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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 internal structure of the skeleton is formed of calcareous structural elements parallel and perpendicular to the growth surface, forming a rectilinear, three-dimensional grid or forming a less regular network of oblique and rectilinear elements, forming a continuous, space-enclosing framework. Reconstructions of the living stromatoporoid animal (see *Treatise Online*, Part E, Revised, Volume 4, Chapter 9F) 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, pachyστεles, 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 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 (1886) 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 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 (1912), whose pioneering and beautiful work on the hypercalcified sponge *Merlia* (KIRKPATRICK, 1910, 1911) was overshadowed by his subsequent unbelievable, and universally rejected, views on the nature of all rocks (KIRKPATRICK, 1913; GOULD, 1980). HEINRICH (1914) 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 section on Functional Morphology (see *Treatise Online*, Part E, Revised, Volume 4, Chapter 9F). 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.

ARCHAEOCYATHA AND SPHINCTOZOA

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 *Preactinostroma* and *Korovinella* by KHALFINA (1960). 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 (1966) 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 archaeocyathans. 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 archaeocyathids from the early Cambrian of Mongolia. The Devonian microfossils grew up from a basal disk, about 0.25 mm across, into a first chamber that may have septa or tubercles. The chamber then was extended upward into an expanding tube up to 2 mm long. Spongiform outgrowths were then formed in the tube and organized into an inner and outer wall. The similarity of these microfossils to the early stages of the much older archaeocyathids (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 archaeocyathans. 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, 1994; DEBRENNE & REITNER, 2001; PRATT & others, 2001).

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 *Treatise Online*, Part E, Revised, Volume 4, Chapter 9F).

CHAETETIDA

In the 19th century, the chaetetids were considered to belong to the phyla Cnidaria or Bryozoa. The discoveries that chaetetids 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 *Treatise Online*, Part E, Revised, Volume 4, Chapter 2A). 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, 1991). 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, 1939; LECOMPTE, 1951–1952, 1952; GALLOWAY, 1957; FLÜGEL & FLÜGEL-KAHLER, 1968; KAZMIERCZAK, 1971; BOL'SHAKOVA, 1973; FLÜGEL, 1975; BOGOYAVLENSKAYA & YANET, 1983; BOGOYAVLENSKAYA, 1984; MORI, 1984; BOGOYAVLENSKAYA & KHROMYKH, 1985). 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 (1886) 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 (1939, p. 4–13) in the *Handbuch der Paläozoologie*. Less detailed comparisons between the fossils and hydrozoans can be found in LECOMPTE (1956), KAZMIERCZAK (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 *Treatise Online*, Part E, Revised, Volume 4, Chapter 9F).

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

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

The disjunctopoids 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 *Gerronostroma* 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. In the chapter where the disjectoporids are described (see *Treatise Online*, Part E, Revised, Volume 4, Chapter 6), 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 (1977, p. 61) recognized some units of "calcite monocrySTALLINES et carénées," which they interpreted as altered triactine spicules. The disjectoporoids are unlikely to be descendants of the early Paleozoic stromatoporoids (but see TERMIER & TERMIER, 1977, 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 and the Paleozoic stromatoporoids was discussed in detail by NESTOR (1981). 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 (1981). 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 (1981) to the similarities between the solid skeletons of *Lophiostroma* and *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 Stromatoporida of the phylum Coelenterata and contain the orders Stromatoporoidea and Sphaeractinoidea. The skeleton of *Acropora* is compared to that of *Gerronostroma*; 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 stromatoporooid-like forms is so great that LECOMPTE (1956) united genera of the two groups in the same families. 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 found in Paleozoic forms.

3. The families Milleporellidae and Milleporidiidae, usually classified as so-called Mesozoic stromatoporooids, 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 stromatoporooids to those of the Hydrozoa or other groups of the Cnidaria. They might also be placed in the chaetetids. KÜHN (1939) 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 in *Treatise Online*, Part E, Revised, Volume 4, Chapter 5, p. 2–3. The time gap between the last of the Paleozoic stromatoporooids and the Mesozoic stromatoporooid-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 stromatoporooids but, like the disjectoporooids, are a poriferan group of convergent morphology. MISTIAEN (1984, 1994) proposed that the Paleozoic stromatoporooids 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 stromatoporooids. Before fossils were investigated using thin sections, these structures were given names like *Megastroma*, *Parastroma*, *Dictyostroma*, and *Neostroma*, which implied a relationship to the stromatoporooids. Most of these genera (see list in KÜHN, 1939), 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 stromatoporooids.

However, KAZMIERCZAK (1976, 1980, 1981) recognized, on the basis of some exceptionally preserved specimens, that the Paleozoic stromatoporooid skeletons composed of laminae, pillars, pachyστεles, and pachystromes were also secreted by

cyanobacteria. He proposed that the astro-rhizae were traces of the filamentous juvenile stages of colonial cyanobacteria (blue-green algae), because in the specimens he investigated they were filled with dark granules. He believed these granules were calcified cells of cyanobacteria and, because they resembled melanospheres within structural elements, that they were also composed of calcified cyanobacteria. KAZMIERCZAK 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. KAZMIERCZAK 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 KAZMIERCZAK 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 KAZMIERCZAK 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 *Treatise Online*, Part E, Revised, Volume 4, Chapter 9F).

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