYATHIDA Okulitch, 1935

[*nom. correct.* Zhuravleva, 1955a, p. 11, *pro* order Archaeocyathina Okulitch, 1935b, p. 90] [=Anthomorphida Okulitch, 1935b, p. 90, *nom. correct.* Okulitch, 1955a, p. 18, *pro* order Anthomorphina Okulitch, 1935b, p. 90; =Syringocnemidida Okulitch, 1935b, p. 90, *nom. correct.* Debrenne, 1964, p. 117, *pro* order Syringocnemina Okulitch, 1935b, p. 90; =Spirocyathida R. Bedford & W. R. Bedford, 1936, p. 13, *nom. correct.* Hill, 1972, p. 103, *pro* order Spirocyathina R. Bedford & W. R. Bedford, 1936, p. 13; =Metacyathida R. Bedford & W. R. Bedford, 1936, p. 16, *nom. correct.* Okulitch, 1955a, p. 14, *pro* order Metacyathina R. Bedford & W. R. Bedford, 1936, p. 16; =order Dictyocyanthina (*sic*) R. Bedford & J. Bedford, 1937, p. 37, *nom. nud.,* proposed conditionally; =Archaeosyconida Zhuravleva, 1955a, p. 12; =superorder Loculicyathina Zhuravleva, 1955a, p. 9, *nom. transl.* Vologdin, 1962a, p. 118, ex order Loculicyathida Zhuravleva, 1955a, p. 9, *nom. correct.* Vologdin, 1961, p. 178, *pro* Loculocyathida Zhuravleva, 1955a, p. 9, invalid name based on *nom. null.*; =Rhizacyathida Zhuravleva, 1955b, p. 629, for discussion, see Hill, 1972, p. 103, 133; =Bicyathida Vologdin, 1956, p. 878; =Syringocnematida Zhuravleva in Zhuravleva, Krasnopeeva, & Chernysheva, 1960, p. 139; =Thalassocyathida Vologdin, 1961, p. 177; =Tersiida Vologdin, 1961, p. 181; =superorder Bicyathina Vologdin, 1962a, p. 117; =Archaeopharetrida Debrenne, 1970a, p. 25; =Metaldetida Debrenne, 1970a, p. 25; =Paranacyathida Debrenne, 1970a, p. 25; =Paracoscinida Debrenne, 1970a, p. 25, for discussion, see Debrenne & Zhuravlev, 1992b, p. 111; =Metacoscinida Debrenne, 1974a, p. 187]

Cup two walled, of solitary or low- to high-modular organization, with septal type of development; inner wall of centripetal type; intervallum with taeniae, pseudosepta, pseudotaenial network, dictyonal network, calicles, or syringes; segmented or independent (membrane and plate) tabulae may be present. *lower Cambrian (Tom.1–Toy.3), middle Cambrian, upper Cambrian (Furongian).*

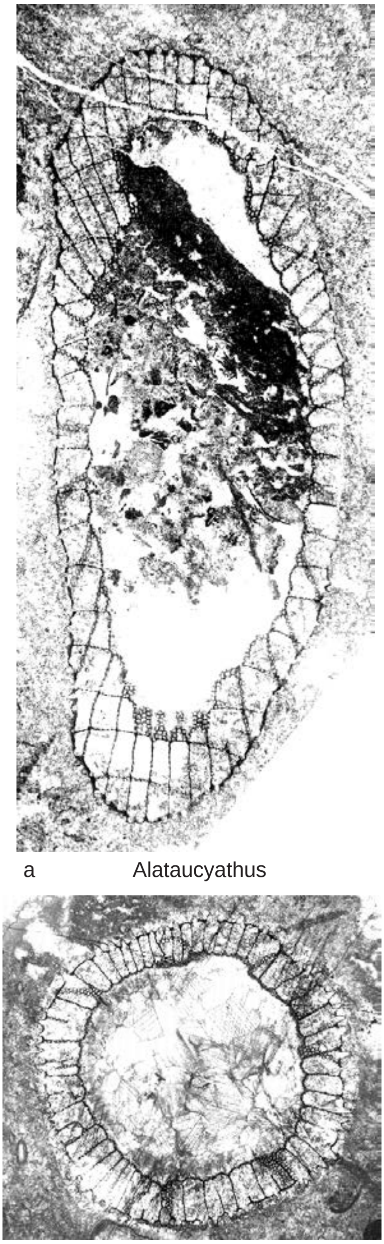


Fig. 611. Alataucyathidae (p. 1033).

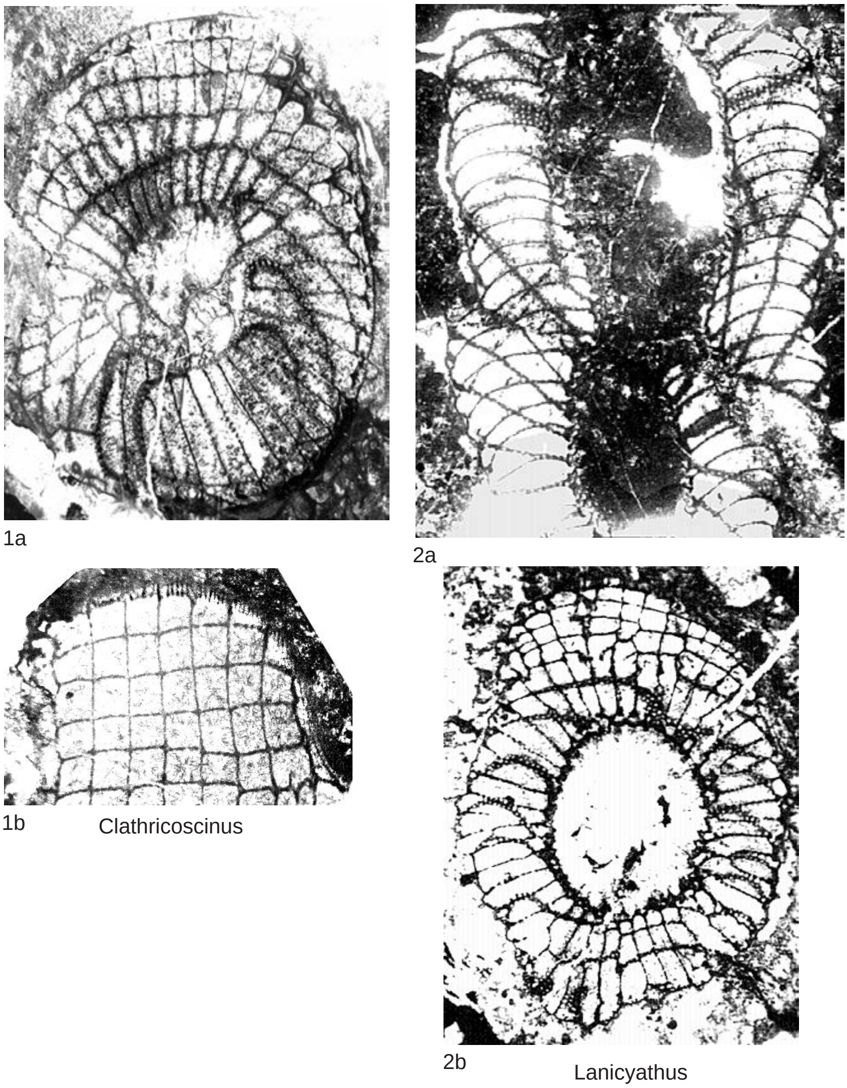


FIG. 612. Clathricoscinidae and Lanicyathidae (p. 1034–1035).

Suborder LOCULICYATHINA Zhuravleva, 1955

[*nom. transl.* DEBRENNE, 1991, p. 219, *ex* superorder Loculicyathina ZHURAVLEVA, 1955a, p. 9, *nom. transl.* VOLOGDIN, 1962a, p. 118, *ex* order Loculicyathida VOLOGDIN, 1961, p. 178, *nom. correct. pro* Loculocyathida ZHURAVLEVA, 1955a, p. 9, invalid name based on *nom. null.*]

Cup modular (pseudocolonies formed by interparietal budding) or rarely solitary; intervallum with pseudosepta; synapticulae and plate tabulae may be present. *lower Cambrian (Tom.1–Bot.3), upper Cambrian (Furongian).*

Superfamily LOCULICYATHOIDEA Zhuravleva, 1954

[*nom. transl. et correct.* DEBRENNE & ZHURAVLEV, 1992b, p.112, *ex* Loculocyathidae ZHURAVLEVA, 1954, p. 27, invalid name based on *nom. null.*]

Outer wall simple, with pores of cambroid type. *lower Cambrian (Tom.1–Bot.3); upper Cambrian (Furongian).*

Family LOCULICYATHIDAE Zhuravleva, 1954

[*nom. correct.* Zhuravleva, 1960b, p.107, *pro* Loculocyathidae Zhuravleva, 1954, p. 27, invalid name based on *nom. null.*] [=Robustocyathidae Debrenne, 1964, p. 113; =Paranacyathidae Debrenne, 1970a, p. 38, *nom. nud.*; =Ardrossacyathidae Gravestock, 1984, p. 109]

Inner wall with simple pores. *lower Cambrian (Tom.1–Bot.3), upper Cambrian (Furongian).*

Loculicyathus Vologdin, 1931, p. 54 (Vologdin, 1928, p. 30, *nom. nud.*) [**L. tolli*; M; lectotype, Vologdin, 1931, pl. 19,*1;* SD Debrenne, Zhuravlev, & Kruse, 2002, p. 1651, TsNIGRm 58a/2956, St. Petersburg] [=*Loculocyathus* Vologdin, 1937b, p. 468, *nom. null.*]. Inner wall with one row of simple pores per intersept; pseudosepta finely porous. *lower Cambrian (Atd.2–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Urals, Australia, Iberia, Sardinia, United States, Mexico.——Fig. 613,*1a–b*. **L. tolli*, Torgashino Formation, Atdabanian, Kameshki, East Sayan, Altay Sayan, Russia; *a,* lectotype, TsNIGRm 58a/2956, transverse section, ×8.5; *b,* paralectotype, TsNIGRm 57a/2956, longitudinal section, ×6 (Vologdin, 1931).

?Antarcticocyathus Debrenne, Rozanov, & Webers, 1984, p. 298 [**A. webersi*; OD; holotype, Debrenne, Rozanov, & Webers, 1984, fig. 5.1–5.2, 6.3, USNM 333901, specimen Ant-1, Washington, D.C.]. Outer wall pores in irregular, undulating quasitransverse (or less commonly quasilongitudinal) rows over entire wall plate; inner wall with one row of simple pores per intersept; pseudosepta coarsely porous. [Genus is otherwise typical of suborder, but bears a continuous outer wall of distinctive porosity, the appropriate taxonomic treatment of which is uncertain.] *upper Cambrian (Furongian: Paibian):* Antarctica.——Fig. 613,*2a–b*. **A. webersi*, Minaret Formation, Springer Peak, Heritage Range, Ellsworth Mountains, Antarctica; *a,* holotype, USNM 333901, specimen Ant-1, longitudinal section, ×4.5 (Debrenne, Rozanov, & Webers, 1984); *b,* paratype, USNM 333906, specimen Ant-2, oblique transverse section, ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

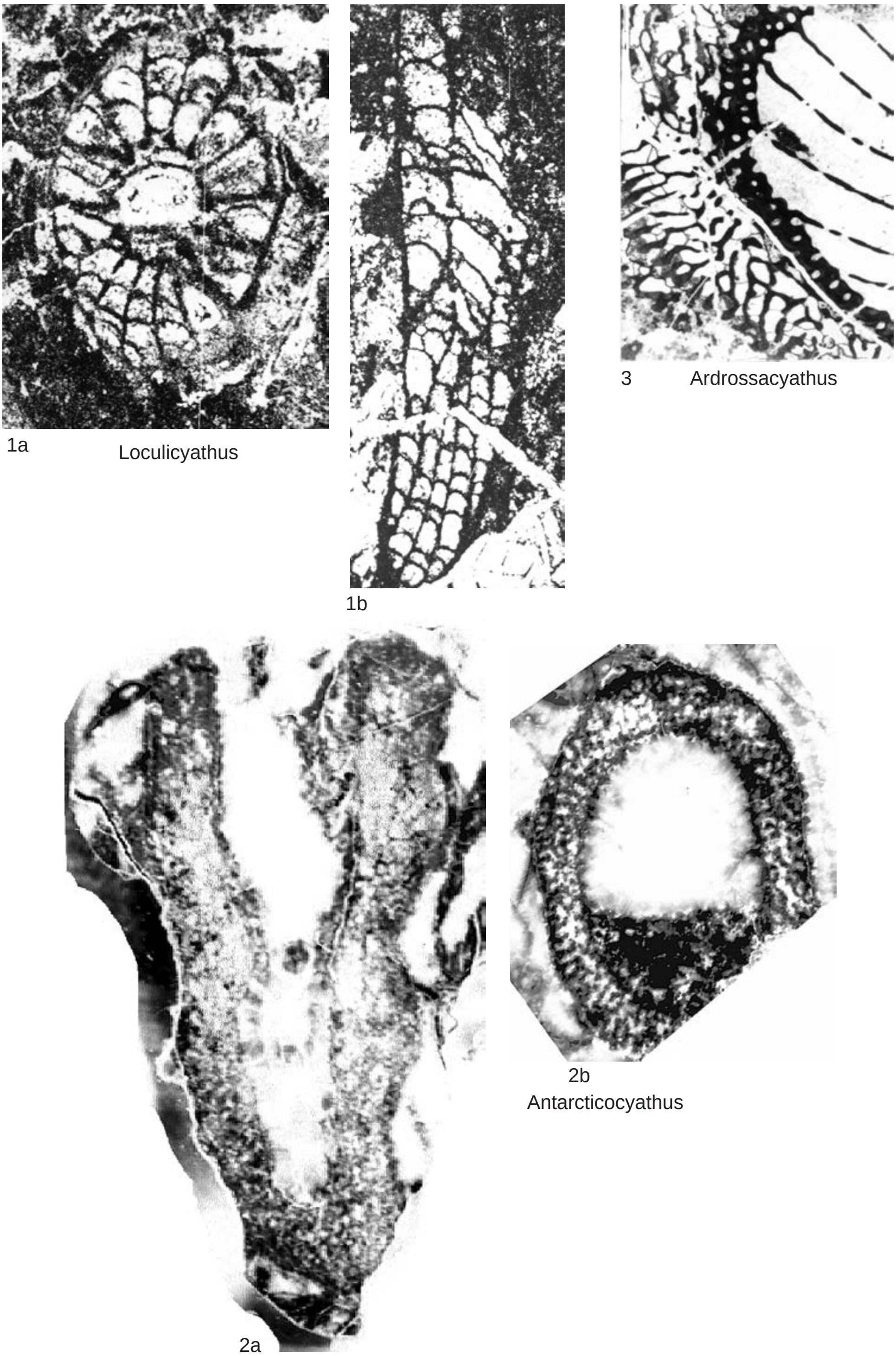
Ardrossacyathus R. Bedford & J. Bedford, 1937, p. 31 [**A. endotheca*; OD; holotype, R. Bedford & J. Bedford, 1937, fig. 125, M, USNM PU86766, specimen 354, Washington, D.C.] [=*Metaldetimorpha* R. Bedford & J. Bedford, 1937, p. 31 (type, *M. yorkei*, OD), for discussion, see Zhuravlev & Gravestock, 1994, p. 31; =*Dzhagdycyathus* Belyaeva in Belyaeva & others, 1975, p. 102 (type, *D. crinitus*, OD); =*Egiinocyathus* Fonin, 1983, p. 12 (type, *E. ornatus*, OD), for discussion, see Debrenne & Zhuravlev, 1992b, p. 121; Zhuravlev & Gravestock, 1994, p. 31]. Inner wall with several rows of simple pores per intersept; pseudosepta finely porous. *lower Cambrian (Bot.1–Bot.3):* Mongolia, Far East, Australia.——Fig. 613,*3*. **A. endotheca*, Botoman, Parara Limestone, Ardrossan, South Australia, Australia, topotype, SAM P32041, tangential section of outer wall, ×7 (Zhuravlev & Gravestock, 1994).

Cambrocyathellus Zhuravleva, 1960b, p. 284 [**C. tschuranicus*; OD; holotype, Zhuravleva, 1960b, pl. 28,*3*, PIN 1161, Moscow, not located] [=*Robustocyathus* Zhuravleva, 1960b, p. 133 (type, *Archaeocyathus robustus* Vologdin, 1937a, p. 25, OD); =*Ramuscyathus* (*Ramuscyathus*) Fonin in Voronin & others, 1982, p. 101 (type, *Loculocyathus tuberculatus* Vologdin, 1940a, p. 87, OD; =*R. (R.) artus* Fonin in Voronin & others, 1982, p. 102); =*Ramuscyathus* (*Parvuscyathus*) Fonin in Voronin & others, 1982, p. 103 (type, *R. (P.) pannonicus*, OD), for discussion, see Debrenne & Zhuravlev, 1992b, p. 122]. Outer wall pores restricted to interseptal areas; inner wall with one row of simple pores per intersept; pseudosepta coarsely porous. *lower Cambrian (Tom.1–Atd.4):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Far East, Kazakhstan, Australia.——Fig. 614,*1a–b*. **C. tschuranicus*, Pestrotsvet Formation, Tommotian; *a,* Churan, Lena River, Sakha (Yakutia), Russia, holotype, PIN 1161, transverse section, ×5.5; *b,* Krestyakh, Lena River, Sakha (Yakutia), Russia, specimen PIN 1161, longitudinal section of modular skeleton (outer wall to right), ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

Mikhnocyathus Maslov, 1957, p. 307 [**M. zolaensis*; OD; lectotype, Maslov, 1957, fig. 2; Debrenne & Zhuravlev, 1992b, pl. 5,*6;* SD Debrenne & Zhuravlev, 1992b, pl. 5, fig. 6 caption, PIN 2038(1), Moscow] [=*Zolacyathus* Vologdin, 1962d, p. 10 (type, *Z. loculosus*, M)]. Inner wall with several rows of simple pores per intersept; pseudosepta coarsely porous; rare plate tabulae. *lower Cambrian (Atd.2–Atd.3):* Altay Sayan, Tuva, Mongolia, Transbaikalia, ?Sardinia.——Fig. 614,*2a–b*. **M. zolaensis*, Bystraya Formation, Atdabanian, Zola Valley, Transbaikalia, Russia, lectotype, PIN 2038(1); *a,* transverse section, ×3.5; *b,* longitudinal section, ×3.5 (Maslov, 1957).

Neoloculicyathus Voronin, 1974, p. 134 [**N. primus*; OD; holotype, Voronin, 1974, pl. 6,*4;* Voronin, 1979, pl. 12,*5;* Debrenne & Zhuravlev, 1992b, pl. 1,*5*, PIN 2742/4, Moscow]. Inner wall with several rows of simple pores per intersept; pseudosepta coarsely porous. *lower Cambrian (Atd.1–Bot.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Urals, Australia, Morocco, Iberia, Germany.——Fig. 614,*3a–b*. **N. primus*, Bazaikha Formation, Atdabanian, Bazaikha River, East Sayan, Altay Sayan, Russia; *a,* paratype, PIN 2742/3, longitudinal section, ×6; *b,* holotype, PIN 2742/4, longitudinal section, ×4 (Voronin, 1974).

Okulitchicyathus Zhuravleva, 1960b, p. 281 [**Ajacicyathus discoformis* Zhuravleva in Zhuravleva & Zelenov, 1955, p. 68; OD; holotype, Zhuravleva & Zelenov, 1955, pl. 1,*1*, PIN 100(1), Moscow, not located] [=*Lermontovaecyathus* Korshunov, 1972, p. 59 (type, *L. isiti*, OD; =*Ajacicyathus discoformis* Zhuravleva in Zhuravleva & Zelenov, 1955, p. 68, for discussion, see Debrenne & Zhuravlev, 1992b, p. 128); =*Alconeracyathus*



1a Loculicyathus

1b

3 Ardrossacyathus

2a

2b Antarcticocyathus

FIG. 613. Loculicyathidae (p. 1037).

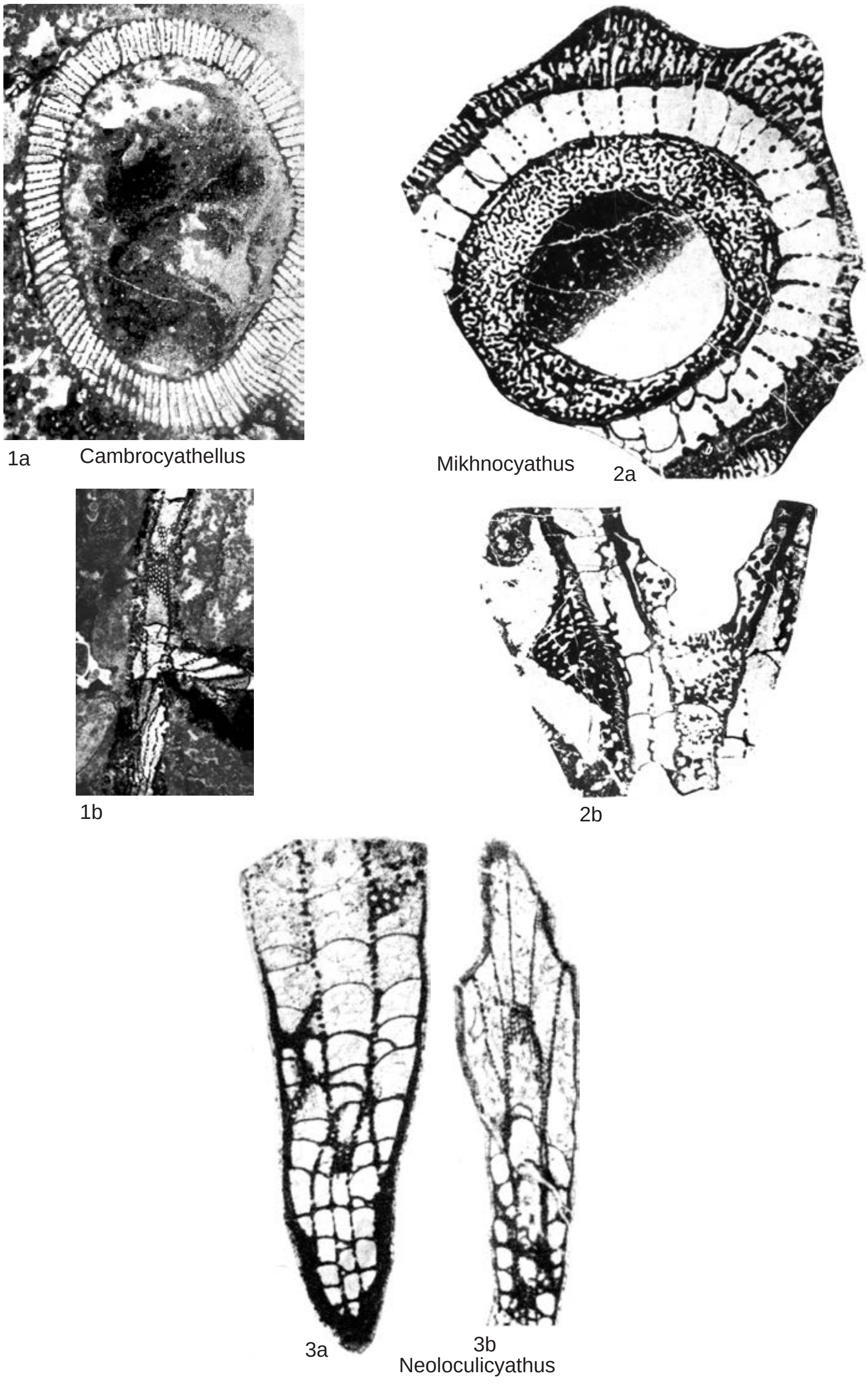


FIG. 614. Loculicyathidae (p. 1037).

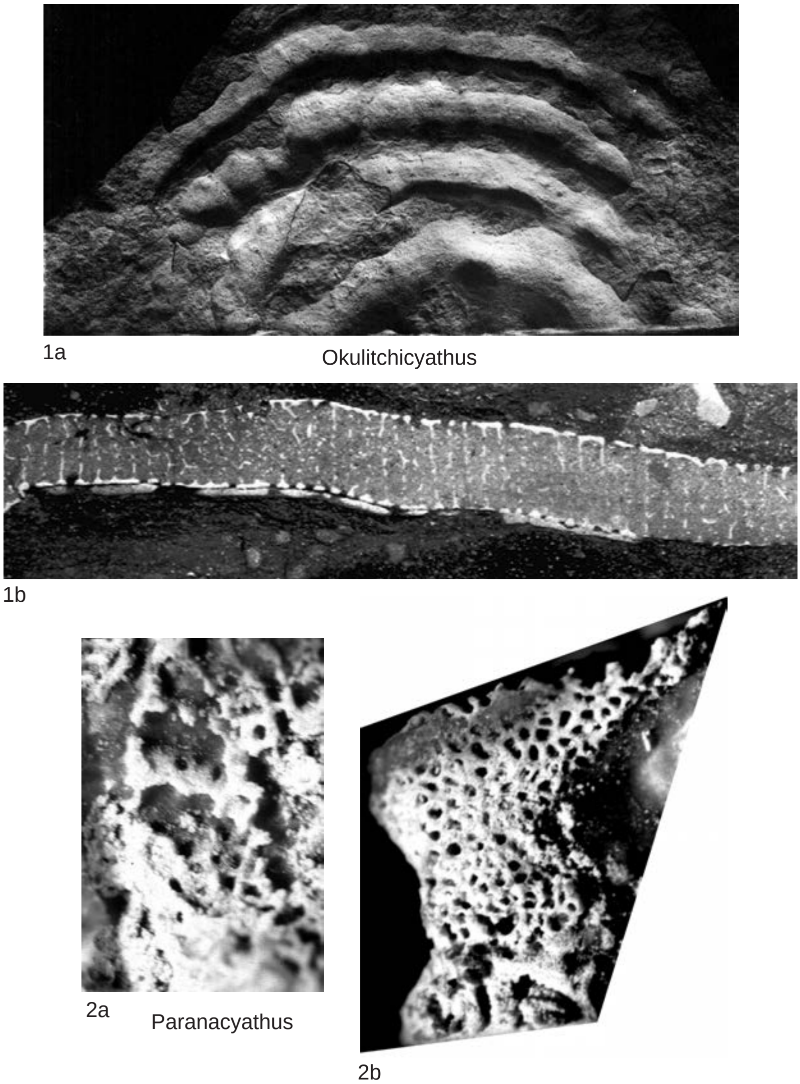


FIG. 615. Loculicyathidae (p. 1037–1041).

PEREJÓN, 1973, p. 185 (type, *A. melendezi*, OD; =*Archaeocyathellus (Archaeofungia) andalusicus* SIMON, 1939, p. 76); =*Andalusicyathus* PEREJÓN in DEBRENNE, 1975, p. 352, *nom. nud.*; =*Andalusicyathus* PEREJÓN, 1976, p. 17 (type, *Archaeocyathellus (Archaeofungia) andalusicus* SIMON, 1939, p. 76, OD); =*Urdacyathus* PEREJÓN & MORENO, 1978, p. 201 (type, *U. pradoanus*, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 119]. Inner wall with several rows of simple pores per intersept; pseudosepta coarsely porous; plate tabulae and synapticulae may be present. *lower Cambrian (Tom.1–Atd.4):* Siberian Platform, Mongolia, Kazakhstan, ?Australia, Iberia.——FIG. 615,*1a–b*. **O. discoformis* (ZHURAVLEVA), Pestrotsvet Formation, Tommotian; *a,* Aldan River, Sakha (Yakutia), Russia, specimen PIN 1162, external view, ×0.6 (Zhuravleva, 1960b); *b,* Churan-Zhurinskiy Mys area, Lena River, Sakha (Yakutia), Russia, specimen MNHN M810058, transverse section (outer wall at top), ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Paranacyathus R. BEDFORD & J. BEDFORD, 1937, p. 34, *nom. nov. pro Paracyathus* R. BEDFORD & W. R. BEDFORD, 1936, p. 17, *non* MILNE-EDWARDS & HAIME, 1848, p. 318 (type, *P. procumbens*, SD MILNE-EDWARDS & HAIME, 1850, p. xv), cnidarian [**Paracyathus parvus* R. BEDFORD & W. R. BEDFORD, 1936, p. 17; OD; holotype, R. BEDFORD

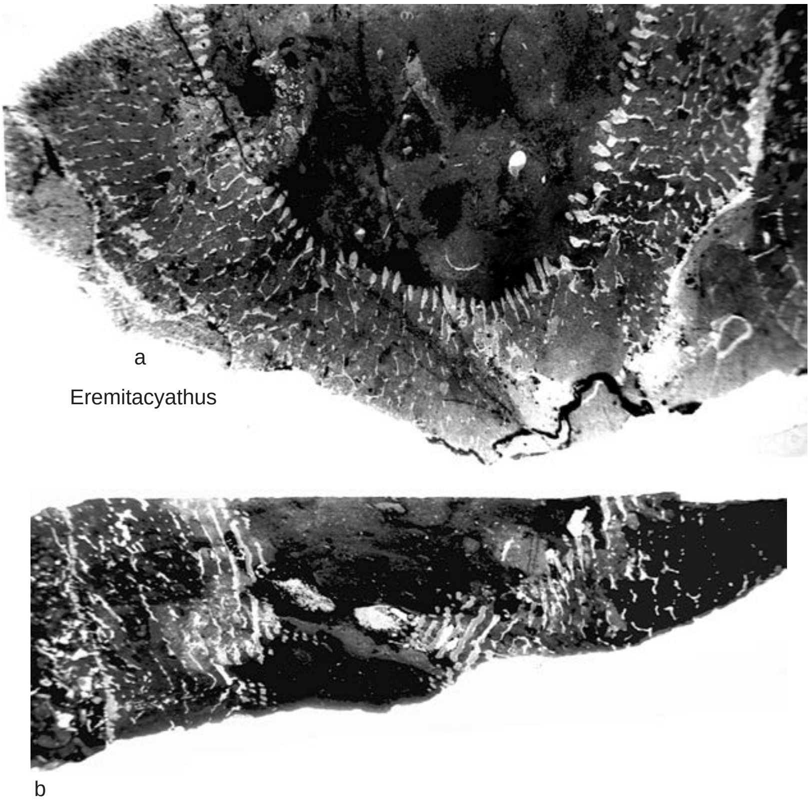


FIG. 616. Eremitacyathidae (p. 1041).

& W. R. Bedford, 1936, fig. 76; Debrenne, 1974c, pl. 19,*1–4;* Debrenne & Zhuravlev, 1992b, pl. 1,*6*, SAM P992-134, -135, M, Adelaide]. Inner wall with one, rarely two rows of simple pores per intersept; pseudosepta finely porous. *lower Cambrian (Bot.1–Bot.3):* ?Altay Sayan, ?Canada, Australia, Antarctica, Morocco.——Fig. 615,*2a–b*. **P. parvus* (R. Bedford & W. R. Bedford), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, SAM P992; *a,* detail of intervallum, longitudinal view (outer wall to left), ×10 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* external longitudinal view of outer wall, ×6 (Debrenne, 1974c).

Family EREMITACYATHIDAE Debrenne, 1992

[Eremitacyathidae Debrenne in Debrenne & Zhuravlev, 1992b, p. 112] [=Eremitacyathidae Zamarreño & Debrenne, 1977, p. 55, *nom. nud.*]

Inner wall with canals. *lower Cambrian (Atd.2).*

Eremitacyathus Zamarreño & Debrenne, 1977, p. 55 [**E. fissus*; OD; holotype, Zamarreño & Debrenne, 1977, pl. 5*a–b;* Debrenne & Zhuravlev, 1992b, pl. 3,*4*, MNHN M84016, specimen Spe 10-1a, Paris]. Inner wall with one canal-like opening per intersept, longitudinally continuous along entire cup, bounded by longitudinal plates bearing denticulate rims and lacking transverse partitions; pseudosepta coarsely porous; synapticulae may be present. *lower Cambrian (Atd.2):* Iberia.——Fig. 616*a–b*. **E. fissus*, Pedroche Formation, Atdabanian, Las Ermitas, Cordoba, Andalusia, Spain, holotype, MNHN M84016, specimen Spe 10-1a; *a,* transverse section, ×2.5; *b,* longitudinal section, ×2.5 (Zamarreño & Debrenne, 1977).

Superfamily SAKHACYATHOIDEA Debrenne & Zhuravlev, 1990

[*nom. transl.* Debrenne & Zhuravlev, 1992b, p. 112, *ex* Sakhacyathidae Debrenne & Zhuravlev, 1990, p. 302]

Outer wall pustular. *lower Cambrian (Tom.2–Atd.2).*

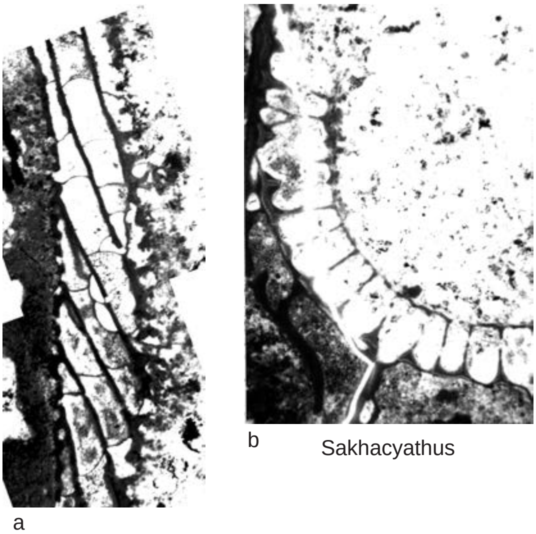


FIG. 617. Sakhacyathidae (p. 1042).

Family SAKHACYATHIDAE
Debrenne & Zhuravlev, 1990

[Sakhacyathidae DEBRENNE & ZHURAVLEV, 1990, p. 302]

Inner wall with simple pores. *lower Cambrian (Tom.2–Atd.2).*

Sakhacyathus DEBRENNE & ZHURAVLEV, 1990, p. 302 [**Paranacyathus subartus* ZHURAVLEVA, 1960b, p. 291; OD; holotype, ZHURAVLEVA, 1960b, pl. 28,*6,* TsSGM 205/149, Novosibirsk] [=*Orbiparanocyathus* BELYAEVA, 1996, p. 109 (type, *O. zolaensis*, OD)]. Inner wall with one, rarely two rows of simple pores per intersept; pseudosepta finely porous. *lower Cambrian (Tom.2–Atd.2):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia.——FIG. 617*a–b*. **S. subartus* (ZHURAVLEVA), Pestrotsvet Formation, Atdabanian, Mukhatta River, Sakha (Yakutia), Russia; *a,* holotype, TsSGM 205/149, longitudinal section (outer wall to left), ×7 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* transverse section, specimen PIN 4451/9, ×15 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

Superfamily
CHANKACYATHOIDEA
Yakovlev, 1959

[*nom. transl.* DEBRENNE & ZHURAVLEV, 1992b, p. 112, *ex* Chankacyathidae YAKOVLEV, 1959, p. 93]

Outer wall with canals. *lower Cambrian (Atd.4–Bot.3).*

Family CHANKACYATHIDAE
Yakovlev, 1959

[Chankacyathidae YAKOVLEV, 1959, p. 93]

Inner wall with simple pores. *lower Cambrian (Bot.1–Bot.3).*

Chankacyathus YAKOVLEV, 1959, p. 91, fig. 1 [**C. strachovi*; OD; *nom. correct.* OKUNEVA, 1969, p. 82, *pro C. strachovii*; holotype not designated, collection not located]. Outer wall with horizontal to upwardly projecting, straight canals, bearing supplementary bracts externally (imparting overall inverted V-shaped appearance to outer wall); inner wall with one row of simple pores per intersept; pseudosepta finely porous. *lower Cambrian (Bot.1–Bot.3):* Far East, ?Australia.——FIG. 618,*1a–b*. **C. strachovi*, Dmitrievka Formation, Botoman, Kar'ernaya, Far East, Russia, specimen PGU 202 133/52; *a,* transverse section of modular skeleton, ×7; *b,* longitudinal section, ×6.5 (Okuneva, 1969).

Family TCHOJACYATHIDAE
Debrenne & Zhuravlev, 1992

[Tchojacyathidae DEBRENNE & ZHURAVLEV, 1992b, p. 113]

Inner wall with canals. *lower Cambrian (Atd.4).*

Tchojacyathus ROZANOV, 1960b, p. 46 [**T. validus*; OD; holotype, ROZANOV, 1960b, pl. 1,*3* (*non* fig. 2); ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 11,*1*, PIN 4297/11, Moscow]. Outer wall with horizontal to upwardly projecting, S-shaped canals; inner wall with one row of horizontal to upwardly projecting, S-shaped canals per intersept; pseudosepta coarsely porous. *lower Cambrian (Atd.4):* Altay Sayan.——FIG. 618,*2a–b*. **T. validus*, Uba Formation, Atdabanian,

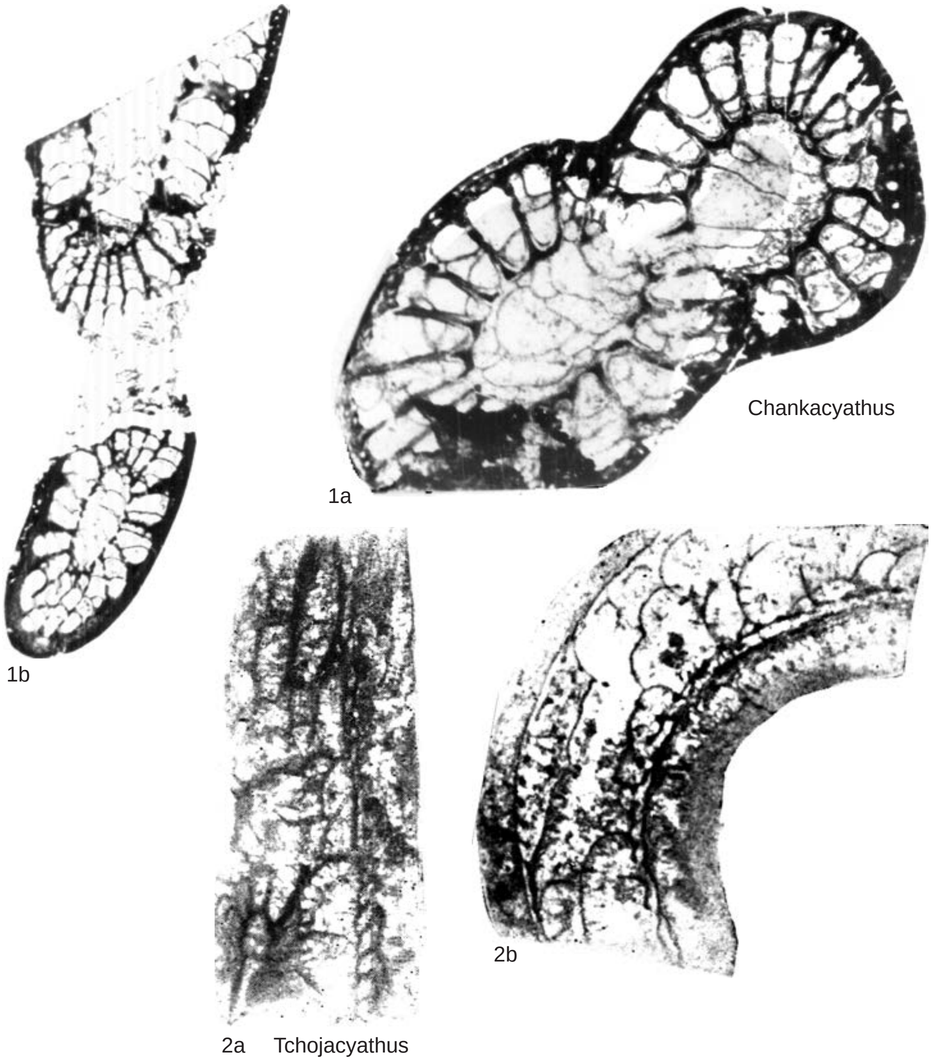


FIG. 618. Chankacyathidae and Tchojacyathidae (p. 1042–1043).

Tyrga River, Altay Mountains, Russia, holotype, PIN 4297/11; *a,* longitudinal section (outer wall to left), ×6; *b,* transverse section, ×6 (Rozanov, 1960b).

Suborder ANTHOMORPHINA Okulitch, 1935

[*nom. transl.* DEBRENNE, 1991, p. 219, *ex* Anthomorphida OKULITCH, 1955a, p. 18, *nom. correct. pro* order Anthomorphina OKULITCH, 1935b, p. 90] [=subclass Anthocyatha OKULITCH, 1943, p. 46; =Araneocyathida VOLOGDIN, 1961, p. 182]

Cup solitary or modular (pseudocolonies formed by external budding); intervallum with pseudosepta and membrane tabulae. *lower Cambrian (Bot.1).*

Superfamily ANTHOMORPHOIDEA Okulitch, 1935

[*nom. transl.* DEBRENNE & ZHURAVLEV, 1992b, p. 113, *ex* Anthomorphidae OKULITCH, 1935b, p. 97]

Outer wall simple, with pores of anthoid type; microporous membranes of similar structure to tabulae may be present. *lower Cambrian (Bot.1).*

Family ANTHOMORPHIDAE Okulitch, 1935

[Anthomorphidae OKULITCH, 1935b, p. 97] [=Anthomorphinae OKULITCH, 1935b, *nom. transl.* FONIN, 1985, p. 121, *ex* Anthomorphidae OKULITCH, 1935b, p. 97; =Araneocyathidae VOLOGDIN, 1956, p. 878; =Serligocyathidae VOLOGDIN, 1959a, p. 670; =Rudicyathinae FONIN in ZHURAVLEV, ZHURAVLEVA, & FONIN, 1983, p. 26; =Vertocyathinae FONIN, 1985, p. 110]

Inner wall with simple pores. *lower Cambrian (Bot.1).*

Anthomorpha BORNEMANN, 1884, p. 705 [**A. margarita*; M; lectotype, BORNEMANN, 1886, pl. 28,*1a,4–6;* DEBRENNE, 1964, pl. 45,*1;* SD DEBRENNE, 1964, p. 233, GML 897a, Halle]. Inner wall with one row of simple pores per intersept; pseudosepta aporose even in early ontogenetic stages; membrane tabulae may be present. *lower Cambrian (Bot.1):* Tuva, ?Far East, Morocco, Iberia, France, Sardinia.——FIG. 619,*1a–b*. **A. margarita*, Matoppa Formation, Botoman; *a,* Cuccuru Contu, Sardinia, Italy, lectotype, GML 897a, transverse section, ×4 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* Gonnesa, Sardinia, Italy, paralectotype, MNHN M84133, specimen C GON 3-7, longitudinal section, ×3 (Debrenne, 1964).

Tollicyathus CHERNYSHEVA, 1960, p. 77 [**T. ishensis*; OD; holotype, CHERNYSHEVA, 1960, pl. 4,*1*, ZSGGU 503/1, Novokuznetsk] [=*Nellicyathus* FONIN in REPINA & others, 1964, p. 247 (type, *N. nelliae*, OD); =*Rudicyathus* FONIN in ZHURAVLEV, ZHURAVLEVA, & FONIN, 1983, p. 26 (type, *R. tersus*, OD); =*Vertocyathus* FONIN, 1985, p. 110 (type, *V. reduncus*, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 67]. Inner wall with one row of simple pores per intersept; pseudosepta with pores restricted to outer wall area, but coarsely porous in early ontogenetic stages; membrane tabulae may be present. *lower Cambrian (Bot.1):* Altay Sayan, Tuva, Mongolia.——FIG. 619,*2a–b*. **T. ishensis*, Verkhneynyrga Formation, Botoman, Bol'shaya Isha River, Altay Mountains, Altay Sayan, Russia, holotype, ZSGGU 503/1; *a,* longitudinal section, ×5; *b,* transverse section, ×5 (Chernysheva, 1960).

Family SHIVELIGOCYATHIDAE Fonin, 1983

[*nom. transl.* DEBRENNE & ZHURAVLEV, 1992b, p. 113, *ex* Shiveligocyathinae FONIN, 1983, p. 12]

Inner wall with canals. *lower Cambrian (Bot.1).*

Shiveligocyathus MISSARZHEVSKIY, 1961, p. 19 [**S. vesiculoides*; OD; holotype, MISSARZHEVSKIY, 1961, pl. 1,*1*, PIN 1914/75M/44, Moscow, not located] [=*Voznesenskicyathus* RODIONOVA in ZHURAVLEVA & others, 1967, p. 99 (type, *V. florens*, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 130]. Inner wall with several rows of horizontal to upwardly projecting, straight communicating canals per intersept; pseudosepta finely porous; membrane tabulae may be present. *lower Cambrian (Bot.1):* Altay Sayan, Tuva, Mongolia.——FIG. 620*a–b*. **S. vesiculoides*, Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Tuva, Russia, paratype, PIN 1914/75M/00; *a,* longitudinal section, ×2 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* oblique transverse section, ×2 (Missarzhevskiy, 1961).

Suborder ARCHAEOCYATHINA Okulitch, 1935

[*nom. transl.* ZHURAVLEVA, 1960b, p. 271, *ex* Archaeocyathida ZHURAVLEVA, 1955a, p. 17, *nom. correct. pro* order Archaeocyathina OKULITCH, 1935b, p. 90] [=Archaeosyconina ZHURAVLEVA, 1955a, p. 12, *nom. transl.* ZHURAVLEVA, 1960b, p. 303, *ex* order Archaeosyconida ZHURAVLEVA, 1955a, p. 12, *nom. correct.* DEBRENNE, 1964, p. 117, *pro* Archaeosyconiina ZHURAVLEVA, 1960b, p. 303; =Dictyocyathina VOLOGDIN, 1956, p. 878, *nom. transl.* FONIN in VORONIN & others, 1982, p. 83, *ex* Dictyocyathida VOLOGDIN, 1956, p. 878; =Chouberticyathina DEBRENNE, 1970a, p. 25, *nom. transl.* FONIN in VORONIN & others, 1982, p. 83, *ex* Chouberticyathida DEBRENNE, 1970a, p. 25]

Cup solitary or modular (latter by external budding and/or longitudinal subdivision; encrusting forms develop by addition of new central cavities); intervallum with taeniae, pseudosepta, or pseudotaenial or dictyonal network; segmented tabulae may be present. *lower Cambrian (Tom.2–Toy.3), middle Cambrian.*

Superfamily DICTYOCYATHOIDEA Taylor, 1910

[*nom. transl.* WOOD, EVANS, & ZHURAVLEV, 1992, p. 492, *ex* Dictyocyathidae TAYLOR, 1910, p. 111]

Outer wall simple, either rudimentary (of marginal intervallar elements only) or basic (of marginal intervallar elements with additional linking lintels); segmented tabulae may be present. *lower Cambrian (Tom.2–Toy.1), middle Cambrian.*

Family DICTYOCYATHIDAE Taylor, 1910

[Dictyocyathidae TAYLOR, 1910, p. 111] [=subfamily Dictyocyathinea HERNÁNDEZ-SAMPELAYO, 1933, p. 159; =Prismocyathidae FONIN, 1960, p. 725; =Paracoscinidae DEBRENNE, 1970a, p. 38, *nom. nud.*; =Paracoscinidae DEBRENNE, 1974a, p. 252; =Chouberticyathidae DEBRENNE, 1974a, p. 192; =Graphoscyphiidae DEBRENNE, 1974a, p. 204, *nom. correct.* KRUSE, 1982, p. 196, *pro* Graphoscyphidae DEBRENNE, 1974a, p. 204]

Inner wall with simple pores. *lower Cambrian (Tom.2–Toy.1), middle Cambrian.*

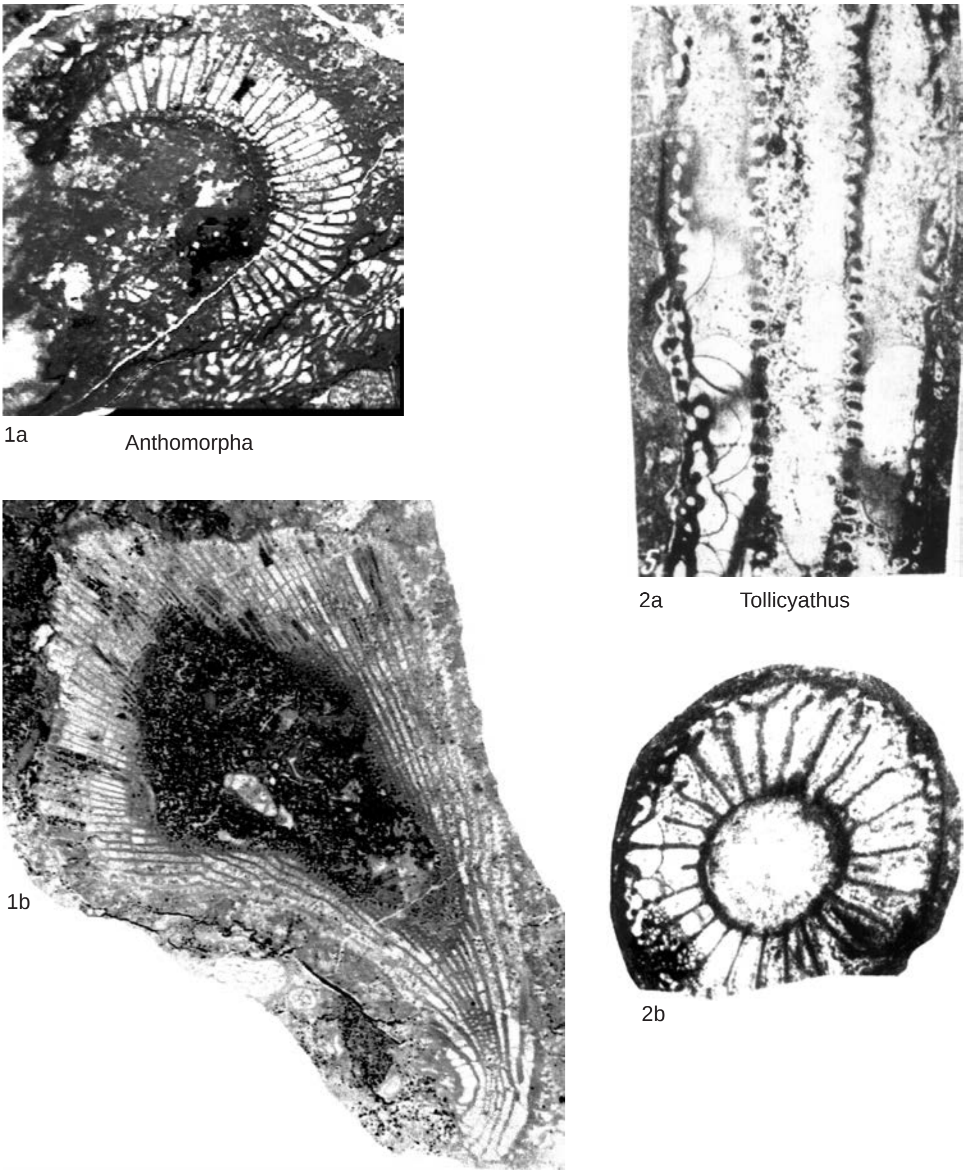


FIG. 619. Anthomorphidae (p. 1044).

Dictyocyathus Bornemann, 1891a, p. 500 [**D. tenerrimus*; M; lectotype, Bornemann, 1891a, pl. 42,*5;* pl. 43,*4–6;* SD Debrenne, 1964, p. 200, not located; =*Coscinocyathus verticillus* Bornemann, 1886, p. 65; lectotype, Bornemann, 1886, pl. 15,*3g;* Debrenne, 1964, pl. 34,*5;* SD Debrenne, 1964, p. 205, GML 899c, Halle] [=*Prismocyathus* Fonin, 1960, p. 725 (type, *P. praesignis*, OD); =*Spongiosicyathus* Zhuravleva in Datsenko & others, 1968, p. 174 (type, *Dictyocyathus translucidus* Zhuravleva, 1960b, p. 275, OD); =*Prismocyathellus* Fonin, 1990, p. 152 (type, *Prismocyathus verisimilis* Fonin, 1960, p. 726, OD; =*Prismocyathus praesignis* Fonin, 1960, p. 725)]. Outer wall basic; inner wall with one row of simple pores per intersept; dictyonal network. *lower Cambrian (Tom.2–Bot.1), middle Cambrian (Guzhangian):* Siberian Platform, Kolyma, Altay Sayan, Tuva, Mongolia, Far East, Kazakhstan, South China, Morocco, Iberia, Sardinia, Germany, *Tom.2–*

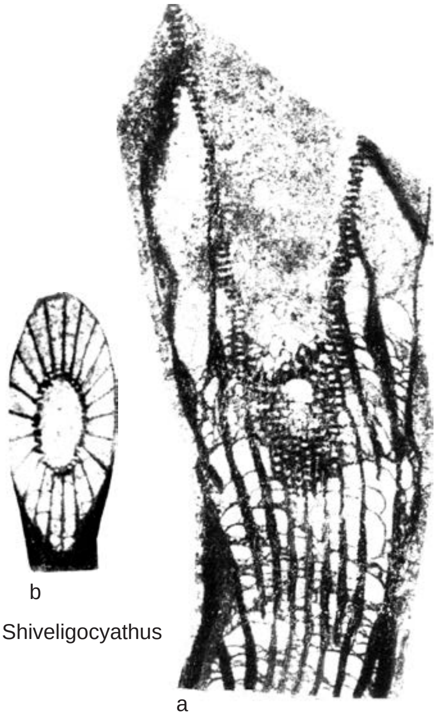


Fig. 620. Shiveligocyathidae (p. 1044).

Bot.1; Antarctica, *Guzhangian.*——Fig. 621,*1a–b.* **D. verticillus* (Bornemann), Matoppa Formation, Botoman, Cuccuru Contu, Sardinia, Italy; *a,* topotype, MNHN M84248, specimen CCC 9-1a, oblique longitudinal section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* lectotype, GML 899c, transverse section, ×6 (Debrenne, 1964).

Cellicyathus Debrenne & Zhuravlev, 1990, p. 300 [**Maturocyathus ornatus* Fonin, 1985, p. 118; OD; holotype, Fonin, 1985, pl. 22,*2,* PIN 1915/280, Moscow]. Outer wall basic, tabular; inner wall tabular, with one row of simple pores per intersept; taeniae coarsely porous; synapticulae and simply porous segmented tabulae may be present. *lower Cambrian (Bot.2–Toy.1):* Siberian Platform, Altay Sayan, Tuva.——Fig. 621,*2a–b.* **C. ornatus* (Fonin), Shangan Formation, Botoman, Ulug-Shangan River, East Tannu-Ola Range, Tuva, Russia; *a,* holotype, PIN 1915/280, transverse section, ×5; *b,* paratype, PIN 1915/300, longitudinal section (outer wall to right), ×3.5 (Fonin, 1985).

Chouberticyathus Debrenne, 1964, p. 208 [**C. clatratus*; OD; holotype, Debrenne, 1964, pl. 32,*1–3,* MNHN M80272, specimen Ki 140 P-6, Paris]. Outer wall imperforate (possibly rudimentary); inner wall with one row of simple pores per intersept; taeniae coarsely porous. *lower Cambrian (Bot.1):* Morocco, Iberia, Sardinia.——Fig. 621,*3a–b.* **C. clatratus*, Issafen Formation, Botoman, Tizi Oumeslema, Morocco, holotype, MNHN M80272, specimen Ki 140 P-6; *a,* transverse view, ×6; *b,* longitudinal view, ×6 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

Graphoscyphia Debrenne in Zhuravleva, 1974a, p. 164 [**Protopharetra graphica* R. Bedford & W. R. Bedford, 1934, p. 4; OD; lectotype, R. Bedford & W. R. Bedford, 1934, fig. 22; Debrenne, 1969a, pl. 12,*5;* SD Debrenne, 1969a, p. 346, NHM S4170, London]. Outer wall basic; inner wall with one row of simple pores per intersept; pseudosepta coarsely porous, linked by synapticulae. *lower Cambrian (Atd.4–Bot.3):* Altay Sayan, Australia, Antarctica, Mexico.——Fig. 621,*4a–b.* **G. graphica* (R. Bedford & W. R. Bedford), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, NHM S4170; *a,* internal longitudinal view of inner wall, ×6; *b,* transverse view, ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Molybdocyathus Debrenne & Gangloff in Debrenne, Gandin, & Gangloff, 1990, p. 92 [**M. juvenilis*; OD; holotype, Debrenne, Gandin, & Gangloff, 1990, pl. 2,*13,* USNM 443573, specimen IR 23.7a', Washington, D.C.]. Outer wall rudimentary; inner wall with one row of simple pores per intersept; dictyonal network. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Tuva, Mongolia, United States.——Fig. 622,*1a–b.* **M. juvenilis*, Valmy Formation, Botoman, Iron Canyon, Nevada, United States; *a,* holotype, USNM 443573, specimen IR 23.7a', transverse and longitudinal sections of modular skeleton, ×8; *b,* paratype, USNM 443568, specimen IR 14.2, longitudinal section of modular skeleton, ×8 (Debrenne, Gandin, & Gangloff, 1990).

Paracoscinus R. Bedford & W. R. Bedford, 1936, p. 18 [**P. mirabile*; OD; holotype, R. Bedford & W. R. Bedford, 1936, fig. 85; Debrenne, 1974a, fig. 37a–b, SAM P988-169, -170, -171, Adelaide]. Outer wall basic, tabular; inner wall with one row of simple pores per intersept, each pore subdivided by median longitudinal rod; pseudosepta finely porous; segmented tabulae. *lower Cambrian (Bot.3–Toy.1):* Altay Sayan, Australia.——Fig. 622,*2a–d.* **P. mirabile*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; *a,* holotype, SAM P988-169, -170, -171, transverse view, ×6 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* paratype, USNM PU86680, specimen 241A, external view of outer wall, ×6 (Debrenne, Zhuravlev, & Kruse, 2002); *c–d,* holotype, SAM P988-169, -170, -171; *c,* longitudinal view, ×4; *d,* internal view of inner wall, ×7 (Debrenne, 1974a).

?Retilamina Debrenne & James, 1981, p. 370 [**R. amourensis*; OD; holotype, Debrenne & James, 1981, pl. 54,*4,* GSC 62128, specimen 169-5acT1, Ottawa]. Encrusting, domelike cup; upper wall (interpreted as outer) with pores regularly arranged but not at each intertaenia; pores commonly produced as chimneys; lower

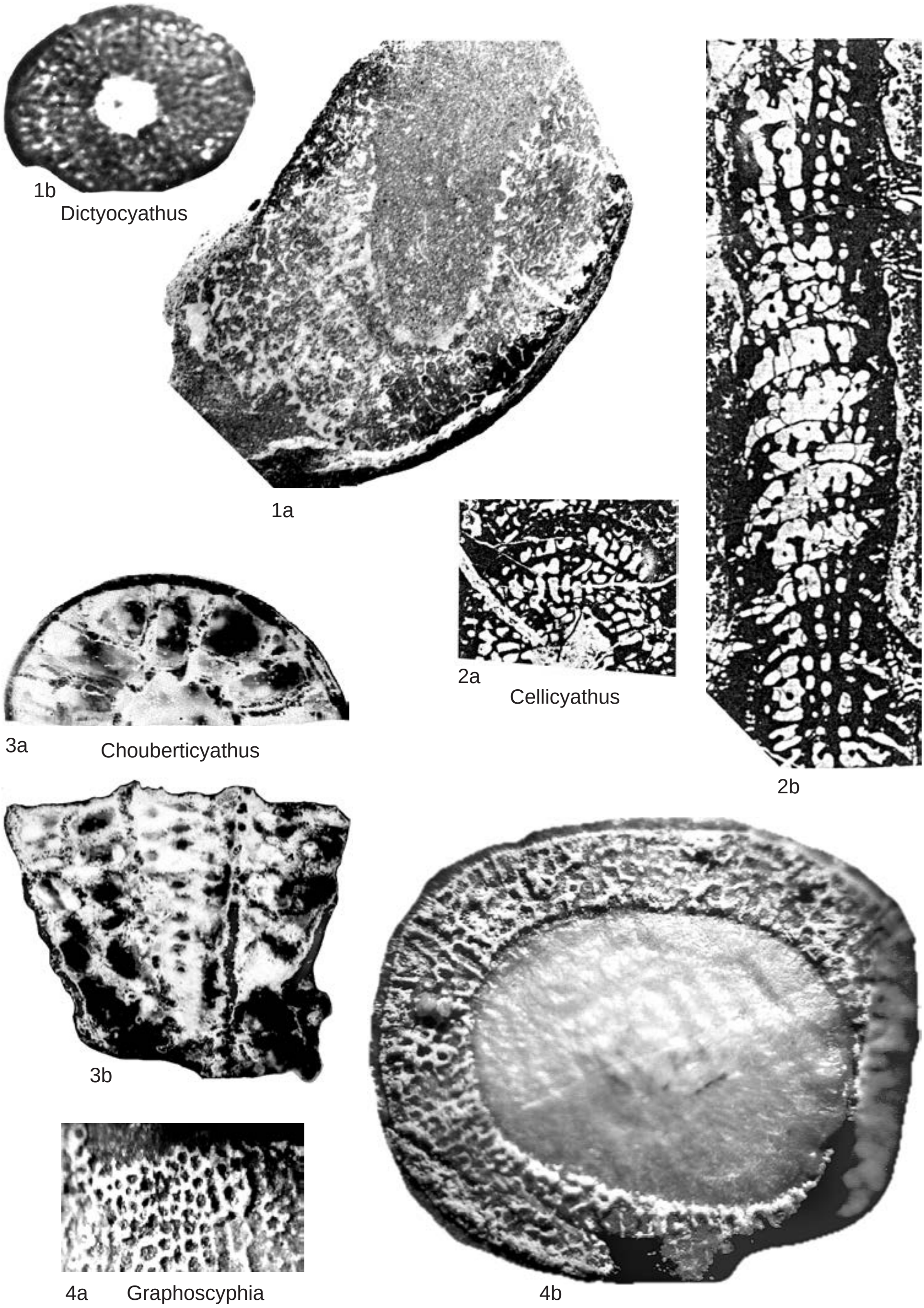


FIG. 621. Dictyocyathidae (p. 1045–1046).

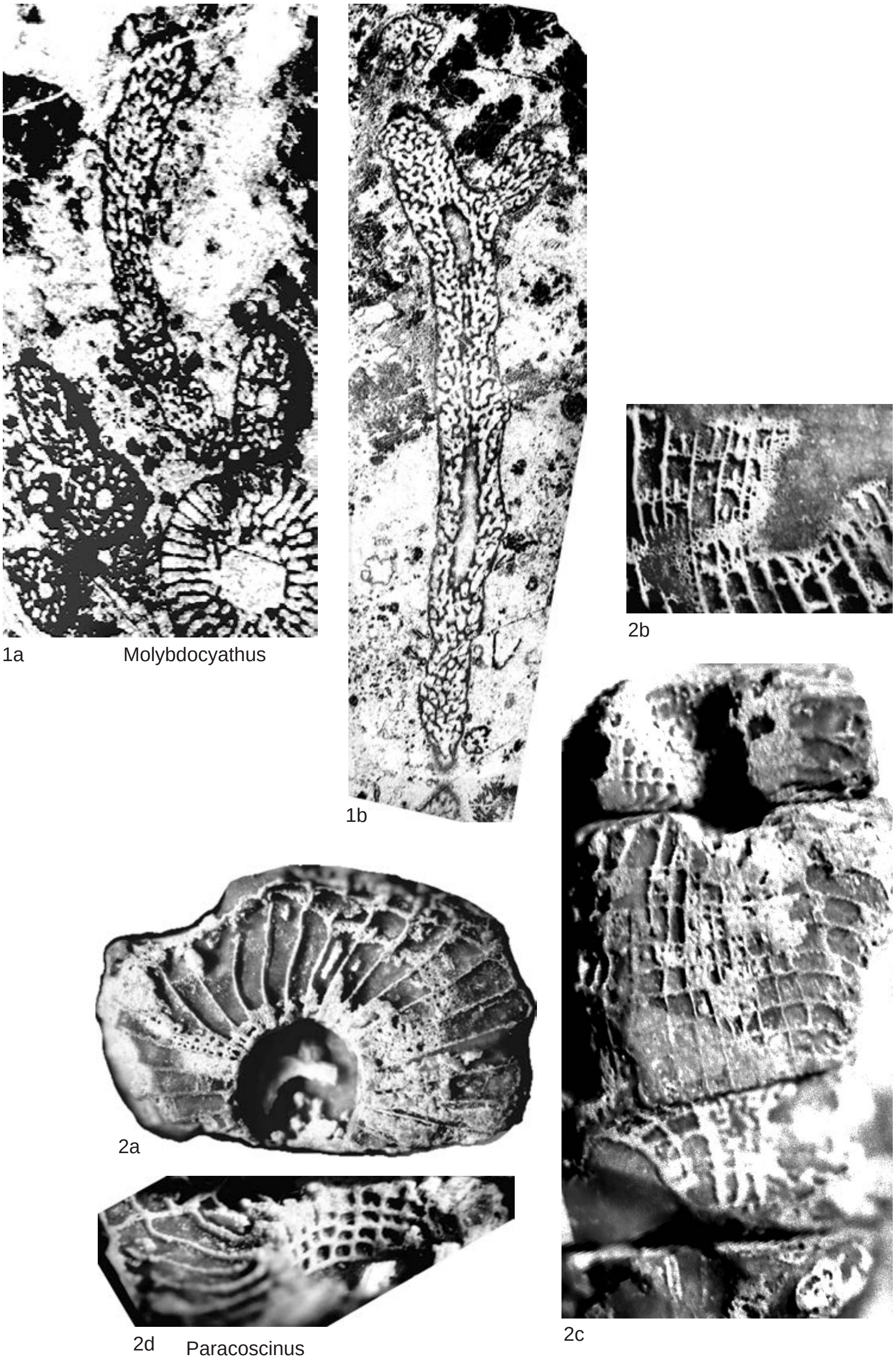


FIG. 622. Dictyocyathidae (p. 1046).

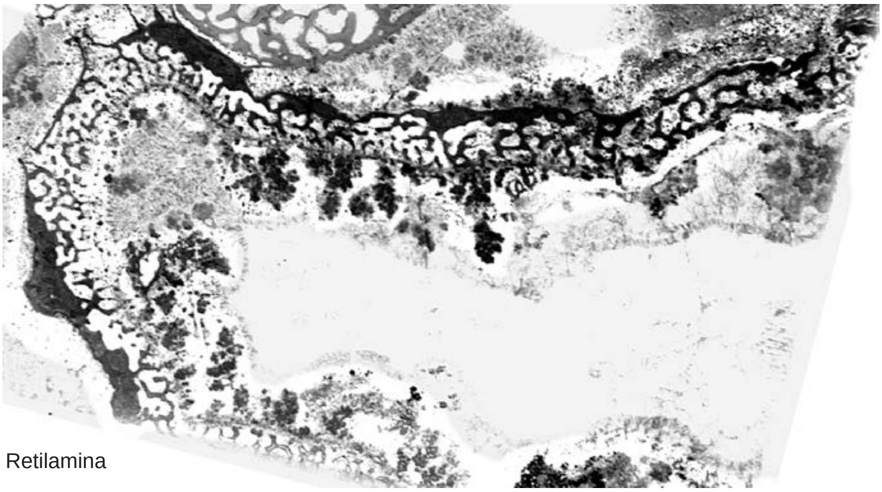


FIG. 623. Dictyocyathidae (p. 1046–1049).

(possibly inner) wall rudimentary; dictyonal or more probably pseudotaenial network. [Atypical cup shape does not provide certainty as to which wall is outer and which inner, and nature of intervallar elements and accepted inner wall remain doubtful.] *lower Cambrian (Bot.2–Bot.3):* Canada, United States, Mexico.——FIG. 623. **R. amourensis*, Forteau Formation, Botoman, Mount St. Margaret, Newfoundland, Canada, holotype, GSC 62128, specimen 169-5acT1, oblique section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Family CLARUSCOSCINIDAE Debrenne & Zhuravlev, 1992

[Claruscoscinidae DEBRENNE & ZHURAVLEV, 1992b, p. 114] [=Claruscoscinidae DEBRENNE in DEBRENNE, GANDIN, & ROWLAND, 1989, p. 167, *nom. nud.*]

Inner wall with bracts, fused bracts, or pore tubes. *lower Cambrian (Bot.1–Toy.1).*

Claruscoscinus HANDFIELD, 1971, p. 74 [**Eucyathus billingsi* VOLOGDIN, 1940b, p. 48; OD; holotype not designated, collection not located] [=*Monstricyathus* VOLOGDIN, 1977, p. 60 (type, *M. tubiformis*, OD); =*Arisacyathus* KASHINA in OSADCHAYA & others, 1979, p. 166 (type, *A. diligens*, OD; =*Eucyathus billingsi* VOLOGDIN, 1940b, p. 48); =*Maturocyathus* FONIN, 1985, p. 114 (type, *M. makarovi*, OD; =*Eucyathus billingsi* VOLOGDIN, 1940b, p. 48); =*Costocyathus* FONIN, 1985, p. 119 (type, *C. mactus*, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 123]. Outer wall basic, tabular; inner wall with one row of pores per intersept, bearing upwardly projecting, straight to S-shaped pore tubes; pseudosepta finely porous; segmented tabulae. *lower Cambrian (Bot.1–Toy.1):* Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Canada, United States.——FIG. 624,*1a–c*. **C. billingsi* (VOLOGDIN), Verkhnemonok Formation, Botoman, Berezovaya River, Abakan River, West Sayan, Altay Sayan, Russia; *a,* unlocated syntype, longitudinal section, ×4 (Vologdin, 1940b); *b,* transverse section, syntype PIN 4754/6, ×5 (Debrenne, Zhuravlev, & Kruse, 2002); *c,* unlocated syntype, longitudinal section, ×4 (Vologdin, 1940b).

Fenestrocyathus HANDFIELD, 1971, p. 72 [**F. complexus*; OD; holotype, HANDFIELD, 1971, pl. 14,*5;* pl. 15,*1*, GSC 25388, Ottawa]. Outer wall basic; inner wall with one row of pores per intersept, bearing upwardly projecting, S-shaped bracts or fused bracts; dictyonal network. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Mongolia, Canada, United States.——FIG. 624,*2*. **F. complexus*, Sekwi Formation, Botoman, Mackenzie Mountains, Northwest Territories, Canada, holotype, GSC 25388, transverse section of modular skeleton, ×5 (Debrenne, Zhuravlev, & Kruse, 2002).

Landercyathus DEBRENNE & GANGLOFF in DEBRENNE, GANDIN, & GANGLOFF, 1990, p. 91 [**L. lewandowskii*; OD; holotype, DEBRENNE, GANDIN, & GANGLOFF, 1990, pl. 1,*13*, USNM 443571, specimen IR 23a, Washington, D.C.]. Outer wall simple; inner wall with one row of horizontal to upwardly projecting, straight to waved canals per intersept; canals may penetrate intervallum forming astrorhizae; dictyonal network. *lower Cambrian (Bot.2):* United States.——FIG. 624,*3*. **L. lewandowskii*, Valmy Formation, Botoman, Iron Canyon, Nevada, United States, holotype, USNM 443571, specimen IR 23a, oblique longitudinal section, ×4 (Debrenne, Gandin, & Gangloff, 1990).

Stevocyathus DEBRENNE in DEBRENNE, GANDIN, & ROWLAND, 1989, p. 166 [**S. elictus*; OD; holotype, DEBRENNE, GANDIN, & ROWLAND, 1989, pl. 12,*1*, MNHN M83100, specimen CR2-8, Paris]. Outer wall basic; inner wall with one row of pores per

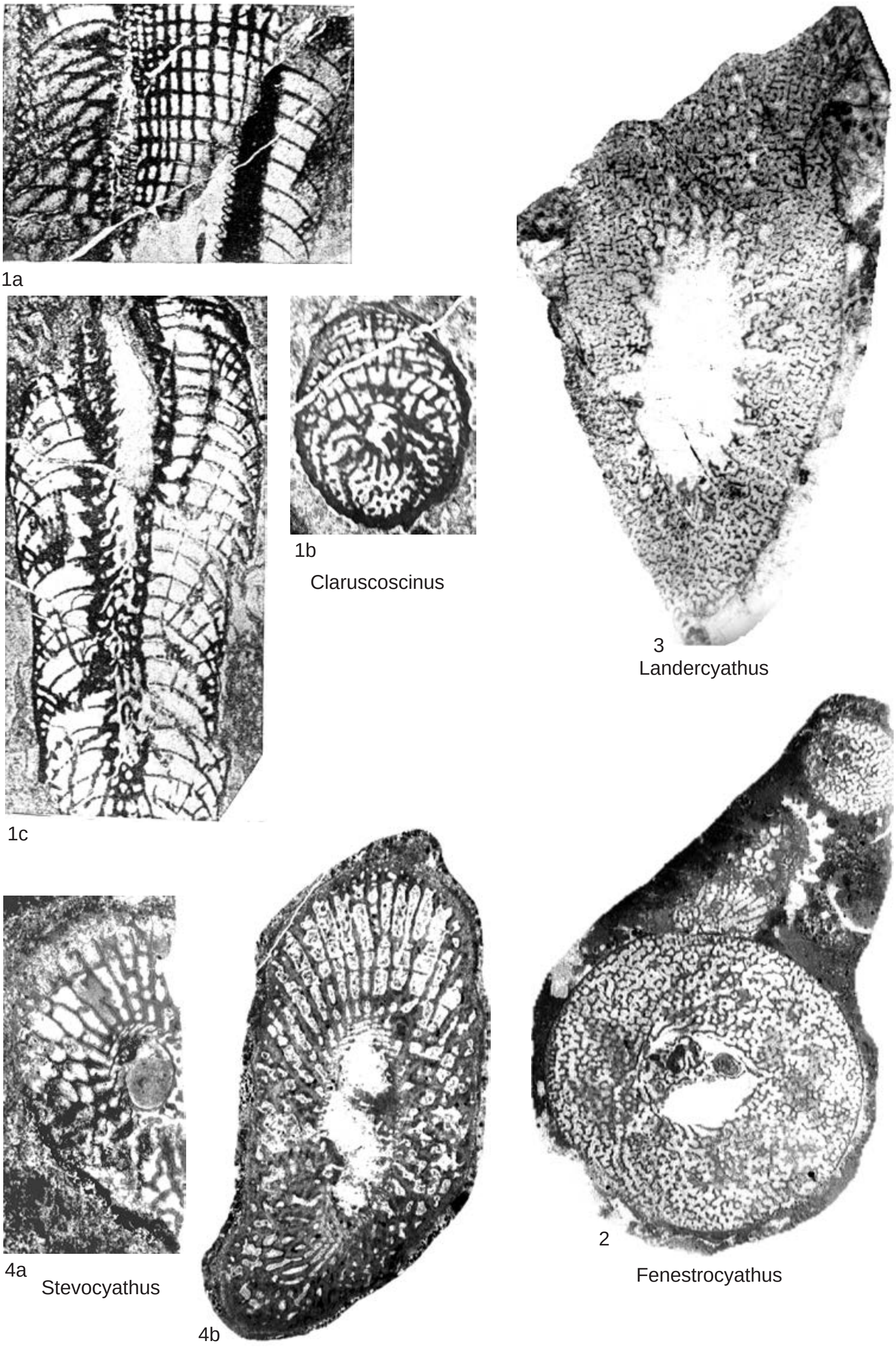


FIG. 624. Claruscoscinidae (p. 1049–1051).

intersept, bearing upwardly projecting, S-shaped bracts or fused bracts; taeniae coarsely porous, linked by synapticulae; simple segmented tabulae may be present. *lower Cambrian (Bot.2):* United States, Mexico.——FIG. 624,*4a–b*. **S. elictus*, Puerto Blanco Formation, Botoman, Caborca, Sonora, Mexico; *a,* paratype, MNHN M83107, specimen CR2*1-8, transverse section, ×6 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* holotype, MNHN M83100, specimen CR2-8, oblique longitudinal section, ×6 (Debrenne, Gandin, & Rowland, 1989).

Family PYCNOIDOCOSCINIDAE Debrenne, 1974

[Pycnoidocoscinidae DEBRENNE, 1974a, p. 256] [=Pycnoidocoscinidae DEBRENNE, 1970a, p. 40, *nom. nud.*]

Inner wall compound. *lower Cambrian (Bot.3).*

Pycnoidocoscinus R. BEDFORD & W. R. BEDFORD, 1936, p. 19 [**P. pycnoideum*; OD; lectotype, R. BEDFORD & W. R. BEDFORD, 1936, fig. 87; SD DEBRENNE, 1970a, p. 40, SAM P990-175, -176, -177, Adelaide]. Outer wall basic; inner wall compound consisting of wall carcass and additional microporous sheath formed by tabulae; pseudosepta finely porous; segmented tabulae. *lower Cambrian (Bot.3):* Australia, ?Canada.——FIG. 625*a–b*. **P. pycnoideum*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM P990-175, -176, -177; *a,* transverse view (outer wall at top), ×4; *b,* tangential view of inner wall, ×6 (Debrenne, Zhuravlev, & Kruse, 2002).

Superfamily ARCHAEOCYATHOIDEA Hinde, 1889

[*nom. correct.* ZHURAVLEV in VORONOVA & others, 1987, p. 32, *pro* Archaeocyathacea SIMON, 1939, p. 6, *nom. transl. ex* Archaeocyathidae TAYLOR, 1910, p. 105, *nom. correct. pro* family Archaeocyathinae HINDE, 1889, p. 141] [=Flindersicyathoidea R. BEDFORD & J. BEDFORD, 1939, p. 78, *nom. correct.* DEBRENNE & KRUSE, 1986, p. 268, *pro* Flindersicyathacea GRAVESTOCK, 1984, p. 115, *nom. transl. ex* Flindersicyathidae R. BEDFORD & J. BEDFORD, 1939, p. 78; =Vadimocyathacea KASHINA in OSADCHAYA & others, 1979, p. 160]

Outer wall concentrically porous. *lower Cambrian (Atd.1–Toy.3).*

Family ARCHAEOPHARETRIDAE R. Bedford & W. R. Bedford, 1936

[Archaeopharetridae R. BEDFORD & W. R. BEDFORD, 1936, p. 17] [=Dictyocoscinidae R. BEDFORD & W. R. BEDFORD, 1936, p. 14, for discussion, see ZHURAVLEV & GRAVESTOCK, 1994, p. 34; =Protopharetridae VOLOGDIN, 1957a, p. 182; =Flindersicoscinidae DEBRENNE, 1974a, p. 246; =Salanycyathidae FONIN in VORONIN & others, 1982, p. 95; =Hawkercyathidae GRAVESTOCK, 1984, p. 115]

Inner wall with simple pores. *lower Cambrian (Atd.1–Bot.3).*

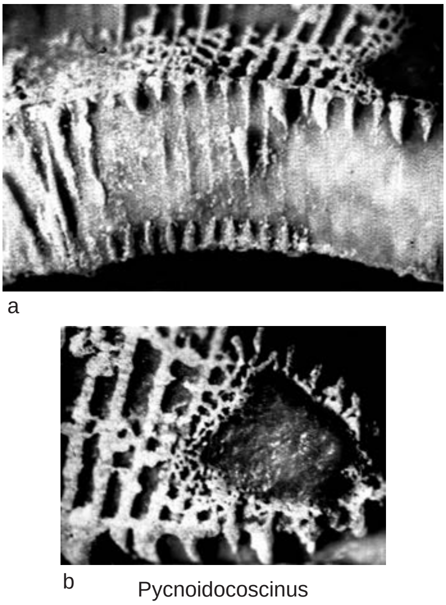


FIG. 625. Pycnoidocoscinidae (p. 1051).

Archaeopharetra R. BEDFORD & W. R. BEDFORD, 1936, p. 17 [**A. typica*; OD; holotype, R. BEDFORD & W. R. BEDFORD, 1936, fig. 75; ZHURAVLEVA, 1963b, fig. 67a; DEBRENNE, 1974a, fig. 3b; SD HILL, 1965, p. 115, SAM P969, Adelaide; =*Dictyocyathus irregularis* TAYLOR, 1910, p. 145; lectotype, TAYLOR, 1910, pl. 12, photo 66; SD DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1665, SAM T1590, Adelaide] [=*Dictyocoscinus* R. BEDFORD & W. R. BEDFORD, 1936, p. 14 (type, *D. beltana*, OD; =*Dictyocyathus irregularis* TAYLOR, 1910, p. 145, for discussion, see ZHURAVLEV & GRAVESTOCK, 1994, p. 34); =*Tubocyathus* VOLOGDIN, 1937b, p. 473 (type, *T. smolianinovae*, M); =*Tubicyathus* VOLOGDIN, 1940a, p. 114, *nom. null.*; =*Tubulocyathus* VOLOGDIN, 1956, p. 880, *nom. null.*; =*Flindersicoscinus* DEBRENNE, 1970a, p. 34 (type, *Flindersicyathus tabulatus* R. BEDFORD & J. BEDFORD, 1937, p. 29, OD); =*Salanycyathus* FONIN in VORONIN & others, 1982, p. 95 (type, *S. marginatus*, OD); =*Hawkercyathus* GRAVESTOCK, 1984, p. 115 (type, *H. insculptus*, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 120]. Inner wall with one row of simple pores per intersept; pseudotaeniae coarsely porous; concentrically porous segmented tabulae may be present. *lower Cambrian (Atd.1–Bot.3):* Altay Sayan, Tuva, Mongolia, Far East, Australia, Antarctica, South Africa (allochthonous), ?South China, ?Iberia.——FIG. 626,*1a–b*. **A. irregularis* (TAYLOR), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; *a,* lectotype, SAM T1590, oblique longitudinal view,

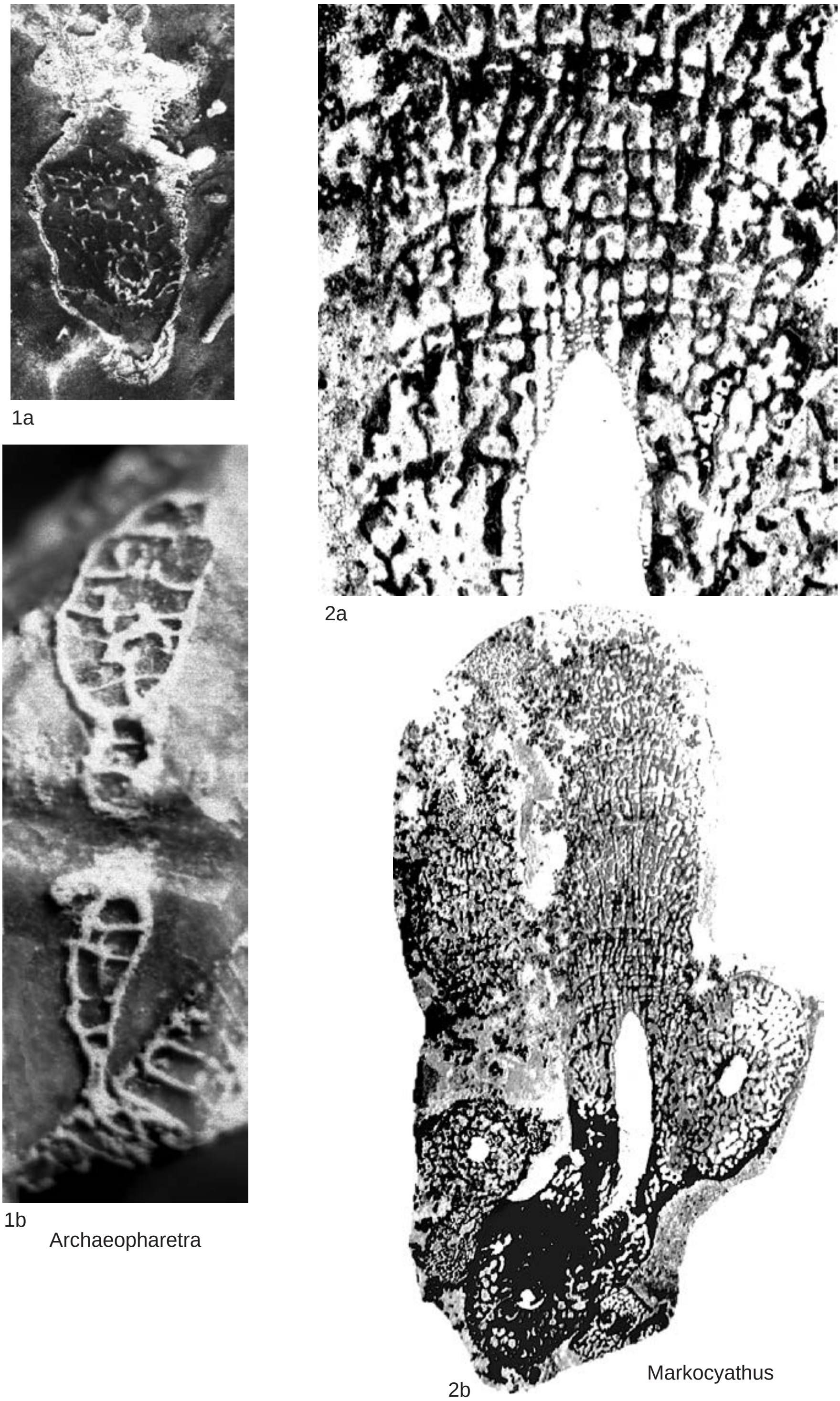


FIG. 626. Archaeopharetridae (p. 1051–1055).

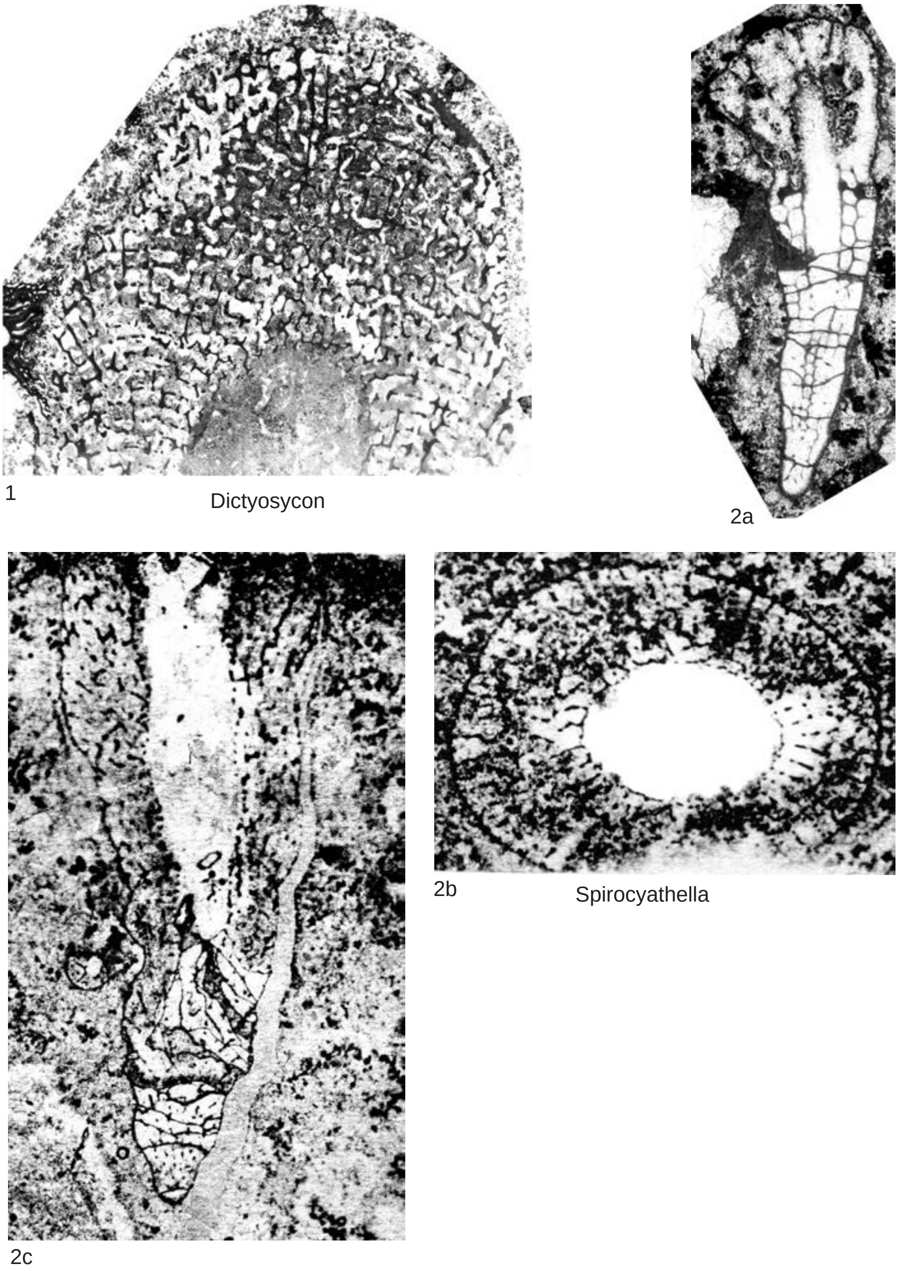


FIG. 627. Archaeopharetridae (p. 1054–1055).

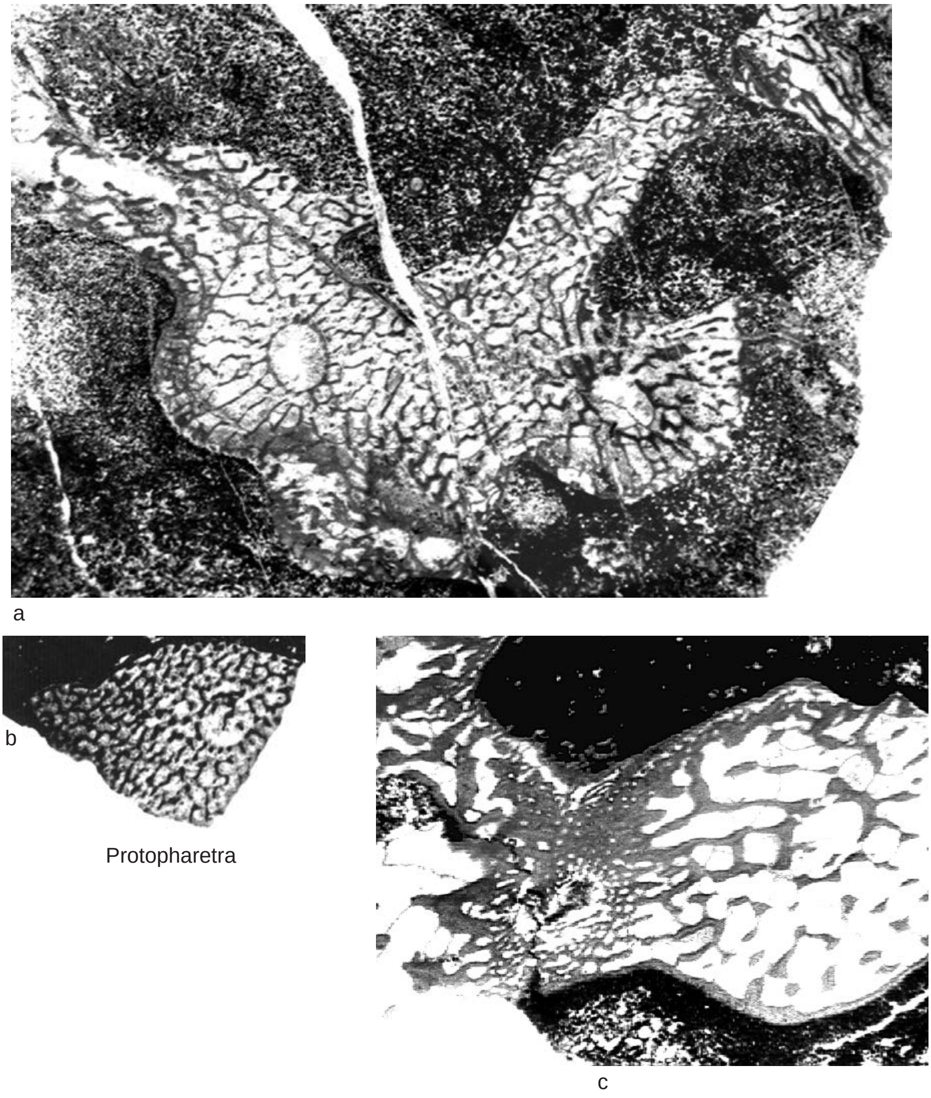


FIG. 628. Archaeopharetridae (p. 1055).

×5 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* holotype [=*A. typica* R. BEDFORD & W. R. BEDFORD], SAM P969, longitudinal view, ×8 (Debrenne, 1974a).

Dictyosycon ZHURAVLEVA, 1960b, p. 307, *nom. transl.* DEBRENNE & ZHURAVLEV, 1992b, p. 124, *ex Sphinctocyathus (Dictyosycon)* ZHURAVLEVA, 1960b, p. 307 [**Sphinctocyathus (Dictyosycon) gravis*; OD; holotype, ZHURAVLEVA, 1960b, pl. 31,*7*, TsSGM 205/169, Novosibirsk]. Inner wall with one row of simple pores per intersept; dictyonal network; simple or concentrically porous segmented tabulae may be present. *lower Cambrian (Atd.1–Atd.4):* Siberian Platform, Altay Sayan, Tuva, Iberia.——FIG. 627,1. **D. gravis*, Pestrotsvet Formation, Atdabanian, Oy-Muran, Lena River, Sakha (Yakutia), Russia, holotype, TsSGM 205/169, oblique longitudinal section, ×4 (Zhuravleva, 1960b).

Markocyathus DEBRENNE in DEBRENNE, GANDIN, & ROWLAND, 1989, p. 165 [**M. clementensis*; OD; holotype, DEBRENNE, GANDIN, & ROWLAND, 1989, pl. 11,*1–2*, MNHN M83096, specimen CL-1e, Paris]. Inner wall with several rows of simple pores per intersept; taeniae coarsely porous; concentrically porous segmented tabulae. *lower Cambrian (Bot.2):* Canada, Mexico.——Fig. 626,*2a–b*. **M. clementensis*, Puerto Blanco Formation, Botoman, Caborca, Sonora, Mexico, holotype, MNHN M83096, specimen CL-1e; *a,* detail of inner wall in tangential section, ×12 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* transverse and longitudinal sections of modular skeleton, ×3 (Debrenne, Gandin, & Rowland, 1989).

Protopharetra Bornemann, 1884, p. 705 (Bornemann, 1883, p. 274, *nom. nud.*) [**P. polymorpha* Bornemann, 1886, p. 46; SD Simon, 1939, p. 34; lectotype, Bornemann, 1886, pl. 5, fig. 4 bottom; SD Simon, 1939, p. 35, not located; topotypes, MNHN M84120, specimens CGR3/3, GLA3.3, GLC10.II.1b, Paris] [=*Volvacyathus* Debrenne, 1960, p. 118 (type, *V. proteus*, OD), for discussion, see Debrenne & Zhuravlev, 1992b, p. 128]. Inner wall with one row of simple pores per intersept; taeniae coarsely porous, linked by rare synapticulae. *lower Cambrian (Atd.1–Bot.3):* Altay Sayan, Tuva, Far East, Tajikistan, Canada, United States, Morocco, Iberia, France, Sardinia, Germany.——Fig. 628*a–c*. **P. polymorpha*, Matoppa Formation, Botoman, Canal Grande, Sardinia, Italy; *a,* topotype, MNHN M84120, transverse section of modular skeleton, ×3 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* lectotype, transverse section, ×3 (Bornemann, 1886); *c,* topotype, MNHN M84120, detail of outer wall in tangential section, ×7 (Debrenne, Zhuravlev, & Kruse, 2002).

Spirocyathella Vologdin, 1939, p. 227 [**S. kyzlartauensis*; OD; holotype not designated, collection not located] [=*Aruntacyathus* Kruse in Walter, 1980, chart, *nom. nud.*; =*Amadedcyathus* Kruse in Walter, 1980, chart, *nom. nud.*; =*Aruntacyathus* Kruse in Kruse & West, 1980, p. 172 (type, *A. toddi*, OD); =*Spirocyathellus* Fonin in Voronin & others, 1982, p. 98, *lapsus calami pro Spirocyathella* Vologdin, 1939, p. 227, for discussion, see Debrenne & Zhuravlev, 1992b, p. 131]. Inner wall with several rows of simple pores per intersept; pseudotaenial network coarsely porous; concentrically porous segmented tabulae. *lower Cambrian (Atd.4–Bot.2):* Altay Sayan, Urals, Canada, United States, Mexico, Australia, Antarctica, Falkland Islands (allochthonous), South Africa (allochthonous), France.——Fig. 627,*2a–c*. **S. kyzlartauensis*, Terekla Formation, Botoman, Mt. Kizlar-Tau, western flank of southern Urals, Russia; *a,* topotype, PIN 4451/26, longitudinal section, ×8 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b–c,* unlocated syntype, 4-M, thin section 4; *b,* transverse section, ×6; *c,* longitudinal section, ×6 (Vologdin, 1939).

Family ARCHAEOCYATHIDAE Hinde, 1889

[*nom. correct*. Taylor, 1910, p. 105, *pro* family Archaeocyathinae Hinde, 1889, p. 141] [=Spirocyathidae Taylor, 1910, p. 112; =Archaeocyathinae Hernández-Sampelayo, 1933, p. 158, *nom. correct*. Fonin, 1985, p. 69, *pro* Archaeocyathinea Hernández-Sampelayo, 1933, p. 158; =Sigmofungiidae R. Bedford & W. R. Bedford, 1936, p. 16, *nom. correct*. Debrenne, 1970a, p. 42, *pro* Sigmofungidae R. Bedford & W. R. Bedford, 1936, p. 16; =Flindersicyathidae R. Bedford & J. Bedford, 1939, p. 78; =Flindersicyathinae R. Bedford & J. Bedford, 1939, p. 78, *nom. transl.* Fonin, 1985, p. 93, *ex* Flindersicyathidae R. Bedford & J. Bedford, 1939, p. 78; =Pycnoidocyathidae Okulitch, 1950b, p. 394; ?=Protocyclocyathidae Vologdin, 1956, p. 878; ?=Protocyclocyathellidae Vologdin, 1956, p. 878, *lapsus calami* Debrenne & James, 1981, p. 366, *pro* Protocyclocyathidae Vologdin, 1956, p. 878; =Syringsellidae Krasnopeeva, 1961, p. 248; =Archaeofungiidae Vologdin, 1962c, p. 90, *nom. correct*. Hill, 1965, p. 58, *pro* Archaeofungidae Vologdin, 1962c, p. 90; =Vadimocyathidae Kashina in Osadchaya & others, 1979, p. 161; =Claruscyathinae Fonin in Zhuravleva & Fonin, 1983, p. 49]

Inner wall with bracts, fused bracts, or pore tubes. *lower Cambrian (?Atd.4, Bot.2–Toy.3).*

Archaeocyathus Billings, 1861, p. 3 [**A. atlanticus* Billings, 1861, p. 5; SD Walcott, 1886, p. 75; holotype, Billings, 1861, fig. 5; Hinde, 1889, pl. 5,*8–10;* Okulitch, 1943, pl. 5,*1–2*, GSC 369, Ottawa] [Original spelling was *Archeocyathus* Billings; subsequent authors have used the diphthong] [=*Spirocyathus* Hinde, 1889, p. 136 (type, *Archeocyathus atlanticus* Billings, 1861, p. 5, M); =*Retecyathus* Vologdin, 1932, p. 20, *nom. nud.*; =*Claruscyathus* Vologdin, 1932, p. 25 (type, *C. cumfundus*, M); =*Eucyathus* Vologdin, 1937b, p. 466, *nom. nud.*; =*Flindersicyathus* R. Bedford & J. Bedford, 1937, p. 28, *nom. nud.*; =*Flindersicyathus* R. Bedford & J. Bedford, 1939, p. 78 (type, *F. decipiens*, OD); =*Eucyathus* Vologdin in Simon, 1939, p. 29 (type, *Claruscyathus cumfundus* Vologdin, 1932, p. 25, OD); =*Retecyathus* Vologdin in Simon, 1939, p. 36 (type, *R. laqueus* Vologdin, 1932, p. 20, SD Simon, 1939, p. 36, =*Claruscyathus cumfundus* Vologdin, 1932, p. 25); =*Syringsella* Krasnopeeva, 1961, p. 248 (type, *S. ynyrgensis*, OD); =*Batenevia* Krasnopeeva, 1961, p. 249 (type, *B. pellisi*, OD); =*Sanxiacyathus* Yuan & Zhang, 1977, p. 8 (type, *S. hubeiensis*, OD); =*Bijacyathus* Krasnopeeva, 1978, p. 81 (type, *Archaeocyathus regularis* Krasnopeeva in Zhuravleva, Krasnopeeva, & Chernysheva, 1960, p. 135, M, =*Retecyathus kusmini* Vologdin, 1932, p. 21); =*Retecyathus (Pararetecyathus)* Yuan & Zhang, 1978, p. 139 (type, *R. (P.) curvatus,* OD); =*Vadimocyathus* Kashina in Osadchaya & others, 1979, p. 161 (type, *V. chikinevae*, OD), for discussion, see Debrenne & Zhuravlev, 1992b, p. 120]. Inner wall with one row of pores per intersept, bearing upwardly projecting, straight pore tubes; pseudotaenial network coarsely porous; concentrically porous segmented tabulae. *lower Cambrian (?Atd.4, Bot.2–Toy.3):* Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East, Uzbekistan, Canada, United States, Mexico, Australia, Antarctica, South China, North China,

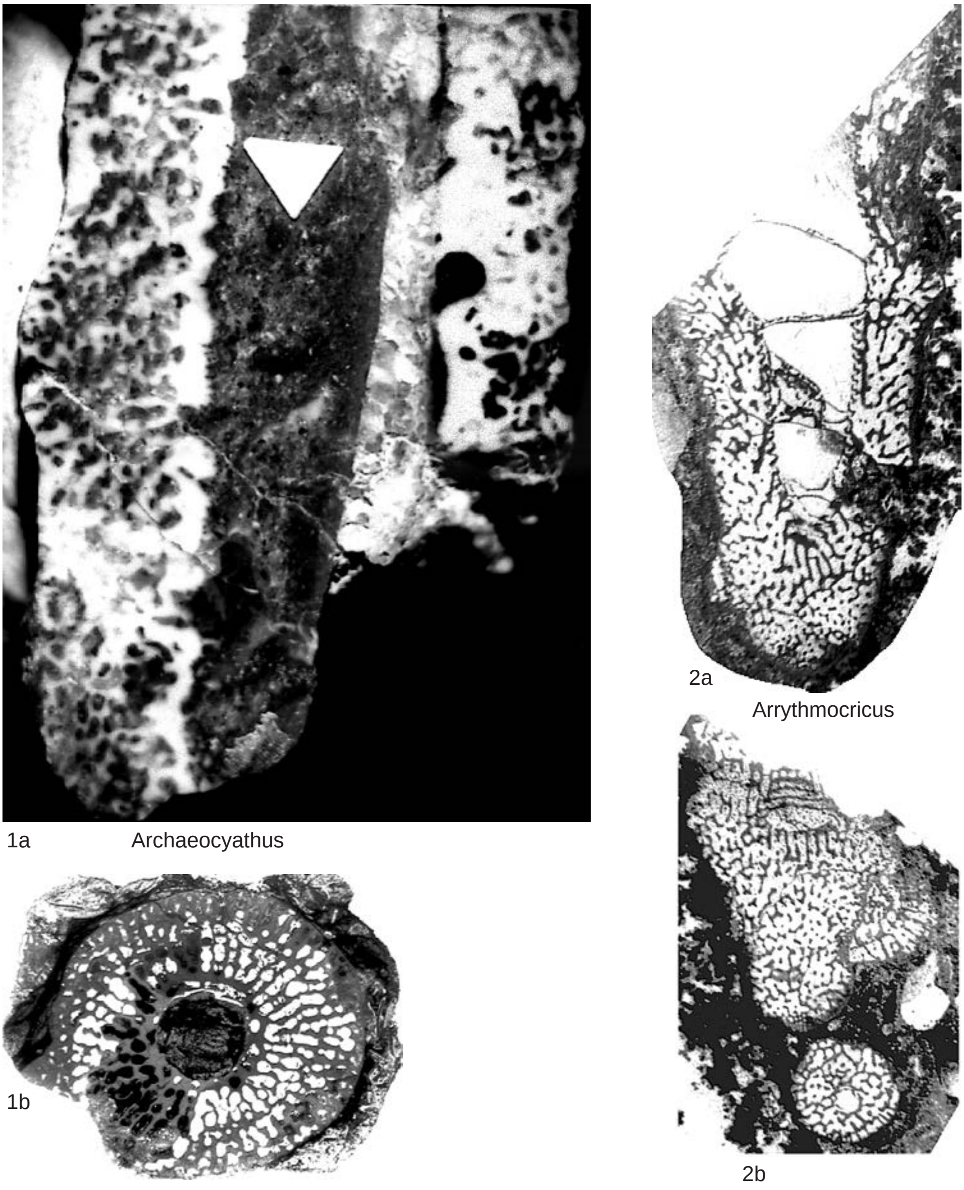


FIG. 629. Archaeocyathidae (p. 1055–1057).

Iberia, Sardinia.——FIG. 629,*1a–b*. **A. atlanticus*, Forteau Formation, Botoman, Anse au Loup, Labrador, Canada, holotype, GSC 369; *a,* longitudinal section (white triangle is adherent paper label), ×2.5 (Okulitch, 1943); *b,* transverse section, ×3 (Debrenne, Zhuravlev, & Kruse, 2002).

Arrythmocricus DEBRENNE & JAMES, 1981, p. 366 [**A. kobluki*; OD; holotype, DEBRENNE & JAMES, 1981, pl. 53,*3–4*, GSC 62123, Ottawa]. Inner wall with one row of pores per intersept, bearing upwardly projecting, S-shaped bracts or fused bracts; pseudotaenial network coarsely porous. *lower Cambrian*

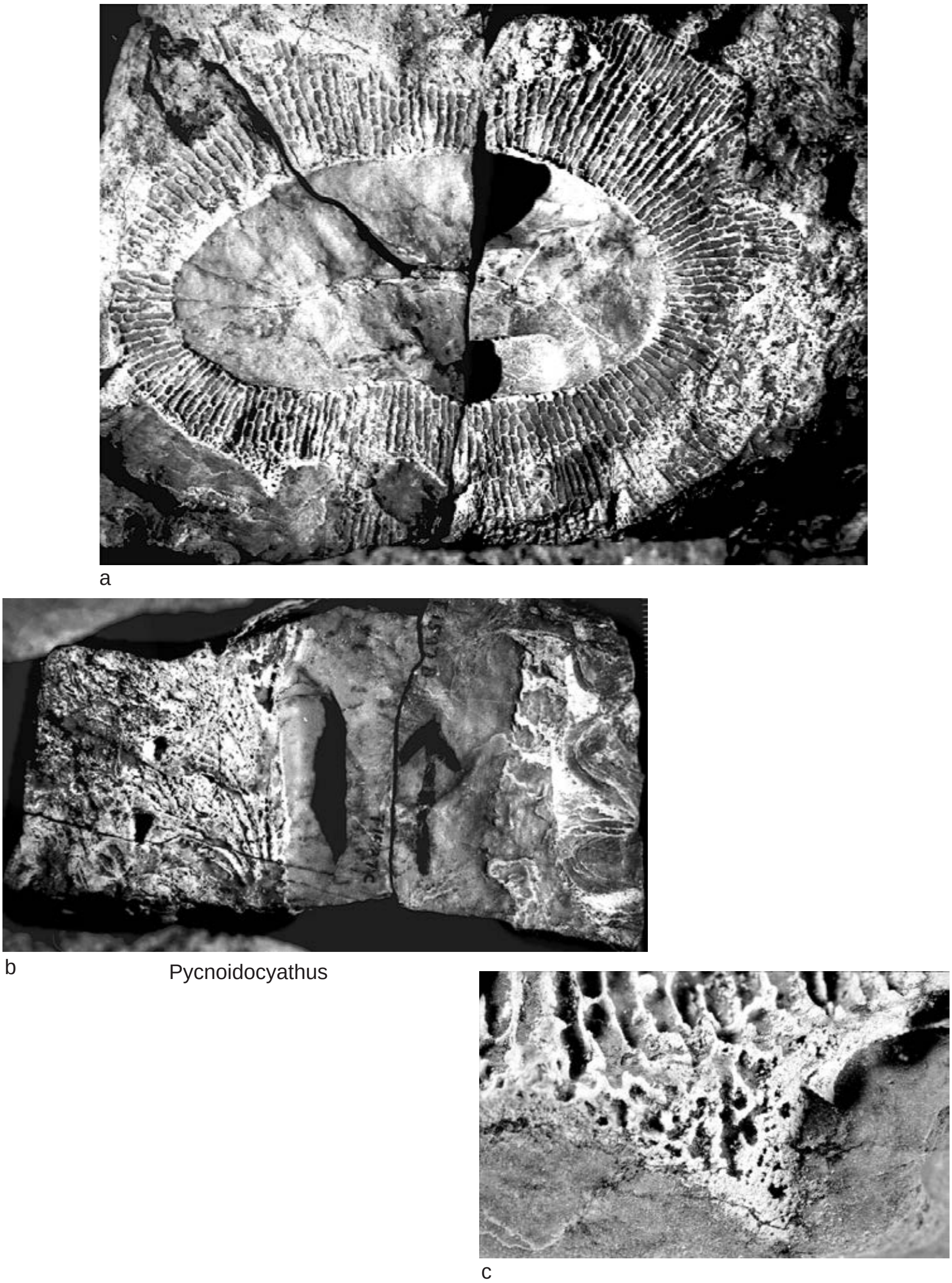


FIG. 630. Archaeocyathidae (p. 1057–1058).

(Bot.1–Bot.3): Canada, United States, Mexico.——FIG. 629,*2a–b*. **A. kobluki*, Forteau Formation, Botoman, Fox Cove, Labrador, Canada, holotype, GSC 62123; *a,* longitudinal section of modular skeleton, ×5; *b,* longitudinal section (inner wall at top), ×5 (Debrenne & James, 1981).

Pycnoidocyathus TAYLOR, 1910, p. 131 [**P. synapticulosus*; SD R. BEDFORD & J. BEDFORD, 1939,

p. 78; lectotype, Taylor, 1910, pl. 12, photo 69; Debrenne, 1974a, fig. 13a–b; SD Debrenne, 1970a, p. 40, SAM T1587A,B,C, Adelaide] [=*Archaeofungia* Taylor, 1910, p. 131 (type, *A. ajax*, M); =*Batenevicyathus* Yaroshevich, 1962, p. 117, 122 (type, *B. zhuravlevae*, OD), for discussion, see Debrenne & Zhuravlev, 1992b, p. 129]. Inner wall with one row of pores per intersept, bearing upwardly projecting, straight pore tubes; taeniae coarsely porous, linked at base by synapticulae; during ontogeny, taeniae become progressively less porous, more planar and without synapticulae. *lower Cambrian (Bot.2–Toy.3):* Altay Sayan, Tuva, Mongolia, Far East, Australia, Antarctica, Falkland Islands (allochthonous), South China, North China, Iberia, Sardinia, Greenland, Canada, United States, Mexico.——Fig. 630*a–c*. **P. synapticulosus*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM T1587A–C; *a,* transverse view, ×1; *b,* longitudinal view, ×1; *c,* detail of outer wall in tangential view, ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

Sigmofungia R. Bedford & W. R. Bedford, 1936, p. 16 [**S. flindersi*; M; lectotype, R. Bedford & W. R. Bedford, 1936, fig. 82; Hill, 1965, pl. 6,*1–2;* Debrenne, 1974a, fig. 30a–b; SD Hill, 1965, p. 89, SAM P963-115, -116, Adelaide] [=*Palmericyathellus* Debrenne, 1970a, p. 37 (type, *Sigmofungia tabularis* R. Bedford & J. Bedford, 1937, p. 29, OD, =*Sigmofungia flindersi* R. Bedford & W. R. Bedford, 1936, p. 16), for discussion, see Debrenne & Zhuravlev, 1992b, p. 130; =*Palmericyathus* Debrenne in Zhuravleva, 1974b, p. 15 (type, *Ethmophyllum lineatus* Greggs, 1959, p. 66, OD), *nom. null.*, *non* Handfield, 1971, p. 44, archaeocyath]. Inner wall with one row of pores per intersept, bearing upwardly projecting, S-shaped pore tubes; taeniae finely porous, linked by synapticulae; concentrically porous, segmented tabulae. *lower Cambrian (Bot.2–Bot.3):* Australia, Antarctica, Mexico.——Fig. 631*a–c*. **S. flindersi*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM P963-115, -116; *a,* transverse and longitudinal views, ×3 (Hill, 1965); *b,* detail of inner wall in oblique view, ×11 (Debrenne, 1974a); *c,* detail of outer wall in tangential view, ×10 (Debrenne, Zhuravlev, & Kruse, 2002).

Family ARCHAEOSYCONIDAE Zhuravleva, 1954

[Archaeosyconidae Zhuravleva, 1954, p. 30]

Inner wall compound. *lower Cambrian (Bot.1–Bot.3).*

Archaeosycon Taylor, 1910, p. 111 [**Archaeocyathus billingsi* Walcott, 1886, p. 74; M; holotype, Walcott, 1886, pl. 3,*3a–c;* Okulitch, 1943, pl. 14,*2–3*, USNM 15302, Washington, D.C.] [=*Pustulacyathellus* Debrenne & Gangloff in Voronova & others, 1987, p. 42 (type, *P. copulatus*, OD), for discussion, see Debrenne & Zhuravlev, 1992b, p. 121]. Outer wall tabular; inner wall compound, comprising wall carcass and tabulae; taeniae coarsely porous; concentrically porous segmented tabulae. *lower Cambrian (Bot.1–Bot.3):* Canada, United States.——Fig. 632*a–b*. **A. billingsi* (Walcott), Forteau Formation, Botoman, Anse au Loup, Labrador, Canada, holotype, USNM 15302; *a,* longitudinal section, ×3; *b,* transverse section, ×3 (Okulitch, 1943).

Superfamily METACYATHOIDEA R. Bedford & W. R. Bedford, 1934

[*nom. correct.* Debrenne & Kruse, 1986, p. 266, *pro* Metacyathacea Fonin, 1983, p. 11, *nom. transl. ex* Metacyathidae R. Bedford & W. R. Bedford, 1934, p. 5] [=Spirillicyathacea Gravestock, 1984, p. 111]

Outer wall compound. *lower Cambrian (Tom.2–Bot.3).*

Family COPLEICYATHIDAE R. Bedford & J. Bedford, 1937

[Copleicyathidae R. Bedford & J. Bedford, 1937, p. 29] [=Tabulacyathellidae Fonin in Voronin & others, 1982, p. 86; =Spirillicyathidae Gravestock, 1984, p. 111].

Inner wall with simple pores. *lower Cambrian (Tom.2–Bot.3).*

Copleicyathus R. Bedford & J. Bedford, 1937, p. 29 [**C. confertus*; OD; holotype, R. Bedford & J. Bedford, 1937, fig. 116; Hill, 1965, pl. 10,*4;* Debrenne, 1974a, fig. 27, USNM PU86741-783, Washington, D.C.]. Outer wall compound with completely subdivided pores; inner wall with several rows of simple pores per intersept; pseudotaenial network coarsely porous. *lower Cambrian (Atd.3–Atd.4):* Australia.——Fig. 633*a–b*. **C. confertus*, Ajax Limestone, Atdabanian, Paint Mine, South Australia, Australia, holotype, USNM PU86741-783; *a,* transverse view, ×5; *b,* longitudinal view, ×5 (Hill, 1965).

Agastrocyathus Debrenne, 1964, p. 209 [**Protopharetra gregaria* Debrenne, 1961, p. 21; OD; holotype, Debrenne, 1961, pl. 2,*5–6*, MNHN M80138, HD71, Paris]. Outer wall compound with incipient subdivision of intervallar cells; inner wall with one row of simple pores per intersept; taeniae coarsely porous, linked by synapticulae. *lower Cambrian (Atd.2–Atd.4):* South China, Morocco, Iberia.——Fig. 634*a–c*. **A. gregarius* (Debrenne), Amouslek Formation, Atdabanian, Jbel Taïssa, Morocco, holotype, MNHN M80138, HD71; *a,* longitudinal section of modular skeleton, ×3; *b,* transverse section of modular skeleton, ×4; *c,* detail of outer wall in tangential section, ×10 (Debrenne, Zhuravlev, & Kruse, 2002).

Gabrielsocyathus Debrenne, 1964, p. 248 [**Metacoscinus gabrielsensis* Okulitch, 1955b, p. 61; OD; holotype, Okulitch, 1955b, pl.

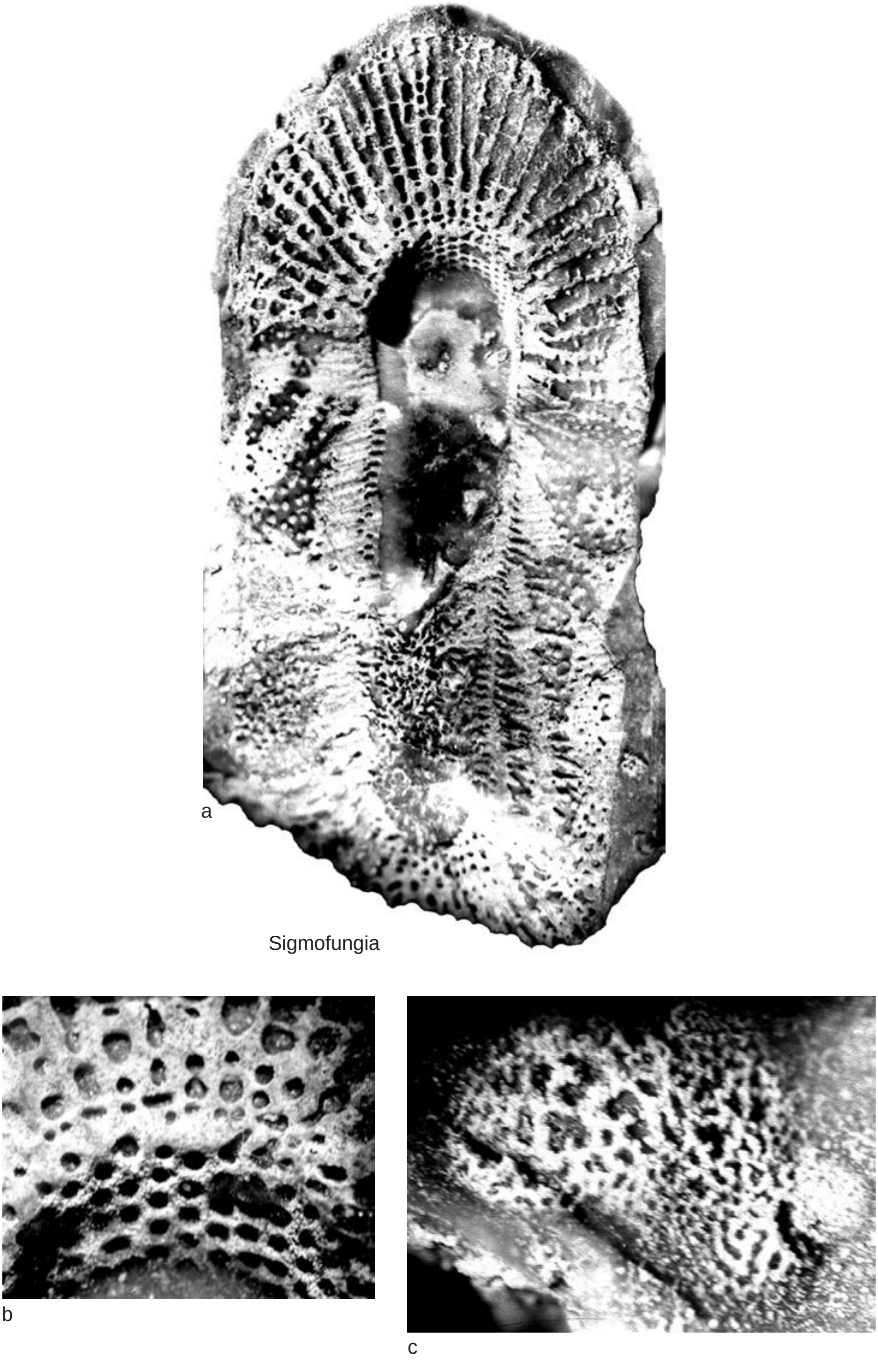


FIG. 631. Archaeocyathidae (p. 1058).

FIG. 632. Archaeosyconidae (p. 1058).

1,*1,2,5*, GSC 12357, Ottawa]. Outer wall compound with completely subdivided pores; inner wall with several rows of simple pores per intersept; taeniae finely porous, linked by synapticulae; simple segmented tabulae. *lower Cambrian (Bot.2):* Canada, United States.——FIG. 635,*1a–c*. **G. gabrielsensis* (OKULITCH), Atan Group, Botoman, McDame Lake, British Columbia, Canada, holotype, GSC 12357; *a,* transverse section, ×2.5; *b,* longitudinal section, ×2.5; *c,* transverse section (outer wall at bottom), ×2.5 (Debrenne, Zhuravlev, & Kruse, 2002).

Metacyathellus DEBRENNE & ZHURAVLEV, 1990, p. 302 [**Metaldetes*? *caribouensis* HANDFIELD, 1971, p. 64; OD; holotype, HANDFIELD, 1971, pl. 11,*2*, GSC 25367, Ottawa]. Outer wall compound with completely subdivided pores; inner wall with one to two rows of simple pores per intersept; taeniae coarsely porous; compound segmented tabulae. *lower Cambrian (Atd.4–Bot.3):* Australia, Antarctica, Falkland Islands (allochthonous), South China, Canada, United States.——FIG. 635,*2a–c*. **M. caribouensis* (HANDFIELD), Sekwi Formation, Botoman; *a,* Caribou Pass, Northwest Territories, Canada, holotype, GSC 25367, transverse section, ×4 (Handfield, 1971); *b,* Mackenzie Mountains, Northwest Territories, Canada, specimen GSC 90187, detail of outer wall in tangential section, ×10 (Voronova & others, 1987); *c,* Caribou Pass, Northwest Territories, Canada, holotype, GSC 25367, longitudinal section, ×6 (Handfield, 1971). [*2a, 2c* are reproduced with the permission of the Minister of Public Works and Government Services Canada, 2006 and courtesy of Natural Resources Canada, Geological Survey of Canada.]

Spinosocyathus ZHURAVLEVA, 1960b, p. 276 [**S. maslennikovae*; OD; holotype, ZHURAVLEVA, 1960b, pl. 25,*1b*, TsSGM 205/134, Novosibirsk]. Outer wall compound with incipient pore subdivision; inner wall with one row of simple pores per intersept; pseudotaenial network coarsely porous; compound segmented tabulae. *lower Cambrian (Tom.2–Atd.2):* Siberian Platform, Mongolia, Iberia.——FIG. 636,*1a–b*. **S. maslennikovae*, Pestrotsvet Formation, Tommotian, Churan, Lena River, Sakha (Yakutia), Russia; *a,* holotype, TsSGM 205/134, transverse section (outer wall at bottom), ×8 (Zhuravleva, 1960b); *b,* oblique longitudinal section of modular skeleton, specimen TsSGM 144-32/4, ×3 (Debrenne, Zhuravlev, & Kruse, 2002).

Spirillicyathus R. BEDFORD & J. BEDFORD, 1937, p. 30 [**S. tenuis*; OD; holotype, R. BEDFORD & J. BEDFORD, 1937, fig. 118; DEBRENNE, 1974a, fig. 10, USNM PU493967, specimen 358, Washington, D.C.] [=*Spiralicyathus* R. BEDFORD & J. BEDFORD, 1937, fig. 118 caption, *nom. null.*]. Outer wall compound with completely subdivided pores; inner wall with one to two rows of simple pores per intersept; pseudotaenial network coarsely porous. *lower Cambrian (Atd.4–Bot.1):* Australia, South China.——FIG. 636,*2a–c*. **S. tenuis*, Ajax Limestone, Atdabanian, Paint Mine, South Australia, Australia; *a–b,* holotype, USNM PU493967, specimen 358; *a,* transverse view, ×9; *b,* longitudinal view, ×9 (Debrenne, 1974a); *c,* Wilkawillina Limestone, Atdabanian, Wilkawillina Gorge, South Australia, Australia, specimen SAM P21741, tangential section of outer wall, ×10 (Gravestock, 1984).

Tabulacyathellus MISSARZHEVSKIY in REPINA & others, 1964, p. 249 [**T. bidzhaensis*; OD; holotype, REPINA & others, 1964, pl. 7,*4–6*, PIN 4297/22, Moscow]. Outer wall compound with completely subdivided pores; inner wall tabular with several rows of simple pores per intersept; pseudotaenial network coarsely porous; compound segmented tabulae. *lower Cambrian (Atd.2):* Altay Sayan, Tuva, Mongolia.——FIG.

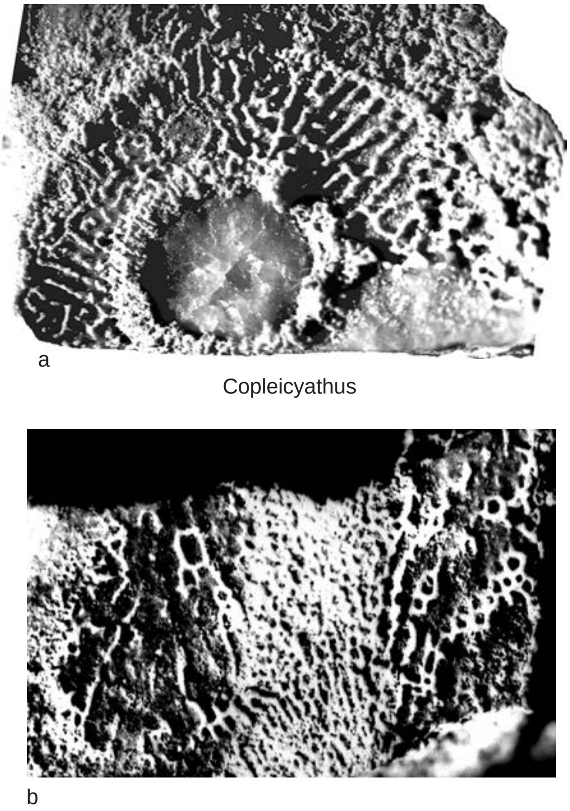


FIG. 633. Copleicyathidae (p. 1058).

637*a–c*. **T. bidzhaensis*, Usa Formation, Atdabanian, Sukhie Solontsy Valley, Batenev Range, Kuznetsk Alatau, Russia, holotype, PIN 4297/22; *a,* tangential section of outer wall, ×5; *b,* longitudinal section (outer wall to left), ×5; *c,* transverse section, ×5 (Repina & others, 1964).

Family JUGALICYATHIDAE Gravestock, 1984

[Jugalicyathidae GRAVESTOCK, 1984, p. 114]

Inner wall with bracts, fused bracts or pore tubes. *lower Cambrian (Atd.4–Bot.2).*

Jugalicyathus GRAVESTOCK, 1984, p. 114 [**J. tardus*; OD; holotype, GRAVESTOCK, 1984, fig. 56H–I, SAM P21747, Adelaide]. Outer wall compound with incipient subdivision of intervallar cells; inner wall with one row of pores per intersept, bearing upwardly projecting, straight pore tubes; pseudosepta finely porous. *lower Cambrian (Atd.4):* Australia.——FIG. 638,*1a–b*. **J. tardus*; *a,* Wilkawillina Limestone, Atdabanian, Wilkawillina Gorge, South Australia, Australia, paratype, SAM P21749, oblique transverse section, ×8 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* Ajax Limestone, Atdabanian, Mount Scott Range, South Australia, Australia, holotype, SAM P21747, longitudinal section, ×1 (Gravestock, 1984).

Alaskacoscinus DEBRENNE, GANGLOFF, & ZHURAVLEV in DEBRENNE & ZHURAVLEV, 1990, p. 300 [**A. tatondukensis*; OD; holotype, DEBRENNE & ZHURAVLEV, 1990, pl. 1,*5*, UAM UA2534, 2535, Fairbanks]. Outer wall tabular, compound with completely subdivided pores; inner wall tabular with one row of pores per intersept, bearing upwardly projecting, S-shaped pore tubes; pseudosepta finely porous; segmented tabulae with subdivided pores. *lower Cambrian (Bot.2):* United States.——FIG. 638,*2a–b*. **A. tatondukensis*, Adams Argillite, Botoman, Tatonduk River, Alaska, United States; *a,* holotype, UAM UA2534, longitudinal section (outer wall to right), ×4; *b,* paratype, UAM UA2536, longitudinal section, ×5 (Debrenne & Zhuravlev, 1990).

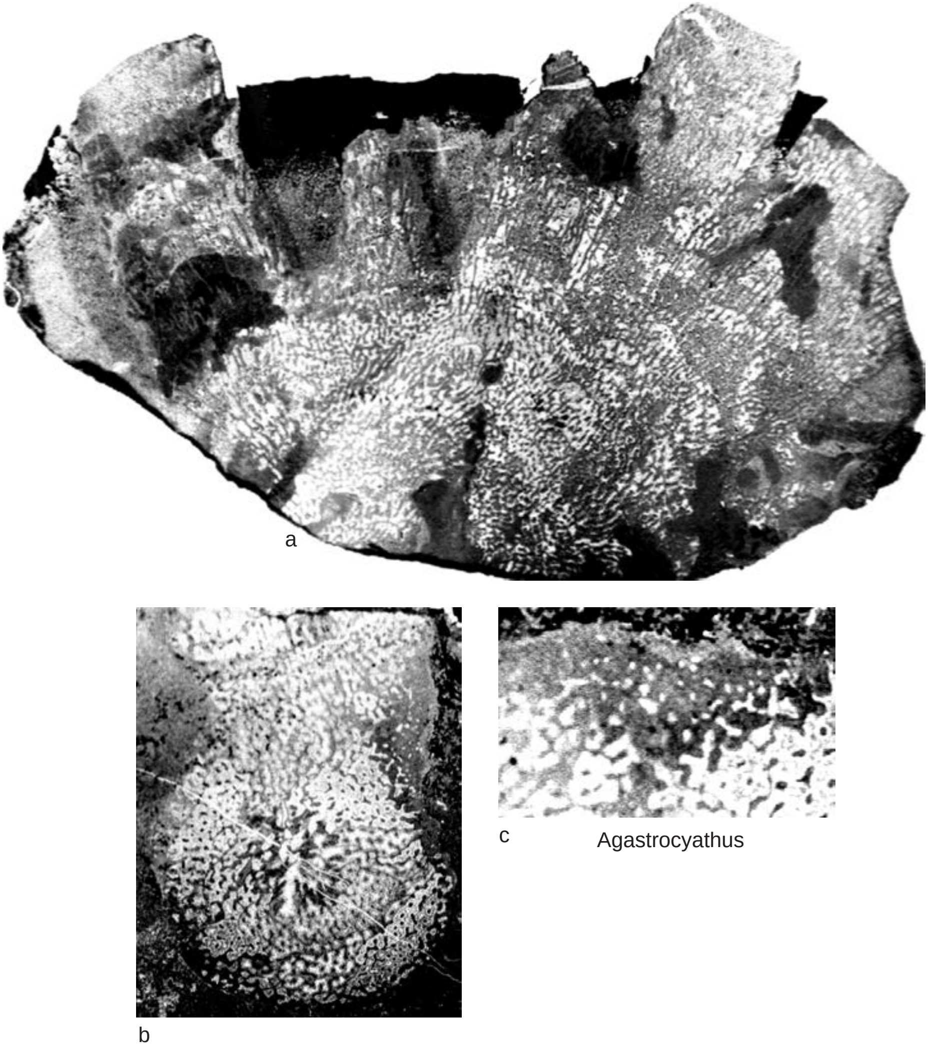


FIG. 634. Copleicyathidae (p. 1058).

Family METACYATHIDAE R. Bedford & W. R. Bedford, 1934

[Metacyathidae R. BEDFORD & W. R. BEDFORD, 1934, p. 5] [=Metacoscinidae R. BEDFORD & W. R. BEDFORD, 1936, p. 18; =Cambrocyathidae OKULITCH, 1937a, p. 251; =Cambrocyathinae OKULITCH, 1937a, p. 251, *nom. transl.* DEBRENNE, 1964, p. 218, *ex* Cambrocyathidae OKULITCH, 1937a, p. 251; =Metaldetinae DEBRENNE, 1964, p. 218; =Metafungiidae DEBRENNE, 1974a, p. 216]

Inner wall compound. *lower Cambrian (Atd.4–Bot.3).*

Metaldetes TAYLOR, 1910, p. 151 [**M. cylindricus*; M; holotype, TAYLOR, 1910, pl. 15, photo 86–88, fig. 11, 37, 38; DEBRENNE, 1974a, fig. 21a–b, M, SAM T1592A, Adelaide] [=*Metafungia* R. BEDFORD & W. R. BEDFORD, 1934, p. 5 (type, *M. reticulata*, M); =*Metacyathus* R. BEDFORD & W. R. BEDFORD, 1934, p. 5 (type, *M. taylori*, M, =*Archaeocyathus dissepimentalis* TAYLOR, 1910, p. 128); =*Metacoscinus* R. BEDFORD & W. R. BEDFORD, 1934, p. 6 (type, *M. reteseptatum*, M, =*Archaeocyathus retesepta* TAYLOR, 1910, p. 120); =*Cambrocyathus* OKULITCH, 1937a, p. 251 (type, *Archaeocyathus profundus* BILLINGS, 1861, p. 4, OD); =*Metethmophyllum* OKULITCH, 1943, p. 78 (type, *Ethmophyllum meeki* WALCOTT, 1889, p. 34, OD); =*Bedfordcyathus* VOLOGDIN, 1957a, p. 182 (type,

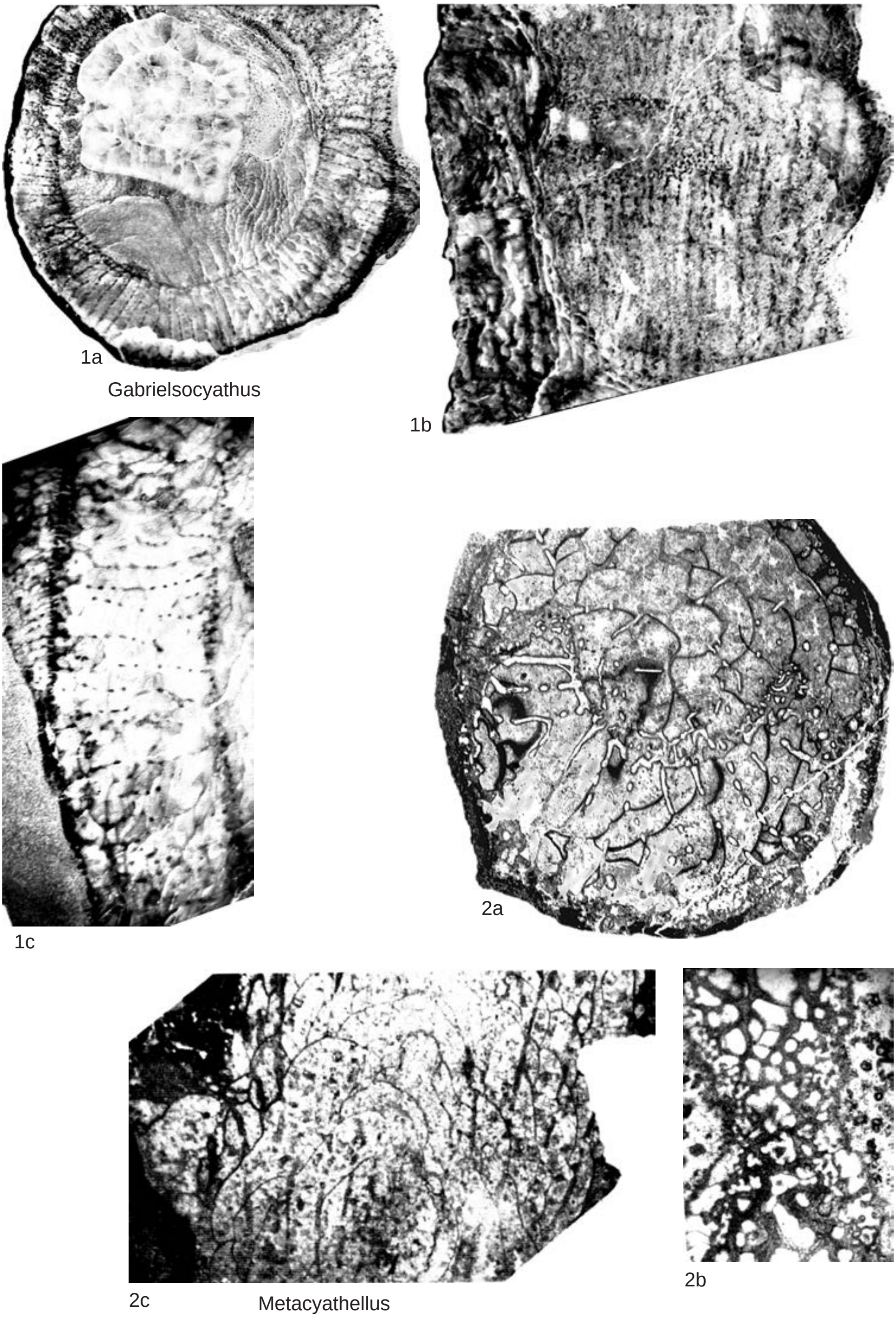


FIG. 635. Copleicyathidae (p. 1058–1060).

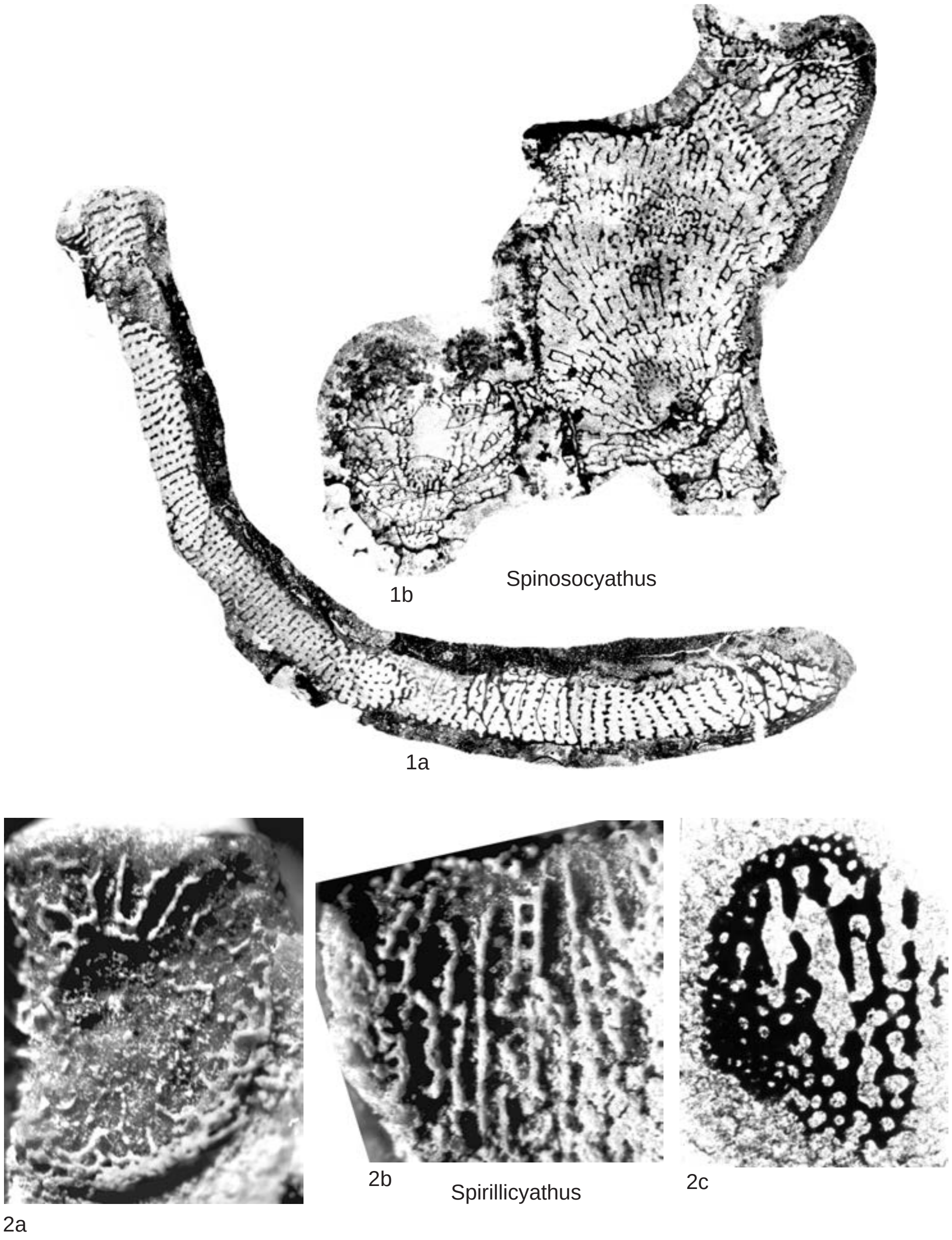


FIG. 636. Copleicyathidae (p. 1060).

Metacyathus irregularis R. BEDFORD & W. R. BEDFORD, 1934, p. 6, M, =*Archaeocyathus dissepimentalis* TAYLOR, 1910, p. 128); =*Praefungia* DEBRENNE in ZHURAVLEVA, 1974b, p. 42, *nom. correct.* DEBRENNE, 1974a, p. 227, *pro Pruefungia, lapsus calami* (type, *Metaldetes superbus* R. BEDFORD & W. R. BEDFORD, 1936, p. 18, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 127]. Outer wall compound with completely subdivided pores; inner wall compound with several rows of completely subdivided pores per intersept; taeniae coarsely porous, linked by synapticulae in early ontogenetic stages but rarely so in mature cups; compound segmented tabulae. *lower Cambrian (Atd.4–Bot.3):* Far East, Australia, Antarctica, Canada, United States, Mexico.——FIG. 639*a–e*. **M. cylindricus*, Wilkawillina Limestone, Botoman, Wilson, South Australia, Australia, holotype, SAM T1592A; *a,* transverse section, ×4; *b,* detail of inner wall in transverse

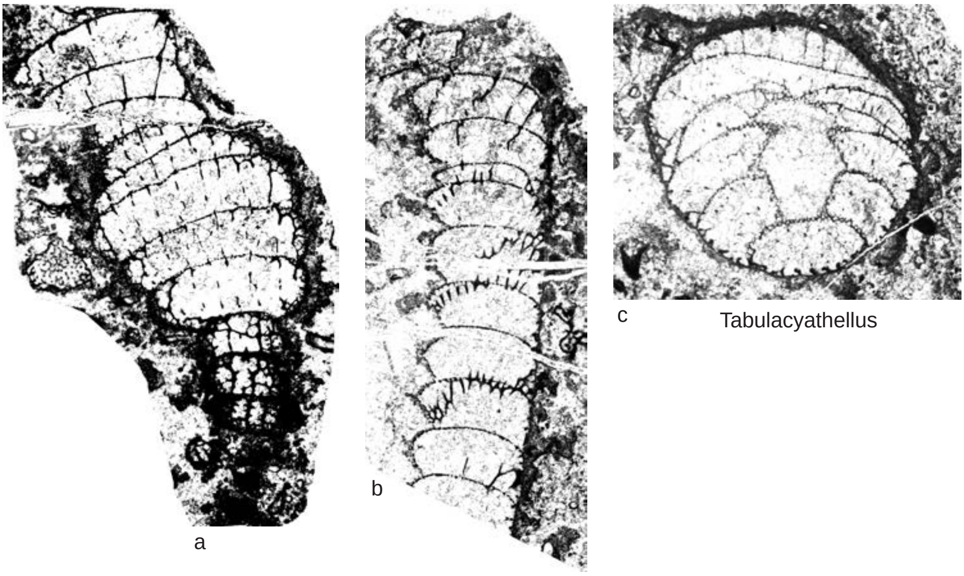


FIG. 637. Copleicyathidae (p. 1060–1061).

section, ×8; *c,* detail of outer wall in transverse section, ×8; *d,* detail of taenia in longitudinal section, ×8; *e,* longitudinal section of modular skeleton, ×4 (Debrenne, Zhuravlev, & Kruse, 2002).

Changicyathus DEBRENNE & ZHURAVLEV, 1990, p. 301 [**Cambrocyathellus tenuicaulus* ZHANG & YUAN, 1985, p. 523; OD; holotype, ZHANG & YUAN, 1985, pl. 2,*6;* DEBRENNE & ZHURAVLEV, 1990, pl. 1,*7*, NIGP 82277, specimen 17f(10-14), Nanjing]. Outer wall compound with completely subdivided pores; inner wall compound with incipient pore subdivision; taeniae coarsely porous; compound segmented tabulae. *lower Cambrian (Bot.1):* ?Tajikistan, South China.——FIG. 640. **C. tenuicaulus* (ZHANG & YUAN), Xiannudong Formation, Botoman, Nanzhen, Sichuan, China, holotype, NIGP 82277, specimen 17f(10-14), oblique longitudinal section of modular skeleton, ×6 (Debrenne & Zhuravlev, 1990).

Superfamily NAIMARKCYATHOIDEA Wrona & Zhuravlev, 1996

[Naimarkcyathoidea WRONA & ZHURAVLEV, 1996, p. 28]

Outer wall pustular. *lower Cambrian (Bot.3).*

Family NAIMARKCYATHIDAE Wrona & Zhuravlev, 1996

[Naimarkcyathidae WRONA & ZHURAVLEV, 1996, p. 29]

Inner wall with bracts, fused bracts or pore tubes. *lower Cambrian (Bot.3).*

Naimarkcyathus WRONA & ZHURAVLEV, 1996, p. 29 [**N. elenae*; OD; holotype, WRONA & ZHURAVLEV, 1996, pl. 7,*2*, ZPAL Ac.I/M10DI, Warsaw]. Inner wall with one row of pores per intersept, bearing upwardly projecting, straight pore tubes; pseudotaenial network coarsely porous. *lower Cambrian (Bot.3):* Antarctica.——FIG. 641*a–b*. **N. elenae*, Polonez Cove Formation (allochthonous), Botoman, Mazurek Point, King George Island, South Shetland Islands, Antarctica; *a,* holotype, ZPAL Ac.I/M10DI, transverse section, ×5; *b,* paratype, ZPAL Ac.I/M10CI, longitudinal section, ×5 (Wrona & Zhuravlev, 1996).

Superfamily WARRIOOTACYATHOIDEA Debrenne & Zhuravlev, 1992

[Warriootacyathoidea DEBRENNE & ZHURAVLEV, 1992b, p. 115]

Outer wall with canals. *lower Cambrian (Atd.3–Atd.4).*

Family WARRIOOTACYATHIDAE Debrenne & Zhuravlev, 1992

[Warriootacyathidae DEBRENNE & ZHURAVLEV, 1992b, p. 115]

Inner wall with bracts, fused bracts or pore tubes. *lower Cambrian (Atd.3–Atd.4).*

Warriootacyathus GRAVESTOCK, 1984, p. 126 [**W. wilkawillinensis*; OD; holotype, GRAVESTOCK, 1984, fig. 62A,D–F, SAM P21806-1, Adelaide]. Outer wall with horizontal to upwardly projecting, straight canals; inner wall with one row of pores

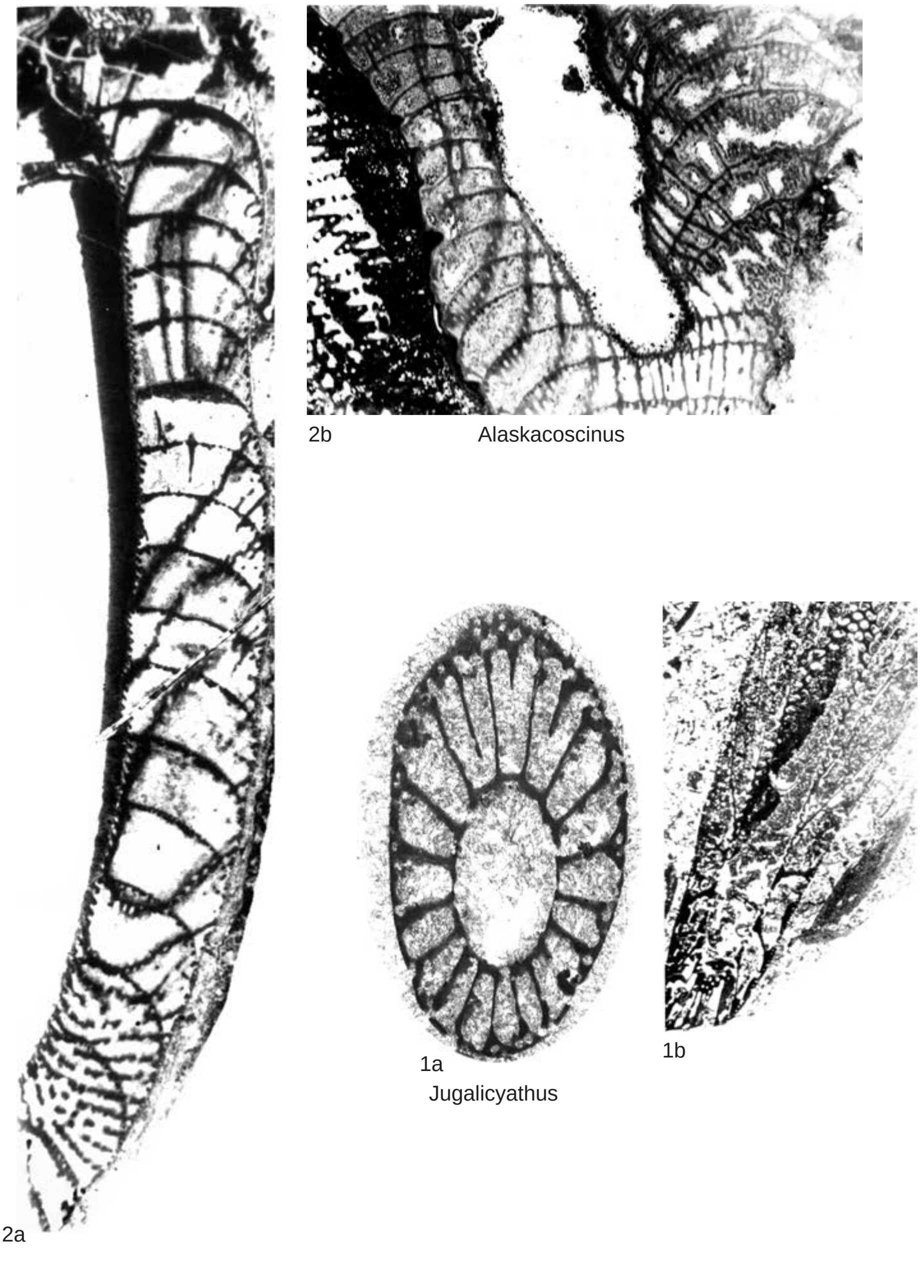


FIG. 638. Jugalicyathidae (p. 1061).

per intersept, bearing upwardly projecting, straight to waved pore tubes; pseudosepta coarsely porous. *lower Cambrian (Atd.3–Atd.4):* Australia.——FIG. 642*a–c*. **W. wilkawillinensis*, Wilkawillina Limestone, Atdabanian, Wilkawillina Gorge, South Australia, Australia, holotype, SAM P21806-1; *a,* tangential section of outer wall, ×7; *b,* tangential section of inner wall, ×3; *c,* longitudinal section of septum (outer wall to right), ×3 (Gravestock, 1984).

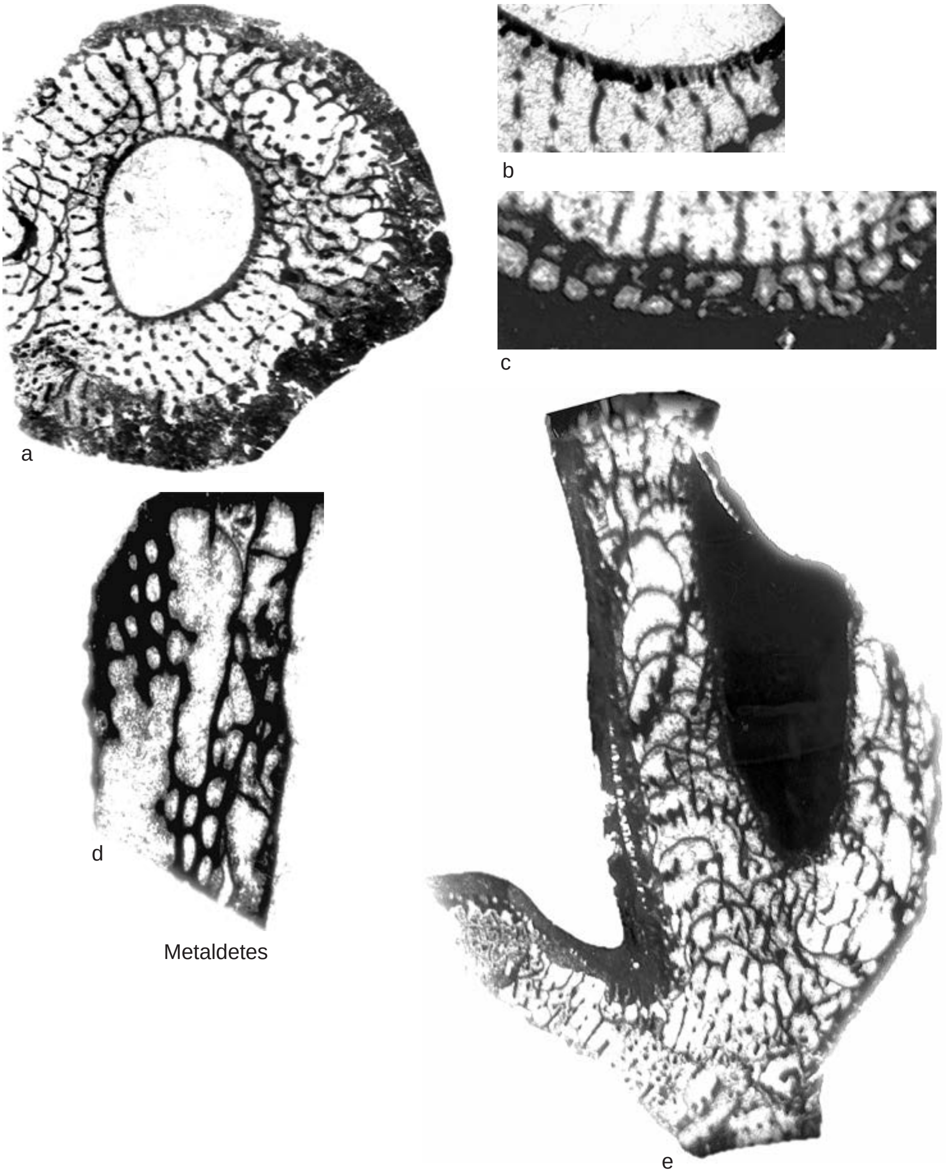


FIG. 639. Metacyathidae (p. 1062–1065).

Superfamily BELTANACYATHOIDEA
Debrenne, 1974

[*nom. correct.* DEBRENNE & ZHURAVLEV, 1992b, p. 115, *pro* Beltanacyathacea GRAVESTOCK, 1984, p. 123, *nom. transl. ex* Beltanacyathidae DEBRENNE, 1974a, p. 243] [=Beltanacyathidae DEBRENNE, 1970a, p. 30, *nom. nud.*]

Outer wall with subdivided canals. *lower Cambrian (Atd.3–Bot.3).*

Family MAIANDROCYATHIDAE
Debrenne, 1974

[Maiandrocyathidae DEBRENNE, 1974a, p. 235]

Inner wall with simple pores. *lower Cambrian (Bot.3).*

Maiandrocyathus DEBRENNE in ZHURAVLEVA, 1974a, p. 209 [**Metacoscinus insigne* R. BEDFORD & W. R. BEDFORD, 1936, p. 18; OD; holotype, R. BEDFORD

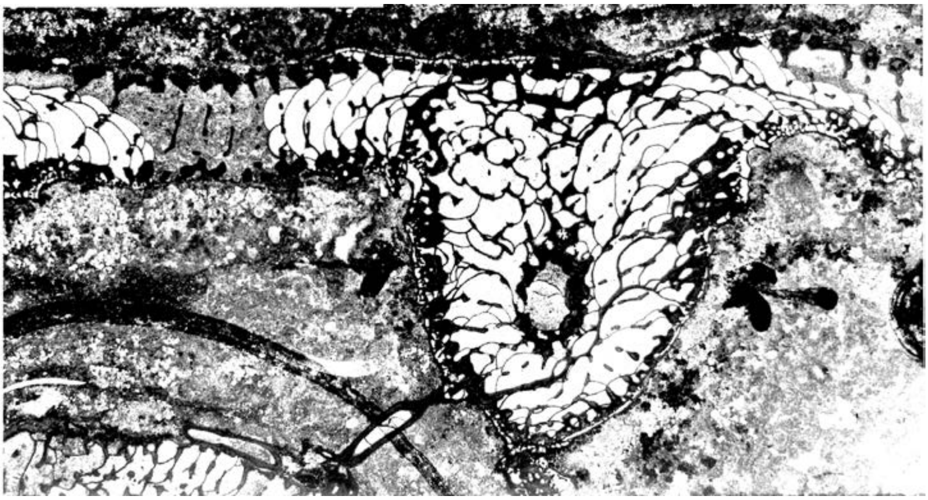


FIG. 640. Metacyathidae (p. 1065).

& W. R. BEDFORD, 1936, fig. 84; DEBRENNE, 1974a, fig. 28, M, SAM P986-167, -168, Adelaide]. Inner wall with one to two rows of simple pores per intersept; taeniae coarsely porous. *lower Cambrian (Bot.3):* Australia.——FIG. 643,*1a–b*. **M. insigne* (R. BEDFORD & W. R. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, SAM P986-167, -168; *a,* tangential view of outer wall, ×3; *b,* longitudinal view of septum and exocyathoid buttress (outer wall to right), ×3 (Debrenne, Zhuravlev, & Kruse, 2002).

Ataxiocyathus DEBRENNE in ZHURAVLEVA, 1974a, p. 52 [**Paranacyathus grandis* R. BEDFORD & J. BEDFORD, 1937, p. 34; OD; holotype, R. BEDFORD & J. BEDFORD, 1937, fig. 140; DEBRENNE, 1974c, pl. 20,*3–4,* M, USNM PU86821, specimen 311, Washington, D.C.]. Inner wall with one row of simple pores per intersept; pseudosepta finely porous. *lower Cambrian (Bot.3):* Australia.——FIG. 643,*2a–c*. **A. grandis* (R. BEDFORD & J. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, USNM PU86821, specimen 311; *a,* transverse view, ×5 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* longitudinal view of septum (outer wall to left), ×6 (Debrenne, Zhuravlev, & Kruse, 2012b); *c,* tangential view of outer wall, ×6 (Debrenne, 1974c).

Family BELTANACYATHIDAE
Debrenne, 1974

[Beltanacyathidae DEBRENNE, 1974a, p. 243] [=Beltanacyathidae DEBRENNE, 1970a, p. 30, *nom. nud.*]

Inner wall with bracts, fused bracts, or pore tubes. *lower Cambrian (Atd.3–Atd.4).*

Beltanacyathus R. BEDFORD & J. BEDFORD, 1936, p. 23 [**B. ionicus*; OD; lectotype, R. BEDFORD & J. BEDFORD, 1936, fig. 95–96; HILL, 1965, pl. 6,*3;* SD HILL, 1965, p. 89, USNM PU86716-271, Washington, D.C.; =*Archaeocyathus wirrialpensis* TAYLOR, 1910, p. 124; holotype, TAYLOR, 1910, pl. 8, photo 43–44; DEBRENNE, 1974a, fig. 33b; M, SAM T1581A-E, Adelaide] [=*Fridaycyathus* GRAVESTOCK, 1984, p. 125 (type, *F. biserialis*, OD); =*Bayleicyathus* GRAVESTOCK, 1984, p. 131 (type, *B. bowmani*, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 122]. Inner wall with one row of pores per intersept, bearing upwardly projecting, straight pore tubes; pseudosepta finely porous; segmented tabulae. *lower Cambrian (Atd.3–Atd.4):* Australia.——FIG. 644*a–d*. **B. wirrialpensis* (TAYLOR); *a–b,* holotype, Wilkawillina Limestone, Atdabanian, Wirrealpa Mine, South Australia, Australia, SAM T1581A-E; *a,* transverse section (outer wall at top), ×2; *b,* longitudinal section (outer wall to left), ×2.5 (Taylor, 1910); *c–d,* lectotype [=*B. ionicus*], Ajax Limestone, Atdabanian, Paint Mine, South Australia, Australia, USNM PU86716-271; *c,* transverse view, ×2; *d,* longitudinal view, ×2 (Hill, 1965).

Superfamily
TABELLAECYATHOIDEA
Fonin, 1963

[*nom. transl.* DEBRENNE & ZHURAVLEV, 1992b, p. 116, *ex* Tabellaecyathidae FONIN, 1963, p. 15] [=Taeniaecyathellacea KONYUSHKOV, 1972, p. 141]

Outer wall tabellar. *lower Cambrian (Bot.2–Bot.3).*

Family TABELLAECYATHIDAE Fonin, 1963

[Tabellaecyathidae FONIN, 1963, p. 15] [=Taeniaecyathellidae KONYUSHKOV, 1972, p. 142; =Karakolocyathidae KONYUSHKOV, 1972, p. 142]

Inner wall with bracts, fused bracts, or pore tubes. *lower Cambrian (Bot.2–Bot.3).*

Taeniaecyathellus ZHURAVLEVA, 1960a, p. 45 [**T. semenovi*; OD; holotype, ZHURAVLEVA, 1960a, fig. 1i–k, TsSGM 273/7, Novosibirsk] [=*Tabellaecyathus* FONIN, 1963, p. 15 (type, *T. totus*, OD); =*Cambronanus* FONIN, 1963, p. 19 (type, *C. multicavitatus*, OD); =*Karakolocyathus* KONYUSHKOV, 1972, p. 142 (type, *K. loculatus*, OD; =*Tabellaecyathus totus* FONIN, 1963, p. 16), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 131]. Inner wall with several rows of pores per intersept, bearing upwardly projecting, straight pore tubes; dictyonal network. *lower Cambrian (Bot.2–Bot.3):* Altay Sayan.——FIG. 645*a–b*. **T. semenovi*, Verkhnemonok Formation, Botoman, Malyy Karakol River, West Sayan, Altay Sayan, Russia, holotype, TsSGM 273/7; *a,* oblique longitudinal section, ×5; *b,* detail of outer wall in tangential section, ×21 (Debrenne, Zhuravlev, & Kruse, 2002).

Suborder DICTYOFAVINA Debrenne, 1991

[Dictyofavina DEBRENNE, 1991, p. 219]

Skeleton solitary or modular, latter as branching or massive pseudocolonies (both by intercalicular budding); intervallum with calicles. *lower Cambrian (Atd.1–Bot.2).*

Superfamily USLONCYATHOIDEA Fonin, 1966

[*nom. transl.* DEBRENNE, ZHURAVLEV, & KRUSE, 2002, p. 1679, *ex* Usloncyathidae FONIN in VOLOGDIN & FONIN, 1966, p. 187] [=Dictyofavoidea DEBRENNE & ZHURAVLEV, 1992a, p. 596]

Outer wall simple. *lower Cambrian (Atd.1–Bot.2).*

Family USLONCYATHIDAE Fonin, 1966

[Usloncyathidae FONIN in VOLOGDIN & FONIN, 1966, p. 187] [=Dictyofavidae DEBRENNE & ZHURAVLEV, 1992a, p. 596]

Inner wall with simple pores. *lower Cambrian (Atd.1–Bot.2).*

Usloncyathus FONIN in VOLOGDIN & FONIN, 1966, p. 188 [**U. miculus*; OD; holotype, VOLOGDIN & FONIN, 1966, fig. 1a, PIN 2486/143, Moscow] [=*Falsocyathus* FONIN in VOLOGDIN & FONIN, 1966, p. 189 (type, *F. vastulus*, OD; =*U. miculus* FONIN in VOLOGDIN & FONIN, 1966, p. 188); =*Nostrocyathus* FONIN in VOLOGDIN & FONIN, 1966, p. 189 (type, *N. aculeatus*, OD; =*U. miculus* FONIN in VOLOGDIN & FONIN, 1966, p. 188); =*Cavocyathus* FONIN in VOLOGDIN & FONIN, 1966, p. 189 (type, *C. pusilus*; OD; =*U. miculus* FONIN in VOLOGDIN & FONIN, 1966, p. 188), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 132; =*Dictyofavus* GRAVESTOCK, 1984, p. 98 (type, *D. obtusus*, OD)]. Outer and inner walls rudimentary; calicles hexagonal in cross section with several pore rows per facet. *lower Cambrian (Atd.1–Atd.4):* Altay Sayan, Tuva, Mongolia, Transbaikalia, Far

FIG. 641. Naimarkcyathidae (p. 1065).

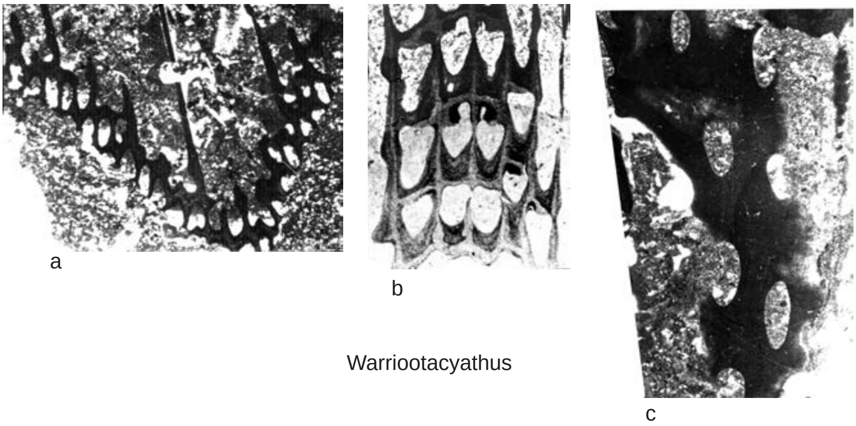


FIG. 642. Warriootacyathidae (p. 1065–1066).

East, Australia, South China.——FIG. 646,*1*. **U. miculus*, Bystraya Formation, Atdabanian, Uslon Valley, Transbaikalia, Russia, holotype, PIN 2486/143, longitudinal section, ×8 (Vologdin & Fonin, 1966).

Kechikacyathus DEBRENNE & ZHURAVLEV, 1992a, p. 598 [**K. natlaensis*; OD; holotype, DEBRENNE & ZHURAVLEV, 1992a, pl. 1,*3*, GSC 90166, Ottawa]. Outer wall basic; inner wall rudimentary; calicles hexagonal in cross section with one pore row per facet. *lower Cambrian (Bot.1–Bot.2):* Canada.——FIG. 646,*2a–b*. **K. natlaensis*, Sekwi Formation, Botoman; *a,* Kechika River, British Columbia, Canada, paratype, GSC 103939, GAM-78-G, detail of outer wall in tangential section, ×10; *b,* Natla, Mackenzie Mountains, Northwest Territories, Canada, holotype, GSC 90166, longitudinal section, ×5 (Debrenne & Zhuravlev, 1992a).

Zunyicyathus DEBRENNE, KRUSE, & ZHANG, 1991, p. 286 [**Agastrocyathus grandis* YUAN & ZHANG, 1980, p. 387; OD; *nom. correct.* DEBRENNE, KRUSE, & ZHANG, 1991, p. 286, *pro Agastrocyathus grandus* YUAN & ZHANG, 1980, p. 387; holotype, YUAN & ZHANG, 1980, pl. 1,*3*, NIGP 56292, Nanjing]. Outer and inner walls rudimentary; calicles tetragonal in cross section with one pore row per facet. *lower Cambrian (Bot.1–Bot.2):* Tajikistan, South China, United States.——FIG. 647. **Z. grandis* (YUAN & ZHANG), Jindingshan (Chintingshan) Formation, Botoman, Jindingshan, Guizhou, China, specimen MNHN 85103, longitudinal section of modular skeleton, ×5 (Debrenne, Kruse, & Zhang, 1991).

Superfamily KERIOCYATHOIDEA
Debrenne & Gangloff, 1992

[Keriocyathoidea DEBRENNE & GANGLOFF in DEBRENNE & ZHURAVLEV, 1992a, p. 598]

Outer wall concentrically porous. *lower Cambrian (Bot.1–Bot.2).*

Family KERIOCYATHIDAE
Debrenne & Gangloff, 1992

[Keriocyathidae DEBRENNE & GANGLOFF in DEBRENNE & ZHURAVLEV, 1992a, p. 598] [=Keriocyathidae DEBRENNE & GANGLOFF in DEBRENNE, GANDIN, & GANGLOFF, 1990, p. 93, *nom. nud.*]

Inner wall with simple pores. *lower Cambrian (Bot.1–Bot.2).*

Keriocyathus DEBRENNE & GANGLOFF in DEBRENNE, GANDIN, & GANGLOFF, 1990, p. 93 [**K. arachnaius*; OD; holotype, DEBRENNE, GANDIN, & GANGLOFF, 1990, pl. 1,*9*, USNM 443557, specimen IR24.10, Washington, D.C.]. Inner wall basic; calicles tetragonal in cross section with one pore row per facet. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Far East, United States.——FIG. 648*a–b*. **K. arachnaius*, Valmy Formation, Botoman, Iron Canyon, Nevada, United States; *a,* holotype, USNM 443557, specimen IR24.10, transverse section, ×7.5; *b,* paratype, USNM 443572, longitudinal section, ×7.5 (Debrenne, Gandin, & Gangloff, 1990).

Superfamily GATAGACYATHOIDEA
Debrenne & Zhuravlev, 1992

[Gatagacyathoidea DEBRENNE & ZHURAVLEV, 1992a, p. 598]

Outer wall compound. *lower Cambrian (Bot.2).*

Family GATAGACYATHIDAE
Debrenne & Zhuravlev, 1992

[Gatagacyathidae DEBRENNE & ZHURAVLEV, 1992a, p. 598]

Inner wall with simple pores. *lower Cambrian (Bot.2).*

Gatagacyathus DEBRENNE & ZHURAVLEV, 1992a, p. 598 [**G. mansyi*; OD; holotype, DEBRENNE

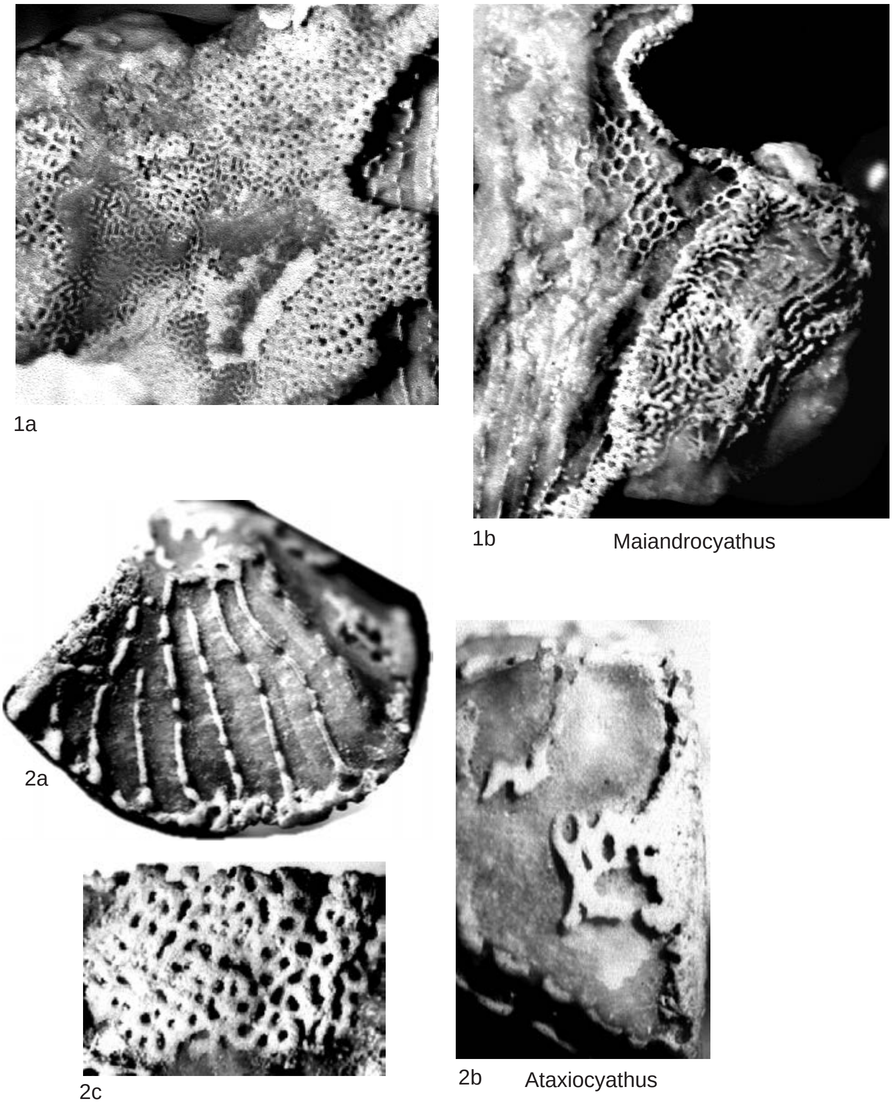


FIG. 643. Maiandrocyathidae (p. 1067–1068).

& ZHURAVLEV, 1992a, pl. 1,*4,* GSC 103942, specimen GAM76.8G.XI.3L, Ottawa]. Outer wall compound with incipient pore subdivision; inner wall rudimentary; calicles hexagonal in cross section with one pore row per facet. *lower Cambrian (Bot.2):* Canada, United States.——FIG. 649. **G. mansyi*, Rosella Formation, Botoman, Kechika River, British Columbia, Canada, holotype, GSC 103942, specimen GAM76.8G.XI.3L, longitudinal section, ×3.5 (Debrenne, Zhuravlev, & Kruse, 2002).

Suborder SYRINGOCNEMINA Okulitch, 1935

[*nom. correct.* DEBRENNE, ZHURAVLEV, & KRUSE, herein, *pro* Syringicnemidina KRASNOPEEVA, 1980, p. 159, *nom. transl. ex* order Syringocnemina OKULITCH, 1935b, p. 90] [=Syringocyathina DEBRENNE, 1991, p. 219]

Skeleton solitary or modular, latter as branching pseudocolonies (by longitudinal fission); intervallum with syringes. *lower Cambrian (Atd.4–Bot.3).*

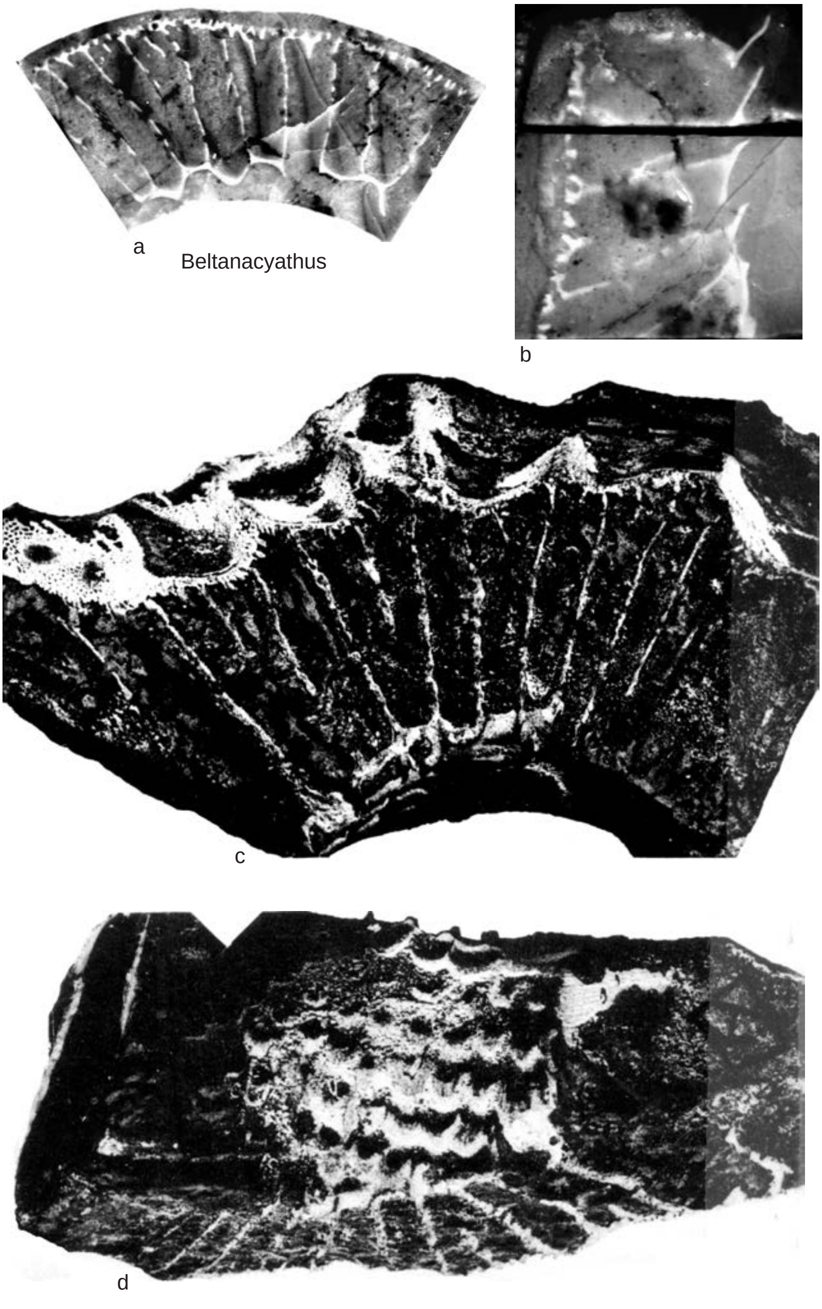


FIG. 644. Beltanacyathidae (p. 1068).

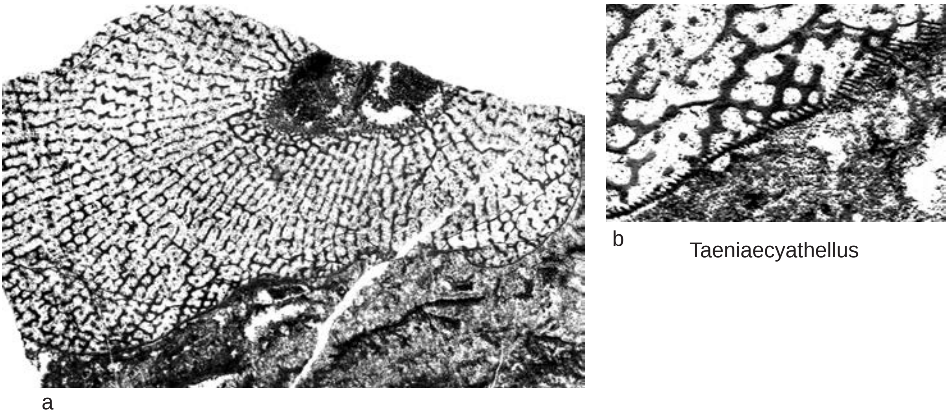


FIG. 645. Tabellaecyathidae (p. 1069).

Superfamily AULISCOCYATHOIDEA Debrenne & Zhuravlev, 1992

[Auliscocyathoidea DEBRENNE & ZHURAVLEV, 1992b, p. 117]

Outer wall simple. *lower Cambrian (Atd.4–Bot.3).*

Family AULISCOCYATHIDAE Debrenne & Zhuravlev, 1992

[Auliscocyathidae DEBRENNE & ZHURAVLEV, 1992b, p. 117]

Inner wall with simple pores. *lower Cambrian (Atd.4–Bot.3).*

Auliscocyathus DEBRENNE in ZHURAVLEVA, 1974a, p. 53 [**Spirocyathus multifidus* R. BEDFORD & W. R. BEDFORD, 1936, p. 14; OD; lectotype, R. BEDFORD & W. R. BEDFORD, 1936, fig. 65; DEBRENNE, 1974a, fig. 8a; SD DEBRENNE, 1974a, p. 199, SAM P950-81, Adelaide]. Outer and inner walls rudimentary; syringes tetragonal in cross section with one pore row per facet. *lower Cambrian (Atd.4–Bot.3):* Tuva, Australia, Antarctica.——FIG. 650*a–c*. **A. multifidus* (R. BEDFORD & W. R. BEDFORD), Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, SAM P950-81; *a,* longitudinal view, ×5 (Debrenne, 1974a); *b,* oblique longitudinal view, ×5; *c,* detail of syringes in longitudinal intervallar view, ×8 (Debrenne, Zhuravlev, & Kruse, 2002).

Superfamily SYRINGOCNEMOIDEA Taylor, 1910

[*nom. correct.* DEBRENNE, ZHURAVLEV, & KRUSE, herein, *pro* Syringocnemidoidea DEBRENNE & ZHURAVLEV, 1992b, p. 117, *nom. transl. ex* Syringocnemidae TAYLOR, 1910, p. 113]

Outer wall concentrically porous. *lower Cambrian (Bot.1–Bot.3).*

Family TUVACNEMIDAE Debrenne & Zhuravlev, 1990

[*nom. correct.* DEBRENNE, ZHURAVLEV, & KRUSE, herein, *pro* Tuvacnemididae DEBRENNE & ZHURAVLEV, 1990, p. 300]

Inner wall with simple pores. *lower Cambrian (Bot.1–Bot.3).*

Tuvacnema DEBRENNE & ZHURAVLEV, 1990, p. 301 [**Syringocnema tannuolensis* RODIONOVA in ZHURAVLEVA & others, 1967, p. 106; OD; holotype, ZHURAVLEVA & others, 1967, pl. 58,*4*, VSEGEI 9594, St. Petersburg, not located]. Inner wall with several rows of pores per syrinx; syringes hexagonal in cross section with several pore rows per facet. *lower Cambrian (Bot.1–Bot.3):* Tuva.——FIG. 651. **T. tannuolensis* (RODIONOVA), Shangan Formation, Botoman, Shivelig-Khem River, East Tannu-Ola Range, Russia, holotype, VSEGEI 9594, transverse section, ×7 (Zhuravleva & others, 1967).

Family SYRINGOCNEMIDAE Taylor, 1910

[Syringocnemidae TAYLOR, 1910, p. 113] [=Syringocnematidae VOLOGDIN, 1928, p. 31; =Syringocnemitidae TING, 1937, p. 370; =Syringocnemididae DEBRENNE, 1964, p. 117; =Pseudosyringocnemididae DEBRENNE, 1975, p. 355]

Inner wall with bracts, fused bracts, or pore tubes. *lower Cambrian (Bot.1–Bot.3).*

Syringocnema TAYLOR, 1910, p. 153 [**S. favus*; M; holotype, TAYLOR, 1910, pl. 14, photos 78–79, M, SAM T1597A,B,E, Adelaide]. Inner wall with one row of pores per syrinx, bearing upwardly projecting, S-shaped pore tubes; syringes hexagonal in cross section with several pore rows per facet. *lower Cambrian (Bot.3):* Australia, Antarctica, ?Falkland Islands (allochthonous).——FIG. 652*a–d*. **S. favus*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; *a–c,* holotype, SAM T1597A,B,E; *a,* transverse view, ×3; *b,* oblique longitudinal view, ×3.5; *c,* detail of

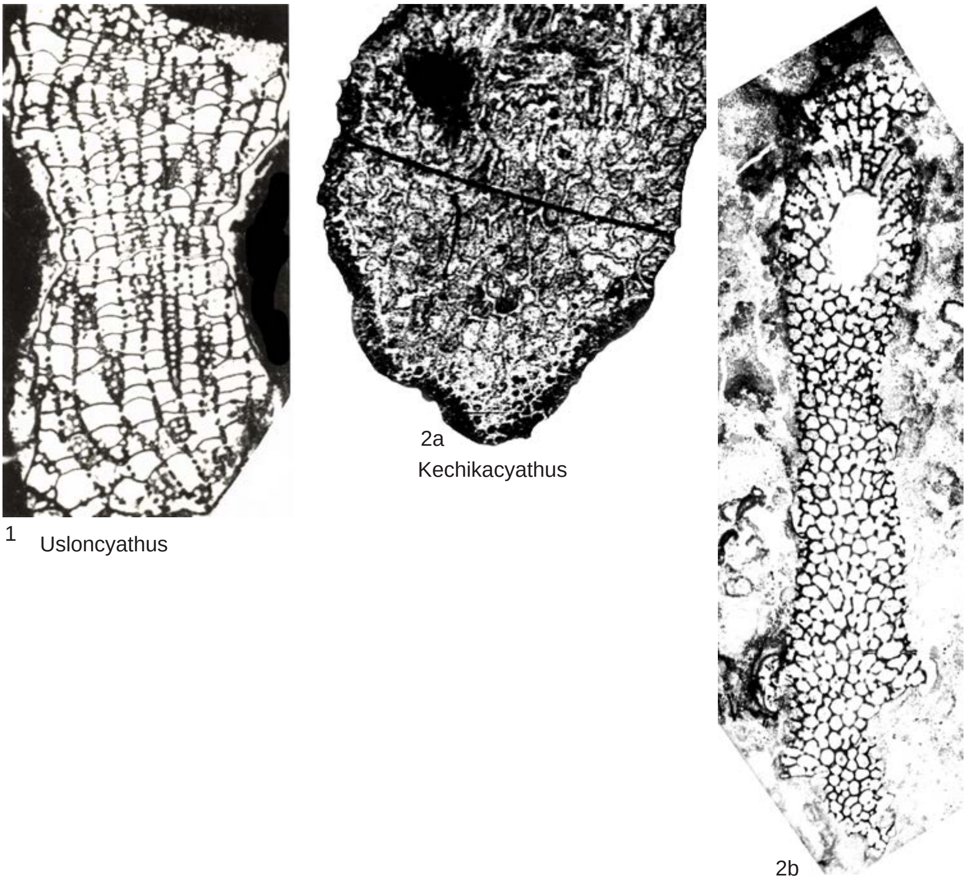


FIG. 646. Usloncyathidae (p. 1069–1070).

syringes in longitudinal view (outer wall to left), ×5; *d,* paratype, SAM T1558, detail of syringes in oblique transverse view, ×5 (Debrenne, Zhuravlev, & Kruse, 2002).

Pseudosyringocnema HANDFIELD, 1971, p. 76 [**P. uniporus*; OD; holotype, HANDFIELD, 1971, pl. 15,*3*, GSC 25392, Ottawa]. Inner wall with one row of pores per syrinx, bearing upwardly projecting, S-shaped pore tubes; syringes hexagonal in cross section with one pore row per transverse facet and several pore rows per lateral facet. *lower Cambrian (Bot.2–Bot.3):* Altay Sayan, Antarctica, Canada, United States.——FIG. 653,*1a–b*. **P. uniporus*, unnamed Sekwi Formation equivalent (map unit 5 of HANDFIELD, 1971), Botoman, Coal River, Yukon Territory, Northwest Territories, Canada, holotype, GSC 25392; *a,* longitudinal section, ×4 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* oblique longitudinal section, ×4 (Handfield, 1971; reproduced with the permission of the Minister of Public Works and Government Services Canada, 2006 and courtesy of Natural Resources Canada, Geological Survey of Canada).

Syringothalamus DEBRENNE, GANGLOFF, & ZHURAVLEV in DEBRENNE & ZHURAVLEV, 1990, p. 301 [**S. crispus*; OD; holotype, DEBRENNE & ZHURAVLEV, 1990, pl. 1,*1*, UCMP D6610, Berkeley]. Inner wall with one row of pores per syrinx, bearing upwardly projecting, S-shaped fused bracts; syringes hexagonal in cross section with one pore row per facet. *lower Cambrian (Bot.1):* United States.——FIG. 653,*2a–c*. **S. crispus*, Poleta Formation, Botoman, Lida, Palmetto Mountains, Nevada, United States; *a,* holotype, UCMP D6610, detail of outer wall in tangential section, ×11 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* paratype, UCMP D6620, transverse section, ×5; *c,* holotype, UCMP D6610, oblique longitudinal section, ×5 (Debrenne & Zhuravlev, 1990).

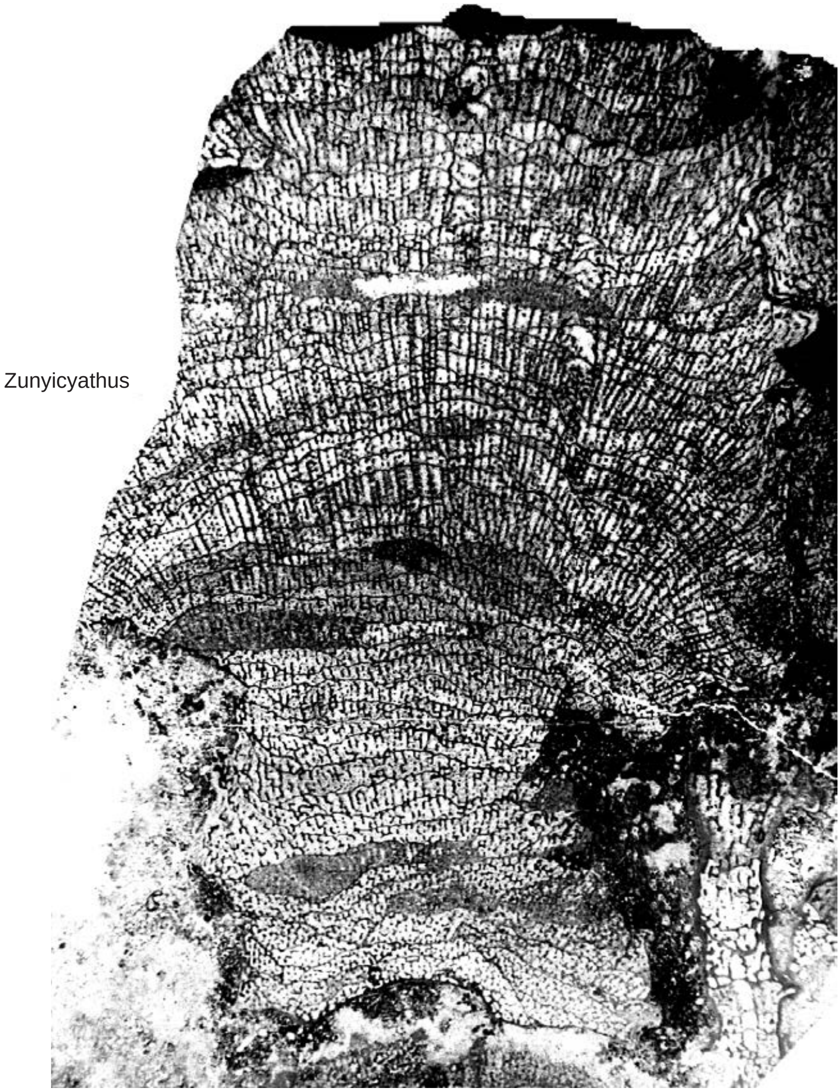


FIG. 647. Usloncyathidae (p. 1070).

Williamicyathus ZHURAVLEV in VORONOVA & others, 1987, p. 34 [**Syringocnema colvillensis* GREGGS, 1959, p. 72; OD; holotype, GREGGS, 1959, pl. 13,*6,* GSC 14317, Ottawa]. Inner wall with one row of pores per syrinx, bearing upwardly projecting, planar, fused bracts; syringes hexagonal in cross section with one pore row per transverse facet and several pore rows per lateral facet. *lower Cambrian (Bot.1–Bot.2):* Canada, United States.——FIG. 654*a–c*. **W. colvillensis* (GREGGS); *a,* Sekwi Formation, Botoman, Mackenzie Mountains, Northwest Territories, Canada, specimen GSC 90169, transverse section, ×7 (Voronova & others, 1987); *b,* Maitlen Formation, Botoman, Colville, Washington, United States, holotype, GSC 14317, transverse section, ×7.5 (Greggs, 1959); *c,* Sekwi Formation, Botoman, Mackenzie Mountains, Northwest Territories, Canada, specimen GSC 90170, oblique transverse section, ×7.5 (Voronova & others, 1987).

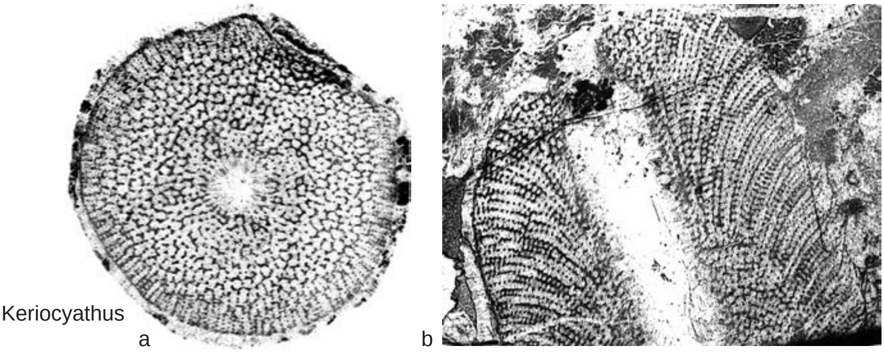


FIG. 648. Keriocyathidae (p. 1070).

Superfamily KRUSEICNEMOIDEA Debrenne & Zhuravlev, 1990

[*nom. correct.* DEBRENNE, ZHURAVLEV, & KRUSE, herein, *pro* Kruseicnemidoidea DEBRENNE & ZHURAVLEV, 1992b, p. 117, *nom. transl. ex* Kruseicnemididae DEBRENNE & ZHURAVLEV, 1990, p. 301]

Outer wall pustular. *lower Cambrian (Bot.3).*

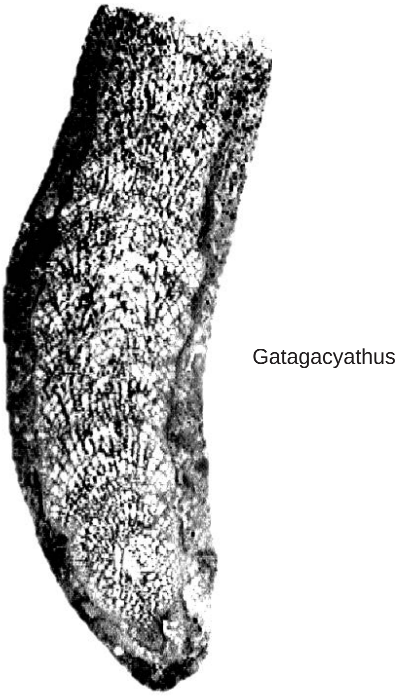


FIG. 649. Gatagacyathidae (p. 1070–1071).

Family KRUSEICNEMIDAE Debrenne & Zhuravlev, 1990

[*nom. correct.* DEBRENNE, ZHURAVLEV, & KRUSE, herein, *pro* Kruseicnemididae DEBRENNE & ZHURAVLEV, 1990, p. 301]

Inner wall with bracts, fused bracts or pore tubes. *lower Cambrian (Bot.3).*

Kruseicnema DEBRENNE, GRAVESTOCK, & ZHURAVLEV in DEBRENNE & ZHURAVLEV, 1990, p. 301 [**Syringocnema gracilis* GORDON, 1920, p. 699; OD; holotype, GORDON, 1920, pl. 4,*43,46,* NHM S10412-10413, London]. Outer wall pustules bearing supplementary multiperforate tumuli; inner wall with one row of pores per syrinx, bearing upwardly projecting, S-shaped pore tubes; syringes hexagonal in cross section with several pore rows per facet. *lower Cambrian (Bot.3):* Australia, Antarctica, South Africa (allochthonous), Falkland Islands (allochthonous).——FIG. 655,*1a–b*. **K. gracilis* (GORDON), allochthonous, Botoman, Weddell Sea, Antarctica, holotype, NHM S10412-10413; *a,* oblique longitudinal section, ×9; *b,* transverse section, ×9 (Gordon, 1920).

Superfamily FRAGILICYATHOIDEA Belyaeva, 1975

[*nom. transl.* DEBRENNE & ZHURAVLEV, 1992b, p. 117, *ex* Fragilicyathidae BELYAEVA in BELYAEVA & others, 1975, p. 117]

Outer wall with canals. *lower Cambrian (Bot.1).*

Family FRAGILICYATHIDAE Belyaeva, 1975

[Fragilicyathidae BELYAEVA in BELYAEVA & others, 1975, p. 117]

Inner wall with bracts, fused bracts, or pore tubes. *lower Cambrian (Bot.1).*

FIG. 650. Auliscocyathidae (p. 1073).

Fragilicyathus BELYAEVA, 1969, p. 98 [**F. zhuravlevae*; OD; holotype, BELYAEVA, 1969, pl. 37,*7*, DVGU 6M/212/15-3, Khabarovsk]. Outer wall with horizontal to upwardly projecting, straight canals; inner wall with one row of pores per syrinx, bearing upwardly projecting, S-shaped pore tubes; syringes hexagonal in cross section with several pore rows per facet. *lower Cambrian (Bot.1):* Far East.——FIG. 655,*2*. **F. zhuravlevae*, Ust'toka unit, Botoman, Gerbikan River, Dzhagdy Range, Far East, Russia, holotype, DVGU 6M/212/15-3, oblique longitudinal section, ×5.5 (Debrenne, Zhuravlev, & Kruse, 2002).

Order KAZACHSTANICYATHIDA
Konyushkov, 1967

[Kazachstanicyathida KONYUSHKOV, 1967, p. 105]

Cup multichambered, solitary or modular, with massive modular types by individualization of modules around new central cavities; development of thalamid type, with stromatoporoid growth pattern; chambers of subspherical to laterally elongate shape, with pillars. *lower Cambrian (Bot.1–Bot.3).*

Suborder KAZACHSTANICYATHINA
Konyushkov, 1967

[*nom. transl.* DEBRENNE & ZHURAVLEV, 1992b, p. 118, *ex* Kazachstanicyathida KONYUSHKOV, 1967, p. 105] [=Kazakhstanicyathida HILL, 1972, p. 130, *nom. null.*; =Korovinellina DEBRENNE, 1991, p. 219]

Initial chambers hollow and elongate; pillars developed in subsequent chambers; inner wall invaginal. *lower Cambrian (Bot.1–Bot.3).*

FIG. 651. Tuvacnemidae (p. 1073).

Family KOROVINELLIDAE Khalfina, 1960

[Korovinellidae KHALFINA, 1960a, p. 80] [=Kazachstanicyathidae KONYUSHKOV, 1967, p. 106; =Kazakhstanicyathidae HILL, 1972, p. 130, *nom.null.*]

Outer and inner walls with simple pores. *lower Cambrian (Bot.1–Bot.3).*

Korovinella RADUGIN in KHALFINA, 1960a, p. 80 [**Clathrodictyon sajanicum* YAVORSKY, 1932, p. 614; OD; holotype, YAVORSKY, 1932, fig. 4–5, M, TsNIGRm 4a,b/4070, St. Petersburg] [=*Kazachstanicyathus* KONYUSHKOV, 1967, p. 106 (type, *K. fistulatus,* OD); =*Kazakhstanicyathus* HILL, 1972, p. 130, *nom. null.*]. Outer and inner walls tabular; chambers of simple segmented tabulae and pillars. *lower Cambrian (Bot.3):* Altay Sayan, Kazakhstan.——FIG. 656,*1a–b*. **K. sajanica* (YAVORSKY), Verkhnemonok Formation, Botoman, Sanashtykgol Spring, West Sayan, Altay Sayan, Russia; *a,* oblique transverse section, topotype, PIN 4754/10, ×10 (Debrenne, Zhuravlev, & Kruse, 2002); *b,* holotype, TsNIGRm 4a,b/4070, transverse section of modular skeleton, ×10 (Yavorsky, 1932).

Bicoscinus DEBRENNE, 1977a, p. 127 [**B. sdzuyi*; OD; holotype, DEBRENNE, 1977a, pl. 14,*2*, MNHN M80058, specimen IRH13-1d, Paris]. Outer wall aporose (possibly rudimentary); inner wall simple; tabulae. *lower Cambrian (Bot.1):* Morocco.——FIG. 656,*2*. **B. sdzuyi*, Issafen Formation, Botoman, Jbel Irhoud, holotype, MNHN M80058, specimen IRH13-1d, oblique longitudinal section, ×5 (Debrenne, 1977a).

Suborder ALTAICYATHINA Debrenne, 1991

[Altaicyathina DEBRENNE, 1991, p. 219]

Initial chambers subspherical; pillars present in initial and subsequent chambers. *lower Cambrian (Bot.1–Bot.2).*

Family ALTAICYATHIDAE Debrenne & Zhuravlev, 1992

[Altaicyathidae DEBRENNE & ZHURAVLEV, 1992b, p. 118]

Outer and inner walls with simple pores. *lower Cambrian (Bot.1–Bot.2).*

Altaicyathus VOLOGDIN, 1932, p. 26 [**A. notabilis*; M; lectotype, VOLOGDIN, 1932, pl. 1,*5;* SD DEBRENNE & ZHURAVLEV, 1992b, p. 48, TsNIGRm 290/2957, St. Petersburg] [=*Praeactinostroma* KHALFINA, 1960a, p. 81 (type, *Actinostroma vologdini* YAVORSKY, 1932, p. 613, OD); =*Cambrostroma* VLASOV, 1961, p. 29 (type, *C. rossicum*, OD); =*Abakanicyathus* KONYUSHKOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 127 (type, *A. karakolensis*, OD), for discussion, see DEBRENNE & ZHURAVLEV, 1992b, p. 119; =*Altaicyathus notabilis* VOLOGDIN, 1932, p. 26)]. Outer and inner walls tabular; chambers of simple segmented tabulae and pillars; exaules and astrorhizae may be present. *lower Cambrian (Bot.1–Bot.2):* Altay Sayan, Mongolia, Far East, United States.——FIG. 657. **A. notabilis*, Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Altay Sayan, Russia, lectotype, TsNIGRm 290/2957, longitudinal section, ×9 (Vologdin, 1932).

NOMINA DUBIA

Adaecyathus FONIN in ZHURAVLEV, ZHURAVLEVA, & FONIN, 1983, p. 28 (FONIN in KRASNOPEEVA, 1978, p. 81, *nom. nud.*) [**A. gravis*; OD].

Araneocyathus VOLOGDIN in SIMON, 1941, p. 5 (VOLOGDIN, 1937b, p. 466, *nom. nud.*) [**A. curvus* VOLOGDIN, 1940a, p. 64; SD SIMON, 1941, p. 5].

Archaeocyathellus FORD, 1873b, p. 135 [**Archaeocyathus? rensselaericus* FORD, 1873a, p. 211; M].

ARCHAEOCYATHOSPONGIA VOLOGDIN, 1940a, p. 27 (class).

Archaeofungiella ZHURAVLEVA in ZHAUTIKOV & others, 1976, p. 137 [**A. chingisiensis*; OD].

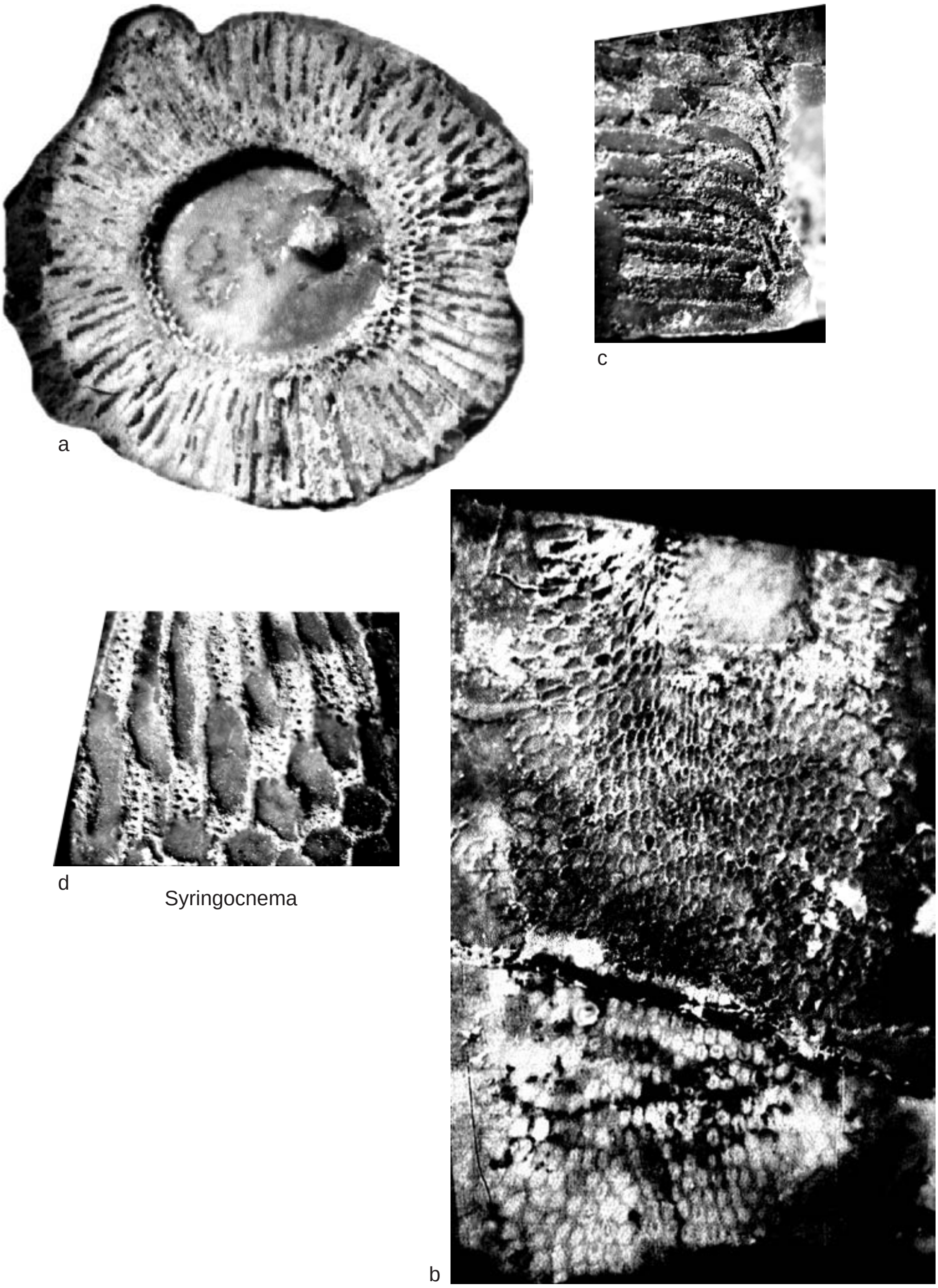


FIG. 652. Syringocnemidae (p. 1073–1074).

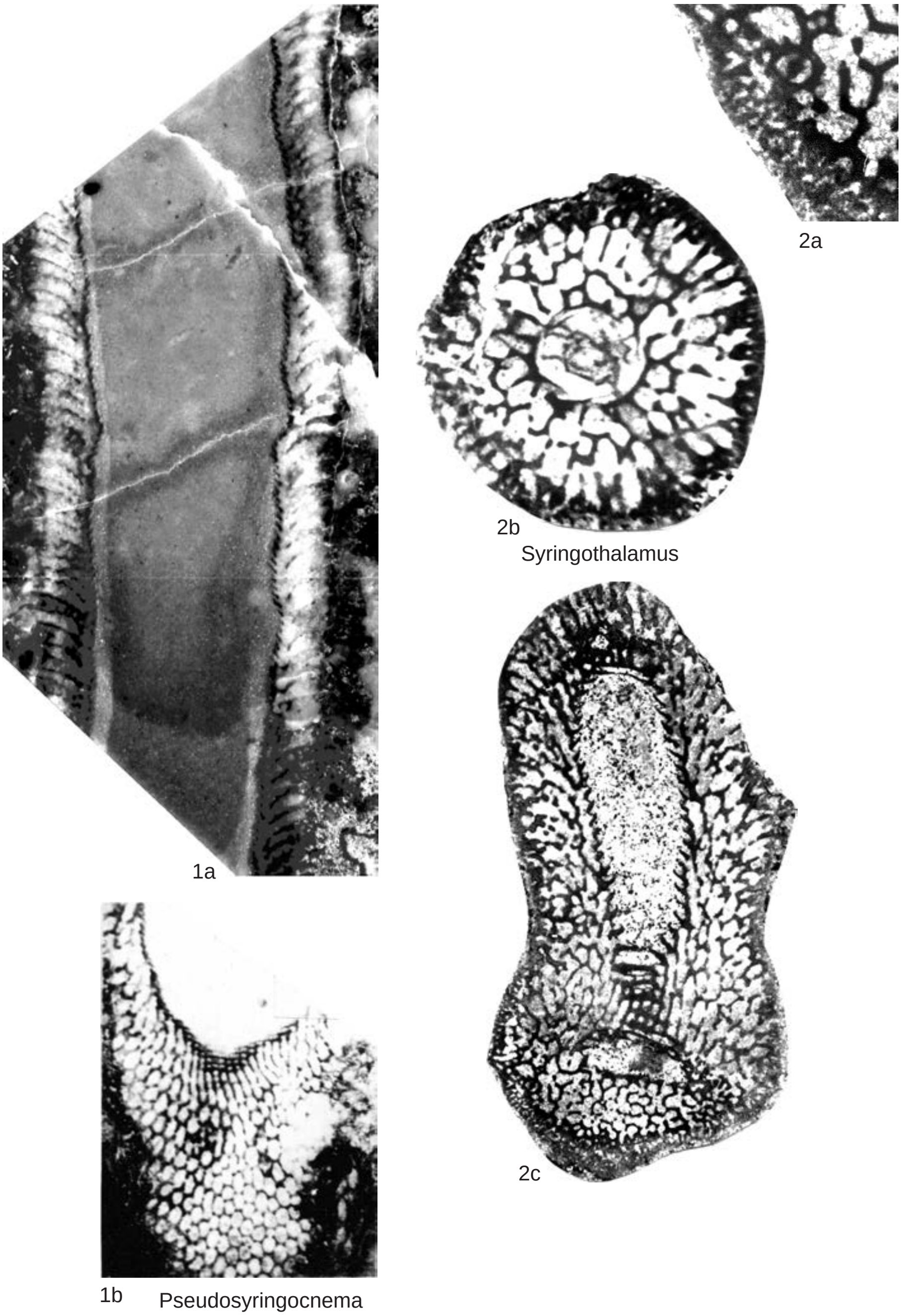


FIG. 653. Syringocnemidae (p. 1074).

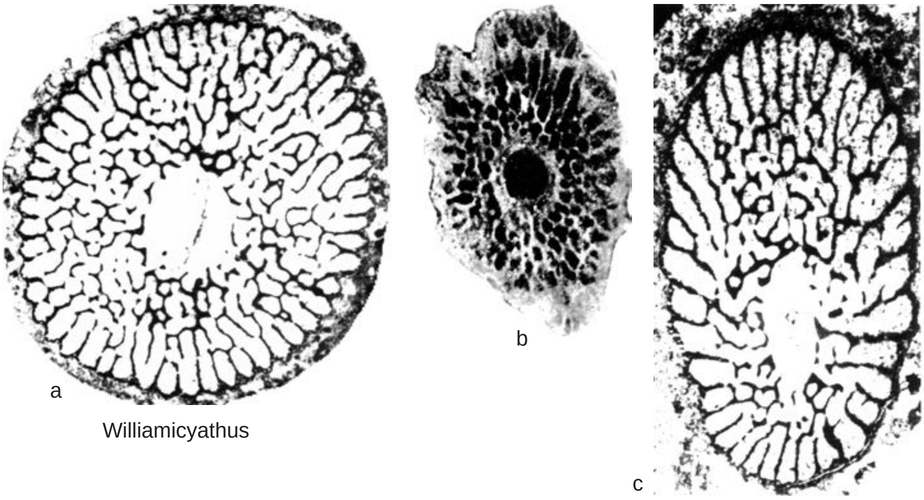


FIG. 654. Syringocnemidae (p. 1075).

ARCHAEOPHYLLIDA OKULITCH, 1943, p. 46, *nom. correct.* OKULITCH, 1955a, p. 10, *pro* order Archaeophyllina OKULITCH, 1943, p. 46.

ARCHAEOPHYLLIDAE VOLOGDIN, 1940b, p. 97 [=Archaeophyllidae VOLOGDIN, 1931, p. 60, *nom. nud.*].

Archaeophyllum VOLOGDIN in SIMON, 1939, p. 21 (VOLOGDIN, 1931, p. 61, *nom. nud.*) [**A. edelsteini* VOLOGDIN, 1931, p. 62; SD SIMON, 1939, p. 21].

BACATOCYATHIDAE ZHURAVLEVA, 1960b, p. 268, *nom. correct.* HILL, 1965, p. 116, *pro* Batchatocyathidae ZHURAVLEVA, 1960b, p. 268.

Bacatocyathus VOLOGDIN, 1940b, p. 95, *nom. correct.* HILL, 1965, p. 116, *pro Bačatocyathus* VOLOGDIN, 1940b, p. 95 [**B. kazakevici*; OD] [=*Batschatocyathus* VOLOGDIN, 1956, p. 878, *nom. null.*; =*Batchatocyathus* ZHURAVLEVA, 1960b, p. 268, *nom. null.*].

Beticocyathus SIMON, 1939, p. 73 [**B. beticus*; OD].

BICYATHIDAE VOLOGDIN, 1937b, p. 472.

Bicyathus VOLOGDIN, 1939, p. 235 (VOLOGDIN, 1937b, p. 472, *nom. nud.*) [**B. angustus*; OD].

Butovia VOLOGDIN, 1931, p. 63 [**B. serrata*; M].

CROMMYOCYATHINA R. BEDFORD & J. BEDFORD, 1939, p. 79 (order).

Dendrocyathus OKULITCH & ROOTS, 1947, p. 44 [**D. unexpectans*; M].

Echinocyathus H. TERMIER & G. TERMIER, 1950, p. 47 [**E. goundafensis*; OD] [=*Dictyocyathus (Echinocyathus)* H. TERMIER & G. TERMIER, 1950, p. 47, *nom. transl.* DEBRENNE, 1964, p. 207, *ex Echinocyathus* H. TERMIER & G. TERMIER, 1950, p. 47].

Echinocyathus VOLOGDIN, 1960, p. 424, *non* H. TERMIER & G. TERMIER, 1950, p. 47 (type, *E. goundafensis,* OD) [**E. bilateralis*; OD].

ETHMOLYNTHIDAE ZHURAVLEVA, 1963b, p. 112, *nom. transl.* HILL, 1972, p. 51, *ex* Ethmolynthinae ZHURAVLEVA, 1963b, p. 112.

Ethmolynthus ZHURAVLEVA, 1963b, p. 112 [**E. rosanovi*; OD].

EXOCYATHA OKULITCH, 1943, p. 42 (subclass).

EXOCYATHIDAE R. BEDFORD & J. BEDFORD, 1939, p. 82.

Exocyathus R. BEDFORD & J. BEDFORD, 1937, p. 32 [**E. australis*; OD].

Gorskinocyathus VOLOGDIN, 1960, p. 422 [**Archaeocyathus gorskinensis* VOLOGDIN, 1940b, p. 60; OD].

Kameschkovia VOLOGDIN, 1957a, p. 183 (VOLOGDIN, 1956, p. 880, *nom. nud.*) [**Labyrinthomorpha perforata* VOLOGDIN, 1940b, p. 40; M].

LABYRINTHOCYATHIDAE YAROSHEVICH, 1962, p. 117.

Labyrinthocyathus YAROSHEVICH, 1962, p. 117 [**L. grandiporosus*; M].

Labyrinthomorpha VOLOGDIN, 1931, p. 35 [**L. tolli*; M] [=*Labirinthomorpha* VOLOGDIN, 1928, p. 32, *nom. nud.*].

LABYRINTHOMORPHIDA VOLOGDIN, 1961, p. 180 (order).

LABYRINTHOMORPHIDAE VOLOGDIN, 1962a, p. 125 [=Labirinthomorphidae VOLOGDIN, 1928, p. 32, *nom. nud.*].

LABYRINTHOMORPHINA VOLOGDIN, 1961, p. 180 (superorder), *nom. transl.* VOLOGDIN, 1962a, p. 125, *ex* order Labyrinthomorphida VOLOGDIN, 1961, p. 180].

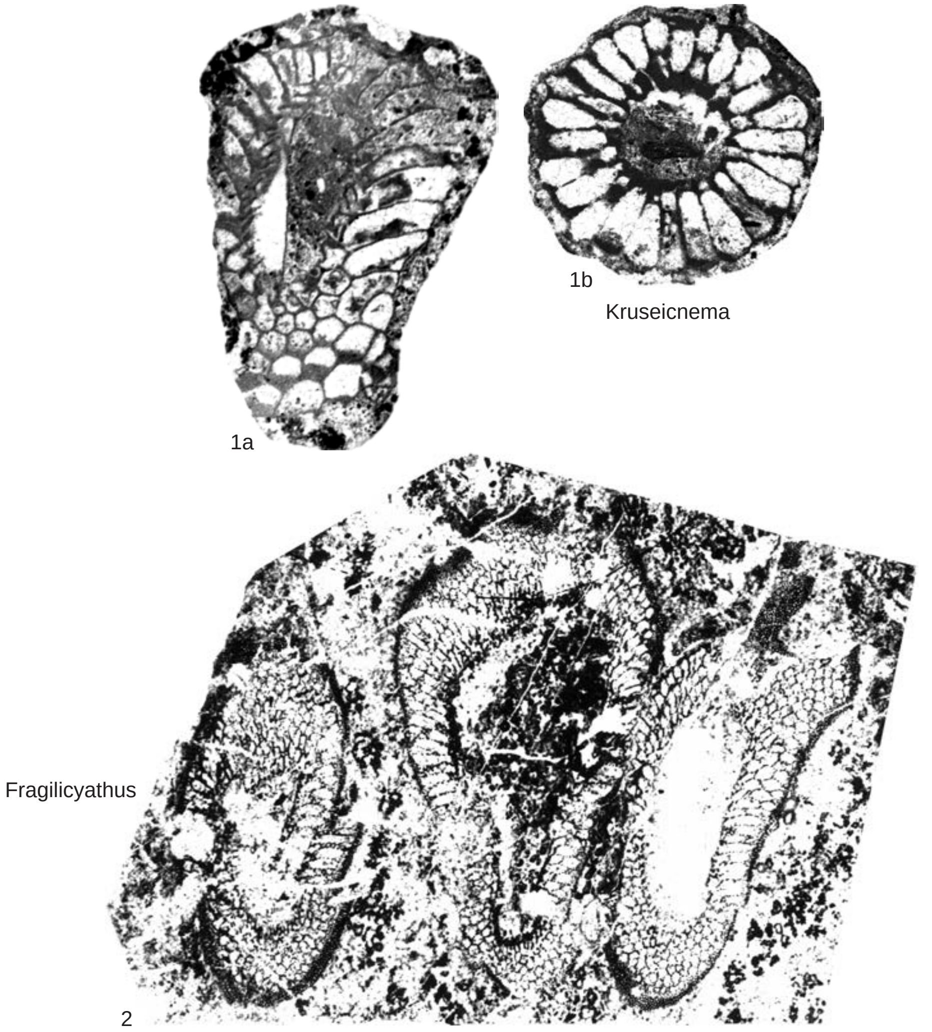


Fig. 655. Kruseicnemidae and Fragilicyathidae (p. 1076–1077).

LEECYATHIDAE Vologdin, 1957c, p. 495 [=Leecyathidae Vologdin, 1956, p. 879, *nom. nud.*].

Leecyathus Vologdin, 1957c, p. 495 [**Archaeocyathus yavorskii* Vologdin, 1931, p. 86; OD] [=*Zeecyathus* Vologdin, 1956, p. 879, *nom. nud., lapsus calami pro Leecyathus*].

Leiocyathus Vologdin, 1959a, p. 671 [**L. inaequitaenialis*; OD].

Nevadacyathus Okulitch, 1943, p. 59 [**Archaeocyathus septaporus* Okulitch, 1935b, p. 101; M].

Pinacocyathus R. Bedford & W. R. Bedford, 1934, p. 4 [**P. spicularis*; M].

Potekhinocyathus Vologdin, 1957d, p. 699 [**P. bateniensis*; M].

Protocyclocyathus Vologdin, 1955, p. 142 [**Cyclocyathus irregularis* Vologdin, 1940b, p. 62; M].

RHIZACYATHIDAE R. Bedford & J. Bedford, 1939, p. 69.

Rhizacyathus R. Bedford & J. Bedford, 1939, p. 69 [**Protopharetra radix* R. Bedford & J. Bedford, 1937, p. 28; OD].

Salopicyathus Vologdin, 1962c, p. 86 [**S. complanatoporosus*; OD].

Septocyathus Vologdin, 1937b, p. 468 [**S. pedaschenkoi*; M].

Serligocyathus Vologdin, 1959a, p. 671 [**S. lukashevi*; OD].

SOMPHOCYATHIDAE Okulitch, 1935b, p. 98.

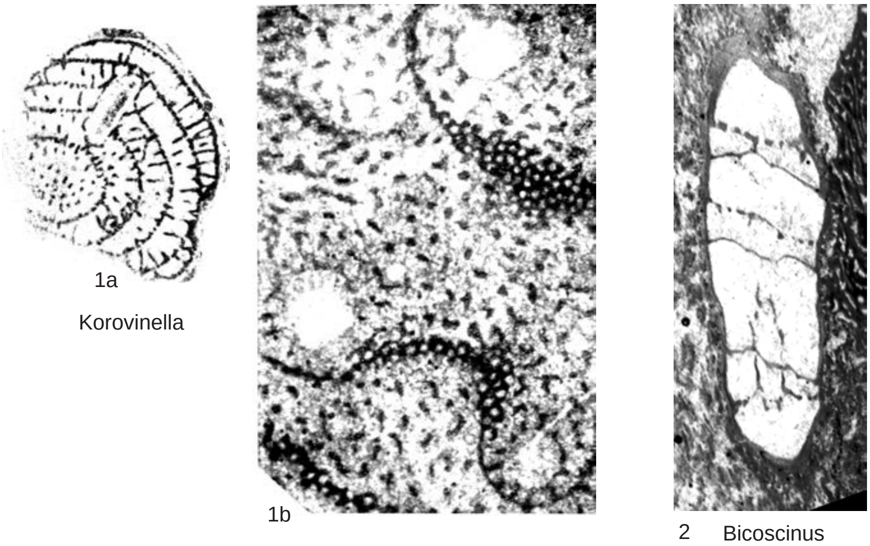


FIG. 656. Korovinellidae (p. 1078).

Somphocyathus TAYLOR, 1910, p. 134 [**S. coralloides*; M].

Sphinctocyathus (Sphinctocyathus) ZHURAVLEVA, 1960b, p. 304 [**S. (S.) oimuranicus*; OD].

Squamella VOLOGDIN, 1977, p. 75, *non* BORY DE SAINT-VINCENT, 1826, p. 90 (type, *S. limulina,* M), rotifer [**S. prima*; OD] [=*Squamellicyathus* VOLOGDIN, 1977, p. 22, *nom. nud.*].

TABULACYATHIDA VOLOGDIN, 1956, p. 878 (order), *nom. correct.* HILL, 1972, p. 121 *pro* Tabulocyathida VOLOGDIN, 1956, p. 878, *lapsus calami.*

TABULACYATHIDAE VOLOGDIN, 1956, p. 878, *nom. correct.* HILL, 1972, p. 123, *pro* Tabulathyathidae VOLOGDIN in REPINA & others, 1964, p. 249, *nom. correct. pro* Tabulocyathidae VOLOGDIN, 1956, p. 878, *lapsus calami.*

Tabulacyathus VOLOGDIN, 1932, p. 30 [**T. taylori;* M] [=*Tabulocyathus* VOLOGDIN, 1937b, p. 471, *nom. null.*].

TABULOIDEA VOLOGDIN, 1957a, p. 183 (class).

TANNUOLACYATHIDAE DEBRENNE, 1964, p. 188.

Tannuolacyathus VOLOGDIN, 1957c, p. 496 [**T. multiplex;* OD].

TEREKTIGOCYATHIDAE VOLOGDIN, 1962b, p. 419.

Terektigocyathus VOLOGDIN, 1962b, p. 420 [**T. primus*; OD].

Tersia VOLOGDIN, 1931, p. 70 [**T. filiforma*; M].

FIG. 657. Altaicyathidae (p. 1078).

Tersiella VOLOGDIN, 1962a, p. 129 [**Tersia nodosa* VOLOGDIN, 1940a, p. 34; OD].

THALASSOCYATHIDAE VOLOGDIN, 1962a, p. 116.

Thalassocyathus VOLOGDIN, 1957d, p. 699 [**T. acutatus*; M].

Torgaschinocyathus VOLOGDIN, 1957d, p. 699 [**T. spinosus*; M].

Turgidocyathus VOLOGDIN, 1960, p. 422 [**T. ippolitovensis*; OD].

Tuvacyathus VOLOGDIN, 1940a, p. 112 (VOLOGDIN, 1937b, p. 471, *nom. nud.*) [**T. mollimurus*; M].

URALOCYATHIDAE VOLOGDIN & ZHURAVLEVA in VOLOGDIN, 1956, p. 878 [=Vacuocyathidae VOLOGDIN, 1962c, p. 77].

Vacuocyathus OKULITCH, 1950a, p. 392, *nom. nov. pro Coelocyathus* VOLOGDIN, 1939, p. 237, *non* SARS, 1857, p. 126, cnidarian, *nec* SCHLÜTER, 1886, p. 899, cnidarian [**Coelocyathus kidrjassovensis* VOLOGDIN, 1939, p. 237; OD; =*Coelocyathus kidrjassovensis* VOLOGDIN, 1937b, p. 478, *nom. nud.*] [=*Uralocyathus* ZHURAVLEVA, 1960b, p. 102 (type, *Coelocyathus kidrjassovensis* VOLOGDIN, 1939, p. 237, OD), *nom. nov. pro Coelocyathus* VOLOGDIN, 1939, p. 237, archaeocyath].

VESICULOIDA VOLOGDIN, 1956, p. 878 (order).

VESICULOIDAE VOLOGDIN, 1931, p. 34, invalid family-group name based on unavailable genus name.

NOTE ADDED IN PROOF

A publication by SKORLOTOVA (2013) could not be included in the present volume. Among other new archaeocyath taxa, the paper describes the following new genera: *Turgorocyathus* SKORLOTOVA, 2013, p. 4 (type, *T. elegans;* OD) in Ajacicyathidae; *Angustocyathus* SKORLOTOVA, 2013, p. 5 (type, *A. porus;* OD) in Densocyathidae; and *Flossocyathus* SKORLOTOVA, 2013, p. 6 (type, *F. squamosus;* OD) in Coscinocyathidae. All are from the *Carinacyathus pinus* Zone (Atd.2), Lena River, Sakha (Yakutia), Russia. Type material is lodged in the Paleontologicheskiy Institut RAN, Moscow, as PIN 5499.

RADIOCYATHS AND POTENTIALLY ALLIED TAXA: SYSTEMATIC DESCRIPTIONS

P. D. KRUSE, A. YU. ZHURAVLEV, and F. DEBRENNE

Radiocyaths show superficial similarity to archaeocyaths in size, shape, and gross morphology, and typically co-occur with them. They were first described from the lower Cambrian of South Australia as *Heterocyathus* R. BEDFORD & W. R. BEDFORD, 1934, a preoccupied name later substituted with *Radiocyathus* OKULITCH, 1937a. This latter was to become the eponymous genus for the entire group (DEBRENNE, H. TERMIER, & G. TERMIER, 1970).

Radiocyath skeletons may range up to 20 cm in height and 12 cm in diameter, although the majority are around 2–5 cm diameter. Apart from some branching *Girphanovella* ZHURAVLEVA and *Gonamispongia* KORSHUNOV, they are solitary. The skeleton may be globular, conical, or pyriform, composed of one or two walls, the walls in the latter being linked by radial rods, thus superficially resembling certain species of the archaeocyath *Dokidocyathus* TAYLOR. Nevertheless, radiocyaths differ fundamentally from archaeocyaths in that their walls are constructed of more or less uniformly arranged nesasters (DEBRENNE, H. TERMIER, & G. TERMIER, 1971): solid starlike structures consisting of 6–20 coplanar rays radiating from a central boss. Walls range from those apparently composed of relatively isolated nesasters, as in the poorly preserved *Kuraya* ROMANENKO (treated herein as a probable synonym of *Uranosphaera* R. BEDFORD & W. R. BEDFORD), to those constructed of nesasters whose rays are intricately linked to form a continuous skeletal network, as in *Radiocyathus* OKULITCH and *Girphanovella* ZHURAVLEVA. Nesasters may be two layered, as, for example, in *Radiocyathus* OKULITCH, in which nesasters have an internal layer of radial rays that fuse with rays of adjacent nesasters at angled junctions, and an external layer of anastomosing rays and tangential linking cross pieces that constitute a microporous sheath (DEBRENNE, H. TERMIER, & G. TERMIER, 1970; KRUSE, 1991).

The lower end of the skeleton appears to have been closed. The upper end is not commonly preserved, and a distal opening is confirmed only in *Uranosphaera* R. BEDFORD & W. R. BEDFORD, which bears a circular opening about one third the equatorial skeleton diameter. Skeletal growth was from the lower end, with intermingling of differently sized nesasters in some taxa implying that additional nesasters may have been subsequently inserted interstitially (ZHURAVLEV, 1986b). Alternatively, the organism may simply have exerted little control over nesaster size at the growing edge, with resultant size variation.

Historically, most studied specimens have been secondarily silicified, dolomitized, or phosphatized. The microstructure of unaltered specimens is typically a mosaic of equant calcite spar, suggestive of an original aragonitic skeletal mineralogy based on the comparative approach of JAMES and KLAPPA (1983). Exceptionally, ZHURAVLEV (1986b) reported what may be an original microstructure: a fabric of interlocking isometric microgranules 3–6 µm in size, although this may represent contamination due to intergrowth with archaeocyaths.

Neither the rank of radiocyathan supra-generic taxa nor the placement of genera within family-rank taxa is universally agreed. ZHURAVLEV and SAYUTINA (1985), in their restudy of *Kuraya* ROMANENKO (?=*Uranosphaera* R. BEDFORD & W. R. BEDFORD) and *Gonamispongia* KORSHUNOV, suggested that one-walled forms are merely incompletely mineralized or preserved two-walled forms. These authors placed *Gonamispongia* KORSHUNOV in their two-walled Radiocyathinae (Hetairacyathidae, herein), as it has rods projecting radially inward from its wall nesasters; they further amalgamated Girphanovellidae with Radiocyathidae (as Radiocyathinae). ZHURAVLEVA and MYAGKOVA (1987) assigned *Gonamispongia* KORSHUNOV to a separate subfamily.

The class has been allied variously with spiculate (especially heteractinide) sponges or archaeocyaths (R. BEDFORD & W. R. BEDFORD, 1934; OKULITCH, 1935b, 1955a; R. BEDFORD & J. BEDFORD, 1937; ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964; ZHURAVLEVA in ZHURAVLEVA, ZADOROZHNAYA, & others, 1967; KORSHUNOV, 1968; ROMANENKO, 1968; ROZANOV & ZHURAVLEV, 1992; FINKS & RIGBY, 2004a), or considered as a problematic class of uncertain affinity (HILL, 1965, 1972). RIGBY and NITECKI (1975), erroneously believing the nesasters to be sutured, claimed for *Uranosphaera* R. BEDFORD & W. R. BEDFORD a close relationship to chancelloriids. These latter are now recognized as a group of nonporiferan epithelium-bearing metazoans (MEHL, 1996; BENGTSON & HOU, 2001; JANUSSEN, STEINER, & ZHU, 2002).

More recent studies have related the class most closely to the Early Ordovician–Permian receptaculitaleans, a group popularly allied with calcareous algae (NITECKI, 1972; CAMPBELL, HOLLOWAY, & SMITH, 1974; RIETSCHEL, 1977; NITECKI & DEBRENNE, 1979; BEADLE, 1988), though most recently regarded as problematic (neither sponges, nor dasycladalean algae) by NITECKI and MUTVEI (1996) and M. H. NITECKI, MUTVEI, and D. V. NITECKI (1999). In the receptaculitalean model, homology is drawn between the receptaculitalean merom (consisting of shaft, inner platelike foot and outer quadribrachial structure with surmounting head plate) and the radiocyathan radial rod connecting corresponding inner and outer nesasters (NITECKI & DEBRENNE, 1979; NITECKI & TOOMEY, 1979; MYAGKOVA, 1985; ZHURAVLEV & SAYUTINA, 1985; ZHURAVLEV, 1986b). This proposed affinity with receptaculitaleans is consistent with microstructural (KRUSE & DEBRENNE, 1989) and mineralogical comparisons (DZIK, 1994; NITECKI & MUTVEI, 1996). Nevertheless, because the possibility of a poriferan affinity remains, the Radiocyatha are included in the present *Treatise* revision.

A dissenting view of phylogenetic relationships was advanced by ZHURAVLEVA and MYAGKOVA (1987). These authors grouped radiocyaths together with heteractinide sponges, chancelloriids, and some receptaculitaleans in a phylum, Receptaculita, itself grouped with the phylum Archaeocyatha, as the subkingdom Archaeata in the kingdom Inferibionta. The Archaeata-Inferibionta concept has not found favor with other researchers.

Radiocyaths appeared on the Siberian Platform in the late Tommotian, spread into adjacent Altay Sayan, Tuva, Mongolia, and Transbaikalia in the early Atdabanian and had reached Morocco, Australia, Antarctica, and Laurentia by the Botoman. As with archaeocyaths, their range contracted thereafter; the latest radiocyaths are from the middle Toyonian of South Australia.

Limited paleoecological studies indicate that at least some radiocyaths were reef dwellers or constructors. They contributed to reefs in the Tommotian of the Siberian Platform, Atdabanian of Mongolia and central Australia, and Toyonian of South Australia (Kennard, 1991; Kruse, 1991; Wood, Zhuravlev, & Chimed Tseren, 1993; Kruse, Zhuravlev, & James, 1995; Kruse & others, 1996).

?Class RADIOCYATHA Debrenne, H. Termier, & G. Termier, 1970

[Radiocyatha Debrenne, H. Termier, & G. Termier, 1970, p. 120] [=order Hetairacyathida R. Bedford & J. Bedford, 1937, p. 27, *nom. correct.* Okulitch, 1955a, p. 18, *pro* order Hetairacyathina R. Bedford & J. Bedford, 1937, p. 27, *nom. nov. pro* order Heterocyathina Okulitch, 1935b, p. 90, based on junior homonym; =order Uranosphaerina R. Bedford & J. Bedford, 1939, p. 82; =subclass Uranocyatha Okulitch, 1943, p. 42; =order Radiocyatales Debrenne, H. Termier, & G. Termier, 1970, p. 120, *nom. transl.* Nitecki & Toomey, 1979, p. 728, *ex* class Radiocyatha Debrenne, H. Termier, & G. Termier, 1970, p. 120; =Radiocyathaceae Okulitch, 1955a, p. 18, *nom. transl.* Zhuravlev & Sayutina, 1985, p. 54, *ex* Radiocyathidae Okulitch, 1955a, p. 18; =order Radiocyathida Zhuravleva & Myagkova, 1987, p. 73]

One- or two-walled globular, conical, or pyriform skeletons constructed of nesasters; corresponding nesasters of inner and outer wall linked by radial rods, which may bifurcate toward outer wall, in two-walled forms; rods project radially inward from wall of some one-walled forms; original skeletal mineralogy aragonitic. [The rank of Radiocyatha is uncertain (Debrenne, H. Termier, & G. Termier, 1970).] *lower Cambrian (Tom.3–Toy.2).*

Family HETAIRACYATHIDAE R. Bedford & J. Bedford, 1937

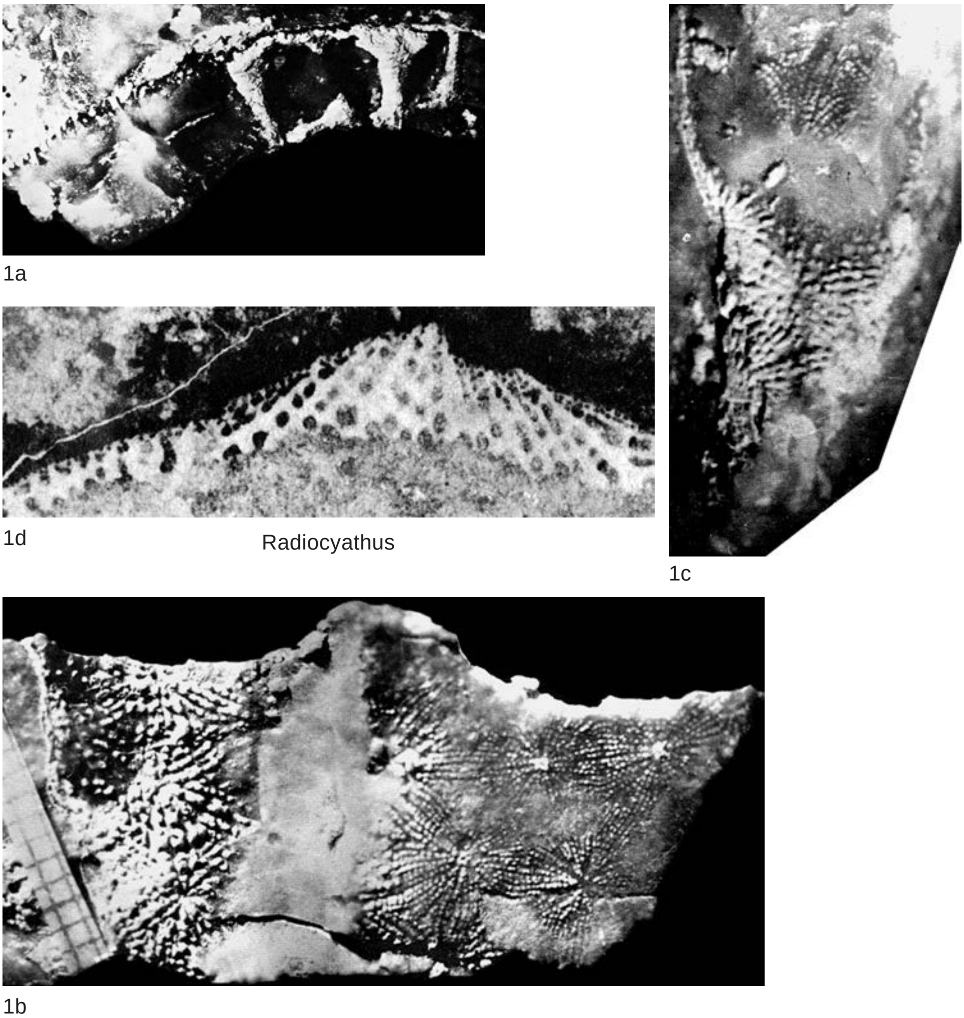
[Hetairacyathidae R. Bedford & J. Bedford, 1937, p. 27, *nom. nov. pro* Heterocyathidae R. Bedford & W. R. Bedford, 1934, p. 6, based on junior homonym] [=Radiocyathidae Okulitch, 1955a, p. 18; =Girphanovellidae Debrenne, H. Termier, & G. Termier, 1971, p. 442; =Kazakovicyathidae Konyushkov, 1972, p. 130; =family Radiocyataceae Okulitch, 1955a, p. 18, *nom. correct.* Nitecki & Toomey, 1979, p. 728, *pro* Radiocyathidae Okulitch, 1955a, p. 18; =family Girvanovellaceae Debrenne, H. Termier, & G. Termier, 1971, p. 442, *lapsus calami pro* Girphanovellaceae, *nom. correct.* Nitecki & Toomey, 1979, p. 728, *pro* Girphanovellidae Debrenne, H. Termier, & G. Termier, 1971, p. 442; =Radiocyathaceae Zhuravlev & Sayutina, 1985, p. 54, *nom. transl. et correct. ex* Radiocyathidae Okulitch, 1955a, p. 18; =Radiocyathinae Okulitch, 1955a, p. 18, *nom. transl.* Zhuravlev & Sayutina, 1985, p. 54, *ex* Radiocyathidae Okulitch, 1955a, p. 18; =Gonamispongiinae Zhuravleva in Zhuravleva & Myagkova, 1987, p. 74]

Cup two-walled. *lower Cambrian (Tom.3–Toy.2).*

Radiocyathus Okulitch, 1937a (April), p. 252, *nom. nov. pro Heterocyathus* R. Bedford & W. R. Bedford, 1934, p. 7 (type, *H. minor*, SD R. Bedford & W. R. Bedford, 1936, p. 20), *non* Milne-Edwards & Haime, 1848, p. 323 (type, *H. aequicostatus*, SD Milne-Edwards & Haime, 1850–1854, p. xv), cnidarian [**Heterocyathus minor* R. Bedford & W. R. Bedford, 1934, p. 7; SD R. Bedford & W. R. Bedford, 1936, p. 20; holotype, R. Bedford & W. R. Bedford, 1934, fig. 32; Hill, 1965, pl. 12,*4;* Debrenne, H. Termier, & G. Termier, 1970, pl. 4,*1-3,* pl. 5,*1;* M, S4196, NHM, London and PU87211, USNM, Washington, D.C.] [=*Hetairacyathus* R. Bedford & J. Bedford, 1937 (September), p. 27, *nom. nov. pro Heterocyathus* R. Bedford & W. R. Bedford, 1934, p. 7 (type, *H. minor*, SD R. Bedford & W. R. Bedford, 1936, p. 20), *non* Milne-Edwards & Haime, 1848, p. 323 (type, *H. aequicostatus,* SD Milne-Edwards & Haime, 1850–1854, p. xv), cnidarian]. Cup conical to pyriform, nesasters linked, of constant size and number of rays; outer wall with microporous sheath. *lower Cambrian (Atd.4–Bot.3)*: Australia, Antarctica, Falkland Islands (allochthonous).——Fig. 658,*1a–d*. **R. minor* (R. Bedford & W. R. Bedford); *a–c,* Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; *a–b,* holotype, USNM PU87211; *a,* transverse view, ×3; *b,* tangential view of outer wall (at left) and inner wall (at right), ×3; *c,* holotype, NHM S4196, tangential view of outer wall (at bottom) and inner wall (at top), ×3 (Debrenne, H. Termier, & G. Termier, 1970); *d,* Wilkawillina Limestone, Botoman, Wirrealpa Mine, South Australia, Australia, specimen SAM P47956, tangential section of outer wall, ×9 (Kruse, 1991).

Blastasteria Debrenne, H. Termier, & G. Termier, 1971, p. 442 [**B. bedfordorum*; OD; holotype, R. Bedford & W. R. Bedford, 1936, fig. 39; M; P922/3, SAM, Adelaide; =*Uranosphaera hexaster* R. Bedford & W. R. Bedford, 1936, p. 10, *non* R. Bedford & W. R. Bedford, 1934, p. 7]. Cup globular, nesasters independent. *lower Cambrian (Bot.3)*: Australia.——Fig.658,*2a–b*. **B. bedfordorum*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, SAM P922/3; *a,* sketch of transverse view, ×3; *b,* sketch of outer wall in tangential view, ×6 (R. Bedford & W. R. Bedford, 1936).

Girphanovella Zhuravleva in Zhuravleva, Zadorozhnaya, & others, 1967, p. 107 [**G. girphanovae*; OD; holotype, Zhuravleva, Zadorozhnaya, & others, 1967, pl. 59,*1–2*, 325, TsSGM, Novosibirsk; =*Archaeocyathus neoproskurjakovi* Vologdin, 1940b, p. 56, holotype not designated, collection not located; =Dokidocyathina? *georgensis* Rozanov in Zhuravleva, Konyushkov, & Rozanov, 1964, p. 100, holotype, Zhuravleva, Konyushkov, & Rozanov, 1964, pl. 16,*8*, GIN3461, PIN, Moscow] [=*Kazakovicyathus* Konyushkov, 1972, p. 130 (type, *K. sajanicus,* OD)]. Cup conical to pyriform, nesasters linked, of variable size



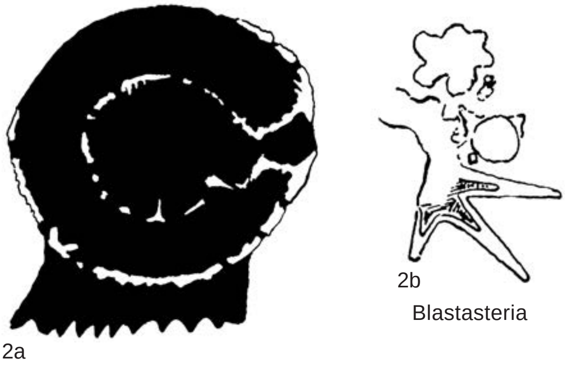


FIG. 658. Hetairacyathidae (p. 1087).

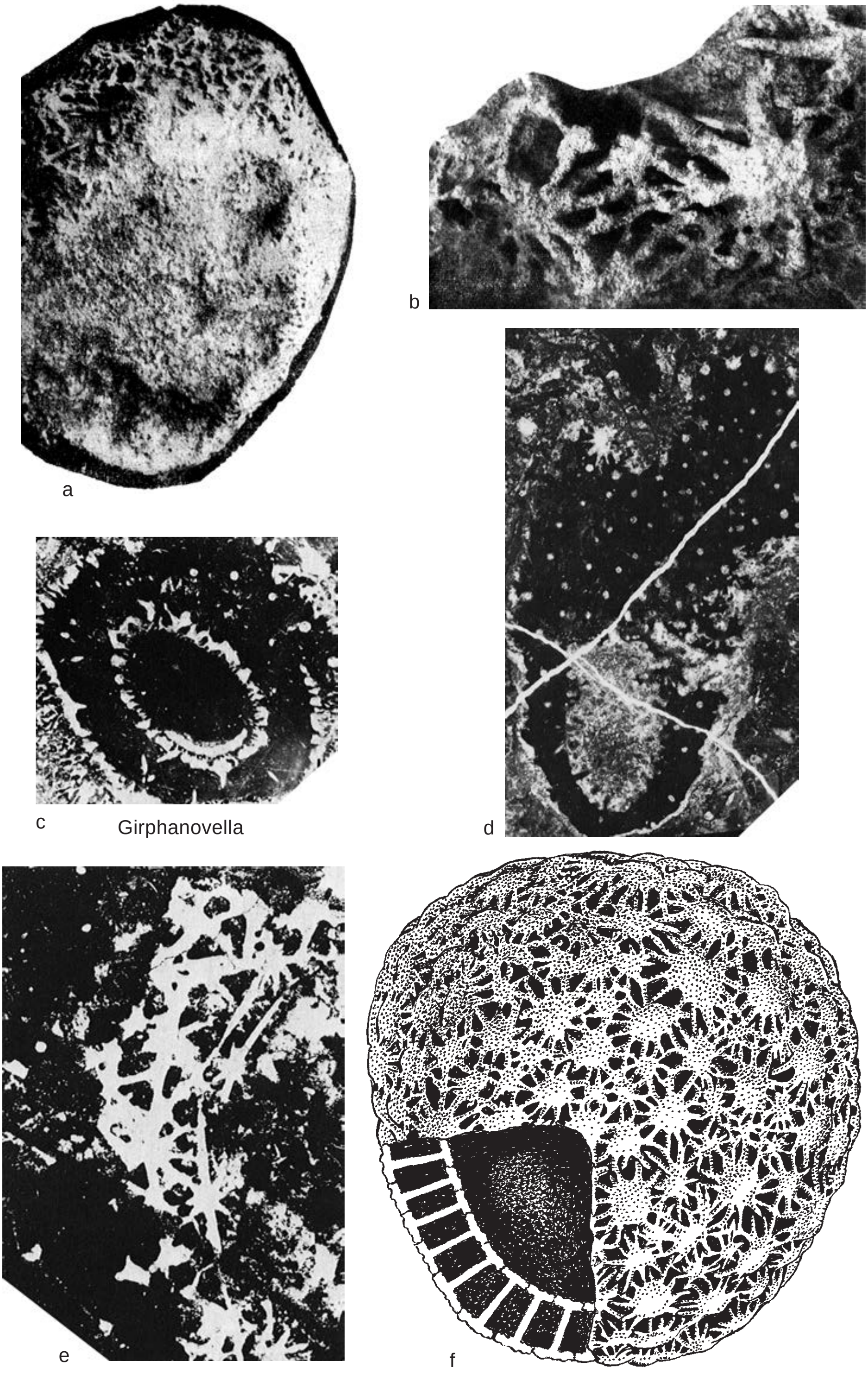


FIG. 659. Hetairacyathidae (p. 1087–1090).

and number of rays; outer wall with possible microporous sheath. *lower Cambrian (Atd.1–Toy.2)*: Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Australia, ?Morocco, Canada.——Fig. 659*a–f. G. neoproskurjakovi* (Vologdin); *a–b,* = *G. girphanovae* Zhuravleva, Shangan Formation, Botoman, Shivelig-Khem River, Eastern Tannu-Ola Range, Tuva, Russia, holotype TsSGM 325; *a,* external view, ×1.8; *b,* tangential view of outer wall, ×10 (Zhuravleva, Zadorozhnaya & others, 1967); *c–e,* = *G. georgensis* (Rozanov); *c,* Bystraya Formation, Atdabanian, Georgievka, Argun' River, Transbaikalia, Russia, specimen PIN 3900/35, oblique transverse section, ×3; *d–e,* Salaany Gol Formation, Atdabanian, Mount Zuune Arts, Tsagaan Oloom province, Mongolia; *d,* specimen PIN 3482/51, oblique longitudinal section, ×3; *e,* specimen PIN 3482/53, tangential section of inner wall, ×6 (Zhuravlev, 1986b); *f,* Shangan Formation, Shivelig-Khem River, Eastern Tannu-Ola Range, Tuva, Russia, reconstruction based on etched specimens, external longitudinal view, ×1.5 (Kruse, Zhuravlev, & Debrenne, 2012).

Gonamispongia Korshunov, 1968, p. 127 [**G. ignorabilis*; OD; holotype, Korshunov, 1968, fig. 1a–v, 84/3, YaFAN, Yakutsk]. Cup conical to pyriform, nesasters linked, of constant size and number of rays; rods extend radially inward from nesaster centers. *lower Cambrian (Tom.3–Atd.1)*: Siberian Platform.——Fig. 660,*1a–b.* **G. ignorabilis*, Pestrotsvet Formation, Tommotian, Knyaz'-Yurakh Creek, Algoma and Gonam rivers, Sakha (Yakutia), Russia, holotype, YaFAN 84/3; *a,* longitudinal section, ×1.5; *b,* detail of wall in tangential section, ×10 (Korshunov, 1968).

Family URANOSPHAERIDAE R. Bedford & J. Bedford, 1936

[Uranosphaeridae R. Bedford & J. Bedford, 1936, p. 22] [=family Uranosphaeraceae R. Bedford & J. Bedford, 1936, p. 22, *nom. correct.* Nitecki & Toomey, 1979, p. 728, *pro* Uranosphaeridae R. Bedford & J. Bedford, 1936, p. 22; =Uranosphaerinae R. Bedford & J. Bedford, 1936, p. 22, *nom. transl.* Zhuravlev & Sayutina, 1985, p. 60, *ex* Uranosphaeridae R. Bedford & J. Bedford, 1936, p. 22]

Cup one-walled. *lower Cambrian (Bot.1–Bot.3).*

Uranosphaera R. Bedford & W. R. Bedford, 1934, p. 7 [**U. polyaster*; SD R. Bedford & W. R. Bedford, 1936, p. 20; holotype, R. Bedford & W. R. Bedford, 1934, fig. 35; Debrenne, H. Termier, & G. Termier, 1971, pl. 29,*3–6;* M, S4199, NHM, London] [?=*Kuraya* Romanenko, 1968, p. 135 (type, *K. sphaerica,* OD)]. Cup globular, nesasters linked. *lower Cambrian (?Bot.1, Bot.3)*: ?Altay Sayan, Australia.——Fig. 660,*2a–c.* **U. polyaster*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, NHM S4199; *a,* distal view, ×2.5; *b,* lower view, ×2.5; *c,* external tangential view of wall, ×6 (Debrenne, H. Termier, & G. Termier, 1971).

Class UNCERTAIN

MORPHOLOGICALLY SIMILAR BUT PROBABLY NOT ALLIED TO ARCHAEOCYATHA OR RADIOCYATHA

Acanthinocyathus R. Bedford & W. R. Bedford and *Osadchiites* Zhuravleva share a morphology of radial rods linking more or less identical units of the inner and outer wall, a character reminiscent of Radiocyatha (Nitecki & Debrenne, 1979, p. 14; Debrenne, Zhuravlev, & Rozanov, 1989, p. 77). In their original description of *Acanthinocyathus*, R. Bedford and W. R. Bedford (1934) drew attention to a similarity with the archaeocyath *Dokidocyathus* Taylor, which also bears radial intervallar rods in some species. R. Bedford & W. R. Bedford (1934) and Okulitch (1935b) viewed the walls as consisting of fused spicular elements, implying affinity with spiculate sponges. Most authors have nevertheless included *Acanthinocyathus* among the Archaeocyatha.

Acanthinocyathus R. Bedford & W. R. Bedford was known only from silicified specimens until well-preserved calcitic specimens with archaeocyath-like microgranular microstructure were described by Kruse (1982). Despite this microstructural similarity, the genus has been excluded from the Archaeocyatha by Debrenne, Zhuravlev, and Rozanov (1989).

Order ACANTHINOCYATHIDA R. Bedford & W. R. Bedford, 1936

[Acanthinocyathida R. Bedford & W. R. Bedford, 1936, p. 11, *nom. correct.* Vologdin, 1962a, p. 131, *pro* order Acanthinocyathina R. Bedford & W. R. Bedford, 1936, p. 11; *nom. nov. pro* Acanthocyathina Okulitch, 1935b, p. 90, invalid name based on junior homonym]

Cup conical to subcylindrical, two-walled; intervallum with radial rods arranged in longitudinal radial planes, rods linking

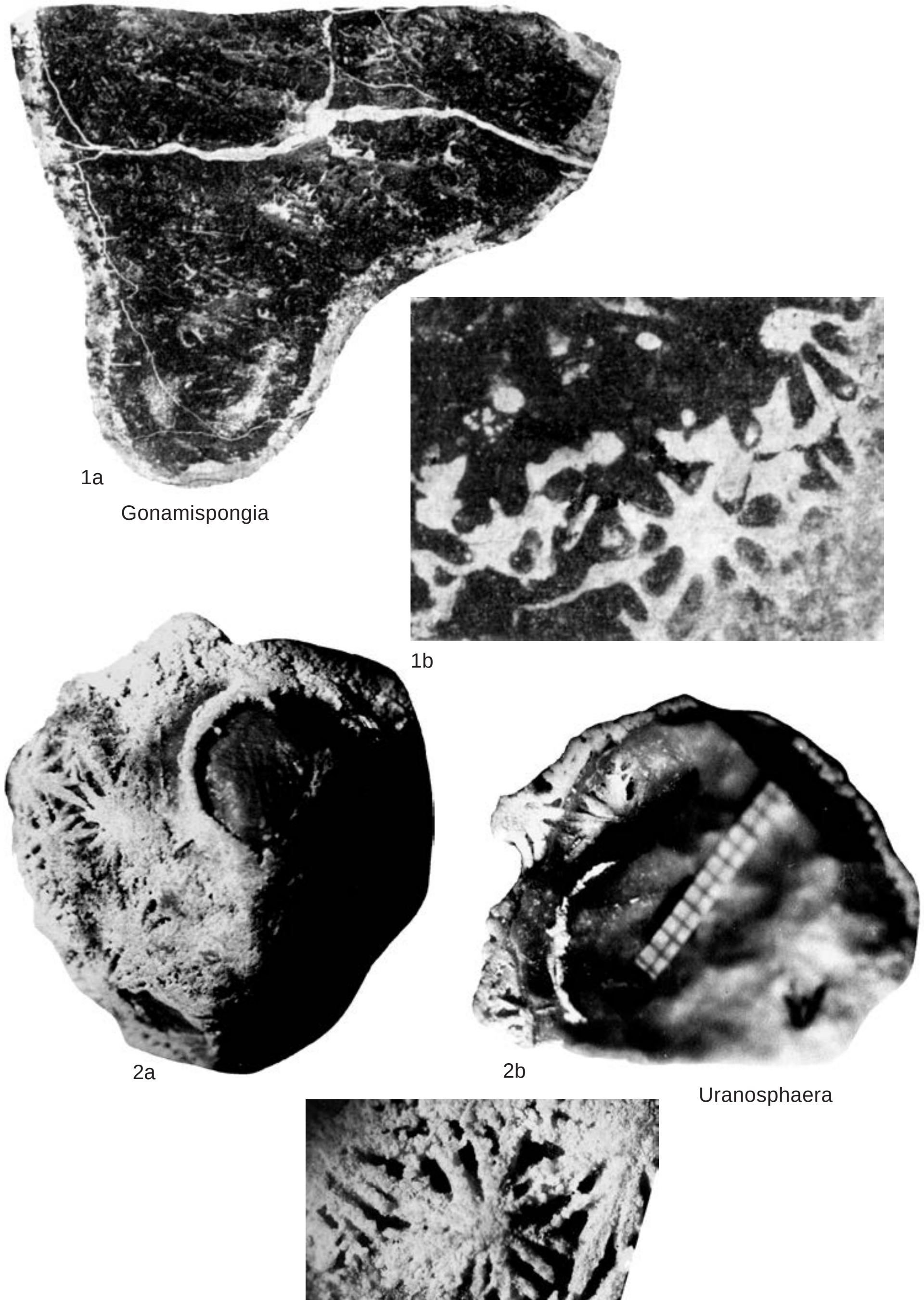


FIG. 660. Hetairacyathidae and Uranosphaeridae (p. 1090).

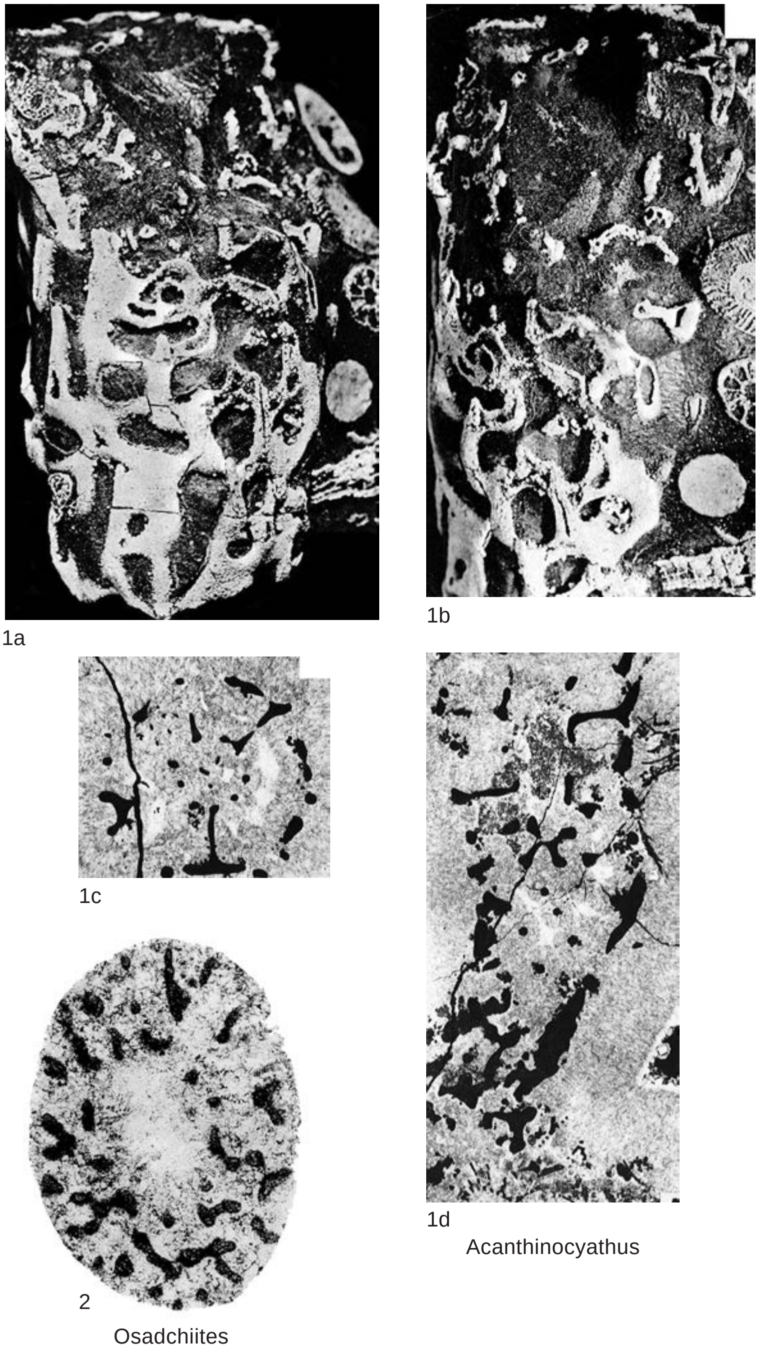


FIG. 661. Acanthinocyathidae (p. 1093).

corresponding intersections of inner and outer wall structures. *lower Cambrian (Atd.1–Bot.3).*

Family ACANTHINOCYATHIDAE R. Bedford & W. R. Bedford, 1936

[Acanthinocyathidae R. BEDFORD & W. R. BEDFORD, 1936, p. 11, *nom. nov. pro* Acanthocyathidae R. BEDFORD & W. R. BEDFORD, 1934, p. 4, invalid name based on junior homonym] [=Acantinocyathidae ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 99, *nom. null.*]

Outer and inner walls simple, each constructed of two sets of intersecting tangential diagonal rods. *lower Cambrian (Atd.1–Bot.3).*

Acanthinocyathus R. BEDFORD & W. R. BEDFORD, 1936, p. 11, *nom. nov. pro Acanthocyathus* R. BEDFORD & W. R. BEDFORD, 1934, p. 4 (type, *A. apertus* R. BEDFORD & W. R. BEDFORD, 1934, p. 4, M), *non* MILNE-EDWARDS & HAIME, 1848, p. 292, cnidarian [**Acanthocyathus apertus* R. BEDFORD & W. R. BEDFORD, 1934, p. 4; M; lectotype, HILL, 1965, pl. 2,*3;* DEBRENNE, 1969a, pl. 2,*3;* SD DEBRENNE, 1969a, p. 307, S4166, NHM, London] [=*Acantinocyathus* ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 100, *nom. null.*]. Outer and inner walls with subrounded to diamond-shaped pores in one longitudinal row per intersept, each outer wall pore bearing an upwardly projecting cornute spine. *lower Cambrian (Bot.3)*: Australia, Antarctica.——FIG. 661,*1a–d*. **A. apertus* (R. BEDFORD & W. R. BEDFORD); *a–b,* Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, NHM S4166; *a,* longitudinal view, ×2.5; *b,* longitudinal view, ×2.5 (Hill, 1965); *c–d,* Cymbric Vale Formation, Botoman, Mount Wright, New South Wales, Australia, AM F.83608; *c,* transverse section, AM FT.14180, ×3; *d,* longitudinal section, AM FT.14179, ×3 (Kruse, 1982).

Osadchiites ZHURAVLEVA in ZHURAVLEVA & others, 1997b, p. 167 [**O. denaevadae*; OD; holotype, ZHURAVLEVA & others, 1997b, pl. 13,*3*, 917/5, TsSGM, Novosibirsk]. Outer and inner walls with subrounded to diamond-shaped pores in one longitudinal row per intersept, each outer wall pore bearing an upwardly projecting cornute spine; intervallar rods linked by subsidiary lintels. *lower Cambrian (Atd.1–Atd.2)*: Altay Sayan, Mongolia.——FIG. 661,*2*. **O. denaevadae*, Usa Formation, Atdabanian, Kiya River, Kuznetsk Alatau, Altay Sayan, Russia, holotype, TsSGM 917/5, transverse section, ×8 (Zhuravleva & others, 1997b).

CRIBRICYATHS AND CRIBRICYATH-LIKE TAXA: SYSTEMATIC DESCRIPTIONS

A. Yu. Zhuravlev and P. D. Kruse

Cribricyaths were first described by Vologdin (1932), who interpreted them as archaeocyathan larvae. In a subsequent monograph, Vologdin (1964a) treated cribricyaths as a class within the phylum Archaeocyatha.

Vologdin (1966, p. 16) defined the class Cribricyathea as having "cups elongate or isometric, one-walled and two-walled. Walls built by transversely oriented ribbonlike platy elements (peripteratae) connected by longitudinal rodlike skeletal elements (baculi)." He compared cribricyaths with one-walled archaeocyaths and considered them to be the descendants of the latter. According to him, the peripterate construction of the wall was a further development of the archaeocyathan perforated wall, wherein pores are confined to tightly constrained horizontal files.

Cribricyaths are small (up to 2 cm in length and 1–2 mm in transverse section), cornute, bilaterally symmetric calcareous fossils, either one walled or two walled. In transverse section they are circular to elliptical, cardioid, or quadrate (subtetragonal). The outer wall consists of ribbonlike elements (peripterates), about 0.1 mm thick, spirally coiled along the cup axis (Fig. 662). External surfaces of peripterates can be covered by longitudinal rodlike elements (baculi). The inner wall, if present, is excentric, fused to one (usually the concave) side of the outer wall. It is porous and consists of transverse, platelike elements (striae) or can be contiguous. Longitudinal lintels may additionally be present.

Jankauskas (1969, 1972) showed that cribricyath ontogenetic development commenced from a nonporous cup 0.03–0.04 mm in diameter. The inner wall appeared after the complication of the outer wall.

Cribricyath skeletal microstructure is microgranular, similar to that of archaeocyaths (Zhuravleva & Okuneva, 1981; Rozanov & Sayutina, 1982). However, the microgranule size (about 2.0 µm) is smaller than the microgranules constituting archaeocyaths from the same locality (Kruse & Debrenne, 1989). As with archaeocyaths, the microstructural type implies a primary magnesium calcite skeletal mineralogy.

Cribricyath affinities are still a matter of debate. Boyarinov (1962) suggested that they were ancestral to conulariids because some cribricyaths have a quadrate transverse section. Jankauskas (1972) considered them to be a separate metazoan phylum, whereas Zhuravleva and Okuneva (1981), Belyaeva (1985), Zhuravleva and Myagkova (1987), and Belyaeva and Zhuravleva (1990) maintained that cribricyaths are simply outgrowths of archaeocyathan cups, similar to some archaeocyathan secondary skeletal structures, or even a specialized mode of archaeocyathan existence somewhat analogous to sporophytes and gametophytes in higher plants. However, evidence for the consistent co-occurrence of any pair or set of archaeocyathan and cribricyathan taxa is lacking. Furthermore, cribricyaths were much more restricted in space and time than were archaeocyaths.

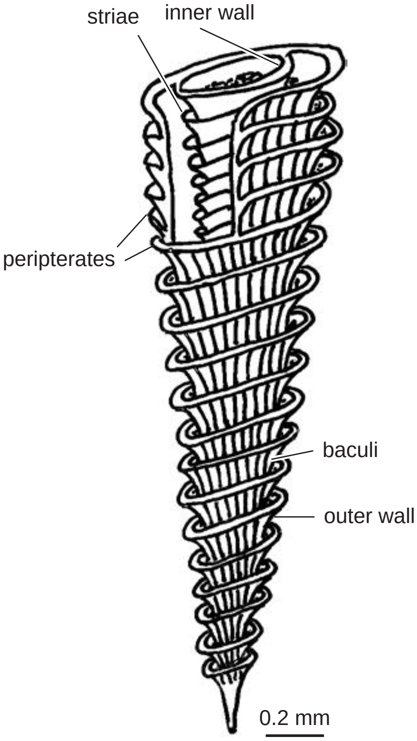


FIG. 662. Reconstruction of cribricyath skeleton as loosely exemplified by *Dolichocyathus* VOLOGDIN, based on etched and thin-sectioned specimens, Tuva, Russia, external longitudinal view, ×10 (Zhuravlev & Kruse, 2012).

Cribricyaths were sessile reef dwellers, and befitting their tiny size, mostly cryptobionts (ZHURAVLEV & WOOD, 1995). Cribricyath habitats were restricted to areas of constant water currents, presumably necessary for filter feeding (WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993). Possibly, some were ectoparasites on archaeocyaths, as their settlement on archaeocyathan skeletons commonly caused malformation of the host (DEBRENNE & ZHURAVLEV, 1992b).

The earliest cribricyaths are known from the middle Tommotian of East Sayan. During the Atdabanian and Botoman, they become widespread along the entire Ural-Mongolian Foldbelt (Urals, Altay Sayan, Tuva, Mongolia, Transbaikalia, and Russian Far East). They are unknown beyond the limits of this region, with the exception of a single Atdabanian species from the Siberian Platform (SUNDUKOV & ZHURAVLEV, 1989).

The pioneering cribricyathan systematics of VOLOGDIN (1964a, 1966) were reworked by JANKAUSKAS (1965, 1969; VOLOGDIN & JANKAUSKAS, 1968) based on rich material from mixed siliciclastic-carbonate rocks of the Krasnoyarsk region (East Sayan). He described a large new group, order Pterocyathida, and later (JANKAUSKAS, 1972, 1973) introduced a morphological key to all cribricyath genera. Through synonymization, he also significantly reduced the number of formal genera having diagnoses based only on single sections. With necessary nomenclatural corrections, his systematics serves as the basis for the present revision.

The following taxonomic criteria, listed with their known character states, are adopted here:

Order: baculi [absent/present]
  Superfamily: cup [one/two]-walled
    Family: peripterates [closed/open]
    Genus: transverse section [circular to elliptical/cardioid/quadrate]
      Peripterates [weakly/well] developed
        If well developed: Peripterates open [internally/externally]
      Inner wall [contiguous/of striae]
        If of striae: Striae [planar/curved]

Class CRIBRICYATHA Vologdin, 1961

[*nom. correct.* ZHURAVLEV & KRUSE, herein, *pro* Cribricyathea VOLOGDIN, 1964a, p. 1392, *nom. correct. pro* Cribrocyathea VOLOGDIN, 1961a, p. 177] [=Protoarchaeocyatha RADUGIN, 1964, footnote, p. 145; =phylum Cribricyatha JANKAUSKAS, 1972, p. 166, *nom. correct.* ZHURAVLEVA & OKUNEVA, 1981, p. 23, *pro* Cribricyathi JANKAUSKAS, 1972, p. 166]

One- or two-walled cornute, bilaterally symmetric aporose cups of circular, elliptical, cardioid, or quadrate (subtetragonal) transverse section; outer wall of ribbonlike peripterates coiled along cup axis to form a spiral chamber that can be either closed or open externally or internally; longitudinal, rodlike baculi may be present on external surface of peripterates; inner wall, if present, is excentric, fused to outer wall on one side, and consists of transverse annular platelike striae or may be a contiguous porous sheet; original magnesium calcite skeletal mineralogy. *lower Cambrian (Tom.2–Bot.3).*

Order VOLOGDINOPHYLLIDA Radugin, 1964

[*nom. correct.* HILL, 1972, p. 137, *pro* order Vologdinophylloidea RADUGIN, 1964, p. 145] [=order Akademiophylloidea RADUGIN, 1964, p. 145; =Pterocyathida JANKAUSKAS, 1969, p. 134, *nom. correct pro* order Pterocyathidae JANKAUSKAS, 1965, p. 439]

Baculi absent. *lower Cambrian (Tom.2–Bot.1).*

Superfamily VOLOGDINOPHYLLOIDEA Radugin, 1964

[*nom. correct.* ZHURAVLEV & KRUSE, herein, *pro* Vologdinophyllacea JANKAUSKAS, 1969, p. 134, *nom. transl. ex* Vologdinophyllidae RADUGIN, 1964, p. 145]

Cup one-walled. *lower Cambrian (Tom.2–Bot.1).*

Family VOLOGDINOPHYLLIDAE Radugin, 1964

[Vologdinophyllidae RADUGIN, 1964, p. 145] [=Eophyllidae RADUGIN, 1966, p. 46; =Monophyllidae RADUGIN, 1966, p. 62; =Costophyllidae RADUGIN, 1966, p. 65; =Anomalophyllidae RADUGIN, 1966, p. 67; =Nefrophyllidae RADUGIN, 1966, p. 68; =Cardiophyllidae RADUGIN, 1966, p. 77; =Polygonophyllidae RADUGIN, 1966, p. 91, *nom. nud.*, invalid family-group name based on unavailable type genus; =Linzophyllidae RADUGIN, 1966, p. 97; =Kaphyllidae RADUGIN, 1966, p. 100]

Peripterates closed. *lower Cambrian (Atd.1).*

Vologdinophyllum RADUGIN, 1962, p. 8 [**V. chachlovi*; OD; holotype, RADUGIN, 1962, fig. 1; RADUGIN, 1964, fig. 1(37), 36–r 12, TPI, Tomsk] [=*Ophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Miophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Mesophyllum* RADUGIN, 1964, p. 146, *nom. nud.*, *non* SCHLÜTER, 1889, p. 325, cnidarian; =*Ellipsophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Nefrophyllina* RADUGIN, 1964, p. 146, *nom. nud.*; =*Nefrophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Dephyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Laphyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Unicophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Costophullum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Kaphyllum* RADUGIN, 1964, p. 146, *nom. nud.*; ?=*Trapecephyllum* RADUGIN, 1964, p. 146, *nom. nud.*; ?=*Quadriphyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Rhombophyllina* RADUGIN, 1964, p. 146, *nom. nud.*; =*Rhombophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Linzophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Vandophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Tephyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Esphyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Ellipsophyllina* RADUGIN, 1964, p. 146, *nom. nud.*; =*Eophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; =*Anomalophyllum* RADUGIN, 1964, p. 146, *nom. nud.*; ?=*Longaevus* JANKAUSKAS, 1965, p. 439, *nom. nud.*; ?=*Crispus* JANKAUSKAS, 1965, p. 439, *nom. nud.*, all invalid genus-group names based on unavailable type species; =*Eophyllum* RADUGIN, 1966, p. 47 (type, *E. falciforme*, OD); =*Circophyllum* RADUGIN, 1966, p. 52, *nom. nud.*, *non* LANG & SMITH, 1939, p. 153, cnidarian; =*Hemiphyllina* RADUGIN, 1966, p. 53 (type, *H. prima,* OD); =*Hemiphyllum* RADUGIN, 1966, p. 54 (type, *H. semicirculare*, OD), *non* TOMES, 1887, p. 98, rugose coral; =*Hemiphyllum (Paraphyllum)* RADUGIN, 1966, p. 56 (type, *H. (P.) cerskii*, OD), *non Paraphyllum* HANCOCK, 1913, p. 40, orthopteran; =*Miophyllum* RADUGIN, 1966, p. 57 (type, *M. biconvexum*, OD); =*Ophyllum* RADUGIN, 1966, p. 58 (type, *O. planiconvexum*, OD); =*Mesophyllum* RADUGIN, 1966, p. 59 (type, *M. ordinare*, OD), *non* SCHLÜTER, 1889, p. 325, cnidarian; =*Ellipsophyllina* RADUGIN, 1966, p. 61 (type, *E. prima*, OD); =*Monophyllum* RADUGIN, 1966, p. 62 (type, *M. obrucevi*, OD), *non* FOMICHEV, 1953, p. 110, cnidarian; =*Vandophyllum* RADUGIN, 1966, p. 64 (type, *V. khalfini*, OD); =*Costophyllum* RADUGIN, 1966, p. 66 (type, *C. nalivkini*, OD); =*Anomalophyllum* RADUGIN, 1966, p. 67 (type, *A. karpinskii*, OD); =*Dephyllum* RADUGIN, 1966, p. 69 (type, *D. tadasi*, OD); =*Laphyllum* RADUGIN, 1966, p. 71 (type, *L. ordinare*, OD); =*Nefrophyllum* RADUGIN, 1966, p. 74 (type, *N. cairkini*, OD); =*Ellipsophyllum* RADUGIN, 1966, p. 87 (type, *E. typicum*, OD); ?=*Quadriphyllum* RADUGIN, 1966, p. 91 (type, *Q. koptevi*, OD); ?=*Trapecephyllum* RADUGIN, 1966, p. 93 (type, *T. unicum*, OD); =*Rhombophyllum* RADUGIN, 1966, p. 95 (type, *R. flexuosum*, OD); =*Linzophyllum* RADUGIN, 1966, p. 97 (type, *L. asimmetricum*, OD); =*Gonophyllum* RADUGIN, 1966, p. 99 (type, *G. zhuravlevae*, OD); =*Kaphyllum* RADUGIN, 1966, p. 101 (type, *K. irregulare*, OD); =*Tephyllum* RADUGIN, 1966, p. 102 (type, *T. mirabile*, OD); =*Esphyllum* RADUGIN, 1966, p. 103 (type, *E. originale*, OD), for discussion, see JANKAUSKAS (1969, p. 141); ?=*Longaevus* JANKAUSKAS, 1969, p. 144 (type, *L. vitalis*, OD); ?=*Crispus* JANKAUSKAS, 1969, p. 145 (type, *C. subdimidiatus*, OD)]. Transverse section circular to elliptical; peripterates well developed. *lower Cambrian (Atd.1)*: Altay Sayan.——FIG. 663,*1*. **V. chachlovi*, Ungut Formation, Atdabanian, Kolba River, Mana River, East Sayan, Altay Sayan, Russia, holotype, TPI 36-r 12, longitudinal section, ×10 (Radugin, 1962).

Manaella JANKAUSKAS, 1964 (April), p. 57 [**M. basaica*; OD; holotype, JANKAUSKAS, 1964, pl. 1,*a*, thin section 187/62, Division of General Geology, TPI, Tomsk; =*Cardiophyllum kelleri* RADUGIN, 1964 (January), p. 146, *nom. nud.*; =*Cardiophyllina mani* RADUGIN, 1964 (January), p. 146, *nom. nud.*; =*Stapephyllum cerskii* RADUGIN, 1964 (January), p. 146, *nom. nud.*; =*Aphyllum lomonosovi* RADUGIN, 1964 (January), p. 146, *nom. nud.*; =*Cephyllum costatum* RADUGIN, 1964 (January), p. 146, *nom.*

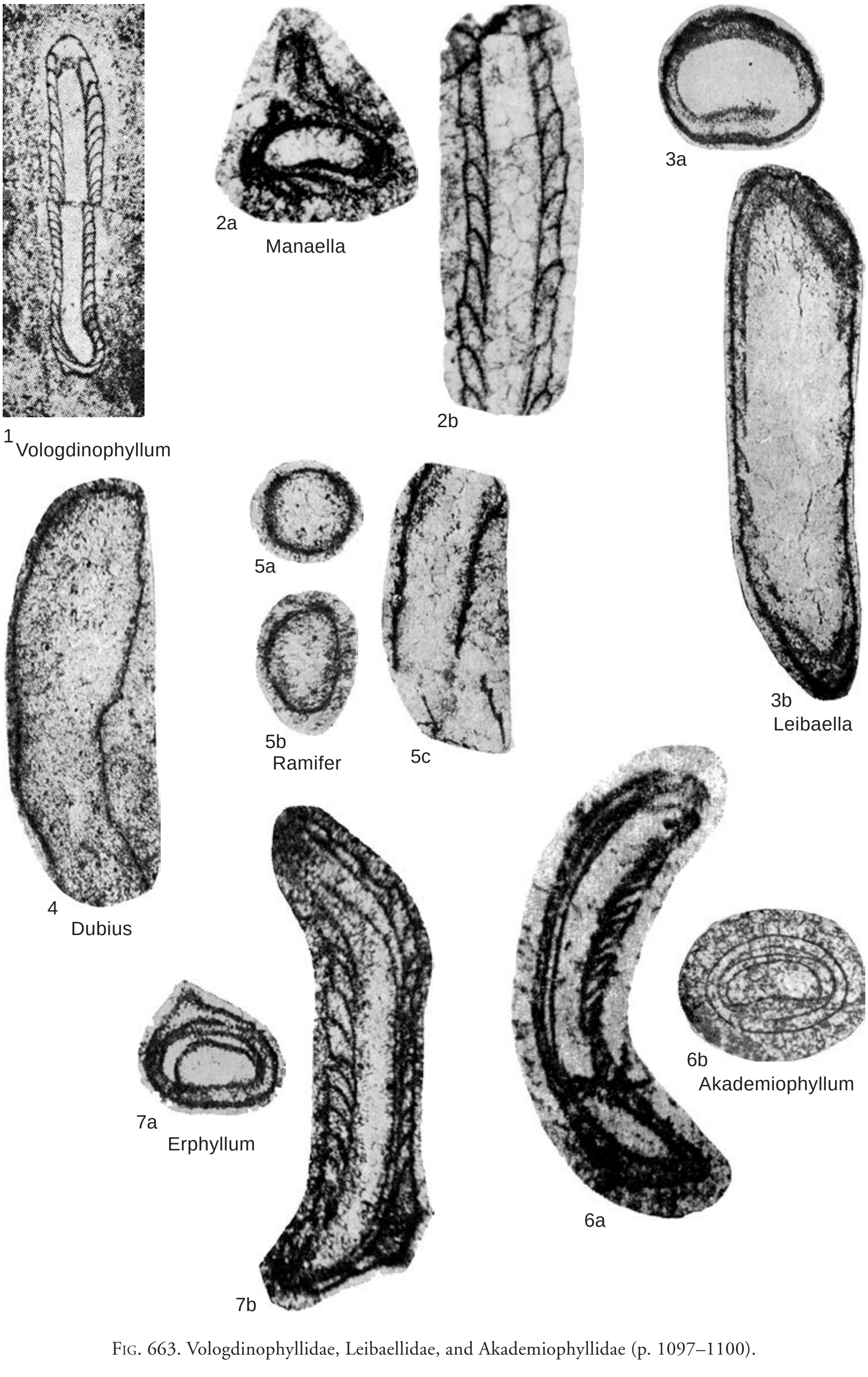


FIG. 663. Vologdinophyllidae, Leibaellidae, and Akademiophyllidae (p. 1097–1100).

nud.; =*Bephyllum lermontovae* Radugin, 1964 (January), p. 146, *nom. nud.*] [=*Cardiophyllum* Radugin, 1964 (January), p. 146, *nom. nud.*; =*Cardiophyllina* Radugin, 1964 (January), p. 146, *nom. nud.*; =*Stapephyllum* Radugin, 1964 (January), p. 146, *nom. nud.*; =*Aphyllum* Radugin, 1964 (January), p. 146, *nom. nud.*, *non Aphyllum* Soshkina, 1937, p. 45, cnidarian; =*Cephyllum* Radugin, 1964 (January), p. 146, *nom. nud.*; =*Bephyllum* Radugin, 1964 (January), p. 146, *nom. nud.*, all invalid genus-group names based on unavailable type species; =*Cardiophyllina* Radugin, 1966, p. 77 (type, *C. manae*, OD); =*Cardiophyllum* Radugin, 1966, p. 79 (type, *C. kelleri*, OD); =*Stapephyllum* Radugin, 1966, p. 81 (type, *S. cerskii*, OD); *Bephyllum* Radugin, 1966, p. 82 (type, *B. lermontovae*, OD); =*Cephyllum* Radugin, 1966, p. 84 (type, *C. costatum*, OD); =*Aphyllum* Radugin, 1966, p. 85 (type, *Aphyllum lomonosovi*, OD), *non* Soshkina, 1937, p. 45, cnidarian, for discussion, see Jankauskas (1969, p. 143)]. Transverse section cardioid; peripterates well developed. *lower Cambrian (Atd.1)*: Altay Sayan.——Fig. 663,*2a–b*. **M. basaica*, Bazaikha Formation, Atdabanian, Bazaikha River, East Sayan, Altay Sayan, Russia; *a,* specimen TPI thin section 318, transverse section, ×40; *b,* specimen TPI thin section 239, longitudinal section, ×20 (Jankauskas, 1965).

Family LEIBAELLIDAE Jankauskas, 1965

[Leibaellidae Jankauskas, 1965, p. 439]

Peripterates open. *lower Cambrian (Tom.2–Bot.1).*

Leibaella Jankauskas, 1964, p. 58 [**L. elovica*; OD; holotype, Jankauskas, 1964, pl. 1,*k;* Jankauskas, 1969, pl. 43,*8*, collection 5, thin section 68, specimen 3, Division of General Geology, TPI, Tomsk; =*L. ungutica* Jankauskas, 1964, p. 59; for discussion, see Jankauskas (1969, p. 138)]. Transverse section circular to elliptical; peripterates well developed, open internally. *lower Cambrian (Tom.4–Atd.3)*: Altay Sayan, Mongolia.——Fig. 663,*3a–b*. **L. elovica*, Ungut Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia; *a,* holotype, TPI collection 5, thin section 68, specimen 3, transverse section, ×20; *b,* paratype, TPI collection 5, thin section 65, specimen 4, longitudinal section, ×20 (Jankauskas, 1969).

Dubius Jankauskas, 1969, p. 135 [**D. uncatus*; OD; holotype, Jankauskas, 1969, fig. 11a, pl. 43,*2*, collection 5, thin section 142/63, specimen 1, TPI, Tomsk]. Transverse section circular to elliptical; peripterates weakly developed. *lower Cambrian (Tom.3–Bot.1)*: Altay Sayan, Mongolia.——Fig. 663,*4*. **D. uncatus*, Ungut Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia, holotype, TPI collection 5, thin section 142/63, specimen 1, longitudinal section, ×20 (Jankauskas, 1969).

Ramifer Jankauskas, 1969, p. 136 [**R. giratus*; OD; holotype, Jankauskas, 1965, fig. 1(1), Jankauskas, 1969, fig. 12, pl. 43,*3*, collection 5, thin section 265, specimen 2, TPI, Tomsk] [=*Ramifer* Jankauskas, 1965, p. 439, *nom. nud.*, invalid genus-group name based on unavailable type species]. Transverse section circular to elliptical; peripterates well developed, open externally. *lower Cambrian (Tom.2–Atd.4)*: Altay Sayan, Mongolia.——Fig. 663,*5a–c*. **R. giratus*, Ungut Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia; *a,* paratype, TPI collection 5, thin section 261, specimen 5, transverse section, ×20; *b,* paratype, TPI collection 5, thin section 261, specimen 8, transverse section, ×20; *c,* holotype, TPI collection 5, thin section 265, specimen 2, longitudinal section, ×20 (Jankauskas, 1969).

Superfamily AKADEMIOPHYLLOIDEA Radugin, 1964

[*nom. correct.* Zhuravlev & Kruse, herein, *pro* Akademiophyllacea Hill, 1972, p. 139, *nom. transl. ex* Akademiophyllidae Radugin, 1964, p. 145] [=Striatocyathacea Vologdin & Jankauskas, 1968, p. 200, *nom. transl.* Jankauskas, 1972, p. 177, *ex* Striatocyathidae Vologdin & Jankauskas, 1968, p. 200; =Pterocyathacea Jankauskas, 1969, p. 146]

Cup two-walled. *lower Cambrian (Atd.1–Bot.1).*

Family AKADEMIOPHYLLIDAE Radugin, 1964

[Akademiophyllidae Radugin, 1964, p. 145] [=Pterocyathidae Jankauskas, 1965, p. 440, *nom. nud.*, invalid family-group name based on unavailable genus name; =Academiophyllidae Radugin, 1966, p. 105, *nom. null.*; =Erphyllidae Radugin, 1966, p. 107; =Pterocyathidae Jankauskas, 1969, p. 146]

Peripterates closed. *lower Cambrian (Atd.1–Bot.1).*

Akademiophyllum Radugin, 1964, p. 145 [**A. cornuforme;* OD; holotype, Radugin, 1964, fig. on p. 147, Radugin, 1966, pl. 7,*39*, collection 61r, specimen 8-100-34, TPI, Tomsk] [=*Akademiophyllum* Jankauskas, 1965, p. 440, *nom. nud.*; =*Lacerathus* Jankauskas, 1965, p. 440, *nom. nud.*; =*Pterocyathus* Jankauskas, 1965, p. 440, *nom. nud.*, all invalid genus-group names based on unavailable type species; =*Academiophyllum* Radugin, 1966, p. 106, *lapsus calami pro Akademiophyllum* Radugin, 1964, p. 145; =*Laceratus* Jankauskas, 1969, p. 149 (type, *L. cuneatus*, OD); =*Pterocyathus* Jankauskas, 1969, p. 150 (type, *P. glausus*, OD)]. Transverse section circular to elliptical; peripterates well developed; inner wall contiguous. *lower Cambrian (Atd.1–Bot.1)*: Altay Sayan, Mongolia, Far East.——Fig. 663,*6a–b*. **A. cornuforme*, Ungut Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia; *a,* holotype TPI collection 61r, specimen 8-100-34, longitudinal section, ×28 (Radugin, 1964); *b,* topotype TPI collection

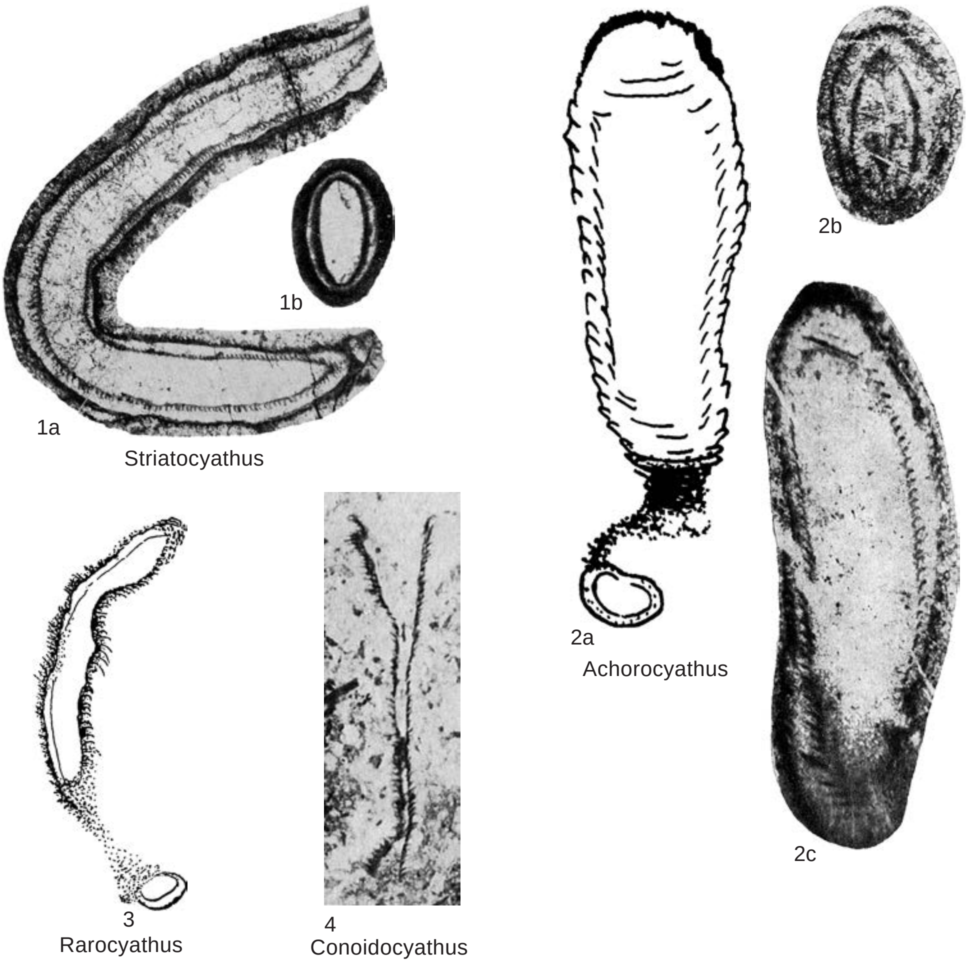


Fig. 664. Striatocyathidae and Conoidocyathidae (p. 1100–1101).

5, locality 61r8, specimen 111, transverse section, ×20 (Jankauskas, 1969).

Erphyllum Radugin, 1966, p. 107 [**E. bephylleforme;* OD; holotype, Radugin, 1966, pl. 7,*36*, collection 61r, specimen 8-46-1, TPI, Tomsk] [=*Erphyllum* Radugin, 1964, p. 146, n*om. nud.*; =*Archaeobullatus* Jankauskas, 1965, p. 440, *nom. nud.*, both invalid genus-group names based on unavailable type species]. Transverse section cardioid; peripterates well developed; inner wall contiguous. *lower Cambrian (Atd.1)*: Altay Sayan.——Fig. 663,*7a–b*. **E. bephylleforme*, Ungut Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia; *a,* topotype, TPI collection 61r, specimen 8, thin section 32, transverse section, ×20; *b,* topotype, TPI specimen 1, thin section 309, longitudinal section, ×20 (Jankauskas, 1969).

Family STRIATOCYATHIDAE
Vologdin & Jankauskas, 1968

[Striatocyathidae Vologdin & Jankauskas, 1968, p. 200] [=Achorocyathidae Jankauskas, 1965, p. 440, *nom. nud.*, invalid family-group name based on unavailable genus name; =Achorocyathidae Jankauskas, 1969, p. 151]

Peripterates open. *lower Cambrian (Atd.1–Bot.1).*

Striatocyathus Vologdin & Jankauskas, 1968, p. 201 [**S. murtukensis*; OD; holotype, Vologdin & Jankauskas, 1968, fig. 1(15), Jankauskas, 1972, fig. 14(1), pl. 29,*2*, thin section 2k-148, TPI, Tomsk] [=*Gracilocyathus* Vologdin & Jankauskas, 1968, p. 201 (type, *G. condensus*, OD); =*Tortocyathus* Vologdin & Jankauskas, 1968, p. 201 (type, *T. ujarensis*, M); =*Iortocyathus* Vologdin & Jankauskas, 1968, p. 201, *nom.*

null., lapsus calami pro Tortocyathus Vologdin & Jankauskas, 1968, p. 201]. Transverse section circular to elliptical; peripterates well developed, open externally; inner wall of curved striae. *lower Cambrian (Atd.1–Bot.1)*: Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Far East.——Fig. 664,*1a–b*. **S. murtukensis*, Siner Formation, Botoman, Murtuk Creek, Mana River, East Sayan, Altay Sayan, Russia; *a,* holotype, TPI thin section 2k-148, longitudinal section, ×15; *b,* paratype, TPI thin section 2k-60, transverse section, ×15 (Jankauskas, 1972).

Achorocyathus Jankauskas, 1969, p. 152 [**A. perbellus*; OD; holotype, Jankauskas, 1965, fig. 1(20); Jankauskas, 1969, fig. 26, collection 5, thin section 62-26-V, specimen 1, TPI, Tomsk] [=*Achorocyathus* Jankauskas, 1965, p. 440, *nom. nud.*; =*Topolinocyathus* Jankauskas, 1965, p. 440, *nom. nud.*, both invalid genus-group names based on unavailable type species; =*Topolinocyathus* Jankauskas, 1969, p. 153 (type, *T. popovi*, OD), for discussion, see Jankauskas (1973, p. 48)]. Transverse section circular to elliptical; peripterates well developed, open internally; inner wall of curved striae. *lower Cambrian (Atd.1–Atd.3)*: Altay Sayan, Mongolia.——Fig. 664,*2a–c*. **A. perbellus*, Krol Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia; *a,* holotype, TPI collection 5, thin section 62-26-V, specimen 1, sketch of longitudinal section, ×20; *b,* paratype, TPI collection 5, thin section 62-26, transverse section, ×15; *c,* paratype, TPI collection 5, thin section 62-26, longitudinal section, ×15 (Jankauskas, 1969).

Rarocyathus Vologdin & Jankauskas, 1968, p. 203 [**R. tubulosus*; M; holotype, Vologdin & Jankauskas, 1968, fig. 1(7); Jankauskas, 1972, fig. 19(1), collection Jankauskas, 1965, thin section 141, specimen 1, TPI, Tomsk]. Transverse section circular to elliptical; peripterates well developed, open externally; inner wall of planar striae. *lower Cambrian (Atd.3–Bot.1)*: Altay Sayan, Transbaikalia, Far East.——Fig. 664,*3*. **R. tubulosus*, Bagrad Formation, Atdabanian, Kiya River, Kuznetsk Alatau, Russia, holotype, TPI collection Jankauskas, 1965, thin section 141, specimen 1, sketch of longitudinal section, ×15 (Vologdin & Jankauskas, 1968).

Order CRIBRICYATHIDA
Vologdin, 1961

[*nom. correct.* Vologdin, 1964a, p. 1392, *pro* Cribrocyathida Vologdin, 1961, p. 177] [=Conoidocyathida Vologdin, 1964a, p. 1392]

Baculi present, imparting cancellate relief where well developed. *lower Cambrian (Atd.1–Bot.3).*

Superfamily
CONOIDOCYATHOIDEA
Vologdin, 1964

[*nom. transl. et correct.* Zhuravlev & Kruse, herein, *ex* Conoidocyathidea Vologdin, 1964a, p. 1392]

Cup one-walled. *lower Cambrian (Atd.1–Bot.3).*

Family CONOIDOCYATHIDAE
Vologdin, 1964

[*nom. correct.* Zhuravlev & Kruse, herein, *pro* Conoidocyathidea Vologdin, 1964a, p. 1392]

Peripterates open. *lower Cambrian (Atd.1–Bot.3).*

Conoidocyathus Vologdin, 1964a, p. 1392 [**C. artus*; M; holotype, Vologdin, 1964a, fig. 1(2); Vologdin, 1966, fig. 4, pl. 1,*5*, 1924/26, PIN, Moscow] [=*Pubericyathus* Vologdin, 1964a, p. 1392, *nom. nud.*, invalid genus-group name based on unavailable type species; ?=*Azyricyathus* Vologdin, 1964a, p. 1392 (type, *A. transseptatus*, OD); =*Pubericyathus* Vologdin, 1966, p. 20 (type, *P. phialiformis*, OD); ?=*Azyrocyathus* Vologdin, 1966, p. 23, *nom. null.*; ?=*Azyrcyathus* Vologdin, 1966, p. 23, *nom. null.*]. Transverse section circular to elliptical; peripterates well developed, open externally; baculi weakly expressed. *lower Cambrian (Atd.1–Bot.3)*: Altay Sayan, Mongolia, Transbaikalia, Urals.——Fig. 664,*4*. **C. artus*, Usa Formation, Botoman, Sukhie Solontsy Valley, Batenev Range, Kuznetsk Alatau, Altay Sayan, Russia, longitudinal section, ×10 (Vologdin, 1966).

Superfamily
PYXIDOCYATHOIDEA
Vologdin, 1964

[*nom. transl.* Zhuravlev & Kruse, herein, *ex* Pyxidocyathidae Vologdin, 1964a, p. 1394]

Cup two-walled. *lower Cambrian (Atd.1–Bot.3).*

Family PYXIDOCYATHIDAE
Vologdin, 1964

[Pyxidocyathidae Vologdin, 1964a, p. 1394] [=Cribricyathidae Vologdin, 1964a, p. 1392, *nom. nud.*, invalid family-group name based on unavailable genus name; =Capillicyathidae Vologdin, 1964a, p. 1394; =Szecyathidae Vologdin in Repina & others, 1964, p. 251; =Cribricyathidae Vologdin, 1966, p. 25]

Peripterates open. *lower Cambrian (Atd.1–Bot.3).*

Szecyathus Vologdin, 1957c, p. 493 [**S. cylindricus*; OD; syntype(s), Vologdin, 1932, fig. 7g–e, Vologdin, 1957c, fig. 1v, holotype not

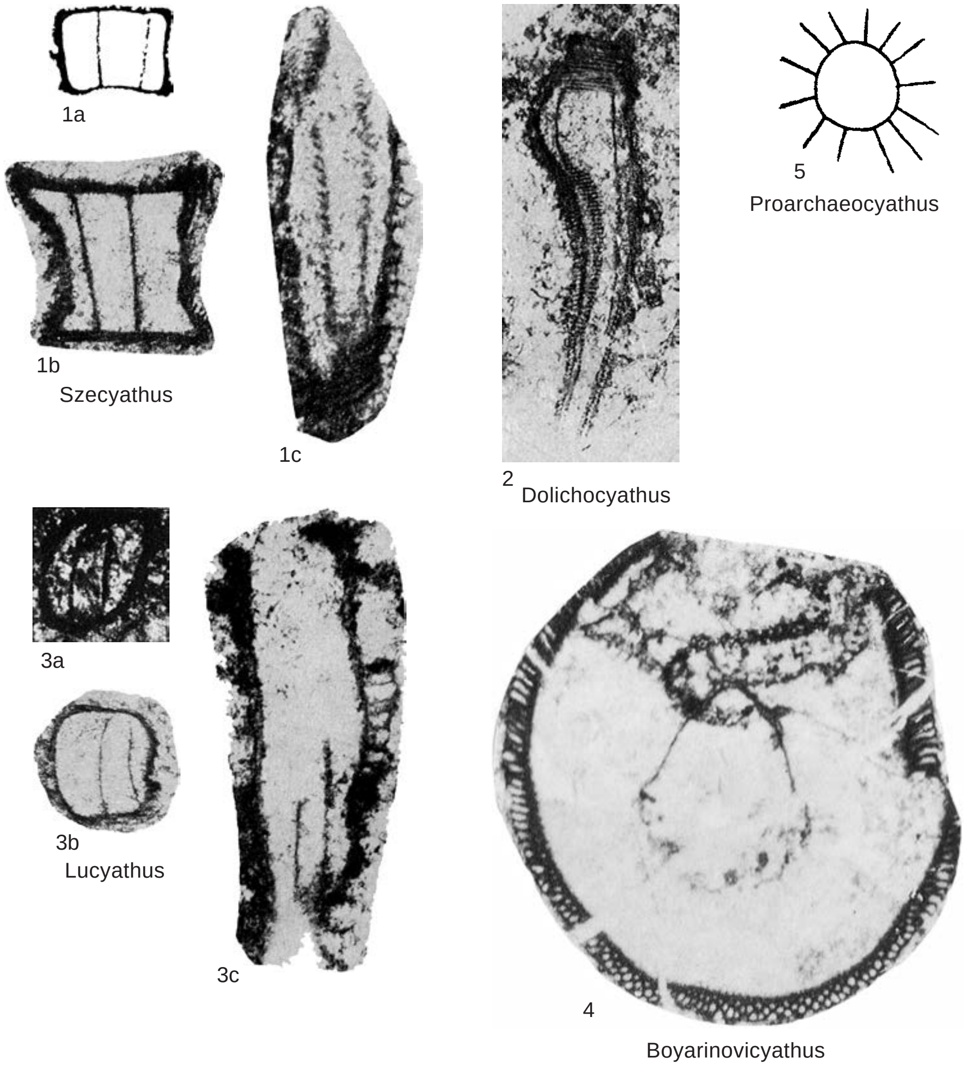


FIG. 665. Pyxidocyathidae, Boyarinovicyathidae, and Cribricyath-like fossils (p. 1101–1103).

designated, collection not located] [=*Cribricyathus* Vologdin, 1964a, p. 1392, *nom. nud.*; =*Lomatiocyathus* Vologdin, 1964a, p. 1392, *nom. nud.*, both invalid genus-group names based on unavailable type species; =*Thecocyathus* Vologdin, 1964a, p. 1392 (type, *T. tetragonus*, OD); =*Pyxidocyathus* Vologdin, 1964a, p. 1394 (type, *P. gracilis*, OD); =*Radicicyathus* Vologdin, 1964a, p. 1394 (type, *R. canaliculatus*, OD); =*Radiacicyathus* Vologdin, 1964a, p. 1394, *nom. null., lapsus calami pro Radicicyathus* Vologdin, 1964a, p. 1394; =*Redicicyathus* Vologdin, 1964a, p. 1394, *nom. null., lapsus calami pro Radicicyathus* Vologdin, 1964a, p. 1394; =*Cribricyathus* Vologdin, 1966, p. 26 (type, *C. longus*, OD); =*Lomaticyathus* Vologdin, 1966, p. 28 (type, *L. clathratus*, OD); =*Thecicyathus* Vologdin, 1966, p. 31, *nom. null., lapsus calami pro Thecocyathus* Vologdin, 1964a, p. 1392; =*Abicyathus* Jankauskas, 1972, p. 172 (type, *Lomaticyathus asymmetricus* Vologdin, 1966, p. 29, OD)]. Transverse section quadrate; peripterates well developed, open externally; inner wall of planar striae. *lower Cambrian (Atd.2–Bot.3)*: Altay Sayan, Mongolia.——FIG. 665,*1a–c*. **S. cylindricus*; *a,* Verkhneynyrga Formation, Botoman, Lebed' River, Altay Mountains, Altay Sayan, Russia, unlocated topotype, sketch of transverse section, ×20 (Vologdin, 1932); *b,* Mazas Formation, Botoman, Mrassu River, Gornaya Shoria, Altay Sayan, Russia, unlocated specimen collection Zhuravleva, 1964, collection 440, specimen 33/41, thin section 2, transverse section, ×20; *c,* Verkhnemonok Formation, Botoman, Kazly River, West Sayan, Altay Sayan, Russia, TPI collection Jankauskas, 1966, specimen IIIa, thin section 19, longitudinal section, ×25 (Jankauskas, 1972).

Dolichocyathus Vologdin, 1964a, p. 1394 [**D. effiguratus*; OD; holotype, Vologdin, 1964a, fig. 1(15); Vologdin, 1966, fig. 20, pl. 2,*12,* M, 1924/741, PIN, Moscow] [?=*Apocyathus* Vologdin, 1964a, p. 1394 (type, *A. ovalis*, OD); ?=*Capillicyathus* Vologdin, 1964a, p. 1394 (type, *C. fimbriatus*, OD); ?=*Lagenicyathus* Vologdin, 1964a, p. 1394 (type, *L. lamellifer*, OD)]. Transverse section circular to elliptical; peripterates well developed, open externally; inner wall of planar striae oriented normal to wall, linked by longitudinal lintels. *lower Cambrian (Bot.1–Bot.3)*: Altay Sayan, Tuva, Transbaikalia.——Fig. 665,*2*. **D. effiguratus*, Usa Formation, Botoman, Sukhie Solontsy Valley, Batenev Range, Kuznetsk Alatau, Russia, holotype, PIN 1924/741, longitudinal section, ×10 (Vologdin, 1966).

Lucyathus Vologdin, 1957c, p. 495 [**L. elegans*; OD; syntype(s), Vologdin, 1932, fig. 7a,b,m; Vologdin, 1957c, fig. 1e,zh, 2a–v [left], holotype not designated, collection not located] [=*Longicyathus* Vologdin, 1964a, p. 1394 (type, *L. pubescens*, OD); =*Sunicyathus* Vologdin, 1964a, p. 1394 (type, *S. pulcher*, M); =*Turricyathus* Vologdin, 1964a, p. 1394 (type, *T. procerulus*, OD); =*Peripteratocyathus* Vologdin, 1964a, p. 1394 (type, *P. cirratus*, OD), for discussion, see Jankauskas (1972, p. 176)]. Transverse section quadrate; peripterates well developed, open externally; inner wall contiguous. *lower Cambrian (Atd.3–Bot.3)*: Altay Sayan, Transbaikalia.——Fig. 665,*3a–c*. **L. elegans*; *a,* Verkhnemonok Formation, Botoman, Sanashtykgol River, West Sayan, Altay Sayan, Russia, unlocated topotype, transverse section, ×20 (Vologdin, 1957c); *b,* Adiak Formation, Atdabanian, Mrassu River, Gornaya Shoria, Altay Sayan, Russia, unlocated specimen collection Zhuravleva, 1961, collection 440, specimen 43/41, thin section 2, transverse section, ×20; *c,* Kacha Formation, Botoman, Kookta River, Transbaikalia, Russia, unlocated specimen collection 451, specimen 321/2, thin section 1, longitudinal section, ×20 (Jankauskas, 1972).

Phylum UNCERTAIN

CRIBRICYATH-LIKE TAXA OF UNCERTAIN AFFINITY

Family BOYARINOVICYATHIDAE Zhuravleva, 1997

[Boyarinovicyathidae Zhuravleva in Zhuravleva & others, 1997b, p. 151]

Boyarinovicyathus Zhuravleva in Zhuravleva & others, 1997b, p. 151 [**B. alexandri*; OD; holotype, Zhuravleva & others, 1997, pl. 8,*10*, 2329/116, ZSGGU, Novokuznetsk]. Two-walled saclike cup of probable magnesium calcite composition; outer wall aporose with honeycomb-like pits that open externally; inner wall with simple pores. *lower Cambrian (Bot.3)*: Altay Sayan.——Fig. 665,*4*. **B. alexandri*, Usa Formation, Botoman, Bol'shaya Belokamenka River, Kuznetsk Alatau, Russia, holotype ZSGGU 2329/116, oblique longitudinal section, ×10 (Zhuravleva & others, 1997b).

Family UNCERTAIN

Proarchaeocyathus Radugin, 1966, p. 112 [**P. manae*; OD; holotype, Radugin, 1964, pl. 1,*1*; Radugin, 1966, pl. 7,*1*, collection 61r, specimen 8-100, TPI, Tomsk] [=*Proarchaeocyathus* Radugin, 1964, p. 146, *nom. nud.*, invalid genus-group name based on unavailable type species]. Hollow possible tube of rounded possible cross section bearing spines or longitudinal ribs on external surface. *lower Cambrian (Atd.1):* Altay Sayan.——Fig. 665,*5*. **P. manae*, Ungut Formation, Atdabanian, Mana River, East Sayan, Altay Sayan, Russia, holotype, TPI collection 61r, specimen 8-100, transverse section, ×7.5 (Radugin, 1964).

ARCHAEOCYATHA AND CRIBRICYATHA *NOMINA NUDA;* TAXA NOT ARCHAEOCYATHA, RADIOCYATHA, OR CRIBRICYATHA

F. Debrenne, A. Yu. Zhuravlev, and P. D. Kruse

ARCHAEOCYATHA AND CRIBRICYATHA *NOMINA NUDA*

Argunicyathus Fonin, 1985, p. 27.
Baculocyathus Vologdin, 1940b, p. 27.
Bijacoscinus Krasnopeeva, 1978, p. 81.
Ceratocyathus Gangloff in Rozanov & Gangloff, 1979, p. 57, *non* Seguenza, 1864, p. 430, cnidarian.
Coscinophyllina Radugin, 1966, p. 110.
Coscinophyllum Radugin, 1966, p. 109.
Demboicyathus Vologdin in Krasnopeeva, 1960, p. 40.
Dissocyathus Vologdin, 1962a, p. 117.
GAMOCYATHIDAE Vologdin, 1961, p. 179, invalid family-group name based on unavailable genus name.
Gunnicyathus Han & others, 2008, p. 26.
Involucrocyathus Yang & others, 2007, p. 91.
Leptosocyathella Rozanov, 1973, p. 110.
LYSOCYATHIDAE Boyarinov in Rozanov, 1973, p. 85, invalid family-group name based on unavailable genus name.
Lysocyathus Boyarinov in Rozanov, 1973, p. 61.
Mongolocyathus Rozanov, 1973, p. 38.
Plenocyathus Vologdin, 1962c, p. 13.
Protophyllum Radugin, 1966, p. 114, invalid genus-group name based on unavailable type species.
Sagacyathellus Kashina in Debrenne & Rozanov, 1983, p. 734.
Saocyathus Kashina & Jankauskas, 1973, p. 181.
Saocyathus Kashina in Zhuravleva, 1974b, p. 86.
Serratocyathus Vologdin, 1960, p. 424.
Sheathcyathus Yang & others, 2005, p. 206.
Taschtagolia Radugin, 1966, p. 111, invalid genus-group name based on unavailable type species.
Ulenicyathus Krasnopeeva in Yaroshevich, 1962, p. 117.
Utukcyathus Vologdin in Debrenne, 1964, p. 231.

TAXA THAT ARE NOT ARCHAEOCYATHA, RADIOCYATHA, OR CRIBRICYATHA

Binatocyathus Vologdin, 1963, p. 948 [**B. obliquoseptatus*; OD]. Possible nonspiculate thalamid sponge.

Cornutocyathus Boyarinov in Zhuravleva & others, 1997b, p. 166 [**C. cornutus*; OD]. One-walled cone of probable magnesium calcite skeletal mineralogy; wall thick with long, curved radial spines externally; possibly an eroded archaeocyath.

Buschmannia Kaever & Richter, 1976, p. 28 [**B. roeringi*; OD; holotype, Kaever & Richter, 1976, pl. 4,*3*, B2-358, UM]. Radiating gypsum crystal bundles; for discussion, see Debrenne & Lafuste, 1979; Glaessner, 1980.

Domophyllum Radugin, 1964, p. 146, *nom. nud.*, invalid genus-group name based on unavailable type species; hyolith transverse section.

Lenaella Korde, 1959, p. 626 [**L. reticulata*; OD; holotype, Korde, 1959, fig. 1(1, 4), 1298/496, PIN, Moscow, not located]. Similar to *Tunkia* R. Bedford & J. Bedford (1936, p. 21), a probable alga or small skeletal fossil; for discussion, see Handfield and Hansman (1967).

Maldeotaina Flügel in Flügel & Singh, 2003, p. 368 [**M. composita*; OD]. Possible microstromatolite (for discussion, see Debrenne, Gangloff, & Zhuravlev, 1990, p. 361) or cyanobacterium, alga, or khasaktiid (see Problematic Early Cambrian Record, in Early Evolution of the Paleozoic Stromatoporoidea, p. 577).

MANACYATHIDAE Jankauskas, 1969, p. 154. Probable cyanobacteria.

Manacyathus Jankauskas, 1969, p. 154 [**M. mikroporosus*; OD]. Probable cyanobacterium with affinities to *Obruchevella* Reitlinger, 1948, and especially *Spirellus* Jiang in Luo & others, 1982.

MATTHEWCYATHIDAE Okulitch, 1943, p. 48. Possibly inorganic.

Matthewcyathus Okulitch, 1940, p. 83 [**Archaeocyathus pavonoides* Matthew, 1886, p. 29; OD]. Possibly inorganic.

Misracyathus Vologdin, 1959b, p. 82 [**M. vindhianus*; OD]. Possible alga.

Mussooriella Flügel in Flügel & Singh, 2003, p. 356 [**M. kroli*; OD]. Possible microstromatolite; for discussion, see Debrenne, Gangloff, and Zhuravlev (1990, p. 361).

Pentaphyllum Radugin, 1964, p. 146, *nom. nud.*, invalid genus-group name based on unavailable type species; hyolith transverse section.

Sphaerocyathus Vologdin, 1962c, p. 76 [**S. plasticus*; OD]. Possible micrite envelope.

Tanchocyathus Vologdin, 1963, p. 947 [**T. amgaensis*; OD]. Possible nonspiculate sponge; for discussion, see Debrenne and Reitner (2001, p. 312).

Trifoliophyllum Radugin, 1966, p. 104 [**T. mirabile*; OD; holotype, Radugin, 1966, pl. 7,*29*, collection 61r, specimen 5, TPI, Tomsk] [=*Trifoliophyllum* Radugin, 1964, p. 146, *nom. nud.*, invalid genus-group name based on unavailable type species]. Possible anabaritid cross section.

Trigonophyllum Radugin, 1966, p. 94 [**T. inexpectum*; OD; holotype, Radugin, 1966, pl. 7,*18*, collection 61r, specimen 8-1, TPI, Tomsk] [=*Trigonophyllum* Radugin, 1964, p. 146, *nom. nud.*, invalid genus-group name based on unavailable type species]. Possible hyolith transverse section.

Tuvinia Krasnopeeva, 1972, p. 146 [**T. prima*; OD]. Possible coralomorph.

TUVINIDAE Krasnopeeva, 1972, p. 146. Possible coralomorphs.

Yakovlevites Korde, 1979, p. 126, *nom. nov. pro Yakovlevia* Vologdin, 1931, p. 36, *non* Fredericks, 1925, p. 7, brachiopod [**Yakovlevia granulosa* Vologdin, 1931, p. 36; M] [=*Yakovleviella* Korde, 1975, p. 246 (type, *Y. tuvaica*; M; =*Yakovlevia granulosa* Vologdin, 1931, p. 36), *non* Fomichev, 1953, p. 318, rugosan]. Possible coralomorph; for discussion, see Hill, 1972, p. 132; Sayutina, 1985, p. 70, 73; Zhuravlev, Debrenne, and Lafuste, 1993, p. 367.

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